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Sistemática, Biogeografia e Ecologia de Arachnida. Parte I

Boletim do Museu Paraense Emílio Goeldi

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IMAGEM DA CAPA
Aranha-lobo da espécie *Lycosa erythrognatha*.
Foto: Leonardo Carvalho.

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CARTA DOS EDITORES

O terceiro número de 2024 do **Boletim do Museu Paraense Emílio Goeldi. Ciências Naturais** traz o resultado da chamada especial para recebimento de artigos sobre "Sistemática, biogeografia e ecologia de Arachnida". Dezesseis artigos científicos foram aprovados para publicação na edição especial. Os oito primeiros trabalhos encontram-se publicados neste número, enquanto os demais serão publicados no primeiro número do próximo ano. Esta edição temática destaca-se pela abrangência taxonômica e geográfica, havendo estudos com aranhas, escorpiões e pseudoescorpiões, desenvolvidos no Brasil, Uruguai, Madagascar, Brunei, Malásia, Indonésia e Singapura.

O primeiro artigo, de autoria de Arias e colaboradores, descreve e ilustra uma nova espécie de tarântula do gênero *Plesiopelma* (família Theraphosidae) com base em espécimes de ambos os sexos encontrados no Uruguai, utilizando dados morfológicos e moleculares.

Ainda sobre descrição de novas espécies, Jäger & Koh apresentaram oito espécies novas de aranhas caçadoras do gênero *Heteropoda* (família Sparassidae), ocorrentes no sudoeste asiático. Seis delas são incluídas em um novo grupo, o *ocyalina*. Além de fornecer dados importantes sobre história natural e distribuição, o trabalho estabelece uma conexão com a ciência cidadã, fornecendo fotografias de animais vivos e utilizando registros fotográficos da página da *internet* iNaturalist sobre uma espécie de *Heteropoda* com marcante padrão de colorido como um meio para suplementar os dados de sua área de distribuição.

Em outro notável trabalho taxonômico, Sherwood & Jäger demonstram a importância da documentação moderna de material-tipo histórico como base para o estudo de um grupo de aranhas pouco pesquisado, o das aranhas-lobo (família Lycosidae) da ilha de Madagascar. Neste estudo, os autores documentam a morfologia dos espécimes-tipo de quatro espécies descritas no século 19 e no início do século 20, discutindo as identidades taxonômicas das únicas seis espécies desta família atualmente conhecidas para a ilha. Este trabalho estabelece um sólido ponto de partida para o estudo taxonômico da fauna de aranhas-lobo malgaxes.

A amostragem de aranhas ainda apresenta importantes questões a serem resolvidas na área da ecologia. Carvalho e colaboradores compararam a amostragem de aranhas em copas bem estruturadas e copas isoladas de árvores de grande porte, sobre os padrões de diversidade das assembleias amostradas. Como resultado, os autores observaram semelhanças entre a abundância e a riqueza, bem como diferenças na composição, discutindo fatores favoráveis ou contrários a estas amostragens.

Na área da etologia, Gonçalves e colaboradores trazem um estudo sobre o comportamento reprodutivo e o cuidado parental do pseudoescorpião (Pseudoscorpiones) da espécie *Americhernes bethaniae* (família Chernetidae) a partir de espécimes coletados em área de cerrado de Goiás. Os autores apresentam análises e observações que elucidam aspectos importantes sobre a identificação do sexo, rituais de cortejo e comportamentos de transferência de espermatóforos.

Em outro estudo sobre comportamento de pseudoescorpiões conduzido em algumas áreas de cerrado do estado de Goiás e São Paulo, Reis e colaboradores apresentaram evidências da predação intraguilda em que duas espécies do gênero *Victorwithius* (família Withiidae) e uma espécie do gênero *Parachernes* (família Chernetidae) foram registradas alimentando-se de imaturos da espécie *Paratemnoides nidificator* (família Atemnidae). *Paratemnoides nidificator* é uma das espécies de pseudoescorpião com maior distribuição geográfica conhecida no Brasil, formando grandes colônias embaixo de cascas de árvores. O estudo mostra a importância desta espécie em múltiplas relações tróficas, previamente não documentadas.

Gonzalez-Filho e colaboradores revisaram a distribuição geográfica das enigmáticas aranhas-caranguejeiras da família Barychelidae. Os autores compilaram informações já publicadas, registros de espécimes de coleções científicas biológicas e ainda dados de ciência cidadã, totalizando 127 novos registros de Barychelidae para o Brasil, um grande esforço para diminuir o déficit wallaceano associado a estas aranhas.

Ainda sobre a distribuição de aranhas, Cajade e colaboradores apresentam os primeiros registros para a América do Sul continental de *Agyneta galapagosensis*, *Erigone autumnalis* e *Mermessus fradeorum*, três espécies de aranhas da família Linyphiidae. Além disso, os autores ainda ampliaram a distribuição da espécie *Neriene redacta* (família Linyphiidae). Estes registros ampliam a distribuição dessas quatro espécies de Linyphiidae, bem como atualizam os dados sobre as condições ambientais em que elas habitam, incluindo ambientes urbanos.

Encerrando esta carta, agradecemos aos avaliadores de várias instituições do Brasil e do exterior, pela dedicação à leitura dos artigos publicados nesta edição, bem como a Rafaele Lima, Adrienny Souza, Luiz Ramiro Cardoso e Talita do Vale, pela dedicação no trabalho de editoração.

Alexandre Bragio Bonaldo, Cláudia Xavier & Leonardo Sousa Carvalho
Editores Convidados

Fernando da Silva Carvalho-Filho
Editor Científico

LETTER FROM THE EDITORS

The third issue of 2024 of the **Boletim do Museu Paraense Emílio Goeldi. Ciências Naturais** presents the results of the special call for articles on "Systematics, Biogeography, and Ecology of Arachnida." Fifteen scientific articles were approved for publication in this special issue. The first eight papers are published in this edition, while the remainder will be included in the first issue of the coming year. This thematic edition stands out for its taxonomic and geographic scope, featuring studies on spiders, scorpions, and pseudoscorpions conducted in Brazil, Uruguay, Madagascar, Brunei, Malaysia, Indonesia, and Singapore.

The first article, authored by Arias and collaborators, describes and illustrates a new tarantula species of the genus *Plesiopelma* (family Theraphosidae) based on specimens of both sexes found in Uruguay, utilizing morphological and molecular data.

Regarding new species descriptions, Jäger & Koh presented eight new species of hunting spiders of the genus *Heteropoda* (family Sparassidae), found in Southeast Asia. Six of these species are included in a new group, *ocyalina*. Besides providing important data on natural history and distribution, the study establishes a connection with citizen science by offering photographs of live specimens and using photographic records from the iNaturalist website to supplement distribution data for a strikingly patterned species of *Heteropoda*.

In another remarkable taxonomic study, Sherwood & Jäger demonstrate the importance of modern documentation of historical type material as a foundation for studying a little-researched group of spiders, the wolf spiders (family Lycosidae) of Madagascar. In this study, the authors document the morphology of type specimens of four species described in the 19th and early 20th centuries, discussing the taxonomic identities of the only six species of this family currently known from the island. This work establishes a solid starting point for the taxonomic study of Malagasy wolf spider fauna.

Spider sampling still presents significant unresolved issues in ecology. Carvalho and collaborators compared spider sampling in well-structured and isolated canopies of large trees, analyzing the diversity patterns of the sampled assemblages. The authors observed similarities in abundance and richness, as well as differences in composition, discussing factors that either favor or hinder these samplings.

In the field of ethology, Gonçalves and collaborators present a study on the reproductive behavior and parental care of the pseudoscorpion (Pseudoscorpiones) species *Americhernes bethaniae* (family Chernetidae) based on specimens collected in the cerrado biome of Goiás. The authors provide analyses and observations elucidating important aspects of sex identification, courtship rituals, and spermatophore transfer behaviors.

In another study on pseudoscorpion behavior conducted in cerrado areas of Goiás and São Paulo, Reis and collaborators provided evidence of intraguild predation involving two species of the genus *Victorwithius* (family Withiidae) and one species of the genus *Parachernes* (family Chernetidae) feeding on immature specimens of the species *Paratemnoides nidificator* (family Atemnidae). *Paratemnoides nidificator* is one of the pseudoscorpion species with the broadest known geographical distribution in Brazil, forming large colonies under tree bark. The study highlights this species' importance in multiple previously undocumented trophic relationships.

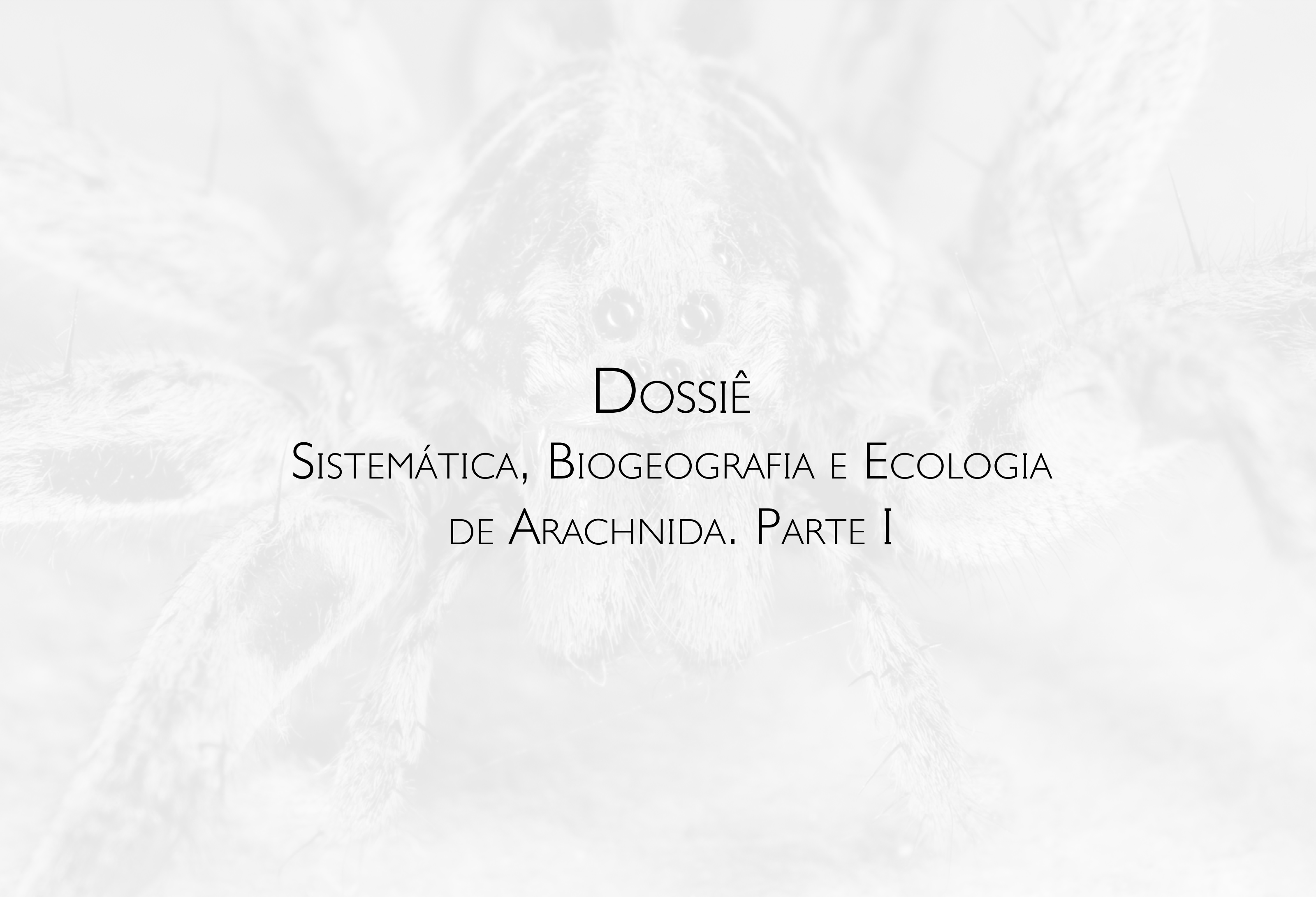
Gonzalez-Filho and collaborators reviewed the geographic distribution of the enigmatic trapdoor spiders of the family Barychelidae. The authors compiled published information, records of specimens from biological scientific collections, and citizen science data, totaling 127 new records of Barychelidae for Brazil—a major effort to reduce the Wallacean shortfall associated with these spiders.

On the topic of spider distribution, Cajade and collaborators report the first records for continental South America of *Agyneta galapagosensis*, *Erigone autumnalis*, and *Mermessus fradeorum*, three species of spiders from the family Linyphiidae. Additionally, the authors expanded the distribution of the species *Neriene redacta* (family Linyphiidae). These records extend the range of these four Linyphiidae species and update data on the environmental conditions in which they inhabit, including urban environments.

To conclude this letter, we extend our gratitude to the reviewers from various institutions in Brazil and abroad for their dedication to reviewing the articles published in this edition. We also thank Rafaele Lima, Adrienny Souza, Luiz Ramiro Cardoso, and Talita do Vale for their dedication to the editorial work.

Alexandre Bragio Bonaldo, Cláudia Xavier & Leonardo Sousa Carvalho
Guest Editors

Fernando da Silva Carvalho-Filho
Scientific Editor



Dossiê

Sistemática, Biogeografia e Ecologia de Arachnida. Parte I

A new species of *Plesiopelma* from Uruguay (Araneae, Theraphosidae, Theraphosinae)

Uma nova espécie de *Plesiopelma* do Uruguai (Araneae, Theraphosidae, Theraphosinae)

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Abstract: We describe and illustrate a new tarantula species of the genus *Plesiopelma* from Lavalleja and Maldonado, Uruguay. *Plesiopelma arevaloae* sp. nov. is distinguished from other known species by morphological characters and molecular evidence.

Keywords: Taxonomy. Morphology. Molecular. Tarantula.

Resumo: Descrevemos e ilustramos uma nova espécie de tarântula do gênero *Plesiopelma* de Lavalleja e Maldonado, Uruguai. *Plesiopelma arevaloae* sp. nov. é distinguida de outras espécies conhecidas por caracteres morfológicos e evidências moleculares.

Palavras-chave: Taxonomia. Morfologia. Molecular. Tarântula.

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INTRODUCTION

Theraphosidae is the most speciose family within Mygalomorphae spiders comprising 168 genera and 1,117 species (World Spider Catalog, 2024). They are mostly large, hairy spiders that live in burrows, under stones or in silken retreats on the ground or on trees (Pérez-Miles, 2020). Theraphosidae occurs mainly in tropical and subtropical regions and occupies habitats from deep caves up to 4,000 m (Mendoza & Francke, 2017; Ferretti et al., 2018). More than a half of the species of the family are included in the subfamily Theraphosinae, endemic of the Neotropics. Due to their homogeneity and conservative morphology, its taxonomy was in a chaotic state (Raven, 1990; Pérez-Miles et al., 1996; Bertani, 2001; Ferretti & Barneche, 2013). However, in the last two decades, theraphosid systematics has progressed considerably, recently the incorporation of molecular characters led several authors to propose well supported phylogenies (Hamilton et al., 2011, 2014, 2016; Hendrixson et al., 2013, 2015; Wilson et al., 2013; Montes de Oca et al., 2016; Ortiz & Francke, 2016, 2017; Mendoza & Francke, 2017, 2020; Turner et al., 2018; Lüddecke et al., 2018; Hüsser, 2018; Fabiano-da-Silva et al., 2019; Foley et al., 2019, 2021; Candia-Ramírez & Francke, 2020; Korba et al., 2022; Galleti-Lima et al., 2023; Biswas et al., 2023). Despite these advances, the diversity of tarantulas, mainly in the New World, probably remains underestimated but molecular markers have demonstrated to be useful tools to reveal cryptic species, redundantly described taxa, and intraspecific and interspecific paraphyly (Hamilton et al., 2016).

The genus *Plesiopelma* Pocock 1901 was described based on a male of the type species *Plesiopelma myodes* Pocock 1901 from Uruguay. *Plesiopelma* is characterized by a combination of characters: the presence of convergent setae on dorsal abdomen, males with a retrolateral basal nodule on metatarsi I; most males with a subapical tooth on palpal bulb; prolateral superior and inferior keels well developed on bulb. Females with two spiral-shaped spermathecal receptacles (Ferretti & Barneche, 2013). The genus comprises thirteen species registered in Argentina, Brazil, Paraguay, Bolivia, Uruguay and Venezuela (World Spider Catalog, 2024). *Plesiopelma* was considered a senior synonym of *Ceropelma* Mello-Leitão 1923 by Pérez-Miles et al. (1996) who transferred their five species and proposed the following combinations: *Plesiopelma flavohirtus* (Simon 1889), *Plesiopelma semiauranticum* (Simon 1897), *Plesiopelma insulare* (Mello-Leitão 1923), *Plesiopelma longisternale* (Schiapelli & Gerschman 1942) and *Plesiopelma gertschi* (Caporiacco 1955). Pérez-Miles et al. (1996) also considered that *Plesiopelma imperatrix* Piza, 1976, was not *Plesiopelma* because of the presence of types I and III urticating setae and the spermathecal morphology with a single receptacle. *Plesiopelma rectimanus* (Mello-Leitão, 1923) was transferred from *Hapalopus* Ausserer 1875 by Pérez-Miles et al. (1996). Yamamoto et al. (2007) transferred *Plesiopelma physopus* (Mello-Leitão, 1926) and *Plesiopelma minensis* (Mello-Leitão 1943) from *Tmesiphantes* Simon 1892 and Yamamoto et al. (2012) transferred *Catanduba flavohirtus* Yamamoto, Lucas & Brescovit 2012 from *Plesiopelma*. Ferretti and Barneche (2013) described *Plesiopelma paganoi* and *Plesiopelma aspidosperma,* both species are restricted to the northern province of Salta, Argentina.

Recently Ferretti et al. (2024) studied several populations from Argentina of the widespread tarantula *P. longisternale* using morphological characters and molecular markers. Their results revealed the presence of a new species from Catamarca, Argentina, *Plesiopelma absconditus* Ferretti, Nicoletta & Soresi 2024.

Studying the material of *Plesiopelma* from several sites of Uruguay deposited in the arachnological collection of the Facultad de Ciencias (FCE-My), we found some individuals from Lavalleja and Maldonado that fit with the diagnosis of the genus but differs from all known species. We collected additional material from the same sites, performed a molecular study, and included it in the phylogeny recently published by Ferretti et al. (2024). Both morphological and molecular results congruently support the presence of a new species, consequently we propose *Plesiopelma arevaloae* sp. nov. which is here diagnosed, described and illustrated.

MATERIAL AND METHODS

Studied individuals were deposited in the arachnological collection of the *Facultad de Ciencias*, Montevideo, Uruguay (Curator: Dr. Miguel Simó). Description style, terms and morphological characters examined are the usually used in the standards of Theraphosidae taxonomy (Pérez-Miles, 2020) and specially used in last *Plesiopelma* studies (Ferretti & Barneche, 2013; Ferretti et al., 2024). All measurements are given in millimeters and were taken with an ocular micrometer and digital caliper. Photographs were taken with a Leica M205A stereomicroscope. Palpal bulbs were removed from palp for examination and photographed in prolateral and retrolateral views. Spermathecae were dissected and cleared by immersion in clove oil to make transparent tissues that cover the structure. For the study of urticating setae, they were removed from six different points of the urticating patch on the abdomen (central and lateral lines, anterior, medial and posterior) using a forceps and examined by an optical microscope (Nikon YS 100). Description and notation for leg and palpal spines follow Petrunkevitch (1925).

Abbreviations: AME = anterior median eyes, ALE = anterior lateral eyes, PME = posterior median eyes, PLE = posterior lateral eyes, PLS = posterior lateral spinneret, PMS = posterior median spinneret, PI = prolateral inferior keel, PS = prolateral superior keel, D =dorsal, V= ventral, P = prolateral, R = retrolateral, PCR = polymerase chain reaction.

This paper and its nomenclatural acts have been registered in ZooBank, the online registration system for the ICZN (http://zoobank.org/ urn:lsid:zoobank.org:pub:2CA474CA-9C5A-456A-B193-C20A3CB90C28).

MOLECULAR PROCEDURES AND ANALYSIS

For DNA extraction, the tissue was digested with proteinase K and lysis buffer, then the proteins were precipitated with sodium chloride while the DNA was precipitated with isopropanol, which was resuspended in water (protocol modified from Miller et al., 1988). The mitochondrial marker cytochrome oxidase subunit 1 (COI) was used. For PCR amplification, the universal primers LCO-1490 and HCO-2198 were used (Folmer et al., 1994). The PCR was performed using NZYtech Green Master Mix following their standard protocol. The PCR was performed in the SimpliAmp thermocycler (appliedbiosystems by thermo fisher scientific) and Ferretti et al. (2024) cycling conditions were followed. The PCR products were sent for purification and subsequent sequencing to the company Macrogen (South Korea), where both strands were sequenced. The chromatograms were inspected and the sequences were edited using MEGA11 (Tamura et al., 2021), obtaining a fragment of 595 base pairs for two individuals (FCE-My 1440, FCE-My 1441).

We added 16 sequences belonging to *Plesiopelma longisternale* and *P. absconditus* and five sequences of *Grammostola* Simon 1892 as an outgroup (Table 1). An alignment was made with the ClustalW algorithm of MEGA11. A genetic distance matrix was calculated using the p-distance model in MEGA11. Three phylogenetic inferences were performed with the softwares MEGA11, IQ-TREE (Nguyen et al., 2015) and BEAST2 (Bouckaert et al., 2014). 1. Phylogeny in MEGA11: Maximum likelihood inference under a Tamura-Nei evolutionary model with 1,000 bootstrap iterations. 2. Phylogeny in IQ-TREE: Maximum likelihood inference performed in the online server (IQ-TREE, n. d.) with 1,000 iterations of 'ultrafast bootstrap.' The automatic model selection using ModelFinder according to the BIC criteria was TIM3+F+G4. 3. Phylogeny in BEAST2: Bayesian inference. The XML file was created in BEAUti, and two independent runs were performed in BEAST2, with the default parameters. The Monte-Carlo Markov chains were run for 100 million generations, and trees were sampled every 10,000 generations, so 10,000 trees were saved. Trees were annotated with TreeAnotator with a burnin of 10%. In TRACER (Rambaut et al., 2018) the convergences of the independent runs were checked. Also, it was confirmed that the estimated sample sizes (ESS) for each parameter were greater than 200, as an indicator of independence

Table 1. Samples taken from the Genbank.

	Sample	NCBI Code
Plesiopelma absconditus	El Singüil 29	PP028752.1
	El Singüil N3	PP028762.1
	El Singüil N4	PP028763.1
Plesiopelma longisternale	Cumbrecita 30	PP028753.1
	Cumbrecita 31	PP028754.1
	Cumbrecita 34	PP028757.1
	Balcarce 36	PP028759.1
	Tandil N5	PP028764.1
	Tandil N6	PP028765.1
	Villa Ojo de Agua 43	PP028760.1
	Villa Ojo de Agua 44	PP028761.1
	Achiras 33	PP028756.1
	Alpa Corral 35	PP028758.1
	FUNKE 27	PP028750.1
	Lihue Calel 32	PP028755.1
	PPET 28	PP028751.1
Out-group	*Grammostola andreleetzi* Vol 2008	KT965218.1
	Grammostola anthracina C.L. Koch 1842	KT965202.1
	Grammostola burzaquensis Ibarra 1946	KT965249.1
	Grammostola pulchra Mello-Leitão 1921	KT965206.1
	Grammostola quirogai Montes de Oca, D'Elía & Pérez-Miles 2016	KT965275.1

between the samples in the run. Following the principles of integrative taxonomy, we delimited the species based on the congruence of the results obtained across the different sources of data (Padial et al., 2010; Schlick-Steiner et al., 2010; Carstens et al., 2013).

RESULTS

PHYLOGENY AND SPECIES DELIMITATION

The results of the three phylogenetic inferences were congruent. In the present study, the greater diversity in *P. logisternale* is related with the number of terminals included in the analysis, due to the greater geographic range. *Plesiopelma* samples from Argentina were resolved into two separate clades corresponding to *P. longisternale* and *P. absconditus*. Individuals from Lavalleja and Maldonado (Uruguay) were grouped as a distinct clade, with individuals from Argentina as a sister group, with high statistical support in the three inferences (bootstrap = 100, ultrafast bootstrap = 100, posterior probability = 1) (Figure 1). In addition, the genetic distances of the *Plesiopelma arevaloae* sp. nov. samples from Uruguay were always higher than 10% in comparison with all other populations considered (Table 2). The results based on molecular evidence were supported by the morphological differences found, particularly in the number of labial and maxillary cuspules, the morphology of the copulatory bulb in males, the morphology of spermathecae in females and the body size (see below).

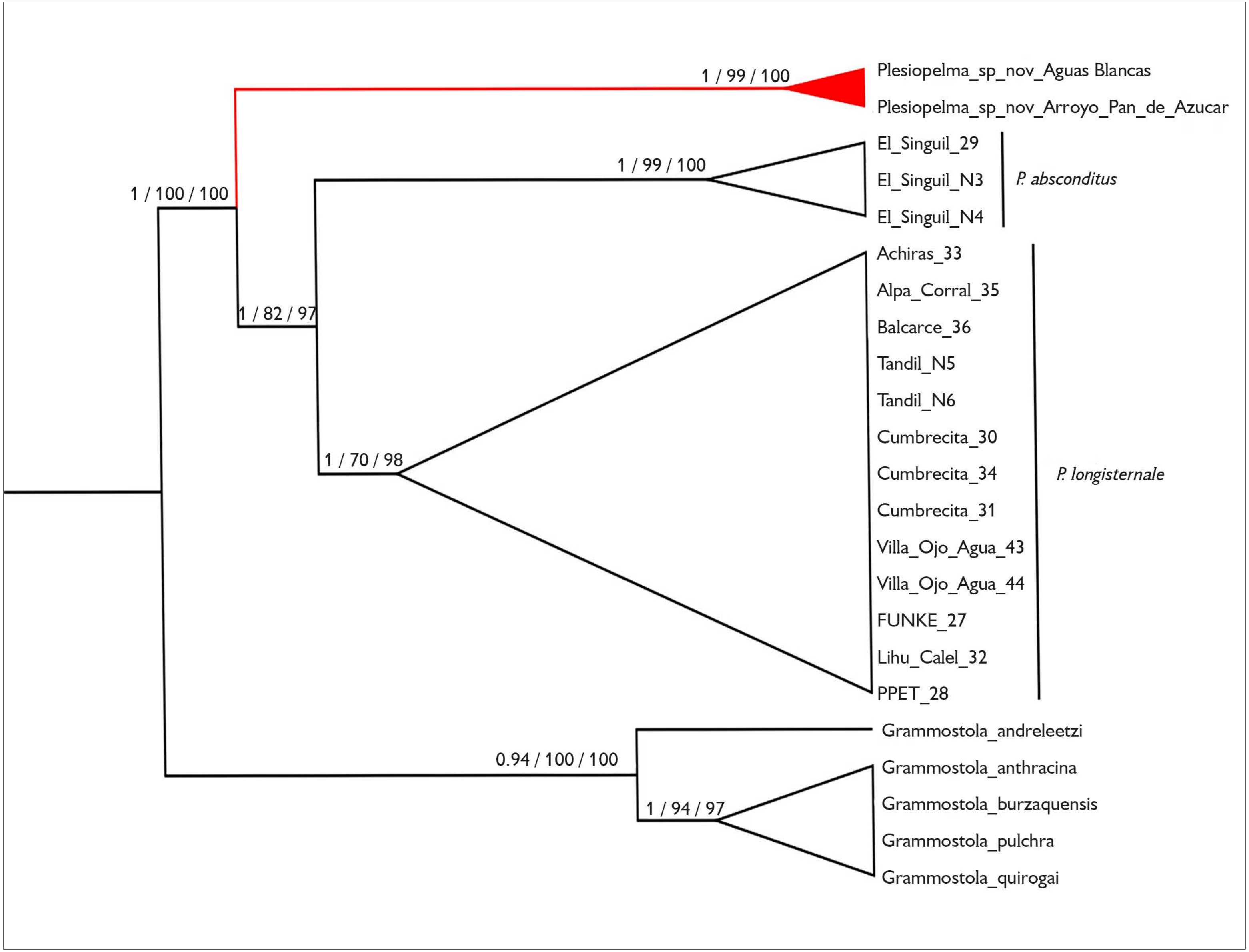

Figure 1. Summary of maximum likelihood and bayesian inference trees showing node support (posterior probability/ultrafast Bootstrap – IQ-TREE/Bootstrap - Mega).

Table 2. Inter-population p-distances calculated for COI sequences: a pairwise genetic distance measure based on nucleotide differences, where the numbers in e-ach column correspond to those of each sample.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
1	Aguas Blancas 1441																						
2	Arroyo Pan de Azucar 1440	0,02																					
3	*Plesiopelma absconditus*	0,12	0,11																				
4	*Plesiopelma absconditus*	0,12	0,11	0,00																			
5	*Plesiopelma absconditus_*	0,12	0,11	0,00	0,00																		
6	Achiras 33	0,11	0,10	0,08	0,08	0,08																	
7	Alpa Corral 35	0,11	0,10	0,08	0,08	0,08	0,00																
8	Balcarce 36	0,10	0,10	0,08	0,08	0,08	0,01	0,01															
9	Tandil N5	0,10	0,10	0,08	0,08	0,08	0,01	0,01	0,01														
10	Tandil N6	0,10	0,10	0,08	0,08	0,08	0,01	0,01	0,00	0,00													
11	Cumbrecita 30	0,11	0,11	0,08	0,08	0,08	0,01	0,01	0,01	0,01	0,01												
12	Cumbrecita 34	0,11	0,11	0,08	0,08	0,08	0,01	0,01	0,01	0,01	0,01	0,00											
13	Cumbrecita 31	0,11	0,11	0,08	0,08	0,08	0,01	0,01	0,01	0,02	0,01	0,00	0,00										
14	Villa Ojo Agua 43	0,11	0,11	0,08	0,08	0,08	0,01	0,01	0,01	0,02	0,02	0,01	0,01	0,01									
15	Villa Ojo Agua 44	0,11	0,11	0,08	0,08	0,08	0,01	0,01	0,01	0,02	0,02	0,01	0,01	0,01	0,00								
16	FUNKE 27	0,12	0,11	0,08	0,08	0,08	0,01	0,01	0,02	0,03	0,03	0,02	0,02	0,02	0,02	0,02							
17	Lihu Calel 32	0,11	0,10	0,08	0,08	0,08	0,00	0,00	0,01	0,02	0,02	0,01	0,01	0,01	0,01	0,01	0,01						
18	PPET 28	0,11	0,10	0,08	0,08	0,08	0,00	0,00	0,01	0,02	0,02	0,01	0,01	0,01	0,01	0,01	0,01	0,00					
19	*Grammostola andreleetzi*	0,15	0,15	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16				
20	*Grammostola anthracina*	0,16	0,15	0,17	0,17	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,16	0,17	0,16	0,16	0,14			
21	*Grammostola burzaquensis*	0,18	0,18	0,17	0,17	0,17	0,18	0,18	0,18	0,18	0,18	0,18	0,18	0,18	0,18	0,18	0,18	0,18	0,18	0,13	0,10		
22	*Grammostola pulchra*	0,17	0,17	0,16	0,16	0,16	0,16	0,16	0,16	0,15	0,15	0,16	0,16	0,16	0,16	0,16	0,17	0,16	0,16	0,14	0,11	0,09	
23	*Grammostola quirogai*	0,17	0,16	0,18	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,17	0,18	0,17	0,17	0,14	0,11	0,11	0,10

TAXONOMY

Family Theraphosidae Thorell, 1869
Subfamily Theraphosinae Thorell, 1870
Genus *Plesiopelma* Pocock 1901
Plesiopelma Pocock, 1901:553; Petrunkevitch, 1911:85; Pérez-Miles et al., 1996:55 (removed of synonymy of *Citharacanthus*)
Citharacanthus Pocock, 1901:551; Pérez-Miles et al., 1996:46 (in part). *Dryptopelma* Simon, 1889:402 (in part)
Eurypelma C. L. Koch, 1850:70 (in part); Roewer, 1942:240 (in part); Brignoli, 1983:137 (in part)
Ceropelma Mello-Leitão, 1923:175; Pérez-Miles et al., 1996:55 (Synonymy with *Plesiopelma*)

Type species: *P. myodes* Pocock, 1901, by monotypy.

Plesiopelma arevaloae Arias & Pérez-Miles sp. nov.
http://zoobank.org/urn:lsid:zoobank.org:act:5D52BDB9-6F88-4CB5-B4CD-E89C695FBBFB
(Figures 2-6, 8, 9; Table 3 and 4)

Type material. Holotype ♂. Uruguay, Lavalleja, Aguas Blancas (34° 32’ S, 55° 24’ W), 15 May 2008, C. Perafán, L. Baruffaldi, F. Pérez-Miles (FCEMy-0773). Paratypes ♀, same locality, 7 July 2000, F.G. Costa, F. Pérez-Miles, M. Pérez, (FCEMy-1415). Aguas Blancas (34° 32’ S, 55° 24’ W): 15 May 2008, 1♂, Baruffaldi, Perafán, Montes de Oca & Pérez-Miles (FCE-My 0772). Aguas Blancas (34° 32’ S, 55° 24’ W): 15 May 2008, 1♂, Baruffaldi, Perafán, Montes de Oca & Pérez-Miles (FCE-My 0777). Aguas Blancas (34° 32’ S, 55° 24’ W): 15 May 2008, 2 ♂, Baruffaldi, Perafán, Montes de Oca & Pérez-Miles (FCE-My 0783). Aguas Blancas (34° 32’ S, 55° 24’ W): 15 May 2008, 1 ♂, Baruffaldi, Perafán, Montes de Oca & Pérez-Miles (FCE-My 0776). Aguas Blancas (34° 32’ S, 55° 24’ W), 2 ♀, (FCE-My 1415).

Non-type material. Maldonado: Sierra de las Animas (34° 42’ S, 55° 19’ W): 19 April 1953, 1♂, P.R. San Martín, L.C Zolessi (FCE-My 0659). Sierra de las Ánimas (34° 42’ S, 55° 19’ W): 19 April 1953, 1 ♂, P.R. San Martín, L.C Zolessi (FCE-My 0660). Sierra de las Ánimas (34° 42’ S, 55° 19’ W): 19 April 1953, 1♂, P.R. San Martín, L.C Zolessi (FCE-My 0450). Sierra de las Ánimas (34° 42’ S, 55° 19’ W): 19 April 1953, 1♀, P.R. San Martín, L.C Zolessi (FCE-My 0520). Sierra de las Ánimas (34° 42’ S, 55° 19’ W): 01 October 1962, 1 ♀, P.R. San Martín (FCE-My 0481). Sierra de las Ánimas (34° 42’ S, 55°19’ W): 13 April 1987, 1♀, (FCE-My 0528). Sierra de las Ánimas (34° 42’ S, 55° 19’ W): 08 December 1984, 1 ♀, M. Menenghel. (FCE-My 0499). Sierra de las Ánimas (34° 42’ S, 55° 19’ W): 13 April 1987, 1 ♀, De Leon, E Gudynas, F. Pérez-Miles (FCE-My 0504). Sierra de las Ánimas (34° 42’ S, 55° 19’ W): 19 April 1953, 1♀, P.R. San Martín, L.C Zolessi (FCE-My 0481). Maldonado, Arroyo Pan de Azúcar (34° 38’ S, 55° 14’ W): 10 June 2023, 1 ♀, F. Pérez-Miles (FCE-My 1440). Uruguay, Lavalleja, Aguas Blancas (54° 32’ S, 55° 24’ W), June 2023, 1 ♀, F. Pérez-Miles (FCE-My 1441).

Figure 2. *Plesiopelma arevaloae* sp. nov. paratype male (FCEMy-783): A) carapace, B) sternum, C) abdomen, dorsal view, D) abdomen, ventral view.

Geographic range. Lavalleja and Maldonado, Uruguay (Figure 7).

Diagnosis. *Plesiopelma arevaloae* sp. nov. differs from most of *Plesiopelma* species, except from *P. insulare* and *P. paganoi*, by the high number of labial and maxillary cuspules;more than 125-138 labial and 251-188 maxillary; male-female (Figures 2B, 6B). In other species the number of labial cuspules is about: 30 to 48 (males), 67 to 90 (females) while maxillary cuspules from 90 to 96 (males) and 67 to 197 (females). Male differs from *P. insulare* by the aspect of the palpal bulb with narrower PS and PI and the more proximal location of the embolus tooth (Figure 3). Additionally, it differs from *P. paganoi* in the presence of embolus tooth and smaller body size. Also differs from male *P. longisternale* in the absence of a group of short thick spines on the metatarsal nodule on leg I (Figures 4A-4B). Additionally, it differs from the male of *P. myodes* in the smaller body size (26 mm total length in *P. myodes* and 14-18 mm in *P. arevaloae* sp. nov.). Females additionally differ from other species in the shorter spermathecal receptacles (Figure 8).

Description. Color *in ethanol* (male holotype FCEMy-0773): carapace and legs dorsally dark brown with whitish setae on carapace border, coxae and trochanters. Abdomen dorsally black with reddish setae on live spiders (Figure 2). Urticating setae type III (on the center of the patch) and IV (on the periphery) present. Total length (not including chelicerae or spinnerets) 16.1. Cephalothorax 8.2 long, 7.2 wide. Abdomen 6.3 long, 4.2 wide. Spinnerets: PMS, 1.0 long, 0.15 wide; PLS, 1.7 basal, 0.95 middle, 1.35 digitiform distal. Eyes: tubercle length 0.9, width 1.2. Clypeus narrow, 0.2. Anterior eyes row procurved, posterior row recurved. Eyes sizes and interdistances: AME 0.18, ALE 0.28, PME 0.15, PLE 0.23, AME – AME 0.25, AME – ALE 0.13, PME – PME 0.55, PME – PLE 0.08, ALE – PLE 0.13. Fovea transverse, procurved, 1.4 wide. Labium length 1.5, width 1.4, with ca.125 cuspules. Maxillae each with ca. 251 cuspules spread over internal face. Sternum: length 3.8, width 2.4. Chelicerae with 10 large teeth on promargin, a group of 6 smaller basal teeth behind promarginal line. Length of legs and palpal segments in Table 3. Tarsi I – IV densely scopulate, scopula I entire, II-IV divided by lines of setae, increasing in width towards posterior legs. Metatarsi I fully scopulate, II-III 1/2 apical scopulate, IV 1/3 apical scopulate. Spination: femora of palp 1D; I 1P; II 1D; III; 1D, IV 0. Tibiae: palp 1D; I 2D, 3V; II 1P, 5V; III 2P, 2R, 5V; IV 2P, 2R, 5V. Metatarsi: I 1 V; II 1D, 2V; III 3P, 1R, 6V; IV 2P, 3D, 2R, 5V. Tarsi I – IV, palps 0. Presence of spiniform setae on the retrolateral face of palpal tibia (Figure 3). Tibia I with ventral apophysis formed by two branches (Figure 4): prolateral smaller, with a basal megaspine, absence of spines on inner face; retrolateral

Figure 3. *Plesiopelma arevaloae* sp. nov. holotype male (FCEMy-773). Left palp, arrow shows a field of spiniform setae, retrolateral view.

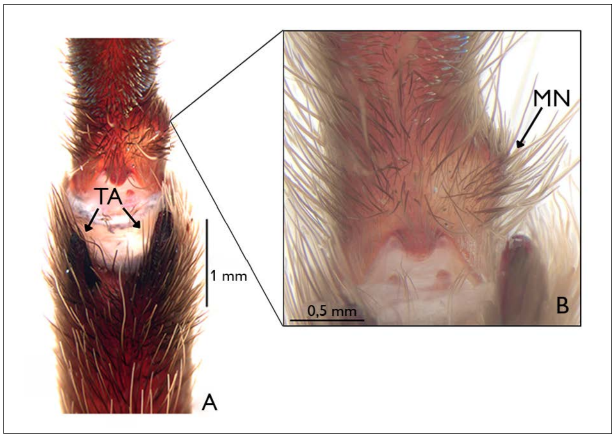

Figure 4. *Plesiopelma arevaloae* sp. nov. holotype male (FCEMy-773): A) left leg I showing tibial apophyses (TA) and metatarsal node (MN), ventral view, B) close up of the metatarsal node (MN).

Table 3. Length of legs and palp of *Plesiopelma arevaloae* sp. nov. holotype male.

	I	II	III	IV	Palp
Femur	7.7	6.5	5.7	7.2	4.2
Patella	4.1	3.4	3.2	3.3	2.4
Tibia	5.4	4.3	3.6	5.6	3.8
Metatarsus	4.3	3.8	3.8	6.0	-
Tarsus	3.2	2.7	3.2	3.8	1.8

larger with a subapical megaspine and five short spines on inner face. Metatarsus of leg I with basal retrolateral rounded nodule slightly developed (Figure 4) and flexes between both branches of tibial apophysis, touching their medial portion. Male palpal bulb piriform, tapering abruptly, with well-developed PI and PS, close and about parallel to each other (Figure 5). Embolus slender, as long as half of the total bulb length. Subapical tooth present on the middle of the embolus length (Figure 5C).

Female. Color *in ethanol* (paratype FCEMy-1415): carapace and legs dorsally brown with whitish setae on carapace border, coxae and trochanters. Abdomen dorsally black with reddish setae in live spiders (Figure 6). Color alive as in Figure 9. Urticating setae type III (on the center of the patch) and IV (on the periphery) present. Total length (not including chelicerae or spinnerets) 18.8. Cephalothorax 7.4 long, 6.3 wide. Abdomen 11.7 long, 7.9 wide. Spinnerets: PMS, 0.9 long, 0.14 wide; PLS, 1.6 basal, 1.15 middle, 1.05 digitiform distal. Eyes: tubercle length 0.7, width 1.10. Clypeus narrow, 0.3. Anterior eyes row procurved, posterior row recurved. Eyes sizes and inter distances: AME 0.13, ALE 0.28, PME 0.13, PLE 0.24, AME – AME 0.28, AME – ALE 0.10, PME – PME 0.55, PME – PLE 0.05, ALE – PLE 0.08. Fovea transverse, procurved, 0.8 wide. Labium length 1.05, width 1.50, with ca. 138 cuspules.

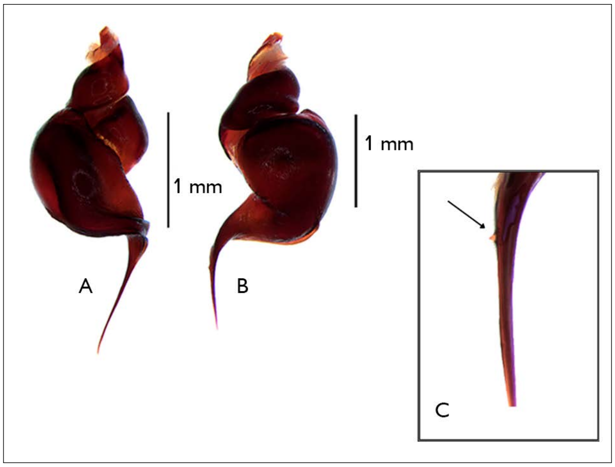

Figure 5. *Plesiopelma arevaloae* sp. nov. holotype male (FCEMy-773). Left palpal bulb. A) Prolateral view, B) retrolateral view, C) close up of distal embolus, arrow shows the tooth.

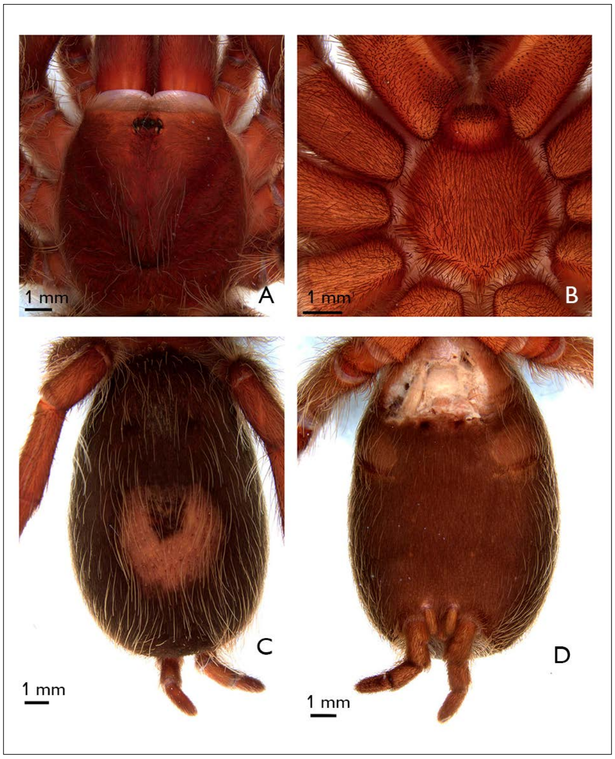

Figure 6. *Plesiopelma arevaloae* sp. nov. paratype female (FCEMy-1415): A) carapace, B) sternum, C) abdomen, dorsal view, D) abdomen, ventral view.

Maxillae each with ca. 188 cuspules spread over internal face. Sternum: length 3.45, width 3.55. Chelicerae with 10 large teeth on promargin, a group of 9 smaller basal teeth behind promarginal line. Length of legs and palpal segments in Table 1. Tarsi I – IV densely scopulate, scopula I entire, II-IV divided by lines of setae, increasing in width towards posterior legs. Metatarsi I 2/3 apical scopulate, II-III 1/2 apical scopulate, IV 1/3 apical scopulate. Spination: femora of palp 0; I 0; II 1D; III and IV 0. Tibiae: palp 3V; I 0; II 0; III 2P, 1R, 1V; IV 2R, 5V. Metatarsi: I 1 V; II 2V; III 3P, 1C, 6V; IV 1P, 2R, 6V. Tarsi I – IV, palps 0. Spermathecae constituted by two separated tubular sinusoidal receptacles with the fundus subglobose; receptacles are shorter than other *Plesiopelma* species (Figure 8).

Etymology. The specific name is a tribute to Julia Arévalo, born in Lavalleja, Uruguay (1898-1985) and the first woman senator in Latin America.

Comments on distribution and habitat. *Plesiopelma arevaloae* sp. nov. was found in the "Sierras del Este" eco-region (Brazeiro, 2015), particularly in stony hills ranges in the departments of Maldonado and Lavalleja where the Cuchilla Grande extends (Figure 10). In these hills, the heights vary between 200 and 500 meters above sea level, the average annual temperature is 17 °C and annual rainfall varies between 1,000 and 1,200 mm, the landscape has a matrix of meadow with patches of tree and shrub vegetation, as well as rocky outcrops (Evia & Gudynas, 2000). The spiders are usually found under rocks, in shelters that they cover with abundant and dense silk; the refuges are similar to those of *P. longisternale* (Pérez-Miles & Ferretti, 2014). The region contains an intermediate level of specific richness of vertebrates and woody species with few endemic species but a considerable number of indicator species (Brazeiro, 2015). Grassland and hill forest vegetation predominate.

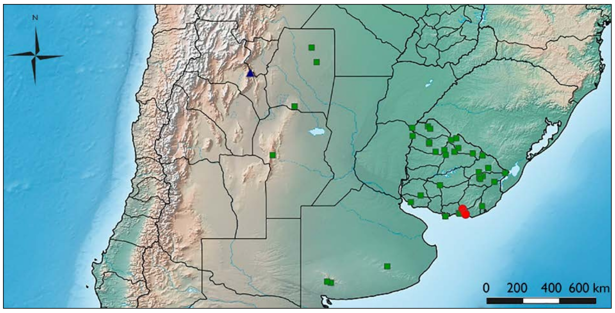

Figure 7. Geographic distribution of *Plesiopelma arevaloae* sp. nov. (red circles), *Plesiopelma longistarnale* (green squares) and *Plesiopelma absconditus* (blue triangle). Map: Arias (2024).

Figure 8. *Plesiopelma arevaloae* sp. nov. paratype female (FCEMy-1415). Spermathecae, ventral view.

Figure 9. *Plesiopelma arevaloae* sp. nov. female, habitus.

Figure 10. Habitat of the type locality of *Plesiopelma arevaloae* sp. nov. in Uruguay, Lavalleja, Aguas Blancas. Photo: González (2024).

Table 4. Length of legs and palp of *Plesiopelma arevaloae* sp. nov. paratype female.

	I	II	III	IV	Palp
Femur	5.2	4.8	3.9	5.6	4.0
Patella	3.4	2.9	2.3	3.0	2.4
Tibia	3.9	3.0	2.5	3.9	2.5
Metatarsus	2.6	2.4	2.8	4.0	-
Tarsus	2.3	2.2	2.2	2.7	2.7

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AUTHORS' CONTRIBUTION

V. Arias contributed to conceptualization, data curation, analysis, methodology, research, and writing (original draft); M. Hilario to data curation, analysis, research, and writing (review and editing); N. Ferretti to analysis, research, and writing (review and editing); and F. Pérez-Miles to conceptualization, analysis, methodology, research, project administration, and writing (review and editing).

On some *Heteropoda* species from Southeast Asia with new data on their biology and distribution range and the resurrection of a new species group (Sparassidae: Heteropodinae)

Novos dados sobre algumas espécies de *Heteropoda* do sudeste asiático sobre a biologia, a área de distribuição e a ressurreição de um novo grupo de espécies (Sparassidae: Heteropodinae)

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Abstract: Eight species of the huntsman spider genus *Heteropoda* Latreille, 1804 are described; *Heteropoda bufocorniculans* spec. nov. (Sabah, Sarawak; female), *H. sederhana* spec. nov. (Java; female), *H. temburong* spec. nov. (Brunei, Sabah, Sarawak; male, female), *H. trifurcata* spec. nov. (Pahang State, Malaysia; male, female), *H. tutula* spec. nov. (Singapore; female), *H. tympanum* spec. nov. (Penang, Malaysia; female), *H. ulna* spec. nov. (Sumatra, Indonesia; female), and *H. uniter* spec. nov. (Kalimantan, Indonesia; female). The latter six species, along with *H. ocyalina* (Simon, 1887) and *H. asa* Jäger, 2024, are included in the newly proposed *ocyalina* species-group. *H. fasciata* (Reimoser, 1927) is removed from synonymy of *H. ocyalina* (Simon, 1887) and considered a *nomen dubium*. The male of *Heteropoda borneensis* (Thorell, 1890) is illustrated for the first time, male and female are redescribed, new distributional data are presented, including the first records from Brunei, Indonesia (Kalimantan Utara), Malaysia (Kuala Lumpur, Sabah), and Singapore. *Heteropoda strandi* Jäger, 2002 and *H. lunula* (Doleschall, 1857) are formally documented for the first time from Singapore, the female of the former is redescribed.

Keywords: Taxonomy. New species. *Nomen dubium*. iNaturalist.

Resumo: Oito espécies do gênero de aranhas caçadoras *Heteropoda* Latreille, 1804 são reconhecidas como novas para a ciência e descritas como *Heteropoda bufocorniculans* spec. nov. (Sabah, Sarawak; fêmea), *H. sederhana* spec. nov. (Java; fêmea), *H. temburong* spec. nov. (Brunei, Sabah, Sarawak; macho, fêmea), *H. trifurcata* spec. nov. (Pahang, Malásia; macho, fêmea), *H. tutula* spec. nov. (Cingapura; fêmea), *H. tympanum* spec. nov. (Penang, Malásia; fêmea), *H. ulna* spec. nov. (Sumatra, Indonésia; fêmea) e *H. uniter* spec. nov. (Kalimantan, Indonésia; fêmea). As últimas seis espécies, juntamente com *H. ocyalina* (Simon, 1887) e *H. asa* Jäger, 2024, estão incluídas no novo grupo de espécies *ocyalina*. *H. fasciata* (Reimoser, 1927) é removido da sinonímia de *H. ocyalina* (Simon, 1887) e considerado um *nomen dubium*. O macho de *Heteropoda borneensis* (Thorell, 1890) é ilustrado pela primeira vez, com macho e fêmea sendo redescritos e apresentados novos dados de distribuição, entre eles os primeiros registros para Brunei, Indonésia (Kalimantan Utara), Malásia (Kuala Lumpur, Sabah) e Cingapura. *Heteropoda strandi* Jäger, 2002 e *H. lunula* (Doleschall, 1857) são formalmente documentados pela primeira vez em Cingapura, sendo redescrita a fêmea de *H. strandi*.

Palavras-chave: Taxonomia. Novas espécies. *Nomen dubium*. iNaturalist.

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INTRODUCTION

Heteropoda Latreille, 1804 is a large genus within the subfamily Heteropodinae, with 203 nominal species and distributed mostly in Asia and Australia (World Spider Catalog, 2024), including the largely synanthropic and pantropic species *Heteropoda venatoria* (Linnaeus, 1767). Revisionary work has been done so far mainly for Southeast Asia and Australia (e.g., Jäger, 2005, 2008a, 2014, 2024; Davies, 1994). The majority of the diversity of the genus is still unrevised or undiscovered (Jäger, unpublished data).

Heteropoda borneensis (Thorell, 1890) was described from a male and a female from Borneo (Malaysia: Sarawak) in the new genus *Urgulania* Thorell, 1890. While acknowledging *Urgulania's* strong similarity in comparison with *Heteropoda* and *Panaretus* Simon, 1880, Thorell (1890, p. 143) stated in three lines in the footnote that *Urgulania* may be distinguished from the two former genera by having legs I longer than legs IV, and from *Heteropoda* by having dense pubescence at the base of the chelicerae ("as in *Panaretus*"). Simon (1880, p. 54) synonymised the genus with *Panaretus* without giving any reason. After Jäger (2002, p. 40) synonymised *Panaretus* with *Heteropoda* and formally transferred the present species to the genus *Heteropoda*, there have been no further references to the species in scientific literature. It has been difficult to identify the species based on the original eight-line description in Latin (Thorell, 1890, p. 143). After examining the type and conspecific material, the male and female are now re-described and data on the species' biology and distribution are provided.

Other material of the genus *Heteropoda* collected on various expeditions or borrowed from natural history collections was examined and eight species were recognised as new to science. They are diagnosed, described, and illustrated. A new species group is proposed to include eight species, comprising two formerly described ones and six new species described in this paper. Additionally, two previously described *Heteropoda* species are formally documented for the first time from Singapore.

