

Three Remarkable New Fungus-Growing Ant Species of the Genus *Myrmicocrypta* (Hymenoptera: Formicidae), With a Reassessment of the Characters That Define the Genus and Its Position Within the Attini

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ABSTRACT Three new species of the fungus-growing ant genus *Myrmicocrypta* Fr. Smith are described from Brazil and Peru, all unique within the genus due to their shared character state of erect pilosity. *Myrmicocrypta erectapilosa* sp. nov. and *Myrmicocrypta bucki* sp. nov. are otherwise typical for the genus in their small size and effaced, tuberculate sculpture, whereas *Myrmicocrypta camargoi* sp. nov. is also unique in its large size and pronounced sculpture. *M. erectapilosa* and *M. bucki* are closely related but can be distinguished by differences in the frontoclypeal and hypostomal teeth, frontal lobes, mesonotal sculpture, and propodeal spines. All castes (workers, gynes, and males) are described for *M. camargoi*, workers and gynes are described for *M. erectapilosa*, and only workers are described for *M. bucki*. Because the erect pilosity encountered in these species contradicts the state previously considered diagnostic for the genus, that of appressed, spatulate or squamiform pilosity found in all other *Myrmicocrypta* species, we necessarily discuss the characters that define the genus *Myrmicocrypta* and review its phylogenetic position within the tribe Attini.

KEY WORDS Brazil, *Myrmicocrypta erectapilosa* sp. nov., *Myrmicocrypta camargoi* sp. nov., *Myrmicocrypta bucki* sp. nov., Myrmicinae

The ant genus *Myrmicocrypta* (Formicidae: Myrmicinae: Attini) was established by Smith (1860) based on an alate gyne collected in São Paulo, Brazil. The genus has never been revised; genus-level taxonomic actions consist solely of a junior synonym (*Glyptomyrme*, Emery 1894), the transfer of nine species to the attine genera *Mycetophylax* Emery, *Kalathomyrmex* Klingenberg & Brandão, *Paramycetophylax* Kusnezov, and *Trachymyrme* Forel (Emery 1913, 1922; Santschi 1922, 1929; Weber 1958; Bolton 1995), and the transfer from the genus *Apterostigma* of the species *Myrmicocrypta uncinatum* (Emery 1894). Currently, the genus comprises 28 described species and subspecies (Bolton 1995, Bolton et al. 2007) distributed in the Neotropics from southern Mexico through Northern Argentina (Kempf 1972, Fernandez and Sendoya 2004). Except for Trinidad and Tobago, which are biotic extensions of the mainland, the genus is unknown in the Caribbean (Wheeler 1922a; Weber 1958, 1968; Wilson 1988; see Kempf 1972 for distributional information).

The genus *Myrmicocrypta* is one of 15 genera within the monophyletic ant tribe Attini (Schultz and Meier

1995, Wetterer et al. 1998, Price et al. 2003, Schultz and Brady 2008). Like all other attine ants, *Myrmicocrypta* species, so far as their biology is known, cultivate fungus gardens upon which they depend for food (Wilson 1971, Garling 1979, Hölldobler and Wilson 1990, Mueller et al. 2005, Schultz et al. 2005). Chief among the putative synapomorphies uniting *Myrmicocrypta* species are the recurved, appressed, squamiform or spatulate setae present in workers and gynes (but not in males). Indeed, the first species described was named *M. squamosa*, of which the author, Smith (1860) (p. 74), wrote, "... covered on every part with separate and not very distant scales, which are of a glittering transparent white,—those on the scape of the antennae and legs most dense, the flagellum alone being naked;..." (Smith 1860). This character state has been cited consistently in the subsequent taxonomic history of the genus and in identification keys (Smith 1860, Mayr 1865, 1887; Emery 1913, 1922; Mann 1916, 1922; Wheeler 1922b, 1925; Santschi 1936, Weber 1937, 1938, 1947, 1958, 1972; Borgmeier 1948, Hölldobler and Wilson 1990, Bolton 1994, Palacio and Fernandez 2003). Here, as part of a larger taxonomic revision and phylogenetic analysis of the genus currently in progress, we describe three new species of *Myrmicocrypta* in which this character state is contradicted, requiring a redefinition of the genus based on previously described as well as newly discovered synapomorphies.

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Materials and Methods

Morphology and Standard Measurements and Indices. Specimens were examined at various magnifications using an MZ125 light stereomicroscope (Leica, Wetzlar, Germany). All measurements were taken to the nearest 0.001 mm and unless otherwise noted are in millimeters. Measurements of paratypes are listed within parentheses. Specimens were photographed using a JVC KY-F70B video camera mounted on an M420 stereomicroscope (Leica) attached to an IBM Intellistation M Pro computer, on which composite images were assembled using Auto-Montage Pro version 5.03.0018 BETA software (Synoptics Ltd., Frederick, MD). Images were cropped and edited using Photoshop CS2 version 9) (Adobe Systems, Mountain View, CA). The measurements, indices, and morphological terminology used throughout follow Gauld and Bolton (1988), Hölldobler and Wilson (1990), Huber and Sharkey (1993), Bolton (1994), and Kugler (1994), with modifications where noted. Anatomical abbreviations are as follows: eye length (EL): in profile, the maximum diameter of the eye measured from the dorsal margin to the ventral margin; frontal lobes distance (FLD): in full-face view, the maximum horizontal distance between the outer borders of the frontal lobes; gaster length (GL), in profile, the length of the gaster from the anteriormost point of first gastral segment (fourth abdominal segment) to the posteriormost point of the last segment; head length (HL), in full-face view, the maximum vertical distance from the posteriormost margin of the head to the midpoint of the anterior clypeal margin, excluding the mandibles; head width (HW), in full-face view, the maximum horizontal width of the cephalic capsule excluding the eyes; mandible length (ML), in full-face view, the maximum diagonal-line distance from the base of the external mandibular insertion to the apical tooth; petiole length (PL), in lateral profile, the straight-line distance from the posteriormost margin of the petiole to the posteriormost margin of the metapleural lobe; postpetiole length (PPL), in lateral profile, the maximum length of the postpetiole; scape length (SL), in full-face view, the maximum length of the scape excluding the basal condyle; total length (TL), HL+ML+WL+PL+PPL+GL; Weber's length (WL), in lateral profile, the diagonal length of the alitrunk as measured from the anteriormost dorsal extent of the pronotum to the posteriormost ventral angle of the propodeum; cephalic index (CI), (HW/HL) \times 100; frontal lobes index (FLI), FLD/HW \times 100; mandibular index (MI), (ML/HL) \times 100; and scape index (SI), (SL/HW) \times 100.

Depositories of Material. The specimens examined were borrowed from and/or have been deposited in the following institutions: CPDC Jacques Delabie Collection, CEPEC/CEPLAC, Itabuna, Bahia, Brazil; INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil; LACM, Natural History Museum of Los Angeles County, Los Angeles, CA; MCZC, Museum of Comparative Zoology, Harvard University, Cambridge, MA; MUSM, Museo de Historia Natural

"Javier Prado," Universidad Nacional Mayor de San Marcos, Lima, Perú; MZSP, Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil; SMNK, Staatliches Museum fuer Naturkunde Karlsruhe, Germany; and USNM, National Museum of Natural History, Washington, DC.

Results and Discussion

Systematic Treatment

Genus *Myrmicocrypta* Mayr

Myrmicocrypta is currently regarded as relatively "primitive" for the tribe Attini, i.e., as retaining many character states considered plesiomorphic for the tribe, including characters of wing venation (Kusnezov 1963); male antennae (Kusnezov 1961); degree of queen/worker polymorphism (Wheeler 1910); monomorphism of the worker caste (Wheeler 1910, Emery 1912); larval morphology, including the form of the galea in some species and straight (rather than curved) body profile (Schultz and Meier 1995); position on the integument of mutualistic *Pseudonocardia* Henssen (Actinomycetes) bacterial symbionts (Currie et al. 1999); and the use, by the nest-founding gyne, of her shed forewing as a platform for the incipient garden (Fernandez-Marin et al. 2004).

Colonies of most *Myrmicocrypta* species are small, consisting of <200 individuals (Weber 1945, Murakami and Higashi 1997, Price et al. 2003). Nest form varies across species, usually consisting of either a single, spherical, shallow chamber in the soil or of a single, irregular chamber within rotting wood (Mann 1916, Weber 1941, 1945, 1947, 1968, 1969; Hölldobler and Wilson 1990, Murakami and Higashi 1997; unpublished data). Workers are cryptic foragers in the leaf litter and thus rarely hand-collected in the field. *Myrmicocrypta* species reportedly use a wide variety of organic matter as substrates for their fungus gardens, including arthropod frass, wood pellets, insect corpses, seeds, flower parts, dry leaves, and other plant debris (Weber 1941, 1945, 1947, 1966, 1968, 1969; Hölldobler and Wilson 1990, Murakami and Higashi 1997, Mueller et al. 2005). The only thorough study of *Myrmicocrypta* biology (Murakami and Higashi 1997) reports that *M. ednaella* Mann garden substrate consists mainly of wood chips and occasional insect corpses and that adult workers feed primarily upon plant nectar and sap, which they share with other workers via trophallaxis.

