UNIVERSIDADE FEDERAL DE MINAS GERAIS

Instituto de Ciências Biológicas

Programa de Pós-Graduação em Zoologia

Mayara Drumond Faustino Magalhães

ADDRESSING KNOWLEDGE GAPS OF ATLANTIC FOREST XENOCTENIDS (ARANEAE: XENOCTENIDAE): a taxonomic, phylogenetic, and biogeographic approach

Belo Horizonte

2024

Mayara Drumond Faustino Magalhães

ADDRESSING KNOWLEDGE GAPS OF ATLANTIC FOREST XENOCTENIDS (ARANEAE: XENOCTENIDAE): a taxonomic, phylogenetic, and biogeographic approach

Tese apresentada ao Programa de Pósgraduação em Zoologia, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais, como requisito para obtenção do título de Doutora em Zoologia.

Linha de Pesquisa: Sistemática e biogeografia

Orientador: Prof. Dr. Adalberto José dos Santos Co-orientadora: Dra. Hannah Wood

Belo Horizonte

2024

Magalhães, Mayara Drumond Faustino. Addressing knowledge gaps of Atlantic Forest xenoctenids (Araneae: Xenoctenidae): a taxonomic, phylogenetic, and biogeographic approach [manuscrito] / Mayara Drumond Faustino Magalhães. – 2024. 135 f. : il. ; 29,5 cm.
Orientador: Adalberto José dos Santos. Coorientador: Hannah Wood. Tese (doutorado) – Universidade Federal de Minas Gerais, Instituto de Ciências Biológicas. Programa de Pós-Graduação em Zoologia.

1. Zoologia. 2. Biogeografia. 3. Floresta Úmida. 4. Aranhas. I. Santos, Adalberto José dos. II. Universidade Federal de Minas Gerais. Instituto de Ciências Biológicas. III. Título.

CDU: 591

Ficha Catalográfica elaborada pelo bibliotecário Rafael Gonçalves Dias (CRB: 6 - 3277)

SEI/UFMG - 3070206 - Folha de Aprovação

https://sei.ufmg.br/sei/controlador.php?acao=documento_imprimir_...



UNIVERSIDADE FEDERAL DE MINAS GERAIS INSTITUTO DE CIÊNCIAS BIOLÓGICAS PÓS-GRADUAÇÃO EM ZOOLOGIA

FOLHA DE APROVAÇÃO DE TESE

Addressing knowledge gaps of Atlantic Forest xenoctenids (Araneae: Xenoctenidae): a taxonomic, phylogenetic, and biogeoghaphic approach

MAYARA DRUMOND FAUSTINO MAGALHÃES

Esta tese foi apresentada em sessão pública e submetida a avaliação em 29 de fevereiro de 2024, sendo aprovada pela Banca Examinadora composta pelos seguintes membros:

Prof. Dr. Adalberto José dos Santos (Orientador / UFMG)

Prof. Dr. Antonio Domingos Brescovit (Membro / Instituto Butantan)

Profa. Dra. Diana Fernanda Silva Davila (Membro / Universidad Nacional Mayor de San Marcos)

Prof. Dr. Guilherme Henrique Fernandes de Azevedo (Membro / Museo Argentino de Ciencias Naturales)

Profa. Dra. Cibele Bragagnolo (Membro / UNIFESP)

sel!

Documento assinado eletronicamente por **Adalberto Jose dos Santos**, **Professor do Magistério Superior**, em 01/03/2024, às 10:35, conforme horário oficial de Brasília, com fundamento no art. 5º do <u>Decreto nº 10.543, de 13 de novembro de 2020</u>.



Documento assinado eletronicamente por **Antonio Domingos Brescovit**, **Usuário Externo**, em 01/03/2024, às 11:00, conforme horário oficial de Brasília, com fundamento no art. 5º do Decreto h° 10.543, de 13 de novembro de 2020.



Documento assinado eletronicamente por **Cibele Bragagnolo**, **Usuária Externa**, em 01/03/2024, às 16:06, conforme horário oficial de Brasília, com fundamento no art. 5º do <u>Decreto nº 10.543</u> de 13 de novembro de 2020. SEI/UFMG - 3070206 - Folha de Aprovação

https://sei.ufmg.br/sei/controlador.php?acao=documento_imprimir_...



Documento assinado eletronicamente por **Diana Fernanda Silva Dávila, Usuária Externa**, em 03/03/2024, às 19:33, conforme horário oficial de Brasília, com fundamento no art. 5º do <u>Decreto</u> nº 10.543, de 13 de novembro de 2020.



Documento assinado eletronicamente por **Guilherme Henrique Fernandes de Azevedo, Usuário** Externo, em 18/03/2024, às 12:08, conforme horário oficial de Brasília, com fundamento no art. 5º do <u>Decreto nº 10.543, de 13 de novembro de 2020</u>.



A autenticidade deste documento pode ser conferida no site <u>https://sei.ufmg.br/sei/</u> <u>controlador_externo.php?acao=documento_conferir&id_orgao_acesso_externo=0</u>, informando o código verificador **3070206** e o código CRC **94EE3A07**.

Referência: Processo nº 23072.212080/2024-81

SEI nº 3070206

Agradecimentos

Ao longo dos anos de desenvolvimento deste projeto pude contar com o apoio de diversas pessoas, entre profissionais, amigos e familiares. Todos os aqui citados foram essenciais para que eu pudesse superar todos os obstáculos enfrentados neste processo, principalmente diante do desafio que a pandemia de COVID-19 trouxe para todos.

Primeiramente, agradeço ao meu orientador, Professor Dr. Adalberto José dos Santos, pelos 10 anos de orientação, que se iniciaram em 2014, quando eu era apenas uma aluna de iniciação científica. Por todos estes anos, agradeço a paciência, dedicação, incentivo e parceria. Agradeço a minha coorientadora, Dra. Hannah Wood, por ter me recebido tão bem em seu laboratório, pelo carinho, paciência e por me inspirar como mulher pesquisadora.

Agradeço à Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) pela bolsa de doutorado e ao programa CAPES-PrInt pelo financiamento do doutoradosanduíche, que me possibilitou desenvolver boa parte deste projeto, além de ampliar conexões acadêmicas e superar limitações. Agradeço a The Rufford Foundation pelo financiamento, sem o qual seria impossível realizar todas as expedições de coleta, que foram essenciais para projeto e me proporcionaram experiências incríveis.

Agradeço ao Programa de Pós-Graduação de Zoologia da UFMG pelo suporte acadêmico e a todos os docentes pelos ensinamentos e colaborações. Agradeço aos técnicos de laboratório do departamento de Zoologia, principalmente à Viviane, pelo zelo e organização da coleção científica de Aracnídeos.

Agradeço aos curadores e funcionários das coleções científicas e museus que cederam empréstimo ao material utilizado nesta pesquisa. Especialmente aos pesquisadores Adriano Kury (MNRJ), Antônio D. Brescovit (IBSP), Diana Silva Dávila (UNMSM), Gustavo Hormiga (GWU), Lauren Esposito (CAS) e Martín Ramirez (MACN), que gentilmente me recebam em seus laboratórios. Agradeço também ao pesquisador Luis Piacentini, pela parceira e colaboração, que resultaram no primeiro capítulo desta tese.

Agradeço aos amigos do laboratório de aracnologia, Richard Torres, Leonardo Carvalho, Ivan Magalhães, Guilherme Azevedo, Ubirajara Oliveira, Alexandre Michelotto, João Victor Cardinali, Philip Russo e Gracielle Braga, pelos bons momentos e discussões acadêmicas. Agradeço especialmente à Bárbara Teixeira Faleiro, Márcia Oliveira Tomasi, Pedro Henrique Martins e Vinícius Sergio Diniz pela parceria de tantos anos, por fazerem os dias de trabalho mais divertidos e por serem a melhor equipe de coleta do mundo. Agradeço também aos colegas, Arthur Galleti Lima, Álvaro Drumond Araujo, Estevão Comitti, Hector Gonzalez Filho e Gabriel Peñaloza Bojacá, que participaram das expedições de coleta e se dispuseram a viajar e contribuir conosco. Agradeço à Cláudia Vaga, Corinthia R. Black, David Adamski, Jonathan Coddington, Megan Ma, Nicholas Hazzi, e Tom Nguyen, pela receptividade e por fazerem minha estadia nos Estados Unidos ser uma experiência ainda mais incrível.

Aos meus pais, Priscila D. F. Magalhães e Aloísio Eduardo C. Magalhães, agradeço por todo o suporte e incentivo, por compreenderem meus momentos de ausência e por sempre acreditarem em mim. Agradeço ao meu companheiro e grande amor, Gustavo H. de Paula Abrantes, por sempre me apoiar e aceitar superar desafios ao meu lado, por estar presente quando eu não pude e pelo cuidado e carinho com os que eu amo.

Agradeço aos membros da banca, Antônio Brescovit, Cibele Bragagnolo, Diana Silva Dávila e Guilherme Azevedo, e aos suplentes, Lica Haseyama e Ubirajara Oliveira, por aceitarem contribuir com este trabalho e fazer parte desta jornada.

Mayara D. F. Magalhães

<u>Resumo</u>

Xenoctenidae é uma família de aranhas errantes que habita a região Neotropical e é composta por quatro gêneros: Incasoctenus Mello-Leitão, 1942; Odo Keyserling, 1887; Paravulsor Mello-Leitão, 1922; e Xenoctenus Mello-Leitão, 1938. No Capítulo 1 relatamos duas espécies de Xenoctenus que são endêmicas e amplamente distribuídas na Caatinga. Redescrevemos e ilustramos Odo vittatus (Mello-Leitão, 1936), que até então era a única espécie de Xenoctenidae encontrada na Caatinga. Com base em um estudo morfológico comparativo da família, transferimos esta espécie para Xenoctenus Mello-Leitão, 1938. Descrevemos o macho de Xenoctenus vittatus comb. nov. e fornecemos novos registros de distribuição para esta espécie, que é restrita a Caatinga e formações vegetais semiáridas próximas. Também descrevemos e ilustramos uma nova espécie, Xenoctenus kaatinga sp. nov., baseado em exemplares machos e fêmeas da Caatinga. Além disso, propomos caracteres diagnósticos para Xenoctenus e redescrevemos a espécie-tipo, X. unguiculatus Mello-Leitão, 1938. No capítulo 2 e 3 estudamos o gênero monotípico Paravulsor, até então conhecido apenas pela sua descrição original. Recentemente, uma hipótese filogenética baseada na morfologia e revisão taxonômica de Xenoctenidae recuperou Odo como um gênero polifilético, com cinco espécies que deveriam ser transferidas para Paravulsor. Além disso, Paravulsor era conhecido somente pela localidade-tipo, mas identificamos que o grupo é amplamente distribuído por toda a Mata Atlântica e apresenta 51 novas espécies. Assim, no Capítulo 2 transferimos as espécies O. blumenauensis Mello-Leitão, 1927, O. obscurus Mello-Leitão, 1936, O. pulcher Keyserling, 1891, 1936 e O. similis Keyserling, 1891 para Paravulsor. Também sinonimizamos O. serrimanus Mello-Leitão, 1936 com O. blumenauensis e redescrevemos e designamos um neótipo para a espécie-tipo, Paravulsor impudicus Mello-Leitão, 1922. Em seguida, o Capítulo 3 explora a posição filogenética de Paravulsor usando métodos filogenômicos e fornece novas evidências para delimitação dos gêneros de Xenoctenidae. Além disso, para desvendar os padrões de distribuição e diversificação dos Xenoctenidae da Mata Atlântica, investigamos cenários biogeográficos do passado baseado em uma filogenia molecular datada e em reconstruções de áreas ancestrais. Nossos resultados apoiam estudos anteriores sobre a taxonomia de Xenoctenidae e recuperaram dois novos gêneros endêmicos da Mata Atlântica. Os padrões de distribuição dos Xenoctenidae da Mata Atlântica correlacionam-se com as áreas de endemismo da Mata Atlântica. Nossos resultados indicam que a diversificação de Paravulsor ocorreu predominantemente durante o Mioceno, associada a reativações tectônicas,

responsáveis por mudanças e formações de rios no sudeste e sul da Mata Atlântica neste período.

Palavras-chave: aranhas; sistemática; biogeografia; floresta tropical; Caatinga.

Abstract

Xenoctenidae is a family of wandering spiders that inhabit the Neotropics and is composed by four genera: Incasoctenus Mello-Leitão, 1942; Odo Keyserling, 1887; Paravulsor Mello-Leitão, 1922; and Xenoctenus Mello-Leitão, 1938. In Chapter 1 we report two species of Xenoctenus that are endemic to, and widely distributed in the Caatinga. We redescribe and illustrate Odo vittatus (Mello-Leitão, 1936), the only xenoctenid species previously known from the Caatinga. Based on a comparative morphological study of xenoctenids, we transfer this species to Xenoctenus Mello-Leitão, 1938. We also newly describe the male of Xenoctenus *vittatus* comb. nov. and provide new records of this species, which was hitherto known only from the type-locality, throughout the Caatinga and nearby semiarid vegetation formations. We also describe and illustrate a new species, Xenoctenus kaatinga sp. nov., based on males and female specimens collected throughout the Caatinga. Additionally, we propose diagnostic characters for *Xenoctenus* and redescribe the type-species, *X. unguiculatus*. In chapters 2 and 3 we studied the monotypic genus *Paravulsor*, previously known only by its original description. Recently, a morphology-based phylogenetic hypothesis and taxonomic revision of Xenoctenidae recovered Odo as a polyphyletic genus, with five species that should be transferred to Paravulsor. Additionally, Paravulsor was previously known only by its type locality, but we identify that it is widely distributed throughout the Atlantic Forest and comprises 51 new species. Thus, in the Chapter 2 we transfer the species O. blumenauensis Mello-Leitão, 1927, O. obscurus Mello-Leitão, 1936, O. pulcher Keyserling, 1891, 1936 and O. similis Keyserling, 1891 to Paravulsor. We also synonymize O. serrimanus Mello-Leitão, 1936 with O. blumenauensis and we redescribe and designated a neotype for the type-species, Paravulsor impudicus Mello-Leitão, 1922. Then, in the Chapter 3 explores the phylogenetic position of *Paravulsor* using phylogenomic data and provides new evidence for delimiting the Xenoctenidae genera. Additionally, it investigates past biogeographical scenarios through dating phylogenies and ancestral area reconstructions to unravel the distribution and diversification patterns of Atlantic Forest xenoctenids. Our results support previous studies about the taxonomy of Xenoctenidae and recovered two new genera endemic to the Atlantic Forest. The distribution patterns of Atlantic Forest xenoctenids correlate with proposed areas of endemism for the Atlantic Forest. Our results indicate that the diversification of Paravulsor occurred predominantly during the Miocene, associated with tectonic reactivations responsible

for changes and formation of rivers in the southeast and south of the Atlantic Forest during this period.

Key words: spiders; systematics; biogeography; rainforest; Caatinga.

Prefácio

É com grande satisfação e gratidão que apresento esta tese aos leitores. Este é o resultado de anos de dedicação, pesquisa e colaboração com diversos profissionais, acadêmicos e instituições. A inspiração para esta investigação teve início em 2017, quando iniciei meus estudos do mestrado sobre a família Xenoctenidae. Assim, tive meu primeiro contato com uma pequena aranha que, à primeira vista, apresentava uma morfologia muito genérica e que muitos diriam ser "sem graça". Descobrimos que estas aranhas, que não eram nada "sem graça", pertenciam ao gênero *Paravulsor* e que existiam mais de dezenas de espécies novas para o grupo, todas restritas a Mata Atlântica.

Esta tese surgiu do desejo de contribuir ainda mais para o avanço do conhecimento sobre os Xenoctenidae, principalmente sobre os processos evolutivos que guiaram a diversificação do grupo. Sendo assim, o primeiro capítulo é destinado à uma revisão das espécies brasileiras de *Xenoctenus*, gênero-tipo de Xenoctenidae. Foram redescritas duas espécies, incluindo a espécie-tipo do gênero, e uma espécie nova endêmica da Caatinga. O segundo e o terceiro capítulo são destinados ao estudo do gênero *Paravulsor* e as demais espécies de Xenoctenidae que ocorrem na Mata Atlântica brasileira. No segundo capítulo, revisamos *Paravulsor*, focando em resolver vários dos problemas taxonômicos que envolviam o grupo. Assim, o terceiro capítulo for destinado ao estudo das relações filogenéticas entre *Paravulsor* e os demais gêneros da família, incluindo as espécies novas dos Xenoctenidae da Mata Atlântica. Além disso, investigamos a história evolutiva dos Xenoctenidae da Mata Atlântica e buscamos compreender os padrões e processos que influenciaram sua diversificação.

Ao final da leitura, espero que este estudo possa enriquecer ainda mais nossa compreensão sobre os Xenoctenidae e que inspire novas investigações. Além disso, espero que assim como eu, o leitor se apaixone por essas aranhas incríveis que fazem parte da biota brasileira e se sintam inspirados para conhecer ainda mais sobre elas.

CHAPTER 1	
THE DESERT WOLF-SPIDER GENUS XE	NOCTENUS: TWO ENDEMIC SPECIES
FROM THE BRAZILIAN CAATINGA, AN	D A REDESCRIPTION OF THE TYPE-
SPECIES, X. UNGUICULATUS (ARANEAE	: XENOCTENIDAE)15
Abstract	
1. INTRODUCTION	
2. MATERIAL AND METHODS	
3. Тахолому	
Xenoctenus unguiculatus Mello-Leitão, 1	93820
Xenoctenus vittatus (Mello-Leitão, 1936)	сомв. NOV
Xenoctenus kaatinga Faustino-Magalhai	ES & SANTOS SP. NOV28
4. Acknowledgements	
5. References	
FIGURE LEGENDS	
CHAPTER 2	40
TAXONOMIC REVIEW OF PARAVULSOR	, AN ENDEMIC GENUS OF THE
AILANIIC FORESI (ARANEAE: XENOC	(IENIDAE)
Abstract	
1. INTRODUCTION	
2. MATERIAL AND METHODS	
3. Abbreviations	
4. TAXONOMY	
PARAVULSOR MELLO-LEITÃO, 1922	
PARAVULSOR IMPUDICUS MELLO-LEITÃO, 1922	
PARAVULSOR BLUMENAUENSIS (MELLO-LEITÃO	, 1927) COMB. NOV48
PARAVULSOR OBSCURUS (MELLO-LEITÃO, 1930	б) сомв. nov53
PARAVULSOR SIMILIS (KEYSERLING, 1891) COM	B. NOV
PARAVULSOR PULCHER (KEYSERLING, 1891) CO	DMB. NOV61
5. References	64
FIGURE LEGENDS	

Summary

CHAPTER 3	70
PHYLOGENETIC AND BIOGEOGRAPHICAL STUDY OF PARAVULSO	DR: AN
ENDEMIC SPIDER TO THE ATLANTIC FOREST (ARANEAE: XENOC	TENIDAE)
••••••	70
Abstract	70
1. INTRODUCTION	70
2. MATERIAL AND METHODS	72
2.1. Taxon sampling and DNA extraction	72
2.2. Ultraconserved elements library construction and enrichment	73
2.3. Phylogenetic analyses	74
2.4. Divergence time estimation	74
2.5. Ancestral range reconstruction	75
3. Results	76
3.1. Taxon sampling and DNA extraction	76
3.2. Phylogenetic analyses	76
4. DISCUSSION	
4.1. Historical biogeography of Xenoctenidae	78
4.2. Historical biogeography of the Atlantic Forest xenoctenids	79
5. References	
FIGURE LEGENDS	91
SUPPLEMENTARY MATERIALS	93
FIGURES	
Chapter 1	
Chapter 2	115
Chapter 3	

CHAPTER 1

The desert wolf-spider genus Xenoctenus: two endemic species from the Brazilian Caatinga, and a redescription of the type-species, X. unguiculatus (Araneae: Xenoctenidae)

Mayara D. Faustino-Magalhaes^{1, 2, 4*}, Luis N. Piacentini^{3, 5} & Adalberto J. Santos^{2, 6}

¹ Pós-graduação em Zoologia, Universidade Federal de Minas Gerais.

² Departamento de Zoologia, Instituto de Ciências Biológicas, Universidade Federal de Minas Gerais. Av. Antônio Carlos 6627, Belo Horizonte, Minas Gerais, Brazil. CEP 31270-901.

³ División de Aracnología, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Av .Angel Gallardo 470, C1405DJR Buenos Aires, Argentina

⁴mayaradfm@hotmail.com; ORCID <u>https://orcid.org/0000-0002-3689-4910</u>

⁵Piacentini@macn.gov.ar; ORCID <u>https://orcid.org/0000-0003-1246-0699</u>

⁶oxyopes@yahoo.com; ORCID <u>https://orcid.org/0000-0002-0010-346X</u>

* Corresponding author

Published in Zootaxa

DOI: 10.11646/ZOOTAXA.5399.5.3

Abstract

The Caatinga is a nucleus of seasonally dry tropical forest (SDTF) known as a hotspot of diversification and endemism. Despite its importance, this biome is still insufficiently sampled, resulting in extensive knowledge gaps regarding its species richness and composition. In this study we report two species of Xenoctenidae that are endemic to, and widely distributed in the Caatinga. We redescribe and illustrate *Odo vittatus* (Mello-Leitão, 1936), the only xenoctenid species previously known from the Caatinga. Based on a comparative morphological study of xenoctenids, we transfer this species to *Xenoctenus* Mello-Leitão, 1938, a genus currently known from six species restricted to Argentina, Bolivia, and Colombia. We also newly describe

the male of *Xenoctenus vittatus* **comb. nov.** and provide new records of this species, which was hitherto known only from the type-locality, throughout the Caatinga and nearby semiarid vegetation formations. We also describe and illustrate a new species, *Xenoctenus kaatinga* **sp. nov.**, based on males and female specimens collected throughout the Caatinga. Additionally, we propose diagnostic characters for *Xenoctenus* and redescribe the type-species, *X. unguiculatus*.

Key words:

seasonally dry tropical forest; spider; taxonomy; dry environments; geographic distribution.

1. Introduction

The Caatinga is the largest and most biodiverse seasonally dry tropical forest (SDTF) of the world, spanning over 860.000 km² in northeastern Brazil (IBGE 2019; Silva *et al.* 2017). Most of the Caatinga are in interplanaltic depressions, with occasional vegetation formations in plateaus (Prado 2003). The biome also has different types of soil, from shallow and rocky to deep and sandy, forming flat surfaces between 300 and 500 meters above sea level. The climate is semiarid, characterized by high temperature, ranging from 25 to 30 °C, and low and intermittent precipitation (Silva *et al.* 2017). All these geomorphologic and climatic features make the Caatinga a particularly harsh and unpredictable habitat surrounded by tropical mesic biomes. It is also a natural laboratory for the study of species adaptation and diversification in stressful environments (Liberal *et al.* 2011; Moro *et al.* 2015; Silva *et al.* 2018; Silva & Souza 2018; Lira *et al.* 2019). Its importance for biogeographic and evolutionary studies is only reinforced by its long-term climatic stability, as the Caatinga apparently passed through the Quaternary climatic oscillations without significant temperature and precipitation changes, though it could have experienced occasional drier conditions (Prado 2003).

Despite its importance as a center of endemism, the Caatinga is still insufficiently sampled, with species records usually concentrated in a small portion of its area (Correia *et al.* 2019; Oliveira *et al.* 2016, 2017; Santos *et al.* 2011). This situation is particularly worrying considering the growing threats to the Caatinga natural habitats and how poorly represented they are in conservation units (Aguiar *et al.* 2002). Additionally, the knowledge gaps about the Caatinga biodiversity are especially pronounced regarding the invertebrate fauna, arthropods in particular (Oliveira *et al.* 2016, 2017).

Regarding its spider fauna, the Caatinga is among the least known biomes in Brazil. The density of species records is particularly low throughout the biome, as 73% of its area remains unsampled (Carvalho *et al.* 2014; Oliveira *et al.* 2017). However, studies on endemic spiders from the Caatinga show interesting results about their ecology, biogeography, and systematics, corroborating the Caatinga as a nucleus of diversification for many taxa (Carvalho *et al.* 2015, Magalhaes *et al.* 2014, 2019; Oliveira *et al.* 2017). For instance, the genus *Sicarius* Walckenaer, 1847 (Sicariidae), which is known only from xeric environments, is represented in the Caatinga by six endemic species (Magalhaes *et al.* 2017), which diversified in isolation from the rest of the genus since at least the last 20 million years (Magalhaes *et al.* 2019). In this study, we report on another (though not so diversified) spider group from the Brazilian Caatinga, the desert wolf spiders (Platnick *et al.* 2020) of the genus *Xenoctenus* Mello-Leitão, 1938.

Xenoctenidae Ramírez & Silva-Davila, 2017 is an exclusively Neotropical family of wandering spiders, which was recently delimited to group 33 species distributed in four genera: *Incasoctenus* Mello-Leitão, 1942; *Odo* Keyserling, 1887; *Paravulsor* Mello-Leitão, 1922; and *Xenoctenus* (Wheeler *et al.* 2017; World Spider Catalog 2023). Despite the importance of recognizing a family for those genera, which have been originally classified in different families, and the accumulated information on their morphology and phylogenetic position (Silva-Dávila 2003; Ramírez 2014; Wheeler *et al.* 2017), most xenoctenid species were not revised after their original description (World Spider Catalog 2023). Consequently, several species of the family might be wrongly positioned in their genera. For instance, in a recent phylogenetic study on the family, we concluded based on morphological characters that the only xenoctenid species described from the Caatinga, *Odo vittatus* Mello-Leitão, 1936, does not compose a monophyletic group with other species of *Odo* (including the type-species) but should belong in *Xenoctenus* (Faustino-Magalhaes 2019, Faustino-Magalhaes & Santos, in prep.).

Xenoctenus comprises four species from Argentina (*X. marmoratus* Mello-Leitão, 1941; *X. pampeanus* Mello-Leitão, 1940; *X. patagonicus* Mello-Leitão, 1940; and *X. unguiculatus* Mello-Leitão, 1938) and two species from Bolivia and Colombia, *X. gomezraggioi* Carcavallo & Martínez, 1967 and *X. proseni* Carcavallo & Martínez, 1967, respectively (World Spider Catalog 2023). Thus, transferring *O. vittatus* to *Xenoctenus* represents not only a new genus record from Brazil, but also a considerable range expansion for the genus. Our extensive survey of xenoctenid collection samples revealed not only that *O. vittatus* is restricted to and widely

distributed in the Caatinga domain, but also an undescribed, and equally endemic new species of *Xenoctenus*.

Our taxonomic research on the family has brought to light a nomenclatural issue concerning Xenoctenus, in addition to numerous challenges related to delineating the boundaries of its various species. The holotypes of X. patagonicus, X. marmoratus, and X. unguiculatus are all juveniles (although those of the latter two were originally reported as adult females), and the three species were described with no illustrations or reference to genital characters (Mello-Leitão 1938; 1940; 1941; Pereira et al. 1999). Prosen (1951) described a male for X. *marmoratus*, including illustrations of the male palp and female epigynum. Those illustrations, which were provided by Max Birabén (Prosen 1951), were reported to represent a male from Santiago del Estero (Argentina) examined by Prosen (1951), and the female holotype. This latter information is a mistake, as the holotype is a juvenile, so it is not clear which specimen was illustrated. Later, Carcavallo & Martínez (1967) revised the genus, describing two new species from Bolivia and Colombia (X. gomezraggioi and X. proseni, respectively) and considered X. unguiculatus and X. patagonicus as species inquirendae. This is particularly vexing because the latter is the type species of the genus. Since the article 67.2.5 of the ICZN (1999) states that type-species of genera should not be species with doubtful status, the identity of the genus in itself would require a clarification of *X. unguiculatus* identity.

In this study we propose a taxonomic and geographic revision of the Brazilian *Xenoctenus* species, by redescribing and illustrating *X. vittatus* **comb. nov.** and describing and illustrating *X. kaatinga* Faustino-Magalhaes & Santos **sp. nov.** for the first time. As a result, we report another spider group endemic to, and widespread throughout the Caatinga. Additionally, we redescribe *X. unguiculatus* based on adult specimens from Argentina, removing the species from the *species inquirenda* status and thus reinstating the validity of the genus. In the process, we also discovered that *X. marmoratus* should be considered a junior synonym of *X. unguiculatus*. However, the remaining non-Brazilian species of the genus remain in need of revision and species redescriptions and illustrations.

2. Material and Methods

The specimens examined are deposited in the following scientific collections: Centro de Coleções Taxonômicas, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil

(UFMG, curator A.J. Santos); Coleção de História Natural da Universidade Federal do Piauí, Piauí, Brazil (CHNUFPI, E.F.B. Lima); Instituto Butantan, São Paulo, Brazil (IBSP, A.D. Brescovit); Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina (MACN, M.J. Ramírez); Laboratorio de Biología Reproductiva Y Evolución, Córdoba, Argentina (LABRE, A.V. Peretti). Museo de La Plata, La Plata, Argentina (MLP, L.A. Pereira); Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brazil (MNRJ, A.B. Kury); Museu Paraense Emílio Goeldi, Belém, Brazil (MPEG, A.B. Bonaldo); National Museum of Natural History, Smithsonian Institution, Washington D.C., USA (NMNH, H. Wood).

Specimens were examined immersed in 80% ethanol under a Labomed Luxeo 4D stereomicroscope and measured under an Olympus SZ40 stereomicroscope or from digital images. All measurements are in millimeters. The female epigynum were removed and cleaned by immersion in a pancreatin solution, following the protocol of Álvarez-Padilla & Hormiga (2007). Because the epigynum and copulatory bulb of *Xenoctenus* species are usually strongly sclerotized, these structures were partially bleached by immersion in 6% hydrogen peroxide for three hours (modified from Wirth & Hildebrandt 2022). One male palp of *X. kaatinga* was accidentally expanded during the bleaching process (Fig. 12A, B). The palp of *X. vittatus* was expanded in 10% KOH for about 8 hours (Fig. 8).

The specimens were illustrated through multifocal digital images taken with a Leica DFC500 digital camera coupled to a Leica M205C stereomicroscope, and a Leica DFC295 digital camera coupled to a Leica M205C stereomicroscope stereomicroscope. Images were assembled into multifocal images using Leica Applications Suite Version 3.8.0 software (Leica Inc.) or with Helicon Focus 6.7.1 Pro (www.heliconsoft.com). Samples for Scanning Electron Microscopy (SEM) were removed from specimens, dried at room temperature, and mounted on stubs using conductive adhesive copper tape. The samples were sputter-coated with 10 nm of gold-palladium and examined in a Quanta 2000 SEM at the Centro de Microscopia of UFMG.

Morphological terminology follows Ramírez (2014). Species descriptions and material examined lists were assembled using spreadsheets developed by Magalhaes (2019). Geographic coordinates were taken from sample labels, when available, or obtained online using Google Earth Pro. The map was assembled and edited using the QGIS 3.30.2 's-Hertogenbosch (available in <u>https://qgis.org</u>).

3. Taxonomy

Family Xenoctenidae Ramírez & Silva-Dávila, 2017

Genus Xenoctenus Mello-Leitão, 1938

Type species. *Xenoctenus unguiculatus* Mello-Leitão, 1938, by monotypy (considered a *nomen dubium* by Carcavallo & Martínez 1967).

Emended diagnosis. *Xenoctenus* species can be differentiated from other Xenoctenidae by the presence of a flexible tarsus in both sexes (Fig. 10B). Males can be distinguished from other xenoctenids by the tip of the cymbium with a thick scopula, without macrosetae (Figs 5, 7A–C, 8, 11A–C, 12A–B, 13A, C). The palp also differs by the retrolateral tegular projection (RTP) long, concave and located anteriorly (Figs 4A–C, 7A–C, 8, 11A–C, 12A–B, 13A, C). Females differ by a strongly sclerotized epigynum and the primary spermathecae long, with irregular margins, and secondary spermathecae anteriorly positioned (Figs 6, 9, 10A, 12C–D).