MATERIAL AND METHODS

The examined spiders are preserved in 70% denatured ethanol. Observations and drawings were made using a Leica MZ 16 stereomicroscope and a Leica DLMS compound microscope, each with a camera lucida attachment. Photographs of preserved specimens were taken with a Canon EOS R and a Canon 100 mm macro lens in combination with a Canon MR 14EX ringlite (or with the same camera mounted on a Leica MZ 16 stereomicroscope). Photographs of live spiders were taken with an AF-S micro-NIKKOR 60 mm ED lens or an AF-S micro-NIKKOR 105 mm 1:2.8G ED lens, attached to a Nikon D7000 camera. Photographs of the female genitalia were taken with Nikon D800E camera either mounted on a Nikon SMZ 18 stereoscopic microscope, or with a series of extension tubes attached to a Nikon E Plan 10X compound microscope objective. Specific photo credits are given in legends. All line drawings and maps were made by P. Jäger. All measurements are given in millimetres. Prosoma length/width is the length/width of the dorsal shield of the prosoma, opisthosoma length/width is the length excluding petiolus and spinnerets. Eye distances were measured in orthogonal views. Leg formula, leg spination pattern and size classes follow Jäger (2001). Palpal and leg lengths are given as: total (femur, patella, tibia, metatarsus, tarsus). The arising points of appendages of the male bulb are given in clock-position of the left palp in ventral view. Colouration is described from specimens in ethanol and live specimens. All specimens were checked for scars as potential traces of mating bites as described in Jäger (2021, 2023) and Eudeline & Jäger (2023). Data in square brackets were retrieved subsequently. Elevation of localities are given in metres (m). The maps were produced using DIVA GIS version 7.5.0.0. Records of *H. borneensis* from iNaturalist unambiguously identifiable by photographs are included in the map, with the caveat that the precision of some of the coordinates given in iNaturalist may not necessarily be punctiliously accurate. Records for '*Heteropoda*' were searched for data associated with Singapore, Sumatra, the southern part of peninsular Malaysia, and the entire 'Borneo' region (namely

Brunei, Sabah, Sarawak, and the Indonesian provinces of Kalimantan). Valid species are listed in alphabetical order; only those close to *H. ocyalina* could be assigned to a species group.

Abbreviations used in the text: ALE = anterior lateral eyes, AME = anterior median eyes, dRTA = dorsal branch of RTA, DS = dorsal shield of prosoma, Fe = femur/femora, Mt = metatarsus/metatarsi, OL = opisthosoma length, OS = opisthosoma, OW = opisthosoma width, Pa = patella/patellae, PL = prosoma length, PLE = posterior lateral eyes, PME = posterior median eyes, PW = prosoma width, RTA = retrolateral tibial apophysis, Ta = tarsus/tarsi, Ti = tibia/tibiae, TL = total length, vRTA = ventral branch of RTA.

Museum collections (with curators): AMNH = American Museum of Natural History, New York, USA (L. Prendini); BMKB = Brunei Museum, Kota Batu, Brunei Darussalam (F. Hamdan); FRC = Forestry Research Centre, Sepilok, Sandakan, Sabah, Malaysia (A. Chung); LKCNHM = Lee Kong Chian Natural History Museum, Singapore (W. Wang); MCSN = Museo Civico di Storia Naturale, Genoa, Italy (M. Tavano); NHM = Natural History Museum, London, UK (J. Beccaloni); NHMW = Naturhistorisches Museum, Vienna, Austria (C. Hörweg); RMNH = Naturalis Biodiversity Center, Leiden, Netherlands (H. Bakker); SMF = Senckenberg Research Institute, Frankfurt am Main, Germany (J. Grüger, P. Jäger); ÜMB = Übersee Museum Bremen, Germany (V. Lohrmann); ZMUC = Zoological Museum of the University, Copenhagen, Denmark (N. Scharff).

This paper and its nomenclatural acts have been registered in ZooBank, the online registration system for the ICZN (http://zoobank.org/urn:lsid:zoobank.org:pub:3461EAFC-DEE4-4A4A-A509-C4FA1B338C69).

TAXONOMY

Sparassidae Bertkau, 1872
Heteropodinae Thorell, 1873
Heteropoda Latreille, 1804
Heteropoda borneensis (Thorell, 1890)
(Figures 1–41)

Urgulania borneensis Thorell 1890: 143 (Description of male and female; 1 female [with epigyne] lectotype; 1 male? [without palps] and 1 female [without epigyne] paralectotypes; from Borneo: [MALAYSIA:] *Sarawak*, Doria & Beccari, MCSN; examined).

Panaretus borneensis Simon 1897: 54 (transfer to *Panaretus*).

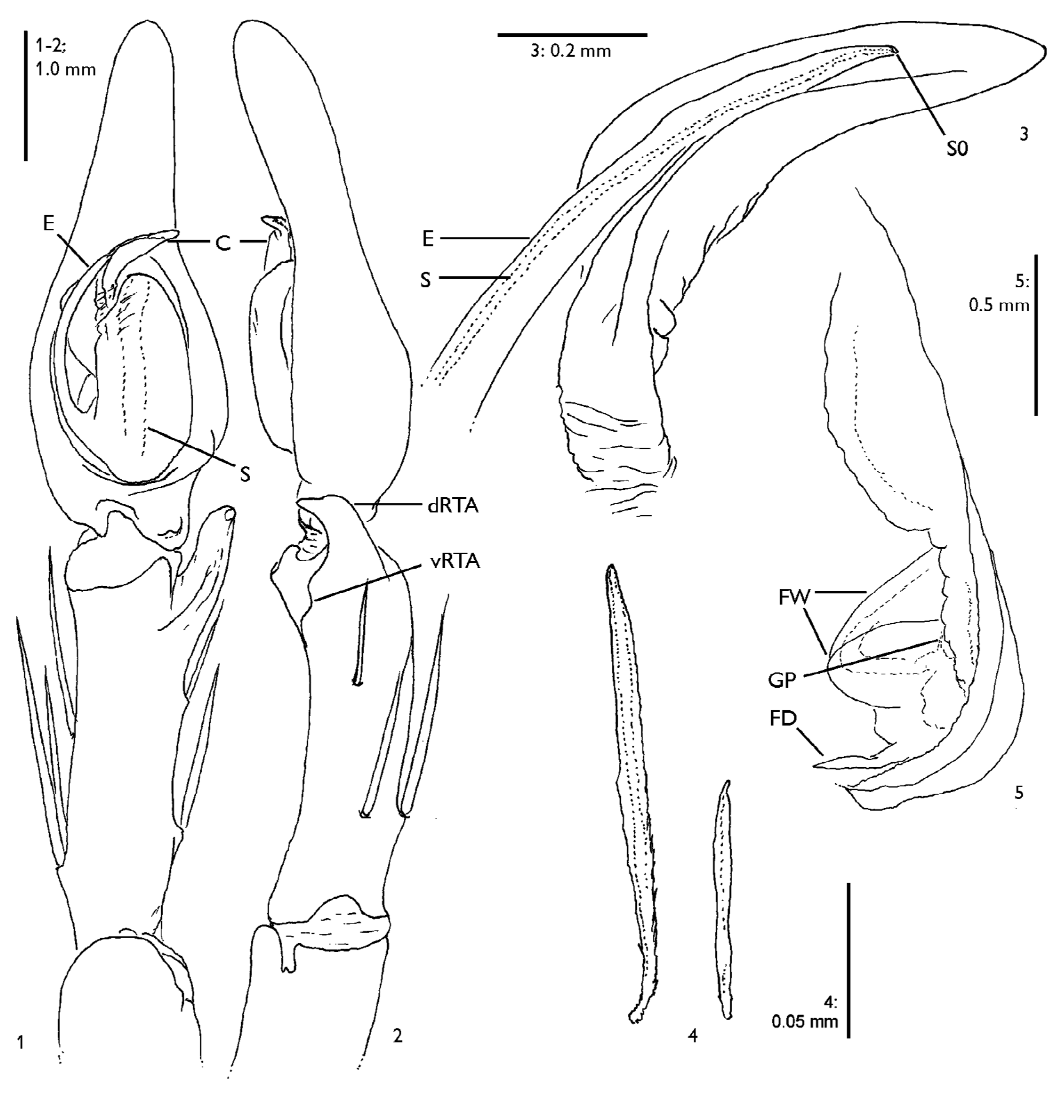
Heteropoda borneensis, Jäger 2002: 42 (transfer and designation of lectotype and paralectotypes).

Heteropoda sp. A—Koh & Bay 2019: 330–331, unnumbered photos of male and female. Koh et al. (2022, p. 493), unnumbered photos of male and female.

Notes. The genus *Panaretus* was synonymised by Jäger (2002, p. 40) with *Heteropoda*, thus formally transferring *Panaretus borneensis* to *Heteropoda*. In the original publication, Thorell (1890, p. 144) reported "Borneo" as its country of origin ("*patria*"). On the original labels, "Sarawak" was added and is considered a more precise indication of the type locality.

Additional material examined. BRUNEI: Belait: 1 female (JK.11.03.26.9002), Melilas, Sungai Ingei, primary forest, 4° 08' 36" N, 114° 43' 16" E [58 m elevation], J.K.H. Koh leg. 26 March 2011 (BMKB). 1 female (JK.11.03.26.9008), with same locality data as for previous specimen (LKCNHM). Tutong: 1 male (JK.11.04.16.1041), Tasek Merimbun, Botanical Trail, 4° 35' 40" N, 114° 40' 15" E [38 m elevation], Joseph K.H. Koh leg. 16 April 2011, 22.00, "orange big" (SMF). 1 female (JK.11.04.14.1012), with same data as for previous specimen (SMF). 1 female (JK.11.04.16.1006), with same locality data as for previous specimen, J.K.H. Koh leg. 16 April 2011 (LKCNHM). 4 females (JK.09.10.13.0001, JK.09.10.13.0008–9), with same locality data as for previous specimen, disturbed forest, J.K.H. Koh leg. 13 October 2009 (LKCNHM). 1 male (JK.10.01.24.3015), 2 females (JK.10.01.24.3001–2), with same locality data as for previous specimens, J.K.H. Koh leg. 24 January 2010 (LKCNHM). 1 female (JK.11.04.16.1006), with same locality data as for previous specimens, J.K.H. Koh leg. 16 April 2011 (LKCNHM). 1 female (JK.12.03.24.1002), with same locality data as for previous specimens, J.K.H.

Koh leg. 24 March 2012 (BMKB). 1 male (JK.09.10.14.2001), Tasek Merimbun Heritage Park, Banunih Trail, disturbed forest, 4° 35' 28" N, 114° 28' 44" E [43 m elevation], J.K.H. Koh leg. 14 October 2009 (BMKB). Temburong: 1 male, Ulu Temburong National Park, Kuala Belalong Field Study Centre [4° 32' 46.73" N, 115° 9' 28.15" E, 107 m elevation], O. Machač leg. 25 January–18 February 2019 (SMF). 1 female (JK.07.04.17.0026), Kampong Lakiun, disturbed secondary forest, 4° 42' 55" N, 115° 8' 15" E [80 m elevation], J.K.H. Koh leg. 17 April 2017. (LKCNHM). 1 male (JK.10.05.08.0008), Peradayan Forest Reserve, off Kampung Lakiun, 4° 45' 0.0" N, 115° 9' 58" E [109 m elevation], J.K.H. Koh leg. 8 May 2010 (BMKB). 4 females (JK.10.05.08.0019, JK.10.05.08.00023, JK.10.05.08.9021, JK.10.05.08.9023), with same locality



Figures 1–5. *Heteropoda borneensis* (Thorell, 1890), male (1–3) and female (4) from Brunei, holotype female (5) from Sarawak. 1–2 Left palp (1 ventral; 2 retrolateral). 3 Conductor and apical part of embolus, ventral. 4 Setae of light dorsal band on tibia IV. 5 Epigyne, lateral. Abbreviations: C = conductor, dRTA = dorsal part of RTA, E = embolus, FD = fertilisation duct, FW = first winding of internal duct system, GP = glandular pore, S = spermophor, SO = spermophor opening, vRTA = ventral part of RTA.

data as for previous specimen, J.K.H. Koh leg. 8 May 2010 (LKCNHM). 1 female (JK.11.08.06.0016), with same locality data as for previous specimens, J.K.H. Koh leg. 6 July 2011 (BMKB). 2 males (JK.12.04.20.0041, JK.12.04.20.0068), 5 females (JK.12.04.20.0002–5, JK.12.04.20.0064), with same locality data as for previous specimens, J.K.H. Koh leg. 20 April 2012. (LKCNHM). MALAYSIA: Kuala Lumpur: 1 female, Pahang Road 6.5 km N Kuala Lumpur [ca. 3° 10' 56.17" N, 101° 42' 5.07" E, 39 m elevation], Robert Traub leg. March–May 1950, US Scrub Typhus Unit (AMNH). Sabah: 1 female (JK.15.06.26.0010), Tawau, Tawau Hill Park, 4° 23' 34" N, 117° 54' 52" E [291 m elevation], C.S.P. Ang & J.M.L. Yeo leg. 26 June 2015 (LKCNHM). 1 female (JK.16.11.04.0057), Maliau Basin, Sky Bridge Trail, 4° 44' 36" N, 116° 58' 13" E [260 m elevation], J.K.H. Koh leg. 4 November 2016 (FSC). Sarawak: 1 male (JK.12.01.21.1016), Gunung Mulu National Park, Night Walk Trail, near Park HQ, 4° 2' 31" N, 114° 48' 54" E [45 m elevation], J.K.H. Koh leg. 21 January 2012 (LKCNHM). SINGAPORE: 1 female (JK.15.11.16.0001), Thomson Nature Park, secondary forest floor, 1° 22' 54" N, 103° 48' 55" E [30 m elevation], J.W.B Koh leg. 16 January 2015 (LKCNHM).

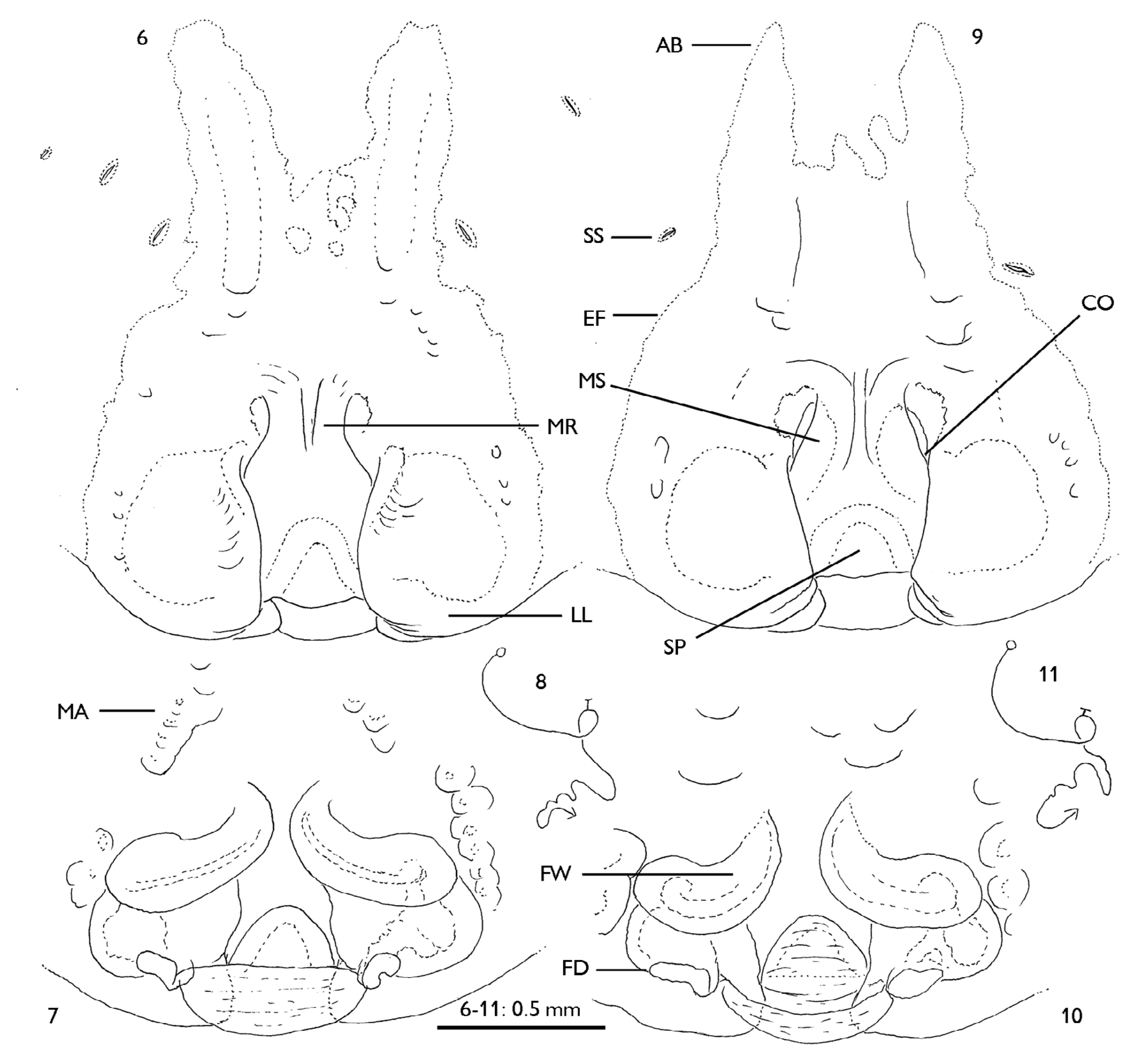
Diagnosis. Males may be diagnosed by the following combination of palpal characters (Figures 1–3): 1. Embolus arising in 7.30-o'clock-position from tegulum, 2. Conductor arising in 11-o'clock-position from tegulum, short, i.e. roughly as long as tegulum width, 3. Spermophor straight, longitudinally running, 4. dRTA with ventrad pointed apex, 5. vRTA with hump and building an obtuse angle with dRTA. Female copulatory organs are similar to those of *Heteropoda afghana* Roewer, 1962, *H. fischeri* Jäger 2005 and *H. robusta* Fage 1924 in having a freely visible median septum and an especially simple internal duct system with the first winding running laterad, then connecting to posterior spermathecae (Figures 6–11), but can distinguished from all three species by the short and broad anterior bands of the epigynal field (cf. Jäger, 2005, figures 7–27, 35–45). Additionally, *H. borneensis* can be distinguished from *H. fischeri* and *H. robusta* by the copulatory opening visible in dorsal view (hidden in dorsal view by first windings in *H. fischeri* and *H. robusta*). *H. borneensis* can be distinguished from *H. afghana* by the round and entire outline of the spermathecae (outline with bulges in *H. afghana*; cf. Jäger, 2005, figures 8, 13, 18, 24, 26, 28). Furthermore, live spiders can be recognised by their striking colouration. Live females (Figures 23–28) are orange, with bicoloured chelicerae: the proximal part orange and distal part black. White and simple setae (i.e. not feathered, Figure 4) cover the dorsal side of tibiae and metatarsi of legs III and IV. The overall colouration of living males (Figures 29–30) is dusty brown. The tibiae and metatarsi of legs I, II, III and IV are covered dorsally by white setae. Their chelicerae are black except for a thin strip of orange hairs near the base (Figure 31). However, such contrasting colouration fades quickly in preserved specimens (Figures 12–22).

Description. Male (JK.11.04.16.1014, from Brunei): Measurements: TL 16.6, PL 9.0, PW 8.3, AW 4.1, OL 7.6, OW 4.5. Eyes: AME 0.51, ALE 0.60, PME 0.45, PLE 0.61, AME-AME 0.25, AME-ALE 0.07, PME-PME 0.42, PME-PLE 0.62, AME-PME 0.40, ALE-PLE 0.44, CH AME 0.76, CH ALE 0.75 (with especially strong setae around eyes; Figure 22). Spination: Pp 131, 101, 2121; Fe I–II 323, III 323(2), IV 321; Pa I–III 101, IV 001; Ti I–III 2126, IV 2026; Mt I–II 1014, III 2014, IV 3036. Mt I–III with dense scopulae along entire length, IV with distal field and double row of stronger setae, with very sparse scopula in distal half. Measurements of palps and legs: Pp 14.6 (4.9, 2.2, 3.4, -, 4.1); I 54.6 (13.8, 4.9, 15.8, 15.7, 4.4); II 58.9 (15.2, 5.1, 17.1, 17.1, 4.4); III 43.9 (12.2, 4.0, 12.5, 12.0, 3.2); IV 52.0 (14.1, 3.9, 14.1, 15.7, 4.2). Leg formula: II-I-IV-III. CH with 3 promarginal and 4 retromarginal teeth, ca. 75–80 denticles and 1 escort seta.

Palp (Figures 1–3). As in diagnosis. RTA arising distally to sub-distally from Ti, vRTA flat, dRTA broad, dorso-apically rounded. Cymbium distinctly longer than Ti, with indistinct small, rounded retro-proximal swelling. Spermophor running from a 12-o'clock- to 6-o'clock-position in ventral view. E with short broad base, narrowing continuously towards tip, subapically with almost undiscernible widening, spermophor opening situated apically. C with broadly pointed retrolaterad tip.

Colouration (Figures 12–14, 22). Orange-brown without distinct pattern. DS with dark fovea and margins. Chelicerae darker and with longitudinal stripes. Sternum and ventral coxae partly suffused with black especially in the anterior parts. OS dorsally with a short light-and-dark transversal pattern in posterior half, ventrally dark behind epigastric furrow with white longitudinal lines; spinnerets light brown.

Female (JK.11.04.16.1012, from Brunei with data of lectotype in square brackets, in spination pattern only when different): Measurements: TL 21.2 [22.6], PL 9.8 [11.2], PW 8.5 [10.2], AW 5.0 [5.4], OL 11.4 [11.4], OW 8.4 [6.9]. Eyes: AME 0.51 [0.52], ALE 0.63 [0.65], PME 0.46 [0.48], PLE 0.63 [0.67], AME-AME 0.26 [0.34], AME-ALE 0.11 [0.14], PME-PME 0.51 [0.53], PME-PLE 0.63 [0.75], AME-PME 0.41 [0.55], ALE-PLE 0.50 [0.56], CH AME

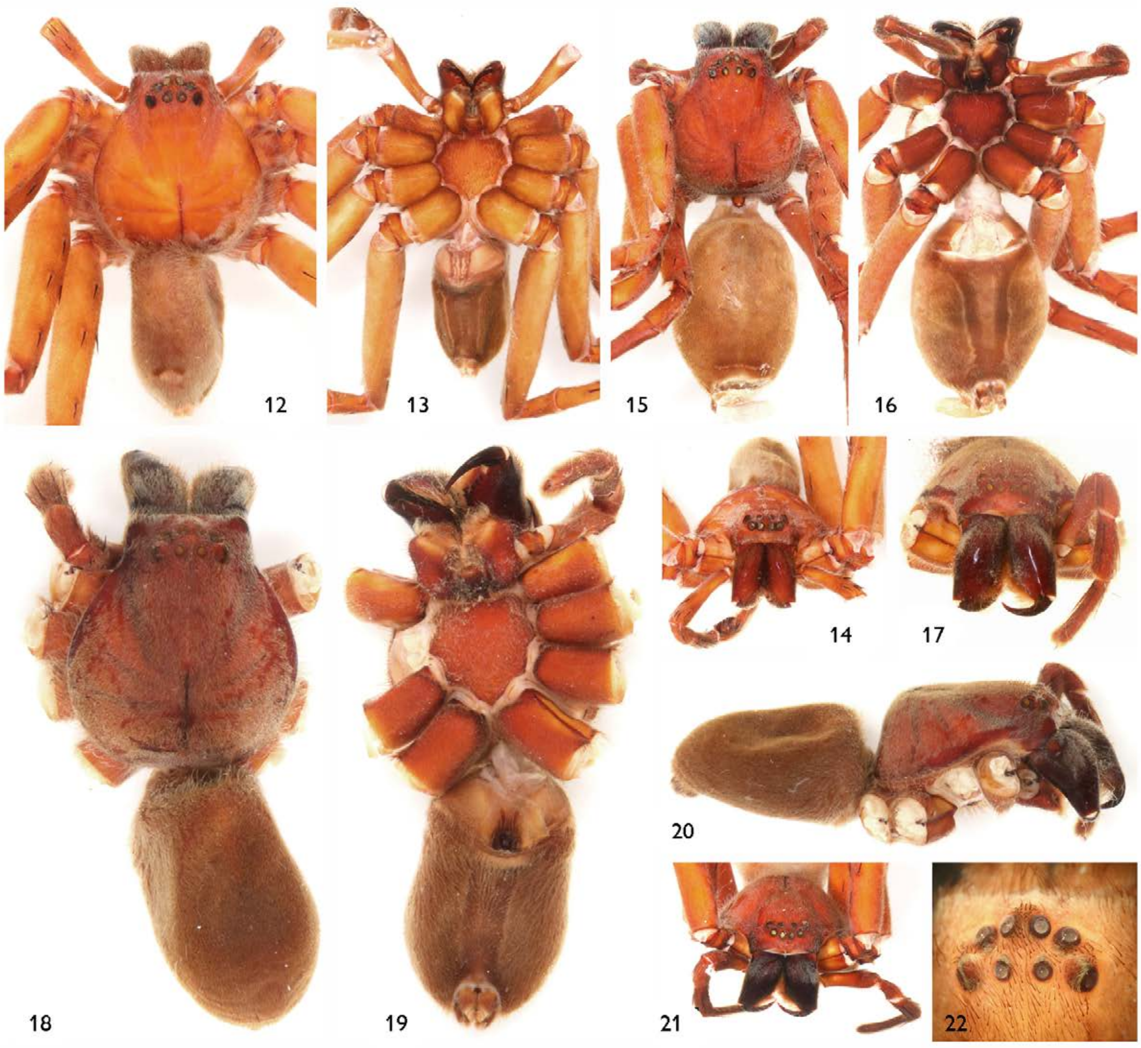


Figures 6–11. *Heteropoda borneensis* (Thorell, 1890), lectotype female from Sarawak (6–8), female from Brunei (9–11). 6, 9 Epigyne, ventral. 7, 10 Vulva, dorsal. 8, 11 Schematic course of internal duct system, dorsal. Abbreviations: AB = anterior bands, CO = copulatory opening, EF = epigynal field, FD = fertilisation duct, FW = first winding of internal duct system, LL = lateral lobes, MA = muscle attachment points, MR = median ridge, MS = median septum, SP = septal pocket, SS = slit sensillum.

◆

0.81 [0.95], CH ALE 0.90 [1.04]. Spination: Pp 131, 101, 2121, 1014; Fe I–II 323, III 322, IV 321; Pa I–IV 001 [III 101]; Ti I–IV 2026; Mt I–II 1014, III 2014, IV 3036. Mt I–III with dense scopulae along entire length, IV with distal field and double row of stronger setae, with very sparse scopula in distal half. Measurements of palps and legs: Pp 14.3 (4.4., 2.1, 3.3, -, 4.5); I 41.7 (11.3, 4.7, 11.6, 11.0, 3.1); II 46.0 (12.7, 5.1, 13.1, 11.8, 3.3); III 35.4 (10.6, 4.3, 9.4, 8.6, 2.5); IV 43.3 (12.4, 4.0, 11.5, 12.0, 3.4) [Pp 17.0 (5.2, 2.6, 4.1, -, 5.1); I 46.7 (12.6, 5.5, 13.3, 11.7, 3.6); II 50.2 (13.9, 6.0, 14.4, 12.3, 3.6); III 40.2 (11.7, 4.9, 11.0, 9.6, 3.0); IV 48.8 (13.9, 4.7, 12.8, 13.4, 4.0)]. Leg formula: II-IV-I-III. CH with 3 promarginal and 4 retromarginal teeth, ca. 90 [90–100] denticles and 1 escort seta. Palpal claw with 8 [9] teeth.

Copulatory organ (Figures 6–11). As in diagnosis. Epigynal field roughly as long as wide, anterior bands fused, with 2 left and 3 right slit sensilla lateral of anterior bands and many muscle attachment points. Median septum longer



Figures 12–22. *Heteropoda borneensis* (Thorell, 1890), male (12–14) and female (15–17) from Brunei, lectotype female from Sarawak (18–21), male from Brunei (22), habitus (12, 15, 18, 22 dorsal; 13, 16, 19 ventral; 14, 17, 21 frontal; 20 lateral). Photos: P. Jäger.

than wide, septal pocket distinctly developed, with distinct median longitudinal ridge in the anterior part of the median septum. Posterior part of internal duct system separated by one width of the first winding in ventral view. Fertilisation ducts short, their tips laterad.

Colouration (Figures 15–21). As in male, but generally darker, especially, chelicerae, ventral side and palps. OS ventrally with light median band. Spinnerets proximally darker.

Variation. Male: TL 18.0–25.0, PL 9.0–12.0, OL 9.0–13.0. While the chelicerae in mature males are almost entirely black (vs bicoloured chelicerae in females), immature males have bicoloured chelicerae, like their sisters and mothers. Living males (Figures 29–32) differ from live females in overall colouration, leg colouration, and cheliceral colouration. They further differ from females in: 1. DS shows a pair of dark patches at the 4 o'clock and 8 o'clock positions (Figures 29–30, absent in the females); 2. Dark patch visible anterior to a black-and-white somewhat transversal line on the posterior half of the OS (Figures 29–30 vs. Figure 23); 3. Venter almost completely black, with only a pair of fine longitudinal lines running behind the epigastric area to the posterior end of the opisthosoma (Figure 32 vs. Figure 26). In subadult males, the chelicerae are bicoloured (Figure 33) in live specimens, like those in females, and not almost black as in adult males (Figure 31). Female: TL 20.1–27.0, PL 9.8–16.0, OL 11.2–16.3. The shape of the epigynal median septum varies rather widely. In some specimens, it is broader than those depicted in Figures 6 and 9, and the posterior margin can be straight, curved slightly backward, or angled with a blunt protrusion at the posterior end (Figures 35–40). While the median ridges of some specimens are conspicuously rugged (Figure 35), others appear merely as a slightly crested, upfolding band; in some specimens it is not recognisable at all. On both sides of the median ridge, the eyebrow-like ridges anterior to the copulatory openings are straight or concave (Figure 35 vs. Figure 38). The number of slit sensilla off the anterior bands of the epigyne varies: in some cases, only a single slit sensillum is visible on the left side; in other cases, the number of sensilla ranges from one to three on one side, without necessarily a corresponding number on the other side. For instance, in one examined specimen, there are three sensilla on the left, but only one on the right. In live spiders, overall colouration is orange (Figures 23–24, 27–28), with a short transversal pattern on the posterior half (Figures 23–24). Chelicerae bicoloured with orange and black (Figures 25, 28). Palps, sternum, ventral coxae, and epigastric area black (Figure 26). A median longitudinal black band, flanked by a pair of fine white lines, running from the epigynal area to the spinnerets contrasting with the orange background, forming a T-shaped black pattern on the entire venter (Figure 26 vs. Figure 32). The orange setae on the female OS are easily dislodged, resulting in some older females showing an almost bare and brownish OS (Figure 24), differing in colouration from a DS densely carpeted by orange setae. In live males, the paired dark patches on the posterior half of the DS often differ in size and shapes. Some specimens have paired dark patches on the anterior half as well, albeit smaller and paler. In some subadult males, the size of these dark patches on the DS can be twice bigger than the norm. In subadults and mature specimens in both sexes, the light-and-dark transversal pattern on the posterior half of the OS show a wide range of differences: from a short straight or wavy line to a moustache-liked bar, or a small white transversal patch (1 female from Kuala Lumpur; iNaturalist). Such a white patch on the posterior half of the opisthosoma is also present in other species of Heteropodinae, e.g., *Pseudopoda confusa* Jäger, Pathoumthong & Vedel, 2006, and may vary in size and shape (Jäger et al., 2006).

Distribution. Malaysia (Kuala Lumpur, Sabah, Sarawak), Singapore, Brunei, Indonesia (Kalimantan Utara) (Figure 41, based on specimens examined and iNaturalist records of unambiguously identified individuals of the species). Additional unmistakably identifiable records were provided on the internet platform Flickr — Malaysia: Sabah: Tawau and Maliau Basin; Selangor: close to Semenyih; Johor: Gunung Panti. Because exact coordinates were not provided, these records are not indicated in the distribution map.

Figures 23–28. *Heteropoda borneensis* (Thorell, 1890), living females (23–24), freshly killed females (25–26), living females with egg sacs (27–28). 23 Female described in the text, from Brunei: Tutong, Tasek Merimbun Heritage Park. 24 Female from Malaysia: Sabah, Maliau Basin. 25 Frontal view showing bicoloured chelicerae, from Brunei: Temburong, Peradayan. 26 Ventral view of a specimen from Brunei: Temburong, Kuala Belalong; scale line: 5.0 mm. 27 Egg sac carried under chelicerae, from Brunei: Temburong, Peradayan Forest Reserve. 28 Egg sac fastened on foliage, from Brunei: Temburong, Peradayan Forest Reserve. Photos: J. K. H. Koh.

Figures 29–32. *Heteropoda borneensis* (Thorell, 1890), living males (29–30), freshly killed male (31–32). 29 the male described in text, from Brunei: Tutong, Tasek Merimbun Heritage Park. 30 Living male in resting pose, from Brunei: Temburong, Peradayan Forest Reserve. 31 Frontal view showing cheliceral colouration in adult male. 32 ventral habitus, scale bar: 5.0 mm. Photos: J. K. H. Koh.

Figures 33–34. *Heteropoda borneensis* (Thorell, 1890), freshly killed subadult male (33), living subadult male (34). 33 Frontal view showing cheliceral colouration in subadult male. 34 Habitus of subadult male. Photos: J. K. H. Koh.

Figures 35–40. *Heteropoda borneensis* (Thorell, 1890), selected epigynes from examined specimens, ventral view. Scale lines: 0.5 mm. 35 from Brunei: Beilait, Sungei Ingei Forest Reserve. 36–38 from Brunei: Temburong, Peradayan Forest Reserve. 39 from Singapore: Thomson Nature Park. 40 from Malaysia: Sabah, Tawau Hill Park. Photos: J. K. H. Koh.

Biology. This spider appears to thrive in dense, moist lowland forests (elevations between 30 and 300 metres). It forages not only on the ground, but also on the fallen logs and foliage up to a metre from the ground. Apart from insects and other spiders, slugs are among its diet (Koh & Leong, 2014, p. 242). In resting position, its legs 3 are often retracted with the femora pointing almost vertically upwards (Figures 23–24, 27, 29–30, as in the jumping spider *Portia*). A mother has been seen fastening egg sac on the upper side of leaves (Figure 28). Before that stage, the discoidal egg-sacs are carried with the fangs under the mother's prosoma, as is usually seen in this genus. In three females, scars were observed (1 female syntype from Sarawak with 1 round scar ventrodistally on coxa II; 1 female from Malaysia: with 1 irregular scar on left femur IV ventro-proximally and 1 round scar on opisthosoma dorso-anteriorly; 1 female from Kuala Lumpur with 1 round scar on left palpal tibia dorso-medially, 1 irregular and 1 round scar on left coxa II ventro-proximally, and 4 round scars on left femur II retrolatero-ventro-proximally). These scars may indicate that males bite females during the mating process as reported in some *Thunberga* spp. (Jäger, 2021; Eudeline & Jäger, 2023), *Micrommata* spp. (Jäger, 2023), and *Heteropoda* spp. (Jäger, 2024; Korai & Jäger, 2024).

Heteropoda bufocorniculans spec. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:64E6BBD6-1725-4D5D-9DE2-81A505DCABE4

(Figures 42–48, 52–66, 169)

Type material. MALAYSIA: Sarawak: holotype female, Kuching, Gading National Park, 1° 41' 26.79" N, 109° 50' 45.14" E [47 m elevation], dipterocarp forest, D. Nazir

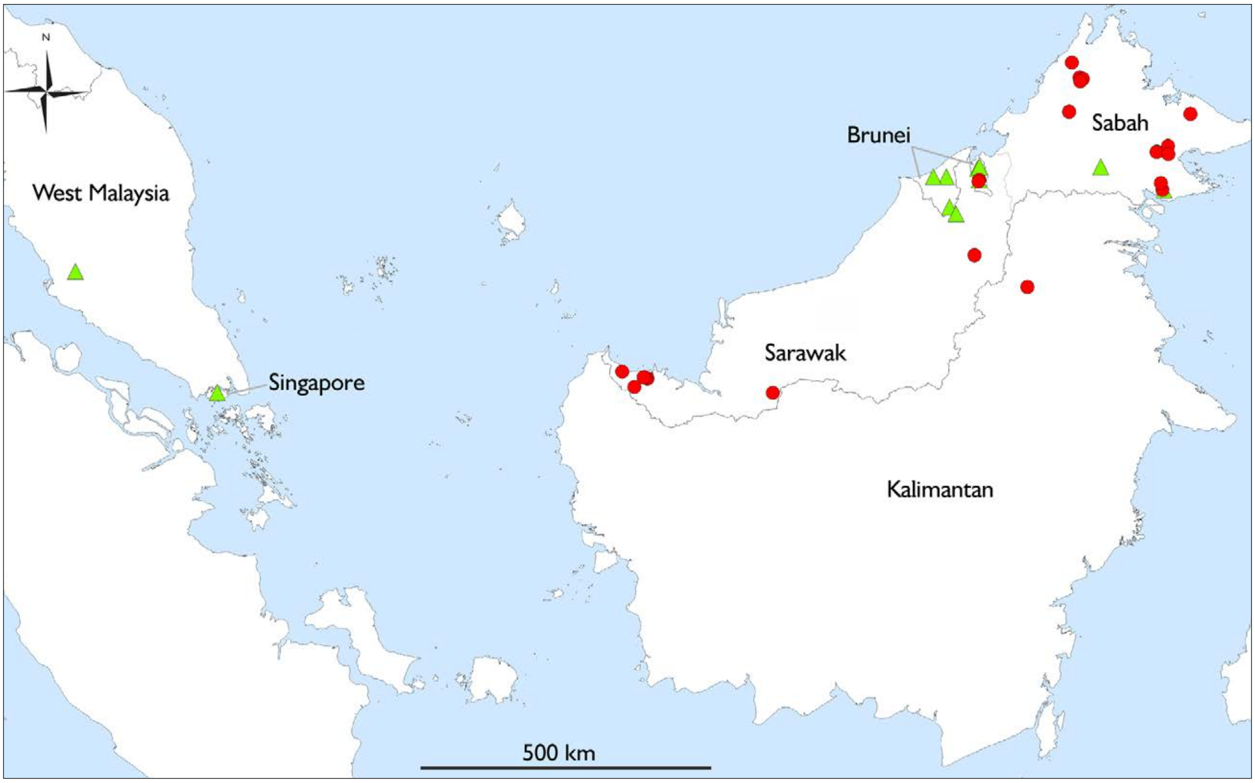


Figure 41. Distribution records of *Heteropoda borneensis* (Thorell, 1890). Green triangles—material examined for this study; red dots—photos from iNaturalist identifiable to species level. The exact type locality in Sarawak is unknown and therefore not pinpointed.

leg. 21 April 2013, DMN 00063, N. Nazir ded. (SMF). Paratype: MALAYSIA: Sabah: 1 female (JK.15.06.26.0005), Tawau, Tawau Hill Park, 4° 23' 34" N, 117° 54' 52" E [291 m elevation], C.S.P. Ang & J.M.L. Yeo leg. 26 June 2015 (FSC).

Material examined for comparison. *Heteropoda gemella* Simon, 1877: holotype female from the PHILIPPINES: Metro Manila: Manila [PL 5.7, OL 6.9; without characters 1–4 listed in the diagnosis below; DS and legs with numerous small dots] (MNHN 1774) (Figures 49–51).

Notes. Although the measured OL (6.9) of the holotype of *H. gemella* is not consistent with the length (7.5) provided by Simon in his original description, the examined specimen is considered the holotype. The ten immature specimens in the same vial as the holotype are not treated as part of the type series, as they were not mentioned in the description by Simon (1877, p. 65, "une femelle").

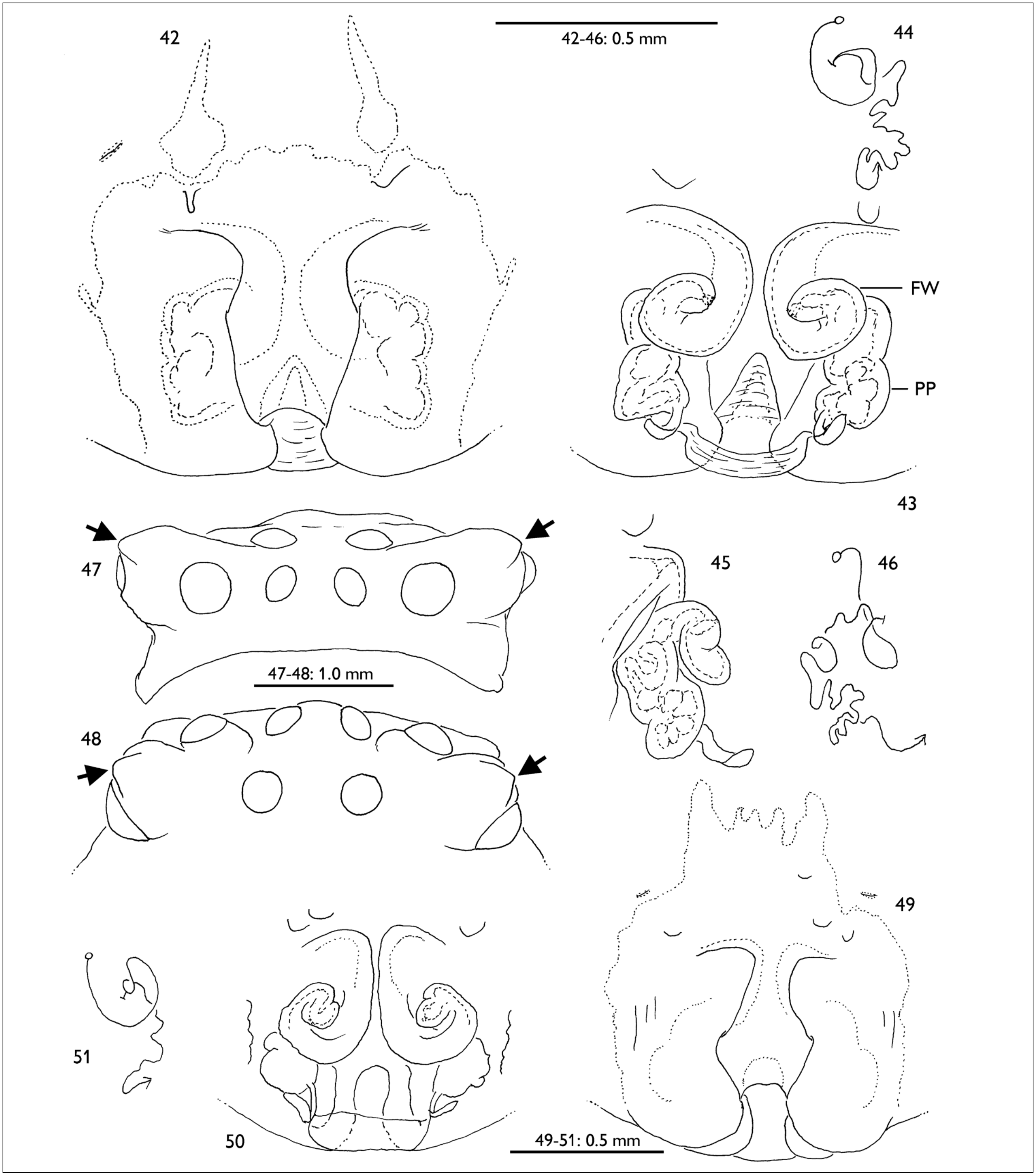
Etymology. The species name is derived from the Latin 'bufo' meaning 'toad' and 'corniculans' meaning 'horned' and refers to toad-like appearance of the species with wart-shaped structures and the "horns" between lateral eyes; adjective.

Diagnosis. Females of this species are unique in having the following characters: 1. Presence of a cone-shaped bulge between lateral eyes (Figures 47–48, 55), 2. Body covered dorsally with tufts of light and dark setae (Figures 52–54, 56, 59–64), 3. Absence of most of retrolateral spines on femora, tibiae and most of lateral spines on metatarsi (see description for details), 4. Presence of erect spines on femora (Figures 57–58), 5. Reduction of metatarsal ventral scopula in legs I–III (see description for details), and 6. Posterior part of opisthosoma widened resulting in an atypical shape (Figures 52–53, 59–60, 62, 64). Female copulatory organs (Figures 42–44, 65–66) are similar to those of *Heteropoda gemella* (Figures 49–51) in having a similarly shaped median septum (narrow waist anteriorly, anterior margins laterad) and internal duct system (first winding postero-laterad, glandular pores mediad to medio-posteriad, posterior part bulging, slightly wider than anterior part), but can be distinguished by: 1. Presence of distinct anterior bands, slightly separated from the field, 2. Anterior waist of median septum wider (i.e. ratio maximum width/waist width 1.3), 3. First windings medially rounded. In contrast, in *H. gemella*, the anterior bands are indistinct, strongly fused to field, waist of median septum narrower (i.e. ratio maximum width/waist width of median septum 2.6), and the first windings are elongate (i.e. median margins partly running parallel).

Description. Male. Unknown.

Female (holotype): Measurements: TL 12.2, PL 5.6, PW 5.4, AW 2.9, OL 6.5, OW 4.5. Eyes: AME 0.30, ALE 0.44, PME 0.29, PLE 0.45, AME-AME 0.29, AME-ALE 0.22, PME-PME 0.48, PME-PLE 0.83, AME-PME 0.29, ALE-PLE 0.61, CH AME 0.37, CH ALE 0.36; lateral eyes separated by cone-shaped bulge. Spination: Pp 130, 101, 2121, 1012; Fe I 321, II 331, III–IV 330; Pa I–IV 000; Ti I 1016, II 1006, III 1004, IV 1003; Mt I 0014, II–III 0004, III 2014, IV 0006(5). Ta I–IV with moderately dense scopulae, Mt I–II with scopula in distal half and proximal field and double row of stronger setae, III with rest of sparse scopula only distally and double row of stronger setae, IV with distal field and double row of stronger setae. Measurements of palps and legs: Pp 6.6 (2.0, 1.2, 1.3, -, 2.1); I 17.3 (5.0, 2.7, 4.7, 3.7, 1.2); II 19.5 (6.0, 2.8, 5.3, 4.0, 1.4); III 16.5 (5.2, 2.3, 4.2, 3.5, 1.3); IV 16.2 (5.4, 2.0, 3.8, 3.7, 1.3). Leg formula: II-I-III-IV. CH with 3 promarginal and 4 retromarginal teeth, 35 denticles and 1 escort seta. Palpal claw with 7 teeth.

Copulatory organ (Figures 42–46). As in diagnosis. Epigynal field wider than long, with 1 slit sensillum on left side and short anteriorly acuminate anterior bands, separated from the field. Subseptal pocket developed, anteriorly tapering. Internal duct system with semicircular first winding running to the distinctly visible glandular pores; posterior part with heavily coiled ducts and bulges; fertilisation ducts long, narrow, and curved, with antero-dorsad tips.



Figures 42–51. *Heteropoda* spp., females, copulatory organs. 42–48 *Heteropoda bufocorniculans* spec. nov., holotype female from Sarawak. 49–51 *Heteropoda gemella* Simon, 1877, holotype female from Philippines. 42, 49 Epigyne, ventral. 43, 45, 50 Vulva (42, 50 dorsal; 45 left half, lateral). 44, 46, 51 Schematic course of internal duct system (44, 51 dorsal; 46 lateral). 47–48 Eye arrangement (47 frontal; 48 dorsal). Abbreviations: FW = first winding of internal duct system, PP = posterior part of the internal duct system. Arrows indicating cone-shaped bulges between lateral eyes,

Figures 52–58. *Heteropoda bufocorniculans* spec. nov., holotype female from Sarawak. 52–54 Habitus (52 dorsal; 53 ventral; 54 frontal). 55 Eye region, dorsal. 56 Opisthosoma, dorsal, showing stiff setae and tufts of light setae. 57–58 Erect femoral spines (57 shortened prolateral distal spine of leg I, dorsal; 58 dorsal spines of leg II, prolateral, with shortened prolateral spine of leg III in the background). Photos: P. Jäger.

Figures 59–66. *Heteropoda bufocorniculans* spec. nov., females from Sabah (59, with egg-sac; 60–63 carrying egg-sac; 60–61 with some freshly hatched spiderlings clinging on the mother's prosoma). 59–64 Habitus (59–62, 64 dorsal; 63 frontal). 65 Epigyne, ventral. 66 Vulva, dorsal. Photos: J. K. H. Koh (59–61, 64–66) and N. Bay (62–63).

Colouration (Figures 52–56). Pale yellow to reddish brown with vivid pattern of dots, patches, light and dark tufts of setae as well as marbled pattern. DS with lighter median band and black tufts of setae laterally. Chelicerae reddish-brown with lighter patch in proximal half. Legs with spine patches and dots in between (decreasing in intensity from leg I to IV), femora ventrally yellowish-brown with many dots. Opisthosoma dorsally with pair of dark triangular patches antero-laterally, anterior half light brown with heart region slightly darker; posterior half darker with rows of lighter tufts of setae; laterally with reticulate, strongly contrasting pattern; ventrally light brown with dots.

Variation. Female (paratype): TL 11.6, PL 5.0, OL 6.6. Chelicerae with 25 denticles in furrow. Epigyne with 1 slit sensillum on each side, anterior bands distinct, but fused to field (Figures 65–66; many setae including tufts are rubbed of).

Distribution. Malaysia (Sarawak, Sabah) (Figure 169).

Biology. These spiders were found on tree trunks in primary rain forests. The egg-sac is held like in other *Heteropoda* species mainly by fangs and palps (Figures 59–63). Hatched spiderlings were bigger in size relative to the mother's body length compared to other *Heteropoda* species (Figures 60–61; Koh & Bay, 2019, p. 335).

Heteropoda lunula (Doleschall, 1857)
(Figures 67–71, 169)

Olios lunula Doleschall 1857: 428 (Description of female; holotype female from Java, NHMW 1858.1.30; examined).

Heteropoda lunula, Jäger 2002: 49, figures 106–117 (illustrations of male and female, removed f from synonymy of *H. thoracica*, synonymy of male previously assigned to *H. lunula* with *H. venatoria*). Jäger 2006: 53, figure 9 (illustration of female).

Material examined. SINGAPORE: 4 males (JK.89.08.24.0003, JK.90.01.01.0001, 90.08.10.0001, JK.92.06.14.0001), Greenwood Avenue, inside old house (now demolished) [1° 20' 3.79" N, 103° 48' 18.87" E, 12 m], J.K.H. Koh, leg. 24 August 1989, 1 January 1990, 10 August 1990, 14 June 1992 respectively (LKCNHM). 1 male (JK.88.10.16.0001), Malcolm Road, inside house, 1° 19' 26" N, 103° 50' 05" E [9 m elevation], J.K.H. Koh leg. 16 October 1988 (LKCNHM), 1 male (JK.88.11.15.0002), Kent Ridge, inside old house (now demolished), 01° 17' 43" N, 103° 46' 34" E [64 m elevation], J.K.H. Koh, leg. 15 November 1988 (LKCNHM). 1 male (JK.14.09.18.0001), Cluny Road, inside house, 01° 19' 10" N, 103° 48' 59" E [16 m elevation], J.K.H. Koh leg. 18 September 2014 (LKCNHM). 1 female (JK.92.05.24.0001), Hillcrest Road, inside old house (now demolished), 01° 19' 48" N, 108° 48' 22" E [12 m elevation], S.C. Tiah, leg. 24 May 1992 (LKCNHM).

Diagnosis. See Jäger (2002).

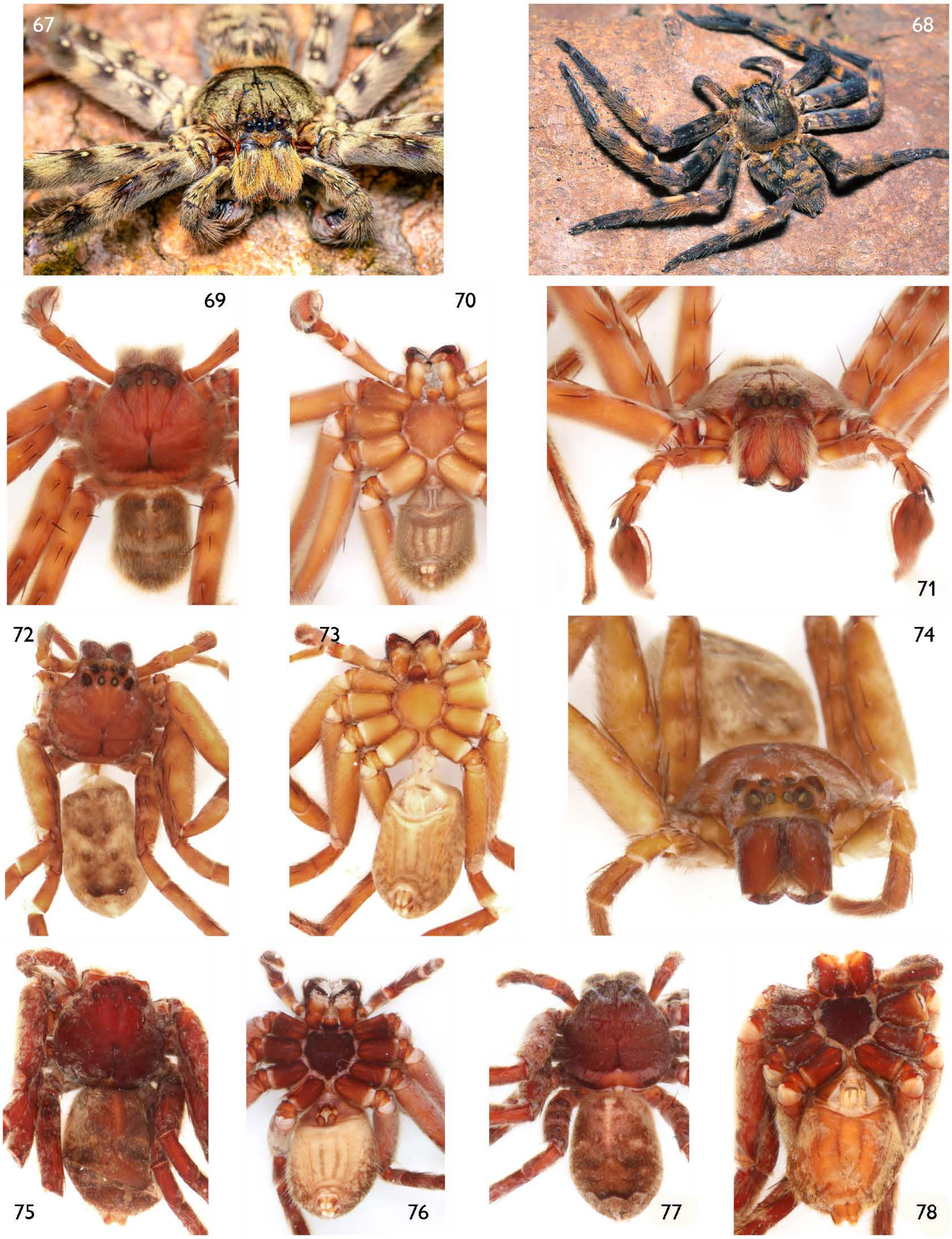
Description. See Jäger (2002). For colouration of preserved male see Figures 69–71, of live males and females see Figures 67–68 and Koh and Bay (2019, p. 326, unnumbered figures) and Koh et al. (2022, p. 505, unnumbered figures).

Distribution. India to Vietnam, Malaysia (Selangor), Indonesia (Java, Sumatra, Kalimantan, Maluku), Singapore new record (Figure 169).