Smith (1860) created the genus *Myrmicocrypta* based on an alate gyne collected in São Paulo, Brazil. Mayr (1865) (p. 24) briefly defined the genus, citing the characters: wings of gynes with short hairs, with submarginal cell enclosed, lacking stigma and lacking discal cell; and very reduced frontal lobes in workers and gynes. Forel (1885) created the genus *Glyptomymex*, based on a single male collected in Orizaba, Mexico, noting its resemblance to males in the genera *Apterostigma* Mayr and *Cyphomyrmex* Mayr. Mayr (1887) described the species *Apterostigma uncinatum*,

based on a worker collected in St. Catharina, Brazil. After examining the type specimen and additional specimens (worker, gyne, and male) collected in Asunción, Paraguay, Emery (1890) (p. 70) transferred this species to *Glyptomyrme*. Referring to the description by Smith (1860) and reexamining the gyne, Emery (1894) (p. 224) synonymized the genus *Glyptomyrme* with *Myrmicocrypta* and synonymized *G. uncinatus* with *M. squamosa*. Subsequently, Forel (1911) (p. 295) revived *uncinata* as a variety of *M. squamosa*.

Interestingly, in his description Smith (1860) (p. 74) points out a possible relationship between *Myrmicocrypta* and *Oecodoma* Latreille, the latter now regarded as a junior synonym of the attine leaf-cutting genus *Atta* F. (Roger (1863) p. 35). Because, contrary to other authors of the day, Smith's (1858) concept of *Oecodoma* seemed to comprise our modern concept of the leaf-cutting attine genera *Atta* and *Acromyrme* Mayr, his suggestion of a relationship between *Oecodoma* and *Myrmicocrypta* was unusually prescient. Forel (1885) was the first researcher to propose the monophyly of the Attini, grouping the seven genera known at the time (including *Myrmicocrypta*), three of which were regarded as "subgenera" of *Atta*. Six years later, however, he expanded his tribal definition to include additional genera ("the former *Cryptocerides* excluding *Cryptocerus* Latreille and *Procryptocerus* Emery"), none of which are fungus growers nor any longer considered to be attines. It was only after the fungus-growing behavior became known for multiple attine genera (Möller 1893, Forel 1893) that the tribal composition became relatively stable.

The Attini are morphologically heterogeneous, with few unreversed synapomorphies. The tribe is characterized by 1) 11 antennal segments in workers and gynes, 13 in males (reduced to 12 in some *Cyphomyrme* Mayr and *Trachymyrme* Forel species, in *Pseudoatta argentina* Gallardo, and in all *Sericomyrme* Mayr species); 2) palpal formula of 4,2 (reduced to 3,2 in all *Apterostigma* species and in *Pseudoatta argentina*); 3) anterior tarsus dilated, with the distal tarsomere long (reversed in some *Cyphomyrme* species); 4) larvae with short, narrow labrum; 5) larval mandibles fleshy, straight, and subconical; 6) larvae with leg vestiges present as open integumental slits (Schultz and Meier 1995); 7) obligate cultivation of fungi for food (Leucoprineaceae or, in some derived *Apterostigma* species, Pterulaceae) (Schultz et al. 2005); 8) presence of a long unpaired median clypeal seta that arises from the border of the clypeus and clypeal apron, secondarily lost in all *Apterostigma* except *A. megacephala* Lattke and in *Kalathomyrme mayri* (Forel) (Lattke 1997, 1999; Brandão and Mayhé-Nunes 2001, Klingenberg and Brandão 2009).

Some, but not all, previous researchers have suggested that members of *Myrmicocrypta* possess the most plesiomorphic characters within the Attini, i.e., that *Myrmicocrypta* species may be morphologically little diverged from the ancestral attine and that the genus may occupy a phylogenetic position near the root of the attine tree. Wheeler (1910) was the first to

propose that *Myrmicocrypta* is the "most primitive" attine genus, based on low degree of worker/queen polymorphism and on the monomorphic worker caste. Emery (1912) produced the first phylogenetic diagram for the tribe, dividing it into two clades, one containing (*Apterostigma* + *Myrmicocrypta*) and the other containing (*Cyphomyrme* + the rest of the attines). A year later he added *Mycocephurus* Forel to the clade containing *Myrmicocrypta* and *Apterostigma*, based on the relative size of the male antennal pedicel (Emery 1913), and subsequently reinforced this grouping (Emery 1922). Kusnezov (1955) (p. 23) also hypothesized that the genera *Myrmicocrypta* + *Apterostigma* + *Mycocephurus* were "primitive" based on nest architecture, number of individuals per colony, fungal substrate, worker monomorphism, and defense behavior. He subsequently grouped the three genera together under the name Paleoattini (Kusnezov 1963). The phylogeny of Schultz and Meier (1995), based solely on morphological characters of larvae, reconstructs *Myrmicocrypta* as paraphyletic with regard to both the remaining Paleoattini (*Mycocephurus* + *Apterostigma*) and the Neoattini.

The Paleoattini share a number of plausible synapomorphies including 1) the presence of a fenestra (clear spot) on the forewings of gynes, to our knowledge unique among ants (Emery 1913, 1922; Fernandez-Marin et al. 2005, T.R.S., unpublished data); 2) inferior corner of the pronotum rounded, entirely lacking a spine, tooth, or angle; 3) male antennal funicular segment I (pedicel) much shorter (almost as twice as short) than funicular segment II; 4) the presence of the *Pseudonocardia* actinomycete symbiont on basisternum II under the forelegs (Currie et al. 1999); and 5) hypostoma of workers and gynes bearing a pair of lateral teeth, secondarily lost in some *Apterostigma* and some *Mycocephurus*. The monophyly of the Paleoattini is also supported by molecular phylogenetic analyses (Schultz and Brady 2008). *Myrmicocrypta* can be separated from the other two Paleoattine genera by the characters listed in the following diagnosis.

Genus *Myrmicocrypta* Fr. Smith, 1860

Myrmicocrypta, Smith, J. Entomol. i. p. 73, t. 4. Figures 14–17 (1860). Type-species: *Myrmicocrypta squamosa* by monotypy.

Junior synonymy of *Myrmicocrypta*.

Glyptomyrme, Forel, Bull. Soc. Vaud. Sci. Nat. (2) xx. p. 50 (1885). Type-species: *Glyptomyrme dilaceratum* by monotypy.

Glyptomyrme as junior synonym of *Myrmicocrypta* Emery, Bull. Soc. Ent. Ital. 26: 224 (1894).

The monophyly of *Myrmicocrypta* is well supported in molecular phylogenetic analyses of DNA sequences from four nuclear protein-coding genes for six species (Schultz and Brady 2008) and one nuclear protein-coding gene and one mitochondrial protein-coding gene for fourteen species (J.S.-C., unpublished data). Putative morphological synapomorphies for the genus include the following.

Worker:

1. Antennal scapes bilobed at the base at the junction of the antennal condyle.
2. Posterior lateral margins of the clypeus, anterior to the frontal lobes, produced into a pair of blunt to acuminate frontoclypeal teeth.
3. Area of propleuron adjacent to the inferior pronotal angle bearing a tooth, tubercle, or carina.
4. Postpetiole with lateral margins usually confluent with the anterior lateral margins of the gaster.
5. Body of most species typically covered with appressed to suberect squamate or spatulate hairs, reversed to erect or simple hairs in *M. camargoi* sp. nov., *M. erectapilosa* sp. nov., and *M. bucki* sp. nov.

Male: Propodeal spines extremely long and thin.