Distribution. The genus is mostly known from xeric environments in Argentina and northeastern Brazil (Caatinga domain), with isolated records in southern Brazil and northeastern Argentina (Figs 14–16). Records from Bolivia and Colombia (Carcavallo & Martínez 1967) require further confirmation.

Xenoctenus unguiculatus Mello-Leitão, 1938

Figs 1F, 2–6, 14, 15

Xenoctenus unguiculatus Mello-Leitão, 1938: 101 (immature holotype from Argentina, San Luis, Desaguadero [33°24'3.05" S, 67°9'14.94"W, alt. 461 m], Bruch coll., deposited in MLP 14093, examined.

Xenoctenus marmoratus Mello-Leitão, 1941: 160, pl. 8, fig. 38 (immature holotype from Argentina, Tucumán, Bañado [26°25'19.71" S, 65°57'44.99"W, alt. 1721 m], Birabén coll., Feb.1939, deposited in MLP 14835, examined. Prosen 1951: 57, figs 1–3; Lehtinen 1967: 457, fig. 407; Carcavallo & Martínez 1967: 78, figs 2, 6. **Syn. nov.**

Xenoctenus sp. — Ramírez 2014 (voucher specimens MACN-Ar 45040 and MACN-Ar 45039, examined).

Diagnosis. Males of *X. unguiculatus* are similar to *X. kaatinga* in the elongated, longer than wide cymbium and copulatory bulb (Figs 5, 11A–C), but can be distinguished by the thinner median apophysis and the acuminated apex of the retrolateral tegular projection (RTP, Figs 4B, 5B). Males of *X. unguiculatus* differ from *X. vittatus* by the presence of the RTA similar to a macrosetae and from *X. kaatinga* by the RTA with the pointed tip (Figs 5B, C). Females of *X. unguiculatus* resemble those of *X. kaatinga* in the elongated epigynum (Figs 6A, C, 12C), but can be differentiated by the presence of posterior, medially directed teeth on the lateral lobes extension (LLE, Fig. 6A, C).

Remarks. The holotype of *X. unguiculatus* are a small juvenile, too old and fragmented to allow the identification of the species (Fig. 2). We identified this species based on specimens collected throughout northern and northwestern Argentina, including samples taken around 60 km from the type-locality (Fig. 15). The holotype of *X. marmoratus* is also a juvenile, though at least with partially preserved color pattern (Fig. 3). We proposed the synonymy of this species with *X. unguiculatus* because the former type-locality is located within the distribution range of the latter (Fig. 15). Our decision is further supported by the absence of any *Xenoctenus* species in collection samples collected near the type locality, except for the one described and illustrated herein.

Description. MALE FROM PARQUE NACIONAL SIERRA DE LAS QUIJADAS, SAN LUIS, ARGENTINA (MACN-AR 45013; FIG. 4). Carapace light brown, with dark brown irregular bands at its margin, dark brown radial lines, enhanced by dark setae, and a median darker line (Fig. 4D). Paler area of the carapace covered with white setae, denser on the cephalic area and the border of the carapace (Fig. 4D). Opisthosoma dorsally light brown with irregular darker areas and patches of white setae dorsally (Fig. 4D). Venter light brown. Eight eyes in two recurved rows surrounded by a dark line, except for the smaller and pale ALE (Figs 2B, 3B, 4D). Chelicerae reddish brown. Labium, endites and sternum light brown. Legs yellowish, with darker dorsal markings on femora and patellae (Fig. 4D), with dense scopula on the tarsus and less dense on metatarsus and the apex of tibia. Pedipalps light brown, tibia with ventral macrosetae, with a small, inconspicuous RTA, which is covered by short, white setae (Fig. 5B, C). Cymbium covered by setae and with an apical thick scopula (Fig. 5). Copulatory bulb sclerotized, dark-brown to black, longer than wide (Figs 4A–C, 5). Conductor membranous and translucent (Fig. 4B, 5B). Embolus flat, with a basal locking lobe (ELL) connected to the subtegular locking lobe (StLL, Fig. 4B). Retrolateral tegular projection (RTP) thick and curved apically (Figs 4B, 5B), followed by an additional retrolateral projection (Fig. 4C, 5C). Tegular distal division (TDD)

triangular (Figs 4B, 5B) Median apophysis longitudinally oriented and flat (Figs 4B, C, 5B, C). Total length 17.82. Carapace length 8.78, width 7.18. Eye diameters: AME 0.30, PME 0.40, ALE 0.25, PLE 0.35. Femur of leg I: 11.97, II 11.70, III 10.77, IV 13.03.

FEMALE FROM PARQUE NACIONAL SIERRA DE LAS QUIJADAS, SAN LUIS, ARGENTINA (MACN-AR 45013; FIG. 6 C, D). Coloration as in male (Fig. 1F). Epigynum with lateral lobes very sclerotized, dark brown, median field membranous (Fig. 6A, C). Internal genitalia sclerotized, dark brown. Primary spermathecae long and secondary spermathecae shorter and rounded, located anteriorly (Fig. 6B, D). Total length 18.49. Carapace length 9.18, width 7.58. Eye diameters: AME 0.37, PME 0.38, ALE 0.30, PLE 0.42. Femur of leg I 9.31, II 8.78, III 8.78, IV 11.04.

Variation. Female body size exhibit significant variation, even among specimens collected from the same locality. Female epigynum vary in orientation of the lateral lobes, which can be near straight (Fig. 6A) to angled (Fig. 6C). Although males are also variable in body size, the palp does not show any significant variation. Total body length: females, 16.63–22.08 (n=10); males, 12.10–23.14 (n=24).

Distribution. Southern Brazil and Argentina, in Buenos Aires and the central and northern zones of western Argentina, in the Chaco, Monte and Pampean biogeographic provinces (*sensu* Morrone *et al.* 2022) (Fig. 15).

Additional material examined. BRAZIL. Rio Grande do Sul: *Porto Alegre*, P. Buck coll., VIII/1962, 1 #ff (IBSP 1787). ARGENTINA. Buenos Aires: L. Coronel coll., VII/1988, 1 #m (IBSP 5022). Salta: *Guachipas*, Magnesita, La Salamanca, Valles Calchaquíes, 7 km de Alemanía [25°37'27.11"S, 65°36'46.49"W, 1184 m], Ramírez, M. J. & Goloboff, P.A., 17/VII/1995, 1 #f (MACN-Ar 17966). Formosa: *Bermejo*, Reserva Natural Formosa, Seccional Río Teuco [24°18'42.20"S, 61°48'44.50"W, 178 m], Izquierdo, M. A., 27/VI-05/VII/2010, 1 #m (MACN-Ar 27353). Chaco: *General Güemes*, El Pintado [24°41'21.95"S, 61°25'37.28"W, 157 m], Bachmann, A., XI/1959, 1 #m (MACN-Ar 5444); Paraje La Armonía [25°10'52.72"S, 61° 5'42.89"W, 138 m], Damer, L., 12/X/2013, 1 #f (MACN-Ar 33414). Catamarca: *La Paz*, Recreo [29°16'34.6''S, 65°3'51.4''W], 4/XII/1956, 1 #m (MACN-Ar 17983); *Andalgalá*, Andalgalá [27°35'30.88"S, 66°19'10.61"W, 1041 m], Enders, 19/X/1972, 2 #m (MACN-Ar 18002); *Villavil*, Frank A. Enders coll., 30/XII/1973, 3 #m 1 #ff (NMNH); ditto, 30/XII/1974, 3 #m 1 #ff 1 imm. (NMNH); 2/XII/1972, 2 #ff 1 imm. (NMNH); 29/X/1972, 1 #m (NMNH); 1 #m (NMNH); 1 #ff 1 imm. (NMNH); 29/X/1972, 2 #ff 1 imm. (NMNH); 30/XII/1973, 1 #ff 1 imm. (NMNH); 30/XII/1973, 1 #ff 1 imm.

(NMNH); 27/I/1972, 1 #ff 1 imm. (NMNH); 23/XI/1972, 1 #m (NMNH); 5/I/1974, 1 #m (NMNH); 11/II/1974, 1 #m 4 imm. (NMNH); 30/XII/1973, 2 #m 2 #ff (NMNH); 23/XI/1972, 2 #ff 1 imm. (NMNH); 25/I/1974, 1 #ff (NMNH – USNMENT 01458297). La Rioja: without exact locality, Viana, J. M., XI/1959, 1 #m (MACN-Ar 17975); Independencia, Patquía, Guayapa [30°2'41.34"S, 66°52'52.54"W, 434 m], Maury, E. A., III/1965, 1 #m (MACN-Ar 17970); Galiano, M. E., X/1963, 1 #m (MACN-Ar 17969); Capital, Dique Los Sauces [29°23'5.75"S, 66°58'47.90"W, 850 m], Maury, E., 7-8/X/1965, 1 #f 3 imm. (MACN-Ar 45040). Santiago del Estero: Guasayan, Santa Catalina [28° 7'18.31"S, 64°46'51.70"W, 436 m], Galiano, M. E., 26/X/1963, 1 #m, 1 #f (MACN-Ar 45039); Moreno, Mercedes, 10 km E de Amamá [27°12'26.22"S, 62°56'7.47"W, 161 m], Vezzani, D., VII/1995, 1 #f 17 imm. (MACN-Ar 17971); Weisburd [27°19'22.55"S, 62°35'9.24"W, 153 m], 22/IX/1947, 1 #f (MACN-Ar 17997); Robles, Fernández [27°55'16.71"S, 63°53'30.37"W, 154 m], Salguero, J., IX/1960, 1 #f 1 imm. (MACN-Ar 17972); Choya, [28°29'42.56"S, 64°51'33.78"W, 384 m], Salguero, J., 12/X/1961, 1 #m 1 imm. (MACN-Ar 17982); Salguero, J., 05/V/1962, 6 #m 1 #f 4 imm. (MACN-Ar 18001); 1 #f (MACN-Ar 34165); Villa La Punta [28°22'12.76"S, 64°47'34.53"W, 389 m], Donado, O., 18/II/1981, 1 #m (MACN-Ar 17974). San Juan: Sierra pie de palo, vega, 25 km (por aire) W de El Bosque [LNP-loc-34] [31°22'50.27"S, 68°8'19.82"W, 996 m], Piacentini, L.N., Ojanguren, A. & Mattoni, C., 20/XII/2014, 1 #f (MACN-Ar 34662); Valle Fértil, Reserva Natural Provincial Valle Fértil, (JPA-Loc-03) [30°41'10.99"S, 67°30'15.97"W, 952 m], Pardó, J., 12/III/2014, 1 #m (MACN-Ar 35606); Caucete, Al costado de la Ruta Provincial N°141, 25 km (por aire) NW de Caucete [LNP-loc-35] [31°45'30.71"S, 68° 3'6.01"W, 687 m], Piacentini, L.N., Ojanguren, A. & Mattoni, C., 20/XII/2014, 1 #f (MACN-Ar 35624). San Luis: Parque Nacional Sierra de las Quijadas [32°29'37.4''S, 66°59'33.5''W, 765 m], C. Grismado et al. coll., 7/XI/2013, 1 #ff (MACN-Ar 31091); Parque Nacional Sierra de las Quijadas, alrededores del área de servicios (CJG-Loc-03a) [32°28'8.40"S, 66°57'39.06"W, 710 m], C.J. Grismado et al. coll., 04/XI/2013, 1 #f (MACN-Ar 33447); Parque Nacional Sierra de las Quijadas, al costado de la ruta, camping viejo [32°29'45.06"S, 67° 0'11.67"W, 817 m], A. Ojanguren et al. coll., 01/II/2022, 1 #m 1 #f (MACN-Ar 45013); Parque Nacional Sierra de las Quijadas, al costado de la ruta, camino al mirador [32°29'43.95"S A Ojanguren et al. coll., 01/II/2022 1 #m (MACN-Ar 66°59'41.30"O, 794 m], 45277); La Capital, San Gerónimo [33° 8'18.76"S, 66°31'20.13"W, 541 m], II/1977, 1 #f (MACN-Ar 18003). Mendoza: Lavalle, Reserva Natural y Cultural Bosques Telteca, 100 m a la redonda del puesto El Pichón (RBT-Loc-11) [32°22'32.11"S, 68° 2'46.78"W, 554 m], Botero Trujillo, R. & Carbajal, A. L., 14/XI/2015, 1 #m (MACN-Ar 35619); 3 imm. (MACN-Ar 38991); 1 #m (MACN-Ar 40932). **Córdoba**: *Ischilin*, Salinas Grandes [29°49'23.88"S, 64°47'34.17"W, 180 m], Equipo LABRE coll., 24/XI/2016 1 #m (LABRE 319); *Pocho*, Chancaní [31°24'59.78"S, 65°26'59.55"W 383 m] Izquierdo, M., pit fall traps, 15/XI/2005 1 #m (LABRE 246); 1 #m (LABRE 244); 1 #m (LABRE 245). **La Pampa**: *Curacó*, Gobernador Duval [38°43'33.95"S, 66°26'19.86"W, 222m], M. Izquierdo & H. Iuri coll., 19/01/2018, 1 #m (LABRE 350).

Xenoctenus vittatus (Mello-Leitão, 1936) comb. nov. Figs 1A–E, 7–10, 13A, B, 14, 16

Horioctenus vittatus Mello-Leitão, 1936: 27, pl. 2, fig. 50 (female holotype from Brazil, Paraíba, Rudolf von Ihering coll., deposited in MNRJ 42491, examined, survived the 2018 fire). Bonnet 1957: 2235.

Odo vittatus — World Spider Catalog 2023 (combination implied by the synonymy of *Horioctenus* Chamberlin, 1916: 265 with *Odo* Keyserling, 1887: 454 by Lehtinen 1967: 239).

Diagnosis. Males of *X. vittatus* can be distinguished from males of all other species by the palp having the tegular distal division (TDD) thin and concave, with a sharp tip (Figs 7A–C, 8, 13A). Additionally, they differ by the median apophysis being large and flat (Figs 7A–C, 8B, C, 13A) and by the copulatory bulb rounded, as long as wide (Figs 7A–C, 8, 13A). Differ from *X. unguiculatus* and *X. kaatinga* by the RTA very reduced, without projection, represented by a dark spot on a ledge (Figs. 7C, 8B). Females of *X. vittatus* differ from those of other *Xenoctenus* by the lateral lobe extension (LLE) ending in the middle of the epigynum, not crossing the lateral lobes, and by the median field (MF) dark, very sclerotized (Figs 9A, C, E, 10A). Females resemble those of *X. pampeanus* in the median field with a longitudinal groove, formed by a central epigynal fold, where the copulatory ducts are connected (Figs 9, 10A, 13B), but differ by the copulatory opening located anteriorly at the epigynum (Fig. 9B, D, F).

Description. *MALE FROM ZONA RURAL, JAGUARIBE, CEARÁ, BRAZIL (CHNUFPI 2521; FIG. 2A–C)*. Carapace light brown, with dark brown lateral bands running from eyes to posterior margin of carapace (Figs 1A, C, E, 7D). Opisthosoma light brown dorsally, anteriorly with dark brown lateral bands, following carapace pattern, and densely covered by setae (Figs 1A, C, E, 7D). Venter fully light brown. Eight eyes in two recurved rows surrounded by dark line, except for the smaller and pale ALE (Fig. 7D). Chelicerae light brown with median dark brown band.

Labium, endites and sternum brown. Legs light brown, with dark spots (Figs 1A, C, E, 7D), with dense tarsal scopula, macrosetae and claw tufts (Fig. 10B) Pedipalps light brown, tibia with ventral macrosetae and retrolateral tibial apophysis small, covered by small setae (Figs 7B, C, 8). Cymbium covered by setae and with apical thick scopula (Figs 7A–C, 8, 13A). Copulatory bulb sclerotized and dark, as long as wide (Figs 7A–C, 8). Conductor membranous, translucent (Figs 7B, C, 8C, 13A). Embolus flat, with basal locking lobe (ELL) connected to subtegular locking lobe (StLL, Figs 7A–C, 8, 13A). Tegular distal division (TDD) concave, with a sharp tip and one median tooth (Figs 7A–C, 8, 13A). Retrolateral tegular projection (RTP) long, concave, following conductor (Figs 7A–C, 8, 13A). Median apophysis large, flat, and bending inwards apically (Figs 7A–C, 8, 13A). Total length 10.80. Carapace length 5.50, width 4.60. Eye diameters: AME 0.31, PME 0.43, ALE 0.20, PLE 0.43. Femur of leg I: 5.60, II 5.50, III 5.90, IV 7.20.

FEMALE FROM FAZENDA VELHA, JEQUIÉ, BAHIA, BRAZIL (UFMG 13690; FIG. 5). Coloration as in male (Figs 1B, D). Epigynum with lateral lobes and median field very sclerotized, dark brown (Fig. 10A). Lateral lobes extension (LLE) located anteriorly and covering partially lateral lobes (Fig. 9A, C, E). Median field with central fold forming a groove where copulatory ducts connect (Figs 9, 13B). Internal genitalia sclerotized, dark brown (Fig. 9B, D, F). Primary spermathecae long; secondary spermathecae shorter, rounded, located anteriorly (Figs 9B, D, F, 13B). Total length 14.50. Carapace length 6.13, width 4.90. Eye diameters: AME 0.35, PME 0.64, ALE 0.26, PLE 0.64. Femur of leg I 5.80, II 5.80, III 5.60, IV 7.10.

Variation. Female body size and genitalia exhibit significant variation, even among specimens collected from the same locality. Female epigynum varies in the edges of the lateral lobes extension (LLE), which can be straight (Fig. 9A) or angled (Fig. 9C, E). Additionally, the median field can be narrow (Fig. 9A) or wide (Fig. 9C, E) and variably sclerotized. Internally, the secondary spermathecae can be medially (Fig. 9B) or anteriorly directed (Fig. 9D, F). Although males also vary in body size, the palp does not show any significant variation. Total body length: female, 9.50–18.0 (n=47); male, 8.13–13.0 (n=196).

Distribution. Northeastern Brazil, within the Caatinga domain. Distribution is known only for xeric environments, in the Caatinga *strictu sensu* but also in transition areas between Caatinga and Cerrado, and in sandy restinga forests (Fig. 16).

Additional material examined. BRAZIL. Bahia: *Brumado*, Magnesita [14°10'51.5''S, 41°42'0.7''W, 623 m], P.H. Martins *et al.* coll., 25/II/2017, 1 #m (UFMG 24328); 1 #ff (UFMG

24329); 1 #ff (UFMG 24330); 1 #m 4 #ff (UFMG 24331); Central, Fazenda do Paulo [11°8'7.86''S, 42°6'41.28''W, 699 m], E.F. Ramos coll., 15/VII/1997, 1 #m 5 #ff 3 imm. (IBSP 13336); Roça do Paulo, E.F.Ramos coll., 9/VII/1997, 1 #ff 1 imm. (IBSP 13341); Toca da Esperança, A.D. Brescovit coll., 21/VII/2000, 1 #ff (IBSP 210255); Zona rural, proximidades da BA-052 [11°10'13.1''s, 41°58'57.6''W, 772 m], L.S. Carvalho & B.T. Faleiro coll., 25/VIII/2016, 1 #ff (UFMG 20534); Guanambi, Fazenda do Seu Washinton [14°10'58.9''S, 42°48'45.9"W, 516 m], V. Mattos & C. Ubinski coll., 12/IV/2015, 1 #m (UFMG 20929); Proximidades do Aeroporto de Guanambi, Fazenda do Seu Luis [14°12'18.6''S, 42°43'33.8''W, 607m], L.S. Carvalho coll., 11/IV/2015, 1 #ff (UFMG 20602); Itaguaçu da Bahia, Proximidades da Toca da Esperança [11°1'52.9''S, 42°4'2''W, 568 m], L.S. Carvalho & B.T. Faleiro coll., 26/VIII/2016, 1 #m (UFMG 20535); 1 #ff (UFMG 20536); Jandaíra, Mangue Seco [11°28'12.92''S, 37°22'10.44''W], J. P. Alvez coll., 2-5/XI/2006, 1 #ff (IBSP 79622); Jequié, Fazenda Velha [13°52'12.8''S, 40°14'16.5''W, 255 m], G.H.F. Azevedo & A.J. Santos coll., 3/XII/2010, 1 #ff (UFMG 13690); ditto, [13°51'32.69''S, 40°5'1.6''W, 208 m], L. Bocardo coll., 1-11/VIII/2004-I/2005, 3 #m (IBSP 66319); ditto, 1-11/VIII/2004-I/2006, 1 #m (IBSP 66325); same collector, 1-11/VIII/2004-I/2007, 1 #m (IBSP 66329); 1-11/VIII/2004–I/2008, 1 #ff (IBSP 66339); 1–11/VIII/2004–I/2009, 2 #m (IBSP 66342); Paulo Afonso, Estação Ecológica Raso da Catarina [9°39'58.1''S, 38°28'15.1''W, 586 m], I.L.F. Magalhães & J.L. Chavari coll., 22-23/V/2012, 1 #ff (UFMG 20930); Senhor do Bonfim, Campus VII da UNEB [10°28'13.57"S, 40°10'10.63"W, 519 m], J.S. Costa coll., III-VIII/2008, 1 #m (IBSP 133717); 1 #m (IBSP 133718); 1 #ff (IBSP 133719); 1 #m (IBSP 133720); 1 #m (IBSP 133721); 1 #ff (IBSP 133723); 1 #m (IBSP 133724); 1 #m (IBSP 133725); 1 #m (IBSP 133726); 1 #m (IBSP 133727); 1 #m (IBSP 133728). Ceará: Aiuaba, Estação Ecológica de Aiuaba [6°36'6.5''S, 40°7'27.8''W, 424 m], I.L.F. Magalhães & A.J. Santos coll., 8/V/2012, 1 #ff (UFMG 20538); Jaguaribe, Zona rural [5°59'57.2''S, 38°32'11.8''W, 235 m], S.C. Sousa coll., 2014, 2 #m 1 #ff (CHNUFPI 2521); ito, 3 #m (UFMG 20056); Pentecoste, Fazenda Experimental Vale do Curu [3°48'28.5''S, 39°20'10''W, 54 m], I.L.F. Magalhães & A.J. Santos coll., 3/V/2012, 1 #m (UFMG 20950); 1 #ff 2 imm. (UFMG 20951); 1 #ff 3 imm. (UFMG 20952); Quixadá, Fazenda Magé [4°56'48.5''S, 39°1'22.8''W, 195 m], I.L.F. Magalhães & A.J. Santos coll., 6/V/2012, 1 #ff (UFMG 20894); 1 #ff (UFMG 27770); Santana do Cariri, Estrada de barro com barrancos para Santana do Cariri [7°7'25.66''S, 39°24'0''W, 750 m], A.B. Kury & A.P.L. Giupponi coll., 18/III/1999, 1 #m 1 imm. (MNRJ 3435). Maranhão: Barreirinhas, Parque Nacional dos Lençóis Maranhenses [2°29'13.27"'S, 43°7'41.94"W, 15 m], Equipe BIOTA coll., 12-18/X/2001, 1 #ff (IBSP 76664); 1 #m (IBSP 76666); 1 #ff (IBSP 76665); 1 #ff (IBSP 76667); Caxias, Reserva Ecológica Inhamum [4°53'31.94"'S, 43°24'49.13"W, 100 m], J.F.B. Lima Lobato & F. Limeira de Oliveira coll., 2-5/X/2007, 1 #ff (IBSP 129042); ito, 26-29/IX/2007, 1 #m (IBSP 129115). Minas Gerais: Itacarambi, Distrito de Fabião II [15°10'19''S, 44°10'49''W], G.F.B. Pereira et al. coll., 5-7/V/2012, 1 #ff (UFMG 13399). Paraíba: Araruna, Pedra da Boca [6°27'24.97''S, 35°40'32.46''W, 376 m], S.C. Dias coll., 3/X/2003, 2 #ff (IBSP 41353); Campina Grande, próximo à PB-138 [7°16'16.14''S, 35°58'19.7''W], 1 #m (UFMG 20537); 1 #ff (UFMG 20539); Malta, km 53 [6°54'23.06''S, 37°31'18.45''W, 260 m], P.F.L.Duarte coll., 25/IV/1978, 1 #ff (IBSP 57518); São João do Cariri [7°23'28.09''S, 36°31'57.07''W, 455 m], S.C. Dias coll., II/2004, 2 #ff (IBSP 43456); 1 #ff (IBSP 43454); Soledade [7°12'42.5''S, 36°16'23.2''W, 573 m], A. Kury & A. Giupponi coll., 16/III/1999, 1 #ff (MNRJ 1739). Pernambuco: Afogados da Ingazeira, Sítio Saco do Queiroz [7°45'3''S, 37°38'21''W], M. Carvalho coll., VI/2008, 1 #ff (UFMG 4327); Itacuruba, near to Riacho Itacuruba [8°47'14.8''S, 38°41'53.7''W, 309 m], S.C. Sousa coll., 2014, 1 #m 1 #ff (CHNUFPI 2508); 6 #m 6 #ff (UFMG 20060); Petrolina [9°11'44.5''S, 40°22'59.5''W, 450 m], A.S. Michelotto & B.A. Huber coll., 30/XI/2022, 1 #ff (UFMG 29171). Piauí: Alvorada do Gurguéia, Fazenda Escola da Universidade Federal do Piauí [8°22'11.5''S, 43°51'30.2''W], D.B.S. Barbosa et al. coll., 30/VI/2018, 13 #m 6 #ff (CHNUFPI 2448); 23 #m (CHNUFPI 2450); Piracuruca, Parque Nacional de Sete Cidades [4°5'56.2''S, 41°43'12.9''W], L.S. Carvalho coll., 27/I/2006, 1 #m (MPEG.ARA 7923); ito, 28/I/2006, 1 #m (MPEG.ARA 7924); 1 #m (MPEG.ARA 7925); 1 #m (MPEG.ARA 7927); 27/I/2006, 1 #m (MPEG.ARA 7928); 1 #ff (MPEG.ARA 7930); 1 #m (MPEG.ARA 7931); L.S. Carvalhoet al. coll., 10/IX/2006, 1 #m (MPEG.ARA 7929); Castelo do Piauí, Fazenda Bonito, ECB Rochas Ornamentais do Brasil LTDA [5°13'54.1''S, 41°42'1.7"W], F.M. Oliveira-Neto coll., 21/X/2005, 15 #m 1 #ff (CHNUFPI 2380); 19/X/2005, 25 #m (CHNUFPI 2381); 22/X/2005, 25 #m (CHNUFPI 2383); 28/X/2005, 21 #m (CHNUFPI 2384); same locality [5°13'46.7"'S, 41°41'29.9", same collector, 22/X/2005, 17 #m 3 #ff (CHNUFPI 2385); [5°13'54.1''S, 41°42'1.7''W, 21/X/2005, 4 #ff (CHNUFPI 2393); [5°13'50.8''S, 41°42'1.1''W], L.S. Carvalho & F.M. Oliveira-Neto coll., 13/IX/2006, 3 #m (MPEG.ARA 7932); 1 #m (MPEG.ARA 7933); 1 #ff (MPEG.ARA 7934); 1 #ff (MPEG.ARA 7935); L.S. Carvalho coll., 12/IX/2006, 2 #m (MPEG.ARA 7936); L.S. Carvalho & F.M. Oliveira-Neto coll., 13/IX/2006, 1 #ff (MPEG.ARA 7937); 1 #ff (MPEG.ARA 7938); F.M. Oliveira-Neto coll., 23/X/2005, 3 #m (MPEG.ARA 7939); 19/X/2005, 1 #ff (MPEG.ARA 7940); Guaribas, Parque Nacional da Serra das Confusões [9°13'12.3''S, 43°29'26.7''W], P.R.R. Silva et al. coll., VI/2007, 31 #ff (CHNUFPI 2398); 62 #m (CHNUFPI 2403); 50 #m

(CHNUFPI 2406); 19 #m (CHNUFPI 2413); [9°13'10''S, 43°29'27''W], Giovana coll., 11-26/I/2002, 1 #ff (IBSP 56027); São Raimundo Nonato, Parque Nacional da Serra da Capivara [8°41'42.82''S, 42°35'10.18''W, 565 m], T. Falotico coll., IX-X/2007-2010, 1 #ff (IBSP 168543); R. Recorder coll., 10-03/II-III/2013, 1 #m 1 #ff (IBSP 168388). Rio Grande do Norte: João Câmara, João Câmara [5°32'15''S, 35°49'11''W], N. Sebastian et al. coll., 1/X/2012, 1 #ff 22 imm. (MPEG.ARA 23631); 1/VI/2012, 1 #m 15 imm. (MPEG.ARA 23632); 1 #ff 3 imm. (MPEG.ARA 23633); 1 #m 4 #ff 15 imm. (MPEG.ARA 23634); 3 #m 6 imm. (MPEG.ARA 23635); 1 #m 4 #ff 12 imm. (MPEG.ARA 23636); 4 #ff 13 imm. (MPEG.ARA 23637); 3 #m 1 #ff 5 imm. (MPEG.ARA 23639); 1 #m 3 #ff 6 imm. (MPEG.ARA 23640); 5 #m 3 #ff (MPEG.ARA 23641); 2 #ff 2 imm. (MPEG.ARA 23642); 2 #ff 15 imm. (MPEG.ARA 23816); 6 #m 1 #ff 11 imm. (MPEG.ARA 23817); 3 #ff 7 imm. (MPEG.ARA 23818); Zona rural [5°34'2.5''S, 35°55'3.3''W, 147m], L.S. Carvalho coll., 5/VI/2015, 1 #m (UFMG 20556); Mossoró [5°11'31.9''S, 37°20'32.57''W, 19 m], U.M. Maia coll., 10/XI/2007, 1 #m (IBSP 91660); Serra Negra do Norte, Estação Ecológica do Seridó [6°35'15.5''S, 37°15'19.62''W, 213 m], M. Maia coll., VI/2008, 1 #ff (IBSP 123381); 10–14/XII/2007, 1 #m (IBSP 124196); VI/2008, 1 #m (IBSP 123373); 1 #m (IBSP 123378); 1 #m 1 #ff (IBSP 123374); 1 #m (IBSP 123375); 1 #ff (IBSP 123379). Sergipe: Carindé do São Franscico, Usina Hidrelétrica do Xingó [9°37'33.77''S, 37°48'8.26''W, 71 m], M.E.V. Calleffo coll., 12-18/X/2002, 1 #m (IBSP 37226).

Xenoctenus kaatinga Faustino-Magalhaes & Santos sp. nov.

Figs 11 12, 13C, D, 14, 16

Type material. HOLOTYPE: BRAZIL. Piauí: *Alvorada do Gurguéia*, Fazenda Escola da Universidade Federal do Piauí [8°22'11.5''S, 43°51'30.2''W], D.B.S. Barbosa *et al.* coll., 30/VI/2018, 1 #m (CHNUFPI 4390). **PARATYPES:** BRAZIL. Piauí: *Alvorada do Gurguéia*, Fazenda Escola da Universidade Federal do Piauí [8°22'11.5''S, 43°51'30.2''W], D.B.S. Barbosa *et al.* coll., 30/VI/2018, 1 #ff (CHNUFPI 4391); *Guaribas*, Parque Nacional da Serra das Confusões [9°13'12.3''S, 43°29'26.7''W], P.R.R. Silva *et al.* coll., VI/2007, 2 #m (UFMG 30406).

Etymology. The specific epithet is the Tupi for white forest (ka'a [forest], tinga [white]), which is also the etymology of the Brazilian semi-arid Caatinga. Tupi is one of the major language families spoken by native people in Brazil.

