



A taxonomic study of the Brazilian turtle ants (Formicidae: Myrmicinae: *Cephalotes*)

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ABSTRACT

We revise the taxonomy of species of the ant genus *Cephalotes* occurring in Brazil. Sixty-four species are recognized, distributed in 14 species groups. Five species are described as new: *Cephalotes gabicamacho* **new species**, *Cephalotes marycorn* **new species**, and *Cephalotes monicaulysea* **new species** (*angustus* group); *Cephalotes liviaprado* **new species** (*fiebrigi* group); and *Cephalotes mariadeandrade* **new species** (*pinelii* group). The soldier and gyne of *C. adolphi* (*angustus* group), and the gyne and male of *C. nilpiei* (*pinelii* group) are described for the first time. *Cephalotes marginatus* is synonymized under *C. atratus*. The *bruchii* and the *laminatus* species groups are synonymized under *fiebrigi* and *pusillus* groups, respectively. The new species group *manni* is proposed, derived from the *basalis* species group. Distribution maps for each species in Brazil are provided. In addition, we provide an illustrated morphological glossary for the genus and illustrated identification keys for workers and soldiers for species groups and for all Brazilian species.

Introduction

The ant genus *Cephalotes* Latreille, 1802, commonly known as turtle ants, is limited to the New World, occurring throughout the Neotropical region and the southern Nearctic region (De Andrade and Baroni-Urbani, 1999). Morphologically, this genus is recognized by the combination of the frontal carinae covering the genae in frontal view, eyes very close to the vertex of the head, deep antennal scrobes, and hard integument (Kempf, 1951; De Andrade and Baroni-Urbani, 1999).

All *Cephalotes* species are exclusively arboreal, nesting in galleries in wood perforated and abandoned by other insects (Powell, 2008; Powell et al., 2014). Almost all species are polymorphic, with soldiers that are responsible for protecting the colony using their highly differentiated heads to block the nest entrance (De Andrade and Baroni-Urbani, 1999; Powell et al., 2020). Its diet consists of pollen and nectar, both very abundant resources available in their foraging zone, as well as the secretions of Hemiptera, bird droppings, and urine deposits of arboreal mammals (Creighton, 1967; Baroni Urbani and De Andrade, 1997; Powell, 2008; Byk and Del-Claro, 2010). One of the most commonly sampled species, *Cephalotes atratus*, is unusual in having the most polymorphic worker caste of any species but no soldier (Corn, 1980).

The biology and ecology of *C. atratus* was extensively studied by Mary Corn (1980), a pioneer in the study of polymorphism and polyethism in this genus, throwing light on our knowledge about the division of labor related to size and age in this species.

The taxonomic history of this genus is exceptionally long, since its first species was described by Linnaeus (1758) in his "Systema Naturae", under the name *Formica atrata*. Latreille, in 1802, described the genus *Cephalotes* by monotypy based on *F. atrata*, which became *Cephalotes atratus*. However, in the next year, Latreille (1803) described *Cryptocerus* also based on *F. atrata*. In 1804, Fabricius synonymized *Cephalotes* under *Cryptocerus* and this name remained valid for more than one century, until the publication of the "priority principle" by the International Code of Zoological Nomenclature in 1905. Wheeler (1913), reverting Fabricius' act, synonymized *Cryptocerus* under *Cephalotes*, rendering *Cephalotes* a valid name again. In 1949, Smith proposed the tribe Cephalotini, including *Cephalotes*, *Zacryptocerus* Wheeler, 1911, *Paracryptocerus* Emery, 1915, *Hypocryptocerus* Wheeler, 1920, *Cyathomyrmex* Creighton, 1933, *Harnedia* Smith, 1949, and *Procryptocerus* Emery, 1887.

The first taxonomic review including *Cephalotes* was performed in 1951 by Kempf, who assessed the entire Cephalotini tribe, recognized six species belonging to *Cephalotes* and described the genus *Eucryptocerus*. In subsequent years, Kempf worked extensively with Cephalotini, dedicating

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almost three decades of his life to this tribe. From 1951 to 1978, Kempf published at least 16 papers on these ants, including revisions (Kempf, 1951, 1952, 1958a, 1969, 1978), descriptions of new species and new records (Kempf, 1953, 1960, 1964, 1967, 1973, 1974), synonymies (Kempf, 1958b, 1963), catalogs (Kempf, 1959), and notes (Kempf, 1965). Among the taxonomic changes proposed by Kempf in his studies, the genera *Paracryptocerus*, *Hypocryptocerus*, *Cyathomyrmex*, and *Harnedia* were synonymized under *Zacryptocerus*, and until 1999 the Cephalotini tribe was constituted by *Cephalotes*, *Zacryptocerus*, *Eucryptocerus*, and *Procryptocerus*.

The last taxonomic revision of the genus, published by De Andrade and Baroni-Urbani in 1999, is one of the most comprehensive and detailed taxonomic works in myrmecology. In this seminal work, the authors synonymized *Zacryptocerus* (75 species) and *Eucryptocerus* (three species) under *Cephalotes* (until then constituted by 10 species). De Andrade (in De Andrade and Baroni-Urbani, 1999) described 30 new species, totaling 118 valid species divided into 24 species groups. Of this total, 59 species from 15 species groups were recognized as being known from Brazil so far. A single species has since been described, *Cephalotes specularis* Brandão, Feitosa, Powell and Del-Claro, 2014. De Andrade and Baroni-Urbani (1999) provided descriptions for all species groups, indicating synapomorphies for each, along with descriptions for all species and new castes for the species known at that time. De Andrade's new species and caste descriptions were remarkably detailed, including the taxonomic history, diagnoses, measurements, photos, illustrations of genitalia, and discussions including comparisons with other species. These authors also provided the first morphological phylogeny and identification keys for the different castes of all species. This work is and will continue to be the basis for any study in *Cephalotes*, and a model for other works in ant taxonomy.

Many authors provided different hypotheses for the position of Cephalotini within Myrmicinae, often relating this tribe to the Paleotropical monotypic tribe Cataulacini, due to the niche (vegetation) and morphological similarity of the genus *Cataulacus* Smith, 1853 (Smith, 1867; Emery, 1893; Ashmead, 1905; Forel, 1906; Emery, 1906, 1914, 1921, 1922). De Andrade and Baroni Urbani (1999) hypothesized Cataulacini as the sister group to Cephalotini. However, a recent molecular phylogeny on Myrmicine ants demonstrated that Cephalotini and Cataulacini are not closely related (Ward et al., 2015). Therefore, the genera in the tribe Cephalotini, *Cephalotes* and *Procryptocerus*, were included in the tribe Attini, as the sister group of *Pheidole* Westwood, 1839, while *Cataulacus*, was transferred to the tribe Crematogastrini as the sister group of *Cardiocondyla* Emery, 1869 + *Ocymyrmex* Emery, 1886 (Ward et al., 2015).

The first molecular phylogeny of the genus, including 61 species, corroborated most of the species' groups by De Andrade and Baroni Urbani's morphological phylogeny, but also showed that some groups are not monophyletic (Price et al., 2014). The *angustus*, *fiebrigi*, *bruchi*, *laminatus* and *pusillus* groups were recovered as paraphyletic and the *pinellii* group as polyphyletic. This analysis was further supported by a subsequent phylogenetic analysis that incorporated molecular and morphological data and had near species-complete coverage of the genus (Price et al., 2016).

In this study, more than 20 years after the revision by De Andrade and Baroni-Urbani (1999), we reviewed the taxonomy of the species of *Cephalotes* occurring in Brazil based on external morphology, geographic distribution and considering previously published and ongoing molecular phylogenetic hypotheses to reclassify the species groups. We provide descriptions and high-resolution images for the new species and for the undescribed castes and sexes of known species. In addition, we update the distribution data regarding the genus in Brazil, providing maps to all species and present an illustrated morphological glossary for the genus. Finally, illustrated identification keys for species groups and for the species in each group known to occur in Brazil are presented, both for workers and soldiers.

Material and methods

We examined and measured adult *Cephalotes* specimens with a Leica S8APO stereomicroscope equipped with an ocular micrometer. Images of specimens available from the AntWeb.org platform were

also included in the morphological study. Entomological collections are referred to by the following acronyms:

ALWC Alex L. Wild Collection, The University of Texas Insect Collection, Austin, Texas, USA.

BMNH The Natural History Museum, London, England.

CASC California Academy of Sciences, San Francisco, California, USA.

CPDC Laboratório de Mirmecologia da Comissão Executiva do Plano da Lavoura Cacaueira, Centro de Pesquisas do Cacau, Ilhéus, Bahia, Brazil.

DZUP Coleção Entomológica Pe. Jesus Santiago Moure, Universidade Federal do Paraná, Curitiba, Paraná, Brazil.

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

IBSP Coleção Entomológica Adolph Hempel, Instituto Biológico de São Paulo, São Paulo, Brazil.

INPA Instituto Nacional de Pesquisas da Amazônia, Manaus, Amazonas, Brazil.

JTLC John T. Longino Collection, University of Utah, Salt Lake City, Utah, USA.

MHNG Musée d'Histoire Naturelle, Geneva, Switzerland.

MIZA Museo de Zoología Agrícola, Universidad Central de Venezuela, Maracay, Aragua, Venezuela.

MNHN Musée National d'Histoire Naturelle, Paris, France.

MPEG Museu Paraense Emílio Goeldi, Belém, Pará, Brazil.

MSNG Museo Civico di Storia Naturale "Giacomo Doria", Genoa, Italy.

MZSP Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil.

NHMB Naturhistorisches Museum, Basel, Switzerland.

NHMW Naturhistorisches Museum Wien, Vienna, Austria.

OUMNH Oxford University Museum of Natural History, Oxford, United Kingdom.

PSWC Philip S. Ward Collection, University of California, Davis, California, USA.

UECE Laboratório de Mirmecologia, Universidade Estadual do Ceará, Fortaleza, Ceará, Brazil.

UCDC Bohart Museum of Entomology, University of California, Davis, California, USA.

UFU Laboratório de Ecologia de Insetos Sociais, Universidade Federal de Uberlândia, Uberlândia, Minas Gerais, Brazil.

UFV Coleção Entomológica do Laboratório de Sistemática de Coleoptera, Universidade Federal de Viçosa, Viçosa, Minas Gerais, Brazil.

UFMG Laboratório de Ecologia de Insetos, Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, Brazil.

USNM National Museum of Natural History, Smithsonian Institution, Washington D.C., USA.

ZMHB Berlin Museum für Naturkunde der Humboldt-Universität, Berlin, Germany.

ZSMC Zoologische Staatssammlung, Munich, Germany.

Measurements were made for all specimens of the new species and undescribed castes and sexes of known species. Measurement values are presented as ranges in mm and follow De Andrade and Baroni-Urbani (1999) and Brandão et al. (2014):

HL: the maximum head length measured in full face view, on the sagittal plane.

HW: the maximum head width posteriorly to the eyes, including any projections on the posterior region of head.

EL: the maximum measurable length of eyes in profile.

PW: the maximum width of the pronotum; in dorsal view, including the pronotal spines.

WL: the diagonal length of mesosoma in profile (Weber's length), from the mid-point of the anterior pronotal declivity to the posterior

ventral angle of the metapleura.

PTL: the maximum length of the petiole in dorsal view.

PTW: the maximum width of the petiole in dorsal view, including the petiolar spines.

PPL: the maximum length of the postpetiole in dorsal view.

PPW: the maximum width of the postpetiole in dorsal view, including the postpetiolar spines.

GL: the maximum length of the first gastral tergite in dorsal view.

HBL: the maximum length of the hind basitarsus.

HBW: the maximum width of the hind basitarsus.

TL: the summed length of HL, WL, PTL, PPL, and GL.

CI: cephalic index. $HW \times 100/HL$.

OI: optical index. $EL \times 100/HW$.

PI: petiolar index. $PTL \times 100/PTW$.

HBI: hind basitarsal index. $HBW \times 100/HBL$.

High-resolution images were obtained with a Zeiss Stereo DiscoveryV20 stereomicroscope attached to a Zeiss Axiocam 305 color video camera in the *Laboratório de Sistemática e Biologia de Formigas – Universidade Federal do Paraná*, Curitiba, Brazil. Photos were combined through image stacking using the software Combine ZP 1.0. Plates for the identification keys are composed by photos taken by the authors and from AntWeb.org. For the specimens from AntWeb.org we provide the unique identifier codes provided by the webpage in the captions of each plate. These photos are here used and edited under Creative Commons license. Some images were edited in Photoshop CS6 (Adobe) to enhance the parameters of brightness and contrast.

Distribution maps were made using QGIS 3.2.3. The occurrence points were based on label information from the examined material (highlighting the new records), and records from literature, which were obtained from references compiled in Antmaps.org (Janicki et al., 2016; Guénard et al., 2017). The literature sources are given by a number in the figure captions, that matches with a reference in the list attached. For the specimens without geographical coordinates in the labels, we used the centroid coordinates of the corresponding municipalities provided by QGIS. The type locality is indicated in the maps for 28 species, including the new species. We do not include the type locality for 19 species, for which the locality is not precise, indicated only for states, countries, or continent. Finally, 17 species have their type localities outside Brazil, so they were not included in maps.

The complete list of the material examined in this study is available as supplementary information (Table S1). The material examined for the new species described here are given in the main text, just below the descriptions. The label information was transcribed *ipsis literis* and organized as follows: country, acronym of the state, specific location, unique identifier labels (composed by the acronym of the Entomological Collection Padre Jesus Santiago Moure – DZUP – plus six numbers), number of specimens and caste between parenthesis, and, finally, the depositary institution in square brackets; a slash, “/”, is used to indicate information on an additional second label in the specimens pin.

The phylogeny presented here is the maximum clade credibility tree from Price et al. (2016), which was based on morphological and molecular data, trimmed to include only those species known from Brazil, and therefore included in this study. The phylogeny does not include the species *C. duckei*, *C. manni*, and *C. solidus*, which were omitted from the analysis by Price et al. (2016) due to difficulty in the determination of their phylogenetic placement. The species *C. marycorn* **new species**, *C. monicaulysea* **new species**, and *C. liviaprado* **new species**, described for the first time in this work, were not included in the Price et al. (2016) analyses. The species *C. mariadeandrade* **new species** and *C. gabicamacho* **new species** are also described here for the first time, but they were included in the previous analysis as *C. sp2* and *C. sp3*, respectively. Thus, they were here included in the phylogeny. We present the labels for species groups in the trimmed phylogeny

according to our proposal (i.e. including the synonymies made here) and present the previous names for the synonymized groups in grey.

The terms for the basic external morphology of *Cephalotes* were compiled in an illustrated glossary (Fig. 1). The illustrations were made in Illustrator CS6 (Adobe) and Photoshop based on morphological schemes published by Kempf (1951), and Powell et al. (2020). The glossary terms follow De Andrade and Baroni Urbani (1999) and Wilson (1955). Terms for external morphology of alate forms follow Boudinot (2015) and for wing descriptions follow Yoshimura and Fisher (2011). Surface sculpturing follows Harris (1979). Following De Andrade and Baroni Urbani (1999), the reproductive females are here called as gynes; and the small individuals and the specialized large individuals are called workers and soldiers, respectively.

The soldier morphotypes are based on the shape of their heads, according to Powell et al. (2020). They are separated into four morphotypes: square, dome, disc, and dish. The square morphotype is defined by the frontal carinae extending posteriorly to form a continuous carina with the vertexal corners, which gives a square shape to the posterior region of head. The dome morphotype has the frontal carinae terminating over the eyes or posteriorly to the eyes, but not reaching the vertexal corners; while the vertex forms an angle with the dorsum of head, forming a dome. For the disc shape, the frontal carinae extend over the eyes, fusing posteriorly with the median-vertexal teeth, creating a unified dorsal disc shape, so that the vertex corners are in a lower plane than the dorsal disc; the median-vertexal teeth may be absent to strongly visible in the posterior margin of the disc. The dish morphotype is similar to the disc shape, but the frontal carinae are fused anteriorly with the frontal lobes, covering completely the mandible in frontal view.

Results

Cephalotes Latreille, 1802

Type-species: *Formica atrata*, by monotypy.

[Type-species not *Formica cephalotes*, unjustified subsequent designation by Wheeler, 1911: 160; corrected by Wheeler, 1913: 78].

Cephalotes as junior synonym of *Cryptocerus*: Fabricius, 1804: 419.

Cephalotes as senior synonym of *Cryptocerus*: Wheeler, 1913: 78.

Cephalotes in Myrmicinae, Cryptocerini: Emery, 1914: 42; Forel, 1917: 246; Wheeler, 1922: 665; Emery, 1924: 303; all subsequent authors to 1949, and Dlussky and Fedoseeva, 1988: 79 (anachronism).

Cephalotes in Myrmicinae, Cephalotini: Smith, 1949: 19; Kempf, 1951: 105; all subsequent authors except the above.

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

General diagnosis: Females: Frontal carinae covering the genae in frontal view. Mandibles small and thick, with two apical teeth. Eyes produced laterally, very close to the vertex. Antennae short, with 11 articles. Deep antennal scrobes. Humeral angles with spines or lamellae. Hard integument. Male: Size smaller than or subequal to gyne. Frontal carinae short to obsolete. Antennae with 13 articles, remarkably longer than in the females. Antennal scrobes vestigial to absent. Propodeum unarmed or armed with a pair of obtuse angles or denticles.

Worker (Fig. 1A): Mandibles small and thick, with two apical teeth. Palpal formula 5:3. Clypeus narrow. Frontal lobes greatly expanded and covering the genae. Frontal carinae divergent posteriorly and reaching the vertex. Antennal scrobes deeply excavated. Antennae with 11 articles. Lateral margins of pronotum with spines, denticles or lamellae. Dorsum of propodeum without a transversal crest. Mid and hind tibiae without apical spurs. The first gastral tergite comprises almost the total length of gaster. Sting reduced or missing.

Soldier (Figs. 1C, D): Present in most species. Differs from the worker by the presence of a variably developed transverse crest or carina on dorsum of pronotum and, in most species, by the head specialization, which varies in degree of modification in four morphotypes (Powell et al., 2020). Of the species present in Brazil, the square morphotype occurs in

the *atratus*, *basalis*, *clypeatus* and *manni* groups. The dome morphotype occurs in the *basalis*, *pusillus*, and *depressus* groups. The disc morphotype occurs in the *angustus*, *depressus*, *grandinosus*, *pinelii*, *umbraculatus*, and *fiebrigi* groups. Finally, the dish morphotype occurs only in the *pallens* group. The soldier for the Brazilian representatives of the *coffea* species group (*Cephalotes trichophorus*) and the *solidus* species group (*Cephalotes solidus*) are currently unknown.

Gyne (Figs. 1E, G): Head generally like the soldier; when the soldier caste is absent, gyne's head is similar to the workers but usually larger and more convex. Eyes comparatively large; ocelli always present. Scutum and scutellum weakly convex to flat. Forewings with Sc+R meeting the strongly pigmented stigma; R extends beyond the stigma, not reaching the external margin of wing; Rs meeting R posteriorly and forming a marginal cell with 2r-rs; M+Cu diverging in M and Cu, forming a discal cell with m-cu; M and Cu extends towards margin after discal cell, but spectral for most of its length, not reaching the wing margin; vein A extends beyond the cu-a, which is interrupted, not connecting M+Cu and A; claval furrow marked by a conspicuous notch; length of R, M, Cu, and A can be variable between specimens, but never reaching the

margin of wing. Hindwing with R+Rs diverging in R1 and Rs; M+Cu diverging in Cu and rs-m+M; vein A extends beyond the cu-a, which is interrupted, not connecting M+Cu and A; length of R1, Rs, Cu, and A can be variable between specimens, but never reaching the wing margin; hamuli variable in number between species. Gaster longer than mesosoma, with four tergites visible, the first one occupying almost the total length of gaster.

Male (Fig. 1B): Size smaller than or subequal to gyne. Head subcircular in dorsal view. Mandibles like workers, but masticatory margins usually with a single apical tooth, often followed by a series of denticles. Clypeus subrectangular. Frontal carinae short to obsolete. Antennal scrobes vestigial to absent. Antennae with 13 articles, remarkably longer than in the females; scape shorter than second funicular segment; pedicel shorter than scape, antennal condyle exposed. Mesosoma with notauli Y-shaped, deeply impressed. Propodeum unarmed or armed with a pair of obtuse angles or denticles. Hind tibiae usually without apical spurs. Petiole cylindrical or nodiform. Wings as in gyne. Gaster usually shorter than mesosoma, with five visible tergites; tergite I always larger than others.

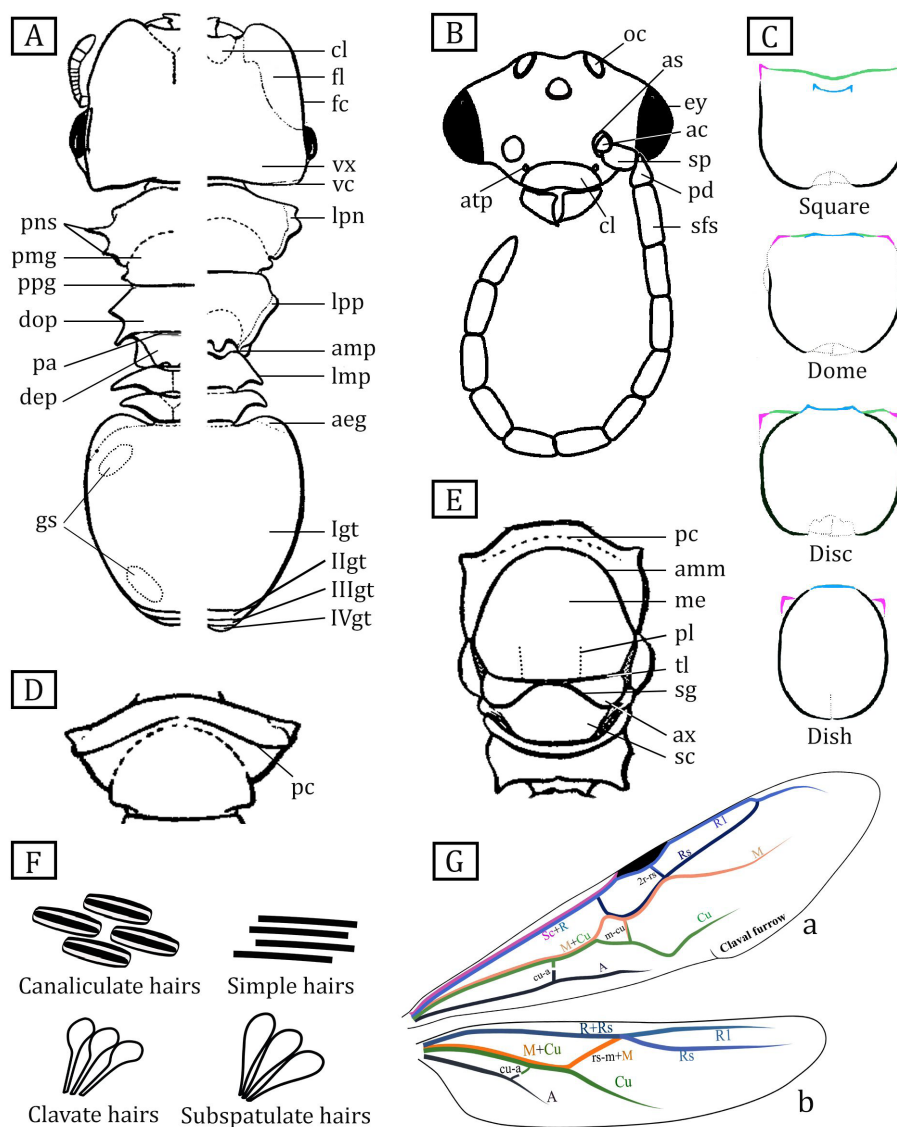


Figure 1 Glossary for basic external morphology of *Cephalotes*. A: Workers. B: Male head. C: Soldiers' head morphotypes (black: frontal carinae, green: vertex, pink: vertex corners, blue: median-vertexal teeth). D: Soldier promesonotum. E: Gyne mesosoma. F: Basic hair types. G: Wing venation (a: forewing, b: hindwing). ac: antennal condyle, aeg: anterior lamellar expansions of gaster, amm: anterior margin of mesoscutum, amp: anterior margin of petiole, as: antennal socket, ax: axilla, cl: clypeus, dep: declivous face of propodeum, dop: dorsal face of propodeum, ey: eye, fc: frontal furrow, fl: frontal lobe, gs: gastral lobe, Igt: gastral tergite I, IIgt: gastral tergite II, IIIgt: gastral tergite III, IVgt: gastral tergite IV, lmp: lateral margin of petiole, lpn: lateral expansions of pronotum, lpp: lateral expansions of propodeum, me: mesoscutum, oc: ocelli, pa: propodeal angle, pc: pronotal carina, pd: pedicel, pl: parapsidal lines, pmg: promesonotal groove, pns: pronotal spines, ppg: propodeal groove, sc: scutellum, sfs: second funicular segment, sg: scutoscutellar groove, sp: scape, tl: transscutal line, vc: vertex corner, vx: vertex.

Taxonomic synopsis of *Cephalotes* for Brazil**angustus species group**

- Cephalotes adolphi* (Emery, 1906)
Cephalotes angustus (Mayr, 1862)
Cephalotes conspersus (Smith, 1867)
Cephalotes frigidus (Kempf, 1960)
Cephalotes gabicamacho **new species**
Cephalotes goeldii (Forel, 1912)
Cephalotes marycorn **new species**
Cephalotes monicaulyssea **new species**
Cephalotes notatus (Mayr, 1866)
Cephalotes pallidicephalus (Smith, 1876)
Cephalotes targionii (Emery, 1894)

atratus species group

- Cephalotes atratus* (Linnaeus, 1758)
 =*Cephalotes marginatus* (Fabricius, 1804) **new synonym**
Cephalotes oculatus (Spinola, 1851)
Cephalotes opacus Santschi, 1920
Cephalotes placidus (Smith, 1860)
Cephalotes serratriceps (Smith, 1858)

basalis species group

- Cephalotes basalis* (Smith, 1876)
Cephalotes complanatus (Guérin-Méneville, 1844)
Cephalotes cordiae (Stitz, 1913)
Cephalotes ramiphilus (Forel, 1904)

clypeatus species group

- Cephalotes clypeatus* (Fabricius, 1804)
Cephalotes membranaceus (Klug, 1824)
Cephalotes ustus (Kempf, 1973)

coffae species group

- Cephalotes trichophorus* De Andrade, 1999

depressus species group

- Cephalotes betoi* De Andrade, 1999
Cephalotes borgmeieri (Kempf, 1951)
Cephalotes cordatus (Smith, 1853)
Cephalotes depressus (Klug, 1824)
Cephalotes eduarduli (Forel, 1921)
Cephalotes palustris De Andrade, 1999
Cephalotes pavonii (Latreille, 1809)

fiebrigi species group

- = *bruchi* species group **new synonym**
Cephalotes bruchi (Forel, 1912)
Cephalotes fiebrigi (Forel, 1906)
Cephalotes guayaki De Andrade, 1999
Cephalotes jheringi (Emery, 1894)
Cephalotes liviaprado **new species**
Cephalotes pilosus (Emery, 1896)
Cephalotes quadratus (Mayr, 1868)
Cephalotes specularis Brandão, Feitosa, Powell and Del-Claro, 2014

grandinosus species group

- Cephalotes grandinosus* (Smith, 1860)
Cephalotes klugi (Emery, 1894)
Cephalotes persimilis De Andrade, 1999
Cephalotes persimplex De Andrade, 1999

manni species group (here proposed)

- Cephalotes manni* (Kempf, 1951)

pallens species group

- Cephalotes pallens* (Klug, 1824)
Cephalotes pallidoides De Andrade, 1999
Cephalotes pallidus De Andrade, 1999
Cephalotes patellaris (Mayr, 1866)
Cephalotes pellans De Andrade, 1999

pinelii species group

- Cephalotes incertus* (Emery, 1906)
Cephalotes liepini De Andrade, 1999
Cephalotes maculatus (Smith, 1876)
Cephalotes mariadeandrade **new species**
Cephalotes nilpiei De Andrade, 1999
Cephalotes pinelii (Guérin-Méneville, 1844)

pusillus species group

- = *laminatus* species group **new synonym**
Cephalotes duckei (Forel, 1906)
Cephalotes inaequalis (Mann, 1916)
Cephalotes laminatus (Smith, 1860)
Cephalotes minutus (Fabricius, 1804)
Cephalotes pusillus (Klug, 1824)
Cephalotes simillimus (Kempf, 1951)
Cephalotes spinosus (Mayr, 1862)

solidus species group

- Cephalotes solidus* (Kempf, 1974)

umbraculatus species group

- Cephalotes umbraculatus* (Fabricius, 1804)

Key to the identification of Brazilian species groups of *Cephalotes* based on workers

(Figs. 2a-r)

- 1 In lateral view, vertexal corners with a pair of spines (pd, pv) (Fig. 2a). Comparatively larger ants.....**atratusgroup**
- 1' Vertexal corners can have projections, but in a different pattern than above, usually as lamellar expansions (vle) (Figs. 2b, c). Comparatively smaller ants.....2
- 2 In dorsal view, mesonotum and propodeum without lateral projections (Fig. 2e).....**solidusgroup**
- 2' Mesonotum and propodeum with lateral projections. These projections can be denticles, spines (ps) (Figs. 2f-h) or lamellar expansions (ple) (Figs. 2i, k-l) sometimes restricted to the declivous face of propodeum (Fig. 42c).....3
- 3 In dorsal view, lateral margins of propodeum with lamellar expansions (ple) (Figs. 2i, k-l) sometimes restricted to the declivous face of propodeum (Fig. 42c).....4
- 3' Lateral margins of propodeum with denticles or spines (ps) (Figs. 2f-h).....7
- 4 In dorsal view, gaster completely surrounded by a lamella (Fig. 2o).....**clypeatusgroup**
- 4' In dorsal view, gaster with lamellar expansions restricted to the anterior portion (ge) (Figs. 2k-l, p-r).....5
- 5 In frontal view, vertexal corner extending laterally, overhanging the eyes (Fig. 2d - dashed). Body color reddish brown (Fig. 2d, i).....**pallensgroup**
- 5' In frontal view, vertexal corners not extending laterally (Fig. 2c - dashed). Body variable in color.....6
- 6 Metafemur with lamellar expansion (fle) on dorsal and/or ventral face, which frequently are crenulate and narrow (Fig. 2k).....**grandinosusgroup**
- 6' Metafemur without lamellar expansions (Fig. 2l).....**pineliigroup**
- 7 In dorsal view, propodeum with two pairs of spines, the anterior one longer than the posterior and curved backwards (Fig. 2g). Spines sometimes with denticles.....**depressusgroup**
- 7' In dorsal view, propodeum with variable number of spines (Fig. 2h); if there are two pairs, the anterior one is never longer than the posterior (Fig. 2f).....8
- 8 In dorsal view, first gastral tergite yellowish, with a cross-shaped dark macula (Fig. 2p).....**umbraculatusgroup**
- 8' First gastral tergite variable in color; macula absent (Fig. 2q) or never cross-shaped (Fig. 2r).....9
- 9 Posterior femora with a median projection (Fig. 2j). Metatibiae usually marginated (Fig. 2j).....**basalisgroup**
- 9' Posterior femora without projections (Fig. 2l). Metatibiae never marginated (Fig. 2l).....10

10 In dorsal view, anterior gastral expansions (ge) without a translucent lamella (Fig. 2q).....11
 10' In dorsal view, anterior gastral expansions (ge) translucent (Fig. 2r)..
12
 11 Dorsal and declivous faces of propodeum meeting at a distinct propodeal angle; lateral margins of the declivous face with broad lamellar expansion from the posterior dorsal spines of propodeum to the petiolar insertion.....**manni**group
 11' Dorsal and declivous faces of propodeum continuous, not meeting at a distinct propodeal angle; lateral margins of declivous face without lamellar expansions.....**fiebrigi**group

12 In dorsal view, propodeum with two pairs of spines, the posterior one longer than the declivous face of propodeum (Fig. 2f).....
 **pusillus** group
 12' In dorsal view, propodeum with variable number of spines, none of them longer than the declivous face of propodeum (Fig. 2h).....
13
 13 In dorsal view, margins of declivous face of propodeum with lamellar expansions (Fig. 2m). In dorsal view, margins of pronotum with lamellar expansion, which can be crenulate, but not forming denticles or spines.....**coffea**group
 13' In dorsal view, margins of declivous face of propodeum without lamellar expansions (Fig. 2n). In dorsal view, margins of pronotum with denticles or spines.....**angustus**group

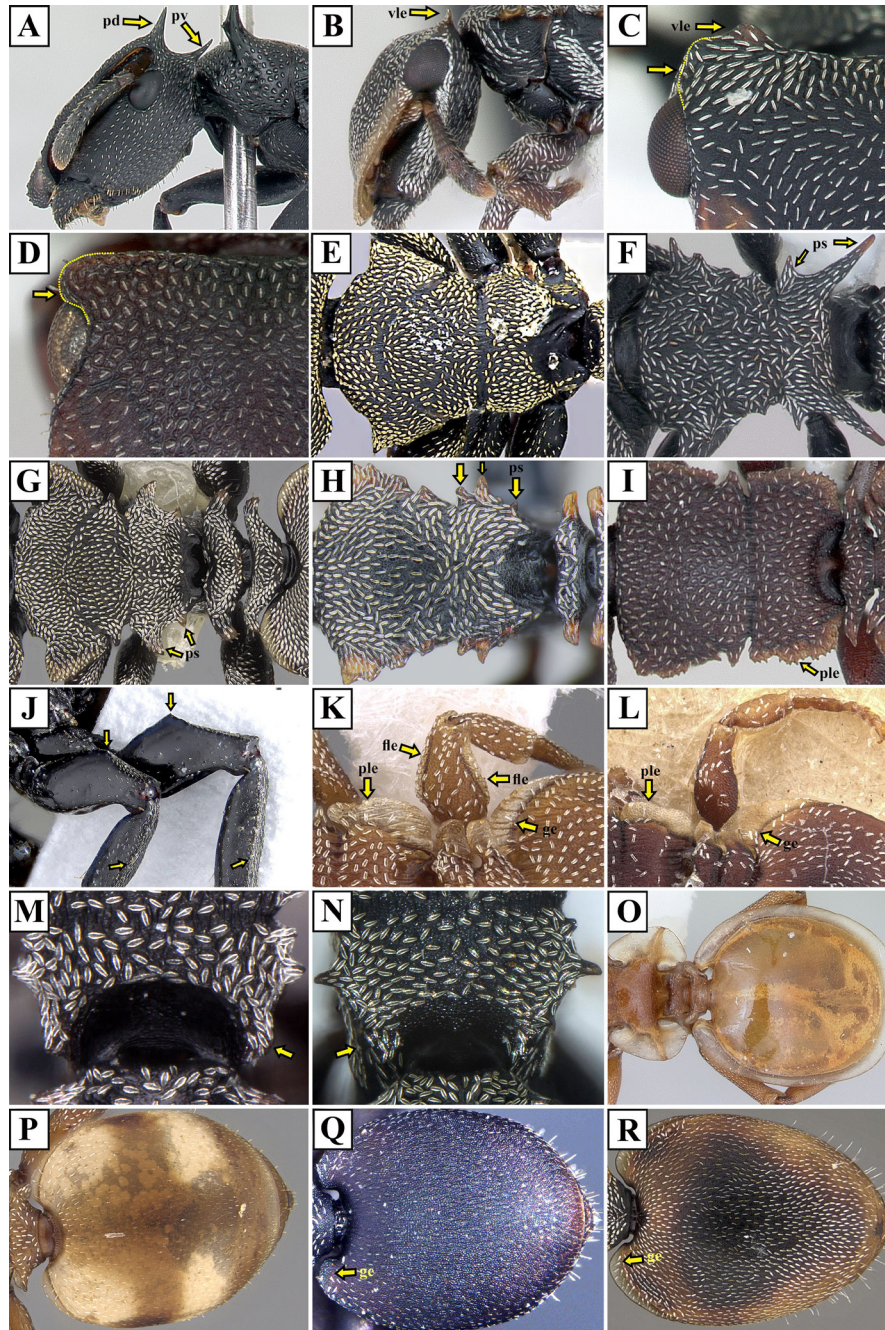


Figure 2 Workers of *Cephalotes*. A: *C. atratus* (*atratus* group) [CASENT0178627]. B: *C. depressus* (*depressus* group) [CASENT0173671]. C and F: *C. pusillus* (*pusillus* group) [CASENT0173703]. D and I: *C. pallens* (*pallens* group) [CASENT0173697]. E: *C. solidus* (*solidus* group). G: *C. cordatus* (*depressus* group) [CASENT0922596]. H: *C. frigidus* (*angustus* group) [UFV-LABÉCOL-004442]. J: *C. basalis* (*basalis* group). K: *C. grandinosus* (*grandinosus* group) [CASENT0922544]. L: *C. maculatus* (*pinelii* group) [CASENT0909295]. M: *C. trichophorus* (*coffea* group). N and R: *C. conspersus* (*angustus* group) [R: CASENT0922530]. O: *C. clypeatus* (*clypeatus* group) [CASENT0173669]. P: *C. umbraculatus* (*umbraculatus* group) [CASENT0922582]. Q: *C. jheringi* (*fiebrigi* group). fle: femoral lamellar expansions. ge: gastral expansions. pd: posterodorsal spine. ple: propodeal lamellar expansions. ps: propodeal spine. pv: posteroventral spine. vle: vertexal lamellar expansions.