Notes. Images of what can be unambiguously identified as *H. lunula* of both sexes have been taken outdoors by Nicky Bay (personal communication) near human habitation in other locations in Malaysia (Johor: Batu Pahat; Sabah: Maliau Basin).

Biology. *H. lunula* may be regarded as a synanthropic species, at least in Singapore, as it is often found on walls and corners inside old houses, and on tree trunks and crevices in highly disturbed or degraded forests. The females are heavy, sluggish, and slow-moving.

Heteropoda sederhana spec. nov.
http://zoobank.org/urn:lsid:zoobank.org:act:F376EB9B-3E5C-43B5-A08B-4FBF941BDF46
(Figures 72–74, 79–81, 169)



Figures 67–78. *Heteropoda* spp., habitus. 67–71 *H. lunula* (Doleschall, 1857), male (67, 69–71) and female (68) from Singapore. 72–74 *H. sederhana* spec. nov., holotype female from Java. 75–78 *H. strandi* Jäger, 2002, females from Sumatra (75–76: holotype) and Singapore (77–78) (67, 71, 74 frontal; 68–69, 72, 75, 77 dorsal; 70, 73, 76, 78 ventral; 73, 78 with epigyne dissected). Photos: C. S. P. Ang (67); J. K. H. Koh (68); P. Jäger (69–78).

Type material. INDONESIA: Jawa Barat: Holotype female, Buitenzorg [= Bogor, ca. 6° 35' 58.46" S, 106° 47' 59.46" E, 250 m], H.J. Jensen leg. 1904, Tilg. 28.8.1916, #275 (ZMUC).

Etymology. The species names is derived from the Indonesian adjective 'sederhana', meaning 'simple,' referring to the simple internal duct system without a loop as in most other *Heteropoda* spp.; term in apposition.

Diagnosis. Females of this species and *H. strandi* are unique among *Heteropoda* spp. in having the following characters (Figures 79–81): 1. Distinct triangular pocket situated anteriorly of copulatory openings, 2. Median septum distinctly narrowing posteriorly (i.e. lateral lobes almost touching each other at posterior margin), 3. Internal duct system simple, with short first winding and one coil anteriorly. Females of *H. sederhana* spec. nov. are distinguished from those of *H. strandi* by 1. Epigynal folds with S-shaped laterad parts in anterior half. 2. Anterior pocket approximately as long as wide. 3. Plain of first winding transversal to cuticular surface (epigynal folds with simple laterad part, anterior pocket distinctly wider than long [although may be bend], plain of first winding parallel to cuticular surface in *H. strandi*, cf. Figures 82–84).

Description. Male. Unknown.

Female (holotype): Measurements: TL 13.9, PL 6.5, PW 6.2, AW 3.4, OL 7.4, OW 4.9. Eyes: AME 0.41, ALE 0.62, PME 0.42, PLE 0.67, AME-AME 0.25, AME-ALE 0.04, PME-PME 0.41, PME-PLE 0.66, AME-PME 0.46, ALE-PLE 0.50, CH AME 0.50, CH ALE 0.31. Spination: Pp 131, 101, 2121, 1014(3); Fe I–II 323, III 333, IV 331; Pa I–IIII 001, IV 000; Ti I–IV 2026; Mt I–II 1014, III 2014, IV 3036. Ta I–IV and Mt I–III with dense scopulae, Mt IV with distal field, double row of stronger setae and very few scopula setae. Measurements of palps and legs: Pp 8.9 (2.6, 1.5, 2.2, -, 2.6); I 23.1 (6.6, 3.1, 6.1, 5.5, 1.8); II 26.2 (7.6, 3.5, 7.0, 6.1, 2.0); III 21.2 (6.5, 2.8, 5.5, 4.8, 1.6); IV 20.7 (6.2, 2.5, 5.4, 5.0, 1.6). Leg formula: II-I-IV-III. CH with 3 promarginal and 4 retromarginal teeth, ca. 35 denticles, most of them in patch close to promarginal teeth and 1 escort seta.

Copulatory organ (Figures 79–81). As in diagnosis. Epigynal field slightly longer than wide, with 2 slit sensilla on each side and short anterior bands, the latter fused to field. Median septum narrowing to narrow posterior part. Anterior pocket regularly triangular. Internal duct system with first winding posteriad, glandular pores not detected; posterior part with lateral bulges; fertilisation ducts narrow and curved, arising medio-posteriorly from posterior part, their tips dorsad.

Colouration (Figures 72–74). DS reddish-brown with light submarginal crescent posteriorly and sparse cover of light pubescence, the latter rubbed off in most parts; fovea, striae, and posterior margins dark. Chelicerae deep reddish-brown. Sternum ventral coxae, and gnathocoxae yellowish to reddish brown, labium deep reddish brown. Legs yellowish to dark yellowish brown with indistinct spine patches and numerous spots on ventral femora. Opisthosoma dorsally yellowish brown with four dark patches around muscle sigilla, between the two pairs a light chevron, dark median zone resulting posteriorly in dark transversal patch in posterior half; laterally mottled with elongate patches; ventrally yellowish, with four indistinct longitudinal bands of small muscle sigilla; spinnerets dorsally and laterally brown, ventrally yellowish.

Distribution. Indonesia (Java: Bogor) (Figure 169).

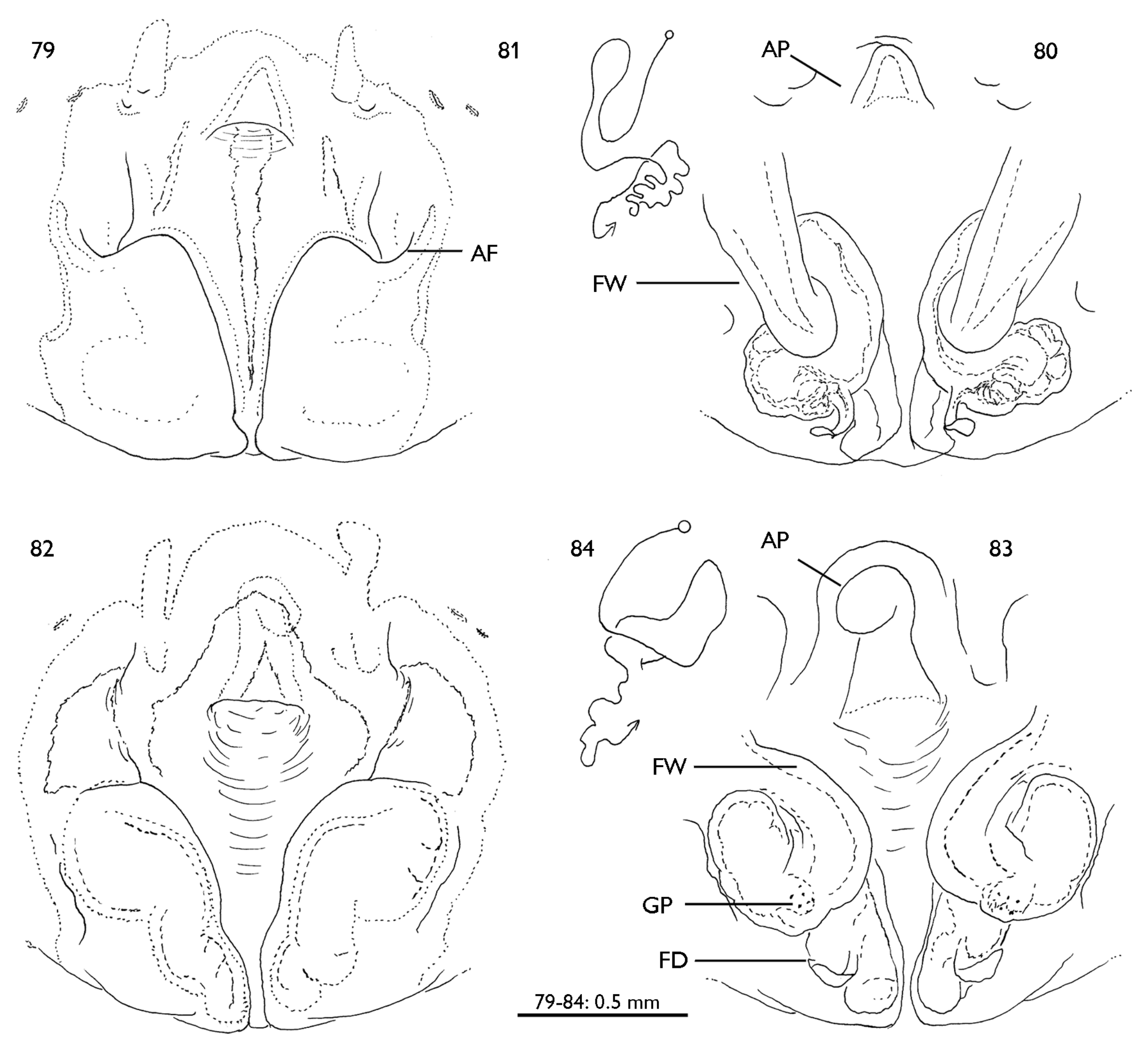
Heteropoda strandi Jäger, 2002
(Figures 75–78, 82–84, 169)

Torania panaretiformis Strand 1913: 119 (Description of female; holotype female from Indonesia, Sumatra, Bungar-Bondar, Schütz leg., SMF 4749; examined).

Heteropoda strandi Jäger 2002: 50, figs 129–131 (illustration of female, replacement name).

Material examined. SINGAPORE: 1 female (JK.03.07.30.0030), Upper Pierce Reservoir [1° 22' 23.65" N, 103° 48' 44.65" E, 20 m], edge of secondary forest, ground, J.K.H. Koh leg. 30 July 2003 (LKCNHM).

Diagnosis. Females of this species and *H. sederhana* spec. nov. are unique in having the following characters (Figures 82–84): 1. Distinct triangular pocket situated anteriorly of copulatory openings, 2. Freely visible median septum, narrowing posteriorly distinctly (i.e. lateral lobes almost touching each other), 3. Internal duct system simple, with short first winding and one coil anteriorly. Females of *H. strandi* are distinguished from those of *H. sederhana* spec. nov. by: 1. Epigynal folds with simple laterad part in anterior half, 2. Anterior pocket distinctly wider than long [although may be bend], 3. Plain of first winding parallel to cuticular surface (epigynal folds with S-shaped laterad parts, anterior pocket approximately as long as wide, plain of first winding transversal to cuticular surface in *H. sederhana* spec. nov., cf. Figures 79–81).



Figures 79–84. *Heteropoda* spp., female copulatory organs. 79–81 *H. sederhana* spec. nov., holotype female from Java. 82–84 *H. strandi* Jäger, 2002, female from Singapore. 79, 82 Epigyne, ventral; 80, 83 vulva, dorsal; 81, 84 schematic course of internal duct system, dorsal. Abbreviations: AF = anterior fold of epigyne, AP = anterior pocket, FD = fertilisation duct, FW = first winding of internal duct system, GP = glandular pores.

Description. Male. Unknown.

Female (Singapore): Measurements: TL 14.1, PL 6.7, PW 6.5, AW 3.7, OL 7.4, OW 5.0. Eyes: AME 0.49, ALE 0.67, PME 0.43, PLE 0.72, AME-AME 0.21, AME-ALE 0.08, PME-PME 0.47, PME-PLE 0.75, AME-PME 0.42, ALE-PLE 0.55, CH AME 0.35, CH ALE 0.24. Spination: Pp 131, 101, 2121, 1014; Fe I–II 323, III 333, IV 331; Pa I–IIII 001, IV 000; Ti I–IV 2026; Mt I–II 1014, III 2014, IV 3036. Ta I–IV and Mt I–III with dense scopulae, Mt IV with distal field, double row of stronger setae and very few scopula setae. Measurements of palps and legs: Pp 8.9 (2.6, 1.5, 2.0, -, 2.8); I 23.1 (6.3, 3.2, 6.3, 5.4, 1.9); II 26.1 (7.5, 3.5, 7.2, 5.9, 2.0); III 21.0 (6.4, 2.6, 5.6, 4.8, 1.6); IV 20.4 (6.1, 2.4, 5.3, 4.8, 1.8). Leg formula: II-I-IV-III. CH with 3 promarginal and 4 retromarginal teeth, 50–55 denticles in patch close to promarginal teeth and 1 escort seta. Palpal claw with 6 teeth.

Copulatory organ (Figures 82–84). As in diagnosis. Epigynal field as long as wide, with 1 slit sensillum on right and 2 slit sensilla on left side, all 3 close to the field, and short anterior bands, the latter fused to field. Median septum narrowing to thin posterior part. Anterior pocket anteriorly bent, tip ventrad. Internal duct system with first winding medio-posteriad, glandular pores indistinct; posterior part stretched converging posteriorly; fertilisation ducts narrow and curved, arising sub-terminally from posterior part, their tips antero-latero-dorsad.

Colouration (Figures 77–78). DS deep reddish-brown with distinct light submarginal crescent posteriorly and sparse cover of light pubescence, the latter denser around eyes; fovea and striae dark, with marbled pattern. Chelicerae deep reddish-brown with 2 thin dark longitudinal lines each. Sternum dark-brown, ventral coxae brown with light marbled pattern in proximal half, labium dark brown with light distal margin, gnathocoxae medially light, externally darker. Legs reddish-brown with cover of light pubescence, indistinct spine patches and numerous spots on ventral femora. Opisthosoma dorsally brown with irregular pattern, light transversal patch in posterior half, the latter anteriorly bordered by W-shaped dark zone and posteriorly with narrow extended part. Ventral part of opisthosoma more lightly coloured in the area posterior to the epigastric groove, with four longitudinal bands of dark setae stopping short 2–3 mm anterior of the spinnerets (more obvious when the specimen was newly preserved. See also Figure 78).

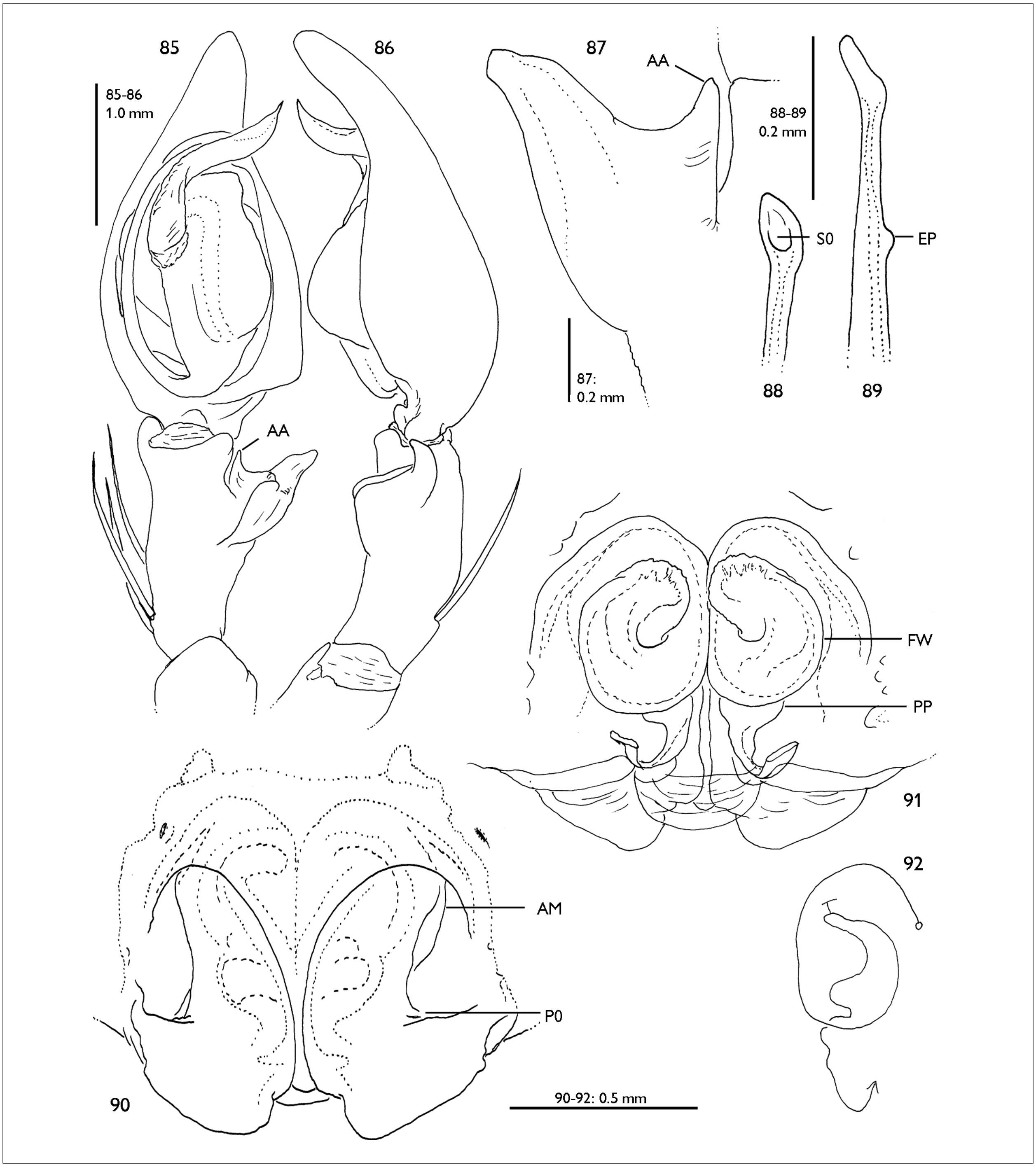
Variation. Female (holotype; Figures 75–76): TL 18.0, PL 8.8, OL 9.2. Anterior pocket straight (i.e. not bent as in the Singapore specimen illustrated in Figure 83).

Distribution. Indonesia (Sumatra), Singapore new record (Figure 169).

Heteropoda ocyalina species-group

Among the *Heteropoda* specimens we have examined in this study are six new species that are noteworthy in having shared diagnostic characters with *H. ocyalina* (Simon, 1887) and *H. asa* Jäger, 2024. We are therefore proposing a new species-group anchored on *H. ocyalina*. Its possible phylogenetic affinities with other species-groups will be discussed at the concluding part of this paper.

Diagnosis. Males may be recognised by the following combination of characters (Figures 85–89, 102–109): 1. dRTA with at least one additional apex, this latter may be reduced and hidden, 2. Tegulum with retrolateral swelling, 3. Embolus with medial to subapical projection, and apical part carrying the spermophor opening forming in most species an obtuse angle with embolus main part. Females may be recognised by: 1. Presence of posteriorly to medially located epigynal pockets (e.g., Figures 110, 124, 144, 152, 155; Jäger & Bayer, 2009, figure 6), and 2. First windings of the internal duct system touching each other along the median line (e.g., Figures 111, 125, 140, 153, 156). Moreover, females of three species (*H. temburong* spec. nov., *H. trifurcata* spec. nov., and *H. tutula* spec. nov.) are known to make and carry an egg-sac that is more bloated, with thicker seams, rather than the flat discoidal egg-sacs more commonly seen in other *Heteropoda* species (Figures 100, 121). The opisthosoma in both sexes is elongated with



Figures 85–92. *Heteropoda temburong* spec. nov., holotype male from Brunei (85–89) and female from Sabah (90–92). 85–87 Left palp (85 ventral; 86 retrolateral; 87 RTA, dorsal). 88–89 Embolus tip (88 distal; 89 dorsal). 90 Epigyne, ventral. 91 Vulva, dorsal. 92 Schematic course of internal duct system, dorsal. Abbreviations: AA = additional apex of dRTA, AM = anterior margins of epigynal pockets, EP = embolus projection, FW = first winding of internal duct system, PO = epigynal pocket, PP = posterior part of internal duct system, SO = spermophor opening.

an acuminate posterior end (e.g., Figures 93, 99, 114, 120, 122, 133, 158, 166). Additionally, the height of the clypeus measuring from the lower edge of the AME is about 1.5 times taller than the height measuring from the lower edge of the ALE (e.g., Figures 98, 121, 132, 160, 168). However, the last two characters (viz. elongated opisthosoma and procurved anterior eye row), by themselves, do not define the species group; they should only be used in combination with one or more of the genitalic characters defined earlier under the diagnosis of this species group. Another somatic character that may be used to discern members of this species-group from other congeners: a bunch of stiff light bristles originating from the ocular area (e.g., Figures 99–100, 120, 161), similar to those in species of the genus *Acantheis* Thorell, 1891 (Ctenidae, Keyserling, 1877).

Species included. *H. asa* Jäger, 2024, *H. ocyalina* (Simon, 1887), *H. temburong* spec. nov., *H. trifurcata* spec. nov., *H. tutula* spec. nov., *H. tympanum* spec. nov., *H. ulna* spec. nov., *H. uniter* spec. nov.

Distribution. Malaysia (Penang, Pahang, Sabah, Sarawak), Singapore, Indonesia (Sumatra, Java, Central Kalimantan) (Figure 169).

IDENTIFICATION KEY FOR SPECIES OF THE *HETEROPODA OCYALINA* SPECIES-GROUP

1a. Males (those of *H. tutula* spec. nov., *H. tympanum* spec. nov., *H. ulna* spec. nov., and *H. uniter* spec. nov. unknown) 2

1b. Females (that of *H. asa* unknown) 5

2a. dRTA distinctly longer that vRTA in ventral view, extending retrolaterally well beyond cymbial margin, conductor with additional ventral furrow (Figures 102–103; Jäger & Bayer, 2009, figures 1–3) 3

2b. dRTA not extending retrolaterally well beyond cymbial margin, conductor simple, without such additional furrow 4

3a. dRTA distally simple, narrow (Figure 103) .... *H. trifurcata* spec. nov.

3b. dRTA distally widened, best seen in retrolateral view, with two apices (Jäger & Bayer, 2009, figures 3–4).... .... *H. ocyalina*

4a. dRTA with one additional apex (Figures 85, 87) .... *H. temburong*

4b. dRTA with two additional apices (Jäger, 2024, figure 3) .... *H. asa*

5a. First windings overlapping medially (Figure 128) .... *H. tympanum* spec. nov.

5b. First windings touching each other medially, running parallel along median axis (Figures 91, 111, 126, 140, ... 153, 156) 6

6a. Median septum anteriorly distinctly broader, i.e. at least twice the posterior width, and with anteriorly diverging epigynal margins (Figures 90, 110, 113, 139, 144) 7

6b. Median septum anteriorly not distinctly broader, i.e. less than or just barely twice the posterior width (Figures 152, 155), or if slightly broader, anterior epigynal margins more or less parallel (Figure 124).......... 9

7a. Epigynal pockets situated in the mid of epigyne, i.e. not reaching epigastric furrow (Figure 90).................... .... *H. temburong* spec. nov.

7b. Epigynal pockets situated posteriorly, i.e. posterior of epigastric furrow (e.g., Figures 110, 113, 139, 144).... 8

8a. Anterior margins of first winding running towards centrally located glandular pores (Figures 140, 145), spiders with distinct, narrow median band on prosoma and opisthosoma (Figures 158, 161)........... *H. ulna* spec. nov.

8b. Anterior margins of first winding running directly to marginally situated glandular pores (Figure 111), spiders with broad dark patch on prosoma and dark lanceolate heart patch on opisthosoma (Figures 117, 122) .... *H. trifurcata* spec. nov.
9a. Epigynal pockets situated posteriorly, reaching epigastric furrow (Figure 152).......... *H. ocyalina*
9b. Epigynal pockets situated in the mid of epigyne, i.e. not reaching epigastric furrow (Figures 124, 155)....... 10
10a. Posterior part of internal duct system pointed, extending laterally distinctly beyond first winding, glandular pores situated centrally, dorsad (Figure 125) .... *H. tutula* spec. nov.
10b. Posterior part of internal duct system rounded, extending laterally not beyond first winding, glandular pores situated marginally, mediad (Figure 156) .... *H. uniter* spec. nov.

Heteropoda temburong spec. nov.

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(Figures 85–101, 169)

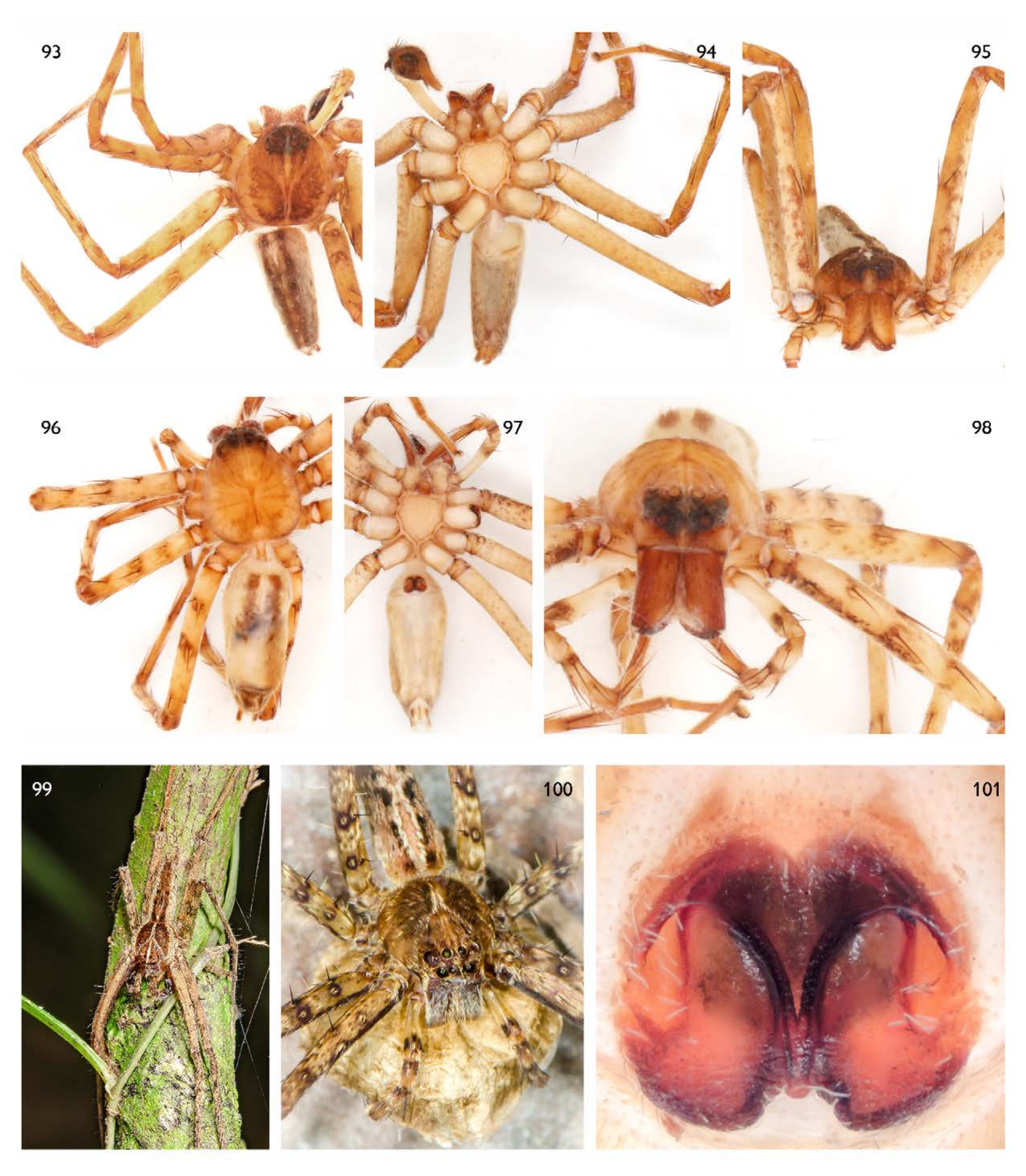
Heteropoda sp. J—Koh & Bay 2019: 336, unnumbered photos of male and female.

Type material. BRUNEI: Temburong: Holotype male (JK.11.04.13.2004), Ulu Temburong National Park, Sungai Seruyu, 4° 33' 50" N, 115° 8' 55" E, 222 m elevation, primary forest, J.K.H. Koh leg. 13 April 2011, "prograde sparassid" (SMF).

Additional material examined. BRUNEI: Temburong: 1 female (JK.12.04.20.0069), Peradayan Forest Reserve, off Kampung Lakiun, 4° 45' 0.0" N, 115° 9' 58" E [109 m elevation], J.K.H. Koh leg. 20 April 2012 (BMKB). 1 female (JK.12.04.20.0062), with same locality data as for previous specimen (LKCNHM). Belait: 1 male (JK.11.03.23.0055), Melilas, Sungai Ingei, primary forest, 4° 08' 36" N, 114° 43' 16" E [58 m elevation], J.K.H. Koh leg. 23 March 2011 (LKCNHM). MALAYSIA: Sabah: 1 female (JK.10.03.16.2017), Sepilok, Orang Utan Rehabilitation Centre, 5° 51' 37" N, 117° 57' 7" E, 49 m elevation, disturbed forest, J.K.H. Koh leg. 16 March 2010, "Prograde Unicorn" (FRC). Sarawak: 1 male (JK.12.01.23.1003), Gunung Mulu National Park, Botanical Walk near Parks' headquarters, 4° 02' 30" N, 114° 48' 52" E [44 m elevation], J.K.H. Koh leg. 23 January 2012 (LKCNHM). 1 female (JK.12.01.23.1002), same locality as for previous specimen (SMF). 1 female (JK.12.01.23.0046), Gunung Mulu National Park, outside Fast Lane Cave 4° 02' 55" N, 114° 49' 10" E [57 m elevation] J.K.H. Koh leg. 23 January 2012 (LKCNHM).

Etymology. The species name refers to the type locality; noun in apposition.

Diagnosis. Males are similar to those of *Heteropoda asa* Jäger, 2024 by having an almost identical palpal arrangement including same arising point and shape of embolus, same arising point and shape of conductor with a pointed, retro-distad tip extending distinctly beyond cymbial margin, presence of additional apex on dRTA, tegulum with right-angled margin retro-distally and right-angled bend of spermophor (Figures 85–89), but can be distinguished by: 1. dRTA with one additional apex, 2. Embolus base narrow, 3. Retrolateral swelling of tegulum bulging distinctly ventrad, 4. Conductor tip with entire proximad margin, 5. Spermophor opening roundish (dRTA with two apices, embolus base broader, narrowing abruptly, retrolateral swelling of tegulum not bulging ventrally, conductor tip with triangular proximad outgrowth, spermophor opening elongated in *H. asa*; cf. Jäger, 2024, figures 1–5). Females similar to those of *H. trifurcata* spec. nov. in having the median septum narrowest in its posterior half, the anterior margins of posterior epigynal pockets reaching copulatory openings (Figures 90–92), but can be distinguished by: 1. Posterior pockets situated medially between copulatory openings and posterior margin of lateral lobes, 2. Lateral margins of first windings extending posteriorly distinctly beyond glandular pore area of internal duct system, 3. Posterior parts of internal duct system less



Figures 93–101. *Heteropoda temburong* spec. nov., holotype male (93–95, 99) and female (96–98, 100–101) from Brunei. 93–100 Habitus of preserved (93–98) and live (99–100) specimens (93, 96, 99–100 dorsal; 94, 97 ventral; 95, 98 frontal). 101 Epigyne, ventral. Photos: P. Jäger (93–98), J. K. H. Koh (99–101).

than one diameter apart from each other (posterior pocket extending posteriorly almost to margin of lateral lobes, lateral margins of first windings not reaching posteriorly to glandular pore area and posterior parts of internal duct system separated by more than one of their diameters in *H. trifurcata* spec. nov.; cf. Figures 110–113).

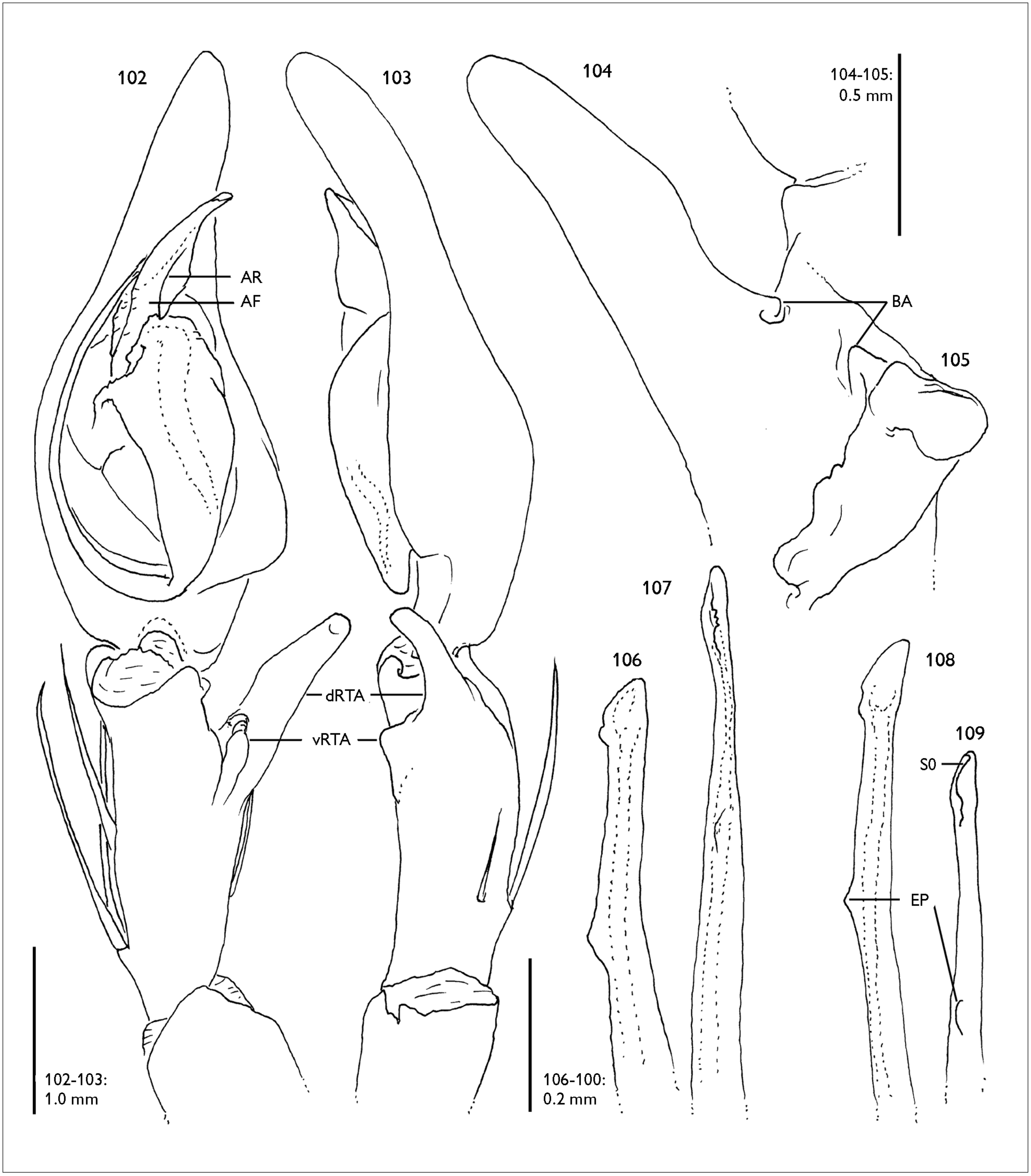
Description. Male (holotype): Measurements: TL 10.6, PL 4.9, PW 4.5, AW 2.0, OL 5.7, OW 2.2. Eyes: AME 0.28, ALE 0.49, PME 0.36, PLE 0.46, AME-AME 0.09, AME-ALE 0.08, PME-PME 0.19, PME-PLE 0.42, AME-PME 0.37, ALE-PLE 0.47, CH AME 0.41, CH ALE 0.26. Spination: Pp 131, 101, 2101; Fe I 323, III 333, IV 331; Pa I–III 101, IV 101(0); Ti I–II 2126, III 2026, IV 2126; Mt I–II 1014, III 2014, IV 3036. Mt I–III with sparse scopulae in distal half and double row of setae in proximal half, IV with distal field and double row of stronger setae. Measurements of palps and legs: Pp 8.4 (2.7, 1.0, 1.7, -, 3.0); I 33.9 (9.0, 2.5, 10.4, 9.1, 2.9); II 34.5 (9.2, 2.6, 10.4, 9.3, 3.0); III 23.3 (6.6, 1.9, 6.8, 6.0, 2.0); IV 30.7 (8.7, 2.0, 8.2, 8.9, 2.9). Leg formula: II-I-IV-III. CH with 3 promarginal and 4 retromarginal teeth, ca. 37 denticles and 1 escort seta.

Palp (Figures 85–89). As in diagnosis. RTA arising medially from Ti, vRTA flat and with right-angled margin ventrally in retrolateral view, dRTA short, slightly bent, and tapering at its tip, the additional apex distad, papering, its tip rounded. Cymbium distinctly longer than Ti, with distinct retro-proximal swelling. E arising from tegulum in 6-o'clock-position running a flat semi-circle, subapically with small rounded projection, spermophor opening situated apically.

Colouration (Figures 93–95). Yellowish-brown with dark pattern consisting of dark setae. DS with light narrow lateral bands and median dark band with an anteriorly trifurcated light line, clypeus with light median patch in front of AME. Chelicerae brown, disto-medially lighter. Sternum, gnathocoxae, ventral coxae light yellow, labium brown. Legs yellowish-brown with dark patches and femora, additionally, with dots ventrally. Opisthosoma dorsally with two dark narrow posteriorly converging bands, these consisting of dark patches, between and lateral to these bands light-brown; laterally light with dots; ventrally pale yellowish-brown with elongate triangle in front of spinnerets, the latter dorsally pale yellowish brown, ventrally and laterally brown. Live spiders or freshly preserved specimens with more distinctly contrasting colouration, with the trifurcate pattern on DS more conspicuous than that in preserved specimens (Figure 99). As median part of the trifurcate pattern, a narrow band of long and forward-directed white seta runs from the fovea, through the gap between the PME, to the anterior edge of the DS between the AME. 2 long and stiff bristles between the AME projects beyond the anterior edge of the DS.

Female (from Sepilok, Sabah): Measurements: TL 10.8, PL 4.6, PW 3.9, AW 2.2, OL 6.2, OW 2.7. Eyes: AME 0.29, ALE 0.49, PME 0.36, PLE 0.43, AME-AME 0.18, AME-ALE 0.02, PME-PME 0.24, PME-PLE 0.46, AME-PME 0.37, ALE-PLE 0.45, CH AME 0.72, CH ALE 0.45. Spination: Pp 131, 101, 2121, 1014; Fe I 323, II–III 333, IV 331; Pa I–II 001, III 101, IV 100; Ti I–IV 2026; Mt I–II 1014, III 2014, IV 3036. Mt I–III with moderately dense scopulae along entire length and few stiff setae very proximally (I–II) or with double row of stiff setae over entire length (III), IV with distal field and double row of stronger setae, with very sparse scopula in distal half. Measurements of palps and legs: Pp 8.1 (2.2, 1.0, 2.0, -, 2.9); I 24.3 (6.5, 2.2, 7.3, 6.2, 2.1); II 24.5 (6.8, 2.3, 7.3, 6.0, 2.1); III 17.9 (5.2, 1.7, 5.0, 4.3, 1.7); IV 23.4 (6.8, 1.8, 6.1, 6.5, 2.2). Leg formula: II-I-IV-III. CH with 3 promarginal and 4(5) retromarginal teeth, ca. 30 denticles and 1 escort seta.

Copulatory organ (Figures 90–92). As in diagnosis. Epigynal field with one slit sensillum on each side, one very close to field, one included in the field. Median septum longer than wide, becoming gradually narrower towards posterior end. Posterior pockets postero-mediad, wide, their internal margin running close to copulatory organ. Copulatory openings situated laterally. Glandular pores of internal duct system antero-mediad, fertilisation ducts arising postero-medially from spermathecae, long and bent, their tips dorsad.



Figures 102–109. *Heteropoda trifurcata* spec. nov., holotype male (102–107) and paratype male (108–109) from Malay peninsula, copulatory organs (102 left palp, ventral; 103 same, retrolateral; 104 RTA, dorsal; 105 same, disto-retrolateral; 106, 108 embolus, ventral; 107, 109 same, distal). Abbreviations: AF = additional furrow of conductor, AR = additional ridge of conductor, BA = basal apex of dRTA, dRTA = dorsal part of RTA, EP = embolus projection, SO = spermophor opening, vRTA = ventral part of RTA.

Colouration (Figures 96–98). As in male, but patch on DS not as distinct. Fe I with dark pattern ventrally, this pattern turning gradually to a dotted pattern towards Fe IV. OS dorsally with less distinct pattern, ventrally paler and many light erect spines on OS. Living spiders with much more distinctly developed pattern (Figure 100). 2 broken bristles and another base of a broken off setae are present between the AME.

Variation. Males: TL 10.2 to 10.8. Female: TL 9.2 to 11.2. Epigyne with both slit sensilla separated from epigynal field (Figure 101). In both sexes, the stiff bristles projecting between the AME in both sexes may vary from one to three. In some specimens, one of the bristles may point upward (dorsally) instead of forward (anteriorly). The dorsal patterns of opisthosoma vary: some do not have a white longitudinal band.

Distribution. Brunei (Temburong, Belait) and Malaysia (Sabah, Sarawak) (Figure 169).

Biology. Although it is occasionally found among forest leaf litter, the species lives and hunts at night mainly above ground: on foliage, twigs and stems, and tree trunks. In their resting position, the males and females of this species (and the two new species described below) tend to direct their legs I and II forward, instead of spreading them sideway, as in other congeners. The egg-sac is more bloated or inflated in shape compared to the flattish discoid egg-sacs more commonly seen in other *Heteropoda* species (Figure 100). Measurements of an egg-sac carried by specimen JK. 12.40.30.0069 from Brunei: 10.3 mm (maximum width) by 8.7 mm (minimum width), and 7.4 mm (thickness).

Heteropoda trifurcata spec. nov.

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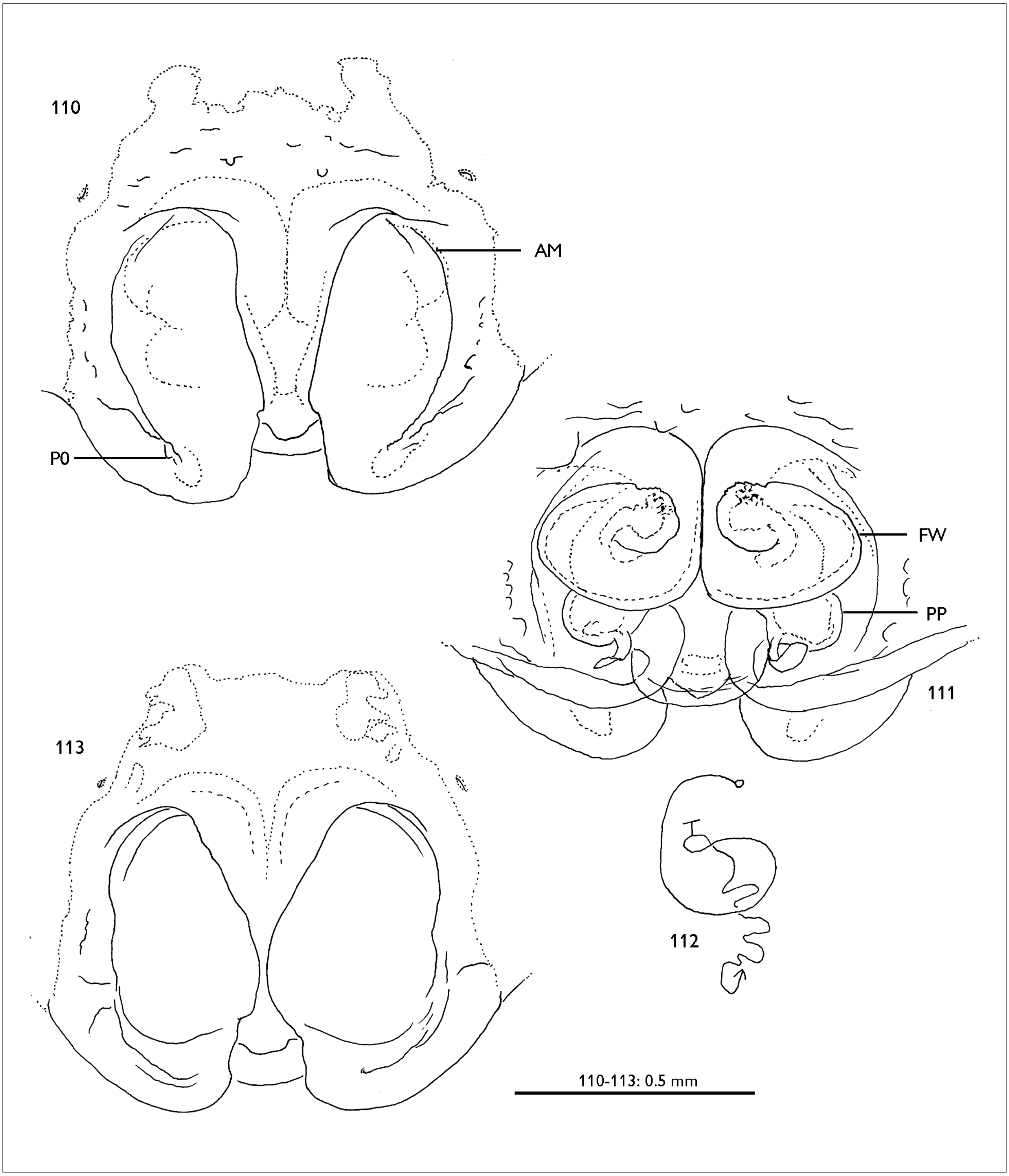
(Figures 102–123, 169)

Type material. MALAYSIA: Pahang State: Holotype male, Bukit Fraser, Jeriau Waterfall, 3° 43' 26.07" N, 101° 42' 36.22" 'E, 1040 m elevation, disturbed primary forest, along trail, at night, by hand, P. Jäger & T. Laufs leg. 13 February 2014 (SMF). Paratypes: 1 female, with same data as for holotype (SMF). 1 male, 1 female, with same data as for holotype, except for: 11 February 2014 (LKCNHM).

Additional material examined. 1 immature, with same data as for holotype (SMF). 2 immatures, with same data as for holotype, except for: 11 February 2014 (LKCNHM).

Etymology. The species name is derived from the Latin 'trifurcatus, -a, -um' meaning 'trifurcated' and refers to the trifurcate pattern on the dorsal shield of prosoma especially of males, characteristic for the *ocyalina* species-group; adjective.

Diagnosis. Males of *H. trifurcata* spec. nov. similar to those of *H. ocyalina* in having a similar arrangement of the palp including almost the same arising point and shape of embolus and conductor, the retro-proximal margin of the conductor with additional furrow and ridge, spermophor very slightly S-shaped, running from 12.30-o'clock-position to the retrolateral part of the embolus base (Figures 102–109), but can be distinguished by: 1. dRTA long and with simple apex, 2. Embolus projection situated freely visible outside of the conductor sheath (dRTA with two small plier-shaped apices, embolus projection situated sub-apically within the conductor sheath in *H. ocyalina*; cf. Jäger & Bayer, 2009, figures 1–5). Female copulatory organs similar to those of *H. ocyalina* in having an epigynal field roughly as long as wide and with only very short or entirely included anterior bands, a very similar internal duct system with first winding running one coil up to glandular pores, these latter anteriad to mediad (Figures 110–112), but can be distinguished by: 1. Median septum narrowest in posterior half, 2. Posterior epigynal pockets extending into anterior half, 3. First winding of internal duct system wider than posterior part, i.e. posterior part extending only posteriorly beyond first winding (median septum roughly with the same width over entire length, slightly narrower in anterior half, posterior pockets situated exclusively in posterior half, first winding not as wide as posterior part of internal duct system, i.e. the latter part extending beyond first winding laterally in *H. ocyalina*; cf. Figures 152–154).



Figures 110–113. *Heteropoda trifurcata* spec. nov., paratype females, copulatory organs (110, 113 Epigyne, ventral; 111 vulva, dorsal; 112 schematic course of internal duct system, dorsal). Abbreviations: AM = anterior margin of epigynal pocket, FW = first winding of internal duct system, PO = epigynal pocket, PP = posterior part of internal duct system.

Description. Male (holotype): Measurements: TL 15.0, PL 6.2, PW 5.8, AW 2.8, OL 8.8, OW 4.5. Eyes: AME 0.38, ALE 0.56, PME 0.41, PLE 0.52, AME-AME 0.19, AME-ALE 0.05, PME-PME 0.19, PME-PLE 0.49, AME-PME 0.42, ALE-PLE 0.59, CH AME 0.95, CH ALE 0.60. Spination: Pp 131, 101, 2101; Fe I 323, II–III 333, IV 331; Pa I–II 101, III 1(0)01, IV 100; Ti I–II 2326, III–IV 2126; Mt I–II 1014, III 2014, IV 3036. Mt I–III with dense scopulae along entire length and stiff setae in proximal half, IV with distal field and double row of stronger setae, with very sparse scopula in distal half. Measurements of palps and legs: Pp 11.2 (3.9, 1.6, 2.3, -, 3.4); I 45.7 (12.4, 3.5, 14.0, 12.3, 3.5); II 47.3 (13.1, 3.6, 14.3, 12.7, 3.6); III 32.3 (9.4, 2.9, 9.3, 8.3, 2.4); IV 39.5 (11.5, 2.8, 10.6, 11.4, 3.2). Leg formula: II-I-IV-III. CH with 3 promarginal and 4 retromarginal teeth, ca. 65 denticles and 1 escort seta.

Palp (Figures 102–107). As in diagnosis. RTA medially to sub-distally from Ti, vRTA developed as small hump, internally connected to basal dRTA apex, the latter small and seen only in dorsal or retrolatero-distal view, dRTA only very slightly bent, distally rounded. Cymbium distinctly longer than Ti, with distinct, rounded retro-proximal swelling. E arising in 5.30-o'clock-position from tegulum, running a flat semicircle to its tip, subapically with small triangular projection, spermophor opening situated apically. C with pointed disto-retrolaterad tip, extending slightly beyond cymbial margin.

Colouration (Figures 114–116). Yellowish-brown with moderately dark pattern. DS with broad black median band with a narrow trifurcate light pattern, reaching from fovea between AME and along border between thoracic and cephalic area; 5 sockets of setae present between AME in a triangular arrangement, with 1 median long stiff seta and shorter lateral setae. Chelicerae light yellowish-brown. Legs yellowish-brown with spine patches on femora and further patches on patellae and tibiae, and many dots on femora ventrally. Opisthosoma dorsally light reddish-brown with dark median lanceolate patch above heart; ventrally yellowish-brown with reddish-brown median band ending in triangle anterior of spinnerets, the latter dorsally reddish-brown, ventrally pale yellowish-brown. Living spiders with much more vividly developed pattern (Figure 120).

Female (paratype, SMF): Measurements: TL 20.1, PL 8.3, PW 7.1, AW 4.1, OL 11.8, OW 6.1. Eyes: AME 0.46, ALE 0.67, PME 0.53, PLE 0.62, AME-AME 0.25, AME-ALE 0.06, PME-PME 0.30, PME-PLE 0.64, AME-PME 0.54, ALE-PLE 0.64, CH AME 1.24, CH ALE 0.84. Spination: Pp 131, 101, 212(1)1, 1014; Fe I 323, II–III 333, IV 331; Pa I 001, II–III 101, IV 100; Ti I–IV 2026; Mt I–II 1014, III 2014, IV 3036. Mt I–III with dense scopulae along entire length and stiff setae in proximal half, IV with distal field and double row of stronger setae, with very sparse scopula in distal half. Measurements of palps and legs: Pp 15.9 (4.5, 2.1, 3.8, -, 5.5); I 45.9 (12.6, 4.6, 13.9, 11.6, 3.2); II 47.0 (13.2, 4.8, 14.1, 11.6, 3.3); III 34.7 (10.4, 3.5, 10.2, 8.4, 2.2); IV 41.6 (12.3, 3.3, 11.3, 11.6, 3.1). Leg formula: II-I-IV-III. CH with 3 promarginal and 4 retromarginal teeth, ca. 75 denticles and 1 escort seta.

Copulatory organ (Figures 110–112). As in diagnosis. Epigynal field with one slit sensillum on each side, very close to field. Median septum longer than wide, with posteriorly bulging transversal margin. Posterior pockets postero-mediad, slit-like, their internal margin running close to copulatory opening. Copulatory openings situated antero-laterally. Glandular pores of internal duct system antero-mediad, fertilisation ducts arising postero-medially from spermathecae, bent, their tips dorsad to antero-dorsad.

Colouration (Figures 117–119). As in male, but generally darker, dark reddish-brown. DS with pair of distinct light patches submarginally in posterior half; 5 sockets of broken off setae between AME. Coxae ventrally vividly dotted. OS dorsally with few long light setae standing upright; laterally dotted; ventrally with dark triangle anterior of spinnerets. In living spiders especially pattern on DS more distinctly developed (Figures 121–123).

Figures 114–123. *Heteropoda trifurcata* spec. nov., holotype male (114–116, 120) and paratype female (117–119, 121–123) from Malay peninsula, habitus of preserved (114–119) and live (120–123) specimens (114, 117, 120, 122 dorsal; 115, 118, 123 ventral; 116, 119, 121 frontal). Photos: P. Jäger.

Variation. Male: TL 16.4, PL 7.3, OL 9.1. Distinctly darker than holotype, DS and OS dorsally with more complete colour pattern; 2 long stiff setae present between AME. Coxae ventrally with few pale dots. Embolus tip with spermophor opening and subapical projection only slightly different from that of holotype (Figures 108–109). Female: TL 18.1, PL 7.2, OL 10.9. Chelicerae laterally with narrow band of light setae. OS dorsally with light patches anterior and posterior of dark lanceolate heart patch. Lateral lobes in paratype (11.2.2014) almost touching each other, anterior bands integrated in epigynal field (Figure 113).

Distribution. Known only from type locality in Pahang State, Malaysia (Figure 169).

Biology. Little is known about the biology of this species. One male was caught on the rooftop of a forest hut, suggesting that the species inhabits also higher strata. One female with an egg-sac was found on the ground in a disturbed primary forest. The egg-sac is similar to those of *H. temburong* spec. nov. and *H. tutula* spec. nov., in contrast to the typically discoidal egg-sacs of most other *Heteropoda* spp. Additionally, it has unique dark streaks of silk on its surface such as those on the egg-sacs of *Argiope bruennichi* (Scopoli, 1772) (Bellmann, 2001, p. 121, unnumbered photo).

Heteropoda tutula spec. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:9D7F591E-9070-4EB3-89C8-14D1FDC767A5

(Figures 124–126, 130–133, 169)

Type material. SINGAPORE: Holotype female (JK.91.01.30.0008), Upper Peirce Reservoir, Pipeline Trail, 1° 23' 11" N, 103° 48' 40" E [42 m elevation], forest floor, J.K.H. Koh leg. 30 September 1991 (LKCNHM).

Etymology. The species name refers to the stiff setae between the AME characteristic for the *ocyalina* species-group and derived from the Latin 'tutulus, -a, -um' meaning 'hair dressed in a high cone over the forehead'; adjective.