Diagnosis. Males of *X. kaatinga* can be distinguished from those of all other species of the genus by the tegular distal division (TDD) oblong, with a straight tip (Figs 11A–C, 12A–B, 13C). Additionally, they differ from *X. vittatus* by the median apophysis thin and cylindrical (Figs 11B, C, 12A, 13C). The RTA of *X. kaatinga* differs from that of *X. vittatus* by the presence of a macrosetae-like projectins, and from *X. unguiculatus* by its straight tip (Figs 11C, 12B). Females of *X. kaatinga* resemble those *X. unguiculagus* in the epigynum longer than wide (Figs 6A, B, 12C, D), but differ by the lateral lobes extension (LLE) ending at the base of the epigynum, parallel to the lateral lobes (Fig. 12C). Females also differ from *X. vittatus* and *X. pampeanus* by the median field without a longitudinal groove (Fig. 12C). The internal female genitalia of *X. kaatinga* resemble that of *X. unguiculatus* in the secondary spermathecae medially curved and thinner than the primary spermathecae, but differ by the secondary spermathecae (Fig. 12D).

Description. *MALE FROM FAZENDA ESCOLA DA UFPI, ALVORADA DO GURGUÉIA, PIAUÍ, BRAZIL (CNHUFPI 2450; FIG. 6).* Carapace light brown, with dark brown lateral bands running from eyes to posterior margin of carapace (Fig. 11D). Opisthosoma light brown dorsally, with dark brown lateral bands, following carapace pattern, and densely covered by long setae anteriorly (Fig. 11D). Chelicerae light brown with median dark brown band. Labium, endites and sternum brown. Legs light brown, with dark spots (Fig. 11D). Pedipalps pale yellow, tibia with ventral macrosetae and entirely covered by setae (Figs 11C, 12B). Cymbium covered by setae and with apical thick scopula (Figs 11A–C, 12A, B, 13C). Copulatory bulb sclerotized, dark, longer than wide (Figs 11A–C, 12A, B). Conductor membranous and translucent (Figs 11A–C, 12A, B, 13C). Tegular distal division (TDD) oblong, with straight tip (Figs 11A–C, 12A, B, 13C). Retrolateral tegular projection apical, long, concave, following conductor (Figs 11A–C, 12A, B, 13C). Median apophysis thin, cylindrical (Figs 11B, C, 12A, 13C). Total length 10.20. Carapace length 5.30, width 4.80. Eye diameters: AME 0.33, PME 0.31, ALE 0.15, PLE 0.36. Femur of leg I: 6.80. II: 6.60. IV: 7.90.

FEMALE FROM FAZENDA ESCOLA DA UFPI, ALVORADA DO GURGUÉIA, PIAUÍ, BRAZIL (CNHUFPI 2448). Coloration as in male. Epigynum sclerotized, oval, longer than wide (Fig. 12C, D). Lateral lobes extension ending at base of epigynum (Fig. 12C). Median field lightly sclerotized, translucent, and without groove (Fig. 12C). Internal genitalia sclerotized, dark brown (Fig. 12D). Primary spermathecae long; secondary spermathecae shorter, thin, posteriorly directed

and medially adpressed to primary spermathecae (Figs 12D, 13D). Total length 14.40. Carapace length 5.90, width 4.80. Eye diameters: AME 0.36, PME 0.43, ALE 0.25, PLE 0.41. Femur of leg I: 5.30. II: 5.30. III: 5.40. IV: 7.00.

Variation. Different from *X. vittatus*, males and females of *X. kaatinga* do not show significant variation in genitalia or in body size. However, this might be a consequence of insufficient sampling, as *X. kaatinga* has a narrower distribution (Fig. 16) and is less represented in collections. Total body length: female, 13.8–14.4 (n=3). Male, 8.75–11.3 (n=21).

Distribution. Northeastern Brazil, at the middle portion of the Caatinga domain, in the Caatinga *stricto sensu* (Fig. 16).

Additional material examined. Bahia: Xique-Xique [10°49'24.05''S, BRAZIL. 42°43'30.08"W, 408 m], P. Rocha coll., 29/II/1996, 1 #m (IBSP 11806). Pernambuco: Buíque, Parque Nacional do Catimbau [8°36'0''S, 37°9'0''W], M.C. Carvalho coll., 2-4/VI/2007, 1 #m (UFMG 4843); Vale do Catimbau [8°35'30.3''S, 37°14'53.8''W], D. Araújo & D.M. Cella coll., 6/XI/2002, 1 #ff (IBSP 36919). Piauí: Alvorada do Gurguéia, Fazenda Escola da Universidade Federal do Piauí [8°22'11.5''S, 43°51'30.2''W], D.B.S. Barbosa et al. coll., 30/VI/2018, 3 #m 1 #ff (CHNUFPI 2448); 10 #m (CHNUFPI 2450); Guaribas, Parque Nacional da Serra das Confusões [9°13'12.3", 43°29'26.7", P.R.R. Silva et al. coll., VI/2007, 1 #m (CHNUFPI 2413); ito [9°13'10''S, 43°29'27''W], Giovana coll., 11–26/I/2002, 1 #m (IBSP 56027); São Raimundo Nonato, Parque Nacional da Serra da Capivara [8°41'42.82''S, 42°35'10.18''W, 565 m], R. Recorder coll., 10/II-3/III/2013, 1 #m (IBSP 168388).

4. Acknowledgements

We are grateful to all collection curators and assistants who make their xenoctenid material available for this study, and to Leonardo S. Carvalho and Alexandre S. Michelotto for providing additional specimens from Caatinga localities. Laboratory procedures were made possible by Kin Master Produtos Químicos, which provided a free sample of pancreatin, and the staff of Centro de Microscopia da UFMG. We are also indebted to Pedro H. Martins, Leonardo S. Carvalho and Hernan Iuri for providing their amazing photographs to illustrate this publication. Finally, our thanks to Diana Silva and Martín Ramírez for sharing their knowledge about Xenoctenidae, and Leonardo S. Carvalho for help in understanding the Caatinga limits, which

was instrumental to improve this study. This study was financially supported by a CAPES doctoral fellowship and a Rufford Foundation grant to MDFM, and by grants from FAPEMIG (PPM-00605-17), CNPq (405795/2016-5; 307731/2018-9, 311843/2022-0), and Instituto Nacional de Ciência e Tecnologia dos Hymenoptera Parasitóides da Região Sudeste Brasileira (http://www.hympar.ufscar.br/, CNPq 465562/2014-0, FAPESP 2014/50940-2) to AJS. In addition, collection expeditions by LNP in Argentina was carried out under grants PIP 2021-2023 11220200101990CO and PICT-2019-00597. LNP would like to thank the Parques Nacionales de Argentina for permission to collect, the staff of the Guardaparques of PN Sierra de las Quijadas, PN El Impenetrable and RN Formosa, in particular Guardaparque Juan Garro of PN Sierra de las Quijadas, Guardaparques Alvaro Becerra and Andres Alberto Vidal of RN Formosa and Gerardo Cerón and Alejandro Serrano of the Rewild Foundation for their willingness to accompany field work.

5. References

- Aguiar, J., Lacher Jr., T.E. & Da Silva, J.M.C. (2002) The Caatinga. *In:* Mittermeier, R.A., Mittermeier, C.G., Gil R.P., Pilgrim, J., Da Fonseca, G.A.B., Brooks, T. & Konstant, W.R. (Eds.). *Wilderness: earth's last wild places*. Cemex, Agrupación Serra Madre, S.C., Mexico, pp. 174–181.
- Álvarez–Padilla, F. & Hormiga, G. (2007) A protocol for digesting internal soft tissues and mounting spiders for scanning electron microscopy. *Journal of Arachnology*, 35, 538– 542.

https://doi.org/10.1636/Sh06-55.1

- Bonnet, P. (1957) Bibliographia araneorum. Analyse méthodique de toute la litérature aranéologique jusqu'en 1939. Tome II, 3me partie: G–M. Systématique des araignées (Étude par ordre alphabétique). Douladoure, Toulouse, 1927–3026.
- Carcavallo, R. U. & Martínez, A. (1967) Revision del genero *Xenoctenus* M. Leitão (Araneae: Ctenidae). *Segunda Jornada Entomoepidemiológica Argentina*, 1 (1965), 75–82.
- Carvalho, L.S., Brescovit A.D., Santos A.J., Oliveira, U. & Guadanucci, J.P.L. (2014) Aranhas da Caatinga. *In:* Bravo, F. & Calor, A. (Eds.) *Artrópodes do Semiárido: Biodiversidade e conservação*. Printmídia, Feira de Santana, pp. 15–32.

Carvalho, L.S., Sebastian, N., Araújo, H.F.P., Dias, S.C., Venticinque, E., Brescovit, A.D. & Vasconcellos, A. (2015) Climatic variables do not directly predict spider richness and abundance in semiarid caatinga vegetation, Brazil. *Environmental Entomology*, 44, 54–63.

https://doi.org/10.1093/ee/nvu003

- Chamberlin, R.V. (1916) Results of the Yale Peruvian Expedition of 1911. The Arachnida. *Bulletin of the Museum of Comparative Zoology*, 60, 177–299, pl. 1–25.
- Correia, R.A., Ruete, A., Stropp, J., Malhado, A.C.M., dos Santos, J.W., Lessa, T., Alves, J.A. & Ladle, R.J. (2019) Using ignorance scores to explore biodiversity recording effort for multiple taxa in the Caatinga. *Ecological Indicators*, 106, 105539.

https://doi.org/10.1016/j.ecolind.2019.105539

- Faustino–Magalhaes, M.D. (2019) Análise filogenética e revisão taxonômica de Xenoctenidae Ramírez & Silva–Dávila (Araneae). MsC. Dissertation, Universidade Federal de Minas Gerais, Belo Horizonte. Available from: http://hdl.handle.net/1843/32080
- IBGE (2019) Biomas e sistema costeiro-marinho do Brasil: compatível com a escala 1:250 000. Instituto Brasileiro de Geografia e Estatística & Coordenação de Recursos Naturais e Estudos Ambientais. IBGE (Ed.), 45: 164 pp. ISSN 0101-2843
- ICZN (1999) *International Code of Zoological Nomenclature*. Fourth edition. International Trust for Zoological Nomenclature, London, xxix + 306 pp.
- Keyserling, E. (1887) Neue Spinnen aus America. VII. Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien, 37, 421–490, pl. 6.

https://doi.org/10.5962/bhl.part.17676

- Lehtinen, P.T. (1967) Classification of the cribellate spiders and some allied families, with notes on the evolution of the suborder Araneomorpha. *Annales Zoologici Fennici*, 4, 199–468.
- Liberal, C.N., De Farias, A.M.I., Meiado, M.V., Filgueiras, B.K.C. & Iannuzzi, L. (2011) How Habitat Change and Rainfall Affect Dung Beetle Diversity in Caatinga, a Brazilian Semi–Arid Ecosystem. *Journal of Insect Science*, 11, 114.

https://doi.org/10.1673/031.011.11401

- Lira, A.F.A., Salomão, R.P. & Albuquerque, C.M.R. (2019) Pattern of scorpion diversity across a bioclimatic dry–wet gradient in Neotropical forests. *Acta Oecologica*, 96, 10–17. https://doi.org/10.1016/j.actao.2019.02.004
- Magalhaes I.L.F. (2019) Spreadsheets to expedite taxonomic publications by automatic generation of morphological descriptions and specimen lists. *Zootaxa*, 4624 (1), 147–150.

https://doi.org/10.11646/zootaxa.4624.1.12

Magalhaes, I.L.F., Oliveira, U., Santos, F.R., Vidigal, T.H.D.A., Brescovit, A.D. & Santos, A.J. (2014) Strong spatial structure, Pliocene diversification, and cryptic diversity in the Neotropical dry forest spider *Sicarius cariri*. *Molecular Ecology*, 23, 5323–5336.

https://doi.org/10.1111/mec.12937

Magalhaes, I.L.F., Brescovit, A.D. & Santos, A.J. (2017) Phylogeny of Sicariidae spiders (Araneae: Haplogynae), with a monograph on Neotropical Sicarius. Zoological Journal of the Linnean Society, 179, 767–864.

https://doi.org/10.1111/zoj.12442

Magalhaes, I.L.F., Neves, D.M., Santos, F.R., Vidigal, T.H.D.A., Brescovit, A.D. & Santos, A.J. (2019) Phylogeny of Neotropical *Sicarius* sand spiders suggests frequent transitions from deserts to dry forests despite antique, broad–scale niche conservatism. *Molecular Phylogenetics and Evolution* 140, 106569.

https://doi.org/10.1016/j.ympev.2019.106569

- Mello-Leitão, C.F. (1936) Contribution à l'etude des Ctenides du Bresil. *Festschrift Embrik Strand*, 1, 1–31.
- Mello-Leitão, C.F. (1938) Algunas arañas nuevas de la Argentina. *Revista del Museo de La Plata (N.S.)*, 1, 89–118.
- Mello–Leitão, C.F. (1940) Arañas de la provincia de Buenos Aires y de las gobernaciones de La Pampa, Neuquén, Río Negro y Chubut. *Revista del Museo de La Plata, N.S., Zool.*, 2, 3–62.

- Mello–Leitão, C.F. (1941) Las arañas de Córdoba, La Rioja, Catamarca, Tucumán, Salta y Jujuy colectadas por los Profesores Birabén. *Revista del Museo de La Plata, N.S., Zool.,* 2, 99–198.
- Moro, M.F., Silva, I.A., De Araújo, F.S., Lughadha, E.N., Meagher, T.R. & Martins, F.R. (2015) The role of edaphic environment and climate in structuring phylogenetic pattern in seasonally dry tropical plant communities. *PLoS ONE*, 10 (3), e0119166.

https://doi.org/10.1371/journal.pone.0119166

- Morrone, J.J., Escalante, T., Rodriguez-Tapia, G., Carmona, A., Arana, M. & Mercado-Gómez, J.D. (2022) Biogeographic regionalization of the Neotropical region: new map and shapefile. *Anais da Academia Brasileira de Ciências*, 94, e20211167.
- Oliveira, U., Paglia, A.P., Brescovit, A.D., de Carvalho, C.J.B., Silva, D.P., Rezende, D.T., Leite, F.S.F., Batista, J.A.N., Barbosa, J.P.P.P., Stehmann, J.R., Ascher, J.S., de Vasconcelos, M.F., De Marco, P., Löwenberg–Neto, P., Dias, P.G., Ferro, V.G. & Santos, A.J. (2016) The strong influence of collection bias on biodiversity knowledge shortfalls of Brazilian terrestrial biodiversity. *Diversity and Distributions*, 22, 1232–1244.

https://doi.org/10.1111/ddi.12489

Oliveira, U., Brescovit, A.D. & Santos, A.J. (2017) Sampling effort and species richness assessment: a case study on Brazilian spiders. *Biodiversity and Conservation*, 26, 1481–1493.

https://doi.org/10.1007/s10531-017-1312-1

- Pereira, L.A., Sutton, C.A. & Ramírez, M.J. (1999) Catálogo de tipos de Araneae (Arachnida) del Museo de La Plata. *Neotrópica*, 45 (113–114), 77–100.
- Platnick N.I., Hormiga, G., Jäger, P., Jocqué, R., Ramírez, M.I. & Raven, R.J. (2020) *Spiders* of the World: A Natural History. Princeton University Press, Princeton, 256 pp.
- Prado, D. (2003) As caatingas da América do Sul. *In:* Leal, I.E., Tabarelli, M. & Da Silva, J.M.C. (Eds.) *Ecologia e Conservação da Caatinga*. Ed. Universitária da Universidade Federal de Pernambuco, Recife, 3–73.

- Prosen, A.F. (1951) El alotipo de Xenoctenus marmoratus Mello-Leitão. Misión Estudios de Patología Regional Argentina, 22(80), 57–59.
- Ramírez, M.J. (2014) The Morphology and Phylogeny of Dionychan Spiders (Araneae: Araneomorphae). *Bulletin of the American Museum of Natural History*, 390, 1–374.

https://doi.org/10.1206/821.1

Santos, J.C., Leal, I.R., Almeida–Cortez, J.S., Fernandes, G.W. & Tabarelli, M. (2011) Caatinga: the scientific negligence experienced by a dry tropical forest. *Tropical Conservation Science*, 4 (3), 276–286.

https://doi.org/10.1177/194008291100400306

Silva, A.C. & Souza, A.F. (2018) Aridity drives plant biogeographical sub regions in the Caatinga, the largest tropical dry forest and woodland block in South America. *PLoS ONE*, 13 (4), e0196130.

https://doi.org/10.1371/journal.pone.0196130

Silva, J.M.C. da, Barbosa, L.C.F., Leal, I.R. & Tabarelli, M. (2017) The Caatinga: Understanding the Challenges. *In:* Silva, J.M.C. da, Leal, I.R. & Tabarelli, M. (Eds). *Caatinga: The Largest Tropical Dry Forest Region in South America*. Springer International Publishing, Heidelberg, pp. 3–19.

https://doi.org/10.1007/978-3-319-68339-3_1

Silva, U.B.T., Delgado–Jaramillo, M., de Souza Aguiar, L.M. & Bernard, E. (2018) Species richness, geographic distribution, pressures, and threats to bats in the Caatinga drylands of Brazil. *Biological Conservation*, 221, 312–322.

https://doi.org/10.1016/j.biocon.2018.03.028

- Silva-Dávila, D. (2003) Higher-level relationships of the spider family Ctenidae (Araneae: Ctenoidea). *Bulletin of the American Museum of Natural History*, 274, 1–86.
- Wheeler, W.C., Coddington, J.A., Crowley, L.M., Dimitrov, D., Goloboff, P.A., Griswold, C.E., Hormiga, G., Prendini, L., Ramírez, M.J., Sierwald, P., Almeida–Silva, L., Alvarez–Padilla, F., Arnedo, M.A., Benavides Silva, L.R., Benjamin, S.P., Bond, J.E., Grismado, C.J., Hasan, E., Hedin, M., Izquierdo, M.A., Labarque, F.M., Ledford, J., Lopardo, L., Maddison, W.P., Miller, J.A., Piacentini, L.N., Platnick, N.I., Polotow, D.,

Silva–Dávila, D., Scharff, N., Szűts, T., Ubick, D., Vink, C.J., Wood, H.M. & Zhang, J. (2017) The spider tree of life: phylogeny of Araneae based on target–gene analyses from an extensive taxon sampling. *Cladistics*, 33, 574–616.

https://doi.org/10.1111/cla.12182

- Wirth, V. von & Hildebrandt, K. (2022) Bleaching of Taxonomically Important Body Structures in Spiders Using the Example of Tarantulas (Araneae: Theraphosidae). *Journal of the British Tarantula Society*, 37, 34–41.
- World Spider Catalog (2023) World Spider Catalog. Version 24.5. Natural History Museum Bern. Available from: https://wsc.nmbe.ch (accessed 24 August 2023)
FIGURE LEGENDS

Figure 1. Xenoctenus spp., habitus of live specimens. A–E, *Xenoctenus vittatus* (Mello-Leitão, 1936) **comb. nov.** A, male and B, female from Guanambi, Bahia, Brazil (UFMG 20929). C, male (UFMG 24328) and D, female (UFMG 24330) from Brumado, Bahia, Brazil. E, male from Itaguaçu da Bahia, Bahia, Brazil (UFMG 20535). F, *Xenoctenus unguiculatus* Mello-Leitão, 1938, female from Parque Nacional Sierra de las Quijadas, San Luis, Argentina (MACN-Ar 45013). Photos by Pedro H. Martins (A–C), Leonardo S. Carvalho (D, E) and Hernán Iuri (F).

Figure 2. Xenoctenus unguiculatus Mello-Leitão, 1938, juvenile holotype (MLP 14093). A, C, habitus dorsal view. B, prosoma, frontal view. D, habitus, ventral view. E, original collection labels.

Figure 3. Xenoctenus marmoratus Mello-Leitão, 1941, juvenile holotype (MLP 14835). A, habitus, lateral view. B, prosoma, frontal view. C, habitus, dorsal view. D, habitus, ventral view. E, original collection vial with labels.

Figure 4. Xenoctenus unguiculatus Mello-Leitão, 1938. A, C, male from Reserva Natural y Cultural Bosques Telteca, Mendoza, Argentina (MACN-Ar 35619), palp. A, prolateral. B, ventral. C, retrolateral. D, habitus, dorsal view. Abbreviations: E, embolus; MA, median apophysis; RTP, retrolateral tegular projection; StLL, subtegular locked lobe. White star on tegular distal division (TDD).

Figure 5. Xenoctenus unguiculatus Mello-Leitão, 1938, male from PN Sierra de las Quijadas, San Luis, Argentina (MACN-Ar 45013). A, C, palp. A, prolateral. B, ventral. C, retrolateral. Abbreviations: C, conductor; E, embolus; MA, median apophysis; RTA, retrolateral tibial apophysis; RTP, retrolateral tegular projection. White star on tegular distal division (TDD).

Figure 6. Xenoctenus unguiculatus Mello-Leitão, 1938, female epigynum (A, C) and internal genitalia (B, D). A, B, female from Caucete, San Juan, Argentina (MACN-Ar 35624). A, ventral. B, dorsal. C, D, female from PN Sierra de las Quijadas, San Luis, Argentina (MACN-Ar 45013). C, ventral. D, dorsal. Abbreviations: CD, copulatory ducts; LL, lateral lobes; LLE, lateral lobes extension; MF, median field; S1, primary spermathecae; S2, secondary spermathecae.

Figure 7. Xenoctenus vittatus (Mello-Leitão, 1936) **comb. nov.** A–C, male from Jaguaribe, Ceará, Brazil (CNHUFPI 2521), bleached palp. A, prolateral. B, ventral. C, retrolateral. D, male from Castelo do Piauí, Piauí, Brazil, habitus (CHNUFPI 2385). Abbreviations: C, conductor; E, embolus; ELL, embolar locked lobe; MA, median apophysis; RTA, retrolateral tibial apophysis; RTP, retrolateral tegular projection; StLL, subtegular locked lobe. White star on tegular distal division (TDD).

Figure 8. Xenoctenus vittatus (Mello-Leitão, 1936) **comb. nov.**, male from Pentecoste, Ceará, Brazil (UFMG 20950). A–C, expanded palp. A, prolateral. B, ventral. C, retrolateral. Abbreviations: C, conductor; E, embolus; ELL, embolar locked lobe; MA, median apophysis; RTA, retrolateral tibial apophysis; RTP, retrolateral tegular projection; StLL, subtegular locked lobe. White star on tegular distal division (TDD).

Figure 9. Xenoctenus vittatus (Mello-Leitão, 1936) **comb. nov.**, bleached female epigynum (A, C, E) and internal genitalia (B, D, F). A–B, female from Jaguaribe, Ceará, Brazil (CNHUFPI 2521). A, ventral. B, dorsal. C–D, female from Guaribas, Piauí, Brazil (IBSP 56027). C, ventral. D, dorsal. E–F, female from Guaribas, Piauí, Brasil (CNHUFPI 2398). E, ventral. F, dorsal. Abbreviations: CD, copulatory ducts; LL, lateral lobes; LLE, lateral lobes extension; MF, median field; MG, median groove S1, primary spermathecae; S2, secondary spermathecae.

Figure 10. Xenoctenus vittatus (Mello-Leitão, 1936) **comb. nov.** from Jequié, Bahia, Brazil (UFMG 13690). A, female epigynum, not bleached. B, leg I, flexible tarsus.

Figure 11. Xenoctenus kaatinga **sp. nov.**, male from Alvorada do Gurguéia, Piauí, Brazil (CNHUFPI 2450). A–C, bleached palp. A, prolateral. B, ventral. C, retrolateral. D. habitus. Abbreviations: C, conductor; E, embolus; ELL, embolar locked lobe; MA, median apophysis; RTA, retrolateral tibial apophysis; RTP, retrolateral tegular projection; StLL, subtegular locked lobe. White star on tegular distal division (TDD).

Figure 12. Xenoctenus kaatinga **sp. nov.**, male and female from Alvorada do Gurguéia, Piauí, Brazil (CNHUFPI 2448). A–B, expanded, bleached male palp. A, prolateral. B, retrolateral. C, bleached female epigynum, ventral. D, bleached internal female genitalia, dorsal. Abbreviations: C, conductor; CD, copulatory ducts; E, embolus; ELL, embolar locked lobe; LL, lateral lobes; LLE, lateral lobes extension; MA, median apophysis; MF, median field; RTA, retrolateral tibial apophysis; RTP; retrolateral tegular projection; S1, primary spermathecae; S2, secondary spermathecae; St, subtegulum, StLL, subtegular locked lobe; T, tegulum. White star on tegular distal division (TDD). *Figure 13*. A–B, *Xenoctenus vittatus* (Mello-Leitão, 1936) **comb. nov.**, male and female from Itacuruba, Pernambuco, Brazil (UFMG 20060). A, male palp, ventral. B, female internal genitalia, dorsal. C–D, *Xenoctenus kaatinga* **sp. nov.**, male and female from Alvorada do Gurguéia, Piauí, Brazil (CHNUFPI 2448). C, male palp, ventral. D, female internal genitalia, dorsal. Abbreviations: C, conductor; CD, copulatory ducts; E, embolus; ELL, embolar locked lobe; MA, median apophysis; RTP, retrolateral tegular projection; StLL, subtegular locked lobe; S1, primary spermathecae; S2, secondary spermathecae. Black star on tegular distal division (TDD).

Figure 14. Geographic distribution records of *Xenoctenus* Mello-Leitão, 1938 in South America.

Figure 15. Geographic distribution records of *Xenoctenus unguiculatus* Mello-Leitão, 1938 in Argentina and southern Brazil. The "?" indicates that the specific locality is unknown as it was described only for the Province of Buenos Aires.

Figure 16. Geographic distribution records of *Xenoctenus kaatinga* **sp. nov.** and *Xenoctenus vittatus* (Mello-Leitão, 1936) **comb. nov.** on northeastern Brazilian Caatinga domain. The type locality of *X. vittatus* is uncertain, as it is reported only as the Brazilian state of Paraiba.

CHAPTER 2

Taxonomic review of Paravulsor, an endemic genus of the Atlantic Forest (Araneae:

Xenoctenidae)

Abstract

Xenoctenidae is a family of wandering spiders that inhabit the Neotropics and is composed by four genera: Incasoctenus Mello-Leitão, 1942; Odo Keyserling, 1887; Paravulsor Mello-Leitão, 1922; and Xenoctenus Mello-Leitão, 1938. Paravulsor is a monotypic genus from the Brazilian Atlantic Forest (BAF), known only from its original description. However, a morphology-based phylogenetic hypothesis and taxonomic revision of Xenoctenidae proposed by Faustino-Magalhães (2019) recovered Odo as a polyphyletic genus, with five species that should be transferred to *Paravulsor*. In the current study, we examined *Paravulsor* specimens collected from several localities throughout the BAF and deposited in scientific collections in, which resulted in an expansion of Paravulsor distribution and in the discovery of over 50 undescribed species. These discoveries demonstrated how poorly studied this group is and the necessity to review the Atlantic Forest xenoctenid's. Thus, in this study we revise the currently known species of Paravulsor. We transfer O. blumenauensis Mello-Leitão, 1927, O. obscurus Mello-Leitão, 1936, O. pulcher Keyserling, 1891, 1936 and O. similis Keyserling, 1891 to Paravulsor. We also synonymize O. serrimanus Mello-Leitão, 1936 with O. blumenauensis and we redescribe and illustrate all species, including the type-species, Paravulsor impudicus Mello-Leitão, 1922. A neotype is also designated for *P. impudicus*.

1. Introduction

The Brazilian Atlantic Forest (BAF) is among the world's most biodiverse and threatened ecosystems (Fundação SOS Mata Atlântica, 2019). Intact forests have been increasingly deforested over the years and currently comprises around 24% of its original extension (Marques et al., 2021). The Atlantic Forest is the biome with the highest proportion of threatened species in Brazil and over 45% of the BAF terrestrial fauna is threatened of extinction (IBGE, 2021). Additionally, this is the better-known biome in Brazil and the one with the highest spider species richness and (Oliveira et al., 2017). However, new species of spiders are still being described from the BAF over the years, which shows that there is still a

lot to be discovered about the Atlantic Forest spider fauna (Francisco et al., 2016; Huber, 2015, 2016; Huber & Rheims, 2011; Magalhães et al., 2016; Rheims, 2010, 2019).

Xenoctenidae Ramírez & Silva-Davila, 2017 is a family composed of wandering spiders that inhabit Neotropical forests and deserts. The family groups 33 species distributed in four genera: Incasoctenus Mello-Leitão, 1942; Odo Keyserling, 1887; Paravulsor Mello-Leitão, 1922; and Xenoctenus Mello-Leitão, 1938 (World Spider Catalog 2024). All these genera originally belonged to the Ctenidae Keyserling, 1877 until Lehtinen (1967) transferred Xenoctenus and Odo to Zoridae Pickard-Cambridge, 1893. The first cladistic analysis with xenoctenid specimens (Silva-Davila, 2003) showed Odo and Xenoctenus forming a separated clade from ctenids and zorids (including the type-species of the later, Zora Koch, 1847). This clade was supported by the presence of a distal division in the tegulum (TDD) of the male copulatory bulb and was the first evidence that these genera might be a separate lineage that deserves family status. Later, Ramírez (2014) considered Zoridae as a junior synonym of Miturgidae Simon, 1886, but suggested that Xenoctenus, Odo and Paravulsor should compose a new family, corroborating Silva-Davila's (2003) results. Wheeler et al. (2017) reproduced the (morphologybased) results of Silva-Davila (2003) and Ramírez (2014) with independent, molecular data and confidently supported the proposition of a family of their own for those three genera, plus Incasoctenus, which was transferred from Ctenidae.

Regarding the family's internal classification, most xenoctenid species were not revised after their original description (World Spider Catalog, 2024). *Incasoctenus* is a monotypic genus from Peru, known only from their original description (Mello-Leitão, 1942). *Odo* is the largest genus, with 25 species from Central America, the Galapagos Islands, The Caribbean, Peru, Chile, Argentina, and the Brazilian Atlantic Forest. Also, Silva-Davila's (2003) analyses provided the first evidence of the genus polyphyly. Recently, Faustino-Magalhaes et al. (2024) transferred *Odo vittatus* Mello-Leitão, 1936 to *Xenoctenus* and described a new species of the genus, both species endemic to the Brazilian Caatinga. Additionally, the type species of *Xenoctenus* (*X. unguiculatus* Mello-Leitão, 1938) was redescribed (Faustino-Magalhaes et al., 2024). Thus, currently *Xenoctenus* comprises 6 species, known from dry environments in Argentina, Bolivia, Colombia, and Brazil (World Spider Catalog, 2024). Besides the importance of this recent publication, the genus still needs to be reviewed.

Paravulsor is a monotypic genus known only from a single locality in from Brazilian Atlantic Forest and from its original description, which lacks appropriate diagnostic information and illustrations, making its identification virtually impossible from the current literature (MelloLeitão, 1922). However, a morphology-based phylogenetic hypothesis and taxonomic revision of Xenoctenidae proposed by Faustino-Magalhães (2019), showed that five species of *Odo*, *O*. *blumenauensis* Mello-Leitão, 1927, *O. obscurus* Mello-Leitão, 1936, *O. pulcher* Keyserling, 1891; *O. serrimanus* Mello-Leitão, 1936 and *O. similis* Keyserling, 1891, all restricted to the BAF, compose a separated clade with *Paravulsor*'s type-species, *P. impudicus* Mello-Leitão, 1922. These species can be distinguished from other xenoctenids by the presence of twisted setae in the tarsus of the female palp and male cymbium, and by the male metatarsus I with a row of ventral, dome-shaped macrosetae. Additionally, all species share the carapace with lateral dark brown bands and a median white band.

Our survey of xenoctenid collection material revealed that *Paravulsor* might be a particularly diverse and widely distributed genus. Based on material from several scientific collections, we identified over 50 undescribed species that fit the *Paravulsor* diagnosis proposed herein, all exclusively from the BAF. This indicates the genus represents a large, BAF endemic lineage. These species are particularly abundant in leaf litter and seem to be limited to microregions of endemism in the southeastern and southern BAF, in addition to a few species from the northern portion of the biome, that could be delimited as two new genera. All these figures show that *Paravulsor* (and those potential undescribed genera) could be a valuable model to study the biogeography of the Brazilian Atlantic Forest, after their taxonomy and phylogeny are resolved.