Key to the identification of Brazilian species groups of *Cephalotes* based on soldiers

(Figs. 3a-p)

Note 1: soldiers are not present in the Brazilian species of *coffea* and *solidus* groups.

Note 2: soldiers have a transversal crest or carina on the dorsum of pronotum (Fig. 1D), except in *atratus* group, which can be identified with the worker's key.

Note 3: for a better comprehension of the morphology of soldier's head see Fig. 1C.

- 1 In frontal view, cephalic dorsum completely covering the mandibles (Fig. 3a).....**pallens**group
- 1' In frontal view, mandibles visible, at least partially (Figs. 3b-e).....2
- 2 In frontal view, dorsum of head completely margined by a carina (blue dotted), forming a disc (Fig. 3b). Vertexal corners (pink dotted) separated from the dorsal cephalic disc (Fig. 3b).....3
- 2' In frontal view, dorsum of head square shaped (Fig. 3c) or dome shaped (Fig. 3d, e), but never disc shaped. In both cases, the vertexal corners (pink dotted) are not separated from the dorsum of head by a carina (blue dotted) (Fig. 3c-e).....8
- 3 In dorsal view, petiole and postpetiole with lateral lamellar expansions (Fig. 3h).....4
- 3' Petiole and postpetiole with lateral acute projections, forming spines or denticles (Figs. 3i, j, m, o, p).....5
- 4 Posterior femora with lamellar expansions in dorsal and/or ventral face (Fig. 3k), which frequently are crenulate and narrow.....**grandinosus**group
- 4' Posterior femora without lamellar expansions (Fig. 3l).....**pinelii**group
- 5 In dorsal view, propodeum with two pairs of spines, the anterior one longer than the posterior one and slightly curved backwards (Fig. 3j).....**depressus**group (in part)

- 5' In dorsal view, propodeum with variable number of spines, if there are two pairs, the anterior one is never longer than the posterior (Figs. 3f, g, i).....6
- 6 Body yellowish; first gastral tergite with a cross-shaped dark macula (Fig. 3p). In dorsal view, pronotum crest with pointed edges (Fig. 3f).....**umbraculatus**group
- 6' Body black to dark brown; gaster macula absent or in a shape different than a cross (Fig. 3o), if cross-shaped, then pronotum crest with rounded or subrectangular edges (Fig. 3g).....7
- 7 In dorsal view, anterior expansions of gaster without a translucent lamella (Fig. 3m).....**fiebrigig**group (in part)
- 7' In dorsal view, anterior gaster expansions with a translucent lamella, usually very thin (Fig. 3o).....**angustus**group
- 8 In frontal view, frontal carinae continuous with the vertexal corners, cephalic dorsum square shaped (Fig. 3c).....9
- 8' In frontal view, frontal carinae ends before reaching the vertexal corners, cephalic dorsum dome shaped (Fig. 3d, e).....11
- 9 Gaster completely surrounded by lamellar expansions (Fig. 3n).....**clypeatus**group
- 9' Lamellar expansions, if any, present only in the anterior portion of the gaster (Fig. 3o, p).....10
- 10 Posterior femora with a median projection, metatibiae margined.....**basalis**group
- 10' Posterior femora without projections, metatibiae never margined.....**manni**group
- 11 In frontal view, head longer than wide, with contiguous foveae and suberect hairs (Fig. 3e).....**fiebrigig**group (in part)
- 11' In frontal view, head subquadrate, with foveae separate by interspaces, and short appressed hairs (Fig. 3d).....12
- 12 Propodeum with two pairs of lateral projections, the posterior one longer than the anterior one (Fig. 3i).....**pusillus**group
- 12' Propodeum with two pairs of lateral projections, the anterior one longer than the posterior one (Fig. 3j).....**depressus**group (in part)

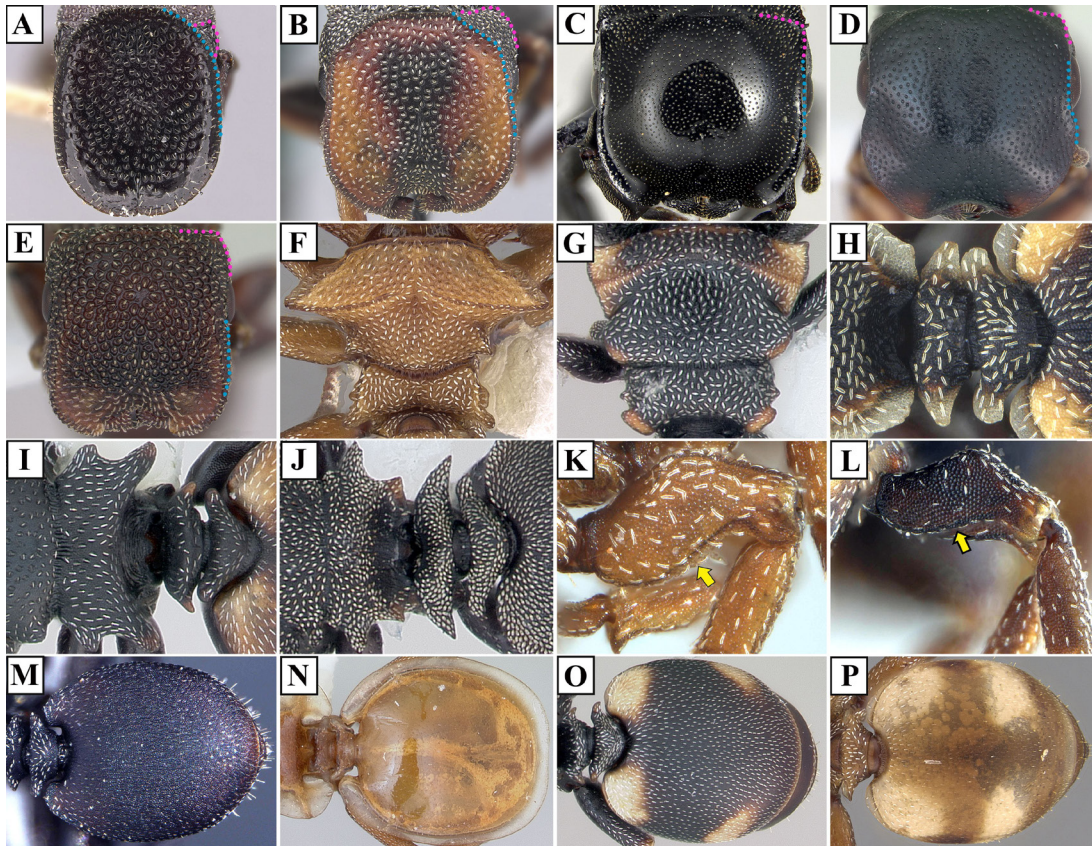


Figure 3 Soldiers of *Cephalotes*. A: *C. decoloratus* (*pallens* group) [CASENT0909299]. B: *C. angustus* (*angustus* group) [CASENT0909276]. C: *C. basalis* (*basalis* group). D and I: *C. minutus* (*pusillus* group) [CASENT0173691]. E: *C. quadratus* (*fiebrigig* group) [CASENT0173705]. F and P: *C. umbraculatus* (*umbraculatus* group) [CASENT0922582]. G and O: *C. targionii* (*angustus* group) [CASENT0173708]. H: *C. nilpiei* (*pinelii* group). J: *C. borgmeieri* (*depressus* group) [CASENT0173664]. K: *C. grandinosus* (*grandinosus* group). L: *C. pinelii* (*pinelii* group). M: *C. jheringi* (*fiebrigig* group). N: *C. clypeatus* (*clypeatus* group) [CASENT0173669].

The *angustus* species group

(Figs. 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16)

The *angustus* group was proposed by Kempf (1958a) based on the subgenus *Harnedia* of the genus *Paracryptocerus*, with 26 species divided into seven subgroups. De Andrade and Baroni Urbani (1999) reorganized this scheme, reducing the *angustus* group to Kempf's *angustus* subgroup, which was composed by *C. adolphi*, *C. angustus*, *C. goeldii*, *C. notatus* (= *P. (Harnedia) fleddermanni* in Kempf, 1958a), *C. pallidicephalus* (= *P. (Harnedia) striativentris* in Kempf, 1958a), and *C. targionii*. These authors also added *C. conspersus* in the group, which was considered by Kempf (1951) as a taxonomically isolated species, and two species described by them, *C. dentidorsum* and *C. palta*. These last two species are known only from Colombia and were not included in this study. All species in this group are exclusively South American.

In the morphological phylogeny by De Andrade and Baroni Urbani (1999, see their Fig. 24), this group was considered the sister group to the clade formed by the *bruchi*, *fiebrigi* and *prodigosus* groups. The current phylogeny confirms the relationships between these groups (Fig. 54). The *bruchi*, *fiebrigi* and *prodigosus* groups are recovered as monophyletic, but they render the *angustus* group paraphyletic, suggesting that all these groups might represent a single lineage (Fig. 54).

Morphologically, these groups share the declivous face of the propodeum continuous with its dorsal face, not meeting at a distinct propodeal angle, and with a variable number of spines, but differing by the anterior expansions of the gaster, which are a thin translucent lamella in the *angustus* group and a thick opaque lamella in *bruchi*, *fiebrigi* and *prodigosus* groups. Although the phylogenetic data (Fig. 54) suggests the *angustus*, *bruchi*, *fiebrigi* and *prodigosus* groups could be synonymized, we decided to keep *angustus* as a valid group until a broader phylogeny, including additional species from all these groups, is available. The Argentinian *prodigosus* group was not included in the present study, due to its absence in Brazil. The discussion about *bruchi* and *fiebrigi* groups is presented in the *fiebrigi* group section below.

Diagnosis: In workers, body with appressed hairs (Fig. 2h). Declivous face of propodeum continuous with dorsal face, not meeting at a distinct propodeal angle, with a variable number of spines (Fig. 2h). If only two pairs of spines are present on propodeum, the anterior one is never the longest, and the posterior one is never longer than the declivous face (Fig. 2h). First tergite of gaster with anterior lamellar expansions translucent (Fig. 2r). In soldiers, propodeum with variable number of spines, if there are two pairs, the anterior one is never longer than the posterior. Anterior gastral expansions with a translucent lamella, usually very thin (Fig. 3o).

Brazilian species of *angustus* group

Cephalotes adolphi (Emery, 1906)

Obsolete combination: *Cryptocerus adolphi*

Cephalotes angustus (Mayr, 1862)

Obsolete combination: *Cryptocerus angustus*

= *Cephalotes angustus clarior* (Forel, 1912)

Obsolete combination: *Cryptocerus angustus clarior*

= *Cephalotes cristatus ruficeps* (Santschi, 1929)

Obsolete combination: *Cryptocerus cristatus ruficeps*

Cephalotes conspersus (Smith, 1867)

Obsolete combination: *Cryptocerus conspersus*

= *Cephalotes denticulatus variegata* (Forel, 1911)

Obsolete combination: *Cryptocerus denticulatus* var. *variegata*

Cephalotes frigidus (Kempf, 1960)

Obsolete combination: *Paracryptocerus frigidus*

Cephalotes gabicamacho new species

Cephalotes goeldii (Forel, 1912)

Obsolete combination: *Cryptocerus goeldii*

Cephalotes marycorn new species

Cephalotes monicaulysea new species

Cephalotes notatus (Mayr, 1866)

Obsolete combination: *Cryptocerus notatus*

= *Cephalotes fleddermanni* (Kempf, 1958a)

Obsolete combination: *Paracryptocerus (Harnedia) fleddermanni*

Cephalotes pallidicephalus (Smith, 1876)

Obsolete combination: *Cryptocerus pallidicephalus*

= *Cephalotes striativentris* (Emery, 1894)

Obsolete combination: *Cryptocerus striativentris*

Cephalotes targionii (Emery, 1894)

Obsolete combination: *Cryptocerus targionii*

= *Cephalotes denticulatus* (Emery, 1894)

Obsolete combination: *Cryptocerus denticulatus*

Key to the identification of Brazilian species of the *angustus* group of *Cephalotes* based on workers

(Figs. 4a-p)

- 1 In lateral view, the second pair of pronotal spines is raised dorsally above the level of the anterior pronotal spines (Fig. 4c).....***C. adolphi***
- 1' In lateral view, the second pair of pronotal spines are in the same level of the anterior pronotal spines (Fig. 4d, e).....2
- 2 First gastral sternite longitudinally costate (Fig. 4o).....***C. pallidicephalus***
- 2' First gastral sternite not longitudinally costate (Fig. 4m), but rugosities can be present (Fig. 4n).....3
- 3 Ventral face of head with longitudinal rugosities towards the cephalic foramen (Fig. 4a).....***C. notatus***
- 3' Ventral face of head microalveolate. Rugosities can be present, but not towards the cephalic foramen (Fig. 4b).....4
- 4 In dorsal view, lateral spines of postpetiole longer than the maximum width of its lamellar part (Fig. 4f).....***C. frigidus***
- 4' In dorsal view, lateral spines of postpetiole as long as or shorter than the maximum width of its lamellar part (Fig. 4g).....5
- 5 In lateral view, dorsum of petiole without a pair of denticles (Fig. 4h).....***C. goeldii***
- 5' In lateral view, dorsum of petiole with a pair of denticles (Fig. 4i).....6
- 6 Pro-, meso- and metapleura striate longitudinally (Fig. 4d).....***C. targionii***
- 6' Pro-, meso- and metapleura not striate longitudinally; if they are striae, it is only on the propleura (Fig. 4e).....7
- 7 In dorsal view, first gastral tergite orange to light brown, with a black lozenge-shaped patch in the middle (Fig. 4j).....***C. conspersus***
- 7' In dorsal view, first gastral tergite black, with or without a pair of anterolateral colored spots, never with a median lozenge (Fig. 4k, l, p).....8
- 8 In dorsal view, first gastral tergite with appressed canaliculate hairs only, without simple hairs (Fig. 4k).....9
- 8' In dorsal view, first gastral tergite with some appressed canaliculate hairs and appressed simple hairs (Fig. 4l, p).....10
- 9 In ventral view, sternite of gaster microalveolate, without longitudinal striae (Fig. 4m).....***C. angustus***
- 9' In ventral view, sternite of gaster with longitudinal striae (Fig. 4n).....***C. monicaulysea* new species**
- 10 Anterior portion of first tergite of gaster, near the postpetiolar insertion, without striae, with abundant appressed canaliculate hairs, the distance between each hair shorter than their length (Fig. 4l).....***C. gabicamacho* new species**
- 10' Anterior portion of first tergite of gaster, near the postpetiolar insertion, with short striae and sparse appressed simple hairs, the distance between each hair longer than their length (Fig. 4p).....***C. marycorn* new species**

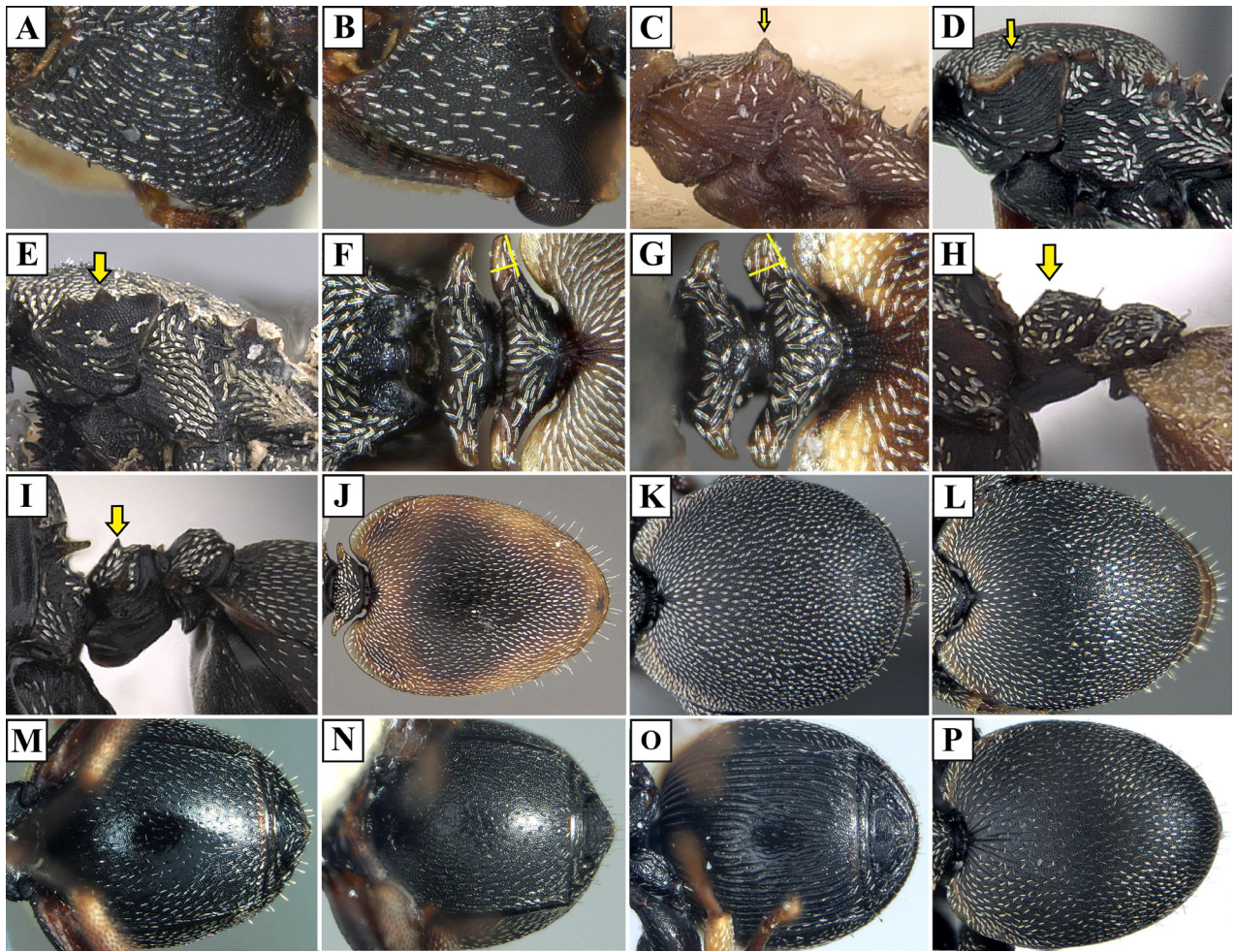


Figure 4 Workers of *angustus* group. A: *C. notatus*. B and H: *C. goeldii* [H: CASENT0922535]. C: *C. adolphi* [CASENT0904906]. D and I: *C. targionii* [D: CASENT0173661, I: CASENT0922537]. E and M: *C. angustus* [E: CASENT0909277]. F: *C. frigidus*. G and J: *C. conspersus* [J: CASENT0922530]. K and N: *C. monicaulysea*. L: *C. gabicamacho*. O: *C. pallidicephalus*. P: *C. marycorn*.

Key to the identification of Brazilian species of the *angustus* group of *Cephalotes* based on soldiers

(Figs. 5a-p)

- 1 Cephalic disc alveolate with suberect to erect hairs (Fig. 5a).....*C. frigidus*
- 1' Cephalic disc foveate with subdecumbent to appressed hairs (Fig. 5b-d).....2
- 2 In dorsal view, dorsum of mesosoma yellowish (Fig. 5k). In lateral view pleurae black, with some yellowish macula (Fig. 5g).....*C. adolphi*
- 2' In dorsal view, dorsum of mesosoma predominantly black, sometimes with the apices of the lateral projections yellowish (Fig. 5j). In lateral view, the entire pleurae black to dark brown (Fig. 5h, i).....3
- 3 Cephalic disc wider than long, at most subquadrate (Fig. 5b).....4
- 3' Cephalic disc longer than wide (Fig. 5c, d).....5
- 4 Pronotum broader than the head width (Fig. 5j).....*C. goeldii*
- 4' Pronotum narrower or as broad as the head width (Fig. 5k).....*C. notatus*
- 5 First gastral sternite with longitudinal rugosities (Fig. 5l).....*C. pallidicephalus*
- 5' First gastral sternite without longitudinal rugosities (Fig. 5m), striae can be present laterally, but the middle of the sternite is smooth (Fig. 5n).....6
- 6 In dorsal view, lateral margins of pronotum straight and subparallel (Fig. 5e).....7
- 6' In dorsal view, lateral margins of pronotum convex and converging posteriorly (Fig. 5f).....9

- 7 In dorsal view, propodeal groove weakly impressed, marked on the sides but absent medially (Fig. 5f).....*C. conspersus*
- 7' In dorsal view, propodeal groove strongly impressed (Fig. 5e).....8
- 8 Foveae of cephalic disc very close, space between them shorter than their diameters; each fovea with an internal subdecumbent hair (Fig. 5d). In dorsal view, pronotal carina weak and interrupted in the middle by a superficial sulcus (Fig. 5f). In lateral view, posterior pair of denticles of propodeum strongly bent dorsally with the apices curved anteriorly.....*C. targionii*
- 8' Foveae of head sparse, space between most foveae equal to or longer than the diameter of each fovea; each fovea with an internal appressed hair (Fig. 5c). In dorsal view, pronotal carina weak and continuous (Fig. 5e). In lateral view, posterior pair of denticles of propodeum gently bent dorsally with apices not curved anteriorly (Fig. 5i).....*C. gabicamacho* new species
- 9 First sternite of the gaster without striae laterally (Fig. 5m). In dorsal view, anterior lamellae of gaster extending posteriorly as a carina (Fig. 5o - dotted line). Pronotal carina well marked, normally forming a crest (Fig. 5g, h).....*C. angustus*
- 9' First sternite of the gaster with striae laterally (Fig. 5n). In dorsal view, anterior lamellae of the gaster not extending posteriorly as a carina (Fig. 5p - dotted line). Pronotal carina weakly marked, not forming a crest (Fig. 5i).....*C. monicaulysea* new species

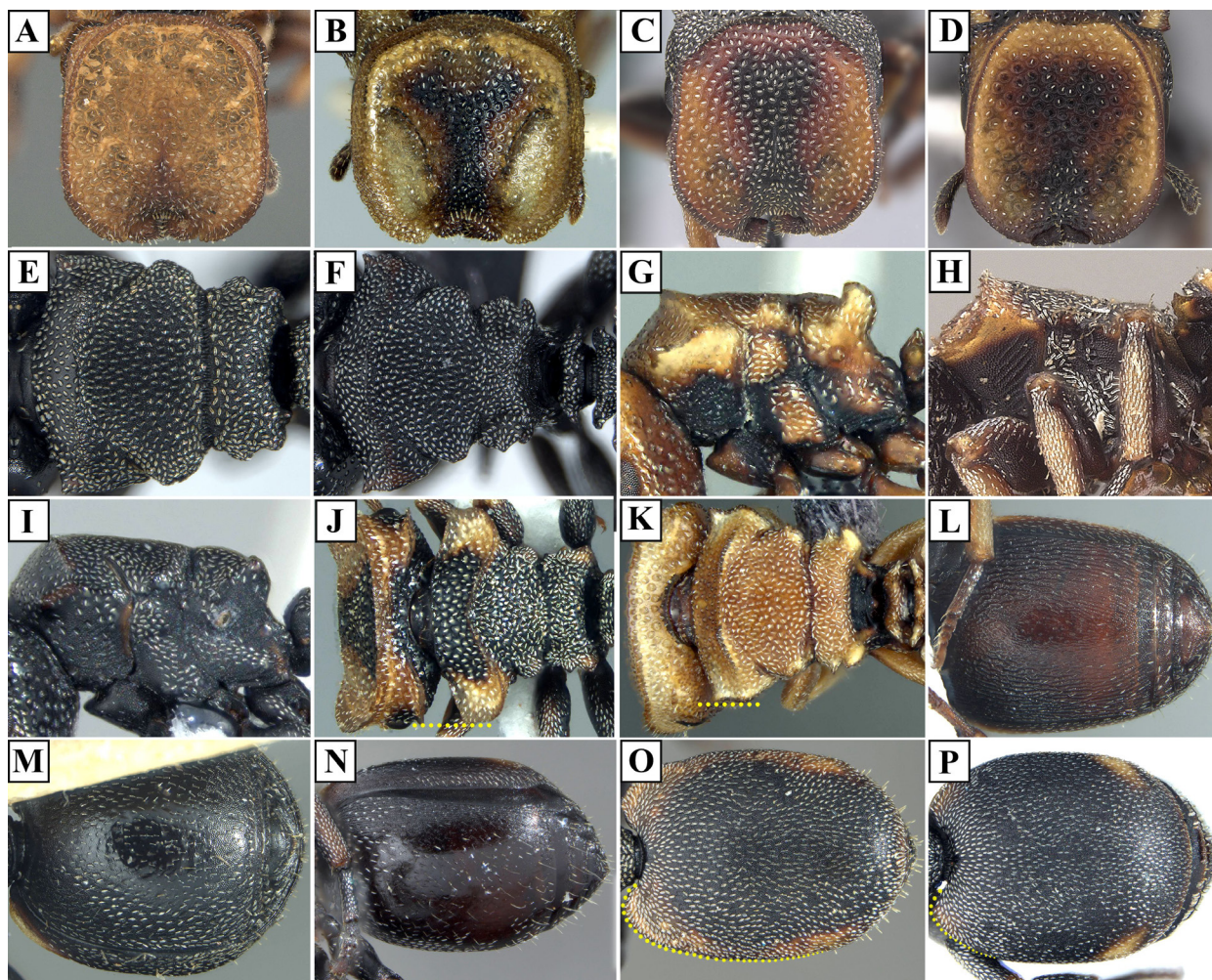


Figure 5 Soldiers of *angustus* group. A: *C. frigidus*. B: *C. goeldii*. C, F, M and O: *C. angustus* [C: CASENT0909276]. D: *C. targionii* [CASENT0922536]. E and I: *C. gabicamacho*. G and K: *C. adolphi*. H: *C. notatus* [CASENT0919600]. J: *C. goeldii*. L: *C. pallidicephalus*. N and P: *C. monicaulysea*.

Cephalotes adolphi

Figs. 6a-c, 7a-c, 15

Holotype: BRAZIL, MT, Coxipó, ix.1900, typus (worker), -15.614986, -56.030674 [MSNG] [examined by images - AntWeb.org CASENT0904906].

Additional material examined: Brazil, MG, Uberlândia, Clube de caça e pesca Itororó, 20.vii.2007, -19.004404 -48.312329, S. Powell cols, Cerrado, / C05-192 (1 soldier) [DZUP], Panga Ecological Reserve, 10.vii.2015, -19.174260 - 48.400940, S. Powell cols, Cerrado, / C15-45 (2 soldiers) [DZUP], Panga Ecological Reserve, 10.vii.2015, -19.174260 - 48.400940, S. Powell col, Cerrado, / C15-45 (1 gyne) [DZUP].

Worker description can be found in De Andrade and Baroni Urbani, 1999, page 733.

Soldier measurements (N=3): HL 1.95-2.12; HW 1.72-1.88; EL 0.33-0.35; PW 1.52-1.76; WL 1.60-1.69; PTL 0.64-0.72; PTW 0.20-0.24; PPL 0.70-0.76; PPW 0.20-0.26; GL 1.88-1.94; HBL 0.46-0.48; HBW 0.11-0.13; TL 6.85-7.16; CI 87.1-89.7; OI 18.6-20; PI 266-327; HBI 23.1-27.2.

Soldier (first description): Head, dorsum of mesosoma and legs yellowish to ferruginous. Propleura predominantly black with the upper surface yellowish; meso- and metapleura predominantly yellowish with dark spots. First gastral tergite yellowish with a transverse dark macula. First gastral sternite brownish (Fig. 6).

Mandibles alveolate; ventral face of head weakly foveate, space between foveae microalveolate; dorsum of head irregularly foveate (Fig. 6a). Dorsum of mesosoma foveate-microalveolate; lateral of mesosoma finely rugose with sparse foveae. Petiole and postpetiole smooth. Gaster microalveolate (Fig. 6c).

Mandibles with appressed canaliculate hairs and erect simple hairs. Head, mesosoma, petiole, postpetiole and legs with appressed canaliculate hairs; frontal carinae with erect simple hairs. Gaster with

appressed simple hairs; posterior portion of first sternite and edges of each tergite and sternite of gaster with erect simple hairs (Fig. 6b).

Head longer than wide (CI 87.1-89.7). Mandibles with a strong longitudinal lateral angle. Clypeus with a pair of denticles (Fig. 6a). Dorsum of head disc shaped, slightly convex anteriorly (Fig. 6b). Frontal carinae crenulate anteriorly. Antennae with a three-segmented club. Roof of antennal scrobes with a lateral carinae and a posterior rounded projection. Lateroventral margins of head without carinae. Vertexal corners forming pointed projections separated of the dorsum cephalic disc (Fig. 6a, b).

In lateral view, pronotum ascending, with a transversal carina raised in a crest; pronotal crest not crenulate, with a median depression (Fig. 6c). In dorsal view, anterior margin of pronotum gently rounded, lateral margins with two pairs of denticles, the anterior one acute, the second one obtuse. Mesonotum and propodeum discontinuous and flat (Fig. 6b); mesonotum with a pair of blunt rounded denticles; propodeal groove impressed; dorsal and declivous faces of propodeum meeting in a distinct propodeal angle; in dorsal view, lateral margins of propodeum with a pair of median spines and obtuse denticles strongly bent dorsally, with the apices curved anteriorly (Fig. 6b). Femora not angulated dorsally, mid, and hind basitarsi not flattened, with subparallel dorsal and ventral faces.

In dorsal view, petiole compressed anteroposteriorly, anterior margin with a discrete median concavity, lateral spines curved backwards, dorsum with a pair of denticles (Fig. 6b), subpetiolar process broader and rounded anteriorly (Fig. 6c). Postpetiole slightly wider and longer than petiole, spines narrow and curved forward, dorsum with a "v" shaped elevation (Fig. 6b), subpostpetiolar process pronounced ventrally and compressed anteroposteriorly (Fig. 6c).

Gaster elongate, with narrow anterior lamellar expansions (Fig. 6c).

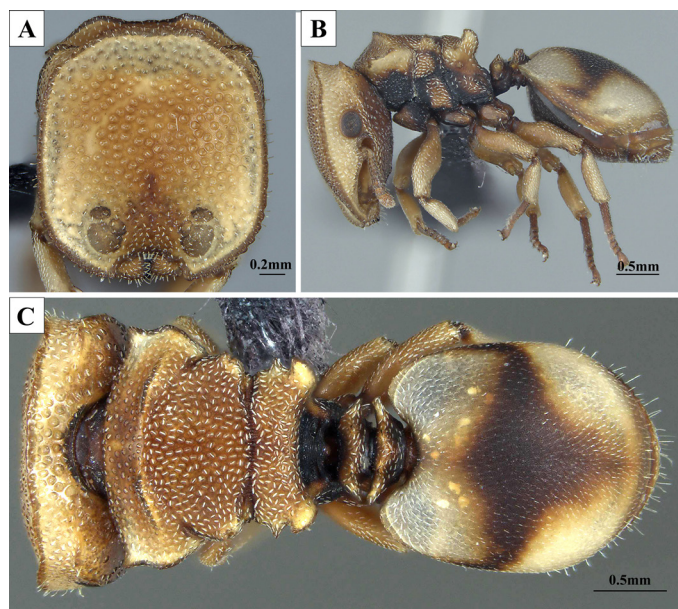


Figure 6 Soldier of *Cephalotes adolphi*. A: frontal view. B: lateral view. C: dorsal view. Brazil: MG, Uberlândia.

Gyne measurements (N=1): HL 1.80; HW 1.64; EL 0.40; PW 1.60; WL 2.05; PTL 0.60; PTW 0.28; PPL 0.70; PPW 0.30; GL 2.56; HBL 0.56; HBW 0.14; TL 7.71; CI 91.1; OI 24.4; PI 214; HBI 25.

Gyne (first description): Body black; dorsum and lateral of head, lateral margins of pronotum and propodeum, central disc of anepisternum, and legs yellowish to ferruginous. First gastral tergite with an anterior and a posterior pair of yellowish spots, each one occupying more than one third of the first tergite length; posterior margins of each tergite and sternite yellowish (Fig. 7).

Sculpture of head, petiole, postpetiole, legs and gaster as in the soldiers. Dorsum of mesosoma with sparse foveae, space between foveae microalveolate. Propleura deeply striate. Anepisternum deeply and densely foveate, without space between foveae; katepisternum and metapleura finely rugose with some sparse foveae (Fig. 7b). Declivous face of propodeum finely rugose and microalveolate.

Pilosity of head as in the soldier. Mesoscutum, axillae and legs with some short erect hairs. First gastral tergite with sparse appressed simple hairs and some short erect hairs; first gastral sternite with short and long appressed simple hairs, and short erect hairs (Fig. 7c)

Head as in the soldier, but shorter (HL 1.80) (Fig. 7a).

In dorsal view, anterior margin of pronotum slightly rounded, lateral margins with a pair of denticles pointed anteriorly, pronotal carina weakly developed, not crenulate, with a median depression (Fig. 7c). Dorsally, mesoscutum subtriangular, anterior margins rounded; notauli absent; parapsidial lines feebly visible and parallel; transscutal line impressed, reaching the lateral margins of mesosoma; scutoscuteellar groove impressed, extending laterally, separating scutellum and axillae; axillae rounded posteriorly (Fig. 7c). Laterally, mesopleural groove dividing anepisternum and katepisternum; metapleura divided in upper and lower metapleura by a deep groove; metapleuropropodeal groove not impressed (Fig. 7b). In dorsal view, posterior margin of propodeum concave with a pair of short, blunt denticles (Fig. 7c). Wings unknown.

In dorsal view, petiole subquadrate, anterior margin concave and lateral margins convex, without lateral or dorsal projections, subpetiolar process narrow. Postpetiole wider than petiole, with a “v” shaped dorsal elevation and lateral blunt projections, subpostpetiolar process pronounced ventrally and compressed anteroposteriorly (Fig. 7b).

Gaster with anteriorly protruding lobes (Fig. 7c).

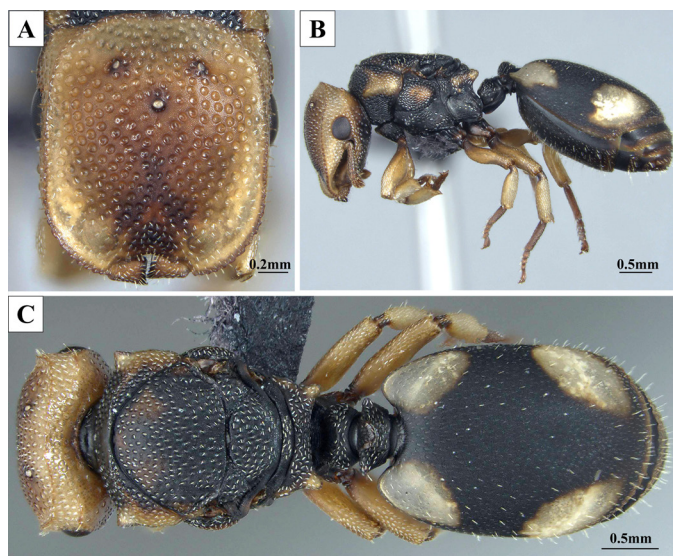


Figure 7 Gyne of *Cephalotes adolphi*. A: frontal view. B: lateral view. C: dorsal view. Brazil: MG, Uberlândia.

Cephalotes gabicamacho new species

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Figs. 8a-c, 9a-c, 10a-c, 15

Holotype: BRAZIL: MG, Uberlândia, Clube de Caça e Pesca Itororó, -19.00473 -48.31253, S. Powell col./C06-94, DZUP 550148 (worker) [DZUP].

