UNIVERSIDADE FEDERAL DO PARANÁ

ALINE MACHADO DE OLIVEIRA

ESTUDO TAXONÔMICO DAS ESPÉCIES DO GÊNERO *CEPHALOTES* LATREILLE, 1802 OCORRENTES NO BRASIL

CURITIBA

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Dissertação apresentada como requisito parcial à obtenção do título de Mestre em Ciências Biológicas (Entomologia) no curso de Pós-Graduação em Entomologia, Setor de Ciências Biológicas, Departamento de Zoologia, Universidade Federal do Paraná.

Orientador: Prof. Dr. Rodrigo Machado Feitosa

Coorientador: Prof. Dr. Scott Powell

CURITIBA

2020

Universidade Federal do Paraná
Sistema de Bibliotecas
(Giana Mara Seniski Silva – CRB/9 1406)

Oliveira, Aline Machado de
Estudo taxonômico das espécies do gênero *Cephalotes* Latreille, 1802 ocorrentes no Brasil. / Aline Machado de Oliveira. – Curitiba, 2020.
97 p.: il.

Orientador: Rodrigo Machado Feitosa
Coorientador: Scott Powell

Dissertação (mestrado) - Universidade Federal do Paraná, Setor de Ciências Biológicas. Programa de Pós-Graduação em Entomologia.

1. Formiga. 2. Taxonomia. 3. Savana. I. Título. II. Feitosa, Rodrigo Machado, 1981-. III. Powell, Scott. IV. Universidade Federal do Paraná. Setor de Ciências Biológicas. Programa de Pós-Graduação em Entomologia.

CDD (22. ed.) 595.796

MINISTÉRIO DA EDUCAÇÃO
SETOR DE CIENCIAS BIOLOGICAS
UNIVERSIDADE FEDERAL DO PARANÁ
PRÓ-REITORIA DE PESQUISA E PÓS-GRADUAÇÃO
PROGRAMA DE PÓS-GRADUAÇÃO CIÊNCIAS BIOLÓGICAS
(ENTOMOLOGIA) - 40001016005P5

TERMO DE APROVAÇÃO

Os membros da Banca Examinadora designada pelo Colegiado do Programa de Pós-Graduação em CIÊNCIAS BIOLÓGICAS (ENTOMOLOGIA) da Universidade Federal do Paraná foram convocados para realizar a arguição da dissertação de Mestrado de **ALINE MACHADO DE OLIVEIRA** intitulada: **ESTUDO TAXONÔMICO DAS ESPÉCIES DO GÊNERO *CEPHALOTES* LETREILLE, 1802 OCORRENTES NO BRASIL**, sob orientação do Prof. Dr. RODRIGO DOS SANTOS MACHADO FEITOSA, que após terem inquirido a aluna e realizada a avaliação do trabalho, são de parecer pela sua aprovação no rito de defesa.

A outorga do título de mestre está sujeita à homologação pelo colegiado, ao atendimento de todas as indicações e correções solicitadas pela banca e ao pleno atendimento das demandas regimentais do Programa de Pós-Graduação.

CURITIBA, 20 de Fevereiro de 2020.

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AGRADECIMENTOS

Ao professor Rodrigo Feitosa pela orientação no desenvolvimento desse trabalho, pela confiança, amizade, todo apoio profissional e principalmente emocional e por ser sempre tão presente no meu *mundus*.

Aos colegas de laboratório Alexandre, Amanda, Ana Carolina, Jaqueline, Mila, Natalia, Paloma, Suiane, Tainara, Weslly e Yasmin, pelo companheirismo diário, pelas conversas e incentivo.

Ao professor Scott Powell pela coorientação, pelo material disponibilizado, pelas discussões e pelo apoio e confiança no desenvolvimento desse projeto.

Aos curadores das instituições depositárias e colegas mirmecólogos que tão gentilmente forneceram material para a execução desse trabalho.

Aos meus pais, Cleide e Nelson, por todo amor, dedicação e apoio incondicional a todas as minhas escolhas.

A família que eu escolhi, Andrey e Thais, por serem tão presentes na minha vida e por me proporcionarem um pouco de vida social longe da rotina acadêmica.

A Fabielle por sempre me manter pé no chão, mesmo quando minha mente e coração queriam voar por aí.

A Gabriela por mesmo distante ser tão presente na minha vida, por acreditar em mim e no meu potencial mesmo quando eu duvidava, por ser um dos meus maiores exemplos como mulher cientista e ser meu ponto de apoio e sensatez.

Aos colegas de pós-graduação pela parceria nos estudos.

Aos professores que tive ao longo dessa trajetória por me ensinarem tanto, dentro e fora da sala de aula.

Ao CNPq pelo auxílio financeiro.

“O cientista não estuda a natureza porque ela é útil; ele a estuda porque se deleita nela, e se deleita nela porque ela é bela. Se a natureza não fosse bela, não valeria a pena ser conhecida, e se não valesse a pena ser conhecida, a vida não valeria a pena ser vivida.”

Henri Poincaré, Ciência e Método, 1908

RESUMO

O gênero *Cephalotes* ocorre exclusivamente no Novo Mundo. Todas as espécies do gênero são exclusivamente arbóreas, com os ninhos localizados em galerias abandonadas por outros insetos. Quase todas as espécies são polimórficas, apresentando soldados, responsáveis pela proteção da colônia, os quais utilizam suas cabeças para bloquear a entrada do ninho. A última revisão taxonômica do gênero foi publicada por De Andrade e Baroni Urbani (1999), que sinonimizaram os gêneros *Zacryptocerus* e *Eucryptocerus* sob *Cephalotes*, reconheceram 118 espécies e forneceram chaves de identificação para todas as espécies. No mesmo trabalho os autores forneceram a primeira filogenia para o gênero baseada em caracteres morfológicos, dividindo as espécies em 24 grupos, com base nos clados da filogenia. No Brasil, ocorrem cerca de 60 espécies, distribuídas em 15 grupos. Desde então, apenas uma espécie foi descrita, *C. specularis* Brandão, Feitosa, Powell e Del-Claro, 2014. A última filogenia do gênero, baseada em dados moleculares, elaborada por Price et al. (2016), corroborou grande parte dos grupos propostos na filogenia morfológica, porém demonstrou que alguns grupos são artificiais. Diante disso, o objetivo desse trabalho foi examinar taxonomicamente as espécies ocorrentes no Brasil, baseando-se em morfologia e nas informações filogenéticas. Após o exame de cerca de 15.000 exemplares, foi possível reconhecer 64 espécies para o Brasil, distribuídas em 13 grupos, sendo cinco espécies novas. São elas: *C.* **sp. n. A**, *C.* **sp. n. B**, *C.* **sp. n. C**, pertencendo ao grupo *angustus*, as duas primeiras conhecidas pela operária, soldado e gine, a terceira conhecida apenas pela operária; *C.* **sp. n. D**, grupo *fiebrigi*, conhecida pela operária e soldado; e *C.* **sp. n. E**, grupo *pinelii*, conhecida por todas as castas e sexos. Além disso, fornecemos descrições para soldado e gine de *C. adolphi*, e para gine e macho de *C. nilpiei*. A espécie *C. marginatus* foi sinonimizada sob *C. atratus* e os grupos *bruchi* e *laminatus* foram sinonimizados sob *fiebrigi* e *pusillus*, respectivamente. As informações sobre distribuição das espécies de cada grupo foram ampliadas e atualizadas e chaves de identificação para os grupos de espécies e para cada grupo são fornecidas para as operárias e soldados.

Palavras-chave: Neotrópico. Revisão taxonômica. Attini. Formigas arbóreas. Floresta. Savana.

ABSTRACT

The ant genus *Cephalotes*, whose members are known as turtle-ants, is uniquely found in the New World. All *Cephalotes* species are exclusively arboreal, nesting in galleries in wood perforated and abandoned by other insects. Almost all species are polymorphic, with soldiers that are responsible for protecting the nest entrance using their heads. The last taxonomic revision on the genus was published by De Andrade and Baroni-Urbani (1999) who synonymized the genera *Zacryptocerus* and *Eucryptocerus* under *Cephalotes* and recognized 118 species divided into 24 species groups. That study also provided a morphological phylogeny, and a key for the identification for all species. According to the same work, about 60 species are known so far to Brazil, divided into 15 species groups. Since then, a single species was described, *C. specularis* Brandão, Feitosa, Powell and Del-Claro, 2014. The last comprehensive phylogeny of the genus, using molecular data, elaborated by Price et al. (2016), showed that some of De Andrade and Baroni-Urbani's groups are evolutionary artificial. So, in this study we propose a re-examination of the Brazilian species based on morphological and phylogenetic data. After examination of more than 15,000 specimens, we were able to recognize 64 species for Brazil distributed in 13 species groups. Five species are described as new: *C.* **sp. n. A**, *C.* **sp. n. B** and *C.* **sp. n. C** of *angustus* group, the two first known for worker, soldier and gyne, the third one known only for the worker; *C.* **sp. n. D**, *fiebrigi* group, known for worker and soldier; and *C.* **sp. n. D**, *pinelii* group, known for all forms (worker, soldier, gyne and male). Descriptions are provided for soldier and gyne of *C. adolphi*, and for gyne and male of *C. nilpiei*. The species *C. maginatus* was synonymized under *C. atratus*. The *bruchi* group was synonymized under *fiebrigi*, and the *laminatus* group was synonymized under *pusillus*. The distribution information of each species group is provided and updated. In addition, illustrated identification keys to workers and soldiers are provided for species groups and for each group.

Keywords: Neotropics. Taxonomic review. Attini. Arboreal ants. Forest. Savanna.

SUMARIO

1. INTRODUÇÃO GERAL

As formigas compreendem uma única família de insetos, Formicidae. Representada por cerca de 13.600 espécies, distribuídas em 336 gêneros e 17 subfamílias. Dentre estas, a subfamília Myrmicinae é a mais diversa, com quase 7.000 espécies, distribuídas em seis tribos e 145 gêneros (Bolton, 2020). A tribo Attini apresenta cerca de 2.600 espécies e 47 gêneros, incluindo *Cephalotes*, um dos mais diversos e antigos gêneros de formigas.

O histórico taxonômico de *Cephalotes* tem início em 1758, com a publicação de um dos trabalhos mais significativos para o estudo e classificação de seres vivos, *Systema Naturae*; neste trabalho, Linnaeus descreveu inúmeros gêneros de organismos, entre eles *Formica*, que dá o nome a família Formicidae, além de diversas espécies pertencentes a este gênero, incluindo *Formica atrata*. Em seguida, Fabricius (1793) descreveu o gênero *Dorylus*. E em 1802, Latreille descreveu o terceiro gênero de formigas conhecido pela ciência, *Cephalotes*, por monotipia com base em *F. atrata*, que a partir de então ganhou o nome de *Cephalotes atratus*. No ano seguinte, em 1803, Latreille descreveu o gênero *Cryptocerus* também baseado em *F. atrata*. Em 1804, Fabricius publicou a sinonímia de *Cephalotes* em *Cryptocerus*. Essa sinonímia perdurou por mais de 100 anos, até a publicação da primeira edição do Código Internacional de Nomenclatura Zoológica, em 1905, no qual foi apresentado o princípio da prioridade. Diante disso, o nome *Cephalotes* tornou-se valido, uma vez que foi descrito anteriormente a *Cryptocerus*, porém a sinonímia só foi publicada no ano de 1913 por Wheeler. No ano seguinte, em 1914, *Cephalotes* foi incluída na subfamília Myrmicinae, na tribo Cryptocerini (Emery, 1914). Em 1949, Smith descreveu a tribo Cephalotini, incluindo nela os gêneros *Cephalotes*, *Zacryptocerus* Wheeler, 1911, *Paracryptocerus* Emery, 1915, *Hypocryptocerus* Wheeler, 1920, *Cyathomyrmex* Creighton, 1933, *Harnedia* Smith, 1949 e *Procryptocerus* Emery, 1887 (Smith, 1949).

A primeira revisão taxonômica incluindo *Cephalotes* foi realizada em 1951 por Kempf, que revisou toda a tribo Cephalotini, reconheceu seis espécies pertencentes a *Cephalotes* e descreveu o gênero *Eucryptocerus*. Porém nos anos seguintes, quatro dos gêneros incluídos em Cephalotini foram sinonimizados: *Cyathomyrmex* e *Harnedia* foram sinonimizados em *Paracryptocerus* (Kempf, 1972); *Paracryptocerus* e *Hypocryptocerus* foram sinonimizados em *Zacryptocerus* (Kempf, 1973).

Kempf foi um grande estudioso da tribo Cephalotini, dedicando cerca de 30 anos de trabalho a essa tribo. Entre os anos de 1951 e 1978, publicou pelo menos 16 trabalhos sobre essas formigas, incluindo revisões (Kempf, 1951, 1952, 1958a, 1969, 1978), descrições de novas espécies (Kempf, 1953, 1960, 1964, 1967, 1972, 1973, 1974), sinonímias (Kempf, 1958b, 1963), catálogos (Kempf, 1959) e notas (Kempf, 1965).

Após a morte de Kempf, outros autores a se dedicarem ao estudo dessas formigas foram De Andrade e Baroni Urbani, que publicaram sua revisão do gênero em 1999. Nesse trabalho, os gêneros *Eucryptocerus*, com três espécies e *Zacryptocerus*, com 75 espécies, foram sinonimizados em *Cephalotes*, até então com apenas 10 espécies. Assim, a tribo Cephalotini passou a ser representada por apenas dois gêneros, *Cephalotes* e *Procryptocerus* (De Andrade & Baroni Urbani, 1999).

Esse trabalho também apresentou a primeira filogenia do gênero baseada em caracteres morfológicos, que subdividiu o gênero em 24 grupos de espécies, designados a partir dos clados gerados na árvore filogenética. Os autores apresentaram descrições para cada uma das até então 118 espécies conhecidas, incluindo as 31 espécies novas descritas no trabalho. Em adição, o estudo abrangeu também as espécies fósseis, apresentando descrições para cada uma delas e sinonimizando o gênero fóssil *Exocryptocerus* Vierbergen & Scheven, 1995 em *Cephalotes.* Filogeneticamente, o estudo propôs *Procryptocerus* como grupo irmão de *Cephalotes* e o gênero do Velho Mundo *Cataulacus* Smith, 1853, como irmão do clado formado pelos dois primeiros. Finalmente, os autores apresentaram chaves de identificação para todas as castas e sexos conhecidos (De Andrade & Baroni Urbani, 1999). Porém, estas chaves podem ser desafiadoras, sendo necessário muitas vezes recorrer a descrição de cada espécie, que por vezes podem ser abrangentes e pouco elucidativas, tornando a identificação precisa das espécies uma tarefa bastante difícil. Apesar disso, esse trabalho ainda é o mais abrangente e atual para a identificação das espécies de *Cephalotes*. Após o trabalho de De Andrade e Baroni Urbani, apenas uma nova espécie foi descrita, *Cephalotes specularis* Brandão, Feitosa, Powell & Del-Claro, 2014.

Em 2015, um trabalho bastante abrangente demonstrou que muitas tribos da subfamília Myrmicinae não eram naturais, incluindo a tribo Cephalotini, seus dois gêneros foram então alocados na tribo Attini. A relação de gêneros irmãos entre *Cephalotes* e *Procryptocerus* foi recuperada, porém o gênero irmão recuperado para esse clado foi *Pheidole*. O gênero considerado como irmão daqueles até então era *Cataulacus*, que nesse trabalho foi recuperado como pertencente à tribo Crematogastrini (Ward et al., 2015).

A distribuição de *Cephalotes* está restrita ao Novo Mundo, cobrindo 30 países, incluindo quase todos os países da América do Sul, grande parte dos países da América Central e o sul dos Estados Unidos (De Andrade & Baroni Urbani, 1999; Antwiki, 2020). Atualmente *Cephalotes* apresenta 119 espécies viventes e 16 espécies fósseis (Bolton, 2020). É o 26º maior gênero da família Formicidae, o 11º maior gênero da subfamília Myrmicinae e o 8º com maior número de espécies fósseis entre os 66 gêneros que apresentam espécies fósseis conhecidas (Antwiki, 2020). O país com a maior diversidade é o Brasil, com 59 espécies registradas (Bolton, 2020), o que representa quase metade das espécies conhecidas. Em comparação, os cinco países com maior diversidade depois do Brasil são: Colômbia (45 espécies); Equador (31); México (27); Peru (26);

e Argentina (24). Dessas 59 espécies, 11 são endêmicas do Brasil (De Andrade & Baroni Urbani, 1999; Brandão et al., 2014; Antwiki, 2020; Sandoval-Gómez & Sánchez-Restrepo, 2019).

Algumas espécies dos clados mais antigos evolutivamente, como *C. atratus*, *C. pusillus* Klug, 1824 e *C. minutus* (Fabricius, 1804), apresentam uma distribuição geográfica extremamente ampla e são numericamente abundantes na maioria dos países e biomas. Já as espécies dos clados mais recentes, como os grupos *fiebrigi* e *angustus*, tem a distribuição mais restrita, concentrando maior diversidade nos ambientes mais áridos, como o Cerrado (De Andrade & Baroni Urbani, 1999, Price et al., 2014, 2016).

Esse gênero é estritamente arbóreo, conhecido por nidificar em cavidades ocas nas copas das árvores, geralmente deixadas por larvas de besouros ou outros insetos (Powell, 2008). Conforme a colônia cresce, novas cavidades precisam ser encontradas, pois essas formigas não possuem habilidade para escavar os troncos das árvores que habitam (Powell, 2014). Essas cavidades fornecem proteção aos ninhos e permitem a estratégia de defesa por meio da fragmose, realizada pelo bloqueio da entrada do ninho pelas cabeças de uma ou mais formigas. Esse bloqueio é feito pelos soldados da colônia, que na maioria das espécies possuem cabeça em formato de disco, encaixando perfeitamente na abertura. Por apresentarem o esclerito extremamente rígido essa forma de defesa é muito eficaz (Creighton & Gregg, 1954; Creighton & Nutting, 1964).

O nível de especialização da cabeça dos soldados para defesa do ninho pode variar de acordo com a espécie, que pode ou não apresentar soldado, ou apresentar diferentes graus de especialização. Quatro morfotipos de cabeça de soldado estão sendo propostos por Powell et al. (in press): tipo quadrado, em que a carena frontal e contínua com os cantos vertexais; tipo domo, com a carena frontal terminando sobre os olhos ou posteriormente aos olhos, não atingindo os cantos vertexais; tipo disco, com a carena frontal fusionada aos dentes vertexais medianos, formando um disco cefálico, de forma que os cantos vertexais estão em um plano inferior ao disco; e tipo prato, semelhante ao disco, porém a carena frontal esta fusionada aos lobos frontais, cobrindo as mandíbulas em vista frontal.

Em espécies sem soldado ou com soldado de cabeça tipo quadrada ou domo, a tendência da colônia é ocupar cavidades com entradas maiores que a circunferência da cabeça de uma única formiga. Assim, são necessários vários indivíduos para fazer a proteção da entrada do ninho (Delabie, 1994; De Andrade & Baroni Urbani, 1999), como ocorre em *C. atratus*, *C. clypeatus* e *C. pusillus* (Powell, 2008). Já em espécies que apresentam a cabeça tipo disco ou prato, a tendência é ocupar cavidades com a mesma circunferência da cabeça de uma única formiga, de forma que apenas um indivíduo seja necessário para proteção da entrada do ninho (Creighton & Gregg, 1954; Creighton 1963; Creighton & Nutting, 1964), como ocorre em *C. depressus* Klug, 1824 e *C. persimilis* De Andrade & Baroni Urbani, 1999 (Powell, 2008).

Powell (2008) demonstrou a relação entre a evolução da especialização ecológica e a morfologia, na qual a presença de cabeças mais especializadas ocorre em linhagens mais recentes, enquanto cabeças menos especializadas ou a ausência de especialização é característica de linhagens mais antigas. Além disso, a maior especialização para a tarefa de defesa do ninho resulta no menor envolvimento dos soldados com a tarefa de forrageamento (Powell, 2008).

O forrageamento em *Cephalotes* geralmente ocorre no dossel das árvores e a dieta varia muito entre as espécies. Há registros de *C. maculatus* Smith, 1876, seguindo as trilhas de forrageamento de *Azteca trigona* Emery, 1893 para explorar suas fontes de alimento (Adams, 1990); enquanto *C. atratus* e *C. pusillus* coletam néctar, secreções de hemípteros, excremento de pássaros, e diversas outras espécies se alimentam de pólen (Creighton, 1967; Baroni Urbani & De Andrade, 1997; Byk & Del-Claro, 2010). Além disso, há associações com diferentes espécies de bactérias encontradas no trato digestivo das formigas, que auxiliam na digestão (Jaffe et al., 2001; Bution et al., 2008).

Uma estratégia de defesa utilizada por *Cephalotes* e muito estudada na espécie *C. atratus* (Yanoviak et al., 2005, 2010, 2011; Yanoviak & Dudley, 2006) é a chamada descida aérea direcionada. Trata-se de uma forma rápida de fugir de possíveis ameaças na qual as operárias saltam de galhos mais altos e planam controlando sua descida com movimentos das pernas, deslizando para o tronco de sua árvore hospedeira, impedindo uma aterrissagem arriscada no sub-bosque e facilitando um rápido retorno ao ninho (Yanoviak et al., 2005). As operárias utilizam pistas visuais para direcionar os locais de pouso, principalmente o brilho das colunas verticais dos troncos e o contraste com a vegetação (Yanoviak & Dudley, 2006), tornando essa estratégia segura e eficaz (Yanoviak et al., 2010, 2011).

Como visto, *Cephalotes* é um gênero muito estudado em relação a sua biologia e aspectos evolutivos. Recentemente, filogenias baseadas em dados moleculares e combinando dados moleculares com morfológicos foram propostas (Price et al., 2014, 2016). Essas filogenias corroboraram a maioria dos clados propostos por De Andrade & Baroni Urbani, porém revelaram alguns grupos artificiais. Nos grupos *fiebrigi*/*bruchi*, a espécie *C. bruchi* aparece interna ao grupo *fiebrigi*. Nos grupos *laminatus*/*pusillus* a espécie *C. pusillus* surge entre as espécies do grupo *laminatus*. Finalmente, o grupo *pinelii* se apresenta polifilético, com algumas espécies relacionadas filogeneticamente ao grupo *grandinosus*, mais apicais na filogenia, enquanto outras espécies do grupo são comparativamente mais basais e relacionadas filogeneticamente aos grupos *bimaculatus* e *texanus*.

Diante disso, o objetivo desse trabalho é unir informações filogenéticas e morfológicas no estudo taxonômico das espécies de *Cephalotes* ocorrentes no Brasil. Assim, reorganizar os grupos de espécies propostos por De Andrade & Baroni Urbani (1999), descrever novas espécies, atualizar os dados sobre distribuição e fornecer novas chaves de identificação ilustradas,

facilitando a identificação acurada dos exemplares e expandindo o conhecimento acerca deste gênero comumente representado em todos os ecossistemas terrestres brasileiros.

A TAXONOMIC STUDY OF THE BRAZILIAN TURTLE-ANTS (FORMICIDAE: MYRMICINAE: *CEPHALOTES*)

2. Abstract

This study analyzed the taxonomy of the Brazilian species of the ant genus *Cephalotes*. We recognize 64 species for Brazil distributed in 13 species groups. Five species are described as new: to *angustus* group, ***C*. sp. n. A**, ***C*. sp. n. B**, known for the worker, soldier and gyne, and ***C*. sp. n. C**, known for worker; to *fiebrigi* group, ***C*. sp. n. D**, known for worker and soldier; to *pinelii* group, ***C*. sp. n. E**, known for all forms (worker, soldier, gyne and male). 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 maginatus* is synonymized under *C. atratus*. The *bruchi* and the *laminatus* species groups are synonymized under *fiebrigi*, and *pusillus* groups, respectively. The distribution information of each species group is provided. In addition, illustrated identification keys to workers and soldiers are provided for species groups and for the species in all groups.

Keywords: Neotropics, Taxonomic review, Attini, Forest, Savanna.

3. Introduction

The ant genus *Cephalotes*, Latreille, 1802, known as the turtle ants, is limited to the New World, occurring throughout the Neotropical region and south of the 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 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, 2014). Almost all species are polymorphic, presenting soldiers that are responsible for protecting the nest entrance using their heads, which is highly differentiated, to block the nest entrance passageway (De Andrade and Baroni Urbani, 1999). 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 the urine deposits of arboreal mammals (Creighton, 1967; Baroni Urbani and De Andrade, 1997; Powell 2008, Byk and Del-Claro, 2010).

The taxonomic history of this genus is very long, since it was described by Linnaeus in 1758, at the Systema Naturae, under the name *Formica atrata*. Latreille, in 1802, described the genus *Cephalotes* by monotypy based on *F. atrata*, which became *Cephalotes atratus*. But in the next year, Latreille described *Cryptocerus* also based on *F. atrata*. So, in 1804, Fabricius synonymized *Cephalotes* under *Cryptocerus*, and this name remained valid for more than one century, until the publication of The International Code of Zoological Nomenclature (ICZN) and the priority principle in 1905, thereby Wheeler synonymized *Cryptocerus* under *Cephalotes* (1913), making *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 reviewed the entire Cephalotini tribe, recognized six species belonging to *Cephalotes* and described the genus *Eucryptocerus*. In the next years, Kempf worked extensively with Cephalotini, dedicating almost three decades of work to this tribe. From 1951 to 1978, Kempf published at least 16 papers on these ants, including reviews (Kempf, 1951, 1952, 1958a, 1969, 1978), descriptions of new species and new records (Kempf, 1953, 1960, 1964, 1967, 1972, 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*.

In the last taxonomic revision of the genus, published by De Andrade and Baroni-Urbani in 1999, the authors synonymized *Zacryptocerus* (75 species) and *Eucryptocerus* (three species) under *Cephalotes* (until then constituted by 10 species). In addition, 31 new species were described by De Andrade in that study, totaling 118 valid species divided into 24 species groups. That study also provided a morphological phylogeny and identification keys for all species. According to the same work, 59 species are known so far to Brazil, divided into 15 species groups. Since then, a single species was described, *C. specularis* Brandão, Feitosa, Powell and Del-Claro, 2014.

The study of De Andrade and Baroni Urbani (1999) provided a discussion about the limits and phylogenetic position of Cephalotini tribe. Based on their phylogeny, the authors hypothesized that the Cephalotini sister group would be the Old World monotypic tribe Cataulacini. However, a recent molecular phylogeny on Myrmicine ants demonstrated that Cephalotini and Cataulacini are not closely related. So, 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*, Smith, 1853*,* the single member of the tribe Cataulacini,

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, containing 61 species, corroborated most of the species groups of De Andrade and Baroni Urbani's morphological phylogeny, but also showed that some groups are evolutionary artificial (Price et al., 2014). The *angustus*, *fiebrigi, bruchi laminatus* and *pusillus* groups, were recovered as paraphyletic and the *pinelii* 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, we examined the species of *Cephalotes* occurring in Brazil based on morphology and considering phylogenetic data 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 and provide illustrated identification keys for species groups and for the species in each group known to occur in Brazil, both for workers and soldiers.

4. Material and Methods

We examined and measured adult ant specimens with a Leica S8APO stereomicroscope equipped with an ocular micrometer. We also examined specimens by images from the Antweb.org platform.

The specimens examined in this study are from the following institutions:

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, BA, 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, SP, Brazil.
INPA Instituto Nacional de Pesquisas da Amazônia, Manaus, AM, Brazil.
JTLC John T. Longino Collection, University of Utah, Salt Lake City, Utah, USA.

MHNG Musée d'Histoire Naturelle, Geneva, Switzerland.

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

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

MPEG Museu Paraense Emilio Goeldi, Belém, PA, Brazil.

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

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

NHMB Naturhistorisches Museum, Basel, Switzerland.

NHMW Naturhistorisches Museum Wien, Viena, 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 Ceara, Fortaleza, CE, Brazil.

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

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

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

UFMG Laboratório de Ecologia de Insetos, Universidade Federal de Minas Gerais, Belo Horizonte, MG, 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. Measurements 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 dorsally on the sagittal plane.

HW: the maximum head width behind the eyes, including the posterior expansions.

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 basal angle of the metapleuron.

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: Maximum length of the hind basitarsus.
HBW: Maximum width of the hind basitarsus.
TL: the summed length of HL, WL, PTL, PPL, and GL.
CI: cephalic index. HW x 100/HL.
OI: optical index. EL x 100/HW.
PI: petiolar index. PTL x 100/PTW.
HBI: hind basitarsal index. HBW x l00/HBL.

High-resolution images were obtained with a Zeiss Stereo DiscoveryV20 steromicroscope attached to a Zeiss Axiocam 305 color video camera in the *Laboratório de Sistemática e Biologia de Formigas* - UFPR. Photos were combined by the stacker of digital image files system Combine ZP 1.0. The plates for the identification keys are composed by photos by the authors and from Antweb.org. For the photos from Antweb.org we provide the unique identifier codes in the captions of each plate. These photos are here used and edited under a Creative Commons license CC BY 3.0. Some images were edited in Photoshop CS6 (Adobe) to enhance parameters of brightness and contrast.

The species distributions are given in tables, with the acronyms of Brazilian states where each species occurs. These tables also contain the records from the last taxonomy revision (De Andrade and Baroni Urbani, 1999), the records from literature since the last revision (after 1999), and the new records provided by this study. The literature records are divided into two columns, one for records exclusively from literature, of which we did not examine the material, and another column for literature and this study, of which we examined material from the same state, confirming the record. All records from the literature in the tables are given by a number which matches with a reference in the list attached. The material examined in this study can be seen in the supplementary material.

The terms for external morphology of adults and pilosity follow De Andrade and Baroni Urbani (1999) and Wilson (1955). Surface sculpturing follows Harris (1979). For alate forms terms for external morphology follow Boudinot (2015) and for wing descriptions follow Yoshimura and Fisher (2012). 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 head of soldiers is here categorized in four morphotypes, square, dome, disc and dish. The square morphotype is defined by frontal carinae forming a continuous carinae with the vertexal corners. The domed morphotype is defined by the frontal carinae terminating posteriorly over the eyes, not continuous with the vertexal corners. The disc morphotype is defined by the frontal carinae forming a continuous carinae over the eyes, fusing with median-vertexal teeth

posteriorly, creating a unified dorsal cephalic disc. The dish morphotype is similar to disc, but frontal carinae and frontal lobes are fused anteriorly covering completely the mandibles in frontal view (Powell et al., 2020 “in press”).

5. 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.

Diagnosis (De Andrade and Baroni-Urbani, 1999; and this study): Frontal carinae covering the genae in frontal view. Mandibles small and thick, with two apical teeth. Eyes very close to the vertex. Deep antennal scrobes. Hard integument.

Worker (after Kempf, 1951; and this study): Mandibles small and thick, with two apical teeth. Palpal formula 5:3. Clypeus narrow. Frontal lobes greatly expanded and covering the genae. Frontal carinae strongly divergent posteriorly and reaching the vertex. Antennal scrobes deeply excavated. Antennae with 11 segments. Lateral margin of pronotum with spines, denticles or lamellae. Mid and hind tibiae without apical spurs. The first tergite of gaster comprises almost the total length of gaster. Sting reduced or missing.

Soldier (De Andrade and Baroni-Urbani, 1999; and this study): Present in almost species. Differs from the worker, in most species, by the head specialization, which varies in degree of specialization in four morphotypes. The square morphotype occurs in *basalis*, *clypeatus* and *depressus* groups. The dome morphotype occurs in *pusillus* group and some species of *fiebrigi*

group. The disc morphotype occurs in *angustus*, *grandinosus*, *pinelii*, *umbraculatus* groups and some species of the *fiebrigi* group. The dish morphotype occurs only in the *pallens* group. And by the presence, in all species, of a transverse carina on the dorsum of pronotum, with variable in degree developed.

Gyne (after Kempf, 1951; De Andrade and Baroni-Urbani, 1999; and this study): Head normally like the soldiers, if such caste is present. Eyes large; ocelli always present. Scutum and scutellum weakly convex to flat. Wing venation developed. Forewing with Sc+R meeting the strongly pigmented stigma in a weak hinge; 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 the middle, M forming a submarginal closed cell with Rs and Rs+M, and a discal cell with Cu and 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 R and Rs; M+Cu diverging in Cu and rs-m+M, which is formed anteriorly by M and posteriorly by rs-m until the junction with Rs; vein A extends beyond the cu-a, which is interrupted, not connecting M+Cu and A; length of R, Rs, Cu, and A can be variable between specimens, but never reaching the margin of wing. Gaster longer than mesosoma, with four tergites visible, the first one occupying almost the total length of gaster.

Male (after Kempf, 1951; and this study): Head subcircular. Mandibles strong, the masticatory margin usually with one apical tooth. Clypeus short. Frontal carinae short to obsolete. Antennal scrobes vestigial to absent. Antennae with 13 segments; scapes shorter than the second funicular segment; the pedicel is shorter than the second segment and the scapes. Thorax usually with the scutum Y-shaped, deeply impressed. Hind tibiae usually without an apical spur. Petiole cylindrical or nodiform. Wing as in gyne. Gaster usually shorter than mesosoma, with five tergites visible, the first one always larger than the others.

