



**GUILHERME CARVALHO PRADO**

**ADDRESSING KNOWLEDGE GAPS IN BRAZILIAN  
CAVE FAUNA: DESCRIPTION OF A NEW GENUS AND NEW  
SPECIES OF PSEUDOSCORPIONS (ARACHNIDA:  
PSEUDOSCORPIONES)**

**LAVRAS - MG  
2026**

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Dissertação apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Ecologia Aplicada, área de concentração em Ecossistemas Fragmentados e Agrossistemas, para obtenção do título de Mestre.

Prof. Dr. Rodrigo Lopes Ferreira  
Orientador

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**PREENCHENDO LACUNAS DE CONHECIMENTO NA FAUNA  
CAVERNÍCOLA BRASILEIRA: DESCRIÇÃO DE UM NOVO GÊNERO E NOVAS  
ESPÉCIES DE PSEUDOESCORPIÕES (ARACHNIDA: PSEUDOSCORPIONES)**

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All things are in a process of change. You  
yourself are subject to constant alteration  
and gradual decay. So too is the whole  
universe. (Aurelius 2002)

## ABSTRACT

The Brazilian subterranean biodiversity remains significantly underexplored, a condition that exacerbates the Linnean and Racovitzian shortfalls – the gaps between known species and their actual existence and distribution in nature. This taxonomic impediment is particularly critical for the order Pseudoscorpiones, where the lack of formal descriptions hinders the legal protection of cave environments increasingly threatened by mining and deforestation. This dissertation addresses these gaps by providing a systematic reassessment of the family Chthoniidae in Brazil, integrating historical data with the description of new taxa from the Amazon, Caatinga, and Atlantic Forest biomes. In the first chapter, the long-standing taxonomic inconsistency regarding the "unusual" species *Pseudochthonius orthodactylus* Muchmore, 1970, is resolved. Based on a detailed morphological analysis of type material and new specimens, the genus *Kayapochthonius* **gen. nov.** is established. This new genus is distinguished by robust, straight chelae and a highly developed chelal apodeme, traits that bridge the morphological gap between *Pseudochthonius* and *Aphrastochthonius*. Within this framework, *P. orthodactylus* is reallocated as *Kayapochthonius orthodactylus* **comb. nov.**, and two new species are described: *Kayapochthonius bacaba* **sp. nov.**, from the ferruginous landscapes of Carajás (PA), and *Kayapochthonius diamantinus* **sp. nov.**, from a cave in Chapada Diamantina (BA). The second chapter focuses on the diversity of the genus *Pseudochthonius* in northeastern Brazil, describing three new species from limestone caves in Ceará state: *Pseudochthonius ubajara* **sp. nov.**, *P. andyratinga* **sp. nov.**, and *P. tejussuoca* **sp. nov.**. Morphological features, such as elongated appendages and reduced ocular structures, led to the classification of *P. ubajara* **sp. nov.** and *P. andyratinga* **sp. nov.** as troglobionts, while *P. tejussuoca* **sp. nov.** is considered a troglophile. Furthermore, this study reports the first documented case of syntopy within the genus *Pseudochthonius*, with *P. ubajara* **sp. nov.** and *P. andyratinga* **sp. nov.** co-occurring in Morcego Branco Cave. Collectively, these results demonstrate that the diversity of Brazilian cave-dwelling pseudoscorpions is significantly underestimated. By formalizing these descriptions and providing identification keys, this work contributes essential data for environmental impact assessments and the legal safeguarding of Brazil's speleological heritage, ensuring that these unique evolutionary lineages receive the protection required by current legislation.

**Keywords:** Amazon, Caatinga, Cave-dwelling, Syntopy, Taxonomy.

## RESUMO

A biodiversidade subterrânea brasileira permanece significativamente subexplorada, condição que exacerba os déficits Linneano e Racovitziano – as lacunas entre as espécies conhecidas e sua real existência e distribuição na natureza. Esse impedimento taxonômico é particularmente crítico para a ordem Pseudoscorpiones, onde a falta de descrições formais dificulta a proteção legal de ambientes cavernícolas crescentemente ameaçados pela mineração e pelo desmatamento. Esta dissertação aborda essas lacunas ao fornecer uma reavaliação sistemática da família Chthoniidae no Brasil, integrando dados históricos com a descrição de novos táxons dos biomas Amazônia, Caatinga e Mata Atlântica. No primeiro capítulo, é resolvida a inconsistência taxonômica de longa data relativa à espécie "incomum" *Pseudochthonius orthodactylus* Muchmore, 1970. Com base em uma análise morfológica detalhada do material-tipo e de novos espécimes, o gênero *Kayapochthonius* **gen. nov.** é estabelecido. Este novo gênero distingue-se pelas quelas robustas e retas e por um apódema quelal altamente desenvolvido, características que preenchem a lacuna morfológica entre *Pseudochthonius* e *Aphrastochthonius*. Dentro deste contexto, *P. orthodactylus* é realocado como *Kayapochthonius orthodactylus* **comb. nov.**, e duas novas espécies são descritas: *Kayapochthonius bacaba* **sp. nov.**, das paisagens ferruginosas de Carajás (PA), e *Kayapochthonius diamantinus* **sp. nov.**, de uma caverna na Chapada Diamantina (BA). O segundo capítulo foca na diversidade do gênero *Pseudochthonius* no nordeste do Brasil, descrevendo três novas espécies de cavernas calcárias no estado do Ceará: *Pseudochthonius ubajara* **sp. nov.**, *Pseudochthonius andyratinga* **sp. nov.** e *Pseudochthonius tejussuoca* **sp. nov.**. Atributos morfológicos, como apêndices alongados e estruturas oculares reduzidas, levaram à classificação de *P. ubajara* **sp. nov.** e *P. andyratinga* **sp. nov.** como troglóbios, enquanto *P. tejussuoca* **sp. nov.** é considerado troglófilo. Além disso, este estudo relata o primeiro caso documentado de sintopia no gênero *Pseudochthonius*, com a coocorrência de *P. ubajara* **sp. nov.** e *P. andyratinga* **sp. nov.** na Gruta do Morcego Branco. Coletivamente, estes resultados demonstram que a diversidade de pseudoescorpiões cavernícolas brasileiros é significativamente subestimada. Ao formalizar estas descrições e fornecer chaves de identificação, este trabalho contribui com dados essenciais para processos de licenciamento ambiental e para a salvaguarda legal do patrimônio espeleológico do Brasil, garantindo que estas linhagens evolutivas únicas recebam a proteção exigida pela legislação vigente.

**Palavras-chave:** Amazônia, Caatinga, Cavernas, Sintopia, Taxonomia.

## **SOCIAL, TECHNOLOGICAL, ECONOMIC AND CULTURAL IMPACTS**

Subterranean biodiversity is a vital component of global biological heritage, yet it remains significantly underexplored due to the shortfalls. This lack of knowledge represents a critical taxonomic impediment, as the formal description of species is a legal prerequisite for the conservation of cave environments under Brazilian legislation. This dissertation addresses these gaps through the systematic study of the family Chthoniidae, resulting in the establishment of the new genus *Kayapochthonius* **gen. nov.** and the description of five new species: *K. bacaba* **sp. nov.**, *K. diamantinus* **sp. nov.**, *Pseudochthonius ubajara* **sp. nov.**, *P. andyratinga* **sp. nov.**, and *P. tejussuoca* **sp. nov.**. These discoveries represent a significant technological and theoretical advance in Brazilian arachnology, utilizing taxonomic methods and high-resolution imaging technologies to resolve historical inconsistencies. The cultural impact of this research is highlighted by the naming of the genus *Kayapochthonius*, which honors the Kayapó Indigenous people and their traditional territories in the Amazon. Economically and socially, the results provide essential data for environmental licensing and conservation decisions in regions under high anthropogenic pressure, such as the ferruginous landscapes of Carajás and the karst areas of Chapada Diamantina and Ubajara. By identifying troglobitic species – which are strictly restricted to subterranean environments – this work directly informs legal protection strategies that determine whether these habitats are preserved or slated for suppression. The study also possesses a strong extensionist character, involving a collaborative network of scientists and students from the Center for Studies in Subterranean Biology (CEBS/UFLA) and the American Museum of Natural History (AMNH), alongside interaction with environmental consultancy firms. The documentation of the first case of syntopy in the genus *Pseudochthonius* further expands the ecological understanding of cave communities. These impacts are aligned with the National Extension Policy thematic areas of Environment, Education, and Culture, and contribute directly to UN Sustainable Development Goal 15 (Life on Land) by halting biodiversity loss, as well as Goal 4 (Quality Education) through scientific training and specialized knowledge production. Ultimately, this research provides the necessary scientific foundation to safeguard Brazil's speleological heritage and ensure the long-term persistence of unique evolutionary lineages.

## SUMMARY

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## FIRST PART

### 1 INTRODUCTION

Pseudoscorpions (Arachnida: Pseudoscorpiones) comprise a monophyletic lineage of small predatory arthropods (BENAVIDES et al., 2019; HARVEY et al., 2025). with a global distribution across terrestrial habitats on six continents, excluding Antarctica (JEONG et al., 2026). They inhabit a variety of environments, including leaf litter, under bark or stones, bird nests, and animal burrows (TURBANOVA et al., 2025). Some families (e.g., Chernetidae and Cheliferidae) are known for specific displacement capabilities, where many species use phoresy – hitching rides on larger animals – to disperse (MUCHMORE, 1971; POINAR et al., 1998); and others (e.g., Chthoniidae, Pseudotyranochthoniidae, Ideoroncidae, Neobisiidae) host species adapted to subterranean environments, that often exhibit troglomorphic traits, such as the absence of eyes, elongation of the appendices and depigmentation (ČERVENÁ et al., 2021). This diverse group of arachnids comprises 27 families (including one extinct family), 477 extant genera, and approximately 4350 species (WORLD PSEUDOSCORPIONES CATALOG, 2022).

In Brazil, 189 species of pseudoscorpions have been recorded, distributed across 16 families and 68 genera (WORLD PSEUDOSCORPIONES CATALOG, 2022; GUIMARÃES et al., 2025). Among these, ten families are found in caves, with some representatives (e.g., Chthoniidae, Chernetidae, Ideoroncidae and Bochicidae) exhibiting troglomorphic adaptations (SCHIMONSKY et al., 2019; VIANA & FERREIRA, 2020). The family Chthoniidae stands out for its diversity, with over 800 species distributed across 51 genera worldwide (WORLD PSEUDOSCORPIONES CATALOG, 2022).

In this group, 11 genera are recorded from Brazil, with *Pseudochthonius* being the most abundant in species richness (23 spp.). The distribution of this genus in the country spans six states across four regions (WORLD PSEUDOSCORPIONES CATALOG, 2022). Traditionally, distinctive characteristics are used as diagnosis, such as plumose coxal spines on coxae I and II and the "S-shaped" form of the chelae, apart from *Pseudochthonius orthodactylus* Muchmore 1970, which lacks this configuration (CHAMBERLIN, 1929).

Despite the richness of the Brazilian pseudoscorpion fauna, it remains largely underexplored. Foundational work was conducted by prominent 19<sup>th</sup> and 20<sup>th</sup> century authors (e.g., Balzan, Banks, Beier, Chamberlin, Ellingsen, Mello-Leitão, With, and Tömösváry), who collectively contributed to approximately 43% of the current records (WORLD PSEUDOSCORPIONES CATALOG, 2022). Today, taxonomic descriptions have improved

significantly in quality, increasingly integrating other disciplines and imaging technologies, which naturally requires more preparation time. Consequently, the relative scarcity of active taxonomists acts as a severe taxonomic impediment (ENGEL et al., 2021). This impediment directly exacerbates the Linnean shortfall – the critical gap between the number of described species and the actual number of species in nature (BRITO, 2010).

This linnean gap is further complicated by the Racovitzan shortfall, which represents the lack of knowledge regarding species distributions due to under-samples habitats. Brazil is estimated to have approximately 300,000 caves (AULER, 2019), yet only about 30,000 are officially registered (CANIE), and even a smaller fraction has been properly sampled for fauna. The taxonomic impediment, combined with these shortfalls, leaves a vast amount of subterranean biodiversity unrecorded and unprotected.

The taxonomic impediment acts as a barrier to resolving the Linnean, Darwinian, and Racovitzian shortfalls, which highlight gaps in knowledge about species existence, their distributions, and their ecological roles in subterranean habitats. This stasis directly impacts the conservation of caves, which are recognized as national heritage but are increasingly threatened by quarry operations and deforestation. Conservation decisions often rely on knowing whether troglobiont species (organisms restricted to subterranean environments) inhabit areas slated for suppression (Pellegrini *et al.* 2023). According to Decree No. 6,640 of 2008, which provides for the protection of natural subterranean cavities within the national territory, the presence of such species can determine whether these habitats are preserved or destroyed (BRASIL, 2008).

This stasis in biodiversity description has direct and immediate impacts on the conservation of caves. Subterranean ecosystems are recognized as national heritage but are increasingly threatened bby quarry operations and deforestation. Environmental licensing and conservation decisions rely heavily on knowing whether troglobiont species (organisms strictly restricted to subterranean environments\_ inhabit areas slated for suppression. According to the current legislation (Decree No. 10,935), the documented presence of such endemic and specialized species can determine whether these habitats are preserved or legally destroyed. Therefore, there is an urgent need to formally describe these species to ensure their legal protection.

The present work has three aims: First, to describe a new genus for Chthoniidae based on two new species from northern and northeastern Brazil, respectively, and the reassessment of a previously described species, *Pseudochthonius orthodactylus* Muchmore, 1970 – originally referred to as “an unusual *Pseudochthonius* from Brazil” and historically treated as an exception to the genus diagnosis (PRADO & FERREIRA, 2024). Second, to better understand the

morphological relationships within *Pseudochthonius*, a challenging genus frequently found in caves, marked by historical inconsistencies in its descriptions and third, to describe three new species, detailing the first documented case of syntopy among Brazilian Pseudoscorpiones.

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**SECOND PART****2 MANUSCRIPT I**

A NEW GENUS OF PSEUDOSCORPIONS (Pseudoscorpiones: Chthoniidae): A  
SYSTEMATIC REASSESSMENT OF AN “UNUSUAL” CHTHONIID FROM BRAZIL

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A new genus of Pseudoscorpions (Pseudoscorpiones: Chthoniidae): a systematic reassessment of an “unusual” chthoniid from Brazil

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## Abstract

The genus *Pseudochthonius* Balzan, 1892 (Arachnida: Pseudoscorpiones: Chthoniidae) has traditionally been characterized by the presence of plumose coxal spines and sigmoid chelae. However, *Pseudochthonius orthodactylus* Muchmore, 1970 has long been regarded as an exception to this diagnosis due to its straight chelae and distinctive chelal dentition. Based on a detailed examination of the type material, from Ducke Reserve, Manaus, Amazonas, together with newly collected specimens from Pará state and the Semi-Arid region, we herein propose the new genus *Kayapochthonius* **gen. nov.** This genus is distinguished by robust, straight chelae, a well-developed chelal apodeme, and acute, well-separated teeth on both chelal fingers. The type species is accordingly transferred to *Kayapochthonius orthodactylus* (Muchmore, 1970) **comb. nov.** In addition, two new species are described: *Kayapochthonius bacaba* **sp. nov.**, from the ferruginous landscapes of Carajás, Pará, and *Kayapochthonius diamantinus* **sp. nov.**, from a cave in Chapada Diamantina, Bahia. These results resolve long-standing taxonomic inconsistencies, bridging the morphological gap between *Pseudochthonius* and *Aphrastochthonius*, and highlight the importance of conserving subterranean habitats in regions under high anthropogenic pressure.

**Keywords:** Amazon, Cave-dwelling, Taxonomy, Pseudoscorpiones

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## Background

Pseudoscorpions (Arachnida: Pseudoscorpiones) are small predatory arthropods with a worldwide distribution across terrestrial ecosystems, including subterranean habitats, where some species exhibit pronounced troglomorphic adaptations (Viana & Ferreira 2019). Within the order, the family Chthoniidae is among the most diverse, comprising more than 800 described species distributed across 51 genera globally (World Pseudoscorpiones Catalog 2022). In Brazil, Chthoniidae is particularly well represented, with *Pseudochthonius* Balzan, 1892 standing out as the most speciose genus, with 23 species described. Species of *Pseudochthonius* are recorded from four Brazilian regions and also occur in Africa, Asia, Europe, and Central America (World Pseudoscorpiones Catalog 2022).

