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DIVERSIFICAÇÃO MORFOLÓGICA E MOLECULAR DO GÊNERO DE GECKOS NEOTROPICAIS *Phyllopezus* PETERS, 1878 (SQUAMATA: GEKKOTA: PHYLLODACTYLIDAE) EM FLORESTAS SECAS DO NORDESTE BRASILEIRO

MARCOS JORGE MATIAS DUBEUX

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Dissertação apresentada ao Programa de Pós-Graduação em Biologia Animal, da Universidade Federal de Pernambuco, como requisito parcial para a obtenção do título de Mestre em Biologia Animal.

Área de concentração: Sistemática e taxonomia de grupos recentes.

Orientador: Prof. Dr. Pedro M. Sales Nunes

Coorientadora: Profa. Dra. Tamí Mott

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Aprovada em 26 de fevereiro de 2021

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Dedico à minha mãe, Nazaré Matias,
pois ao contrário de uma ave de gaiola
que vive presa, ela me ensinou a voar.

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A todos que acreditaram e contribuíram em minha formação, seja através de exemplos, inspiração, financiamento, conselhos ou críticas, dedicando seu tempo e paciência, o meu muito obrigado. Agradeço aos gerentes e curadores das Coleções Herpetológicas visitadas pela ajuda e disponibilidade e a Fundação de Amparo à Ciência e Tecnologia do Estado de Pernambuco – FACEPE pela bolsa concedida.

Um bom cientista se revela, se realiza no laboratório, isso é logico, ninguém escapa, mas um cientista feliz é aquele que se integra na mata virgem; A mata é uma dessas coisas em que o todo é mais que a soma das partes, não é só essa luz, essas plantas, esses bichos, essas vozes, mas é esse todo que penetra a gente, que dá uma felicidade, uma tranquilidade imensa. Eu já estou há mais de 50 anos nessa lida e lógico que meu tempo útil está chegando ao fim, e o pavor que eu tenho é um dia não poder mais vir, não é que eu queira ver muito bicho, ver muita coisa, mas estar na mata, pra mim, é uma felicidade [...]. O zoólogo, geralmente, entra na profissão se apaixonando enquanto menino ainda, por um grupo zoológico. O zoólogo vai, aprofunda a sistemática, entra pela ecologia do bicho, entra pela evolução, pelo comportamento, e acaba afinal entrando no ambiente do bicho. Eu já disse ao meu filho e gostaria de dizer ao meu neto... "Vá lá, veja o que eu vi, e goste como eu gostei" [...].

Vanzolini, Paulo Emílio 1992

Os calangos do boiaçu

RESUMO

Estudos moleculares identificaram uma elevada diversidade entre representantes do gênero de lagartixas *Phyllopezus*, sendo indicada a presença de múltiplas linhagens de espécies crípticas não formalmente descritas. Nos anos seguintes, muito pouco foi discutido sobre a diversidade morfológica do gênero e a instabilidade taxonômica de *Phyllopezus* permanece. Nesse estudo, objetivamos ampliar o conhecimento acerca da diversidade genética, morfológica e hemipeniana de populações dos três táxons nominais de *Phyllopezus* com ocorrência para o Nordeste do Brasil, avaliando seus relacionamentos filogenéticos e limites de espécies através de uma abordagem integrativa. O estudo está organizado em dois capítulos: No Capítulo I, tratamos da diversidade e variação morfológica entre e dentro das populações do Nordeste do Brasil, identificamos e designamos morfogrupos e morfotipos ao longo da distribuição dos táxons, realizamos as primeiras descrições de hemipênis para o gênero e ampliamos a representatividade de amostras e localidades na filogenia molecular atual. No Capítulo II, descrevemos duas novas espécies de *Phyllopezus* para o Nordeste do Brasil, baseado na congruência entre evidências morfológicas e moleculares. Embora ainda não estejamos próximos de resolver a taxonomia do gênero *Phyllopezus*, o presente trabalho traz contribuições importantes para a definição de características diagnósticas e a descrição formal de espécies no gênero e descreve uma diversidade morfológica há décadas negligenciada.

Palavras-chave: Diversidade críptica. Filogenia. Hemipênis. Lagarto. Variação morfológica.

ABSTRACT

Molecular studies have identified a high diversity within representatives of the geckos' genus *Phyllopezus*, indicating the presence of multiple lineages of cryptic species not formally described. In the following years, little was discussed about the morphological diversity of the genus, and the taxonomic instability of *Phyllopezus* remains. In this study, we aimed to expand the knowledge about the genetic, morphological and hemipenial diversity of populations of the three nominal taxa of *Phyllopezus* occurring in Northeast Brazil, evaluating their phylogenetic relationships and species limits through an integrative approach. The study is organized in two chapters: In Chapter I, we dealt with the diversity and morphological variation between and within the populations of Northeast Brazil, we identified and designated morphogroups and morphotypes throughout the distribution of the taxa, we carried out the first descriptions of hemipenial morhology for the genus and we expand the representativeness of samples and locations in the current molecular phylogeny. In Chapter II, we described two new species of *Phyllopezus* for Northeastern Brazil, based on the congruence between morphological and molecular evidence. Although in this point we are still far away to solving the taxonomy of the *Phyllopezus* genus, the present work brings important contributions to the definition of diagnostic characteristics and the formal description of species in the genus and describes a neglected morphological diversity for decades.

Keywords: Cryptic diversity. Phylogeny. Hemipenis. Lizard. Morphological variation.

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1 INTRODUÇÃO

A família de gecos transatlânticos Phyllodactylidae (Gamble et al., 2008) é atualmente composta por 151 espécies, alocadas em 10 gêneros e amplamente distribuídas na África, na região do Mediterrâneo, nas Américas Central e do Sul e nas ilhas do Caribe (Uetz & Hosek, 2021). Dentre os gêneros da família, seis tem distribuição no continente americano (*Garthia* [2 spp.], *Gymnodactylus* [5 spp.], *Homonota* [13 spp.], *Phyllodactylus* [58 spp.], *Phyllopezus* [6 spp.] e *Thecadactylus* [3 spp.]), três estão distribuídos no continente africano (*Asaccus* [19 spp.], *Haemodracon* [2 spp.] e *Ptyodactylus* [12 spp.]) e apenas o gênero *Tarentola* (31 spp.) apresenta representantes em ambos os continentes (Gamble et al., 2011; Uetz & Hosek, 2021). Embora a ampla diversidade morfológica dos phyllodactylídeos tenha dificultado até o momento a identificação de caracteres morfológicos diagnósticos e não ambíguos em nível de família, o monofiletismo de Phyllodactylidae é sustentado por diferentes marcadores moleculares, tendo como uma de suas principais sinapomorfias a deleção de três pares de base no gene nuclear codificador de proteína "fosducina" (PDC) (Gamble et al., 2008, 2011).

Dentre os Phyllodactylidae do Novo Mundo, o gênero de lagartixas neotropicais *Phyllopezus* Peters, 1878 abriga animais de hábito saxícola e arbóreo, em geral noturnos, e predominantemente distribuídos em áreas abertas dos biomas secos da América do Sul (Werneck et al., 2012; Cacciali et al., 2018). Atualmente, o gênero é composto por seis espécies nominais: *P. heuteri* Cacciali, Lotzkat, Gamble & Köhler, 2018 (restrito ao bioma Chaco na Cordillera de Los Altos, Paraguai; Cacciali et al., 2018), *P. lutzae* (Loveridge, 1941) (restrito ao bioma da Mata Atlântica dos estados da Paraíba à Bahia, Brasil; Albuquerque et al., 2019), *P. maranjonensis* Koch, Venegas & Böhme, 2006 (restrito às florestas secas da bacia do alto Marañon, Peru; Koch et al., 2006), *P. periosus* Rodrigues, 1986 (restrito à região norte do bioma Caatinga dos estados do Ceará à Pernambuco), *P. pollicaris* (Spix, 1825) (amplamente distribuído nos biomas da Caatinga e Cerrado, Brasil; Werneck et al., 2012) e *P. przewalskii* Koslowsky, 1895 (distribuída no bioma Chaco no Paraguai e ao norte da Argentina e no bioma Cerrado, abaixo do Planalto Central do Brasil, nos estados do Mato Grosso e Mato Grosso do Sul, Brasil; Cacciali et al., 2018).

Desde muito cedo, o gênero *Phyllopezus* apresentou uma história taxonômica confusa. A primeira espécie do gênero foi descrita por Spix (1825) para alocar uma população do interior do estado da Bahia (atualmente alocada em *P. pollicaris*), com localidade-tipo designada apenas como "interior do estado da Bahia" ("*habitat sub córtice arborum in sylvis interioris Bahiae campestribus*"; Spix, 1825: 17 [58]). Originalmente atribuída ao gênero

Thecadactylus, a descrição desse táxon (ainda em latim) não apresentou grande riqueza de detalhes, com uma caracterização sucinta e com pouca ou nenhuma diagnose específica, apenas com uma ilustração em vista dorsolateral. Isso foi suficiente para que Cuvier (1829), poucos anos depois, baseado na ilustração de *T. pollicaris* de Spix (1825: Tab. XVII [2]) e sem examinar qualquer exemplar-tipo, sinonimizasse esse táxon à lagartixa-africana, introduzida no Brasil, *Hemidactylus mabouia* (Moreau-de-Jonnès, 1818), justificando que o táxon poderia representar uma variação etária da espécie. Essa sinonímia foi amplamente aceita pelos autores posteriores e se manteve por mais de um século (Müller & Brongersma, 1933).

O gênero *Phyllopezus* só foi proposto no ano de 1878 para comportar *P. goyazensis* Peters, 1878, descrito para o estado de Goiás (sem maiores especificações), até então designado como "*Hemidactylus goyazensis"* (Behn, *nom. nud.*). Müller & Brongersma (1933), analisando os exemplares de *T. pollicaris* de Spix depositados nas coleções herpetológicas do *Rijksmuseum van Natuurlijke Historie* em Leiden na Holanda e *Zoological State Collection* em Munique na Alemanha, designaram o espécime ZSM 2510/0 como lectótipo do táxon por melhor se enquadrar às medidas fornecidas na descrição original de Spix, redescrevendo este espécime, agora com maiores detalhes. Outros dois exemplares, considerados pertencentes a série-tipo, passaram a ser tratados como paralectótipos [ZSM 165/0/1-2(a, b)] e são também caracterizados nesse trabalho. A partir dessa análise mais refinada os autores notaram a grande semelhança morfológica entre *T. pollicaris* e *P. goyazensis*, propondo assim a sinonímia desses dois táxons, permanecendo a proposta do novo táxon genérico [*Phyllopezus pollicaris* (Spix, 1825) comb. nov.].

Ainda, uma terceira espécie foi descrita no gênero para o oeste do estado do Mato Grosso ("*Descalvados, distrito San Luis de Cáceres, en Matto-Grosso*"), *P. przewalskii* Koslowsky, 1895, logo também sinonimizada a *P. goyazensis* (= *P. pollicaris*) (Boulenger, 1897). Vanzolini (1953), em uma revisão do gênero, identificou alguns caracteres morfológicos diagnósticos entre *P. pollicaris* e *P. przewalskii*, embora com grande sobreposição, e conferiu a *P. przewalskii* o status subespecifico dentro de *P. pollicaris*, proposta posteriormente reforçada por diferenças marcantes no cariótipo entre representantes das duas subespécies (número e forma dos cromossomos; Pellegrino et al., 1997). Assim, por mais de três décadas o gênero *Phyllopezus* se manteve taxonomicamente estável e monotípico, com duas subespécies (*P. p. pollicaris* e *P. pollicaris przewalskii*), até recentes descrições de novos táxons.

Rodrigues (1986) descreveu *P. periosus* para o município de Cabaceiras, Paraíba, uma área de Caatinga no Nordeste do Brasil. Essa espécie, encontrada em simpatria com *P. p. pollicaris*, era particularmente diferente dos representantes até então conhecidos para o gênero, podendo ser facilmente diagnosticada por caracteres morfológicos. Já no início dos anos 2000 é descrita *P. maranjonensis*, uma espécie alopátrica do gênero encontrada nos vales interandinos da bacia do alto Marañon, nas proximidades de Balsas, Departamento do Amazonas, Peru (Kock et al., 2009).

Até então, toda a taxonomia de *Phyllopezus* havia sido baseada exclusivamente em dados morfológicos e cariotípicos e apenas mais recentemente espécies do gênero foram inclusas em estudos moleculares. Gamble et al. (2008), visando investigar a diversificação dos gecos do Novo Mundo, incluíram representantes de *P. maranjonensis* e das duas subespécies de *P. pollicaris* entre representantes de outros 31 gêneros em uma amostragem de cinco marcadores nucleares (RAG1, RAG2, c-mos, ACM4 e PDC). Nesse estudo, os autores recuperaram o monofiletismo de *Phyllopezus*, relacionando-o aos gêneros sul-americanos *Homonota* e *Phyllodactylus*, todos pertencentes a família Phyllodactylidae. Utilizando os mesmos marcadores nucleares e ampliando a representatividade geográfica e taxonômica de seu conjunto de dados (representando 60 gêneros de gecos), Gamble et al. (2011) identificaram resultados intrigantes relacionados ao gênero *Phyllopezus*. Além da alta diversidade genética entre os representantes da espécie nominal *P. pollicaris*, com distâncias genéticas similares àquelas encontradas entre espécies irmãs reconhecidas, *Phyllopezus* foi recuperado parafilético em relação à *Bogertia* Loveridge, 1941, gênero monotípico de lagartixas endêmico da Mata Atlântica. Os autores também atribuíram uma nova reorganização filogenética em nível de gênero, recuperando *Phyllopezus* + *Bogertia* como o clado irmão de *Gymnodactylus* (não incluído nos estudos anteriores) e o clado composto por *Phyllopezus*/*Bogertia* + *Gymnodactylus* grupo irmão dos demais gêneros de Phyllodactylidae do Novo Mundo (exceção para *Thecadactylus* e *Tarentola* que não formaram um grupo monofilético com os demais). Tais achados, forneceram hipóteses específicas a serem testadas acerca das relações filogenéticas de *Phyllopezus* e *Bogertia*. Assim, Gamble et al. (2012) utilizando marcadores mitocondriais (16SrRNA) e nucleares (RAG1, RAG2, ACM4 C-MOS), com uma maior amostragem geográfica e incluindo todas as espécies até então conhecidas de *Phyllopezus* e *Bogertia*, confirmaram a não reciprocidade monofilética entre os dois gêneros, sendo *B. lutzae* recuperada como espécie irmã de *P. maranjonensis* com elevado suporte estatístico. Tal fato, somado às similaridades na morfologia externa (Loveridge, 1941; Vanzolini, 1953), osteológica (Russell & Bauer, 1988; Abdala, 1996), muscular (Russell &

Bauer, 1988) e de cariótipo (Pellegrino et al., 1997) já identificadas entre os gêneros, sustentou a proposta de sinonímia, transferindo *Bogertia* a sinônimo júnior de *Phyllopezus* (Gamble et al., 2012). Em relação aos representantes de *P. pollicaris*, a linhagem de *P. pollicaris przewalskii* foi recuperada monofilética em todas as análises, corroborando as diferenças morfológicas e cariotípicas já identificadas (Vanzolini, 1953; Pellegrino et al., 1997). No entanto, a hipótese de reciprocidade monofilética entre as duas subespécies foi rejeitada. Além disso, uma elevada diversidade filogenética entre representantes de *P. pollicaris* foi identificada, sendo indicada a presença de múltiplas linhagens de espécies crípticas associadas a este táxon nominal.

A revelação da presença de uma diversidade subestimada sob o táxon nominal *P. pollicaris* reforçou a necessidade de uma maior representatividade geográfica e a inclusão de diferentes abordagens para testar as hipóteses de espécies (Gamble et al., 2012). Com esse objetivo, dentre outros, Werneck et al. (2012) desenvolveram um dos estudos genéticos mais densamente amostrados em termos de cobertura geográfica (63 localidades ao longo da distribuição do complexo), número de marcadores (dois mitocondriais e 11 nucleares em rápida evolução) e indivíduos (N = 393) para um complexo de espécies de lagartos neotropicais, até então restringindo suas análises ao complexo de espécies crípticas *P. pollicaris* (Gamble et al., 2012). Nesse estudo foi identificada uma marcante estruturação genética entre três grandes clusters geográficos que correspondem aos biomas de ocorrência do complexo (Caatinga, Cerrado e Chaco). Em uma avaliação mais refinada, oito clusters genéticos foram delimitados com alta divergência genética e suporte estatístico (Clados I – VIII), passando a serem tratados como espécies candidatas.

Nos anos seguintes, muito pouco foi discutido sobre a diversidade morfológica do gênero *Phyllopezus* e as questões taxonômicas a serem tomadas como consequência das hipóteses filogenéticas moleculares disponíveis. De fato, os estudos morfológicos não conseguiram acompanhar o crescente avanço da pesquisa filogenética molecular. Recentemente, Cacciali et al. (2018) avaliando a diversidade morfológica e molecular de populações de *Phyllopezus* ocorrentes no Chaco paraguaio, revalidaram o táxon nominal específico *P. przewalskii* para acomodar as populações pertencentes ao “Clado V” de Werneck et al. (2012), baseado nas informações morfológicas e cariotípicas disponíveis (Vanzolini, 1953, 1968; Pellegrino et al., 1997) e nas novas evidências moleculares (Gamble et al. 2011, 2012; Werneck et al., 2012; Cacciali et al., 2018). Além disso, descreveram uma nova espécie para o gênero, relacionada a *P. przewalskii* e nunca incluída nos estudos moleculares anteriores: *Phyllopezus heuteri*, com localidade-tipo na cadeia de montanhas da

Cordillera de Los Altos, Departamento de Cordillera, Paraguai. Essas novas propostas taxonômicas tornaram o táxon nominal *P. pollicaris* parafilético e, embora representem avanços importantes na taxonomia do grupo, estão longe de resolver a instabilidade taxonômica do gênero.

As evidências moleculares de uma riqueza de espécies subestimada nesse gênero de lagartixas Neotropicais revelam a necessidade de estudos integrativos adicionais para investigar e delimitar as linhagens crípticas presentes no gênero *Phyllopezus*. Uma revisão morfológica ampla e detalhada a fim de diagnosticar e descrever essa diversidade por décadas negligenciada é necessária. Nesse contexto, esse trabalho teve como objetivos: (1) ampliar a representatividade geográfica dos dados genéticos do gênero e explorar diferentes análises, métodos e modelos de delimitação de espécies a fim de refinar a compreensão da diversidade e diversificação das linhagens previamente reveladas em estudos anteriores e, eventualmente, delimitar novas linhagens ainda não identificadas; (2) caracterizar a morfologia externa e hemipeniana de populações representantes de cada linhagem genética ocorrentes no Nordeste do Brasil, ampliando o conhecimento sobre variação morfológica no gênero e buscando determinar os melhores preditores morfológicos para a distinção das linhagens; (3) utilizar a taxonomia integrativa por congruência para avaliar o status taxonômico e posicionamento filogenético das linhagens analisadas; e por fim, (4) propor adequações taxonômicas às novas hipóteses, com a descrição/redescrição de novos táxons, revalidação ou proposta de novos nomes para as linhagens a serem identificadas/ diagnosticadas.

Esse estudo, desenvolvido e apresentado como dissertação junto ao PPGBA-UFPE, foi originalmente proposto como projeto de mestrado, cujo objetivo geral era caracterizar a diversidade morfológica e molecular e avaliar o posicionamento filogenético das populações de *Phyllopezus* ocorrentes no Nordeste do Brasil. Até o início de 2021 (segundo semestre do mestrado), o projeto vinha se desenvolvendo dentro dos prazos e cinco Coleções Herpetológicas do Nordeste já haviam sido visitadas. Devido à atual pandemia de COVID-19, as visitas técnicas aos acervos das universidades e museus, bem como os procedimentos laboratoriais relacionados às abordagens moleculares planejadas para os semestres seguintes tiveram de ser canceladas/adiadas. Recentemente, buscamos a readequação do projeto na tentativa de convertê-lo em Doutorado, ampliando os objetivos e abordagens e contemplando toda a diversidade taxonômica e cobertura geográfica do gênero. Obtivemos sucesso com o pleito de progressão de nível junto ao mesmo Programa de Pós-Graduação, sendo o novo projeto de Doutorado intitulado “REVISÃO TAXONÔMICA DO GÊNERO DE GECOS NEOTROPICAIS *Phyllopezus* PETERS, 1878 (SQUAMATA: GEKKOTA:

PHYLLODACTYLIDAE)” com conclusão prevista para 2023. Dessa forma, os objetivos originais que não puderam ser alcançados devido aos atrasos/contratempos associados à pandemia da COVID-19, deverão ser alcançados com o novo prazo, além do acréscimo de novos objetivos não previstos anteriormente. Dessa forma, o estudo aqui apresentado está dividido em dois capítulos e organizado a seguir em forma de manuscritos em construção, seguindo a formatação sugerida pelas revistas *Zoological Journal of the Linnean Society* (Capítulo I) e *Zootaxa* (Capítulo II). Adicionalmente, um terceiro artigo, relacionado a gênero-foco da dissertação e também em fase final de construção (seguindo a formatação da revista *CheckList*), se encontra anexado ao final do documento (Anexo 1).

Vale salientar que os dados utilizados como base para a construção do primeiro capítulo dessa dissertação correspondem a dados parciais e preliminares que serão utilizados como ponto de partida para o projeto de doutorado. Estamos cientes que o artigo referente ao Capítulo I carece de uma maior amostragem geográfica, taxonômica e metodológica, afim de alcançar os objetivos nele propostos.

Cabe ressaltar ainda que embora tenhamos restringindo no documento a linha de coautoria dos manuscritos aos orientadores, este projeto, assim como seus produtos, conta com a parceria e colaboração de pesquisadores da Universidade Federal do Rio Grande do Norte (UFRN), Universidade Federal do Paraná (UFPR), Universidade de São Paulo (USP), Instituto de Pesquisas da Amazônia (INPA) e University of Minnesota. Embora estejam redigidos em inglês os manuscritos ainda não passaram por revisão da língua por um profissional ou nativo.

2 CAPÍTULO I – MOLECULAR DIVERSITY, MORPHOLOGICAL VARIATION AND SPECIES LIMITS IN THE GENUS *Phyllopezus* PETERS, 1878 (SQUAMATA: GEKKOTA: PHYLLODACTYLIDAE)

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ABSTRACT

In tropical regions, where levels of endemism are high, widely distributed reptile species commonly correspond to cryptic lineages, morphologically similar and with complex evolutionary histories. This is the case of *Phyllopezus*, a genus of Neotropical geckos widely distributed in dry open biomes of South America and north of Atlantic Forest biome. Recent molecular studies have identified a high phylogenetic diversity in the genus, with the presence of multiple lineages of cryptic species not formally described. In fact, the morphological and taxonomic studies failed to keep track with the increasing advance of molecular phylogenetic research and, consequently, morphological limits for most putative lineages remain unknown. Herein we analyzed 353 specimens from 78 localities representing the three nominal taxa of *Phyllopezus* occurring in northeastern Brazil. We expand the geographic coverage of the genetic data (17 samples from four localities) and present a detailed systematic revision of the morphology, including hemipenial morphology, pholidosis (14 characters) and morphometrics (22 characters) information for the genus. The new genetic samples are nested within lineages representing the clade that comprised most of the localities in the Caatinga (Clade VIII). Hemipenial morphology revealed informative characters which are diagnostic of different lineages. Geographic variation in morphological characters was not identified in *P. lutzae* and *P. periosus*. In *P. pollicaris*, two large morphogroups (A and B) and nine morphotypes (A1-A4 and B1-B5) were diagnosed based on external morphology. For many of the locations analyzed, no genetic and/or hemipenial data were available, reinforcing the

need for further studies to fill these sampling gaps in order to better understand the variation and morphological limits and describe species diversity for decades neglected.

Keywords: Cryptic diversity; Hemipenis; Phylogeny; Integrative taxonomy; Morphology.