Key to the identification of Brazilian species groups of *Cephalotes* based on workers
(Figure 1)

1 In lateral view, vertexal corners with two pairs of spines, one posterodorsal (pd) and other posteroventral (pv) (Fig. 1a)… ***atratus* group**

1’ In lateral view, vertexal corners can present projections, but in a different conformation than that above, usually formed by lamellar expansions (le) (Fig. 1b, 1c)… 2

2 In dorsal view, propodeum without lateral projections (Fig. 1e)… ***solidus* group**

2’ In dorsal view, propodeum with lateral projections. These projections can be spines (ps), denticles (Fig. 1f, 1g, 1h) or lamellar expansions (ple) (Fig. 1i, 1k, 1l, 1o), even present only on declivous face of propodeum (Fig. 21c)… 3

3 In dorsal view, lateral margins of propodeum with lamellar expansions (le) (Fig. 1i, 1k, 1l, 1p), even present only on declivous face of propodeum (Fig. 33c)… 4

3’ In dorsal view, lateral margins of propodeum with spines (ps) or denticles (Fig. 1f, 1g, 1h)… 7

4 In dorsal view, gaster thoroughly surrounded by lamellar expansions (Fig.1o)… ***clypeatus*** **group**

4’ In dorsal view, gaster with lamellar expansions restricted to the anterior portions (leg) (1k, 1l)… 5

5 In frontal view, vertexal corners extending laterally above the eyes (Fig. 1d). Body color reddish brown… ***pallens*** **group**

5’ In frontal view, vertexal corners not extending laterally above the eyes (Fig. 1c). Body variable in color… 6

6 Posterior femora with lamellar expansions (fle) in dorsal and/or ventral face, which frequently are crenulate and narrow (Fig. 1k)… ***grandinosus*** **group**

6’ Posterior femora without lamellar expansions (Fig. 1l)… ***pinelii*** **group**

7 In dorsal view, propodeum with two pairs of spines (disregarding possible denticles in the spines), the anterior one longer than the posterior one and curved backwards (Fig. 1g)… ***depressus*** **group**

7’ In dorsal view, propodeum with variable number of spines, if there are two pairs, the anterior one is never longer than the posterior (Fig. 1f, 1h)… 8

8 In dorsal view, first gastral tergite yellowish, with a cross-shaped dark macula (Fig. 1p)… ***umbraculatus*** **group**

8’ In dorsal view, first gastral tergite variable in color. Macula absent or in a shape different than a cross (Fig. 1r)… 9

9 Posterior femora with a median projection (Fig. j). Posterior tibiae usually emarginated (Fig. j)… ***basalis*** **group**

9’ Posterior femora without projections (Fig. j). Posterior tibiae never emarginated (Fig. 1l)… 10

10 In dorsal view, anterior gastral expansions (ge) without a translucid lamella (Fig. 1q)… ***fiebrigi*** **group**

10’ In dorsal view, anterior gastral expansions (ge) with a translucid lamella (Fig. 1r)… 11

11 In dorsal view, propodeum with two pairs of spines, the posterior one longer than the declivous face of propodeum (Fig. 1f)… ***pusillus*** **group**

11’ In dorsal view, propodeum with variable number of spines, none of them longer than the declivous face of propodeum (Fig. 1h)… 12

12 Margins of declivous face of propodeum with lamellar expansions (Fig. 1m). In dorsal view, margins of pronotum with lamellar expansion, which can be crenulate, but not forming denticles or spines. … ***coffeae*** **group**

12’ Margins of declivous face of propodeum without lamellar expansions (Fig. 1n). In dorsal view, margins of pronotum with denticles or spines... ***angustus* group**

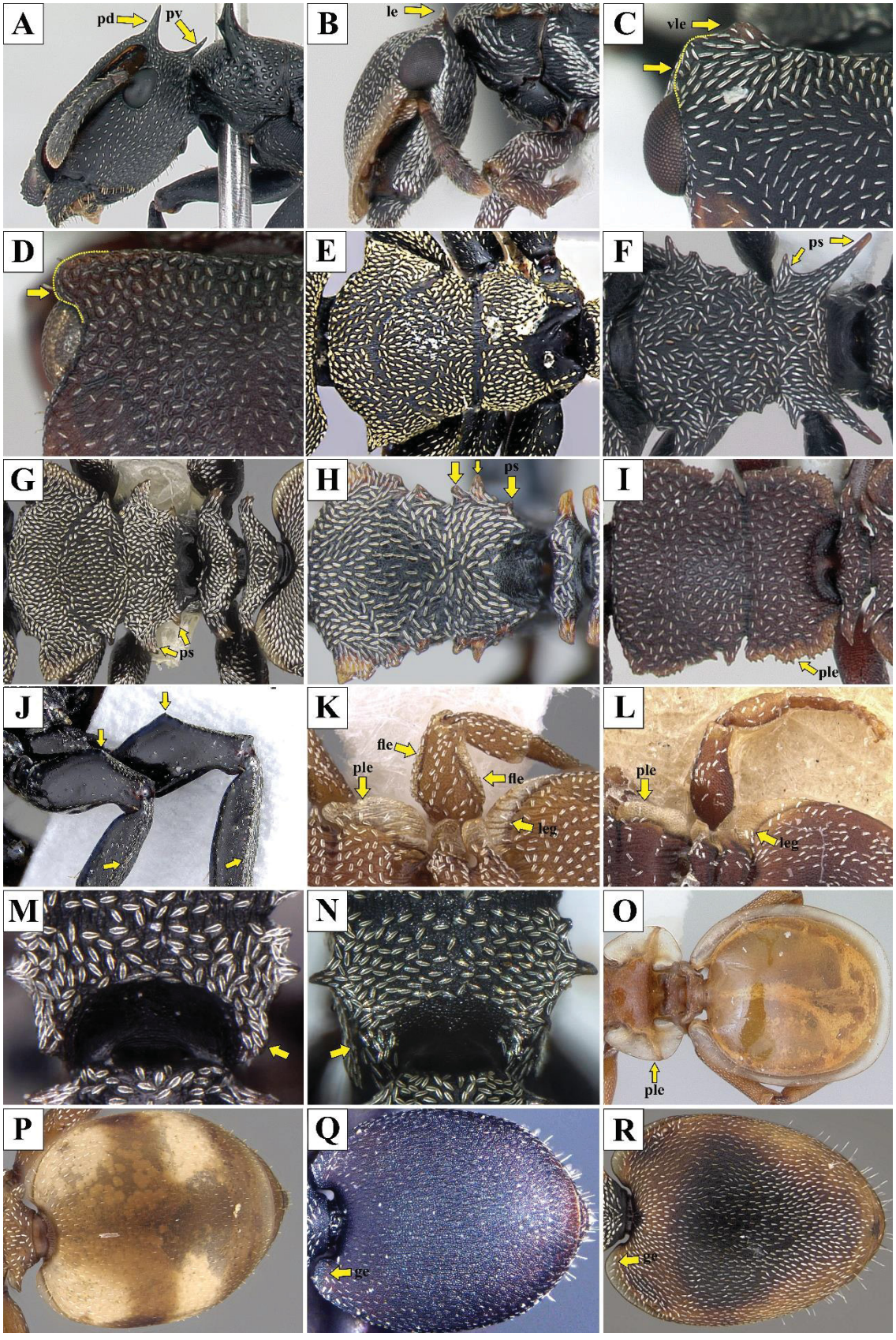

Figure 1: Workers of *Cephalotes*. A: *Cephalotes atratus* (*atratus* group) [CASENT0178627]. B:

Cephalotes depressus (*depressus* group) [CASENT0173671]. C, F: *Cephalotes pusillus* (*pusillus* group) [CASENT0173703]. D, I. *Cephalote pellans* (*pallens* group) [CASENT0173697]. E. *Cephalotes solidus* (*solidus* group). G: *Cephalotes cordatus* (*depressus* group) [CASENT0922596]. H. *Cephalotes frigidus* (*angustus* group) [UFV-LABECOL-004442]. J: *Cephalotes basalis* (*basalis* group) K: *Cephalotes grandinosus* (*grandinosus* group) [CASENT0922544]. L: *Cephalotes maculatus* (*pinelii* group) [CASENT0909295]. M: *Cephalotes trichophorus* (*coffeae* group). N: *Cephalotes angustus* (*angustus* group). O: *Cephalotes clypeatus* (*clypeatus* group) [CASENT0173669]. P: *Cephalotes umbraculatus* (*umbraculatus* group) [CASENT0922582]. Q: *Cephalotes jheringi* (*fiebrigi* group). R: *Cephalotes angustus* (*angustus* group) [CASENT0922530]. Pd: posterodorsal spine. Pv: posteroventral spine. Ple: propodeal lamellar expansion. Vle: vertexal lamellar expansions. Fle: femoral lamellar expansions. Ps: propodeal spine. Leg: Gastral lamellar expansions. Ge: Gastral expansions.

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

(Figure 2)

Note: soldiers are not present in the *atratus*, *coffeae* and *solidus* groups.

1 In frontal view, cephalic dorsum dish shaped, completely covering the mandibles (Fig. 2a) ... ***pallens* group**

1’ In frontal view, mandibles visible, even partially (Fig. 2b, 2c, 2d, 2e) ... 2

2 In frontal view, the vertexal corners are in a lower level than the dorsal surface of the head; cephalic dorsum completely emarginate, disc shaped (Fig. 2b) ... 3

2’ In frontal view, the vertexal corners are in the same level as the dorsal surface of the head; cephalic dorsum square or dome shaped (Fig. 2c, 2d, 2e) ... 7

3 Petiole and postpetiole with lateral lamellar expansions (Fig. 2j) ... 4

3’ Petiole and postpetiole with lateral acute projections, forming spines or denticles (Fig. 2g, 2h, 2o, 2q) ... 5

4 Posterior femora with lamellar expansions in dorsal and/or ventral face, which frequently are crenulate and narrow (Fig. 2m) ... ***grandinosus* group**

4’ Posterior femora without lamellar expansions (Fig. 2n) ... ***pinelii* group**

5 Body yellowish; first gastral tergite with a cross-shaped dark macula (Fig. 2r). Pronotum crest with pointed edges (Fig. 2f) ... ***umbraculatus* group**

5’ Body black to dark brown; gaster macula absent or in a shape different than a cross (Fig. 2q), if cross-shaped, then pronotum crest with rounded or subrectangular edges (Fig. 2i) ... 6

6 In dorsal view, anterior expansions of gaster without a translucid lamella and without yellow spots (Fig. 2o) ... ***fiebrigi* group** (in part)

6’ In dorsal view, anterior gaster expansions with a translucid lamella, usually very thin, and with one or two yellow spots (Fig. 2q) ... ***angustus* group**

7 In frontal view, frontal carinae ends before reaching the vertexal corners, cephalic dorsum dome shaped (Fig. 2d, 2e) ... 8

7’ In frontal view, frontal carinae continuous with the vertexal corners, cephalic dorsum square shaped (Fig. 2c) ... 11

8 In frontal view, head longer than broad, with contiguous foveae and suberect hairs (Fig. 2e) ... ***fiebrigi*** **group** (in part)

8’ In frontal view, head subquadrate, foveae separate by interspace, with short appressed hairs (Fig. 2d) ... 9

9 Propodeum with two pairs of lateral projections, the posterior longer than the anterior (Fig. 2g) ... ***pusillus*** **group**

9’ Propodeum with two pairs of lateral projections, the anterior longer than the posterior (Fig. 2h) ... ***depressus*** **group** (in part)

11 Gaster thoroughly surrounded by lamellar expansions (Fig. 2p) ... ***clypeatus*** **group**

11’ Lamellar expansions, if any, present only in the anterior portion of the gaster (Fig. 2q, 2r) ... 12

12 In lateral view, propodeum with continuous dorsal and declivous face (Fig. 2k) ... ***depressus*** **group** (in part)

12’ In lateral view, propodeum with distinct dorsal and declivous face (Fig. 2l) ... ***basalis*** **group**

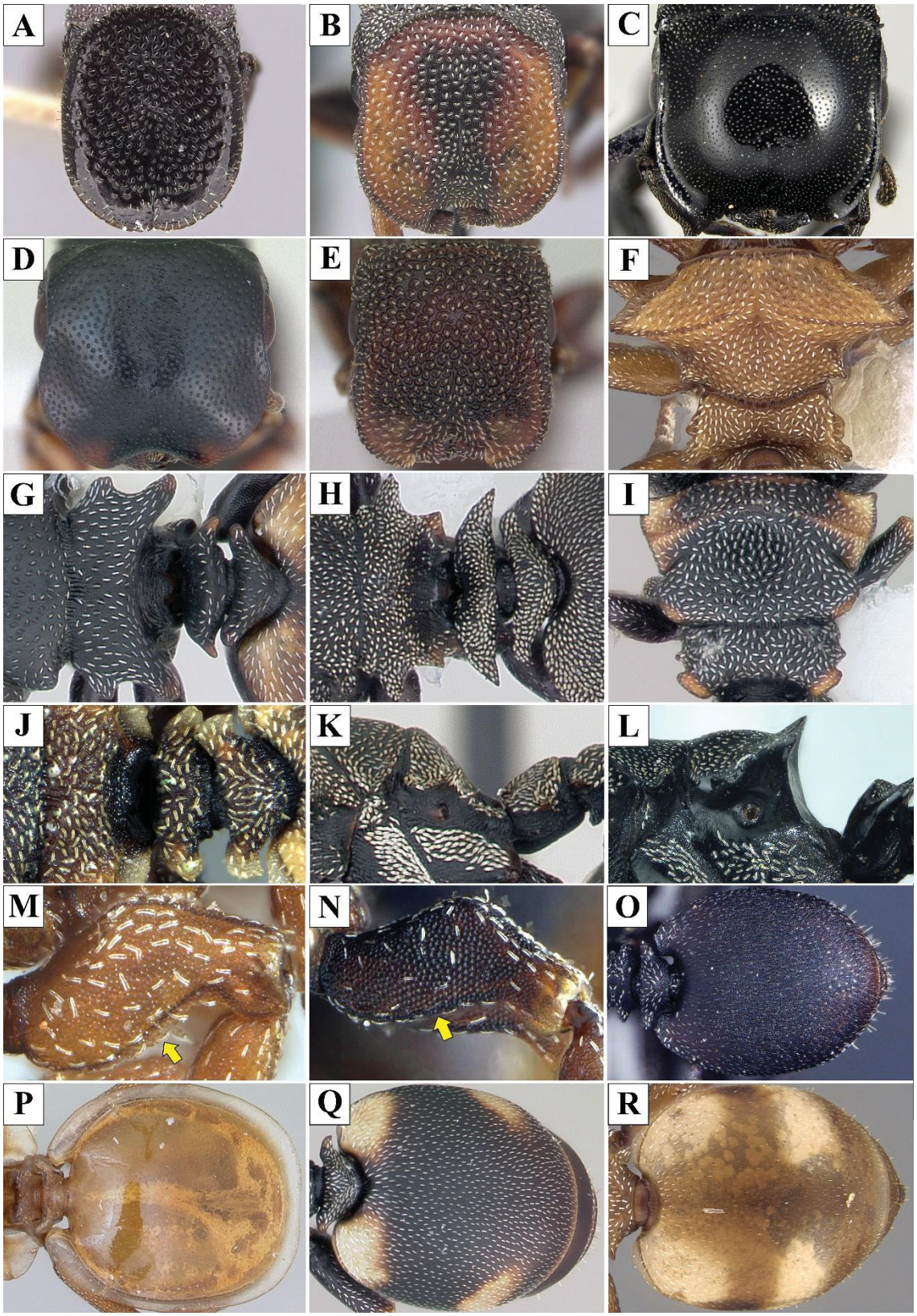

Figure 2: Soldiers of *Cephalotes*. A: *Cephalotes decoloratus* (*pallens* group) [CASENT0909299]. B: *Cephalotes angustus* (*angustus* group) [CASENT0909276]. C, L: *Cephalotes basalis* (*basalis* group). D, G: *Cephalote minutus* (*pusillus* group) [CASENT0173691]. E. *Cephalotes quadratus* (*fiebrigi* group) [CASENT0173705]. F, R: *Cephalotes umbraculatus* (*umbraculatus* group) [CASENT0922582]. H. *Cephalotes borgimeiri* (*depressus* group) [CASENT0173664]. I, Q: *Cephalotes targionii* (*angustus* group) [CASENT0173708]. J: *Cephalotes nilpiei* (*pinelii* group). K: *Cephalotes depressus* (*depressus* group) [CASENT0173672]. M: *Cephalotes grandinosus*

(*grandinosus* group). N: *Cephalotes pinelii* (*pinelii* group). O: *Cephalotes jheringi* (*fiebrigi* group). P: *Cephalotes clypeatus* (*clypeatus* group) [CASENT0173669].

5.1 The *angustus* species group

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

In the morphological phylogeny by De Andrade and Baroni Urbani (1999), this group was considered the sister group of the clade formed by *prodigiosus*, *fiebrigi* and *bruchi* groups. The subsequent phylogenies including molecular data confirm the intrinsic relationship between these groups. The *prodigiosus* and *fiebrigi/bruchi* groups are recovered as monophyletic, but they make the *angustus* group paraphyletic, suggesting these all groups might represent a unique evolutive lineage.

Morphologically, these groups share the declivous face of propodeum continuum with dorsal face, with a variable number of spines, but differ by the anterior expansions of the gaster, which are lamellar in the *angustus* group and lobate in *prodigiosus* and *fiebrigi/bruchi* groups. The Argentinian *prodigidous* group was not included in the present study. Although the phylogenetic data suggest that *angustus*, *bruchi*, *fiebrigi* and *prodigiosus* groups could be synonymized we decided to keep *angustus* as a group apart until a broader phylogeny including additional species from all these groups is available.

Diagnosis: Body with appressed hairs. Declivous face of propodeum continuum with dorsal face, with a variable number of spines. If there only two pairs of spines on propodeum, the first one never is the longer, and the second one never is longer than the declivous face. Gaster with anterior lamellar expansions.

Brazilian species of *angustus* group

Cephalotes adolphi (Emery, 1906)
Cephalotes angustus (Mayr, 1862)

Cephalotes conspersus (Smith, 1867)
Cephalotes frigidus (Kempf, 1960)
Cephalotes goeldii (Forel, 1912)
Cephalotes notatus (Mayr, 1866)
Cephalotes pallidicephalus (Smith, 1876)
Cephalotes targionii (Emery, 1894)
Cephalotes **new species A** Oliveira, Feitosa &Powell, 2020
Cephalotes **new species B** Oliveira, Feitosa &Powell, 2020
Cephalotes **new species C** Oliveira, Feitosa &Powell, 2020

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

(Figure 3)

1 In lateral view, the second pair of pronotal spines are raised dorsally above the level of the anterior spines (Fig. 3c)… ***C. adolphi***

1' In lateral view, the second pair of pronotal spines are in the same level of the anterior spines (Fig. 3d, 3e)… 2

2 First gastral sternite longitudinally costate (Fig. 3o)… ***C. pallidicephalus***

2' First gastral sternite not longitudinally costate (Fig. 3m); rugosities can be present (Fig. 3n)… 3

3 Ventral face of head with longitudinal rugosities towards the cephalic foramen (Fig. 3a)… ***C. notatus***

3' Ventral face of head microalveolate. Rugosities can be present, but not towards the cephalic foramen (Fig. 3b)… 4

4 In dorsal view, lateral spines of postpetiole longer than the maximum width of lamellar part of petiole (Fig. 3f)… ***C. frigidus***

4' In dorsal view, lateral spines of postpetiole as long as or shorter than the maximum width of lamellar part of petiole (Fig. 3g)… 5

5 In lateral view, dorsum of petiole without a pair of denticles (Fig. 3h)… ***C. goeldii***

5' In lateral view, dorsum of petiole with a pair of denticles (Fig. 3i)… 6

6 Propleuron, mesopleuron and metapleuron striate longitudinally (Fig. 3d)… ***C. targionii***

6' Propleuron, mesopleuron and metapleuron not striate longitudinally; if they are striae, it is only on the propleuron (Fig. 3e)… 7

7 Propleuron completely with well defined striate (Fig. 3d) … 8

7' Propleuron without striae; if it is present, are short, not occupying completely the propleuron, or restrict to lower propleuron (Fig. 3e)… 9

8 Gaster brownish with a dark lozenge in the middle… ***C. conspersus***

8'Gaster black, some yellowish spots can be present… ***C.* sp. n. B**

9 In dorsal view, gastral lamellar expansions surpassing the spiracles of the first tergite and extending posteriorly as a carina (Fig. 3j).… ***C. angustus***

9' In dorsal view, gastral lamellar expansions not surpassing the spiracles of the first tergite, if it is surpassing the spiracles, not extends posteriorly as a carina (Fig. 3k)… 10

10 Gaster with caniculate abundant hairs, equally distributed on the tergite (Fig. 3l)… ***C.* sp. n. A**

10' Gaster with simple sparse hairs in the middle, caniculate are present on the anterior portion and posterior portion of the tergite (Fig. 3p)… ***C.* sp. n. C**

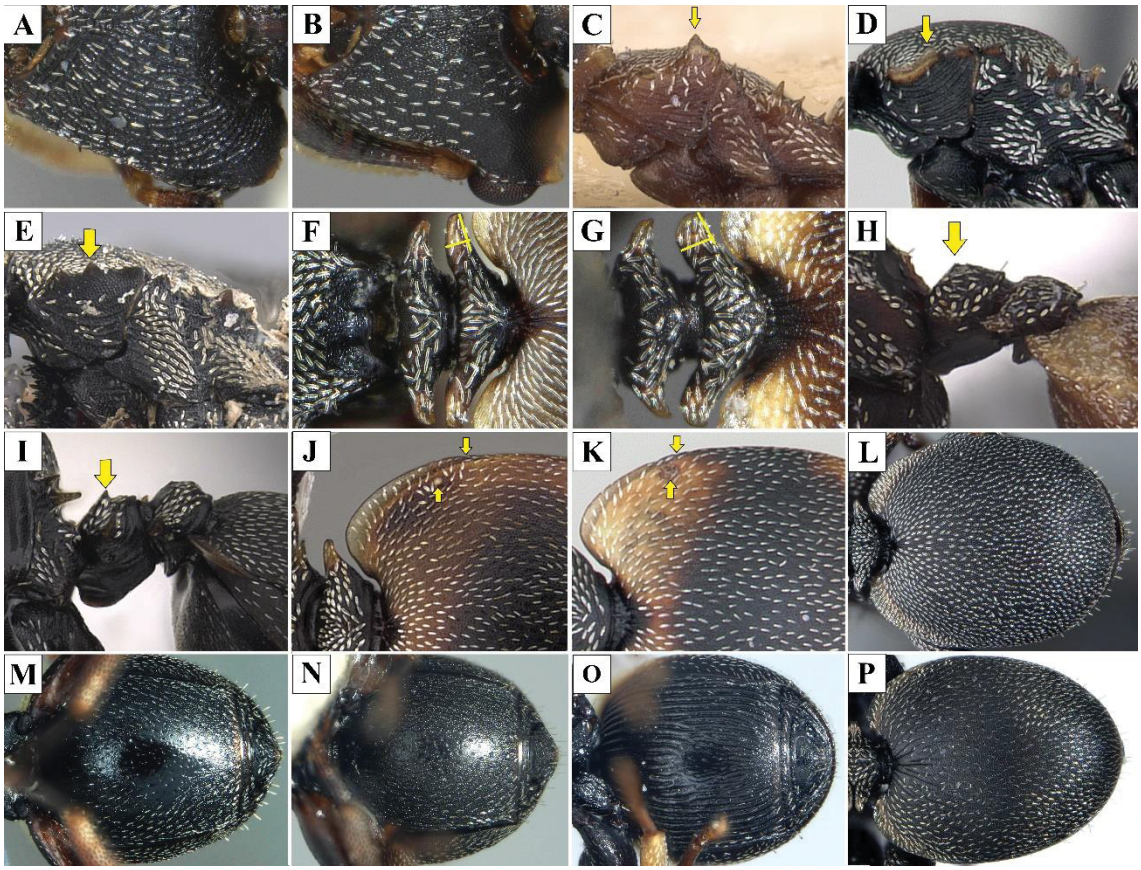

Figure 3: Workes of *angustus* group. A: *Cephalotes notatus*. B: *Cephalotes goeldii*. C: *Cephalotes adolphi* [CASENT0904906]. D: *Cephalotes targionii* [CASENT0173661]. E: *Cephalotes angustus* [CASENT0909277]. F: *Cephalotes frigidus*. G: *Cephalotes conspersus*. H: *Cephalotes goeldii* [CASENT0922535]. I: *Cephalotes targionii* [CASENT0922537]. J: *Cephalotes targionii* [CASENT0173707]. K: *Cephalotes conspersus* [CASENT0173707]. L, N: *Cephalotes* sp. n. A. M: *Cephalotes angustus.* O: *Cephalotes pallidicephalus*. P: *Cephalotes* sp. n. C.

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

(Figure 4)

1 Cephalic disc alveolate with suberect to erect hairs (Fig. 4a).... ***C. frigidus***

1’ Cephalic disc foveate with subdecumbent to appressed hairs (Fig. 4b, 4c, 4d).... 2

2 In dorsal view, dorsum of mesosome yellowish (Fig. 4k). In lateral view, the upper surface of the mesosoma yellowish, the lower surface dark (Fig. 4g)... ***C. adolphi***

2’ In dorsal view, dorsum of the mesosome predominantly black, the apexes of the lateral projections may be yellowish (Fig. 4i). In lateral view, the entire lateral surface black to dark brown (Fig. 4h, 4i)... 3

3 Cephalic disc wider than long, at most subquadrate (Fig. 4b)... 4

3’ Cephalic disc longer than wide (Fig. 4c, 4d)... 5

4 Lateral expansions of the pronotum broader than the width of the posterior expansions of head (Fig. 4j) ... ***C. goeldii***

4’ Lateral expansions of the pronotum narrower or of the same width as posterior expansions of head (Fig. 4k) ... ***C. notatus***

5 First gastral sternite with longitudinal rugosities (Fig. 4l)... ***C. pallidicephalus***

5’ First gastral sternite without longitudinal rugosities (Fig. 4m), striae can be present laterally, but the middle of the sternite is smooth (Fig. 4n)... **6**

6 In dorsal view, lateral margins of pronotum straight and subparallel (Fig. 4e). The posterior pair of denticles of propodeum gently bent dorsally; short, apexes not curved anteriorly (Fig. 4e)… 7

6’ In dorsal view, lateral margins of pronotum convex and converging posteriorly (Fig. 4f). The posterior pair of denticles of propodeum strongly bent dorsally, with the apexes curved anteriorly (fig. 4f)…8

7 In dorsal view, propodeal groove strongly impressed (Fig. 4e)… ***C.*** **sp. n. B**

7’ In dorsal view, propodeal groove weakly impressed; marked on the sides but absent medially (Fig. 4f)… ***C. conspersus***

8 Foveae of cephalic disc very near, space between them is less than their diameter; each fovea with a subdecumbent hair (Fig. 4d) … ***C. targionii***

8’ Foveae of head sparse, space between most foveae equal to or larger than the diameter of each fovea; each fovea with an appressed hair (Fig. 4c)… 9

9 First sternite of the gaster without striae laterally (Fig. 4m). Anterior lamellae of the gaster extending posteriorly as a carina (Fig. 4o). Pronotal carina well marked, normally forming a crest … ***C. angustus***

9’ First sternite of the gaster with striae laterally (Fig. 4n). Anterior lamellae of the gaster not extending posteriorly as a carina (Fig. 4p). Pronotal carina weakly marked, not forming a crest. ***C.* sp n. A**

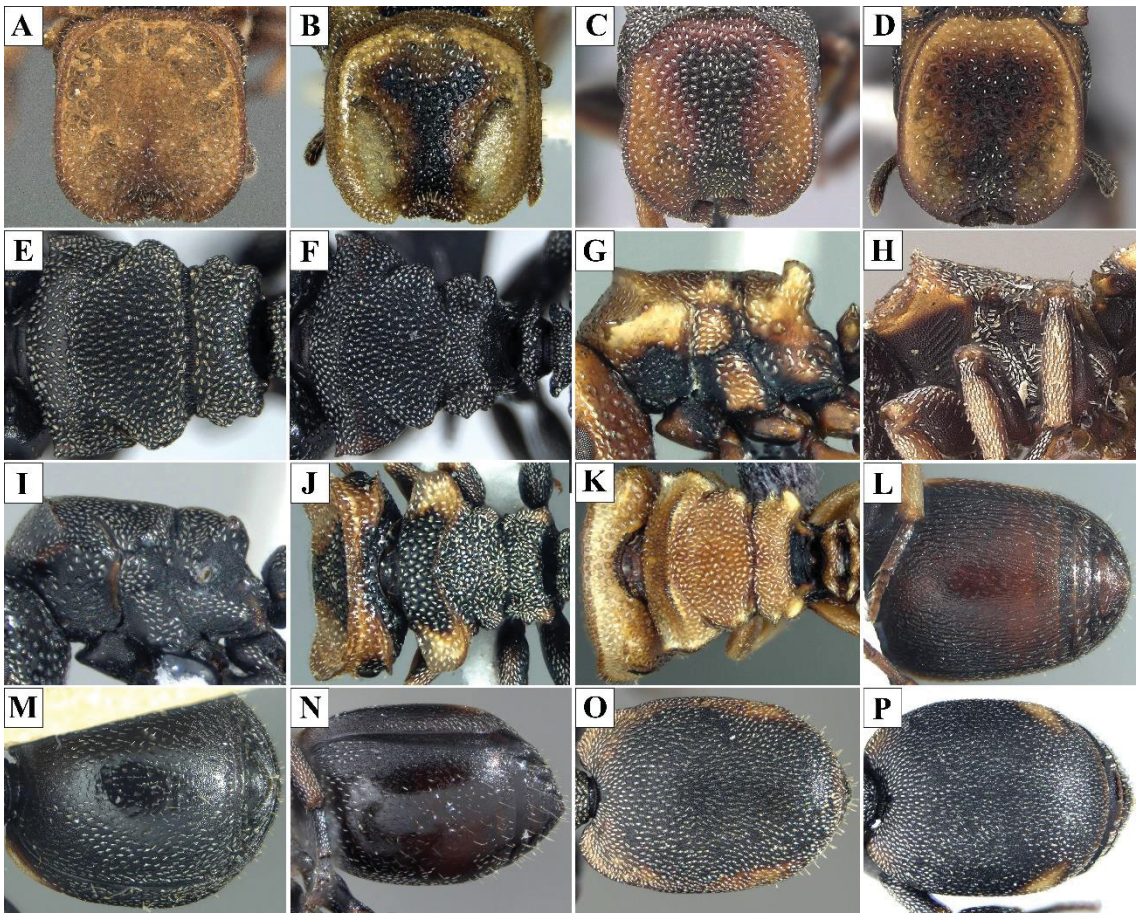

Figure 4: Soldiers of *angustus* group. A: *Cephalots frigidus*. B: *Cephalotes goeldii*. C: *Cephalotes angustus* [CASENT0909276]. D: *Cephalotes targionii* [CASENT0922536]. E, I: *Cephalotes* sp. n. B. F: *Cephalotes angustus*. G, K: *Cephalotes adolphi*. H: *Cephalotes notatus* [CASENT0919600]. J: *Cephalotes goeldii*. L: *Cephalotes pallidicephalus*. M, O: *Cephalotes angustus*. N, P: *Cephalotes* sp. n. A.

5.1.1 *Cephalotes* new species A Oliveira, Feitosa and Powell, 2020

Figs. 5, 6, 7

Holotype: Brazil: MG, Santana do Riacho, Serra do Cipó, 1267m, -19.294090 -43.587950, 10.vii.2018, S. Powell col., Campo rupestre (*Vellozia*), C18-32 (worker) [DZUP].

Paratype: same data as holotype (1 worker, 1 soldier, 1 gyne) [DZUP], (2 workers, 1 soldier) [MZSP], (2 workers, 1 soldier) [USNM]; 1258m, -19.294040 -43.587760, 17.vii.2019, S. Powell col. *Vellozia*, C19-22 (1 worker, 1 gyne) [DZUP], (1 worker, 1 gyne) [USNM].

Diagnosis: A member of *angustus* species group, with incomplete striae on propleuron. Denticles on the dorsum of the petiole. First sternite of the gaster laterally striate; anterior lamellar

expansions of the gaster not extending posteriorly as a carina; hairs of the first tergite caniculate and abundant.

Worker measurements (N=8): HL 0.85-1.20; HW 1.00-1.38; EL 0.30-0.38; PW 0.79-0.25; WL 0.93-1.35; PTL 0.17-0.24; PTW 0.46-0.60; PPL0.17-0.28; PPW 0.49-0.66; GL 1.05-1.76; HBL 0.28-0.41; HBW 0.10-0.11; TL3.43-4.11; CI 108.33-117.65; OI 25.19-31.30; PI 37.93-43.33; HBI 26.32-34.63.

Worker description: Color black; frontal lobes and apex of each segment of head yellowish (Fig. 5c).

Mandibles, internal surface of antennal scrobes and gaster microalveolate. Head, mesosoma, legs, petiole and postpetiole foveate-microalveolate. Propleuron striate-microalveolate, striae not fully occupying the propleuron. Declivous face of propodeum with some striae. First tergite of gaster microalveolate with some anterior striae, first sternite medially smooth and shiny, laterally striate-microalveolate (Fig. 5).

Body with appressed caniculate hairs (Fig. 5c), more concentrated on meso and metapleuron. Declivous face of propodeum hairless. Anterior margin of clypeus and mandibles with suberect clavate and simple hairs (Fig. 5a). First sternite of gaster with long erect simple hairs. (Fig. 5b).

Head wider than long (CI 105.33-117.65), slight convex (Fig. 5a). 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, gentle bent dorsally over the eyes (Fig. 5c). Antennae with a three-segmented club. In frontal view, eyes rounded. Lateroventral margins of head with posterior carinae extending beyond the eyes until vertexal corners. Vertexal corners with a narrow irregular lamellar expansion.

Mesosoma convex in lateral view (Fig. 5b). In dorsal view, lateral margins of pronotum with variable number of denticles, normally three, the posterior one bifurcate or trifurcate. Promesonotal groove absent (Fig. 5c). Mesonotum with a pair of short denticles. Propodeal groove impressed only laterally. Dorsal and declivous faces of propodeum continuous; lateral margins of propodeum with two anterior denticles and a row of minor denticles posteriorly, near to petiole insertion (Fig. 5c). Femora not angulated dorsally; mid and hind basitarsi not flattened, with subparallel dorsal and ventral faces.

Anterior margin of petiole concave; laterally with a pair of spines curved backwards; dorsum with a pair of denticles; subpetiolar process broader and rounded (Fig. 5b). Postpetiole longer than petiole (Fig. 5c); with a pair of spines broader than spines of petiole and curved backwards; dorsum of postpetiole without carina or denticles (Fig. 5c); subpostperiolar process pronounced and flattened anteroposteriorly (Fig. 5b).

Gaster suboval; with broad anterior lamellar expansions, not extend posteriorly in a carina (Fig. 5c).

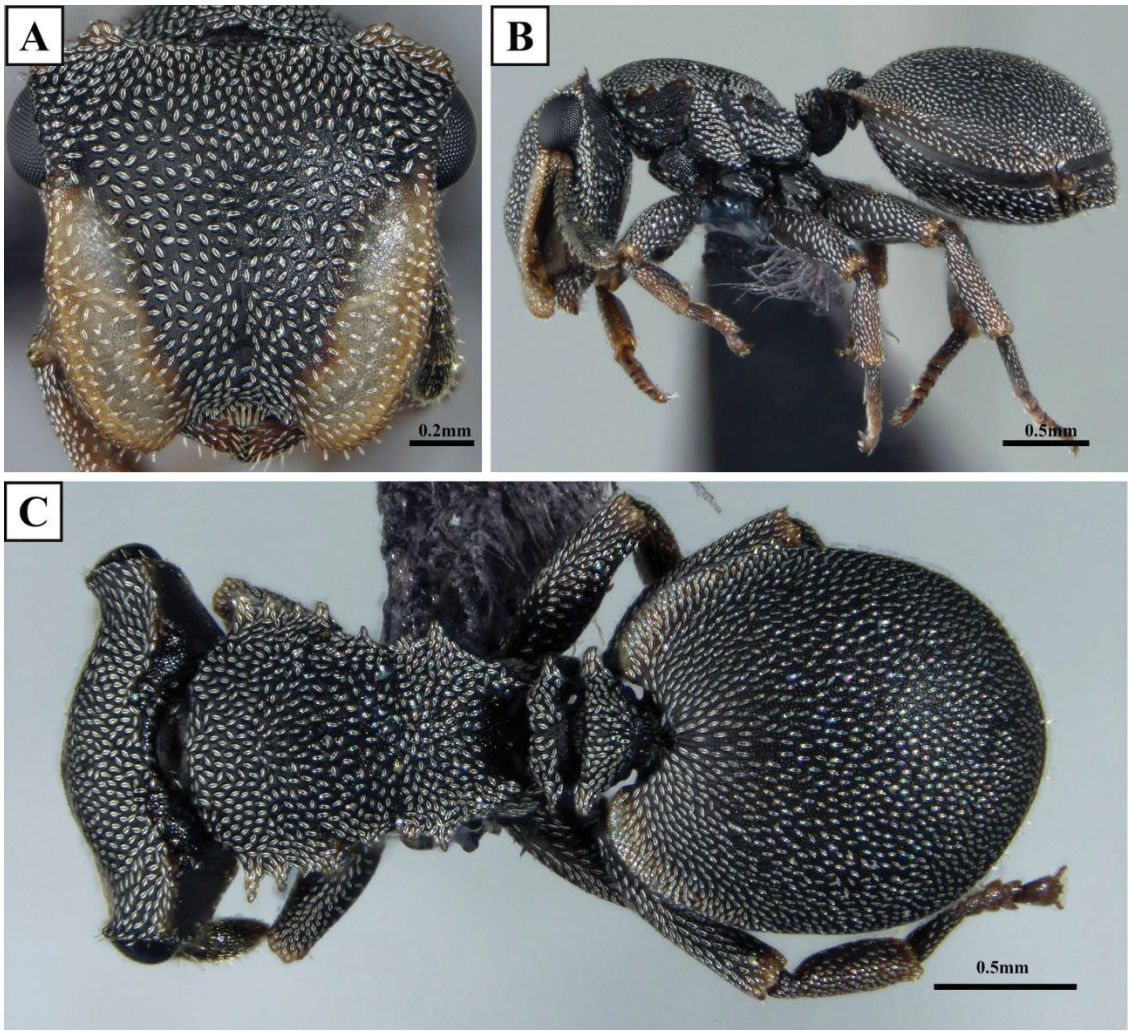

Figure 5: Worker of *Cephalotes* sp. n. A. A: frontal view. B: lateral view. C: dorsal view. Brazil: MG, Santana do Riacho.