Paratypes: same data as holotype: DZUP 550149 (2 workers), DZUP 550150 (1 worker, 1 soldier), DZUP 550151 (1 soldier, 1 gyne), DZUP 550152 (1 gyne) [DZUP], DZUP 550159 (1 worker, 1 soldier) [MZSP], DZUP 550157 (1 worker, 1 soldier) [USNM]; -19.00124 -48.31239, S. Powell col./C05-134, DZUP 550153 (3 workers), DZUP 550154 (2 soldiers) [DZUP], DZUP 550158 (1 worker, 1 soldier) [MZSP], DZUP 550156 (1 soldier) [USNM], DZUP 550163 (2 workers), DZUP 550162 (1 soldier) [INPA], DZUP 550161 (2 workers) DZUP 550160 (1 soldier) [MPEG], Paraopeba, iii.2011, C.R. Ribas, Cerrado, pitfall arbóreo [unique specimen identifier UFV-LABECOL-004439] (1 worker) [DZUP].

Diagnosis: A member of the *angustus* species group. In workers, propleura striate. First gastral sternite microalveolate, without striae (Fig. 4m). First gastral tergite anteriorly without striae, with abundant appressed canaliculate hairs, the distance between each hair shorter than their length, appressed simple hairs present on middle of tergite (Fig. 8c). In soldiers, in dorsal view, lateral margins of pronotum straight and subparallel (Fig. 9c). Propodeal groove strongly impressed, forming a depression (Fig. 9c).

Worker measurements (N=15): HL 0.95-1.20; HW 0.98-1.28; EL 0.30-0.34; PW 0.82-1.03; WL 1.10-1.24; PTL 0.18-0.23; PTW 0.53-0.60; PPL 0.22-0.25; PPW 0.54-0.63; GL 1.40-1.64; HBL 0.35-0.40; HBW 0.08-0.10; TL 3.85-4.46; CI 95.1-120; OI 24.9-31.6; PI 30-38.3; HBI 20-26.3.

Worker description: Body black; frontal lobes, anterior spots on gastral tergite, apices of each segment of legs, and external face of tibiae yellowish (Fig. 8).

Mandibles, legs and gaster microalveolate. Head, mesosoma, petiole and postpetiole foveate-microalveolate. Propleura totally striate. Declivous face of propodeum sparsely striate.

Body with appressed canaliculate hairs (Fig. 8c), more concentrated on meso- and metapleura. Mandibles and anterior margin of clypeus with suberect clavate and simple hairs (Fig. 8a). Declivous face of propodeum glabrous. First sternite of gaster with long erect simple hairs (Fig. 8b). Posterior edge of the gastral tergites with erect hairs.

Head slightly wider than long (CI 95.1-120), dorsum slight convex (Fig. 8b). Mandibles with weakly developed lateral angle. Anterior margin of clypeus concave, without lateral denticle. Frontal carinae notched anteriorly to eyes, not bent dorsally over eyes (Fig. 8c). Antennae with three-segmented club. Lateroventral margins of head with posterior carinae extending posteriorly to eyes until vertexal corners. Vertexal corners with narrow, irregular lamellar expansion (Fig. 8a).

Mesosoma weakly convex in lateral view (Fig. 8b). In dorsal view, lateral margins of pronotum with three denticles, anterior two acute, posterior broad and sometimes bifid, almost forming fourth denticle; promesonotal groove absent (Fig. 8c). Mesonotum with a pair of short denticles. Propodeal groove impressed only laterally. Dorsal and declivous faces of propodeum continuous, not meeting in a distinct propodeal angle; lateral margins of propodeum with variable number of denticles (Fig. 8c). Femora not angulated dorsally, mid and hind basitarsi not flattened, with subparallel dorsal and ventral faces.

In dorsal view, anterior margin of petiole concave, laterally with pair of spines (Fig. 8c), dorsum with a pair of tiny denticles (Fig. 8b), subpetiolar process broader anteriorly with narrow translucent lamellae (Fig. 9b). Postpetiole wider and longer than petiole (Fig. 8c), with a pair of spines curved backwards broader than spines of petiole, dorsum without carina or denticles (Fig. 8c), subpostpetiolar process pronounced and compressed anteroposteriorly (Fig. 8b).

Gaster suboval, deeply concave anteromedially, with broad anterior lamellar expansions, not extended posteriorly in a carina (Fig. 8c).

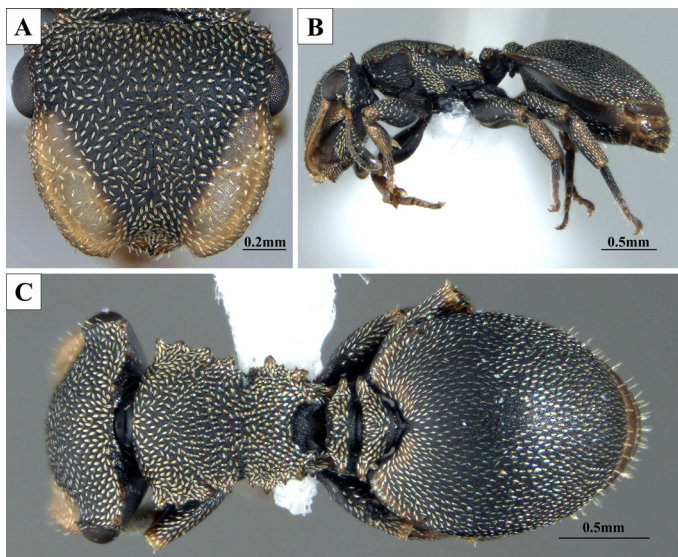


Figure 8 Worker of *Cephalotes gabicamacho*. A: frontal view. B: lateral view. C: dorsal view. Brazil: MG, Uberlândia.

Soldier measurements (N=10): HL 1.43-1.72; HW 1.15-1.58; EL 0.33-0.36; PW 1.18-1.48; WL 1.40-2.00; PTL 0.20-0.33; PTW 0.53-0.68; PPL 0.28-0.32; PPW 0.63-0.73; GL 1.72-2.06; HBL 0.36-0.42; HBW 0.10-0.12; TL 5.17-6.09; CI 77.1-98.2; OI 20.1-28.3; PI 34.4-50.8; HBI 23.8-31.6.

Soldier description: Body black; dorsum and lateral of head, apices of femora and external face of tibiae ferruginous. First gastral tergite with an anterior and a posterior pair of yellowish spots, each one occupying less than one third of the first tergite length; posterior margins of each tergite and sternite yellowish (Fig. 9).

Sculpturing as in the workers, except by propleura with striae not fully occupying the propleura, often on the lower part of the surface (Fig. 9b). Pilosity as in the workers, except by gaster, which has appressed simple hairs (Fig. 9b, c).

Head longer than wide (CI 77.1-98.2). Mandibles with a strong longitudinal lateral angle. Clypeus slightly concave without a pair of denticles (Fig. 9a). Dorsum of head disc shaped and slightly concave anteriorly. Frontal carinae crenulate anteriorly. Antennal club ill-defined. Roof of antennal scrobes with a lateral carinae and a posterior denticle (Fig. 9b). Lateroventral margins of head without carinae. Vertex corners forming pointed projections separated of the dorsum cephalic disc (Fig. 9a, b).

In lateral view, pronotum ascending, with a transversal carina not raised in a crest; pronotal carina weakly developed, not crenulate, medially interrupted (Fig. 9c). In dorsal view, anterior margin of pronotum gently rounded, lateral margins subparallel, with a pair of anterior denticles. Mesonotum and propodeum discontinuous and flat (Fig. 9b); mesonotum with a pair of blunt rounded projections; propodeal groove well impressed;

dorsal and declivous faces of propodeum meeting in a distinct propodeal angle (Fig. 9b); in dorsal view, lateral margins of propodeum with two pairs of projections, the anterior obtuse, the posterior acute, short, not curved anteriorly (Fig. 9b). Legs as in the worker.

In dorsal view, anterior margin of petiole slightly concave, laterally with a pair of spines curved backwards (Fig. 9c), dorsum with a pair of denticles (Fig. 9b), subpetiolar process broader anteriorly with an acute projection. Postpetiole wider and longer than petiole (Fig. 9c), with a pair of spines broader than spines of petiole and curved anteriorly, dorsum of postpetiole with a transversal elevation (Fig. 9c), subpostpetiolar process pronounced and compressed anteroposteriorly (Fig. 9b).

Gaster elongate, protruding anteriorly, without anterior lamellae or carinae (Fig. 9c).

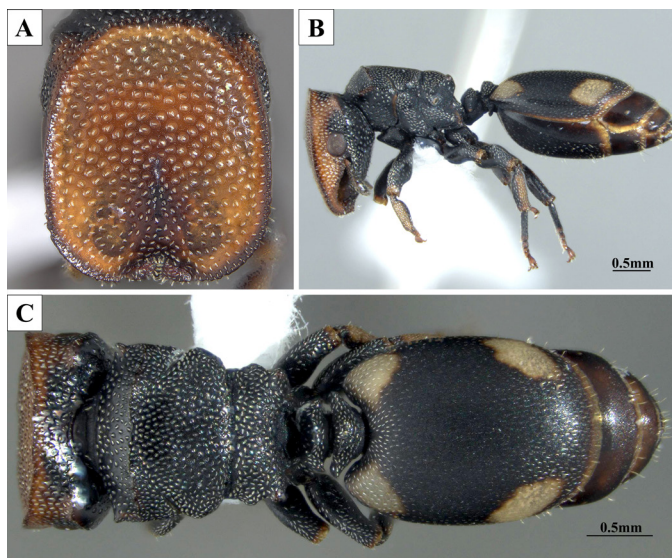


Figure 9 Soldier of *Cephalotes gabicamacho*. A: frontal view. B: lateral view. C: dorsal view. Brazil: MG, Uberlândia.

Gyne measurements (N=2): HL 1.32-1.40; HW 1.28-1.38; EL 0.32-0.35; PW 1.38-1.43; WL 1.85-1.88; PTL 0.33-0.34; PTW 0.48-0.50; PPL 0.35-0.38; PPW 0.63; GL 2.31-2.40; HBL 0.46-0.50; HBW 0.12; TL 6.20-6.36; CI 96.6-98.2; OI 25.1-25.4; PI 65-75.8; HBI 24.0-26.1.

Gyne description: Body black; head predominantly black, with the edges of dorsum and part of lateral face yellowish. Apices of femora, tarsi and external face of tibiae yellowish. First gastral tergite with an anterior and a posterior pair of yellowish spots, each one occupying about one fifth of the first tergite length; posterior margins of each tergite and sternite yellowish (Fig. 10).

Sculpturing and pilosity as in the soldiers, except by some erect hairs on mesoscutum and first tergite of gaster.

Head as in the soldier (CI 96.6-98.2), but with frontal carinae converging posteriorly (Fig. 10a).

In dorsal view, anterior margin of pronotum slightly rounded, narrower than in the soldiers, lateral margins with a pair of denticles pointed forwards, pronotal carina weakly developed (Fig. 10b). Dorsally, mesoscutum subtriangular, anterior margin rounded; notauli absent; parapsidial lines feebly visible and parallel; transscutal line weakly impressed, reaching the lateral margins of mesosoma; scutoscuteellar groove weakly impressed, arched; scutellum well delimited and broader anteriorly; axillae rounded posteriorly (Fig. 10c). Laterally, mesopleural groove dividing anepisternum and katepisternum; metapleura divided in upper metapleura and lower metapleura by a groove; metapleuropropodeal groove not impressed (Fig. 10b). In dorsal view, posterior margin of propodeum concave, with a pair of denticles (Fig. 10b). Wings as in genus description.

Petiole and postpetiole as in the soldier, but longer (Fig. 10b, c).

Gaster elongated, protruding anteriorly, without anterior lamellae or carinae (Fig. 10c).

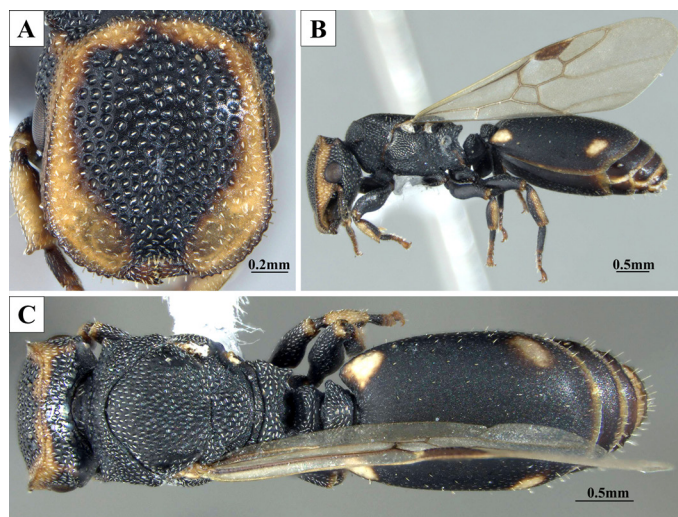


Figure 10 Gyne of *Cephalotes gabicamacho*. A: frontal view. B: lateral view. C: dorsal view. Brazil: MG, Uberlândia.

Comments: This species differs from *C. marycorn new species* and *C. monicaulysea new species* by the anterior portion of the first tergite of gaster, near of the postpetiolar insertion, not striate, while the two first species present short striae in this portion. Also, the first gastral tergite in *C. gabicamacho* is covered by appressed canaliculate hairs anteriorly and posteriorly, with a narrow central portion with appressed simple hairs, while *C. marycorn new species* has appressed canaliculate hairs only laterally on anterior portion and posterior edges of tergite, the central portion has sparse appressed simple hairs, and *C. monicaulysea new species* has abundant appressed canaliculate hairs evenly distributed over the tergite. *Cephalotes gabicamacho* is the species *C. sp. 3* in the molecular phylogenies of Price et al. (2014, 2016), where it is placed as sister to the clade containing all other members of the *angustus*, *fiebrigi* and *prodigious* groups and thus contributes to the paraphyly of the *angustus* group (Fig. 54).

Natural history: This species was collected in two cities of state of Minas Gerais, both in the core region of the Brazilian biome Cerrado, a savanna physiognomy. In Paraopeba, a single worker was collected in an arboreal pitfall trap, in a Cerrado area, at 750m a.s.l. In Uberlândia, the specimens were collected in two points at the Private Natural Heritage Reserve of Clube Caça e Pesca Itororó. This reserve is a 640 ha area, with Cerrado *sensu strictu* as predominant vegetation. This Cerrado physiognomy is characterized by tree canopies approximately 3-6 m high, annual average temperature between 18 and 24°C, and altitude 850 m a.s.l. Annual average precipitation is 1,700 mm, with two well-defined seasons, rainy summer (October to March) and dry winter (April to September) (Pinese et al., 2015). The colonies from the Reserve of Clube Caça e Pesca Itororó were discovered in April 2005 (paratype C05-134) and July 2006 (holotype C06-94), respectively, as part of a larger survey of *Cephalotes* diversity at the reserve (see Powell, 2008, 2016). In both cases, discovery occurred during a transect baiting approach, designed to maximize the discovery of *Cephalotes* forager recruitment (See Powell, 2008 for explanation). For each colony, all occupied nests were located using dense baiting within the home tree and visually tracking recruits back to their nest (following methods of Powell, 2009). Collections were made by sealing each nest in the early morning, when foragers are not active, and then removing the intact branches for dissection in the laboratory (following methods of

Powell, 2009). The colonies occupied six and eleven nests, respectively. The two colonies occupied different tree species, indicating no tree species preference. Nevertheless, nest entrance size was limited to sizes that closely fit a single soldier head (see data for *C. sp3* in Powell, 2016), characteristic of species with a disc-headed soldier morphology (Powell et al., 2020).

Distribution: Minas Gerais, Brazil.

Etymology: This species is named, in apposition, after the Brazilian myrmecologist Gabriela Procópio Camacho, for her important contribution to our current knowledge on Hymenoptera evolution, especially Ectatommine ants. Gabriela is a close friend of the three authors and her work and career trajectory have provided personal inspiration, as well as inspiring many other female myrmecologists.

Cephalotes marycorn new species

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Figs. 11a-c, 16

Holotype: BRAZIL: MG, Manga, Parque Estadual da Mata Seca, ix.2011, -14.84833 -43.96555, R. Garro & R. Antoniazzi cols. Dossel 15.5m, in *Myracrodruon urundeuva*, DZUP 550164 (worker) [DZUP].

Paratypes: same data as holotype, -14.84833 -43.96694, dossel 14m, DZUP 550169 (1 worker) [DZUP]; -14.84833 -43.98805, dossel 10.3m, DZUP 550165 (1 worker) [DZUP]; -14.84833 -43.98861, dossel 10.3m, DZUP 550168 (1 worker) [MZSP]; -14.84833 -43.98777, dossel 23m, DZUP 550167 (1 worker) [DZUP]; -14.848333 -43.965555, dossel 11.8, in *Handroanthus chrysotrichus*, DZUP 550166 (1 worker) [DZUP]; -14.848333 -43.98805, dossel 15.8, in *Handroanthus chrysotrichus* dossel 15.8m, DZUP 550170 (1 worker) [USNM].

Diagnosis: A member of *angustus* species group. Workers with incomplete striae on propleura. First sternite of gaster laterally striate. Anterior portion of first tergite of gaster, near to the postpetiolar insertion, with short striae and sparse appressed simple hairs, the distance between each hair longer than their length; appressed canaliculate hairs present only laterally on gastral anterior portion (Fig. 11).

Worker measurements (N=7): HL 0.98-1.08; HW 1.13-1.33; EL 0.28-0.32; PW 0.92-1.10; WL 0.90-1.16; PTL 0.18-0.21; PTW 0.50-0.57; PPL 0.21-0.25; PPW 0.53-0.60; GL 1.35-1.68; HBL 0.34-0.40; HBW 0.10; TL 4.10-4.34; CI 111-123; OI 23.8-25.5; PI 17.6-19.0; HBI 24.0-28.0.

Worker description: Body black; mandibles, frontal lobes, apices of femora, dorsal face of tibiae and tarsi yellowish to brownish (Fig. 11).

Mandibles, legs, gaster and declivous face of propodeum microalveolate. Head, mesosoma, petiole and postpetiole foveate-microalveolate. Propleura striate-microalveolate, striae not fully occupying the propleura. First tergite of gaster microalveolate with some anterior striae near of the postpetiole insertion; first sternite medially smooth and shiny, laterally striate-microalveolate.

Body with appressed canaliculate hairs (Fig. 11c). Mandibles and anterior margin of clypeus with suberect clavate and simple hairs (Fig. 11a). Declivous face of propodeum glabrous. First tergite of gaster with sparse appressed simple hairs, first sternite with short erect simple hairs (Fig. 11b). Some erect hairs present on the posterior edge of the gastral tergites.

Head wider than long (CI 111-123), dorsum slight convex (Fig. 11b). Mandibles with a weakly developed lateral angle. Anterior margin of clypeus concave without a pair of denticles. Frontal carinae sinuous anterior to the eyes, not bent dorsally over the eyes (Fig. 11c). Antennae

with a three-segmented club. Lateroventral margins of head with posterior carinae extending beyond the eyes until vertexal corners. Vertexal corners with a narrow, irregular lamellar expansion (Fig. 11a).

Mesosoma convex in lateral view (Fig. 11b). In dorsal view, lateral margins of pronotum with three denticles, the anterior two acute, the posterior broad and sometimes bifid, almost forming a fourth denticle; promesonotal groove absent (Fig. 11c). Mesonotum with a pair of short denticles. Propodeal groove impressed only laterally. Dorsal and declivous faces of propodeum continuous, not meeting in a distinct propodeal angle; lateral margins of propodeum with variable number of denticles (Fig. 11c). Femora not angulated dorsally, mid and hind basitarsi not flattened, with subparallel dorsal and ventral faces.

In dorsal view, anterior margin of petiole concave, laterally with a pair of spines (Fig. 11c), petiolar dorsum with a pair of tiny denticles (Fig. 11b), subpetiolar process broader anteriorly (Fig. 11b). Postpetiole wider and longer than petiole (Fig. 11c), with a pair of spines curved backwards, broader than the spines of petiole. Dorsum of postpetiole without carinae or denticles (Fig. 11c), subpostpetiolar process pronounced and compressed anteroposteriorly (Fig. 11b).

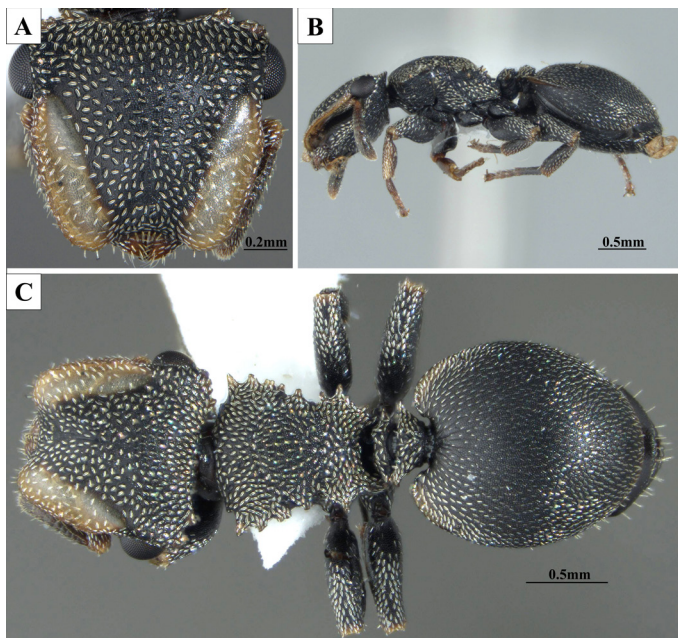


Figure 11 Worker of *Cephalotes marycorn*. A: frontal view. B: lateral view. C: dorsal view. Brazil: MG, Manga.

Gaster suboval, deeply concave anteromedially, with broad anterior lamellar expansions, not extending posteriorly in a carina (Fig. 11c).

Comments: This species differs from *C. gabicamacho* and *C. monicaulysea new species* by the anterior portion of the first tergite of gaster, near the postpetiolar insertion, which presents short striae and sparse appressed simple hairs, while in *C. gabicamacho* this portion is not striate and covered by abundant, appressed canaliculate hairs, and in *C. monicaulysea new species* this portion has short striae, but the hairs are canaliculate and evenly distributed.

Natural history: The only series of this species known so far was collected at the Parque Estadual da Mata Seca, an area of successional stages where had no anthropogenic intervention for at least 60 years. There are trees exceeding 20 m in height and fewer new trees and lianas when

compared with other adjacent areas at different levels of regeneration. That area is a transition zone between three Brazilian biomes: Cerrado and Caatinga (Brazilian savanna), and Mata Atlântica (Brazilian Atlantic Forest). That locality is at almost 500 m a.s.l., with average annual temperature of 25°C, and average annual precipitation of 818 mm, the rainiest months are November and April (Antoniuzzi et al., 2019).

Workers were sampled in arboreal pitfalls which contained water and soap, on the canopy of two tree species, between 10 and 23 meters. *Handroanthus chrysotrichus* (Mart. ex DC.) (Bignoniaceae), known as Golden trumpet tree (in Brazil, ipê), is found in open formation of Atlantic Forest, in dry forests, on top of hills, disturbed areas, associated with sandy soils, and is widely used as ornamental tree in urban areas (Bittencourt Junior and Moraes, 2010). This species presents extrafloral nectaries located on leaves (Gonzalez, 2013), which is highly attractive for ants, and *Cephalotes* genus are often sampled on these trees. *Myracrodruon urundeuva* Allemão (Anacardiaceae), known as Aroeira, has an ethnobotany role, as an important species for communities in northeastern Brazil, because of its use for medicinal, construction, fuel and forage purposes (Barros et al., 2016). However, precisely because of its importance for the community, this species was evaluated as one of the ten most priority for conservation, in comparison with almost 150 species with medicinal use endemic from Brazil (Campos and Albuquerque, 2020).

Distribution: Minas Gerais, Brazil.

Etymology: This species is named, in apposition, after Mary Lynne Corn, an early pioneer in the study of *Cephalotes* ants. Her dissertation on *Cephalotes atratus* from 1976 was groundbreaking in its detailed examination of *Cephalotes* biology. Her work represents as an essential contribution to our knowledge of this remarkable group of ants and stands as an inspiration to all students of *Cephalotes* biology.

Cephalotes monicaulysea new species

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Figs. 12a-c, 13a-c, 14a-c, 16

Holotype: BRAZIL: MG, Santana do Riacho, Serra do Cipó, 1267m, -19.294090 -43.587950, 25.vii.2018, S. Powell col., Campo rupestre (*Vellozia*) |C18-32, DZUP 550180 (worker) [DZUP].

Paratypes: same data as holotype: DZUP 550181 (2 workers, 1 soldier), DZUP 550182 (1 worker, 1 soldier, 1 gyne) [DZUP]; -19.29370 -43.588160, 13.viii.2017, DZUP 550186 (1 worker, 1 soldier) [MZSP]; 1258m, -19.294040 -43.587760, 17.vii.2019, S. Powell col. *Humiria balsamifera* |C19-27, DZUP 550183 (1 worker, 1 gyne), DZUP 550184 (1 worker) [DZUP], DZUP 550185 (1 worker, 1 gyne) [USNM].

Diagnosis: A member of *angustus* species group. Workers with incomplete striae on the propleura. First gastral tergite with short striae near of postpetiole insertion, and with evenly distributed appressed canaliculate hairs, without simple hairs (Fig. 12c). In soldiers, in dorsal view, lateral margins of pronotum convex and converging posteriorly (Fig. 13c). Propodeal groove weakly impressed, marked on the sides but absent medially (Fig. 13c). First sternite of the gaster with striae laterally (Fig. 5n).

Worker measurements (N=8): HL 0.85-1.20; HW 1.00-1.38; EL 0.30-0.38; PW 0.79-1.25; WL 0.93-1.35; PTL 0.17-0.24; PTW 0.46-0.60; PPL 0.17-0.28; PPW 0.49-0.66; GL 1.05-1.76; HBL 0.28-0.41; HBW 0.10-0.11; TL 3.43-4.77; CI 105-117; OI 25.2-36.0; PI 37.9-43.3; HBI 26.3-34.6.

Worker description: Body black; frontal lobe, vertexal lamellar expansions, apices of femora, tarsi, dorsal face of tibiae, and gastral lamellar expansions yellowish (Fig. 12).

Head, mesosoma, legs, petiole and postpetiole foveate-microalveolate. Propleura striate-microalveolate, striae not fully covering propleura. Propodeal declivity with some striae. First tergite of gaster microalveolate,

with some short striae in the anterior portion, near to the postpetiolar insertion; first sternite medially smooth and shiny, laterally striate-microalveolate (Fig. 12b, c).

Body with appressed canaliculate hairs (Fig. 12c), more concentrated on meso-, metapleura and anterior lamellar expansions of the gaster. Mandibles and anterior margin of clypeus with erect clavate and simple hairs (Fig. 12a). Declivous face of propodeum glabrous. First sternite of gaster with long erect simple hairs (Fig. 12b).

Head wider than long (CI 105-117), dorsum slightly convex (Fig. 12b). Mandibles with a weakly developed lateral angle. Anterior margin of clypeus concave with a pair of denticles. Frontal carinae sinuous to notched anteriorly the eyes, in frontal view (Fig. 12a), gently bent dorsally over the eyes, in posterior view (Fig. 12c). Antennae with three-segmented club. Lateroventral margins of head with posterior carinae extending posteriorly to vertexal corners, in lateral view. Vertexal corners with a narrow irregular lamellar expansion (Fig. 12a).

Mesosoma convex in lateral view (Fig. 12b). In dorsal view, lateral margins of pronotum with variable number of denticles, often three, the posterior one bifurcate or trifurcate; promesonotal groove absent (Fig. 12c). Mesonotum with a pair of short denticles. Propodeal groove impressed only laterally. Dorsal and declivous faces of propodeum continuous, not meeting in a distinct propodeal angle; lateral margins of propodeum with a pair of anterior denticles and row of minor denticles posteriorly near petiolar insertion (Fig. 12c). Femora not angulated dorsally, mid and hind basitarsi not flattened, with subparallel dorsal and ventral faces.

In dorsal view, anterior margin of petiole concave; lateral margin with posteriorly curved spine, dorsum with a pair of denticles, subpetiolar process in lateral view with an anterior angle (Fig. 12b). Postpetiole wider and longer than petiole (Fig. 12c), with lateral spines broader than petiolar spines and curved backwards, dorsum without carinae or denticles, subpostpetiolar process in lateral view pronounced and compressed anteroposteriorly (Fig. 12b).

Gaster suboval, deeply concave anteromedially with broad anterior anterolateral lamellar expansions, not extending posteriorly as a carina (Fig. 12c).

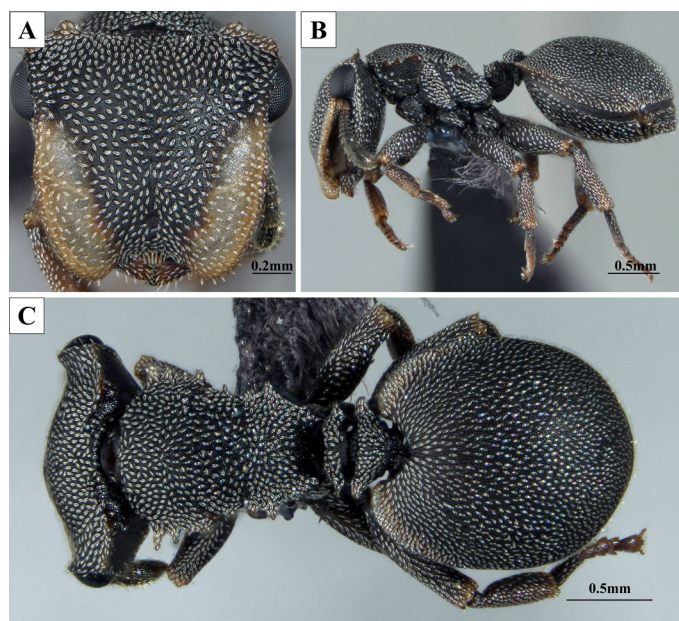


Figure 12 Worker of *Cephalotes monicaulyseae*. A: frontal view. B: lateral view. C: dorsal view. Brazil: MG, Santana do Riacho.

Soldier measurements (N=3): HL 1.80-2.00; HW 2.00-2.16; EL 0.40-0.43; PW 1.88-2.03; WL 1.73-2.00; PTL 0.30-0.35; PTW 0.73-0.80; PPL 0.33-0.38; PPW 0.80-0.88; GL 2.30-2.55; HBL 0.44-0.48; HBW 0.14-0.20; TL 5.76-7.28; CI 109-111; OI 19.7-20.0; PI 41.4-43.7; HBI 32.0-43.4.

Soldier description: Body mostly black; anterolateral face and edges of the dorsum of head ferruginous, only central portion of the cephalic disc black. Lateral margins of pronotum with ferruginous spots. Apices of femora, tarsi and dorsal face of tibiae ferruginous. First gastral tergite with an anterior and a posterior pair of weakly yellowish spots, each one occupying less than one fourth of the first tergite length (Fig. 13).

Sculpturing and pilosity as in workers, except by the presence of appressed simple hairs on the first tergite of gaster, and the erect short hairs on the posterior edge of the tergites and sternites (Fig. 13b).

Head slightly wider than longer (CI 106-111). Mandibles with strong longitudinal lateral angle. Clypeus slightly concave with a pair of denticles (Fig. 13a). Dorsum of head disc shaped and concave anteriorly. Frontal carinae crenulate anteriorly. Antennal club ill-defined. Roof of antennal scrobe with lateral carinae and posterior denticle. Lateroventral margin of head without carina. Vertexal corners forming pointed projections separated of the dorsum cephalic disc (Fig. 13a, b).

In lateral view, pronotum ascending, with a transversal carina not raised in a crest; pronotal carinae weakly developed, not crenulate (Fig. 13c). In dorsal view, anterior margin of pronotum gently rounded, lateral margins slightly concave and converging posteriorly, with anterolateral denticle. Mesonotum and propodeum continuous and flat (Fig. 13b); mesonotum with blunt rounded posterolateral projection; propodeal groove impressed only laterally; dorsal and declivous faces of propodeum meeting in a distinct propodeal angle; in dorsal view, lateral margin of propodeum with three projections, the anterior one obtuse, the median one broad and acute, the posterior one acute and long, with the apices curved anteriorly. Legs as in worker.

Petiole and postpetiole as in worker, except for the presence of a transverse elevation of dorsum of postpetiole.

Gaster elongated, with narrow anterior lamellae, not extending posteriorly as a carina (Fig. 13c).

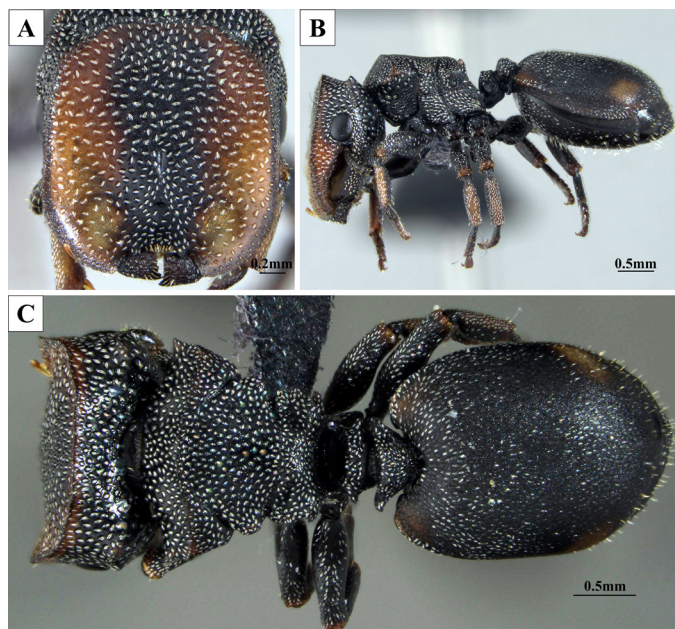


Figure 13 Soldier of *Cephalotes monicaulyseae*. A: frontal view. B: lateral view. C: dorsal view. Brazil: MG, Santana do Riacho.

Gyne measurements (N=3): HL 1.88-2.16; HW 1.88-1.96; EL 0.43-0.46; PW 1.80-1.88; WL 2.52-2.60; PTL 0.32-0.44; PTW 0.71-0.78; PPL 0.45-0.51; PPW 0.86-0.93; GL 0.33-0.36; HBL 0.56-0.58; HBW 0.15-0.17; TL 5.59-5.97; CI 90.7-101; OI 22.4-24.5; PI 44.1-61.6; HBI 26.1-31.2.

Gyne description: Color, sculpturing and pilosity as in soldiers, except for some erect hairs on mesoscutum (Fig. 14).

Head as in the soldier (CI 90.7-101), but longer (Fig. 14a).

In dorsal view, anterior margin of pronotum slightly rounded, narrower than in the soldiers, lateral margin with a pair of denticles pointed forward, pronotal carina weakly developed (Fig. 14c). Dorsally, mesoscutum subtriangular, anterior margin rounded; notauli absent; parapsidal line well developed and parallel; transscutal line impressed, reaching lateral margin of mesosoma; scutoscuteellar groove deeply impressed, arched, and scrobiculate; scutellum well delimited, broadest anteriorly; axillae rounded posteriorly (Fig. 14c). Laterally, mesopleural groove dividing anepisternum and katepisternum; metapleura divided in upper metapleura and lower metapleura by groove; metapleuropropodeal groove not impressed (Fig. 14b). In dorsal view, posterior margin of propodeum slightly concave with a pair of short denticles (Fig. 14b). Wings unknown.

Petiole and postpetiole as in the soldier, but longer (Figs. 14b, c).

Gaster elongated, anteriorly with narrow carinae, not extending posteriorly (Fig. 14c).

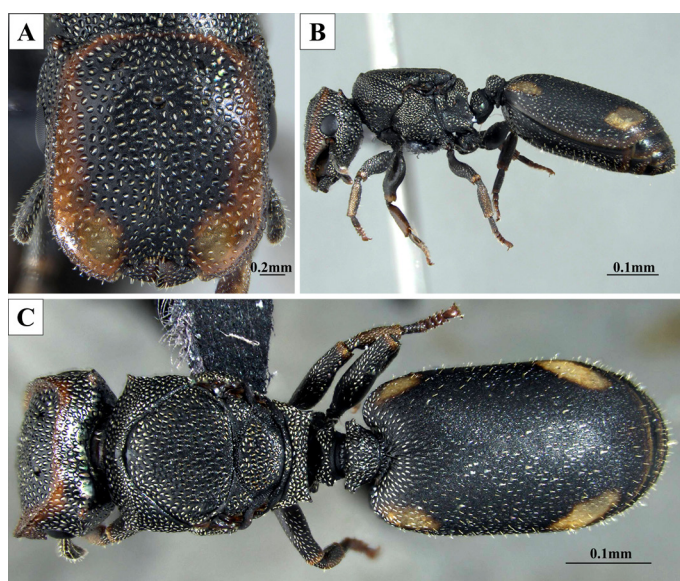


Figure 14 Gyne of *Cephalotes monicaulysea*. A: frontal view. B: lateral view. C: dorsal view. Brazil: MG, Santana do Riacho.

