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YESENIA MARGARITA CARPIO DÍAZ

COMPOSIÇÃO TAXONÔMICA E VARIAÇÕES FUNCIONAIS DOS ISÓPODES TERRESTRES (ISOPODA: ONISCIDEA) EM HABITATS EPÍGEOS E HIPÓGEOS DA REGIÃO NEOTROPICAL

SÃO CARLOS – SP
2026

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Tese apresentada ao Programa de Pós-Graduação em Ecologia e Recursos Naturais da Universidade Federal de São Carlos, como parte dos requisitos para obtenção do título de Doutora em Ciências, área de concentração: Ecologia e Recursos Naturais

Orientadora: Profª. Drª. Maria Elina Bichuette
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UNIVERSIDADE FEDERAL DE SÃO CARLOS

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ao meu marido Chars,

a meus pais Sandra e Iván,

e a minha família y amigos.

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"Es sencillo hacer que las cosas sean complicadas,

pero es difícil hacer que sean sencillas"

Friedrich Nietzsche

RESUMO

Os habitats subterrâneos (cavernas e espaços de dimensões menores) representam ecossistemas singulares que abrigam espécies altamente especializadas. A exploração de variações funcionais nesses habitats fornece pistas fundamentais para compreender padrões de diversidade, permitindo conhecer sobre os processos ecológicos e evolutivos subjacentes, além de subsidiar estratégias e/ou planos de conservação. Entre os organismos mais frequentes e abundantes nesses ambientes estão os invertebrados, especialmente os isópodes terrestres, que desempenham papéis essenciais no fluxo de carbono nos solos. Ao atuar na fragmentação da matéria orgânica, esses organismos promovem a transferência de nutrientes e estimulam o metabolismo microbiano, contribuindo para o aumento das taxas de decomposição. A conservação de habitats subterrâneos torna-se cada vez mais urgente, uma vez que muitas espécies troglóbias apresentam distribuição geográfica restrita, baixa capacidade de dispersão e elevada sensibilidade a distúrbios ambientais. Esses fatores as tornam particularmente vulneráveis às mudanças climáticas e aos impactos antrópicos, como atividades minerárias, expansão urbana, turismo desordenado e poluição. Nesse contexto, as pesquisas sobre a caracterização da biodiversidade subterrânea e avaliação da sua diversidade não apenas amplia o conhecimento científico, mas também fortalece ações de manejo e conservação em regiões cársticas neotropicais. Diante desse panorama, os objetivos do presente projeto foram: (i) descrever a taxonomia dos isópodes terrestres associados aos habitats subterrâneos da Colômbia; (ii) descrever a taxonomia dessas espécies em habitats epígeos e hipógeos do sudeste do Brasil, com ênfase no bioma da Mata Atlântica; e (iii) avaliar as variações funcionais desses organismos em habitats epígeos e hipógeos do Parque Estadual Turístico do Alto Ribeira (PETAR), sudeste do Brasil. Para atingir esses objetivos, foram analisados espécimes depositados em coleções científicas, incluindo o Laboratório de Estudos Subterrâneos da UFSCar (LES-UFSCar), o Museo de Zoologia da Universidade de São Paulo (MZUSP), e na Colección del Laboratorio de Biología da Universidad de Cartagena (CBUDC). A metodologia consistiu na revisão taxonômica das espécies provenientes do PETAR, SP, e de sistemas de cavernas da Colômbia, resultando na descrição de novas espécies de isópodes terrestres. Para a avaliação da diversidade taxonômica e funcional, foram utilizados os espécimes pertencentes ao PETAR. As análises incluíram a estrutura de números efetivos de espécies baseada em números de Hill, e métricas de diversidade funcional (FRic, FEve e FDiv), além da estimativa de dissimilaridade taxonômica e funcional por meio da abordagem de Baselga. A distância funcional foi calculada com a distância de Gower. Todas as análises foram realizadas no software RStudio v. 4.4.1. Em relação ao primeiro objetivo, como resultados, o exame dos exemplares da Colômbia resultou na descrição de novas espécies de isópodes terrestres do gênero *Ctenorillo*, com publicação no periódico Tropical Zoology. Para o segundo objetivo, o estudo dos exemplares do sudeste do Brasil identificou 309 indivíduos pertencentes a 29 espécies, cinco famílias e nove gêneros, provenientes principalmente de habitats subterrâneos da Mata Atlântica, com destaque para o PETAR, no estado de São Paulo. Esses dados fundamentaram um artigo sobre a fauna de oniscídeos da região do Alto Ribeira, incluindo o PETAR, o PEI, o PECD e áreas contíguas, com a descrição de três novas espécies e novos registros para a área cárstica do Alto Ribeira. Para o terceiro objetivo, os resultados indicaram maior riqueza funcional nas assembleias epígeas, enquanto a diversidade beta foi elevada tanto nas dimensões taxonômica quanto funcional. Este padrão foi impulsionado principalmente pela substituição de espécies (turnover), evidenciando diferenciação marcante na estrutura das assembleias entre os habitats. A Análise de Coordenadas Principais revelou segregação parcial das assembleias epígeas e hipógeas no espaço funcional, além de agrupamento de traços por família, destacando o papel da história evolutiva na conformação da composição funcional. Esses resultados contribuem para a compreensão dos mecanismos que estruturam a biodiversidade ao longo de gradientes ambientais da Mata Atlântica e reforçam a importância de integrar perspectivas taxonômicas e funcionais para orientar ações de conservação. A proteção simultânea dos habitats epígeos e hipógeos em sistemas cársticos ameaçados é essencial para preservar a diversidade biológica e os processos ecológicos que sustentam esses ecossistemas. Por fim o conhecimento gerado por este trabalho oferece ferramentas para a tomada de decisões em políticas de conservação de áreas estratégicas, manejo de habitats subterrâneos tropicais e mitigação dos efeitos das mudanças climáticas.

Palavras-chave:

Alfa funcional; Beta funcional; Habitat epígeo; Habitat hipógeo; Isópodes terrestres; Mata Atlântica.

ABSTRACT

Subterranean habitats (caves and smaller spaces) represent unique ecosystems that harbor highly specialized species. Exploring functional variations in these habitats provides fundamental clues to understanding diversity patterns, allowing us to learn about the underlying ecological and evolutionary processes, as well as supporting conservation strategies and/or plans. Among the most frequent and abundant organisms in these environments are invertebrates, especially terrestrial isopods, which play essential roles in carbon flow in soils. By acting in the fragmentation of organic matter, these organisms promote nutrient transfer and stimulate microbial metabolism, contributing to increased decomposition rates. The conservation of subterranean habitats is becoming increasingly urgent, since many troglobitic species have restricted geographic distribution, low dispersal capacity, and high sensitivity to environmental disturbances. These factors make them particularly vulnerable to climate change and anthropogenic impacts, such as mining activities, urban expansion, unregulated tourism, and pollution. In this context, research on the characterization of subterranean biodiversity and the assessment of its diversity not only expands scientific knowledge but also strengthens management and conservation actions in tropical karst regions. Given this scenario, the purposes of this project were: (i) to describe the taxonomy of terrestrial isopods associated with subterranean habitats in Colombia; (ii) to describe the taxonomy of these species in epigean and hypogean habitats in southeastern Brazil, with emphasis on the Atlantic Forest biome; and (iii) to evaluate the functional variations of these organisms in epigean and hypogean habitats of the Parque Estadual Turístico do Alto Ribeira (PETAR), southeastern Brazil. To achieve these purposes, specimens deposited in scientific collections were analyzed, including the Laboratório de Estudos Subterrâneos of UFSCar (LES-UFSCar), the Museo de Zoologia da Universidade de São Paulo (MZUSP), and Colección del Laboratorio de Biología de la Universidad de Cartagena (CBUDC). The methodology consisted of a taxonomic review of species from PETAR, SP, and cave systems in Colombia, resulting in the description of new species of terrestrial isopods. For the assessment of taxonomic and functional diversity, specimens from PETAR were used. The analyses included the effective species number structure based on Hill numbers, and functional diversity metrics (FRic, FEve, and FDiv) by habitats, in addition to the estimation of taxonomic and functional dissimilarity by habitats using the Baselga approach. Functional distance was calculated using Gower distance. All analyses were performed using RStudio v. 4.4.1 software. Regarding the first purpose, the examination of specimens from Colombia resulted in the description of new species of terrestrial isopods of the genus *Ctenorillo*, with a publication in the journal Tropical Zoology. For the second purpose, the study of specimens from southeastern Brazil identified 309 individuals belonging to 29 species, five families, and nine genera, mainly from subterranean habitats in the Atlantic Forest, especially PETAR, in the state of São Paulo. These data formed the basis of an article on the oniscid fauna of the Alto Ribeira region, including PETAR, PEI, PECD, and contiguous areas, with the description of three new species and new records for the karst area of Alto Ribeira. For the third purpose, the results indicated greater functional richness in epigean assemblages, while beta diversity was high in both taxonomic and functional dimensions. This pattern was mainly driven by species turnover, highlighting marked differentiation in the structure of assemblages between habitats. Principal Coordinate Analysis revealed partial segregation of epigean and hypogean assemblages in functional space, as well as grouping of traits by family, highlighting the role of evolutionary history in shaping functional composition. These results contribute to the understanding of the mechanisms that structure biodiversity along environmental gradients in the Atlantic Forest and reinforce the importance of integrating taxonomic and functional perspectives to guide conservation actions. The simultaneous protection of epigean and hypogean habitats in threatened karst systems is essential to preserve biological diversity and the ecological processes that sustain these ecosystems. Finally, the knowledge generated by this work offers tools for decision-making in conservation policies for strategic areas, management of tropical subterranean habitats, and mitigation of the effects of climate change.

Keywords:

Atlantic Forest; Epigean habitat; Functional alpha; Functional beta; Hypogean habitat; Terrestrial isopods.

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APRESENTAÇÃO E ESTRUTURA DA TESE

Esta tese de doutorado enfoca o estudo dos isópodes terrestres (Oniscidea) em sistemas cársticos da Colômbia e do Brasil, integrando abordagens taxonômicas, biogeográficas e funcionais para compreender a diversidade, a distribuição e a conservação do grupo em ambientes epígeos e hipógeos. A pesquisa está organizada em três capítulos, cada um com objetivos específicos, porém complementares, contribuindo para uma compreensão abrangente da biodiversidade de Oniscidea em contextos neotropicais.

O primeiro capítulo, *The genus Ctenorillo Verhoeff, 1942 (Oniscidea, Armadillidae) from Colombia: new records, new species, and conservation comments*, publicado na revista *Tropical Zoology*, apresenta a revisão do gênero *Ctenorillo* (Armadillidae) na Colômbia, com base em material proveniente de sete departamentos das regiões Caribe e Andina, e também inclui material das cavernas do Caribe colombiano. Foram reconhecidas oito espécies do gênero, das quais seis são novas para a ciência (*C. binomio*, *C. humboldti*, *C. mincaensis*, *C. orientalis*, *C. papagayoensis* e *C. tayrona*). Além disso, ampliou-se a distribuição conhecida de *C. dazai* e *C. tuberosus*. Os resultados revelam que a maior parte das espécies ocorre na Floresta Tropical Seca, um dos ecossistemas mais ameaçados do mundo, destacando a urgência de ações de conservação voltadas aos Oniscidea associados a esses ambientes.

O segundo capítulo, *Bridging taxonomic gaps: three new species and novel distributional records of terrestrial isopods (Isopoda: Oniscidea) from epigean and hypogean habitats in the Alto Ribeira karst area, southeastern Brazil* (em preparação), apresenta uma revisão abrangente da fauna de isópodes terrestres em ambientes epígeos e hipógeos da região cárstica do Alto Ribeira, área de elevada relevância biogeográfica na Mata Atlântica. A partir de um extenso esforço de amostragem, três espécies foram reconhecidas como novas para a ciência: *Benthana* n. sp. e *Metaprosekia* n. sp. (Philosciidae), e *Novamundoniscus* n. sp. (Dubioniscidae), sendo esta última o primeiro registro de Dubioniscidae no Alto Ribeira. Também são apresentados diversos novos registros de distribuição, incluindo o primeiro registro de Armadillidae para a região. O capítulo fornece informações relevantes sobre história natural, micro-hábitats e diversidade em ambientes contrastantes, reforçando o papel fundamental da taxonomia para a compreensão e conservação da biodiversidade subterrânea.

O terceiro capítulo, *Contrasting taxonomic and functional diversity of terrestrial isopods (Oniscidea) in epigean and hypogean Atlantic Forest habitats* (em preparação), integra abordagens de ecologia funcional e análises de diversidade para comparar comunidades de isópodes em ambientes epígeos e hipógeos no Parque Estadual Turístico do Alto Ribeira, PETAR (Brasil). Os resultados mostram que, embora a diversidade alfa taxonômica não apresente diferenças significativas entre os ambientes, a riqueza funcional é maior em comunidades epígeas, enquanto as comunidades cavernícolas exibem traços mais especializados, associados à vida subterrânea. A alta diversidade beta, dominada pelo turnover, indica forte diferenciação na composição das comunidades. As análises também revelam segregação parcial no espaço funcional e agrupamento de traços por família, sugerindo influência marcante da história evolutiva sobre a composição funcional. Esse capítulo evidencia que os traços funcionais são fortemente estruturados pelo tipo de ambiente e reforça a importância de integrar taxonomia, ecologia e funcionalidade para subsidiar estratégias de conservação em sistemas cársticos ameaçados.

Ao longo do doutorado, participei como coautora em diversos trabalhos relacionados à taxonomia e à diversidade de isópodes terrestres em cavernas do Brasil e na Colômbia. Colaborei na descrição de novas espécies do gênero *Diploexochus* provenientes da Colômbia, incluindo a primeira espécie troglóbia registrada para o país (Anexo 1). Adicionalmente, perticipei na descrição de 11 novas espécies do gênero *Trichorhina*, algumas provenientes do PETAR (SP, Brasil), área que constitui o foco de estudo deste projeto (Anexo 2); além de colaborar em outras publicações relacionadas a novos registros e à descrição de táxons neotropicais em ambientes subterrâneos (Anexos 3–6).

Em conjunto, os três capítulos revelam a importância dos isópodes terrestres como componentes-chave da biodiversidade neotropical, ao documentar espécies novas, ampliar distribuição e elucidar padrões de diversidade taxonômica e funcional em gradientes ambientais. A tese destaca não apenas a relevância da taxonomia como base para estudos ecológicos e conservacionistas, mas também evidencia a necessidade de fortalecer a pesquisa em fauna subterrânea e a proteção dos ecossistemas ameaçados onde esses organismos ocorrem.

INTRODUÇÃO GERAL

Habitats subterrâneos

Os habitats subterrâneos (cavernas e espaços de dimensões menores) são considerados um dos ecossistemas mais interessantes e únicos no planeta, pois constituem refúgios para diversas espécies, as quais apresentam especializações únicas, relacionadas ao isolamento nestes habitats (Muñoz-Saba, 1998; Ardila-Rodríguez, 2006; Culver & Pipan, 2009; Castellanos-Morales, 2018). Uma caverna é definida como uma cavidade natural em um ambiente rochoso acessível ao ser humano, representando janelas aos espaços de dimensões menores (Monroe, 1972; Trajano & Bichuette, 2006; Culver & Pipan, 2009, 2019). Em geral, possuem particularidades em termos de recursos tróficos e espaciais (Culver & Pipan, 2009, 2019).

As cavernas são ecossistemas frágeis e apresentam relações ecológicas únicas (Culver & Pipan, 2009, 2019; Muñoz-Saba & Lasso, 2020). O meio epígeo ou superficial às cavernas é exposto à luz direta ou indiretamente, de forma regular, enquanto o meio hipógeo (subterrâneo) apresenta uma zonação de acordo com a distância ou influência do meio epígeo (Culver & Pipan, 2009, 2019). A ausência de luz repercute na fauna que vive nesses ambientes, apresentando especializações únicas, muitas adaptativas, como uma otimização na percepção de cheiros e estímulos mecânicos (Culver & Pipan, 2019). As cavernas são divididas em três zonas principais (Culver & Pipan, 2009, 2019; Lee *et al*., 2012): 1) zona de entrada, a mais próxima da superfície, recebe luz solar direta e tem temperaturas e umidade variáveis, além de pouca vegetação; 2) zona de penumbra, a qual tem incidência indireta de luz, e a temperatura tende a ser constante, mas ainda pode oscilar junto com o clima da superfície; e 3) zona afótica ou profunda, a qual corresponde à área onde não há luz, a temperatura permanece constante, e a umidade do ar geralmente é elevada (Figura 1).

A flutuação das variáveis ambientais também é reduzida nos habitats subterrâneos, com exceções. Contrastando, os habitats superficiais apresentam ampla variação na temperatura e umidade relativa do ar, geralmente seguindo a sazonalidade climática local/regional (Lee *et al*., 2012).

Existe uma proposta de classificação onde os organismos que habitam as cavernas e outros habitats subterrâneos são categorizados (**sensu** Schiner, 1854, modificado por Racovitza, 1907), a saber: troglóbios, inclui as populações só encontradas nas cavernas, são caracterizadas tanto por redução até perdas morfológicas (como redução dos olhos, pigmento e adelgamento da cutícula em artrópodes), quanto por ganhos (como aumento de estruturas sensoriais extraópticas, alongamento dos apêndices, antenas, etc.); troglófilos, são populações que ocorrem tanto em habitats superficiais quanto em subterrâneos; e trogloxenos, essas espécies geralmente são encontradas em cavernas, e necessitam sair para completarem seus ciclos de vida como alimentação ou reprodução (Trajano & Bichuette, 2006; Culver & Pipan, 2009, 2019).

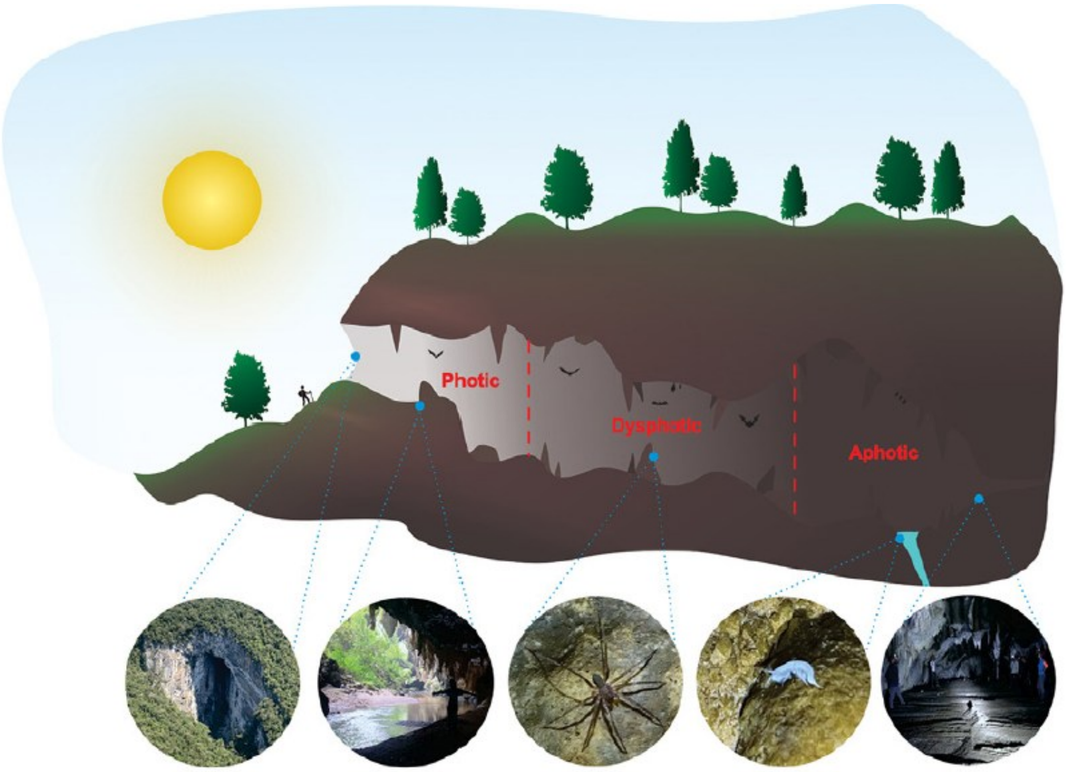

Figura 1. Diagrama geral das principais áreas dentro de uma caverna: área de entrada, com alta incidência de luz; zona crepuscular ou penumbra, transição entre a entrada e a escuridão; e a zona profunda (afótica) com ausência de luz. Extraído de Kato *et al*. (2024).

As cavernas e seu entorno fornecem uma série de serviços ecossistêmicos, incluindo: purificação ou disponibilização de água; produção de guano como fonte de abrigo e alimento para muitos invertebrados detritívoros; além de benefícios econômicos e sociais para as comunidades, relacionados às possibilidades esportivas e de ecoturismo oferecidas pela exploração subterrânea, entre outros (Muñoz-Saba & Lasso, 2020). Ainda, as cavernas são excelentes laboratórios naturais para o estudo das mudanças climáticas globais devido à estabilidade ecológica e térmica, onde se torna importante considerar os organismos subterrâneos como espécies modelo para estudos ecológicos relacionados às mudanças climáticas e estender tais investigações a outros sistemas subterrâneos ao redor o mundo (Mammola *et al*., 2017). No entanto, sabemos que as alterações climáticas afetam todos os ecossistemas, incluindo os habitats subterrâneos, e um aumento das temperaturas à superfície pode levar a um aumento das temperaturas nas cavernas, ameaçando a biota subterrânea e os serviços ecossistêmicos (Medina *et al*., 2023).

Atualmente, o Brasil há registro de cerca de 24.000 cavernas, porém, menos da 50% tem sua informação validada, e 10% apresentam informações errôneas sobre sua localização geoespacial (Massuqueto *et al*., 2021; CANIE, 2023). Ainda, há um potencial para a descoberta de milhares de novas cavernas devido à extensão do seu território e áreas inexploradas (Auler, 2017; Massuqueto *et al*., 2021). A geração de conhecimento sobre a fauna dos ecossistemas subterrâneos do Brasil concentrou-se nas áreas cársticas (rochas sedimentares carbonáticas e/ou dolomitas composto de carbonato de cálcio e magnésio) dos estados de Bahia, São Paulo e Minas Gerais (Gallão & Bichuette, 2018; CANIE, 2023).

Por outro lado, a Colômbia possui uma grande riqueza de locais com potencial para cavidades (Muñoz-Saba, 1998). Até o momento, a Associação Espeleológica da Colômbia (ESPELEOCOL) registrou mais de 500 cavidades cuja informação espeleométrica (dados gerais de topografia e mapeamento) é escassa e, em alguns casos inexistentes (Valdivieso-Bohórquez, 2022). Embora estime-se que este número possa ultrapassar 1000 cavidades, o que tornará o país com grande potencial do ponto de vista bioespeleológico, o conhecimento da fauna associada a estas formações ainda é incipiente (Muñoz-Saba & Lasso, 2020). A geração de conhecimento sobre a fauna dos ecossistemas subterrâneos da Colômbia concentrou-se nos departamentos de Santander e Tolima (região central do país), agrupando 86% das pesquisas sobre biologia subterrânea (Castellanos-Morales *et al*., 2015). Portanto, ainda faltam informações e estudos para outros departamentos, principalmente para a região do Caribe.

Ainda, há uma escassez de informações sobre outros grupos funcionalmente importantes, como os isópodes terrestres. Portanto, é possível que haja uma perda de biodiversidade ainda não conhecida, causada principalmente pela alteração de habitats naturais, pressão antrópica, turismo e mineração descontrolados, entre outros fatores de ameaça a tais ambientes (Muños-Saba & Lasso, 2020).

Diversidade funcional em ecossistemas subterrâneos

A diversidade funcional é definida como a variedade de modos pelas quais os organismos utilizam os recursos, bem como transformam o meio ambiente (Cleland, 2011; Garnier *et al*., 2015; Salgado-Negret, 2015). Este componente da ecologia inclui um valor baseado em traços funcionais, que permite descrever as estratégias de vida das espécies e o funcionamento de um ecossistema (Violle *et al*., 2007; Moore, 2013). Essas características incluem os atributos morfológicos ou fisiológicos, relacionado ao uso do habitat e pode ser qualitativo ou quantitativo, e refletem as qualidades cuja variação tem impacto no sucesso individual (Violle *et al*., 2007; Song *et al*., 2014; Arnan *et al*., 2016). O estudo da diversidade funcional tem aumentado nos últimos anos, pois permite obter informações e compreender a resposta das espécies à variação ambiental e seu impacto nos processos ecossistêmicos (Díaz & Cabido, 2001; Garnier *et al*., 2015; Salgado-Negret, 2015).

A exploração de variações funcionais em habitats estratégicos, como os subterrâneos, fornece pistas para a compreensão dos padrões de diversidade, o que pode fornecer conhecimento sobre os processos evolutivos e ecológicos, os quais podem ser implementados em estratégias e/ou planos de conservação (Gibert & Deharveng, 2002). A fauna mais numerosa e frequente dos habitats subterrâneos são os invertebrados, como os isópodes terrestres, que desempenham um papel essencial no fluxo de carbono nos solos (Gibert & Deharveng, 2002; Fišer *et al*., 2012; Deharveng & Bedos, 2018; Barriga *et al*., 2019). Estes organismos alimentam-se principalmente de matéria orgânica em decomposição, razão pela qual desempenham um papel fundamental na transformação e distribuição da matéria orgânica do solo (Hassall *et al*., 2018). Eles têm sido utilizados como bioindicadores de impactos ambientais e antrópicos e como organismos modelo de investigação (Paoletti & Hassall, 1999; De Smedt *et al*., 2022). Ainda são organismos sensíveis às alterações na disponibilidade de água no solo e às variações de temperatura, o que influencia sua dinâmica, afetando padrões de crescimento, sobrevivência, reprodução e distribuição (Hassall *et al*., 2018).

Um dos métodos para medir a diversidade funcional consiste em classificar os táxons em grupos funcionais de acordo com a similaridade de suas características (Cleland, 2011; Moore, 2013). Os isópodes terrestres são particularmente interessantes para explorar a relação entre peso corporal, hábito e taxa de perda de água (Broly *et al*., 2015; Ooms *et al*., 2020). Por outro lado, foi demonstrado que estes organismos utilizam as suas antenas para se orientarem em direção às fontes de alimento (quimiorrecepção de contato), fornecendo informações sobre a resposta adaptativa em ambientes subterrâneos (Ooms *et al*., 2020). A avaliação destas características funcionais é considerada importante em isópodes terrestres porque ajudam a compreender a resposta da montagem destes organismos e a influência no funcionamento destes ecossistemas, razão pela qual têm sido utilizados em diferentes trabalhos abordando ecologia funcional (Fernandes, 2015; Fernandes *et al*., 2016; Deharveng & Bedos, 2018). Fernandes *et al*. (2016) avaliaram a diversidade funcional de comunidades subterrâneas de isópodes terrestres, a partir de traços comportamentais, fisiológicos e morfológicos, encontrando maior valor dessa diversidade nos habitats subterrâneos em comparação com os epígeos. Além disso, sugeriram que as cavernas mantêm condições ambientais e de predação favoráveis para a diversificação destes organismos, o que reforça a necessidade de sua proteção.

Portanto, a avaliação de isópodes terrestres em habitats subterrâneos permite compreender o papel que desempenham no meio ambiente, melhorando a transferência de nutrientes e promovendo o metabolismo microbiano, que por sua vez aumenta a taxa de decomposição da matéria orgânica nesses ambientes (Gibert & Deharveng, 2002). Além disso, compreender sua ecofisiologia pode ser útil para explicar a distribuição geográfica e a utilização de microhabitats de espécies em um contexto de alterações climáticas (Antoł *et al*., 2021).

Pelo exposto, as perguntas do presente projeto são: qual é a composição de espécies de isópodes terrestres associados aos ecossistemas subterrâneos da região Neotropical, com ênfase na região sudeste do Brasil e na Colômbia? e como os habitats (epígeos e hipógeos) condicionam a diversidade taxonômica e funcional dos isópodes terrestres associados aos habitats subterrâneos da Mata Atlântica no sudeste do Brasil.

Isópodes terrestres (Crustacea, Isopoda, Oniscidea)

Com aproximadamente 4,000 espécies descritas distribuídas em mais de 500 gêneros e 38 ou 39 famílias, a subordem Oniscidea agrupa espécies de crustáceos estritamente terrestres, comumente conhecidos como "tatuzinhos de jardim" (Sfenthourakis & Taiti, 2015; Campos-Filho & Taiti, 2021). Evolutivamente desenvolveram adaptações morfofisiológicas que estão ligadas às necessidades de viver em diferentes ambientes. Dentre essas adaptações está o desenvolvimento de estruturas respiratórias (pulmões pleopodais), localizadas nos exópodes dos pleópodes (Figura 2). Essas estruturas são especializadas para a respiração aérea, substituindo as brânquias das espécies aquáticas, conseguindo variar desde simples áreas respiratórias como diminuição do espessamento da cutícula dos exópodes, até uma estrutura ramificada, complexa e interna que pode atingir as proximidades do coração, e são amplamente utilizados na identificação taxonômica (Ferrara *et al*., 1994; Schmidt & Wägele, 2001).

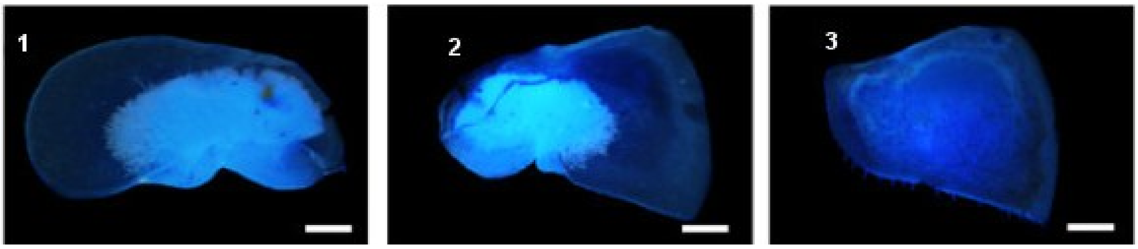

Figura 2. Pulmões pleopodais em *Porcellio scaber* Latreille, 1804. Estruturas pulmonares dentro do primeiro (1) segundo (2) e terceiro pleópode (3). Extraído de Inui *et al*. (2022).

Outro exemplo de adaptação ao ambiente terrestre é o comportamento gregário de algumas espécies (Figura 3), que é parcialmente responsável pela resistência à perda de água e como estratégia de defesa contra predadores (Broly *et al*., 2013). Esse comportamento é estimulado por feromônios de agregação ou reprodução capturados pelos estetascos, que são cerdas sensoriais específicas dispostas nos dois pares de antenas. O hábito gregário também traz benefícios adicionais, relacionados a diferentes aspectos da história natural dos isópodes terrestres, como redução do consumo de oxigênio, aumento do crescimento corporal, estímulos bióticos para reprodução, possíveis defesas compartilhadas contra predadores, estimulação da coprofagia, alimentação e aquisição de endossimbiontes (Broly *et al*., 2013).

Os isópodes terrestres podem ser encontrados vivendo na zona supralitoral, manguezais, desertos, floresta tropical seca, floresta andina, paramos, ecossistemas subterrâneos e urbanos, entre outros (Schmalfuss, 2003). Estes organismos alimentam-se principalmente de matéria orgânica em decomposição, razão pela qual desempenham um papel essencial aos processos de formação do solo e reciclagem de nutrientes (Zimmer & Topp, 1999). Eles aumentam a taxa de decomposição da matéria orgânica (Abd El-Wakeil, 2015), e, além disso, são consideradas pragas emergentes, uma vez que foram observados ataques às lavouras (Waller, 2018; Fusaro *et al*., 2024).

Figura 3. Comportamento gregário da espécie *Pulmoniscus turbanaensis* López-Orozco, Carpio-Díaz & Campos-Filho, 2017. Fonte da autora.

Fatores ambientais como temperatura e umidade desempenham um papel essencial na dinâmica das comunidades terrestres de isópodes, afetando seu crescimento, sobrevivência e reprodução (Rushton & Hassall, 1987). Por outro lado, a riqueza e abundância das comunidades de isópodes terrestres podem ser afetadas pela intervenção dos seus habitats e pela redução da humidade relativa (Oliveira *et al*., 2019).

Para o Brasil já foram registradas mais de 93 espécies de isópodes terrestres associados a cavernas, sendo 43 troglóbias, concentrou-se nas áreas cársticas dos estados de Bahia, São Paulo e Minas Gerais (Campos-Filho *et al*., 2014, 2018, 2019, 2020, 2022a, 2022b, 2022c, 2023; Cardoso et a., 2020a, 2020b, 2021; Cardoso & Ferreira, 2023).

Porém, para a Colômbia, apenas seis espécies de isópodes terrestres foram registradas em habitats subterrâneos, todas para o departamento de Santander, área centro-norte da Colômbia: para as cavernas Hoyo del Aire e Indio do Parque Natural Nacional Cueva de los

Guácharos, registraram a presença de espécie pertencente ao gênero *Neosanfilippia* Brian, 1957 (Scleropactidae) (Castellanos-Morales *et al*., 2015); para a caverna El Caracol um espécime pertencente à família Philosciidae Kinahan, 1857; para a caverna Las Sardinas uma espécie do gênero *Ischioscia* Verhoeff, 1928 (Philosciidae); para as cavernas El Caracol e Los Carracos uma espécie do gênero *Colomboniscus* Vandel, 1972 (Scleropactidae); para as cavernas La Tronera, Las Sardinas e Los Carracos foi registrada uma espécie do gênero *Colomboscia* Vandel, 1972 (Scleropactidae); e para as cavernas La Tronera e Los Carracos uma espécie do gênero *Sphaeroniscus* Gerstäcker, 1854 (Scleropactidae) foi registrada. Esses registos demonstram a necessidade de ampliação de estudos tanto em áreas conhecidas como inexploradas, buscando uma melhor compreensão da fauna associada, considerando a preservação destes habitats e de sua biodiversidade para a Colômbia (Muñoz-Saba & Lasso, 2020).

A necessidade de conhecer a biodiversidade das cavernas e a funcionalidade dos seus organismos reside na oportunidade de compreender a resposta da fauna às alterações climáticas e a influência no funcionamento destes ecossistemas (Mammola *et al*., 2017). Estes ambientes subterrâneos estão a atrair cada vez mais interesse e preocupação de conservação, porque a maioria das espécies troglóbias são geograficamente restritas e muitas vezes raras, tornando-as vulneráveis a perturbações ambientais, devido à baixa capacidade das espécies subterrâneas em responder ao estresse ambiental (Trajano & Bichuette, 2006; Culver & Pipier, 2009, 2019; Gallão & Bichuette, 2018).

O baixo nível de conhecimento sobre a biologia, ecologia e distribuição dos grupos funcionalmente importantes, como isópodes terrestres impossibilita o reconhecimento de possíveis áreas estratégicas para a conservação, gestão e uso sustentável da biodiversidade (Myers *et al*., 2000). Provavelmente, muitas espécies da fauna associadas aos ecossistemas subterrâneos de países como Colômbia não foram descritas pela ciência, e esse conhecimento ainda é incipiente (Barriga *et al*., 2019).

Considerando o que está estabelecido na Lei No. 2237 de 8 de julho de 2022 (Congresso da República de Colômbia) em seu artigo 1, devem ser adotadas medidas para a conservação, estudo científico, identificação, restauração e uso sustentável do patrimônio espeleológico colombiano. Portanto, estes princípios devem ser promovidos e utilizados em locais estratégicos para contribuir para o desenvolvimento do conhecimento e para a conservação da biodiversidade e do meio ambiente (Congreso de la República, 2022).

Levando em consideração o acima, este estudo nos ajuda a compreender como a análise da diversidade taxonômica e funcional pode explicar a co-ocorrência de espécies em diversas assembleias comunitárias, além disso, fornecem novas evidências dos processos de assembleia de comunidades em ambientes subterrâneos. Com esses resultados são gerados conhecimentos para a tomada de decisões em ações de conservação de sítios estratégicos, gestão de habitats subterrâneos tropicais e mitigação das mudanças climáticas.

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OBJETIVOS E HIPÓTESES

Objetivo geral

- ❖ Avaliar a composição taxonômica e as variações na diversidade funcional de isópodes terrestres (Isopoda, Oniscidea) em habitats epígeos e hipógeos da região Neotropical, com ênfase na Mata Atlântica no sudeste do Brasil e da Colômbia.

Objetivos específicos

- ❖ Determinar e descrever as espécies de isópodes terrestres associados aos habitats epígeos e hipógeos da Colômbia;
- ❖ Determinar e descrever as espécies de isópodes terrestres associados aos habitats subterrâneos da Mata Atlântica na região sudeste do Brasil;
- ❖ Avaliar as mudanças na diversidade taxonômica e funcional de isópodes terrestres associados aos habitats epígeos e hipógeos da Mata Atlântica (região sudeste) do Brasil.

Desses objetivos, o último foi planejado com as seguintes hipóteses:

1. Espera-se que as dimensões da diversidade dos oniscídeos estudados difiram entre ambientes epígeos e hipógeos, com a assembleia epígea apresentando maior diversidade taxonômica e funcional, enquanto a assembleia hipógea apresente uma maior afetação ou simplificação destes devido à filtragem ambiental.
2. Devido às pressões contrastantes nesses ambientes, espera-se uma alta dissimilaridade nas comunidades, impulsionada principalmente pela substituição de espécies ou traços (em vez de aninhamento), refletindo a diferenciação adaptativa em habitats contrastantes.
3. Espera-se que cada tipo de habitat apresente regiões distintas de espaço funcional, com as assembleias epígeas exibindo maior variabilidade de traços que refletem as condições da superfície, enquanto as assembleias hipógeas exibem fortes efeitos de filtragem ambiental.

CAPÍTULO 1: The genus *Ctenorillo* Verhoeff, 1942 (Oniscidea, Armadillidae) from Colombia: new records, new species, and conservation comments

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The genus *Ctenorillo* Verhoeff, 1942 (Oniscidea, Armadillidae) from Colombia: new records, new species, and conservation comments

1. Abstract

The Armadillidae are the most diverse family within the Oniscidea, widely distributed around the world. To date, only seven species of the family are known from Colombia. After the examination of a collection from the Colombian departments of Atlántico, Bolívar, Cesar, Magdalena, Risaralda, Santander, and Sucre, eight species were recognized as belonging to the genus *Ctenorillo*, of which six are considered to be new to science: *C. binomio*, *C. humboldti*, *C. mincaensis*, *C. orientalis*, *C. papagayoensis*, and *C. tayrona*. Moreover, the distribution knowledge of *C. dazai* and *C. tuberosus* has expanded. *Ctenorillo* species in Colombia are predominantly distributed in Tropical Dry Forest areas, which is one of the most endangered ecosystems in the world. Considering the new taxa presented here, allied with other Oniscidea groups, there is an urgent need to raise the awareness level regarding the conservation status of this ecosystem in the country.

Keywords: Neotropical, terrestrial isopods, new species, Tropical Dry Forest.

2. Introduction

Terrestrial isopods (Oniscidea) are the unique crustacean lineage completely adapted to terrestrial habitats (Schmalfuss, 2003; Hornung, 2011; Richardson & Araujo, 2015; Taiti, 2018a). To date, the group comprises more than 4,000 species in more than 500 genera in 38 or 39 families distributed in almost all types of habitats (Sfenthourakis & Taiti, 2015; Lins *et al*., 2017; Dimitriou *et al*., 2019; Campos-Filho & Taiti, 2021).

The family Armadillidae holds the highest diversity, including ca. 650 species in 80 genera widely distributed in Neotropical, Afrotropical, Oriental, and Australian regions (Taiti *et al*., 1998; Schmalfuss, 2003; Sfenthourakis & Taiti, 2015; López-Orozco *et al*., 2022; Boyko *et al*., 2023a). The family has a great morphological diversity (Schmalfuss & Ferrara, 1983; Schmalfuss, 1985, 1996; Taiti *et al*., 1998; Taiti, 2014), and most of its representatives have the ability to roll up into a ball (Schmalfuss, 1984).

To date, in the Neotropics, only eight genera have been recorded so far, *Acanthoniscus* Gosse, 1851, *Ctenorillo* Verhoeff, 1942, *Cubaris* Brandt, 1833, *Diploexochus* Brandt, 1833, *Gabunillo* Schmalfuss & Ferrara, 1983, *Pseudodiploexochus* Lewis, 1998, *Synarmadillo* Dollfus, 1891, and *Venezillo* Verhoeff, 1928 (Pearse, 1915; Schmidt, 2001; Campos-Filho *et al*., 2014, 2017, 2018; Carpio-Díaz *et al*., 2018; Rodríguez-Cabrera & Armas, 2023).

In Colombia, only seven species of Armadillidae are known, i. e., *Ctenorillo dazai* Carpio-Díaz, López-Orozco & Campos-Filho, 2018, *C. tuberosus* (Budde-Lund, 1904), *Synarmadillo ruthveni* (Pearse, 1915), *Venezillo brevispinis* (Pearse, 1915), *V. gigas* (Miers, 1877), *V. grenadensis* (Budde-Lund, 1893), and *V. vincentis* (Budde-Lund, 1904) (Richardson, 1912; Pearse, 1915; Carpio-Díaz *et al*., 2018; Campos-Filho *et al*., 2017; López-Orozco *et al*., 2022). It is worth mentioning that Van Name (1936) and Vandel (1972) recorded the pantropical species *Cubaris murina* Brandt, 1833 from the country, but both authors did not provide the localities where the specimens were collected, and therefore, these records are considered doubtful.

In the present work six new species of the genus *Ctenorillo* were described, i.e., *Ctenorillo binomio* Carpio-Díaz, Bichuette & Campos-Filho, 2023 from the department of Bolívar, *Ctenorillo humboldti* Carpio-Díaz, López-Orozco & Campos-Filho, 2023 from the department of Risaralda, *Ctenorillo mincaensis* López-Orozco, Carpio-Díaz & Campos-Filho, 2023, *Ctenorillo tayrona* López-Orozco, Borja-Arrieta & Campos-Filho, 2023 from the department of Magdalena, *Ctenorillo orientalis* Carpio-Díaz, Taiti & López-Orozco, 2023 from the department of Cesar, and *Ctenorillo papagayoensis* Carpio-Díaz, Borja-Arrieta & Campos-Filho, 2023 from the department of Santander. In addition, *C. dazai* and *C. tuberosus* have the knowledge on their distribution expanded.

3. Material and Methods

Specimens were preserved in ethanol 75%. The identifications are based on morphological characters with the use of micropreparations in Hoyer’s medium (Anderson, 1954). The illustrations were made with the aid of a camera lucida mounted on Wild M3 and M20 microscopes. The final illustrations were prepared using the software GIMP (v. 2.8) with the method proposed by Montesanto (2015, 2016). The respiratory structures were classified as in Paoli *et al*. (2002). The maps were constructed with the ArcMap (v. 10) software with the layers as in Morrone et al. (2022).

The material examined is deposited in the Collection of the Universidad de Cartagena, Cartagena (CBUDC-CRU), Collection of Terrestrial Invertebrates of the Instituto Alexander von Humboldt, Villa de Leyva (IAvH-I), and Collection of the Instituto de Ciencias Naturales, Nacional University of Colombia, Bogotá, Colombia (ICN-CR-is).

4. Results

Systematic account

Family Armadillidae Brandt, 1831

Genus ***Ctenorillo*** Verhoeff, 1942

Type species: *Ctenorillo buddelundi* Verhoeff, 1942 [= *Ctenorillo regulus* (Van Name, 1920)], by monotypy (see Schmidt & Leistikow, 2004).