INTRODUCTION

In tropical regions, where levels of endemism are high, widely distributed reptile species commonly correspond to cryptic lineages, morphologically similar and with complex evolutionary histories (Bickford et al., 2007; see below), and several studies with neotropical lizards have reinforced this scenario (e.g., Domingos et al., 2014; Werneck et al., 2012; Nunes et al., 2012; Recoder et al., 2014; Sturaro et al., 2018). In fact, although our understanding about the diversity and diversification of the lineages have been growing, in some cases, morphological and taxonomic studies failed to keep track with the increasing advance of molecular phylogenetic research (Werneck et al., 2012; Recoder et al., 2014; Rodrigues et al. 2014; Cacciali et al., 2018; Lanna et al., 2018). Consequently, morphological diagnoses for such putative lineages remain unknown, hampering new taxonomic proposals and conservation policies.

The trans-Atlantic geckos in family Phyllodactylidae (Gamble et al., 2008) currently consist of 151 species, allocated in 10 genera widely distributed in Central and South Americas, the Caribbean islands, Africa and in the Mediterranean region (Uetz & Hosek, 2021). For several decades, molecular studies have been reporting high levels of cryptic diversity within Phyllodactylidae (Pellegrino et al., 2005; Weiss et al., 2007; Gamble et al., 2008a, b, 2012; Domingos et al., 2014; Werneck et al., 2012; Ramírez-Reyes et al., 2018, 2020). In fact, in the last 15 years, almost 30% of the species currently recognized were described.

Among the New World Phyllodactylidae, *Phyllopezus* Peters, 1878 has a confusing taxonomic history. The first species of the genus was described by Spix (1825) to allocate a population from the hinterlands of the State of Bahia, in northeastern Brazil (currently *P. pollicaris*), originally attributed to the genus *Thecadactylus*. A few years later, Cuvier (1829) synonymized this taxon with the African gecko, *Hemidactylus mabouia* (Moreau-de-Jonnès, 1818), an invasive species in South America. The genus *Phyllopezus* was only established in 1878, to include *P. goyazensis* Peters, 1878, described for the State of Goiás, Brazil (Peters, 1878). Later, Müller & Brongersma (1933) synonymized *T. pollicaris* and *P. goyazensis*,

keeping the species in the latter genus as *Phyllopezus pollicaris* (Spix, 1825). A third species, *P. przewalskii* Koslowsky, 1895, was described west of the State of Mato Grosso, Brazil, being latersynonymized with *P. goyazensis* (= *P. pollicaris*) (Boulenger, 1897).

Vanzolini's (1953) revision of the *Phyllopezus* genus using morphological data identified some diagnostic characters, although with high overlap, and gave *P. przewalskii* a subspecific status within *P. pollicaris.* This taxonomic arrangement was supported by karyotypic evidence, distinguishing these two subspecies (Pellegrino et al., 1997). Thus, during more than three decades, the genus *Phyllopezus* remained taxonomically stable, monotypic, with two subspecies (*P. p. pollicaris* and *P. pollicaris przewalskii*). Only two species were described subsequently: *P. periosus* Rodrigues, 1986 from the municipality of Cabaceiras, State of Paraíba, Brazil (Rodrigues, 1986) and *P. maranjonensis* Kock, Venegas & Böhme, 2006, from the inter-Andean valleys of the upper Marañon basin, Department of Amazonas, Peru (Kock et al., 2009).

Until then, the taxonomy of the genus had been based exclusively on morphological and karyotypic data.Onlyrecently, species of *Phyllopezus* were included in molecular studies (Gamble et al., 2008, 2011, 2012; Werneck et al., 2012; Cacciali et al., 2018). Gamble et al. (2011), included representatives of *P. pollicaris* and *P. maranjonensis* among 60 other gecko genera, and used five nuclear markers for phylogenetic inference. They recovered the paraphyly of *Phyllopezus* with the monotypic genus of Atlantic Forest lizards *Bogertia* Loveridge, 1941. Such findings generated hypotheses to be tested about the phylogenetic relationships in the genus. Gamble et al. (2012) included all previously recognized species of *Phyllopezus* and *Bogertia* in a larger geographic sampling in their phylogenetic studies using mitochondrial and nuclear markers. Their results confirmed the non-monophyletic reciprocity between the two genera, as *B. lutzae* was recovered as the sister species of *P. maranjonesis*. This fact, in addition to external morphology (Loveridge, 1941; Vanzolini, 1953), osteological (Russell & Bauer, 1988; Abdala, 1996), muscular (Russell & Bauer, 1988) and karyotypic (Pellegrino et al., 1997) similarities, supported a synonymy proposal, with *Bogertia* being treated as a junior synonym of *Phyllopezus* (Gamble et al., 2012). In addition, an unexpected phylogenetic diversity among representatives of *P. pollicaris* was identified, indicating the presence of multiple lineages of cryptic species associated with this nominal taxon, with genetic distances similar to those found among recognized sister species.

The discovery of an underestimated diversity under the nominal taxon *P. pollicaris* reinforced the need for additional studies with larger geographic coverage and with the use of different approaches to test and to expand the preliminary results of delimiting species already

obtained (Gamble et al., 2012). With this objective Werneck et al. (2012) developed one of the most densely sampled genetic studies for a complex of neotropical lizard species so far, in terms of geographic coverage (63 locations along the distribution of the complex), number of markers (two mitochondrial and 11 rapidly evolving nuclear markers) and individuals (N = 393). In this study, eight genetic clusters were recovered with high genetic divergence and statistical support (Clades I – VIII), and treated as candidate species.

In the following years, little was discussed about the morphological diversity of the genus, and the taxonomic instability of *Phyllopezus* remains. Recently, Cacciali et al. (2018) evaluated the morphological and molecular diversity of *Phyllopezus* populations occurring in the Paraguayan Chaco. They resurrected the specific nominal taxon *P. przewalskii* to accommodate populations belonging to "Clade V" of Werneck et al. (2012), based on the available morphological and karyotypic information (Vanzolini, 1953, 1968; Pellegrino et al., 1997) and on new molecular data. In addition, they described a new species for the genus, related to *P. przewalskii* and not yet included in previous molecular studies: *Phyllopezus heuteri* Cacciali, Lotzkat, Gamble & Köhler, 2018, with a type-locality in the Cordillera de Los Altos mountain range, Department of Cordillera, Paraguay. These new taxonomic proposals made the nominal taxon *P. pollicaris* paraphyletic and despite the remarkable recent advances in the taxonomy of the group, it is far from solving the taxonomic instability of the genus.

The great revealed diversity not adequately diagnosed under the name *Phyllopezus pollicaris* and the consequent need of taxonomic actions reveal the need for integrative studies aiming at investigating the morphological variation, to diagnose properly the candidate species and to formally describe the diversity present in the genus. Herein we expand the geographic coverage of the genetic data already available and present a detailed systematic revision of the morphology of the genus, including hemipenial, pholidotic and morphometric data. Our main goal is to determine the taxonomic status and phylogenetic position of the cryptic lineages of *Phyllopezus* genus based on an integrative approach.

MATERIAL AND METHODS

External morphological data and statistical analyses

We examined a total of 353 specimens of *Phyllopezus* (Fig. 1; Appendix I), being 15 specimens of *P. lutzae* from six locations; 77 of *P. periosus* from 13 locations; 11 of *P.*

pollicaris “Clade I” from a single location; 86 of *P. pollicaris* “Clade VIII” from 11 locations, and 164 specimens of *P. pollicaris* sensu lato from 50 locations not included in earlier molecular studies (unassigned clades). Specimens were housed in the following herpetological collections: *Coleção Herpetológica* do *Museu de História Natural da Universidade Federal de Alagoas* (MUFAL or field number acronym LABI), *Coleção Herpetológica* da *Universidade Federal da Paraíba* (CHUFPB), *Coleção Herpetológica* da *Universidade Federal de Pernambuco* (CHUFPE or field number acronyms PMSN and CAT), *Coleção Herpetológica* da *Universidade Federal do Rio Grande do Norte* (UFRN) and *Laboratório de Herpetologia da Universidade de São Paulo* (USP [Field number acronym JC]). The comparisons with type series (paralectotypes of *P. pollicaris* [ZSM 165/0/1–2]) and congeners which we did not have access to physical material (*P. heuteri*, *P. maranjonensis* and *P. przewalskii*) were based on data from the literature and/or photographs (Spix, 1825; Koslowsky, 1895; Müller & Brongersma, 1933; Koch et al., 2006; Cacciali et al., 2018).

Sex was determined by direct inspection of gonads (when dissected), by the presence of eggs (females) or hemipenis (when everted) or by a small lateral insertion at the base of the tail when not everted (in search for the hemipenis or the hemipenial retractor muscle). Measurements and scale counts were taken under a stereomicroscope. Measurements followed Cassimiro & Rodrigues (2009), and Sturaro et al. (2018), and were taken using a digital caliper with 0.1 mm precision (in right side of specimens whenever possible): snout-vent length (SVL, from tip of snout to cloacal opening), distance between limbs (DBL, from axilla to groin), tail base width (TBW, taken at the base of the organ just posterior to the cloaca), tail length (TL, from cloacal opening to tip of tail, only in specimens with intact, non-regenerated tails), head length (HL, from tip of snout to anterior margin of ear-opening), head width (HW, on the widest part of head), head depth (HD, on the highest part of head), snout length (SL, from tip of snout to anterior margin of eye), nares-snout distance (NSD, from tip of snout to anterior border of nares), nares-eye distance (NED, to posterior border of nares to anterior edge of eye), eye-snout distance (ESD, from tip of snout to center of eye), eye diameter (ED, in widest section of the eye), interorbital distance (IOD, between the upper margins of eyes), internarial distance (IND, between the upper margins of nares), length of humerus (LH, from insertion of humerus to elbow), length of forearm (LF, from tip of elbow to wrist), length of thigh (LT, from insertion of femur to knee), length of tibia (LTB, from knee to ankle), width of mental scale (WM, between lateral corners), length of mental scale (LM, between anterior and posterior corners), width of rostral scale (WR, between lateral corners) and length of rostral scale (LR, between anterior and posterior corners).

Scale counts and others meristic characters were recorded according to Rodrigues (1986), and Cassimiro & Rodrigues (2009), taken as follows: number of rostrals (R), number of postrostrals (PR), number of postnasals (PN), number of supralabials (SL), number of infralabials (IL), number of mentals (M), number of postmentals (PM), scales that surround the postmental (SSP), number of ventrals in a longitudinal row (VLR, along a midventral line, from anterior margin of forelimbs to anterior margin of hind limbs), number of dorsal tubercles in a longitudinal row (DT, along a middorsal line, from anterior margin of forelimbs to tail), number of lamellae under the fourth finger (L4F), number of lamellae under the fourth toe (L4T), number of postcloacal tubercles at the sides of the vent (TP), and total number of postcloacal pores (CP).

To identify the existence of diagnosable sexual dimorphism of size in SVL, univariate analysis of variance (ANOVA) was performed for each species/morphotype separately. To identify variation between the sexes in the other morphometric characters, multivariate analyses of variance (MANOVA) were performed using the dataset corrected by size (SVL) through Linear Regression Analysis (here treated as "shape"). When the number of samples was smaller than the number of dependent variables, data variation was summarized through a Principal Component Analysis (PCA). For SVL, exploratory analyses of barplots were performed. For all analyzes, individuals considered outliers (non-normal) and juveniles (with SVL <50 mm for *P. pollicaris*; following Recoder et al., 2012) were excluded. To assess data normality and homoscedasticity, Shapiro-Wilks and Levene tests were performed. When significant variation between sex was identified, males and females were tested separately. The interespecifc variation in morphometric characters was summarized with a PCA (without previous identification of groups). To test the segregation of previously defined morphological groups, Discriminant Function Analyzes (DFA; classifying the identified morphotypes) was performed. All analyses were performed on the R Studio software and in paleontological statistics software (PAST; Hammer et al., 2001), with significance considered when $P < 0.05$.

Hemipenial morphology

For the characterization of the hemipenis, we preferentially selected individuals who had the organ totally or partially everted in all the identified morphogroups and removed it through a cut at its base (next to the cloacal opening). In individuals who did not have the previously everted hemipenis, we removed the organ through a longitudinal incision at the

base of the tail (D'Angiolella et al., 2016). For the preparation of the organ, we followed the protocol of Manzani & Abe (1988) with modifications proposed by Pesantes (1994) and Zaher & Prudente (2003). Then the removed hemipenis were immersed for a few seconds in a solution of potassium hydroxide (KOH) and then filled with a solution of petroleum jelly and paraffin stained with blue aniline and preserved in 70% ethanol. Terminology of hemipenial morphology and ornamentation follows Dowling & Savage (1960), Klaver & Böhme (1986), Keogh (1999) and Zaher (1999).

Measurements followed or were adapted from Das & Purkayastha (2012) and were measured with the aid of the ImageJ v.1.50i software using staggered photographs: hemipenis length (HPL, from base of hemipenis to tip of lobe), hemipenis width (HPW, on the widest part of hemipenial body), lobe length (LL, from basal region to tip of lobe), lobe width (LW, on the widest part of lobe), trunk length (TRL, from base of hemipenis to basal region of lobe), sulcus spermaticus width (SSW, in widest section of sulcus spermaticus) and spermaticus lips width (SLW, in widest section of spermaticus lips).

Molecular data and phylogenetic analyses

We complemented with new samples the existent dataset for *Phyllopezus* genus of partial sequence data from two mitochondrial genes: cytochrome b (cytb) and NADH dehydrogenase subunit 2 (ND2). We included 17 new samples from specimens *P. pollicaris* from four locations in Northeast of Brazil (see Appendix II for GenBank accession numbers, vouchers, and localities). The DNA extraction methods, amplification protocols, primers used and regions of the gene follow the same methods used and described by Werneck et al. (2012). All DNA sequences were obtained by Dra. Fernanda Werneck and she will be the coauthor of this manuscript from the next stages of its development.

The sequences obtained were aligned with other 404 representatives of all *Phyllopezus* species available on GenBank (the entire database for the most complete phylogeny for genus [available in Werneck et al., 2012] and information about additional sequences is available in Appendix II) using MAFFT software v7.310 and default parameters (Katoh & Standley, 2013). Additionally, representatives of the phyllodactylids *Phyllodactylus* and *Homonota* (distributed in the New World) and *Tarentola* (only species distributed in Old World) were included as external groups (Gamble et al., 2011). Genetic distances within and between clades were then estimated using p-distance (p-D) with complete deletion of gaps, implemented in MEGA software v.7.0.26 (Tamura et al., 2013).

A Maximum Likelihood Analysis was carried out with the set of concatenated mitochondrial genes in the RAxML v.8.2.12 software (Stamatakis, 2006) implemented in the online platform CIPRES v.3.3. The choice of the best evolutionary model for the character matrix was performed in the PartitionFinder software v.2.1.1 (Lanfear et al., 2012) using the Bayesian Information Criterion (BIC) and default settings. The analysis consisted of 100 independent searches of maximum likelihood and 1,000 replicates of non-parametric bootstraps to test the support of the clusters. The majority consensual tree was visualized using the FigTree software v.1.3.1 (Rambault & Drummond, 2008). The African phyllodactylid *Tarentola mauritanica* (Linnaeus, 1758) was used for rooting the tree following the phylogenetic proposal of Gamble et al. (2011) and Pyron et al. (2013). Values of bootstrap above 0.70 were considered with high support and are indicated in the tree.

RESULTS

External morphology

The representatives of *P. lutzae* analyzed came almost exclusively from the northernmost distribution of the species (Fig. 1), and do not include important geographic regions, such as the State of Bahia, the type-locality of the species. In addition, the representativeness of specimens from southern Atlantic Forest, south of the São Francisco River, one of the main historical geographical barriers within the current distribution of *P. lutzae*, is very small so far (N = 1), making it impossible to verify the existence of morphological variations in populations in the opposite banks of the River. Regarding the analyzed specimens, *P. lutzae* did not present diagnostic sexual dimorphism in relation to SVL (ANOVA, $F_{1,14} = 2.60$; $P = 0.13$) or shape (MANOVA, $F_{1,14} = 0.81$; $P = 0.56$). In relation to the other morphometric characters, significant dimorphism was found only in IOD, LT and LR (See Table 1). The specimens available of *P. lutzae* present very conserved external morphology (Figs. 2A and 3A) and regional differences or morphogroups were not identified.

In *P. periosus*, sexual dimorphism was also not diagnosed in relation to SVL (ANOVA, $F_{1.76} = 0.52$; $P = 0.47$), despite a representative sample of each sex was available (58♂ and 19♀). However, shape significantly differed between males and females (MANOVA, $F_{1.76} = 2.00$; $P = 0.02$). In the other morphometric characters, significant differences were found in IOD, LH, LTB and TBW (Table 1), the latterwith males presenting

higher values (TBW = 29.6 ± 2.26) when compared to females (TBW = 11.6 ± 1.7). This difference may be associated with the presence of the hemipenis, which is large and robust in *P. periosus* (see "*Hemipenial morphology*" section). The populations of *P. periosus* analyzed present very conserved external morphology throughout its distribution (Figs. 2B and 3B) and regional differences or morphogroups were not identified.

For *P. pollicaris*, two major morphological groups were identified. Among the observed differences, stands out differences in size and disposition of the gular scales; shape, size and disposition of the dorsal tubercles; and dorsal color pattern (characteristics described in detail below), in addition to the marked difference in the average SVL (ANOVA, Males $F_{1,134}$ = 198.1; *P* = <0.01; Females $F_{1,124}$ = 143.3; *P* = <0.01; Fig. 4; Table 2). Such morphological variation presents a certain geographical congruence, being the first morphogroup (hereafter referred as *P. pollicaris* A) composed predominantly of populations located further east in the distribution of *P. pollicaris* in Northeast Brazil, in ecotonal areas of Caatinga or in Atlantic Forest remnants in low or high elevations within the Caatinga biome. The second morphogroup (hereafter referred to as *P. pollicaris* B) is represented by interior (Western) populations, in the Caatinga and Cerrado ecoregions. The PCA based on morphometric characters identified high segregation in the morpho-space, with little overlap between the two morphological groups, both in females and males (Fig. 5A–B). In addition, differences in scale counts (Table 3), shape in females (MANOVA, Females $F_{1,124}$ = 0.74; *P* = 0.05; Table 2) and in most other morphometric characters were identified (Table 2). Thus, from here on, both sexual dimorphism and morphological variation tests in *P. pollicaris* were conducted independently for each morphogroup.

Among the representatives of *P. pollicaris* A, four morphotypes were identified, presenting variation congruent with the geographic distribution and little variation within each morphotype. Those morphotypes are morphologically distinct from each other, especially regarding the arrangement of the dorsal tubercles, dorsal color pattern, proportions of the head and the robustness of the body and limbs. The PCA's with morphometric characters performed only with the representatives of *P. pollicaris* A, recovered clusters in the morpho-space for almost all the morphotypes, with low overlap in both sexes (Fig. 5C–D), although for some morphotypes the sample was reduced or there were no representatives available for one of the sexes.

The first morphotype (*P. pollicaris* A1; Figs. 3C and 6A) is distributed in the Atlantic Forest and transition areas (*Agreste* region) of the State of Alagoas (municipalities of Boca da Mata, Limoeiro de Anadia, Coruripe, Igaci, Quebrangulo and Traipú), and was also identified

in a locality of Caatinga in the State of Pernambuco – the Catimbau National Park, municipality of Buíque and in a *brejo de altitude* in the municipality of Areia, in the hinterlands of State of Paraíba (Fig. 7). The other three morphotypes are distributed in locations in the state of Bahia: the second morphotype (*P. pollicaris* A2; Fig. 6B) is from the northern portion of the *Serra do Espinhaço* Mountain Range, in the Chapada Diamantina National Park, municipality of Mucugê (Fig. 7); the third morphotype (*P. pollicaris* A3; Figs. 3D and 6C) is from *Serra da Jiboia*, a mountain range located in the southern portion of the *Recôncavo Baiano*, municipality of Elísio Medrado (Fig. 7); and the fourth morphotype (*P. pollicaris* A4; Figs. 3E and 6D), represented by a single individual, was collected in the municipality of Condeúba, in the south of the Bahia state (Fig. 7).

Representatives of *P. pollicaris* A have proportionally shorter members (LH+LF/SVL = 0.33; LT+LTB/SVL = 0.37); larger dorsal tubercles, corresponding to about six granules, elongated and generally slightly keeled; dorsal color pattern in irregular, semi-regular cross bars or forming semi-continuous longitudinal lines; absence of a light cervical band delimiting the dark bars; wider head (HW/HL = 0.71); in most specimens (96%) the mental scale does not extend beyond the anterior margin of the second infralabial (Fig. 9C–E); elongated postmental scales (Fig. 9C-E); first rows of reduced scales that surround the enlarged scales of the postmental region do not extend beyond the posterior margin of the third infralabial (Fig. 9C-E); first and second infralabial of the same width (Fig. 9C–E); and larger size (females 72.38–101.6 mm, males 75.97–108.44 mm). Only *P. pollicaris* A2 showed significant sexual dimorphism in relation to SVL (ANOVA, $F_{1.10} = 5.43$; $P = 0.04$) and in most other morphometric characters (Table 2). However, for *P. pollicaris* A3 and A4, dimorphism tests were not performed because they presented few or no samples for one sex (≤ 1). Sexual color dimorphism was not identified in any of the morphotypes. Differences and variations in the other morphometric characters and scale counts are provided in Table 3. Main differences between *P. pollicaris* A morphotypes are described below.

Phyllopezus pollicaris A1 can be distinguished from the other representatives of its respective morphogroup (between parentheses) because it presents coloration in semi-regular transverse bars that can form semi-continuous longitudinal lines (coloration in irregular bars and/or never forming longitudinal lines; Fig. 6), absence or up to two tubercles in angular region between the upper and lower edges of the opening of the auditory meatus and eyes (more of four tubercles in this region), presence of increased scales on the upper and lower sides of the labial commissure (homogeneous scales of the same size in this region) and absence of postcloacal pores in most specimens [75%] (absent in *P. pollicaris* A4, always

present in the others). *Phyllopezus pollicaris* A2 can be distinguished by presenting longer head [HL/HW = 1.5] (shorter [HL/HW = 1.3]), shorter trunk [DBL/SVL = 0.41] (longer [DBL/SVL = 0.44]), longer snout [SL/HL = 0.42] (shorter [SL/HL = 0.40]). *Phyllopezus pollicaris* A3 can be distinguished by having a short postmental central pair (twice longer than wide), a central scale that surrounds the postmentals, the one that contacts both postmentals, increased, about two times larger than the others (of similar sizes), coloration in irregular and sparse bars (coloration in regular or semi-regular transverse bars; Fig. 6). *Phyllopezus pollicaris* A4 can be distinguished by presenting dorsal stains in semi-regular transverse bars with well-demarcated posterior margin, becoming lighter previously (stains of irregular bars and/or with homogeneous dark spots; Fig. 6), three postmental scales in contact with the mental (two postmental scales), absence of postcloacal pores (absent in most *P. pollicaris* A1, always present in the others).

Representatives of *P. pollicaris* B have less expressive external morphology variation among morphotypes when compared to the morphotypes of the morphogroup *P. pollicaris* A. However, morphological variations were observed and five morphotypes could be defined. The main differences observed among the morphotypes are related to the robustness of the body, limbs, neck and tail, proportion of the limbs and snout, shape of the scales of the auditory meatus, and the presence and number of postcloacal tubercles. The PCA's with morphometric characters performed with the representatives of *P. pollicaris* B presented great overlap in most of the morphotypes, mainly in males. However, there was some segregation in relation to the far north morphotypes (*P. pollicaris* B4 and B5) compared to the southernmost representatives (Fig. 5E-F). In the DFA's with morphometric characters a greater segregation was recovered between the morphotypes of *P. pollicaris* B and, although there is overlap in the morpho-space, DF1 successfully discriminated against representatives of *P. pollicaris* B1 and B2 in relation to the other morphotypes, while DF2 successfully discriminated representatives of *P. pollicaris* B1 in relation to *P. pollicaris* B2 (Fig. 5G–H).

