# UNIVERSIDADE FEDERAL DO PARANÁ

LEONARDO POLIZELI AGUIAR

PHYLOGENY OF THE GIANT COCKROACHES OF BRACHYCOLINI AND A TAXONOMIC REVISION OF *BIONOBLATTA* REHN, 1940 (INSECTA: BLATTODEA: BLABERIDAE)



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Dissertação apresentada ao Programa de Pós-Graduação em Ciências Biológicas (Entomologia), Departamento de Zoologia, Setor de Ciências Biológicas, Universidade Federal do Paraná, como requisito parcial para a obtenção do título de mestre em Ciências Biológicas (Entomologia).

Orientador: Prof. Dr. Ângelo Parise Pinto (DZoo/UFPR)

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#### **RESUMO**

A taxonomia e os relacionamentos filogenéticos das baratas Neotropicais de Brachycolini assim como do gênero Bionoblatta Rehn, 1940 tem sido pouco estudada desde a primeira espécie descrita para este grupo. Entretanto, ainda que seja um táxon pouco estudado, a compreensão sore a composição e classificação da tribo tem mudado inúmeras vezes nos últimos 200 anos. Esta linhagem pode ser considerada um táxon chave para investigar a evolução de Blaberidae, devido aos muitos aspectos interessantes presentes em seus representantes como o possível comportamento social, tendências ao braquipterismo, hipertrofia dos elementos discais, e a distribuição endêmia ao Neotrópico. Os objetivos específicos deste estudo foram (1) disponibilizar uma revisão taxonômica do gênero Bionoblatta; e realizar uma análise filogenética para inferir a história evolutiva de Brachycolini. Portanto, buscou-se contribuir para o conhecimento sobre este grupo de baratas Neotropicais. Baseado em análises morfológicas comparativas, nós disponibilizamos uma revisão taxonômica abrangente para Bionoblatta, dividida em dois capítulos. No primeiro capítulo, Parahormetica hylaeceps é considerada como um sinônimo sênior de Bion mastrucatus syn. nov., e Bionoblatta hylaeceps (Miranda-Ribeiro, 1936) deve ser considerado como nome valido. No segundo capítulo Bionoblatta é revisada, assim como diagnosticada dos outros gêneros da tribo Brachyolini, a composição é atualizada, resultando em seis espécies inclusas no gênero, e Bionoblatta marcelli sp. nov. é proposta como uma nova espécie. Além disto, diagnoses, mapa de distribuição, imagens dos espécimes-tipo e de espémices-não-tipo, assim como notas sobre a história natural e variações morfológicas são disponibilizadas. No terceiro capítulo desta dissertação por meio de uma análise filogenética investigamos as relações filogenéticas de Brachycolini, baseada em 92 caracteres morfológicos codificados para 33 táxons terminais,. As análises filogenéticas foram realizadas com diferentes estratégias de busca e parâmetros, e foram realizados testes de estabilidade de ramos. Nossos resultados suportam a monofilia de Brachycolini com alta estabilidade. Brachycolini inclui oito gêneros já descritos-Brachycola Serville 1839, Bionoblatta Rehn, 1940, Hormetica Burmeister, 1839, Lucihormetica Zompro & Fritzsche, 1999, Parahormetica Brunner von Watttenwyl, 1865, Oxycercus Bolivar, 1881, Quadrihormetica Vidlička, 2019, e Sibylloblatta Rehn, 1937-e dois gêneros para serem introduzidos como novos. As relações internas entre os táxons foram inferidas, e as implicações filogenéticas e evolucionárias sobre táxons-chave e bem suportados são discutidas.

Palavras-chave: Blaberinae; Neotrópico; parcimônia cladística; sistemática; Zetoborinae.

#### ABSTRACT

The intricate taxonomic and phylogenetic knowledge about the Neotropical cockroaches belonging to Brachycolini as well as the genus Bionoblatta Rehn, 1940 have been poor studied, since the first described species to this taxa. However, yet it is a poor studied taxon the understanding, composition and their classification status have been changing numerous times during last almost 200 years. This lineage is a very interesting taxon to investigate the evolution of blaberids due many important aspects as the putative social behavior, trend to brachypterism, hypertrophy of diskal elements, and distribution endemic to the neotropics. The specific objectives of this project were to (1) make available a taxonomic revision of the genus *Bionoblatta*; and (2) perform a phylogeny analysis to infer the evolutionary history of Brachycolini. Therefore contributing to the knowledge about this Neotropical group of cockroaches. Based on a comparative morphological analysis, we provide a comprehensive taxonomic revision of the genus Bionoblatta. On first chapter Parahormetica hylaeceps is considered a senior synonym of Bion mastrucatus syn. nov., hence the valid name should be Bionoblatta hylaeceps (Miranda-Ribeiro, 1936). On second chapter Bionoblatta is reviewed and diagnosed from other Brachycolini genera, and the composition is updated resulting in the genus with six species, and Bionoblatta marcelli sp. nov. introduced as a new species. We made available diagnosis, distribution map, images of type and non-type specimens, and notes on natural history and morphological variations. On third chapter thought a phylogenetic analysis based on 92 morphological characters coded for 33 terminal taxa was investigated the relationships of Brachycolini. The phylogenetic analyses were undertaken with different search strategies and parameters, as well as tests of branch stability. Our results supports the monophyly of Brachycolini with high levels of clade stability. Brachycolini stat. rev. comprise eight already described genera-Brachycola Serville 1839, Bionoblatta Rehn, 1940, Hormetica Burmeister, 1839, Lucihormetica Zompro & Fritzsche, 1999, Parahormetica Brunner von Watttenwyl, 1865, Oxycercus Bolivar, 1881, Ouadrihormetica Vidlička, 2019, and Sibylloblatta Rehn, 1937-and two genera waiting to be introduced. The internal relationships among taxa was inferred, and evolutionary and systematics implications on key and well-supported taxa are discussed.

Key words: Blaberinae; cladistic parsimony; Neotropic; sistematics; Zetoborinae.

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#### **1 INTRODUCTION**

The monophyletic group that includes cockroaches and termites is known as the order Blattodea. Representatives of this order exhibit great morphological, behavioral, and lifestyle diversity (Bell et al. 2007). They are among the main decomposers in terrestrial ecosystems and have an unquestionable importance for organic matter cycling (Evangelista 2019). The order contains approximately 7,570 species (Beccaloni and Eggleton 2013), and the paraphyletic group, which corresponds to cockroaches, comprises approximately 4,650 living species (Beccaloni and Eggleton 2013). Even though they are significant in ecosystems, have great diversity, and some species are among the most common insects in human daily life today, the biodiversity of Blattodea is relatively little studied (see Roth 2003; Marques and Lamas 2006). Therefore, there is still much to be researched and learned in different areas of the knowledge about the diversity of cockroaches.

The order Blattodea contains 17 families and Blaberidae is the third richest with about 1200 species, which represents 25% of all cockroaches (cf. Beccaloni and Eggleton, 2013). The family includes cockroaches ranging from medium size to the some of the largest known, presents a variety of colors and their representatives are distributed in the Pantropical region (Djernæs et al. 2020). Phylogenetic analyzes using morphological data and more recently phylogenomic data have contributed to the understanding of the evolutionary history of the group (Legendre et. al. 2017; Djernæs et al. 2020), but in lower levels than family some relationships needs more investigations. The Brachycolini are among the lineages of Blaberidae whose evolutionary history we are beginning to understand.

The subject of this study focuses on the taxonomy and phylogenetic knowledge about the Neotropical cockroaches of Brachycolini and its genus *Bionoblatta* Rehn, 1940. Several studies have contributed to the taxonomic knowledge and the understanding of the evolutionary history of this lineage (McKittrick 1964; Roth 1970; Grandcolas 1993; Zompro & Fritzsche 1999; Legendre et al. 2017; Vidlička 2019; Polizeli and Pinto 2024). However, it is still necessary to search for taxonomic and systematic solutions to problems recognized for Brachycolini and *Bionoblata*. Such problems will be explained and addressed in each chapter of this dissertation.

Keeping an up-to-date knowledge and making efforts to reduce gaps on the knowledge about biodiversity are fundamental contributions, as well as significant advances in how we understand and interact with biodiversity. Therefore, the completeness of knowledge have implications for inferences about biological processes, development of new knowledge, and to elaborate conservation actions, if necessary. The lack of information or unresolved problems can negatively influence the development of knowledge about the Neotropical cockroaches. This thesis aims to contribute to the systematics of blaberids and it was divided into three chapters, which correspond to independent scientific papers. The first chapter addresses the taxonomic status of two names included in the genus *Bionoblatta*. Through a comparative morphological analysis and a detailed study of the type material, the synonymy of the two specific names is proposed. The second chapter makes available a revision of *Bionoblatta*. Therefore, addressing the taxonomic status and nomenclatural validity of the valid species included in the genus. The third chapter investigate the phylogeny of Brachycolini, by means of a phylogenetic analysis based on morphological data. The monophyly of the tribe and its genera was evaluated, and it the internal relationships among taxa was inferred.

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# **2 OBJECTIVES**

# 2.1 General objective

The objective of this study is to contribute to the taxonomic and phylogenetic knowledge of Neotropical Brachycolini cockroaches.

# 2.2 Specific objectives

The specific objectives are listed below, and each chapter has its own objectives.

- (1) Make available a taxonomic revision of the genus *Bionoblatta*.
- (2) Perform a phylogeny analysis to infer the evolutionary history of Brachycolini.

# 3 CHAPTER 1 - ON THE TAXONOMIC STATUS OF TWO GIANT COCKROACHES OF *Bionoblatta* (BLATTODEA: BLABERIDAE) COLLECTED BY JOSÉ PINTO DA FONSECA, A FOUNDER OF THE BRAZILIAN SOCIETY OF ENTOMOLOGY

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Blaberinae, Brachycolini, Neotropical, nomenclature, systematics, taxonomy, trilobite cockroaches, Zetoborinae

# Abstract

The blaberids *Parahormetica hylaeceps* Miranda-Ribeiro, 1936 and *Bion mastrucatus* Rehn, 1937 were described in the 1930s from single males collected by José Pinto da Fonseca (JPF) in the 1910s. Both specimens came from the region of Mariana municipality, Minas Gerais State, an ecotonal formation between Atlantic Forest and Cerrado domains in southeastern Brazil. Recently, *P. hylaeceps* was transferred to *Bionoblatta* Rehn, 1940 and its strong morphological similarity with *Bion mastrucatus* (already in *Bionoblatta*) was highlighted, indicating the need to investigate the validity of these names. Here we addressed this question analyzing photos of type material, comparing original descriptions, and data on both the collecting site and collector's history. We concluded that *Parahormetica hylaeceps* should be *Bionoblatta hylaeceps* (Miranda-Ribeiro, 1936). We also provide a new diagnosis, synonymy and a review of the distribution for this species,

as result *Bionoblatta hylaeceps* is endemic to the Itacolomi Peak region. We also present a short account on JPF, his relevance to the Brazilian entomology and itinerary for collecting these specimens. Therefore, *Bionoblatta* have five poorly known species of blaberids which, despite recent advances in the genus taxonomy, are still pending review.

#### **3.1 Introduction**

Scientific collections are of great importance to the development of scientific thinking and have been used in collections-based science from the 18<sup>th</sup> century to the present day (see Funk 2018). Specimens held in natural history collections provide the primary data or evidence to understand the natural world through studies on biodiversity, and they are also mandatory to meet the requirements of scientific practices (e.g., vouchers and type specimens; see Huber 1998, Halm 2023, Nanglu et al. 2023).

Natural history collections grew for centuries by contributions from many collectors and naturalists, among them José Pinto da Fonseca (1896–1982, hereafter just JPF). He was an important collector and preparator of birds (Vasconcelos et al. 2014) as well as a memorable Brazilian entomologist (Ide et al. 2005). During 1911 until 1919 he centered his scientific collection efforts around Mariana municipality, Minas Gerais State, Brazil (Martins 1982, Vasconcelos et al. 2014). Among all the material that he collected in that region, there are some cockroaches which a few years later were recognized as new taxa—*Parahormetica hylaeceps* Miranda-Ribeiro, 1936 and the genus *Bion* Rehn, 1937, which included *Bion mastrucatus* Rehn, 1937 as its single species (Miranda-Ribeiro 1936, Rehn 1937).

*Parahormetica hylaeceps* was described based on a single male collected by JPF from Mariana municipality in the state of Minas Gerais, Brazil. The holotype was deposited in the Museu Nacional, Federal University of Rio de Janeiro (MNRJ) and it was lost in the catastrophic fire of 2018 (S. F. Lopes 2021, personal communication; see Kury et al. 2018 and De Almeida et al. 2021 for additional data on the impact of the fire to the entomological collection).

In turn, *Bion* and its single species, *Bion mastrucatus*, were described based on a single male from "Serra do Itacolomi" in Mariana Municipality, also collected by JPF, but the locality was originally mistakenly indicated as from the state of São Paulo by Rehn (1937). However, this record was corrected years later by Gurney (1955: 272) that indicated Itacolomi as located in the state of Minas Gerais. Just a few years after its description, Rehn (1940) renamed the genus *Bion* to *Bionoblatta* Rehn, 1940, after discovering it as a homonym of *Bion* Cambridge, 1898, a genus of orb-weaver spiders (Araneae: Araneidae).

We recently transferred *Parahormetica hylaeceps* to *Bionoblatta* based on characters from the original description and examination of photo of the habitus of a male, which was considered its putative holotype (Polizeli and Pinto 2024). We also pointed out the strong morphological similarity between the putative holotype of *P. hylaeceps* and the holotype of *Bion mastrucatus* and suggested that the status of two nomina should be investigated (Polizeli and Pinto 2024). Because, both specimens were collected by JFP, virtually at the same site and the strong similarity that finds correspondence in the original descriptions (see Miranda-Ribeiro 1936, Rehn 1937, Polizeli and Pinto 2024). We recognize that this weakens the supports to keep them as two distinct names and a reassessment is needed.

Today, both names, *Parahormetica hylaeceps* Miranda-Ribeiro, 1936 and *Bion mastrucatus* Rehn, 1937, are combined with *Bionoblatta* (Polizeli and Pinto 2024). Thus, after transfers and descriptions of new species throughout the years *Bionoblatta* now include six species of brachypterous blaberids with a hormeticoid-shaped. All are endemic to the Atlantic Forest in Southeastern Brazil (see Gurney 1955, Rocha e Silva Albuquerque 1957, Polizeli and Pinto 2024). As part of the ongoing taxonomic revision of the *Bionoblatta* our goal in this study is to address the taxonomic status of *Parahormetica hylaeceps* and *Bion mastrucatus*.

## 3.2 Materials and methods

We evaluated the taxonomic validity of *P* hylaeceps and *Bion mastrucatus* comparing the original descriptions, available images of the holotypes of *Bionoblatta* species, original data from the collecting site and collector's history. The nomenclature of specific names was evaluated following the International Code of Zoological Nomenclature (ICZN 1999).

The original descriptions of Miranda-Ribeiro (1936) and Rehn (1937) were critically analyzed and compared to recognize the proposed characters present in both descriptions. Photos of the holotype of *Bion mastrucatus* and the putative holotype of *Parahormetica hylaeceps* (Fig. 1) were also utilized to propose the characters used in the Table 1. Outlines of terminalia were elaborated (Fig. 2C) from photos of specimens or illustrations from the original descriptions. Morphological terminology was largely based on Polizeli and Pinto (2024), while the areas of the wings (e.g., humeral) were named following Li et al. (2018).

A photo from a male identified as *P. hylaeceps* held in MNRJ was sent to us by Sonia Maria Fraga Lopes. The photo was taken by Edivar Heeren de Oliveira in the 2010s, but not as part of the digitization collections project of the MNRJ (S. Lopes and E. Oliveira 2021, personal communication, see also De Almeida et al. 2021 for data on the collections digitization project). This putative holotype was lost in the fire of 2018 (S. Lopes and E. Oliveira 2021, personal communication). To help investigate the status of the name-bearing type of *P. hylaeceps*, we compared this putative holotype with the original description, trying to determin whether the original description was based on that particular specimen. Photos of the *Bion mastrucatus* holotype, made by Heidi Hopkins, are available in the Cockroach Species File – CSF (Beccaloni 2023) under Creative Commons Attribution 4.0 International License (CC-BY).

Review of literature and search for specimens in collections were conducted in digital databases (e.g., Biodiversity Heritage Library, Google Scholar, GBIF, Taxonomic Catalog of Brazilian Fauna). We looked for the full names *Bionoblatta mastrucata* and *Parahormetica hylaeceps*, or through the following keywords "Bionoblatta, Parahormetica, hylaeceps, mastrucata", which were searched individually or combined.

#### 3.2.1 Abbreviations of institutions:

- ANSP Entomology Collection of the Academy of Natural Sciences of Drexel University, Philadelphia, United States of America;
- **MNRJ** Entomological collection, Department of Entomology, Museu Nacional, Federal University of Rio de Janeiro, Rio de Janeiro, Brazil;
- MZSP Entomological collection, Museum of Zoology, University of São Paulo, São Paulo, Brazil.

## 3.3 Results

Based on our comparison, we concluded that there is no evidence to support the taxonomic validity of the two names, and they must be treated as a single taxon. Thus, based on principle of priority (Art. 23 of the Code, ICZN 1999), *Parahormetica hylaeceps* Miranda-Ribeiro, 1936 has precedence over *Bion mastrucatus* Rehn, 1937, which is deemed its junior synonym. A synonymy, catalog, status of the type material, diagnosis, remarks about provenance of the specimens and updated distribution are made available in the sections below.

The comparative analysis between both original descriptions and specimens' photos (Figs 1– 2, Table 1) validates the strong morphological similarity between Bion mastrucatus and Parahormetica hylaeceps. Many characters used by Rehn (1937) to characterize and diagnose Bion mastrucatus are similar to those of original description of the P. hylaeceps (Table 1). They share the following major characters (character numbers in the Table 1 are shown in parentheses): Head - (1) anterior surface of head reddish-brown to dark brown, (2) with pale orange brown spots; Pronotum -(6) a pair of diskal anterolateral tubercle-like processes (DTP); (7) posterior margin of diskal horseshoe-like process (DHP) adjacent to posterior margin of pronotum; (8) inner area of disk reddish-orange; (9-10) lateral portion of pronotum with a pale orange elongated spot on dorsal and ventral surfaces; Tegmina - (12) short, not touching nor overlapping mesially and largely rounded; (13) rough, with dense and deep punctuation; (14) overall color dark brown with humeral area reddish-brown; (15) no venation with ill-defined veins basally at radial area; Abdomen - (19) dorsal surface densely rugose, covered with callosities and rough and (20) narrowly bordered of reddishorange; (21) supraanal plate orange ochre dorsally; Dimensions - (25) total length about of 35 mm; (26) length of pronotum 12 mm, (28) length of tegmina 10.5 mm. Furthermore, they were collected by the same collector at the same site (see below on José Pinto da Fonseca and the provenance of these specimens).

#### 3.3.1 On the putative holotype of P. hylaeceps

A photo from a male identified as *P. hylaeceps* held in MNRJ, took in the 2010s by Edivar Heeren de Oliveira (EHO) was sent to us by Sonia Maria Fraga Lopes 2021 (Fig. 1D). The photo has no data on the specimen labels, and further than to the original description, it was the only information about this species to survive the fire in MNRJ (Sonia Maria Fraga Lopes 2021, personal communication).

The careful comparison of the putative holotype and the original description and illustration of *P. hylaeceps* (see Table 1), reveals a strong similarity among them. The major similarities are the tip of tegmina reaching the second abdominal segment (Fig. 1) exactly was mentioned by Miranda-Ribeiro (1936), the shape and arrangement of the supraanal and subgenital plates (Fig. 2), in the coloration of the supraanal plate and posterior margin of subgenital plate (Fig. 1; see fig. 2 in Miranda-Ribeiro (1936)). Even though we know that caution is need when analyzing the illustration of the supraanal plates drew by Miranda-Ribeiro due to putative inaccuracies (see Gurney 1955), we saw a very high similarity between the terminalia illustrated and the photo (Fig. 2). Moreover,

some of the proportions of the specimens are also similar (total length / pronotum maximum width = 1.84 vs. 1.86; total length / tegmina length = 3.33 vs. 3.13; pronotum maximum width / tegmina length = 1.80 vs. 1.67), but some are distinct (total length / pronotum maximum length = 2.91 vs. 3.43; pronotum maximum width / pronotum maximum length = 1.58 vs. 1.84; pronotum maximum length / tegmina length = 1.14 vs. 0.91). All these minor incongruences in proportions are related to the pronotum maximum length, these disparities may be caused by inconsistencies in the acquisition of the measurements because of many aspects, including the angle of the image. This set of evidence led us to associate the photo as the main candidate to represent the specimen described and illustrated by Miranda-Ribeiro (1936), as well as anticipated by Polizeli and Pinto (2024).

