



# Molecular and morphological recognition of species boundaries in the neglected ant genus *Brachymyrmex* (Hymenoptera: Formicidae): toward a taxonomic revision

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## Abstract

*Brachymyrmex* is a neglected genus of Formicinae because of its small body size, soft mesosoma, and superficially monotonous external morphology. These features have complicated the documentation of morphological variation, resulting in poorly defined and incompletely described species. Consequently, the taxonomy of the genus is complex and problematic, which has impeded research and conservation efforts. Here, we integrate molecular and morphological data to recognize species boundaries in *Brachymyrmex* and to guide its long-overdue revision. Specifically, we (1) redefine the limits of all described species, subspecies, and varieties based on intra- and interspecific morphological variation in workers; (2) document this variation quantitatively by constructing morphospace occupation and statistically analyzing measurements; (3) synthesize our findings on diagnostic traits in a dichotomous, illustrated identification key; and (4) examine the significance of our morphological identification system with molecular evidence from four gene fragments (EF1aEF1, EF1aEF2, WG, and COI). We recognize 40 species, of which four are new to science: *Brachymyrmex bahamensis*, *Brachymyrmex bicolor*, *Brachymyrmex iridescens*, and *Brachymyrmex sosai*. Furthermore, *Brachymyrmex attenuatus* and *Brachymyrmex bonariensis* are raised to species, and we propose 25 new synonyms. Morphometrics indicated that even poorly distinguishable species pairs show statistically significant differences in some traits, and that taxonomically problematic cases relate to taxa that demonstrate large intraspecific trait variance. Our molecular analysis supports the monophyly of the genus based on increased taxon sampling, and of the 19 species that were included 18 were retrieved as monophyletic. The single case of incongruence was also flagged in morphological analyses and requires extended geographic sampling before it can be resolved. In conclusion, the molecular work corroborates the morphologically recognized species boundaries. We also document the presence of worker dimorphism and putative worker-queen intercastes in several *Brachymyrmex* species, which indicates that the genus may present a promising study system to understand caste evolution in ants.

**Keywords** *Brachymyrmex* · Formicinae · Phylogeny · Taxonomy · Neotropics · Morphometrics

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## Introduction

*Brachymyrmex* is a neglected genus of Formicinae that consists of minute ants (maximum length ~3 mm), which are morphologically diagnosed by the presence of an acidopore and antennae with nine segments lacking a club (Bolton 2003). The combination of their small body size, soft metasoma, and at least superficially monotonous external morphology complicate the observation and interpretation of morphological variation. *Brachymyrmex* is native to America and predominantly Neotropical. It ranges from the south of Canada to Argentina and Chile, including the Caribbean islands (Kempf 1972; Brandão 1991; Bolton 1995; Bolton

2007). Creighton (1950) pointed out that these tiny ants are easily transported with living plants, and beyond the native distribution some species have been introduced to, among others, various places in Africa (Forel 1895a; Dejean et al. 2010), Europe (Forel 1874), and Asia (Guénard 2018; Yoshimura pers. comm.). *Brachymyrmex heeri* and *Brachymyrmex longicornis*, for example, were described by Forel (1874, 1907) from ant colonies in European greenhouses and *Brachymyrmex cordemoyi* was described from Réunion (Forel 1895a). Some *Brachymyrmex* species, like *Brachymyrmex patagonicus*, are notorious invaders which are considered pests in the southern USA (MacGown et al. 2007) and probably beyond.

The only complete taxonomic treatment of *Brachymyrmex* was published by Santschi (1923a) and included 27 species and 15 subspecies and varieties. The work was based on worker morphology, but unfortunately the identification key is difficult to use because it includes polytomous steps with strongly overlapping character suites. Furthermore, character descriptions are regularly ambiguous and contain contradictions. As a result, species, subspecies, and varieties are often poorly defined and incompletely described (De Zollesi et al. 1978). The small size and taxonomic ambiguity prompted Creighton (1950) to label *Brachymyrmex* as a “miserable little genus” in his treatment of the ants of North America, and for more than a century colleagues (Wheeler 1903; Kusnezov 1959; Wilson and Taylor 1967) have raised warnings on the taxonomic challenges in this genus. Since Santschi (1923a), Alayo (1974) examined the species from Cuba and Wheeler and Wheeler (1978) those from the USA. More recently, Quirán and collaborators (Quirán et al. 2004; Quirán 2005, 2007) reported on the *Brachymyrmex* species from Argentina, and Ortiz and Fernández (2014) reviewed the species with tumuliform metathoracic spiracles. Additionally, Wilson et al. (2016) documented the male genitalia of *Brachymyrmex*. Currently, 44 species with 17 subspecies and varieties are attributed to the genus in the online catalog of the ants of the world (Bolton 2018). However, the biology, diversity, and phylogeny of the genus remain poorly understood and a comprehensive revision is long-overdue (see Wilson and Taylor 1967).

A detailed account of opinions on the phylogenetic position of *Brachymyrmex* within Formicinae is provided by Wilson et al. (2016). Agosti (1991) divided the subfamily in four groups based on morphological characters, with *Brachymyrmex* included in the “*Pseudolasius* genus group” based on the widely separated hind coxae, the petiole that is ventrally u-shaped and the simple helcium that is antero-ventrally often concealed by the anteriorly fused sternite and tergite, which meet laterally. Bolton (2003), also based on morphology, assigned *Brachymyrmex* (and *Pseudolasius*) to the Plagiolepidini, which is one of three tribes of the lasiine group. More recently, Blaimer et al. (2015) obtained strong support for a sister group relationship between *Brachymyrmex*

and *Myrmelachista* upon analysis of ultraconserved elements (UCEs), and these genera form a well-supported sister group to all other formicines. Therefore, Ward et al. (2016) resurrected the tribe Myrmelachistini (= *Brachymyrmicini*) for these two genera. This tribe is morphologically characterized by 9–10 antennal segments, five mandibular teeth, an anteriorly inclined petiole with a long posterior peduncle, and an anterior tergo-sternal fusion of the third abdominal segment.

Here, we work toward a comprehensive revision of *Brachymyrmex* by (1) redefining the limits of all of the described species, subspecies, and varieties in light of intra- and interspecific morphological variation in workers; (2) documenting this variation both qualitatively and quantitatively; (3) summarizing these findings on diagnostic traits with a new, dichotomous, illustrated identification key to increase reproducibility and to make the diversity of *Brachymyrmex* more accessible for future research; and (4) examining the significance of our morphological identification system and the monophyly of the genus in light of molecular evidence. Finally, we also report on the biogeographical distribution of the recognized species and how our taxonomic framework compares with previous studies.

In summary, we recognize a total of 40 species, 4 of which are newly described here. We also synonymize 25 previously described species/subspecies and raise two former subspecies to species status. The proposed species delimitations follow a new, dichotomous identification key that is supported by quantitative morphological studies. More importantly, we tested our morphological identification system with molecular data for half of the recognized species and found strong congruence (18 of the 19 included species were retrieved as monophyletic), indicating its overall validity. During our studies, it also became clear that several samples contain specimens that presumably belong to undescribed species, but we prefer to await more material before formal description. This remark includes, but is not limited to, several potentially new species from Central America. We also observed that some species have dimorphic workers and others a possible intercaste between worker and queen. However, confirming the presence of an intercaste necessitates distinguishing it from ergatoid queens, which requires dissections of the ovaries and demographic data (Peeters 1991). Unfortunately, such confirmation is not usually possible based on the museum specimens studied here, but we discuss the issue where relevant. In general, it warrants further study and for now, we highlight such specimens as putative intercastes. If intercastes would be confirmed in the future beyond dimorphic workers, *Brachymyrmex* would present a promising study system to understand caste evolution in ants (Ortiz and Fernández 2014).

## Material and methods

### Material and repositories

Authors of previous taxonomic studies of *Brachymyrmex* (e.g., Santschi 1923a; Creighton 1950; Quirán et al. 2004; Quirán 2005, 2007) have mainly or exclusively focused on the morphology of workers, for which abundant material is available in existing museum collections. Consequently, we adopt the same focus here. A comparative framework is largely lacking for queens and males, because they are not available for all species, and even when collections exist they are often poorly preserved. Nevertheless, we provide a genus-level diagnosis of queens and males with selected pictures for illustrative purposes. The morphological terminology used follows Bolton (1994), that for hair inclination Kugler (1994), and for sculpture Harris (1979).

We examined a total of 1303 *Brachymyrmex* samples. This material belongs to the following institutions, and it includes all relevant types and many additional specimens; most collection acronyms follow Ward (1989). In some collections, not all specimens have individual voucher numbers. In such cases, we assigned an identifier (either a personal code or number, such as CMOS 000032, or a Smithsonian database reference number, such as USNMENT00757197) to the relevant specimen, preceded by the acronym of the proprietary institution. These unique identifiers are used here for traceability.

ALWC	Alex L. Wild Personal Collection, University of Texas, Austin, TX, USA
CASC	California Academy of Sciences, San Francisco, CA, USA
CPDC	Laboratório de Mirmecologia do Centro de Pesquisas do Cacau, Comissão Executiva do Plano da Lavoura Cacaueira (CEPLAC), Itabuna, Bahia, Brazil
IAvH	Instituto Humboldt, Claustro San Agustín, Villa de Leyva, Boyacá, Colombia
ICN	Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá D.C., Colombia
INBC	Instituto Nacional de Biodiversidad, Santo Domingo de Heredia, Costa Rica
INSUE	Instituto Superior de Entomología, Universidad Nacional de Tucumán, San Miguel de Tucumán, Argentina
JTLC	John Longino Collection, the University of Utah, Salt Lake City, UT, USA
MACN	Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina
MCZC	Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA

MCSN	Museo Civico di Storia Naturale “Giacomo Doria”, Genoa, Italy
MfNB	Museum für Naturkunde, Berlin, Germany
MLP	Museo de La Plata, Buenos Aires, Argentina
MHNG	Muséum d’Histoire Naturelle, Genève, Switzerland
MPEG	Museu Paraense “Emílio Goeldi”, Belém, Pará, Brazil
MZSP	Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil
NHMB	Naturhistorisches Museum, Basel, Switzerland
NHMW	Naturhistorisches Museum, Wien, Austria
PSWC	Philip S. Ward Collection, University of California, Davis, CA USA
RBINS	Royal Belgium Institution of Natural Sciences, Bruxelles, Belgium
UFUC	Universidade Federal de Uberlândia, Uberlândia, Minas Gerais, Brazil
UNMSM	Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru
USNM	Department of Entomology, National Museum of Natural History Smithsonian Institution, Washington DC, USA
WEMC	William and Emma MacKay, Personal Collection, El Paso Texas, TX, USA

### Georeferencing and mapping

Although we tried to georeference all studied samples, some were excluded because locality information was too ambiguous for georeferencing (e.g., when only a country name was available). Furthermore, specimens from the same collecting event were sometimes separated over replicate samples. After removing such “duplicates,” 747 georeferenced localities remained, of which 736 represented specimens from the native range. These were mapped in R v3.2.1. (R Core Team 2015) using the packages maps v3.0.1. (Brownrigg et al. 2015) and mapdata v2.2-5 (Brownrigg 2015), and subsequently projected on the ETOPO1 global topographic map of Amante and Eakins (2009).

### Images

Photographs were taken in dorsal, lateral, and full-face view. At the MCZC, we used an imaging system that consisted of a Leica MZ16 stereomicroscope equipped with a Leica DCF 420 digital camera, software from Leica Application Suite 3.7 and Helicon Focus 5.1 for auto-montage; at the USNM the imaging system consisted of a Leica Z16APO stereomicroscope with a JVC KY-F75U digital camera mounted to the Leica motor-focus

system. Composite images made with this system were assembled using Auto-Montage Pro Version 5.03.0018 BETA (Synoptics Ltd.); at the MZSP, the imaging system consisted of a Leica M250c stereomicroscope and Auto-Montage Professional software LAS3.6.0. Some images were obtained from [www.antweb.org](http://www.antweb.org), which is specified in the figure captions. Images were processed with Adobe Photoshop CS5.

### Analysis of measurements and indices

Measurements were made using an advanced optical microscope, a Leica Z16 APO microscope, and a Zeiss StereoDiscovery V20 in combination with an ocular micrometer. All measurements were taken at  $\times 80$ – $120$  magnification and are reported in mm to an accuracy of two decimal places. Indices were calculated from these measurements following Ortiz and Fernández (2014) (Fig. 1).

Head length<sub>1</sub> (HL<sub>1</sub>) The maximum length of the head excluding the mandibles in full-face view. HL<sub>1</sub> is measured as the straight-line distance from the mid-point of the anterior margin of the clypeus to the mid-point of the posterior (= vertexal) margin of the head (for major workers the posterior mid-point is located at the middle of the virtual line between the posterior apices of the head)

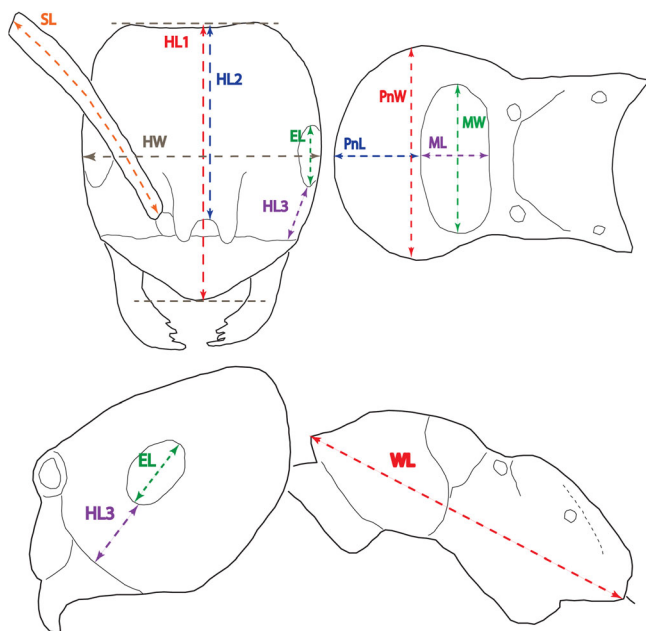


Fig. 1 Morphological measurements for *Brachymyrmex* workers. See text for details

Head length <sub>2</sub> (HL <sub>2</sub> )	Distance from the posterior margin of the frontal triangle (see Bolton, 1994, p. 192) to the vertexal margin in full-face view
Head length <sub>3</sub> (HL <sub>3</sub> )	Measurement of the gena in lateral view; this measurement equals the distance from the anterior margin of the eye to the posterior edge of the clypeus, parallel to the longest axis of the eye
Head width (HW)	The maximum width of the head measured in full-face view. Eyes are included in the measurement if they project laterally from the head
Scape length (SL)	The maximum length of the scape, excluding the basal constriction just distal to the condylar bulb
Eye length (EL)	Maximum diameter of the compound eye
Weber's length (WL)	The diagonal length of the mesosoma in lateral view, i.e., from the anterior-most point of the pronotum to the posterior-most basal angle of the metapleuron (this measurement excludes the cervical neck of the pronotum)
Pronotum length (PnL)	The length along the midline between the anterior and posterior edges of the pronotum in dorsal view (this measurement excludes the cervical neck of the pronotum)
Pronotum width (PnW)	The maximum width of the pronotum in dorsal view
Mesonotum length (ML)	The length between the anterior edge of the mesonotum and the mesometanotal suture in dorsal view
Mesonotum width (MW)	The maximum width of the mesonotum in dorsal view
Cephalic index (CI)	$(HW/HL_1) \times 100$
Scape index <sub>1</sub> (SI <sub>1</sub> )	$(SL/HW) \times 100$
Scape index <sub>2</sub> (SI <sub>2</sub> )	$(SL/HL_2) \times 100$
Ocular index <sub>1</sub> (OI <sub>1</sub> )	$(EL/HW) \times 100$
Ocular index <sub>2</sub> (OI <sub>2</sub> )	$(HL_3/HL_1) \times 100$
Ommatidia	The number of facets in the compound eye along its maximal diameter

In total, 347 specimens of 38 species were measured. In some cases, it was not possible to reliably measure all features, e.g., because of the preservation of the specimen or the way it was mounted. The ranges of the obtained measurements are described in the systematic treatment, but we also performed a statistical analysis of morphometric variables.

First, we ordinated these data with non-metric multidimensional scaling (nmMDS) using functions of *vegan* v2.3-0 (Oksanen et al. 2015) and *MASS* v7.3-41 (Venables and Ripley 2002). As this rank-based method does not allow missing data, we selected only specimens for which all measurements were taken, i.e., a subset of 240 individuals for 38 species. We converted this dataset into a Euclidean distance matrix and ordinated it in two dimensions using 1000 random starting configurations to find the solution with minimal stress without getting trapped in local minima. The resulting stress value obtained, i.e., the goodness-of-fit, was multiplied by 100 and evaluated using the criteria of Kruskal (1964) and Clarke (1993). We also examined how individual morphometric variables (i.e., the measurements, indices, and counts) contributed to the morphospace occupation with the “*envfit*” function of *vegan* using 1000 permutations.

Subsequently, we conducted statistical tests for the univariate morphometric variables on all species that were represented with at least 5 specimens, resulting in a subset of 286 specimens for 20 species. (Specimens with missing data were allowed for these tests.) Given that the data of several species differed significantly from a normal distribution, we used non-parametric Dunn’s tests to test pairwise differences between species for each measurement and index. These tests were performed in R using functions of the package *dunn.test* v1.3.4. (Dinno 2017), and the resulting *p* values were adjusted with a Benjamini-Hochberg correction, i.e., using the false discovery rate (Benjamini and Hochberg 1995). These results were represented with boxplots, featuring letters to indicate significance levels of comparisons.

## Molecular phylogenetics

We examined the monophyly of the genus with a dataset that has substantially enhanced taxon sampling compared to previous efforts (Brady et al. 2006; Moreau et al. 2006; Blaimer et al. 2015), and we examined the molecular support of the here proposed morphological identification system. The specimens used for genetics are indicated in Supplementary material Table S1, i.e., 82 specimens covering 19 *Brachymyrmex* species and 6 specimens of 5 *Myrmelachista* species (the sister-genus of *Brachymyrmex* [Blaimer et al. 2015]). *Acanthoponera minor*, *Manica rubida*, and *Rhytidoponera metallica* were used as outgroups.

DNA extraction, amplification, and sequencing were carried out at the Laboratories of Analytical Biology (LAB) of the Smithsonian National Museum of Natural History, Washington, DC. Genomic DNA was extracted using the Qiagen DNEasy Tissue Kit. Fragments of four protein-coding genes were amplified, i.e., one fragment for each of the nuclear genes elongation factor 1-alpha paralog F1 (EF1 $\alpha$  F1), elongation factor 1-alpha paralog F2 (EF1 $\alpha$  F2) and wingless (*wg*), and two of the mitochondrial gene cytochrome

oxidase subunit 1 (COI). Primer sequences used for polymerase chain reaction (PCR) amplification are those used by LaPolla et al. (2010). PCR products were sequenced on an ABI sequencer (ABI 377 or ABI 3100) using Big Dye Cycle Sequencing chemistry. Fragments were sequenced bidirectionally, and the resulting chromatograms were assembled and edited with *SEQUENCHER* v.4.8.

Furthermore, our dataset includes unpublished sequences that are available in GenBank by the International Barcode of Life Consortium. These sequences are provided without species identification, but they are linked to an image database, and we included specimens for which unambiguous identification was possible based on the available images. Additional sequences with specimen images were kindly provided by David Donoso and John Longino, and we used the same criteria for inclusion as for GenBank sequences.

Sequences for each gene fragment were aligned using *MAFFT* v.7 (Katoh and Standley 2013) and results were visually inspected in *MESQUITE* v.2.10 (Maddison and Maddison 2017) to determine codon positions. We tested for substitutional saturation using *DAMBE* v.5.5.9 (Xia 2013) but none of the gene fragments used were saturated. Models of sequence evolution were fit with *PARTITION FINDER* v.1.1.1 (Lanfear et al. 2012) to individual gene fragments accounting for potential differences between codon positions. The resulting model fit was examined with a corrected akaike information criterion (AICc). Subsequently, the data for the individual fragments was concatenated into a total dataset with seven partitions (Supplementary material Table S2) and phylogenetically analyzed with maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI). MP analyses were performed in *PAUP\** v.4.0b10 for Windows (Swofford 2002) with gaps treated as fifth state, 10,000 bootstrap replicates, and tree-bisection-reconnection branch swapping. ML analyses were performed with the *RAXML* BlackBox (Stamatakis et al. 2008) with 100 replicates and the implemented GTR +  $\Gamma$  model, individually parameterized for each of the 7 partitions. BI analyses were executed in *MrBayes* v.3.2.6 (Ronquist et al. 2012) as implemented in *CYPRES* v.3.3 (Miller et al. 2010). Two independent Markov chain Monte Carlo (MCMC) runs were conducted for 20 million generations and sampled every 1000 generations. Each run was distributed across four chains with a heating parameter of 0.2 and 25% of the samples were discarded as burnin. Convergence between runs was examined using the *sump* command and by inspecting effective sample sizes for the parameters in *TRACER* v.1.6 (Rambaut et al. 2013). The maximum clade credibility tree was visualized with *FigTree* v.1.4.0 (Rambaut 2012) and the bootstrap support for clades retrieved under MP and ML was added. Sequences are deposited in GenBank and accession numbers are indicated in Supplementary Table S1.

## Automated species delimitation

We identified hypothetical species entities from sequence data with an automated procedure. Our specific aim was to evaluate the congruence of automated species delimitation and our morphological identification system, and thus to test the reliability of that identification system. Multiple such methods exist (Pons et al. 2006; Leliaert et al. 2014; Da Silva et al. 2018) and results may vary considerably among methods (Da Silva et al. 2018) related to the size of the dataset, the methodological procedures adopted, variation in underlying population genetic parameters, and evolutionary processes. Many of the potentially influencing biological factors are poorly known for *Brachymyrmex*. We used the automatic barcode gap discovery method (ABGD; Puillandre et al. 2011), i.e., a fast single-locus method, on the barcoding fragment of COI, because of the exceptional suitability of this fragment for species identification as well as species delimitation and discovery in Metazoa (Hebert et al. 2003). The ABGD method is generally considered to be conservative as to the number of hypothetical species lineages it detects (Da Silva et al. 2018). We performed the analysis on the ABGD website (<http://www.wabi.snv.jussieu.fr/public/abgd/abgdweb.html>, accessed 8 October 2018) using default parameters except for relative gap width, which was set to 1.0.

## Data availability

Sequence data is deposited in NCBI Genbank and accession numbers are indicated in Supplementary Table S1.

## Results and discussion

### Genus account

*Brachymyrmex* Mayr

*Plagiolepis* (in part): Roger (1863: 162).

*Brachymyrmex* Mayr, 1868: 163. Type species: *B. patagonicus*, by monotypy.

*Brachymyrmex* subgenus *Bryscha* Santschi, 1923a: 652.

*Brachymyrmex* senior synonym of *Bryscha*: Smith (1979: 1424).

*Brachymyrmex*: Kempf (1972), Bolton (1995, 2003, 2018).

**Diagnosis.** *Brachymyrmex* differs from most other formicine genera by having workers with nine antennal segments. Some species of *Myrmelachista* also have nine antennal segments, but these have a well-defined antennal club, whereas such a club is absent in *Brachymyrmex*. Some *Agraulomyrmex* species from Africa also have nine antennal segments without club (unpublished results), but *Brachymyrmex* differs from these by the presence of a mesometanotal suture. Workers are monomorphic to dimorphic; some species have a putative worker-queen intercaste.

**Worker. Head.** Usually longer than wide, cordate in some species, with sparse to dense pubescence and hairs in variable orientation (appressed, decumbent, erect). Mandibles with five teeth, of which intercalary (central) and basal teeth are smaller than the others and the apical tooth is largest. Maxillary palps and labial palps with six and four segments, respectively. Maxillary palps usually reach the occiput and bear several long ventral hairs. The clypeus has a rounded anterior margin or in some taxa, notably *B. nebulosus*, its medio-anterior portion forms a “lip.” In monomorphic species, the clypeus bears five long, erect hairs of which one usually conspicuous hair is near the anterior margin, two are in mediolateral position and the other two close to the toruli; other hairs are markedly shorter and appressed or decumbent. In dimorphic species, the clypeus is larger and with a row of long thick hairs near the anterior margin. Toruli either touch the posterior clypeal margin in oblique anterodorsal view or surpass it. Compound eye conspicuous, positioned usually on the cephalic midline or anterior to it; with 3–14 ommatidia along its maximal diameter. Number of ocelli either 0, 1, or 3, but when present often inconspicuous. Antennae with nine segments, without antennal club; flagelomeres sometimes gradually increasing apically in diameter; scapes variable in length, with appressed, decumbent or erect hairs.

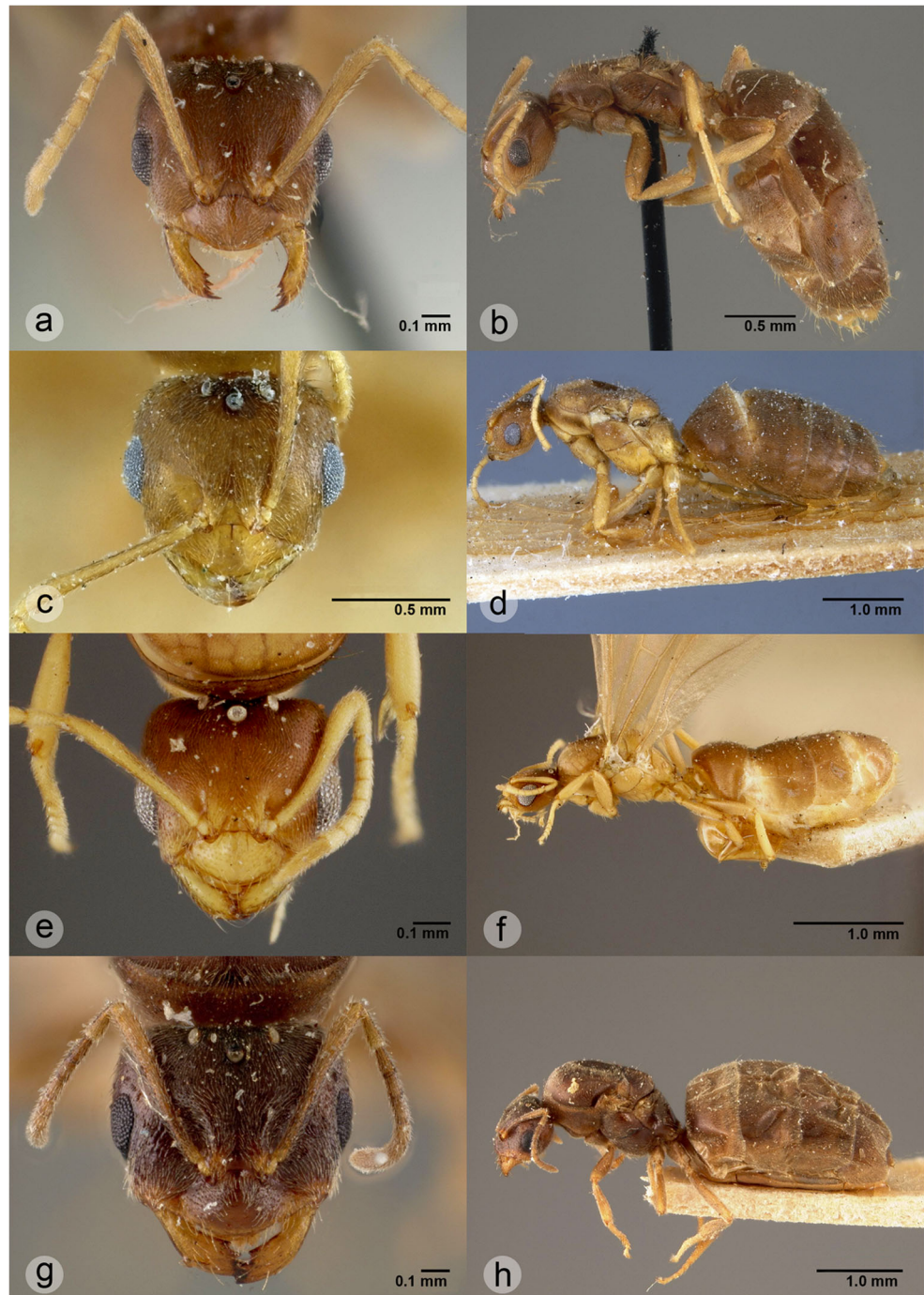
**Mesosoma.** With sparse or dense pubescence and hairs in variable orientation. The pronotum and mesonotum typically bear two erect hairs each, but sometimes additional suberect hairs on one or both are present, or erect hairs may be absent from the mesonotum. The pronotum is slightly to strongly convex, and the promesonotal suture, i.e., the line of junction between the pronotum and mesonotum, is always present. The mesonotum may bulge dorsally above the propodeum, and the mesometanotal suture, i.e., the line of junction between the mesonotum and the metanotum, is usually conspicuous, although the mesonotum and metanotum appear fused in some species. The metanotum is reduced to a transverse groove, the metanotal groove, which separates the mesonotum from the propodeum on the mesosomal dorsum. The metanotal groove is variable, from absent to wide and deep. The metathoracic spiracles are dorsal near the midline or dorsolateral, and not, slightly or very strongly protruding, i.e., tumiliform. The propodeal suture, i.e., the line of junction between either the mesonotum (if the metanotal groove is absent) or the metanotal groove anteriorly and the propodeum posteriorly, is present as a dorsal fold with variable lateral extension. Dorsum of the propodeum flat or convex and usually shorter than the propodeal slope. Propodeal spiracles circular and positioned near the posterior propodeal margin. Petiole usually with a low scale, reduced to a narrow subcylindrical segment that is overhung from behind by the gaster, but in dimorphic species the scale of the petiole may be high and visible in dorsal view. Hairs on the legs may be appressed, decumbent, or erect.

**Gaster.** Of variable size, with five segments that bear sparse or dense pubescence and usually erect hairs, mainly but not exclusively along the posterior edges of the segments.

**Color and sculpture.** Body color ranges from light yellow to dark brown and black; most often, it is uniform, but some species display markedly contrasting patterns, e.g., with the head and/or the gaster darker than the rest of the body. Body usually smooth and shiny, but in some species the head and/or mesonotum bear microsculpture.

**Queen** (Fig. 2). Head wider than long, with abundant, fine pubescence, and with long erect hairs; eyes large, located laterally along the cephalic midline; three ocelli present; frontal lobes well-developed; scapes usually extending beyond the posterior margin of the head; palpal formula: 6,4. Mesosoma with moderately dense, fine pubescence, and several erect hairs; anepisternum and katapisternum separated by a distinct suture. Anterior wing with a single dark brown cell, i.e., pterostigma, the first submarginal cell is closed, others open.

**Fig. 2** Habitus of a selection of queens of *Brachymyrmex*: head and lateral view of **a, b** *B. admotus*, **c, d** *B. antennatus*, **e, f** *B. aphidicola*, and **g, h** *B. giardi*



Posterior wing with five to seven hammuli. Gaster with moderately dense, fine pubescence, and erect hairs along the posterior edges of the segments. Body color ranges from yellow to dark brown, and it is uniform or sometimes with the head and/or gaster darker than the rest of the body.

**Male** (Fig. 3). Head wider than long, with fine, sparse pubescence, lacking erect hairs except on mouthparts, and with smooth, shiny integument; maxillary palps with four segments,

labial palps with two; mandibles unidentate; frontal lobes reduced; ocelli and eyes well-developed; antennae with ten segments. Mesosoma with sparse pubescence and shiny integument, without erect hairs. Gaster shiny, lacking pubescence, with scattered erect hairs on the last few segments. Head dark brown to almost black, rest of body, including appendages, very light brown or concolorous. Wilson et al. (2016) described the morphology of the male genitalia in detail.

**Fig. 3** Habitus of a selection of males of *Brachymyrmex*: head and lateral view of **a, b** *B. coactus*, **c, d** *B. myops*, **e, f** *B. longicornis* var. *immunis* (junior synonym of *B. admotus*), and **g, h** *B. australis* var. *curta* (junior synonym of *B. australis*)



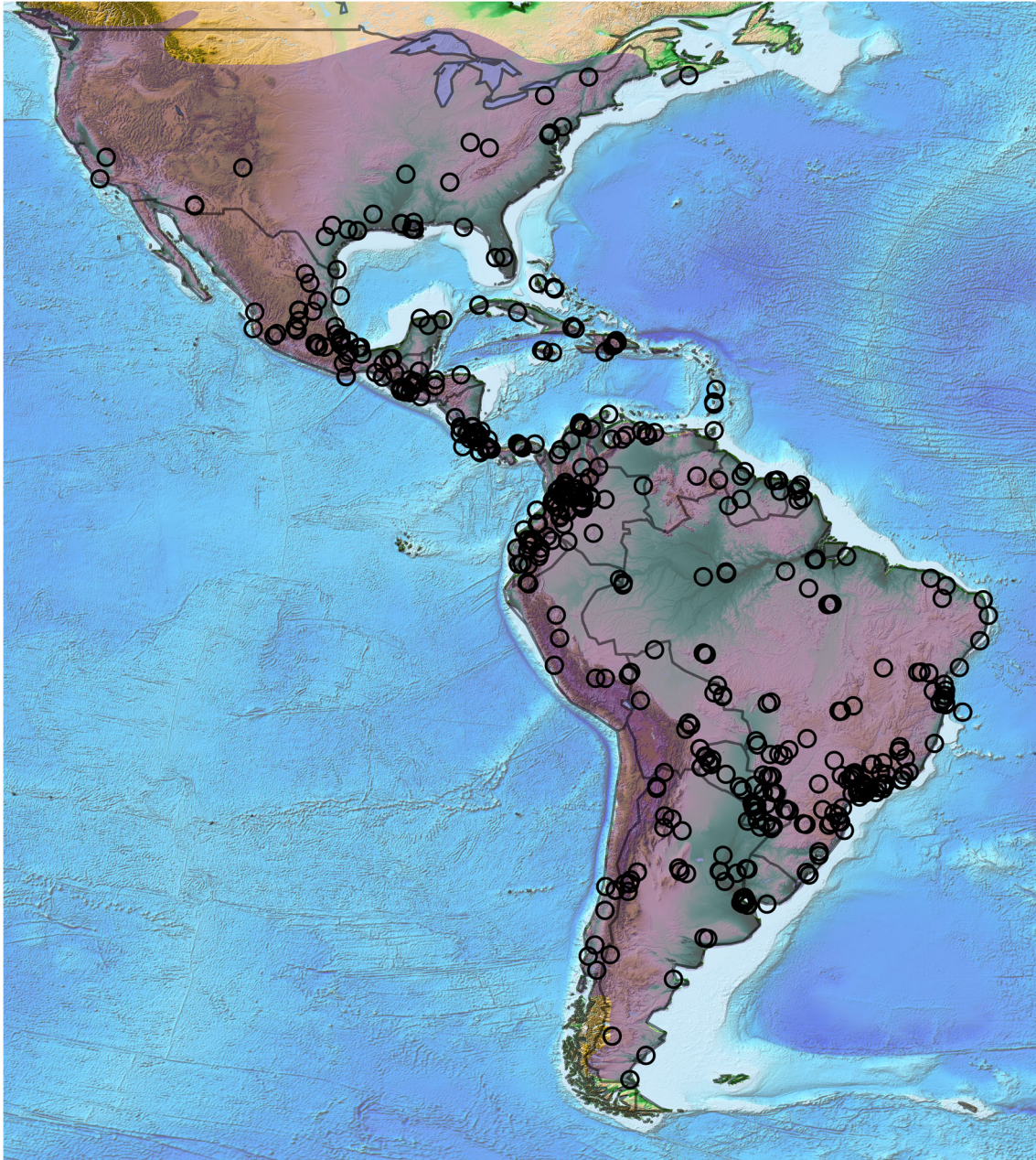


**Distribution.** Neotropical and Nearctic, with introductions elsewhere. The native distribution of *Brachymyrmex* is illustrated in Fig. 4.

**Biology.** *Brachymyrmex* is commonly collected from leaf-litter and some species occur in association with epiphytes; nests are found under stones, among plant roots, in trees, in rotten wood (Wheeler 1942; LaPolla and Longino 2006), and in urban buildings (MacGown et al. 2007). The biology and natural history of the genus are poorly known although habitat information exists for some species, such as the arboreal *B.*

*nebulosus* (LaPolla and Longino 2006). As mentioned, some *Brachymyrmex* species are notorious invaders which are considered pests (MacGown et al. 2007).

Interestingly, *Brachymyrmex* species occur sometimes in association with other insects. Santschi (1923a) mentioned associations of *Brachymyrmex depilis*, *Brachymyrmex giardi*, and *B. heeri* with mealybugs (Hemiptera: Coccidae) and observed that some species live in or very close to termite nests (*Brachymyrmex fiebrigi*, *Brachymyrmex modestus*, *Brachymyrmex myops*, *Brachymyrmex termitophilus*).



**Fig. 4** The native distribution range of *Brachymyrmex* as reconstructed from the unique georeferenced localities of the here studied material (black circles) and the *Brachymyrmex* records available in the Global

Ant Biodiversity Informatics database (Guénard et al. 2017) as viewed in [www.antmaps.org](http://www.antmaps.org) (Janicki et al. 2016; shaded area)

Moretti et al. (2011) suggested a possible association between *B. cordemoyi* and the cockroach *Pycnoscelus surinamensis* (Blaberoidea: Blaberidae), whereas Delssine (pers. comm.) found a staphylinid beetle in a nest of *B. modestus* in Ecuador.

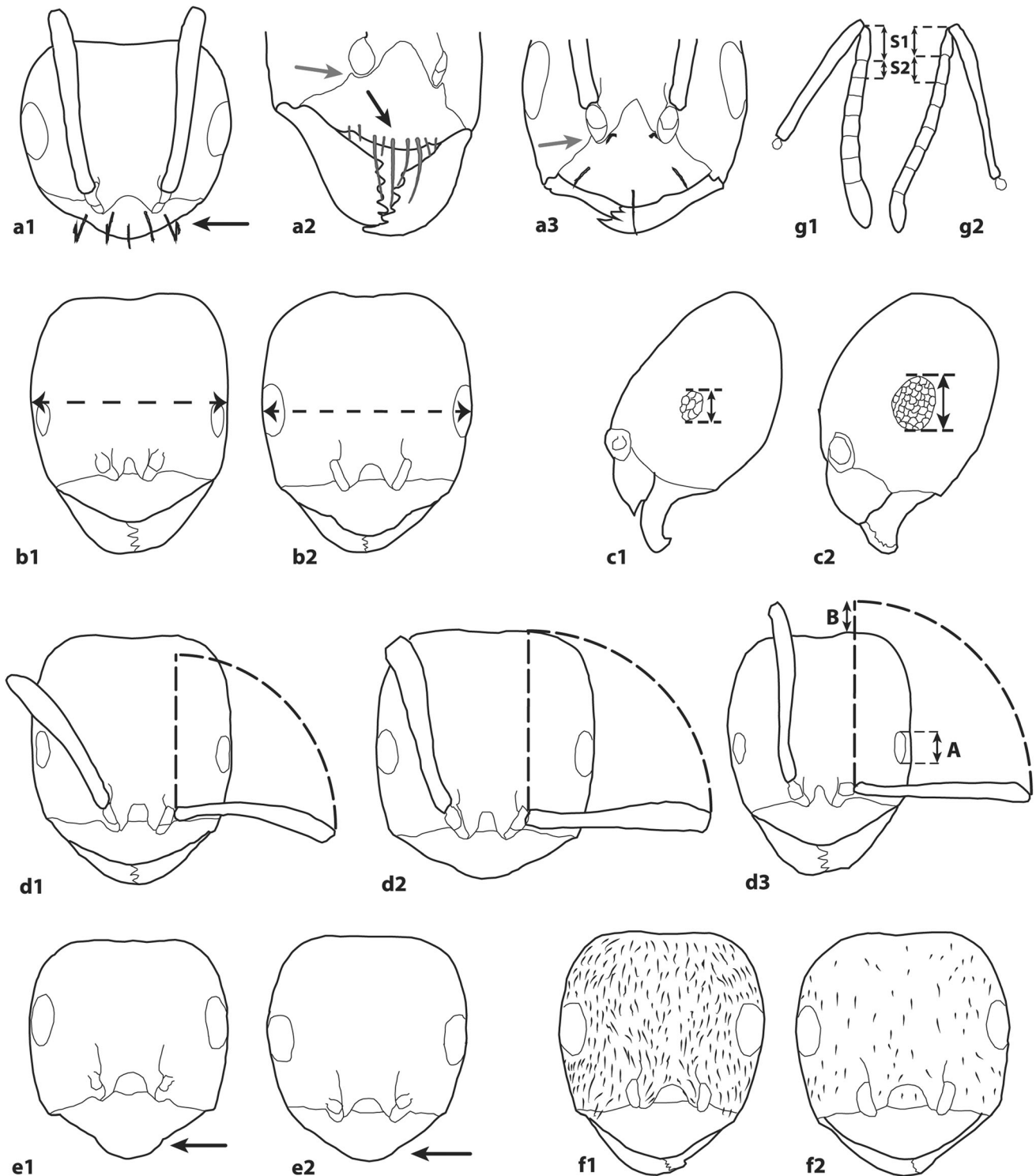
### Synonymy of species

*B. admotus* Mayr, 1887  
 = *B. longicornis* var. *immunis* Forel, 1908 n. syn.  
*B. antennatus* Santschi, 1929  
*B. aphidicola* Forel, 1909  
 = *B. heeri* var. *fallax* Santschi, 1923a  
 = *B. longicornis* var. *hemiops* Santschi, 1923a n. syn.  
*B. attenuatus* Santschi, 1929 n. st.  
*B. australis* Forel, 1901  
 = *B. australis* var. *curta* Santschi, 1922 n. syn.  
 = *B. longicornis* Forel, 1907 n. syn.  
*B. bahamensis* n. sp.  
*B. bicolor* n. sp.  
*B. bonariensis* Santschi, 1933 n. st.  
*B. brasiliensis* Ortiz & Fernández, 2014  
*B. bruchi* Forel, 1912a  
 = *B. bruchi* var. *rufipes* Forel, 1912a  
 = *B. giardi* var. *nitida* Santschi, 1922 n. syn.  
 = *B. laevis* var. *andina* Santschi, 1923a n. syn.  
*B. cavernicola* Wheeler, 1938  
*B. coactus* Mayr, 1887  
 = *B. coactus* var. *nictitans* Emery, 1906 n. syn.  
 = *B. constrictus* Santschi, 1923a n. syn.  
 = *B. coactus* var. *robustus* Santschi, 1923b n. syn.  
*B. cordemoyi* Forel, 1895a  
 = *B. laevis* var. *fuscula* Emery, 1906 n. syn.  
 = *B. brevicornis* Emery, 1906 n. syn.  
 = *B. patagonicus* var. *brevicornoides* Forel, 1914 n. syn.  
 = *B. cordemoyi* var. *nigricans* Santschi, 1916  
 = *B. cordemoyi* var. *distinctus* Santschi, 1923a n. syn.  
*B. degener* Emery, 1906  
 = *B. admotus* r. *niger* Forel, 1912a n. syn.  
 = *B. incisus* Forel, 1912a n. syn.  
 = *B. luederwaldti* Santschi, 1923a n. syn.  
*B. delabiei* Ortiz & Fernández, 2014  
*B. depilis* Emery, 1893  
 = *B. depilis* subsp. *flavescens* Grundmann, 1952.  
 = *B. nanellus* Wheeler, 1903  
*B. donisthorpei* Santschi, 1939  
*B. feitosai* Ortiz & Fernández, 2014  
*B. fiebrigi* Forel, 1908  
 = *B. fiebrigi* var. *funicularis* Santschi, 1922 n. syn.  
 = *B. fiebrigi* var. *fumida* Santschi, 1923a n. syn.  
*B. flavidulus* Roger, 1863  
*B. gagates* Wheeler, 1934  
*B. gaucho* Santschi, 1917  
*B. giardi* Emery, 1895

= *B. melensis* De Zolessi, Abenante & Gonzalez, 1978 n. syn.  
*B. heeri* Forel, 1874  
 = *B. goeldii* Forel, 1912a n. syn.  
 = *B. giardi* var. *cordobensis* Santschi, 1929 n. syn.  
 = *B. physogaster* Kusnezov, 1960 n. syn.  
*B. iridescens* n.sp.  
*B. micromegas* Emery in Santschi, 1923a  
*B. minutus* Forel, 1893  
*B. modestus* Santschi, 1923b  
*B. musculus* Forel, 1899  
*B. myops* Emery, 1906  
*B. nebulosus* LaPolla & Longino, 2006  
*B. obscurior* Forel, 1893  
*B. oculatus* Santschi, 1919  
*B. patagonicus* Mayr, 1868  
 = *B. laevis* Emery, 1895 n. syn.  
 = *B. patagonicus* var. *atratala* Santschi, 1923a  
*B. pictus* Mayr, 1887  
 = *B. heeri* var. *basalis* Wheeler, 1921. n. syn.  
 = *B. pictus* subsp. *balboae* Wheeler, 1942 n. syn.  
*B. pilipes* Mayr, 1887  
*B. santschii* Menozzi, 1927  
*B. sosai* n. sp.  
*B. termitophilus* Forel, 1895b.  
*B. tristis* Mayr, 1870

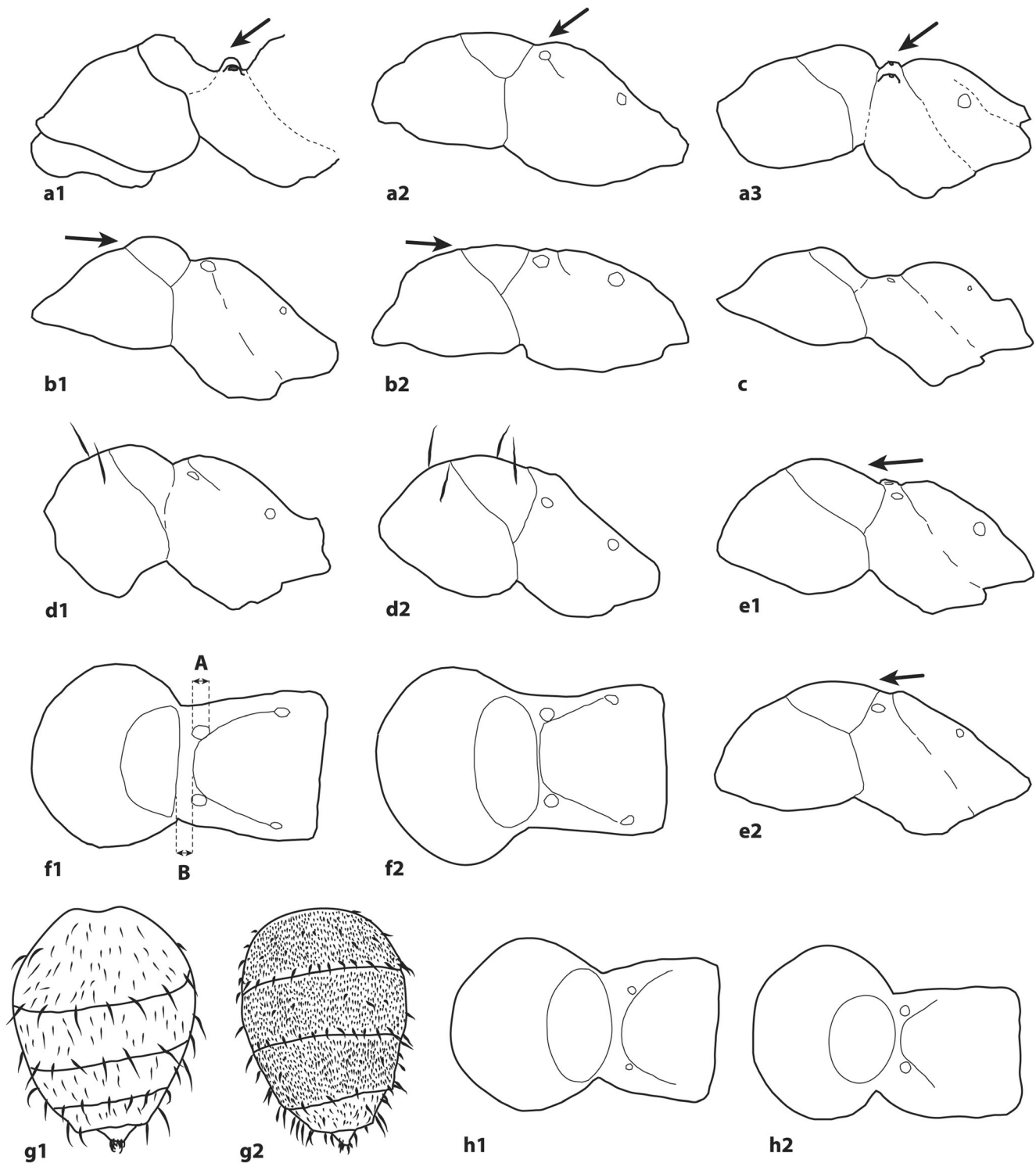
### Identification key to *Brachymyrmex* species

- 1 Clypeus with a single long apical hair near the anterior margin, two lateral hairs medially and two hairs near the toruli (Fig. 5(a1)); monomorphic .....2  
 - Clypeus with a row of long thick hairs near the anterior margin (Fig. 5(a2)), remaining pilosity not as above; dimorphic .....39  
 2(1) Metathoracic spiracles tumuliform (i.e., strongly protruding dorsally) (Fig. 6(a1)); known only from Brazil .....3  
 - Metathoracic spiracles not (Fig. 6(a2)) or slightly protruding but not tumiliform (Fig. 6(a3)); naturally occurring throughout the Neotropics .....5  
 3(2) Toruli surpassing the posterior clypeal margin in oblique anterodorsal view (Fig. 5(a3)); head and mesosoma smooth and shiny .....4  
 - Toruli touching the posterior clypeal margin but never surpassing it in oblique anterodorsal view (Fig. 5(a2)); head and mesosoma finely punctate and opaque .....*B. brasiliensis*  
 4(3) Mesosoma without erect hairs; gaster with scattered long erect hairs, except for the first segment which has dense yellowish pubescence .....*B. feitosai*  
 - Mesosoma with two erect hairs on pronotum and two on mesonotum; gaster with scattered long erect hairs, also on the first segment .....*B. delabiei*



**Fig. 5** Morphological characteristics of the head of *Brachymyrmex*. (a1) clypeus with five hairs of which a single long apical hair is positioned near the anterior margin, two in mediolateral position and two near the toruli (black arrow); (a2) clypeus with a row of long, thick hairs near the anterior margin (black arrow), toruli touching but not surpassing the posterior clypeal margin in oblique anterodorsal view (gray arrow); (a3) toruli surpassing the posterior clypeal margin in oblique anterodorsal view (gray arrow); (b1) eyes below the cephalic midline; (b2) eyes on cephalic midline; (c1) eyes with three or four ommatidia along the maximal diameter of the eye; (c2) eyes with more than four ommatidia along

the maximal diameter of the eye; (d1) scapes short and not reaching the posterior margin of the head; (d2) scapes just reaching the posterior margin of the head; (d3) scapes long and surpassing the posterior margin of the head; the length by which the scapes surpass this margin is compared to the length of the maximal diameter of the eye; (e1) anterior clypeal margin with the medial portion forming a “lip”; (e2) anterior clypeal margin evenly convex without antero-medial “lip”; (f1) head with dense pilosity; (f2) head with sparse decumbent hairs; (g1) second segment of the antennal funiculus shorter than the first; (g2) second segment of the antennal funiculus as long or longer than the first



**Fig. 6** Morphological characteristics of the mesosoma and gaster of *Brachymyrmex*. (a1) metathoracic spiracles tumiliform; (a2) metathoracic spiracles not protruding; (a3) metathoracic spiracles slightly protruding, but not tumiliform; (b1) mesonotum inflated and bulging dorsally above the pronotum in lateral view; (b2) mesonotum not inflated or bulging dorsally above the pronotum in lateral view; (c) dorsal margin of the mesosoma of conspicuous sinusoidal shape; (d1) mesometanotal suture inconspicuous (dashed line); (d2) mesometanotal suture directly visible; (e1) mesonotum strongly antero-posteriorly inclined and thus elongated

in lateral view; (e2) mesonotum weakly antero-posteriorly inclined in lateral view; (f1) metanotal groove deep and wider than the diameter of the metathoracic spiracles; (f2) metanotal groove shallow and narrower than the diameter of the metathoracic spiracles; (g1) gaster with scattered pubescence; (g2) gaster with dense pubescence, in both cases illustrated with long erect hairs near the edges of the segments; (h1) mesonotum laterally extended and oval in dorsal view; (h2) mesonotum almost circular in dorsal view

- 5(2)** Dorsum of the head, mesosoma and gaster with thick erect black hairs (as in *Nylanderia*) that contrast with the body color (head and gaster may be darker than mesosoma) .....*B. cavernicola*  
 - Dorsum of the head, mesosoma and gaster without hairs, or with thin hairs that do not contrast with the body color .....**6**
- 6(5)** Eyes positioned below the cephalic midline (Fig. 5(b1)), with three or four ommatidia along the maximal diameter of the eye (EL) (Fig. 5(c1)) .....**7**  
 - Eyes usually positioned on the cephalic midline (Fig. 5(b2)), with more than four ommatidia along the maximal diameter of the eye (Fig. 5(c2)) .....**9**
- 7(6)** Mesonotum not bulging dorsally above the pronotum in lateral view (Fig. 6(b1)) .....**8**  
 - Mesonotum bulging dorsally above the pronotum in lateral view (Fig. 6(b2)) .....*B. modestus*
- 8(7)** Scapes short, just reaching the posterior margin of the head or surpassing it by a length shorter than the maximal diameter of the eye (Fig. 5(d1, d2)) .....*B. donisthorpei*  
 - Scapes long, surpassing the posterior margin of the head by a length approximately equal to the maximal diameter of the eye (Fig. 5(d3)) .....*B. myops*
- 9(6)** Two erect hairs between the metathoracic spiracles **10**  
 - Without erect hairs between the metathoracic spiracles .....**11**
- 10(9)** Scapes surpass the posterior cephalic margin by a length of approximately  $1.5 \times$  the maximal diameter of the eye (Fig. 5(d3):  $2A \leq B$ ); hairs on scapes decumbent; body uniform in color (usually dark brown) .....*B. admotus*  
 - Scapes surpass the posterior cephalic margin by a length of approximately  $1.0 \times$  the maximal diameter of the eye (Fig. 5(d3):  $2A > B$ ); hairs on scapes appressed; head and mesosoma light brown, gaster darker .....*B. bonariensis* n. sp.
- 11(9)** Dorsal margin of the mesosoma having a marked sinusoidal shape (Fig. 6(c)) .....**12**  
 - Dorsal margin of the mesosoma not sinusoidal or only of sub-sinusoidal shape (Figs. 6(a2, a3, b1, b2, d1, d2, e1, e2)) .....**13**
- 12(11)** Clypeus with its medial anterior portion forming a “lip” (Fig. 5(e1)); head and mesosoma partially or completely alveolate (sometimes alveolate-strigate); dorsum of the mesosoma with many erect hairs; body uniform in color .....*B. nebulosus*  
 - Clypeus without anteromedial “lip” (Fig. 5(e2)); entire body non-alveolate; dorsum of the mesosoma without erect hairs; head and gaster black; mesosoma yellowish .....*B. bicolor* n. sp.
- 13(11)** Head with strong alveolate sculpture .....**14**  
 - Head without alveolate sculpture .....**15**
- 14(13)** Metanotal groove wider than the diameter of the metathoracic spiracles (Fig. 6(f1):  $A \leq B$ ); scapes surpassing the posterior margin of the head by approximately  $1.0 \times$  the maximal diameter of the eye (Fig. 5(d3)); gaster with scattered pubescence (Fig. 6(g1)) .....*B. santschii*  
 - Metanotal groove narrower than the diameter of the metathoracic spiracles (Fig. 6(f2):  $A > B$ ); scapes just reaching the posterior margin of the head (Fig. 5(d2)); gaster with dense pubescence (Fig. 6(g2)) .....*B. iridescens* n. sp.
- 15(13)** Mesometanotal suture inconspicuous (Fig. 6(d1)) .....**16**  
 - Mesometanotal suture readily visible (Fig. 6(d2)) .....**17**
- 16(15)** Pronotum without erect hairs; scapes short or reaching the posterior margin of the head (Fig. 5(d1, d2)); gaster with dense pubescence (Fig. 6(g2)) .....*B. flavidulus*  
 - Pronotum with two erect hairs (Fig. 6(d1)); scapes surpassing the posterior margin of the head (Fig. 5(d3)); gaster without dense pubescence, but with scattered appressed hairs (Fig. 6(g1)) .....*B. minutus*
- 17(15)** Gaster with dense appressed or decumbent pubescence (Fig. 6(g2)) .....**18**  
 - Gaster with sparse pubescence, but with scattered, appressed hairs (Fig. 6(g1)) .....**28**
- 18(17)** Metanotal groove absent or when present shallow and narrower than the diameter of the metathoracic spiracles (Fig. 6(f2):  $A > B$ ) .....**19**  
 - Metanotal groove deep and wider than the diameter of the metathoracic spiracles (Fig. 6(f1):  $A \leq B$ ) .....**26**
- 19(18)** Mesonotum bulging dorsally above the pronotum in lateral view (Fig. 6(b1)) .....**20**  
 - Mesonotum not bulging dorsally above the pronotum in lateral view (Fig. 6(b2)) .....**22**
- 20(19)** Scapes just reaching the posterior margin of the head or surpassing it by a length of less than  $1.0 \times$  the maximal diameter of the eye (Fig. 5(d2,d3):  $A > B$ ) .....**21**  
 - Scapes surpassing the posterior margin of the head by a length of approximately  $1.0 \times$  the maximal diameter of the eye (Fig. 5(d3):  $A \approx B$ ) .....*B. heeri*
- 21(20)** Body usually dark brown; eye with on average nine ommatidia along its maximal diameter; scapes on average  $> 0.5$  mm; known only from South America .....*B. giardi*  
 - Body yellowish; eye with on average six ommatidia along its maximal diameter; scapes on average  $< 0.5$  mm; known only from Canada, Mexico, USA .....*B. depilis*
- 22(19)** Body yellowish .....**23**  
 - Body dark brown .....**25**
- 23(22)** Scapes not or barely reaching the posterior margin of the head (Fig. 5(d1, d2)) .....*B. fiebrigi*  
 - Scapes surpassing the posterior margin of the head (Fig. 5(d3)) .....**24**
- 24(23)** About six erect hairs on the pronotum and two on the mesonotum, each hair with a length of about  $2.0 \times$  the maximal diameter of the eye; known only from the Bahamas .....*B. bahamensis* n. sp.  
 - Two erect hairs on the pronotum and two on the

mesonotum, each with a length shorter than the maximal diameter of the eye; widespread .....*B. termitophilus*

**25(22)** Dorsum of the head and mesosoma with light-colored, dense pubescence; gaster with dense appressed pubescence; eye with on average 11 ommatidia along its maximal diameter, head on average long ( $HL_1 > 0.5$  mm) and wide ( $HW > 0.4$  mm) .....*B. cordemoyi*

- Dorsum of the head and mesosoma with less conspicuous dense pubescence; gaster with dense decumbent pubescence; eye with on average nine ommatidia along its maximal diameter, head on average short ( $HL_1 < 0.5$  mm) and narrow ( $HW < 0.4$  mm) .....*B. obscurior*

**26(18)** Dorsum of the mesosoma without conspicuous sculpture; metathoracic spiracles fully dorsal in position; dorsal margin of the mesonotum strongly antero-posteriorly inclined (Fig. 6(e1)) .....*B. sosai* n. sp.

- Dorsum of the mesosoma with imbricate sculpture; metathoracic spiracles in dorsolateral position; dorsal margin of the mesonotum not or slightly antero-posteriorly inclined (Fig. 6(e2)) .....**27**

**27(26)** Second segment of the antennal funiculus shorter than the first antennal segment (Fig. 5(g1):  $S_2 < S_1$ ); scapes with appressed hairs; metathoracic spiracles protruding slightly dorsally, but not tumiliform (Fig. 6(a3)); hairs lighter in color than the body, which is brownish .....*B. attenuatus* n. st

- Second segment of the antennal funiculus as long or longer than the first antennal segment (Fig. 6(g2):  $S_2 \geq S_1$ ); scapes with decumbent hairs; methatoracic spiracles not protruding (Fig. 6(a2)) hairs darker in color than the body, which is yellowish .....*B. antennatus*

**28(17)** Eyes large, with a maximal diameter  $> 1/4$ th of the length of the head ( $HL_1$ ), usually with  $> 14$  ommatidia along their maximal diameter .....*B. oculus*

- Eyes small, with a maximal diameter of approximately  $1/4$ th the length of  $HL_1$ , typically with  $< 14$  ommatidia along their maximal diameter .....**29**

**29(28)** Metanotal groove absent, or, when present, shallow and narrower than the diameter of the metathoracic spiracles (Fig. 6(f2):  $A > B$ ) .....**30**

- Metanotal groove deep and wider than the diameter of the metathoracic spiracles (Fig. 6(f1):  $A \leq B$ ) .....**34**

**30(29)** Head and thorax yellowish; gaster black or yellowish with a black spot,  $OI_2$  usually  $> 27$  .....*B. pictus*

- Body of uniform color,  $OI_2$  usually  $< 25$  .....**31**

**31(30)** Body yellowish, usually with a narrow mesonotum ( $MW \sim 16$ ) and 8–9 ommatids along the maximum diameter of the eye .....**32**

- Body brownish or dark brown, usually with a wide mesonotum ( $MW \sim 20$  or more) and 10 or more ommatids along the maximum diameter of the eye .....**33**

**32(31)** Scapes surpassing the posterior margin of the head by a length exceeding the maximal diameter of the eye (Fig. 5(d3):  $A < B$ ) .....*B. aphidicola*

- Scapes surpassing the posterior margin of the head by a length smaller than or equal to the maximal diameter of the eye (Fig. 5(d3):  $A \geq B$ ) .....*B. australis*

**33(31)** Scapes surpassing the posterior margin of the head by a length smaller than the maximal diameter of the eye (Fig. 5(d3):  $A > B$ ); usually with two erect hairs on the pronotum and two on the mesonotum .....*B. patagonicus*

- Scapes surpassing the posterior margin of the head by a length approximately equal to the maximal diameter of the eye (Fig. 5(d3):  $A \approx B$ ); usually with more than two erect or decumbent hairs on the pronotum and two erect hairs on the mesonotum .....*B. bruchi*

**34(29)** Legs and antennae with erect hairs; second segment of the antennal funiculus as long as or longer than the first (Fig. 5(g2):  $S_2 \geq S_1$ ) .....*B. gaucho*

- Legs and antennae with decumbent or appressed hairs; second segment of the antennal funiculus shorter than the first (Fig. 5(g1):  $S_2 < S_1$ ) .....**35**

**35(34)** Mesonotum not bulging dorsally above the pronotum in lateral view (Fig. 6(b2)); metathoracic spiracles low, not protruding dorsally (Fig. 6(a2)) .....*B. musculus*

- Mesonotum bulging dorsally above the pronotum in lateral view (Fig. 6(b1)); metathoracic spiracles protruding slightly in lateral view but not tumiliform in shape (Fig. 6(a3)) .....**36**

**36(35)** Head and thorax yellow or brown, gaster darker .....*B. coactus*

- Body uniform in color .....**37**

**37(36)** Head with dense decumbent pubescence (Fig. 5(f1)) .....*B. tristis*

- Head with sparse decumbent pubescence (Fig. 5(f2)) **38**

**38(37)** Mesonotum laterally extended and therefore oval in dorsal view (Fig. 6(h1)); body light brown .....*B. degener*

- Mesonotum almost circular in dorsal view (Fig. 6(h2)); body dark brown or black .....*B. gagates*

**39(1)** Mesosoma mostly smooth and shiny, except for longitudinal striations restricted to the metapleura; body uniform light brown .....*B. micromegas*

- Mesosoma entirely covered with fine longitudinal striations; gaster darker than the rest of the body .....*B. pilipes*

## Species accounts

### *Brachymyrmex admotus* Mayr

(Fig. 7, supplementary material Fig. S1)

*Brachymyrmex admotus* Mayr, 1887: 523 (w.q.). Lectotype worker (NHMW: USNMENT00757197) and paralectotype workers, queen (NHMW: USNMENT00757196, 00757198-00757200; here designated): five workers, one queen [examined]. **BRAZIL:** Santa Catharina. Other relevant descriptions: Wheeler and Wheeler (1982: 178) (l.). See also: Santschi (1923a: 669); Quirán (2005: 762).

**Fig. 7** *Brachymyrmex admotus*: **a, c, e** head, dorsal, and lateral view of the lectotype worker; **b, d, f** *B. longicornis* var. *immunis* n. syn.: head, dorsal, and lateral view of a syntype worker



=*Brachymyrmex longicornis* var. *immunis* Forel, 1908: 400 (w.q.m.). (MHNG: USNMENT00757148): two workers [examined]. **BRAZIL:** São Paulo. See also: Forel (1911: 308); Santschi (1923a: 668) n. syn.

**Additional material examined.** **ARGENTINA: Misiones:** A.A. Oglobin, three workers (NHMB: USNMENT00758065-00758067). **BRAZIL: Bahia:** Itacaré, -14.30917 -39.01944, 26 June 1998, Santos, J.R.M. dos, two workers (CPDC: USNMENT00757769); Ituberá, 08 May 1994, 4815, J.H.C. Delabie, three workers (CPDC: USNMENT00757772); **Mato Grosso do Sul:** 8 km SE Ponta Pora, 15 Oct. 1989, W.P. MacKay #12523, two workers (WEMC: USNMENT00759009); **Minas Gerais:** Alfenas, 05 May 2011, one worker (ICN: USNMENT00759050); Cristina, Luederwaldt, nine workers (NHMB: USNMENT00758053, 00758059, 00758061); Cristina, MP17192, two workers (MZSP: USNMENT00757765, 00757819); Cocais das Estrelas, -19.73333 -43.41667, 19–22

June 2007, D.L. Braga #5512, 1 worker (CPDC: USNMENT00757768); Serra Caraça, 1380 m, Nov. 1961, Kloss, Lemko, 2713, Martins & Silva, nine workers, three males (MCZC: USNMENT00757252, 00757253, 00757764); Viçosa, Mata do Paraiso, Dec. 1993–1994, P.S.F. Ferreira, three workers (CPDC: USNMENT00757770); **Paraná:** Antonina, Parque Estadual do Pauçó, -25.57597 -48.88875, 6–11 May 2002, R.R. Silva & B.H. Dietz, 24 workers (ICN: MZSP016, 018, 019); Rio Negro, Goeldi, two workers (MCZC: USNMENT00757235); **Rio de Janeiro:** Reischensperger, eight workers (NHMB: USNMENT00758056-00758058); Goeldi, 1 worker (NHMB: USNMENT00758050); Floresta de Tijuca, D. Federal, 16 Dec. 1959, C.A.C. Seabra, five workers (MZSP: USNMENT00757766); Itatiaia, 17 Oct. 1933, one worker (NHMB: USNMENT00758068); Petropolis 77 9, T. Borgmeier, five workers, one queen (MCZC: USNMENT00757233, 00757234, 00757236); **Santa**

**Catarina:** Blumenau, Reichensperger, nine workers (NHMB: USNMENT00758055, 00758060, 00758064); Blumenau, Rev. P.M. Witte, two workers (NHMB: USNMENT00758063); Blumenau, Rev. Wittz, 19 workers (NHMB: USNMENT00758051, 00758052, 00758062); Palhoça, PE Serra do Tabuleiro, -27.74111 -48.69722, 02–10 June 2003, R.R. Silva, B.H. Dietz & A. Tavares, 25 workers (ICN: MZP030, 031, 035, 040); São Bento do Sul, APA Rio Vermelho, -26.36417 -49.27111, 30 Mar.–04 Apr. 2001, R.R. Silva & Eberhardt, 27 workers (ICN: MZP043, 134, 137); São Bento do Sul, APA Rio Vermelho, -26.36417 -42.27111, 30 Mar.–04 Apr. 2001, R.R. Silva & R.M. Feitosa, five workers (ICN: MZP044); **São Paulo:** Agudos, 24 Jan. 1955, W.S. Kempf leg 1337, three workers (MZSP: USNMENT00757767); Barueri, n 297, 17 Dec. 1957, K. Lenko, five workers (MZSP: USNMENT00757775); Iguape, EE Jureia-Itatins, Nucleo Rio Verde, -24.54417 -47.23556, 5–14 Mar. 2001, A.A. Tavares, 13 workers (ICN: MZP157, 158); Ipiranga Ihering, four workers (MHNG); Ipiranga (x.60), Ihering, two workers (MHNG); Jardim Botânico, Agua Funda, wet Forest, 08 Feb. 1967, W.L. Brown, five workers, one queen, one male (MCZC: USNMENT00757961, 00757771, 00757773, 00757774, CMOS00148, 00153); Jundiá, Serra Do Japi, 03 Jan. 2009, S. Diniz, four workers (ICN: USNMENT00759039); Miracatu, Serra do Mar, Clube pesca & Cia, 04–07 Sep. 2004, R.M. Feitosa, 11 workers (ICN: MZP092, 097); Picinguaba, PE Serra do Mar, -23.33611 -44.83758, 30 Mar.–04 Apr. 2001, Brandão C.R.F. & Eq, 52 workers, one queen (ICN: MZP060–062, 064); Picinguaba, PE Serra do Mar, -23.33611 -44.83758, 30 Mar.–04 Apr. 2001, Brandão, Albuquerque & Silva, 15 workers (ICN: MZP063); Piedade, Floresta Atlantica “Theomar,” Mar 2010, G. Bieber, one worker (ICN: USNMENT00759040); Piedade, Floresta Atlantica, Jurupará, Apr. 2009, G. Bieber, 1 worker (ICN: USNMENT00759041); Serra du Cantareira, Horto Florestal, 20 Feb. 1967, R. Crozier, nine workers (MCZC: USNMENT00757774, CMOS000089, 000090); **PANAMA: Colon Province:** San Lorenzo Forest, 9–16 Feb. 2004, Springate & Pinzon, one worker, (PSWC: USNMENT00757747). **PARAGUAY: Canindeyú:** Reserva Natural, Bosque Mbaracayú, Jejuimi, -24.10000 -55.50421, 15 Aug. 1996, A. Wild #AW0295, three workers (ALWC: USNMENT00757763).

**Diagnosis.** *Brachymyrmex admotus* morphologically resembles *B. bonariensis* n. st., because both species have long scapes, a conspicuous metanotal groove, a pair of thin erect hairs between the metathoracic spiracles, and a gaster with scarce pubescence. However, *B. admotus* is usually more uniform brownish in color, it has longer scapes (i.e., the scapes surpass the posterior cephalic margin with a length of approximately 1.5× the maximal diameter of the eye) with decumbent hairs, and its metathoracic spiracles are positioned more dorsally. *Brachymyrmex admotus* also resembles *B.*

*cavernicola* in having a pair of erect hairs between the dorsal metathoracic spiracles, but these hairs are thinner in *B. admotus* and they are not darker in color than the body.

**Lectotype measurements** (mm). HL<sub>1</sub> 0.51; HL<sub>2</sub> 0.35; HL<sub>3</sub> 0.12; HW 0.45; SL 0.49; EL 0.10; WL 0.49; PnL 0.14; PnW 0.31; ML 0.08; MW 0.18; **Indices** CI 88.46; SI<sub>1</sub> 108.70; SI<sub>2</sub> 138.89; OI<sub>1</sub> 21.74; OI<sub>2</sub> 23.08.

**Paralectotypes measurements** (mm) (n = 3). HL<sub>1</sub> 0.51–0.57; HL<sub>2</sub> 0.35–0.39; HL<sub>3</sub> 0.12–0.14; HW 0.45–0.49; SL 0.55–0.59; EL 0.10; WL 0.53–0.59; PnL 0.14–0.21; PnW 0.31–0.35; ML 0.08–0.12; MW 0.18–0.21; **Indices** CI 86.21–92.59; SI<sub>1</sub> 112.00–121.74; SI<sub>2</sub> 140.00–155.60; OI<sub>1</sub> 20.00–21.74; OI<sub>2</sub> 23.08–25.93.

**Additional material examined measurements** (mm) (n = 16). HL<sub>1</sub> 0.46–0.57; HL<sub>2</sub> 0.30–0.43; HL<sub>3</sub> 0.11–0.14; HW 0.43–0.51; SL 0.47–0.57; EL 0.09–0.13; WL 0.46–0.61; PnL 0.16–0.22; PnW 0.29–0.34; ML 0.09–0.13; MW 0.17–0.21; **Indices** CI 87.72–96.6; SI<sub>1</sub> 105.26–120.00; SI<sub>2</sub> 131.91–155.88; OI<sub>1</sub> 18.87–26.92; OI<sub>2</sub> 21.43–28.30.

**Description.** **Head.** Slightly longer than wide in full face view, with scattered appressed hairs except for two frontal rows of erect hairs; posterior cephalic border slightly concave. Dorsum of the head with sparse appressed pubescence. Clypeus with a rounded anterior margin and five long, erect hairs of which a single, usually conspicuous apical hair is near the anterior margin, two lateral hairs in medial position and two more near the toruli; other hairs on the clypeus are markedly shorter and appressed or decumbent. Toruli surpassing the posterior clypeal margin in oblique anterodorsal view. Scapes extend beyond the posterior cephalic margin by a length of ~1.5× the maximum eye diameter or more. The scapes typically have appressed, sometimes decumbent, but never erect hairs. A single central ocellus is present, but sometimes inconspicuous. Eyes are positioned on the cephalic midline and have 7–9 ommatidia along their maximal diameter.

**Mesosoma.** Usually with two erect hairs on the pronotum and two on the mesonotum; sometimes with additional suberect hairs on both. In lateral view, the mesonotum is not or slightly inflated and it does not or only slightly bulge dorsally above the pronotum. Metanotal groove deep and wider than the diameter of the metathoracic spiracles. Metathoracic spiracles fully dorsal and slightly protruding, they are closer to the propodeal than to the mesometanotal suture, but not touching any suture. Between the metathoracic spiracles two simple erect hairs are present, which are shorter than those on the pronotum and mesonotum. Dorsum of the propodeum flat and ~1/3th of the length of the propodeal slope. Propodeal spiracles circular, positioned ventrally of the posterior propodeal margin slightly posterior of the middle of the propodeal slope. Legs with appressed and scattered hairs. Petiole short and inclined forward.



*Gaster*. With scattered pubescence and scattered long suberect hairs.

**Color and sculpture.** Body overall smooth and shiny, except for the sometimes slightly imbricate sculpture on the dorsum of the mesosoma; body typically uniform dark brown in color, although in some specimens the head and mesosoma may be light brownish and the gaster darker brown.

**Distribution** (Supplementary material Fig, S1). *Brachymyrmex admotus* is mainly known from Argentina, Brazil, and Paraguay, but we also examined a specimen from Panamá that appears to belong to this species.

**Biology.** This species makes nests in rotting wood [USNMENT00757763] and it has been collected from below rocks [USNMENT00759009].

**Remarks.** We synonymize *B. longicornis* var. *immunis* Forel, 1908 under *B. admotus*, because the workers have all morphological characteristics of *B. admotus*, although they are slightly larger and of somewhat darker color. Forel (1908) did not specify a holotype for *B. longicornis* var. *immunis* but considered it to differ from *B. longicornis* in color, size, and the position of the metathoracic spiracles. The similarity between *B. admotus* and *B. longicornis* var. *immunis* was previously pointed out by Santschi (1923a) and Quirán (2005), who suggested that the main difference between both relates to the size and position of the metathoracic spiracles. However, these traits appear to be variable among populations and we have not found consistent differences between both taxa. For example, Santschi's collection (MHNB) includes syntype specimens of *B. longicornis* var. *immunis* that match the diagnostic traits of *B. admotus* entirely. Hence, synonymization seems appropriate.

Quirán (2005) indicated that *B. admotus* has three small ocelli, but in the samples that we studied we only observed one central ocellus, although this trait is inconspicuous.

*Brachymyrmex antennatus* Santschi

(Fig. 8, supplementary material Fig. S2)

*Brachymyrmex (Bryscha) antennatus* Santschi, 1929: 312 (w.q.). Lectotype worker (NHMB: USNMENT00758161) and paralectotype worker, queen (NHMB: USNMENT00758161; here designated): two workers, one queen (without USNMENT number) [examined]. **BRAZIL: Paraná, Rio Negro.**

**Additional material examined. ARGENTINA: Misiones:** Iguazu, PNI, Garganta, 28 Feb.–03 Mar. 2009, -25.70323 -54.42992, P.E. Hanisch & C.I Paris, Bait T4S10a, one worker (MACN-Bar-Ins-3120). **BRAZIL: Ceará:** Meruoca (Baixa, Gnd), ±970 m, -3.550 -40.467, July 2003, Y. Quinet, three workers (CPDC: USNMENT00757781). **São Paulo:** Ubatuba, P.E. Serra do Mar, N. Picinguaba, -23.297 -44.789, 800 m, 03–14 Mar. 2008, armadilha subterrânea #4, F.A. Esteves & R.M. Feitosa, three workers (MZSP: USNMENT00757777, 00757591).

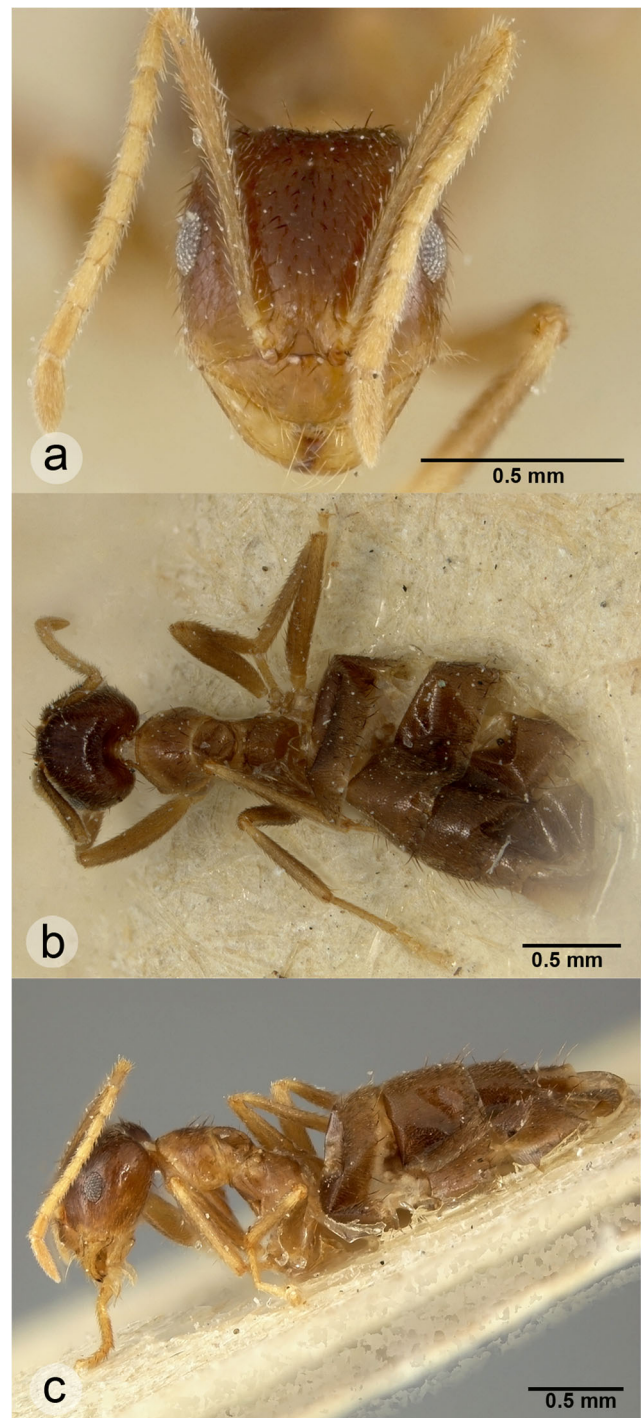


Fig. 8 *Brachymyrmex antennatus*: a–c head, dorsal, and lateral view of the lectotype worker

**COLOMBIA: Quindío:** Génova, Vereda El Cedral, Finca Buenos Aires, 1600 m, 4.235 -75.775, 26 Oct. 1999, E. Gonzales & J. Sossa, one worker (IAvH-E 74166). **ECUADOR: Napo:** Carlos Julio Arosemena Tola, -1.150 -77.883, 500 m, 11 Dec. 2003. A. L. Wild #AW2300, one worker (ALWC: USNMENT00757782). **FRENCH**

**GUIANA:** Petit, Satn Basse vie, June–July 2000, S. Durou, J. Delabie, A. Dejean & A. Gibernau, two workers (CPDC: USNMENT00757779, 00757780). **PERU: Madre de Dios:** Reserva Nacional Tambopata, Centro Sachacavayoc, -12.85583 -69.36194, 210 m, 19–31 July 2012, two workers (ICN: USNMENT00757627). Tambopata, Cuzco Amazónico, 15 km NE Puerto Maldonado, 24 June 1989, 200 m, S.P. Cover & J.E. Tobin, CA-115, one worker, one queen (MCZC: USNMENT00757630). **SURINAME:** Maripahewel, IX-1959 14–XX–29 I.v.d. Drift, one worker (MZSP: USNMENT00757778).

**Diagnosis.** *Brachymyrmex antennatus* morphologically resembles *B. gaucho*, because both species have legs and antennae with suberect hairs and both have an antennal funiculus with the second segment as long as or longer than the first. However, they differ from one another because *B. antennatus* has abundant, suberect hairs on the dorsum of the head and mesosoma, its gaster has dense pubescence, and its body is lighter and yellowish. *Brachymyrmex antennatus* also resembles *B. cavernicola* in having suberect hairs on the mesosoma that are generally darker in color than the tegument, but *B. antennatus* has a more elongated head, a longer second segment of the antennal funiculus, as mentioned above, thinner hair on its body and denser pubescence on the gaster.

*Lectotype and paralectotype measurements* (mm) ( $n = 2$ ). HL<sub>1</sub> 0.68–0.71; HL<sub>2</sub> n.a.; HL<sub>3</sub> 0.19–0.23; HW 0.68–0.71; SL 0.68–0.80; EL 0.15; WL 0.87; PnL 0.31–0.33; PnW 0.45; ML 0.21; MW 0.27; *Indices* CI 95.50–95.80; SI<sub>1</sub> 100.00–123.00; SI<sub>2</sub> n.a.; OI<sub>1</sub> 22.22–23.25; OI<sub>2</sub> 27.94–31.41.

*Additional material examined measurements* (mm) ( $n = 5$ ). HL<sub>1</sub> 0.54–0.60; HL<sub>2</sub> 0.38–0.41; HL<sub>3</sub> 0.12–0.16; HW 0.54–0.58; SL 0.52–0.63; EL 0.09–0.14; WL 0.60–0.71; PnL 0.15–0.22; PnW 0.35–0.40; ML 0.14–0.18; MW 0.20–0.24; *Indices* CI 92.31–100.00; SI<sub>1</sub> 93.33–130.23; SI<sub>2</sub> 130.23–155.56; OI<sub>1</sub> 15.38–26.67; OI<sub>2</sub> 21.67–29.03.

**Description.** *Head.* Longer than wide in full face view; posterior cephalic border concave. Dorsum of the head with scattered decumbent hairs. Clypeus with a rounded anterior margin and five long, erect hairs of which a single, usually conspicuous apical hair is near the anterior margin, two lateral hairs in medial position and two more near the toruli; other hairs on the clypeus are conspicuously shorter and appressed or decumbent. Toruli surpassing the posterior clypeal margin (in oblique anterodorsal view). Scapes surpass the posterior cephalic margin by a length of 1.5× the maximum eye diameter or more. The second segment of the antennal funiculus is as long as the first or longer. The scapes typically have suberect and erect hairs. Three ocelli present. Eyes are positioned on the cephalic midline and have 7–9 ommatidia along their maximal diameter.

*Mesosoma.* With conspicuous, thin erect hairs of darker color than the tegument. Pronotum anteroposteriorly

elongated. The mesonotum is slightly antero-posteriorly inclined, weakly inflated, and it does not bulge dorsally above the pronotum in lateral view. Metanotal groove deep and wider than the diameter of the metathoracic spiracles. Metathoracic spiracles in dorsolateral position and slightly protruding, closer to the propodeal than to the mesometanotal suture, but not touching any suture. Dorsum of propodeum flat and equal in length to the propodeal slope. Propodeal spiracles circular, situated ventral of the posterior propodeal margin. Legs with suberect and erect hairs. Petiole short and inclined forward.

*Gaster.* With dense pubescence and scattered long suberect hairs, mainly at the edges of the segments.

*Color and sculpture.* Body typically uniformly light brown, although some specimens may be light brownish with the head and gaster darker brown.

**Distribution** (Supplementary material Fig. S2). Known from Argentina, Brazil, Colombia, Ecuador, French Guiana, Perú and Suriname.

**Biology.** Unknown.

**Remarks.** The ant at the top of pin USNMENT00758161 is designated here as lectotype and the one immediately below as paralectotype. Santschi's collection (MHNB) contains three additional pins with four workers from the same locality but they are not considered to be part of the type collection as they have no type label. Santschi (1929) described the queen from a sample that does not contain any workers but expressed confidence that it belongs to *B. antennatus*; the issue may require verification from independent material. Substantial variation exists in the body size of workers of *B. antennatus* from various locations that were studied here, and the cause of this variation remains uncertain.