The first morphotype (*P. pollicaris* B1; Figs. 3F and 8A) is from Caatinga areas in the south of the São Francisco River in the states of Sergipe (municipalities of Porto da Folha, Poço Redondo and Canindé do São Francisco) and Bahia (municipalities of Paulo Afonso and Curaça; Fig. 7). The second morphotype (*P. pollicaris* B2; Figs. 3G and 8B) is from areas of Caatinga in regions close to the north bank of the São Francisco River in the State of Alagoas (municipality of Delmiro Gouvêia, Piranhas and Água Branca), being also identified in a locality of Caatinga in the State of Pernambuco – National Park of Catimbau, municipality of Buíque, where it co-occurs with *P. pollicaris* A1 (Fig. 7). The third morphotype (*P. pollicaris*

B3; Figs. 3H and 8C) is from mountain ranges and rock formations in the states of Piauí and Maranhão (e. g. *Serra das Confusões*, *Serra da Capivara*, see Appendix I for a complete list of locations), areas in western Caatinga and in ecotones with the Cerrado and Amazon ecoregions (Fig. 7). The fourth morphotype (*P. pollicaris* B4; Figs. 3I and 8D) is distributed in rock formations in the state of Ceará and in the northwest of the State of Pernambuco (Fig. 7; Appendix I). The fifth morphotype (*P. pollicaris* B5; Figs. 3J and 8E) is widely distributed in the northeast of the Caatinga, in the states of Rio Grande do Norte, Paraíba and Pernambuco, and is also recorded in some transition areas with the Atlantic Forest ecoregion (Fig. 7; Appendix I).

Representatives of *P. pollicaris* B have proportionally longer members (LH+LF/SVL = 2.71; LT+LTB/SVL = 3.32); smaller dorsal tubercles, corresponding to about four granules, subcircular or elliptical, with no keels; staining dorsal pattern in irregular transverse bars delimited medially by a light cervical band; narrower head (HW/HL = 0.71); mental scale reaching or exceeding the anterior margin of the second infralabial (Fig. 9F-H); postmental scales of similar width and length (Fig. 9F–H); first rows of reduced scales that surround the enlarged scales of the postmental region always extending beyond the posterior margin of the third infralabial (Fig. 9F-H); second infralabial wider than the first (Fig. 9F–H); and smaller size (females 55.93–87.11 mm, males 58.89–88.68 mm). Differences and variations in the other morphometric characters and scale counts are given in Table 3. No morphotype showed significant sexual dimorphism in relation to SVL (ANOVA, $P > 0.05$ in all comparisons). However, in relation to shape, all morphotypes presented significant sexual dimorphism (MANOVA, $P \leq 0.02$; Table 1). Sexual color dimorphism was not identified in any of the morphotypes. Significant values for others morphometric characters are provided in Table 2. Differences and variations in the other morphometric characters and scale counts are provided in Table 3. Main differences between *P. pollicaris* B morphotypes are described below.

Phyllopezus pollicaris B1 can be distinguished from the other representatives of its respective morphogroup (between parentheses) because it presents more robust body (robust in *P. pollicaris* B5, slender in the others); wider neck region, with width similar to the maximum width of the head (slightly narrower in *P. pollicaris* B4 and B5, narrow in the others), rostral remarkably divided (little divided or not divided), smaller size [up to 81.25 mm] (larger size [up to 88.68 mm]). *Phyllopezus pollicaris* B2 can be distinguished because it presents very slender (more robust) body and limbs, narrower head [HW/HL = 0.70] (wider [HW/HL = 0.72–0.74]). *Phyllopezus pollicaris* B5 can be distinguished because it presents a natural thickening of the tail just after the region of the autotomy point (without enlargement),

up to four [in 20% of specimens; Fig. 9H] postmental scales (up to three in the others; Fig. 9F-G).

Hemipenial morphology

The descriptions of hemipenial morphology for *Phyllopezus*are presented below, followed by the differences noticed in each nominal taxon or morphogroup. Only representatives of the nominal taxa *P. periosus* and *P. pollicaris* had the hemipenial preparations available, and their morphology was characterized herein. For *P. pollicaris*, only two of the morphotypes (one belonging to each identified morphogroup) were characterized (*P. pollicaris* A1 and *P. pollicaris* B2).

The hemipenis of *Phyllopezus* species are characterized by hemipenial body longer than wide, bilobed, capitulated or not, Y or T-shaped, ending in two large and symmetric lobes. The hemipenial body long, smooth and cylindrical, unadorned, with thin and transparent skin. Sulcus spermaticus single, longitudinal, varying in width and depth, starting at the base, extending in the middle of the lobular fork and reaching to the apical region of the hemipenial body, being visible or not on the asulcate face. Although the hemipenis body is bilobed the sulcus spermaticus does not branch in the lobular fork. The semen dispersion for the lobes can occur through some shallow depressions present in the lobes. Spermatic lips broad and poorly developed, represented by a thickening of skin on the margins of the sulcus spermaticus, and extending from the base of the hemipenis to the base of the lobes. The lobes are arranged almost perpendicular to the longitudinal axis of the hemipenis and in opposition to each other. Short lobe represents about 20% of the total length of the hemipenis. Dermal folds on the walls of the lobes chalice-shaped,differing in size and development from the vertical walls of chalices. Each lobe has a cylindrical shape, wider than longer.

The main differences identified between taxa or morphogroups are related to the shape and disposition of the lobes, presence of capitulation and chalices, width, depth and disposition of the sulcus spermaticus and spermaticus lips thickness. Below we described the interspecific variations and between the analyzed morphotypes.

Phyllopezus periosus (N = 2; Fig. 10A): (CHUFPE) CAT416 – Catimbau National Park, municipality of Buíque, Pernambuco state; MUFAL 12431 – Estação Ecológica do Seridó, municipality of Serra Negra do Norte, Rio Grande do Norte state. HPL 135.5 mm, HPW 41.6 mm, LL 22.9 mm, LW 43.5 mm, TRL 92.0 mm, SSW 1.0 mm, SLW 7.9. Hemipenial body longer than wide (HPL/HPW = 3.11), capitulated, with slightly Y-shaped.

The hemipenial body long (TRL/HPL = 0.67) and unadorned. Sulcus spermaticus narrow and shallow (SSW/TRW = 0.02), being visible on the asulcate face. The sulcus spermaticus presents a slight narrowing in the region between the lobes. Spermatic lips broad (SLW/TRW = 0.18) and poorly developed. Lobe short, representing about 16% of the total length of the hemipenis (LL/HPL = 0.16), being wider than the hemipenial body (LW/TRW = 1.04). Lobe wide than longer (LW/LL = 1.89). Small calyces on the walls of the lobes. The apex of the lobe is almost flat, showing some depressions that communicate with the sulcus spermaticus. On the lower portion of each lobe there is a wide and deep sulcus capitular that delimits the wall of the hemipenial body and connects on the asulcate face with the termination of the sulcus spermaticus and on the sulcate face it is delimited by the spermatic lips.

Phyllopezus pollicaris **A1** (N = 2; Fig. 10C): MUFAL 12168, 12400, Mata da Barra do Tamanduá, municipality of Limoeiro de Anadia, Alagoas state. HPL 100.4 mm, HPW 30.2 mm, LL 24.5 mm, LW 32.3 mm, TRL 69.9 mm, SSW 3.3 mm, SLW 7.3. Hemipenial body longer than wide (HPL/HPW = 3.10), non-capitulated, slightly T-shaped, hemipenial body extending after insertion of the lobes. The hemipenial body is long (TRL/HPL = 0.69), with remarkable calycular ornamentations in its upper portion both on the asulcate face and at the apex of the body. Sulcus spermaticus wider and deeper at the base of the hemipenial body and narrowing towards the apex (SSW/TRW = 0.11). Spermatic lips developed throughout its length, slightly wider near the base of the hemipenis, extending from the base of the hemipenis to the locular crotch. Lobe short, represents 24% of the total length of the hemipenis (LL/HPL = 0.24), narrower than the hemipenial body (HPW/TRW = 1.06). Lobe wider than longer (LW/LL = 1.31). Enlarged calyces on the walls of the lobes, with vertical walls of calyces developed, distinctly larger on the asulcate face. The apex of the lobe is rounded, showing some depressions that communicate with the sulcus spermaticus.

Phyllopezus pollicaris **B2** (N = 1; Fig. 10B): (CHUFPE) PMSN920, Wildlife Refuge Morros do Craunã e do Padre, municipality of Água Branca, Alagoas state. HPL 74.3 mm, HPW 20.5 mm, LL 13.8 mm, LW 20.8 mm, TRL 54.2 mm, SSW 2.4 mm, SLW 5.5. Hemipenial body longer than wide (HPL/HPW = 3.56), non-capitulated, slightly T-shaped, hemipenial body extending after insertion of the lobes. The hemipenial body is long (TRL/HPL = 0.72), unadorned. Sulcus spermaticus wider and deeper at the base of the hemipenial body and narrowing towards the apex (SSW/TRW = 0.11), starting at the base of the hemipenial body and extending to the apical region. In the region between the lobes, the sulcus spermaticus is very narrow and the spermaticus lips come into contact, forming a channel that opens at the apex of the hemipenial body, close to the region of the lobular fork.

Spermatic lips developed, twice wider near the base of the hemipenis and progressively narrowing to the region of the lobular fork. Spermatic lips extend from the base of the hemipenis to the base of the lobes. Lobe short, represents about 18% of the total length of the hemipenis (LL/HPL = 0.18), narrower than the hemipenial body (HPW/TRW = 1.01). Lobe wider than long (HPW/LL = 1.50). On the walls of the lobes are small dermal folds in calycular shape, aproviding a striated texture. The apex of the lobe is rounded, showing some depressions that communicate with the sulcus spermaticus.

Molecular data and phylogenetic analyses

The final mitochondrial dataset included 1,785 base pairs (Cytb = 909 bp; ND2 = 878 bp) for 426 samples, of which 17 were obtained in this study. The best evolutionary model selected for the dataset was GTR + G. The topology obtained by the concatenated mitochondrial phylogenetic tree based on the Maximum Likelihood analysis (Fig. 11) recovered the monophyly of the genus *Phyllopezus* with high statistical support (Bootstrap = 1.0) in relation to the other genera of Phyllodactylidae included in the analysis. *Phyllopezus periosus* was recovered as the sister of the remaining lineages in the genus (Bootstrap = 0.86), showing high statistical support and little genetic divergence between the co-specific sequences (N = 12) and localities (N = 4) (Bootstrap = 0.99).

Phyllopezus maranjonensis and *P. lutzae* were represented by a single sequence each of the ND2 gene. Although with low statistical support, *P. maranjonensis* was recovered as the sister (Bootstrap = 0.45) to the clade including *P. lutzae* and all representatives of *P. pollicaris* complex (Bootstrap = 0.26). The *P. pollicaris* species complex, although monophyletic, presented low statistical support (Bootstrap = 0.52). The internal relationships among the sequences belonging to this complex did not differ from those presented by Werneck et al. (2012) and all previously identified clades were recovered in our topology (Clades I–VIII).

Phyllopezus heuteri (not included in the topology of Werneck et. al. [2012]) was recovered as monophyletic, with high statistical support (Bootstrap = 1.0). However, *P. heuteri* was nested within the paraphtletic *P. przewalskii*. The sequences of *P. heuteri* were recovered as a sister lineage to the populations of *P. przewalskii* of the Chaco biome in Paraguay and Argentina, although this group presented low statistical support (Bootstrap = 0.56). The clade formed by *P. heuteri* + populations of *P. przewalskii* of Chaco was recovered

as the sister group to the populations of *P. przewalskii* from Cerrado (State of Mato Grosso do Sul, Brazil), with high statistical support (Bootstrap = 0.99).

The 17 new sequences obtained here, including the two new localities (municipality of Santa Quitéria, Ceará state [N = 2] and municipality of Serra Talhada, Pernambuco state [N = 1]), were all recovered in the strongly supported clade that includes most of the Caatinga locations (Bootstrap = 0.70; Clado VIII).

DISCUSSION

Morphological approach

External morphology

Representatives of *P. pollicaris* showed high morphological variation. Two main morphological groups were identified, being easily diagnosed by morphometric, meristic characters and dorsal color patterns. The first morphogroup (*P. pollicaris* A) is morphologically very distinct from the representatives previously characterized of the *P. pollicaris* complex (Spix, 1825; Koslowsky, 1895; Müller & Brongersma, 1933; Vanzolini, 1953; Cacciali et al., 2018). Among the observed differences, stands out differences in size and disposition of the gular scales; shape, size and disposition of the dorsal tubercles; and dorsal color pattern, and the marked difference in the average SVL. In addition to the morphological discrepancy, these populations have a distribution largely associated with regions of the Atlantic Forest and transition areas (*Agreste* region) in Northeast Brazil. This differs from the standard commonly described for *P. pollicaris* sensu lato and formally described species of the *P. pollicaris* complex (*P. przewalskii* and *P. heuteri*), which are associated with the dry diagonal formations of South America (Werneck et al., 2012; Cacciali et al., 2018).

The second morphological group (*P. pollicaris* B) has a more conserved and similar morphology to that described for *P. pollicaris* stricto sensu (Spix, 1825; Müller & Brongersma, 1933), *P. heuteri* and *P. przewalskii* (Koslowsky, 1895; Vanzolini, 1953; Cacciali et al., 2018). Representatives of *P. pollicaris* B share with the other nominal species of the complex, characteristics such as number, size and disposition of the gular scales, dorsal color pattern, number, size and shape of the dorsal tubercles and body size. Such variation among the two morphogroups identified here may indicate a deep diversification among these

populations in the Northeast of Brazil, and although geographically closer to *P. pollicaris* A populations (presenting areas of co-occurrence), the representatives of *P. pollicaris* B may be more related to the populations of the complex that occur in Cerrado and Chaco.

The representatives of *P. periosus* analyzed come from almost all the known distribution, however, the currently known distribution this species may be overestimated. Although it is considered to be widely distributed from the state of Ceará to the state of Bahia (Koch et al., 2006; Cacciali et al., 2018; Uetz & Hosek, 2021), so far, its southern distribution in Northeast Brazil has been confirmed only for the state of Pernambuco, 455 km north of the the southernmost registration point in the Bahia state. The photographs and/or specimens attributed to *P. periosus* in localities between Alagoas and Bahia (all in Atlantic Forest areas) are probably representatives of *P. pollicaris* A, who may have been mistakenly associated with *P. periosus* due to the large size and dorsal color pattern in cross bars (Carvalho et al., 2005; Couto-Ferreira et al., 2011; Gonçalves, 2012; Roberto et al., 2015). If these records are in fact *P. pollicaris* A, it also reinforces the strong association of this morphogroup of *Phyllopezus* with areas of Atlantic Forest in the Northeast of Brazil.

Hemipenial morphology

Phyllopezus has a long hemipenian body and a massive apex, ending in two lobes, pattern found in most Gekkota (Böhme, 1988; Rösler, 1998; Das & Purkayastha, 2012; Brennan & Bauer, 2017). The hemipenial morphology of *Phyllopezus* is similar to that described for representatives of Gekkonidae, the most phylogenetically related family (Gamble et al., 2011), sharing characteristics such as thin skin, lobes arranged parallel to the axis of the sulcus spermaticus, covered by chalices and devoid of additional ornamental structures such as fringes and thorns (Das & Purkayastha, 2012). The descriptions of hemipenial morphology for *Phyllopezus* presented here are the first for the genus and indicates the hemipenis as potential source of diagnostic information for distinguishing different lineages within the group. However, a larger number of samples is still necessary to confirm that these characteristics represent a pattern within the morphotypes. Additionally, the general morphology of the *Phyllopezus* hemipenis presents striking difference in comparison with those known for other Gekkota species, revealing great potential in systematic studies (Böhme, 1988; Rösler, 1998; Das & Purkayastha, 2012; Brennan & Bauer. 2017).

Despite this, the knowledge about the Gekkota hemipenian morphology is still incipient. Although for several species of Gekkonidae significant advances in the description of hemipenial morphology have been obtained in the last decades (Böhme, 1988; Rösler, 1998; Glaw et al., 2006; Rösler & Böhme, 2006; Das & Purkayastha, 2012), in relation to the other two New Word geckos' families little is known. For Sphaerodactylidae, a few species present the hemipenial morphology described (Batista et al., 2017; Meneses-Pelayo & Ramírez, 2020), and for Phyllodactylidae, there was not formal hemipenian description available until now. Thus, the new information presented herein represents an important advance in the knowledge of the hemipenial morphology of the New World phyllodactylids.

Molecular approach

Phylogenetic inference

Phyllopezus was recovered monophyletic, with high statistical support, in relation to the other genera of phyllodactylids included in the analysis. These results corroborate the hypothesis of monophyly proposed in previous studies involving the different lineages within Gekkota (Gamble et al., 2008, 2011) and even in more comprehensive phylogenetic hypotheses (Pyron et al., 2013).

The cluster of *P. periosus* sequences (N = 12) showed high statistical support and low intraspecific genetic divergence being recovered as sister of all other species. Incongruencies about the phylogenetic positioning of *P. periosus* have been identified in previous studies. Gamble et al. (2012), recovered the same relationships identified here using a dataset concatenated with different nuclear (RAG 1, RAG 2, C-MOS, ACM4 and PDC) and mitochondrial (16S rRNA) markers. However, Cacciali et al. (2018) recovered different phylogenetic arrangement using three mitochondrial markers (16Sr RNA, Cytb and ND2). In the Baeysian Inference analysis, they recovered *P. periosus* [N = 4] as the sister clade to the *P. pollicaris* complex. But, using the same dataset, the authors recovered *P. periosus* as the sister lineage to a clade composed of *P. lutzae* and *P. maranjonensis* in a species tree inference analysis. This instability in the relationships regarding the phylogenetic placement of *P. periosus* may be an artifact of the low number of samples in the forementioned studies and the presence of different signatures contained in different genomes. To these relationship hypotheses, there is still a need of a broader sampling, both in the number of individuals and in the number of markers.

Phyllopezus maranjonesis was recovered as a sister clade of the remaining species, followed by *P. lutzae*, these relationships showed low nodal support (Botstrap < 0.70). Unlike the topology presented here, *P. maranjonensis* and *P. lutzae* have been recovered as sister lineages strongly supported, in previous studies that used a greater number of markers and individuals (Gamble et al., 2011, 2012; Cacciali et al., 2018; Dubeux et al., in preparation – Chapter 2 of this Dissertation). Herein, the non-recovery of the clade formed by *P. lutzae* and *P. maranjonensis* probably reflect an artifact due our limited sampling (both species were represented by a single individual each and with information available only for the ND2 gene).

The *P. pollicaris* species complex, was recovered monophyletic in our analyzes, with low statistical support. The relationships among the major genetic lineages of the complex did not differ significantly from those previously identified (Werneck et al., 2012). The new sequences added in the topology, included two locations never sampled, and they nested within Clade VIII.

In addition, the topology recovered with the inclusion of the newly described *P. heuteri*, made *P. przewalskii* paraphyletic (Fig. 11B). The monophyletic reciprocity of these two nominal taxa was strongly supported by mitochondrial markers, including both used in this study (Cacciali et al., 2018). However, the 16SrRNA gene (marker not evaluated in the present study) was the one that presented more information on the recovery of these lineages (Cacciali et al., 2018; Dubeux et al., In preparation – Chapter 2 of this Dissertation). The paraphyly of *P. przewalskii* in relation to *P. heuteri* may be an artifact of the lack of information contained in the genes used here, and reinforces the importance of the information contained in the 16SrRNA gene for the understanding of *Phyllopezus* phylogenetic relationships, especially in relation to the most recent lineages (Gamble et al., 2012; Cacciali et al., 2018).

Integrative approach

The representatives of the two putative lineages of *P. pollicaris* with localities analyzed here (Clade I [*P. pollicaris* A2, Fig. 6B] and Clade VIII [*P. pollicaris* B, Fig. 8]; Fig. 11) showed substantial morphological distinctiveness, and multiple diagnostic characteristics were found. The morphological distinctiveness between these two morphotypes is congruent with the high genetic divergence between these lineages (12.4%-14.3%). Likewise, the morphological and molecular data are also congruent in diagnosis of

the representatives of *P. pollicaris* A1 (Fig. 6A), which although has not available genetic samples for the genes analyzed here, was recovered as the highly supported sister clade of *P. pollicaris* A2 using the 16S rRNA gene (Dubeux et al. in preparation – Chapter 2 of this Dissertation). The high genetic divergence and the presence of multiple diagnostic morphological characteristics reinforces the need for new taxonomic proposals and these two morphotypes of *P. pollicaris* A (A1 and A2) are already in the process of formal description (Dubeux et al., in preparation – Chapter 2 of this Dissertation).

Two other morphotypes of the morphogroup *P. pollicaris* A (*P. pollicaris* A3 and A4), although morphologically distinct, do not yet have available genetic samples and the representativeness of specimens evaluated for external morphology is still low (N = 1 - 5). Both morphotypes are distributed in the state of Bahia, that present records of four different lineages belonging to the *P. pollicaris* complex in your limits (Clade I, III, VI and VIII; Werneck et al., 2012), but none of the morphotypes is geographically close to a location with molecular information available. The lack of correspondence between specimens and/or localities with genetic and morphological available samples hamper us to determine which lineage a certain morphological group belongs to or possibly to associate the morphotype with a lineage not previously identified. This scenario makes clear the need to incorporate these localities in new genetic studies in order to assess their phylogenetic positions and determine whether the morphological similarity associated with these populations is related to phylogenetic proximity or adaptive convergence.

Five different morphotypes were identified within morphogroup *P. pollicaris* B. Each morphotype is composed of specimens collected on geographically close locations, many of which are arranged in the same mountain range or rock formation. The morphotypes *Phyllopezus pollicaris* B1 and B2 were those with the closest distribution (< 1km apart between the closest localities), however these morphotypes are distributed on opposite banks of the São Francisco River. Although the distribution of morphotypes shows certain congruence with the geographic distribution of these populations, all morphotypes have locations with available genetic vouchers. These sequences are highly nestled in the clade that comprises most locations in the Caatinga (*P. pollicaris* Clade VIII). The topology obtained here presents low resolution within the internal lineages of this Clade VIII, and samples from the same location are recovered at different terminals throughout the clade. These same relationships were obtained by Werneck et al. (2012), who recovered the Clade VIII in one of the most derived positions in topology, presenting more recent diversification in the evolutionary history of the genus (~ 2 Ma). In this way, new sources of evidence (e.g.,

karyotype, niche modeling) as well as the expansion of the current molecular database (new location and markers), is essential to better understand the diversification of these Caatinga lineages.

In addition, representatives of *P. pollicaris* from the municipality of Cabaceiras in the state of Paraíba, were recovered in two different clades (*P. pollicaris* Clades VI and VIII; Fig. 11). Although the genetic vouchers for this location have not been analyzed for external morphology, the representatives of *P. pollicaris* from Cabaceiras (who do not have available genetic data) show great morphological divergence with specimens belonging to *P. pollicaris* Clade VIII from other locations. This specimens of Cabaceiras, together with samples from geographically close locations in the state of Paraíba, Rio Grande do Norte and west of the state of Pernambuco (areas not yet assessed in molecular studies) form a particular morphotype (*P. pollicaris* B5), morphologically diagnosable. The morphological analysis of the genetic representatives of these locations where the sympatric lineages occur becomes essential, to investigate whether the differences observed in the morphology are due geographic variation (in case the analyzed samples belong to *P. pollicaris* Clade VIII) or diagnostic characters between the lineages (if they belong to *P. pollicaris* Clade VI).

The inclusion of sequences of all morphological groups identified here as well nuclear markers are essential pieces for solving this taxonomic puzzle. The presence of lineages with widely disjunct distribution (e. g. *P. pollicaris* Clades II and VI) and the presence of localities with co-occurrence of lineages/morphotypes (e. g. Catimbau National Park, Pernambuco state [*P. pollicaris* Clade VIII and *P. pollicaris* A1] and municipality of Cabaceiras, Paraíba state [*P. pollicaris* Clades VI and VIII) reinforces the need of filling sampling gaps, in order to understand the geographical limits of these lineages and eventual cases of overlap or sympatry in distributions and/or mitochondrial introgression.

In conclusion, the external morphology and hemipenial variations found in *Phyllopezus* matches with the molecular diversity previously identified. Further studies are need to expand geographically and taxonomically the representativeness of the genus.