#### 3.3.2 Bionoblatta Rehn, 1940

Zoobank: http://zoobank.org/NomenclaturalActs/BB0A6D6B-E9E3-4334-8746-4268FDA173D3

*Bion* Rehn, 1937: 252 (original description, homonym of *Bion* Cambridge, 1898). *Bionoblatta* Rehn, 1940: 60 (replacement of homonym by a new substitute name).

**Type species**: *Bion mastrucatus* Rehn, 1937 (by original designation), a junior synonym of *Parahormetica hylaeceps* Miranda-Ribeiro, 1936.

Generic composition (see discussion): *Bionoblatta diabolus* (Saussure, 1864), *Bionoblatta hylaeceps* (Miranda-Ribeiro, 1936), *Bionoblatta itatiayae* (Miranda-Ribeiro, 1936), *Bionoblatta oiticicai* Rocha e Silva Albuquerque, 1957, and *Bionoblatta punctata* (Saussure, 1873).

#### 3.3.3 Bionoblatta hylaeceps (Miranda-Ribeiro, 1936)

Zoobank: <u>http://zoobank.org/NomenclaturalActs/025457AE-67E6-47D3-87F4-C8D6E3E68093</u> (Figs 1A–D; 2A–C)

- Parahormetica hylaeceps Miranda-Ribeiro, 1936: 218–219, fig. 2 (description of male holotype from Mariana municipality, Minas Gerais State, Brazil in MNRJ 14250); —Camargo-Andrade (1937: 794, mention); —Princis (1963: 118, catalog); —Rocha e Silva Albuquerque (1964: 4, checklist to Brazil, record to Rio de Janeiro State); —Rocha e Silva Albuquerque (1982: 3, checklist to Rio de Janeiro municipality); —Pelles and Grandcolas (2008: 57, catalog to Brazil); —Lopes et al. (2009: 231, record from Rio de Janeiro State based on Rocha e Silva Albuquerque 1982).
- Bion mastrucatus Rehn, 1937: 208, 253–256, 258 (description of male holotype from Serra do Itacolomi, [state of Minas Gerais], Brazil in MZSP [probably under loan to ANSP], figs 18, 22, 29, subgenital plate and tip abdomen in ventral view, and habitus in dorsal view); —Zompro and Fritzsche (1999: 212, mention). syn. nov.

- *Bionoblatta mastrucatus* (Rehn, 1937): —Rehn (1940: 60, comb. nov.); —Rocha e Silva Albuquerque (1964: 5, record to Minas Gerais); —Polizeli and Pinto (2024: 4, 6, figs1d–f, taxonomic notes, photos of tegmina and abdomen of holotype in dorsal view).
- Bionoblatta mastrucata (Rehn, 1937): —Gurney (1955: 272, 277, key and remarks about type locality); —Rocha e Silva Albuquerque (1957: 408, key and synonymic list); —Princis (1963: 119, catalog); —Vanschuytbroeck (1969: 5, mention); —Pelles and Grandcolas (2008: 48, catalog to Brazil).

Bionoblatta hylaeceps (Miranda-Ribeiro, 1936): -Polizeli and Pinto (2024: 280, comb. nov.).

**Type material:** *Parahormetica hylaeceps* **Holotype** (by monotypy): BRAZIL • ♂; Minas Gerais State, Mariana municipality; José Pinto da Fonseca leg.; MNRJ 14250. Lost in the fire of 2018 (S. F. Lopes, 2021, personal communication; see remarks).

*Bion mastrucatus* **Holotype** (by original designation): BRAZIL • ♂; [Minas Gerais State, Mariana municipality], Serra do Itacolomi; Apr. 1919; José Pinto da Fonseca leg.; MZSP 22,074, provisionally in ANSP Type 9367. Examined by photos (Fig. 1A–C).

### 3.3.3.1 Diagnosis

*Bionoblatta hylaeceps* is a dark and reddish-brown hormeticoid-shape brachypterous blaberid; tegmina largely rounded, reaching the anterior margin of the second abdominal segment and almost touching mesialy, dorsal surface deeply punctuated, coloration dark brown, humeral area reddish-brown; small arolium; dorsal surface of the abdomen densely rugged and with few callosities, coloration dark brown, dull, except for narrow reddish-brown lateral borders. The inner area of the disk and the lateral pale portion of the diskal horseshoe-like process (DHP) of pronotum reddish-orange, as wells as supraanal plate orange ochre, may help in its identification. Based on the coloration pattern, *Bionoblatta hylaeceps* resembles the poorly known *Bionoblatta punctata* (Saussure, 1873) from which can be misidentified. It would be possible to differentiate it from *B. punctata* by its large rounded, oval-like tegmina, largely dark brown, with humeral area reddish-brown (tegmina possibly trapezoidal, black colored with brown humeral area in *B. punctata*); abdomen dark brown narrowly bordered of reddish-orange dorsally (black in *B. punctata*) and legs reddish-brown (black in *B. punctata*).

#### 3.3.3.2 José Pinto da Fonseca (JPF) and the provenance of the specimens of Bionoblatta

JPF born in Mariana municipality in the state of Minas Gerais, Brazil in 1896 and soon moved to Lorena in the state of São Paulo (Martins 1982). The day and month of his birth are not clear, as there are two dates in the literature (see Martins 1982, Ide et al. 2005). At the age of 16 he

returned to Mariana to study humanities, philosophy and theology. At the institution he began to dedicate himself to the knowledge of biological sciences, influenced by his masters in Natural Sciences (Martins 1982). He collected many animals, among them insects, and firstly his specimens were sent to the MNRJ and later to the Museu Paulista (nowadays Museu de Zoologia da Universidade de São Paulo, MZSP) where he joined as a traveling naturalist in 1919 (see Martins 1982). Paulo Miranda-Ribeiro described *P. hylaeceps* based on a male individual deposited in MNRJ and collected in Mariana municipality by JPF but does not specify the date of collection (Miranda-Ribeiro 1936). Interestingly, Alípio de Miranda-Ribeiro, Paulo's father, recommended JPF as a traveling naturalist to the director of the Museu Paulista (Martins 1982, Pombal Jr. 2002). We assume that holotype of *P hylaeceps* deposited at the MNRJ has been collected before 1919, but after 1912, indicating it was before JPF started sending specimens to the Museu Paulista and after him started to have interest in Natural Sciences.

**Table 1.** Characters of holotypes of *Bion mastrucatus* and *Parahormetica hylaeceps* and the putative holotype of *Parahormetica hylaeceps* (in MNRJ, without data). Data was extracted from original descriptions by Miranda-Ribeiro (1936) and Rehn (1937), those from the putative holotype of *Parahormetica hylacaeps* is from this study. n.o. = Not observed. Character from Miranda-Ribeiro (1936) adapted from Portuguese.

	Character / Specimen	Bion mastrucatus	Parahormetica hylaeceps	Putative holotype of Parahormetica hylaeceps
1.	Coloration of anterior surface of head	Liver brown	Dark reddish-brown	n.o.
2.	Pale spots at anterior surface of head	Four paired dots of vinaceous-rufous placed immediately mesad of antennal scrobes and at proximo-lateral angles of clypeus	A light reddish-brown spot lateral to the base of antenna, and another below	n.o. r
3.	Antennae coloration	Pitch brown	Dark reddish-brown (incomplete)	n.o.
4.	Pronotum	Median length faintly less than three-fourths the greatest breadth [] general arcuation	Large, wide, convex and parabolic	Wider than long, semicircular
5.	Anterior margin of pronotum	Dorsal recurving, thickening	Strongly protruded upward	Projected dorsally (upwards)
6.	Diskal anterolateral tubercle-like processes (DTP)	Pair of elevated, smoothly but not glabrously rounded, large boss-like tubercles	Pair of huge smooth tubercles	Pair of large and smooth (rounded) tubercles
7.	Posterior margin of diskal horseshoe-like process (DHP)	In contact with the caudal margin of the pronototum, from which it is separated by a narrow sulcation	Almost fused (undifferentiated) to the posterior margin of pronotum	Adjacent to posterior margin of pronotum

# Table 1. Continuation

	Character / Specimen	Bion mastrucatus	Parahormetica hylaeceps	Putative holotype of Parahormetica hylaeceps
8.	Inner area of disk coloration	Auburn to orange rufous	Testaceous, reddish- yellow	Reddish-orange
9.	Pronotum coloration laterally to the DHP (dorsal view)	Lateral crescents [] auburn to orange rufous	Elongated reddish- yellow spot, testaceous	Pale orange
10.	Pronotum coloration in ventral view	Broader crescents of zinc orange to vinaceous-rufous	Elongated reddish- yellow spot, testaceous	n.o.
11.	Scupturation around the disk	Criboso-punctate	Wrinkled (rugose)	Rough [?]
12.	Tegmina	Subcircular, separated mesad	Trapezoidal-like with rounded angles [] posteriorly reaching the second abdominal segment	Subcircular, not touching nor overlapping mesially, tip reaching the second abdominal segment
13.	Scupturation of dorsal surface of	Deeply impressed	Shagreen-like [rough]	Rough, with dense and
14.	Tegmina color	Dark brown with humeral area reddish- brown	Dark reddish-brown, lighter towards to the humeral area	Dark brown with humeral area reddish-
15.	Humeral trunk [Radial area]	A cicatriform ridge, definite only proximad	Strong, elevated, with two branches disappearing distally	Visible as a carina
16.	Humeral area [marginal field]	Broad, almost equal in width to a third of the entire tegmen, its dorsal surface appreciably concave	Wide with thickened margin [carinated]	Wide, concave, with thickened margin [carinated]
17.	Hind wings	Wings rudimentary, present but hidden beneath tegmina	Scale-like, vestigial, almost wingless	n.o.
18.	Meso- and metathorax coloration	Liver brown, each crossed by a narrow wavering band of zine orange	Reddish-yellow, [testaceous], with black marks	Reddish-orange, with brown to black marks
19.	Scupturation of dorsal surface of abdomen	Strongly corasely and irregularly eroso- shagreenous, to strongly rugose	Rugose	Densely rugose, covered with callosities and rough
20.	Dorsal surface of abdomen coloration	Narrowly bordered with madder brown	Dark brown to black, very finely bordered by reddish-brown	Dark brown,bordered by reddish-brown
21.	Supraanal plate coloration	Dull zine orange	Reddish-yellow, [testaceous]	Pale orange
22.	Subgenital plate	Subtrigonal, [] apex well rounded	Rounded triangular	Not visible [Posterior margin rounded]
23.	Legs coloration	Vinaceous-rufous to mahogany red	Reddish-brown	Reddish-brown
24.	Legs spurs coloration	Color of tibiae proximad [reddish- brown], becoming pitch brown distad	Dark brown	Reddish-brown to dark brown, tip black

	Character / Specimen	Bion mastrucatus	Parahormetica hylaeceps	Putative holotype of Parahormetica hylaeceps
25.	Total length (mm)	35.5	35	n.o.
26.	Pronotum maximum length (mm)	12	12	n.o.
27.	Pronotum maximum width (mm)	16.9	19	n.o.
28.	Tegmina length (mm)	10.5	10.5	n.o.

#### **Table 1. Continuation**

JPF collected the holotype of *Bion mastrucatus* in 1919 and sent to the Museu Paulista. This material was received and deposited in that institution with collection number #22,074 and recorded in the catalog of the collection containing natural history notes which reveal unknown data about the biology of this species (Fig. 2A–B). In free translation "These Orthopteros were found by José Pinto da Fonseca in the highlands of the Serra do Itacolumy, about 300 m below the rock known as "Pedra Menina" [in the Itacolomi Peak]. They appear just when the sun is very strong [hot days], in such manner that is useless [looking for them] on a cold day". Gurney (1955) in his synopsis on *Bionoblatta* mentioned that this material was in the Museu Paulista (now MZSP), however this material is currently at Academy of Natural Sciences of Philadelphia, USA (ANSP). Most likely, it was not returned to MZSP when borrowed for study by James Abram Garfield Rehn, who spent most of his career at ANSP (Gurney 1965), and the holotype has remained deposited in that institution since then.

Throughout his life JPF demonstrated a successful career, at the end of the decade of 1920 he was hired as a technical assistant in entomology at the Biological Institute of São Paulo and in the same period in this institution founded the Adolph Hempel Entomological Collection (Ide et al. 2005). He was one of the pioneers of biological control in Brazil, thanks to his studies on the wasp *Prorops nasuta* Waterson, 1923 in the control of the "Broca-do-Café"—coffee berry borer, *Hypothenemus hampei* (Ferrari, 1867). In 1937 he was one of the founding members and first president of the Brazilian Society of Entomology (Carrera 1987). Since 1938 he was chair of the Entomology Section of the Instituto Biológico, a position he held until his retirement in 1966 and during his prolific career published hundreds of studies compiled in Ide et al. (2005).

#### 3.3.3.3 Distribution

*Bionoblatta hylaeceps* (cited as *P. hylaeceps*) has been recorded in many studies for the state of Rio de Janeiro (Rocha e Silva Albuquerque 1964, 1982, Pelles and Grandcolas 2008, Lopes et al.

2009), however no voucher specimens were reported in support these records. Most of them only replicated the record from the seminal paper by Rocha e Silva Albuquerque (1964). In her paper of 1982, Rocha e Silva Albuquerque (1982) mentioned which records have been based on literature or on voucher specimens, the record of *P. hylaeceps* for Rio de Janeiro municipality evidently was based on literature. We believe the occurrence record in Rio de Janeiro is a misinterpretation of the study of Miranda-Ribeiro (1936). Thus, it is suggested that this species be removed from the list of cockroaches recorded in the state of Rio de Janeiro, pending evidence such as *bona fide* specimens collected in this state.

As mentioned, the holotype of *Bion mastrucatus* was collected about 300 m below the rock known as Pedra Menina in the Itacolomi Peak, Mariana municipality. While the holotype of *P. hylaeceps* has also been collected in Mariana, there is no further information about the locality. The specimen and any supposed additional data from the labels or field and collection notebooks were permanently lost during the fire in the MNRJ. However, because *P. hylaeceps* was collected by the same person and municipality with few years of difference to that of *Bion mastrucauts* holotype, we are convinced it also came also from the "Serra do Itacolomi". We considered *B. hylaeceps* endemic to the "Serra do Itacolomi" [Itacolomi Peak] in Minas Gerais State due to the records of this species being limited to that region.

Itacolomi Peak is currently located within the protected area of Itacolomi State Park, which was created by law n° 4,495, of June 14th of 1967 encompassing an area of approximately 7,000 hectares between the municipalities of Mariana and Ouro Preto (Minas Gerais 1967). Although we do not know the conservation status of this species, the type locality is within a protected area, which may favor the maintenance of the population of this species.

#### **3.4 Discussion**

In this study, we formally proposed *P. hylaeceps* as senior synonym to *Bion mastrucatus* as suggested by Polizeli and Pinto (2024). Therefore, contributing to the biological understanding of two names related to the same area, and recognized as distinct species for approximately 90 years. As result, *Bionoblatta* contains now five species: *Bionoblatta diabolus* (Saussure, 1864), *Bionoblatta hylaeceps* (Miranda-Ribeiro, 1936), *Bionoblatta itatiayae* (Miranda-Ribeiro, 1936), *Bionoblatta oiticicai* Rocha e Silva Albuquerque, 1957 and *Bionoblatta punctata* (Saussure, 1873).

We believe that even if there was not the photo of the putative holotype for comparison, the data from the original descriptions of two species and photos of the holotype of *Bion mastrucatus*, combined with provenance data, is sufficient to support the synonymy. We are aware that interpret a photo of an unlabeled specimen as belonging to the type specimen requires caution. In despite of this, the similarities among the three data sources (original descriptions, available images and original data from the collecting site) given high support to the synonymy.

Our study is a minor example of how collection efforts and scientific collections are extremely important to know the extant biodiversity. With the re-study of these specimens, taxonomic important contributions to the knowledge of *Bionoblatta hylaeceps* were made. It gives new meaning to a poorly known species that has its holotype lost, provides new data about its natural history, increases the knowledge about its morphology, aids in the comprehension of local diversity, serves as an alert to the importance of monitoring this population, and facilitates further specimens' associations with *Bionoblatta* species. It also is a minor example of how the loss of these biological and cultural collections, in this case the loss of a heritage with more than 200 years and 20 million artifacts, makes humanity loss its history, culture and scientific documents (Zamudio et al 2018).

*Bionoblatta* is still a poorly known genus because the knowledge about its species is based solely on a few taxonomic surveys, virtually entirely on exclusively on the type specimens and original descriptions (see Rehn 1937, Gurney 1955, Rocha e Silva Albuquerque 1957, Polizeli and Pinto 2024). Therefore, additional researches are required to improve and update our understanding of taxonomy and phylogenetic relationships in *Bionoblatta*.

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### **Author Contribution**

Both authors contributed to the conceptualization, formal analysis, data curation, visualization of results and review and editing of the manuscript. LP was responsible to the original draft. All authors approved the final draft of the manuscript.

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## **Conflict of interest**

The authors declare no competing interests.

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**Fig. 1**. Habitus and labels of the name-bearing specimen of *Bion mastrucatus* and habitus of the putative holotype of *Parahormetica hylaeceps*. **A–C**. Holotype of *Bion mastrucatus*: **A.** dorsal view; **B.** ventral view; **C.** collection labels; **D.** Putative holotype of *P. hylaeceps* in dorsal view. **A–C**. Photos by H Hopkins, available in Cockroach Species File – CSF (Beccaloni 2023); **D.** Photo by EH de Oliveira.

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**Fig. 2.** Page of catalog of the collections of Museu Paulista (now Museu de Zoologia da USP) and outlines of terminalia of specimens of *Bion mastrucatus* and *Parahormetica hylaeceps*. **A.** Page with record of entry of José Pinto da Fonseca's specimen to museum holding; **B.** Zoom-in the entry of the holotype of *Bion mastrucatus*; **C.** outlines of terminalia based on original description illustration and photos from specimens. Abbreviations: cc = cercus, sap = supraanal plate, sgp = subgenital plate. **A–B.** Adapted from photo by AM Vasques.

4 CHAPTER 2 - Revisiting the Brazilian giant cockroaches of the genus *Bionoblatta* (Blattodea: Blaberidae): a taxonomic revision with description of *Bionoblatta marcelli* sp. nov. from Serra do Caraça, mountain range in Minas Gerais State<sup>1</sup>

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#### ABSTRACT

Bionoblatta Rehn 1940, along with other seven genera, is allocated in the poorly know and intriguing Brachycolini, a Neotropical tribe including 44 blaberid species. Because of the braquipterism, pronotum shape, callosities on abdomen and being montane species, it is outstanding genus of cockroaches, endemic to Brazil. Nevertheless, all taxonomic knowledge is based on a small number of male specimens. In this study we revisit the taxonomy of Bionobaltta based on a comparative morphological analysis, providing a comprehensive overview of the genus, including assessments on its composition, as well as the taxonomic status and nomenclatural validity of available names, aiming to provide a synoptic and updated information about their species. Our results support Bionoblatta as a taxonomically distinguishable genera comprising six species with distribution range exclusively in southeastern Brazil and an identification key is given. Bionoblatta marcelli sp. nov., is herein introduced (holotype male deposited in DZUP: Brazil, Minas Gerais State, Catas Altas) based on males, female and nymph. For the species diagnosis, distribution map, images of type and non-type specimens, and notes on natural history and morphological variations are provided. We hope this study encourage further investigations on this amazing groups of cockroaches-such as phylogenetic and biogeographic analyses, habitat and social studies, and examination of morphological variations in Bionoblatta diabolus-which are essential to

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understand the evolutionary history of living biodiversity.

**Keywords:** Blaberinae, Brachycolini, Mountain Ranges, Neotropical, New species, Systematics, Trilobite cockroaches, Zetoborinae

#### 4.1 Introduction

Recently the taxonomy of the blaberid cockroaches of Brachycolini has received considerable attention with introduction of new taxa, generic and specific revisions, new combinations and high-level rank transferences, which resulted in deep nomenclatural and taxonomic changes (e.g., Legendre et al. 2017; Vidlička 2019; Djernæs et al. 2020; Polizeli and Pinto 2024a). The Brachycolini has eight genera and 44 species (Polizeli and Pinto 2024a, in press). Further to its type genus, *Brachycola* Serville, 1838, the tribe (sensu Vidlička 2019) also include *Bionoblatta* Rehn, 1940, *Hormetica* Burmeister, 1838, *Lucihormetica* Zompro & Fritzsche, 1999, *Oxycercus* Bolívar, 1881, *Parahormetica* Brunner von Wattenwyl, 1865, *Quadrihormetica* Vidlička, 2019 and *Sibylloblata* Rehn, 1937. Due to the intricate phylogenetic position allied to some brachypterous trend and general morphology the tribe represent an intriguing and key-group to research and help to understand the blaberid evolutionary history.