Traditionally, the diagnosis of *Pseudochthonius* has relied primarily on the presence of plumose coxal spines on coxae I and II and, most notably, on the characteristic sigmoid (“S-shaped”) configuration of the chelae. These traits are consistently observed in nearly all species

of the genus, including an extinct representative, with a single notable exception: *Pseudochthonius orthodactylus* Muchmore, 1970. Collected from leaf litter, at Ducke Reserve, near Manaus, Amazonas state, Brazil, this species has long posed a challenge to the generic concept due to its straight (non-sigmoid) chelae, a distinct chelal dentition, and additional taxonomically informative features that have not been previously emphasized, including the morphology of the chelal apodeme and the apical setae of the manducatory process. Although Muchmore (1970) recognized a close morphological affinity between *P. orthodactylus* and the North American genus *Aphrastochthonius* Chamberlin, 1962, he conservatively retained the species within *Pseudochthonius* to avoid destabilizing the taxonomy at the time. Notably, he explicitly acknowledged that compelling arguments existed for the establishment of a separate genus, a point later briefly mentioned by Mahnert (2001), yet the systematic placement of the species remained unresolved.

Interestingly, recent biodiversity surveys in cave conducted in the Brazilian Amazon and the Brazilian Semi-Arid region have led to the discovery of two previously unknown species that share a suite of morphological synapomorphies with *P. orthodactylus*. These shared characters include straight chelae, identical trichobothrial patterns, comparable morphology of the fixed and movable chelal fingers, and a similarly developed chelal apodeme. Despite their wide geographic separation, both regions are subject to intense anthropogenic pressures (Araujo et al., 2023; Pellegrini et al., 2022), underscoring the importance of accurate species delimitation and taxonomic resolution for environmental impact assessments and the legal protection of vulnerable habitats.

The recognition of these new species demonstrates that *P. orthodactylus* does not represent an isolated morphological anomaly but instead belongs to a morphologic distinct lineage. This lineage warrants formal separation from *Pseudochthonius* and from its closest known relative, *Aphrastochthonius*. Although members of this lineage resemble *Aphrastochthonius* in chelal configuration, they lack several diagnostic features of that genus, including the lateral transverse short seta at the apex of the manducatory process and the bisetose intercoxal tubercle, differences that are addressed in detail below.

Accordingly, this study proposes the establishment of a new genus within Chthoniidae, based on the newly discovered species from the Brazilian Amazon and Semi-Arid regions, together with the reallocation of *Pseudochthonius orthodactylus*. By formalizing this taxonomic framework, we aim to resolve long-standing systematic ambiguities, clarify morphological boundaries between *Pseudochthonius* and *Aphrastochthonius*, and contribute to a more comprehensive understanding of subterranean biodiversity in Brazil.

## Materials and methods

### Study area

#### *Carajás*

The Serra dos Carajás region is part of the Dissected Plateau of Southern Pará, characterized by residual massifs with flat or undulating summits and lower-lying terrains. The area includes Serra Norte, Serra Leste (where *Kayapochthonius bacaba* **sp. nov.** was collected), Serra da Bocaina, Serra do Tarzan, and Serra Sul, with elevations averaging 700 meters and altitudinal differences of 300 meters (Piló & Auler 2009).

Locally called *Canga* plateaus, the Serra dos Carajás highlands feature ferruginous duricrust overlying Archean ferriferous rocks from the Carajás Formation (Grão-Pará Group). These plateaus, renowned for their ecological and geological significance, host unique evolutionary processes and hold some of the world's largest iron ore reserves, making this region a crucial Ferruginous Geosystem (Piló & Auler 2009). The specimens were collected from multiple incursions to the region, in October 2014; August, July and September 2015; March, April, May, June and October 2016; July 2019 and January, February and October 2020. Such material is from environmental analysis for iron mining companies; the collects were done by several consultancy companies.

#### *Chapada Diamantina*

Located in central Bahia, northeastern Brazil, the Chapada Diamantina is a major geological and geomorphological region covering roughly 65,600 km<sup>2</sup> and encompassing dozens of municipalities (Parra et al, 2025). It acts as an important hydrological divide, channeling surface waters westward to the São Francisco River basin and eastward to Atlantic-draining systems, particularly the Paraguaçu River. The landscape is marked by rugged mountain chains, extensive plateaus, and well-developed karst features, shaped through a long geological history involving sedimentary and metasedimentary rocks of Proterozoic age within the structural context of the São Francisco Craton (Pedreira, 1997; Pereira, 2010). This complex evolution underpins the region's distinctive topography, hydrology, and mineral resources. Climatically, Chapada Diamantina is influenced by tropical atmospheric circulation and strong altitudinal gradients, resulting in a tropical highland climate with moderate temperatures and pronounced seasonality in rainfall. Mean annual temperatures are around 24 °C, with average precipitation close to 1,060 mm, concentrated mainly in a humid season from December to March and followed by a well-defined dry period between June and September (INMET, 2022), patterns that strongly regulate ecological dynamics and water availability across the region.

### **Field sampling**

Fieldwork for the collection of recent material was conducted during multiple campaigns in October 2014; August, July, and September 2015; March, April, May, June, and October 2016; July 2019; and January, February, and October 2020. These surveys were carried out as part of several research initiatives led by scientists from the Center for Studies in Subterranean Biology, as well as projects associated with environmental consultancy companies, all focusing primarily on cave community ecology. Sampling was performed using untimed direct intuitive searches (*sensu* Wynne et al., 2019). All invertebrate specimens were carefully collected with a fine brush and preserved in vials containing 70% ethanol.

### **Analysis and preparation**

Field sampled specimens were examined under a Zeiss Axio Scope A1 stereomicroscope, with measurements and observations supported by ZEN 2012 software. Detailed illustrations of the coxae were prepared using a drawing tube attached to a Leica DM750 optical microscope. Images of additional structures, fine morphological details, and measurements were obtained with a Zeiss Axio Zoom V16 microscope and processed using ZEN 2.1 software. All images were subsequently vectorized in Inkscape 1.1 (Montesanto 2015; available at: [inkscape.org](http://inkscape.org)). The male holotype of *Kayapochthonius orthodactylus* **comb. nov.** was examined at American Museum of Natural History (AMNH) by using a U3CMOS series microscopy camera attached on a light microscope. The holotype of the two new species is deposited in the Subterranean Invertebrates Collection of Lavras (ISLA). The holotype of *Kayapochthonius orthodactylus* **comb. nov.** is still deposited at AMNH.

### **Terminology**

Terminology follows Chamberlin (1931), Harvey (1992), Judson (2007) and Zaragoza (2017).

### **Results**

#### **Family Chthoniidae Daday, 1889**

#### **Subfamily Chthoniinae Daday, 1889**

#### **Genus *Kayapochthonius* gen. nov.**

#### **Type species: *Pseudochthonius orthodactylus* Muchmore, 1970**

**Etymology.** The generic name *Kayapochthonius* refers to the Caiapó (also spelled Kayapó) Indigenous people of Brazil, whose traditional territories encompass parts of north

Brazil, including regions where representatives of this genus occur. The name should be treated as a noun in apposition.

**Diagnosis.** *Kayapochthonius* most closely resembles *Pseudochthonius*, as they share the following combination of characters: Plumose coxal spines arranged transversally on coxae I and II; two large apical setae at the apex of the manducatory process; *sb* trichobothrium closer to *b* than to *st*; *ame* not abutting or adjacent to the epistome but displaced towards *al* seta. They differ as follows: straight and robust chelae (slender and s-shaped chelae in *Pseudochthonius*); well developed and sclerotized chelal apodeme (short and barely visible in *Pseudochthonius*) and acute and well separate teeth on both chelal fingers, with or without alternate dentition (*Pseudochthonius* with acute but more constricted teeth).

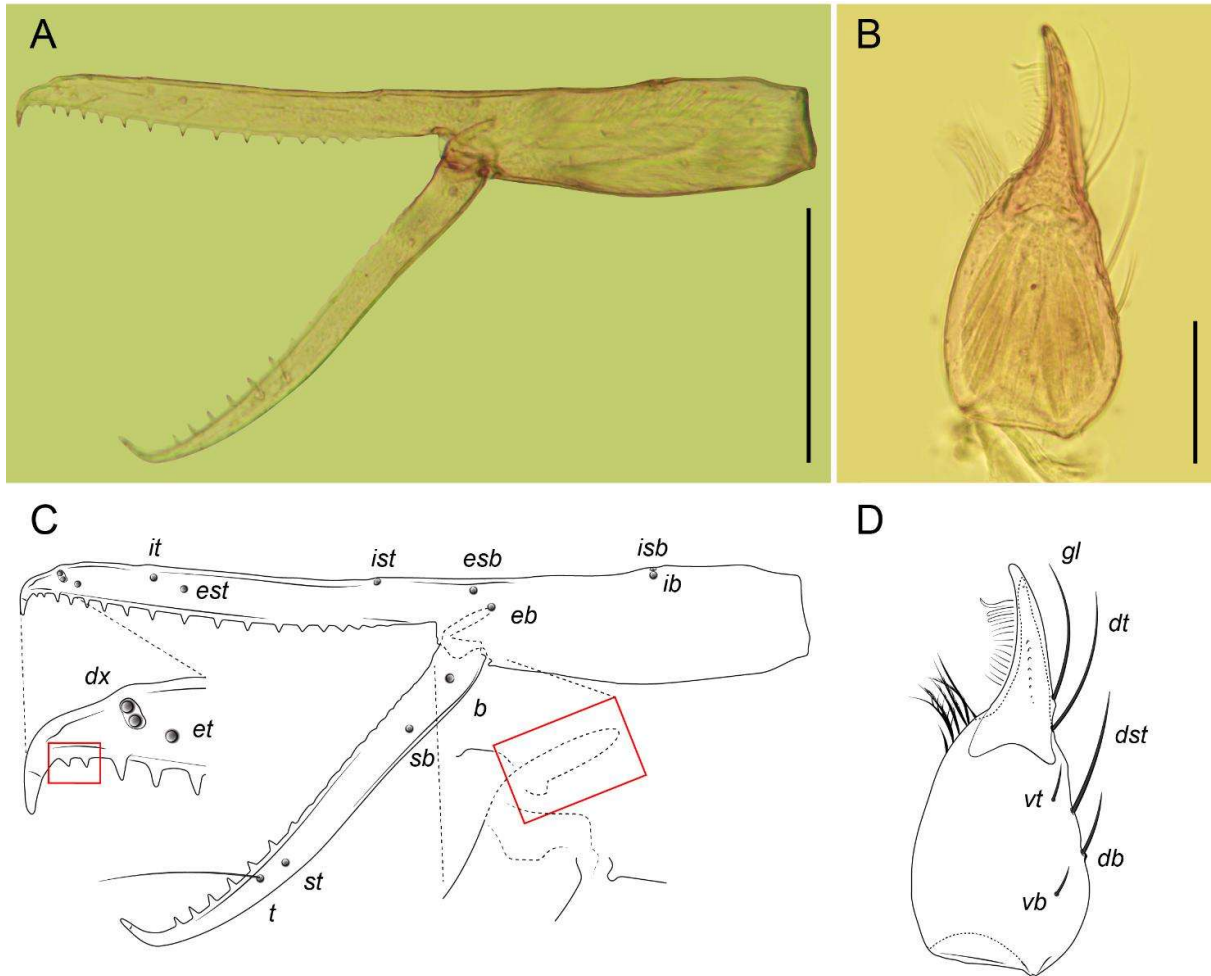
**Remarks.** The new genus has some resemblance to *Aphrastochthonius* by the shape and dentition of the chelae, but it differs by the absence of lateral short thin and turned medially setae at the apex of the maxilla; by the absence of intercoxal tubercle and by the arrangement of the setae in the male genitalia, characteristics that resembles the genus *Pseudochthonius* along with the presence of 7 pinnate blades on the rallum and the position of the *ist* trichobothrium somewhere between *esb* and *est* and not grouped as in *Aphrastochthonius*.

***Kayapochthonius orthodactylus* comb. nov.**

Figs 1, 2.

**Material examined.** **Holotype** adult male (WM 634.01001), preserved in ethanol: Belém, Pará, Brazil, 8 February 1959, leg. A. M. Nadler. **Other Material.** MPEG.PSE 000142 (5 males and 2 tritonymphs), preserved in ethanol: Belém, Pará, Fazenda Velha, Estrada da CEASA, 04 December 1974, leg. Silva, S., det. Mahnert, V. MPEG.PSE 000145 (1 male), preserved in ethanol: Mocambo, Belém, Pará, Brazil, no date, det. Mahnert, V. MPEG.PSE 000150 (1 tritonymph), same locality and det. as previous. MPEG.PSE 000152 (1 male and 1 female), preserved in ethanol: Parque Estadual do Utinga, Belém, Pará, Brazil, 09 March 1977, det. Mahnert, V.z

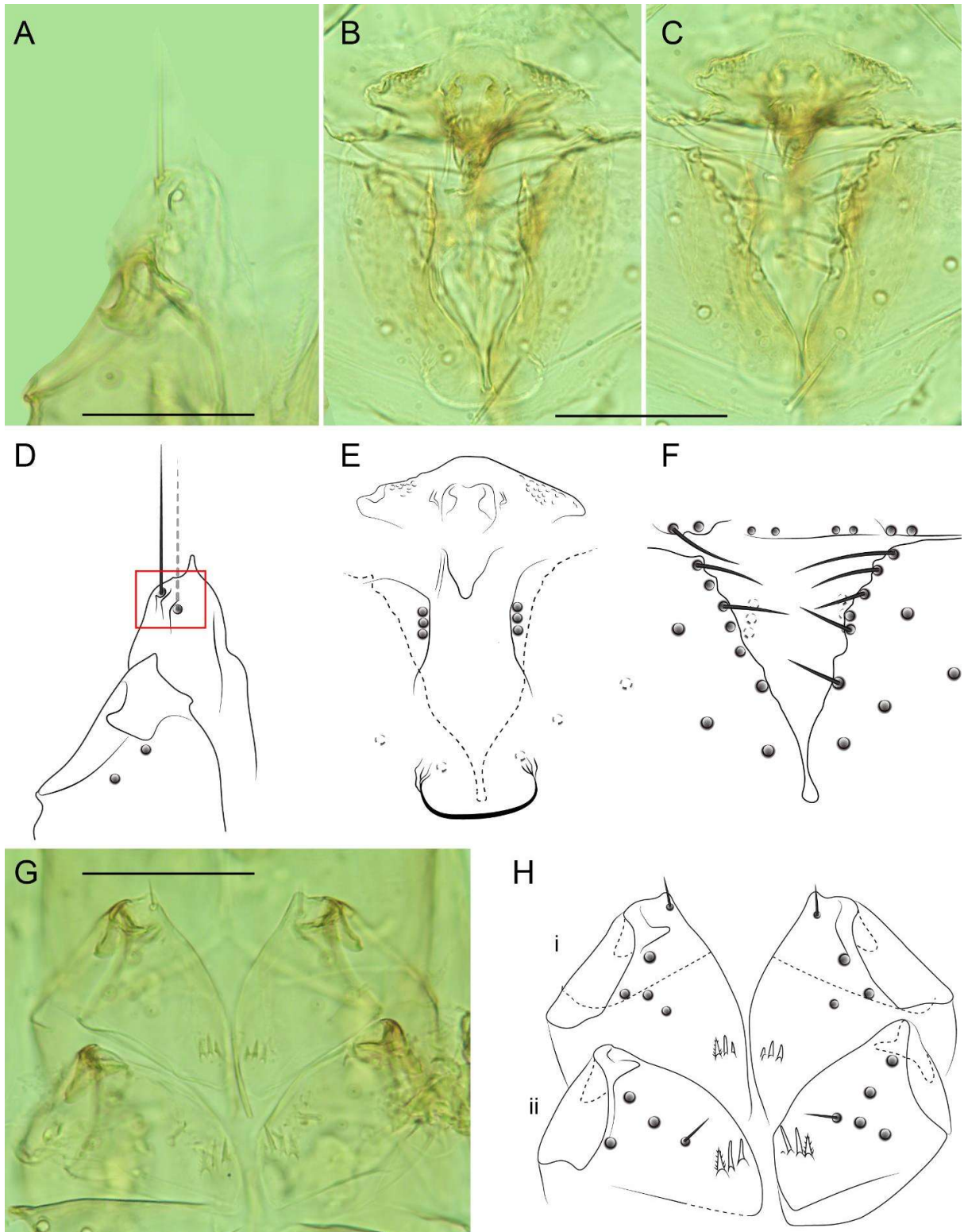
**Diagnosis.** *Kayapochthonius orthodactylus* **comb. nov.** resembles *Kayapochthonius diamantinus* **sp. nov.** as they exhibit two well-developed eyes, large acute and spaced teeth on fixed and movable chelal fingers and large chelal apodemes. They differ from each other in the following combination of characteristics: *Kayapochthonius diamantinus* **comb. nov.** with *esb-ist/ist-est* ratio of 1.86–1.96 (*K. diamantinus* **sp. nov.** with trichobothrial ratio of 1.01) and *K. orthodactylus* with two acute small teeth at tip of chelal fixed finger (*K. diamantinus* **sp. nov.** lacks the trait).