Remarks

To date, the genus *Ctenorillo* Verhoeff, 1942 comprises 15 species: *C. ausseli* Dollfus, 1893 from the Canary Islands; *C. bananae* (Van Name, 1920) from Angola, Cameroon and Congo; *C. dazai* from Colombia; *C. fagei* (Paulian de Félice, 1941) from Ivory Coast; *C. ferrarai* Campos-Filho, Araujo & Taiti, 2014 from Brazil; *C. gabunensis* (Schmalfuss & Ferrara, 1983) from Gabon; *C. guinensis* (Schmalfuss & Ferrara, 1983) from Guinea; *C. kenyensis* Schmölzer, 1974 from Tanzania and Uganda; *C. legai* (Arcangeli, 1941) from Ethiopia; *C. meyeri* Taiti, 2018 from South Africa; *C. mineri* (Van Name, 1936) from Guyana and Venezuela; *C. parituberculatus* (Taiti & Ferrara, 1987) from Malawi; *C. regulus* (Van Name, 1920) from Kenya, Somalia, Uganda and Zaire; *C. strinatii* (Schmalfuss & Ferrara, 1983) from Congo; and *C. tuberosus* (Budde-Lund, 1904) from Brazil and Haiti (Boyko *et al*., 2023b).

The genus was recently redefined by Carpio-Díaz *et al*. (2018). As mentioned by Campos-Filho *et al.* (2014) and Taiti (2018b), the best taxonomic characteristics to distinguish the species of the genus are the number and arrangement of the dorsal tubercles and bosses of the cephalon, pereon, and pleon.

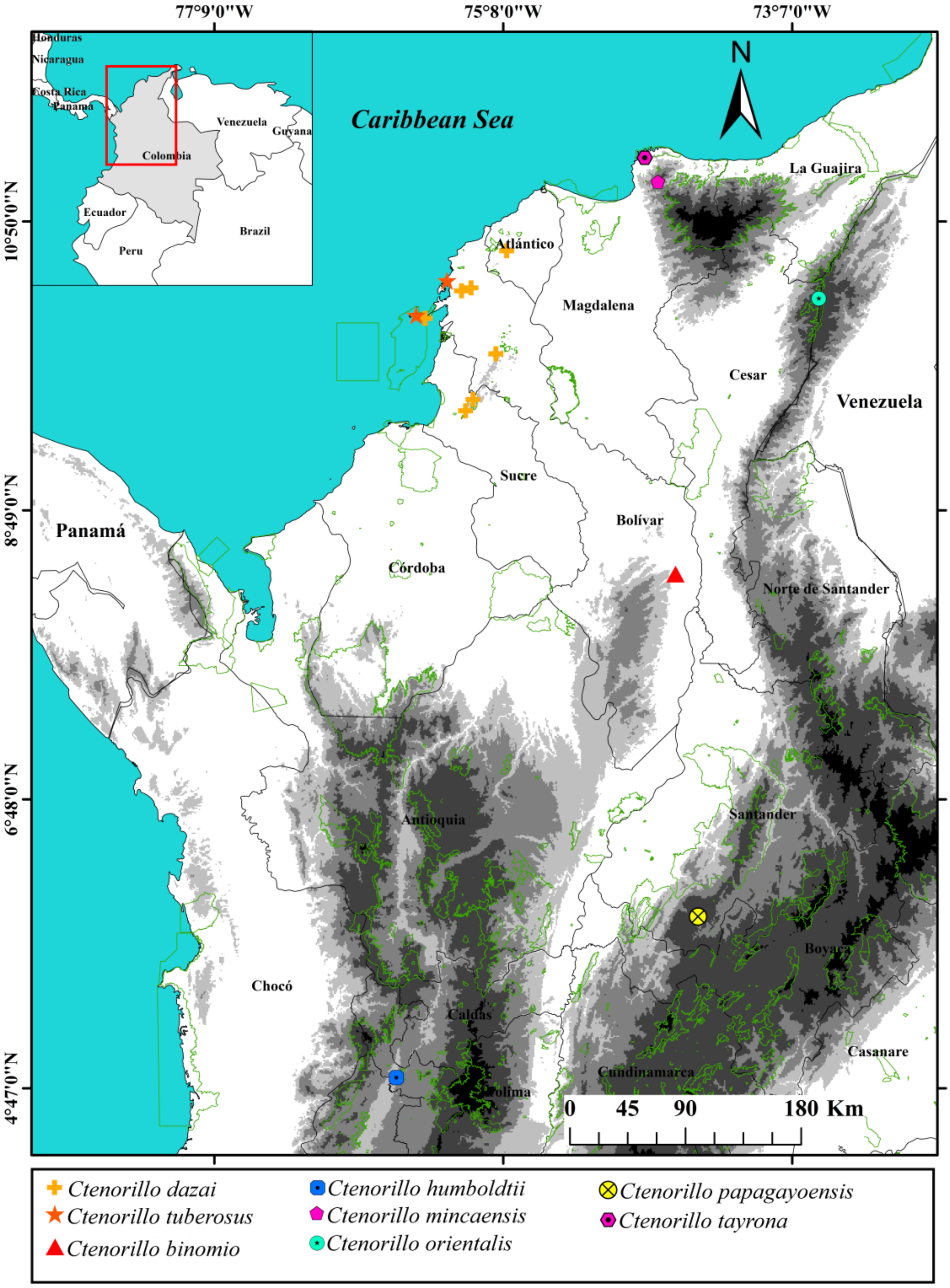

Figure 1. Map of *Ctenorillo* species from Colombia. Light to dark gray areas = Andean Cordillera; Light green areas= Tropical Dry Forest; Dark green lines = Colombian conservation units.

Ctenorillo dazai Carpio-Díaz, López-Orozco & Campos-Filho, 2018

Figure 1

Ctenorillo dazai Carpio-Díaz *et al*. (2018): 311, figs 5, 51-74.

Material examined

COLOMBIA: **Atlántico**, 2 ♂♂, 1 ♀ (CUDC-CRU 410), Luruaco, Arroyo de Piedra, around La Mojana cave (outside), 10°37'38.15"N 75°6'35.89"W, 25 March 2017, leg. C.M. López-Orozco and R. Borja-Arrieta; **Bolívar**, 9 ♂♂, 9 ♀♀ (CBUDC-CRU 334), Cartagena de Indias, Barú, Calablanca, 10°9'20.62"N 75°40′44.39″W, 5 October 2017, leg. L.D. Luna; 1 ♂, 2 ♀♀ (CBUDC-CRU 335), San Jacinto, Brasilar, 9°54'33"N 75°11'6"W, 20 October 2018, leg. W. Zapata and M. Carrillo; 2 ♂♂, 2 ♀♀ (CBUDC-CRU 336), Turbaco, Cañaveral, 10°22'7.1"N 75°21'30.5"W, 15 October 2018, leg. W. Zapata and M. Carrillo; **Sucre**, 1 ♀ (CBUDC-CRU 409), Chalán, Reserva Natural Altamira, 9°35'22.46"N 75°20'41.76"W, 16 July 2018, leg. C.M. López-Orozco and R. Borja-Arrieta; 2 ♀♀ (CBUDC-CRU 377), Tolúviejo, La Piche, Campo Aventura Roca Madre, 9°30'51.5"N 75°23'37.3"W, 13 July 2018, leg. C.M. López-Orozco and R. Borja-Arrieta; 1 ♀ (CBUDC-CRU 378), 1 ♀ (CBUDCCRU 379), same locality and collectors as previous, 14 July 2018.

Distribution

This species was previously recorded from the Botanical Garden Guillermo Piñeres (Tropical Dry Forest area - TDF), Turbaco, North of Bolívar, Colombian Caribbean (Carpio-Díaz *et al*., 2018). The present records extend the knowledge of its distribution to the departments of Atlántico and Sucre (Montes de María). The localities where the specimens were collected are placed in TDF areas (see Figure 1).

Ctenorillo tuberosus (Budde-Lund, 1904)

Figure 1

Armadillo tuberosus Budde-Lund (1904): 109, pl. X figs 1-4. *Ctenorillo tuberosus*; López-Orozco *et al*. (2022): 38, fig. 2L.

Material examined

COLOMBIA: **Bolívar**, 3 ♀♀ (CUDC-CRU 56), Cartagena de Indias, Cerro de la Popa, Salto del Cabrón, 10°25'9.03"N 75°31'33.37"W, 13 July 2017, leg. C.M. López-Orozco.

Distribution

Brazil, Colombia, and Haiti (Schmalfuss, 2003; Campos-Filho *et al*., 2017; López-Orozco *et al*., 2022). This species has been recorded in the Colombian Caribbean from Isla Grande, department of Bolívar (López-Orozco *et al*., 2022). The present work extends the knowledge of its distribution to the continental part of the Colombian Caribbean (see Figure 1).

Ctenorillo binomio Carpio-Díaz, Bichuette & Campos-Filho, 2023

Figures 1-4

Material examined

COLOMBIA: Holotype ♂ (parts in micropreparations) (CBUDC-CRU 412), **Bolívar**, Morales, Arcadia, San Miguel cave, 8°22’21.22”N 73°55’54.17”W, 20 April 2018, leg. C.M. López-Orozco and R. Borja-Arrieta. Paratype*:* 1 ♀ (parts in micropreparations) (CBUDC-CRU 337), same data as holotype.

Description

Maximum length: male and female 5 mm. Color dark gray. Dorsum covered with small triangular tubercles, arranged as follows (Figure 2A,B): cephalon with 10 tubercles in three rows, anterior and middle rows with two tubercles each, posterior row with six tubercles; pereonite 1 with four tubercles on anterior row, 12 tubercles on middle arranged in two rows of six tubercles each, and five tubercles on posterior row; pereonites 2-6 with eight tubercles on anterior row, and nine tubercles on posterior row; pereonite 7 with six tubercles on anterior row, and nine tubercles on posterior row; pleonites 3 and 4 with four tubercles, pleonite 5 and telson with two tubercles each. Dorsal surface with short triangular scale-setae (Figure 2C). Pereonites 1-7 with one line of noduli laterales per side inserted on postero-lateral surface of second outer tubercle. Cephalon (Figure 2D-F) with frontal shield rectangular, slightly protruding above vertex, and slightly bent over vertex; eyes of 12 ommatidia. Pereonite 1 epimera slightly grooved on lateral margin for about half length, inner lobe of schisma rounded, not extending beyond posterior margins of outer lobe; pereonites 2-4 epimera rectangular, pereonite 2 with ventral lobe subtriangular, distal margin rounded, not extending beyond posterior margin of epimera (Figure 2A,F,G). Pleonites 35 epimera rectangular (Figure 2H,I). Telson (Figure 2H) hourglass-shaped, proximal part broader than distal part, slightly convex distal margins.

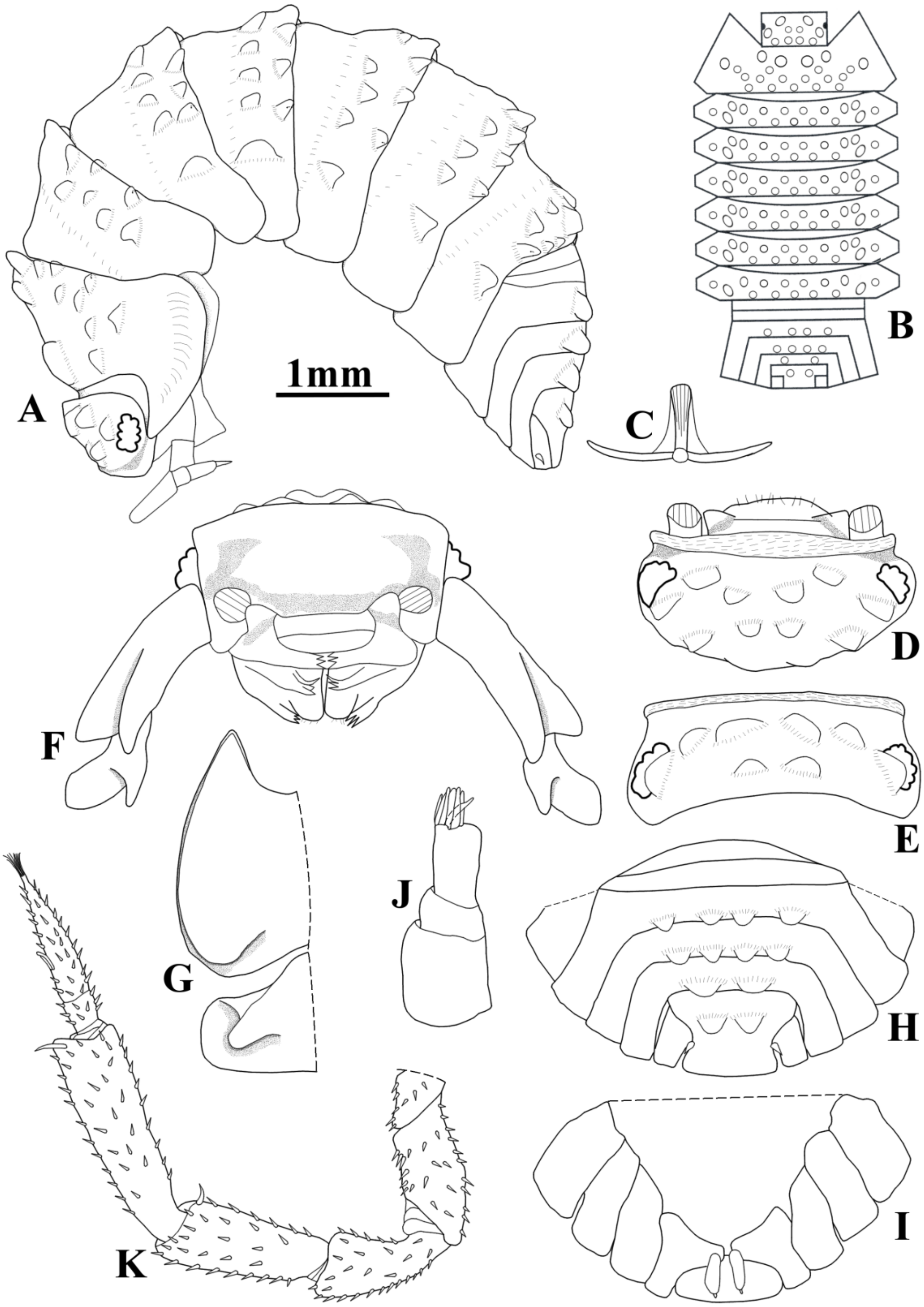

Figure 2. *Ctenorillo binomio* Carpio-Díaz, Bichuette & Campos-Filho, 2023, ♀: A, habitus, lateral view; B, dorsal tubercles scheme; C, dorsal scale-seta; D, cephalon, dorsal view; E, cephalon, posterior view; F, cephalon and pereonites 1 and 2, frontal view; G, pereonites 1 and 2 epimera, ventral view; H, pleon, telson, and uropods, dorsal view; I, pleonites 3-5, telson, and uropods, ventral view; J, antennula; K, antenna.

Antennula (Figure 2J) of three articles, proximal and distal articles subequal in length, distal article bearing seven apical aesthetascs. Antenna (Figure 2K) short and stout, not surpassing posterior margin of cephalon when extended backwards; flagellum of two articles, distal article about three times as long as proximal article, bearing two lateral aesthetascs; apical organ short. Mandibles with molar penicil semi-dichotomized bearing several plumose branches, left mandible (Figure 3A) with 2+1 penicils, right mandible (Figure 3B) with 1+1 penicils. Maxillula (Figure 3C) inner branch distal margin rounded bearing two long penicils; outer branch composed of 4+5 simple teeth. Maxilla (Figure 3D) bilobate, inner lobe covered with thick setae; outer lobe about three times as wide as inner lobe covered with thin setae. Maxilliped (Figure 3E) basis rectangular bearing sparse setae; palp proximal article with two distinct setae; endite subrectagular, medial seta strong, distal margin with two hook-like setae.

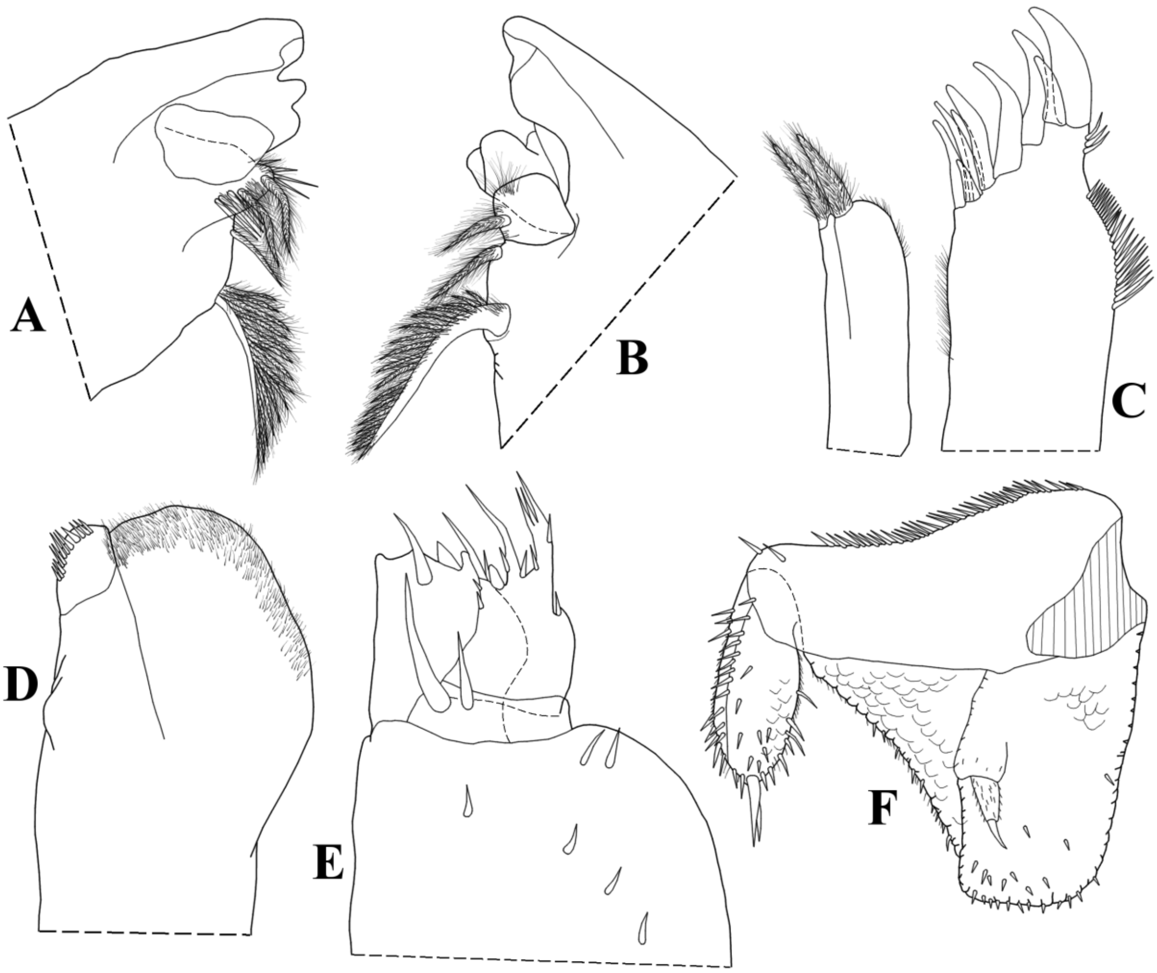

Figure 3. *Ctenorillo binomio* Carpio-Díaz, Bichuette & Campos-Filho, 2023, ♀: A, left mandible; B, right mandible; C, maxillula; D, maxilla; E, maxilliped; F, uropod.

Pereopod 1 carpus with antennal grooming brush transverse, and distal setae apically cleft; dactylus with ungual and dactylar seta simple. Uropod (Figure 3F) protopod trapezoidal, flattened, basal part enlarged, medial margin slightly concave; exopod short, inserted dorsally on distinct lobe near medial margin; endopod inner margin bearing fringe of setae. Pleopods 1-5 exopods with monospiracular lungs.

Male

Pereopod 1 and 7 (Figure 4A,B) with no particular modifications. Genital papilla as in Figure 4C. Pleopod 1 (Figure 4C) exopod subtriangular, slightly wider than long, outer margin slightly crenulate bearing five short setae; endopod three times as long as exopod, distal part tapering, and slightly bent outwards. Pleopod 2 (Figure 4D) exopod triangular, outer margin concave bearing eight short setae; endopod flagelliform longer than exopod. Pleopod 3 and 4 exopods as in Figure 4E and F, respectively. Pleopod 5 exopod (Figure 4G) rhomboid, outer margin slightly concave bearing many setae.

Etymology

The new species is named after the Vallenata music group "Binomio de Oro", dedicated to its singer and founder Rafael Orozco.

Remarks

In the arrangement of the dorsal tubercles of the pleon, *Ctenorillo binomio* is similar to *C. gabunensis* and *C. tuberosus*; however, it can be distinguished in the shape, number and arrangement of the dorsal tubercles of the cephalon and pereon (see Schmalfuss & Ferrara, 1983; Campos-Filho *et al*., 2017). Moreover, in comparison with the other Neotropical species, it differs in having the cephalon with 10 tubercles (vs. 12 in *C. dazai* and *C. mineri*; 14 in *C. ferrarai*), pereonite 1 with 21 tubercles (vs. 23 in *C. dazai*; 22 in *C. ferrarai*), pereonites 2-6 with 17 tubercles and pereonite 7 with 15 tubercles (vs. pereonites 2-7 with 15 tubercles in *C. dazai*; pereonites 2-7 with 12 tubercles in *C. ferrarai*), pleonites 3-5 composed of 4+4+2 tubercles (vs. 3+3+3 in *C. dazai*; 4+4+4 in *C. ferrarai* and *C. mineri*); antennula with seven aesthetascs (vs. six in *C. dazai*; eight in *C. ferrarai*), uropod exopod short inserted bellow the dorsal lobe (vs. tiny and inserted above the dorsal lobe in *C. dazai* and *C. ferrarai*), and male pleopod 1 exopod with the distal-medial part broad (vs. triangular in *C. dazai* and *C. ferrarai*) (see Vandel, 1952; Campos-Filho *et al*., 2014; Carpio-Díaz *et al*., 2018).

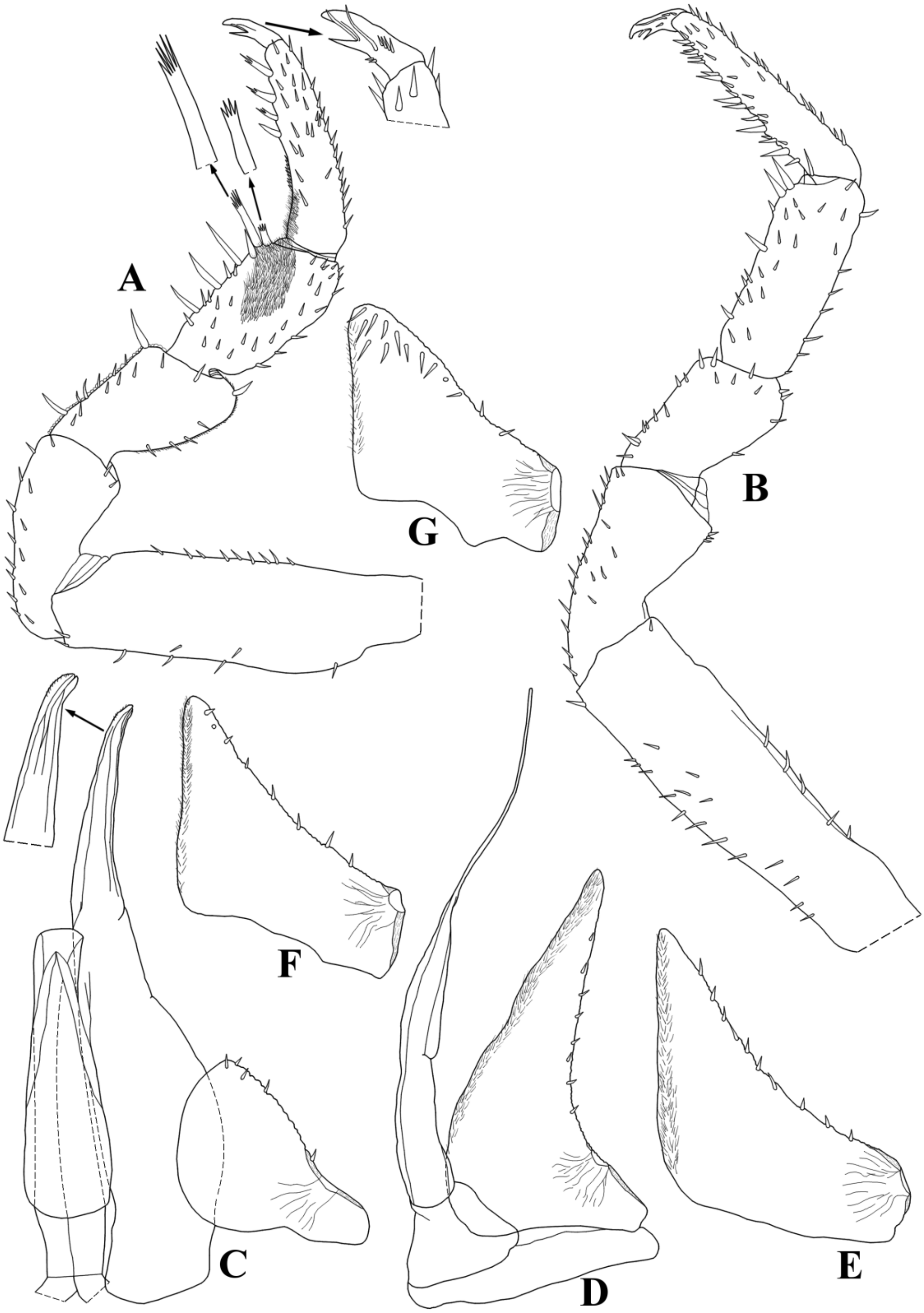

Figure 4. *Ctenorillo binomio* Carpio-Díaz, Bichuette & Campos-Filho, 2023, ♂: A, pereopod 1; B, pereopod 7; C, pleopod 1 and genital papilla; D, pleopod 2; E, pleopod 3 exopod; F, pleopod 4 exopod; G, pleopod 5 exopod.

Ctenorillo humboldti Carpio-Díaz, López-Orozco & Campos-Filho, 2023

Figures 1,5-7

Material examined

COLOMBIA: Holotype ♂ (IAvH-I-508), **Risaralda**, Pereira, Vereda Los Cerritos - Hacienda Alejandría, 4°51'27"N 75°52'49"W, 1000 m a.s.l., November 2004, leg. M. Bustamante. Paratype: 1 ♂ (parts in micropreparations) (IAvH-I-508), same data as holotype.

Description

Maximum length: 4 mm. Color brown; upper portion of tubercles, anterior corner of pereonite 1 epimera, pereonites 2-7 and pleonites 3-5 epimera depigmented. Dorsum covered with triangular tubercles, arranged as follows (Figure 5A,B): vertex of cephalon with eight tubercles in three rows, anterior and posterior rows with two tubercles each, middle row with four tubercles; pereonite 1 with four tubercles on anterior row, six tubercles on middle, and two tubercles on posterior row; pereonites 2-7 with six tubercles on anterior row, and two tubercles on posterior row; pleonites 3-5 without tubercles; telson with two tubercles. Dorsal surface with short triangular scale-setae (Figure 5C). Pereonites 1-7 epimera with one line of noduli laterales per side inserted on postero-lateral surface of second outer tubercle. Cephalon (Figure 5D-F) with frontal shield rectangular, slightly protruding above vertex, and slightly bent over vertex; eyes of 18 ommatidia. Pereonite 1 epimera grooved on lateral margins for about two thirds of length, inner lobe of schisma rounded, not extending beyond posterior margin of outer lobe; pereonites 2-7 epimera rectangular, pereonite 2 with ventral lobe subtriangular, distal margin rounded, not extending beyond posterior margin of epimera (Figure 5A,F-H). Pleonites 3-5 epimera rectangular (Figure 5I,J). Telson (Figure 5I) hourglass-shaped, proximal part broader than distal part, straight distal margin. Antennula (Figure 5K) of three articles, proximal and distal articles subequal in length, distal article bearing seven aesthetascs. Antenna (Figure 5L) short and stout, slightly surpassing posterior margin of cephalon when extended backwards; flagellum of two articles, distal article about twice as long as proximal article, bearing two lateral aesthetascs; apical organ short. Buccal pieces (Figure 6A-E) as in *Ctenorillo binomio*.

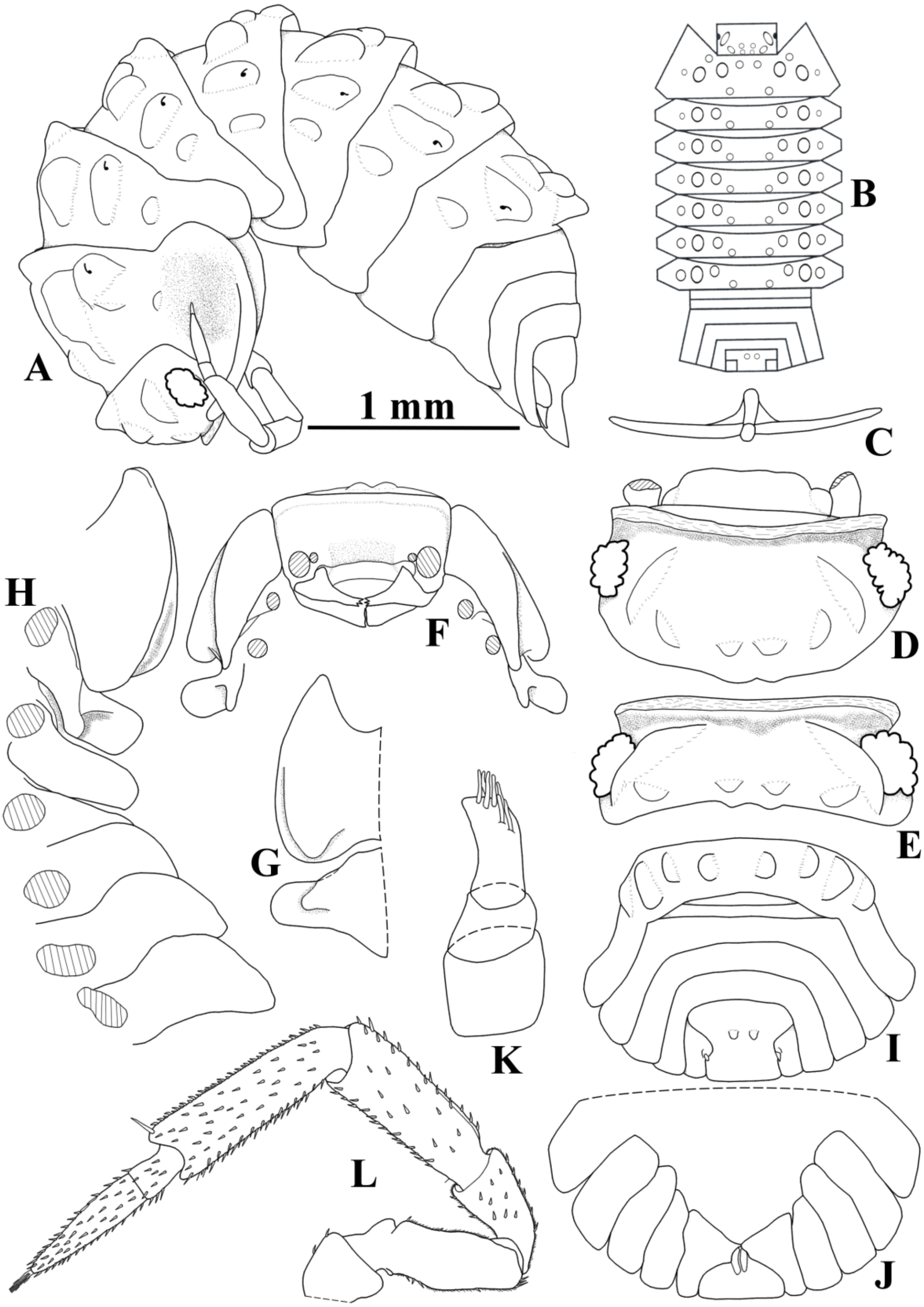

Figure 5. *Ctenorillo humboldti* Carpio-Díaz, López-Orozco & Campos-Filho, 2023, ♂: A, habitus, lateral view; B, dorsal tubercles scheme; C, dorsal scale-seta; D, cephalon, dorsal view; E, cephalon, posterior view; F, cephalon and pereonites 1 and 2, frontal view; G, pereonites 1 and 2 epimera, ventral view; H, pereonites 1-7 epimera, ventral view; I, pereonite 7, pleon, telson, and uropods, dorsal view; J, pereonite 7, pleonites 3-5, telson and uropods, ventral view; K, antennula; L, antenna.

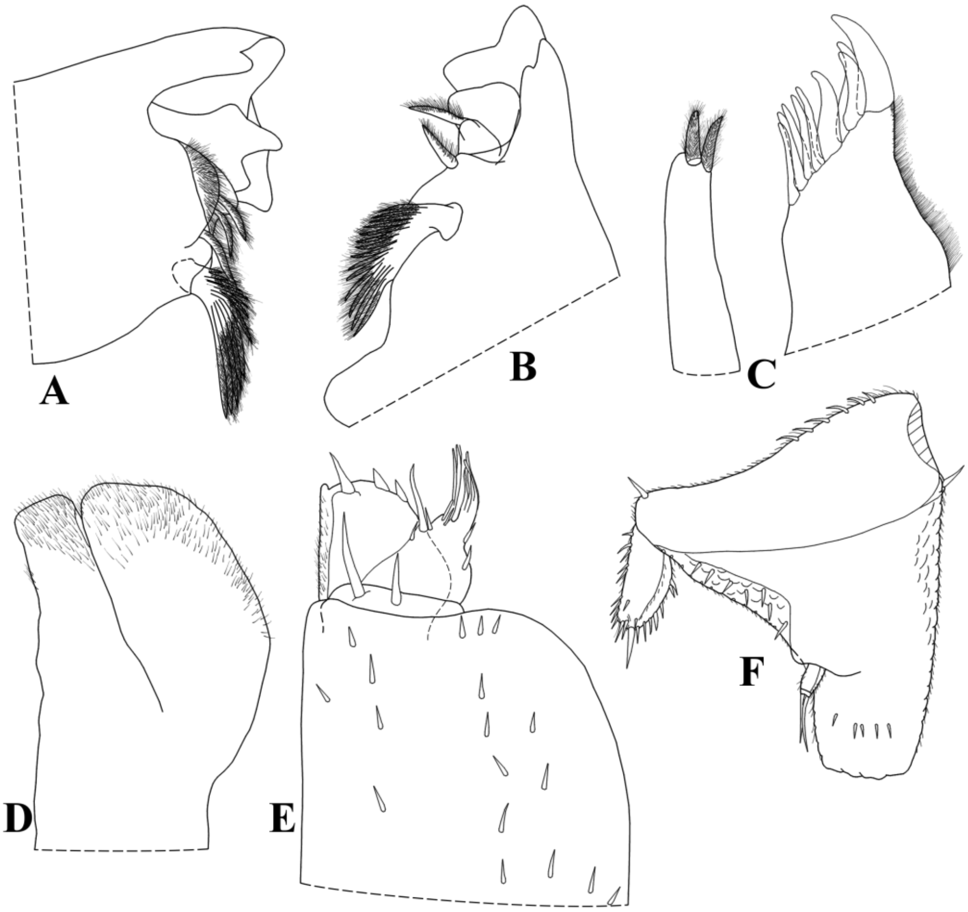

Figure 6. *Ctenorillo humboldti* Carpio-Díaz, López-Orozco & Campos-Filho, 2023, ♂: A, left mandible; B, right mandible; C, maxillula; D, maxilla; E, maxilliped; F, uropod.

Pereopod 1 carpus with antennal grooming brush transverse, and distal setae apically cleft; dactylus with ungual and dactylar seta simple. Uropod (Figure 6F) protopod trapezoidal, flattened, basal part enlarged, medial margin concave; exopod short, inserted dorsally below distinct lobe near median margin; endopod inner and outer margins bearing fringe of setae. Pleopods 1-5 exopods with monospiracular lungs.

Male

Pereopod 1 and 7 (Figure 7A,B) with no particular modifications. Genital papilla as in Figure 7C. Pleopod 1 (Figure 7D) exopod triangular, as long as wide, outer margin slightly concave, inner and outer margins bearing many short setae; endopod about three times as long as exopod, distal part tapering. Pleopod 2 (Figure 7E) exopod triangular, outer margin concave bearing many short setae; endopod flagelliform longer than exopod. Pleopod 3 and 4 exopods as in Figure 7F and G, respectively. Pleopod 5 exopod (Figure 7H) rhomboid, outer margin slightly sinuous bearing many short setae.

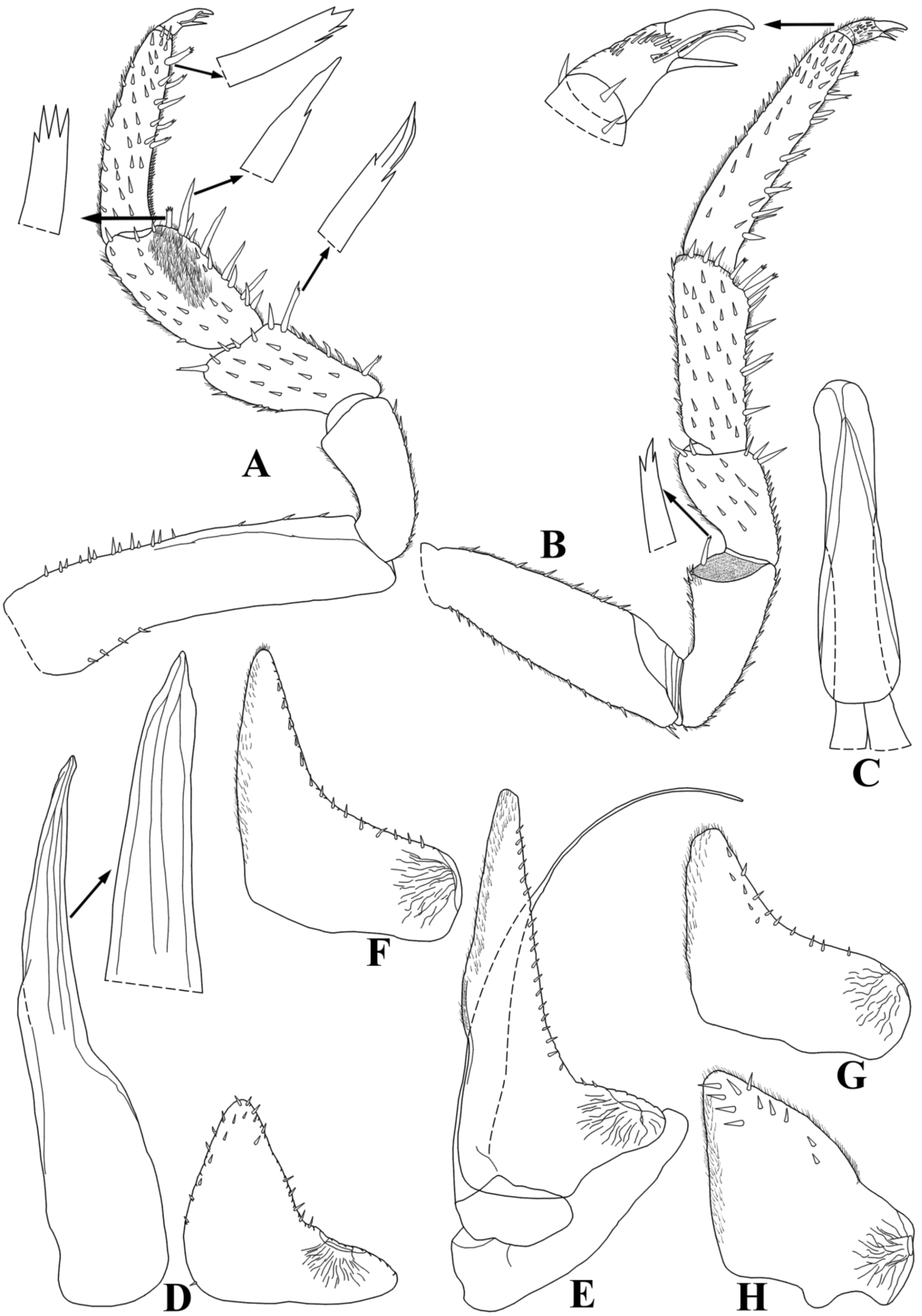

Figure 7. *Ctenorillo humboldti* Carpio-Díaz, López-Orozco & Campos-Filho, 2023, ♂: A, pereopod 1; B, pereopod 7; C, genital papilla; D, pleopod 1; E, pleopod 2; F, pleopod 3 exopod; G, pleopod 4 exopod; H, pleopod 5 exopod.

Etymology

The new species is named after the German naturalist and explorer Friedrich Wilhelm Heinrich Alexander von Humboldt, also known as Baron von Humboldt, famous for his biogeographic expeditions to South America.

Remarks

In the absence of the dorsal tubercles of the pleon, *Ctenorillo humboldti* is similar to *C. strinatii*, from which it can de distinguished by the shape, number and arrangement of the dorsal tubercles of the cephalon and pereon, and shape of the male pleopod 1 exopod (see Schmalfuss & Ferrara, 1983). Moreover, it differs from the Neotropical species in the cephalon with eight tubercles, pereonite 1 with 12 tubercles, pereonites 2-7 with eight tubercles, pleonites 3-5 smooth, antennula with seven aesthestascs, uropod exopod short inserted below the dorsal median lobe, and the male pleopod 1 exopod with outer margin concave (see previous remarks). *Ctenorillo humboldti* also differs from *C. binomio*, in the number and arrangement of the dorsal tubercles of the cephalon and pereon, pleonites 3-5 smooth and shape of the male pleopod 1 exopod.

Ctenorillo mincaensis López-Orozco, Carpio-Díaz & Campos-Filho, 2023

Figures 1,8-10

Material examined

COLOMBIA: Holotype ♂ (CBUDC-CRU 411), **Magdalena**, Santa Marta, Minca, Betoma 11°6′42.26″N 74°3′13.98″W, 20 February 2018, leg. F. Cala. Paratypes*:* 1 ♂, 1 ♀ (parts in micropreparations) (CBUDC-CRU 347), same data as holotype; 13 ♂♂, 27 ♀♀ (CBUDCCRU 348), same locality and collector as holotype, 21 February 2018.

Description

Maximum length: male 4 mm, female 6 mm. Color dark brown with typical pale muscular insertions; pereonites 1-7 median portion and epimera more pigmented; upper portion of dorsal tubercles depigmented. Dorsum covered with short triangular and elongated tubercles, arranged as follows (Figure 8A,B): vertex of cephalon with 12 tubercles in three rows, anterior row with four tubercles, middle row with two tubercles, posterior row with six tubercles; pereonite 1 with six tubercles on anterior row, 12 tubercles on middle, and three tubercles on posterior row; pereonites 2-6 with two tubercles on anterior row, ten tubercles on middle row, and three tubercles on posterior row; pereonite 7 with two tubercles on anterior row, six tubercles on middle, and three tubercles on posterior row; pleonite 3 with four small tubercles, pleonites 4 and 5 and telson with two tubercles each, more prominent on telson. Dorsal surface with short triangular scalesetae (Figure 8C). Pereonites 1-7 with one line of noduli laterales per side. Cephalon (Figure 8D-F) with frontal shield rectangular, not protruding above vertex, and slightly bent over vertex; eyes of 16 ommatidia. Pereonite 1 epimera grooved on lateral margin, inner lobe of schisma rounded, not extending beyond posterior margin of outer lobe; pereonites 2 and 3 epimera subrectangular, 4-7 rectangular; pereonite 2 with ventral lobe subtriangular, distal margin rounded, not extending beyond posterior margin of epimera (Figure 8A,F,G). Pleonites 3-5 epimera rectangular (Figure 8H, I). Telson (Figure 8H) hourglass-shaped, proximal part broader than distal part, straight distal margin. Antennula (Figure 8J) of three articles, proximal and distal articles subequal in length, distal article bearing six to seven aesthetascs inserted apically. Antenna (Figure 8K) short and stout, not surpassing posterior margin of cephalon when extended backwards; flagellum of two articles, distal article three times as long as proximal article, bearing two lateral aesthetascs; apical organ short. Buccal pieces (Figure 9A-E) as in *Ctenorillo binomio*. Pereopod 1 carpus with antennal grooming brush transverse, and distal setae apically cleft; dactylus with ungual and dactylar seta simple. Uropod (Figure 9F) protopod trapezoidal, flattened, basal part enlarged, medial margin concave; exopod tiny, inserted dorsally on distinct lobe near median margin; endopod inner margin bearing fringe of setae. Pleopods 1-5 exopods with monospiracular lungs.