Amongst the brachycolines genera included in this tribe are the *Bionoblatta* a genus poorly known. Bionoblatta have five species that are southeastern Brazilian endemic, which pending additional investigations on many biological and evolutionary issues, also needying a taxonomic review. Its taxonomic history started confusing, once it was introduced as Bion Rehn, 1937, a junior homonym of a genus of orb-weaver spiders, thus must be replaced of Bionoblatta Rehn, 1940 (see Polizeli and Pinto in press). Originally monotypic, the genus included only its types species Bion *mastrucatus* Rehn, 1937, a montane cockroach endemic to a small area in the state of Minas Gerais, Brazil (Rehn 1937, 1940). When reviewed the genus, Gurney (1955) transferred two montane Atlantic Forest species from Hormetica to Bionoblatta, creating the new combinations: Bionobaltta diabolus (Saussure, 1864) and Bionobaltta itatiayae (Miranda Ribeiro, 1936). In addition, provided illustrations, photos, key and diagnoses for the three recognized species. Subsequently, Bionobaltta oiticicai Rocha e Silva Albuquerque, 1957 was described from a transitional region between Atlantic Forest and Cerrado in the State of São Paulo. In 2018 there was a catastrophe at Museu Nacional (MNRJ) and the holotypes of *B. hylaeceps*, *B. oiticicai* and *B. itatiavae* were destroyed by the fire. Polizeli and Pinto (2024a), reviewed Parahormetica and based on its new concept transferred the Brazilian Parahormetica punctata Saussure, 1873 and Parahormetica hylaeceps (Miranda Ribeiro, 1936) to Bionoblatta. We (Polizeli and Pinto in press) also suggested the synonym *B. mastrucatus* and *B. hylaeceps* based on strong similarities between them, but they were synonymized by us after a careful study (Polizeli and Pinto in press), resulting in the composition of genus with five species.

*Bionoblatta* species are distributed in southeastern Brazil, mainly on Atlantic Forest in the states of Minas Gerais, Rio de Janeiro and São Paulo. Gurney (1955) indicated that the evolutionary history of the species may be highly related to mountain ranges. After two years from the Gurney study, the *B. oiticicai* was described based on a single male from Pirassununga municipality, state of São Paulo at 546 m a.s.l., apparently the first known non-mountainous species. The distribution range and biogeography of *Bionoblatta* yet are not fully understood, as well as the preference of habitat choice and putative social behavior of the species (see Pellens et al. 2007: fig. 5–6).

When diagnosed *Bionoblatta*, Rehn (1937) differentiated it from similar genera by having a "hormeticoid shape", pronotum with tubercles and sculptures (similar to the genus *Parahormetica*), ovate tegmina, not touching mesially with heavily and deeply shagreened surface, lacking any trace of venation except a weakly indicated humeral trunk, heavily and solidly rugose of dorsal surface of the abdomen and small arolium. Gurney (1955), which expanded the composition of the genus, also highlighted the sculpture, shape of tip and the length of the tegmina to differentiate *Bionoblatta* from *Hormetica* and *Parahormetica*. Roth (1970b: fig. 209–211) detailed studied the masculine genitalia and made available the first images of phallomeres of *B. itatiayae*, contributing to characterization of the genus. In the most recent emended diagnosis of the genus the sculpturation at tegmina and abdomen were also highlighted to differentiate it from *Parahormetica* (see Polizeli & Pinto 2024a: 281).

From 1937 until 1960, *Bionoblatta* was included in the subfamily Perisphaerinae, thus considered closely related to *Brachycola, Hormetica, Parahormetica* and *Sybilloblatta*, but possibly as a sibling genus of *Parahormetica* (Rehn 1937). Rehn (1951: 86) concept of Brachycolinae was applied just to *Hormetica* and *Brachycola*, consequently Gurney (1955: 271). indicated that *Bionoblatta* could also belong the Brachycolinae. In his monumental catalog Princis (1960: 437) included *Bionoblatta* within the subfamily Brachycolinae. In meantime in the milestone intuitive phylogenetic study of McKittrick (1964: 34) Brachycolinae was synonymized with Blaberinae, whereas Roth (1970b: 310) based on morphology of male genitalia defined Blaberinae as divided into the tribes Blaberini, Monastriini, and Brachycolini, the last included *Bionoblatta*. Then based on his studies on the male genitalia he indicated that *Bionoblatta* have a putative close relationship with *Parahormetica* and *Oxycercus* Bolívar, 1881 (Roth 1970b: 340). In more contemporary phylogenetic investigations, *Bionoblatta* was sampled in the morphological studies by Grandcolas (1993a, 1993b, 1998) and Pellens et al. (2007), however relationships between the sampled genera of Brachycolini were largely unsolved. Further and recent phylogenetic hypotheses based on

molecular data (e.g., Legendre et al., 2014, 2015, 2017; Djernaes et al., 2020) have consistently recovered two representatives of Brachycolini as closely related to Zetoborinae instead to Blaberinae such proposed by McKittrick (1964), therefore it is possible that all genera included in Brachycolini representing a distinct monophyletic lineage more close related to some Zetoborinae than Blaberinae genera.

*Bionoblatta* and its first species (*Bionoblatta hylaeceps*), were described almost nine decades ago, however the taxonomic knowledge of this Neotropical cockroaches are limited to less than ten papers, most focused on species descriptions, making it largely poorly known. Even though it has been characterized morphologically (Polizeli and Pinto 2024a), there is a need to update the diagnosis of the genus, as well as to review limits among species. Most of current knowledge is biased and limited to the external morphology of males, thus descriptions and images of females, nymphs and internal morphology would expand the knowledge about the genus. Also, the relationship between these cockroaches and mountain complexes where they occur, as well as their unknown preference of habitat choice and social behavior needs to be illuminated by new data.

Refining the knowledge (revise, updating and making new data available) about these cockroaches will facilitate the achievement of several objectives and enable the development of more accurate knowledge about the group. The goals of this study are (1) review the generic status and composition of the genus; (2) assess the taxonomic status and nomenclatural validity at species-level; (3) synthetize and update data on morphology, distribution and natural history. A new species from Serra do Caraça in the Atlantic Forest of state of Minas Gerais in Brazil is also described.

## 4.2 Material and methods

#### 4.2.1 Taxonomy and nomenclature

A nomenclatural evaluation was conducted to assess the status of genus- and species-group names in accordance with the International Code of Zoological Nomenclature (ICZN, 1999). The taxonomic status of species-group names was evaluated through a morphological comparative analysis of all names once combined with *Bionoblatta*. The taxonomic decisions were based on qualitative analysis. The bibliographic research was made with the following keywords: Blaberidae; Blaberinae, Brachycolini, Bionoblatta, diabolus, hylaeceps, itatiayae, punctata, oiticicai. The single or combined key words were searched in any year within the database (e.g., Web of Science, Biodiversity Heritage Library).

#### 4.2.2 Species delimitation
We based our taxonomic decisions, thus hypothesis at species- or genus-levels, thought comparison of specimens with aid of stereomicroscope, photographs of holotype and literature data (e.g., Rehn 1937; Rocha e Silva Albuquerque 1957; Roth 1970b; Polizeli and Pinto in press). Taxonomic works used for identification are the following: Saussure (1864a, b, 1873), Gurney (1955) and Rocha e Silva Albuquerque (1957). The characters used to propose species- and genus-level hypotheses were: (1) coloration of body and structures; (2) dimensions of tegmina and arolium; (3) discal morphology and esculpturation (4) Genitalia, mainly phallomeres L2d and L2vm. Data on natural history were obtained from notes of collectors, specimens labels, and literature. Because nymphs are largely unknown and have no same diagnostic characters proposed to the species, they were identified through association with adults.

#### 4.2.3 Terminology and photographs

Morphological terminology follows that described in our previous studies (Polizeli and Pinto 2024a, in press). The preparation of genitalia was based on techniques described in Roth (1969b) and Klass (1997). Stacked images of habitus and details of morphology were generated with digital cameras (EOS Rebel SL3), equipped with microlens (up to 10x), attached to a motorized rail system (MJKZZ). Source photographs were stacked in Helicon Focus, the resulting images were improved using techniques of editing images on a dedicated software. Photos of the holotypes of *Parahormetica itatiayae* and *Bionoblatta oiticicai* was made available by the Projeto Informatização da Coleção Entomológica do Museu Nacional; those of *Bion mastrucatus* holotype by Heidi Hopkins, and are available in the Cockroach Species File – CSF (Beccaloni 2024, CC BY 4.0); while the credits of photos from holotype of *Brachycola diabolus* in MNHN is to Depraetere Marion – 2014 and is available under CC BY-ND 4.0 (https://creativecommons.org/).

#### 4.2.4 Georeferenced data and maps

Occurrence records were compiled from the labels of voucher material and literature, organized in a DwC spreadsheet (<u>https://dwc.tdwg.org/</u>) and used to elaborate the map of species occurrences. Records were georeferenced using the data on the specimens labels, using the data available in Base Cartográfica Contínua do Brasil ao Milionésimo – BCIM (IBGE 2011) or OpenStreetMap (2024) coordinates (Open Database License) or the data available in Base Cartográfica Contínua do Brasil ao Milionésimo – BCIM (IBGE 2011). Map was created in QGIS 3.28.13, QGIS Geographic Information System Software (https://qgis.org) with georeferenced sites

preferentially to locality level, alternatively to municipality. Collections during this project were undertaken under Chico Mendes Institute for Biodiversity Conservation (ICMBio permission 86093-1).

#### 4.2.5 Measurements

The total and pronotal length, as wells as pronotal maximum width were obtained with a caliper rule. All other measurements were made with the aid of a stereomicroscope equipped with an eyepiece micrometer. The minimum distance spaces interocular and interantennal were acquired in anterio view, while the intertegminal space in dorsal view.

## 4.2.6 Collections

Whenever possible the updated version of Arnett et al. (1993) available in Evenhuis (2016) was used for the list of collection acronyms. The following institutions are mentioned in the text:

- ANSP Academy of Natural Sciences of Drexel University, Philadelphia, United States of America;
- CEIOC Entomology Collection of Oswaldo Cruz Institute, Fundação Oswaldo Cruz, Rio de Janeiro, Brazil;
- DZRJ Entomological Collection Professor José Alfredo Pinheiro Dutra, Department of Zoology, Institute of Biology, Federal University of Rio do Janeiro, Rio de Janeiro, Brazil;
- DZUP Entomological Collection Padre Jesus Santiago Moure, Department of Zoology, Federal University of Paraná, Curitiba, Brazil;
- MCN Natural History Museum of Pontifical Catholic University of Minas Gerais, Pontifical Catholic University of Minas Gerais, Belo Horizonte, Brazil;
- UFVB Museum of Entomology of Federal University of Viçosa, Federal University of Viçosa, Viçosa, Brazil;
- MNHN National Museum of Natural History, Paris, France;
- MNRJ Entomological Collection, Museu Nacional, Federal University of Rio de Janeiro, Rio de Janeiro, Brazil;
- MZSP Museum of Zoology, University of São Paulo, São Paulo, Brazil;
- CCT-UFMG Entomological Collection, Taxonomic Collection Center of UFMG, Institute of Biology, Federal University of Minas Gerais, Belo Horizonte, Brazil.

#### 4.3 Results

#### 4.3.1 Taxonomy

#### 4.3.1.1 The genus Bionoblatta Rehn, 1940

(Figs. 1–7)

Zoobank: https://zoobank.org/NomenclaturalActs/bb0a6d6b-e9e3-4334-8746-4268fda173d3

- *Bion* Rehn, 1937 (*nec* Cambridge, 1898): 248, 252–353 (original description, preoccupied); —Estrada-Álvarez (2022: 213, remarks about etymology).
- Bionoblatta Rehn, 1940: 60, 309 (replacement for the junior homonym *Bion*); —Gurney (1955: 271, taxonomic review, key to species); —Rocha e Silva Albuquerque (1957: 405, catalog and key to species); —Princis (1960: 437, catalog); —Princis (1963: 119–120, catalog); —Roth (1969a: 200, table 9, mention); —Roth (1970b: 308, 310, 328, 340–341, comparison of male genitalia among genera of Blaberinae); —Grandcolas (1993a: 204, 211, 212–213, figs. 30–31, phylogenetic analysis); —Grandcolas (1996: 527, phylogenetic analysis); —Grandcolas (1997: 129, mention); —Grandcolas (1998: 119, 121–122, fig. 1–3; phylogenetic analysis); —Grandcolas (1999: 212–213, key to genera); —Baaren et al. (2002: 246, mention); —Roth (2003: 39, 141, mention); Pellens et al. (2007: 27–28, figs. 5–6, phylogenetic analysis); —Pellens & Grandcolas (2008: 48, catalog); —Vidlička (2019: 155, mention); —Estrada-Álvarez (2022: 213, etymology); —Grandcolas, Pellens & Constantino (2024: 337, mention); —Polizeli & Pinto (2024a: 277–278, 280–281, 300, taxonomic discussion); —Polizeli & Pinto (in press: synonymy and generic composition).

#### **Diagnosis:**

Representatives of *Bionoblatta* are hormeticoid-shaped brachypterous blaberids, with general coloration ranging from dark orange to black (except *B. oiticicai* which is brown), dorsal surface of the abdomen uniformly reddish-brown to black with a wide longitudinal mesial yellow stripe, often supraanal plate yellow; pronotum diskal horseshoe-like process (DHP) protruded and well-defined, sculpture of disk and diskal tubercle-like process (DTP) slightly larger in males than in females; tegmina short, reaching at maximum the anterior margin of S2 distallly, suboval trapezoid narrow (Fig. 1A) or quadrate large (Fig. 1B), intertegminal space narrow or wide, in *Bionoblatta marcelli* sp. nov. often touch mesially (Fig. 2A); dorsal surface of the tegmina very sculptured with medium to large, rounded puncture-like depressions; hindwing rudimentary, vestigial; arolia small to fairly well-developed; dorsal surface of abdomen strongly sculptured, rugose to densely rugose and frequently with several callosities.

*Bionoblatta* is a distinctive Brachycolini (sensu Vidlička, 2019) genus, but the specimens of these genera may resemble representatives of *Sibylloblatta* or *Parahormetica*. Species of

*Bionoblatta*, *Sibylloblatta* and *Parahormetica* are brachypteous, with the tip of tegmina close to the first and second abdominal segments (S1–2). *Sibylloblatta pustulata* (Hebard, 1929) have callosities at abdominal tergites of S4–7, which can resemble *B. itatiayae* and *B. oiticicai*. However, *Bionoblatta* differs from *Sibylloblata* by the pronotal disk with a distinct horseshoe-like process (DHP), surfaces of tegmen and abdomen very rugged and by L2d curved toward the L2vm. *Bionoblatta* and *Parahormetica* was recently diagnosed by Polizeli and Pinto (in press) being is possible to differentiate them by (*Parahormetica* characters in parentheses) the dorsal surface of the tegmen very sculptured with deep punctuation (less rough with few shallow punctuations) and by the dorsal surface of the abdomen densely rugose, covered with callosities and rough (smooth, with sparse minute pits and no callosities).

**Type species** (by original designation): *Bion mastrucatus* Rehn, 1937, a junior synonymy of *Bionoblatta hylaeceps* (Miranda-Ribeiro, 1936).

#### 4.3.1.2 Key to adults of Bionoblatta

The taxonomic key available below was almost exclusively based on males, so is better for identification of specimens of this sex, because just the females of *B. marcelli* **sp. nov.**, *B. itatiayae*, and *B. punctata* are known and could be examined. The figures and diagnoses should be used in combination with the key to achieve more confident identifications and they also can be used to associate either to unknown females.

 1. General coloration of dorsal surface of abdomen brown to dark red with black areas on S1 (Figs.

 1C-1D); abdominal tergites with small light-brown callosities, more abundant on posterior segments

 2

 1'. General coloration of dorsal surface of abdomen black (Figs. 1B, 4A) or black with a wide longitudinal yellow stripe; abdominal tergites with numerous large callosities in all segments or deep rugged (Figs. 1A, 3A)

 3
 2(1). Tegmen, meso- and metanotum black (Figs. 1C, 5C)

 Bionoblatta itatiayae

 2'. Tegmen light brown with a small black basal spot, meso- and metanotum brown, with a broad black band laterally (Figs. 1D)

 Bionoblatta oiticicai

 3(1'). Narrow intertegminal space, tegmen large, almost touching each other mesially, humeral area orange to red

 4

 3' Large intertegminal space, tegmen narrow (raton L/W = 00), largely separated mesially, humeral area black

4(3). Diskal and lateral areas of DHP black; tegmen orange with a small black spot on the humeral field; abdominal tergites with a wide longitudinal yellow band (Figs. 3, 5A) *Bionoblatta marcelli* **sp. nov.** 

4'. Diskal areas brick-red and lateral areas of DHP orange; tegmen black	with humeral field red,
abdominal tergites almost uniformly brick-red (Fig. 1B)	Bionoblatta hylaeceps
5 (3'). Disk black; arolium large (Figs. 1A, 4B–C)	Bionoblatta diabolous
5'. Disk yellow to brick-red; arolium small (Figs. 4A, 5D)	Bionoblatta punctata

# 4.3.1.3 Species of Bionoblatta

#### 4.3.1.3.1 Bionoblatta diabolus (Saussure, 1864)

(Figs. 1A, 2A, 4B-C, 6E-L, 7)

Zoobank: https://zoobank.org/NomenclaturalActs/8CA18E3F-1422-434F-9BFE-70D0BA3495C7

- *Brachycola diabolus* Saussure, 1864a: 345 (original description based on a male from Brazil in MNHN); —Walker (1868: 54, mention); —Kirby (1904: 197, catalog); —Rehn (1937: 253, mention).
- Brachycolla diabolus Saussure, 1864a 345 [lapsus calami] (implicit combination with Brachycolla);
- Hormetica diabolus (Saussure, 1864): —Saussure (1864b: 182-183, description); —Saussure (1869: 278, catalog and note about arolium); —Saussure (1870: 99, taxonomic discussion); —Finot (1897: 216, catalog, *Hormetica diablus* lapsus calami).
- Bionoblatta diabola (Saussure, 1864): —Gurney (1955: 272–274, fig. 1–4, 9, comb. nov., remarks about distribution, key, photo of dorsal habitus and illustrations of morphology, specimen from Serra da Bocaina, SP State); Rocha e Silva Albuquerque (1957: 408, key and catalog).
- Bionoblatta diabolus (Saussure, 1864): —Princis (1963: 119, catalog); —Rocha e Silva Albuquerque (1964: 4, record to São Paulo State); —Pelles and Grandcolas (2008: 48, catalog); —Polizeli and Pinto (2024a: 280, mention); Polizeli and Pinto (in press, mention).

Bionoblatta diabolus nec (Saussure, 1864): -- Vanschuytbroeck (1969: 5, misidentification).

**4.3.1.3.1.1 Type Material. Holotype** (by monotypy): **BRAZIL**. 1*<sup>(2)</sup>*; [Capitainerie du Rio de Janeiro]: 1815 [lapsus calami], A. Saint-Hilaire leg., 39, MNHN(EP)-1248, *Brachycola diabolus* Brésil Sauss. Type repository MNHN (EP). Examined by photo (Figs. 1A, 2A); access granted by MNHN, <u>http://coldb.mnhn.fr/catalognumber/mnhn/ep/ep1248</u>.

**4.3.1.3.1.2** *Other material examined.* **BRAZIL** • 1♂; Rio de Janeiro State, Mauá municipality; Dez.1998; R. Gonçalves leg.; (DZRJ) • 1♂; Rio de Janeiro State, Paraty municipality, Rodovia RJ-165; 23°11'23"S, 44°50'14"W; 47 m a.s.1.;13 Dez.2015; A. C. Delciello leg.; ex-DZRJ (DZUP 267084).

**4.3.1.3.1.3** *Male measurements (mm, n = 2).* Total length 37.80–45.10; interocular space 4.05–4.65; interantennae space 4.00–4.20; pronotum maximum length 11.50–12.50; pronotum maximum width 13.00–15.80; Fw costal margin length 9.00–10.00; Fw anal margin length 7.00–9.00; Fw basal width 5.00–8.00; intertegminal space 2.62–6.06.

**4.3.1.3.1.4 Diagnosis.** General body coloration dark brown to black, with a longitudinal pale-yellow band on abdominal tergites; dorsal surface of pronotum and DHP dark red to black; tegmen subelliptic, black with costal margin brown, mesonotum and metanotum black; arolium well-developed, large; dorsal surface of abdomen dark with a broad reddish-brown band medially, all segments with numerous whitish-yellow callosities, more dense mesially on pale band. The broad longitudinal pale-yellow band on abdomen resembles that of *Bionoblatta marcelli* **sp. nov.**, but tegmen in *B. diabolus* are narrower and black (wider and reddish-brown in *Bionoblatta marcelli* **sp. nov.**), as well as arolium is large and prepuce has few spines (arolium vestigial and prepuce with several lines and columns of spines in *Bionoblatta marcelli* **sp. nov.**).

**4.3.1.3.1.5 Remarks.** The holotype of *B. diabolous* was collected by Augustin François C. P. de Saint-Hilaire. Specimens collected by him have round labels, which are categorized by color or numbering, those categories reefers to the region of collection locality (Papavero 1971). The white label of the holotype (Fig. 1A) indicates that it comes from Rio de Janeiro/Captaincy of Rio de Janeiro (see Papavero 1971). Therefore, most likely the collection site is near the Rio de Janeiro municipality, different from the type locality Serra da Bocaina such was proposed by Gurney (1955: 273). Although Saussure (1864a) referred to the last abdominal segments as black, the supraanal plate of the holotype also has yellow areas (Fig. 1A).