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 0.30-0.55; HBL 0.44-0.48; HBW 0.14-0.20; TL 5.99-7.28; CI 109.59-111.11; OI 19.68-20.00; PI 41.38-43.75; HBI 32.00-43.45.

Soldier description: Color black; dorsum of head with lateral maculae, only central region black; lateral margin of pronotum with ferruginous spot; first tergite of gaster with two pairs of yellow spots (Fig. 6c).

Sculpturing and pilosity as the workers, except by gaster, which dorsally has some appressed simple hairs and ventrally has short erect hairs.

Head slightly wider than longer (CI 106.56-111.11). Dorsum of head disc shaped and concave anteriorly.

Mandibles with a strong longitudinal lateral angle. Frontal carinae crenulate anteriorly. Clypeus slightly concave with a pair of denticles (Fig. 6a). Antennal club ill-defined. Roof of antennal scrobes with a lateral carinae and a posterior denticle. Lateroventral margins of head without carinae. Vertexal corners with a pair of pointed projections (Fig. 6a).

In profile, pronotum ascending, meso and metanotum continuous and flat (Fig. 6b). In dorsal view, anterior margin of pronotum gently rounded; lateral margins concave and converging posteriorly, with a pair of anterior denticle; pronotal carina weakly developed, not crenulate (Fig. 6c). Mesonotum with a pair of blunt rounded projections. Propodeal groove impressed only laterally. Propodeum with well differentiate dorsal and declivous faces; in dorsal view, lateral margins of propodeum with three pairs of projections, the anterior obtuse, the second broad and acute, the posterior acute, long, with the apex curved anteriorly. Legs as the worker.

Petiole and postpetiole as the worker, except by the dorsum of postpetiole, which has a transversal elevation.

Gaster elongate, with narrow anterior lamellae not extending posteriorly in a carina g. 6c).

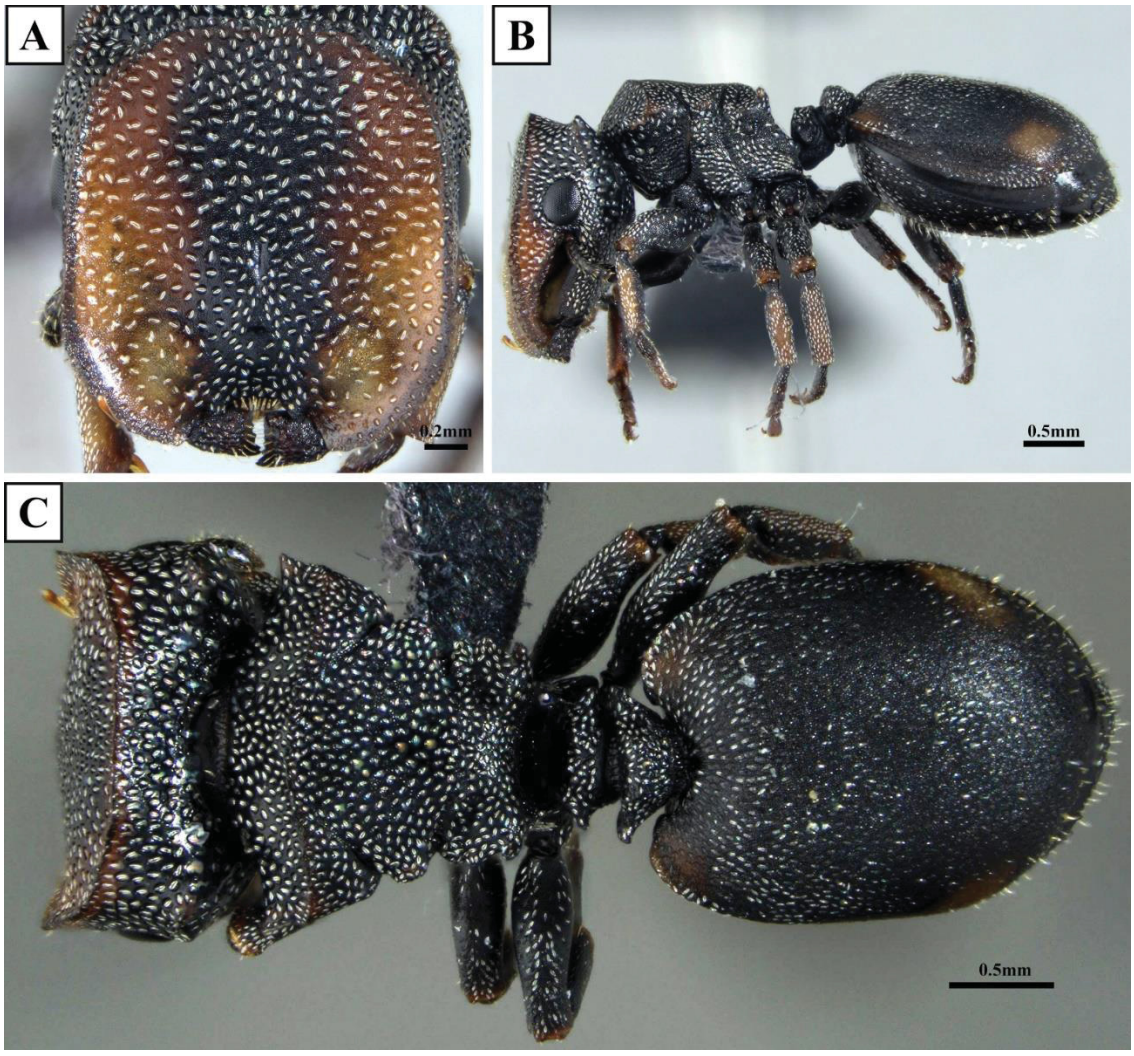

Figure 6: Soldier of *Cephalotes* sp. n. A. A: frontal view. B: lateral view. C: dorsal view. Brazil: MG, Santana do Riacho.

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 0.72-0.78; PPL 0.45-0.51; PPW 0.8-0.93; GL 0.33-0.36; HBL 0.56-0.58; HBW 0.15-0.17; TL 5-59-5.97; CI 90.74-101.06; OI 22.37-24.53; PI 44.09-61.60; HBI 26.09-31.18.

Gyne description: Color, sculpturing and pilosity as the soldier, except by some erect hairs on mesoscutum.

Head as the soldier (CI 90.74-71.06), but longer (Fig. 7a).

Mesosoma flattened in lateral view (Fig. 7b). 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, medially interrupted (Fig. 7c). Dorsally mesoscutum large and subtriangular, anterior margin rounded; notauli absent; parapsidial lines well visible and parallel; transscutal line impressed, reaching the lateral margins of mesosoma; scutoscutellar groove deeply impressed, arched, and cross by short striae; scutellum well delimited and broader anteriorly; axillae rounded posteriorly (Fig. 7c). Laterally, mesopleural groove impressed dividing anepisternum and katepisternum; metapleuron divided in upper metapleuron and lower metapleuron by a groove; metapleuropropodeal groove not impressed (Fig. 7b). In dorsal view, posterior margin of propodeum slightly concave and meeting the declivous face in a pair of short denticles (Fig. 7b). Wings unknown.

Petiole and postpetiole as the soldier, but longer (Fig. 7b, 7c).

Gaster as the genus description; anteriorly with a narrow carina, not extending anteriorly (Fig. 7c).

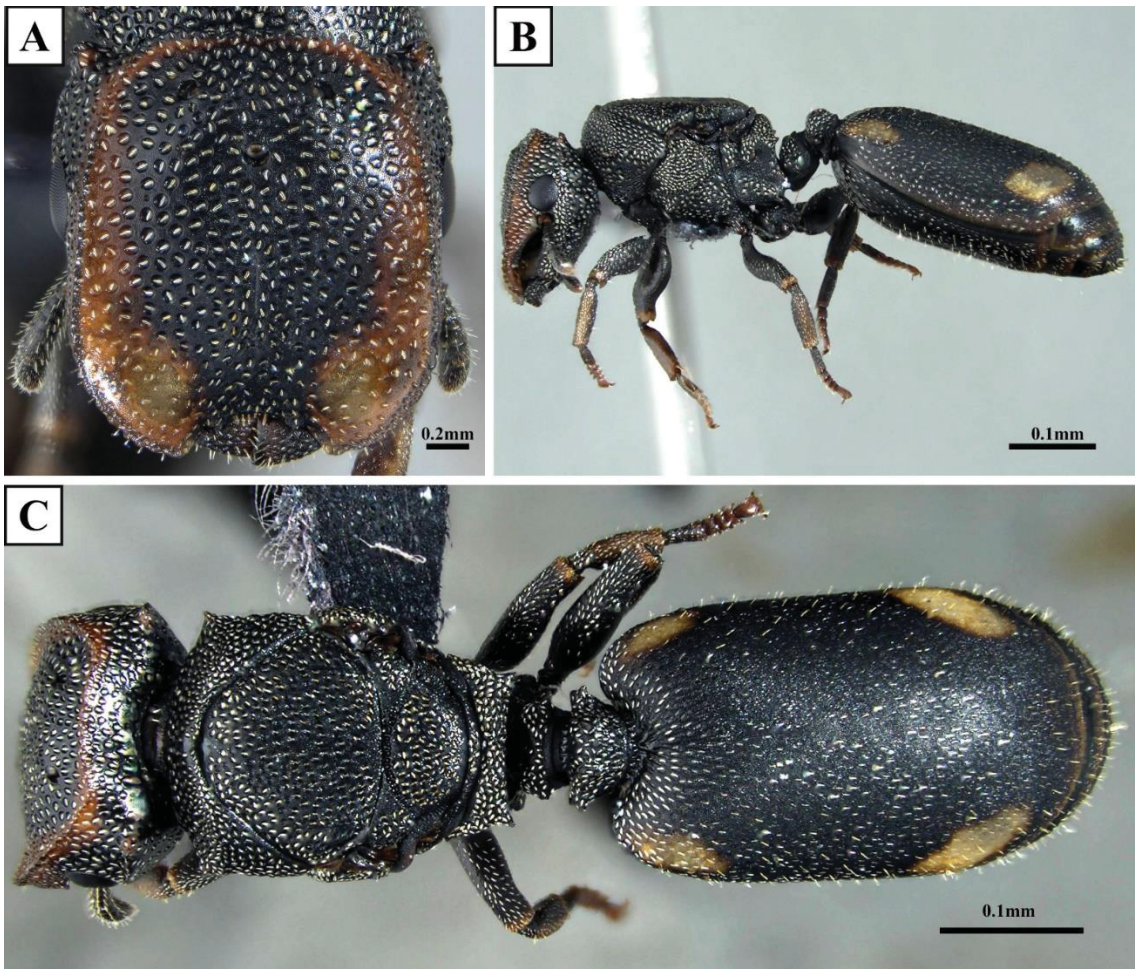

Figure 7: Gyne of *Cephalotes* sp. n. A. A: frontal view. B: lateral view. C: dorsal view. Brazil: MG, Santana do Riacho.

Distribution: Minas Gerais, Brazil.

Comments: This species is very similar to *C. angustus* and *C.* sp. n. C. Differing from the first by the striae on first sternite of gaster and by anterior lamella not extending posteriorly as a carina; and differs from the second by pilosity pattern on first tergite of gaster, which is caniculate and abundant in new species A and simple and sparse in new species B. This species was found only in altitudes above 1200m always foraging in *Vellozia*, which is a very common shrub genus, found especially in Brazilian savannas, occurs in altitudes between 1000 and 2000 meters.

5.1.2 *Cephalotes* new species B Oliveira, Feitosa and Powell, 2020

Figs. 8, 9, 10

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

Paratype: same data as holotype (2 workers, 2 soldiers, 1 gyne) [DZUP], (2 workers, 1 soldier) [MZSP], (1 workers, 1 soldier) [USNM]; -19.00124 -48.31239, S. Powell col. C05-134; (2 workers, 2 soldiers) [DZUP], (2 workers, 1 soldier) [MZSP], (2 workers, 1 soldier) [USNM], (2 workers, 1 soldier) [INPA], (2 workers) [MPEG]; Paraopeba, iii.2011, C.R. Ribas, Cerrado, pitfall arboreo [unique specimen identifier UFV-LABECOL-004439] (1 worker) [DZUP].

Diagnosis: A member of *angustus* species group, with propleuron completely with well-marked striae. Denticles on the dorsum of the petiole. First sternite of the gaster black, normally with an anterior pair of maculae; first sternite microalveolate, without striae.

Worker measurements (N=16): 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 0.95-148.72; OI 24.90-32.82; PI 30-40.91; HBI 20.00-28.57.

Worker description: Color black; frontal lobes, anterior spots on gaster and apex of each segment of head yellowish (Fig. 8c).

Mandibles, legs and gaster microalveolate. Head, mesosoma, petiole and postpetiole foveate-microalveolate. Propleuron with well marked striae fully occupying the propleuron. Declivous face of propodeum with some striae (Fig. 8).

Body with appressed caniculate hairs (Fig. 8c), more concentrated on meso and metapleuron. Declivous face of propodeum hairless. Anterior margin of clypeus and mandibles with suberect clavate and simple hairs (Fig. 8a). First sternite of gaster with long erect simple hairs (Fig. 8b).

Head slightly wider than long (CI 0.95-148.72), subquadrate, slight convex (Fig. 8a). Mandibles with a weakly developed lateral angle. Anterior margin of clypeus concave without a pair of denticles. Frontal carinae notched anteriorly the eyes, not bent dorsally over the eyes (Fig. 8c). Antennae with a three-segmented club. In frontal view, eyes rounded. Lateroventral margins of head with posterior carinae extending beyond the eyes until vertexal corners. Vertexal corners with a narrow lamellar irregular expansion.

Mesosoma gentle convex in lateral view (Fig. 8b). In dorsal view, lateral margins of pronotum with three denticles, the two anterior acute, the posterior broad and sometimes with two acute apices, almost forming a 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; lateral margins of propodeum with variable number of denticle (Fig. 8c). Femora not angulated dorsally; mid and hind basitarsi not flattened, with subparallel dorsal and ventral faces.

Anterior margin of petiole concave; laterally with a pair of spines; dorsum with a pair of denticles; subpetiolar process broader anteriorly with a narrow translucid lamella (Fig. 8b). Postpetiole longer than petiole (Fig. 8b); with a pair of spines broader than spines of petiole and curved backwards; dorsum of postpetiole without carina or denticles (Fig. 8c); subpostperiolar process pronounced and flattened anteroposteriorly (Fig. 8b).

Gaster suboval; with broad anterior lamellar expansions, not extend posteriorly in a carina (Fig. 8c).

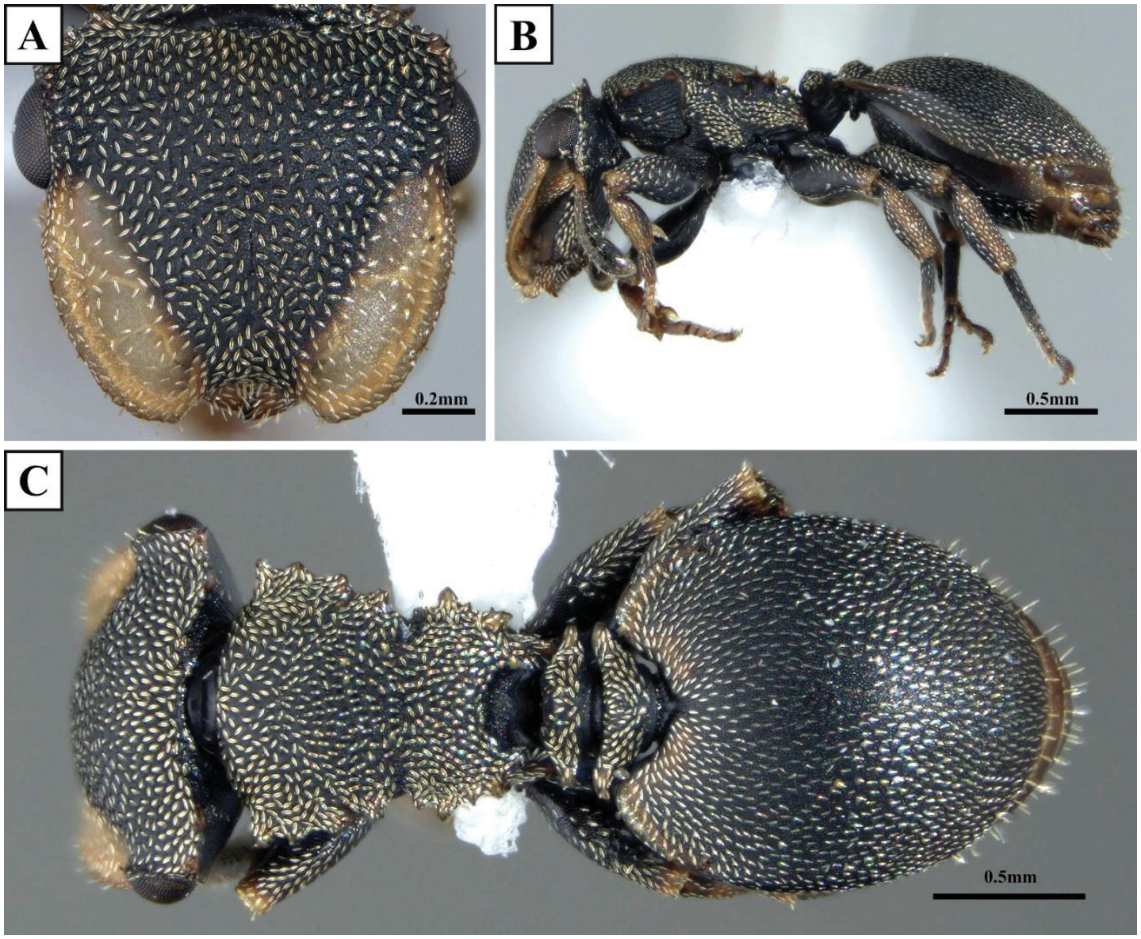

Figure 8: Worker of *Cephalotes* sp. n. B. A: frontal view. B: lateral view. C: dorsal view. Brazil: MG, Uberlândia.

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 010.-012; TL 5.17-6.09; CI 77-97-98.25; OI 20.97-28.26; PI 34.38-50.78; HBI 23.81-31.58.

Soldier description: Color black; dorsum of head, apex of femora and dorsal face of tibiae ferruginous; gaster with two pairs of yellowish spots (Fig. 9).

Sculpturing and pilosity as the workers, except by propleuron with striae not fully occupying the propleuron and gaster dorsally with appressed simple hairs and ventrally with short and long erect hairs.

(Fig. 9a, 9c).

Head longer than wide (CI 77-97-98.25). Dorsum of head disc shaped and slightly concave anteriorly.

Mandibles with a strong longitudinal lateral angle. Frontal carinae crenulate anteriorly. Clypeus slightly concave without a pair of denticles (Fig. 9a). Antennal club ill-defined. Roof of antennal scrobes with a lateral carinae and a posterior denticle. Lateroventral margins of head without carinae. Vertexal corners with a pair of pointed projections (Fig. 9a).

In profile, pronotum ascending, meso and metanotum continuous and flat (Fig. 9b). In dorsal view, anterior margin of pronotum gently rounded; lateral margins subparallel, with a pair of anterior denticle; pronotal carina weakly developed, not crenulate, interrupted in middle (Fig. 9c). Mesonotum with a pair of blunt rounded projections. Propodeal groove well impressed. Propodeum with well differentiate dorsal and declivous faces; 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 the worker.

Anterior margin of petiole slightly concave; laterally with a pair of spines curved backwards; dorsum with a pair of denticles; subpetiolar process broader anteriorly with an acute projection. Postpetiole longer than petiole (Fig. 9b); with a pair of spines broader than spines of petiole and curved backwards; dorsum of postpetiole with a transversal elevation (Fig. 9c); subpostperiolar process pronounced and flattened anteroposteriorly (Fig. 9b).

Gaster suboval, protunding anteriorly, without lamella or carinae (Fig. 9c).

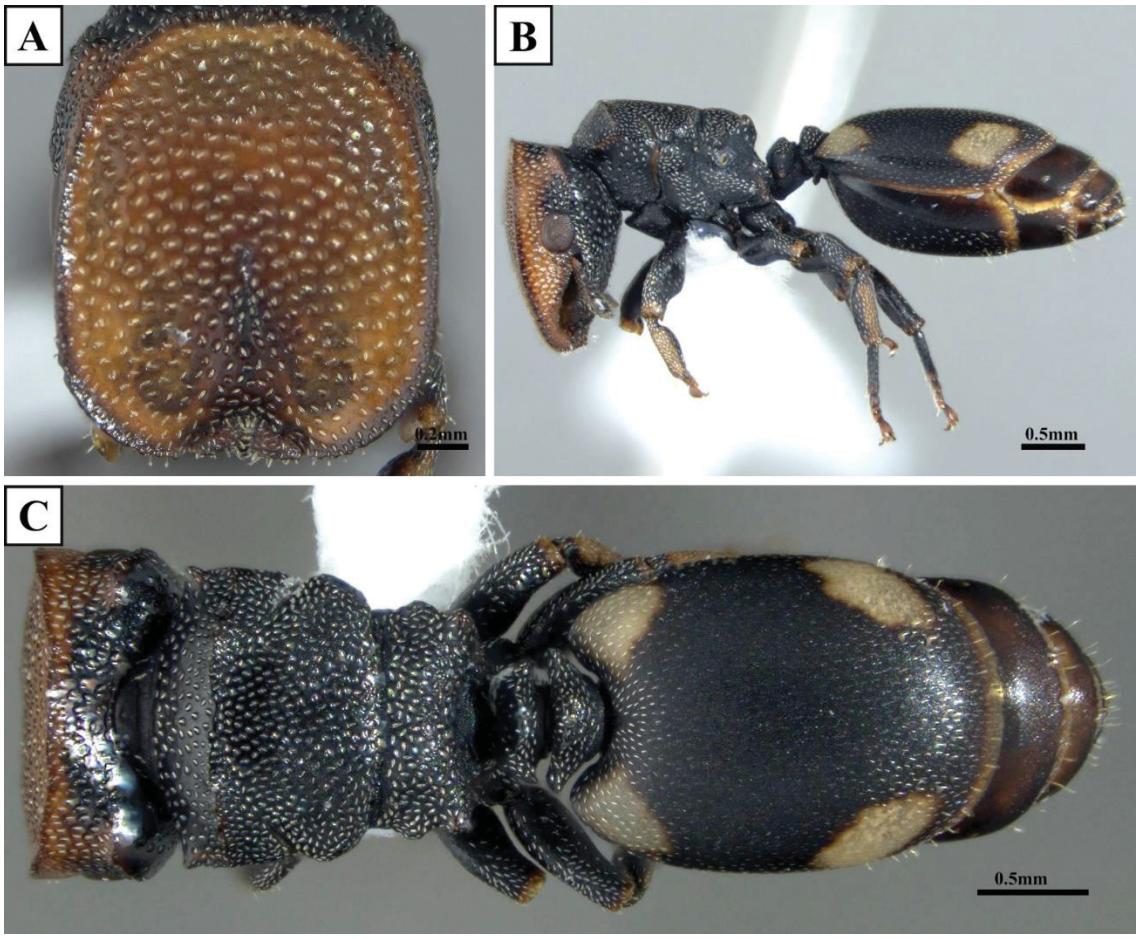

Figure 9: Soldier of *Cephalotes* sp. n. B. A: frontal view. B: lateral view. C: dorsal view. Brazil: MG, Uberlândia.

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 96.59-98.21; OI 25.10-25.45; PI 65.00-71.58; HBI 24.00-26.09.

Gyne description: Color as the soldier, except by dorsum of head with lateral maculae, only central region black (Fig. 10a).

Sculpturing and pilosity as the soldier, except by some erect hairs on mesoscutum.

Head as the soldier (CI 96.59-98.21), but with frontal carina converging posteriorly (Fig. 10a).

Mesosoma flattened in lateral view (Fig. 10b). In dorsal view, anterior margin of pronotum slightly rounded, narrow than in the soldiers; lateral margins with a pair of denticles pointed forwards; pronotal carina weakly developed (Fig. 10c). Dorsally mesoscutum large and subtriangular, anterior margin rounded; notauli absent; parapsidial lines feebly visible and parallel; transscutal line weakly impressed, reaching the lateral margins of mesosoma; scutoscutellar groove weakly impressed, arched; scutellum well delimited and broader anteriorly; axillae rounded posteriorly (Fig. 10c). Laterally, mesopleural groove impressed dividing

anepisternum and katepisternum; metapleuron divided in upper metapleuron and lower metapleuron by a groove; metapleuropropodeal groove not impressed (Fig. 10b). In dorsal view, posterior margin of propodeum concave and meeting the declivous face in a pair of denticles (Fig. 10b). Wings as the genus description.

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

Gaster as the genus description; protruding anteriorly, without lamella or carinae (Fig. 10c).

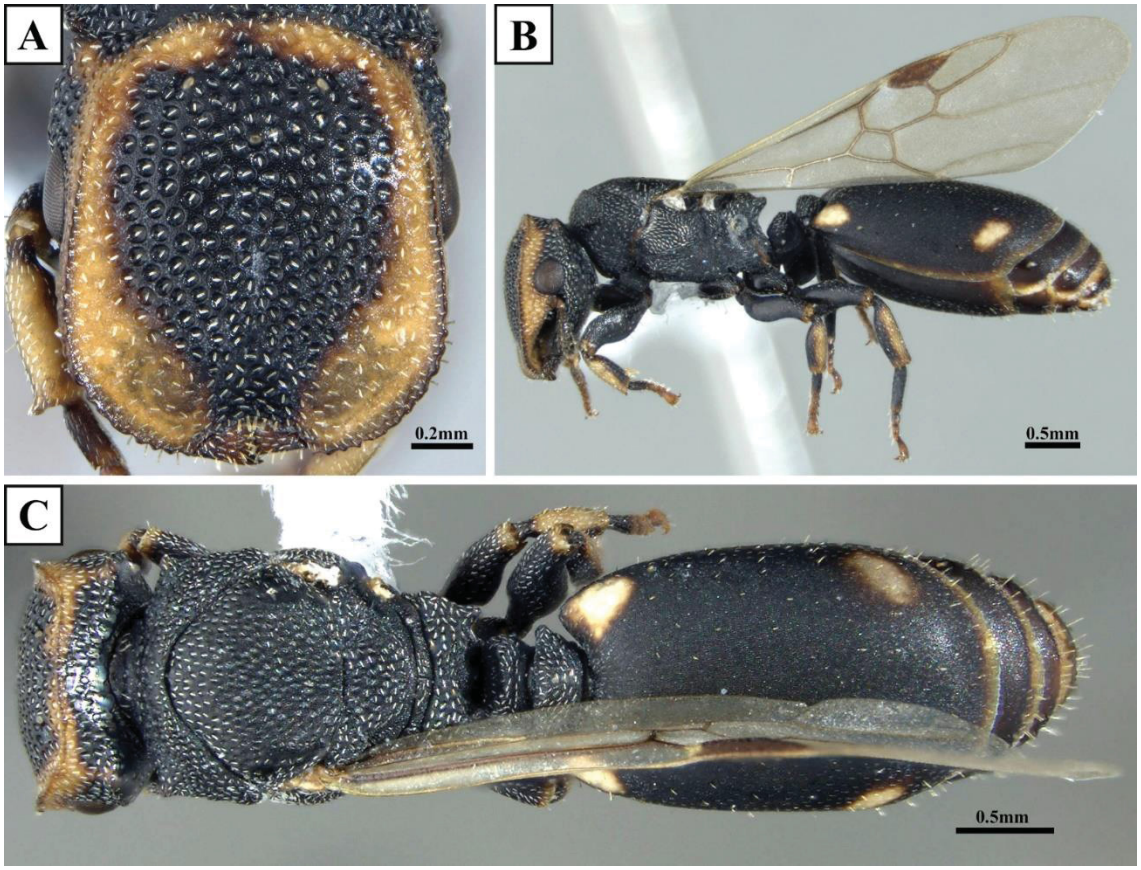

Figure 10: Gyne of *Cephalotes* sp. n. B. A: frontal view. B: lateral view. C: dorsal view. Brazil: MG, Uberlândia.

Distribution: Minas Gerais, Brazil.

Comments: This species is very similar to *C. conspersus*, differing by the absent of carinae or denticles on dorsum of postpetiole, femur not angulate and gaster black. This species is the C. sp. 3 in the molecular phylogenies by Price et al. (2014, 2016), which was in the base of the paraphyletic grouping formed by other species of *angustus* group, *fiebrigi* and *prodigious* groups.

5.1.3 *Cephalotes* new species C Oliveira Feitosa and Powell, 2020

Figs. 11

Holotype: Brazil: MG, Manga, Parque Estadual da Mata Seca, ii.2011, -14.84833 -43.96555, R. Garro & R. Antoniazzi cols. Dossel 15.5m, in *Myracrodruon urundeuva* (worker) [DZUP].
Paratype: same data as holotype, -14.84833 -43.96555, dossel 14m (1 worker), -14.84833 -43.98805, dossel 15.8m (1 worker) [DZUP]; -14.84833 -43.98805, dossel 10.3m (2 workers) [MZSP]; -14.84833 -43.96555, dossel 11.8m, in *Handroanthus chrysotrichus* (1 worker), dossel 23m (1 worker) [USNM].

Diagnosis: A member of *angustus* species group, with incomplete striae on propleuron. Denticles on the dorsum of the petiole. First sternite of the gaster laterally striate; anterior lamellar expansions of the gaster not extending posteriorly as a carina; hairs of the first tergite simple and sparse, caniculate hair are present only on anterior region.

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 021-0.25; PPW 0.53-0.60; GL 1.35-1.68; HBL 0.34-0.40; HBW 0.10; TL 4.10-4.34; CI 111.90-123.26; OI 23.83-25.53; PI 17.64-19.02; HBI 24.00-28.01.
Worker description: Color black; frontal lobes, apex of femora and dorsal face of tibiae yellowish (Fig. 8c).

Mandibles, legs, gaster and declivous face of propodeum microalveolate. Head, mesosoma, petiole and postpetiole foveate-microalveolate. Propleuron striate-microalveolate, striae not fully occupying the propleuron. First tergite of gaster microalveolate with some anterior striae, first sternite medially smooth and shiny, laterally striate-microalveolate (Fig. 8).

Body with appressed caniculate hairs (Fig. 8c). Declivous face of propodeum hairless. Anterior margin of clypeus and mandibles with suberect clavate and simple hairs (Fig. 11a). First tergite of gaster with sparse appressed simple hairs, first sternite with short erect simple hairs (Fig. 11b).

Head wider than long (CI 111.90-123.26), slight convex (Fig. 11a). Mandibles with a weakly developed lateral angle. Anterior margin of clypeus concave without a pair of denticles. Frontal carinae sinuous anteriorly 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 lamellar irregular expansion.

Mesosoma gentle convex in lateral view (Fig. 11b). In dorsal view, lateral margins of pronotum with three denticles, the two anteriorly acute, the posterior broad and sometimes with two acute apices, 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; lateral margins of propodeum with variable number of

denticle (Fig. 11c). Femora not angulated dorsally; mid and hind basitarsi not flattened, with subparallel dorsal and ventral faces.

Anterior margin of petiole concave; laterally with a pair of spines; dorsum with a pair of denticles; subpetiolar process broader anteriorly (Fig. 11b). Postpetiole longer than petiole (Fig. 11c); with a pair of spines broader than spines of petiole and curved backwards; dorsum of postpetiole without carina or denticles (Fig. 11c); subpostperiolar process pronounced and flattened anteroposteriorly (Fig. 11b).

Gaster suboval; with broad anterior lamellar expansions, not extend posteriorly in a carina (Fig. 11c).

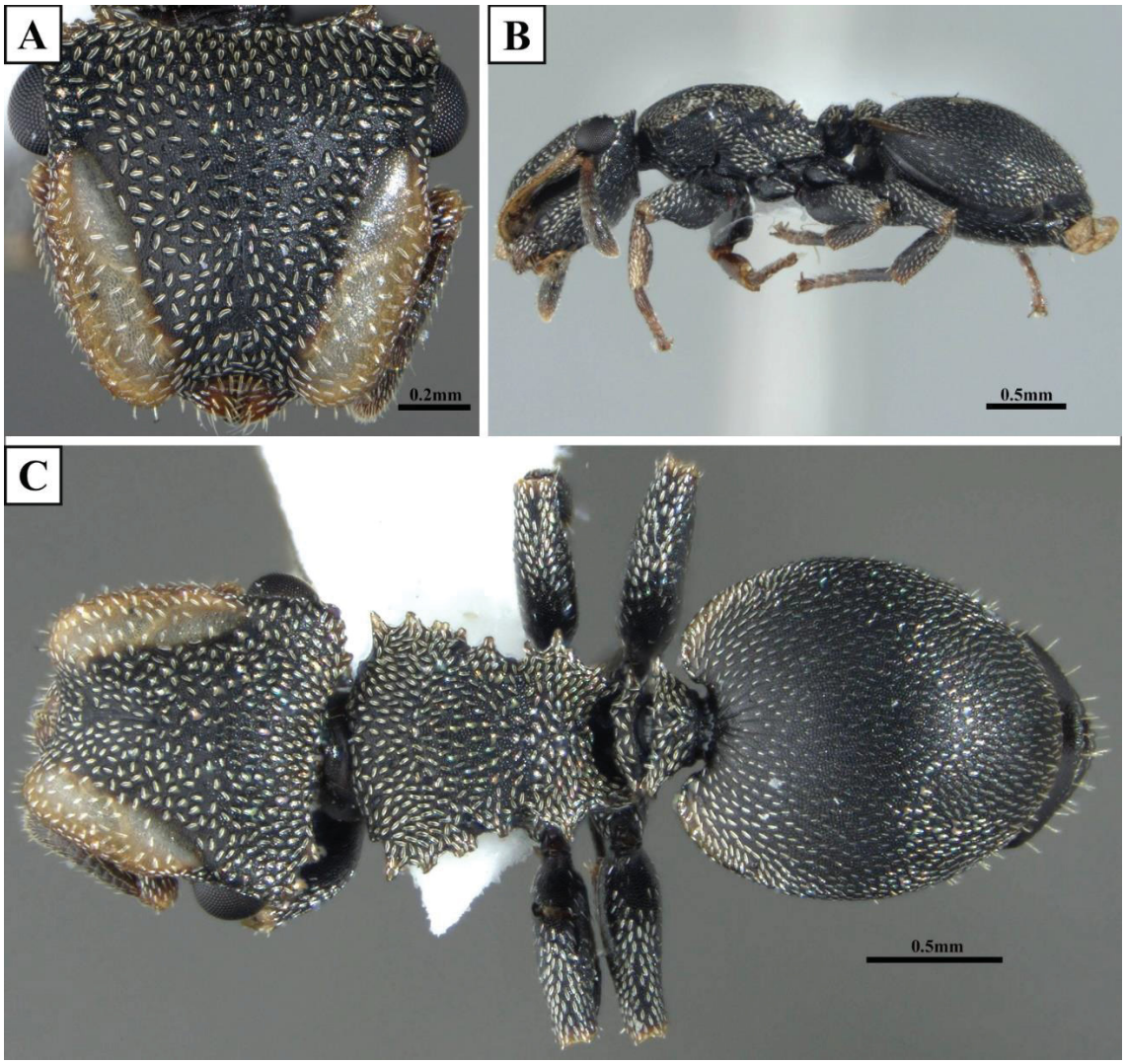

Figure 11: Worker of *Cephalotes* sp. n. C. A: frontal view. B: lateral view. C: dorsal view. Brazil: MG, Manga.