Male

Pereopod 1 and 7 (Figure 10A,B) with no particular modifications. Genital papilla as in Figure 10C. Pleopod 1 (Figure 10C) exopod triangular, wider than long, outer margin slightly concave, outer and inner margins bearing many short setae; endopod more than twice as long as exopod, distal part tapering bearing short median setae. Pleopod 2 (Figure 10D) exopod triangular, outer margin concave bearing many short setae; endopod distinctly longer than exopod. Pleopod 3 and 4 exopods as in Figure 10E,F, respectively. Pleopod 5 exopod (Figure 10G) rhomboid, outer margin almost straight bearing many short setae.

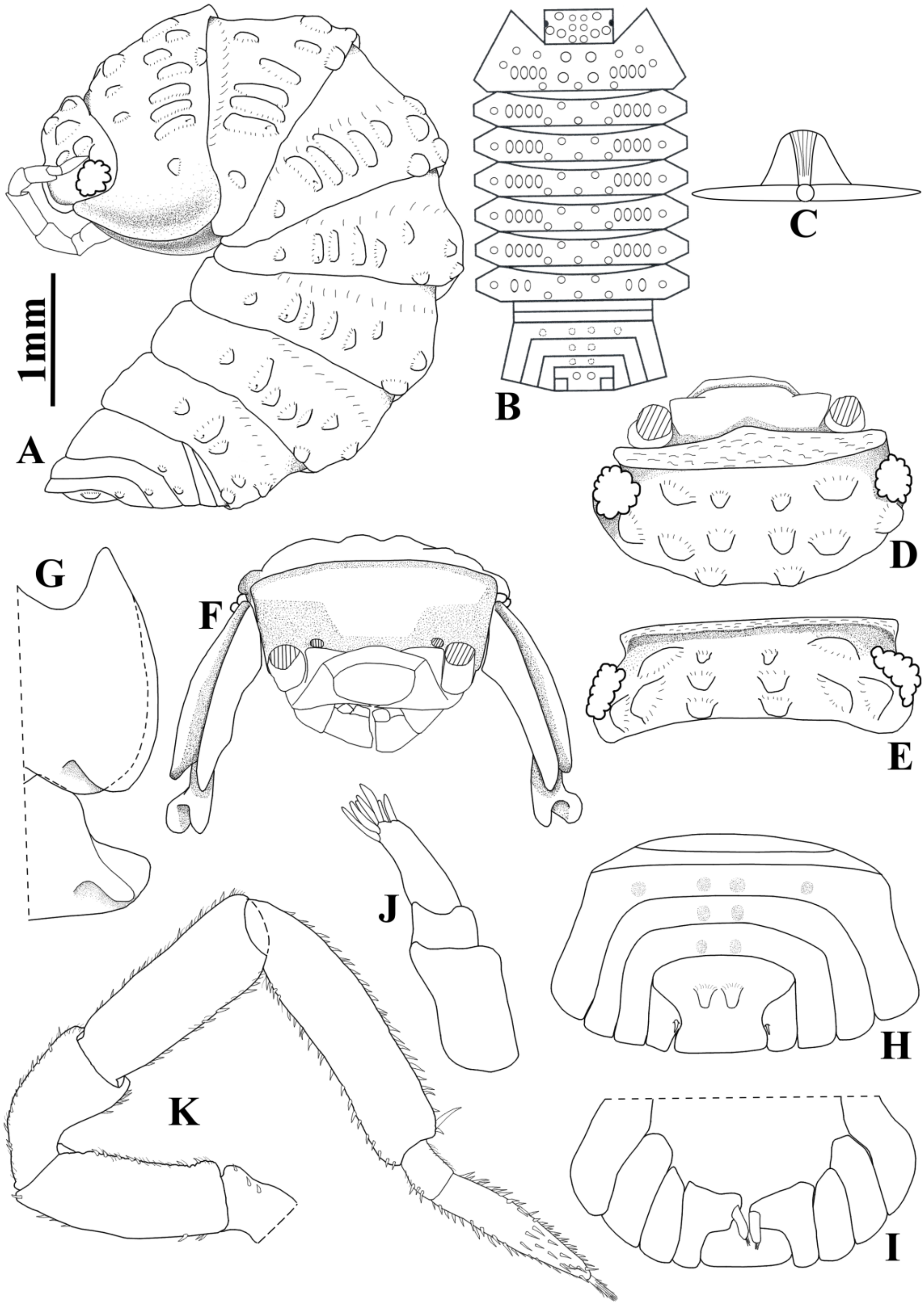

Figure 8. *Ctenorillo mincaensis* López-Orozco, Carpio-Díaz & Campos-Filho, 2023, ♀: A, habitus, lateral view; B, dorsal tubercles scheme; C, dorsal scale-seta; D, cephalon, dorsal view; E, cephalon, posterior view; F, cephalon and pereonites 1 and 2, frontal view; G, pereonites 1 and 2 epimera, ventral view; H, pleon, telson, and uropods, dorsal view; I, pleonites 3-5, telson, and uropods, ventral view; J, antennula; K, antenna.

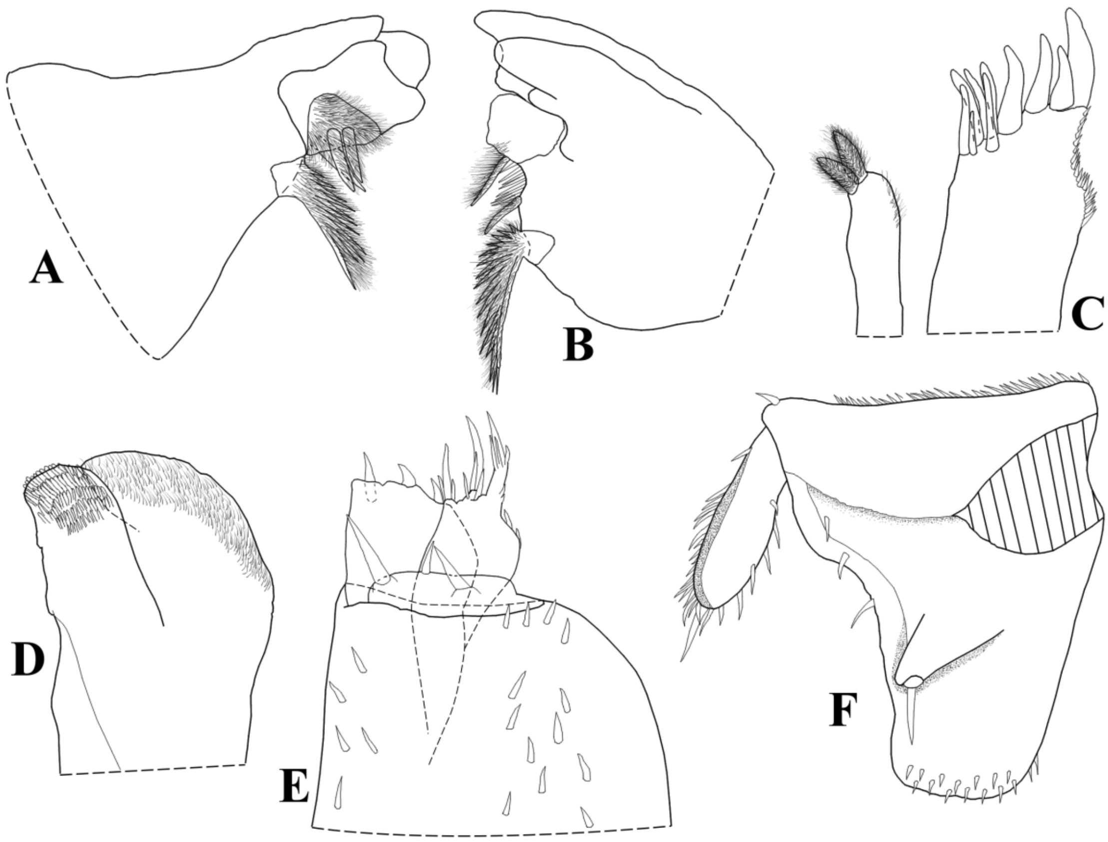

Figure 9. *Ctenorillo mincaensis* López-Orozco, Carpio-Díaz & Campos-Filho, 2023, ♀: A, left mandible; B, right mandible; C, maxillula; D, maxilla; E, maxilliped; F, uropod.

Etymology

The new species is named after the locality where the specimens were collected: Minca.

Remarks

In the arrangement of the dorsal tubercles of the pleon, i.e., pleonite 3 with four tubercles, pleonites 4 and 5 and telson with two tubercles, *Ctenorillo mincaensis* resembles *C. guinensis*, from which it can easily be distinguished by the shape and arrangement of the dorsal tubercles of the cephalon and pereon, and shape of the male pleopod 1 (see Schmalfuss & Ferrara, 1983). Moreover, it differs from the Neotropical species in the cephalon with 12 tubercles, pereonite 1 with 21 tubercles, pereonites 2-6 with 15 tubercles and pereonite 7 with 11 tubercles, pleonites 3-5 with 4+2+2 tubercles, male pleopod 1 exopod with outer margin concave in the middle (see *C. binomio* remarks). *Ctenorillo mincaensis* also differs from the previous new species in the shape, number and arrangement of the dorsal tubercles of the cephalon, pereon and pleon, and shape of the male pleopod 1 exopod.

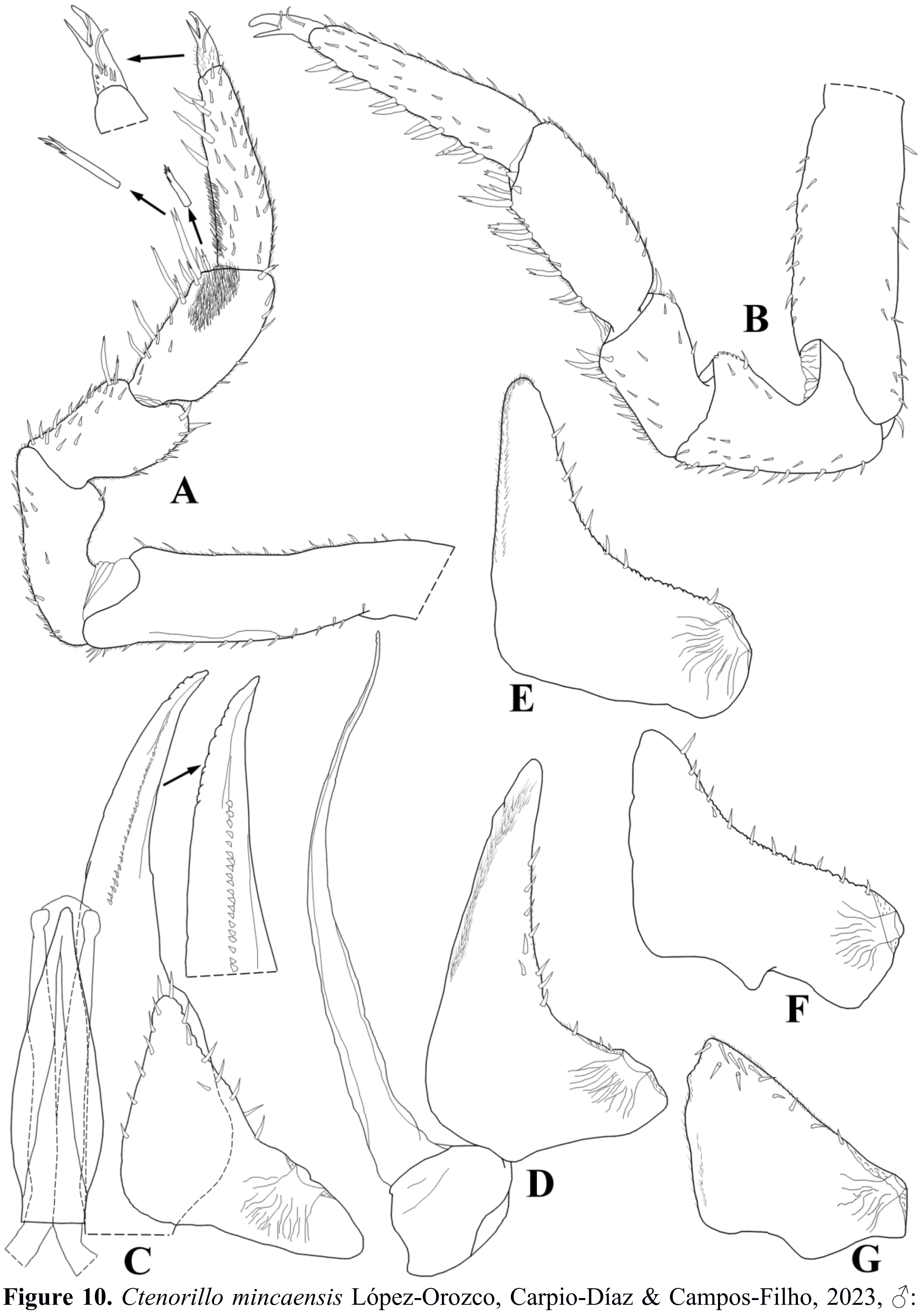

Figure 10. *Ctenorillo mincaensis* López-Orozco, Carpio-Díaz & Campos-Filho, 2023, ♂: A, pereopod 1; B, pereopod 7; C, pleopod 1 and genital papilla; D, pleopod 2; E, pleopod 3 exopod; F, pleopod 4 exopod; G, pleopod 5 exopod.

Ctenorillo orientalis Carpio-Díaz, Taiti & López-Orozco, 2023

Figures 1,11-13

Material examined

COLOMBIA: Holotype ♀ (CUDC-CRU 57), **Cesar**, Manaure, San José de Oriente, Serranía de Perijá, 10°17'40.4"N 72°55'52.1"W, 13 August 2015, leg. C.M. López-Orozco and Y. Herrera-Medina. Paratypes*:* 1 ♀ (parts in micropreparations) (CUDC-CRU 355), 5 ♀♀ (CUDC-CRU 356), same data as holotype.

Description

Maximum length: 4.5 mm. Color brown; antennae and pereopods strongly pigmented; pereonites 1-7 and pleon with median and paramedian portions depigmented; pereonite 1 epimera anterior and posterior corners depigmented; pereonites 2-7 epimera lateral margins with large depigmented spot. Dorsum covered with short triangular tubercles, arranged as follows (Figure 11A,B): vertex of cephalon with 16 tubercles in three rows, anterior row with six tubercles, middle row with four tubercles, posterior row with six tubercles; pereonite 1 with four tubercles on anterior row, 14 tubercles on middle row, and seven tubercles on posterior row; pereonites 2-7 with eight tubercles on anterior row, nine tubercles on posterior row; pleonites 3 and 4 with four tubercles, pleonite 5 and telson with two tubercles each. Dorsal surface with semi-circular scale-setae (Figure 11C). Pereonites 1-7 epimera with one line of noduli laterales per side inserted on antero-lateral surface of second outer tubercle. Cephalon (Figure 11D-F) with frontal shield rectangular, slightly protruding above vertex, and slightly bent over vertex; eyes of 17-19 ommatidia. Pereonite 1 epimera grooved on lateral margins, for about one quarter of length, inner lobe of schisma rounded, not extending beyond posterior margin of outer lobe; pereonites 2 epimera subtriangular, 3-7 rectangular; pereonite 2 with ventral lobe subrectangular, distal margin rounded, not extending beyond posterior margin of epimera (Figure 11A,F,G). Pleonites 3-5 epimera rectangular (Figure 11H,I). Telson (Figure 11H) hourglass-shaped, proximal part broader than distal part, slightly convex distal margin. Antennula (Figure 11J) of three articles, proximal and distal articles subequal in length, distal article bearing five subapical aesthetascs. Antenna (Figure 11K) short and stout, slightly surpassing posterior margin of cephalon when extended backwards; flagellum of two articles, distal article three times as long as proximal article, and bearing two lateral aesthetascs; apical organ short. Buccal pieces (Figure 12A-E) as in *Ctenorillo binomio*.

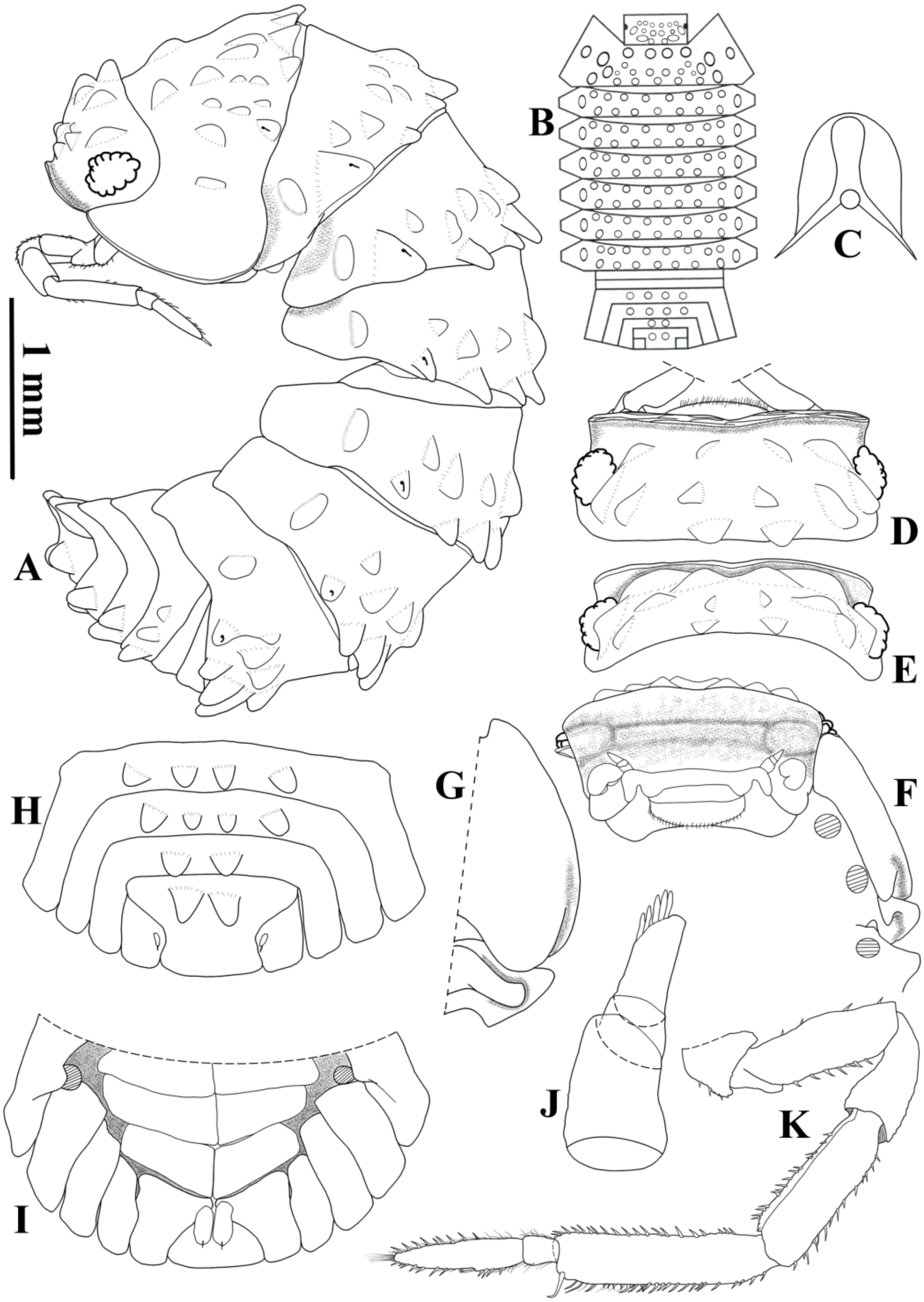

Figure 11. *Ctenorillo orientalis* Carpio-Díaz, Taiti & López-Orozco, 2023, ♀: A, habitus, lateral view; B, dorsal tubercles scheme; C, dorsal scale-seta; D, cephalon, dorsal view; E, cephalon, posterior view; F, cephalon and pereonites 1-3, frontal view; G, pereonites 1 and 2 epimera, ventral view; H, pleonites 3-5, telson, and uropods, dorsal view; I, pereonite 7, pleonites 3-5, telson, and uropods, ventral view; J, antennula; K, antenna.

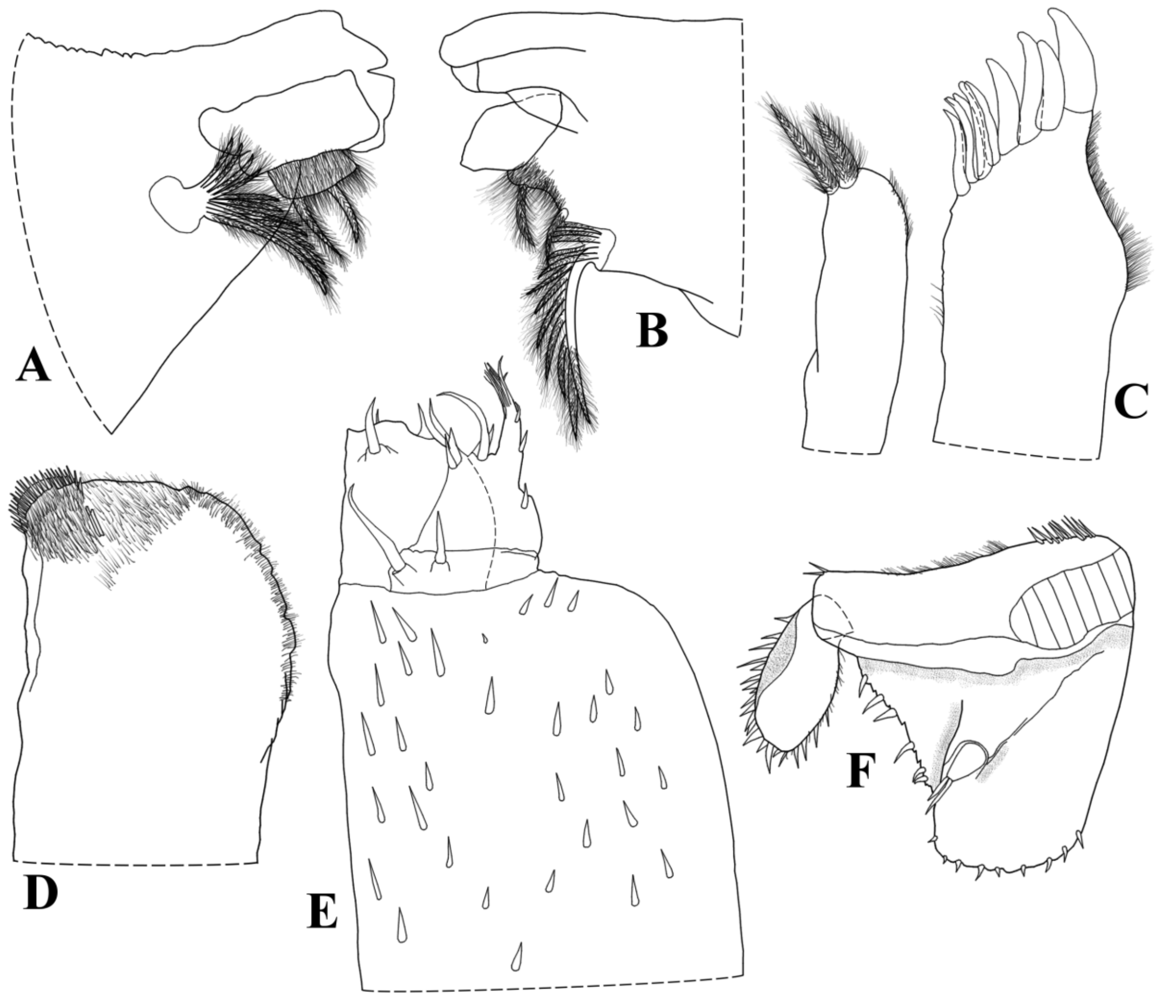

Figure 12. *Ctenorillo orientalis* Carpio-Díaz, Taiti & López-Orozco, 2023, ♀: A, left mandible; B, right mandible; C, maxillula; D, maxilla; E, maxilliped; F, uropod.

Pereopods 1-7 (Figure 13A,B) with no particular modifications; pereopod 1 carpus with antennal grooming brush transverse, distal setae apically cleft; dactylus with ungual and dactylar seta simple. Uropod (Figure 12F) protopod trapezoidal, flattened, basal part enlarged, medial margin slightly concave; exopod short, inserted dorsally below distinct lobe near medial margin; endopod inner and outer margins bearing fringe of setae. Pleopods 1-5 exopods with monospiracular lungs. Pleopod 1 exopod (Figure 13C) twice as wide as long, distal margin almost straight. Pleopod 2 exopod (Figure 13D) subtriangular, outer margin concave bearing many short setae. Pleopod 3 and 4 exopods (Figure 10E,F) subrectangular, distal margin slightly concave and bearing many short setae. Pleopod 5 exopod (Figure 13G) rhomboid, outer margin almost straight bearing many short setae.

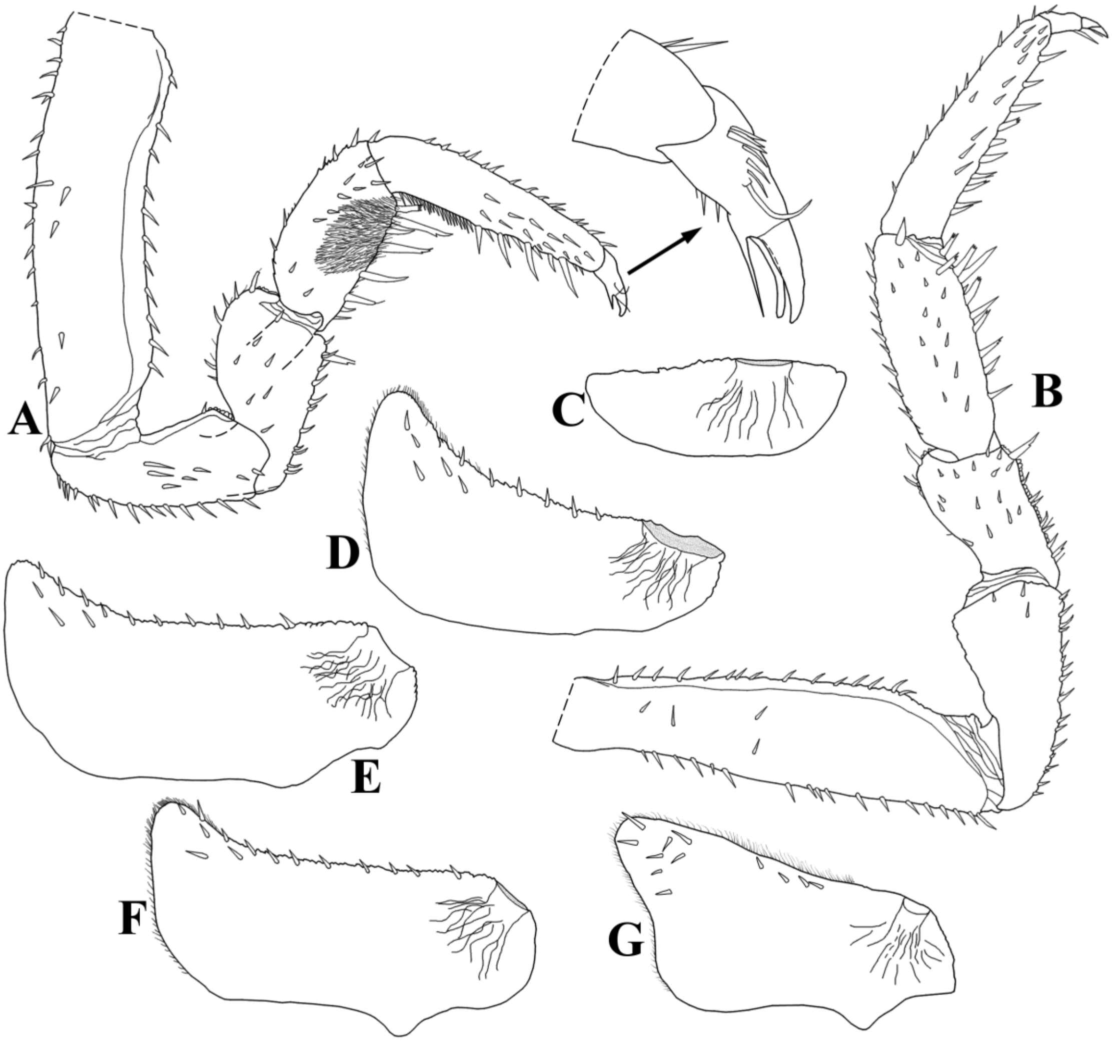

Figure 13. *Ctenorillo orientalis* Carpio-Díaz, Taiti & López-Orozco, 2023, ♀: A, pereopod 1; B, pereopod 7; C, pleopod 1 exopod; D, pleopod 2 exopod; E, pleopod 3 exopod; F, pleopod 4 exopod; G, pleopod 5 exopod.

Etymology

The new species name refers to the geographical location of the locality where the specimens were collected: Cordillera Oriental de Colombia.

Remarks

Despite the absence of male specimens, *Ctenorillo orientalis* exhibits a unique arrangement of the dorsal tubercles of the cephalon and pereon. In the arrangement of the dorsal tubercles of the pleon, the new species is similar to *C. gabunensis*, *C. tuberosus* and *C. binomio*. It can de distinguished by the shape, number and arrangement of the dorsal tubercles of cephalon and pereon (see Schmalfuss & Ferrara, 1983; Campos-Filho *et al*., 2017).

Ctenorillo papagayoensis Carpio-Díaz, Borja-Arrieta & Campos-Filho, 2023

Figures 1,14-16

Material examined

COLOMBIA: Holotype ♂ (parts in micropreparations) (ICN-CR-is 72), **Santander**, Bolívar, Los Papagayos cave, 5°58’47.65”N 73°46’24.44”W, 22 June 2008, leg. D. Casallas and M. Hoyos. Paratypes*:* 1 ♂, 1 ♀ (parts in micropreparations) (ICN-CR-is 72), same data as holotype.

Description

Maximum length: male 5 mm, female 5.5 mm. Color brown with typical pale muscular insertions; pereonites 1-7 median portion and epimera, and pleon strongly pigmented. Dorsum covered with short rounded tubercles, arranged as follows (Figure 14A,B): vertex of cephalon with 12 tubercles in three rows, anterior row with four tubercles, middle row with two tubercles, posterior row with six tubercles; pereonite 1 with four tubercles on anterior row, six tubercles on middle row, and two tubercles on posterior row; pereonites 2-7 with two tubercles on anterior row, six tubercles on posterior row; pleonites 3-5 plus telson smooth. Dorsal surface with short triangular scale-setae (Figure 14C). Pereonites 1-7 epimera with one line of noduli laterales per side inserted on postero-lateral surface of second outer tubercle. Cephalon (Figure 14D-F) with frontal shield rectangular, not protruding above vertex, and slightly bent over vertex; eyes of 16 ommatidia. Pereonite 1 epimera grooved on lateral margins for about two thirds of length, inner lobe of schisma rounded, not extending beyond posterior margin of outer lobe; pereonites 2-7 rectangular; pereonite 2 with ventral lobe subtriangular, distal margin rounded, not extending beyond posterior margin of epimera (Figure 14A,F,G). Pleonites 3-5 epimera rectangular (Figure 14H,I). Telson (Figure 14H) hourglass-shaped, proximal part broader than distal part, straight distal margin. Antennula (Figure 14J) of three articles, proximal and distal articles subequal in length, distal article bearing five apical aesthetascs. Buccal pieces (Figure 15A-E) as in *Ctenorillo binomio*. Pereopod 1 carpus with antennal grooming brush transverse, distal setae apically cleft; dactylus with ungual and dactylar seta simple. Uropod (Figure 15F) protopod trapezoidal, flattened, basal part enlarged, medial margin concave; exopod short, inserted dorsally below distinct lobe near median margin.

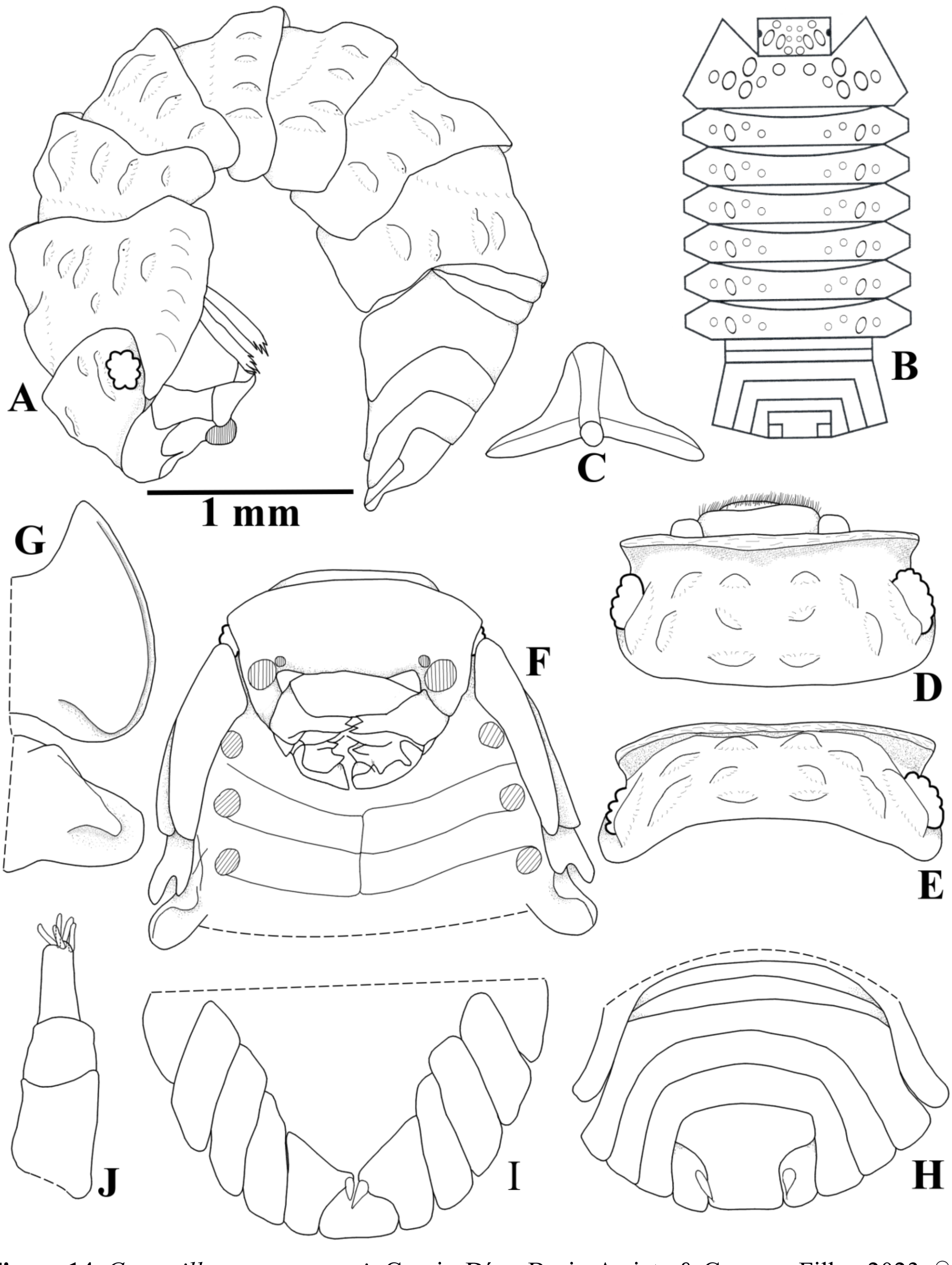

Figure 14. *Ctenorillo papagayoensis* Carpio-Díaz, Borja-Arrieta & Campos-Filho, 2023, ♀: A, habitus, lateral view; B, dorsal tubercles scheme; C, dorsal scale-seta; D, cephalon, dorsal view; E, cephalon, posterior view; F, cephalon and pereonites 1-3, frontal view; G, pereonites 1 and 2 epimera, ventral view; H, pereonite 7, pleon, telson, and uropods, dorsal view; I, pereonite 7, pleonites 3-5, telson, and uropods, ventral view; J, antennula; K, antenna.

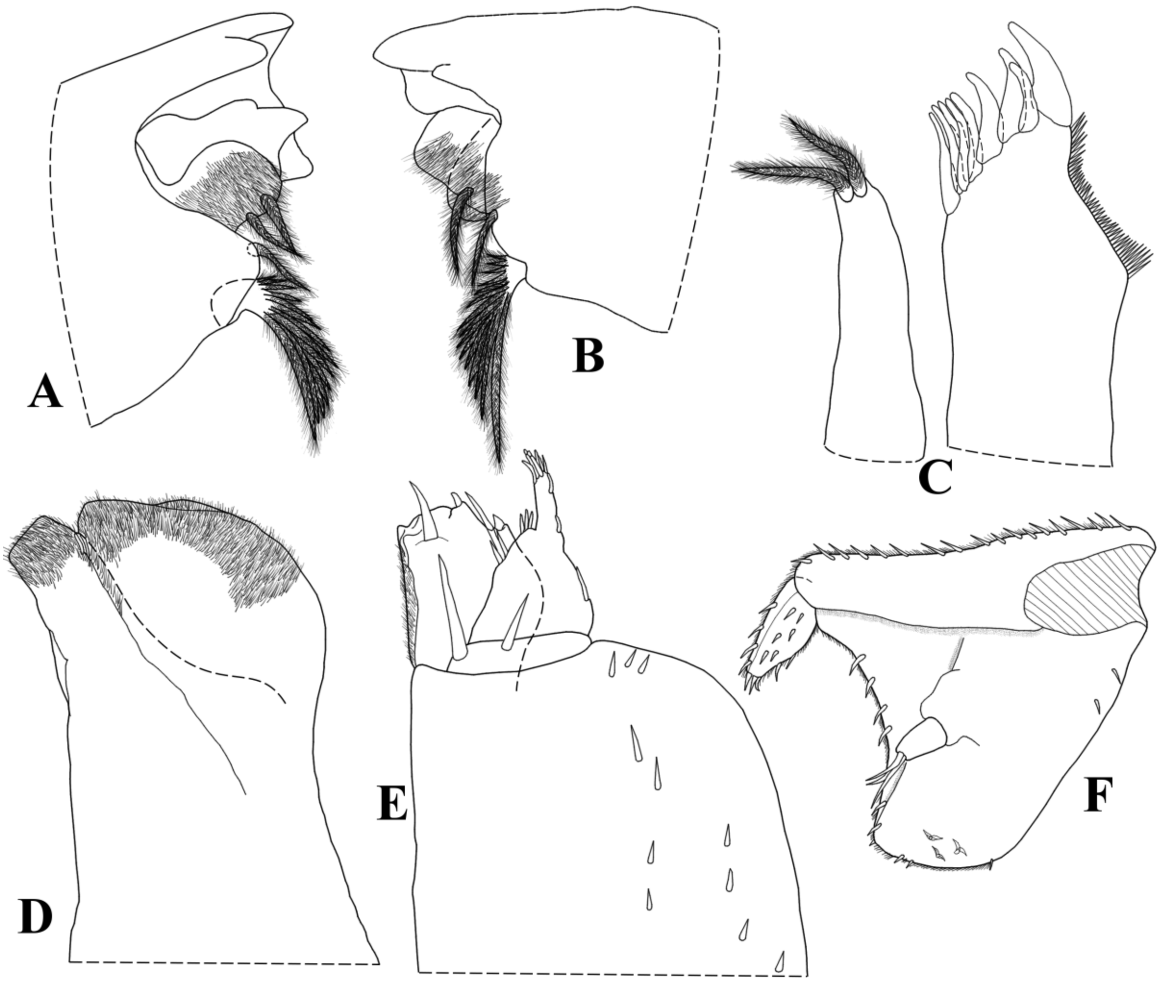

Figure 15. *Ctenorillo papagayoensis* Carpio-Díaz, Borja-Arrieta & Campos-Filho, 2023, ♀: A, left mandible; B, right mandible; C, maxillula; D, maxilla; E, maxilliped; F, uropod.

Pleopods 1-5 exopods with monospiracular lungs.

Male

Pereopod 1 (Figure 16A) with no particular modifications. Pereopod 7 (Figure 16B) ischium with rostral surface slightly depressed distally. Genital papilla as in Figure 16C. Pleopod 1 (Figure 16D) exopod triangular, longer than wide, outer margin slightly concave, outer and inner margins bearing many short setae; endopod twice as long as exopod, distal part tapering bearing short setae on medial margin. Pleopod 2 (Figure 16E) exopod triangular, outer margin concave bearing many short setae. Pleopod 3 and 4 exopods as in Figure 16F,G, respectively. Pleopod 5 exopod (Figure 16H) triangular, outer margin almost straight bearing many short setae.

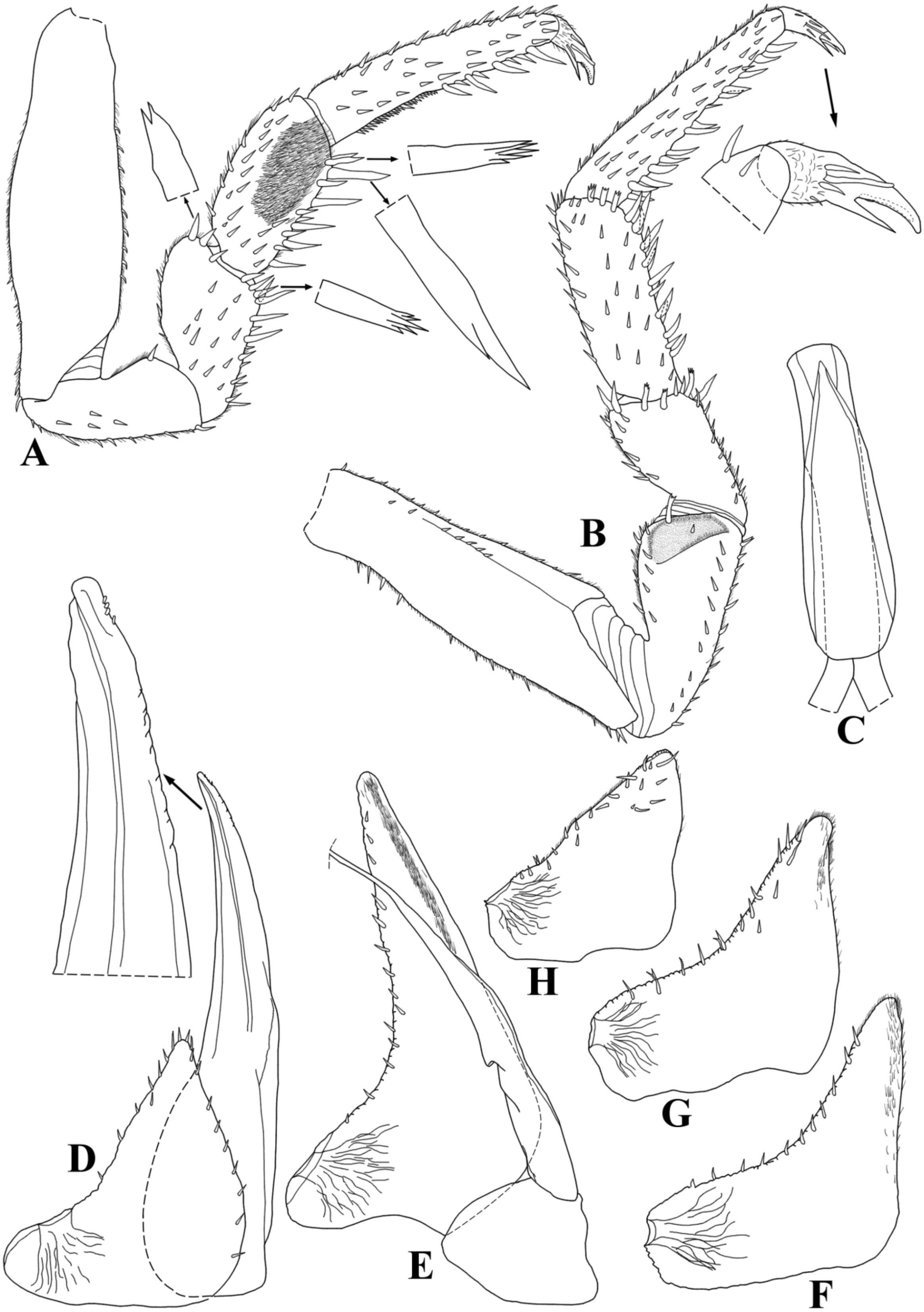

Figure 16. *Ctenorillo papagayoensis* Carpio-Díaz, Borja-Arrieta & Campos-Filho, 2023, ♂: A, pereopod 1; B, pereopod 7; C, genital papilla; D, pleopod 1; E, pleopod 2; F, pleopod 3 exopod; G, pleopod 4 exopod; H, pleopod 5 exopod.