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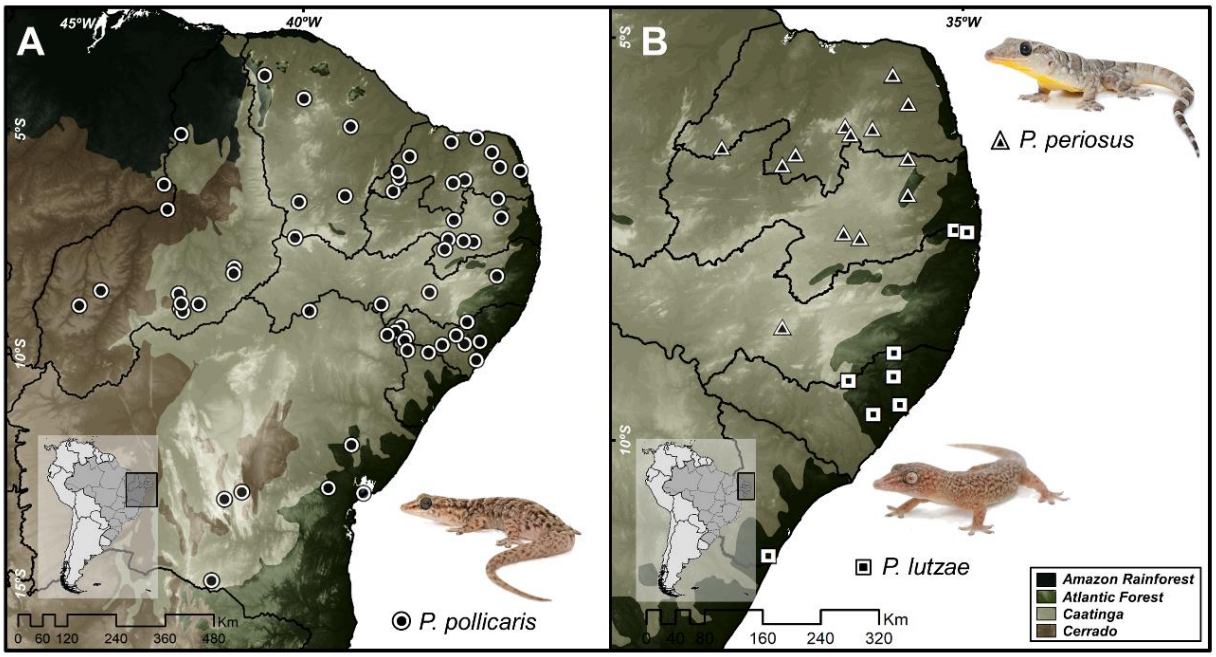


FIGURE 1. Geographic distribution of morphological vouchers analyzed in this study. (A) *Phyllopezus pollicaris*, circles, (B) *P. periosus*, triangles, and *P. lutzae*, squares. Inset map: South America.

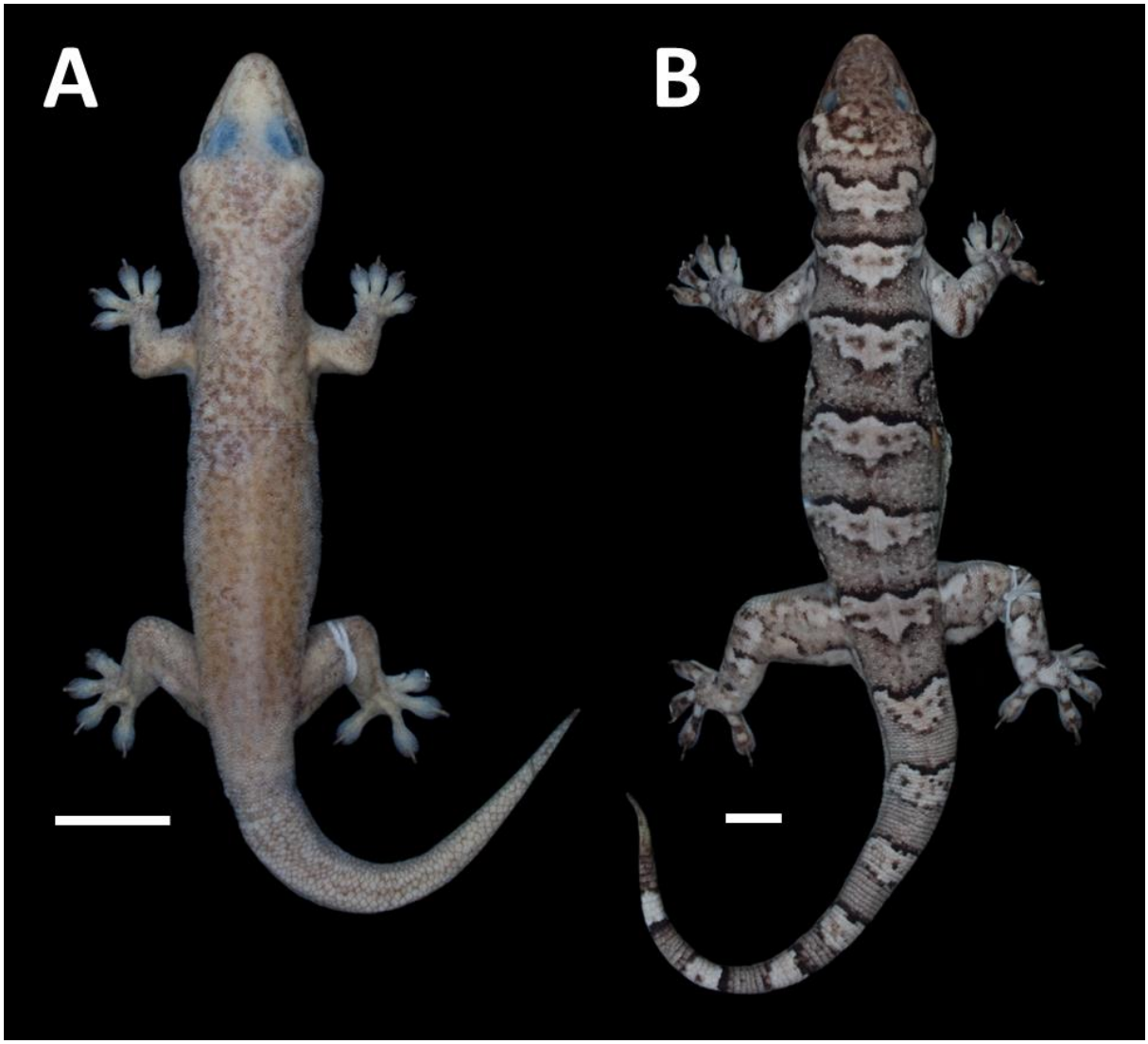


FIGURE 2. General morphology and dorsal color pattern in preservative of (A) *Phyllopezus lutzae* [CHUFPB 19518] and (B) *P. periosus* [MUFAL 12431] representatives. Scale bar = 10mm.

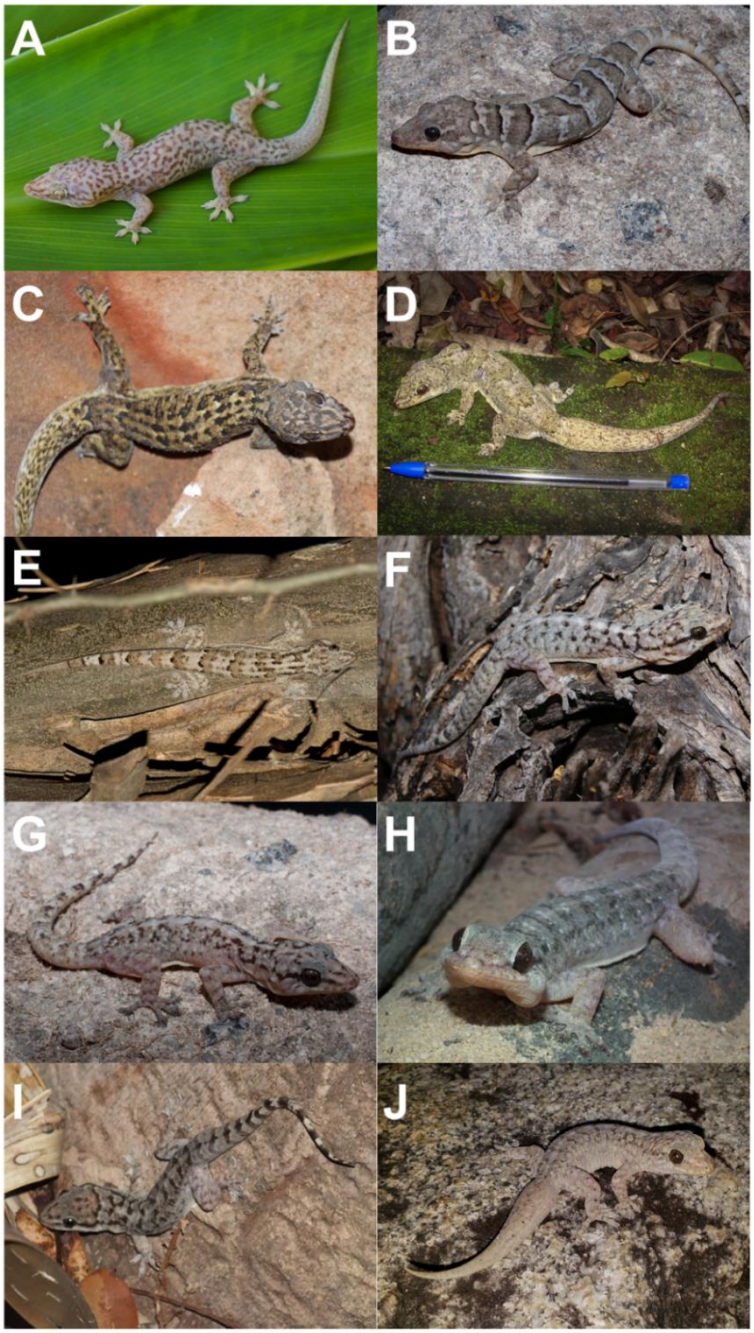


FIGURE 3. General morphology and dorsal color pattern in life of representatives of (A) *Phyllopezus lutzae* [municipality of Maceió, Alagoas state], (B) *P. periosus* [municipality of Serra Negra do Norte, Rio Grande do Norte state], (C) *P. pollicaris* A1 [municipality of Boca da Mata, Alagoas state], (D) *P. pollicaris* A3 [municipality of Elísio Medrado, Bahia state], (E) *P. pollicaris* A4 [municipality of Condeúba, Bahia state], (F) *P. pollicaris* B1 [municipality of Curaça, Bahia state], (G) *P. pollicaris* B2 [municipality of Piranhas, Alagoas state], (H) *P. pollicaris* B3 [municipality of Gilbués, Piauí state], (I) *P. pollicaris* B4 [municipality of Crato, Ceará state], (J) *P. pollicaris* B5 [municipality of Venturosa, Pernambuco state]. For *P. pollicaris* A2 photos in life not available from localities with specimens analyzed. Photos: A and C (Ubiratan Gonçalves); D, E and J (Marco de Freitas); H (Sarah Mângia); I (Raquel Soares).

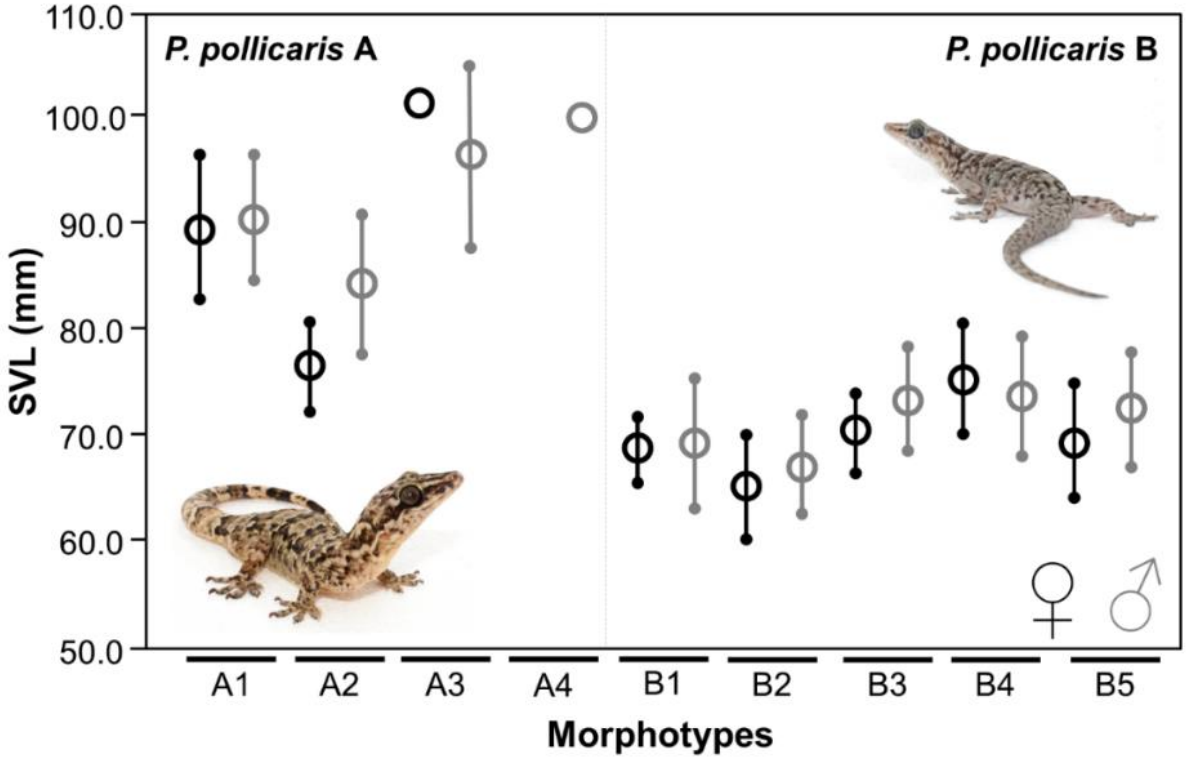


FIGURE 4. Average Snout Vent Length [SVL] in millimeters for females (black) and males (gray) of each morphotype of *Phyllopezus pollicaris* analyzed for Northeast Brazil. Vertical bars correspond to the standard deviation of each sample.

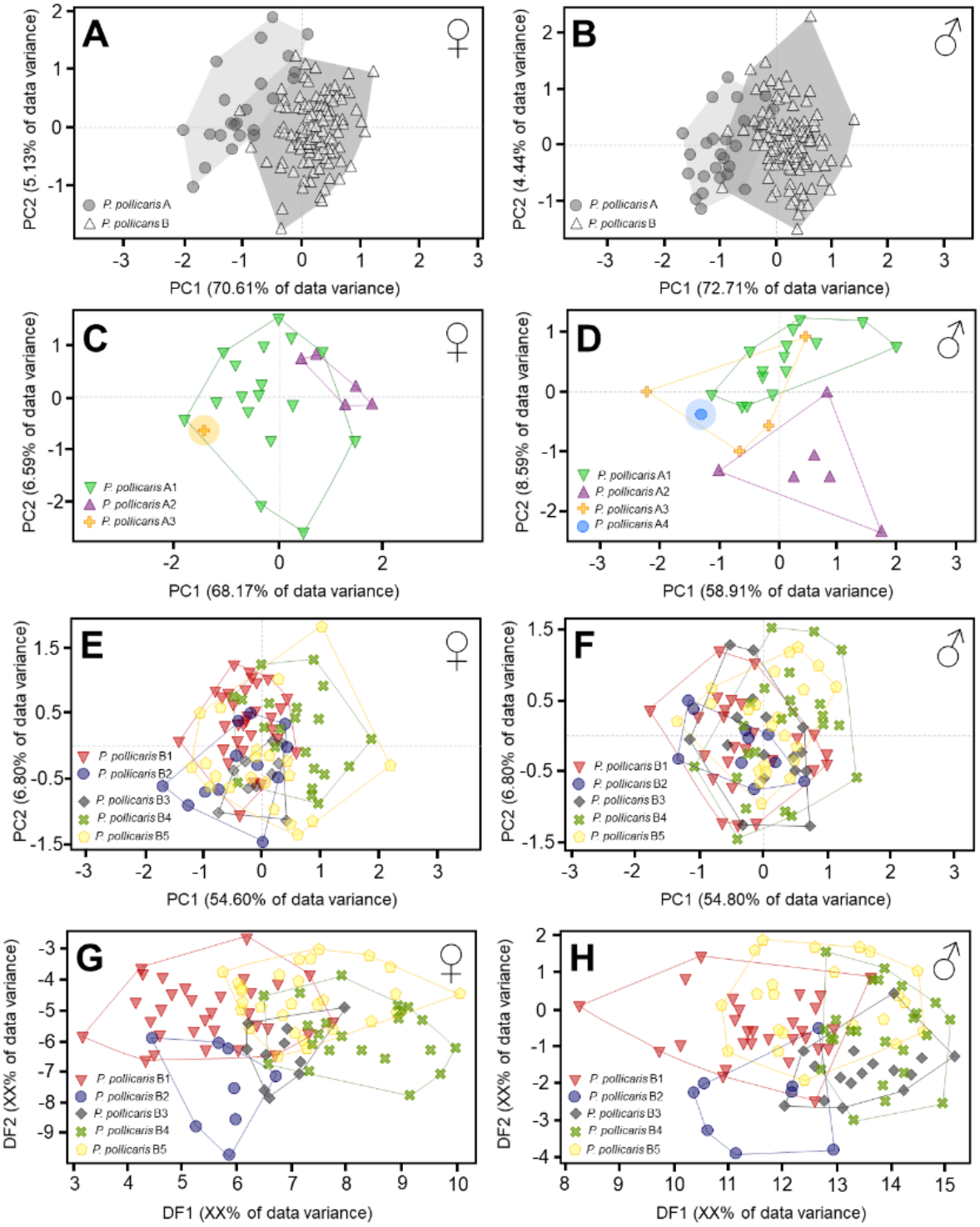


FIGURE 5. Principal Component (A – F) and Discriminant Function (G – H) analysis for females (left) and males (right) based on 20 morphometric characteristics. (A – B) all analyzed populations of *Phyllopezus pollicaris*, (C – D) only the *P. pollicaris* A populations and (E – H) only the *P. pollicaris* B populations occurring in northeastern Brazil. The scores of Principal Components (PC) and Discriminant Functions (DF) are available in Appendix III.

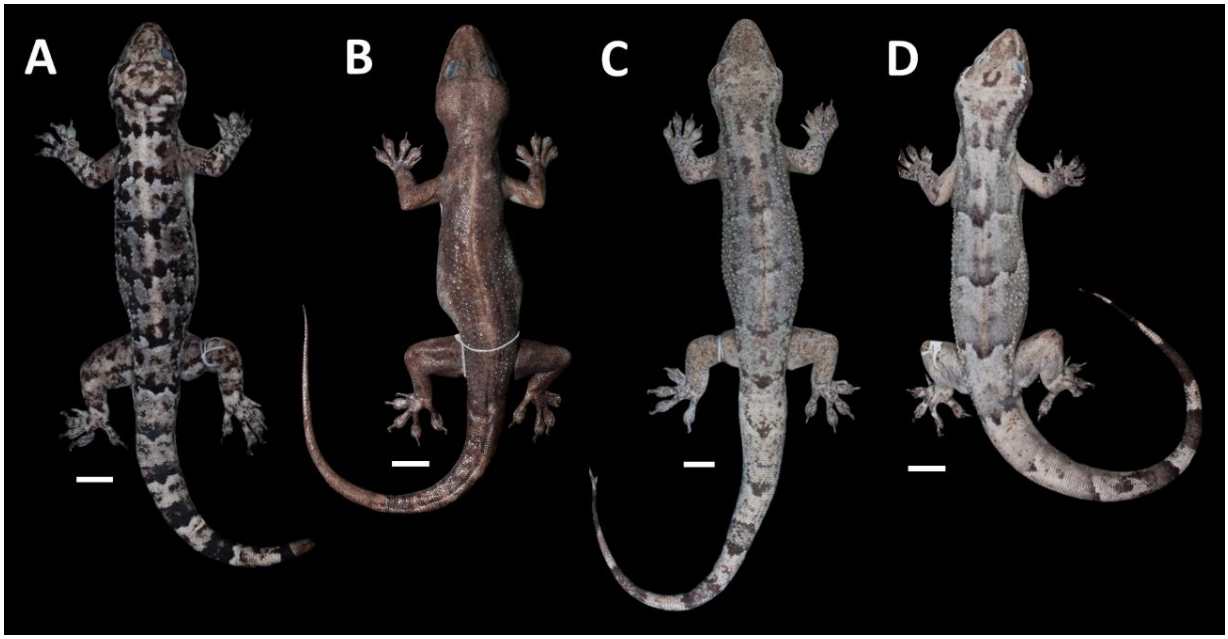


FIGURE 6. General morphology and dorsal color pattern in preservative of (A) *Phyllopezus pollicaris* A1 [♂ MUFAL 12396], (B) *P. pollicaris* A2 [♀ JC 1234], (C) *P. pollicaris* A3 [♂ CHUFPB 20626] and (D) *P. pollicaris* A4 [♂ CHUFPB 25804] representatives. Scale bar = 10mm.

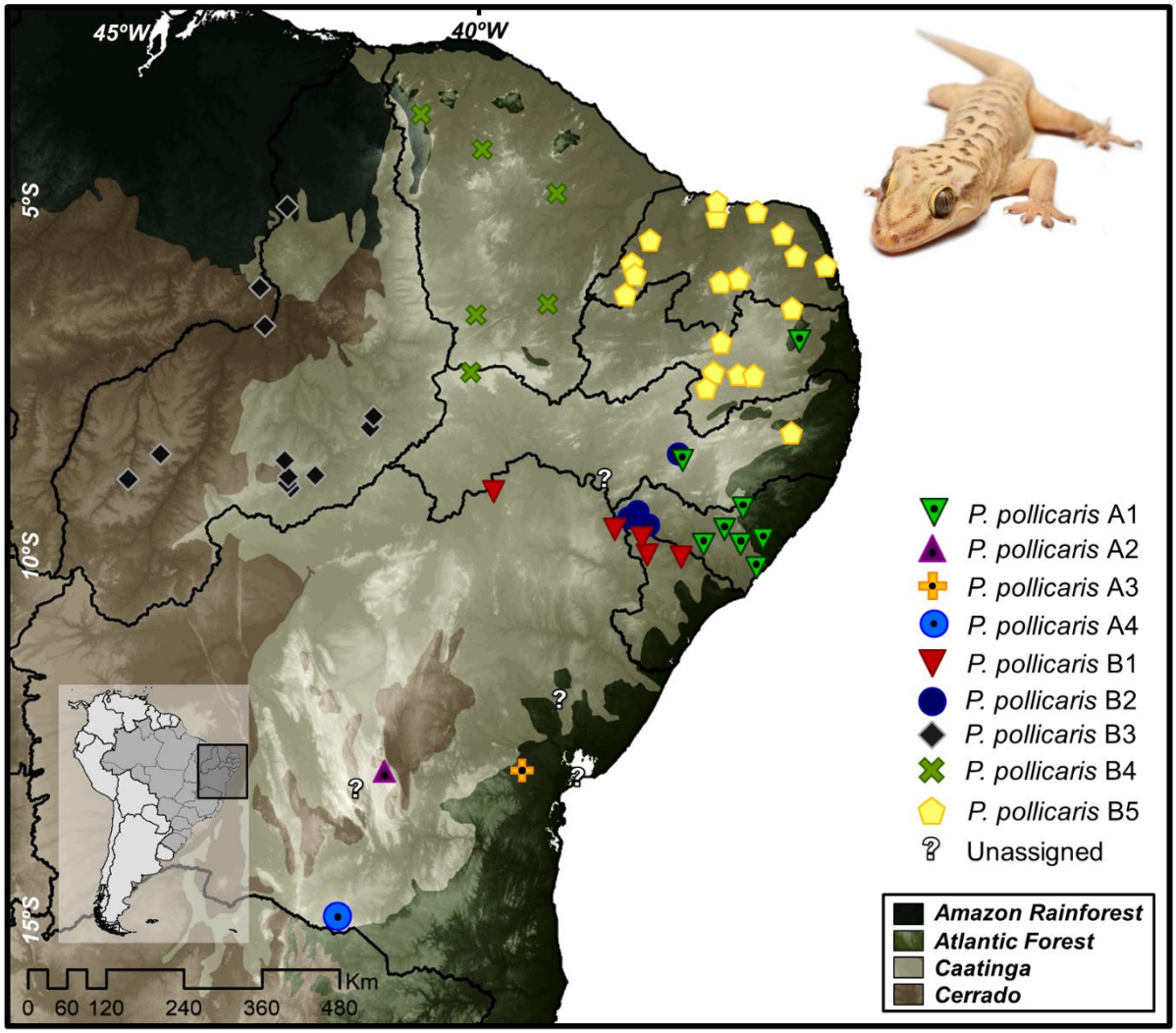


FIGURE 7. Geographic distribution of *Phyllopezus pollicaris* morphotypes identified in northeastern Brazil. Inset map: South America. Black dots denote morphotypes of *P. pollicaris* A.