**Figure 1.** *Kayapochthonius orthodactylus* **comb. nov.** male holotype (WM 634.01001). **A** Optic microscopic image of left chela, antiaxial view. **B** Optic microscopic image of left chelicera, antiaxial view. **C** Illustration of left chela, highlighting distal microteeth and apodeme, antiaxial view. **D** Illustration of left chelicera, antiaxial view. Scale bars: 0.1 mm (B, D), 0.2 mm (A, C).

**Complementary description.** Genital operculum of male (Figs 2B–C, E–F). Anterior genital operculum (2<sup>nd</sup> tergite) with 8 discal setae (4 groups of 2 setae [Figs 2C, F]), posterior genital operculum (3<sup>rd</sup> tergite) with 6 marginal setae on each side, and 4 setae along the sternite with 3 microlateral setae on each side, near the spiracle [Fig. 2C, F].

Coxal area (Figs 2A, D, G, H). Manducatory process with 2 apical setae (lateral ones slightly dislocated dorsal-anteriorly [Figs 2A, D]); palpal coxae with 3 setae arranged in a triangle; delicate lamellae outlined by 7 small spines. Pedal: plumose coxal spines arranged transversally in coxae I (3) and II (3) (Figs 2G, H), chaetotaxy: 3–4(1): 4–5: 7–8: 7; intercoxal tubercle absent.



**Figure 2.** *Kayapochthonius orthodactylus* **comb. nov.** male holotype (WM 634.01001). **A** Left manducatory process, ventral view. **B** Medial region of male genitalia, ventral view. **C** External region of male genitalia, ventral view. **D** Illustration of left manducatory process, highlighting apical setae, ventral view. **E** Illustration of medial male genitalia. **F** Illustration of external male genitalia setae. **G** Coxae I and II ventral view.

H Illustration of coxae I and II, exhibiting setae and coxal spines arrangement. Scale bars: 0.1 mm (B–C, E–F), 0.2 mm (A, D, G, H).

***Kayapochthonius bacaba* sp. nov.**

Figs 3A–F.

**Material examined.** **Holotype** male (MPEG.PSE 000004), preserved in ethanol: Bacaba, Canaã dos Carajás Municipality, Brazil, (-6.382661, -49.980997), 30 March 2017, Col. Carste LTDA *et al.* **Allotype** female (MPGE.PSE 000006), same location, date and collector as holotype. **Paratype** male (MPGE.PSE 000005), same location, date and collector as holotype.

**Etymology.** The specific epithet refers to the type locality, Bacaba, located in the municipality of Canaã dos Carajás, Pará state, Brazil. The name is to be treated as a noun in apposition.

**Diagnosis.** *Kayapochthonius bacaba* sp. nov. resembles *Kayapochthonius orthodactylus* comb. nov. in exhibiting two well-developed eyes, large acute and spaced teeth on a single row on both fixed and movable chelal fingers, and large chelal apodemes. The two species can be distinguished by the following combination of characters: *Kayapochthonius bacaba* sp. nov. presents an *esb-ist/ist-est* trichobothrial ratio of approximately 2.82–3.09 (*K. orthodactylus* comb. nov. with a ratio of 1.86–1.96); *K. bacaba* sp. nov. lacks the two small acute teeth at the tip of the chelal fixed finger that are present in *K. orthodactylus* comb. nov.; *K. bacaba* sp. nov. with larger space between teeth on fixed chelal finger, with 5 distal teeth from the tip to *est* trichobothrium (*K. orthodactylus* comb. nov. with 7 distal teeth from the tip to *est* trichobothrium), and on movable chelal finger, with 4 distal teeth from the tip to *st* trichobothrium (*K. orthodactylus* comb. nov. with 6 distal teeth from the tip *st* trichobothrium and *K. bacaba* sp. nov. with second and third distal teeth on cheliceral movable finger highly grouped on a small hump (*K. orthodactylus* comb. nov. lacks this trait state).

**Description.** *Adults, male and female.* Body pale, slightly translucent; chelicerae slightly darker, abdomen beige. Vestitural setae thin and anteriorly projected on the prosoma and posteriorly projected on the opisthosoma

Chelicera (Fig. 3D). Hand with 5 setae (fig. 3D); movable finger with 1 subbasal seta; galea present as a tubercle in female; fixed finger with 12 small acute teeth and well distinguishable (Fig. 3B); movable finger with 9 small acute teeth and well distinguishable (second and third grouped on a single hump [fig. 3D]), including a distal one slightly displaced from the main teeth row; rallum with 7 unilaterally pinnate blades; serrulae exterior and interior with 11 blades.

Palp (Figs 3B, C). Trochanter 1.22–1.56 times longer than wide, patella 1.99–2.23 times longer than wide, femur 5.78–5.87 times longer than wide. Femur chaetotaxy 5: 4: 3: 5: 1. Trichobothrial pattern: *ib* and *isb* located at the half portion of the hand, adjacent to each other, *eb* proximal to *esb*, *ist* distal to *esb*, *it* proximal to *est*, *et* proximal to *dx*; *ist* almost exactly between *esb* and *est* (ratio distance  $ist-est/ist-esb = 2.82-3.09$ ). Fixed and movable chelal finger straight (Fig. 3B). Fixed chelal finger with 11 acute and well-separate teeth (2 small distal ones), and two micro distal teeth at tip (Fig. 3B). Movable finger with 5 distal acute and well separate teeth, and about 6 basal vestigial teeth.

Cephalothorax (Fig. 3A). 1.18 times longer than broad; anterior margin fully serrated; two small eyes present; epistome small, triangular and serrate; posterior margin of carapace smooth; chaetotaxy: 4(2): 4: 4: 2: 2 (18).

Abdomen. Pleural membrane papillate; tergites and sternites undivided, setae uniseriate and acuminate. Tergal chaetotaxy 4: 4: 4: 4: 5: 6: 6: 7: 6: 2. Sternal chaetotaxy (3)10(3): (3)8(3): (1)6(1): (1)6(1): (1)6(1): 4: 4sen: 2sen: (1sen)2(1sen). Anal operculum with 2 ventral setae and without dorsal ones.

Coxal area. Manducatory process with 2 apical setae (lateral ones slightly dislocated dorsally); palpal coxae with 3 setae arranged in a triangle; delicate lamellae outlined by 9 small spines. Pedal: plumose coxal spines arranged transversally in coxae I (2–3) and II (3–4), chaetotaxy: 3(1): 5: 7: 7; intercoxal tubercle absent.

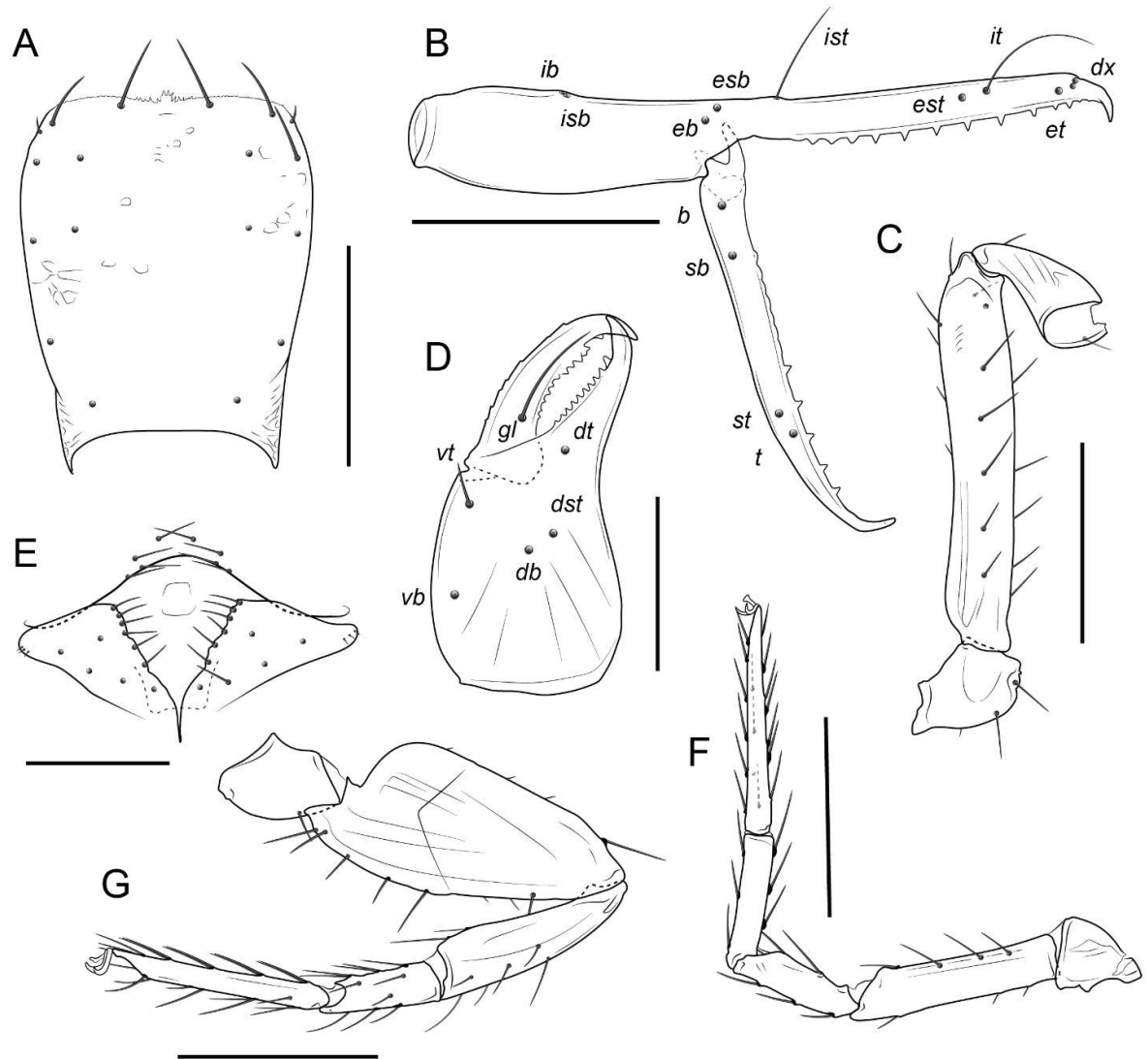
Leg IV (Fig. 3G). Arolia simple and undivided, slightly shorter than claws.

Genital operculum of male (Fig. 3E). Anterior genital operculum (2<sup>nd</sup> tergite) with 8 discal setae (2 apical and a lateral cluster of 3 setae on each side [Fig. 3E]), posterior genital operculum (3<sup>rd</sup> tergite) with 6 marginal setae on each side, and 5 setae along the sternite with 3 microlateral setae on each side, near the spiracle [Fig. 3E]).

Genital operculum of female. setae distributed in 3 transversal rows (2: 2: 2), genital opening bifurcated.

Measurements (length/width or depth in mm and ratios in parenthesis calculated using three significant digits). Male holotype (female paratype in brackets). Body length 1.226 [0.974]. Carapace 0.357 / 0.302 (1.18) [0.313 / 0.265 (1.18)]. Palps: trochanter 0.101 / 0.083 (1.22) [0.122 / 0.078 (1.56)], femur 0.476 / 0.081 (5.88) [0.399 / 0.069 (5.78)], patella 0.181 / 0.091 (1.99) [0.156 / 0.070 (2.23)], chela 0.691 / 0.125 (5.53) [0.569 / 0.086 (6.61)], movable finger length 0.360 [0.303]. Leg I: trochanter [0.093 / 0.069 (1.35)], femur 0.235 / 0.054 (4.35) [0.213 / 0.051 (4.18)], patella 0.143 / 0.043 (3.33) [0.131 / 0.037 (3.54)], femur/patella 1.643 [1.626], tibia 0.148 / 0.030 (4.93) [0.136 / 0.031 (4.39)], tarsus 0.244 / 0.028 (8.71) [0.229 /

0.026 (8.81)]. Leg IV: Trochanter: 0.097 / 0.080 (1.21) [0.120 / 0.077 (1.56)], femur + patella 0.380 / 0.149 (2.55) [0.326 / 0.141 (2.31)], tibia 0.251 / 0.062 (4.05) [0.216 / 0.061 (3.54)], basitarsus 0.134 / 0.046 (2.91) [0.121 / 0.041 (2.95)], telotarsus 0.246 / 0.027 (9.11) [0.221 / 0.026 (8.5)].



**Figure 3.** *Kayapochthonius bacaba* sp. nov. male holotype (MPEG.PSE 000004). **A** Carapace, dorsal view. **B** Right chela, antiaxial view. **C** Left pedipalp, dorsal view **D** Left chelicera, dorsal view **E** Male genital operculum, ventral view **F** Leg I, antiaxial view **G** Leg IV, antiaxial view. Scale bars: 0.1 mm (E), 0.2 mm (A–D, F–G).

***Kayapochthonius diamantinus* sp. nov.**

Figs 4A–G.

**Material examined.** **Holotype** female (ISLA 151511, Fig. 5D, E), preserved in ethanol: Igatu district, Andaraí Municipality, Brazil, Lava Pé Cave (-12.895138, -41.317972), 17 September 2008, leg. R.L Ferreira. **Paratype** tritonymph (ISLA 151512), same location, date and collector as holotype.

**Etymology.** The specific epithet is an adjective from the toponym Chapada Diamantina, referring to the type locality region. This term should be treated as an adjective in apposition.

**Diagnosis.** *Kayapochthonius diamantinus* **sp. nov.** resembles *Kayapochthonius orthodactylus* **comb. nov.** in exhibiting two well-developed eyes and large chelal apodemes. The two species can be distinguished by the following combination of characters: *Kayapochthonius diamantinus* **sp. nov.** presents an *esb-ist/ist-est* trichobothrial ratio of approximately 1.01 (*K. orthodactylus* **comb. nov.** with a ratio of 1.86–1.96), lacks the two small acute teeth at the tip of the chelal fixed finger that are present in *K. orthodactylus* **comb. nov.**, the new species presents alternate teeth row (heterodonty) (21 acute and well-separate teeth on total, the 15 distal ones in alternate rows on fixed chelal finger and movable chelal finger with 20 teeth (10 distal ones acute, well separate and in alternate rows), *K. orthodactylus* **sp. nov.** with a single simple row of 15 teeth on fixed chelal finger and 6 teeth on movable chelal finger.

**Description.** *Female adult.* Body pale, slightly translucent; chelicerae slightly darker, abdomen beige. Vestitural setae thin and anteriorly projected on the prosoma and posteriorly projected on the opisthosoma.

Chelicera (Fig. 4B). Hand with 5 setae (fig. 4B); movable finger with 1 subbasal seta; galea present as a tubercle in female; fixed finger with 10 small acute teeth and well distinguishable (Fig. 4B); movable finger with 9 small acute teeth and well distinguishable, including a distal one slightly displaced from the main teeth row; rallum with 7 unilaterally pinnate blades; serrulae exterior and interior with 12 blades.

Palp (Figs 4C, F). Patella 2.16 times longer than wide, femur 5.08 times longer than wide. Femur chaetotaxy 5: 3: 4: 6: 1. Trichobothrial pattern: *ib* and *isb* located at the half portion of the hand, adjacent to each other, *eb* proximal to *esb*, *ist* distal to *esb*, *it* proximal to *est*, *et* proximal to *dx*; *ist* almost exactly between *esb* and *est* (ratio distance *ist-est/ist-esb* = 1.02). Fixed and movable chelal finger straight (Fig. 4C). Fixed chelal finger with 21 acute and well-separate teeth (the 15 distal ones in alternate rows, giving an impression of heterodonty [fig. 4C]), including an acute distal lateral tooth (Fig. 4C). Movable finger with 20 teeth (10 distal ones acute, well separate and in alternate rows [Fig. 4C], 10 basal ones rounded and vestigial).

Cephalothorax (Fig. 4A). 1.0 times longer than broad; anterior margin partially serrated (ranging from epistome to seta *ame*); two eyes present; epistome small, rounded and serrate; posterior margin of carapace smooth; chaetotaxy: 4(2): 4: 4: 2: 2 (18).