Diagnosis (Worker). Monomorphic. Posterior border of head in full-face view convex, interrupted by a median concavity and sometimes by blunt tubercles but never by teeth or spines. Eyes of variable size, strongly convex, hemispherical, or globose. Lacking ventral subocular prominence. Antennal scapes long usually surpassing occipital corners and bilobed at base at junction of antennal condyle. Clypeal apron ("anteclypeus" of Brandão and Mayhé-Nunes 2001) always present as smooth to weakly sculptured shining strip. Posterior lateral margins of clypeus, anterior to frontal lobes, produced into a pair of blunt to acuminate frontoclypeal teeth. Frontal lobes narrow, in some species incompletely covering antennal sockets, and always separated by fingerlike posterior projection of clypeus. Lateral corners of hypostoma with acute hypostomal teeth (hypostomal teeth rounded or absent in *Apterostigma* and *Mycocepurus*). Area of propleuron adjacent to inferior pronotal angle bearing a tooth, tubercle, carina, or otherwise sculptured and bearing erect hairs (sculpture and hairs absent in *Mycocepurus* and sculpture absent in *Apterostigma*). Promesonotum usually with spines or tubercles, rarely reduced to low ridges or carinae (as in *Apterostigma*), anteriorly with three pairs of spines or tubercles, but never with a crown of well-differentiated spines (as in *Mycocepurus*). Petiole with long peduncle and well-defined petiolar node lacking spines but sometimes with posterior carina (petiolar node weakly defined in *Apterostigma* and armed with two pairs of spines in *Mycocepurus*). Postpetiole, in dorsal view, usually trapezoidal with or without posterior margin emarginate, lateral margins usually confluent with anterior lateral margins of gaster. First gastral segment somewhat longer than wide; in dorsal view, its anterior and posterior margins straight, the lateral margins convex and anteriorly carinate. Sting present, protruding, and visible; frequently large. Body of most species covered with appressed to suberect squamate or spatulate hairs, in rare cases (described below) with erect or simple hairs (in *Apterostigma* hairs always long, simple, and flexuous [Lattke 1997, 1999], in *Mycocepurus* simple, short, and either erect, curved, or decumbent [Kempf 1963]).

Type Species. *Myrmicocrypta squamosa* Fr. Smith.

Myrmicocrypta camargoi Sosa-Calvo & Schultz,
new species
(Figs. 1–15)

Diagnosis (Worker). The largest known species of *Myrmicocrypta* (TL > 4 mm); body covered with erect hairs; frontal lobes, in full-face view, evenly rounded and, in profile, strongly protruding; antennal scapes covered with simple, suberect hairs; lateral pronotal and lateral mesonotal spines long, the latter longer than the former and blunt at apex.

Type Material. HOLOTYPE. Worker, labeled: "Brasil: São Paulo, Botucatu, 29-XI-2002, 23°15' S 48°15' W, 825 m., nest series, pasture, (RS Camargo)." (MZSP). USNM No. 00412647. PARATYPES. Nine workers, same data as holotype. Deposited in MCZC (1) USNM ENT No. 00537327; MZSP (3) USNM ENT Nos. 00537318, 00537309, 00413572; and USNM (5) USNM ENT Nos. 00413572, 00413574, 00413577, 00412653, 00412649, 00412651; 1 gyne labeled: "Brasil: Jataí, Goiás, Faz. Aceiro, 30-X-1962, Exp. Dep. Zool. Cerrado" (MZSP) USNM ENT No. 00537319; 1 gyne labeled: "São Paulo, Botucatu, 5-X-1991, (BH Dietz)" (MZSP) USNM ENT No. 00537310; 2 males labeled: "Brasil: GB [refers to state of Guanabara, actually state of Rio de Janeiro (RJ)], Rio de Janeiro (Floresta da Tijuca), IV-1966, (M Alvarenga)." (MZSP) USNM ENT Nos. 00537311, 00537311; 2 males labeled: "Brasil: Espírito Santo, Santa Teresa, XI-1928, (O Conde)." (MZSP) USNM ENT No. 00537320.

Worker. Measurements: TL = 4.58 (4.49–4.89); WL = 1.36 (1.33–1.46); HL = 0.97 (0.94–1.02); HW = 0.74 (0.72–0.80); SL = 1.13 (1.10–1.19); ML = 0.61 (0.58–0.69); EL = 0.12 (0.11–0.12); PL = 0.39 (0.39–0.42); PPL = 0.22 (0.21–0.23); GL = 1.03 (0.97–1.13); CI = 76 (76–81); SI = 153 (147–154); MI = 63 (60–71); FLD = 0.31 (0.28–0.34) ($n = 10$).

Head. Almost 1.3× as long as wide (excluding mandibles); in full-face view head narrowing posterior to eyes, posterior corners more or less evenly rounded; head dorsally with erect, spatulate hairs on carinae, areas between carinae lacking pilosity; sculpture on head restricted to discrete carinae, areas in between smooth, minutely punctate; in full-face view, frontal carinae branching posteriorly into fully developed median vertexal carinae and continuing laterally to connect with a carina arising in area of eye, possibly preocular carina; denticles occur at junctions of carinae forming, in lateral view, projections of almost similar size and shape; eyes with seven to eight ommatidia in longest row and 37–42 in total; eyes globose, located posterior to middle of head at level above frontal lobes; antennal scapes very long and thin, slightly thickened at apex; antennae with 11 segments; antennal flagellum gradually thickened distally rather than abruptly clubbed, last three segments noticeably larger than rest, last two very much so, all typical for Attini; antennal scapes surpassing occipital corners by >0.4× scape length; anterior border of clypeus hyaline, shining, and imbricate, with a distinct median angle; clypeal setae arising from posterior margin of clypeal apron and consisting of six to seven pairs of

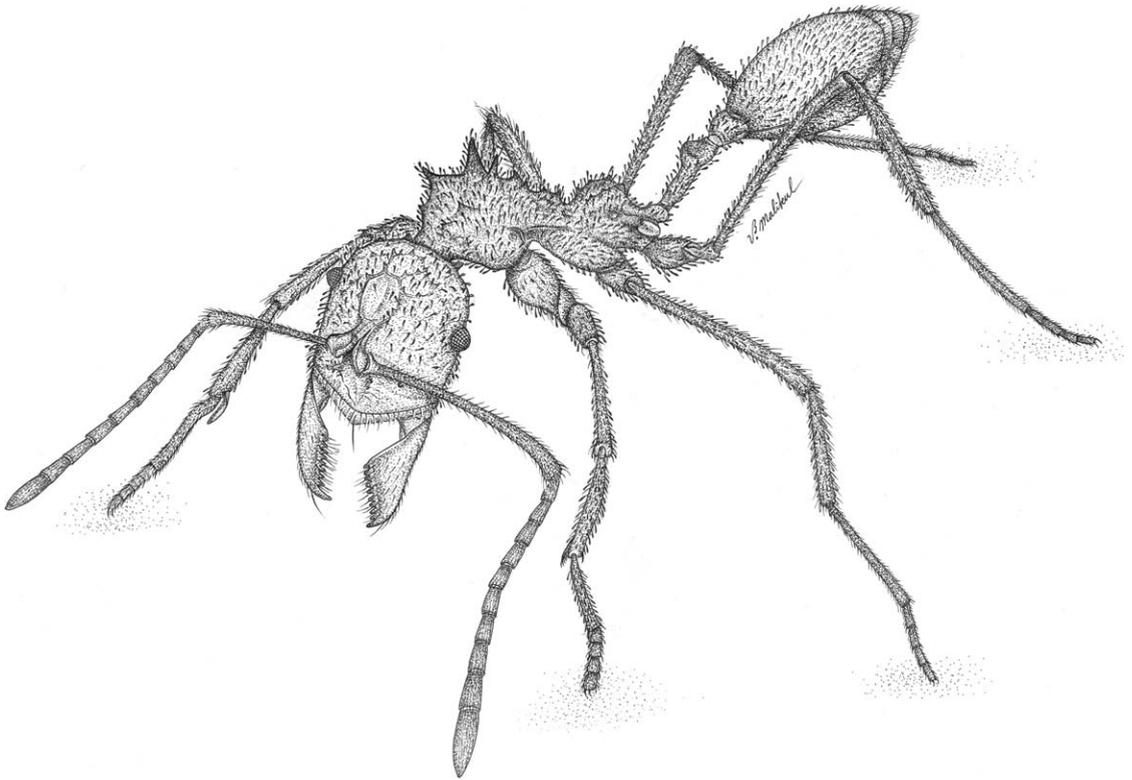
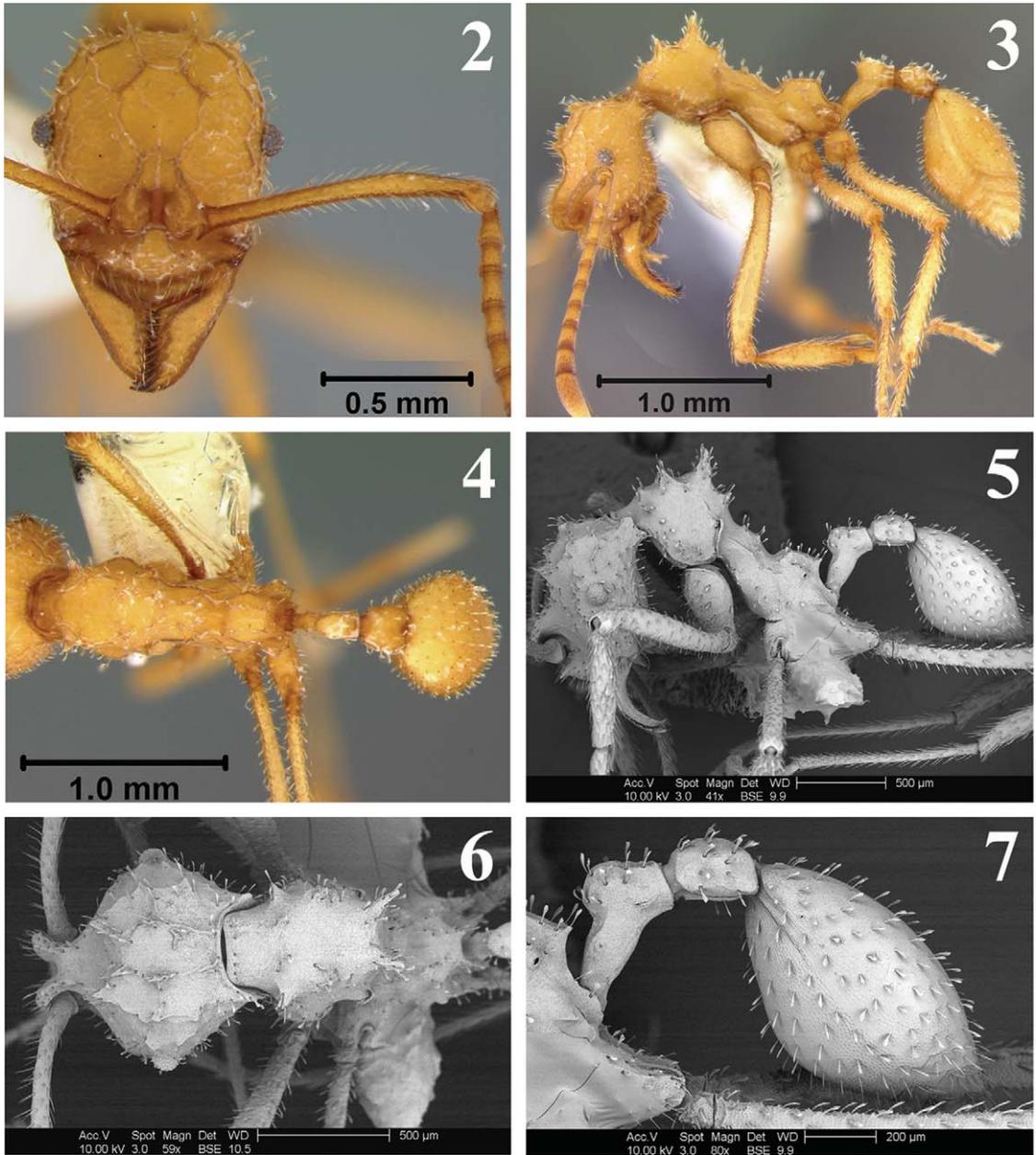