Given the importance of these new discoveries, in this study we propose a taxonomic revision of *Paravulsor*, attempting to clarify the taxonomic status of the currently known species. This will be a first step towards using the genus as a biogeographic model, which will be followed by the description of the dozens of undescribed species in a future study.

2. Material and Methods

Xenoctenidae specimens were obtained from field work and scientific collections. We carry out extensive field expeditions all over the Atlantic Forest (Chapter 3: fig. 3). Additionally, we obtained material from the following scientific collections (abbreviations and curators in parentheses): Centro de Coleções Taxonômicas, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil (UFMG, A.J. Santos); Instituto Butantan, São Paulo, Brazil (IBSP, A.D. Brescovit); Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brazil (MNRJ, A.B. Kury); Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto

Alegre, Brazil (MCTP, R. Teixeira); Museu de Ciências Naturais, SEMA Porto Alegre, Brazil (MCN, R. Ott); Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil (MZUSP, R. Pinto-da-Rocha); The Natural History Museum, London, UK (NHML, J. Beccaloni).

Specimens were examined in 80% ethanol under a Labomed Luxeo 4D stereomicroscope and measured using an eyepiece reticule attached to an Olympus SZ40 stereomicroscope, or from digital images using the Leica Applications Suite Version 3.8.0 software (Leica Inc.) software. All measurements are in millimeters. The female epigyna were removed and cleaned by immersion in a pancreatin solution, following the protocol of Álvarez-Padilla & Hormiga (2007).

The specimens were illustrated through multifocal digital images taken with a Leica DFC500 digital camera coupled to a Leica M205C stereomicroscope, and a Leica DFC295 digital camera coupled to a Leica M205C stereomicroscope. Images were assembled into multifocal images using Leica Applications Suite Version 3.8.0 software (Leica Inc.) or with Zerene Stacker Version 1.04 (Zerene Systems, LLC). Samples for Scanning Electron Microscopy (SEM) were removed from specimens, dried at room temperature, and mounted on stubs using conductive adhesive copper tape. Then, the samples were sputter-coated with 10 nm of gold-palladium and examined in a Quanta 2000 SEM at the Centro de Microscopia of UFMG.

Morphological terminology follows Ramírez (2014), and species descriptions and material examined lists were assembled using spreadsheets developed by Magalhaes (2019). Geographic coordinates were taken from sample labels, when available, or obtained online using Google Earth Pro. The map was assembled and edited using QGIS 3.30.2 's-Hertogenbosch (available in <u>https://qgis.org</u>).

3. Abbreviations

C – Conductor; CD – Copulatory ducts; CE –Central Expansion; DL –Distal lobe; dRTA – dorsal RTA; E – Embolus; HD – Hood; LB – Lateral Lobe; MA – Median Apophysis; DM – Dorsal Macrosetae; MF – Median Field; ML – Median Lobe; mRTA – median RTA; TNL – Tegular Narrowed Lobe; PL – Proximal Lobe; PP – Posterior Pockets; RTA – Retrolateral Tibial Apophysis; RTP – Retrolateral Tegular Projection; S1 – Primary spermathecae; S2 – Secondary spermathecae; **TDD** – Tegular Distal Division; **TE** – Tegular Expansion; **TL** – Transversal Lobe; **vRTA** – ventral RTA.

4. Taxonomy

Xenoctenidae Ramírez & Silva-Davila, 2017 in Wheeler et al. 2017

Paravulsor Mello-Leitão, 1922

Paravulsor Mello-Leitão, 1922: 37–38. Petrunkevitch 1928: 176; Strand 1934: 274; Mello-Leitão 1936: 26, 28; Roewer 1955: 658; Bonnet 1958: 3339; Ramírez, 2014: 342; Wheeler et al., 2017: 609.

Type species. Paravulsor impudicus Mello-Leitão, 1922 (Figure 1)

Emended diagnosis. *Paravulsor* can be distinguished from other Xenoctenidae by the palp with twisted setae in the female tarsus and male cymbium (Fig. 2A–C). Males of *Paravulsor* differ from those of *Odo* and *Xenoctenus* by the presence of a complex RTA, composed by ventral, median and dorsal branches (vRTA, mRTA and dRTA, respectively; Figs 3B, C, 6B, C, 7, B, C, 8B, C), and by the metatarsus I with a row of ventral, dome-shaped macrosetae. Females can be distinguished from other Xenoctenidae by the complex and sclerotized median field of the epigynum (Figs. 3D, 6D, 7D, 9D, 10D).

Description. *MALE* (FIG. 3F). **Carapace** light brown to brown, covered by short setae with median white setae and dark brown lateral bands. Chelicerae brown, labium, endites, and sternum light brown. **Eyes** 4-4, recurved, all rounded with similar size, equidistant. **Legs** light brown or brown, with several macrosetae and tarsal scopula. Metatarsus I with a row of dome-shaped ventral macrosetae, metatarsus II with a row of two pairs of ventral macrosetae. **Abdomen** dorsum covered by short setae and anterior median white setae, light brown with dark spots and lateral dark bands, venter light brown to brown. **Total length** 4.33–5.07. **PALP** (**FIG 3A–C**). **Cymbium** with a basal, retrolateral expansion. Covered by setae, with apico-prolateral twisted setae and a dorsal scopula. **Tegulum** with an apical-retrolateral tegular process (RTP). **Median apophysis** retrolateral, hook-shaped. **Conductor** apical and translucent. **Embolus** prolateral, arising at the base of the tegulum and ending close to the RTP, cylindrical. **Tegular distal division (TDD)** wide, covering the embolus, arising at the base of

45

the embolus, ending at the apex of the tegulum. **Patella** with one dorsal macrosetae. **Tibia** with a wide retrolateral concavity and long ventral setae. **Retrolateral tibial apophysis (RTA)** covered by setae, usually divided in a fully sclerotized ventral RTA (vRTA), and dorsal RTA (dRTA). The dRTA can be divided in up to three lobes: proximal lobe (PL), median lobe (ML) and distal lobe (DL).

FEMALE (FIGS 1, 2, 3G). **Carapace** light brown to brown, covered by short setae, with median white setae and lateral dark brown bands. Chelicerae brown, labium, endites, and sternum light brown. **Eyes** 4-4, recurved, all rounded with similar size, equidistant. **Legs** light brown to brown, with several macrosetae and tarsal scopula. **Palp** with tarsal, twisted ventral setae. **Abdomen** dorsum covered by short setae and anterior median white setae, dorsum light brown with dark spots and lateral dark bands, venter light brown to brown. **Total length** 5.22–7.66. **GENITALIA** (**FIG. 3D, E**). **Epigynum** divided into median field and lateral lobes. **Median field** sclerotized, wide, conspicuous. **Lateral lobes** with posterior pockets medially directed and located at the posterior extremity. **Median field and lateral lobes** extending through the genital opening (Figs 5F, 6F) forming a sclerotized lobe or plate. **Internal genitalia** sclerotized. **Primary spermathecae** elongated, duct-shaped. **Secondary spermathecae** rounded. **Copulatory ducts** connected anteriorly to the median field. **Fertilization ducts** sclerotized, thinner than the copulatory ducts and covered by the *uterus externus* membrane.

Distribution & Habitat. All *Paravulsor* species are found in the leaf litter of the Atlantic Forest, in southeastern and southern Brazil. Most species occur in high altitude regions, throughout the mountain ranges of the Brazilian littoral and some interior areas. These species are usually found in well preserved environments (Fig. 11).

Species included. 5 species: *Paravulsor blumenauensis* (Mello-Leitão, 1927) **comb. nov.**, *Paravulsor obscurus* (Mello-Leitão, 1936) **comb. nov.**, *Paravulsor impudicus* Mello-Leitão, 1922, *Paravulsor pulcher* (Keyserling, 1891) **comb. nov.**; *Paravulsor similis* (Keyserling, 1891) **comb. nov.**

Paravulsor impudicus Mello-Leitão, 1922

(Figs 1, 2, 3, 11, 12)

Paravulsor impudicus Mello-Leitão, 1922: 38. (Female holotype from Pinheiro, nowadays comprising the municipality of Pinheiral, Rio de Janeiro, Brazil; Mello-Leitão coll.,

deposited in MNRJ - MLPC 092; not found, lost. Female neotype here designated from *Volta Redonda*, Área de Relevante Interesse Ecológica Floresta da Cicuta [S22.54836°, W44.08753°], M.D.F. Magalhães et al. coll., 19–20/VI/2021, 1 #ff deposited in UFMG 28018. Silva-Moreira et al., 2010: 7, 30.

Remarks. The original description of *P. impudicus* (Mello-Leitão,1922) is based on a female from Pinheiro (currently municipalities of Pinheiral and Piraí, state of Rio de Janeiro) deposited in the Museu Nacional do Rio de Janeiro (voucher nº 92 in Mello-Leitão Personal Collection - MLPC). In this publication, Mello-Leitão described only the body coloration and setae patterns of the specimen, with no mention of genitalic characters or illustrations. Thus, this description fits any *Paravulsor* specimen from throughout the BAF, since all share similar color patterns, body size and spinulation. To make matters worse, a type-material catalog of the MNRJ (Silva-Moreira et al., 2010) states that no specimen labelled as MLPC 92 was ever found in the collection, and that a Mello-Leitão's handwritten card file indicates a female previously identified as *Odo pulcher* (MNRJ 737) as the type of *P. impudicus*. This specimen was collected in Petrópolis (state of Rio de Janeiro), a locality far away from the one described in the original publication. Based on this evidence, Silva-Moreira et al. (2010) considered this exemplar as the real holotype of *P. impudicus*.

During a visit to the MNRJ arachnology collection in 2017, MDFM could not find either the MLPC 92 or MNRJ 737 specimens. We also checked the whereabouts of those samples with curators of other collections and colleagues who previously studied xenoctenids, but no one could provide any information about them. It is currently safe to presume that both samples were probably lost before 2017 or, if misplaced within the collection, destroyed in the 2018 fire that completely obliterated the MNRJ arachnology collection and laboratory (Kury et al. 2018).

The taxonomic status of *Paravulsor impudicus* is of particular importance as it is the type species of the genus. The situation described above is justification enough to designate a neotype in order to fix the uncertain identity of the species (ICZN 1999: art. 75). Given that both MLPC 92 and MNRJ 737 lots are most probably lost, together with all Mello-Leitão's documentation, we can only rely on subsequently collected material. The museum specimens we examined from localities around Petrópolis belong to a different species examined from nearby Pinheiral. Considering the information available, we think it would be preferrable to rely on the information from the original publication, so we chose the species from around the early Pinheiral area to fix *P. impudicus* name.

Article 75 of the ICZN (1999) states that a neotype should be consistent with what is known of the type-species' original description and come from as nearly as practicable from the original type locality. The surroundings of the early municipality of Pinheiral are currently extremely deforested. Thus, we selected as the neotype a specimen collected by us from the Floresta da Cicuta, in the municipality of Volta Redonda (approx. 9 km away from Pinheiral). This conservation unity is the largest of the few remaining forest fragments in the region, and probably represents one of the few, if not the only site to preserve a *P. impudicus* population.

Finally, based at the type species of *Paravulsor impudicus*, we concluded that *O. blumenauensis* Mello-Leitão, 1927, *O. obscurus* Mello-Leitão, 1936, *O. pulcher* Keyserling, 1891, *O. serrimanus* Mello-Leitão, 1936 and *O. similis* Keyserling, 1891 should be transferred from *Odo* to *Paravulsor*.

Diagnosis. Males of *P. impudicus* differ from all others *Paravulsor* species by the vRTA lobe with a tuft of setae and the dRTA long, with a pointed apex, reaching the tegulum in retrolateral view (Fig. 3B, C). *Paravulsor impudicus* resembles *P. blumenauensis* in the RTP with an apical and a median lobe but differ by the apical lobe of the RTP longer than the median lobe (Figs 3C, 6C). Females of *P. impudicus* can be distinguished from other *Paravulsor* species by the lateral lobes lightly curved medially (Fig. 3D). The epigynum of this species is a bit like that of *P. similis*, but those species can be further distinguished in spermathecae located below the copulatory opening in *P. impudicus*.

Description. MALE FROM ÁREA DE RELEVANTE INTERESSE ECOLÓGICA FLORESTA DA CICUTA, VOLTA REDONDA, RIO DE JANEIRO, BRAZIL (IBSP 48937; FIG 3F). **Carapace** light brown, with several setae, and dark lateral bands. Chelicerae brown, labium, endites and sternum light brown. **Legs** dark brown, with several macrosetae. **Abdomen** dorsum covered by short setae and median white setae, dorsum light brown with irregular dark spots and lateral dark bands, venter light brown. **Total length** 4.52. **Carapace** length 2.47, width 2.11. **Leg IV:** femur (fe) 2.37, patella (pa) 0.96, tibia (ti) 2.14, metatarsus (mt) 2.97, tarsus (ta) 1.15. **Abdomen:** length 1.87, width 1.24. PALP: **Retrolateral tegular process (RTP)** one apical pointed lobe and one median lobe. **Median apophysis** hook-shaped, curved, shorter than the RTP and TDD. **Embolus** cylindrical. **Tegular distal division (TDD)** narrow, with a narrowed posterior lobe. **Patella** with one dorsal macrosetae, similar sized with the patella length. **Tibia** with long ventral setae and a wide concavity. **Retrolateral tibial apophysis** (**RTA**) divided in two apophysis covered by setae. **Retrolateral tibial apophysis** vRTA lobe with a tuft of setae, dRTA simple, long, reaching the tegulum, with a pointed apex. FEMALE FROM ÁREA DE RELEVANTE INTERESSE ECOLÓGICA FLORESTA DA CICUTA, VOLTA REDONDA, RIO DE JANEIRO, BRAZIL (IBSP 48937; FIGS 1, 2, 3G). **Carapace** light brown, with several setae, dark lateral bands. Chelicerae brown, labium, endites, and sternum light brown. **Legs** light brown, with dark brown spots and several macrosetae. **Abdomen** dorsum covered by short setae, dorsum light brown with irregular dark spots and lateral dark bands, venter light brown. **Total length** 5.67. **Carapace** length 2.16, width 1.60. **Leg IV:** femur (fe) 2.07, patella (pa) 0.72, tibia (ti) 1.89, metatarsus (mt) 2.41, tarsus (ta) 1.32. **Abdomen:** length 3.08, width 2.12. **GENITALIA (FIG. 3D, E): Epigynum** median field and lateral lobes lightly curved medially; posterior pockets medially directed in a triangular lobe. **Median field and lateral lobes** extend through the genital opening. **Primary spermathecae** elongated and spiral, duct-shaped. **Secondary spermathecae** rounded, located bellow to the copulatory ducts opening. **Copulatory ducts** open centrally, anteriorly to the median field. **Fertilization duct** sclerotized, curved, thinner than the copulatory ducts and covered by the *uterus externus* membrane.

Distribution & Habitat. *P. impudicus* is known only from in the Cicuta forest, the only wellpreserved Atlantic Forest fragment in the region comprising Volta Redonda, Pinheral, and Piraí (state of Rio de Janeiro). We highlight the possibility of this species being threatened of extinction (Fig. 11, 12).

Additional material examined. BRAZIL. Rio de Janeiro: *Volta Redonda*, Área de Relevante Interesse Ecológica Floresta da Cicuta, trilha principal, Busca ativa [S22.54836°, W44.08753°, 387 m], M.D.F. Magalhães et al. coll., 19–20/VI/2021, 7 #m 10 #ff (UFMG 28018), Área de Relevante Interesse Ecológico Floresta da Cicuta, Busca ativa [S22.54837°, W44.08753°, 387 m], M.D.F. Magalhães et al. coll., 4/III/2020, 1 imm. (UFMG 27964), same locality [S22.54883°, W44.09274°], E.L.C. Silva et al coll., 01–03/X/2004, 1 #ff (IBSP 48937).

Paravulsor blumenauensis (Mello-Leitão, 1927) comb. nov.

(Figs 4, 5, 6, 11, 13)

Odo blumenauensis Mello-Leitão, 1927: 405, plate 15, figs 1-2 (syntype, 1#f from Brazil, Santa Catarina, Blumenau, Pitfall [S26.92096°, W49.07441°], Luederwaldt coll., XI/1924, deposited in MZUSP DZ 8946 (824), 1 #ff, deposited in MZUSP DZ 8947 (949), 1#m from the same locality, Mello-Leitão coll., examined). Mello-Leitão, 1936: 28, plate 4, fig. 54. Ramírez, 2014: p. 222, fig. 150B).

Odo serrimanus Mello-Leitão, 1936: 29, plate 4, fig. 57. (holotype from Brazil, Rio Grande do Sul, Porto Alegre, Pitfall [S30.05417°, W51.12613°], Pe. Balduíno Rambo coll., 1 #m, deposited in MNRJ 41704, examined). Mello-Leitão, 1943: 197, fig. 26. **Syn. nov.**

Remarks. The male holotype of *O. serrimanus* lost both palps, so we have only the description and illustrations, and additional specimens from the type-locality to confirm the species identity. *Paravulsor blumenauensis* has the widest distribution range within the genus and can be found in many places in southern Brazil. Most importantly, this is the sole species we could find in collections and in our field expeditions at and around the type-locality of *O. serrimanus*. Additionally, the male palp illustrations of *O. serrimanus*, though sketchy, perfectly fit in the specimens of *O. blumenauensis* we examined Thus, the available evidence supports the synonymization of *O. serrimanus* with *P. blumenauensis*.

Diagnosis. Males of *P. blumenauensis* can be distinguished from other *Paravulsor* species by the presence of a tegular posterior expansion and by the presence of a mRTA (Figs. 5A, B, 6A, B). Additionally, it also differs by the vRTA ventrally curved and the dRTA larger than the vRTA, dorsolaterally curved with a small spine at the apex (Figs 5B, C, 6B, C). *P. blumenauensis* resemble *P. impudicus* in the narrow TDD but differ by the presence of a median constriction in the same sclerite (Figs 3A, 5A). Females of *P. blumenauensis* resemble those of *P. similis* and *P. obscurus* by the copulatory ducts connected medially (Figs 5D, E, 6D, E, 7D, E, 9D, E) but can be distinguished from all other species of *Paravulsor* by the median field rounded and prominent (Figs. 5D, 6D).

Description. MALE FROM ROÇA GRANDE, IMBITUBA, SANTA CATARINA, BRAZIL (IBSP 136858; FIGS 4, 6G)). **Carapace** light brown, covered by short setae and median white setae, dark lateral bands. Chelicerae brown, labium, endites, and sternum light brown. **Legs** light brown, with dark brown spots and several macrosetae. **Abdomen** dorsum covered by short setae and median white setae, dorsum light brown with irregular dark spots and lateral dark bands, venter light brown. **Total length** 4.63. **Carapace** length 2.26, width 2.09. **Leg IV:** femur (fe) 2.36, patella (pa) 0.85, tibia (ti) 2.17, metatarsus (mt) 3.02, tarsus (ta) 1.58. **Abdomen:** length 2.43, width 1.46. **PALP (FIG 5A–C, 6A–C). Retrolateral tegular process (RTP)** one apical lobe, with a straight and wide tip and one smallest median lobe. **Median apophysis** hook-shaped, curved, shorter than the RTP and TDD. **Embolus** cylindrical. **Tegular distal division (TDD)** narrow, medially constricted, with a narrowed posterior lobe. **Patella** with one dorsal macrosetae, smallest than the patella length. **Tibia** with long ventral setae and a wide concavity. **Retrolateral tibial apophysis (RTA)** divided in three apophysis covered by setae. **Retrolateral tibial apophysis** vRTA fully sclerotized, ventrally pointed, mRTA fully sclerotized and smallest than the others, dRTA simple, longer than others, without projections.

FEMALE FROM ROÇA GRANDE, IMBITUBA, SANTA CATARINA, BRAZIL (IBSP 136858). Carapace light brown, with several setae, dark lateral bands. Chelicerae brown, labium, endites, and sternum light brown. Legs light brown, with dark brown spots and several macrosetae. Abdomen dorsum covered by short setae, dorsum light brown with dark lateral bands, venter light brown. Total length 6.31. Carapace length 2.8, width 2.3. Leg IV: femur (fe) 2.50, patella (pa) 0.94, tibia (ti) 2.17, metatarsus (mt) 2.77, tarsus (ta) 1.31. Abdomen: length 3.29, width 2.21. GENITALIA (FIGS 5D–F, 6D–F). Epigynum median field and lateral lobes divides from the middle of the epigynum. Median field rounded and prominent. Lateral lobes posterior pockets medially directed. Median field and lateral lobes extend through the genital opening. Primary spermathecae elongated and spiral, duct-shaped. Secondary spermathecae rounded, parallel to the copulatory ducts opening. Copulatory ducts open in a central hole, anteriorly to the median field. Fertilization duct sclerotized, curved, thinner than the other ducts, and covered by the *uterus externus* membrane.

Variation. The vRTA can be shorter or longer, and more or less pointed in different specimens. In some specimens the mRTA can be very small, almost indistinguishable. The dRTA can be wider or narrower.

Distribution & Habitat. *P. blumenauensis* can be found in the coastal Atlantic Forest or in fragments of interior forests in the states of Paraná, Rio Grande do Sul and Santa Catarina (Figs 11, 13).

Additional material examined. BRAZIL. Paraná: *Foz do Iguaçu*, Parque Nacional do Iguaçu, trilha do Poço Preto, Córrego Carlos Giovanni, Busca ativa [S25.61281°, W54.43101°, 205m], M.D.F. Magalhães et al. coll., 7/I/2022, 1 #m 2 #ff 1 imm. (UFMG 27944), 1 #m (UFMG 28057), 1 #ff (UFMG 28058), 1 #ff (UFMG 28059); *Mangueirinha*, Reservatório do Rio Jordão Candói, Usina Hidrelétrica de Segredo [S25.80036°, W52.10738°], Sem Coletor coll., 24–04/IV–V/1996, 2 #ff (IBSP 62909); *Pinhão*, Pitfall [S25.68389°, W51.65644°], S.M. Hefler coll., II/X/2003, 1 #ff (IBSP IB-57897). **Paraná:** *Capitão Leonidas Marques*, Rio Iguaçú, Salto Caxias [S25.54073°, W53.5014°], A. B. Bonaldo coll., 23–23/II–III/1993, 1 #ff 1 imm. (MCN 23461); *Foz do Iguaçu*, Refúgio Biológico de Bela Vista [S25.44525°, W54.58381°], A.B. Bonaldo coll., 09–11/XI/1991, 1 #ff (MCN 21644); *Guarapuava* [S25.39094°, W51.46117°], Equipe PROFAUPAR coll., 23/II/1987, 1 #ff (MCN 20506); *Morretes* [S25.47723°,

W48.82522°], Arno Antônio Lise et al. coll., 9/I/1995, 1 #m (MCTP 7426); Ponta Grossa [S25.09841°, W50.13185°], Arno Lise coll., 5/IV/1968, 1 #ff (MCN 3785), same collector, 8/IV/1967, 1 #ff (MCN 566). Rio Grande do Sul: Canela [S29.31745°, W50.84162°], A.A. Lise coll., 2/VIII/1965, 1 #ff (MCN 16681); Cidreira [S30.17273°, W50.22158°], Pinto, J. A. M. coll., 6/IX/2003, 8 #m 1 #ff 1 imm. (MCTP 22438), Pitfall, same collector, 4/X/2003, 9 #m 4 #ff (MCTP 22445), 9 #m 1 #ff (MCTP 22446), 8 #m 2 #ff (MCTP 22449), same collector, 1/XI/2003, 11 #m 4 #ff (MCTP 22455), 7 #m 2 #ff (MCTP 22458), 8 #m 2 #ff (MCTP 22461), Pitfall, same collector, 29/XI/2003, 22 #m 3 #ff (MCTP 22464), 31 #m 3 #ff (MCTP 22469), 11 #m 2 #ff (MCTP 22471), Pitfall, 9 #m 3 #ff 2 imm. (MCTP 22472), same collector, 24/I/2004, 13 #m 2 #ff (MCTP 22483), 10 #m 3 #ff (MCTP 22484), 2 #m 5 #ff (MCTP 22487), same collector, 20/II/2004, 3 #m 4 #ff 2 imm. (MCTP 22494); Maquiné, Fepagro [S29.66323°, W50.21246°], Equipe Biota coll., 18–27/II/2002, 1 #ff (IBSP 60070); Porto Alegre, Refúgio de Vida Silvestre São Pedro, trilha principal, Busca ativa [S30.17776°, W51.10539°, 66m], M.D.F. Magalhães et al. coll., 18/II/2022, 8 #ff 3 imm. (UFMG 27963), 1 #ff (UFMG 28107), 1 #ff (UFMG 28108); São Francisco de Paula, Floresta Nacional do Ibama [S29.42281°, W50.38672°], E.L.C.Silva et al coll., 16–23/VIII/1999, 1 #m (IBSP 48363), Trilha da Cascata da Represa, Floresta Nacional de São Francisco de Paula [S29.42128°, W50.38992°, 907m], M.D.F. Magalhães et al. coll., 16/II/2022, 1 #m 15 #ff 10 imm. (UFMG 27962), Busca ativa, 1 #ff (UFMG 28103), 1 #ff (UFMG 28104), 1 #ff (UFMG 28105), 1 #ff (UFMG 28106) [S29.45964°, W50.54687°], Teixeira, R. A. coll., 10/XII/2012, 1 #m 1 #ff (MCTP 37210). Santa Catarina: Florianópolis, Costa do Santinho, Morro das Aranhas [S27.4702°, W48.37943°], F. Albertoni et al. coll., 2007, 28 #m 11 #ff 1 imm. (IBSP 144229), Itacorubi, UCAD [S27.53111°, W48.37943°], C. Carlos et al. coll., 05/I–12/I/2004, 1 #ff (IBSP 144327), Pitfall, same collector, 03/II–10/II/2004, 1 #ff (IBSP 144343), same collector, 03–10/XI/2003, 1 #ff (IBSP 144368), Pitfall, 1 #ff (IBSP 144376), Lagoa do Peri [S27.71667°, W48.53333°], M.I.M. Hernándes coll., 2007, 26 #m 12 #ff (IBSP 117352), Lagoa do Peri, Restinga e Mata umbrofila densa [S27.72721°, W48.53333°], F. Albertoni coll., 08/V-11/V/2007, 5 #ff (IBSP 92194), 2 #m 3 #ff (IBSP 92195), Praia do Pântano do Sul [S27.78315°, W48.507°], E.N. Saito coll., VII/2008, 2 #ff (IBSP 155657), Santo Antônio de Lisboa, Pitfall [S27.50733°, W48.51579°], C. Carlos coll., 05/VII/2004, 1 #m (IBSP 144412), same collector, 29/IX/2003, 1 #ff (IBSP 144426), same collector, 03/VIII/2004, 1 #m (IBSP 144434), same collector, 03/V/2004, 1 #ff (IBSP 144435), Unidade de Conservação Ambiental Desterro, Pitfall [S27.53111°, W48.37943°], C. Carlos et al. coll., 03–10/XI/2003, 1 #ff (IBSP 144378), Busca ativa, same locality [S27.52803°, W48.51151°, 160m], M.D.F. Magalhães et al. coll.,

10/II/2022, 29 #m 15 #ff 1 imm. (UFMG 27957), 1 #ff (UFMG 28080), 1 #ff (UFMG 28081), 1 #ff (UFMG 28082), 1 #m (UFMG 28083), 1 #m (UFMG 28086), 1 #m (UFMG 28087) [S27.63025°, W48.49654°], Arno Antônio Lise coll., 6/X/1995, 1 #m (MCTP 11794), Pitfall, Arno Antônio Lise et al. coll., 15/IV/1994, 2 #m 4 #ff (MCTP 5008), Arno Antônio Lise coll., 15/4/1994, 1 #ff (MCTP 5009), same collector, 15/IV/1994, 1 #ff (MCTP 5010), Pitfall, Arno Antônio Lise et al. coll., 13/X/1994, 4 #m 3 #ff (MCTP 5151), 3 #m 2 #ff 37 imm. (MCTP 5162), Arno Antônio Lise coll., 3/V/1995, 3 #ff (MCTP 6312), 10 #m 2 #ff (MCTP 6313), Pitfall, 1 #m 1 #ff (MCTP 6314), Arno Antônio Lise et al. coll., 14/IV/1994, 4 #ff (MCTP 6399), 2 #ff 1 imm. (MCTP 6400), Pitfall, Arno Antônio Lise coll., 5/X/1995, 1 #ff (MCTP 7475), A.D. Brescovit coll., 14/XI/1993, 2 #m (IBSP IB-62910); Guarda do Embaú [S27.90302°, W48.58837°], A.J.Santos coll., 2/XII/09–15/X/2001, 1 #m (IBSP 58343); *Imbituba*, Praia do Rosa [S28.12496°, W48.64193°], A.B. Bonaldo coll., 08–15/II/1998, 3 #ff 21 imm. (MCN 28972), Roça Grande [S28.32163°, W48.71989°], Equipe Biota coll., I/2003, 2 #m 1 #ff (IBSP 136850), 1 #m (IBSP 136851), 2 #m (IBSP 136852), 1 #ff (IBSP 136853), 1 #m 1 #ff (IBSP 136854), 1 #m 1 #ff (IBSP 136855), 1 #m (IBSP 136856), 1 #m 1 #ff (IBSP 136857), 2 #m 1 #ff (IBSP 136858), 1 #ff (IBSP 136859), 2 #m 1 #ff (IBSP 136861), 3 #m (IBSP 136862), 2 #m (IBSP 136863), 7 #m 1 #ff (IBSP 136864), 4 #m (IBSP 136866), 4 #m 1 #ff (IBSP 136867), 4 #m (IBSP 136867), 1 #m 1 #ff (IBSP 136868), 3 #m (IBSP 136869), 4 #m (IBSP 136870), 4 #m 1 #ff (IBSP 136871), 1 #m (IBSP 136872), 2 #m (IBSP 136873), 1 #m 1 #ff (IBSP 136874), 1 #m (IBSP 136875), 1 #m 1 #ff (IBSP 136876), 1 #ff (IBSP 136877), 1 #ff (IBSP 136878), 2 #m 1 #ff (IBSP 136879), 2 #m (IBSP 136881), 1 #ff (IBSP 136882), 2 #m 1 #ff (IBSP 136883), 2 #m 1 #ff 1 imm. (IBSP 136884), 3 #m (IBSP 136885), 2 #m (IBSP 136886), 1 #ff (IBSP 136887), 1 #m (IBSP 136888), 1 #m (IBSP 136889), 1 #m 1 #ff (IBSP 136890), 2 #m (IBSP 136891), 1 #m 3 #ff (IBSP 136892), 2 #ff (IBSP 136893), 5 #m 1 #ff (IBSP 136894), 1 #m 1 #ff (IBSP 136897), Winkler, Equipe BIOTA et. al. coll., same date, 3 #m (IBSP IB-136880); Indaial, Instituto de Permacultura Vale do Itajaí (IPEVI), Busca ativa [S26.96635°, W49.18029°, 184m], M.D.F. Magalhães et al. coll., 9/II/2022, 7 #ff 2 imm. (UFMG 27956), 1 #ff (UFMG 28076), 1 #m (UFMG 28077), 1 #ff (UFMG 28078), 1 #ff (UFMG 28079); Paulo Lopes, Parque Estadual do Tabuleiro [S27.91667°, W48.7°], Equipe Biota col. coll., 10–20/I/2003, 1 #ff (IBSP 60450), 1 #ff (IBSP 60451), 1 #ff (IBSP 60507), Pitfall, Equipe BIOTA et. al. coll., same date, 1 #ff (IBSP IB-60448); Siderópolis, Reserva Biológica do Aguaí, Busca ativa [S28.59694°, W49.59093°, 432m], M.D.F. Magalhães et al. coll., 14/II/2022, 2 #m 13 #ff 1 imm. (UFMG 27960), 1 #ff (UFMG 28093), 1 #ff (UFMG 28094), 1 #ff (UFMG 28095), 1 #ff (UFMG 28096), 1 #ff (UFMG 28097), 1 #m (UFMG 28098), 1 #m (UFMG 28099) [S28.54494°, W49.53604°], R. A. Teixeira coll., 01/VII/2006, 1 #ff (IBSP 84832); *Treviso*, Trilha dos Dois Dedos, Reserva Biológica do Aguaí [S28.51738°, W49.53024°, 368m], M.D.F. Magalhães et al. coll., 15/II/2022, 1 #m 2 #ff 9 imm. (UFMG 27961), Busca ativa, 1 #m (UFMG 28100), 1 #ff (UFMG 28101), 1 #ff (UFMG 28102)., 1 #m 1 #ff (IBSP 136896).