Abdomen: Pleural membrane papillate; tergites and sternites undivided, setae uniseriate and acuminate. Tergal chaetotaxy 4: 4: 4: 4: 6: 6: 6: 6: 6: 2. Sternal chaetotaxy (3)10(3): (3)8(3): (1)6(1): (1)6(1): (1)6(1): 6: 4sen: 2sen: (1sen)2(1sen). Anal operculum with 2 ventral setae and without dorsal ones.

Coxal area (Fig. 4D). Manducatory process with 2 apical setae (lateral ones dislocated dorsally); palpal coxae with 3 setae arranged in a triangle; delicate lamellae outlined by 7 small spines. Pedal: plumose coxal spines arranged transversally in coxae I (2) and II (3–4), chaetotaxy: 3(1): 5: 7: 8; intercoxal tubercle absent.

Leg IV (Fig. 4E). Arolia simple and undivided, slightly shorter than claws.

Genital operculum of female. setae distributed in 2 transversal rows (4: 2), genital opening bifurcated.

Measurements (length/width or depth in mm and ratios in parenthesis calculated using three significant digits). Female holotype. Body length 1.241. Carapace 0.346/0.345 (1.0). Palps: femur 0.467/0.092 (5.08), patella 0.175/0.081 (2.16), chela 0.658/0.127 (5.18), movable finger length 0.353. Leg I: trochanter 0.089/0.079 (1.13), femur 0.260/0.051 (5.10), patella 0.142/0.042 (3.38), femur/patella 1.831, tibia 0.154/0.032 (4.81), tarsus 0.

*Tritonymph*. Body pale, mostly depigmented, chelicerae and chelae light beige, abdomen pale with tergite plates not distinguishable. Vestitural setae, anteriorly projected on the carapace and posteriorly projected in opisthosoma.

Chelicera. Hand with 5 setae and 1 on the movable finger; galea present as a tubercle; rallum with 6 unilaterally pinnate blades.

Palp. Femur 5.5 x, patella 2.08 x and chela 6.95 times longer than broad, chelal movable finger 1.8 times longer than hand. Fixed chelal finger with 7 trichobothria (*ib*, *eb*, *esb*, *ist*, *est*, *it*, *et*). Fixed chelal finger with 31 acute and widely spaced teeth and two distal micro teeth, and movable chelal finger with 29 teeth, basal ones projected backwards and distal ones acute.

Cephalothorax. 1.19 times longer than broad; eyes absent.

Abdomen. Tergal chaetotaxy 4: 4: 4: 4: 6: 6: 6: 6: 6: 4: 2. Sternal chaetotaxy 2: (2)8(2): (2)8(2): 8: 6: 6: 6: 4: 4: 4. Anal operculum with 2 ventral setae and without dorsal ones.

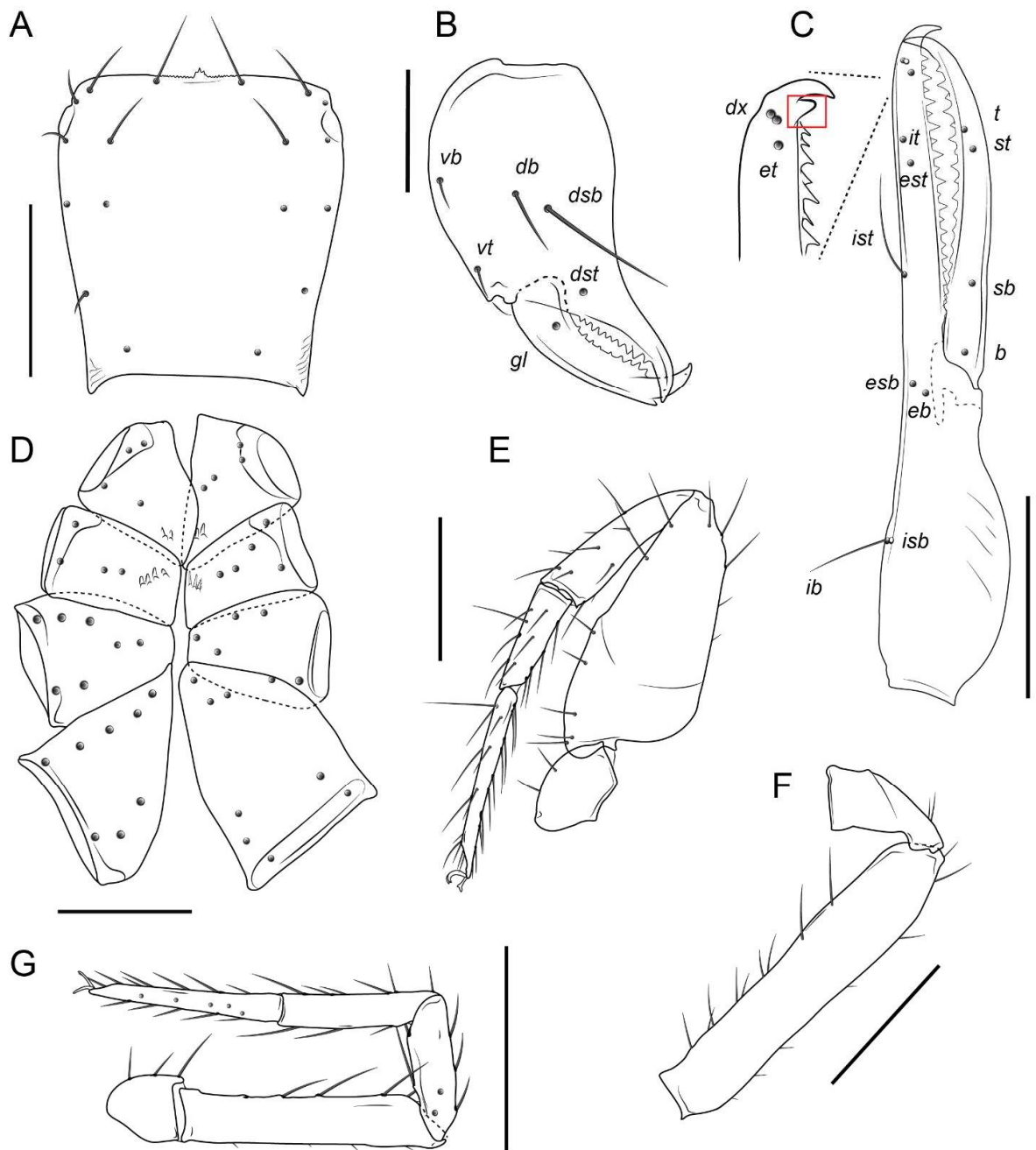
Legs. much as in adults.

Measurements. Body length 1.75. Palps: femur 0.55/0.1, patella 0.21/0.101, chela 0.779/0.112. hand length 0.278, movable finger length 0.501. Carapace 0.592/0.498.

### **Habitat and Threats**

Igatu Village, in the Chapada Diamantina region (Fig. 5A), developed rapidly during the mid-19th century as a major diamond-mining center, with peak extraction between about 1846 and 1871. Mining continued into the early 20th century, but its decline triggered economic contraction and severe depopulation, leaving fewer than 500 residents today. The legacy of this activity is clearly imprinted on the surrounding caves, which exhibit extensive anthropogenic alteration resulting from historical mining (Parra *et al.*, 2025). These modifications include the enlargement of natural conduits and the excavation of artificial galleries, as observed in Lava-pé Cave (the only known locality of *K. diamantinus* **sp. nov.**) where stone walls, accumulations of excavation debris, and rock-cut passages have substantially transformed the original cave morphology (Fig. 5B, C).

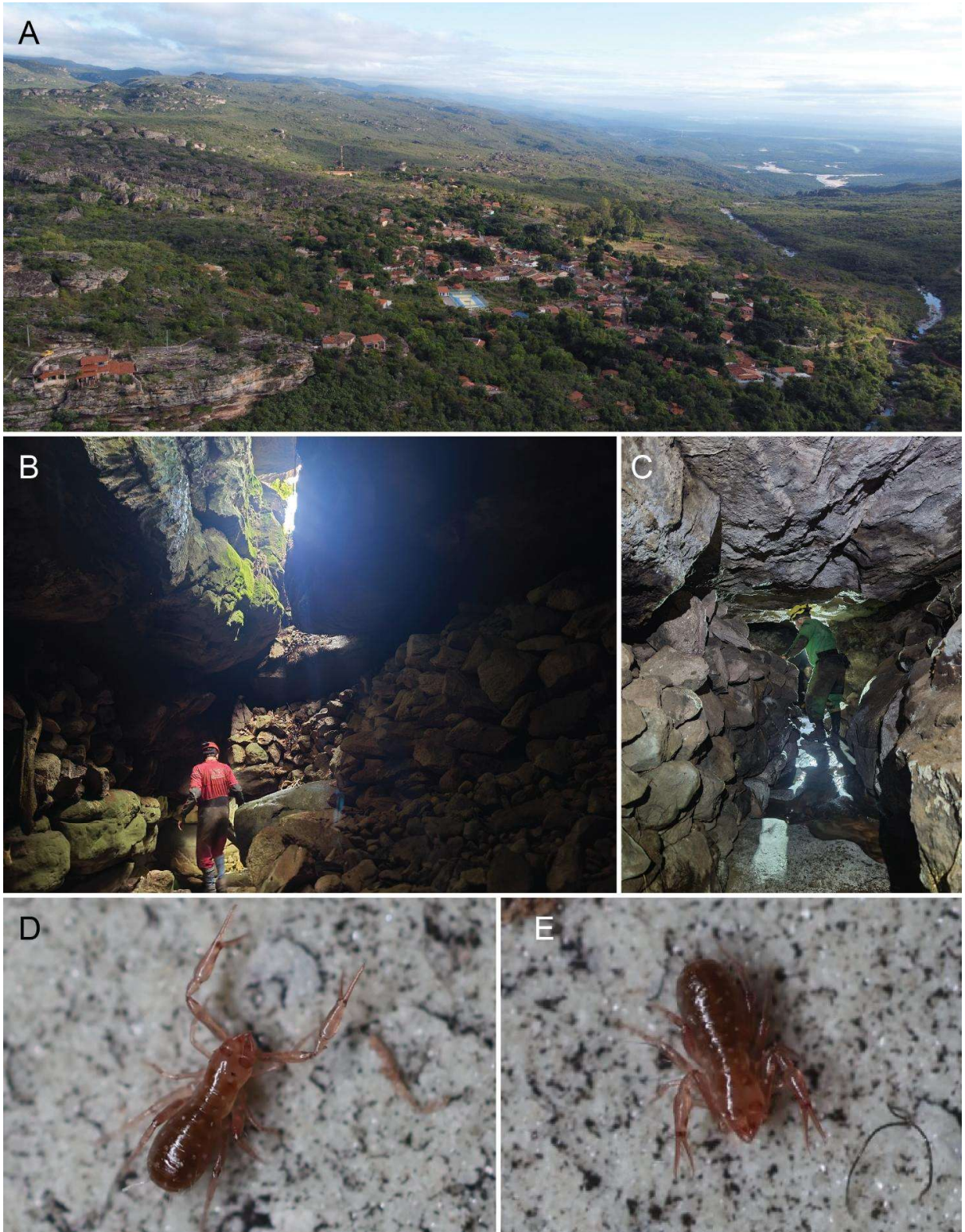
Despite biological surveys conducted in other caves in the region, *K. diamantinus* **sp. nov.** is currently known from a single specimen collected in Lava-pé Cave. The individual was found near an entrance, beneath a rock block on the cave floor. Organic resources within the cave are primarily derived from plant detritus transported by water flow, with minor guano deposits. These resources sustain springtail populations, which are likely to constitute prey for *K. diamantinus* **sp. nov.** Given the absence of conspicuous troglomorphic traits, it is plausible that the species also occurs in epigeal habitats; however, the lack of targeted surface sampling prevents any assessment of its true distribution.



**Figure 4.** *Kayapochthonius diamantinus* sp. nov. female holotype (ISLA 151511). **A** Carapace, dorsal view. **B** Right chelicera, dorsal view. **C** Right chela, antiaxial view **D** Coxae region, ventral view **E** Leg IV, antiaxial view **F** Right pedipalp, dorsal view **G** Leg I, antiaxial view. Scale bars: 0.1 mm (B, D), 0.2 mm (A, C, E–G).

Considering that the species is presently known from a single, heavily disturbed cave, further research is strongly recommended. Future efforts should prioritize surveys in additional caves and surrounding surface environments, as well as the establishment of monitoring

programs at known sites, to better assess population status and identify potential threats to the long-term persistence of the species.



**Figure 5.** Habitat and habitus of *Kayapochthonius diamantinus* **sp. nov.** **A** Igatu municipality. **B** Lava Pé cave main entrance. **C** Conduct of collection of the new species at Lava Pé cave **D** Female holotype habitus, with extended palps **E** Female holotype habitus, with retracted palps.

### Discussion

The understanding of Chthoniidae diversity in Brazil has long been hindered by taxonomic inertia and historical gaps. Early taxonomic work on the family within the country was conducted predominantly by foreign researchers during the late 19<sup>th</sup> and early-to-mid 20<sup>th</sup> centuries (e.g. Balzan, Banks, Beier, Chamberlin, Ellingsen, Mello-Leitão, With, and Tömösváry). Despite a marked increase in species descriptions over recent decades (particularly within the genus *Pseudochthonius*) the broader systematic framework of Brazilian chthoniids has remained largely unchanged. This taxonomic inertia has likely contributed to an underestimation of generic diversity among Brazilian Chthoniidae (Assis et al., 2021; von Schimonsky et al., 2022; Prado & Ferreira, 2023, 2024; von Schimonsky, 2024; Guimarães et al., 2025a, b).

Importantly, the notion that chthoniid diversity in Brazil has been historically underestimated is not new. More than five decades ago, Muchmore (1970) reported the discovery of an “unusual” pseudoscorpion from the Amazon, described as *Pseudochthonius orthodactylus*, and explicitly noted that this taxon did not conform well to existing generic concepts (Muchmore, 1970; Mahnert, 1979). In the original description – based solely on a single male – Muchmore emphasized morphological similarities between *P. orthodactylus* and the North American genus *Aphrastochthonius*, interpreting shared traits (such as straight, robust chelae, well-separated teeth on both chelal fingers, and a well-developed chelal apodeme) as representing a plesiomorphic condition within Chthoniidae (Muchmore, 1970). Subsequently, Mahnert (1979), through the examination of additional material from the Brazilian Amazon, attributed new specimens to *P. orthodactylus*, thereby expanding both its known morphological variation and geographic distribution. The present study builds upon and reinforces these observations, which gain additional significance as the morphological diversity of *Pseudochthonius* continues to be more thoroughly explored.

The establishment of *Kayapochthonius* **gen. nov.** resolves these historical taxonomic inconsistencies. The recognition of this new genus is supported by a consistent set of morphological characters, including features of the chelae, manducatory structures, and coxal chaetotaxy, which in combination clearly distinguish this lineage from *Pseudochthonius* and other closely related chthoniid genera, such as *Aphrastochthonius*. Furthermore, morphological

analysis reveals that these diagnostic traits are conserved across both male and female specimens, reinforcing the stability and validity of this new group.

The description of *Kayapochthonius diamantinus* **sp. nov.** further elucidates this evolutionary pattern. This species exhibits a combination of characters interpreted as plesiomorphic, particularly with respect to chelal morphology, including straight chelal fingers and acute teeth on both the fixed and movable fingers (Muchmore 1970). At the same time, it displays traits traditionally associated with *Pseudochthonius*, such as apparent heterodont dentition (Mahnert 2001). However, as previously noted by Mahnert (2001) and subsequent authors, this apparent heterodonty likely results from alternating tooth displacement rather than from true differentiation in tooth type. When examined in ventral view, the chelal dentition exhibits a biseriata arrangement, producing the visual effect of alternating larger and smaller teeth in antiaxial view, a pattern also documented by Assis et al. (2021) in *Pseudochthonius lubueno*.

Taken together, this mosaic of character states supports the interpretation of *Kayapochthonius* as a distinct evolutionary lineage that retains ancestral features while also sharing derived traits with *Pseudochthonius*. This combination of morphological attributes provides robust justification for the recognition of *Kayapochthonius* as a new genus within Chthoniidae.

**Author's contributions:** All authors contributed equally to the manuscript.

**Competing interests:** GCP and RLF declare that they have no conflict of interest.

**Availability of data and materials:** The collected materials are deposited in the Coleção de Invertebrados Subterrâneos de Lavras (ISLA). Type material of *Kayapochthonius orthodactylus* **comb. nov.** is deposited at American Museum of Natural History (AMNH).