Fig. 1. *M. camargoi*, new species, life habitus reconstruction by V. Malikul.

simple, appressed hairs slightly overhanging mandibles and single thick, long (0.16–0.19 mm) unpaired median seta that originates from posterior of clypeal apron, slightly anterior to junction of clypeal apron and body of clypeus (sensu Kugler 1994:22 defined as: “the medial portion of the clypeus anterior to the frontal lobes and dorsal to the clypeal apron”); frontoclypeal teeth acute, covered with suberect simple hairs; mandibles with eight to 10 teeth, increasing uniformly in size from base to apex; sculpture on dorsal surface of mandibles rugulose-strigulate, frontal lobes evenly rounded, expanded laterally (0.28–0.34 mm), covering antennal insertions; in profile, frontal lobes strongly protruding; posterior margin of hypostoma with simple hairs that project over hypostomal plate. Dorsum of hypostomal plate shining and glabrous; anterior-lateral margin of hypostoma with a pair of acute teeth; in profile, occiput drawn out posterolaterally into an enlarged bilobed “neck” or “collar” that extends backwards, covering anterior-lateral portions of pronotum. *Mesosoma*: median pronotal tubercles present, small; humeral tubercles present, $\approx 1.5\times$ length of median pronotals; lateral pronotal tubercles long and robust, $\approx 2\times$ length of median pronotals, directed forward; lateral mesonotal tubercles longest on mesosoma, $\approx 2\times$ length of lateral pronotals; first median anterior mesonotal tubercles absent; second median posterior mesonotal tubercles present, acute, subequal in length to humeral tubercles; first and second posterior mesonotal tubercles present, small, sub-

equal, joined by carinae, similar in size to median pronotals; inferior angle of pronotum evenly rounded; propleuron, adjacent to inferior pronotal edge, lacking distinct tubercles, site bearing roughenings and erect, spatulate hairs. mesonotal groove shallow but conspicuous. Metanotal groove deep and conspicuous, with median longitudinal carina. Base of propodeum, in profile, flat and slightly longer than declivity; both laterally carinate; propodeal spines reduced to tubercles. Base of forecoxa with a conspicuous and lamellate carina. *Metasoma*: petiolar peduncle lacking ventral process; node of petiole, in dorsal view, rounded anteriorly and longer than wide and, in lateral view, anteriorly rounded and posteriorly straight; postpetiole, in dorsal view, $1.3\times$ wider than long; posterior border emarginate; postero-lateral postpetiolar processes absent; dorsum of abdominal segment IV (gaster) finely reticulate and covered with short, erect, spatulate hairs; very subtle longitudinal sculpturing visible anteriorly; anterior margin straight, anterior lateral carinae absent. Individuals yellow to light ferruginous; pilosity restricted mainly to tubercles and carinae, spoon-shaped or spatulate; antennal scapes and legs with simple, erect hairs.

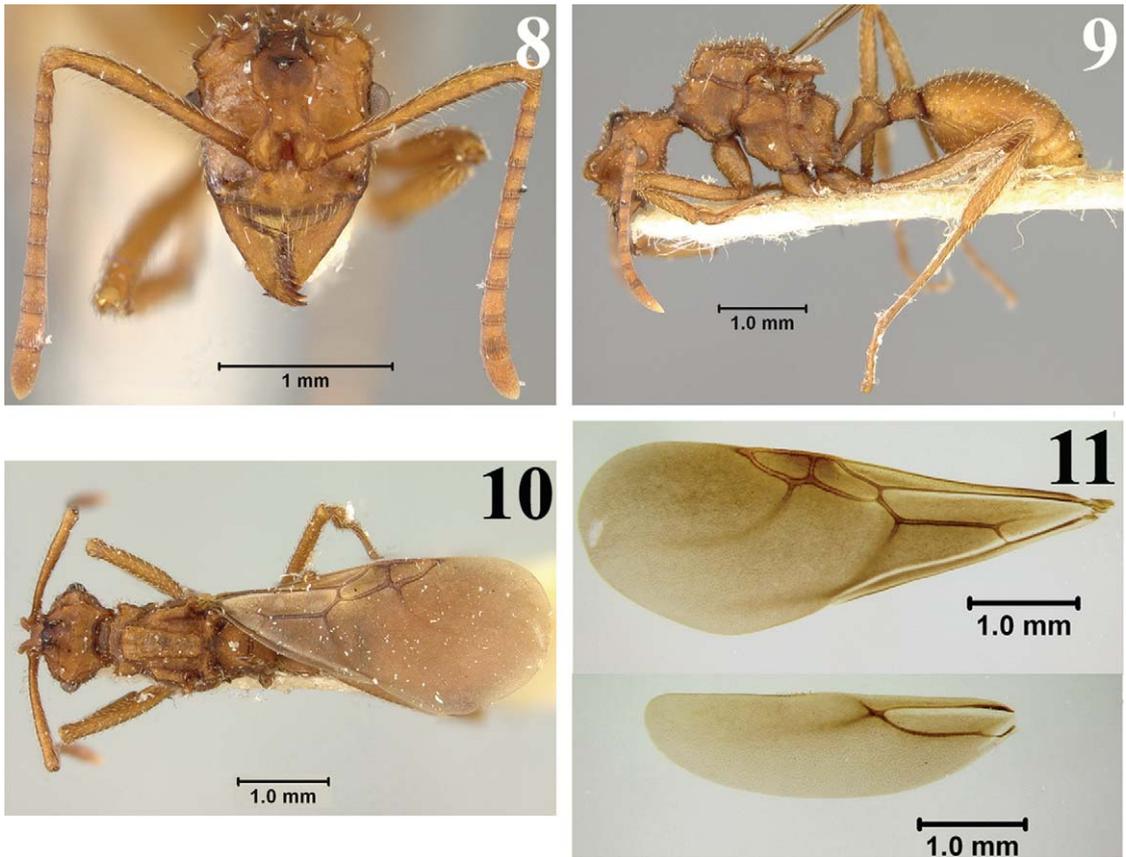
Gyne. Measurements: TL = 7.42–7.51; WL = 2.13–2.18; HL = 1.20–1.24; HW = 1.05–1.13; SL = 1.44; ML = 0.42; EL = 0.22–0.25; PL = 0.67–0.72; PPL = 0.38–0.39; GL = 2.15–2.22; CI = 85–94; SI = 127–137; MI = 67–69; FLD = 0.42–0.43 ($n = 2$).