*Brachymyrmex aphidicola* Forel

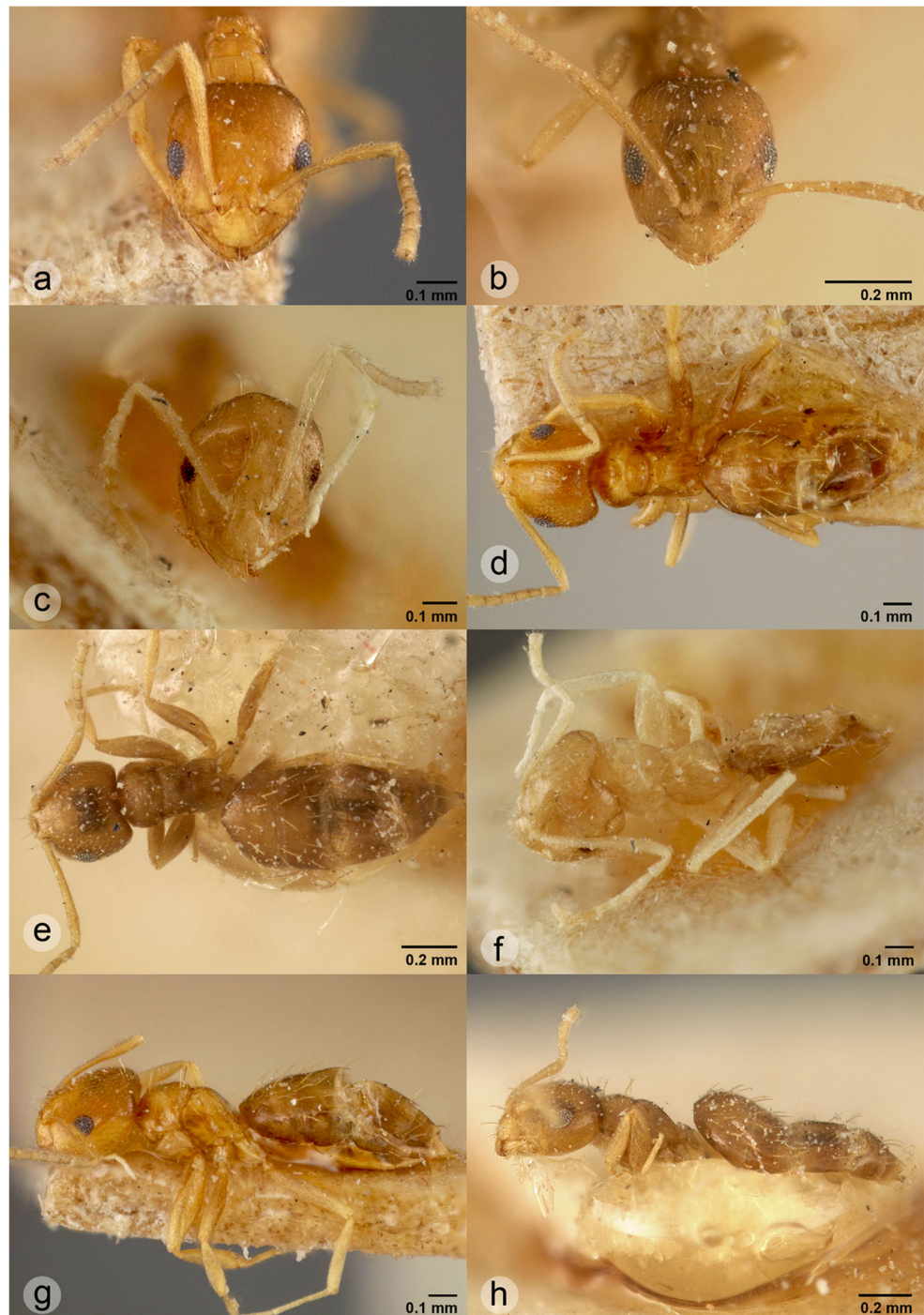
(Fig. 9, supplementary material Fig. S3)

*Brachymyrmex heeri* var. *aphidicola* Forel, 1909: 263 (w.). Lectotype worker (MHNG: USNMENT00757130) and paralectotype workers (MHNG: USNMENT00757129, 00757130, 00758121–00718123; here designated): 11 workers [examined]. **PARAGUAY:** San Bernardino. Other relevant descriptions: Forel (1912a: 62) (q.). (MHNG: USNMENT00757128): one queen. **BRAZIL: Santa Catarina:** Blumenau. Raised to species: Wild (2007: 43).

= *B. heeri* var. *fallax* Santschi, 1923a: 665 (w.). (NHMB: USNMENT00757697): one worker [examined]. **PARAGUAY.** Junior synonym of *B. aphidicola*: Wild (2007: 43).

= *B. longicornis* var. *hemiops* Santschi 1923a: 668 (w.). (NHMB: USNMENT00757188–00757190) 11 workers, three queens [examined]. **BRAZIL:** São Paulo, Ypiranga. n. syn.

**Fig. 9** *Brachymyrmex aphidicola*: **a, d, g** head, dorsal and lateral view of the lectotype worker; **b, e, h** *B. heeri* var. *fallax*: head, dorsal, and lateral view of a syntype worker; **c, f** *B. longicornis* var. *hemiops* n. syn: head and dorsal view of a syntype worker



**Additional material examined. ARGENTINA: Entre Ríos:** 8.63 km W Concordia, -31.42048 -58.11700, 16 m, 27 Dec. 2007, W. & E. MacKay, one worker, one male (WEMC: USNMENT00757975). **Misiones:** Parque Provincial Cañadón de Profundidad, -27.56020 -55.70988, 160 m, 29 Dec. 2007, W. & E. MacKay leg #22710, #22711, #22712, #22724, #22732, 10 workers (WEMC: USNMENT00757617, 00757897, 00757901, 00757924, 00757925, 00757929, 00757930, 00757956, 00757992). **BOLIVIA: Santa Cruz:** Parque

Nacional Noel Kempff, Mercado, -18.800 -60.383, 700 m, 04 Dec. 1993, P.S. Ward #12285-46, two workers, one queen (PSWC: USNMENT00757910). **BRAZIL: Amazonas:** 61 km N Manaus, om Caracai Rd., “caatinga,” 10 June 1972, W.L. & D.E. Brown, three workers (MCZC: UNSMENT00757619). **Goias:** Anapolis, 12 Feb. 1958, W. Kempf, two workers (MZSP: USNMENT00757921). Ouro Verde, Faz Boa Vista, -16.29847 -49.21183, 01-07 Aug. 2005, R.R. Silva & R.M. Feitosa, five workers (ICN:

MZSP123). **Mato Grosso:** Chapada dos Guimarães, -15.43333 -55.44874, 740 m, 03 Sep. 1996, P.S. Ward leg #13203–7, three workers (PSWC: USNMENT00757911). **Mato Grosso do Sul:** 24 km W Campo Grande, 07 Oct. 1989, W. MacKay, two workers (WEMC: USNMENT00758000). 48 km E Campo Grande, 12 Oct. 1989, S. Porter #12791, two workers (WEMC: USNMENT00759011). 8 km SE Punta Bora, 15 Oct. 1989, W.P. MacKay #12508, two workers (WEMC: USNMENT00759003). Río de Alegria, 17 Oct. 1989, W.P. MacKay #12950, two workers (WEMC: USNMENT00759022). **Pará:** Melgaço, Caxiuanã-ECFPn, 27 June–03 Dec. 2001, I. Andrade, five workers (MPEG: USNMENT00757674, 00757927, 00758030, 00759030). Melgaço, Caxiuanã-ECFPn, -1.78155 -51.59758, 30 Oct. 2003, A.Y. Harada, E.P. Fagundes, C.J.M. Ribeiro, C.E.D. Sanhudo, C.A.R. Moura, J.L.P. Souza, C. Renato, two workers (MPEG: AYH112, 127). Serra Norte, Calderiã, 20 Oct. 1980, two workers (MPEG: MPEG\_HYM11505158, USNMENT00757902). **Rio de Janeiro:** Teresópolis, P.N. Serra dos Orgãos, -22.45333 -42.99806, 23–28 Nov. 1999, Dietz, Silva & Rocha, eight workers (ICN: MZSP130). **Rondônia:** Ouro Preto do Oeste, 03 Apr. 1985, Linha 212 N 0375, 339, W. França, four workers (MPEG: USNMENT00757899, 00757914, 00757915, 00758999). Ouro Preto do Oeste, 04 May 1985, Linha 212, W. França, three workers (MPEG: USNMENT00757913, 00757938, 00758038). Ouro Preto do Oeste, 25 Mar. 1985, ResINPA0035, J. Dias, two workers (MPEG: USNMENT00757914, 00757936). **São Paulo:** Ipiranga, 2371, two workers (MZSP: USNMENT00757926]. Itirapina, Dec. 2008, D.P. Silva, one worker (MPEG: AYH008). **COLOMBIA: Cundinamarca:** Bogotá-Villavicencio Km 88 (Susumuko), 1100 m, 28 June 1976, W.L. & D.E. Brown, one worker, one queen (MCZC: USNMENT00757746). Caqueza, 29 Dec. 1975, W. & E. MacKay #945, two workers (WEMC: USNMENT00757686). **Huila:** 4 km NE Rivera, 30 Dec. 1986, W. & E. MacKay, three workers (WEMC: USNMENT00757903). La Vega, A280, 14–17 Jul 1975, W. MacKay, one worker, one male (WEMC: USNMENT00757912). **Magdalena:** 4 km San Pedro, 10.95 -74.05, 550 m, 14 Aug. 1985, P.S. Ward #17912–36, three workers (PSWC: USNMENT00757585). **Meta:** San Juan de Arama, RNN La Macarena, Caño La Curia, 580 m, 13 July 1992, Est. U. Nacional, one worker (ICN: USNMENT00758035). **Tolima:** Mendez, 15 Nov. 1995, F. Fernández, one worker (IAvH: USNMENT00759058). **Valle del Cauca:** Medio Calima, 24 June 1989, E. MacKay #11746 (WEMC: USNMENT00758041). **COSTA RICA: Heredia:** Estación biológica La Selva, 10.417 -84.000, 50 m, 21 Oct. 1991, J. Longino #3126-s, one worker, one queen (JTLC: INBIOCRI001238064). **ECUADOR: Loja:** Estación San Francisco, 2200 m, 14 Sep. 2011, 14 workers (ICN: USNMENT00759036, 00759037). Estación San Francisco, 17 Sep. 2011, two workers (ICN: USNMENT00759034). **Napo:** 11 km SE Consaga, -0.66667 -77.80000, 1640 m, 09 Dec. 2003, A.L. Wild #AW2263, four workers (ALWC: USNMENT00757586, 00757928). **GUATEMALA:** Alta Vera Paz, Parque Nacional Las Victorias, 15.47492 -90.37528, 206 m, 18 July 2004, W. & E. MacKay, one worker (WEMC: USNMENT00758018). **GUYANA: Karto:** Pt. Mazaruni-Potaru Dist. J. Weintraub, two workers, one queen (MCZC: USNMENT00757931). **MEXICO: Guanajuato:** Highway 57, Km 306, Rancho Jardin, 10 Aug. 1965, Cornell University, two workers, one queen (MCZC: USNMENT00759002). Yuriria, 03 Feb. 1964, P. Reyes C. & H. Romero, one worker (MZSP: USNMENT00757616). **NICARAGUA: Río San Juan:** Bartola, 8 km SE El Castillo, 10.97303 -84.33897, 47 m, 12 July 2003, W. & E. MacKay #20187, two workers (WEMC: USNMENT00758029). **PANAMA: San Blas:** Nusegandi, 08 June 1992, L.E. Tennant, one worker, one queen (MZSP: USNMENT00757923). **PARAGUAY: Amambay:** Parque Nacional Cerro Corá, -22.650 -56.017, 13 May 1997, A. Wild #AW0563, one worker (ALWC: USNMENT00757625). **Canindeyu:** Reserva Natural del Bosque, Mbaracayú, Jejuimi, -24.1 -55.5, 19 Sep. 1996, A. Wild #AW0563, six workers (ALWC: USNMENT00757584, 00757895). Reserva Natural del Bosque, Mbaracayú, Jejuimi, -24.1 -55.5, 16–23 May 1996, A.C.F. Costa, one worker (ALWC: USNMENT00757868). Reserva Natural del Bosque, Mbaracayú, Jejuimi, -24.1 -55.5, 11 Oct 1996, A. Wild #AW0334, one worker (ALWC: USNMENT00757893). Reserva Natural del Bosque, Mbaracayú, Jejuimi, -24.1 -55.5, 28 Jan. 1997, A. Wild #AW384, three workers (ALWC: USNMENT00757894). Reserva Natural del Bosque, Mbaracayú, Jejuimi, -24.1 -55.5, 12 Mar. 1997, A. Wild #AW0490, three workers (ALWC: USNMENT00757896). **PERU: Huanuco:** 42 km E. Tingo Maria, 1100 m, 10 Dec. 1954, one worker (CASC: CASENT0196020). **Madre de Dios:** Reserva Nacional Tambopata, Centro Sachavacayoc, -12.85583 -69.36194, 19–31 July 2012, Curso de hormigas, seven workers (ICN: CAB-120725-1). Reserva Nacional Tambopata, Centro Sachavacayoc, casa camping, -12.85583 -69.36194, 198 m, 26 July 2012, GSNMBU, one worker (ICN: USNMENT00757613). **USA: Louisiana:** East Baton Rouge Par. Baton Rouge, Kennilworth & Perkins Rd. BREC Perkins Park, 03 Apr. 2003, S.T. Dash, one worker (WEMC: USNMENT00759023). **VENEZUELA: Bolivar:** Canaima, Orchid Is, 14 Oct. 1988, W. MacKay #11159, one worker (WEMC: USNMENT00757906).

**Diagnosis.** *Brachymyrmex aphidicola* is morphologically similar to *B. australis*, *B. minutus*, and *B. termitophilus*, because all of them typically have smooth and shiny yellowish bodies, their mesonotum does not bulge dorsally above the pronotum, their eyes are positioned on the cephalic midline, and the metanotal groove is either absent or narrower than the

diameter of the metathoracic spiracles. However, *B. aphidicola* differs from *B. australis* by having scapes that surpass the posterior margin of the head by a length longer than the maximal diameter of the eye; from *B. minutus* by having a well-differentiated mesometanotal suture and by the presence of two erect hairs on the pronotum and two on the mesonotum; and from *B. termitophilus* by having scattered pubescence on the gaster.

**Lectotype measurements** (mm). HL<sub>1</sub> 0.41; HL<sub>2</sub> 0.29; HL<sub>3</sub> 0.10; HW 0.37; SL 0.39; EL 0.10; WL 0.41; PnL 0.10; PnW 0.25; ML 0.08; MW 0.18; **Indices** CI 90.48; SI<sub>1</sub> 105.26; SI<sub>2</sub> 133.33; OI<sub>1</sub> 26.32; OI<sub>2</sub> 23.81.

**Paralectotype measurements** (mm) (*n* = 4). HL<sub>1</sub> 0.43–0.45; HL<sub>2</sub> 0.27–0.31; HL<sub>3</sub> 0.10; HW 0.37; SL 0.39–0.41; EL 0.10; WL 0.41–0.43; PnL 0.14–0.17; PnW 0.23–0.29; ML 0.08–0.10; MW 0.16–0.18; **Indices** CI 82.61–86.36; SI<sub>1</sub> 105.26–110.53; SI<sub>2</sub> 125.00–142.86; OI<sub>1</sub> 26.32; OI<sub>2</sub> 21.74–22.73.

**Additional material examined measurements** (mm) (*n* = 20). HL<sub>1</sub> 0.36–0.55; HL<sub>2</sub> 0.26–0.37; HL<sub>3</sub> 0.08–0.13; HW 0.33–0.51; SL 0.32–0.54; EL 0.09–0.12; WL 0.35–0.58; PnL 0.09–0.18; PnW 0.24–0.36; ML 0.07–0.12; MW 0.14–0.20; **Indices** CI 84.21–95.65; SI<sub>1</sub> 94.74–112.5; SI<sub>2</sub> 117.14–157.89; OI<sub>1</sub> 21.82–28.57; OI<sub>2</sub> 20.62–28.89.

**Description.** *Head.* Slightly longer than wide in full face view; posterior cephalic margin flat or slightly concave. Dorsum of the head with scattered appressed hairs. Clypeus with a rounded anterior margin and five long, erect hairs of which a single, usually conspicuous hair is near the anterior margin, two hairs are in mediolateral position, and two more near the toruli; other hairs on the clypeus are markedly shorter and appressed or decumbent. Toruli surpassing the posterior clypeal margin in oblique anterodorsal view. The scapes surpass the posterior margin of the head by a length larger than the maximal diameter of the eye, and typically bear appressed, sometimes decumbent, but never erect hairs. Three ocelli usually present, but sometimes inconspicuous. Eyes are positioned on the cephalic midline and have 7–10 ommatidia along their maximal diameter.

*Mesosoma.* Typically with two erect hairs on the pronotum and two on the mesonotum. In lateral view, the mesonotum is not or weakly inflated and does not bulge dorsally above the pronotum. Metanotal groove absent or shallow and narrower than the diameter of the metathoracic spiracles. Metathoracic spiracles in dorsolateral position, not protruding, and usually touching the propodeal suture. Dorsum of propodeum slightly convex and ~ 1/3th of the length of the propodeal slope. Propodeal spiracles circular, positioned ventrally of the posterior propodeal margin, and slightly posterior of the middle of the propodeal slope. Legs with appressed and scattered hairs. Petiole short and inclined forward.

*Gaster.* With scattered pubescence and scattered long suberect hairs, especially along the posterior edges of the segments.

*Color and sculpture.* Body smooth and shiny, yellowish.

**Distribution** (Supplementary material Fig. S3). *Brachymyrmex aphidicola* is widely distributed and known

from Argentina, the Bermudas, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, Guatemala, Guyana, Mexico, Nicaragua, Panama, Paraguay, Peru, the USA, and Venezuela.

**Biology.** Specimens of this species have been found under stones, in rotten wood, on epiphytes (USNMENT00757619), and on *Conostegia setosa* (USNMENT00757923). *Brachymyrmex aphidicola* nests underground or in organic litter, and it appears to be abundant in Paraguayan forests (Wild, 2007).

**Remarks.** Some specimens from Argentina have expanded gasters and Forel (1912a) highlighted a worker identified as *B. aphidicola* from Santa Catharina (Brazil) that also has a somewhat expanded gaster, but this specimen has not been studied and its identification remains to be confirmed. The original description of Forel (1909) indicates *B. aphidicola* to occur in both Paraguay and the Bermudas; however, a type locality is not designated. In the type series of Forel's collection (NHMG), only specimens from Paraguay are present. Nevertheless, Santschi's collection (NHMB) contains a decapitated specimen from Bermudas that is labeled as the type of *B. aphidicola*. Given this complication, only the specimens from Forel's collection are designated here as lectotype and paralectotypes.

We concur with Wild (2007) that *B. heeri* var. *fallax* is a junior synonym of *B. aphidicola*. The workers of the type series of this variation have all the diagnostic characteristics of *B. aphidicola*. The description of *B. longicornis* var. *hemiops* (Santschi, 1923a) only specifies color and the smaller size of the body and eyes of this variation in comparison to *B. longicornis*; however, detailed study of the syntype renders it indistinguishable from *B. aphidicola*.

#### *Brachymyrmex attenuatus* Santschi NEW STATUS

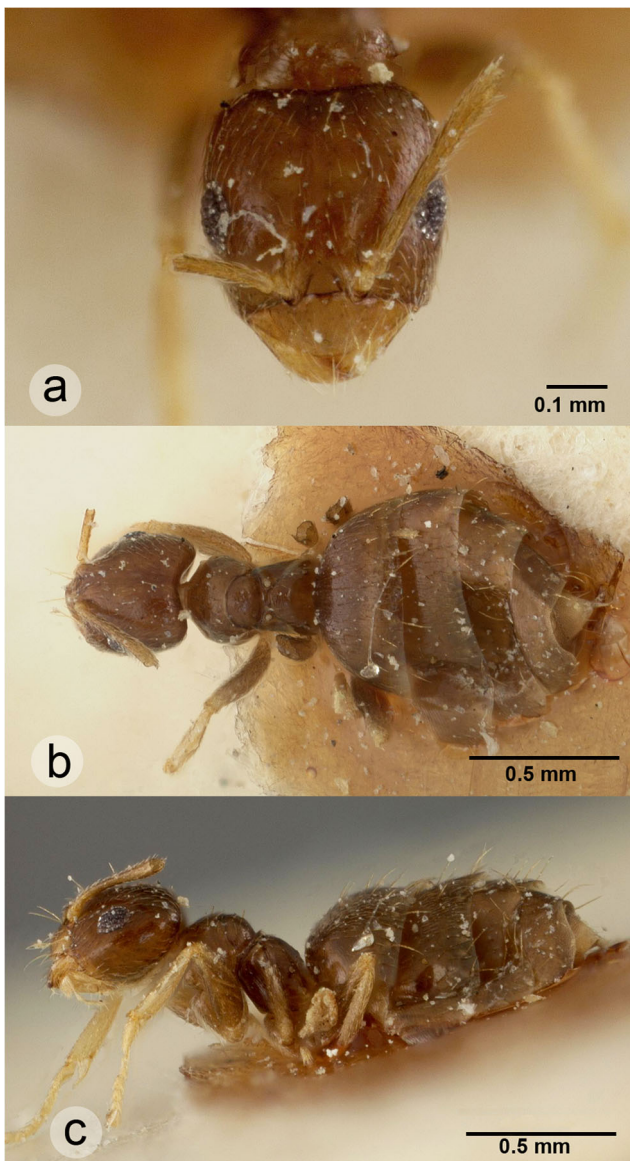
(Fig. 10, supplementary material Fig. S4)

*Brachymyrmex luederwaldti* st. *attenuatus* Santschi, 1929: 310 (w.). Lectotype worker (NHMB: USNMENT00757177) and Paralectotype worker (NHMB: USNMENT00757177; here designated) two workers [examined]. **BRAZIL: Santa Catarina:** Blumenau.

**Diagnosis.** *Brachymyrmex attenuatus* n. st. morphologically resembles *Brachymyrmex degener*, because both have long scapes that extend beyond the posterior margin of the head, they have faint sculpture on the mesosomal dorsum, and dorsally positioned, slightly protruding metathoracic spiracles. *Brachymyrmex attenuatus* n. st. differs from *B. degener*, however, by having a gaster with dense pubescence.

**Lectotype worker measurements** (mm) HL<sub>1</sub> 0.47; HL<sub>2</sub> 0.28; HL<sub>3</sub> 0.11; HW 0.43; SL n.a.; EL 0.12; WL 0.52; PnL 0.09; PnW 0.31; ML 0.12; MW 0.21; **Indices** CI 90.74; SI<sub>1</sub> n.a.; SI<sub>2</sub> n.a.; OI<sub>1</sub> 28.57; OI<sub>2</sub> 23.15.

**Paralectotype worker measurements** (mm) HL<sub>1</sub> 0.43; HL<sub>2</sub> 0.31; HL<sub>3</sub> 0.11; HW 0.39; SL 0.45; EL 0.13; WL 0.46; PnL 0.14; PnW 0.29; ML 0.11; MW 0.15; **Indices** CI 91.84; SI<sub>1</sub> 113.33; SI<sub>2</sub> 145.71; OI<sub>1</sub> 33.33; OI<sub>2</sub> 25.51.



**Fig. 10** *Brachymyrmex attenuatus*: a–c head, dorsal, and lateral view of the lectotype worker

**Description.** *Head.* Slightly longer than wide in full face view; posterior cephalic margin slightly concave. Dorsum of head with scattered appressed hairs. Clypeus with a rounded anterior margin and five long, erect hairs of which a single, usually conspicuous hair is near the anterior margin, two hairs are in mediolateral position, and two more near the toruli; other hairs on the clypeus are substantially shorter and appressed or decumbent. Toruli surpassing the posterior clypeal margin in oblique anterodorsal view. The scapes extend beyond the posterior cephalic margin by a length approximately equal to the maximum diameter of the eye (and not more than 1.5× this diameter), and have decumbent hairs. A single central ocellus seems to be present but is inconspicuous. Eyes are positioned on the cephalic midline and have 7–9 ommatidia along their maximal diameter.

*Mesosoma.* Typically with two erect hairs on the pronotum and two on the mesonotum, sometimes with additional suberect hairs, mainly on pronotum. In lateral view, the mesonotum is inflated, but it does not bulge dorsally above the pronotum. Metanotal groove deep and wider than the diameter of the metathoracic spiracles. Metathoracic spiracles fully dorsal in position, slightly protruding and not touching the mesometanotal or propodeal sutures. Dorsum of propodeum slightly convex and shorter than the propodeal slope. Propodeal spiracles circular, positioned ventrally of the posterior propodeal margin, and slightly posteriorly of the middle of the propodeal slope. Legs with appressed and scattered hairs. Petiole short and inclined forward.

*Gaster.* With appressed dense pubescence and several scattered long erect hairs.

*Color and sculpture.* Body overall smooth and shiny, with faint sculpture on mesosomal dorsum. Body uniformly light or dark brownish, but the legs and antennae are yellowish.

**Distribution** (Supplementary material Fig. S4). *Brachymyrmex attenuatus* is currently only known from Brazil.

**Biology.** Unknown.

**Remarks.** Here, we designate the lectotype as the specimen closest to the pin (USNMENT00757177); the paralectotype has lighter brownish color in comparison with the lectotype. This species was described by Santschi (1929) as a subspecies of *B. luederwaldti* that has a smaller body size in comparison with *B. luederwaldti*. Additionally, *B. attenuatus* has weaker sculpture, a shinier body, especially on pronotum, a more concave posterior cephalic border, smaller eyes and a more convex mesonotum than *B. luederwaldti*. All these characteristics are somewhat subjective, because they represent differences in intensity rather than state and as such it is difficult to determine clear boundaries. A more marked difference is the presence of pubescence on the gaster, which is clearly present in *B. attenatus* n. st., but absent in *B. luederwaldti*. The presence or absence of pubescence is an important trait to delimit other *Brachymyrmex* species, and hence we raise *B. attenatus* n. st. to species level.

*Brachymyrmex australis* Forel

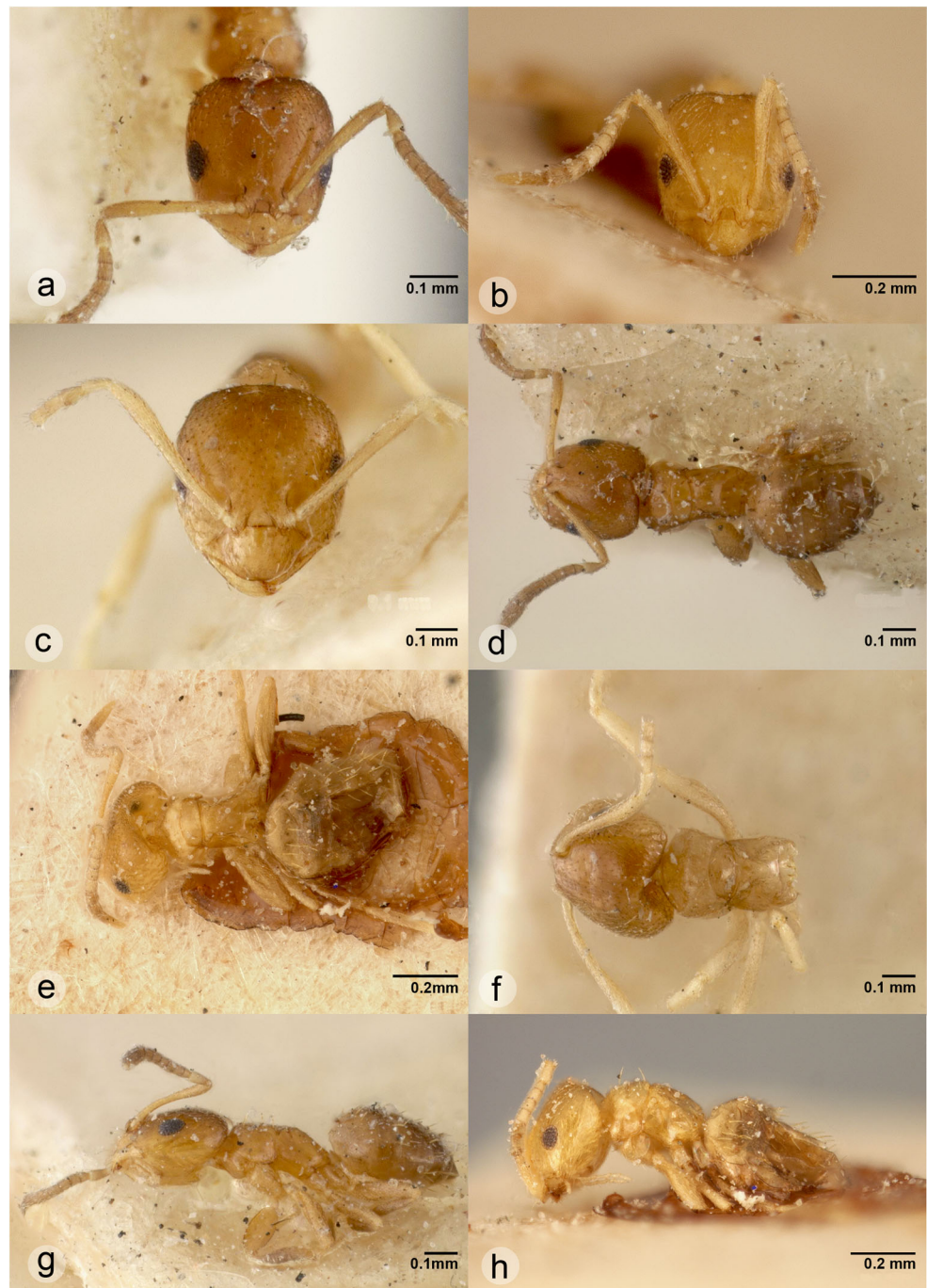
(Fig. 11, supplementary material Fig. S5)

*Brachymyrmex minutus* r. *australis* Forel, 1901b: 302 (w.). Lectotype worker (MHNG: USNMENT00757156) and paralectotype worker (MHNG: USNMENT00758102; here designated): two workers [examined]. **BRAZIL: Rio Grande do Sul:** Pelotas. Raised to species: Santschi (1922: 260). See also: Santschi (1923a: 662).

= *Brachymyrmex australis* var. *curta* Santschi, 1922: 260 (w.q.m.). (NHMB: USNMENT00757700–00757703, 00758069–00758071): 17 workers, two queens, seven males [examined]. **ARGENTINA: Cordoba:** Alta Gracia [Also described as a new variety in Santschi (1923a: 663)]. n. syn.

= *Brachymyrmex longicornis* Forel, 1907: 9 (w.). (MHNG: USNMENT00757144): two workers [examined]. **BRAZIL:** Porto Alegre. Other relevant descriptions: Forel (1912a: 62)

**Fig. 11** *Brachymyrmex australis*: **a, d, g** head, dorsal, and lateral view of the lectotype worker; **b, e, h** *B. australis* var. *curta* n. syn.: head, dorsal, and lateral view of a syntype worker; **c, f** *B. longicornis* n. syn.: head and dorsal view of a syntype worker



(q.). (MHNG: USNMENT00757145): one queen [examined].

**BRAZIL:** São Paulo. n. syn.

**Additional material examined. ARGENTINA: Santa Cruz:** O. Bondensköld, three workers (MCZC: USNMENT00759000). **Tucumán:** 11 km N Tafi Viejo, -26.63333 -65.23333, 820 m, 01 Feb. 1995, P.S. Ward #12826–25, three workers (PSWC: USNMENT00757628). **BAHAMAS: Exumas:** unnamed cay, 175 m N of NW tips of Obrien's Cay, 05 May 1995, J. W. Morrison 321–92, two workers (PSWC: USNMENT00758991). **BRAZIL:**

**Bahia:** Ilheus, CEPEC, Antonio 455E, two workers, two queens (CPDC: USNMENT00757922). Lençóis, Chap. Diamantina, -12.55 -41.38, 25 Mar. 2001, Santos, J.R.M. dos, two workers, one queen (CPDC: USNMENT00757909). **Goias:** Ouro verde, Faz Boa Vista, -16.29847 -49.21183, 01–07 July 2005, R.R. Silva & R.M. Feitosa, four workers (ICN: MZSP122). **Minas Gerais:** Alfenas, Porto, 06 Oct. 2011, I.A. Dos Santos, six workers (ICN: USNMENT00759048, 00759049). **Pará:** Melgaço, Caxiuanã, ECFPn, -1.73584 -51.48762, II: transecto (4–

600), 23–25 Oct. 2005, Equipe A.Y. Harada, three workers (MPEG: AYH036). **Rio de Janeiro:** Teresópolis, P.N. Serra dos Orgãos, -22.45333 -42.99806, 23–28 Nov. 1999, Dietz, Silva & Rocha, 6 workers (ICN: MZSP130). **Santa Catarina:** São Bento do Sul, APA Rio Vermelho, -26.36417 -42.99806, 30 Mar.–04 Apr. 2001, R. Silva & Eberhardt, five workers (ICN: MZSP134 135). **São Paulo:** Ilha da Vitória, 16–27 Mar. 1964, Exp. Dep. Zool. 3592, 5 workers, one queen (MCZC: USNMENT00757932); Itirapina, 10 Feb. 2009, S. Sendoya, 20 workers (ICN: USNMENT00759046); Jundiá, Sierra Do Japi, Apr. 2009, S. Diniz, three workers (ICN: USNMENT00759043); Piedade, Floresta Atlantica, “Cristo,” Mar. 2010, G. Bieber, three workers (ICN: USNMENT00759045); Tapirai, -24.03208 -47.46556, 08–14 Jan. 2001, R. Silva & Eberhard, four workers (ICN: MZSP170). **COLOMBIA:** **Bolivar:** Zambrano, Hacienda Monterrey, 9.617 -74.900, 9–75 m, 04 Aug. 1992, A. Molano, three workers (ICN: USNMENT00757898). **Caldas:** Municipio Aranzazu, Vereda Alegrias, Finca Betania, La Esperanza, 5.29811 -75.4904, 1990 m, L.E. Franco & J. Cruz, two workers (IAvH: IAvH27305); Aranzazu, Vereda Alegrias, Finca Villa Rosita, 5.30603 -75.4849, 1825 m, 06–08 Aug. 2003, L.E. Franco & J. Cruz, one worker (IAvH: IAvH25467). **Caquetá:** PNN Serranía de Chiribiquete, Cuñané-Anuí, 26 Feb. 2001, two workers (IAvH: IAvH-E71471). **Cauca:** El Hortigal, Holanda, Mar. 2002, Valderrama, one worker (ICN: USNMENT00757937). **Cundinamarca:** Fusagasugá, 08 Dec. 1975, W. & E. MacKay, two workers (WEMC: USNMENT00757907). **Guajira:** Serranía de Macuira, 6–8 km S Nazareth, 70–200 m, 13 June 1957, W.L. Brown & Kugler, two workers (IAvH: IAvH-E74171). **Huila:** 21 Km W La Plata Gallego, 03 Jan. 1984, W.P. MacKay #7153, six workers (WEMC: USNMENT00757623, 00757624, 00759014); Neiva, 05 Dec 1975, W. & E. MacKay, two workers (WEMC: USNMENT00757620). **Magdalena:** PNN Tayrona, Cañaveral, 11.33 -74.03, 30 m, 20–27 Apr. 2000, C. Sarmiento, one worker (IAvH: USNMENT00759056). Meta and Cundinamarca border: 28 Dec. 1975, W. & E. Mackay, four workers (WEMC: USNMENT00757917, 00757939). **Meta:** Puerto Gaitán, 21 Dec. 1975, W. & E. MacKay #783, two workers (WEMC: USNMENT00757672). **Quindío:** Buenavista, Vereda El Infierno, Finca Guadalajara, 4.3767 -75.7694, 1160 m, 16 Nov. 1999, E. Gonzalez, two workers (IAvH: IAvH-E74165); Filandia, Vereda Cruces, Finca Los Micos, 4.70424 -75.65917, 12–13 July 2002, E. Jimenez & L.E. Franco, one worker (IAvH: IAvH27232). **Risaralda:** Apia La Felisa, Cafetal de sol (S-I), 5.13 -75.95, 1480 m, 29 Oct. 2001, one worker (IAvH: IAvH-E74174). **Valle del Cauca:** Dagua, 07 Jan. 1976, W. & E. MacKay, five workers (WEMC: USNMENT00758993); Medio Calima, 24 June 1989, E. MacKay #11740 #11743 #11744, two workers (WEMC: USNMENT00757738, 00759005, 00757908, 00759012).

**Vichada:** Cumaribo, Corregimiento Santa Rita, PNN El Tuparro, 5.3075 -67.9500, 135 m, 14–16 Feb. 2004, I. Quintero & E. Gonzalez, two workers (IAvH: USNMENT00759057). **COSTA RICA:** **Guanacaste:** Provincia Maritza field Station, 03 May 1995, R. Anderson #17716, three workers (WEMC: USNMENT00757671). **Puntarenas:** Pen. Osa. Par. Nat. Corcovado, Llorona, 8.058 -83.70, 5 m, 30 Dec. 1981, J. Longino, one worker (JTLC: JTLC000005948). **CUBA:** **Holguín:** 6 km S Yamanigüey, 20.55 -74.73, 25 m, 23 Aug. 2001, P.S. Ward #14437–19, three workers (PSWC: USNMENT00757919). **DOMINICAN REPUBLIC:** 16 km ENE Pedernales, 18.11667 -71.62361, 800 m, 9 Sep. 1992, P.S. Ward #11726–22, three workers (PSWC: USNMENT00757959); Prov. La Vega, Jarabacoa to El Rio, shady ravine, 80–1500 m, Feb. 1975, W.L. & D.E. Brown, two workers (MCZC: USNMENT00757736). **ECUADOR:** Guayaquil, 10 m, Dec. 1997, Forero, two workers (IAvH: USNMENT00759054). **FRENCH GUIANA:** Petit Saut Basse Vie II/III, 2001, A. Dejean, one worker (CPDC: USNMENT00757734); Reserve Naturel de Nouragues–Inselbery forest, Oct. 2009, Sara Groc, four workers (ICN: USNMENT00759033). **GUATEMALA:** **El progreso:** 5 km W El Rancho, 14.91667-90.06666, 400 m, 17 Nov. 2003, A.L. Wild #AW2002, three workers (ALWC: USNMENT00757957). **Suchitepéquez:** Cocales (Mpio. San Antonio), 14.39206 -91.19347, 242 m, 31 Aug. 2004, W & E. MacKay #20820, one worker (WEMC: USNMENT00758995). **GUYANA:** Demerara-Mahaica: Wales, 6.67 58.25, 50 m, 23 Jan. 1981, two workers, one queen (JTLC: JTLC000005920); Rupununi, Karanambo, 3.75-59.3, 100 m, 01 Jan. 1981, one worker (JTLC: JTLC000005926). **MAURITUS:** Mgne. Brise Fer, -20.37 57.43, 600 m, 07 May 1989, P.S. Ward #10518–2, three workers (PSWC: USNMENT00757934). **MEXICO:** **Chiapas:** 10 km S Palenque, 30 May 1988, 31 May 1988, W. MacKay #10611 #10613, eight workers (WEMC: USNMENT00757588, 00757677, 00757678). **Veracruz:** Los Tuxtlas, 26 July 1974, R.L. Jeanne, one worker (MCZC: USNMENT00757735). **Yucatan:** 25.7 km E Progreso, 12 Apr. 1982, Smalley Thien & Bradburn, one worker (MCZC: USNMENT00757618). **PARAGUAY:** **Boquerón:** Enciso, -21.20 -61.67, 03–06 Nov 2001, M. LePonce & T. Delsinne, two workers (ALWC: USNMENT00757904). **Central:** Areguá, CHP center, -25.30 -57.38, 01 Oct. 1995, A. Wild #AW 0059, one worker (ALWC: USNMENT00757905). **Presidente Hayes:** Monte Lindo, -23.86667 -58.46667, 800–1500 m, Feb. 1975, W.L. & D.E. Brown, two workers (MCZC: USNMENT00757736). **PERU:** **Madre de Dios:** Reserva Nacional Tambopata, Centro Sachavacayoc, Centre, -12.85583 -69.36194, 209 m, 19–31 Jul 2012, R. Feitosa, one worker (ICN: USNMENT00757611). **URUGUAY:** Montevideo, L. Pastre, one worker (CPDC: USNMENT00757684).



**Diagnosis.** *Brachymyrmex australis* is very similar in morphology to *B. aphidicola*, *B. minutus*, and *B. termitophilus*, because all these species have a mesonotum that does not bulge dorsally above the pronotum in lateral view, their bodies are smooth, shiny and yellowish, and their eyes are positioned on the cephalic midline. However, *B. australis* differs from *B. aphidicola* by somewhat shorter scapes, although they still reach to the posterior margin of the head or surpass it by a length equal to or smaller than the maximal diameter of the eye; it differs from *B. minutus* by having a well-marked mesometanotal suture and two erect hairs on the pronotum and two on the mesonotum; finally, it has scattered pubescence on the gaster whereas that of *B. termitophilus* is dense.

*Lectotype worker measurements* (mm) HL<sub>1</sub> 0.37; HL<sub>2</sub> 0.27; HL<sub>3</sub> 0.10; HW 0.29; SL 0.29; EL 0.10; WL 0.35; PnL n.a.; PnW 0.23; ML 0.08; MW 0.17; *Indices* CI 78.95; SI<sub>1</sub> 100.00; SI<sub>2</sub> 107.14; OI<sub>1</sub> 33.33; OI<sub>2</sub> 26.31.

*Additional material examined measurements* (mm) ( $n = 13$ ). HL<sub>1</sub> 0.32–0.54; HL<sub>2</sub> 0.21–0.38; HL<sub>3</sub> 0.08–0.15; HW 0.29–0.53; SL 0.26–0.48; EL 0.08–0.14; WL 0.29–0.55; PnL 0.08–0.20; PnW 0.21–0.32; ML 0.06–0.11; MW 0.14–0.20; *Indices* CI 82.61–97.09; SI<sub>1</sub> 89.09–104.54; SI<sub>2</sub> 114.29–135.29; OI<sub>1</sub> 15.38–30.91; OI<sub>2</sub> 19.35–28.33.

**Description.** *Head.* Slightly longer than wide in full face view; posterior cephalic margin slightly concave. Dorsum of the head with scattered appressed hairs. Clypeus with a rounded anterior margin and five long, erect hairs of which a single, usually conspicuous hair is near the anterior margin, two hairs are in mediolateral position, and two more near the toruli; other hairs on the clypeus are markedly shorter and appressed or decumbent. Toruli surpassing the posterior clypeal margin in oblique anterodorsal view. The scapes extend beyond the posterior margin of the head by a length equal to or smaller than the maximal diameter of the eye; they typically have appressed, sometimes decumbent, but never erect hairs. Three inconspicuous ocelli. Eyes on the cephalic midline, with 7–14 ommatidia along their maximal diameter.

*Mesosoma.* Typically with two erect hairs on the pronotum and two on the mesonotum. The mesonotum is not inflated and it does not bulge dorsally above the pronotum in lateral view. Metanotal groove absent or shallow and narrower than the diameter of the metathoracic spiracles. Metathoracic spiracles in dorsolateral position, not protruding, and usually touching both the mesometanotal and propodeal sutures. Dorsum of the propodeum flat or weakly convex and ~ 1/3th of the length of the propodeal slope. Propodeal spiracles circular, positioned ventrally of the posterior propodeal margin slightly posterior of the middle of the propodeal slope. Legs with appressed and scattered hairs. Petiole short and inclined forward.

*Gaster.* With scattered pubescence and scattered long suberect hairs.

*Color and sculpture.* Body smooth and shiny, uniform yellowish in color.

**Distribution** (Supplementary material Fig. S5). *Brachymyrmex australis* is known from Argentina, the Bahamas, Brazil, Colombia, Costa Rica, Cuba, the Dominican Republic, Ecuador, French Guiana, Guatemala, Guyana, Mexico, Paraguay, Peru, and Uruguay. It has also been introduced in Mauritius.

**Biology.** Some specimens have been found under stones and among leaf litter. The type material of *B. longicornis* (here considered a junior synonym of *B. australis*) was collected from orchids.

**Remarks.** Forel (1901b) described *B. australis* as a variety of *B. minutus* but did not indicate diagnostic traits to separate it from typical *B. minutus*. Subsequently, Santschi (1922) raised *B. australis* to species level, described a new variety to it (*B. australis* var. *curta*), again without clear motivation, although he pointed out morphological similarities between the males of *B. australis* and *B. fiebrigi*. Later, Santschi (1923a) indicated that *B. australis* has a conspicuous mesometanotal suture, and *B. minutus* does not, and that *B. australis* var. *curta* is smaller and shinier than typical *B. australis*.

The type material of *B. australis* var. *curta* and *B. longicornis* share the same diagnostic traits and display only minor variation in body size and the length of the scapes compared with *B. australis*. Most of the specimens of *B. longicornis* we studied are yellowish, but one was brownish, and the nature of this variation remains to be documented. In any case, Forel (1907) originally described *B. longicornis* as “yellowish brown.” Considering our observations *B. australis* var. *curta* and *B. longicornis* are synonymized here to *B. australis*.

Santschi (1923a) identified a specimen (one worker, NHMB) from a termite nest in Sao Leopoldo, Rio Grande do Sul, Brazil, i.e., the type locality of *B. termitophilus* (which has also been recored from termite nests), as *B. australis* but this specimen has the diagnosis traits of *B. fiebrigi*; additional specimens (two workers, NHMB) from Uruguay, Nueva Helvetia (Mme.v. Steiger) that he identified as *B. australis* var. *curta* have the diagnostic traits of *B. termitophilus*.

#### *Brachymyrmex bahamensis* NEW SPECIES

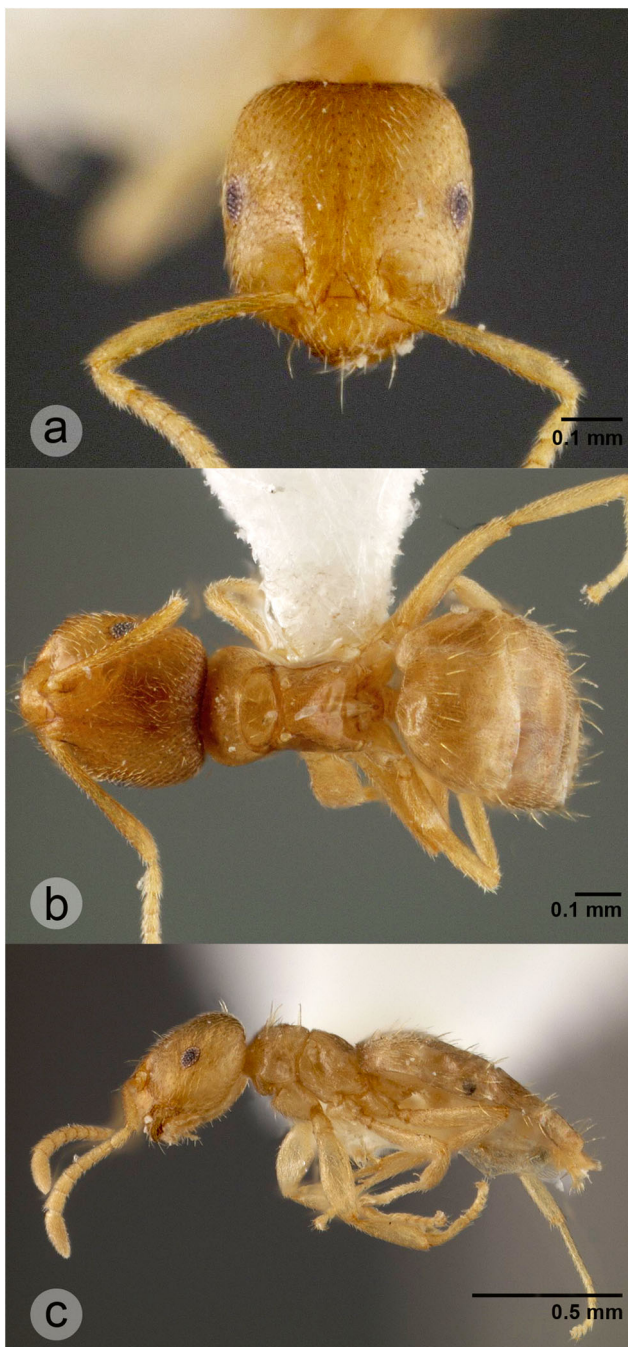
(Fig. 12, supplementary material S6)

Holotype worker (MCZC: USNMENT00757689) and Paratype workers (MCZC: USNMENT00757689, PSWC: USNMENT00757726); five workers. **BAHAMAS:** Exuma, unnamed cay, 175 m S of Staniel Cay, 21 May 1990, L.W. Morrison 101–90.

**Additional material examined. BAHAMAS:** Andros Island, May–June 1904, col. W.M. Wheeler, 13 workers, two queens (MCZC: USNMENT00757690).

**Etymology:** In reference of the type locality.

**Diagnosis.** *Brachymyrmex bahamensis* resembles *B. termitophilus* because both species have scapes that are surpass



**Fig. 12** *Brachymyrmex bahamensis* n.sp.: a–c head, dorsal, and lateral view of the holotype worker

the posterior margin of the head by a length smaller than the maximal diameter of the eye, their mesonotum does not bulge dorsally above the pronotum, they have erect or suberect hairs on the mesosoma, a gaster with dense pubescence, and yellowish body color. However, the unique feature of *B. bahamensis* is that it has approximately six erect hairs on the pronotum and two on the mesonotum that are very long, i.e., about twice the length of the maximal diameter of the eye. *Brachymyrmex bahamensis* also resembles *B. heeri*, but this latter species has a mesonotum that bulges out dorsally above the pronotum.

**Holotype measurements** (mm). HL<sub>1</sub> 0.46; HL<sub>2</sub> 0.31; HL<sub>3</sub> 0.13; HW 0.41; SL 0.38; EL 0.09; WL 0.45; PnL 0.13; PnW 0.29; ML 0.09; MW 0.19; **Indices** CI 88.46; SI<sub>1</sub> 91.30; SI<sub>2</sub> 120.00; OI<sub>1</sub> 21.74; OI<sub>2</sub> 28.85.

**Paratype measurements** (mm) ( $n = 2$ ). HL<sub>1</sub> 0.47–0.48; HL<sub>2</sub> 0.32; HL<sub>3</sub> 0.14; HW 0.43–0.44; SL 0.39–0.40; EL 0.09–0.10; WL 0.47–0.49; PnL 0.13–0.16; PnW 0.30–0.31; ML 0.09–0.12; MW 0.21; **Indices** CI 90.57–90.74; SI 91.67–91.84; SI<sub>2</sub> 122.22–125.00; OI<sub>1</sub> 22.45–25; OI<sub>2</sub> 27.78–28.30.

**Description.** **Head.** Slightly longer than wide in full face view; posterior cephalic margin slightly concave. Dorsum of head with appressed hairs and with two rows of erect hairs. Clypeus with a rounded anterior margin and five long, erect hairs of which a single, usually conspicuous hair is near the anterior margin, two hairs are in mediolateral position, and two more near the toruli; other hairs on the clypeus are markedly shorter and appressed or decumbent. Toruli surpassing the posterior clypeal margin in oblique anterodorsal view. The scapes surpass the posterior cephalic margin by a length smaller than the maximal diameter of the eye; they typically have appressed, sometimes decumbent but never erect hairs. Ocelli absent. Eyes are positioned on the cephalic midline and have 8–9 ommatidia along their maximal diameter.

**Mesosoma.** Approximately six long, erect hairs on the pronotum and two on the mesonotum, each having a length of about twice the maximal diameter of the eye. In lateral view, the mesonotum is not inflated and it does not bulge dorsally above the pronotum. Metanotal groove absent or shallow and narrower than the diameter of the metathoracic spiracles. Dorsum of the propodeum is flat and  $\sim 1/3$ th of the length of the propodeal slope. Metathoracic spiracles in dorsolateral position, not protruding, and usually touching the propodeal suture, but not the mesometanotal suture. Propodeal spiracles circular, positioned ventrally of the posterior propodeal margin, posterior of the middle of the propodeal slope. Legs with appressed and scattered hairs. Petiole short and inclined forward.

**Gaster.** With dense pubescence and several scattered conspicuous long erect hairs.

**Color and sculpture.** Body usually smooth and shiny, yellowish.

**Distribution** (Supplementary material S6). Currently exclusively known from the Bahamas.

**Biology.** Unknown.

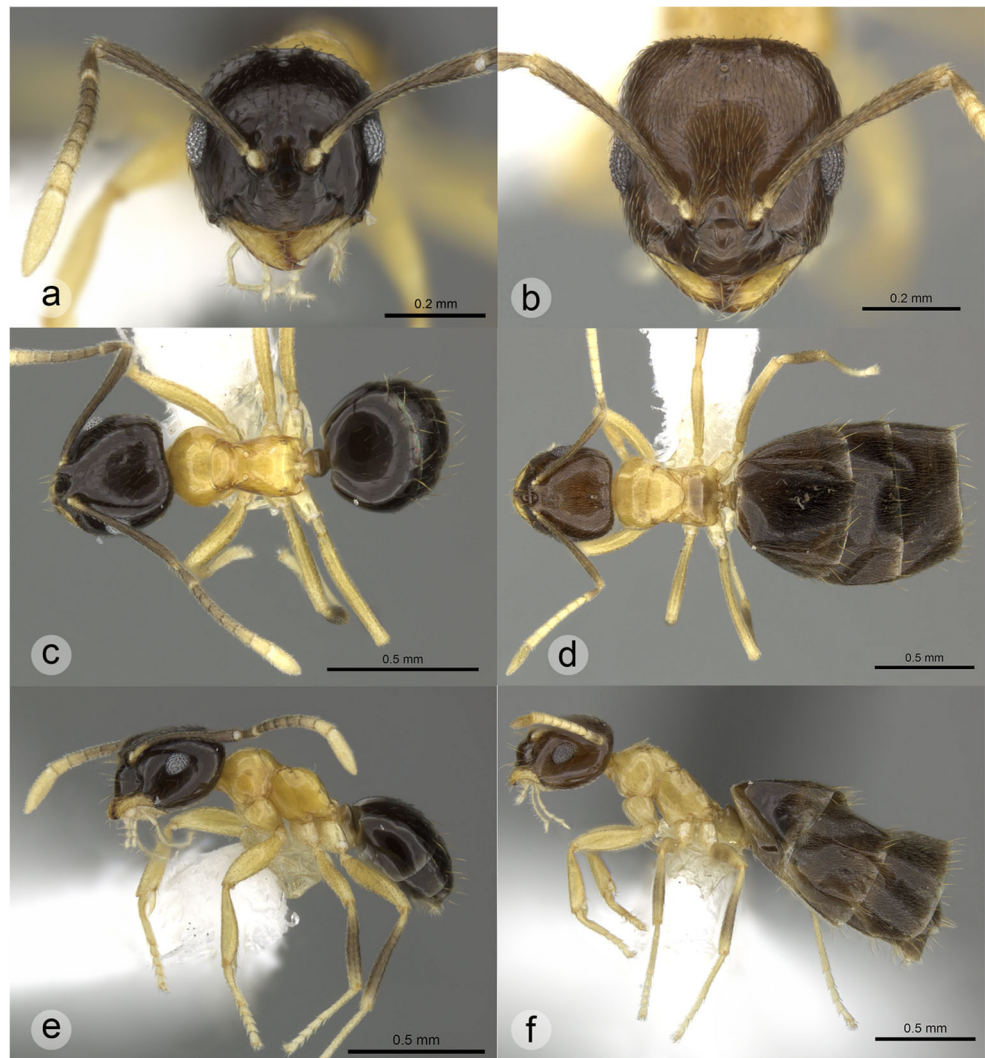
**Remarks.** The holotype is located at the top of pin USNMMENT00757689, with the two paratypes below.

#### *Brachymyrmex bicolor* NEW SPECIES

(Fig. 13, supplementary material S7)

Holotype worker (USNM: CASENT0615272) and Paratype worker, putative worker-queen intercastes (USNM: CASENT0615274 (putative worker-queen intercaste); CASENT0615277, 0615294, 0617077 (destroyed) (three workers), 0615292 (one queen); MCZC: CASENT0615273

**Fig. 13** *Brachymyrmex bicolor* n. sp.: **a, c, e** head, dorsal, and lateral view of a paratype worker; **b, d, f** head, dorsal, and lateral view of a syntype specimen of the putative worker-queen inter-caste. (from [www.antweb.org](http://www.antweb.org); photographer: Ryan Perry)



(putative worker-queen intercaste), 0615276 (one worker)): five workers, one queen, two putative worker-queen intercastes. **HONDURAS: Comayagua:** PN Cerro Azul Meambar, 14.87092, -87.89917, 1120 m, 20 May 2010, LLAMA#Wa-C-04-1-31.

**Etymology:** The epithet *bicolor* reflects the conspicuous body coloration with black head and gaster and yellow mesosoma.

**Diagnosis.** The conspicuous color pattern allows distinguishing *B. bicolor* from any other *Brachymyrmex* species.

**Holotype measurements** (mm). HL<sub>1</sub> 0.43; HL<sub>2</sub> 0.30; HL<sub>3</sub> 0.10; HW 0.38; SL 0.44; EL 0.11; WL 0.48; PnL 0.12; PnW 0.28; ML 0.10; MW 0.16; **Indices** CI 88.78; SI<sub>1</sub> 114.94; SI<sub>2</sub> 147.06; OI<sub>1</sub> 27.59; OI<sub>2</sub> 22.45.

**Paratype measurements** (mm). HL<sub>1</sub> 0.43; HL<sub>2</sub> n.a.; HL<sub>3</sub> 0.10; HW 0.41; SL 0.45; EL 0.11; WL 0.48; PnL 0.12; PnW 0.28; ML 0.11; MW 0.15; **Indices** CI 94.90; SI<sub>1</sub> 109.68; SI<sub>2</sub> n.a.; OI<sub>1</sub> 25.81; OI<sub>2</sub> 22.45.

**Worker description.** **Head.** Slightly longer than wide in full face view; posterior cephalic margin slightly convex. Dorsum of the head with appressed hairs. Clypeus with a rounded anterior margin and five long, erect hairs of which a single, usually conspicuous hair is near the anterior margin, two hairs are in mediolateral position, and two more near the toruli; other hairs on the clypeus are clearly shorter and appressed or decumbent. Toruli surpassing the posterior clypeal margin in oblique anterodorsal view. The scapes surpass the posterior margin of the head by a length larger than the maximal diameter of the eye and have appressed pubescence. Three conspicuous ocelli. Eyes are positioned on the cephalic midline and have eight ommatidia along their maximal diameter.

**Mesosoma.** Without erect hairs and in lateral view approximately hour-glass shaped (this condition is absent in the presumed intercast) with a constriction between the bulging promesonotum and propodeum. In lateral view, the mesonotum is anteriorly inclined, but it does not bulge dorsally above the

pronotum. Metanotal groove present and wider than the diameter of the metathoracic spiracles. Dorsum of the propodeum is convex and shorter than the propodeal slope. Metathoracic spiracles in dorsal position, not protruding, not touching any sutures. Propodeal spiracles circular, positioned just ventrally of the posterior propodeal margin slightly posterior of the middle of the propodeal slope. Legs with appressed and scattered hairs. Petiole short and inclined forward.

**Gaster.** With scarce pubescence and several scattered long erect hairs at the edge of the segments.

**Color and sculpture.** Body smooth and shiny, with a conspicuous bicolored pattern. The head and gaster are blackish in color, however, the mandibles, the labial and maxillary palps, the bulbi and bases of the antennae, the terminal antennomeres and hairs are conspicuously yellow in color. Additionally, the mesosoma and legs are yellowish, with the tibia of the second and third pairs of legs being dark brownish, like most of the scape.

**Intercaste description.** The presumed worker-queen intercaste differs from the worker mainly by its larger body size, the shape of the mesosoma in lateral view, and its dense pubescence on the gaster. The dorsum of the head bears two rows of erect hairs. Eyes have around ten ommatidia along their maximal diameter; the promesonotum is bluntly angular, with the mesonotum being not inflated or bulging out dorsally above the pronotum in lateral view, mesonotum in dorsal view posteriorly extended along the midline. Metanotal groove absent. Dorsum of the propodeum is flat and shorter than the length of the propodeal slope. Metathoracic spiracles in dorsolateral position, not protruding, not touching any sutures. Gaster with dense pubescence and several scattered long erect hairs at the edges of the segments.

**Distribution** (Supplementary material S7). Currently exclusively known from Honduras.

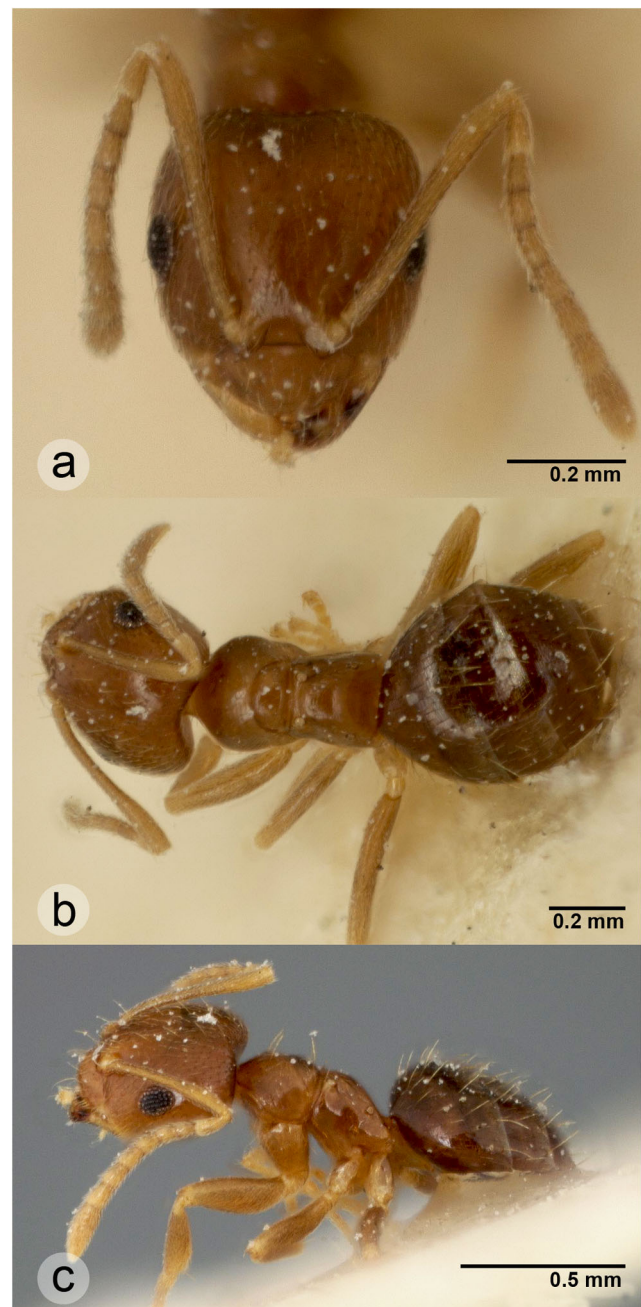
**Biology.** Specimens were collected from leaf litter in cloud forest.

**Remarks.** Further comments on the putative worker-queen intercaste in *Brachymyrmex* are provided in the remarks on *B. giardi*.

*Brachymyrmex bonariensis* Santschi NEW STATUS  
(Fig. 14, supplementary material Fig. S8)

*Brachymyrmex constrictus* st. *bonariensis* Santschi, 1933: 122 (w.). Lectotype worker (NHMB: USNMENT00757706) and paralectotype worker (NHMB: USNMENT00757705; here designated): two workers [examined]. **ARGENTINA: Buenos Aires:** Buenos Aires, 08 Mar. 1803, C. Bruch. n. st.

**Diagnosis.** *Brachymyrmex bonariensis* n. st. resembles *B. admotus* because they both have scapes that surpass the posterior margin of the head, a pair of simple erect hairs between the dorsal methathoracic spiracles, a wide metanotal groove, and a gaster with scarce pubescence. However, in *B. bonariensis* n. st., the head and mesosoma are light brownish in color, and the gaster is darker, whereas the body of *B.*



**Fig. 14** *Brachymyrmex bonariensis* n. st.: a–c head, dorsal, and lateral view of the lectotype worker

*admotus* is uniformly colored. The scapes of *B. bonariensis* are shorter than those of *B. admotus* and surpass the posterior margin of the head with a length approximately equal to the maximal diameter of the eyes. The metathoracic spiracles of *B. bonariensis* are furthermore positioned more laterally and are not protruding. Like *B. admotus*, *B. bonariensis* could be confused with *B. cavernicola* because this latter species also has a pair of erect hairs between the methathoracic spiracles, however in *B. cavernicola* these hairs are very thick, and they are darker in color than the body.

**Lectotype measurements** (mm) HL<sub>1</sub> 0.53; HL<sub>2</sub> 0.36; HL<sub>3</sub> 0.15; HW 0.48; SL 0.49; EL 0.13; WL 0.50; PnL 0.14; PnW 0.31; ML 0.12; MW 0.20; **Indices** CI 90.00; SL<sub>1</sub> 102.78; SL<sub>2</sub> 134.55; OI<sub>1</sub> 22.78; OI<sub>2</sub> 27.50.

**Paralectotypes measurements** (mm). HL<sub>1</sub> 0.53; HL<sub>2</sub> 0.35; HL<sub>3</sub> 0.15; HW 0.50; SL 0.50; EL 0.13; WL 0.53; PnL 0.18; PnW 0.34; ML 0.11; MW 0.18; **Indices** CI 92.59; SL<sub>1</sub> 101.33; SL<sub>2</sub> 143.40; OI<sub>1</sub> 26.67; OI<sub>2</sub> 27.16.

**Description.** *Head.* Slightly longer than wide in full face view; posterior cephalic margin slightly concave. Dorsum of head with scattered, appressed hairs and usually two rows of erect hairs. Clypeus with a rounded anterior margin and five long, erect hairs of which a single, usually conspicuous hair is near the anterior margin, two hairs are in mediolateral position, and two more near the toruli; other hairs on the clypeus are markedly shorter and appressed or decumbent. Toruli surpassing the posterior clypeal margin in oblique anterodorsal view. The scapes surpass the posterior margin of the head by a length approximately equal to the maximal diameter of the eyes. Ocelli appear to be present but are inconspicuous. Eyes are positioned on the cephalic midline and have 8–9 ommatidia along their maximal diameter.

*Mesosoma.* With two erect hairs on the pronotum and two on the mesonotum. In lateral view, the mesonotum is somewhat inflated, but it does not bulge dorsally above the pronotum. Metanotal groove wider than the diameter of the metathoracic spiracles. Metathoracic spiracles in dorsolateral position, not protruding, but touching the propodeal suture. Between the metathoracic spiracles two thin erect hairs are present, but they are shorter than those on the pronotum and mesonotum. Dorsum of the propodeum flat and ~1/3th of the length of the propodeal slope. Propodeal spiracles circular, positioned on the posterior propodeal margin slightly posterior of the middle of the propodeal slope. Legs with appressed and scattered hairs. Petiole short and inclined forward.

*Gaster.* With scattered pubescence, and scattered suberect hairs, mainly along the edges of the segments.

*Color and sculpture.* Body overall smooth and shiny, except for the slightly imbricate sculpture on the dorsum of the mesosoma in some specimens. Head and mesosoma light brown, gaster darker in color.

**Distribution** (Supplementary material Fig. S8). Exclusively known from Argentina.

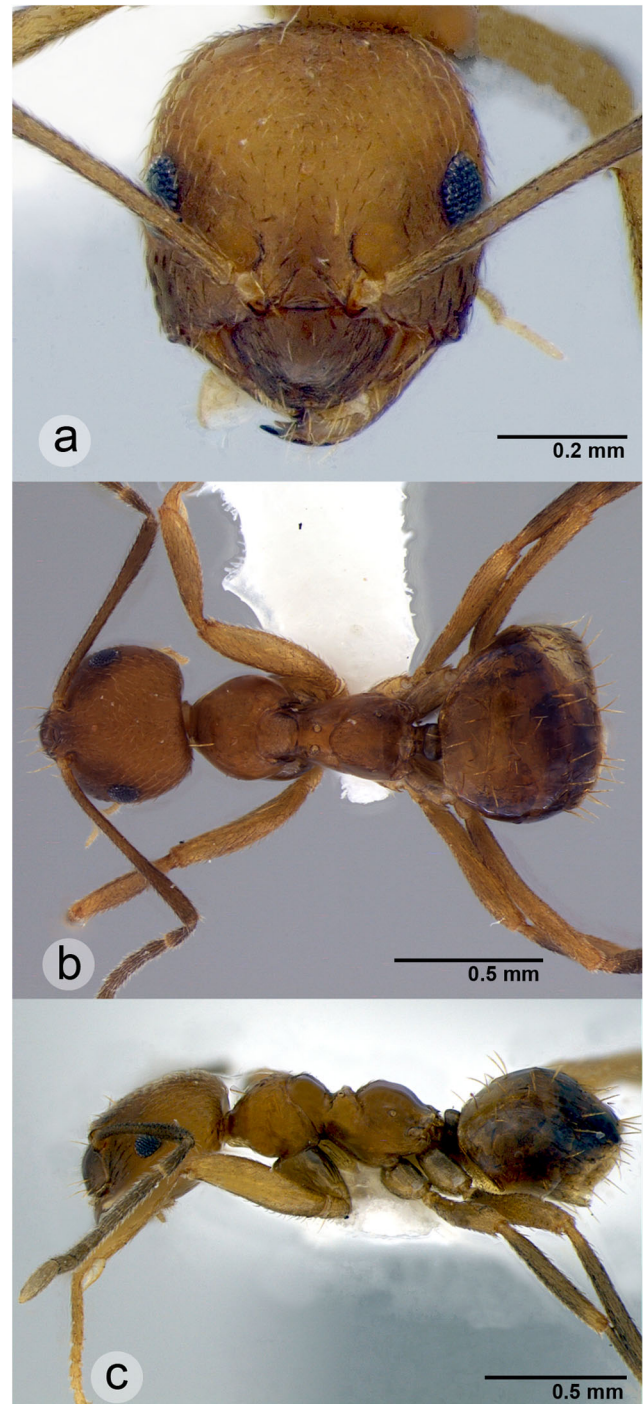
**Biology.** Unknown.

**Remarks.** *Brachymyrmex bonariensis* was first described by Santschi (1933) as a variety of *B. constrictus* because it has the thorax less strongly inflated, a little wider head, and more concave posterior margin of the head in comparison with *B. constrictus*. However, in our opinion, *B. bonariensis* is morphologically very different than *B. constrictus*: it has a mesonotum that does not bulge dorsally above the pronotum in lateral view whereas that of *B. constrictus* does; *B. constrictus* does not have erect hairs between the metathoracic

spiracles and moreover it has a uniformly dark brownish body. As mentioned before, *B. bonariensis* resembles *B. admotus* more closely (see diagnosis).

*Brachymyrmex brasiliensis* Ortiz & Fernández (Fig. 15, supplementary material Fig. S9)

*Brachymyrmex brasiliensis* Ortiz and Fernández, 2014: 22, Figs. 19, 20, and 21 (w). Holotype worker (MZSP:



**Fig. 15** *Brachymyrmex brasiliensis*: a–c head, dorsal, and lateral view of the holotype worker

USNMENT00757748) and paratype worker (UFUC: USNMENT00757833): two workers. **BRAZIL: Rio de Janeiro:** Nova Friburgo, Fazenda Barreto, -22.161242 -42.524302, 1068 m, 11–12 June 2011, T.M.S. Mesquita.

**Additional material examined. BRAZIL: Goias:** Anapolis, 12 Feb. 1958, W. Kempf, one worker (MZSP: USNMENT00757820). **ECUADOR: Zamora:** Chinchipe, -3.98228 -79.083528, one worker (RBINS: 4048410).

**Diagnosis.** *Brachymyrmex brasiliensis* differs from other *Brachymyrmex* species by having tumuliform metathoracic spiracles, in combination with a smooth and shiny gaster as well as an opaque head and mesosoma.

**Description.** See Ortiz and Fernández (2014).

*Brachymyrmex bruchi* Forel

(Figs. 16 and 17, supplementary material Fig. S10)

*Brachymyrmex bruchi* Forel, 1912a: 64 (w.m.). Lectotype worker (MHNG: USNMENT00757159), and paralectotype workers, males (MHNG: USNMENT007157–007159, 00758104, 00758149–00758181; here designated): 21 workers, three males [examined]. **ARGENTINA: Catamarca:** Aconquija, Filo blanco, 4300 m, Bruch. Santschi (1929: 309) (q.).

= *Brachymyrmex bruchi* var. *rufipes* Forel, 1912a: 65 (w.). (MHNG: USNMENT00757160, 00757161): three workers [examined]. **ARGENTINA: Catamarca:** Huasan; synonymy by Quirán et al. (2004: 279). See also: Santschi (1923a: 660).

= *Brachymyrmex giardi* var. *nitida* Santschi, 1922: 261 (w.). (NHMB: USNMENT00757182): one worker [examined]. **CHILE:** Los Lagos, Petrohué, 1922, Schiller. Snelling and Hunt (1975: 114) as junior synonym of *Brachymyrmex giardi*. n.syn.

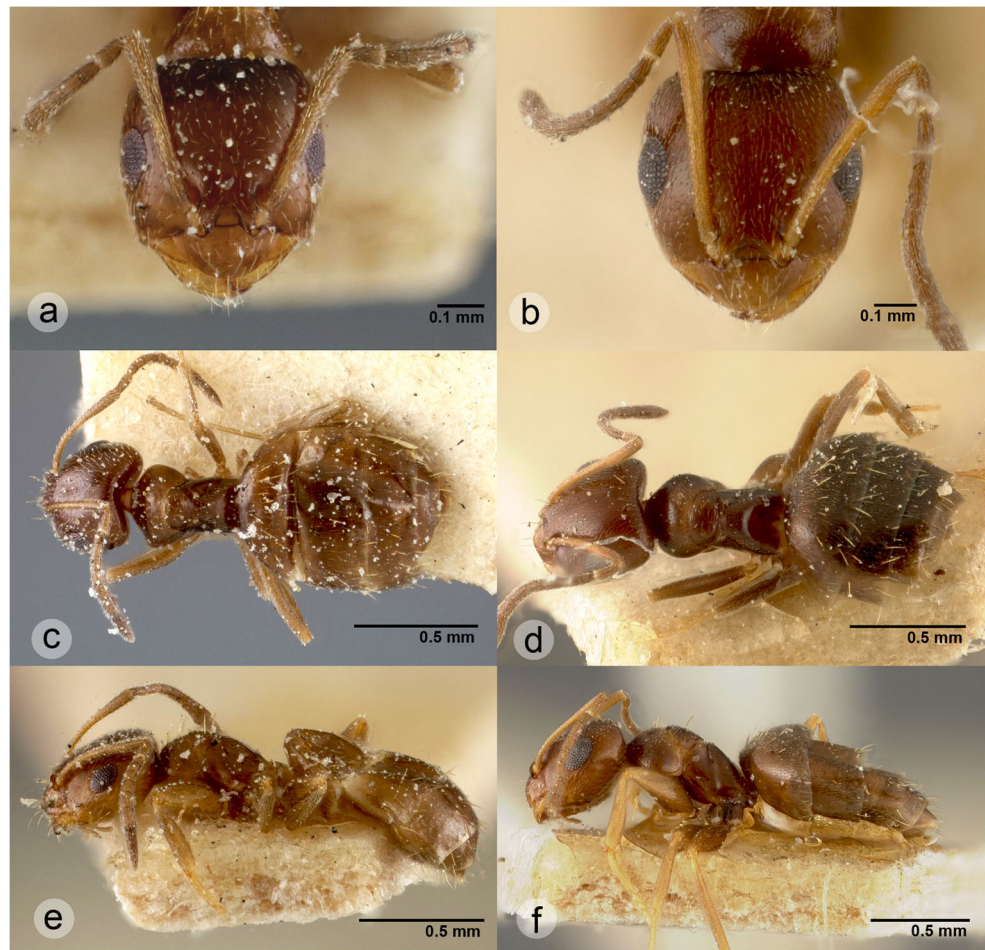
= *B. laevis* var. *andina* Santschi, 1923a: 659 (w.). (NHMB: USNMENT00758161, 00757186, 00757187; MHNG: USNMENT00758129): 16 workers [examined]. **ARGENTINA: Jujuy:** Puna, 4000 m, D. Witter. n. syn.

**Additional material examined. ARGENTINA: Entre Ríos:** 8.63 km W Concordia, -31.42303 -58.11672, 16 m, 26 Dec. 2007, W. & E. MacKay, seven workers, one male, one queen (WEMC: USNMENT00757969, 00757997, 00758001, 00758003, 00758004, 00758013, 00759019) **Santa Fe:** 10 km E Santa Fe, -31.6666 -60.5833, 12 Oct. 2002, A.L. Wild & N. Helle, one worker (ALWC: USNMENT00757998). **Tucumán:** Lara, 4000 m, Feb. 2003, G.A. Baer, two workers (MCSN: USNMENT00757709). **BOLIVIA: Santa Cruz:**

**Fig. 16** *Brachymyrmex bruchi*: a, c, e head, dorsal, and lateral view of the lectotype worker; b, d, f *B. giardi* var. *nitida*: head, dorsal, and lateral view of a syntype worker



**Fig. 17** *Brachymyrmex bruchi*: **a**, **c**, **e** *B. laevis* var. *andina*: head, dorsal, and lateral view of a syntype worker; **b**, **d**, **f** *B. bruchi* var. *rufipes*: head, dorsal, and lateral view of a syntype worker



Perforación, 68 km ESE Charagua, -19.91667 -62.56667, 470 m, 11 Dec. 1993, P.S. Ward, three workers (PSWC: USNMENT00758008). **BRAZIL:** Brasília D.F., Aug. 1996, R.M. Oliveira, six workers (CPDC: USNMENT00758011). **CHILE:** Temuco, 24 Nov. 1967, W.W. Kempf, six workers (PSWC: USNMENT00758015–00758022). **COLOMBIA:** **Quindío:** Génova, Vereda El Cedral, Finca Venecia, 4.2275 -75.7586, 1800 m, 19 Oct. 1999, E. González & J. Sossa, one worker (IAvH: IAvH-E74162). **Risaralda:** Apia, La Clarita, 3.13 -75.95, 1550 m, 26 Oct. 2001, I. Armbrrecht, one worker (IAvH: IAvH-E74173). **DOMINICAN REPUBLIC:** 28 km SSE Constanza, 18.7 -70.9, 2220 m, 11 Nov. 1992, P.S. Ward #11757, three workers (PSWC: USNMENT00758034). **La Vega:** Reserva Valle Nuevo, 18.81667 -70.68333, 2240 m, 01 Sep. 2001, A.L. Wild #AW1348, two workers, one queen (ALWC: USNMENT00757682); Cervantía, 18.85 -70.70, 1730 m, 01 Sep. 2001, A.L. Wild, two workers (ALWC: USNMENT00757988). **ECUADOR:** **Napo:** near Dureno, 0.0780 -76.7307, 287 m, 20 July 2005, W. & E. MacKay #21277, two workers (WEMC: USNMENT00759007). **GUATEMALA:** **Sacatepéquez:** Finca El Pilar, near Antigua, 14.55 -90.72, 1700 m, 13 Nov. 2003, A.L. Wild,

three workers (ALWC: USNMENT00757963). **PARAGUAY:** **Boquerón:** Filadelfia, -22.35 -60.03, 22 Sep. 1994, B. Garcete, one worker (ALWC: USNMENT00758005). **Canindeyú:** Reserva Natural Bosque Mbaracayú Lagunita, -24.13 -55.43, 12 Feb. 1997, A. Wild, three workers (ALWC: USNMENT00757999). **Concepción:** Concepción centro, -23.42 -57.35, 7 Feb. 1998, A. Wild, three workers (ALWC: USNMENT00757976). **Presidentes Hayes:** Villa Hayes, -25.10 -57.57, 21 Sep. 1994, B. Garcete, two workers (ALWC: USNMENT00757996). **USA:** **Arizona:** Pima Co. Tucson International Airport, 32.11667 -110.93333, 800 m, 07 Aug. 2001, P.S. Ward #14412, two workers (PSWC: USNMENT00757972). **Florida:** Florida Gulf Co. Wewahitchka Steele Rd./GCI Bond, 30.1 -85.2, 13.6 m, 23 Dec. 2000, Corrie Saux, one worker (MCZC: USNMENT00758014). **Louisiana:** Audubon Park, New Orleans, 29 Apr. 1995, A.L. Wild, two workers (ALWC: USNMENT00757979); Baton Rouge, 01 Oct. 2000, B. Raphaël, five workers (CPDC: USNMENT00757980); E. Baton Rouge Par. Baton Rouge. Kenniloworth & Perkins Rd. BREC Perkins Park, 03 Apr. 2003, J. Rosson, one worker (CPDC: USNMENT00757967). Plaquemines

Co. St. Bernard St. Pk., 22 Aug. 1987, W. MacKay, 22 Aug. 1987, W. MacKay, two workers (WEMC: USNMENT00757970). **Texas:** Austin, Travis Co., 30.25167 -97.76722, 160 m, 21 Nov. 2006, A.L. Wild, three workers (ALWC: USNMENT00757977). **URUGUAY:** Montevideo, Nov. 2000, L. Pastre, two workers (CPDC: USNMENT00757978). **Salto:** Salto Parque Municipal Benito Solari, 25 Dec. 2007, W. & E. MacKay, one worker (WEMC: USNMENT00758047).

**Diagnosis.** *Brachymyrmex bruchi* is morphologically most similar to *B. patagonicus* and *B. oculatus* because these species have scapes that surpass the posterior margin of the head, typically two erect hairs on the mesonotum, their metanotal groove is either absent or narrower than the diameter of the metathoracic spiracles, their mesonotum does not bulge dorsally above the pronotum in lateral view, their gaster has several scattered long erect hairs and sparse pubescence, and they have brownish bodies. However, *B. bruchi* differs from *B. patagonicus* by having a larger body size, abundant suberect hairs on the dorsum of the pronotum, and scapes that surpass the posterior margin of the head by a length approximately equal to the maximal diameter of the eye. It differs from *B. oculatus* by having smaller eyes with less than 14 ommatidia along the maximal diameter, which approximately equal only a quarter of the length of the head (HL<sub>1</sub>).

*Lectotype and paralectotypes measurements* (mm) ( $n = 4$ ). HL<sub>1</sub> 0.58–0.64; HL<sub>2</sub> 0.41–0.45; HL<sub>3</sub> 0.14–0.18; HW 0.57–0.60; SL 0.55–0.62; EL 0.16–0.18; WL 0.64–0.78; PnL 0.20–0.25; PnW 0.39–0.45; ML 0.18–0.21; MW 0.27–0.31; *Indices* CI 90.63–100.00; SI<sub>1</sub> 93.33–103.45; SI<sub>2</sub> 130.43–142.86; OI<sub>1</sub> 26.67–31.03; OI<sub>2</sub> 21.88–28.13.

*Additional material examined measurements* (mm) ( $n = 25$ ). HL<sub>1</sub> 0.41–0.61; HL<sub>2</sub> 0.29–0.42; HL<sub>3</sub> 0.09–0.16; HW 0.37–0.60; SL 0.31–0.59; EL 0.10–0.20; WL 0.40–0.72; PnL 0.10–0.20; PnW 0.25–0.44; ML 0.09–0.20; MW 0.16–0.29; *Indices* CI 70.98–96.97; SI<sub>1</sub> 78.13–136.36; SI<sub>2</sub> 106.67–156.76; OI<sub>1</sub> 23.91–45.45; OI<sub>2</sub> 19.23–28.00.

**Description.** *Head.* Slightly longer than wide in full face view; posterior cephalic margin slightly concave. Dorsum of the head with sparse and appressed hairs. Clypeus with a rounded anterior margin and five long, erect hairs of which a single, usually conspicuous hair is near the anterior margin, two hairs are in mediolateral position, and two more near the toruli; other hairs on the clypeus are markedly shorter and appressed or decumbent. Toruli surpassing the posterior clypeal margin in oblique anterodorsal view. The scapes surpass the posterior cephalic margin with a length that approximately equals the maximal diameter of the eye; they typically have appressed and decumbent hairs. Three inconspicuous ocelli present. Eyes are positioned on the cephalic midline and have 8–13 ommatidia along their maximal diameter.

*Mesosoma.* Typically with two erect hairs on the pronotum and two on the mesonotum, sometimes with additional

suberect hairs, mainly on the pronotum. The mesonotum is not inflated and does not bulge dorsally above the pronotum in lateral view. Metanotal groove absent or narrower than the diameter of the metathoracic spiracles. Metathoracic spiracles in dorsolateral position, not protruding, but touching the propodeal suture. Dorsum of the propodeum slightly convex and shorter than the posterior slope. Propodeal spiracles circular, positioned on the posterior propodeal margin at the middle of the propodeal slope. Legs with appressed and scattered hairs. Petiole short and inclined forward.

*Gaster.* With sparse pubescence and several scattered long erect hairs.

*Color and sculpture.* Body overall smooth and shiny, except for the sometimes slightly imbricate sculpture on the dorsum of the mesosoma; typically brownish.

**Distribution** (supplementary material Fig. S10). *Brachymyrmex bruchi* is known from Argentina, Bolivia, Brazil, Chile, Colombia, the Dominican Republic, Ecuador, Guatemala, Paraguay, Uruguay, and the USA

**Biology.** Unknown.

**Remarks.** The here designated lectotype is the specimen at the top of pin MHNG: USNMENT00757159, and the ants below are paralectotypes. The type material of *B. bruchi*, *B. giardi* var. *nitida*, *B. laevis* var. *andina*, and *B. bruchi* var. *rufipes* shares a common set of diagnostic characters, i.e., the brownish body color, scapes that surpass the posterior cephalic margin by a length that approximately equals the maximal diameter of the eye, the metanotal groove is lacking or narrow, and scattered pubescence on the gaster. As such, these species and varieties are synonymized here.

*Brachymyrmex giardi* var. *nitida* was considered to be a junior synonym of *B. giardi* by Snelling and Hunt (1975); however, we disagree with this synonymization taking in account both the description of Santschi (1922) and our own observations of important differences in diagnostic traits: *B. giardi* var. *nitida* differs from *B. giardi* by having erect hairs on the pronotum, a darker body color and scarce pubescence on the body.

Quirán et al. (2004) suggested *B. bruchi* var. *rufipes* to be a junior synonym of *B. bruchi* based on the original description by Forel (1912a), which only specifies a difference in body color. Quirán et al. (2004) argued that this difference is not taxonomically informative and therefore they proposed synonymization. We agree that body color is variable in several *Brachymyrmex* species, and therefore we follow the suggestion of Quirán et al. (2004) here. Nevertheless, it is noteworthy that some individuals of *B. bruchi* var. *rufipes* have somewhat denser pubescence on the gaster than pointed out in our description above (see Fig. 17d, f). Such moderately dense pubescence on the gaster has been also observed in some of the examined specimens of *B. laevis* var. *andina*. Future studies on *B. bruchi* and its geographical variation is required.