Distribution: Minas Gerais, Brazil.

Comments: This species differs from others in new species 1 by the hairs on first tergite of gaster, which is simple and sparse, with caniculate hairs only on anterior region, while new species 1 has caniculate hairs abundant and equally distributed. The species known from this species was

collected in two species of plants, *Handroanthus chrysotrichus* and *Myracrodruon urundeuva*. These trees are important components on Brazilian Savanna, but widely found on urban regions.

5.1.4 *Cephalotes adolphi* (Emery, 1906)

Figs. 12, 13

Holotype: BRASIL, Mato Grosso, Coxipó, ix.900, typus [MSNG] [examined by photo on Antweb.org CASENT0904906].

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 87.09-89.74; OI 18.62-20.00; PI 266.67-327.50; HBI 23.15-27.16.

Soldier (first description): Head, dorsum of mesosoma and legs yellowish; lateral of mesosoma dark; gaster yellowish with a transverse macula (Fig. 12c).

Mandibles alveolate, ventral face of head weakly foveate, space between foveae microalveolate. Dorsum of head regularly foveate (Fig. 5a). Internal surface of antennal scrobes microalveolate. Dorsum of mesosoma foveate-microalveolate; lateral of mesosoma finely rugose with sparse foveae; petiole and postpetiole smooth. Gaster microalveolate.

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

Head longer than wide (CI 87.09-89.74). Dorsum of head disc shaped, slightly convex anteriorly (Fig. 12a). Mandibles with a strong longitudinal lateral angle. Frontal carinae crenulate anteriorly. Clypeus with a pair of denticles (Fig. 12a). 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 with a pair of narrow projections (Fig. 12a).

In profile, pronotum ascending, meso and metanotum continuous and flat (Fig. 12b). In dorsal view, anterior margin of pronotum gently rounded; lateral margins with two pairs of denticles, the anterior one acute, the second one obtuse; pronotal carina weakly marked, not crenulate, medially interrupted (Fig. 12c). Mesonotum with a pair of blunt rounded denticles. Propodeal groove impressed. Propodeum with well differentiate dorsal and declivous faces; in dorsal view, lateral margins of propodeum with a pair of median obtuse denticles and a pair of well-developed spines, directed upwards, broad basally with apex acute and curved anteriorly (Fig. 12c). Femora not angulated dorsally; mid and hind basitarsi not flattened, with subparallel dorsal and ventral faces.

Petiole compressed anteroposteriorly, anterior margin with a discreet median concavity; lateral spines curved backwards; dorsum with a pair of denticles; subpetiolar process broader and rounded anteriorly (Fig. 12c). Postpetiole slightly longer than petiole, spines narrow and straight, dorsum with a "v" sharped elevation; subpostperiolar process pronounced ventrally and flattened anteroposteriorly (Fig. 12c).

Gaster elongate, with narrow anterior lamellae (Fig. 12c).

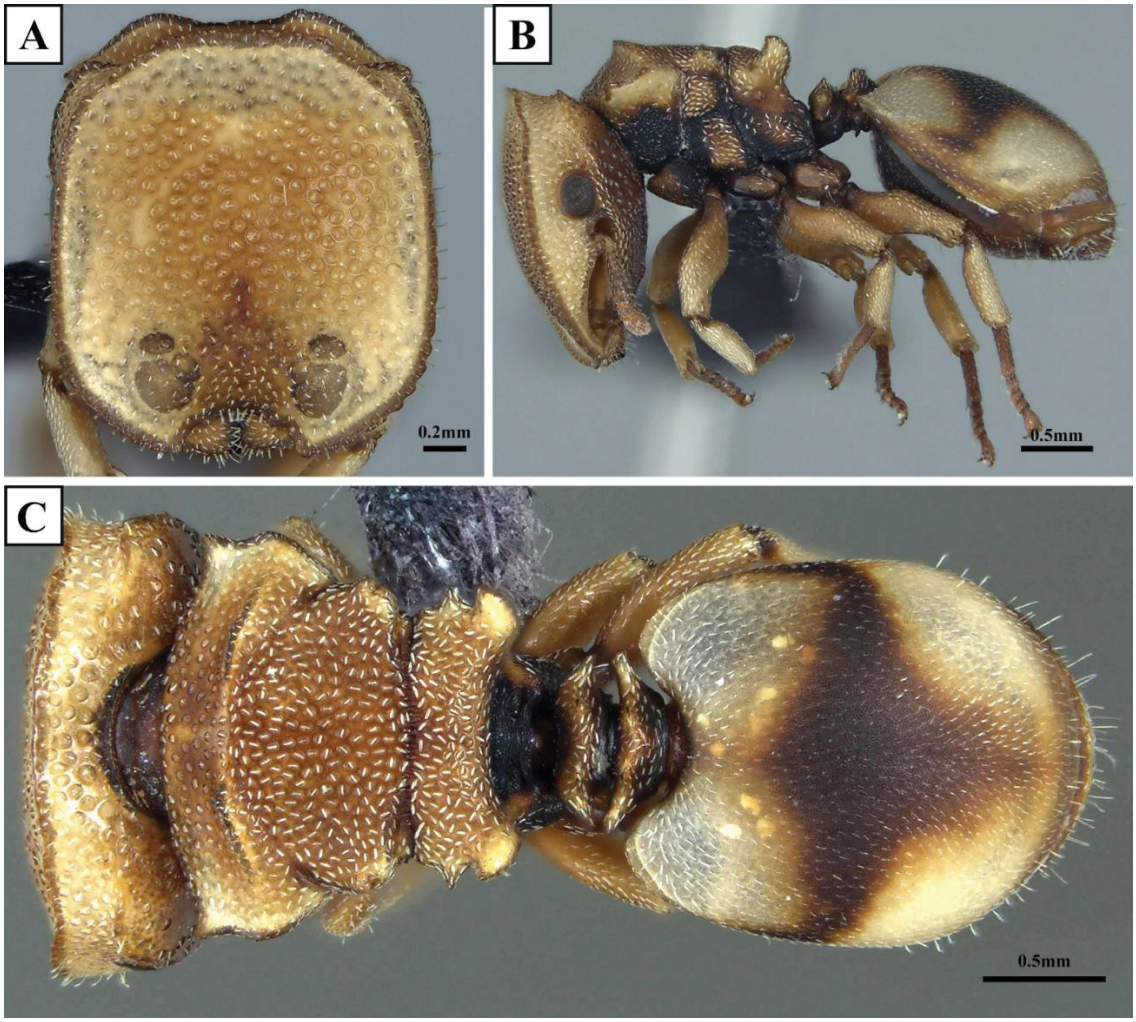

Figure 12: Soldier of *Cephalotes adolphi*. A: frontal view. B: lateral view. C: dorsal view. Brazil: MG, Uberlândia.

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 91.11; OI 24.39; PI 214.29; HBI 25.

Gyne (first description): Color black; head, lateral of pronotum and legs yellowish; gaster with four yellowish spots (Fig. 13).

Sculpture of head, petiole, postpetiole, legs and gaster as the soldiers. Dorsum of mesosoma, petiole and postpetiole with sparse foveae, space between foveae microalveolate.

Propleuron deeply striate. Anepisternum deeply foveate, without space between foveae; katepisternum and metapleuron finely rugose (Fig. 13b). Declivous face of propodeum finely rugose and microalveolate.

Pilosity of head as the soldiers. Mesosoma, petiole, postpetiole and legs with subdecumbent to appressed caniculate hairs; mesoescutum, axillae and legs with some short erect hairs. Dorsum of gaster with appressed simple hairs and some short erect hairs more abundant on the posterior edge of tergites; ventral face with sparse short and long erect simple hairs (Fig. 13b).

Head as the soldier (CI 91.11), but longer (Fig. 13a).

Mesosoma flattened in lateral view (Fig. 13b). 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. 13c). Dorsally, mesoscutum large and subtriangular, anterior margins rounded; notauli absent; parapsidial lines feebly visible and parallel; transscutal line impressed, reaching the lateral margins of mesosoma; scutoscutellar groove impressed, not extending to lateral margins; scutellum and axillae separated by a weak groove; axillae rounded posteriorly (Fig. 13c). Laterally, mesopleural groove impressed dividing anepisternum and katepisternum; metapleuron divided in upper metapleuron and lower metapleuron by a deep groove; metapleuropropodeal groove not impressed (Fig. 13b). In dorsal view, posterior margin of propodeum concave and meeting the declivous face in a pair of short, blunt denticles (Fig. 13c). Wings unknown.

Petiole subquadrate, anterior margin concave and lateral convex; without lateral or dorsal projections; subpetiolar process narrow. Postpetiole longer than petiole with a "v" sharped dorsal elevation and lateral blunt projections, subpostpetilar process pronounced ventrally and flattned anteroposterioly (Fig. 13c).

Gaster as the genus description, with protruding anteriorly lobes (Fig. 13c).

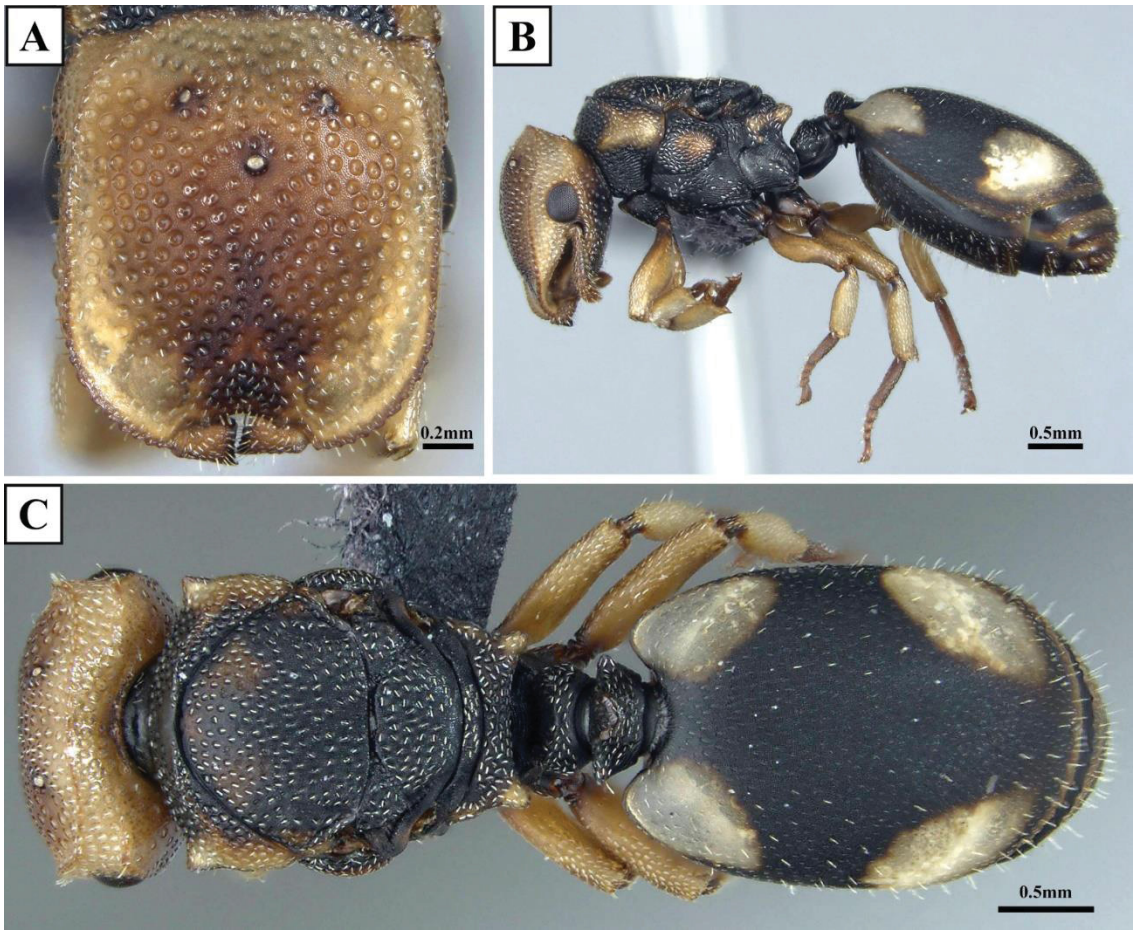

Figure 13: Gyne of *Cephalotes adolphi*. A: frontal view. B: lateral view. C: dorsal view. Brazil: MG, Uberlândia.

Distribution of the *Cephalotes* species of *angustus* group in Brazil

Species	Records from De Andrade and Baroni-Urbani, 1999	Records from literature, after 1999	Records from this study and literature, 1999	New records from this study
Cephalotes adolphi	MT	MG (7; 8)	DF (39)	PA
Cephalotes angustus	BA, MG, PR, RJ, RS, SC, SP	-	-	ES
Cephalotes conspersus	AM, AP, GO, MS, MT, RO	-	-	AC, MG
Cephalotes frigidus	BA, MG, RJ	GO (41; 21)	DF (39)	ES
Cephalotes goeldii	BA, ES, RJ	MG (41; 50; 45; 39), MT (40)	-	-
Cephalotes notatus	RJ, SP	MG (30)	-	GO
Cephalotes pallidicephalus	BA, MG, RJ, PR, SC, SP, RJ, RS	-	-	-
Cephalotes targionii	MT, SP	-	-	MG, RJ

5.2 The *atratus* species group

The *atratus* group was proposed for the first time by De Andrade and Baroni Urbani (1999). Before that, the species *C. alfaroi*, *C. atratus* and *C. serraticeps* were separated from the other species of the group, which were in the genus *Eucryptocerus*, comprised by *C. oculatus*, *C. opacus* and *C. placidus*. *Cephalotes alfaroi* is not included in this study, since it does not occur in Brazil. In the morphological phylogeny by De Andrade and Baroni Urbani (1999) 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) this relationship is inverse, and the *atratus* group is the most basal group in the topology. The *atratus* and *hamulus* groups share the absence of the soldier caste.

Diagnosis: Vertexal corners of head with two pairs of spines, one posterodorsal and one posteroventral. Pronotum with a pair of long dorsalateral spines always present; a pair of short median spine can be present in some species, even weakly developed. Postoccipital carinae with ventral expansions.

Brazilian species of *atratus* group

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

Note: The synapomorphies so far accepted for *C. marginatus* include abundant suberect pilosity on the first gastral sternite and median pronotal spines with ¼ of the size of the lateral ones. However, these traits are considerably variable among samples and do not support *marginatus* as a valid species. So, we here propose the synonymy of *Cephalotes marginatus* under *Cephalotes atratus*.

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

(Figure 14)

1 In lateral view, eyes positioned ventrally in relation to the antennal scrobes (Fig. 14a)… 2

1’ In lateral view, eyes positioned posteriorly in relation to the antennal scrobes (Fig. 14b)… 3

2 Body shiny. In lateral view, postpetiolar dorsal spines shorter than the subpostpetiolar process (Fig. 14d)… ***C. atratus***

2’ Body opaque. In lateral view, postpetiolar dorsal spines longer than the subpostpetiolar process (Fig. 14e)… ***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. 14f)… ***C. oculatus***

3’ In dorso-oblique view, dorsal and lateral faces of mesonotum and propodeum continuous, without carina (Fig. 14g)…4

4 Propodeal spines shorter than the declivous face of propodeum (Fig. 14c)… ***C. opacus***

4’ Propodeal spines longer than the declivous face of propodeum (Fig. 14e, 14e).. ***C. placidus***

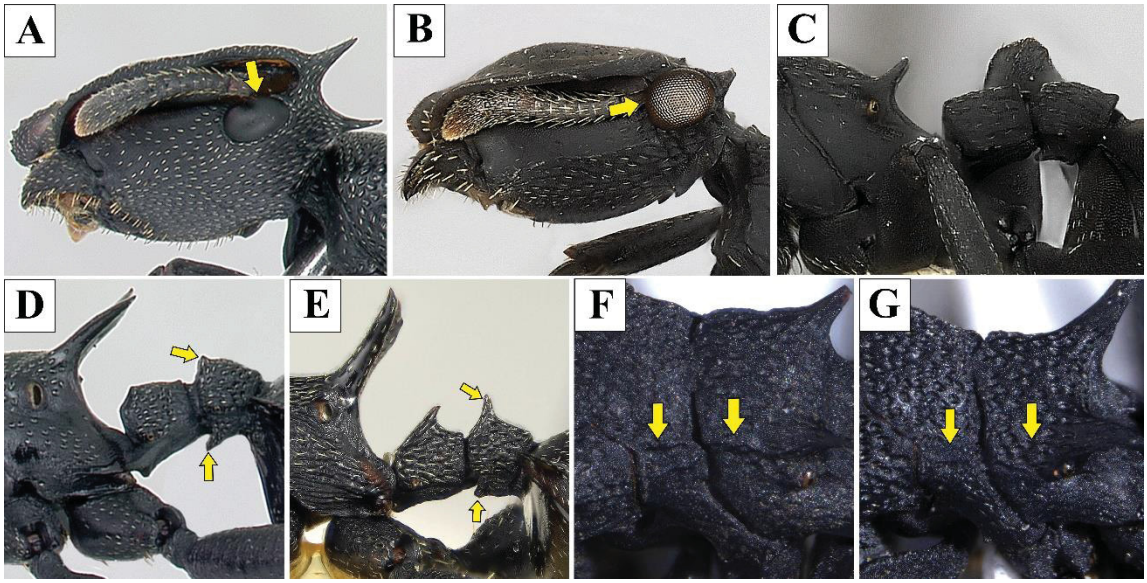

Figure 14: Workers of *atratus* group. A, D: *Cephalotes atratus* [CASENT0178627]. B, C: [CASENT0217839]. E: *Cephalotes serraticeps*. F: *Cephalotes oculatus*. G: *Cephalotes placidus*.

Distribution of the *Cephalotes* species of *atratus* group in Brazil

Species	Records from De Andrade and Baroni-Urbani, 1999	Records from literature, after 1999	New records from this study
Cephalotes atratus	AC, AP, AM, BA, DF, ES, GO, MA, MT, MS, MG, PA, PB, PR, PE, PI, RJ, RO, RR, SP, SE	-	TO
Cephalotes oculatus	AP, BA, PA	AM (52), MT (56; 33)	RO
Cephalotes opacus	AC, AM, BA, ES, MT, PA, RO	-	AP, SE
Cephalotes placidus	AC, AM, AP, MT, PA, RO		-
Cephalotes serraticeps	AM, AP, MA, PA, RO	AC (54)	-

5.3 The *basalis* species group

The *basalis* group of De Andrade and Baroni Urbani (1999), include the *complanatus* group of *Paracryptoceus* by Kempf (1951), the isolate species *C. basalis* and *C. manni,* and a new species described by De Andrade in De Andrade and Baroni Urbani (1999), *C. mompox*. According to the molecular phylogeny, this group forms a clade with exclusively North and Central American species groups (*multispinosus*, *wheeleri* and *texanus* groups). All species recorded for Brazil occur only in the North and Midwest regions.

Diagnosis: Declivous face of propodeum and anterior face of petiole truncate. Fore femora with a median projection dorsally. Mid and hind basitarsi anteroposteriorly strongly flattened, with proximal region broad and distal region narrow.

Brazilian species of *basalis* group

Cephalotes basalis (Smith, 1876)
Cephalotes complanatus (Guérin-Méneville, 1844)
Cephalotes cordiae (Stitz, 1913)
Cephalotes manni (Kempf, 1951)
Cephalotes ramiphilus (Forel, 1904)

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

(Figure 15)

1 In dorsal view, propodeum with one pair of spines (Fig. 15e)… ***C. cordiae***

1’ In dorsal view, propodeum with two or more pairs of spines (Fig. 15f, 15g)… 2

2 In dorsal view, lateral margins of pronotum tridentate (Fig. 15c)… ***C. manni***

2’ In dorsal view, lateral margins of pronotum without denticles (Fig. 15d)… 3

3 In dorsal view, frontal carinae upturned dorsally above the eyes (Fig. 15a)… ***C. basalis***

3’ In dorsal view, frontal carinae not upturned dorsally above the eyes (Fig. 15b)… 4

4 Declivous face of propodeum finely striate (Fig. 15h)… ***C. ramiphilus***

4’ Declivous face of propodeum microalveolate, never striate (Fig. 15i)... ***C. complanatus***

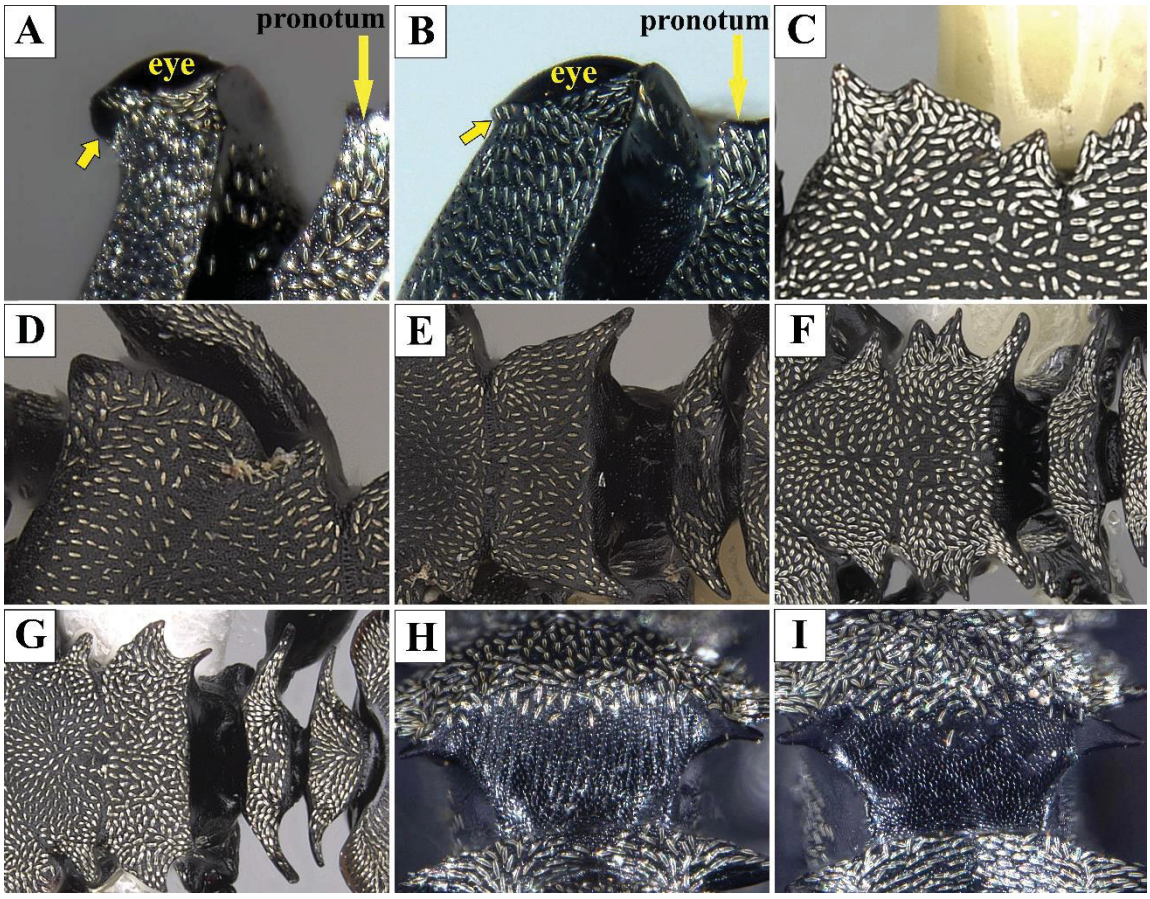

Figure 15: Workers of *basalis* group. A, I: *Cephalotes complanatus*. B: *Cephalotes basalis*. C: *Cephalotes manni* [CASENT0627955]. D, E: *Cephalotes cordiae* [CASENT0919596]. F: *Cephalotes basalis* [CASENT0922591]. G: *Cephalotes complanatus* [CASENT0922595]. H: *Cephalotes ramiphilus*.

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

(Figure 16)

1 In dorsal view, propodeal spines longer than petiolar spines (Fig. 16a) ... ***C. cordiae***

1’ In dorsal view, propodeal spines shorter than petiolar spines (Fig. 16b, 16c) ... 2

2 Gaster without lamellar anterior expansions (Fig. 16d) ... ***C. complanatus***

2’ Gaster with lamellar anterior expansions (Fig. 16e) ... 3

3 Metapleura with more than 30 hairs (Fig. 16f) ... ***C. basalis***

3’ Metapleura with less than 15 hairs (Fig. 16g) ... ***C. ramiphilus***

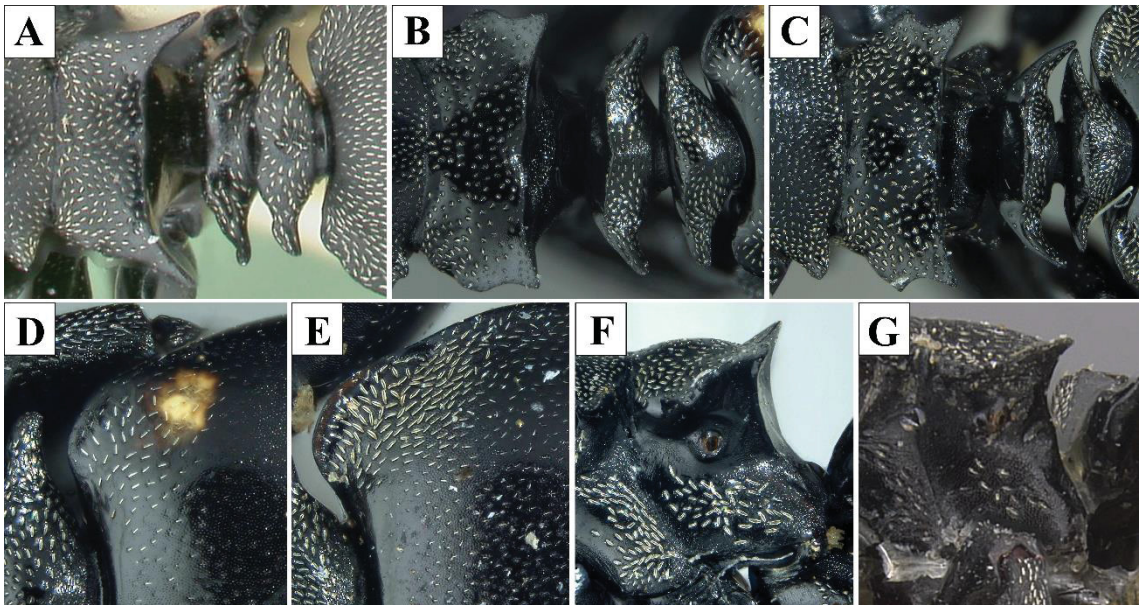

Figure 16: Soldiers of *basalis* group. A: *Cephalotes cordiae* [FOCOL2143]. B, D: *Cephalotes complanatus*. C, E, F: *Cephalotes basalis*. G: *Cephalotes ramiphilus* [CASENT0909261].

Distribution of the *Cephalotes* species of *basalis* group in Brazil

Species	Records from De Andrade and Baroni-Urbani, 1999	Records from literature, after 1999	New records from this study
Cephalotes basalis	-	-	RO
Cephalotes complanatus	AM, MT, PA, RO	AC (10)	GO
Cephalotes cordiae	AC	-	-
Cephalotes manni	AM, PA, RO	-	-
Cephalotes ramiphilus	AM	-	AC

5.4 The *clypeatus* species group

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

Diagnosis: Pronotal and propodeal spines fused with a lamella. Gaster surrounded by lamella.

Brazilian species of *clypeatus* group

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

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

(Figure 17)

1 In dorsal view, gaster smooth and shiny (Fig. 17a)… ***C. clypeatus***

1' In dorsal view, gaster sculptured and opaque (Fig. 17b, 17c)… 2

2 Gaster yellowish to brownish with sparse hairs (Fig. 17b)… ***C. membranaceus***

2' Gaster black, with abundant hairs (Fig. 17c)… ***C. ustus***

Figure 17: Workers and soldiers of *clypeatus* group. A: *Cephalotes clypeatus* [CASENT0173669]. B: *Cephalotes membranaceus* [FOCOL2117]. C: *Cephalotes ustus*.

Distribution of the *Cephalotes* species of *clypeatus* group in Brazil

Species	Records from De Andrade and Baroni-Urbani, 1999	New records from this study
Cephalotes clypeatus	AC, AM, AP, BA, GO, MA, MG, MS, MT, PE, PI, PR, RO, RR, SP	CE, SE, TO
Cephalotes membranaceus	ES, RJ	-
Cephalotes ustus	BA, MG	-

5.5 The *coffeae* species group

Kempf (1951) created the monotypic *coffeae* subgroup, within the *angustus* group, in the subgenus *Harnedia* of the genus *Paracryptocerus*. De Andrade and Baroni Urbani raised this subgroup to a group of *Cephalotes*, adding the species *C. setulifer* and the two new species described by De Andrade in De Andrade and Baroni Urbani (1999), *C. peruviensis* and *C.*

trichophorus. *Cephalotes trichophorus* occurs in Brazil and Peru; the other species occur in Central America and northeastern of South America. The recent molecular phylogeny (Price et al., 2016) recovered *coffeae* as the sister group of the clade formed by *patei*, *emeryi* and *crenaticeps* groups, none of them occurring in Brazil.

Diagnosis: Declivous face and dorsal face of propodeum continuum. 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 *coffeae* group

Cephalotes trichophorus De Andrade, 1999

Distribution of the *Cephalotes* species of *coffeae* group in Brazil

Species	Records from De Andrade and Baroni-Urbani, 1999	New records from this study
Cephalotes coffeae	AM	AC

5.6 The *depressus* species group

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) this group is sister to the clade formed by *coffeae, patei, emeryi* and *crenaticeps* groups. All species in *depressus* group occurs in Brazil.

Diagnosis: Propodeum with continuous dorsal and declivous face, with two pairs of spines, the anterior longer than the posterior.

Brazilian species of *depressus* 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)

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

(Figure 18)

1 In dorsal view, postpetiole subquadrate, at most twice wider than length (Fig. 18k)… ***C. depressus***

1' In dorsal view, postpetiole subrectangular, three to five times wider than long (Fig. 18d, 18e, 18f, 18j, 18l, 18m)… 2

2 Erect hairs present on mesosoma, petiole, postpetiole and gaster (Fig. 18n)… ***C. eduarduli***

2' Erect hairs predominantly absent, present only on the apex of spines (Fig. 18o)… 3

3 In frontal view, color of the frontal lobes similar to the rest of the head (Fig. 18a). In dorsal view, posterior margins of petiolar spines weakly curved backwards (Fig. 18e - dotted). … ***C. borgmeieri***

3' In frontal view, color of frontal lobes lighter than rest of the head (Fig. 18b, 18c). In dorsal view, posterior margins of petiolar spines strongly curved backwards (Fig. 18f, 18g, 18j, 18l, 18m - dotted). … 4

4 In dorsal view, petiole with an angle separating the anterior and lateral margin (Fig. 18g, 18m - line)… 5

4' In dorsal view, petiole with anterior and lateral margin continuous (Fig. 18e, 18f, 18j - line 18l)… 6

5 Posterior third of declivous face of propodeum striate (Fig. 18h)… ***C. betoi***

5 Posterior third of declivous face of propodeum not striate; some striae can be present, but not reaching the posterior third (Fig. 18i)… ***C. pavonii***

6 In dorsal view, lateral expansions of pronotum subrectangular, followed by a shorter projection (Fig. 18d)… ***C. palustris***

6' In dorsal view, lateral expansions of pronotum triangular (Fig. 18f)… ***C. cordatus***

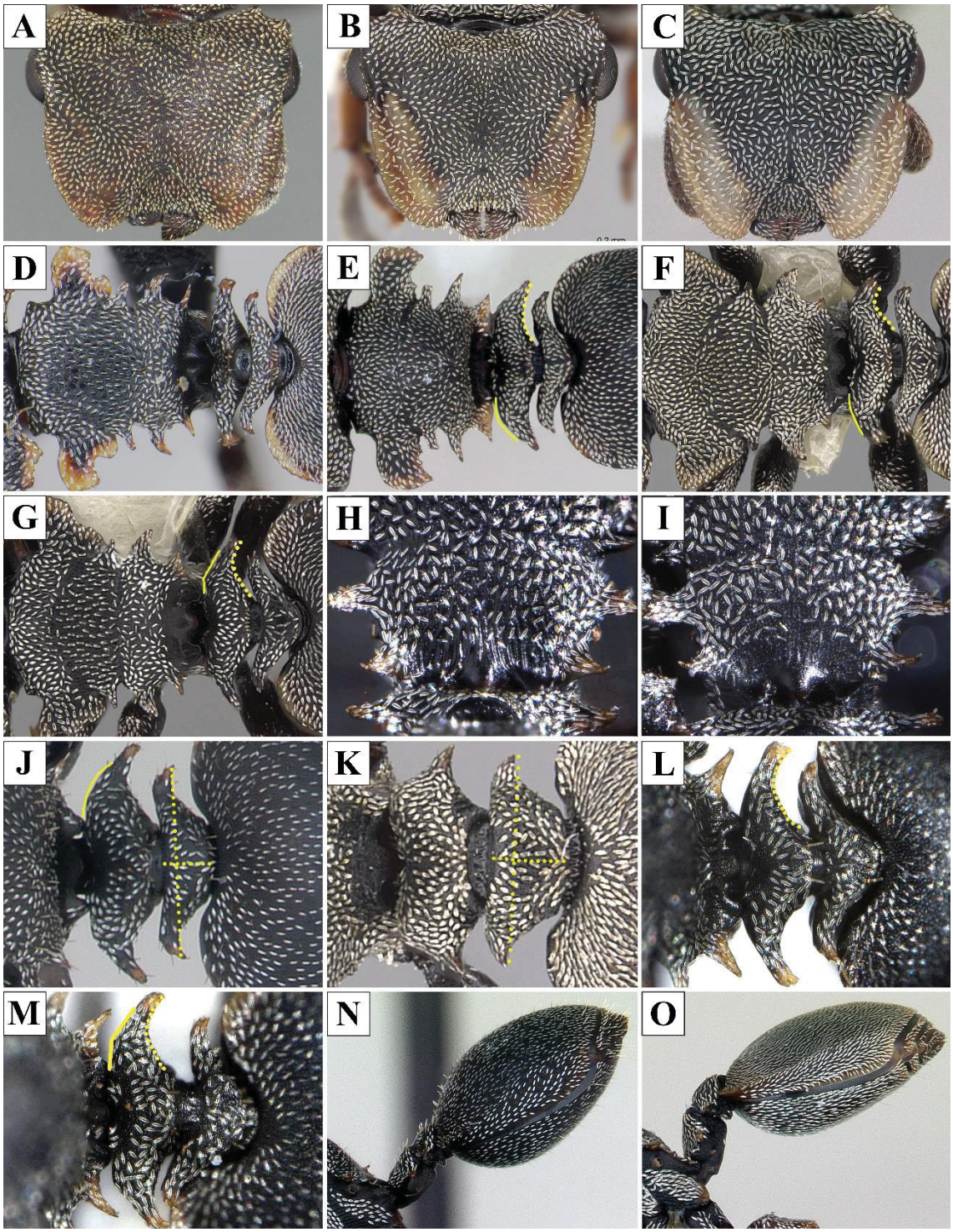

Figure 18: Workers and soldiers of *depressus* group. A, E: *Cephalotes borgmeieri* [CASENT0173665]. B, F: *Cephalotes cordatus* [CASENT0922596]. G: *Cephalotes pavonii* [CASENT0922611]. I, M: *Cephalotes pavonii*. C, O: *Cephalotes depressus* [CASENT0173671], K: *Cephalotes depressus* [CASENT0909272]. D: *Cephalotes palustris* [UFV-LABECOL-004489]. H: *Cephalotes betoi.* I, L: *Cephalotes betoi*. J, N: *Cephalotes eduarduli* [CASENT0173676]

Distribution of the *Cephalotes* species of *depressus* group in Brazil

Species	Records from De Andrade and Baroni-Urbani, 1999	Records from literature, after 1999	Records from this study and literature	New records from this study
Cephalotes betoi	BA, DF, GO, MS, MT, PI, SP	-	MG (54; 18; 26; 1; 40)	CE, MA, PE, TO
Cephalotes borgmeieri	MG, MS, MT, SP	-	-	ES, PR
Cephalotes cordatus	AC, AP, AM, GO, MA, MT, PA, PI, RO	BA (54; 18), MG (7; 8)	-	DF, TO
Cephalotes depressus	AP, AM, BA, GO, MG, MS, MT, PA, PE, RJ, RO, RS, SC, SP	SE (17)	DF (16, 39, 49)	CE, PR, TO
Cephalotes eduarduli	BA, GO, MS, MT, PA, SP	PE (31), MS (34)	MA (36), MG (54; 9; 7; 8; 18; 41)	PR, RO, TO
Cephalotes palustris	PA	-	-	AM, MG
Cephalotes pavonii	AP, AM, BA, ES, GO, MT, PA, RJ, RR	-	AC (32; 29), DF (16), MA (37) MG (42; 30; 54; 11; 18)	-

5.7 The *fiebrigi* species group

Kempf (1958) created the *jheringi* subgroup of the *angustus* group in *Paracryptocerus (Harnedia)* with seven species. Later, De Andrade and Baroni Urbani (1999) separated it in 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 *prodigiosus* group with the species *C. bivestitus* and *C. prodigiosus*, characterized by the concave cephalic disc in soldiers. Finally, the remaining species of the *jheringi* subgroup were transferred to Kempf's *pilosus* group, originally formed by *C. fiebrigi*, *C. liogaster,* and *C. pilosus*. This last act resulted 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) the *bruchi* group was recovered as sister to the *fiebrigi* group. The authors argued that the cephalic disc incomplete could be a secondary loss, and the unknown ancestor of *C. bruchi* should have had both soldiers and gynes with a complete disc but kept the species in a separated group. However, the molecular phylogenies (Price et al., 2014, 2016) recovered *C. bruchi* within the *fiebrigi* group, as sister to the grouping formed by *C. jheringi*, *C. bohlsi* and *C. specularis*. Then, based on morphological

and molecular evidence, we here transfer *C. bruchi* to the *fiebrigi* group, extinguishing the *bruchi* species group.