Etymology

The new species is named after of the locality where the specimens were collected: Los Papagayos cave.

Remarks

Ctenorillo papagayoensis differs from all other species of the genus in the absence of tubercles on pleon and telson, and in the number and arrangement of the dorsal tubercles of the cephalon and pereon.

Ctenorillo tayrona López-Orozco, Borja-Arrieta & Campos-Filho, 2023

Figures 1,17,18

Material examined

COLOMBIA: Holotype ♀ (parts in micropreparations) (CBUDC-CRU 342), **Magdalena**, Santa Marta, Sierra Nevada de Santa Marta, Sector Bahía Concha, 11°17'32.28"N 74°9'12.8"W, 16 August 2018, leg. C.M. López-Orozco and R. Borja-Arrieta.

Description

Length: 2.5 mm. Color brown with typical pale muscular insertions; entire body strongly pigmented. Dorsum covered with short rounded tubercles, arranged as follows (Figure 17A,B): vertex of cephalon with ten tubercles in three rows, anterior row with four tubercles, middle row with two tubercles, posterior row with four tubercles; pereonite 1 with four tubercles on anterior row, eight tubercles on middle, and seven tubercles on posterior row; pereonites 2-7 with six tubercles on anterior row, and nine tubercles on posterior row; pleon smooth, telson with two median tubercles. Dorsal surface with short triangular scale-setae (Figure 17C). Pereonites 1-7 epimera with one line of noduli laterales per side inserted on postero-lateral surface of second outer tubercle. Cephalon (Figure 17D-F) with frontal shield rectangular, not protruding above vertex; eyes of eight ommatidia. Pereonite 1 epimera grooved on lateral margins, inner lobe of schisma rounded, slightly extending beyond posterior margin of outer lobe; pereonites 2 and 3 epimera subtriangular, outer margin rounded, epimera 4-7 rectangular; pereonite 2 with ventral lobe subtriangular, distal margin rounded, slightly extending beyond posterior margin of outer lobe (Figure 17A,F,G). Pleonites 3-5 epimera rectangular (Figure 17H,I).

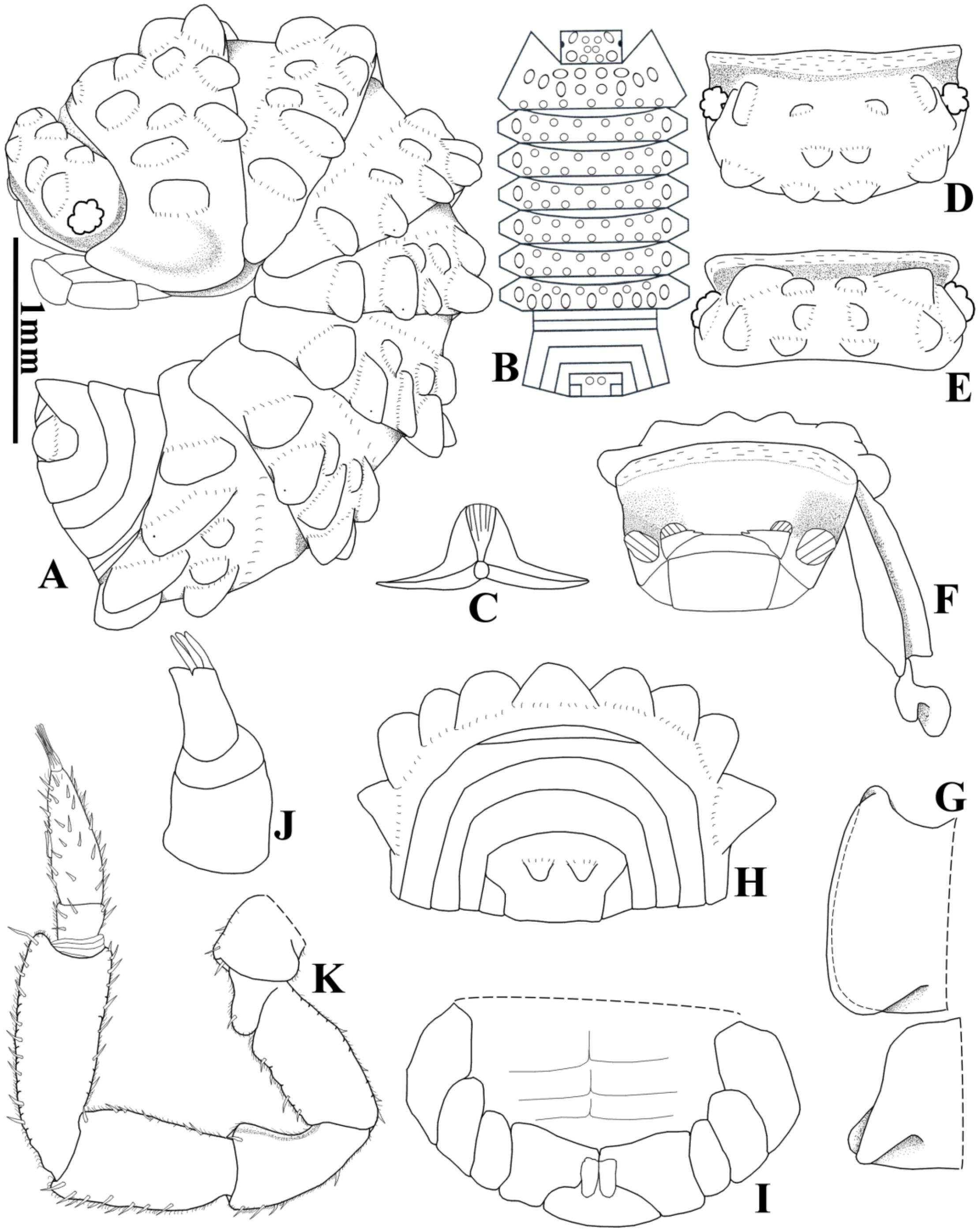

Figure 17. *Ctenorillo tayrona* López-Orozco, Borja-Arrieta & Campos-Filho, 2023, ♀: A, habitus, lateral view; B, dorsal tubercles scheme; C, dorsal scale-seta; D, cephalon, dorsal view; E, cephalon, posterior view; F, cephalon and pereonites 1 and 2, frontal view; G, pereonites 1 and 2 epimera, ventral view; H, pereonite 7, pleon, telson, and uropods, dorsal view; I, pleonites 3-5, telson, and uropods, ventral view; J, antennula; K, antenna.

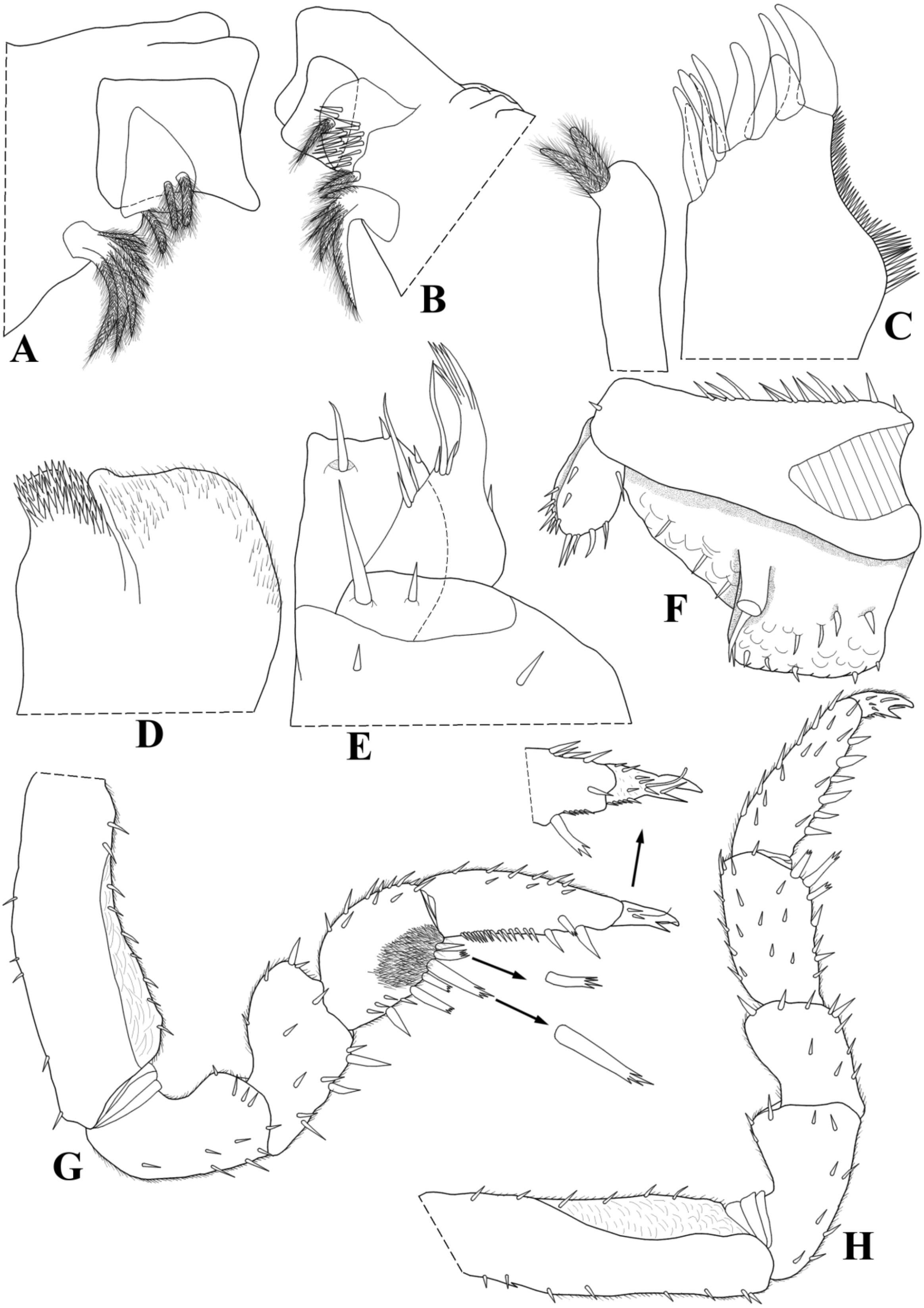

Figure 18. *Ctenorillo tayrona* López-Orozco, Borja-Arrieta & Campos-Filho, 2023, ♀: A, left mandible; B, right mandible; C, maxillula; D, maxilla; E, maxilliped; F, uropod; G, pereopod 1; H, pereopod 7.

Telson (Figure 17H) hourglass-shaped, proximal part broader than distal part, straight distal margin. Antennula (Figure 17J) of three articles, proximal and distal articles subequal in length, distal article bearing three apical aesthetascs. Buccal pieces (Figure 18AE) as in *Ctenorillo binomio*. Uropod (Figures 17I, 18F) protopod trapezoidal, flattened, basal part enlarged, medial margin straight; exopod tiny, inserted dorsally below distinct lobe near median margin. Pereopods 1 and 7 (Figure 18G,H) with no particular modifications; pereopod 1 carpus with antennal grooming brush transverse, and distal setae apically cleft; dactylus with ungual and dactylar seta simple. Pleopods 1-5 exopods with monospiracular lungs.

Etymology

The new species is named after the Tayrona people, an indigenous group that inhabited areas of the Sierra Nevada de Santa Marta.

Remarks

In the absence of the dorsal tubercles of the pleon, *Ctenorillo tayrona* is similar to *C. strinatii* and *C. humboldti*. It can de distinguished by the shape, number and arrangement of the dorsal tubercles of the cephalon and pereon (see Schmalfuss & Ferrara, 1983). In the comparison with the Neotropical species, it differs in having the cephalon with 10 tubercles, pereonite 1 with 19 tubercles, pereonites 2-7 with 15 tubercles, and antennula with three aesthetascs.

5. Discussion

To date, 46 species of Armadillidae are known from South America, distributed as follows, 20 from Brazil, one from Chile, seven from Colombia, five from Paraguay, and 13 from Venezuela (Schultz, 1995; Schmidt, 2001; Pérez-Schultheiss, 2009; Schmalfuss, 2003; Campos-filho *et al*., 2018, 2023; Cardoso *et al*., 2023). The present work considerably increases the biodiversity of the Armadillidae for Colombia, from seven to 13 species. In addition, it represents the first record of terrestrial isopods for the departments of Atlántico, Risaralda, and Santander. Despite the number of species described here, this work also suggests the need of more surveys in other regions of the country where the knowledge of the group is poorly known, such as Andina, Pacífico, Amazonía, Sucre, and Orinoquía.

The members of the Armadillidae are mainly distributed in lower altitudes of the Colombian Caribbean, mostly associated with TDF areas (Figure 1), one of the most threatened ecosystems in the world (Janzen, 1988; Etter, 1993; García *et al*., 2014). In the Neotropical region, the TDF areas show a disjointed distribution, and hold high levels of endemic taxa (Olson *et al*., 2001; Lamoreux *et al*., 2006; Pennington *et al*., 2006; Morrone, 2014; Banda-R *et al*., 2016). In Colombia, only 5% of this ecosystem is protected through the National System of Protected Areas. Considering the number of new taxa proposed here, allied with other studies of Oniscidea for the country, there is an evident need to raise the level of awareness of this ecosystem in order to propose strategic areas for conservation efforts.

Regarding the Neotropical regionalization proposed by Morrone *et al*. (2022), Colombia holds nine provinces in three main biogeographic regions, the Pacific domain in the north, the South American Transition domain as a corridor in the center, and Boreal Brazilian domain in the south. Most of the records of the *Ctenorillo* species are in the Pacific domain, especially in Magdalena province, and one record in the Transition domain, Páramo province. In Colombian Caribbean four regions were recognized: 1, Península de La Guajira; 2, Sierra Nevada de Santa Marta; 3, Serranía de San Jacinto; and 4, Serranía del Perijá.

Colombia holds a high diversity of ecosystems, fauna and flora, due to its latitudinal extension as well as its complex geological history (Morrone & Lopretto, 2001; Hooghiemstra *et al*., 2006; Guerrero *et al*., 2008; Cardona *et al*., 2010; Llorente-Bousquets & LeCrom, 2013; Solari *et al*., 2013; López-O. *et al*., 2014; Morrone, 2014; Campos & Lasso, 2015; González-Orozco, 2021). It is clear that with more surveys along its territory, the biodiversity of Armadillidae, as well as of other Oniscidea members, will increase, as is common in tropical countries. It will be very interesting, using also molecular approaches (see for instance López-Orozco *et al*., 2022) to check whether the distribution of the Oniscidea in Colombia reflects the geological history of the country. Therefore, it is of fundamental importance to support the human capacity of taxonomists, ecologists and molecular biologists, with more financial support to conduct more studies on the group within the country.

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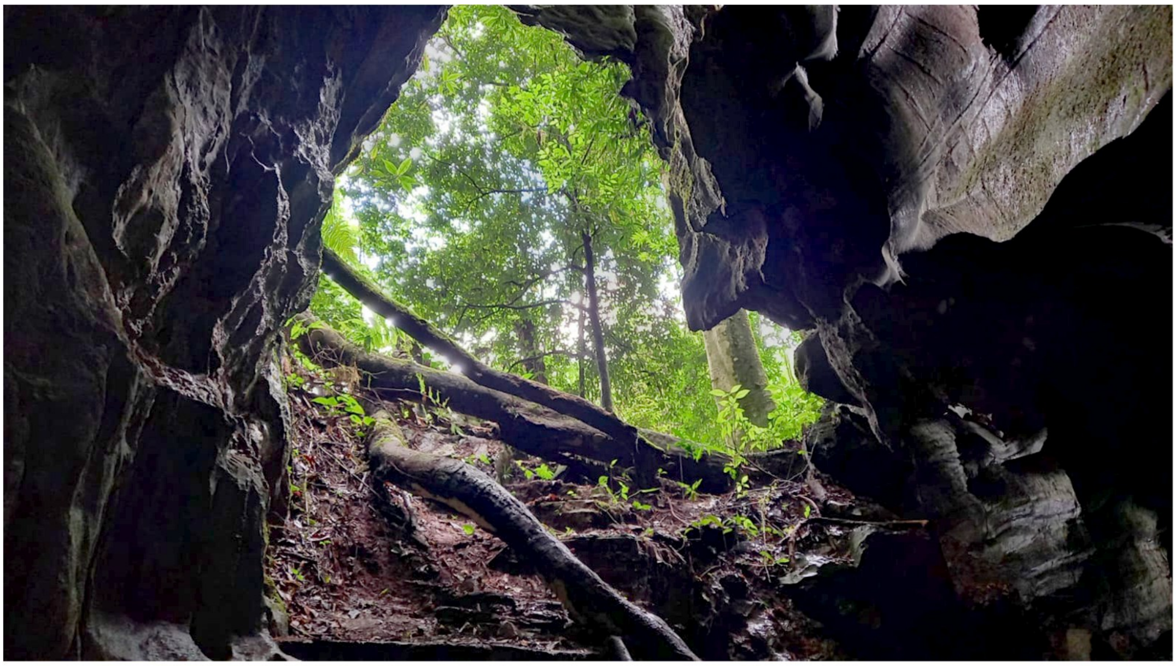
CAPÍTULO 2: Bridging taxonomic gaps: three new species and novel distributional records of terrestrial isopods (Isopoda: Oniscidea) from epigean and hypogean habitats in the Alto Ribeira karst area, southeastern Brazil



Editorial status: Manuscript in preparation.

Bridging taxonomic gaps: three new species and novel distributional records of terrestrial isopods (Isopoda: Oniscidea) from epigean and hypogean habitats in the Alto Ribeira karst area, southeastern Brazil

1. Abstract

Terrestrial isopods are an important component of both epigean and hypogean habitats of the Atlantic Forest in southeastern Brazil, yet the fauna of the Alto Ribeira karst area remains incompletely characterized. In this study, we revise the terrestrial isopod assemblage of this region based on extensive material collected in surface (epigean) and inside cave (hypogean) environments. We describe three new species: *Benthana* **sp. n.**, *Metaprosekia* **sp. n.** (Philosciidae) and *Novamundoniscus* **sp. n.** (Dubioniscidae), the latter representing the first record of Dubioniscidae in the Alto Ribeira karst area. We also provide new distributional records for *Cylindroniscus flaviae*, *Styloniscus spinosus* (Styloniscidae), *Atlantoscia antennamaculata*, *A. floridana*, *A. inflata*, *Benthana carijos*, *B. cairensis*, *B. picta* (Philosciidae), *Trichorhina tomentosa* (Platyarthridae), *Neotroponiscus carolii* (Bathytropidae) and *Pseudodiploexochus gibbus* (Armadillidae), the latter constituting the first record of Armadillidae for this region. Natural history remarks and habitat information are provided for all species examined. Our findings reveal the high diversity and ecological significance of terrestrial isopods in both epigean and hypogean habitats of the Alto Ribeira karst area, underscoring the importance of continued taxonomic research for advancing the knowledge and conservation of subterranean biodiversity in the Atlantic Forest.

Keywords: Atlantic Forest, Cave woodlice, Karst areas, Neotropical region, taxonomy.

2. Introduction

Terrestrial isopods (Oniscidea) groups species of strictly terrestrial crustaceans and comprise more than 4,000 described species in more than 500 genera and across 38 or 39 families (Sfenthourakis & Taiti, 2015; Campos-Filho & Taiti, 2021; De Smedt, *et al.*, 2025). The species of the groupd are distributed in almost all terrestrial habitats, inhabiting the supralittoral zone, mangroves, deserts, tropical forests, caves and urban areas, among others, and are considered an essential component in soil formation and nutrient recycling processes (Schmalfuss, 2003; Zimmer & Topp, 1999). To date, more than 210 species are known from

Brazil, and more than 110 species are recorded from subterranean environments (Campos-Filho *et al*., 2014, 2015a, 2016, 2017a, 2017b, 2019, 2020, 2022a, 2022b, 2023a, 2023b, 2023c; Cardoso *et al*., 2017, 2020a, 2020b, 2021, 2023, 2024a, 2024b; López-Orozco *et al*., 2024a, 2024b, 2024c).

The Atlantic Forest in southeastern Brazil harbors a high diversity of cave systems and unique subterranean biota (Fundação & Brasil, 2010; Fundação Florestal, 2018; Santos & Brilha, 2024). Although it is an important component of the protected areas of Brazil, this biome remains critically threatened by habitat loss and fragmentation (Myers *et al*., 2000; Fundação Florestal, 2018; Silva *et al*., 2024). The Alto Ribeira karst area in the Atlantic Forest, including limestone caves, are notable for supporting many troglobitic species with restricted distributions (Trajano, 2000; Silva *et al*., 2011; Trajano *et al*., 2016). To date, 13 species in six genera and four families of terrestrial isopods are recorded in this karst area, i.e., *Alboscia jotajota* Campos-Filho, Bichuette & Taiti, 2020, *Atlantoscia inflata* Campos-Filho & Araujo, 2015, *Benthana iporangensis* Lima & Serejo, 1993, *B. longicornis* Verhoeff, 1941, *B. olfersii* (Brandt, 1833), *B. picta* (Brandt, 1833), *B. taeniata* Araujo & Buckup, 1994 (Philosciidae), *Cylindroniscus flaviae* Campos-Filho, Araujo & Taiti, 2017 (Styloniscidae), *Neotroponiscus iporangaensis* Cardoso & Araujo, 2017 (Bathytropidae), *Trichorhina acrux* Campos-Filho, Sfenthourakis & Bichuette, 2023, *T. jurai* Campos-Filho, Gallão & Bichuette, 2023, *T. quadriocellata* Campos-Filho, Borja-Arrieta & Bichuette, 2023, and *T. tomentosa* (Budde-Lund, 1893) (Platyarthridae) (Lima & Serejo, 1993; Campos-Filho *et al*., 2017, 2020, 2023a, 2023b; Cardoso *et al*., 2017).

After the examination of a large collection of terrestrial isopods from the Alto Ribeira karst area, south of the state of São Paulo, Brazil, 14 species in 9 genera (six families) were recognized, of which three are considered new to the science. Moreover, distribution maps and subterranean classification are provided.

3. Material and methods

Study area: Alto Ribeira karst area, state of São Paulo, southeastern Brazil

The Alto Ribeira karst area is located in the south of the state of São Paulo, Brazil, in an area of mountainous relief, with natural elevations ranging from 80 to 1,146 m (Figure 1).

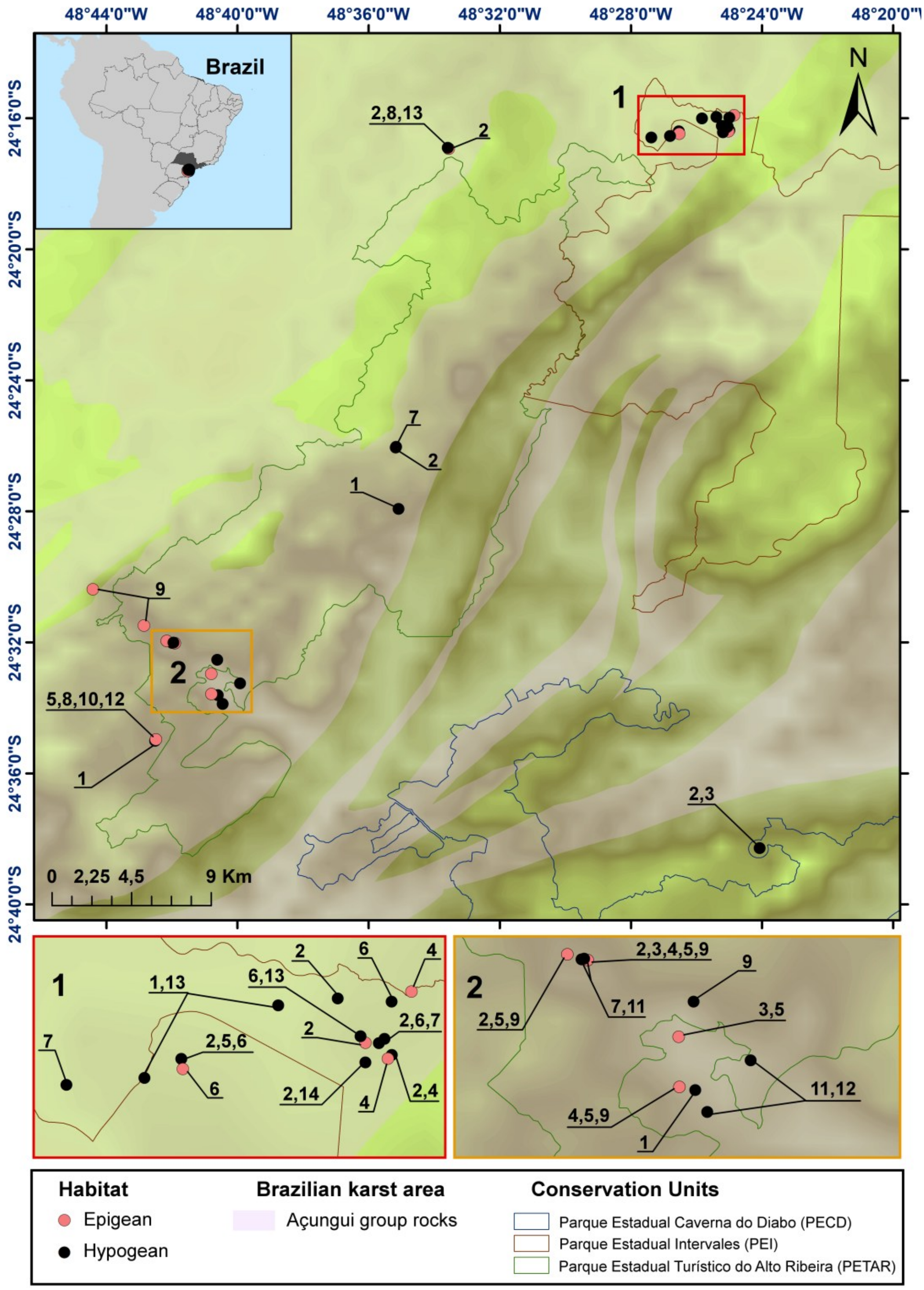


Figure 1. Study area and species distribution in Alto Ribeira karst area, southeastern Brazil. **1.** *Cylindroniscus flaviae* Campos-Filho, Araujo & Taiti, 2017; **2.** *Styloniscus spinosus* (Patience, 1907); **3.** *Atlantoscia antennamaculata* Campos-Filho, Cardoso & Araujo, 2018; **4.** *A. floridana* (Van Name, 1940); **5.** *A. inflata* Campos-Filho & Araujo, 2015; **6.** *Benthana carijos* Costa, Campos-Filho & Araujo, 2014; **7.** *B. cairensis* Sokolowicz, Araujo & Boetler, 2008; **8.** *B. picta* (Brandt, 1833); **9.** *Benthana* **n. sp.**; **10.** *Metaprosekia* **n. sp.**; **11.**

Novamundoniscus **n. sp.**; **12.** *Trichorhina tomentosa* (Budde-Lund, 1893); **13.** *Neotroponiscus carolii* Arcangeli, 1936; **14.** *Pseudodiploexochus gibbus* (Lemos de Castro, 1972).

Dense ombrophilous forest predominates over karst soil, and is considered one of the most important remnants of preserved Atlantic Forest in the country, and a global biodiversity hotspot due to its rich flora and fauna, often endemic and endangered (SEMA, 1997; Myers *et al*., 2000; Ab'Saber, 2007; Gallão & Bichuette, 2018). This region is inserted in the Atlantic, Araucaria Forest and Paraná Forest Provinces, Chacoan Subregion (Morrone, 2014). These caves are located in limestone formations belonging to the Açungui Group, dating from the Proterozoic period (Figure 2) (Auler *et al*., 2001). The regional climate is humid subtropical, with hot summers and evenly distributed rainfall throughout the year, and is predominantly classified as Cfa, according to the Köppen-Geiger climate classification. However, higher altitude areas near the park may present Cfb type characteristics, defined as a humid temperate climate with mild summers (Alvares *et al*., 2013; Bedek *et al*., 2018, 2020).

The specimens were collected in three conservation units from this region: Parque Estadual Turistico do Alto Ribeira (PETAR), Parque Estadual da Caverna do Diabo (PECD), and Parque Estadual Intervales (PEI), from state Sao Paulo, southeastern Brazil (Figure 1). The region plays a fundamental role in sustainable tourism and environmental conservation, and its trails and caves offer unique opportunities for ecotourism, while also promoting environmental education and appreciation of the Ribeira Valley's natural and cultural heritage.

Specimen collection, preparations and taxonomy

Specimens were collected manually and preserved in 70% ethanol. Descriptions are based on morphological characters, after micropreparations in Hoyer's medium (Anderson, 1954). For already described species, the synonym list includes the original description and subsequent records from Brazilian caves; moreover, distribution and remarks, are given. For each new species, type material, description, and remarks are provided. The subterranean classification follows Trajano & Carvalho (2017). Descriptions and morphological terms follow Campos-Filho *et al*. (2014).

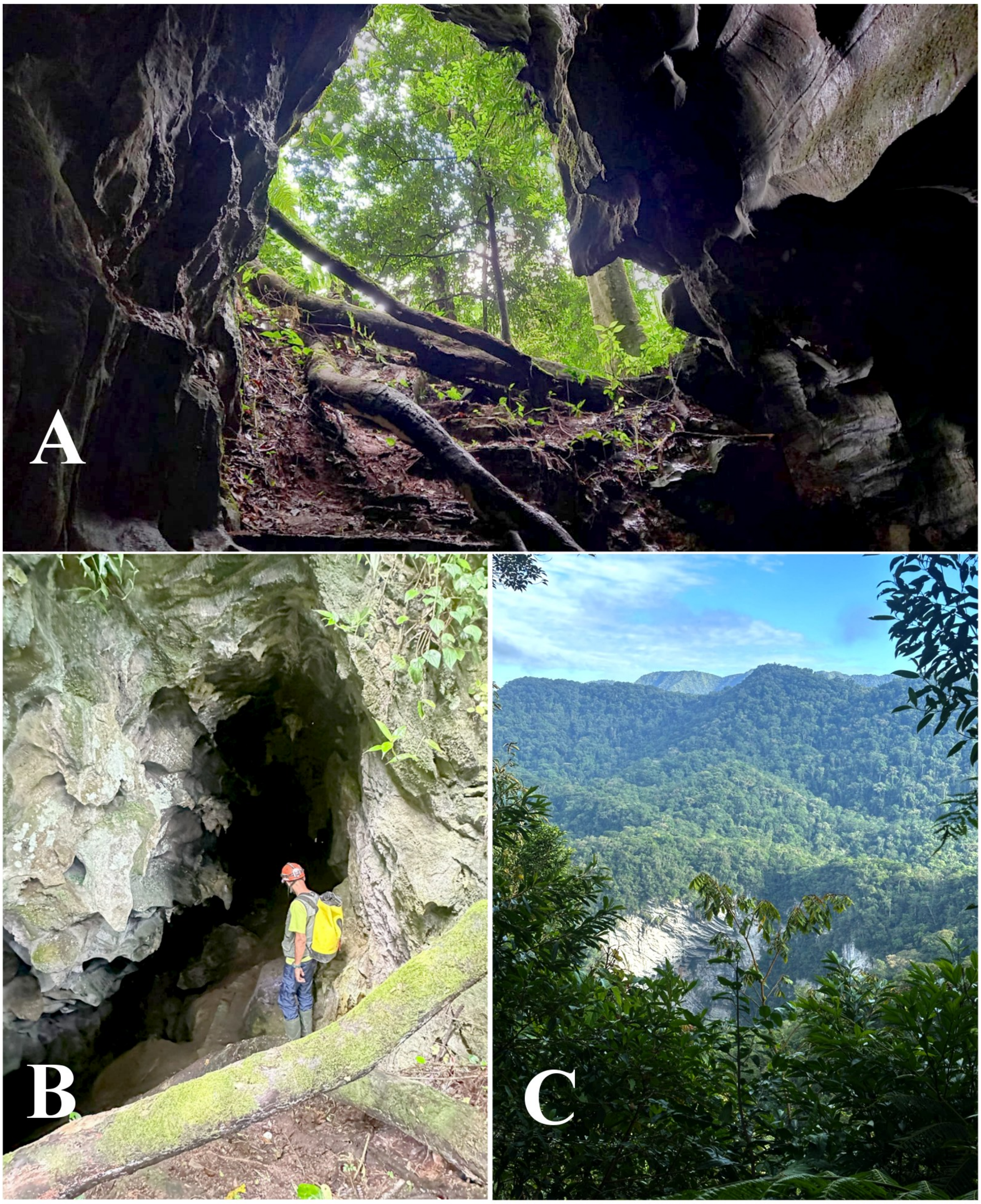


Figure 2. Study area: **A**, Ressurgência das Areias de Água Quente (PETAR), inside; **B**, Ressurgência das Areias de Água Quente (PETAR), outside; **C**, outcrops and rainforest cover of Alto Ribeira karst system, Iporanga, state of São Paulo. Photos A and C by Y.M. Carpio-Díaz, and B by M. E. Bichuette.

The images of each species were obtained with a stereomicroscope Nikon SMZ800N with an adapted Prime Life Science camera and edited using GIMP (v. 2.8). Illustrations were made with the aid of a camera lucida mounted on a Wild M3 microscope. The final illustrations were prepared using GIMP (v. 2.8), using the method proposed by Montesanto (2015, 2016). The collected material is deposited in the Brazilian scientific collection of the Laboratório de Estudos Subterrâneos (LES) Universidade Federal de São Carlos, São Carlos, Brazil (curator: Maria Elina Bichuette).

4. Results

Systematic account

Suborder Oniscidea Latreille, 1802

Family Styloniscidae Vandel, 1952

Genus ***Cylindroniscus*** Arcangeli, 1929

Type species: *Cylindroniscus seurati* Arcangeli, 1929, by monotypy.

Cylindroniscus flaviae Campos-Filho, Araujo & Taiti *in* Campos-Filho *et al*. 2017: 229, figs 1C, 2–5.

Figures 1, 3A

Material examined

São Paulo, Iporanga, Parque Estadual Turístico do Alto Ribeira (PETAR): 1 male (WWF_2_062), Lajeado Artificial Mine, 24°35'0.316"S, 48°42'30.463"W, 08 november 2023, leg. M.E. Bichuette, M.V.S.A. Duarte, J.A. dos Santos, J. Barbosa; 1 female (WWF_2_150), Baralho Artificial Mine, 24°33'36.799"S, 48°40'35.63"W, 09 november 2023, same leg. As previous; 1 female (WWF3_076), Gruta do Monjolinho cave, 24°27'55.598"S, 48°35'4.898"W, 10 may 2024, M.E. Bichuette, J.S. Gallo, J.E. Gallão, Gambarini, J. Barbosa. Parque Estadual Intervales (PEI): 1 male, 1 female (FOG-003), Gruta do Fogo cave, 24°16'0.48"S, 48°25'49.439"W, 27 october 2023, leg. J.S. Gallo, M.V.S.A. Duarte, E.L. Silva, M.F.C. Zancheta, A. Jackson; 1 female (FOG-015), same data as previous; 1 female (ROD-052), Gruta dos Rodriguez cave, 24°16'32.412"S, 48°26'48.184"W, 08 april 2023, leg. J.E. Gallão, J.S. Gallo, I. Ribeiro, E.C. Igual.

Remarks

The specimens were found living exclusively inside caves, occurring in very humid clay, guano, or rocky substrates rich in organic matter, between the twilight and aphotic zones. This species had been previously considered troglophilic (Campos-Filho *et al*., 2017). However, despite extensive and repeated surveys conducted in the epigean environments of the karst region, we did not record its presence outside caves. These findings suggest that the species may in fact be troglobitic.

Distribution

Endemic from Brazil, with wide distribution in several caves of the Açungui karst area from state Sao Paulo (Campos-Filho *et al*., 2017). The present records extend the knowledge of its distribution for hypogean habitats in the Atlantic Forest, southeast of São Paulo.

Genus *Styloniscus* Dana, 1853

Type species: *Styloniscus longistylis* Dana, 1853 type by subsequent designation.

Styloniscus spinosus (Patience, 1907)

Figures 1, 3B

Trichoniscus spinosus Patience, 1907: 85, pl. III.

Styloniscus spinosus; Campos-Filho *et al*. 2018a: 5 (for full Brazilian references).

Material examined

São Paulo, Eldorado, Parque Estadual da Caverna do Diabo (PECD): 1 female (CD-I-171), Gruta da Tapagem cave, 24°38'16.998"S, 48°24'3.996"W, 26 march 2021, leg. M.E. Bichuette, J.E. Gallão, V.F. Sperandei, T. Zepon; 1 male, 2 females (CD-IV-043), same locality as previous, 16 february 2022, leg. M.E. Bichuette, T. Zepon, L.R. Penoni; 1 female, 1 juvenile (CD-IV-106), 17 february 2022, same locality and leg. as previous; 1 female (CD-

V-025), same local as previous, 11 october 2022, leg. M.E. Bichuette, J.E. Gallão. Guapiara, Parque Estadual Intervales (PEI): 1 female (ARA-076), outside Gruta Aracaeiro II cave, 24°16'16.957"S, 48°25'11.053"W, 10 june 2023, leg. J.S. Gallo, C.M. López-Orozco, L.F. Dos Santos, B.D. Lenhare, E.C. Igual, I.A. Ribeiro; 1 male, 5 females (POR-042), Gruta Mamica da Porca cave, 24°16'54.001"S, 48°33'34.999"W, same data as previous; 1 female, 1 juvenile (POR-067), outside Gruta Mamica da Porca cave, 24°16'55.913"S, 48°33'33.418"W, same data as previous. Iporanga, Parque Estadual Intervales (PEI): 1 juvenile (2TATU-015), Gruta do Tatu cave, 24°16'17.101"S, 48°25'05.199"W, 26 october 2023, leg. J.S. Gallo, M.V.S.A. Duarte, E.L. Silva, M.F.C. Zancheta, A. Jackson; 1 juvenile (CHU-040), Gruta Abismo da Chuva cave, 24°15'57.47"S, 48°25'23.253"W, 11 june 2023, leg. J.S. Gallo, C.M. López-Orozco, L.F. Dos Santos, B.D. Lenhare, E.C. Igual, I.A. Ribeiro; 1 juvenile (COL-049), Gruta Colorida cave, 24°16'55.601"S, 48°25'11.1"W, 10 february 2023, leg. M.E. Bichuette, J.E. Gallão, J.S. Gallo, M.V.S.A. Duarte, B.C.M. Oliveira, L.F. Dos Santos, M.F.C. Zancheta, E.L. Silva; 2 females (PAIVA-V-031), Gruta dos Paiva cave, 24°16'23.999"S, 48°26'31.999"W, 09 june 2023, leg. J.S. Gallo, C.M. López-Orozco, L.F. Dos Santos, B.D. Lenhare, E.C. Igual, I.A. Ribeiro; 1 female (PED-008B), Abismo da Pedreira cave, 24°16'22.321"S, 48°24'59.497"W, 19 november 2023, leg. M.E. Bichuette, J.E. Gallão, B.C. Mafra. Parque Estadual Turistico do Alto Ribeira (PETAR): 1 male (sem triagem), Gruta do Chapéu Mirim II, 24°26'1.68"S, 48°35'9.24"W, 26-30 march 2009, F. Pellegatti-Franco; 1 female (PET-EPI-011), outside Caverna do Couto cave, 24°32'1.614"S, 48°41'54.408"W, 19 june 2025, leg. M.E. Bichuette, C.M. López-Orozco, R. Borja-Arrieta, J. Barbosa, Y.M. Carpio-Díaz; 1 male, 1 female (PET-EPI-016), same data as previous; 2 females (PET-EPI-019), same data as previous; 2 males, 4 females (PET-EPI-023), same data as previous; 1 female (PET-EPI-036), left bank of the Roncador river, 24°31'57.336"S, 48°42'9.252"W, same data as previous.

Remarks

The specimens were found living leaf litter and trunk outside of caves with high humidity, and inside the caves, occurs in very humid clay or rocky substrate with organic matter, in all three zones of the cave (entrance, twilight, and aphotic zone). Moreover, tis species was recorded living in greenhouses from several countries (Schmalfuss, 2003). Due to distribution of this species, it being considered a troglophilic species.

Distribution

Great Britain, Hawaii (USA), Madagascar, Mauritius and Réunion (Schmalfuss, 2003). In Brazil this species is considered introduced and was recorded from the states of Paraná, São Paulo and Santa Catarina (Magrini *et al*., 2010, 2011; Campos-Filho *et al*., 2017, 2018a). This is the first record of the species for hypogean habitats in the Atlantic Forest, southeast of São Paulo.