Vanschuytbroeck (1969: 5) listed 40 specimens identified as *Bionoblatta diabolous* held in the Royal Belgian Institute of Natural Sciences, Brussels, Belgium (RBINS). We examined photos of these specimens kindly sent by Jérôme Constant and we concluded they don't belong to *Bionoblatta*.

The identity of *B. diabolus*, thus its intraspecific limits are still inconclusive. When reviewed the genus Gurney (1955) not examined the holotype, and the male studied and illustrated by him (his fig. 9) differs from the original description and the holotype. The series examined by us consists of two males from Rio de Janeiro State held in DZRJ and DZUP. They show minor to major differences from the holotype and one each may be associated with either Saussure' or Gurney's specimens. The specimen from Mauá municipality (DZUP 267084) agrees fair-well with Saussure (1864b *apud* Gurney, 1955) while that from Paraty (DZUP 267084) differs significantly

from the diagnosis. This specimen has vellow callosities while they are white on the holotype and the two last abdominal segments are yellow while they are black on the holotype. From the other side the specimen from Mauá in DZRJ has a yellow spot at anterior portion of pronotum while the pronotum is entirely black on the holotype, and the large longitudinal band on abdomen is brown (most likely due preservation condition) while it is reddish-brown on holotype, the posterior area of supraanal plate is yellow (black on the holotype). These males herein studied also have differencessignificantly each other, as the shape of tegmen (Mauá's male it is narrow with a wide intertegminal space, however in the Paraty's specimen is wider and larger with a narrower intertegminal space), the coloration of venter of abdomen (it is black in Mauá specimen and yellow in the Paraty specimen); the subgenital plate is longer in Paraty specimen; the anterior tip of L2vm is more rounded in Mauá specimen and quadrangular in Paraty specimen, the posterior tip are slightly different (the left portion of L2d is rounded at Mauá specimen and quadrangular in Paraty specimen); the amount of the spines and place in relation to L2d are similar at both specimens. In despite of these differences, we tentatively proposed the male of Paraty as being no more than a morphological variation of the B. diabolous (see discussion section). In addition, the specimen studied by Gurney (1955: fig. 9) is herein considered as from the same morphotype as Paraty specimen, because they share many characters including the large and rounded tegmen and coloration of abdomen.

**4.3.1.3.1.6 Distribution.** The type locality is most likely in highlands areas near of Rio de Janeiro municipality, Rio de Janeiro State, Brazil. This species has been recorded to Mauá and Paraty municipalities in the state of Rio de Janeiro State and São José do Barreiro municipality in the São Paulo.

#### 4.3.1.3.2 Bionoblatta hylaeceps (Miranda Ribeiro, 1936)

(Figs: 1B, 2B, 7)

Zoobank: http://zoobank.org/NomenclaturalActs/025457AE-67E6-47D3-87F4-C8D6E3E68093

- Parahormetica hylaeceps Miranda Ribeiro, 1936: 218–219, fig. 2 (description of male holotype from Mariana municipality, Minas Gerais State in MNRJ); —Camargo-Andrade (1937: 794, mention); —Princis (1963: 118, catalog); —Rocha e Silva Albuquerque (1964: 5, checklist to Brazil, mistakenly recorded to Rio de Janeiro State); —Rocha e Silva (1982: 3, mistakenly recorded to Rio de Janeiro State); —Pelles and Grandcolas (2008: 57, catalog); —Lopes et al. (2009: 231, mistakenly recorded to Rio de Janeiro State).
- *Bion mastrucatus* Rehn, 1937: 253–256, 258, pl. XIV, XVII, figs. 18, 22, 29 (description of the male holotype from Serra do Itacolomi, state of Minas Gerais, Brazil in ANSP; ventral view illustration of subgenital plate, photo from dorsal view of habitus holotype and ventral view of the abdomen); —Gurney (1955: 272, mention); —

Vanschuytbroeck (1969: 5, mention); -Zompro and Fritzsche (1999: 212, mention).

- *Bionoblatta mastrucatus* (Rehn, 1937): —Rehn (1940: 60, comb. nov.); —Rocha e Silva Albuquerque (1964: 5, record to Minas Gerais).
- *Bionoblatta mastrucata* (Rehn, 1937): —Gurney (1955: 272, 277, remarks about type locality and key); —Rocha e Silva Albuquerque (1957: 408, key modified from Gurney (1955) and synonymy list); —Princis (1963: 119, catalog); —Pelles and Grandcolas (2008: 48, catalog).
- *Bionoblatta hylaeceps* (Miranda Ribeiro, 1936): —Polizeli and Pinto (2024a: 280, comb. nov. and taxonomic discussion); —Polizeli and Pinto (in press, syn. nov.).

**4.3.1.3.2.1 Type material of** *Parahormetica hylaeceps.* **Holotype** (by monotypy): BRAZIL • 13; Minas Gerais State, Mariana municipality; José Pinto da Fonseca leg.; MNRJ 14250. Lost in the fire of 2018 (Polizeli and Pinto, in press).

**4.3.1.3.2.2.** Male measurements (mm). Data from Miranda-Ribeiro (1936) and Rehn (1937). Total length 35.0-35.5; Pronotum maximum length 12; Pronotum maximum width 16.9-19; Tegmina length 10.5.

4.3.1.3.2.3 Diagnosis. This species was diagnosed by Polizeli and Pinto (in press), except by the comparison with newly introduced species the diagnosis presented here is very similar. General body coloration dark and reddish-brown; rounded dark brown tegmina with reddish-brown humeral area, its large leaving a small intertegminal space; mesonotum and metanotum liver brown, each crossed by a narrow wavering band of zine orange; arolium small; dorsal surface of abdomen dark brown with a narrow reddish-brown lateral borders, densely rugged with few and minute callosities. Dorsal surface of pronotum dark with the coloration of discal inner area, medially of DHP and an elongated spot external to the DHP ranging from auburn to testaceous yellow, which may help in the identification, but can resembles B. punctata (Saussure, 1873) also due dark coloration and irregular surface of abdomen. It can be distinguished from *B. punctata* by the rounded dark brown tegmina with reddish-brown humeral area (black in *B. punctata*), and large tegmina leaving a small intertegminal space; liver brown mesonotum and metanotum, abdomen dark brown narrowly bordered of reddish-orange dorsally and legs reddish-brown. Bionoblatta marcelli sp. nov. also have a large and wide tegmina with a short or null intertegminal space similar to B. hylaeceps, but can be differentiated from it by the auburn to testaceous yellow areas of pronotum and dorsal surface of abdomen dark brown with a narrow reddish-brown lateral borders.

#### 4.3.1.3.2.4 Remarks.

The holotype of Parahormetica hylaeceps was lost in the fire of 2018 (see Polizeli and Pinto, in

press). Due to the inalterability of the type specimens of each specific name (article 72.9; ICZN, 1999), the holotype of *Bion mastrucatus* is the specimen designed by Rehn (1937: 253). This specimen is at the Academy of Natural Sciences of Philadelphia, USA (ANSP). For more detailed information about morphological characteristics, provenance of type specimens, synonyms and biological information check Polizeli and Pinto (in press). Virtually the entire knowledge about this species was constructed based on two males collected by José Pinto da Fonseca in the 1910s. Despite that the male morphology is well-studied, females and nymphs are yet unknown.

**4.3.1.3.2.5 Distribution.** The type locality is "Serra do Itacolomi" at Mariana municipality, Minas Gerais State, Brazil. See Polizeli and Pinto (in press) for additional data on the distribution of this species.

# 4.3.1.3.3 Bionoblatta itatiayae (Miranda Ribeiro, 1936)

(Figs: 1C, 2C, 5C, 7)

Zoobank: https://zoobank.org/NomenclaturalActs/6F3165A1-5187-438D-AFD6-DA87D6DC2011

Hormetica itatiayae Miranda-Ribeiro, 1936: 217–218, f. 1 (syntypes description, from Itatiaya, Minas Gerais State).
Bionoblatta itatiayae (Miranda-Ribeiro, 1936): —Gurney (1955: 272, 274-276, f.5-8, designation of lectotype, key, description, note about type locality, photo of habitus, illustration of tegmina, supraanal and subgenital plates);
—Rocha e Silva (1957: 408, key and catalog); —Princis (1963: 119, catalog); —Rocha e Silva Albuquerque (1964: 5, checklist to Rio de Janeiro State); —Roth (1970b: 335, 339, figs. 174, 209–211, photo from habitus and genitalia of specimen from Serra do Itatiaia); —Roth (1971: 137, mention); —Pelles and Grandcolas (2008: 48, catalog); —Lopes et al. (2009: 230, record from Rio de Janeiro State); —Polizeli and Pinto (in press, mention).

**4.3.1.3.3.1 Type Material: Lectotype** (fixed by Gurney, 1955: 275). **BRAZIL.** • 1♂; Rio de Janeiro State, Itatiaya [municipality], Mont-Serrat; [-22.4525, -44.6075, 834 m a.s.l.]; 02 Mar. [1]921; [illegible], Lobo leg.; (MNRJ-ENT2-12, MNN 542). Type repository MNRJ (lost in the fire of 2018 that affected MNRJ—SIBBr 2024). Examined by photos (Fig. 1; photos by Department of Entomology, MNRJ).

**4.3.1.3.3.2 Other material examined. BRAZIL.** • 1♂; Rio de Janeiro State, Itatiaia municipality; Jun. [19]54; J. L. Lima leg.; MZSP 0992 • 1♀; Mina Gerais State, Itamonte municipality, Parque Nacional do Itatiaia, Brejo da Lapa; -22.3590, -44.7372; 2142 m a.s.l.; 13 Jan. 2023; AP Pinto, AC Domahovski, J Ehlert & LP Aguiar leg.; active collect; DNA SAMPLE LABSIA 516; DZUP 267064; (Fig. 5C) • 1♀; São Paulo State, Cruzeiro municipality, Serra da Mantiqueira; 22°29'47"S,

45°09'11"; Nov. 2013; W Hans Tomassen leg.; embaixo de pedra com apróx. 20 indivíduos agregados; (UFMG IBL 230008). 1 male, without data (CEOIC 42315—[invalid catalog number, CEOIC curator Márcio Felix 2022, personal communication]).

**4.3.1.3.3.3 Measurements (mm). Male (n = 1):** Total length 32.00; interocular space 4.05; interantennae space 3.75; pronotum maximum length 11.50; pronotum maximum width 13.00; Fw costal margin length 7.00; Fw anal margin length 8.00; Fw basal width 6.00; intertegminal space 4.00.

Female measurements (mm, n = 1): Total length 31.00; interocular space 3.50; interantennae space 3.35; pronotum maximum length 10.50; pronotum maximum width 11.00; Fw costal margin length 7.00; Fw anal margin length 6.00; Fw basal width 4.00; intertegminal space (not measured due tegmina position).

**4.3.1.3.3.4 Diagnosis.** General body coloration black and dark reddish, abdomen dorsally brown to dark red; surface of pronotum black with the DHP dark red, sometimes with a yellow spot external to the DHP; sub oval black tegmina, narrow with large intertegminal space; meso- and metanotum black; dorsal surface of abdomen entirely brown to dark red, some individuals black on the fS1 or sparse in other segments; arolium large. The narrow tegmina easily distinguish *B. itatiayae* from *B. hylaeceps* and *Bionoblatta marcelli* **sp. nov.** The coloration of pronotum, mesonotum, metanotum, and tegmina of *B. itatiayae* are very similar to *B. diabolus*. The entire brown to dark red abdomen helps easily distinguish *B. itatiayae* from *B. diabolus*, also *B. hylaeceps*, *B. punctata* and *Bionoblatta marcelli* **sp. nov.**, but specimens with brown abdomen can resemble specimens of *B. oiticicai*, which *B. itatiayae* can be distinguished by the black coloration on pronotum, mesonotum, metanotum, metanotum, and tegmina.

**4.3.1.3.3.5 Remarks.** The lectotype labels (Fig. 1C) do not contain a label with the N° Proc 11426– 11428 or 14248, cited by Miranda-Ribeiro (1936: 218), this could raise doubts about whether this specimen was part of the type series. However, other specimens collected by Bruno Lobo at Mont Serrat on March of 1921 (e.g., MPEG DIC 18000948—*Hormetica* sp.) have labels with N° Proc (14253) very close to that of lectotype. Therefore, due to the provenance label of the lectotype we were able to associate it with the "N° Proc" labels cited by Miranda-Ribeiro (1936). Even though the "N° Proc" label was not included in the photo, what would be a clear proof that the lectotype was part of the type series, clearly Gurney (1955: 275) made a valid lectotype designation.

The abdomen of the lectotype is brown (Fig. 1C), but some specimens analyzed have reddish-brown to dark red abdomen with shades of black. The dorsal surface of the abdomen of

males and females are rugose, but males have yellowish-white callosities mesially.

An adult female (DZUP 267064) was found solitary in a cavity of a rotten trunk of 5–10 cm diameter, during the day at a cold weather. This trunk had a several fans above, it was still upright but was not live and was broken to find the specimen. The female was reared for approximately one month after collection, but no immature forms were born. According to the label of the UFMG IBL 230008 specimen, it was found approximately 20 individuals together under a rock, but we don't know if the aggregate was of males and females adults, adult females with nymphs, adult males or adult males with nymphs. This information may indicate that at some stage of life these cockroaches live as gregarious.

**4.3.1.3.3.6 Distribution.** The type locality is the old farm of Mont-Serrat, currently the region of the visitors' center at the lower part of the National Park of Itatiaia, Itatiaia municipality, Rio de Janeiro State, Brazil. This species is recorded from Itamonte (Minas Gerais State), Itatiaia (Rio de Janeiro State), and Cruzeiro municipalities (São Paulo State).

#### 4.3.1.3.4 Bionoblatta marcelli sp. nov.

(Figs: 3A-E, 5A-B, 6A-D, 7)

Zoobank: https://zoobank.org/NomenclaturalActs/683396E9-2154-423C-983B-958867E020B7

**4.3.1.3.4.1 Type Material Examined: Holotype. BRAZIL** • 13; Minas Gerais State, Catas Altas municipality, [Serra do Caraça], Pico do Inficionado; [-20.1347, -43.4513]; 2.050 m a.s.l.; Campo Rupestre; 04 May 2012; M. F. Vasconcelos leg.; DZUP 267083 ([ex]MCN-INV 289, MCN-INV B01); type repository DZUP (Fig. 3). Paratypes (7 females, 7 males) • 1 $\paratephi$ ; same data of the holotype but Serra do Caraça, Pico do Inficionado; 2.050 m a.s.l.; 13 Aug. 1999; Campo rupestre, sob pedra; M. F. Vasconcelos [leg.], collection number 600; UFMG IBL 230006; • 13; same data but 1.950 m a.s.l.; 11 Out. 1999; collection number 601; UFMG IBL 230005 • 13; same data but 2.020 m a.s.l.; 22 Mar. 2000; UFMG IBL 2300001 • 333; same data but 1.940 m a.s.l., 23 Mar. 2000; UFMG IBL 2300004 • 13; same data but 2.050 m a.s.l.; 02 May 2012; MCN-INV 288, MCN-INV B02 • 13; same data but 03 May 2012; MCN-INV 287, MCN-INV B05 DZUP267082 • 1 $\pmphi$ ; same data but 04 May 2012; MCN-INV 291, MCN-INV B03 • 1 $\pmphi$ ; same data but 20°07'S, 43°27'W; 03 Nov. 2017; MCN-INV B04 • 2 $\pmphi$ ; same data but 20°08'05"S, 43°27'05"W; 19 Set. 2021; MCN-INV B195 and B196 (DZUP267081). • 1 $\pmphi$ ; Minas Gerais State, Santa Bárbara municipality, Faz. Bocaina; 20°00'02"S, 43°28'16"W; 751 m; 24–26 Aug. 2018; I. SARAIVA leg.; active collection;

**4.3.1.3.4.2. Other material. BRAZIL.** • 1 nymph; Minas Gerais State, Catas Altas municipality, Serra do Caraça, Pico do Inficionado; 1.950m; 24 Nov. 1999; M. F. Vasconcelos [leg.], collection number 610; campo rupestre, sob pedra; UFMG IBL 230007;

**4.3.1.3.4.3 Diagnosis**. General body coloration orange, pronotum dark, and abdomen with a yellow longitudinal band on dorsally; pronotum dark red to black, with dark red carinated margins, DHP dark red to black; sub rectangular orange tegmen, wide and large, with a narrow intertegminal space (tegmina may touching mesially Fig. 3A, 5A); visible parts of meso- and metanotum reddish-brown to dark brown; arolium small; abdominal tergites orange brown to dark red with a broad yellow to yellowish-red longitudinal mesial band, numerous yellow to whitish-yellow callosities, mainly on band. The abdominal coloration easily allow distinguish this species from *B. hylaeceps*, *B. itatiayae*, *B. punctata* and *B. oiticicai*. The broad yellow band on abdomen can be similar to *B. diabolus*, but *Bionoblatta marcelli* sp. nov. have a large subretangular orange tegmina.

#### 4.3.1.3.4.4 Description of the male holotype

Head (Fig. 3B). Head mostly dark brown, oval shape, with the maximum width at anterior region of reniform eyes; punctures concentrated on posterior region of the frons and in the occipital region; a median black stripe from the postclypeus to the suture in the middle of the face; minute yellow spot in the ocellar region; labrum with a long black band, covering 0.8 the width of the sclerite, anterior and posterior margins yellow; anteclypeus brown, lateral margins and a central line from anterior to posterior margin yellowish, two black lines at anterior margin; postclypeus anterior half dark brown to black, a median black irregular mark from anterior portion of postclypeus to the middle of frons; lateral regions of frons orange-brown; postclypeus and frons slightly wrinkled; maxillary and labial palps dark brown to black with golden hair-like setae, more numerous on the last segment of palp; gena black; mandible proximal part orange-brown and distal part dark-brown; anterior tentorial pit black; antennifer yellowish-white, edge of antennifer and surrounding area black, scape dark brown with distal margin yellow, pedicel black, first flagellomere approximately 1.5 times the size of the pedicel and larger than the rest of the flagellomeres, 2-8 flagellomeres rectangular, wider than long, with many punctures and shiny, next flagellomeres dull with many white setae, proximally very flattened and flagellomeres distally longer than wide, 4 terminal segments wedge; intraocular space same distance to the intra-antennal space.

Thorax (Figs. 3A-3B). Pronotum large, reddish-brown, dark red to black colored, very

sculptured, covering the head dorsally, about as wide as abdomen in dorsal view; margins reddishbrown to dark red, discal horseshoe-like process (DHP) dark red, remaining of the surface black, including most of discal inner area (DIA); hemisphere-shaped, 1.4 times wider than long; margins carinated, thickener at posterolateral angles, anterior margin convex and upwards mesially, posterior margin almost straight, downward laterally, ending an obtuse posterolateral angle; external surface to the disk covered with numerous deep punctures; discal inner area heavily sculptured by elongated, sinuous dark red processes, diskal horseshoe-like process (DHP), wider than long, discal anterolateral tubercle-like processes (DTP) protruded into a large smooth hill-like dorsoposterior tubercle, with scattered minute punctures; ventrally pronotal surface yellow with black dots, darkening to brown mesially covered by scattered short hair-like setae, margins orange.

Visible part of mesonotum reddish-brown. Tegmen reddish-orange with irregular brown areas at margins, and dark brown to black humeral trunk; surface rough, with dense and deep punctuation; base of humeral trunk thick with a deep humeral groove; reaching the anterior margin of S2, anal margins basally separated (with a very short intertegminal space), in contact toward to tip mesially, left tegmen slightly overlapping the right one; roughly square-shaped with rounded angles, anal margin and costal margin convex, costal carinated, marginal field downward. Metanotum and hind wing covered by tegmina.

Legs pale, orange red to orange brown with irregular yellow areas on coxae, dark brown on articulations, carinae, sutures, around to setal socket and trochanter, black mark on the anterior suture; femora brown-orange to orange, with dark brown antero-ventral and posteroventral margins, on meso- and meta femur a thin brown ill-defined line close to dorsomedial region, anteroventral margin of profemur with five piliform setae equidistant each other on proximal half and a fringe of piliform setae on distal half, a submarginal short dark brown spur distally (similar to the armament type C1 sensu Roth 2003); on meso- and metafemora with scattered setae and a submarginal spur distally, posteroventral margin of the profemur with few hair-like setae, meso- and metafemora with several hair-like setae; a single dorsoapical spur on meso- and metafemora; tibia orange-red covered by strong spurs, reddish-orange basally, tip black reddish brown on posterior region of the pro tibiae; Tarsus dark brown to black, first tarsomere brown, reddish-brown basally on the meso- and metatarsi, the first and fifth longer than 2–4 together; pulvilli yellowish-orange, right meta leg the first and second pulvilli abnormally dark brown, fifth tarsomere with a medial yellow-orange carina taking the place of puvillus; pretarsal claws dark brown, symmetrical and simple (unspecialized sensu Roth 2003), minute arolium (vestigial).