Figs. 2-7. *M. camargoi*, new species. Automontage photographs of worker habitus: 2, full-face (dorsal) view; 3, profile; 4, dorsal view. Scanning electron micrographs of worker habitus: 5, profile; 6, dorsal view; and 7, waist segments and gaster in lateral view.

Similar to worker except for differences typical of caste. *Head*: In full-face view, excluding mandibles, slightly longer than wide with lateral and posterior margins straight, posterior corners more angular and less rounded than in worker; vertexal carinae conspicuous and lamellate, each produced into a series of three processes: a pair of obtuse, triangular denticles flanking anterior ocellus, a pair of rectangular lamellae overhanging posterior ocelli, and a pair of long, acute, spinelike denticles mounted on vertex; cephalic mar-

gin with raised carina; posterior ocelli very small, median ocellus small (0.06 mm in diameter); frontal carinae complete to junction with vertexal carinae, but lateral branches absent (present in worker); supraocular tubercle present; mandibles with 11 teeth; clypeus as in worker and likewise with 7-9 pairs of hairs and with a long unpaired median seta (length = 0.22-0.23 mm). *Mesosoma*: Median and lateral pronotal and humeral tubercles present, well developed; inferior margin of pronotum evenly rounded; in lateral



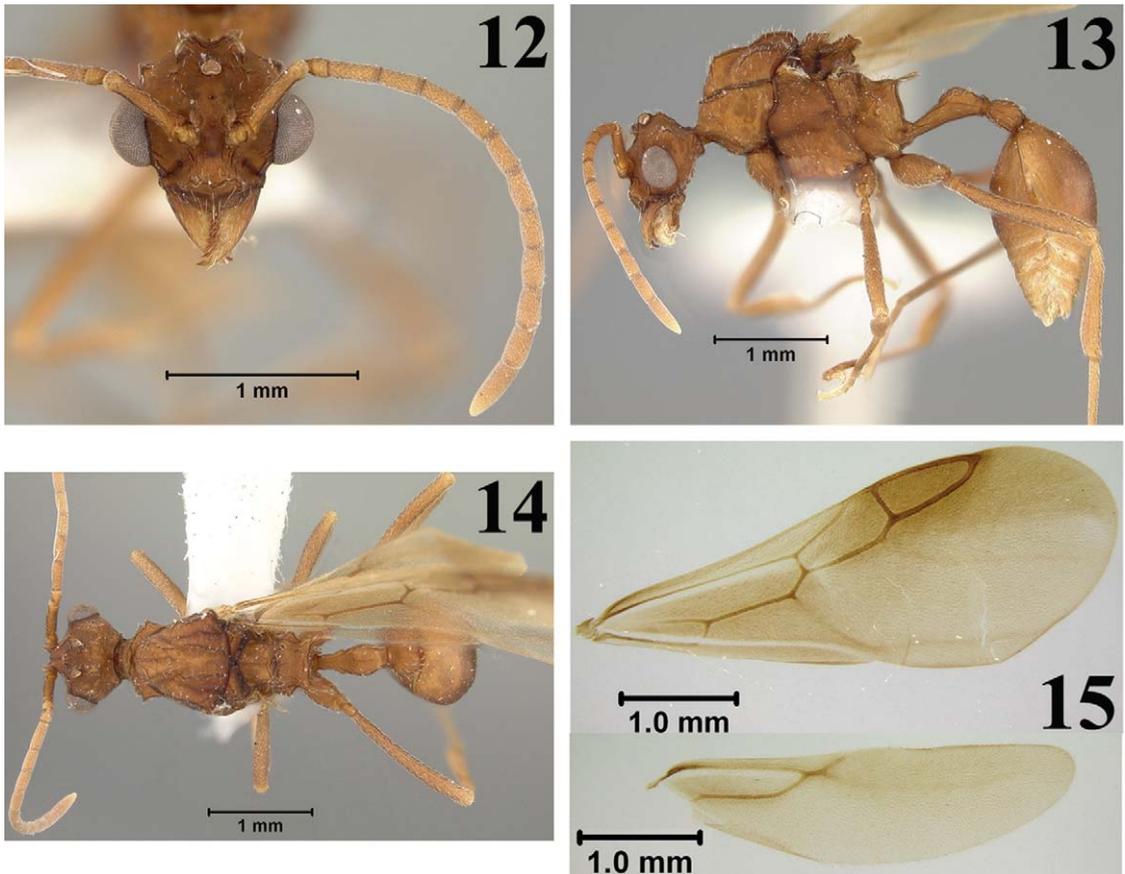
Figs. 8–11. Gyne of *M. camargoi*. 8, full-face view; 9, profile; 10, dorsal view; 11, fore and hind wings.

view, propleuron adjacent to inferior pronotal edge weakly and obtusely angulate; median pronotal spines connected by a weak carina, easily visible in fronto-dorsal view; mesoscutum with notauli (i.e., median pair of longitudinal carinae) carinate and extending through entire length of mesoscutum, developed anteriorly into blunt triangular denticles; median sulcus present as a low raised carina on anterior half of mesoscutum; parapsidal lines present as carinae in posterior half of mesoscutum; transscutal articulation present; parascutal lobes prominent and well developed, in lateral view posteriorly narrowed to a blunt, acute angle, tip bearing a transverse lamella on its outer face visible in oblique or dorsal view; axillae large, in dorsal view tapering posteriorly, dorsal and lateral margins developed into lamellae that form excavated, hemispherical concavities visible in posterior view; scutellum without lateral projections and ending posteriorly as two prominent dorsoventrally extended, laterally compressed, distally rounded processes; base and declivity of propodeum laterally carinate, carinae continuing downward to join propodeal lobes; propodeal teeth short, triangular; pleural suture wide and deep. *Metasoma*: Peduncle of petiole with a pair of dorsolateral longitudinal carinae along nearly entire length; petiole with a pair of ventral carinae that may (one individual) or may not (one individual) end

anteriorly in a small tooth-like process, visible laterally; node of petiole dorsolaterally carinate; postpetiole in dorsal view 1.9× wider than long, with pronounced posterolateral corners, posteriorly emarginate; tergite of abdominal segment IV finely reticulate-punctate. *Wings*: Forewing (length 4.80 mm) with very reduced fenestra, which appears as a rounded spot near apical margin (Fig. 5.9); hind wing (length 3.57 mm) with one closed cell. Head and body dark ferruginous; gaster yellowish to light ferruginous; wings smoky. Pilosity as in worker.

Male. Measurements: TL = 5.96–6.34; WL = 1.90–1.98; HL = 0.90–0.94; HW = 0.77–0.83 (including eyes = 1.08); SL = 0.48–0.54; ML = 0.48–0.58; EL = 0.37–0.40; PL = 0.64–0.73; PPL = 0.23–0.33; GL = 1.64–1.86; CI = 82–92; SI = 58–70; MI = 53–62; FLD = 0.25–0.29 ($n = 4$).