Forel (1912a) indicated that *B. bruchi* and *B. patagonicus* are very similar as to their mesosoma, and Santschi (1923a) likewise compared *B. laevis* var. *andina* with *B. patagonicus* var. *atrátula*, which has been synonymized with *B. patagonicus* (Quirán et al. 2004). We concur with these authors that *B. bruchi* and *B. patagonicus*, including their type material, are morphologically very similar, but as noted in the diagnosis above, consistent differences also exist between both species. Furthermore, our morphometric and phylogenetic analyses tentatively confirm these taxa to be distinct, although further studies on the morphology and phylogenetics of these species as well as their ecology and biology are admittedly needed.

Santschi (1929) and Quirán et al. (2004) also referred specimens from Jujuy: Pueblo Viejo (Weiser), Catamarca: Aconquija and Tucuman (Argentina) to *B. bruchi*; however, this material was not studied here.

*Brachymyrmex cavernicola* Wheeler

(Fig. 18, supplementary material Fig. S11)

*Brachymyrmex cavernicola* Wheeler, 1938: 252 (w.m.). Lectotype worker (USNM: USNMENT00529073) and Paralectotype workers, male (USNM: USNMENT00529073; MCZC: M.C.Z. Cotype 17–1922428, M.C.Z. Cotype 11–1322428, M.C.Z. Cotype 23–2522428, M.C.Z. Cotype 14–1622428, M.C.Z. Cotype 1–322428, M.C.Z. Cotype 5–722428, M.C.Z. Cotype 422428; here designated): 21 workers, one male [examined]. **MEXICO: Yucatan:** Chichenitza, Balaam Canche Cave, H.S. Pearse, 13 June 1936.

**Additional material examined. BRAZIL: Amazonas:** Manaus, BR.174 km 45 EEST-S1, 12 Nov. 1990, Eq. A. Y. Harada, A. G Baineira, one worker (MPEG: USNMENT00757857). **Pará:** Melgaço, Caxiuanã ECFPn, -1.73584 -51.48762, 12–14 Oct. 2006, Equipe A.Y. Harada, one worker (MPEG: AYH051). Melgaço, Caxiuanã ECFPn, -1.75444 -51.52241, 28 Oct. 2003, A.Y. Harada, E.P. Fagundes, C.J.M. Ribeiro, C.E.D. Sanhudo, C.A.R. Moura, J.L.P. Souza, C. Renato, one worker (MPEG: AYH067). Melgaço, Caxiuanã ECFPn, -1.73584 -51.48762, 30 Oct. 2003, A.Y. Harada, E.P. Fagundes, C.J.M. Ribeiro, C.E.D. Sanhudo, C.A.R. Moura, J.L.P. Souza, C. Renato, three workers (MPEG: AYH086, AYH088, AYH126). Serra Norte, Est. Do. Mang, 6 Sep. 1983, 12 Sep. 1983, 29 Feb. 1984, 12 May 1984, 15 May 1984, 22 May 1984, Lote: 2105, 2108, 2195, 2197, 2208, 2213, 2214, 2223, 2227, 2231, 2232, 2235, 11 workers (MPEG: MEPEG\_HYM11505683, 11505907, 11505913, 11505945, 11505960, 11505969, 11505999, 11506007, 11506023, 11506030, 11506036). **COLOMBIA: Cauca:** Isla Gorgona, 17 Sep. 1989, M. Baena #GQA-05, one worker (WEMC: USNMENT00757854). Isla Gorgona, 16 Jan. 1990, M. Baena #Gacd-19, two workers (WEMC: USNMENT00757855, 00757856). **Cundinamarca:** La

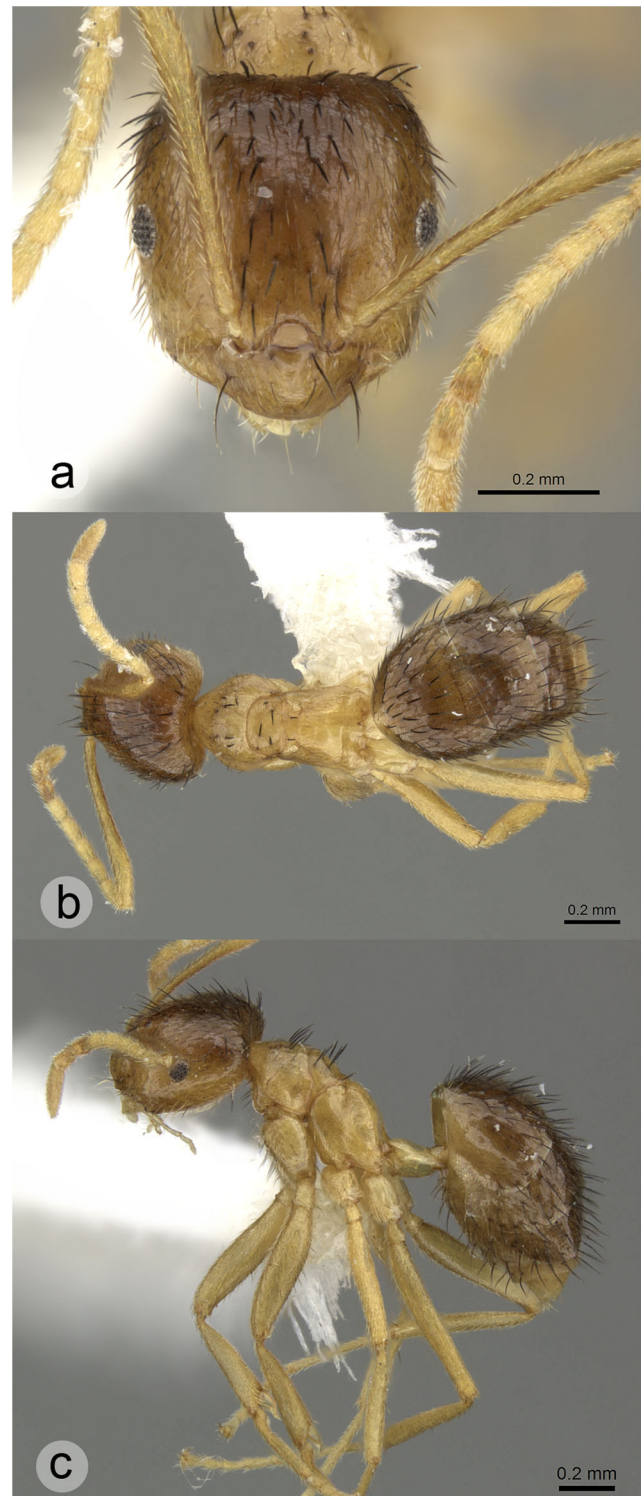


Fig. 18 *Brachymyrmex cavernicola*: a–c head, dorsal, and lateral view of a worker (from [www.antweb.org](http://www.antweb.org); photographer: Estella Ortega)

Vega, R.N. Natautá, 5.00 -74.33, 1040 m, 10 Nov. 2010, F. Fernández, two workers (IAVH: USNMENT00757859). **Nariño:** Barbacoas, Tajadas, 100 m, one worker (ICN: USNMENT00757858). **Quindío:** Buenavista, Finca Ceilán,

Bs., 4.35833 -75.78472, 1100 m, 15 Nov. 1999. E. Gonzalez, one worker (IAvH: IAvH-E744170). **COSTA RICA: Guanacaste:** Prov. Maritza field, Sta., 800 m, 03 May 1995, R. Anderson #17714, four workers (WEMC: USNMENT00757844, 00757845). **Heredia:** Estación Biológica, La Selva, 10.433 -84.017, 50–150 m, 01 June 1993, INBio-OET, one worker (JTLC: INBIOCRI001276875). Puerto Viejo, #733, 25 June 1979, J. Raich, seven workers (MCZC: USNMENT00757273, 00757275). **ECUADOR: Endesa:** Forest Reserve Pichincha Province, 25 Jan. 1994, L.E. Tennant, one worker (MCZC: USNMENT00757274). **Pichincha:** La Unión del Río Toachi, -0.31889 -78.95442, 770 m, 15 Jul. 2005, W. & E. MacKay #21169, two workers (WEMC: USNMENT00757841, 00757842). **MEXICO: Chiapas:** 8.8 km SE Salto de Agua, 17.51328 -92.29515, 50 m, 14 July 2007, J.L. Cozar ANTC#4225, one worker (JTLC: CASENT0600011). 10 km S Palenque, 30 May 1988, A. Rabeles, two workers (WEMC: USNMENT00757848). 10 km S Palenque, 30 May 1988, W. MacKay #10563, #10571, #10627, #10674, 15 workers (WEMC: USNMENT00757849, 00757850, 00757851, 00757852, 00757853, 00758028). 10 km S Palenque, 30 May 1988, VIAL, D. Gonzalez, one worker (WEMC: USNMENT00757846.). **Veracruz:** Los Tuxtlas, 10 km NNW Sontecomapan, 18.583 -95.083, 500 m, 21 Mar. 1985, P.S. Ward #7366, three workers (PSWC: USNMENT00757843). **PERU: Madre de Dios:** Prov. Tambopata, Cuzco Amazónico, 15 km NE Puerto Maldonado, CA-130, 200 m, 13 June 1989, S.P. Cover & J.E. Tobin, six workers (MCZC: USNMENT00757260, 00757269, 00757270). Prov. Tambopata, Cuzco Amazónico, 15 km NE Puerto Maldonado, CA-601 JT79, CA-601 JT80, CA-365, CA-659 JT138, CA-116, CA-141, June 1989, S.P. Cover & J.E. Tobin, 17 workers (MCZC: USNMENT00757260–00757272).

**Diagnosis.** The feature that allows distinguishing *B. cavernicola* from all other *Brachymyrmex* species is the presence of conspicuous thick black hairs on the head, mesosoma and gaster, which contrast strongly with the yellowish body, a condition reminiscent of *Nylanderia*. *Brachymyrmex antennatus* also has erect hairs on the mesosoma that are darker than the tegument; however, these are not as thick as those of *B. cavernicola*, and in other features these species are very different.

*Additional material examined measurements* (mm) ( $n = 10$ ). HL<sub>1</sub> 0.51–0.57; HL<sub>2</sub> 0.35–0.41; HL<sub>3</sub> 0.13–0.18; HW 0.45–0.51; SL 0.54–0.63; EL 0.09–0.10; WL 0.51–0.63; PnL 0.19–0.21; PnW 0.29–0.35; ML 0.10–0.13; MW 0.18–0.22; *Indices* CI 83.33–91.67; SI<sub>1</sub> 118.18–134.62; SI<sub>2</sub> 139.53–166.67; OI<sub>1</sub> 17.54–20.83; OI<sub>1</sub> 25.00–31.25.

**Description.** *Head.* Slightly longer than wide in full face view; posterior cephalic margin slightly concave. Thick hairs cover the front of the head. Clypeus with a rounded anterior

margin and five long, erect hairs of which a single hair is near the anterior margin, two hairs are in mediolateral position, and two more near the toruli; other hairs on the clypeus are markedly shorter and appressed or decumbent. Toruli surpassing the posterior clypeal margin in oblique anterodorsal view. The scapes surpass the posterior cephalic margin by a length of approximately 2.0× the maximal diameter of the eyes and bear appressed or decumbent hairs. Ocelli are absent or one central ocellus is present. Eyes are positioned on the cephalic midline and have 7–8 ommatidia along their maximal diameter.

*Mesosoma.* With several thick erect hairs on the promesonotum (> 2), and two between the metathoracic spiracles, but none on the propodeum. The mesonotum is not inflated and does not bulge dorsally above the pronotum in lateral view. Metanotal groove wider than the diameter of the metathoracic spiracles. Metathoracic spiracles in dorsolateral position, not protruding, and not touching any suture. Dorsum of the propodeum is weakly convex and shorter than the posterior slope. Propodeal spiracles circular, positioned just ventrally of the posterior propodeal margin slightly posterior of the middle of the propodeal slope. Legs with appressed and scattered suberect hairs. Petiole short and inclined forward.

*Gaster.* With scarce pubescence but densely covered by thick, erect hairs.

*Color and sculpture.* Body smooth and shiny, except for the dorsum of the mesosoma which sometimes has slightly imbricate sculpture. The body color is typically yellowish, although the head and gaster are sometimes darker than the mesosoma. Tegument color contrasts with the thick black hairs.

**Distribution** (Supplementary material Fig. S11). *Brachymyrmex cavernicola* is known from Argentina, Brazil, Colombia, Costa Rica, Ecuador, Mexico, and Peru.

**Biology.** Nests of this species have been found in the soil under stones.

**Remarks.** The lectotype is the top specimen on pin USNMENT00759073, whereas the specimens below are the paralectotypes. As indicated in the diagnosis and pointed out before by Wheeler (1938), *B. cavernicola* resembles *Nylanderia* species by its thick hairs that cover the entire body.

*Brachymyrmex coactus* Mayr

(Figs. 19 and 20, supplementary material Fig. S12)

*Brachymyrmex coactus* Mayr, 1887: 523 (w.q.m.). Lectotype worker (NHMW: USNMENT00757191) and paralectotype workers, males, queens (NHMW: USNMENT00757191–00757195; here designated): three workers, three males, two queens [examined]. **BRAZIL: Santa Catharina** (Hetscko). See also: Santschi (1923a: 669); Santschi (1923b: 272).

= *Brachymyrmex coactus* var. *nictitans* Emery, 1906: 178 (w.). (MCSN: USNMENT 00757209): one worker [examined]. **COSTA RICA.** See also: Santschi (1923a: 670). n. syn.

**Fig. 19** *Brachymyrmex coactus*: **a, c, e** head, dorsal, and lateral view of the lectotype worker; **b, d, f** *B. coactus* var. *nictitans* n. syn.: head, dorsal, and lateral view of a syntype worker



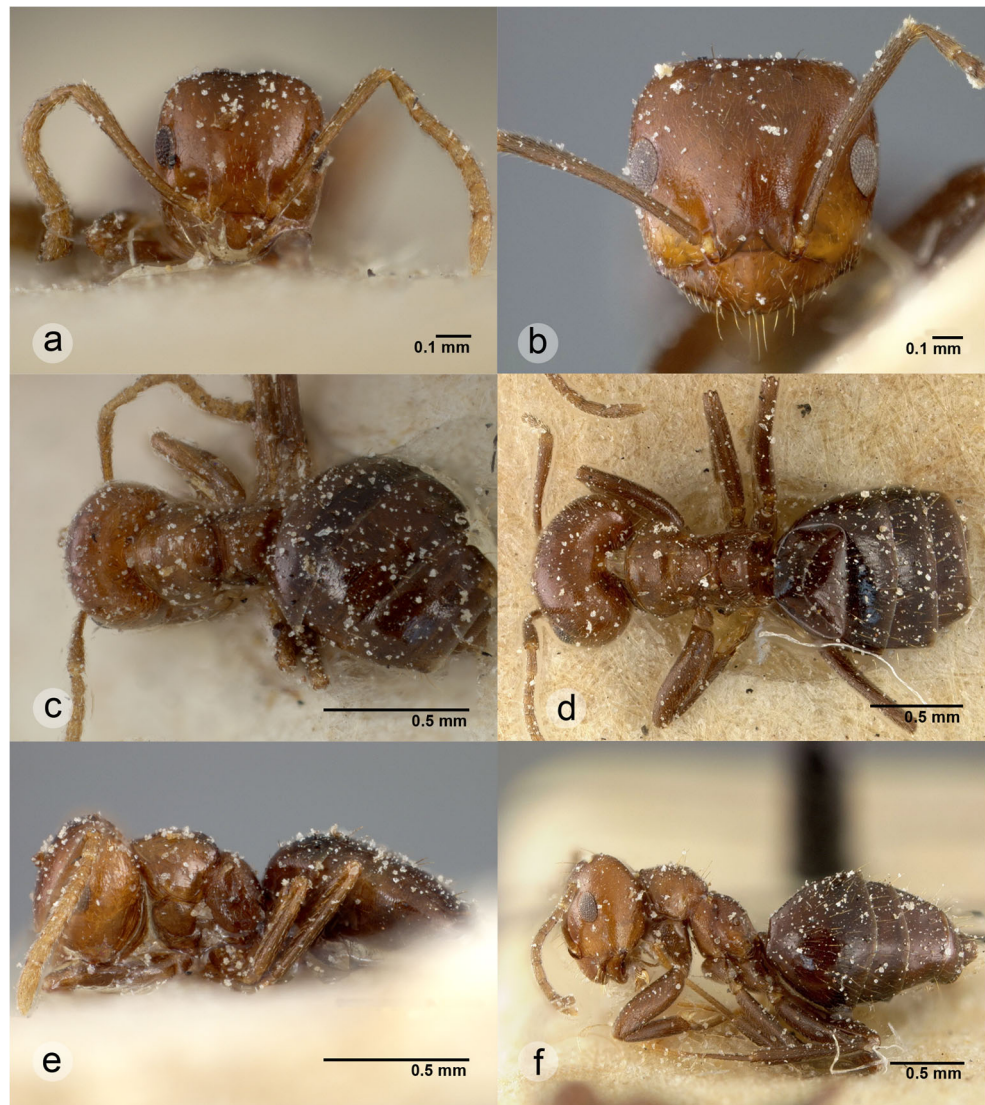
= *Brachymyrmex constrictus* Santschi, 1923a: 671, Figs. 5 and 38, 61 (w.). (NHMB: USNMENT00758087): one worker [examined]. **BOLIVIA: La Paz:** Mapiiri. n. syn.

= *Brachymyrmex coactus* var. *robustus* Santschi, 1923b: 272 (w.). (NHMB: USNMENT00757224): four workers [examined]. **BRAZIL: Santa Catharina:** Encano alto; (NHMB: USNMENT00758085, 00758086): six workers [examined]. **BRAZIL: Santa Catharina:** Blumenau. n. syn.

**Additional material examined.** **ARGENTINA:** “Fives Lile,” four workers, five queens, one male (NHMB: USNMENT00758083, 00758084). **BRAZIL: Alagoas:** Maceió–Emília Flores, Hm For 68, For 91, 18 Mar. 2005, 04 June 2005, #5460, M.C.C. Diniz, eight workers (CEPLAC: USNMENT00757552, 00757553, 00757555); **Bahia:** Barreiras, Serra do Mimo, 24 Apr. 2010, S. Souza & B. Santos, three workers (CEPLAC: USNMENT00757564); Esplanada, Baixio, -12.11444 -37.69944, June–Oct. 2010, M.L.O. Travassos, one worker (CEPLAC:

USNMENT00757556); Porto Seguro, Troncoso, 12 June 1991, J. Delabie 4451, three workers (CEPLAC: USNMENT00757559); UNA-ESMAI, Estação Experimental Lemos Maia, Em coqueiro-anão, Oct. 2005, J.R.M. Santos, eight workers (CEPLAC: USNMENT00757558, 00757559, 00757562); **Goias:** Ouro Verde, Faz Boa Vista, -16.29847 -49.21183, 01–07 July 2005, R.R. Silva & R.M. Feitosa, three workers (ICN: MZSP123); **Santa Catharina:** Blumenau, M. Witte #150, nine workers (MCZC: USNMENT00757238, 00757239, 00757251); **Paraíba:** Independência, Mann & Heath, -7.15194 -34.90556, three workers, one queen (MZUSP: USNMENT00757240); **São Paulo:** ANHEMBI, Faz B. Rio, 14 Feb. 1969, W. Kemf, J.C. Mahalhães, L.T.F., M. Kulmann, two workers, one queen (MZUSP: USNMENT00757563); Sete Barras, PE Carlos Bothelo, -24.20833 -47.97056, 200 m, 11–15 May 2009, F. Esteves leg. two workers (MZUSP: USNMENT00757560). **COSTA**

**Fig. 20** *Brachymyrmex coactus*: **a, c, e** *B. constrictus* n. syn.: head, dorsal, and lateral view of a syntype worker; **b, d, f** *B. robustus*: head, dorsal, and lateral view of a syntype worker



**RICA: Puntarenas:** Sirena, Corcovado National Park, 8.48333 -83.60000, 10 m, 24 Dec. 1981, J. Longino, one worker, one male (JTLC: JTLC000005905); Peninsula Osa, 8.46667 -83.58333, 50 m, 24 Dec. 1981, J. Longino, one worker, one male (MCZC: USNMENT00757243). **ECUADOR: Zamora-Chinchipe:** Copalinga, -4.09122 -69.93591, Jacquemin, Col id 5087, one worker (RBINS) **GUYANA: Rupunini:** Kananambo, 16 Jan. 1981, 3.75 -59.3, 100 m, J. Longino, one worker (JTLC: JTLC000005907). **PANAMA: Barro Colorado I:** Canal Zone, B50, Jan 1960, W.L. Brown, E.S. McCluskey, three workers (MCZC: CMOS0000097). **PARAGUAY:** Fortin mayor infante Rd., trans Chaco locality 1, 01 Oct. 2004, T. Delsinne, one worker (RBINS: Coll.RIScNB SID SPM\_ID 30833); **Boquerón:** Enciso, -21.20 -61.67, 3–6 Nov. 2001, M. LePonce & T. Delsinne, Dry Chaco, Pitfall trap, three workers (ALWC: USNMENT00757554); Boquerón: Enciso, -21.20609 -61.65748, 04–06 Nov. 2001, 23–25 Sep. 2004, M. LePonce, T. Delsinne, Col ID4132, Col ID 13623,

two workers (RBINS: Coll.RIScNB SID SPM\_ID 22607, ID27462); Nueva Asunción, -20.69190 -61.92925, 02–06 Nov 2001, M. LePonce, Col ID 3948, one worker (RBINS: Coll.RIScNB SID SPM\_ID 30542); **Canindeyú:** Reserva Natural Bosque Mbaracayú, Jejuimi, -24.10 -61.67, 02 Apr. 1996, A.L. Wild, 6three workers (ALWC: USNMENT00757561); **Cordillera:** Caacupé, Camp. J. Noment, -25.36667 -57.08333, 19 Jan. 1994, B. Garcete #AW0395, one worker (ALWC: USNMENT00757567); **Misiones:** 8 km SE San Juan Bautista, -26.71666 -57.06667, 150 m, 10 Dec. 2002, A.L. Wild & B. Garcete #AV1781, one worker (ALWC: USNMENT00757570). **PERU: Madre de Dios:** Reserva Nacional Tambopata, Centro Sachavacayoc, -12.85583 -69.36194, 210 m, 19–31 July 2012, R.M. Feitosa, two workers (ICN: USNMENT00757614, 00757612); Reserva Nacional Tambopata, Centro Sachavacayoc, -12.82667 -69.37056, 198 m, 26 July 2012, GSNMBU, two workers (ICN: USNMENT00757615, 00757838).

**Diagnosis.** *Brachymyrmex coactus* is morphologically very similar to *B. degener* as both species have scapes that surpass the posterior margin of the head, faint sculpture on the mesosoma, a mesonotum that is inflated and bulges dorsally above the pronotum in lateral view, a wide metanotal groove, metathoracic spiracles that are slightly protruding dorsally, and a gaster with scarce pubescence. However, *B. coactus* has a brown yellowish head and mesosoma, but a darker gaster, whereas *B. degener* has a uniformly brownish body.

*Lectotype and paralectotypes measurements* (mm) ( $n = 3$ ). HL<sub>1</sub> 0.72–0.84; HL<sub>2</sub> 0.44–0.55; HL<sub>3</sub> 0.21–0.25; HW 0.64–0.82; SL 0.68–0.80; EL 0.16–0.21; WL 0.53–0.88; PnL 0.21; PnW 0.43–0.55; ML 0.14–0.20; MW 0.23–0.35; *Indices* CI 94.29–97.67; SI<sub>1</sub> 97.62–106.06; SI<sub>2</sub> 144.00–152.17; OI<sub>1</sub> 24.24–28.57; OI<sub>2</sub> 29.73–31.43.

*Additional material examined measurements* (mm) ( $n = 10$ ). HL<sub>1</sub> 0.52–0.88; HL<sub>2</sub> 0.34–0.60; HL<sub>3</sub> 0.16–0.25; HW 0.50–0.82; SL 0.51–0.82; EL 0.13–0.21; WL 0.53–0.98; PnL 0.18–0.25; PnW 0.36–0.57; ML 0.13–0.23; MW 0.18–0.35; *Indices* CI 93.33–101.45; SI<sub>1</sub> 92.86–105.36; SI<sub>2</sub> 126.67–165.38; OI<sub>1</sub> 23.53–35.71; OI<sub>2</sub> 26.67–32.5.

**Description.** *Head.* Slightly longer than wide in full face view; posterior cephalic margin flat or slightly concave. Dorsum of the head has scattered appressed hairs. Clypeus with a rounded anterior margin and five long, erect hairs of which a single, usually conspicuous hair is near the anterior margin, two hairs are in mediolateral position, and two more near the toruli; other hairs on the clypeus are markedly shorter and appressed or decumbent. Toruli surpassing the posterior clypeal margin in oblique anterodorsal view. The scapes extend beyond the posterior margin of the head by a length that is equal to the maximal diameter of the eye or larger, and they bear appressed and decumbent hairs. Three ocelli are present. Eyes are positioned on the cephalic midline and have 10–14 ommatidia along their maximal diameter.

*Mesosoma.* Typically with two erect hairs on the pronotum and two on the mesonotum; sometimes with additional suberect hairs, mainly on pronotum. Dorsum of the mesosoma with imbricate sculpture. The mesonotum is inflated and bulges dorsally above the pronotum in lateral view. Metanotal groove wider than the diameter of the metathoracic spiracles. Metathoracic spiracles in dorsolateral position, slightly protruding, and not touching any sutures. Dorsum of the propodeum strongly convex and shorter than the propodeal slope. Propodeal spiracles conspicuous and circular, positioned on the propodeal margin, anterior of the middle of the propodeal slope. Legs with appressed hairs. Petiole short and inclined forward.

*Gaster.* With scattered pubescence and several scattered long erect hairs.

*Color and sculpture.* Head and gaster are smooth and shiny, but the dorsum of the mesosoma usually has imbricate sculpture. Head and mesosoma are brown yellowish, whereas the gaster is darker.

**Distribution** (Supplementary material Fig. S12). *Brachymyrmex coactus* occurs in Argentina, Bolivia, Brazil, Costa Rica, Guyana, Panama, Paraguay, and Peru.

**Biology.** The specimens from UNA-ESMAI in Bahia (Brazil) were found in dwarf coconuts (CEPLAC: USNMENT00757557, 00757558), those from Canindeyú (Paraguay) on shrubs (ALWC: USNMENT00757561), and those from St. Catharina underneath bark in association with a beetle of the genus *Claviger* (Mayr 1887).

**Remarks.** The worker on pin USNMENT00757191 is designated here as lectotype. Emery (1906) considered *B. coactus* var. *nictitans* to be a separate variety because it has smaller eyes than *B. coactus*, but he also expressed doubt on the level of consistency of this difference.

Santschi (1923a) did not provide a motivation to distinguish *B. constrictus* from *B. coactus* but indicated that *B. constrictus* has more finely imbricate sculpture on the mesosoma and smaller metathoracic spiracles. Subsequently, he (Santschi 1923b) reported that his original description (Santschi 1923a) of *B. coactus* refers to *B. coactus* var. *robusta*. This variety has a larger body size, more sculpture on the mesosoma, and a somewhat bigger head than the “typical” form of *B. coactus*. Both varieties of *B. coactus* were described from the same type locality, however.

After examining specimens of all these varieties and *B. constrictus*, we consider the main morphological differences to relate to variation in body size. This trait is, however, very variable even within localities (including among specimens mounted on the same pin). As these taxa all have the same diagnostic features, we here synonymize *B. coactus* var. *nictitans*, *B. coactus* var. *robustus*, and *B. constrictus* with *B. coactus*.

*Brachymyrmex cordemoyi* Forel

(Figs. 21, 22, and 23, supplementary material Fig. S13)

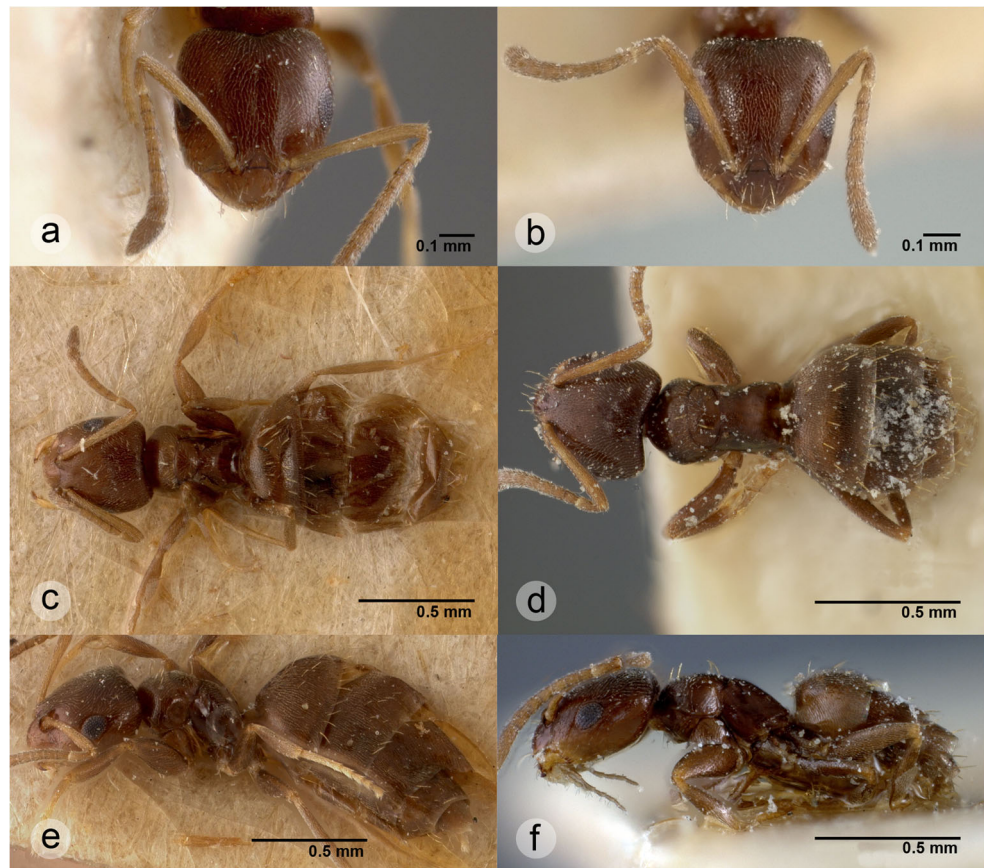
*Brachymyrmex patagonicus* var. *cordemoyi* Forel, 1895a: 49 (w.). (MHNG) [not examined]. **REUNION.** See also: Emery (1906: 180) (q.m.). Raised to species: Emery (1906: 179). Subspecies of *Brachymyrmex patagonicus*: Forel (1908: 399); Forel (1912b: 165); Santschi (1912: 533). Revived status as species: Wheeler (1922: 1036); Emery (1925: 41). See also Forel (1912a: 62).

= *Brachymyrmex laevis* var. *fuscula* Emery, 1906: 178 (w.q.). (MCSN: USNMENT00757216, 00757217; MHNG00758131–00758133): ten workers, one queen [examined]. **ARGENTINA: Mendoza:** Mendoza, Punta de vacas; (MCSN: USNMENT00757215): eight workers [examined]. **ARGENTINA: Buenos Aires:** Buenos Aires. n. syn.

= *Brachymyrmex brevicornis* Emery, 1906: 180, Figs. 38, 40, and 41 (w.q.m.). (MCSN: USNMENT00757210–00757214): 16 workers, one queen, one male [examined]. **ARGENTINA: Buenos Aires:** Santa Catalina. See also Quirán (2005: 765). n. syn.

= *Brachymyrmex patagonicus* var. *brevicornoides* Forel, 1914: 287 (w.q.m.). (MHNG: USNMENT00758141–

**Fig. 21** *Brachymyrmex cordemoyi*: **a, c, e** *B. laevis* var. *fuscula* n. syn: head, dorsal, and lateral view of a syntype worker; **b, d, f** *B. cordemoyi* var. *nigricans*: head, dorsal, and lateral view of a syntype worker



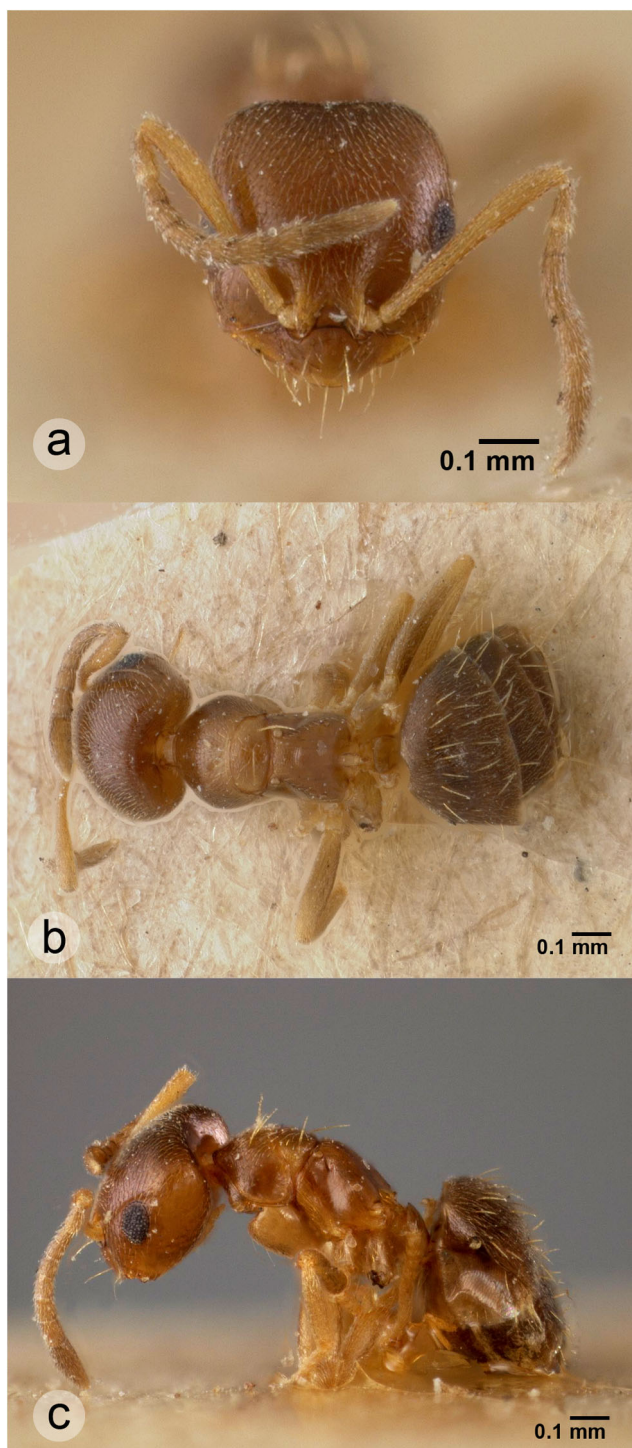
00758143): four workers, three males [examined]. **ARGENTINA: Buenos Aires:** Tapalquén. Junior synonym of *Brachymyrmex nigricans*: Santschi (1923a: 657). [*Brachymyrmex brevicorneoides* has priority as senior name, *Brachymyrmex nigricans* is its junior synonym: Bolton (1995: 81)]. n. syn.

= *Brachymyrmex cordemoyi* var. *nigricans* Santschi, 1916: 395 (w.). (NHMB: USNMMENT00758081): three workers [examined]. **ARGENTINA: Río de la plata,** Isla Martin Garcia; (NHMB: USNMMENT00758078, 00758080): ten workers. **ARGENTINA: Buenos Aires:** Buenos Aires. [First available use of *Brachymyrmex patagonicus cordemoyi nigricans* Santschi (1912: 533) unavailable name]. Raised to species: Santschi (1923a: 657). Junior synonym of *Brachymyrmex nigricans*: Santschi (1923a: 657) [As mentioned above *Brachymyrmex brevicorneoides* has priority over *B. nigricans*].

= *Brachymyrmex cordemoyi* var. *distincta* Santschi, 1923a: 658, Figs. 6 and 50, 59 (w.q.). (NHMB: USNMMENT00757178, 00757179): three workers [examined]. **ARGENTINA: Santa Cruz:** (NHMB: USNMMENT00758089): nine workers [examined]. **ARGENTINA: Delta del Paraná.** n. syn.

**Additional material examined. ARGENTINA: Buenos Aires:** Buenos Aires, E.V. Steigen, three workers (MZUSP:

USNMMENT00759023); Buenos Aires, Universidad de Buenos Aires, 18 workers (ICN: USNMMENT00759032); La Plata, Silvestri, four workers (NHMB: USNMMENT00758088), eight workers (MCZC: USNMMENT00757244); **Entre Ríos:** 8.63 km Concordia, -31.41667 -58.11667, 16 m, 26 Dec. 2007, W. & E. MacKay #22670, one worker (WEMC: USNMMENT00757638); Isla frente Puerto Victoria, -32.63333 -60.16667, 10 m, 29 Oct. 2002, A.L. Wild & N. Heller, one worker (ALWC: USNMMENT00757966); **Misiones:** 48.93 km N Campinas de America, -25.8565 -53.9939, 360 m, 03 Jan. 2008, W. & E. MacKay #22794, one worker (WEMC: USNMMENT00757728); **San Juan:** 8.59 km S Villa Aberastain, -31.72528 -68.55447, 592 m, 10 Jan. 2008, W. MacKay #22879, one worker (WEMC: USNMMENT00757737). **BRAZIL: Bahia:** Boa Vista do Tupim, x06 Dec. 2010, V.M.S. Cameiro & J.J. Resende, one worker (CEPLAC: USNMMENT00757887); **Mato Grosso do Sul:** ~70 km E Corumbá, Faz. Maria Bonita, -19.16666 -57.16666, 22 Aug. 1998, A. L. Wild #AW0657, one worker (ALWC: USNMMENT00759025); 10 km Posto Chapadao, 18 Oct. 1989, S. Porter, three workers (WEMC: USNMMENT00758994); 3 km Anastácio, 17 Oct. 1989, W. MacKay #12605, three workers (WEMC: USNMMENT00757652); Passo da Lontra, -19.53333 -57.01667,

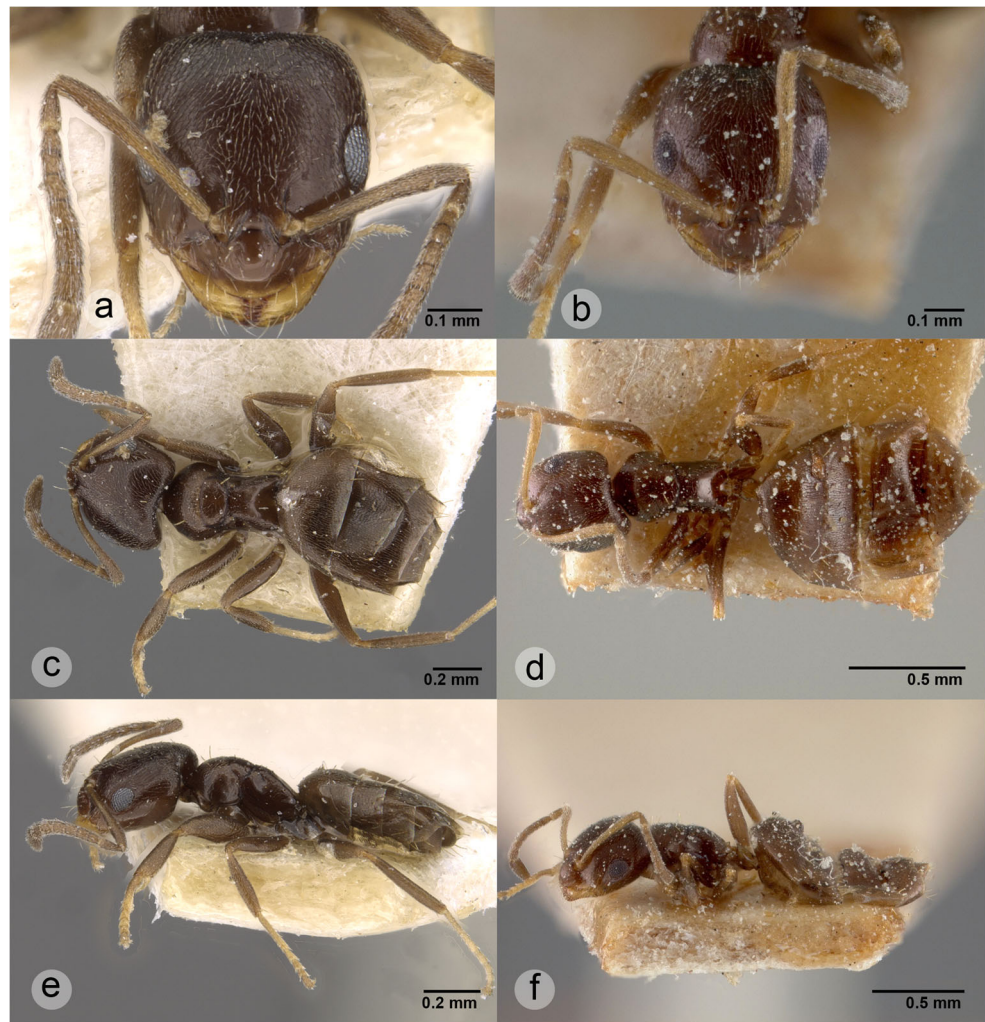


**Fig. 22** *Brachymyrmex cordemoyi*: **a–c** *B. brevicornis* n. syn: head, dorsal, and lateral view of a syntype worker

80 m, 08 Sep. 1996, P.S. Ward #13222, one worker, one male (MCZC: CMOS000020); **Para**: Santarem, Taperinha, -2.9 -54.3, July 1975, R.L. Jeanne, 440, four workers (MCZC: CMOS000015, CMOS000016); **Rio Grande do Norte**: Ceará, Mirim, W.M. Mann, 10 workers (MCZC: CMOS000124,

CMOS000125); **Rondônia**: Ji Parana, 27 Aug. 1984, W. Overall, two workers (MPEG: USNMMENT00757583, 00757964); Ouro Preto do Oeste, 25 Mar. 1985, W. França, Res INPA 0050, three workers (MPEG: USNMMENT00757984, 00758043); **São Paulo**: Aguas de São Pedro, May–June 1985, S. Silva, one worker (ICN: USNMMENT00757670); Caraguatatuba, Res. Florest rain for, 40–80 m 18–22 May 1971, W.L. & D.E. Brown, six workers (MCZC: CMOS000017, CMOS000019, CMOS000021); José Bonifacio, 17 Nov. 1970, J. Diniz, two workers, one queen (MZUSP: USNMMENT00757582). **COLOMBIA**: **Caqueta**: Florencia, two workers (ICN: LEV127); **Huila**: 17 km NW, La Plata, 03 Jan. 1984, W. & E. MacKay #7138, two workers (WEMC: USNMMENT00757673); **Meta**: 65 km E Puerto Lopez, 30 Jan. 1973, W.P. MacKay #7365, three workers (WEMC: USNMMENT00757636); Villavicencio, 17 Dec. 1975, W. & E. MacKay, two workers (WEMC: USNMMENT00757648); Vista Hermosa, 25 Dec. 1975, W. & E. MacKay #75812, #815, seven workers, one queen, one male (WEMC: USNMMENT00757653, 00757675, 00757985). **COSTA RICA**: **Limón**: Guapiles, R. Toro Amarillo vic., 15 Feb.–09 Mar. 1966, W.L. Brown, three workers (MCZC: USNMMENT00757647); **Puntarenas**: 8 km WNW Potrero Grande, 9.03 -85.26, 200 m, 01 Aug. 1985, P.S. Ward #7791, three workers (PSWC: USNMMENT00757877). **CUBA**: **Guantanamo**: Baracoa, 20.35 -74.5 m, 26 Aug. 2001, P.S. Ward #14462–14, three workers (PSWC: USNMMENT00757881); **Pinar del Río**: Viñales del Río, 14 June 1953, E.O. Wilson #11, three workers (MCZC: CMOS000018). **DOMINICAN REPUBLIC**: 28 km SSE Constanza, -9.29576 -75.99786, 11 Sep. 1992, P.S. Ward #11757, one worker, one queen (PSWC: USNMMENT00758016). **ECUADOR**: **Loja**: Estación San Francisco, 2200 m, 11 & 14 Sep. 2011, F. Fernandez, 46 workers (ICN: USNMMENT00759034, 00759036, 00759037); **Napo**: near Dureno, 0.07778 -76.73056, 287 m, 20 July 2005, W. & E. MacKay #21273 #21277, four workers (WEMC: USNMMENT00757581, 00757637); **Pichincha**: Mitad del Mundo, 00.00 -78.45, 2483 m, 07 Dec. 2003, A.L. Wild & J.M. Vieira #AW 2235, one worker (ALWC: USNMMENT00757888). **EL SALVADOR**: **La Libertad**: Quezaltepeque, 500 m, 19 June 1963, D.Q. Cavagnaro & M.E. Irwin, ANTC 10258, one worker (CASENT: CASENT0196000). **GUATEMALA**: **Suchitepéquez**: Finca Tarrales, 12.3 km N Patulul, 14.52256 -91.13642, 740 m, 30 July 2004, W. & E. Mackay #20782, three workers (WEMC: USNMMENT00758045, 00758046). **GUYANA**: Kartabo, July–Aug. 1920, W.M. Wheeler, 16 workers (MCZC: CMOS000022–000027). **MEXICO**: **Morelos**: Cuernavaca, 25 May 1989, W. MacKay #11418, two workers (WEMC: USNMMENT00757981); **Oaxaca**: 45 km N. San Pedro Pochutla, 1000 m, 03 June 1988, W. MacKay #10755, six

**Fig. 23** *Brachymyrmex cordemoyi*: **a, c, e** *B. brevicornoeides* n. syn: head, dorsal, and lateral view of a syntype worker (from [www.antweb.org](http://www.antweb.org); photographer: Zach Lieberman); **b, d, f** *B. cordemoyi* var. *distincta* n. syn: head, dorsal, and lateral view of a syntype worker



workers (WEMC: USNMENT00758032, 00757649); **Veracruz:** Los Tuxtlas, 10 June 1994, L. Quiroz, two workers (ICN: USNMENT00757661). **NEW CALEDONIA:** Kuto Penin. Ile des Pins, -22.6666 167.4333, 5 m, 11 May 1980, P.S. Ward #4294-9, three workers (PSWC: USNMENT00757882); Noumea, 0-100 m, N.L.H. Krauss, one worker (CASENT: CASENT0196015). **PARAGUAY:** **Central:** Guarambaré, -25.48 -57.45, 25 Apr. 1997, A. Wild #AW0514, one worker (ALWC: USNMENT00757645); **Guairá:** Roque Gonzalez, -25.88333 -57.28333, 14 Jan. 1995, B. Garcete #AW0457, one worker (ALWC: USNMENT00759028). **PERU:** **Madre de Dios:** Tambopata, Cuzco Amazónico, 15 km NE Puerto Maldonado, June 1989, S.P. Cover & J.E. Tobin, CA-275, six workers, one queen (MCZC: USNMENT00757276-00757279); **San Martín:** Con. Mun. Zona Barreal 23 km S Picota, -7.09111 -76.31361, 335 m, 06-15 Mar. 2005, M.E. Irwin & J.D. Vasquez, ANTC1447, one worker (CASENT: CASENT0066404). **SEYCHELLES:** La Dique Island, 1 m, 09 Nov 1993, Alpert et al., two workers (MCZC: USNMENT00757245).

**SOLOMON ISLAND:** Guadalcanal, Honiara, 0-100 m, Mar 1986, N.L.H. Krauss, ANTC 10277, one worker (CASENT: CASENT0196019). **SURINAME:** Dirkshoop, May 1959, I. V. d. Drift, three workers (MPEG: USNMENT00757580). **USA:** **Arizona:** Pima Co. Tucson, 32.23417 -110.96666, A.L. Wild #AW2826 (ALWC: USNMENT00757958). **VANUATU:** Tafea, Tanna, 0-100 m, Dec. 1985, N.L.H. Krauss, ANTC 10270, 10271, two workers (CASENT: CASENT0196012, 0196013). **VENEZUELA:** **Lara:** Barquisimeto, to Carora km 19, 29 June 1971, W.L. & D.E. Brown, two workers (MCZC: USNMENT00757884); **Miranda:** D.F. Inst. Estud. Avan. Caracas, 10 Oct 1988, W. MacKay #11144-2 #11146-6, four workers (WEMC: USNMENT00757654, 00757744).

**Diagnosis.** *Brachymyrmex cordemoyi* strongly resembles *B. obscurior* and to some extent also *B. patagonicus*. All these species have scapes that reach or surpass the posterior cephalic margin, but by less than the maximal diameter of the eye; their mesonotum does not bulge dorsally above the pronotum in lateral view, and the metanotal groove is absent or narrower than the diameter of methathoracic spiracles. In general, *B.*



*cordemoyi* has a longer pronotum and mesonotum than *B. obscurior* and *B. patagonicus*, but these characters show important intraspecific variation. Furthermore, it differs from *B. patagonicus* by having considerably denser pubescence on the gaster, and from *B. obscurior* by having a larger head, more ommatidia along the maximal diameter of the eye, and lighter-colored pubescence which is denser on the dorsum of the entire body and appressed on the gaster instead of decumbent in *B. obscurior*.

**Additional material examined measurements** (mm) ( $n = 20$ ). HL<sub>1</sub> 0.39–0.62; HL<sub>2</sub> 0.27–0.41; HL<sub>3</sub> 0.10–0.16; HW 0.33–0.59; SL 0.27–0.53; EL 0.08–0.16; WL 0.37–0.60; PnL 0.10–0.20; PnW 0.23–0.39; ML 0.08–0.18; MW 0.16–0.29; *Indices* CI 84.38–96.78; SI<sub>1</sub> 82.35–106.38; SI<sub>2</sub> 100.00–142.86; OI<sub>1</sub> 23.33–34.69; OI<sub>2</sub> 20.00–29.63.

**Description.** *Head.* Slightly longer than wide in full face view; posterior cephalic margin slightly concave. Dorsal hairs dense and appressed. Clypeus with a rounded anterior margin and five long, erect hairs of which a single, usually conspicuous hair is near the anterior margin, two hairs are in mediolateral position, and two more near the toruli; other hairs on the clypeus are markedly shorter and appressed or decumbent. Toruli surpassing the posterior clypeal margin in oblique anterodorsal view. Scapes reach the posterior cephalic margin or surpass it by a length up to the maximal diameter of the eye; they have appressed hairs. Three inconspicuous ocelli are usually present. Eyes are positioned on the cephalic midline and have 10–12 ommatidia along their maximal diameter.

*Mesosoma.* Typically with two erect hairs on the pronotum and two on the mesonotum; sometimes with additional suberect hairs, mainly on the pronotum. The mesonotum is not inflated and does not bulge dorsally above the pronotum in lateral view. Metanotal groove absent or narrower than the diameter of the metathoracic spiracles. Metathoracic spiracles in dorsolateral position, not protruding, and typically touching the mesometanotal and propodeal sutures. Dorsum of the propodeum slightly convex and shorter than the posterior slope. Propodeal spiracles circular, positioned on the posterior propodeal margin, slightly posterior of the middle of the propodeal slope. Legs with appressed hairs. Petiole short and inclined forward.

*Gaster.* With dense yellowish pubescence and several scattered and sub-erect hairs, mainly but not exclusively along the edges of the segments.

**Color and sculpture.** Body smooth, shiny, and brownish in color.

**Distribution** (Supplementary material Fig. S13). *Brachymyrmex cordemoyi* is widespread and known from Argentina, Brazil, Colombia, the Dominican Republic, Ecuador, El Salvador, Guatemala, Guyana, Mexico, Paraguay, Peru, Suriname, the USA, Venezuela, and it has been introduced in New Caledonia, Seychelles, Vanuatu,

Solomon Island, Saudi Arabia (Sharaf et al., 2016), Europe, and Asia (Ortiz-Sepulveda, pers. obs.).

**Biology.** Some specimens were collected from under stones (PSWC: USNMENT00757877, 00757881; MCZC: CMOS000020), or on cacti (WEMC: USNMENT00757981).

**Remarks.** We refrain from designating a lectotype because we did not come across the type series of *B. cordemoyi* at the MHNG. However, we studied the original description and the type series of its varieties (i.e., *distincta*, *nigricans*) (Santschi 1916; Santschi 1923a). Hence, the taxonomic decisions made here are based on these data together with the overall morphological framework we developed for the genus.

The type series of *B. cordemoyi* was collected in Reunion, and Forel (1895a) already suggested that it represents an introduction from the Neotropics. Forel (1895a) indicated that *B. cordemoyi* resembles *B. patagonicus*, and originally described it as a variety of the latter species that has more pubescence. Such dense pubescence is also observed in *B. patagonicus* var. *brevicornoeides*. Forel (1914) did not provide diagnostic features to distinguish *B. patagonicus* var. *brevicornoeides* and typical *B. patagonicus*. However, he suggested that the scapes in *B. patagonicus* var. *brevicornoeides* resemble those of *B. brevicornis*, but are slenderer, and that *B. patagonicus* var. *brevicornoeides* has somewhat larger eyes than *B. brevicornis*. Before, Emery (1906) had suggested that *B. brevicornis* is closely related to *B. cordemoyi* because they have similar integument and pubescence, although the integument is slightly more lucid in *B. brevicornis*. Furthermore, the head and antennal funiculi of *B. brevicornis* are somewhat longer than those of *B. cordemoyi*, the clypeus slightly more prominent, and the eyes smaller. However, many of these differences could represent geographic variation rather than specific differences. It is noteworthy that *B. cordemoyi* is variable in most of these features, and therefore we synonymize *B. patagonicus* var. *brevicornoeides* and *B. brevicornis* to it here. Quirán (2005) redescribed *B. brevicornis* but did not compare or relate it to other *Brachymyrmex* species.

Another example of the variability within *B. cordemoyi* represents *Brachymyrmex cordemoyi* var. *distinta*, which was obtained from various places in Argentina, and which has somewhat shorter scapes than specimens of the typical *B. cordemoyi* (Santschi 1923a). Beyond this feature, the only difference that Santschi (1923a) remarked is the body color of queens. Santschi (1923a) also synonymized *B. patagonicus* var. *brevicornoeides* with *B. nigricans*, which he previously (Santschi 1916) considered a variety of *B. cordemoyi*. Studying the type material of *B. nigricans* we agree with this taxonomic decision, but *brevicornoeides* has taxonomic priority over *nigricans* (Bolton 1995: 81), so that *B. nigricans* is also synonymized to *B. cordemoyi* here.

The type specimens of *B. laevis* var. *fuscula* are morphologically more similar to *B. cordemoyi* than they are to *B. laevis*, and the only difference Emery (1906) described between *B. laevis* and *B. laevis* var. *fuscula* is body color; however, from our observations, both differ also in other traits, notably the pubescence of the gaster, resulting in their synonymization to *B. patagonicus* and *B. cordemoyi*, respectively.

In summary, *B. cordemoyi* has several diagnostic features; however, we also observed considerable intraspecific variation in various traits. This variation may hint to a potential species complex. *Brachymyrmex cordemoyi* is very widespread and a more comprehensive study of the variation within and between its populations would be required to fully resolve the taxonomic status of this species.

*Brachymyrmex degener* Emery

(Figs. 24 and 25, supplementary material Fig. S14)

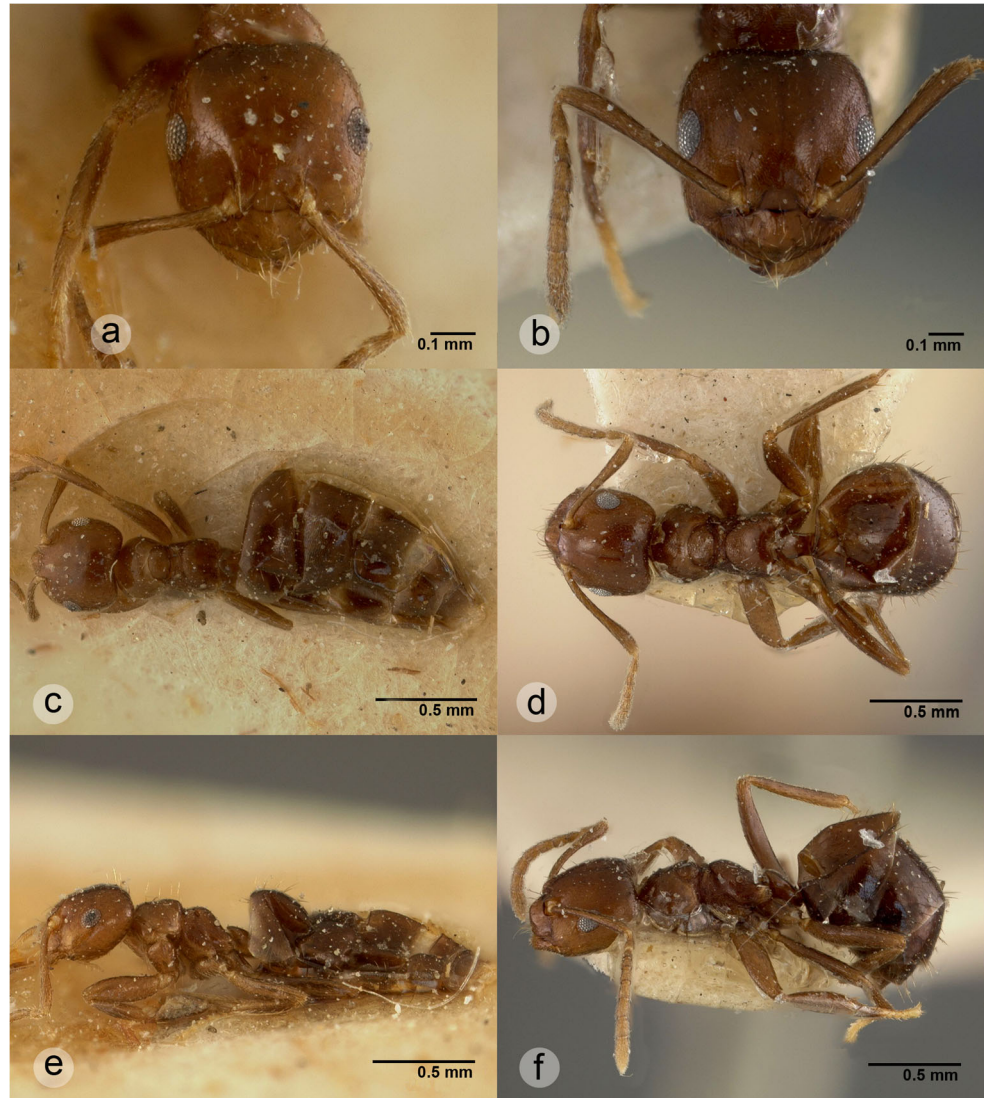
*Brachymyrmex coactus* subs. *degener* Emery, 1906: 177 (w.). Lectotype worker (MCSN: USNMMENT00757208) and paralectotype workers (MCSN: USNMMENT 00757207, MCZC: M.C.Z. Cotypte 01435; here designated): four workers [examined]. **BRAZIL: MATTO GROSSO:** Cuiaba. Raised to species: Santschi (1923a: 670).

= *Brachymyrmex admotus* r. *niger* Forel, 1912a: 62 (w.). (MHNG: USNMMENT00757162, 00757163, 00758155): seven workers [examined]. **BRAZIL: Ceara.** Assigned as *B. degener* st. *niger* by Santschi (1923a: 671). n. syn.

= *Brachymyrmex incisus* Forel, 1912a: 63 (w.m.). (MHNG: USNMMENT00758134–00758139, 00757141–00757143; NHMB: USNMMENT00758096): 24 workers, one male [examined]. **COLOMBIA:** Naranjo. n. syn.

= *Brachymyrmex luederwaldti* Santschi, 1923a: 672, Fig. 36, 66 (w.). (NHMG: USNMMENT00758140; NHMB: USNMMENT00758097, 00758098): six workers [examined]. **BRAZIL: São Paulo:** Alcatrazes. n. syn.

**Fig. 24** *Brachymyrmex degener*: **a, c, e** head, dorsal, and lateral view of the lectotype worker; **b, d, f** *B. admotus* r. *niger* n. syn.: head, dorsal, and lateral view of a syntype worker



**Fig. 25** *Brachymyrmex degener*: **a, c, e** *B. incisus* n. syn.: head, dorsal, and lateral view of a syntype worker; **b, d, f** *B. luederwaldti* n. syn.: head, dorsal, and lateral view of a syntype worker



**Additional material examined. BRAZIL: Bahia:** Canavieiras, -15.69028 -39.00722, 17 July 1998, J.C.S. Carmo & J.R.M. Santos, four workers (CEPLAC: USNMENT00757566); **Para:** Serra Norte, Serraria, -6.08276 -50.16666, 22 Oct. 1984, one worker (MPEG: MPEG\_HYM11506088). **COLOMBIA: Caldas:** Aguadas, Cañón del Río Arma, 5.61472 -75.45972, 1995, C. Sarmiento CES096, three workers (IAvH: USNMENT00757575); **Guajira:** Quebrada Guacoche, nr. Don Diego, forest, 10.72305 -72.96972, 10 m, 22 July 1976, W.L. Brown & R.C. Kugler, eight workers (MCZC: USNMENT00757565, CMOS000094-CMOS000096); **Huila:** 4 km NE Rivera, 30 Dec. 1986, W. MacKay #9023, three workers (WEMC: USNMENT00758026); **Tolima:** Cunday, vereda “El Eden,” 4.08333 -74.66667, 450 m, 01 Oct. 1999, Mejia et al., two workers (ICN: MPUJ\_ENT0000416); **Valle del Cauca:** 08 Jan. 1976, W. & E. MacKay, two workers (WEMC:

USNMENT00758162). **GUATEMALA: El Progreso:** 5 km W Morazan, 14.93 -90.20, 800 m, 19 Nov. 2003, A.L. Wild #AW2121, two workers (ALWC: USNMENT00757576). **FRENCH GUIANA:** Basse Vie-foret, 04 July 1999, S. Durou, two workers, one queen (CEPLAC: USNMENT00757568); Petit Saut, May 2003, J. Orivel & J. Le Breton, three workers (CEPLAC: USNMENT00757573). **PANAMA:** Barro Colorado, Canal Zone, Jan. 1960, W.L. Brown & E.S. McCluskey, three workers (MCZC: USNMENT00758033). **PARAGUAY: Amambay:** Parque Nacional Cerro Corá, -22.65 -56.05, 13 May 1997, A. Wild #AW0576, three workers (ALWC: USNMENT00757569); **Boqueron:** Enciso N.P. (Southern side), -21.20609 -61.65748, 01–02 Oct. 2002, T. Delsinne, two workers (RBINS: Coll.RIScNB SID SPM\_ID11523); Enciso N.P. (Southern side), -21.20609 -61.65748, 01–02 Oct. 2002, M. Leponce, one worker (RBINS: Coll.RIScNB SID SPM\_ID31985); Estancia Maria

Vicenta, -20.92130 -61.39321, T. Delsinne, one worker (RBINS: Coll.RIScNB SID SPM\_ID26822); **Canindeyú:** Residencias, 6 km N Ygatimi, -24.06667 -55.63333, 21 Feb. 1997, A. Wild #AW0451, one worker (AWLC: USNMENT00757577). **TRINIDAD AND TOBAGO:** Cumuto, 24 Apr. 1929, Darlinhton, one worker (MCZC: USNMENT00757578).

**Diagnosis.** *Brachymyrmex degener* morphologically resembles *B. coactus* as both species have scapes that surpass the posterior margin of the head, they have faint sculpture on the mesosoma, a mesonotum that is inflated and that bulges dorsally above the pronotum in lateral view, a wide metanotal groove, metathoracic spiracles that are slightly protruding dorsally, and their gasters have sparse pubescence. However, *B. degener* has a uniformly brownish body, whereas the gaster is conspicuously darker than the rest of the body in *B. coactus*.

*Lectotype and paralectotypes measurements* (mm) ( $n = 3$ ). HL<sub>1</sub> 0.51–0.55; HL<sub>2</sub> 0.35–0.41; HL<sub>3</sub> 0.16; HW 0.49–0.55; SL 0.37–0.53; EL 0.12–0.14; WL 0.55–0.68; PnL 0.16–0.20; PnW 0.31–0.37; ML 0.12–0.16; MW 0.20–0.23; *Indices* CI 96.15–100.00; SI<sub>1</sub> 76.00–96.43; SI<sub>2</sub> 105.56–135.00; OI<sub>1</sub> 21.43–25.93; OI<sub>2</sub> 28.57–30.77.

*Additional material examined measurements* (mm) ( $n = 24$ ). HL<sub>1</sub> 0.53–0.70; HL<sub>2</sub> 0.29–0.49; HL<sub>3</sub> 0.12–0.20; HW 0.51–0.73; SL 0.55–0.68; EL 0.12–0.20; WL 0.60–0.79; PnL 0.14–0.23; PnW 0.33–0.50; ML 0.12–0.21; MW 0.20–0.31; *Indices* CI 87.50–112.50; SI<sub>1</sub> 82.22–117.86; SI<sub>2</sub> 137.04–233.33; OI<sub>1</sub> 20.00–30.30; OI<sub>2</sub> 22.22–33.33.

**Description.** *Head.* Slightly longer than wide in full face view; posterior cephalic margin slightly concave. Dorsum of the head has scattered appressed hairs. Clypeus with a rounded anterior margin and five long, erect hairs of which a single, usually conspicuous hair is near the anterior margin, two hairs are in mediolateral position, and two more near the toruli; other hairs on the clypeus are markedly shorter and appressed or decumbent. Toruli surpassing the posterior clypeal margin in oblique anterodorsal view. The scapes surpass the posterior cephalic margin by a length smaller or equal to the maximal diameter of the eye, and they bear appressed and decumbent hairs. Three ocelli are present. The eyes are positioned on the cephalic midline and have 8–14 ommatidia along their maximal diameter.

*Mesosoma.* Typically with two erect hairs on the pronotum and two on the mesonotum; sometimes with additional suberect hairs, mainly on the pronotum. The mesonotum is inflated and bulges dorsally above the pronotum in lateral view. Metanotal groove wider than the diameter of the metathoracic spiracles. Metathoracic spiracles in dorsolateral position, slightly protruding, and not touching any sutures. Dorsum of the propodeum strongly convex and shorter than the posterior slope. Propodeal spiracles conspicuous and

circular, positioned on the propodeal margin or just dorsal of it, at the anterior margin of the propodeal slope. Legs with appressed hairs. Petiole short and inclined forward.

*Gaster.* With scattered pubescence and several scattered long erect hairs.

*Color and sculpture.* Body shiny and uniformly brownish in color. Head and gaster smooth whereas the dorsum of the mesosoma usually bears imbricate sculpture.

**Distribution** (supplementary material Fig. S14). *Brachymyrmex degener* occurs in Brazil, Colombia, Guatemala, French Guiana, Trinidad, and Tobago.

**Biology.** Unknown.

**Remarks.** The lectotype of *B. degener* is the top specimen on pin USNMENT00758155, whereas the others on that pin are paralectotypes.

*Brachymyrmex degener* was first described as a subspecies of *B. coactus* by Emery (1906) and Santschi (1923a) subsequently raised it to species. *Brachymyrmex degener* indeed resembles *B. coactus* closely, and in retrospect we are uncertain that it represents a separate species. However, the issue of *B. degener* and *B. coactus* is taxonomically very complex and involves several other previously described species and subspecies that warrant synonymization too. Perhaps this process is best performed incrementally, which is the approach taken here.

One of these other taxa involved is *B. admotus* r. *niger* which was described by Forel (1912a) with the following diagnostic traits: the metanotal groove is deep, the mesonotum bulges out dorsally above the pronotum (in lateral view), the body is shiny, and the head and gaster smooth whereas faint sculpture is present on the mesosoma. Upon examination, the type specimens of *B. admotus* r. *niger* have the diagnostic traits of *B. degener*, but lack some of those for *B. admotus*, such as the presence of a pair of thin erect hairs between the metathoracic spiracles, which are positioned fully dorsal instead of dorsolaterally, and the absence of sculpture on the mesosoma. These criteria that motivated Santschi (1923a) to reclassify the race as *B. degener* st. *niger*, and whereas we agree with this reclassification, we do not consider there to be sufficient differences to prevent synonymization of *niger* to *B. degener*.

In the description of *B. incisus* Forel (1912a) likewise indicated similarities to *B. coactus* and *B. admotus*, but again some of the diagnostic traits of *B. admotus* are absent. Moreover, whereas the specimens resemble *B. coactus* closely they do not have a gaster that is conspicuously darker in color than the head and mesosoma, and hence *B. incisus* is here synonymized to *B. degener*.

As to *B. luederwaldti*, Santschi (1923a) indicated similarities to *B. coactus*, and even more so to *B. admotus* r. *niger* (Forel 1912a), from which he distinguished *B. luederwaldti* mainly by its fainter propodeal suture. We consider this

variation to be intraspecific here and consequently also synonymize *B. luederwaldti* to *B. degener*.

Upon describing *degener* as a variety of *B. coactus*, Emery (1906) indicated that this variety differs from typical *B. coactus* mainly in body and eye size, which are traits with a lot of intraspecific variation as we already indicated in the remarks of *B. coactus*. We did not find consistent differences in body size, nor in the number of ommatidia along the maximal diameter of the eye between both taxa. Emery (1906) further emphasized that the medial antennomeres are somewhat longer than wide in *B. degener*, and vice versa in *B. coactus*. However, we cannot confirm this putative difference from the type material of both species. Although some putatively diagnostic differences between *B. coactus* and *B. degener* are indicated in the diagnosis, the taxonomic importance of these differences remains to be examined. Our morphometric measurements confirm the difficulty to establish consistent differences between both taxa, and furthermore our phylogenetic analyses (see below) recovered *B. degener* nested within *B. coactus*. However, a deep phylogenetic branch separates *B. degener* from *B. coactus* as is also recognized by in the ABGD analysis (see below), and given the taxonomic complexity surrounding *B. coactus*, it is possible that the one specimen identified as *B. coactus* that renders the species paraphyletic in fact belongs to a distinct taxon. With the sampling that is currently available, this issue cannot be resolved and therefore we do not further synonymize *B. coactus* and *B. degener* here.

*Brachymyrmex delabiei* Ortiz & Fernández

(Fig. 26, supplementary material Fig. S15)

*Brachymyrmex delabiei* Ortiz and Fernández, 2014: 24, Figs. 22, 23, and 24 (w). Holotype worker (MZSP: USNMENT00757718) and paratype workers (CPDC: USNMENT00757719, ICN: USNMENT00757720, USNM: USNMENT00757721): four workers. **BRAZIL: São Paulo:** Tapirai, -24.03208 -47.65556, 08–14 Jan. 2001, R.R. Silva & Eberhardt.

**Additional material examined. BRAZIL: Bahia:** Boa Nova, João Mata, 13 Aug. 2003, J.R.M. Santos & J.C.S. Carmo, one worker (CPDC: USNMENT00757610); A61 Camacan, 27 Aug. 1999, -15.60111 -39.52111, col. J.R.M. dos Santos, one worker (CPDC: USNMENT00757837); **Santa Catharina:** Palhoça, PE Serra do Tabuleiro, 02–10 Nov. 2003, -27.74111 -48.69722, R.R. Silva, B.H. Dietz and A. Tavares, one worker (MZSP: USNMENT00757725); **São Paulo:** São Bernardo do Campo, 01 June 1971, W.L. & D.E. Brown, one worker (MCZC: USNMENT00757835).

**Diagnosis.** *Brachymyrmex delabiei* is most similar in morphology to *B. brasiliensis* and *B. feitosa*, because they all have tumuliform metathoracic spiracles; however, it differs from *B. brasiliensis* by its entirely smooth and shiny body, and from *B. feitosa* by the presence of two erect hairs on



Fig. 26 *Brachymyrmex delabiei*: a–c head, dorsal, and lateral view of the holotype worker

the pronotum and two on the mesonotum, the lack of dense pubescence on the first segment of the gaster, and the yellowish body.

**Description.** See Ortiz and Fernández (2014).

*Brachymyrmex depilis* Emery

(Fig. 27, supplementary material Fig. S16)

*Brachymyrmex heeri* subsp. *depilis* Emery, 1893: 635 (w.q.). Lectotype worker (MCSN: USNMENT00757228) and paralectotype workers, queen, male (MCSN:

**Fig. 27** *Brachymyrmex depilis*: **a, c, e** head, dorsal, and lateral view of the lectotype worker; **b, d, f** *B. depilis* subsp. *flavescens*: head, dorsal, and lateral view of a syntype worker



USNMENT00757225–00757232; here designated): 37 workers, one queen, ten males [examined]. **USA: District of Columbia:** Georgetown College, 10 Aug. 1885, leg. Pergrande. Wheeler and Wheeler (1953: 139) (l.). Raised to species: Santschi (1923a: 663).

= *Brachymyrmex nanellus* Wheeler, 1903: 102, Fig. 7b (w.m.). (MCZC: MCZ Cotype 22,939): five workers [examined]. **USA: Texas:** Austin, 25 May 1901. Synonymy by Creighton (1950: 359).

= *Brachymyrmex depilis* subsp. *flavescens* Grundmann, 1952: 117 (w.). (USNM: USNMENT00529204): three workers [examined]. **USA: Utah:** near Salt Lake City. Lower portion of Big Cottonwood Canyon, 24 June 1947. Synonymy by Cole (1953: 266).

**Additional material examined. CANADA :** **Nova Scotia:** Halifax, 15 m, 44.63333 -63.61667, 25 Oct. 1996, P.S. Ward #13234, two workers, one queen (PSWC: USNMENT00757818). **MEXICO: Tamaulipas:** Gomez Parias, 25 Sep. 1987, W. MacKay #10073, 2 workers (WEMC: USNMENT00757816); **Veracruz:** Las Hamacas,

17 km. N Santiago Tuxtla, 26–28 Aug. 1953, E.O. Wilson, five workers, one queen (MCZC: CMOS000114–000115); Los Tuxtlas, 10 km NNW Sontecomapan, 18.58333 -95.08333, 200 m, 20 Mar. 1985, P.S. Ward #7333–55, three workers (PSWC: USNMENT00757815). **USA: Alabama:** Marshall Co. JCT 420 7 km S Morgna city, 34.41111 -86.52361, 09 June 1998, MacKay fam. #188203, two workers (WEMC: USNMENT00757813); **Arkansas:** Cross Co. Village Cr. St. Pk. 14 Aug. 1988, R. Anderson, three workers (WEMC: USNMENT00757805–00757807); **California:** 8 km S, Brans. Wiask, 10 Feb. 1943, W.S. Ross, ANTC10266, four workers (CASENT: CASENT0196008); Santa Barbara Co, Figueroa Crk., Sedgwick Ranch, 34.71667 -120.03333, 350 m, 02 Mar. 1996, P.S. Ward #12963, three workers (PSWC: USNMENT00757590); **District of Columbia:** Washington D.C. 25 May 1948, F. Bonet #1718, three workers (MZUSP: USNMENT00757798). **Florida:** Highlands Co. Archbold Biol. Station, 22 Aug. 1995, A. Wild, five workers (ALWC: USNMENT00757817); **Kentucky:** Floyd Co. Jennie Wiley

St. Pk., 07 July 1968, S. Peck Ber #134, one worker (MCZC: CMOS000028); **Louisiana:** Tammany Par. Abita, Springs, Money Hills Golf Course, 30.55156 -89.95488, 08 Sep. 2000, A.M. Pranschke, two workers (CEPLAC: USNMENT00757801); **New Mexico:** Sandoval Co, Bandelier, Nat. Mon, 21 Aug. 1986, W. & E. MacKay #8784, two workers (WEMC: USNMENT00757814); **New York:** Newark, Morris Farm, U. Delaware, Liriadendrofagus, 18 Apr. 1976, S. Handel, two workers (MCZC: CMOS000116, 000117); Ontario Co. Gannet Hill, 42.7 -77.4, 640 m, 27–29 Aug 2003, A.L. Wild #AW1970, two workers, one queen (ALWC: USNMENT00757799); Ontario Co. Gannet Hill, 42.7 -77.4, 640 m, 10 Sep. 1995, A.L. Wild #AW0719, three workers (ALWC: USNMENT00757799); **Texas:** 16 km S San Antonio, 18 Feb. 1942, E.S. Ross, ANTC10267, three workers (CASENT: CASENT0196009); Houston Co. Big Stough Wild Area, 09 May 1988, R. Anderson #12760, four workers (WEMC: USNMENT00757811–00757812, 00758040); Sabino Co. 14.5 K E Nerwphill, 11 May 1988, R. Anderson #12763, #12763, six workers (WEMC: USNMENT00757808–00757810); **Vermont:** Nr. Burlington, Temperate Forest, Nov 2001, R. Blatrix, nine workers (CEPLAC: USNMENT00757802–00757804).

**Diagnosis.** *Brachymyrmex depilis* resembles *B. heeri* and *B. giardi* as all three taxa have the mesonotum bulging dorsally above the pronotum in lateral view, and a gaster with dense pubescence. However, *B. depilis* differs from *B. heeri* by its shorter scapes and the lack of erect hairs on the mesosoma, and from *B. giardi* by its smaller eyes, its appressed hairs on the dorsum of the mesosoma, its yellowish color, and its Nearctic distribution, i.e. from the South of Canada to the North of Mexico.

**Lectotype and paralectotypes measurements** (mm) ( $n = 10$ ). HL<sub>1</sub> 0.47–0.49; HL<sub>2</sub> 0.33–0.37; HL<sub>3</sub> 0.10–0.18; HW 0.39–0.45; SL 0.35–0.41; EL 0.08–0.12; WL 0.39–0.51; PnL 0.12–0.20; PnW 0.27–0.33; ML 0.10–0.14; MW 0.20–0.21; **Indices** CI 80.00–92.00; SI<sub>1</sub> 85.71–100.00; SI<sub>2</sub> 100.00–117.65; OI<sub>1</sub> 18.18–30.00; OI<sub>2</sub> 20.00–36.00.

**Additional material examined measurements** (mm) ( $n = 10$ ). HL<sub>1</sub> 0.31–0.50; HL<sub>2</sub> 0.19–0.35; HL<sub>3</sub> 0.05–0.14; HW 0.29–0.46; SL 0.27–0.42; EL 0.08–0.10; WL 0.31–0.46; PnL 0.08–0.18; PnW 0.22–0.31; ML 0.07–0.13; MW 0.17–0.22; **Indices** CI 88.89–94.74; SI<sub>1</sub> 85.71–95.74; SI<sub>2</sub> 110.71–142.86; OI<sub>1</sub> 19.57–30.30; OI<sub>2</sub> 17.14–30.00.

**Description.** **Head.** Slightly longer than wide in full face view; posterior cephalic margin slightly concave. Clypeus with a rounded anterior margin and five long, erect hairs of which a single, usually conspicuous hair is near the anterior margin, two hairs are in mediolateral position and two more near the toruli; other hairs on the clypeus are markedly shorter and appressed or decumbent. Toruli surpassing the posterior clypeal margin in oblique anterodorsal view. The scapes are short, usually barely

reaching the posterior margin of the head, and never surpassing it by a length that equals the maximal diameter of the eye. Ocelli are absent. Eyes are small and positioned on the cephalic midline; they have 6–8 ommatidia along their maximal diameter.

**Mesosoma.** Not bearing any erect hairs. The mesonotum is inflated and bulges dorsally above the pronotum in lateral view. Metanotal groove absent or narrower than the diameter of the metathoracic spiracles. Metathoracic spiracles are small, in dorsolateral position, not protruding, but touching the propodeal suture. Dorsum of the propodeum is weakly convex and much shorter than the propodeal slope. Propodeal spiracles are circular, positioned on the posterior propodeal margin at the middle of the propodeal slope. Legs with appressed hairs. Petiole short and inclined forward.

**Gaster.** With dense pubescence and scattered long erect hairs at the edges of the segments.

**Color and sculpture.** Body opaque with inconspicuous sculpture. Body yellowish, sometimes with the gaster a bit darker than the mesosoma.

**Distribution** (supplementary material Fig. S16). *Brachymyrmex depilis* is known from Canada, México, and the USA.

**Biology.** Grundmann (1952) collected a nest of *B. depilis* subsp. *flavescens* from among the roots of the scrub oak *Quercus gambelii* and suggested that this species is subterranean and tends aphids and coccids on the roots of plants. This association was also highlighted by Jensen et al. (1980) and Wheeler and Wheeler (1986). Small colonies of *B. depilis* were found in the soil under stones or in rotting wood in a wide variety of habitats: open forest, dense moist forest, grass lands, and dry fields (Wheeler and Wheeler 1986). Surprisingly, Jensen et al. (1980) reported *B. depilis* from an intertidal halophyte-covered mud flat in the Gulf of California in Mexico, where colonies are regularly inundated by sea water. The authors suggest that the mechanisms that allow the species to survive heavy rains elsewhere may have preadapted their survival in this unusual habitat. Page (1982) reported on copulatory behavior and observed a queen of *B. depilis* with attached to her abdomen three motionless males, that she dragged around. As such he suggested that *B. depilis* seems to have multiple copulations but whether insemination occurs by several partners is unknown.

**Remarks.** The lectotype is designated here as the worker on pin USNMENT00757229 and the other specimens are paralectotypes.

*Brachymyrmex depilis* was originally described as a subspecies of *B. heeri* by Emery (1893), and he distinguished it from typical *B. heeri* because *B. depilis* lacks erect hairs on the mesosoma. Santschi (1923a) raised the subspecies to species but did not provide criteria to support his decision. Nevertheless, we consider this decision justified given the differences we mention here in the diagnosis.

In the original description of *B. nanellus*, Wheeler (1903) reported a comparison of his material to alleged specimens of

*B. depilis*, and he described a series of differences to support the status of *B. nanellus* as a separate species. Santschi (1923a) accepted this taxonomic decision, but as Creighton (1950) pointed out the comparative material unlikely belonged to *B. depilis*, and after a further comparison of both taxa he synonymized *B. nanellus* with *B. depilis*, which we support here after re-examining the material.

*Brachymyrmex depilis* subsp. *flavescens* was originally distinguished from *B. depilis* by having a lighter body color, smaller eyes, an opaquer body due to its shriveled integument, scarcer pubescence, and hairs (Grundmann 1952). However, after examining this material, we agree with the conclusion of Cole (1953) that these specimens appear to be part of an incipient colony, which adequately explains all these morphological differences outlined by Grundmann (1952).

Fisher and Cover (2007) suggested that *B. depilis* may constitute a complex of several species. The material studied here is perhaps too limited to accurately comment on this issue; however, we did not find consistent morphological differences between samples, except perhaps in body size.

*Brachymyrmex donisthorpei* Santschi

(Fig. 28, supplementary material Fig. S17)

*Brachymyrmex donisthorpei* Santschi, 1939: 320, Figs. 4 and 5 (w.). Lectotype worker (NHMB: USNMENT00757183) and paralectotype workers (NHMB: USNMENT00757184–00757185; here designated): three workers [examined]. **COLOMBIA**, Mar. 1937, Paul Robá, leg.

**Additional material examined. BRAZIL: Bahia:** Vargito, -15.40 -39.55, 22 Mar. 1999, J.R.M. dos Santos, one worker (CEPLAC: USNMENT00757839); **São Paulo:** Iguape, E.E. Jureia-Itatins, Nucleo Rio verde, -24.54417 -47.23556, 5–14 Mar. 2001, A.A. Tavares, one worker (ICN: MZSP158). **COLOMBIA: Magdalena:** El Campano, 11.12 -74.10, 1300 m, 13 Aug. 1985. P.S. Ward #7891–23, two workers, one queen (PSWC: USNMENT00757840); **Nariño:** territorio Kofan, 0.47481 -77.17913, 1000 m, 28 Sep. 1998, one worker (IAvH). **ECUADOR: Zamora-Chinchipe:** Copalinga, -4.09122 -78.96069, 17–19 Oct. 2009, Jacquemin, one worker (RBIN: Coll.RIScNB SID SPM\_ID3753921). **PARAGUAY: Boquerón:** Enciso N.P. (Southern side), -21.20298 -61.65909, 04–06 Nov. 2001, M. Leponce.

**Diagnosis.** *Brachymyrmex donisthorpei* morphologically resembles *B. modestus* and *B. myops* because they all have dense, short pubescence over the entire body, scapes with short suberect hairs, eyes that are positioned below the cephalic midline, a metanotal groove that is either absent or narrower than the diameter of the metathoracic spiracles, and yellowish body color. *Brachymyrmex donisthorpei* differs from *B. modestus* and *B. myops* by its short scapes that approximately reach the posterior margin of the head or surpass it by less than the maximal diameter of the eye.