Comments: This species is very similar to *C. angustus*, differing by the presence of striae on the first sternite of gaster and the gastral anterior lamellae not extending posteriorly as a carina. *Cephalotes monicaulysea* differs from new species *C. marycorn* and

C. gabicamacho by the first tergite of gaster with abundant appressed canaliculate hairs evenly distributed. While *C. gabicamacho* has appressed canaliculate hairs anteriorly and posteriorly, with a narrow central portion with appressed simple hairs, and *C. marycorn* has appressed canaliculate hairs only laterally of anterior portion and posterior edge of tergite, the central portion has sparse appressed simple hairs.

Natural history: This species was collected at the same locality in three different years (2017, 2018 and 2019), at Serra do Cipó, the southern part of the mountainous system of Serra do Espinhaço, Minas Gerais state. The local climate is well-defined, with fresh and rainy summers and dry season, the annual average temperature is 18°C, and the annual average precipitation is 1,600 mm. The dominant vegetation of the region is the Cerrado, a Neotropical savanna (Callisto et al., 2001). The specimens were only collected in altitudes above 1200m, in a phytophysiognomy know as Campo Rupestre, despite targeted *Cephalotes* sampling at nearby locations at 1000m and 800m. Campo Rupestre is characterized by occurring exclusively on top of mountains, above 900m, with rocky outcrops, shallow soils, and vegetation herbaceous-shrubs (Vasconcelos, 2011). It has been inferred that 30% of the taxa occurring in campos rupestres are restricted to this formation (Lousada et al., 2011). The larger colony collection (C18-32) was taken from four nests in the thicker basal stems of a *Vellozia* Vand. plant, a shrub typical of Campo Rupestres, occurring between 1000 and 2000 m a.s.l. (Lousada et al., 2011). This colony was discovered initially with baiting, and subsequent baiting across *Vellozia* individuals showed that *Cephalotes monicaulysea* occupied most plants of this species within the vegetation patch. Viable populations of *Cephalotes monicaulysea* may then be highly dependent on *Vellozia* at this altitude. Nevertheless, the second collection, a small incipient colony (C19-27), was made inadvertently when opening dead stems of a *Humiria balsamifera* Aubl. (Humiriaceae) tree within the same vegetation patch as C18-32. Additionally, a large reproductively mature colony of *Cephalotes monicaulysea* was also collected from dead stems of a *Vochysia thyrsoidea* Pohl. (Vochysiaceae) tree in the same patch. This indicates that despite the high density of this *Cephalotes monicaulysea* in *Vellozia* plants, it is not indicative of an obligate ant-plant relationship. Nevertheless, the discovery of this high-density population at 1200m a.s.l. and not at lower elevations does suggest that *C. monicaulysea* may be restricted to high altitude in Campos Rupestres.

Distribution: Minas Gerais, Brazil.

Etymology: This species is named, in apposition, after Mônica Antunes Ulysséa, a Brazilian myrmecologist, poetess, activist, and agroecologist, for her contribution to the knowledge of Neotropical ants, especially the taxonomy of Myrmicinae. Besides being a great friend, Mônica's protagonism in academic feminism has been an inspiration for contemporary and future generations of female myrmecologists.

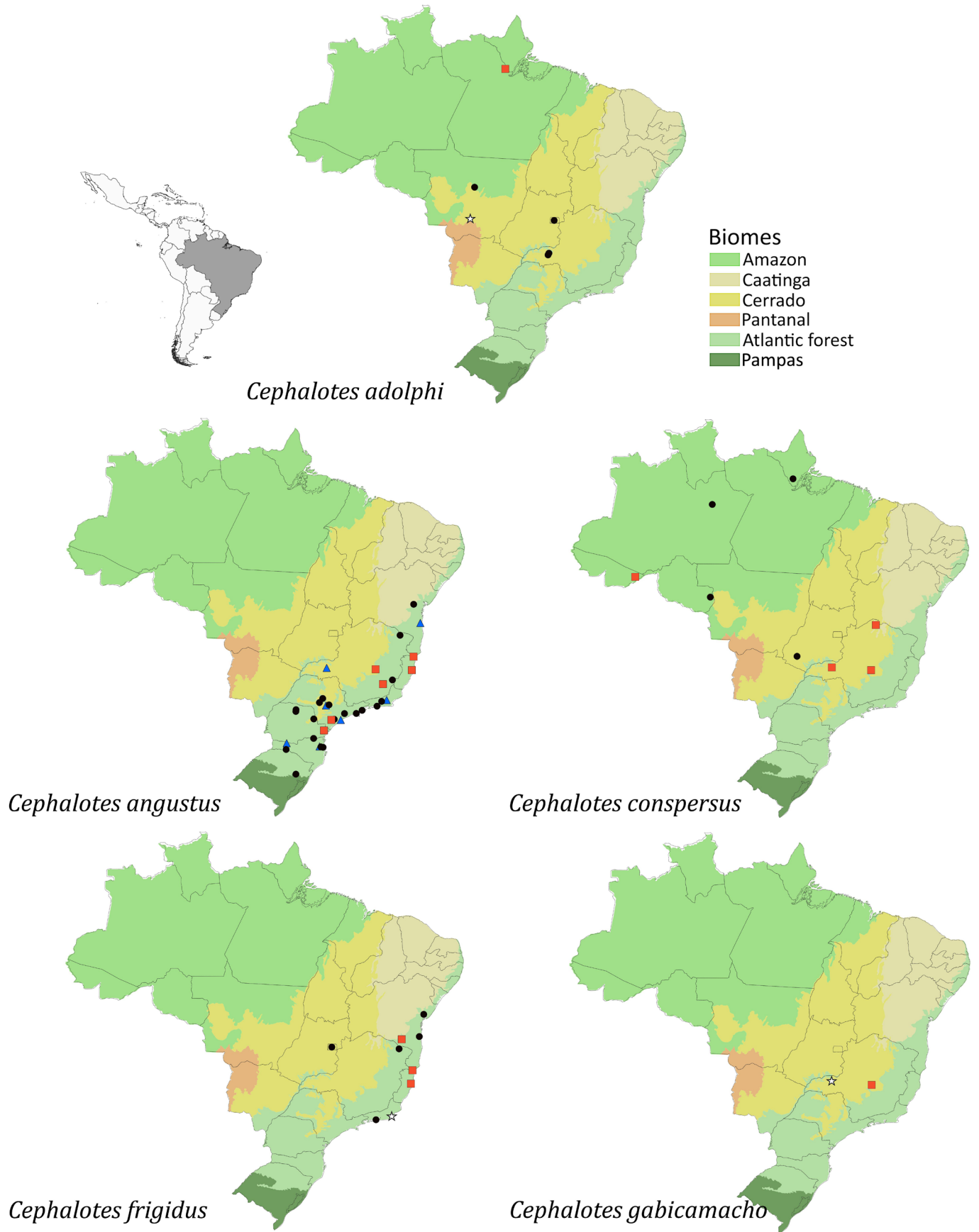


Figure 15 Distribution maps of *angustus* group in Brazil "part 1". White stars: type locality. Black circles: material examined. Red squares: new records. Blue triangles: records not examined from literature. (Literature source: 4, 13, 30).

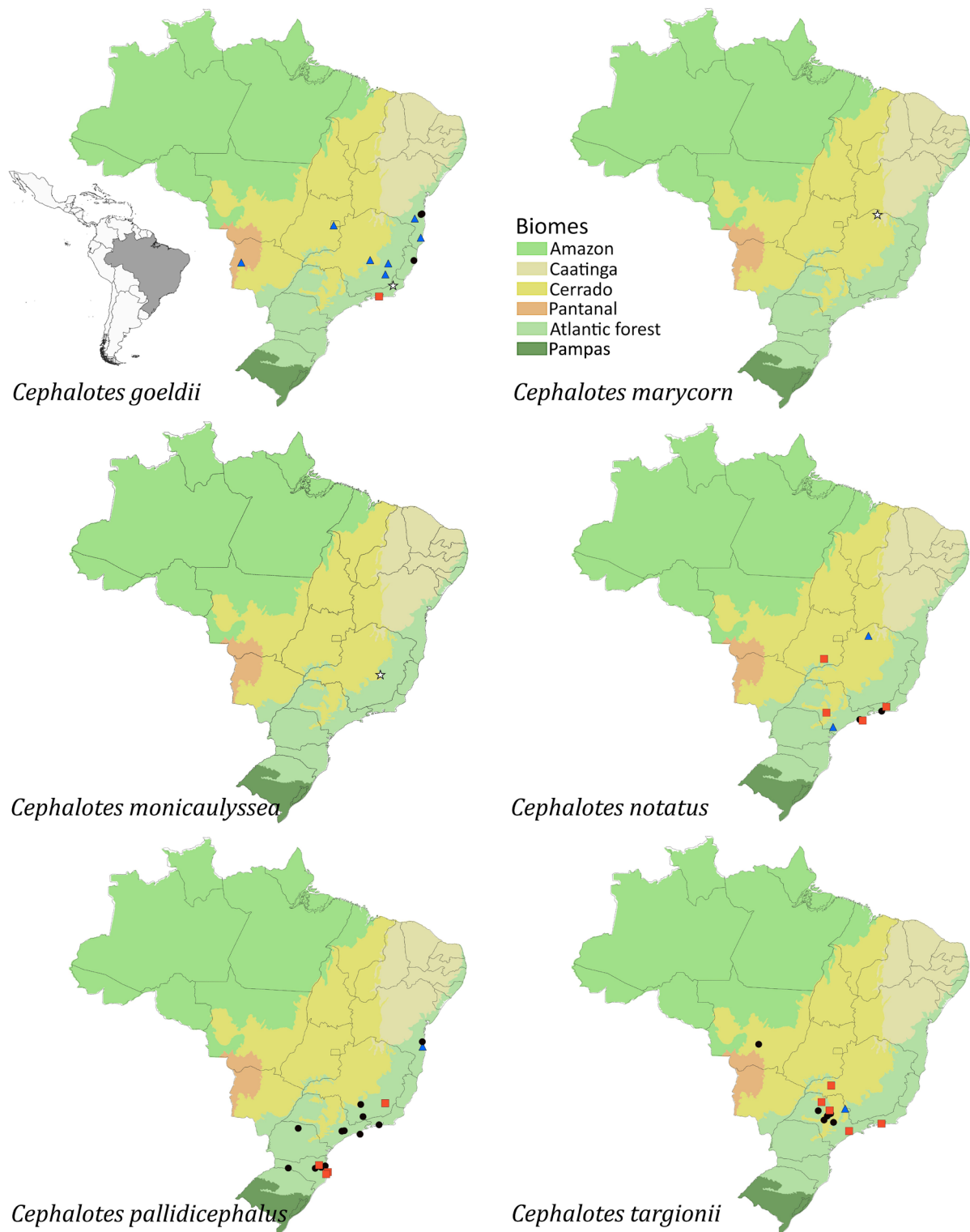


Figure 16 Distribution maps of *angustus* group in Brazil "part 2". White stars: type locality. Black circles: material examined. Red squares: new records. Blue triangles: records not examined from literature. (Literature source: 13, 14, 40, 47 48, 49, 56, 64).

The *atratus* species group

(Figs. 17, 18)

The *atratus* group was proposed for the first time by De Andrade and Baroni Urbani (1999). Before that, the species *C. alfaro*, *C. atratus* and *C. serraticeps* belonged to the genus *Cephalotes*, while the species *C. oculatus*, *C. opacus* and *C. placidus* belonged to the genus *Eucryptocerus*. The species *C. alfaro* was not included in this study since it does not

occur in Brazil. In the morphological phylogeny by De Andrade and Baroni Urbani (1999, see their Fig. 24), the Central American *hamulus* group is the sister group of all other groups in *Cephalotes*, followed by the *atratus* group. In the recent molecular phylogenies (Price et al., 2014, 2016, see their Fig. S3) this relationship is inverse, and the *atratus* group is the sister-most group in the topology (Fig. 54). The *atratus* and *hamulus* groups share the absence of the soldier caste in some species

of *atratus* and all species of *hamulus*. The species *C. alfaroi*, *C. opacus*, and *C. serraticeps* have known soldiers, while the species *C. atratus*, *C. oculatus*, and *C. placidus* do not have soldiers, as far as we know. Of these, large colony series of *C. atratus* have revealed that while this species certainly lacks morphologically differentiated soldiers and any pronounced allometric morphological scaling, the worker caste is highly variable in size within mature colonies (Corn, 1980). This species is broadly distributed, and frequently collected (Fig. 18), and is the second most common species of the genus in Brazil, after *C. pusillus*. The other species without soldiers are not highly variable in size, and their distribution is more restricted (Amazon/Atlantic Forest (Fig. 18)).

Diagnosis: In workers and soldiers vertexal corners of head, in lateral view, with a pair of spines (Fig. 2a). Pronotum always with a pair of long dorsolateral spines; a pair of short median spines can be present in some species, sometimes weakly developed. Postoccipital carinae with ventral expansions (Fig. 17a-b).

Brazilian species of *atratus* group

Cephalotes atratus (Linnaeus, 1758)

Obsolete combinations: *Cryptocerus atratus*, *Formica atrata* = *Cephalotes atratus crassispina* Santschi, 1920
= *Cephalotes atratus erectus* Kempf, 1951
= *Cephalotes atratus nitidiventris* Santschi, 1920
= *Cephalotes atratus quadridens* (De Geer, 1773)

Obsolete combinations: *Cephalotes quadridens*, *Formica quadridens*

= *Cephalotes atratus rufiventris* (Emery, 1894)

Obsolete combination: *Cryptocerus atratus rufiventris*

= *Cephalotes dubitatus* (Smith, 1853)

Obsolete combination: *Cryptocerus dubitatus*

= *Cephalotes marginatus* (Fabricius, 1804) **new synonym**

Obsolete combination: *Cryptocerus marginatus*

Cephalotes oculatus (Spinola, 1851)

Obsolete combination: *Cryptocerus oculatus*

= *Cephalotes aethiops* (Smith, 1853)

Obsolete combination: *Cryptocerus aethiops*

Cephalotes opacus Santschi, 1920

= *Cephalotes abdominalis* Santschi, 1929

Cephalotes placidus (Smith, 1860)

Obsolete combination: *Cryptocerus placidus*

= *Cephalotes fenestralis* (Smith, 1876)

Obsolete combination: *Cryptocerus fenestralis*.

Cephalotes serraticeps (Smith, 1858)

Obsolete combination: *Cryptocerus serraticeps*

Note: The synapomorphies so far accepted for *C. marginatus* include abundant suberect pilosity on the first gastral sternite, instead of sparse as in *C. atratus*, and median pronotal spines at least with $\frac{1}{4}$ of the size of the dorsolateral ones, instead of minute or absent as in *C. atratus* (De Andrade and Baroni Urbani, 1999).

Cephalotes marginatus was described by Fabricius (1804), synonymized under *C. atratus* by Klug (1824), and then revived by De Andrade and Baroni Urbani (1999). In the latter study, the species *C. decemspinus* Santschi, 1920 was synonymized under *C. marginatus*. Kempf (1951) has already argued that the status of this species should be changed, as there were individuals in series of *C. atratus* with the same characteristics of *C. decemspinus*.

After a careful examination of both species based on specimens from a wide range of distribution, we found great variation of the putative synapomorphic characters of *C. marginatus* among samples of *C. atratus*. *Cephalotes marginatus* is known only for the Amazonian arch in South America, while *C. atratus* is widely distributed from Mexico to north of Argentina and is one of the most commonly sampled species of *Cephalotes*.

Therefore, considering morphological and geographic evidence, we here propose the synonymy of *C. marginatus* under *C. atratus*.

Key to the identification of Brazilian species of the *atratus* group of *Cephalotes* based on workers and soldiers

- (Figs. 17a-g)
- 1 In lateral view, eyes positioned ventrally to the antennal scrobes (Fig. 17a).....2
 - 1' In lateral view, eyes positioned posteriorly the antennal scrobes (Fig. 17b).....3
 - 2 Body shiny. In lateral view, postpetiolar dorsal spines shorter than the subpostpetiolar process (Fig. 17d).....*C. atratus*
 - 2' Body opaque. In lateral view, postpetiolar dorsal spines longer than the subpostpetiolar process (Fig. 17e).....*C. serraticeps*
 - 3 In dorso-oblique view, dorsal and lateral faces of mesonotum and propodeum meeting in a carina, not necessarily extending to the propodeal spines (Fig. 17f).....*C. oculatus*
 - 3' In dorso-oblique view, dorsal and lateral faces of mesonotum and propodeum continuous, without carina (Fig. 17g).....4
 - 4 Propodeal spines shorter than the declivous face of propodeum (Fig. 17c).....*C. opacus*
 - 4' Propodeal spines longer than the declivous face of propodeum (Fig. 17d, e).....*C. placidus*

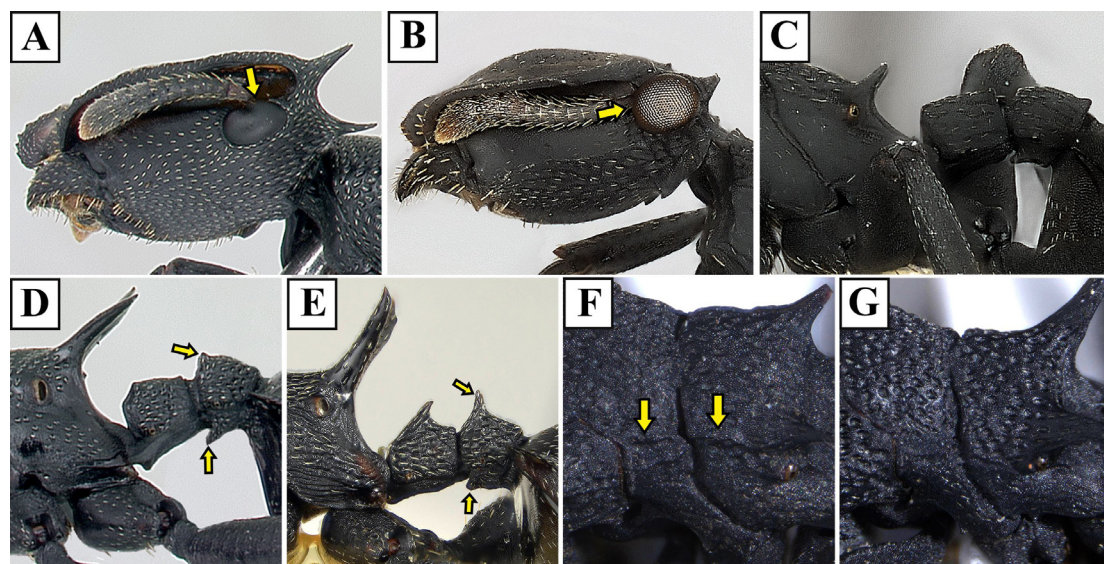


Figure 17 Workers of *atratus* group. A and D: *C. atratus* [CASENT0178627]. B and C: *C. opacus* [CASENT0217839]. E: *C. serraticeps*. F: *C. oculatus*. G: *C. placidus*.

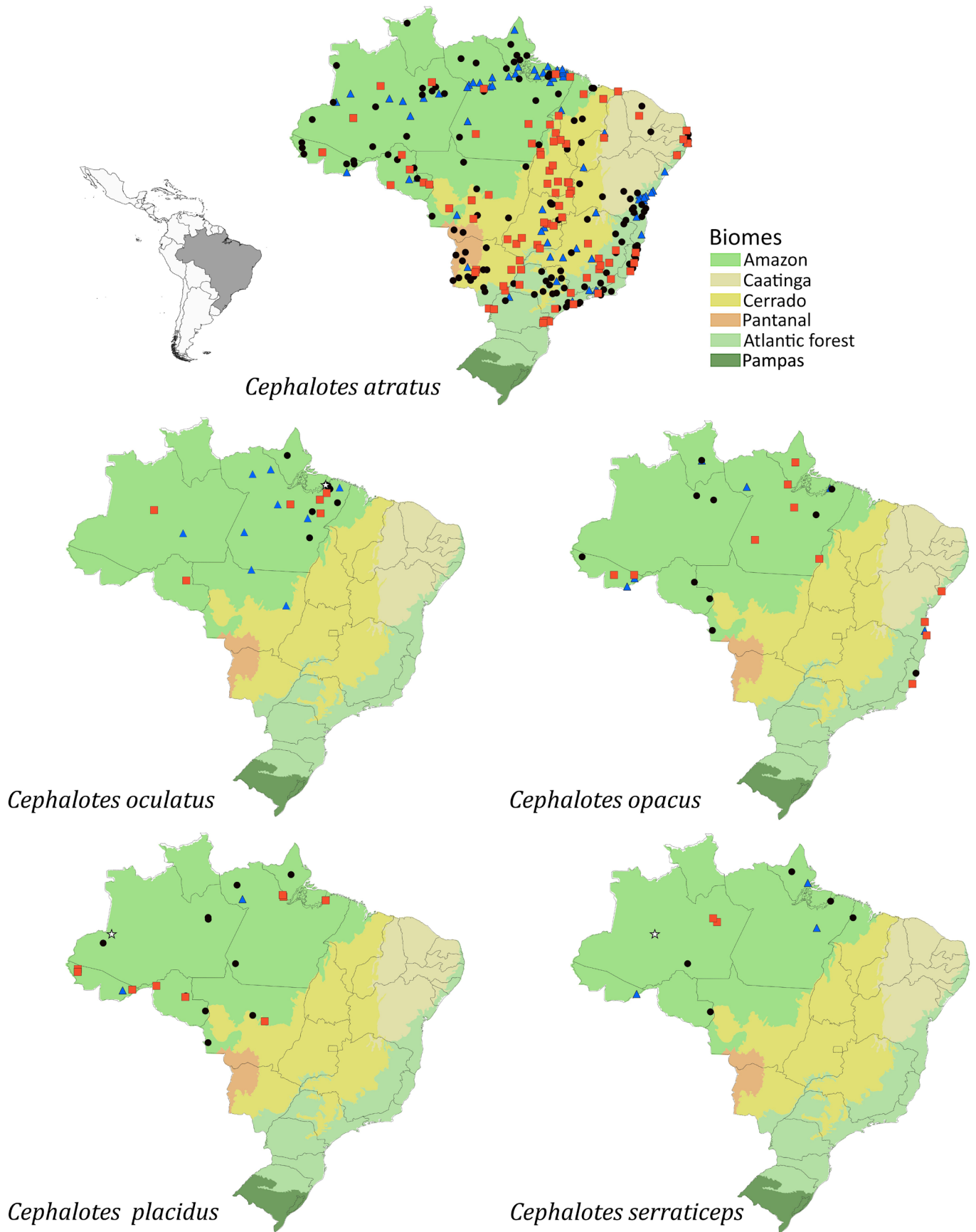


Figure 18 Distribution maps of *atratus* group in Brazil. White stars: type locality. Black circles: material examined. Red squares: new records. Blue triangles: records not examined from literature. (Literature source: 1, 4, 5, 8, 11, 13, 22, 23, 34, 36, 37, 42, 43, 49, 51, 52, 54, 57, 61, 63, 68, 69, 71, 72, 75).

The *basalis* species group

(Figs. 19, 20, 21)

The *basalis* group of De Andrade and Baroni Urbani (1999) includes the *complanatus* group of *Paracryptoceus* by Kempf (1951) (*C. complanatus*, *C. cordiae*, *C. ramiphilus*), and two isolated species, *C. basalis* and *C. manni*. Additionally, there are five other species that do not occur in Brazil (*C. brevispineus*, *C. cordiventris*, *C. femoralis*, *C. inca* and *C. mompox*). *Cephalotes manni* is morphologically very distinct and can be easily separated from all other species in the group, by the combination of dentiform lamellar expansions on pronotum, declivous face of propodeum and anterior face of petiole concave, apices of anterior lamellar expansion of gaster near to postpetiole insertion, and median dorsal projection on hind femora absent. Thus, we transfer *C. manni* to the monotypic *manni* species group, proposed here as discussed in its respective section.

According to the molecular phylogeny (Price et al., 2016, see their Fig. S3), *basalis* group forms a clade with the exclusively North and Central American *multispinosus*, *wheeleri* and *texanus* species groups. All species of *basalis* group recorded for Brazil occur only in the North and Midwest regions (Fig. 21).

Diagnosis: In workers and soldiers, margin of pronotum with lamellar expansions, without denticles or spines. Declivous face of propodeum and anterior face of petiole truncate (Fig. 19c-d). Hind femora with a median projection dorsally (Fig. 2j). In dorsal view, the anterior lamellar expansions of the gaster with apices distally directed in relation to the postpetiole insertion.

Brazilian species of *basalis* group

Cephalotes basalis (Smith, 1876)

Obsolete combination: *Cryptoceus basalis*

= *Cephalotes multispinus* (Emery, 1890)

Obsolete combinations: *Cryptoceus cordatus multispinus*,
Cryptoceus multispinus

Cephalotes complanatus (Guérin-Méneville, 1844)

Obsolete combination: *Cryptoceus complanatus*

= *Cephalotes angulatus* (Smith, 1858)

Obsolete combination: *Cryptoceus angulatus*

= *Cephalotes multispinus amazonensis* (Forel, 1911)

Obsolete combination: *Cryptoceus multispinus amazonensis*

Cephalotes cordiae (Stitz, 1913)

Obsolete combination: *Cryptoceus cordiae*

Cephalotes ramiphilus (Forel, 1904)

Obsolete combination: *Cryptoceus complanatus ramiphilus*

Key to the identification of Brazilian species of the *basalis* group of *Cephalotes* based on workers

(Figs. 19a-f)

- 1 In dorsal view, propodeum with one pair of spines (Fig. 19c).....*C. cordiae*
- 1' In dorsal view, propodeum with two or more pairs of spines (Fig. 19d).....2
- 2 In dorsal view, frontal carinae upturned dorsally above the eyes (Fig. 19a).....*C. basalis*
- 2' In dorsal view, frontal carinae not upturned dorsally above the eyes (Fig. 19b).....4
- 3 Declivous face of propodeum finely striate (Fig. 19e).....*C. ramiphilus*
- 3' Declivous face of propodeum microalveolate, never striate (Fig. 19f).....*C. complanatus*

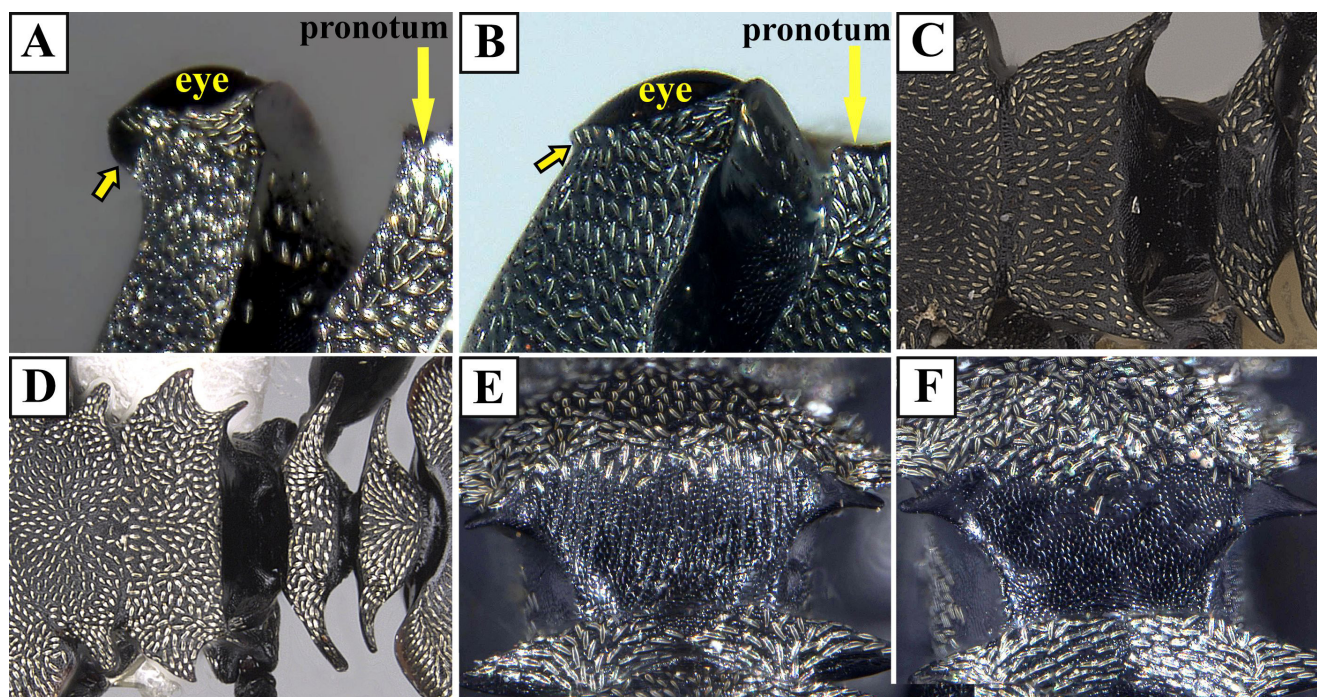


Figure 19 Workers of *basalis* group. A, D and F: *C. complanatus* [D: CASENT0922595]. B: *C. basalis*. C: *C. cordiae* [CASENT0919596]. E: *C. ramiphilus*.

Key to the identification of Brazilian species of the *basalis* group of *Cephalotes* based on soldiers

(Figs. 20a-g)

- 1 In dorsal view, propodeal spines longer than petiolar spines (Fig. 20a).....***C. cordiae***
- 1' In dorsal view, propodeal spines shorter than petiolar spines (Fig. 20b, c).....2

- 2 In dorsal view, gaster without translucent lamellar anterior expansions (Fig. 20d).....***C. complanatus***
- 2' In dorsal view, gaster with translucent lamellar anterior expansions (Fig. 20e).....3
- 3 Metapleura with more than 30 hairs (Fig. 20f).....***C. basalis***
- 3' Metapleura with less than 15 hairs (Fig. 20g).....***C. ramiphilus***

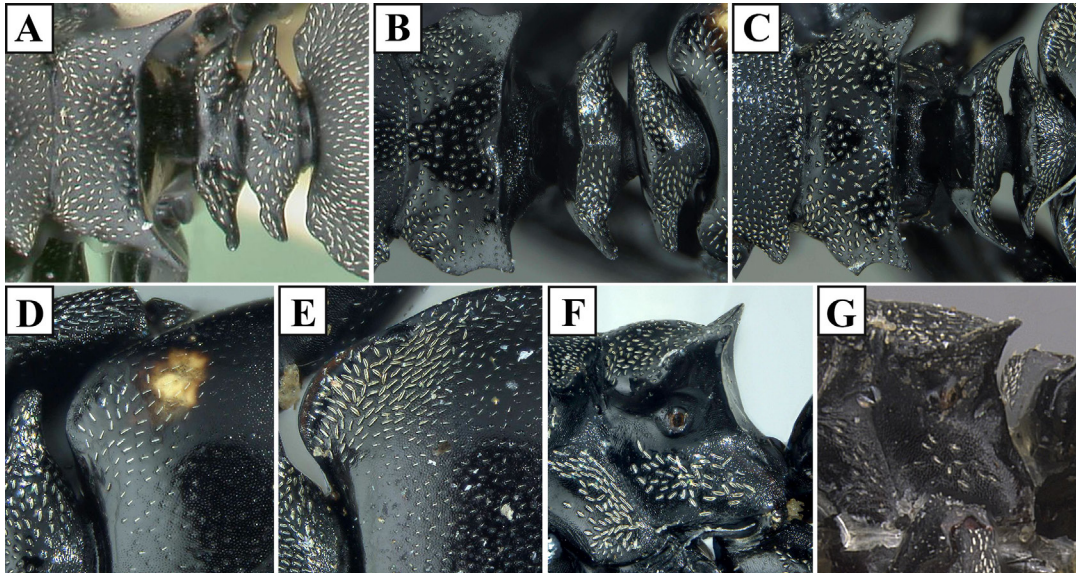


Figure 20 Soldiers of *basalis* group. A: *C. cordiae* [FOCOL2143]. B and D: *C. complanatus*. C, E and F: *C. basalis*. G: *C. ramiphilus* [CASENT0909261].

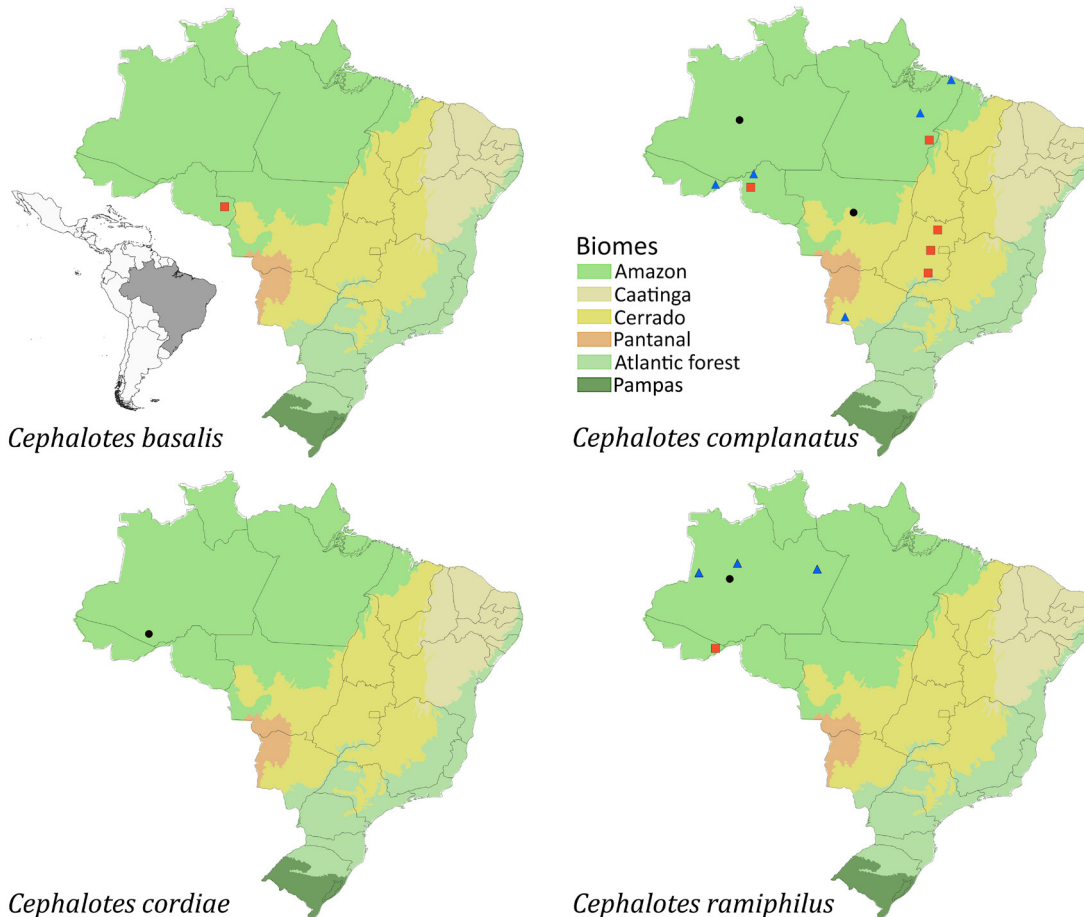


Figure 21 Distribution maps of *basalis* group in Brazil. Black circles: material examined. Red squares: new records. Blue triangles: records not examined from literature. (Literature source: 12, 13, 72).

The *clypeatus* species group

(Figs. 22, 23)

The *clypeatus* group was proposed by De Andrade and Baroni Urbani (1999) to include three species from the former genus *Zacryptocerus*. The authors stated that the diagnostic characters of this group (triangular vertexal angles, and pronotal and propodeal spines fused by lamella) could indeed be enough to keep them in a separated genus from *Cephalotes*. However, this would render *Cephalotes* paraphyletic since the phylogeny shows this group as a clade within the genus *Cephalotes* (Fig. 54). All species in this group are exclusively South American.