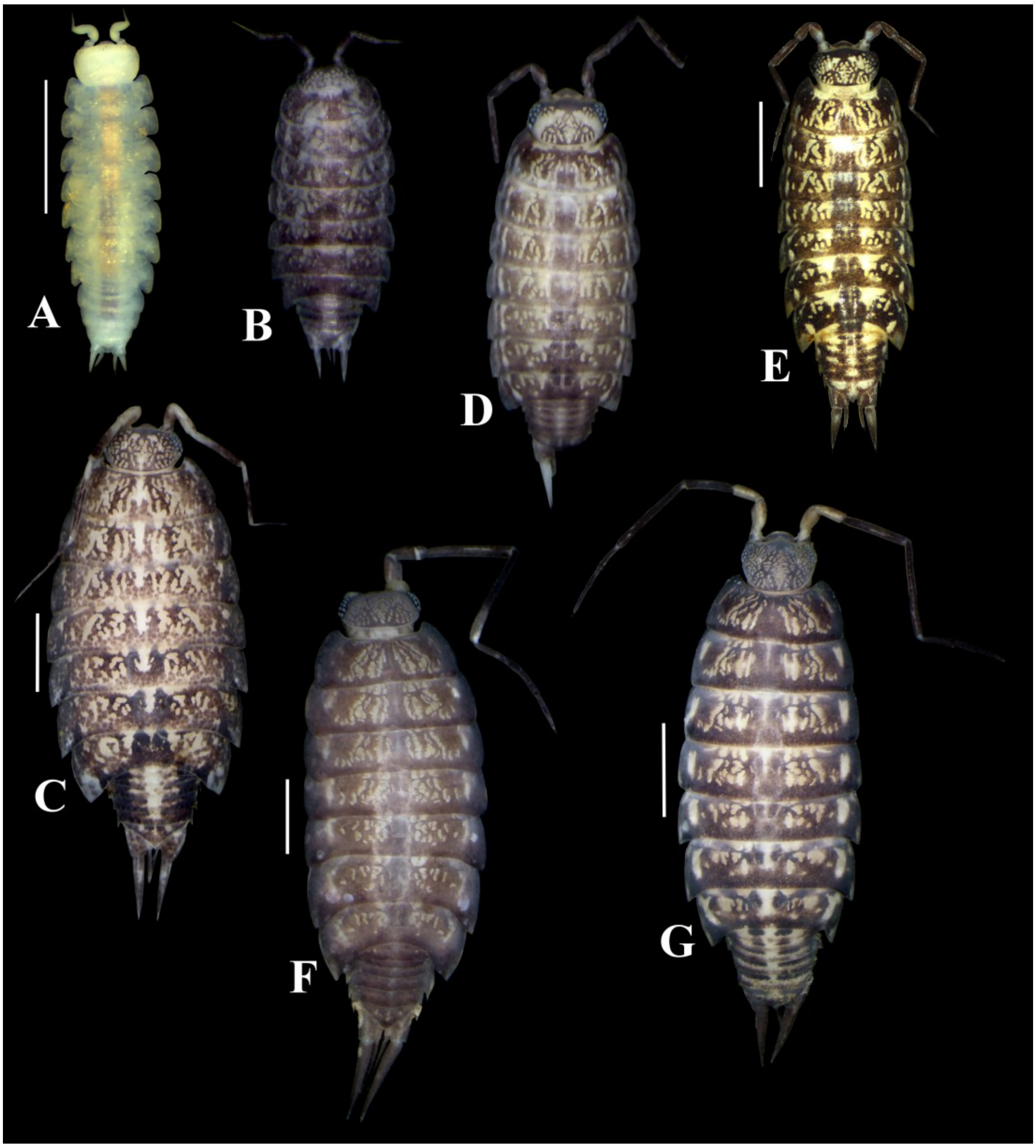


Figure 3. Habitus in dorsal view of species. **A.** *Cylindroniscus flaviae* Campos-Filho, Araujo & Taiti, 2017; **B.** *Styloniscus spinosus* (Patience, 1907); **C.** *Atlantoscia antennamaculata* Campos-Filho, Cardoso & Araujo, 2018; **D.** *A. floridana* (Van Name, 1940); **E.** *A. inflata*

Campos-Filho & Araujo, 2015; **F.** *Benthana carijós* Costa, Campos-Filho & Araujo, 2014; **G.** *B. cairensis* Sokolowicz, Araujo & Boetler, 2008.

Family Philosciidae Kinahan, 1857

Genus ***Atlantoscia*** Ferrara & Taiti, 1981

Type species: *Atlantoscia alceui* Ferrara & Taiti, 1981.

Atlantoscia antennamaculata Campos-Filho, Cardoso & Araujo, 2018

Figures 1, 3C

Atlantoscia antennamaculata Campos-Filho, Cardoso & Araujo *in* Zimmermann *et al*. 2018: 553, figs 1–3.

Atlantoscia antennamaculata Campos-Filho *et al*. 2018a: 7 (for full Brazilian references).

Material examined

São Paulo, Iporanga, Parque Estadual Turístico do Alto Ribeira (PETAR): 1 male, 1 female (PET-EPI-001), left bank of the Betari river, 24°32'57.696"S, 48°40'47.784"W, 18 june 2025, leg. M.E. Bichuette, C.M. López-Orozco, R. Borja-Arrieta, J. Barbosa, Y.M. Carpio-Díaz; 1 male, 1 female (PET-EPI-005), same data as previous; 1 female, 1 juvenile (PET-EPI-010), same data as previous; 1 male, 4 females (PET-EPI-014), outside Caverna do Couto cave, 24°32'1.614"S, 48°41'54.408"W, 19 june 2025, same leg. as previous; 1 female (PET-EPI-024), same data as previous. Eldorado, Parque Estadual da Caverna do Diabo (PECD): 1 male (CD-I-164), Gruta da Tapagem cave, 24°38'15.30"S, 48°24'03.30"W, 26 march 2021, leg. M.E. Bichuette, J.E. Gallão, V.F. Sperandei, T. Zepon; 1 male (CD-III-062), same local as previous, 13 november 2021, leg. M.E. Bichuette, T. Zepon, V.F. Sperandei.

Remarks

The specimens were found living leaf litter, trunk and dry leaves outside of caves with high humidity, and inside the caves, occurs in very humid clay or rocky substrate with organic matter, between the twilight and aphotic zones. Due to distribution of this species, it being considered a troglophilic species.

Distribution

Endemic to Brazil, with records from Santa Catarina state (Zimmermann *et al*., 2018a). This is the first record of the species in caves and state of São Paulo.

Atlantoscia floridana (Van Name, 1940)

Figures 1, 3D

Philoscia floridana – Van Name (1940): 113, fig. 4.

Atlantoscia floridana; Campos-Filho *et al*. 2018a: 7 (for full Brazilian references).

Material examined

São Paulo, Iporanga, Parque Estadual Intervales (PEI): 1 male (PED-008), Abismo da Pedreira cave, 24°38'15.30"S, 48°24'03.30"W, 19 november 2023, leg. M.E. Bichuette, J.E. Gallão, B.C. Mafra; 3 males, 7 females (PED-044), outside Abismo da Pedreira, 24°16'23.902"S, 48°25'1.178"W, same data as previous; 1 male, 3 females, 1 juvenile (RIO-058), Quiosque riverbank, 24°15'54.392"S, 48°24'50.878"W, same data as previous, leg. M.E. Bichuette, J.E. Gallão, B.C. Mafra, Jaqueline, E.C. Igual, I.A. Ribeiro. Parque Estadual Turistico do Alto Ribeira (PETAR): 1 male (WWF_246), outside Gruta dos Lagos Suspensos cave, 24°33'34.459"S, 48°40'47.251"W, 14 march 2023, leg. M.E. Bichuette, J.E. Gallão, M.V.S.A. Duarte; 5 females (PET-EPI-066), same locality as previous, 20 june 2025, leg. M.E. Bichuette, C.M. López-Orozco, R. Borja-Arrieta, J. Barbosa, Y.M. Carpio-Díaz; 1 female (PET-EPI-372), outside Caverna do Couto cave, 24°32'1.614"S, 48°41'54.408"W, 19 june 2025, same leg. as previous.

Remarks

The specimens were found living leaf litter, trunk and dry leaves outside of caves, and inside the caves occurs in substrate with organic matter, in the entrance zone. Due to distribution of this species, it being considered a troglophilic species.

Distribution

USA, Argentina, coastal regions of Ascension and St. Helena Island, and Brazil (Van Name, 1940; Schmalfuss, 2003; Campos-Filho *et al*., 2013, 2018). In Brazil, it is widely distributed (Campos-Filho *et al*., 2013, 2018a). This is the first record of the species in caves.

Atlantoscia inflata Campos-Filho & Araujo, 2015

Figures 1, 3E, 9B

Atlantoscia inflata Campos-Filho & Araujo *in* Zimmermann *et al*. 2015: 705, figs 1–2, 5–6, tables 1–3.

Atlantoscia inflata; Campos-Filho *et al*. 2018a: 7 (for previous Brazilian references); Campos-Filho *et al*. 2020: 16, fig 14.

Material examined

São Paulo, Iporanga, Parque Estadual Intervales (PEI): 1 male, 1 female (Paiva_177b), Gruta dos Paiva cave, 24°16'23.999"S, 48°26'31.999"W, 27 march 2022, leg. M.E. Bichuette, J.E. Gallão, J.S. Gallo. Parque Estadual Turistico do Alto Ribeira (PETAR): 1 male (WWF_264), outside Gruta dos Lagos Suspensos cave, 24°33'34.459"S, 48°40'47.251"W, 14 march 2023, leg. M.E. Bichuette, J.E. Gallão, M.V.S.A. Duarte; 1 female (WWF_284), same data as previous; 1 female (WWF_287), same data as previous; 3 males, 1 female (WWF_292), same data as previous; 3 females, 3 juveniles (PET-EPI-059), same local as previous, 20 june 2025, leg. M.E. Bichuette, C.M. López-Orozco, R. Borja-Arrieta, J. Barbosa, Y.M. Carpio-Díaz; 1 male (PET-EPI-068), same data as previous; 1 male, 1 female (PET-EPI-048), outside Lajeado Artificial Mine, 24°34'57.762"S, 48°42'29.202"W, 20 june 2025, same leg. as previous; 2 females (PET-EPI-052), same data as previous; 2 males, 1 female (PET-EPI-026), outside Caverna do Couto cave, 24°32'1.614"S, 48°41'54.408"W, 19 june 2025, same leg. as previous; 2 males, 6 females, 1 juvenile (PET-EPI-008), left bank of the Betari river, 24°32'57.696"S, 48°40'47.784"W, 18 june 2025, same leg. as previous; 6 males, 6 females (PET-EPI-009), same data as previous; 1 male (PET-EPI-030), left bank of the Roncador river, 24°31'57.336"S, 48°42'9.252"W, 19 june 2025, same leg. as previous; 1 male, 3 females (PET-EPI-035), same data as previous.

Remarks

The specimens were found inside cave, occurs in leaf litter in the entrance zone. Outside of cave, were found living leaf litter and trunk with high humidity.

Distribution

Endemic to Brazil, with records from states Rio Grande do Sul, São Paulo and Paraná (Zimmermann *et al*., 2015; Campos-Filho *et al*., 2018a, 2020). In caves, was recorded from PETAR, São Paulo (Campos-Filho *et al*., 2020). The present record extends the knowledge of its distribution for epigean and hypogean habitats in the Atlantic Forest, southeast of São Paulo.

Genus ***Benthana*** Budde-Lund, 1908

Type species: *Philoscia picta* Brandt, 1833, by subsequent designation (Van Name, 1936).

Benthana carijos Costa, Campos-Filho & Araujo, 2014

Figures 1, 3F

Benthana carijos Costa, Campos-Filho & Araujo, 2014: 170, figs 1–3.

Benthana carijos Campos-Filho *et al*. 2018a: 9 (for full Brazilian references).

Material examined

São Paulo, Guapiara, Parque Estadual Intervales (PEI): 2 females (ARA-018), Gruta Aracaeiro II cave, 24°16'14.045"S, 48°25'13.252"W, 10 june 2023, leg. J.S. Gallo, C.M. López-Orozco, L.F. Dos Santos, B.D. Lenhare, E.C. Igual, I.A. Ribeiro. Iporanga, PEI: 1 female (DETRÁS-024), Gruta Detrás cave, 24°16'15.2"S, 48°25'2.701"W, 12 february 2023, leg. M.E. Bichuette, J.E. Gallão, J.S. Gallo, M.V.S.A. Duarte, B.C.M. Oliveira, L.F. Dos Santos, M.F.C. Zancheta, E.L. Silva; 1 juvenile (DETRÁS-028), same data as previous; 1 juvenile (DETRÁS-043), same data as previous; 1 female (DETRÁS-044), same data as previous; 1 female (DETRÁS-051), same data as previous; 1 female (DETRÁS-061), same data as previous; 1 male (DETRÁS-067b), same data as previous; 2 females (DETRÁS-073), same data as previous; 1 female (DETRÁS-093), same data as previous; 1 female, 1 juvenile (2TATU-002), Gruta do Tatu cave, 24°16'17.101"S, 48°25'05.199"W, 26 october 2023, leg. J.S. Gallo, M.V.S.A. Duarte, E.L. Silva, M.F.C. Zancheta, A. Jackson; 1 female (TATU-012B), same locality as previous, 08 june 2023, leg. J.S. Gallo, C.M. López-Orozco, L.F. Dos Santos, B.D. Lenhare, E.C. Igual, I.A. Ribeiro; 1 female (TATU-021), same data as previous; 1 male, 2 females (TATU-031), same data as previous; 1 female (MEN-073), Toca dos Meninos cave, 24°15'58.835"S, 48°24'59.565"W, 12 february 2023, leg. M.E. Bichuette, J.E. Gallão, J.S. Gallo, M.V.S.A. Duarte, B.C.M. Oliveira, L.F. Dos Santos, M.F.C. Zancheta, E.L. Silva; 3 males, 2 females (PAIVA-011), Gruta dos Paiva cave, 24°16'23.999"S, 48°26'31.999"W, 27 march 2022, leg. M.E. Bichuette, J.E. Gallão, J.S. Gallo; 1 male, 1 female (PAIVA-177), same data as previous;1 female (PAIVA-V-020), same locality as previous, 09 june 2023, leg. J.S. Gallo, C.M. López-Orozco, L.F. Dos Santos, B.D. Lenhare, E.C. Igual, I.A. Ribeiro; 1 male, 1 female (PAIVA-IV-050), same locality as previous, 07 april 2023, leg. J.E. Gallão, J.S. Gallo, I. Ribeiro, E.C. Igual; 1 male (PAIVA-IV-078), same data as previous; 1 female (PAIVA-III-107), outside Gruta dos Paiva cave, 24°16'28.427"S, 48°26'31.34"W, 11 february 2023, leg. M.E. Bichuette, J.E. Gallão, J.S. Gallo, M.V.S.A. Duarte, B.C.M. Oliveira, L.F. Dos Santos, M.F.C. Zancheta, E.L. Silva.

Remarks

The specimens were found inside of several caves, foraging on guano, occurs in the walls, in substrate with organic matter and in very humid clay or rocky substrate, between the entrance and the twilight zone of the caves. This reflects a high degree of plasticity of this species in occupying different microhabitats within caves. Due to distribution of this species, it being considered a troglophilic species.

Distribution

Endemic to Brazil, with records from São Paulo and Santa Catarina states (Campos-Filho *et al*., 2015b). This is the first record of this species in caves.

Benthana cairensis Sokolowicz, Araujo & Boetler, 2008

Figures 1, 3G

Benthana cairensis Sokolowicz, Araujo & Boetler, 2008: 315, figs 1–28.

Benthana cairensis Campos-Filho *et al*. 2018a: 9 (for full Brazilian references).

Material examined

São Paulo, Iporanga, Parque Estadual Turistico do Alto Ribeira (PETAR): 1 male, 3 females (LES 636), Gruta do Chapéu Mirim I cave, 24°26'03"S, 48°35'10"W, 26–30 march 2009, leg. F. Pellegatti-Franco; 2 males, 2 females (LES 1783), Caverna do Couto cave, 24°32'00.9"S, 48°41'56"W, 16–20 september 2009, leg. F. Pellegatti-Franco. Iporanga, Parque Estadual Intervales (PEI); 1 male, 1 female (DETRÁS-047), Gruta Detrás cave, 24°16'15.2"S, 48°25'2.701"W, 12 february 2023, leg. M.E. Bichuette, J.E. Gallão, J.S. Gallo, M.V.S.A. Duarte, B.C.M. Oliveira, L.F. Dos Santos, M.F.C. Zancheta, E.L. Silva; 1 female (DETRÁS-067), same data as previous; 1 female (TATU-012), Gruta do Tatu cave, 24°16'17.101"S, 48°25'05.199"W, 08 june 2023, leg. J.S. Gallo, C.M. López-Orozco, L.F. Dos Santos, B.D. Lenhare, E.C. Igual, I.A. Ribeiro. Guapiara, Parque Estadual Intervales (PEI): 1 female (MINO2-051), Gruta do Minotauro II cave, 24°16'35.436"S, 48°27'22.528"W, 09 april 2023, leg. J.E. Gallão, J.S. Gallo, I. Ribeiro, E.C. Igual; 1 female (MINO2-057), same data as previous; 1 male (MINO2-073), same data as previous.

Remarks

The specimens were found living inside of several caves foraging on guano, in unconsolidated substrates, occurs in the walls, in substrate with organic matter or rocky substrate, between the entrance and the twilight zone of the caves. This species occupies different microhabitats within caves possibly due to the availability of resources and favorable conditions and its high degree of plasticity of this species in occupying different microhabitats. Due to distribution of this species, it being considered a troglophilic species.

Distribution

Endemic to Brazil, with records from São Paulo, Paraná, Santa Catarina and Rio Grande do Sul states (Campos-Filho *et al*., 2015b, 2018a; Zimmermann *et al*., 2015a). The present work constitutes the first record of this species from caves.

Benthana picta (Brandt, 1833)

Figures 1, 4A, 9A

Philoscia picta Brandt, 1833: 183.

Benthana picta Campos-Filho *et al*. 2018a: 9 (for full Brazilian references); Zimmermann *et al*. 2024: 3, figs 1 and 2, table 1.

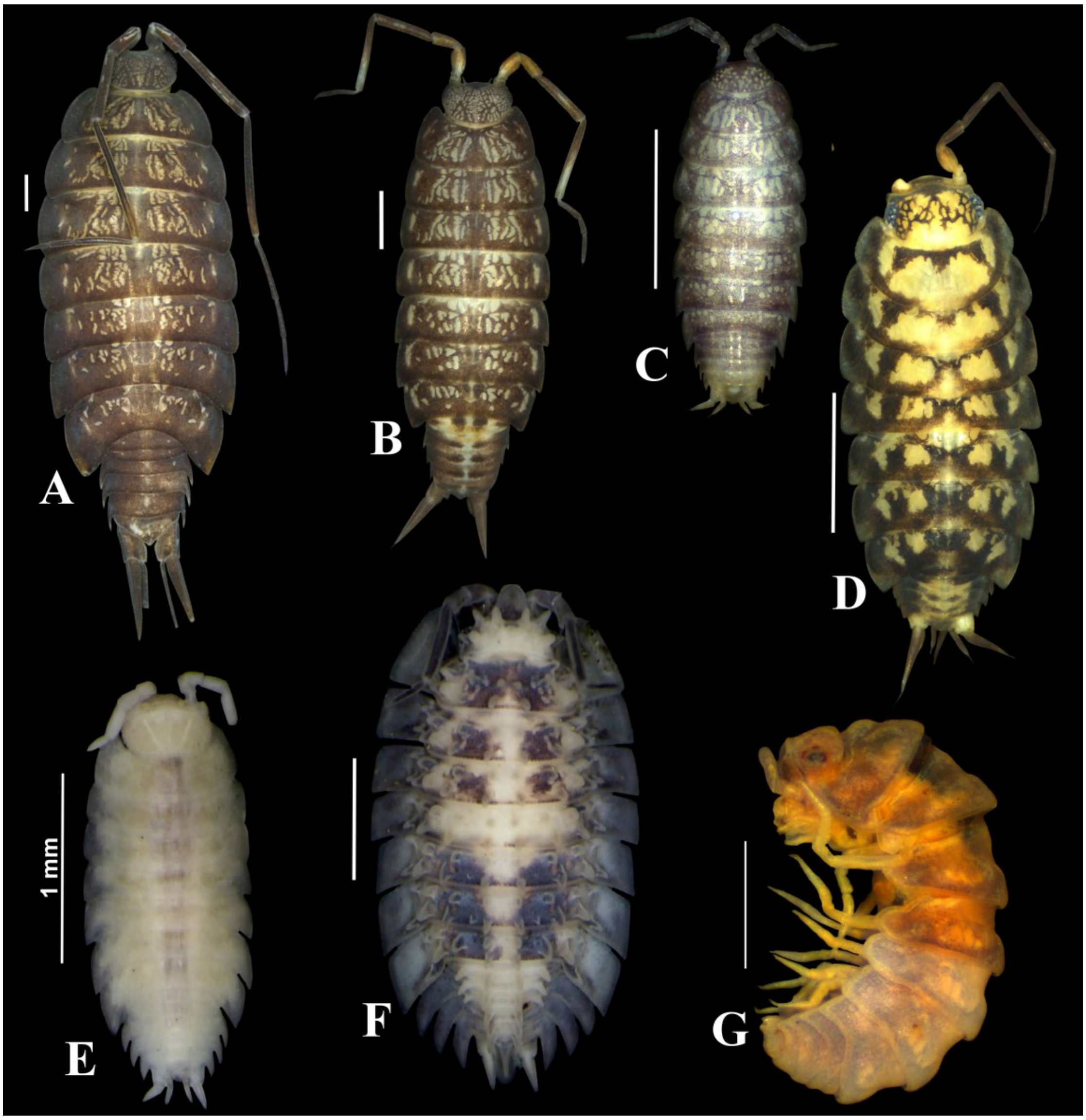


Figure 4. Habitus in dorsal and lateral view of species. **A.** *Benthana picta* (Brandt, 1833); **B.** *Benthana* **n. sp.**; **C.** *Metaprosekia* **n. sp.**; **D.** *Novamundoniscus* **n. sp.**; **E.** *Trichorhina tomentosa* (Budde-Lund, 1893); **F.** *Neotroponiscus carolii* Arcangeli, 1936; **G.** *Pseudodiploexochus gibbus* (Lemos de Castro, 1972).

Material examined

São Paulo, Guapiara, Parque Estadual Intervales (PEI): 1 female (POR-011), Gruta Mamica da Porca cave, 24°16'54.001"S, 48°33'34.999"W, 10 june 2023, leg. J.S. Gallo, C.M. López-Orozco, L.F. Dos Santos, B.D. Lenhare, E.C. Igual, I.A. Ribeiro; 3 males, 2 females (POR-028), same data as previous: 1 female (PET-EPI-041), outside Lajeado Artificial Mine, 24°34'57.762"S, 48°42'29.202"W, 20 june 2025, leg. M.E. Bichuette, C.M. López-Orozco, R. Borja-Arrieta, J. Barbosa, Y.M. Carpio-Díaz.

Remarks

The specimens were found living inside cave occurs about blocks of rock substrate with organic matter, in the entrance zone of the caves.

Distribution

Recorded from Brazil and Paraguay (Schmalfuss, 2003). In Brazil, it is distributed in Atlantic Forest areas from the state of Espírito Santo to Rio Grande do Sul (Campos-Filho *et al*., 2015b, 2020). In caves, it is recorded from several caves of Alto Ribeira karst area (Campos-Filho *et al*., 2020). The present record extends the knowledge of its distribution for caves in the state of São Paulo, inserted in the Atlantic Forest.

Benthana n. sp.

Figures 1, 4B, 5–6

Material examined

São Paulo, Iporanga, Parque Estadual Turistico do Alto Ribeira (PETAR): *Holotype* male (WWF_2_193) (part in micropreparations), outside Mina Artificial Jaguatirica, 24°31'29.42"S, 48°42'50.88"W, 09 november 2023, leg. M.E. Bichuette, M.V.S.A. Duarte, J.A. dos Santos, J. Barbosa. *Paratypes* 1 female (WWF_2_033), outside Gruta do Calcário Branco cave, 24°30'22.705"S, 48°44'24.316"W, 07 november 2023, leg. M.E. Bichuette, M.V.S.A. Duarte, J.A. dos Santos, J. Barbosa; 1 female (Disc_PET_285), Gruta do Ouro Grosso cave, 24°32'31.92"S, 48°40'36.84"W, 01 december 2024, leg. Disciplina PPGERN_2024; 1 male, 2 females (PET-EPI-022), outside Caverna do Couto cave, 24°32'1.614"S, 48°41'54.408"W, 19 june 2025, leg. M.E. Bichuette, C. M. López-Orozco, R. Borja-Arrieta, J. Barbosa, Y. M. Carpio-Díaz; 1 female (PET-EPI-027), same data as previous; 1 female (PET-EPI-031), left bank of the river Roncador, 24°31'57.336"S, 48°42'9.252"W, same data and collector as previous; 1 male (PET-EPI-034), same data as previous; 1 female (PET-EPI-037), same data as previous; 1 female (PET-EPI-058), outside Gruta dos Lagos Suspensos cave, 24°33'34.459"S, 48°40'47.251"W, 20 june 2025, same leg. as previous; 1 male, 1 female (PET-EPI-067), same data as previous.

Description

Maximum body length: male 7.2 mm, female 10.25 mm. Color brown (Figure 4B). Cephalon with irregular unpigmented spots; pereonites 1–7 with irregular unpigmented spots on medial portion, epimera more pigmented; pleonites 1–5 and telson with unpigmented spots on medial portion, pleonites 3–5 more pigmented on paramedian and median portions; telson pigmented (Figure 4B). Body convex, outline as in Figures 4B, 5A. Dorsum smooth, covered with sparse long triangular scale-setae (Figure 5B). *Noduli laterales* piliform; d/c and b/c coordinates as in Figure 5C and 5D, respectively. Cephalon (Figure 5E) with lateral lobes not well-developed, frontal line absent, suprantennal line bent downwards in middle; eyes composed of 22 ommatidia arranged in five rows. Pereonites 1–4 with corners rounded and posterior margins straight; pereonites 5–7 more acute and gradually arched (Figures 4B, 5A). Pleon (Figure 4B, 5A) narrower than pereon, epimera of pleonites 3–5 triangular and directed backward. Telson (Figure 5F) triangular with lateral margins slightly concave, and acute apex. Antennula (Figure 5G) of three articles, distal article longest, bearing nine lateral aesthetascs plus apical pair. Antenna (Figure 5H) very long, reaching pereonite 4 when extended backward; flagellum as long as fifth article of peduncle, third flagellar article longer than first and second; apical organ short, bearing two shorts free sensilla. Mandibles with molar penicil of eight branches; left mandible (Figure 5I) with 2 + 1 penicils, right mandible (Figure 5J) with 1 + 1 penicils. Maxillula (Figure 5K) inner endite with two apical penicils, distal margin rounded; outer endite with 4 + 5 teeth, five of them pectinate, one short and simple. Maxilla (Figure 5L) inner lobe rounded, covered with thick setae; outer lobe about two times as wide as inner lobe, with distal margin sinuous. Maxilliped (Figure 5M) palp with two stout setae on proximal article; endite rectangular, medial seta surpassing distal margin, distal margin slightly straight, two hooks on distal margin, rostral surface with longitudinal ridge bearing dense setae. Uropod (Figure 6A) protopod subquadrangular; protopod and exopod outer margins grooved, bearing glandular pores; exopod twice as long as endopod, endopod inserted proximally. Pleopod exopods with Benthana-type respiratory areas. Pereopods rather slender (Figure 6B,C) merus to propodus bearing sparse setae on sternal margin, pereopod 1 carpus with short transverse antennal grooming brush and distal seta hand-like; dactylus with inner claw reaching distal margin of outer claw, dactylar and ungual setae simple, not surpassing outer claw.

Male

Pereopods 1 and 7 without sexual dimorphism (Figure 6B,C). Genital papilla (Figure 6D) bearing triangular ventral shield, papilla slightly longer than ventral shield with two subapical orifices. Pleopod 1 (Figure 6E) exopod elongated with heart-shaped, inner margin with lobe, distal margin slightly acute and with medium indentation, dentiform protrusion convex; endopod longer than exopod, stout and slightly directed outwards and bearing small setae on medial portion. Pleopod 2 (Figure 6F) exopod triangular, outer margin concave bearing three setae; endopod slender distinctly longer than exopod. Pleopod 3 and 4 exopods as in Figure 6G and H, respectively. Pleopod 5 exopod (Figure 6I) triangular, outer margin sinuous bearing 5 setae.

Remarks

The genus *Benthana* comprises 30 species with a distribution restricted to South America, with records in Brazil from Atlantic Forest and Amazon biome, and only *Benthana picta* (Brandt, 1833) in Paraguay (Lemos de Castro, 1958; Andersson, 1960a; Leistikow, 2001; Leistikow & Araujo, 2006; Sokolowicz *et al*., 2008; Campos-Filho & Araujo, 2011; Campos-Filho *et al*., 2013, 2014, 2015b, 2018a, 2019, 2020; Costa *et al*., 2014; Cardoso & Ferreira, 2023).

Benthana **n. sp.** is similar to *B*. *picta*, *B*. *longicornis* Verhoeff, 1941 and *B*. *cairensis* Sokolowicz, Araujo & Boetler, 2008 in the shape of the male pleopod 1 exopod, and it is distinct in the number of ommatidia having 22 (vs. 24 in *B*. *picta*; 22–24 in *B*. *longicornis*; 22–25 in *B*. *cairensis*), antennula with 9+2 aesthetascs (vs. 10+2 in *B*. *picta*; 13+2 in *B*. *longicornis*; 15+2 in *B*. *cairensis*), by the outer margin of the male pleopod 1 exopod lacking setae (vs. six in *B*. *longicornis* and *B*. *cairensis*), and maxillula outer endite with proximal tooth with 5 denticles (vs. 6 in *B*. picta and *B*. *cairensis*; 7 in *B*. *longicornis*).

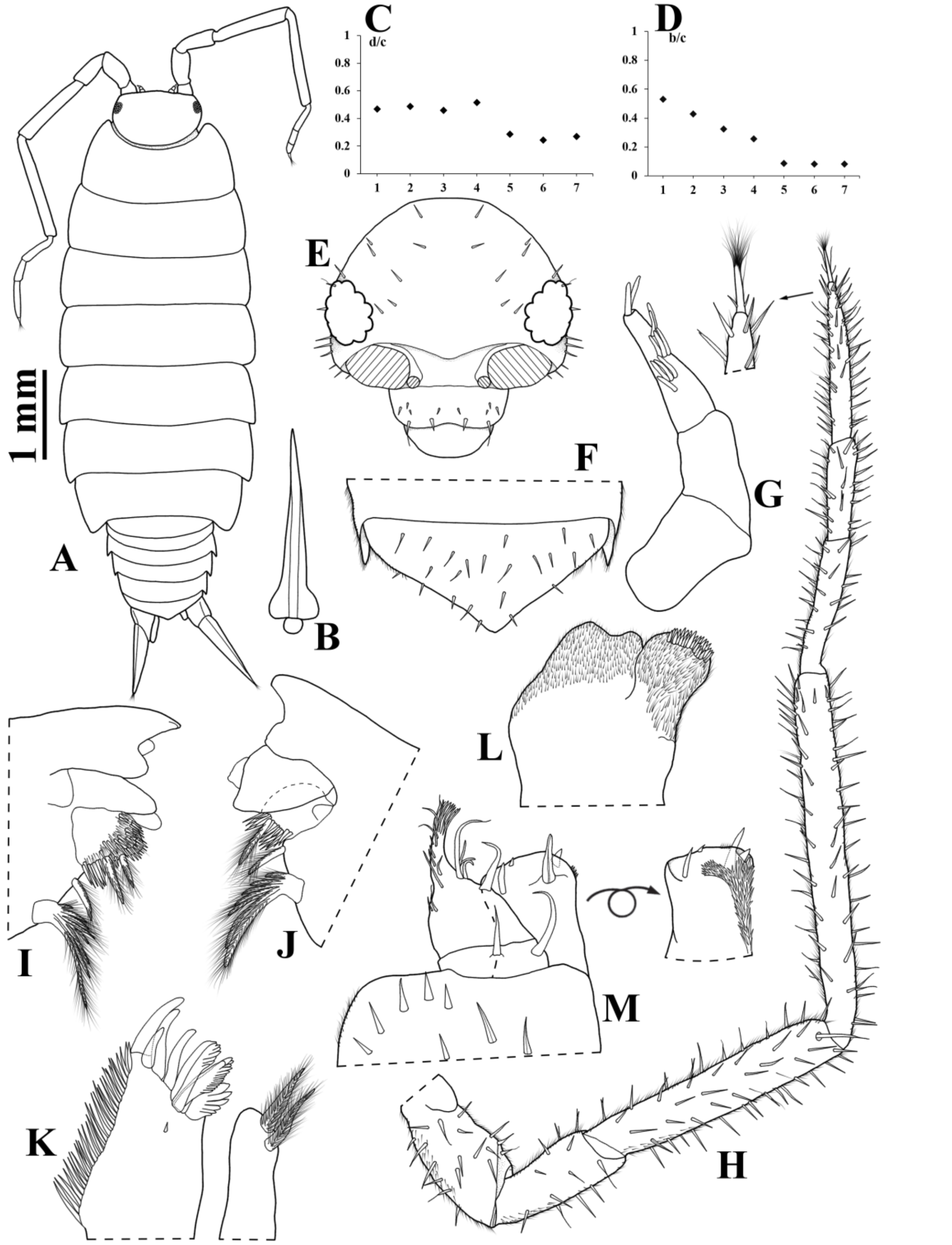


Figure 5. *Benthana* **n. sp.**. A, Habitus, dorsal view; B, Dorsal scale-seta; C, *Noduli laterales* d/c coordinates; D, *Noduli laterales* b/c coordinates; E, Cephalon, frontal view; F, Pleonite 5 and telson; G, Antennula; H, Antenna; I, Left mandible; J, Right mandible; K, Maxillula; L, Maxilla; M, Maxilliped.

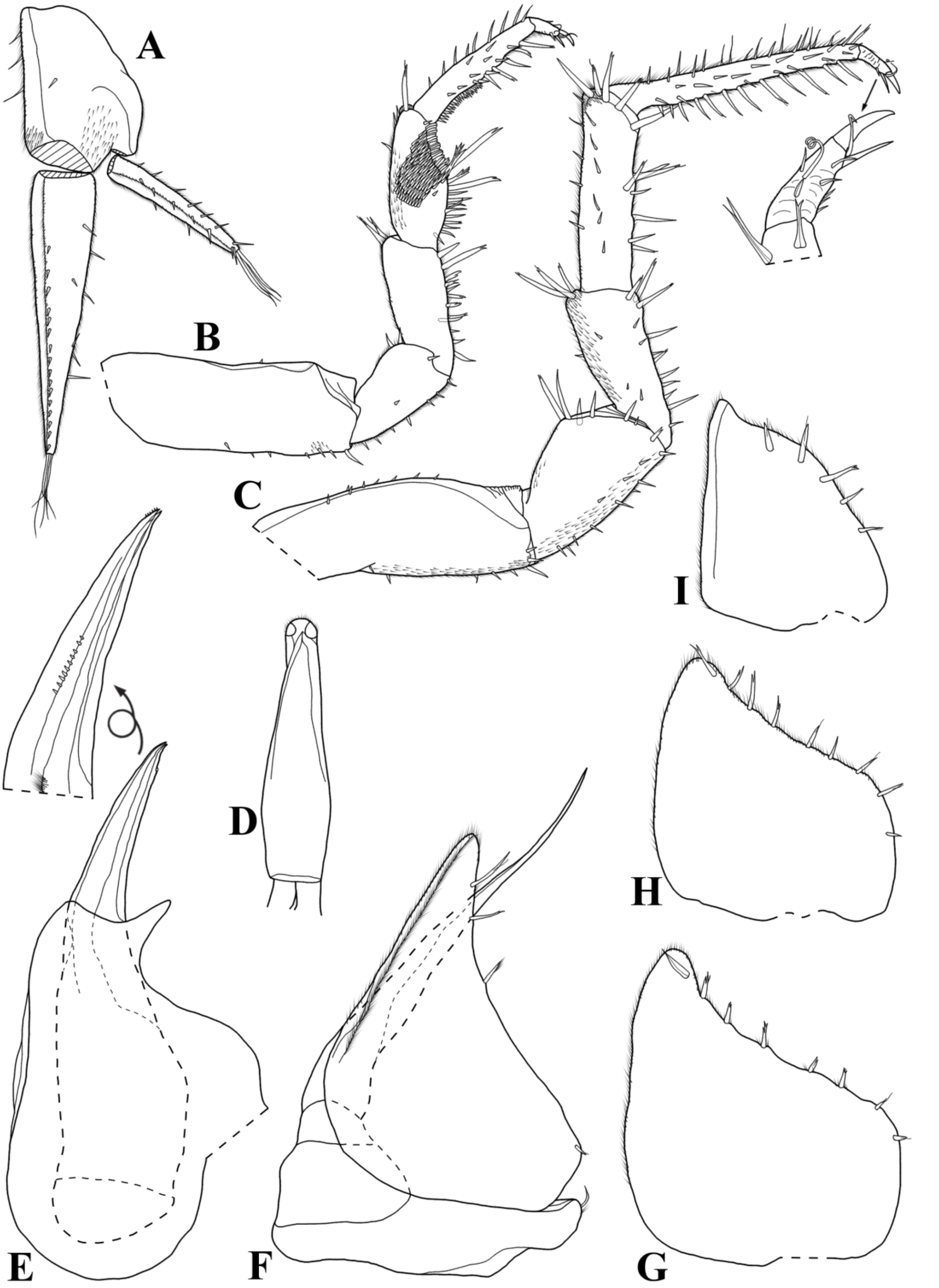


Figure 6. *Benthana* **n. sp.**. A, Uropod; B, Pereopod 1; C, Pereopod 7; D, Genital papilla; E, Pleopod 1; F, Pleopod 2; G, Pleopod 3 exopod; H, Pleopod 4 exopod; I, Pleopod 5 exopod.

The specimens were found living in leaf litter, trunk and dry leaves, outside of caves with high humidity such as the left bank of the river Roncador, and inside the caves, occurs in very humid clay or rocky substrate with organic matter, in the entrance zone. Based on the presence of specimens both hypogean and epigean habitats, and to the absence of troglomorphic characters, the new species is considered to be a troglophile.

Genus ***Metaprosekia*** Leistikow, 2000

Type species: *Metaprosekia nodilinearis* Leistikow, 2000, by original designation and monotypy.

Metaprosekia n. sp.

Figures 1, 4C, 7–8, 9C

Material examined

São Paulo, Iporanga, Parque Estadual Turistico do Alto Ribeira (PETAR): *Holotype* male (PET-EPI-046) (part in micropreparations), outside Lajeado Artificial Mine, 24°34'57.762"S, 48°42'29.202"W, 20 june 2025, leg. M.E. Bichuette, C.M. López-Orozco, R. Borja-Arrieta, J. Barbosa, Y.M. Carpio-Díaz. *Paratypes* 4 males, 6 females (PET-EPI-046), same data as holotype; 1 male, 1 female (PET-EPI-047), same data as holotype; 3 females (PET-EPI-050), same data as holotype; 1 male, 1 female (PET-EPI-056), same data as holotype; 2 males, 8 females (PET-EPI-057), same data as holotype; 3 females (PET-EPI-635), same data as holotype.

Description

Maximum body length: male 2.55 mm, female 3 mm. Color light brown with typical muscle spots insertions, cephalon with irregular pale spots, pleonite 5, telson and uropods less pigmented (Figure 4C, 9C). Body outline as in Figures 4C, 7A. Dorsum covered with sparse pointed scale setae (Figure 7B). *Noduli laterales* piliform (Figure 7C); d/c and b/c coordinates as in Figure 7D and 7E, respectively. Cephalon (Figure 7F) with lateral lobes not well-developed, frontal line absent, suprantennal line slightly sinuous; eyes composed of seven ommatidia. Pereonite 1 epimera with anterior corners slightly directed frontwards; pereonites 1–4 with posterior margins straight, 5–7 gradually arched (Figures 4C, 7A).

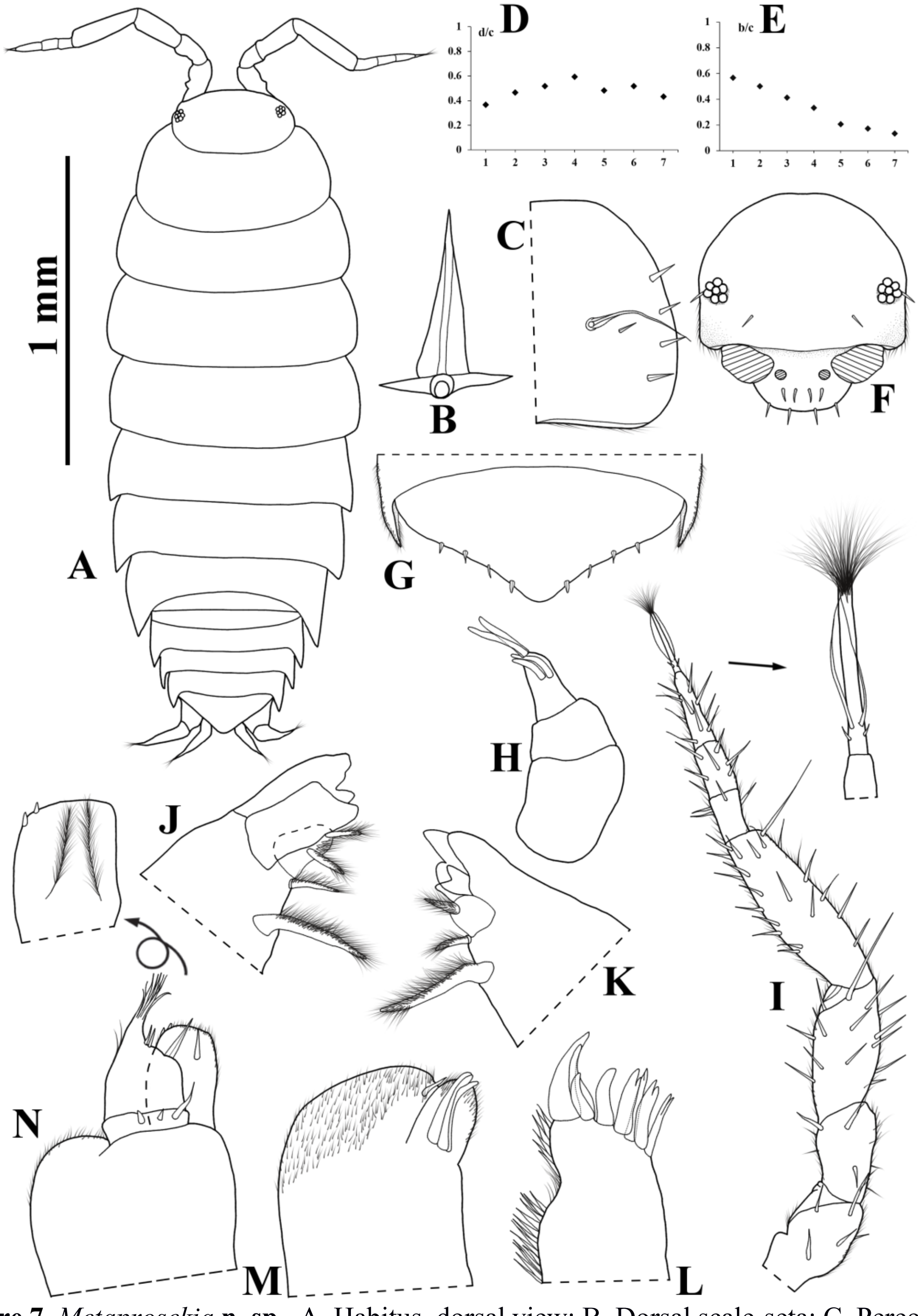


Figure 7. *Metaprosekia* **n. sp.**. A, Habitus, dorsal view; B, Dorsal scale-seta; C, Pereonite 1 epimeron, dorsal view; D, *Noduli laterales* d/c coordinates; E, *Noduli laterales* b/c coordinates; F, Cephalon, frontal view; G, Pleonite 5 and telson; H, Antennula; I, Antenna; J, Left mandible; K, Right mandible; L, Maxillula; M, Maxilla; N, Maxilliped.

Pleon (Figures 4C, 7A) narrower than pereon, epimera of pleonites 3–5 short and directed backward. Telson (Figure 7G) twice as wide as long, triangular with lateral margins slightly concave, and rounded apex. Antennula (Figure 7H) of three articles, distal article longest, bearing two lateral aesthetascs plus apical pair. Antenna (Figure 7I) reaching pereonite 2 when extended backward; flagellum as long as fifth article of peduncle, third flagellar article longer than first and second; apical organ long, bearing two shorts free sensilla.

Mandibles with dense cushion of setae on incisor process, molar process simple; left mandible (Figure 7J) with 2 + 1 penicils, right mandible (Figure 7K) with 1 + 1 penicils. Maxillula (Figure 7L) inner endite with two apical penicils (not illustrated); outer endite with 4 + 4 teeth, inner set with four teeth apically cleft. Maxilla (Figure 7M) inner lobe rounded, covered with thick setae; outer lobe about three times as wide as inner lobe, with distal margin rounded. Maxilliped (Figure 7N) palp with three setae on proximal article; endite subrectangular, medial seta surpassing distal margin, distal margin bearing outer tip, rostral surface with setose sulcus. Uropod (Figure 8A) protopod subquadrangular; protopod and exopod outer margins grooved; exopod twice as long as endopod, endopod inserted proximally. Pereopods 1–7 (Figure 8B,C) merus to propodus bearing sparse setae on sternal margin, pereopod 1 carpus with short transverse antennal grooming brush and distal seta hand-like; dactylus of two claws, inner claw shorter, dactylar and ungual setae simple, ungual seta overpassing outer claw.