**Abdomen** (Figs. 1A–D). Dorsally with a mesial yellow band throughout, as wide as 0.4 of abdomen, with several callosities, except on supraanal plate; the ellipsoid-shaped callosities arranged into 2–3 rows close to each other; lateral regions rough, orange brown with few scattered

small yellow callosities. Tergites rectangular-shaped dorsally, posterior margin slightly sinuous convex on S2 gradually changing to concave on S8, protruded into an acute angle with a blunt tip at lateral edge; tergite of S1 under tegmina; T4 wider, with posterior margin almost straight. Supraanal plate yellow with irregular dark areas mesially and orange posterior margin, overlapping entirely the subgenital plate in dorsal view, posterior margin slightly bilobed, sparse tiny setae. Cercus somewhat flat, in dorsal view extended slightly beyond of the supraanal plate, maximum width at midlength slightly tapering toward to tip, dark brown on inner surface and light brown in outer surface, sutures dividing segments visible, the last segment triangular with rounded margins, in ventral view black covered with yellow minute callosities and numerous spike-like and hair-like setae, last two segments light brown with fewer setae. Sterna smooth, brown to orange, with irregular orange spots and sinuous lines in a reticulated pattern mesially at S2–4 and throughout S5–6; Subgenital plate with posterior margin upward, rounded and asymmetric to the left side, anterior region orange brown with irregular brown areas, lightening to orange posteriorly, marginally with yellow line, thicker in left style insertion; style orange brown of similar size.

#### 4.3.1.3.4.5 Morphological variation

Only differences from the holotype are reported here.

**4.3.1.3.4.5.1 Males paratypes. Holotype measurements (mm).** Total length 27.0; interocular space 3.65; interantennae space 3.60; pronotum maximum length 9.00; pronotum maximum width 13.00; Fw costal margin length 7.5; Fw anal margin length 7.5; Fw basal width 7.0; intertegminal space 1.75. Male paratypes are very similar to holotype, but in some the head is lighter colored, tegmina not touching mesially, tergites with brown marks on the yellow band, with larger brownish areas instead of yellow areas, or paler than holotype with yellow areas larger and smaller black spots.

**Head**. Head orange brown, without dark marks from the postclypeus to the occipital region; labrum black or with anterior margin light-brown; postclypeus anterior half (0.50) orange brown to brown, the median black irregular mark almost absent, just a small dark line at the middle of the anterior region of frons; gena orange-brown to brown; mandible proximal part brown; scape distal margin dark brown.

**Thorax.** Width 1.2 to 1.5 times greater than length; disc with thick and sinuous black raised lines without a defined shape; pronotum ventral surface, mesially orange brown with black dots. Tegmen slightly separated, light brick red at posterior margin and anal region dark red; mesothorax brown to black in visible parts between tegmina.

Metafemur without a thin brown ill-defined line close to dorsomedial region; anteroventral margin of the pro femora with 1–3 spurs proximally; tibia dark red-brown, spurs dark red; brown to black pulvilli; 5 tarsomere yellow; pretarsal claws black to black at base and red in tip.

Abdomen. Tergum with the central yellow band with brown lines, lateral regions orange brown with black marks. Supraanal plate yellow to red with a black mark from median to posterior margin, anterior margin orange, posterior margin not overlapping the tip of the subgenital plate. Cercus, yellow tip; in ventral view, brown to black; sternum with almost absent orange lines and dots or with marks larger than those on the holotype. Subgenital plate anterior region orange to dark-brown, stylus black.

**Genitalia** (Figs. 6A–D). The male genitalia of the *Bionoblatta marcelli* **sp. nov.** paratype differs from other *Bionoblatta*'s, it has posterior tip of L2vm arrow shaped with an acute angle on posterior margin; sinuous posterior margin of the phallomere L2d with a small lobe-process on right portion; the posterior margin of the prepuce with several lines and columns of small to median robust spines; R2 and L1 are very similar with other *Bionoblatta* and *Parahormetica*.

#### 4.3.1.3.4.5.2 Females (Fig. 5A). General coloration darker than males.

**Head.** Head darker or lighter than holotype; from small dark brown marks to totally dark brown to black from the postclypeus to the occipital region; black in the ocellar region; anteclypeus lateral margins brownish; postclypeus black; dark brown to black lateral regions frons; gena dark-brown; mandible proximal part brown or completely black; antennifer white; from surrounding area of antennifer to the mandible black, scape black.

**Thorax.** Pronotum width 1.5 times greater than length; posterior region black; some females have black raised lines at disc and black elevated horseshoe-like process, the rounded hill-like tubercle anterolateral region of DHP at females are smaller than males; pronotum ventral surface dark brown.

Tegmina slight separated or with right tegmina overlapping the left (due preservation?), marginal field orange as tegmina, light red brick at posterior margin and anal region dark red; brown to black mesothorax visible in a small space between tegmina; tegmina posterior angles straighter.

Coxae dark brown to black; femora antero-ventral and posteroventral margins orange; tibia dark brown to black, spurs dark red; tarsomeres black; whitish-yellow pulvilli.

Abdomen. Tergites callosities not close to each other as on the holotype; the central yellow band with brown lines; lateral regions dark red with black marks; Supraanal plate not overlapping the tip of the subgenital plate, posterior margin with orange marks, posterior margin rounded without sparse tiny setae inserted at orange points; Cercus in dorsal view black, with tip brown, not reaching the tip of supraanal plate, segments in cercus ill-defined, cercus in ventral view black with dark-brown tip; Sternites dark red with black spots laterally, black marks at T1 and T2; Subgenital plate very broad, symmetrical, reddish to light-brown, anterior margin with a black disform band covering almost entire length of the sclerite or a black spot laterally.

**4.3.1.3.4.5.3** Nymph (Fig. 5B). The nymph is very similar to the adults but can be differentiated because it does not have great sculpturation in pronotum, wings, nor the yellow band on the abdomen.

**Head**. Head dark brown to black, without a median black stripe at the face as the holotype; labrum black; postclypeus dark brown; frons concave with a carina Y-shaped, dark brown to black; mandible dark-brown; from surrounding area of antennifer to the mandible black, scape dark-brown, 2–11 flagellomeres shiny, terminal flagellomeres not present/broken.

**Thorax.** Pronotum dark red, bordered by punctures; 1.5 times wider than long; margins carinated, orange; posterior margin almost straight with lateral ending acute at the connection with the lateral margin; disk with a pattern of dark red marks similar the raised sculptures in adults, but without raised lines, portions and horseshoe-like process, with a minute elevation of the rounded hill-like tubercle at anterolateral region of DHP; ventral surface of pronotum yellow.

Mesothorax rectangular (4.3 times wider than long), mostly red with sparse punctures; anterior region with dark red to black shapeless marks; anterior margin covered by pronotum, lateral margins carinated and slightly curved; posterior margin convex (from anterior to posterior direction); metathorax similar to the mesothorax, but anterior margin covered by the mesotórax and posterior margin with a little curve, forming a little vertex in the center of the margin.

Legs yellow to dark brown; coxae brown, meso- and meta coxae with yellow tip; trochanter yellow; femora yellow at proximal margin and in posterior region, brown distally; tibiae dark brown, spurs and tarsi as the holotype, whitish pulvilli.

**Abdomen.** Tergites dark red to black, with orange callosities in the medial region and posterior region; anterior region of each tergite with a black band; Supraanal plate as holotype; Cerci, in dorsal view, black with dark brown tip, not reaching the tip of supra-anal plate, segments ill-defined, cerci in ventral view black with dark-brown tip; Sternites orange to dark red with black spots laterally in each segment; subgenital plate of size of males, rounded and symmetric, red with small black dots and lines; style orange-brown of similar size.

**4.3.1.3.4.6 Measurements (mm). Holotype.** Total length 27.0; interocular space 3.65; interantennae space 3.60; pronotum maximum length 9.00; pronotum maximum width 13.00; Fw costal margin length 7.5; Fw anal margin length 7.5; Fw basal width 7.0; intertegminal space 1.75.

**Male paratypes (n = 5).** Total length 29.50–33.00; interocular space 3.65-4.55; interantennae space 3.40-4.05; pronotum maximum length 9.20-11.00; pronotum maximum width 13–15.5; Fw costal margin length 6.0-9.5; Fw anal margin length 8.00-9.50; Fw basal width 5.00-9.00; intertegminal space 0.75-2.75.

Female paratype (n = 5). Total length 25.00-32.0; interocular space 3.25-3.50; interantennae space 3.05-3.35; pronotum maximum length 7.50-9.00; pronotum maximum width 11.00-13.00; Fw costal margin length 5.00-6.50; Fw basal part of anal margin length 6.00-7.00; Fw basal width 5.00-7.00; intertegminal space 0.50-2.25.

**Nymph** (n = 1). Total length 30.0; interocular space 3.95; interantennae space 3.56; pronotum maximum length 9.50; pronotum maximum width 13.00.

**4.3.1.3.4.7 Etymology.** Specific name marcelli (genitive singular), from the classical Latin origin Marcellus a masculine name diminutive of Marcus. We honor Marcelo Ferreira de Vasconcelos, the collector of the type series, whose efforts resulted in a great series of specimens of the new name group proposed in this work. Examining these specimens, we have advanced our understanding of intraspecific morphological variations and made the first-ever association of a nymph with a species of the genus *Bionoblatta*.

**4.3.1.3.4.8 Remarks.** Marcelo Vasconcelos (2023–2024, personal communication) provided rich notes about the collection habitat, and we reproduce in free translation below. "These specimens live in the accumulation of organic matter under stone slab in the highest points on the region of Peak of Inficionado, Serra do Caraça, Catas Altas municipality, Minas Gerais State, between 1,900 and 2,050 m a.s.l. All specimens were always found alone under the stone slabs. These stone slabs occur in rocky outcrops exposed to intense sunlight and orographic mist and are covered by rupestrian field vegetation predominantly composed of *Vellozia compacta* Mart. ex Schult. & Schult.f. (Velloziaceae), *Vriesea marceloi* Versieux & T.M. Machado (Bromeliaceae), *Hippeastrum carassense* Campos-Rocha & R.C. Mota (Amaryllidaceae) e *Phlegmariurus ruber* (Cham. & Schlecht.) B.Øllg. (Lycopodiaceae). Epiphytic specimens of *Sophronitis coccinea* (Lindl.) Rchb.f. (Orchidaceae) may occur on *V. compacta*". Marcelo also states that all specimens were collected solitary, information that may provide an indication of the putative solitary behavior of this species.

**4.3.1.3.4.9 Distribution.** The type locality is the "Pico do Inficionado", Catas Altas municipality, Minas Gerais State, Brazil. Almost all specimens were collected at this same locality, but a female was recorded from Santa Bárbara municipality near Catas Altas municipality.

#### 4.3.1.3.5 Bionoblatta oiticicai Rocha e Silva, 1957

(Figs: 1D, 2D, 7)

Zoobank: https://zoobank.org/NomenclaturalActs/355ab31b-45b6-4a63-a045-488f38a5101e

Bionoblatta oiticicai Rocha e Silva, 1957: 406–408, fig. 1–5 (description of male holotype from Pirassununga, São Paulo State, Brazil, photo of habitus, illustration of arolium, subgenital, supraanal plates and hind wing); — Princis (1963: 120, catalog); —Rocha e Silva Albuquerque (1964: 5, checklist to Brazil); —Lopes and Oliveira (2000: 4, information about holotype); —Pelles and Grandcolas (2008: 58, catalog); —Polizeli and Pinto ( in press, mention).

**4.3.1.3.5.1 Type Material Examined. Holotype** (by original designation). **BRAZIL.** 1∂; São Paulo State, Pirassununga municipality; Mar. [1]944; N. Santos leg.; N° 581 Proc. 446, M.N N. 545, 36, 11, MNRJ-ENT2-11. Type repository MNRJ (lost in the fire of 2018 that affected MNRJ). Examined by photos (Figs. 1D, 2D; photos by Department of Entomology, MNRJ).

**4.3.1.3.5.2** *Male measurements (mm).* Data from Rocha e Silva Albuquerque (1957). Total length: 38–39.

**4.3.1.3.5.3 Diagnosis.** General body coloration brown; dorsal surface of pronotum with dark red carinated margins, brown margins areas, DHP red, surrounding by black, disk brown, clearly bilateral divided with large black marks, lines, and dots; tegmen brown with a black spot on anterior margin, subelliptic, narrow with a large intertegminal space; meso- and metanotum brown, laterally with broad black bands; arolium large; abdominal tergites brown with lateral black marks on S1. The narrow tegmina distinguishes it from *B. hylaeceps* and *B. marcelli* **sp. nov.** The brown abdominal coloration help to easily distinguish *B. oiticicai* from *B. diabolus*, *B. hylaeceps*, *B. punctata* and *Bionoblatta marcelli* **sp. nov.**, but it is shared with some specimens of *B. itatiayae*, from which *B. oiticicai* can be distinguished by the brown coloration on pronotum, mesonotum, metanotum, and tegmina (black in *B. itatiayae*).

**4.3.1.3.5.4 Remarks.** Further to the holotype, which was lost during the fire on MNRJ in 2018, no additional specimen of *B. oiticicai* was found in other collections. The holotype was collected in Pirassununga by the eminent odonatologist Newton Dias dos Santos, unfortunately the labels lacking indication a specific locality. This municipality has 727,118 km<sup>2</sup> (IBGE, 2024) and is in an ecotonal area between Atlantic Forest and Cerrado phytophysiognomies. Newton Santos collected in several localities of this municipality in 1944, at least in the Estação Experimental de Caça e

Pesca (nowadays Centro Nacional de Pesquisa e Conservação da Biodiversidade Aquática Continental-CEPTA), Laranja Azeda and Rio Jaguari (see collection localities in Santos 1945, 1953). Lopes and Oliveira (2000) mentioned that the holotype was collected at an anthropic savanna. In 2023, we were in Pirassununga for a collecting expedition with duration of five days, our efforts were focused on CEPTA area, but we were unable to collect any specimen of *B. oiticicai*.

**4.3.1.3.5.4 Distribution.** *Bionoblatta oiticicai* is known just from its type locality, Pirassununga municipality, São Paulo State, Brazil.

#### 4.3.1.3.6 Bionoblatta punctata (Saussure, 1873)

(Figs: 4A, 5D, 6M-P, 7)

Zoobank: http://zoobank.org/NomenclaturalActs/EBD3F1B3-2E17-4AC7-B5FA-993931A09013

- Parahormetica punctata Saussure, 1873: 145–146 (description, material-type from Brazil); —Finot (1897: 218, catalog); Kirby (1904: 198, catalog); —Princis (1963: 118, catalog); —Rocha e Silva Albuquerque (1964: 4, record to Brazil); —Pelles and Grandcolas (2008: 58, catalog).
- *Bionoblatta punctata* (Saussure, 1873): —Polizeli and Pinto (2024a: 280, comb. nov. and taxonomic discussion); Polizeli and Pinto (in press, taxonomic discussion).

**4.3.1.3.6.1 Type Material Examined. BRAZIL**. Possibly syntypes, but no material from the type series or indication of its repository collection was found (see remarks).

**4.3.1.3.6.2 Other material examined. BRAZIL.** • 1 $\degree$ ; Minas Gerais State, Ibitipoca, Parque Estadual do Ibitipoca, [-21.7117, -43.9029; 1,365 m a.s.l.]; 15 Mar. 2019; Ana Carolina N. [leg.] col.; MNRJ 743 MRNJ-ENT2-2557; (Fig. 4A) • 1 $\degree$ ; same data as for preceding but MNRJ 744 MRNJ-ENT2-2558 • 1 $\degree$ ; same data as for preceding but 3–10 Fev. 2019; Tatiana S. & Ana Carolina N. [leg.] cols; MNRJ 419 MRNJ-ENT2-2209 • 1 $\degree$ ; same state, coordinates and m a.s.l, Lima Duarte municiality, Pq. Florestal do Ibitipoca; 21 Fev. [19]90; F. A. da Silveira [leg.]; UFV.

**4.3.1.3.6.3 Measurements (mm). Male measurements (mm, n = 2):** Total length 27.4–34.0; interocular space 4.05-4.55; interantennae space 3.60-4.00; pronotum maximum length 9.50-11.50; pronotum maximum width 13.00-15.00; Fw costal margin length 7.00-9.00; Fw anal margin length 3.00-4.00; Fw basal width 5.00-6.00; intertegminal space 4.65-5.20.

**Female measurements (mm, n = 2):** Total length 27.0–30.0; interocular space 3.50-4.05; interantennae space 2.60-3.50; pronotum maximum length 8.50-9.00; pronotum maximum width

11.00–12.00; Fw costal margin length 6.00–7.00; Fw anal margin length 3.00–6.00; Fw basal width 4.00–6.00; intertegminal space 4.40–4.50.

**4.3.1.3.6.4 Diagnosis.** General body coloration black, disk dark red to orange, with a yellow spot on lateral of DHP (crescent) and supraanal plate; tegmen black, trapezoidal (strongly similar to *Parahormetica* species), narrow with a large intertegminal space; meso- and metanotum black; arolium small; abdominal tergites strongly irregular, surface densely punctured, lacking callosities, coloration black, in females black with dark red areas. A very distinctive species, unique in have almost entirely black coloration, trapezoidal tegmen and irregular ornamentation of abdomen. Due to the coloration of pronotum and supraanal plate *B. punctata* reassemble *B. hylaeceps*, but the narrow trapezoidal black tegmen and overall black coloration allows distinguished from it.

**4.3.1.3.6.5 Remarks.** *Parahormetica punctata* was described by Saussure (1873) based on specimens from Brazil, including at least a male, he did not mention sex, number of specimens nor deposit collection of the type series (see Saussure 1873). With the goal to investigate the type series of *P. punctata*, we contacted the curators Alexander Riedel (SMNG), Brendon Boudinot and Patricia Peters (SDEI), Birgit Jaenicke (ZMHB), Daniela Matenaar (HLMD), Harald Bruckner (NHMW), John Hollier (MHNG) and Katja Neven (ZSM). Curators from institutions where several type specimens described by Saussure were deposited (see Pellens and Grandcolas 2008) or curators of collections that he mentions at his acknowledges in Mélanges Orthoptérologiques (see Saussure 1873: 2). They did not locate any material corresponding to the type series of *Parahormetica punctata*. Moreover, Hollier checked the databases of the NHMUK and MNHN and did not found specimens of *P punctata* (Polizeli and Pinto 2024a). Therefore, most likely the type series of *P punctata* is lost.

Through comparison with original description (Saussure 1873), we confidently identified the examined specimens as *B. punctata*. The original description and the specimens are very similar and except for minor differences reported below. The examined specimens have black meso- and metanotum, while Saussure (1873) mentions an orange-yellow transversal band that does not cover the posterior margin, and the original description mentions that the DHP is poor protruded while in males the DHP is strongly protruded. If the type series of this species was found, we will know more about a species described 151 years ago. Our material indicates that an evolutionary lineage within the *Bionoblatta* group is associated with the ecosystem characteristics found where Ibitipoca Park is located.

The *Bionoblatta* species have spines at posterior region of prepuce of male genitalia, such as *B. diabolus*, *B. itatiayae*, and *B. oiticicai* have a single line of spines at prepuce, *Bionoblatta* 

*marcelli* **sp. nov.** have more lines of spines (see Fig. 6C). The L2d of the specimens are curved toward the L2vm and almost all analyzed individuals have the L2d unlinked to L2vm. The structures of the genitalia of the dissected individual of *B. punctata* are similar to those expected for *Bionoblatta* (*e.g.*, as small spines, and the L2d curved toward L2vm), however, the L2d is linked with the L2vm (fig. 6O), an unexpected feature (see Discussion).

**4.3.1.3.6.6 Distribution.** The type locality is unknown. All specimens examined are from Minas Gerais State, Ibitipoca municipality, Ibitipoca State Park.

#### **4.4 DISCUSSION**

*Bionoblatta* is a taxonomically distinguishable genus among other Brachycolini genera. The revised composition of the genus includes six species taxonomically recognized. To genus and species delimitation we used morphological characteristics largely used in studies within Blattodea (Hopkins 2014, Li and Wang 2017, Luo et al. 2023), Blaberinae (Tarli et al. 2018) and Zetoborinae (Roth 1970a), and in genera and species of Brachycolini (Vidlička 2019, Polizeli and Pinto 2024a). Males from all species and females from *B. itatiayae*, *Bionoblatta marcelli* **sp. nov.**, and *B. punctata* were utilized to define the species. Also, nymphal stage of *Bionoblatta marcelli* **sp. nov.** was described. However, the females of *B. oiticicai*, *B. diabolus* and *B. hylaeceps* and nymphs of the other five species yet are unkown.