Diagnosis: In workers and soldiers, pronotal and propodeal spines fused by lamellae (Fig. 2o). Gaster surrounded by a lamella (Fig. 22).

Brazilian species of *clypeatus* group

***Cephalotes clypeatus* (Fabricius, 1804)**

Obsolete combination: *Cryptocerus clypeatus*

***Cephalotes membranaceus* (Klug, 1824)**

Obsolete combination: *Cryptocerus membranaceus*
= *Cephalotes fervidus* (Smith, 1876)

Obsolete combination: *Cryptocerus fervidus*

***Cephalotes ustus* (Kempf, 1973)**

Obsolete combination: *Zacryptocerus ustus*

Key to the identification of Brazilian species of the *clypeatus* group of *Cephalotes* based on workers and soldiers

(Figs. 22a-c)

- 1 In dorsal view, gaster smooth and shiny (Fig. 22a).....***C. clypeatus***
- 1' In dorsal view, gaster sculptured and opaque (Fig. 22b, c).....2
- 2 Gaster yellowish to brownish with sparse hairs (Fig. 22b).....***C. membranaceus***
- 2' Gaster black, with abundant hairs (Fig. 22c).....***C. ustus***



Figure 22 Workers and soldiers of *clypeatus* group. A: *C. clypeatus* [CASENT0173669]. B: *C. membranaceus* [FOCOL2117]. C: *C. ustus*.

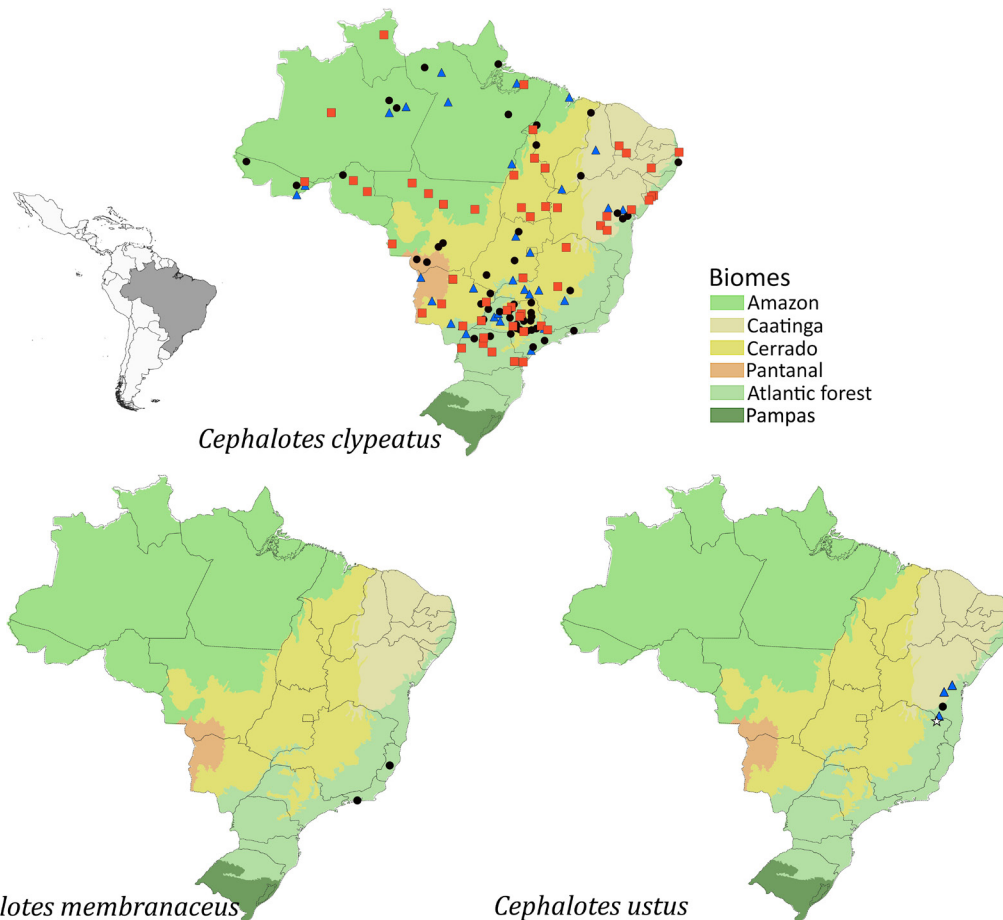


Figure 23 Distribution maps of *clypeatus* group in Brazil. White stars: type locality. Black circles: material examined. Red squares: new records. Blue triangles: records not examined from literature. (Literature source: 4, 12, 13, 15, 20, 34, 37, 45, 49, 61, 62, 63, 68, 71).

The *coffea* species group

(Fig. 24)

Kempf (1951) created the monotypic *coffea* subgroup, within the *angustus* group, in the subgenus *Harnedia* of the genus *Paracryptocerus*. De Andrade and Baroni Urbani (1999) raised this subgroup to a group of *Cephalotes*, adding *C. setulifer*, *C. peruviensis* and *C. trichophorus*. *Cephalotes trichophorus* occurs in Brazil and Peru; the other species occur in Central America and northwestern South America. The recent molecular phylogeny (Price et al., 2016, see their Fig. S3) recovered *coffea* as the sister group of the clade formed by *patei*, *emeryi* and *crenaticeps* groups, none of which occur in Brazil, but this collection of small clades was itself sister to the species rich *depressus* group which has numerous members throughout Brazil (Fig. 54).

Diagnosis: In workers, declivous and dorsal faces of propodeum continuous, not meeting at a distinct propodeal angle. Propodeum with two pairs of denticles, the posterior one longer than the anterior one, but never longer than the declivous face. Postpetiole wider than petiole. Gaster with a narrow anterior lamella; first tergite with erect hairs; first sternite with longitudinal striae.

Brazilian species of *coffea* group

Cephalotes trichophorus De Andrade, 1999

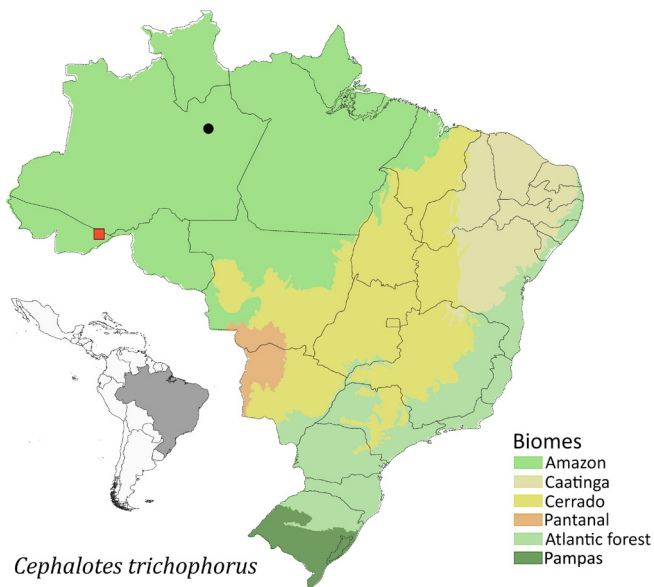


Figure 24 Distribution map of *coffea* group in Brazil. Black circle: material examined. Red square: new record.

The *depressus* species group

(Figs. 25, 26)

The *depressus* group is composed by the former *pavonii* group of *Paracryptocerus* by Kempf (1951), and the species *C. betoi* and *C. palustris*,

described by De Andrade in De Andrade and Baroni Urbani (1999). In the recent molecular phylogeny (Price et al., 2016, see their Fig. S3) this group is sister to the clade formed by *coffea*, *patei*, *emeryi* and *crenaticeps* groups. The majority of species in the *depressus* group occur in Brazil. *Cephalotes cristatus* is the only member that does not occur in Brazil.

Diagnosis: In workers and soldiers, dorsal and declivous face of propodeum continuous, not meeting in a distinct propodeal angle, with two pairs of spines, the anterior one longer than the posterior one (Fig. 25d-i).

Brazilian species of *depressus* group

Cephalotes betoi De Andrade, 1999

Cephalotes borgmeieri (Kempf, 1951)

Obsolete combination: *Paracryptocerus borgmeieri*

Cephalotes cordatus (Smith, 1853)

Obsolete combination: *Cryptocerus cordatus*

= *Cephalotes cordatus boliviensis* (Santschi, 1921)

Obsolete combination: *Cryptocerus cordatus boliviensis*

Cephalotes depressus (Klug, 1824)

Obsolete combination: *Cryptocerus depressus*

= *Cephalotes depressus sorocabensis* (Forel, 1912)

Obsolete combination: *Cryptocerus depressus sorocabensis*

Cephalotes eduarduli (Forel, 1921)

Obsolete combination: *Cryptocerus eduarduli*

Cephalotes palustris De Andrade, 1999

Cephalotes pavonii (Latreille, 1809)

Obsolete combination: *Cryptocerus pavonii*

Key to the identification of Brazilian species of the *depressus* group of *Cephalotes* based on workers and soldiers

(Figs. 25a-o)

- 1 In dorsal view, postpetiole at most twice wider than long (Fig. 25k).....*C. depressus*
- 1' In dorsal view, postpetiole three to five times wider than long (Fig. 25d-g, j, l, m).....2
- 2 Erect hairs present on mesosoma, petiole, postpetiole and gaster (Fig. 25n).....*C. eduarduli*
- 2' Erect hairs mostly absent, present only on the apices of spines (Fig. 25o)....3
- 3 In frontal view, color of the frontal lobes similar to the rest of the head (Fig. 25a). In dorsal view, posterior margins of petiolar spines weakly curved backwards (Fig. 25e - dotted).....*C. borgmeieri*
- 3' In frontal view, color of frontal lobes lighter than rest of the head (Fig. 25b, c). In dorsal view, posterior margins of petiolar spines strongly curved backwards (Fig. 25f, g, j, l, m - dotted).....4
- 4 In dorsal view, anterior and lateral margins of the petiole meeting in a distinct angle (Fig. 25g, m - line).....5
- 4' In dorsal view, anterior and lateral margins of the petiole continuously curved (Fig. 25e, f, j, l - line).....6
- 5 Posterior third of declivous face of propodeum striate (Fig. 25h).....*C. betoi*
- 5' Posterior third of declivous face of propodeum not striate; some striae can be present on propodeum, but not reaching the posterior third (Fig. 25i).....*C. pavonii*
- 6 In dorsal view, lateral expansions of pronotum subrectangular, followed by a shorter projection (Fig. 25d).....*C. palustris*
- 6' In dorsal view, lateral expansions of pronotum triangular (Fig. 25f).....*C. cordatus*

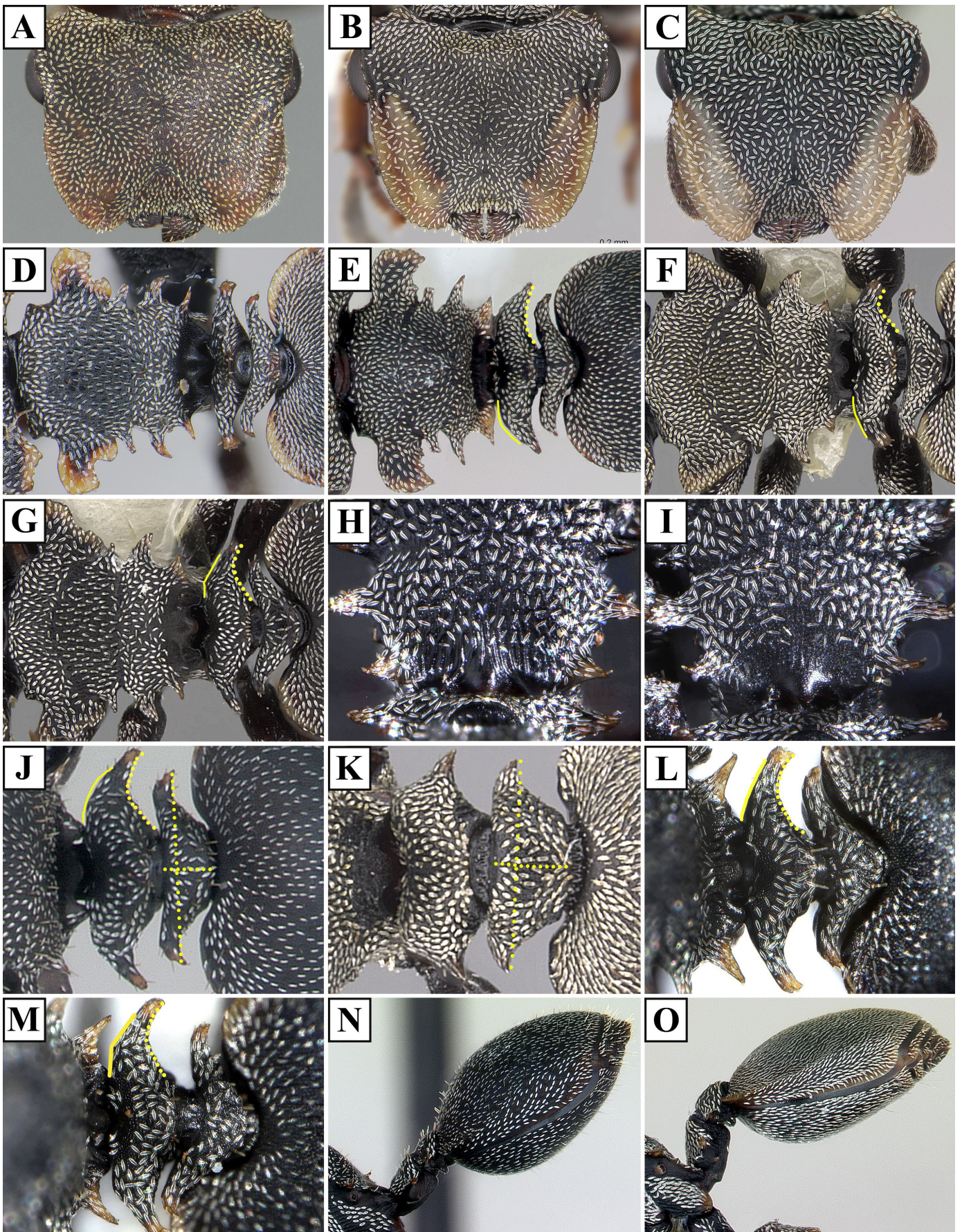


Figure 25 Workers and soldiers of *depressus* group. A and E: *C. borgmeieri* [E: CASENT0173665]. B and F: *C. cordatus* [CASENT0922596]. G, I and M: *C. pavonii* [G: CASENT0922611]. C, K and O: *C. depressus* [C, O: CASENT0173671, K: CASENT0909272]. D: *C. palustris* [UFV-LABECOL-004489]. H and L: *C. betoi*. J and N: *C. eduarduli* [CASENT0173676].

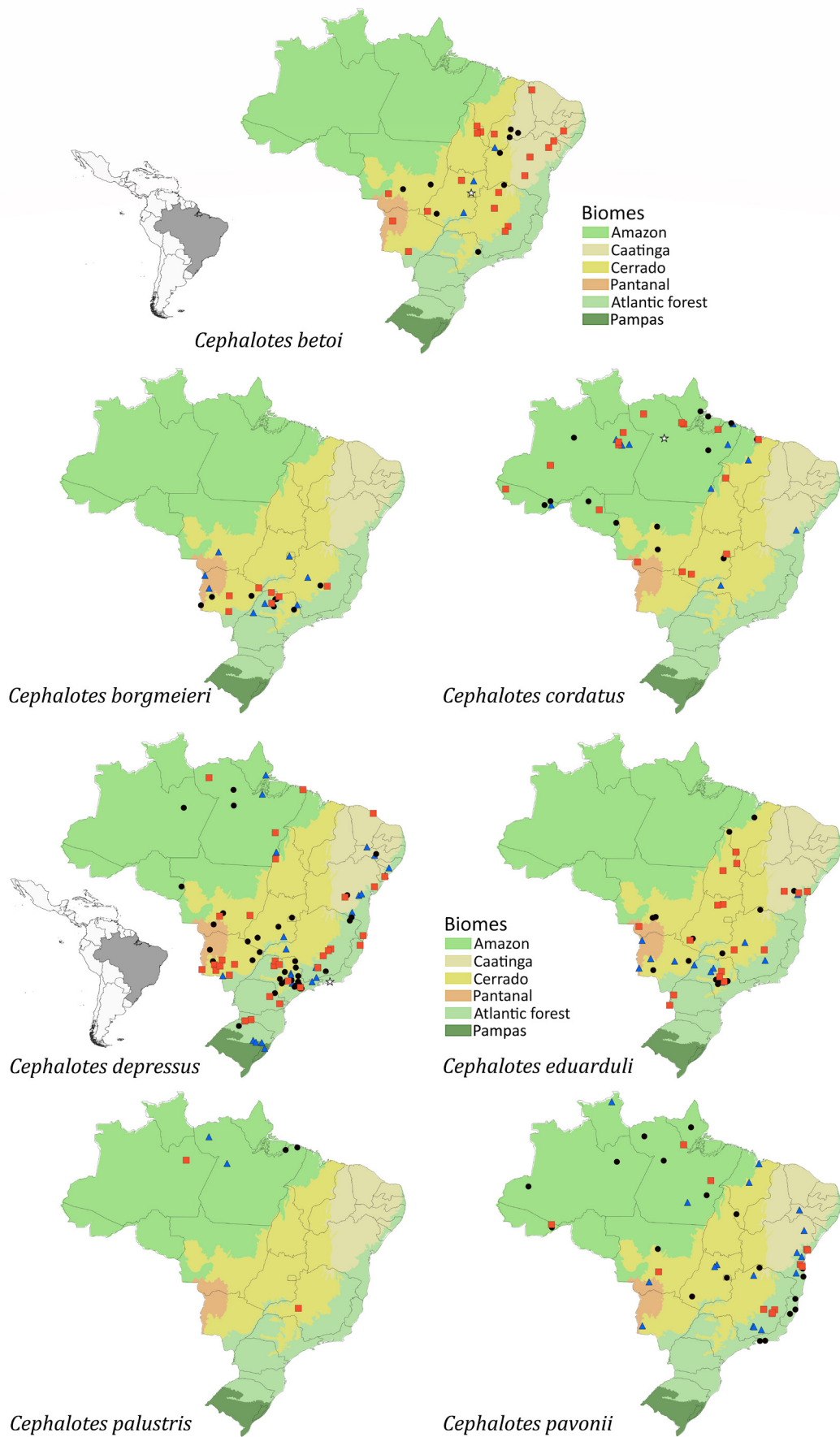


Figure 26 Distribution maps of *depressus* group in Brazil. White stars: type locality. Black circles: material examined. Red squares: new records. Blue triangles: records not examined from literature. (Literature source: 4, 9, 11, 12, 13, 15, 16, 17, 18, 21, 23, 25, 28, 35, 40, 41, 44, 45, 46, 49, 56, 60, 61, 63, 66, 70, 71, 76).

The fiebrigi species group

(Figs. 27, 28, 29, 30, 31, 32)

Kempf (1958a) created the *jheringi* subgroup of the *angustus* group in *Paracryptocerus* (*Harnedia*) with seven species (*C. bivestitus*, *C. bohlsi*, *C. bruchi*, *C. fossithorax*, *C. jheringi*, *C. prodigious*, and *C. quadratus*). Later, De Andrade and Baroni Urbani (1999) separated it into three groups of *Cephalotes*. The first is the monotypic *bruchi* group, characterized by cephalic disc incomplete in soldiers and gynes, a significant character in their analysis. The second is the exclusively Argentinian *prodigiousus* group with the species *C. bivestitus* and *C. prodigiousus*, characterized by the concave cephalic disc in soldiers. Finally, the four remaining species of the *jheringi* subgroup were joined to the Kempf's *pilosus* group, originally formed by *C. fiebrigi*, *C. liogaster*, and *C. pilosus*; resulting in the current *fiebrigi* group, with the addition of *C. guayaki*, *C. lanuginosus*, and *C. supercilii* described by De Andrade in De Andrade and Baroni Urbani, 1999.

In the morphological phylogeny (De Andrade and Baroni-Urbani, 1999, see their Fig. 24) the *bruchi* group was recovered as sister to the *fiebrigi* group. The authors argued that the incomplete cephalic disc could be a secondary loss in *bruchi* group, and the unknown ancestor of *C. bruchi* should have had both soldiers and gynes with a complete disc, but they kept the species in a separated group. However, the molecular phylogenies (Fig. 54) recovered *C. bruchi* within the *fiebrigi* group, as sister to the grouping formed by *C. jheringi*, *C. bohlsi* and *C. specularis*. Therefore, based on morphological and molecular evidence, we here transfer *C. bruchi* to the *fiebrigi* group, extinguishing the *bruchi* species group (Fig. 54).

Diagnosis: In workers, dorsal and declivous faces of propodeum continuous, not meeting in a distinct propodeal angle, and converging posteriorly towards the petiolar insertion, the lateral margins without lamellar expansions (Fig. 2n). Anterior portion of gaster with opaque expansion, never extending posteriorly in the form of translucent lateral lamellae (Fig. 2q). In soldiers, propodeum with variable number of spines, if there are two pairs, the anterior one is never longer than the posterior. Anterior gastral expansions not translucent (Fig. 2q).

Brazilian species of fiebrigi group***Cephalotes bruchi* (Forel, 1912)**

Obsolete combination: *Cryptocerus bruchi*
= *Cephalotes jheringi pampaensis* (Santschi, 1931)
= *Cephalotes ridiculus* (Santschi, 1915)
Obsolete combination: *Cryptocerus ridiculus*

***Cephalotes fiebrigi* (Forel, 1906)**

Obsolete combination: *Cryptocerus pilosus fiebrigi*

= *Cephalotes guttifer* (Santschi, 1919)

Obsolete combination: *Cryptocerus* (*Paracryptocerus*) *guttifer*

Cephalotes guayaki* De Andrade, 1999**Cephalotes jheringi* (Emery, 1894)**

Obsolete combination: *Cryptocerus jheringi*

= *Cephalotes peltatus* (Emery, 1896)

Obsolete combination: *Cryptocerus peltatus*

= *Cephalotes peltatus ellenriederi* (Forel, 1911)

Obsolete combination: *Cryptocerus peltatus ellenriederi*

Cephalotes liviaprado* new species**Cephalotes pilosus* (Emery, 1896)**

Obsolete combination: *Cryptocerus pilosus*

***Cephalotes quadratus* (Mayr, 1868)**

Obsolete combination: *Cryptocerus quadratus*

= *Cephalotes convexus* (Santschi, 1916)

Obsolete combination: *Cryptocerus convexus*

Cephalotes specularis* Brandão, Feitosa, Powell and Del-Claro, 2014*Key to the identification of Brazilian species of the fiebrigi group of *Cephalotes* based on workers**

(Figs. 27a-l)

- 1 Body with long, flexuous and abundant hairs (Fig. 27j).....2
- 1' Pilosity with a different pattern (Fig. 27g, h, k).....3
- 2 In frontal view, frontal carinae with a lateral projection anteriorly to the eyes (Fig. 27d).....*C. liviaprado* new species
- 2' In frontal view, frontal carinae straight (Fig. 27e).....*C. pilosus*
- 3 In dorsal view, frontal carinae strongly bent dorsally over the eyes (Fig. 27f).....*C. bruchi*
- 3' In dorsal view, frontal carinae not bent dorsally over the eyes (Fig. 27c)....4
- 4 In lateral view, first gastral tergite with erect hairs (Fig. 27h, k).....5
- 4' In lateral view, first gastral tergite without erect hairs (Fig. 27g)....6
- 5 First gastral tergite with less than 50 erect hairs (Fig. 27h).....*C. guayaki*
- 5' First gastral tergite with more than 100 erect hairs (Fig. 27k).....*C. fiebrigi*
- 6 In lateral view, head very convex, forming deep depressions anterior to the eyes (Fig. 27a).....*C. quadratus*
- 6' In lateral view, head slightly convex or straight, not forming deep depressions (Fig. 27b).....7
- 7 Gaster shiny, with equal sized hairs, evenly distributed throughout the tergite (Fig. 27i).....*C. specularis*
- 7' Gaster opaque, with shorter and sparser hairs in the central portion, and longer and more abundant hairs in the anterior portion (Fig. 27l).....*C. jheringi*

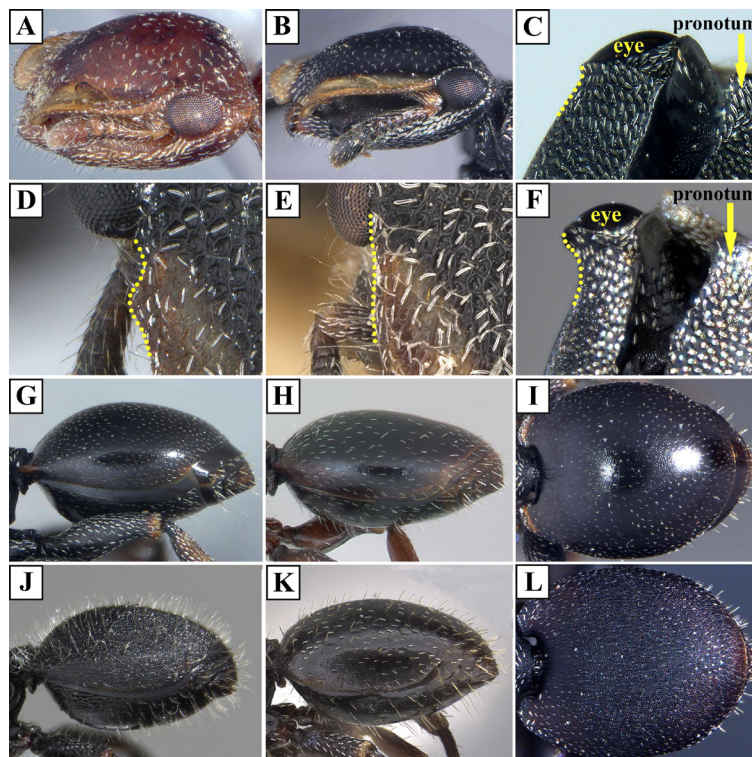


Figure 27 Workers of *fiebrigi* group. A: *C. quadratus*. B, G and I: *C. specularis*. C: *C. complanatus* (*basalis* group). D and J: *C. liviaprado*. E: *C. pilosus* [CASENT0904912]. F: *C. basalis* (*basalis* group). H: *C. guayaki* [CASENT0173677]. K: *C. fiebrigi* [CASENT0922539]. L: *C. jheringi*.

Key to the identification of Brazilian species of the *fiebrigi* group of *Cephalotes* based on soldiers

(Figs. 28a-l)

- 1 In frontal view, cephalic dorsum dome shaped, not totally marginated by a carina (blue dotted), and continuous with the vertexal corners (pink dotted) (Fig. 28c).....2
- 1' In frontal view, cephalic dorsum disc shaped, totally enclosed by a carina (blue dotted), which separate the dorsum from the vertexal corners (pink dotted) (Fig. 28a, b, d, e).....3
- 2 In dorsal view, propodeal groove strongly impressed forming a depression in the integument (Fig. 28g).....*C. quadratus*
- 2' In dorsal view, propodeal groove weakly impressed, without depression in the integument (Fig. 28h).....*C. guayaki*
- 3 In lateral view, dorsum of first gastral tergite only with appressed hairs (Fig. 28l).....4
- 3' In lateral view, dorsum of first gastral tergite with erect hairs (Fig. 28j); appressed hairs can be present (Fig. 28k).....6
- 4 Cephalic dorsum with erect clavate hairs (Fig. 28f).....*C. specularis*
- 4' Cephalic dorsum with appressed canaliculate hairs (Fig. 28i).....5

- 5 In frontal view, the distance between the anterior and posterior margins of the dorsum of head greater than the distance between the eyes (Fig. 28a).....*C. jheringi*
- 5' In frontal view, distance between the anterior and posterior margins of the dorsum of head shorter than or equal to the distance between the eyes (Fig. 28b).....*C. bruchi*
- 6 In lateral view, first gastral tergite without canaliculate appressed hairs. Simple sparse appressed hairs can be present laterally (Fig. 28j).....*C. liviaprado* new species
- 6' In dorsal view, first gastral tergite with evenly distributed, canaliculate appressed hairs (Fig. 28k).....7
- 7 In frontal view, the long hairs posterior to the eyes are as long as the length eyes (Fig. 28d). Dorsum of head with comparatively small foveae, and canaliculate suberect hairs present only anteriorly (Fig. 28d).....*C. pilosus*
- 7' In frontal view, the long hairs posterior to the eyes are shorter than half length eyes (Fig. 28e). Dorsum of head with comparatively large foveae and canaliculate suberect hairs evenly distributed (Fig. 28e).....*C. fiebrigi*

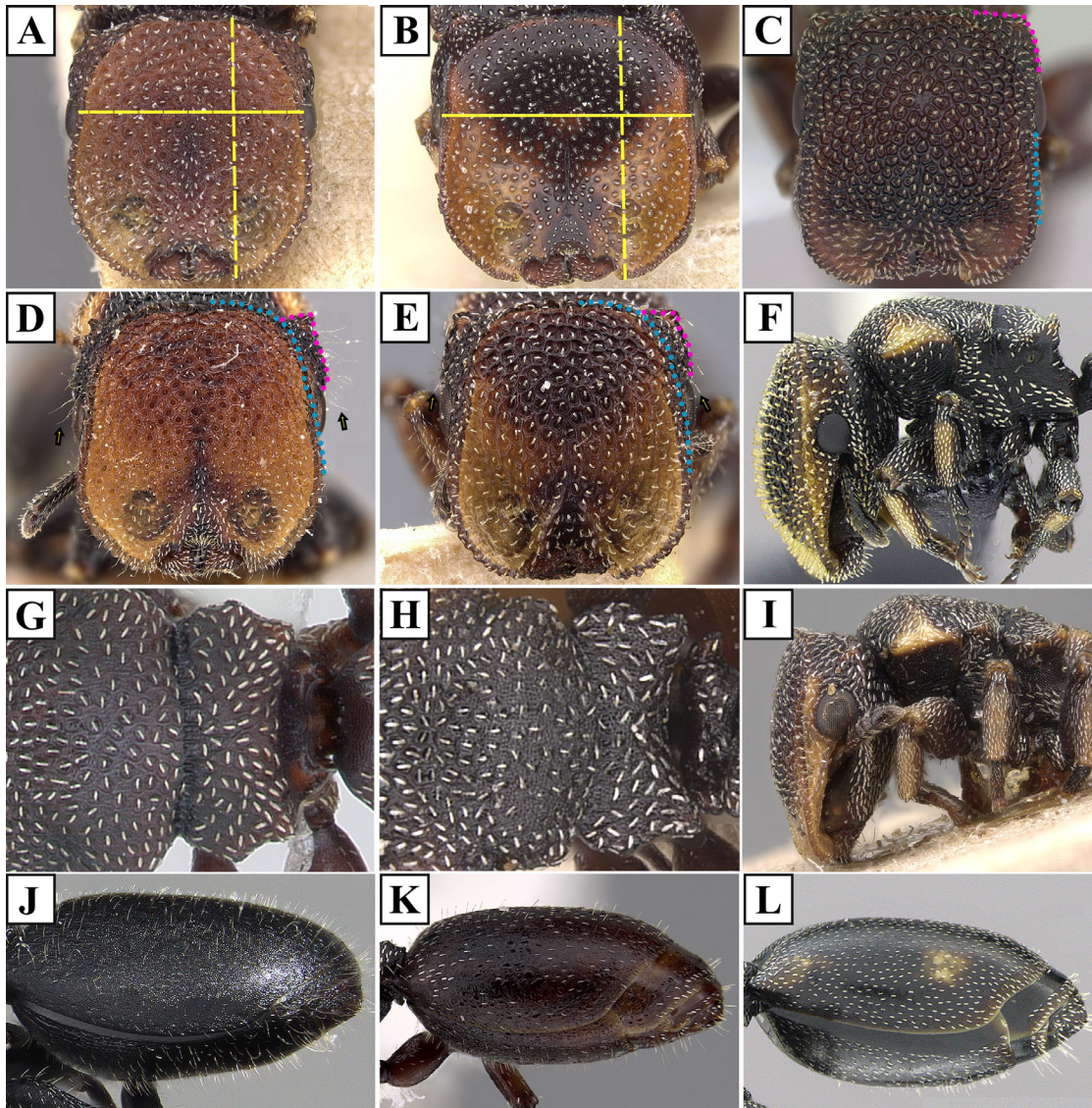


Figure 28 Soldiers of *fiebrigi* group. A and I: *C. jheringi* [A: CASENT0912601, I: CASENT0904919]. B: *C. bruchi* [CASENT0912591]. C and G: *C. quadratus* [CASENT0173705]. D: *C. pilosus* [CASENT0904911]. E and K: *C. fiebrigi* [E: CASENT0909290, K: CASENT0922538]. F and L: *C. specularis* [Brandão et al., 2014]. H: *C. guayaki* [CASENT0904920]. J: *C. liviaprado*.

***Cephalotes liviaprado* new species**

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Figs. 29a-c, 30a-c, 32

Holotype: BRAZIL, MS, Porto Murtinho, 28.i.2015 (diq, espinho *P. ruscifolia*), P. R. Souza, DZUP 550171 (worker) [DZUP].

Paratypes: same data as holotype: DZUP 550173 (2 workers, 1 soldier), DZUP 550172 (1 worker, 1 soldier) [DZUP], DZUP 550174 (2 workers, 1 soldier) [MZSP], DZUP 550175 (1 worker, 1 soldier) [INPA].

Diagnosis: A member of *fiebrigi* species group. Workers with long flexuous hairs (Fig. 29b). In frontal view, frontal carinae with a lateral projection anteriorly to the eyes (Fig. 27d). In soldier, first gastral tergite, with erect hairs, few and sparse appressed hairs can be present (Fig. 30).

Worker measurements (N=7): HL 1.08-1.23; HW 1.18-1.33; EL 0.32-0.38; PW 1.10-1.25; WL 1.21-1.34; PTL 0.26-0.29; PTW 0.62-0.64; PPL 0.26-0.31; PPW 0.66-0.75; GL 1.50-1.80; HBL 0.41-0.48; HBW 0.13-0.14; TL 4.36-4.92; CI 104-109; OI 26.4-29.8; PI 37.5-44.3; HBI 27.2-30.8.

Worker description: Body black; frontal lobes, mandibles, and apices of each segment of legs brownish to ferruginous (Fig. 29).

Mandibles, dorsum of head, mesosoma, petiole and postpetiole foveate-rugose, space between foveae microalveolate (Fig. 29a, c). Frontal lobes weakly striate (Fig. 29a); ventral face of head and lateral of mesosoma areolate-rugose; rugosities of dorsum of mesosoma extending to the middle of propodeum declivous face, lower portion of propodeum microalveolate. Legs microalveolate, except by tibiae, which external face is areolate-rugose. Gaster microalveolate, the anterior half of first tergite with short longitudinal striae originating near the postpetiole insertion (Fig. 29c); first sternite laterally with some irregular weak rugosities.

Body with abundant flexuous hairs, and some sparse appressed canaliculate hairs. Anterior margin of clypeus with suberect canaliculate hairs (Fig. 29a).

Head slightly wider than long (CI 104-109), dorsum weakly convex (Fig. 29b). Mandibles with a weakly developed lateral angle. Anterior margin of clypeus slightly concave, with a pair of lateral denticles. Frontal carinae notched anteriorly to the eyes, forming a lateral angle (Fig. 29a). Antennal club ill-defined. Lateroventral margins of head without carinae. Vertexal corners with irregular lamellar expansions (Fig. 29a).

Mesosoma strongly convex in lateral view (Fig. 29b). In dorsal view, lateral margins of pronotum with three pairs of denticles, the anterior one acute and the two posterior obtuse; promesonotal groove absent (Fig. 29c). Mesonotum with a pair of short blunt denticles. Propodeal groove absent. Dorsal and declivous faces of propodeum continuous, not meeting in a distinct propodeal angle; lateral margins of propodeum with an anterior pair of short blunt denticles, followed by a pair of large and acute and a row of minor acute denticles near petiolar insertion, the number and degree of development of the denticles vary even between sides of the same specimen (Fig. 29c). Femora not angulated dorsally, mid and hind basitarsi not flattened, with subparallel dorsal and ventral faces.

In dorsal view, petiole compressed anteroposteriorly, in dorsal view, anterior margin with a discrete median concavity, lateral spines curved backwards, dorsum with a pair of denticles (Fig. 29b), subpetiolar process acute anteriorly (Fig. 29b). Postpetiole slightly longer than petiole, without dorsal projections, lateral spines broad and curved backwards (Fig. 29c), subpostpetiolar process pronounced and compressed anteroposteriorly (Fig. 29b).