**Consent for publication:** Not applicable.

**Ethics approval consent to participate:** Not applicable.

#### **List of Abbreviations**

Abbreviations for the trichobothria: *b* = basal; *sb* = sub-basal; *st* = sub-terminal; *t* = terminal; *ib* = interior basal; *isb* = interior sub-basal; *ist* = interior sub-terminal; *it* = interior terminal; *eb* = exterior basal; *esb* = exterior sub-basal; *est* = exterior sub-terminal; *et* = exterior terminal. Other abbreviations: *al* = anterolateral setae of carapace; *ame* = anteromedial setae of carapace; *an* = anterior setae row of carapace; *il* = intermedian lateral setae of carapace; *in* = intermedian setae row of carapace; *me* = median setae row of carapace; *ml* = median lateral

setae of carapace; *mm* = median medial setae of carapace; *oc* = ocular setae row of carapace; *ol* = lateral ocular setae of carapace; *om* = medial ocular setae of carapace; *osl* = sublateral ocular setae of carapace; *pl* = posterolateral setae of carapace; *pm* = posteromedial setae of carapace; *po* = posterior setae row of carapace. Abbreviations for repositories: ISLA = Coleção de Invertebrados Subterrâneos de Lavras; AMNH = American Museum of Natural History.

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### 3 MANUSCRIPT II

THREE CAVE-DWELLING *Pseudochthonius* (Pseudoscorpiones: Chthoniidae) FROM  
NORTHEASTERN BRAZIL, WITH THE FIRST DOCUMENTED CASE OF SYNTOPY IN  
THE GENUS.

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Three new cave-dwelling *Pseudochthonius* (Pseudoscorpiones: Chthoniidae) from northeastern Brazil, with the first documented case of syntopy in the genus

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Date of submission: 26/11/2025

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## Abstract

Three new pseudoscorpion species (Arachnida: Pseudoscorpiones: Chthoniidae), *Pseudochthonius ubajara* **sp. nov.**, *Pseudochthonius andyratinga* **sp. nov.** (both cave-restricted) and *Pseudochthonius tejussuoca* **sp. nov.** are herein described from caves in northeastern Brazil. These species exhibit a combination of diagnostic traits that clearly differentiate them from their congeners, including distinctive chelal dentition, male genital morphology, ocular structures, and morphometric features. In addition, we provide ecological notes for each species, outline potential threats to their habitats, and present an identification key to the *Pseudochthonius* species of northeastern Brazil. Finally, we report and discuss the first documented case of syntopy within the genus *Pseudochthonius*.

**Keywords:** Cave-dwelling, co-occurrence, taxonomy, troglomorphisms, Pseudoscorpiones

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## Background

Pseudoscorpions are a meso-diverse order of small predatory arachnids that inhabit a wide variety of environments, including leaf litter, bark, stones, bird nests, and mammal burrows. Numerous species also occur in subterranean habitats (particularly caves) where they may exhibit traits associated with subterranean adaptation (Harms 2018; Viana et al. 2021). Their diversity is distributed across 27 families (including one extinct) and 476 extant genera (World Pseudoscorpiones Catalog 2024).

Among these families, Chthoniidae is the most species-rich, reflecting its nearly global distribution, with approximately 954 valid species recorded from all continents except Antarctica. In the Neotropics, most chthoniid species descriptions date to the 1990s, while recent taxonomic advances have been concentrated in the genus *Pseudochthonius* Balzan, 1892 (Assis et al. 2021; Schimonsky et al. 2022; Prado and Ferreira 2023 2024; Schimonsky 2024; Guimarães et al. 2025a 2025b), which includes approximately 46% of the Brazilian representatives of the family.

The genus *Pseudochthonius* is characterized by the presence of plumose transverse coxal spines on coxae I and II, and by the sigmoid shape of the chelae (except in *Pseudochthonius orthodactylus* Muchmore, 1970, which lacks this trait) (Muchmore 1970). Species may possess

fully developed eyes, reduced ocular structures, or be completely anophthalmic, a condition frequently associated with subterranean environments (Prado & Ferreira 2024).

In addition to the formal descriptions of three new species, this study provides a comparative assessment of their morphology relative to other regional congeners, detailed ecological observations with emphasis on potential threats, and a brief account of the occurrence of two distinct *Pseudochthonius* species within a single cave.

## **Materials and methods**

### **Study area**

Specimens of *P. ubajara* **sp. nov.** and *P. andyratinga* **sp. nov.** were collected in three and one limestone caves, respectively, within Ubajara National Park (PARNA Ubajara), situated in the northwestern portion of Ceará State, Brazil (Fig. 9A). Established in 1959, the park was created primarily to safeguard the Ubajara Cave. The area harbors notable paleontological sites (De Oliveira 2011; De Oliveira 2017; Trajano and Ferrarezzi 1995) and serves as a refuge for several threatened species (Machado et al. 2008), underscoring its conservation importance. The regional climate is classified as tropical hot sub-humid (Aw, Köppen–Geiger), with mean annual temperatures ranging from 22 to 26 °C and an average annual rainfall of approximately 1,277 mm (De Oliveira 2019). Precipitation is concentrated in the rainy season, which occurs from January to April (mean monthly values between 134 and 265 mm), whereas the dry season extends from July to October, when rainfall is markedly reduced (1.8–18.5 mm).

Specimens of *P. tejuçuoca* **sp. nov.** were collected in a limestone cave located within the Parque Municipal de Tejuçuoca, also known as Parque Ecológico Furna dos Ossos (Fig. 9C). This protected area lies about 12–13 km southwest of the town of Tejuçuoca, in the north-central region of Ceará state. The climate is classified as tropical semi-arid (BSh, Köppen–Geiger), characterized by consistently high temperatures (between 26 °C and 28 °C), irregular rainfall restricted to a few months, and a prolonged dry season, with an average annual rainfall of approximately 660 mm. The vegetation cover corresponds to Caatinga, which in this locality is relatively well preserved and exhibits structural and compositional heterogeneity. The geological setting is marked by karst formations, including caves and sinkholes, developed in metacalciferous rocks such as marble and crystalline limestones, underlain by metamorphic units of the Ceará Complex (NEED REFS).

### **Field sampling**

Fieldwork was conducted in December 2006, September 2008, September 2019, September 2024, and April 2025 as part of several research initiatives led by scientists from the

Center for Studies in Subterranean Biology, focusing on cave community ecology surveys, followed untimed direct intuitive searches (sensu Wynne et al. 2019). All invertebrates were carefully collected using a fine brush and preserved in vials containing 100% ethanol.

### **Analysis and preparation**

Specimens were examined under a Zeiss Axio Scope A1 stereomicroscope, with measurements and observations supported by ZEN 2012 software. Detailed illustrations of the coxae and male genitalia were prepared using a drawing tube attached to a Leica DM750 optical microscope. Images of additional structures, fine morphological details, and measurements were obtained with a Zeiss Axio Zoom V16 microscope and processed using ZEN 2.1 software. All images were subsequently vectorized in Adobe Illustrator 2020. The holotype, allotype, and paratypes are deposited in the Subterranean Invertebrates Collection of Lavras (ISLA).

### **Terminology**

Terminology follows Chamberlin (1931), Harvey (1992), Judson (2007) and Zaragoza (2017).

### **Results**

<http://zoobank.org/urn:lsid:zoobank.org:pub:F9B1B430-7481-43F8-ADCE-1D91D38A09B2>

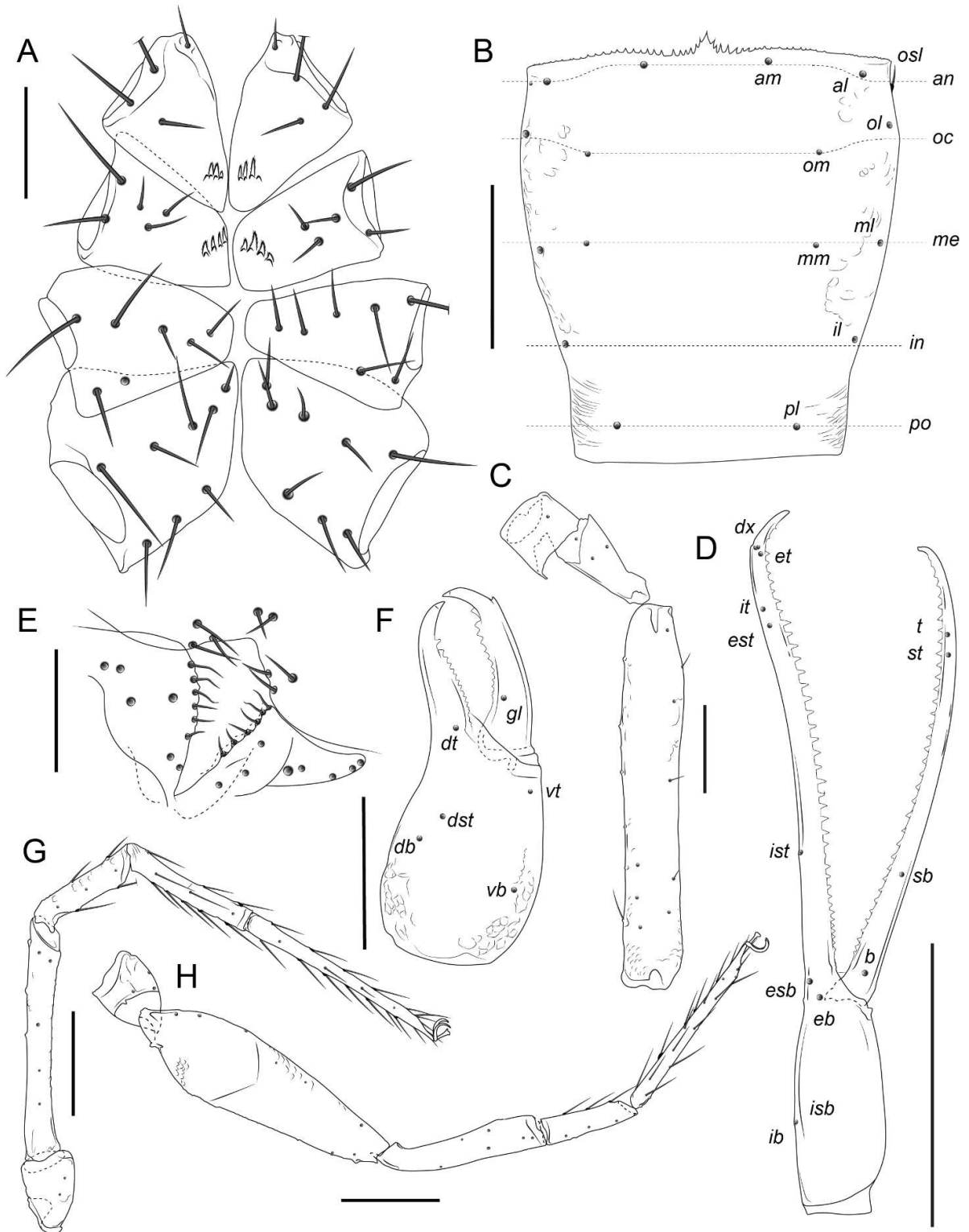
### **Family Chthoniidae Daday, 1889**

### **Subfamily Chthoniinae Daday, 1889**

### **Genus *Pseudochthonius* Balzan, 1892**

### ***Pseudochthonius ubajara* sp. nov.**

Figs 5A–H.



**Figure 1.** *Pseudochthonius ubajara* sp. nov. **A** Male holotype (ISLA 151472) coxal region **B** Female allotype (ISLA 151473) carapace, dorsal view **C** Female allotype pedipalp, dorsal view **D** Female allotype right chela, antiaxial view **E** Male holotype genitalia **F** Female allotype right chelicera, dorsal view **G** Female allotype

right leg I, antiaxial view **H** Female allotype right leg IV, paraxial view. Scale bars: 1 mm (**A**, **E**); 2 mm (**B–D**, **F–H**).

**Material examined. Holotype** male (ISLA 151472, Fig. 4C), preserved in ethanol: Ubajara, Ceará, Brazil, Ubajara Cave (-3.831611 E, -40.898599 N), 12 April 2025, leg. R.L Ferreira. **Allotype** female (ISLA 151473), same location, date and collector as holotype. **Paratypes:** tritonymph (ISLA 151476) and female (ISLA151477), Gruta do Urso Fóssil Cave (-3.832953 E, -40.892814 N), 26 September 2019, leg. R.L Ferreira; deutonymph, two females and a male (ISLA 151478), same location as tritonymph, 15 April 2025, leg. R.L Ferreira; one male and one female (ISLA 151474), same location as holotype, 30 December 2006, leg. R.L Ferreira; female (ISLA 151475), Gruta do Morcego Branco Cave (-3.831453 E, -40.900264 N), 13 April 2025, leg. R.L Ferreira.

**Etymology.** The specific epithet is an adjective formed from the toponym Ubajara, referring to the type locality. This term should be treated as a noun in apposition.

**Diagnosis.** The new species most resembles *Pseudochthonius aware* Prado and Ferreira 2024 by the absence of eyes or eyespots, anterior margin of the carapace fully serrated, number and morphology of the chelal fixed finger dentition, *et* trichobothrium near *dx* and *ist* trichobothrium twice as near to *esb* than to *est* – represented by ratio distance *ist-est/ist-esb* close to 2.0. *Pseudochthonius ubajara* **sp. nov.** differs from *P. aware* in the following combination of characteristics: chelal movable finger teeth medially and distally acute and basally projected backwards (*P. aware* with tiny and projected backwards teeth on chelal movable finger), slightly isolated tooth on cheliceral fixed finger (*P. aware* lacks the trait), two microteeth at tip of chelal fixed finger (*P. aware* with only one microtooth), male genitalia discal setae arranged in groups (*P. aware* with male genitalia discal setae equally sparse, not forming any clusters) and chelal length of 1.122 – 1.245 (*P. aware* chelal length of 0.871–0.884).

**Description** (Fig. 4C). *Adults.* Body pale, slightly translucent; chelicerae slightly darker, abdomen beige. Vestitural setae thin and anteriorly projected on the prosoma and posteriorly projected on the opisthosoma.

Chelicera (Fig. 1F). Hand with 5 setae; movable finger with 1 subbasal seta; galea present as a tubercle in females and absent in males; fixed finger with 11–13 well separate teeth (including a distally isolated inclined tooth) decreasing in size towards the base (Figs 1F); movable finger with 12 small and well defined teeth, including a small isolated acute tooth; rallum with 7 unilaterally pinate blades, including a distal large one; serrulae exterior with 13 and interior with 11 blades, respectively. Similar in females?!

Palp (Figs 1C, D). Trochanter 1.85 (1.56), patella 2.49 (2.59) and femur 5.65 (6.08) times longer than wide. Femur chaetotaxy 6: 4: 2: 6: 2. Trichobothrial pattern: *ib* and *isb* located at the half portion of the hand, adjacent to each other and slightly dislocated to the paraxial face of the chela, *eb* proximal to *esb*, *ist* distal to *esb*, *it* proximal to *est*, *et* proximal to *dx*; *ist* almost exactly two times closer to *esb* than to *est* (ratio distance  $ist-est/ist-esb = 1.76-2.04$ ). Fixed and movable chelal finger bent (Fig. 1D). Fixed chelal finger with 34–37 acute teeth (5 distal small, 22–23 medial heterodont [alternate] and 7–10 proximal round ones); tip of fixed chelal finger with two micro teeth. Movable finger with 32–38 teeth (distal and medial teeth acute and basal ones slightly projected backwards) (Fig. 1D).

Cephalothorax (Fig. 1B). 1.22 (1.05) times longer than broad, constricted posteriorly showing a difference between ocular width and posterior width of 0.1 (0.06) mm; anterior margin fully serrated; eyes absent; epistome large, acute and with two adjacent projections (Fig. 5B); posterior margin of carapace smooth; chaetotaxy 4(2): 4: 4: 2: 2 (18).

Abdomen. Pleural membrane papillate; tergites and sternites undivided, setae uniseriate and acuminate; tergal chaetotaxy 4: 4: 4: 4: 4: 6: 6: 6: 6: 4: 2, sternal chaetotaxy (3)10(3)–(3)12(3): 8: 8: 8: 8: 6: 5: 4. Anal operculum with 2 ventral setae and without dorsal ones.

Coxal area (Fig. 1A). Manducatory process with 2 apical setae (medial ones slightly dislocated forwards); palpal coxae with 3 setae arranged in a triangle; delicate lamellae outlined by 10 small spines. Pedal: plumose coxal spines arranged transversally in coxae I (3–4) and II (4), chaetotaxy: 3(1): 5: 7: 8–9; intercoxal tubercle absent.