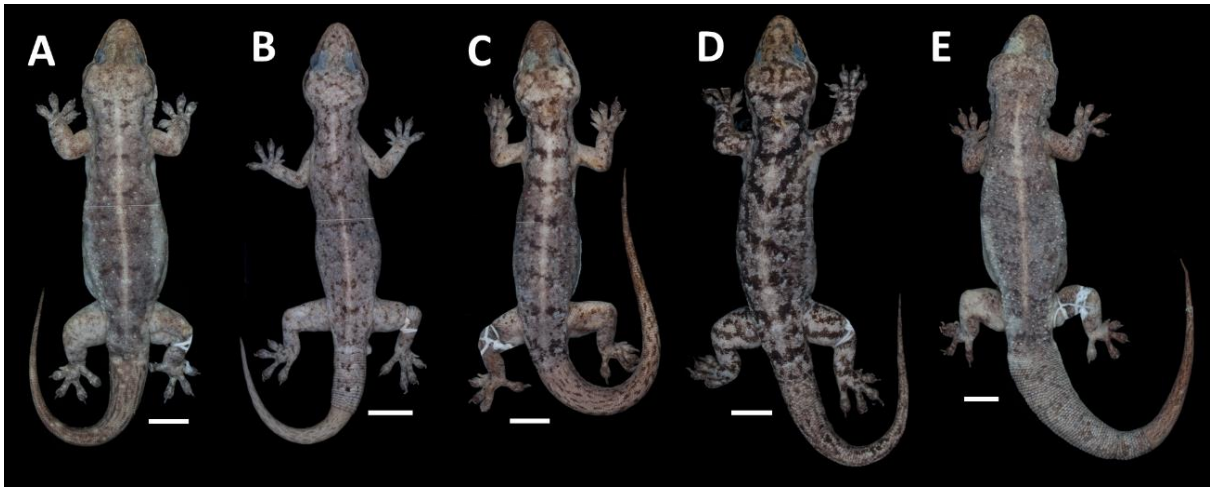


FIGURE 8. General morphology and dorsal color pattern in preservative of (A) *Phyllopezus pollicaris* B1 [♂ CHUFPB 18662], (B) *P. pollicaris* B2 [♂ LABI 643], (C) *P. pollicaris* B3 [♂ CHUFPB 22349], (D) *P. pollicaris* B4 [♂ CHUFPB 17403] and (E) *P. pollicaris* B5 [♂ CHUFPB 10229] representatives. Scale bar = 10mm.

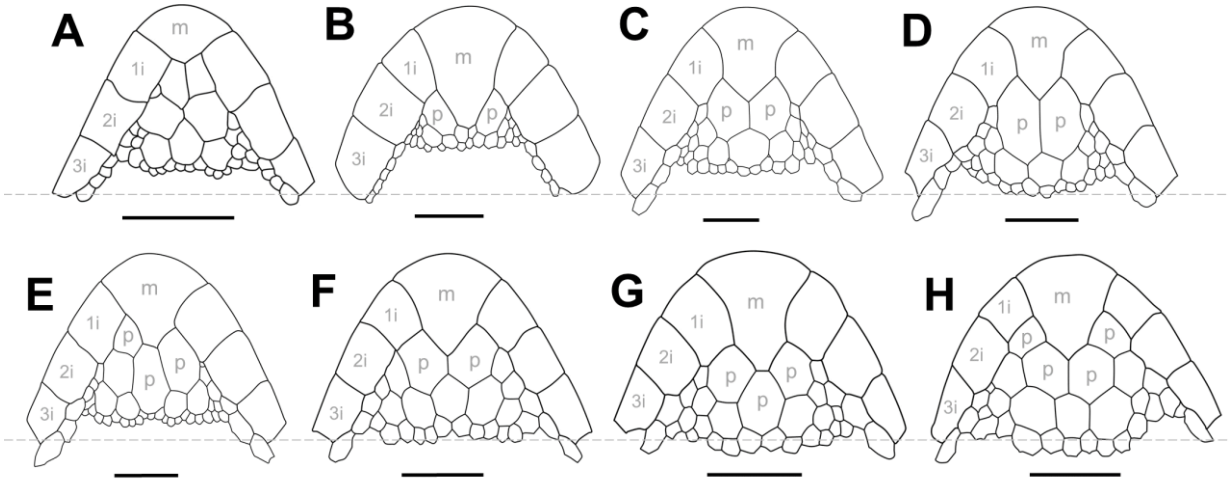


FIGURE 9. Scheme of the main arrangement of scales in the gular region of *Phyllopezus* species/morphotypes from Northeastern Brazil. (A) *P. lutzae* [based on CHUFPB 19518], (B) *P. periosus* [based on CHUFPB 1936], (C) *P. pollicaris* A3 [based on CHUFPB 20626], (D) *P. pollicaris* A1 and A2 [based in CHUFPB 6185], (E) *P. pollicaris* A4 [based on CHUFPB 25804], (F - H) representatives of *P. pollicaris* B: (F) two postmental scales [based on CHUFPB 17403], (G) three postmental scales [based on CHUFPB 18662], and (H) four postmental scales [observed only in *P. pollicaris* B5; based on CHUFPB 10229]. m = mental scale, p = postmental scales (increased scales in direct contact with mental scale), 1i = first infralabial scale, 2i = second infralabial scale, 3i = third infralabial scale. Dashed gray line marks the posterior margin of the third infralabial scale. After the area illustrated, the gular scales reduce in size and become granular. Scale bar = 3mm.

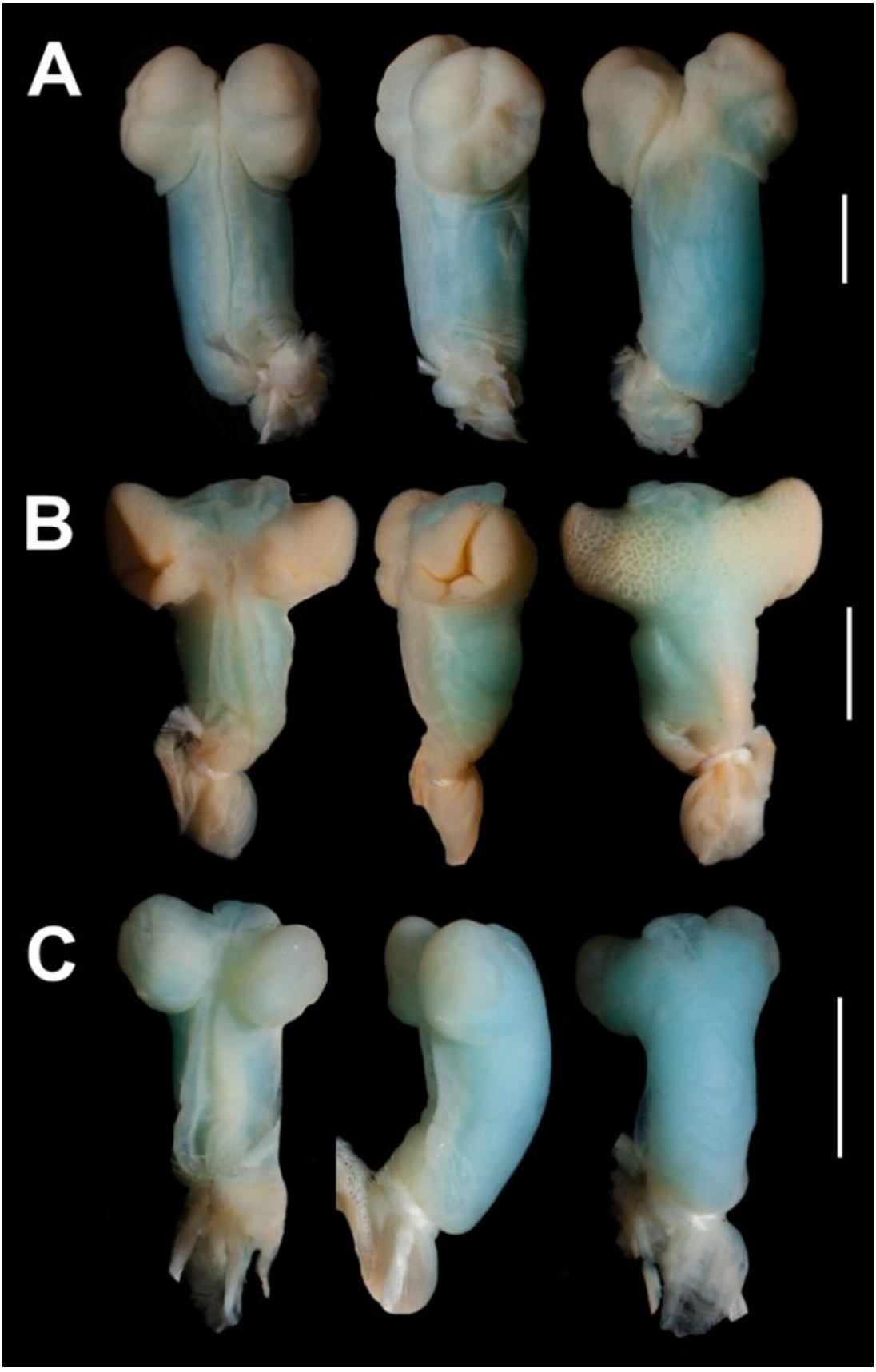


FIGURE 10. Sulcate, lateral and asulcate faces of hemipenis of (A) *Phyllopezus periosus* [CAT 416], (B) *P. pollicaris* A1 [MUFAL 12168] and (C) *P. pollicaris* B2 [PMSN 920]. Scale bar = 3mm.

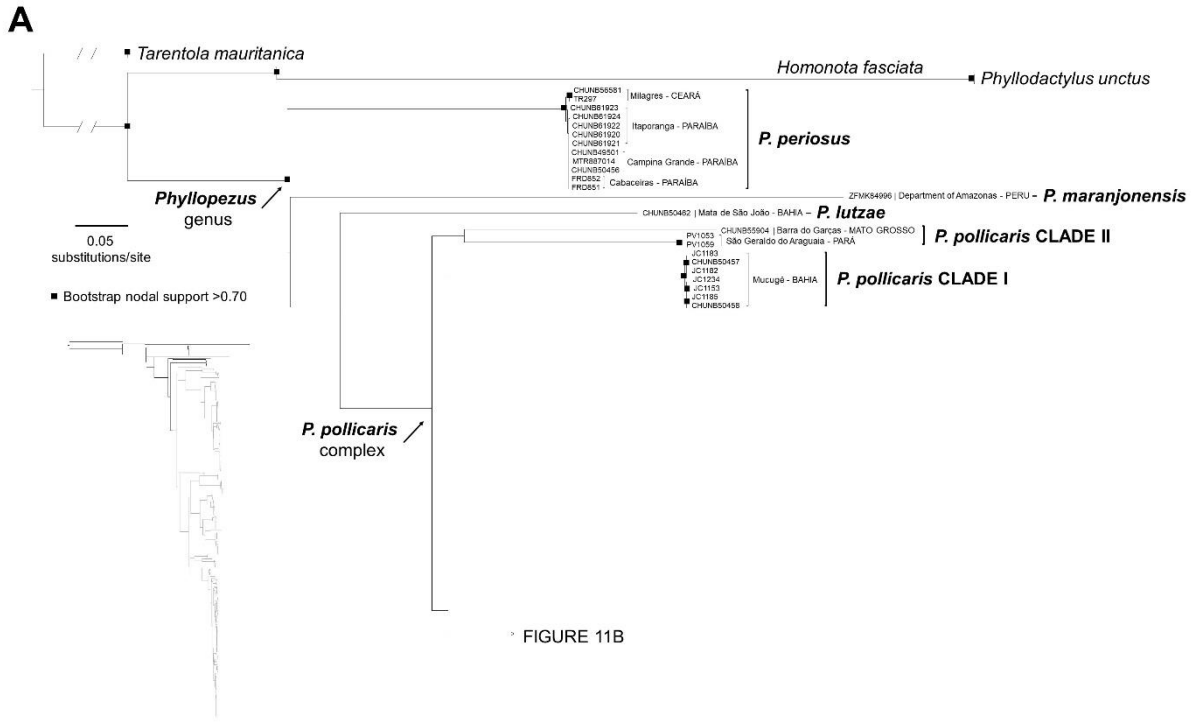


FIGURE 11. A partial view of the concatenated mitochondrial phylogenetic tree based on the Maximum Likelihood analysis (1,785 bp) of *Phyllopezus*. *Phyllopezus pollicaris* Clades follow the definitions by Werneck et al. (2012). Sequences obtained in this study are highlighted in bold.

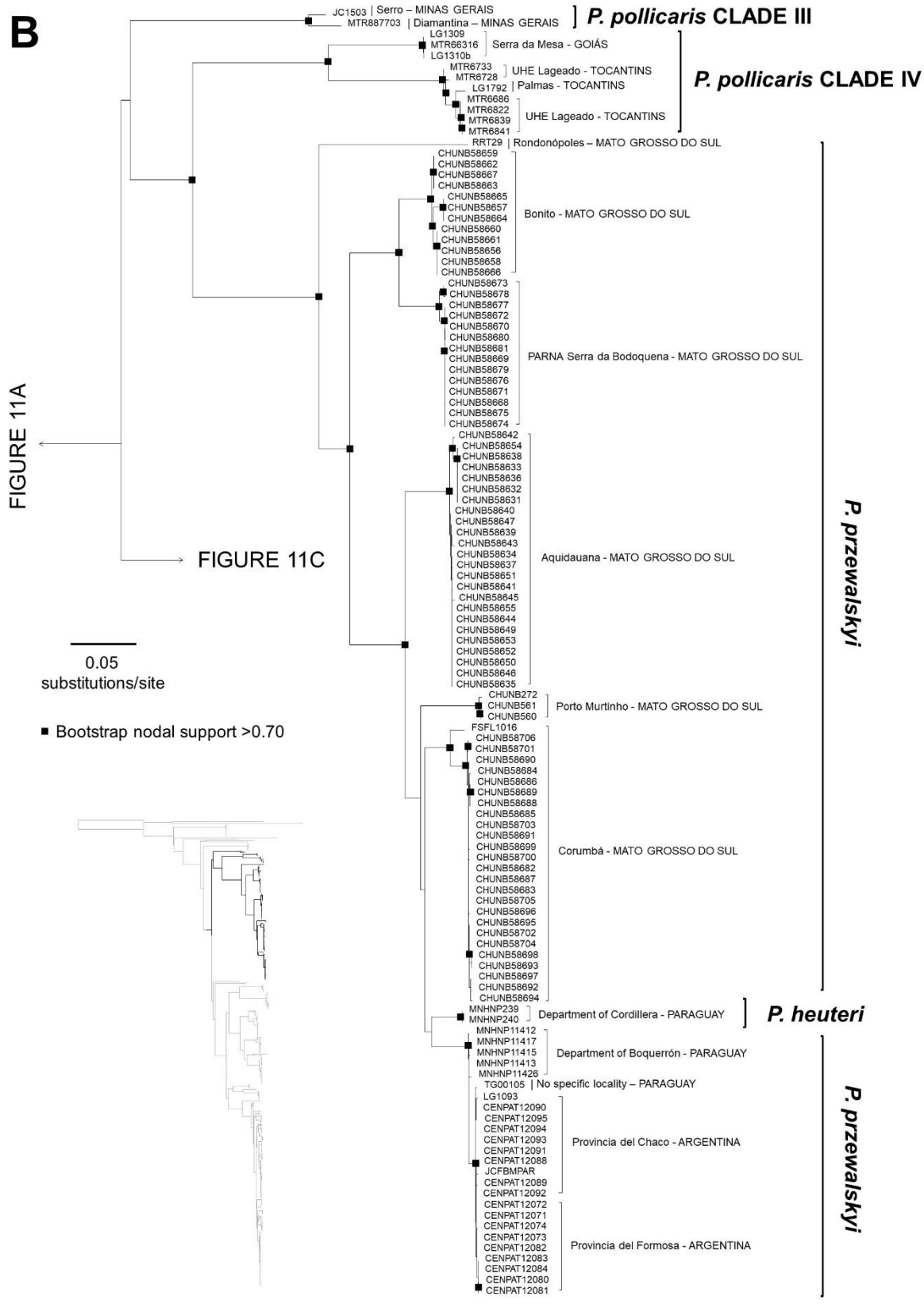
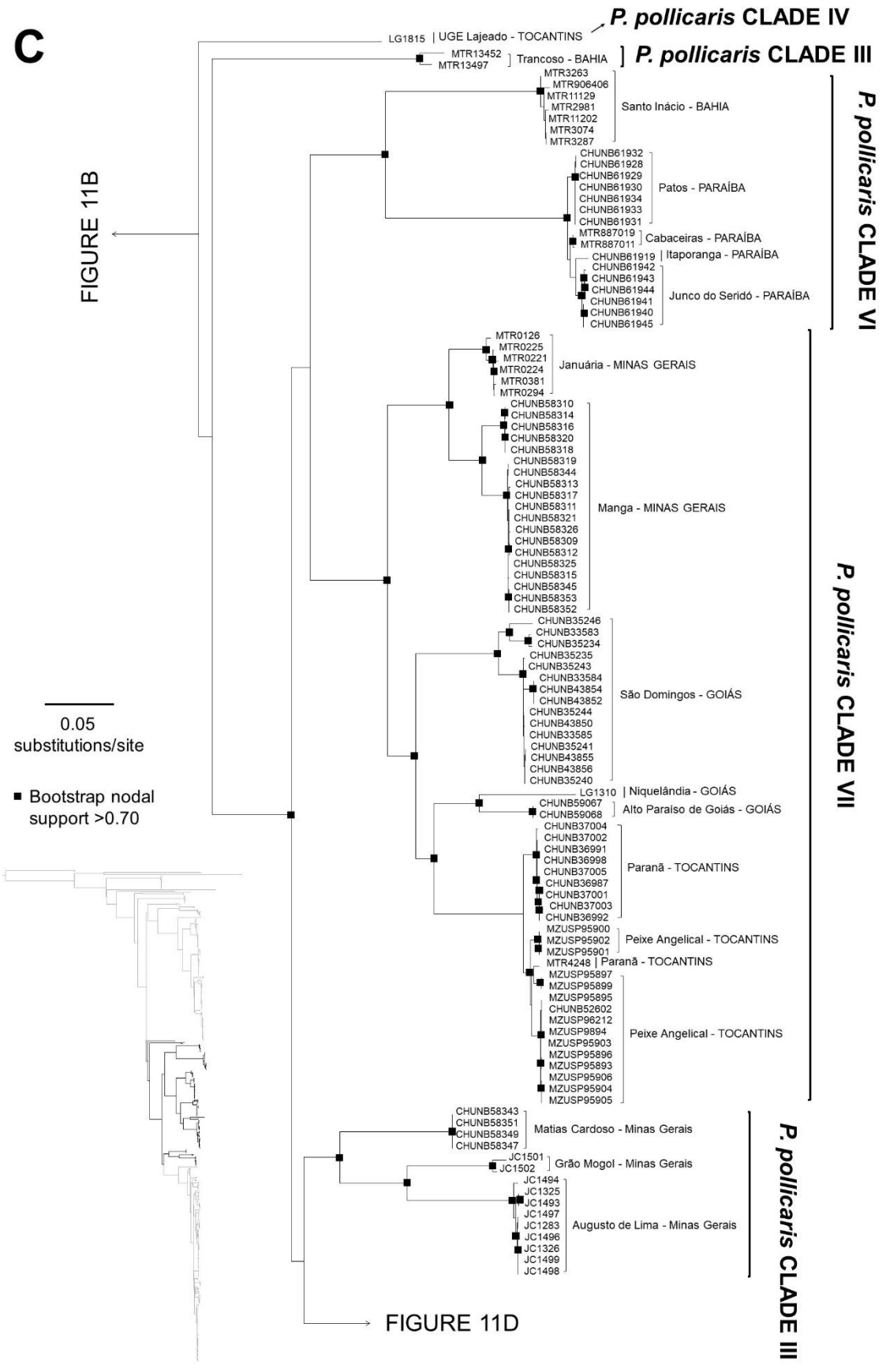


FIGURE 11. Continued.