Of the seven available specific names combined with *Bionoblatta*, four have virtually their name bearing types lost —*P. hylaeceps*, *H. itatiayae*, *P. punctata* and *B. oiticiai*. This study was largely beneficiated by projects that promoted the digitization of metadata from specimens and sharing these data (e.g., Projeto Informatização da Coleção Entomológica do Museu Nacional; Cockroach Species File – CSF). In total, we analyzed five name bearing type specimens being that four were thought images. These images of name-bearing types were essential to a better taxonomic delimitation at species level and to assessment the nomenclatural status of specimens. The two nomina that the specimens of the series type were not analyzed because the type series of *P. punctata* remain lost, and the holotype of *P. hylaeceps* was not photographed before being destroyed by the fire at MNRJ, 2018 (Polizeli and Pinto, in press).

We are aware that the proposition of new species must be based on a broad and integrated dataset (see discussion in Silva et al. 2020). Therefore, in this study we proposed *Bionoblatta marcelli* **sp. nov.** based on a large series with adult males and females and a nymph. The strong morphological differences between the specimens herein identified as *B. diabolus* made us consider whether they represent different species. Due to the low number of specimens possibly the intra-

and interspecific variation has not been thoroughly addressed. Therefore, considering guidelines recommended by Dayrat (2005), we decided to consider these morphological differences as intraspecific of *B. diabolus*. We recommend new studies to get additional specimens and data of both populations from the state of Rio de Janeiro and Serra da Bocaina in the states of Rio de Janeiro and São Paulo (see *B. diabolus* section) and assess whether they are the same species. Furthermore, the specific limits of *B. punctata* are starting to be understood due to the associations of specimens with this name based the original description (Saussure, 1873). A male (MNRJ-ENT2-2557) has the L2vm connected to the L2d, this being an unexpected feature for representatives of Brachycolini. However, the connection between these structures has already been documented for *Parahormetica bilobata* (Saussure, 1864), another Brachycolini species (Polizeli and Pinto, 2024a). The implications of this feature to the delimitation of the Brachycolini yet needs to be thoroughly addressed.

The genus yet is poor understood, representatives of the genus were found only in southeastern Brazil. Few occurrence points or just one are known for the species and were used to understand the specific distribution, most likely being an incomplete knowledge about the geographic distribution, such as Wallaccean shortall (Hortal et al., 2015). The low sampling of this material must be due to the under-sampling (see Coddington et al., 2009). As well as there is no phylogenetic hypothesis for the relationships of the species considered Darwinian shortall (Hortal et al. 2015). Although the distribution and speciation within *Bionoblatta* may have been influenced by mountain complexes as proposed by Gurney (1955), both shortfalls can compromise the accuracy, generality, and realism of such inference (the specialization within Bionoblatta is due the emergence of geographic structures-e.g. mountains and rivers. The majority of collected specimens were found solitary in the adult stage, what can mean that the representatives of this genus can be of solitary behavior on adult stage. Although a female of B. itatiayae (UFMG IBL 230008) was observed with other 20 individuals grouped (not all were collected), this may be the case of a female with the breed. Moreover, Bionoblatta marcelli sp. nov. specimens were found under accumulation of organic matter under stone slab and B. itatiayae was found inside dead wood or under rock, this can indicate the habitat of the representatives Bionoblatta are under or inside habitats with organic matter. However, we reinforce the suggestion that new studies must be elaborated with efforts to sample representatives of this genus.

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#### Nomenclature

Zoobank registration number

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## **Author Contribution**

Both authors contributed to the conceptualization, formal analysis and revision of the manuscript. LP was responsible to the original draft, data curation and visualization of results. All authors approved the final draft of the manuscript.

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#### Declarations

The authors declare no competing interests.

#### **Data Availability**

All data supporting the findings of this study are available within the paper, listed as material examined and references.

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**Fig. 1**. Habitus dorsal and labels of the name-bearing specimens of *Bionoblatta* **A**. Holotype of *Brachycola diabolus* **B**. Holotype of *Bion mastrucatus*. **C**. Holotype of *Hormetica itatiayae*. **D**. Holotype of *Bionoblatta oiticicai*. Copyights at Materials and Methods section.



**Fig. 2**. Habitus ventral of the name-bearing specimens of *Bionoblatta* **A**. Holotype of *Brachycola diabolus* **B**. Holotype of *Bion mastrucatus*. **C**. Holotype of *Hormetica itatiayae*. **D**. Holotype of *Bionoblatta oiticicai*. Copyights at Materials and Methods section



Fig. 3. View of the habitus (A-B), details of terminalia (C-D) and labels (C), of the of name-bearing specimen of *Bionoblatta marcelli* sp. nov. (DZUP 267083). A. Dorsal view and B. ventral view of the habitus. C. Terminalia in C. dorsal and D. in ventral view. E. Labels pin with the specimen.



**Fig. 4**. Habitus in dorsal and ventral view of males of *Bionoblatta*. **A**. Dorsal and ventral view of a specimen identified as *Bionoblatta punctata* (MRNJ-ENT2-2209). **B** and **C** figures were identified as *B. diabolous* (see discussion). **B**. Dorsal and ventral view of individual from Mauá - RJ (DZRJ). **C**. Dorsal and ventral view of specimen from Paraty - RJ (DZUP 267084).



# Bionoblatta itatiayae



# Bionoblatta marcelli sp nov.

# Bionoblatta punctata

Fig. 5. Habitus in dorsal and ventral views of females and a nymph of *Bionoblatta*. A. Female of *Bionoblatta* sp. nov. (UFMG IBL 230006). B. Nymph *Bionoblatta marcelli* sp. nov. (UFMG IBL 230007). C. Female of *Bionoblatta itatiayae* (DZUP267064). D. Female of *Bionoblatta punctata* (MEUFV).



Fig. 6. Genitália of males of *Bionoblatta*. A–D. *Bionoblatta marcelli* sp. nov. (UFMG IBL 2300003): A. sgp; B. L1; C. L2vm, L2d and P; D. R2. E–H *Bionoblatta diabolous*, Paraty - RJ (DZUP 267084): E. sgp; F. L1; G. L2vm, L2d and P; H. R2. I–L *Bionoblatta diabolous*, Mauá - RJ (DZRJ): I. sgp; J. L1; K. L2vm, L2d and P; L. R2. M–P *Bionoblatta punctata* (MRNJ-ENT2-2557): M. sgp; N. L1; O. L2vm, L2d and P; P. R2.



Fig. 7. Map of the southeastern of Brazil with ocurrence records for species of *Bionoblatta*. pink circle = *B. diabolous*; purple pentagon = *B. hylaeceps*; yellow rombhus = *B. itatiayae*; red triangle = *B. oiticicai*; blue star = *B. punctata*; and white trapezoid = *Bionoblatta marcelli* sp. nov.
# 5 CHAPTER 3 - PHYLOGENY OF BRACHYCOLINI: A PHYLOGENETIC SURVEY ABOUT THE EVOLUTIONARY HISTORY OF THIS LINEAGE (INSECTA: BLATTODEA: BLABERIDAE)<sup>2</sup>

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# Abstract

Brachycolini is a unique evolutionary lineage of blaberids, and it have been recognized as a taxon in biological classifications for approximately 200 years. However, few comprehensive studies and phylogenetic analyses have been conducted investigating this group, leaving doubts about the monophyly of the tribe, its relationships with other Blaberidae taxa, and the internal relationships of the group. We made available a comprehensive phylogenetic hypothesis for this tribe, based on 92 morphological character statements coded for 33 terminal taxa, phylogenetic analyses with different search strategies and parameters, and tests for branch stability. Brachycolini stat. rev. was supported as a monophyletic group with high level of clade stability and 16 synapomorphies, being composed by ten genera, eight already described—*Brachycola*, *Bionoblatta*, *Hormetica*, *Lucihormetica*, *Parahormetica*, *Oxycercus*, *Quadrihormetica*, and *Sibylloblatta*—and two waiting to be introduced. Relationships among *the* taxa are proposed, and evolutionary and systematics implications on key and well-supported clades are discussed. The relationships among Clades B (exclusively macropterous cockroaches of *Brachycola* + *Lucihormetica* + *Quadrihormetica*), D (*Hormetica* + *Sibylloblatta* + *Parahormetica* + Gen. nov. A + *Bionoblatta* + Gen. nov. B + *Oxycercus*), and, the

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brachypterous clade E (remaining genera excluding *Hormetica*) are examples of more general divisions within the tribe that show high support and can reveal general relationships among brachycolines. *Hormetica*, *Parahormetica*, and *Bionoblatta* show be either paraphyletic or polyphyletic genera. However, interpreting the results of the analyses, we see that these relationships are still sensitive and inconclusive. Some of the clades found herein are similar to the old classifications. Lastly, we propose that expanding the sampling for *Lucihormetica*, deepening the study of relationships within the genus *Hormetica*, improve the quality of data for some terminals and also integrate with other sources of data such DNA-based, which are all necessary to improve more the comprehension of Brachycolini relationships.

# Key words

Blaberinae, Evolution, monophyletic group, morphological data, non-monophyletic group, Neotropical, Systematics, Zetoborinae

# 5.1. Introduction

The Brachycolini genera are among the lineages of Blaberidae whose evolutionary history we are beginning to better understand. The representatives of the tribe occur exclusively in the Neotropical region, but some genera are endemic to smaller areas (e.g., *Parahormetica* to the southern and southeastern Atlantic Forest, *Bionoblatta* to the chain mountains of southeastern Brazil, and *Lucihormetica* to the Amazonia). Most members of this tribe have a protruded horseshoe-shaped process (DHP) on pronotal disk, with a hormeticoid-shaped, and may be from macropterous, brachypterous, vestigial tegmen or even wingless. However, the tribe is delimited by characteristics of the male genitalia, such as the phallomere L2vm separated by a membrane from the phallomere L2d and prepuce covered by small and few spines (Roth, 1970b).

Since the introduction of first species—*Brachycola tuberculata* (Dalman, 1823)—or of the first genus—*Hormetica* Burmeister, 1838—our knowledge of this evolutionary lineage has started about 200 years ago. The understanding, composition and classification status of the Brachycolini lineages have been changing along all these years (e.g., Burmeister, 1838; Saussure, 1864b; Walker, 1868, 1869; Rehn, 1937; Princis, 1963; Roth, 1970b; Zompro & Fritzsche, 1999; Vidlička, 2019; Djernæs, 2020). As well as changes in understanding of the relationships of this lineage with other more inclusive groups (Bunner von Wattenwyl, 1865, 1893; Rehn, 1951; McKittrick, 1964; Grandcolas, 1993; Djernæs, 2020).

A study that seemed to bring relative stability to its intricate taxonomic treatment was presented by Roth (1970b) where he redefined the group as a tribe of Blaberinae. He did not

perform a formal phylogenetic analysis, instead he used morphological data into an intuitive approach. Roth's delimitation and composition for the tribe has been followed as a basis for numerous other studies after it (e.g., Vidlička, 2019; Polizeli and Pinto, 2024a).

Because of many interesting aspects of their biology (putative social behavior), morphology (trend to brachypterism and hypertrophy of diskal elements), and distribution (endemic to the neotropics), Brachycolini is a key taxon to study to understand the evolution of blaberids. Formal phylogenetic analyses with Blaberidae started to be carried out in the 1990s with the pioneers' hypotheses of Grandcolas (1993, 1996, 1998) based on morphological data which supported the monophyly of Brachycolini as member of Blaberinae. However, phylogenetic hypotheses based on molecular data, still that with low sampling to investigate relationships among Brachycolini species, support that species of Lucihormetica and Hormetica are more closely related to representatives of Zetoborinae, instead than Blaberinae (Legendre et al., 2017; Djernæs et al., 2020). These results call back to the intuitive analysis of McKittrick (1964), in which this relationship had already been recognized. In his investigation McKittrick (1964) used data on the internal morphology of genitalia of both sexes, proventriculus and behavioral observations. Also, these molecular-based analyses recognized Phoetalia as being closer to other groups of Zetoborinae than Brachycolini (Legendre et al. 2017; Djernæs et al., 2020), contrary to Roth (1970) that has supported this genus in Brachycolini. Based on just two terminal taxa of two genera from the 43 species and eight genera in Brachycolini (see Polizeli & Pinto, in press), Djernæs et al. (2020) transferred Hormetica and Lucihormetica from Blaberinae to Zetoborinae.

Currently there is no formal classification that include the results of comprehensive phylogenetic analyses and would help to clearly define the composition of this lineage. Taking into consideration the classification history and recent studies, Polizeli & Pinto (2024a, updated) recognized the tribe sensu Vidlička (2019) as composed by 43 species in the following genera and species: *Bionoblatta* Rehn, 1940 (6 spp.), *Brachycola* Serville, 1839 (2 spp.), *Hormetica* Burmeister, 1838 (14 spp.), *Lucihormetica* Zompro & Fritzsche, 1999 (13 spp), *Oxycercus* Bolivar, 1881 (1 sp.), *Parahormetica* Brunner von Wattenwyl, 1865 (4 spp.), *Quadrihormetica* Vidlička, 2019 (1 sp.) and *Sibylloblatta* Rehn, 1937 (2 spp.).

As mentioned, the knowledge about the Brachycolini has grown thanks to studies of comparative morphology, descriptions of genera and species, reviews, synopses and phylogenetic analyses (Rehn, 1937; Gurney, 1955; Roth, 1970b; Zompro and Fritzsche, 1999; Legendre et. al., 2017; Vidlička, 2019; Djernæs et al., 2020). However, the last study with a comprehensive sampling of the Brachycolini genera was in the intuitive classification of Roth (1970b). Studies that performed phylogenetic analyses have indicated that this tribe is monophyletic (McKittrick, 1964; Grandcolas, 1993; Legendre et. al., 2017; Djernæs et al., 2020), but some have not established

relationships between the genera, or they are inconclusive because of the resolution of the tree or the low taxon sampling. Issues about the monophyly of Brachycolini and of its genera, as well as the relationship between species are still pending investigation through comprehensive and integrative methods of 21<sup>st</sup> century systematics.

This study aimed to contribute to the understanding of the phylogenetic relationships of Brachycolini. We performed the very first phylogenetic analysis to test the monophyly of Brachycolini sampling all genera and aims to circumscribe genera and to infer the phylogenetic relationship between them.

# 5.2. Materials and Methods

#### 5.2.1. General procedures and material studied

Detailed information about the material examined for each terminal taxa are on Supplementary Material 1. The terminology for general external morphology was based on Roth (2003), cephalic morphology on Wipfler et al. (2016), areas of the wings on Li et al. (2018) and structures of the genitalia on Roth (1970b).

#### 5.2.2. Taxon sampling

For the ingroup we followed the Brachycolini composition proposed by Polizeli and Pinto (2024a) and available as supplementary material of that paper. *Phoetalia* was not included in Brachycolini because this genus has been recovered as closely related with other Zetoborinae lineages than the Brachycolini lineage (see introduction, Legendre et. al., 2017; Djernaes et al., 2020). Hypothesis about relationships among subfamilies within Blaberidae following Djernaes et al. (2020). A total of 33 species were included as terminal taxa in this study (Table 1). The branch of *Panchlora* was selected for rooting the tree, looking to avoid artificial relationships between the taxa. The outgroup consisted of 11 species, among them four of Blaberinae (Blaberini and Monastriini) and four representatives of Zetoborinae, some putatively closely related to Brachycolini taxa. This composition, consequently, the analysis configuration aimed to act as strong test the monophyly of the tribe.

To infer the relationships between Brachycolini lineages, the composition of the ingroup aimed to cover the largest number of species of the tribe and that met our criteria. We selected terminal taxa considering the following criteria: (1) availability of material, (2) lineage coverage, thus including phenotypic, distributional and phylogenetics diversity, (3) minimum number of taxa to test the monophyly of the included genera, (4) nomenclatural implication with inclusion of type species for use in nomenclatural purposes, (5) potential of taxon belonging to Brachycolini, (6) overall quality of available data of the terminal, such as number of specimens, available of images and availability of molecular data. The ingroup consists of 22 terminal taxa (Table 1), being 20 valid species of all 8 genera in Brachycolini. Two terminals labeled as Gen. Nov. A and B were added on our analyses due to the specimens were identified as probably being of new genera within Brachycolini.

#### 5.2.3. Analysis

Data matrix was elaborated with help of the WINCLADA software version 1.61, by K. Nixon (1999-2004) and characters statements (homologues or primary homology) following structure of Sereno (2007). Phylogenetic analyses were performed on TNT software version 1.6 (Goloboff & Morales, 2023). Characters were treated as unordered (Fitch, 1971). The selection for the best hypothesis of phylogenetic relationships was made using cladistic parsimony (Farris, 1983), all searches for the best tree solution were undertaken through heuristic solution methods. The searches were performed using equal weights (EW) or with extended implied weighting (EIW, Goloboff, 2022) using different values of constant of concavity as reference (K = 3, 5, 10, 15, 20, 25, and 30). A first and exploratory approximation was performed using EW with random addition sequence plus tree bisection and reconnection (RAS + TBR, TNT commands set as thr replic 1000 hold 10 ras). Strategies aiming to solve composite optima problems was conducted using a combination of global optima algorithms (Sectorial Searches, Parsimony Ratchet, Tree-Drifting and Tree-Fusing; Goloboff, 1999; Nixon, 1999), with commands set as replications 100 hits 10 rss fuse 25 drift 500 ratchet 500. For the searches that selected more than one optimal tree techniques of consensus was adopted. We used extended implied weighting because its purpose is to handle with missing and inapplicable data minimizing high weighting to characters with no potential of homoplasy (Goloboff 2022), the *default* parameters was used (to deal with missing data) and the value of constant concavity (K) for reference was set to K = 10. The tree obtained using the value of K = 10and undertaken through strategies aiming to solve composite optima problems and it was used as the main hypothesis of relationships. To evaluate branch stability four strategies were adopted: (1) symmetric resampling with 2000 pseudoreplicates analyzed with either Bootstrap; and (2) Jackknife (p = 0.33), both with difference frequency values (GC) (Goloboff 2008, 2022); (3) Relative Bremer support (Goloboff, 2022); and a (4) sensitive analyses applying with the following value of Ks = 3. 5, 15, 20, 25, and 30, Resampling and sensitive Analysis with EIW was made via composite optima solving approach (parameters set as replication 100 hits 10 level 10 chklevel 2). Relative Bremer support (BS) was made with EIW - RAS + TBR and conducted by a suboption survey in ratio of number of steps and fit.

# 5.3. Results

## 5.3.1. Dataset, Character statements

Our comparative analyses of specimens resulted in 92 morphological character statements coded for 33 terminal taxa (Supplementary Material 2). The list of characters is made available below, consisting 8 of the head, 36 from thorax, 26 from legs and 19 from the abdomen. There are 32 multistate and 60 binary characters, among them 6 autapomorphic characters.

# 5.3.1.1. Head

0. Vertex, dorsally, visible: exposed (0), or, hidden (1).

1. Female, antenna, 1° flagellomere, length: shorter (0), or, longer (1), than the next 2 + 3 flagellomeres.

2. Interocular space on vertex, width: short,  $\leq 0.25$  (0), or, long,  $\geq 0.50$  (1), of the maximum width of the head.

3. Ocellus, size: large  $\leq 0.25$  (0), or, minute,  $\geq 0.50$  (1), of the maximum width of the head.

4. Compound eye, ventral margin, level relative to the ventral margin of circumantennal ridge: surpassing (0), or, not surpassing (1).

5. Compound eye, inner ventral margin, shape relative to circumantennal ridge ventrally: no projected (0), or projected (1).

6. Anterior tentorial pit, shape: straight (0), curved (1).

7. Anteclypeus, posterior margin, width: narrow (0), or, wide (1), to the maximum width of dorsal margin.

#### 5.3.1.2. Thorax

8. Pronotum, anterior margin, thickness: thinner (0), thicker (1), or, similar (2), to than other margins.

9. Pronotum, surface sculpture: irregular (diskal elements defined) (0), or, smooth (no diskal elements) (1).

10. Pronotum, male diskal elements, shape: smooth (0) or, protruded dorsally into a diskal horseshoe-like process (DHP sensu Polizeli and Pinto, 2024a) (1).

11. Pronotum, male diskal horseshoe-like process (DHP), shape: barely protruded (0), protruded (1), or, strongly protrude (2).

12. Pronotum, female diskal elements, shape: smooth (0) or, protruded dorsally into a diskal horseshoe-like process (DHP sensu Polizeli and Pinto, 2024a) (1).

13. Pronotum, female diskal horseshoe-like process (DHP), shape: barely protruded (0), protruded into a diskal horseshoe-like process (DHP sensu Polizeli and Pinto, 2024a) (1).

14. Pronotum, surface, coloration: pale (0), with dark marks, spots or stripes (1), almost all uniformly dark colored (2).

15. Pronotum, anteromesial region, coloration: pale (0), or, dark (1).

16. Pronotum, lateral area adjacent to the disk, sculpture: smooth (0), minute punctures (1) or deep punctures (2).

17. Pronotum, disk, inner area of the horseshoe-like process (DHP), sculptures: lines and dots (0), or, with large yellow rounded processes (1).