Diagnosis: Declivous face of propodeum continuum with the dorsal face. Anterior region of gaster with lobes, never extending posteriorly in the form of lateral lamellae.

Brazilian species of *fiebrigi* group

Cephalotes bruchi (Forel, 1912)
Cephalotes fiebrigi (Forel, 1906)
Cephalotes guayaki De Andrade, 1999
Cephalotes jheringi (Emery, 1894)
Cephalotes pilosus (Emery, 1896)
Cephalotes quadratus (Mayr, 1868)
Cephalotes specularis Brandão, Feitosa, Powell and Del-Claro, 2014
Cephalotes **new species D** Oliveira, Feitosa and Powell, 2020

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

(Figure 19)

1 Body with long, flexuous and abundant hairs (Fig. 19j) ... 2

1’ Pilosity with a different pattern (Fig. 19g, 19h, 19k) ... 3

2 In frontal view, frontal carinae with a lateral projection anterior to the eyes, (Fig. 19d) ... ***C.* sp. n. D**

2’ In frontal view, frontal carinae straight (Fig. 19e) ... ***C. pilosus***

3 In dorsal view, frontal carinae strongly bent dorsally over the eyes (Fig. 19f) ... ***C. bruchi***

3’ In dorsal view, frontal carinae not bent dorsally over the eyes (Fig. 19c) ... 4

4 In lateral view, first gastral tergite with erect hairs (Fig. 19h, 19k) ... 5

4’ In lateral view, first gastral tergite without erect hairs (Fig. 19g)... 6

5 First gastric tergite with less than 50 erect hairs (Fig. 19h) ... ***C. guayaki***

5’ First gastral tergite with more than 100 erect hairs (Fig. 19k) ... ***C. fiebrigi***

6 In lateral view, head very convex, forming deep depressions anterior to the eyes (Fig. 19a) .... ***C. quadratus***

6’ In lateral view, head slightly convex or straight, not forming deep depressions (Fig. 19b)... 7

7 Gaster shiny, with equal sized hairs, evenly distributed throughout the tergite (Fig. 19i).. ***C. specularis***

7’ Gaster opaque, with shorter and sparser hairs in the central region, with longer and more abundant hairs in the anterior region (Fig. 19l)...***C. jheringi***

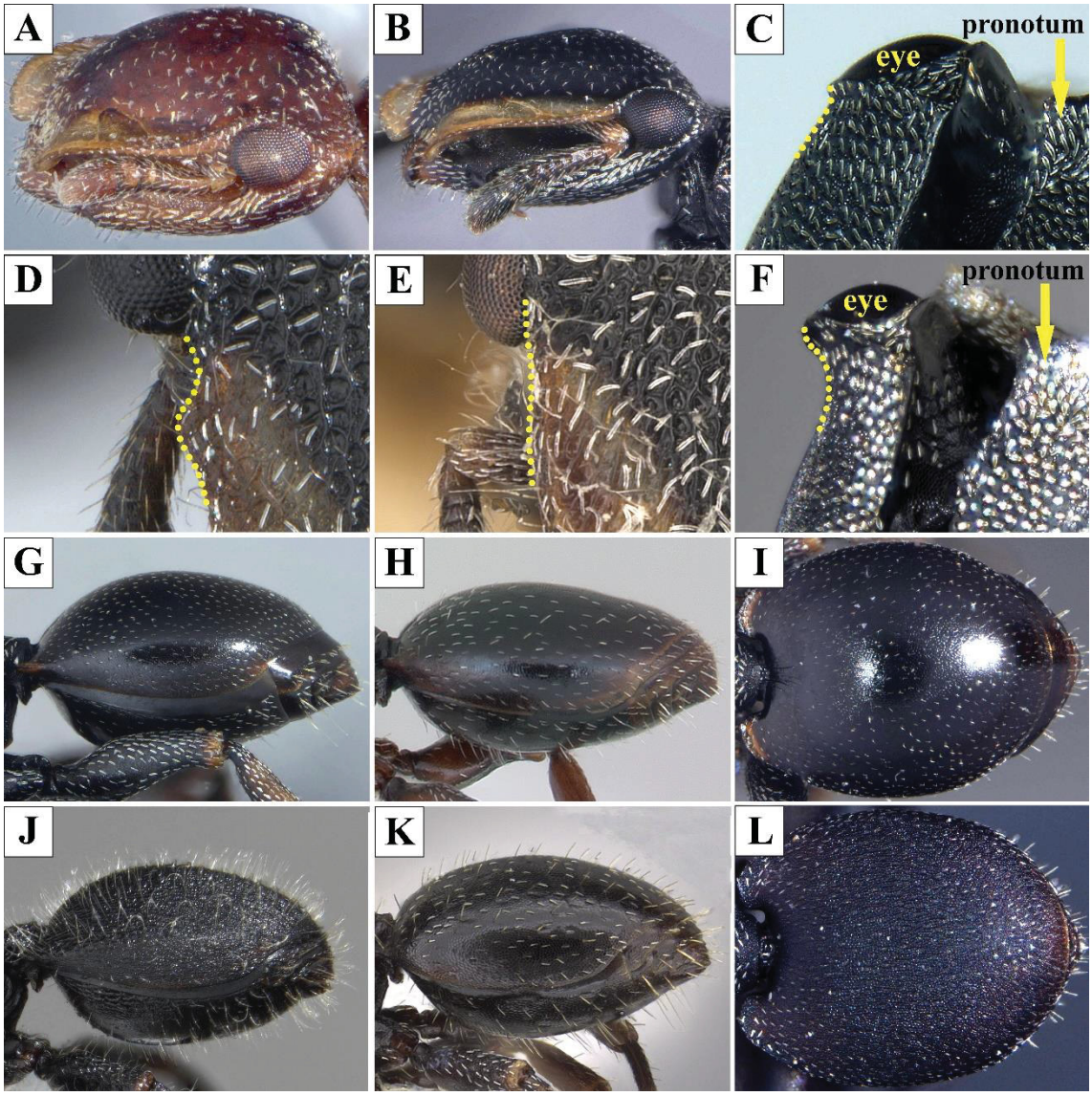

Figure 19: Workers of *fiebrigi* group. A: *Cephalotes quadratus*. B, G, I: *Cephalotes specularis*. C: *Cephalotes complanatus* (*basalis* group). D, J: *Cephalotes* sp. n. D. E: *Cephalotes pilosus* [CASENT0904912]. F: *Cephalotes basalis* (*basalis* group). H: *Cephalotes guayaki* [CASENT0173677]. K: *Cephalotes fiebrigi* [CASENT0922539]. L: *Cephalots jheringi*.

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

(Figure 20)

1 In frontal view, cephalic dorsum disc shaped, totally emaginated by carina (Fig. 20a) ... 2

1’ In frontal view, cephalic dorsum dome shaped, not totally emaginated by carina (Fig. 20b, 20c) ... 5

2 Body with abundant and flexuous hairs, most abundant in the gaster (Fig. 20j) ... ***C.* sp. n. D**

2’ Body with short erect and appressed hairs (Fig. 20k, 20l) ... 3

3 In lateral view, dorsum of mesosoma with more than 40 erect hairs (Fig. 20f) ... ***C. fiebrigi***

3’ In lateral view, dorsum of the mesosoma with appressed hairs, at most 20 erect hairs (Fig. 20d, 20e) ... 4

4 Cephalic disc with erect clavate hairs (Fig. 20d) ... ***C. specularis***

4’ Cephalic disc with appressed caniculate hairs (Fig. 20e) ... ***C. jheringi***

5 Mesosoma with long and flexuous hairs (Fig. 20g) ... ***C. pilosus***

5’ Mesosoma with appressed hairs (Fig. 20d, 20e) ... 6

6 In frontal view, distance between the anterior and posterior margins of the dorsum of head less than or equal to the distance between the eyes (Fig. 20b) ... ***C. bruchi***

6’ In frontal view, the distance between the anterior and posterior margins of the dorsum of head greater than the distance between the eyes (Fig. 20c) ... 7

7 In dorsal view, propodeal groove strongly impressed forming a depression in the integument (Fig. 20h) ... ***C. quadratus***

7’ In dorsal view, propodeal groove weakly impressed, without depression in the integument (Fig. 20i) ... ***C. guayaki***

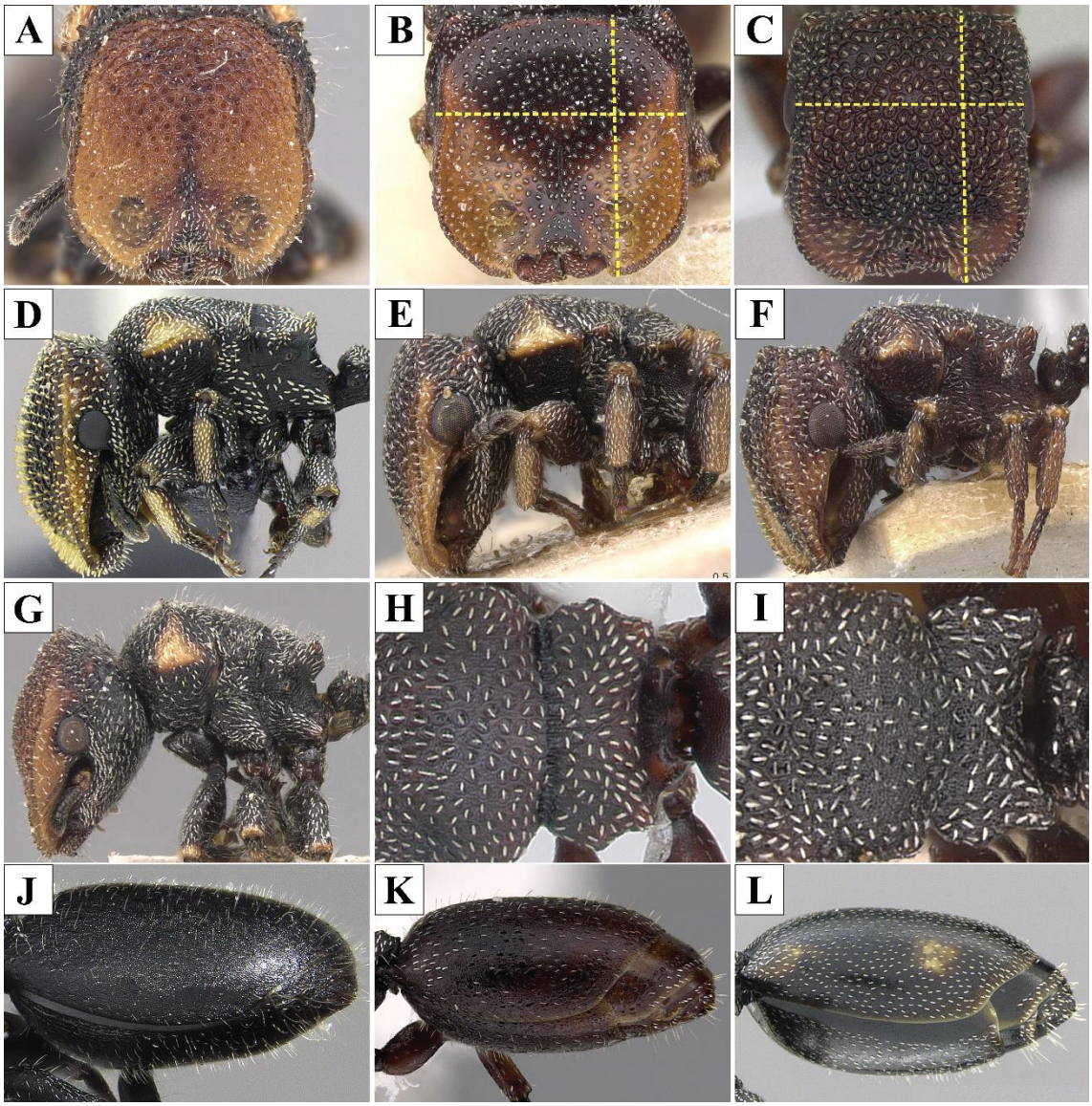

Figure 20: Soldiers of *fiebrigi* group. A, G: *Cephalotes pilosus* [CASENT0904911]. B: *Cephalotes bruchi* [CASENT0912591]. C, H: *Cephalotes quadratus* [CASENT0173705]. D, L: *Cephalotes specularis* [Brandão et al., 2014]. E: *Cephalotes jheringi* [CASENT0904919]. F: *Cephalotes fiebrigi* [CASENT0909290]. I: *Cephalotes guayaki* [CASENT0904920]. J: *Cephalotes* sp. n. D. K: *Cephalotes fiebrigi* [CASENT0922538].

5.7.1 *Cephalotes* new species D Oliveira, Feitosa and Powell, 2020

Figs. 21, 22

Holotype: BRASIL: Mato Grosso do Sul, Porto Murtinho, 28.i.2015 (dique, espinho *P. ruscifolia*), P. R. Souza (worker) [DZUP].

Paratype: same data as holotype (4 workers, 2 soldiers) [DZUP], (1 worker) [MZSP], (1 worker) [INPA], (1 worker, 1 soldier) [USNM].

Diagnosis: A member of *fiebrigi* species group, with long and flexuous hairs. The frontal carinae notched anteriorly to the eyes, forming a lateral angle. Lateral margins of propodeum with an anterior pair of short and blunt lateral denticles, followed by a large and acute denticle, and a row of minor acute denticles.

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 4.36-4.952; CI 104.91-109.57; OI 26.42-29.79; PI 37.50-44.35; HBI 77.17-30.77.

Worker description: Color dark brown to black; frontal lobes yellowish (Fig. 21c). Mandibles, apices of the antennal scapes, apex of each segment of the legs, and body spines tips light brownish to ferruginous (Fig. 21b).

Mandibles, dorsum of head, mesosoma, petiole and postpetiole foveate-rugose, space between foveae microalveolate (Fig. 21c). Frontal lobes weakly striate (Fig. 21a). Internal surface of antennal scrobes microalveolate with incomplete striae. 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 of which external face is areolate-rugose. Gaster microalveolate, the anterior half of first tergite with longitudinal rugosities, originating near to the postpetiole insertion (Fig. 21c); sternite with some irregular weak rugosities.

Body with abundant flexuous hairs, and some sparse appressed caniculate hairs (Fig. 21b). Anterior margin of clypeus with suberect caniculate hairs.

Head slightly wider than long (CI 104.91-109.57), weakly convex. Mandibles with a weakly developed lateral angle; Anterior margin of clypeus slightly concave, with a pair of lateral denticles. Frontal carinae notched below the eyes, forming a lateral angle (Fig. 21a). Antennal club ill-defined. In frontal view, eyes broader anteriorly. Lateroventral margins of head without carinae. Vertexal corners with irregular lamellar expansions.

Mesosoma convex in lateral view (Fig. 21b). In dorsal view, lateral margins of pronotum with three pairs of denticles, the anterior one acute and the two posterior obtuse. Promesonotal groove impressed only on the pleuron (Fig. 21c). Mesonotum with a pair of short blunt denticles. Propodeal groove absent. Dorsal and declivous faces of propodeum continuous; 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, which extends to declivous face; the number and degree of development of the denticles vary even between sides of the same specimen (Fig 21c). Femora not angulated dorsally; mid and hind basitarsi not flattened, with subparallel dorsal and ventral faces.

Petiole compressed anteroposteriorly, anterior margin with a discreet median concavity; lateral spines curved backwards; dorsum with a pair of denticles (Fig. 21c); subpetiolar process acute anteriorly (Fig. 21b). Postpetiole slightly longer than petiole (Fig. 21c); without dorsal projections; lateral spines broad and curved backwards (Fig. 21c); subpostperiolar process pronounced and flattened anteroposteriorly (Fig. 21b).

Gaster elongated, with a pair of well-developed thick anterolateral lobes, not extending posteriorly in the form of a lateral lamella (Fig. 21c).

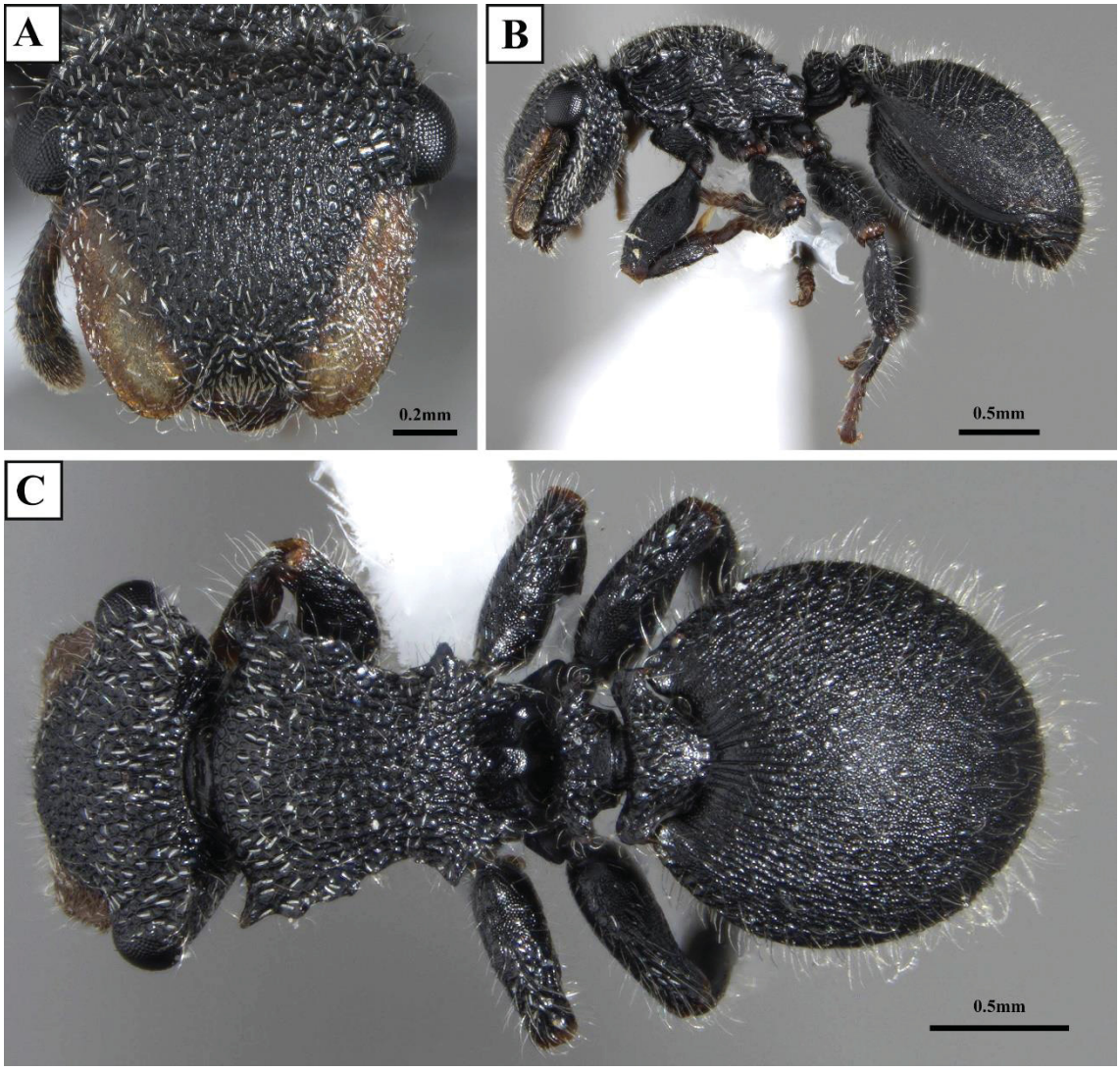

Figure 21: Worker of *Cephalotes* sp. n. D: frontal view. B: lateral view. C: dorsal view. Brazil: MS, Porto Murtinho.

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 89.60-94.90; OI 21.30-21.98; PI 37.65-42.19; HBI 29.87-33.33.

Soldier description: Color black, frontal lobes brownish (Fig. 22).

Mandible, ventral face of head (Fig. 22a), promesonotum and mesonotum foveate, space between foveae microalveolate (Fig. 22c). Dorsum of head with small foveae anteriorly, increasing in diameter posteriorly. Internal surface of antennal scrobes as the worker. Dorsal face of mesosoma, 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. 22b). Legs microalveolate; except by tibiae which external face is areolate-rugose. Gaster microalveolate, with a few short weakly marked longitudinal rugosities, originating near the postpetiole insertion (Fig. 22c).

Body with abundant flexuous hairs (Fig. 22b), except on dorsum of head, which has tiny suberect simple hairs (Fig. 22a). Mandibles, lateral and ventral face of head, meso and metapleuron with few appressed caniculate hairs. Anterior margin of clypeus with suberect caniculate hairs. Gaster with sparse appressed simple hairs (Fig. 22c).

Head longer than wide (CI 89.60-94.90). Dorsum of head disc shaped, convex medially (Fig. 22a). Mandibles with a strong longitudinal lateral angle. Frontal carinae crenulate converging posteriorly. Clypeus with a pair of denticles (Fig. 22a). Antennal club ill-defined. Roof of antennal scrobes with lateral carinae and a posterior denticle. Lateroventral margins of head without carinae. Vertexal corners with a pair of broad projections (Fig. 22a).

In profile, pronotum ascending, meso and metanotum continuous and flat (Fig. 22b). In dorsal view, anterior margin of pronotum rounded; lateral margins with two pairs of denticle, the anteriorly one acute, the posterior one obtuse; pronotal carina weakly marked and crenulate (Fig. 22c). Mesonotum with a pair of blunt rounded projections. Propodeal groove impressed. Propodeum with well differentiate dorsal and declivous faces, in dorsal view, lateral margins of propodeum with a pair of median obtuse denticles and a pair of well-developed spines, directed upwards (Fig. 22c). Legs as the worker.

Petiole and postpetiole as the worker.

Gaster elongate, with the anterolateral lobes protruding anteriorly (Fig. 22c).

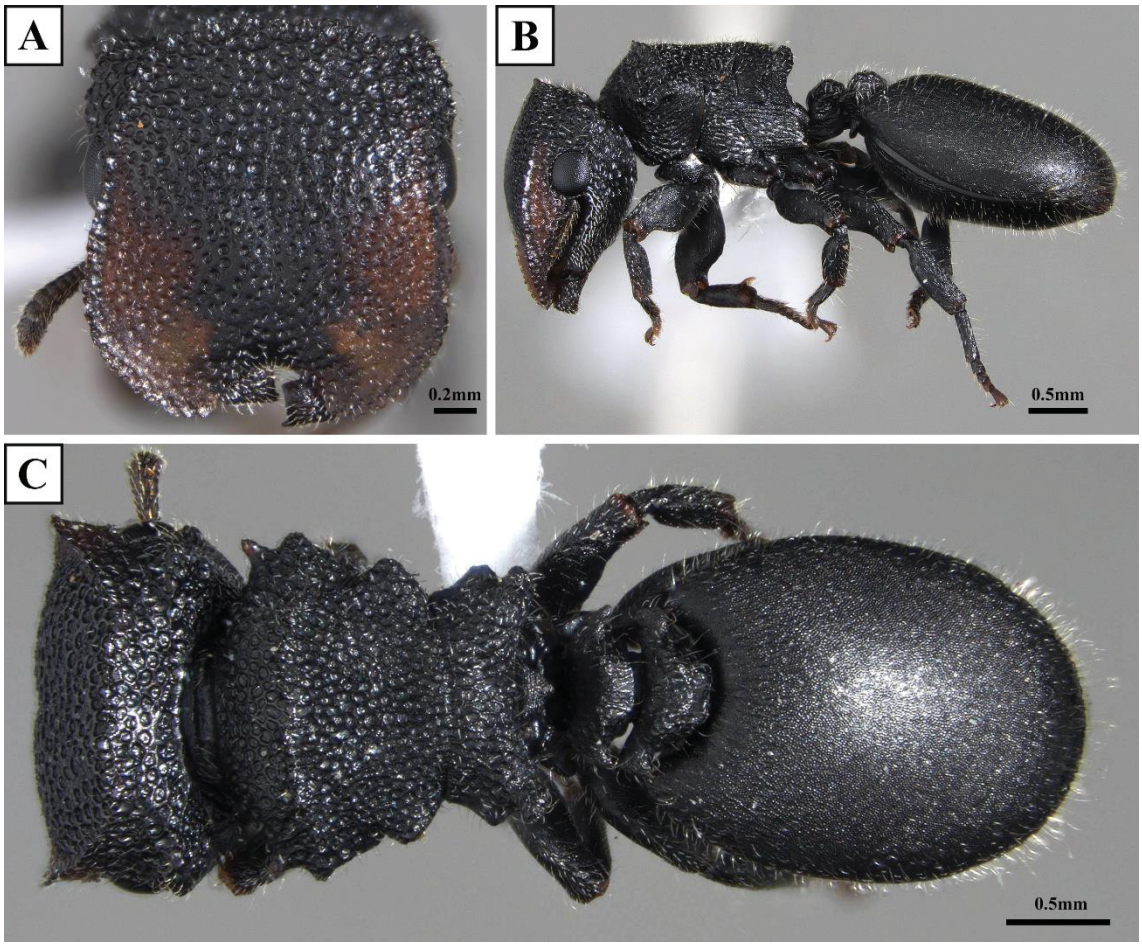

Figure 22: Soldier of *Cephalotes* sp. n. D: frontal view. B: lateral view. C: dorsal view. Brazil: MS, Porto Murtinho.

Distribution: Mato Grosso do Sul, Brazil.

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 hairs less abundant and shorter; in *C. pilosus* the frontal carinae is evenly straight to slightly depressed anterior to the eyes, but never forming a lateral angle.

Distribution of the *Cephalotes* species of *fiebrigi* group in Brazil

Species	Records from De Andrade and Baroni-Urbani, 1999	Records from literature, after 1999	Records from this study and literature	New records from this study
Cephalotes bruchi	MS	AM (20)	-	MT
Cephalotes fiebrigi	BA, MS, PI	-	-	MG, MT, PA
Cephalotes guayaki	MS	-	-	-
Cephalotes jheringi	RS	-	-	MS, PR
Cephalotes pilosus	BA, RN, SP	-	-	MS
Cephalotes quadratus	-	-	-	BA, MS, MT
Cephalotes specularis	-	-	MG (original description)	-

5.8 The *grandinosus* species group

The *grandinosus* group was first proposed by De Andrade and Baroni Urbani (1999), including five species, *C. persimplex*, 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 the species *C. incertus*, *C. maculatus*, *C. pinelii,* and *C. scutulatus*.

The groups *grandinosus* and *pinelii* are sister groups in the morphological phylogeny (De Andrade and Baroni Urbani, 1999), sharing many characters, as body strongly dorsoventrally flattened, dorsum of mesosoma continuous, 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), the *grandinosus* and *pinelii* groups are recovered as paraphyletic. The species *C. foliaceus* (*grandinosus* group) is sister to *C.* sp. 2 (here described as new species E, of the *pinelii* group). The clade formed by the other species of the *grandinosus* group (*C. grandinosus¸ C. klugi*, *C. persimplex* and *C. persimilis*) is the sister group of a clade formed by species of the *pinelii* group (*C. maculatus*, *C. liepini*, *C. nilpiei*, *C. pinelii* and *C. pileini*).

The morphological similarities and phylogenetic association between species of *pinelii* and *grandinosus* groups, suggests that these species likely represent a unique evolutive lineage. However, in this study the species of both groups occurring outside Brazil were not examined,

what would help to better understand the relationships between these species and redefine these groups.

Diagnosis: Body strongly flattened dorsoventrally. Dorsum of mesosoma continuous, with lamellar lateral expansions in dorsal view. Petiole and postpetiole with lamellar lateral expansions. Hind femora with a ventral or dorsal lamellar crest, usually crenulate and narrow.

Brazilian species of *grandinosus* group

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

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

(Figure 23)

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. 23c) ... ***C. grandinosus***

1’ In dorsal view, anterior portion of the lamellar expansions of the gaster bent dorsally, not continuous with the gastral tergite (Fig. 23d) ... 2

2 Body hairs relatively broad and uniform, without a submedian constriction (Fig. 23a) ... ***C. persimplex***

2’ Body hairs relatively narrow, with a submedian constriction (Fig. 23b) ... ***C. persimilis***

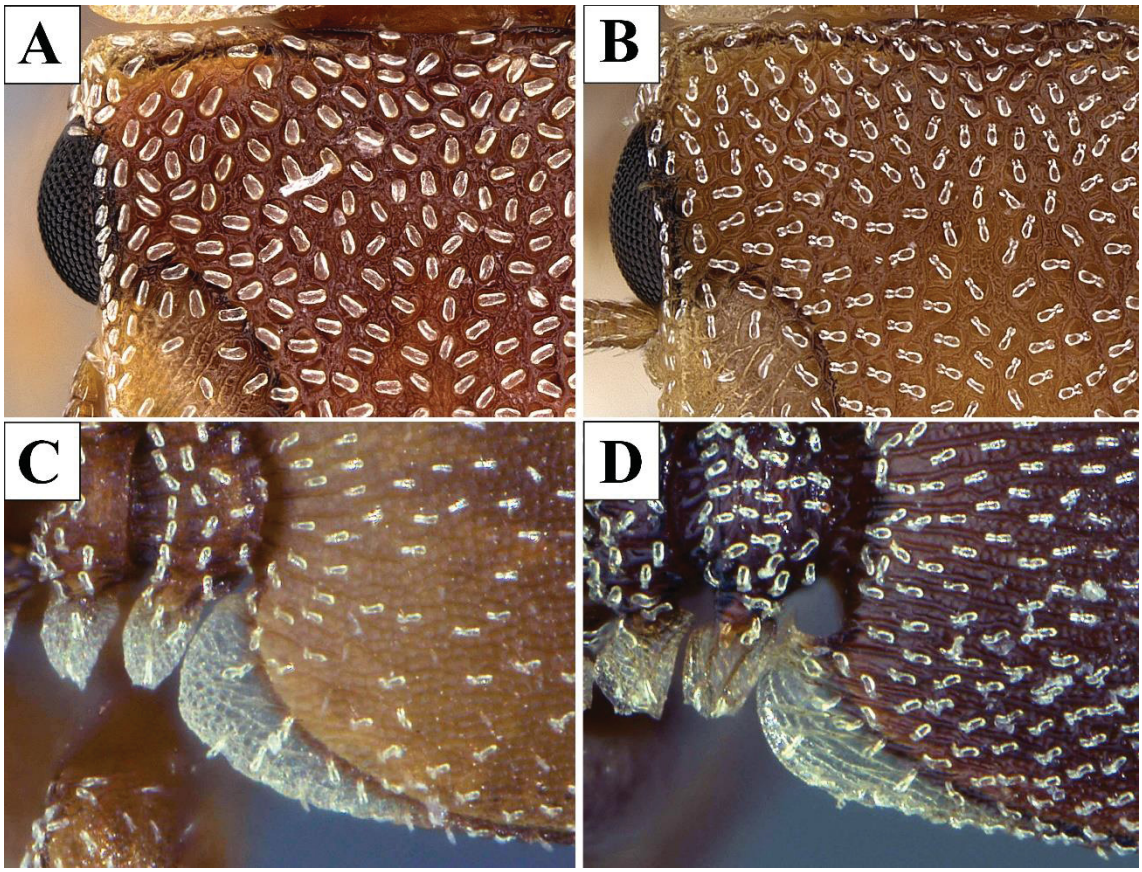

Figure 23: Workers of *grandinosus* group. A: *Cephalotes persimplex* [CASENT0922544]. B: *Cephalotes persimilis* [CASENT0922542]. C: *Cephalotes grandinosus*. D: *Cephalotes persimilis*.