Diagnosis. Females of *H. tutula* spec. nov. are similar to those of *H. ocyalina* in having indistinct epigynal pockets and the posterior part of internal duct system wider than first winding (Figures 124–126), but can be distinguished by: 1. Posterior pockets with their anterior margins reaching copulatory openings, 2. Lateral margins of first winding extending posteriorly beyond glandular pores, 3. Posterior part of internal duct system distinctly bent laterally (posterior pockets situated in posterior half, lateral margins of first winding situated anterior of glandular pores, posterior part of internal duct system longitudinally straight in *H. ocyalina*; cf. Figures 152–154).

Description. Male: Unknown.

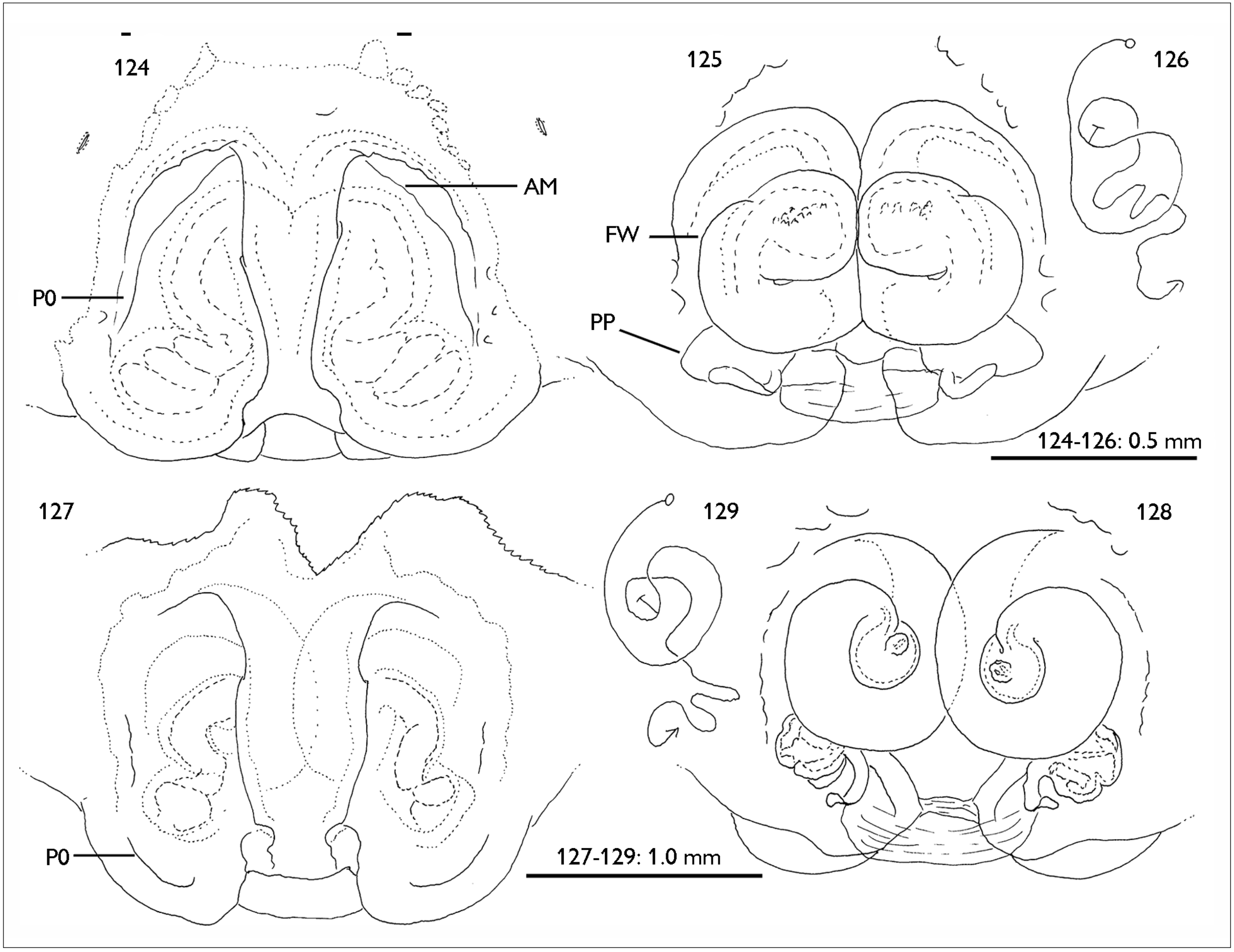
Female (holotype): Measurements: TL 12.1, PL 4.6, PW 4.3, AW 2.3, OL 7.5, OW 3.8. Eyes: AME 0.30, ALE 0.49, PME 0.37, PLE 0.47, AME-AME 0.19, AME-ALE 0.05, PME-PME 0.20, PME-PLE 0.46, AME-PME 0.37, ALE-PLE 0.41, CH AME 0.77, CH ALE 0.45. Spination: Pp 131, 101, 2(1)121, 1014; Fe I 323, II–III 333, IV 331; Pa I 001, II 101, III 100, IV 000; Ti I–IV 2026; Mt I–II 1014, III 2014, IV 3036. Mt I–III with dense scopulae along entire length and few stiff setae very proximally (I–II) or double row of setae in proximal half (III), IV with distal field and double row of stronger setae, with very sparse scopula in distal half. Measurements of palps and legs: Pp 8.5 (2.4, 1.2, 2.0, -, 2.9); I 24.3 (6.6, 2.3, 7.3, 6.0, 2.1); II 24.6 (6.8, 2.3, 7.3, 6.1, 2.1); III 17.7 (5.2, 1.8, 4.9, 4.2, 1.6); IV 23.2 (6.8, 1.9, 6.0, 6.4, 2.1). Leg formula: II-I-IV-III. CH with 3 promarginal and 4 retromarginal teeth, ca. 55–60 denticles and 1 escort seta.

Copulatory organ (Figures 124–126). As in diagnosis. Epigynal field slightly trapezoid, narrowing anteriorly, with one slit sensillum on each side. Median septum longer than wide covered by lateral lobes a bit in posterior half, with posteriorly concave transversal margin. Posterior pockets posteriad, slit-like. Copulatory openings situated antero-laterally. Glandular pores of internal duct system anteriad, turning point wide, fertilisation ducts arising postero-medially from spermathecae, bent, their tips latero-dorsad.

Colouration (Figures 130–132). Deep yellowish- to light reddish-brown with reddish-brown pattern. DS reddish brown with broad margins and median stripe light yellowish, the latter over entire length of DS; with 5 sockets of broken off setae between AME. PS ventrally pale yellow, without pattern. Chelicerae darker reddish-brown than DS, with 3 longitudinal bands each. Legs yellowish-brown with patches at spines on femora and on patellae and proximal tibia, femora ventrally dotted. Opisthosoma dorsally reddish-brown, becoming darker posteriorly, with light median band along entire length; ventrally pale yellowish, with indistinct patch anterior of spinnerets, the latter dorsally and laterally reddish-brown, ventrally pale yellow. Living spiders with distinctly more contrasting pattern and more details (Figure 133).

Distribution. Known only from type locality in Singapore (Figure 169).

Biology. Like the egg-sacs of the two preceding species in the ocyalina species-group, the egg-sac is more inflated and thicker than those seen in most other *Heteropoda* species.



Figures 124–129. *Heteropoda* spp., females, copulatory organs. 124–126 *Heteropoda tutula* spec. nov., holotype from Singapore. 127–129 *Heteropoda tympanum* spec. nov., holotype from Penang, Malaysia (124, 127 epigyne, ventral; 125, 128 vulva, dorsal; 126, 129 schematic course of internal duct system, dorsal). Abbreviations: AM = anterior margin of epigynal pocket, FW = first winding of internal duct system, PO = epigynal pocket, PP = posterior part of internal duct system.

Heteropoda tympanum spec. nov.

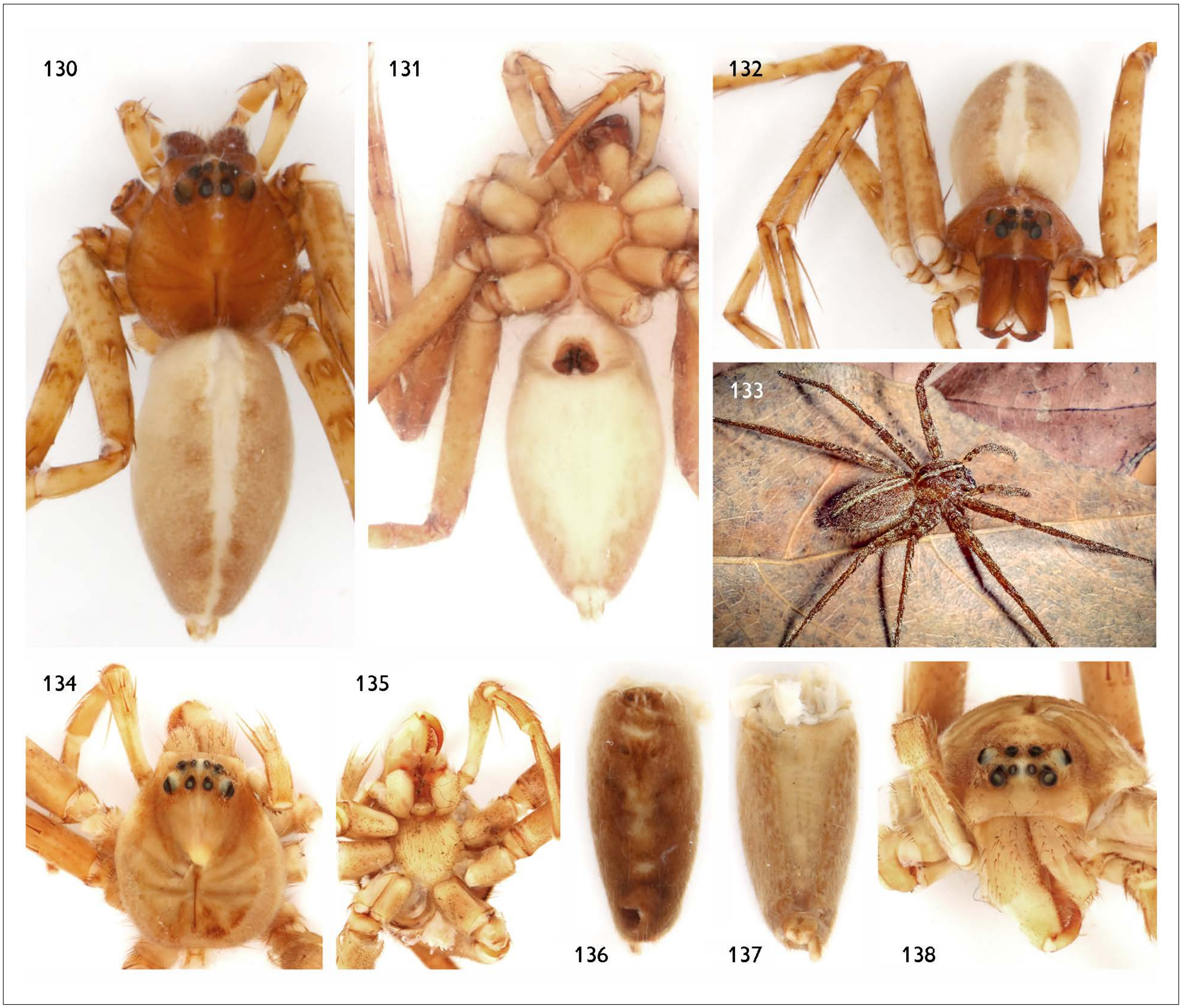
http://zoobank.org/urn:lsid:zoobank.org:act:845687EE-2CE1-4071-A136-BD8C760EA78B

(Figures 127–129, 134–138, 169)

Type material. MALAYSIA: Penang: Holotype female, Penang [ca. 5° 22' 46.64" N, 100° 15' 12.08" E, 352 m elevation], March 1898, 42., F.H. Gravely det. 1930 as *Heteropoda* sp. (NHM).

Etymology. The species name is derived from the Latin word 'tympanum', meaning 'tambourine-shaped drum' and refers to the round medially overlapping first winding of the internal duct system; noun in apposition.

Diagnosis. Females of *H. tympanum* spec. nov. are similar to those of the *H. ocyalina* species-group in having a similar course of internal duct system, posterior pockets (although indistinct), and an elongate opisthosoma, but can be distinguished from all females by the medially overlapping



Figures 130–138. *Heteropoda* spp., habitus of preserved (130–132, 134–138) and live (133) specimens. 130–133 *Heteropoda tutula* spec. nov., holotype female from Singapore. 134–138 *Heteropoda tympanum* spec. nov., holotype female from Penang, Malaysia (130, 133–134, 136 dorsal; 131, 135, 137 ventral; 132, 138 frontal). Photos: P. Jäger (130–132, 134–138), C. S. P. Ang (133).

first winding (first winding not overlapping medially, but running parallel along median axis in all other species of that group).

Description. Male: Unknown.

Female (holotype): Measurements: TL 18.0, PL 7.8, PW 7.0, AW 3.6, OL 10.2, OW 4.7. Eyes: AME 0.40, ALE 0.61, PME 0.46, PLE 0.57, AME-AME 0.27, AME-ALE 0.07, PME-PME 0.28, PME-PLE 0.55, AME-PME 0.43, ALE-PLE 0.56, CH AME 1.16, CH ALE 0.81. Spination: Pp 131, 101, 2121, 1014; Fe I -, II 333, III 332, IV 331; Pa I–II 101, III -, IV 100; Ti I–IV 2026; Mt I–II 1014, III 2014, IV 3036. Mt I–III with dense scopulae along entire length and few stiff single setae very proximally (III), IV with distal field and double row of stronger setae, with very sparse scopula in distal half. Measurements of palps and legs: Pp 15.1 (4.3, 2.1, 3.2, -, 5.5); I -; II - (13.3, -, -, -, -); III 17.1 (10.1, 3.4, 10.7, 8.8, 2.7); IV - (10.2, -, -, 12.1, 3.2). Leg formula: -. CH with 3 promarginal and 4 retromarginal teeth, ca. 100 denticles and 1 escort seta.

Copulatory organ (Figures 127–129). As in diagnosis. Epigynal field roughly rectangular, anterior part not recognisable due to damage. Median septum longer than wide, with posteriorly slightly convex transversal margin. Posterior pockets and their anterior margins indistinct. Copulatory openings situated anteriorly. Glandular pores of internal duct system medio-anteriad, situated on small hump, turning point narrower than first winding, dorsal part of internal duct system wider posteriorly, fertilisation ducts arising postero-medially to medially from spermathecae, bent, their tips dorsad.

Colouration (Figures 134–138). Yellowish-brown with opisthosoma darker. No pattern recognisable due to degraded condition of specimen.

Distribution. Known only from type locality in Penang, Malaysia (Figure 169).

Heteropoda ulna spec. nov.

http://zoobank.org/urn:lsid:zoobank.org:act:6B5F7D26-3BAA-4BB5-A644-BA40826799F4

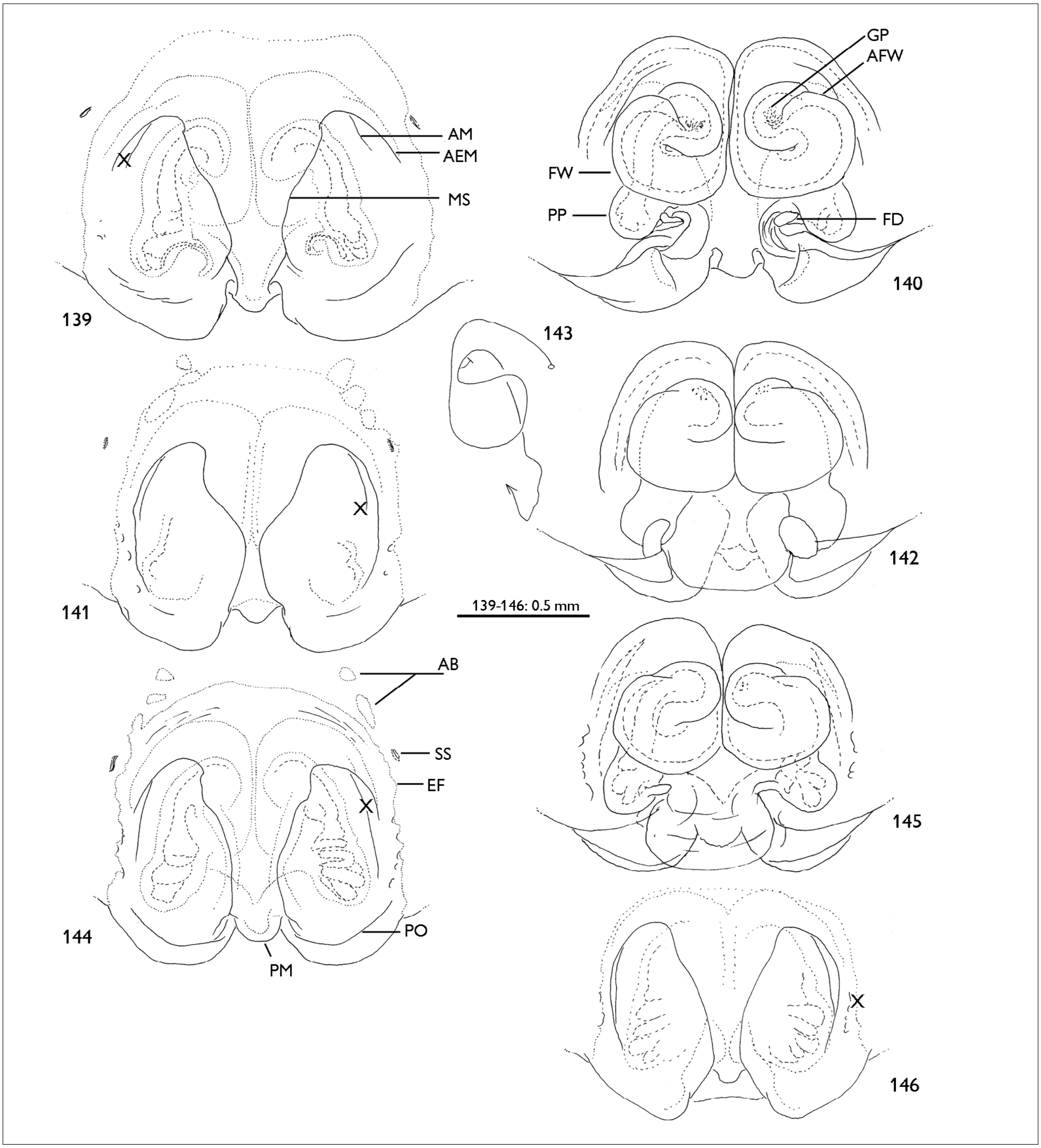
(Figures 139-151, 158-165, 169)

Type material. INDONESIA: Sumatera Barat: Holotype female, Fort de Kock [Bukkittingi, ca. 0° 19' 29.51" S, 100° 22' 12.22" E, 910 m elevation], Eusparassidae, Coll. Roewer, No. 12974, PJ 85 (SMF 9912974). Paratypes: 2 females, with same data as for holotype, PJ 86–87 (SMF).

Additional material examined. Sumatera Utara: 2 females, Soekaranda [south of Medan, ca. 3° 26' 21.99" N, 98° 40' 44.56" E, 108 m elevation], Dohrn [leg.], Jenner [=January] [18]82, PJ 3144–3145 (ÜMB). Aceh: 1 female, Ketambe, Gunung Leuser [ca. 3° 32' 56.47" N, 97° 41' 51.55" E, 470 m elevation], fr[om] leaves, tr. 4.2., Suh. Djojosudharmo leg. 3 May [19]86, *Urgularius* [Deeleman det.], Coll. Deeleman, PJ 3146 (RMNH). Riau: 1 female, Buru [ca. 0° 56' 26.76" N, 103° 27' 18.01" E, 13 m elevation], 034. (NHMW).

Etymology. The species name is derived from the Latin noun 'ulna', meaning 'elbow' and refers to the anterior epigynal margins bent like an elbow; noun in apposition.

Diagnosis. Females of *H. ulna* spec. nov. are similar to those of *H. trifurcata* spec. nov. in having a posteriorly distinctly converging median septum in combination with the dorsal part of internal duct system posteriorly widening (Figures 139–151), but can be distinguished by: 1. Posterior pockets and their anterior margins discontinuous, 2. First winding running into central part of glandular region, 3. Prosoma length 4.1–5.2 (posterior pockets connected with their anterior margins, first winding running marginally to glandular region, prosoma length 7.2–8.3 in *H. trifurcata* spec. nov.; cf. Figures 110–113). Females are also similar to those of *H. tutula* spec. nov. in having a similar internal duct system with a similar arrangement of the glandular pores in the centre of the turning point region and anterior margin of first winding running into this area (Figures 139–151), but can be distinguished by: 1. Anterolateral epigynal margin and anterior margin of posterior pocket leaving a narrow slit-like space, 2. Median septum distinctly diverging anteriorly, 3. Epigynal field only little narrower anteriorly then posteriorly, i.e. roughly square, 4. Posterior part of internal duct system



Figures 139–146. *Heteropoda ulna* spec. nov., females from Sumatra, Indonesia (139–140 holotype from Bukkittingi; 141–143 paratype from Bukkittingi; 144–146 specimens from Soekaranda), copulatory organs (139, 141, 144, 146 epigyne, ventral; 140, 142, 145 vulva, dorsal; 143 schematic course of internal duct system, dorsal). Abbreviations: AB = anterior band, AEM = anterior epigynal margin, AFW = anterior margin of first winding, AM = anterior margin of epigynal pocket, EF = epigynal field, FD = fertilisation duct, FW = first winding of internal duct system, GP = glandular pores, MS = median septum, PM = convex posterior margin of median septum, PO = epigynal pocket, PP = posterior part of internal duct system, SS = slit sensillum, x indicating narow slit.

laterally rounded (anterolateral epigynal margin and anterior margin of posterior pockets leaving a wide space, median septum in its anterior half with parallel margins, and posterior part of internal duct system with pointed laterad bulges in *H. tutula* spec. nov.; cf. Figures 124–126). In addition, *H. ulna* spec. nov. has a wide light median band on the opisthosoma dorsally distinctly bordered by a dark pattern (Figures 158, 161, 163), whereas in *H. tutula* spec. nov. this band is distinctly narrower and without distinct dark border (Figures 130, 133).

Description. Male: Unknown.

Female (holotype): Measurements: TL 10.8, PL 4.6, PW 4.1, AW 2.2, OL 6.2, OW 2.5. Eyes: AME 0.22, ALE 0.41, PME 0.30, PLE 0.41, AME-AME 0.20, AME-ALE 0.05, PME-PME 0.16, PME-PLE 0.39, AME-PME 0.33, ALE-PLE 0.42, CH AME 0.75, CH ALE 0.47. Spination: Pp 131, 101, 2121, 1014; Fe I 323, II–III 333, IV 331; Pa I–II 000(1), III–IV 100; Ti I 2(1)024, II 2025, III 2024, IV 2025(6); Mt I–II 1014, III 2014, IV 3036(5). Mt I–III with dense scopulae along entire length and few stiff setae very proximally (III), IV with distal field and double row of stronger setae, with very sparse scopula in distal half. Measurements of palps and legs: Pp 8.5 (2.5, 1.2, 1.8, -, 3.0); I 26.2 (7.3, 2.4, 7.8, 6.5, 2.2); II 26.4 (7.5, 2.4, 7.7, 6.6, 2.2); III 18.9 (5.5, 1.8, 5.3, 4.5, 1.8); IV 24.5 (7.4, 1.8, 6.3, 6.9, 2.1). Leg formula: II-I-IV-III. CH with 3 promarginal and 4 retromarginal teeth, ca. 45 denticles and 1 escort seta; palpal claw with 6 teeth.

Copulatory organ (Figures 139–140). As in diagnosis. Epigynal field anteriorly rounded, anterior bands indistinct, with one slit sensillum on each side. Median septum longer than wide covered by lateral lobes in posterior half, with convex posterior transversal margin. Posterior pockets indistinct, shallow. Copulatory openings situated antero-laterally. Glandular pores of internal duct system anteriad, situated in the centre of the second winding, fertilisation ducts arising medially from spermathecae, bent, their tips latero-dorsad.

Colouration (Figures 158–160). Pale yellowish- to light reddish-brown with reddish-brown pattern. DS yellowish brown with broad slightly darker margins and pale median stripe, the latter over entire length of DS; with 5 sockets (4 of which with broken off setae, 1 with stiff white setae) between AME. PS ventrally pale yellow, without pattern. Chelicerae yellowish-brown, with indistinct pattern. Legs yellowish-brown with indistinct small spine patches on femora, femora ventrally dotted. Opisthosoma dorsally pale reddish-brown, becoming darker posteriorly, with light median band along entire length, this latter bordered by reddish-brown pattern; ventrally pale yellowish, with indistinct pattern in posterior half; spinnerets dorsally and laterally reddish-brown, ventrally pale yellow.

Variation. Female TL 10.0–14.2, PL 4.1–5.2, OL 5.9–9.0. Spination: Pa I–II 001, III 100(1), IV 101; Ti I 2024(5/6), II 2024(6), III 2024(5/6), IV 2026. Chelicerae with ca. 50 intermarginal denticles. Colouration (Figures 161–165): Some specimens darker. Femoral dots may fused proximally or along entire femora. White stiff setae between AME present in female from Gunung Leuser. Epigynal field with anterior bands, these partly fragmented (Figures 141–151).

Distribution. Known from various localities in Indonesia: Sumatra (Figure 169).

Heteropoda uniter spec. nov.

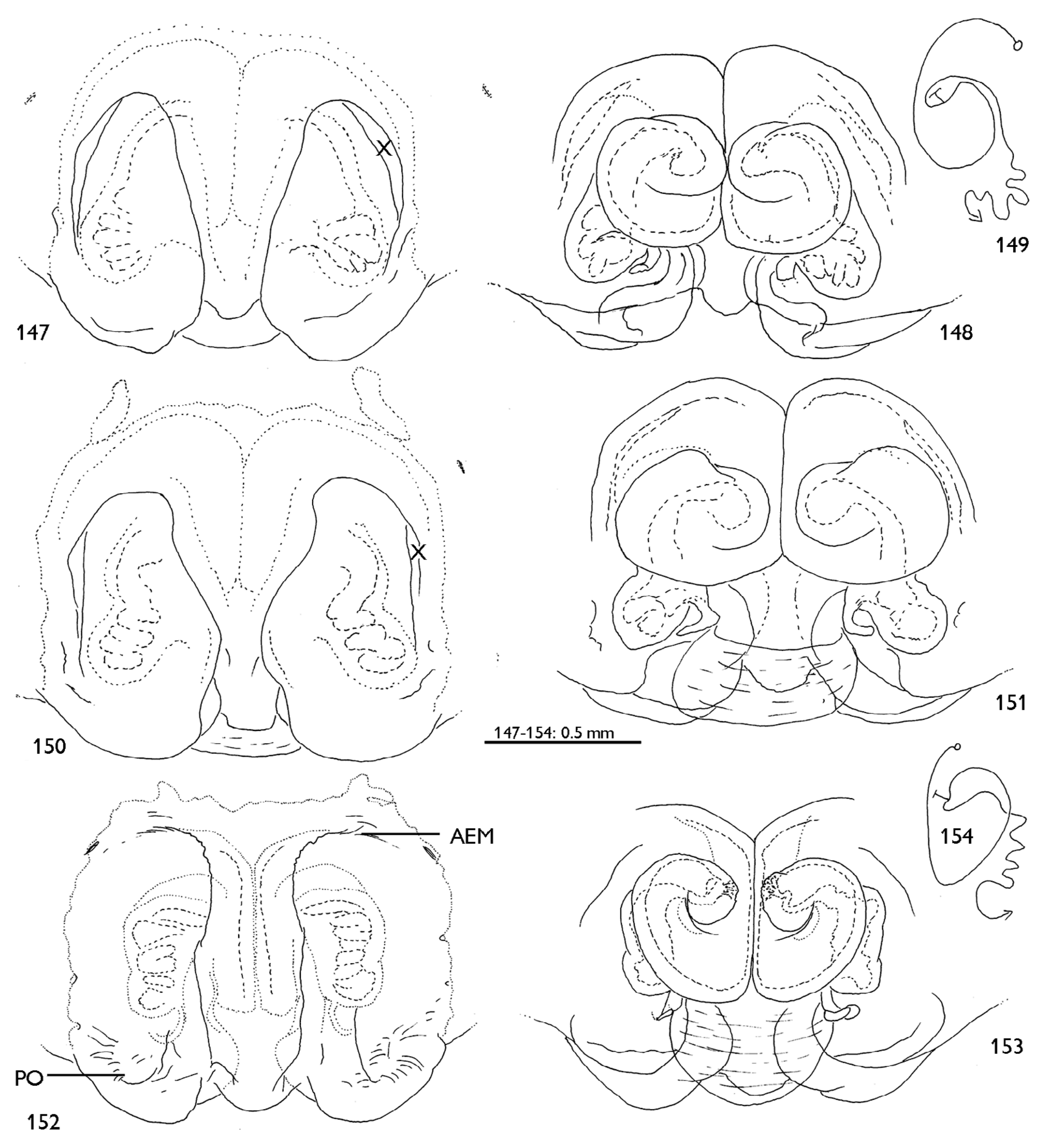
http://zoobank.org/urn:lsid:zoobank.org:act:79B5AB44-58BA-43AE-8427-2921DC4F4F60

(Figures 155–157, 166–169)

Type material. INDONESIA: Kalimantan Tengah: Holotype female, Kaharian, 2° 2' N, 113° 40' E [c. 50 m elevation], swampy primary forest, leaf litter, Suh. Djojosudharmo leg. 2–16 September 1985, 0208–0217; PJ 3147 (RMNH).

Etymology. The species name is derived from the Latin 'uniter,' meaning 'united in one' and refers to the first windings of the internal duct system joining along the median axis; adverb in apposition.

Diagnosis. Females of *H. uniter* spec. nov. are similar to those of *H. temburong* spec. nov. in having epigynal pockets with their anterior margins extending to the middle part of epigyne and the anterior bands short and attached to epigynal field (Figures 155–157), but can be distinguished by: 1. Glandular pores mediad, glandular regions touching each other medially, 2. Lateral lobes distinctly separated over their entire length, 3. Posterior part of internal duct system as wide as first winding (glandular pores anteriad, glandular regions separated, lateral lobes almost touching each other medially in posterior half, posterior part of internal duct system distinctly narrower than first winding in *H. temburong* spec. nov.; cf. Figures 90–92).



Figures 147–154. *Heteropoda* spp., females from Indonesia (147–151 *H. ulna* spec. nov. from Pulau Buru [147–149] and Gunung Leuser [150–151], 152–154 *H. ocyalina* from the South coast of Java), copulatory organs (147, 150, 152 epigyne, ventral; 148, 151, 153 vulva, dorsal; 149, 154 schematic course of internal duct system, dorsal). Abbreviations: AEM = anterior epigynal margin, PO = epigynal pocket, x indicating narow slit (152–154 from Jäger & Bayer, 2009).

Description. Male: Unknown.

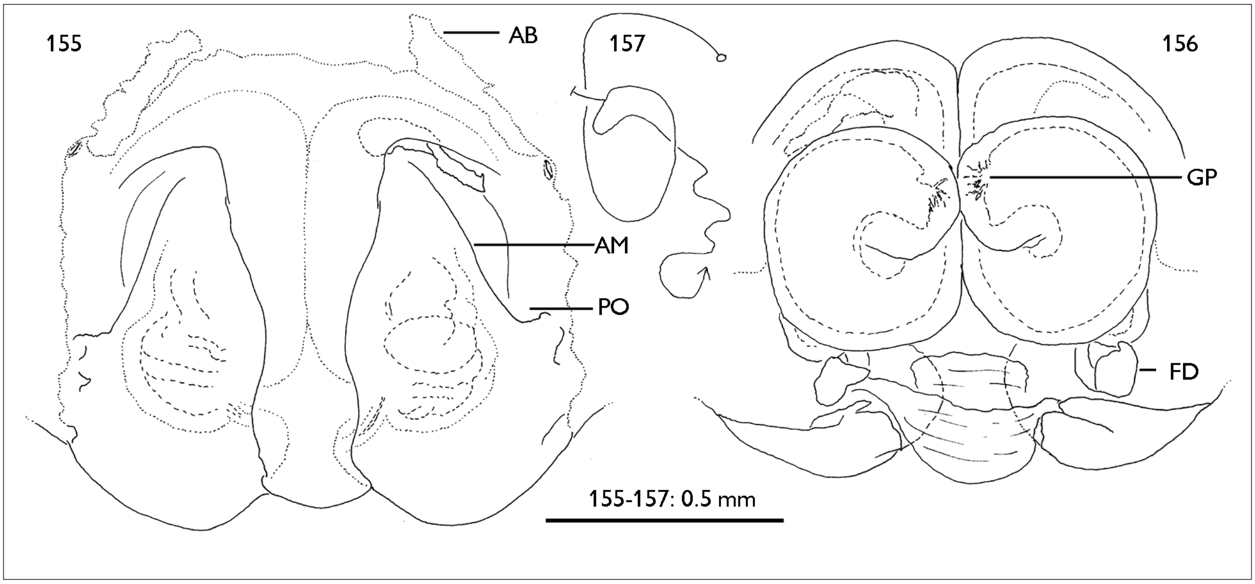
Female (holotype): Measurements: TL 9.3, PL 4.4, PW 3.4, AW 2.0, OL 4.9, OW 2.0. Eyes: AME 0.25, ALE 0.45, PME 0.32, PLE 0.42, AME-AME 0.16, AME-ALE 0.03, PME-PME 0.17, PME-PLE 0.40, AME-PME 0.29, ALE-PLE 0.57, CH AME 0.67, CH ALE 0.40. Spination: Pp 131, 101, 2121, 1014; Fe I–II 323, III 333, IV 331; Pa I–II 001, III–IV 000; Ti I 2024, II–III 2025, IV 2024(5); Mt I–II 1014, III 2014, IV 3036. Mt I–III with dense scopulae along entire length and four stiff setae in proximal half (III), IV with distal field and double row of stronger setae, with very sparse scopula in distal half. Measurements of palps and legs: Pp 7.6 (2.2, 1.0, 1.8, -, 2.6); I 22.4 (6.3, 2.0, 6.7, 5.6, 1.8); II 29.0 (8.4, 2.7, 8.6, 7.0, 2.3); III 22.0 (6.0, 2.1, 6.7, 5.4, 1.8); IV 22.0 (6.6, 1.8, 5.7, 6.0, 1.9). Leg formula: II-I-(IV-III). CH with 3 promarginal and 4 retromarginal teeth, ca. 45 denticles and 1 escort seta.

Copulatory organ (Figures 155–157). As in diagnosis. Epigynal field roughly rectangular, with one slit sensillum on each side, included in the field. Median septum longer than wide, slightly wider anteriorly, with posteriorly convex transversal margin. Posterior pockets slit-like, running diagonally. Copulatory openings situated antero-laterally. Fertilisation ducts arising postero-medially from spermathecae, bent, their tips antero-dorsad.

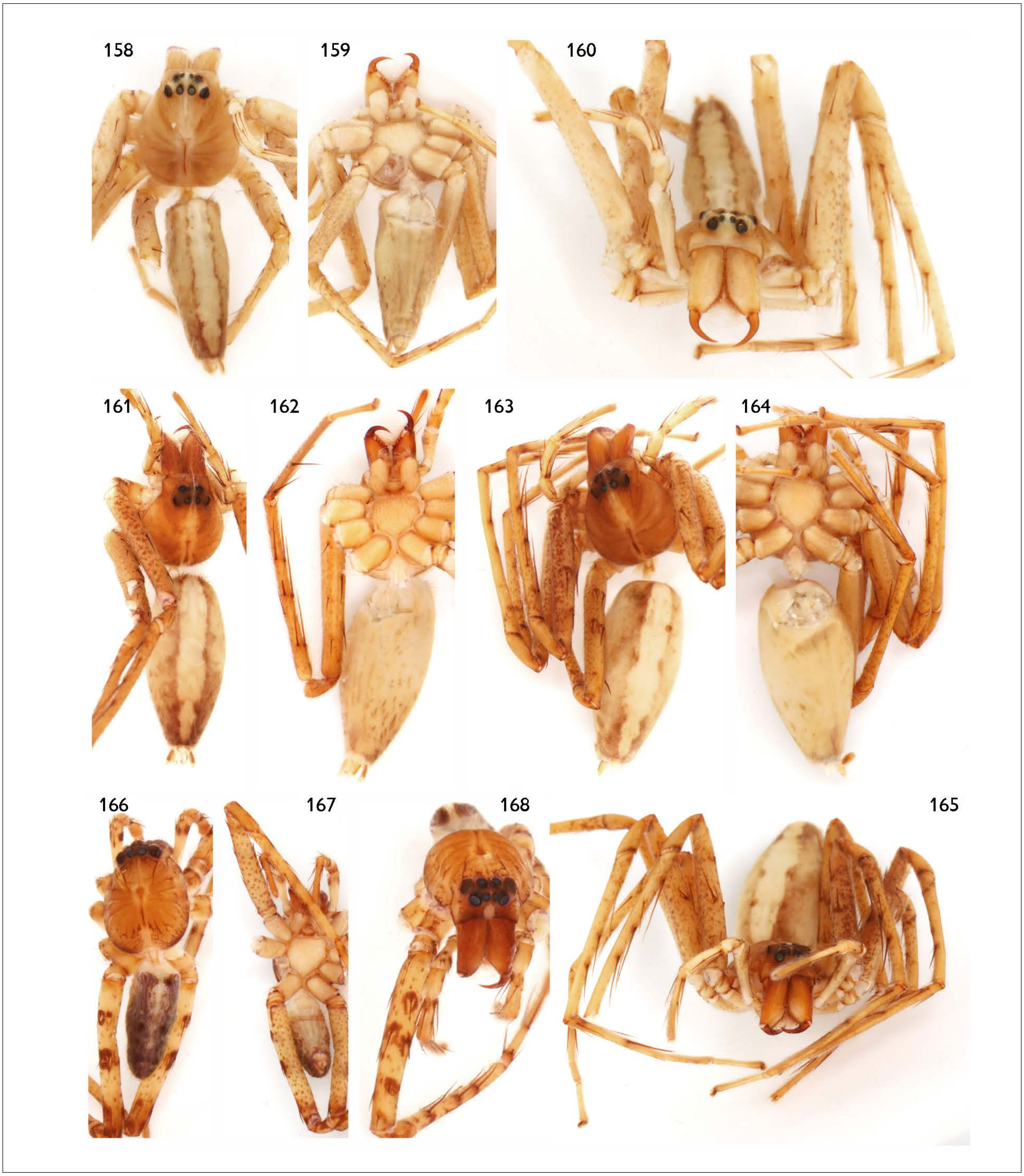
Colouration (Figures 166–168). Deep yellowish- to light reddish-brown with distinct reddish-brown pattern. DS reddish brown with indistinct light median stripe, fovea dark with round dark patch in front; with 4 sockets in a linear arrangement of broken off setae between AME. PS ventrally pale yellow, without pattern. Chelicerae slightly darker reddish-brown. Legs yellowish-brown with distinct and partly fused patches at spines on femora and on patellae and proximal tibia, femora ventrally, less so dorsally dotted. Opisthosoma dorsally dark brown, with indistinct light median band especially in anterior half; ventrally pale yellowish, with distinct patch anterior of spinnerets, the latter dorsally and laterally reddish-brown, ventrally pale yellow.

Distribution. Known only from type locality in Kaharian, Kalimantan, Indonesia (Figure 169).

Biology. The holotype female was recorded in a swampy forest in the leaf litter.



Figures 155–157. *Heteropoda uniter* spec. nov., holotype female from Sarawak, Malaysia, copulatory organ (155 epigyne, ventral; 156 vulva, dorsal; 157 schematic course of internal duct system, dorsal). Abbreviations: AM = anterior margin of epigynal pocket, AB = anterior band, FD = fertilisation duct, GP = glandular pores, PO = epigynal pocket.



Figures 158–168. *Heteropoda* spp., habitus of preserved female specimens. 158–165 *Heteropoda ulna* spec. nov. from Sumatra, Indonesia (158–160 holotype from Bukkittingi, 161–162 specimens from Gunung Leuser, 163–165 specimen from Soekaranda). 166–168 *Heteropoda uniter* spec. nov., holotype female from Sarawak, Malaysia (158, 161, 163, 166 dorsal; 159, 162, 164, 167 ventral; 160, 165, 168 frontal). Photos: P. Jäger.

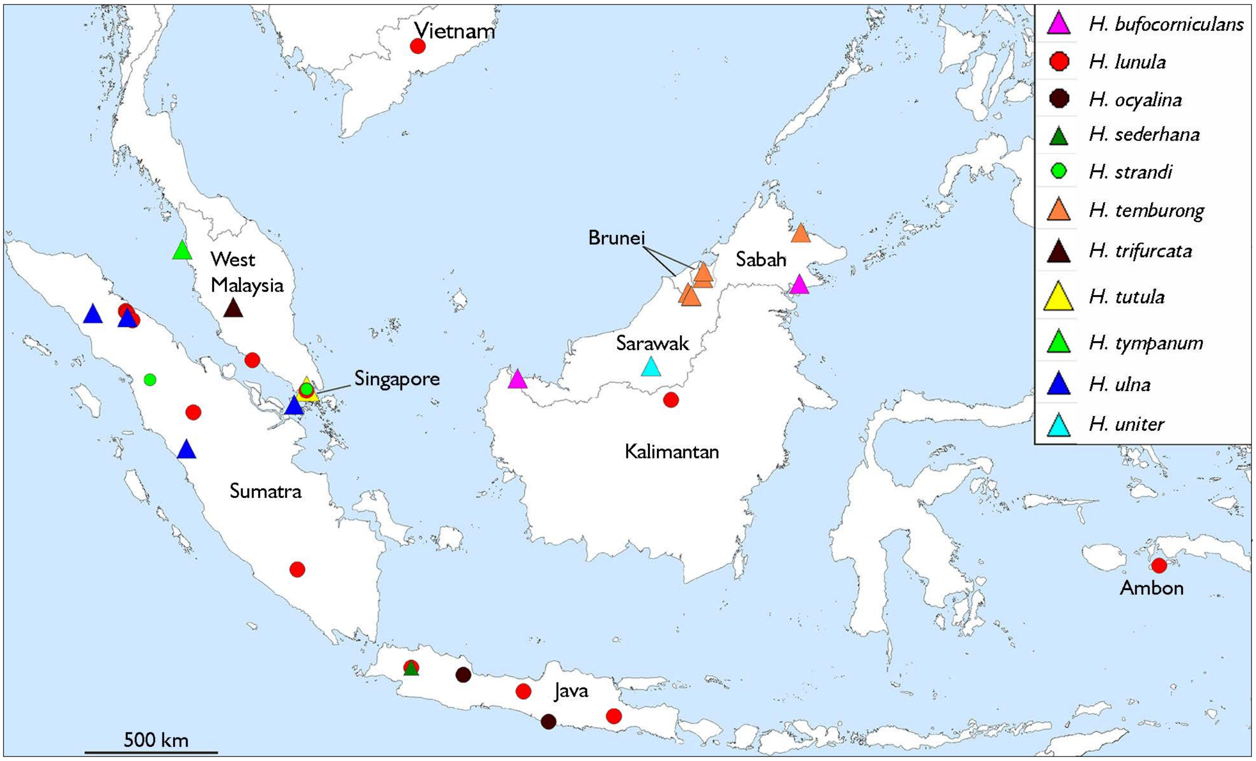


Figure 169. Distribution records of *Heteropoda* spp. in Southeast Asia of new species (triangles) and previously described species (circles).

Heteropoda fasciata (Reimoser, 1927) *nomen dubium*

Parhedrus fasciatus Reimoser, 1927: 1 (description of immature; immature holotype, PJ 1624, label: INDONESIA: Sumatra: Pulau Berhala [ca. 0° 51' 33.37" S, 104° 24' 23.27" E, 24 m], van der Meer Mohr leg., NHMW, examined).

Heteropoda ocyalina,— Jäger & Bayer 2009: 368 (synonymy).

Notes. This species name was considered a junior synonym of *H. ocyalina* by Jäger and Bayer (2009, p. 368) by its elongated opisthosoma and similar colour pattern. At that time, both authors underestimated the diversity within this genus in general and within this species-group in particular. Given the fact that there are much more species of similar appearance described in the present paper and most likely even more undescribed species and that there are various gradual states of elongation in the opisthosoma in different species in this group, we now no longer consider *H. fasciata* conspecific with *H. ocyalina* because it has a much more slender opisthosoma than all other members of this species-group. The fact that the holotype of *H. fasciata* is immature does not weaken the argument that *H. fasciata* has an exceptionally slender opisthosoma. Immatures of *H. trifurcata* spec. nov., but also of members of other groups, such as *H. boiei*, show the same opisthosomal shape as the adults. Therefore, we remove *H. fasciata* from the synonymy of *H. ocyalina*. Separately, since the holotype of *H. fasciata* is immature and its identity cannot be clarified, we consider it a *nomen dubium*.

DISCUSSION

Considering the many shared diagnostic characters among *H. ocyalina*, *H. asa*, and six of the new species described in the present paper, it seems justifiable to erect a new species-group encompassing all eight species. Jäger and Bayer (2009) considered *H. ocyalina* a member of the *H. dagmarae*-group based on their similarity of the palpal organs. However, they also highlighted the differences between *H. ocyalina* and the *dagmarae* species-group, such as the elongated opisthosoma with no black venter in *H. ocyalina* (otherwise in the *dagmarae* species-group), and the different positions of their respective conductor apophyses. Whether the *ocyalina* species-group is more closely related to the *H. javana*-group, given their similarities such as having an additional apex on dRTA, should be investigated in the future.

Based on impressions after six years of quarterly field trips in Brunei Darussalam (J.K.H. Koh, unpublished), it may be said that *H. borneensis* is one of the most common *Heteropoda* species in Brunei forests. The species is also notable in that the external appearance of its epigyne is highly variable. The variability is discernible even among population within the same locality. However, the internal duct system in the vulva appears consistent among the specimens collected in Sarawak, Sabah, Brunei, and Singapore. As *H. borneensis* is one of the extraordinary species of huntsman spiders with a unique striking colouration, it was possible to unmistakably assign several records in iNaturalist to that species and gather additional information on its distribution range (among others, the first record for Indonesia: North Kalimantan; Figure 41). However, there are other species of Heteropodinae with similar characteristic white lines on the dorsal side of the legs (e.g., an unidentified *Heteropoda* species from Indonesia, Sumatra; P. Jäger, unpublished data). Even some species of the genus *Pseudopoda* Jäger, 2000 exhibit this remarkable character, which is why an unambiguous identification of *H. borneensis* is valid only after a more holistic check encompassing other diagnostic indicators, including size, the colouration of the male and female bodies, legs and chelicerae, and occurrence on forest floor and only occasional occurrence in ground vegetation (i.e., never arboreal, nor near streams) etc.

The wide distribution pattern of *Heteropoda borneensis* is reminiscent of that of *H. davidbowie* Jäger, 2008, also occurring in northern Borneo, peninsular Malaysia and Singapore, in addition to Indonesia (Sumatra) and southern Thailand. Further studies are required to explain the wide distribution of *H. borneensis*. There are two questions that need to be addressed: first, why it is more frequently sighted in Borneo and less so in Singapore and peninsular Malaysia by iNaturalist contributors; second, whether its presence in Singapore and peninsular Malaysia could have been introduced through the exports of plants. In the context of the first question, it should be noted that the species has often been seen and photographed in Singapore, but not posted on the iNaturalist platform. In the context of the latter question, while *H. davidbowie* has been observed on ornamental plants at Bukit Fraser in peninsular Malaysia (P. Jäger, unpublished data), *H. borneensis* has never been seen in gardens or other artificially cultivated habitats in Singapore. On the other hand, the latter species has been photographed on the forest floor in forest reserves in Johor and Selangor in peninsular Malaysia, and in the more pristine forest patches in nature reserves in Singapore, including the Bukit Timah Nature Reserve which has been protected since 1883 (J.K.H. Koh, from unpublished records of other nature photographers).

Some morphological characters in *Heteropoda bufocorniculans* spec. nov. are unique not only in the genus *Heteropoda*, but also in the entire family. Striking features are the erect femoral spines and the absence of spines in many positions of some leg segments. Apparently, both characters evolved together, since erect spines in retrolateral positions, e.g. in femora would disturb a smooth movement of the legs. A similar reduction is known from femur IV in almost all Sparassidae: retrolateral proximal spines are reduced because they would interfere with the antero-lateral part of the opisthosoma during locomotion. While it cannot be explained easily how these modifications (erect spines) occurred, the tufted body could be explained by a selective advantage in certain habitats, where the spider is better camouflaged. Similar colour and setal modifications are known, e.g., from *Pandercetes* L. Koch, 1875 (lichen huntsmen) or *Barylestis saaristoi* Jäger 2008, all living also on bark of tree trunks.

A more general remark concerns the usage of photos posted on platforms like iNaturalist or Flickr: it is clear that only a small fraction of spider species with unmistakably recognisable morphological characters can be identified accurately purely from photos. On the other hand, for this small group, these platforms offer an added avenue to ascertain the full extent of their distribution range, and even provide information on their ecology or biology. In the present paper we used only data for one species, *H. borneensis*, but there are more candidates, like *H. bufocorniculans* spec. nov. and *H. lunula*, identifiable by their unique shape or colour pattern. Another example shows that unknown sexes can be found on such platforms: after the species *H. dede* Jäger, 2024 was described, a photo of a male Sparassidae from Tawau Hill, Sabah, ca. 50 km south of the type locality, Danum Valley, Sabah, posted in 2021 by Wong Tsu Shi was identified as being conspecific. However, a critical recheck should be done when photos are used as lone base for identification.

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AUTHORS' CONTRIBUTION

P. Jäger contributed to conceptualization, data curation, formal analysis, investigation, methodology, visualization, and writing (original draft, review and editing); and J. K. H. Koh contributed to data curation, investigation, visualization, and writing (original draft).

* * *

Identity check: documenting the type specimens of historical Malagasy wolf spiders (Araneae: Lycosidae)

Verificação de identidade: documentando os espécimes-tipo de aranhas-lobo malgaxes históricas (Araneae: Lycosidae)

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Abstract: This work aims to digitize and disseminate knowledge on historical specimens of Malagasy lycosids, as a foundation for future researchers intending to undertake a comprehensive review of this fauna. The types of *Arctosa atroventrosa* (Lenz, 1886), *Geolycosa nossibeensis* (Strand, 1907), *Hippasosa fera* (Strand, 1907), and *Trochosa urbana hova* Strand, 1907 were examined, figured, and their taxonomic identities discussed herein. *Arctosa atroventrosa* is proposed as a *nomen dubium*. *Geolycosa nossibeensis* is clearly misplaced in *Geolycosa* Montgomery, 1904 and is transferred to *Trochosa* C. L. Koch, 1847 as *Trochosa nossibeensis* comb. nov. Likewise, *H. fera* is a valid species but is misplaced in *Hippasosa* Roewer, 1960 and does not belong to this genus. *Trochosa urbana hova*, recently synonymised with the nominal species is confirmed in its current taxonomic placement. *Lycosa madagascariensis* Vinson, 1863 is treated as a *species inquirenda* as the types cannot be located but the mention of specific localities in Madagascar could allow future workers to designate a neotype to recognise this species. *Lycosa signata* Lenz, 1886 is treated as a valid species, although a neotype designation will be required in future as the holotype was destroyed as a result of bombing raids on the Museum of Lübeck during the World War II and its vulva never previously illustrated.

Keywords: Morphology. Taxonomy. *Arctosa*. *Hippasosa*. *Lycosa*. *Trochosa*.

Resumo: Este trabalho tem como objetivo digitalizar e disseminar conhecimento sobre espécimes históricos de licosídeos malgaxes, como base para futuros pesquisadores que queiram revisar de forma abrangente esta fauna. Os tipos de *Arctosa atroventrosa* (Lenz, 1886), *Geolycosa nossibeensis* (Strand, 1907), *Hippasosa fera* (Strand, 1907) e *Trochosa urbana hova* Strand, 1907 foram examinados e documentados, e suas identidades taxonômicas são discutidas aqui. *Arctosa atroventrosa* é proposto como um *nomen dubium*. *Geolycosa nossibeensis* claramente não pertence a *Geolycosa* Montgomery, 1904 e é transferido para *Trochosa* C. L. Koch, 1847 como *Trochosa nossibeensis* comb. nov. Da mesma forma, *H. fera* é uma espécie válida, mas está mal alocada em *Hippasosa* Roewer, 1960 e não pertence a este gênero. *Trochosa urbana hova*, recentemente sinonimizada com a espécie nominal, é confirmada em sua atual posição taxonômica. *Lycosa madagascariensis* Vinson, 1863 é tratada como uma *species inquirenda*, pois os tipos não podem ser localizados, mas a menção de localidades específicas em Madagascar pode permitir que futuros pesquisadores designem um neótipo para reconhecer esta espécie. *Lycosa signata* Lenz, 1886 é tratada como uma espécie válida, embora uma designação de neótipo seja necessária no futuro, pois o holótipo foi destruído como resultado de bombardeios no Museu de Lübeck durante a Segunda Guerra Mundial e sua vulva nunca foi ilustrada anteriormente.

Palavras-chave: Morfologia. Taxonomia. *Arctosa*. *Hippasosa*. *Lycosa*. *Trochosa*.

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INTRODUCTION

Lycosidae Sundevall, 1833, known globally as wolf spiders, are a ubiquitous group presently containing 134 genera and 2473 species (World Spider Catalog, 2024). Afrotropical Lycosidae prove a particular challenge, with many species known only from written descriptions (without illustrations) from the Victorian and Edwardian periods, but modern revisions are slowly improving knowledge of these taxa (e.g. Logunov, 2023; Sherwood et al., 2023).

Madagascar is an island renowned for its biodiversity (Myers et al., 2000), with many spider groups receiving attention from modern workers (e.g. Gregorič et al., 2015; Henrard & Jocqué, 2017; Jäger, 2020, 2021; Griswold et al., 2022). However, according to the World Spider Catalog (2024) only eight lycosid species are known to occur on the island, none having been illustrated or redescribed in the twenty first century. The Madagascan lycosid fauna is likely underestimated. However, before future studies with modern material can ascertain this, historical taxa must be addressed.

According to Vinson (1863) the species *Pardosa cinerascens* (Roewer, 1951) [as *Lycosa cinerea* Vinson, 1863] and *Pardosa vinsoni* (Roewer, 1951) [as *Lycosa nigra* Vinson, 1863] do not occur in Madagascar, as currently stated by the World Spider Catalog (2024) and thus the current count of eight must be reduced by two. These pardosine species are outside the scope of this contribution and should be addressed by future workers.

In this work, in order to lay a foundation for future workers, we assess the six species of lycosid spiders known from Madagascar, addressing the taxonomy of all but one of these species, and considering a further two recorded by the World Spider Catalog (2024) as being erroneous distribution records.