Leg IV (Fig. 1H). Arolia simple and undivided, slightly longer as claws.

Genital operculum of male (Fig. 1E). Anterior genital operculum (2<sup>nd</sup> tergite) with 8 discal setae (2 apical and a lateral cluster of 3 setae on each side [Fig. 1E]), posterior genital operculum (3<sup>rd</sup> tergite) with 6 marginal setae on each side, and 5 setae along the sternite with 3 microlateral setae on each side, near the spiracle [Fig. 1E]).

Genital operculum of female. 6 setae distributed in two horizontal rows (2: 4), genital opening bifurcated.

Measurements (length/width or depth in mm and ratios in parenthesis calculated using three significant digits). Male holotype (female paratype in brackets). Body length 1,173 [1.596]. Carapace 0.429 / 0.351 (1.22) [0.494 / 0.469 (1.05)]. Palps: trochanter 0.226 / 0.122 (1.85) [0.228 / 0.146 (1.56)], femur 0.778 / 0.145 (5.36) [0.841 / 0.136 (6.18)], patella 0.333 / 0.134 (2.49) [0.342 / 0.132 (2.59)], chela 1.122 / 0.153 (7.33) [1.166 / 0.154 (7.57)], movable finger length 0.744 [0.766]. Leg I: trochanter 0.147 / 0.107 (1.37) [0.102 / 0.104 (0.98)], femur 0.424 / 0.075 (5.65) [0.426 / 0.070 (6.08)], patella 0.217 / 0.067 (3.24) [0.231 / 0.053 (4.36)],

femur/patella 1.954 [1.844], tibia 0.234 / 0.051 (4.59) [0.243 / 0.045 (5.4)], tarsus 0.406 / 0.037 (10.97) [0.403 / 0.039 (10.33)]. Leg IV: Trochanter: 0.145 / 0.121 (1.2) [0.195 / 0.112 (1.74)], femur + patella 0.631 / 0.179 (3.53) [0.65 / 0.196 (3.32)], tibia 0.422 / 0.081 (5.21) [0.425 / 0.078 (5.45)], basitarsus 0.227 / 0.063 (3.6) [0.222 / 0.062 (3.58)], telotarsus 0.432 / 0.034 (12.71) [0.437 / 0.036 (12.14)].

*Tritonymph*. Body pale, mostly depigmented, chelicerae and chelae light beige, abdomen pale with tergite plates not distinguishable. Vestitural setae, anteriorly projected on the carapace and posteriorly projected in opisthosoma.

Chelicera. Hand with 5 setae and 1 on the movable finger; galea present as a tubercle; rallum with 7 unilaterally pinnate blades.

Palp. Femur 5.5 x, patella 2.08 x and chela 6.95 times longer than broad, chelal movable finger 1.8 times longer than hand. Fixed chelal finger with 7 trichobothria (*ib, eb, esb, ist, est, it, et*). Fixed chelal finger with 31 acute and widely spaced teeth and two distal micro teeth, and movable chelal finger with 29 teeth, basal ones projected backwards and distal ones acute.

Cephalothorax. 1.19 times longer than broad; eyes absent.

Abdomen. Tergal chaetotaxy 4: 4: 4: 4: 6: 6: 6: 6: 6: 4: 2. Sternal chaetotaxy 2: (2)8(2): (2)8(2): 8: 6: 6: 6: 4: 4: 4. Anal operculum with 2 ventral setae and without dorsal ones.

Legs. much as in adults.

Measurements. Body length 1.75. Palps: femur 0.55/0.1, patella 0.21/0.101, chela 0.779/0.112. hand length 0.278, movable finger length 0.501. Carapace 0.592/0.498.

*Deutonymph*. Body, chelicerae and chelae depigmented, abdomen pale light beige. Vestitural setae, anteriorly projected on the carapace and posteriorly projected in opisthosoma.

Chelicera. Hand with 4 setae and 1 on the movable finger; galea present as a tubercle.

Palp. Femur 4.6 x, patella 1.83 x and chela 6.65 times longer than broad, chelal movable finger 1.94 times longer than hand. Fixed chelal finger with 6 trichobothria (*ib, esb, ist, est, it, et*). Fixed chelal finger with 26 acute and widely spaced teeth and two distal micro teeth, and movable chelal finger with 23 teeth, basal ones projected backwards and distal ones acute.

Cephalothorax. 1.04 times longer than broad; eyes absent.

Abdomen. Tergal chaetotaxy 4: 4: 4: 6: 6: 6: 6: 6: 6: 4: 2. Sternal chaetotaxy (1)4(1): (1)4(1): 6: 6: 6: 6: 6: 6: 3: 4. Anal operculum with 2 ventral setae and without dorsal ones.

Legs. much as in adults.

Measurements. Body length 0.880. Palps: femur 0.341/0.074, patella 0.146/0.08, chela 0.512/0.077. hand length 0.174, movable finger length 0.338. Carapace 0.257/0.247.

### Habitat and Ecological Remarks

*Pseudochthonius ubajara* **sp. nov.** was recorded in three limestone caves within Ubajara National Park, which encompasses a relatively small remnant of Atlantic Forest in northeastern Brazil. The type locality, Gruta de Ubajara cave (Figs 4C, 5B), has been a show cave open to visitors since 1975. The initial section of the cave, including conduits and chambers near the entrance, is illuminated by electric lighting, and approximately 420 m of passageways are accessible to tourists. The total surveyed extension of the cave, however, is about 1,120 m, with most of its length remaining close to visitation. The deeper portions, reachable by descending beyond the tourist route, are traversed by a perennial stream and remain inaccessible to the public (Fig. 4C). Specimens of *P. ubajara* **sp. nov.** (Fig. 4C) were collected in these inner sectors, which consist of a single passage crossed by the stream. Individuals were observed walking freely on muddy substrates and occasionally beneath rocks on the cave floor. Potential food sources include insectivorous and hematophagous bat guano, while likely prey comprise mainly springtails (Collembola) and booklice (Psocoptera: Psyllipsocidae). The population appears to be small but persistent, as only a few specimens were found during collection. Environmental measurements indicate an average temperature of 23.5°C and relative humidity of 99% in the inner parts of the cave where the species occurs (Santos et al. 2013).

Specimens of *P. ubajara* **sp. nov.** were also observed in two additional caves within the park: Morcego Branco (Fig. 4B) and Urso Fóssil (Fig. 4A). Both are considerably smaller than Gruta de Ubajara. Morcego Branco Cave may represent a secondary entrance or branch of the Ubajara system, as a small stream flowing inside the cave (likely originating from the Ubajara cave) emerges at the surface at its entrance. Populations in both Morcego Branco and Urso Fóssil caves appear smaller, with individuals consistently found under rocks on the cave floor. This sheltering behavior may be associated with the less humid and less stable microclimatic conditions of these caves, which each have more than one entrance. In both systems, organic input consists mainly of guano deposits and plant debris, with springtails and other macroinvertebrates representing the likely prey for *P. ubajara* **sp. nov.** Notably, in Morcego Branco Cave, *P. ubajara* **sp. nov.** co-occurs with another species of *Pseudochthonius* described herein.

It is noteworthy that all caves in which the species was recorded are located within the boundaries of Ubajara National Park, where the surrounding environment remains relatively well preserved and legally protected. However, these caves are subject to visitation at varying intensities, ranging from heavy tourist use (as in Ubajara Cave) to occasional visits by speleologists and local residents. In Ubajara Cave, the population of the species appears to be

shielded from visitor impacts, particularly trampling, as it occurs in areas distant from the tourist route. By contrast, the other two caves experience less regulated visitation, which poses potential risks to the species.

***Pseudochthonius andyratinga* sp. nov.**

**Material examined.** **Holotype** male (ISLA 151479, Fig. 4B), preserved in ethanol: Ubajara, Ceará, Brazil, Gruta do Morcego Branco Cave (-3.831453 E, -40.900264 N), 13 April 2025, leg. R.L Ferreira. **Allotype** female (ISLA 151480), same location, date and collector as holotype.

**Etymology.** The specific epithet *andyratinga* is derived from the Tupi-Guarani language, combining the words *and'-yrã* (“bat”) and *tinga* (“white”). It refers to the type locality of the species, Morcego Branco Cave (“White Bat Cave”). The epithet is to be treated as a noun in apposition.

**Diagnosis.** The new species most resembles *Pseudochthonius ramalho* Assis et al. 2021 by the presence of two weak eyes (although *P. Ramalho* only exhibits two eyes only in females), by the calix shape of the carapace, similar numbers and morphologies of chelal movable-finger teeth and cheliceral teeth and by rallum with 7 blades. *Pseudochthonius andyratinga* sp. nov. differs from *P. ramalho* in the following combination of characteristics: trichobothrial ratio distance *ist-est/ist-esb* of 2.03–2.14 (4.71 in *P. ramalho*), absence of microteeth adjacent to any teeth on the chelal fixed finger (microteeth present medially and distally between the main teeth row in *P. ramalho*), male genitalia with 6 lateral setae (7–8 in *P. ramalho*) and *et* trichobothrium near *dx* (*et* close to *it* in *P. ramalho*).

**Description** (Fig. 4B). Body pale, slightly translucent; chelicerae slightly darker, abdomen beige. Vestitural setae thin and anteriorly projected on the prosoma and posteriorly projected on the opisthosoma.

Chelicera (Fig. 2B). Hand with 5 setae; movable finger with 1 subbasal seta; galea present as a tubercle in both sexes; fixed finger with 9 teeth (distal ones grouped in a small hump) (Fig. 2B); movable finger with 10 teeth acute small teeth; rallum with 7 unilaterally pinnate blades; serrulae exterior with 13 and interior with 10 blades, respectively.

Palp (Figs 2D, H). Trochanter 1.54 (1.38) times longer than wide, patella 2.1 (1.96) times longer than wide, femur 5.09 (4.99) times longer than wide. Femur chaetotaxy 5: 6: 3: 6: 2. Trichobothrial pattern: *ib* and *isb* located at the half portion of the hand, adjacent to each other and slightly dislocated to the paraxial face of the chela, *eb* proximal to *esb*, *ist* distal to *esb*, *it* proximal to *est*, *et* proximal to *dx*; *ist* almost exactly twice as closer to *esb* than to *est* (ratio

distance *ist-est/ist-esb* = 2.03–2.14). Fixed chelal finger slightly bent (Fig. 2H), movable finger slightly curved. Fixed chelal finger with 34 teeth and two micro distal teeth. Movable finger with 32 small and heavily projected backwards teeth.

Cephalothorax (Fig. 2C). 1.14 (1.19) times longer than broad, slightly constricted posteriorly showing a difference between ocular width and posterior width of 0.04 mm; anterior margin fully serrated; two eyes with weak lens present; epistome with a single large and acute projection; posterior margin of carapace smooth; chaetotaxy 4(2): 4: 4: 2: 2 (18).

Abdomen: Pleural membrane papillate; tergites and sternites undivided, setae uniseriate and acuminate; tergal chaetotaxy 4: 4: 4: 4: 6: 6: 6: 6: 5: 4: 0, sternal chaetotaxy (2)12(2): (1)8(1): (1)4(1): (1)4(1): 6: 6: 6: 5: 2. Anal operculum with 2 ventral setae and without dorsal ones.

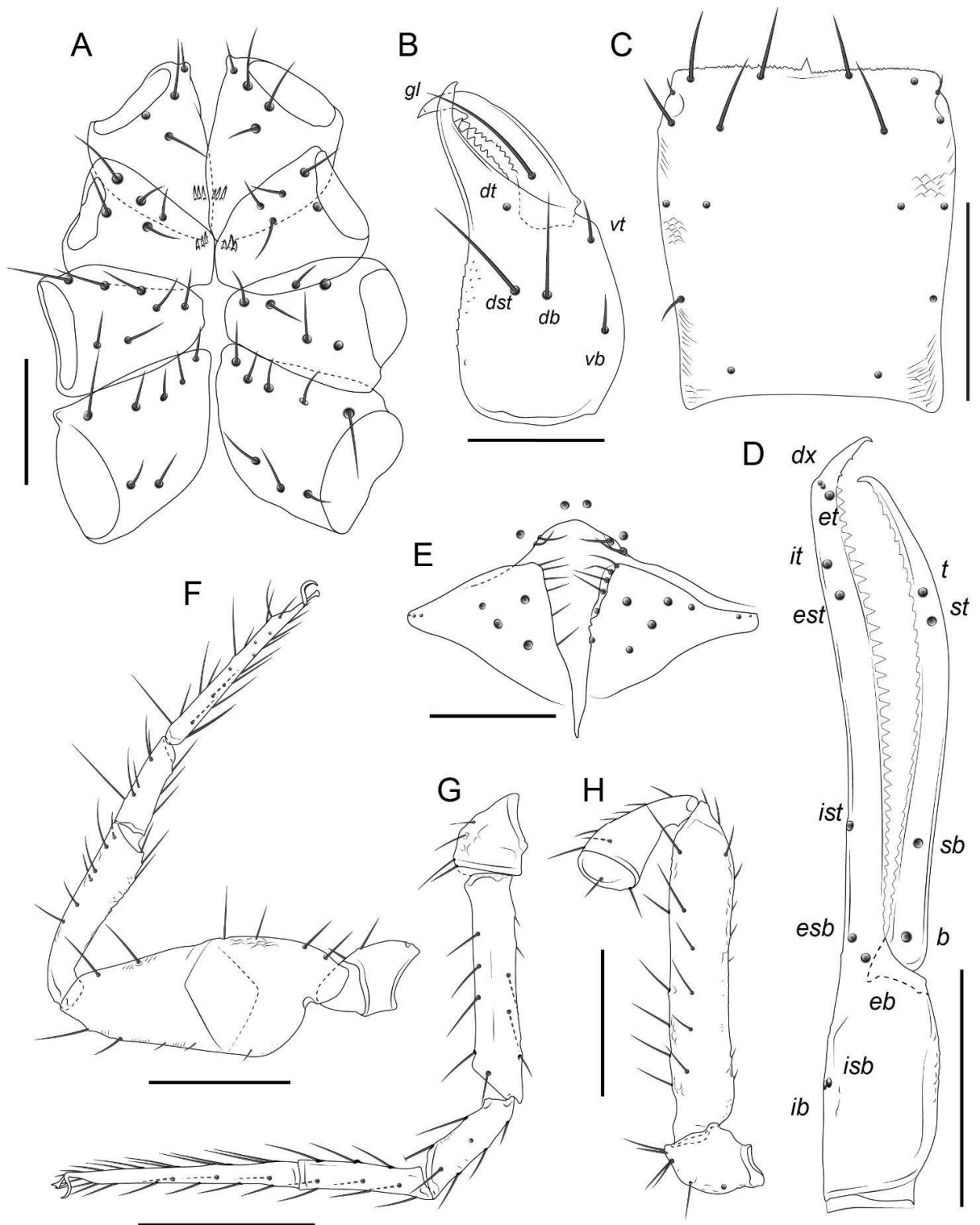
Coxal area (Fig. 2A). Manducatory process with 2 apical setae (medial ones slightly dislocated forwards); palpal coxae with 3 setae arranged in a triangle; delicate lamellae outlined by 9 small spines. Pedal: plumose coxal spines arranged transversally in coxae I (3) and II (3), chaetotaxy: 3(1): 5: 7: 7–8; intercoxal tubercle absent.

Leg IV (Fig. 2F). Arolia simple and undivided, slightly shorter than claws.

Genital operculum of male (Fig. 2E). Anterior genital operculum (2<sup>nd</sup> tergite) with 8 discal setae (2 apical and a lateral cluster of 3 setae on each side [Fig. 2E]), posterior genital operculum (3<sup>rd</sup> tergite) with 6 marginal setae on each side, and 5 setae along the sternite with 3 microlateral setae on each side, near the spiracle [Fig. 2E]).

Genital operculum of female. 6 setae distributed in three horizontal rows (2: 2: 2), genital opening bifurcated.