Male

Pereopods 1 and 7 without sexual dimorphism (Figure 8B,C). Genital papilla (Figure 8D) bearing triangular ventral shield, papilla slightly longer than ventral shield with two subapical orifices. Pleopod 1 (Figure 8E) exopod rounded, with outer and inner margins convex; endopod more than twice as long as exopod, distal portion tapering, slightly directed outwards and bearing small setae on subapical medial margin. Pleopod 2 (Figure 8F) exopod triangular, outer margin concave bearing one seta; endopod slightly longer than exopod. Pleopod 3 and 4 exopods as in Figure 8G and H, respectively. Pleopod 5 exopod (Figure 8I) rhomboid, outer margin convex, bearing three long setae, inner margin grooved to accommodate pleopod 2 endopod.

Remarks

The genus *Metaprosekia* comprises five species: *M. nodilinearis* Leistikow, 2000 from Venezuela, *M. caupe* Campos-Filho, Araujo & Taiti, 2014, *M. quadriocellata* CamposFilho, Araujo & Taiti, 2014, *M. igatuensis* Campos-Filho, Fernandes & Bichuette, 2020 and *M. utiariti* Campos-Filho, Sfenthourakis & Bichuette, 2023 from Brazil (Leistikow, 2000; Campos-Filho *et al*., 2014, 2020, 2023c). The genus is mainly defined by specimens with small size, dorsal surface covered with fan-shaped or pointed scale-setae, pereonites 1–7 epimera with noduli laterales inserted at same level from lateral margins, cephalon with suprantennal line and eyes of 3–4 ommatidia, antennula with one lateral tuft of aesthetascs plus apical pair, maxillula outer endite with 4+4 teeth (some of them cleft at apex), maxilliped endite with rostral penicil, and pleopod exopods without respiratory structures (see Leistikow, 2000, 2001; Campos-Filho *et al*., 2014, 2020, 2023c).

Metaprosekia **n. sp.** differs from congeneric species in the shape of the male pleopod 1 exopod rounded and pleopod 2 endopod slightly longer than exopod, and by the eye with seven instead of three–four ommatidia. Moreover, it differs in having the mandibles with molar penicil simple (vs. dichotomized in *M. utiariti*, *M. quadriocellata*, *M. caupe* and *M. nodilinearis*), suprantennal line slightly sinuous (vs. suprantennal line bent downwards in the middle in *M. utiariti* and *M. igatuensis*; vs. straight in *M. caupe* and *M. nodilinearis*), antennula with two lateral aesthetascs (vs. three lateral aesthetascs in *M. utiariti*; six in *M. caupe*; five in *M. igatuensis*, *M. nodilinearis*, and *M. quadriocellata*), antenna with apical organ slightly shorter than distal article of flagellum (vs. longer in *M. nodilinearis*; subequal in length in *M. caupe* and *M. quadriocellata*), male pleopod 1 endopod with distal portion tapering, slightly directed outwards (vs. distal portion narrow and not apically bended in *M. utiariti*; tapering and apically bent outwards in *M. caupe*, *M. nodilinearis*, and *M. quadriocellata*), male pleopod 2 endopod slightly longer than exopod (vs. almost three times as long as exopod in *M. utiariti*; twice as long as exopod in *M. caupe*; one and a half times longer than exopod in *M. igatuensis*, *M. nodilinearis* and *M. quadriocellata*), and male pleopod 5 exopod rhomboid with distal portion not elongated and rounded (vs. triangular with distal portion elongated and acute in *M. utiariti*; subtriangular with distal portion not elongated and right-angled in *M. caupe*; subrhomboid with distal portion not elongated and rounded in *M. igatuensis*; subtriangular with distal portion not elongated and rounded in *M. nodilinearis*; triangular with distal portion not elongated and right-angled in *M. quadriocellata*).

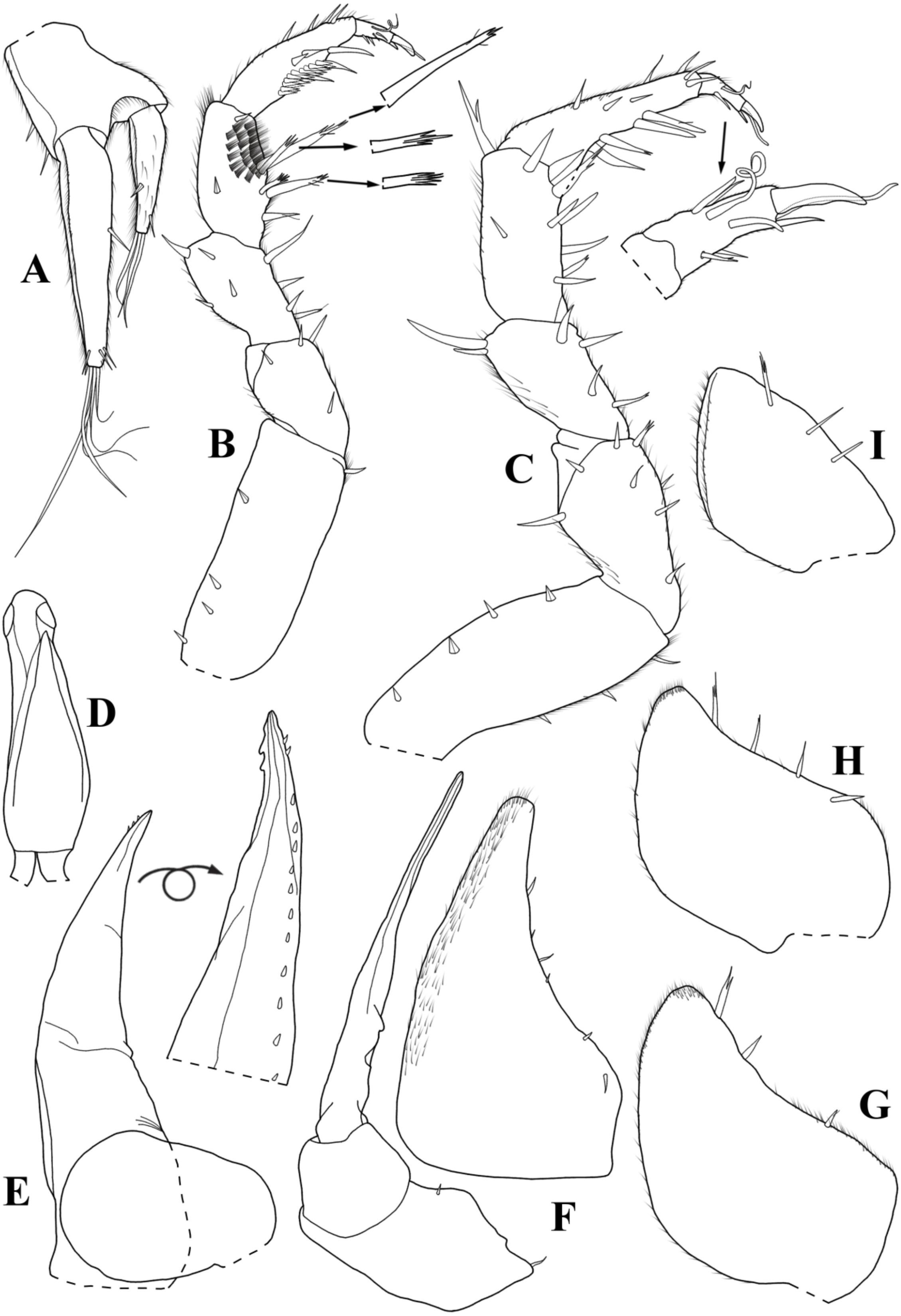


Figure 8. *Metaprosekia* **n. sp.**. A, Uropod; B, Pereopod 1; C, Pereopod 7; D, Genital papilla; E, Pleopod 1; F, Pleopod 2; G, Pleopod 3 exopod; H, Pleopod 4 exopod; I, Pleopod 5 exopod.

The specimens were found living in tree trunks and leaf litter, outside the Lajeado Artificial Mine, in patches of Atlantic Forest. The presence of the new species in this Biome of southeastern Brazil is significant, being the sixth known species of the genus, and the first recorded for this region. Additionally, thorough explorations of this artificial mine are required to verify if the species is present within it.

Family Dubioniscidae Schultz, 1995

Genus ***Novamundoniscus*** Schultz, 1995

Type species: *Phalloniscus vandeli* Lemos de Castro, 1960, by original designation (see Schmidt & Leistikow 2004).

Novamundoniscus n. sp.

Figures 1, 4D, 10–11

Material examined

São Paulo, Iporanga, Parque Estadual Turistico do Alto Ribeira (PETAR): *Holotype* male (WWF_018) (part in micropreparations), Gruta do Alambari de Baixo cave, 24°33'15.001"S, 48°39'55"W, 11 march 2023, leg. M.E. Bichuette, J.E. Galllão, M.V.S.A. Duarte. *Paratypes* 1 male, 1 female (WWF_025), same data as holotype; 2 males, 4 females (LES 4426), Gruta do Morro Preto cave, 24°32'0.499"S, 48°41'57.001"W, 30 september 2012, leg. Disciplina Cavernas; 1 male (PET-0185), same data as previous; 1 female (PET-0383), same data as previous; 1 male (PET-0174), same data as previous; 2 males, 2 females (Disc_PET_292), Ressurgência das Areias de Águas Quentes cave, 24°33'52.801"S, 48°40'26.799"W, 29 november 2024, leg. Disciplina Cavernas PPGERN_2024.

Description

Maximum body length: male 3.9 mm, female 4.9 mm. Color brown with typical muscle spots insertions; cephalon, pereonites 1-7 and pleonites with a median pale area; pleonites epimera and telson strongly pigmented (Figure 4D). Body outline as in Figures 4D, 10A. Pereonite 1 slightly directed frontwards, not surpassing cephalon, pereonites 2-7 gradually more arched and directed backwards (Figures 4D, 10A). Dorsum densely covered with fan-shaped scale setae (Figure 10B). *Noduli laterales* piliform; d/c and b/c coordinates as in Figure 10C and 10D, respectively. Cephalon (Figure 10E) with short lateral lobes and lacking frontal line, suprantennal line slightly sinuous; eyes composed of 14 ommatidia. Pleonites 3-5 epimera well developed, acute and directed backwards (Figures 4D, 10A,F). Telson (Figure 10F) with lateral sides concave, apex slightly acute. Antennula (Figure 10G) with proximal and distal articles subequal in length, distal article bearing about four aesthetascs in two rows plus one apical.

Figure 9. Natural habitat and habitus of species: **A**, *Benthana picta* (Brandt, 1833); **B**, *Atlantoscia. inflata* Campos-Filho & Araujo, 2015; **C**, *Trichorhina tomentosa* (Budde-Lund, 1893) and *Metaprosekia* **n. sp.**.

Antenna (Figure 10H) reaching pereonite 4 when extended backward; flagellum with first and second articles subequal in length, third article reduced and bearing lateral aesthetascs; apical organ bearing two long free sensilla. Mandibles with molar penicil of about five branches; left mandible (Figure 10I) with 2 + 1 penicils, right mandible (Figure 10J) with 1 + 1 penicils. Maxillula (Figure 10K) inner endite with two apical penicils; outer endite with 4 + 4 teeth apically simple, outer margin strongly concave with short setae. Maxilla (Figure 10L) inner lobe rounded, covered with thick setae; outer lobe about three times as wide as inner lobe, with distal margin sinuous. Maxilliped (Figure 10M) palp with two long setae on proximal article; endite subrectangular, medial seta surpassing distal margin, distal margin rounded. Uropod (Figure 11A) protopod subquadrangular; protopod and exopod outer margins grooved; exopod three times longer than endopod, endopod insertion slightly proximal. Pereopods 1–7 (Figure 11B,C) with merus to propodus bearing sparse setae on sternal margin, pereopod 1 carpus with short transverse antennal grooming brush and distal seta hand-like; dactylus of two claws subequal in length, dactylar and ungual setae simple, not surpassing outer claw.

Male

Pereopods 1 and 7 without sexual dimorphism (Figure 11B,C). Genital papilla (Figure 11D) bearing triangular ventral shield, papilla slightly longer than ventral shield with two subapical orifices. Pleopod 1 (Figure 11D) exopod triangular, with inner margin rounded, outer margin concave; endopod more than twice as long as exopod, distal portion tapering, almost straight and bearing small setae on subapical medial margin. Pleopod 2 (Figure 11E) exopod triangular, outer margin concave bearing short one seta; endopod distinctly longer than exopod. Pleopod 3 and 4 exopods as in Figure 11F and G, respectively. Pleopod 5 exopod (Figure 11H) triangular, outer margin convex, bearing three short setae.

Remarks

The genus *Novamundoniscus* comprise 12 species: *N. vandeli* (Lemos de Castro, 1960), *N. dissimilis* (Lemos de Castro, 1960), *N. macrophthalmus* (Lemos de Castro 1960), *N. singularis* (Lemos de Castro, 1967), *N. gracilis* Lopes & Araujo, 2003, *N. altamiraensis* Campos-Filho, Araujo & Taiti, 2014, *N. adhara* Campos-Filho & Cardoso, 2018, *N. canopus* Campos-Filho, Gallo & Gallão, 2023, *N. kayabi* Campos-Filho, Sfenthourakis & Araujo, 2023, and *N. mandacaru* Campos-Filho, Araujo & Bichuette, 2023 from Brazil, and *N. marcuzzii* (Vandel, 1952) and *N. persimilis* (Vandel, 1952) from Venezuela (Vandel, 1952; Lemos de Castro, 1960, 1967; Lopes & Araujo, 2003; Campos-Filho *et al*. 2014, 2018b, 2023b;).

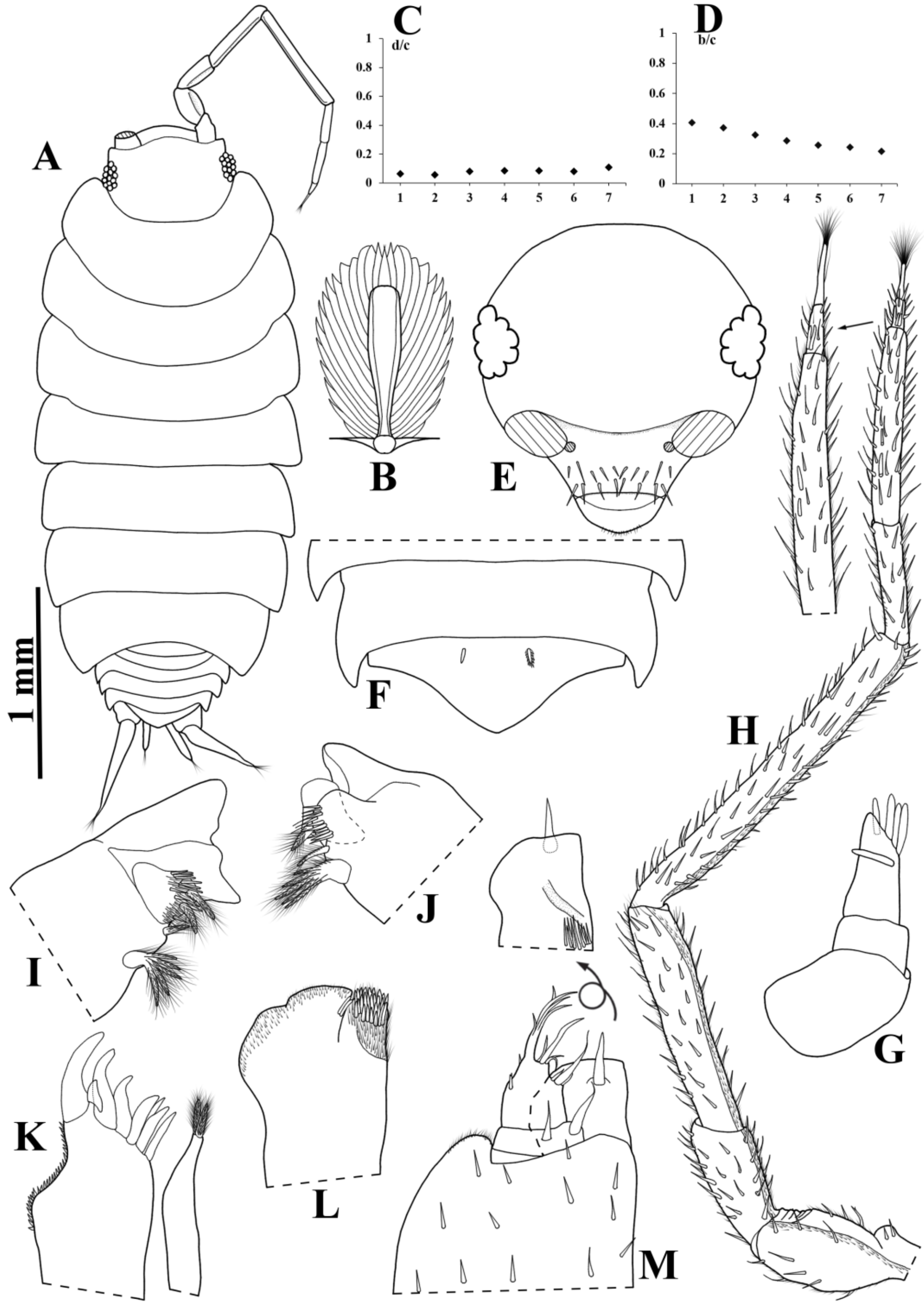


Figure 10. *Novamundoniscus* **n. sp.**. A, Habitus, dorsal view; B, Dorsal scale-seta; C, *Noduli laterales* d/c coordinates; D, *Noduli laterales* b/c coordinates; E, Cephalon, frontal view; F,

Pleonite 5 and telson; G, Antennula; H, Antenna; I, Left mandible; J, Right mandible; K, Maxillula; L, Maxilla; M, Maxilliped.

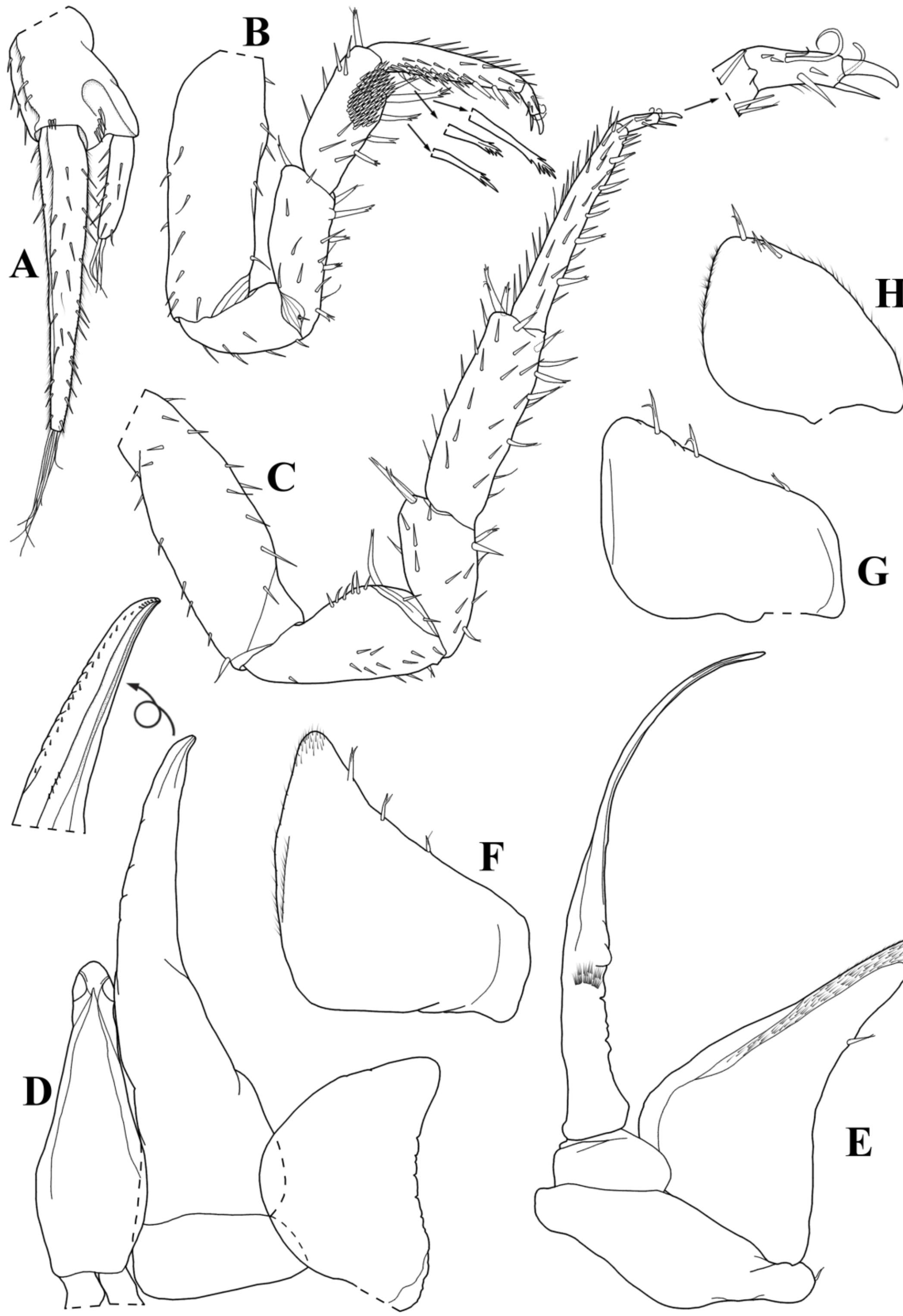


Figure 11. *Novamundoniscus* **n. sp.**. A, Uropod; B, Pereopod 1; C, Pereopod 7; D, Genital papilla and Pleopod 1; E, Pleopod 2; F, Pleopod 3 exopod; G, Pleopod 4 exopod; H, Pleopod 5 exopod.

Novamundoniscus n. sp. differs from congeneric Brazilian species in the shape of the male pleopod 1 exopod triangular, cephalon with short lateral lobes, in having the antennal flagellum with third article reduced and by the eye with 14 ommatidia. Moreover, it differs in having mandibles with molar penicil of about five branches (vs. seven in *N. adhara*; five-seven in *N. altamiraensis*; ten in *N. canopus*; 11 in *N. kayabi*), maxillula outer endite with four teeth apically simple (vs. four cleft in *N. adhara*, *N. canopus*, *N. macrophthalmus*, *N. altamiraensis*, *N. vandeli*; two cleft in *N. mandacaru*), uropod exopod three times longer than endopod (vs. twice in *N. adhara*, *N. mandacaru*, *N. canopus*, *N. altamiraensis*; similar in length in *N. kayabi*).

The specimens were found living inside the caves, occurs in artificial rocky substrate with organic matter, in the entrance zone. The new species is considered to be a troglophile due to the absence of troglomorphic characters. This is the first record of the family Dubioniscidae from the Alto Ribeira karst region, southeast Brazil.

Family Platyarthridae Verhoeff, 1949

Genus ***Trichorhina*** Budde-Lund, 1908

Type species: *Bathytropa thermophila* Dollfus, 1896 [= *Trichorhina tomentosa* (Budde-Lund, 1893)] by original designation (see Schmidt & Leistikow 2004)

Trichorhina tomentosa (Budde-Lund, 1893)

Figures 1, 4E, 9C

Alloniscus tomentosa – Budde-Lund (1893): 126.

Trichorhina tomentosa Campos-Filho *et al*., 2018a: 23 (for full Brazilian references); Fernandes *et al*. 2019: 1115, table 1; Campos-Filho *et al*. 2023a: 7, fig. 1.

Material examined

São Paulo, Iporanga, Parque Estadual Turistico do Alto Ribeira (PETAR): 9 females (LES 1772), Gruta do Alambari de Baixo cave, 24°33'15.001"S, 48°39'55"W, 16-20 september 2009, leg. F. Pellegatti-Franco; 2 females (WWF-009), same locality as previous, 11 march 2023, leg. M.E. Bichuette, J.E. Gallão, M.V.S.A. Duarte; 3 females (WWF_017), same data as previous; 2 females, 1 juvenile (WWF_024), same data as previous; 7 females (WWF_028), same data as previous; 2 females, 1 juvenile (WWF_035), same data as previous; 9 females (WWF_040), same data as previous; 10 females (WWF_044), same data as previous; 2 females, 1 juvenile (WWF_056), same data as previous; 2 females (WWF_061), same data as previous; 2 females, 3 juveniles (WWF_075), same data as previous; 1 females (WWF_080), same data as previous; 1 female (LES 4421), Ressurgência das Areias de Águas Quentes cave, 24°33'52.801"S, 48°40'26.799"W, 29 september 2012, leg. Disciplina; 1 female (LES 24807), same locality as previous, 21 november 2017, leg. M.E. Bichuette, T. Zepon, J.E. Gallão, J.S. Gallo; 2 females (LES 24808), same data as previous; 4 females, 5 juveniles (LES 24809), same data as previous; 1 female (LES 24814), same locality as previous, 10 april 2018, leg. T. Zepon, C.M. Borges, G.F. Damasceno; 1 female (LES 24818), same locality as previous, 31 july 2018, leg. T. Zepon, C.S. Fernandes, B.G.O do Monte; 2 females, 1 juvenile (WWF_187), same locality as previous, 13 march 2023, leg. M.E. Bichuette, J.E. Gallão, M.V.S.A. Duarte; 2 females (WWF_193), same data as previous; 1 female (WWF_211), same data as previous; 12 females (WWF_335), same data as previous; 4 females, 1 juvenile (Disc_PET_092), same locality as previous, 29 november 2024, Disciplina PPGERN_2024; 1 female (Disc_PET_159), same data as previous; 12 females (Disc_PET_180), same data as previous; 2 females (Disc_PET_267), same data as previous; 17 females (Disc_PET_294), same data as previous; 21 females (Disc_PET_314), same data as previous; 1 female (Disc_PET_344); 1 female (PET-EPI-044), outside Lajeado Artificial Mine, 24°34'57.762"S, 48°42'29.202"W, 20 june 2025, M.E. Bichuette, C.M. López-Orozco, R. Borja-Arrieta, J. Barbosa, Y.M. Carpio-Díaz; 2 females (PET-EPI-053), same data as previous.

Remarks

The specimens were found living leaf litter, trunk and dry leaves outside of caves, and inside the caves, occurs in several microhabitats such as very humid clay, guano, unconsolidated substrates or rocky substrate with organic matter, from the entrance to the aphotic zone of the cave.

Distribution

Pantropical species (Schmalfuss, 2003). In Brazil, it has been recorded in the states of Minas Gerais, São Paulo, and Rio Grande do Sul (Zimmermann *et al*., 2015, 2018a). In caves, it has been recorded from states of São Paulo, Minas Gerais, Goiás and Mato Grosso (Fernandes *et al*., 2019; Campos-Filho *et al*., 2023a). The present work expands the knowledge of its distribution from Alto Ribeira karts area, southeast Brazil.

Family Bathytropidae Vandel, 1952

Genus ***Neotroponiscus*** Arcangeli, 1936

Type species: *Neotroponiscus carolii* Arcangeli, 1936, by monotypy.

Neotroponiscus carolii Arcangeli, 1936

Figures 1, 4F

Neotroponiscus carolii Arcangeli, 1936: 15, figs. 1–4.

Neotroponiscus carolii Campos-Filho *et al*., 2018a: 25 (for full Brazilian references).

Material examined

São Paulo, Guapiara, Parque Estadual Intervales (PEI): 1 male (ARA-001), Gruta Aracaeiro II cave, 24°16'14.045"S, 48°25'13.252"W, 10 june 2023, leg. J.S. Gallo, C.M. López-Orozco, L.F. Dos Santos, B.D. Lenhare, E.C. Igual, I.A. Ribeiro; 1 female (ARA-010), same data as previous; 1 female (POR-053), Gruta Mamica da Porca cave, 24°16'54.001"S, 48°33'34.999"W, same data as previous. Iporanga, PEI: 1 male (FOG-031), Gruta do Fogo cave, 24°16'0.48"S, 48°25'49.439"W, 27 october 2023, leg. J.S. Gallo, M.V.S.A. Duarte, E.L. Silva, M.F.C. Zancheta, A. Jackson; 2 males, 2 females (ROD-008), Gruta dos Rodriguez cave, 24°16'32.412"S, 48°26'48.184"W, 08 april 2023, leg. J.E. Gallão, J.S. Gallo, I. Ribeiro, E.C. Igual.

Remarks

The specimens were found inside the caves living dry organic matter such as guano and plants, occurs also in unconsolidated substrates or rocky substrate, between the entrance and twilight zone of the cave.

Distribution

Endemic to Brazil, with records from states of Bahia, Espírito Santo and São Paulo (Lemos de Castro, 1970; Lenko, 1971; Lisboa *et al*., 2013; Campos-Filho *et al*., 2018a). This is the first record of this species in caves.

Family Armadillidae Brandt, 1831

Genus ***Pseudodiploexochus*** Lewis, 1998

Type species: *Diploexochus tabularis* Barnard, 1932 (= *Pseudodiploexochus tabularis* (Barnard, 1932) by original designation).

Pseudodiploexochus gibbus (Lemos de Castro, 1972)

Figures 1, 4G

Reductoniscus gibbus – Lemos de Castro (1972b): 347, figs 1–5.

Pseudodiploexochus gibbus Campos-Filho *et al*., 2018a: 25 (for full Brazilian references).

Material examined

São Paulo, Iporanga, Parque Estadual Intervales (PEI): 5 females (COL 98_16), Gruta Colorida cave, 24°16'55.601"S, 48°25'11.1"W, 1998.

Remarks

The specimens were found inside the caves living dry organic matter such as guano and plants, occurs also in unconsolidated substrates or rocky substrate, between the entrance and twilight zone of the cave. The presence of this species in this karst system suggests resources and favorable micro-habitat conditions associated with low humidity (Fernandes *et al*., 2016, 2019).

Distribution

Endemic to Brazil, with records from state of São Paulo (Lemos de Castro, 1972; Campos-Filho *et al*., 2018a). This is the first record of this species in caves, being considered a troglophilic species. Furthermore, it is the first record of the family Armadillidae from the Alto Ribeira karst region, southeast Brazil and being the southernmost record of the family from Brazil.

5. Discussion

The current knowledge of terrestrial isopods from subterranean habitats in Brazil has increased considerably in recent years, with more than 110 species recorded. Among Brazilian cave system, the Sistema Areias in the Ribeira valley, Atlantic Forest, southeast São Paulo, stands out as one of the richest in troglobitic species with more than 60 obligate cave fauna and is recognized as a global hotspot of subterranean biodiversity (Trajano, 2000; Trajano *et al*., 2016; Bichuette & Trajano, 2018; Gallão & Bichuette, 2018).

The present work increases the known biodiversity of Oniscidea in epigean and hypogean habitats of the Alto Ribeira karst area, in the Atlantic Forest of southeastern Brazil, from 13 to 21 species, and surpass 118 species documented in Brazilian caves. Additionally, we recorded, for the first time, the family Dubioniscidae and Armadillidae in this karstic system. These results suggest that these karst areas harbor a higher potential for terrestrial isopods of another families and species with high ecological plasticity and generalist strategies for occupying microhabitats in epigean and hypogean environments, and therefore the subterranean faunal inventories may be underestimated.

The species *S. spinosus* (an exotic species) has been considered a bioindicator of anthropogenic disturbances in the Atlantic Forest, as it may benefit from the mosaic of vegetation create by such impacts (Magrini *et al*., 2011). The presence of this species in highly sensitive habitats such as caves and their surroundings can generate negative impacts (Nicolosi *et al*., 2023). It is found distributed in several caves in the Ribeira Valley region, and may co-occur with troglobitic species such as vertebrates as the blind catfish, invertebrates such as terrestrial isopods of the genus *Benthana*, amphipods of the genus *Hyallela* Smith, 1874 and crabs of the genus *Aegla* Leach, 1820, among other invertebrates such as arachnids and myriapods (Trajano *et al*., 2016; Bichuette & Trajano, 2018; Gallão & Bichuette, 2018).

Although most of the recorded species are found within conservation areas, this biome remains seriously threatened by habitat loss and fragmentation, groundwater pollution, and biological invasions. Many of these caves serve as ecotourism destinations, providing sustainable livelihoods for local communities while supporting conservation initiatives (Lobo, 2008). However, uncontrolled tourism can lead to the transformation of these ecosystems and favor the establishment of exotic species adapted to environmental disturbances and ecosystem changes, potentially competing with native species and leading to environmental imbalance.

Therefore, taxonomic studies that reflect the existing native biodiversity in subterranean systems, particularly in vulnerable biomes such as the karst areas of the Atlantic Forest, are necessary for conservation planning.

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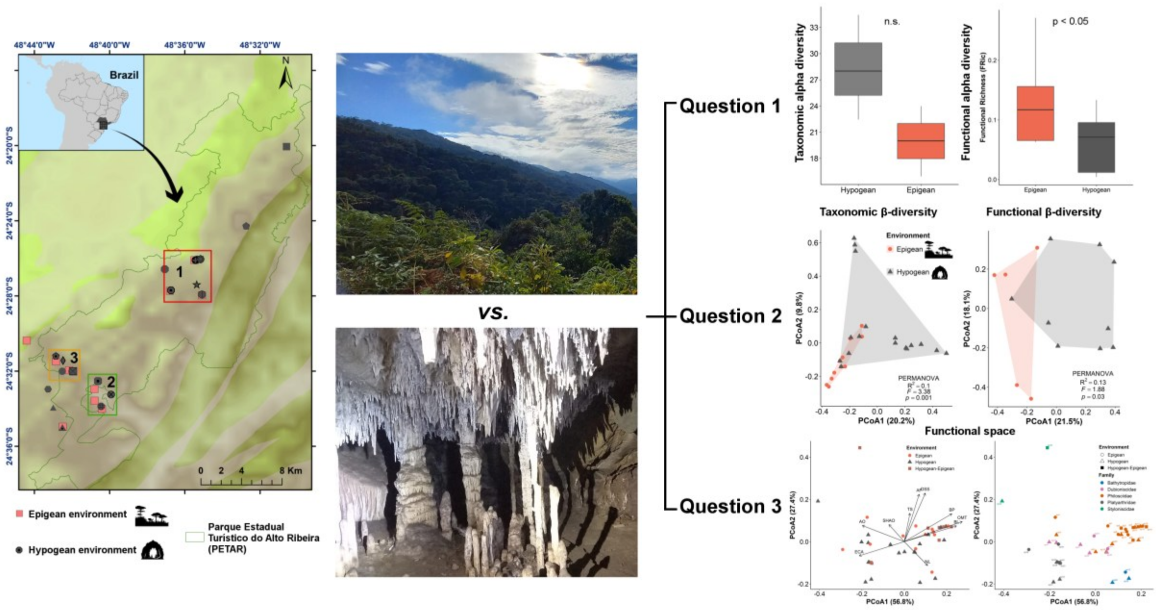
CAPÍTULO 3: Contrasting taxonomic and functional diversity of terrestrial isopods (Oniscidea) in epigean and hypogean Atlantic Forest habitats



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Contrasting taxonomic and functional diversity of terrestrial isopods (Oniscidea) in epigean and hypogean Atlantic Forest habitats

1. Abstract

Subterranean environments are considered strong ecological filters that select for specific traits, resulting in functionally distinct communities from those in surface environments. To investigate how the taxonomic and functional diversity of terrestrial isopods is structured in epigean and hypogean habitats, we studied assemblages in karst landscapes of the Atlantic Forest, southeastern Brazil. We tested the hypotheses that hypogean communities would exhibit lower functional and taxonomic diversity and be dominated by specialist species. A total of 22 hypogean and ten epigean habitats were sampled in the Parque Estadual Turístico do Alto Ribeira. We recorded 40 species/morphospecies belonging to five families across all sites, with distinct taxonomic composition in the different environments. While taxonomic alpha diversity did not differ significantly between habitats, functional richness was higher in epigean communities. Beta diversity was high across both taxonomic and functional dimensions, driven primarily by turnover, indicating marked differentiation in assemblage structure in each habitat. Principal Coordinate Analysis revealed partial segregation of assemblages in functional space and clustering of traits by family, highlighting the role of evolutionary history in shaping functional composition. Species in epigean habitats exhibited greater trait variability compared to hypogean habitats, which showed traits associated with cave specialization. These findings suggest that functional traits are strongly structured by habitat type and that epigean and hypogean assemblages represent distinct functional entities. Our results highlight the importance of integrating different perspectives on diversity to understand community assemblage and support conservation strategies that preserve epigean and hypogean biodiversity in threatened karst systems.

Keywords: Beta diversity, Biodiversity patters, Cave ecosystem, Community assembly, Oniscideans traits.

2. Introduction

Functional diversity refers to the range of strategies organisms employ to utilize resources and engage with their environment (Garnier *et al*., 2015). Unlike taxonomic diversity, which focuses on species richness and identity, functional diversity emphasizes on trait-based that reflect the life strategies of species and their roles in the ecosystem (Violle *et al*., 2007; Moore, 2013). These traits include morphological, ecological, physiological or behavioral attributes related to habitat use and life history, and reflect the qualities whose variation impacts individual success (Violle *et al*., 2007; Song *et al*., 2014; Arnan *et al*., 2016). In recent decades, the study of functional diversity has increased, as it provides information into species responses to environmental variation and their contribution to ecosystem processes (Fernandes *et al*., 2016; de Bello *et al*., 2021). Taxonomic diversity is commonly used in biodiversity assessments and combining it with functional diversity offers a broader perspective on biodiversity patterns across various dimensions (Chao *et al*., 2021). This integration allows for the evaluation of morphological traits that define habitat preferences, physiological aspects that enhance survival under specific environmental conditions, and efficiencies in resource processing (Moore, 2013), helping the development and the implementation of conservation strategies.

Examining taxonomic and functional diversity in subterranean environments (hypogean), such as caves, can help inform understanding of ecological and evolutionary processes, and contribute to a more comprehensive perspective on community responses in these habitats (Gibert & Deharveng, 2002). Subterranean systems act as environmental filters, selecting for organisms capable of tolerating conditions such as permanent darkness, low nutrient availability and reduced temperature variation. At the same time, they may offer ecological opportunities, including lower predation pressure and access to niche space that is absent in epigean habitats. Due to this combination of constraints and opportunities, caves serve as useful natural laboratories for examining biodiversity responses to environmental pressures, including those related to climate change (Gibert & Deharveng, 2002; Mammola *et al*., 2018), particularly when compared with superficial environments (epigean). In this context, terrestrial isopods (Isopoda, Oniscidea) are particularly valuable as model organisms, being of the numerous and frequent invertebrate fauna in subterranean habitats, which play an essential role in soil carbon cycling (Trajano & Bichuette, 2006; Fišer *et al*., 2012;

Deharveng & Bedos, 2018). These organisms contribute significantly to the transformation and redistribution of soil organic matter (Quadros & Araujo, 2007; Ellers *et al*., 2018), and are sensitive bioindicators of environmental and anthropogenic disturbances (Paoletti & Hassall, 1999; De Smedt *et al*., 2022), responding strongly to variations in soil moisture and temperature that influence their growth, reproduction and distribution (Hassall *et al*., 2018).

Functional diversity can be measured by classifying species into functional groups based on shared ecological traits (Cleland, 2011; Moore, 2013; Garnier *et al*., 2015). Terrestrial isopods are particularly interesting for exploring the relationship between body weight, habit, water loss rate, and sensory adaptations, which are closely linked to survival in distinct environments (Broly *et al*., 2015; Ooms *et al*., 2020). For instance, antennae-mediated chemoreception plays a key role in food detection in subterranean habitats, highlighting behavioral adaptations to resource-limited systems (Ooms *et al*., 2020). Assessing these functional traits improves our understanding of community assembly rules and ecosystem functioning, supporting their frequent use in functional ecology studies (Fernandes *et al*., 2016; Deharveng & Bedos, 2018). Fernandes *et al*. (2016) evaluated the functional diversity of epigean-hypogean communities of terrestrial isopods, based on behavioral, physiological, and morphological traits, finding greater value in subterranean habitats compared to epigean ones from karst areas of the Bambuí geomorphological group, within the Cerrado and Caatinga domains. Furthermore, they suggested that caves acting as ecological filters, maintain favorable environmental and predation conditions for the diversification of these organisms, which reinforces the need for their protection. Such studies help clarify the ecological roles of terrestrial isopods in nutrient cycling and microbial metabolism, processes that accelerate organic matter decomposition in these unique environments (Gibert & Deharveng, 2002), and can be useful in explaining the geographic distribution and microhabitat use of species under future climate change scenarios (Antoł *et al*., 2021).

These patterns are particularly relevant in strategic ecosystems, such as the Atlantic Forest in southeastern Brazil, which harbors a high diversity of cave systems and unique subterranean biota (Fundação & Brasil, 2010; Fundação Florestal, 2018; Santos & Brilha, 2024). Although it is an important component of the protected areas of Brazil, this biome remains critically threatened by habitat loss and fragmentation (Myers *et al*., 2000; Fundação Florestal, 2018; Silva *et al*., 2024). Subterranean system in the Atlantic Forest, including limestone caves, are notable for supporting many troglobitic species with restricted distributions (Trajano, 2000; Silva *et al*., 2011; Trajano *et al*., 2016). Assessing taxonomic and functional diversity across epigean and hypogean in this context provides insights into community assembly processes and has direct implications for biodiversity conservation (Mammola *et al*., 2018).

The purpose of this study was to evaluate the taxonomic and functional diversity of terrestrial isopods in subterranean environments of the Atlantic Forest of southeastern Brazil. We addressed the three following questions: (1) Are there differences in the taxonomic and functional alpha diversity of terrestrial isopods between epigean and hypogean environments in Atlantic Forest areas? We hypothesized that both taxonomic and functional diversity differ between habitats, with epigean assemblages exhibiting higher diversity, whereas hypogean assemblages show reduced diversity due to strong environmental filtering typical of subterranean systems (Gibert & Deharveng, 2002; Mammola *et al*., 2019a, 2019b); (2) Is there taxonomic and functional dissimilarity between epigean and hypogean assemblages in Atlantic Forest areas, and which process (turnover or nestedness) modulates this dissimilarity? Given the contrasting environmental conditions and the filtering associated with subterranean habitats, we expect high dissimilarity between assemblages, driven mainly by species or trait turnover rather than nestedness, reflecting adaptive differentiation between these environments (Fichaux *et al*., 2019; Mammola *et al*., 2019c, 2024); (3) How are terrestrial isopod assemblages structured in functional space, and which functional traits explain the separation between epigean and hypogean habitats in Atlantic Forest areas? We expect distinct regions of functional space for each habitat type. Epigean assemblages should exhibit broader trait variability associated with surface conditions (e.g., wider ranges of body size, pigmentation, eye development, and mobility-related traits). In contrast, hypogean assemblages are expected to possess traits shaped by environmental filtering in caves (reduced or absent eyes, loss of pigmentation and elongated appendages) (Fernandes *et al*., 2016; Mammola *et al*., 2024). These shifts in trait composition are expected to drive functional turnover between habitats, independently of differences in alpha diversity.

3. Material and methods

Study area

The Parque Estadual Turístico do Alto Ribeira (acronym in Portuguese PETAR) is located in southern São Paulo state, Brazil (Figure 1), between the municipalities of Apiaí and Iporanga, with approximately 35,772.5 ha (Fundação Florestal, 2018). The predominant vegetation is dense ombrophilous forest, on karst soil, considered one of the most important remnants of preserved Atlantic Forest in Brazil, protected by law and under Conservation Units (SEMA, 1997; Fundação Florestal & Brasil, 2010; Fundação Florestal, 2018). It is also a global biodiversity hotspot, noted for its rich flora, fauna, high endemism, and considerable threat status (Myers *et al*., 2000; Gallão & Bichuette, 2018).