Gaster oval, with a pair of well-developed thick opaque anterior expansions, not extending posteriorly forming a lateral lamella (Fig. 29c).

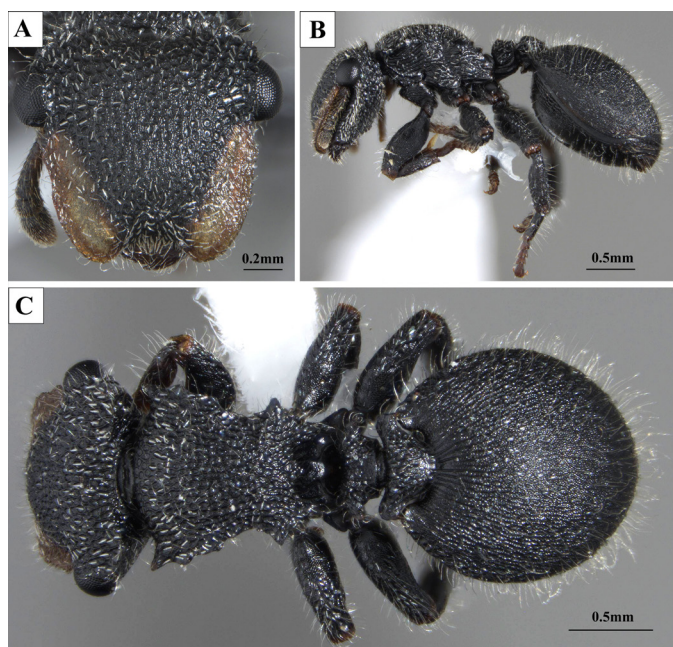


Figure 29 Worker of *Cephalotes liviaprado*. A: frontal view. B: lateral view. C: dorsal view. Brazil: MS, Porto Murtinho.

Soldier measurements (N=4): HL 1.96-2.09; HW 1.82-1.96; EL 0.40-0.43; PW 1.75-1.94; WL 1.66-1.88; PTL 0.32-0.38; PTW 0.85-0.89; PPL 0.33-0.39; PPW 0.88-0.90; GL 2.04-2.40; HBL 0.44-0.48; HBW 0.14-0.15; TL 6.31-7.13; CI 89.6-94.9; OI 21.3-21.2; PI 37.6-42.2; HBI 29.9-33.3.

Soldier description: Body black; frontal lobes and apices of each segment of legs brownish to ferruginous (Fig. 30).

Mandible, ventral face of head (Fig. 30a), promesonotum and mesonotum foveate, space between foveae microalveolate to smooth (Fig. 30c). Dorsum of head with small foveae anteriorly, increasing in diameter posteriorly. Dorsal face of propodeum, petiole and postpetiole foveate, without space between foveae; declivous face of propodeum microalveolate, with some striae on upper surface; lateral of mesosoma areolate-rugose (Fig. 30b). Legs microalveolate, except tibiae which external face is areolate-rugose. Gaster microalveolate, with a few short weakly marked longitudinal striae, originating near the postpetiole insertion (Fig. 30c).

Body with abundant flexuous hairs (Fig. 30b), except on dorsum of head, which has tiny suberect simple hairs (Fig. 30a). Mandibles, lateral and ventral face of head, meso- and metapleura with few appressed canaliculate hairs. Anterior margin of clypeus with suberect canaliculate hairs. Gaster with sparse appressed simple hairs (Fig. 30b, c).

Head longer than wide (CI 89.6-94.9). Mandibles with a strong longitudinal lateral angle. Clypeus with a pair of denticles (Fig. 30a). Dorsum of head disc shaped, convex medially (Fig. 30a). Frontal carinae crenulate converging posteriorly. Antennal club ill-defined. Roof of antennal scrobes with lateral carinae and a posterior denticle. Lateroventral margins of head without carinae. Vertexal corners forming pointed projections separated of the dorsum cephalic disc (Fig. 30a, b).

In lateral view, pronotum ascending, pronotal carina weakly marked and crenulate (Fig. 30b, c). In dorsal view, anterior margin of pronotum rounded, lateral margins with two pairs of denticles, the anteriorly one acute, the posterior one obtuse. Mesonotum and propodeum continuous and flat (Fig. 30b); mesonotum with a pair of blunt rounded projections; propodeal groove impressed; dorsal and declivous faces of propodeum meeting in

a distinct propodeal angle, in dorsal view, lateral margins of propodeum with a pair of median obtuse denticles and a pair of well-developed spines, directed upwards (Fig. 30c). Legs as in the worker.

Petiole and postpetiole as in the worker.

Gaster elongate, with the anterolateral expansions protruding anteriorly (Fig. 30c).

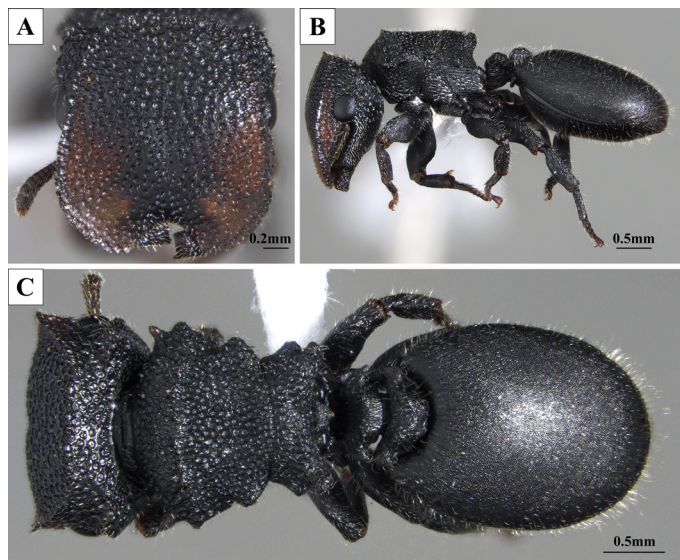


Figure 30 Soldier of *Cephalotes liviaprado*. A: frontal view. B: lateral view. C: dorsal view. Brazil: MS, Porto Murtinho.

Comments: This species is similar to *C. pilosus* but can be distinguished by the frontal carinae notched anterior to the eyes, forming a lateral angle and by the less abundant and shorter pilosity; in *C. pilosus* the frontal carinae is evenly straight to slightly depressed anterior to the eyes, but never forming a lateral angle and the pilosity is long and dense.

Natural history: *Cephalotes liviaprado* was collected in the Chaco formation. This ecosystem is part of the diagonal zone of seasonally-dry open areas in South America. The so called “Gran Chaco” occurs in northern Argentina, western Paraguay, southeastern Bolivia, and the extreme western of Mato Grosso do Sul state in Brazil, exclusively in the city Porto Murtinho (Prado, 1993). The vegetation is represented by shrub, deciduous, and spinous vegetation, usually associated with saline soils (Silva et al., 2000). The Chaco extends from tropical latitudes (18° S) to subtropical zones (31° S), and the climate is marked by strong seasonality, with more severe summers, and winter frosts (Werneck, 2011). The Brazilian Chaco (*Chaco sensu stricto*) occupy a subregion of the Pantanal biome, and extends over about 7% of its territory (Silva et al., 2000). Despite its relatively small area in Brazil, this formation is considered of high priority for conservation (Tálamo and Caziani, 2003). However, the anthropic use in this area for agriculture and logging has been a serious threat for the maintenance of this ecosystem and the species that live in it (Pott and Pott, 2003).

Cephalotes liviaprado was collected in the thorns of the tree species *Prosopis ruscifolia* Griseb. (Fabacea: Mimosoideae), which is endemic to the Chaco (Fuster, 2012). This tree species is adapted to edaphic conditions, and marshy and salty environments, and is known as a pioneer and colonizer plant. It has large stem thorns (10 to 30 length and 2 cm diameter) and extrafloral nectaries (Vilela and Palacios, 1997) which favors nesting by arboreal ants, like *Cephalotes* (Fuster, 2012). So far, *C. liviaprado* has been collected only in this location exclusively associated with *P. ruscifolia*. If these species are intimately related and endemic of Chaco, they must be extremely threatened.

Distribution: Mato Grosso do Sul, Brazil.

Etymology: The specific epithet, in apposition, is in honor of Livia Pires do Prado, a Brazilian myrmecologist and passionate historian of science, for her contributions to the taxonomy of Brazilian ants and the rescue of extremely relevant names and facts involving the history of Brazilian entomologists of all generations. Her work and dedication to science stands as an inspiration to female myrmecologists and students of the history of science alike.

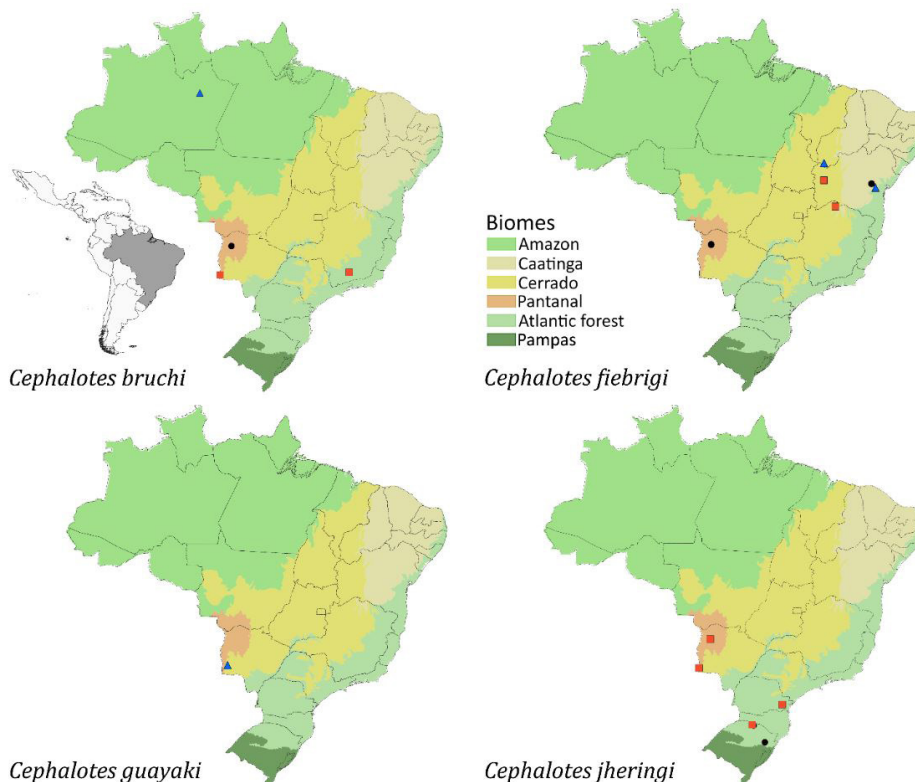


Figure 31 Distribution maps of *fiebrigi* group in Brazil “part 1”. Black circles: material examined. Red squares: new records. Blue triangles: records not examined from literature. (Literature source: 13, 29, 71).

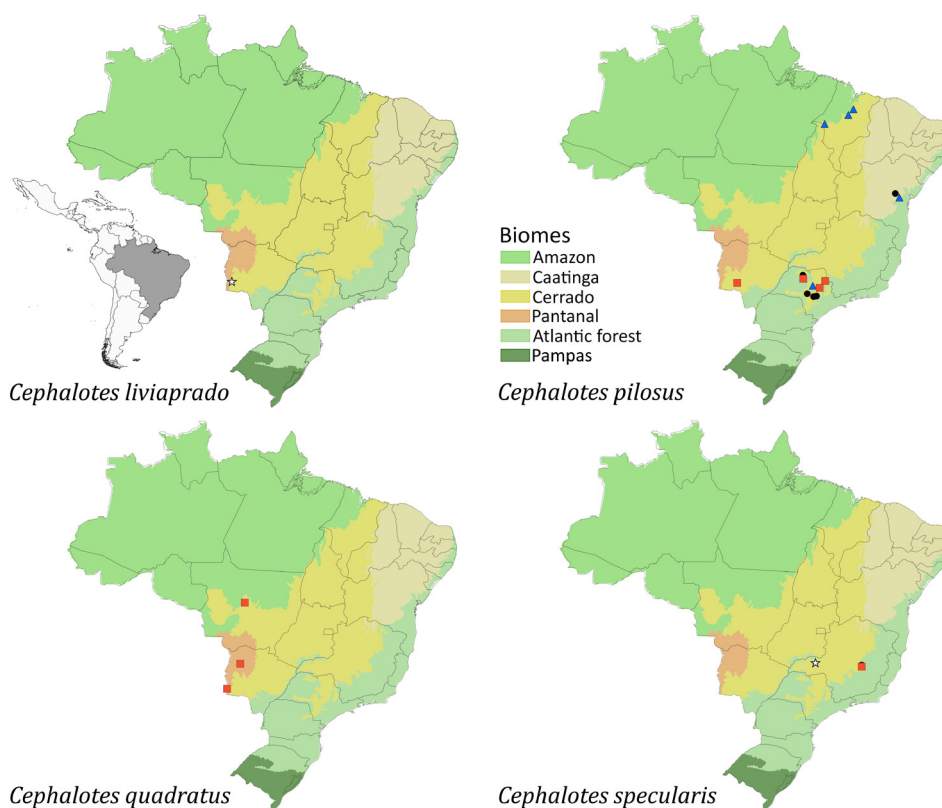


Figure 32 Distribution maps of *fiebrigii* group in Brazil "part 2". White stars: type locality. Black circles: material examined. Red squares: new records. Blue triangles: records not examined from literature. (Literature source: 13, 45, 71).

The *grandinosus* species group

(Figs. 33, 34, 35)

The *grandinosus* group was first proposed by De Andrade and Baroni Urbani (1999) including five species: *C. persimilis*, described by De Andrade in De Andrade and Baroni Urbani (1999), *C. klugi*, known only for the gyne, *C. persimilis*, *C. grandinosus*, and *C. foliaceus*. These last three composed the former *pinelii* group by Kempf (1952), along with *C. incertus*, *C. maculatus*, *C. pinelii*, and *C. scutulatus*.

Grandinosus and *pinelii* are sister groups in the morphological phylogeny (De Andrade and Baroni Urbani, 1999, see their Fig. 24), sharing many characters, as the strongly dorsoventrally flattened body, dorsum of mesosoma continuous, and lamellar expansions on mesosoma, petiole, postpetiole and gaster. Both groups differ only by the presence of a lamella on hind femora and the lighter color in *grandinosus*.

In the molecular phylogeny (Price et al., 2016, see their Fig. S3), the *grandinosus* and *pinelii* groups are recovered as paraphyletic. *Cephalotes foliaceus* (*grandinosus* group) is sister to *C. sp. 2* (here described as *C. mariadeandrade* **new species**, of the *pinelii* group). The clade formed by the other species of the *grandinosus* group (*C. grandinosus*, *C. klugi*, *C. persimilis* and *C. persimilis*) is the sister group of a clade formed by some of the previously designated species of the *pinelii* group (*C. maculatus*, *C. liepini*, *C. nilpiei*, *C. pinelii* and *C. pileini*) (Fig. 54).

The morphological similarities and phylogenetic association between species of the *pinelii* and *grandinosus* groups suggest they likely represent a single evolutionary lineage (Fig. 54). Even being paraphyletic, these groups are morphologically diagnosable, thus we kept it separate here, since we have not examined the species occurring outside Brazil in this study, what would help to better understand the relationships and limits between these species and redefine these groups.

Diagnosis: In workers, body strongly flattened dorsoventrally. In dorsal view, dorsum of mesosoma continuous, with lamellar lateral expansions. In workers and soldiers, hind femora with a ventral and/or

dorsal lamellar crest, usually crenulate and narrow (Fig. 2k, 3k). Petiole and postpetiole with lamellar lateral expansions.

Brazilian species of *grandinosus* group

Cephalotes grandinosus (Smith, 1860)

Obsolete combination: *Cryptocerus grandinosus*
= *Cephalotes grandinosus nevadensis* (Forel, 1912)

Obsolete combination: *Cryptocerus grandinosus nevadensis*

Cephalotes klugi (Emery, 1894)

Obsolete combination: *Cryptocerus klugi*

Cephalotes persimilis De Andrade, 1999

Cephalotes persimilis De Andrade, 1999

Key to the identification of Brazilian species of the *grandinosus* group of *Cephalotes* based on workers

(Figs. 33a-d)

Note: *Cephalotes klugi* is known only for the gyne.

- 1 In dorsal view, anterior portion of the lamellar expansions of the gaster flat, continuous with the gastral tergite (Fig. 33c).....***C. grandinosus***
- 1' In dorsal view, anterior portion of the lamellar expansions of the gaster bent dorsally, not continuous with the gastral tergite (Fig. 33d).....2
- 2 Body hairs appressed, relatively broad and uniform, without a submedian constriction (Fig. 33a).....***C. persimilis***
- 2' Body hairs relatively narrow, with a submedian constriction, which is not appressed to the body like the remain part of the hair (Fig. 33b).....***C. persimilis***

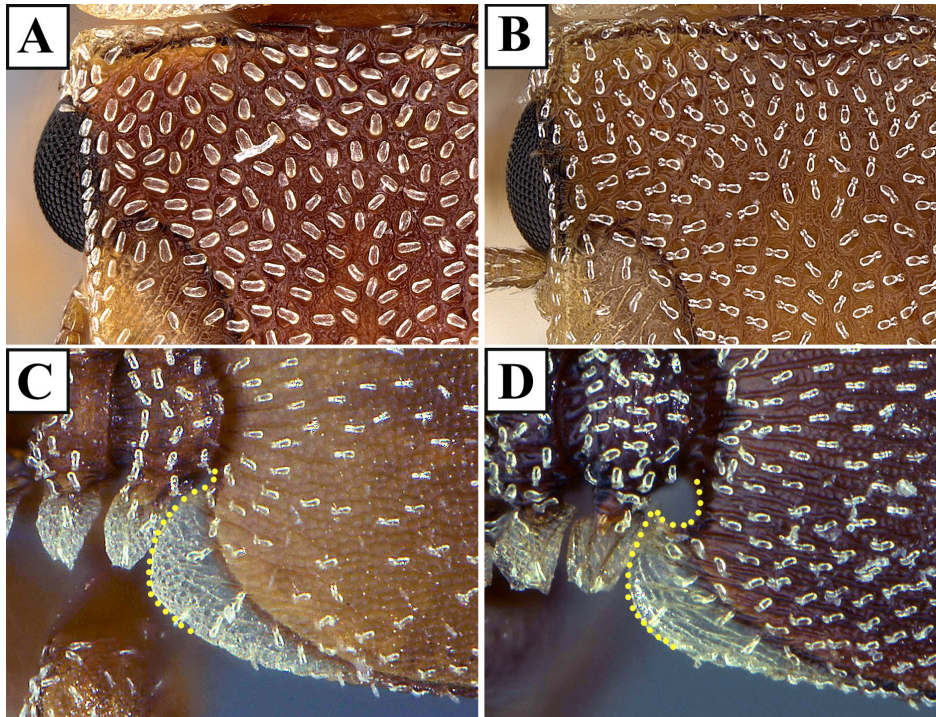


Figure 33 Workers of *grandinosus* group. A: *C. persimlex* [CASENT0922544]. B and D: *C. persimilis* [B: CASENT0922542]. C: *C. grandinosus*.

Key to the identification of Brazilian species of the *grandinosus* group of *Cephalotes* based on soldiers
(Figs. 34a-f)

Note: *Cephalotes klugi* is known only for the gyne.

1 In frontal view, cephalic disc areolate (Fig. 34a).....*C. grandinosus*

1' In frontal view, cephalic disc foveate, space between foveae microalveolate (Fig. 34b).....2
2 In lateral view, hairs of lateral face of head abundant, most hairs touching each other (Fig. 34c).....*C. persimlex*
2' In lateral view, hairs of lateral face of head sparse, hairs never touching each other (Fig. 34f). Hairs of head subrectangular (Fig. 34e).....*C. persimilis*

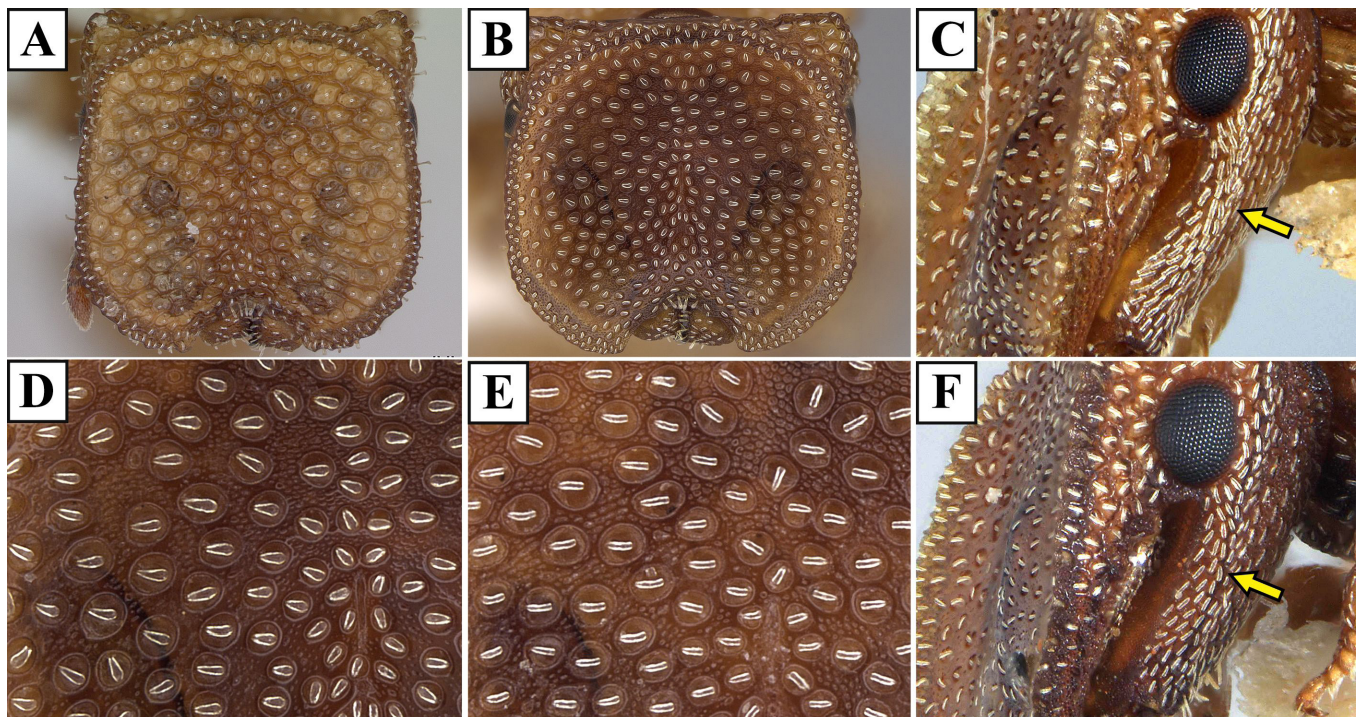


Figure 34 Soldiers of *grandinosus* group. A: *C. grandinosus* [CASENT0173699]. B, C and D: *C. persimlex* [B, D: CASENT0922543]. E and F: *C. persimilis* [E: CASENT0922541].

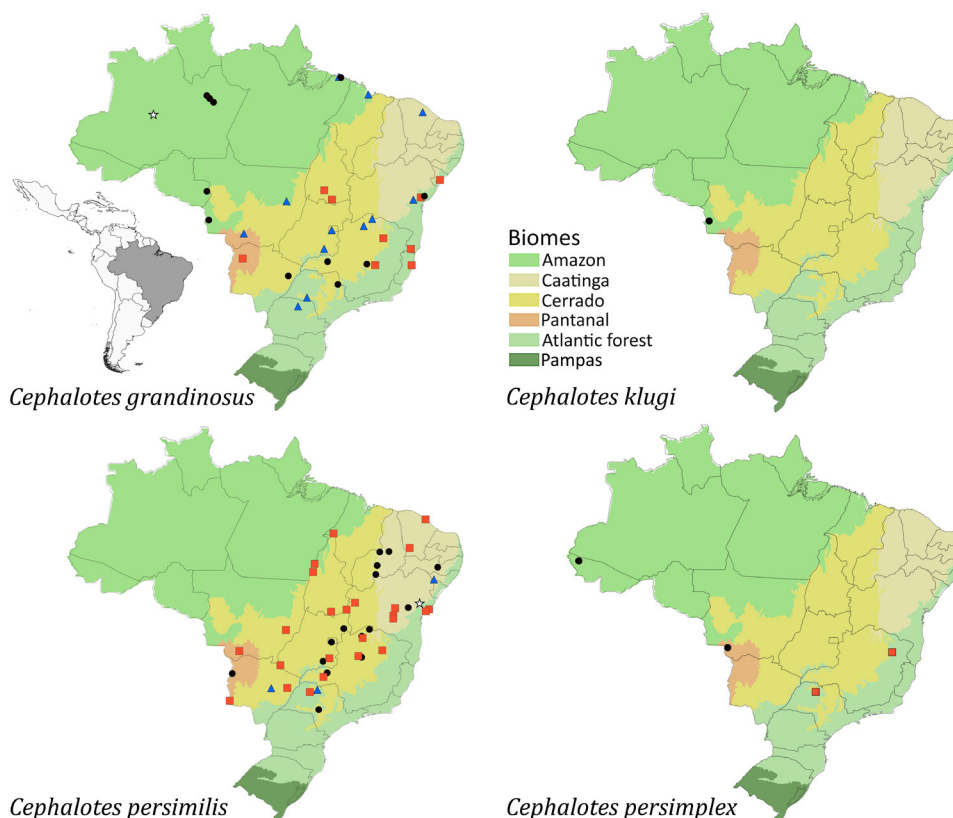


Figure 35 Distribution maps of *grandinosus* group in Brazil. White stars: type locality. Black circles: material examined. Red squares: new records. Blue triangles: records not examined from literature. (Literature source: 13, 19, 21, 27, 32, 40, 43, 45, 49, 59, 67, 70, 71, 76).

The *manni* species group

(Fig. 36)

The monotypic *manni* species group is here created to accommodate the species *C. manni*, formerly a member of the *basalis* species group. This species was described by Kempf (1951), as an “isolated species” without any defined group. However, De Andrade and Baroni Urbani (1999) included this species in the *basalis* group.

Cephalotes manni differs from the species in the *basalis* group by many characters. All species in the *basalis* group have lamellar expansions on the margins of the pronotum, in dorsal view, while *C. manni* has three pairs of dentiform projections. The declivous face of propodeum and anterior face of petiole are flat in the species of the *basalis* group, and concave in *C. manni*. The species in the *basalis* group have a median dorsal projection on the hind femora, which is absent in *C. manni*. In dorsal view, the anterior lamellar expansions of the gaster of species of *basalis* group have their apices distant to the postpetiole insertion, while in *C. manni* the apices of the lamellar expansions are near the postpetiole insertion.

In the morphological phylogeny, *C. manni* is the sister species of the rest of the *basalis* group (De Andrade and Baroni Urbani, 1999, see their Fig. 24), but this species was not included in the molecular phylogeny (Price et al., 2016), which could corroborate its phylogenetic position.

In Brazil, *C. manni* occurs only in the North Region, in the Amazon Forest, like some species of *basalis* group, but not in sympatry with other members of this group.

Diagnosis: In workers, in lateral view, eyes occupying more than 1/3 of the length of the head. In dorsal view, margin of pronotum with three pairs of lamellar dentiform projections. Fore femora very increased in size relative to the mid and hind femora. Lateral margins of the declivous face with broad lamellar expansion extending to the posterior dorsal spines of propodeum towards to petiolar insertion (Fig. 2m). In soldiers, mesonotal spines curved dorsally. Posterior femora without projections, metatibiae never marginated.

Brazilian species of *manni* group

Cephalotes manni (Kempf, 1951)

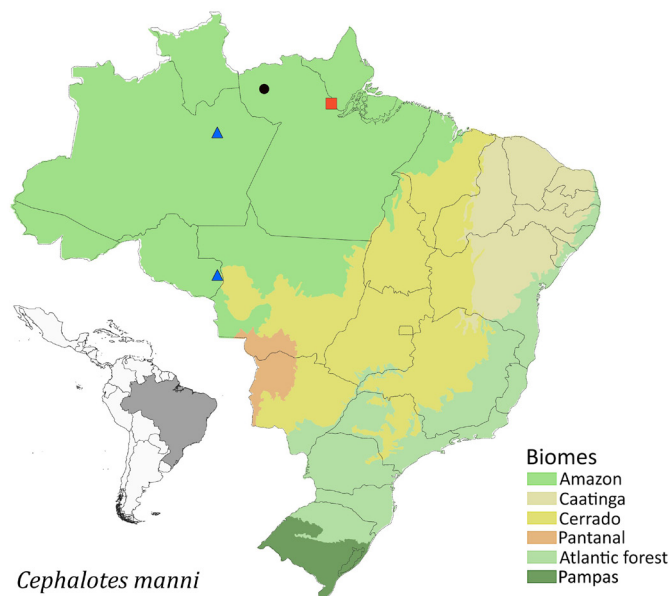


Figure 36 Distribution map of *manni* group in Brazil. Black circle: material examined. Red square: new record. Blue triangles: records not examined from literature. (Literature source: 13).

The *pallens* species group

(Figs. 37, 38, 39)

The *pallens* group was proposed by De Andrade and Baroni Urbani (1999) with 10 species. It includes *C. jamaicensis*, *C. pallens*, *C. patellaris*,

C. porrasi, *C. varians* and the new species described by De Andrade in De Andrade and Baroni Urbani (1999) (*C. decolor*, *C. decoloratus*, *C. pallidooides*, *C. pallidus*, and *C. pellans*). Of these species, only five occur in Brazil – *C. pallens*, *C. pallidooides*, *C. pallidus*, *C. patellaris*, and *C. pellans*.

This is the most morphologically homogeneous group of *Cephalotes*. Therefore, is the most challenging group regarding species delimitation, especially if the workers are the only caste available. In the identification key for workers, De Andrade and Baroni Urbani (1999) provided a note about this difficulty and recommended verification of the soldier's identification key before applying a name.

In addition to the characters employed by De Andrade and Baroni Urbani (1999), here we provide an illustrated identification key for workers based on characters as the shape of frontal carinae in relation to eyes, and sculpture patterns on pleura. Regarding the identification key for soldiers, the most informative characters are the sculpture and pilosity patterns.

The *pallens* group is sister to the clade formed by the *grandinosus* and *pinelii* groups (Fig. 54), with all of these groups sharing a worker body shape that is strongly flattened dorsoventrally.

Diagnosis: In worker, body strongly flattened dorsoventrally. Body color reddish brown. In frontal view, vertexal corner extending laterally overhanging the eye (Fig. 2d). In soldier, in frontal view, cephalic dorsum completely covering the mandibles to form a “dish” head type (Fig. 38).

Brazilian species of *pallens* group

Cephalotes pallens (Klug, 1824)

Obsolete combinations: *Cryptocerus pallens*, *Zacryptocerus pallens*
= *Cephalotes araneolus* (Smith, 1853)

Obsolete combination: *Cryptocerus araneolus*
= *Cephalotes discocephalus* Smith, 1853

Obsolete combination: *Cryptocerus discocephalus*

Cephalotes pallidooides De Andrade, 1999

Cephalotes pallidus De Andrade, 1999

Cephalotes patellaris (Mayr, 1866)

Obsolete combination: *Cryptocerus patellaris*

Cephalotes pellans De Andrade, 1999

Key to the identification of Brazilian species of the *pallens* group of *Cephalotes* based on workers

(Figs. 37a-i)

- 1 In dorsal view, lamellar expansions of the propodeum with a symmetrical posterior notch on both sides; an additional notch may be present anteriorly, but in this case, it is always symmetrical. The notch is never present on one side only or are asymmetrical (Fig. 37g).....***C. pallens***
- 1' In dorsal view, lamellar expansions of propodeum without notches. If any, they are asymmetric, probably caused by breaking (Fig. 37h).....2
- 2 In lateral view, frontal carinae narrow, ending over the eyes, so that the posterior portion of the eyes is confluent with the dorsal face of the head (Fig. 37a).....3
- 2' In lateral view, frontal carinae broad, extending beyond eyes length, separating eyes from dorsal face of head (Fig. 37b, c).....4
- 3 Lateral surface of the mesosoma rugose (Fig. 37f).....***C. pellans***
- 3' Lateral surface of the mesosoma microalveolate; some incomplete rugosities may be present (Fig. 37i).....***C. pallidooides***
- 4 In ventral view, head rugose (Fig. 37d).....***C. patellaris***
- 4' In ventral view, head totally microalveolate, without rugosities (Fig. 37e).....***C. pallidus***

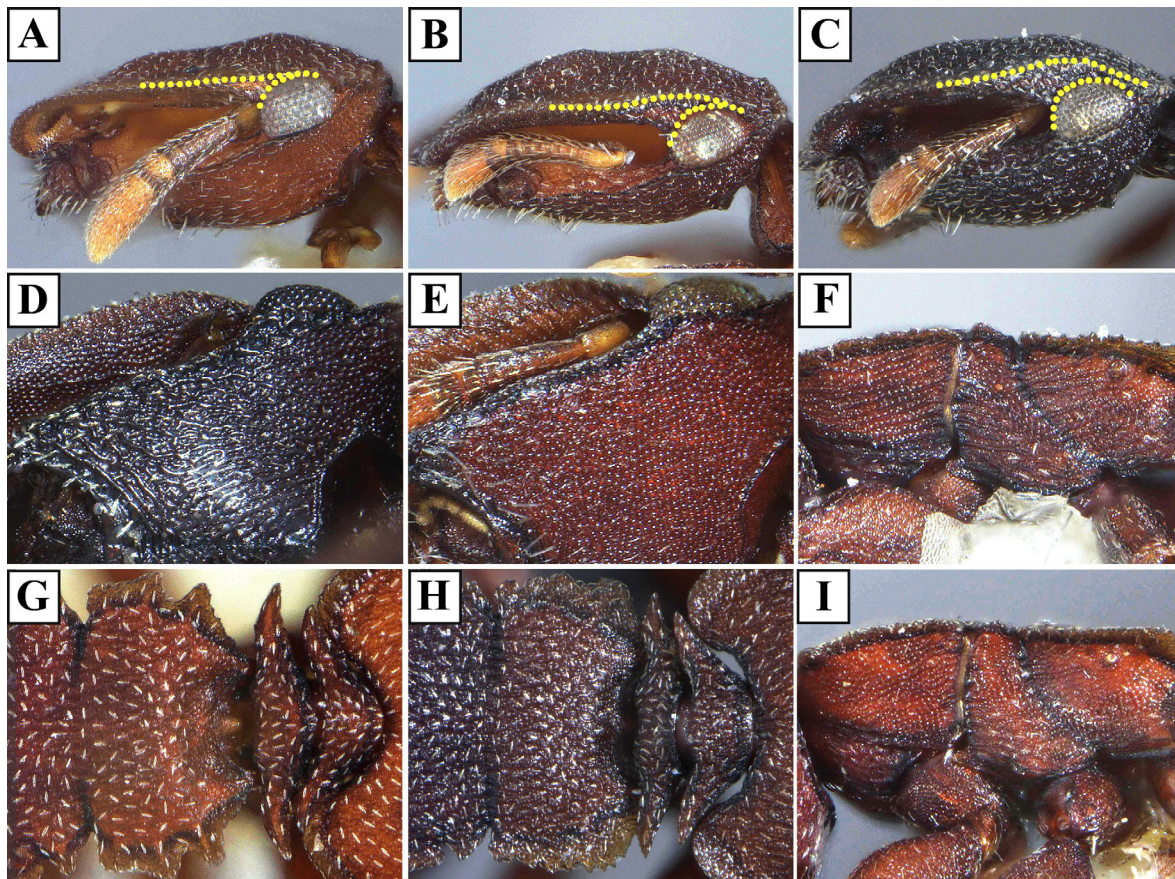


Figure 37 Workers of *pallens* group. A, F and H: *C. pellans*. B and E: *C. pallidus*. C and D: *C. patellaris*. G: *C. pallens*. I: *C. pallidooides*.