18. Pronotum, disk, diskal anterolateral tubercle-like processes (DTP), amount: one (0), two (1), three (2) tubercles.

19. Pronotum, dorsal region above the head, morphology (Grandcolas, 1993, modified): regular (0), shallow groove and ill-defined process (1) or, with deep grooves forming a rounded process (2).

20. Pronotum, posterior margin, shape: straight (0), convex (1) or acute projected (2).

21. Pronotum, lateral angles of posterior margin in dorsal view, shape (Tarli et al, 2018): almost right (0), inclined (1), seemly have a new margin, or, obtuse (2).

22. Pronotum, lateral margin configuration, shape: flattened, keeping the dorsal plane (0), or, curved downward, changing the plane (1).

23. Male pronotum, anterior margin, direction: not curved, towering anteriorly (0), curved, towering dorsally, (1), or strongly curved, towering posteriorly (2).

24. Pronotum, posterolateral angle, shape (Tarli et al., 2018, modified): regular, not projected into a tubercle (0), or, irregular, projected into a blunt spine-like tubercle (1).

25. Mesothorax: winged (0), or, wingless (1).

26. Metathorax: winged (0), or, wingless (1).

27. Female tegmen, length: macropterous (0), semibrachypterous (1), brachypterous (2), or, vestigial (3).

28. Female hindwing, length: macropterous (0), semibrachypterous (1), brachypterous (2).

29. Male tegmen, length: macropterous (0), semibrachypterous (1), brachypterous (2), or, vestigial (3).

30. Macropterous tegmen, length: slightly short or as long as the tip of abdomen (0), or, beyond the tip of abdomen (1).

31. Female, brachypterous tegmen, shape: oblong (L 3x > W) (0); ovate (L 2x < W) (1); quadrangular-shaped (L 1.5x < W) (2); rectangular (L 1.5x > W) (3); trapezoid-shaped (4).

32. Male tegmen, humeral area, sculptures: minute punctures (0), deep punctures (1), or, smooth (2).

33. Male, tegmen, humeral area, surface: smooth (0), or, with several hair-like setae (1).

34. Male tegmen, claval furrow (cfr): well-defined (0), or, ill-defined (1).

35. Tegmina, sculptures: smooth (0), or rugose (1)

36. Tegmen, level of sclerotization (thickness): low (0), medium (1), or, high (2).

37. Tegmen, humeral trunk and adjacent region, coloration: uniformly dark (0), pale, spotted by dark marks (1), uniformly pale (2).

38. Tegmen, coloration, pattern: uniform dark (0), punctate marked, large well-defined dark spots (1), reticulated marked, with small spots and stripes (2), basal single-marked, a large transverse elongated spot (3), striped marked, multiple elongated spots (4); uniform pale (5).

39. Tegmen, costal margin, coloration: dark (0), pale (1).

40. Tegmina, median furrow (mrf), length: smaller than 0.2 of the tegmina (0), or, longer than 0.5 of the tegmina (1).

41. Intertegminal space, width: none, tegmina fully touch (0), narrow, anterior margin not in touch, exposing a triangular area of mesonotum (1), or, fully separated (2).

42. Mesonotum, anteromesial area between tegmina, sculptures: smooth (0), minute punctures (1), or, large punctures (2).

43. Mesonotum, posterior region, sculptures: with a deep arcuated furrow (0), or, shallow arcuated furrow (1).

44. Metanotum, posterolateral angles, size: small, not covering the lateral margin of S1 (0), or, large, covering the lateral margin of S1 (1).

#### 5.3.1.3. Legs

45. Male procoxa, surface: smooth (0), or, sulcate (1).

46. Female procoxa sulcus, shape: complete (0); basal (1), interrupted mesially (2).

47. Profemur, anteroventral carina, length: long, > 0.8 (0), or, short, < 0.5 (1), of the total length of femur.

48. Profemur, proximal half of anteroventral margin, setae shape: hair-like (0), spurs (1), or, spurs and hair-like (2).

49. Profemur, proximal half of anteroventral margin, armament (coverage): almost glabrous (0), few or scattered setae (1), or, several setae (2).

50. Profemur, distal half of antero-ventral margin, setae shape: hair-like setae (0), spine-like setae (1).

51. Profemur, distal half of anteroventral margin, armament (coverage): few or scattered setae (1), or, several setae (2).

52. Profemur, posteroventral margin, armament (coverage): almost glabrous (0), hair-like (1), spurs and hair-like (2).

53. Profemur, tip of anteroventral margin, armament: smooth (0), or, with a spur (1).

54. Profemur, tip of anteroventral margin, length of spur: long, 3x long as width (0), or, short, <2x as long width (1).

55. Profemur, tip of posteroventral margin, armament: smooth (0), or, with a spur (1).

56. Protibia, shape: claviform (0), or, rectangular (1).

57. Proleg, first tarsomere, length: longer than tarsomeres 2+3 (0), or, as long as to the tarsomere 2 (1).

58. Pretarsus, arolium, size: defined, large (0), or, vestigial (1), defined, small.

59. Pretarsus, arolium, insertion: dorsally (0), or, ventrally (1), to the base of the tarsal claws.

60. Proleg, lateral surface of the first three tarsomeres, armament: smooth (0), or, with small robust spines (1).

61. Mesofemur, tip of dorsal margin, armament: with a spur (0), or, smooth (1).

62. Meron 3, shape: globose (0), or, flattened (1).

63. Pretarsus, tarsal claw, ventral margin, shape: unspecialized (0), or, specialized (1).

64. Mesofemur, posteroventral margin surface, armament: with hair-like setae (0), with one or more stout spine (1), or, with several small setae (2).

65. Metafemur, tip of posteroventral margin, armament: smooth (0), or, with a spur (1).

66. Metafemur, tip of anteroventral margin, armament: smooth (0), or, with a spur (1).

67. Metafemur, tip of anteroventral margin, shape of spur: long and thin (0), or, short and robust (1).

68. Metafemur, tip of dorsal margin, armament: smooth (0), or, with a spur (1).

69. Metafemur, tip of dorsal margin, shape of spur: long and thin (0), or, short and robust (1).

70. Metafemur, posteroventral margin surface, armament: with few hair-like setae (0), with one or more stout spine (1), with several small setae (as a comb) (2), or, smooth (3).

71. Leg, tibia, spurs, length: long (0), or, small (1).

# 5.3.1.4. Abdomen

72. Abdominal tergum, shape: convex (0), or, concave (1).

73. Male, abdomen, cercus, segmentation: well-defined separated segments (0), or, fused segments (1).

74. Male, abdomen, cercus, length: long,  $\geq 2.5x$  width (0), or, short  $\leq 2.0x$  (1).

75. Female, abdomen, cercus, segmentation: well-defined separated segments (0), or fused segments (1).

76. Abdomen in ventral view, lateral margins of tergite, shape: small expansions of lateral margins(0), or, large expansions of lateral margins (1).

77. Male, abdomen, dorsal surface, sculptures callosities: lacking (0), with minute (1), or, large.

78. Male, abdomen, dorsal surface, sculptures: smooth (0), rugose laterally (1), or, overall rugose (2).

79. Male abdomen, tergites, dorsal surface, callosities distribution: S5-10 (0), or, almost S1-10 (1).

80. Female, dorsal surface of abdomen, mesial sculptures: smooth (0), or, with callosities (1).

81. Abdomen, dorsal surface, coloration: uniform (0), or, with two or more colors (1).

82. Colored abdomen, general coloration: a large yellow band mesially (0), variegated, with black lines and dots on the yellow background (1), with a large semicircular black area with pale margins (2), a dark brown band mesially (3), or, yellow band on final tergites (4).

83. Female, bilobed supraanal plate, shape of mesial groove: deep (0), or, shallow (1).

84. Females, cercus, length: greater than 2,5x(0), or, smaller than 2,0x the width (1).

85. Cercus, shape: falciform (0), lanceolate (1), or, truncated (2).

86. Subgenital plate, stylus, length: symmetrical (0), or, asymmetrical (1).

87. Subgenital plate, right stylus, length: medium/long (0), or, minute (1).

88. Connection between the L2vm and L2d, sclerotization: weak, membranous (unlinked) (0), or, strong, sclerotized (linked) (1).

89. Left margin of the L2d in relation to the posterior margin of L2vm, position: to the left (0), at the beginning of the left side (1), or, on the right side or beyond (2).

90. Prepuce, spines: absence (0), or, presence (1).

91. L2d in relation to the L2vm, orientation: perpendicular (0), or, parallel (1).

# 5.3.2. Analysis Results

The equal weighting analysis retained 18 most parsimonious trees (MPTs) with steps = 337, consistency index CI = 0.395 and retention index RI = 0.669. All analyses using extended implied

weighting (EIW) selected just one hypothesis for each reference value of constant of concavity (K). The tree (Fig. 1) obtained using the value of K base = 10 and adopting strategies of composite optima (search combination of SS, PR, TD and TF) was used as the preferred hypothesis of relationships (fit = 14.45512, steps = 337, CI = 0.395, RI = 0.669) and was utilized to optimize the characters using accelerated-transformation ACCTRAN criterium (Fig. 2). This tree is one of the 13 MPTs selected with EW.

Brachycolini was supported as monophyletic herein represented as the clade A (Fig. 1), as well the group including *Brachycola*, *Lucihormetica* and *Quadrihormetica* (clade B), the group with *Sibylloblatta*, *Parahormetica*, Gen. nov. A and B, *Oxycercus* and *Bionoblatta* (clade E), *Sibylloblatta* (clade F), and the group including *Oxycercus* and Gen. Nov. B (clade L). On our analyses, the clade A is the best supported, it was retained on analyses with all values of reference concavity (K) and obtained high indexes of branch stability BO = 98, JK = 98 and BS = 45. The clades D, E and L are among the better supported nodes. The genus *Hormetica* (among clade D and E) and *Parahormetica* (among clade G and I) were obtained as paraphyletic and *Bionoblatta* as polyphyletic including the Gen. nov. B and *Oxycercus* (clade J). However, *Hormetica* monophyly was obtained in majority of the 18 trees retained with EW and with the analyses with K = 3 and 5 what can mean that *Hormetica* genera are among the weakly supported nodes, due to the low branch stability and sensitivity analyses as showed in the Fig. 1.

The tree with characters optimized using ACCTRAN is available in the Fig. 2. Below we present the labeled clades and their number of synapomorphies (Fig. 2): Clade A representing Brachycolini = 16 synapomorphies; Clade B including *Brachycola*, *Lucihormetica* and *Quadrihormetica* = 4 synapomorphies; Clade C including *Lucihormetica* and *Quadrihormetica* = 4 synapomorphies; Clade C including *Lucihormetica* and *Quadrihormetica* = 4 synapomorphies; Clade C including *Lucihormetica* and *Quadrihormetica* = 4 synapomorphies; Clade C including *Lucihormetica* and *Quadrihormetica* = 10 synapomorphies; Clade E including *Sibylloblatta*, *Parahormetica*, Gen. nov. A and B, *Oxycercus* and *Bionoblatta* = 10 synapomorphies; Clade E including *Sibylloblatta*, *Parahormetica*, Gen. nov. A and B, *Oxycercus* and *Bionoblatta* = 9 synapomorphies; Clade F including *Sibylloblatta* = 5 synapomorphies; Clade G including *Parahormetica*, Gen. nov. A and B, *Oxycercus* and *Bionoblatta* = 5 synapomorphies. Clade H including "*Parahormetica*" = 1 synapomorphies. Clade I including Gen. nov. A and B, *Oxycercus* and *Bionoblatta* = 5 synapomorphies. Clade J including *B. punctata*, Gen. nov. B, Oxycercus and "*Bionoblatta*" = 7 synapomorphies. Clade K including Gen. nov. B and *Oxycercus* = 10 synapomorphies. Clade M including "Bionoblatta" = 4 synapomorphies.

## 5.4. Discussion

The monophyly of Brachycolini (Clade A) was an expected result, due the intuitive classifications that grouped representatives of Brachycolini (e.g. Burmeister, 1838; Rehn 1937, 1951; Princis, 1963; Roth, 1970b), recent phylogenetic investigations indicating support to the tribe (Grandcollas, 1993; Legendre et. al., 2017; Djarneaes et al., 2020), and its unique biological and phenotypic features. Brachycolini as monophyletic show high values of branch stability and 26 characters as synapomorphies, corroborating what was already expected and indicates that it is a lineage with its own evolutionary history. Also, in our analyses *Phoetallia* was not recovered as a Brachycolini member, supporting hypothesis that these genera must be more related with other subfamilies of Blaberidae (Legendre et. al., 2017; Djernaes et al., 2020). However, our studies are the very first formal phylogenetic analysis that could test its monophyly and infer their relationships among the genera of the tribe. Also, most studies that included representatives at analyses used few genera to infer the relationships, which increases the difficulty in comparing our results with the literature.

The first divergence in Brachycolini separates clade B from clade D (Fig. 1). Within the clade B, *Lucihormetica*, as a sister group to *Quadrihormetica* (clade C), is a strongly expected result due to them being the only genera with yellow spots on the disk. Considering the results of all analyses, clade D indicated that most likely *Hormetica* is the sister group of the brachypterous clade E. Although *Hormetica* seems paraphyletic in the selected topology (Fig. 1), the monophyly of this genus was retained in some of our analyses with EW and EIW, thus its paraphyly would be an artifact of our research.

In our analyses the clade E (*Bionoblatta* + Oxycercus + Parahormetica + Sibylloblatta + Gen. nov. A + Gen. nov. B) is a very interesting group with emphasis that all members have brachypterous, vestigial wings (Gen. nov. B) or is wingless (Oxycercus), the tegmina have illdefined humeral furrow and is high sclerotized. Following our hypothesis the genera forming the clade E are more related between them. Its differing of relationships already proposed by some authors as *Hormetica* and *Parahormetica* as closest related groups (Hebard, 1921 apud Roth, 1970b) and McKitrick (1964) proposed that *Hormetica* is more related with *Parahormetica* than *Brachycola*, and *Hormetica* as sister-group of *Lucihormetica* (Legendre et. al. 2017; Djernaes et al. 2020). However, the relationships presented in these studies are dependent on the sampling of these few taxa. Nonetheless, some studies with a larger sampling of taxa indicated relationships that are similar to our results. As Rehn (1937) that proposed *Bionoblatta* and *Sibylloblatta* nearer *Parahormetica* than *Hormetica* a relationship that can resemble the composition of the clade E herein presented, but without Oxycercus and Gen. nov. A and B. These genera were not sampled by Rehn (1937). Also, Roth (1970b) indicated that *Bionoblatta* is near of *Parahormetica* and *Oxycercus*, a composition very similar with our clade J, excluding the Gen. nov. B, a taxon not sampled by Roth. Another result that agrees with Brachycolini sensu Roth 1970b is that *Oxycercus* is a Brachycolini member.

The genera *Parahormetica* and *Bionoblatta* were not recovered as monophyletic, challenging the classification proposed at the latest taxonomic revisions of these genera (Polizeli and Pinto, 2024a, c—unpublished data). However, the nodes indicating the non-monophyly of these genera are not well-supported, which can be interpreted as an inconclusive relationship. Additionally, the terminals *P. monticollis* and *O. peruvianus* were coded based on photographs, affecting the quality of the data, potentially causing a bias in the analysis. Finally, we suggest that to improve the understanding of Brachycolini relationships, it is necessary to increase the sampling for *Lucihormetica*, enhance the investigation of relationships within the genus *Hormetica*, and improve the quality of some of terminals.

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#### **Author Contribution**

Both authors contributed to the conceptualization, formal analysis, data curation and visualization of results. LP was responsible to the original draft. All authors approved the final draft of the manuscript

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Table 1. Terminal taxa composition. Species composition, classification and status in the analysis. Detailed information about the examined material can be found in Appendix 1. Classification according to Vidlička (2019), Djernæs (2020), and Polizeli and Pinto (2024a).

Terminal taxa	Subfamily	Tribe	Status		
Panchlora sp.	Panchlorinae	-	outgroup		
Pycnoscelus surinamensis	Pycnoscelinae	-	outgroup		
<i>Epilampra</i> sp.	Epilamprinae	Epilamprini	outgroup		
Blaberus giganteus	Blaberinae	Blaberini	outgroup		
Blaptica formosa	Blaberinae	Blaberini	outgroup		
<i>Monastria</i> sp.	Blaberinae	Monastriini	outgroup		
Petasodes dominicana	Blaberinae	Monastriini	outgroup		
Phoetalia pallida	Zetoborinae	-	outgroup		
Tribonium morroferrensis	Zetoborinae	Triboniini	outgroup		
<i>Lanxoblatta</i> sp.	Zetoborinae	Phortioecini	outgroup		
Zetobora signaticollis	Zetoborinae	Phortioecini	outgroup		
Oxycercus peruvianus	Blaberinae	Brachycolini	ingroup		
Brachycola sp.	Blaberinae	Brachycolini	ingroup		
Hormetica atlas	Zetoborinae	Brachycolini	ingroup		
Hormetica kemneri	Zetoborinae	Brachycolini	ingroup		
Hormetica laevigatta	Zetoborinae	Brachycolini	ingroup		
Hormetica luteomarginatta	Zetoborinae	Brachycolini	ingroup		
Lucihormetica fenestrata	Zetoborinae	Brachycolini	ingroup		
Quadrihormetica onorei	Blaberinae	Brachycolini	ingroup		
Sibylloblatta panesthoides	Blaberinae	Brachycolini	ingroup		
Sibylloblatta pustulata	Blaberinae	Brachycolini	ingroup		
Gen. nov. A sp. nov.	Blaberinae	Brachycolini	ingroup		
Gen. nov. B sp. nov.	Blaberinae	Brachycolini	ingroup		
Bionoblatta diabolus	Blaberinae	Brachycolini	ingroup		
Bionoblatta hylaeceps	Blaberinae	Brachycolini	ingroup		
Bionoblatta itatiayae	Blaberinae	Brachycolini	ingroup		
Bionoblatta punctata	Blaberinae	Brachycolini	ingroup		
Bionoblatta oiticicai	Blaberinae	Brachycolini	ingroup		
Bionoblatta marcelli	Blaberinae	Brachycolini	ingroup		
Parahormetica bilobata	Blaberinae	Brachycolini	ingroup		
Parahormetica cicatricosa	Blaberinae	Brachycolini	ingroup		
Parahormetica monticollis	Blaberinae	Brachycolini	ingroup		
Parahormetica museunacional	Blaberinae	Brachycolini	ingroup		



Figure 1. Preferred tree with values of branch stability: Single most parsimonious tree obtained from extended implied weighting (reference K = 10) with unordered characters containing a phylogenetic hypothesis of Brachycolini (33 terminal taxa, 92 characters, fit = 14.45512, steps = 337, CI = 0.395, RI = 0.669). Node labels show clade stability, when not displayed there is no support. Resampling value cutoff BO and JK < or = to 0 and BS > or = to 50. Black value cutoff BO and JK < or = to 0 and BS > or to 50. Black squares represent branches supported with K = N. A–M = labeled nodes; EW = equal weighting; K = constant of concavity; BO = symmetric bootstrap with difference frequency (GC); JK = symmetric jackknife with p = 33; BS = relative Bremer support.



Figure 2. Preferred tree with characters optimized: single most parsimonious tree obtained from extended implied weighting (reference K = 10) with unordered characters containing a phylogenetic relationship of Brachycolini (33 terminal taxa, 92 characters). Preferred hypothesis tree with characters optimized using ACCTRAN criteria. Characters statements enumerated from 0 to 91. Black square corresponds unique transformation and with to multiple. A-M = labeled nodes.