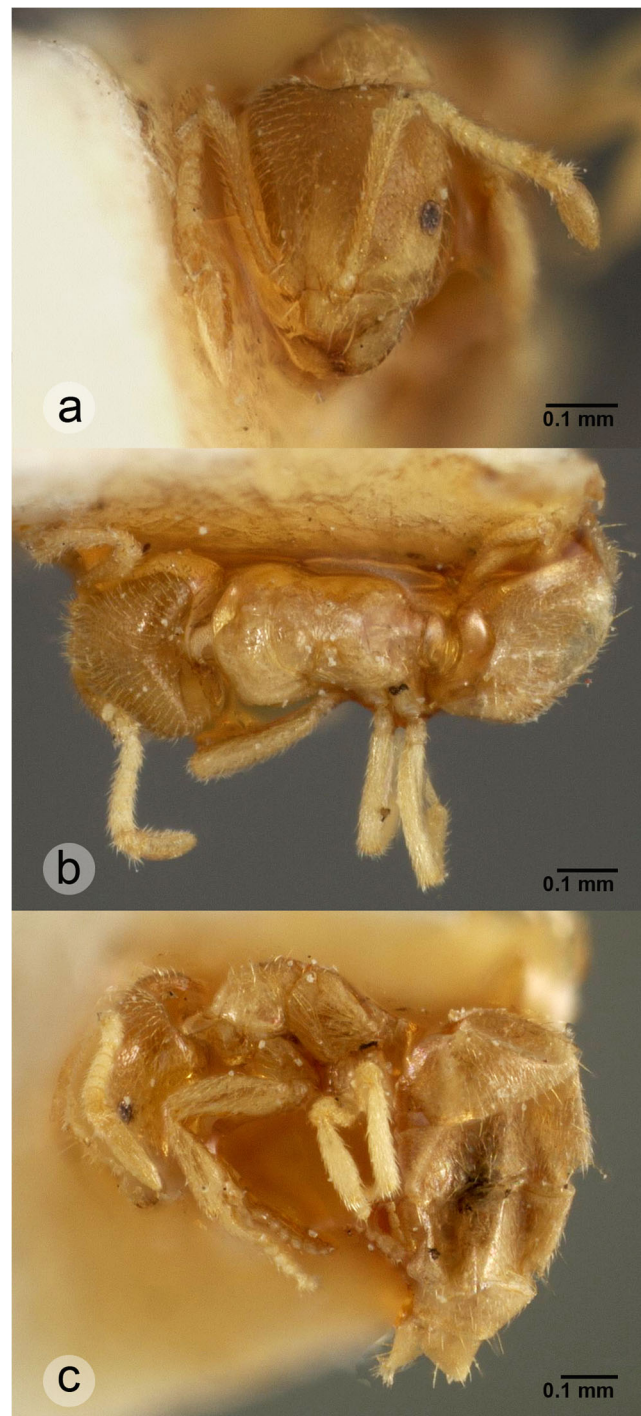


Fig. 28 *Brachymyrmex donisthorpei*: a–c head, dorsal, and lateral view of the lectotype worker

*Lectotype and paralectotype measurements* (mm) ( $n = 2$ ). HL<sub>1</sub> 0.39–0.41; HL<sub>2</sub> 0.25–0.27; HL<sub>3</sub> 0.08; HW 0.33–0.35; SL 0.27–0.29; EL 0.05; WL 0.39; PnL 0.10; PnW 0.27–0.29; ML 0.10; MW 0.20; *Indices* CI 85.00–85.71; SI<sub>1</sub> 82.35–83.33; SI<sub>2</sub> 107.14–107.69; OI<sub>1</sub> 13.89–14.71; OI<sub>2</sub> 19.05–20.00.

*Additional material examined measurements* (mm) ( $n = 4$ ). HL<sub>1</sub> 0.32–0.38; HL<sub>2</sub> 0.22–0.29; HL<sub>3</sub> 0.07–0.09; HW 0.26–



0.33; SL 0.24–0.29; EL 0.04; WL 0.27–0.38; PnL 0.11–0.12; PnW 0.20–0.23; ML 0.06–0.09; MW 0.13–0.16; *Indices* CI 80.55–86.05; SI<sub>1</sub> 86.49–96.55; SI<sub>2</sub> 96.97–112.00; OI<sub>1</sub> 13.51–16.67; OI<sub>2</sub> 22.22–23.26.

**Description.** *Head.* Substantially longer than wide in full face view; posterior cephalic margin slightly concave. Clypeus with a rounded anterior margin and five long, erect hairs of which a single, usually conspicuous hair is near the anterior margin, two hairs are in mediolateral position, and two more near the toruli; other hairs on the clypeus are markedly shorter and appressed or decumbent. Toruli surpassing the posterior clypeal margin in oblique anterodorsal view. Dorsum of the head has conspicuous appressed pubescence and several suberect hairs. The scapes approximately reach the posterior margin of the head or surpass it by a length smaller than the maximal diameter of the eye, and they have appressed and decumbent hairs. Ocelli absent. The eyes are positioned below the cephalic midline and have only 3–4 ommatidia along their maximal diameter.

*Mesosoma.* With several short appressed and sub-erect hairs. The mesonotum is not inflated and does not bulge dorsally above the pronotum in lateral view. Metanotal groove absent or narrower than the diameter of the metathoracic spiracles. Metathoracic spiracles dorsolateral in position, not protruding, and touching the propodeal suture. Dorsum of the propodeum flat and much shorter than propodeal declivity. Propodeal spiracles circular, small and inconspicuous, positioned on the posterior propodeal margin, slightly posterior of the middle of the propodeal slope. Legs with appressed and sub-erect hairs. Petiole short and inclined forward.

*Gaster.* With appressed dense pubescence and some sub-erect hairs near the edges of the segments.

*Color and sculpture.* Body yellowish, with imbricate sculpture on the dorsum of the mesosoma.

**Distribution** (supplementary material Fig. S17). *Brachymyrmex donisthorpei* is known from Brazil, Colombia, Ecuador and Paraguay.

**Biology.** Unknown.

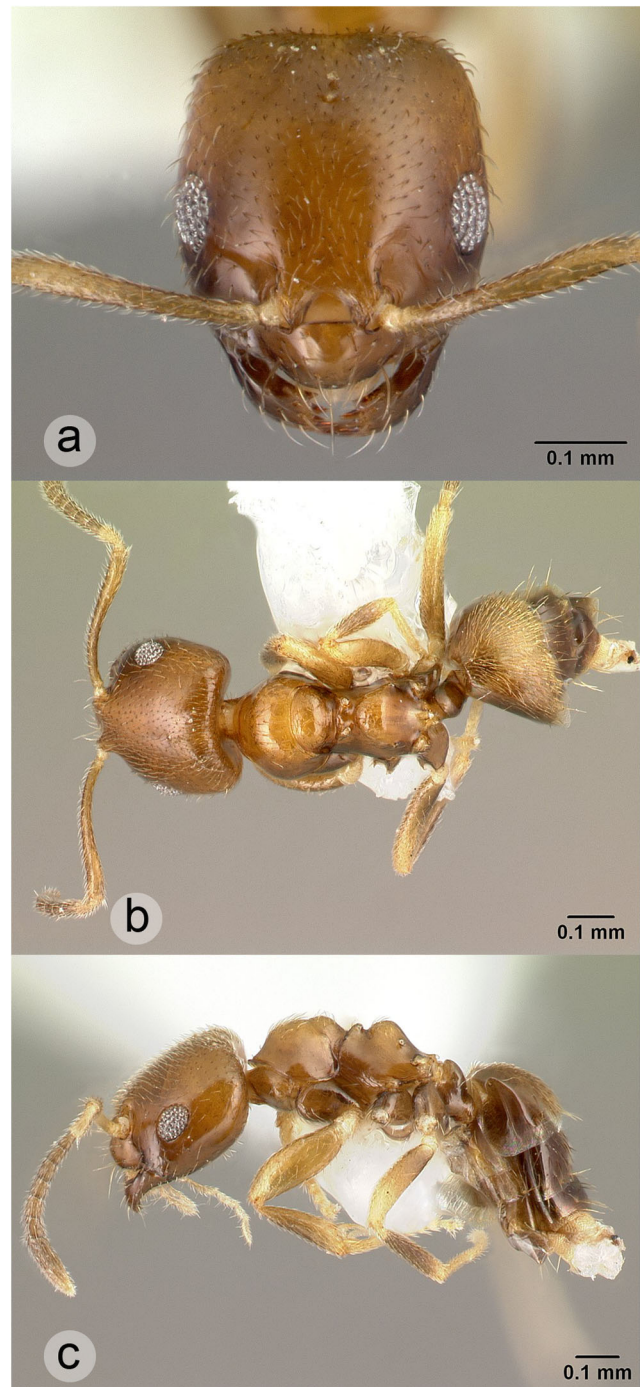
**Remarks.** No specific geographic information is available on the type material beyond Colombia.

*Brachymyrmex feitosa* Ortiz & Fernández

(Fig. 29, supplementary material Fig. S18)

*Brachymyrmex feitosa* Ortiz and Fernández, 2014: 27, Figs. 25, 26, and 27 (w). Holotype worker and paratype workers (MZSP: USNMENT00757694): three workers. **BRAZIL: Rio de Janeiro:** Floresta de Tijuca, D. Federal. 16 Dec. 1959, C.A: Campos Seabra.

**Additional material examined. BRAZIL: Minas Gerais:** Lavras, Ijaci e Perdões, -21.24528 -44.99972, Fragmento, 06 Dec. 2002, M.S. Santos & N.S. Dias, four workers (CPDC: USNMENT00757836, 00759008); **São Paulo:** Piedade, Floresta Atlantica “Theomar,” -23.73846 -47.38957, 16



**Fig. 29** *Brachymyrmex feitosa*: a–c head, dorsal, and lateral view of a worker (from [www.antweb.org](http://www.antweb.org); photographer: Erin Prado)

Nov. 2008, G. Bieber, three workers (ICN: USNMENT00759038); Sete Barras, PE Carlos Botelho, 600 m, -24.20833 -47.97056, 11–15 May 2009, armadilha subterrânea #18, F. Esteves et al., one worker (MZSP: ANTWEB CASENT0217326).

**Diagnosis.** *Brachymyrmex feitosa* resembles *B. brasiliensis* and *B. delabiei* because they all have tumuliform metathoracic spiracles. However, *B. feitosa* differs from *B.*

*brasiliensis* by its entirely smooth and shiny body, that is more brownish, and by the dense yellowish pubescence on the first gastral segment. It differs from *B. delabiei* by the presence of many suberect hairs on the pronotum and mesonotum and its dense yellowish pubescence on the first gastral segment.

**Description.** See Ortiz and Fernández (2014).

*Brachymyrmex fiebrigi* Forel

(Figs. 30 and 31, supplementary material Fig. S19)

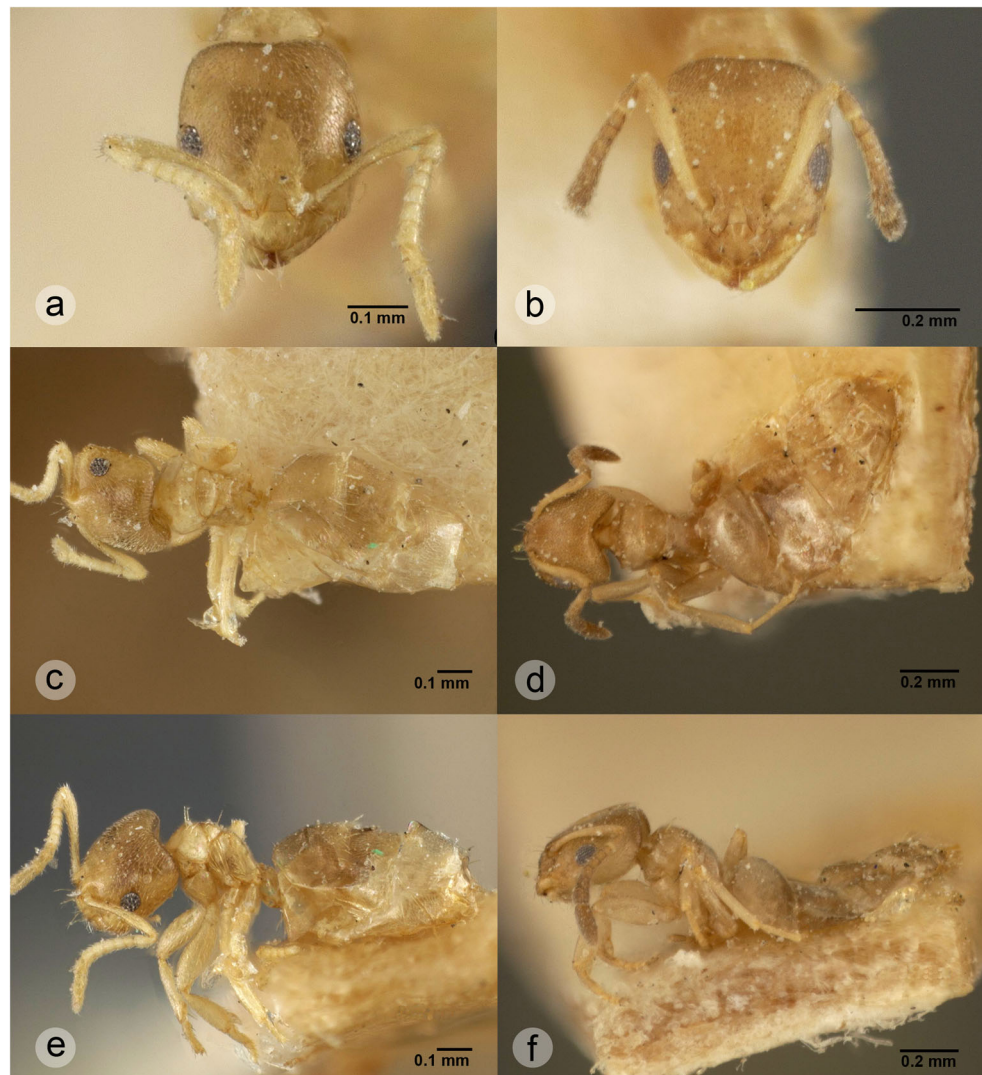
*Brachymyrmex fiebrigi* Forel, 1908: 400 (w.). Lectotype worker (MHNG: USNMENT00757164) and paralectotype workers (MHNG: USNMENT00757164–00757165; here designated): four workers [examined]. **PARAGUAY:** San Bernardino, Fiebrig leg. Santschi (1922: 260) (q.m.). See also: Santschi (1923a: 661).

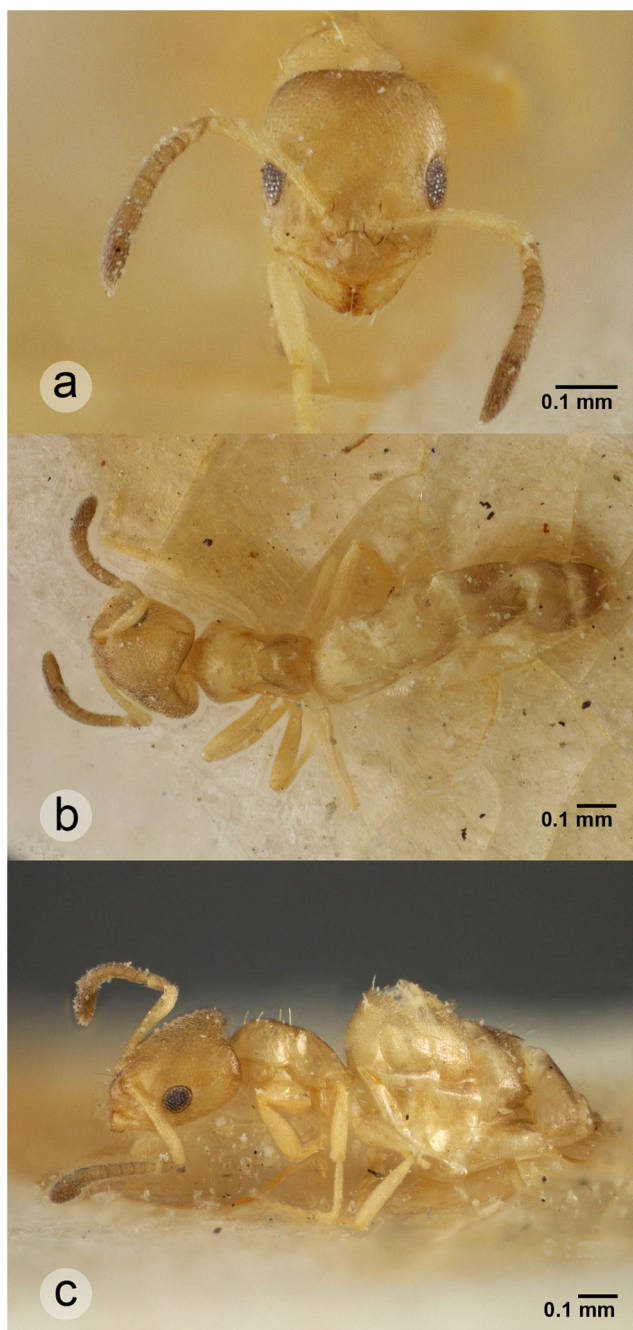
= *Brachymyrmex fiebrigi* var. *funicularis* Santschi, 1922: 260 (w.). (NHMB: USNMENT00757180–007581, 00758094): 22 workers [examined]. **ARGENTINA: Córdoba:** Alta Gracia. n. syn.

= *Brachymyrmex fiebrigi* var. *fumida* Santschi, 1923a: 661 (w.). (MHNB: USNMENT00757704, 00758157): four workers [examined]. **ARGENTINA: Buenos Aires:** Cerro “Ruinas”; (MHNB: USNMENT00758093, NHMG: USNMENT00758153): three workers [examined]. **ARGENTINA: Córdoba:** La Cabana. n. syn.

**Additional material examined. ARGENTINA: Córdoba:** Alta Gracia, Bruchi, two workers (MZUSP: USNMENT00757548). **BRAZIL: Bahia:** Canavieiras, -15.56361 -39.01722, 24 Aug. 1998, J.C.S. Carmo & J.R.M. Santos, one worker (CEPLAC: USNMENT00757962; Esplanada Baixio, -12.11444 -37.69694, June–Oct. 2010, M.L.O. Travassos, #5644, one worker (CEPLAC: USNMENT00757545). **Minas Gerais:** Lavras, 06–122, 002, M.S. Santos, N.S. Dias, two workers (CEPLAC: USNMENT00759008). **São Paulo:** Iguape, EE Jureia-Itatins, Nucleo Rio verde, -24.54417 -47.23556, 05–14 Mar. 2001, A.A. Tavares, one worker (ICN: MZSP158). **COSTA RICA: Heredia:** Cantarrana, 11 km ESE La Virgen,

**Fig. 30** *Brachymyrmex fiebrigi*: **a, c, e** head, dorsal, and lateral view of the lectotype worker; **b, d, f** *B. fiebrigi* var. *fumida* n. syn.: head, dorsal, and lateral view of a syntype worker





**Fig. 31** *Brachymyrmex fiebrigi*: **a–c** *B. fiebrigi* var. *funicularis* n. syn.: head, dorsal, and lateral view of a syntype worker

10.33516 -84.04856, 300 m, 26 Feb. 2007, Marcos-Deimer-Joel, one worker (JTLC: INBIO0003646597); **Limón**: Casa Verde, Tortuguero, 10.58333 -83.51667, 5 m, 24 June 1988, J. Longino #2154, three workers (JTLC: INBIOCRI001280321, 001280326, 001280331); **Puntarenas**: 8 km WNW Potrero grande, 9.03 -85.25, 200 m, 01 Aug. 1985, P.S. Ward #7792, three workers (PSWC: USNMENT00757549); La Pita, rd. To Monteverde 10.16667 -84.91667, 120 m, 13 July 1984, J. Longino, one worker (JTLC: JTLC000005902). **CUBA**: **Viñales**: Pinar del Rio, 14 June 1953, E.O. Wilson #10, two

workers, one male (MCZC: USNMENT00757546). **MEXICO**: **Quintana Roo**: Municipio Leona Vicario, Reserva Ecológica “El Edén,” 21.21667 -87.18333, 03 July 1997, G.M. Daniel, one worker (ICN: USNMENT00757626); **PARAGUAY**: **Boquerón**: Garrapatal, -21.44306 -61.87500, 04–06 Nov. 2001, M. Leponce, one worker (RBIN: Coll.RIScNB SID SPM\_ID14544); Garrapatal, -21.43965 -61.48899, 05–06 Nov. 2001, M. Leponce, one worker (RBIN: Coll.RIScNB SID SPM\_ID25159); Enciso, -21.20 -61.67, 03–06 Nov. 2001, M. Leponce & T. Delsinne #4123–9/3, three workers (ALWC: ANTWEB CASENT0173481); Enciso N.P. (Southern side), -21.19978 -61.66084, 17–18 Sep. 2003, T. Delsinne, one worker (RBIN: Coll.RIScNB SID SPM\_ID31851); Enciso N.P. (Southern side), -21.19978 -61.66084, 04–06 Nov. 2003, M. Leponce, one worker (RBIN: Coll.RIScNB SID SPM\_ID32154); Fortín Mayor Infante Rivarola, -21.67146 -62.41312, 02–06 Nov. 2001, M. Leponce, one worker (RBIN: Coll.RIScNB SID SPM\_ID30618); Mister Long, -20.60386 -62.05053, 05–06 Nov. 2001, M. Leponce, one worker (RBIN: Coll.RIScNB SID SPM\_ID25477); Mister Long, -20.60386 -62.05053, 17–18 Sep. 2003, T. Delsinne, two workers (RBIN: Coll.RIScNB SID SPM\_ID26023, Coll.RIScNB SID SPM\_ID27108); Mister Long, -20.60386 -62.05053, 01–04 Oct 2004, T. Delsinne, one worker (RBIN: Coll.RIScNB SID SPM\_ID30953); Nueva Asunción, -20.68896 -61.92886, 17–18 Sep. 2003, T. Delsinne, one worker (RBIN: Coll.RIScNB SID SPM\_ID27184); **Central**: Capiata, -25.35 -57.42, 22 Feb. 1994, B. Garcete #ibn 197, one worker (ALWC: USNMENT00757544); **Itapúa**: Isla Yacyretá E Melgarejo, -22.42 -56.50, 11 Nov. 1997, B. Barrios #ibn 217, two workers (ALWC: USNMENT00757891). **SURINAME**: Paramaribo, Apr. 1959, I.v.d. Drif, three workers (MZUSP: USNMENT00757547).

**Diagnosis.** *Brachymyrmex fiebrigi* morphologically resembles *B. depilis*, because they both have short scapes that do not or just reach the posterior margin of the head, a gaster with dense pubescence, a yellowish body, and eyes that are positioned on the cephalic midline. *Brachymyrmex fiebrigi* differs from *B. depilis* by its mesosoma, which usually bears several erect hairs, two on the pronotum and two on the mesonotum and by its geographic distribution, which ranges from the South of Mexico until Paraguay, including Cuba.

*Lectotype and paralectotypes measurements* (mm) ( $n = 3$ ). HL<sub>1</sub> 0.35–0.37; HL<sub>2</sub> 0.23; HL<sub>3</sub> 0.08–0.10; HW 0.31; SL 0.25–0.29; EL 0.08–0.10; WL 0.27–0.31; PnL 0.12; PnW 0.20–0.25; ML 0.06; MW 0.16–0.20; *Indices* CI 87.21–88.89; SI<sub>1</sub> 81.25–93.75; SI<sub>2</sub> 108.33–125.00; OI<sub>1</sub> 25.00–31.25; OI<sub>2</sub> 21.05–27.78.

*Additional material examined measurements* (mm) ( $n = 12$ ). HL<sub>1</sub> 0.32–0.46; HL<sub>2</sub> 0.22–0.34; HL<sub>3</sub> 0.07–0.13; HW 0.27–0.41; SL 0.22–0.36; EL 0.08–0.10; WL 0.26–0.40; PnL 0.09–0.14; PnW 0.20–0.28; ML 0.06–0.11; MW 0.15–

0.20; *Indices* CI 75.71–88.46; SI<sub>1</sub> 80.00–93.75; SI<sub>2</sub> 96.77–115.38; OI<sub>1</sub> 21.74–33.33; OI<sub>2</sub> 20.00–28.85.

**Description.** *Head.* Slightly longer than wide in full face view; posterior cephalic margin flat. Dorsum of the head with appressed hairs. Clypeus with a rounded anterior margin and five long, erect hairs of which a single, usually conspicuous hair is near the anterior margin, two hairs are in mediolateral position, and two more near the toruli; other hairs on the clypeus are markedly shorter and appressed or decumbent. Toruli surpassing the posterior clypeal margin in oblique anterodorsal view. The scapes are short, usually approximately reaching the posterior margin of the head, and they bear appressed and decumbent hairs. Ocelli apparently absent. Eyes are positioned on the cephalic midline and have 6–9 ommatidia along their maximal diameter.

*Mesosoma.* Typically with two erect hairs on the pronotum and two on the mesonotum. The mesonotum is not inflated and does not bulge dorsally above the pronotum in lateral view. Metanotal groove absent or narrower than the diameter of the metathoracic spiracles. Metathoracic spiracles dorsolateral in position, not protruding, and touching the propodeal suture. Dorsum of the propodeum flat and much shorter than the posterior slope. Propodeal spiracles circular, small and inconspicuous, positioned on the posterior propodeal margin slightly posterior of the middle of the propodeal slope. Legs with appressed hairs. Petiole short and inclined forward.

*Gaster.* With dense pubescence and scattered suberect hairs at the edges of the segments.

*Color and sculpture.* Body usually smooth, shiny and yellowish.

**Distribution** (supplementary material Fig. S19). *Brachymyrmex fiebrigi* is known from Argentina, Brazil, Costa Rica, Cuba, Mexico, Paraguay, and Suriname.

**Biology.** Some specimens have been collected from below stones (PSWC: USNMENT00757549); Forel (1908) suggested that this species nests in dry branches of bushes.

**Remarks.** The lectotype is the second ant from the top on pin USNMENT00757164, whereas the other specimens on that pin are paralectotypes. Santschi (1922) considered *B. fiebrigi* var. *funicularis* as a variety of *B. fiebrigi* mainly based on its darker-colored funiculus and posterior segments of the gaster, but otherwise the type specimens of this variety are very similar in measurements, head shape, and gastric pubescence compared to the type material of *B. fiebrigi*. Overall, we consider these differences to represent intraspecific variation.

Santschi (1923a) considered *B. fiebrigi* var. *fumida* as a variety that only differs from the typical *B. fiebrigi* by its somewhat darker body color, and the overall light yellowish scapes and tibia. As for *B. fiebrigi* var. *funicularis*, we consider these differences to represent intraspecific variation and both varieties are synonymized here.

*Brachymyrmex flavidulus* (Roger)  
(Supplementary material Fig. S20)

*Plagiolepis flavidula* Roger, 1863: 162 (w.). Lectotype worker (MfNB: 19185: GBIF-D/FoCol2900; GBIF-D/FoCol2910; here designated): one worker [examined]. **CUBA.** Attributed to *Brachymyrmex* by Smith (1955:99).

**Additional material examined.** **COLOMBIA: Valle del Cauca:** Bosque Yotoco, 1575 m, 25 June 1989, W.P. MacKay #11562, two workers (WEMC: USNMENT00757634). **COSTA RICA: Puntarenas:** Monteverde, 10.29564 - 84.79009, 1540 m, 10 Dec. 1987, J. Longino #1975-s, one worker, one queen (JTLC: JTLC0000005251). **JAMAICA:** Trelawny: 5 km N Quick Step, 18.26667 -77.71667, 360 m, A.L. Wild #AW1382, one worker (ALWC: USNMENT00757658).

**Diagnosis.** *Brachymyrmex flavidulus* resembles *B. fiebrigi*, *B. giardi*, and *B. depilis* in that they all have short scapes that approximately reach the posterior margin of the head or surpass it by less than one maximal diameter of the eye, their gaster bears dense pubescence, their eyes are located on the cephalic midline, and their bodies are yellowish. *Brachymyrmex flavidulus* differs from *B. depilis* and *B. giardi* by its mesonotum that does not bulge dorsally above the pronotum in lateral view, and from *B. fiebrigi* by the absence of erect hairs on the pronotum and mesonotum.

**Description.** *Head.* Slightly longer than wide in full face view; posterior cephalic margin slightly convex. Clypeus with a rounded anterior margin and five long, erect hairs of which a single, usually conspicuous hair is near the anterior margin, two hairs are in mediolateral position, and two more near the toruli; other hairs on the clypeus are markedly shorter and appressed or decumbent. Toruli surpassing the posterior clypeal margin in oblique anterodorsal view. The scapes are short and barely reach the posterior margin of the head. Ocelli apparently absent. Eyes are positioned on the cephalic midline and have 7–9 ommatidia along their maximal diameter.

*Mesosoma.* Without erect hairs. The mesonotum does not bulge dorsally above the pronotum in lateral view. Metanotal groove absent. Metathoracic spiracles dorsolateral in position, not protruding, and touching the propodeal suture. Dorsum of the propodeum shorter than posterior slope. Propodeal spiracles circular, positioned on the posterior propodeal margin, slightly posterior of the middle of the propodeal slope. Legs with appressed hairs. Petiole short and inclined forward.

*Gaster.* With dense pubescence.

*Color and sculpture.* Body usually smooth, shiny, and yellowish.

**Distribution** (Supplementary material Fig. S20). This species is known from Colombia, Costa Rica, Cuba, and Jamaica.

**Biology.** Unknown.

**Remarks.** *Brachymyrmex flavidulus* is a problematic species for several reasons. It was described by Roger (1863) as a species of *Plagiolepis*. Smith (1955) transferred it to

*Brachymyrmex*, seemingly based in geographic reasons, i.e., that *Plagiolepis* is not native to the neotropics. We agree with the attribution to *Brachymyrmex* because the type of *Brachymyrmex flavidulus* has 9 antennal segments, which is a diagnostic trait of *Brachymyrmex*, whereas *Plagiolepis* has 11 antennal segments (Bolton 2003). The type series consist of a single individual of which the mesosoma and gaster are mounted on a pin, and the head is prepared on a microscope slide. This preservation hampers us to document the arrangement of hairs on scapes, head, and clypeus as well as the number of ommatidia in the maximal diameter of the eye.

The worker on pin JTLC0000005251 is unusual in comparison to the other specimens of *B. flavidulus* in having sparser gastral pubescence and somewhat longer scapes. Additional material from Costa Rica would be required to adequately characterize the morphological variation in these populations, and to verify its species attribution.

This species is morphologically very similar to *B. fiebrigi*. *Brachymyrmex flavidulus* lacks the erect hairs on the mesosoma that are present in *B. fiebrigi*, but as the number of specimens available of *B. flavidulus* is very limited we cannot currently comment on the consistency of this difference. An in-depth comparison with *B. fiebrigi* is required when more specimens of *B. flavidulus* become available, especially from Cuba, where both species occur.

*Brachymyrmex gagates* Wheeler

(Fig. 32, supplementary material Fig. S21)

*Brachymyrmex gagates* Wheeler, 1934: 206 (w.). Lectotype worker (USNM: USNMENT00529454) and paralectotype workers (USNM: USNMENT00529454; MCZC: M.C.Z. Cotype 1–321436, M.C.Z. Cotype 4–621436; here designated): nine workers [examined]. **MEXICO: Veracruz:** Mirador, 20 Apr. 1929.

**Additional material examined. PANAMA: Colon:** San Lorenzo Forest, 9.28333 -79.97194, J. Schmidt & J. Bail, fogging, two workers (ICN: USNMENT00759031).

**Diagnosis.** *Brachymyrmex gagates* resembles *B. degener* and *B. gaucho* in morphology, because they all have smooth, shiny, and dark brown or black bodies, scapes that surpass the posterior margin of the head, and a gaster with scarce pubescence. *Brachymyrmex gagates* differs from *B. degener* by its darker body and by having a mesonotum that is almost circular in dorsal view and that does not bulge above the pronotum in lateral view. It differs from *B. gaucho* by having a slightly concave posterior cephalic margin, scapes with decumbent hairs, a second segment of the antennal funiculus that is conspicuously shorter than the first antennal segment, and its almost circular mesonotum in dorsal view that does not bulge above the pronotum in lateral view.

**Lectotype measurements** (mm). HL<sub>1</sub> 0.59; HL<sub>2</sub> 0.39; HL<sub>3</sub> 0.18; HW 0.55; SL 0.51; EL 0.16; WL 0.59; PnL 0.18; PnW



Fig. 32 *Brachymyrmex gagates*: a–c head, dorsal, and lateral view of the lectotype worker

0.39; ML 0.16; MW 0.20; *Indices* CI 93.33; SI<sub>1</sub> 92.86; SI<sub>2</sub> 130.00; OI<sub>1</sub> 28.57; OI<sub>2</sub> 30.00.

**Description.** *Head.* Slightly longer than wide in full face view; posterior cephalic border slightly concave. Dorsum of the head with scattered appressed hairs. Clypeus with a rounded anterior margin and five long, erect hairs of which a single, usually conspicuous hair is near the anterior margin, two hairs

are in mediolateral position, and two more near the toruli; other hairs on the clypeus are markedly shorter and appressed or decumbent. Toruli surpassing the posterior clypeal margin in oblique anterodorsal view. The scapes bear decumbent hairs and surpass the posterior margin of the head by a length smaller than the maximal diameter of the eye. Three ocelli present. Eyes are positioned slightly posteriorly to the cephalic midline and have 10–12 ommatidia along their maximal diameter.

**Mesosoma.** Typically bearing two erect hairs on the pronotum and two on the mesonotum, sometimes with some additional appressed hairs on the dorsum of the mesonotum. The mesonotum is inflated but does not bulge dorsally above the pronotum in lateral view; it is almost circular in dorsal view. Metanotal groove wider than the diameter of the metathoracic spiracles. Metathoracic spiracles in dorsolateral position, protruding slightly, and either just or just not touching the propodeal suture. Dorsum of the propodeum convex and somewhat shorter than the posterior declivity. Propodeal spiracles circular, positioned on the posterior propodeal margin, anterior of the middle of the propodeal slope. Legs have appressed hairs. Petiole short and inclined forward.

**Gaster.** With scattered pubescence and several scattered long erect hairs.

**Color and sculpture.** Head and gaster are smooth and shiny, whereas the dorsum of the mesosoma is slightly imbricate. Body uniformly dark brown, apart from the terminal segments of the tarsus and the hairs, which are lighter.

**Distribution** (Supplementary material Fig. S21). *Brachymyrmex gagates* is known from Mexico and Panama.

**Biology.** The type specimens were collected from an epiphytic bromelia (*Tillandsia streptophylla*) (Wheeler 1934).

**Remarks.** The lectotype is the ant at the top of pin USNM: USNMENT00529454, whereas the others on that pin are paralectotypes. Wheeler (1934) pointed out that *B. gagates* is similar to but nevertheless different from *B. incisus* (which is here synonymized to *B. degener*) of which he had specimens from Panama in his collection. He reported that *B. gagates* has a wider head, a much more prominent mesonotum, a more distinct and impressed promesonotal suture, longer funicular joints, and darker body color. We are uncertain as to what he exactly implied about the promesonotal suture, because it is very distinctive in all *Brachymyrmex* species, and the mesonotum bulges dorsally above the pronotum in lateral view in *B. degener*, whereas it does not in *B. gagates* (see diagnosis). We agree that generally *B. incisus* (and thus *B. degener*) generally have much lighter body color than *B. gagates*, but as mentioned in the remarks of *B. degener* and *B. coactus* the variation in body color in these species requires more detailed documentation.

*Brachymyrmex gaucho* Santschi

(Fig. 33, supplementary material Fig. S22)

*Brachymyrmex gaucho* Santschi, 1917: 283 (w.). (NHMB) [examined, but the type is severely damaged].

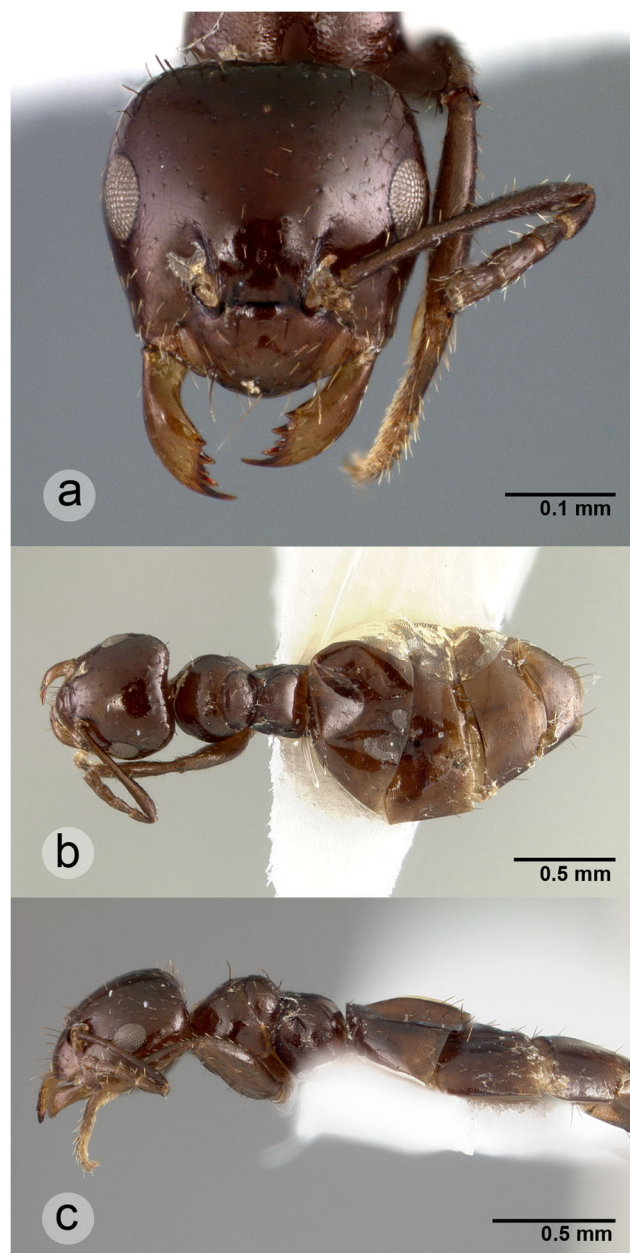


Fig. 33 *Brachymyrmex gaucho*: a–c head, dorsal, and lateral view of a worker

**ARGENTINA: Córdoba:** Unquillo, M. Birabén. Combination in *Brachymyrmex* (*Bryscha*) by Santschi (1923a: 674). See also: Quirán (2005: 767).

**Diagnosis.** *Brachymyrmex gaucho* is morphologically similar to *B. antennatus* because both have legs and antennae with erect hairs and a second segment of the antennal funiculus that is as long as or longer than the first. However, *B. gaucho* differs from *B. antennatus* by having a flat posterior cephalic margin, a dark brown body, erect hairs on the scape, and the dorsum of the head, a mesonotum that bulges dorsally above the pronotum, and a gaster with scarce pubescence.

**Description.** *Head.* Almost equally wide as long in full face view; the posterior cephalic margin is flat and the posterior side of the head is wider than the anterior side. Dorsum of the head bears scattered erect hairs. Clypeus with a rounded anterior margin and five long, erect hairs of which a single, usually conspicuous hair is near the anterior margin, two hairs are in mediolateral position, and two more near the toruli; other hairs on the clypeus are clearly shorter and decumbent. Toruli surpassing the posterior clypeal margin in oblique anterodorsal view. The scapes surpass the posterior cephalic margin by a length smaller than 1.5× the maximal diameter of the eye and have erect hairs. The second segment of the antennal funiculus is as long as or longer than the first. Three ocelli are present. Eyes are positioned on the cephalic midline and have 13–14 ommatidia along their maximal diameter.

*Mesosoma.* With several thin, erect hairs. The mesonotum is inflated, anteroposteriorly inclined and bulges dorsally above the pronotum in lateral view. Metanotal groove usually absent, but when present narrower than the diameter of the metathoracic spiracles. Metathoracic spiracles in dorsolateral position, slightly protruding, and near the propodeal suture. Dorsum of the propodeum flat and equal in length to the propodeal slope. Propodeal spiracles circular, positioned just dorsally of the posterior propodeal margin and slightly posterior of the middle of the propodeal slope. Legs have suberect and erect hairs. Petiole short and inclined forward.

*Gaster.* With scattered pubescence and several scattered long erect hairs.

*Color and sculpture.* Head and gaster are smooth and shiny, whereas the dorsum of the mesosoma is imbricate. Body uniformly dark brown.

**Distribution** (Supplementary material Fig. S22). *Brachymyrmex gaucho* is currently only known from Argentina.

**Biology.** Unknown.

**Remarks.** The type specimen in the NHMB is damaged but Quirán deposited three workers belonging to this species from Argentina, Córdoba II-2001, E. Quirán, leg. at the NHMB, which we also examined. These specimens come from the same state as the type material, but they are no types. We studied these specimens, one of which is illustrated in Fig. 33. More type material would exist at the MACN (5 workers) and the MLP (1 worker) (Quirán 2005), but it is not studied here.

*Brachymyrmex giardi* Emery

(Fig. 34, supplementary material Fig. S23)

*Brachymyrmex giardi* Emery, 1895: 215 (w.q.). Lectotype worker (MSNG: USNMENT00757220) and paralectotype workers, putative worker-queen intercaste, queen, male (MSNG: USNMENT00757218–00757220, MHNG: USNMENT00758105–00758109; here designated): six

workers, nine putative worker-queen intercastes, one queen, one male [examined]. **CHILE:** Santiago de Chile. Emery (1906: 178) (m.).

= *Brachymyrmex melensis* De Zolessi et al., 1978: 26 (w.q.l.). **URUGUAY: Cerro Largo:** Melo. [not examined]. n. syn.

**Additional material examined.** **CHILE:** Valparaiso, two workers (MCZC: M.C.Z. Cotype22940).

**Diagnosis.** *Brachymyrmex giardi* resembles *B. depilis* and *B. heeri* as these species have a mesonotum that bulges dorsally above the pronotum in lateral view, and a gaster with dense pubescence. Additionally, *B. giardi* and *B. depilis* have bodies without erect hairs; they can be distinguished because *B. giardi* has dense decumbent pubescence on the head and mesosoma, usually a dark brownish body, and it is geographically restricted to Chile and Uruguay. Furthermore, *B. giardi* differs from *B. heeri* by having short scapes, and no erect hairs on the pronotum or mesonotum.

*Lectotype and paralectotype measurements* (mm) ( $n = 8$ ). HL<sub>1</sub> 0.45–0.68; HL<sub>2</sub> 0.29–0.42; HL<sub>3</sub> 0.10–0.32; HW 0.35–0.68; SL 0.33–0.59; EL 0.10–0.18; WL 0.39–0.89; PnL 0.10–0.21; PnW 0.25–0.57; ML 0.08–0.35; MW 0.16–0.52; *Indices* CI 78.26–105.00; SL<sub>1</sub> 84.85–100.00; SL<sub>2</sub> 113.33–142.86; OI<sub>1</sub> 23.53–33.33; OI<sub>2</sub> 21.74–50.00.

**Worker description.** *Head.* Slightly longer than wide in full face view; posterior cephalic margin is flat. Dorsum of the head has dense appressed hairs. Clypeus with a rounded anterior margin and five long, erect hairs of which a single, usually conspicuous hair is near the anterior margin, two hairs are in mediolateral position, and two more near the toruli; other hairs on the clypeus are clearly shorter and appressed or decumbent. Toruli surpassing the posterior clypeal margin in oblique anterodorsal oblique view. The scapes surpass the posterior cephalic margin by a length smaller than the maximal diameter of the eye and have decumbent hairs. Three ocelli appear to be present. Eyes are positioned on the cephalic midline and have 7–9 ommatidia along their maximal diameter.

*Mesosoma.* Without erect hairs. The mesonotum is inflated and bulges dorsally above the pronotum in lateral view. Metanotal groove usually absent, or narrower than the diameter of the metathoracic spiracles. Metathoracic spiracles in dorsolateral position, not protruding, and touching the propodeal suture. Dorsum of the propodeum slightly convex and shorter than the posterior propodeal margin. Propodeal spiracles circular, positioned on the posterior propodeal margin slightly posterior of the middle of the propodeal slope. Legs with appressed hairs. Petiole short and inclined forward.

*Gaster.* With dense pubescence and scattered long erect hairs along the edges of the segments. Some specimens have the same morphology as a regular worker as to the head and mesosoma, but have a gaster that is somewhat expanded, i.e., they are somewhat physogastric.

**Fig. 34** *Brachymyrmex giardi*: **a**, **c**, **e** head, dorsal, and lateral view of the lectotype worker; **b**, **d**, **f** head, dorsal, and lateral view of a putative worker-queen intercaste



**Color and sculpture.** Body smooth and shiny, usually dark brownish with yellowish legs and pubescence.

**Intercaste description.** The morphology of the putative worker-queen intercaste differs from that of the worker by its larger size, the eyes that have around nine ommatidia along their maximal diameter, the pronotum that bears several semi-erect hairs, the enlarged mesonotum that does not bulge dorsally above the pronotum in lateral view, and that does not bear erect but several subdecumbent hairs, the sharper posterior ending of the mesonotum in dorsal view, the deep metanotal groove that is wider than the metathoracic spiracles, the almost laterally positioned metathoracic spiracles, that do not protrude and do not touch any suture, and the uniform yellowish body color (albeit with lighter-colored legs).

**Distribution** (Supplementary material Fig. S23). *Brachymyrmex giardi* is known to occur in Chile and Uruguay.

**Biology.** The biology of *B. giardi* has not recently been studied; however, Emery (1895) indicated that Prof. Giard

observed an association between *B. giardi* and the coccid *Margadores vitium*. As to the biology of *B. melensis*, which we synonymize here with *B. giardi*, De Zolessi et al. (1978: 39) provided detailed habitat information including specifications on the landscape, soil and vegetation. Their nest was subterranean, with several chambers between 15 and 50 cm deep, each chamber being about 3 cm high and 3 to 5 cm long and wide. Some repletes were found hanging from the roof together with normal workers as is observed in *Mymecocystus hortideorum*.

**Remarks.** The second ant from the top in pin MSNG: USNMENT00757220 is designated here as lectotype, whereas the other specimens are paralectotypes. In the original description of *B. giardi*, Emery (1895: 215) described a worker, a replete, and a queen, and the replete is what we consider here as a putative worker-queen intercaste, because a regular queen was also reported by Emery (1895). Note that this queen was indicated to be wingless; however, after studying the material, we confirm that it represents a real queen rather than an



ergatoid, and the replete has, as mentioned above, a hybrid morphology between queen and worker. Upon dissection of the abdomen of the replete, Emery (1895: 215) reported that the crop is full of honey-like liquid, but also that the ovaries are more developed than in normal workers, and that these repletes likely have a reproductive function. Nevertheless, he considered nourishment their primary function, as is confirmed by De Zolessi et al. (1978). In summary, the exact affinity of these repletes is uncertain: if it were ergatoid queens we would not expect a regular queen to be present (Peeters 1991), which points to an intercaste, because intercastes co-exist with a regular queen. However, intercastes do not usually participate in reproduction (Peeters 1991). Given all the available data, we consider these specimens for now to be a putative worker-queen intercaste, as mentioned before, but the intriguing issue of the repletes in *B. giardi* requires further study.

We have not been able to locate the type material of *B. melensis* and have therefore studied it from the detailed work of De Zolessi et al. (1978). These authors subdivided the putative worker-queen intercaste into two categories: the first for specimens that resemble normal workers but have the gaster somewhat expanded, and the second for the putative intercaste, which displays a strongly enlarged gaster with the ability to store liquids. De Zolessi et al. (1978) indicate that *B. melensis* resembles *B. physogaster* Kusnezov (1960) most, a species here synonymized to *B. heeri*, but that both differ in size and in the number of ocelli (see additional differences in the diagnosis above). These authors did not compare *B. melensis* and *B. giardi*, but upon doing so we did not find any trait that allows distinguishing these taxa and hence we synonymize *B. melensis* here. *Brachymyrmex giardi* and *B. heeri* are indeed quite similar, not in the least by the presence of a putative worker-queen intercaste, and further in-depth study of both species is required.

*Brachymyrmex giardi* var. *nitida* was previously suggested to be a junior synonym of *B. giardi* (Snelling and Hunt 1975), but in our opinion, it is a junior synonym of *B. bruchi* (see above). *Brachymyrmex giardi* var. *cordobensis* on the other hand appears to be a junior synonym of *B. heeri* (see below).

*Brachymyrmex heeri* Forel

(Figs. 35 and 36, supplementary material Fig. S24)

*Brachymyrmex heeri* Forel, 1874: 91, Figs. 16 and 20 (w.). Lectotype worker (MHNG: USNMENT00757169) and paralectotype workers, males, queen (MHNG: USNMENT00757167–00757171, USNMENT00758116–00758120); here designated): 15 workers, three males, one queen [examined]. **SWITZERLAND: Zurich:** Serra des orchidiées. Forel (1876: 52) (q.m.). See also: Santschi (1923a: 664).

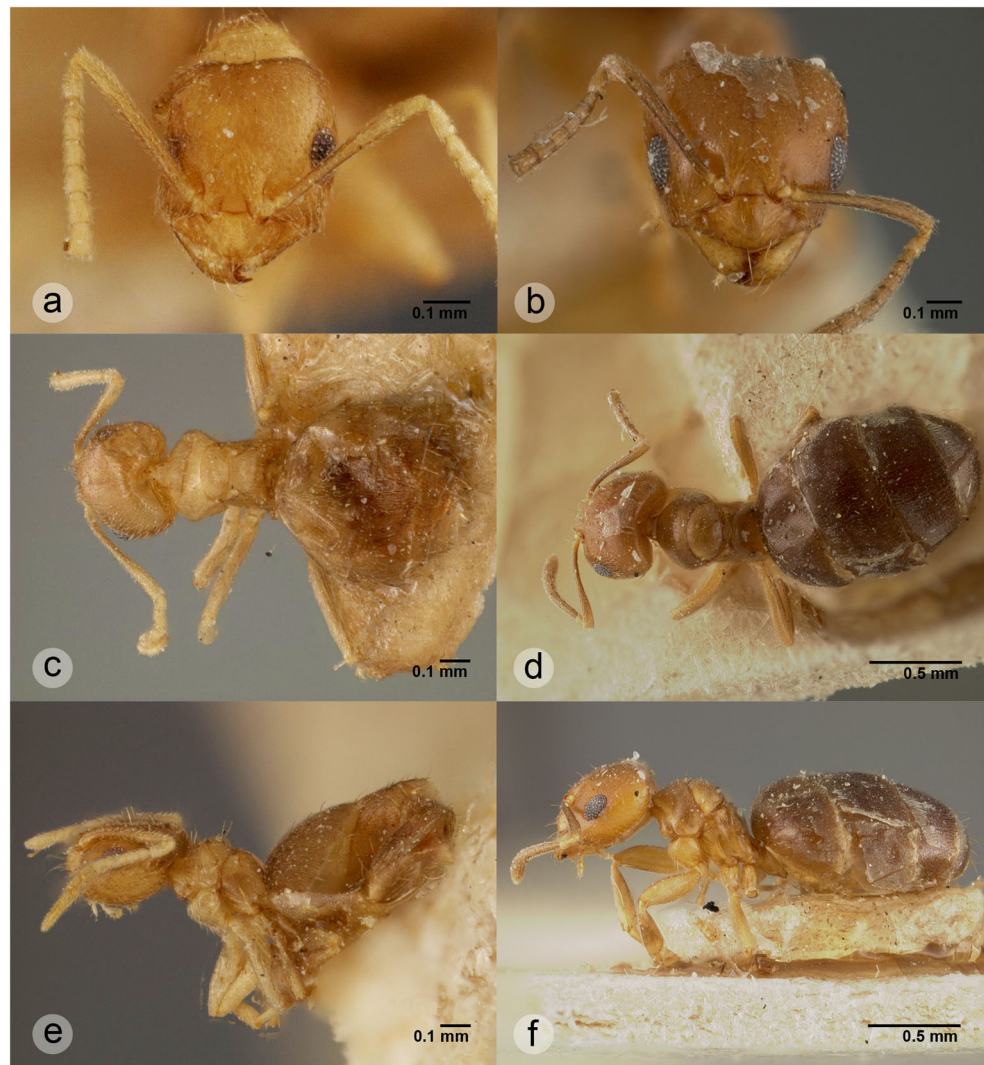
= *Brachymyrmex goeldii* Forel, 1912a: 65 (w.). (MHNG: USNMENT00757166): one worker [examined]. **BRAZIL: São Paulo:** Botucatu. n. syn.

= *Brachymyrmex giardi* var. *cordobensis* Santschi, 1929: 309 (w.). (NHMB: USNMENT00757698, 00757699, CASENT0911600): 23 workers [examined]. **ARGENTINA: Cordoba:** Alta Gracia. n. syn.

= *Brachymyrmex physogaster* Kusnezov, 1960: 382, Figs. 1, 2, 3, and 4 (w.). (INSUE): seven workers [examined]. **ARGENTINA: Salta:** National park Estancia El Rey. n. syn.

**Additional material examined. ARGENTINA: Misiones:** Loreto, C. Bruch, one worker (NHMB: USNMENT00758095). **BOLIVIA: Santa Cruz:** 10 km NW Terevinto, -17.67 -63.45, 380 m, 09 Dec. 1993, P.S. Ward #12314–61, two workers (MCZC: USNMENT00757940); Buena Vista, -17.45 -63.67, 350 m, 18 Dec. 1993, P.S. Ward #12438–79, three workers (PSWC: USNMENT00757745); Las Gamas, Parque Nacional Noel Kempff Mercado, -14.80 -60.38, 700 m, 04 Dec. 1993, six workers (PSWC: USNMENT00757941, 00758024). **BRAZIL: Goiás:** Campo Limpo, faz conceição, -16.33083 -49.16367, 01–07 July 2005, R.R. Silva & R.M. Feitosa, eight workers (ICN: MZSP120, 121); **Minas Gerais:** Serra Caraça, 1380 m, Oct. 1961, Martins & Silva, two workers, three putative worker-queen intercastes (MZSP: USNMENT00757603); Serra Caraca, Kloss, Lenko, Nov. 1961, Martins & Silva, three workers, one putative worker-queen intercaste (MCZC: USNMENT00757598); **Pará:** Melgaço, Caixuanã, ECFPn, -1.77803 -51.42694, 27 Nov.–03 Dec. 2001, two workers (MPEG: USNMENT00757592, 00757550); Melgaço, Caixuanã, ECFPn, -1.70661 -51.45909, 25–27 Oct. 2005, Equipe A.Y. Harada, 11 workers (MPEG: AYH057); Melgaço, Caixuanã, ECFPn, -1.75444 -51.52241, 24–26 Jan. 2006, Equipe A.Y. Harada, five workers (MPEG: AYH023); Melgaço, Caixuanã, ECFPn, -1.75444 -51.52241, 28 Oct. 2003, A.Y. Harada, E.P. Fagundes, C.J.M. Ribeiro, C.E.D. Sanhudo, C.A.R. Moura, J.L.P. Souza, C. Renato, eight workers (MPEG: AYH083); **Santa Catarina:** São Bento do Sul, APA Rio Vermelho, -26.36417 -49.27111, 30 Mar.-04 Apr. 2001, R.R. Silva & Everhardt, two workers (ICN: MZSP043); **São Paulo:** Barueri, K. Lenko, four workers, one queen (MZSP: USNMENT00757602); Caraguatubá, Reserva Florestal, 13 July 1965, Exp. Dep. Zool. 3487, four workers, one queen (MZSP: USNMENT00757597); Cunha, PE Serra do Mar, Nucleo Cunha-Indara, -23.25083 -45.00722, 21–22 Apr. 2001, A.A. Tavares & R.R. Silva, 15 workers (ICN: MZSP151). **COLOMBIA: Caldas:** Aranzazu, Vereda Cuatro Esquinas, Finca Tres Esquinas, 5.31870 -75.48947, 1837 m, 06–08 Aug. 2003, L.E. Franco & J. Cruz, two workers (IAvH: IAvH27322); Aranzazu, Vereda La Guaira, Finca Alto Bonito, 5.27883 -75.48461, 2056 m, 25–26 July 2003, L.E. Franco & J. Cruz, one worker (IAvH: IAvH27303); Aranzazu, Vereda Sabana Larga, Finca Las Colinas de Zega, 5.31713 -75.47556, 2000 m, 25–27 July 2003, L.E. Franco & J. Cruz, five

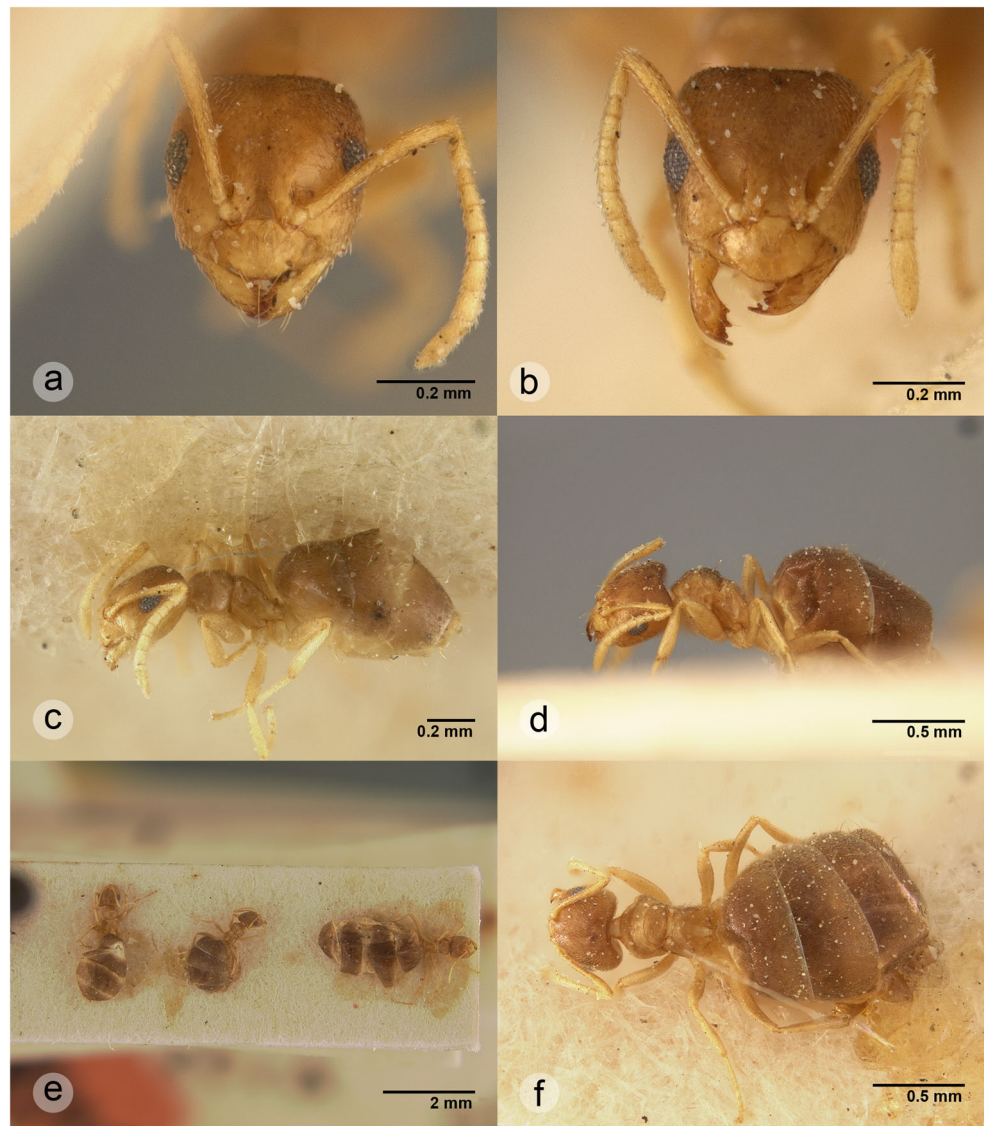
**Fig. 35** *Brachymyrmex heeri*: **a**, **c**, **e** head, dorsal, and lateral view of the lectotype worker; **b**, **d**, **f** *Brachymyrmex* var. *goeldii* n. syn.: head, dorsal, and lateral view of a syntype worker



workers, one queen (IAvH: IAvH25458, 25,459); Salamina, Vereda El Cedrito, Finca El Cedrito, 5.33117 -75.46744, 1960 m, 27–29 Aug. 2002, L.E. Franco & J. Cruz, one worker (IAvH: IAvH25465); **Huila**: 8 km S. Neiva, 20 Mar. 1976, W. & E. MacKay, four workers (WEMC: USNMENT00757948, 00757949); Neiva, 23 Mar. 1976, W. & E. MacKay, four workers, one queen, one male (WEMC: USNMENT00757733, 00757946, 00757947); **Nariño**: Altaquer, Barro Nambi, C. Sanda #22, two workers (ICN: USNMENT00757633); **Quindío**: Calarcá, Vereda Pradera Baja, Finca La Holanda, 4.55694 -75.63917, 1575 m, 29 Nov. 1999, E. Gonzalez & J. Sossa, one worker (IAvH: IAvH-E74153); Calarcá, Vereda Santo Domingo, Finca Santa Librada, 4.55694 -75.63917, 1575 m, 16 Mar. 2000, J. Sossa, one worker (IAvH: IAvH-E74154); Filandia, Vereda Cruces, Finca Pavas, 4.70422 -76.63250, 1900 m, 04–06 June 2002, E. Jimenez & M.F. Reina, two workers (IAvH: IAvH27228); Génova, Vereda El Cedral, Finca Buenos Aires, 4.235 -75.77556, 1600 m, 26 Oct. 1999, E. Gonzalez

& J. Sossa, two workers (IAvH: IAvH-E74166, 74,167); **Risaralda**: Apia, La María, Cafetal de sol (S-III), 3.13 -75.95, 1405 m, 28 Jan. 2002, L. Rivera, one worker (IAvH: IAvH-E74175); Pereira, Vereda La Suiza, SFF Otún Quimbaya, 4.72800 -75.57744, 1900 m, 24–26 Nov. 2002, M. Reina & L.E. Franco, two workers, one putative worker-queen intercaste (IAvH: IAvH27279); Pereira, Vereda La Suiza, Finca Pez Fresco, 1890 m, 22–24 Nov. 2002, E. Jimenez & M.F. Reina, one worker (IAvH: IAvH27285); **Valle del Cauca**: Cairo, Vereda Llano Grande, Finca Encanto, 4.73603 -76.21698, 1650 m, 03 Apr. 2003, J. Henao, one worker (IAvH: IAvH25147); Medio Calima Campamento DR., C.H.M. Aldana, one worker (ICN: USNMENT00757551). **COSTA RICA**: **Guanacaste**: Cerro Cacao, 10.92682 -85.46823, 1100 m, 09 Feb. 1989, J. Longino #2342, one worker (INBIOCRI001280503); **Heredia**: 16 km N Vol. Barba, 10.283 -84.083, 950 m, 12 July 1986, J. Longino #1367, one worker, one queen (JTLC: JTLC000005274); 16 km SSE La Virgen, 10.26871

**Fig. 36** *Brachymyrmex heeri*: **a**, **c**, **e** *B. giardi* var. *cordobensis*: head, dorsal, and lateral view of a syntype worker; **b**, **d**, **f** head, dorsal, and lateral view of a syntype of the putative worker-queen intercaste



-84.08572, 1100 m, 09 Mar. 2001, one worker (JTLC: INBIO0003205132); coffee farms vic. Heredia, 1100 m, 01 July 1991, I. Perfecto, one worker (JTLC: LACM ENT 139924); **Puntarenas**: Monteverde, 10.3 -84.8, 1500 m, 17 May 2001, S. Yanoviak & J. Gering, one worker, one queen (JTLC: JTLC000002089, JTLC000002253); Monteverde, 10.301 -84.806, 1500 m, 14 July 1984, J. Longino 1556, one worker, one queen (JTLC: JTLC000005268); 3 km SE Monteverde, 10.283 -84.783, 1200 m, 02 Mar. 1994, J. Longino #3578-s, one worker (JTLC: INBIO CRI001282749); 4 km S San Vito, 8.783 -82.967, 1200 m, 30 June 1995, J. Longino #3702-s, one worker (JTLC: INBIOCRI001280752); Sirena, Parque Nacional Corcovado, 8.467 -83.583, 0–100 m, 23 Sep. 1982, J. Longino, one worker (JTLC: JTLC000005266); **ECUADOR**: 3.2–13 km N of Puyo, Napo, Pastaza, 953 m, 09 Feb. 1955, R.I. Schlinger & E.S. Ross, ANTC10200, one worker (CASENT:

CASENT0196022); **Pichincha**: Maquipucuna, 5 km ESE Nanegal, 0.116 -78.633, 1500 m, 17 Aug. 1991, P.S. Ward #11503–19, two workers, one queen (PSWC: USNMENT00757596); **Zamora-Chinchipe**: Copalinga, -4.09122 -78.96069, 1000 m, 01–03 Oct. 2009, Delsinne & Arias. **FRENCH GUIANA**: Basse Vie (Petit Saut), Aug. 1999, S. Dorou, three workers, two males (CPDC: USNMENT00757952). **GUATEMALA**: El Progreso, 20 km N Estancia de la Virgen, 1800–1900 m, 08 June 1991, R.S. Anderson, one worker (JTLC: CASENT0601427); Sololá, 1 km N San Andrés, Semetabaj, 14.75 -91.13, 1840 m, 16 Nov. 2003, A.L. Wild #AW2059, A.L. Wild #AW 2059, three workers (ALWC: USNMENT00757942). **MEXICO**: **Chiapas**: 15.1 km N.W. Bochil, 17.09120 -92.99138, 1930 m, 24 Sep. 1992, R.S. Anderson, one worker (JTLC: CASENT0603200); 29 km E La Trinitaria, 16.106 -91.772, 1520 m, 21 July 2007, J.

Longino #6100, one worker (JTLC: JTLC000010323); 3.8 km ESE Custepec, 15.71205 -92.93387, 1900 m, 18 July 2007, J. Longino #6072-2, two workers, one queen, one male (JTLC: JTLC000010342, 000010343); **Jalisco:** 6.76 km SW Mazamitla, 19.89222 -103.07722, 1997 m, 22 June 2000, W. & E. MacKay, one worker, one male (WEMC: USNMENT00757739); **Nuevo León:** Monterrey, Mesa de Chipinque, 1365 m, 16–18 July 1965, two workers, one queen (MCZC: USNMENT00757666); **Veracruz:** 2.7 km N Teocelo, 1128 m, 22–24 July 1973, A. Newton, two workers (WEMC: USNMENT00757945, 00757607); Km 38 on Fortin-Huatusco road, Cornell University, 1965, two workers, one queen (MCZC: USNMENT00757954); Las Hamacas, 17 km N Santiago Tuxtla, 26–28 Aug. 1853, E.O. Wilson #357, two workers (MCZC: USNMENT00757951); Los Tuxtlas, 10 km NNW Sontecomapan, 18.58333 -95.08333, 500 m, 21 Mar. 1985, P.S. Ward #7364, one worker; 5.5 km NE Coscomatepec, 05 June 1988, W. MacKay #10844, two workers, one male (PSWC: USNMENT00757950); 5.5 km NE Coscomatepec, 05 June 1988, W. MacKay #10844, two workers, one male (WEMC: USNMENT00757944). **NICARAGUA: Granada:** Mombacho Volcano, 11.93394 -85.97858, 1150 m, 18 July 2003, W. & E. Mackay, two workers, one queen (WEMC: USNMENT00758042). **PANAMA: Canal zone:** 3 km NW Gamboa, 9.13333 -79.71667, 40 m, 10 Dec. 1983, P.S. Ward #6391-14, three workers (PSWC: USNMENT00757542); **Chiriqui:** Parque Nacional Volcan Baru Boquete, 1850 m, 18 June 1995, R. Anderson #17810, one worker (WEMC: USNMENT00757943). **PARAGUAY: Canindeyú:** Reserva Natural Bosque Mbaracayú, Jejuimini, -24.1 -55.5, 24 July 1996, A. Wild #AW0235, two workers, one queen (ALWC: USNMENT00758025); Reserva Natural Bosque Mbaracayú, Jejuimini, -24.1 -55.5, 11 Mar. 1997, A. Wild #AW0477, #AW0478, three workers, one queen (ALWC: USNMENT00757543, 00757955). **VENEZUELA: Aragua:** Parque Nacional Henri Pittier, La Toma, 10.59233 -68.14031, 1169 m, 09–19 Aug. 2008, one worker (ICN: USNMENT00757740); **Lara:** 9 km SE Barbacoas, 9.77 -70.06, 2000 m, 22 Aug. 1987, P.S. Ward #8922, two workers, one queen (PSWC: USNMENT00757953).

**Diagnosis.** *Brachymyrmex heeri* resembles *B. depilis* and *B. giardi* closely, because all three species have a mesonotum that bulges above the pronotum in lateral view, and a gaster with dense pubescence. However, *B. heeri* differs from *B. depilis* and *B. giardi* by having scapes that surpass the posterior margin of the head.

*Lectotype and paralectotypes measurements* (mm) ( $n = 5$ ). HL<sub>1</sub> 0.39–0.43; HL<sub>2</sub> 0.27–0.30; HL<sub>3</sub> 0.10; HW 0.35–0.41; SL 0.37–0.39; EL 0.10–0.11; WL 0.39–0.45; PnL 0.10; PnW 0.25–0.31; ML 0.08–0.12; MW 0.16–0.20; *Indices* CI 90.00–100.00; SI<sub>1</sub> 90.48–111.11; SI<sub>2</sub> 126.67–142.86; OI<sub>1</sub> 23.81–27.78; OI<sub>2</sub> 22.72–25.00.

*Additional material examined measurements* (mm) ( $n = 5$ ). HL<sub>1</sub> 0.41–0.60; HL<sub>2</sub> 0.27–0.39; HL<sub>3</sub> 0.10–0.13; HW 0.40–0.66; SL 0.36–0.52; EL 0.09–0.19; WL 0.35–0.68; PnL 0.11–0.16; PnW 0.27–0.45; ML 0.09–0.21; MW 0.18–0.35; *Indices* CI 93.75–110.81; SI<sub>1</sub> 78.05–93.62; SI<sub>2</sub> 114.29–135.71; OI<sub>1</sub> 21.74–29.27; OI<sub>2</sub> 16.22–28.00.

**Description.** *Head.* Slightly longer than wide in full face view; posterior cephalic margin slightly concave. Clypeus with a rounded anterior margin and five long, erect hairs of which a single, usually conspicuous hair is near the anterior margin, two hairs are in mediolateral position, and two more near the toruli; other hairs on the clypeus are markedly shorter and appressed or decumbent. Toruli surpassing the posterior clypeal margin in oblique anterodorsal view. The scapes surpass the posterior margin of the head by a length smaller than the maximal diameter of the eye; they bear decumbent hairs. Ocelli absent. Eyes are positioned on the cephalic midline and have 6–7 ommatidia along their maximal diameter.

*Mesosoma.* With several decumbent hairs and usually two erect hairs on the pronotum and two on the mesonotum, but sometimes those on the mesonotum or on both are absent. The mesonotum is inflated and bulges dorsally above the pronotum in lateral view. Metanotal groove absent or narrower than the diameter of the metanotal spiracles. Metathoracic spiracles in dorsolateral position, not protruding, and touching the propodeal suture. Dorsum of the propodeum convex and shorter than the propodeal slope. Propodeal spiracles circular, positioned on the posterior propodeal margin, slightly posterior of the middle of the propodeal slope. Legs with appressed hairs. Petiole short and inclined forward.

*Gaster.* With dense pubescence and scattered long erect hairs at the edges of the segments. Some specimens of *B. heeri* resemble the regular worker in head and mesosoma, but they have a strongly expanded gaster (physogastry).

*Color and sculpture.* Head and gaster smooth, dorsum of the mesosoma with imbricate sculpture, body opaque and yellowish, sometimes with a somewhat darker gaster.

**Distribution** (Supplementary material Fig. S24). We have studied *B. heeri* from localities in Argentina, Bolivia, Brazil, Colombia, Costa Rica, Ecuador, French Guiana, Guatemala, Mexico, Nicaragua, Panama, Paraguay, Uruguay, Venezuela, and from populations that were introduced in Switzerland. Santschi (1923a) also reported this species from Puerto Rico, Jamaica, Haiti, and Guyana, but we have not studied this material.

**Biology.** *Brachymyrmex heeri* was originally described from specimens collected in a tropical orchid greenhouse in Switzerland (Forel 1874). The species was found climbing on various plants, and was associated with aphids, but the nest was not located. Santschi (1929) reported that the nest of the type specimens of *B. giardi* var. *cordobensis* was found at the base of a tree, and *B. physogaster* was collected in the heavily

humic, finely loamy soil in the shadow of trees, where both excessive moisture and eventual drought are unlikely (Kusnezov 1960).

**Remarks.** The lectotype is designated here as the ant in the middle of their holder MHNG: USNMENT00757169, whereas the other specimens are paralectotypes. Forel (1874) described the worker of *B. heeri*, but did not indicate physogastry in his description, and Santschi (1923a) did not comment on this issue neither. In the description of *B. giardi* var. *cordobensis* (which is here synonymized under *B. heeri*) Santschi (1929) referred to physogastric specimens, and also to “worker-queens” with a strongly expanded gaster. He does not provide any additional description of these worker-queen specimens, but upon examination of this material and other samples of *B. heeri*, we exclusively found worker-like specimens with a normal or robust mesosoma and an expanded gaster. These specimens do not have morphological features reminiscent of a queen, but rather differ from regular workers by having a larger body size, a subquadrate head, with the posterior cephalic margin slightly concave to almost flat, scapes that barely reach the posterior margin of the head, three ocelli, eyes that have approximately 11 ommatidia along their maximal diameter, a deep metanotal groove that is wider than the diameter of the metathoracic spiracles, and as already mentioned, a strongly expanded gaster. To exclude the possibility that the museum samples we studied reflect a mixture of two species, we sequenced specimens of both morphs, and found them to be genetically very similar. In summary, *B. heeri* either has dimorphic workers, or a putative worker-queen intercaste, and whereas we consider the first scenario more likely (because we did not find specimens with a hybrid worker-queen morphology), the issue requires more study. These observations also apply to *B. physogaster*, and this species and *B. giardi* var. *cordobensis* are synonymized here with *B. heeri* because they contain all its morphological features. Forel (1912a) distinguished *B. goeldii* from other *Brachymyrmex* species principally based on the form of the head, and he mainly compared it with *B. bruchi*; however, this material appears to belong to a “robust worker” of *B. heeri*. Interestingly, as for *B. heeri* before, Forel (1912a) does not mention physogastry.

Two varieties have been assigned to *B. heeri*, namely *B. heeri* var. *fallax*, and *B. heeri* var. *basalis*. As indicated before, *B. heeri* var. *fallax* is attributed here to *B. aphidicola*, and *B. heeri* var. *basalis* is synonymized under *B. pictus* (see below) here.

It is noteworthy that *B. heeri* has a wide geographic distribution and a study of the morphological variation within the species in a molecular and geographic context would be required. Likewise, it would be interesting to study the biology of the various morphs within a colony, including the underlying developmental processes and their distribution and behavior within the colony. Indeed, some colleagues (Kusnezov 1960) have labeled physogastric specimens here assigned to *B. heeri* as honey pot workers and have observed them hanging from the

ceiling of the chambers of the nest, as in *Myrmecocystus*, and *B. melensis* (see *B. giardi* above). However, why physogastry is present in some *Brachymyrmex* species, but not in others remains unclear. Kusnezov (1960) suggested that it may relate to a trophobiotic lifestyle, whereas others suggested it is an adaptation to periodically arid conditions or food scarcity (Forel 1902; Wheeler 1910). However, Creighton (1950) argued exactly the opposite by suggesting that physogastry may develop when a xerophyte species encounters and adapts to less arid and more resource-rich habitats. Clearly, more work on this issue is required, but as mentioned above, the habitat from which *B. physogaster* was reported by Kusnezov (1960) does not appear to confirm the “scarcity hypothesis.” This future work should perhaps also consider potential intrinsic causes of physogastry beyond the putative environmental drivers discussed above.

#### *Brachymyrmex iridescens* NEW SPECIES

(Fig. 37, supplementary material Fig. S25)

Holotype worker (MZSP: USNMENT00757758) and paratype workers (MZSP: USNMENT00757757): five workers. **BRAZIL: Santa Catharina:** Chapecó, July 1960, F. Plaumann 9878.

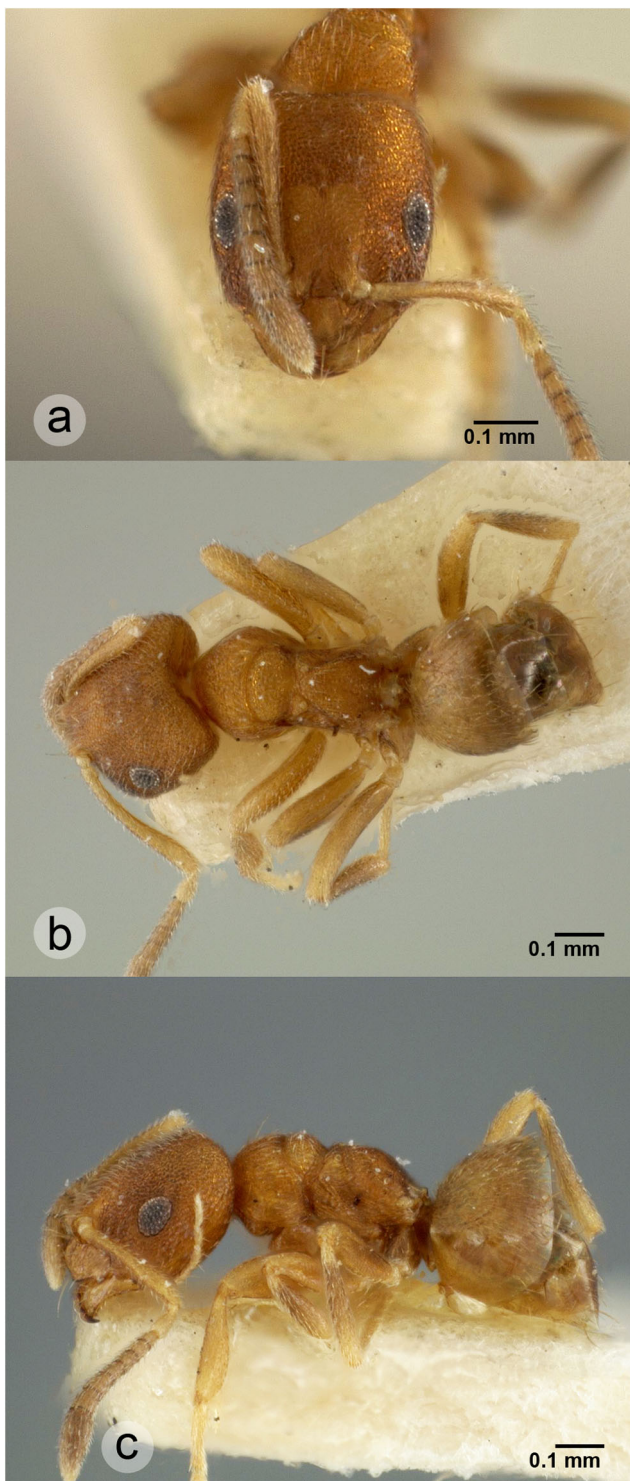
**Additional material examined. ARGENTINA: Misiones:** Parque Nacional Iguazú, -25.71847 -54.43319, 23 Sep. 1999, Leponce, Roisin & Theunis, one worker (MACN: MACN\_En 18283, MACN\_En 18201, MACN\_En 18,242); Parque Nacional Iguazú, one worker (RBINS: Coll. RIScNB SID SPM\_ID01612). **BRAZIL: Parana:** Londrina, Nov. 2004, D.T. Lopes, one worker (CPDC: USNMENT00757755); **Santa Catharina:** Teutônia, June 1961, F. Plaumann, 8219, three workers (MZSP: USNMENT00757756).

**Etymology:** The epithet *iridescens* refers to the conspicuous iridescent appearance of this species under stereoscope illumination.

**Diagnosis.** *Brachymyrmex iridescens* morphologically resembles *B. santschii*, because both have conspicuous, strongly alveolate sculpture on the head and mesosoma. However, they differ from one another because *B. iridescens* has a metanotal groove that is narrower than the diameter of the metathoracic spiracles, scapes that approximately reach the posterior margin of the head, and a gaster with dense pubescence.

**Holotype and paratype measurements** (mm) ( $n = 2$ ). HL<sub>1</sub> 0.40–0.43; HL<sub>2</sub> 0.29–0.30; HL<sub>3</sub> 0.09; HW 0.35–0.37; SL 0.30–0.34; EL 0.09–0.10; WL 0.39–0.40; PnL 0.13; PnW 0.22–0.25; ML 0.09–0.11; MW 0.13–0.16; **Indices** CI 85.42–86.67; SI<sub>1</sub>80.95–82.5; SI<sub>2</sub> 100.00; OI<sub>1</sub> 23.81–25.00; OI<sub>2</sub> 23.81–25.00.

**Additional material examined measurements** (mm) ( $n = 2$ ). HL<sub>1</sub> 0.37–0.42; HL<sub>2</sub> 0.26–0.30; HL<sub>3</sub> 0.07–0.11; HW 0.29–0.38; SL 0.28–0.30; EL 0.09; WL 0.39–0.42; PnL 0.12–0.13; PnW 0.22–0.22; ML 0.09–0.11; MW 0.13–0.18; **Indices** CI



**Fig. 37** *Brachymyrmex iridescens* n. sp.: a–c head, dorsal, and lateral view of the holotype worker

78.57–89.36; SI<sub>1</sub> 80.95–93.94; SI<sub>2</sub> 100.00–106.90; OI<sub>1</sub> 23.81–30.30; OI<sub>2</sub> 19.05–25.53.

**Description.** *Head.* Slightly longer than wide in full face view; posterior cephalic margin slightly concave or flat. Dorsum of the head with decumbent hairs. Clypeus with a

rounded anterior margin and five long, erect hairs of which a single, usually conspicuous hair is near the anterior margin, two hairs are in mediolateral position, and two more near the toruli; other hairs on the clypeus are markedly shorter and appressed or decumbent. Toruli surpassing the posterior clypeal margin in oblique anterodorsal view. The scapes are short and approximately reach the posterior margin of the head; they have decumbent and suberect hairs. Three ocelli are present. Eyes are positioned on the cephalic midline and have 8–9 ommatidia along their maximal diameter.

*Mesosoma.* With several decumbent hairs, and on the pronotum some suberect hairs. The mesonotum is inflated and bulges dorsally above the pronotum. The metanotal groove is narrower than the diameter of the metathoracic spiracles. Metathoracic spiracles dorsal, slightly protruding, and not touching the mesonotal nor propodeal suture. Dorsum of the propodeum slightly convex and shorter than the propodeal slope. Propodeal spiracles circular, positioned on the posterior propodeal margin at the middle of the propodeal slope. Legs with appressed hairs. Petiole short and inclined forward.

*Gaster.* With decumbent, dense pubescence and several scattered long erect hairs.

*Color and sculpture.* Head and thorax finely alveolate, gaster smooth, and shiny. The body is uniformly brownish.

**Distribution** (supplementary material Fig. S25). *Brachymyrmex iridescens* is known from Argentina and Brazil.

**Biology.** Unknown.

**Remarks.** *Brachymyrmex iridescens* resembles *B. santschii*, but their distributions are strongly disjunct: *B. iridescens* is only known from Brazil and Argentina, whereas *B. santschii* from Costa Rica and Panama.

*Brachymyrmex micromegas* Emery

(Fig. 38, supplementary material Fig. S26)

*Brachymyrmex (Brytscha) micromegas* Emery in Santschi, 1923a: 675, Figs. 30 and 32 (w.). Lectotype minor worker (MCSN: USNMENT00757222) and paralectotype minor workers, major workers (MCSN: USNMENT00757222–00757223; MZSP: USNMENT00758145–00758146, 00757825–00757827, 00757830; NHMG: USNMENT00758145–00758146): four major workers, five minor workers [examined]. **BRAZIL: São Paulo:** São Paulo city, Ipiranga. See also: Ortiz and Fernández (2014: 16, Figs. 1, 2, 3, 4, 5, and 6).

**Additional material examined. BRAZIL: São Paulo:** Agudos, 05 Nov. 1967, W. Kempf, one minor worker (MZSP: USNMENT00757830); Anhembi, Faz B. Rico, 14 Feb. 1969, W. Kempf, J.C. Magalhães, L.T.F.M. Kulman, one minor worker (MZSP: USNMENT00757834).

**Diagnosis.** *Brachymyrmex micromegas* morphologically resembles *B. pilipes* because both species have a dimorphic

**Fig. 38** *Brachymyrmex micromegas*: **a, c, e** head, dorsal, and lateral view of the lectotype worker; **b, d, f** head, dorsal, and lateral view of a soldier



worker caste, a clypeus with a row of long thick hairs near the anterior margin, toruli that touch the posterior clypeal margin, but never surpass it in oblique anterodorsal view, and tumuliform metathoracic spiracles. However, *B. micromegas* differs from *B. pilipes* by having a smooth and shiny body, with very fine longitudinal striations restricted to the metapleura.

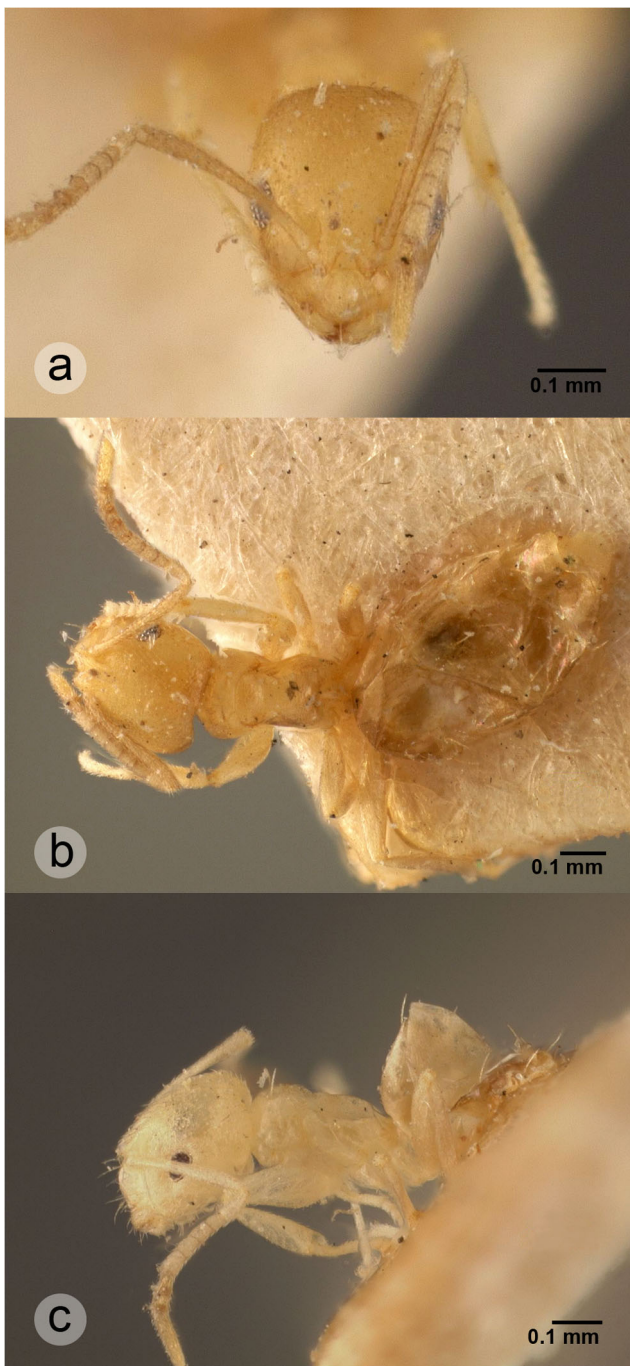
**Description.** See Ortiz and Fernández (2014).