Paravulsor obscurus (Mello-Leitão, 1936) comb. nov.

(Figs 7, 11, 14)

Odo obscurus Mello-Leitão, 1936: 28, plate 3, figs 55-56. (syntypes from Brazil, São Paulo, Iguape, [S24.6926°, W47.54464°], pitfall, 2 #m, deposited in MNRJ 41900, examined).

Diagnosis. Males of *P. obscurus* differ from other *Paravulsor* species by the RTP apical lobe wide (Fig 7C). Males resemble *P. impudicus*, *P. pulcher* and *P. similis* in the RTA with vRTA and dRTA (Figs. 3B, C, 7B, C, 9B, C, 10, B, C) but can be distinguished from all other species by the vRTA macrosetae-like (Fig 7B, C). Also, differ by the dRTA longer, reaching the bulb, with a DL narrow and straight tip and a ML spiniform. Females can be distinguished from other *Paravulsor* by the median field with a posterior lobe, which is two times wider than the anterior part, and by the lateral lobes with two hoods above the median field (Fig. 7D, E). Females resemble *P. impudicus* in the secondary spermathecae bellow to the copulatory ducts opening (Fig. 3D, E).

Description. MALE FROM JARDIM ÂNGELA, RESERVATÓRIO DO GUARAPIRANGA, SÃO PAULO, SÃO PAULO, BRAZIL (IBSP 131663; FIG. 7F). **Carapace** brown, covered by short setae and median white setae, dark lateral bands. Chelicerae, labium, endites and sternum brown. **Legs** brown, with several macrosetae. **Abdomen** dorsum covered by short setae and median white setae, dorsum brown with irregular dark spots and lateral dark bands, venter brown. **Total length** 5.07. **Carapace** length 2.56, width 2.23. **Leg IV:** femur (fe) 2.42, patella (pa) 0.77, tibia (ti) 2.21, metatarsus (mt) 2.97, tarsus (ta) 1.68. **Abdomen:** length 2.52, width 1.79. **PALP (FIG. 7A–C): Retrolateral tegular process (RTP)** one apical lobe. **Median apophysis** hook-shaped, curved, shorter than the RTP and TDD. **Embolus** cylindrical. **Tegular distal division (TDD)** wide, medially constricted. **Patella** with one dorsal macrosetae, longer than the patella length. **Tibia** with long ventral setae and a wide concavity. **Retrolateral tibial apophysis** (**RTA**) divided in two apophysis covered by setae. **Retrolateral tibial apophysis** vRTA macrosetaelike, dRTA longer, reaching the bulb, with a narrow and straight tip and a median spine. FEMALE FROM JARDIM ÂNGELA, RESERVATÓRIO DO GUARAPIRANGA, SÃO PAULO, SÃO PAULO, BRAZIL (IBSP 131663; FIG. 7G). **Carapace** light brown, with several setae, dark lateral bands. Chelicerae brown, Labium light brown, Endites light brown, Sternum light brown. **Legs** light brown, with dark brown spots and several macrosetae. **Abdomen** dorsum covered by short setae, dorsum light brown with irregular dark spots and lateral dark bands, venter light brown. **Total length** 7.66. **Carapace** length 2.6, width 2.21. **Leg IV:** femur (fe) 2.40, patella (pa) 0.83, tibia (ti) 2.36, metatarsus (mt) 2.62, tarsus (ta) 1.49. **Abdomen:** length 4.63, width 2.86. **GENITALIA (FIG. 7D, E). Epigynum** median field and lateral lobes divides from the middle of the epigynum. **Median field** longer than wide, with a posterior lobe two times wider than the superior part. **Lateral lobes** with two hoods above the median field and posterior pockets medially. **Median field and lateral lobes** extend through the genital opening. **Primary spermathecae** elongated, duct-shaped. **Secondary spermathecae** rounded, located bellow to the copulatory ducts opening. **Copulatory ducts** open in a central hole, anteriorly to the median field. **Fertilization duct** sclerotized, curved, thinner than the other ducts, and covered by the *uterus externus* membrane.

Variation. Males of *P. obscurus* can present differences in the RTA. The vRTA is always macrosetae-like but can be longer or more curved. The dRTA, that can be narrowed at the tip and some specimens may present a third apical median spine. The bulb apophysis do not present significant variations.

Distribution & Habitat. *P. obscurus* can be found mostly in the surroundings of the Serra do Mar mountain range in São Paulo state, but its distribution can extend to Santa Catarina state (Figs 11, 14).

Additional material examined. NON-TYPE MATERIAL: BRASIL. Santa Catarina: *Joinvile*, Parque Municipal Morro do Finder, Busca ativa [S26.26407°, W48.83543°, 99m], M.D.F. Magalhães et al. coll., 5/II/2022, 1 #ff (UFMG 27950); *Urussanga*, Rio Molha [S28.42233°, W49.31347°], R. Teixeira coll., 04–11/IX/2007, 2 #m (IBSP 133913). São Paulo: *Biritiba Mirim*, Barragem do Rio Biritiba [S23.60208°, W46.08424°], Equipe IBSP coll., 30/VII/2004, 2 #ff (IBSP 119846), 1 #ff (IBSP 119851), 1 #ff (IBSP 119852), 1 #m (IBSP 119854); *Cananéia*, Parque Estadual da Ilha do Cardoso [S25.13361°, W47.96167°], E.M. Venticinque col. coll., 11–13/VIII/1988, 1 #ff 2 imm. (IBSP 62938), same collector, 15–17/XII/1987, 2 #ff (IBSP 62939), same collector, 26/IX/1987, 1 #m (IBSP 62942), same collector, 01–06/III/1986, 3 #ff 5 imm. (IBSP 62943), same collector, 17/VII/1987, 1 #m 4 #ff (IBSP 62945), same collector, 16/III/1988, 2 #ff (IBSP 62946), A. J. Santos coll., 09–15/VII/2007, 1 #m (IBSP 92203), Pitfall, E.M. Venticinque et al. coll., 16-26/IX/1987, 1 #ff 1 imm. (IBSP IB-62940), same collector, 11–13/VIII/1988, 1 #ff 1 imm. (IBSP IB-62948); Cocaia, Represa nova, Pitfall [S23.70478°, W46.6505°], H. Urban coll., 7/XI/1948, 1 #m (MZUSP 10735), Pitfall [S23.81592°, W45.35741°], H. Urban coll., 8/X/1950, 2 #m 2 #ff 2 imm. (MZUSP 10741), same collector, 3/XII/1951, 1 #m (MZUSP 11434); Cotia, Reserva Morro Grande, Busca ativa [S23.77464°, W47.00897°, 1011m], M.D.F. Magalhães et al. coll., 25/XI/2020, 3 #m 4 #ff (UFMG 27987), same locality [S23.67603°, W46.99414°, 954m], same collector and date, 3 #m (UFMG 27989), same locality, 2 #m 1 #ff (MZUSP 74400), 2 #m 1 #ff (MZUSP 74401), 1 #m 2 #ff (MZUSP 74402), Pitfall, 3 #m (MZUSP 74403), 3 #m (MZUSP 75503), 3 #ff (MZUSP 75507), 2 #ff (MZUSP 75508), 2 #ff (MZUSP 75513), Reserva Morro Grande - Area-D, Pitfall [S23.73018°, W46.96403°], 26/III/2003, 2 #ff (MZUSP 75505), Reserva Morro Grande -Torres, Pitfall, 09/III/2003, 2 #ff (MZUSP 75504), M. B. S. coll., 13/XI/2003, 1 #m (MZUSP 75506); Cubatão, Mata de encosta da Copebrás [S23.835°, W46.39778°], Nogueira et al coll., VI–IX–XII/2008, 1 #ff (IBSP 123237), 1 #ff (IBSP 123240), 1 #ff (IBSP 123241), 2 #ff (IBSP 123242), 1 #m 1 #ff (IBSP 123243), 1 #ff (IBSP 123244), 1 #ff (IBSP 123245), 1 #ff (IBSP 123246), 1 #m (IBSP 123247); Embu-Guaçu [S23.83136°, W46.81569°], R. P. Zanun & C. Borrely coll., 12–13/XI/2007, 1 #m (IBSP 88504); Iguape [S24.6926°, W47.54464°], Leonardos, O. coll., 2 #ff (MNRJ 3439); Ilhabela, Parque Estadual de Ilhabela [S23.85154°, W45.33598°], Equipe Biota coll., 23-30/VII/2001, 1 #m (IBSP 57185), same collector, 09-15/X/2001, 1 #ff (IBSP 57187), 1 #m (IBSP 57188), 1 #m (IBSP 57189), 1 #m (IBSP 57190), 1 #ff (IBSP 57192), 1 #ff (IBSP 57193), 1 #ff (IBSP 57194), 2 #m (IBSP 57196), 2 #ff (IBSP 57197), 2 #m (IBSP 57198), 1 #m (IBSP 57199), 1 #ff (IBSP 57200), 1 #ff (IBSP 57201), 1 #ff (IBSP 57202), 1 #m (IBSP 57203), 1 #m (IBSP 57204), 2 #ff (IBSP 57205), 1 #ff (IBSP 57206), 1 #m (IBSP 57208), 1 #ff (IBSP 57210), 1 #m (IBSP 57211), 1 #ff (IBSP 57212), 1 #m (IBSP 57213), 1 #m (IBSP 57214), 1 #ff (IBSP 57215), 2 #m (IBSP 57216), 1 #m (IBSP 57217), 1 #ff (IBSP 57218), 1 #m (IBSP 57219), 3 #m (IBSP 57220), 1 #ff (IBSP 57222), 1 #m (IBSP 57223), 1 #m (IBSP 57224), 1 #m (IBSP 57226), 2 #m (IBSP 57227), 1 #m 1 #ff (IBSP 57230), 1 #m (IBSP 57231), 2 #m (IBSP 57232), 1 #m (IBSP 57235), 1 #ff (IBSP 57237), 1 #m (IBSP 57239), 1 #ff (IBSP 57240), 1 #m (IBSP 57241), 1 #m (IBSP 57242), 1 #m (IBSP 57243), 1 #ff (IBSP 57244), Pitfall, Equipe BIOTA et. al. coll., 09–15/XI/2001, 2 #ff (IBSP IB-57186), same collector, 9-15/X/2001, 1 #m (IBSP IB-57195), same collector, 09-15/X/2001, 2 #m (IBSP IB-57209); *Miracatu*, Morro do Fau, Pitfall [S24.24814°, W47.45979°], R. Pinto da Rocha, R. S. Bérnils, E. Howaldt & M. Matsumoto coll., 19/XII/1998, 1 #ff (MZUSP 16981), 1 #ff (MZUSP 17013); Mogi das Cruzes, Parque Natural Municipal da Serra do Itapety [S23.48673°, W46.19498°], Equipe Biota coll., 17–19/XII/2003, 1 #ff (IBSP 55043), RPPN Botujuru, trilha para a Pedra do Lagarto, Busca ativa [S23.48333°, W46.17717°, 839m], M.D.F. Magalhães et al. coll., 22/VI/2021, 1 #ff (UFMG 28020), 8 #m 11 #ff (UFMG 28021), 1 #ff (UFMG 28022), 1 #m (UFMG 28023), 1 #m (UFMG 28024); Peruibe, Estação Ecológica Juréia-Itatins [S24.55417°, W47.22478°], A. D. Brescovit et. al. coll., 26-3/IV-V/1999, 6 #m 9 #ff 2 imm. (IBSP 24963), same locality [S24.55417°, W47.1895°], R. Bertani & O.Marques coll., 02/XI/1995, 5 #m 7 #ff 1 imm. (IBSP 6347), O.Marques coll., 23/II/1997, 1 #m 1 #ff (IBSP 9538), A.D. Brescovit et.al. coll., 17–21/III/1997, 1 #ff (IBSP 9593), A.D.Brescovit et.al. coll., same date, 16 #m 12 #ff 4 imm. (IBSP 9612), A.D. Brescovit et.al. coll., same date, 2 #m (IBSP 9725), 1 #ff (IBSP 9750), 2 #ff (IBSP 9832), A.D.Brescovit et.al. coll., same date, 1 #m 1 #ff (IBSP 9848), 3 #m (IBSP 9927); Peruíbe, A.D. Brescovit et al. coll., 26/IV-03/V/1999, 1 #ff (IBSP 24809), 1 #m (IBSP 24851), 1 #ff (IBSP 24882), 1 #ff (IBSP 25040), 1 #m (IBSP 25123), 1 #ff (IBSP 25143), 1 #ff (IBSP 25185), 1 #ff (IBSP 25188), 1 #ff (IBSP 25209), 1 #m (IBSP 25240), 1 #ff 1 imm. (IBSP 25352), 1 #m 1 #ff (IBSP 25660), 1 #ff (IBSP 25661), 1 #ff (IBSP 25662), 1 #m 1 #ff (IBSP 25663), 1 #m (IBSP 25668), 1 #ff (IBSP 25669), 2 #m 1 imm. (IBSP 25670), 1 #m 1 #ff (IBSP 25674), 1 #m (IBSP 25677), 1 #m (IBSP 25678), 1 #ff (IBSP 25683), 1 #ff (IBSP 25685), 1 #ff (IBSP 25687), 1 #ff (IBSP 25691), 1 #ff (IBSP 25694), 1 #ff 2 imm. (IBSP 25695), 1 #m (IBSP 25701), 1 #m (IBSP 25702), 1 #m (IBSP 25703), 1 #ff (IBSP 25704), 1 #ff (IBSP 25709), 1 #ff (IBSP 25711), 3 #m (IBSP 25712), 1 #ff (IBSP 25713), 1 #m (IBSP 25715), 1 #m (IBSP 25726), 1 #ff (IBSP 25729), 1 #ff (IBSP 25736), 1 #ff (IBSP 25737), 1 #m (IBSP 25748), 1 #ff (IBSP 25751), 1 #ff (IBSP 25769), 1 #m (IBSP 25773), 1 #ff (IBSP 25774), 1 #m (IBSP 25778), Estação Ecológica Juréia-Itatins, A.D. Brescovit et al. coll., 1 #ff (IBSP 22077), 1 #m (IBSP 22110), 1 #m (IBSP 22112), 1 #m (IBSP 22133), 1 #m (IBSP 22141), same collector, 18/XII/1998, 1 #ff (IBSP 22183), same collector, 16/XII/1998, 1 #m (IBSP 22348), 1 #m (IBSP 22457), 1 #ff (IBSP 22725), same collector, 17/XII/1998, 1 #ff (IBSP 22983), Estação Ecológica Juréia-Itatins - Base Perequê, trilha da água, Busca ativa [S24.37583°, W47.08417°, 286m], M.D.F. Magalhães et al. coll., 26/X/2021, 9 #m 6 #ff 1 imm. (UFMG 28039), 1 #m (UFMG 28040), 1 #m (UFMG 28041), 1 #ff (UFMG 28042), 1 #ff (UFMG 28043), Estação Ecológica Juréia-Itatins, Núcleo Arpoador, Pitfall [S24.38711°, W47.01758°, 13m], G.H.F. Azevedo & J.P.P. Pena-Barbosa coll., 21–26/IV/2012, 5 #m 4 #ff (UFMG 13078), 1 #ff (UFMG 20353), 1 #ff (UFMG 20354), 1 #m (UFMG 20355); Pindamonhangaba [S22.92389°, W45.46167°], R.Martins coll., 16/II/1997, 3 #ff (IBSP 20007); Santo Amaro, Engenheiro Masilac, Pitfall [S23.86236°, W46.75377°], P. Biasi coll., 30/XII/1966, 1 #m (MZUSP 11775), Busca ativa, same collector, 16-17/XII/1966, 1 #m 1 #ff

(MZUSP 5410); Santos, Vale do Rio Jurubatuba [S23.86475°, W46.30436°], Nogueira et al coll., III-XII/2007, 1 #m (IBSP 123198), 3 #m (IBSP 123201), 1 #m (IBSP 123203), 2 #m (IBSP 123205), 1 #ff (IBSP 123207), Nogueira et al. coll., same date, 1 #m (IBSP IB-123202), Busca ativa, 1 #m (IBSP IB-123204) [S23.95887°, W46.33162°], E.O. Machado coll., 01-05/X/2007, 1 #ff (IBSP 118401); São Bernardo do Campo, Clube de Campo São Camilo [S23.79038°, W46.54498°], C.V. Janini et al. coll., 13-20/X/2008, 2 #m (IBSP 136553), Parque Estoril [S23.77064°, W46.51951°], C.V. Janini et al. coll., 04–09/I/2008, 1 #m (IBSP 117851), same collector, 21–29/X/2007, 1 #ff (IBSP 117853), same collector, 04–09/I/2008, 1 #m (IBSP 117854), same collector, 17/III/2008, 1 #ff (IBSP 117855), same collector, 21-29/X/2007, 1 #m (IBSP 117856), same collector, 12–17/III/2006, 1 #ff (IBSP 117857), same collector, 15–19/XII/2007, 2 #m (IBSP 117859), same collector, 27/VIII–03/IX/2007, 1 #ff (IBSP 117860), same collector, 04–09/I/2008, 1 #ff (IBSP 117861), Pitfall, B. Távora et al. coll., 15-19/XII/2006, 1 #ff (IBSP 117863), C.V. Janini coll., 21-29/X/2007, 1 #m (IBSP 118736), B. Távora et al. coll., 05–12/XII/2006, 1 #m (IBSP 118737), 2 #m (IBSP 118739), 1 #ff (IBSP 118741), C.V. Janini coll., 04-09/I/2008, 1 #m (IBSP 118746), same collector, 12-19/III/2008, 1 #m (IBSP 118747), B. Távora et al. coll., 2006, 1 #m (IBSP 118748), C.V. Janini coll., 21–29/X/2007, 1 #m (IBSP 118749), B. Távora et al. coll., 31/I–07/II/2007, 1 #ff (IBSP 118752), C.V. Janini coll., 12-19/III/2008, 1 #ff 1 imm. (IBSP 118753), same collector, 04-09/I/2008, 1 #ff (IBSP 118755), same collector, 21-29/X/2007, 1 #ff (IBSP 118756), same collector, 04-09/I/2008, 1 #m (IBSP 118760), same collector, 12-19/III/2008, 1 #ff (IBSP 118765), same collector, 04–09/I/2008, 1 #m (IBSP 118767), same collector, 12–19/III/2008, 1 #ff (IBSP 118771), B. Távora et al. coll., 31/I-07/II/2007, 1 #ff (IBSP 118775), same collector, 05–12/XII/2006, 1 #ff (IBSP 118871), same collector, 31/I–07/II/2007, 1 #ff (IBSP 118874), C.V. Janini et al. coll., 21–29/X/2007, 1 #ff (IBSP 118877), 2 #m (IBSP 118882), 1 #ff (IBSP 118887), same collector, 31/I–07/II/2007, 2 #ff (IBSP 118889), B. Távora et al. coll., 05-12/XII/2006, 1 #m (IBSP 118892), C.V. Janini et al. coll., 27/VIII-03/IX/2007, 1 #m (IBSP 118950), s/col. coll., 28/IX-02/X/2006, 1 #m (IBSP 90442), 1 #m (IBSP 90445), 1 #m (IBSP 90449), 1 #m (IBSP 90450), 1 #ff (IBSP 90455), 3 #m (IBSP 90457), 1 #m (IBSP 90464), 4 #m (IBSP 90465), 1 #m (IBSP 90471), 1 #ff (IBSP 90480), 1 #m (IBSP 90482), 2 #m (IBSP 90484), 1 #m (IBSP 90487), 1 #m (IBSP 90495), 1 #m (IBSP 90495), Pitfall, B. Távora et al. coll., 7–12/XII/2006, 1 #ff (IBSP IB-118769), same collector, 31–7/I–II/2007, 1 #ff (IBSP IB-118777), C. V. Janini et al. coll., 27-3/VIII-IX/2007, 2 #m (IBSP IB-118888); São Luiz do Paraitinga, Parque Estadual Serra do Mar - Núcleo Santa Virgínia, Busca ativa [S23.43772°, W45.24414°, 803m], M.D.F. Magalhães et al. coll., 18/XI/2020, 3 #m 1 #ff (UFMG 27971);

São Miguel Arcanjo, Parque Estadual de Carlos Botelho [S24.13822°, W47.99264°], A. B. Bonaldo coll., 14/X/1990, 1 #ff (MCN 20483); São Paulo, Batêa, Pitfall, F. Lane coll., 2/XI/1940, 2 #m (MZUSP 10253), Campus USP, Reserva Florestal da CUASO [S23.56667°, W46.71667°], alunos USP coll., V/2001, 1 #ff (IBSP 41737), D. F. Candiani coll., 16-23/II/2000, 1 #ff (IBSP 42239), 1 #ff (IBSP 42240), 1 #ff (IBSP 42241), 1 #ff (IBSP 42242), 1 #ff (IBSP 42244), same collector, 16–23/XI/1999, 1 #m (IBSP 42246), 1 #m (IBSP 42248), 1 #m (IBSP 42249), same collector, 16–23/VIII/1999, 1 #m (IBSP 42254), 1 #m (IBSP 42255), 1 #m (IBSP 42256), Pitfall, same locality [S23.56286°, W46.72937°], Alunos USP coll., V/2001, 1 #ff (IBSP IB-41790), Horto Florestal, Cidade Universitária [S23.58333°, W46.666667°], Sem coletor coll., XII/1972, 70 #m 7 #ff 4 imm. (IBSP 62937), Jardim Ângela, Reservatório do Guarapiranga [S23.70374°, W46.76947°], R. P. Indicatti coll., 06–12/XI/1999, 9 #m (IBSP 131655), 9 #m (IBSP 131657), 13 #m 2 #ff (IBSP 131658), same collector, 09– 15/IX;06–12/XI/1999, 14 #m (IBSP 131659), same collector, 06–12/XI/1999;06–12/V/2000, 11 #m 1 #ff (IBSP 131660), same collector, 09–15/IX/1999;06–12/XI/1999;06–12/V/2000, 11 #m (IBSP 131661), same collector, 06–12/XI/1999;06–12/V/2000, 11 #m (IBSP 131662), same collector, 09-15/IX/1999;06-12/V/2000, 5 #m 6 #ff (IBSP 131663), I. Cizauskas & C.R.M Garcia col. coll., 7-13/X/2004, 1 #m 1 #ff (IBSP 66927), I. Cizauskas & C.R.M. Garcia col. coll., 07–13/IV/2005, 1 #ff (IBSP 75023), 1 #ff (IBSP 75032), 7 #m 1 #ff (IBSP 75034), 4 #m 1 #ff (IBSP 75035), 3 #m (IBSP 75037), 1 #ff (IBSP 75040), 3 #m 1 #ff (IBSP 75041), 1 #ff (IBSP 75042), 1 #m (IBSP 75045), I. Cizauskas & C.R.M. Garcia coll., 07-13/X/2004, 4 #m (IBSP IB-75022), same locality [S23.73686°, W46.73572°], R. P. Indicatti coll., XI/2000, 1 #m (IBSP 27346), Parque da Previdência [S23.58028°, W46.727°], D. F. Candiani coll., 16-23/VIII/1999, 1 #m (IBSP 42264), 2 #m (IBSP 42265), same locality [S23.56667°, W45.71667°], D.F. Candiani col. coll., V/2000 – II/2001, ? #m ? #ff ? imm. (IBSP 76530), same locality [S23.56667°, W46.71667°], same collector and date, 10 #m 5 #ff (IBSP 76530), Parque do Estado [S23.65163°, W46.62616°], J.R.Valvassori coll., 16-23/VII/2002, 1 #m 1 #ff (IBSP 59167), 1 #m 1 #ff (IBSP 59168), 1 #m (IBSP 59170) [S23.5603°, W46.63731°], D. F. Candiani coll., 16–23/IV/1999, 1 #m (IBSP 42258), 1 #ff (IBSP 42260), same collector, 16– 23/VIII/1999, 1 #m (IBSP 42263), 1 #m (IBSP 42266), same locality [S22.92389°, W45.46167°], same collector, 16-23/II/2000, 1 #m (IBSP 42268); São Paulo, Parque da Previdência [S23.58028°, W46.727°], F.S. Cunha coll., 22/II/2001, 1 #m (IBSP 32920); Ubatuba, Fazenda Angelin [S23.39732°, W45.06416°], C. Rheims & R. Indicatti coll., VIII/2002, 1 #m (IBSP 52266).

Paravulsor similis (Keyserling, 1891) comb. nov.

(Figs 2, 8, 9, 11, 15)

Odo similis Keyserling, 1891: 44, plate 1, fig. 19 (syntypes from Brazil, Rio de Janeiro state, Rio de Janeiro, Corcovado, Prof. Göldi coll., 3 #f, 1 #m, deposited in NHML 1311-12, examined by photographs. Male herein designated as lectotype). Mello-Leitão, 1936: 28, plate 2, fig. 53.

Remarks. *Odo pulcher* and *Odo similis* were described by Keyserling (1891) based on males and females collected in the state of Rio de Janeiro, Brazil. *O. pulcher* type specimens are from Palmeiras, nowadays known as Palmeira da Serra, and *O. similis* type-locality is the Corcovado, a famous mountain in the city of Rio de Janeiro. These localities are very far from each other, about 63 km in straight line. However, among the specimens examined for this study, we found several females from the Parque Nacional da Tijuca (which includes the Corcovado), which fit our images of *O. pulcher* female syntype. Those females were found always associated with males that match the images of *O. similis* male syntype and original illustrations. We could not find any female similar to *O. similis* female syntypes in that locality. After examining dozens of specimens, we concluded that males and females of *O. pulcher* and *O. similis* were mismatched. Finally, the illustrations provided by Mello-Leitão (1936) do not correspond to *Odo similis*, but to an undescribed species.

Diagnosis. Males of *P. similis* resemble *P. pulcher* in the vRTA pointed, thorn-shaped, and the dRTA composed by three projections (Figs 8A-C, 9A-C, 10A-C). *P. similis* differ from *P. pulcher* in the vRTA wider, laterally expanded. Also, differ from *P. pulcher* in the dRTA with PL spiniform, ventrally curved, the ML more sclerotized than the DL, finger-shaped, and the DL wider at the base, narrowing at the tip (Figs 8A-C, 9A-C, 10A-C). Males resemble *P. impudicus* in the apical RTP pointed (Figs 3A-C, 8A-C, 9A-C) but differ by the absence of the median RTP. Females of *P. similis* resemble *P. impudicus* and *P. pulcher* in the median field longer than wide and differ by presence of a narrow posterior lobe and by the lateral lobes straight, opening posteriorly (Figs 3D, E, 8D, 9D, E, 10D).

Description. MALE FROM PARQUE NACIONAL DA TIJUCA, MATA DO PAI RICARDO, RIO DE JANEIRO, RIO DE JANEIRO, BRAZIL (MNRJ 7482; FIGS 8E, 9F). **Carapace** light brown, with several setae, dark lateral bands. Chelicerae brown, labium, endites and sternum light brown. **Legs** brown, with several macrosetae. **Abdomen** dorsum covered by short setae, dorsum light

brown with irregular dark spots and lateral dark bands, venter light brown. **Total length** 4.33. **Carapace** length 2.2, width 1.84. **Leg IV:** femur (fe) 2.39, patella (pa) 0.79, tibia (ti) 2.09, metatarsus (mt) 3.03, tarsus (ta) 1.53. **Abdomen** length 2.09, width 1.36. **PALP (FIGS 8A–C, 9A–C). Retrolateral tegular process (RTP)** one apical pointed lobe. **Median apophysis** hook-shaped, straight, shorter than the RTP and TDD. **Tegular distal division (TDD)** wide, with a narrowed posterior lobe. **Patella** with one dorsal macrosetae, smallest than the patella length. **Tibia** with long ventral setae and a wide concavity. **Retrolateral tibial apophysis** (**RTA**) divided in two apophysis. vRTA fully sclerotized, ventrally pointed, with a lateral expansion, dRTA composed by three projections: PL fully sclerotized, long, reaching the concavity of the tibia, spiniform and ventrally curved; ML smallest and more sclerotized than the DL, finger-shaped; DL, wider than other lobes, narrowing at the tip.

FEMALE FROM PARQUE NACIONAL DA TJUCA, MATA DO PAI RICARDO, RIO DE JANEIRO, RIO DE JANEIRO, BRAZIL (MNRJ 7482; FIGS 8F, 9G). **Carapace** light brown, with several setae, dark lateral bands. Chelicerae brown, Labium light brown, Endites light brown, Sternum light brown. **Legs** light brown, with dark brown spots and several macrosetae. **Abdomen** dorsum covered by short setae, dorsum light brown with irregular dark spots and lateral dark bands, venter light brown. **Total length** 5.22. **Carapace** length 2.49, width 1.92. **Leg IV:** femur (fe) 2.27, patella (pa) 0.78, tibia (ti) 2.01, metatarsus (mt) 2.63, tarsus (ta) 1.42. **Abdomen** length 2.96, width 2.13. **GENITALIA (FIGS 8D, 9D, E). Epigynum** median field and lateral lobes divides from the upper half of the epigynum. **Median field** longer than wide, with median constriction and a narrower posterior lobe. **Lateral lobes** straight medially; posterior pockets medially directed in a triangular lobe. **Median field and lateral lobes** extend through the genital opening. **Primary spermathecae** elongated and spiral, duct-shaped. **Secondary spermathecae** rounded, duct-shaped, located above to the copulatory ducts opening. **Copulatory ducts** open in a central hole, anteriorly to the median field. **Fertilization duct** sclerotized, curved, thinner than the other ducts, and covered by the *uterus externus* membrane.

Distribution & Habitat. *P. similis* occurs mostly in the Parque Nacional da Tijuca, a national park in Rio de Janeiro city, which is part of the Serra do Mar mountain range. Additionally, it can be found in a few localities in the states of Espírito Santo and São Paulo (Figs. 11, 15).