Key to the identification of Brazilian species of the *pallens* group of *Cephalotes* based on soldiers

(Figs. 38a-i)

- 1 Cephalic dish irregularly areolate-rugose (Fig. 38a).....*C. pallidus*
- 1' Cephalic dish regularly alveolate (Fig. 38b) or foveate (Fig. 38c).....2
- 2 Cephalic dish with erect to suberect hairs (Fig. 38d, g).....3
- 2' Cephalic dish with subdecumbent to appressed hairs (Fig. 38e, f).....4
- 3 Cephalic dish with a median protuberance (Fig. 38d).....*C. patellaris*
- 3' Cephalic dish flat or with a weak median protuberance (Fig. 38g).....
-*C. pallidoides*

- 4 Cephalic dish without a median protuberance (Fig. 38e). Translucent edges of the cephalic disc internally with long hairs larger than the diameter of the foveae (Fig. 38e). Declivous face of propodeum always rugose (Fig. 38h).....*C. pellans*
- 4' Cephalic dish with a median protuberance, weakly developed (Fig. 38f). Translucent edges of the cephalic disc internally with short hairs smaller than the diameter of the foveae (Fig. 38f). Declivous face of propodeum predominantly microalveolate, some tiny rugosities can be present (Fig. 38i).....*C. pallens*

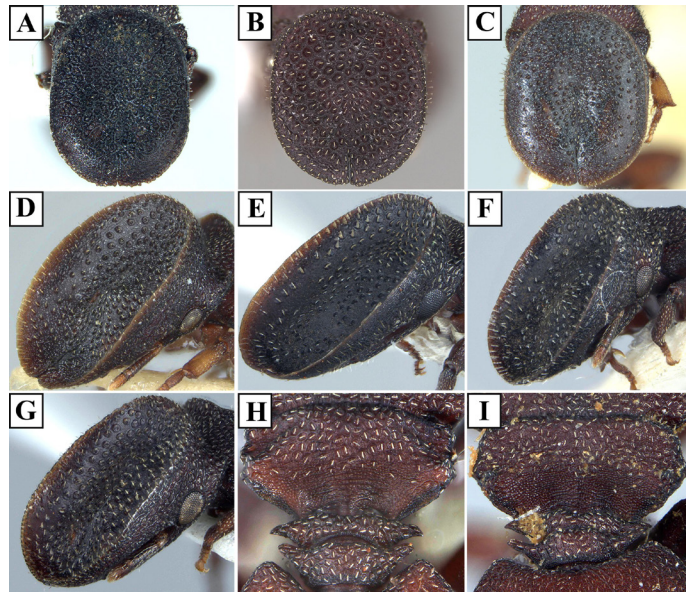


Figure 38 Soldiers of *pallens* group. A: *C. pallidus*. B: *C. pallidoides* [CASENT0922516]. C and D: *C. patellaris*. E and H: *C. pellans*. F and I: *C. pallens*. G: *C. pallidoides*.

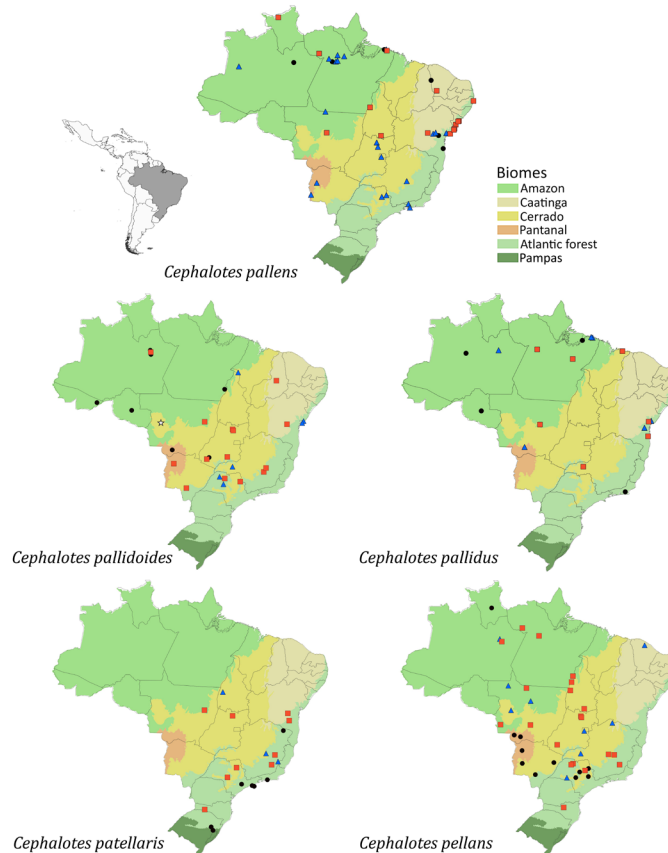


Figure 39 Distribution maps of *pallens* group in Brazil. White stars type locality. Black circles: material examined. Red squares: new records. Blue triangles: records not examined from literature. (Literature source: 2, 3, 4, 13, 15, 33, 36, 38, 39, 48, 49, 56, 58, 59, 61, 69, 71, 72).

The *pinelii* species group

(Figs. 40, 41, 42, 43, 44, 45, 46, 47, 48)

The *pinelii* group was first proposed by Kempf (1952), including six species (*C. foliaceus*, *C. grandinosus*, *C. incertus*, *C. maculatus*, *C. pinelii*, and *C. scutulatus*). Later, De Andrade and Baroni Urbani (1999) separated it in two groups, *grandinosus* and *pinelii*. The species *C. foliaceus*, and *C. grandinosus* were included in the *grandinosus* group, and the other four species in the *pinelii* group, along with *C. kukulcan* and three new species described by De Andrade in De Andrade and Baroni Urbani (*C. liepini*, *C. pileini* and *C. nilpiei*).

In the morphological phylogeny (De Andrade and Baroni Urbani, 1999, see their Fig. 24), the group *pinelii* is recovered as monophyletic, with the species *C. kukulcan*, *C. scutulatus* and *C. incertus* forming a deeply nested grouping within the clade. In the molecular phylogeny (Price et al., 2016, see their Fig. S3), the relationships between *C. kukulcan*, *C. scutulatus* and *C. incertus* were supported, but they were recovered as sister group of the *texanus* and *bimaculatus* groups, not related with the other species of the *pinelii* group. The remaining species of the *pinelii* group were recovered as related to the *grandinosus* group (Fig. 54), rendering the *pinelii* group proposed by De Andrade and Baroni Urbani (1999) polyphyletic. Morphology and molecular data suggest that *C. kukulcan*, *C. scutulatus* and *C. incertus* might form an additional group within *Cephalotes*, but the first two species were not included in this study, since they not occur in Brazil. On the other hand, the species of *pinelii* that occur in Brazil and are closely related to the *grandinosus* group likely form a monophyletic group with it, as discussed under the *grandinosus* group section.

Diagnosis: In workers, body strongly flattened dorsoventrally. In dorsal view, dorsum of mesosoma continuous, with lamellar lateral expansions. In workers and soldiers, hind femora without crest, lamellae, or angles (Fig. 21, 31). Petiole and postpetiole with lamellar lateral expansions.

Brazilian species of *pinelii* group

Cephalotes incertus (Emery, 1906)

Obsolete combination: *Cryptocerus incertus*

Cephalotes liepini De Andrade, 1999

Cephalotes maculatus (Smith, 1876)

Obsolete combination: *Cryptocerus maculatus*

= *Cephalotes grandinosus magdalenensis* (Forel, 1899)

Obsolete combination: *Cryptocerus grandinosus magdalenensis*

= *Cephalotes maculatus nanus* (Forel, 1912)

Obsolete combination: *Cryptocerus maculatus nanus*

Cephalotes mariadeandrade new species

Cephalotes nilpiei De Andrade, 1999

Cephalotes pinelii (Guérin-Méneville, 1844)

Obsolete combination: *Cryptocerus pinelii*

Key to the identification of Brazilian species of the *pinelii* group of *Cephalotes* based on workers

(Figs. 40a-i)

- 1 In dorsal view, petiole and postpetiole as long as or longer than wide (not including lateral lamellar expansions) (Fig. 40e).....*C. incertus*
- 1' In dorsal view, petiole and postpetiole wider than long (not including lateral lamellar expansions) (Fig. 40d).....2
- 2 In dorsal view, anterior portion of the lamellar expansions of the gaster bent dorsally, not continuous with the gastral tergite (Fig. 40g).....*C. liepini*
- 2' In dorsal view, anterior portion of the lamellar expansions of the gaster flat, continuous with the gastral tergite (Fig. 40h).....3
- 3 In dorsal view, lamellar expansions of propodeum present only on the declivous face, absent dorsally (Fig. 40c).....*C. mariadeandrade* new species
- 3' In dorsal view, propodeum entirely margined by lamellar expansions (Fig. 40f, i).....4
- 4 In frontal view, frontal carinae concave anteriorly the eyes (Fig. 40a). In lateral view, eyes occupying 1/3 of the length of the head.....*C. maculatus*
- 4' In frontal view, frontal carinae straight anteriorly the eyes (Fig. 40b). In lateral view, eyes occupying less 1/3 of the length of the head5
- 5 In dorsal view, propodeal groove deep, forming a depression (Fig. 40f).....*C. nilpiei*
- 5' In dorsal view, propodeal groove weak, not forming a depression (Fig. 40i).....*C. pinelii*

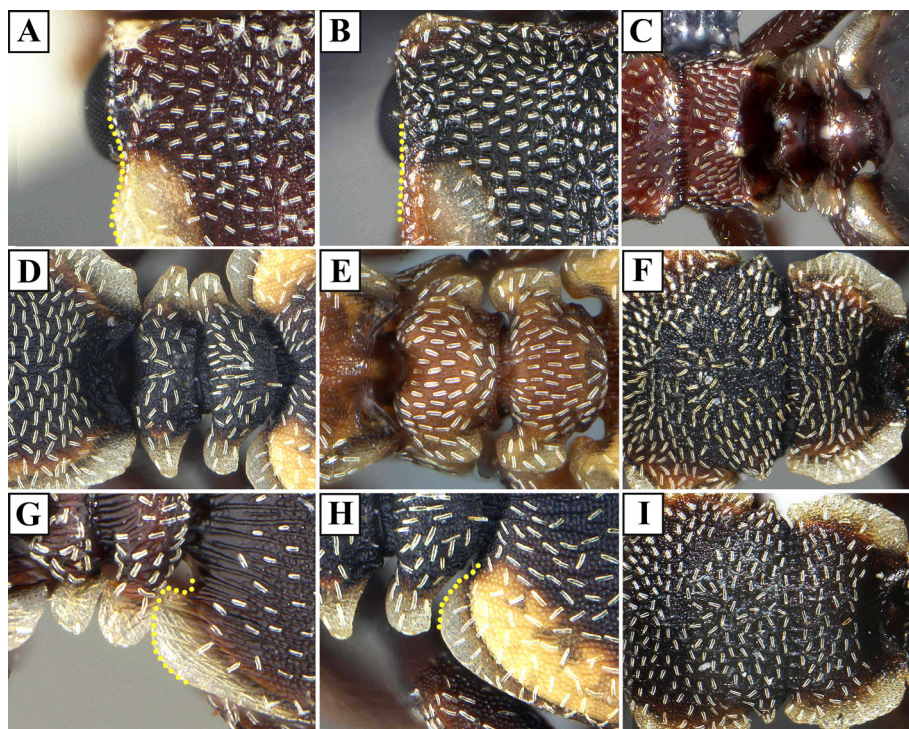


Figure 40 Workers of *pinelii* group. A: *C. maculatus*. B and I: *C. pinelii*. C: *C. mariadeandrade*. D, F and H: *C. nilpiei*. E: *C. incertus*. G: *C. liepini*.

Key to the identification of Brazilian species of the *pinellii* group of *Cephalotes* based on soldiers

(Figs. 41a-i, 43)

- 1 Cephalic disc full of many tubercular elevations (Fig. 43).....
*C. mariadeandrade* new species
- 1' Cephalic disc without tubercular elevations (Fig. 41a-c).....2
- 2 Cephalic disc with contiguous foveae (Fig. 41a).....*C. liepini*
- 2' Cephalic disc with foveae separate by interspaces (Fig. 41b, c).....3
- 3 In frontal view, posterior portion of the head with a circular depression (Fig. 41b).....*C. pinellii*
- 3' In frontal view, posterior portion of head flat, without a depression (Fig. 41c).....4
- 4 Lateral expansions of pronotum with same color as the rest of the mesosoma (Fig. 41d). Dorsal face of propodeum meeting the declivous face at an angle of almost 90° (Fig. 41h).....*C. maculatus*
- 4' Lateral expansions of pronotum lighter than the rest of the mesosoma (Fig. 41e). Dorsal face of propodeum continuous with the declivous face, not meeting at a distinct propodeal angle (Fig. 41g).....5
- 5 In dorsal view, petiole and postpetiole as long as or longer than wide (not including lateral lamellar expansions) (Fig. 41f).....*C. incertus*
- 5' In dorsal view, petiole and postpetiole wider than long (not including lateral lamellar expansions) (Fig. 41i).....*C. nilpiei*

***Cephalotes mariadeandrade* new species**

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 (Figs. 42a-c, 43a-c, 44a-c, 45a-c, 48)

Holotype: BRAZIL, MG, Uberlândia, -19.033630 -48.318400, 860m, 03.viii.2016. S. Powell et al. col. /C16-64, DZUP 550137 (worker) [DZUP].

Paratypes: same data as holotype: DZUP 550138 (1 worker, 1 soldier, 1 male), DZUP 550139 (1 worker, 1 soldier, 1 gyne), DZUP 550140 (1 worker, 1 male), DZUP 550141 (1 worker, 1 soldier, 1 gyne), DZUP 550142 (1 worker, 2 soldiers) [DZUP], DZUP 550145 (1 worker, 1 soldier, 1 gyne), DZUP 550146 (1 worker, 1 soldier, 1 male) [MZSP], DZUP 550147 (1 worker, 1 soldier) [MPEG], DZUP 550143 (1 worker, 1 male), DZUP 550144 (1 worker, 1 soldier, 1 gyne) [USNM].

Diagnosis: A member of *pinellii* species group. Workers with lateral lamellar extensions of the propodeum on the declivous face but not on the dorsal face (Fig. 42c). Soldier with cephalic disc covered with many tubercular elevations (Fig. 43a-c).

Worker measurements (N=11): HL 0.78-0.84; HW 0.89-0.99; EL 0.25-0.28; PW 0.70-0.78; WL 0.84-0.89; PTL 0.13-0.19; PTW 0.48-0.53; PPL 0.14-0.19; PPW 0.51-0.62; GL 0.94-1.08; HBL 0.35-0.38; HBW 0.09; TL 2.89-3.16; CI 110-123; OI 26.3-29.9; PI 25.0-37.5; HBI 23.3-25.0.

Worker description: Body dark brown; frontal lobes and lamellar expansions of pronotum, propodeum, petiole, postpetiole and gaster yellowish to translucent. Gaster darker than the rest of body (Fig. 42).

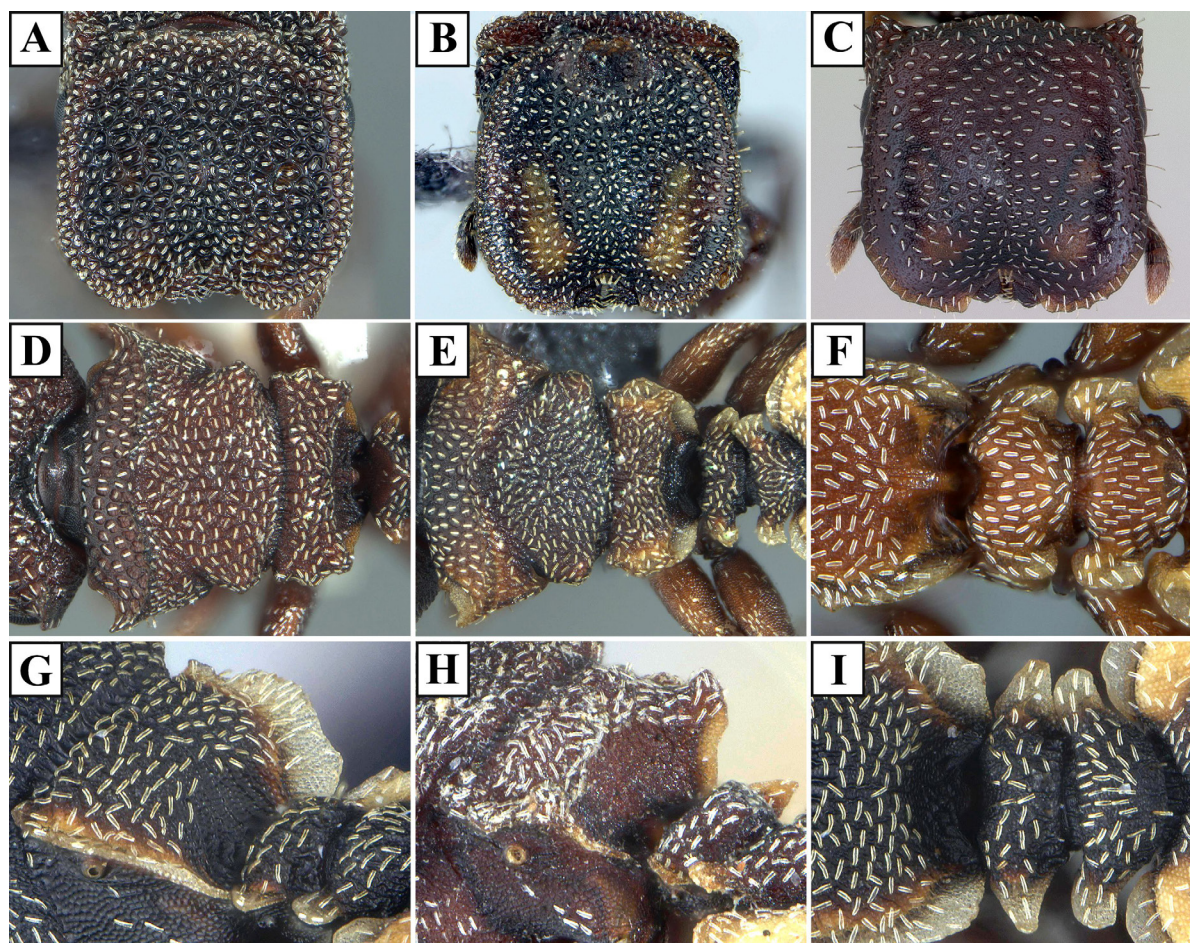


Figure 41 Soldiers of *pinellii* group. A: *C. liepini*. B: *C. pinellii*. C, D and H: *C. maculatus* [C: CASENT0173689]. E, G and I: *C. nilpiei*. F: *C. incertus*.

Mandibles rugose-microalveolate. Dorsum of head and mesosoma foveate, space between foveae smooth; ventral face of head areolate-microalveolate. Legs and gaster microalveolate.

Body with appressed canaliculate hairs, more abundant on dorsum of pronotum (Fig. 42c). Mandibles and anterior margin of clypeus with suberect clavate hairs. Declivous face of propodeum glabrous. Petiole and postpetiole with hairs forming a transverse dorsal strip; anterior and posterior portions glabrous (Fig. 42c). Gaster with sparse short appressed simple hairs, anterior lamellar expansions glabrous (Fig. 42c).

Head slightly wider than long (CI 110-123), dorsum very convex medially, with two longitudinal elevations posteriorly, and depressions in front of eyes. Mandibles with a weakly developed lateral angle. Anterior margin of clypeus concave without denticles. Frontal carinae strait anteriorly of eyes; pointed upwards over eyes (Fig. 42c). Antennae with a two-segmented club. Lateroventral margins of head with posterior carinae extending beyond the eyes until vertexal corners. Vertexal corners with a narrow lamellar expansion.

Mesosoma almost flat in lateral view, with a gently ascendant pronotum (Fig. 42b). In dorsal view, lateral margins of pronotum with concave lamellar expansions, broader anteriorly; promesonotal groove absent, instead of it is an elevation on dorsum of pronotum (Fig. 42c). Mesonotum with a pair of short denticles pointed upwards. Propodeal groove deeply impressed. Dorsal and declivous faces of propodeum well differentiated, meeting in a distinct propodeal angle; lateral margins of the dorsum of propodeum without lamellar expansions, declivous face with lateral lamellar expansions pointed upwards (Fig. 42c). Femora not angulated dorsally, mid and hind basitarsi not flattened, with subparallel dorsal and ventral faces.

In dorsal view, petiole compressed anteroposteriorly, anterior margin with a discrete median concavity, with lateral lamellar expansions broader posteriorly, dorsally with pair of obtuse denticles, subpetiolar process broader and rounded anteriorly (Fig. 42b). Postpetiole narrower than petiole (Fig. 42b), with lateral lamellar expansions, dorsum of postpetiole with a transverse elevation (Fig. 42c), subpostpetiolar process pronounced and compressed anteroposteriorly (Fig. 42b).

Gaster suboval, deeply concave anteromedially, with broad anterior lamellar expansions, not extending posteriorly in a carina (Fig. 42c).

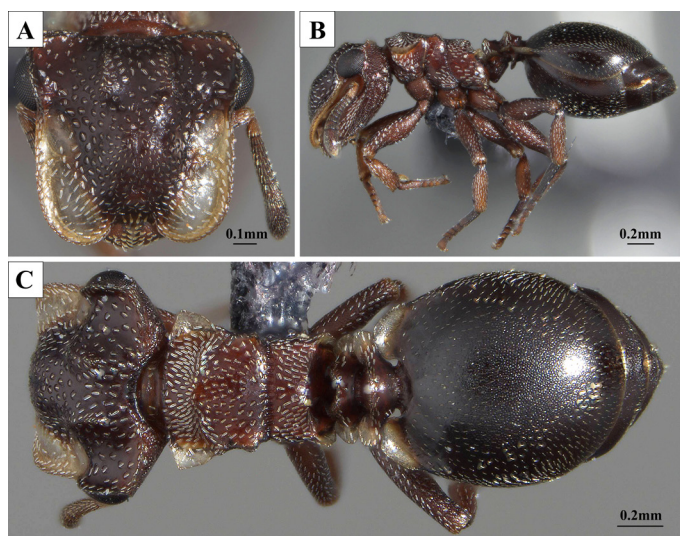


Figure 42 Worker of *Cephalotes mariadeandrade*. A: frontal view. B: lateral view. C: dorsal view. Brazil: MG, Uberlândia.

Soldier measurements (N=9): HL 0.91-1.00; HW 1.09-1.19; EL 0.25-0.28; PW 0.94-1.13; WL 0.97-1.13; PTL 0.15-0.19; PTW 0.50-0.56; PPL 0.18-0.21; PPW 0.54-0.64; GL 1.04-1.19; HBL 0.32-0.38; HBW 0.10-0.11; TL 3.27-3.65; CI 118-122; OI 21.2-24.4; PI 29.5-36.4; HBI 26.7-33.7.

Soldier description: Body dark brown; frontal lobes and lamellar expansions of pronotum, propodeum, petiole, postpetiole and gaster yellowish to translucent. Gaster dark brown with an anterior and a posterior pair of small yellowish spots (Fig. 43).

Mandibles alveolate. Ventral face of head areolate-microalveolate; dorsum of head with many tubercular elevations, space between tubercles scabrous (Fig. 43a); frontal lobes weakly rugose. Pronotum scabrous (Fig. 43c). Meso- and metanotum, meso- and metapleura foveate-microalveolate. Petiole and postpetiole with shallow foveae. Legs, and gaster as in the workers (Fig. 43c).

Pilosity as in the workers, except by anterior portion of head with erect clavate hairs, dorsum of head with canaliculate hairs on tubercles, and dorsum of pronotum with sparse canaliculate hairs.

Head slightly wider than longer (CI 118-122). Mandibles with a strong longitudinal lateral angle. Clypeus without denticles (Fig. 43a). Dorsum of head disc shaped and convex, strongly tuberculate with a posteriorly pair of distinct larger tubercle (Fig. 43a, b). Frontal carinae crenulate laterally. Antennae with a two-segmented club. Roof of antennal scrobes with a lateral crenulate carinae. Lateroventral margins of head with a posterior carinae extending beyond the eyes until vertexal corners. Vertexal corners forming a pair of broad projections pointed upwards (Fig. 43b, c).

In lateral view, pronotum ascending, pronotal carina well marked and crenulate, medially interrupted (Fig. 43c). In dorsal view, anterior margin of pronotum gently rounded, lateral margins pointed anteriorly. Mesonotum and propodeum discontinuous and flat (Fig. 43b). Mesonotum, propodeum, legs, petiole, postpetiole and gaster as in workers; except by the narrow lamellar expansions on the declivous face of propodeum (Fig. 43c).

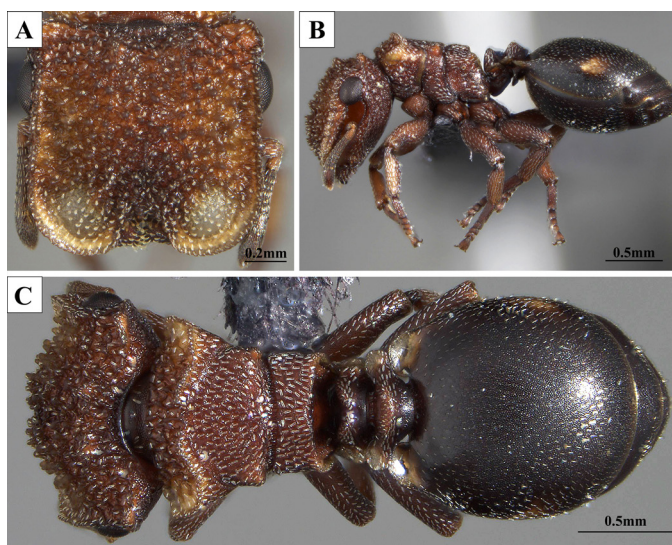


Figure 43 Soldier of *Cephalotes mariadeandrade*. A: frontal view. B: lateral view. C: dorsal view. Brazil: MG, Uberlândia.

Gyne measurements (N=4): HL 1.13-1.18; HW 1.22-1.27; EL 0.30-0.31; PW 1.27-1.34; WL 1.63-1.88; PTL 0.25-0.32; PTW 0.50-0.51; PPL 0.30-0.32; PPW 0.70-0.72; GL 1.80-1.88; HBL 0.44-0.50; HBW 0.13-0.15; TL 5.18-5.49; CI 106-110; OI 23.4-25.2; PI 50-63.4; HBI 27.5-33.3.

Gyne description: Body black; frontal lobes anteriorly translucent; dorsum of head, pronotum and legs brownish to yellowish. First gastral tergite with an anterior and a posterior pair of whitish spots, each one occupying less than one third of the first tergite length; posterior margins of each tergite and sternite yellowish (Fig. 44).

Sculpturing of mandibles, dorsal and ventral face of head, pronotum, legs, and gaster as in the soldier. Dorsum of mesonotum, mesopleuron, upper metapleura foveate-microalveolate, lower metapleura rugose-microalveolate (Fig. 44b). Propodeum foveate. Petiole and postpetiole with shallow foveae (Fig. 44c).

Pilosity as in the soldier, but hairs more abundant on propodeum.

Head as in the soldier (CI 106-110). The two posterior ocelli positioned in the posterior tubercular elevations (Fig. 44a).

In dorsal view, anterior margin of pronotum slightly rounded, narrower than in the soldiers, lateral margins with a pair of denticles pointed forwards, pronotal carina weakly developed, crenulate, medially interrupted (Fig. 44c). Dorsally, mesoscutum subtriangular, anterior margin rounded; notauli absent; parapsidial lines feebly visible and parallel; transscutal line impressed, reaching the lateral margins of mesosoma; scutoscutellar groove deeply impressed, arched, and scrobiculate; scutellum well delimited and broader anteriorly; axillae rounded posteriorly (Fig. 44c). Laterally, mesopleural groove dividing anepisternum and katepisternum; metapleura divided in upper metapleura and lower metapleura by a groove; metapleuropropodeal groove impressed (Fig. 44b). In dorsal view, posterior margin of propodeum concave with a pair of short, blunt denticles (Fig. 44c). Wing venation as in the genus description.

In dorsal view, petiole subrectangular, lateral margins straight, without lamellar expansions and without dorsal projections, subpetiolar process narrow (Fig. 44c). Postpetiole longer than petiole, with a pair of lateral broad opaque projections (Fig. 44c), without projection on dorsum, subpostpetiolar process pronounced and compressed anteroposteriorly.

Gaster protruding anteriorly (Fig. 44c).

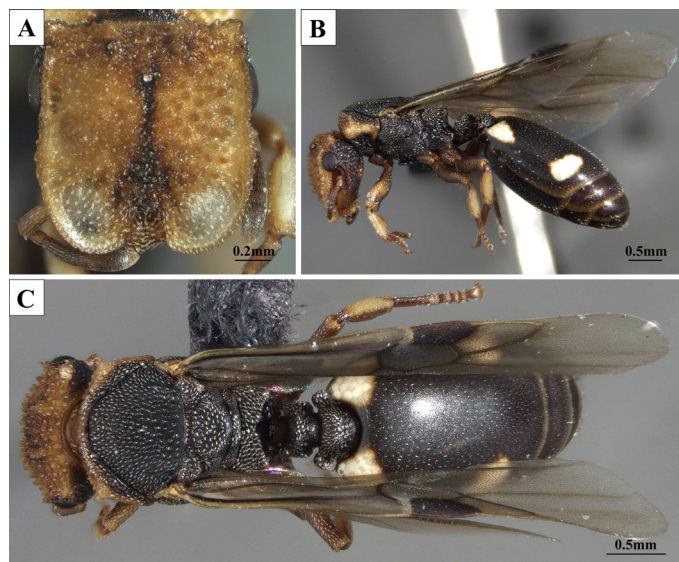


Figure 44 Gyne of *Cephalotes mariadeandrade*. A: frontal view. B: lateral view. C: dorsal view. Brazil: MG, Uberlândia.

Male measurements (N=4): HL 0.58-0.60; HW 0.78-0.81; EL 0.30-0.31; PW 0.80-0.84; WL 1.24-1.28; PTL 0.21-0.25; PTW 0.31-0.34; PPL 0.20-0.22; PPW 0.33-0.39; GL 0.75-0.81; HBL 0.38-0.44; HBW 0.06-0.08; TL 3.03-3.13; CI 130-138; OI 36.9-40.1; PI 66.7-74.8; HBI 15.6-18.2.

Male description: Body brownish to black; femora brownish to yellowish, tibiae and tarsi yellowish (Fig. 45).

Mandibles, head and dorsum of mesosoma microalveolate with sparse shallow foveae. Propleura and mesopleuron weakly striate; metapleura and propodeum rugose. Legs, petiole, postpetiole and gaster microalveolate.

Body with long and flexuous hairs, more abundant on mandibles, dorsum of head and mesosoma. Legs with long hairs only in the internal face of coxae and femur. Hairs shorter on gaster (Fig. 45b).

Head wider than longer (CI 130-138), broader posteriorly. Mandibles with one apical tooth, lateral angle weakly developed to absent. Clypeus with a median elevation, posterior margin rounded. Frontal carinae not extending posteriorly. The central portion of head strongly elevated. Eyes occupying more than half of head length (Fig. 45a). Ocelli positioned at a central elevation. Antenna as the genus description.

In dorsal view, anterior margin of pronotum strongly rounded (Fig. 45c). Mesoscutum subtriangular; notauli present; parapsidial lines feebly visible and parallel; transscutal line reaching lateral margins of mesosoma; scutoscutellar groove deeply impressed, arched, and scrobiculate; scutellum well delimited and broader anteriorly; axillae rounded posteriorly (Fig. 45c). Laterally, mesopleural groove dividing anepisternum and katepisternum; metapleura divided in upper metapleura and lower metapleura by a groove; metapleuropropodeal groove inconspicuous (Fig. 45b). Dorsal face of propodeum concave, with rounded lateral angles. Wings as in genus description.

In dorsal view, petiole and postpetiole concave anteriorly, with lateral acute projections near to the anterior margin, without dorsal projections, subpetiolar and subpostpetiolar process weakly developed (Fig. 45c).

First tergite of gaster as broad as mesosoma, occupying half or less than the total length of gaster (Fig. 45b), without anterior projection (Fig. 45c).

Comments: This species differs from others in *pinelii* group by the presence of two longitudinal elevations on the posterior portion of head dorsum, lack of lateral lamellar expansions on dorsum of propodeum declivous face, and body robust, not strongly flattened dorsoventrally. *Cephalotes mariadeandrade* is the species *C. sp. 2* in the molecular phylogenies by Price et al. (2014, 2016), recovered at the base of the paraphyletic grouping formed by the *grandinosus* and *pinelii* groups (Fig. 54).

Natural history: A complete colony of *C. mariadeandrade* species was collected in Uberlândia (Minas Gerais) in a region of Neotropical savanna (biome Cerrado). The colony occupied four individual nests on the same tree occupied by an aggressive species of *Crematogaster* of similar size and dark brown color. Workers of *C. mariadeandrade* were observed running in the well-established foraging trails of the *Crematogaster* species, which could indicate a parasitic relation between these species, like that described to *Cephalotes specularis* and *Crematogaster ampla* Forel, 1912. In that case, *C. specularis* mimics the behavior and posture of their host *C. ampla*, so they can use the foraging networks and exploit food resources of their hyperaggressive host without being notice (Powell et al., 2014). *Cephalotes mariadeandrade* workers also moved like the *Crematogaster* workers whose trails they integrated with and they were similarly undetected by the *Crematogaster* foragers.

Distribution: Minas Gerais, Brazil.

Etymology: The specific epithet, in apposition, is in honor of Maria de Andrade, a Brazilian taxonomist, who dedicated years of work conducting the most comprehensive study of the genus *Cephalotes* to date. This seminal

contribution provided the basis for the development of the present study and the foundation upon which all current *Cephalotes* research is based.

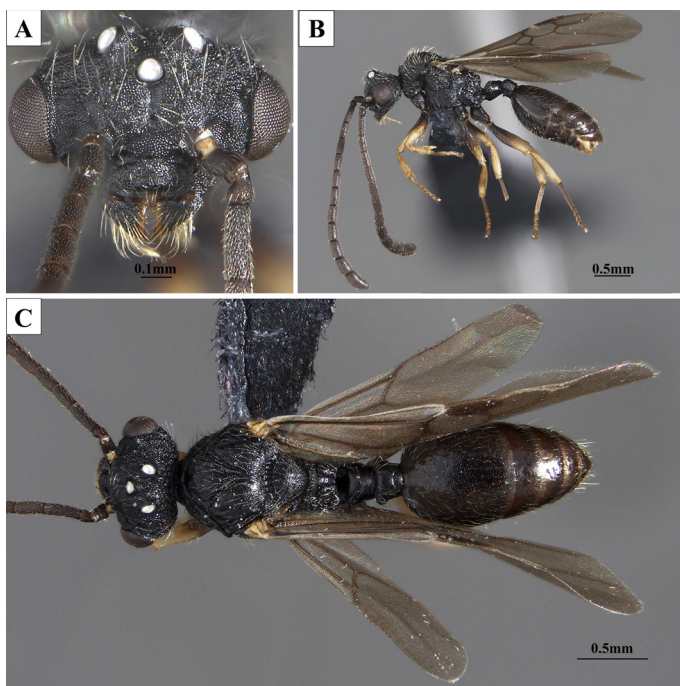


Figure 45 Male of *Cephalotes mariadeandrade*. A: frontal view. B: lateral view. C: dorsal view. Brazil: MG, Uberlândia.

Cephalotes nilpiei

Figs. 46a-c, 47a-c, 48

Holotype: BRAZIL, Rio de Janeiro, Parque Nacional de Itatiaia, 15.xii.1966, 950-1000m, H. Reichardt [MZSP] [examined].

Additional material examined: Brazil, MG, Santana do Riacho, Capão, 1253m, -19.206740 -43.495630, S. Powell, 31.vii.2018 /C18-208 (3 gynes, 3 males) [DZUP].

Gyne measurements (N=3): HL 1.73-1.75; HW 1.55; EL 0.35; PW 1.43-1.48; WL 2.15-2.20; PTL 0.63-0.68; PTW 0.28-0.35; PPL 0.78-0.80; PPW 0.30-0.38; GL 2.60-2.70; HBL 0.54-0.58; HBW 0.18-0.20; TL 7.48-8.02; CI 88.6-89.8; OI 22.6; PI 84.4-84.6; HBI 33.3-37.0.

Worker and soldier descriptions can be found in De Andrade and Baroni Urbani, 1999, page 381.

Gyne (first description): Body black to brownish; frontal lobes, lateral margins of pronotum and propodeum, and legs brownish to ferruginous. First gastral tergite with an anterior and a posterior pair of yellowish spots, each one occupying more than one third of the first tergite length (Fig. 46).