Head. In full-face view, triangular, wider posteriorly and laterally angulate, cephalic margin interrupted laterally by a pair of tubercles and medially (behind posterior ocelli) by a pair of denticulate tubercles mounted on posterior extensions of vertexal carinae; ocelli larger than those in gynes, median ocellus 0.12 mm in diameter and with its anterior margin slightly concave or straight, posterior margin evenly rounded; frontal carinae extending posterad to intersect with vertexal carinae, not continuing laterad; low



Figs. 12–15. Male of *M. camargoi*. 12, full-face view; 13, profile; 14, dorsal view; 15, fore and hind wings.

tubercles present at point of intersection; a median carina extends from between frontal lobes to anterior margin of median ocellus, more pronounced anteriorly, weaker posteriorly; dorsum of mandibles punctate; masticatory margin with eight to nine teeth gradually diminishing in size toward base; outer margin of mandibles slightly convex; frontoclypeal teeth present, short, blunt; anterior margin of clypeus hyaline, shining, and imbricate; three to four pairs of lateral clypeal hairs barely exceeding the anterior clypeal margin, a single thick median seta ≈ 0.07 mm in length; body of clypeus with a median carina arising posterior to hyaline border at socket of median clypeal seta, extending posterad and dividing into two carinae that intersect frontoclypeal teeth; posterior border of clypeus carinate; antennae with 13 segments; antennal scapes barely surpassing cephalic margin, shorter than funicular segments I–III combined; funicular segment II $> 2\times$ longer than funicular segment I (antennal pedicel); posterior margin of head, in profile, concave; with a median longitudinal carina that originates at occipital carina and extends to level of vertexal tubercles; occipital collar present laterally, short and, in lateral view, quadrate; hypostomal teeth large and rounded at tip. *Mesosoma*: Pronotum with humeral and lateral tubercles present, short and angulate; median

pronotal spines absent, replaced by a transverse carina that connects lateral spines; inferior margin of pronotum evenly rounded; propleuron adjacent to inferior pronotal edge with a low tubercle bearing simple hairs; mesoscutum and scutellum similar to those of gyne, axillary concavities less pronounced; propodeal spines long and dorsolaterally compressed, in lateral view appearing somewhat expanded apically, in dorsal view appearing apically blunt, but in dorsolateral (edge-on) view appearing linear; base of propodeum with a pair of lateral carinae (Rio de Janeiro specimens; carinae absent in Espiritu Santo specimens), declivity with a pair of lamellate carinae (Rio de Janeiro specimens; carinae lower in Espiritu Santo specimens). *Metasoma*: Petiole pedunculate; in profile, node of petiole low and evenly convex; petiole with dorso-lateral carinae that extend along entire length of petiole, petiolar node with single median (Espiritu Santo specimens) or a few longitudinal carinae (Rio de Janeiro specimens); petiole with a pair of ventral lateral longitudinal carinae extending its entire length; node of petiole $1.6\times$ longer than wide; node of postpetiole $1.7\times$ wider than long; abdominal tergite IV finely reticulate. *Wings*: as in female but lacking fenestra. Forewing length = 4.56–4.68 mm; hind wing length = 3.25–3.47 mm.



Fig. 16. *M. erectapilosa*, new species, life habitus reconstruction by E. Hodges.

Individuals ferruginous in color; antennae and legs testaceous; pilosity on antennal scape simple and appressed; head and mesosoma with hook-like hairs mostly on carinae and tubercles; legs with simple appressed or decumbent hairs; abdominal tergite IV with very short simple appressed hairs.

Etymology. It gives us great pleasure to name this striking and unusual fungus-growing ant after its discoverer, Roberto S. Camargo.

Natural History. Workers of this species have been collected in Cerrado habitat in Botucatu (São Paulo) and Jatai (Goiás) and in Mata Atlantica (Atlantic forest) in Floresta da Tijuca (Rio de Janeiro) and Santa Teresa (Espírito Santo). The nest series from Botucatu was collected while digging out a colony of *Atta capiguara* Gonçalves in a pasture field composed mostly of *Brachiaria* spp. and *Paspalum* spp. (Poaceae: Panicoideae). Workers were observed carrying small pieces of dry grass, but the nest entrance was not located (R. S. Camargo, personal communication).

Myrmicocrypta erectapilosa Sosa-Calvo & Schultz,
new species
(Figs. 16–22)

Diagnosis (Worker). body covered with erect simple hairs; hypostomal teeth short, triangular, and acute; sculpture on mesosoma reduced; frontal lobes

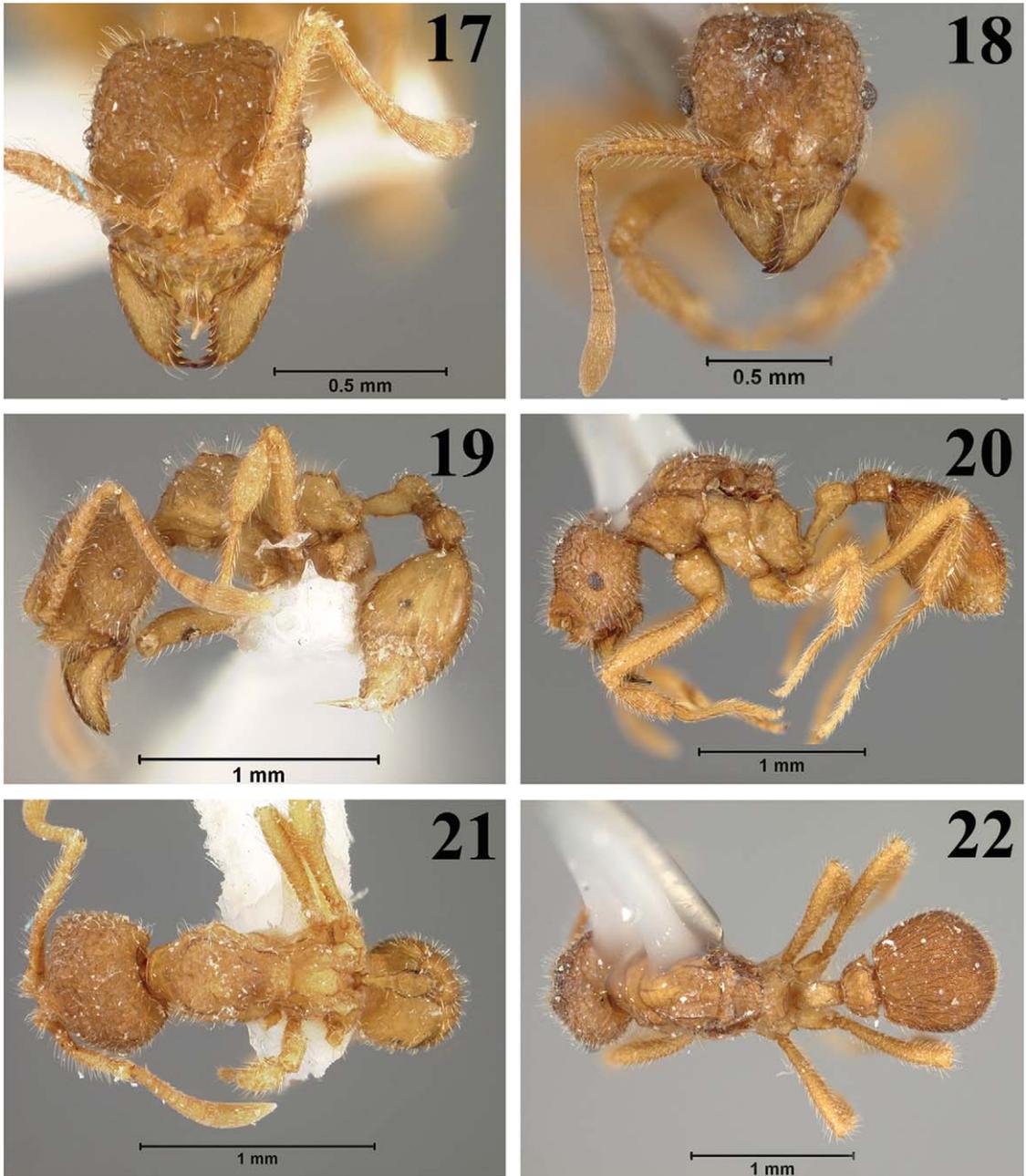
triangular and partially covering the antennal insertions.

Type Material. HOLOTYPE. Worker, labeled: "Brazil: Amazonas, Manaus, BR. 174 Km 45 EEST 51, 13-IX-1991, (AY Harada and AG Bandeira)." (INPA USNM ENT No. 00537305).

Paratypes. 2 workers, same locality as holotype; one dealate gyne, same locality as holotype. (INPA USNM ENT No. 00537305; one worker labeled: "Brazil: Amazonas 4832, Manaus, Dimona Camp, RS 2108, 21-X-93, plot C-5, (AB Casimiro) P. Coleção do Laboratório de Myrmecologia # 62 (CEPEC)" USNM ENT No. 00537329).

Worker. Measurements: TL = 3.22 (3.23–3.33); WL = 0.87 (0.84–0.91); HL = 0.67 (0.66–0.71); HW = 0.58 (0.57–0.63); SL = 0.60 (0.61–0.65); ML = 0.46 (0.44–0.47); EL = 0.05 (0.05–0.06); PL = 0.36 (0.29–0.33); PPL = 0.16 (0.15–0.16); GL = 0.70 (0.76–0.78); CI = 87 (86–89); SI = 103 (103–107); MI = 69 (63–68); FLD = 0.22 (0.21–0.24) ($n = 4$).