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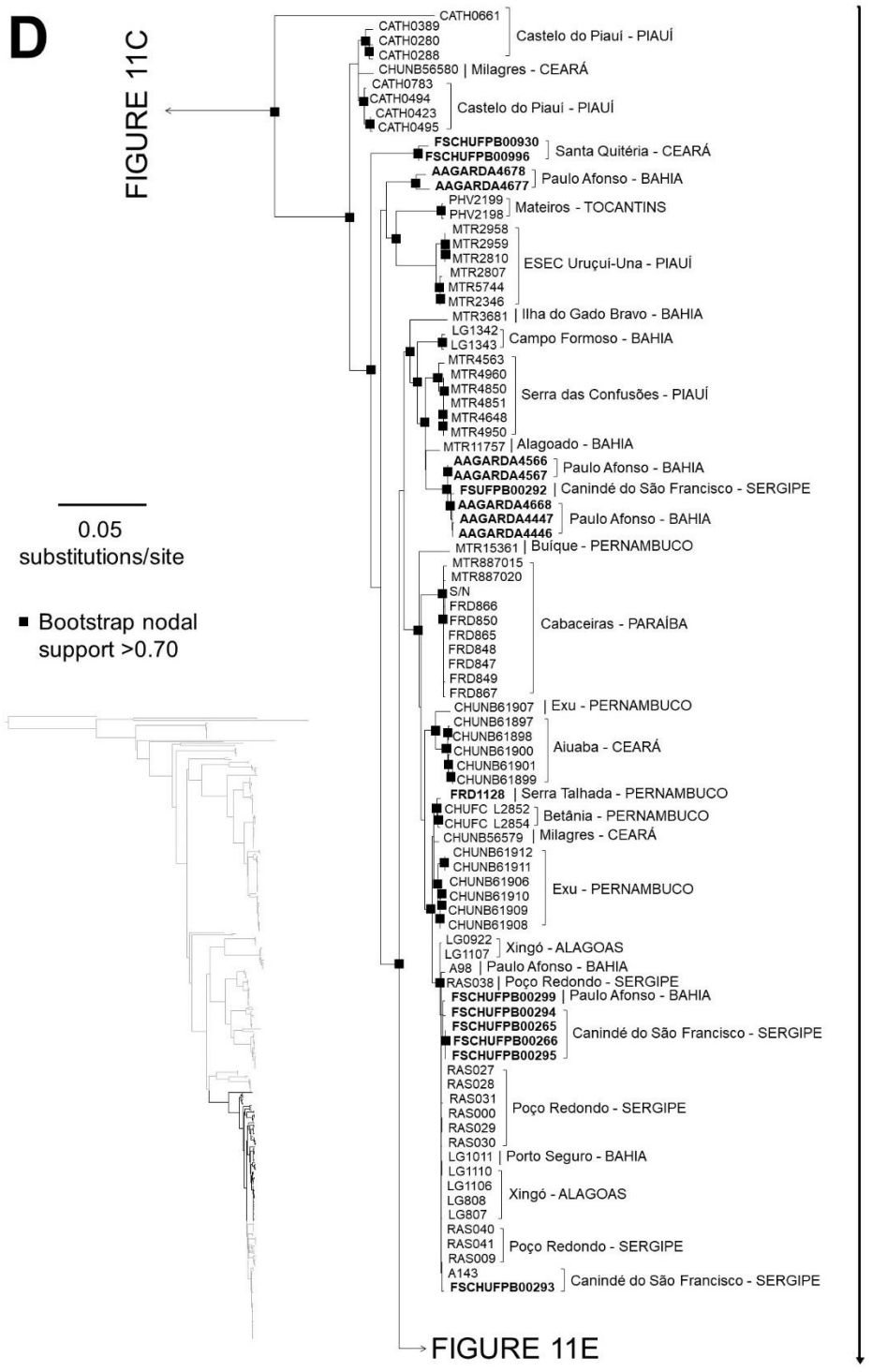

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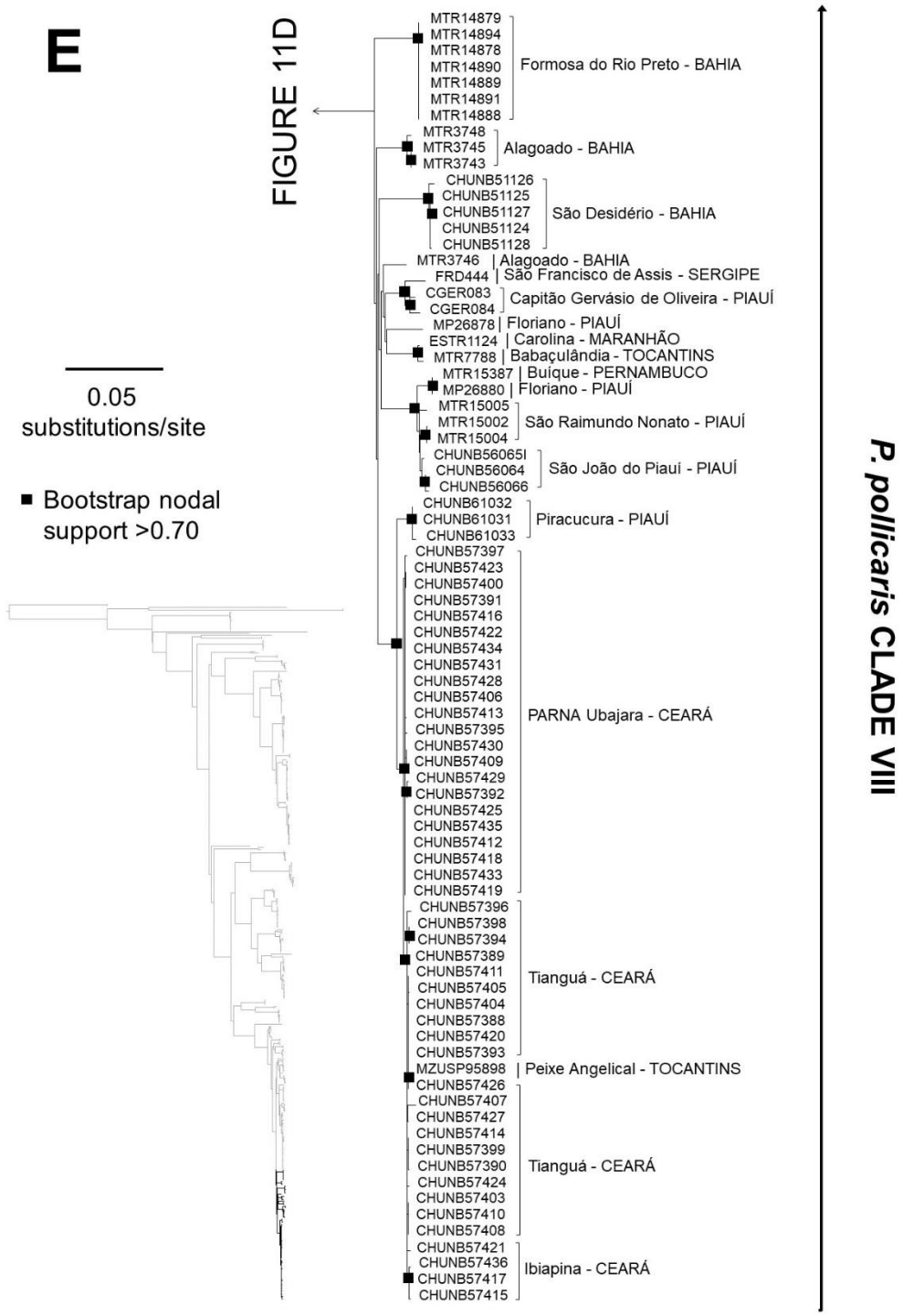

FIGURE 11. Continued.

TABLE 1. Results of univariate and multivariate analysis of variance (ANOVA and MANOVA, respectively) based on 20 morphometric characters comparing the sexes of *Phyllopezus* species/morphotypes analyzed in Northeast Brazil. Significant *P* values (<0.05) are in bold. The values used for shape analysis (MANOVA) were corrected for size (SVL). *P. pollicaris* A3 and A4 were not included in the analyzes because they presented N sample below that indicated for one of the sexes.

	P. lutzae		***P. periosus***		***P. pollicaris* A1**		***P. pollicaris* A2**		***P. pollicaris* B1**		***P. pollicaris* B2**		***P. pollicaris* B3**		***P. pollicaris* B4**		***P. pollicaris* B5**	
	$F_{1,14}$	*P*	$F_{1,76}$	*P*	$F_{1,27}$	*P*	$F_{1,10}$	*P*	$F_{1,56}$	*P*	$F_{1,15}$	*P*	$F_{1,24}$	*P*	$F_{1,46}$	*P*	$F_{1,54}$	*P*
SVL	2.60	0.13	0.52	0.47	0.11	0.74	5.43	**0.04**	1.78	0.18	0.79	0.40	3.55	0.07	1.54	0.22	2.63	0.11
DBL	3.32	0.09	2.01	0.16	0.03	0.84	6.36	**0.03**	2.06	0.15	11.94	**<0.01**	0.25	0.61	2.07	0.15	1.29	0.26
TBW	0.13	0.71	13.82	**<0.01**	5.62	**0.02**	7.56	**0.02**	1.64	0.20	0.23	0.63	2.68	0.11	15.27	**<0.01**	4.10	**0.04**
HL	1.89	0.19	0.28	0.59	0.04	0.83	3.69	0.08	0.02	0.86	7.12	**0.01**	4.64	**0.04**	6.03	**0.01**	18.11	**<0.01**
HW	2.55	0.13	1.69	0.19	1.13	0.29	5.93	**0.03**	0.96	0.33	8.32	**0.01**	4.62	**0.04**	20.69	**<0.01**	15.51	**<0.01**
HD	0.02	0.88	0.99	0.32	13.94	**<0.01**	5.44	**0.04**	0.17	0.67	12.4	**<0.01**	0.47	0.49	8.12	**<0.01**	11.94	**<0.01**
SL	1.05	0.32	0.95	0.33	0.04	0.82	7.25	**0.02**	1.35	0.24	10.24	**<0.01**	1.81	0.19	8.13	**<0.01**	25.91	**<0.01**
NSD	0.06	0.81	0.00	0.99	0.33	0.57	3.15	0.10	3.71	**0.05**	0.10	0.75	0.23	0.63	0.59	0.44	0.06	0.79
ESD	2.15	0.16	0.85	0.35	0.25	0.61	5.00	**0.05**	0.01	0.89	13.25	**<0.01**	3.14	0.08	5.37	**0.02**	5.92	**0.01**
ED	0.85	0.37	0.25	0.61	0.79	0.38	1.14	0.31	0.80	0.37	3.32	0.08	0.09	0.76	0.11	0.73	12.89	**<0.01**
IOD	12.75	**<0.01**	4.58	**0.03**	0.02	0.87	5.70	**0.04**	0.94	0.33	10.36	**<0.01**	0.17	0.68	16.51	**<0.01**	4.62	**0.03**
IND	1.18	0.29	0	0.98	0.05	0.81	1.07	0.32	0.23	0.63	0.73	0.40	0.10	0.74	2.46	0.12	0.18	0.67
LH	1.18	0.29	9.21	**<0.01**	0.01	0.90	6.44	**0.03**	0.19	0.65	9.99	**<0.01**	1.84	0.18	1.23	0.27	8.82	**<0.01**
LF	1.19	0.29	3.01	0.08	0.34	0.56	6.24	**0.03**	1.09	0.30	22.8	**<0.01**	6.65	**0.01**	0.71	0.40	10.05	**<0.01**
LT	6.71	**0.02**	2.88	0.09	1.83	0.18	6.49	**0.03**	1.86	0.17	4.94	**0.04**	0.10	0.74	8.62	**<0.01**	12.76	**<0.01**
LTB	0.76	0.39	5.12	**0.02**	0.43	0.51	3.67	0.08	0.69	0.40	10.07	**<0.01**	3.63	0.06	5.64	**0.02**	3.95	0.06
WR	0.56	0.46	0.06	0.80	0.54	0.46	5.98	**0.03**	0.00	0.97	7.13	**0.01**	0.19	0.66	0.81	0.37	0.63	0.43
LR	4.56	**0.05**	0.73	0.39	0.45	0.50	9.30	**0.01**	0.04	0.83	4.11	0.06	0.09	0.76	2.62	0.11	8.38	**<0.01**
WM	0.12	0.73	0.43	0.51	0.10	0.74	6.22	**0.03**	0.01	0.89	8.16	**0.01**	2.01	0.16	1.70	0.19	5.19	**0.02**
LM	0.01	0.89	0.30	0.58	0.13	0.71	12.4	**<0.01**	1.98	0.16	2.3	0.15	0.31	0.57	0.64	0.42	21.04	**<0.01**
Shape	0.81*	0.56	2.00	**0.02**	2.86	0.06	0.58	0.71*	2.06	**0.02**	7.94*	**<0.01**	2.06	**0.02**	2.92	**<0.01**	2.78	**<0.01**

***** Analysis performed using the residuals of a PCA = $F_{1,5}$

TABLE 2. Results of univariate and multivariate analysis of variance (ANOVA and MANOVA, respectively) based on 20 morphometric characters comparing the two morfogroups (A and B) of *Phyllopezus pollicaris* in Northeast Brazil. Significant *P* values (<0.05) are in bold. The values used for shape analysis (MANOVA) were corrected for size (SVL).

	P. pollicaris			
	Males		*Females*	
	$F_{1,134}$	*P*	$F_{1,124}$	*P*
SVL	198.1	**<0.01**	143.3	**<0.01**
DBL	107.7	**<0.01**	79.4	**<0.01**
TBW	34.85	**<0.01**	14.95	**<0.01**
HL	172.6	**<0.01**	162.7	**<0.01**
HW	91	**<0.01**	81	**<0.01**
HD	48.32	**<0.01**	7.53	**<0.01**
SL	221.9	**<0.01**	179.8	**<0.01**
NSD	41.23	**<0.01**	31.36	**<0.01**
ESD	130.8	**<0.01**	97.81	**<0.01**
ED	82.72	**<0.01**	64.32	**<0.01**
IOD	43.55	**<0.01**	39.71	**<0.01**
IND	67.73	**<0.01**	67.63	**<0.01**
LH	149.4	**<0.01**	124.9	**<0.01**
LF	127.5	**<0.01**	108.9	**<0.01**
LT	216.4	**<0.01**	141.1	**<0.01**
LTB	157.1	**<0.01**	192.1	**<0.01**
WR	167.8	**<0.01**	143	**<0.01**
LR	97.42	**<0.01**	69.62	**<0.01**
WM	142.2	**<0.01**	70.94	**<0.01**
LM	44.3	**<0.01**	21.25	**<0.01**
Shape	1.42	0.15	1.74	**0.05**

TABLE 3. Morphometrics (in mm) and meristics data [mean ± standard deviation (range)] of *Phyllopezus* species/morphotypes occurring in northeastern Brazil. Details of acronyms of characteristics are mentioned in Material and methods section.

	P. lutzae		***P. periosus***		***P. pollicaris* A1**		***P. pollicaris* A2**		***P. pollicaris* A3**		***P. pollicaris* A4**
	Female (n = 7)	Male (n = 8)	Female (n = 19)	Male (n = 58)	Female (n = 17)	Male (n = 15)	Female (n = 5)	Male (n = 6)	Female (n = 1)	Male (n = 4)	Male (n = 1)
SVL	57.1±3.1 (53.2-61.2)	59.8±4.3 (51-64.9)	107.1±3.3 (97.3-111.9)	108.1±5.4 (99.1-120.2)	89.7±6.8 (75.4-99.5)	90.8±5.8 (76-100.2)	76.7±4 (72.4-82.4)	84.7±6.7 (76.4-96.3)	101.6	96.7±8.7 (87.5-108.4)	99.86
DBL	23.9±1.8 (20.9-26.2)	25.5±2.1 (23.5-29.8)	47.3±4.7 (42.1-65.2)	45.8±3.8 (37.6-52.4)	39.5±4.2 (31.1-46.8)	39.2±3.3 (32.5-43.1)	31.5±2.4 (28.1-34.1)	35.6±2.9 (32.1-39.1)	46.22	40.9±4.5 (36.2-46)	47.42
TBW	6.4±0.6 (5.4-7.4)	6.4±0.5 (5.4-6.8)	11.7±1.7 (8.4-15.4)	13.7±2.1 (7-22)	9.8±1.3 (6.7-12.3)	11±0.9 (8.9-12.2)	6.9±0.5 (6.4-7.5)	8.5±1.2 (6.6-10.1)	13.23	11.2±1.7 (9.7-13.6)	11.32
HL	16.5±1 (15.1-18.2)	17.3±1.3 (15.1-18.6)	29.9±1.1 (27.4-31.7)	29.6±2.3 (21.3-34.5)	24.4±1.5 (21.7-27)	24.7±1.5 (21.4-26.8)	22.1±1.1 (21.1-23.9)	24.1±2.1 (21.5-27.8)	26.44	26.4±2.4 (23.7-29.2)	27.26
HW	11.1±0.7 (10.3-12.2)	11.7±0.9 (10.8-13.2)	21.4±0.9 (19-23.1)	22±2 (13.2-26.5)	17.3±1.4 (14.5-19.5)	17.9±1.1 (15.6-20.2)	14.3±0.7 (13.2-14.9)	16.4±1.8 (13.5-19.2)	20.09	19.4±1.5 (18-21.2)	20.02
HD	5.9±0.8 (4.6-7)	6±0.5 (5.4-6.7)	11.8±0.9 (10.3-13.8)	12.1±1.2 (9.6-16.5)	8.4±0.9 (6.4-9.7)	9.9±0.9 (7.9-11.2)	7.2±0.4 (6.6-7.6)	8.1±0.7 (7.3-9.1)	9.91	10.6±1.9 (9.4-13.4)	12.19
SL	7±0.4 (6.3-7.6)	7.2±0.5 (6.4-7.8)	12.7±0.4 (12.1-13.2)	13±1.3 (8.6-19.5)	9.9±0.6 (8.9-11.1)	10±0.7 (8.5-11)	9±0.5 (8.5-9.7)	10±0.7 (8.9-11)	10.7	10.6±0.7 (9.7-11.5)	10.86
NSD	1.7±0.2 (1.5-2)	1.7±0.2 (1.4-2)	2.6±0.4 (2.1-3.3)	2.6±0.4 (1.8-4.7)	2.2±0.3 (1.7-2.8)	2.2±0.3 (1.6-2.6)	1.9±0.1 (1.8-2)	2.1±0.2 (1.9-2.4)	2.55	2.5±0.5 (2.1-3.2)	2.54
ESD	5.3±0.4 (4.6-5.7)	5.6±0.3 (5.1-6.2)	10.1±0.5 (8.7-10.6)	10.2±0.7 (7.5-11.9)	7.6±0.5 (6.6-8.3)	7.5±0.6 (6.2-8.4)	7±0.3 (6.8-7.3)	7.8±0.7 (6.8-8.8)	7.62	8±0.5 (7.4-8.7)	8.84
ED	3.3±0.3 (2.9-3.5)	3.4±0.3 (3-3.9)	6.3±0.4 (5.7-7.6)	6.4±0.7 (3.5-8.5)	5.1±0.4 (4.4-6.1)	5.2±0.4 (4.6-5.7)	4.7±0.5 (4.1-5.2)	5.2±1.1 (3.7-6.9)	5.33	5.7±0.7 (5-6.7)	5.49
IOD	5.2±0.3 (4.8-5.6)	6±0.6 (5-6.8)	9.6±0.9 (8.4-11.8)	10.2±1 (7.9-12.5)	8.2±0.6 (7.1-9.4)	8.1±0.8 (6.1-9.3)	6.4±0.7 (5.7-7.1)	7.5±0.8 (6.7-8.9)	9.05	9.3±1.1 (8-10.3)	8.89
IND	2.3±0.3 (1.9-2.7)	2.4±0.3 (2-2.9)	3.7±0.2 (3.2-4.1)	3.7±0.5 (2.8-5.9)	3.2±0.3 (2.8-3.8)	3.2±0.4 (2.5-4)	2.8±0.3 (2.5-3.2)	3±0.3 (2.6-3.4)	3.52	3.3±0.3 (3-3.7)	3.18
LH	10.9±0.6 (10-11.7)	11.3±1 (9.9-12.7)	22.4±1.7 (19.3-25.5)	23.7±1.6 (20.5-26.9)	18.2±1.3 (15-20.1)	18.4±1.6 (16.5-21.9)	16.1±0.5 (15.7-16.7)	18.1±1.6 (16.4-21)	20.87	20±2.1 (18.3-22.9)	19.87
LF	6.9±0.4 (6.1-7.4)	7.1±0.5 (6.4-7.7)	14.6±0.7 (13.3-15.8)	15±0.9 (13.2-17.2)	11.2±0.7 (9.6-12.3)	11.5±0.7 (10.3-12.8)	10.9±0.5 (10.4-11.4)	11.9±0.7 (10.9-13.1)	12.06	12±0.8 (11.1-12.9)	12.75
LT	12±0.4 (11.5-12.7)	12.6±0.6 (11.7-13.5)	25.2±1.1 (23-27.2)	25.9±1.5 (21-29.5)	19.3±1.6 (15.3-21.2)	20.5±1.9 (17.7-24.1)	18.4±1.1 (17.3-19.6)	20.2±1.2 (18.3-22)	21.31	20.6±1.7 (18.5-22.6)	21.13
LTB	8.2±0.5 (7.3-8.7)	8.4±0.5 (7.6-9)	18.1±0.7 (16.5-19.1)	18.8±1.2 (15.7-21.9)	13.8±0.9 (12.3-15.3)	14.1±0.8 (12.8-15.4)	13.1±0.7 (12.2-13.9)	14.1±0.9 (12.6-15.4)	14.7	14.4±1.6 (13-16.8)	15.67
WR	2.3±0.2 (2.1-2.7)	2.4±0.1 (2.2-2.5)	4.4±0.2 (3.9-4.9)	4.4±0.5 (3.4-6.5)	3.9±0.4 (3.3-4.5)	3.9±0.3 (3.3-4.3)	3.4±0.2 (3.1-3.8)	3.8±0.2 (3.6-4.1)	3.98	4±0.3 (3.7-4.4)	4.17
LR	1±0.1 (0.8-1.2)	1.2±0.2 (0.9-1.4)	2.2±0.3 (1.8-2.6)	2.3±0.4 (1.6-3.2)	2±0.2 (1.5-2.3)	2±0.2 (1.6-2.3)	1.6±0.2 (1.4-1.9)	1.9±0.2 (1.6-2.2)	2.17	1.9±0.1 (1.8-2)	2.6
WM	2.5±0.3 (2.1-3)	2.6±0.4 (2.1-3.1)	4.7±0.2 (4.4-5.1)	4.8±0.4 (4-6)	3.9±0.4 (3.2-4.6)	4±0.2 (3.6-4.3)	3.7±0.4 (3.1-4.2)	4.4±0.4 (3.7-4.8)	4.96	4.4±0.5 (3.7-4.7)	4.43
LM	1.6±0.2 (1.3-2)	1.6±0.1 (1.4-1.8)	6.1±0.4 (5.5-7.2)	6.2±0.7 (3-8.8)	3.9±0.5 (3-5)	3.9±0.4 (3.3-4.5)	3.3±0.4 (2.8-3.7)	4.1±0.3 (3.7-4.6)	3.68	4.4±0.4 (4-5)	4
R	1±0 (1-1)	1.6±0.5 (1-2)	1±0 (1-1)	1±0 (1-1)	1±0 (1-1)	1.1±0.4 (1-2)	1±0 (1-1)	1±0 (1-1)	1	1.3±0.5 (1-2)	2
PR	3±0 (2-3)	2.7±0.5 (2-3)	2±0 (2-2)	2.1±0.4 (2-4)	2.1±0.2 (2-3)	2±0 (2-2)	2±0 (2-2)	2.3±0.5 (2-3)	2	2.5±0.6 (2-3)	2
PN	2±0 (2-3)	2±0 (2-2)	2.7±0.5 (2-3)	2.8±0.4 (2-4)	2±0 (2-2)	2.1±0.3 (2-3)	2±0 (2-2)	2±0 (2-2)	2	2±0 (2-2)	2
SL	9±1 (8-9)	7.9±0.4 (7-8)	7.5±0.6 (7-9)	7.9±0.9 (7-11)	7.3±0.6 (6-8)	7±0.5 (6-8)	7±0 (7-7)	7±0.6 (6-8)	6	6.5±0.6 (6-7)	8
IL	8±1 (7-8)	6.9±0.4 (6-7)	7.7±0.6 (7-9)	7.6±0.7 (7-9)	6.8±0.4 (6-7)	6.4±0.5 (6-7)	6.6±0.5 (6-7)	6.8±0.4 (6-7)	6	6±0 (6-6)	6
PM	2±0 (1-2)	2±0 (2-2)	4.6±1 (3-7)	4.9±1.2 (3-8)	2±0 (2-2)	2±0 (2-2)	2±0 (2-2)	2±0 (2-2)	2	2±0 (2-2)	3
SSP	4±1 (3-5)	4.1±0.4 (4-5)	12.8±2 (10-16)	12.3±1.9 (7-18)	6.1±1.1 (4-8)	6.5±1.5 (5-10)	4.4±0.5 (4-5)	5.2±1.7 (3-7)	5	5.8±1 (5-7)	8
VLR	61±3 (57-64)	58±3.7 (56-66)	44.9±3.6 (39-52)	45.2±3.4 (38-52)	45.9±1.8 (42-51)	46.7±1.7 (44-51)	54.6±1.9 (52-57)	56±2.8 (51-59)	52	52.3±4.3 (46-55)	59
DT	35±6 (29-43)	27.9±10 (20-42)	42.3±4.8 (31-52)	43.4±5.4 (24-54)	42.8±3.4 (32-47)	45.7±3.3 (41-53)	46.6±2.7 (43-50)	44.7±4.9 (38-52)	44	48.8±3 (45-52)	52
L4F	10±1 (9-11)	9.6±0.8 (9-11)	13.3±0.9 (12-15)	13.3±0.8 (12-15)	12.8±1 (11-14)	13.3±0.8 (12-14)	12.2±0.8 (11-13)	11.8±1 (11-13)	13	13.5±0.6 (13-14)	14
L4T	11±1 (10-12)	10±0.8 (9-11)	13.5±0.8 (12-15)	13.7±0.8 (12-16)	13.4±0.8 (12-14)	13.7±1 (12-15)	12.6±0.9 (12-14)	13±0.9 (12-14)	13	13.3±0.5 (13-14)	15
TP	0±0 (0-0)	0±0 (0-0)	1.3±0.8 (0-2)	2.1±0.6 (0-3)	2.2±1 (0-3)	1.7±1 (0-3)	2±0 (2-2)	2.2±0.4 (2-3)	2	2.3±0.5 (2-3)	2
CP	1±1 (0-1)	0±0 (0-0)	1±0 (1-1)	1±0.1 (0-1)	0.2±0.4 (0-1)	0.3±0.5 (0-1)	1±0 (1-1)	1±0 (1-1)	0	0.3±0.5 (0-1)	1

TABLE 3. Continuation.