*Brachymyrmex minutus* Forel

(Fig. 39, supplementary material Fig. S27)

*Brachymyrmex minutus* Forel, 1893: 346 (w.q.). Lectotype worker (MHNG: USNMENT00757150) and paralectotype workers, queen (MHNG: USNMENT00757149–00757151; USNMENT00758110–00758112; here designated): 15 workers, one queen [examined]. **ANTILLES:** Saint Vincent. See also: Santschi (1923a: 667).

**Additional material examined. BOLIVIA: Santa Cruz:** Aserradero Moira, -14.57 -61.20, 180 m, 27 Nov. 1993, P.S. Ward #12174–49, three workers (PSWC: USNMENT00757587), three workers (MCZC: USNMENT00757305); 10 km NW Terevinto, -17.67 -63.45, 380 m, 09 Dec. 1993, P.S. Ward #12314–62, #12314–63, two workers (PSWC: USNMENT00757870), five workers (MCZC: USNMENT00757303–00757304); 35 km SSE Flor de Oro, -13.833 -60.867, 450 m, 29 Nov. 1993, P.S. Ward #12199–73, seven workers (MCZC: USNMENT00757301–00757302); Las Gamas, Parque Natural Noel Kempff Mercado, -14.80 -60.38, 700 m, 03 Dec. 1993, P.S. Ward #12266–43, four workers (MCZC: USNMENT00757299–00757300); Las Gamas, Parque Natural Noel Kempff Mercado P, -14.80 -60.38, 700 m, 04 Dec. 1993, P.S. Ward #12266–45, six workers (MCZC: USNMENT00757297–00757298). **BRAZIL: Ceará:**



**Fig. 39** *Brachymyrmex minutus*: **a–c** head, dorsal, and lateral view of the lectotype worker

Guaramiranga (Pq. Tr.), -4.267 -38.933, 900 m, 22 Feb. 2002, Y. Quinet, one worker (CPDC: USNMENT00757874); **Goiás**: Campo Limpo, faz conceição, -16.33083 -49.16367, 20–24 Jan. 2005, R.R. Silva, nine workers (ICN: MZSP071); Campo Limpo, faz conceição, -16.33083 -49.16367, 01–07 July 2005, R.R. Silva & R.M. Feitosa, 15 workers (ICN: MZSP120 - MZSP121); **Pará**: Belem, 07 Aug. 1962, P.F. Doullington. B.F. 14, one worker (MCZC: USNMENT00757256); Melgaço, Caxiuanã ECFPn,

-1.70661 -51.45909, 10–12 Oct. 2006, Equipe A.Y. Harada, one worker (MPEG: AYH018); 10–11 Oct. 2006, one worker (MPEG: AYH019); 10–12 Oct. 2005, seven workers (MPEG: AYH041); 24–26 Jan. 2007, six workers (MPEG: AYH003, 069, 115, 122, 124); 28–30 Jan. 2006, five workers (MPEG: AYH001, 007); 23–25 Apr. 2007, one worker (MPEG: AYH005); A.Y. Harada, E.P. Fagundes, C.J.M. Ribeiro, C.E.D. Sanhudo, C.A.R. Moura, J.L.P. Souza, C. Renato, three workers (MPEG: AYH076); -1.72484 -51.42979, 26 Oct. 2006, A.Y. Harada, E.P. Fagundes, C.J.M. Ribeiro, C.E.D. Sanhudo, C.A.R. Moura, J.L.P. Souza, C. Renato, 45 workers one Queen (MPEG: AYH005, 016, 032, 052, 053, 068, 070, 078, 087, 093, 097, 100, 102, 106, 113, 136); 12–14 Oct. 2006, Equipe A.Y. Harada, one worker (MPEG: AYH045); 20–22 July 2006, two workers (MPEG: AYH095); 20–22 Oct. 2005, two workers (MPEG: AYH082, 105); 21–23 Oct. 2005, one workers (MPEG: AYH006); 22–24 Apr. 2005, two workers (MPEG: AYH082, 105); 23–25 Feb. 2006, one worker (MPEG: AYH033); 24–26 July 2003, 10 workers (MPEG: AYH066, 084, 108, 119, 133, 135); 26–28 Nov. 2003, A.Y. Harada, E.P. Fagundes, C. Renato, one worker (MPEG: AYH117); 07–09 Feb. 2003, one worker (MPEG: AYH060); Melgaço, Caxiuanã ECFPn, -1.73360 -51.51054, 27 Oct. 2003, Equipe A.Y. Harada, three workers (MPEG: AYH014, 061); Melgaço, Caxiuanã ECFPn, -1.73360 -51.51053, 27 Oct. 2003, A.Y. Harada, E.P. Fagundes, C.J.M. Ribeiro, C.E.D. Sanhudo, C.A.R. Moura, J.L.P. Souza, C. Renato, three workers (MPEG: AYH101, 035, 050); 14–16 Oct. 2006, Equipe A.Y. Harada, 15 workers, two queens (MPEG: AYH107, 081, 116); 23–25 July 2006, one worker (MPEG: AYH104); 12–14 Oct. 2006, Equipe A.Y. Harada, three workers (MPEG: AYH051); Melgaço, Caxiuanã ECFPn, -1.73584 -51.48762, 30 Oct. 2003, A.Y. Harada, E.P. Fagundes, C.J.M. Ribeiro, C.E.D. Sanhudo, C.A.R. Moura, J.L.P. Souza, C. Renato, one worker (MPEG: AYH091); 13–15 Oct. 2005, Equipe A.Y. Harada, five workers (MPEG: AYH031, 056); 15–17 Jan. 2006, one worker (MPEG: AYH132); 21 Apr. 2006, one worker (MPEG: AYH080); 22–24 July 2006, one worker (MPEG: AYH121); 23–25 Oct. 2005, three workers (MPEG: AYH017, 027, 030); 23–28 Oct. 2005, one worker (MPEG: AYH022); 25–27 Jan. 2006, one worker (MPEG: AYH128); 26–28 Jan. 2007, two workers (MPEG: AYH075); -1.75444 -51.52241, 28 Jan. 2003, AY Harada, E.P. Fagundes, C.J.M. Ribeiro, C.E.D. Sanhudo, C.A.R. Moura, J.L.P. Souza, C. Renato, one worker (MPEG: AYH011); 28 Oct. 2003, 10 workers (MPEG: AYH028, 079, 089, 092, 118); 01–03 Nov. 2004, Equipe A.Y. Harada, one worker (MPEG: AYH020); 01–05 Nov. 2004, one worker (MPEG: AYH004); 19–21 Oct. 2007, one worker (MPEG: AYH026); 20–22 July 2007, three workers (MPEG: AYH025, 065); 22–24 Oct. 2003, one worker (MPEG: AYH085); 22–24 Oct. 2005, two workers (MPEG:



AYH110, 123); 24–26 Oct. 2006, one worker (MPEG: AYH040); Melgaço, Caxiuana ECFPn, -1.78155 -51.59197, 24–26 Oct. 2007, one worker (MPEG: AYH009); 30 July–01 Aug. 2003, two workers (MPEG: AYH010); 02 Oct. 2006, A.Y. Harada, E.P. Fagundes, C.J.M. Ribeiro, C.E.D. Sanhudo, C.A.R. Moura, J.L.P. Souza, C. Renato, two workers (MPEG: AYH077); 30 Oct. 2003, two workers (MPEG: AYH125, 130); 02 Nov. 2003, one worker (MPEG: AYH120); 12–14 Oct. 2006, Equipe A.Y. Harada, one worker (MPEG: AYH054); 14–16 Oct. 2006, one worker (MPEG: AYH043); 15–17 Oct. 2006, one worker (MPEG: AYH055); 15–17 Oct. 2010, 16 workers (MPEG: AYH013, 024); 23–25 Apr. 2003, one worker (MPEG: AYH096); 23–25 July 2007, six workers (MPEG: AYH002, 042, 072); 23–25 May 2003, one worker (MPEG: AYH114); 24–26 July 2006, two workers (MPEG: AYH015); 25–27 Jan. 2007, two workers (MPEG: AYH064, 090); 25–27 June 2007, one worker (MPEG: AYH012); 30 July–01 Aug. 2003, three workers (MPEG: AYH103, 131); 30 July–01 Aug. 2003, A.Y. Harada, E.P. Fagundes, C. Renato, two workers (MPEG: AYH098, 109); **Rondônia:** Ouro Preto do Oeste, 04 Apr. 1985, F.F. Ramos, Res. INPA N°0388, two workers (MPEG: USNMENT00757865, 00757866); **São Paulo:** Jundiá, Serra Do Japi, Jan. 2009, S. Diniz, three workers (ICN: USNMENT00759044); Tapirai, -24.03208 -47.46556, 08–14 Jan. 2001, R.R. Silva & Everhardt, one worker, two males (ICN: MZSP172). **COLOMBIA:** **Amazonas:** Leticia, one worker (ICN); Parque Nacional Natural Amacayacu, Matamata, -3.68 -70.25, 150 m, 23 Oct. 2000, one worker (ICN); **Cundinamarca:** La Vega, Reserva Natural Natautá, 5.00 -74.33, 1040 m, 10 Nov. 2010, F. Fernández, one worker (ICN: USNMENT00757873); **Magdalena:** 4 km N San Pedro, 10.95 -74.05, 550 m, 14 Aug. 1985, P.S. Ward #7912–35, three workers (PSWC: USNMENT00757863); **Norte de Santander:** 2 km N Barrancabermeja, Dec. 1962, leafmodd Berles. J. Archer; **Quindío:** Buenavista, Vereda El infierno, Finca Guadalajara, 4.37667 -75.76944, 1160 m, 16 Nov. 1999, E. Gonzalez, three workers (IAvH: IAvH-E74164); Calarca, Vereda Santo Domingo, Finca Santa Librada, 4.55694 -75.63917, 1575 m, 16 Jan. 2000, J. Sosa, five workers, one queen (IAvH: IAvH-E74163, 74,157); Circasia, Vereda Buenavista, Finca Calamar, 4.59806 -75.69861, 1450 m, 12 Oct. 1999, E. Gonzalez, two workers (IAvH: IAvH-E74168); **Risaralda:** La Celia, 5.00361 -76.00444, 1900 m, 27 Jan. 2011, Gustavo Zabala, two workers (ICN); **Valle del Cauca:** Cairo, Vereda Vallecitos, Finca El Maladero, 4.75803 -76.22732, 1850 m, 29 Mar. 2003, J. Henao, one worker (IAvH: IAvH25152); **Victada:** Cumaribo, Corregimiento Santa Rita, PNN El Tuparro, 5.3075 -67.9500, 135 m, 14–16 Feb. 2004, I. Quintero & E. Gonzalez, one worker (IAvH: USNMENT00759055). **COSTA RICA:** **Heredia:** Estación Biológica La Selva, 10.43691 -84.01374, 50 m, 19 Mar. 93, J. Longino, one

worker (JTLC: JTLC000007845); La Selva, 12 June 1991, L.E. Tennant, two workers (MCZC: USNMENT00757284, 00757285); **Puntarenas:** Estación Biológica Los Llanos, 10.30487 -84.83735, 1150 m, 28 Feb. 2004, J. Longino #5249-s, one worker (JTLC: JTLC000004545); Peninsula Osa, Parque Natural Corcovado, Sirena, 8.467 -83.583, 11 Aug. 1980, J. Longino, one worker (MCZC: USNMENT00757289); Parque Natural Corcovado, Sirena, 8.48333 -83.60000, 10 m, 27 June 1982, J. Longino, one worker (JTLC: JTLC000005929); **San José:** San Jose, 9.933 -84.083, 1100 m, 14 June 1999, J. Longino #4040-s, one worker (JTLC: LACM ENT 143521). **CUBA:** **Holguín:** 2 km N La Melba, 20.467 -74.817, 400 m, 22 Aug. 2001, P.S. Ward #14424–16, three workers (PSWC: USNMENT00757862); **Manicaragua:** Trinidad Mts, 01 Aug. 1953, E. O. Wilson #65, three workers, one queen (MCZC: USNMENT00757295). **DOMINICAN REPUBLIC:** 16 km ENE Pedernales, 18.1167 -71.6167, 800 m, 10 Sep. 1992, P.S. Ward #11751–16, three workers (PSWC: USNMENT00757872). **ECUADOR:** **Pichincha:** Reserva Forestal ENDESA, 0.083 -79.033, 25 Jan. 1994, L.E. Tennant, three workers (MCZC: USNMENT00757293, 00757869); Reserva Forestal ENDESA, 0.13 -79.05, 600 m, 05 Dec. 2003, A. L. Wild #AW2195, one worker (ALWC: USNMENT00757861); **Zamora-Chinchipe:** Copalinga, -4.09122 -78.96069, 1000 m, 28–30 Sep. 2009, Delsinne/Arias, col. id 35,155, 35,161, 15 workers (RBINS: Coll.RIScNB SID SPM\_ID3515505, 3,516,111); 30 Sep.–02 Oct. 2009, Delsinne/Arias, col. id 34,651, 39,654, three workers (RBINS: Coll.RIScNB SID SPM\_ID3465109, 3,465,404); 01–03 Oct. 2009, Delsinne/Arias, col. id34663, 34,671, 34,673, 14 workers (RBINS: Coll.RIScNB SID SPM\_ID3466304, 3,467,107, 3,467,305); 07 Oct. 2009, Delsinne/Arias, col. Id 34,715, 34,733, 29 workers (RBINS: Coll.RIScNB SID SPM\_ID3471501, 3,473,311); 04–06 Oct. 2009, Delsinne/Arias, col. id34695, 34,703–34,705, 34,709), 19 workers (RBINS: Coll.RIScNB SID SPM\_ID3469506, 3,470,305, 3,470,405, 3,470,504, 3,470,909); 05–07 Oct. 2009, Delsinne/Arias, col. id34746, 34,751, 34,753, five workers (RBINS: Coll.RIScNB SID SPM\_ID3474605, 3,475,106, 3,475,305). **FRENCH GUIANA:** Araguez, Inselbery forest, Sara Groc, three workers (ICN: USNMENT00757864); Kaw Mountains, Oct. 2008, Sara Groc, two workers (ICN: USNMENT00757867); Oct. 2009, Sara Groc, six workers (ICN: USNMENT00759035). **GUATEMALA:** **Zacapa:** 8.5 km NE Tukulután, 15.058717 -89.67638, 1100 m, 06 July 2001, J. Longino #6016-s, one worker (JTLC: JTLC000009864). **MEXICO:** **Oaxaca:** 7.2 km S Valle Nacional, 490 m, 11–18 Aug. 1973, A. Newton, two workers (MCZC: USNMENT00757286, 00757287); **Veracruz:** Los Tuxtlas, 10 km NNW Sontecomapan, 18.583 -95.083, 500 m, 21 Mar. 1995, P.S. Ward #1369–39, two workers

(PSWC: USNMENT00757871); Sa. Teoviscocla, nr. Cuichapa to 1600 m trop. For w. coffe, 04 Aug. 1965, Cornell Univ. Mexico Field Party, six workers, 1 queen (MCZC: USNMENT00757290, 00757291, 00757296). **PANAMA:** Barro Colorado I., Canal Zone, Jan. 1960, m-16 Strays, W.L. Brown, E.S. McCluskey, one worker (MCZC: USNMENT00757288); **PARAGUAY:** **Canindeyú:** Reserva Natural del Bosque, Mbaracayú, Jejuimi, -24.1 -55.5, 02 May 1996, A. Wild #0132, three workers, one queen (ALWC: USNMENT00757601); 11 Feb. 1997, A. Wild #AW 0409, one worker (ALWC: USNMENT00757860). **PERU:** **Madre de Dios:** Reserva Nacional Tambopata, Centro Sachavacayoc, -12.85583 -69.36194, 19–31 July 2012, curso de hormigas, seven workers (ICN: JSC120726-LS01). **SURINAME:** Tambahredjo, June 1959, I. V. d. Drift, one worker (MPEG: USNMENT00757876). **VENEZUELA:** **Aragua:** Parque Nac. Henri Pittier, La Toma, 10.34924 -67.68251, 1169 m, 09–19 Aug. 2008, Ant Course, three workers, one queen (ICN: USNMENT00757600, 00758023); Rancho Grande, 1100 m, 23–27 June 1967, W.L. Brown, one worker (MCZC: USNMENT00757294); 12 Aug. 1967, R.W. Poole, three workers (MCZC: USNMENT00757875).

**Diagnosis.** *Brachymyrmex minutus* morphologically resembles *B. australis*, *B. aphidicola*, and *B. termitophilus*, because all these species have eyes located on the cephalic midline, a mesonotum that does not bulge dorsally above the pronotum in lateral view, and yellowish body color. *Brachymyrmex minutus* differs from the three other species, or any other *Brachymyrmex* species for that matter, by having a very inconspicuous mesometanotal suture, giving the impression that the mesonotum and metanotum are fused. Additionally, *B. minutus* differs from *B. termitophilus* by having scattered pubescence on the gaster, from *B. aphidicola* by the presence of only two erect hairs on the pronotum and from *B. australis* by having scapes that surpass the posterior margin of the head by a length that is smaller than the maximal diameter of the eye.

*Lectotype and paralectotypes worker measurements* (mm) ( $n = 4$ ). HL<sub>1</sub> 0.37–0.40; HL<sub>2</sub> 0.25–0.31; HL<sub>3</sub> 0.07–0.10; HW 0.32–0.36; SL 0.32–0.36; EL 0.08–0.11; WL n.a.; PnL n.a.; PnW 0.20–0.24; ML 0.06–0.07; MW 0.14–0.15; *Indices* CI 85.88–89.29; SI<sub>1</sub> 92.59–108.00; SI<sub>2</sub> 107.14–126.67; OI<sub>1</sub> 26.03–29.63; OI<sub>2</sub> 20.00–25.27.

**Description.** *Head.* Slightly longer than wide in full face view; posterior cephalic margin weakly convex. Dorsum of the head with sparse hairs. Clypeus with a rounded anterior margin and five long, erect hairs of which a single, usually conspicuous hair is near the anterior margin, two hairs are in mediolateral position, and two more near the toruli; other hairs on the clypeus are markedly shorter and appressed or decumbent. Toruli surpassing the posterior clypeal margin in oblique anterodorsal oblique view. The scapes surpass the posterior margin of the head by a length that is smaller than the maximal

diameter of the eye; they have appressed pubescence. Ocelli absent. Eyes are positioned on the cephalic midline and have 8–9 ommatidia along their maximal diameter.

*Mesosoma.* Typically with two erect hairs on the pronotum and without erect hairs on the mesonotum. The mesonotum is not inflated and does not bulge dorsally above the pronotum in lateral view. Mesometanotal suture inconspicuous, giving the impression that the mesonotum and metanotum are fused. Metanotal groove absent or narrower than the diameter of the metathoracic spiracles. Metathoracic spiracles in dorsolateral position, not protruding, and touching the propodeal suture. Dorsum of the propodeum slightly convex and shorter than the propodeal slope. Propodeal spiracles circular, positioned on the posterior propodeal margin, just dorsally at the middle of the propodeal slope. Legs with appressed and scattered hairs. Petiole short and inclined forward.

*Gaster.* With scarce pubescence and several scattered long suberect hairs.

*Color and sculpture.* Body smooth, or finely granulated and shiny, sometimes with some imbricate sculpture on the dorsum of the mesosoma. Body usually yellowish, but sometimes reddish.

**Distribution** (Supplementary material Fig. S27). *Brachymyrmex minutus* is known to occur in Bolivia, Brazil, Colombia, Costa Rica, Cuba, the Dominican Republic, Ecuador, French Guiana, Guatemala, Mexico, Panama, Paraguay, Peru, Suriname, and Venezuela.

**Biology.** Forel (1893) found several colonies subterranean at the roots of sod, usually where it overgrows rocks, typically within the forest and/or nearby streams. The nest of *B. minutus* consists of large tunnels with small chambers at intervals. Colonies contain ~ 50 to 100 individuals, with a single queen.

**Remarks.** The lectotype is designated here as the second ant counting from the top of pin MHNG: USNMENT00757150, whereas the other specimens on that pin are paralectotypes.

Forel (1893) admitted having confused this species for *B. heeri* before but provided several morphological differences. However, *B. minutus* is morphologically more similar to the species indicated here in the diagnosis.

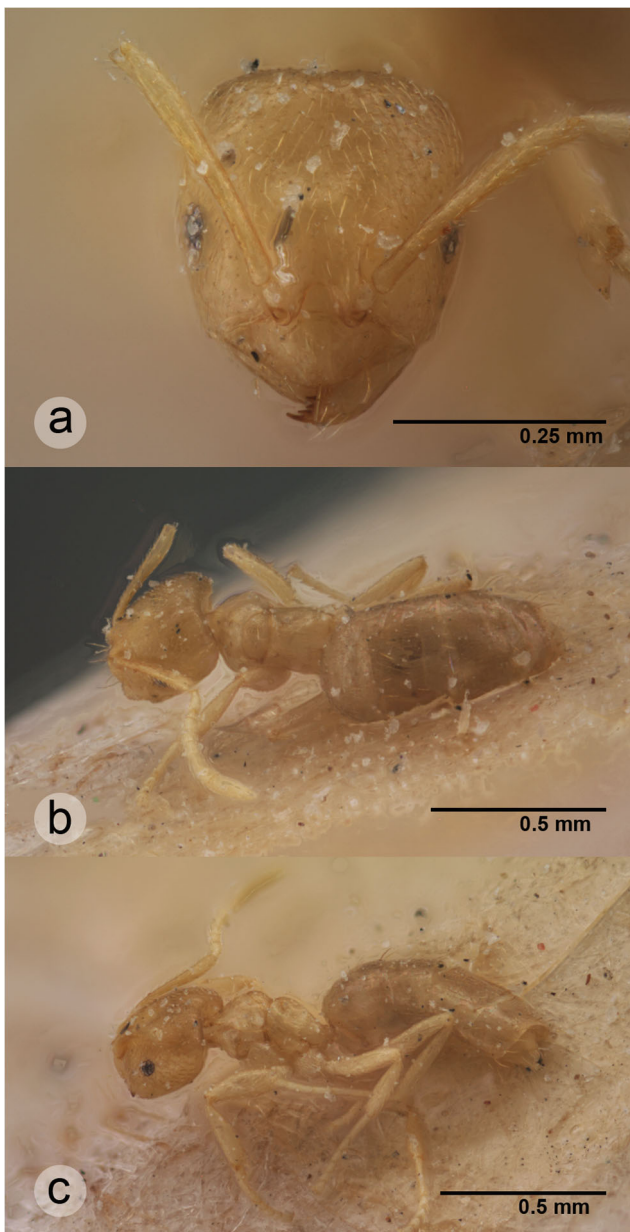
*Brachymyrmex modestus* Santschi

(Fig. 40, supplementary material Fig. S28)

*Brachymyrmex modestus* Santschi, 1923b: 271 (w.). Lectotype worker (NHMB: USNMENT00758099) and paralectotype workers (NHMB: USNMENT00758099, 00758100; here designated): three workers [examined].

**BRAZIL: Santa Catarina:** Blumerau, A. Reinchensperger leg.

**Additional material examined.** **BRAZIL: Santa Catarina:** Palhoça, PE Serra do Tabuleiro, -27.74111 -48.69722, 02–10 June 2003, R.R. Silva, B.H. Dietz & A. Tavares, one worker (ICN: MZSP033); São Bento do Sul, APA Rio Vermelho,



**Fig. 40** *Brachymyrmex modestus*: **a–c** head, dorsal, and lateral view of the lectotype worker

-26.36417 -49.27111, 30 Mar.-04 Apr. 2004, R. Silva & Eberhardt, eight workers (ICN: MZSP138); **São Paulo:** Cunha, PE Serra do Mar, Nucleo Cunha-Indara, -23.25083 -45.00722, 21–22 Apr. 2001, A.A. Tavares & R.R. Silva, 12 workers (ICN: MZSP149); Praia grande, PE Serra do Mar, nucleo pilhões-Cubatão, -23.9753 -46.5400, 26–27 May 2001, A.A. Tavares & R.R. Silva, five workers (ICN: MZSP165). **COLOMBIA: Amazonas:** Leticia, Reserva Forestal del Rio Calderón, Estación Biológica El Zafre, -4.00583, -69.89861, 150 m, 02–04 Dec. 2007, L.E. Franco & S. Florez, two workers (IAvH); **Caldas:** Aranzazu, Vereda Chambery, Finca Los Planes, 5.29231 -75.47283, 1910 m, 01–03

Aug. 2003, L.E. Franco & Cruz, one worker (IAvH: IAvH27307); Finca maranduba, 5.30731 -75.47250, 2050 m, 30 July–01 Aug. 2003), L.E. Franco & Cruz, two workers (IAvH: IAvH27288); Vereda La Guiaira, Finca Villa Ofelia, 5.286 -75.465, 1965 m, 01–03 Aug. 2003, L.E. Franco & Cruz, one worker, one queen (IAvH: IAvH27320); Vereda Sabana Larga, Finca Cañada Brujas, 5.30883 -75.47281, 1920 m, 31 July–02 Aug. 2003, L.E. Franco & Cruz, three workers (IAvH: IAvH55442); **Quindío:** Circasia, Finca Calamar, 4.60 -75.70, 1450 m, 12 Oct. 1999, E. Gonzalez, one worker (IAvH: IAvH 74,169); Filandia, Vereda Cruces, Finca Aranjuez, 4.70826 -75.64679, 1750 m, 13–15 July 2002, E. Jiménez & L.E. Franco, two workers (IAvH: IAvH27261); Finca La Cha, 4.70468 -75.60982, 1920 m, 28–30 Aug. 2002, E. Jiménez & L.E. Franco, one worker, one queen (IAvH: IAvH27233); 4.69617 -75.61056, 1920 m, 28–30 Aug. 2002, E. Jiménez & L.E. Franco, two workers (IAvH: IAvH27239); **Risaralda:** Pereira, Vereda El Manzano, Finca Santa Isabel, 4.70515 -75.62377, 1860 m, 15–17 July 2002, E. Jiménez & L.E. Franco, three workers (IAvH: IAvH27234); Vereda La Suiza, Finca El Amparo de Niños, 4.74624 -75.59830, 1810 m, 28–30 Nov. 2002, L.E. Franco, three workers (IAvH: IAvH27273); 4.75013 -75.60278, 1780 m, 26–28 Nov. 2002, L.E. Franco & E. Londoño, two workers (IAvH: IAvH27281); Finca Pez Fresco, 4.73838 -75.58016, 1910 m, 22–24 Nov. 2002, E. Jiménez & M.F. Reina, one worker, one queen (IAvH: IAvH27275); Finca Tesorito, 4.72141 -75.56186, 1940 m, 27–29 Nov. 2002, E. Jiménez, L.E. Franco & E. Londoño, two workers, one queen (IAvH: IAvH27280); Santuario, 26 Feb. 2003, one worker (IAvH: IAvH27286). **ECUADOR: Pichincha:** Maquipucuna, 5 km, ESE Nanegal, 0.11667 -78.63333, 1500 m, 17 Aug. 1991, P.S. Ward #11503–19, five workers (MCZC: USNM00757255, 00757283).

**Diagnosis.** *Brachymyrmex modestus* morphologically resembles *B. donisthorpei* and *B. myops* because these species have short dense hairs on the head and the mesosoma, short suberect hairs on the scapes, eyes below the cephalic midline of the head, the metanotal groove is either absent or narrower than the diameter of the metathoracic spiracles, their gaster bears dense pubescence, and their bodies are yellowish. *Brachymyrmex modestus* differs from *B. donisthorpei* by having scapes that surpass the posterior margin of the head, and from *B. myops* by having a mesonotum that bulges dorsally above the pronotum in lateral view.

*Lectotype and paralectotypes measurements* (mm) ( $n = 3$ ) HL<sub>1</sub> 0.49–0.51; HL<sub>2</sub> n.a.; HL<sub>3</sub> 0.14–0.16; HW 0.45; SL 0.43; EL 0.08–0.09; WL 0.49–0.55; PnL 0.10–0.14; PnW 0.29–0.39; ML 0.08–0.16; MW 0.20–0.25; *Indices* CI 88.46–92.00; SI<sub>1</sub> 95.65; SI<sub>2</sub> n.a.; OI<sub>1</sub> 17.39–19.57; OI<sub>2</sub> 20.00–25.27.

*Additional material examined measurements* (mm) ( $n = 3$ ). HL<sub>1</sub> 0.41–0.46; HL<sub>2</sub> 0.29–0.32; HL<sub>3</sub> 0.11–0.12; HW 0.38–

0.45; SL 0.38–0.40; EL 0.06–0.07; WL 0.45–0.49; PnL 0.12–0.13; PnW 0.22–0.28; ML 0.10–0.12; MW 0.18–0.22; *Indices* CI 91.49–100.00; SI<sub>1</sub> 90.00–97.78; SI<sub>2</sub> 120.00–133.33; OI<sub>1</sub> 15.56–18.61; OI<sub>2</sub> 23.53–27.66.

**Description.** *Head.* Slightly longer than wide in full face view; posterior cephalic margin flat. Dorsum of the head with appressed and several suberect hairs. Clypeus with a rounded anterior margin and five long, erect hairs of which a single, usually conspicuous hair is near the anterior margin, two hairs are in mediolateral position, and two more near the toruli; other hairs on the clypeus are markedly shorter and appressed or decumbent. Toruli surpassing the posterior clypeal margin in oblique anterodorsal view. The scapes surpass the posterior margin of the head by a length approximately equal to the maximal diameter of the eye and bear decumbent hairs. Ocelli appear to be absent. Eyes are positioned below the cephalic midline and have 3–4 ommatidia along their maximal diameter.

*Mesosoma.* Usually with two erect hairs on the pronotum and two on the mesonotum; sometimes additional decumbent hairs are present, mainly on the pronotum. The mesonotum is inflated, somewhat anteriorly inclined, and bulges dorsally above the pronotum in lateral view. Metanotal groove usually absent or narrower than the diameter of the metathoracic spiracles. Metathoracic spiracles small and in dorsolateral position, not protruding, and touching the propropodeal suture. Dorsum of the propodeum convex and shorter than the propodeal slope. Propodeal spiracles circular and positioned on the posterior propodeal margin, ventrally and slightly posterior of the middle of the propodeal slope. Legs with appressed hairs. Petiole short and inclined forward.

*Gaster.* With dense pubescence and some long erect hairs at the edges of the segments.

*Color and sculpture.* Head and gaster smooth and shiny, dorsum of the mesosoma slightly imbricate. Body yellowish, with the gaster sometimes being darker in color.

**Distribution** (Supplementary material Fig. S28). *Brachymyrmex modestus* is known from Brazil, Colombia, and Ecuador.

**Biology.** The type material of *B. modestus* was collected in association with termites (Santschi 1923b).

**Remarks.** The here designated lectotype is the specimen without expanded gaster on pin NHMB: USNMENT00758099, whereas the other specimen is one of the paralectotypes.

Santschi (1923b) mentioned the presence of physogastric workers in *B. modestus*, and we also observed some physogastric individuals in other samples (ICN: MZSP138, 149). These specimens are characterized by having a larger body in comparison to regular workers, and they have shorter scapes that barely reach the posterior margin of the head.

*Brachymyrmex musculus* Forel

(Fig. 41, supplementary material Fig. S29)

*Brachymyrmex tristis* r. *musculus* Forel, 1899: 124 (w.). Lectotype worker (MHNG: USNMENT00757155) and paralectotype workers (MHNG: USNMENT00757153–00757155; USNMENT00758113–00758115; MCSN: USNMENT00757152; here designated): 16 workers

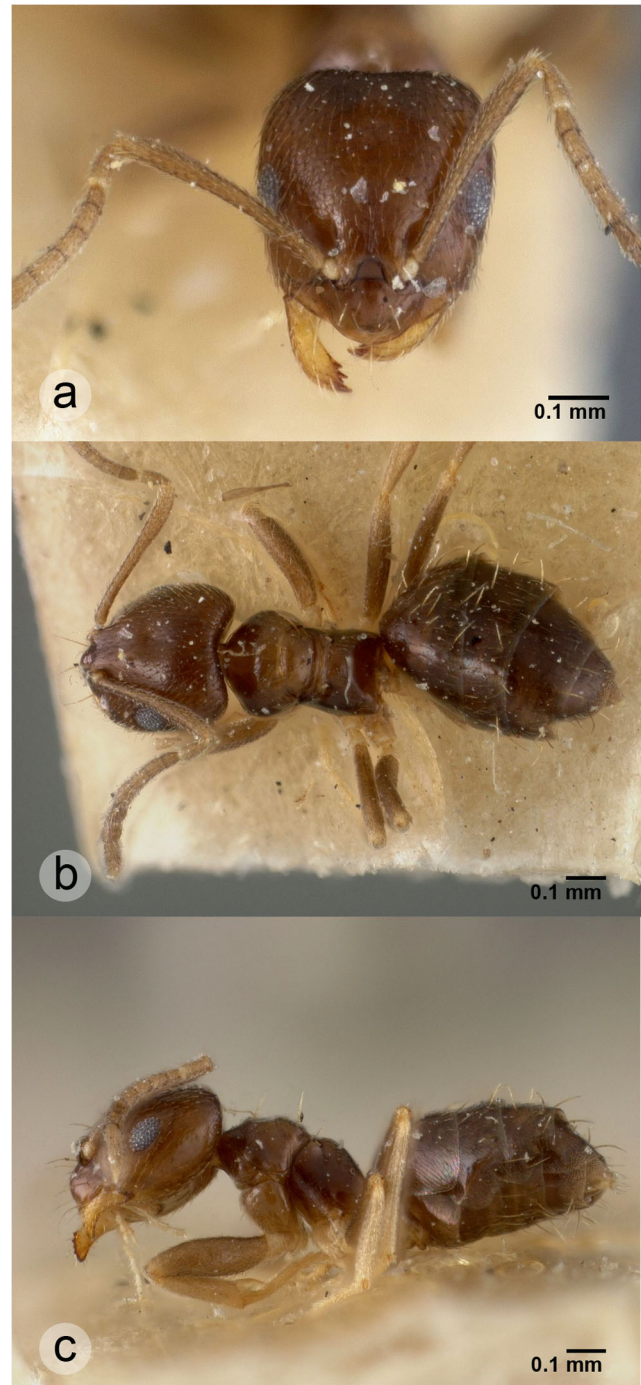


Fig. 41 *Brachymyrmex musculus*: a–c head, dorsal, and lateral view of the lectotype worker

[examined]: **COSTA RICA:** Pittier; Forel (1901a: 135) (q.). Raised to species: Forel (1901a: 135). See also: Santschi (1923a: 673).

**Additional material examined. ARGENTINA:** **Mendoza:** 22.81 km W Villa Seca, -33.58515 -69.41708, 1835 m, 06 Jan. 2008, W. MacKay, one worker (WEMC: USNMENT00757974); **Santa Cruz:** 12 km S Bajo Caracoles, 640 m, E.I. Schlinger & M.E. Trwin, ANTC10276, one worker (CASC: CASENT0196018). **COLOMBIA: Quindío:** Filandia, Vereda Cruces, Finca Los Micos, 4.70239 -75.64665, 1800 m, 12–14 July 2002, E. Jimenez & L.E. Franco, one worker (IAvH: IAvH27235). **COSTA RICA: Puntarenas:** Monteverde, 10.301 -84.806, 1500 m, 27 June 1984, J. Longino, two workers, one queen (JTLC: JTLC000005951, JTLC000005953). **MEXICO:** 6.5 km E Chalma, 26 May 1988, W.P. MacKay #10386, one worker, two males, one queen (WEMC: USNMENT00759016). **PARAGUAY: Amambay:** Pedro Juan Caballero, -22.567 -55.617, 20 Aug. 1998, A. Wild #AW0642, one worker (ALWC: USNMENT00757965). **VENEZUELA: Lara:** 9 km SE Barbacoas, 9.77 -71.06, 2000 m, 22 Aug. 1987, P.S. Ward #8923, three workers (PSWC: USNMENT00757589).

**Diagnosis.** *Brachymyrmex musculus* morphologically resembles *B. bruchi*, *B. patagonicus*, and *B. oculatus*, because all four species have scapes that surpass the posterior margin of the head, a mesonotum that does not bulge dorsally above the pronotum in lateral view, a gaster with scattered pubescence and a brownish body. However, *B. musculus* differs from the three other species by having a metanotal groove that is wider than the diameter of the metathoracic spiracles.

*Lectotype and paralectotype measurements* (mm) ( $n = 5$ ). HL<sub>1</sub> 0.43–0.48; HL<sub>2</sub> 0.30–0.33; HL<sub>3</sub> 0.10–0.11; HW 0.39–0.42; SL 0.39–0.42; EL 0.10–0.12; WL 0.42–0.46; PnL 0.11; PnW 0.25–0.29; ML 0.08–0.10; MW 0.18–0.20; *Indices* CI 87.16–91.26; SI<sub>1</sub> 98.92–100.00; SI<sub>2</sub> 117.65–136.76; OI<sub>1</sub> 23.16–30.00; OI<sub>2</sub> 21.10–23.81.

*Additional material examined measurements* (mm) ( $n = 3$ ) HL<sub>1</sub> 0.48–0.51; HL<sub>2</sub> 0.33–0.37; HL<sub>3</sub> 0.10–0.12; HW 0.44–0.47; SL 0.43–0.47; EL 0.12–0.14; WL 0.35–0.51; PnL 0.10–0.14; PnW 0.30–0.32; ML 0.10–0.12; MW 0.19–0.20; *Indices* CI 89.09–92.59; SI<sub>1</sub> 97.87–102.04; SI<sub>2</sub> 125.00–131.58; OI<sub>1</sub> 26.00–30.61; OI<sub>2</sub> 21.15–24.07.

**Description.** *Head.* Slightly longer than wide in full face view; posterior cephalic margin slightly concave. Dorsum of the head has sparse appressed hairs. Clypeus with the medial anterior margin somewhat forming a lip and five long, erect hairs of which a single, usually conspicuous hair is near the anterior margin, two hairs are in mediolateral position, and two more are near the toruli; other hairs on the clypeus are markedly shorter and appressed or decumbent. Toruli surpassing the posterior clypeal margin in oblique anterodorsal view.

The scapes surpass the posterior cephalic margin with a length up to the maximal diameter of the eye; with appressed hairs. Three ocelli are present but inconspicuous. Eyes are positioned on the cephalic midline with 9–11 ommatidia along their maximal diameter.

*Mesosoma.* Typically with two erect hairs on the pronotum and two on the mesonotum; sometimes with additional suberect hairs mainly on the pronotum. The mesonotum is not inflated and does not bulge dorsally above the pronotum in lateral view. Metanotal groove wider than the diameter of the metathoracic spiracles. Metathoracic spiracles in dorsolateral position, not protruding, and close to the propodeal suture. Dorsum of the propodeum convex and shorter than the posterior propodeal slope. Propodeal spiracles circular, positioned on the posterior propodeal margin at the middle of the propodeal slope. Legs with appressed hairs. Petiole short and inclined forward.

*Gaster.* With scattered pubescence and several scattered long erect hairs.

*Color and sculpture.* Body overall smooth and shiny, except for the sometimes slightly imbricate sculpture on the dorsum of the mesosoma. Body typically brownish; however, the bulbi of the antennae are whitish, and the antenna and legs, especially the tarsi, are somewhat lighter in color than the body.

**Distribution** (Supplementary material Fig. S29). *Brachymyrmex musculus* is known from Argentina, Colombia, Costa Rica, Mexico, Paraguay, and Venezuela.

**Biology.** Unknown.

**Remarks.** The lectotype is here designated as the ant at the top of pin MHNG: USNMENT00757155, whereas the other specimens in the pin are paralectotypes.

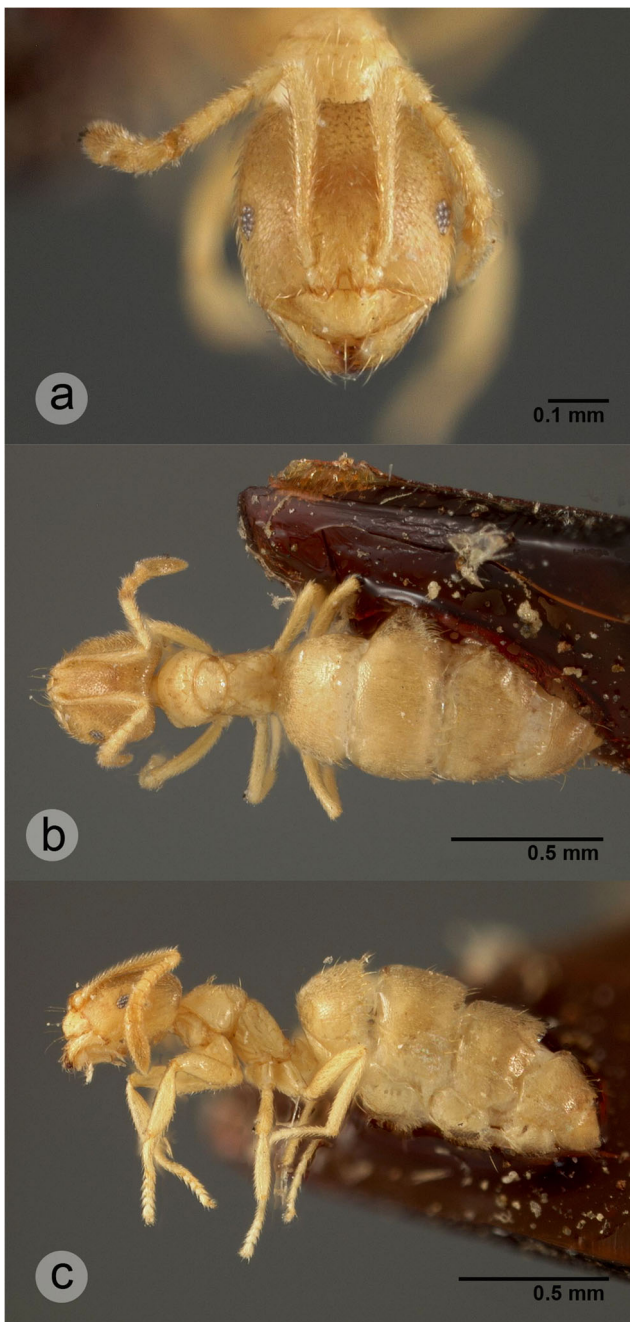
Forel (1899) originally described *B. musculus* as a race of *B. tristis*, but later indicated that the difference in size urged him to elevate it to a separate species (Forel 1901a). We agree with this decision, because *B. tristis* differs from *B. musculus* by having dense decumbent hairs on the head and the dorsum of the mesosoma, a mesonotum that bulges dorsally above the pronotum, and metathoracic spiracles that protrude slightly.

*Brachymyrmex myops* Emery

(Fig. 42, supplementary material Fig. S30)

*Brachymyrmex myops* Emery, 1906: 182, footnote, Fig. 42 (w.m.). Lectotype worker (NHMB: USNMENT00757221) and paralectotype male (NHMB: USNMENT00757221; here designated): one worker, one male [examined]. **BRAZIL: Santa Catarina:** Joinville, J. P. Schmalz, leg. See also: Santschi (1923a: 663).

**Additional material examined. BOLIVIA: Santa Cruz:** 35 km SSE Flor de Oro, -13.833 -60.867, 450 m, 29 Nov. 1993, P.S. Ward #12199–74, five workers (MCZ: USNMENT00757254, 00757892), three workers (PSWC: USNMENT00758027); **BRAZIL: Rondônia:** Jaru, R.M.



**Fig. 42** *Brachymyrmex myops*: a–c head, dorsal, and lateral view of the lectotype worker

Feitosa, five workers (ICN: MZSP178); **Pará**: Belém, 07 Aug. 1962, P.F. Doullington. B.F. 14, one worker (MCZC: USNMENT00757257); 14 Aug. 1962, P.F. Doullington. B.F. 19, two workers (MCZC: USNMENT00757258); 14 Aug. 1962, P.F. Doullington. B.F. 19, one worker (MCZC: USNMENT00757259); Melgaço, Caxiuanã ECFPn, -1.70661 -51.45909, 01 Nov. 2003, A.Y. Harada, E.P. Fagundes, C.J.M. Ribeiro, C.E.D. Sanhudo, C.A.R. Moura, J.L.P. Souza, C. Renato, one worker (MPEG: AYH094); 10–12 Oct. 2006, Equipe A.Y. Harada, one worker (MPEG: AYH046); 10–12

Oct. 2007, Equipe A.Y. Harada, two workers (MPEG: AYH038); 20–22 Oct. 2006, Equipe A.Y. Harada, eight workers (MPEG: AYH058); 20–22 Oct. 2007, Equipe A.Y. Harada, four workers (MPEG: AYH021, 047, 059); 25–27 Oct. 2007, Equipe A.Y. Harada, three workers (MPEG: AYH039, 048, 099); -1.73584 -51.48762, 13–15 Oct. 2005, Equipe A.Y. Harada, five workers (MPEG: AYH037); 25–27 Jan. 2007, Equipe A.Y. Harada, one worker (MPEG: AYH111); -1.78155 -51.59753, 15–17 Oct. 2007, Equipe A.Y. Harada, three workers (MPEG: AYH013, 044); 24–26 Oct. 2007, Equipe A.Y. Harada, one worker (MPEG: AYH029); 25–27 Jan. 2007, Equipe A.Y. Harada, one worker (MPEG: AYH062); 27–29 Jan. 2006, Equipe A.Y. Harada, five workers (MPEG: AYH034); 30 July–01 Aug. 2003, Equipe A.Y. Harada, 13 workers (MPEG: AYH134); A.Y. Harada, E.P. Fagundes, C. Renato, three workers (MPEG: AYH129). **COLOMBIA: Cauca**: PNN Gorgona, Mancora, 2.967 -78.183, 60 m, 02 Feb. 2000, D. Campos, 16 workers (IAvH).

**Diagnosis.** *Brachymyrmex myops* morphologically resembles *B. donisthorpei* and *B. modestus* because all three species have dense short hairs on the head and mesosoma, scapes with short suberect hairs, eyes that are positioned below the cephalic midline of the head, a metanotal groove that is absent or narrower than the diameter of the metathoracic spiracles, a gaster with dense pubescence, and yellowish body color. However, *B. myops* differs from *B. donisthorpei* by having scapes that surpass the posterior margin of the head and from *B. modestus* by having a mesonotum that does not bulge dorsally above the pronotum.

*Lectotype measurements* (mm) HL<sub>1</sub> 0.41; HL<sub>2</sub> 0.29; HL<sub>3</sub> 0.12; HW 0.37; SL 0.35; EL 0.06; WL 0.41; PnL 0.14; PnW 0.25; ML 0.12; MW 0.20; *Indices* CI 90.48; SI<sub>1</sub> 94.74; SI<sub>2</sub> 120.00; OI<sub>1</sub> 15.79; OI<sub>2</sub> 28.57.

*Additional material examined measurements* (mm) ( $n = 3$ ). HL<sub>1</sub> 0.37–0.38; HL<sub>2</sub> 0.27–0.30; HL<sub>3</sub> n.a.; HW 0.33–0.34; SL 0.34–0.36; EL 0.05–0.06; WL 0.36; PnL 0.09–0.10; PnW 0.22–0.23; ML 0.06–0.07; MW 0.15–0.18; *Indices* CI 88.10–88.37; SI<sub>1</sub> 102.70–105.40; SI<sub>2</sub> 111.76–130.00; OI<sub>1</sub> 15.79–18.92; OI<sub>2</sub> n.a.

**Description.** *Head.* Slightly longer than wide in full face view; posterior cephalic margin slightly concave. Dorsum of the head with appressed and several suberect hairs. Clypeus with a rounded anterior margin and five long, erect hairs of which a single, usually conspicuous hair is near the anterior margin, two hairs are in mediolateral position, and two more are near the toruli; other hairs on the clypeus are markedly shorter and appressed or decumbent. Toruli surpassing the posterior clypeal margin in oblique anterodorsal view. The scapes surpass the posterior margin of the head by a length approximately equal to the maximal diameter of the eye and have decumbent and suberect hairs. Ocelli absent. Eyes are positioned below the cephalic midline and have 3–4 ommatidia along their maximal diameter.

**Mesosoma.** Usually two erect hairs on the pronotum and two on the mesonotum; sometimes decumbent hairs are present, mainly on the pronotum. The mesonotum is somewhat inflated, but it does not bulge dorsally above the pronotum in lateral view. Metanotal groove absent or narrower than the diameter of the metathoracic spiracles. Metathoracic spiracles inconspicuous, in dorsolateral position, not protruding, and not touching any suture. Dorsum of the propodeum weakly convex and much shorter than the propodeal slope. Propodeal spiracles circular but inconspicuous, positioned on the posterior propodeal margin, slightly posterior of the middle of the propodeal slope. Legs with appressed hairs. Petiole short and inclined forward.

**Gaster.** With dense pubescence and several long erect hairs, mainly along the edges of the segments.

**Color and sculpture.** Head and gaster smooth and shiny, dorsum of the mesosoma slightly imbricate. Body usually uniformly yellowish, but sometimes with a darker gaster.

**Distribution** (Supplementary material Fig. S30). *Brachymyrmex myops* is known from Bolivia, Brazil, and Colombia.

**Biology.** Emery (1906) described *B. myops* from specimens that were collected in the nest of the termite *Anoplotermes ater*.

**Remarks.** The worker on pin NHMB: USNMENT00757221 is designated here as the lectotype. *Brachymyrmex myops* has been described from one worker and a male, which makes it currently impossible to determine the intraspecific variation. *Brachymyrmex modestus* has also been collected from termite nests, has a very similar geographic distribution as *B. myops*, and both species resemble one another morphologically (see diagnosis). They differ in whether the mesonotum bulges dorsally above the pronotum in lateral view, which is a trait of diagnostic value to delimit several *Brachymyrmex* species, however, the conditions in *B. myops* and *B. modestus* are not strongly different, and both species may be conspecific.

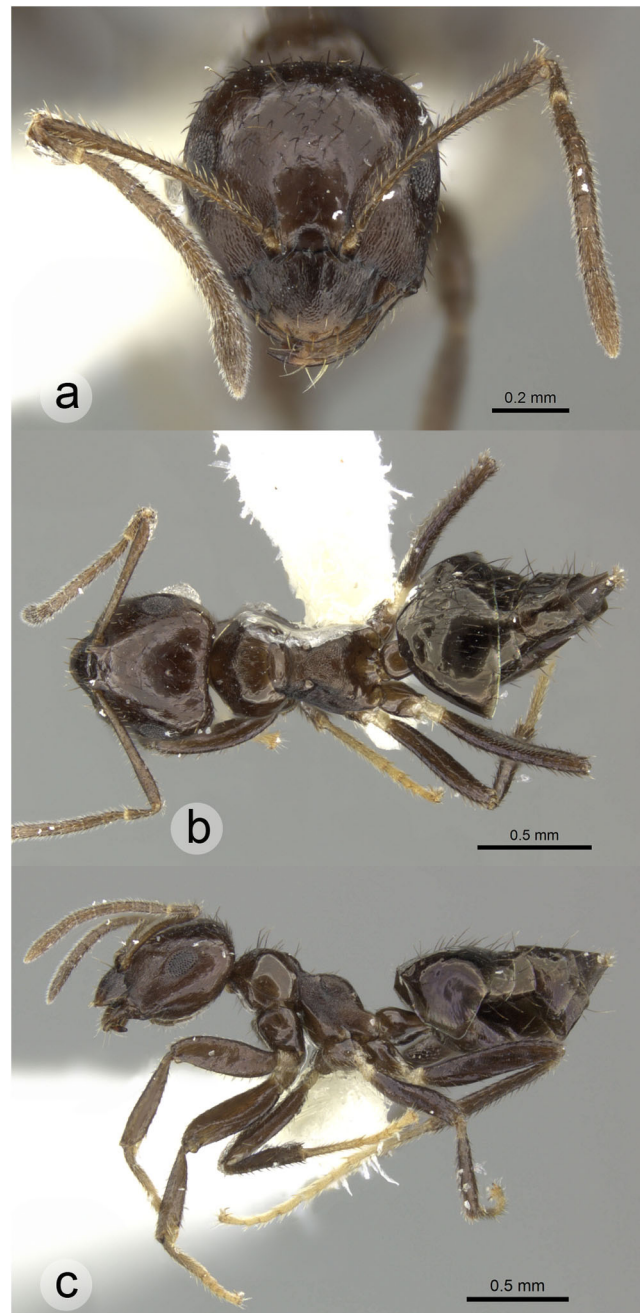
*Brachymyrmex nebulosus* LaPolla & Longino (Fig. 43, supplementary material Fig. S31)

*Brachymyrmex nebulosus* LaPolla and Longino, 2006: 299, Fig. 1 (w.). **COSTA RICA: Puntarenas:** 6 km south of Monteverde, 10.25 -84.82, 800 m, 22 June 1999, J. Longino #4050, LACM ENT 143550 (INBC).

Paratype examined. **COSTA RICA: Puntarenas:** Ojo de agua, rd to Monteverde, 800 m, 05 July 1991, J. Longino, leg. (JTLC #2965), two workers (INBIO).

**Additional material examined. MEXICO: Chiapas:** Sierra Morena, 16.15427–93.58961, 1150 m, 11 May 2008, J. Longino #6218-s, two workers (JTLC: JTLC0000007379; CASENT0609689).

**Diagnosis.** *Brachymyrmex nebulosus* differs from other *Brachymyrmex* species in having a clypeus with its medial



**Fig. 43** *Brachymyrmex nebulosus*: **a–c** head, dorsal, and lateral view of a worker (from [www.antweb.org](http://www.antweb.org); photographer: Ryan Perry)

portion forming a conspicuous “lip,” its hour-glass shaped mesosoma and it has portions of the head and mesosoma that bear alveolate sculpture. *Brachymyrmex musculus* is the only other *Brachymyrmex* species known to date that has a clypeus with a somewhat developed medial lip, but it is less conspicuous than in *B. nebulosus*.

**Paratype measurements** (mm). HL<sub>1</sub> 0.67; HL<sub>2</sub> 0.40; HL<sub>3</sub> 0.24; HW 0.63; SL 0.62; EL 0.18; WL 0.80; PnL 0.29; PnW 0.45; ML 0.26; MW 0.23; **Indices** CI 94.67; SI<sub>1</sub> 97.18; SI<sub>2</sub> 153.33; OI<sub>1</sub> 28.17; OI<sub>2</sub> 36.00.

*Additional material examined measurements (mm) (n = 1).* HL<sub>1</sub> 0.80; HL<sub>2</sub> 0.49; HL<sub>3</sub> 0.23; HW 0.73; SL 0.72; EL 0.20; WL 0.92; PnL 0.31; PnW 0.50; ML 0.12; MW 0.27; *Indices* CI 91.11; SI<sub>1</sub> 98.78; SI<sub>2</sub> 111.76; OI<sub>1</sub> 15.79; OI<sub>2</sub> n.a.

**Description.** See LaPolla and Longino (2006).

**Distribution.** (supplementary material Fig. S31). This species is known from Costa Rica and Mexico.

**Biology.** *Brachymyrmex nebulosus* was collected from sites at about 800 m elevation in moist forest at the transition between lowland dry forest and cloud forest. All collected workers were obtained from open scrubby vegetation. In the field, these ants look and behave remarkably like *Crematogaster* (LaPolla and Longino 2006).

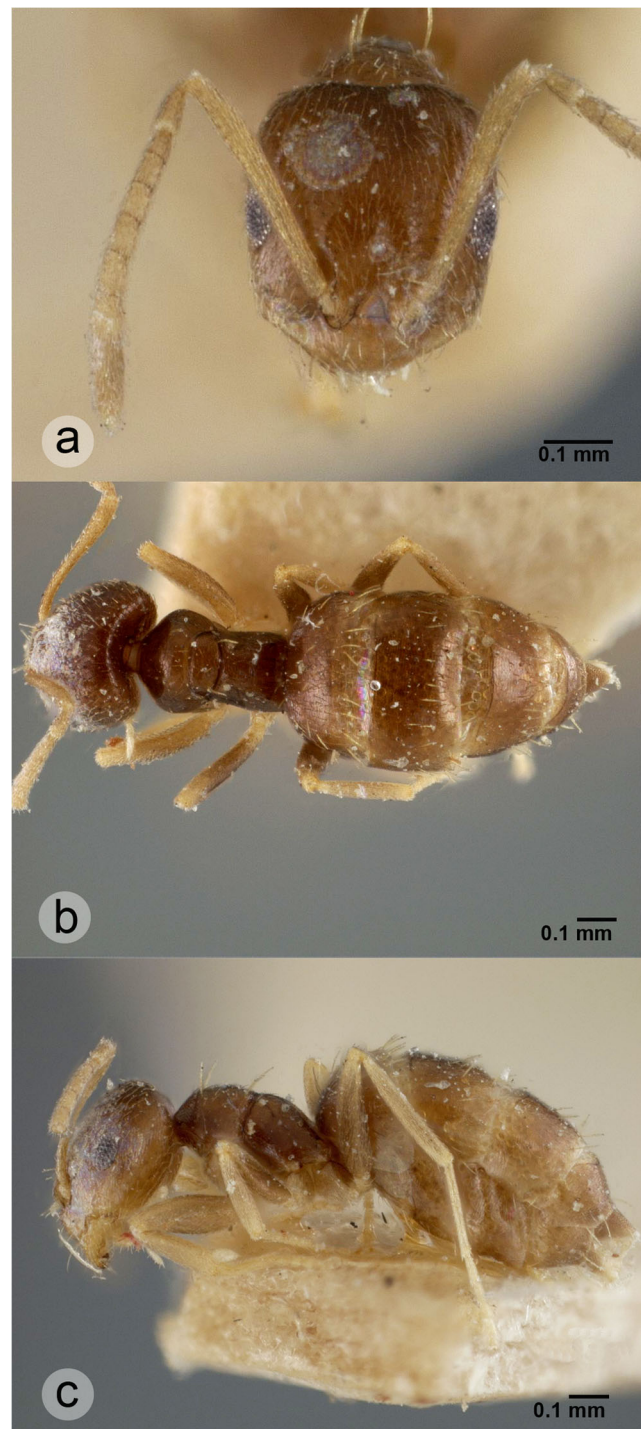
**Remarks.** *Brachymyrmex nebulosus* has been originally described from Costa Rica, but during our studies we came across two specimens from Mexico that very strongly resemble this species. The only differences are that the Mexican specimens have a more squared head, and stronger alveolate sculpture on the head and the dorsum of the mesosoma. Considering these differences and the geographical distribution, these Mexican specimens may be a variety of *B. nebulosus*, or potentially a different species, although more material and further study would be required to resolve this issue.

*Brachymyrmex obscurior* Forel

(Fig. 44, supplementary material Fig. S32)

*Brachymyrmex heeri* var. *obscurior* Forel, 1893: 345 (w.q.m.). Lectotype worker (MHNG: USNMENT00757132) and paralectotype workers, queens, males (MHNG: USNMENT00757132–00757135; USNMENT00758124–00758128; here designated): 16 workers, three queens, three males [examined]. **ANTILLES:** Saint Vincent. Subspecies of *Brachymyrmex heeri*: Forel (1897: 298); Forel (1912a: 62). Raised to species: Wilson and Taylor (1967: 92). See also Santschi (1923a: 666).

**Additional material examined. ARGENTINA: Chubut:** 3 km N. Puerto Lobos, 20 m, 14 Dec. 1966, E.I. Schlinger & M. Irwin, ANTC 10275, one worker (CASC: CASENT0196017). **BRAZIL: Bahia:** CEPEC, 11 Nov. 1997, L.S. Ramos, one worker (CPDC: USNMENT00757668); **São Paulo:** Caraguatatuba, Reserva Florestal, 40–80 m, 12–22 May 1971, W.L. & D.E. Brown, two workers, one queen (MCZC: USNMENT00757659); Itirapina, cerrado, Dec. 2008, D.P. Silva, three workers (ICN: USNMENT00759042); Ubatuba, Picinguaba, July 2011, two workers (ICN: USNMENT00759051). **CHILE:** Santiago, Nov. 1996, C. Errard, three workers (CPDC: USNMENT00757683). **COLOMBIA: Córdoba:** Monteria, Finca Betania, 29 June 2009, Juan C. Abadia, four workers (IAvH); Valencia, Villa Mary, 02 June 2009, Juan C. Abadia, four workers (IAvH); **Huila:** 17 km NW La Plata, 03 Jan. 1984, W.P. MacKay #7133, one worker (WEMC:



**Fig. 44** *Brachymyrmex obscurior*: **a–c** head, dorsal, and lateral view of the lectotype worker

USNMENT00759021); 17 km N La Plata, 03 Jan. 1984, W.P. MacKay #7139, one worker one queen (WEMC: USNMENT00758996); **Magdalena:** Parque Nacional Tayrona, Cañaveral, 11.33 -74.03, 30 m, 18–20 Aug. 2002, M. Sharkey, P. Arias & E. Torres, seven workers (IAvH); **Valle del Cauca:** Cairo, vereda Llano Grande, Finca Encanto, 4.73620 -76.21698, 1550 m, 31 Mar. 2003, R. Garcia,



one worker (IAVH: IAVH25144). **DOMINICAN REPUBLIC:** La Vega: 12 km NW Bonao, 19.03333 -70.48333, 890 m, 31 Aug. 2001, A.L. Wild #AW1324, two workers (ALWC: USNMENT00757987); 5 km N El Río, 19.02 -70.60, 1230 m, 01 Sep. 2001, A.L. Wild #AW1339, one worker (ALWC: USNMENT00757657); Casabito For. El Rio - Bona Km 8, 07 Feb. 1975, W.L. & D.E. Brown, two workers (MCZC: USNMENT00757664). **FRENCH GUIANA:** 20 km Sinnamary, 12 Feb 1994, A. Dejean #17025, two workers (ICN: USNMENT00757660). **GUATEMALA: El Progreso:** 5 km El Rancho, 14.9167 -90.0667, 400 m, 17 Nov. 2003, P.S. Ward #15076-3, three workers (PSWC: USNMENT00757667); **Escuintla:** Escuintla, 30 Dec. 1911, W.M. Wheeler, three workers (MCZC: USNMENT00759001). **JAMAICA:** Manchester, Gourie Forest Res., 18.20 -77.52, 860 m, 10 Sep. 2001, A.L. Wild #AW1375, one worker (ALWC: USNMENT00757669). **MEXICO: Chiapas:** Custepec, 15.72196 -92.95037, 1530 m, 19 May 2008, J. Longino #6280, one worker, one queen (JTLC: JTLC000007437, JTLC 000007438); **Jalisco:** 7 km SW Tamazula, 19.68056 -103.32194, 992 m, 22 June 2000, W. & E. Mackay, two workers (WEMC: USNMENT00757729). **NEW CALEDONIA:** Road to My. Koghi, Dec. 1985, N.L.H. Krauss, ANTC10279, one worker (CASC: CASENT0196021). **USA: Florida:** Sarasota Co. Longino Ranch. T38S, R22E Sect, 27.15 -82.12, 20 m, 07 June 1981, J. Longino, two workers (JTLC: JTLC0000005943); **Texas:** Del Mar, 26.01167 -97.31861, 26 Sep. 1972, W.S. Ross, ANTC 10263 10264, two workers (CASC: CASENT0196005, 0196006).

**Diagnosis.** *Brachymyrmex obscurior* morphologically resembles *B. cordemoyi* and *B. patagonicus* because all three species have a metanotal groove that is absent or narrower than the diameter of metathoracic spiracles, their mesonotum does not bulge dorsally above the pronotum, their scapes usually surpass the posterior margin of the head, and their bodies are brownish. *Brachymyrmex obscurior* and *B. cordemoyi* differ from *B. patagonicus*, however, because they have dense pubescence on the gaster. *Brachymyrmex obscurior* differs from *B. cordemoyi* by having less conspicuous dense pubescence on the dorsum of the head and the mesosoma, dense decumbent pubescence on the gaster, and eyes with fewer ommatidia along their maximal diameter (on average 9 instead of 10–12).

*Lectotype and paralectotypes workers measurements* (mm) ( $n = 8$ ). HL<sub>1</sub> 0.39–0.47; HL<sub>2</sub> 0.27–0.35; HL<sub>3</sub> 0.10–0.12; HW 0.35–0.48; SL 0.35–0.45; EL 0.10–0.15; WL 0.31–0.53; PnL 0.09–0.15; PnW 0.23–0.30; ML 0.06–0.14; MW 0.15–0.23; *Indices* CI 79.17–106.67; SI<sub>1</sub> 96.59–115.79; SI<sub>2</sub> 125.71–1146.67; OI<sub>1</sub> 25.00–31.25.

*Additional material examined measurements* (mm) ( $n = 2$ ). HL<sub>1</sub> 0.44–0.47; HL<sub>2</sub> 0.30–0.32; HL<sub>3</sub> 0.11–0.12; HW 0.37–0.42; SL 0.38–0.41; EL 0.11–0.12; WL 0.42–0.47; PnL 0.11–

0.13; PnW 0.26–0.30; ML 0.11; MW 0.18–0.19; *Indices* CI 84.34–88.89; SI<sub>1</sub> 96.25–102.86; SI<sub>2</sub> 126.32–128.33; OI<sub>1</sub> 28.57–28.75; OI<sub>2</sub> 24.10–24.44.

**Description.** *Head.* Slightly longer than wide in full face view; posterior cephalic margin slightly concave. Dorsum of the head with sparse appressed hairs. Clypeus with a rounded anterior margin and five long, erect hairs of which a single, usually conspicuous hair is near the anterior margin, two hairs are in mediolateral position, and two more near the toruli; other hairs on the clypeus are clearly shorter and appressed or decumbent. Toruli surpassing the posterior clypeal margin in oblique anterodorsal view. The scapes surpass the posterior cephalic margin by a length up to the maximal diameter of the eye, and they have appressed hairs. Ocelli absent. Eyes are positioned on the cephalic midline and have 8–10 ommatidia along their maximal diameter.

*Mesosoma.* Typically with two erect hairs on the pronotum and two on the mesonotum. The mesonotum is not inflated and does not bulge dorsally above the pronotum in lateral view. Metanotal groove absent or narrower than the diameter of the metathoracic spiracles. Metathoracic spiracles in dorsolateral position, not protruding, and typically touching the mesometanotal and propodeal sutures. Dorsum of the propodeum convex and shorter than the propodeal slope. Propodeal spiracles circular and positioned on the posterior propodeal margin, slightly anterior of the middle of the propodeal slope. Legs with appressed hairs. Petiole short and inclined forward.

*Gaster.* With decumbent dense pubescence and several scattered long erect hairs.

*Color and sculpture.* Body smooth and shiny, except for the dorsum of the mesosoma which is sometimes slightly imbricate. Body uniformly brownish, but with slightly lighter antenna and legs.

**Distribution** (supplementary material Fig. S32). *Brachymyrmex obscurior* is widespread and known from the Antilles, Argentina, Brazil, Chile, Colombia, the Dominican Republic, French Guiana, Guatemala, Hawaii, Jamaica, and Mexico. It has also been introduced in New Caledonia, the USA, and other colleagues have reported it from Samoa and Hawaii (Wilson and Taylor, 1967), but we did not examine this material.

**Biology.** In the original description, Forel (1893) mentioned that this species forms colonies of a few hundred individuals. Nests are usually constructed on open ground, typically under a stone, or at the roots of grass and weeds. The nest consists of only one or two simple chambers that are connected with a short passage. Forel (1893) indicated that *B. obscurior* occurs from sea level up to 800 m of altitude, but here we report new records from localities above 800 m.

**Remarks.** The specimen at the top of pin MHNG: USNMENT00757132 is designated here as the lectotype, whereas the other ants are paralectotypes. Forel (1893)

described *B. obscurior* as a variety of *B. heeri* and indicated that it differs from typical *B. heeri* by having a brownish instead of yellowish body and slightly denser pubescence on the gaster. We observed that both species can readily be distinguished as to whether or not the mesonotum bulges dorsally above the pronotum in lateral view. Forel (1893) also reported that *B. obscurior* resembles *B. patagonicus* but that both taxa differ as to the presence or absence of ocelli, in body size, as to pubescence and the length of the scapes. He further considered *B. obscurior* to be a difficult “form” that represents a morphological transition between *B. patagonicus* and *B. heeri* (Forel 1912a). We agree that *B. obscurior* and *B. patagonicus* are morphologically very similar (see diagnosis), and molecular studies of both taxa will be required to examine whether they are distinct species. Wilson and Taylor (1967) recognized *B. heeri* var. *obscurior* as a distinct species as a provisional measure in anticipation of a full-scale revision of the genus. We agree with this decision, based on the morphological differences indicated above, but we cannot for now comment on their proposed synonymization of *B. heeri* var. *aphidicola* Wheeler, 1934 to *B. obscurior*, as this material from Hawaii was not available to us.

*Brachymyrmex oculatus* Santschi

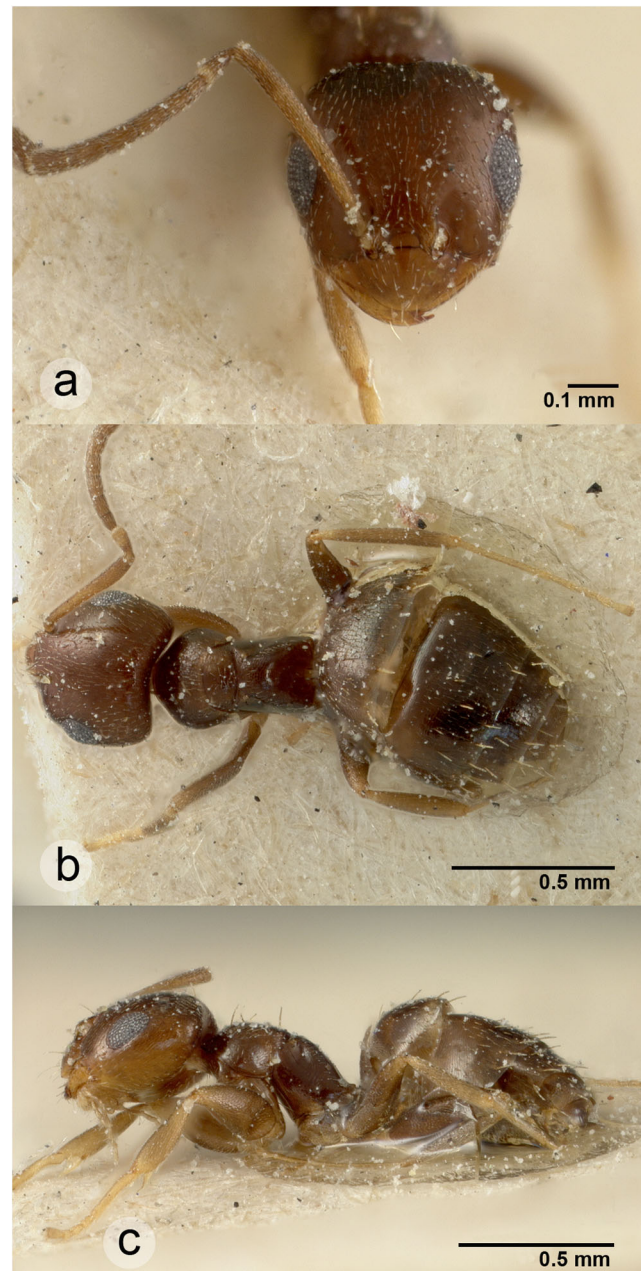
(Fig. 45, supplementary material Fig. S33)

*Brachymyrmex oculatus* Santschi, 1919: 55 (w.). Lectotype worker (NHMB: USNMENT00758101) and paralectotype workers (NHMB: USNMENT00758101; here designated): six workers [examined]. **ARGENTINA: Buenos Aires:** Sierra de las Ventanas, Bruch leg. Quirán et al. (2004: 282) (m).

**Additional material examined. ARGENTINA: Entre Ríos:** Vilcaguay, Bruchi, three workers (MZSP: USNMENT00757776); **Santa Fé:** “Fives Lilles”, Wiser, six workers (MCZC: USNMENT00757250).

**Diagnosis.** *Brachymyrmex oculatus* morphologically resembles *B. bruchi* and *B. patagonicus*, because all three species have scapes that surpass the posterior margin of the head, they usually have two erect hairs on the mesonotum, their mesonotum does not bulge dorsally above the pronotum in lateral view, a metanotal groove is absent or narrower than the diameter of the metathoracic spiracles, their gaster has scarce pubescence, and several scattered long erect hairs and their body is brownish. *Brachymyrmex oculatus* differs from *B. bruchi* and *B. patagonicus*, however, by having larger eyes, with a maximal diameter that approximates a third of the length of the head ( $HL_1$ ). They usually have more than 14 ommatidia along their maximal diameter.

*Lectotype and paralectotypes worker measurements* (mm) ( $n = 4$ ).  $HL_1$  0.45–0.50;  $HL_2$  0.35–0.41;  $HL_3$  0.11–0.14; HW 0.48–0.58; SL 0.45–0.50; EL 0.15–0.18; WL 0.53–0.61; PnL 0.15–0.17; PnW 0.30–0.39; ML 0.14–0.20; MW 0.23–0.27;



**Fig. 45** *Brachymyrmex oculatus*: a–c head, dorsal, and lateral view of the lectotype worker

*Indices* CI 106.67–115.15;  $SI_1$  86.84–93.75;  $SI_2$  122.22–133.33;  $OI_1$  31.25–34.29;  $OI_2$  21.88–27.27.

**Description.** *Head.* Slightly longer than wide in full face view; posterior cephalic border flat. Dorsum of the head with sparse appressed hairs. Clypeus with a rounded anterior margin and five long, erect hairs of which a single, usually conspicuous hair is near the anterior margin, two hairs are in mediolateral position, and two more near the toruli; other hairs on the clypeus are markedly shorter and appressed or decumbent. Toruli surpassing the posterior clypeal margin in oblique anterodorsal view. The scapes surpass the posterior cephalic

margin by a length that is shorter than the maximal diameter of the eye; they have appressed hairs. Ocelli absent. Eyes are positioned on the cephalic midline and usually have more than 14 ommatidia along their maximal diameter.

**Mesosoma.** Dorsum of the mesosoma with sparse appressed hairs, and typically with two erect hairs on the pronotum and two on the mesonotum; sometimes with additional suberect hairs, mainly on pronotum. The mesonotum is not inflated and does not bulge dorsally above the pronotum in lateral view. Metanotal groove absent or narrower than the diameter of the metathoracic spiracles. Metathoracic spiracles in dorsolateral position, not protruding, and touching the propodeal suture. Dorsum of the propodeum slightly convex and shorter than the propodeal slope. Propodeal spiracles circular, positioned on the posterior propodeal margin, at the middle of the propodeal slope. Legs with scattered appressed hairs. Petiole short and inclined forward.

**Gaster.** With scattered pubescence and several scattered long erect hairs, mainly at the edges of the segments.

**Color and sculpture.** Body overall smooth and shiny, with the dorsum of the mesosoma slightly imbricate. Body uniformly brownish.

**Distribution** (Supplementary material Fig. S33). *Brachymyrmex oculatus* is exclusively known from Argentina. Quirán et al. (2004) examined material from additional localities throughout the country.

**Biology.** Unknown.

**Remarks.** The specimen at the top of pin NHMB: USNMENT00757132 is here designated as lectotype, whereas the other ants in that pin are paralectotypes. Santschi (1919) suggested that *B. oculatus* can be confused with *B. bruchi* based on overall similarity. *Brachymyrmex patagonicus* is also very similar, and as mentioned in the diagnosis *B. oculatus* differs mainly from these species by its larger eyes. Whereas *B. patagonicus* has two erect hairs on the pronotum and *B. bruchi* usually more than two, the number of erect hairs on the pronotum is variable in *B. oculatus*.

Quirán et al. (2004) designated a male to be the lectotype of *B. oculatus*, because it was labeled as “typus,” and the associated workers were designated to be paralectotypes. However, the original description by Santschi (1919) exclusively described the worker morphology, and therefore logic dictates that the lectotype should be a worker. As such, we redesignated a worker of Santschi (1919) type series as lectotype here.

*Brachymyrmex patagonicus* Mayr

(Figs. 46, and 47, supplementary material Fig. S34)

*Brachymyrmex patagonicus* Mayr, 1868: 164 (w.m.). (NHMW), Emery (1906: 178) (q.). **ARGENTINA: Buenos Aires:** Rio Negro. See also: Santschi (1923a: 657).

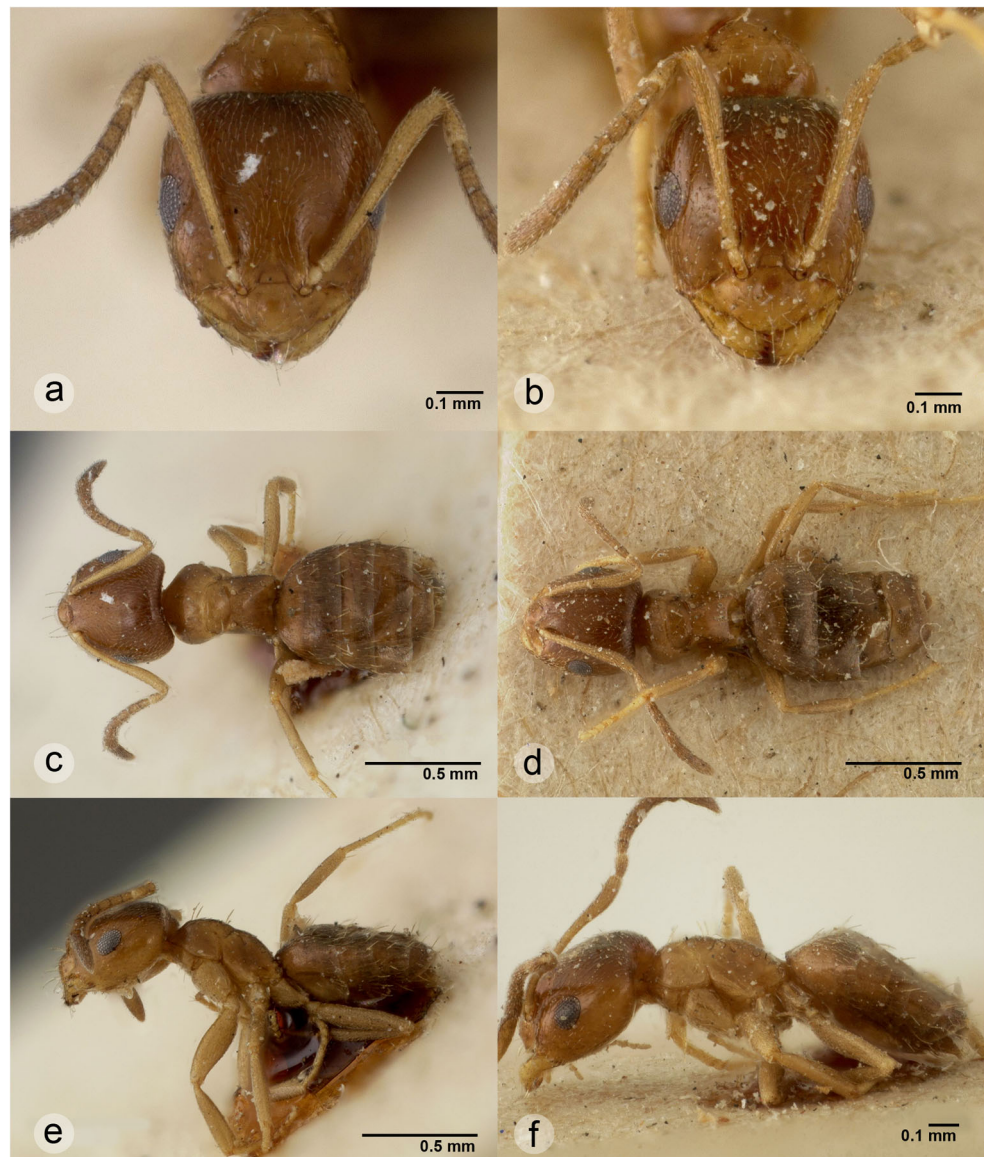
= *Brachymyrmex patagonicus* var. *atrátula* Santschi, 1923a: 657, Fig. 3 (w.). (NHMB: USNMENT00757695):

two workers [examined] **ARGENTINA: Jujuy:** Alfarito; synonym proposed by Quirán et al. (2004: 275). See also: Santschi (1923a: 657).

= *Brachymyrmex laevis* Emery, 1895: 216 (w.). (MSNG: USNMENT00757205, 00757206; MHNG: USNMENT00758130): four workers [examined] **CHILE: Valdivia.** See also: Forel (1908: 400); Forel (1912a: 62); Santschi (1923a: 659). n. syn.

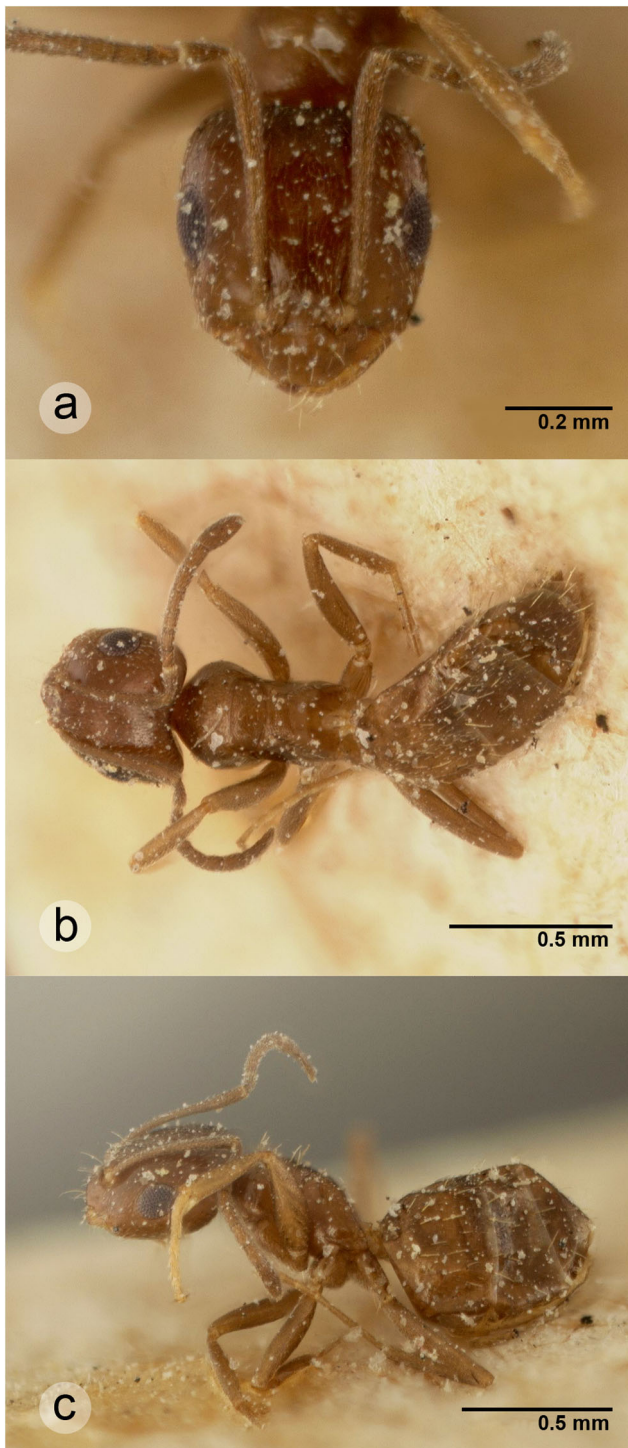
**Additional material examined. ARGENTINA: Entre Ríos:** 8.63 km W Concordia, -31.42303 -58.11672, 16 m, 26 Dec. 2007, W. MacKay #22667, one worker (WEMC: USNMENT00758002); **Las Heras:** Agua de las zorras, Paramillo de Uspallata, 13 km NW of Villavicencio, -32.48011 -69.16467, 2750 m, three workers one queen (MCZC: USNMENT00759011); **Mendoza:** 22.81 km W Villa Seca, -33.58515 -69.41708, 1835 m, 06 Jan. 2008, W. MacKay, four workers, one queen (WEMC: USNMENT00757968, 00757973, 00759018, 00759020); **Santiago del Estero:** two workers (ICN: USNMENT00759047). **BRAZIL: Pará:** Melgaço, Caxiuanã ECFPn, -1.73584 -51.48762, 23–25 Oct. 2005, Equipe A.Y. Harada, five workers (MPEG: AYH036); -1.72484 -51.42979, 26 Oct. 2003, A.Y. Harada, E.P. Fagundes, C.J.M. Ribeiro, C.E.D. Sanhudo, C.A.R. Moura, J.L.P. Souza, C. Renato, two workers (MPEG: AYH053); Santarem, Taperinha, -2.90 -54.33, July 1975, R. L. Jeanne, three workers (MCZC: USNMENT00757990); **São Paulo:** Cananéia, P.E. Ilha Do Cardoso, -22.30 -47.88, 02 Nov. 2007, C. Bottcher & E.R. Pereira, 1 worker (ICN: USNMENT00757730); **Itirapina:** 11 Feb. 2009, S. Sendoya, 23 workers (ICN: USNMENT00759052). **COLOMBIA: Caldas:** Aranzazu, Vereda Alegrias, Finca Betania, La Esperanza, 5.29831 -75.49053, 1990 m, 08–09 Aug. 2003, L.E. Franco & J. Cruz, three workers (IAvH: 55576); Finca Villa Rosita, 5.30603 -75.48489, 1825 m, 06–08 Aug. 2003, L.E. Franco & J. Cruz, two workers (IAvH: IAvH25467, 25,468); Vereda Buenavista, Naranjal Finca Bizerta, 5.28431 -75.48942, 2065 m, 25–27 July 2003, L.E. Franco & J. Cruz, one worker (IAvH: IAvH25471); 4.285 -75.489, 2065 m, 25–27 July 2003, L.E. Franco & J. Cruz, two workers, one queen (IAvH: IAvH27267); Finca La Herradura, 5.27936 -75.49744, 2020 m, 5–7 Aug. 2003, L.E. Franco & J. Cruz, one worker (IAvH: IAvH27291); Vereda Chambery, Finca Las Garzas, 5.29481 -75.47292, 1980 m, 5–6 July 2003, L.E. Franco & J. Cruz, three workers (IAvH: IAvH55563); Vereda Chupaleros, Finca Alegrias, 5.30633 -75.50028, 1960 m, 27–29 July 2003, L.E. Franco & J. Cruz, three workers (IAvH: IAvH25466); Veredada El Eden, Finca Los Guayacanes, 5.29606 -75.49428, 1984 m, 26 July 2003, L.E. Franco & J. Cruz, one worker, one male (IAvH: IAvH27294); Vereda San José, Finca Casa Roja 5.33348 -75.48892, 1777 m, 07–09 Aug. 2003, L.E.