Head. In full-face view 1.13×–1.15× as long as wide (excluding mandibles); cephalic margin with shallow median concavity, posterior corners evenly convex, lacking sharp angles, spines, or tubercles; frontal carinae vestigial, past level of eyes merging with abundant scabrous sculpture; eyes very small (six to eight ommatidia total) and in full-face view located approximately midway between posteriormost margin of head



Figs. 17–22. *M. erectapilosa*, new species. 17, 19, and 21 worker habitus (17, full-face view; 19, profile; and 21, dorsal view). 18, 20, and 22 gyne habitus (18, full-face view; 20, profile; and 22, dorsal view).

and insertion of mandibles; antenna with 11 segments; antennal scape slightly wider at midpoint; hairs on antennal scape long and erect or semierect; antennal scapes surpassing cephalic margin by nearly $1.8\times$ their apical width; clypeal apron evenly convex, transparent, and shiny with shallow transverse striae and with five pairs of simple, long, slender, appressed hairs that originate on posterior margin of clypeal apron and overhang mandibles; medially with unpaired long

(0.14–0.16 mm), thick seta; frontoclypeal teeth prominent, triangular, dentiform, and covered with simple erect hairs; mandibles with six to seven teeth increasing in size from base to apex; dorsal surface of mandibles striate and bearing hairs, shorter and more appressed on lateral margins, longer and suberect toward tips. Frontal lobes, in full face view, triangular and partially covering antennal insertions; hypostomal teeth short, triangular, and acute; hypostoma glabrous,

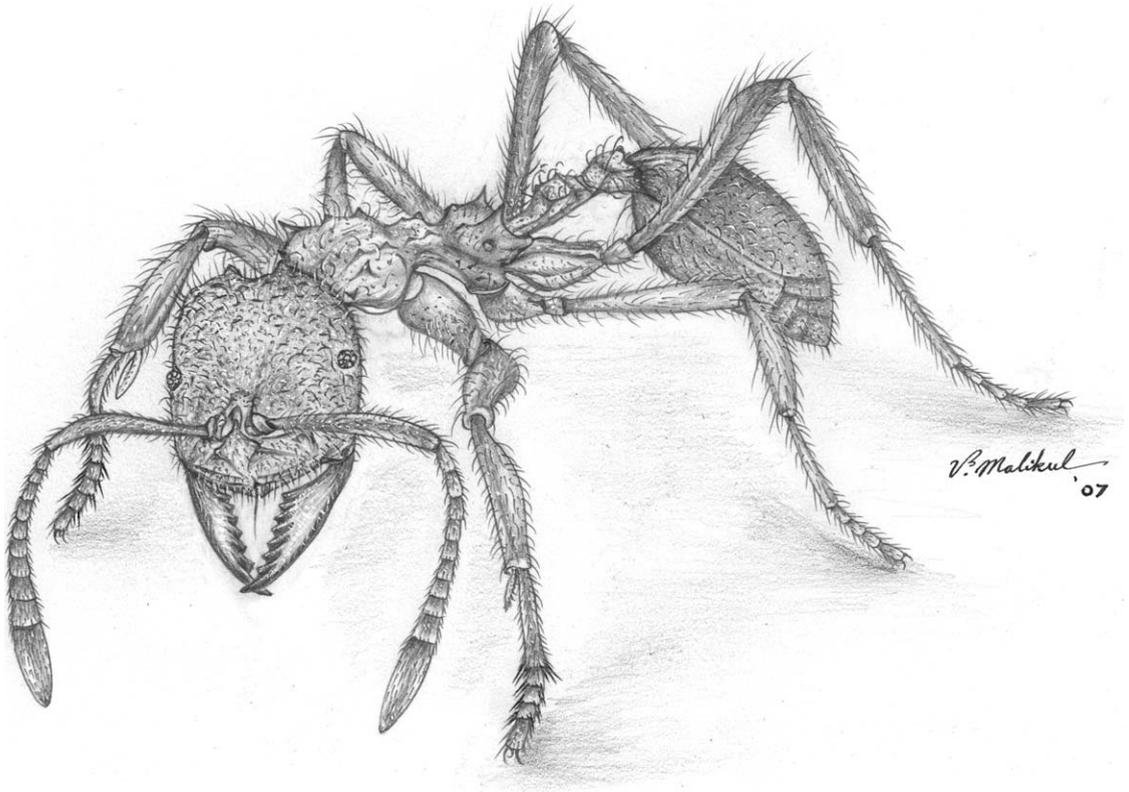


Fig. 23. *M. bucki*, new species, life habitus reconstruction by V. Malikul.

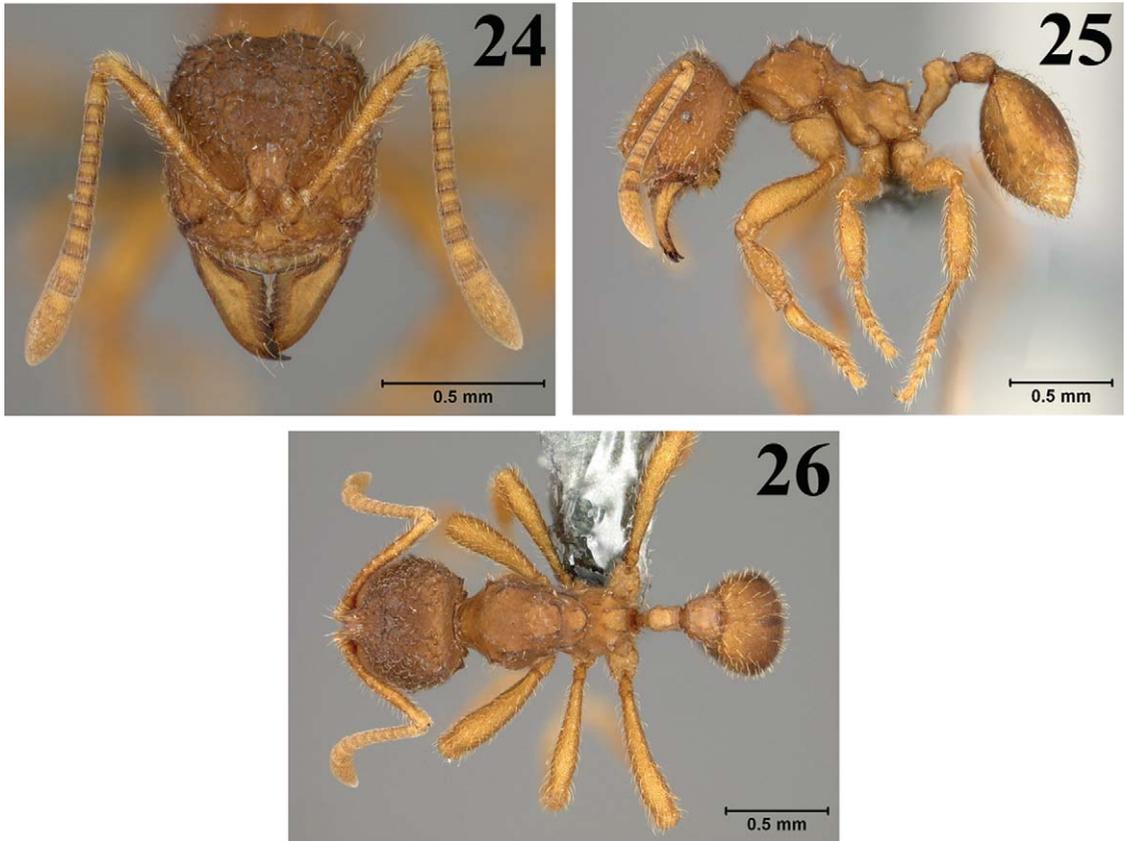
smooth, and shiny; occiput not extended into a "neck" or "collar." Head covered mainly with erect and suberect hairs; integument evenly reticulate-rugose. *Mesosoma*: pronotal humeral and lateral spines reduced to eroded tubercles occurring at intersections of carinae; anterior pronotal spines absent; dorsum of pronotum with a median longitudinal carina arising at anterior pronotal margin and extending posteriorly at least to level of lateral pronotal spines; dorsum of pronotum sometimes with low wrinkles; inferior pronotal margin evenly rounded; propleuron adjacent to inferior pronotal edge with one or two very small tubercles, each bearing a simple hair; all mesonotal spines reduced to carinae; anterior propodeal spines absent; posterior portion of propodeum with short, blunt teeth; base of propodeum, in profile, flat and as long as declivity of propodeum; declivity of propodeum with a very reduced but conspicuous lamella on each side. *Metasoma*: petiole pedunculate; ventrally with a pair of closely approximated longitudinal median carinae that end anteriorly in a slightly raised process that, when viewed laterally, looks like a single longitudinal carina ending in a very small tooth; node of petiole in profile rounded, in dorsal view ellipsoidal and with a longitudinal carina; postpetiole in profile longer than high and dorsally convex; posterior edge of postpetiole in dorsal view slightly emarginate and with distinct lateral corners; postpetiole wider than long (1.6–1.9 \times). In lateral view, base of abdominal

segment IV at junction with postpetiole ventrally evenly convex and smooth; in dorsal view, base of abdominal segment IV at junction with postpetiole with a transverse carina with lateral corners; laterally a few short carinae extend posterad from these corners. Dorsum of abdominal segment IV punctulate-reticulate.