Mandibles and dorsum of head foveate; anterolateral portion of cephalic disc rugose with sparse foveae (Fig. 46a); ventral face of head longitudinally rugose-microalveolate. Declivous face of propodeum, legs and gaster microalveolate. Dorsum of mesosoma, petiole and postpetiole microalveolate with shallow foveae (Fig. 46c); lateral of mesosoma microalveolate. Propleura and lower surface of metapleura weakly rugose. Anepisternum and katepisternum weakly foveate (Fig. 46b). Dorsum of gaster anteriorly finely rugose (Fig. 46c).

Body with appressed canaliculate hairs. Mandibles, mesosoma, petiole and postpetiole with short erect simple hairs; mandibles and anterior margin of clypeus with short erect clavate hairs (Fig. 46a). Gaster with appressed simple hairs and some short erect hairs (Fig. 46b).

Head longer than wide (CI 88.6-89.8). Mandibles with a longitudinal lateral angle. Clypeus without pair of denticles (Fig. 46a). Dorsum of

head disc shaped, slightly concave anteriorly. Frontal carinae crenulate anteriorly. Antennae with a three-segmented club. Roof of antennal scrobes with lateral carinae without projections. Lateroventral margins of head without carinae. Vertexal corners forming a pair of broad projections (Fig. 46c).

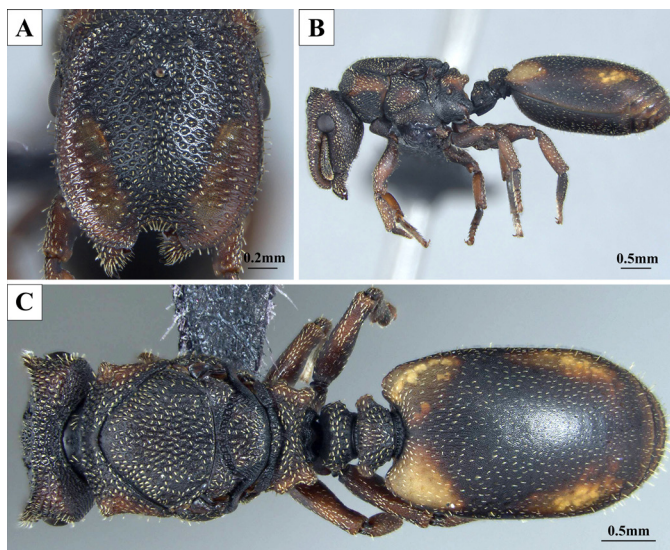


Figure 46 Gyne of *Cephalotes nilpiei*. A: frontal view. B: lateral view. C: dorsal view. Brazil: MG, Santana do Riacho.

In dorsal view, anterior margin of pronotum slightly rounded, anterolateral margins with blunt projection, pronotal carina weakly developed, crenulate, medially interrupted (Fig. 46c). Dorsally, mesoscutum subtriangular, anterior margin convex; notauli absent; parapsidal lines visible and parallel; transscutal line reaching lateral margins of mesosoma; scutoscutellar groove impressed, arched, and scrobiculate; scutellum well delimited and broader anteriorly; axillae acute posteriorly (Fig. 46c). Laterally, mesopleural groove dividing anepisternum and katepisternum; metapleura divided in upper metapleura and lower metapleura by groove; metapleuropropodeal groove not impressed (Fig. 46b). In dorsal view, posterior margin of propodeum concave with a pair of short, blunt denticles (Fig. 46c). Wings unknown.

In dorsal view, petiole subrectangular, anterior margin concave and lateral margins with a tiny denticle (Fig. 46c), subpetiolar process narrow with an acute projection anteriorly (Fig. 46b). Postpetiole longer and wider than petiole, without dorsal elevations, with lateral blunt projections (Fig. 46c), subpostpetiolar process short and compressed anteroposteriorly (Fig. 46b).

Gaster elongate with a narrow anterior lamellar expansion (Fig. 46c).

Male measurements (N=3): HL 0.58-0.64; HW 0.93-1.00; EL 0.38; PW 1.03-1.10; WL 1.48-1.60; PTL 0.40-0.45; PTW 0.30-0.32; PPL 0.40-0.45; PPW 0.28-0.30; GL 0.93-0.98; HBL 0.54-0.56; HBW 0.8; TL 3.82-4.07; CI 153-166; OI 37.5-40.5; PI 125-140; HBI 14.3-14.8.

Male (first description): Body predominantly black; apices of femora, tibiae and tarsi, and edges of each sternite and tergite brownish to yellowish (Fig. 47b).

Mandibles, head, pronotum and metanotum microalveolate with sparse shallow foveae (Fig. 47). Anepisternum, katepisternum and lower mesopleuron rugose; upper mesopleuron and propodeum scabrous (Fig. 47b). Legs, petiole, postpetiole and gaster weakly microalveolate (Fig. 47c).

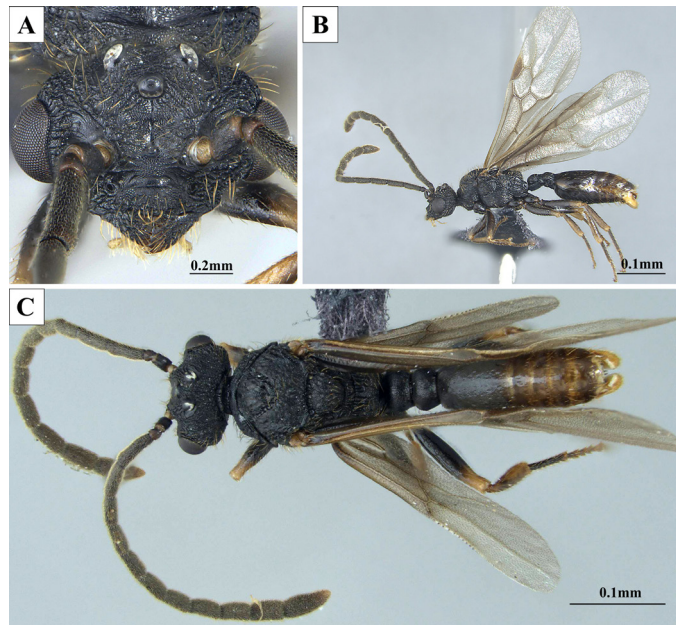


Figure 47 Male of *Cephalotes nilpiei*. A: frontal view. B: lateral view. C: dorsal view. Brazil: MG, Santana do Riacho.

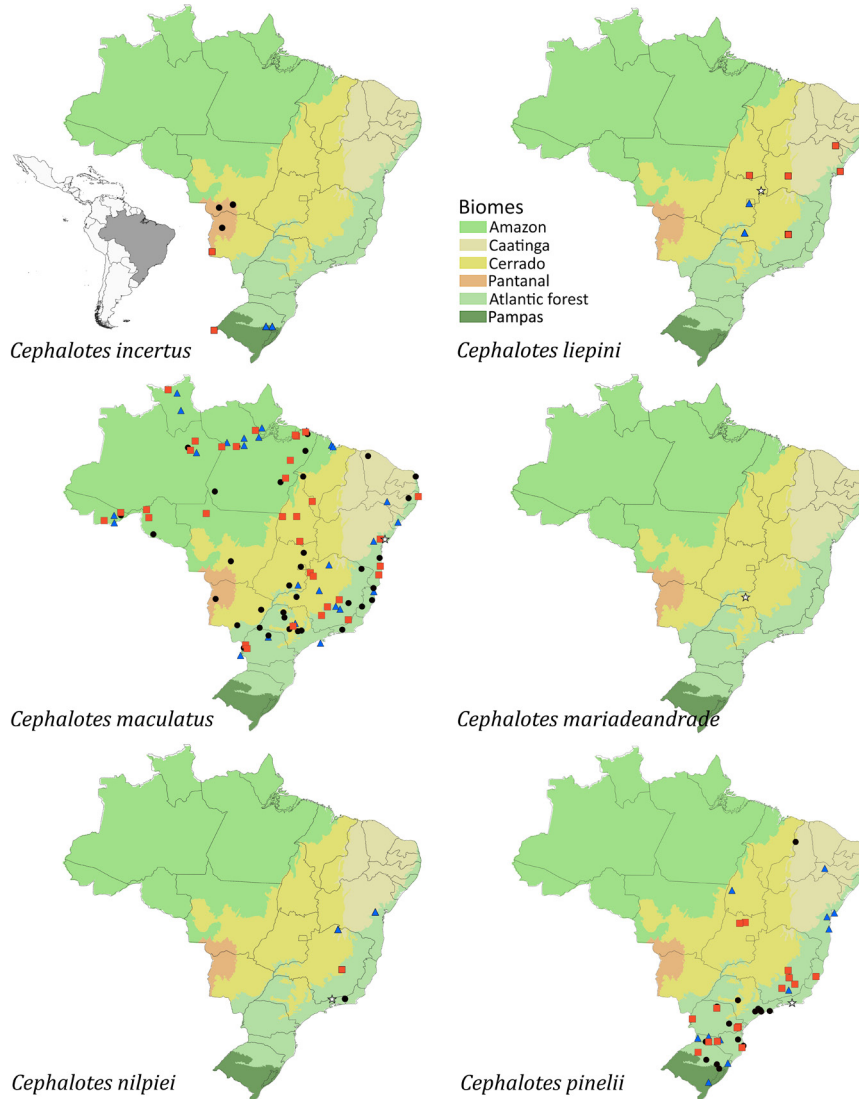


Figure 48 Distribution maps of *pinelii* group in Brazil. White stars: type locality. Black circles: material examined. Red squares: new records. Blue triangles: records not examined from literature. (Literature source: 2, 4, 11, 13, 16, 23, 26, 30, 32, 36, 37, 40, 41, 45, 50, 53, 56, 68, 71, 72, 74).

Body with long and flexuous hairs, more abundant on mandibles, dorsum of head and dorsum of mesosoma. Legs with long hairs only in the internal face of coxae and femur. Hairs shorter on gaster (Fig. 47b).

Head wider than longer (CI 153-166), broader posteriorly. Mandibles with one to three apical teeth, lateral angle absent (Fig. 47a). Clypeus with a median elevation, posterior margin rounded. Frontal carinae not extending posteriorly. The central portion of head slightly elevated. Eyes occupying more than half of head length (Fig. 47a). Ocelli positioned at a central elevation. Antenna as the genus description.

In dorsal view, anterior margin of pronotum slightly rounded, laterally angular (Fig. 47c). Mesoscutum subtriangular; notauli deeply impressed; parapsidal lines visible and parallel; transscutal line reaching the lateral margins of mesosoma; scutoscuteellar groove deeply impressed, arched, and scrobiculate; scutellum well delimited and broader anteriorly; axillae with posterior denticles (Fig. 47c). Laterally, mesopleural groove dividing anepisternum and katepisternum; metapleura divided in upper metapleura and lower metapleura by a groove; metapleuropropodeal groove inconspicuous (Fig. 47b). Dorsal face of propodeum straight and with a rounded angle (Fig. 47b). Wings as in the genus description.

In dorsal view, petiole and postpetiole wider than longer, laterally rounded, without lateral or dorsal projections, subpetiolar and subpostpetiolar process weakly developed (Fig. 47c).

Gaster as long as mesosoma. The first tergite narrower than mesosoma and occupying half or less than the total length of gaster (Fig. 47b), without anterior projection. (Fig. 47c).

The *pusillus* species group

(Figs. 49, 50, 51)

The *spinus* group by Kempf (1951) comprised the De Andrade and Baroni Urbani's *laminatus* and *pusillus* groups, which share the following characters: anterolateral pronotum angulate, separate from the pronotal expansions; propodeum with two pairs of spines or denticles, with the posterior one longer than anterior; dorsal and declivous faces of propodeum differentiated, meeting in a distinct propodeal angle; gaster with distinct anterolateral lamellate borders.

Despite the shared characters, De Andrade and Baroni Urbani (1999) separated the former Kempf's *spinus* group in *laminatus* and *pusillus* groups. The synapomorphy for the *pusillus* group is the absence of fine reticulation on the cephalic ventral face and the absence of angulate hind femora. However, both characters are the same in the *laminatus* group, which includes the remaining species of Kempf's *spinus* group and *C. duckei*, that had been considered an isolated species by Kempf (1951). The synapomorphy for *laminatus* group, according to De Andrade and Baroni Urbani (1999), is the vertexal corners with a truncate lamella, but this character is also present in other groups, including the *pusillus* group. The characters used by Kempf (1951) to join the members of the *pusillus* and *laminatus* groups within the *spinus* group seem more robust. Concordantly, the molecular phylogeny by Price et al. (2016, see their Fig. S3) recovered *C. pusillus* and *C. columbicus* within the *laminatus* group, rendering the *laminatus* group paraphyletic. Based on this molecular and morphological evidence, we here recognize the members of *pusillus* and *laminatus* groups as a unique group, under the name "*pusillus*", since *C. pusillus* is the oldest species in the group (Fig. 54).

Most species in this group occur in Brazil, except for *C. christopherseni*, known so far only from Colombia, Venezuela, and Panama, and for *C. columbicus*, known from Colombia and Venezuela.

Diagnosis: In workers and soldiers, dorsal and declivous faces of propodeum differentiated, meeting in a distinct propodeal angle; propodeum with two pairs of spines, the posterior longer than the anterior (Fig. 2f). Mid and hind basitarsi not flattened.

Brazilian species of *pusillus* group

Cephalotes duckei (Forel, 1906)

Obsolete combination: *Cryptocerus duckei*

Cephalotes inaequalis (Mann, 1916)

Obsolete combination: *Cryptocerus inaequalis*

Cephalotes laminatus (Smith, 1860)

Obsolete combination: *Cryptocerus laminatus*

Cephalotes minutus (Fabricius, 1804)

Obsolete combination: *Cryptocerus minutus*

= *Cephalotes cognatus* (Smith, 1862)

Obsolete combination: *Cryptocerus cognatus*

= *Cephalotes exiguus* (Smith, 1867)

Obsolete combination: *Cryptocerus exiguus*

= *Cephalotes quadrimaculatus* (Klug, 1824)

Obsolete combination: *Cryptocerus quadrimaculatus*

= *Cephalotes volxemi* (Emery, 1878)

Obsolete combination: *Cryptocerus volxemi*

Cephalotes pusillus (Klug, 1824)

Obsolete combination: *Cryptocerus pusillus*

= *Cephalotes caustica* (Pohl & Kollar, 1832)

Obsolete combination: *Formica caustica*

= *Cephalotes elongatus* (Klug, 1824)

Obsolete combination: *Cryptocerus elongatus*

= *Cephalotes obtusus* (Smith, 1858)

Obsolete combination: *Cryptocerus obtusus*

= *Cephalotes pusillus brevispinosa* (Santschi, 1921)

Obsolete combination: *Cryptocerus pusillus brevispinosa*

Cephalotes simillimus (Kempf, 1951)

Obsolete combination: *Paracryptocerus simillimus*

Cephalotes spinosus (Mayr, 1862)

Obsolete combination: *Cryptocerus spinosus*

= *Cephalotes laminatus peruvianus* (Forel, 1911)

Obsolete combination: *Cryptocerus laminatus peruvianus*

= *Cephalotes punctatus* (Mayr, 1862)

Obsolete combination: *Cryptocerus punctatus*

Key to the identification of Brazilian species of the *pusillus* group of *Cephalotes* based on workers

(Figs. 49a-l)

- 1 In dorsal view, petiole subrectangular, a small denticle of the same color as petiole can be present (Fig. 49g).....***C. pusillus***
- 1' In dorsal view, petiole of another shape, with spines with translucent tips (Fig. 49d-f, h-k).....2
- 2 In dorsal view, mesonotal spines absent (Fig. 49d).....***C. spinosus***
- 2' In dorsal view, mesonotal spines present (Fig. 49c, e, h, i).....3
- 3 In posterodorsal view, declivous face of the propodeum with well-marked longitudinal striae occupying the entire surface (Fig. 49j).....***C. minutus***
- 3' In posterodorsal view, declivous face of propodeum without longitudinal striae; if any, they are weakly marked and not occupying the entire surface (Fig. 49k, l).....4
- 4 In dorsal view, posterior propodeal spines curved anteriorly (Fig. 49e).....***C. duckei***
- 4' In dorsal view, posterior propodeal spines curved posteriorly (Fig. 49c, d, h, i).....5
- 5 In frontal view, the distance between the eyes is shorter or at most equal to the length of the head (Fig. 49a).....***C. simillimus***
- 5' In frontal view, distance between eyes greater than head length (Fig. 49b).....6
- 6 In dorsal view, propodeal groove weakly impressed; marked on the sides but absent medially (Fig. 49h).....***C. laminatus***
- 6' In dorsal view, propodeal groove strongly impressed on the entire dorsum (Fig. 49i).....***C. inaequalis***

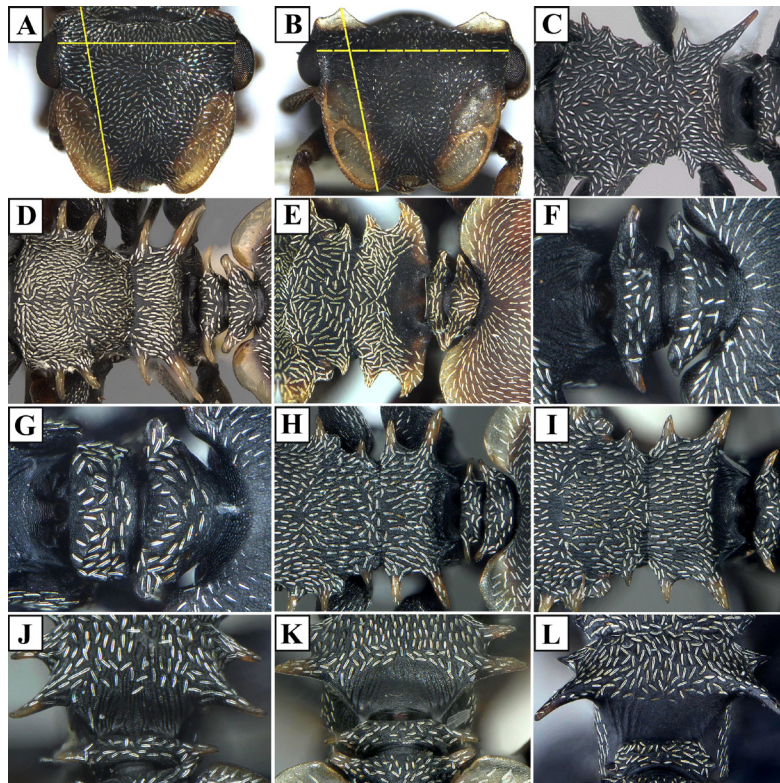


Figure 49 Workers of *pusillus* group. A: *C. simillimus*. B, H and K: *C. inaequalis*. C, G and L: *C. pusillus* [C: CASENT0173703]. D: *C. spinosus* [CASENT0900244]. E: *C. duckei*. F: *C. minutus*. I: *C. laminatus*. J: *C. minutus*.

Key to the identification of Brazilian species of the *pusillus* group of *Cephalotes* based on soldiers

(Figs. 50a-i)

- 1 In dorsal view, petiole subrectangular, without spines; at most with a very tiny denticle (Fig. 50a)..... ***C. pusillus***
- 1' In dorsal view, petiole of another shape; if subrectangular, there are spines with translucent tips (Fig. 50b-g)..... 2
- 2 Margins of declivous face of propodeum with lateral lamellar expansions (Fig. 50c, f, i)..... 3
- 2' Margins of declivous face of propodeum without lateral lamellar expansions (Fig. 50b, d, e, g, h)..... 4
- 3 In dorsal view, posterior propodeal spines curved anteriorly (Fig. 50c)..... ***C. duckei***

- 3' In dorsal view, posterior propodeal spines curved posteriorly (Fig. 50f)..... ***C. simillimus***
- 4 In dorsal view, gastral lamellae width shorter than or equal to the width of the postpetiolar spines (Fig. 50b - yellow arrows)..... ***C. minutus***
- 4' In dorsal view, gastral lamellae width is at least twice the width of the postpetiolar spines (Fig. 50d, e, g - yellow arrows)..... 5
- 5 In dorsal view, gastral lamellae glabrous (Fig. 50e)..... ***C. spinosus***
- 5' In dorsal view, gastral lamellae with hairs (Fig. 50d, g)..... 6
- 6 Posterior propodeal spines bifurcated, spines black with yellowish tips (Fig. 50d)..... ***C. inaequalis***
- 6' Posterior propodeal spines not bifurcated, spines completely black (Fig. 50g)..... ***C. laminatus***

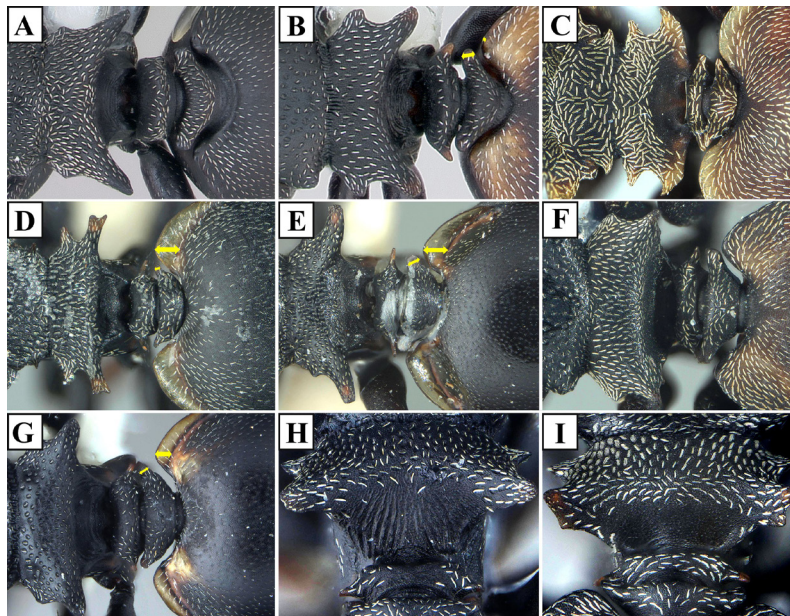


Figure 50 Soldiers of *pusillus* group. A: *C. pusillus*. B and H: *C. minutus*. C: *C. duckei*. D: *C. inaequalis*. E: *C. spinosus*. F and I: *C. simillimus*. G: *C. laminatus*.

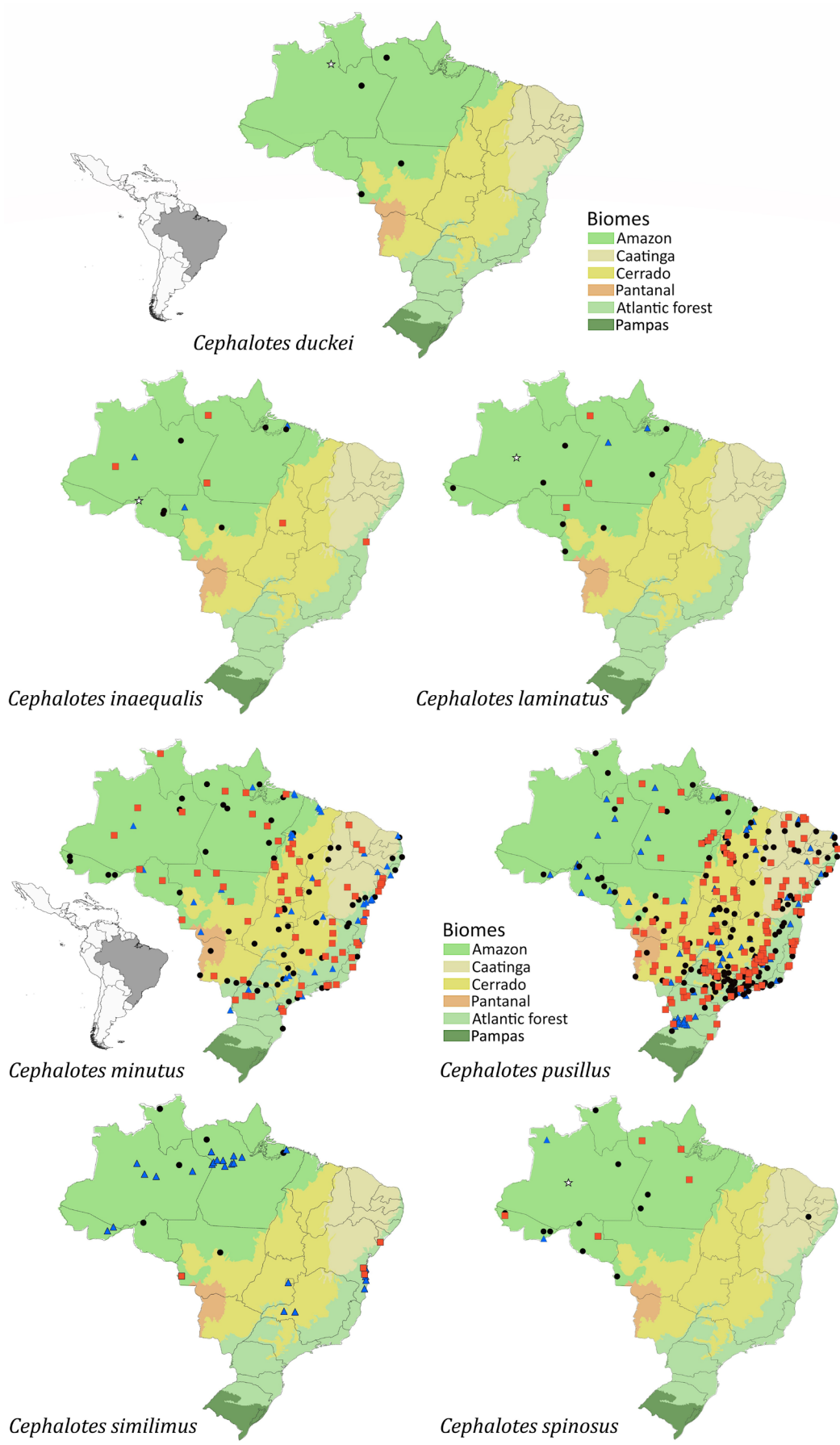


Figure 51 Distribution maps of *pusillus* group in Brazil. White star: type locality. Black circles: material examined. Red squares: new records. Blue triangles: records not examined from literature. (Literature source: 4, 6, 7, 8, 10, 11, 13, 14, 15, 21, 22, 23, 24, 27, 30, 31, 34, 36, 37, 40, 42, 43, 45, 47, 49, 50, 52, 55, 56, 61, 62, 65, 67, 68, 71, 72, 73).

The *solidus* species group

(Fig. 52)

The *solidus* group is monotypic. Its unique species was described by Kempf (1974) as *Zacryptocerus solidus*, within the *angustus* group. The *angustus* and *solidus* groups share the dorsal and declivous faces of propodeum continuous, not meeting in a distinct propodeal angle, but differ by the mesonotum and propodeum unarmed in *solidus*, while in *angustus* there is a pair of denticles on the mesonotum and a series of denticles on propodeum.

In the morphological phylogeny by De Andrade and Baroni Urbani (1999, see their Fig. 24), *C. solidus* is not related with the *angustus* group species, being more closely related to the *pusillus* group. Nevertheless, most of the characters used in their morphological analysis are based on soldiers. However, *C. solidus* is a rarely collected species, with only five workers known so far from northern Brazil (Fig. 52). This species was not included in the molecular phylogeny (Price et al., 2016).

Diagnosis: Dorsal and declivous faces of propodeum continuous, not meeting in a distinct propodeal angle. Metanotum and propodeum unarmed (Fig. 2e).

Brazilian species of *solidus* group

Cephalotes solidus (Kempf, 1974)

Obsolete combination: *Zacryptocerus solidus*

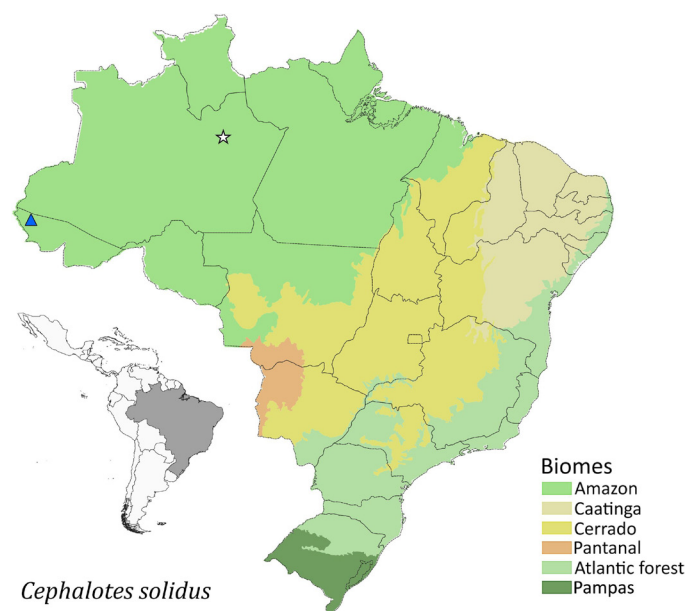


Figure 52 Distribution map of *solidus* group in Brazil. White star: type locality. Blue triangle: record not examined from literature. (Literature source: 13).

The *umbraculatus* species group

(Fig. 53)

The monotypic *umbraculatus* group was created by Kempf (1958a). He discussed the position of the species, which shares characters with the *angustus* and *pinelii* groups, but is different enough to be

separated from them. Kempf's proposal was corroborated by the morphological and molecular phylogenies (De Andrade and Baroni Urbani, 1999, see their Fig. 24; Price et al., 2014, 2016, see their Fig. S3), both phylogenies recover this species as a monophyletic lineage. The recent molecular phylogenies by Price et al. (2014, 2016) recovered *umbraculatus* as a sister group of the clade formed by the *angustus*, *fiebrigi* and *prodigosus* groups (Fig. 54). *Cephalotes umbraculatus* is broadly distributed in Central America and north of South America.

Diagnosis: In workers, body with appressed hairs. Dorsal and declivous face of propodeum continuous, not meeting in a distinct propodeal angle, with a variable number of spines. Dorsum of petiole without denticles. Gaster yellowish with a cross-shaped dark macula, anteriorly with lamellar expansions (Fig. 2p). In soldiers, in dorsal view, pronotum crest with pointed edges (Fig. 3f).

Brazilian species of *umbraculatus* group

Cephalotes umbraculatus (Fabricius, 1804)

Obsolete combination: *Cryptocerus umbraculatus*
= *Cephalotes elegans* (Smith, 1853)

Obsolete combination: *Cryptocerus elegans*
= *Cephalotes flavomaculatus* (Mayr, 1862)

Obsolete combination: *Cryptocerus flavomaculatus*
= *Cephalotes quadriguttatus* (Guérin-Méneville, 1844)

Obsolete combination: *Cryptocerus quadriguttatus*

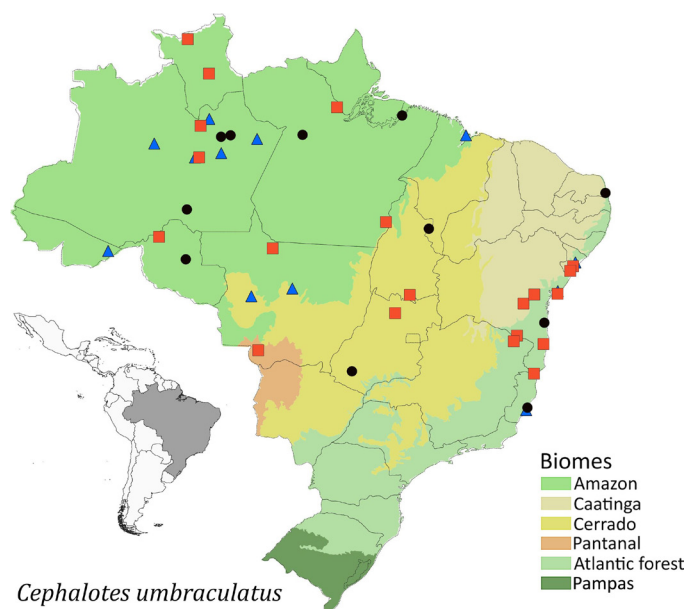


Figure 53 Distribution map of *umbraculatus* group in Brazil. Black circles: material examined. Red squares: new records. Blue triangles: records not examined from literature. (Literature source: 12, 13, 23, 36, 45, 68, 72).

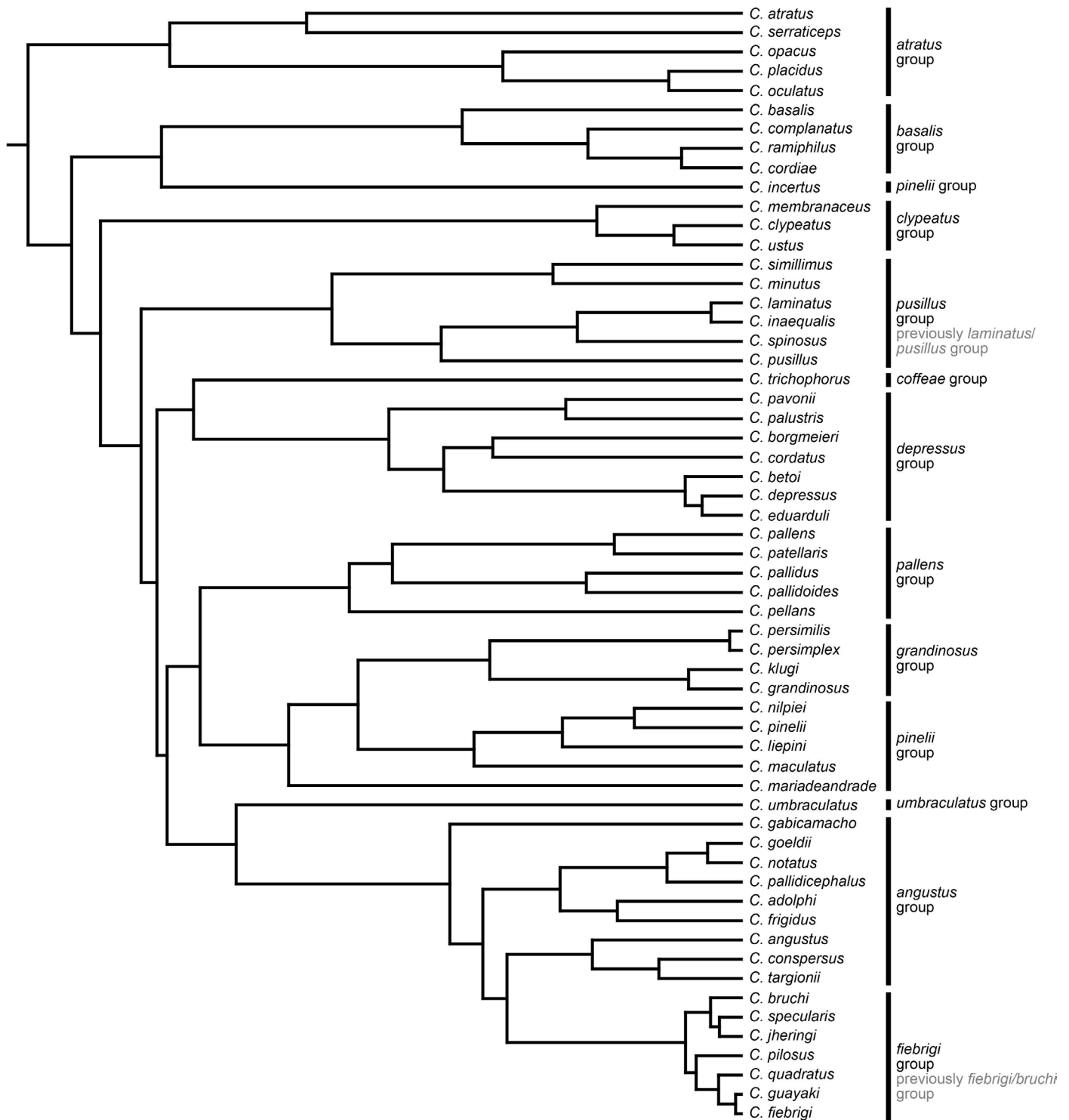


Figure 54 The maximum clade credibility tree from phylogenetic analyses performed by Price et al. (2016) based on morphological and molecular data. The tree has been trimmed to include only those species known from Brazil. The labels for the species groups follow our proposals, including the synonymies, and the previous names for the synonymized groups are shown in grey.

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Conflicts of interest

None.

Author contribution statement

All authors contributed to the concept and design of the study. AMO examined the specimens, described the ants, took photos, made identification keys and the distribution maps. RMF requested loan specimens and contributed to the delimitation of the species. SP sampled specimens and produced the trimmed phylogeny. All authors wrote the manuscript and approved the final version.

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Supplementary material

The following online material is available for this article:

Table S1 - Complete list of the material examined in the present study