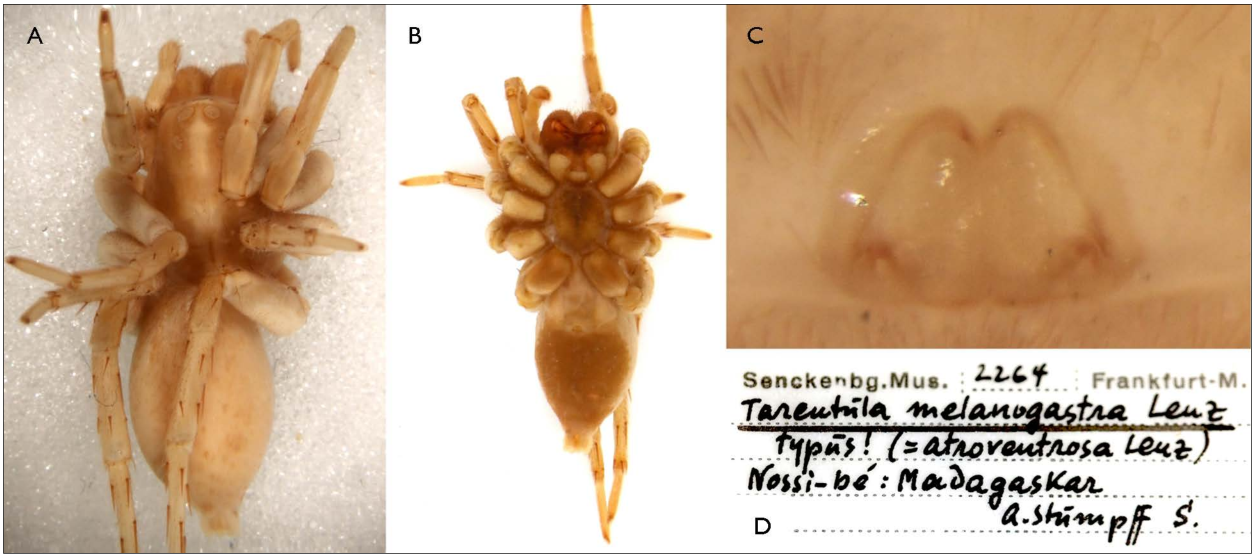
MATERIAL AND METHODS

Specimens were examined under binocular microscopes. Photographs were made (except those of *H. fera* which were made by Nadine Dupérré using a custom BK Labs imaging system) using a Canon EOS 6D Mark II attached to a Leica MZ12.5 stereomicroscope, with images stacked using Helicon Focus software. Abbreviations, Institutes: MLB = Lübeck Museum, Lübeck, Germany; MNHN = Muséum National d'Histoire Naturelle, Paris, France (collection staff: Christine Rollard and Elise-Anne Leguin); SMF = Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt am Main, Germany (collection staff: PJ); ZMB = Museum für Naturkunde, Berlin, Germany (collection staff: Jason Dunlop); ZMH = Zoologisches Museum, Universität Hamburg, Germany (collection staff: Danilo Harms and Nadine Dupérré). Structures: ALE = anterior lateral eyes, AME = anterior median eyes, PLE = posterior lateral eyes, PME = posterior median eyes. Other: det. = determined by; leg. = legit. Leg formulae start with the longest leg to the shortest in order of decreasing size, e.g. 4123. The diagnoses given herein are only between other known species on Nosy Be, this is simply because the state of lycosid taxonomy precludes a proper analysis against all relevant congeners. The purpose of this work is to provide full information on the type specimens of existing species only, as a foundation for future workers. Total lengths exclude chelicerae. All measurements are in mm and were measured with an ocular micrometer. Non-ocular measurements are given to one decimal point, measurements of eyes and eye interdistances are conversely measured to two decimal points due to their much smaller size. In accordance with Article 8 of the International Code of Zoological Nomenclature, this work was preregistered in ZooBank prior to publication. LSID: urn:lsid:zoobank.org:pub:719F1B50-9979-4177-9C57-E4DF50048D26

TAXONOMY

Arctosa atroventrosa (Lenz, 1886) *nomen dubium*

(Figure 1)



Senckenbg.Mus. 2264 Frankfurt-M.
Tarentūla melanogastra Lenz
typūs! (=atroventrosa Lenz)
Nossi-bé : Madagaskar
a.Stūmpff S.

Figure 1. *Arctosa atroventrosa* (Lenz, 1886) *nomen dubium*: holotype immature female (SMF 2264). A) Habitus, dorsal view, B) habitus, ventral view, C) pre-epigyne, ventral view, D) data label.

Lycosa atroventrosa Lenz, 1886: 401, pl. 10, fig. 11 (imm. ♀, as *Lycosa melanogaster* [preoccupied] in main text but *L. atroventrosa* used in figure legend, thereby available).
Tarentula melanogaster: Strand, 1916: 79.
Hogna lenzi Roewer, 1951: 440 (superfluous replacement name).
Arctosa lenzi: Roewer, 1955: 229.
Arctosa atroventrosa: Roewer, 1960: 645, figs. 363a–b (imm. ♀).

Type material. Holotype imm. ♀ (SMF 2264), Nossi-bé [Nosy Be], A. Stumpf leg., examined.

Complimentary morphological data. Total length: 11.5. Carapace: 5.2 long, 4.0 wide, abdomen 6.2 long, 3.7 wide. Chelicerae with 3 promarginal and 4 retromarginal teeth, no denticles and a single escort seta.

Remarks. The holotype (Figures 1A–1D) is an immature female with a pre-epigyne (Figure 1C). It is not diagnosable from other taxa on Nosy Be and as an immature specimen is not informative for a tenable morphological diagnosis. Thus, is hereby proposed as a *nomen dubium*.

Trochosa nossibeensis (Strand, 1907) comb. nov.
(Figures 2–4)

Tarentula nossibeensis Strand, 1907: 743 (imm.).
Geolycosa nossibeensis: Roewer, 1955: 242.
Geolycosa nossibeensis: Roewer, 1960: 715, figs. 400a–c (♀).

Type material. Holotype imm. (Museum of Lübeck), destroyed during WWII; neotype ♀ (SMF 9910480) [designated by Roewer, 1960], Madagascar, Nossibé [Nosy Be], Roewer det. 1957, examined.

Diagnosis. *Trochosa nossibeensis* comb. nov. is readily distinguished from known sympatric congeners by the dumbbell-shaped median septum, with absence of pronounced sclerotization on the outer edges of the basal part (median septum anchor-shaped in *T. urbana*; I-shaped and with pronounced sclerotization of outer edges of basal part in *H. fera*).

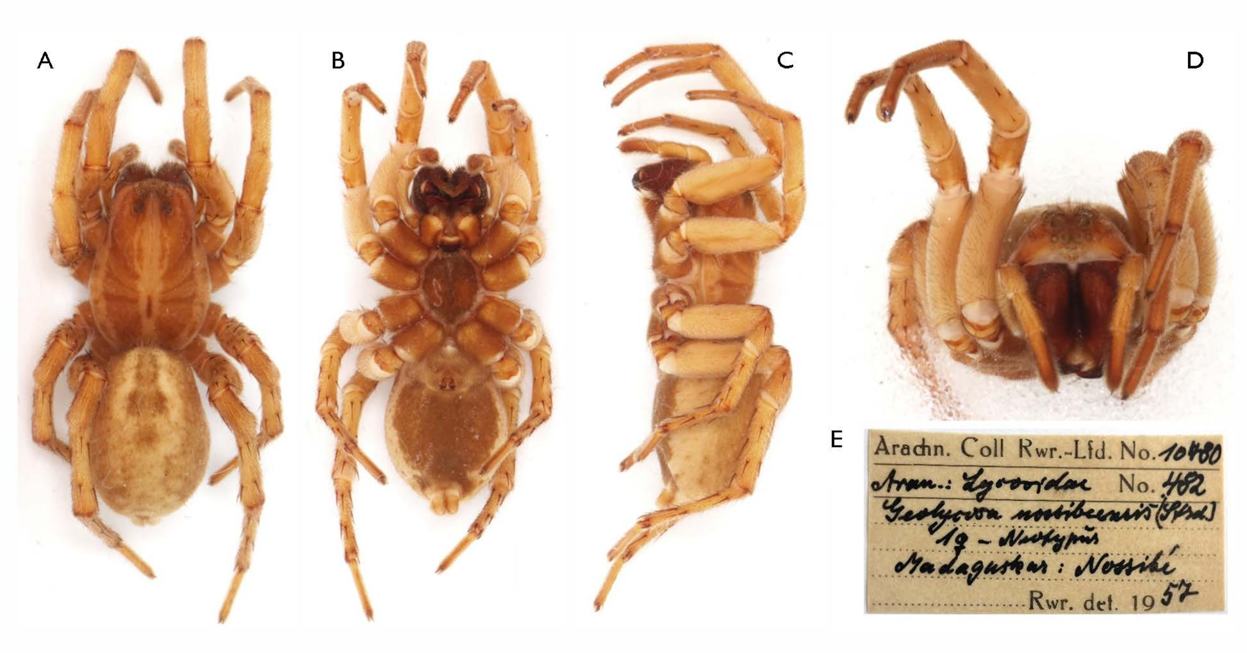
Redescription of neotype female (SMF 9910480): Total length: 15.7. Carapace: 7.7 long, 5.6 wide. Eye sizes and interdistances: AME 0.36, ALE 0.30, PME 0.65, PLE 0.51, AME–AME 0.09, AME–ALE 0.05, PME–PME

0.31, PME–PLE 0.49, AME–PME 0.20, ALE–PLE 0.96. Abdomen: 8.0 long, 5.6 wide. Leg formula: 4123. Leg measurements: I 17.4 (5.0+2.7+4.1+3.3+2.3), II 16.3 (4.5+2.7+3.7+3.2+2.2), III 15.5 (4.2+2.9+3.1+3.6 +2.3), IV 20.7 (5.3+2.6+4.6+5.4+2.8). Chelicerae with 3 promarginal and 3 retromarginal teeth, no denticles and a single escort seta. Epigyne and vulva: epigyne (Figures 3C, 4A) with median septum dumbbell-shaped, longer than wide, lateral sides tapering distally (septal length/width ratio 3.8 at its narrowest part); length of septum and posterior transverse plate essentially equal; hoods wide and deep, separated by distance slightly less than width of each hood; vulva (Figures 4B–4D) with receptacles sinuous medially, terminating in elongate and rounded spermathecae, fertilisation ducts situated posteriorly, directed outwards. Colour (in alcohol): yellowish-brown; carapace with two wide lateral bands, medially with fovea dark and two parallel narrow lines between fovea and eyes, marginally with single patches; ventrally overall dark brown; chelicerae reddish-brown, with proximo-lateral humps yellow; opisthosoma dorsally light yellowish-brown with darker heart patch, laterally yellowish-brown with irregular pattern, ventrally dark-brown, spinnerets yellowish-brown (Figures 2A–2D, 3A–3B).

Male. Unknown.

Distribution. Known only from the type locality, Nosy Be, Madagascar.

Remarks. This species is clearly misplaced in *Geolycosa* Montgomery, 1904. The ocular arrangement, carapace colouration, and general form of the epigyne are congruent with that of *Trochosa ruricola* (De Geer, 1778), the type species of *Trochosa* C. L. Koch, 1847, suggesting this species is at the very least a member of the *Trochosa sensu lato*. Therefore, we herein transfer *G. nossibeensis* to this genus, creating the new combination *Trochosa nossibeensis* comb. nov., and suggest future workers attempt to collect topotypic material to better understand its placement. A global revision of *Trochosa* is warranted, but entirely outside the scope of the present work.



Arachn. Coll Rwr.-Lfd. No. 10480
Aran.: Lycosidae No. 482
Geolycosa nossibeensis (Strd.)
1♀ - Neotypus
Madagaskar : Nossibé
Rwr. det. 1957

Figure 2. *Trochosa nossibeensis* (Strand, 1907) comb. nov.: holotype female (SMF 9910480). A) Habitus, dorsal view, B) habitus, ventral view, C) habitus, lateral view (left-hand side), D) cephalothorax, frontal view, E) data label.

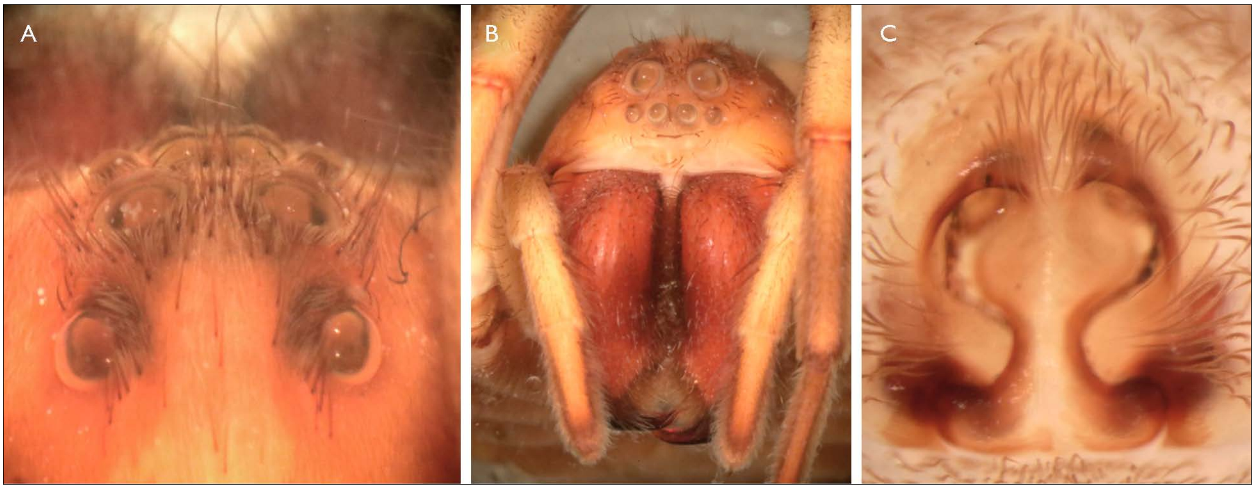


Figure 3. *Trochosa nossibeensis* (Strand, 1907) comb. nov.: holotype female (SMF 9910480). A) Close-up of eyes, dorsal view, B) same, frontal view, C) epigyne (undissected), ventral view.

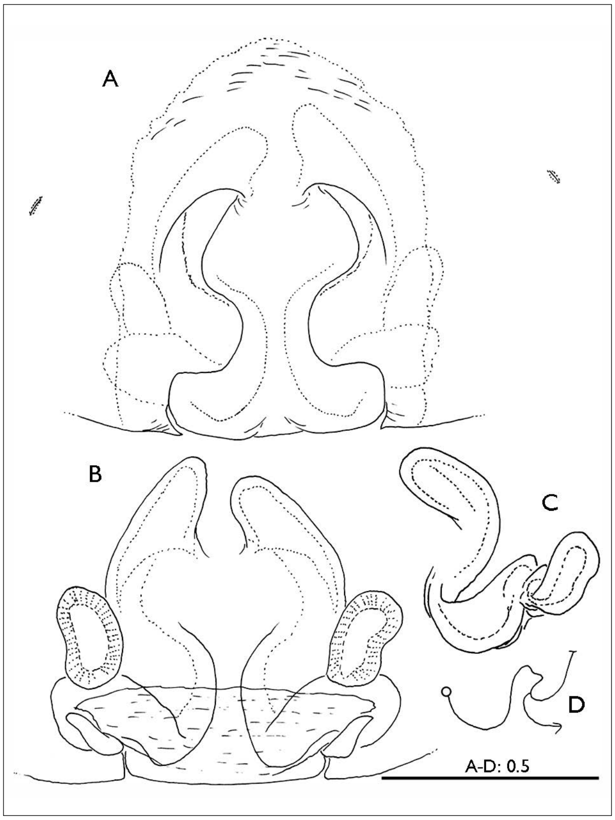


Figure 4. *Trochosa nossibeensis* (Strand, 1907) comb. nov.: holotype female (SMF 9910480), illustrations of epigyne and vulva. A) Epigyne (dissected), ventral view, B) vulva, dorsal view, C) detail of copulatory ducts, lateral view, D) schematic course of duct, lateral view. Scale bar = 0.5 mm.

Hippasosa fera (Strand, 1908)

(Figure 5)

Lycosa robusta Lenz, 1891: 171, pl. 1, fig. 7 (♀, preoccupied).
Ocyale fera Strand, 1908a: 155 (replacement name).
Ocyale fera: Roewer, 1960: 814, figs. 452a–b (♀).
Ocyale fera: Alderweireldt, 1996: 1364 (states as misplaced in *Ocyale*).
Hippasosa fera: Sherwood, 2022: 583 (transferred from the pisaurid genus *Ocyale*).

Type material. Holotype ♀ (ZMH-A0003552), Nossi-Bé [Nosy Be], Albr. O'Swald leg., ded. 02/07/1888, examined by photographs only.

Diagnosis. *Hippasosa fera* can be distinguished from females of *H. dewinterae* (Alderweireldt, 1996), *H. discrepans* (Roewer, 1960), *H. ghost* (Jocque & Jocqué, 2017), *H. grandis* (Alderweireldt, 1996), *H. guttata* (Karsch, 1878), *H. pilosa* Roewer, 1960, and *H. qiongzhongensis*(Ying & Peng, 1997) by the wide anterior flaring of the median septum (absent, anterior of septum extremely straight and thin in *H. dewinterae*, *H. discrepans*, *H. ghost*, *H. grandis*, *H. guttata*, *H. pilosa* and *H. qiongzhongensis*). The female genitalia of *H. kumari* (Dyal, 1935), *H. lanca* (Karsch, 1879), and *H. pelliona* (Audouin, 1826) are unknown but can be tentatively differentiated based on their disjunct localities (Pakistan, Sri Lanka, Egypt and Algeria, respectively vs. Madagascar). The shape of the medium septum readily differentiates this species from other lycosid species presently described from Madagascar.

Complimentary redescription of holotype female. Total length: 9.87. Carapace: 5.14 long, 3.43 wide. Eye sizes and interdistances: AME 0.43, ALE 0.30, PME 0.22, PLE 0.19, AME–AME 0.36, AME–ALE 0.46, PME–PME 0.20, PME–PLE 0.08, AME–PME 0.12, ALE–PLE 0.57. Abdomen: 4.73 long, 2.70 wide. Leg formula: 4123. Leg measurements: I 12.89 (3.58+1.71+2.40+3.10+2.10); II 12.61 (3.64+1.45+2.48+3.05+1.99); III 12.56 (3.40+1.41+2.12+3.80+1.83); IV 16.99 (4.24+1.94+3.40+4.71+2.70). Chelicerae with 3 promarginal and 3 retromarginal teeth, no denticles and a single escort seta (Figure 5C). Epigyne and vulva: epigyne (Figures 5D–5E) T-shaped, median septum longer than wide, narrow medially, wide in posterior and anterior thirds, (septal length/width ratio 4.0 at its narrowest part); length of septum and posterior transverse plate essentially equal, anterior hoods laterally situated, shallow and indistinct, base of septum with outer edges heavily sclerotised; vulva (Figure 5F) with gently sinuous S-shaped copulatory ducts, leading to circular spermathecae, fertilisation ducts situated posteriorly, directed inwards. Colour (in alcohol): margins of carapace dark brown, rest light brown, abdomen beige with dark brown speckles all over; spinnerets light brown (Figure 5A); legs light brown with faint dark brown annulations; ventrally overall light brown except for legs which show faint dark brown annulations.

Distribution. Known only from the type locality, Nosy Be, Madagascar.

Remarks. We update the redescription given by Roewer (1960), who paid particular detail in (accurately) describing the colouration and leg spination but whose drawings of the genitalia are schematic. This species is certainly misplaced in *Hippasosa* Roewer, 1960, Alderweireldt (1996) postulated it may belong to *Lycosa sensu lato*, but we suspect instead it belongs to another genus. However, it is imperative that topotypic material be collected and material from mainland Madagascar be examined before any such taxonomic act is taken, especially since so many historical lycosid genera remain without any published illustrations of the genitalia.

Lycosa madagascariensis Vinson, 1863 *species inquirenda*

Lycosa madagascariensis Vinson, 1863: 297 (♀).
Lycosa madagascariensis: Roewer, 1955: 271.

Type material. Not located in MNHN, SMF, ZMB or ZMH, probably lost.

Remarks. Vinson (1863, p. 16) states this species occurs "le lit de la rivière de Ranomafana près du village de Voizanliar ou Bout-Zanaar", which provides a type locality that can be approximated today to the confines of the Ranomafana National Park. The description is not particularly useful for identification purposes, but we prefer to keep the species as valid until such time as it is possible for future workers to attempt to collect topotypes. Therefore, we treat *Lycosa madagascariensis* Vinson, 1863 as a *species inquirenda*.

Lycosa signata Lenz, 1886

Lycosa signata Lenz, 1886: 402, pl. 10, fig. 10 (♀).

Allohogna signata: Roewer, 1955: 212.
Allohogna signata: Roewer, 1960: 737, figs. 415a–b (♀).

Type material. Holotype ♀ (MLB), Nosy Be, Madagascar, destroyed during WWII.

Remarks. A drawing of the epigyne is presented by Lenz (1886, pl. 10, fig. 10), which shows the medium septum is flared medially, unlike that of the other known lycosids of Nosy Be. It is thus clearly not synonymous with any of the other species on that island. Unfortunately, the holotype is lost, precluding further study, and it is necessary that future topotypic material be collected with matching morphology

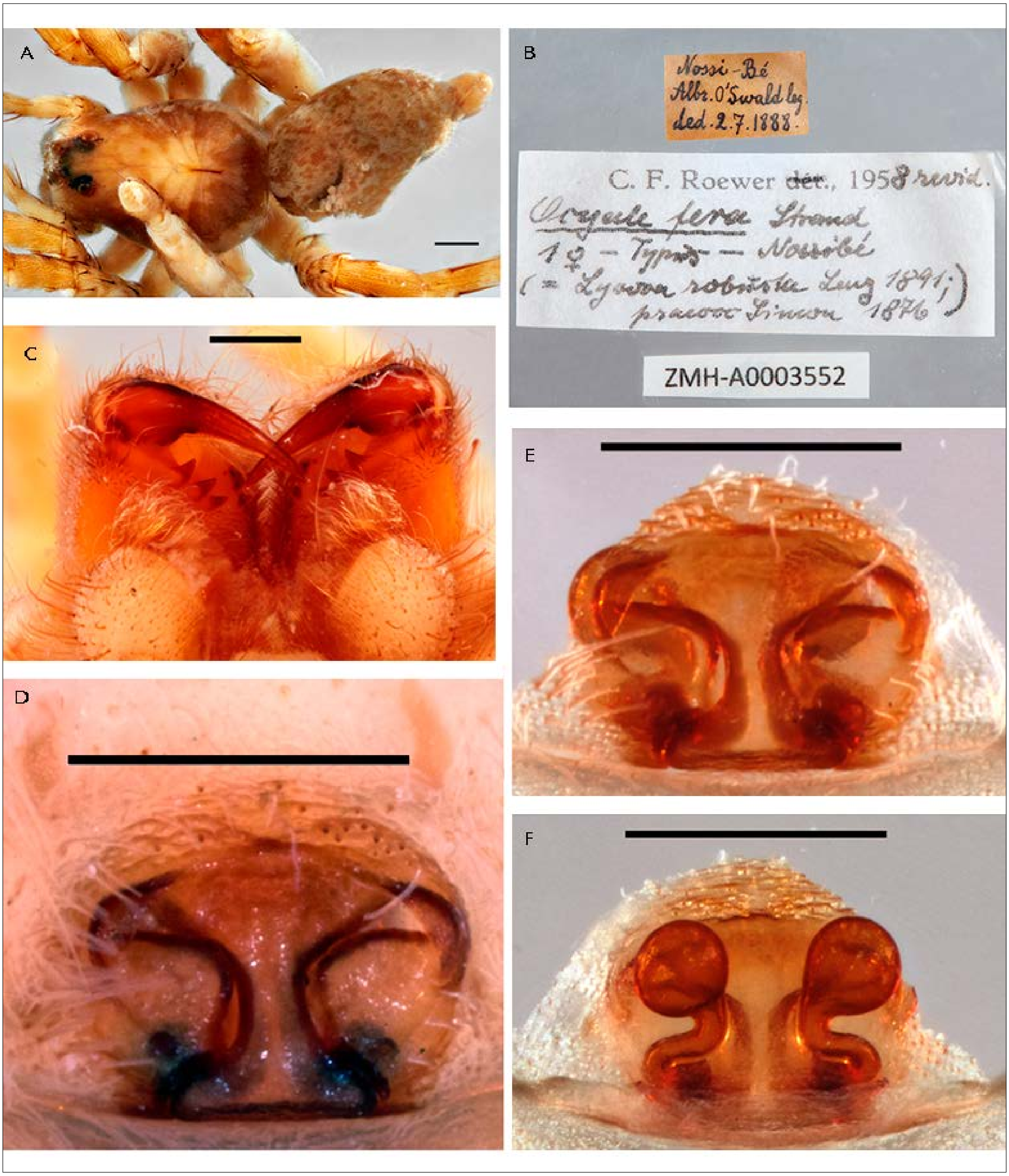


Figure 5. *Hippasosa fera* (Strand, 1908): holotype female (ZMH-A0003552). A) Carapace and abdomen, dorsal view, B) data labels, C) chelicerae, ventral view, D) epigyne (undissected), ventral view, E) epigyne (dissected and cleared), ventral view, F) vulva, dorsal view. Scale bars = 0.5 mm. Photographs by, and courtesy of, Nadine Dupérré (ZMH).

of the median septum before more can be said about the generic placement of this species.

Trochosa urbana O. Pickard-Cambridge, 1876
(Figure 6)

Trochosa urbana O. Pickard-Cambridge, 1876: 601, pl. 60, fig. 14 (♂♀).
Tarentula urbana gofensis Strand, 1906: 685 (♀).
Tarentula urbana hova Strand, 1907: 744 (♀). syn. conf.
Tarentula sansibarensis Strand, 1907: 743 (♀).
Tarentula urbana molensis Strand, 1908b: 48 (♂).
Trochosina arctosaeformis Caporiacco, 1940: 798 (imm.).
Trochosa urbana: Marusik, Nadolny & Koponen, 2020: 482, 487, 488, 489, figs. 1a–c, 2a–d, 3a–c, 4a–c, 4g,

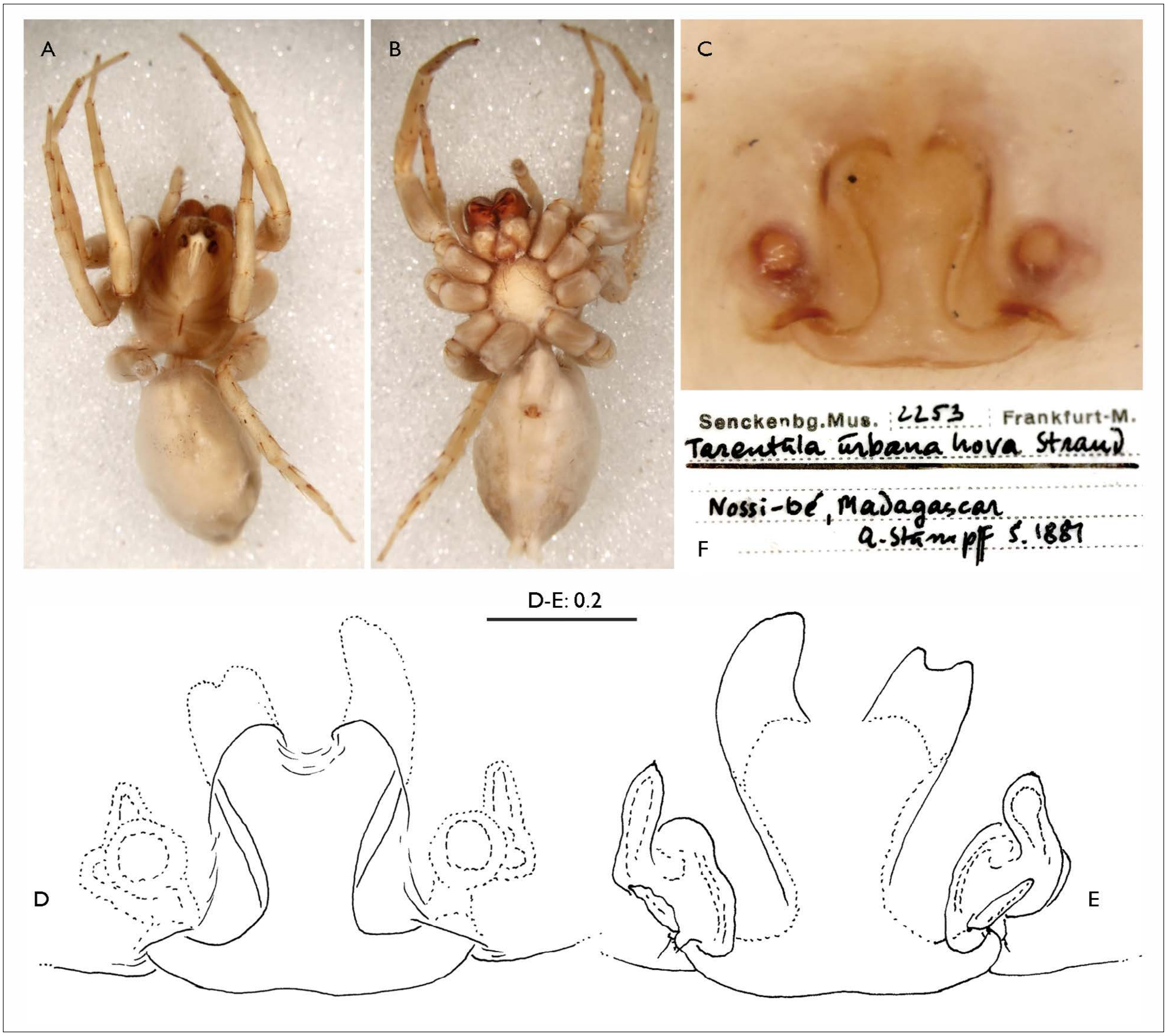


Figure 6. *Trochosa urbana* O. Pickard-Cambridge, 1876: holotype of *Tarentula urbana hova* Strand, 1907 (SMF 2253). A) Habitus, dorsal view, B) habitus, ventral view, C) epigyne (undissected), ventral view, D) illustration of epigyne (dissected and cleared), ventral view, E) illustration of vulva, dorsal view, F) data labels. Scale bar: 0.2 mm (D–E).

suppl. figs. 1A–E, 2.7–9, 3A–B, D, 4C–D, 5C (♂♀, synonomy of *Tarentula urbana hova*).

For full synonymy list, see World Spider Catalog (2024).

Type material. Holotype ♀ (SMF 2253), Madagascar, Nossi-bé [Nosy Be], A. Stumpff leg. 1881; for type material of other synonyms and the original material of Pickard-Cambridge (1876), see Marusik et al. (2020).

Complimentary morphological data. Total length: 11.1. Carapace: 4.8 long, 3.5 wide. Abdomen: 6.3 long, 3.9 wide. Chelicerae with 3 promarginal (distal tooth broken off on left chelicera) and 3 retromarginal teeth, no denticles and a single escort seta.

Remarks. Our examination of the female in SMF confirms the synonymy of the subspecies *T. urbana hova*, as proposed by Marusik et al. (2020). At present, *T. urbana* is the only non-native species of wolf spider currently known from Nosy Be and Madagascar broadly.

ACKNOWLEDGEMENTS

We would like to thank Nadine Dupérré (ZMH) for the high-quality photographs of *H. fera* and Jason Dunlop (Zoologisches Museum, Berlin) for searching for Malagasy lycosid material in the ZMB collections. Luis Piacentini (Museo Argentino de Ciencias Naturales, "Bernardino Rivadavia") is thanked for valuable comments on an early draft of this work. Finally, we thank Abel Bustamante (Museu Paraense Emílio Goeldi, Brazil) and an anonymous reviewer for comments which improved the final work.

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AUTHOR'S CONTRIBUTION

D. Sherwood contributed to conceptualization, data curation, formal analysis, investigation, methodology, project administration, and writing (original draft, review and editing); and P. Jäger contributed to conceptualization, data curation, formal analysis, investigation, methodology, project administration, and writing (review and editing).

What is better for sampling canopy spiders in the Amazon rainforest: a good tree or a good canopy?

O que é melhor para amostrar aranhas de dossel na floresta amazônica: uma boa árvore ou um bom dossel?

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Abstract: Despite being one of the largest Neotropical biomes, the Amazon rainforest presents a strong sampling bias. Most of its known spider fauna is reported from easily accessed environments, while canopy spider fauna is understudied. Sampling canopy spider fauna using fogging machines is based on two distinct approaches: (1) sampling the canopy of a target tree species ('single species'); or (2) sampling the fauna from a closed canopy, with overlapping branches of different tree species ('closed canopy'). These approaches have never been compared before. In the present manuscript, we provided evidence that fogging samples in both approaches yield a similar number of adult spiders and species. However, species composition is differs between the two methods. The pros and cons of each approach are discussed and the choice between them should depend on project goals.

Keywords: Fogging. Araneae. Community ecology. Eltonian shortfall.

Resumo: Apesar de ser um dos maiores biomas neotropicais, a floresta amazônica apresenta um forte viés de amostragem. Grande parte da fauna de aranhas conhecida provém de ambientes de fácil acesso, enquanto a fauna de aranhas do dossel é pouco estudada. A amostragem da fauna de aranhas do dossel usando máquinas de nevoeiro baseia-se em duas abordagens distintas: (1) amostrar o dossel de uma espécie de árvore-alvo ('uma única espécie'); ou (2) amostrar a fauna de um dossel fechado, com galhos sobrepostos de diferentes espécies de árvores ('dossel fechado'). Essas abordagens nunca foram comparadas antes. No presente manuscrito, fornecemos evidências de que as amostras de nevoeiro em ambas as abordagens resultam em um número semelhante de aranhas adultas e espécies. No entanto, a composição das espécies difere entre os dois métodos. Os prós e contras de cada abordagem são discutidos e a escolha entre elas deve depender dos objetivos do projeto.

Palavras-chave: *Fogging*. Araneae. Ecologia de comunidades. Déficit eltoniano.

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INTRODUCTION

The Amazon forest is well recognized as the most species rich tropical forest in the world, also serving as a primary source for Neotropical biodiversity (Antonelli et al., 2018). However, for spiders, this pattern is not fully recovered, in part owing to strong sampling biases (Oliveira et al., 2016, 2017). While the Amazon forest occupies an area ca. 3.8 times that of Atlantic forest, the Amazon forest presents ca. 62% of the spider species richness recorded for the Atlantic forest (1,036 vs 1,672 spp., respectively; Oliveira et al., 2017). These differences reflect sampling heterogeneity: only about 12% of the Amazon forest area presents at least one spider distribution record, while about 92% of the Atlantic forest area has records of spider species (Oliveira et al., 2017). Disregarding this sampling deficiency, both of these biomes share a particular bias with regard to the known taxa: they are mostly known from easily accessible environments, while the leaf litter and the forest canopy are poorly studied microhabitats (Basset, 2001; Oliveira et al., 2017).

A significant part of this biodiversity is found in the forest canopy, a critical habitat that harbors a unique and often underexplored array of species (Basset, 2001; Erwin, 1989). The canopy, functioning as a distinct ecosystem, plays a key role in photosynthesis, sexual reproduction, light absorption, shading, nutrient cycling, atmospheric-meteorological interaction, hydrologic interactions, and biological diversity (Shaw & Bible, 1996). Its complex vertical stratification supports different species assemblages compared to the forest floor (e.g., Lindo & Winchester, 2006; Oguri et al., 2014), making it essential for understanding overall forest biodiversity. However, sampling the canopy spider fauna is not an easy task, in terms of access and spatial heterogeneity (Mupepele et al., 2014; Ozanne, 2005). For example, at low canopy sites (e.g., under 20 m) the sampling can be carried out from the ground (e.g., fogging and branch clipping) (Adis et al., 1984; Ozanne, 2005). However, at sites with higher canopy (e.g., over 20 m), effective sampling can only be attained from within the canopy (e.g., rope climbing, hoisting the fogging machine, or using drones, hoisted pitfall traps, canopy sweeping or arboreal traps) (Madden et al., 2022; Matevski et al., 2020; Ozanne, 2005; Sena et al., 2010; Viana-Junior et al., 2021). Among the methods used, fogging (i.e., chemical knockdown) is arguably the most effective and widely used sampling method for assessing the canopy fauna (Ozanne, 2005).

The knowledge regarding the Brazilian canopy spider fauna is scarce, highly concentrated in a few localities and mostly based on samplings with fogging. During the 80s and 90s, several papers investigated the ecology of canopy spiders at Amazonian forest sites near Manaus (Adis et al., 1984, 1997; Höfer et al., 1994). Later, samplings were carried out in the Pantanal of Poconé (Battirola et al., 2004, 2016; Marques et al., 2006, 2007; Yamazaki et al., 2017), in the urban Atlantic Forest remains at Salvador (Sena et al., 2010) and in the Cerrado of Brasília (Gurgel-Gonçalves et al., 2006). These studies could be divided into two different sampling approaches. Most of them focused on the spider canopy fauna from a single tree species (Adis et al., 1997; Adis et al., 1998b; Battirola et al., 2004, 2016; Höfer et al., 1994; Marques et al., 2006, 2007; Yamazaki et al., 2017), while only a few studies focused on the canopy fauna from general forested sites (Adis et al., 1984; Sena et al., 2010), presumably with a closed canopy.

The effect of sampling with fogging using these two different approaches has never been tested. Samplings carried out in other regions worldwide share the same duality, either sampling single tree species (Floren et al., 2008, 2011; Mupepele et al., 2014; Otto & Floren, 2010; Pashkevich et al., 2022; Wildermuth et al., 2023) or, less commonly, closed canopies (Junggebauer et al., 2021; Ramos et al., 2022; Sørensen, 2004). Most of these studies were carried out in temperate forests, where targeting specific tree species is a viable alternative, owing to the particularly low tree diversity compared to tropical and subtropical moist forest biomes (Cazzolla-Gatti et al., 2022). However, in tropical forests, areas where the crown canopy architecture and overlapping branches of different tree species hamper the process of carrying out fogging for single tree species, making it impossible to associate each animal species to specific tree species (Erwin, 1989). Owing to these structural characteristics of tropical forest trees, Erwin (1989) proposed that fogging should be carried out targeting single tree species, a proposal later followed as a rule of thumb (see Adis et al., 1998a).

In the present study, we aimed to compare the spider assemblages from an Amazon forest locality, collected using these two approaches for canopy fogging: sampling target tree species (hereafter only 'single species'), or sampling at sites with a closed canopy. Our study also provides an unique opportunity to discuss the vertical stratification of spider assemblage in the Amazon biome, as the spider fauna from the study site can be considered relatively well-known (Bonaldo & Dias, 2010; Carvalho et al., 2010; Dias & Bonaldo, 2012).

MATERIAL AND METHODS

SAMPLING SPIDERS

The study site is located at the Base de Operações Geólogo Pedro de Moura (4° 51' 7" S, 65° 16' 59" W), an oil and gas drilling area of the Petrobras S.A., at the Urucu River basin, Coari, Amazonas, northern Brazil. The area has approximately 520,000 hectares of continuous Amazon forest and it is located about 650 km west of the city of Manaus, Amazonas. The region is covered by dense, uniform-canopy *terra firme* rainforest, with few floodable areas, with *várzea* occurring only along the sandy banks of the Urucu River. Notable changes in vegetation structure occur where the soil is poorly drained or in clearings opened artificially for natural gas and oil exploration and production (see Bonaldo & Dias, 2010). The trees range between 23-32 meters in height and have low densities of epiphytes and lianas (Lima-Filho et al., 2001).

The sampling was carried out with canopy fogging in two occasions, at haphazard sampling sites. In the first expedition, nine areas (i.e., nine independent samples for statistical purposes) with closed canopies formed by a mixture of tree species with overlapping branches were sampled from October 28 to November 4, 2008. At each sampling, the spiders were intercepted by 13 fabric sheets of 1.5 x 4 m (total of 78 m^2 of interception area per sampling) placed directly under the sampled canopy (Figure 1A). In the second sampling, eight canopies (i.e., eight independent samples for statistical purposes) of *Eschweilera atropetidata* S.A. Mori (Lecythidaceae), commonly known as '*matá-matá branco*' or '*castanha-vermelha*', were sampled from August 30 to September 7, 2009. The sampled trees were selected according to the rule of thumb for single species fogging (see Adis et al., 1998a), by choosing a common species (for allowing replication), without flowers or fruits, and with few epiphytes. The genus *Eschweilera* is the most abundant angiosperm tree genus in the study site, although it is also one that most host epiphytes too (Irume et al., 2013). At each sampling, the spiders were intercepted by 7-8 fabric sheets (same as for closed canopy samplings; total of 42-48 m^2 of interception area per sampling) placed directly under the sampled canopy. The number of fabric sheet used in each sampling differed owing to logistical reasons. These differences were considered in the analytical methods applied.

In both expeditions, the fogging was carried out in the morning to take advantage of the lower wind circulation, preventing the cloud of chemical droplets from dissipating away from the target canopy (Figures 1C-1D). A fogger model pulsFOG K-10 / 6 volt 0.5 A / 24 CV was used for 30 minutes per sample, with the smoke jet directed from the ground towards the tree canopies (Figure 1B). A non-residual synthetic pyrethroid (K-Othrine® insecticide) diluted in diesel oil at a concentration of 10% and permethrin (100 ml) was used as the active ingredient to increase the

Figure 1. Canopy fogging carried out at Urucu River basin: (A) fabric sheet disposed for intercepting the spiders before fogging application; (B) fogging application; (C-D) cloud of knockdown chemicals during fogging application. Photos: S. C. Dias (2008).

knockdown effect on organisms (see Adis et al., 1997). The collected individuals were fixed in 80% alcohol, stored in labeled vials, and later identified. Juveniles were not considered for the present study. Adults of both expeditions were grouped and identified to the species level or assigned to morphospecies when the identification to the species level was not possible. All specimens are deposited in the arachnological collection of the Museu Paraense Emílio Goeldi, Belém, Pará, Brazil (MPEG; curator A.B. Bonaldo).

STATISTICAL ANALYSES

The number of males and females was compared using chi-squared tests for equal proportions. A species richness estimative was calculated using the 'iNEXT' function of the package 'iNEXT', for $q = 0$ (Hsieh et al., 2016), which is based on the methods proposed in Chao (1984, 1987). The mean numbers of adult spiders and species per fabric sheet used in each sample was compared between treatments (i.e., 'closed canopy' vs. 'single species') using generalized linear models with gaussian distribution of errors. Dispersion issues were checked based on the raw dispersion parameters and using the 'rdiagnostic' function of the package 'RT4Bio' (Reis Jr. et al., 2015). To compare the spider species composition among treatments, we performed a permutational multivariate analysis of variance using distance matrices – PERMANOVA, using Bray-Curtis dissimilarity index (function 'adonis2', package 'vegan' Oksanen et al., 2024). To represent graphically the dissimilarity among spider assemblages from each treatment, we also performed a nonmetric multidimensional scaling – NMDS, using Bray-Curtis dissimilarity index and calculated for two dimensions (function 'metaMDS', package 'vegan' Oksanen et al., 2024). Whittaker plots of the species abundance data were produced for each assemblage (function 'racurve', package 'goeveg'; von Lampe & Schellenberg, 2024). All analyses were carried out in R programming, through RStudio 2024.04.2 Build 764 (RStudioTeam, 2020).

RESULTS AND DISCUSSION

We collected 723 adult spiders, including 338 males and 385 females (sex ratio males/females = 0.88; x^2 = 3.05, df = 1, p = 0.08). Closed canopy fogging yielded 431 adults, including 192 males and 239 females (sex ratio = 0.80; x^2 = 5.125, df = 1, p = 0.02); while single species fogging yielded 292 adults, including 146 males and 146 females (sex ratio = 1.0; x^2 = 0, df = 1, p = 1). Spider abundance in both treatments was not significantly different (deviance = 0.212, df = 15, p = 0.777; Figure 2). The biased sampling towards females is similar to that observed for other spider inventories, not based on passive (i.e., pitfall traps) sampling methods (e.g., Bomfim et al., 2021; Mendes et al., 2018; Prado & Baptista, 2023; Rodrigues et al., 2009), including canopy fogging samplings (e.g., Battirola et al., 2004). In fact, it is widely known that adult male spiders are relatively short lived and wander in search of mating pairs, which induces a higher mortality than in females (Coddington et al., 2009; Vollrath & Parker, 1992), but increases their capture by passive sampling methods (e.g., Engelbrecht, 2013).

A total of 272 spider species were recorded with fogging at the Urucu River basin, of which only 56 species (20.6%) were collected in both fogging treatments (Table 1). 197 species were collected in the closed canopy fogging, including 141 exclusive species (71.6%). 131 species were collected in the single species canopy fogging, including 75 exclusive species (57.3%). Spider species richness in both treatments was not significantly different (deviance = 0.592, df = 15, p = 0.4345; Figure 2).

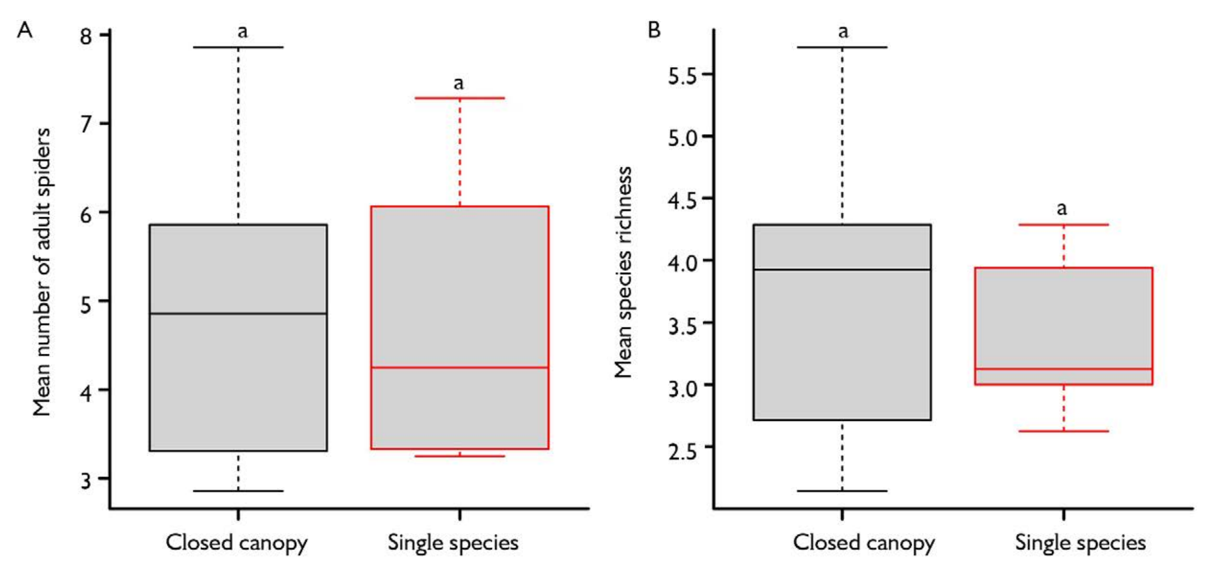

Figure 2. Comparison of the mean number of adult spiders (A) and mean species richness (B) collected per fabric sheet by fogging at closed canopy sites ('Closed canopy') and under the canopy of *Eschweilera atropetidata* ('Single species').