**Fig. 46** *Brachymyrmex patagonicus*: **a, c, e** head, dorsal, and lateral view of the lectotype worker; **b, d, f** *B. laevis* n. syn.: head, dorsal, and lateral view of a syntype worker



Franco & J. Cruz, two workers (IAvH: IAvH25462, 25,463); Salamina, Vereda El Cedrito, Finca El Cedrito, 5.33197 -75.46785, 1960 m, 27–28 July 2003, L.E. Franco & J. Cruz, three workers (IAvH: IAvH25470, 25472); **Córdoba**: Monteria, 29 June 2009, Juan C. Abadia, three workers (ICN); **Cundinamarca**: Villeta, Conjunto Residencial Las Acacias, 5.01361 -74.47306, 11 Jan. 2010, C.M. Ortiz, 8 workers (ICN); **Quindío**: Filandia, Vereda Cruces, Finca Los Micos, 4.70452 -75.64665, 1800 m, 12–14 July 2002, E. Jimenez & L.E. Franco, two workers (IAvH: IAvH27227, 27240); **Valle del Cauca**: bosque Yotoco, 1575 m, 23 June 1989, W.P.MacKay #11720, one worker (WEMC: USNMENT00757995); Medio Calima, 24 June 1989, E. MacKay #11744, three workers, one queen (WEMC: USNMENT00759012, 00759013). **COSTA RICA**: **Alajuela**: Juan Santa Maria airport, 9.98 -84.20,

900 m, 09 Jan. 1999, J. Longino #3958-s, one worker (JTLC: LACM ENT 142311); **Heredia**: Estación Biológica la Selva, 10.433 -84.017, May 1994, J. Longino #3625, one worker (JTLC: INBIOCRI001260979); 10.423 -84.001, 50 m, 04 Aug. 2004, W. & E. Mackay #20890, one worker (WEMC: USNMENT00758039); 06 Aug. 2004, W. & E. Mackay #20917, one worker (WEMC: USNMENT00757982); **Limon**: 3 km SSE Cahuita, 9.71667 -82.83333, 70 m, 24 Dec. 1983, P.S. Ward #6530–40, three workers (PSWC: USNMENT00758007); **Puntarenas**: Estación Biológica Los Llanos, 10.30487 -84.83735, 1150 m, 28 Feb. 2004, J. Longino, one worker (JTLC: JTLC000005287); 6 km S Monteverde, 10.25 -84.82, 800 m, 22 June 1999, J. Longino, one worker, one queen (JTLC: LACM ENT 143543). **ECUADOR**: **Chimborazo**: Huigra, -2.29417 -78.98861, 1200 m, 18



**Fig. 47** *Brachymyrmex patagonicus*: **a–c** *B. patagonicus* var. *atratula*: head, dorsal, and lateral view of a syntype worker

Feb. 2004, Roger Vila I-457, two workers (ICN: USNMENT00758037). **GUATEMALA: El Progreso:** 3.8 km E. San Cristobal, 14.91850 -90.04075, 302 m, 19 July 2004, W. & E. MacKay #20586, three workers (WEMC: USNMENT00759006); **Santa Rosa:** 5 km SW Cuilapa, 14.23333 -90.33333, 575 m, 14 Nov. 2003, A.L.

Wild #AW2030, one worker (ALWC: USNMENT00758009); **Suchitepéquez:** Finca Tarrales, 12.3 km N Patulul, 14.52256 -91.13642, 740 m, 30 July 2004, W. & E. MacKay #20782, two workers (WEMC: USNMENT00757688, 00757983). **HONDURAS:** La Lima, 23 Jan. 1960, C. Evers, UFC-217-35 (6871), five workers, one male (MZSP: USNMENT00757621, 00757622). **JAPAN:** Hyogo, Kob, Port Island, 34.67 135.20, 18 Sep. 2007, M. Yoshimura, one worker (ICN: MY1862–12). **MEXICO: Federal:** Mexico City, 6.5 km E Chalma, 26 May 1998, W. MacKay #10386, one worker, two males (WEMC: USNMENT00757993); **Guanajuato:** Highway 57, km 306, Rancho Jardin, 21.14224 -100.95341, 10 Aug. 1965, Cornell University, one worker (MCZC: USNMENT00759002); **Jalisco:** 6 km N El Tuito, 20.3667 -105.3167, 730 m, 31 Dec. 1987, P.S. Ward #9327–11, two workers (PSWC: USNMENT00757679); **Nuevo Leon:** 8 km W. Iturbide, 09 Nov. 1946, W.S. Ross, ANTC10261, two workers (CPDC: CASENT0196003); **Nayarit:** 19.3 km S Rosamorada, 21.94389 -105.20639, 51 m, 19 June 2000, W. & E. MacKay #19126, two workers (WEMC: USNMENT00757983); **Oaxaca:** 148 km NE Oaxaca Rt175, 17.02647 -96.71947, 1210 m, 04 June 1988, W. MacKay #10825, three workers (WEMC: USNMENT00757732); 1.6 km E Reforma, near Tuxtepec, 18.08078 -96.13677, 12–15 Aug. 1973, A. Newton, one worker (MCZC: USNMENT00757680); **Puebla:** 6.5 km W Izucar Matamoros, 1220 m, 26 May 1988, W. MacKay, one worker, one male (WEMC: USNMENT00757991); **San Luis de Potosi:** 10 km S San Luis Potosi, 21 May 1988, W.P. MacKay #10307 #10308, six workers, two males, one queen (WEMC: USNMENT00757685, 00759015, 00759017); 16 km S San Luis Potosi, 21 May 1988, W.P. MacKay #10307, two workers, one male (WEMC: USNMENT00758006); 11 km N Cardenas, 1720 m, 09 June 1988, W. MacKay #1095, one worker, two males (WEMC: USNMENT00759027); **Tamaulipas:** 32.3 km SE Ciudad Victoria, 23.49161 -96.97775, 289 m, 24 Mar. 2008, W. & E. MacKay #22930, two workers (WEMC: USNMENT00757681, 00757687); Gomez Farias, 25 Sep. 1987, A. Rebeles #10096, one worker (WEMC: USNMENT00757994); **Veracruz:** Los Tuxlas, July 2001, A. Pezon, one worker (CPDC: USNMENT00757989); Xalapa, V. Rico Gray #17209, four workers (MCZC: USNMENT00759026, 00758044). **PARAGUAY: Canindeyú:** Reserva Natural Bosque Mbaracayú, Aguara Ñu, -24.18333 -55.28333, 240 m, 16 Nov. 2002, A. L. Wild, one worker (ALWC: USNMENT00757971); **Itapúa:** Isla Yacyretá, -27.41667 -56.75417, 25 Sep. 1997, B. Barrios #ibn 216, one worker (ALWC: USNMENT00757683); **Presidente Hayes:** 5 km SSE Pozo Colorado, -23.55 -58.77, 140 m, 05 Dec. 2002, A.L. Wild #AW1764, one worker (ALWC: USNMENT00758010). **URUGUAY: Salta:** Salta,

Parque Municipal Benito Solari, 25 Dec. 2007, W. & E. MacKay #22634, one worker (WEMC: USNMENT00757731).

**Diagnosis.** *Brachymyrmex patagonicus* morphologically resembles *B. bruchi* and *B. oculatus*, because all three species have scapes that surpass the posterior margin of the head by a length approximately equal to the maximum diameter of the eye or less, they usually have two erect hairs on the mesonotum, which does not bulge dorsally above the pronotum in lateral view, the metanotal groove is absent or narrower than the diameter of the metathoracic spiracles, their gaster has scarce pubescence and several scattered long erect hairs, the body is uniformly brownish. *Brachymyrmex patagonicus* differs from *B. bruchi*, however, by usually having two erect hairs on the pronotum and two on the mesonotum and from *B. oculatus* by having smaller eyes, with a maximal diameter of approximately 1/4th of the length of the head ( $HL_1$ ) and usually with less than 14 ommatidia along their maximal diameter.

*Types measurements* (mm) ( $n = 2$ ).  $HL_1$  0.45–0.53;  $HL_2$  0.33–0.37;  $HL_3$  0.10–0.13; HW 0.38–0.49; SL 0.40–0.48; EL 0.14–0.17; WL 0.38–0.51; PnL 0.11–0.15; PnW 0.26–0.33; ML 0.07–0.11; MW 0.17–0.24; *Indices* CI 85.29–92.50;  $SI_1$  97.30–103.45;  $SI_2$  120.00–128.57;  $OI_1$  33.78–36.21;  $OI_2$  22.06–25.00.

*Additional material examined measurements* (mm) ( $n = 13$ ).  $HL_1$  0.40–0.59;  $HL_2$  0.28–0.39;  $HL_3$  0.07–0.16; HW 0.33–0.51; SL 0.35–0.49; EL 0.09–0.14; WL 0.35–0.55; PnL 0.09–0.20; PnW 0.23–0.35; ML 0.07–0.14; MW 0.15–0.23; *Indices* CI 81.40–93.33;  $SI_1$  92.00–128.95;  $SI_2$  116.22–163.33;  $OI_1$  22.22–32.5;  $OI_2$  18.18–28.57.

**Description.** *Head.* Slightly longer than wide in full face view; posterior cephalic margin slightly concave. Dorsum of head with sparse appressed hairs. Clypeus with a rounded anterior margin and five long, erect hairs of which a single, usually conspicuous hair is near the anterior margin, two hairs are in mediolateral position, and two more near the toruli; other hairs on the clypeus are markedly shorter and appressed or decumbent. Toruli surpassing the posterior clypeal margin in oblique anterodorsal view. The scapes surpass the posterior cephalic margin by a length that is shorter than the maximal diameter of the eye; they have appressed hairs. At least one central ocellus is present. Eyes are positioned on the cephalic midline and have 8–12 ommatidia along their maximal diameter.

*Mesosoma.* Dorsum of the mesosoma with sparse appressed hairs, typically with two erect hairs on the pronotum and two on the mesonotum. The mesonotum is not inflated and does not bulge dorsally above the pronotum. Metanotal groove absent or narrower than the diameter of the metathoracic spiracles. Metathoracic spiracles in dorsolateral position, not protruding, and touching the propodeal suture. Dorsum of

the propodeum slightly convex and shorter than the propodeal slope. Propodeal spiracles circular, situated on the posterior propodeal margin, at the middle of the propodeal slope. Legs with appressed and scattered hairs. Petiole short and inclined forward.

*Gaster.* With scattered pubescence and several scattered long erect hairs, mainly at the edges of the segments.

*Color and sculpture.* Body overall smooth and shiny, except for the sometimes slightly imbricate sculpture on the dorsum of the mesosoma, and typically uniformly brownish.

**Distribution** (supplementary material Fig. S34). *Brachymyrmex patagonicus* is widespread and known from Argentina, Brazil, Colombia, Chile, Costa Rica, Ecuador, Guatemala, Honduras, Mexico, Paraguay, Uruguay, and it has been introduced in Japan (Ortiz-Sepulveda pers. obs.) and the USA (MacGown et al. 2007).

**Biology.** MacGown et al. (2007) indicated that *B. patagonicus* nests in a variety of habitats, both natural and disturbed, ranging from pine forests over mixed forest and prairie to urban environments. Colonies may contain many hundreds of workers packed into a small sheltered area. Where this species is found, colonies are often abundant and within a few centimeters from one another. Nests can be found in loose tree bark, at the base of plants, in soil, dead wood and organic litter, or below natural and man-made objects. The species is considered a nuisance pest, as both alates and foraging workers may enter man-made structures to forage and/or nest (MacGown et al. 2007).

**Remarks.** As Quirán et al. (2004) already indicated Mayr (1868) described *B. patagonicus* based on specimens from Argentina. However, the specimens in the NHMW: USNMENT00757201–00757204 that were examined and identified as types by Mayr are from Chile. Either the locality indicated in the original description may be wrong, or specimens from Argentina may be lacking from the collection, and as such we do not designate a lectotype here.

Emery (1895), upon describing *B. laevis* (which is sometimes misspelled as *B. levis*, e.g., Emery (1906: 178); Santschi (1923a: 659)), indicated that it is closely related to *B. patagonicus* and to the dark forms of *B. heeri*, but he considered *B. laevis* distinct by having a smooth and shiny tegument of the head. However, a description of the species is not provided, and after examining the type material of *B. laevis* we have not identified any consistent morphological differences compared to *B. patagonicus* so that we synonymize the species here.

*Brachymyrmex patagonicus* displays variation in color from light to dark brown; *B. patagonicus* var. *atrátula* was described by Santschi (1923a) as a variety with darker, almost black tegument, and a smooth and shiny body. Evaluating these morphological differences Quirán et al. (2004) suggested that *B. patagonicus* var. *atrátula* is a junior synonym of *B. patagonicus*, and we agree with this decision.

Guénard (2018) reports the first record of *B. patagonicus* from continental Asia (Hong Kong); however, the specimen illustrated in the paper does not display the diagnostic features of this species, but rather those of *B. cordemoyi*. It is noteworthy that *B. patagonicus* is very abundant and geographically widespread, but its morphological variation and genetic diversity as well as other biological features remain poorly studied. An in-depth study of these features in a geographic context would be required to determine if *B. patagonicus* is a distinct species, a species complex, or conspecific with some other taxa, e.g., *B. bruchi* and *B. obscurior*.

*Brachymyrmex pictus* Mayr

(Fig. 48, supplementary material Fig. S35)

*Brachymyrmex pictus* Mayr, 1887: 522 (w.q.). Lectotype worker (NHMW: ANTWEB CASENT0915735) and paralectotype worker (NHMW; MHNG: USNMENT00758144; here designated): three workers [examined]. **BRAZIL: Santa Catharina.**

= *B. heeri* var. *basalis* Wheeler, 1921: 166 (w.). [not examined]. **GUYANA.** Kartabo, Puruni trail. n. syn.

= *B. pictus* subsp. *balboae* Wheeler, 1942: 253 (w.q.m.). (MCZC: M.C.Z. Cotype 1–3, 4–6, 7–9, 21,438): two workers, eight queens, two males [examined]. **PANAMA:** Balboa. n. syn.

**Additional material examined. BOLIVIA: Santa Cruz:** 35 km SSE Flor de Oro, -13.83333 -60.87763, 450 m, 01 Dec. 1993, P.S. Ward #12232, three workers, one male (MCZC: CMOS000012, CMOS000013). **BRAZIL: Amazonas:** 11 Sep. 1962, W.L. Brown, three workers (MCZC: CMOS000002); Aleixo nr. Manaus, 11 Sep. 1962, W. L. Brown, eight workers, two males, six queens (MCZC: CMOS000004, CMOS000006, CMOS000009–000011); Peredão Rd. S. of Manaus, 02 Sep. 1962; W. L. Brown, 12 workers (MCZC: CMOS000003, CMOS000005, CMOS000007, CMOS000008); **Bahia:** Ilheus, 27 Mar. 1997, C.S.F. Mariano, four workers (CPDC: USNMENT00757794); **Espirito Santo:** Nov. 1977, M. Alvarenga, four workers (MZSP: USNMENT00757785); **São Paulo:** Caraguatutuba, Reserva Florestal, 40 m, 22 May–01 June 1962, Exp. Dep. Zool. 2056, eight workers (MZSP: USNMENT00757676, 00757783); Ilha dos Pescadores (Ilha da Vitoria), 24 Mar. 1964, two workers, two queens (MZSP: USNMENT00757604); Ubatuba, Picinguaba, July 2011, nine workers (ICN: USNMENT00759053). **COLOMBIA: Cauca:** Isla Gorgona, 11 Sep. 1989, M. Baena #GQA-05, three workers (WEMC: USNMENT00757796, 00757797); **Magdalena:** 2 km ESE Minca, 11.13 -74.10, 780 m, 13 Aug. 1985, P.S. ward #7895, two workers, one queen (PSWC: USNMENT00757792); **Putumayo:** Parque Nacional La Paya, Cabaña La Paya, -0.03, -75.20, 330 m, 15–30 Sep. 2002, A. Morales, one worker (IAvH). **COSTA**

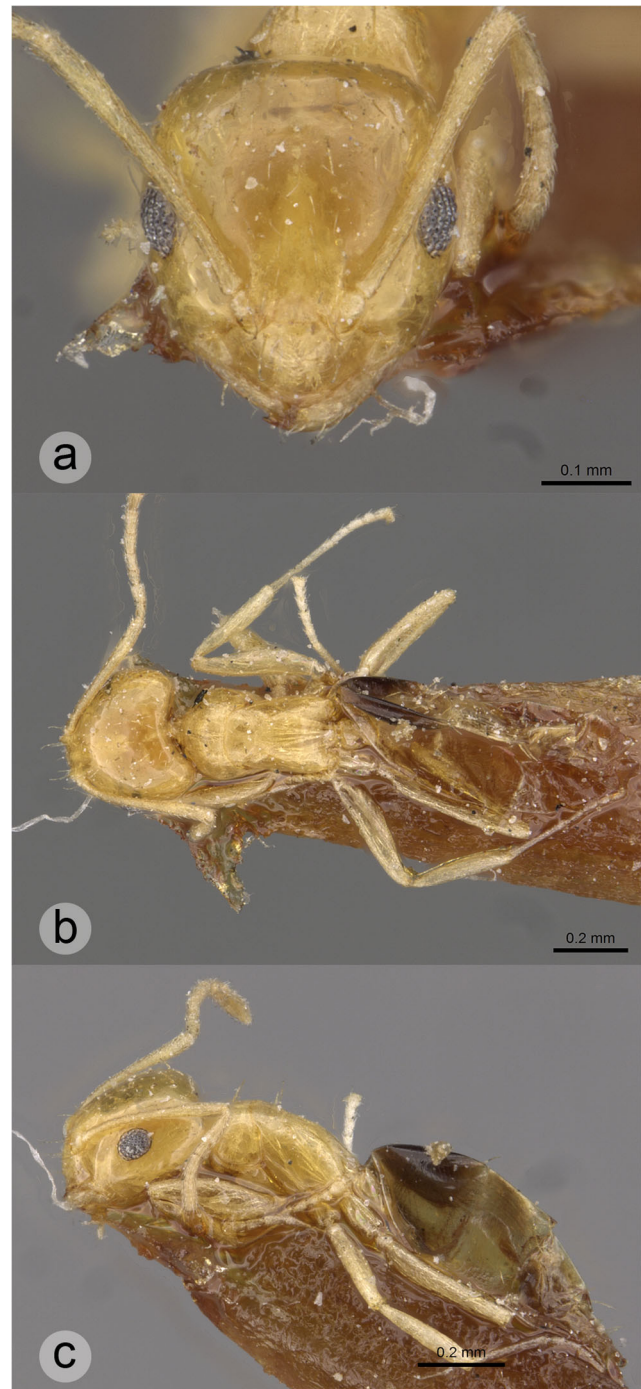


Fig. 48 *Brachymyrmex pictus*: a–c head, dorsal, and lateral view of a syntype worker (from [www.antweb.org](http://www.antweb.org); photographer: Zach Lieberman)

**RICA: Puntarenas:** Parque Natural Corcovado, Sirena, 8.483 -83.583; 23 Apr. 1981, J. Longino, one worker, one queen (JTLC000005913, 000005914); 14 June 1982, J. Longino, two workers (MCZC: USNMENT00757793); Reserva Biologica Carara, 9.78 -84.60, 30 m, 24 July 1985, P.S. Ward #7615, two workers, one queen (PSWC: USNMENT00757784); Reserva Biologica Carara, Estación Quebrada Bonita, 9.78 -84.60, 30 m, 24 July 1985, J.

Longino #0562, one worker, one queen (JTLC: JTLC000006051). **ECUADOR: Esmeraldas:** 6.1 km E Rio Verde, 1.07694, -79.41389, 13 July 2005, W. & E. MacKay #21098, one worker (WEMC: USNMENT00757791); **Manabí:** 20 km NE Chone, 300 m, 1976, S. & J. Peck, two workers (MCZC: CMOS000014); **Pichincha:** Cotopaxi, 19 km ENE La Maná, -0.88 -79.05, 1100 m, 10 Aug. 1991, P.S. Ward #11418-23, one worker (MCZC: USNMENT00758017). **FRENCH GUIANA:** Saint Elie-K, 4.82261, -53.27649, Apr. 2002, J. Orivel & J. Le Breton, six workers, one queen (CPDC: USNMENT00757786, 00757787). **GUATEMALA: Petén:** Finca Ixobel, 83 km SE Flores, 16.30367, -89.42353, 365 m, 25 July 2004, W. & E. MacKay #20694, one worker, one male, one queen (WEMC: USNMENT00758998); **GUYANA:** Rupununi, Apoteri, 4.08333 -58.58333, 100 m, 12 Jan. 1981, J. Longino, one worker (JTLC: JTLC000005918). **JAMAICA:** Saint Andrew: Cinchona, 18.067 -76.650, 1450 m, 19 Mar. 1984, one worker (JTLC: JTLC000005924). **PANAMA:** Gamboa, Parque, 9.11722 -79.69972, 24 Apr. 1988, D. Quintero #1, two workers (WEMC: USNMENT00757795). **PERU: Madre de Dios:** Tambopata, 15 km NE Puerto Maldonado, June 1989, S.P. Cover & J.E. Tobin, JT 219 CA-740, two workers (MCZC: CMOS000032). **VENEZUELA: Bolívar:** Canaima, Orchid Is., 14 Oct. 1988, W. MacKay #11165, eight workers, three males, one queen (WEMC: USNMENT0075778800757790, 00757960, 00758997).

**Diagnosis.** The unique feature for *B. pictus* is a conspicuous color difference between the head and thorax, which are yellow and the gaster, which is black, or yellow with (a) black spot(s).

*Additional material examined measurements* (mm) ( $n = 1$ ). HL<sub>1</sub> 0.43; HL<sub>2</sub> n.a.; HL<sub>3</sub> 0.08; HW 0.38; SL 0.38; EL 0.11; WL 0.44; PnL n.a.; PnW n.a.; ML 0.09; MW 0.18; *Indices* CI 89.58; SI<sub>1</sub> 100.00; SI<sub>2</sub> n.a.; OI<sub>1</sub> 26.83; OI<sub>2</sub> 28.57.

**Description.** *Head.* Slightly longer than wide in full face view; posterior cephalic margin flat. Dorsum of the head has sparse appressed hairs. Clypeus with a rounded anterior margin and five long, erect hairs of which a single, usually conspicuous hair is near the anterior margin, two hairs are in mediolateral position, and two more near the toruli; other hairs on the clypeus are markedly shorter and appressed or decumbent. Toruli surpassing the posterior clypeal margin in oblique anterodorsal view. The scapes surpass the posterior cephalic margin by a length that is smaller than the maximal diameter of the eye; they have appressed hairs. Three ocelli present. Eyes are positioned on the cephalic midline and have 7–10 ommatidia along their maximal diameter.

*Mesosoma.* Typically with two erect hairs on the pronotum and two on the mesonotum. The mesonotum is not inflated and does not bulge dorsally above the pronotum in lateral view. The mesometanotal suture is directly visible; however, there is no marked constriction between the

mesonotum and metanotum, and as a result the metanotal groove is absent. Metathoracic spiracles widely separated in dorsolateral position, not protruding, and touching the propodeal suture. Dorsum of the propodeum flat and shorter than the propodeal slope. Propodeal spiracles circular, situated slightly ventral to the posterior propodeal margin, and slightly posterior of the middle of the propodeal slope. Legs with appressed and scattered hairs. Petiole short and inclined forward.

*Gaster.* With scattered pubescence and several scattered long erect hairs.

*Color and sculpture.* Body smooth and shiny. The head and thorax are yellowish, whereas the gaster is either totally black or yellowish with one or more black spots.

**Distribution** (Supplementary material Fig. S35). *Brachymyrmex pictus* is known to occur in Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guatemala, Guyana, Jamaica, Panama, Peru, and Venezuela.

**Biology.** The colony of *B. heeri* var. *basalis* reported by Wheeler (1921) and Wheeler (1942) was small but nevertheless contained brood. It was found in hollow petioles of a small *Tachigalia paniculata* tree on the Puruni trail at Kartabi, Guyana. Several colonies of *B. pictus* subsp. *balboae* were found to be nesting in hollow twigs of *Tripalis americana* at Balboa, Panama (Wheeler 1942). No biological information exists on typical *B. pictus*, but it seems this species is arboreal.

**Remarks.** One of the specimens determined as a syntype of *B. pictus* (NHMW: CASENT0915734) displays the diagnostic features of *B. admotus*. Given that both species were described by Mayr (1887) in the same publication from the same type locality, we consider the identification of this specimen to be a labeling mistake. Upon describing *B. pictus*, Mayr (1887) did not provide any information on the diagnostic features he considered relevant to distinguish *B. pictus* from other *Brachymyrmex* species. Wheeler (1921) described *B. heeri* var. *basalis*, but he did not provide any morphological description for his typical *B. heeri* specimens nor for the variety. The only feature described for *B. heeri* var. *basalis* is its yellow body with a black first segment of the gaster (which to our knowledge only fits with the characters of *B. pictus*). Other complications are that the material has not been illustrated, that both the typical form and the variety were found on the same tree species and the same locality, and that we have not been able to locate the material. Later, Wheeler (1942) continued to consider his specimens of *B. heeri* and *B. heeri* var. *basalis* to be distinct of *B. pictus*. Given the information available, we consider it likely that *B. heeri* var. *basalis* belongs to *B. pictus*, but we cannot comment on the taxonomic status of his typical *B. heeri* specimens for now.

Fortunately, Wheeler (1942) provided a description of *B. pictus* subsp. *balboae*, which indicates that it differs from the typical *B. pictus* only by being smaller. It is indeed somewhat



smaller (1.0–1.2 mm) than the typical form described by Mayr (1887; 1.3–1.6 mm); however, after studying the material, we consider this difference to likely represent geographic variation, and we synonymize this subspecies here, although a better characterization of the variation in *B. pictus* is required.

*Brachymyrmex pilipes* Mayr

(Fig. 49, supplementary material Fig. S36)

*Brachymyrmex pilipes* Mayr, 1887: 524 (q.m.). Lectotype queen (NHMW) and paralectotype queen, male (NHMW): two queens, one male [examined]. **BRAZIL: Santa Catharina.** Santschi (1929: 310) (w.). (NHMB): two major workers, two minor workers, one queen [examined]. **BRAZIL: Parana: Rio Negro.** Combination in *Brachymyrmex* (*Brytscha*): Santschi (1923a: 674). See also: Ortiz and Fernández (2014: 19, Figs. 7, 8, 9, 10, 11, and 12).

**Diagnosis.** *Brachymyrmex pilipes* morphologically resembles *B. micromegas* because both species have a dimorphic

worker caste, tumuliform metathoracic spiracles, toruli that touch the posterior clypeal margin, but never surpass it (best observed in oblique anterodorsal view) and a clypeus with a row of long thick hairs near the anterior margin. However, *B. pilipes* differs from *B. micromegas* by the fine, longitudinal striations on most of the mesosoma, and by usually having a gaster of darker color than the rest of the body.

**Description.** See Ortiz and Fernández (2014).

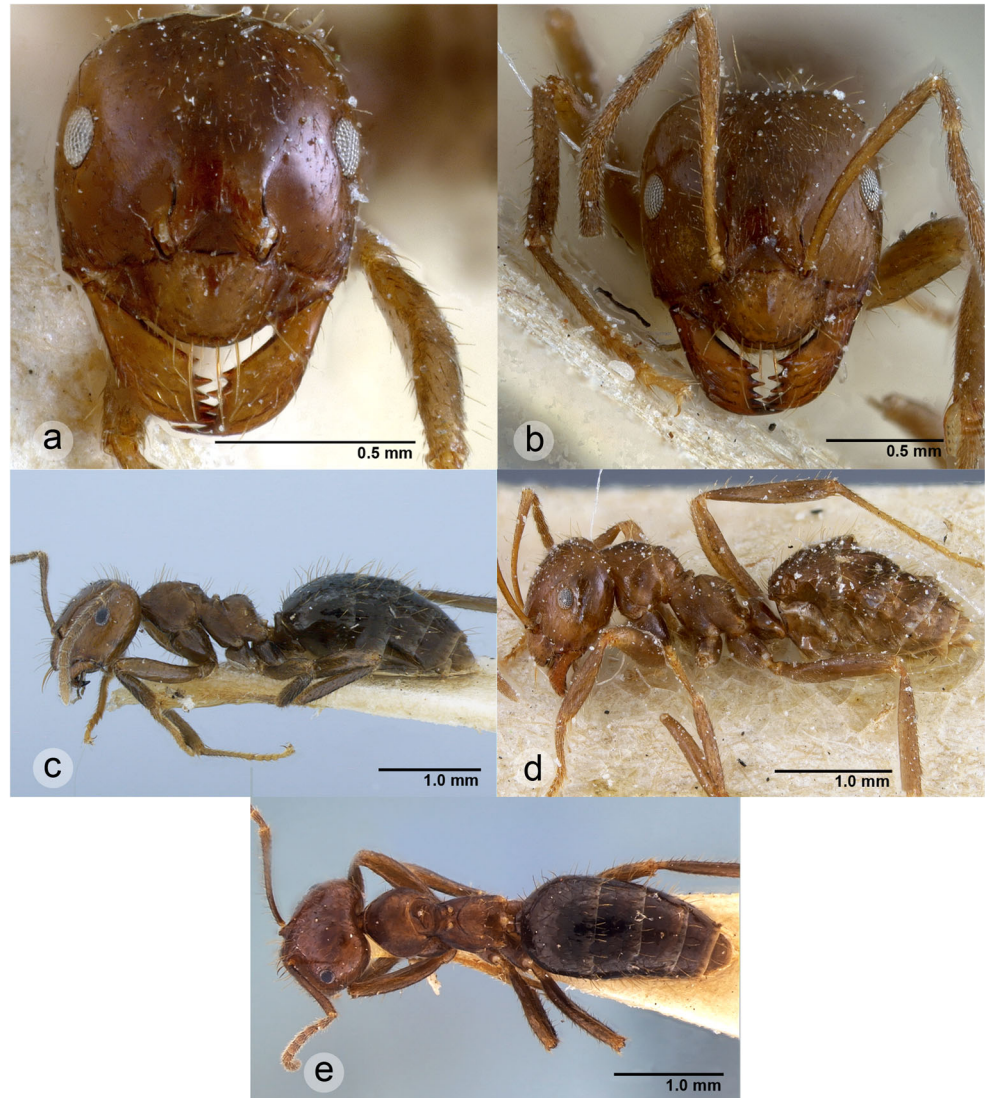
*Brachymyrmex santschii* Menozzi

(Fig. 50, supplementary material Fig. S37)

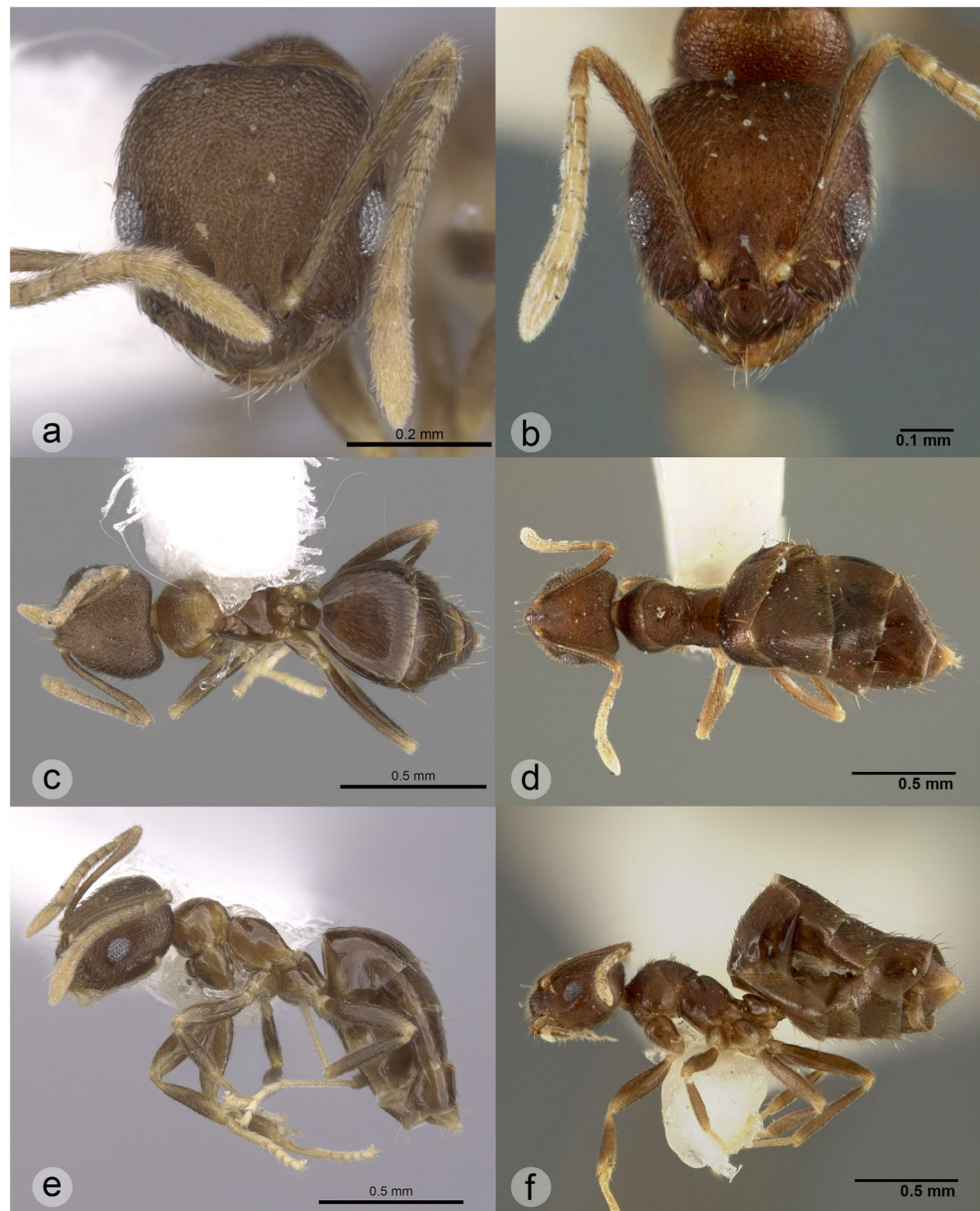
*Brachymyrmex santschii* Menozzi, 1927: 338, Fig. 5 (w.). [not examined]. **COSTA RICA: San José.**

**Additional material examined. COSTA RICA: Cartago:** 2 km N Cervantes, 1600 m, Jan. 1973, W.L. Brown, four workers, two putative worker-queen intercastes (MCZC: CMOS000098, USNMMENT00757750–00757751); **Guanacaste:** Rincon de la Vieja, Las Pailas 7676,

**Fig. 49** *Brachymyrmex pilipes*: a, c, e head, dorsal, and lateral view of the minor worker lectotype; b, d head, dorsal, and lateral view of a major worker



**Fig. 50** *Brachymyrmex santschii*: **a, c, e** head, dorsal, and lateral view of a worker (from [www.antweb.org](http://www.antweb.org); photographer: Will Ericson); **b, d, f** head, dorsal, and lateral view of a putative worker-queen intercaste



10.77556–85.34528, 1400 m, 18 Feb. 1996, R. Anderson, two workers (WEMC: USNMENT00757753, 00757754); **Puntarenas:** Monteverde, 10.30–84.83, 1400 m, Apr.–May 1987, S. Little, one worker (JTLC: JTLC000005243); Monteverde, 10.2964–84.7831, 1550 m, 18 Jan. 2003, L.A. Schonberg, one worker (JTLC: JTLC000005055); **San José:** Cerros de Escazu, 2 km S Antonio, 1650 m, 13 June 1997, R. Anderson #186880C, one worker (WEMC: USNMENT00757593). **PANAMA: Chiriqui:** Volcan Hartman's, Finca #17815, 1450 m, 14 June 1996, R.S. Anderson, one worker (WEMC: USNMENT00757752).

**Diagnosis.** *Brachymyrmex santschii* morphologically resembles *B. iridescens*, because both species have the head and the mesosoma with strongly alveolate sculpture. However, they can be distinguished from one another because *B. santschii* has a

metanotal groove that is wider than the diameter of the metathoracic spiracles, scapes that surpass the posterior margin of the head, and a gaster with scattered pubescence.

*Additional material examined measurements* (mm) ( $n = 4$ ). HL<sub>1</sub> 0.40–0.44; HL<sub>2</sub> 0.29–0.30; HL<sub>3</sub> 0.08–0.10; HW 0.37–0.40; SL 0.39–0.42; EL 0.09–0.11; PnL 0.11–0.13; PnW 0.24–0.28; ML 0.09; MW 0.13–0.17; *Indices* CI 89.80–91.82; SI<sub>1</sub> 102.27–109.76; SI<sub>2</sub> 136.36–138.24; OI<sub>1</sub> 24.39–26.84; OI<sub>2</sub> 20.00–24.44.

**Worker description.** *Head.* Longer than wide in full face view; posterior cephalic margin flat or slightly concave. Dorsum of the head with subdecumbent hairs. Clypeus with a rounded anterior margin and five long, erect hairs of which a single, usually conspicuous hair is near the anterior margin, two hairs are in mediolateral position, and two more near the

toruli; other hairs on the clypeus are markedly shorter and appressed or decumbent. Toruli surpassing the posterior clypeal margin in oblique anterodorsal view. The scapes surpass the posterior margin of the head by a length approximately equal to the maximal diameter of the eye; they bear appressed hairs. Three conspicuous ocelli are present. Eyes are positioned on the cephalic midline and have 8–9 ommatidia along their maximal diameter.

**Mesosoma.** Dorsum subsinusoidal in lateral view. Without erect hairs, but with decumbent hairs on the promesonotum. The mesonotum is variable, typically not or weakly inflated, and not or slightly bulging dorsally above the pronotum in lateral view. Metanotal groove wider than the diameter of the metathoracic spiracles. Metathoracic spiracles in dorsal position, not protruding and not touching any sutures. Dorsum of the propodeum slightly convex and shorter than the propodeal slope. Propodeal spiracles circular, positioned on the posterior propodeal margin, at the middle of the propodeal slope. Legs with appressed hairs. Petiole short and inclined forward.

**Gaster.** With scattered pubescence and long erect hairs at the edges of the segments.

**Color and sculpture.** Head and dorsum of the mesosoma finely alveolate, those parts that are not sculptured, including the gaster, are smooth and shiny. The body is brownish, but sometimes the antennae, tarsi, and articulations of the legs are more yellowish.

**Intercaste description.** The morphology of the putative worker-queen intercaste differs from that of the worker by its larger body size, the eyes that have around ten ommatidia along their maximal diameter, its strongly expanded mesonotum, the absence of a metanotal groove, the dorsolateral position of the metathoracic spiracles, the less convex dorsum of the propodeum, and a markedly expanded gaster with dense pubescence.

**Distribution** (Supplementary material Fig. S37). *Brachymyrmex santschii* is known from Costa Rica and Panama.

**Biology.** Unknown.

**Remarks.** Menozzi (1927) considered *B. santschii* to differ from any other *Brachymyrmex* species by its sculpture and pubescence. He described the sculpture as strongly punctuate-reticulate; however, following the terminology of Harris (1979), we consider it rather alveolate. We do not designate a lectotype here, as we have not studied the type series, which would be deposited at the German Entomological Institute in Berlin-Dahlem.

#### *Brachymyrmex sosai* NEW SPECIES

(Fig. 51, supplementary material Fig. S38)

Holotype worker (UNMSM: USNMENT00757760) and paratype workers (UNMSM: USNMENT00759061, 00759062): 3 workers, (USNM: USNMENT01128655, 01128760): two workers, one vial (USNM: USNMENT00526429): 15 workers, five pupae, five larvae,

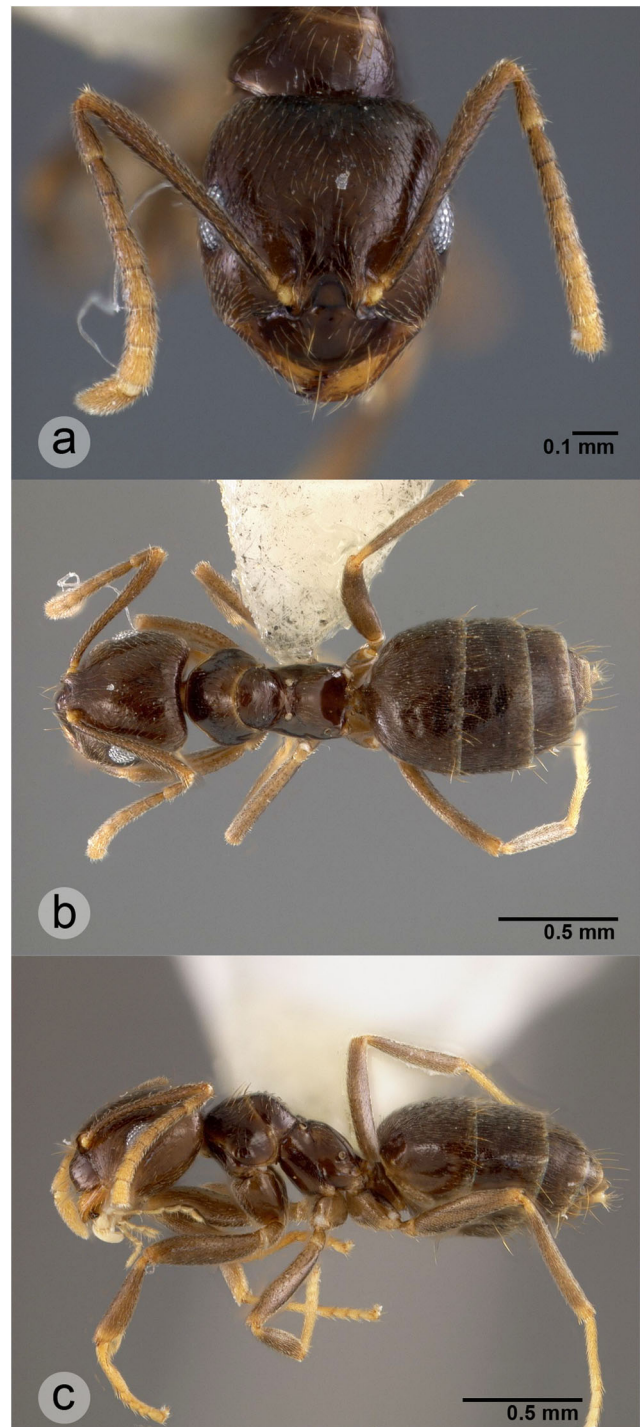


Fig. 51 *Brachymyrmex sosai* n. sp.: a–c head, dorsal, and lateral view of the holotype worker

one vial in Biorepository (USNM: USNMENT01414589): five workers, (USNMENT 01128762): one queen. **PERU:** Cusco: Paucartambo, Kcosñipata, Predio Los Wayqechas, ACCA [Asociacion para la Conservacion de la Cuenca Amazonica], -13.17956 -71.60556, 2825 m, Andean Forest, J. Sosa-Calvo, JSC040920–04.

**Additional material examined. BOLIVIA: Santa Cruz:** 32.8 km N Comparapa, Kara Huasi, -18.05972 -63.91056, 21 Jan. 1999, R. Anderson #18567, one worker (WEMC: USNMENT00759024); **PERU: Lima:** Zárate forest, 2850 m, N. Valencia, I. Frank, 16 workers (MCZC: USNMENT00757314–00757320).

**Etymology:** In honor of Dr. Jeffrey Sosa-Calvo, the collector, for his unconditional support and friendship.

**Diagnosis.** *Brachymyrmex sosai* n. sp. does not have a specific unique feature but rather a unique combination of features that render it distinct: its scapes surpass the posterior margin of the head by a length approximately equal to the maximal diameter of the eye, the dorsum of the mesosoma does not have conspicuous sculpture, a metanotal groove is present, the metathoracic spiracles are in dorsal position, and the dorsal margin of the mesonotum is strongly antero-posteriorly inclined. Some features of this species are reminiscent of *B. antennatus*; however, *B. sosai* differs from this species in body color, the color of the hairs, the length of the scapes, and in having an antennal funiculus with the second segment shorter than the first.

**Holotype measurements** (mm) HL<sub>1</sub> 0.57; HL<sub>2</sub> 0.35; HL<sub>3</sub> 0.16; HW 0.53; SL 0.59; EL 0.14; WL 0.68; PnL 0.21; PnW 0.33; ML 0.16; MW 0.21; **Indices** CI 93.10; SI<sub>1</sub> 111.11; SI<sub>2</sub> 166.67; OI<sub>1</sub> 25.93; OI<sub>2</sub> 27.59.

**Paratypes measurements** (*n* = 3) HL<sub>1</sub> 0.60–0.62; HL<sub>2</sub> 0.41–0.43; HL<sub>3</sub> 0.16–0.20; HW 0.57–0.60; SL 0.59–0.62; EL 0.14–0.16; WL 0.68–0.72; PnL 0.20–0.23; PnW 0.41; ML 0.18–0.20; MW 0.14–0.27; **Indices** CI 93.55–96.88; SI<sub>1</sub> 103.23–103.45; SI<sub>2</sub> 142.86–145.45; OI<sub>1</sub> 22.58–27.59; OI<sub>2</sub> 25.81–31.25.

**Description.** *Head.* Slightly longer than wide in full face view; posterior cephalic margin flat or slightly concave. Dorsum of the head with scattered appressed hairs. Clypeus with a rounded anterior margin and five long, erect hairs of which a single, usually conspicuous hair is near the anterior margin, two hairs are in mediolateral position, and two more near the toruli; other hairs on the clypeus are markedly shorter and appressed or decumbent. Toruli surpassing the posterior clypeal margin in oblique anterodorsal view. The scapes surpass the posterior margin of the head by a length that exceeds the maximal diameter of the eye. Ocelli typically appear to be absent but some workers have a central ocellus. Eyes are positioned on the cephalic midline and have 9–10 ommatidia along their maximal diameter.

*Mesosoma.* With several semi-erect hairs on the pronotum and scattered decumbent hairs on the promesonotum. The mesonotum is slightly inflated, antero-posteriorly inclined, and it bulges dorsally above the pronotum in lateral view. Metanotal groove present and wider than the diameter of the metathoracic spiracles. Metathoracic spiracles in fully dorsal position, not protruding, and not touching any sutures. Dorsum of the propodeum weakly convex and shorter than

the propodeal slope. Propodeal spiracles circular, positioned slightly ventral of the posterior propodeal margin; they are posterior of the middle of the propodeal slope. Legs with appressed hairs. Petiole short and inclined forward.

*Gaster.* With dense pubescence and scattered long hairs at the edges of the segments.

*Color and sculpture.* Body smooth and shiny, and usually dark brown, but with conspicuously lighter hairs. Additionally, the bulbi of the antennae, the terminal funiculus, the tarsi, and the articulations of the legs are conspicuously yellowish.

**Distribution** (Supplementary material Fig. S38). *Brachymyrmex sosai* is known from Bolivia and Peru.

**Biology.** This species was collected from sandy soil, from below a rock.

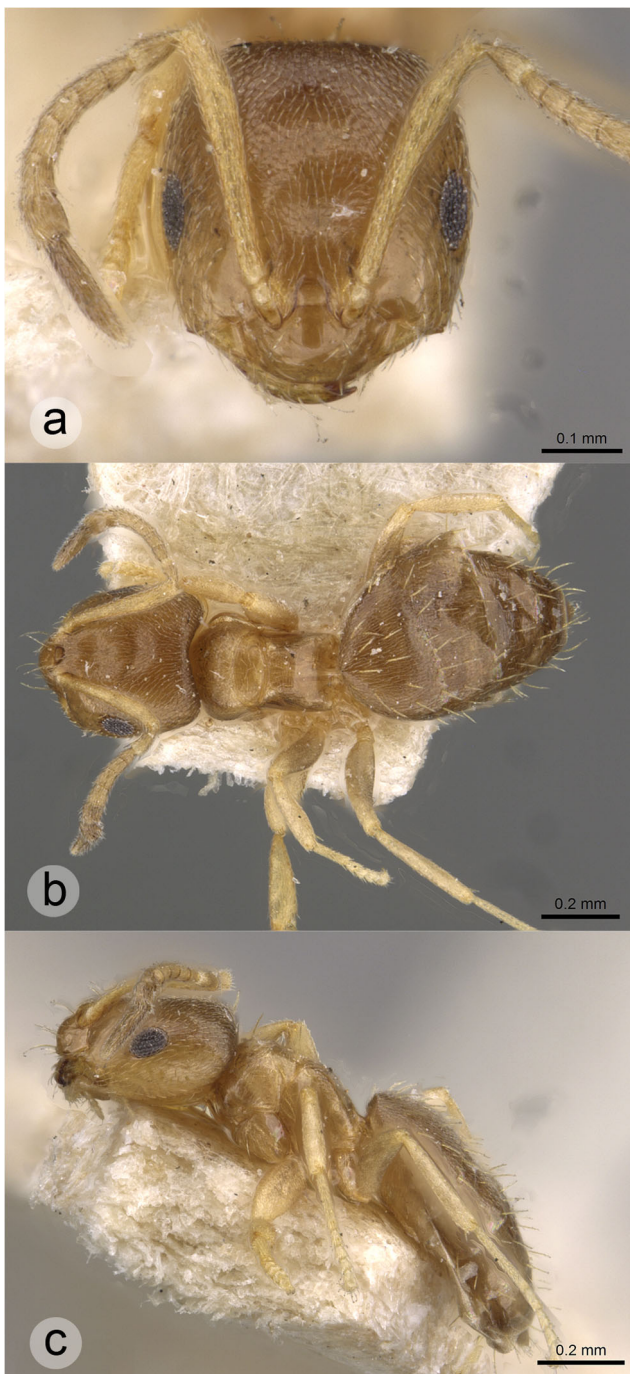
**Remarks.** The single specimen of *B. sosai* known from Bolivia (WEMC: USNMENT00759024) differs in color from the specimens from Peru: its head and thorax are more yellowish than brown and the gaster is darker than the rest of the body. We consider it to be part of *B. sosai* as all other traits match. Currently, *B. sosai* is only known from three localities, and more specimens from additional localities will be required to characterize the intraspecific variation in body color.

*Brachymyrmex termitophilus* Forel

(Fig. 52, supplementary material Fig. S39)

*Brachymyrmex heeri* var. *termitophilus* Forel, 1895b: 179 (w.). Lectotype worker (MHNG: USNMENT00757137) and paralectotype workers, queen (MHNG: USNMENT00757136–00757138; NHMB: USNMENT00758159; MSNG: USNMENT00757139; here designated): six workers, one queen [examined]. **BRAZIL: Rio Grande do Sul:** San Leopoldo, col. Wasmann. Raised to species: Wild (2007: 44).

**Additional material examined. BRAZIL: São Paulo:** Tapirai, -24.03208 -47.46556, 08–14 Jan. 2001, R.R. Silva & Everhardt, two workers (ICN: MZSP170). **COLOMBIA: Norte de Santander:** Parque Nacional Natural Tamá, Vereda El Diamante, Alto Herrera, 7.12278 -72.23472, 1000 m, 26 Nov. 1999, one worker (IAvH: USNMENT00759060). **COSTA RICA: Guanacaste:** Maritza field Station, 10.95694 -85.49389, 03 May 1995, R. Anderson #17716, three workers (WEMC: USNMENT00757632); **DOMINICAN REPUBLIC: Pedemales:** Parque Nacional Sierra Baoruco, “Las Abejas,” 18.15 -71.62, 1320 m, 02 Sep. 2001, A.L. Wild #AW1359, one worker, one male, one queen (ALWC: USNMENT00757918). **MEXICO: Puebla:** 17 km NE Teztlutlán, 1940 m, 07 June 1988, W. MacKay #10879, one worker, one queen (WEMC: USNMENT00758036). **PARAGUAY: Itapúa:** San Miguel Potrero, c/Villa Yacyreta, -27.03 -56.20, 17 Jan. 1996, N.E. Lopez #ibn 227, one worker (ALWC: USNMENT00757662). **USA: Texas:** Sabino Co., 14.5 km E Nempfil, 11 May 1988,



**Fig. 52** *Brachymyrmex termitophilus*: **a–c** head, dorsal, and lateral view of the lectotype worker (from [www.antweb.org](http://www.antweb.org); photographer: Zach Lieberman)

R. Anderson #12763, one worker (WEMC: USNMMENT00758031).

**Diagnosis.** *Brachymyrmex termitophilus* morphologically resembles *B. aphidicola*, *B. australis*, *B. cordemoyi*, and *B. obscurior* because these species have scapes that are usually surpassing the posterior cephalic margin, their eyes are positioned on the cephalic midline, they have two erect hairs on the pronotum and two on the mesonotum, and their

mesonotum does not bulge dorsally above the pronotum in lateral view. *Brachymyrmex termitophilus* differs from *B. australis* and *B. aphidicola*, however, by having dense pubescence on the gaster, and from *B. cordemoyi* and *B. obscurior* by having a yellowish body instead of brownish. *Brachymyrmex termitophilus* also resembles *B. bahamensis* somewhat, but *B. termitophilus* typically bears two erect hairs on the pronotum, whereas *B. bahamensis* approximately six that are moreover much longer.

**Lectotype and paralectotype measurements (mm) ( $n=2$ ).** HL<sub>1</sub> 0.45; HL<sub>2</sub> 0.29–0.31; HL<sub>3</sub> 0.10–0.12; HW 0.39; SL 0.41–0.43; EL 0.10; Pnl 0.12; PnW 0.25–0.27; ML 0.08; MW 0.18; **Indices** CI 89.96; SI<sub>1</sub> 105.00–110.00; SI<sub>2</sub> 131.25–146.67; OI<sub>1</sub> 25.00; OI<sub>2</sub> 21.74–26.09.

**Additional material examined measurements (mm) ( $n=2$ ).** HL<sub>1</sub> 0.43–0.44; HL<sub>2</sub> 0.30; HL<sub>3</sub> 0.10; HW 0.38–0.39; SL 0.33–0.40; EL 0.10; WL 0.42; PnL 0.12; PnW 0.25–0.27; ML 0.08–0.09; MW 0.16–0.18; **Indices** CI 89.80–90.00; SI<sub>1</sub> 85.23–101.11; SI<sub>2</sub> 110.29–133.82; OI<sub>1</sub> 25.56–26.14; OI<sub>2</sub> 22.00–22.45.

**Description.** **Head.** Slightly longer than wide in full face view; posterior cephalic margin flat. Dorsum of the head with sparse appressed hairs. Clypeus with a rounded anterior margin and five long, erect hairs of which a single, usually conspicuous hair is near the anterior margin, two hairs are in mediolateral position, and two more near the toruli; other hairs on the clypeus are markedly shorter and appressed or decumbent. Toruli surpassing the posterior clypeal margin in oblique anterodorsal view. The scapes surpass the posterior margin of the head by a length equal to the maximal diameter of the eye or less; they have appressed hairs. Ocelli inconspicuous. Eyes are positioned on the cephalic midline and have 7–9 ommatidia along their maximal diameter.

**Mesosoma.** Typically with two erect hairs on the pronotum and two on the mesonotum. The mesonotum is not inflated and does not bulge dorsally above the pronotum in lateral view. Metanotal groove absent or narrower than the diameter of the metathoracic spiracles. Metathoracic spiracles in dorso-lateral position, not protruding, and usually touching the propodeal sutures. Dorsum of the propodeum is convex and shorter than the propodeal slope. Propodeal spiracles circular, positioned slightly ventral of the posterior propodeal margin, at the middle of the propodeal slope. Legs with appressed and scattered hairs. Petiole short and inclined forward.

**Gaster.** Usually with dense pubescence, and scattered long erect hairs, among others at the edges of the segments.

**Color and sculpture.** Body smooth, shiny, and yellowish.

**Distribution** (Supplementary material Fig. S39). *Brachymyrmex termitophilus* is known from Brazil, Colombia, Costa Rica, the Dominican Republic, Mexico, Paraguay, and the USA.

**Biology.** Forel (1895b) indicated that this species was collected in association with termites.

**Remarks.** The type material of *B. termitophilus* at the MHNG is somewhat problematic and may have caused confusion as to the diagnostic traits of the species (see below). This material consists of specimens mounted on three pins of which one (USNMENT00757136) holds an undescribed queen; the second (USNMENT00757137) holds a brownish worker with dense pubescence on the gaster, which is here designated as lectotype, and the gaster of another worker of which the rest of the body is missing; the third pin (USNMENT00757138) holds two workers with yellowish heads and mesosoma, and a darker gaster which bears scarce pubescence.

Originally, Forel (1895b) described *B. termitophilus* as a variety of *B. heeri* that is slightly smaller than the typical form, that has longer scapes, and a somewhat sparser pubescence but denser, thicker erect hairs, mainly on the gaster. Wild (2007) subsequently elevated *B. termitophilus* to species level reporting two differences with *B. heeri*, i.e., the length of the scapes and the lateral morphology of the mesosoma. The first trait is suspect, however, as he reports the scapes of *B. termitophilus* to barely reach the posterior margin of the head, which contrasts strongly with the original statement by Forel (1895b). We believe that this error caused Wild (2007) to suggest that *B. termitophilus* may be conspecific with *B. fiebrigi*. The latter species has indeed scapes that do not reach the posterior margin of the head. Rather than *B. fiebrigi*, *B. termitophilus* resembles the species here mentioned in the diagnosis. The status of *B. termitophilus* is unclear: Several of the specimens in the type series of *B. termitophilus* morphologically resemble *B. australis* and *B. aphidicola* in having scarce pubescence on the gaster. Additionally, Santschi (1923a) mentioned that *B. termitophilus* and *B. australis* are both found in association with termites. As mentioned in the diagnosis, also the differences with *B. cordemoyi* and *B. obscurior* are limited, and *B. termitophilus* may be conspecific with one or several of these four species mentioned in the diagnosis. We tentatively preserve the current status of *B. termitophilus* awaiting more material and study.

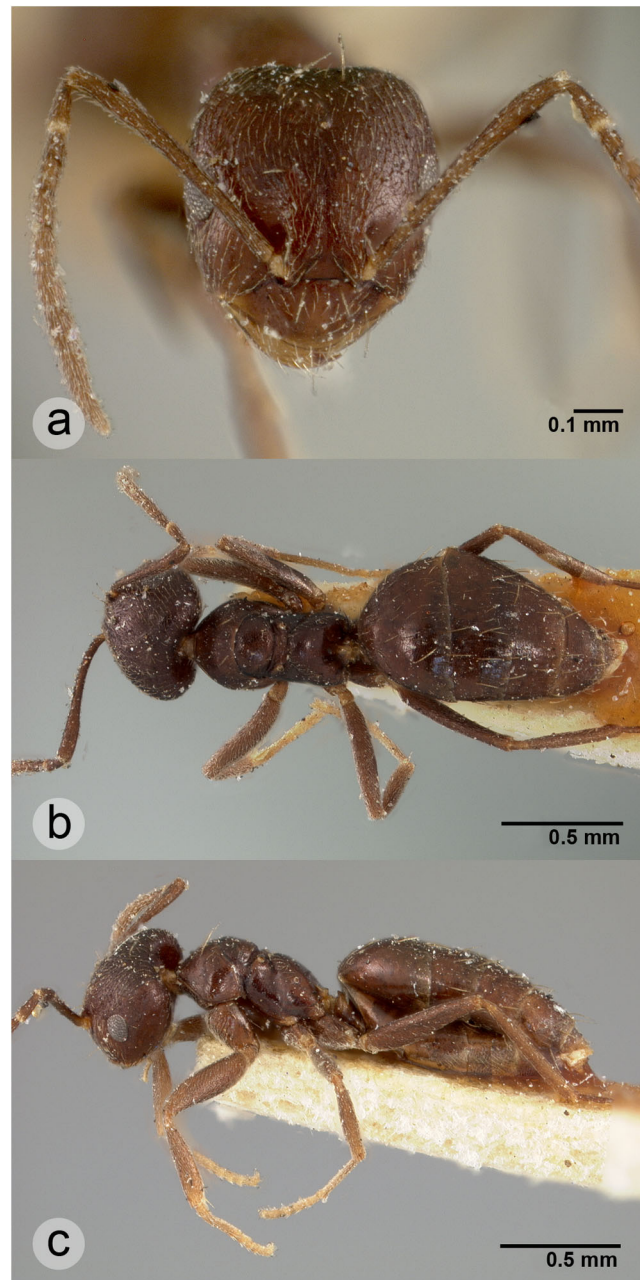
*Brachymyrmex tristis* Mayr

(Fig. 53, supplementary material Fig. S40)

*Brachymyrmex tristis* Mayr, 1870: 389 (w.). Lectotype worker (NHMW: ANTWEB CASENT0915737; here designated): one worker [examined]. **COLOMBIA:** Santafé de Bogotá. See also: Santschi (1923a: 673).

**Additional material examined.** **COLOMBIA: Boyacá:** Chinquinquirá, 07 Dec. 1975, W. & E. MacKay #572, 2 workers (WEMC: USNMENT00757574); **Cundinamarca:** Mosquera to La Mesa, km 8, > 2600 m, arid slope, under rock, 30 June 1976, W.L. & D.E. Brown, 18 workers, 2 queens, 3 males (MCZC: USNMENT00757280–00757282, 00757306–00757311).

**Diagnosis.** *Brachymyrmex tristis* morphologically resembles *B. degener* and *B. coactus*, because all three species have



**Fig. 53** *Brachymyrmex tristis*: a–c head, dorsal, and lateral view of the lectotype worker

scapes that surpass the posterior margin of the head, they have faint sculpture on the mesosoma, their mesonotum bulges dorsally above the pronotum in lateral view, their metanotal groove is wider than the diameter of the metathoracic spiracles, the metathoracic spiracles slightly protrude, and the gaster has sparse pubescence. *Brachymyrmex tristis* differs from *B. coactus* by having a uniform body color and dense decumbent hairs on the head. It differs from *B. degener* by having many decumbent hairs on the head.

*Lectotype worker measurements* (mm). HL<sub>1</sub> 0.61; HL<sub>2</sub> 0.38; HL<sub>3</sub> 0.15; HW 0.56; SL 0.61; EL 0.15; WL 0.70; PnL

0.17; PnW 0.39; ML 0.17; MW 0.30; *Indices* CI 92.50; SI<sub>1</sub>108.11; SI<sub>2</sub> 160.00; OI<sub>1</sub> 27.03; OI<sub>2</sub> 25.00.

**Description.** *Head.* Slightly longer than wide in full face view; posterior cephalic margin slightly concave. Dorsum of the head with dense decumbent pubescence. Clypeus with a rounded anterior margin and five long, erect hairs of which a single, usually conspicuous hair is near the anterior margin, two hairs are in mediolateral position, and two more near the toruli; other hairs on the clypeus are markedly shorter and appressed or decumbent. Toruli surpassing the posterior clypeal margin in oblique anterodorsal view. The scapes surpass the posterior margin of the head by a length up to 1.5× the maximal diameter of the eye; they have appressed hairs. Three ocelli are present. Eyes are positioned on the cephalic midline and have 10–12 ommatidia along their maximal diameter.

*Mesosoma.* With two erect hairs on the pronotum and usually also two on the mesonotum. The mesonotum is slightly inflated and bulges dorsally above the pronotum in lateral view. Metanotal groove wider than the diameter of the metathoracic spiracles. Metathoracic spiracles in dorsolateral position, slightly protruding, and not touching any sutures. Dorsum of the propodeum slightly convex and shorter than propodeal slope. Propodeal spiracles circular, positioned ventral of the posterior propodeal margin, at the middle of the propodeal slope. Legs with appressed hairs. Petiole short and inclined forward.

*Gaster.* With scattered pubescence and several scattered long erect hairs.

*Color and sculpture.* Head and gaster are smooth and shiny, whereas the mesosoma has faint sculpture; body uniformly dark brown apart from the tarsi of the legs which are lighter in color.

**Distribution** (supplementary material Fig. S40). *Brachymyrmex tristis* is only known from Colombia.

**Biology.** Unknown.

**Remarks.** *Brachymyrmex tristis* is as mentioned morphologically very similar to *B. degener* and *B. coactus* and further studies are required to assess whether these species are distinct or conspecific. For now, we follow previous authors in maintaining them as separate species.

Forel (1899) initially considered *B. musculus* to be a race of *B. tristis*; however, we agree with his later decision to consider *B. musculus* distinct (Forel 1901a). Santschi (1923a) also considers *B. musculus* to be closely related to *B. tristis*; however, the first species has a mesonotum that does not bulge dorsally above the pronotum in lateral view, and its metathoracic spiracles are not protruding.

### Additional taxonomic remarks

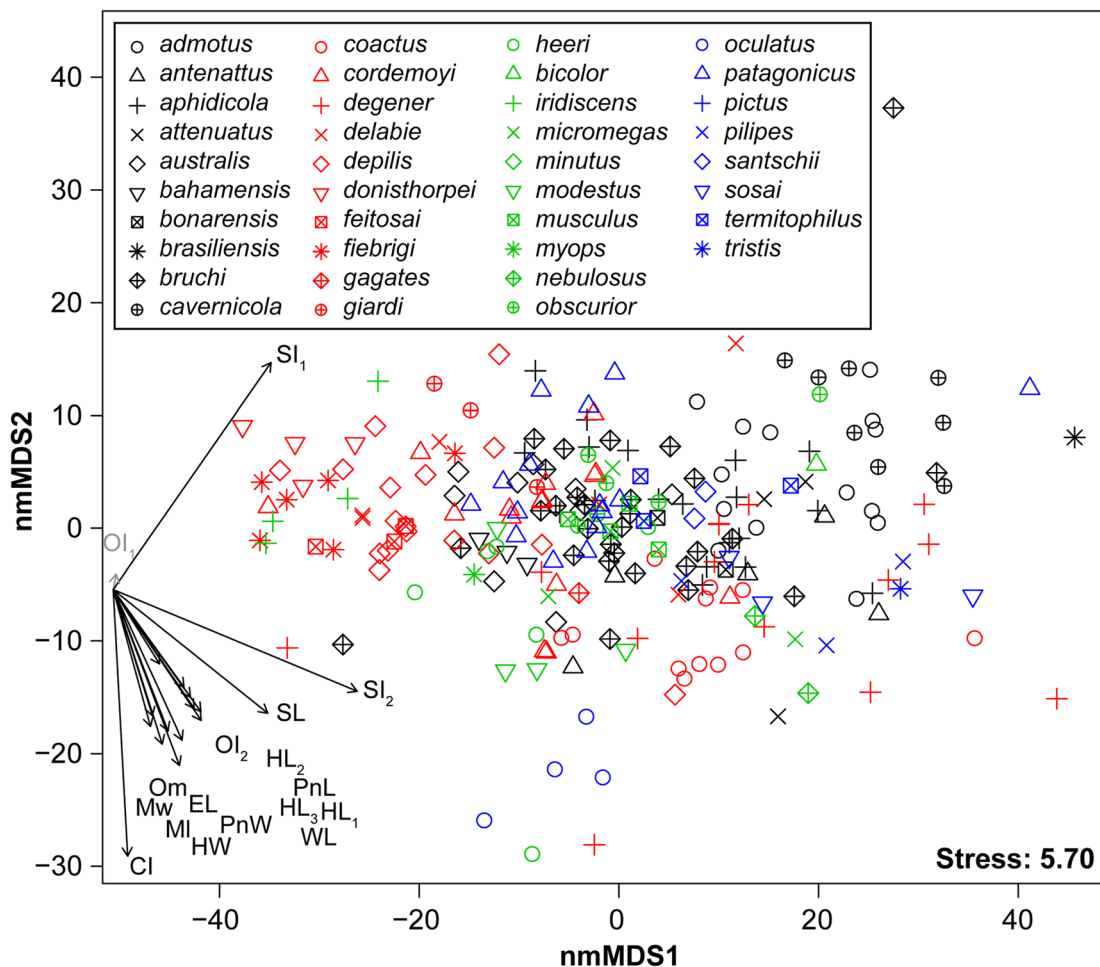
We could not include information on *B. longicornis* var. *pullus* Santschi, 1933 in the above because the type

series consists of a single, destroyed worker (NHMB). As such, we could only re-examine the morphological descriptions of Santschi (1933), from which we conclude that *B. longicornis* var. *pullus* seems to be morphologically similar to *B. patagonicus* and *B. bruchi*. *Brachymyrmex longicornis* var. *pullus* has a shiny body that is black or dark brownish, the scapes surpass the posterior margin of the head, it has large eyes that occupy a third of the sides of the head, and the thorax would have been similar to that of *B. longicornis* which indicates that the mesonotum did not bulge dorsally above the pronotum in lateral view. Santschi (1933) did not describe the pubescence on the gaster, and so in the above we consider the pubescence to be similar to that of typical *B. longicornis* (here synonymized to *B. australis*), *B. longicornis* var. *hemiops* (here synonymized to *B. aphidicola*), and *B. longicornis* var. *immunis* (here synonymized to *B. admotus*). If this assumption were not true, *B. longicornis* var. *pullus* would resemble *B. cordemoyi* and *B. obscurior* more than *B. bruchi* and *B. patagonicus*.

### Morphometric measurements

Although the abovementioned identifications mention morphometric measurements, indices, and count data, our identification system and the key were constructed before analysis of quantitative data, and thus somewhat independent from the quantitative comparison that follows. Here, we examine how well measurements corroborate the established identification system.

The morphospace occupation of the various species is displayed in Fig. 54. The stress associated with nmMDS is small (5.70), indicating that this ordination is reliable and the risk of drawing false inferences very limited. The contribution of the individual morphometric variables (measurements, indices, and counts) to the morphospace is indicated with a biplot. Permutation tests revealed that all variables contributed significantly to the morphospace occupation of taxa, apart from OI<sub>1</sub>, and therefore we excluded this index from further statistical tests. Overall, many of the 38 species included occupy very similar regions of the morphospace, which testifies to the cryptic nature of morphological differences among these taxa, and therefore to the legacy of difficulties with species identifications that have plagued workers of *Brachymyrmex* (see Wheeler 1903; Santschi 1923a; Creighton 1950; Kusnezov 1959; Wilson and Taylor 1967). Indeed, the observation that several species overlap in the central region of the morphospace suggests that the genus is overall characterized by a large degree of morphological conservatism. However, upon more detailed examination, we also perceive that most taxa occupy rather restricted regions of the morphospace, despite measurements typically deriving from



**Fig. 54** Morphospace occupation of 38 of the here studied *Brachymyrmex* species as reconstructed with non-metric multidimensional scaling. The limited stress (5.70) indicates that the ordination is robust

and the biplot displays how the various morphometric variables contribute to the morphospace occupation. OI<sub>1</sub> is indicated in gray, as this variable did not contribute significantly to the morphospace

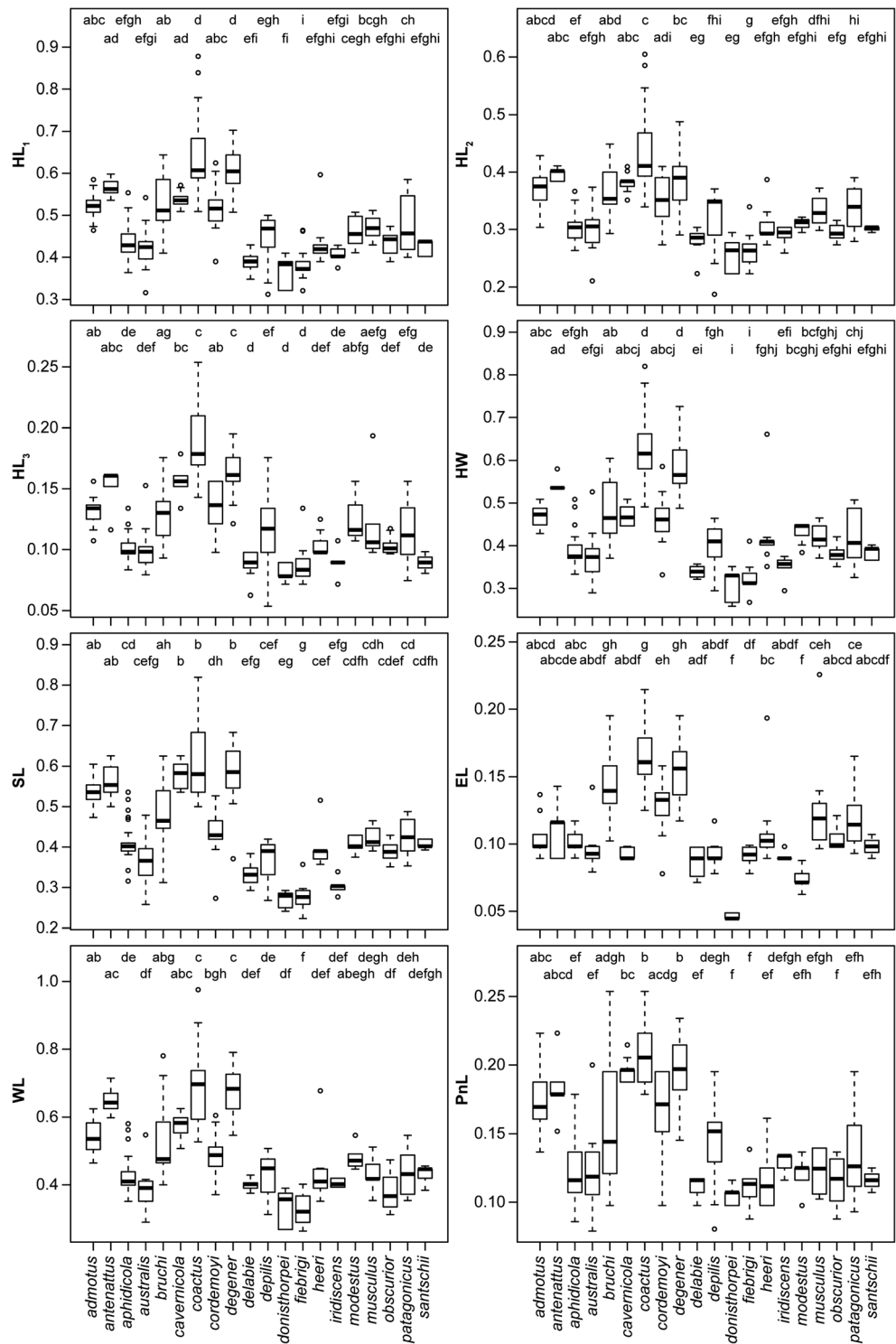
specimens obtained from distant localities. For example, even widespread species, such as *B. patagonicus*, occupy a rather restricted region of the morphospace. One notable exception is *B. bruchi*, which displays large variation on both nmMDS1 and 2, and which is difficult to characterize morphologically (although molecular analyses suggest our identification system works well for this species too [see below]). Beyond the measured traits, the first nmMDS axis also reflects general differences in body size, with small species (*B. depilis*, *donisthorpei*, *fiebrigi*, *iridescens*, and *feitosai*) plotting along the most negative and large species (*B. admotus*, *cavernicola*, and *degener*) along the most positive values. The overall restricted morphospace occupation of individual species testifies to the possibility to distinguish many species in one-on-one comparisons, and we examine this issue for univariate variables, because such univariate comparisons may be more helpful than multivariate comparisons for colleagues aiming to identify specimens directly in the field.

Boxplots (Figs. 55 and 56) highlight similarities and differences among 20 *Brachymyrmex* species for the 16 univariate

variable (after exclusion of OI<sub>1</sub>) with statistical pairwise comparisons. Here, we will not exhaustively compare all these species for each of the variables, as this would lead to 3040 pairwise comparisons. Rather, we will focus on comparing five species pairs that are difficult to distinguish, i.e., *aphidicola-australis*, *bruchi-patagonicus*, *coactus-degener*, *cordemoyi-obscurior*, and *donisthorpei-modestus*, with the aim to find additional criteria that may allow differentiating these taxa. *Brachymyrmex aphidicola-australis* differ significantly in SI<sub>1</sub> and SI<sub>2</sub>, but not in other variables. *Brachymyrmex bruchi-patagonicus* display significant differences in HL<sub>1</sub>, HL<sub>2</sub>, HW, SL, EL, WL, PnL, and PnW suggesting that the main difficulty differentiating these taxa relates to the very variable nature of *B. bruchi*, as already highlighted above. *Brachymyrmex coactus* and *B. degener* are effectively very difficult to distinguish as the only significant difference we found is in OI<sub>2</sub>, which was admittedly very variable for *B. degener*. Although *B. cordemoyi* and *B. obscurior* overlapped strongly in morphospace occupation, they can nevertheless be distinguished based on HL<sub>1</sub>, HL<sub>2</sub>, HL<sub>3</sub>, HW, EL, PnL, PnW,



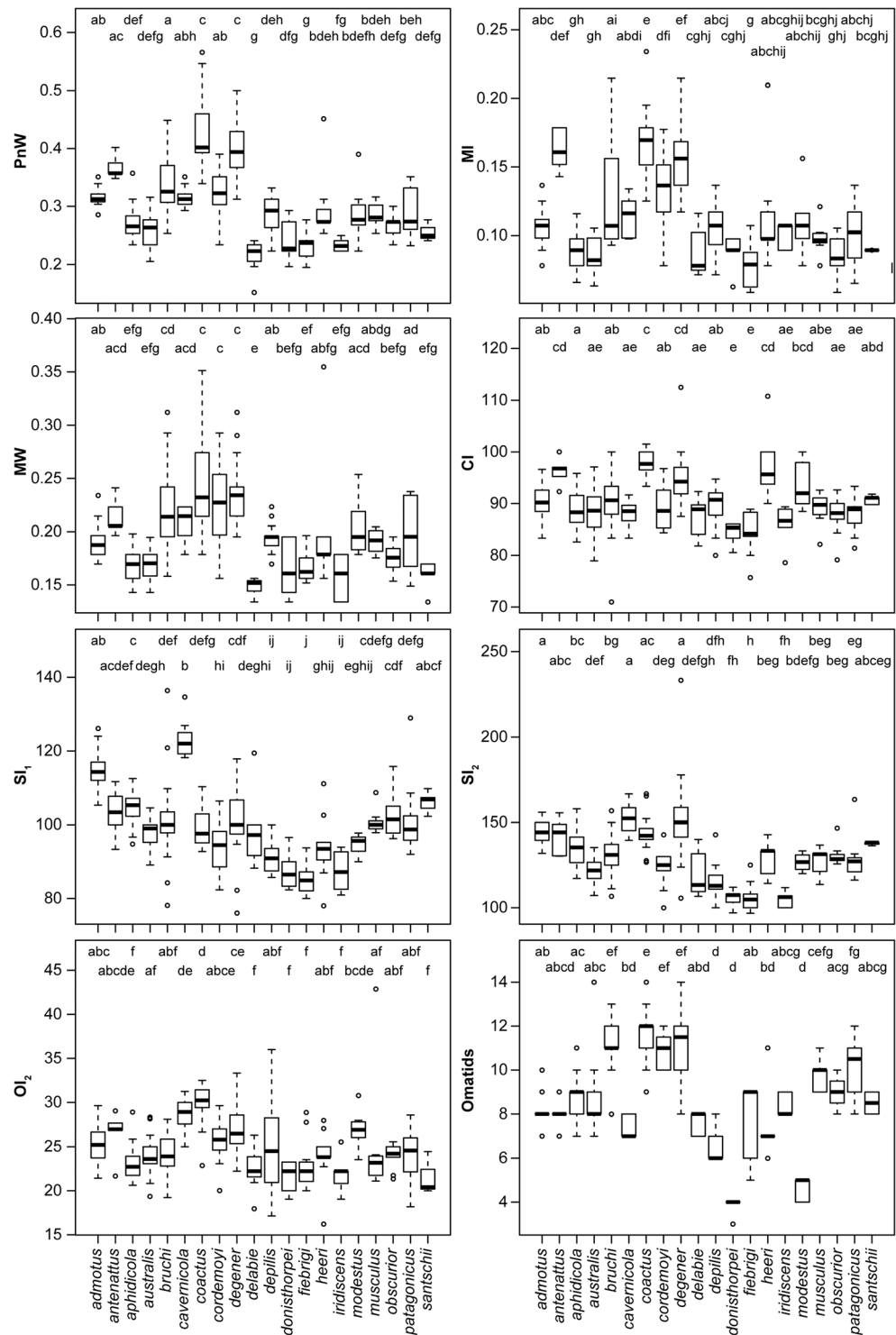
**Fig. 55** Boxplots representing intraspecific variation and interspecific differences for eight morphometric traits. Interspecific differences are tested with Benjamini-Hochberg corrected pairwise Dunn's tests, with significance levels indicated by letter codes (if species carry at least one identical letter than observed differences are insignificant, if they carry no identical letter, the observed differences for the studied trait are significant)



MI, MW,  $SI_1$ , and the number of ommatidia. For several of these variables, *B. obscurior* showed limited variation, despite the inclusion of ten specimens from four different countries, which may have driven statistical significance. Finally, *B. donisthorpei* and *B. modestus* differed significantly in  $HL_1$ ,  $HL_3$ , HW, SL, WL, MW, CI, and  $OI_2$ . In summary, the

morphometric variables confirm significant morphological differences for all five species pairs. Interestingly, as we will document in the next section, the two species pairs with the most limited number of differences, i.e., *aphidicola-australis* and especially *coactus-degener* are phylogenetically closely related (see below).

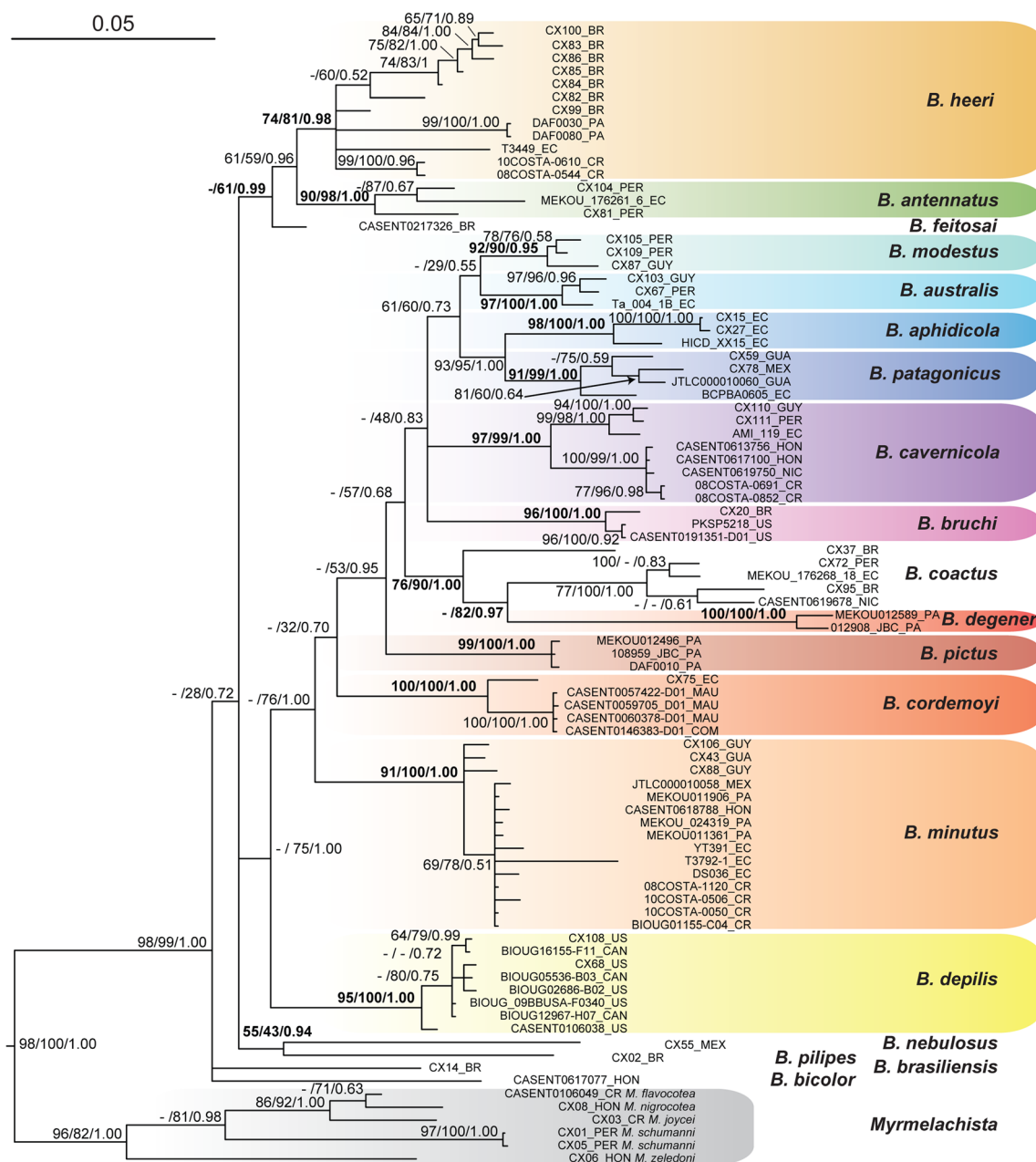
**Fig. 56** Boxplots representing intraspecific variation and interspecific differences for eight morphometric traits. Interspecific differences are tested with Benjamini-Hochberg corrected pairwise Dunn's tests, with significance levels indicated by letter codes (if species carry at least one identical letter than observed differences are insignificant, if they carry no identical letter, the observed differences for the studied trait are significant)



**Phylogenetic inference**

Our phylogenetic analyses with maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI) on 5 gene fragments (3 nuclear, 2 mitochondrial) for 19 *Brachymyrmex* species, 5 species of its sister clade *Myrmelachista* and outgroups retrieved *Brachymyrmex* and

*Myrmelachista* as a well-supported monophyletic clade (MP = 98, ML = 100, BPP = 1.00; Fig. 57). This finding agrees with recent studies of the deep phylogenetic relationships within the subfamily Formicinae based on UCES (ultraconserved elements: Blaimer et al. 2015; Ward et al. 2016); however, this previous study contained only two *Brachymyrmex* and one *Myrmelachista* species. Under



**Fig. 57** Maximum clade credibility tree of *Brachymyrmex* and *Myrmelachista* based on five gene fragments (see Supplementary material Table S1). Analyses were run under maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI) with bootstrap support values and Bayesian posterior probabilities indicated above

expanded taxon sampling, *Brachymyrmex* and *Myrmelachista* were found to be reciprocally monophyletic, with high support for each genus (MP = 98, ML = 100, BPP = 1.00, and MP = 96, ML = 82, BPP = 1.00, respectively). This finding suggests that the morphological criteria currently used to delimit these genera are unambiguous autapomorphies. Examining *Brachymyrmex* in more detail, many of the nodes of intermediate depth are poorly supported, indicating that more markers are required, or at least more complete sampling

nodes (MP/ML/BI). Support for species-level clades is indicated in bold; specimens were assigned to clades based on the morphological identification system, which proves to be overall in good agreement with the genealogy, apart from *B. degener* and *B. coactus*

of markers across taxa, to reveal the phylogenetic relationships between individual *Brachymyrmex* species. Given that our analysis includes half of the currently recognized *Brachymyrmex* species, increased taxon sampling may also help to resolve phylogenetic relationships among the species.