	P. pollicaris B1		*P. pollicaris* B2		*P. pollicaris* B3		*P. pollicaris* B4		*P. pollicaris* B5	
	Female (n = 7)	Male (n = 8)	Female (n = 7)	Male (n = 8)	Female (n = 7)	Male (n = 8)	Female (n = 7)	Male (n = 8)	Female (n = 7)	Male (n = 8)
SVL	69±3.1 (59.4-74.6)	70.5±5.1 (58.9-81.3)	66.8±4.6 (55.9-71.8)	70.2±6.7 (60.9-85.6)	70.6±3.7 (63.9-75.2)	74.7±5.2 (67.1-88.7)	75.2±5.1 (67.3-87.1)	74.4±5.4 (64.2-85)	69.4±6.1 (59.1-85.7)	71.3±3.5 (61.8-75.5)
DBL	30.4±2.3 (24.6-36.2)	31.3±3 (23.2-36.5)	28.4±2.3 (24.1-31.2)	30.3±3.6 (23.4-38.8)	30.8±2.7 (27.2-35.1)	32.1±3.4 (26.6-40)	32.8±3.2 (25.5-37.4)	32±2.7 (28.2-38.6)	30±2.9 (24.3-35.5)	31.4±2.7 (25.4-36.1)
TBW	8.7±1.1 (5.6-10.3)	8.8±1.3 (5.8-11.5)	7.1±0.7 (5.8-8.1)	8.3±1.4 (6.7-12.2)	7.4±0.9 (5.5-8.7)	8.2±1 (6.6-10.3)	8.6±1 (6.2-11.6)	9.3±1.3 (6.6-13.1)	7.4±1.1 (5.7-11.1)	8.7±1 (6.9-10.6)
HL	19.1±0.9 (16.7-21.1)	19.7±1.4 (16.7-22.5)	18.9±1.5 (16.2-20.8)	20.1±2.1 (17.3-25.3)	19.4±0.8 (17.4-20.7)	20.6±1.4 (18.9-24.2)	20.7±1.3 (18.6-23.5)	21±1.4 (18.4-23.5)	19.5±1.7 (16.8-24.9)	20.1±1.1 (17.4-21.8)
HW	13.8±0.7 (12-14.9)	14.6±1.2 (11.4-17.1)	13.5±1.1 (11.4-15.1)	14.4±1.5 (12.2-18.3)	13.8±0.5 (13-14.9)	15±1.3 (13.2-18.7)	15.1±1.2 (12.3-17.5)	15.6±1.1 (13.1-17.3)	13.6±1.2 (12.1-16.9)	14.6±1.4 (12.3-19.5)
HD	7.5±0.7 (6.1-9.4)	7.7±0.9 (5.9-9.8)	7.1±1.2 (4.8-9.1)	7.2±1.6 (5.1-10.4)	7.4±0.6 (6.4-8.2)	7.9±0.9 (6.8-9.9)	8.2±0.9 (6.7-9.7)	8.4±0.9 (6.5-11.2)	7.4±0.8 (6.2-9.3)	8±1 (6.1-9.7)
SL	7.6±0.4 (6.9-8.6)	7.7±0.5 (6.9-8.8)	7.5±0.6 (6.3-8.3)	8±0.9 (6.9-10.3)	7.7±0.4 (7-8.4)	8.2±0.5 (7.7-9.5)	8.3±0.5 (7.4-9.3)	8.4±0.5 (7.4-9.4)	7.8±0.7 (6.8-9.7)	8.1±0.4 (7.4-9)
NSD	1.7±0.2 (1.3-2.3)	1.9±0.2 (1.4-2.4)	1.7±0.3 (1.1-2.2)	1.9±0.2 (1.6-2.5)	1.8±0.2 (1.5-2.1)	1.9±0.2 (1.5-2.4)	1.8±0.2 (1.4-2.2)	1.9±0.3 (1.4-2.6)	1.9±0.3 (1.3-2.6)	1.8±0.3 (1.3-2.2)
ESD	6.1±0.5 (5.3-7.3)	6.2±0.5 (5.4-7.5)	5.8±0.8 (4.8-7)	6±0.5 (5.2-6.7)	6.1±0.2 (5.7-6.4)	6.5±0.5 (5.8-7.6)	6.5±0.5 (5.7-7.8)	6.6±0.4 (5.7-7.4)	6.2±0.5 (5.3-7.4)	6.3±0.3 (5.8-6.7)
ED	4.1±0.3 (3.5-5.3)	4.1±0.3 (3.5-4.7)	4.2±0.4 (3.4-4.8)	4.3±0.5 (3.7-5.5)	4.3±0.1 (4.1-4.5)	4.5±0.4 (3.8-5)	4.4±0.4 (3.3-5.1)	4.5±0.4 (3.9-5.1)	4.4±0.5 (3.5-5.5)	4.5±0.4 (3.7-5.1)
IOD	6.6±0.5 (5.9-8.2)	6.8±0.7 (5.4-8)	6.5±0.7 (4.8-7.3)	6.8±0.6 (6-8.4)	6.5±0.6 (5.2-7.1)	7.1±0.9 (6-9.6)	7.4±0.6 (6.2-8.7)	7.4±0.6 (5.9-8.6)	6.6±0.6 (5.5-7.7)	6.9±0.8 (5.2-9)
IND	2.6±0.2 (2.1-3.1)	2.6±0.2 (2.1-2.9)	2.5±0.4 (1.8-3.1)	2.7±0.3 (2.4-3.5)	2.4±0.3 (2-2.9)	2.6±0.3 (2-3)	2.7±0.3 (2.1-3.3)	2.6±0.3 (2.2-3.3)	2.5±0.2 (2.1-3.1)	2.6±0.3 (2.2-3.3)
LH	13.8±0.8 (11.8-15.6)	14.5±1.4 (11.6-17.1)	14.1±1.5 (11.8-17)	14.4±1.4 (12.5-17.8)	14.6±0.8 (13.5-15.6)	15.1±1.1 (13.8-17.7)	15.3±1.2 (12.6-18.4)	15.3±1.5 (11.9-18)	14.3±1.6 (12.1-19)	14.7±1.1 (11.6-16.1)
LF	8.7±0.7 (6.1-9.7)	9.1±0.8 (7.4-10.5)	8.4±0.7 (7.3-9.4)	9.2±0.9 (8.2-11)	9.5±0.8 (8-10.9)	10.1±1 (8.6-12.7)	9.7±0.6 (8.7-11)	9.7±0.9 (7.6-11.3)	9.4±1.1 (8-13.2)	9.5±0.8 (7.7-10.7)
LT	14.8±0.8 (13.1-16.5)	15.2±1.2 (13-17.3)	15.3±1.1 (12.4-16.5)	15.6±1.6 (14.1-19.8)	15.8±0.7 (14.6-16.8)	16.3±1.1 (14.8-18.6)	16.4±1.1 (14.5-18.1)	16.6±1.1 (14.4-18.1)	15.5±1.5 (12.1-18)	15.9±1.2 (13.4-17.8)
LTB	10.6±0.6 (9.5-11.6)	10.7±0.9 (8.7-12.2)	10.3±0.7 (8.7-11.5)	11.2±1.2 (9.8-14.3)	11.1±0.7 (9.7-12)	11.7±1 (9.9-14.4)	11.6±0.7 (10.3-13.1)	11.8±1 (10.2-13.9)	11.1±0.9 (9.7-13)	11.1±0.9 (9-12.3)
WR	2.9±0.2 (2.3-3.3)	3±0.3 (2.1-3.6)	3±0.3 (2.7-3.8)	3.1±0.4 (2.7-4.1)	2.9±0.2 (2.5-3.2)	3±0.2 (2.5-3.4)	3.1±0.3 (2.6-3.6)	3.1±0.4 (2.5-3.9)	2.9±0.4 (2.3-3.7)	2.9±0.2 (2.4-3.3)
LR	1.4±0.2 (1.2-2)	1.5±0.2 (1.2-1.9)	1.5±0.2 (1.2-1.8)	1.5±0.2 (1.4-1.9)	1.5±0.2 (1.2-2)	1.6±0.2 (1.2-2)	1.5±0.2 (1.2-1.9)	1.6±0.2 (1.2-1.9)	1.5±0.2 (1.2-1.9)	1.6±0.2 (1.2-2)
WM	3±0.3 (2.1-3.6)	3.1±0.3 (2.5-3.8)	3.1±0.2 (2.6-3.4)	3.3±0.3 (2.8-4.1)	3.1±0.3 (2.6-3.6)	3.2±0.3 (2.7-3.6)	3.4±0.4 (2.9-4.4)	3.3±0.4 (2.1-4.1)	3.2±0.4 (2.7-4.4)	3.1±0.3 (2.4-3.7)
LM	3.1±0.4 (2.5-3.9)	3.2±0.5 (2.5-4.3)	3±0.4 (2.2-3.6)	3.4±0.4 (2.7-3.8)	3.2±0.3 (2.8-4)	3.5±0.4 (2.7-4.2)	3.5±0.5 (2.6-4.8)	3.5±0.4 (2.8-4.3)	3.5±0.4 (2.7-4.6)	3.5±0.4 (3-4.5)
R	2±0.2 (1-2)	1.8±0.4 (1-2)	1.1±0.3 (1-2)	1.1±0.3 (1-2)	1.5±0.5 (1-2)	1.4±0.5 (1-2)	1.1±0.3 (1-2)	1.3±0.5 (1-2)	1.2±0.4 (1-2)	1.2±0.4 (1-2)
PR	2±0 (2-2)	2±0 (2-2)	2±0 (2-2)	2±0 (2-2)	2.1±0.3 (2-3)	2.1±0.3 (2-3)	2±0.2 (2-3)	2±0 (2-2)	2±0 (2-2)	2±0 (2-2)
PN	2±0 (2-2)	2±0 (2-2)	1.8±0.4 (1-2)	2±0 (2-2)	2±0 (2-2)	2±0 (2-2)	2±0.2 (2-3)	2±0 (2-2)	2±0 (2-2)	2±0 (2-2)
SL	6.9±0.2 (6-7)	6.8±0.5 (6-8)	6.8±0.8 (6-8)	6.8±0.7 (6-8)	7.3±0.5 (7-8)	7.2±0.7 (6-9)	7.1±0.4 (6-8)	7±0.5 (6-9)	7.1±0.5 (6-8)	7.4±0.7 (6-9)
IL	6.1±0.3 (6-7)	6.1±0.3 (6-7)	6.2±0.4 (6-7)	6.2±0.4 (6-7)	6.7±0.5 (6-7)	6.4±0.5 (6-7)	6.1±0.3 (6-7)	6.2±0.4 (6-7)	6.5±0.6 (6-8)	6.5±0.6 (6-8)
PM	2.3±0.4 (2-3)	2.4±0.5 (2-3)	2±0 (2-2)	2±0 (2-2)	2.2±0.4 (2-3)	2.3±0.6 (2-4)	2.2±0.5 (2-4)	2.1±0.4 (2-4)	2.3±0.6 (2-4)	2.4±0.7 (2-4)
SSP	5.8±1 (4-8)	6.5±1.2 (5-9)	6.9±2.8 (5-14)	6.1±1 (5-8)	5.5±0.7 (5-7)	6.1±1.7 (3-10)	5.8±0.9 (5-8)	5.6±0.8 (5-8)	5.5±0.7 (5-7)	5.8±1.1 (4-9)
VLR	43.7±2.7 (36-48)	44±3.6 (38-53)	45.3±3.8 (37-51)	46.7±3.1 (42-55)	48.2±5.2 (39-55)	47.3±5.2 (40-60)	46.1±3.2 (37-52)	45.5±3.5 (39-53)	45±3.8 (38-54)	44.7±3.5 (39-54)
DT	35.8±3.1 (30-43)	37±2.9 (32-44)	40.8±5.7 (33-50)	38.8±3.7 (34-44)	39.2±3.7 (34-45)	39.3±3.6 (32-45)	39.8±3.7 (34-47)	38.6±3.5 (34-47)	36.3±3.6 (29-42)	36.6±3.5 (30-45)
L4F	11.3±1 (10-13)	11.2±0.9 (10-13)	11.2±1.4 (9-14)	11.1±1.1 (10-14)	10.7±1.2 (9-13)	11.1±0.8 (10-12)	11.1±1 (9-13)	11.4±1.2 (10-13)	11.5±0.9 (10-13)	11.1±0.9 (10-13)
L4T	11.6±0.8 (10-14)	11.8±0.8 (10-13)	11.3±0.9 (10-13)	11.5±0.7 (10-12)	11.1±1 (9-12)	11.4±0.7 (10-13)	12±0.9 (10-14)	11.6±0.9 (10-14)	12.1±0.7 (11-13)	11.6±0.8 (10-13)
TP	2.2±1.4 (0-4)	3±0.8 (0-4)	3.1±0.9 (1-4)	2.5±1.2 (0-4)	2±1.6 (0-4)	2.3±1.3 (0-4)	3.4±0.8 (1-4)	3±0.8 (1-4)	2.3±1.2 (0-4)	2.6±0.8 (0-3)
CP	0.7±0.5 (0-1)	0.7±0.5 (0-1)	0.3±0.5 (0-1)	0.3±0.5 (0-1)	0.3±0.5 (0-1)	0.2±0.4 (0-1)	0.6±0.5 (0-1)	0.4±0.5 (0-1)	0.4±0.5 (0-1)	0.5±0.5 (0-1)

APPENDIX I. Specimens examined

***Phyllopezus lutzae*:** BRAZIL: **Paraíba**: Pedras de Fogo (CHUFPB 19517, 19518, 19519); Caaporã (CHUFPB 24979); **Alagoas**: Maceió (UFRN 36, 236; LABI 181, 182, 183); Quebrangulo (LABI 651, 653); **Sergipe**: Castro (UFRN 1427).

***Phyllopezus periosus*:** BRAZIL: **Paraíba**: Araruna (CHUFPB 9118); Cabaceiras (Topotypes – CHUFPB 1646, 1930, 1931, 1932, 1934, 1935, 1936, 1938, 1939, 1940, 1940, 1947, 1949, 1950, 10187, 10188); São João do Cariri (UFRN 511, CHUFPB 1955, 1992, 5952, 8644, 8645, 8647, 8912, 8913, 8914, 9005); São João dos Cordeiros (CHUFPB 9327); **Pernambuco**: Buíque (CHUFPB 11150, 13015, 13016, 14287, 14289, 25656, CAT 416); **Rio Grande do Norte**: Alexandria (UFRN 3976); Caicó (CHUFPB 13306); Currais Novos (UFRN 5550, 5551, 5552, 5553, 5554, 5556, 5557, 5558, 5559); Equador (UFRN 5173); João Câmara (CHUFPB 6541, 6546, 6547, 6544); Lages Pintadas (UFRN 5562, 5563, 5565); Lagoa Nova (UFRN 4693, 4694, 4960); Santa Maria (UFRN 3150, 3151, 3153); Serra Negra do Norte (MUFAL 12408, 12409, 12410, 12423, 12426, 12427, 12428, 12430, 12431, 12432, 12433, 12435, 12436, 12437, 12438, 12440).

***Phyllopezus pollicaris* A1:** BRAZIL: **Alagoas**: Boca da Mata (MUFAL 13481, 13482, 13485); Coruripe (MUFAL 12128, 12449); Igaci (MUFAL 12200, 12201, 12202); Limoeiro de Anadia (MUFAL 12166, 12167, 12168, 12169, 12170, 12172, 12196, 12197, 12198, 12396, 12397, 12398, 12400); Quebrangulo (MUFAL 12401, LABI 648); Traipú (MUFAL 9309, 9331, 9412, 9762, 12399); **Paraíba**: Areia (CHUFPB 1981, 6185, 6671, 24994); **Pernambuco**: Buíque (CHUFPB 23514).

***Phyllopezus pollicaris* A2:** BRAZIL: **Bahia**: Mucugê (JC 1234, 1176, 1185, 1180, 1219, 1153, 1222, 1182, 1227, 1184, 1183).

***Phyllopezus pollicaris* A3:** BRAZIL: **Bahia**: Serra da Jiboia (CHUFPB 20625, 20626, 20627, 20630, 4579).

***Phyllopezus pollicaris* A4:** BRAZIL: **Bahia**: Condeúba (CHUFPB 25804).

***Phyllopezus pollicaris* A [unassigned]:** BRAZIL: **Bahia**: Santa Barbara (CHUFPB 1989).

***Phyllopezus pollicaris* B1:** BRAZIL: **Bahia**: Curaça (UFRN 3813), Paulo Afonso (CHUFPB 11294, 11295, 11296, 11297, 11298, 11299, 11300, 12058, 22330, 25018, 25111, 25137, 25569); **Sergipe**: Canindé do São Francisco (CHUFPB 18559, 18562, 18563, 18567, 18568, 18570, 18573, 18581, 18587, 18592, 18594, 18595, 18602, 18605, 18626, 18633); Poço Redondo (CHUFPB 18657, 18659, 18661, 18662, 18663, 18664, 18665, 18666, 18668, 18672, 18674, 18681, 18686, 18689); Porto da Folha (CHUFPB 18645, 18646, 18647, 18648, 18649, 18673, 18918, 18923, 19390, 19392, 19393, 19394, 19397).

***Phyllopezus pollicaris* B2:** BRAZIL: **Alagoas**: Água Branca (PMSN 0914, 0920, 0938, 0940, 0946, UGS 698, LABI 645, 639, 643, 646, 644, 640, 641, 642); Delmiro Gouvêia (LABI 552); Piranhas

(LABI 551); **Pernambuco**: Buíque (CHUFPE 23509, 25026, 25562, 25973, CAT 272, 391, 271, 388, 392).

***Phyllopezus pollicaris* B3:** BRAZIL: **Maranhão**: São Francisco do Maranhão (CHUFPB 8696); **Piauí**: São Raimundo Nonato (CHUFPB 25050, 25153); Andorinha (CHUFPB 22324, 22349, 22364, 22450, 22473, 22603); Coronel José Dias (CHUFPB 14603, 14606, 14608, 14611, 14614, 14616, 14617, 14618); Floriano (CHUFPB 8699); Museu (CHUFPB 22304); Palmeiras (CHUFPB 8698); São Francisco de Assis do Piauí (CHUFPB 268); Teresina (CHUFPB 11767); Uruçuí (CHUFPB 8697); Serra da Capivara (CHUFPB 8697, 23519, 25051, 25170, 25975, 25984).

***Phyllopezus pollicaris* B4:** BRAZIL: **Ceará**: Aiuaba (CHUFPB 5145, 5147, 5153, 5159, 5160, 5161, 5162, 5163, 5165, 5324, 5325, 5326, 5327, 5328, 5329, 13767, 13768, 13769, 13778, 13780, 13788); Quixadá (CHUFPB 25009, 25017, 25157, 25191, 25858); Santa Quitéria (CHUFPB 10681, 11850); Ubajara (CHUFPB 26129, 26894, 26916); Várzea da Conceição (CHUFPB 239, 324); Crato (CHUFPB 17403, 17405, 17411, 17412, 17413, 17414, 17419, 17423, 17430,17431, 17435, 17442, 17445).

***Phyllopezus pollicaris* B5:** BRAZIL: **Paraíba**: Araruna (CHUFPB 9093); Cabaceiras (CHUFPB 10224, 10225, 10228, 10229, 10230, 10231); São João do Cariri (CHUFPB 1980, 1983, 1985, 1987, 5953, 5954, 8796, 8916, 8918, 9007); São José dos Cordeiros (CHUFPB 6070, 6887); Sumé (CHUFPB 9328); **Rio Grande do Norte**: Alexandria (UFRN 3974); Alto do Rodrigues (UFRN 4825); Felipe Guerra (UFRN 4260, 4261, 4262); Galinhos (CHUFPB 25770); João Câmara (CHUPB 6549, 6552, 6553, 25870, 25022, 25549); Lagoa Nova (UFRN 4732); Martins (CHUFPB 25076, 25543); Riacho da Cruz (UFRN 4840, 4842, 4845, 4847, 4849, 4850, 4851, 4852); Santa Maria (UFRN 2935, 3031, 3156); Tenente Laurentino Cruz (UFRN 2724); **Pernambuco**: Paranamirim (CHUFPB 24998, 25089, 2559); Bezerros (CHUFPB 1991).

***Phyllopezus pollicaris* B [unassignet]**: BRAZIL: **Bahia**: Piatã (CHUFPB 25799); Itaparica (CHUFPB 1988).

APPENDIX II. Additional Cytb and ND2 mitochondrial genes sequences of *Phyllopezus* species used in this study. New sequences obtained in the present study are highlighted in bold.

Species	Voucher	Locality	Cytb	ND2
Phyllopezus pollicaris	**AAGARDA4446**	Paulo Afonço, Bahia		
Phyllopezus pollicaris	**AAGARDA4447**	Paulo Afonço, Bahia		
Phyllopezus pollicaris	**AAGARDA4566**	Paulo Afonço, Bahia		
Phyllopezus pollicaris	**AAGARDA4567**	Paulo Afonço, Bahia		
Phyllopezus pollicaris	**AAGARDA4568**	Paulo Afonço, Bahia		
Phyllopezus pollicaris	**AAGARDA4677**	Paulo Afonço, Bahia		
Phyllopezus pollicaris	**AAGARDA4678**	Paulo Afonço, Bahia		
Phyllopezus pollicaris	**FSCHUFPB0299**	Paulo Afonço, Bahia		
Phyllopezus pollicaris	**FSCHUFPB0265**	Canindé do São Francisco, Sergipe		
Phyllopezus pollicaris	**FSCHUFPB0266**	Canindé do São Francisco, Sergipe		
Phyllopezus pollicaris	**FSCHUFPB0292**	Canindé do São Francisco, Sergipe		
Phyllopezus pollicaris	**FSCHUFPB0293**	Canindé do São Francisco, Sergipe		
Phyllopezus pollicaris	**FSCHUFPB0294**	Canindé do São Francisco, Sergipe		
Phyllopezus pollicaris	**FSCHUFPB0295**	Canindé do São Francisco, Sergipe		
Phyllopezus pollicaris	**FSCHUFPB0930**	Santa Quitéria, Ceará		
Phyllopezus pollicaris	**FSCHUFPB0996**	Santa Quitéria, Ceará		
Phyllopezus pollicaris	**FDR1128**	Serra Talhada, Pernambuco		
Phyllopezus heuteri	MNHNP 2 39	Cordillera Department, Paraguay	MH397468.1	MH397468.1
Phyllopezus heuteri	MNHNP 2 40	Cordillera Department, Paraguay	MH397467.1	MH397467.1
Phyllodactylus unctus	MVZ 236276	Baja California Sur, Mexico	NC_020038.1	NC_020038.1
Phyllodactylus unctus	MVZ 236276	Baja California Sur, Mexico	HQ896027.1	HQ896027.1
Homonota fasciata	-	-	AB738953.1	AB738953.1
Tarentola mauritanica	MNCN/ADN7216	Las Gaviras-Granada, Spain	EU443255.1	EU443255.1

APPENDIX III. Residues of Principal Component (PC) and Discriminat Functions (DF) analysis based on 20 morphometrics characteristics for all analyzed populations of *Phyllopezus pollicaris*, only the *P. pollicaris* A populations, and only the *P. pollicaris* B populations occurring in northeastern Brazil.