Additional material examined. BRAZIL. Espírito Santo: *Cariacica*, Reserva Biológica Duas Bocas, Pitfall [S20.28998°, W40.52132°, 653m], C.F. Sperber et al. coll., 17–19/VII/2012, 5 #ff (UFMG 28046). **Rio de Janeiro:** *Rio de Janeiro*, Jacarepaguá, Pedra Branca, INEA -Núcleo Pau da Fome [S22.93225°, W43.44128°], AF García, AB Kury & MA Medrano coll.,

17/IV/2022, 1 #m 1 #ff (UFMG 28047), Parque Nacional da Tijuca, Pitfall [S22.94439°, W43.27153°], Mário Eugenio, Irmão coll., 1 #m (MNRJ 58294), Pedroso, D. R., Almeida, D. F. & Giupponi, A. P. L. coll., 3/III/2001, 1 #ff (MNRJ 7487), 4 #ff 3 imm. (MNRJ 7499), Winkler, 14 #m 1 #ff (MNRJ 7501), same locality [S22.9515°, W43.28586°], same collector and date, 6 #m 1 imm. (MNRJ 7509), Pitfall, same locality [S22.95189°, W43.44233°, 563m], E.S.S. Álvares coll., II/2004, 3 #m 3 #ff (UFMG 1777), Busca ativa, same locality [S22.95417°, W43.28889°, 528m], M.D.F. Magalhães et al. coll., 1/II/2020, 9 #m 8 #ff (UFMG 27939), same locality [S22.96°, W43.27528°, 368m], same collector and date, 5 #m 1 #ff (UFMG 27940), Parque Nacional da Tijuca [S22.9515°, W43.28586°], 1 #ff (MNRJ 7515), Parque Nacional da Tijuca, Archer, Pitfall [S22.95203°, W43.28803°], 3 #m 3 #ff (MNRJ 7486), 1 #ff (MNRJ 7502), Parque Nacional da Tijuca, Belmiro, Winkler [S22.95179°, W43.28964°], Moreira, T.S. coll., I/2005, 10 #m 1 #ff 2 imm. (MNRJ 7498), 2 #ff (MNRJ 7511), Parque Nacional da Tijuca, Cochrane, Pitfall [S22.98139°, W43.26528°], Baptista, R. L. C. coll., 20/I/2005, 1 #ff (MNRJ 7485), Parque Nacional da Tijuca, Gávea, Pitfall [S23.00136°, W43.29549°], Pedroso, D. R. coll., 18/I/2005, 1 #m 2 imm. (MNRJ 7484), Parque Nacional da Tijuca, Mata do Pai Ricardo, Pitfall [S22.96214°, W43.24811°], R. L. C. Baptista coll., 21/i/2005, 1 #m 1 #ff (MNRJ 7479), Wienskoski, E. H. coll., same date, 1 #m (MNRJ 7480), Costa, C. S. coll., same date, 1 #ff (MNRJ 7481), R. L. C. Baptista coll., III/2005, 19 #m 9 #ff 5 imm. (MNRJ 7482), Sampaio, C. coll., 21/I/2005, 1 #ff (MNRJ 7497), 28 #m 8 #ff (MNRJ 7500), Parque Nacional da Tijuca, Sumaré, Winkler [S22.95112°, W43.2334°], Baptista, R. L. C. coll., 22/I/2005, 1 #ff (MNRJ 7483), Parque Nacional da Tijuca, Vale da Gávea. [S23.00136°, W43.29549°], Moreira, T.S. coll., 18/I/2005, 1 #ff 4 imm. (MNRJ 7510), Urca, Pitfall [S22.95198°, W43.16044°], Batista, R. L. C. coll., III/1995, 1 #ff (MNRJ 7513), Pitfall [S22.9431°, W43.22917°], Rosa, M. coll., 1 #m (MNRJ 42684); Rio do Janeiro, Represa Rio Grande, Pitfall [S22.95764°, W43.44477°], Alvarenga coll., I/1967, 1 #m (MZUSP 10817). São Paulo: Ubatuba, Parque Estadual da Ilha Anchieta [S23.41667°, W46.61667°], Equipe Biota coll., 13–18/X/2003, 1 #m (IBSP 56395), same collector, 23–30/VII/2001, 1 #ff (IBSP 56397), 1 #ff (IBSP 56405).

Paravulsor pulcher (Keyserling, 1891) comb. nov.

(Figs 10, 11, 16)

Odo pulcher Keyserling, 1891: 42, plate 1, fig. 18 (syntypes from Brazil, Rio de Janeiro, Paulo de Frontin, Palmeiras [nowadays Palmeira da Serra], Prof. Göldi coll., 1 #f, 1 #m, deposited in NHML 1313-15, examined by photographs. Male herein designated as lectotype). Mello-Leitão, 1936: 28, plate 2, fig. 52.

Remarks. Given the information presented above for *Paravulsor similis*, we assumed that the *Odo pulcher* male syntype and *Odo similis* female syntypes belong to the same species. However, none of the species that we collected nearly to the type locality of *O. pulcher* match completely with them. Since we examined these syntypes only by photographs, a future confirmation must be made based on an in-person examination.

Diagnosis. Males of *P. pulcher* resemble *P. similis* in the vRTA pointed, thorn-shaped, and the dRTA composed by three projections (Figs 9A-C, 10A-C). *P. pulcher* differ from *P. similis* in the vRTA smaller, pointed, and ventrally curved (Figs 9A-C, 10A-C). Also, differ from *P. similis* in the dRTA with PL sinuous, not curved; DL sinuous, and ML wide, rounded at the apex (Figs 9B, C, 10B, C). Females of *P. pulcher* resemble *P. impudicus* and *P. similis* in the median field longer than wide but differ in the lateral lobes anteriorly expanded and widely spaced posteriorly (Figs 3D, 9D, 10D).

Description. MALE FROM PALMEIRAS, PAULO DE FRONTIN, RIO DE JANEIRO, BRAZIL (NHML 1313-15; FIG. 10E). **Carapace** light brown, with several setae, dark lateral bands. Chelicerae brown, labium, endites and, sternum light brown. **Legs** brown, with several macrosetae. **Abdomen** dorsum covered by short setae, dorsum light brown with irregular dark spots and lateral dark bands, venter light brown. Male. **Total length** 4.87. **Carapace** length 2.42, width 2.05. **Abdomen** length 2.38, width 1.42. **PALP (FIG. 10A–C). Retrolateral tegular process** (**RTP**) one apical pointed lobe. **Median apophysis** hook-shaped, shorter than the RTP and TDD. **Tegular distal division (TDD)** wide, with a narrowed posterior lobe. **Patella** with one dorsal macrosetae, smallest than the patella length. **Tibia** with long ventral setae and a wide concavity. **Retrolateral tibial apophysis (RTA)** divided in two apophysis. vRTA fully sclerotized, ventrally pointed, thorn-shaped, dRTA composed by three projections: PL fully sclerotized, spiniform and sinuous; ML sinuous and DL smallest than other lobes, rounded at the apex.

FEMALE FROM PALMEIRAS, PAULO DE FRONTIN, RIO DE JANEIRO, BRAZIL (NHML 1313-15; FIG.10F). **Carapace** light brown, with several setae, dark lateral bands. Chelicerae brown, Labium light brown, Endites light brown, Sternum light brown. **Legs** light brown, with dark brown spots and several macrosetae. **Abdomen** dorsum covered by short setae, dorsum light brown with irregular dark spots and lateral dark bands, venter light brown. **Total length** 6.20. **Carapace** length 2.78, width 2.22. **Abdomen:** length 3.42, width 2.06. **GENITALIA (FIG. 10D)**. **Epigynum** median field and lateral lobes divides from the middle of the epigynum. **Median** field longer than wide, with a posterior lobe. **Lateral lobes** present a central expansion

anteriorly to the median field, posterior pockets wide, medially directed. **Primary spermathecae** elongated and spiral, duct-shaped. **Secondary spermathecae** rounded, parallel to the copulatory ducts opening.

Distribution & Habitat. P. similis is known only from the type locality (Figs 11, 16).

5. References

- Álvarez-Padilla F. & Hormiga G. (2008) A Protocol for Digesting Internal Soft Tissues and Mounting Spiders for Scanning Electron Microscopy. *Journal of Arachnology* 35: 538– 542.
- Bonnet, P. (1958) Bibliographia araneorum. Analyse méthodique de toute la littérature aranéologique jusqu'en 1939. Tome II. Systématique des araignées (Étude par ordre alphabétique) (4me partie: N-S). Douladoure, Toulouse, pp. 3027-4230.
- Faustino-Magalhães, M.D. (2019) Análise filogenética e revisão taxonômica de Xenoctenidae Ramírez & Silva-Dávila (Araneae). Master's dissertation. Universidade Federal de Minas Gerais, Brazil.
- Faustino-Magalhaes, M.D., Piacentini, L.N. & Santos, A.J. (2024) The desert wolf-spider genus *Xenoctenus*: two endemic species from the Brazilian Caatinga, and a redescription of the type-species, *X. unguiculatus* (Araneae: Xenoctenidae). *Zootaxa*, 5399(5), 517–539. https://doi.org/10.11646/zootaxa.5399.5.3
- Francisco, R.C., Ott, R. & Teixeira, R.A. (2016) A new species of the genus *Apollophanes* O. Pickard-Cambridge, 1898 (Araneae: Philodromidae) with the first record to the Atlantic rainforest. *Zootaxa*, 4171 (1), 178–182. https://doi.org/10.11646/zootaxa.4171.1.9
- Fundação SOS Mata Atlântica. (2019). *Relatório Anual*. Available in: https://doi.org/https://www.sosma.org.br/relatorio-anual-2019.
- Huber, B.A. (2015) Small scale endemism in Brazil's Atlantic Forest: 14 new species of *Mesabolivar* (Araneae, Pholcidae), each known from a single locality. *Zootaxa*, 3942 (1), 1–60. https://doi.org/10.11646/zootaxa.3942.1.1
- Huber, B.A. (2016) Spider diversity and endemism in a South American hotspot: 20 new species of *Carapoia* (Araneae: Pholcidae) from Brazil's Atlantic Forest. *Zootaxa*, 4177 (1), 1–69. https://doi.org/10.11646/zootaxa.4177.1.1
- Huber, B.A. & Rheims, C.A. (2011) Diversity and endemism of pholcid spiders in Brazil's Atlantic Forest, with descriptions of four new species of the Atlantic Forest endemic genus *Tupigea* (Araneae: Pholcidae). *Journal of Natural History*, 45 (5–6), 275–301. https://doi.org/10.1080/00222933.2010.524319

- IBGE (2021) Ecosystem accounts: species threatened with extinction in Brazil: 2014 (IBGE, Department of Natural Resources and Environmental Studies, & Department of National Accounts, Eds.).
- International Commission on Zoological Nomenclature (1999) *International Code of Zoological Nomenclature*. Fourth Edition. International Trust for Zoological Nomenclature, London, XXIX, 306 pp.
- Keyserling, E. (1877) Ueber Amerikanische Spinnenarten Der Unterordnung Citigradae. Verhandlungen Der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien, 26, 609–708.
- Keyserling, E. (1887) Neue Spinnen Aus America. Vii. Verhandlungen Der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft In Wien, 37. 421–490.
- Keyserling, E. (1891) Die Spinnen Amerikas. Brasilianische Spinnen. Bauer & Raspe, Nürnberg 3, 1–278. doi:10.5962/bhl.title.64832
- Koch, C.L. (1847) Die Arachniden. Nürnberg, Vierzehnter Band, Pp. 89–210, Funfzehnter Band, Pp. 1–136, Sechszehnter Band, Pp. 1–80.
- Kury, A.B., Giupponi, A.P. & Mendes, A.C. (2018) Immolation of Museu Nacional, Rio de Janeiro–unforgettable fire and irreplaceable loss. *Journal of Arachnology*, 46 (3), 556– 558.
- Lehtinen, P.T. (1967) Classification of the Cribellate Spiders and Some Allied Families, With Notes on The Evolution of The Suborder Araneomorpha. *Annales Zoologici Fennici*, 4, 199–468.
- Magalhaes, I.L.F. (2019) Spreadsheets to expedite taxonomic publications by automatic generation of morphological descriptions and specimen lists. *Zootaxa*, 4624 (1), 147–150. https://doi.org/10.11646/zootaxa.4624.1.12
- Magalhães, I., Fernandes, L., Ramírez, M. & Bonaldo, A. (2016) Phylogenetic position and taxonomic review of the *Ianduba* spiders (Araneae: Corinnidae) endemic to the Brazilian Atlantic rainforest. *Arthropod Systematics & Phylogeny*, 74 (2), 127–159. https://doi.org/10.3897/asp.74.e31843
- Marques, M.C.M., Trindade, W., Bohn, A. & Grelle, C.E.V. (2021) The Atlantic Forest: An Introduction to the Megadiverse Forest of South America. *In*: Marques, M.C.M. &

Grelle, C (Eds.), *The Atlantic Forest*. Springer, Heidelberg. Pp. 3–23. International Publishing. https://doi.org/10.1007/978-3-030-55322-7_1

- Mello-Leitão, C.F. de (1922) Novas Clubionidas Do Brasil. Archivos Da Escola Superior De Agricultura e Medicina Veterinaria, Rio De Janeiro, 6, 17–56.
- Mello-Leitão, C.F. de (1927) Arachnideos de Santa Catharina (Brasil). Revista do Museu Paulista, 15, 393–418.
- Mello-Leitão, C.F. de (1936) Contribution à l'etude des Ctenides du Bresil. *Festschrift Embrik Strand*, 1 1–31.
- Mello-Leitão, C.F. de (1938) Algunas Arañas Nuevas De La Argentina. *Revista Del Museo De La Plata* (N.S), 1, 89–118.
- Mello-Leitão, C.F. de (1942) Cinco Aranhas Novas do Perú. *Revista Brasileira de Biologia*, 2, 429–434.
- Mello-Leitão, C. F. de (1943) Catálogo das aranhas do Rio Grande do Sul. *Arquivos do Museu Nacional do Rio de Janeiro* 37: 147–245, 24 pls.
- Oliveira, U., Brescovit, A.D. & Santos, A.J. (2017). Sampling effort and species richness assessment: a case study on Brazilian spiders. *Biodiversity and Conservation*, 26 (6), 1481–1493. https://doi.org/10.1007/s10531-017-1312-1
- Petrunkevitch, A. (1928) Systema Aranearum. *Transactions of the Connecticut Academy of* Arts and Sciences, 29, 1–270.
- Pickard-Cambridge, F.O. (1893) Handbook To the Study of British Spiders (Drassidae And Agalenidae). *British Naturalist*, Supplement 3, 117–170.
- Ramírez, M.J. (2014) The Morphology and Phylogeny of Dionychan Spiders (Araneae: Araneomorphae). Bulletin of the American Museum of Natural History, 390, 1–374. https://doi.org/10.1206/821.1
- Rheims, C.A. (2010) *Caayguara*, a new genus of huntsman spiders from the Brazilian Atlantic Forest (Araneae: Sparassidae). *Zootaxa*, 2630, 1–29. doi:10.11646/zootaxa.2630.1.1
- Rheims, C.A. (2019) *Extraordinarius* gen. nov., a new genus of Sparianthinae spiders (Araneae: Sparassidae) from southeastern Brazil. *Zootaxa*, 4674 (1), 83–99. https://doi.org/10.11646/zootaxa.4674.1.4

- Roewer, C.F. (1955) Katalog der Araneae von 1758 bis 1940, bzw. 1954. 2. Band, Abt. a (Lycosaeformia, Dionycha [excl. Salticiformia]). 2. Band, Abt. b (Salticiformia, Cribellata) (Synonyma-Verzeichnis, Gesamtindex). Institut royal des Sciences naturelles de Belgique, Bruxelles, 1751 pp.
- Silva-Davila, D. (2003) Higher-Level Relationships of the Spider Family Ctenidae (Araneae: Ctenoidea). *Bulletin of the American Museum of Natural History*, 274, 1–86.
- Silva-Moreira, T.D., Baptista, R.L., Kury, A.B., Giupponi, A.P., Buckup, E.H. & Brescovit, A.D. (2010) Annotated check list of Arachnida type specimens deposited in the Museu Nacional, Rio de Janeiro. II—Araneae. *Zootaxa*, 2588 (1), 1–91.
- Simon, E. (1886) Etudes Arachnologiques. 18e Mémoire. Xxvi. Matériaux Pour Ouvel À La Faune Des Arachnides Du Sénégal. Annales De La Société Entomologique De France, (6) 5, 345–396.
- Strand, E. (1934) Miscellanea nomenclatorica Zoológica et palaeontologica, VI. Folia Zoologica et Hydrobiologica, Rigā, 6, 271–277.
- Wheeler, W.C., Coddington, J.A., Crowley, L.M., Dimitrov, D., Goloboff, P.A., Griswold, C.E., Hormiga, G., Prendini, L., Ramírez, M.J., Sierwald, P., Almeida-Silva, L., Alvarez-Padilla, F., Arnedo, M.A., Benavides Silva, L.R., Benjamin, S.P., Bond, J.E., Grismado, C.J., Hasan, E., Hedin, M., Izquierdo, M.A., Labarque, F.M., Ledford, J., Lopardo, L., Maddison, W.P., Miller, J.A., Piacentini, L.N., Platnick, N.I., Polotow, D., Silva-Dávila, D., Scharff, N., Szűts, T., Ubick, D., Vink, C.J., Wood, H.M. & Zhang, J. (2017) The spider tree of life: phylogeny of Araneae based on target-gene analyses from extensive taxon sampling. Cladistics. 33. 574-616. an https://doi.org/10.1111/cla.12182World Spider Catalog (2024) World Spider Catalog. Version 25.0. Natural History Museum Bern, online at http://wsc.nmbe.ch. Accessed in 8 February 2024.

FIGURE LEGENDS

Figure 1. Paravulsor impudicus Mello-Leitão, 1922. Female habitus, dorsal view. Photo: Pedro H. Martins

Figure 2. Paravulsor similis (Keyserling, 1891) comb. nov. Female palp with twisted setae.

Figure 3. Paravulsor impudicus Mello-Leitão, 1922, male and female from Área de Relevante Interesse Ecológica Floresta da Cicuta, Volta Redonda, Rio de Janeiro, Brazil (UFMG 28018). A–C, male palp. A, prolateral. B, ventral. C, retrolateral. D, female epigynum. E, female internal genitalia. F, male habitus, dorsal view. G, female habitus, dorsal view.

Figure 4. Paravulsor blumenauensis Mello-Leitão, 1900. A, male habitus, dorsal view. B, female habitus, dorsal view. Photo: Pedro H. Martins.

Figure 5. Paravulsor blumenauensis (Mello-Leitão ,1927) **comb. nov.**, male and female *syntypes* from Blumenau, Santa Catarina, Brazil (MZUSP DZ 8947[949]). A–C, male palp. A, prolateral. B, ventral. C, retrolateral. D, female epigynum. E, female internal genitalia. F, female epigynum, posterior view.

Figure 6. Paravulsor blumenauensis (Mello-Leitão, 1927) **comb. nov.**, male and female from Blumenau, Santa Catarina, Brazil (IBSP 136858). A–C, male palp. A, prolateral. B, ventral. C, retrolateral. D, female epigynum. E, female internal genitalia. F, male habitus, dorsal view. G, female habitus, dorsal view.

Figure 7. Paravulsor obscurus (Mello-Leitão, 1936) **comb. nov.**, male and female from Jardim Ângela, Reservatório do Guarapiranga, São Paulo, SP, Brazil (IBSP 131663). A–C, male palp. A, prolateral. B, ventral. C, retrolateral. D, female epigynum. E, female internal genitalia. F, male habitus

Figure 8. Paravulsor similis (Keyserling, 1891) **comb. nov.**, male and female *syntypes* from Corcovado, Rio de Janeiro, RJ, Brazil (NHML 1311-12). A, C, male palp. A, ventral. B, C, retrolateral. D, female epigynum. E, male habitus, dorsal view. F, female habitus, dorsal view.

Figure 9. Paravulsor similis (Keyserling, 1891) **comb. nov.**, male and female from Parque Nacional da Tijuca, Rio de Janeiro, RJ, Brazil (MNRJ 7482). A–C, male palp. A, prolateral. B,

ventral. C, retrolateral. D, female epigynum. E, female internal genitalia. F, male habitus, dorsal view. G, female habitus, dorsal view.

Figure 10. Paravulsor pulcher (Keyserling, 1891) **comb. nov.**, male and female *syntypes* from Palmeiras, Rio de Janeiro, RJ, Brazil (NHML 1313-15). A, C, male palp. A, ventral. B, C, retrolateral. D, female epigynum. E, male habitus, dorsal view. F, female habitus, dorsal view.

Figure 11. Geographic distribution of Paravulsor in the Brazilian Atlantic Forest.

Figure 12. Geographic distribution of the type locality of *Paravulsor impudicus* in Rio de Janeiro state, Brazil.

Figure 13. Geographic distribution of *P. blumenauensis* in Paraná, Santa Catarina and Rio Grande do Sul states (Southern Atlantic Forest).

Figure 14. Geographical distribution of *P. obscurus* in São Paulo and Santa Catarina states (Southeastern and Southern Atlantic Forest).

Figure 15. Geographic distribution of *P. similis* in Espírito Santo, Rio de Janeiro, and São Paulo states (Southeastern Atlantic Forest).

Figure 16. Geographic distribution of *P. pulcher* type locality in Rio de Janeiro state (Southeastern Atlantic Forest).

<u>CHAPTER 3</u>

Phylogenetic and biogeographical study of *Paravulsor*: an endemic spider to the Atlantic Forest (Araneae: Xenoctenidae)

Abstract

Xenoctenidae Ramirez & Silva-Davila, 2017 is a Neotropical family of spiders composed of four genera: Incasoctenus Mello-Leitão, 1942; Odo Keyserling, 1887; Paravulsor Mello-Leitão, 1922; and Xenoctenus Mello-Leitão, 1938: A recent morphological phylogeny of the family, resulted in many discoveries about the monotypic genus Paravulsor. This genus, which was previously known only by its type locality, is widely distributed throughout the Atlantic Forest and comprises 56 species, including 51 new species. Furthermore, some of the new species may compose two new Atlantic Forest genera. Thus, this chapter explores the phylogenetic position of Atlantic Forest xenoctenids using phylogenomic data and provides new evidence for delimiting the Xenoctenidae genera. Additionally, it investigates past biogeographical scenarios through dating phylogenies and ancestral area reconstructions to unravel the distribution and diversification patterns of Atlantic Forest xenoctenids. Our results support previous studies about taxonomic problems of Xenoctenidae and recovered two new genera (Gen.nov.01 and Gen.nov.02) endemic to the Atlantic Forest. The distribution patterns of Atlantic Forest xenoctenids correlate with proposed centers of endemism for the Atlantic Forest. Also, Gen.nov.01 and Gen.nov.02 are associated with historically stable regions in the northern Atlantic Forest, and Paravulsor in the less stable southern portion of the biome. Despite a strong correlation with climatically stable areas, Pleistocene refugia didn't drive speciation, as most divergences occurred during the Miocene. Finally, the diversification of the north genera was likely influenced by global cooling, while in the south, it was associated with river formation due to tectonic activity.

1. Introduction

The Atlantic Forest is the second largest tropical forest in South America with a territory of 1.6 million ha, spanning the northeast to the south of Brazil, reaching the borders of

Paraguay and Argentina (Figure 1;Fundação SOS Mata Atlântica, 2019; Marques et al., 2021). This biome is among the most biodiverse ecosystems of the world and the geographical and climatic variation throughout its latitudinal and attitudinal gradients results in high habitat heterogeneity (Joly et al., 2014; Oliveira-Filho et al., 2000). Congruent endemism patterns have been observed between different taxa and at least five centers of endemism have been recognized for the Brazilian Atlantic Forest (BAF): Pernambuco, Central Bahia (the interior of the Chapada Diamantina region), Coastal Bahia (southern coast of Bahia), Serra do Mar, and Paraná/Araucaria (Carnaval et al., 2009; Carnaval & Moritz, 2008; Oliveira et al., 2015; Peres et al., 2020).

Over the years, the patterns of endemism and distribution observed in the Atlantic Forest biota has aroused the interest of biogeographers (Marques et al., 2021). Some hypotheses have emerged to explain its origin and diversification, such as: (1) the Pleistocene refuge theory, which proposes that the Quaternary glaciations fragmented the Atlantic Forest and led to the formation of areas of endemism that are associated with climatically stable regions (Ashcroft, 2010; Carnaval & Moritz, 2008; Dhorta et al., 2011; Porto et al., 2013); (2) the Neotectonism hypothesis, which predicts that tectonic reactivations in the Brazilian shield since the Neogene led to the Continental Rift of Southeastern Brazil, created new favorable environments for species diversification, and also rearranged important rivers in Southeastern Brazil, such as the Ribeira do Iguape and Paraíba do Sul, which may act as barriers for some taxa (Dantas et al., 2011; C., Riccomini et al., 2004; C. Riccomini & Assumpção, 1999; Souza et al., 2021); (3) the rivers-as-barriers hypothesis, which posits that large rivers prevent the dispersal of some lineages, thereby acting as a barrier to gene flow (Dantas et al., 2011; Pellegrino et al., 2005; Siedchlag et al., 2010; Thomé et al., 2010).

Xenoctenidae Ramirez & Silva-Davila, 2017 is a Neotropical family of spiders composed of four genera: *Incasoctenus* Mello-Leitão, 1942; *Odo* Keyserling, 1887; *Paravulsor* Mello-Leitão, 1922; and *Xenoctenus* Mello-Leitão, 1938 (Wheeler et al., 2017; World Spider Catalog, 2024). The family was recently reviewed by Faustino-Magalhaes (2019) based on a morphological phylogeny and resulted in new discoveries in its genera and species (see also Chapter 1). According to this study, *Odo* is polyphyletic and some of its species should be transferred to *Paravulsor* and *Xenoctenus*. Also, a recent review of the Brazilian *Xenoctenus* transferred *Odo vittatus* to *Xenoctenus* and described a new species (Faustino-Magalhaes et al., 2024).

One of the main discoveries about this family involves the monotypic genus *Paravulsor* Mello-Leitão, 1922. Although it was previously known only from the type locality, the genus is in fact widely distributed throughout the Atlantic Forest, comprising 56 species, of which 51 are new to science and 5 were transferred from *Odo* (see Chapter 1). These are wandering-spiders that hunt actively during the night and are very abundant in some regions, reaching almost 50% of the relative abundance of ground spiders (Castanheira et al., 2016; Raub et al., 2014). The genus also aroused scientific interest due to its distribution patterns, with microendemic species that occur in some BAF recognized centers of endemism of the Atlantic Forest. Additionally, some of the new species may consist of two new genera.

Besides the recent advances regarding the Atlantic Forest xenoctenids, the phylogenetic relationships of these genera still need to be better studied, as the processes that drive its distribution and diversification still need to be examined. Thus, in this chapter, we test the phylogenetic position of the Atlantic Forest xenoctenids, which includes *Paravulsor* and all new species or genera. Based on Ultraconserved Elements (UCEs) phylogenomic data, and we will also uncover new evidence for the delimitation of Xenoctenidae genera. Additionally, to understand the distribution and diversification patterns of the Atlantic Forest xenoctenids, we explored biogeographical scenarios from the past based on a dated phylogeny and ancestral area reconstructions.

2. Material and Methods

2.1. Taxon sampling and DNA extraction

We sequenced 72 specimens of Xenoctenidae comprising 51 specimens of *Paravulsor*, 4 specimens of *Gen.nov.01*; 1 specimen of *Gen.nov.02*, 8 specimens of *Odo* and 8 specimens of *Xenoctenus*. For the outgroup we selected 15 species, comprising 5 families of Dionycha, 4 families of the Oval Calamistrum Clade and *Dysdera crocrata* was used to root the phylogeny, selected according to Wheeler et al. (2017). The UCE sequences were obtained by Azevedo et al. (2022) and downloaded from the GenBank (see Table 1 in supplementary material).

Xenoctenidae specimens were obtained from field work and scientific collections. We collected fresh specimens from 153 sampling sites throughout the Atlantic Forest (Figure 3). Specimens collected during our field expeditions were kept in 100% ethanol and
stored in a -20 °C freezer. Additionally, we also obtained older specimens that were preserved in 70–80% ethanol and maintained at room temperature from the following collections: Coleção de História Natural da Universidade Federal do Piauí, Floriano, Brazil (CHNUFPI); Instituto Butantan, São Paulo, Brazil (IBSP); Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru (UNMSM); Museu Nacional do Rio de Janeiro, Rio de Janeiro, Brazil (MNRJ); National Museum of Natural History, Smithsonian Institution, Washington D.C., US (NMNH); Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Brazil (MCTP); Centro de Coleções Taxonômicas, Universidade Federal de Minas Gerais, Belo Horizonte, Brazil (UFMG).

We extracted DNA from tissue of up to four legs, depending on the size and preservation condition for each specimen. We performed a phenol-chloroform extraction protocol using the GenePrep DNA isolation system (GENE PREP STAR PI-480), following the manufactures protocol. The extracted DNA was quantified using high-sensitivity Qubit fluorometry (Life Technologies, Inc.). Fragment length was assessed using gel electrophoresis on a 1.5% agarose gel.

2.2. Ultraconserved elements library construction and enrichment

Libraries were prepared and enriched following protocols described in Faircloth et al. (2015) with the Kapa Hyper Prep Library kit (Kapa Biosystems). For each sample, we sheared the DNA with shearing time (from 0-60 seconds) based on the DNA quality by sonication (Q800R, Qsonica Inc.). We added the End Repair & A-Tailing buffer and incubate the solution on a thermocycler following the thermal protocol (Kapa Biosystems). The solution was then incubated on a thermocycler, followed by a post-ligation bead cleanup using Kapa beads. For adapter ligation, we used Illumina TruSeq-style adapters (Faircloth & Glenn, 2012). For amplification, the PCR reactions were assembled using the post-ligation library, Kapa HiFi Hot-Start Ready Mix, and i5 and i7 primers. The post-PCR cleanup was done with a bead clean Kapa Pure Beads (Kapa Biosystems) and the DNA was quantified using Qubit Broad Range and fragment length was assessed using gel electrophoresis on a 1.5% agarose gel. Then, libraries were combined into pools of eight samples at equimolar ratios, followed by Qubit Broad Range assay to measure DNA concentration.

The pools where enriched using the 'spider-specific' probe-set (Kulkarni et al., 2020), following the myBaits v5.02 protocol (Diacel Arbor Biosciences). We purified the resulting reactions using the bead clean Kapa Pure Beads (Kapa Biosystems) and we measured the post-PCR DNA concentration using Qubit Broad Range assay. All pools were then combined into a single pool at equimolar rations and sent to Admera Health Biopharma Services, NJ (via Genohub: www.genohub.com) for sequencing in a single lane of a paired-end run on an Illumina HiSeq X (2x150bp rapid run).

2.3. Phylogenetic analyses

The assembly, alignment, trimming and concatenation of data were done using the PHYLUCE pipeline (publicly available at <u>https://phyluce.readthedocs.io/en/latest/tutorials/tutorial-1.html</u>). We applied gene occupancies of 20% to all data and screened for orthologous and duplicate loci with the minimum identity and coverage of 65 and 65 as suggested by Kulkarni *et al.* (2020).

First, we estimated a phylogeny on non-partitioned data matrices (N = 100) in using RAxML v8.2 (Stamatakis, 2014) and performed a maximum likelihood best tree and bootstrap searches with a rapid bootstrap algorithm (bootstrap replicates N = 100 and the GTRGAMMA model; Stamatakis et al., 2008). In this initial analysis we assess the quality of the generated UCE sequences and got initial insights about the relationships between the taxa.

Then, we used PartitionFinder2 to select best-fit partitioning schemes (Lanfear et al., 2017) and ModelFinder to estimate the best evolution model (Kalyaanamoorthy et al., 2017). We use the partitioned tree to estimate the branch support values using IQ-TREE 2.2.0.7 via 5,000 ultrafast bootstrap replicates and the consensus tree was constructed from 5000 bootstrap trees (Minh et al., 2020; Hoang et al., 2017). Ultrafast bootstrap above 95 was considered as high support as suggested by Minh et al. (2013). All analyses were conducted on the Smithsonian Institution High Performance Cluster (SI/HPC).

2.4. Divergence time estimation

Due to the size of the resulting data matrix, we were unable to conduct divergence dating using Bayesian methods, such as BEAST (Drummond et al., 2012) or BEAST2 (Bouckaert et al., 2019). Thus, we chose MCMCTree, which is part of PAML v4.9 (Dos Reis et al., 2017; Yang, 1993), because it is a more efficient program. Due to a lack of

informative fossils for this group, we set node age priors on outgroup nodes of Salticidae based in the species *Almolinus ligula* Wunderlich, from Eocene Baltic amber (43–47.8 Ma; Magalhaes et al., 2020) and Lycosidae, based in a juvenile from the Dominican Ambar (15–20 Ma; Penney, 2001). The root was set based on Araneophorphae age (300–380 Ma; Magalhaes et al., 2020).

The analysis was based on the topology inferred by IQ-TREE. We choose the 'exact likelihood' method and estimated divergence dates through a molecular clock with independent rates, where the rates follow a log-normal distribution. We choose HKY85+G5 as a substitution model with Gamma shape parameter $\alpha = 0.5$ and rate priors adjusted to set the gamma-Dirichlet prior. Although our results indicated the GTR model as the best fit, the MCMCtree set of parameters does not have this option, so we choose the closest one (Egan & Crandall, 2006). To ensure proper MCMC convergence, we discarded the first 2,000 iterations as burn-in, and then ran the MCMC for 2 x 100,000 iterations, resulting 202,000 iterations. We used Tracer v1.7.1 (Rambaut et al., 2018) to assess convergence.