The Park is characterized by its mountainous landscape, with altitudes ranging from 80 to 1,146 m, with rounded formations on granite and intrusive phyllites, and more dissected formations in the limestone areas (Fundação Florestal & Brasil, 2010; Silva *et al*., 2024). The presence of porous limestone rocks, highly susceptible to dissolution by water and acids, has resulted in more than 400 caves within the Conservation Unit of Integral Protection (SEMA, 1997; Silva *et al*., 2024; CECAV, 2025). Many caves serve as ecotourism destinations that provide sustainable livelihoods for local communities while supporting conservation initiatives (Lobo, 2008). These karst systems belong to the Açungui Group, dating from the Proterozoic period (Auler *et al*., 2019). This region has a subtropical humid climate, characterized by high temperatures in summer and consistent rainfall throughout the year, classified as Cfa according to the Köppen-Geiger climate classification. In higher altitudes, areas near the Park may exhibit Cfb characteristics, defined as a humid temperate climate with mild summers (Alvares *et al*., 2013).

Sampling methods and taxonomic identification

The specimens collected correspond to 22 caves and their surrounding surface habitats under the limits of the PETAR and its buffer zone (Figure 1), from several expeditions (2008-2025) by the Laboratório de Estudos Subterrâneos (LES), Universidade Federal de São Carlos, São Paulo, Brazil. For hypogean habitats (inside each cave), direct intuitive searches (DIS) were used in some types of microhabitats (e.g., cave floor, wall, rock blocks, guano, plant organic matter, etc.), across entrance, twilight, and aphotic zones (Bichuette *et al*., 2015; Wynne *et al*., 2019). For epigean habitats (outside the cave, in the forest), Winkler litter extraction was applied to 1 m² plots, and DIS were used, during four hours per observer (three observer) in the accessible microhabitats (fallen logs, soil, leaf litter, bark, rocks, etc.) for each site, resulting in 60 hours of searching (Karasawa, 2022; López-Orozco *et al*., 2024). Specimens were collected using fine brushes or manually.

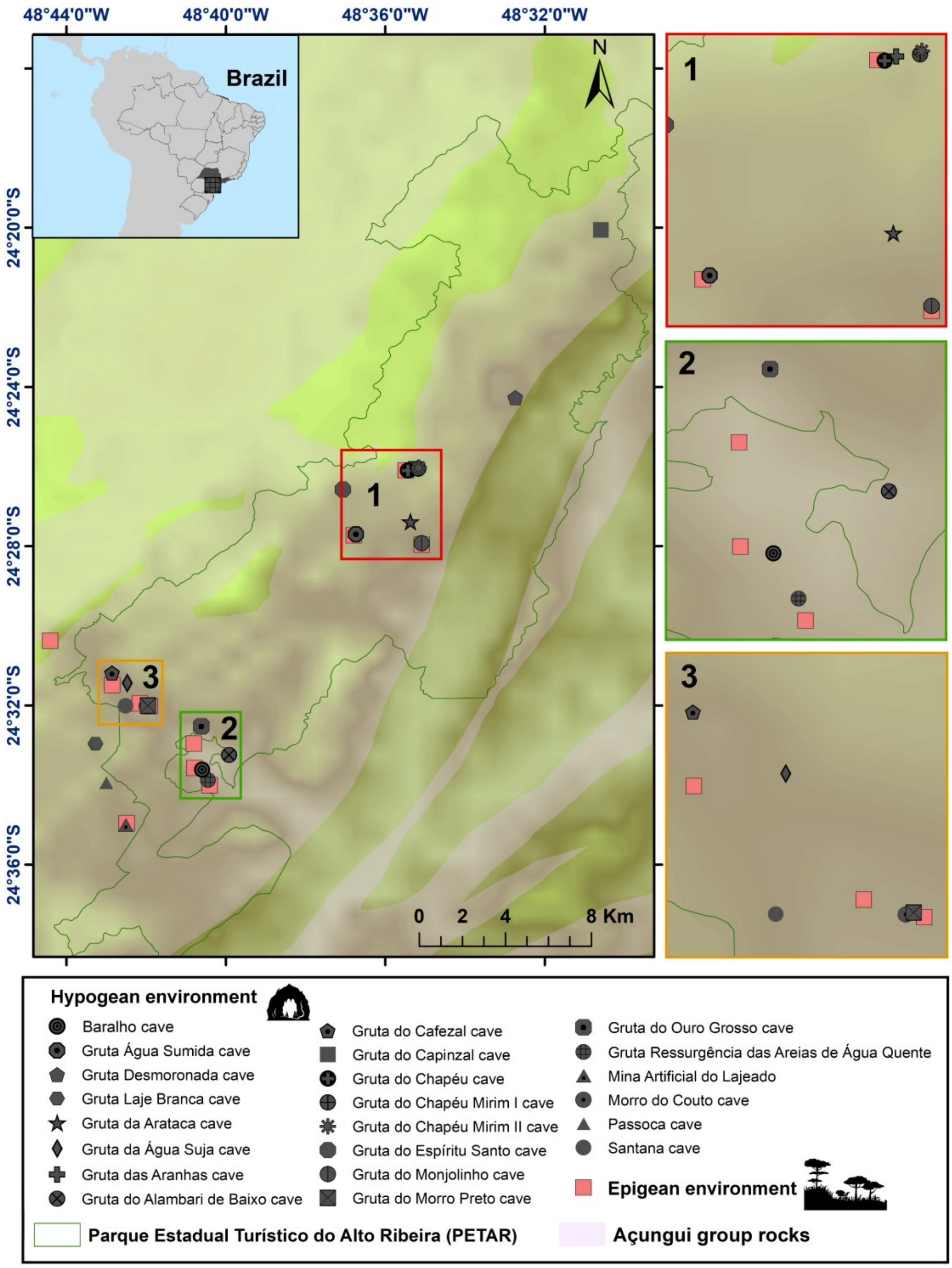

Figure 1. Map of the study area showing the spatial distribution of sampling sites in epigean (pink squares) and hypogean (gray symbols) environments within the Parque Estadual Turístico do Alto Ribeira (PETAR), southeastern Brazil. Insets (1, 2 and 3) provide detailed views of cave clusters and epigean sites across three sectors of the Park.

All specimens were preserved in 70% ethanol and deposited in the LES collection (curator: Maria Elina Bichuette). Identifications were based on morphological characters examined through permanent slide mounts in Hoyer's medium (Anderson, 1954). Species identification was confirmed by comparison with type specimens deposited in the LES and MZUSP collections, and supported by taxonomic keys (Campos-Filho *et al*., 2015, 2017, 2020, 2023; Cardoso *et al*., 2017).

Oniscideans functional traits

Due to limited information on functional traits in terrestrial isopods, we measured a set of morphological attributes with potential ecological relevance, reflecting species' interactions with environmental conditions in epigean and hypogean environments. Further details on the traits measured are available in the supplementary information (Supplementary material 1). These measurements were taken using an ocular micrometer mounted on an Olympus binocular stereomicroscope, with magnifications ranging from 0.67× to 4.0×. In addition, we incorporated traits related to the ecological roles, morphology and ecomorphology of each species (Schmalfuss, 1984; Fernandes *et al*., 2016; Ellers *et al*., 2018). Table 1 presents the 19 selected traits, including details about their variable type and functional relevance to the study.

Table 1. The list of terrestrial isopods traits and their functional importance. SHO: short; LON: long; FRE: free; INV: involved; SIM: simple; ROB: robust; ABS: absent, PRE: present; FS: fan-shaped; PF: piliform; TS: tricorn-shaped; LS: lanceolate-shaped; RED: reduced; CRE: creeper; RUN: runner; CLI: clinger; CLA: clay soil; ART: artificial substrate; FAL: fallen leaves; GUA: guano; ORG: organic plant matter; ROC: rocks; LL: leaf litter; SOI: soil; LOG: logs.

Traits	Abbreviations	Type	Unit	Functional importance
Body length	BL	Continuous	mm	Attribute that affects physiology, ecology, evolution and life history, such as resource utilization increasing with body size, or a larger body size could contribute significantly to reduce water loss rate (Antoł *et al*., 2021).

Traits	Abbreviations	Type	Unit	Functional importance
Cephalothorax width	CW	Continuous	mm	Character related to larger mandibular muscles that may allow greater capture of food resources (Zimmer, 2002).
Antenna length	AL	Continuous	mm	Help to orientation, and function as gustatory organs in food localization by using their aestetascs, or contact chemoreception, providing information on their adaptive response in environments (Schmalfuss, 1998; Hornung, 2011; Ooms *et al*., 2020).
Number of articles of antennal flagellum	AF	Ordinal	-	Morphological adaptations such as the evolutionary reduction in the number of flagellar segments are paralleled by an increase in olfactory capacity (e.g., the number of chemoreceptors) (Indicator of foraging speed, locomotion, associated to habitat complexity, and being able to be more efficient and faster in heterogeneous environments (Schmalfuss, 1998; Zimmer, 2002).
Antennal flagellum length	AFL	Continuous	mm	A reduction in antennal size may favor increased visual and olfactory performance (Schmalfuss, 1998; Zimmer, 2002).

Traits	Abbreviations	Type	Unit	Functional importance
Antenna length/body length ratio	AL/BL	Continuous	mm	Its trait can to provide information on their adaptive response in environments (Schmalfuss, 1998).
Pereiopod 1 length	P1L	Continuous	mm	Indicator of foraging speed, locomotion, associated to habitat complexity, and being able to be more efficient and faster in heterogeneous environments (Schmalfuss, 1984).
Pereiopod 1 length/body length ratio	P1L/BL	Continuous	mm	Attribute that can to provide information on their adaptive response in environments (Schmalfuss, 1984).
Pereiopod 7 length	P7L	Continuous	mm	Indicator of foraging speed, locomotion, associated to habitat complexity, and being able to be more efficient and faster in heterogeneous environments (Schmalfuss, 1984).
Pereiopod 7 length/body length ratio	P7L/BL	Continuous	mm	Its trait can to provide information on their adaptive response in environments (Schmalfuss, 1984).
Size of the apical organ of the antenna (in relation to the distal article of antennal flagellum)	AO: SHO (0), LON (1)	Binary	-	Its trait can to provide information on their adaptive response in environments (Schmalfuss, 1998; Zimmer, 2002).
Sensory hairs of the apical organ	SHAO: FRE (1), INV (0)	Binary	-	Has a gustatory and olfactory function (Schmalfuss, 1998).
Distal aesthetascs of the antennule	DAA: SIM (0), ROB (1)	Binary	-	Sensory structure, is essential in the task of

Traits	Abbreviations	Type	Unit	Functional importance
				finding suitable humidity conditions for short and long-term survival (Schmalfuss, 1998; Hornung, 2011).
Noduli laterales	NL: ABS (0), PRE (1)	Binary	-	Sensory structure, are innervated cuticular extensions mediate sensory information of behavioral responses (Hornung, 2011).
Number of ommatidia	OMT	Ordinal	-	Well-developed eyes several ommatidia allows optic perception of shapes and plays an important role in the orientation of the animals in their environment. In reduction of this can perceive only different shades of light or dark; hypogean isopods species have smaller eyes compared to epigean species (Schmalfuss, 1998).
Dorsal scale-setae	DSS: FS (1), PF (2), TS (3), LS (4)	Categorical	-	Sensory structure, are innervated cuticular extensions mediate sensory information of behavioral responses (Hornung, 2011).
Body pigments	BP: ABS (0), RED (0.5), PRE (1)	Categorical	-	The coloration of many isopods varies from gray to dark brown or even dark gray, so we can consider them species with cryptic colors, an ecological strategy to blend in with their environment and avoid detection by predators. Although they can also present albinism, being common in endogenous

Traits	Abbreviations	Type	Unit	Functional importance
				and cave-dwelling species (Ďurajková *et al*., 2025).
Ecomorphological category	ECA: CLI (1), RUN (2), CRE (3)	Categorical	-	Are classified according to their antipredatory strategies reflect their morphology, behavior and habitat use, e.g.: runners with fast moving, narrow and elongated bodied ones with a smooth surface and long pereopods, that only run as defense against predators; clingers with flat and broad bodies, strong and short pereopods, either cling to a solid substrate or run to avoid predation; creeper inhabits crevices in the soil, are small and narrow species, present tubercles, ribs, or many curved scales that protrude upwards help preventing attachment of small soil particles (Schmalfuss, 1984; Tuf & Ďurajková, 2022).
Type of substratum	TS: CLA (1), ART (2), FAL (3), GUA (4), ORG (5), ROC (6), LL (7), SOI (8), CLA+ROC (9), SOI+LL (10), LOG+CLA (11), LOG+LL (12), CLA+GUA+LOG+LL (13)	Categorical	-	Substrate type selection by terrestrial isopods is generally related to humidity, temperature, and diet quality, and their respond to spatial and temporal changes in the availability of food by varying their feeding tactics (Zimmer, 2002).

Data standardization was performed using the decostand function from the vegan package (Oksanen *et al*., 2024). To select the traits used in the analysis, we first conducted a pairwise correlation test, excluding those with correlation coefficients greater than |0.9|

(Supplementary material 2). We assessed multicollinearity using the Variance Inflation Factor (VIF), with a threshold of 10, employing the vifstep function from the usdm package (Naimi *et al*., 2014). This procedure resulted in the selection of 10 functional traits for subsequent analysis (Table 2). Excluded traits and their corresponding values are listed in the Supplementary Information (Supplementary material 3).

Data analyses

To avoid potential biases in the analysis of abundance data caused by sampling differences, analyses were conducted using raw incidence data of the species across sampling points within each environment. All statistical analyses were performed using RStudio v4.2.0 (R Core Team, 2020). Alpha and beta diversity, and functional space graphics were generated using the ggplot2 package (Wickham, 2016).

Sampling completeness

Sampling completeness was evaluated using rarefaction and extrapolation curves based on sample coverage, with the iNEXT package (Hsieh *et al*., 2024). The analysis focused on species richness (Hill number q = 0), using raw incidence data and 999 bootstrap pseudoreplicates to estimate confidence intervals (Colwell *et al*., 2012; Chao *et al*., 2014; Chao & Jost, 2015).

Taxonomic and functional alpha diversity

Taxonomic alpha diversity was evaluated using the effective numbers of species framework based on Hill numbers. This approach allows for the representation of three orders of true diversity: q = 0, the effective number of observed species, corresponding to species richness; q = 1, the effective number of common species, calculated as the exponential of the Shannon index; and q = 2, the effective number of dominant species, calculated as the inverse of the Simpson index (Hill, 1973; Moreno *et al*., 2011; Colwell *et al*., 2012). The analyses were performed using the iNEXT online platform, applying 999 bootstrap pseudoreplicates to calculate 95% confidence intervals (Chao *et al*., 2016). Differences in taxonomic alpha diversity across environments were evaluated by assessing the overlap of confidence intervals (Moreno *et al*., 2011; Chao *et al*., 2016).

Functional alpha diversity was estimated using the multidimensional framework proposed by Villéger *et al*. (2008), through the calculation of three complementary indices: functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv). Under an incidence-based approach, FRic represents the volume of functional space occupied by the species within an assemblage; FEve quantifies the regularity of species distribution within this space; and FDiv reflects the degree to which species diverge in their trait values within the occupied functional space (Villéger *et al*., 2008; Mouchet *et al*., 2010). These metrics were computed across environments and all species, using the dbFD function from the FD package (Laliberté & Legendre, 2010; Laliberté *et al*., 2014).

To detect possible differences in alpha functional diversity indices values between environments, pairwise comparisons were conducted using Generalized Linear Models (GLMs). A Gaussian distribution was applied to Fric and FDiv, while a quasipoisson distribution was used for FEve. Statistical significance was assessed using the anova function by comparing each full model to its corresponding null model. These analyses were performed using the glm function of glmnet package (Friedman *et al*., 2010).

Taxonomic and functional beta diversity

Taxonomic dissimilarity in species composition between environments was calculated using the additive partitioning framework for beta diversity proposed by Baselga (2010). To assess dissimilarity in functional composition, we applied the analogous method developed by Villéger *et al*. (2013). This approach decomposes total beta diversity into two components: (1) turnover component (βtur), which captures changes in composition due to species or functional replacement; and (2) nestedness component (βnes), which reflects differences in species or functional richness resulting from nested patterns.

Total taxonomic compositional variation, along with its nestedness and species turnover components, was calculated using the Jaccard dissimilarity index, implemented via the beta.pair and beta.multi functions. For functional beta diversity, we used the scores of the first two axes from a Principal Coordinate Analysis (PCoA), conducted with the pcoa function from the vegan package (Oksanen *et al*., 2024), which represent synthetic functional traits derived from the complete set of species attributes (Villéger *et al*., 2013). Using the presence–absence matrix of communities containing three or more species and these synthetic traits, functional dissimilarity was estimated with the functional.beta.multi and functional.beta.pair functions. Both taxonomic and functional beta diversity were calculated using the betapart package (Baselga & Orme, 2012).

From the matrices obtained for total beta diversity and its components, we constructed ternary plots using the ggtern function from the ggtern package (Hamilton & Ferry, 2018), to explore pairwise relationships among sites and to visualize which dissimilarity component dominates beta diversity, in both taxonomic and functional dimensions (Baselga, 2012). To test for significant differences in assemblage structure between environments, we conducted a one-way Permutational Analysis of Variance (PERMANOVA) based on the Jaccard dissimilarity index, using 999 permutations with adonis2 function from the vegan package (Oksanen *et al*., 2024). This test evaluates the null hypothesis that assemblage composition does not differ between environments (Anderson, 2001). To visualize the results of PERMANOVA, we performed a Principal Coordinates Analysis (PCoA). Both analyses (PERMANOVA and PCoA) were conducted separately for total beta diversity and each of its components.

Functional composition

To assess whether the functional composition of the terrestrial isopod assemblage differed across environments, we calculated Gower's functional distance (Gower, 1971) using the gowdis function from the FD package (Laliberté & Legendre, 2010; Laliberté *et al*., 2014). This method is widely used in functional ecology as it accommodates mixed data types in the construction of functional trait spaces (Pavoine *et al*., 2009). A PCoA was then performed on the resulting distance matrix to describe the structure of functional space and to visualize the traits potentially driving differences among assemblages across environments.

4. Results

Species composition and sampled completeness

We analyzed 493 individuals of 39 terrestrial isopod species/morphospecies representing in 10 genera and five families (Table 2). Of these, 19 species were found exclusively inside caves, 12 exclusively outside the caves, and eight occurred in both habitats.

Table 2. Values of functional traits measured in this study, according to correlation analyses and VIF. N: number of individuals measured; BL: body length; AF: number of articles of antennal flagellum; AO: size of the apical organ of the antenna; SHAO: sensory hairs of the apical organ; NL: noduli laterales; DSS: dorsal scale-setae; OMT: number of ommatidia; BP: body pigments; ECA: ecomorphological category; TS: type of substratum.

Family/Species	Species code	Environment	N	BL	AF	AO	SHAO	NL	DSS	OMT	BP	ECA	TS
Philosciidae													
Metaprosekia sp.	sp1	Epigean	28	2.59 (±0.140)	3	0	0	1	2	7	1	2	12
Alboscia jotajota	sp2	Hypogean	1	4.13	3	0	0	1	3	13	0	2	1
Alboscia sp.	sp3	Hypogean	1	3.5	3	1	0	1	2	0	0	2	1
Alboscia sp.	sp4	Epigean	1	1.7	3	1	0	1	2	0	0	2	12
Atlantoscia floridana	sp5	Epigean	6	5.16 (±0.163)	3	0	0	1	2	20	1	2	12
Atlantoscia inflata	sp6	Epigean	92	4.03 (±0.281)	3	0	0	1	2	17	1	2	13
Atlantoscia inflata	sp7	Hypogean	1	3.53	3	0	0	1	2	17	1	2	13
Atlantoscia sp.1	sp8	Epigean	34	8.30 (±0.735)	3	0	0	1	2	22	1	2	13
Atlantoscia sp.1	sp9	Hypogean	1	6.3	3	0	0	1	2	22	1	2	13
Atlantoscia sp.3	sp10	Epigean	6	3.78 (±0.025)	3	0	0	1	2	15	1	2	8
Atlantoscia sp.4	sp11	Epigean	9	6.18 (±1.022)	3	0	0	1	2	20	1	2	8
Atlantoscia sp.5	sp12	Epigean	5	5.88 (±0.672)	3	0	0	1	2	20	1	2	10
Atlantoscia sp.6	sp13	Hypogean	4	6	3	0	0	1	2	14	1	2	8
Benthana cairensis	sp15	Hypogean	8	7.35 (±0.350)	3	0	0	1	2	25	1	2	13
Benthana iporangensis	sp16	Hypogean	10	7.52 (±0.188)	3	0	0	1	2	18	0	2	8
Benthana longicornis	sp17	Hypogean	1	11	3	0	0	1	2	24	1	2	13

Family/Species	Species code	Environment	N	BL	AF	AO	SHAO	NL	DSS	OMT	BP	ECA	TS
Benthana picta	sp18	Epigean	2	15.35	3	0	0	1	2	24	1	2	12
Benthana picta	sp19	Hypogean	4	14.75	3	0	0	1	2	24	1	2	12
Benthana sp.1	sp20	Epigean	12	9.00 (±0.922)	3	0	0	1	2	25	1	2	13
Benthana sp.1	sp21	Hypogean	1	9.7	3	0	0	1	2	25	1	2	13
Benthana sp.2	sp22	Hypogean	3	5.30 (±0.236)	3	0	0	1	2	23	1	2	1
Benthana sp.3	sp23	Epigean	1	12.4	3	0	0	1	2	24	1	2	13
Benthana sp.4	sp24	Hypogean	6	5.08 (±0.102)	3	0	0	1	2	17	0.5	2	8
Benthana taeniata	sp25	Epigean	15	6.22 (±0.093)	3	0	0	1	2	19	1	2	3
Benthana taeniata	sp26	Hypogean	1	6.1	3	0	0	1	2	19	1	2	3
Styloniscidae													
Cylindroniscus flaviae	sp27	Hypogean	9	2.37 (±0.098)	4	1	0	0	3	0	0	3	9
Styloniscus spinosus	sp37	Epigean	12	2.17 (±0.185)	3	1	1	0	4	3	1	3	13
Styloniscus spinosus	sp38	Hypogean	1	3.45	3	1	1	0	4	3	1	3	13
Bathytropidae													
Neotroponiscus iporangaensis	sp30	Hypogean	3	5.25	2	0	0	1	1	16	1	1	4
Neotroponiscus sp.	sp31	Hypogean	1	6.33	2	0	0	1	1	15	0.5	1	8
Bathytropidae gen. sp.	sp14	Epigean	3	3.68 (±0.846)	2	0	0	1	1	18	1	1	7
Dubioniscidae													
Dubioniscus sp.1	sp28	Epigean	1	5.48	3	0	0	1	1	15	1	3	6
Dubioniscus sp.2	sp29	Hypogean	5	4.97 (±0.306)	3	1	0	1	1	14	0	3	8
Novamundoniscus sp.1	sp32	Hypogean	6	3.01 (±0.467)	3	0	0	1	1	6	0.5	3	11

Family/Species	Species code	Environment	N	BL	AF	AO	SHAO	NL	DSS	OMT	BP	ECA	TS
Novamundoniscus sp.2	sp33	Hypogean	5	4.43 (±0.467)	3	0	0	1	1	14	1	3	2
Novamundoniscus sp.4	sp34	Hypogean	1	3.76	3	0	0	1	1	13	0.5	3	8
Novamundoniscus sp.5	sp35	Epigean	29	2.81 (±0.131)	3	0	0	1	1	8	1	3	12
Novamundoniscus sp.6	sp36	Hypogean	1	4.3	3	1	0	1	1	10	0	3	8
Platyarthridae													
Trichorhina acrux	sp39	Hypogean	7	2.60 (±0.328)	2	0	0	1	1	5	0	3	5
Trichorhina jurai	sp40	Hypogean	11	2.82 (±0.107)	2	0	0	1	1	0	0	3	13
Trichorhina quadriocellata	sp41	Epigean	3	2.13	2	0	0	1	1	4	0	3	12
Trichorhina quadriocellata	sp42	Hypogean	2	2.2	2	0	0	1	1	4	0	3	12
Trichorhina sp.1	sp43	Hypogean	8	2.18 (±0.274)	2	0	0	1	1	0	0	3	13
Trichorhina sp.2	sp44	Hypogean	1	2.1	2	0	0	1	1	0	0	3	4
Trichorhina sp.3	sp45	Epigean	14	2.20 (±0.267)	2	1	0	1	1	5	0	3	12
Trichorhina sp.4	sp46	Epigean	14	2.61 (±0.266)	2	1	0	1	1	4	1	3	5
Trichorhina tomentosa	sp47	Epigean	3	2.51 (±0.212)	2	0	0	1	1	1	0	3	13
Trichorhina tomentosa	sp48	Hypogean	100	3.35 (±0.220)	2	0	0	1	1	1	0	3	13

Sampling coverage was greater than 70% in both habitats (Supplementary material 4), indicating an efficiency of the applied sampling in capturing terrestrial isopods. Coverage-based rarefaction and extrapolation presented sample completeness slightly higher in epigean samples (75.6%) compared to hypogean samples (72.4%), the number of observed species was greater in the hypogean environment (28 vs. 20), as higher estimated total species richness (39 vs. 27).

Taxonomic and functional alpha diversity

Taxonomic alpha diversity revealed highest number of effective species (q0) in hypogean habitats with eight species more than epigean habitats, likewise, the effective number of common species (q1) was greater for the same habitat, and dominant species (q2) was similar in both habitats, however, these differences were not statistically significant (Figures 2a, b, c). In contrast, functional alpha diversity metrics only revealed significant differences between habitats for FRic which was higher in epigean assemblage (Figures 2d, e, f, Supplementary material 5, 6), while FDiv was higher in hypogean communities, and FEve was slightly similar in both habitats, that was not statistically different.

Taxonomic and functional beta diversity

Both taxonomic and functional beta diversity was significantly different between epigean and hypogean habitats, primarily driven by species and trait turnover rather than nestedness (Figures 3, 4). Ternary plots indicate a high taxonomic and functional beta diversity, with turnover as the dominant component and nestedness contributing slightly (Figure 3a, b). Principal Coordinate Analysis (PCoA), further supported these results, which taxonomic beta diversity showed clear separation of assemblages by habitat, and functional beta diversity also showed habitat-based structuring, which turnover of species and traits differed significantly between environments (Figure 4).

Composition of functional space in oniscideans

PCoA ordination showed that communities are functionally structured in the functional space, reveals partial segregation between epigean and hypogean assemblages along the first two axes of the functional space (Figure 5).

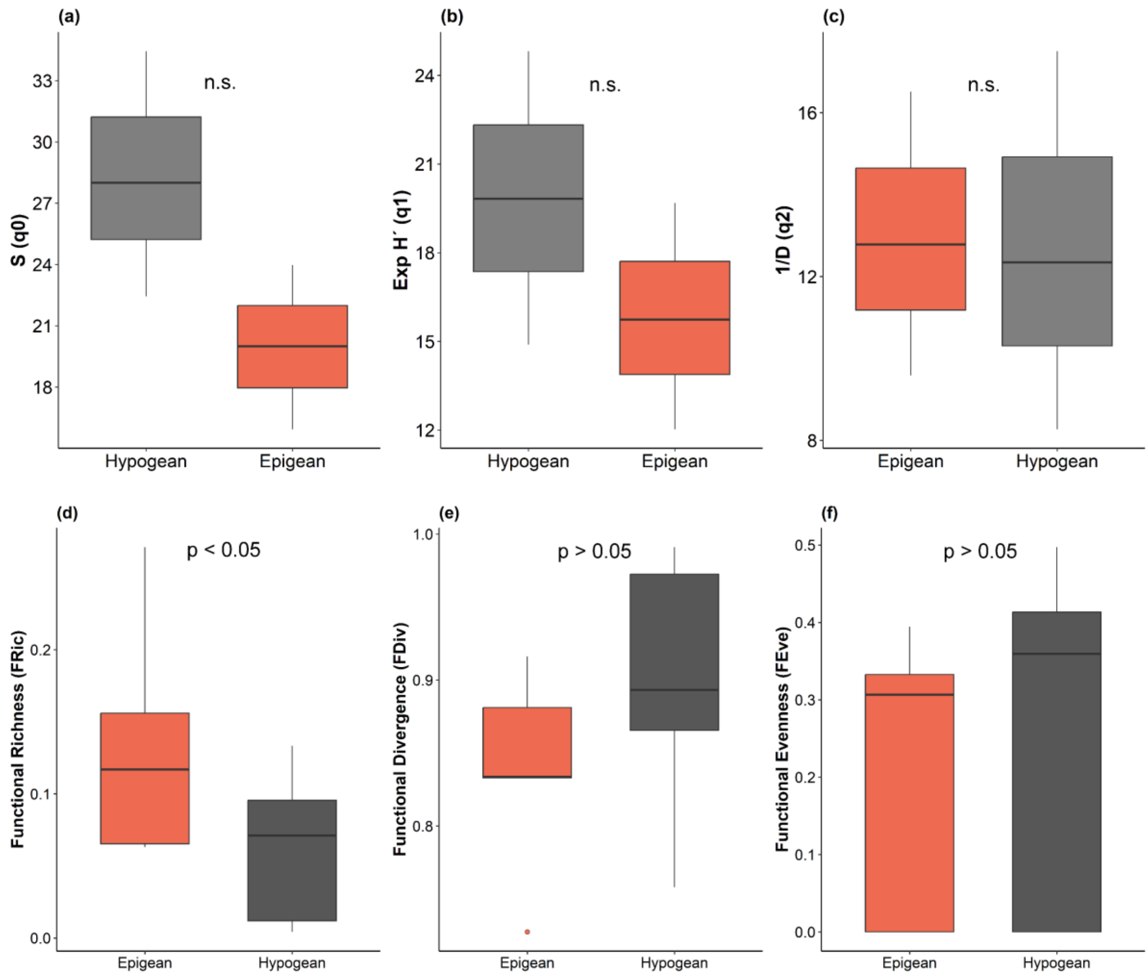

Figure 2. Taxonomic and functional alpha diversity of terrestrial isopod assemblages in epigean and hypogean environments of the Parque Estadual Turístico do Alto Ribeira (PETAR), southeastern Brazil. (a) species richness (q0), (b) Shannon diversity (q1), (c) Simpson diversity (q2), (d) functional richness (FRic), (e) functional divergence (FDiv), and (f) functional evenness (FEve). The p-value for functional alpha diversity indices indicates the result of GLMs and ANOVA test comparing values between environments (see Table S2, S3).

Most hypogean species were clustered slightly to the left and related with ECA values, while epigean species clustered to the right, linked to higher values of BP, OMT and BL, and communities found in both habitats occupy intermediate positions (Figure 5a). When analyzed by family identity and habitat preference, distinct patters emerged (Figure 5b): Philosciidae dominate both habitats and showed a wide distribution along the PCoA1 axis; Dubioniscidae exhibited habitat-specific segregation, with some species restricted to either epigean or hypogean environments; Platyarthridae were predominantly associated with hypogean habitats, characterized by the absent of BP or low BL and OMT values; Bathytropidae and Styloniscidae occupied peripheral positions in functional space, suggesting the presence of specialized traits adapted to particular microhabitat conditions.

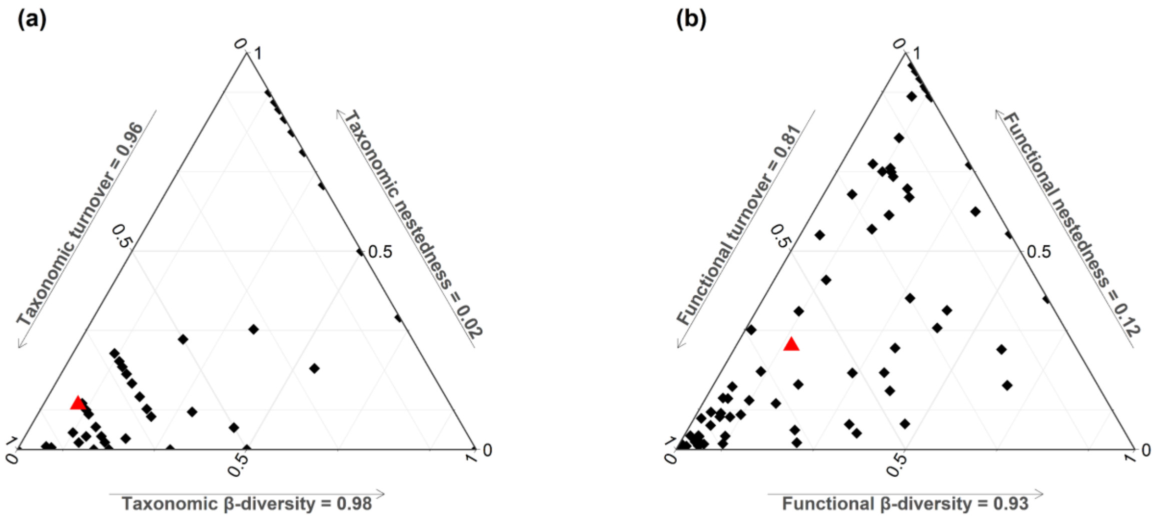

Figure 3. Ternary plots of (a) taxonomic and (b) functional beta diversity of terrestrial isopod assemblages in epigean and hypogean environments in the Parque Estadual Turístico do Alto Ribeira (PETAR), southeastern Brazil, calculated using the Jaccard index. Each point represents a pairwise comparison between communities, illustrating the relative contributions of species turnover, nestedness, and total dissimilarity to overall beta diversity. Red triangle indicate score centroids.

5. Discussion

This study integrated taxonomic and functional perspectives to evaluate how terrestrial isopod assemblages respond to contrasting epigean and hypogean environments within an Atlantic Forest karst system. While taxonomic alpha diversity did not differ significantly between habitats, functional richness (FRic) was markedly higher in epigean environments. In addition, beta diversity patterns and trait composition revealed clear separation between habitat types, driven predominantly by species and trait turnover. The partial segregation of assemblages in functional space further indicates that habitat conditions shape trait organization and niche differentiation.

Taxonomic and functional alpha diversity

Our findings revealed contrasting trends between epigean and hypogean assemblages of oniscideans regarding to initial predictions. Only FRic was significantly greater in epigean habitats, likely because the higher environmental heterogeneity and resource variability at the surface support a wider range of ecological strategies and trait combinations. These conditions allow the coexistence of species with different functional attributes, expanding the overall volume of functional space occupied by epigean assemblages (Mammola *et al.*, 2016; Premate *et al.*, 2023). In contrast, hypogean habitats are characterized by environmental stability, low light and limited food resources, likely act as environmental filters selecting specialized taxa and promoting trait convergence (Mammola *et al.*, 2016; Gibert & Deharveng, 2002; Culver & Pipan, 2019).

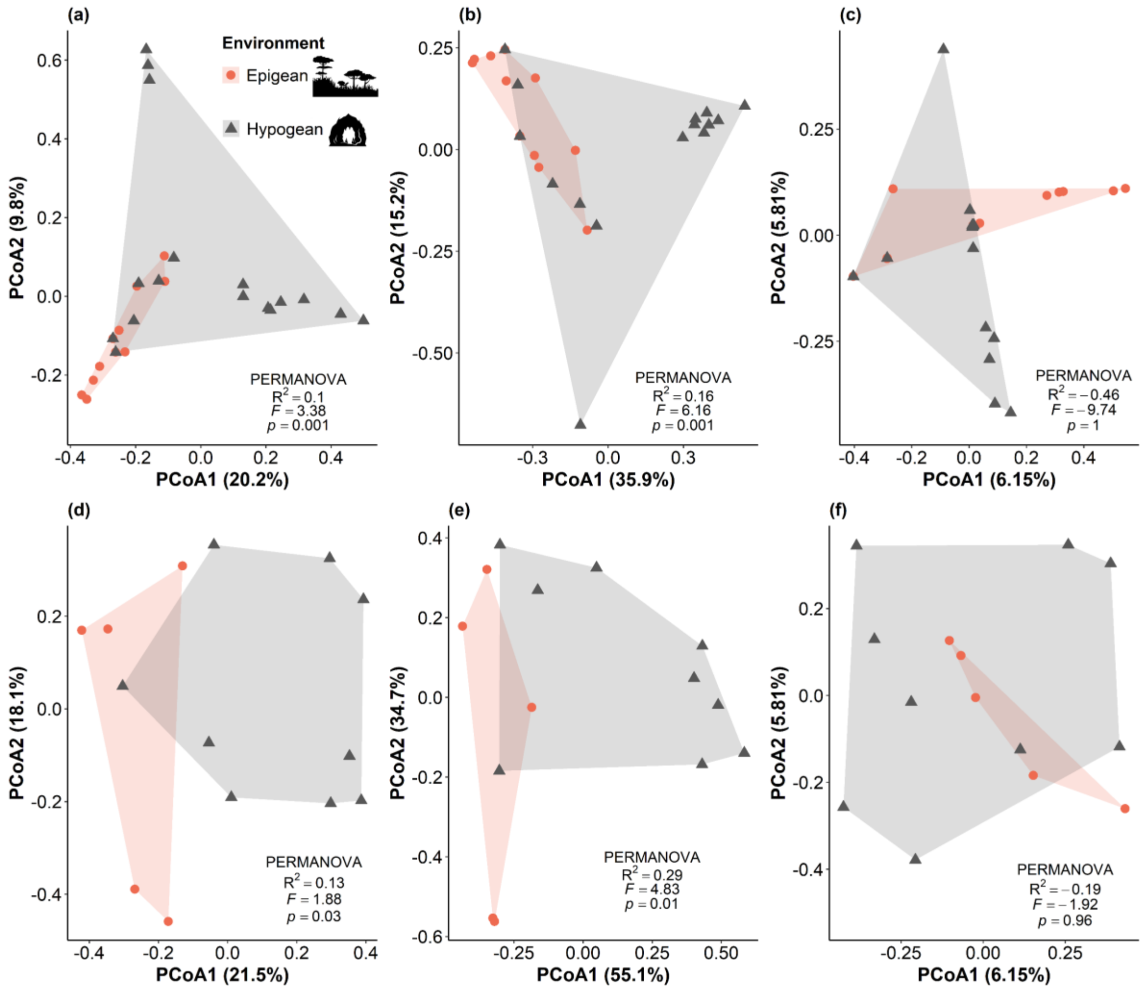

Figure 4. Principal Coordinates Analysis (PCoA) of terrestrial isopod assemblages from epigean and hypogean environments in the Parque Estadual Turístico do Alto Ribeira (PETAR), southeastern Brazil, based on the Jaccard dissimilarity index. (a) total taxonomic beta diversity, (b) taxonomic turnover, (c) taxonomic nestedness, (d) total functional beta

diversity, (e) functional turnover, and (f) functional nestedness. Percentages of variation explained by the first two axes are indicated.

Regarding the selected traits, body length, pigmentation, noduli laterales and number of ommatidia were lower in hypogean habitats than in epigean sites, reflecting the influence of surface conditions in maintaining a broader expression of these traits. Attributes as body size can increasing a resource utilization, or could contribute significantly to reduce water loss rate in this group that depend to humidity (see Table 1). The lack of significant differences in other functional metrics such as functional evenness (FEve) and divergence (FDiv) suggests that trait distribution within the functional space is relatively similar across both environments, taking into account the differences in species distribution in the multidimensional functional space, and cave communities can be influenced by several attributes common to epigean ecosystems (Mammola *et al*., 2016; Legras & Gaertner, 2018; Mendes-Rabelo *et al*., 2020).

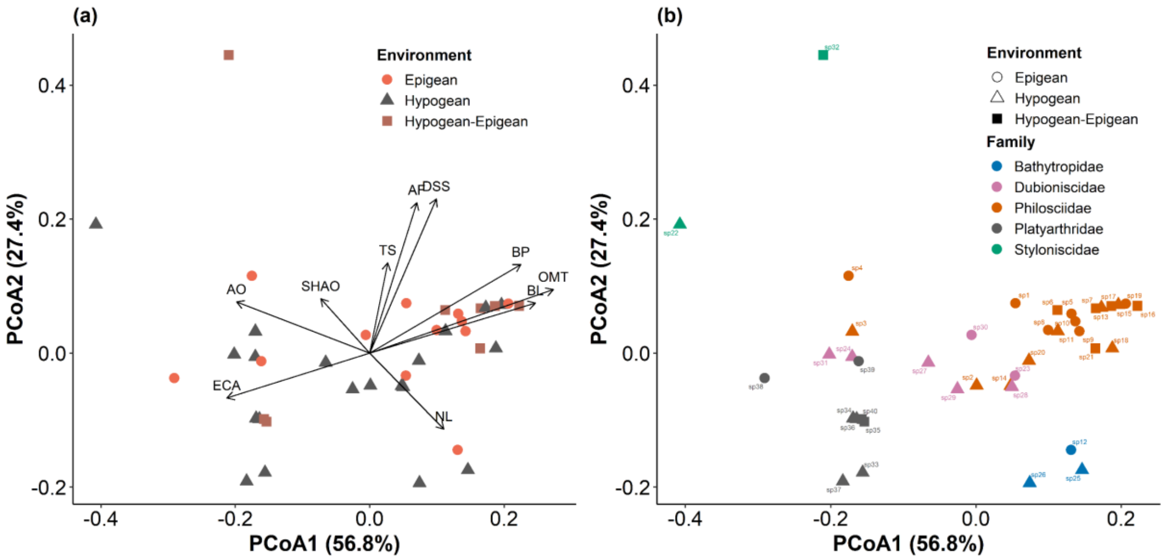

Figure 5. Representation of the functional space of terrestrial isopod assemblages from epigean and hypogean environments in the Parque Estadual Turístico do Alto Ribeira (PETAR), southeastern Brazil, based on Principal Coordinates Analysis (PCoA) using Gower distance computed from a matrix of functional traits. (a) Ordination plot showing the distribution of species and the direction and strength of functional trait vectors, (b) Ordination plot of species color-coded by family, highlighting differences between epigean and hypogean assemblages. AF: number of articles of antennal flagellum; AO: size of the apical organ of the antenna; BL: body length; BP: body pigments; DSS: dorsal scale-setae; ECA: ecomorphological category; NL: noduli laterales; OMT: number of ommatidia;

SHAO: sensory hairs of the apical organ; TS: type of substratum. Percentages of variation explained by the first two axes are indicated. Species code in Table 2.

Our results differ from those found by Fernandes *et al*. (2016), where they found greater functional diversity inside caves than outside them, in limestone outcrop between the Cerrado and the Caatinga domains in central Brazil, suggesting phenotypic overdispersion. In contrast, our results show greater functional richness in epigean habitats. This suggests that, in our study area, surface environments support a wider range of ecological strategies and trait combinations, due to higher environmental heterogeneity, more dynamic resource availability, and greater opportunities for niche differentiation. While the caves we studied harbor a notable number of troglomorphic/endogean species, their functional traits tend to converge on a narrow set of adaptations to stable, resource-limited, and light-deprived conditions, resulting in lower functional diversity despite taxonomic distinctiveness. In contrast, epigean environments especially in the Atlantic Forest, with its structural complexity and diverse microhabitats, appear to promote a broader spectrum of functional traits, including those associated with different foraging strategies, body sizes, and microhabitat preferences. The presence of endogean species with reduced pigmentation and limited visual structures (such as family Platyarthridae, Dubioniscidae and some Philosciidae) in epigean habitats further illustrates that similar morphological traits can arise under different selective pressures, without necessarily implying cave adaptation. Overall, our findings suggest that functional diversity is not only a product of taxonomic richness, but is also shaped by the ecological breadth and the filtering intensity of each environment. In our study, the traits that most clearly differed between habitats were pigmentation, eye development (number of ommatidia), body size, and the development of noduli laterales. These traits indicate that surface environments promote a broader functional expression, likely influenced by the more variable microclimatic conditions of the Atlantic Forest (such as greater fluctuations in humidity, light, temperature and resource availability), which can favor species with wider ecological tolerances and heterogeneous trait combinations. In contrast, the reduced pigmentation, eye regression, and smaller body sizes found in hypogean assemblages suggest the action of strong environmental filtering associated with cave stability, permanent darkness, and limited resources. Thus, the divergence between our results and those of Fernandes *et al*. (2016) may reflect regional differences in subterranean system configuration and microclimatic context, as well as distinct historical patterns of colonization and biogeographic processes (Trajano, 1995; Gnaspini, 1997; Bryson *et al*., 2014). These contrasts highlight the importance of incorporating trait-based approaches in broader comparative analyses across Neotropical karst landscapes.