Despite ambiguity as to interspecific relationships, species-level nodes (indicated in bold in Fig. 57) are overall well-supported, and of the 14 *Brachymyrmex* species that were sampled with 2–15 specimens, 13 proved to be monophyletic.

This finding largely confirms our assessment of intraspecific and interspecific components of morphological variation, the phylogenetic value of the morphological traits used, and thus the significance of our proposed morphological system of species delimitations. The only species that was not retrieved as monophyletic is *B. coactus*, which included the monophyletic *B. degener*. *Brachymyrmex coactus* and *B. degener* are morphologically very similar (as indicated already above in the taxonomic treatment and morphometrics), and they mainly differ in body color, which may be a trait with large intraspecific variation. Significant differences between both species were also found in  $OI_2$ , although *B. degener* is very variable as to this index. On the other hand, the genetic differentiation between *B. coactus* and *B. degener* is substantial, as indicated by the branch lengths in Fig. 57, suggesting that both may be part of a larger clade with cryptic diversity, and that the observed bimodal distribution in body color may hint at interspecific differences. Considering the substantial genetic differentiation, we do not synonymize both species but rather postpone our assessment until more specimens become available, especially of *B. coactus* from Brazil. Another possible indication of cryptic species diversity relates to *B. cavernicola*, which contains two well-supported subclades, one with specimens from Central America, and the other clade with specimens from South America. More in-depth studies are required to test whether this split relates to different species, or rather variation between geographically-separated populations. The hypothesis of cryptic diversity is furthermore supported by the ABGD analysis (see below).

For *B. feitosa*, *B. nebulosus*, *B. pilipes*, *B. brasiliensis*, and *B. bicolor* n. sp., only a single individual per species was included in the phylogenetic analyses so that it is difficult to make conclusions on the integrity of these species; however, all these species are deeply split from other *Brachymyrmex* species, suggesting that they are truly distinct. It was particularly important for us to include *B. pilipes*, because this species has very distinctive and different morphological traits (see species description) in comparison to most other *Brachymyrmex* species. Interestingly, the species seems to have a basal position in our phylogeny and revealing its position in the future may yield important insights into trait evolution within the genus. Nevertheless, our phylogenetic analysis confirms that *B. pilipes* is part of *Brachymyrmex*, rather than an independent lineage.

### Automated species delimitation

A total of 24 hypothetical species entities were retrieved within *Brachymyrmex* upon analyzing the barcoding fragment of COI (658 basepairs) with ABGD. Overall, these entities are in good agreement with the morphologically-recognized species indicated in Fig. 57, and the differences are limited to the

potential further subdivision of morphologically recognized species by ABGD. Within *B. heeri*, four groups are recognized, with each group containing the specimens from one country in the phylogeny. *Brachymyrmex antennatus* is subdivided in two groups, with one group consisting of specimen CX81 from Peru and the other contains the additional specimens. *Brachymyrmex cavernicola* was subdivided in two groups also, along the main subdivision observed in Fig. 57 and discussed above, indicating that differentiation and perhaps cryptic speciation is taking place along a geographic gradient. The final difference relates to the *B. coactus/degener* clade. The ABGD analysis recognized three groups: one group containing only specimen CX37 from Brazil, the remainder of *B. coactus* as a second group, and the third group contains the specimens identified as *B. degener*. In summary, the ABGD analysis corroborates our morphological classification system. It suggests that this classification is conservative and that more cryptic diversity may exist within *Brachymyrmex*.

### Conclusions

For over a century, the ant genus *Brachymyrmex* has been in dire need of revision, and here we present such a revision based on the morphology of workers, validated with morphometric and molecular data. Currently, the strategy to focus on workers is the most effective solution to revise the genus, because other castes (queens and males) are poorly known for most *Brachymyrmex* species. We studied 1303 samples that have been assigned to 40 species based on the established morphological identification system as represented in a dichotomous identification key, which we tested with previous and new material. Additionally, this key was tested independently by several colleagues (Fabiana Cuezco (Argentina), John Latke and Livia Pires do Prado (Brazil)), and the obtained identifications were in good agreement with our own diagnoses, suggesting that it effectively allows discerning interspecific differences from intraspecific variation. Beyond these qualitative tests, we also complemented our identifications with measurements to reconstruct the distribution of species in morphospace, and we statistically analyzed individual measurements as univariate variables. These efforts suggest that even species pairs that are qualitatively difficult to discern can be separated statistically, and they illustrated that taxonomically problematic cases relate to taxa that have high intraspecific trait variance. The species pair that was most difficult to discern based on measurements proved to be *B. coactus* and *B. degener*, and interestingly, these taxa represent the only disagreement between our morphological identification system and our phylogenetic analysis based on five gene fragments. *Brachymyrmex degener* was nested within *B. coactus* but considering the deep phylogenetic splits in the *coactus-degener*

clade and the results from automated species delimitation, we await more material to resolve the status of the morphospecies in this clade. In summary, 13 of the 14 morphologically identified species that were included in molecular work with 2–15 individuals each were recovered as monophyletic, indicating the overall robustness of our proposed morphological identification system, and by extension our taxonomic revision. Finally, we have reported dimorphic workers for some *Brachymyrmex* species and the existence of a putative worker-queen intercaste in others. As such, the genus altogether may represent a promising system to study caste evolution in ants.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

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## Molecular and morphological recognition of species boundaries in the neglected ant genus *Brachymyrmex* (Hymenoptera: Formicidae): toward a taxonomic revision

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### Online Supplementary tables

**Table S1.** Species identification, locality and GenBank accession numbers for the taxa studied in the phylogenetic approach. <sup>a</sup> in the last column indicates sequences generated by David Donoso, <sup>b</sup> by the International Barcode of Life consortium, <sup>c</sup> by John Longino and <sup>d</sup> by J.R. Dewaard et al. (unpublished).

Collection code	Specimen code Voucher	Taxon	Country	GenBank accession numbers					From
				COI <sub>1</sub>	COI <sub>2</sub>	EF1aF1	EF1aF2	WG	
n.a.	CASENT0039772	<i>Acanthoponera minor</i>	Costa Rica	n.a.	n.a.	EF013209	EF013371	EF013661	Brady et al 2006
n.a.	CASENT0106288	<i>Manica rubida</i>	Poland	n.a.	n.a.	KJ860556	KJ859751	KJ861827	Ward et al 2015
n.a.	RA0310	<i>Rhytidoponera metallica</i>	n.a.	DQ353374	DQ353374	n.a.	n.a.	DQ353097	Moreau et al 2006
JSC041006-10;TRS041006-01-LS10	CX-104	<i>B. antennatus</i>	Peru	n.a.	MK634356	MK634392	MK634413	MK634439	this study
ARCAE303_17	MEKOU_176261_6	<i>B. antennatus</i>	Ecuador	D. Donoso pending	n.a.	n.a.	n.a.	n.a.	this study <sup>a</sup>
USNM ENT 00757627	CX-81	<i>B. antennatus</i>	Peru	MK992375	MK634357	n.a.	MK634414	MK634440	this study
JSC090320-01	CX-100	<i>B. heeri</i>	Brazil	MK992376	MK634373	MK634401	MK634426	MK634453	this study
JSC090320-10	CX-86	<i>B. heeri</i>	Brazil	MK992377	MK634377	MK634406	MK634430	MK634458	this study
JSC090320-09	CX-83	<i>B. heeri</i>	Brazil	MK992378	n.a.	MK634404	MK634428	MK634456	this study
JSC090320-08	CX-85	<i>B. heeri</i>	Brazil	MK992379	MK634376	MK634405	MK634429	MK634457	this study
JSC090320-08	CX-84	<i>B. heeri</i>	Brazil	MK992380	MK634374	MK634402	MK634427	MK634454	this study
JSC080922-LS05	CX-82	<i>B. heeri</i>	Brazil	n.a.	MK634375	MK634403	n.a.	MK634455	this study
ARCAE055_17	T3449	<i>B. heeri</i>	Ecuador	D. Donoso pending	n.a.	n.a.	n.a.	n.a.	this study <sup>a</sup>
JSC080922-LS10	CX-99	<i>B. heeri</i>	Brazil	n.a.	MK634378	MK634407	MK634431	MK634459	this study
BCIFO1157-13	DAF0030	<i>B. heeri</i>	Panama	MK758449	n.a.	n.a.	n.a.	n.a.	this study <sup>a</sup>

BCIFO1256-13	DAF0080	<i>B. heeri</i>	Panama	MK768440	n.a.	n.a.	n.a.	n.a.	this study <sup>a</sup>
ACGAD611_10	10COSTA-0610	<i>B. heeri</i>	Costa Rica	HQ545883	n.a.	n.a.	n.a.	n.a.	this study <sup>b</sup>
ACGAB032_09	08COSTA-0544	<i>B. heeri</i>	Costa Rica	GU708679	n.a.	n.a.	n.a.	n.a.	this study <sup>b</sup>
BR01	CASENT0217326	<i>B. feitosa</i>	Brazil	n.a.	n.a.	KT443149	KT443205	KT443261	Blaimer et al 2015
TRS061016-WS07	CX-103	<i>B. australis</i>	Guyana	MK992381	MK634358	MK634393	MK634415	MK634441	this study
USNM ENT 00757611	CX-67	<i>B. australis</i>	Peru	MK992382	MK634359	n.a.	MK634416	MK634442	this study
YASFO434-16	Ta_004_1B	<i>B. australis</i>	Ecuador	D. Donoso pending	n.a.	n.a.	n.a.	n.a.	this study <sup>a</sup>
USNM ENT 00757688	CX-59	<i>B. patagonicus</i>	Guatemala	n.a.	MK634381	n.a.	MK634434	MK634463	this study
USNM ENT 00757687	CX-78	<i>B. patagonicus</i>	Mexico	MK992383	MK634382	n.a.	n.a.	n.a.	this study
JTL6015-s	JTLC000010060	<i>B. patagonicus</i>	Guatemala	MK992403	n.a.	n.a.	n.a.	n.a.	this study <sup>c</sup>
PBA0605	BCPBA0605	<i>B. patagonicus</i>	Ecuador	KU985505	n.a.	n.a.	n.a.	n.a.	this study <sup>a</sup>
n.a.	CX-15	<i>B. aphidicola</i>	Ecuador	MK992384	MK634384	MK634410	n.a.	MK634465	this study
n.a.	CX-27	<i>B. aphidicola</i>	Ecuador	MK992385	MK634385	n.a.	MK634436	MK634466	this study
YASFO053-16	HICD_XX15	<i>B. aphidicola</i>	Ecuador	D. Donoso pending	n.a.	n.a.	n.a.	n.a.	this study <sup>a</sup>
JSC041009-019; TRS041009-01-LS19	CX-105	<i>B. modestus</i>	Peru	n.a.	MK634369	MK634398	MK634424	n.a.	this study
JSC041002-13; TRS041002-01-LS13	CX-109	<i>B. modestus</i>	Peru	n.a.	MK634370	MK634399	n.a.	MK634451	this study
TRS061022-LS03	CX-87	<i>B. modestus</i>	Guyana	n.a.	MK634371	MK634400	MK634425	MK634452	this study
TRS061022-LS02	CX-110	<i>B. cavernicola</i>	Guyana	MK992386	MK634362	MK634395	MK634419	MK634444	this study
JSC041006-02; TRS041006-01-LS2	CX-111	<i>B. cavernicola</i>	Peru	MK992387	MK634363	MK634396	MK634420	MK634445	this study
YASFO499_16	AMI_119	<i>B. cavernicola</i>	Ecuador	D. Donoso pending	n.a.	n.a.	n.a.	n.a.	this study <sup>a</sup>
Wm-C-07-1-10	CASENT0613756	<i>B. cavernicola</i>	Honduras	JN270706	n.a.	n.a.	n.a.	n.a.	this study <sup>c</sup>
Wa-C-04-2-06	CASENT0617100	<i>B. cavernicola</i>	Honduras	JN270709	n.a.	n.a.	n.a.	n.a.	this study <sup>c</sup>
JTL7550	CASENT0619750	<i>B. cavernicola</i>	Nicaragua	MK992404	n.a.	n.a.	n.a.	n.a.	this study <sup>c</sup>
ACGAB179_09	08COSTA-0691	<i>B. cavernicola</i>	Costa Rica	GU709009	n.a.	n.a.	n.a.	n.a.	this study <sup>b</sup>
ACGAB340_09	08COSTA-0852	<i>B. cavernicola</i>	Costa Rica	GU709019	n.a.	n.a.	n.a.	n.a.	this study <sup>b</sup>
MZSP176	CX-20	<i>B. bruchi</i>	Brazil	MK992388	n.a.	MK634408	n.a.	MK634462	this study
ASPNA1434-10	PKSP5218	<i>B. bruchi</i>	United States	HQ551103	n.a.	n.a.	n.a.	n.a.	this study <sup>b</sup>
ASANE612_10	CASENT0191351-D01	<i>B. bruchi</i>	United States	HQ925273	n.a.	n.a.	n.a.	n.a.	this study <sup>b</sup>
MZSP 123	CX-37	<i>B. coactus</i>	Brazil	MK992389	MK634364	n.a.	n.a.	MK634446	this study

USNM ENT 00757612	CX-72	<i>B. coactus</i>	Peru	MK992390	MK634365	n.a.	MK634421	MK634447	this study
ARCAE189_17	MEKOU_176268_18	<i>B. coactus</i>	Ecuador	D. Donoso pending	n.a.	n.a.	n.a.	n.a.	this study <sup>a</sup>
USNM ENT 00757556	CX-95	<i>B. coactus</i>	Brazil	n.a.	MK634366	n.a.	MK634422	MK634448	this study
JTL7481	CASENT0619678	<i>B. coactus</i>	Nicaragua	MK992405	n.a.	n.a.	n.a.	n.a.	this study <sup>c</sup>
BCIFO879-13	MEKOU012589	<i>B. degener</i>	Panama	MK769755	n.a.	n.a.	n.a.	n.a.	this study <sup>a</sup>
012908_JBC	012908_JBC	<i>B. degener</i>	Panama	MK758176	n.a.	n.a.	n.a.	n.a.	this study <sup>a</sup>
MEKOU012496	MEKOU012496	<i>B. pictus</i>	Panama	MK758552	n.a.	n.a.	n.a.	n.a.	this study <sup>a</sup>
108959_JBC	108959_JBC	<i>B. pictus</i>	Panama	MK768698	n.a.	n.a.	n.a.	n.a.	this study <sup>a</sup>
DAF0010	DAF0010	<i>B. pictus</i>	Panama	MK767905	n.a.	n.a.	n.a.	n.a.	this study <sup>a</sup>
USNM ENT 00757880	CX-75	<i>B. cordemoyi</i>	Ecuador	MK992391	MK634361	n.a.	MK634418	n.a.	this study
ASMA067_05	CASENT0057422- D01	<i>B. cordemoyi</i>	Mauritus	EF609727	n.a.	n.a.	n.a.	n.a.	Smith and Fisher 2009
ASMA136_05	CASENT0059705- D01	<i>B. cordemoyi</i>	Mauritus	EF609722	n.a.	n.a.	n.a.	n.a.	Smith and Fisher 2009
ASMA288_05	CASENT0060378- D01	<i>B. cordemoyi</i>	Mauritus	EF609763	n.a.	n.a.	n.a.	n.a.	Smith and Fisher 2009
ASANP101_09	CASENT0146383- D01	<i>B. cordemoyi</i>	Comoros	GU710679	n.a.	n.a.	n.a.	n.a.	this study <sup>b</sup>
JSC061014-LS04	CX-106	<i>B. minutus</i>	Guyana	n.a.	MK634379	n.a.	MK634432	MK634460	this study
JTLC000009864	CX-43	<i>B. minutus</i>	Guatemala	n.a.	MK634380	n.a.	MK634433	MK634461	this study
TRS061022- LS10	CX-88	<i>B. minutus</i>	Guyana	MK992392	MK634391	MK634412	n.a.	MK634469	this study
JTL6046-s	JTLC000010058	<i>B. minutus</i>	Mexico	MK992406	n.a.	n.a.	n.a.	n.a.	this study <sup>c</sup>
MEKOU011906	MEKOU011906	<i>B. minutus</i>	Panama	MK767899	n.a.	n.a.	n.a.	n.a.	this study <sup>a</sup>
Go-C-08-2-01	CASENT0618788	<i>B. minutus</i>	Honduras	MK992407	n.a.	n.a.	n.a.	n.a.	this study <sup>c</sup>
MEKOU_024319	MEKOU_024319	<i>B. minutus</i>	Panama	KM224720	n.a.	n.a.	n.a.	n.a.	Donoso 2013
MEKOU011361	MEKOU011361	<i>B. minutus</i>	Panama	JF863683	n.a.	n.a.	n.a.	n.a.	this study <sup>b</sup>
BCYT391	BCYT391	<i>B. minutus</i>	Ecuador	KY442006	n.a.	n.a.	n.a.	n.a.	Tied et al 2017
ARCAE052_17	T3792-1	<i>B. minutus</i>	Ecuador	D. Donoso pending	n.a.	n.a.	n.a.	n.a.	this study <sup>a</sup>
ARCAE201_17	DS036	<i>B. minutus</i>	Ecuador	D. Donoso pending	n.a.	n.a.	n.a.	n.a.	this study <sup>a</sup>
ACGAB608_09	08COSTA-1120	<i>B. minutus</i>	Costa Rica	GU709339	n.a.	n.a.	n.a.	n.a.	this study <sup>b</sup>
ACGAD507_10	10COSTA-0506	<i>B. minutus</i>	Costa Rica	HQ545796	n.a.	n.a.	n.a.	n.a.	this study <sup>b</sup>

ACGAD050_10	10COSTA-0050	<i>B. minutus</i>	Costa Rica	HM919664	n.a.	n.a.	n.a.	n.a.	this study <sup>b</sup>
ACGAH028_11	BIOUG01155-C04	<i>B. minutus</i>	Costa Rica	KC418964	n.a.	n.a.	n.a.	n.a.	Smith et al 2014
MGB2036	CX-108	<i>B. depilis</i>	United States	MK992393	MK634367	MK634397	MK634423	MK634449	this study
SMTPJ4104_14	BIOUG16155-F11	<i>B. depilis</i>	Canada	KR884779	n.a.	n.a.	n.a.	n.a.	Hebert et al 2016
USNM ENT 00757799	CX-68	<i>B. depilis</i>	United States	MK992394	MK634368	n.a.	n.a.	MK634450	this study
SMTPB3340_13	BIOUG05536-B03	<i>B. depilis</i>	Canada	KR873789	n.a.	n.a.	n.a.	n.a.	Hebert et al 2016
BBHYA3116_12	BIOUG02686-B02	<i>B. depilis</i>	United States	KM996564	n.a.	n.a.	n.a.	n.a.	Eagalle and Smith 2014
USFOR340_10	BIOUG_09BBUSA-F0340	<i>B. depilis</i>	United States	HQ984902	n.a.	n.a.	n.a.	n.a.	this study <sup>b</sup>
CNKJP241_14	BIOUG12967-H07	<i>B. depilis</i>	Canada	KR402540	n.a.	n.a.	n.a.	n.a.	this study <sup>d</sup>
PSW14995	CASENT0106038	<i>B. depilis</i>	United States	n.a.	n.a.	EF01323	EF013395	EF01368	Brady et al 2006
JTLC000007379	CX-55	<i>B. nebulosus</i>	Mexico	MK992395	MK634372	n.a.	n.a.	n.a.	this study
n.a.	CX-02	<i>B. pilipes</i>	Brazil	MK992396	MK634383	MK634409	MK634435	MK634464	this study
USNM ENT 00757748	CX-14	<i>B. brasiliensis</i>	Brazil	MK992397	MK634360	MK634394	MK634417	MK634443	this study
Wa-C-04-1-24	CASENT0617077	<i>B. bicolor nsp</i>	Honduras	MK992408	n.a.	n.a.	n.a.	n.a.	this study <sup>c</sup>
PSW15279	CASENT0106049	<i>Myrmelachista flavocotea</i>	Costa Rica	n.a.	n.a.	EF013295	EF013457	EF013725	Brady et al 2006
JTL7100	CX-08	<i>Myrmelachista nigrocotea</i>	Honduras	MK992398	MK634387	n.a.	n.a.	MK634467	this study
JTL5 509	CX-03	<i>Myrmelachista joycei</i>	Costa Rica	MK992399	MK634386	n.a.	MK634437	n.a.	this study
n.a.	CX-01	<i>Myrmelachista schumanni</i>	Peru	MK992400	MK634388	n.a.	MK634438	MK634468	this study
n.a.	CX-05	<i>Myrmelachista schumanni</i>	Peru	MK992401	MK634389	MK634411	n.a.	n.a.	this study
JTL6972	CX-06	<i>Myrmelachista zeledoni</i>	Honduras	MK992402	MK634390	n.a.	n.a.	n.a.	this study

**Table S2.** Best-supported substitution models for each gene fragment and codon position as identified with PARTITION FINDER v.1.1.1 (Lanfear et al. 2012).

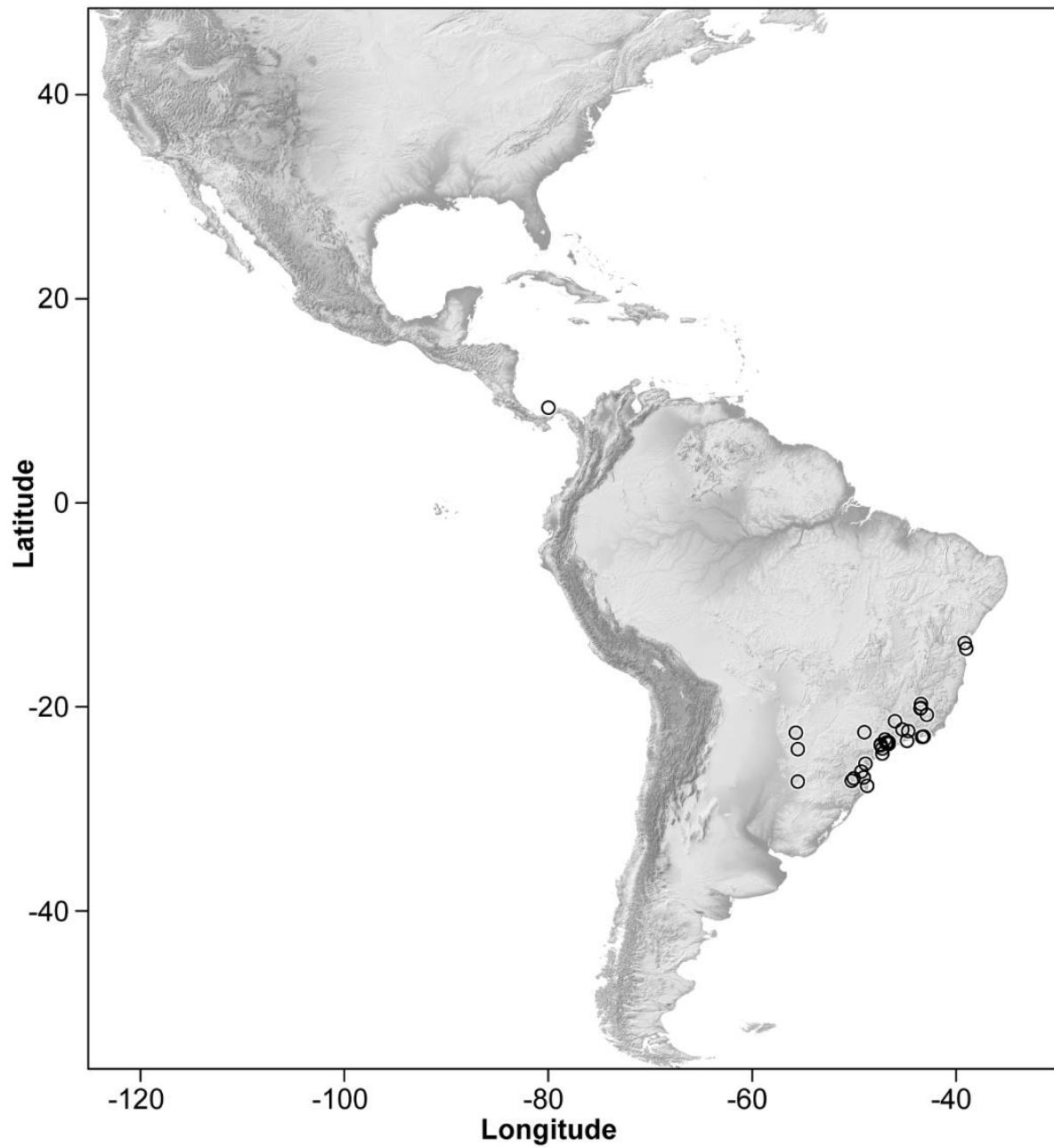
<b>Fragment</b>	<b>Model (AICc)</b>
COI pos1	GTR+I+G
COI pos2	HKY+I+G
COI pos3	GTR+G
EF1 pos1	GTR+G
EF1 pos2	HKY+I
EF1 pos3	GTR+G
EF2 pos1	GTR+G
EF2 pos2	F81+I
EF2 pos3	HKY
WG pos1	GTR+G
WG pos2	GTR+G
WG pos3	GTR

## REFERENCES

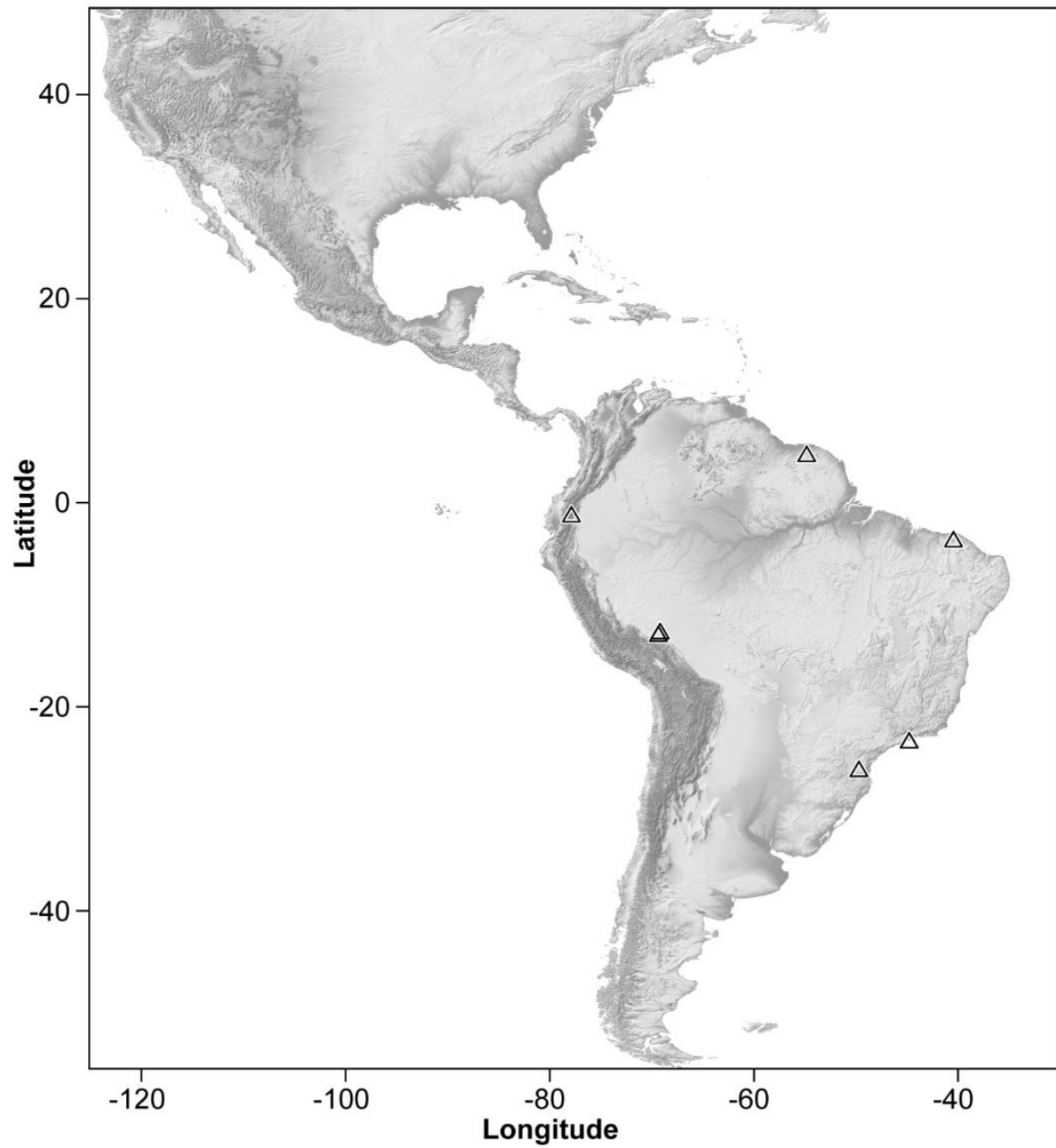
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**Online Supplementary Figures**

**Figure S1.** Geographic distribution of *B. admotus* (n=34).

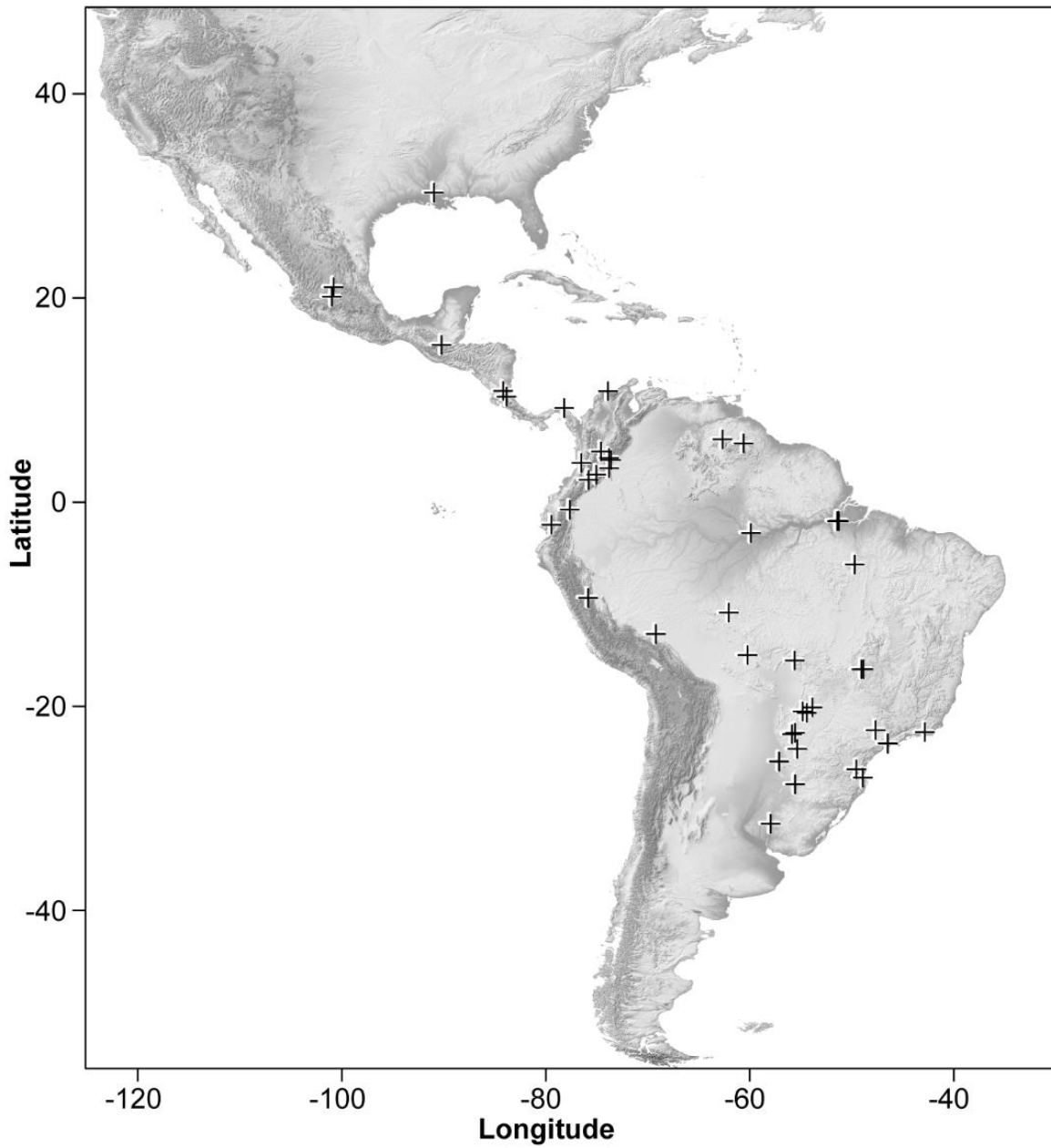


**Figure S2.** Geographic distribution of *B. antennatus* (n=8).

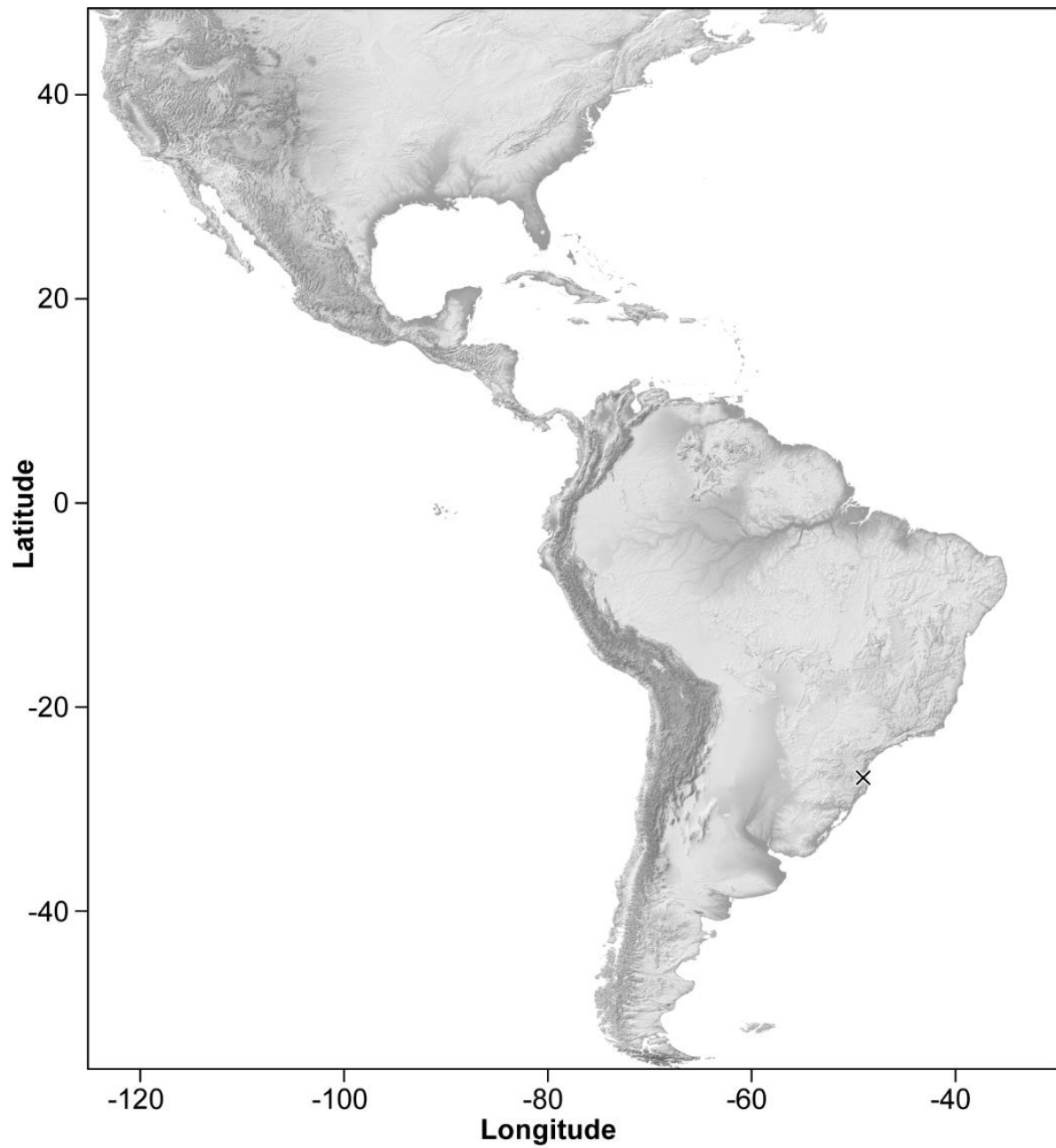




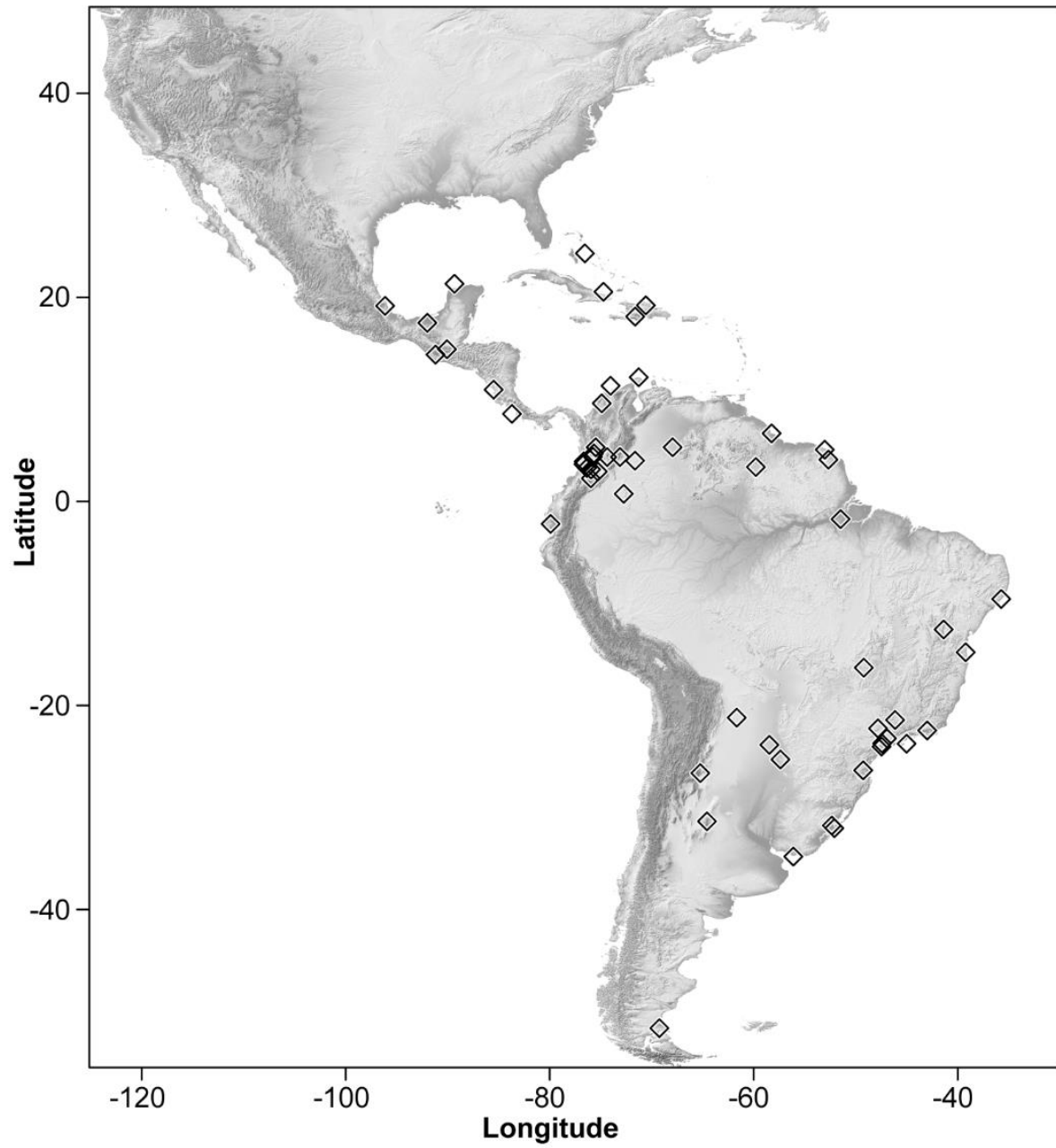
**Figure S3.** Geographic distribution of *B. aphidicola* (n=52).



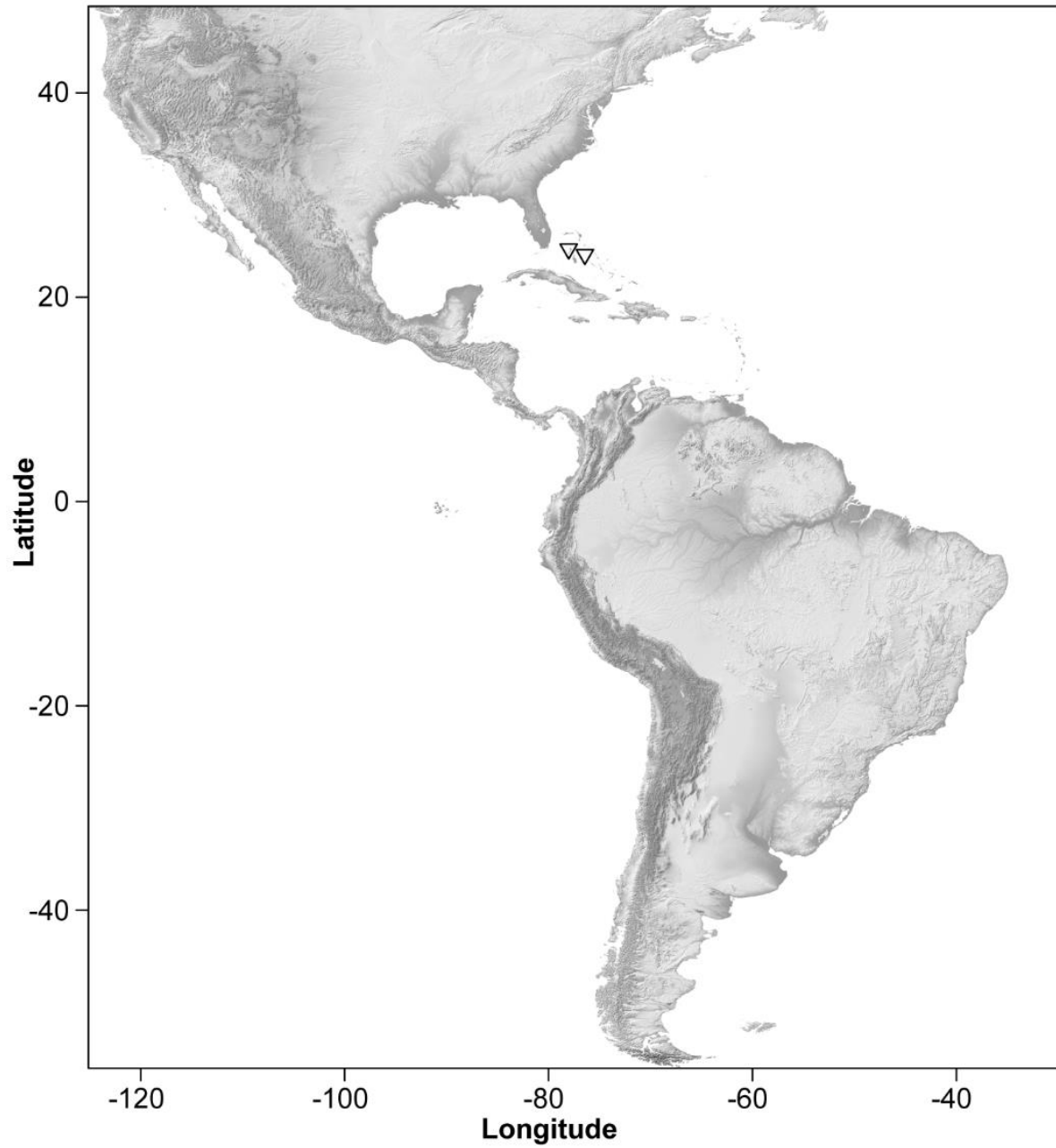
**Figure S4.** Geographic distribution of *B. attenuatus* (n=1).



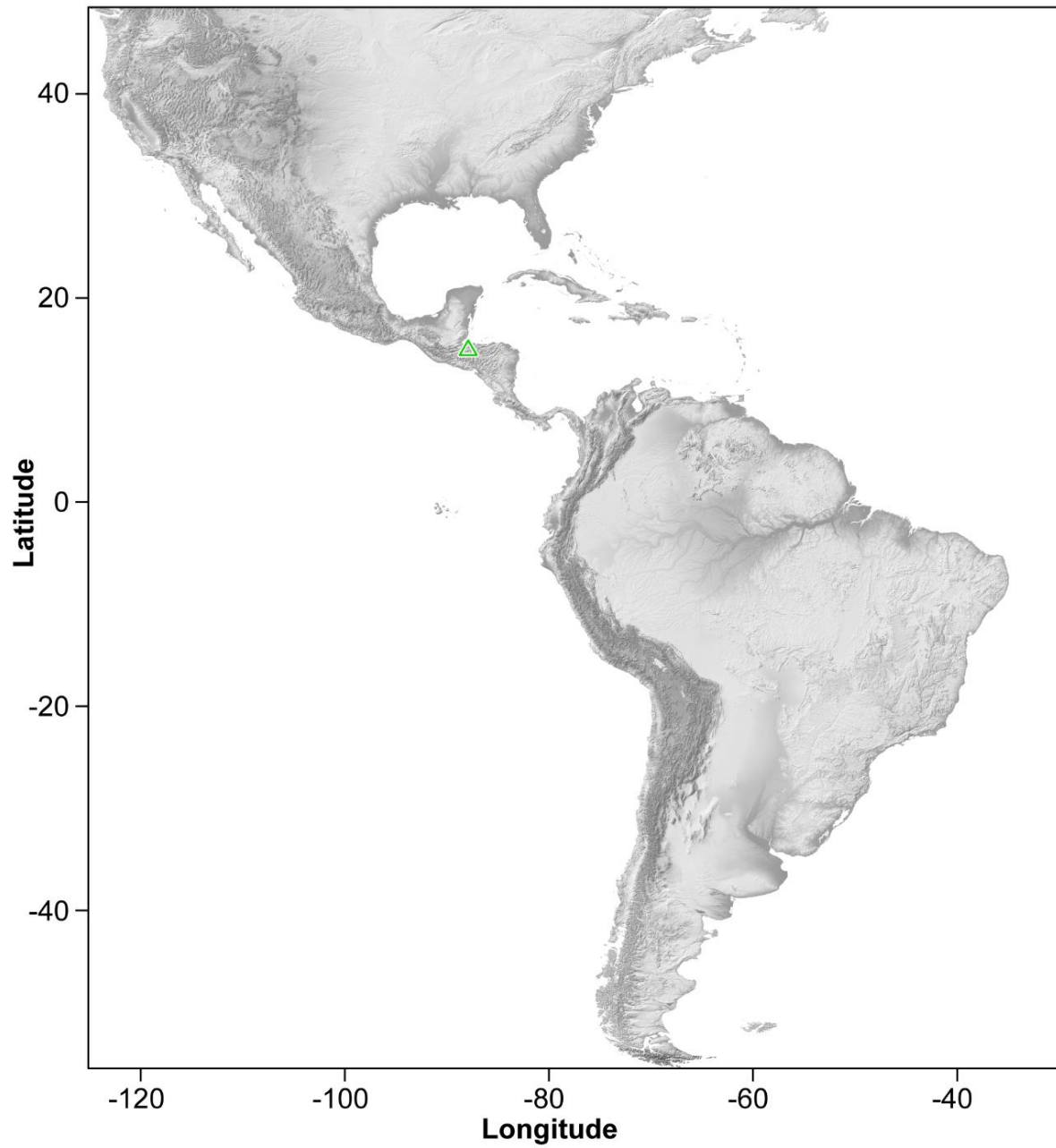
**Figure S5.** Geographic distribution of *B. australis* (n=56).



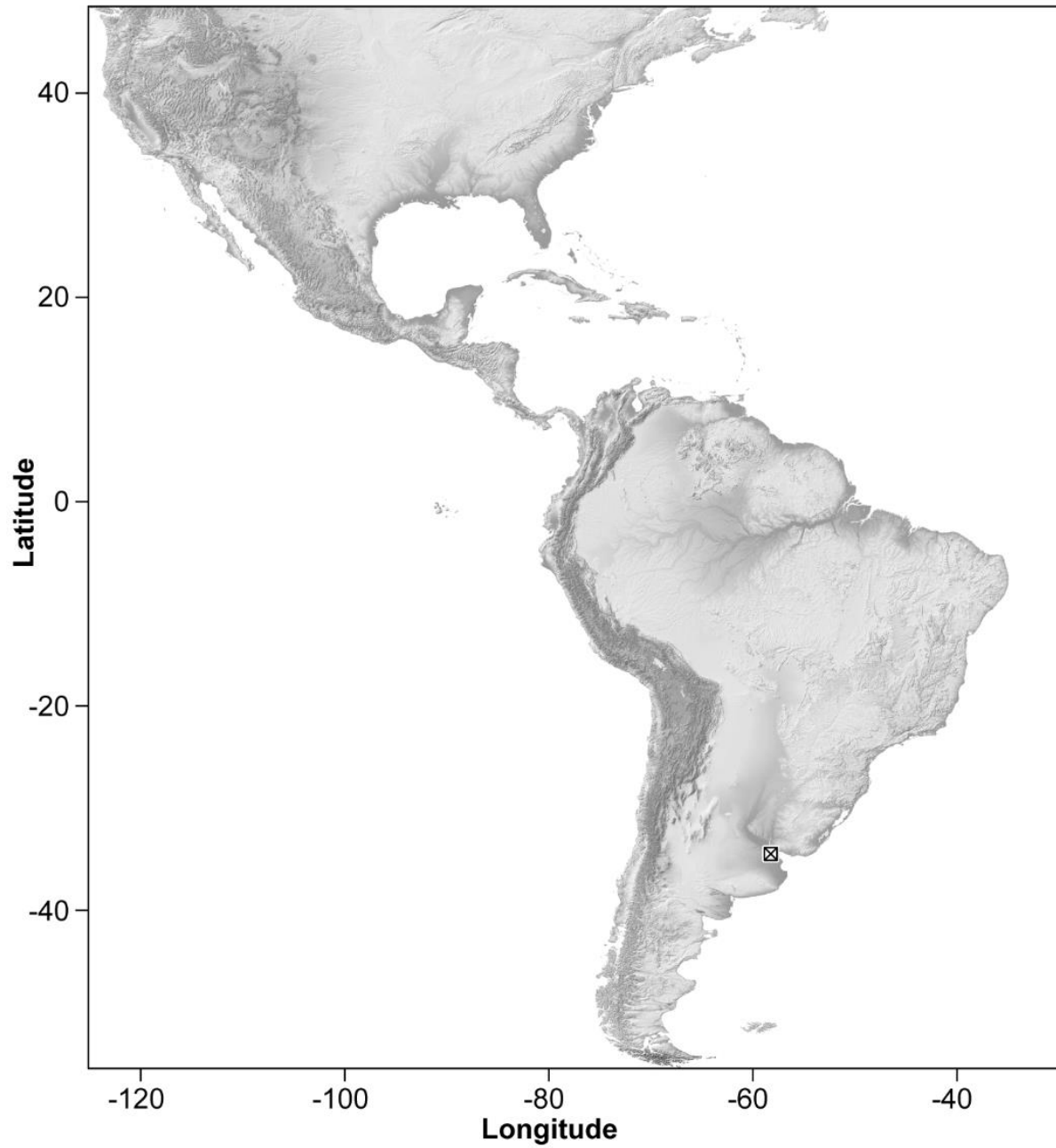
**Figure S6.** Geographic distribution of *B. bahamensis* **n. sp.** (n=2).



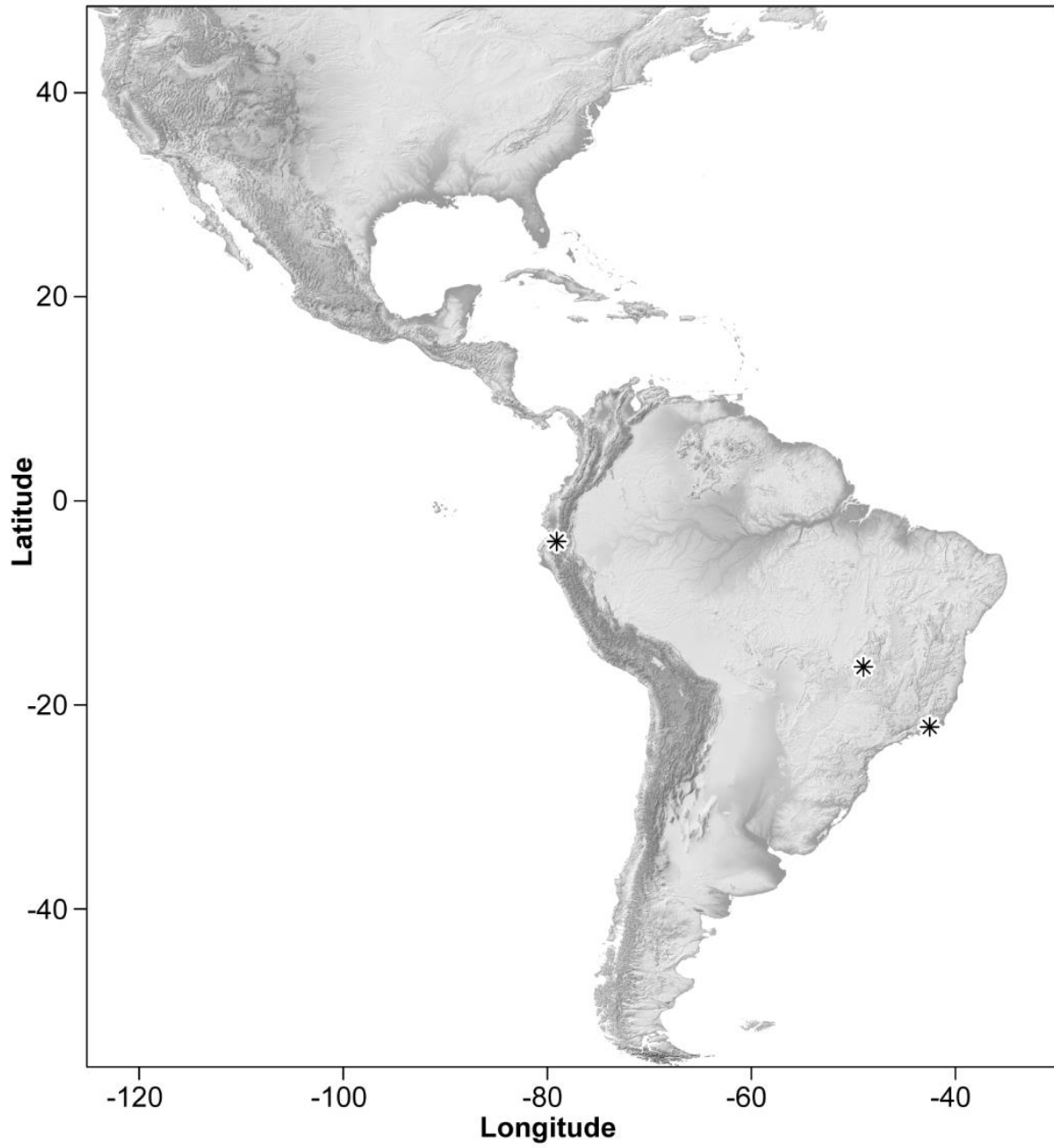
**Figure S7.** Geographic distribution of *B. bicolor* n. sp. (n=1).



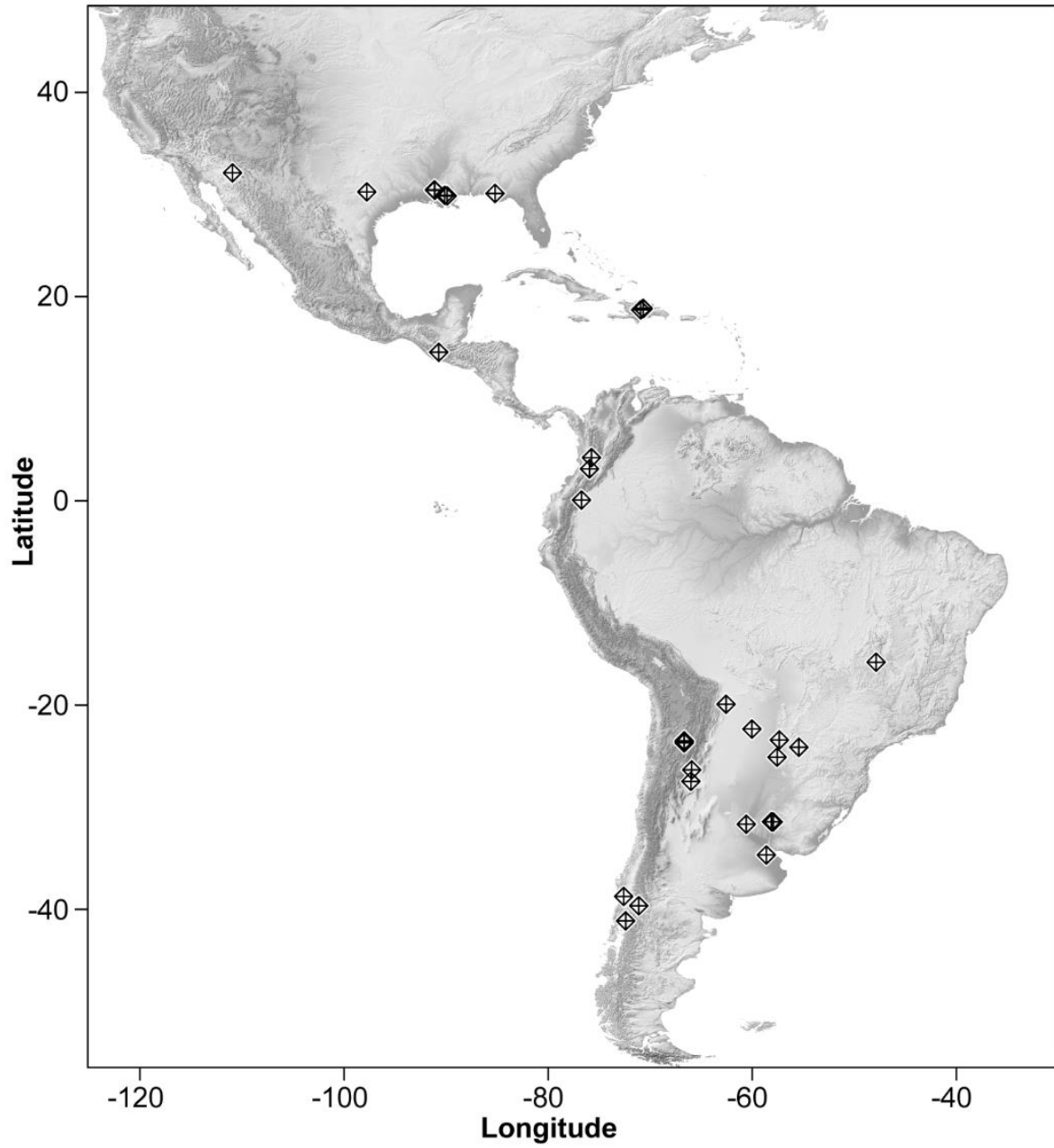
**Figure S8.** Geographic distribution of *B. bonariensis* **n. st.** (n=1).



**Figure S9.** Geographic distribution of *B. brasiliensis* (n=3).

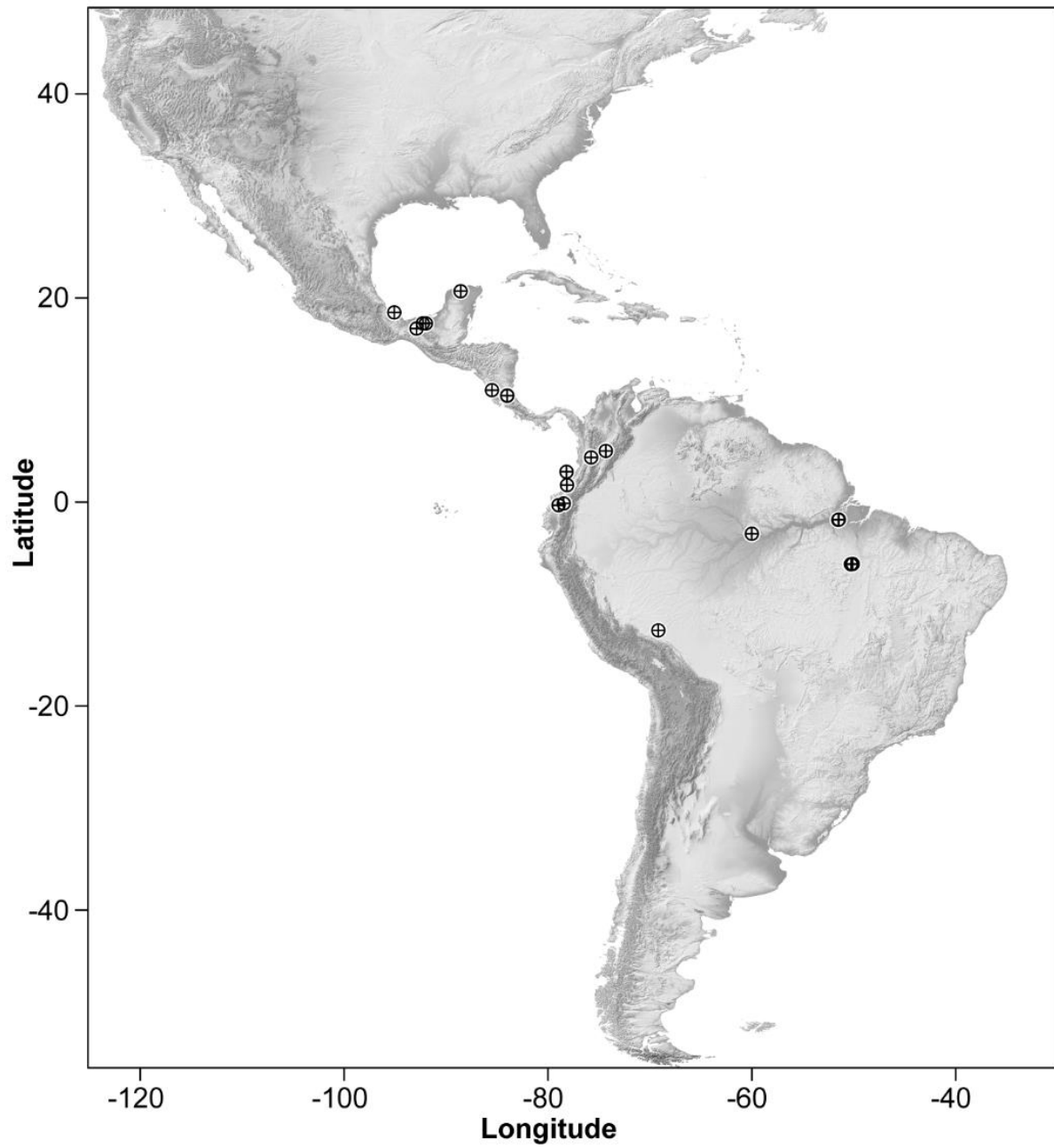


**Figure S10.** Geographic distribution of *B. bruchi* (n=32).

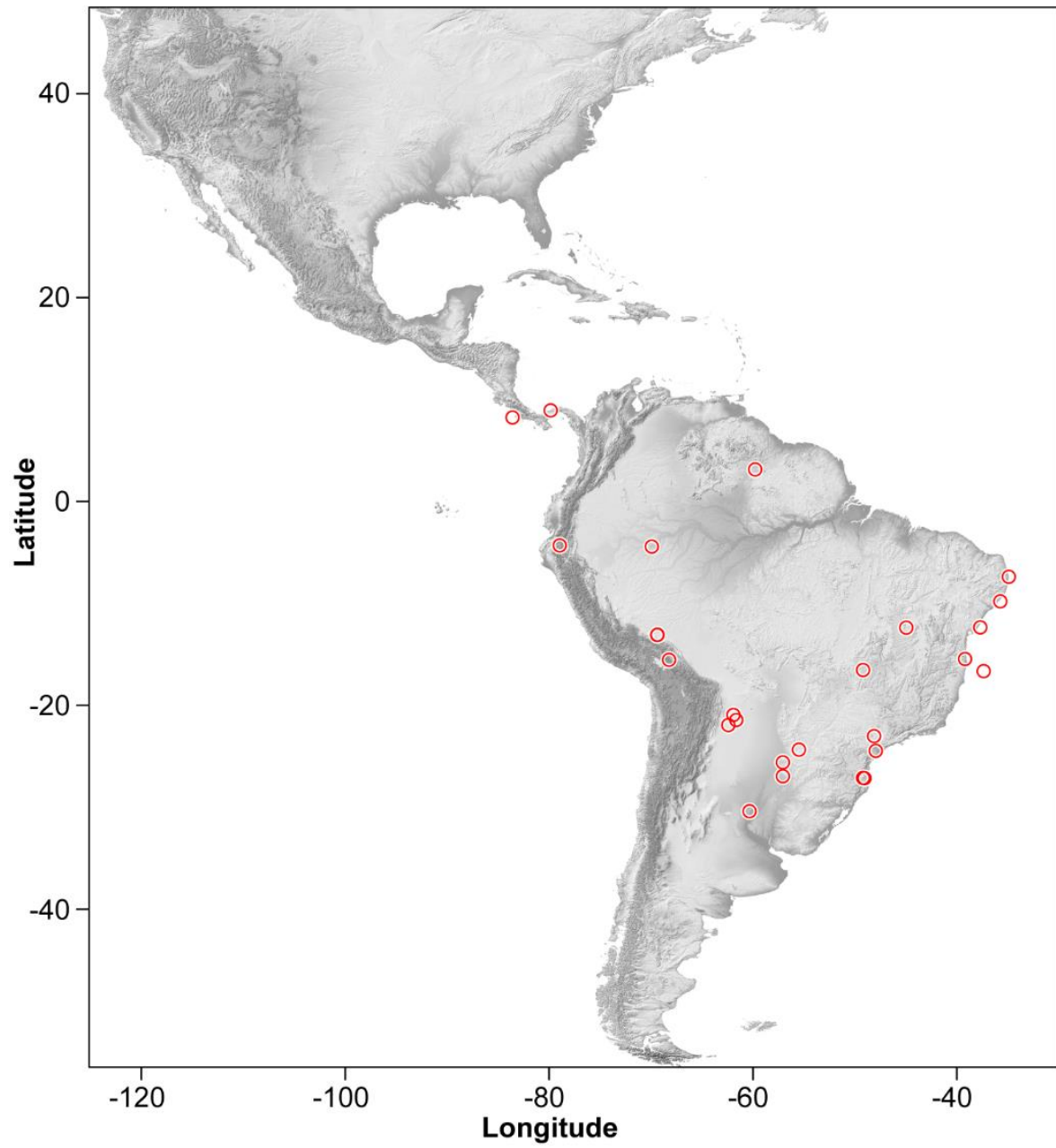




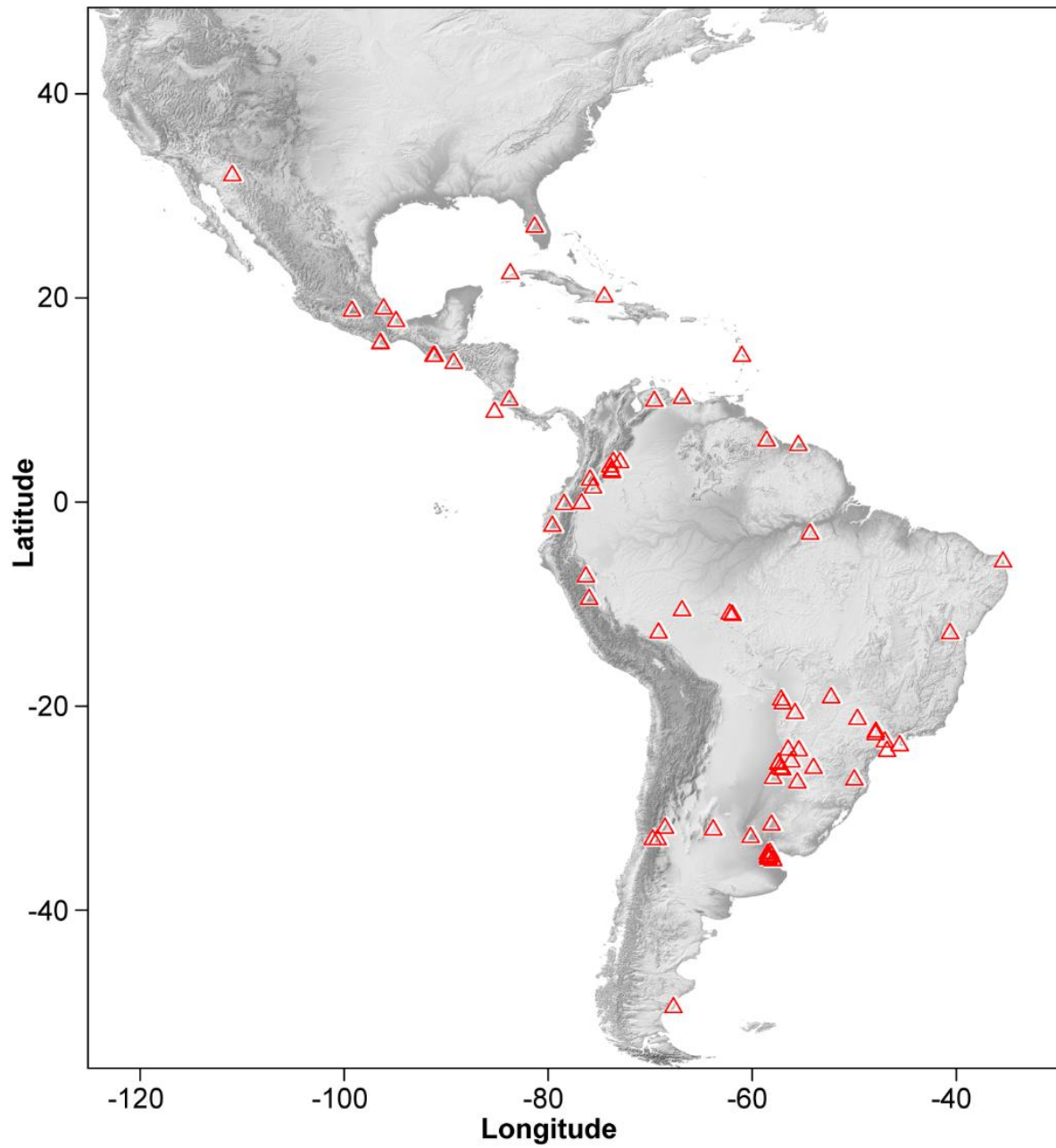
**Figure S11.** Geographic distribution of *B. cavernicola* (n=21).



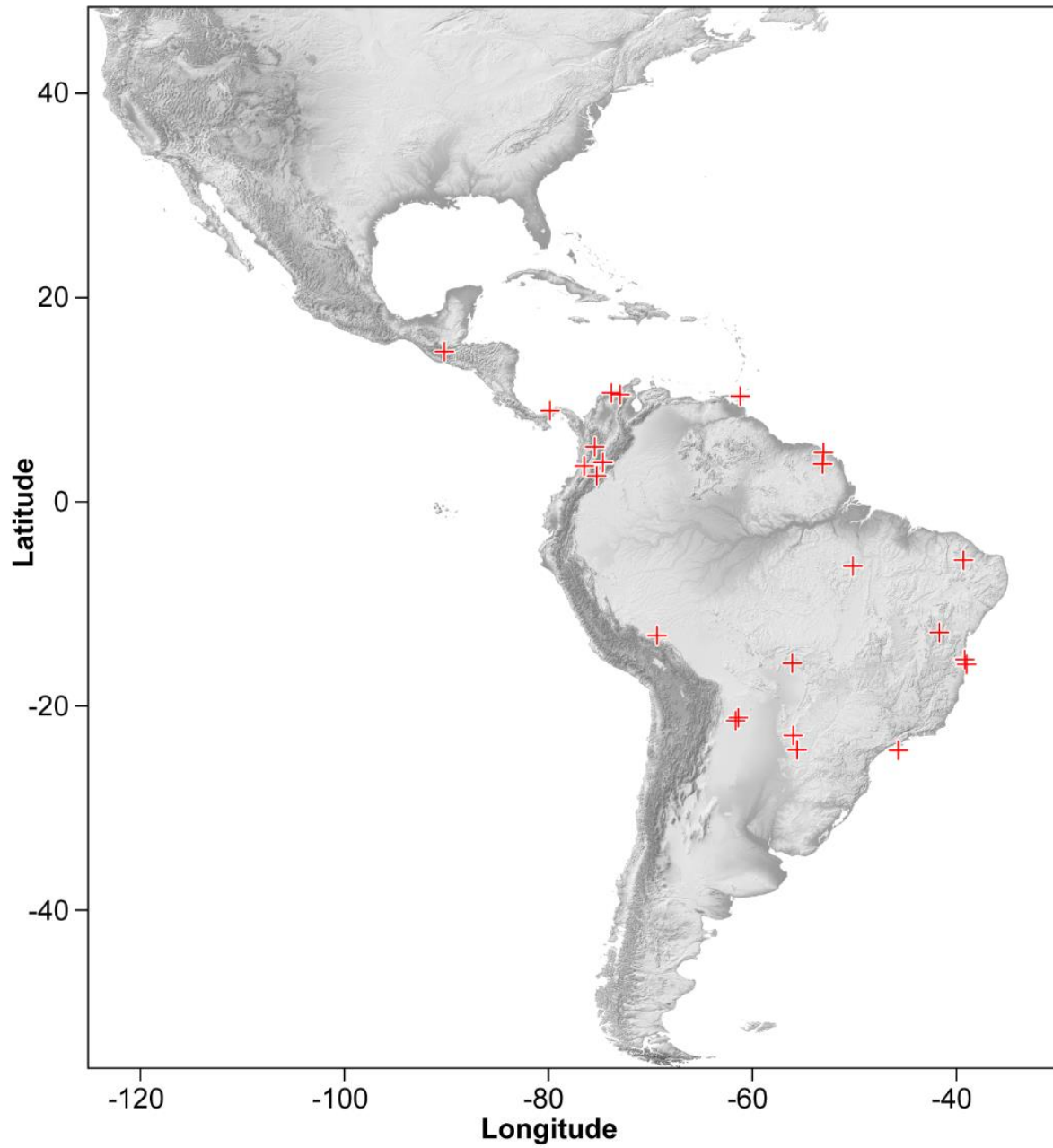
**Figure S12.** Geographic distribution of *B. coactus* (n=28).



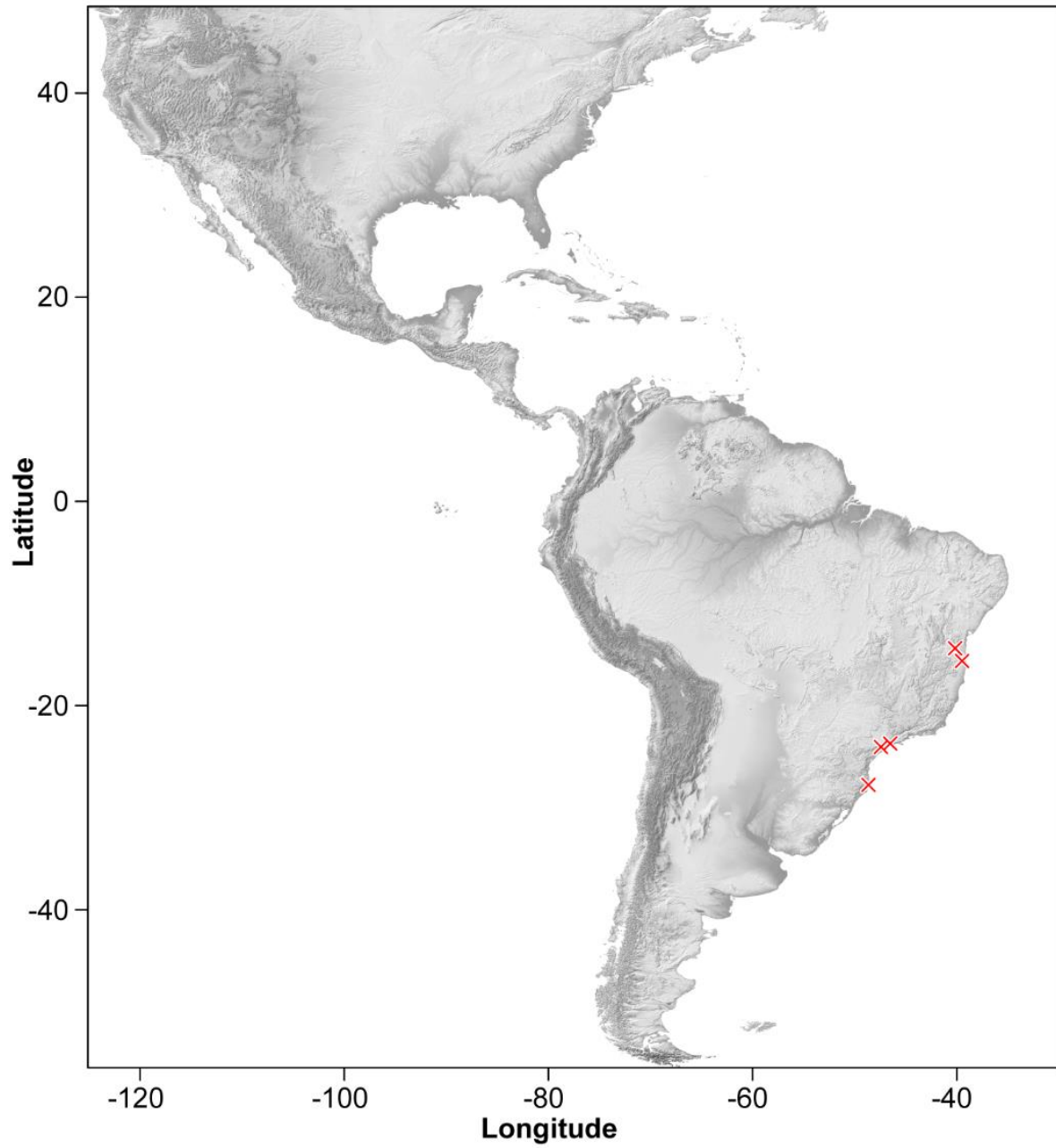
**Figure S13.** Geographic distribution of *B. cordemoyi* (n=79).



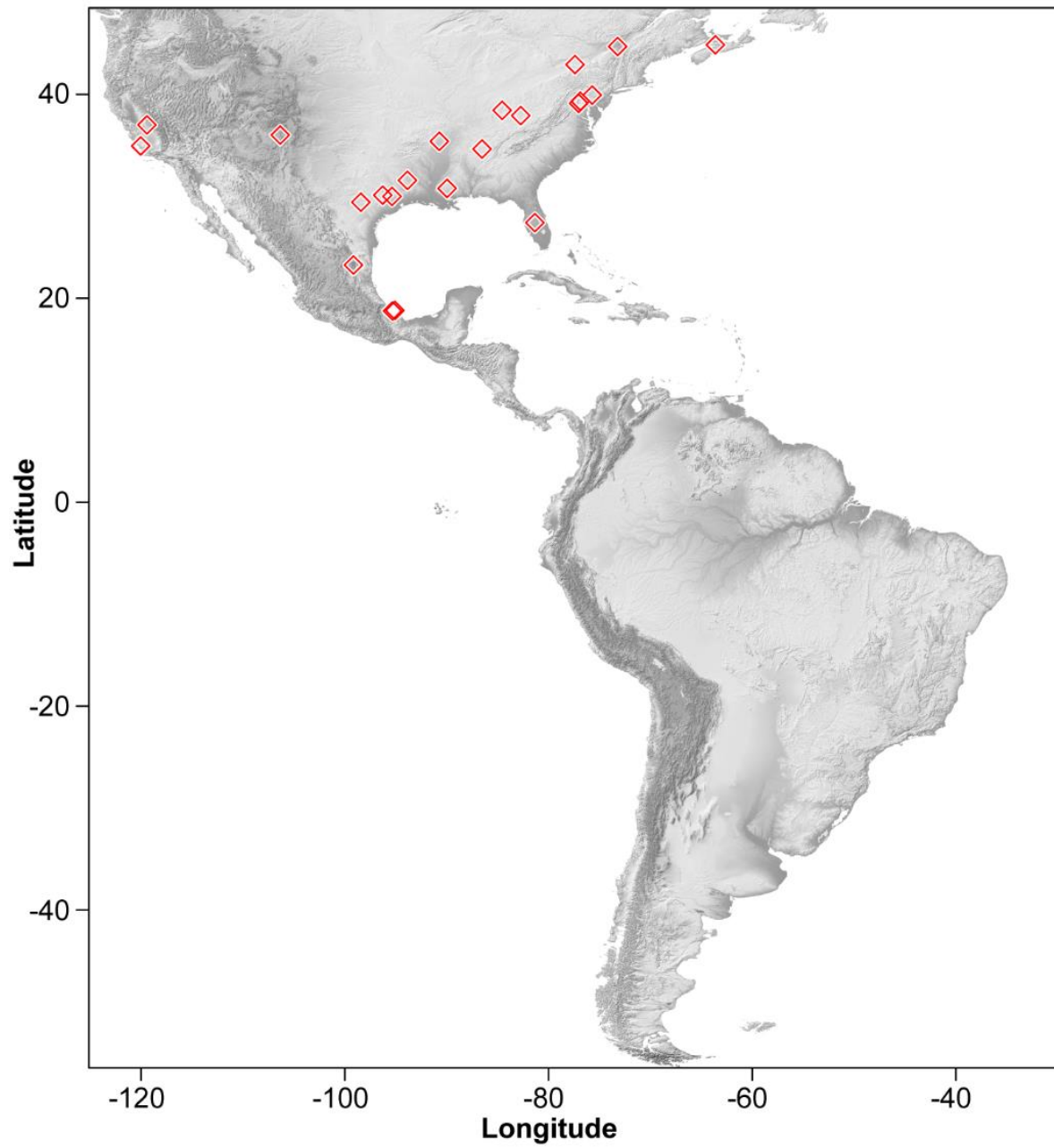
**Figure S14.** Geographic distribution of *B. degener* (n=24).



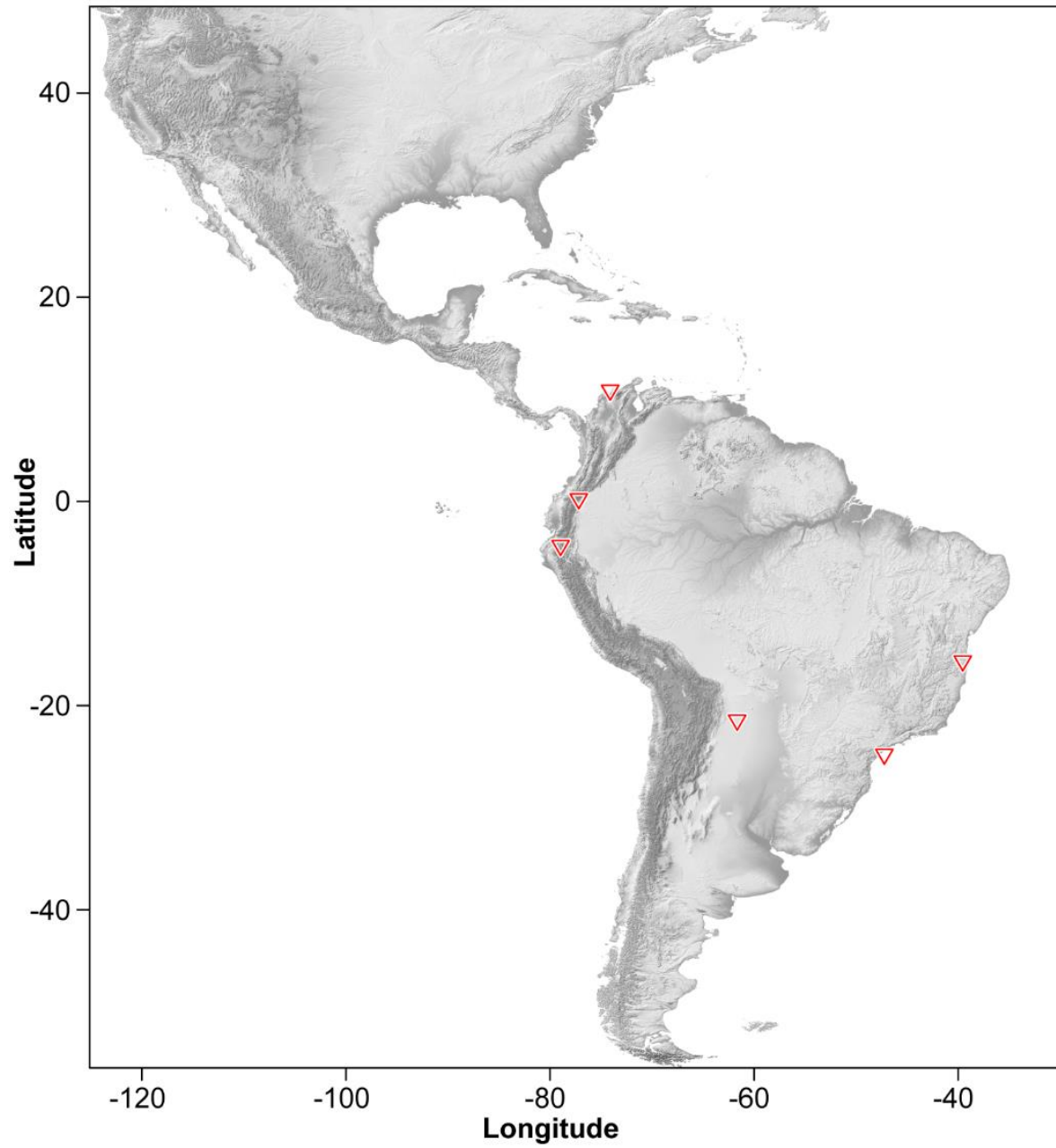
**Figure S15.** Geographic distribution of *B. delabiei* (n=5).