2.5. Ancestral range reconstruction

We used the R package BioGeoBEARS (Matzke, 2013; 2018) to reconstruct the biogeographical history of the Atlantic Forest xenoctenids (*Paravulsor*, *Gen.nov.01*, *Gen.nov.02*), based on the dating phylogeny inferred by MCMCtree. BioGeoBEARS implements three biogeographic models, each one with an additional "jump-dispersal" parameter (+J), for a total of six models: DEC, DEC + J, DIVALIKE, DIVALIKE+J, BAYAREALIKE, BAYAREALIKE+J. We estimated the ancestral range of xenoctenids under all six models and we selected the best fit model using the Akaike information criterion – AIC (Akaike, 1992; Table 2 in supplementary materials) and Akaike weights – AICc (Wagenmakers et al., 2004; Table 3 in supplementary materials).

We selected seven biogeography areas, based on the known distribution of Xenoctenidae: Caatinga dry forest (C); Central America dry forest (A); Central Bahia Atlantic Forest (B); Northeast Atlantic Forest (N); Peruvian Deserts (D), South Atlantic Forest (S); Southeast Atlantic Forest (E) (see Figure 4). The areas are delimited based on geographical or climatic barriers, such as mountain ranges, ecoregions, or biomes.

3. Results

3.1. Taxon sampling and DNA extraction

From the initial pool of 72 extractions, just one sample, *Paravulsor 40* (vchMDF56), presented DNA values too low to be detected (Table 1). Even so, we include all 72 samples into library preparation. Trinity results assembled 777 to 100,147 contigs per sample, with an average of 24,606 contigs per sample. When we matched the contigs to the probe set, we recovered a range of 6 to 1049 UCE loci per sample (see Table 1 and Figure S1 for more details).

After several tests we found that the specimens with less than 100 UCE loci were being attracted to each other and formed a misplaced clade. Except for the outgroup, we excluded 22 specimens with low loci counts (6–87 loci), as they were not successfully placed in the phylogeny. Thus, our final analysis comprises 50 samples, 35 from *Paravulsor*, 4 from *Gen.nov.01*, 1 from *Gen.nov.02*, 5 from *Xenoctenus* and 5 from *Odo* (Table 1), plus 15 outgroup samples.

3.2. Phylogenetic analyses

PartitionFinder2 resulted in 409 partitions and 264,660 total sites (15.5% missing data) for the 65 taxa. GTR was selected as the best model fit. We recovered 92% of nodes with high support values (< 95) for the ingroup based on the Ultrafast bootstrap results (Figure 11, 14).

Our results corroborate with Faustino-Magalhães (2019) and Silva-Davila (2003) by recovering *Odo* as a polyphyletic group, also in agreement with the Chapter 1 results. Thus, *Odo patricius* was recovered in the *Xenoctenus* clade, and *Odo obscurus*, *Odo blumenauensis* and *Odo similis* were recovered in the same clade as *Paravulsor impudicus* (the type species of *Paravulsor*) (Figure 12). *Xenoctenus* was recovered as monophyletic, forming a clade with the Peruvian species, *Odo patricius*, *X. sp.01*, *X. sp.02*, and *X. sp.03*, and another with the Brazillian species, *X. vittatus* and *X. kaatinga* (in agreement with Faustino-Magalhaes et al., 2024). Regarding the Atlantic Forest xenoctenids, we confirmed that *Gen.nov.01* and *Gen.nov.02* should be described as new genera. All the other new species formed an isolated clade with *Paravulsor impudicus*, restricted to Southeast and South of the Atlantic Forest (Figure 12).

3.3. Divergence time and ancestral range reconstruction

The divergence time analysis recovered a crown age of Xenoctenidae of *c*. 48.4 Ma (95% HPD: 32.7–68.9 Ma) that comprises the Middle and Late Eocene, when the most recent common ancestor (MRCA) split into two major clades (Fig. 12). *Odo* and *Xenoctenus* present a stem age of *c*. 33 Ma (95% HPD: 15.2–49.1 Ma) at the Early Oligocene. *Xenoctenus* is the youngest xenoctenid genus, presenting an initial diversification of *c*. 9.3 Ma (95% HPD: 5.2–14.2 Ma) during the Late Miocene (Figs 4, 12, 13).

Regarding the Atlantic Forest xenoctenids, we recovered a crown age of *c*. 32.3 Ma (95% HPD: 22.5–49.4 Ma), similar in age to the *Odo+Xenoctenus* clade. For *Gen.nov.01*, we recovered a crown age of *c*. 17.5 Ma (95% HPD: 10.5–26.3 Ma) also during the Early Oligocene. The *Gen.nov.02* and *Paravulsor* presented a stem age of *c*. 29.1 Ma (95% HPD: 20.2–39.6 Ma). The divergence time of *Paravulsor* recovered a crown age of 18.9 Ma (95% HPD: 14.7–23.7 Ma), during the Early Miocene. The greater part of speciation events in *Paravulsor* occurred between the Middle Miocene and Pliocene (*c*. 18–4 Ma; see Figure 12 for more detail).

Regarding the BioGeoBEARS results, AIC and AICc values indicated the DIVA-like+J as the best-fitting model (AIC: 91.39, AICc: 91.91, Log-likelihood=-44.78; see Table 2 and Table 3). The results indicate that the ancestor of the Atlantic Forest xenoctenids and the *Odo+Xenoctenus* clade occurred in the rainforests of the Brazilian Northeast, and in dry forests of the Central America, with the speciation occurring due to a vicariance event that split the lineage into two regions: the Brazilian Northeast and the Central America (Figure 2, 4, 12, 13).

The Atlantic Forest xenoctenid ancestor occupied a range comprising of the rainforests in the Northeast, Central Bahia, and Southeast Brazil (Figs 4, 12, 13). Given the results, the speciation of the three genera (*Gen.nov.01*, *Gen.nov.02* and *Paravulsor*) occurred due to vicariance events during the Oligocene. *Gen.nov.01* have a distribution range that comprises the northeast cost the Atlantic Forest, occurring in rainforests of Pernambuco and Alagoas states (Fig. 5). Also, *Gen.nov.02* present records of distribution only from in the mountain ranges of Central Bahia, in the municipality of Catolés, Bahia state (Figure 5). The ancestral of *Paravulsor* initially occupied the Southeast of the Atlantic Forest and later disperse throughout the South. As a result, two major clades diversified separately

into these regions, the Southeast clade, and the South clade. These regions comprise large mountain ranges where *Paravulsor* species occurs, as the Serra do Mar, Serra da Mantiqueira, Quadrilátero Ferrífero, and Serra Geral (Figs 4,10 12, 13).

4. Discussion

This study makes an important contribution to the Xenoctenidae literature, filling in some gaps in our knowledge about the evolutionary history of this group. Our results corroborate the taxonomical changes proposed in Chapter 1 and in Faustino-Magalhães (2019), recovering *Odo* as a polyphyletic genus and *Paravulsor* as an endemic group from the Atlantic Forest consisting of over 50 species (Figs 11, 12, 14). Our molecular phylogeny also corroborates the delimitation of the two new genera, *Gen.nov.01* and *Gen.nov.02*, endemic to the Atlantic Forest (Figs 2, 5, 12). *Xenoctenus* was recovered as a monophyletic group, in agreement with Faustino-Magalhaes et al. (2024) (Fig. 12). Thus, we elucidated some taxonomic problems about the delimitation of the Xenoctenidae genera.

Regarding the biogeography of the group, our results demonstrate the strong influence of geological and climatic barriers in species distributions, which may be associated with their poor dispersal ability. Additionally, many species are microendemics, restricted to small ecoregions or biomes (Figs 4–10). In the following, we focus on the Atlantic Forest xenoctenids and discuss the biogeographic events of the past, which may have driven the diversification patterns in Xenoctenidae.

4.1. Historical biogeography of Xenoctenidae

The genetic divergence between the two major clades of Xenoctenidae (*Odo+Xenoctenus* clade and Atlantic Forest xenoctenids clade) occur during the late Paleocene (*c*. 48 Ma; Fig. 12), a time when the Everwet Tropical Biome dominated the Neotropical region (Bernardes-de-Oliveira et al., 2014). According with our ancestral range results, the ancestor of Xenoctenidae lived in a widespread area that comprises the Northeast Atlantic Forest, Central Bahia, and Central America (Figs 2, 4). Because the formation of Central America and Panama Isthmus is more recent than Xenoctenidae divergence (Crews & Esposito, 2020; Montes et al., 2012; O'Driscoll et al., 2012), it may be that this lineage diversified in the Brazillian Northeast and Central Bahia areas, and dispersed to Central America later (Figs 2, 4, 12). Therefore, the ancestor of Xenoctenidae probably lived in

an Everwet Tropical Biome, an environment similar to the modern Neotropical rainforests, and the favorable climate during the Paleocene, may have allowed its dispersal through the continent.

The divergence between *Odo* and *Xenoctenus* occurred at *c*. 33 Ma, during the early Oligocene. However, the diversification of *Xenoctenus* occurred only during the Late Miocene, at *c*. 9 Ma (Figs 4, 12). The ancestor of *Xenoctenus* occurred in a range that comprises the Peruvian deserts and the Brazilian Caatinga, both dry forests. The genus is also known to occur in other Neotropical dry forests, like the Argentinean Monte and Chaco provinces (Faustino-Magalhaes et al., 2024). The global cooling that started in the Middle Miocene and the subsequent expansion of the Antarctic ice sheet during the Late Pliocene increased the aridity in the subtropical region, resulting in the expansion of the savannas, as the Brazilian Cerrado (Luebert, 2021). According to Pennington et al. (2000), the existence of a wider historical area of seasonally dry tropical forests connected these regions, allowing the dispersal of many taxa. Thus, the expansion of the Cerrado, due to unique characteristics, may have isolated lineages of *Xenoctenus* which resulted in the species divergence.

4.2. Historical biogeography of the Atlantic Forest xenoctenids

The distribution patterns of the Atlantic Forest xenoctenids are correlated with the centers of endemism previously proposed for the Atlantic Forest (Carnaval & Moritz, 2008; Dasilva et al., 2015; Oliveira et al., 2015; Peres et al., 2020). *Gen.nov.01* and *Gen.nov.02* are associated with regions of historical stability in the northern portion of the Atlantic Forest, Pernambuco, and Bahia refugia, respectively (Figure 2, 4; Carnaval & Moritz, 2008). *Paravulsor* is distributed throughout the southern portion of the Atlantic Forest, a region with records of small forest refugia (Carnaval et al., 2014; Costa et al., 2018) and several small areas of endemism for spiders (Figs 2, 6–10, 12; Oliveira et al., 2015).

Although our results indicate that the Atlantic Forest xenoctenids are associated with climatically stable areas in the biome, the Pleistocene glacial refugia probably did not promote speciation in these groups, as most of the divergences occurred during the Miocene. Nevertheless, due to low extinction rates, refuges can maintain high levels of taxonomic and phylogenetic diversity, including high levels of endemism (Costa et al., 2018). In fact, we observe a higher diversity of *Paravulsor* species associated with lower

stability regions of the southern portion of the Atlantic Forest, compared with the northern regions, as suggested by Carnaval et al. (2009).

The divergence of the three Atlantic Forest genera occurred during the Oligocene (33.9–23.03 Ma), a period of global cooling and arid expansion that led to the retreat of the Everwet Tropical Biome and the expansion of the Summerwet Subtropical Biome (Bergue & Coimbra, 2014; Bernardes-de-Oliveira et al., 2014). Thus, the divergence of these groups may have been influenced by the expansion of a dryer biome, resulting in the isolation of these groups in fragments of wet forests.

Gen.nov.01 diversify through the coastal region of northeastern Brazil (Figs 2, 4, 5), a region of Atlantic rainforest considered a center of endemism for many taxa, known as the Pernambuco refuge (Dasilva et al., 2015; França et al., 2020; Oliveira et al., 2015). The diversification of this genus occurred mostly during the Neogene (23.3–2.58 Ma), a period known by the uplift of the Borborema Plateau in the Brazilian Northeast. The formation of the Borborema Plateau originated an orographic barrier to air masses entering from the Atlantic, which increased the precipitation at the coastal side and allowed the subsistence of the Atlantic Forest (Hoorn et al., 2014). Thus, the formation of this plateau may have supported a climatically stable area favorable to the *Gen.nov.01* diversification.

The genus *Paravulsor* is distributed through the southern part of the BAF, comprising the Serra do Mar, Serra da Mantiqueira, and Serra Geral, among other mountains (Figs 4, 6–10). The Serra do Mar is an important mountain located on the southeastern coast of Brazil and is known to be a center of endemism that comprises several small endemic regions, as was observed by Oliveira et al. (2015). *Paravulsor* species presented a distribution restricted to small areas, in agreement with the small centers of endemism through the Serra do Mar. Such a pattern is usually recovered in taxa with reduced dispersal ability and narrower environmental tolerance (Peres et al., 2020).

As observed in *Gen.nov.01*, the diversification of *Paravulsor* occurred predominantly during the Miocene (23–5.33 Ma). The older divergence among *Paravulsor* species resulted in the split of two lineages between the Southeast and South of the Ribeira do Iguape River (Southeast clade and South clade; Fig. 10). The Ribeira do Iguape River is situated in a tectonic depression in the Ribeira do Iguape valley in São Paulo state and is assumed to be related with to the Serra do Mar Rift System (Melo et al., 1989).

During the Miocene, tectonic reactivations along the Precambrian shear zones in the Brazilian coast resulted in the uplift flanks and denudation processes of Serra do Mar and Serra da Mantiqueira. These processes led to drainage and reorganization of the course of important rivers such as Ribeira do Iguape and Paraíba do Sul River (Souza et al., 2021). As discussed by Peres et al. (2020), rivers can act as a barrier to species distribution resulting in genetic differentiation between populations, mostly for species with low dispersal ability. Therefore, we expected that the Ribeira do Iguape River influenced the divergence between the Southeast and South clades. Additionally, tectonic reactivations associated with processes of reorganization of rivers in the mountain ranges of the Atlantic Forest's southeastern coast may also have influenced the diversification of *Paravulsor* species.

Finally, we proposed that the diversification of lineages from the northern part of the BAF (*Gen.nov.01* and *Gen.nov.02*) was influenced by the global cooling that led to the contraction of rainforests due to the increased aridity. Also, the diversification of *Paravulsor* in the southern part of the BAF seems to be associated with the formation of rivers due to tectonics reactivations, which might have acted as vicariant barriers in the past. Additionally, given the increasing habitat loss due to anthropogenic disturbance, we highlight that many of these species may be threatened with extinction.

5. References

- Ashcroft, M. B. (2010). Identifying refugia from climate change. Journal of Biogeography, 37(8), 1407–1413. https://doi.org/10.1111/j.1365-2699.2010.02300.x
- Azevedo, G. H. F., Bougie, T., Carboni, M., Hedin, M., & Ramírez, M. J. (2022). Combining genomic, phenotypic and Sanger sequencing data to elucidate the phylogeny of the two-clawed spiders (Dionycha). *Molecular Phylogenetics and Evolution*, 166. https://doi.org/10.1016/j.ympev.2021.107327
- Bartoleti, L. F. de M., Peres, E. A., Fontes, F. von H. M., da Silva, M. J., & Solferini, V. N. (2018). Phylogeography of the widespread spider Nephila clavipes (Araneae: Araneidae) in South America indicates geologically and climatically driven lineage diversification. *Journal of Biogeography*, 45(6), 1246–1260. https://doi.org/10.1111/jbi.13217
- Bell, J. R., Bohan, D. A., Shaw, E. M., & Weyman, G. S. (2005). Ballooning dispersal using silk: world fauna, phylogenies, genetics, and models. *Bulletin of Entomological Research*, 95(2), 69–114. https://doi.org/10.1079/ber2004350
- Bergue, C. T., & Coimbra, J. C. (2014). Os ostracodes psicrosféricos do Atlântico Sul e os eventos climáticos do Paleógeno. In I. de S. Carvalho, M. J. Garcia, O. J. Strohschoen, & C. C. Lana (Eds.), *Paleontologia: Cenários da vida Paleoclimas* (Vol. 5). Editora Interciência.
- Bernardes-de-Oliveira, M. E. C., Garcia, M. J., Caramês, A. G., Dino, R., Antonioli, L., & Saad, A. R. (2014). Evolução Paleoclimática Paleógena no Brasil: Dados Paleobotânicos e Palinológicos. In I. de S. Carvalho, M. J. Garcia, O. Strohschoen Jr., & C. C. Lana (Eds.), *Paleontologia: Cenários da Vida Paleoclimas* (Vol. 5). Editora Interciência.
- Bouckaert, R., Vaughan, T. G., Barido-Sottani, J., Duchêne, S., Fourment, M., Gavryushkina, A., Heled, J., Jones, G., Kühnert, D., De Maio, N., Matschiner, M., Mendes, F. K., Müller, N. F., Ogilvie, H. A., du Plessis, L., Popinga, A., Rambaut, A., Rasmussen, D., Siveroni, I., ... Drummond, A. J. (2019). BEAST 2.5: An advanced software platform for Bayesian evolutionary analysis. *PLOS*

 Computational
 Biology,
 15(4),
 e1006650.

 https://doi.org/10.1371/journal.pcbi.1006650
 15(4),
 1006650.

- Cardoso, P., Erwin, T. L., Borges, P. A. V., & New, T. R. (2011). The seven impediments in invertebrate conservation and how to overcome them. *Biological Conservation*, 144(11), 2647–2655. https://doi.org/10.1016/j.biocon.2011.07.024
- Carnaval, A. C., & Moritz, C. (2008). Historical climate modelling predicts patterns of current biodiversity in the Brazilian Atlantic Forest. *Journal of Biogeography*, 35(7), 1187–1201. https://doi.org/10.1111/j.1365-2699.2007.01870.x
- Dantas, G. P. M., Cabanne, G. S., & Santos, F. R. (2011). How Past Vicariant Events Can Explain the Atlantic Forest Biodiversity? In *Ecosystems Biodiversity*. InTech. https://doi.org/10.5772/24032
- Dasilva, M. B., Pinto-da-Rocha, R., & Desouza, A. M. (2015). A protocol for the delimitation of areas of endemism and the historical regionalization of the Brazilian Atlantic Rain Forest using harvestmen distribution data. *Cladistics*, 31(6), 692–705. https://doi.org/10.1111/cla.12121
- de Queiroz, L. P., Cardoso, D., Fernandes, M. F., & Moro, M. F. (2017). Diversity and Evolution of Flowering Plants of the Caatinga Domain. In *Caatinga* (pp. 23–63). Springer International Publishing. https://doi.org/10.1007/978-3-319-68339-3_2
- d'Horta, F. M., Cabanne, G. S., Meyer, D., & Miyaki, C. Y. (2011). The genetic effects of Late Quaternary climatic changes over a tropical latitudinal gradient: Diversification of an Atlantic Forest passerine. *Molecular Ecology*, 20(9), 1923– 1935. https://doi.org/10.1111/j.1365-294X.2011.05063.x
- Dos Reis, M., Álvarez-Carretero, S., & Yang, Z. (2017). *MCMCTree tutorials*. www.r-project.org
- Drummond, A. J., Suchard, M. A., Xie, D., & Rambaut, A. (2012). Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, 29(8), 1969–1973. https://doi.org/10.1093/molbev/mss075

- Faircloth, B. C., & Glenn, T. C. (2012). Not all sequence tags are created equal: Designing and validating sequence identification tags robust to indels. *PLoS ONE*, 7(8). https://doi.org/10.1371/journal.pone.0042543
- Faircloth, B. C., Branstetter, M. G., White, N. D., & Brady, S. G. (2015). Target enrichment of ultraconserved elements from arthropods provides a genomic perspective on relationships among hymenoptera. *Molecular Ecology Resources*, 15(3), 489–501. https://doi.org/10.1111/1755-0998.12328
- Faustino-Magalhães, M. D. (2019). Análise filogenética e revisão taxonômica de Xenoctenidae Ramírez & Silva-Dávila (Araneae) [Master]. Universidade Federal de Minas Gerais.
- Fine, P. V. A., & Lohmann, L. G. (2018). Importance of dispersal in the assembly of the Neotropical biota. In *Proceedings of the National Academy of Sciences of the United States of America* (Vol. 115, Issue 23, pp. 5829–5831). National Academy of Sciences. https://doi.org/10.1073/pnas.1807012115
- Garcia, M. J., Bernardes-de-Oliveira, M. E. C., Caramês, A. G., Dino, R., Antonioli, L., & Bistrichi, C. A. (2014). Evolução Paleoclimática Neógena, No Brasil Sudeste E Estado Do Paraná, Com Base Em Dados Paleobotânicos E Palinológicos. In I. de S. Carvalho, M. J. Garcia, O. Strohschoen Jr., & C. C. Lana (Eds.), *Paleontologia: Cenários de Vida Paleoclimas* (Vol. 5). Editora Interciência.
- Hamilton, C. A., Formanowicz, D. R., & Bond, J. E. (2011). Species delimitation and phylogeography of Aphonopelma hentzi (araneae, mygalomorphae, theraphosidae):
 Cryptic diversity in north american tarantulas. *PLoS ONE*, *6*(10). https://doi.org/10.1371/journal.pone.0026207
- Hoang, D.T., Chernomor, O., von Haeseler, A., Quang Minh, B., Sy Vinh, L., & Rosenberg, M. S. (2017). UFBoot2: Improving the Ultrafast Bootstrap Approximation. *Mol. Biol. Evol*, 35(2), 518–522. https://doi.org/10.5281/zenodo.854445
- Hochkirch, A., Samways, M. J., Gerlach, J., Böhm, M., Williams, P., Cardoso, P., Cumberlidge, N., Stephenson, P. J., Seddon, M. B., Clausnitzer, V., Borges, P. A. V., Mueller, G. M., Pearce-Kelly, P., Raimondo, D. C., Danielczak, A., & Dijkstra,

K. D. B. (2021). A strategy for the next decade to address data deficiency in neglected biodiversity. *Conservation Biology*, *35*(2), 502–509. https://doi.org/10.1111/cobi.13589

- Hoorn, C., Bernardes-de-Oliveira, M. E. C., Dino, R., Garcia, M. J., Antonioli, L., Casado, F. da C., & Hooghiemstra, H. (2014). NEOGENE CLIMATE EVOLUTION IN AMAZONIA AND THE BRAZILIAN NORTHEAST. In I. de S. Carvalho, M. J. Garcia, O. Strohschoen Jr., & C. C. Lana (Eds.), *Paleontologia: Cenários de Vida Paleoclimas* (Vol. 5). Editora Interciência.
- Hoorn, C., Wesselingh, F. P., ter Steege, H., Bermudez, M. A., Mora, A., Sevink, J., Sanmartín, I., Sanchez-Meseguer, A., Anderson, C. L., Figueiredo, J. P., Jaramillo, C., Riff, D., Negri, F. R., Hooghiemstra, H., Lundberg, J., Stadler, T., Särkinen, T., & Antonelli, A. (2010). Amazonia Through Time: Andean Uplift, Climate Change, Landscape Evolution, and Biodiversity. *Science*, *330*(6006), 927–931. https://doi.org/10.1126/science.1194585
- Jaramillo, C. (2023). The evolution of extant South American tropical biomes. In New Phytologist (Vol. 239, Issue 2, pp. 477–493). John Wiley and Sons Inc. https://doi.org/10.1111/nph.18931
- Joly, C. A., Metzger, J. P., & Tabarelli, M. (2014). Experiences from the Brazilian Atlantic Forest: Ecological findings and conservation initiatives. In *New Phytologist* (Vol. 204, Issue 3, pp. 459–473). Blackwell Publishing Ltd. https://doi.org/10.1111/nph.12989
- Kalyaanamoorthy, S., Minh, B. Q., Wong, T. K. F., Von Haeseler, A., & Jermiin, L. S. (2017). ModelFinder: Fast model selection for accurate phylogenetic estimates. *Nature Methods*, 14(6), 587–589. https://doi.org/10.1038/nmeth.4285
- Keyserling, E. (1887). Neue Spinnen Aus America. Vii. Verhandlungen Der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft In Wien 37: 421-490.
- Keyserling, E. (1891). Die Spinnen Amerikas. Brasilianische Spinnen. Bauer & Raspe, Nürnberg 3, 1-278.

- Kulkarni, S., Wood, H., Lloyd, M., & Hormiga, G. (2020). Spider-specific probe set for ultraconserved elements offers new perspectives on the evolutionary history of spiders (Arachnida, Araneae). *Molecular Ecology Resources*, 20(1), 185–203. https://doi.org/10.1111/1755-0998.13099
- Lanfear, R., Frandsen, P. B., Wright, A. M., Senfeld, T., & Calcott, B. (2017). Partitionfinder 2: New methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution*, 34(3), 772–773. https://doi.org/10.1093/molbev/msw260
- Luebert, F. (2021). The two South American dry diagonals. *Frontiers of Biogeography*, *13*(4). https://doi.org/10.21425/F5FBG51267
- Magalhaes, I. L. F., Azevedo, G. H. F., Michalik, P., & Ramírez, M. J. (2020). The fossil record of spiders revisited: implications for calibrating trees and evidence for a major faunal turnover since the Mesozoic. *Biological Reviews*, 95(1), 184–217. https://doi.org/10.1111/brv.12559
- Maizatto, J. R., Castro, P. de T. A., & Regali, M. da S. P. (2014). Análise Biocronoestratigráfica E Paleoclimática Com Base Em Palinologia Dos Depósitos Cenozoicos Das Bacias Do Gandarela E Fonseca . In I. de S. Carvalho, M. J. Garcia, O. Strohschoen Jr., & C. C. Lana (Eds.), *Paleontologia: Cenário de Vida – Paleoclimas* (Vol. 5). Editora Interciência.
- Marques, M. C. M., Trindade, W., Bohn, A., & Grelle, C. E. V. (2021). The Atlantic Forest: An Introduction to the Megadiverse Forest of South America. In M. C. M. Marques & C. Grelle (Eds.), *The Atlantic Forest* (pp. 3–23). Springer International Publishing. https://doi.org/10.1007/978-3-030-55322-7_1
- Martins, F. de M., & Domingues, M. V. (2011). Filogeografia. *Revista Da Biologia*, 7, 26–30. https://doi.org/10.7594/revbio.07.05
- Matzke, J. N. (2018). *nmatzke/BioGeoBEARS: BioGeoBEARS: BioGeography with Bayesian (and likelihood) Evolutionary Analysis with R Scripts (v1.1.1).* Zenodo.
- Matzke, N. J. (2013). Probabilistic historical biogeography: new models for founderevent speciation, imperfect detection, and fossils allow improved accuracy and

model-testing.FrontiersofBiogeography,5(4).https://doi.org/10.21425/f5fbg19694

- Mello-Leitão, C. F. De (1922). Novas Clubionidas Do Brasil. Archivos Da Escola Superior De Agricultura E Medicina Veterinaria, Rio De Janeiro 6: 17-56.
- Mello-Leitão, C. F. de (1927). Arachnideos de Santa Catharina (Brasil). Revista do Museu Paulista 15: 393-418.
- Mello-Leitão, C. F. De (1938). Algunas Arañas Nuevas De La Argentina. Revista Del Museo De La Plata (N.S) 1: 89-118.
- Mello-Leitão, C. F. De (1942). Cinco Aranhas Novas Do Perú. Revista Brasileira De Biologia 2: 429-434.
- Mello-Leitão, C. F. De. (1936). Contribution À L'etude des Ctenides Du Bresil. Festschrift Embrik Strand 1: 1-31.
- Minh, B. Q., Nguyen, M. A. T., & Von Haeseler, A. (2013). Ultrafast approximation for phylogenetic bootstrap. *Molecular Biology and Evolution*, 30(5), 1188–1195. https://doi.org/10.1093/molbev/mst024
- Minh, B. Q., Schmidt, H. A., Chernomor, O., Schrempf, D., Woodhams, M. D., von Haeseler, A., & Lanfear, R. (2020). IQ-TREE 2: New Models and Efficient Methods for Phylogenetic Inference in the Genomic Era. *Molecular Biology and Evolution*, 37(5), 1530–1534. https://doi.org/10.1093/molbev/msaa015
- Montes, C., Cardona, A., McFadden, R., Morón, S. E., Silva, C. A., Restrepo-Moreno, S., Ramírez, D. A., Hoyos, N., Wilson, J., Farris, D., Bayona, G. A., Jaramillo, C. A., Valencia, V., Bryan, J., & Flores, J. A. (2012). Evidence for middle Eocene and younger land emergence in central Panama: Implications for Isthmus closure. *Bulletin of the Geological Society of America*, 124(5–6), 780–799. https://doi.org/10.1130/B30528.1
- Myers, N., Mittermeier², R. A., Mittermeier², C. G., Da Fonseca³, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. In *NATURE* / (Vol. 403). www.nature.com

- O'Dea, A., Lessios, H. A., Coates, A. G., Eytan, R. I., Restrepo-Moreno, S. A., Cione, A. L., Collins, L. S., De Queiroz, A., Farris, D. W., Norris, R. D., Stallard, R. F., Woodburne, M. O., Aguilera, O., Aubry, M. P., Berggren, W. A., Budd, A. F., Cozzuol, M. A., Coppard, S. E., Duque-Caro, H., ... Jackson, J. B. C. (2016). Formation of the Isthmus of Panama. In *Science Advances* (Vol. 2, Issue 8). American Association for the Advancement of Science. https://doi.org/10.1126/sciadv.1600883
- Oliveira-Filho, A. T., Auré, M., & Fontes, L. (2000). Patterns of Floristic Differentiation among Atlantic Forests in Southeastern Brazil and the Influence of Climate 1. In *BIOTROPICA* (Vol. 32, Issue 4b).
- Oliveira, U., Brescovit, A. D., & Santos, A. J. (2017). Sampling effort and species richness assessment: a case study on Brazilian spiders. *Biodiversity and Conservation*, 26(6), 1481–1493. https://doi.org/10.1007/s10531-017-1312-1
- Ortiz-Jaureguizar, E., & Cladera, G. A. (2006). Paleoenvironmental evolution of southern South America during the Cenozoic. *Journal of Arid Environments*, 66(3 SPEC. ISS.), 498–532. https://doi.org/10.1016/j.jaridenv.2006.01.007
- Pellegrino, K. C. M., Rodrigues, M. T., Waite, A. N., Morando, M., Yassuda, Y. Y., & Jr, J. W. S. (2005). Phylogeography and species limits in the Gymnodactylus darwinii complex (Gekkonidae, Squamata): genetic structure coincides with river systems in the Brazilian Atlantic Forest. In *Biological Journal of the Linnean Society* (Vol. 85). https://academic.oup.com/biolinnean/article-abstract/85/1/13/2701430
- Peres, E. A., Pinto-da-Rocha, R., Lohmann, L. G., Michelangeli, F. A., Miyaki, C. Y., & Carnaval, A. C. (2020). Patterns of Species and Lineage Diversity in the Atlantic Rainforest of Brazil. In V. Rull & A. C. Carnaval (Eds.), *Neotropical Diversification: Patterns and Processes* (pp. 415–447). https://doi.org/10.1007/978-3-030-31167-4_16
- Porto, T. J., Carnaval, A. C., & da Rocha, P. L. B. (2013). Evaluating forest refugial models using species distribution models, model filling and inclusion: A case study with 14 Brazilian species. *Diversity and Distributions*, 19(3), 330–340. https://doi.org/10.1111/j.1472-4642.2012.00944.x

- Potter, P. E., & Szatmari, P. (2009). Global Miocene tectonics and the modern world. In *Earth-Science Reviews* (Vol. 96, Issue 4, pp. 279–295). https://doi.org/10.1016/j.earscirev.2009.07.003
- Rambaut, A., Drummond, A. J., Xie, D., Baele, G., & Suchard, M. A. (2018). Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology*, 67(5), 901–904. https://doi.org/10.1093/sysbio/syy032
- Riccomini, C., & Assumpção, M. (1999). Quaternary tectonics in Brazil. *Episodes*, 22(3), 221–225. https://doi.org/10.18814/epiiugs/1999/v22i3/010
- Rull, V. (2011). Neotropical biodiversity: Timing and potential drivers. In *Trends in Ecology and Evolution* (Vol. 26, Issue 10, pp. 508–513). https://doi.org/10.1016/j.tree.2011.05.011
- Siedchlag, A. C., Benozzati, M. L., Passoni, J. C., & Rodrigues, M. T. (2010). Genetic structure, phylogeny, and biogeography of Brazilian eyelid-less lizards of genera Calyptommatus and Nothobachia (Squamata, Gymnophthalmidae) as inferred from mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution*, 56(2), 622– 630. https://doi.org/10.1016/j.ympev.2010.04.027
- Sobral-Souza, T., Lima-Ribeiro, M. S., & Solferini, V. N. (2015). Biogeography of Neotropical Rainforests: past connections between Amazon and Atlantic Forest detected by ecological niche modeling. *Evolutionary Ecology*, 29(5), 643–655. https://doi.org/10.1007/s10682-015-9780-9
- Souza, D. H., Hackspacher, P. C., Silva, B. V., Siqueira-Ribeiro, M. C., & Hiruma, S. T. (2021). Temporal and spatial denudation trends in the continental margin of southeastern Brazil. *Journal of South American Earth Sciences*, 105. https://doi.org/10.1016/j.jsames.2020.102931
- Stamatakis, A. (2014). RAxML version 8: A tool for phylogenetic analysis and postanalysis of large phylogenies. *Bioinformatics*, 30(9), 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

- Stamatakis, A., Hoover, P., & Rougemont, J. (2008). A rapid bootstrap algorithm for the RAxML web servers. *Systematic Biology*, 57(5), 758–771. https://doi.org/10.1080/10635150802429642
- Thomé, M. T. C., Zamudio, K. R., Giovanelli, J. G. R., Haddad, C. F. B., Baldissera, F. A., & Alexandrino, J. (2010). Phylogeography of endemic toads and post-Pliocene persistence of the Brazilian Atlantic Forest. *Molecular Phylogenetics and Evolution*, 55(3), 1018–1031. https://doi.org/10.1016/j.ympev.2010.02.003
- Troudet, J., Grandcolas, P., Blin, A., Vignes-Lebbe, R., & Legendre, F. (2017). Taxonomic bias in biodiversity data and societal preferences. *Scientific Reports*, 7(1). https://doi.org/10.1038/s41598-017-09084-6
- Wheeler, W. C., Coddington, J. A., Crowley, L. M., Dimitrov, D., Goloboff, P. A., Griswold, C. E., Hormiga, G., Prendini, L., Ramírez, M. J., Sierwald, P., Almeida-Silva, L., Alvarez-Padilla, F., Arnedo, M. A., Benavides Silva, L. R., Benjamin, S. P., Bond, J. E., Grismado, C. J., Hasan, E., Hedin, M., ... Zhang, J. (2017). The spider tree of life: phylogeny of Araneae based on target-gene analyses from an extensive taxon sampling. *Cladistics*, *33*(6), 574–616. https://doi.org/10.1111/cla.12182
- World Spider Catalog. (2024). World Spider Catalog. Version 24.5. Natural History Museum Bern. https://doi.org/10.24436/2
- Yang, Z. (1993). User Guide PAML: Phylogenetic Analysis by Maximum Likelihood. http://abacus.gene.ucl.ac.uk/software/paml.html

FIGURE LEGENDS

Figure 1. The Atlantic Forest biome.