Measurements (length/width or depth in mm and ratios in parenthesis calculated using three significant digits). Male holotype (female paratype in brackets). Body length 1.196 [1.271]. Carapace 0.339/0.298 (1.14) [0.370/0.312 (1.19)]. Palps: trochanter 0.145/0.094 (1.54) [0.117/0.085 (1.38)], femur 0.447/0.088 (5.08) [0.474/0.095 (4.99)], patella 0.185/0.088 (2.10) [0.190/0.097 (1.96)], chela 0.644/0.097 (6.64) [0.681/0.109 (6.25)], movable finger length 0.420 [0.446]. Leg I: trochanter 0.106/0.076 (1.40) [0.130/0.078 (1.67)], femur 0.262/0.052 (5.04) [0.277/0.058 (4.78)], patella 0.141/0.042 (3.36) [0.142/0.046 (3.09)], femur/patella 1.86 [1.95], tibia 0.150/0.032 (4.69) [0.154/0.032 (4.81)], tarsus 0.263/0.027 (9.74) [0.262/0.027 (9.70)]. Leg IV: Trochanter: 0.163/0.094 (1.73) [0.119/0.090 (1.32)], femur + patella 0.410/0.171 (2.40) [0.422/0.167 (2.53)], tibia 0.269/0.063 (4.27) [0.265/0.064 (4.14)], basitarsus 0.144/0.047 (3.06) [0.152/0.047 (3.23)], telotarsus 0.281/0.028 (10.04) [0.276/0.029 (9.52)].



**Figure 2.** *Pseudochthonius andyratinga* sp. nov. **A** Male holotype (ISLA 151479) coxal region **B** Male holotype right chelicera, dorsal view **C** Male holotype carapace, dorsal view **D** Male holotype right chela, antiaxial view **E** Male holotype genitalia **F** Male holotype left leg IV, antiaxial view **G** Female allotype (ISLA 151480) left leg I, antiaxial view **H** Male holotype pedipalp, dorsal view. Scale bars: 1 mm (**A**, **E**); 2 mm (**B–D**, **F–H**).

### **Habitat and Ecological Remarks**

*Pseudochthonius andyratinga* **sp. nov.** was recorded in Morcego Branco Cave, located within the boundaries of Ubajara National Park. This cave is likely connected to the Ubajara Cave system, as its main entrance corresponds to the resurgence of a drainage that presumably flows through both caves. Organic inputs are primarily derived from guano deposits and plant debris, the latter entering through small secondary openings at the base of the limestone outcrop. Potential prey available to *P. andyratinga* **sp. nov.** includes springtails and other microinvertebrates.

This species occurs in syntopy with *P. ubajara* **sp. nov.**, however, it exhibits more discrete troglomorphic traits which, although less pronounced than those of the latter species, still suggest a restriction to subterranean environments. Nonetheless, because no systematic surveys were conducted in the surrounding epigeal habitats, the species' true distribution remains unknown and warrants further investigation (see *Discussion*). Therefore, the occurrence of *P. andyratinga* **sp. nov.** within Ubajara National Park provides an added layer of protection, as the park maintains a relatively high degree of habitat preservation and legal safeguarding of the surrounding landscape.

### ***Pseudochthonius tejussuoca* sp. nov.**

**Material examined. Holotype** male (ISLA 151483), preserved in ethanol: Tejuçuoca, Ceará, Brazil, Gruta do Veado Campeiro Cave (-4.028712 E, -39.662569 N), 17 September 2008, leg. R.L Ferreira. **Allotype** female (ISLA 151482), same location, date and collector as holotype. **Paratypes**: one tritonymph and one female (ISLA 151481), same location as holotype, 17 September 2008, leg. R.L Ferreira.

**Etymology.** The specific epithet is an adjective formed from the toponym Tejuçuoca, referring to the type locality. This term should be treated as a noun in apposition.

**Diagnosis.** The new species most resembles to *Pseudochthonius itakuatiara* Prado and Ferreira 2024 by the presence of two eyes, chelal dentition number and morphology, *ist* trichobothrium twice as near to *esb* than to *est*, represented by ratio distance *ist-est/ist-esb* close to 2.0 and rallum with 7 unilaterally pinnate blades. *Pseudochthonius tejussuoca* **sp. nov.** differs from *P. itakuatiara* by the following combination of characteristics: calix shape of carapace (almost rectangular in *P. itakuatiara*), cheliceral dentition highly constricted in both fingers (cheliceral movable finger teeth acute and well sparse in *P. itakuatiara*), two microteeth at tip

of chelal fixed finger (*P. itakuatiara* with only one microtooth), epistome narrow, squared and highly dentate (epistome broad, triangular, small and with tiny projections in *P. itakuatiara*).

**Description.** *Male and Female adults.* Body pale, slightly translucent; chelicerae slightly darker, abdomen beige. Vestitural setae thin and anteriorly projected on the prosoma and posteriorly projected on the opisthosoma.

Chelicera (Fig. 3B). Hand with 5 setae (fig. 3B); movable finger with 1 subbasal seta; galea present as a tubercle in females and absent in males; fixed finger with 10 teeth highly constricted and barely differentiable (Figs 3B); movable finger with 8 constricted teeth including a small distal one slightly isolated; rallum with 7 unilaterally pinnate blades; serrulae exterior with 11 and interior with 9 blades, respectively.

Palp (Figs 3D, F). Trochanter 1.48 (1.57) times longer than wide, patella 1.93 (1.97) times longer than wide, femur 4.46 (5.02) times longer than wide. Femur chaetotaxy 5: 6: 3: 6: 2. Trichobothrial pattern: *ib* and *isb* located at the half portion of the hand, adjacent to each other and slightly dislocated to the paraxial face of the chela, *eb* proximal to *esb*, *ist* distal to *esb*, *it* proximal to *est*, *et* proximal to *dx*; *ist* almost exactly twice as close to *esb* than to *est* (ratio distance  $ist-est/ist-esb = 1.76-2.05$ ). Fixed chelal finger slightly bent; movable finger slightly curved (Fig. 3F). Fixed chelal finger with 36 acute teeth including two micro distal ones. Movable finger with 33 small and heavily projected backwards teeth.

Cephalothorax (Fig. 3C). 1.179 (1.078) times longer than broad, slightly constricted posteriorly showing a difference between ocular width and posterior width of 0.03 (0.08) mm; anterior margin partially serrated (ranging from epistome to seta *ame*); two eyes with well-developed lens present; epistome small, narrow, quadrangular and highly dentate; posterior margin of carapace smooth; chaetotaxy: 4(2): 4: 4: 2: 2 (18).

Abdomen: Pleural membrane papillate; tergites and sternites undivided, setae uniseriate and acuminate. Tergal chaetotaxy 4: 4: 4: 4: 6: 6: 6: 6: 5: 2. Sternal chaetotaxy (2)10(2): (1)8(1): 6: 6: 6: 6: 6: 6. Anal operculum with 2 ventral setae and without dorsal ones.

Coxal area (Fig. 3A). Manducatory process with 2 apical setae (medial ones slightly dislocated forwards); palpal coxae with 3 setae arranged in a triangle; delicate lamellae outlined by 10 small spines. Pedal: plumose coxal spines arranged transversally in coxae I (2) and II (3), chaetotaxy: 4(1): 5: 5: 6-8; intercoxal tubercle absent.

Leg IV (Fig. 3F). Arolia simple and undivided, slightly shorter than claws.

Genital operculum of male (Fig. 3E). Anterior genital operculum (2<sup>nd</sup> tergite) with 8 discal setae (2 apical and 3 lateral setae aligned [Fig. 3E]), posterior genital operculum (3<sup>rd</sup> tergite)

with 7 marginal setae on each side, and 3 setae along the sternite with 3 microlateral setae on each side, near the spiracle [Fig. 3E]).

Genital operculum of female. setae distributed in 3 transversal rows (2: 2: 2, rows being comparatively distant one to another), genital opening bifurcated.

Measurements (length/width or depth in mm and ratios in parenthesis calculated using three significant digits). Male holotype (female paratype in brackets). Body length 1.179 [1.708]. Carapace 0.369/0.356 (1.04) [0.423/0.450 (0.94)]. Palps: trochanter 0.139/0.094 (1.48) [0.203/0.125 (1.62)], femur 0.433/0.097 (4.46) [0.593/0.135 (4.39)], patella 0.193/0.100 (1.93) [0.248/0.144 (1.72)], chela 0.664/0.114 (5.83) [0.839/0.158 (5.31)], movable finger length 0.413 [0.534]. Leg I: trochanter 0.106/0.076 (1.40) [0.121/0.109 (1.11)], femur 0.248/0.055 (4.51) [0.347/0.072 (4.82)], patella 0.140/0.042 (3.33) [0.181/0.056 (3.23)], femur/patella 1.771 [1.917], tibia 0.148/0.035 (4.23) [0.197/0.044 (4.48)], tarsus 0.263/0.029 (9.07) [0.329/0.036 (9.14)]. Leg IV: Trochanter: 0.124/0.083 (1.45) [0.156/0.117 (1.33)], femur + patella 0.438/0.186 (2.36) [0.556/0.229 (2.43)], tibia 0.268/0.067 (4.0) [0.370/0.089 (4.16)], basitarsus 0.148/0.050 (2.96) [0.195/0.066 (2.96)], telotarsus 0.258/0.029 (8.90) [0.350/0.038 (9.21)].

*Tritonymph*. Body pale, mostly depigmented, chelicerae and chelae light beige, abdomen in beige. Vestitural setae, anteriorly projected on the carapace and posteriorly projected in opisthosoma.

Chelicera. Hand with 5 setae and 1 on the movable finger; galea present as a tubercle; rallum with 7 unilaterally pinnate blades.

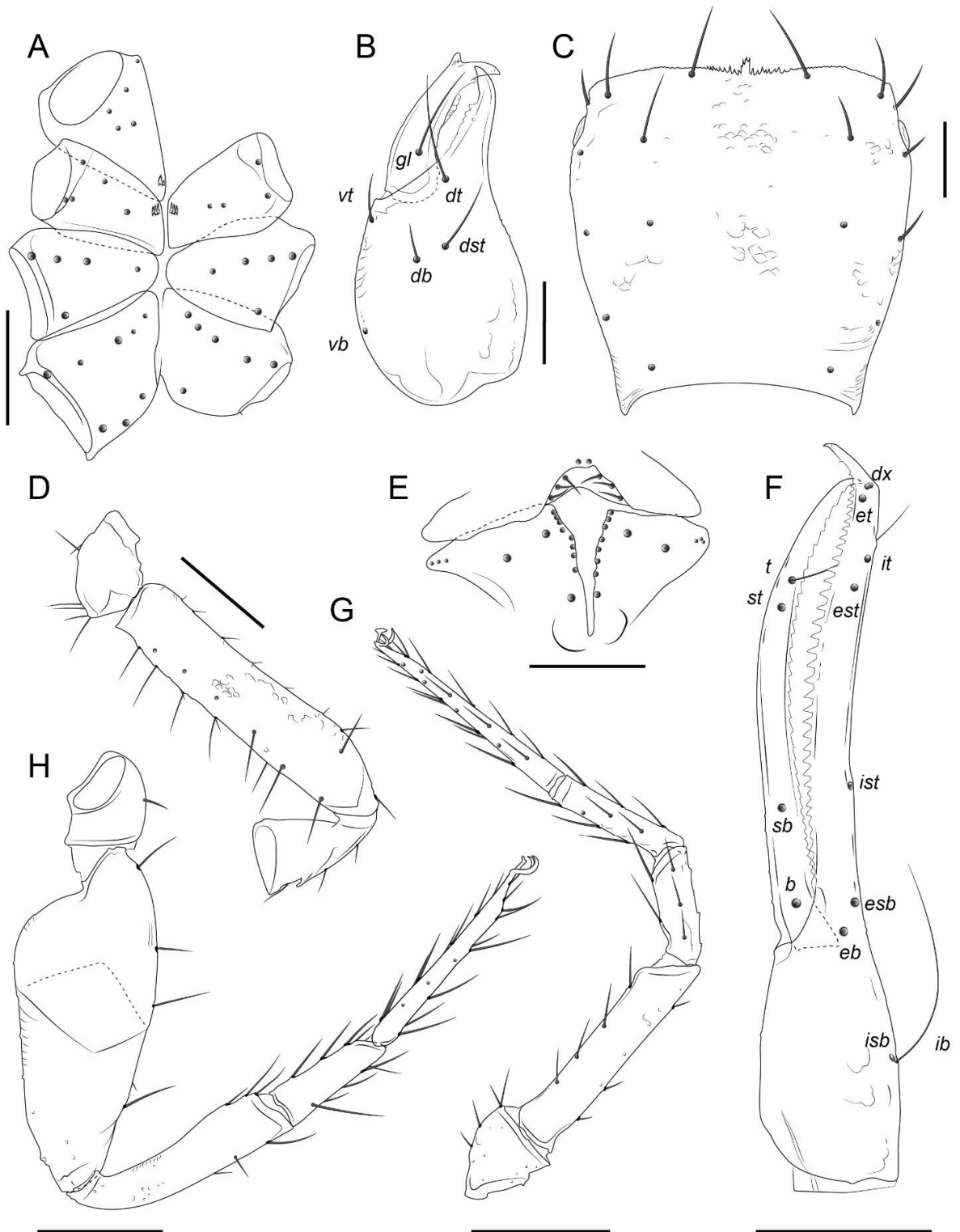
Palp. Femur 4.6 x, patella 1.92 x and chela 4.93 times longer than broad, chelal movable finger 1.93 times longer than hand. Fixed chelal finger with 7 trichobothria (*ib*, *eb*, *esb*, *ist*, *est*, *it*, *et*). Fixed chelal finger with 26 acute and widely spaced teeth and two distal micro teeth, and movable chelal finger with 21 tiny highly projected backwards teeth.

Cephalothorax. 1.15 times longer than broad; eyes present.

Abdomen. Tergal chaetotaxy 4: 4: 4: 4: 6: 6: 6: 6: 6: 6: 4: 2. Sternal chaetotaxy 2: (1)(1): (1)6(1): 6: 6: 6: 4: 5: 4: 4. Anal operculum with 2 ventral setae and without dorsal ones

Legs. much as in adults.

Measurements. Body length 0.846. Palps: femur 0.303/0.066, patella 0.140/0.073, chela 0.404/0.082, hand length 0.138, movable finger length 0.266. Carapace 0.279/0.242.



**Figure 3.** *Pseudochthonius tejuosuoca* sp. nov. **A** Male holotype (ISLA 151483) coxal region **B** Female allotype (ISLA 151482) left chelicera, dorsal view **C** Female allotype carapace, dorsal view **D** Female allotype pedipalp, dorsal view **E** Male holotype genitalia **F** Female allotype left chela, antiaxial view **G** Female allotype

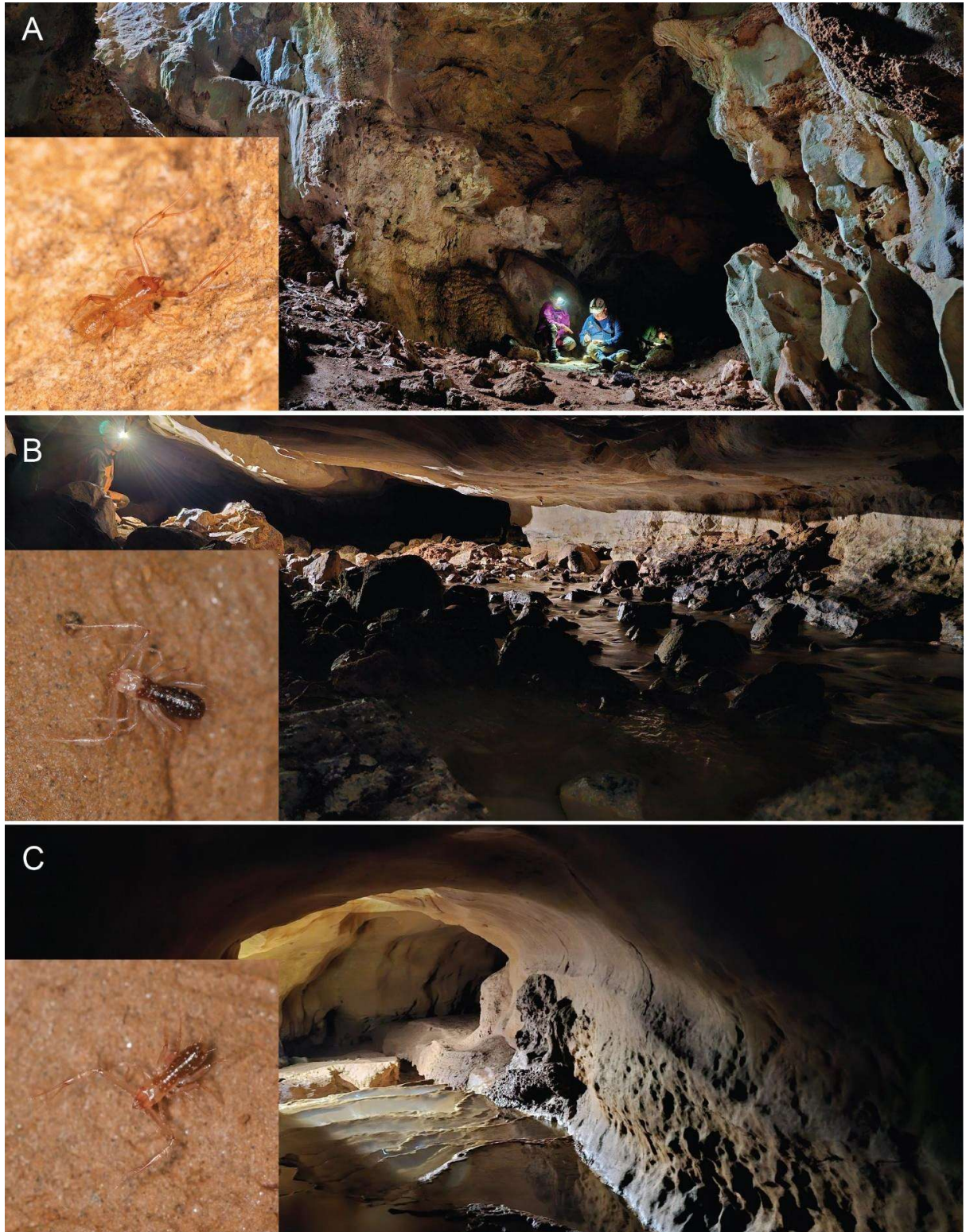
left leg I, antiaxial view **H** Female allotype left leg IV, antiaxial view. Scale bars: 1 mm (**A–C**, **E**); 2 mm (**D**, **F–H**).