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

(Figure 24)

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

1 In frontal view, foveae on the cephalic disc continuous, without spaces between them (Fig. 24a) ... ***C. grandinosus***

1’ In frontal view, foveae on the cephalic disc separated by conspicuous spaces (Fig. 24b) ... 2

2 In lateral view, hairs of lateral face of head abundant, most hairs touching each other (Fig. 24c). Hairs of head subtriangular (Fig. 24d) ... ***C. persimplex***

2’ In lateral view, hairs of lateral face of head sparse, hairs never touching each other (Fig. 24f). Hairs of head subrectangular (Fig. 24e) ... ***C. persimilis***

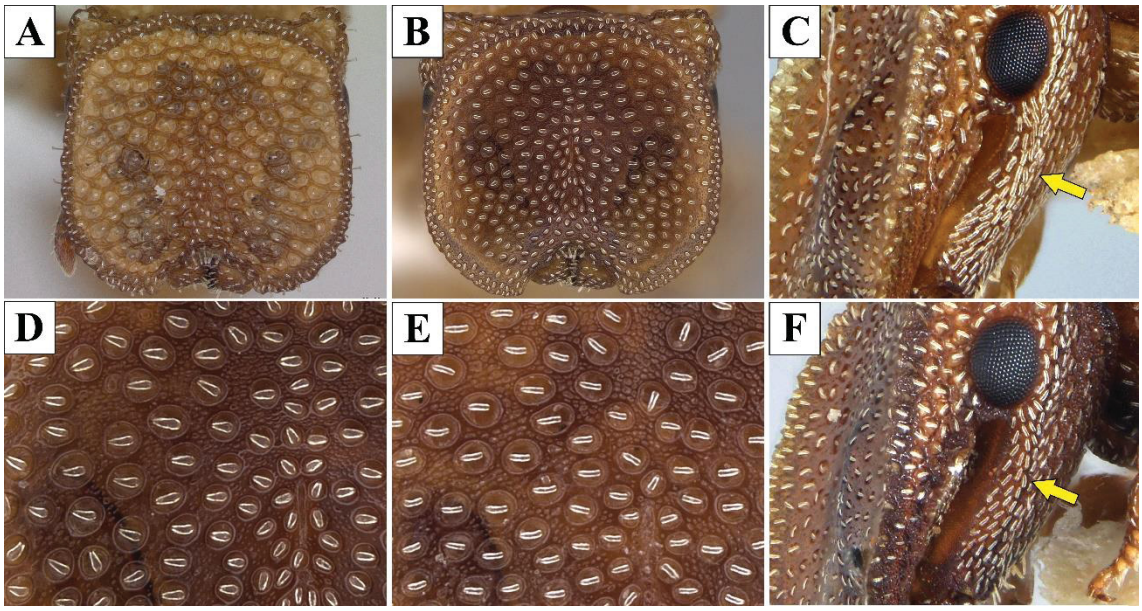

Figure 24: Soldiers of *grandinosus* group. A: *Cephalotes grandinosus* [CASENT0173699]. B, D: *Cephalotes persimplex* [CASENT0922543] C: *Cephalotes persimplex*. E: *Cephalotes persimilis* [CASENT0922541]. F: *Cephalotes persimilis*.

Distribution of the *Cephalotes* species of *grandinosus* group in Brazil

Species	Records from De Andrade and Baroni-Urbani, 1999	Records from literature, after 1999	Records from this study and literature	New records from this study
Cephalotes grandinosus	AM, BA, MS, MT, PA, RO, SP	RR (38; 51), CE (14), PR (19)	GO (41; 23; 45; 15; 22; 16; 21), MG (41; 30; 54; 7; 8; 18; 26)	ES, SE, TO
Cephalotes klugi	MT	-	-	-
Cephalotes persimilis	BA, CE, DF, GO, MG, MS, MT, PA, PI, SP	-	PE (18; 2)	MA, RO, RR, TO
Cephalotes persimplex	AC, MG, MT	-		SP

5.9 The *pallens* group

The *pallens* group was proposed by De Andrade and Baroni Urbani (1999) with 10 species. Including *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. pallidoides*, *C. pallidus*, *C. pellans*). Of these species, only five occurs in Brazil, (*C. pallens*, *C. pallidoides*, *C. pallidus*, *C. patellaris*, *C. pellans*).

This is the most morphologically homogeneous group of *Cephalotes*. Therefore, it is the most difficult group in regard to species identification, especially based only on the workers. 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 identification key for workers based on characters as the shape of frontal carinae in relation to eyes, and sculpture patterns on pleuron. The identification key for soldiers we mainly used sculpture and pilosity patterns.

In both morphological and molecular phylogenies, the *pallens* group is related with the *grandinosus* and *pinelii* groups, with which the species of *pallens* share the body strongly flattened dorsoventrally.

Diagnosis: Body color reddish brown. Frontal carinae posteriorly broadly incised over the eyes.

Brazilian species of *pallens* group

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

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

(Figure 25)

1 In dorsal view, lamellar expansions of the propodeum with a symmetrical posterior notch on both sides; it is possible that there is an additional notch anteriorly, but always symmetrical. The notch is never present on one side only or are asymmetrical (Fig. 25g) ... ***C. pallens***

1' In dorsal view, lamellar expansions of propodeum without notches. If any, they are asymmetric, probably caused by breaking (Fig. 25h) ... 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. 25a)... 3

2'In lateral view, frontal carinae broad, extending beyond eyes length, separating eyes from dorsal face of head (Fig. 25b, 25c) 4

3 Lateral of the mesosoma rugose (Fig. 25f) ... ***C. pellans***

3' Lateral of the mesosoma microalveolate; some incomplete rugosities may be present (Fig. 25i) ... ***C. pallidoides***

4 In ventral view, head rugose (Fig. 25d) ... ***C. patellaris***

4’ In ventral view, head totally microalveolate, without rugosities (Fig. 25e) ... ***C. pallidus***

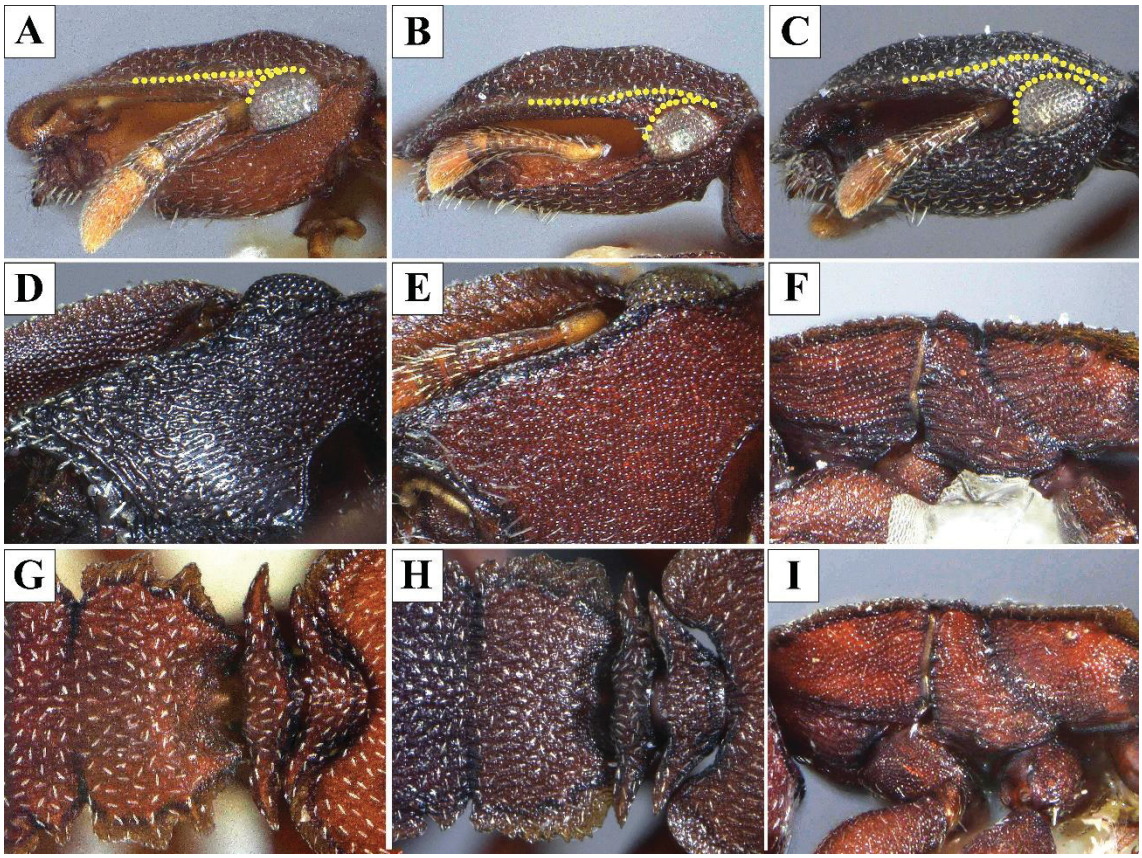

Figure 25: Workers of *pallens* group. A, F, H: *Cephalotes pellans*. B, E: *Cephalotes pallidus*. C, D: *Cephalotes patellaris*. G: *Cephalotes pallens*. I: *Cephalotes pallidoides.*

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

(Figure 26)

1 Cephalic disc irregularly areolate-rugose (Fig. 26a) ... ***C. pallidus***

1’ Cephalic disc regularly alveolate (Fig. 26b) or foveate (Fig. 26c) ... 2

2 Cephalic disc with erect to suberect hairs (Fig. 26d, 26g)... 3

2’ Cephalic disc with subdecumbent to appressed hairs (Fig. 26e, 26f)... 4

3 Cephalic disc with a median protuberance (Fig. 26d)... ***C. patellaris***

3’ Cephalic disc without or with weakly a median protuberance (Fig. 26g)... ***C. pallidoides***

4 Cephalic dish without a media protuberance (Fig. 26e). Translucent edges of the cephalic disc internally with long hairs larger than the diameter of the foveae (Fig. 26e). Declivous face of propodeum always rugose (Fig. 26h) … ***C. pellans***

4’ Cephalic dish with a media protuberance, even weakly developed (Fig. 26f). Translucent edges of the cephalic disc internally with short hairs smaller than the diameter of the foveae (Fig. 26f). Declivous face of propodeum predominantly microalveolate, some tiny rugosities can be present (Fig. 26i)… ***C. pallens***

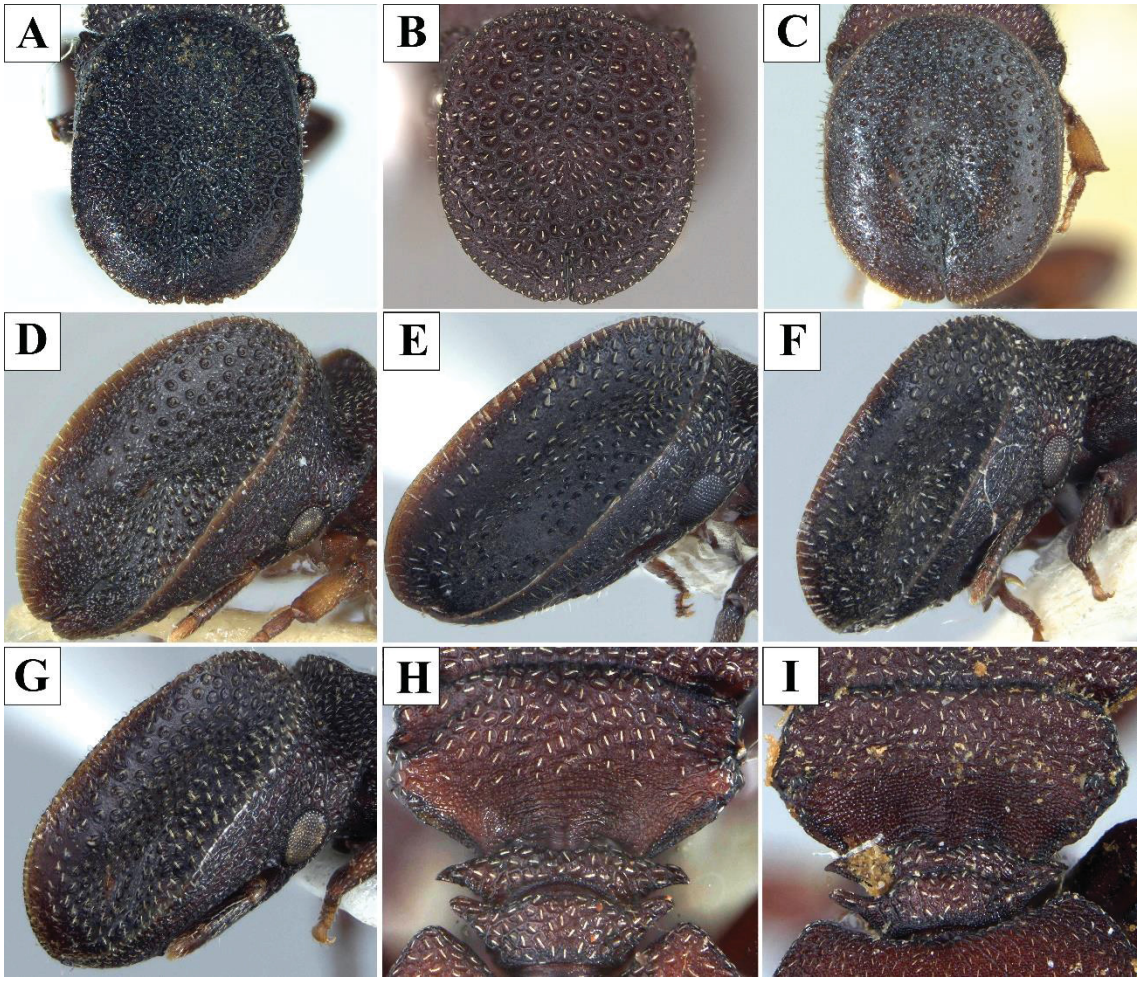

Figure 26: Soldiers of *pallens* group. A: *Cephalotes pallidus*. B: *Cephalotes pallidoides* [CASENT0922516]. C, D: *Cephalotes patellaris*. E, H: *Cephalotes pellans*. F, I: *Cephalotes pallens*. G: *Cephalotes pallidoides.*

Distribution of the *Cephalotes* species of *pallens* group in Brazil

Species	Records from De Andrade and Baroni-Urbani, 1999	Records only from literature, after 1999	Records from this study and literature	New records from this study
Cephalotes pallens	AM, BA, PA	MG (54; 18), MS (40; 12), RJ (46; 28), SP (49; 48), SC (54)	CE (54; 18), MT (12), GO (49; 40; 12)	MA, PE, RR, SE, TO
Cephalotes pallidoides	AM, GO, MT, PA, SP		AC (32; 29), BA (47), MG (7; 8)	MS, PI, RO
Cephalotes pallidus	AM, BA, PA, RJ	SC (13)	MT (5)	MA, RO
Cephalotes patellaris	MG, RJ, RS, SC, SP	TO (3)	-	BA, GO, MT, PA
Cephalotes pellans	MG, MS, MT, SP	CE (54; 18), BA (27)	AM (38; 51), RR (4; 52; 38; 51)	GO, PA, SC, TO

5.10 The *pinelii* species group

The *pinelii* group was first proposed by Kempf (1952), including six species. Later, De Andrade and Baroni Urbani (1999) separated it in two groups, *grandinosus* and *pinelii* groups. The current *pinelii* group includes four species from the former group in addition to three new species described by Andrade in De Andrade and Baroni Urbani (*C. liepini*, *C. pileini* and *C. nilpiei*), and *C. kukulcan* Snelling, 1999.

In the morphological phylogeny (De Andrade and Baroni Urbani, 1999), the group is recovered as monophyletic, with the species *C. kukulcan*, *C. scutulatus* and *C. incertus* forming an apical group within the clade. In the molecular phylogeny (Price et al., 2016), the relationship between these species was recovered, but the group formed by them is the sister group of the *texanus* and *bimaculatus* groups, not related with the other species of *pinelii* group. These other species of *pinelli* were recovered as related to the *grandinosus* group, rendering both groups paraphyletic. Morphology and molecular data suggest that *C. kukulcan*, *C. scutulatus* and *C. incertus* might form an additional group within *Cephalotes*, but the two first species were not included in this study, since they not occur in Brazil. On the other hand, the species of *pinelli* related with *grandinosus* group likely form a monophyletic group with it, as discussed under the *grandinosus* group.

Diagnosis: Dorsum of mesosoma continuous, with lamellar expansions in dorsal view. Petiole and postpetiole with lateral lamellar expansions. Hind femora without crest, lamellae or angles.

Brazilian species of *pinelii* group

Cephalotes incertus (Emery, 1906)
Cephalotes liepini De Andrade, 1999
Cephalotes maculatus (Smith, 1876)
Cephalotes nilpiei De Andrade, 1999
Cephalotes pinelii (Guérin-Méneville, 1844)
Cephalotes **new species E** Oliveira, Feitosa and Powell, 2020

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

(Figure 27)

1 In dorsal view, petiole and postpetiole longer than broad (not including lateral lamellar expansions) (Fig. 27e) ... ***C. incertus***

1' In dorsal view, petiole and postpetiole broader than long (not including lateral lamellar expansions) (Fig. 27d) ... 2

2 In dorsal view, anterior portion of the lamellar expansions of the gaster bent dorsally, not continuous with the gastral tergite (Fig. 27g) ... ***C. liepini***

2' In dorsal view, anterior portion of the lamellar expansions of the gaster flat, continuous with the gastral tergite (Fig. 27h) ... 3

3 In dorsal view, lamellar expansions of propodeum present only on the declivous face (Fig. 27c) ... **C. sp. n. E**

3' In dorsal view, propodeum entirely emarginated by lamellar expansions (Fig. 27d, 27f, 27i) ... 4

4 In frontal view, frontal carinae concave below the eyes (Fig. 27a). In lateral view, eyes occupying 1/3 of the length of the head ... ***C. maculatus***

4' In frontal view, frontal carinae straight below the eyes (Fig. 27b). In lateral view, eyes occupying less 1/3 of the length of the head... 5

5 In dorsal view, propodeal groove deep, forming a depression (Fig. 27f) ... ***C. nilpiei***

5' In dorsal view, propodeal groove weak, not forming a depression (Fig. 27i) ... ***C. pinelii***

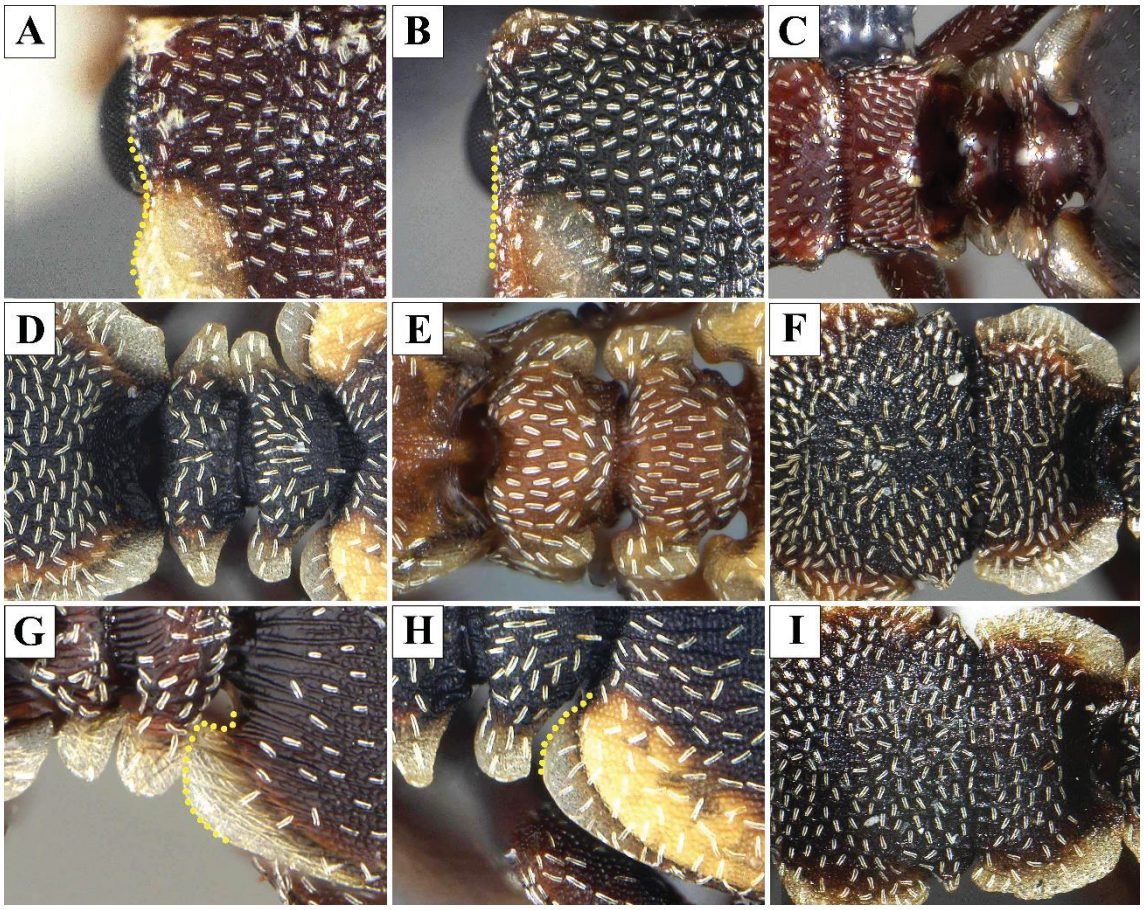

Figure 27: Workers of *pinelii* group. A: *Cephalotes maculatus*. B, I: *Cephalotes pinelii*. C: *Cephalotes* sp. n. E. D, F, H: *Cephalotes nilpiei*. E: *Cephalotes incertus*. G: *Cephalotes liepini*.

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

(Figure 28)

1 Cephalic disc totally tuberculate (Fig. 30a)… ***C.* sp. n. E**

1’ Cephalic disc not tuberculate (Fig. 28a, 28b, 28c)…2

2 Cephalic disc with contiguous foveae (Fig. 28a) ... ***C. liepini***

2’ Cephalic disc with foveae separate by interspace (Fig. 28b, 28c) ... 3

3 In dorsal view, posterior region of the head with a circular depression (Fig. 28b) ... ***C. pinelii***

3’ In dorsal view, posterior region of head flat, without a depression (Fig. 28c) ... 4

4 Lateral expansions of pronotum of the same color as the rest of the mesosoma (Fig. 28d). Dorsal face of propodeum meeting the declivous face at an angle of almost 90° (Fig. 28h)... ***C. maculatus***

4’ Lateral expansions of pronotum lighter than the rest of the mesosoma (Fig. 28e). Dorsal face of propodeum continuous with the declivous face (Fig. 28g) ... 5

5 In dorsal view, postpetiole as long as or longer than wide (Fig. 28f)... ***C. nilpiei***

5’ In dorsal view, postpetiole wider than long (Fig. 28fi)... ***C. incertus***

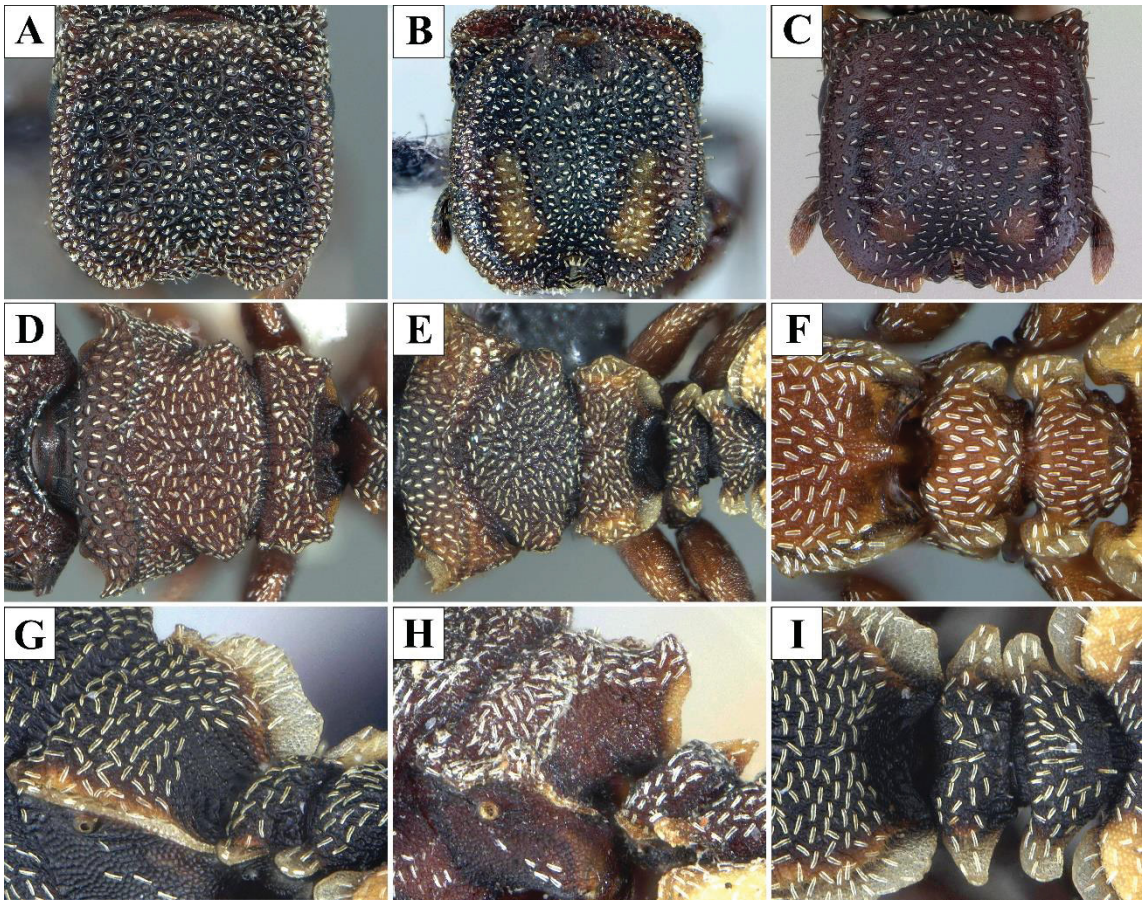

Figure 28: Soldiers of *pinelli* group. A: *Cephalotes liepini*. B: *Cephalotes pinelii*. C: *Cephalotes maculatus* [CASENT0173689]. D, H: *Cephalotes maculatus*. E, G, I: *Cephalotes nilpiei*. F: *Cephalotes incertus*.

5.10.1 *Cephalotes* new species E Oliveira, Feitosa and Powell, 2020

Figs. 29, 30, 31, 32

Holotype: BRASIL: MG, Uberlândia, -19.033630 -48.318400, 860m, 03.viii.2016. S. Powell *et al.* col. (worker) [DZUP].

Paratype: same data as holotype (4 workers, 3 soldiers, 2 gynes, 2 males) [DZUP], (2 worker, 2 soldiers) [MZSP], (2 worker, 2 soldiers) [INPA], (2 worker, 2 soldiers, 2 gynes, 2 males) [USNM].

Diagnosis: A member of *pinelii* species group, with dorsum of propodeum without lamellar expansions, which is present only on the declivous face.

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 110.94-123.44; OI 26.28-29.87; PI 25.00-37.50; HBI 23.33-25.00.

Worker description: Color dark brown; frontal lobes and body lamellar expansions yellowish to translucid (Fig. 29a); lateral margin of pronotum and fore tibiae yellowish.

Mandibles rugose-microalveolate. Dorsum of head and mesosoma foveate, space between foveae smooth (Fig. 29a, 29c). Ventral face of head areolate-microalveolate. Frontal lobes, propodeum declivous face, petiole and postpetiole smooth (Fig. 29c). Internal surface of antennal scrobes, legs and gaster microalveolate.

Body with appressed caniculate hairs, more abundant on pronotum and dorsal face of propodeum (Fig. 29c). Declivous face of propodeum hairless. Anterior margin of clypeus and mandibles with suberect clavate hairs. Petiole and postpetiole with hairs forming a transverse dorsal strip; anterior and posterior regions hairless (Fig. 29c). Gaster with sparse short appressed simple hairs; anterior lamellar expansions hairless (Fig. 29c).

Head as wide as long (CI 110.94-123.44), very convex medially, with two longitudinal elevations on the posterior regions, and depressions in front of the eyes (Fig. 29). Mandibles with a weakly developed lateral angle. Anterior margin of clypeus concave without denticles. Frontal carinae strait below the eyes; pointed upwards over the eyes (Fig. 29c). Frontal lobe extends until the eyes. Antennae with a two-segmented club. In frontal view, eyes rounded. 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. 29b). In dorsal view, lateral margins of pronotum with concave lamellar expansions, broader anteriorly. Promesonotal groove marked by a change in the hair pattern (Fig. 29c). Mesonotum with a pair of short denticles pointed upwards. Propodeal groove impressed. Dorsal and declivous faces of propodeum not continuous; lateral margins of propodeum without projections, declivous face with lateral lamellar expansions pointed upwards (Fig. 29c). Femora not angulated dorsally; mid and hind basitarsi not flattened, with subparallel dorsal and ventral faces.

Petiole compressed anteroposteriorly, anterior margin with a discreet median concavity; with lateral lamellar expansions, broader posteriorly; dorsum with a pair of obtuse denticles; subpetiolar process broader and rounded anteriorly (Fig. 29b). Postpetiole narrower than petiole (Fig. 29b); with lateral lamellar expansions; dorsum of postpetiole with a transverse elevation (Fig. 29c); subpostperiolar process pronounced and flattened anteroposteriorly (Fig. 29b).

Gaster suboval; with broad anterior lamellar expansions, not extend posteriorly (Fig. 29c).

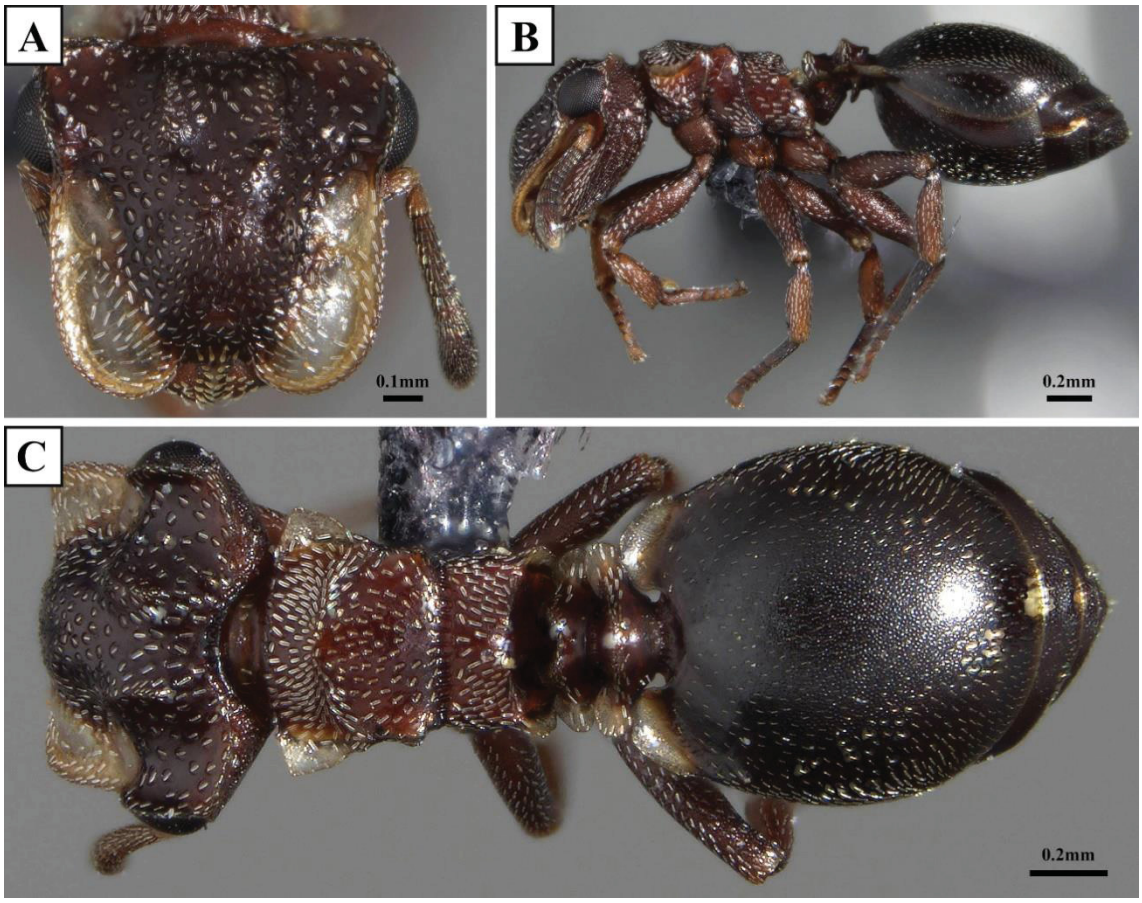

Figure 29: Workers of *Cephalotes* sp. n. E. A: frontal view. B: lateral view. C: dorsal view. Brazil: MG, Santana do Riacho.

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 118.00-122.10; OI 21.19-24.40 ; PI 29.53-36.36; HBI 26.67-33.75.

Soldier description: Color brownish; frontal lobes and body lamellar expansions yellowish to translucid; lateral margin of pronotum and fore tibiae yellowish; gaster dark brown with two pairs of yellowish spots (Fig. 30c).

Mandible alveolate; ventral face of head areolate-microalveolate. Dorsum of head with many tubercles, space between tubercles scabrous (Fig. 30a). Frontal lobes weakly rugose. Internal surface of antennal scrobes, legs, and gaster as the workers. Pronotum scabrous (Fig. 30c). Dorsum of meso and metanotum, meso and metapleuron foveate-microalveolate. Petiole and postpetiole with shallow foveae (Fig. 30c).

Pilosity as the workers, except by mandibles, clypeus, and anterior region of head with clavate hairs; and dorsum of head with caniculate hairs on tubercles.

Head slightly wider than longer (CI 118.00-122.10). Dorsum of head disc shaped and convex, strongly tuberculate with a posteriorly pair of distinct larger tubercle (Fig. 30a). Mandibles with a strong longitudinal lateral angle. Frontal carinae crenulate laterally. Clypeus

without denticles (Fig. 30b). Antennae with a three-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 with a pair of broad projections pointed upwards (Fig. 30c).

In profile, pronotum ascending, meso and metanotum continuous and flat (Fig. 30b). In dorsal view, anterior margin of pronotum gently rounded; lateral margins pointed anteriorly; pronotal carina well marked and crenulate, medially interrupted (Fig. 30c). Mesonotum, propodeum, legs, petiole, postpetiole and gaster as workers; except by the narrow lamellar expansions on the declivous face of propodeum (Fig. 30).