Figure 2. Geographic distribution records of the Atlantic Forest xenoctenid's (Gen.nov.01, Gen.nov.02, Paravulsor Mello-Leitão, 1922) in Brazil.

Figure 3. Geographical distribution of collection sites where Xenoctenidae specimens were found (orange stars) and collection sites where they were not found (red stars).

Figure 4. Geographical distribution of Xenoctenidae species included in the phylogeny. Colors represent areas delimited in the BioGeoBEARS analysis. Brazilian Northeast – N; Central America – A; Central Bahia – B; Peruvian Deserts – D; South Atlantic Forest – S; Southeast Atlantic Forest – E.

Figure 5. Geographic distribution of *Gen.nov.01* and *Gen.nov.02* species in the North.... Atlantic Forest.

Figure 6. Geographic distribution of *Paravulsor* species that compose the Clade 01, in the Southeast Atlantic Forest.

Figure 7. Geographic distribution of *Paravulsor* species that compose the Clade 02, in the Southeastern Atlantic Forest.

Figure 8. Geographic distribution of *Paravulsor* species that compose the Clade 03, in the Southern Atlantic Forest.

Figure 9. Geographic distribution of *Paravulsor* species that compose the Clade 04, in the Southeastern and Southern Atlantic Forest.

Figure 10. Geographic distribution of Clades 1, 2, 3 and 4 of *Paravulsor* phylogeny, showing the gap existent between clades from Southeast (Clade 1 and 2) and South (Clade 3). Clade 04 is the only one that presented species in both areas.

Figure 11. Xenoctenidae phylogeny with ultrafast bootstrap values.

Figure 12. Chronogram of Xenoctenidae. Colors represent biogeographical areas recovered by the ancestral range estimative under the DIVA-like model.

Figure 13. Ancestral area estimative under BioGeoBEARS DIVA-Like+J on Xenoctenidae (ancstates: global optim, d=0.1385; e=0; j=0.0051; LnL=-42.69). Areas: Brazilian Northeast – N; Central America – A; Central Bahia – B; Peruvian Deserts – D; South Atlantic Forest – S; Southeast Atlantic Forest – E

SUPPLEMENTARY MATERIALS

Table 1. Lane results.

FAMILY	SPECIES	VOUCHER	LOCI	PERC CONTIGS	CONTIGS	DUPE PROBE MATCH	REMOVED MULTI CONTIG HITS	REMOVED MULTI UCE HITS	ORIGIN	YEAR	COLLECTION
Cheiracanthiidae	Cheiracanthium mildei	Cmildei	179	0.27	65236	0	29	21	Azevedo et al., 2022	-	-
Dysderidae	Dysdera crocata	Dcrocata	111	0.21	53235	0	18	23	Azevedo et al., 2022	-	-
Corinnidae	Falconina grassa	Fgrassa	594	0.31	192552	0	599	393	Azevedo et al., 2022	_	-
Corinnidae	Ianduba varia	Ivaria	113	0.98	11489	0	10	16	Azevedo et al., 2022	-	-
Prodidomidae	Lygromma volcan	Lvolcan	113	0.86	13114	0	9	19	Azevedo et al., 2022	-	-
Salticidae	Lyssomanes pauper	Lpauper	111	0.84	13165	0	13	22	Azevedo et al., 2022	-	-
Miturgidae	Miturga albopunctata	Malbopunctata	96	0.91	10562	0	12	16	Azevedo et al., 2022	-	-
Oxyopidae	Peucetia longipalpis	Plongipalpis	543	1.81	29974	0	223	203	Azevedo et al., 2022	-	-
Philodromidae	Philodromus insperatus	Pinsperatus	80	1.23	6483	0	5	9	Azevedo et al., 2022	-	_
Prodidomidae	Prodidomus flavipes	Pflavipes	85	0.36	23794	0	50	28	Azevedo et al., 2022	_	_

Corinnidae	Pronophaea natalica	Pnatalica	38	1.41	2692	0	2	3	Azevedo et al., 2022	-	-
Lycosidae	Schizocosa rovneri	Srovneri	548	0.72	75918	0	651	728	Azevedo et al., 2022	-	_
Philodromidae	Tibellus oblongus	Toblongus	102	0.61	16759	0	17	21	Azevedo et al., 2022	-	-
Zoropsidae	Uliodon sp.	Uliodonsp	485	0.22	224076	0	872	687	Azevedo et al., 2022	-	-
Miturgidae	Zora sp.	Zorasp	111	0.47	23527	0	19	22	Azevedo et al., 2022	-	-
Xenoctenidae	Gen.nov.01 sp01	vchMDF34	606	2.6	23287	0	515	114	Fresh	2022	UFMG
Xenoctenidae	Gen.nov.01 sp02	vchMDF13	920	2.34	39362	0	520	151	Fresh	2022	UFMG
Xenoctenidae	Gen.nov.01 sp03	vchMDF08	655	1.77	36988	0	809	231	Fresh	2022	UFMG
Xenoctenidae	Gen.nov.01 sp04	vchMDF24	408	5.36	7616	0	88	26	Fresh	2022	UFMG
Xenoctenidae	Gen.nov.02 sp01	vchMDF12	705	2.12	33262	0	583	107	Fresh	2022	UFMG
Xenoctenidae	Odo agilis	vchMDF67	11	1.24	888	0	0	0	Collection	1970	IBSP
Xenoctenidae	Odo insularis	vchMDF68	6	0.39	1528	0	1	0	Collection	1948	NMNH
Xenoctenidae	Odo lenis	vchMDF66	294	2.2	13367	0	11	10	Collection	1998	IBSP
Xenoctenidae	Odo patricius	vchMDF65	461	1.25	36897	0	56	18	Collection	2012	IBSP
Xenoctenidae	Paravulsor 01	vchMDF27	253	3.58	7064	0	49	12	Fresh	2021	UFMG
Xenoctenidae	Paravulsor 02	vchMDF25	458	5.02	9131	0	36	20	Fresh	2021	UFMG
Xenoctenidae	Paravulsor 04	vchMDF49	54	0.13	41478	0	7	2	Collection	2007	UFMG
Xenoctenidae	Paravulsor 05	vchMDF50	24	0.72	3320	0	1	0	Collection	2010	UFMG
Xenoctenidae	Paravulsor 06	vchMDF51	894	2.99	29866	0	210	58	Collection	2010	UFMG
Xenoctenidae	Paravulsor 07	vchMDF41	50	0.27	18271	0	3	2	Collection	2009	MNRJ

Xenoctenidae	Paravulsor 08	vchMDF38	764	4.01	19063	0	289	69	Fresh	2020	UFMG
Xenoctenidae	Paravulsor 09	vchMDF40	172	5.5	3126	0	37	3	Fresh	2020	UFMG
Xenoctenidae	Paravulsor 10	vchMDF43	38	0.17	22041	0	2	2	Collection	2003	MNRJ
Xenoctenidae	Paravulsor 11	vchMDF33	1004	2.1	47745	0	334	97	Fresh	2021	UFMG
Xenoctenidae	Paravulsor 12	vchMDF03	184	8.53	2158	0	38	9	Fresh	2020	UFMG
Xenoctenidae	Paravulsor 13	vchMDF46	26	0.13	19853	0	4	0	Collection	2008	IBSP
Xenoctenidae	Paravulsor 15	vchMDF19	109	6.45	1690	0	14	2	Fresh	2020	UFMG
Xenoctenidae	Paravulsor 16	vchMDF52	7	0.32	2161	0	1	0	Collection	2009	МСТР
Xenoctenidae	Paravulsor 17	vchMDF44	20	0.33	5977	0	2	0	Collection	2007	IBSP
Xenoctenidae	Paravulsor 18	vchMDF10	600	3.88	15482	0	299	57	Fresh	2021	UFMG
Xenoctenidae	Paravulsor 19	vchMDF28	521	3.38	15422	0	211	32	Fresh	2022	UFMG
Xenoctenidae	Paravulsor 20	vchMDF14	994	2.46	40419	0	354	101	Fresh	2020	UFMG
Xenoctenidae	Paravulsor 21	vchMDF16	635	1.93	32830	0	492	115	Fresh	2020	UFMG
Xenoctenidae	Paravulsor 22	vchMDF09	164	9.65	1699	0	21	6	Fresh	2020	UFMG
Xenoctenidae	Paravulsor 23	vchMDF53	64	2.29	2797	0	5	2	Collection	2009	UFMG
Xenoctenidae	Paravulsor 24	vchMDF11	295	4.76	6203	0	91	16	Fresh	2020	UFMG
Xenoctenidae	Paravulsor 25	vchMDF42	150	0.59	25509	0	6	6	Collection	2012	MNRJ
Xenoctenidae	Paravulsor 26	vchMDF29	468	5.11	9152	0	79	28	Fresh	2020	UFMG
Xenoctenidae	Paravulsor 27	vchMDF47	51	0.76	6675	0	3	0	Collection	2007	IBSP
Xenoctenidae	Paravulsor 28	vchMDF54	13	0.85	1533	0	2	1	Collection	2008	UFMG
Xenoctenidae	Paravulsor 29	vchMDF26	675	3.69	18306	0	100	43	Fresh	2022	UFMG
Xenoctenidae	Paravulsor 30	vchMDF01	632	3.45	18335	0	287	73	Fresh	2020	UFMG
Xenoctenidae	Paravulsor 32	vchMDF48	283	2.32	12176	0	32	8	Collection	2003	IBSP

Xenoctenidae	Paravulsor 34	vchMDF55	26	0.65	4024	0	1	1	Collection	2001	IBSP
Xenoctenidae	Paravulsor 36	vchMDF30	753	4.24	17744	0	201	48	Fresh	2022	UFMG
Xenoctenidae	Paravulsor 37	vchMDF31	519	5.66	9173	0	94	20	Fresh	2022	UFMG
Xenoctenidae	Paravulsor 40	vchMDF56	20	0.06	31069	0	3	1	Collection	1987	IBSP
Xenoctenidae	Paravulsor 41	vchMDF57	1049	1.05	100147	0	408	99	Collection	2014	UFMG
Xenoctenidae	Paravulsor 44	vchMDF35	656	2.46	26622	0	353	79	Fresh	2022	UFMG
Xenoctenidae	Paravulsor 45	vchMDF06	283	6.17	4590	0	90	10	Fresh	2022	UFMG
Xenoctenidae	Paravulsor 45	vchMDF21	509	3.98	12780	0	55	28	Fresh	2022	UFMG
Xenoctenidae	Paravulsor 47	vchMDF58	30	1.55	1937	0	3	2	Collection	1997	IBSP
Xenoctenidae	Paravulsor 49	vchMDF45	13	0.55	2371	0	1	0	Collection	2007	IBSP
Xenoctenidae	Paravulsor 50	vchMDF39	216	6.62	3262	0	54	15	Fresh	2020	UFMG
Xenoctenidae	Paravulsor 51	vchMDF07	688	2.62	26224	0	438	100	Fresh	2021	UFMG
Xenoctenidae	Paravulsor 52	vchMDF32	28	3.55	788	0	7	0	Fresh	2022	UFMG
Xenoctenidae	Paravulsor 53	vchMDF17	87	1.71	5087	0	13	2	Fresh	2022	UFMG
Xenoctenidae	Paravulsor 55	vchMDF37	515	4.88	10561	0	101	28	Fresh	2020	UFMG
Xenoctenidae	Paravulsor 56	vchMDF23	750	1.95	38405	0	470	103	Fresh	2021	UFMG
Xenoctenidae	Paravulsor 57	vchMDF59	116	1.41	8254	0	30	3	Collection	2016	UFMG
Xenoctenidae	Paravulsor 59	vchMDF36	642	2.48	25905	0	375	67	Fresh	2022	UFMG
Xenoctenidae	Paravulsor 60	vchMDF20	309	3.88	7972	0	52	11	Fresh	2022	UFMG
Xenoctenidae	Paravulsor 61	vchMDF02	657	2.81	23401	0	490	77	Fresh	2020	UFMG
Xenoctenidae	Paravulsor 62	vchMDF22	1021	2.97	34330	0	330	106	Fresh	2021	UFMG
Xenoctenidae	Paravulsor 63	vchMDF60	14	0.89	1573	0	1	0	Collection	2009	IBSP

Xenoctenidae	Paravulsor blumenauensis	vchMDF15	765	1.87	40829	0	574	125	Fresh	2022	UFMG
Xenoctenidae	Paravulsor impudicus	vchMDF04	813	2.99	27162	0	452	111	Fresh	2020	UFMG
Xenoctenidae	Paravulsor obscurus	vchMDF05	602	4.01	15021	0	314	50	Fresh	2020	UFMG
Xenoctenidae	Paravulsor similis	vchMDF18	621	3.44	18029	0	106	45	Fresh	2020	UFMG
Xenoctenidae	Xenoctenus kaatinga	vchMDF61	763	3.4	22447	0	176	49	Collection	2018	CHNUFPI
Xenoctenidae	Xenoctenus marmoratus	vchMDF63	44	0.09	47869	0	9	2	Collection	1988	IBSP
Xenoctenidae	Xenoctenus pampeanus	vchMDF64	19	0.2	9665	0	1	0	Collection	1974	NMNH
Xenoctenidae	Xenoctenus sp.nov.01	vchMDF69	64	8.24	777	0	4	0	Fresh	2019	MUSM
Xenoctenidae	Xenoctenus sp.nov.02	vchMDF71	489	10.18	4805	0	142	32	Fresh	2019	MUSM
Xenoctenidae	Xenoctenus sp.nov.03	vchMDF70	892	0.98	90630	0	683	167	Fresh	2019	MUSM
Xenoctenidae	Xenoctenus sp.nov.04	vchMDF72	751	1.54	48770	0	653	140	Fresh	2019	MUSM
Xenoctenidae	Xenoctenus vitattus	vchMDF62	692	2.97	23281	0	176	48	Collection	2018	CHNUFPI

Models	LnL	numparams	d	е	j	AIC	AIC_wt
DEC	-48.53	3	0.052	1.00E-07	0.014	103.1	0.0019
DEC+J	-44.14	3	0.13	1.00E-12	0.0031	94.28	0.15
DIVALIKE	-44.78	2	0.2	1.00E-12	0	93.56	0.21
DIVALIKE+J	-42.69	3	0.14	1.00E-12	0.0051	91.39	0.63
BAYAREALIKE	-62.91	2	0.3	0.89	0	129.8	2.90E-09
BAYAREALIKE+J	-48.53	3	0.052	1.00E-07	0.014	103.1	0.0019

Table 2. Relative probability of each of six models, using AIC.

Table 3. Relative probability of each of six models, using AICc.

Models	LnL	numparams	d	е	j	AICc	AICc_wt
DEC	-48.53	3	0.052	1.00E-07	0.014	103.6	0.0018
DEC+J	-44.14	3	0.13	1.00E-12	0.0031	94.8	0.14
DIVALIKE	-44.78	2	0.2	1.00E-12	0	93.81	0.24
DIVALIKE+J	-42.69	3	0.14	1.00E-12	0.0051	91.91	0.61
BAYAREALIKE	-62.91	2	0.3	0.89	0	130.1	3.20E-09
BAYAREALIKE+J	-48.53	3	0.052	1.00E-07	0.014	103.6	0.0018



Figure S14. UCEs sequencing results using old material from museums and fresh and wellpreserved material.

FIGURES

Chapter 1



Figure 1. Xenoctenus spp., habitus of live specimens. A–E, *Xenoctenus vittatus* (Mello-Leitão, 1936) **comb. nov.** A, male and B, female from Guanambi, Bahia, Brazil (UFMG 20929). C, male (UFMG 24328) and D, female (UFMG 24330) from Brumado, Bahia, Brazil. E, male from Itaguaçu da Bahia, Bahia, Brazil (UFMG 20535). F, *Xenoctenus unguiculatus* Mello-Leitão,

1938, female from Parque Nacional Sierra de las Quijadas, San Luis, Argentina (MACN-Ar 45013). Photos by Pedro H. Martins (A–C), Leonardo S. Carvalho (D, E) and Hernán Iuri (F).



Figure 2. *Xenoctenus unguiculatus* Mello-Leitão, 1938, juvenile holotype (MLP 14093). A, C, habitus dorsal view. B, prosoma, frontal view. D, habitus, ventral view. E, original collection labels.



Figure 3. Xenoctenus marmoratus Mello-Leitão, 1941, juvenile holotype (MLP 14835). A, habitus, lateral view. B, prosoma, frontal view. C, habitus, dorsal view. D, habitus, ventral view. E, original collection vial with labels.



Figure 4. *Xenoctenus unguiculatus* Mello-Leitão, 1938. A, C, male from Reserva Natural y Cultural Bosques Telteca, Mendoza, Argentina (MACN-Ar 35619), palp. A, prolateral. B, ventral. C, retrolateral. D, habitus, dorsal view. Abbreviations: E, embolus; MA, median apophysis; RTP, retrolateral tegular projection; StLL, subtegular locked lobe. White star on tegular distal division (TDD).



Figure 5. *Xenoctenus unguiculatus* Mello-Leitão, 1938, male from PN Sierra de las Quijadas, San Luis, Argentina (MACN-Ar 45013). A, C, palp. A, prolateral. B, ventral. C, retrolateral. Abbreviations: C, conductor; E, embolus; MA, median apophysis; RTA, retrolateral tibial apophysis; RTP, retrolateral tegular projection. White star on tegular distal division (TDD).



Figure 6. *Xenoctenus unguiculatus* Mello-Leitão, 1938, female epigynum (A, C) and internal genitalia (B, D). A, B, female from Caucete, San Juan, Argentina (MACN-Ar 35624). A, ventral. B, dorsal. C, D, female from PN Sierra de las Quijadas, San Luis, Argentina (MACN-Ar 45013). C, ventral. D, dorsal. Abbreviations: CD, copulatory ducts; LL, lateral lobes; LLE, lateral lobes extension; MF, median field; S1, primary spermathecae; S2, secondary spermathecae.



Figure 7. *Xenoctenus vittatus* (Mello-Leitão, 1936) **comb. nov.** A–C, male from Jaguaribe, Ceará, Brazil (CNHUFPI 2521), bleached palp. A, prolateral. B, ventral. C, retrolateral. D, male from Castelo do Piauí, Piauí, Brazil, habitus (CHNUFPI 2385). Abbreviations: C, conductor; E, embolus; ELL, embolar locked lobe; MA, median apophysis; RTA, retrolateral tibial apophysis;



Figure 8. *Xenoctenus vittatus* (Mello-Leitão, 1936) **comb. nov.**, male from Pentecoste, Ceará, Brazil (UFMG 20950). A–C, expanded palp. A, prolateral. B, ventral. C, retrolateral. Abbreviations: C, conductor; E, embolus; ELL, embolar locked lobe; MA, median apophysis; RTA, retrolateral tibial apophysis; RTP, retrolateral tegular projection; StLL, subtegular locked lobe. White star on tegular distal division (TDD).



Figure 9. *Xenoctenus vittatus* (Mello-Leitão, 1936) comb. nov., bleached female epigynum (A, C, E) and internal genitalia (B, D, F). A–B, female from Jaguaribe, Ceará, Brazil (CNHUFPI 2521). A, ventral. B, dorsal. C–D, female from Guaribas, Piauí, Brazil (IBSP 56027). C, ventral. D, dorsal. E–F, female from Guaribas, Piauí, Brasil (CNHUFPI 2398). E, ventral. F, dorsal.
Abbreviations: CD, copulatory ducts; LL, lateral lobes; LLE, lateral lobes extension; MF, median field; MG, median groove S1, primary spermathecae; S2, secondary spermathecae.



Figure 10. *Xenoctenus vittatus* (Mello-Leitão, 1936) **comb. nov.** from Jequié, Bahia, Brazil (UFMG 13690). A, female epigynum, not bleached. B, leg I, flexible tarsus.



Figure 11. *Xenoctenus kaatinga* **sp. nov.**, male from Alvorada do Gurguéia, Piauí, Brazil (CNHUFPI 2450). A–C, bleached palp. A, prolateral. B, ventral. C, retrolateral. D. habitus. Abbreviations: C, conductor; E, embolus; ELL, embolar locked lobe; MA, median apophysis; RTA, retrolateral tibial apophysis; RTP, retrolateral tegular projection; StLL, subtegular locked lobe. White star on tegular distal division (TDD).



Figure 12. *Xenoctenus kaatinga* **sp. nov.**, male and female from Alvorada do Gurguéia, Piauí, Brazil (CNHUFPI 2448). A–B, expanded, bleached male palp. A, prolateral. B, retrolateral. C, bleached female epigynum, ventral. D, bleached internal female genitalia, dorsal. Abbreviations: C, conductor; CD, copulatory ducts; E, embolus; ELL, embolar locked lobe; LL, lateral lobes; LLE, lateral lobes extension; MA, median apophysis; MF, median field; RTA, retrolateral tibial apophysis; RTP; retrolateral tegular projection; S1, primary spermathecae; S2, secondary spermathecae; St, subtegulum, StLL, subtegular locked lobe; T, tegulum. White star on tegular distal division (TDD).



Figure 13. A–B, *Xenoctenus vittatus* (Mello-Leitão, 1936) **comb. nov.**, male and female from Itacuruba, Pernambuco, Brazil (UFMG 20060). A, male palp, ventral. B, female internal genitalia, dorsal. C–D, *Xenoctenus kaatinga* **sp. nov.**, male and female from Alvorada do Gurguéia, Piauí, Brazil (CHNUFPI 2448). C, male palp, ventral. D, female internal genitalia, dorsal. Abbreviations: C, conductor; CD, copulatory ducts; E, embolus; ELL, embolar locked lobe; MA, median apophysis; RTP, retrolateral tegular projection; StLL, subtegular locked lobe; S1, primary spermathecae; S2, secondary spermathecae. Black star on tegular distal division (TDD).



Figure 14. Geographic distribution records of Xenoctenus Mello-Leitão, 1938 in South America.



Figure 15. Geographic distribution records of *Xenoctenus unguiculatus* Mello-Leitão, 1938 in Argentina and southern Brazil. The "?" indicates that the specific locality is unknown as it was described only for the Province of Buenos Aires.



Figure 16. Geographic distribution records of *Xenoctenus kaatinga* **sp. nov.** and *Xenoctenus vittatus* (Mello-Leitão, 1936) **comb. nov.** on northeastern Brazilian Caatinga domain. The type locality of *X. vittatus* is uncertain, as it is reported only as the Brazilian state of Paraiba.

Chapter 2



Figure 15. Paravulsor impudicus Mello-Leitão, 1922. Female habitus, dorsal view. Photo: Pedro H. Martins



Figure 16. Paravulsor similis (Keyserling, 1891) comb. nov. Female palp with twisted setae.



Figure 17. Paravulsor impudicus Mello-Leitão, 1922, male and female from Área de Relevante Interesse Ecológica Floresta da Cicuta, Volta Redonda, Rio de Janeiro, Brazil (UFMG 28018). A–C,

male palp. A, prolateral. B, ventral. C, retrolateral. D, female epigynum. E, female internal genitalia. F, male habitus, dorsal view. G, female habitus, dorsal view.



Figure 18. Paravulsor blumenauensis Mello-Leitão, 1900. A, male habitus, dorsal view. B, female habitus, dorsal view. Photo: Pedro H. Martins.



Figure 19. Paravulsor blumenauensis (Mello-Leitão ,1927) **comb. nov.**, male and female *syntypes* from Blumenau, Santa Catarina, Brazil (MZUSP DZ 8947[949]). A–C, male palp. A, prolateral. B, ventral. C, retrolateral. D, female epigynum. E, female internal genitalia. F, female epigynum, posterior view.



Figure 20. Paravulsor blumenauensis (Mello-Leitão, 1927) **comb. nov.**, male and female from Blumenau, Santa Catarina, Brazil (IBSP 136858). A–C, male palp. A, prolateral. B, ventral. C, retrolateral. D, female epigynum. E, female internal genitalia. F, male habitus, dorsal view. G, female habitus, dorsal view.



Figure 21. Paravulsor obscurus (Mello-Leitão, 1936) **comb. nov.**, male and female from Jardim Ângela, Reservatório do Guarapiranga, São Paulo, SP, Brazil (IBSP 131663). A–C, male palp. A,

prolateral. B, ventral. C, retrolateral. D, female epigynum. E, female internal genitalia. F, male habitus



Figure 22. Paravulsor similis (Keyserling, 1891) **comb. nov.**, male and female *syntypes* from Corcovado, Rio de Janeiro, RJ, Brazil (NHML 1311-12). A, C, male palp. A, ventral. B, C, retrolateral. D, female epigynum. E, male habitus, dorsal view. F, female habitus, dorsal view.



Figure 23. Paravulsor similis (Keyserling, 1891) **comb. nov.**, male and female from Parque Nacional da Tijuca, Rio de Janeiro, RJ, Brazil (MNRJ 7482). A–C, male palp. A, prolateral. B,



ventral. C, retrolateral. D, female epigynum. E, female internal genitalia. F, male habitus, dorsal view. G, female habitus, dorsal view.

Figure 24. Paravulsor pulcher (Keyserling, 1891) **comb. nov.**, male and female *syntypes* from Palmeiras, Rio de Janeiro, RJ, Brazil (NHML 1313-15). A, C, male palp. A, ventral. B, C, retrolateral. D, female epigynum. E, male habitus, dorsal view. F, female habitus, dorsal view.



Figure 25. Geographic distribution of Paravulsor in the Brazilian Atlantic Forest.



Figure 26. Geographic distribution of the type locality of *Paravulsor impudicus* in Rio de Janeiro state, Brazil.



Figure 27. Geographic distribution of *P. blumenauensis* in Paraná, Santa Catarina and Rio Grande do Sul states (Southern Atlantic Forest).



Figure 28. Geographical distribution of *P. obscurus* in São Paulo and Santa Catarina states (Southeastern and Southern Atlantic Forest).



Figure 29. Geographic distribution of *P. similis* in Espírito Santo, Rio de Janeiro, and São Paulo states (Southeastern Atlantic Forest).



Figure 30. Geographic distribution of *P. pulcher* type locality in Rio de Janeiro state (Southeastern Atlantic Forest).

Chapter 3



Figure 31. The Atlantic Forest biome.



Figure 32. Geographic distribution records of the Atlantic Forest xenoctenids (Gen.nov.01, Gen.nov.02, Paravulsor Mello-Leitão, 1922) in Brazil.



Figure 33. Geographical distribution of collection sites where Xenoctenidae specimens were found (orange stars) and collection sites where they were not found (red stars).



Figure 34. Geographical distribution of Xenoctenidae species included in the phylogeny. Colors represent areas delimited in the BioGeoBEARS analysis. Brazilian Northeast – N; Central

America – A; Central Bahia – B; Peruvian Deserts – D; South Atlantic Forest – S; Southeast Atlantic Forest – E.



Figure 35. Geographic distribution of *Gen.nov.01* and *Gen.nov.02* species in the Northern Atlantic Forest.



Figure 36. Geographic distribution of *Paravulsor* species that compose the Clade 01, in the Southeast Atlantic Forest.



Figure 37. Geographic distribution of *Paravulsor* species that compose the Clade 02, in the Southeastern Atlantic Forest.



Figure 38. Geographic distribution of *Paravulsor* species that compose the Clade 03, in the Southern Atlantic Forest.



Figure 39. Geographic distribution of *Paravulsor* species that compose the Clade 04, in the Southeastern and Southern Atlantic Forest.



Figure 40. Geographic distribution of Clades 1, 2, 3 and 4 of *Paravulsor* phylogeny, showing the gap existent between clades from Southeast (Clade 1 and 2) and South (Clade 3). Clade 04 is the only one that presented species in both areas.



Figure 41. Xenoctenidae phylogeny with ultrafast bootstrap values.



Figure 42. Chronogram of Xenoctenidae. Colors represent biogeographical areas recovered by the ancestral range estimative under the DIVA-like model.



Figure 43. Ancestral area estimative under BioGeoBEARS DIVA-Like+J on Xenoctenidae (ancstates: global optim, 3 areas max. d=0.1385; e=0; j=0.0051; LnL=-42.69). Areas: Brazilian



Northeast – N; Central America – A; Central Bahia – B; Peruvian Deserts – D; South Atlantic Forest – S; Southeast Atlantic Forest – E.

Figure -44. Xenoctenidae phylogeny with age uncertainty displayed as bars on nodes.