- Panchlora sp. Burmeister, 1838. BRASIL 1∂; Santa Catarina state, Nova Teutônia municipality; May. 1977; Fritz Plaumann col. [leg.]; (DZUP 528278) 1♀; same data but Fev. 1977; (DZUP 528276); 1♀; same data but Fev. 1976 (DZUP 528279); 1♀; same data but Set. 1977; (DZUP 528290); 1♀; same data but Nov. 1975 (DZUP 528349). Genitalia from Roth (1971).
- Pycnoscelus surinamensis (Linnaeus, 1758). BRAZIL. 1♀; Paraná state, Palotina municipality, Bosque setor UFPR; -24.2930, -53.8416; 100 m a.s.l.; 13-15 Dez. 2020; Jacobina A. leg.; (DZUP 267055); 1♀; Curitiba municipality; 2018; Eurich. J. leg. (DZUP 528708); 1♀; Paranaguá municipality; 20 Fev. 2019; B. A. Cardoso leg.; (DZUP 528713); 1♀; Avorada do Sul municipality.; 01 Mar. 2019; Katia Justi leg.; (DZUP 528714); Piraquara municipality; 25°27'26.8"S 49°09'28.1"W; 20–27 May 2019; CMP dos Reis col. [leg.]; (DZUP 528715); 6♀; Mato Grosso State, Chap. Guimarães; 18 Nov. 1983; Exc. Dep. Zool-UFPR (Polonoroeste); (DZUP 528244–528249); 1♀; Santa Catarina State, Joinville municipality; 23 Jan. 1972 (DZUP 528250).
- *Epilampra* sp. Burmeister, 1838. BRAZIL. 1 ♂; Paraná State, Piraquara municipality, Parque Estadual Pico do Marumbi, Mananciais da Serra (SANEPAR), Trilha da Chaminé; 25.488586°, -48.997824°; 27 Fev. 2022; L. R. Caramori & A. P. Pinto leg. (DZUP 266841); 1 ♂; Rio de Janeiro State; Parque Nacional do Itatiaia, Setor Lago Azul; -22.450306, 44.615361; 830 m a.s.l.; active collection; 12–14 Jan. 2023; AP Pinto, AC Domahovski, J Ehlert & LP Aguiar leg. (DZUP 266982) 1♀; São Paulo State, Pirassununga municipality, CEPTA/ICMBIO; -21.9312, -47.3728; 560 m a.s.l., 14–17.XII.2023, ativa noturna, AP Pinto, E Denck, L Polizeli & RC Varella leg. (DNA sample LABSIA 743, DZUP 267067). Genitalia from Roth (1970c).
- Blaberus giganteus (Linnaeus, 1758). COSTA RICA 1♂; Turrialba; 600 m a.s.l.; 20 Mar 1973, V.
  O. Becker col.; (DZUP 528092); BRAZIL; 1♀; Acre State, Mancio Lima municipality, Pq.
  Nac. Serra Divisor, Sede Rio Moa; 7°26'58"S, 73°39'42"W; 240 m a.s.l.; 7–14 Out. 2018; O.
  Mielke, Casagrande, Dolibaina & Medeiros leg. (DZUP 528258). Genitalia from Roth (1970b: figs 41-43).
- Blaptica formosa Lopes & Oliveira, 2005 cf. BRASIL 1♂; Rio grande do Sul State, Viamão municipality; 15 Out.1989; Quadros, F.C. col. [leg]; (18274-1 MCTP); 1♀; same data but 18275-1 MCTP. Genitalia from Lopes and Oliveira (2005: figs 15, 21, 29-30).
- Monastria sp. Saussure, 1864. BRASIL 1♂; Paraná State, Curitiba municipality; 25.3958, -49.2610; 15 Fev. 2023; Gnoato, M. E. col. [leg.] (DZUP 267092); • 1♀; Paraná State,

Piraquara municipality, Parque Estadual do Pico do Marumbi, Mananciais da Serra (SANEPAR), active collection; 15 Fev. 2020; Lic. IAP 03.20; L. R. Caramori & L. Polizeli leg. (DZUP 266747). Genitalia from Tarli at al. (2018).

- Petasodes dominicana (Burmeister, 1838). BRASIL 1♂; São Paulo State; May. 1957; K. Lenko [leg.]; (DZUP 528080); 1♀; Pirassununga municipality, Centro Nac de Pesq. e Conserv da Biodiv. Aquática Continental (CEPTA/ICMBio), restauração/polígono; -21.9436, -47.3796; 595 m a.s.l.; 16 Dez. 2023; AP Pinto, E Denck, L Polizeli & RC Varella leg.; (DZUP: 267080); active night collection. Genitalia from Roth (1970b: figs 154-156).
- Phoetalia pallida (Brunner von Wattenwyl, 1865). BRASIL 1♂; Paraná State, Curitiba municipality, UFPR, Centro Politécnico; 12 Mar. 2019; F. R. Marcondes [leg.]; (DZUP 528710) 1♂ same data but 16 Mar. 2019; (DZUP 528709); 1♂; same data but 25 Apr. 2019; (DZUP 528711); 1♂; Minas Gerais State; Santa Barbára municipality, Rio Piracicaba; 19°58'53.5"S 43°14'31.8"W; 628m; Active collection; Dez.2022; Neves, M.A.G [leg.]; (MCN-INV B185) 1♀; same data but (MCN-INV B187). Genitalia from Roth (1970b: figs 175-177).
- Tribonium morroferrensis De Oliveira Cardoso da Silva & Lopes, 2015 cf. BRASIL 1♂; Paraná State, Curitiba municipality, Jardim Botânico; -25.4412, -492395; 917 m a.s.l.; 19 Nov. 2023;
  L. Polizeli leg.; (DZUP 267095); under tree bark, nymphs and adults grouped together; 1♀; same data but DZUP 267099. Genitalia from Silva and Lopes (2015: figs 14-16).
- Lanxoblatta sp. Hebard, 1931. BRASIL 1♀; Pará State, Belém municipality, IAN [locality]; 2
  Ago. 1962; J. Bechyné col. [leg.]; (MZSP 2053); 1♀; same data but 18 Dez. 1962; (MZUSP 2046). Genitalia from Roth (1970a: figs 48-56).
- Zetobora signaticollis Burmeister, 1838. BRASIL 1♂; Paraná State, Curitiba municipality, C. Politécnico UFPR, SCB; [-25.4481, -49.2330]; 06 Out. 2023; L Polizeli [leg.]; (DZUP 267103); 1♀; São Paulo State; Barueri municipality; 10 Out. 1960; K. Lenko col. [leg.]; (MZSP 1970). Genitalia from (Roth 1970a: figs 22-26).
- Oxycercus peruvianus Bolivar, 1881. PERU 1♀; Peru central; Museum Paris MNHN (EP) 1249; coll pantel; Muséum paris; Syntype test. M. Paris, 1991. Examined by photos available in Cockroach Species File CSF (Becaloni 2024). Genitalia from Roth (1970b: figs 206-208).
- Brachycola sp. Serville, 1839. BRASIL 1♂; Rio de Janeiro State, Nova Friburgo municipality, Mury [district]; Mar. 1972; Gred & Guimarães col. [leg.] (MZSP 0994); • 1♀; Rio de Janeiro municipality, Horto florestal; Out. 1957; Altamiro B. Pereira [leg.]; (DZUP 528118). Genitalia from Roth (1970b: figs 193-194).
- Hormetica atlas Rehn, 1911 cf. BRASIL 1♂; 1♀; São Paulo State, Mata atrás da Praia de Guaratuba; Set. 1984; Col. F. Mello [leg.]; (MZSP).

*Hormetica kemneri* Princis, 1946 cf. **BRASIL** • 1♂; São Paulo State, São Paulo municipality; 1952; J. J. Ferraciolli leg.; (MZSP 1017); • 1♀; Ypiranga; Set. 1942; (MZSP 1015).

- Hormetica laevigatta Burmeister, 1838. BRASIL 1♂; Rio de Janeiro State, Itatiaia municipality;
  02 Apr. [19]48; J. F. Zikan [leg.]; (CEOIC 42309); 1♀; same data but Parque Nacional do Itatiaia, Setor Lago Azul; -22.450306, -44.615361; 830 m a.s.l.; 12–14 Jan. 2023; AP Pinto, AC Domahovski, J Ehlert & LP Aguiar leg.; night, active collection; emerged 08.II.2023; (DNA SAMPLE LABSIA 512 DZUP 266959). Genitalia from Roth (1970b: figs 181-183).
- Hormetica luteomarginatta Bruijning, 1949. BRASIL 1∂; Minas Gerais State, Viçosa municipality; Vanetti [leg.]; (UFV) 1♀; Minas Gerais State, Viçosa municipality, 12 Fev. 1984; Col. L. Chandler [leg]; (UFV).
- Lucihormetica fenestrata Zompro & Fritzsche, 1999. **BRASIL** 1♂; Amazonas State, [Presidente Figueiredo municipality], UHE Balbina; 22 Jan. 1988; B. Mascarenhas [leg.]; (MPEG DIC 18000985); 1♀; Manaus municipality, Sítio Vida Tropical; 02°51'47"S, 59°55'55"W; manual collection at decomposig log, keep in laboratory; 03 Out. 2006; J. A. Rafael col. [leg.]. Genitalia from Zompro & Fritzsche (1999: figs 4-6).
- Quadrihormetica onorei Vidlicka, 2019 ECUADOR 1♂; Lumbaqui, Sucumbios (before 1993 Napo) Province; Set. 1984; G. Onore leg. (deposited in PUCE, Quito, Ecuador); 1♂; El Reventador, Sucumbios (before 1993 Napo) Province; May. 1985, G. Onore leg. (deposited in IZ SAS, Bratislava, Slovakia); 1♀; Lumbaqui, Sucumbios Province; 7 Apr. 1993; GTZ. Bauin (deposited in PUCE, Quito, Ecuador). Examined by photos from Vidlička (2019: figs 1-5).
- Sibylloblatta panesthoides (Walker, 1868) **JAMAICA** 1♀; (BMNH (E) #876294). Examined by photos available in Cockroach Species File CSF (Becaloni 2024). Genitalia from Roth (1970b: fig. 198).
- Sibylloblatta pustulata (Hebard, 1929) 1♂; Bonaire, W. Indies. SimonColl. Purch. Rosenberg. 1900–255. Hormetica pustulata Type, Hebard cln. BMNH (E) 876284. Examined by photos available in Cockroach Species File – CSF (Becaloni 2024).
- Gen. nov. A [Brachycola\_PARNASO]. BRASIL 1♂; Rio de Janeiro State, Guapimirim municipality, Parque Nacional da Pedra do Sino; 22°28'28,0"S 43°03'17.0"W; 2275 m a.s.l.; 28 Fev. 2026; A. A. Alves [leg.]; (DZRJ).
- Gen. nov. B BRASIL 1♂; Minas Gerais State, Alto Caparaó municipality, Parque Nacional do Caparaó, Acampamento Macieira, área do camping; -20.4809, -41.8296; 1866 m a.s.l.; night, active collection; 14 May. 2024; A P Pinto, B Clarkson, L H Gil-Azevedo, L Hoehne & N O Paiva leg. (DZUP 267075); 1♀; same data but DZUP 267076.

- Bionoblatta diabolus (Saussure, 1864). BRAZIL 1♂; Rio de Janeiro State, Mauá municipality; Dez. 1998; R. Gonçalves leg.; (DZRJ) 1♂; Rio de Janeiro State, Paraty municipality, Rodovia RJ-165; 23°11'23"S, 44°50'14"W; 47 m a.s.l.; 13 Dez.2015; A. C. Delciello leg.; ex-DZRJ (DZUP 267084).
- Bionoblatta hylaeceps (Miranda-Ribeiro, 1936). BRAZIL 1♂; [Minas Gerais State, Mariana municipality], Serra do Itacolomi; Apr. 1919; José Pinto da Fonseca leg.; (MZSP 22,074), provisionally in ANSP Type 9367. Examined by photos available in Cockroach Species File CSF (Becaloni 2024), by H Hopkins.
- Bionoblatta itatiayae (Miranda-Ribeiro, 1936). BRAZIL. 1♂; without collection data (CEOIC 42315— [invalid catalog number, Márcio Felix 2022, personal communication]); 1♀; Mina Gerais State, Itamonte municipality, Parque Nacional do Itatiaia, Brejo da Lapa; -22.359001, 44.737234; 2142 m a.s.l.; 13 Jan. 2023; AP Pinto, AC Domahovski, J Ehlert & LP Aguiar leg.; active collect; DNA SAMPLE LABSIA 516; DZUP267064. Genitalia from Roth (1970b: figs 209-211).
- Bionoblatta punctata (Saussure, 1873). BRAZIL. 1♂; Minas Gerais State, Ibitipoca, Parque Estadual do Ibitipoca, [-21.7117, -43.9029; 1365 m a.s.l.]; 3–10 Fev. 2019; Tatiana S. & Ana Carolina N. cols [leg.]; (MNRJ 419, MRNJ-ENT2-2209); 1♀; Lima Duarte municiality, Pq. Florestal do Ibitipoca; 21 Fev. [19]90; F. A. da Silveira [leg.]; (UFV).
- *Bionoblatta oiticicai* Rocha e Silva, 1957. **BRAZIL**. 1♂; São Paulo State, Pirassununga municipality; Mar. [1]944; N. Santos leg.; (N° 581 Proc. 446, M.N N. 545, 36, 11, MNRJ-ENT2-11).
- Bionoblatta marcelli. BRASIL 1♂; Mina Gerais State, Catas Altas, Serra do Caraça, Pico do Inficionado, campo rupestre, 1940 m a.s.l.; 23 Mar. 2000, M. F. Vasconcelos leg.; (UFMG IBL 2300000); 1♀; same data but (20°07'S, 43°27'W); 03 Nov. 2017; (MCN-INV B04).
- Parahormetica bilobata (Saussure, 1864). BRASIL 1♂; Paraná State, Monjolinho municipality, [ex-]F. Justus Jr. collection, Jan. [19]43; (DZUP 528060); 1♀; Curitiba municipality, Campus Jardim Botânico UFPR, Matriz I, 13 Mar. 2020; A. P. Pinto & V. A. Silva leg.; (DZUP 266818). Genitalia from Polizeli and Pinto (2024a: figs 7a–d).
- Parahormetica cicatricosa (Saussure, 1869). BRASIL 1♂; Paraná State, Morretes municipality, Estrada da Graciosa, Viaduto Nova Graciosa; -25.3492, -48.8874; 10 Mar. 2024; BR Araujo leg.; (DZUP 267070); 1♀; Campo Largo municipality; 29 Ago. 2020; M.R.S. Tavares leg.; (DZUP 266837; DNA sample LABISIA 402). Genitalia from Polizeli and Pinto (2024a: figs 7e–h).
- Parahormetica monticollis (Burmeister, 1838). BRASIL 1∂; Min[as] Ger[ais State]; Bes[cke] leg. (MLUH); • 1♀; Rio de Janeiro State, Nova Friburgo municipality; [-22.281944, -

42.5308333]; (MLUH). Examined by photos (©2021, Zoological Collection of Martin-Luther University, J. Haendel).

Parahormetica museunacional (Polizeli and Pinto, 2024). BRASIL • 1♂; Paraná State, Norte; [ex-]
F. Justus Jr. collection n° 3103; Mar. [19]44; A. Meister [leg.?]; (DZUP 528062). • 1♀;
Barueri municipality; Dez. 1966; [ex-]MZSP collection n° 1047 (DZUP 266854). Genitalia from Polizeli and Pinto (2024a: figs 7i–1).

Taxon/character	1	2	3	4	5	6	7	8	9	9
	0	0	0	0	0	0	0	0	0	2
1. Panchlora sp.	0000011100	0-0-0010	210000000	1000000051	100000002	0110-11000	000000111	101020000-	00-0100000	00
2. Pycnoscelus surinamensis	0110001001	2010	221-000000	A000000151	1000?-0002	1111010000	0000011010	000-100??-	012110????	??
3. Epilampra sp.	0000001000	0-0-1010	2200000000	1020000121	1000000012	1121011000	1001101010	101000000-	0110010010	00
4. Blaberus giganteus	1000010100	0-0-1010	2200000000	1001001141	10-??00022	01-1011011	0000201010	211000100-	0120010010	10
5. Blaptica formosa	1100000100	0-0-1011	0000000220	1400001141	110?001022	0121010111	0000101011	200001100-	0110-21011	10
6. <i>Monastria</i> sp.	1100000110	0-0-1022	1200100120	1300001001	11000131-0	0000-01111	01-0000-1-	210001100-	00-1110010	10
7. Petasodes dominicana	1100011010	0-0-0002	1202100000	1000001151	110??131-0	0001101011	000000-11	01-000100-	00-0011010	10
8. Phoetalia pallida	0000010020	0-0-1100	0200000000	1000000151	110??00011	1121011000	0000101010	100020000-	01210002	10
9. Tribonium morroferrensis	0110001100	0-0-1011	0100000000	1000001121	1120?131-0	0010-01000	0100000-0-	01-020100-	0?-1-11001	00
10.Lanxoblatta sp.	1001001000	0-0-1021	1100100000	1000001051	112??131-1	0100-01100	0100000-0-	010000100-	0?-001??01	00
11.Zetobora signaticollis	1000010100	0-0-1011	0100000000	1000001000	1120?13001	0110-01100	0100000-11	00?-20100-	00-1110001	00
12.Gen. nov. A sp. nov.	10111-0010	12101A1010	0011000222	-200102131	0101000011	0121110110	0010201111	200111000-	00-11001??	??
13.Gen. nov. B sp. nov.	10111-0010	12??210000	00110013-3	-12010200-	021110-002	0111110110	0010201111	20011?000-	-13??011??	??
14.Brachycola sp.	10101-0010	1111112000	0011000000	0000001111	012??00001	011110-120	0010200-11	210011000-	0121100000	10
15.Lucihormetica fenestrata	10101-0010	1210102100	0011000000	0000001141	012??00001	0111110100	0010201111	200020000-	0121100102	11
16.Quadrihormetica onorei	10111-0010	120-102100	0011000000	0000001151	012??00001	0111110120	00-02?????	200010000-	0021100100	10
17.Hormetica atlas	10111-0010	1110101000	0011000111	-100001131	000??00011	01?1110120	0010201111	2000110101	00-11011??	??
18.Hormetica kemneri	10111-0010	1110002000	0011000111	-100001141	0000000011	0121110120	0010101111	1000110100	00-11011??	??
19.Hormetica laevigatta	10111-0010	1210002010	0011000111	-100001151	0000000011	0121110110	0010101111	1000100100	00-1101002	11
20.Hormetica luteomarginatta	10111-0010	1211102020	0011000000	1000001131	00-??02011	0121110120	0010101111	1000100?0?	-?-11010??	??
21.Sibylloblatta panesthoides	10111-0010	111010?000	001100-222	-400102131	021100-001	01110020	002?????	200-110?0-	012110??02	11
22.Sibylloblatta pustulata	10111-0010	11??21?000	001100-222	-400102131	021?00-002	011?00??	0?-0-?????	-00-1?0200	-14??0?1??	??
23.0xycercus peruvianus	11111-0000	10??21?000	0010011	0	1110-002	01110?012?	0?-0-??-??	000?11-10?	-0-110??01	10
24.Parahormetica bilobata	10111-0010	1210102010	0011000222	-400102131	0201000021	0111110110	0010201111	100011000-	0111101111	10
25.Parahormetica cicatricosa	10111-0010	1210102010	0011000222	-400102131	0201002021	01B1110110	0010201111	100011000-	0111101101	10
26.Parahormetica monticollis	101-110	1110101010	0011000222	-400102131	02-?00-0?1	-10110	00-0-?????	200-11-00-	011110????	??
27.Parahormetica museunacional	110111-1010	1211102020	0011000222	-400102131	0201000021	0111110110	0010201111	200010-00-	0111101001	10
28.Bionoblatta diabolus	10111-0010	12??212010	0011000222	-C10112000	021100-001	0111110120	001020A111	20001?0211	-10??00001	10
29.Bionoblatta hylaeceps	10111010	12??11?000	0011000222	-210112001	02-??0-0-?	?1??0120	00-0-0????	-00-1?0121	-1-??0?1??	??
30.Bionoblatta itatiavae	10111-0010	1211212010	0011000222	-110112000	0201002001	0101110120	0010001111	100-100211	10-110?100	10
31.Bionoblatta marcelli	10111-0010	1210212000	0011000222	-210112151	010??00011	0111110110	0010201111	2000100211	1101101100	10
32.Bionoblatta oiticicai	10110010	12??10?010	0011000222	-1?0112131	02-100-001	01??0120	0?-020????	-00-1?0211	-0-??0?1??	??
33.Bionoblatta punctata	10111-0-10	1211112010	0011000222	-410112000	0211000011	0121110110	0010201111	100111002-	00-1101111	10
7		0				0				

Supplementary Material 2: Morphological dataset matrix with 92 characters and 33 terminal taxa. Polymorphism codes: A = [0,1], B = [1,2], C = [1,4].

#### **6 CONCLUSION**

After the development of this project, the genus *Bionoblatta* comprises now six species. All species have been delimited and can be identified using illustrations, diagnoses and identification key. The type-species *Bion mastrucatus* Rehn, 1937 was recognized as a junior synonym of *Parahormetica hylaeceps* Miranda Ribeiro, 1936, and *Bionoblata marcelli* **sp. nov.** is proposed as a new species. Currently, the genus consists of the following valid nomina: *B. diabolus, B. hylaeceps, B. itatiayae, B. marcelli* **sp.** nov., *B. punctata*, and *B. oiticicai*.

For the first time, a phylogenetic hypothesis covering 46% of the species and 100% of the genera of the tribe Brachycolini is available, which supports it as monophyletic, being the most stable clade in our analyses. Some more inclusive clades within the tribe appear stable (clades B, D, and E) and can show a trend of relationship among taxa. Some relationships among genera and the monophyly of some of them are still inconclusive.

In summary, this study aimed to revise the genus *Bionoblatta* and provide a comprehensive phylogenetic hypothesis for Brachycolini. The results contribute to the taxonomic and phylogenetic knowledge of the group by resolving pertinent issues of the genus *Bionoblatta* and providing objective hypotheses about the phylogenetic relationships of the tribe. Finally, by providing these studies, we hope to contribute proactively to the construction of the scientific knowledge about neotropical cockroaches.

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