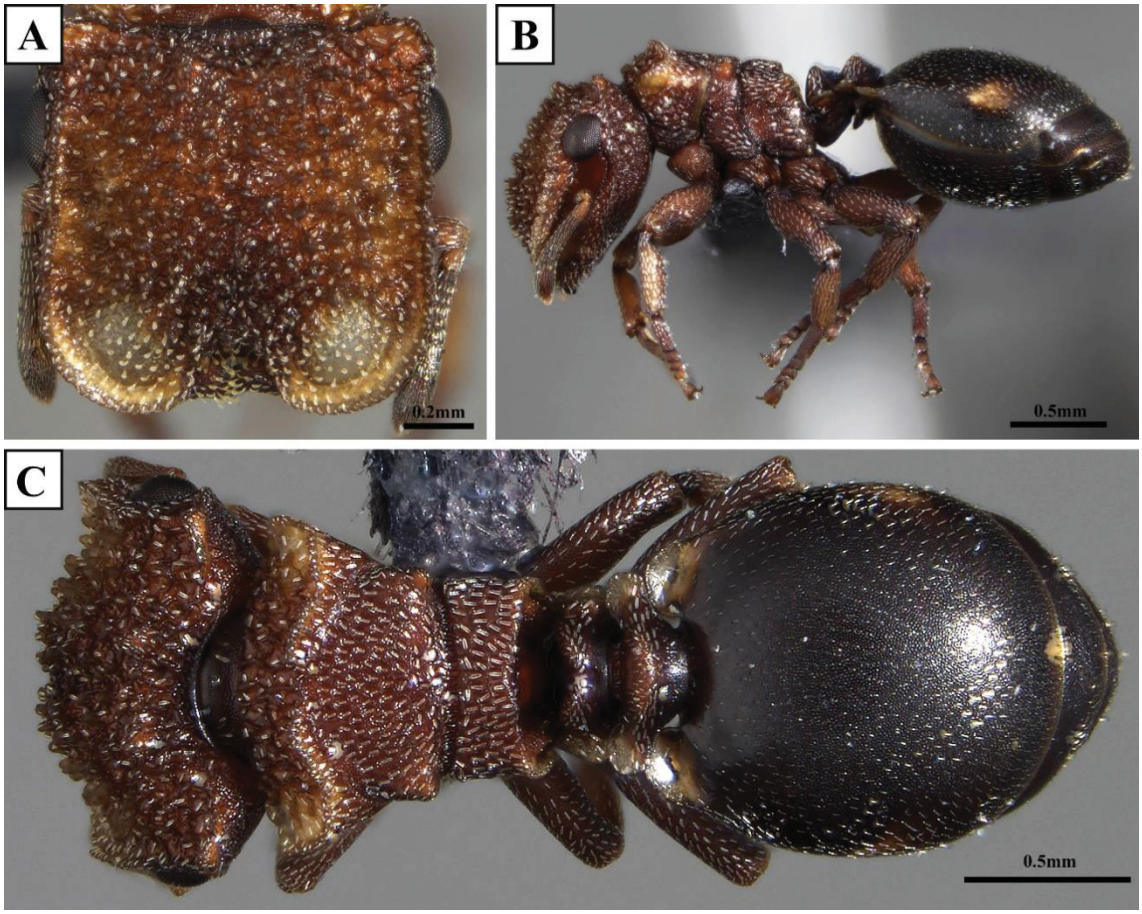

Figure 30: Soldiers of *Cephalotes* sp. n. E. A: frontal view. B: lateral view. C: dorsal view. Brazil: MG, Santana do Riacho.

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 106.38-110.00; OI 23.36-25.25; PI 50.00-63.49; HBI 27.50-33.33.

Gyne description: Color brown to yellowish; frontal lobes anteriorly translucid; gaster with four yellow spots (Fig. 31c).

Mandible, dorsal and ventral face of head, and pronotum as soldier. Internal surface of antennal scrobes, legs, and gaster as the worker. Dorsum of mesonotum, mesopleuron, upper metapleuron foveate-microalveolate; lower metapleuron rugose-microalveolate (Fig. 31b). Propodeum foveate. Petiole and postpetiole with shallow foveae (Fig. 31c).

Pilosity as the soldiers.

Head as the soldier (CI 106.38-110.00). The two posterior ocelli positioned in the posterior elevations (Fig. 31a).

Mesosoma flattened in lateral view (Fig. 31b). 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. 31c). Dorsally mesoscutum large and 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 cross by short striae; scutellum well delimited and broader anteriorly; axillae rounded posteriorly (Fig. 31c). Laterally, mesopleural groove impressed dividing anepisternum and katepisternum; metapleuron divided in upper metapleuron and lower metapleuron by a groove; metapleuropropodeal groove impressed (Fig. 31b). In dorsal view, posterior margin of propodeum concave and meeting the declivous face in a pair of short, blunt denticles (Fig. 31b). Wing venation as the genus description.

Petiole subrectangular, lateral margins straight, without lamellar expansions and dorsal projections; subpetiolar process narrow (Fig. 31c). Postpetiole longer than petiole (Fig. 31b); with a pair of lateral broad projections (Fig. 31c); without projection on dorsum; subpostperiolar process pronounced and flattened anteroposteriorly (Fig. 31b).

Gaster as the genus description; protruding anteriorly with narrow lamellae (Fig. 31c).

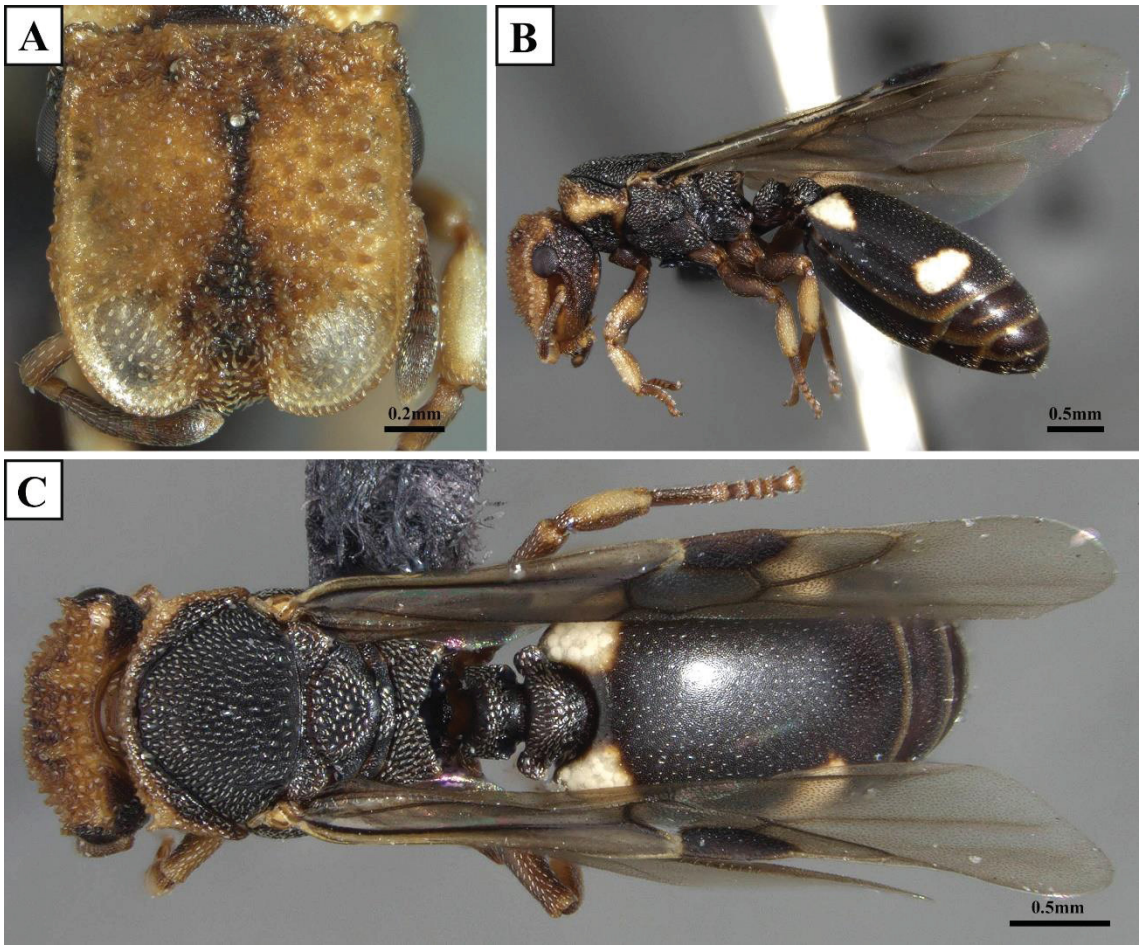

Figure 31: Gyne of *Cephalotes* sp. n. E. A: frontal view. B: lateral view. C: dorsal view. Brazil: MG, Santana do Riacho.

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 0.31-0.24; 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 130.00-138.34; OI 36.92-40.06; PI 66.67-74.81; HBI 15.63-18.17.

Male description: Color brownish to black; legs lighter than body (Fig. 32b).

Mandibles, head and dorsum of mesosoma microalveolate with sparse shallow foveae. Propleuron and mesopleuron weekly striate; metapleuron and propodeum rugose. Legs, petiole, postpetiole and gaster microalveolate.

Body with long and flexuous hairs, more abundant on mandibles, dorsum of head and mesosoma (Fig. 32b). Legs with long hairs only in the internal face of coxae and femur. Hairs shorter on gaster (Fig. 32b).

Head wider than longer (CI 130.00-138.34), broader posteriorly. Mandibles with one apical tooth; lateral angle weakly developed. Clypeus with a median elevation; posterior margin rounded. Frontal carinae not extending posteriorly; the central region of head strongly elevated. Eyes occupying more than half of head length (Fig. 32a). Antenna as the genus description.

In dorsal view, pronotum strongly rounded (Fig. 32c). Mesoscutum shield-shaped; notauli present; parapsidial lines feebly visible and parallel; transscutal line impressed, reaching the lateral margins of mesosoma; scutoscutellar groove deeply impressed, arched, and cross by short striae; scutellum well delimited and broader anteriorly; axillae with rounded posteriorly (Fig. 32c). Laterally, mesopleural groove impressed dividing anepisternum and katepisternum; metapleuron divided in upper metapleuron and lower metapleuron by a groove; metapleuropropodeal groove inconspicuous (Fig. 32b). Dorsal face of propodeum straight and meeting the declivous face in rounded angle. Wing as the genus de description.

Petiole and postpetiole subtriangular, concave anteriorly, with lateral acute projections, without dorsal projections; subpetiolar and subpostpetiolar process weakly developed (Fig. 32c).

Gaster as the genus description, but the first tergite as broad as mesosoma, occupying half or less than the total length of gaster (Fig. 32b), without anterior projection (Fig. 32a).

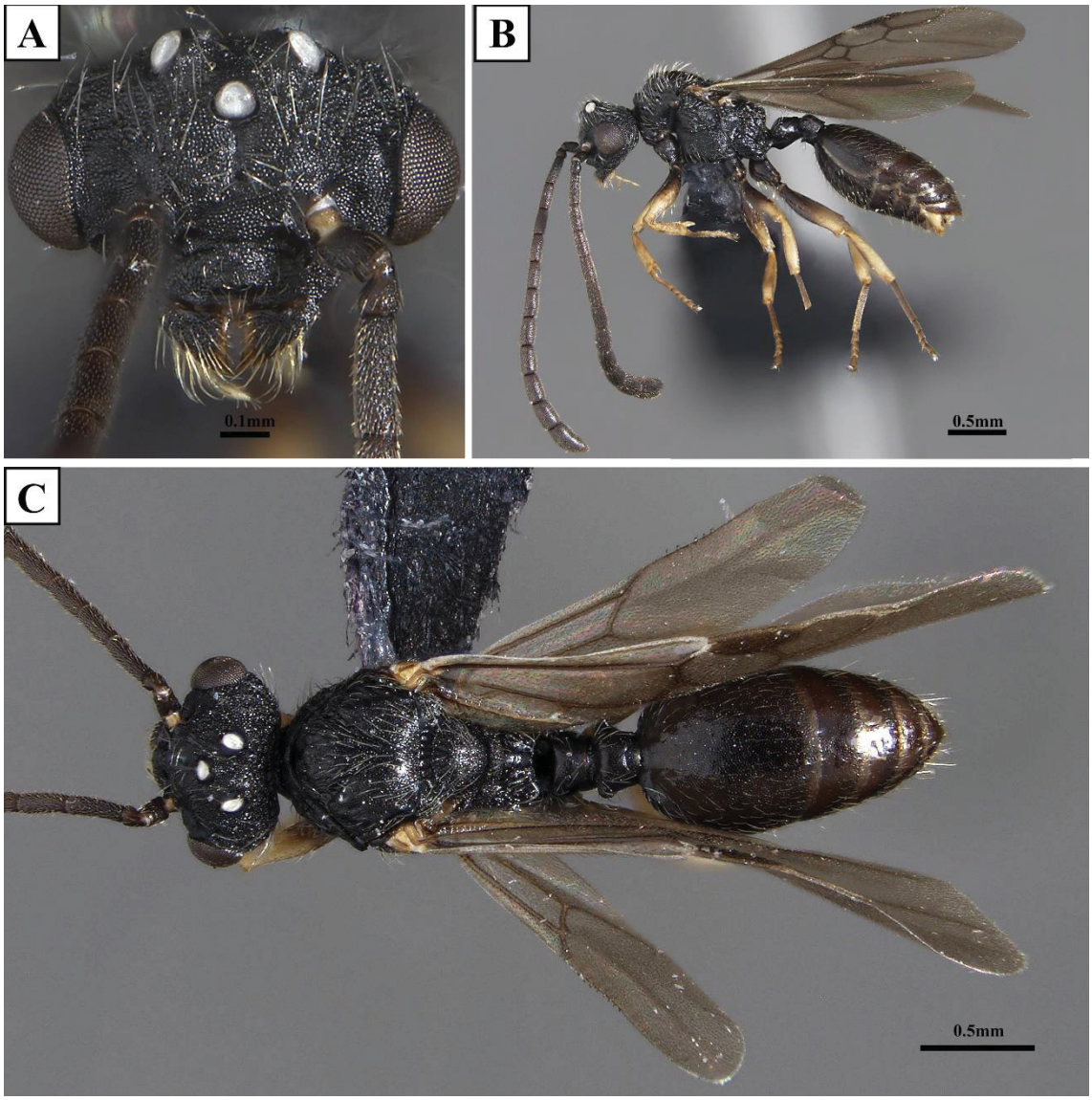

Figure 32: Male of *Cephalotes* sp. n. E. A: frontal view. B: lateral view. C: dorsal view. Brazil: MG, Santana do Riacho.

Distribution: Minas Gerais, Brazil.

Comments: This species differs from others in *pinelii* group by the lack of lateral lamellar expansions on dorsum of propodeum, and by the body not strongly flattened dorsoventrally.

5.10.2 *Cephalotes nilpiei* De Andrade, 1999

Figs. 33, 34

Holotype: BRASIL, Rio de Janeiro, Parque Nacional de ltatiaia, 15.XII.1966, 950-1000m, H. Reichardt [MZSP] [examined].

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 0.25-0.35; 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 88.57-89.86; OI 22.58; PI 84.38-84.65; HBI 33.33-37.04.

Gyne (first description): Color black to brownish; lateral of pronotum and legs lighter; gaster with four light brown spots (Fig. 33c).

Mandibles and dorsum of head foveate; anterolateral region of cephalic disc rugose with sparse foveae (Fig. 33a). Ventral face of head longitudinally rugose-microalveolate. Internal surface of antennal scrobes, legs, declivous face of propodeum and gaster microalveolate. Dorsum of mesosoma, petiole and postpetiole microalveolate with shallow foveae (Fig. 33c). Lateral of mesosoma microalveolate. Propleuron weakly rugose. Anepisternum and katepisternum weakly foveate (Fig. 33b). Dorsum of gaster anteriorly finely rugose (Fig. 33c).

Mandibles, mesosoma, petiole and postpetiole with appressed caniculate and short erect simple hairs. Head with appressed caniculate hairs; frontal carinae with short erect clavate hairs (Fig. 33a). Gaster with appressed simple hairs and some short erect hairs (Fig. 33b).

Head longer than wide (CI 88.57-89.86). Dorsum of head disc shaped, slightly concave anteriorly. Mandibles with a longitudinal lateral angle. Frontal carinae crenulate anteriorly. Clypeus without a pair of denticles (Fig. 33a). Antennae with a three-segmented club. Roof of antennal scrobes with a lateral carinae without projections. Lateroventral margins of head without carinae. Vertexal corners with a pair of broad projections (Fig. 33c).

Mesosoma flattened in lateral view (Fig. 33b). In dorsal view, anterior margin of pronotum slightly rounded; lateral margin with a pair of acute denticle; pronotal carina weakly developed, crenulate, medially interrupted (Fig. 33c). Dorsally mesoscutum large and subtriangular, anterior margin convex; notauli absent; parapsidial lines visible and parallel; transscutal line impressed, reaching the lateral margins of mesosoma; scutoscutellar groove impressed, arched, and cross by short striae; scutellum well delimited and broader anteriorly; axillae acute posteriorly (Fig. 33c). Laterally, mesopleural groove impressed dividing

anepisternum and katepisternum; metapleuron divided in upper metapleuron and lower metapleuron by groove; metapleuropropodeal groove not impressed (Fig. 33b). In dorsal view, posterior margin of propodeum concave and meeting the declivous face in a pair of short, blunt denticles (Fig. 33c). Wings unknown.

Petiole subrectangular, anterior margin concave and lateral margins with a tiny denticle (Fig. 33c); subpetiolar process narrow (Fig. 33b). Postpetiole longer and wider than petiole, without dorsal elevations, with lateral blunt projections (Fig. 33c); subpostperiolar process short and flattened anteroposteriorly (Fig. 33b).

Gaster as the genus description, with a narrow anteriorly lamella (Fig. 33c).

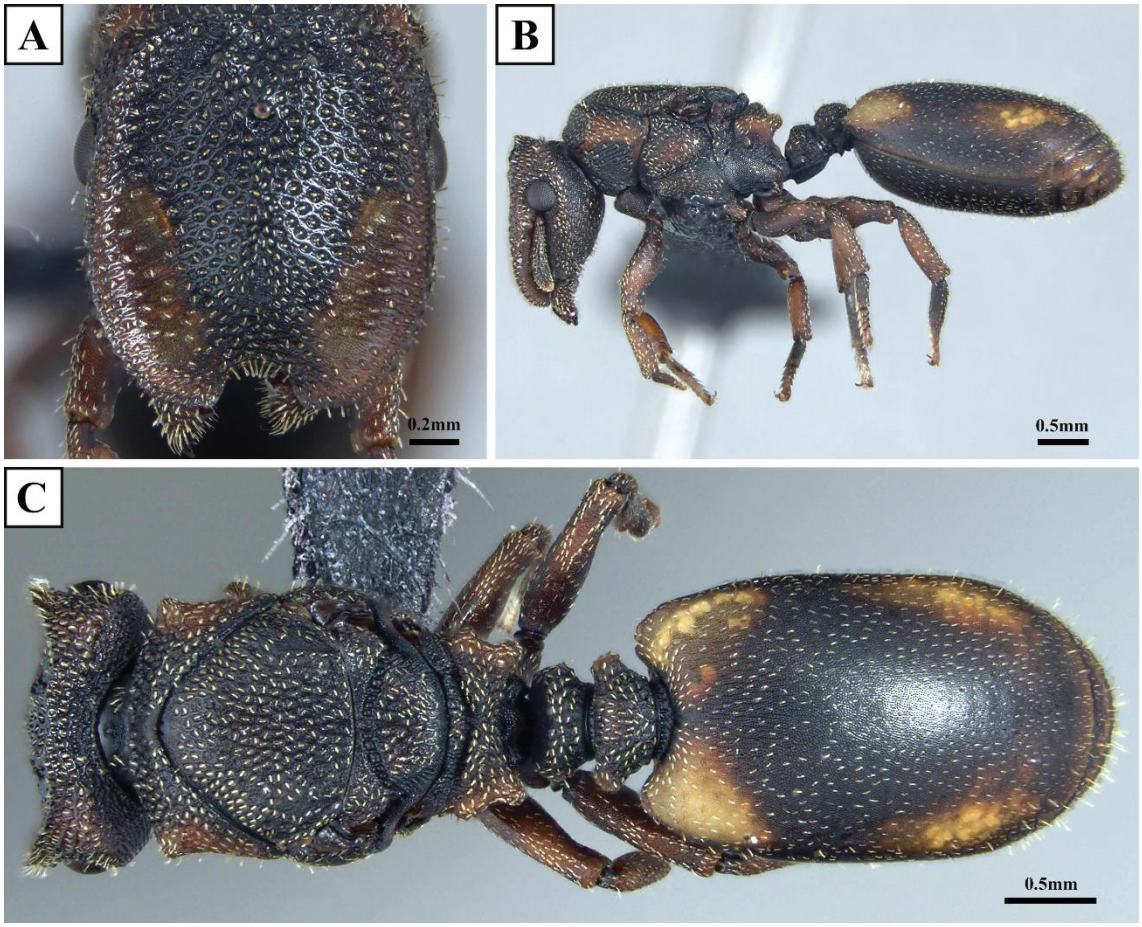

Figure 33: Gyne of *Cephalotes nilpiei*. A: frontal view. B: lateral view. C: dorsal view. Brazil: MG, Santana do Riacho.

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 153.13-166.67; OI 37.50-40.54; PI 125.00-140.63; HBI 14.29-14.81.

Male (first description): Color predominantly black; legs lighter than body (Fig. 34b).

Mandibles, head, pronotum and metanotum microalveolate with sparse shallow foveae (Fig. 34). Anepisternum, katepisternum and lower mesopleuron rugose; upper mesopleuron and propodeum scabrous (Fig. 34b). Legs, petiole, postpetiole and gaster weakly microalveolate (Fig. 34c).

Body with long and flexuous hairs, more abundant on mandibles, dorsum of head and dorsum of mesosoma (Fig. 34b). Legs with long hairs only in the internal face of coxae and femur. Hairs shorter on gaster (Fig. 34b).

Head wider than longer (CI 153.13-166.67); broader posteriorly. Mandibles with one to three apical teeth; lateral angle weakly developed (Fig. 34a). Clypeus with a median elevation; posterior margin rounded. Frontal carinae not extending posteriorly; the central region of head slightly elevated. Eyes occupying more than half of head length (Fig. 34a). Antenna as the genus description.

In dorsal view, pronotum slightly rounded, angulated laterally (Fig. 34c). Mesoscutum shield-shaped; notauli present; parapsidial lines visible and parallel; transscutal line impressed, reaching the lateral margins of mesosoma; scutoscutellar groove deeply impressed, arched, and cross by short striae; scutellum well delimited and broader anteriorly; axillae with a denticle posteriorly (Fig. 34c). Laterally, mesopleural groove impressed dividing anepisternum and katepisternum; metapleuron divided in upper metapleuron and lower metapleuron by a groove; metapleuropropodeal groove inconspicuous (Fig. 34b). Dorsal face of propodeum straight and meeting the declivous face in rounded angle (Fig. 34b). Wing as the genus de description.

Petiole and postpetiole wider than longer, laterally rounded, without lateral or dorsal projections; subpetiolar and subpostpetiolar process weakly developed (Fig. 34c).

Gaster as the genus description, but as long as mesosoma. The first tergite narrow than mesosoma, occupying half or less than the total length of gaster (Fig. 34b), without anterior projection. (Fig. 34c).

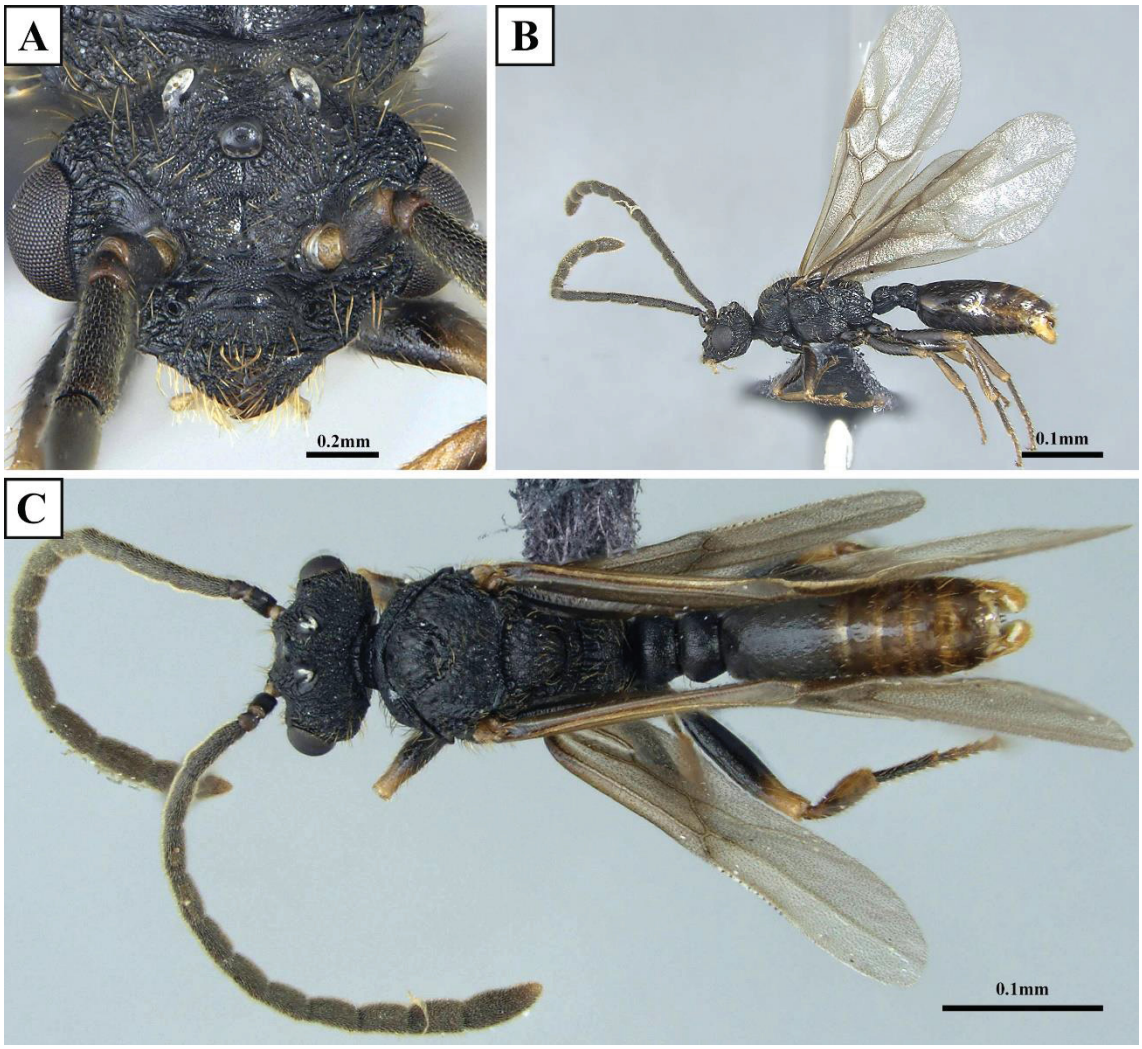

Figure 34: Male of *Cephalotes nilpiei*. A: frontal view. B: lateral view. C: dorsal view. Brazil: MG, Santana do Riacho.

Distribution of the *Cephalotes* species of *pinelii* group in Brazil

Species	Records from De Andrade and Baroni-Urbani, 1999	Records from literature, after 1999	Records from this study and literature	New records from this study
Cephalotes incertus	MS, MT, RS	-	-	-
Cephalotes liepini	GO	-	MG (7; 8)	BA, TO
Cephalotes maculatus	AC, AM, AP, BA, CE, ES, GO, MG, MS, MT, PA, PE, PR, RJ, RN, RO, SP	SE (17)	MA (36), RR (38; 51)	DF, SC, TO
Cephalotes nilpiei	RJ		MG (30; 54; 18)	
Cephalotes pinelii	MG, PI, PR, SC, SP, RJ, RS	TO (3), PE (31; 18), BA (47; 43; 25)	-	AC, ES, GO

5.11 The *pusillus* species group

The *spinosus* group by Kempf (1951) comprised the De Andrade and Baroni Urbani's *laminatus* and *pusillus* groups, which share the follows characters: shoulders of pronotum angulate, separate from the pronotal expansions; propodeum with two spines or denticles on each side, the posterior spines longest, never shorter than the anterior spines; declivous face differentiated from dorsal face of propodeum; gaster with distinct anterolateral lamellate border.

Despite the characters in common, De Andrade and Baroni Urbani (1999) separated *C. pusillus* and *C. columbicus* from Kempf's *spinosus* group, to include them in their *pusillus* group, based on their morphological phylogeny. The synapomorphy for *pusillus* group is the presence of fine reticulation under the head and the absence of angulate femora. However, both characters are also present in the *laminatus* group, which comprehends the remaining species of Kempf's *spinosus* group and *C. duckei*. The synapomorphy for this group, according De Andrade and Baroni Urbani, is the vertexal corners of the worker 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 current *pusillus* and *laminatus* groups seem more robust. Besides, the molecular phylogeny by Price et al. (2016) recovered *C. pusillus* and *C. columbicus* within the *laminatus* group, rendering the *laminatus* group paraphyletic. Then, based on molecular and morphologic 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. Most species in this group occurs in Brazil, except by *C. christopherseni*, known so far only from Colombia, Venezuela and Panama.

Diagnosis: Cephalic lamellar expansions of head truncate. Propodeum with two pairs of spines, the posterior longer than the anterior (except by the rarely collected *C. duckei*). Mid and hind basitarsi not flattened. Anterior region of gaster lamellar.

Brazilian species of *pusillus* group

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)

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

(Figure 35)

1 In dorsal view, petiole subrectangular, a small denticle of the same color as petiole can be present (Fig. 35g) ... ***C. pusillus***

1’ In dorsal view, petiole of another shape, spines are long with translucent tips (Fig. 35d, 35e, 35f, 35h, 35i) ... 2

2 In dorsal view, mesonotal spines absent (Fig. 35d) ... ***C. spinosus***

2’ In dorsal view, mesonotal spines present (Fig. 35c, 35f, 35h, 35i) ... 3

3 In posterodorsal view, declivous face of the propodeum with well-marked longitudinal striae occupying the entire surface (Fig. 35j) ... ***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. 35k, 35l)... 4

4 In dorsal view, posterior propodeal spines curved anteriorly (Fig. 35f) ... ***C. duckei***

4’ In dorsal view, posterior propodeal spines curved posteriorly (Fig. 35c, 35h, 35i) ... 5

5 In frontal view, the distance between the eyes is shorter or at most equal to the length of the head (Fig. 35a) ... ***C. simillimus***

5’ In frontal view, distance between eyes greater than head length (Fig. 35b) ... 6

6 In dorsal view, propodeal groove weakly impressed; marked on the sides but absent medially (Fig. 35h) ... ***C. laminatus***

6’ In dorsal view, propodeal groove strongly impressed on the entire dorsum (Fig. 35i) ... ***C. inaequalis***

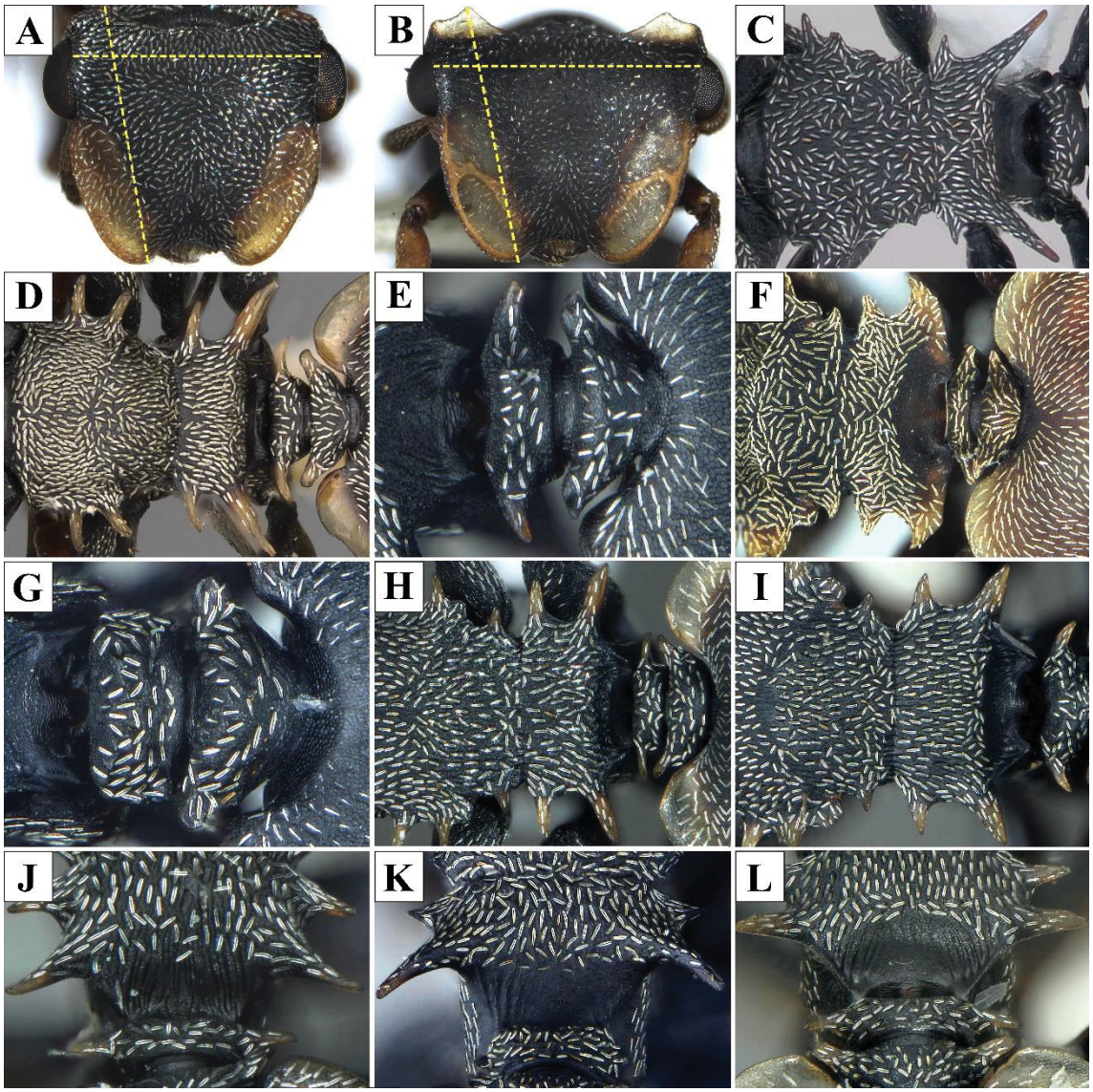

Figure 35: Workers of *pusillus* group. A: *Cephalotes similimus*. B, H, L: *Cephalotes inaequalis*. C: *Cephalotes pusillus* [CASENT0173703]. D: *Cephalotes spinosus* [CASENT0900244]. E: *Cephalotes minutus* [CASENT0173693]. F: *Cephalotes duckei*. G, K: *Cephalotes pusillus*. I: *Cephalotes laminatus*. J: *Cephalotes minutus*.