Table 1. List of adult spider species collected in both inventories carried out at Urucu River basin. 'Single species' refers to canopy fogging sampled carried out under *Eschweilera atropetidata* trees. 'Closed canopy' refers to canopy fogging samples under forests with closed canopies of different trees. (Continue)

Taxa	Single species		Closed canopy		Total
	M	F	M	F	
Anyphaenidae	13	9	19	17	58
Isigonia limbata Simon, 1897	0	0	0	1	1
Macrophyes sp.1	0	0	2	0	2
Anyphaenidae sp.1	0	2	0	5	7
Anyphaenidae sp.10	0	1	0	0	1
Anyphaenidae sp.11	0	0	3	1	4
Anyphaenidae sp.12	2	0	0	1	3
Anyphaenidae sp.13	0	0	1	1	2
Anyphaenidae sp.14	0	0	2	2	4
Anyphaenidae sp.2	1	1	0	1	3
Anyphaenidae sp.3	6	1	1	0	8
Anyphaenidae sp.4	1	0	5	1	7
Anyphaenidae sp.5	0	1	0	0	1
Anyphaenidae sp.6	0	1	1	1	3
Anyphaenidae sp.7	3	1	0	0	4
Anyphaenidae sp.8	0	1	0	1	2
Anyphaenidae sp.9	0	0	4	2	6
Araneidae	16	14	30	42	102
Alpaida chickeringi Levi, 1988	0	0	1	0	1
Alpaida delicata (Keyserling, 1892)	0	0	2	1	3
Alpaida guto Abrahim & Bonaldo, 2008	0	0	0	1	1
Alpaida truncata (Keyserling, 1865)	0	0	0	1	1
Alpaida sp.1	2	0	2	1	5
Alpaida sp.2	1	0	0	0	1
Alpaida sp.3	1	0	0	1	2
Alpaida sp.4	0	0	2	0	2
Alpaida sp.6	1	0	0	0	1
Amazonepeira sp.1	0	1	1	2	4
Bertrana elinguis (Keyserling, 1883)	0	0	0	3	3
Cyclosa fililineata Hingston, 1932	0	1	0	0	1
Enacrosoma sp.1	0	0	0	1	1
Encyosaccus sp.1	2	0	0	0	2
Eustala sp.1	0	0	0	1	1
Eustala sp.2	0	0	0	1	1
Eustala sp.4	0	0	2	0	2
Hypognatha belem Levi, 1996	2	1	0	0	3
Hypognatha sp.1	0	1	0	2	3

Table 1. (Continue)

Taxa	Single species		Closed canopy		Total
	M	F	M	F	
Hypognatha sp.2	1	0	1	0	2
Hypognatha sp.3	0	0	1	0	1
Mangora sp.1	0	0	1	2	3
Mangora sp.2	0	0	1	0	1
Mangora sp.3	2	3	0	0	5
Mangora sp.4	0	0	0	1	1
Metazygia sp.1	1	0	0	1	2
Micrathena acuta (Walckenaer, 1841)	0	0	1	1	2
Micrathena aff. agriliformis (Taczanowski, 1879)	0	0	1	0	1
Micrathena aureola (C. L. Koch, 1836)	0	1	0	0	1
Micrathena clypeata (Walckenaer, 1805)	0	0	0	2	2
Micrathena miles Simon, 1895	0	0	0	5	5
Micrathena pungens (Walckenaer, 1841)	0	0	0	1	1
Micrathena sexspinosa (Hahn, 1822)	0	1	0	0	1
Micrathena triangularispinosa (De Geer, 1778)	0	1	0	2	3
Micrathena vigorsi (Perty, 1833)	0	0	0	2	2
Micrathena sp.1	0	0	1	0	1
Ocrepeira sp.1	0	0	1	1	2
Ocrepeira sp.2	0	0	0	1	1
Parawixia divisoria Levi, 1992	0	0	1	0	1
Parawixia kochi (Taczanowski, 1873)	0	0	1	1	2
Parawixia sp.1	0	0	1	0	1
Spintharidius rhomboidalis Simon, 1893	0	0	1	0	1
Testudinaria quadripunctata Taczanowski, 1879	1	2	0	0	3
Verrucosa sp.1	0	1	5	3	9
Verrucosa sp.2	0	0	0	1	1
Wagneriana jelskii (Taczanowski, 1873)	0	0	1	0	1
Wagneriana sp.1	0	0	1	0	1
Xylethrus sp.1	0	0	1	0	1
Araneidae sp.1	1	0	0	0	1
Araneidae sp.2	1	1	0	0	2
Araneidae sp.4	0	0	0	1	1
Araneidae sp.5	0	0	0	2	2
Clubionidae	0	0	1	3	4
Elaver sigillata (Petrunkevitch, 1925)	0	0	1	3	4
Corinnidae	7	7	17	14	45
Castianeira sp.1	6	5	1	0	12
Castianeira sp.2	0	0	2	0	2

Table 1. (Continue)

Taxa	Single species		Closed canopy		Total
	M	F	M	F	
Castianeira sp.3	0	0	1	0	1
Corinna ducke Bonaldo, 2000	0	0	0	1	1
Corinna sp.1	0	0	3	1	4
Corinna sp.3	0	0	0	1	1
Corinna sp.4	0	0	2	2	4
Creugas sp.1	0	1	0	0	1
Myrmecium sp.1	0	0	1	2	3
Myrmecotypus sp.1	0	0	6	2	8
Myrmecotypus sp.2	1	0	0	1	2
Parachemmis sp.1	0	1	0	0	1
Parachemmis sp.2	0	0	0	1	1
Sphecotypus niger (Perty, 1833)	0	0	0	1	1
Stethorrhagus lupulus Simon, 1896	0	0	0	1	1
Tupirinna sp.1	0	0	0	1	1
Tupirinna sp.2	0	0	1	0	1
Ctenidae	0	0	1	1	2
Ctenus crulsi Mello-Leitão, 1930	0	0	0	1	1
Ctenus sp.2	0	0	1	0	1
Deinopidae	0	0	0	1	1
Deinopis sp.1	0	0	0	1	1
Dictynidae	4	2	0	0	6
Thallumetus sp.1	3	1	0	0	4
Dictynidae sp.1	1	1	0	0	2
Gnaphosidae	1	0	1	2	4
Zimiromus sp.1	0	0	1	2	3
Gnaphosidae sp.1	1	0	0	0	1
Hahniidae	0	5	0	0	5
Hahnia sp.n 1	0	5	0	0	5
Hersiliidae	0	0	1	0	1
Ypypuera crucifera (Vellard, 1924)	0	0	1	0	1
Linyphiidae	1	0	0	0	1
Linyphiidae sp.1	1	0	0	0	1
Mimetidae	1	0	0	1	2
Ero sp.1	1	0	0	1	2
Oonopidae	17	29	0	1	47
Gradunguloonops mutum Grismado et al., 2015	5	9	0	0	14

Table 1. (Continue)

Taxa	Single species		Closed canopy		Total
	M	F	M	F	
Gradunguloonops urucu Grismado et al., 2015	1	4	0	0	5
Orchestina sp.1	2	6	0	0	8
Orchestina sp.2	5	6	0	0	11
Oonopidae sp.1	4	1	0	1	6
Oonopidae sp.2	0	1	0	0	1
Oonopidae sp.3	0	1	0	0	1
Oonopidae sp.4	0	1	0	0	1
Oxyopidae	3	2	2	8	15
Oxyopes argyrotrichius Mello-Leitão, 1929	0	0	0	5	5
Oxyopes hemorrhous Mello-Leitão, 1929	1	1	0	0	2
Oxyopes holmbergi Soares & Camargo, 1948	2	0	0	0	2
Oxyopes incertus Mello-Leitão, 1929	0	0	0	1	1
Oxyopes sp.1	0	1	0	0	1
Oxyopes sp.2	0	0	0	1	1
Schaenicoscelis sp.1	0	0	1	1	2
Schaenicoscelis sp.2	0	0	1	0	1
Pholcidae	5	1	10	16	32
Carapoia fowleri Huber, 2000	0	0	1	0	1
Mesabolivar aurantiacus (Mello-Leitão, 1930)	1	0	4	4	9
Metagonia beni Huber, 2000	1	0	1	2	4
Metagonia taruma Huber, 2000	3	1	4	10	18
Pisauridae	0	2	0	1	3
Architis cymatilis Carico, 1981	0	1	0	0	1
Architis tenuis Simon, 1898	0	1	0	0	1
Thaumasia sp.1	0	0	0	1	1
Salticidae	19	18	27	59	123
Aillutticus sp.1	1	0	0	0	1
Amycus sp.1	0	0	0	7	7
Amycus sp.2	0	0	0	1	1
Breda lubomirskii (Taczanowski, 1878)	0	0	0	1	1
Colonus aff. vaccula (Simon, 1900)	0	0	0	1	1
Coryphasia sp.1	0	1	0	0	1
Coryphasia sp.2	0	3	0	0	3
Cotinusa sp.1	0	1	0	0	1
Encolpius sp.1	0	0	0	1	1
Eustiromastix sp.1	0	0	0	1	1

Table 1. (Continue)

Taxa	Single species		Closed canopy		Total
	M	F	M	F	
Hasarius adansoni (Audouin, 1826)	0	0	2	2	4
Hypaeus sp.1	1	0	0	0	1
Hypaeus sp.2	5	0	0	0	5
Hypaeus sp.3	0	0	0	3	3
Hypaeus sp.4	0	0	0	1	1
Itata sp.1	0	0	0	4	4
Itata sp.2	0	0	0	1	1
Lyssomanes nigropictus Peckham et al., 1889	1	1	2	1	5
Lyssomanes sp.1	0	1	0	0	1
Lyssomanes sp.2	1	0	1	0	2
Lyssomanes sp.4	1	1	0	0	2
Lyssomanes sp.5	0	0	2	0	2
Lyssomanes sp.6	0	0	1	0	1
Lyssomanes sp.7	0	0	1	0	1
Lyssomanes sp.8	0	0	0	1	1
Matinta acutidens (Simon, 1900)	0	0	1	0	1
Myrmapana mocamboensis (Galiano, 1974)	1	1	0	0	2
Myrmarachne sp.1	0	1	0	0	1
Noegus niveomarginatus Simon, 1900	0	0	2	1	3
Nycerella sp.1	0	0	1	0	1
Pachomius sp.1	0	0	2	0	2
Psecas sp.1	0	1	0	0	1
Psecas sp.2	0	0	0	1	1
Scopocira tenella Simon, 1900	1	0	1	5	7
Sidusa sp.1	0	0	1	0	1
Salticidae sp.1	2	0	0	10	12
Salticidae sp.10	0	0	0	1	1
Salticidae sp.11	0	0	0	2	2
Salticidae sp.12	0	0	0	1	1
Salticidae sp.13	0	0	1	2	3
Salticidae sp.15	0	0	1	0	1
Salticidae sp.16	0	0	1	0	1
Salticidae sp.17	0	0	1	0	1
Salticidae sp.18	0	0	1	0	1
Salticidae sp.19	0	0	0	1	1
Salticidae sp.2	1	2	0	1	4

Table 1. (Continue)

Taxa	Single species		Closed canopy		Total
	M	F	M	F	
Salticidae sp.20	0	0	0	1	1
Salticidae sp.21	0	0	0	1	1
Salticidae sp.3	3	2	0	0	5
Salticidae sp.4	1	0	0	1	2
Salticidae sp.5	0	1	0	1	2
Salticidae sp.6	0	1	1	0	2
Salticidae sp.7	0	1	1	0	2
Salticidae sp.8	0	0	1	4	5
Salticidae sp.9	0	0	2	1	3
Scytodidae	6	3	0	2	11
Scytodes altamira Rheims & Brescovit, 2000	1	0	0	2	3
Scytodes romitii Caporiacco, 1947	4	3	0	0	7
Scytodes sp.1	1	0	0	0	1
Selenopidae	1	0	2	1	4
Selenops sp.1	1	0	2	1	4
Senoculidae	0	1	1	3	5
Senoculus sp.1	0	1	1	2	4
Senoculus sp.2	0	0	0	1	1
Sparassidae	0	0	1	1	2
Vindullus gracilipes (Taczanowski, 1872)	0	0	1	1	2
Tetrablemmidae	0	1	0	0	1
Tetrablemmidae sp.1	0	1	0	0	1
Tetragnathidae	1	0	0	0	1
Tetragnatha sp.1	1	0	0	0	1
Theridiidae	40	41	42	42	165
Achaearanea trapezoidalis (Taczanowski, 1873)	0	0	1	0	1
Achaearanea sp.1	0	0	0	1	1
Achaearanea sp.2	0	0	0	1	1
Achaearanea sp.3	1	0	0	0	1
Achaearanea sp.4	0	1	0	0	1
Anelosimus eximius (Keyserling, 1884)	0	0	0	1	1
Cerocida ducke Marques & Buckup, 1989	0	0	1	2	3
Chrysso sp.1	0	1	0	1	2
Cryptachaea dalana (Buckup & Marques, 1991)	0	0	2	1	3
Cryptachaea pydanieli (Buckup & Marques, 1991)	1	0	1	0	2
Dipoena atlantica Chickering, 1943	2	0	2	0	4

Table 1. (Continue)

Taxa	Single species		Closed canopy		Total
	M	F	M	F	
Dipoena duodecimpunctata Chickering, 1943	3	1	1	0	5
Dipoena esra Levi, 1963	1	2	0	1	4
Dipoena militaris Chickering, 1943	4	0	1	0	5
Dipoena tingo Levi, 1963	2	1	1	1	5
Dipoena sp.1	5	3	3	3	14
Dipoena sp.2	0	2	0	2	4
Dipoena sp.3	0	0	1	0	1
Dipoena sp.4	0	0	1	0	1
Dipoena sp.5	1	0	0	0	1
Dipoena sp.6	0	1	0	0	1
Dipoena sp.7	1	0	0	0	1
Episinus immundus (Keyserling, 1884)	1	0	2	2	5
Episinus sp.1	0	0	2	0	2
Euryopis sp.1	0	0	0	3	3
Euryopis sp.2	0	1	0	0	1
Euryopis sp.3	1	4	0	0	5
Helvibis sp.1	1	0	8	6	15
Janula bicruciata (Simon, 1895)	0	0	1	2	3
Janula salobrensis (Simon, 1895)	3	8	1	2	14
Lasaeola donaldi (Chickering, 1943)	1	0	0	0	1
Phoroncidia studo Levi, 1964	0	2	0	0	2
Phoroncidia sp.1	1	0	0	0	1
Phycosoma altum (Keyserling, 1886)	1	3	0	0	4
Spintharus sp.1	0	0	2	3	5
Theridion sp.1	0	0	0	1	1
Theridion sp.2	1	0	0	0	1
Theridion sp.3	0	1	0	0	1
Thwaitesia affinis O. Pickard-Cambridge, 1882	1	0	1	0	2
Thwaitesia bracteata (Exline, 1950)	0	0	6	3	9
Thymoites piarco (Levi, 1959)	1	0	2	2	5
Theridiidae sp.1	1	7	0	1	9
Theridiidae sp.10	1	0	0	0	1
Theridiidae sp.11	1	0	0	0	1
Theridiidae sp.13	1	0	0	0	1
Theridiidae sp.2	2	2	0	0	4
Theridiidae sp.3	0	0	2	0	2
Theridiidae sp.5	0	0	0	1	1
Theridiidae sp.7	0	0	0	1	1
Theridiidae sp.8	0	0	0	1	1

Table 1. (Continue)

Taxa	Single species		Closed canopy		Total
	M	F	M	F	
Theridiidae sp.9	1	1	0	0	2
Theridiosomatidae	1	1	1	0	3
Chthonos sp.1	0	1	1	0	2
Theridiosomatidae sp.1	1	0	0	0	1
Thomisidae	4	3	17	8	32
Aphantochilus rogersi O. Pickard-Cambridge, 1871	0	0	0	1	1
Epicadus sp.1	0	1	4	0	5
Epicadus sp.2	0	0	3	0	3
Epicadus sp.3	0	0	0	1	1
Tmarus sp.1	1	0	0	2	3
Tmarus sp.2	0	0	2	0	2
Tmarus sp.3	0	0	4	1	5
Tmarus sp.4	0	1	0	0	1
Tmarus sp.5	0	1	0	0	1
Tmarus sp.6	1	0	0	0	1
Tmarus sp.7	1	0	0	0	1
Tmarus sp.8	0	0	0	1	1
Tmarus sp.9	0	0	0	1	1
Thomisidae sp.1	1	0	0	0	1
Thomisidae sp.2	0	0	0	1	1
Thomisidae sp.3	0	0	1	0	1
Thomisidae sp.4	0	0	1	0	1
Thomisidae sp.5	0	0	1	0	1
Thomisidae sp.6	0	0	1	0	1
Trachelidae	1	2	5	5	13
Orthobula sp.1	1	0	0	1	2
Trachelas sp.1	0	2	5	3	10
Trachelas sp.2	0	0	0	1	1
Trechaleidae	2	2	5	5	14
Cupiennius bimaculatus (Taczanowski, 1874)	0	0	1	0	1
Rhoicinus urucu Brescovit & Oliveira, 1994	0	0	0	1	1
Syntrechalea adis Carico, 2008	0	1	2	2	5
Syntrechalea sp.1	0	0	0	1	1
Trechalea sp.1	2	1	2	1	6
Uloboridae	3	3	9	6	21
Miagrammopes sp.1	3	2	6	3	14
Miagrammopes sp.2	0	0	0	2	2

Table 1. (Conclusion)

Taxa	Single species		Closed canopy		Total
	M	F	M	F	
Philoponella sp.1	0	0	1	1	2
Philoponella sp.2	0	0	1	0	1
Zosis sp.1	0	1	0	0	1
Uloboridae sp.1	0	0	1	0	1
Total	146	146	192	239	723

The observed species richness represents about 43.7% of the maximum species richness ever reported for the same locality in previous studies (393 spp. in Bonaldo & Dias, 2010; 623 spp. in Dias & Bonaldo, 2012). As the specimens' identifications between the present and past studies were not standardized, it is not possible to evaluate the proportion of the spider fauna from the Urucu River basin that lives exclusively in the forest canopy. However, this provides a good estimate of the spider assemblage in these different vertical strata. Only one additional locality in the Amazon biome has similar data for comparison. For the Reserva Florestal Adolpho Ducke, a nearby locality in Manaus, 62 species were reported from tree canopies (Höfer et al., 1994), representing ca. 12% of the total spider fauna (Höfer & Brescovit, 2001). For tropical dry forest from the Colombian Caribbean (Quijano-Cuervo et al., 2019) and Tanzanian montane forest (Quijano-Cuervo et al., 2019; Sørensen, 2003), there are also evidence of higher spider species richness in lower strata. Similarly, for insects, up to 50% of the fauna is likely to be exclusive to the canopy (Ozanne, 2005). Nonetheless, in the present sampling, there is evidence that the observed canopy fauna is not necessarily exclusive to that environment. Several recorded species are known to live in the understory vegetation (e.g., *Metagonia taruma*, *Wagneriana jelskii* and *Micrathena vigorsi*), tree trunks (e.g., *Syntrechalea adis* and *Ypypuera crucifera*) or are associated with the leaf litter layer (e.g., *Cupiennius bimaculatus* and *Ctenus crulsi*) (Bonaldo et al., 2009; Carico, 2008; Carvalho et al., 2010; Levi, 1991; Rego et al., 2007; Rheims & Brescovit, 2004). This suggests that the composition of Amazon forest canopy spider assemblages is complex and requires further studies to evaluate its uniqueness compared to other strata.

The relatively low species richness recorded also reflects the low sampling intensity, not reaching three individuals per species, on both treatments (Table 2). This results in a high proportion of singletons (50.4%) and doubletons (17.2%), in the closed canopy and single species treatments (Table 2). Consequently, the estimated species richness for both treatments was about twice the observed, with 406 and 317 species, respectively for the closed canopy and single species treatments (Table 2). The number of singletons was much higher than the average frequently reported (32%) for tropical arthropods surveys (Coddington et al., 2009). As canopy spider diversity is positively correlated with sampling effort (Mupepele et al., 2014), intensified additional sampling effort should be carried out, if aiming to provide a realistic survey for the canopy spider fauna from the Urucu River basin.

As expected, owing to a similar spider abundance and species richness, both treatments yielded similar rank-abundance curves, thus suggesting an overall similarity in spider abundance patterns as well (Figure 3A). The species composition, however, was statistically significant between treatments ($R^2 = 15.2\%$, $F = 2.692$, $p = 0.001$; Figure 3B). The results shown in the present study do not corroborate our previous expectations. Single species fogging is likely to sample a more homogeneous canopy structure, which was expected to provide a lower species richness. On the other hand, the closed canopy approach, samples a canopy formed by overlapping branches of different tree species and/or individuals, yielding a more heterogeneous canopy and a higher expected spider species richness. In fact, previous studies have shown that spider abundance, biomass and species richness correlate positively with structural complexity of the vegetation (Wildermuth et al., 2023). As such, the association of spiders with their host trees can be significant (Mupepele et al., 2014), as spiders rely on structural attributes during microhabitat selection, such as leaf shape, branch and leaf density and bark structure (Mupepele et al., 2014; Villanueva-Bonilla et al., 2021). Therefore, our results suggest that the canopy sampled at both approaches had a similar level of structural complexity and/or biomass (hence supporting a similar number of specimens and species), but different structures that form the canopies (hence supporting different spider assemblages).

Table 2. Summary of the spider assemblage parameters collected by fogging at closed canopy sites ('Closed canopy') and under the canopy of *Eschweilera atropetidata* ('Single species'). Abbreviations: "sd", standard deviation; "se", standard error.

Parameters	Closed canopy	Single species	Total
Males	192	146	338
Females	239	146	385
Total specimens	431	292	723
Mean number of spiders per fabric sheet (± sd)	4.95 (±1.62)	4.73 (±1.56)	4.84 (±1.54)
Sex ratio (males/females)	0.80	1.00	0.88
Observed species richness (exclusive)	197 (141)	131 (75)	272
Mean species richness per fabric sheet (± sd)	3.75 (±1.18)	3.38 (±0.61)	3.57 (±0.94)
Sampling intensity	2.19	2.23	2.66
Singletons (% of total)	114 (57.9%)	82 (62.6%)	137 (50.4%)
Doubletons (% of total)	31 (15.7%)	18 (13.7%)	47 (17.2%)
Estimated species richness (± se)	406 (±44)	317 (±51)	471 (±39)
Sampling completeness	48.52%	41.32%	57.75%

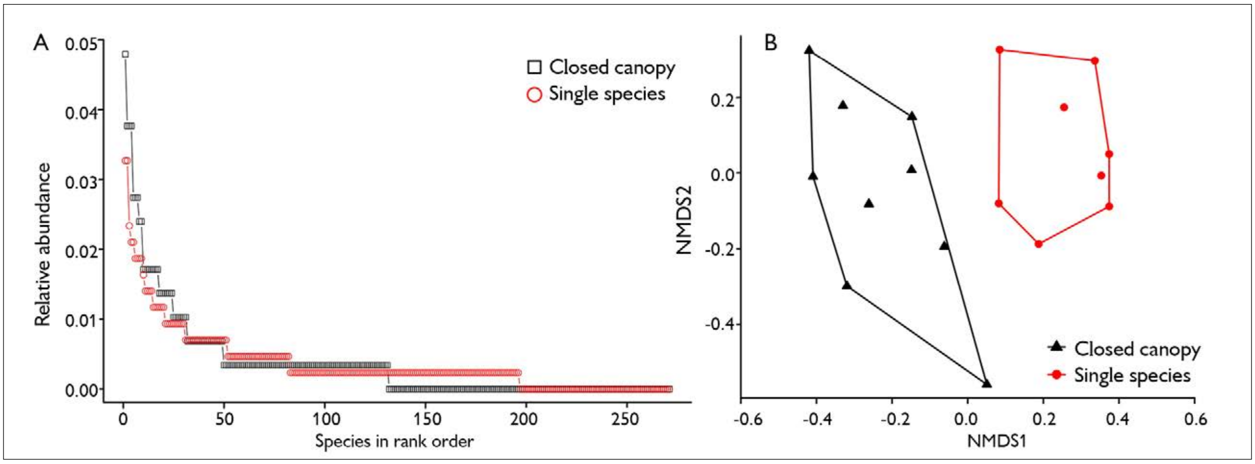

Figure 3. Rank-abundance plots (A) and nonmetric multidimensional scaling ordination using a Bray-Curtis similarity matrix of adult spider abundance (B; stress = 0.198), collected by fogging at closed canopy sites (in black; 'Closed canopy') and under the canopy of *Eschweilera atropetidata* (in red; 'Single species').

The rules of thumb followed for single species design should be reconsidered. The proposal for choosing tree specimens with fewer epiphytes and without flowers (taken from Adis et al., 1998a), might bias the samplings negatively. This proposal is based on the idea that epiphytic plants, phytotelmata and perched litter would hamper the penetration of knock down agents or prevent the dead specimens from falling from the trees (Erwin, 1989). However, in experimental studies, trees with epiphytes presented disproportionately more preys (such as insects) and predators (such as spiders), than those from which epiphytes were removed (Cruz-Angón et al., 2009; Díaz et al., 2012).

The present study revealed a canopy spider fauna from a central Amazonia locality much more diverse than previously reported for this region (see Höfer et al., 1994). We have shown that the choice between carrying out canopy spider inventories following the single species or the closed canopy approaches has its pros and cons. The closed canopy approach would be less time-consuming, as it does not require a previous survey for mapping isolated target trees that match the previously proposed rules of thumb. Conversely, this approach hampers getting information about the interactions among trees and spiders (i.e., the Eltonian shortfall; Hortal et al., 2015). The opposite would occur with the single species approach. A study aiming to collect as many species as possible (i.e., a taxonomy survey) for a given locality, should be treated as equally relevant as a study focusing on getting ecological information (e.g., species interactions). As such, a purely taxonomic study should include samples taken from both approaches to maximize the number of sampled species from a given locality, as they yield different assemblages. Therefore, to choose among both approaches, it is paramount to evaluate the goals of each study.

A purely taxonomic survey should focus on choosing the most structurally complex canopy site for sampling (i.e., based on a previous selection), which is likely to reveal a higher species richness; and include samples of single tree species fogging. The absence of ecological information regarding tree-spider interactions should not be considered a significant negative result, considering the expedition goals. Conversely, a study aiming to evaluate the ecological interactions among trees and spiders (i.e., the Eltonian shortfall; Hortal et al., 2015), should focus on targeting specific tree individuals and focusing on sampling on them. However, contrarily to what is historically suggested (see Adis et al., 1998a; Erwin, 1989), maybe individuals trees with a high abundance of epiphytes, flowers or fruits should not be disregarded as preferable targets. Besides, studies focused on assessing the spider assemblage of a forested area, for conservation purposes, should not ignore its canopy fauna. Although this fauna is not easily accessible, it is highly diversified and exclusive, thus representing a significant portion of the spider fauna from the Amazon forest.

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AUTHORS’ CONTRIBUTION

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Mating behavior and parental care in the neotropical pseudoscorpion *Americhernes bethaniae* Mahnert, 1979 (Arachnida: Chernetidae)

Comportamento de acasalamento e cuidado parental no pseudoescorpião neotropical *Americhernes betaniae* Mahnert, 1979 (Arachnida: Chernetidae)

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Abstract: Pseudoscorpions reproduce indirectly, transferring a spermatophore deposited on the substrate. In Cheliferoidea, males perform an elaborate ritual involving pedipalps vibrations and a mating 'dance' before depositing the spermatophore in the presence of the female. Thus, this study investigated the reproductive behavior and parental care of the neotropical pseudoscorpion *Americhernes bethaniae*, from populations collected in the Brazilian *Cerrado*. Pseudoscorpions were collected from live tree trunks and stored in the laboratory for behavioral observations. In the case of *A. bethaniae*, courtship involved ritual vibration of the pedipalps, followed by eight distinct reproduction stages: approach, sex identification, fixation, dance, spermatophore formation, spermatophore transfer, and then either a fight or resumption of the process. Females built silk nests and produced an embryonic sac about 15 days after mating. Three days after the first ecdysis of the juveniles, the mother left the silk chamber. The male remained with the female until she sealed herself inside the silk nest, but did not contribute to the offspring care. This guarding behavior may suggest a strategy to ensure paternity.

Keywords: Spermatophore transfer. Courtship. Reproductive behavior. *Cerrado*. Pseudoscorpiones.

Resumo: Os pseudoescorpiões se reproduzem de forma indireta, por meio da transferência de espermatóforo depositado no substrato. Em Cheliferoidea, os machos realizam um elaborado ritual envolvendo vibrações dos pedipalpos e uma 'dança' de acasalamento antes de depositarem o espermatóforo na presença da fêmea. Assim, este estudo investigou o comportamento reprodutivo e o cuidado parental do pseudoescorpião neotropical *Americhernes bethaniae*, a partir de populações coletadas no Cerrado brasileiro. Os pseudoescorpiões foram coletados em troncos de árvores vivas e acondicionados em laboratório para observações comportamentais. O cortejo em *A. bethaniae* envolveu um ritual de vibração dos pedipalpos, seguido por oito estágios distintos de reprodução: aproximação, identificação de sexo, fixação, dança, formação de espermatóforo, transferência do espermatóforo e, em seguida, luta ou retomada do processo. As fêmeas construíram seus ninhos de seda e produziram uma bolsa embrionária cerca de 15 dias após o acasalamento. Três dias após a primeira ecdise dos juvenis, a mãe abandonou a câmara de seda. O macho permaneceu junto da fêmea até que ela se selasse no interior no ninho de seda, porém não contribuiu com o cuidado à prole. Este comportamento de guarda pode sugerir uma estratégia para assegurar a paternidade.

Palavras-chave: Transferência de espermatóforo. Cortejo. Comportamento reprodutivo. Cerrado. Pseudoscorpiões.

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INTRODUCTION

The order Pseudoscorpiones is one of the oldest and most diverse groups of arachnids (Shear et al., 1989; Schawaller et al., 1991; Harms & Dunlop, 2017), represented by 25 families, 474 genera, and 4,272 species (World Arachnida Catalog, 2024). Pseudoscorpions are small (2-8 mm), solitary animals that are generally aggressive upon intraspecific contact (Weygoldt, 1969; Zeh & Zeh, 1997). Despite their diversity, the biology of many species is still poorly studied (Weygoldt, 1969; Zeh & Zeh, 1997). Most studies on the behavior and natural history of pseudoscorpions have focused on the superfamily Cheliferoidea (Harvey, 1992; Zeh & Zeh, 1997).

Reproduction in the pseudoscorpions of the superfamily Cheliferoidea is characterized by an elaborate courtship display, in which the male performs a series of rituals before depositing the spermatophores (Zeh & Zeh, 1997). During the courtship phase, the male engages in a series of vibrational and pedipalpal movements, which can be described as a kind of 'dance' (Zeh, 1987; Andrade & Gnaspini, 2003). The courtship and behavior vary according to species or even between families (Weygoldt, 1969; Zeh & Zeh, 1997; Kirchmair & Raspotnig, 2021).

The Chernetidae family is very diverse, with more than 733 described species, distributed in different habitats around the world, from tropical forests to temperate regions. The reproductive behavior of the pseudoscorpions in this family is particularly interesting and complex (Zeh & Zeh, 1997; Palen-Pietri et al., 2019). Males often perform an elaborate courtship ritual that may include mating dances to attract females. During mating, the male deposits a spermatophore on the substrate, which is then collected by the female. Understanding these reproductive interactions is crucial for the conservation and study of the ecology of the Chernetidae, revealing important aspects of their biology and evolution.

Chernetidae represent a large part of the diversity of pseudoscorpions in South America. Approximately 70 species of Chernetidae are known from Brazil (World Arachnida Catalog, 2024), with the genus *Americhernes*, being widely distributed with seven species (Mahnert, 1979; Adis & Mahnert, 1985; Aguiar & Bührnheim, 1998). Of these, at least four have been documented in the Brazilian Central Amazon region, with *A. bethaniae* Mahnert, 1979 being the most abundant (Mahnert, 1979). Subsequent studies have identified this species in other regions of the Amazon (Adis & Mahnert, 1985; Aguiar & Bührnheim, 1998). Nevertheless, *A. bethaniae* is often found under the bark of living trees in the *Cerrado* region (Del-Claro & Tizo-Pedroso, 2009; Tizo-Pedroso & Del-Claro, 2014). Therefore, the aim of this study was to investigate courtship, reproduction, parental care and post-embryonic development of *A. bethaniae* under laboratory conditions.

MATERIAL AND METHODS

The *Cerrado* is the second-largest biome in Brazil, characterized by predominantly savanna vegetation with grasses, scattered shrubs, and trees adapted to poor and acidic soils. This highly diverse biome harbors numerous endemic plant and animal species, and plays a crucial role in regulating the hydrological and climatic regimes of the central region of the country (Oliveira & Marquis, 2002; Colli et al., 2020). Pseudoscorpions were collected from August to October 2017 and 2018 in two seasonal semi-deciduous forests separated by approximately 115 km (Morrinhos municipality, 17° 43' 39" S, 49° 07' 54" W, and Araras Farm, Ipameri municipality, 17° 66' 99" S, 48° 16' 13" W) in the state of Goiás, Brazil.

We searched for pseudoscorpions on live tree trunks. In each area, we searched 60 trunks (15 trunks in 2017 for each area and 15 in 2018) at a height between 30cm and 150cm from the ground. The bark of these trees was manually removed, and individuals were collected (comprising 3 tritonymphs, 29 males, 32 nonpregnant females, and 6 pregnant females) using a thin brush, which prompted the pseudoscorpions to grasp it. Captured individuals were then placed in 10 mL transparent plastic vials for transportation to the laboratory.

The pseudoscorpions were transported to the Laboratory Diversity, Behavior and Conservation of Arachnids at the State University of Goiás. Upon arrival, they were transferred to 5 cm diameter petri dishes, each containing a fragment of tree bark and a piece of moist cotton (Tizo-Pedroso & Del-Claro, 2005). These dishes were covered with red cellophane. Subsequently, the sex of each individual was determined through direct observation using a stereomicroscope.

The pseudoscorpions were individually housed in Petri dishes for a period of 20 days to ensure that the females did not produce brood sacs. Live termites (*Armitermes* sp.) were provided as food twice a week. Following this period, a randomly selected male was transferred from its original dish and introduced into the Petri dish with a resident female. Each dish was assigned a code indicating the animals' origin, collection date, and sex. In total, 18 dishes were prepared, each containing one male and one female, while 6 dishes contained only one pregnant female at the time of collection.

Observations of reproductive behaviors were conducted within one to three days after the formation of pairs in the Petri dishes, between 6 pm-9 pm. The initial step involved transferring one male from its original dish to a dish containing one female. Ten minutes after the introduction of the male, the dish was placed under a stereomicroscope for observation of the subsequent behavioral interactions. The observation of courtship and agonistic behaviors was conducted over the course of two 20-minute sessions, with a 10-minute interval between each session. This approach was employed using the sequential sampling method (Altmann, 1974; Del-Claro, 2010). Over the subsequent 30 days, the dishes were monitored every three days for behavioral changes related to reproduction, with 10 minutes of observation per day. The various developmental milestones, including the period until the formation of the brood sac, the establishment of the silk chamber, embryonic development within the sac, the hatching of protonymphs, and dispersal time, were recorded.

RESULTS

In general, we found one or two individuals of *Americhernes bethaniae* per tree. On one occasion, we found 14 individuals on the same tree in Morrinhos, but without the formation of aggregations. The individuals were scattered along the trunk.

MALE–FEMALE IDENTIFICATION AND THE BEGINNING OF COURTSHIP

The reproductive behavior of *A. bethaniae* was investigated under laboratory conditions, and this species was shown to be an easily manageable model organism. Adults survived well under laboratory conditions, with courtship behavior initiating promptly upon introducing a male to a dish containing a female. Post-manipulation, males typically begin exploring the dish in search of hiding spots, often encountering females in the process.

The male's approach to the female was cautious and deliberate. Upon detecting the female, the male paused for three to five minutes before slowly advancing toward her, extending his pedipalps with chelae open. This deliberate movement continued until the male made contact with the female or until the female exhibited aggression. Every time a male initiated a contact, it swiftly grasped one or both female pedipalps in an attempt to immobilize her or deflect her attacks (Figures 1A-1B). In cases where the male failed to restrain the female, it quickly retreated but resumed the approach shortly after, repeating the process until he successfully grasped her with his pedipalps.

Once the female was immobilized, a ritual resembling a struggle ensued, likely a test of strength. The female attempted to draw her pedipalps close to her cephalothorax, pulling the male toward her chelicerae, while he sought to retreat and find refuge in a crevice.

Given the larger size and robustness of females, they often manage to break free or release one of their pedipalps from the male's grasp. In response, the male promptly resumed control to prevent retaliation. This interaction persisted for an average of seven minutes (±2.5 SD; n = 12), ceasing only when the female inflicted injury, dragged the male into a crevice, or intimidated him with aggressive displays. Eventually, the male succeeded in engaging the female in a courtship dance, coaxing her away from the crevice by 2 to 4 cm. Subsequently, the female's aggression waned, and she remained near the male, receptive to courtship signaled by his pedipalp vibrations.

COURTSHIP AND SPERM TRANSFER

After a brief rest and pedipalp grooming lasting two to three minutes, courtship commenced. The male positioned himself approximately 2 mm from the female and initiated a series of pedipalp vibrations. No discernible pattern or variation was observed in the sequence of vibrations among different males; instead, the form and duration appeared contingent upon the female's receptiveness. At the conclusion of the pedipalp-based courtship, the female either rejected the male, retreated to her previous hiding spot, or progressed to the next stage of the reproductive process.

The subsequent stage commenced with renewed pedipalp interactions. The male again secured the female, who exhibited reduced aggression and led her aimlessly around the dish. At times, the male released one of the female pedipalps, vibrating his pedipalp in her direction, almost making contact, before reseizing it, repeating this sequence several times (Figure 1D). When he finished vibrating one of his pedipalps, the male moved away about 1 cm, vibrating both pedipalps many times. In response, the female approached him, and the two pseudoscorpions reconnected (Figure 1E). However, the male adjusted his grasp, holding one of the female's chelae with one pedipalp and the femur-tibial joint of her pedipalp with the other, as they moved across the bark fragment surface (Figure 1F). The male then deposited its spermatophore without releasing the female, engaging in a back-and-forth 'dance' until she was successfully positioned over the spermatophore (Figure 1G). Once the spermatophore was inserted into

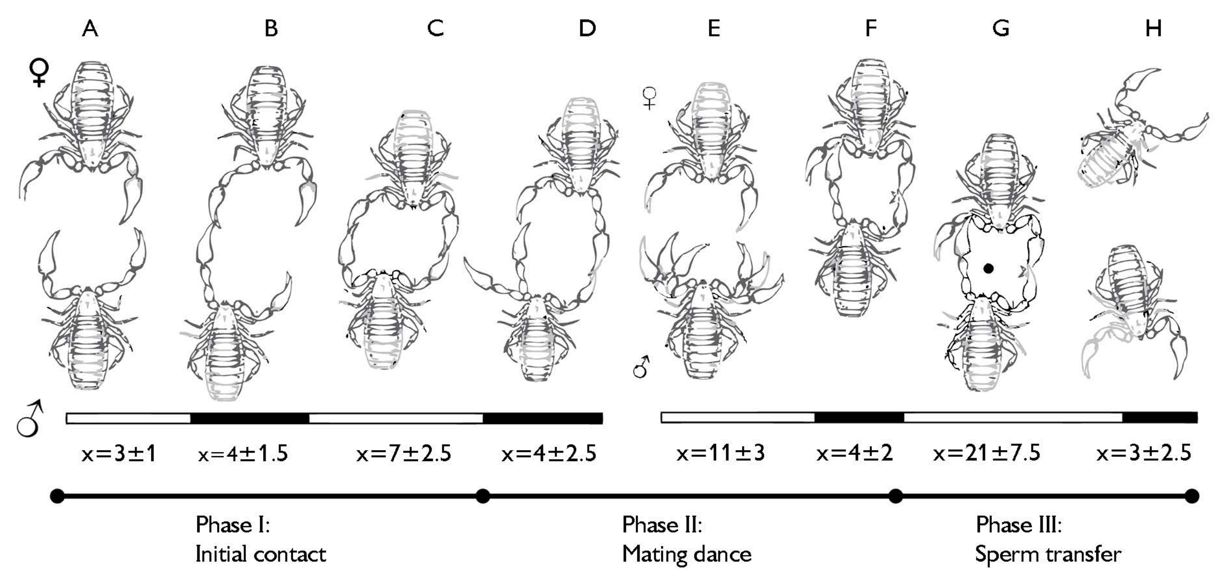

Figure 1. Stages of the courtship process in the pseudoscorpion *Americhernes bethaniae*: A) placement of the individuals and approximation; B) contact of the pedipalps and sex recognition; C) attachment, strength competition, and pushing; D) male signaling with one pedipalp; E) confirmation of female receptivity and vibration of both pedipalps; F) dance position and possible detection of the place for spermatophore deposition; G) spermatophore deposition (black dot) and sperm transfer; H) separation of the pair or fight. The lower bar indicates the average ± standard deviation time (in minutes) spent in each stage of courtship. Photos: Illustrations by the authors.

the female's genital opening, the male held her over it, presumably until she absorbed its entire sperm content. Following sperm transfer, the pair separated, either fleeing or initiating the courtship and spermatophore transfer process anew (Figure 1H). The number and specific shape of spermatophores transferred during the reproductive process were not recorded. On average, the whole mating behavior took about 57 minutes (Figure 1). The sequence of behaviors and possible modifications was organized in a flowchart (Figure 2).

CONSTRUCTION OF THE SILK CHAMBER AND POSTEMBRYONIC DEVELOPMENT

The fertilized females were left undisturbed in their dishes for further observation of reproductive behavior, postembryonic development, and maternal care. Similarly, the males were retained in the dishes, except in cases where the female exhibited aggression toward them. Approximately two weeks following sperm transfer, the females (consisting of 10 females retained in the dishes and six females collected already pregnant) commenced the construction of the silk chamber. The formation of the brood sac occurred approximately six days (±2) after the onset of construction, with the completion of silk chamber building typically taking between four and eight days (±3) (Figure 3). Upon completion, the female rested inside the chamber, providing nourishment to her embryos through a nutritive fluid until the protonymphs hatched. The embryos within the sac reached the second embryonic stage within approximately seven days (±1). The average total duration of development through the first and second embryonic stages within the brood sac was six days (±1). Protonymph hatching occurred approximately five days later (±1 day; n = 13). *Americhernes bethaniae* females exhibited relatively high fecundity, although the exact number of embryos was not accurately recorded. Following hatching, each female produced an average of 24 protonymphs (±4; n = 13).

PARENTAL CARE AND DISPERSAL

After the protonymphs hatched, the female remained in the nest, tending to clean the juveniles for three days. The protonymphs fed on the remaining nutritive fluid in the brood sac until it was fully depleted. During this time, the juveniles moved actively within the chamber, which, although relatively small for the female and the protonymphs, provided enough space for the juveniles to avoid constant contact. On the third day (±1 day) within the chamber, the female used her pedipalps and chelicerae to break the silk wall, creating a small exit hole. This event likely marked the dispersal of females, as some remained nearby, while others ventured farther from the nest, depending on the dish.

Juveniles remained inside the chamber for two more days after the female's departure before dispersing. However, they were kept in Petri dishes for observation of their development and interactions with adult females. This stage proved unsuccessful, as the juveniles constantly moved around the dish and rarely fed until exhaustion and death ensued. They seemed to actively avoid proximity to the adult(s). Only a few number of nymphs reached the second developmental stage (around three nymphs per brood), and none reached to the third stage.

No further parental care was provided after the female left the nest. Female showed no interest in the nymphs, did not touch them, did not bring prey near the nest, and did not allow the juveniles to share it prey. However, no instances of maternal cannibalism or aggressive rejection of the juveniles were observed. By the end of the observation period, it was decided to leave the females in their dishes, resulting in 50% (8 out of 16 females) producing additional broods, with one female even producing a third brood sac. The reproductive season was noted for this species, with pregnant or brood-sac-guarding females observed in *Cerrado* trees between October and April (wet season) (for 2017 and 2018). Reproduction occurred in the laboratory between

October and July. The animals were provided food and kept in Petri dishes until they reached their senility and died. This provided data on the adult lifespan of this species, with adults surviving for approximately one and a half years on average in the laboratory. Voucher specimens were deposited in the arachnid collection of the Arachnid Diversity, Behavior and Conservation Laboratory (State University of Goiás).

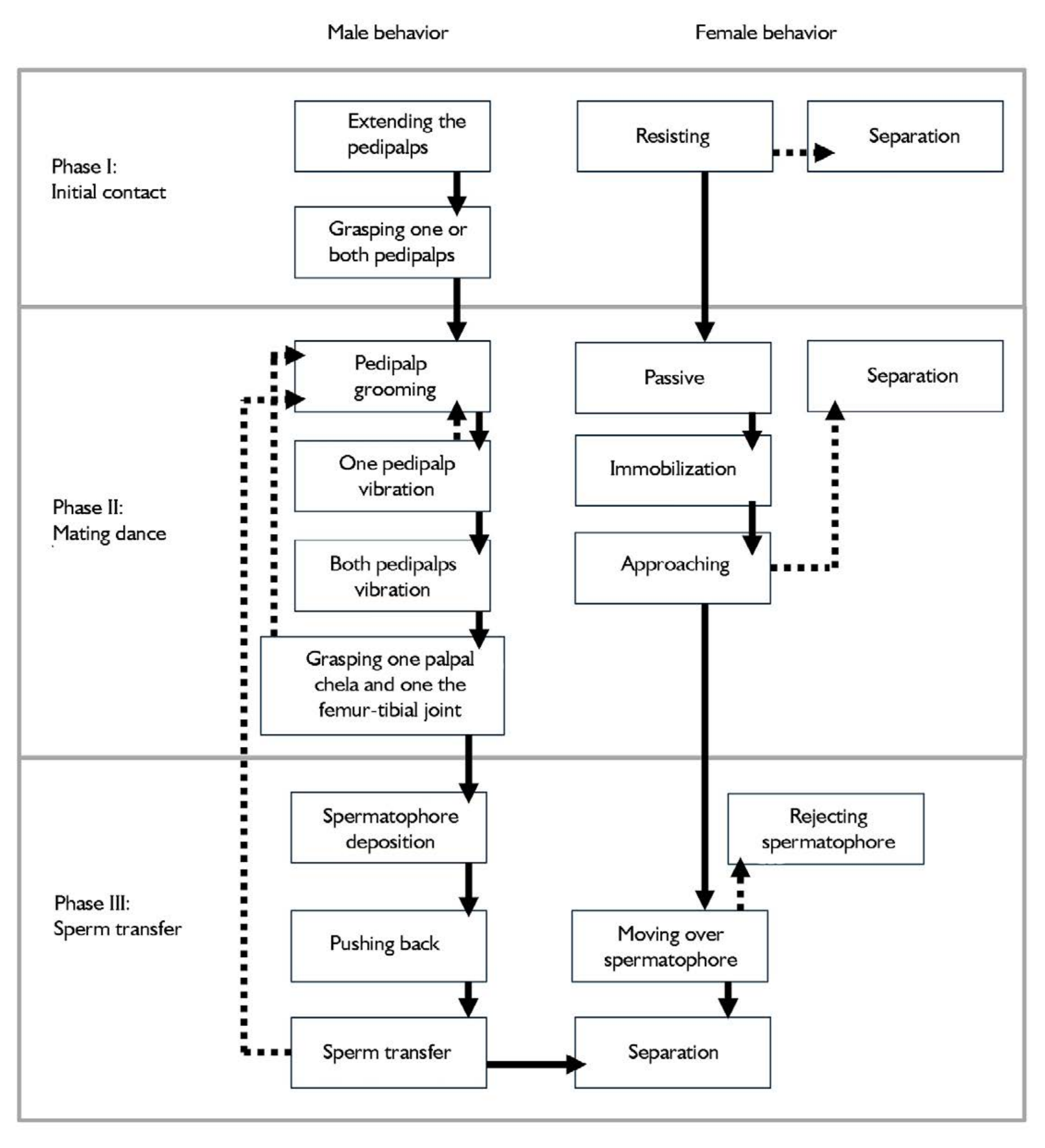

Figure 2. Sequence of behaviors during courtship and sperm transfer in *Americhernes bethaniae*. The phases indicate the three stages of transfer, the boxes indicate the behavioral types, and the lines indicate the sequences. Solid lines indicate the successful sequences in the sperm transfer process, while dotted lines indicate modifications in the sequence. The organization of the flowchart and behavioral types followed Palen-Pietri et al. (2019) and Kirchmair and Raspotnig (2021).

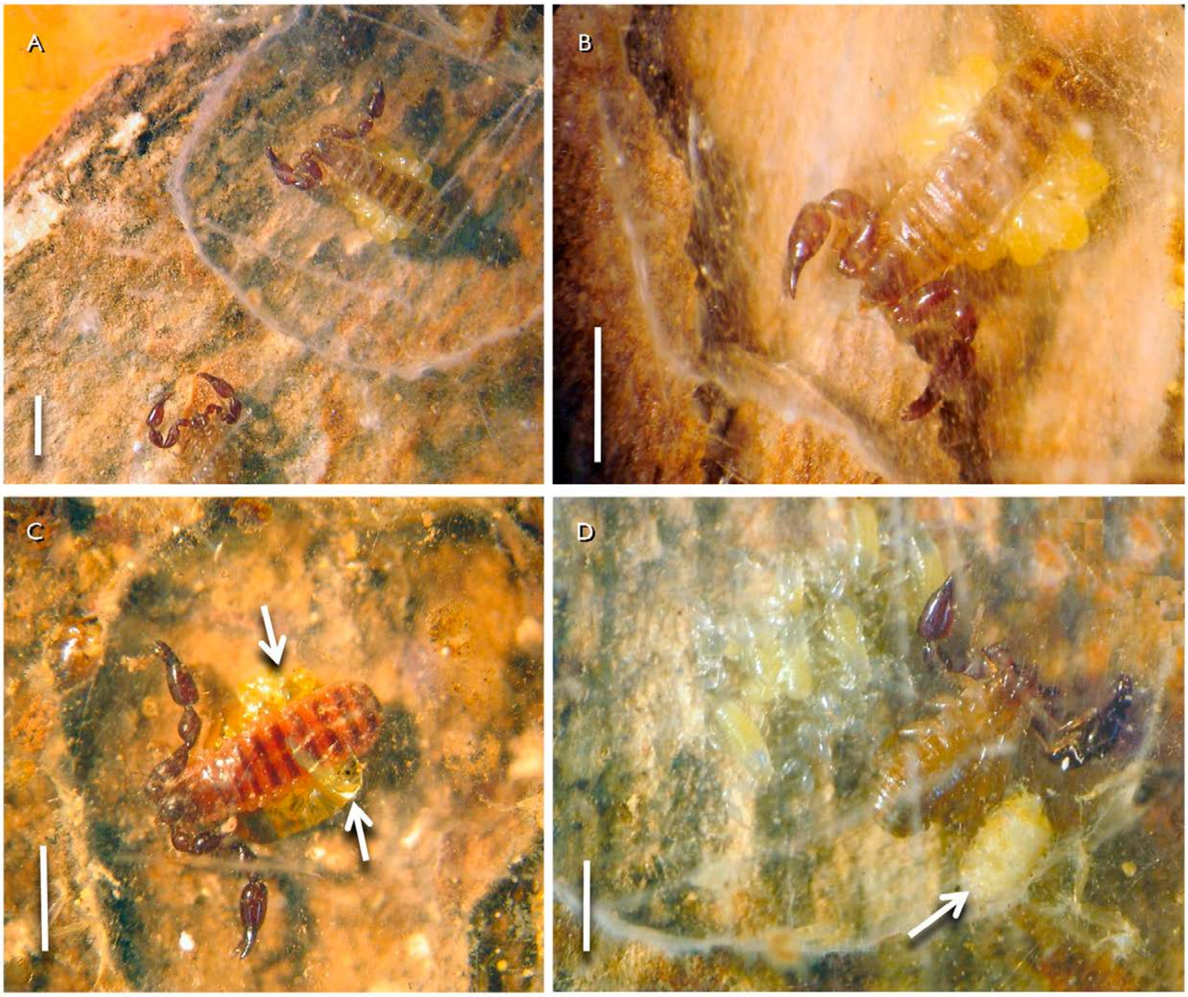

Figure 3. Females of *A. bethaniae* inside the silk chamber after sperm transfer. The images show three different females: A) female 1 resting inside the silk chamber carrying the brood sac with second-instar embryos attached to the genital opening; B) female 1 with a brood sac one day before hatching; C) female 2 inside the nest, with the arrow indicating the nutritive fluid secreted to feed the juveniles; D) female 3 inside the nest with her protonymph two days before dispersal, with the arrow indicating the remains of the brood sac after nymphal hatching and feeding. Scale bars: 1 mm.

DISCUSSION

Sex identification behaviors and female receptivity vary among pseudoscorpion species, even within the Chernetidae family. In *Americhernes bethaniae*, adults can detect and locate conspecifics at approximately 3 cm distances. The relative location between pseudoscorpions during these behaviors appears to be influenced by their movement through the substrate, although the exact distance between pseudoscorpions remains inconclusive based on the present study. Similar occasional perceptions of other individuals with minimal physical contact have been observed in other Chernetidae species (Andrade & Gnaspini, 2003) and Neobisiidae (Weygoldt, 1969). However, such identification behaviors are absent in Chthoniidae species, possibly due to their asexual reproduction (Weygoldt, 1969).

Although intersexual encounters in *A. bethaniae* are cautious and not highly aggressive, agonistic interactions have been observed in other species within the same family (Weygoldt, 1969; Zeh & Zeh, 1997). Nonetheless, non-receptive *A. bethaniae* females may attack and injure males to repel them. Instances of aggressive pedipalp vibrations and attacks by non-receptive females have also been observed in other Chernetidae species, such as *Maxchernes iporangae,* though without resulting in male fatality (Andrade & Gnaspini, 2003). The precise significance of these signaling forms during individual encounters remains unclear, but they likely signal to the other individual who is a potential reproductive partner rather than prey.

The method through which pseudoscorpions identify the sex of conspecifics remains unclear, although it may involve chemical or tactile cues. In some Chernetidae and Cheiridiidae species, males identify only females during leg or pedipalp vibrations (Weygoldt, 1969). However, certain Chernetidae species exhibit marked sexual dimorphism, such as *Dinocheirus arizonensis* (Banks, 1901) and *Cordylochernes scorpioides* (Linnaeus, 1758), where males possess more robust pedipalps than females, and sex identification occurs upon pedipalp contact or after competition from spermatophore deposition (Zeh & Zeh, 1997). In *Lustrochernes argentinus* (Thorell, 1877), females have larger pedipalps than males (Palen-Pietri et al., 2019). The observed behaviors in *A. bethaniae* suggest that sex identification occurs upon pedipalp contact. However, attachment, akin to strength competition, transpires only between individuals of different sexes and not between males. This behavior in *A. bethaniae* is distinct from that in other species, where it seems to determine female receptivity. Overall, females consistently responded covertly to male approaches and only accepted sperm transfer or attacked males post-attachment dancing, indicating that strength competition might serve as a mechanism of sexual selection preceding courtship and sperm transfer.

Courtship and spermatophore transfer behaviors vary uniquely among pseudoscorpion species, with each stage having distinct significance. In *A. bethaniae*, the reproductive process consists of eight stages: approximation, sex identification, attachment, dance, spermatophore formation, sperm transfer, and either fight or continuation. These stages differ among species, and there is no consensus on whether any patterns exist across families, although Andrade and Gnaspini (2003) reviewed the presence or absence of different stages. Attempting to identify a pattern may not be the most effective strategy for understanding these small animals; rather, it may simply underscore their individual differences. Notably, the components of pseudoscorpion reproductive behaviors are strongly influenced by environmental conditions, particularly habitat characteristics (Zeh & Zeh, 1997).

Despite the diversity in sexual behaviors among pseudoscorpion species, there are minimal variations in their nest-building behaviors and embryonic development. Pregnant *A. bethaniae* females construct a silk chamber a few days before the formation of the brood sac. Juveniles are deposited into the brood sac while the chamber is still partially built, consistent with observations in other species and families (Weygoldt, 1969). The most significant differences lie in the number of embryos produced and the timing of juvenile dispersal. For instance, species in the genus *Chthonius* C.L. Koch, 1843 (Chthoniidae) typically produce fewer than ten embryos, while *Neobisium* Chamberlin, 1930 (Neobisiidae) and *Pselaphochernes scorpioides* (Hermann, 1804) (Chernetidae) produce 15 to 25 embryos. The most notable deviation in behavior is observed in some species of the genera *Apocheiridium* Chamberlin, 1924, and *Cheiridium* Menge, 1855 (both Cheiridiidae), where chamber construction does not occur. Instead, females produce a few (3-5) large embryos and guard them until the protonymphs hatch. In Cheliferidae species, the number of embryos ranges from 20 to 40 (Weygoldt, 1969).

Minor variations are also evident among species in the juvenile dispersal stage and in maternal care. For instance, in *Chthonius tetrachelatus* (Preyssler, 1790), the nymphs disperse as deutonymphs after hatching. In contrast, in other Chthoniidae species, females wait for juveniles to hatch, consume the remains of the brood sac, and then disperse. The dispersal pattern in *A. bethaniae* mirrors that of another Chernetidae species, *Pselaphochernes scorpioides*, where the protonymphs disperse four days after the mother abandons the nest. However, in species such as *Serianus carolinensis* Muchmore, 1968, and *Atemnus politus* (Simon, 1878) (Atemnidae), the female disperses only after all the nymphs have left the chamber (Weygoldt, 1969). In these cases, maternal care is limited to the embryonic development period. However, an elaborate form of parental care is found in the family Atemnidae, where females of the social pseudoscorpion *Paratemnoides nidificator* (Balzan, 1888) provide extended care by guarding the nymphs and offering them food until they reach adulthood (Tizo-Pedroso & Del-Claro, 2007).

The findings of the present study revealed that *A. bethaniae* reproduces during the hot and rainy seasons when climatic conditions are more favorable and food is abundant. Pseudoscorpions in the superfamily Neobisioidea, associated with permanent environments such as litter, reproduce year-round. Conversely, reproductive efforts of Cheliferoidea species are concentrated in the most favorable season (Zeh & Zeh, 1997). The existence of a reproductive season is believed to be linked to species inhabiting ephemeral environments such as tree trunks, a pattern broadly applicable to Cheliferoidea pseudoscorpions (Weygoldt, 1969; Zeh & Zeh, 1997). However, in the social pseudoscorpion *P. nidificator*, seasonal reproduction is regulated by food availability and energy allocation during the dry season. Reproductive cycles may deviate from seasonal patterns when food is abundant (Tizo-Pedroso & Del-Claro, 2007). Nevertheless, in *A. bethaniae*, reproduction remains seasonal even in the presence of abundant food. Our understanding of pseudoscorpion reproduction remains fragmented, with reproductive behaviors still unknown in 11 out of 24 families (Harvey, 1992). However, understanding reproductive behavior is crucial for understanding the ecology (Zeh & Zeh, 1997) and evolution (Harvey, 1992; Proctor, 1993) of pseudoscorpions in a given environment, warranting further study within this group.

CONCLUSION

The diverse spectrum of reproductive behaviors observed among pseudoscorpion species, particularly within the Chernetidae family, underscores the complexity of reproductive strategies within this intriguing group of arachnids. Through meticulous observation and analysis, this study elucidated key aspects of sex identification, courtship rituals, and spermatophore transfer behaviors in *A. bethaniae*, shedding light on the intricacies of pseudoscorpion reproductive biology. The findings highlight the significance of environmental factors in shaping reproductive patterns and emphasize the need for further investigation into the mechanisms driving these behaviors across different taxa.

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AUTHOR'S CONTRIBUTION

T. N. Gonçalves contributed to formal analysis, data curation, investigation, and writing (original draft); A. F. S. Tizo contributed to formal analysis, data curation, investigation, and writing (original draft and edition); and E. Tizo-Pedroso contributed to acquisition of funding, conceptualization, data curation, investigation, supervision, validation, and writing (review and edition).

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Hunting the hunter: evidence of intraguild predation among bark-dwelling pseudoscorpions in the Brazilian savanna

Caçando o caçador: evidências de predação intraguilda entre pseudoescorpiões arborícolas no cerrado brasileiro

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Abstract: Intraguild predation, in which animals within the same guild prey on each other, is quite common among arachnids, especially dwelling on the ground. While pseudoscorpions can be found on the ground, tree trunks, and canopies, there is limited evidence of predation among pseudoscorpion species in their natural habitats. This study reports predatory interactions among four species of bark-dwelling pseudoscorpions in the Brazilian *Cerrado*. We observed two species of *Victorwithius* (Withiidae) (*V. similis* and *V. rufus*) opportunistically attacking and feeding on nymphs of *Paratemnoides nidificator* (Atemnidae). Additionally, *Parachernes melanopygus* (Chernetidae) acted as a social parasite, feeding on juveniles within colonies. These observations were made in six different regions of the Brazilian *Cerrado*. In all cases, *P. nidificator* was placed as the intraguild prey, while the other species acted as intraguild predators. In this system, *Paratemnoides* colonies may represent a predictable food resource for other pseudoscorpions, especially during the dry season when prey is scarce.

Keywords: Arachnida. *Cerrado* biome. Neotropical savanna. Pseudoscorpiones. Species interactions.

Resumo: Predação intraguilda é um fenômeno relativamente comum entre aracnídeos, especialmente aqueles da fauna edáfica. Pseudoescorpiões ocorrem no solo, assim como em troncos de árvores e copas, mas há poucas evidências de predação entre espécies de pseudoescorpiões no ambiente natural. Aqui, relatamos interações de predação entre quatro espécies de pseudoescorpiões arborícolas no Cerrado brasileiro. Encontramos duas espécies de *Victorwithius* (Withiidae) (*V. similis* e *V. rufus*) que atacam e se alimentam oportunisticamente de ninfas de *Paratemnoides nidificator* (Atemnidae), enquanto registramos indivíduos de *Parachernes melanopygus* (Chernetidae) agindo como parasitas sociais e se alimentando de juvenis nas colônias. Os registros foram feitos em seis regiões diferentes do Cerrado brasileiro e, em todos os casos, *P. nidificator* atuou como uma presa IG e as outras espécies como predadores IG. Neste sistema, as colônias de *Paratemnoides* podem representar um recurso alimentar mais previsível para outros pseudoescorpiões, principalmente na estação seca, quando as presas são escassas.

Palavras-chave: Arachnida. Bioma Cerrado. Savana neotropical. Pseudoescorpiões. Interações entre espécies.