Individuals uniformly brown ferruginous; antennal scapes, head, and mesosoma covered with simple, erect hairs restricted mainly to carinae or tubercles; hairs on dorsum of abdominal segment IV hook-like.

Gyne. Measurements: TL = 4.24; WL = 1.19; HL = 0.81; HW = 0.71; SL = 0.75; ML = 0.51; EL = 0.12; PL = 0.46; PPL = 0.22; GL = 1.05; CI = 88; SI = 106; MI = 63; FLD = 0.28. ($n = 1$).

Characters similar to those in worker with modifications expected for caste and with following differences: *Head*: Frontal carina extending posterad to almost level of mid-ocellus and splitting into two low carinae, vertexal ones being more conspicuous; eyes large, containing eight ommatidia in largest row, ≈ 45 ommatidia in total; ocelli small (maximum length of middle ocellus = 0.06); occipital collar (neck) moderately developed laterally, with both upper and lower extensions small and blunt, lower one slightly larger than upper. *Mesosoma*: Dorsum of pronotum conspicuously rugose; humeral and lateral pronotal tubercles present; propleuron adjacent to inferior pronotal edge



Figs. 24–26. Habitus of worker of *M. bucki*, new species. 24, full-face view; 25, lateral view; 26, dorsal view.

somewhat angulate and bearing several curved hairs; mesoscutum overall rugose; mesoscutal sulcus, in dorsal view, conspicuous and short, not extending >one third length of mesoscutum; notauli absent; parapsidal lines conspicuous and extending nearly to anterior margin of mesoscutum; transscutal articulation conspicuous; scutellum posteriorly bidentate, dorsally rugose; propodeum with a pair of short denticles; declivity of propodeum with a conspicuous lamella on each side. *Metasoma*: Petiole as in worker; postpetiole 2.5x wider than long, with projecting latero-posterior corners; dorsum of abdominal tergite IV densely reticulate, basally with widely spaced, short costulae and with conspicuous antero-lateral carinae, as in worker. Individual's body dark yellow or light brown; pilosity as in worker.

Etymology. The name *erectapilosa* derives from the latin *erecta* = standing and *pilosa* = hairy and refers to the erect hairs present in this species, the first such species to come to our attention.

Myrmicocrypta bucki Sosa-Calvo & Schultz,
new species
(Figs. 23–26)

Diagnosis. Similar in size and habitus to *M. erectapilosa*, but differing from it by having frontal lobes ves-

tigial, failing to cover antennal insertions; hypostomal teeth long; vertexal carina present; humeral and lateral pronotal spines acute; dorsum of pronotum smooth and glabrous; propodeal spines long and acute; petiole subquadrate.

Type Material. HOLOTYPE. One worker, labeled: "Peru: Madre de Dios, Centro de Investigación y Capacitación Río Los Amigos (CICRA), Otorongo Trail, 12°33' 42.28" S 70°05' 32.64" W, elevation 276 m, 19-XI-2005, (J. Sosa-Calvo), nest series, hand collected, forest (JSC051119-09)" USNM ENT No. 00537326. (MUSM).

Paratypes. Fourteen workers, part of the same nest series as holotype. (USNM). USNM ENT Nos. 00537307, 00537308, 00537317, 00537325, and 00301761 (alcohol); four workers, labeled: "Brazil: Amapa, Serra do Navio (*Silverstone*)." (LACM 42302). USNM ENT Nos. 00537306 and 00537316; 1 worker labeled: "Brazil, Amazonas, Manaus, 9-v-2003, (C. Rabeling and M. Verhaagha)." (USNM). USNM ENT No. 00537315.

Worker. Measurements: TL = 3.56 (3.28–3.65); WL = 0.97 (0.91–1.01); HL = 0.75 (0.72–0.77); HW = 0.64 (0.62–0.67); SL = 0.69 (0.66–0.72); ML = 0.51 (0.45–0.54); EL = 0.07 (0.05–0.07); PL = 0.35 (0.31–0.35); PPL = 0.17 (0.16–0.19); GL = 0.81 (0.72–0.83); CI = 85 (86–88); SI = 108 (101–109); MI = 68 (63–71); FLD = 0.13 (0.11–0.14) ($n = 9$).

Head. Head almost $1.2\times$ longer than broad; posterior margin convex, convexity interrupted by two carinate tubercles in vertexal area; integument matte and strongly rugole-reticulate; frontal carinae obsolete or vestigial; eye very small with seven to nine ommatidia in total; eyes above middle of head; antennal scape reticulate and long, surpassing cephalic corners by twice its apical width; clypeal apron convex and medially slightly angulate, hyaline, and transversely weakly striate; clypeal pilosity originating near posterior margin of apron and extending over mandibles, consisting of five to six pairs of lateral hairs and of one median unpaired seta, much thicker and $3x$ as long (length holotype = 0.15, paratypes = 0.13–0.15 mm) as lateral hairs; clypeus with a pair of blunt frontoclypeal teeth covered with simple, curved hairs; mandibles with six to seven teeth decreasing in size from apex to base; dorsal surface of mandibles striolate; frontal lobes strongly reduced, exposing antennal condyles in full-face view; hypostomal teeth long; occipital “collar” (neck) reduced to two low, blunt tubercles; antennal scape wider near its apex than at rest of its length; anterior edge of antennal scape minutely denticulate; in full-face view anterior and posterior edges of antennal scape bearing suberect to erect hairs; hairs on ventral portion of head narrowly spatulate. **Mesosoma:** Integument of mesosoma minutely punctate. Dorsum of pronotum smooth and glabrous with low humeral tubercles; lateral spines acute and dentiform, longer and more discrete than other mesosomal tubercles; lacking anterior pronotal tubercles or spines; inferior corner of pronotum evenly rounded; propleuron adjacent to inferior pronotal edge with a broadly obtuse angle and with some subdecumbent or suberect, simple or extremely narrowly spatulate hairs; mesonotum with lateral tubercles reduced to carinae, anterior tubercles low; mesonotal groove smooth and glabrous; median mesonotal tubercles low; posterior mesonotal tubercles blunt apically and slightly longer than or similar in size to median tubercles; metanotal groove with a single median longitudinal carina that extends from posterior portion of mesonotum through anterior portion of propodeum; propodeum anteriorly carinate, lacking anterior spines or tubercles; posterior propodeal spines long and acute; dorsum and declivous of propodeum with lateral carinae extending to propodeal lobes; base of propodeum flat, in profile subequal to declivity of propodeum. **Metasoma:** Petiole pedunculate; node of petiole, in profile, with two small anterior tubercles and two larger posterior tubercles connected by sometimes incomplete carinae; node in lateral view subquadrate, in dorsal view slightly longer than broad; in dorsal view, postpetiole $>1.5\times$ broader than long; posteriorly emarginate; latero-posterior corners with inferior wing-like projections giving it a trapezoidal shape; shape of postpetiole, in profile, longer than higher ($1.2\text{--}1.3\times$); tergite of abdominal segment IV punctulate-reticulate; in dorsal view, base of tergite at junction with postpetiole slightly carinate (as in all *Myrmicocrypta* spp.), but lacking lateral carinae beyond this junction, i.e., antero-lateral gastral carinae

absent; pilosity on dorsum of abdominal tergite IV consisting of widely separated, extremely narrowly spatulate hairs, all curved at tips and directed backward.

Individuals brown ferruginous; pilosity restricted to wrinkles, tubercles, spines, carinae, appendages, antennal scapes, and gaster, absent elsewhere. Legs and antennal scapes strongly reticulate.

Gynes and Males: Unknown.

Etymology. Named in honor of Dr. Peter Buck in recognition of his support for science at the Smithsonian’s National Museum of Natural History.

Comments. *M. bucki* is similar in size and habitus to *M. erectapilosa* but differs from it by having simple, curved hairs (simple but entirely erect in *M. erectapilosa*); frontoclypeal teeth blunt (large and acute in *M. erectapilosa*); hypostomal teeth long (short and triangular in *M. erectapilosa*); frontal lobes narrow (triangular in *M. erectapilosa*) exposing part of the antennal condyles; vertexal carinae forming a pair of tubercles on cephalic margin in full-face view (these tubercles absent in *M. erectapilosa*); humeral and lateral tubercles acute (reduced in *M. erectapilosa*); node of petiole subquadrate in profile (rounded in *M. erectapilosa*). *M. bucki* can be separated from any other *Myrmicocrypta* species by the presence of simple, semierect hairs.

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