Several studies suggest a complex historical connection between the Atlantic Forest and the Amazon Forest, shaped by Quaternary climatic fluctuations and the subsequent formation of xeric corridors in central Brazil (Marques *et al*., 2021). This broader biogeographic context is important because it helps explain why different oniscidean lineages may show distinct functional patterns across epigean and hypogean habitats. If lineages have experienced different historical routes of colonization, isolation or persistence, their present-day trait combinations may reflect not only current environmental filtering but also past biogeographic constraints and diversification histories. Thus, the functional differences we observed (such as variation in pigmentation, visual structures, and body size), may be partially influenced by these historical processes, which shaped the distribution and ecological breadth of each lineage before their colonization of cave systems. Understanding these regional biogeographic dynamics is therefore essential for interpreting why some groups show strong trait convergence in hypogean habitats, while others retain broader functional variation. Future studies focused on lineage-specific biogeographic histories could help clarify how past events influence present-day functional structure in both cave and surface assemblages (Rivera *et al*., 2002; Costa, 2003).

Taxonomic and functional beta diversity

Overall, there is considerable local heterogeneity in terms of species and traits composition between habitats. Beta diversity showed clear and significant differentiation between epigean and hypogean assemblages. Due to their environmental requirements, some arthropods can present narrower distribution ranges, that explains why they present higher beta diversity values between habitats (Cardoso, 2012). We observed that turnover was the main driver of both taxonomic and functional dissimilarity, with nestedness playing a minor role. Taxonomic and functional turnover likely reflects the presence of habitat specialists, and trait combinations, especially in subterranean environments, where many species show restricted distributions and low dispersion capacity, maintain the potential for diversification by differentiation of niches (Culver & Pipan, 2009; Fišer *et al*., 2012; Deharveng & Bedos, 2018). These results suggest that these epigean and hypogean sites, at local scale, are completely different in terms of community and trait composition, indicating a high rate of endemism, and cave and surface communities tend to express different functions (Lopes *et al*., 2005; Mammola *et al*., 2024). This is consistent with the high rate of endemism that has been recorded for the Atlantic Forest, including its karst areas (Trajano, 2000; Trajano *et al*., 2016; Bichuette & Trajano, 2018). Moreover, it is possibly shaped by different environmental filters, the role of niche-based processes, and evolutionary history of species (Mammola *et al*., 2019c; Mammola *et al*., 2024).

This high turnover component indicates that species and functional traits are largely replaced between epigean and hypogean habitats, rather than simply lost or gained. Such a pattern suggests that each habitat harbors distinct ecological strategies, reinforcing the idea that functional space is structured not only by the availability of resources but also by the ecological filters imposed by each environment. In the case of hypogean systems, strong environmental filtering selects for a narrow suite of traits, resulting in assemblages that are compositionally and functionally distinct from their surface (Fichaux *et al*., 2019; Mammola *et al*., 2019c,2024). On the other hand, epigean habitats, with more variable and heterogeneous conditions, allow for a broader spectrum of functional strategies and trait combinations. Therefore, the pronounced taxonomic and functional turnover observed in our study highlights the ecological distinctiveness of hypogean and epigean habitats, and underscores the importance of considering both dimensions of diversity when assessing patterns of community differentiation (Cardoso, 2012). These findings align with the idea that beta diversity is a key component of regional diversity (Dambros *et al*., 2024), especially in karst systems, where physical discontinuities and microhabitat specialization promote compositional divergence (Bonacci *et al*., 2009). From a conservation perspective, this emphasizes the need to protect both habitat types to preserve the biodiversity and the ecological functions they support.

Composition of functional space in oniscideans

The PCoA ordination revealed a partial segregation between epigean and hypogean assemblages, supporting the idea of habitat-based clustering of species and maintain the niche differentiation. Epigean assemblages was associated with traits such as increased body size and pigmentation (BL, BP), greater number of ommatidia (OMT), and broader substrate use (TS). These traits are typical of species adapted to the heterogeneous and dynamic epigean conditions (Mammola et al., 2016; Premate et al., 2023). Philosciidae, dominant in both habitats, within the runner ecomorphological category, relatively long with strong pereopods and smooth tergites, suggesting species with high ecological plasticity and generalist strategies (Schmalfuss, 1984; Hornung, 2011). In contrast, hypogean assemblages showed a strong association with traits related to cave specialization, including reduced pigmentation (BP) and eye development, commonly observed in Platyarthridae. These taxa are generally endogenous species, soil-dwelling species within the creepers category, with elongated and convex bodies, and short appendages. These organisms depend on high humidity conditions due to their high rates of cuticular evaporation, reflect adaptations to low-light and low resources (Schmalfuss, 1984). There was clustered in peripheral regions of the functional space, indicating niche specialization and a narrower set of trait combinations (Gibert & Deharveng, 2002; Mammola *et al*., 2016; Culver & Pipan, 2019). The family Dubioniscidae, with creepers species (Schmalfuss, 1984), showed a scattered distribution, with species occurring both in epigean and hypogean habitats, suggesting transitional or intermediate traits, exhibiting partial trait adaptations to subterranean life while retaining some generalist features. The family Bathytropidae, within the clinger ecomorphological category, are either slow moving animal with flat and broad bodies, strong and short pereopods, and generally have tuberculated tergites, which helps increase the strength of the grip on the substrate without loosening the animal, was clustered in peripheral regions, indicating niche specialization. Finally, Styloniscidae with creeper species, showed largely restricted to hypogean environments. This family clustered in peripheral regions of the functional space, indicating niche specialization and a narrower set of trait combinations. Only two species this family were recorded, *Cylindroniscus flaviae* Campos-Filho, Araujo & Taiti, 2017, it is widely distributed in several caves in the Alto Ribeira region (Campos-Filho et al. 2017), while *Styloniscus spinosus* (Patience, 1907) (an exotic species), has been considered as bioindicator to anthropogenic disturbances in the Atlantic Forest, due to this specie may benefit from the vegetation mosaic produced by disturbance (Magrini *et al*., 2011). Furthermore, this would be the first record of this species in caves in Brazil. The presence of this species in highly sensitive environments such as caves can generate negative impacts, primarily related to increased competition with native species (Nicolosi *et al*., 2023).

Clustering patterns by family identity highlight the role of evolutionary history in shaping functional diversity. Phylogenetic constraints may determine the availability and combination of traits within lineages, influencing how species respond to environmental pressures (Costa, 2003). These results emphasize the importance of combining different diversity approaches to understand biodiversity patterns in subterranean systems, particularly in vulnerable biomes such as the Atlantic Forest karst areas.

6. Conclusions and perspectives

This study provides an assessment of terrestrial isopod assemblage structure in terms of taxonomic and functional diversity across surface (epigean) and subterranean (hypogean) habitats within the Atlantic Forest karst system. By integrating taxonomic and functional biodiversity dimensions and analyzing patterns at the alpha and beta levels, we addressed our central questions regarding the functional structuring of isopod communities and the role of environmental filters in shaping their trait composition. Our results partially confirmed the proposed hypotheses. As expected, epigean assemblages exhibited higher functional richness (FRic), reflecting greater environmental heterogeneity and the presence of generalist species adapted to more dynamic and variable surface conditions. In contrast, hypogean assemblages were characterized by lower trait variation and the predominance of specialized taxa. These findings support the hypothesis that hypogean habitats act as environmental filters, promoting trait convergence and niche specialization.

We also found strong taxonomic and functional turnover between epigean and hypogean habitats, reinforcing the idea that these environments host distinct communities with low functional redundancy. High beta diversity, which is mainly influenced by species turnover instead of nestedness, suggests that distinct ecological strategies are present in each habitat, and local environmental factors along with historical conditions play important roles in shaping community assembly processes.

Species ordination in functional space showed clustering by family and ecomorphological strategies, highlighting the influence of evolutionary history in shaping trait distributions. The dominance of Philosciidae in both environments, with broader functional dispersal, contrasts with the restricted distributions of Styloniscidae and Platyarthridae in subterranean habitats, emphasizing the lineage-specific responses of each to environmental constraints.

These results demonstrate that incorporating different diversity metrics provides a better understanding of how epigean and hypogean habitats support biodiversity. We also highlight the need to preserve these habitats to maintain their biodiversity. Given the increasing threats to subterranean biodiversity, such as habitat fragmentation, groundwater contamination, and biological invasions, understanding the functional role of species in these environments is essential for conservation planning. Our findings suggest integrating phylogenetic research to better understand how evolutionary history influences trait convergence or divergence among habitat types. Overall, our study highlights the ecological and evolutionary processes that shape functional diversity in understudied subterranean assemblages, such as terrestrial isopods, reinforcing the importance of integrating multiple dimensions of diversity to aid in biodiversity assessments and conservation strategies in both habitat types to preserve biodiversity in karst ecosystems.

7. References

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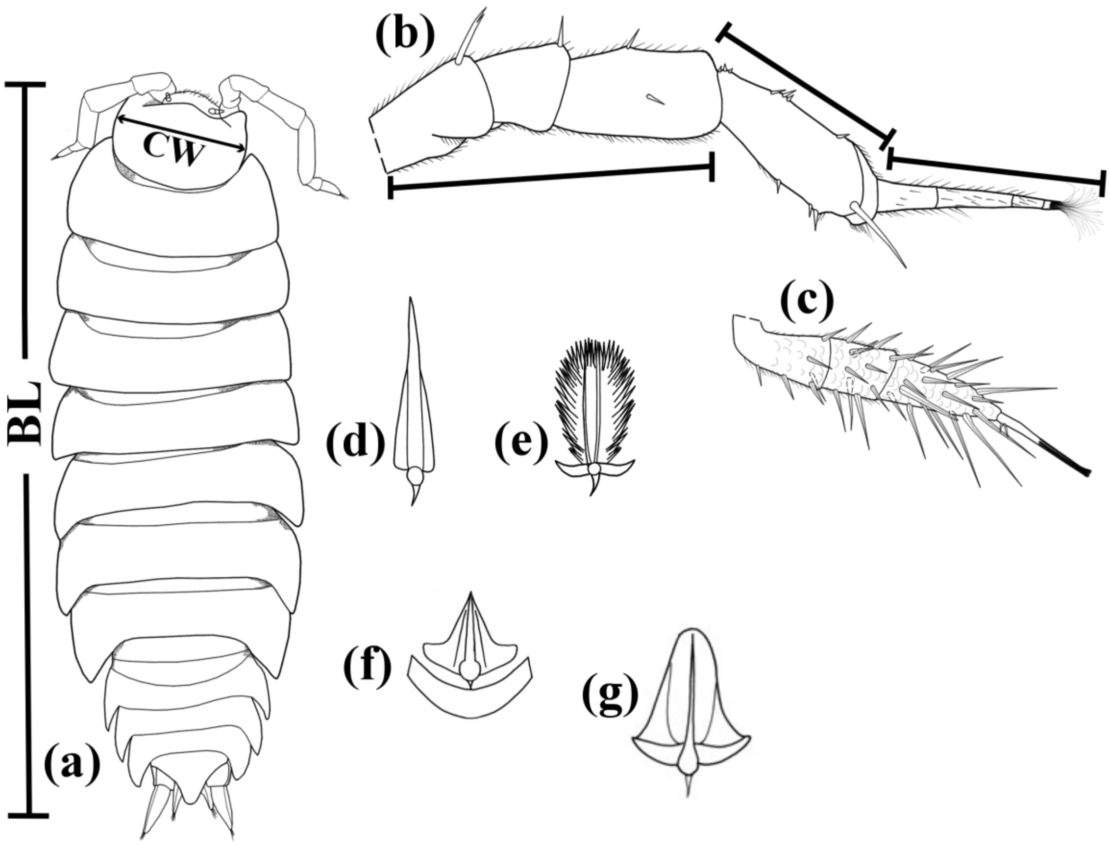
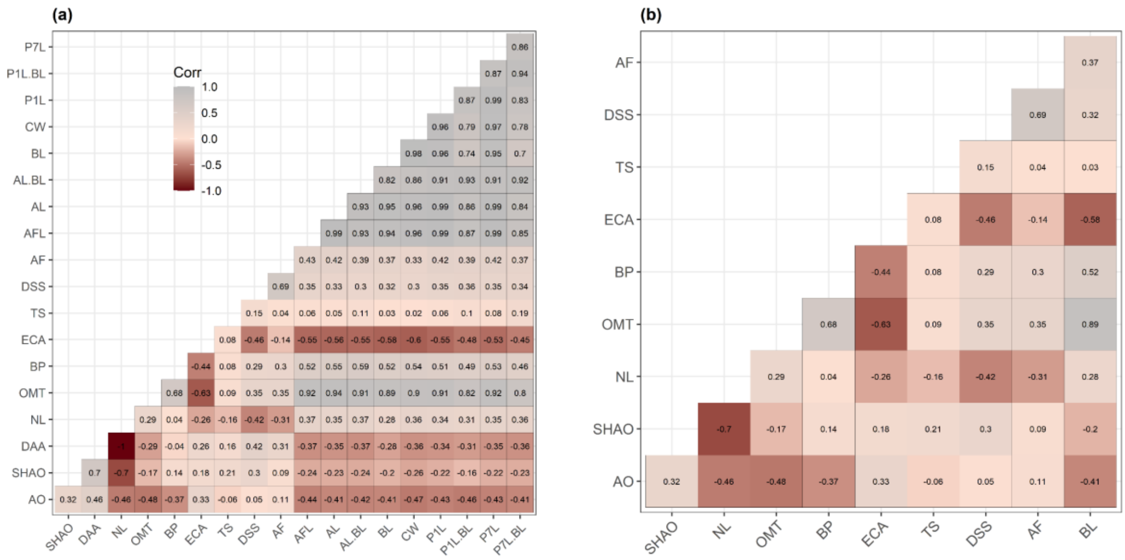
1. Supplementary Information

Supplementary material 1. Examples of functional traits used in this study. (a) Schematic of the dorsal habitus of a terrestrial isopod showing body length and cephalothorax width measurements; (b) antenna with free apical organ; (c) antennal flagellum with wrapped apical organ; (d–g) types of dorsal setae analyzed: (d) piliform, (e) fan-shaped, (f) tricorn-shaped, and (g) lanceolate-shaped.



Supplementary material 2. Correlation plot of all initially analyzed functional traits (a) and of the subset of traits selected for analysis after correlation and multicollinearity filtering (b).



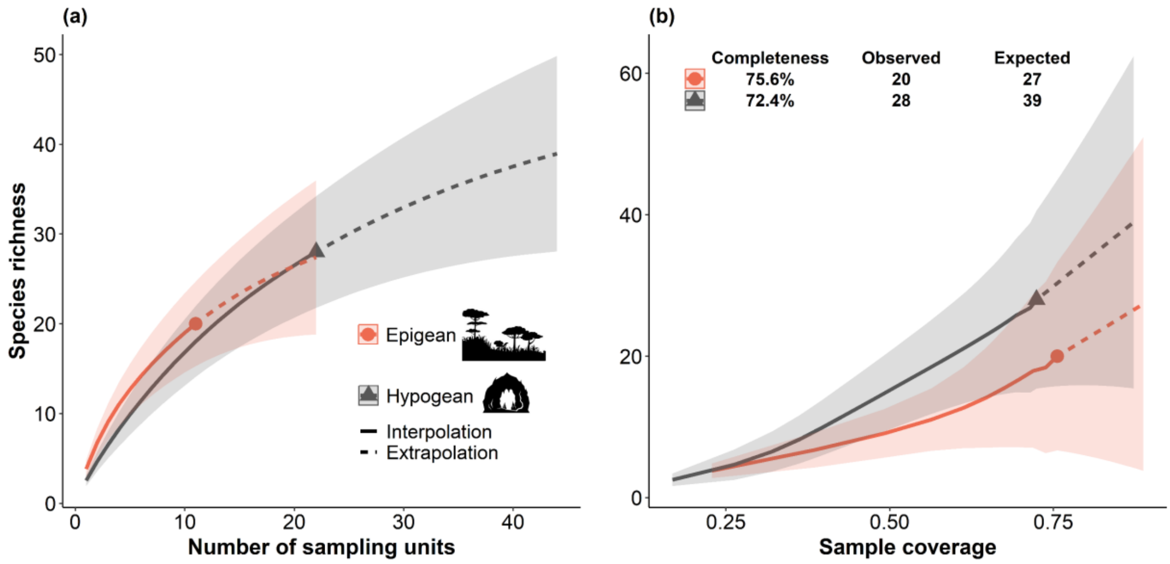
Supplementary material 3. Excluded traits due to multicollinearity and correlation. N: number of individuals measured; AFL: antennal flagellum length; AL: antenna length; AL/BL: antenna length/body length ratio; DAA: distal aesthetascs of the antennule; CW: cephalothorax width; P1L: pereiopod 1 length; P1L/BL: pereiopod 1 length/body length ratio; P7L: pereiopod 7 length; P7L/BL: pereiopod 7 length/body length ratio.

Family/Species	Species code	Environment	N	AFL	AL	AL/BL	DAA	CW	P1L	P1L/BL	P7L	P7L/BL
Philosciidae												
aff. Metaprosekia sp.	sp1	Epigean	28	0.42 (±0.006)	1.38 (±0.012)	0.13 (±0.007)	0	0.57 (±0.006)	1.04 (±0.026)	0.10 (±0.003)	1.23 (±0.034)	0.12 (±0.005)
Alboscia jotajota	sp2	Hypogean	1	0.63	1.95	0.12	0	0.88	1.65	0.1	1.93	0.12
Alboscia sp.	sp3	Hypogean	1	0.38	1.25	0.09	0	0.7	1.03	0.07	1.23	0.09
Alboscia sp.	sp4	Epigean	1	0.25	0.83	0.12	0	0.38	0.5	0.07	0.83	0.12
Atlantoscia floridana	sp5	Epigean	6	1.00 (±0.200)	3.45 (±0.425)	0.17 (±0.015)	0	1.19 (±0.063)	2.05 (±0.175)	0.10 (±0.005)	2.89 (±0.263)	0.14 (±0.008)
Atlantoscia inflata	sp6	Epigean	92	0.77 (±0.057)	2.53 (±0.177)	0.31 (±0.010)	0	0.93 (±0.049)	1.69 (±0.116)	0.21 (±0.006)	2.34 (±0.155)	0.29 (±0.013)
Atlantoscia inflata	sp7	Hypogean	1	0.83	2.5	0.18	0	0.9	1.5	0.11	2.45	0.17
Atlantoscia sp.1	sp8	Epigean	34	1.85 (±0.135)	6.36 (±0.462)	0.39 (±0.018)	0	1.65 (±0.114)	3.70 (±0.215)	0.22 (±0.008)	5.30 (±0.195)	0.33 (±0.024)
Atlantoscia sp.1	sp9	Hypogean	1	1.25	4.2	0.33	0	1.5	2.75	0.22	4.4	0.35
Atlantoscia sp.3	sp10	Epigean	6	0.83 (±0.075)	2.65 (±0.100)	0.35 (±0.016)	0	1.10 (±0.050)	1.63 (±0.025)	0.22 (±0.005)	2.48 (±0.275)	0.33 (±0.039)
Atlantoscia sp.4	sp11	Epigean	9	1.30 (±0.152)	4.18 (±0.561)	0.34 (±0.016)	0	1.27 (±0.097)	2.55 (±0.258)	0.21 (±0.011)	3.92 (±0.655)	0.32 (±0.006)
Atlantoscia sp.5	sp12	Epigean	5	1.16 (±0.114)	4.01 (±0.480)	0.34 (±0.018)	0	1.26 (±0.133)	2.36 (±0.290)	0.20 (±0.008)	3.64 (±0.644)	0.31 (±0.024)
Atlantoscia sp.6	sp13	Hypogean	4	1.4	3.6	0.3	0	1.4	2.55	0.21	3.9	0.33
Benthana cairensis	sp15	Hypogean	8	1.83 (±0.125)	6.28 (±0.225)	0.43 (±0.036)	0	1.35 (±0.050)	3.10 (±0.300)	0.21 (±0.010)	4.33 (±0.325)	0.29 (±0.008)

Family/Species	Species code	Environment	N	AFL	AL	AL/BL	DAA	CW	P1L	P1L/BL	P7L	P7L/BL
Benthana iporangensis	sp16	Hypogean	10	1.53 (±0.073)	5.18 (±0.433)	0.35 (±0.033)	0	1.40 (±0.058)	3.70 (±0.247)	0.25 (±0.014)	5.50 (±0.306)	0.37 (±0.015)
Benthana longicornis	sp17	Hypogean	1	3	9.95	0.9	0	2.4	4.8	0.44	7.6	0.69
Benthana picta	sp18	Epigean	2	4.75	14.25	0.46	0	3	7.1	0.23	11.7	0.38
Benthana picta	sp19	Hypogean	4	3.35	11.55	0.39	0	2.4	5.3	0.18	10.05	0.34
Benthana sp.1	sp20	Epigean	12	2.00 (±0.252)	6.55 (±0.700)	0.36 (±0.021)	0	1.58 (±0.167)	3.93 (±0.650)	0.22 (±0.016)	5.78 (±1.031)	0.32 (±0.027)
Benthana sp.1	sp21	Hypogean	1	2.4	7.75	0.4	0	1.75	4.15	0.21	7	0.36
Benthana sp.2	sp22	Hypogean	3	1.58 (±0.167)	4.97 (±0.233)	0.47 (±0.035)	0	1.27 (±0.017)	2.63 (±0.101)	0.25 (±0.017)	3.93 (±0.101)	0.37 (±0.011)
Benthana sp.3	sp23	Epigean	1	3.75	12.35	0.5	0	2.5	6	0.24	10.05	0.41
Benthana sp.4	sp24	Hypogean	6	1.11 (±0.056)	3.63 (±0.179)	0.36 (±0.015)	0	1.04 (±0.046)	2.21 (±0.048)	0.22 (±0.007)	2.90 (±0.123)	0.29 (±0.013)
Benthana taeniata	sp25	Epigean	15	1.48 (±0.101)	5.15 (±0.180)	0.41 (±0.018)	0	1.33 (±0.044)	2.88 (±0.148)	0.23 (±0.012)	4.42 (±0.186)	0.36 (±0.015)
Benthana taeniata	sp26	Hypogean	1	1.32	3.96	0.65	0	1.2	2.4	0.39	3.9	0.64
Styloniscidae												
Cylindroniscus flaviae	sp27	Hypogean	9	0.23 (±0.016)	0.74 (±0.055)	0.08 (±0.004)	1	0.50 (±0.021)	0.69 (±0.024)	0.07 (±0.003)	0.79 (±0.049)	0.08 (±0.003)
Styloniscus spinosus	sp37	Epigean	12	0.28 (±0.017)	0.86 (±0.065)	0.10 (±0.006)	1	0.45 (±0.022)	0.78 (±0.051)	0.09 (±0.007)	0.92 (±0.069)	0.11 (±0.007)
Styloniscus spinosus	sp38	Hypogean	1	0.23	1	0.07	1	0.58	0.98	0.07	1.18	0.09
Bathytropidae												
Neotroponiscus iporangaensis	sp30	Hypogean	3	0.64	2.6	0.14	0	1.08	1.58	0.09	1.75	0.1
Neotroponiscus sp.	sp31	Hypogean	1	0.73	2.97	0.16	0	1.23	1.87	0.1	2.23	0.12
Bathytropidae gen. sp.	sp14	Epigean	3	0.56 (±0.124)	2.11 (±0.458)	0.19 (±0.016)	0	0.94 (±0.195)	1.44 (±0.349)	0.13 (±0.004)	1.89 (±0.531)	0.17 (±0.017)
Dubioniscidae												
Dubioniscus sp.1	sp28	Epigean	1	0.58	2.3	0.12	0	1.08	1.55	0.08	2.01	0.11

Family/Species	**Species code**	**Environment**	**N**	**AFL**	**AL**	**AL/BL**	**DAA**	**CW**	**P1L**	**P1L/BL**	**P7L**	**P7L/BL**
Dubioniscus sp.2	sp29	Hypogean	5	0.92 (±0.085)	3.26 (±0.279)	0.19 (±0.012)	0	1.04 (±0.085)	1.94 (±0.160)	0.11 (±0.006)	2.59 (±0.300)	0.15 (±0.014)
Novamundoniscus sp.1	sp32	Hypogean	6	0.49 (±0.154)	1.69 (±0.396)	0.14 (±0.011)	0	0.63 (±0.080)	1.18 (±0.262)	0.10 (±0.007)	1.38 (±0.302)	0.11 (±0.007)
Novamundoniscus sp.2	sp33	Hypogean	5	0.90 (±0.029)	3.14 (±0.102)	0.21 (±0.015)	0	0.99 (±0.029)	1.75 (±0.117)	0.12 (±0.004)	2.45 (±0.146)	0.16 (±0.007)
Novamundoniscus sp.4	sp34	Hypogean	1	0.73	2.04	0.16	0	0.73	1.34	0.1	1.75	0.14
Novamundoniscus sp.5	sp35	Epigean	29	0.36 (±0.015)	1.40 (±0.146)	0.14 (±0.008)	0	0.61 (±0.087)	1.09 (±0.073)	0.11 (±0.002)	1.46 (±0.233)	0.15 (±0.017)
Novamundoniscus sp.6	sp36	Hypogean	1	0.98	3.18	0.18	0	0.95	2.1	0.12	2.55	0.15
Platyarthridae												
Trichorhina acrux	sp39	Hypogean	7	0.36 (±0.022)	1.18 (±0.098)	0.12 (±0.007)	0	0.58 (±0.076)	0.93 (±0.121)	0.09 (±0.003)	1.14 (±0.129)	0.11 (±0.002)
Trichorhina jurai	sp40	Hypogean	11	0.33 (±0.015)	1.14 (±0.083)	0.10 (±0.006)	0	0.65 (±0.033)	0.88 (±0.154)	0.08 (±0.014)	1.29 (±0.095)	0.11 (±0.005)
Trichorhina quadriocellata	sp41	Epigean	3	0.25	0.83	0.1	0	0.55	0.88	0.1	1.18	0.14
Trichorhina quadriocellata	sp42	Hypogean	2	0.33	1.1	0.13	0	0.63	0.7	0.08	1	0.11
Trichorhina sp.1	sp43	Hypogean	8	0.30 (±0.014)	0.66 (±0.331)	0.12 (±0.011)	0	0.54 (±0.022)	0.82 (±0.065)	0.09 (±0.005)	0.94 (±0.044)	0.11 (±0.010)
Trichorhina sp.2	sp44	Hypogean	1	0.3	0.93	0.11	0	0.55	0.73	0.09	0.93	0.11
Trichorhina sp.3	sp45	Epigean	14	0.32 (±0.036)	1.18 (±0.156)	0.13 (±0.008)	0	0.51 (±0.051)	0.82 (±0.065)	0.09 (±0.004)	1.09 (±0.145)	0.12 (±0.005)
Trichorhina sp.4	sp46	Epigean	14	0.30 (±0.014)	1.18 (±0.123)	0.11 (±0.004)	0	0.60 (±0.050)	0.88 (±0.058)	0.08 (±0.004)	1.11 (±0.131)	0.11 (±0.004)
Trichorhina tomentosa	sp47	Epigean	3	0.34 (±0.013)	1.28 (±0.050)	0.13 (±0.006)	0	0.63	0.95	0.10 (±0.008)	1.16 (±0.038)	0.12 (±0.014)
Trichorhina tomentosa	sp48	Hypogean	100	0.39 (±0.011)	1.41 (±0.060)	0.11 (±0.006)	0	0.68 (±0.075)	1.24 (±0.067)	0.09 (±0.006)	1.57 (±0.088)	0.12 (±0.007)

Supplementary material 4. Rarefaction and extrapolation curves based on sample size (a) and sample coverage (b) for terrestrial isopod assemblages in epigean and hypogean environments of the Parque Estadual Turístico do Alto Ribeira (PETAR), southeastern Brazil. Solid lines represent interpolated values, while dashed lines indicate extrapolated estimates. Shaded areas denote 95% confidence intervals.



Supplementary material 5. Summary of Generalized Linear Models (GLMs) applied to functional alpha diversity indices of terrestrial isopod assemblages across environments (epigean vs. hypogean). A Gaussian family was used for functional richness and functional divergence, and quasipoisson family for functional evenness.

		Estimate	**Std. Error**	**z value**	**Pr(>|z|)**	**Signif. Code**
Functional richness	(Intercept)	- 0.13	0.03	4.79	0.0004	***
	Environment	-0.07	0.03	-2.10	**0.057**	.
Functional divergence	(Intercept)	0.83	0.03	23.86	1.76e-11	***
	Environment	0.06	0.04	1.45	0.171	n.s.
Functional evenness	(Intercept)	0.13	0.03	4.79	0.00043	***
	Environment	-0.07	-0.03	-2.1	0.06	n.s.

Signif. code: 0 '***', 0.001 '**', 0.01 '*', 0.05 '.', n.s. = Not significative

Supplementary material 6. ANOVA test of Generalized Linear Models (GLMs) assessing the effect of environment on the functional diversity indices of terrestrial isopod assemblages. A Gaussian family was used for functional richness and functional divergence, and quasipoisson family for functional evenness. Likelihood ratio (lr x^2), degrees of freedom (d.f.).

Response variables	Explanatory variable	lr x^2	d.f.	p-value
Functional richness		0.017	1	**0.035 ***
Functional divergence	Environment	0.013	1	0.145
Functional evenness		0.084	1	0.496

CONSIDERAÇÕES FINAIS

Esta pesquisa destaca a importância da integração de diversas abordagens à biodiversidade, fundamentais para a compreensão dos processos de assembleias epígeas e hipógeas em sistemas cársticos tropicais. A descrição de novas espécies e ampliação dos registros de isópodes terrestres para a região do Alto Ribeira demonstram que o estudo de grupos tradicionalmente negligenciados continua sendo uma forma eficaz de revelar processos ecológicos e evolutivos da biodiversidade até então desconhecidos. Além disso, os padrões identificados reforçam a importância da inclusão de registros de coleções científicas como ferramentas estratégicas para superar lacunas no conhecimento histórico, especialmente em biomas altamente ameaçados, como a Mata Atlântica.

As análises de diversidade funcional revelaram que os habitats epígeos abrigam maior riqueza funcional, possivelmente associada à heterogeneidade ambiental e à disponibilidade de recursos orgânicos nesses ambientes. Em contraste, as comunidades hipógeas apresentaram uma diversidade funcional mais restringida no espaço funcional, refletindo fortes pressões seletivas e histórico evolutivo associado à especialização trófica, morfológica e comportamental. A elevada diversidade beta, principalmente impulsionada pelo turnover entre habitats, indica que processos de substituição de espécies são determinantes para a estruturação das assembleias ao longo do gradiente epígeo–hipógeo. Tal padrão sugere que a modificação dos habitats ou a homogeneização de condições ambientais pode comprometer não apenas a riqueza taxonômica local, mas também a diversidade de estratégias funcionais que sustentam o fluxo de energia e matéria nesses ecossistemas.

Diante desse cenário, a proteção simultânea dos habitats subterrâneos e de seus ambientes adjacentes revela-se essencial. As espécies troglóbias apresentam grande vulnerabilidade ecológica devido à dispersão limitada, taxas de reprodução reduzidas e dependência de microhabitats estáveis, enquanto as comunidades epígeas contribuem com funções ecológicas que possivelmente alimentam a dinâmica subterrânea, como o aporte de detritos e a transferência de nutrientes. Pressões antrópicas como a mineração, turismo desordenado, poluição de aquíferos, urbanização e introdução de espécies exóticas, comprometem diretamente esses processos e podem gerar desequilíbrios ambientais. A presença de espécies exóticas nesses sistemas, como observado em cavernas do sudeste do

Brasil, pode ter como consequência a substituição de espécies nativas por organismos tolerantes a perturbações.

Assim, o conhecimento gerado por este trabalho oferece bases científicas para ações de manejo e políticas para a conservação das regiões cársticas tropicais. A incorporação de métricas de diversidade funcional aos programas de monitoramento ambiental pode auxiliar na identificação de áreas prioritárias, na mitigação de impactos e na preservação de processos ecológicos essenciais. Finalmente, com o incremento das mudanças climáticas e do aumento da pressão antropogênica, torna-se urgente fortalecer iniciativas que aliem pesquisa científica, gestão de áreas protegidas e educação ambiental, garantindo a continuidade da biodiversidade hipógea e epígea da Mata Atlântica.

ANEXOS

Anexo 1. Coautoria em trabalho sobre novas espécies de *Diploexochus* na Colômbia.

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Research Article

From surface to caves: new species of *Diploexochus* Brandt, 1833 (Oniscidea, Armadillidae) from Colombia, with the description of the first troglobitic species

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Abstract

Two new species of *Diploexochus* are described, *Diploexochus cacique* **sp. nov.** from Cerro Bañaderos in Hatonuevo, La Guajira, and *Diploexochus troglobius* **sp. nov.** from Roca Madre Cave, Toluviejo, Sucre, both from the Tropical Dry Forest (TDF) areas of the Colombian Caribbean. The latter represent the first troglobitic species of the genus. Moreover, based on specimens from Sierra Nevada de Santa Marta, Magdalena (type locality), *Venezillo brevispinis* is placed into *Diploexochus* and an identification key for all species of the genus is given. The present work describes the first troglobitic species of the genus, and expand the knowledge of its distribution in northern South America.

Key words: Cave-dwelling, Colombian Caribbean, Neotropical, subterranean systems, terrestrial isopods, Tropical Dry Forest

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Introduction

Terrestrial isopods (Oniscidea) are considered one of the most diverse groups of crustaceans, comprising approximately 4,000 species in more than 500 genera in 38 or 39 families, distributed in almost all terrestrial habitats, including caves (Schmalfuss 2003; Hornung 2011; Sfenthourakis and Taiti 2015; Campos-Filho et al. 2017a, 2018, 2023a, 2023b; Taiti 2017; Dimitriou et al. 2019; Campos-Filho and Taiti 2021). Within Oniscidea, the family Armadillidae Brandt, 1831 is the most diverse, including more than 600 species in 81 genera and distributed in Neotropical, Afrotropical, Oriental, and Australian regions (Taiti et al. 1998; Schmalfuss 2003; Sfenthourakis and Taiti 2015; Rodríguez-Cabrera and Armas 2023). In Colombia, 13 species of the family are known: *Ctenorillo binomio* Carpio-Díaz, Bichuette & Campos-Filho, 2023, *C. dazai* Carpio-Díaz, López-Orozco & Campos-Filho, 2018, *C. humboldti* Carpio-Díaz, López-Orozco & Campos-Filho,

Anexo 2. Coautoria em trabalho sobre novas espécies de *Trichorhina* no Brasil.

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Article

Everything is similar, everything is different! *Trichorhina* Budde-Lund, 1908 (Oniscidea, Platyarthridae) from Brazilian caves, with descriptions of 11 new species

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CAMPOS-FILHO, I.S., LÓPEZ-OROZCO, C.M., CARPIO-DÍAZ, Y.M., BORJA-ARRIETA, R.L., GALLÃO, J.E., TAITI, S., SFENTHOURAKIS, S., BICHUETTE, M.E. **Everything is similar, everything is different! *Trichorhina* Budde-Lund, 1908 (Oniscidea, Platyarthridae) from Brazilian caves, with descriptions of 11 new species.** Biota Neotropica 23(4): e20231545. https://doi.org/10.1590/1676-0611-BN-2023-1545

Abstract: The present work describes 11 new species of the genus *Trichorhina* from Brazilian caves in the states of Bahia, Mato Grosso do Sul, Minas Gerais, Pará, and São Paulo. Moreover, the distribution of *T. tomentosa* has been expanded to include the states of Mato Grosso and Minas Gerais. Additionally, a distribution map and a key for all Brazilian species of *Trichorhina*, including epigean ones, are provided.
Keywords: *Terrestrial isopods; cave-dwellers; subterranean environments; Neotropics.*

Tudo é parecido, tudo é diferente! *Trichorhina* Budde-Lund, 1908 (Oniscidea, Platyarthridae) de cavernas brasileiras, com descrições de 11 novas espécies

Resumo: O presente trabalho descreve 11 novas espécies do gênero *Trichorhina* de cavernas brasileiras nos estados da Bahia, Mato Grosso do Sul, Minas Gerais, Pará e São Paulo. Além disso, a distribuição de *T. tomentosa* foi ampliada para incluir os estados de Mato Grosso e Minas Gerais. Adicionalmente, são fornecidos um mapa de distribuição e uma chave para todas as espécies brasileiras de *Trichorhina*, incluindo as epígeas.
Palavras-chave: *Isópodes terrestres; habitantes de cavernas; ambientes subterrâneos; Neotrópicos.*

Introduction

Terrestrial isopods (Oniscidea) comprise about 4,000 species in 38 or 39 families distributed in almost all types of terrestrial habitats (Schmalfuss 2003, Javidkar et al. 2015, 2017, Sfenthourakis & Taiti 2015, Dimitriou et al. 2019, Campos-Filho & Taiti 2021). The cave-dwelling Oniscidea includes over 400 species, predominantly from northern regions of the globe (*e.g.*, Vandel 1981, Taiti 2004, Taiti & Gruber 2008, Taiti & Xue 2012, Tabacaru & Giurginca 2013, Taiti et al. 2018, Bedek et al. 2019a, 2019b, 2019c).

In all of South America, only 2% of the territory has suitable lithology for the development of karst systems, of which Brazil has the highest number of systems and caves, approximately 23,000 caves in 19 karst areas (Auler 2002, 2017, CECAV 2018, Rubbioli et al. 2019). In recent years, numerous surveys conducted in these karst systems have revealed a significant potential for the occurrence of Oniscidea (*e.g.*, Gallão & Bichuette 2015, 2018, Silva & Ferreira 2015, Pellegrini & Ferreira 2016, Fernandes et al. 2019), and a high diversity of obligatory species has been described (Campos-Filho et al. 2011, 2014, 2015a, 2016, 2017a, 2017b, 2019, 2020, 2022a, 2022b, 2023a, 2023b, 2023c, Souza et al. 2006, 2010, 2015, Bastos-Pereira et al. 2017, 2022, Fernandes et al. 2018, Cardoso et al. 2020a, 2020b, 2021, 2022a, 2022b, 2023, Cardoso & Ferreira 2023).

To date, more than 230 species of terrestrial isopods have been identified in Brazil (Campos-Filho et al. 2018a, 2018b, 2019, 2020, Cardoso et al. 2020a, 2020b, 2021, Cardoso & Ferreira 2023), of which 93 have been recorded in subterranean environments (see Campos-Filho et al. 2022c, 2023c, Cardoso & Ferreira 2023).

The family Platyarthridae comprises 130 species in the genera *Cephaloniscus* Ferrara & Taiti, 1989, *Echinochaetus* Ferrara & Schmalfuss, 1983, *Gerufa* Budde-Lund, 1909, *Lanceochaetus* Schmalfuss & Ferrara, 1978, *Manibia* Barnard, 1932, *Niambia* Budde-Lund, 1908, *Papuasoniscus* Vandel, 1973, *Platyarthrus* Brandt, 1833,

Anexo 3. Coautoria em trabalho sobre novas espécies de isópodes terrestres do Brasil.

Shedding light into Brazilian subterranean isopods (Isopoda, Oniscidea): expanding distribution data and describing new taxa

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Anexo 4. Coautoria em trabalho sobre novas espécies de isópodes terrestres do Brasil.

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Research article

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Iron-isopods: new records and new species of terrestrial isopods (Isopoda, Oniscidea) from Brazilian Amazon iron ore caves

Carlos Mario LÓPEZ-OROZCO[1,*], Ivanklin Soares CAMPOS-FILHO[2], Jéssica S. GALLO[3], Jonas E. GALLÃO[4], Yesenia M. CARPIO-DÍAZ[5], Ricardo BORJA-ARRIETA[6] & Maria Elina BICHUETTE[7]

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Abstract. Two new species of terrestrial isopods are described from iron ore caves in Brazil, within the Amazon biome, *Circoniscus mendesi* López-Orozco, Campos-Filho & Bichuette sp. nov. and *C. xikrin* López-Orozco, Campos-Filho & Carpio-Díaz sp. nov. (Scleropactidae). In addition, the knowledge of the distribution of *Ctenorillo ferrarai* Campos-Filho, Araujo & Taiti, 2014 (Armadillidae) is extended to Parauapebas, and *Benthanoides tarzan* Cardoso & Ferreira, 2023 to south area of the Campos Ferruginosos National Park, both in the State of Pará. Moreover, a distribution map and photographs of the species are given.

Keywords. Neotropical, iron caves, Parauapebas, Canaã dos Carajás, woodlice.

Anexo 5. Coautoria em trabalho sobre novas espécies de isópodes terrestres do Brasil.

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Research Article

First amphibious Crinocheta (Isopoda, Oniscidea) from the Neotropics with a troglobitic status: a relictual distribution

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Abstract

The first freshwater amphibian representative of Crinocheta (Oniscidea) from the Neotropics is described from caves within the Brazilian Cerrado biome, state of Mato Grosso do Sul. *Kadiweuoniscus rebellis* **gen. et sp. nov.** is placed in the family Philosciidae. The present work represents a significant contribution to future studies seeking to understand the ecological and evolutionary processes of Crinocheta within the Neotropical region. Moreover, it highlights the importance of biodiversity surveys in subterranean environments toward effective conservation efforts of these unique habitats and their surroundings.

Key words: Cave fauna, new genus, new species, Serra da Bodoquena, southwestern Brazil, terrestrial isopods, troglobitic species

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Introduction

Terrestrial isopods (Oniscidea) are considered the most diverse group of isopods, with more than 4000 species in more than 500 genera in 38 or 39 families (Schmalfuss 2003; Taiti 2004; Javidkar et al. 2015; Sfenthourakis and Taiti 2015; Dimitriou et al. 2019; Campos-Filho and Taiti 2021). These organisms are distributed in almost all terrestrial environments on the planet, ranging from the supralittoral zone to high mountains, and from tropical zones to deserts (Schmalfuss 2003; López-Orozco et al. 2022). Additionally, a considerable number of species inhabit subterranean environments (Vandel 1973; Schmalfuss 2003; Taiti and Gruber 2008; Bedek et al. 2011; Taiti and Xue 2012; Tabacaru and Giurginca 2013; Reboleira et al. 2015).

Regarding the phylogeny of the group, morphological studies show Oniscidea as monophyletic, including the Sections Ligiidae, Tylidae, Mesoniscidae, Synocheta, and Crinocheta (Schmalfuss 1989; Wägele 1989; Erhard 1998; Schmidt 2008). All these authors recognized Synocheta as the sister group of Crinocheta. The last section is the most diverse, representing more than 80% of the entire suborder inhabiting various types of habitats (Schmidt 2002, 2003,

Anexo 6. Coautoria em trabalho sobre novas espécies de isópodes terrestres do Brasil.

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RESEARCH ARTICLE

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Describing to preserve – three new species of *Xangoniscus* (Oniscidea, Styloniscidae) of unprotected caves in dry areas from Bahia state, northeastern Brazil

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Abstract

Three new troglobitic amphibious species of *Xangoniscus* (Styloniscidae) have been described from limestone caves of the Bambui Group semiarid ecosystems (Chacoan subregion) in the state of Bahia: *Xangoniscus antiquus* **sp. nov.**, *X. chaimowiczi* **sp. nov.**, and *X. jonasi* **sp. nov.** Natural history information is provided for *X. chaimowiczi* **sp. nov.** and *X. jonasi* **sp. nov.** Considering the differences between the known species of *Xangoniscus* and those described in this study, we redefined the diagnostic characteristics of the genus. Moreover, the distribution of *Xangoniscus* is discussed. The species described in this study, along with those previously reported, serve as fundamental tools for decision-making processes aimed at conserving Brazil's speleological natural heritage.

Keywords

Amphibious Oniscidea, Cerrado, Caatinga, troglobitic, woodlice