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INTRODUCTION

Intraguild predation is a phenomenon in which two or more species that share similar resources also engage in predatory interactions. It is recognized for its complexity in disrupting traditional trophic hierarchies and influencing the dynamics of food webs and ecological communities (Polis et al., 1989; Holt & Polis, 1997; Arim & Marquet, 2004; Wang et al., 2019; Parimuchova et al., 2021). This intricate form of interaction is particularly evident among arachnids, which are known for their diverse predatory strategies and behavioral adaptations (Rypstra & Samu, 2005; Punzo, 2007; Houser et al., 2014; Petráková et al., 2016; Wise et al., 2023).

Arachnids represent one of the most diverse groups of terrestrial arthropods, characterized by a wide array of life strategies and feeding habits (Schausberger, 2022; Agnarsson, 2023). In this group, there are active predators like hunting spiders and scorpions, as well as more specialized species like pseudoscorpions and whip scorpions that wait for prey. The intraguild predation among these arachnids occurs in different ecological environments, from tropical forests to arid deserts, involving direct competitors and opportunistic predators (Lira et al., 2017; Hambäck et al., 2021; Silva-Júnior et al., 2021; Wise et al., 2023). To understand the dynamics of intraguild predation among arachnids, it is important to analyze factors such as competition for resources, prey selection, and the behavioral adaptations driving species interactions (Hambäck et al., 2021; Cubas-Rodríguez et al., 2024). Additionally, the influence of ecological factors on the occurrence of intraguild predation, as well as its impacts on the structure of arachnid communities and the evolution of predation strategies, represent key research issues in understanding ecological interactions (Hambäck et al., 2021; Wise et al., 2023).

Pseudoscorpions are generalist predators that live in a wide variety of habitats and feed on small insects and arachnids (Weygoldt, 1969; Harms & Dunlop, 2017; Bedoya-Roqueme & Tizo-Pedroso, 2021). Despite being one of the most diverse orders of arachnids, with over 4,200 species worldwide (World Pseudoscorpiones Catalog, 2024), the behavioral ecology of pseudoscorpions is still little known, especially in the context of Brazilian ecosystems. In Brazil, there are over 184 species of pseudoscorpions. These animals are found in all Brazilian biomes, living in environments ranging from leaf litter and canopy layers to tree trunks. Among these species, *Paratemnoides nidificator* (Balzan, 1888) is notable as one of the most widespread pseudoscorpions in Brazil. They form large colonies under tree bark and cooperate in prey capture of large arthropods (Moura et al., 2018, 2021; Ribeiro et al., 2018; Tizo-Pedroso & Del-Claro, 2018).

In the Brazilian *Cerrado* biome, several pseudoscorpion species share the same habitat, the bark of living trees, and rely on similar prey (Tizo-Pedroso & Del-Claro, 2007, 2014; Moura et al., 2018; Bedoya-Roqueme et al., 2023; Gonçalves et al., 2024; Tizo-Pedroso et al., 2024), which increases the likelihood of intraguild predation among them. Given these overlapping ecological niches, our study aims to investigate intraguild predation within this group. Specifically, we document the first observed case of intraguild predation involving pseudoscorpions in the *Cerrado*, with individuals of the genus *Victorwithius* (Feio, 1945), preying on juveniles of the social pseudoscorpion *Paratemnoides nidificator*. This study explores the ecological implications of this interaction, analyzing its potential impact on the dynamics of pseudoscorpion communities in this unique neotropical savanna.

MATERIAL AND METHODS

The data includes information from various field data collection events. Four data sets were recorded during previous years: in 2012, 2015, 2016, and 2018. These studies focused on the behavior and ecology of bark-dwelling pseudoscorpions and were conducted in different locations in the southeastern (Ribeirão Preto, São Paulo State) and central-western regions of Brazil (Abadia de Goiás, Anápolis, Caldas Novas, Morrinhos, and Piracanjuba, Goiás State). More recently, field observations of pseudoscorpion behavior in 2023 have also been included. The region is covered by the *Cerrado* biome, a tropical savannah formation, and the observations occurred within a mesophilic forest type phytophysiognomy (Figure 1).

During our observations, we saw pseudoscorpion species interacting with colonies of *Paratemnoides nidificator*. Pseudoscorpion behaviors were recorded in situ by one or two researchers simultaneously ad libitum (Altmann, 1974). Each observation lasted 20 minutes per tree. The total sampling effort for all plots was approximately 200 hours. After each observation, the pseudoscorpions were collected for identification in the laboratory, and the trees where they were found were identified. This allowed us to describe the interactions between pseudoscorpion species.

RESULTS

The observations were carried out at six different locations across three Brazilian states. Pseudoscorpions were found on four tree species. It's worth noting that the structure of the trunks varied significantly among the tree species. *Cenostigma pluviosum* (DC.) had a more complex trunk

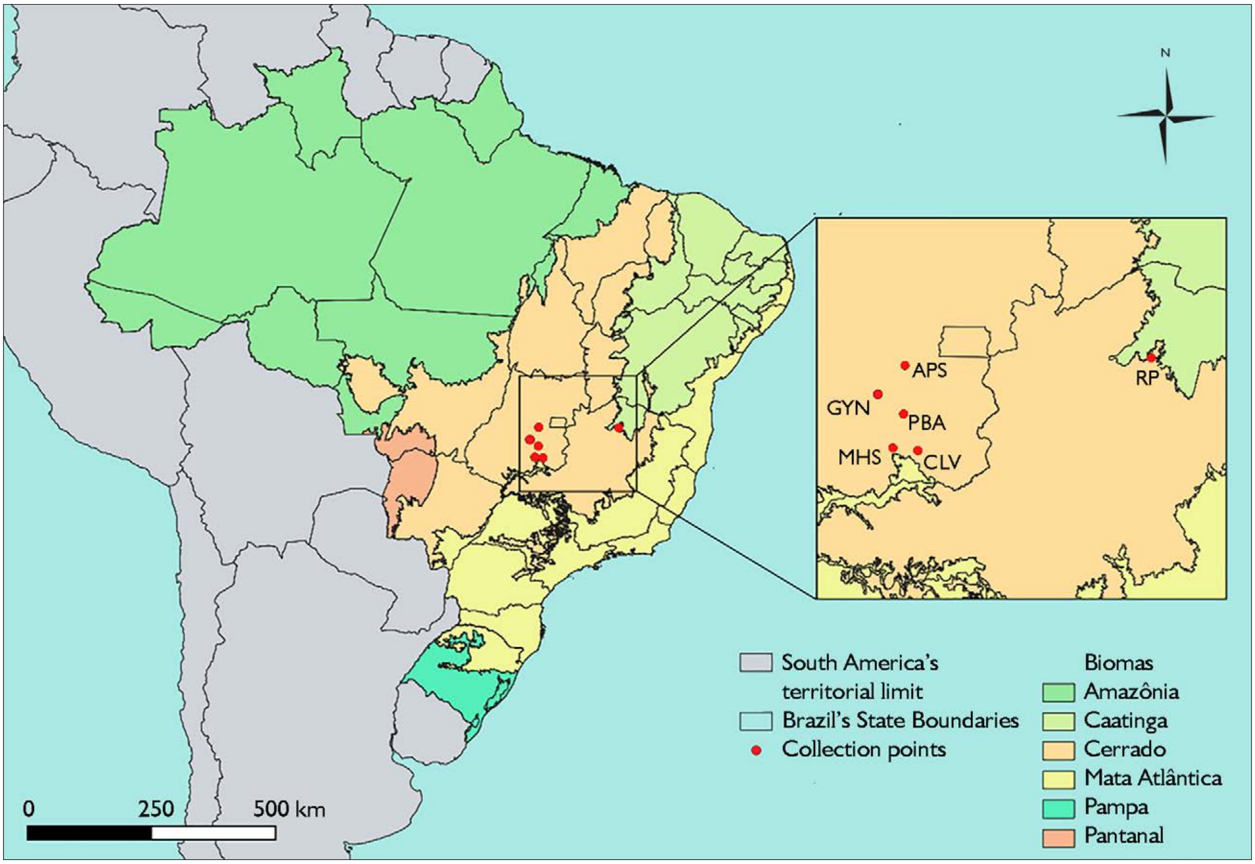

Figure 1. Map of Brazilian states and biomes. The samples were collected in the states of São Paulo, Minas Gerais and Goiás. The red dots highlight the mesophytic forest vegetation collection sites in the municipalities of Ribeirão Preto (RP) (21° 9' 54.91" S, 47° 51' 18.08" W), Anápolis (APS) (16° 18' 31.41" S, 48° 57' 19.05" W), Abadia de Goiás (GYN) (16° 45' 31.88" S, 49° 26' 11.21" W), Piracanjuba (PBA) (17° 18' 21.84" S, 49° 2' 5.19" W), Morrinhos (MHS) (17° 43' 42.14" S, 9° 7' 57.59" W) and Caldas Novas (CLV) (17° 46' 9.12" S, 48° 39' 36.99" W). Map: edited by J. S. Reis.

structure with long bark fragments. *Apuleia leiocarpa* (Vogel) J.F. Macbr and *Dipteryx alata* Vogel had intermediate structures with scale-like bark fragments well distributed along the trunk, while *Vochysia haenkeana* Mart. had a simpler, smoother trunk appearance, with scale-like bark formation near the base (Figure 2).

During the field study, we identified seven pseudoscorpion species across all six locations. In the family Atemnidae, we found colonies of *Paratemnoides nidificator*. In the family Chernetidae, we observed *Americhernes bethaniae* (Mahnert, 1979), *Pachychernes subrobustus* (Balzan, 1892), *Pachychernes baileyi* (Feio, 1945), and *Parachernes melanopygus* (Beier, 1959). Additionally, in the family Withiidae, we found *Victorwithius similis* (Beier, 1959) and *Victorwithius rufus* (Balzan, 1887). We recorded a total of 18 interaction events between pseudoscorpion species.

These observations involved *P. nidificator* colonies and at least one of three other pseudoscorpion species: *P. melanopygus*, *V. similis*, or *V. rufus*. In all instances, one of these three pseudoscorpion species was seen attacking and feeding on *P. nidificator* nymphs. *Parachernes melanopygus*, known as a social parasite, lives in *P. nidificator* colonies, using their silk chambers and preying on the nymphs, particularly during the pre-ecdysis torpor. On the other hand, *Victorwithius* species, which are solitary, do not behave in the same way. They are not found within *P. nidificator* colonies. When *Victorwithius* and *P. nidificator* coexist on the same tree, *Victorwithius* usually shelters in pieces of bark near the *Paratemnoides* colonies.

At times, adult *Victorwithius* were seen approaching *Paratemnoides* colonies. These individuals would take on a lurking posture, moving slowly with their pedipalps facing forward. Upon reaching the edge of the bark piece housing the *Paratemnoides* colony, the *Victorwithius* adult would remain motionless, with its pedipalps extended forward for several minutes. Even though *Paratemnoides* adults might approach or touch *Victorwithius*, they showed no reactions, exploratory behaviors, or agonistic responses.

Figure 2. Examples of the structure of the trunks of the trees sampled in this study: A) *Cenostigma pluviosum*; B) *Apuleia leiocarpa*; C) *Dipteryx alata*; D) and *Vochysia haenkeana*. Photos: by J. S. Reis (2024).

* * *

When *Paratemnoides* touched *Victorwithius*, the latter remained still with its pedipalps extended. It only started capturing the *Paratemnoides* nymph when approached, swiftly grabbing and dragging it away from the colony. After killing the nymph, *Victorwithius* assumed a defensive posture and began feeding. Sometimes, *Victorwithius* attacked multiple *Paratemnoides* nymphs, feeding on one and leaving the others even after killing them.

Despite *Paratemnoides* adults defending their colonies against predators, such as being aggressive towards conspecifics from other colonies, we did not observe *Paratemnoides* adults attacking or repelling *Victorwithius*. Later, in the laboratory, we confirmed that two species of *Victorwithius*, *V. rufus* and *V. similis*, preyed on *P. nidificator* nymphs (Figure 3). After confirming *Victorwithius* predation in the field, we photographed and collected the pseudoscorpions (Figure 4). We also collected *Paratemnoides* colonies to analyze their structure and composition in the laboratory, aiming to determine whether the colonies had sufficient numbers of adults for defense and whether *Victorwithius* targeted small or large colonies. The detailed information about *P. nidificator* colonies, the species involved in predation interactions, host trees, localities, and year of observation can be found in Table 1.

Figure 3. Pseudoscorpion species in the intraguild predation system in the Brazilian *Cerrado*: A) a female of *Paratemnoides nidificator*; B) a female of *Parachernes melanopygus*; C) a male of *Victorwithius rufus*; D) a male of *Victorwithius similis*. Scale bars = 1 mm.

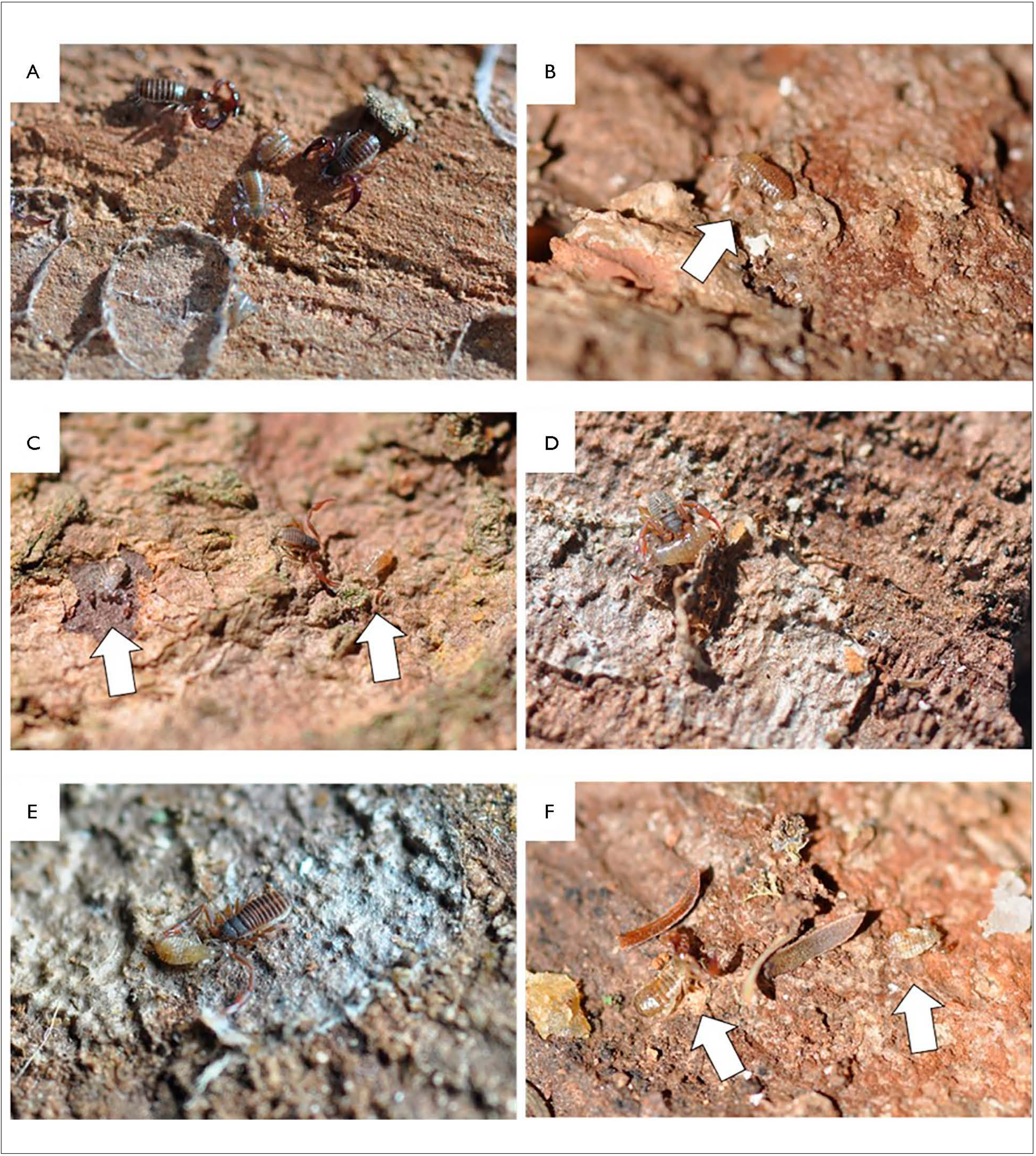

Figure 4. Relationships among pseudoscorpions in the Brazilian savannah: A) a small colony of *Paratemnoides nidificator*, with its silk chambers, and constituted in the image with two adults and two nymphs; B) a deutonymph of *Paratemnoides* moving away from the silk chambers; C) an adult of *Victorwithius rufus* after killing a tritonymph and deutonymph of *P. nidificator*; D) an adult of *V. rufus* feeding on a deutonymph of *P. nidificator*; E) an adult of *V. similis* feeding on a *P. nidificator* deutonymph; F) an exoskeleton of a deutonymph of *P. nidificator* discarded after an adult of *V. similis* had completed feeding.

◆

Table 1. Composition of *Paratemnoides nidificator* colonies and cases of predation by other pseudoscorpions species.

Colony composition	Predator	Tree species	Year	Season	Location
7 adults, 18 nymphs	*Parachernes melanopygus*, 3 adults	*Cenostigma pluviosum*	2016	Dry	Morrinhos, Goiás
3 adults, 8 nymphs	*Parachernes melanopygus*, 2 adults; 3 nymphs	*Cenostigma pluviosum*	2018	Dry	Anápolis, Goiás
5 adults, 7 nymphs	*Parachernes melanopygus*, 2 adults; 2 nymphs	*Cenostigma pluviosum*	2018	Dry	Caldas Novas, Goiás
4 adults, 3 nymphs	*Victorwithius similis*, 1 male	*Cenostigma pluviosum*	2015	Wet	Caldas Novas, Goiás
12 adults, 15 nymphs	*Victorwithius similis*, 1 nymph	*Cenostigma pluviosum*	2012	Dry	Ribeirão Preto, Minas Gerais
13 adults, 28 nymphs	*Victorwithius similis*, 1 female; *Victorwithius rufus*, 1 nymph	*Dipteryx alata*	2023	Wet	Piracanjuba, Goiás
5 adults, 23 nymphs	*Victorwithius rufus,* 1 male	*Dipteryx alata*	2023	Wet	Piracanjuba, Goiás
8 adults, 34 nymphs	*Victorwithius similis*, 1 female	*Dipteryx alata*	2023	Wet	Piracanjuba, Goiás
17 adults, 52 nymphs	*Victorwithius similis,* 1 nymph	*Dipteryx alata*	2023	Wet	Piracanjuba, Goiás
16 adults, 47 nymphs	*Victorwithius similis,* 2 males	*Dipteryx alata*	2023	Wet	Piracanjuba, Goiás
2 adults, 15 nymphs	*Victorwithius rufus,* 1 male	*Dipteryx alata*	2023	Wet	Piracanjuba, Goiás
1 adult, 4 nymphs	*Victorwithius similis,* 2 males	*Apuleia leiocarpa*	2023	Wet	Piracanjuba, Goiás
12 adults, 27 nymphs	*Victorwithius rufus,* 1 male	*Apuleia leiocarpa*	2023	Wet	Piracanjuba, Goiás
11 adults, 28 nymphs	*Victorwithius rufus,* 1 female	*Apuleia leiocarpa*	2023	Wet	Piracanjuba, Goiás
3 adults, 25 nymphs	*Victorwithius rufus,* 1 male	*Dipteryx alata*	2023	Wet	Piracanjuba, Goiás
3 adults, 4 nymphs	*Victorwithius rufus,* 1 nymph	*Vochysia haenkeana*	2024	Wet	Abadia de Goiás, Goiás
7 adults, 23 nymphs	*Victorwithius rufus,* 1 nymph, 1 male	*Dipteryx alata*	2024	Wet	Abadia de Goiás, Goiás
1 adult, 22 nymphs	*Victorwithius similis,* 1 male	*Vochysia haenkeana*	2024	Wet	Abadia de Goiás, Goiás

DISCUSSION

Intraguild predation is quite common among arachnids, especially in ground spiders and scorpions. However, evidence of such predation among pseudoscorpions in natural environments is limited. Pseudoscorpions are cryptic animals found in various biomes worldwide, often living in leaf litter, tree bark, or the canopy. Their small size makes it difficult to observe their behavior in the field (Del-Claro & Tizo-Pedroso, 2009; Bedoya-Roqueme & Tizo-Pedroso, 2021; Bedoya-Roqueme et al., 2023). Hence, intraguild predation may be more common among pseudoscorpions than is currently known, especially given their high diversity and tendency to co-occur and compete for similar prey.

Paratemnoides nidificator is a social pseudoscorpion species found throughout South America. Colonies of this species can be quite large, sometimes numbering in the hundreds (Tizo-Pedroso & Del-Claro, 2005, 2007). These pseudoscorpions capture cooperatively various arthropods living in trees, such as ants, beetles, bugs, and spiders. Their prey can range in size from a few millimeters to 4 or 5 cm (Moura et al., 2018, 2021; Ribeiro et al., 2018; Tizo-Pedroso & Del-Claro, 2018). Solitary pseudoscorpions, on the other hand, depend mainly on small prey (< 2 mm). So, considering that *Paratemnoides* colonies demand a high amount of food, mainly because of the numerous nymphs, in this system there must be marked competition for small prey, especially during the dry season, when food is scarcer.

Alternatively, the high abundance and year-round presence of *P. nidificator* colonies suggests that they may serve as a consistent and predictable food source (Figure 5) (Tizo-Pedroso & Del-Claro, 2007; Garcia et al., 2016; Moura et al., 2018; Ribeiro et al., 2018; Bedoya-Roqueme & Tizo-Pedroso, 2023). Therefore, *Victorwithius* species may take advantage of these colonies opportunistically due to their predictable availability. This predictability of resources is especially beneficial during the dry season, when the population of other arthropods tends to be low, potentially improving the survival prospects for *Victorwithius*.

In this system, there are seven pseudoscorpion species present. We found no evidence of predation by the *Americhernes* and *Pachychernes* species. However, we observed multiple instances where adult *Americhernes bethaniae* individuals were captured and killed by *P. nidificator* when they approached their colonies. Although *Paratemnoides* did not prey on *Americhernes*, they still ended up being killed and expelled from the colony. Interestingly, we did not see adult *Paratemnoides*

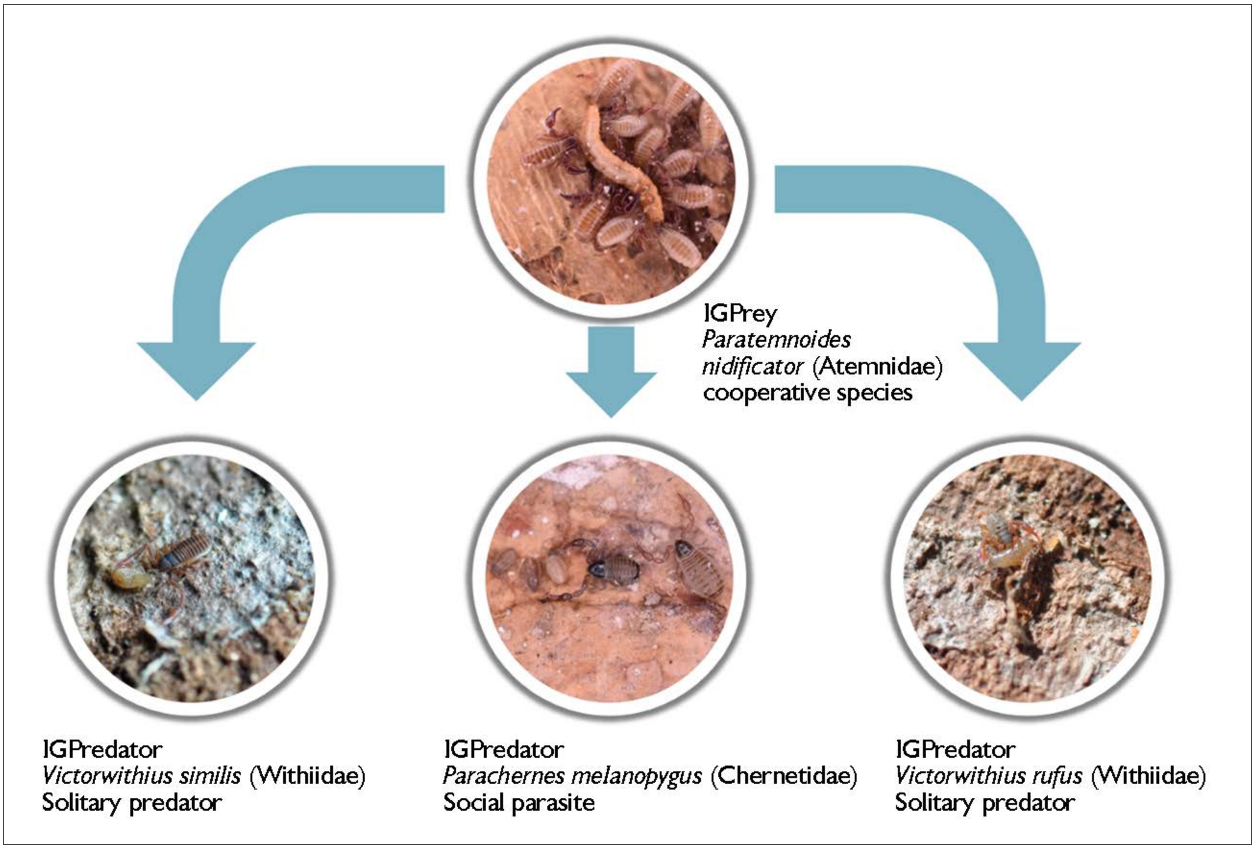

Figure 5. Schematic description of the relationship of intraguild predation among pseudoscorpions in the Brazilian savannah. In this system, *Paratemnoides nidificator* acts as an Intraguild Prey (IG Prey), serving as food for three other species of pseudoscorpions, which act as Intraguild Predators in the system, *Victorwithius similis* and *V. rufus*, both generalist solitary predators and probably opportunistic consumers of *Paratemnoides nidificator*, while *Parachernes melanopygus* adopts a life strategy as a social parasite, being a specialized predator.

repelling *Victorwithius*. *Victorwithius* species were found in smaller colonies with fewer adults, which may make them less likely to be detected. On the other hand, the *Parachernes melanopygus*, a known social parasite, can disguise itself chemically and invade colonies without being noticed (Tizo-Pedroso & Del-Claro, 2014). The lack of aggression between *Paratemnoides* and *Victorwithius* seems notable and warrants further investigation.

The fact that intraguild predation among pseudoscorpions has been observed in areas hundreds of kilometers apart suggests that this behavior isn't isolated and may occur across different pseudoscorpion populations. Understanding these intraguild relationships is fundamental for advancing our knowledge of the life history, behavior and ecology of pseudoscorpions, especially in regions like the Brazilian savanna.

CONCLUSION

In the Brazilian *Cerrado*, intraguild predation among pseudoscorpions involves social species as prey and two solitary species as predators. It seems that competition for the same food resource is not the main driver of this behavior. The abundance and predictability of *Paratemnoides* colonies as a food source for other predators may lead to opportunistic interactions between pseudoscorpion species. This behavior appears to be relatively common among pseudoscorpion populations due to the wide geographic distribution of these species.

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AUTHOR'S CONTRIBUTION

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Updated geographical distribution of the family Barychelidae Simon, 1889 from Brazil (Araneae: Mygalomorphae)

Distribuição geográfica atualizada da família Barychelidae Simon, 1889 do Brasil (Araneae: Mygalomorphae)

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Abstract: Spiders of the family Barychelidae, the sister group to Theraphosidae, are mainly concentrated in the Southern Hemisphere. In the Neotropical region, Barychelidae is represented by five genera found in Brazil, Colombia, Cuba, Ecuador, Panama, Peru and Venezuela. Barychelid spiders are known for their sedentary behavior, spending most of their lives in burrows constructed with a hinged trapdoor made of silk and soil. This habit and the difficulty in identifying and locating their camouflaged burrows, poses challenges to obtaining specimens thereby obscuring the group's true diversity. Examination of numerous specimens from different zoological collections allowed us to expand the distribution of Barychelidae spiders adding 95 new records. In addition to geographic data from colleted material, we were able to find 56 iNaturalist observations of barychelid spiders, with 29 in unpublished locations, totaling 124 new records in Brazil. Overall, the expanded geographical distribution of Barychelidae spiders in Brazil has revealed remarkable diversity, with numerous species covering a variety of habitats. This distribution mapping can provide valuable information for the study of populations variation and evolutionary relationships and help in the biogeographical research of the family Barychelidae.

Keywords: Citizen science. New records. Neotropical region. Trapdoor spiders. Theraphosidae. iNaturalist.

Resumo: As aranhas da família Barychelidae, grupo irmão de Theraphosidae, estão principalmente concentradas no Hemisfério Sul. Na região neotropical, Barychelidae é representada por cinco gêneros encontrados em Brasil, Colômbia, Cuba, Equador, Panamá, Peru e Venezuela. Aranhas Barychelidae são conhecidas pelo seu hábito sedentário, passando a maior parte de suas vidas em tocas construídas com um alçapão articulado, feito de seda e solo. Este hábito e a dificuldade de identificar e localizar suas tocas camufladas representam desafios na obtenção de espécimes, mascarando a real diversidade do grupo. O exame de vários espécies de diferentes coleções zoológicas nos permitiu expandir a distribuição geográfica de aranhas Barychelidae, acrescentando 95 novos registros. Adicionalmente aos dados geográficos de material de coleta, foi possível identificar 56 observações de aranhas Barychelidae no iNaturalist, 29 delas para locais não publicados, totalizando 124 novos registros no Brasil. Em geral, a distribuição geográfica expandida de Barychelidae no Brasil revelou uma notável diversidade, com inúmeras espécies cobrindo uma variedade de habitats. Este mapeamento da distribuição pode fornecer valiosas informações para o estudo da variação populacional e relações evolutivas, além de auxiliar em pesquisas biogeográficas da família Barychelidae.

Palavras-chave: Ciência cidadã. Novos registros. Região neotropical. Aranha-de-alçapão. Theraphosidae. iNaturalist.

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INTRODUCTION

The family Barychelidae, commonly known as brush-footed trapdoor spiders, is phylogenetically related to the family Theraphosidae Thorell, 1869 as its sister group (Hedin & Bond, 2006; Bond et al., 2012; Wheeler et al., 2017; Opatova et al., 2020). It consists of two subfamilies, Barychelinae and Sasoninae, including 39 genera and 285 species (World Spider Catalog, 2024). Barychelid spiders can be distinguished by having a short and domed apical segment of posterior spinnerets, the absence of a third claw, well-developed claw tufts on all tarsi, the presence of scopula on metatarsi and tarsi I and II, a few clavate trichobothria grouped for only half the length of the tarsus, and a small anterior lobe of the maxillae (Raven, 1985, 1994; Guadanucci, 2012; Mori & Bertani, 2020).

Barychelidae displays typical Gondwanan distribution with the current highest species richness found in Oceania and the Pacific, followed by the African continent, the Neotropical region, India, Sri Lanka, Socotra Island, and Hawaii (Raven, 1994). In the Neotropical region, Barychelidae is represented by five genera found in countries such as Brazil, Colombia, Cuba, Ecuador, Panama, Peru, and Venezuela (World Spider Catalog, 2024). Among these countries, Brazil hosts five known genera: *Cosmopelma* Simon, 1889, *Idiophthalma* Pickard-Cambridge, 1877, *Neodiplothele* Mello-Leitão, 1917, *Paracenobiopelma* Feio, 1952, and *Strophaues* Ausserer, 1875. Currently, among the 27 Brazilian federative units (26 states + Distrito Federal), the Barychelidae family was registered for 16 of them: Amazonas, Bahia, Ceará, Espírito Santo, Goiás, Minas Gerais, Mato Grosso do Sul, Paraíba, Pernambuco, Piauí, Rio de Janeiro, Rio Grande do Norte, Santa Catarina, Sergipe, São Paulo, and Tocantins (Pickard-Cambridge, 1896; Gonzalez-Filho et al., 2015; Mori & Bertani, 2016, 2020).

These spiders construct burrows with silk and soil trapdoors, which can be highly camouflaged, often making them difficult to detect even at close proximity (Raven, 1994). These burrows can be constructed in various microhabitats, such as ravines, litter attached to the underside of logs, rocks, or leaves (most genera), attached to a tree, within rolling logs, or built into a shallow depression in the tree with abutting doors lush with bark surface (Raven, 1994).

Recently, new tools have emerged to offer researchers the opportunity to access an additional information, such as localities of difficult or restricted accessibility (Mesaglio & Callaghan, 2021). Citizen science is one of the main tools for disseminating possibly relevant data for scientific research and can be defined as a research technique that involves the voluntary and conscious participation of citizens in conjunction with professional researchers. iNaturalist (n. d.) is a tool that exemplifies the power of community-driven collaboration. This free-access platform is designed to facilitate the sharing of a multitude of organisms, accessible through both a dedicated website and a mobile application (Mesaglio & Callaghan, 2021). This online platform serves as a powerful tool for scientific research, offering an additional pathway to acquire essential locality data. It provides researchers with a valuable platform to engage in collaborative species identification, facilitating a collective effort to enhance our understanding of biodiversity (Rosa et al., 2022; Forti & Szabo, 2023).

Given the limited information on distribution records of barychelids spiders, this study contributes to an updated scenario regarding the geographic distribution of Barychelidae in Brazil. We obtained a total of 124 unpublished localities using two data sources: zoological collections, with 95 new records, and the iNaturalist platform, with 29 new records.

MATERIAL AND METHODS

Geographic coordinates were obtained through information on the original museum labels. Localities from museum samples without coordinates were georeferenced using Google Earth®. The geographic distribution of the specimens was created using SimpleMappr (Shorthouse, 2010). Data from the iNaturalist platform was initially sorted by selecting all records of Infraorder Mygalomorphae taxa for Brazil, excluding duplicates from the research base. After that, all specimens identified as belonging to Barychelidae were selected and thoroughly reviewed by the authors. In addition to the general appearance of the body, the following criteria were used to identify a specimen of photographic record as Barychelidae: the presence of claw tufts, density and distribution of the scopula, shape of the eye group and pattern of spots and stripes on legs, carapace and abdomen. Each record was organized with all information available in each observation, in the following order: state, city, specific location, coordinates, data of the observation, citizen science, and the link of the observation.

Institutional abbreviations (curators in parentheses). The material examined is deposited in the following collections: CAD = Coleção Aracnológica Diamantina, São Paulo, Brazil (J. P. L. Guadanucci); IBSP = Instituto Butantan, São Paulo, Brazil (A. D. Brescovit); MACN = Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina (M. J. Ramirez); MNRJ = Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brazil (A. B. Kury); MPEG = Museu Paraense Emílio Goeldi, Belém, Brazil (A. B. Bonaldo); MZUSP = Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (R. Pinto-da-Rocha); UFMG = Universidade Federal de Minas Gerais, Belo Horizonte, Brazil (A. J. Santos).

RESULTS

Despite all the challenges to study and identify the neotropical barychelid spiders, combining the two types of sampling, the newly registered locations of Brazilian barychelids add up to 124 unpublished locations summarized in two maps (Figure 1). Through an analysis of 7 zoological collections, we added up 95 new records, among them, Barychelidae was recorded for the first time for seven Brazilian federal units: Alagoas, Distrito Federal, Goiás, Mato Grosso, Maranhão, Pará and Rondônia (Figure 1A, circles). We conducted an extensive search on the platform iNaturalist, in which we filtered and analyzed images of all Mygalomorphae specimens from Brazil, resulting in 56 observations of barychelid spiders, disregarding duplicate records, among these records, 29 are in new locations (Figure 1A, blue star). Additionally, as the vast majority of the new points belong to the genus *Neodiplothele*, the new records have been indicated at species level, or the lowest taxonomic level possible (Figure 1B). The points indicated as '*Neodiplothele* spp.' represent specimens whose specific identification was not possible or taxa that do not belong to any described species of the genus.

Class Arachnida Lamark, 1801
Order Araneae Clerck, 1757
Infraorder Mygalomorphae Pocock, 1892
Family Barychelidae Simon, 1889

Barychelidae Simon, 1889: 192; Raven 1985: 111

Diagnosis. Barychelidae differs from Theraphosidae by the short apical segment of the posterior lateral spinnerets, weakly produced anterior lobe of the maxillae, and a few clavate trichobothria grouped for only half the length of the tarsus (Raven, 1985, 1994; Guadanucci, 2012; Mori & Bertani, 2020).

Distribution. Brazil: Pará, Amazonas, Maranhão, Piauí, Ceará, Rio Grande do Norte, Tocantins, Paraíba, Pernambuco, Alagoas, Sergipe, Bahia, Mato Grosso, Rondônia, Goiás, Brasília, Distrito Federal, Minas Gerais, Espírito Santo, Mato Grosso do Sul, Rio de Janeiro, São Paulo, Paraná and Santa Catarina (Figure 1).

New records. Brazil: <u>Pará</u>: APA de Aramanaí, Belterra, 2° 42' 44.8" S, 54° 59' 56.2" W, 28.IV-06.V.2010, Equipe Butantan leg., 1♂= (IBSP217236); Alter do Chão, Santarém, 2° 31' 40.4" S, 54° 56' 58.2" W, 1.XI.2014, A. Coronato, D. Chirivi, J. Cabra & C. Sampaio leg., 1♀ (IBSP220066); Moju, 2° 10' 45.6" S, 48° 48' 06.1" W, Ochoa leg., 1♀ (MPEG38759); Barcarena, 1° 30' 13.7" S, 48° 36' 52.5" W, A.B. Bonaldo leg., 1♀ (MPEG38757); Belém, 1° 26' 36.7" S, 48° 26' 43.2" W, 14.VI.1966,

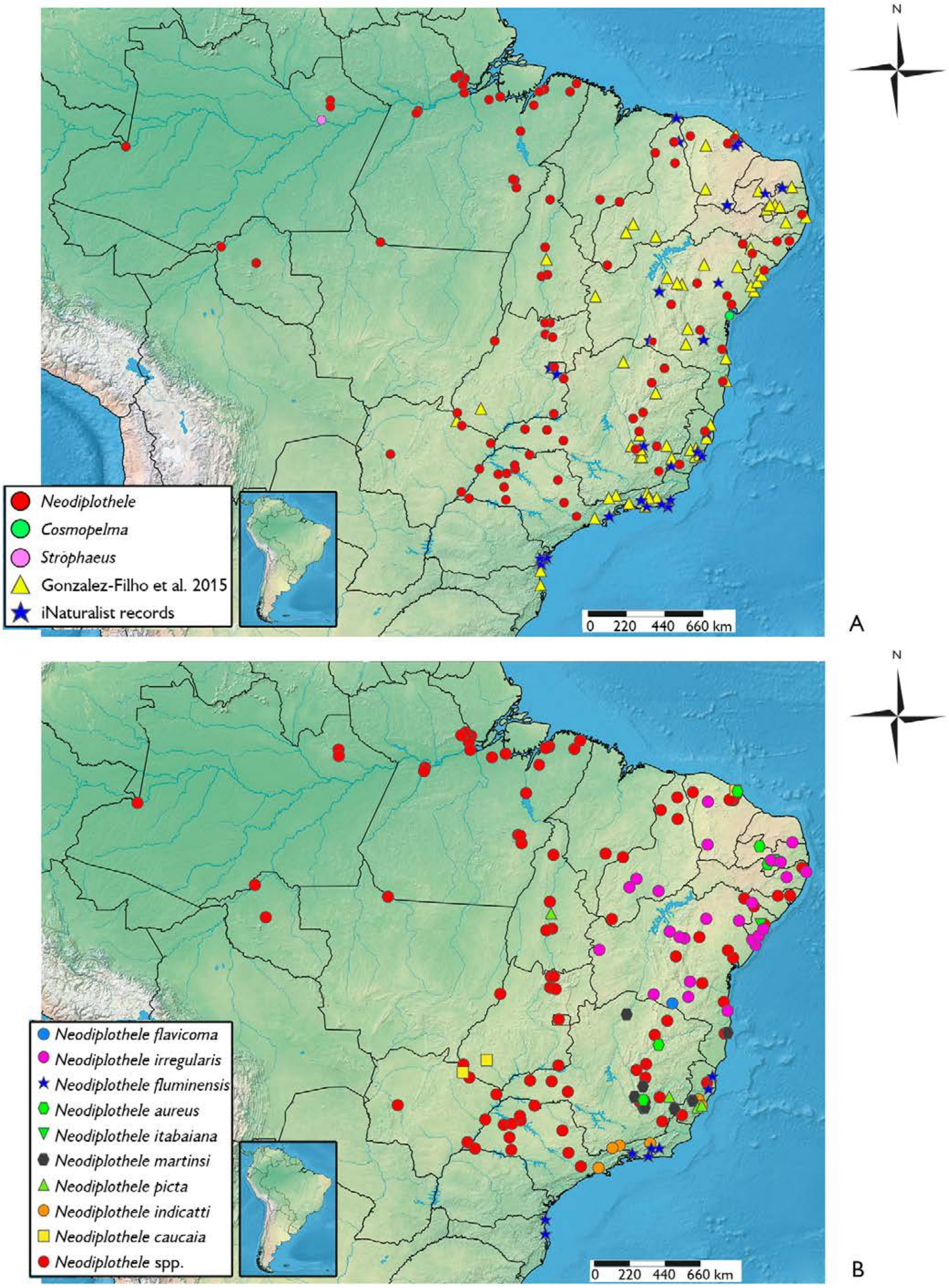

Figure 1. Distribution maps of Barychelidae from Brazil. A). Circles represent new records for Barychelidae from museum data, triangles show previous records, and stars indicate iNaturalist platform. B). Distribution map of *Neodiplothele* from Brazil, colored shapes correspond to specific *Neodiplothele* species. Map: elaborated by the authors (2024).

1♀ (MACN34705); FLONA Carajás, Canaã dos Carajás, 6° 29’ 49.0” S, 49° 52’ 40.0” W, 22-28.IX.2010, R. Andrade & I. Cizauskas et al. leg., 1♀ (IBSP175394); Bragança, 1° 06’ 44.3” S, 46° 48’ 14.2” W, 12.VII.2008, R. Reis leg., 1♂ (MPEG38756); Portel, 1° 59’ 28” S, 51° 25’ 48” W, 23.V.2006, G. Maschio leg., 1♂ (MPEG038750); Estação Científica Ferreira Penna, Floresta Nacional de Caxiunã, Melgaço, 1° 48’ 30.9” S, 50° 42’ 54.6” W, 09-11.IV.2002, J.A.P. Barreiros leg., 1♂ (MPEG210); Patauateua, Ourém, 1° 33’ 02.3” S, 47° 06’ 27.6” W; D. Guimarães leg., 1♀ (MPEG4638); Parque Ambiental de Belém, Mocambo, Belém, 1° 24’ 47.2” S, 48° 25’ 59.2” W, 9.II.1977, P. Waldir leg., 1♀ (MPEG5078); Reserva do Pacanari, Monte Dourado, Almeirim, 0° 51’ 55.1” S, 52° 31’ 43.3” W, 05.XII.2002, 1♀ (MPEG195); Jari, Almeirim, 0° 42’ 33.0” S, 52° 46’ 57.0” W, 22.VI.2005, T. Gardner & M.A. Ribeiro Junior leg., 1♂ (MPEG7462); same collection data as for preceding, 1° 11’ 28.0” S, 52° 38’ 51.0” W, 7.III.2005, T. Gardner leg., 1♂ (MPEG7457); 0° 41’ 25.0” S, 52° 49’ 09.0” W, 11.II.2005, same collector data as for preceeding, 1♂ (MPEG7594); 1° 36’ 14.0” S, 52° 34’ 02.0” W; 28.VIII-03.IX.2004, same collector data as for preceeding, 1♂ (MPEG7465); 0° 50’ 09.0” S, 53° 02’ 49.0” W, 28.VIII-03.IX.2004, same collector data as for preceeding, 1♂ (MPEG7463); Projeto Serra Leste, Curionópolis, 6° 05’ 37.5” S, 49° 57’ 29.6” W, 2010, R. Zampaulo leg., 1♀ (CAD1333); Ilha de Germoplasma, Usina Hidrelétrica de Tucuruí, Tucuruí, 3° 52’ 08.8” S, 49° 38’ 33.3” W, 12.VII.2008, D. Candiani leg., 1♂ (MPEG38760); Floresta Nacional de Carajás, Parauapebas, 6° 03’ 55.8” S, 50° 03’ 33.9” W, 2010, R. Zampaulo leg., 1♀ (CAD1336); Floresta Nacional de Carajás, Parauapebas, 6° 03’ 51.1” S, 50° 03’ 26.6” W, 2007-2009, Equipe Carste leg., 1♀ (IBSP213441); Amazonas: Ilha Furo de Santa Luzia, UHE de Balbina, Presidente Figueiredo, 1° 44’ 07.0” S, 59° 26’ 29.0” W, 22-24.VI.2016, D. Stork-Tonon leg., 1♂ (IBSP305067); Ilha Beco do Catitu, UHE de Balbina, Presidente Figueiredo, 01° 15’ 04” S, 59° 42’ 27” W, 22-24.VI.2016, D. Stork-Tonon leg., 1♂ (IBSP305069); Benjamin Constant, 4° 22’ 58.0” S, 70° 01’ 51.0” W, 2014, P.S. Pompeu et al. leg., 1♂ (IBSP209863); Reserva Ducke, Manaus, 3° 00’ 09.0” S, 59° 56’ 34.5” W, 19.IV.1991, H. Mesquita leg., 1♀ (MACN22599); Maranhão: Campo Mamão, São Raimundo das Mangabeiras, 07° 02’ 17” S, 45° 28’ 26.7” W, 24.VII.2023, A.Galleti-Lima, R.P. Indicatti, B. Gambaré & J.P.L. Guadanucci leg., 1♀ (CAD1439); Piauí: Estrada Bar do Bode, Corrente, 10° 28’ 30.4” S, 45° 08’ 35.9” W, 20.VII.2023, A. Galleti-Lima, R.P. Indicatti, B. Gambaré & J.P.L. Guadanucci leg., juvenile (CAD1450); Fazenda União, Topo da Chapada, Uruçui, 7° 13’ 44.0” S, 44° 33’ 21.0” W, 21-26.X.2007, F.M. Oliveira-Neto leg., 5♂ (MPEG11658); Parque Nacional de Sete Cidades, Piracuruca, 4° 5’ 55.4” S, 41° 42’ 32.2” W, 17.IX.2005, W. A. Rocha leg., 1♂ (MPEG38743); Fazenda Nazareth, José de Freitas, 4° 45’ 23” S, 42° 34’ 32” W, 1♀ (MPEG38729); Fazenda Bonito, ECB Rochas Ornamentais LTDA, Castelo do Piauí, 5° 13’ 49.0” S, 41° 41’ 28.0” W, 07.XII.2005, F.M. Oliveira-Neto leg., 1♂ (MPEG2333); Ceará: Pacatuba, 3° 57’ 07.1” S, 38° 36’ 57.7” W, 03.I.2021, M.U.A. Lima leg., 1♂ (CAD1143); Comunidade Diamante, Redenção, 04° 14’ 23.2” S, 38° 45’ 55.4” W, 27.III.2021, R. Azevedo & K. Falcão leg., 1♀ (CAD1321); Sítio São Luis, Pacoti, 04° 13’ 45.5” S, 38° 53’ 27.9” W, 27.II.2021, same collector as proceeding, 1♀ (CAD1324); Distrito Pernambuquinho, Pico Alto, Terras do Sr. Marcelo Cocão, Guaramiranga, 04° 12’ 50.9” S, 38° 57’ 59” W, 19.IX.2020, same collector as proceeding, 1♀ (CAD1325); Parque Nacional de Ubajara, Ubajara, 3° 49’ 30.7” S, 40° 53’ 35.0” W, 08.X.2022, T. Valença leg., 1♀ (CAD1338); Tocantins: Matinha Paredão de Pedra UFNT, Araguaiana, 07° 06’ 26.4” S, 48° 12’ 31.2” W, 28.VII.2023, A.Galleti-Lima, R.P. Indicatti, B. Gambaré & J.P.L. Guadanucci leg., juvenile (CAD1451); U.H.E. Luis Eduardo Magalhães, Porto Nacional, 10° 58’ 56.7” S, 48° 16’ 37.0” W, 20.II.2003, I. Knysak, R. Martins & G. Puorto leg., 1 juvenile (IBSP110439); Brejinho de Nazaré, 11° 04’ 00.0” S, 48° 34’ 50.3” W, 14-23.II.2003, I. Knysak, R. Martins & G. Puorto leg., 2♀, 4 juvenile (IBSP110434); Miracema do Tocantins, 9° 34' 02.5" S, 48° 23' 44.0" W, 18-25-IV.2002, I. Knysak, R. Martins & G. Puorto leg., 1♀ (IBSP111275); Pernambuco: Campo de Instrução Marechal Newton Cavalcante (CIMNC), Araçoiaba, 07° 46' 55" S, 35° 09' 02" W, 2009-2010, A. Costa leg., 2♂ (IBSP285459 and IBSP285474); Alagoas: Reserva Biológica de Pedra Talhada, Quebrangulo, 09° 15' 30.91" S, 36° 25' 49.20" W, 26-27.IV.2022, M.D.F. Magalhães, P.H. Martins & H.M.O. Gonzalez-Filho leg., 1♂ (CAD1299); ESEC Murici, Murici, 9° 14' 39.1" S, 35° 47' 25.7" W, 29.IV.2022, M.D.F. Magalhães, P.H. Martins & H.M.O. Gonzalez-Filho leg., 1♂ (CAD1300); Sergipe: Poço Redondo, 09° 48' 21" S, 37° 41' 06" W, 2009, F.F.A. Gomes leg., 1♂ (IBSP226803); FAFEN, Laranjeiras, 10° 46' 06" S, 37° 07' 44.8" W, 2010, J.O. Dantas leg., 1♂ (IBSP245623); Bahia: Chapada Diamantina, Seabra, 12° 26' 25" S, 41° 46' 45" W, IV-V.2016, H.J. Souza leg., 1♂ (IBSP225401); Serra de São José, Feira de Santana, 12° 06' 56.6" S, 39° 03' 09.1" W, 2009-2010, G.S.C. Ferreira leg., 12♂, 1♀ (IBSP251512-IBSP251524); Serra de Monte Alto, Palmas de Monte Alto, 14° 25' 38.8" S, 42° 56' 52.3" W, 2009, A. Pimental & I. Soares leg., 1♀ (IBSP232232); Itabuna, 14° 49' 36.8" S, 39° 16' 04.1" W, Cepec-Ceplac leg., 1♀ (IBSP220111); Jaguaripe, 13° 06' 48.4" S, 38° 53' 34.5" W, 2014, C.M.P. Leite leg., 1 juvenile (IBSP220109); Monumento Nacional Canions do Subaé, Santo Amaro, 12° 30' 41.4" S, 38° 46' 39.7" W, 05.III.2022, M.D.F. Magalhães, A. Galleti-Lima & P.H. Martins leg., 1♀ (CAD1286); Rio das Contas, 13° 50' 30.7" S, 40° 24' 00.9" W, 21.I.2021, F.J.S. Cunha, M.J.A. Morales & R. Vergílio leg., 1♀ (CAD1287); Parque Nacional do Pau Brasil, Porto Seguro, 16° 29' 10.43" S, 39° 13' 33.22" W, 24-28.III.2022, H.M.O. Gonzalez-Filho, W.J Moeller & R.P. Indicatti leg., 1♀ (CAD1296); Parque Estadual Sete Passagens, Miguel Calmon, 11° 25' 30.1" S, 40° 32' 56.3" W, 6-12.I.2018, V.E.O. Rodrigues leg., 1♂ (IBSP249669); Ilha do Urubu, Paulo Afonso, 9° 23' 33.3" S, 38° 11' 50.6" W, 2008, E. Daniele leg., 1♂, (IBSP125014); Mato Grosso: Fazenda Globo, Cocalinho, 14° 23' 57.6" S, 50° 59' 50.4" W, IX.1997, M. Celleffo leg., 1♀ (IBSP111277); Rio Teles Pires, alto Tapajós, 9° 18' 10.8" S, 56° 53' 26.0" W, VIII.1950, 1♀ (MNRJ06809); Rondônia: Mutum 7 (amostra M7P2A2), Porto Velho, 9° 34' 16" S, 65° 03' 18" W, 17.XI.2011, R.P. Indicatti leg., 1♀ (MZSP44316); Monte Negro, 10° 22' 57.0" S, 63° 18' 09.2" W, 17.XII.2013, P.H. Martins leg., 1♀ (UFMG17237); Distrito Federal: Brasília, 15° 44' 23.5" S, 47° 55' 38.3" W, III-IV.2000, D. Brianc leg., 1♂, 1 juvenile (IBSP111281); Goiás: Estrada Igrejinha, Colinas do Sul, 14° 08' 60.0" S, 48° 05' 25.9" W, 02.VIII.2023, A. Galleti-Lima, R.P. Indicatti, B. Gambaré & J.P.L. Guadanucci leg., 1♀ (CAD1452); mata preservada nos arredores de Cana Brava, Cana Brava, 13° 29' 26" S, 48° 20' 59.3" W, 01.VIII.2023, A. Galleti-Lima, R.P. Indicatti & J.P.L. Guadanucci leg., 1♂ (CAD1438); estrada para propriedade do Luiz de Abreu, Minaçu, 13° 29' 33.6" S, 48° 11' 05.2" W, 31.VII.2023, A. Galleti-Lima, R.P. Indicatti, B. Gambaré & J.P.L. Guadanucci leg., juvenile (CAD1437); Parque Nacional das Emas, Mineiros, 18° 06' 23.0" S, 52° 55' 40.0" W, II.1999, C. Nogueira & P. Vardujo leg., 1♀ (IBSP111526); Serra da Mesa, 14° 03' 39.0" S, 48° 22' 57.7" W, 18-21.III.1996, Silvestre, Brandão & Yamamoto leg., 1 juvenile (MZSP18991); Catalão, 18° 09' 24.8" S, 47° 56' 43.8" W, 30.I.2023, 1♂ (CAD1275); Minas Gerais: Rampa de Vôo, Pirapanema, Muriaé, 21° 05' 30.6" S, 42° 30' 05.3" W, 07.III.2017, C.A.R. Souza leg., 1♀, 1 juvenile (IBSP282836); Mina do Serro/Cave AAS02, Serro, 18° 36' 24.9" S, 43° 23' 08.5" W, VI.2014, L. Silva leg., 1♀ (IBSP189798); Serra do Gandaerla/Cave GAND-95, Rio Acima, 20° 03' 55" S, 43° 40' 11" W, 10.II-20.III.2014, Equipe Carste et al. leg., 1♀ (IBSP202681); Zelandia, Santa Juliana, 19° 32' 12.0" S, 47° 27' 10.0" W, 16-21.VIII.2010, F. Natali leg., 1♂ (UFMG9534); Taiobeiras, 15° 48' 40.9" S, 42° 14' 08.6" W, 08-17.IV.2002, Equipe Biota leg., 1♂ (IBSP113160); Uberlândia, 18° 59' 29.5" S, 48° 18' 02.8" W, V-VIII.1996, D. Cunha leg., 1♂ (IBSP111279); Fronteira, 20° 16' 04.0" S, 49° 11' 56.0" W, 18.II.1983, J.H. Vieira leg., 1♀ (IBSP111283); Vale das Cancelas, Grão Mogol, 16° 33' 28.5" S, 42° 53' 30.8" W, X.2011, D.R. Pedroso

leg., 1♂ (MNRJ04412); Reserva Particular do Patrimônio Natural Morro Gavião, Dionísio, 19° 49' 41.0" S, 42° 38' 03.3" W, X-XI.2005, J.C.R. Fontenelle leg., 1♂ (UFMG21269); Fazenda Requijão, Gouveia, 18° 23' 48.54" S, 43° 51' 9.06" W, 15.II.2012, P.H. Martins leg., 1♀ (UFMG20077); Parque Estadual do Rio Preto, São Gonçalo do Rio Preto, 18° 05' 09.7" S, 43° 20' 26.5" W, 12.I.2012, J.P.L. Guadanucci leg., 1♀ (CAD573); Ituiutaba, 18° 56' 49.6" S, 49° 25' 56.7" W, 1♀ (CAD1302); Espírito Santo: PEAMA - Polo de Educação Ambiental da Mata Atlântica/Ifes - *Campus* de Alegre, Alegre, 20° 45' 46.4" S, 41° 27' 45.0" W, 12.XII.2021, A. Michelotto leg., 1♂ (CAD1290-1291); REBIO Sooretama, Sooretama, 19° 03' 17.75" S, 40° 08' 50.94" W, 18-23.III.2022, H.M.O. Gonzalez-Filho, W.J Moeller & R.P. Indicatti leg., 1♀ (CAD1295); Mato Grosso do Sul: Fazenda São Roque, Chapadão do Sul, 18° 47' 42.5" S, 52° 37' 05.5" W, X.2007, C. Pritsch leg., 1♂ (IBSP115381); Horto Barra do Moeda, Três Lagoas, 20° 59' 40.3" S, 51° 47' 11.7" W, 16.V.2009, M. Uehara-Prado leg., 1♂ (UFMG5876); UHE Porto Primavera, Anaurilândia, 22° 11' 16.0" S, 52° 43' 04.0" W, XII.1998, I. Knysak & R. Martins leg., 1♂ (IBSP110310); Agachi, Miranda, 20° 14' 27.0" S, 56° 22' 43.0" W, 2♀, 1 juvenile (IBSP102968); Fazenda Ponta Nova, Paranaíba, 19° 40' 29.3" S, 51° 11' 54.4" W, 16.IV.2004, Equipe Jauru leg., 1♀ (IBSP113762); São Paulo: Santa Bárbara do Oeste, 22° 44' 14.1" S, 47° 25' 13.3" W, 16.X.1995, G.C. Garcia leg., 1♂ (IBSP111284); Planalto Paulista, São Paulo, 21° 02' 18.5" S, 49° 55' 34.1" W, VIII.2007, Donizeti leg., 5♂ (IBSP114313); Macaubal, 20° 48' 33.9" S, 49° 57' 50.2" W, VIII.2007, Donizeti leg., 1♂ (IBSP114308); Estação Ecológica de Jataí, Luís Antônio, 21° 34' 13.9" S, 47° 44' 09.2" W, 12-18.IV.2010, A. G. Cristovão leg., 3♂ (IBSP165158); Tupã, 21° 56' 06.0" S, 50° 30' 50.0" W, V.2007, G.R.S. Ruiz leg., 1♀ (IBSP115318); Parque Estadual do Jaraguá, São Paulo, 23° 27' 33.0" S, 46° 46' 02.0" W, 28.IX.1969, O. Franchlich leg., 1 juvenile (IBSP108831); Bento de Abreu, 21° 16' 15.0" S, 50° 48' 43.0" W, 25.IV.1969, R. Moreira leg., 2♀ (IBSP103919); Rua dos Fundos, Araçatuba, 21° 13' 19.5" S, 50° 22' 59.8" W, 23-24.XI.2019, A. Galleti-Lima & R.P. Indicatti leg., 1♂ (CAD1231); Trilha do Morro do Diabo, Teodoro Sampaio, 22° 30' 58.0" S, 2° 19' 20.0" W, 9-16.II.2021, A. Galleti-Lima, R.P. Indicatti & J.P.L. Guadanucci leg., 1♀ (CAD1306); Estação Ecológica de Assis, Assis, 22° 35' 18.9" S, 50° 25' 15.9" W, VII.2008-V.2009, F.T.S. Morimoto leg., 1♀ (IBSP220873).