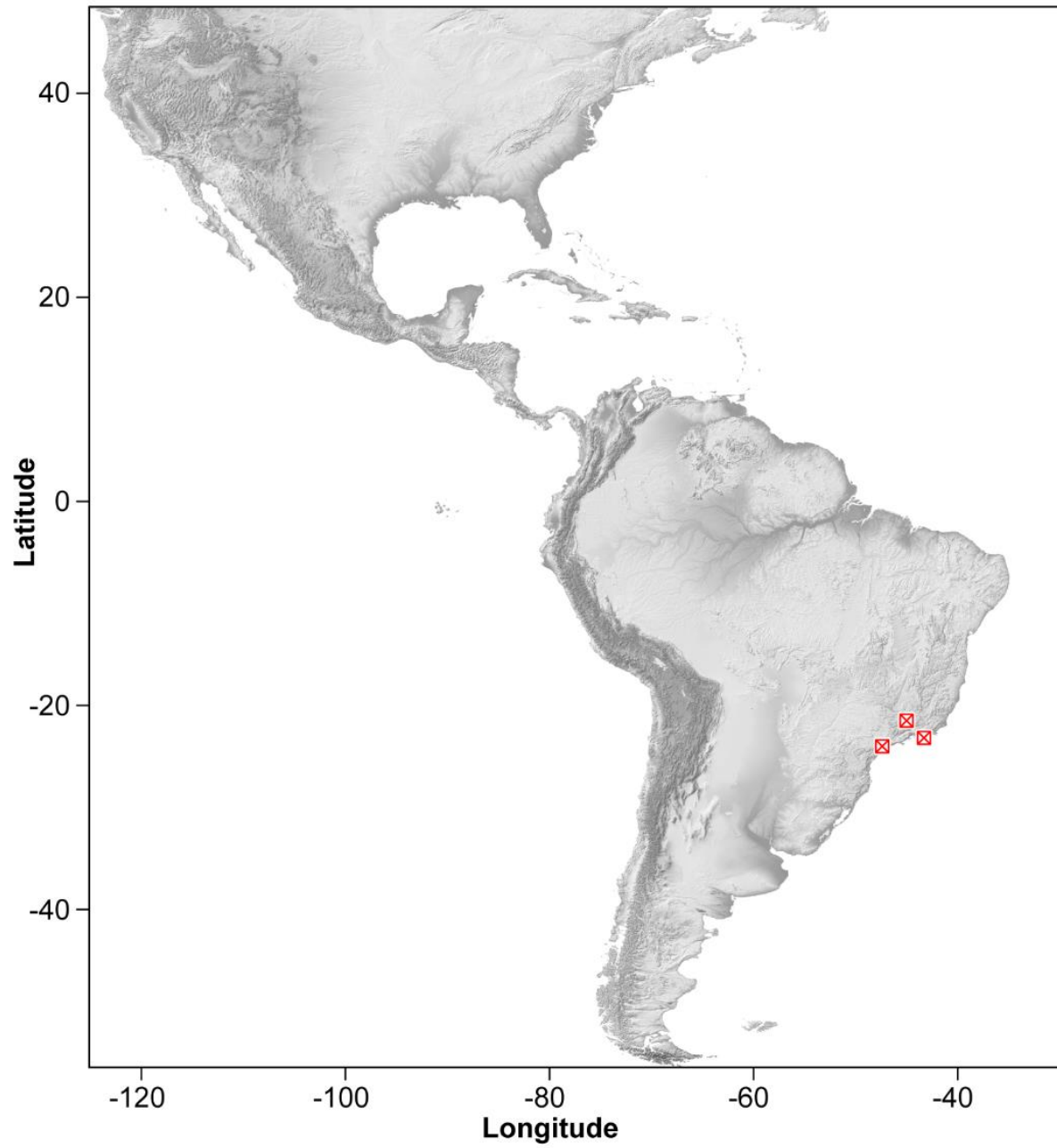
**Figure S16.** Geographic distribution of *B. depilis* (n=22).



**Figure S17.** Geographic distribution of *B. donisthorpei* (n=6).

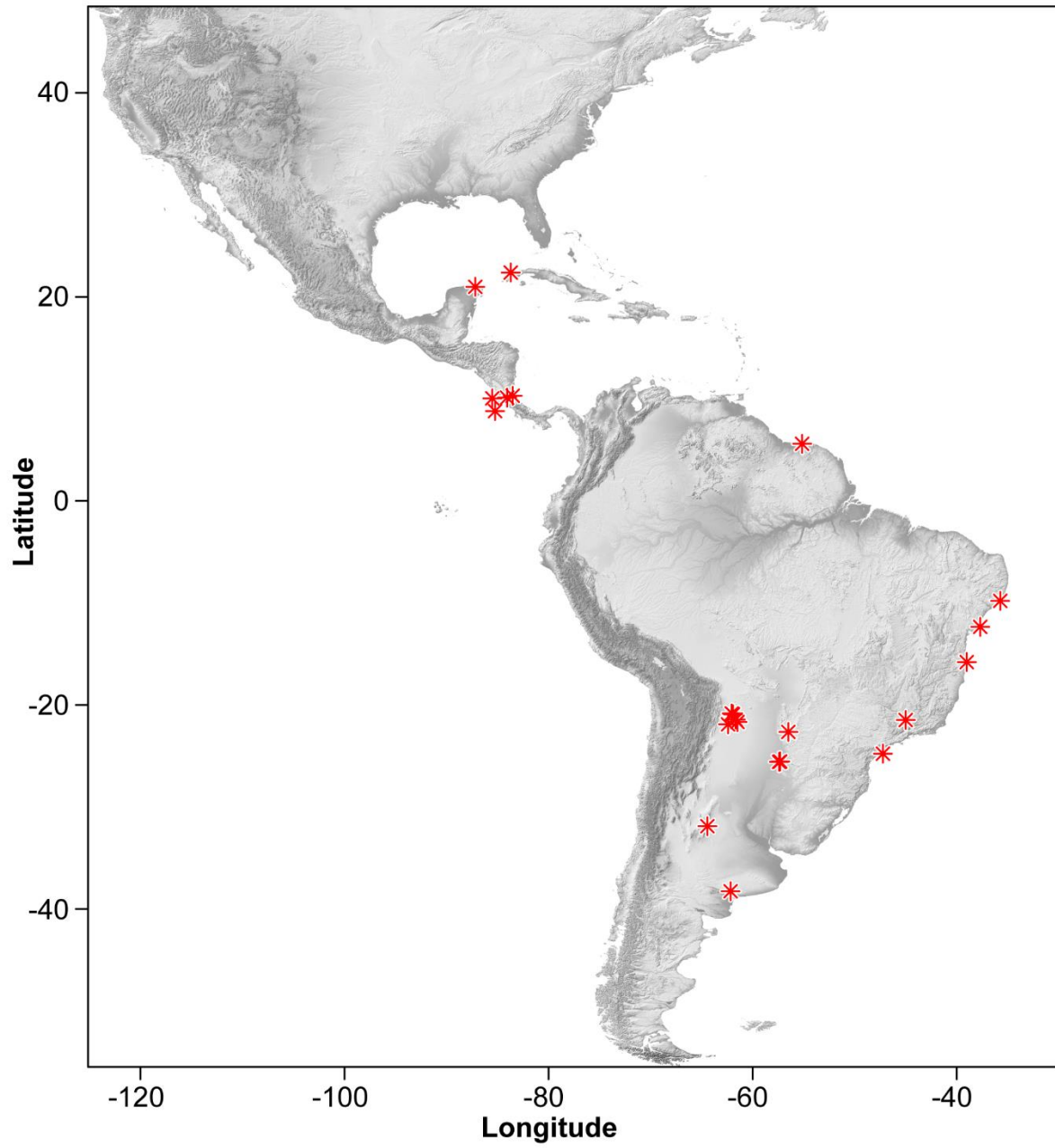


**Figure S18.** Geographic distribution of *B. feitosai* (n=3).

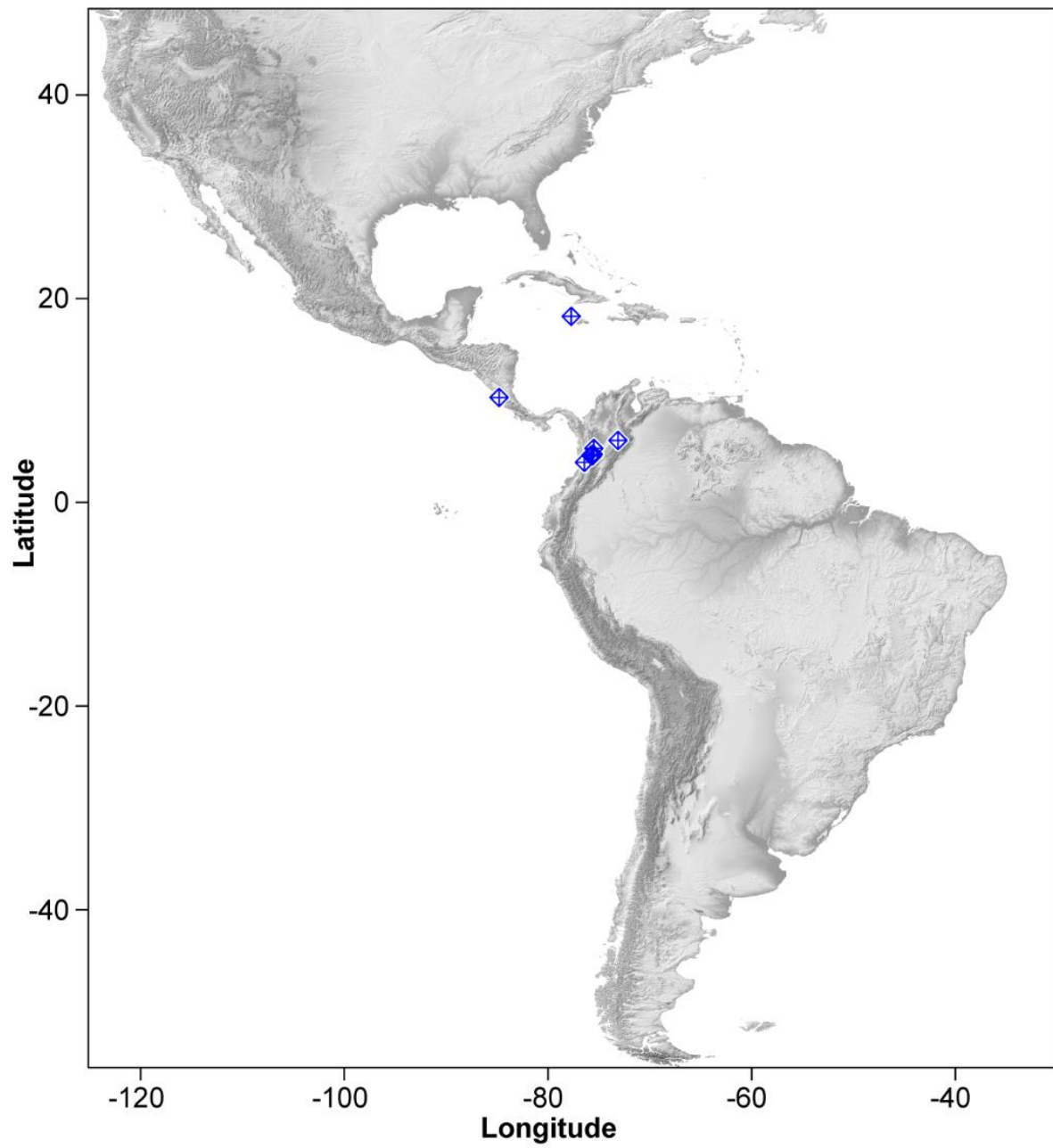




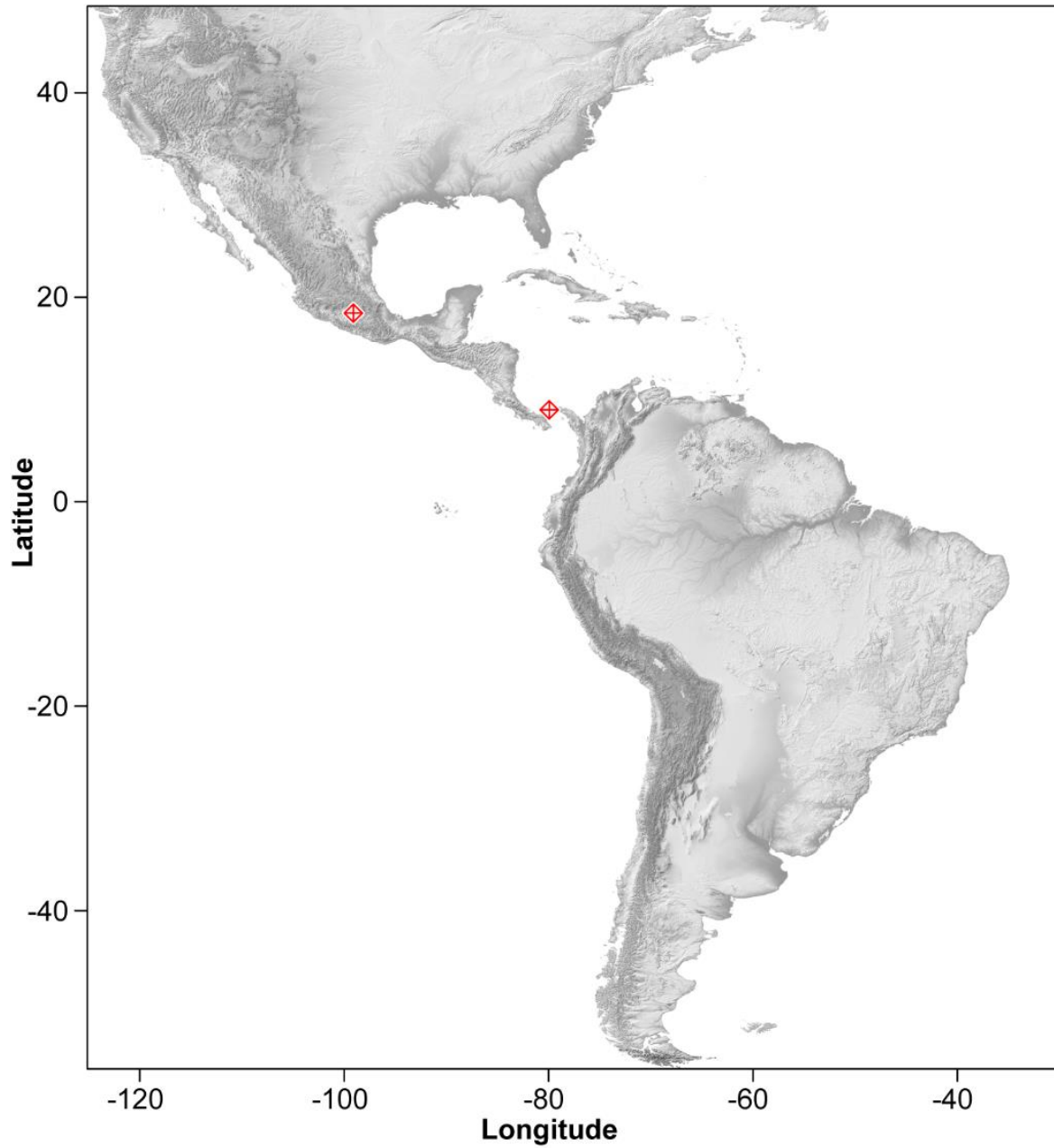
**Figure S19.** Geographic distribution of *B. fiebrigi* (n=24).



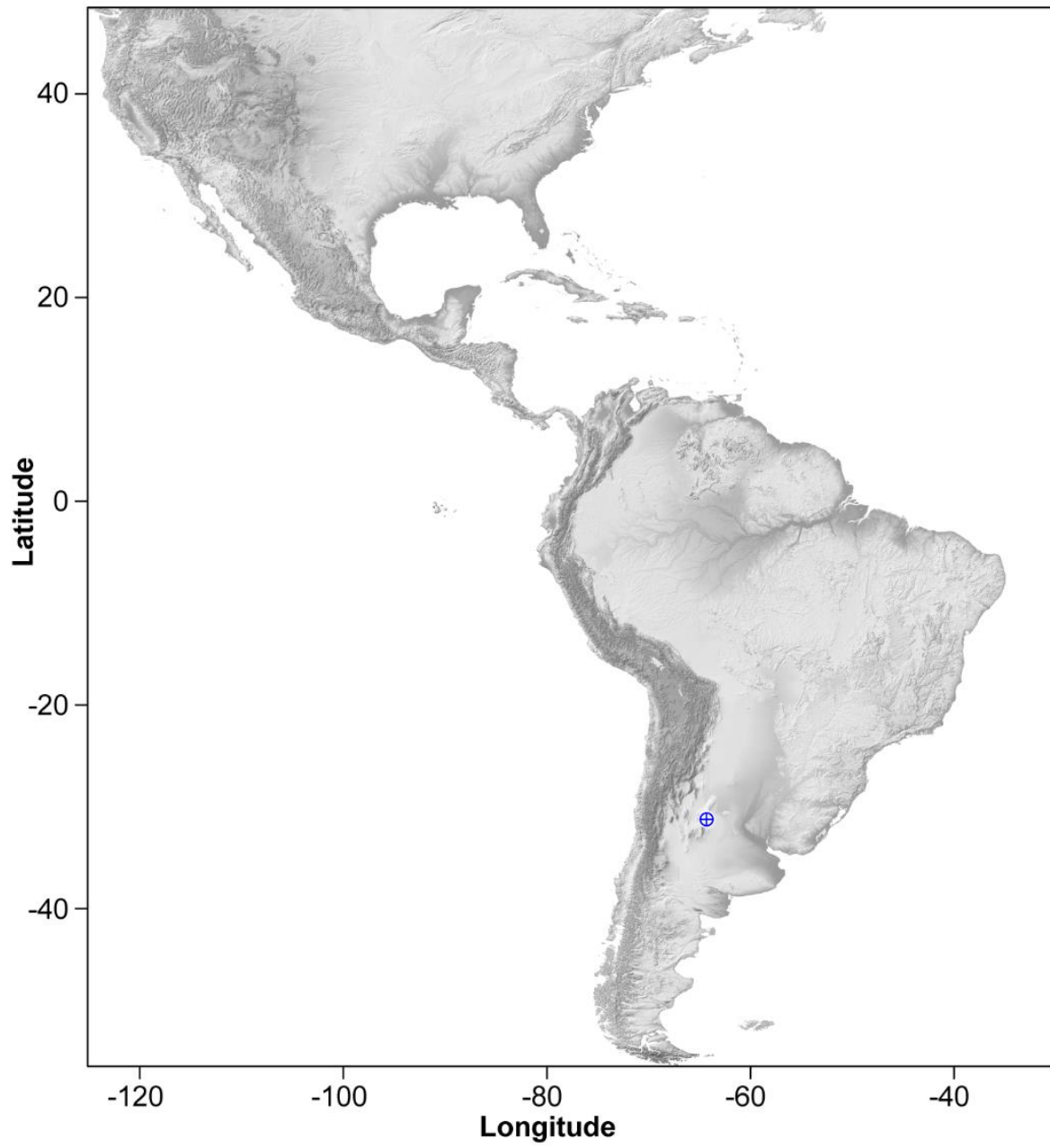
**Figure S20.** Geographic distribution of *B. flavidulus* (n=19).



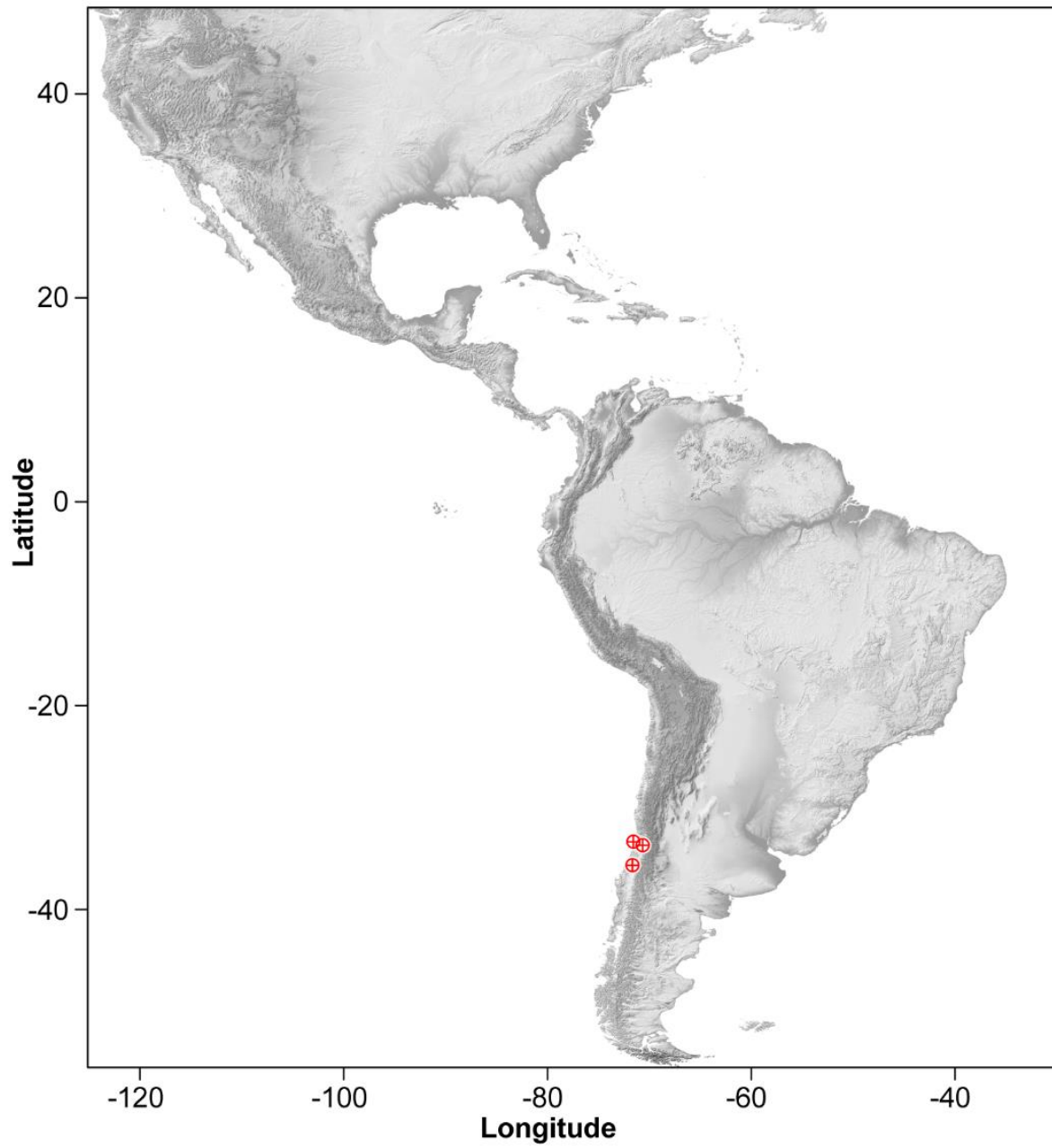
**Figure S21.** Geographic distribution of *B. gagates* (n=2).



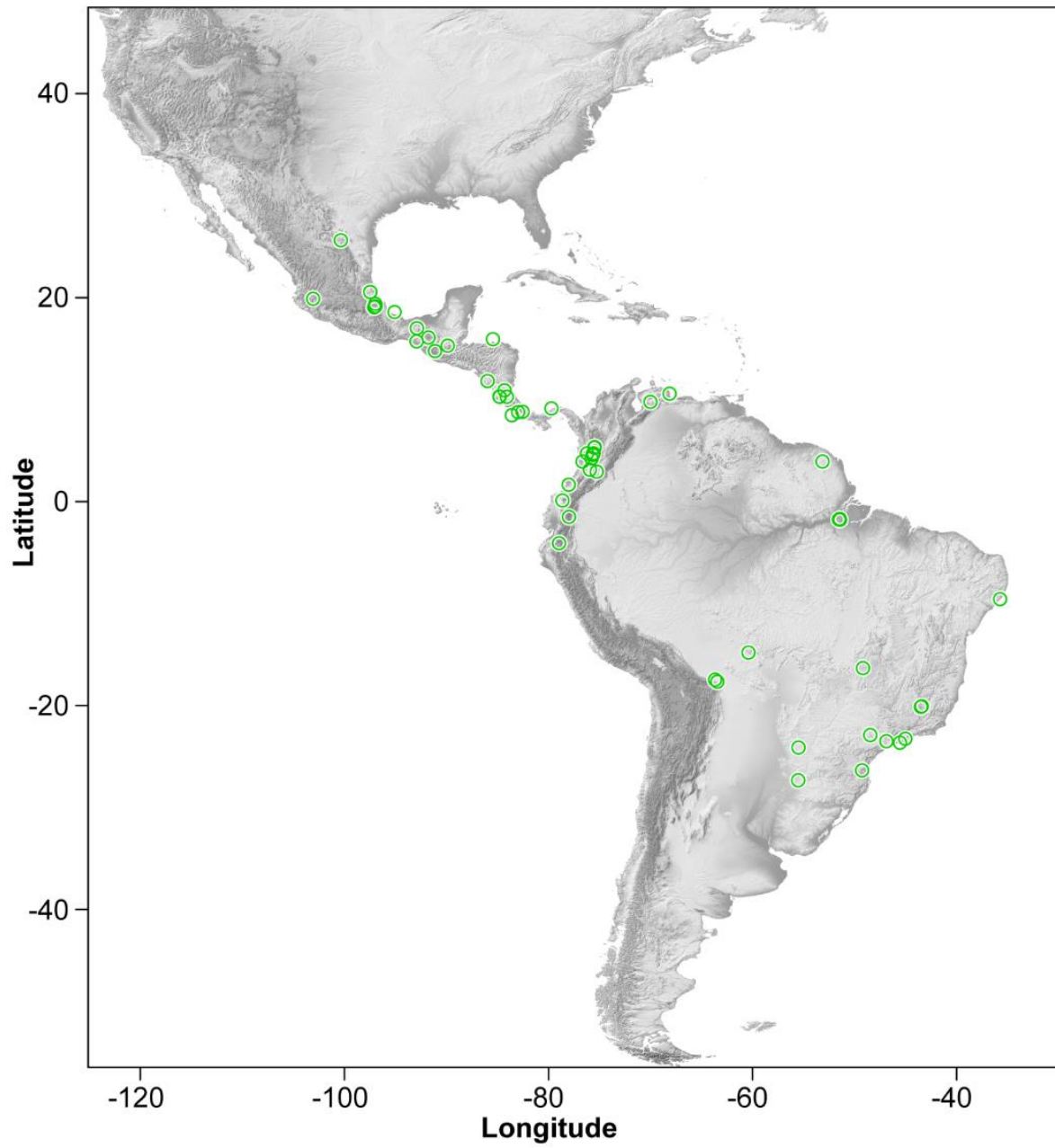
**Figure S22.** Geographic distribution of *B. gaucho* (n=1).



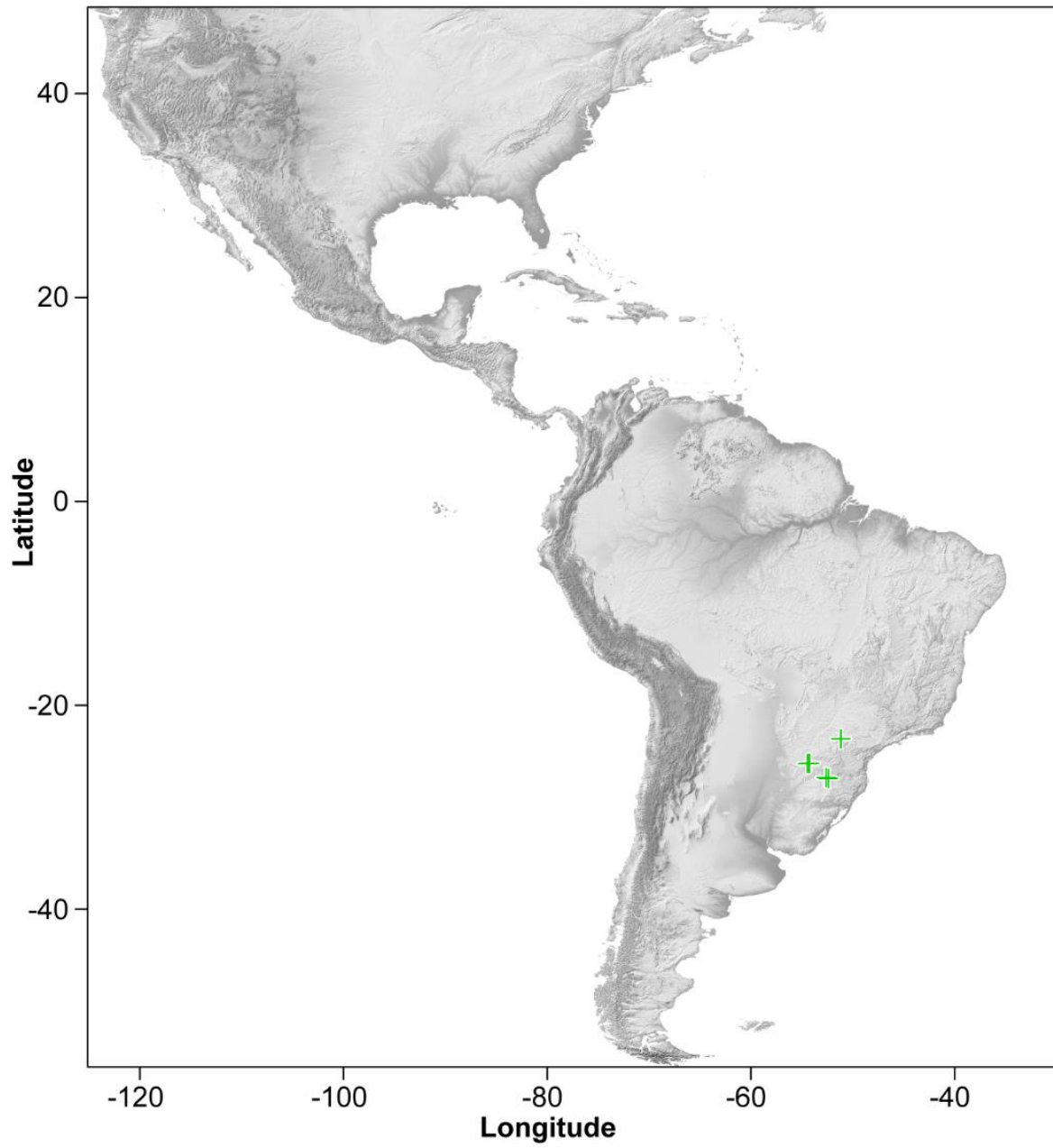
**Figure S23.** Geographic distribution of *B. giardi* (n=4).



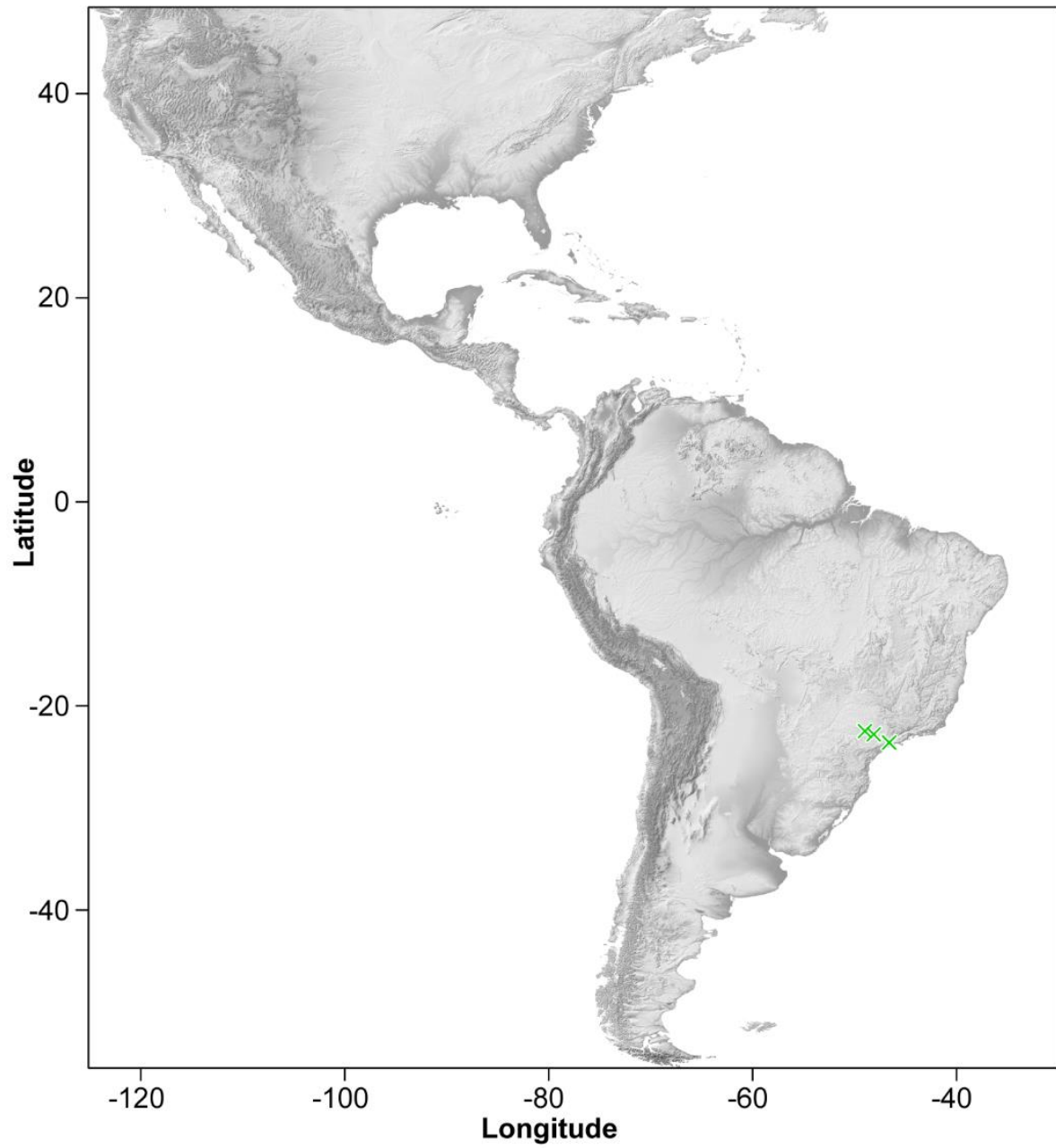
**Figure S24.** Geographic distribution of *B. heeri* (n=63).



**Figure S25.** Geographic distribution of *B. iridiscens* **n. sp.** (n=5).

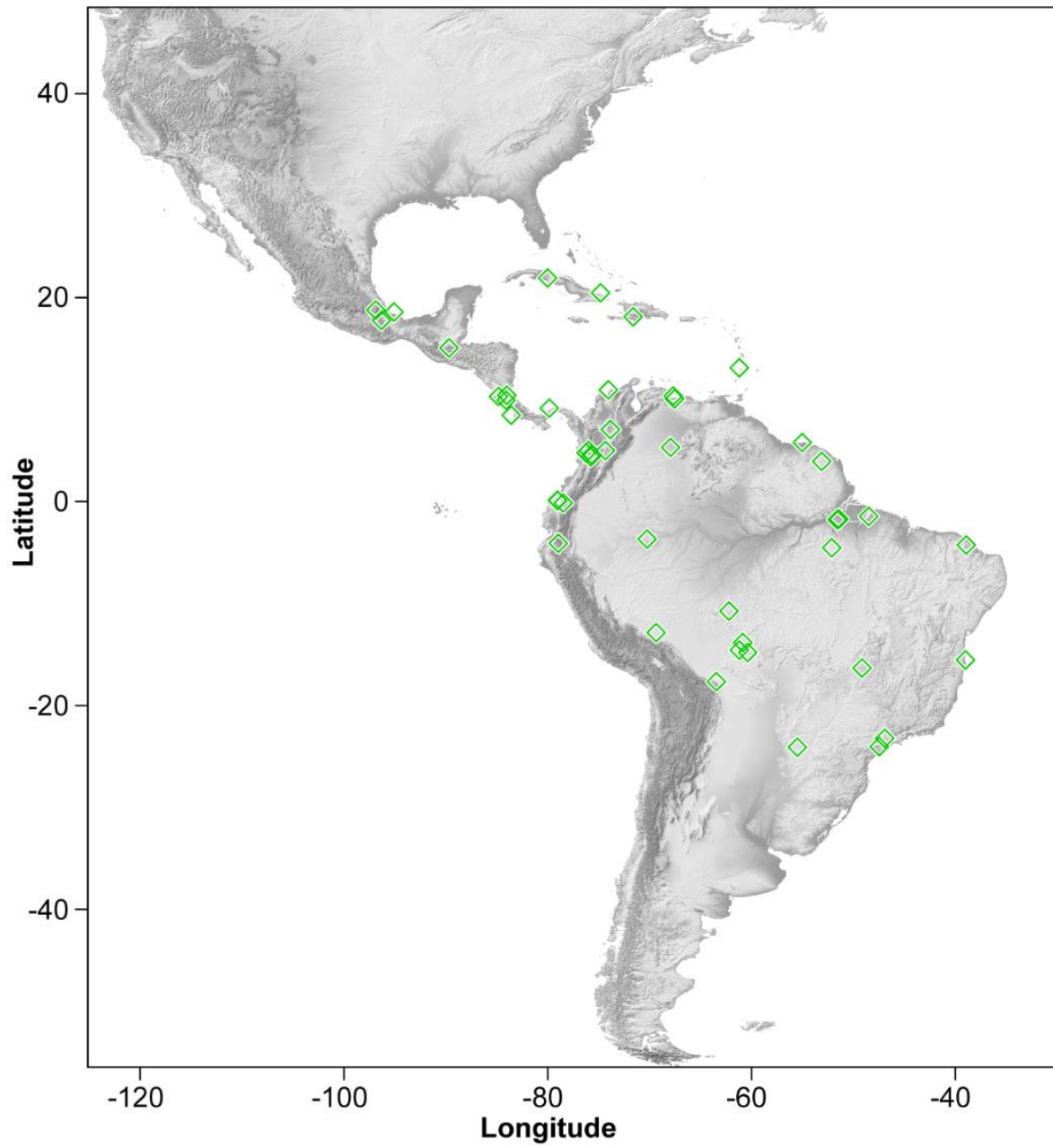


**Figure S26.** Geographic distribution of *B. micromegas* (n=5).

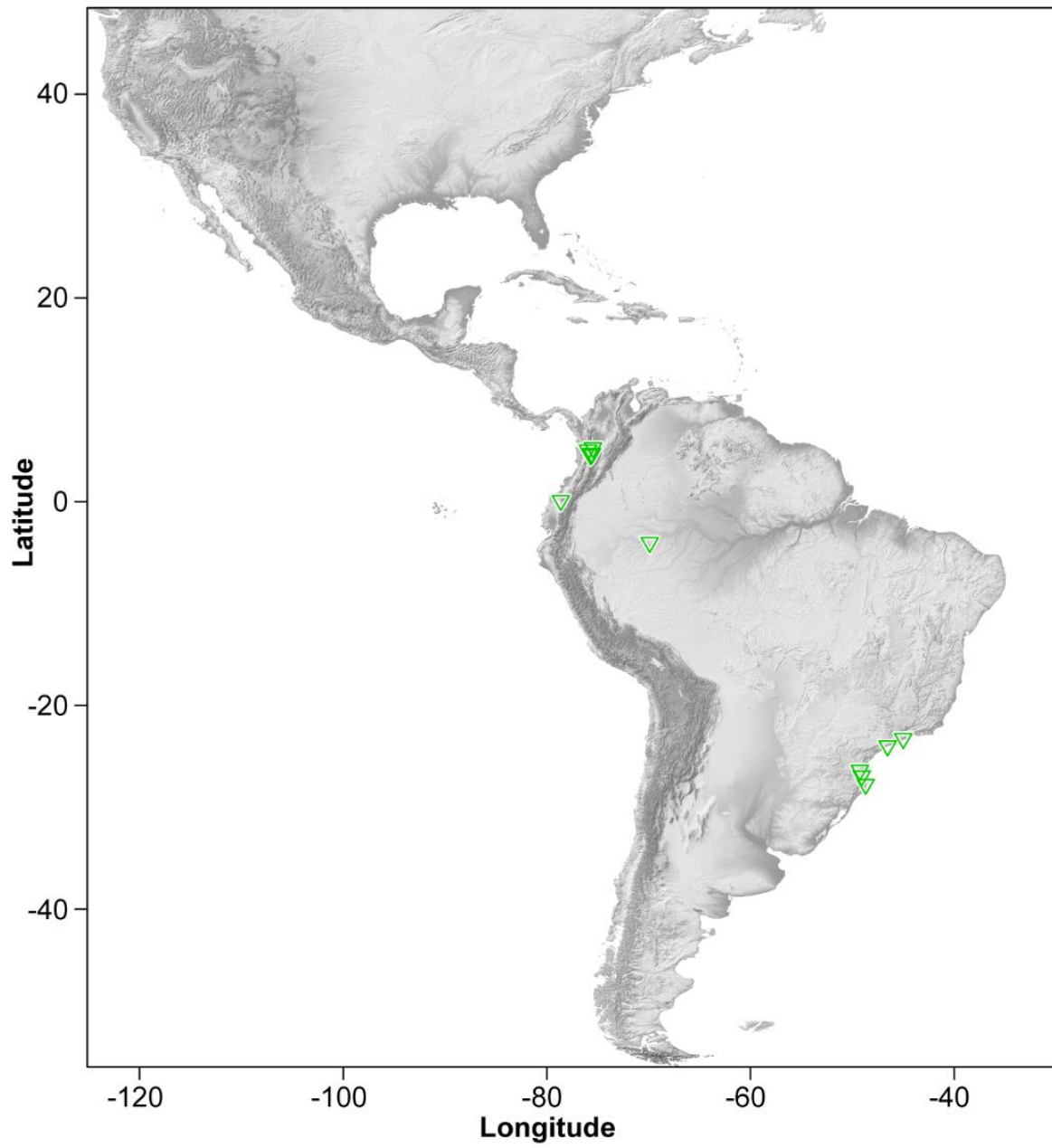




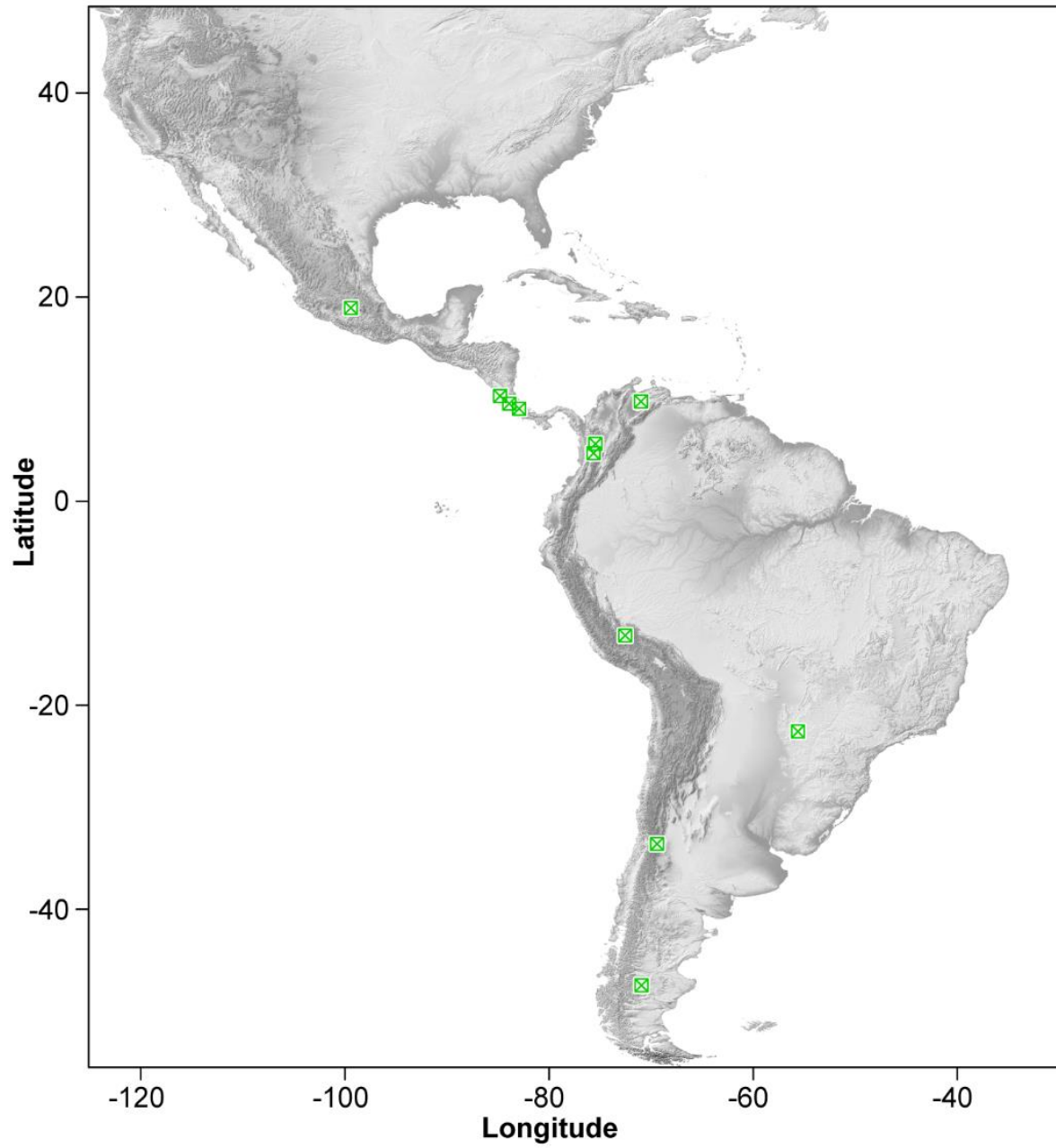
**Figure S27.** Geographic distribution of *B. minutus* (n=54).



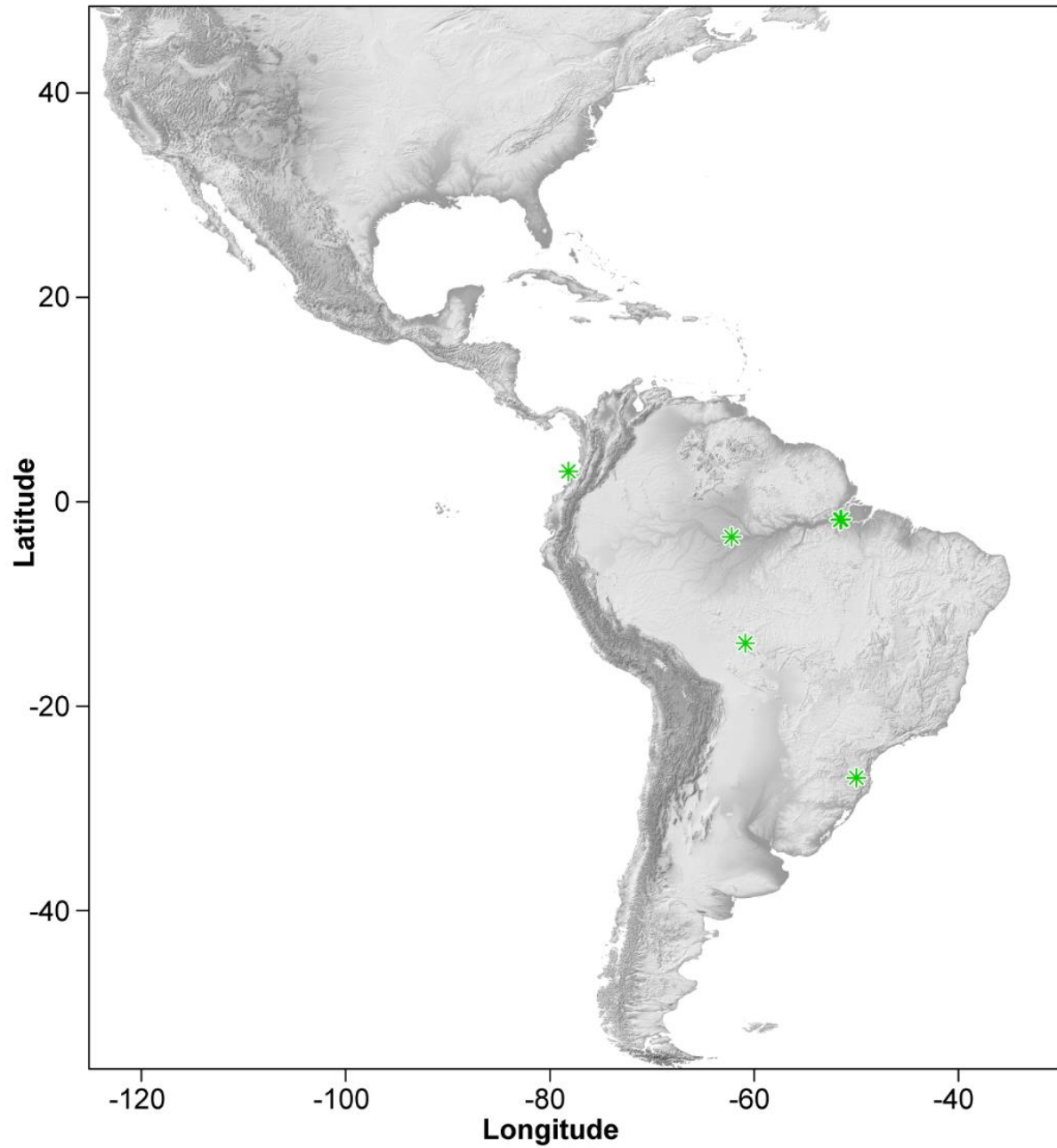
**Figure S28.** Geographic distribution of *B. modestus* (n=21).



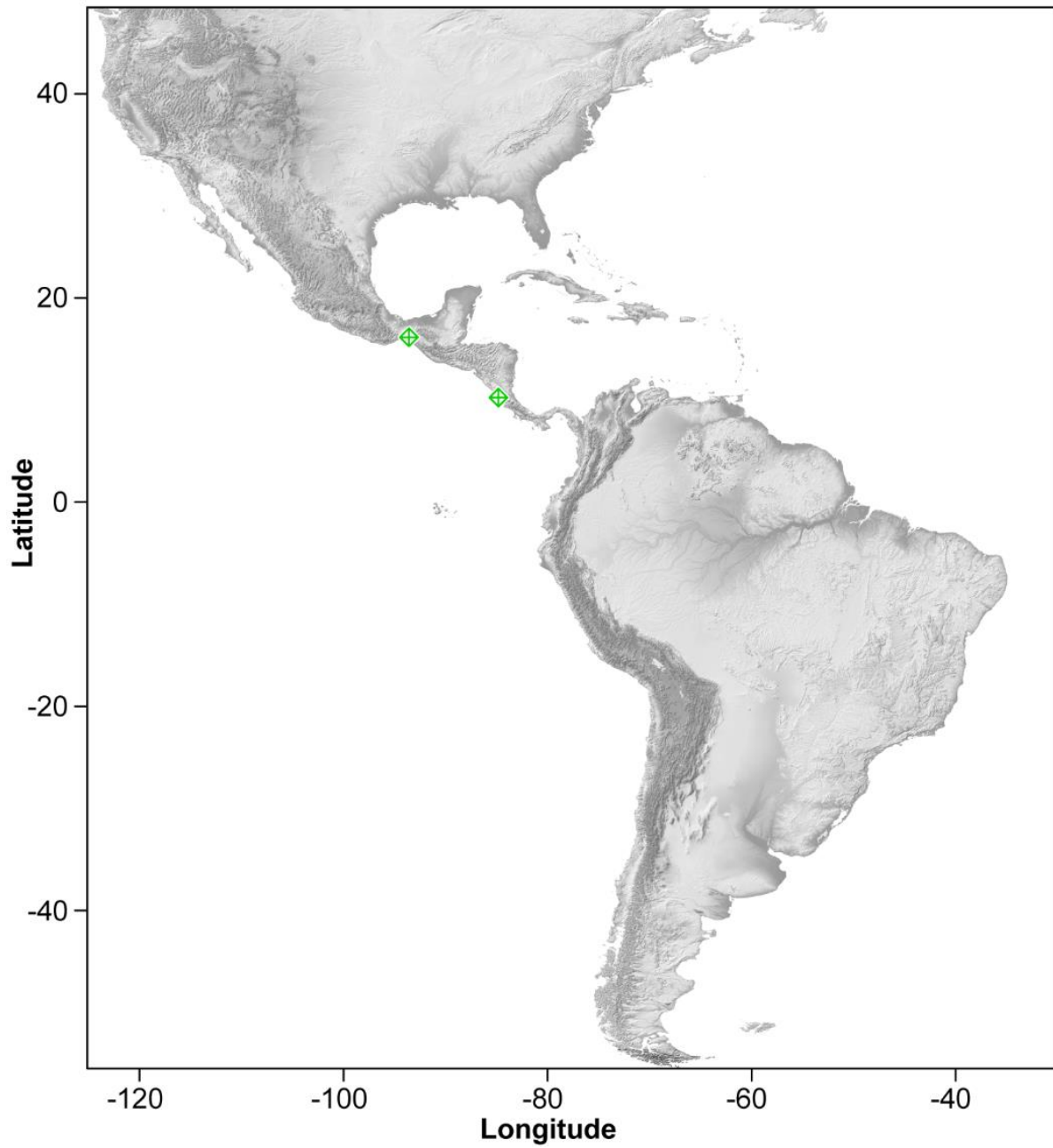
**Figure S29.** Geographic distribution of *B. musculus* (n=11).



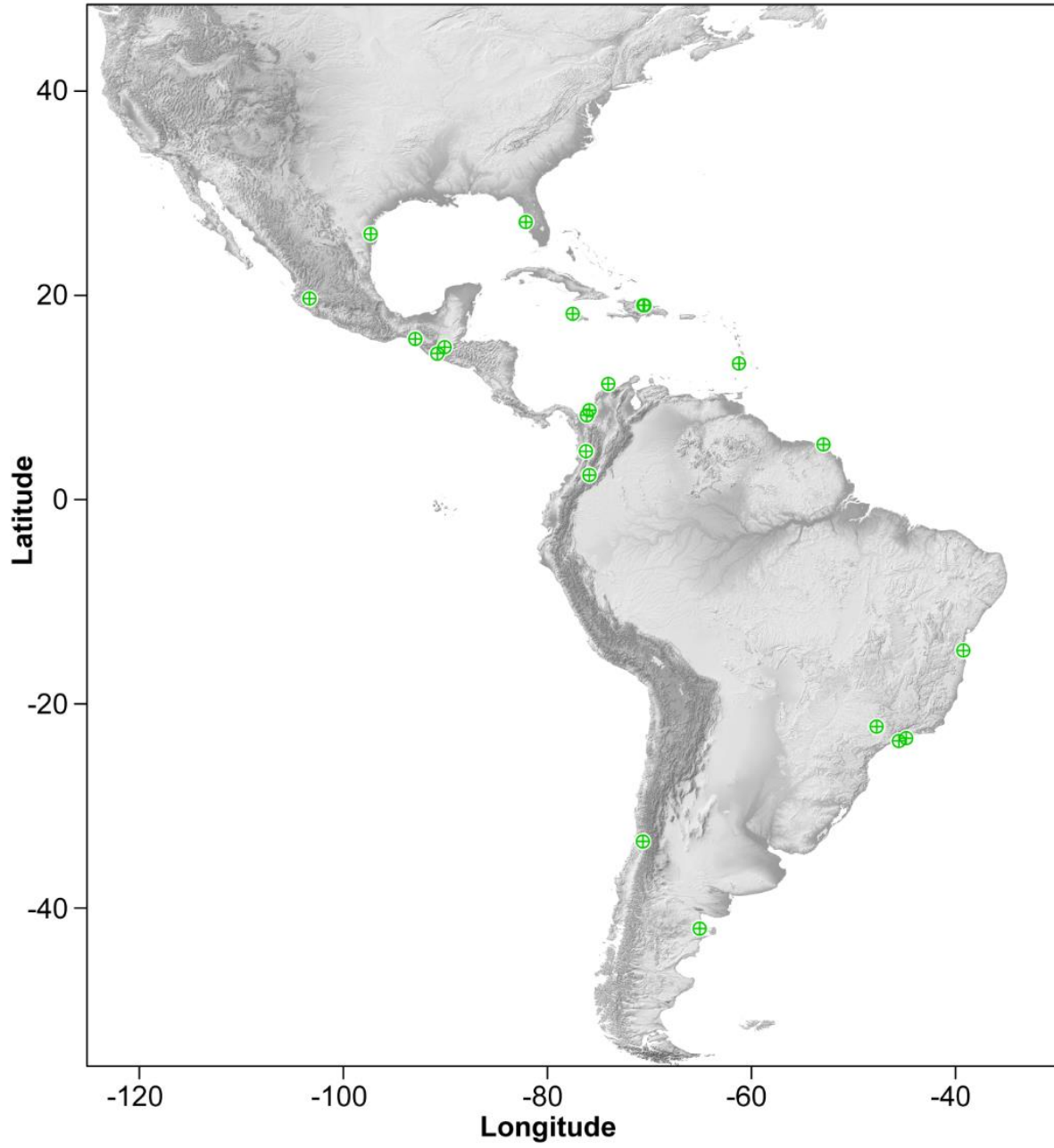
**Figure S30.** Geographic distribution of *B. myops* (n=7).



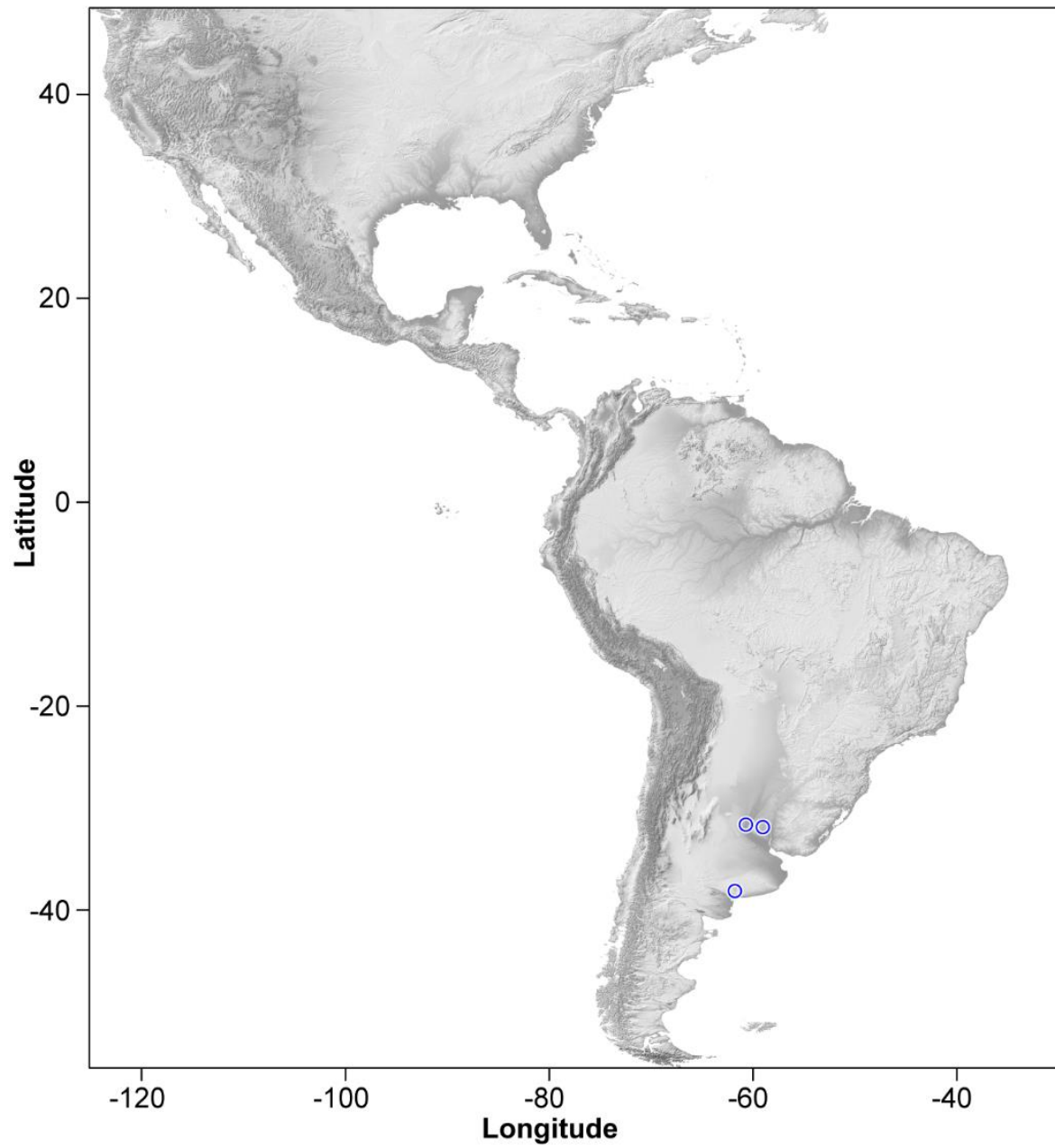
**Figure S31.** Geographic distribution of *B. nebulosus* (n=2).



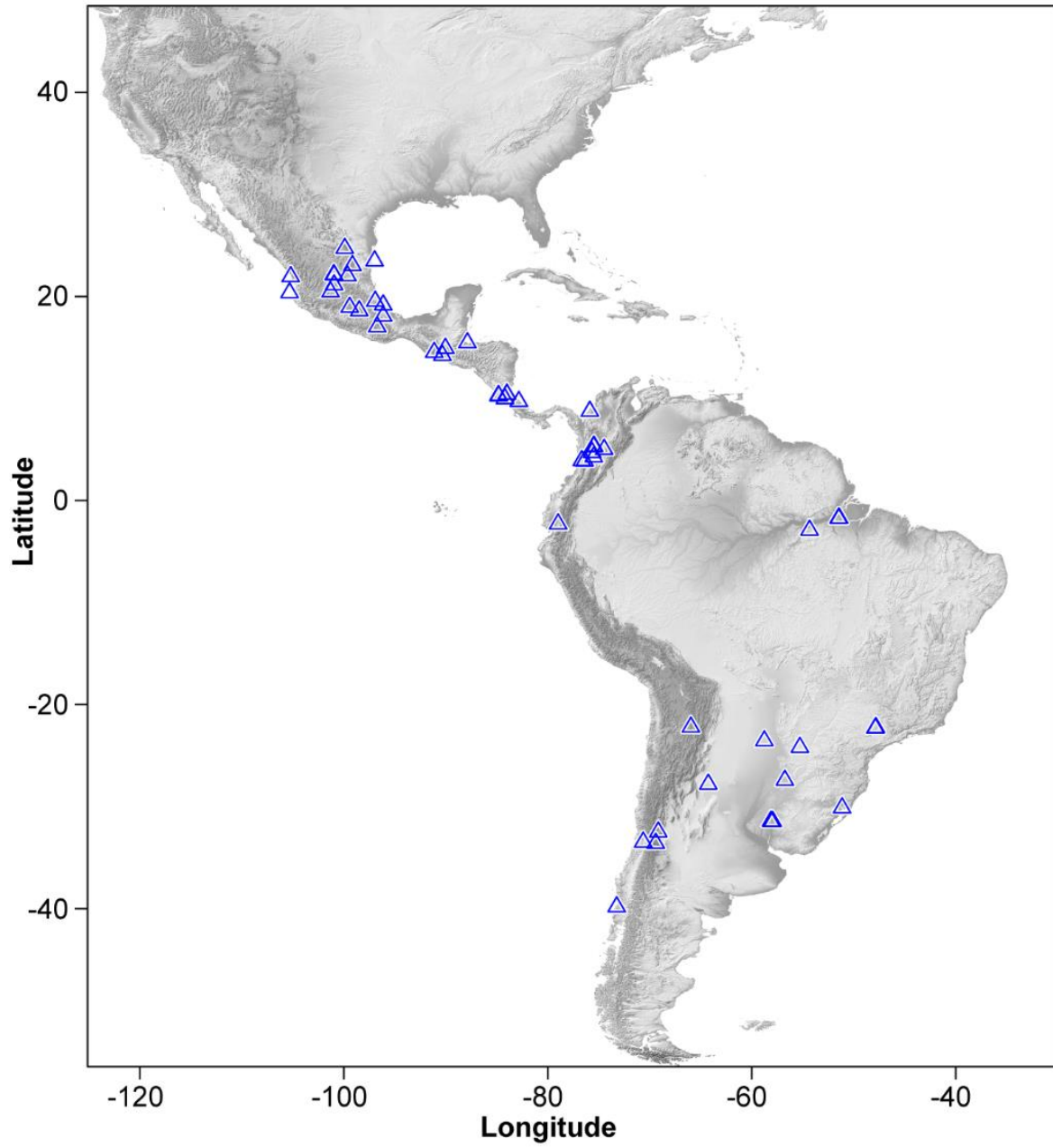
**Figure S32.** Geographic distribution of *B. obscurior* (n=23).



**Figure S33.** Geographic distribution of *B. oculatus* (n=3).

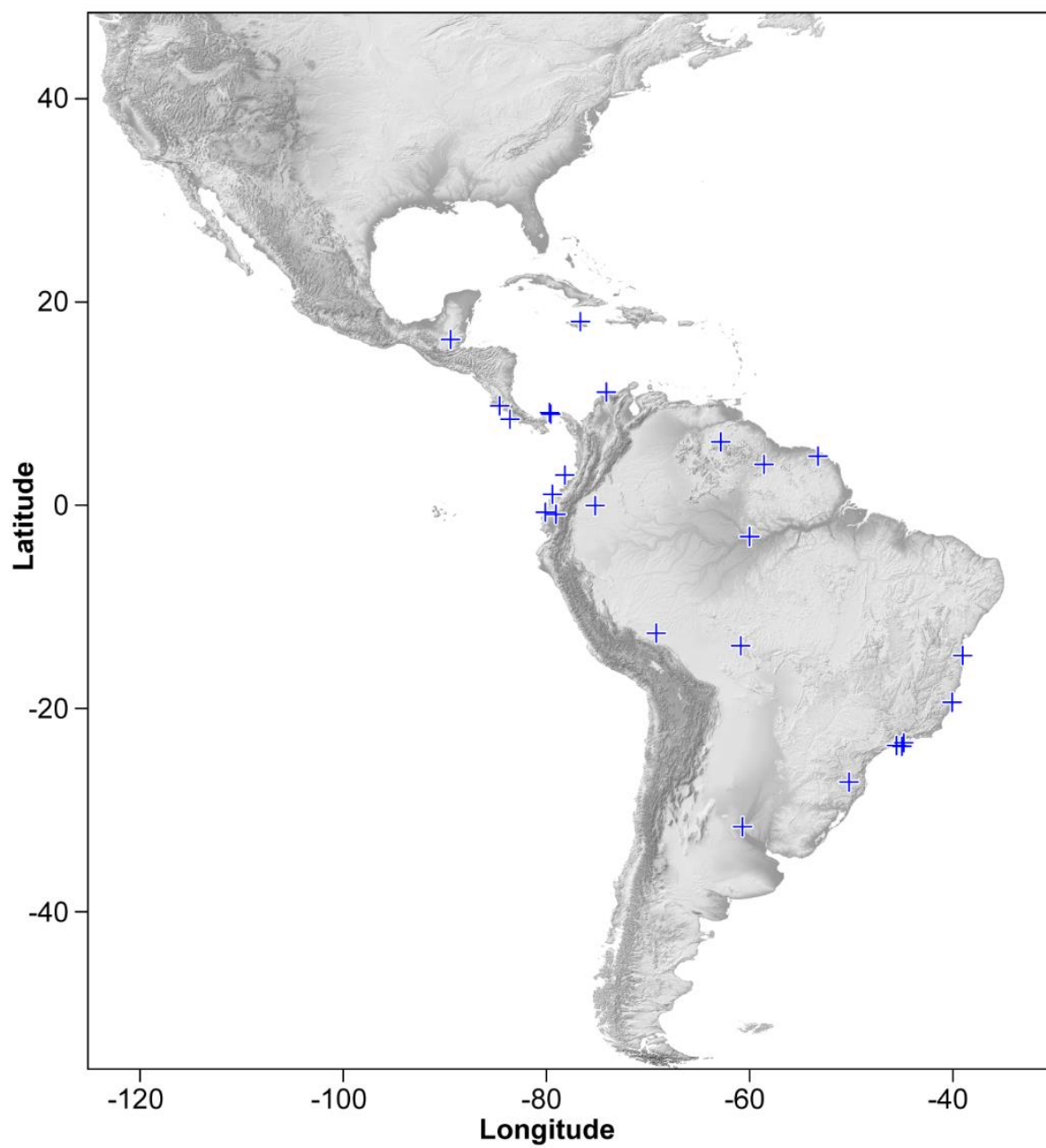


**Figure S34.** Geographic distribution of *B. patagonicus* (n=62).

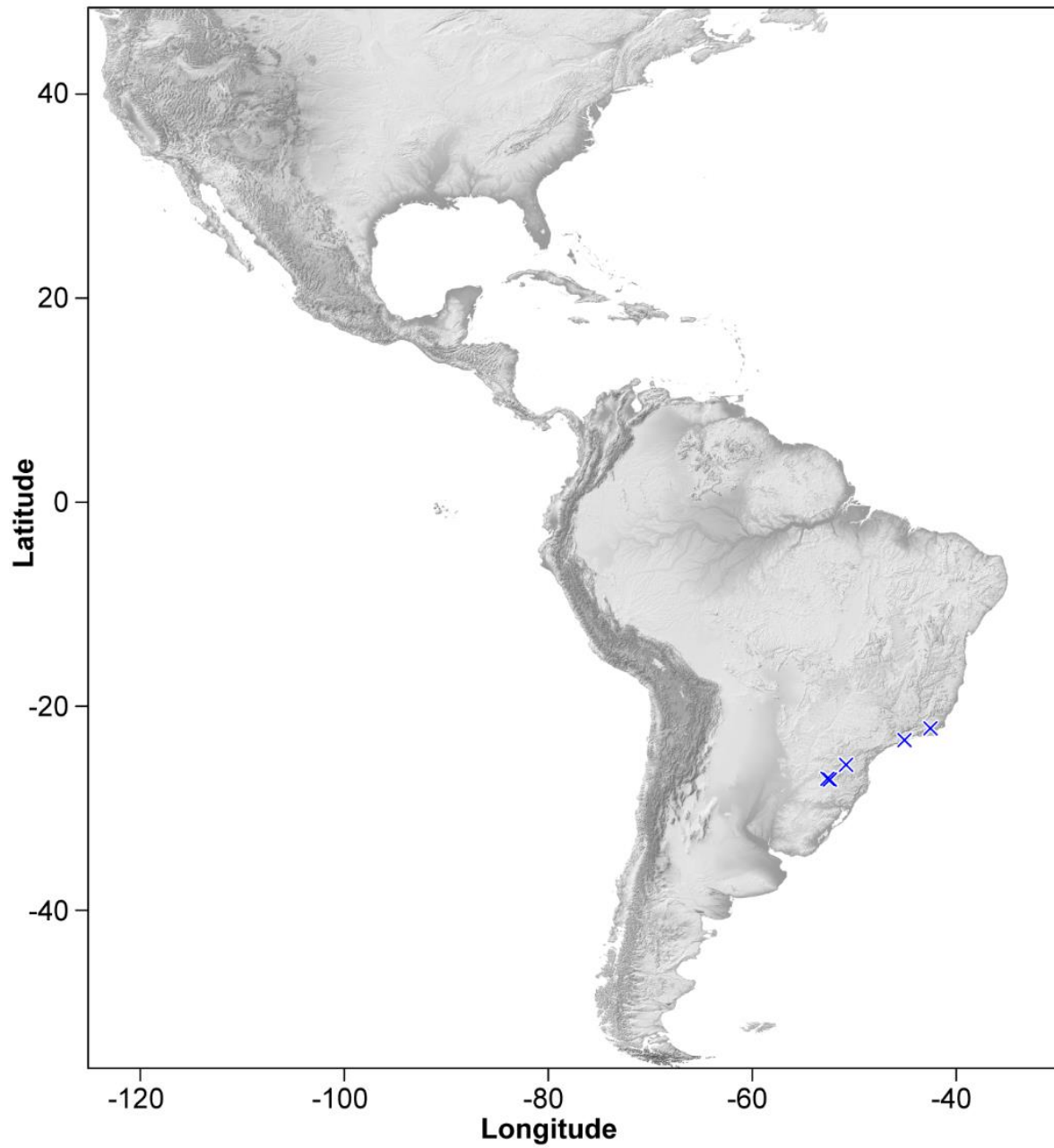




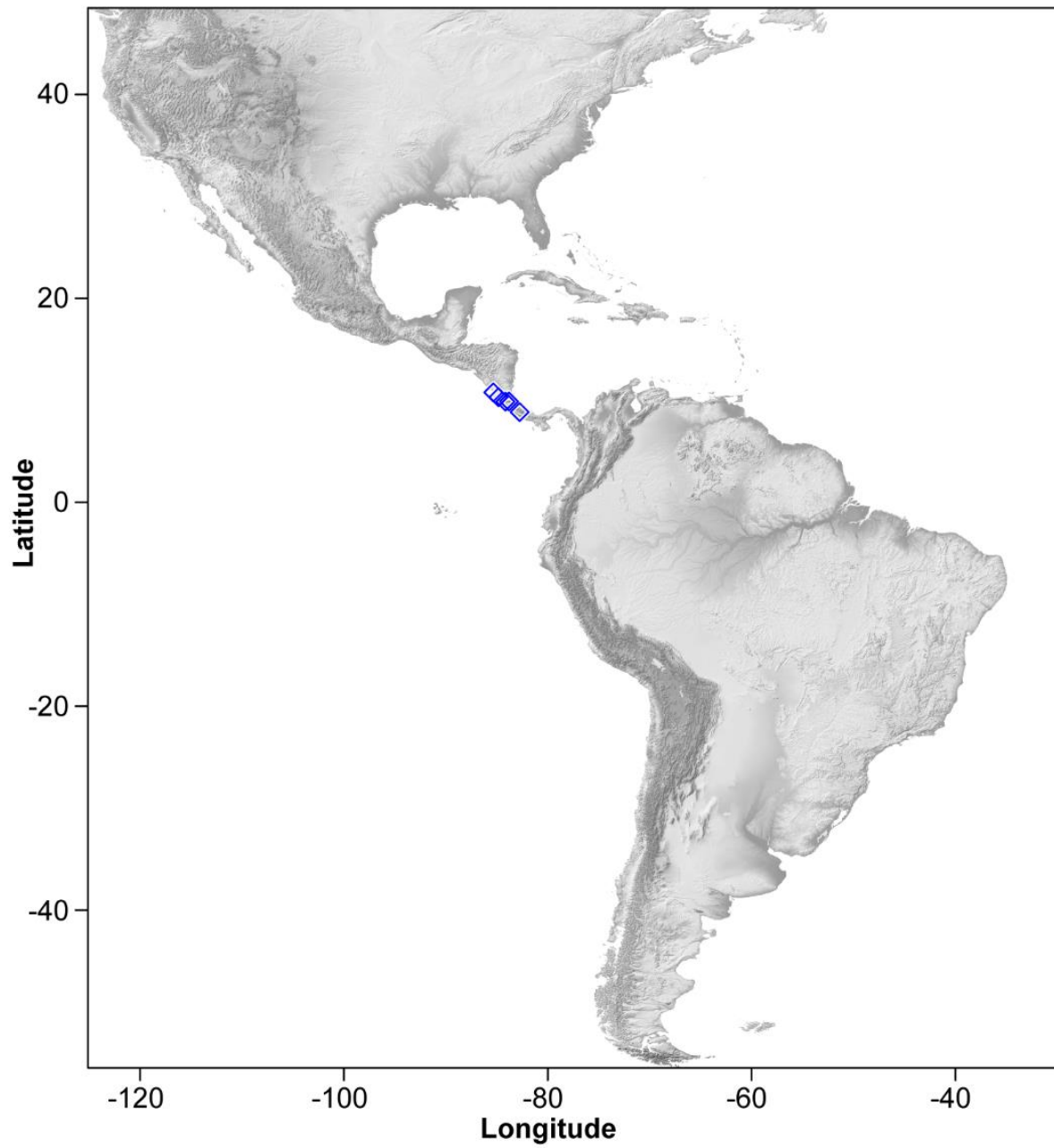
**Figure S35.** Geographic distribution of *B. pictus* (n=26).



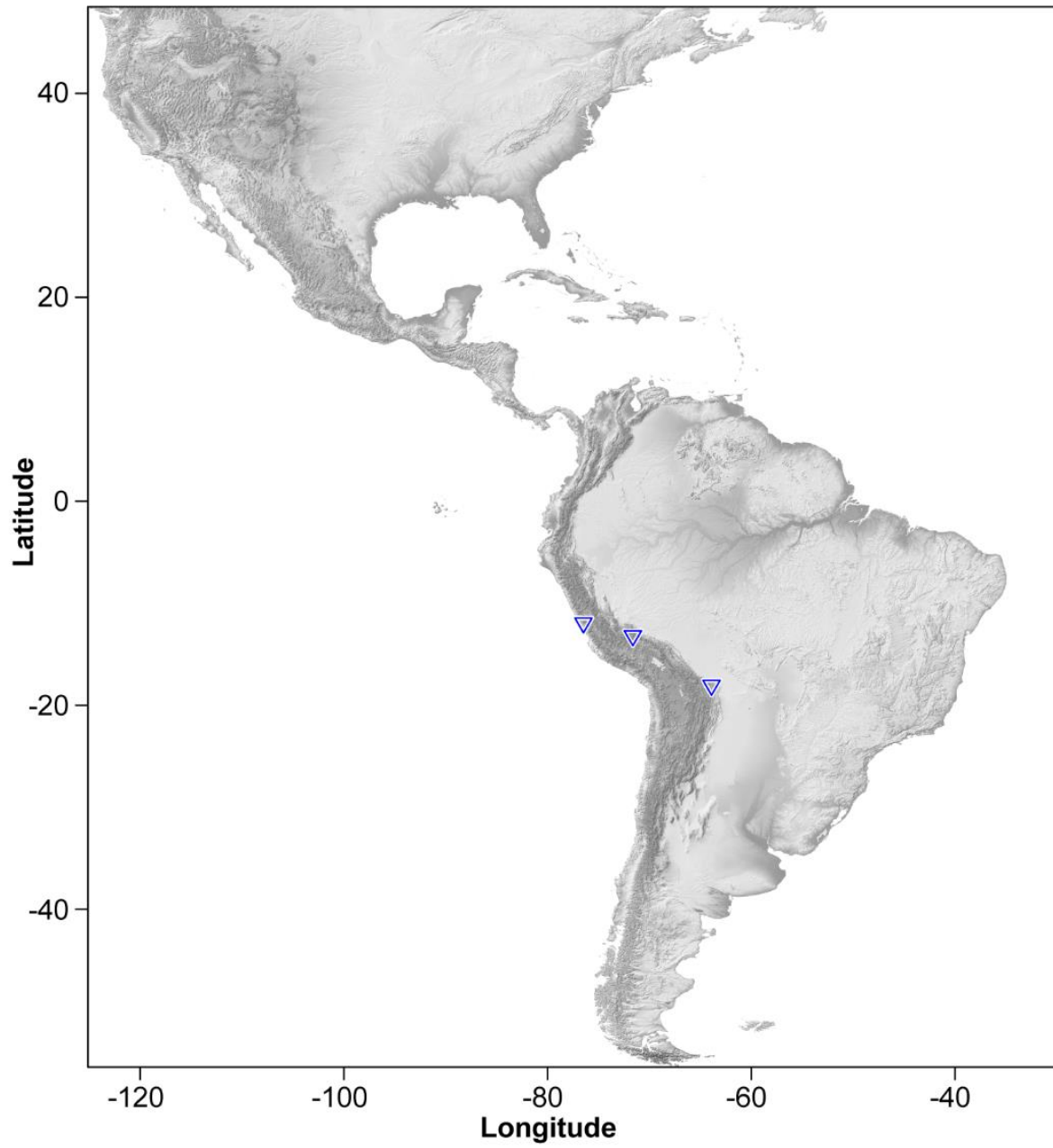
**Figure S36.** Geographic distribution of *B. pilipes* (n=5).



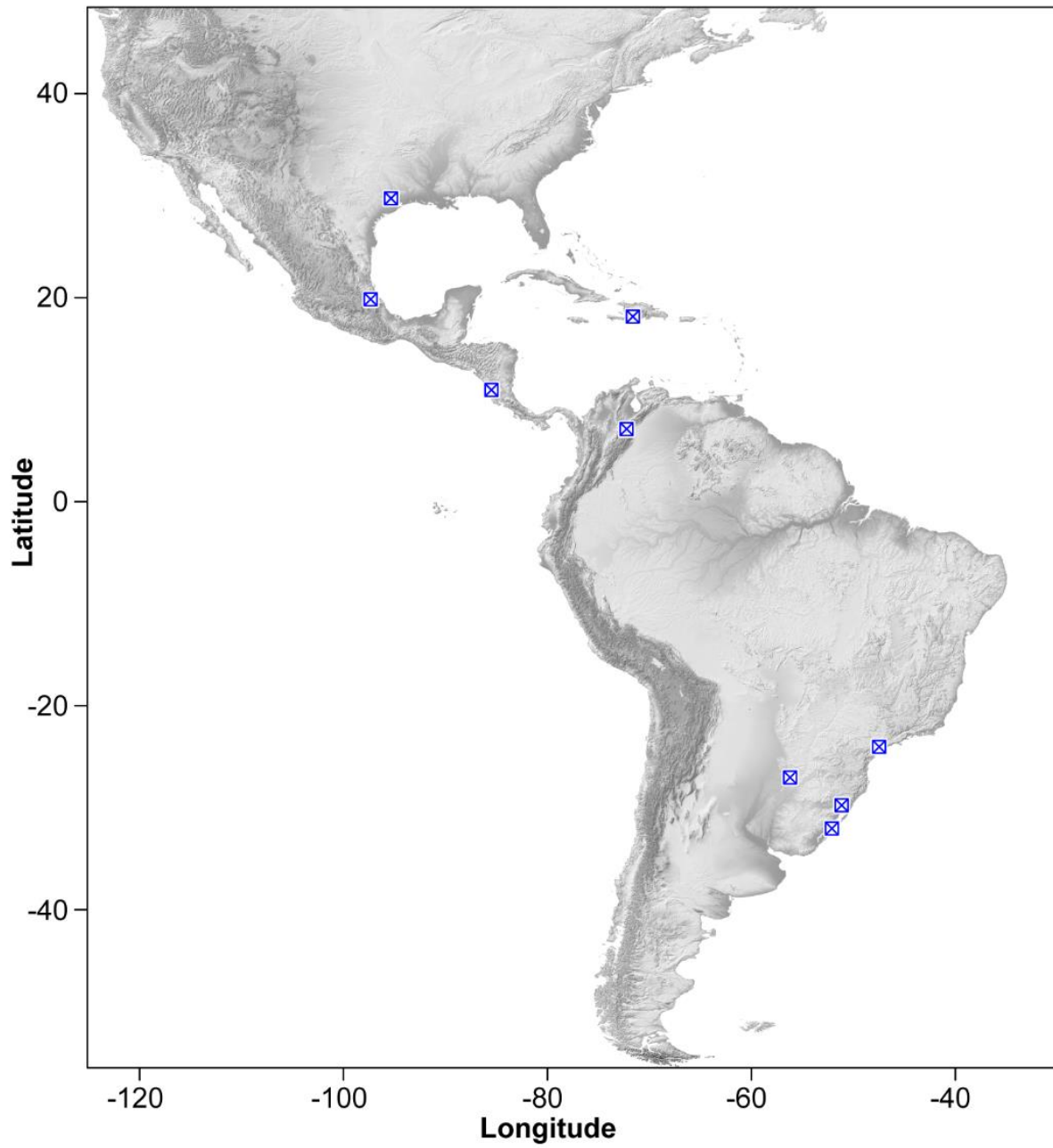
**Figure S37.** Geographic distribution of *B. santschii* (n=6).



**Figure S38.** Geographic distribution of *B. sosai* n. sp. (n=3).



**Figure S39.** Geographic distribution of *B. termitophilus* (n=9).



**Figure S40.** Geographic distribution of *B. tristis* (n=2).