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

(Figure 36)

1 In dorsal view, petiole subrectangular, without spines; at most with a very tiny denticle (Fig. 36a) ... ***C. pusillus***

1' In dorsal view, petiole of another shape; if subrectangular, there are spines with translucent tips (Fig. 36b, 36c, 36d, 36e, 36f, 36g) ... 2

2 Declivous face of propodeum with lateral lamellar expansions (Fig. 36c, 36f, 36i)... 3

2’ Declivous face of propodeum without lateral lamellar expansions (Fig. 36b, 36d, 36e, 36g, 36h) ... 4

3 In dorsal view, posterior propodeal spines curved anteriorly (Fig.36c) ... ***C. duckei***

3’ In dorsal view, posterior propodeal spines curved posteriorly (Fig. 36f) ... ***C. simillimus***

4 In dorsal view, gastral lamellae width shorter than or equal to the width of the postpetiolar spines (Fig. 36b) ... ***C. minutus***

4’ In dorsal view, gastral lamellae width is at least twice the width of the postpetiolar spines (Fig. 36d, 36e, 36g) ... 5

5 In dorsal view, gastral lamella glabrous (Fig. 36e) ... ***C. spinosus***

5’ In dorsal view, gastral lamella with hairs (Fig. 36d, 36g) 6

6 Posterior propodeal spines bifurcated, spines black with yellowish tips (Fig. 36d) ... ***C. inaequalis***

6’ Posterior propodeal spines not bifurcated, spines completely black (Fig. 36g)... ***C. laminatus***

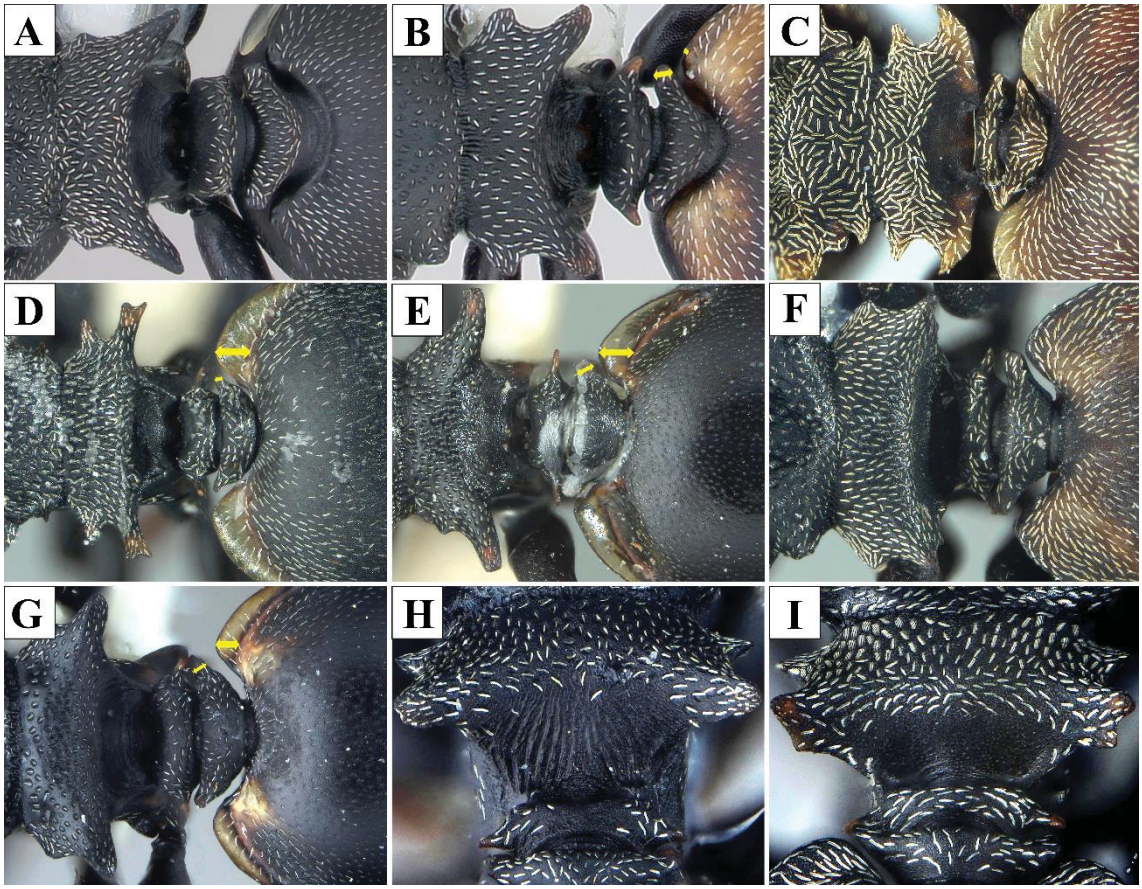

Figure 36: Soldiers of *pusillus* group. A: *Cephalotes pusillus*. B, H: *Cephalotes minutus*. C: *Cephalotes duckei*. D: *Cephalotes inaequalis*. E: *Cephalotes spinosus*. F, I: *Cephalotes simillimus*. G: *Cephalotes laminatus*.

Distribution of the *Cephalotes* species of *pusillus* group in Brazil

Species	Records from De Andrade and Baroni-Urbani, 1999	Records from literature, after 1999	Records from this study and literature	New records from this study
Cephalotes duckei	AM, MT, PA	-		-
Cephalotes inaequalis	AM, MT, PA, RO	-		TO
Cephalotes laminatus	AC, AM, MT, PA, RO	-		BA
Cephalotes minutus	AC, AL, AP, AM BA, CE, DF, ES, GO, MA, MT, MS, MG, PA, PR, PE, PI, PJ, PN, RO, SP, SE	-	SC (44)	RR, TO
Cephalotes pusillus	all states	-		-
Cephalotes simillimus	AC, AM, BA, MT, PA, RO, RR	GO (41; 21); MG (6; 24; 7)		SE
Cephalotes spinosus	AC, AM, BA, MT, PA, PE, RO, RR	-		-

5.12 The *solidus* species group

The *solidus* group is monotypic. Its unique species was described by Kempf (1974) as *Zacryptocerus solidus*, in the *angustus* group. Despite of the great morphological similarity between *C. solidus* and the members of the *angustus* group, in the morphological phylogeny by De Andrade and Baroni Urbani (1999) *C. solidus* is not related with the *angustus* group species. 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.).

Diagnosis: Declivous face of propodeum continuum with the dorsal face. Propodeum unarmed.

Brazilian species and distribution of *solidus* group

Cephalotes solidus (Kempf, 1974) Brazil (AC, AM)

5.13 The *umbraculatus* species group

The monotypic *umbraculatus* group was created by Kempf (1958). He discussed the position of the species, which would share characters with *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; Price et al., 2014), both phylogenies recover this species as a monophyletic group. Both phylogenies by Price et al. (2014, 2016) recovered *umbraculatus* as a sister group of the complexes groups *angustus*, *fiebrigi* and *prodigiosus*. *Cephalotes umbraculatus* is broadly distributed in Central America and north of South America.

Diagnosis: Body with appressed hairs. Declivous face of propodeum continuous with dorsal face, with a variable number of spines. Dorsum of petiole without denticles. Gaster yellowish with cross-shaped dark macula, anteriorly with lamellar expansions.

Brazilian species of *umbraculatus* group

Cephalotes umbraculatus (Fabricius, 1804)

Distribution of the *Cephalotes* species of *umbracuclatus* group in Brazil

Species	Records from De Andrade and Baroni-Urbani, 1999	Records from this study and literature	New records from this study
Cephalotes umbraculatus	AC, AM, BA, ES, GO, MT, PA, RN, RO	MA (36), RR (51; 4; 38), SE (17)	MG, TO

6. References

Antwiki, 2020. https,//www.antwiki.org (accessed 30 January 2020).

Baroni-Urbani, C., De Andrade, M.L., 1997. Pollen eating, storing and spitting by ants. Naturwissenschaften. 84, 256–258. https://doi.org/10.1007/s001140050392

Baroni Urbani, C., 1998. The number of castes in ants, where major is smaller than minor and queens wear the shield of the soldiers. Insectes Sociaux. 45, 315–333. https://doi.org/10.1007/s000400050091

Bolton, B., 2020. An Online Catalog of the Ants of the World. Disponível em http,//www.antcat.org. Acessado 30/01/2020.

Boudinot, B.E., 2015. Contributions to the knowledge of Formicidae (Hymenoptera, Aculeata), a new diagnosis of the Family, the first global male-based key to subfamilies, and a treatment of early branching lineages. European Journal of Taxonomy. 120, 1–62. https://doi.org/10.5852/ejt.2015.120

Brandão, C.R.F., Feitosa, R.M., Powell, S., Del-Claro, K., 2014. Description of *Cephalotes specularis* n. sp. (Formicidae, Myrmicinae) - the mirror turtle ant. Zootaxa. 3796(3), 568-578. https://doi.org/10.11646/zootaxa.3796.3.9

Bution, M.L., Caetano, F.H., 2007. Ileum of the *Cephalotes* ants, A specialized structure to harbor symbionts microorganisms. Micron. 39, 897-909. https://doi.org/10.1016/j.micron.2007.11.008

Byk, J., Del-Claro, K., 2010. Nectar and pollen gathering *Cephalotes* ants provide no protection against herbivory, a new manipulative experiment to test ant protective capabilities. Acta Ethol. 13, 33-38. https://doi.org/10.1007/s10211-010-0071-8

Creighton, W.S., 1933. *Cyathomyrmex*, a new name for the subgenus *Cyathocephalus* Emery. Psyche. 40, 98-100. https://doi.org/10.1155/1933/60232

Creighton, W.S., 1963. Further studies on the habits of *Cryptocerus texanus* Santschi (Hymenoptera, Formicidae). Psyche. 70, 133–143. https://doi.org/10.1155/1963/78162

Creighton, W.S., 1967. Studies on free colonies of *Cryptoceros texanus* Santschi (Hymenoptera, Formicidae). Psyche. 74, 34–41. https://doi.org/10.1155/1967/54234

Creighton, W.S., Gregg, R.E., 1954. Studies on the habits and distribution of *Cryptocerus texanus* Santschi (Hymenoptera, Formicidae). Psyche. 61, 41–57. https://doi.org/10.1155/1954/37696

Creighton, W.S., Nutting. W.L., 1964. The habits and distribution of *Cryptocerus rohweri* Wheeler (Hymenoptera, Formicidae). Psyche. 72, 59–64. https://doi.org/10.1155/1965/79407

De Andrade, M.L., Baroni Urbani, C., 1999. Diversity and adptation in the ant genus *Cephalotes* past and present. Stuttgarter Beiträge zur Naturkunde. Serie B (Geologie und Paläontologie). 271, 1-889.

Delabie, J.H.C., 1994. Cooperative shield phragmosis by minor workers of *Zacryptocerus pusillus* (Hymenoptera, Formicidae, Cephalotini). Etologia. 4, 99 -102.

Dlussky, G.M., Fedoseeva, E.B., 1987. Origin and early stages of evolution in ants, in: Ponomarenko, A.G. (ed.), Cretaceous biocenotic crisis and insect evolution. Moskva: Nauka, pp. 232.

Emery, C., 1914. Intorno alla classificazione dei Myrmicinae. Rendiconti delle Sessioni della Reale Accademia delle Scienze dell'Istituto di Bologna. Classe di Scienze Fisiche. 18, 29-42.

Emery, C., 1924. Hymenoptera. Fam. Formicidae. Subfam. Myrmicinae. [concl.]. Genera Insectorum. 174: 207-397.

Fabricius, J.C., 1793. Entomologia systematica emendata et aucta. Secundum classes, ordines, genera, species, adjectis synonimis, locis observationibus, descriptionibus. Tome 2, C. G. Proft, Hafniae [= Copenhagen]. https://doi.org/10.5962/bhl.title.122153

Fabricius, J.C., 1804. Systema Piezatorum, secundum ordines, genera, species, adjectis synonymis, locis, observationibus, descriptionibus, Brunswick, C. Reichard, Illinois. https://doi.org/10.5962/bhl.title.10490

Haris, R.A., 1979. A glossary of surface sculpture. Occasional Papers of the Bureau of Entomology of the California Department of Agriculture. 28, 1-32.

Jaffe, K., Caetano, F.H., Sanchez, P., Hernandez, J.V., Caraballo L., Vitelli-Flores J., Monsalve, W., Dorta, B., Lemoine, V.R., 2001. Sensitivity of ant (*Cephalotes*) colonies and individuals to antibiotics implies feeding symbiosis with gut microorganisms. Canadian Journal of Zoology. 79, 1120–1124. https://doi.org/10.1139/z01-079

Kempf, W.W., 1951. A taxonomic study on the ant tribe Cephalotini (Hymenoptera, Formicidae). Revista de Entomologia (Rio de Janeiro). 22, 1-244.

Kempf, W.W., 1952. Synopsis of the pinelii-complex in the genus *Paracryptocerus* (Hymenoptera: Formicidae). Studia Entomologica. 1, 1-30.

Kempf, W.W., 1953. Uma nova espécie de *Paracryptocerus* da Colombia, praga do cafeeiro (Hymenoptera, Formicidae). Papeis Avulsos do Departamento de Zoologia, Secretaria da Agricultura (São Paulo). 10, 79-88.

Kempf, W.W., 1958. New studies of the ant tribe Cephalotini (Hymenoptera, Formicidae). Studia Entomologica. 1, 1-168.

Kempf, W.W., 1958b. Synonymic note on ants of the genus *Paracryptocerus* Emery (Hymenoptera, Formicidae). Entomological News. 4, 108-110.

Kempf, W.W., 1959. Sobre algumas formigas "Cephalotini" do Museu de Oxford (Hymenoptera, Formicidae). Revista Brasileira de Biologia. 19 (1), 91-98.

Kempf, W.W., 1960. Miscellaneous studies on Neotropical ants (Hymenoptera, Formicidae). Studia Entomologica. 3, 417-466.

Kempf, W.W., 1963. Nota sinonímica acerca de formigas da tribo Cephalotini (Hymenoptera, Formicidae). Revista Brasileira de Biologia. 23 (4), 435-438.

Kempf, W.W., 1964. Addditions to the knowledge of the Cephalotini ants (Hymenoptera, Formicidae). Papeis Avulsos do Departamento de Zoologia, Secretaria da Agricultura (São Paulo). 16, 245 -255.

Kempf, W.W., 1965. Nota preliminar sobre algumas formigas neotropicais, descritas por Frederick Smith (hym, formi). Revista Brasileira de biologia. 25 (2), 181-186.

Kempf, W.W., 1969. Miscellaneous studies on Neotropical ants. V. (Hymenoptera, Formicidae). Studia Entomologica. 12, 273-296.

Kempf, W.W., 1972. Catálogo abreviado das formigas da região Neotropical. Studia Entomologica. 15, 3-344.

Kempf, W.W., 1973. A new *Zacryptocerus* from Brazil, with remarks on the generic classification of the tribe Cephalotini (Hymenoptera, Formicidae). Studia entomologica. 16, 449- 462.

Kempf, W.W., 1974. Taxonomic and faunistc notes on some neotropical Cephalotini ants (Hymenoptera, Formicidae). Revista Brasileira de entomologia. 18(2), 67-76.

Kempf, W.W., 1978. A preliminary zoogeographical analysis of a regional ant fauna in Latin America. Studia Entomologica. 20, 43-62.

Kempf. W.W., 1967. A new revisionary note on the genus *Paracryptocerus* Emery (Hum. Formicidae). Studia Entomologica. 10 (1-4), 361-368.

Latreille, P.A., 1802. Histoire naturelle générale et particulière des Crustacés et des insectes. Tome 3, Familles naturelles des genres, F. Dufart, Paris.

Latreille, P.A., 1803. Histoire naturelle générale et particulière des Crustacés et des insectes. Tome 5, F. Dufart, Paris.

Linnaeus, C., 1758. Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata, L. Salvii, Holmiae [= Stockholm]. https://doi.org/10.5962/bhl.title.542

Powell, S., 2008. Ecological specialization and the evolution of a specialized caste in *Cephalotes* ants. Functional Ecology. 22, 902–911. https://doi.org/10.1111/j.1365-2435.2008.01436.x

Powell, S., 2014. Mirmicry and eavesdropping enable a new form of social parasitismo in ants. American Naturalist. 184(4). https://doi.org/10.1086/677927

Price, S.L., Powell, S., Kronauer, D.J.C., Tran, L.A.P., Pierce, N.E., Wayne, R.K., 2014. Renewed diversification is associated with new ecological opportunity in the Neotropical turtle ants. Journal of Evolutionary Biology. 27, 242–258. https://doi.org/10.1111/jeb.12300

Smith, M.R., 1949. On the status of *Cryptocerus* Latreille and *Cephalotes* Latreille (Hymenoptera, Formicidae). Psyche (Cambridge). 56, 18-21. https://doi.org/10.1155/1949/47236

Ward, P.S., Brady, S.G., Fisher, B.L., Schultz, T.R., 2015. The evolution of myrmicine ants, phylogeny and biogeography of a hyperdiverse ant clade (Hymenoptera, Formicidae). Systematic Entomology. 40, 61-81. https://doi.org/10.1111/syen.12090

Wheeler, W.M., 1911. A list of the type species of the genera and subgenera of Formicidae. Annals of the New York Academy of Science. 21, 157-175. https://doi.org/10.1111/j.1749-6632.1911.tb56932.x

Wheeler, W.M., 1913. Corrections and additions to "List of type species of the genera and subgenera of Formicidae". Annals of the New York Academy of Sciences. 23, 77-83. https://doi.org/10.1111/j.1749-6632.1914.tb56938.x

Wheeler, W.M., 1922. Ants of the American Museum Congo expedition, Bulletin of the American Museum of Natural History, New York.

Wilson, E.O., 1955. A monographic revision of the ant genus *Lasius*. Bulletin of the Museum of Comparative Zoology. 113 (1), 3-199.

Yanoviak, S.P., 2010. The directed aerial descent of arboreal ants, in, Lach L, Parr CL, Abbott K, (Eds.), Ant ecology. Oxford University Press, Oxford, pp. 223–224.

Yanoviak, S.P., Dudley, R., 2006. The role of visual cues in directed aerial descent of *Cephalotes atratus* workers (Hymenoptera, Formicidae). J Exp Biol. 209, 1777–1783.

Yanoviak, S.P., Dudley, R., Kaspari, M., 2005. Directed aerial descent in canopy ants. Nature. 433, 624–626. https://doi.org/10.1038/nature03254

Yanoviak, S.P., Yonatan, M., Dudley, R., 2011. Evolution and ecology of directed aerial descente in arboreal ants. Integrative and Comparative Biology. 51(6), 944–956. https://doi.org/10.1093/icb/icr006

Yoshimura, M., Fisher, B.L., 2012. A revision of male ants of the Malagasy region (Hymenoptera, Formicidae), Key to genera of the subfamily Dolichoderinae. Zootaxa. 2794, 1–34. https://doi.org/10.11646/zootaxa.2794.1.1

7. List of references cited in the species distribution tables

1. Antoniazzi, R., Garoo, R.N.S.L., Dattilo, W.S., Ribeiro, P., Neves, F.S., 2019. Ant species richness and interactions in canopies of two distinct successional stages in a tropical dry forest. The Science of Nature. 106, 20. https://doi.org/10.1007/s00114-019-1614-0
2. Arnan X., Arcoverde, G.B.M., Pie, R., Ribeiro-Neto, J.D., Leal, I.R., 2018. Increased anthropogenic disturbance and aridity reduce phylogenetic and functional diversity of ant communities in Caatinga dry forest. Science of the Total Environment. 631–632, 429–438. https://doi.org/10.1016/j.scitotenv.2018.03.037
3. Arruda, F.V., Pesquero, M.A., Marcelino, D.G., Leiter, G.A., Delabie, J.H.C., Fagundes, R., 2015. Size and condition of bamboo as structural factors behind the vertical stratification of the bamboo-nesting ant community. Insects Sociaux. 63(1), 99-107. https://doi.org/10.1007/s00040-015-0440-4
4. Baccaro, F.B., De Souza, J.L.P., Franklin, E., Lemes Landeiro, V., Magnusson, W.E., 2012. Limited effects of dominant ants on assemblage species richness in three Amazon forests. Ecological Entomology. 37, 1-12. https://doi.org/10.1111/j.1365-2311.2011.01326.x
5. Battirola, L.E., Marques, M.I., Adis J., Delabie, J.H.C., 2005. Composicao da comunidade de Formicidae (Insecta, Hymenoptera) em copas de *Attalea phalerata* Mart. (Arecaceae), no Pantanal de Pocone, Mato Grosso, Brasil. Revista Brasileira de Entomologia. 49(1), 107-115. https://doi.org/10.1590/S0085-56262005000100011
6. Byk J., Del-Claro, K., 2010. Nectar- and pollen-gathering *Cephalotes* ants provide no protection against herbivory: a new manipulative experiment to test ant protective capabilities. Acta Ethol. 13, 33-38. https://doi.org/10.1007/s10211-010-0071-8
7. Camacho, G.P., Vasconcelos, H.L., 2015. Ants of the Panga Ecological Station, a Cerrado Reserve in Central Brazil. Sociobiology. 62(2), 281-295. https://doi.org/10.13102/sociobiology.v62i2.281-295
8. Camarota, F., Powell, S., Melo, A.S., Priest, G., Marquis, R.J., Vasconcelos, H.L., 2016. Co-occurrence patterns in a diverse arboreal ant community are explained more by competition than habitat requirements. Ecology and Evolution. 6(24), 8907-8918. https://doi.org/10.1002/ece3.2606
9. Costa-Milanez, C.B., Lourenco-Silva, G., Castro, P.T.A., Majer, J.D., Ribeiro, S.P., 2014. Are ant assemblages of Brazilian veredas characterised by location or habitat type?. Braz. J. Biol. 74(1), 89-99. https://doi.org/10.1590/1519-6984.17612
10. Da Silva de Oliveira, A.B.S., Schmidt., F.A., 2019. Ant assemblages of Brazil nut trees Bertholletia excelsa in forest and pasture habitats in the Southwestern Brazilian Amazon. Biodiversity and Conservation. 28(2), 329-344. https://doi.org/10.1007/s10531-018-1657-0
11. De Queiroz, A.C.M., Rabello, A.M., Braga, D.L., Santiago, G.S., Zurlo, L.F., Philpott, S.M., Ribas, C.R., 2017. Cerrado vegetation types determine how land use impacts ant biodiversity. Biodiversity and Conservation. https://doi.org/10.1007/s10531-017-1379-8
12. Demetrio, M.F., Silvestre, R., Robson de Souza, P., Aoki. C., 2015. Checklist of ants (Hymenoptera, Formicidae) from Mato Grosso do Sul, Brazil. Iheringia, Serie Zoologia 107, e2015126. https://doi.org/10.1590/1678-4766e2017126
13. Favretto, M.A., Bortolon dos Santos, E., Geuster, C.J., 2013. Entomofauna from West of Santa Catarina State, South of Brazil. EntomoBrasilis. 6 (1), 42-63. https://doi.org/10.12741/ebrasilis.v6i1.271
14. Filho, P.A.A., Andrade do Vale, L.L., Ferreira de Carvalho Lavor, M.T., Ribeiro Neto, J.D., Coelho Melo, M.V., Hites, N., Biseau, J.C., De Quinet, Y.P., 2003. Biodiversity of the

myrmecofauna (Hymenoptera:Formicidae) in a primary forest of the Serra de Baturité-Ceará. Ciencias e Tecnologia 5(2), 15-29.

15. Frizzo, T.L.M., Campos, R.I., Vasconcelos, H.L., 2012. Contrasting Effects of Fire on Arboreal and Ground-Dwelling Ant Communities of a Neotropical Savanna. Biotropica 44(2), 254-261. https://doi.org/10.1111/j.1744-7429.2011.00797.x
16. Gallego-Ropero, M.C., Feitosa, R.M. Pujol-Luz, J.R., 2013. Formigas (Hymenoptera, Formicidae) Associadas a Ninhos de *Cornitermes cumulans* Kollar (Isoptera, Termitidae) no Cerrado do Planalto Central do Brasil. Entomo Brasilis. 6(1), 97-101. https://doi.org/10.12741/ebrasilis.v6i1.283
17. Gomes, E.C.F., Ribeiro, G.T., Souza, T.M.S., Sousa-Souto, L., 2014. Ant assemblages (Hymenoptera: Formicidae) in three different stages of forest regeneration in a fragment of Atlantic Forest in Sergipe, Brazil. Sociobiology 61(3), 250-257. https://doi.org/10.13102/sociobiology.v61i3.250-257
18. Leal, I.R., Ribeiro-Neto, J.D., Arnan, X., Oliveira, F.M.P., Arcoverde, G.B., Feitosa, R.M., Andersen, A.N., 2015. Ants of the Caatinga: diversity, biogeography, and functional responses to anthropogenic disturbance and climate change, in: Silva, J.M.C., Leal, I.R., Tabarelli, M., (eds), Caatinga, Springer, Cham, pp 65-95. https://doi.org/10.1007/978-3-319-68339-3_3
19. Lopes, D.T., Lopes, J., Cardoso do Nascimento, I., Delabie, J.H., 2010. Epigeic ants diversity (Hymenoptera, Formicidae) in three environments in Mata dos Godoy State Park, Londrina, State of Paraná, Brazil. Iheringia, Serie Zoologia. 100(1), 84-90. https://doi.org/10.1590/S0073-47212010000100012
20. Lopes, M.C., Lamarre, G.P.A., Baraloto, C., Fine, P.V.A., Vincentini, A., Baccaro, F.B., 2019. The Amazonas-trap: a new method for sampling plant-inhabiting arthropod communities in tropical forest understory. Entomologia Experimentalis et Applicata. 167(6), 534-543. https://doi.org/10.1111/eea.12797.
21. Madureira, M.S., Sobrinho, T.G., Schoereder, J.H., 2018. The influence of extrafloral nectaries on arboreal ant species richness in tree communities. Sociobiology. 65(2), 162-169. https://doi.org/10.13102/sociobiology.v65i2.1939
22. Maravalhas, J., Delabie, J.H.C., Macedo, R.G., Morais, H.C., 2012. Tree-dwelling ants: contrasting two Brazilian Cerrado plant species without extrafloral nectaries. Psyche. ID 172739. https://doi.org/10.1155/2012/172739
23. Maravalhas, J., Morais, H.C., 2009. Association between Ants and a Leafhopper (Cicadellidae: Idiocerinae) in the Central Brazilian Cerrado. The Florida Entomologist. 92(4) :563-56 https://doi.org/10.1653/024.092.0405
24. Marques, G.D.V., Del-Claro, K., 2006. The Ant Fauna in a Cerrado area: The Influence of Vegetation Structure and Seasonality (Hymenoptera: Formicidae). Sociobiology. 47(1), 1-18.
25. Marques, T.E.D., Borges de Azevedo Koch, E., Silva dos Santos, I., Raimundo Maia dos Santos, J., Dos Santos Ferreira Mariano, C., Delabie, J.H.C., 2018. The diversity of ants (Hymenoptera: Formicidae) interacting with the invasive hibiscus mealybug *Maconellicoccus hirsutus* (Green 1908) (Hemiptera: Pseudococcidae) on ornamental and cultivated plants in Bahia, Brazil. Arthropod-Plant Interactions. 12, 237–246. https://doi.org/10.1007/s11829-017-9563-z
26. Marques, T., Espirito-Santo, M.M., Neves, F.S., Schoereder, J.H., 2015. Ant assemblage structure in a secondary tropical dry forest: the role of ecological succession and seasonality. Sociobiology. 64(3), 261-275. https://doi.org/10.13102/sociobiology.v64i3.1276

27. Martins, L.C.B., dos Santos, J.R.M., do Nascimento, I.C., Lopes, N.S., Delabie, J.H.C., 2006. Assembléias de Formicidae epigéas no entorno do Parque Nacional da Chapada Diamantina, Bahia, Brasil. Sitientibus Série Ciências Biológicas. 6(4), 306-316.
28. Montine, P.S.M., Viana, N.F., Dattilo, W., Santanna, A.S., Martins, L., Vargas, A.B., 2014. Seasonality of Epigaeic Ant Communities in a Brazilian Atlantic Rainforest. Sociobiology. 61(2), 158-183. https://doi.org/10.13102/sociobiology.v61i2.178-183
29. Nakayama Miranda, P., Oliveira, M.A., Baccaro, F.B., Morato, E.F., Delabie, J.H.C., 2012. Check list of ground-dwelling ants (Hymenoptera: Formicidae) of the eastern Acre, Amazon, Brazil. Check List. 8(4), 722–730. https://doi.org/10.15560/8.4.722
30. Neves, F.S., Queiroz-Dantas, K.S., Da Rocha, W.D., Delabie, J.H.C., 2013. Ants of Three Adjacent Habitats of a Transition Region Between the Cerrado and Caatinga Biomes: The Effects of Heterogeneity and Variation in Canopy Cover. Neotrop Entomol. 42, 258–268. https://doi.org/10.1007/s13744-013-0123-7
31. Oliveira, F.M.P., Ribeiro-Neto, J.D., Andersen, A., Leal, I.R., 2016. Chronic anthropogenic disturbance as a secondary driver of ant community structure: interactions with soil type in Brazilian Caatinga. Environmental Conservation. 4(2), 115-123. https://doi.org/10.1017/S0376892916000291
32. Oliveira, M.A., Della Lucia, T.M.C., Marinho, C.G.S., Delabie, J.H.C., Morato, E.F., 2009. Ant Diversity in an Area of the Amazon Forest in Acre, Brazil. Sociobiology. 54(1), 242-382.
33. Paolucci, L.N., Schoereder, J.H., Brando, P.M., Andersen, A.N., 2015. Fire-induced forest transition to derived savannas: Cascading effects on ant communities. Biological Conservation. 214, 295-302. https://doi.org/10.1016/j.biocon.2017.08.020
34. Pereira, M.C., Delabie, J.H.C., Suarez, Y.R., Antonialli Junior, W.F., 2013. Spatial connectivity of aquatic macrophytes and flood cycle influence species richness of an ant community of a Brazilian floodplain. Sociobiology. 60(1), 41-49. https://doi.org/10.13102/sociobiology.v60i1.41-49
35. Pereira Souza, J.L., Beggiato Baccaro, F., Lemes Landeiro, V., Franklin, E., Magnusson, W.E., Aurelio, P., Lima Pequeno, C., Oliveira Fernandes, I., 2015. Taxonomic sufficiency and indicator taxa reduce sampling costs and increase monitoring effectiveness for ants. Diversity and Distributions. 2(1),1-12.
36. Prado, L.P., Feitosa, R.M., Triana, S.P., Gutiérrez, J.A.M., Rousseau, G.X., Silva, R.A., Siqueira, G.M., Santos, C.L.C.S., Silva, F.V., Silva, T.S.R., Casadei-Ferreira, A., Silva, R.R., Andrade-Silva, J., 2019. Na overview of the ant fauna (Hymenoptera: formicidae) of the state of Maranhão, Brazil. Papeis Avulsos de Zoologia. 59, e20195938. http://doi.org/10.11606/1807-0205/2019.59.38
37. Reis, P.C.J., Darocha, W.D., Falcao, L., Guerra, T.J., Neves, F.S., 2013. Ant Fauna on *Cecropia pachystachya* Trécul (Urticaceae) Trees in an Atlantic Forest Area, Southeastern Brazil. Sociobiology. 60(3), 222-228. https://doi.org/10.13102/sociobiology.v60i3.222-228
38. Ribas, C.R., Shoereder. J.H., 2007. Ant communities, environmental characteristics and their implications for conservation in the Brazilian Pantanal. Biodivers. Conserv. 16, 1511-1520. https://doi.org/10.1007/s10531-006-9041-x
39. Ribas, C.R., Schoereder, J.H., Pic, M., Soares, S.M., 2003. Tree heterogeneity, resource availability, and larger scale processes regulating arboreal ant species richness. Austral Ecology. 28(3), 305-314. https://doi.org/10.1046/j.1442-9993.2003.01290.x
40. Ribeiro, L.F., Solar, R.R.C., Sobrinho, T.G., Muscardi, D.C., Schoereder, J.H., Andersen, A.N., 2019. Different trophic groups of arboreal ants show differential responses to resource supplementation in a neotropical savanna. Oecologia. 190(2), 433-443. https://doi.org/10.1007/s00442-019-04414-z

41. Santos, L.R., Feitosa, R.M., Carneiro, M.A.A., 2015. The role of senescent stem-galls over arboreal ant communities structure in Eremanthus erythropappus (DC.) MacLeish (Asteraceae) trees. Sociobiology. 64(1), 7-13. https://doi.org/10.13102/sociobiology.v64i1.1174
42. Santos Lopes, J.F., Martins dos Reis Hallack, N., Archanjo de Sales, T., Silva Brugger, M., Ribeiro, L.F., Hastenreiter, I.N., da Silva Camargo, R., 2012. Comparison of the Ant Assemblages in Three Phytophysionomies: Rocky Field, Secondary Forest, and Riparian Forest—A Case Study in the State Park of Ibitipoca, Brazil. Psyche. ID 928371. https://doi.org/10.1155/2012/928371
43. Santos, R.J., Azevedo Koch, E.B., Machado, C., Leite, P., Porto, T.J., Delabie, J.H.C., 2015. An assessment of leaf-litter and epigaeic ants (Hymenoptera: Formicidae) living in different landscapes of the Atlantic Forest Biome in the State of Bahia, Brazil. Journal of Insect Biodiversity. 5(19), 1-19. https://doi.org/10.12976/jib/2017.5.19
44. Schmid, V.S., Langner, S., Steiner, J., Zillikens, A., 2014. Inflorescences of the Bromeliad *Vriesea friburgensis* as Nest Sites and Food Resources for Ants and Other Arthropods in Brazil. Psyche. ID 396095. http://dx.doi.org/10.1155/2014/396095
45. Schoereder, J.H., Sobrinho, T.G., Madureira, M.S., Ribas, C.R., Oliveira, P.S., 2010. The arboreal ant community visiting extrafloral nectaries in the Neotropical cerrado savanna. Terrestrial Arthropod Reviews. 3, 3-27. https://doi.org/10.1163/187498310X487785
46. Schütte, M.S., Queiroz, J.M., Mayhé-Nunes, A.J., dos S. Pereira, M.P., 2007. Structured inventory of ants (Hymenoptera, Formicidae) in atlantic slope rain-forest of Marambaia Island, RJ. Iheringia, Serie Zoologia. 97(1), 103-110. https://doi.org/10.1590/S0073-47212007000100015
47. Silva Melo, T., Lima Peres, M.C., Chavari, J.L., Domingos Brescovit, A., Delabie, J.H.C., 2014. Ants (Formicidae) and Spiders (Araneae) listed from the Metropolitan Region of Salvador, Brazil. Check List. 10(2), 355-365. https://doi.org/10.15560/10.2.355
48. Silva, R.R., Brandao, C.R.F., Silvestre, R., 2004. Similarity Between Cerrado Localities in Central and Southeastern Brazil Based on the Dry Season Bait Visitors Ant Fauna. Studies on Neotropical Fauna and Environment. 39(3),191-199. https://doi.org/10.1080/01650520412331271783
49. Silvestre, R., Brandão, C.R.F., Silva da, R.R., 2003. Grupos funcionales de hormigas: el caso de los gremios del cerrado, in: Fernández, F. (Ed.), 2003. Introducción a las hormigas de la región Neotropical. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Bogotá, pp. xxvi-424.
50. Demetrio, M.F., Silvestre, R., Robson de Souza, P., Aoki, C., 2015. Checklist of ants (Hymenoptera, Formicidae) from Mato Grosso do Sul, Brazil. Iheringia, Serie Zoologia 107, e2015126. https://doi.org/10.1590/1678-4766e2017126
51. Sobrinho, T.G., Schoereder, J.H., 2007. Edge and shape effects on ant (Hymenoptera: Formicidae) species richness and composition in forest fragments. Biodivers Conserv. 16, 1459–1470. https://doi.org/10.1007/s10531-006-9011-3
52. Souza, J.L.P., Baccaro, F.B., Pequeno, P.A.C.L., Franklin, E., Magnusson, W.E., 2018. Effectiveness of genera as a higher-taxon substitute for species in ant biodiversity analyses is not affected by sampling technique. Biodiversity and Conservation. 27(13), 3425–3445. https://doi.org/10.1007/s10531-018-1607-x
53. Souza, J.L.P., Baccaro, F.B., Landeiro, V.L., Franklin, E., Magnusson, W.E., 2012. Trade-offs between complementarity and redundancy in the use of different sampling techniques for ground-dwelling ant assemblages. Applied Soil Ecology. 56, 63– 73. https://doi.org/10.1016/j.apsoil.2012.01.004

54. Souza Santos, R., Delabie, J.H.C., 2018. Epigaeic ants in a forest remnant in the state of Acre, Brazil and new records for the state. Brazilian Journal of Agriculture. 93(1), 24-32.
55. Ulyssea, M.A., Brandao, C.R.F., 2013. Ant species (Hymenoptera, Formicidae) from the seasonally dry tropical forest of northeastern Brazil: a compilation from field surveys in Bahia and literature records. Revista Brasileira de Entomologia. 57(2), 215–224. https://doi.org/10.1590/S0085-56262013005000002
56. Vicente, R.E., Prado, L.P., Izzo, T.J., 2016. Amazon rainforest ant-fauna of Parque Estadual do Cristalino: understory and ground-dwelling ants. Sociobiology. 63(3), 894-908. https://doi.org/10.13102/sociobiology.v63i3.1043