iNaturalist new records. Piauí: Brasileira, Piripiri, 4° 06' 53.3" S, 41° 29' 47.6" W, 23.IV.2023, L. Serafim 1♀ (<https://www.inaturalist.org/observations/163394392>); Parnaíba, 2° 53' 25.3" S, 41° 43' 59.5" W, 18.II.2018, J. Martins, 1♀ (<https://www.inaturalist.org/observations/71699270>); Ceará: São José, Abaiara, 7° 23' 00.6" S, 38° 59' 53.3" W, 14.III.2022, G. Augusto, 1♀ (<https://www.inaturalist.org/observations/151119266>); Monte Alegre, Pacatuba, 3° 57' 29.8" S, 38° 37' 51.7" W, 12.VII.2017, C. Moura Neto, 1♀ (<https://www.inaturalist.org/observations/66987539>); Jubaia, 4° 02' 58.4" S, 38° 42' 46.6" W, 19.VIII.2023, Carlos, 1♀ (<https://www.inaturalist.org/observations/179270271>); Paraíba: Cutié, Sítio Olho d'Água da Bica, 6° 29' 42.5" S, 36° 09' 32.7" W, 25.IV.2023, P. Couto, 1♀ (<https://www.inaturalist.org/observations/163715250>); UFCG *Campus*, Cuité, 6° 29' 39.3" S, 36° 09' 32.4" W, 04.IV.2023, P. Couto, 1♀ (<https://www.inaturalist.org/observations/153512651>); Junco do Seridó, 6° 58' 03.6" S, 36° 46' 52.4" W, 06.XI.2023, P. Santos, 1♀ (<https://www.inaturalist.org/observations/190593604>); Bahia: Guanambi, Mutãs, 14° 21' 26.7" S, 42° 59' 43.9" W, 03.I.2023, F. Ronan, 1♀ (<https://www.inaturalist.org/observations/145793336>); Ipupiara, 11° 49' 47.1" S, 42° 30' 13.0" W, 23.XI.2022, F. Amorim, 1♀ (<https://www.inaturalist.org/observations/142764658>); Boa Nova, 14° 20' 03.2" S; 40° 12' 55.3" W, 07.XII.2021, S. Sampaio, 1♀ (<https://www.inaturalist.org/observations/102684199>); Pereira, Santaluz, 11° 20' 55.7" S, 39° 39' 47.4" W, 14.IV.2023, T. Santos, 1♀ (<https://www.inaturalist.org/observations/200452758>); Distrito Federal:

Ceilândia, 15° 46’ 18.9” S, 48° 07’ 55.0” W, 08.VI.2023, J.D.M. de Paiva, juvenile (<https://www.inaturalist.org/observations/166289724>); Goiás: Cidade Ocidental, 16° 06’ 43.3” S, 47° 46’ 24.6” W, 05.XII.2020, M. Barroso, 1♀ (<https://www.inaturalist.org/observations/66267949>); Minas Gerais: Caeté, 19° 51’ 52.0” S, 43° 44’ 00.1” W, 14.VII.2016, J.D.M. de Paiva, 1♀ (<https://www.inaturalist.org/observations/85522591>); Espírito Santo: Santa Leopoldina, 20° 06’ 32.4” S, 40° 31’ 55.4” W, 30.III.2023, L. Felipe Teixeira, 1♀ (<https://www.inaturalist.org/observations/153072767>); Reserva Biológica de Sooretama, Sooretama, 19° 09’ 05.0” S, 40° 04’ 14.9” W, 28.XII.2017, M.S. Ferreira, 1♂ (<https://www.inaturalist.org/observations/66621437>); Convento da Penha, Vila Velha, 20° 19’ 47.5” S, 40° 17’ 14.0” W, 10.I.2022, F. Mendes, 1♀ (<https://www.inaturalist.org/observations/104734343>); Rio de Janeiro: Parque Natural Municipal de Nova Iguaçu, Nova Iguaçu, 22° 46’ 44.6” S, 43° 27’ 23.9” W, 13.VII.2023, R. Depes, juvenile (<https://www.inaturalist.org/observations/172744936>); Arraial do Cabo, 22° 56’ 32.9” S, 42° 03’ 25.7” W, 17.VII.2019, A.S. Michelotto, 1♀ (<https://www.inaturalist.org/observations/29031385>); Tinguá, Nova Iguaçu, 22° 36’ 12.7” S, 43° 26’ 08.5” W, 15.X.2016, D. Luiz, 1♀ (< https://www.inaturalist.org/observations/30214282>); Cabo Frio, 22° 53’ 16.1” S, 42° 01’ 33.9” W, 08.I.2017, D. Luiz, 1♂ (<https://www.inaturalist.org/observations/31156713>); Angra dos Reis, 23° 07’ 20.4” S, 44° 12’ 49.5” W, 05.VII.2021, Uriel, 1♀ (<https://www.inaturalist.org/observations/86221897>); Natividade, 20° 58’ 24.9” S, 41° 55’ 00.3” W, 08.X.2023, R. Danilo, 1♀ (<https://www.inaturalist.org/observations/188650320>); São Paulo: Ubatuba, 23° 26’ 01.7” S, 45° 05’ 09.5” W, 28.XII.2010, C. Moura Neto, 1♀ (<https://www.inaturalist.org/observations/67056153>); Paraná: Ilha do Mel, Paranaguá, 25° 33’ 56.9” S, 48° 18’ 52.3” W, 26.XII.2021, A. Aguiar, 1♂, (<https://www.inaturalist.org/observations/103714198>); Pontal do Paraná, 25° 36’ 52.0” S, 48° 28’ 03.0” W, 26.XII.2010, Antônio, 1♂ (<https://www.inaturalist.org/observations/69624612>); Guaratuba, 25° 53’ 24.8” S, 48° 35’ 14.0” W, 24.X.2021, H. de Oliveira Bonato, 1♂ (<https://www.inaturalist.org/observations/99212306>); Ilha dos Valadares, Paranaguá, 25° 32’ 17.5” S, 48° 30’ 31.7” W, 31.VIII.2023, R. Danilo, 1♂ (<https://www.inaturalist.org/observations/196423301>).

DISCUSSION

Barychelid spiders are known for their behavior of constructing burrows with a hinged trapdoor made of silk and soil or other materials. These burrows are cylindrical, lined internally with silk, closed with circular trapdoors that are thin, malleable, made of silk and aggregated materials such as soil, leaves and branches (Figures 2-3). Many species have burrows with two openings on opposite sides, each with its own trapdoor (Figures 3B, 3H). Live specimens of Barychelidae found in Brazil can generally be recognized by their small size, a coloration pattern ranging from a darker brown to an orange-brown pattern, with a light band of bristles on the central part of the cephalothorax, striped legs, and a pattern of spots on the abdomen (Figures 4-7).

The sedentary habit and the difficulty in identifying and locating the burrows, arising from the camouflage of the trapdoors, hinder the obtaining of materials, masking the real diversity of the group in Brazil and in the Neotropical region (Figures 2-3). Therefore, in view of this special difficulty and scarcity of studies, phylogenetic analyses and taxonomic reviews are necessary to understand the evolutionary history of the group in the Neotropics. Furthermore, there remains a substantial amount of knowledge yet to be gained regarding their taxonomy, ecology, and distribution. Barychelidae exhibits significantly greater diversity in the Pacific region compared to other areas worldwide, due to the extensive review of this family in Australia and Western Pacific (Raven, 1994). According to Mori and Bertani (2016), neotropical barychelids are one of the most neglected groups, as many genera have never been revised and for many groups only the original descriptions are available.

Figure 2. Collection site of barychelid spiders: A) Parque Nacional do Itatiaia, Itamonte, Minas Gerais; B) Araçatuba, São Paulo; C-D) Circle showing the camouflaged burrow: Catalão, Goiás (C); Parque Nacional do Itatiaia, Itamonte, Minas Gerais (D); E-F) *Neodiplothele indicattii* (IBSP165132) from Parque Nacional da Serra dos Órgãos, Teresópolis, Rio de Janeiro: Arrow indicates the burrow (E); Specimens lurking (F); Arrow indicates closed trapdoors from Araçatuba, São Paulo (G-H). Photo credits: Rafael P. Indicatti (2011-2013) (A, D-F); Arthur Galleti Lima (2019) (B, G-H); José Paulo L. Guadanucci (2010) (C).

Figure 3. Collection site of barychelid spiders: A-B) Specimen from Paranapiacaba, Santo André, São Paulo: Circle indicates the trapdoors closed (A); Burrows with the two doors opened (B); C-D) Specimen from Estação Ecológica Mata de Acauã, Leme do Prado, Minas Gerais: Circle indicates the burrow (C); Burrow with the door open (D); E-H) Specimen from Parque Nacional da Serra dos Órgãos, Teresópolis, Rio de Janeiro: Circle indicates the trapdoors closed (E); Burrow with the door opened (F); Arrows indicate the burrows (G); Burrows with the two doors closed (H). Photo credits: Rafael P. Indicatti (2023, 2010-2011) (A-B, E-H); Pedro H. Martins (2013) (C-D).

Figure 4. Live specimens, dorsal habitus. A) *Neodiplothele aureus* (female) from Monumento Nacional Canions do Subaé, Santo Amaro, Bahia; B) *Neodiplothele irregularis* (female) from Parque Nacional da Serra da Capivara, São Raimundo Nonato, Piauí; C) *Neodiplothele irregularis* (female) from Monumento Nacional Canions do Subaé, Santo Amaro, Bahia; D) *Neodiplothele* sp. (male) from Reserva Biológica de Una, Una, Bahia; E) *Neodiplothele caucaia* (male) from Pacatuba, Ceará; F) *Neodiplothele* sp. (female) from Trilha do Morro do Diabo, Teodoro Sampaio, São Paulo; G-H) *Neodiplothele itabaiana* (female and male) from Parque Nacional da Serra de Itabaiana, Areia Branca, Sergipe. Photo credits: Wolf J Moeller (2022-2023) (A-F); Pedro H. Martins (2023) (G); Hector M. O. Gonzalez Filho (2022) (H).

Figure 5. Live specimens, dorsal habitus. A) *Neodiplothele* aff. *picta* (male) from PEAMA - Polo de Educação Ambiental da Mata Atlântica/ Ifes - *Campus* de Alegre, Alegre; B) *Neodiplothele fluminensis* (male) from Parque Nacional Serra dos Órgãos, Teresópolis, Rio de Janeiro; C) *Neodiplothele* sp. (female) from Parque Nacional da Serra da Capivara, Coronel José Dias, Piauí; D) Female from Catalão, Goiás; E) *Neodiplothele aureus* (female) from Leme do Prado, Minas Gerais; F) *Neodiplothele* sp. (female) from Belém, Pará; G) *Neodiplothele martinsi* (male) from Alto Caparaó, Minas Gerais; H) *Neodiplothele* sp. (female) from Parque Nacional da Serra dos Órgãos, Teresópolis, Rio de Janeiro. Photo credits: Alexandre S. Michelotto (2021) (A); Rafael P. Indicatti (2010) (B, H); Leonardo S. Carvalho (2013) (C); José Paulo L. Guadanucci (2012) (D); Pedro H. Martins (2013-2023) (E, G); Igor Cizauskas (2016) (F).

Figure 6. Live specimens, dorsal habitus. A) *Neodiplothele* sp. (juvenile) from Parque Nacional do Pau Brasil, Porto Seguro, Bahia; B) *Neodiplothele* sp.; C) *Neodiplothele* sp. (female) from Tupã, São Paulo; D) *Neodiplothele* sp. (male) from Parque Natural Municipal Professor João Vasconcelos Sobrinho - Serra dos Cavalos, Caruaru, Pernambuco; E-F) *Neodiplothele* sp. (juvenile and male) from Reserva Biológica de Pedra Talhada, Quebrangulo; G) *Neodiplothele* sp. (female) from Parque Nacional Serra do Cipó, Santana do Riacho, Minas Gerais; H) *Neodiplothele* sp. (female) from Estação de Preservação e Desenvolvimento de Peti, São Gonçalo do Rio Abaixo, Minas Gerais. Photo credits: Wolf J Moeller (2022) (A); Rafael P. Indicatti (2010) (B-C); Pedro H. Martins (2023) (D-H).

Figure 7. Live specimens, dorsal habitus. A) *Neodiplothele martinsi* (female) from Gouveia, Minas Gerais; B) *Neodiplothele indicattii* (female) from Parque Nacional do Itatiaia, Itamonte, Minas Gerais; C-D) *Neodiplothele* sp. (male and female) from Estação de Preservação e Desenvolvimento de Peti, São Gonçalo do Rio Abaixo, Minas Gerais; E-F) *Neodiplothele martinsi* (female and male) from Estação Ecológica Mata de Acauã, Leme do Prado, Minas Gerais; G) *Neodiplothele* sp. (female) from Mutum, Porto Velho, Rondônia; H) *Neodiplothele* aff. *indicattii* (male) from Paranapiacaba, Santo André, São Paulo. Photo credits: Pedro H. Martins (2012, 2012, 2013) (A, C-F); Rafael P. Indicatti (2013, 2011, 2023) (B, G-H).

As demonstrated by Rosa et al. (2022), the existence of a platform dedicated to accessible biodiversity records such as iNaturalist, which has a mobile application, makes it more accessible for the common population to record fauna and flora throughout the planet. Taking into account that smartphone cameras have a satisfactory resolution, it is possible that we have images with a reasonable quality to arrive at a concise identification, reaching at least the family level. These characteristics make iNaturalist a platform of scientific importance, generating geographic data, seasonality graphs, life stage and sex of several clades.

Other positive points of the platform are the unpublished records of fauna and flora in life, in which species were only known through illustrations of old scientific works or for the simple fact of being rare species and even the discovery of new species. This can be proven by the observation made in iNaturalist (<https://www.inaturalist.org/observations/30214282>) of the species *Paracenobiopelma gerecormophilum* Feio, 1952, which could be easily identified by one of the authors (HMOGF) due the unique pattern of the abdomen (see Feio, 1952, figure 7). This monotypic genus is only known by the types deposited in the Museu Nacional do Rio de Janeiro, Rio de Janeiro (MNRJ). This rare specimen was recorded in Tinguá, Nova Iguaçu, Rio de Janeiro, 50km close to the type-locality of Niteroi, Rio de Janeiro. In the data analyzed in the present work, some new Neodiplothele species were recognized, which are already in the description process (Figures 4A, 4F, 5D, 5H, 6H). Thus, citizen science platforms like this one help researchers plan field trips to collect specimens, contributing to better use of public research funding and collection efficiency.

CONCLUSION

Overall, the expanding geographic distribution of the Barychelidae spiders from Brazil has revealed remarkable diversity, with numerous specimens spanning a variety of habitats, including the Amazon rainforest, Atlantic forests, Cerrado (savanna fields), and Caatinga, highlighting their ability to adapt to varied ecological conditions within Brazil. Mapping the distribution can provide valuable information for studying population variations, and aids in biogeographic research, enabling the investigation of historical processes, such as dispersal, and evolutionary relationships among different populations. Even among described species, there is a distinct lack of knowledge regarding their distribution and biogeography, as well as basic biology, such as life histories, feeding habits, and habitat preferences of this group.

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AUTHORS’ CONTRIBUTION

H. M. O. Gonzalez Filho contributed to conceptualization, data curation, methodology, investigation, visualization, project administration, and writing (original draft, review and editing); P. H. D. S. Costa to formal analysis, visualization, and writing (review and editing); J. M. D. Paiva to formal analysis, visualization, investigation, methodology, and writing (review and editing); and J. P. L. Guadanucci to resources, funding acquisition, supervision, and writing (review and editing).

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On the first South American records of widespread linyphiid spiders (Araneae)

Sobre os primeiros registros sul-americanos de aranhas Linyphiidae (Araneae) de ampla distribuição

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Abstract: The linyphiid species *Agyneta galapagosensis* (Baert, 1990), *Erigone autumnalis* Emerton, 1882 and *Mermessus fradeorum* (Berland, 1932) are recorded for the first time on the continental South America. In addition, the distribution data of *Neriene redacta* Chamberlin, 1925 is expanded. Figures of the habitus, a distribution map of the new records and new data about the natural history of these species are provided. These results show the high dispersal capacity and adaptability of these linyphiid spiders to different environmental conditions, such as agroecosystems and urban areas.

Keywords: Agrobionts. Invasive species. Cosmopolitan species. Dispersal.

Resumo: *Agyneta galapagosensis* (Baert, 1990), *Erigone autumnalis* Emerton, 1882 e *Mermessus fradeorum* (Berland, 1932), espécies de Linyphiidae, são citadas pela primeira vez para a América do Sul continental. Os dados de distribuição de *Neriene redacta* Chamberlin, 1925 são ampliados. Fornecemos figuras do *habitus*, mapa de distribuição atualizado com os novos registros e informações inéditas sobre a história natural destas espécies. Nossos resultados demonstram a grande capacidade de dispersão e tolerância dessas espécies de aranhas, que as permite viver em diferentes condições ambientais, como agroecossistemas e áreas urbanas.

Palavras-chave: Agrobiontes. Espécies exóticas. Espécies cosmopolitas. Dispersão.

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INTRODUCTION

Linyphiidae Blackwall, 1859 is the second most speciose spider family in the world, with 4855 described species (WSC, 2024). Many species of linyphiids have a wide global distribution or are cosmopolitan (Nentwig, 2015). One the hypothesis for that scenario is their great dispersal ability through ballooning (Thomas et al., 2003) and their tolerance to living in environments modified by human activity, like agroecosystems (Nyffeler & Sunderland, 2003; Thorbek et al., 2004; Rodrigues et al., 2009; Bao et al., 2018) and urban areas (Rodrigues et al., 2008). This study aimed to present new data on the distribution of some linyphiid species in South America, using material deposited in arachnological collections from Uruguay. We report the first records for South America of *Agyneta galapagosensis* (Baert, 1990), *Erigone autumnalis* Emerton, 1882 and *Mermessus fradeorum* (Berland, 1932). Furthermore, new distributional records of *Neriene redacta* Chamberlin, 1925 are registered. We provided detailed images of habitus, genitalia, data of natural history and maps with the updated distribution of all species mentioned above in continental Uruguay.

MATERIAL AND METHODS

Specimens examined are preserved in 70% ethanol and deposited at the Arachnological Collection of Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay (FCE-Ar, curator: M. Simó). Morphological examination was performed using a Leica M205 A stereomicroscope. Female genitalia and male palps were immersed in methyl salicylate (Holm, 1979; Hormiga, 2000; Hormiga et al., 2023) for examination of internal structures. Detailed micro-photographs were obtained using a Nikon SMZ-445 and a Leica DMC 2900 camera, attached with Leica M205 A stereomicroscope enabled with a Leica LAS-X-Z and SW software. *In vivo* photographs of the specimens were taken with a Panasonic DMC-ZS1 Lumix digital camera. Higher-magnification images were taken using a JEOL 5900 scanning electron microscope (SEM) at Facultad de Ciencias, Universidad de la República. Spider corporal structures used in the SEM were cleaned with ultrasonic bath (Álvarez-Padilla & Hormiga, 2007) and sputter-coated with gold. Photographs were edited using GIMP software (GIMP, n. d.) and plates were made in Inkscape software (Inkscape, n. d.). Terminology follows van Helsdingen (1969), Hormiga (1994, 2000), Miller (2007), Tanasevitch (2010), Dupérré (2013) and Irfan et al. (2022). When the exact coordinates of the location of the material examined are unknown, they were estimated using Google Earth (n. d.) and appear in square brackets [ ]. Data on previous distribution of the species was compiled from Word Spider Catalog. A distribution map of the species was made using SimpleMappr (Shorthouse, 2010).

Abbreviations used in the figures: A = atria; APPO = apical pocket of paracymbium; APO = anterior pocket of paracymbium; ARP = anterior radical process; AT = anterior tooth of radix; DP = dorsal plate; DSA = distal suprategular apophysis; DTA = dorsal tibial apophysis; E = embolus; EM = embolic membrane; GD = glabrous depression of cymbium; LC = lamella characteristica; PC = paracymbium; PT = protegulum; R = radix; RTA = retrolateral tibial apophysis; SPT = suprategulum; ST = subtegulum; T = tegulum; TA = terminal apophysis; TP = tailpiece of the radix; VP = ventral plate.

TAXONOMY

Family Linyphiidae Blackwall, 1859

New records

Agyneta galapagosensis (Baert, 1990)
(Figures 1A, 4A and 5)

Material examined. Uruguay: Durazno: Establecimiento Rincón del Río, *Eucalyptus dunnii* Maiden, 1905 plantation, in natural grassland, 32° 33' 9.5" S, 55° 41' 17.9" W, 17.x.2022, collected with pitfall trap, M. Simó leg., 1M (FCE-Ar 15369); Establecimiento La Selva, *E. dunnii* plantation, in natural grassland, 32° 31' 58.8" S, 55° 44' 18.9" W,

Figure 1. Habitus (dorsal and lateral view). A) *Agyneta galapagosensis* (male), B) *Erigone autumnalis* (male), C-D) *Mermessus fradeorum* (C: male, D: female), E-F) *Neriene redacta* (E: male, F: female). Scale bars: 1 mm. Photos: M. Cajade (2024).

17–21.v.2022, collected with G-Vac, M. Simó & B. Maldonado leg., 1M (FCE-Ar 14419); Río Negro: Protected Area Esteros y Algarrobales del Río Uruguay, Establecimiento La Mafalda, in "blanqueal," [32° 53' 00" S, 58° 2' 47" W], 22–23.iv.2022, collected manually, M. Simó leg., 1M (FCE-Ar 15313).

Distribution. Ecuador (Galapagos Islands), Brazil (Fernando de Noronha Island) and Uruguay (Figure 5).

Natural history. In Uruguay it was registered in a natural environment known as "blanquelaes" (alkaline soil areas) and natural grasslands.

Erigone autumnalis Emerton, 1882

(Figures 1B, 2, 3A-3C and 5)

Figure 2. *Erigone autumnalis* habitus (dorsal). A-B) Male, C-D) female. Photos: M. Cajade (2024).

Material examined. Uruguay: Canelones: INIA Las Brujas, in "espinillar", 34° 39' 41.17" S, 56° 20' 25.49" W, 7–14.vii.2014, collected with pitfall trap, Brussa, Da Silva & Muñoz leg., 1M (FCE-Ar 5049); Cerro Largo: Paso Centurión, Aduana, in hillside forest, 32° 8' 1.89" S, 53° 43' 57.31" W, 4.xi.2017, collected with G-Vac (diurnal), Á. Laborda & D. Hagopián leg., 1M (FCE-Ar 8717); same locality, 13–16.iv.2017, collected with G-Vac (diurnal, on foliage), Á. Laborda leg., 1F (FCE-Ar 6384); Durazno: Establecimiento La Teja, in natural grassland, 32° 40' 17" S, 55° 39' 55" W, 17.xii.2021, collected with pitfall trap, M. Simó & Á. Laborda leg., 1M (FCE-Ar 15471); near La Paloma city, in natural grassland, 32° 32' 40.52" S, 55° 42' 51.74" W, 26.viii.2021, collected with pitfall trap, M. Simó & Á. Laborda leg., 1F (FCE-Ar 13543); Establecimiento La Teja, in natural grassland, 32° 40' 11.27" S, 55° 42' 12.02" W, 17.x.2022, collected with pitfall trap, M. Simó & B. Maldonado leg., 2MM (FCE-Ar 15346); Establecimiento La Teja, in firebreak of *E. dunnii* plantation, 32° 40' 12.84" S, 55° 39' 30.34" W, 17–20.v.2022, collected with pitfall trap, M. Simó & Á. Laborda leg., 1F, 2MM (FCE-Ar 14605); Establecimiento La Teja, in natural grassland, 32° 39' 34" S, 55° 40' 46" W, 17.v.2022, collected with G-Vac, Á. Laborda leg., 1M (FCE-Ar 14609); Establecimiento La Teja, in firebreak of *E. dunnii* plantation, 32° 39' 18.47" S, 55° 39' 3.09" W, 17–21.x.2022, collected with G-Vac, D. Hagopián leg., 1F, 1M (FCE-Ar 15103); Establecimiento La Teja, in natural grassland, 32° 39' 36.15" S, 55° 40' 53.39" W, 17.x.2022, collected with G-Vac, Á. Laborda leg., 1M (FCE-Ar 15013); Establecimiento La Teja, in firebreak of *E. dunnii* plantation, 32° 40' 21.39" S, 55° 40' 22.96" W, 17–21.v.2022, collected with pitfall trap, M. Simó leg., 1F, 1M (FCE-Ar 14826); Establecimiento Rincón del Río, in firebreak of *E. dunnii* plantation in a landscape of natural grassland, 32° 40' 21.12" S, 55° 42' 12.15" W, 17.x.2022, collected with pitfall trap, M. Simó leg., 2MM (FCE-Ar 15356); Establecimiento Rincón del Río, in natural grassland, 32° 33' 7.2" S, 55° 41' 17.88" W, 17.x.2022, collected with pitfall trap, M. Simó & Á. Laborda leg., 1F, 6MM (FCE-Ar 15362); Establecimiento Rincón del Río, in natural grassland, 32° 31' 25.54" S, 55° 44' 23.14" W, 17–21.x.2022, collected with pitfall trap, M. Simó & B. Maldonado leg., 1M (FCE-Ar 15882); Establecimiento Rincón del Río, in firebreak of *E. dunnii* plantation,

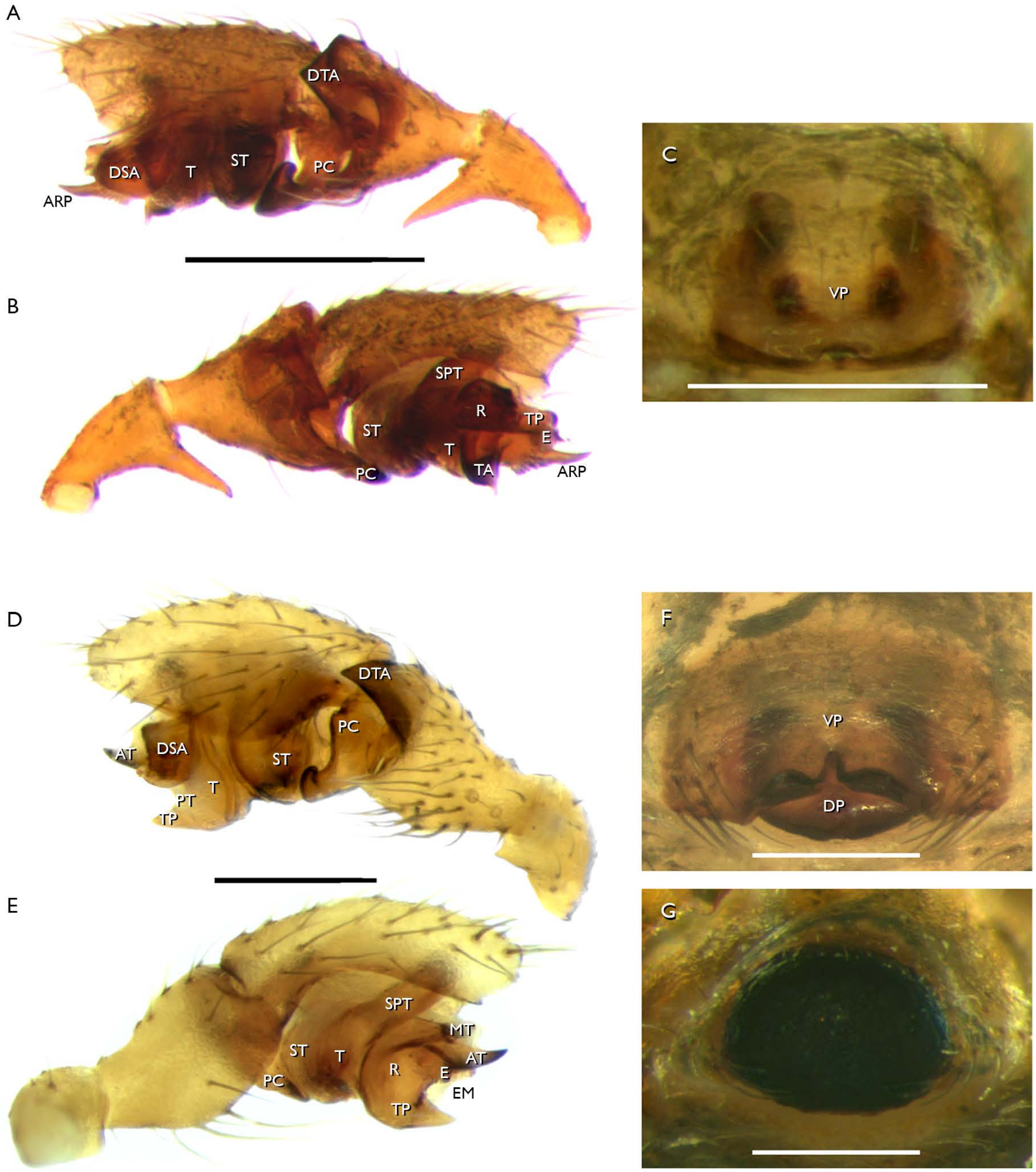

Figure 3. A-C) *Erigone autumnalis*, D-G) *Mermessus fradeorum*. A-B, D-E: male pedipalp in retrolateral (upper) and prolateral (down) view. C, F: female epigynum (ventral view). G: female epigynum with epigynal plug (ventral view). Scale bars: 0.2 mm. Photos: M. Cajade (2024).

32° 31' 26.54" S, 55° 44' 32.46" W, 17–22.x.2022, collected with pitfall trap, M. Simó & B. Maldonado leg., 3MM (FCE-Ar 15890); Establecimiento Rincón del Río, in firebreak of *E. dunnii* plantation, 32° 32' 41.06" S, 55° 42' 41.04" W, 17.v.2022, collected with pitfall trap, M. Simó leg., 2FF, 2MM (FCE-Ar 15613); Establecimiento Rincón del Río, in natural grassland, 32° 32' 40.69" S, 55° 42' 48.6" W, 17–21.v.2022, collected with pitfall trap, M. Simó leg., 1M (FCE-Ar 14967); Establecimiento Rincón del Río, in natural grassland, 32° 32' 40.67" S, 55° 42' 48.6" W, 17–21.x.2022, collected with G-Vac, D. Hagopián leg., 2FF, 1M (FCE-Ar 15074); Establecimiento Rincón del Río, in firebreak of *E. dunnii* plantation, 32° 33' 8.89" S, 55° 41' 19.72" W, 17–21.v.2022, collected with pitfall trap, M. Simó leg., 2MM (FCE-Ar 14960). Flores: Establecimiento Rincón de Piedra, in pasture, 33° 52' 21" S, 56° 58' 49" W, 1. viii. 2019, G. Pompozzi leg., 2MM (FCE-Ar 11339); Maldonado: Sierra de Carapé, in natural grassland, 34° 30' 32.2" S, 54° 58' 59.7" W, 12.x.2019, collected with pitfall trap, M. Simó leg., 1F (FCE-Ar 13215); same locality, 30.iv.2019, collected with pitfall trap, M. Simó leg., 1M (FCE-Ar 10102); Montevideo: Malvín Norte, Facultad de Ciencias field campus, [34° 52' 55.59" S, 56° 7' 7.85" W], 10.x.2000, M. Martínez leg., 9MM (FCE-Ar 15971); Río Negro: Negro river, Establecimiento El Matorral, in riparian forest, 33° 1' 12" S, 57° 33' 57.2" W, 28.v.2020, collected manually, D. Hagopián leg., 1F (FCE-Ar 11723); Salto: Establecimiento Corrales Viejos, in natural grassland, 31° 21' 36" S, 56° 46' 10" W, 14.xi.2019, G. Pompozzi leg., 9FF, 7MM (FCE-Ar 14356); Treinta y Tres: Charqueada, in rice crop of first year, 33° 12' 8.15" S, 53° 50' 47.98" W, 9.ix.2014, L. Bao leg., 2MM (FCE-Ar 11207).

Distribution. Antarctica, Azores, Bermuda, Canada, Czech Republic, Cuba, France, Germain, Hawaii, Italy, New Caledonia, Puerto Rico, Slovenia, Russia, Spain, Panama, Trinidad and Tobago, United Arab Emirates, United States of America and Uruguay (Figure 5).

Natural history. In Uruguay, these species inhabit mainly in open areas like natural grasslands, firebreaks in *E. dunnii* plantations, pastures, rice crops and urban parks. Also, can be found in woodlands like: riparian forests, hillside forests and "espinillares" (park forests of *Vachellia caven* (Molina) Seigler & Ebinger).

Mermessus fradeorum (Berland, 1932)

(Figures 1C-1D, 3D-3G and 5)

Material examined. Uruguay: Durazno: Establecimiento San Eduardo, in natural grassland, 32° 35' 32" S, 55° 42' 43" W, 16.iv.2019, G. Pompozzi leg., 2FF (FCE-Ar 15959); Establecimiento San Eduardo, in sown pasture (mainly *Avena* sp.), 32° 35' 59" S, 55° 42' 2" W, 12.viii.2019, G. Pompozzi leg., 1F (FCE-Ar 11350); Establecimiento La Teja, in two years old *E. dunnii* plantation, 32° 31' 57.75" S, 55° 44' 30.34" W, 17–20.v.2022, collected with G-Vac and leaf litter examination, M. Simó & D. Hagopián leg., 3MM (FCE-Ar 14299); Rivera: Establecimiento Mi lucha, in pasture, 31° 25' 3.7" S, 55° 16' 5.3" W, 10.vii.2019, G. Pompozzi leg., 3FF, 2MM (FCE-Ar 14658); Treinta y Tres: Da Fonseca, in rice crop of second year, 33° 11' 1.57" S, 54° 2' 4.90" W, 4.xi.2015, L. Bao leg., 1M (FCE-Ar 7022).

Distribution. Known for North America. Introduced to Azores, China, Cyprus, Saudi Arabia, South Africa, New Zealand (WSC, 2024), and now in Uruguay (Durazno, Rivera and Treinta y Tres Departments) (Figure 5).

Natural history. In Uruguay *M. fradeorum* was found in natural grasslands, pastures, rice crops and young *E. dunnii* plantations.

Neriene redacta Chamberlin, 1925

(Figures 1E-1F, 4B-4E and 5)

Material examined. Uruguay: Artigas: Rincón de Franquía, in park forest, [30° 12' 21.01" S, 57° 37' 37.02" W], 17–18.xi.2015, collected with G-Vac, M. Simó leg., 1F (FCE-Ar 7722); same locality, in grassland of tall tall tussock grasses,

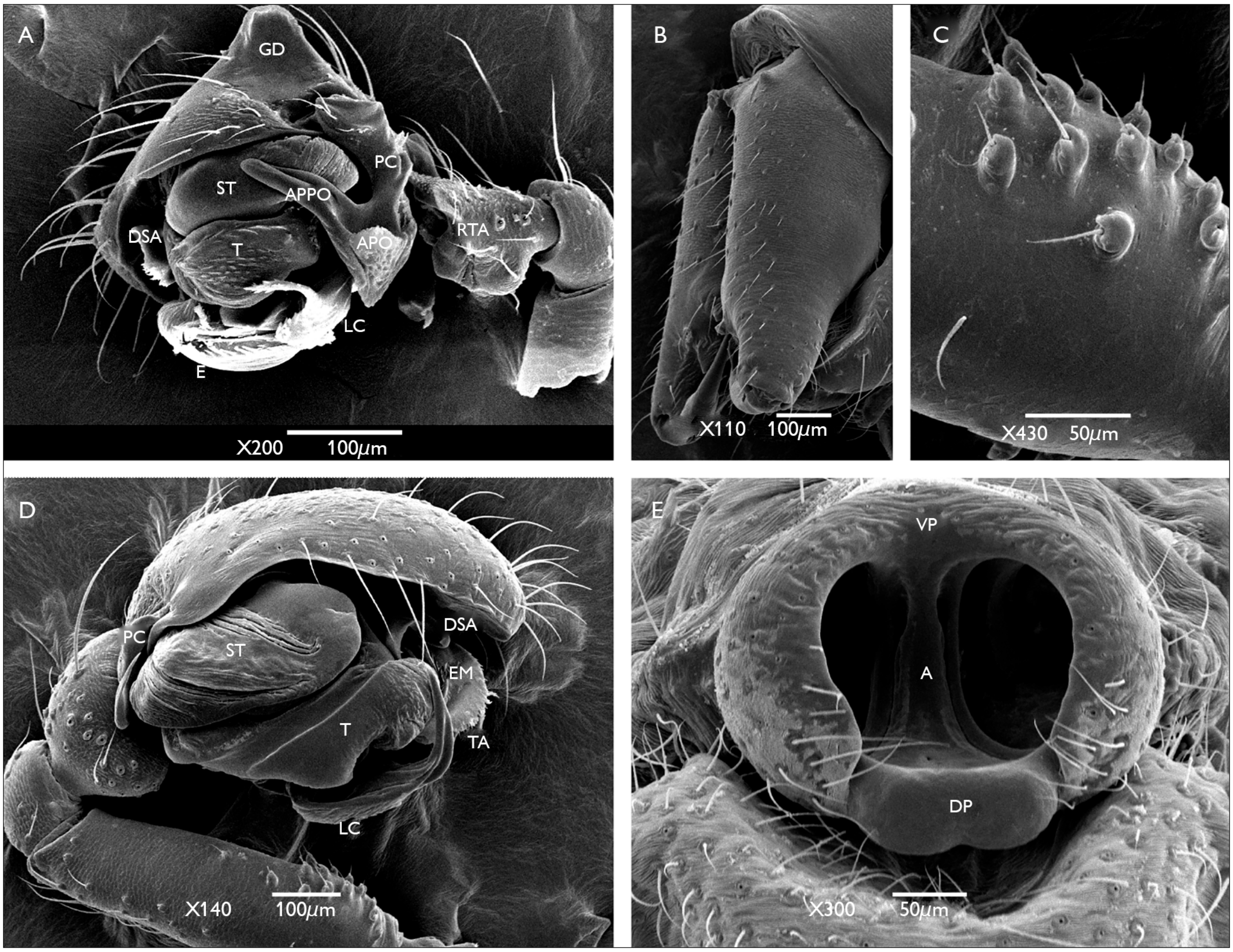

Figure 4. SEM images. A) *Agyneta galapagosensis*, male pedipalp in retrolateral view, B-E) *Neriene redacta*: chelicerae (male) (B), male pedipalp femur (C), male pepipalp in retrolateral view (D), epigynum in ventral view (E). Photos: M. Simó (2023).

collected with G-Vac, 29–30.iv.2015, collected with G-Vac, S. Fabius leg., 1F (FCE-Ar 7024); Canelones: INIA Las Brujas, in "espinillar", 34° 40' 10.08" S, 56° 20' 42.09" W, 7–14.vii.2014, Brussa, Da Silva & Muñoz leg., 3FF, 1Juv. (FCE-Ar 5834); same data, 3FF, 2Juv. (FCE-Ar 5036); same location and collectors, 21–28.iv.2014, 3FF, 3Juv. (FCE-Ar 4989); same data, 2MM (FCE-Ar 5010); same location and collectors, 29.x.2014, 2FF, 1Juv. (FCE-Ar 5873); same data, 1M (FCE-Ar 5916); Cerro Largo: Paso Arriera, in natural grassland, 32° 00' 34.4" S, 54° 26' 29.4" W, 5.vi.2020, collected manually, M. Simó & D. Hagopián leg., 1F (FCE-Ar 12304); same location, 10.xi.2019, collected with G-Vac, M. Simó & D. Hagopián leg., 1F (FCE-Ar 11599); Durazno: Establecimiento La Teja, in natural grassland, 32° 31' 25.78" S, 55° 44' 30.55" W, 17–21.v.2022, A. Laborda & M. Cajade, leg, 1M (FCE-Ar 13593); same data 1F (FCE-Ar 13594); same locality and collectors, 26.viii.2021, collected with pitfall trap, 1M (FCE-Ar 13452); same data, 1F (FCE-Ar 11599); Establecimiento La Teja, in natural grassland, 32° 32' 40.52" S, 55° 42' 51.74" W, 17–21.v.2022, collected with G-Vac, A. Laborda & M. Cajade leg, 1F, 1Juv. (FCE-Ar 13620). Montevideo: Melilla, in natural grassland, 34° 43' 57.10" S, 56° 19' 21.48" W, 24.xi.2021, D. Hagopián leg., 2F, 1Juv. (FCE-Ar 10507).

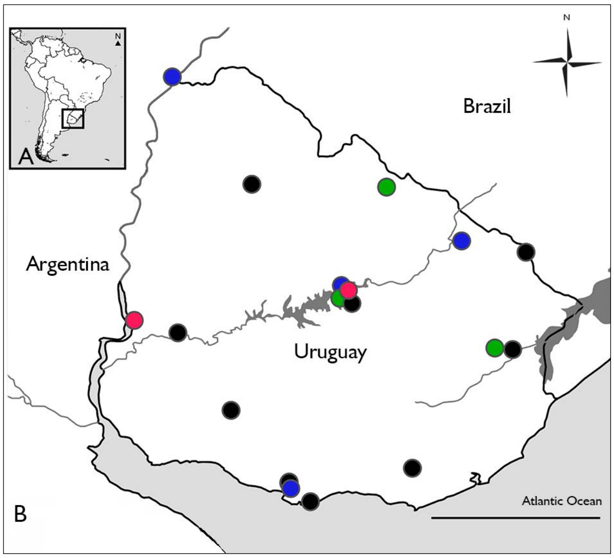

Figure 5. Distribution map. A) South America, B) rectangle in A enlarged. Red circles: *Agyneta galapagosensis*, black circles: *Erigone autumnalis*, green circles: *Mermessus fradeorum* and blue circles: *Neriene redacta*. Scale bar: 279 km. Map: M. Cajade (2024).

Distribution: Brazil, USA and Uruguay (Figure 5).

Natural history: In Uruguay *N. redacta* was found in natural grasslands, park forests and young *E. dunnii* plantations. Females webs were found inside tussock grasses in natural grasslands.

DISCUSSION

Many spider species have worldwide distribution (WSC, 2024), and most of them are a consequence of human transport and trade in the last centuries (Kobelt & Nentwig, 2008). Synanthropic species were favored in this process, expanding their distribution in urban habitats around the world, as reported for some spider species (Simó et al., 2011; Pompozzi et al., 2013). Other exotic species invaded new areas, displacing native species (Nentwig, 2015). Linyphiids show are highly dispersed and many species are associated with human activities, in this way several species show a cosmopolitan or widespread distribution (WSC, 2024). In Europe, Linyphiidae is the third most commonly established family in order of the number of alien species (Nentwig, 2015).

Agyneta galapagosensis, previously known for Galapagos Islands and Fernando de Noronha Island (WSC, 2024), is recorded for the first time for continental South America. This finding constitutes the southernmost records of this species. In Uruguay, *A. galapagosensis* is associated with natural grasslands and "blanqueales". Previous studies found this species in island urban areas, crops and volcanic areas (Baert, 1990; Rodrigues et al., 2008). As hypothesized by Rodrigues et al. (2008, p. 252) "if *A. galapagosensis* is widely distributed in South America, it has not been detected because of the few studies involving the Neotropical linyphiid fauna".

Erigone autumnalis, is native to North America but has a wide global distribution (Nentwig, 2015). In Uruguay, it is recorded for natural grasslands, pastures, urban parks, *Eucalyptus dunnii* plantations and riparian forests. This species is formally cited for the first time in South America. Also, these findings constitute the southernmost records of this species. In addition, in the Global Biodiversity Information Facility (GBIF) exist previous records from Argentina of unconfirmed (cf.) individuals of this species. *Erigone autumnalis* seems to be one of the most common of the epigean spider species in Uruguay (in a wide variety of environments). Males leave the webs (if they actually spin ones) to search for prey or find a female.

Mermessus fradeorum is a widespread species (WSC, 2024). In Uruguay, we found specimens of *M. fradeorum* in natural grasslands, pastures, rice crops and young *E. dunnii* plantations. It is formally recorded for the first time for the continent, in spite of the existence of records in GBIF for Brazil (but unpublished in any taxonomic or biodiversity work) and it is mentioned in Zapata and Grismado (2015), but without the reference to material examined. *Neriene redacta* was originally described for the United States of America and was known from a single specimen in Brazil for sugarcane crops (Rinaldi et al., 2002). In Uruguay, this species is distributed in natural grasslands, park forests and young *E. dunnii* plantations. We hypothesize that this species may have arrived to the continent by the plant traffic of sugarcane, since alien species may be transported by agrciculture crops (Hulme et al., 2008), and then dispersed and adapted to natural grasslands and other open or semi-open environments with herbaceous vegetation.

Some studies (Levine & D'Antonio, 2003; Kobelt & Nentwig, 2008) expect the introduction of at least one alien spider species per year in Europe as well as plants, molluscs and insects in the USA. Based on those, is not farfetched to expect similar rates in other parts of the world such as South America. Future faunistic studies or revision of material in arachnological collections may reveal new South American records of linyphiid species with widespread distribution.

These results confirm the great dispersion of the studied species, mainly by human activities and their tolerance to live in different environmental conditions.

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AUTHORS' CONTRIBUTION

M. Cajade contributed to project administration, formal analysis, conceptualization, data curation, investigation, methodology, validation, visualization, and writing (original draft, review and editing); E. N. L. Rodrigues to formal analysis, supervision, validation, and writing (review and editing); D. Hagopián to data curation, investigation, and writing (review and editing); Á. Laborda to data curation, investigation, and writing (review and editing); A. D. Brescovit to formal analysis, supervision, validation, and writing (review and editing); M. Simó to acquisition of funding, formal analysis, data curation, resources, software, supervisión, validation, and writing (review and editing).

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Todas as figuras (ilustrações, gráficos, imagens, diagramas etc.) (PDF com imagens) devem ser apresentadas em páginas separadas e numeradas, com as respectivas legendas no idioma do texto e em inglês, e submetidas na plataforma online como PDF. As imagens também devem ser submetidas separadamente (em arquivos individuais) e ter resolução mínima de 300 dpi e tamanho mínimo de 1.500 pixels, em formato JPEG ou TIFF, obedecendo, se possível, as proporções do formato de página do Boletim, nos limites de 16,5 cm de largura e 20 cm de altura (para uso em duas colunas) ou 8 cm de largura e 20 cm de altura (para uso em uma coluna). As informações de texto presentes nas figuras, caso possuam, devem estar em fonte Arial, com tamanho entre 7 e 10 pts. O texto deve, obrigatoriamente, fazer referência a todas as tabelas, gráficos e ilustrações.

Chaves devem ser apresentadas no seguinte formato:

1. Lagarto com 4 patas minúsculas 2
   Lagarto com 4 patas bem desenvolvidas 3
2. Dígitos geralmente sem unhas, dorsais lisas .... *Bachia flavescens*
   Dígitos com unhas, dorsais quilhadas .... *Bachia panoplia*
3. Mãos com apenas 4 dedos 4
   Mãos com 5 dedos 5
4. Escamas dorsais lisas .... *Gymnophthalmus underwoodii*
   Escamas dorsais quilhadas .... *Amapasaurus tetradactylus*
5. Cabeça com grandes placas 6
   Cabeça com escamas pequenas 7
6. Placas posteriores da cabeça formam uma linha redonda .... *Alopoglossus angulatus*
   Placas posteriores da cabeça formam uma linha reta .... *Arthrosaura kockii*
7. Etc.
   Etc.

Pede-se destacar termos ou expressões por meio de aspas simples. Apenas termos científicos latinizados ou em língua estrangeira devem constar em itálico. Observar cuidadosamente as regras de nomenclatura científica, assim como abreviaturas e convenções adotadas em disciplinas especializadas. Os artigos deverão seguir as recomendações da APA 7th Edition - Citation Guide (https://apastyle.apa.org/style-grammar-guidelines/references/examples) para uso e apresentação de citações e de referências. Todas as obras citadas ao longo do texto devem estar corretamente referenciadas ao final do artigo.

Estrutura básica dos trabalhos

Título – No idioma do texto e em inglês (quando este não for o idioma do texto). Deve ser escrito em caixa baixa, em negrito, centralizado na página.

Resumo e Abstract – Texto em um único parágrafo, ressaltando os objetivos, métodos e conclusões do trabalho, com, no máximo, duzentas palavras, no idioma do texto (Resumo) e em inglês (Abstract). A versão para o inglês é de responsabilidade do(s) autor(es).

Palavras-chave e Keywords – Três a seis palavras que identifiquem os temas do trabalho, para fins de indexação em bases de dados.

Introdução – Deve conter uma visão clara e concisa de conhecimentos atualizados sobre o tema do artigo, oferecendo citações pertinentes e declarando o objetivo do estudo.

Material e métodos – Exposição clara dos métodos e procedimentos de pesquisa e de análise de dados. Técnicas já publicadas devem ser apenas citadas e não descritas. Termos científicos, incluindo espécies animais e vegetais, devem ser indicados de maneira correta e completa (nome, autor e ano de descrição).

Resultados e discussão – Podem ser comparativos ou analíticos, ou enfatizar novos e importantes aspectos do estudo. Podem ser apresentados em um mesmo item ou em separado, em sequência lógica no texto, usando tabelas, gráficos e figuras, dependendo da estrutura do trabalho.

Conclusão – Deve ser clara, concisa e responder aos objetivos do estudo.

Agradecimentos – Devem ser sucintos: créditos de financiamento; vinculação do artigo a programas de pós-graduação e/ou projetos de pesquisa; agradecimentos pessoais e institucionais. Nomes de instituições devem ser por extenso, de pessoas pelas iniciais e sobrenome, explicando o motivo do agradecimento.

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Artigo de periódico: Gans, C. (1974). New records of small amphisbaenians from northern South America. *Journal of Herpetology, 8*(3), 273-276. http://dx.doi.org/10.2307/1563187.

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Keys have to be presented in the following format:

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   Fingers and toes with nails, dorsals keeled................. *Bachia panoplia*
3. Hands with only 4 fingers...4
   Hands with 5 fingers...5
4. Dorsal scales smooth.................................*Gymnophthalmus underwoodii*
   Dorsal scales keeled.................................*Amapasaurus tetradactylus*
5. Head with large scales...6
   Head with small scales...7
6. Posterior scales of head forming a rounded line .... *Alopoglossus angulatus*
   Posterior scales of head forming a straight line................. *Arthrosaura kockii*
7. Etc. Etc.

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Acknowledgements – Acknowledgements are brief and can mention: support and funding; connections to graduate programs and/or research projects; acknowledgement to individuals and institutions. The names of institutions should be written in full, those of individuals with initials and family name, indicating what motivated the acknowledgement.

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