### **Habitat and Ecological Remarks**

*Pseudochthonius tejussuoca* **sp. nov.** has so far been recorded exclusively from Veado Campeiro Cave, situated within the Municipal Park of Tejuçuoca, Ceará State, Brazil. The cave possesses two entrances that provide access to its innermost conduit, which extends for approximately 34 m. It is characterized as a dry cave, although certain substrates retain moisture, particularly beneath rocks.

Specimens of *P. tejussuoca* **sp. nov.** were found under rocks in zones distant from the entrances. The species does not exhibit conspicuous troglomorphic traits, suggesting that it may also occur in surface habitats, which were not sampled during our surveys. Furthermore, as collections were carried out during the dry season, it cannot be excluded that individuals of *P. tejussuoca* **sp. nov.** may use caves as temporary refuges in periods of unfavorable surface conditions. Alternatively, the species may be troglophilic.

The Municipal Park of Tejuçuoca, encompassing approximately 1,200 hectares, preserves a representative fragment of the Caatinga biome and plays an important role in maintaining regional biodiversity and ecosystem services. However, this area is subject to conservation challenges, including recurrent seasonal fires, soil degradation, and increasing anthropogenic pressures, all of which threaten the integrity of both epigeal vegetation and subterranean habitats. Given the absence of troglomorphic features in *P. tejussuoca* **sp. nov.**, further surveys in surface environments surrounding the cave are strongly recommended to clarify the species' actual distribution and its ecological relationship with cave habitats.



**Figure 4.** Habitat on the background and habitus of new species on left bottom corners. **A** *Pseudochthonius ubajara* sp. nov. female paratype habitus and Gruta do Urso Fossil Cave. **B** *Pseudochthonius ubajara* sp. nov. male paratype habitus and Gruta do Morcego Branco Cave. **C** *Pseudochthonius ubajara* sp. nov. male holotype habitus and Gruta de Ubajara Cave.

## Discussion

Brazilian *Pseudochthonius* diversity has increased sharply in recent years: approximately 54% (23 spp.) of all known species of the genus have been described since 2001. This abrupt rise is largely due to the examination of previously unstudied cave-derived material accumulated over past decades within biological collections. Despite this progress, the genus has long presented several taxonomic complications and conceptual inconsistencies, some of which dating back to the description of the type species *Pseudochthonius simoni* Balzan 1892, originally proposed as a subgenus of *Chthonius* – another species-rich genus that has undergone multiple revisions before its present circumscription (Zaragoza 2017).

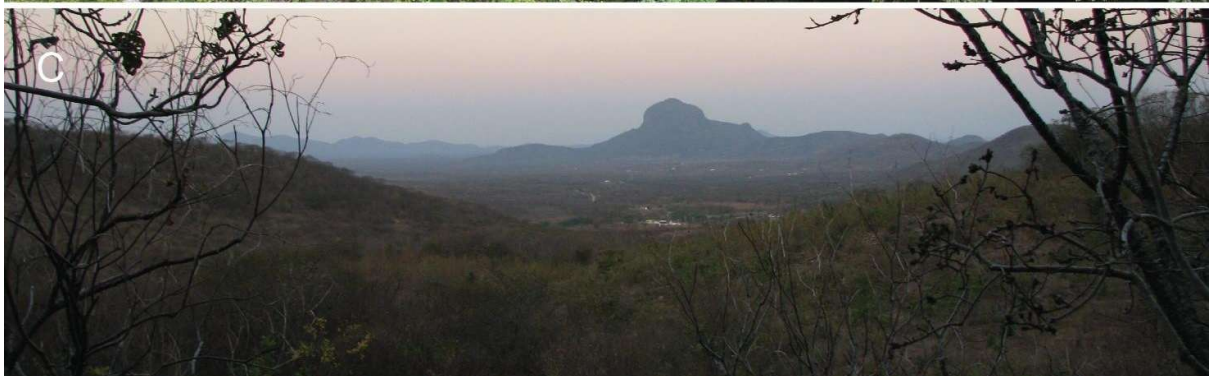
Several classical arachnologists working on the group (e.g., Max Beier, Volker Mahnert, William B. Chamberlin) noted these discrepancies and others, including the unexplained variation in the position of the trichobothrium *et*, which may occur either adjacent to *dx* or basally displaced toward *it*. Equally variable is the morphology of the chelal movable-finger dentition, which can range from acute, well-spaced teeth to strongly constricted teeth projected backwards. The latter configuration has so far always been associated with *et* positioned near *dx*.

Importantly, the opposite condition (*et* close to *it*) shows no consistent correlation with movable-finger dentition. Species exhibiting this trichobothrial arrangement may present either: (i) acute, erect teeth on the movable finger, as observed in *Pseudochthonius cesarioensis* Guimarães et al. 2025, *P. diamachi* Prado and Ferreira 2023, and *P. koinopoliteia* Prado and Ferreira 2023; or (ii) small, posteriorly projected teeth, as found in *P. ramalho* and *P. aware*.

Additionally, *P. orthodactylus* represents an especially unusual case, exhibiting a suite of markedly divergent morphological traits. Muchmore himself suggested in the original description that this species may warrant recognition as a distinct genus (Muchmore 1970). Such cases underscore the substantial work still required to achieve a comprehensive understanding of the group.

To advance the resolution of this complex taxonomic framework, new species descriptions that emphasize detailed and integrative morphological characteristics are essential, as they provide the foundation for future rearrangements within the genus and potentially for its eventual subdivision. In this context, we describe three new species of *Pseudochthonius*, two of which (*P. ubajara* **sp. nov.** and *P. andyratinga* **sp. nov.**) were found in syntopy within Morcego Branco Cave, an ecological condition never before recorded for the genus or for any

Brazilian chthoniid, although the coexistence of two chthoniid species in a single cave has been reported in China (Hou et al. 2022).



**Figure 5.** Caves surroundings. **A** Limestone outcrop at Ubajara National Park (PARNA Ubajara). **B** Gruta de Ubajara Cave entrance. **C** Parque Ecológico Furna dos Ossos, type locality of *Pseudochthonius tejussuoca* **sp. nov.**

#### *On the troglotic status of the new species*

*Pseudochthonius ubajara* **sp. nov.** lacks eyes or eyespots, possesses strikingly elongated appendages (see *Measurements*), and exhibits an extended anterior carapace margin, traits commonly associated with strict subterranean life (Hou et al. 2022; Guimarães et al. 2025; Laibe et al. 2025). *Pseudochthonius andyratinga* **sp. nov.** bears two weakly developed eyes and also displays elongated appendages (leg I femur 1.9–2.0× the length of the patella; leg IV femur + patella 4.1–4.3× longer than wide), even when compared with another troglotic member of the genus, *Pseudochthonius biseriatus* Mahnert 2001 (leg I femur 1.73–1.88× patella; leg IV femur + patella 2.7–3.3× longer than wide). In contrast, *P. tejussuoca* **sp. nov.** possesses two well-developed eyes and comparatively shorter appendages (chelal length 0.61–0.83 mm; leg IV femur + patella 2.2–2.4× longer than wide), values typically observed in epigeal representatives of the genus (e.g., *Pseudochthonius homodentatus* Mahnert 1979, chelal length 0.67–0.70 mm; leg IV femur + patella 2.4–2.5× longer than wide) (Mahnert 1979).

Based on these morphological features, we classify *P. ubajara* **sp. nov.** and *P. andyratinga* **sp. nov.** as troglotients, whereas *P. tejussuoca* **sp. nov.** is considered a troglophile. We emphasize, however, that confirming a species as a troglotient ultimately requires external sampling to demonstrate its ecological restriction to subterranean habitats. Finally, *P. ubajara* **sp. nov.** and *P. andyratinga* **sp. nov.** may represent relictual lineages of Atlantic Forest taxa, now isolated in habitat patches within the Brazilian semi-arid region, potentially qualifying them as rare species of conservation concern.

#### **Conclusions**

The discovery and description of *Pseudochthonius ubajara* **sp. nov.**, *P. andyratinga* **sp. nov.**, and *P. tejussuoca* **sp. nov.** expand the known diversity of *Pseudochthonius* in northeastern Brazil and highlight the complexity of morphological variation within the genus. The coexistence of two species within a single cave represents the first documented case of syntopy for *Pseudochthonius*, providing novel ecological insight into chthoniid assemblages. Our findings underscore the importance of cave systems as reservoirs of evolutionary lineages, including both highly troglomorphic and potentially troglotic taxa, and emphasize the urgent

need for continued exploration, integrative taxonomic work, and conservation efforts in Brazilian karst landscapes.

### List of Abbreviations

Abbreviations for the trichobothria: *b* = basal; *sb* = sub-basal; *st* = sub-terminal; *t* = terminal; *ib* = interior basal; *isb* = interior sub-basal; *ist* = interior sub-terminal; *it* = interior terminal; *eb* = exterior basal; *esb* = exterior sub-basal; *est* = exterior sub-terminal; *et* = exterior terminal. Other abbreviations: *al* = anterolateral setae of carapace; *ame* = anteromedial setae of carapace; *an* = anterior setae row of carapace; *il* = intermedian lateral setae of carapace; *in* = intermedian setae row of carapace; *me* = median setae row of carapace; *ml* = median lateral setae of carapace; *mm* = median medial setae of carapace; *oc* = ocular setae row of carapace; *ol* = lateral ocular setae of carapace; *om* = medial ocular setae of carapace; *osl* = sublateral ocular setae of carapace; *pl* = posterolateral setae of carapace; *pm* = posteromedial setae of carapace; *po* = posterior setae row of carapace. Abbreviations for repositories: ISLA = Coleção de Invertebrados Subterrâneos de Lavras.

### Key to *Pseudochthonius* from Northeastern Brazil

- 1 Eyes absent in at least one of the sexes..... 2
  - Two eyes or eyespots ..... 11
- 2 *est-ist/ist-esb* trichobothrial distance ratio around 1.0 or less..... 3
  - *est-ist/ist-esb* trichobothrial distance ratio higher than 1.0 ..... 4
- 3 Carapace with calix shape (anterior margin much larger than posterior margin) ..... *Pseudochthonius diamachi*
  - Carapace with rectangular shape (anterior margin, ocular breadth and posterior margin almost the same breadth value) ..... *Pseudochthonius koinopoliteia*
- 4 Cheliceral rallum with 7 blades..... 5
  - Cheliceral rallum with either 5 or 9 blades ..... 10
- 5 *est-ist/ist-esb* trichobothrial distance ratio higher than 3.0 ..... 6
  - *est-ist/ist-esb* trichobothrial distance ratio lower than 3.0 ..... 7
- 6 Tergite I with two simple setae, trichobothrium *et* near *dx*..... *Pseudochthonius caesarioensis*
  - Tergite I with four simple setae, trichobothrium *et* basally displaced from *dx*, near *it* ..... *Pseudochthonius ramalho*
- 7 Chelal movable finger with tiny highly projected backwards teeth..... 8

- Chelal movable finger with acute and slightly projected backwards teeth  
.....  
..... *Pseudochthonius ubajara* **sp. nov.**
- 8 Trichobothrium *et* near *dx*..... 9
- Trichobothrium *et* basally displaced from *dx*, near *it*  
.....  
..... *Pseudochthonius pali* Prado and Ferreira 2023
- 9 Cheliceral fixed finger with 9 large and irregular teeth and one ventral seta on palpal femur ..... *Pseudochthonius gonssalo* Guimarães et al. 2025
- Cheliceral fixed finger with 11 well separated and homogeneous teeth and two ventral setae on palpal femur ..... *Pseudochthonius aware*
- 10 Cheliceral rallum with 9 blades..... *Pseudochthonius biseriatus*
- Cheliceral rallum with 5 blades..... *Pseudochthonius lubueno* Assis et al. 2023
- 11 Carapace with calix shape (anterior margin much larger than posterior margin)..... 12
- Carapace with rectangular shape (anterior margin, ocular breadth and posterior margin almost the same breadth value)..... 13
- 12 Two well developed eyes, anterior margin of carapace medially serrated (not extending *ame* setae), male genitalia lateral discal setae with linearly displayed  
.....  
..... *Pseudochthonius tejuusuoca* **sp. nov.**
- Two weak lens present, anterior margin of carapace fully serrated, male genitalia lateral discal setae clustered in a triangle shape..... *Pseudochthonius andyratinga* **sp. nov.**
- 13 Sigmoid chelae; both fingers fully dentate..... 14
- Chelae straight; fixed finger with large, widely spaced teeth; movable finger with large, widely spaced teeth restricted to the medial–distal region, basal portion lacking teeth.  
..... *Pseudochthonius orthodactylus*
- 14 Chelal fixed finger with 23–26 small, constricted, pointed and alternate teeth  
.....  
..... *Pseudochthonius gracilimanus* Mahnert 2001
- Chelal fixed finger with 36 acute teeth: the 8 distal and 19 basal teeth uniseriate, the 9 median teeth biseriate..... *Pseudochthonius itakuatiara*

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### THIRD PART

#### 4 GENERAL CONCLUSION

The present dissertation represents a significant advancement in the understanding of the pseudoscorpion family Chthoniidae in Brazil, directly addressing the Linnean shortfall that hinder the conservation of subterranean biodiversity. By integrating historical taxonomic reassessments with the description of novel fauna, this work highlights the hidden diversity of less studied arachnids in Neotropics.

The establishment of the genus *Kayapochthonius* **gen. nov.** resolves a long-standing taxonomic inconsistency regarding *Pseudochthonius orthodactylus* Muchmore, 1970. The morphological analysis confirmed that this lineage, now comprising *Kayapochthonius orthodactylus* **comb. nov.**, *Kayapochthonius bacaba* **sp. nov.**, and *Kayapochthonius diamantinus* **sp. nov.**, possesses distinct plesiomorphic traits, such as straight chelae and specific dental arrangements, which phylogenetically distinguish it from *Pseudochthonius* and bridge the gap with the genus *Aphrastochthonius*. These findings underscore the importance of the Amazonian and Caatinga formations, specifically the Carajás and Chapada Diamantina regions, as reservoirs of unique evolutionary lineages.

Furthermore, the investigation of the genus *Pseudochthonius* in northeastern Brazil revealed important diversity within the Caatinga and Atlantic Forest remnants. The description of *Pseudochthonius ubajara* **sp. nov.**, *Pseudochthonius andyratinga* **sp. nov.**, and *Pseudochthonius tejussuoca* **sp. nov.** not only expands the number of known species but also provides new ecological insights. The documentation of *P. ubajara* **sp. nov.** and *P. andyratinga* **sp. nov.** co-occurring in Morcego Branco Cave constitutes the first record of syntopy within this genus.

Collectively, these results demonstrate that the Brazilian Pseudoescorpiones cave fauna remains largely underestimated and is characterized by high levels of endemism and morphological specialization. Given the increasing anthropogenic pressures on these ecosystems, particularly from mining and deforestation, the taxonomic descriptions provided herein are essential tools for environmental impact assessments and the legal protection of Brazil's speleological heritage, given that the type locality of these species must be legally protected.