	P. pollicaris				***P. pollicaris* A**				***P. pollicaris* B**				***P. pollicaris* B**			
	Fêmeas		**Machos**		**Fêmeas**		**Machos**		**Fêmeas**		**Machos**		**Fêmeas**		**Machos**	
	PC1	*PC2*	*PC1*	*PC2*	*PC1*	*PC2*	*PC1*	*PC2*	*PC1*	*PC2*	*PC1*	*PC2*	*DF1*	*DF2*	*DF1*	*DF2*
SVL	-15388	0.01610	-15713	0.016784	-0.9892	0.11274	-10310	0.14483	14176	-0.009969	14270	-0.04613	0.18849	0.00489	0.014098	-0.32003
DBL	-14126	-0.17682	-14515	0.014463	-0.9236	0.07706	-0.8837	0.13636	11781	0.172256	12027	-0.14948	0.07726	-0.0104	-0.17684	0.29924
TBW	-0.9668	-0.94936	-12201	0.211828	-0.8765	0.07539	-0.8057	0.59521	0.6573	0.937248	10375	0.17152	0.03923	0.43952	-0.62688	0.66509
HL	-15300	0.04348	-15736	0.054535	-0.9488	0.17707	-10081	-0.05642	14137	0.050726	14452	0.02191	-0.6546	0.45136	0.05422	-0.73526
HW	-14511	-0.31144	-14767	0.036387	-0.9621	-0.04356	-0.9235	0.31205	12456	0.389162	12984	-0.07856	0.28803	-0.2392	0.23311	0.33251
HD	-10034	-0.83143	-12858	0.095479	-0.8167	-0.37009	-0.8063	0.38636	0.9825	0.574637	10633	-0.01443	-0.1125	-0.3762	0.31939	0.69909
SL	-15345	0.09768	-15576	-0.049366	-0.9904	0.14220	-10128	-0.21421	13996	-0.038702	13641	-0.06775	-17176	-0.0795	0.65583	1.86150
NSD	-0.9335	0.07425	-0.9932	-1046092	-0.5327	-0.80125	-0.7424	-0.12684	0.5157	0.221660	0.2797	-104634	0.90582	0.65890	-0.99021	-0.83435
ESD	-14301	0.15613	-14462	0.031474	-0.8843	0.21472	-0.9225	-0.30666	12562	-0.167038	12947	-0.04756	1.6415	0.64979	0.9475	0.483616
ED	-13283	0.28403	-12987	-0.099366	-0.8232	0.22720	-0.7459	0.05241	10849	-0.333455	0.9635	0.08829	1.5046	-1.0693	0.46280	0.590540
IOD	-12276	-0.43698	-12773	-0.019514	-0.7778	-0.03891	-0.8898	0.11335	0.9881	0.404702	10333	-0.04778	-0.8614	0.17718	0.57677	-0.46521
IND	-11761	-0.16529	-11183	-0.869601	-0.7725	-0.27028	-0.7352	0.16174	0.6643	0.669908	0.4355	-110283	0.32622	0.65868	0.10447	-0.35400
LH	-14703	0.11407	-14635	0.096835	-0.9626	0.05749	-0.7499	0.05158	12561	-0.122585	12704	0.04547	0.18366	-0.0595	-0.09788	0.013982
LF	-13997	0.34104	-14767	0.039112	-0.7654	0.12195	-0.8769	-0.27864	12357	-0.287847	12778	-0.09471	0.83578	-0.0360	0.04076	0.44526
LT	-14101	0.24038	-14795	0.036728	-0.7383	0.37092	-0.7797	-0.19245	12005	-0.148560	12129	0.10173	-0.2788	0.04433	0.30614	0.19448
LTB	-14463	0.20596	-14958	0.090975	-0.8101	0.11801	-0.9224	-0.07024	12639	-0.011055	13010	0.02084	-0.2083	-0.6427	0.32210	-0.78576
WR	-13830	0.35699	-14095	0.005596	-0.8784	0.04903	-0.8217	-0.00635	10292	-0.512941	10122	-0.16498	-0.5176	0.75970	-1.65112	-0.39114
LR	-12306	0.13263	-12411	0.373813	-0.8378	-0.30049	-0.4899	-0.11209	0.7583	-0.559244	0.7776	0.60669	0.03975	-0.5939	0.92374	-0.16284
WM	-12841	0.33693	-12205	0.227961	-0.6399	-0.28649	-0.2076	-0.85608	10579	-0.368050	0.7366	0.47964	0.01710	-3.1197	-0.14931	-0.47018
LM	-11000	-0.08890	-11945	0.409142	-0.8273	-0.06113	-0.5965	-0.50068	0.9025	-0.239380	10766	0.27801	-0.4911	0.48620	-1.03201	0.29685

3 CAPÍTULO II – Two new species of geckos of the genus *Phyllopezus* Peters, 1878 (Squamata: Gekkota: Phyllodactylidae) from northeastern Brazil

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Abstract

We describe two new species of geckos of the genus *Phyllopezus* based on morphological and molecular data. The first species is currently known from a relictual Cerrado enclave, "*campos rupestres*", in the altitudinal area in State of Bahia, Brazil. The second species is known from Atlantic Forest and transitional areas with Caatinga biome in the State of Alagoas, in northeastern Brazil. The two new species are reciprocally monophyletic and correspond to the sister clade to the remaining species in the *Phyllopezus pollicaris* species complex. These new species can be morphologically distinguished from their congenerics by meristic and morphometric characters, in addition to color pattern.

Key words: Cryptic diversity; integrative taxonomy; lizard; morphological data; molecular phylogeny.

Introduction

The genus *Phyllopezus* Peters, 1878 includes saxicoulous and arboreal lizards distributed predominantly in the Dry Open Biomes of South America (Werneck *et al.* 2012; Cacciali *et al.* 2018). The genus is morphologically diagnosed by the presence of thin skin with small granular scales with equidistant larger tubercles, tail with small rhomboid scales, a single series of lamellae, not cloven, under the base of the fingers andtoes and, by the two distal phalanges of all five fingers and toes, which are narrowed towards the claw (Vanzolini 1953; Vanzolini *et al.* 1980; Boulenger 1885; Rodrigues 1986). Additionally, the monophyly of the genus is supported by molecular data, including mitochondrial (16SrRNA, Cytb and ND2) and nuclear (*e. g.* RAG1, RAG2, C-MOS and ACM4) genes (Gamble *et al.* 2012; Werneck *et al.* 2012; Cacciali *et al.* 2018).

Currently *Phyllopezus* is composed of six species: *P. heuteri* Cacciali, Lotzkat, Gamble & Köhler, 2018 (restrict to the Chaco biome in the Cordillera de Los Altos mountain range, Paraguay; Cacciali *et al.* 2018), *P. lutzae* (Loveridge, 1941) (restrict to the Atlantic Forest biome of northeastern Brazil, with distribution extending from the State of Paraíba to the State of Bahia; Albuquerque *et al.* 2019), *P. maranjonensis* Koch, Venegas & Böhme, 2006 (distributed in the dry forests of the upper Marañon basin, Peru; Koch *et al.* 2006), *P. periosus* Rodrigues, 1986 (distributed in the north region of Caatinga biome of states of Ceará to Pernambuco), *P. pollicaris* (Spix, 1825) (widely distributed in the Caatinga and Cerrado biomes and entering the Atlantic Forest in the eastern coast of Brazil; Werneck *et al.* 2012), and *P. przewalskii* Koslowsky, 1895 (distributed in the Chaco biome of Paraguay and north of Argentina and in the Cerrado biome, in the Central Brazilian Shield, in the states of Mato Grosso and Mato Grosso do Sul; Cacciali *et al.* 2018).

Contrasting with other taxa in the genus, the nominal species *P. pollicaris* has a wide distribution, including the Brazilian Seasonally Dry Tropical Forest and the Atlantic Forest. However, different studies have already revealed a hidden diversity associated with this taxon (*e. g.* Pellegrino *et al.* 1997; Gamble *et al.* 2012) and the presence of multiple evolutionary lineages (Gamble *et al.* 2012; Werneck *et al.* 2012) that still wait for formal descriptions. Werneck *et al.* (2012) recovered eight lineages associated to *P. pollicaris* sensu lato in the Caatinga, Cerrado, and Chaco biomes (Clades I – VIII), and treated them as candidate species. Later, Cacciali et al. (2018) ressurrected the nominal taxon *P. przewalskii* to accommodate populations belonging to Clade V and described a new lineage related to this

species (*P. heuteri*), thus making the nominal *P. pollicari*s a parafiletic taxon. The presence of high genetic diversity and the presence of reciprocally monophyletic groups, reinforces the need for additional studies for delimiting, and describing this cryptic diversity.
Herein we use an integrative approach, including molecular data and external morphology to describe two new species of *Phyllopezus* (assigned *P. pollicaris* complex) for Northeastern Brazil.

Material and methods

Material analized. We examined 146 specimens of *Phyllopezus* (Fig. 1; Appendix I). All *P. pollicaris* specimens analyzed for external morphology come from localities represented in the molecular datasets used in recent phylogenies (*i. e.* Gamble *et al.* 2012; Werneck *et al.* 2012). Specimens are deposited in the following herpetological collections: *Coleção Herpetológica* do *Museu de História Natural da Universidade Federal de Alagoas* (MUFAL), *Coleção Herpetológica* da *Universidade Federal da Paraíba* (CHUFPB), *Coleção Herpetológica* da *Universidade Federal de Pernambuco* (CHUFPE), and *Coleção Herpetológica* da *Universidade Federal do Rio Grande do Norte (*UFRN). Paralectotypes of *Phyllopezus pollicaris* (ZSM 165/0/1–2) were examined by photographs.

Phylogenetic inference and distance analyses. *Phyllopezus pollicaris* Clade I (population distributed in the municipality of Mucugê, state of Bahia, hereafter treated as *Phyllopezus* sp.1) has been previously considered as a candidate species (Gamble *et al.* 2012; Werneck *et al.* 2012; Cacciali *et al.* 2018). When analyzing the morphology of this candidate species, we noticed its similarity with some specimens occurring in the state of Alagoas, which although morphologically different from *P. pollicaris* sensu stricto, had never been included in a molecular study. We complemented the existent dataset of partial sequence of the 16SrRNA mitochondrial gene with representatives of three different locations (see Appendix II for GenBank accession numbers, vouchers, and localities; representatives of *P. pollicaris* Clades II and III of Werneck *et al*. [2012] were not included due the lack of 16SrRNA samples).
Total genomic DNA was extracted using phenol/chloroform protocol (Sambrook & Russel 2001). Subsequently, a fragment of the 16SrRNA mitochondrial gene was amplified through polymerase chain reaction (PCR), using the primers 16Sar-L and 16Sbr-H (Palumbi *et al.*

2002). Reactions consisted of 25µl with 12.5µl of Master Mix PCR Buffer with 0.4 mM of each dNTP and 3 mM of $MgCl_2$, 8.4 µl of nuclease-free water, 0.5 µl of Taq DNA polymerase (5U/µl), 0.8 µl of each primer (10pmol) plus 2 µl of DNA template (20 – 100ng/µl). Samples were amplified with: (1) initial denaturation at 94 °C for 90 sec followed by 35 cycles of denaturation at 94 °C for 45 sec, (2) annealing at 48 °C for 60 sec, and (3) extending at 72 °C for 60 sec. Samples were then purified using isopropanol to remove PCR residuals and sent to be unidirectional sequenced using Sanger method at the *Laboratório Central da Universidade Federal de Pernambuco* (LABCEN).

Sequences obtained were aligned with other 43 sequences (Appendix II) representative of all *Phyllopezus* species available on Genbank using MAFFT software v7.310 using default parameters (Katoh & Standley 2013). Genetic distances within and between species and among clades recovered by Werneck *et al.* (2012) were then estimated using Kimura 2-parameters evolutionary models (K2P) and p-distance (p-D) with complete deletion of gaps, implemented in software MEGA X (Kumar *et al.* 2018).

Bayesian analysis was performed in Mr. Bayes software version 3.2 (Ronquist *et al.* 2012). *Phyllodactylus xanti* was used for rooting the tree following Gamble *et al.* (2012). The choice of the best evolutionary model for the character matrix was performed in the PartitionFinder software v.2.1.1 (Lanfear *et al.* 2012) using the Bayesian Information Criterion (BIC) and default settings. The analysis consisted of two independent runs of 10 million generations each, being evaluated every 1,000 generations. The first 25% of the trees was discarded as burn-in, the majority consensual tree was visualized using the program FigTree software v.1.3.1 (Rambault & Drummond 2008). Values of posterior probability above 0.95 were considered with high support.

Species delimitation analyses. Four different methods for species delimitation based on a single locus were performed using the aforementioned matrix (excluding external groups). (1) We calculated a cutoff point for probable intraspecific divergence, specifically for our data set, using the Local Minima function of the Species Identity and Evolution in R package (SPIDER; Brown *et al.* 2012) implemented in the R Studio software v. 1.2.1 (R Core Team 2020). This analysis is based on the concept of a barcode gap, and species identification is not provided a priori. When the analysis detects a drop in the density of genetic distances, a possible transition between intra and interspecific distance values is suggested. (2) For the detection of hypothetical species, we performed an analysis of Automatic Barcode Gap

Discovery (ABGD; Puillandre *et al.* 2011) implemented on the ABGD online platform (https://bioinfo.mnhn.fr/abi/public/abgd/). This method is based on the general genetic divergences between the sequences of the matrix, using values from a series of previous intraspecific divergences. For this analysis, the sites with gaps were excluded, resulting in a matrix of 347 base pairs. The previous values for minimum and maximum intraspecific divergence were defined based on the results of Local Minima, and we also tested for values of interspecific divergence found between species already recognized in the genus (Gamble *et al.* 2012; Cacciali *et al.* 2018), and among Gekkota sister genus (Rocha *et al.* 2009; Fujita *et al.* 2010). Values between 0.001 and 1.5 of relative gap were tested. (3) To delimit species based on the topology recovered, an analysis of Bayesian implementation of the Poisson Tree Process (bPTP; Zhang *et al.* 2013) was performed. This model uses a rooted phylogenetic tree to model speciation or branching events in terms of the number of substitutions. The analysis was performed on the PTP web servers (https://species.h-its.org/ptp/) using default settings and clusters with support above 0.95 were indicated in the tree. (4) Finally, the Bayesian implementation of the Generalized Mixed Yule Coalescent model (bGMYC; Pons *et al.* 2006) was conducted. This model uses different topologies to model and to identify likely transition points between coalescence events and cladogenesis of alleles, incorporating phylogenetic uncertainties through a Bayesian extension (Reind & Carstens 2012). The topologies were obtained from a random selection of 100 trees resulting from a Baeysian inference implemented in the BEAST software v.1.8.4 (Suchard *et al.* 2018). The bGMYC analysis was performed in the R Studio software for 100,000 generations with a burn-in of 90,000 and a dilution interval of 100 samples. A cut-off point for the probability of recognition of genetic clusters of 50% was adopted.

External morphology. Measurements and scale counts were taken under a stereomicroscope. Measurements followed Rodrigues (1986), Cassimiro & Rodrigues (2009), and Sturaro *et al.* (2018), and were taken using a digital caliper with 0.1 mm precision (in right side of specimens whenever possible): snout-vent length (SVL, from tip of snout to cloacal opening), distance between limbs (DBL, from axilla to groin), tail base width (TBW, taken at the base of the organ just posterior to the cloaca), tail length (TL, from cloacal opening to tip of tail, only in specimens with intact, non-regenerated tails), head length (HL, from tip of snout to anterior margin of ear-opening), head width (HW, on the widest part of head), head depth (HD, on the highest part of head), snout length (SL, from tip of snout to

anterior margin of eye), nares-snout distance (NSD, from tip of snout to anterior border of nares), nares-eye distance (NED, to posterior border of nares to anterior edge of eye), eye-snout distance (ESD, from tip of snout to center of eye), eye diameter (ED, in widest section of the eye), interorbital distance (IOD, between the upper margins of eyes), internarial distance (IND, between the upper margins of nares), length of humerus (LH, from insertion of humerus to elbow), length of forearm (LF, from tip of elbow to wrist), length of thigh (LT, from insertion of femur to knee), length of tibia (LTB, from knee to ankle), width of mental scale (WM, between lateral corners), length of mental scale (LM, between anterior and posterior corners), width of rostral scale (WR, between lateral corners) and length of rostral scale (LR, between anterior and posterior corners).

Scale counts and scale definition followed Rodrigues (1986), and Cassimiro & Rodrigues (2009), and were counted as follows: number of rostrals (R), number of postrostrals (PR), number of postnasals (PN), number of supralabials (SL), number of infralabials (IL), number of mentals (M), number of postmentals (PM), scales that surround the postmental (SSP), number of ventrals in a longitudinal row (VLR, along a midventral line, from anterior margin of forelimbs to anterior margin of hind limbs), number of dorsal tubercles in a longitudinal row (DT, along a middorsal line, from anterior margin of forelimbs to tail), number of lamellae under the fourth finger (L4F), number of lamellae under the fourth toe (L4T), number of postcloacal tubercles at the sides of the vent (TP), and number of postcloacal pores (CP).

Sex was determined by direct inspection of gonads (when dissected), by the presence of eggs (females) or hemipenis (when everted) or by a small lateral insertion at the base of the tail when not everted (presence of the hemipenis or the hemipenial retractor muscle).

To identify whether there was sexual dimorphism in SVL, univariate analysis of variance (ANOVA) was performed. To identify variation between the sexes in the other morphometric characters, multivariate analysis of variance (MANOVA) was made. Due to the large number of dependent variables (N = 19) and the low number of samples for some species (N = 10 – 87), the data variation was summarized through a Principal Component Analysis (PCA) using the residuals of a linear regression considering the SVL as a factor. The interespecifc variation was summarized with PCA and Analyses3 for meristic and morphometric characters separately. In addition, these analyses were performed for the complete data set (including all species of the genus) and for a data set containing only the representatives of *Phyllopezus pollicaris* complex. All analysis were performed in the R Studio software.

For coloration description, we used the terminology proposed by Köhler (2012) with their corresponding color codes. For *P. heuteri*, *P. maranjonensis* and *P. przewalskii* morphological data for comparations were obtained from literature and/or photographs (Koslowsky 1895; Koch *et al.* 2006; Cacciali *et al.* 2018).

Results

Molecular approach

Phylogenetic inference and genetic distance analyses. The dataset included three new 16SrRNA sequences generated in this study and 45 obtained from Genbank. The best evolutionary model for the dataset was GTR + I + G. The Bayesian analysis recovered the monophyly of the *Phyllopezus pollicaris* complex (posterior probability *PP* = 0.99; sensu Werneck *et al.* 2012; Fig. 2). The two individuals of *Phyllopezus* sp.1 from xxx with identical haplotypes were recovered as sister of *Phyllopezus* sp.2 from xxx with high statistical support (*PP* = 1.0; genetic divergence between groups GD = K2P 0.093, p-D 0.087). The three individuals of *Phyllopezus* sp.2 from three different localities in Alagoas state (geographic distance between collecting sites from 33 to 76 km) also present identical haplotypes. The genetic divergence between *Phyllopezus* sp.1 and *Phyllopezus* sp.2 (GD *Phyllopezus* sp.1 x *Phyllopezus* sp.2 = K2P 0.093, p-D 0.087) was similar to that found among other recognized species of the genus (GD *P. heuteri* x *P. przewalskii* = K2P 0.096, p-D 0.089; see Table 1). This clade (*Phyllopezus* sp.1 and *Phyllopezus* sp.2, hereafter treated as "Group A" due to the sharing of morphological characteristics, see section Morphological approach) was recovered as sister of the remaining lineages belonging to the *P. pollicaris* complex. The Group A corresponds to the sister lineage (*PP* = 0.99) of the clade ((*P. pollicaris* Clade IV (*P. heuteri*; *P. przewalskyi*)) (*P. pollicaris* Clade VI (*P. pollicaris* Clade VII; *P. pollicaris* Clade VIII))) (hereafter treated as “Group B”; *PP* = 0.98). High intraspecific genetic divergences in two methods were observed in *P. pollicaris* clades IV and VII (GD = 0.047 and 0.061, respectively).

Species delimitation analyses. The ABGD analysis indicated the most likely transition point between inter and intraspecific genetic distances around 3–7% (Fig. 3B). The Local Minima function identified a first depression in the distance density curve at 5.73% (N =

1176, Bandwidth = 0.00975). The ABGD analyses did not show great variation between the number of delimited genetic clusters and varied from 15 clusters in relative widths of the range less than 1.0 to 16 clusters in relative widths of the range between 1.0 and 1.5 (Fig. 3). The analysis of bPTP and bGMYC recovered 20 genetic clusters, although in bPTP the subdivisions in the clades of *P. przewalskii* and *P. pollicaris* Clade VIII showed low support (less than 95%). Although the cut-off point of 50% was used for the probability of recognition of genetic clusters in bGMYC analysis, it was observed that even adopting a less conservative cut-off point of 90%, only one more genetic cluster was identified. In all analyses *Phyllopezus* sp.1 and *Phyllopezus* sp.2 were recovered in different genetic clusters with high statistical support (> 95%).

Morphological approach

External morphology. For *Phyllopezus* sp.1, significant values were identified regarding the difference in SVL between sexes (N = 6♂, 4♀; $F_{1.9} = 5.43$, $P = 0.04$). For *Phyllopezus* sp.2, there was not sexual dimorphism in relation to the SVL (N = 9♂, 12♀; $F_{1.19} = 0.15$, P = 0.70). However, we cannot affirm the presence or absence of sexual dimorphism in morphometric characters due to the low number of samples. There were also no variations between sexes considering all other morphometric characteristics: *Phyllopezus* sp.1 ($F_{1.19} = 2.381$, $P = 0.105$) and *Phyllopezus* sp.2 ($F_{1.8} = 0.179$, $P = 0.906$). Morphometric values are available in Appendix III.

When all species were analyzed together (Fig. 4A – B; residues available on Appendix III), *P. periosus* and *P. lutzae* were recovered in morphogroups reciprocally segregated in the PCAs and DFAs in all datasets used, with no overlap with the other morphotypes (exceptionally in some *P. periosus* outliers in the PCA for meristics data; Fig. 4A). In relation to the representatives of the *P. pollicaris* complex (Fig. 4C – D), the PCAs recovered morphogroups with low overlap, mainly in relation to the representatives of *P. pollicaris* sensu lato. For analyzes performed only with representatives of the *P. pollicaris* complex (Fig. 4E – H), morphogroups with almost no overlap in the morpho-space were recovered. Only in PCA using meristics characters *Phyllopezus* sp.1 and *Phyllopezus* sp.2 showed some overlap (Fig. 4E).

Taxonomic implications

Two main clades are recovered in the *Phyllopezus pollicaris* complex (Group A and B) showing high genetic divergence between them (GD = K2P 0.159, p-D 0.142), similar divergence found between more external specific lineages of the genus (*P. periosus*, *P. lutzae*, *P maranjonensis*; GD = 0.165 – 0.195). Morphologically the lineages belonging to Group A can be distinguished from those belonging to Group B (in parentheses) because the postmental scales in hexagonal-shaped, twice longer than wide (heptagonal-shaped with similar wight and length); larger dorsal tubercles, corresponding to about six granules, elongated and generally slightly keeled (smaller dorsal tubercles, corresponding to about four granules, subcircular or elliptical); first rows of reduced scales that surround the enlarged scales of the postmental region do not extend beyond the posterior margin of the third infralabial (always extend beyond the posterior margin of the third infralabial); and their larger size – SVL 88.5 ± 7.25 / 74.4 – 100.2 (SVL 71.7 ± 5.3 / 59.4 – 87.1; ANOVA, $F_{1,117}$ = 1.833, P = 0.031). For more details on the variations see the Comparison with congeners section.

Based on the external morphology and genetic data, two lineages belonging to Group A of the *Phyllopezus pollicaris* complex are identified and described herein as new species.

Species descriptions

***Phyllopezus* sp. nov. 1**

(Figs. 5, 6, 9A – D, 10A – E, 11G)

[http://zoobank.org/urn:lsid:zoobank.org:act: *incluido no momento da publicação*]

Phyllopezus pollicaris: Cassimiro & Rodrigues (2009); Freitas *et al.* (2012)
Phyllopezus pollicaris Clade A: Gamble *et al.* (2012)
Phyllopezus pollicaris Clade I: Werneck *et al.* (2012); Cacciali *et al.* (2018)
Phyllopezus sp.1 (aff. *pollicaris*): Dubeux *et al.* (*present study*)

Holotype. XX, an adult female (field number JC1234) from XX (XXºS, XXºW; XX m above sea level [a.s.l.]), municipality of Mucugê, Bahia state, Brazil, collected by J. Cassimiro on XX.

Paratypes. Adult females (JC, 1227, 1180, 1182, 1184, 1221, 1153) and adult males (JC 1176, 1183, 1185, 1219, 1222) from same locality of holotype (topotypes), collected by J. Cassimiro on XX.

Etymology. *Removido do texto*

Diagnosis. *Phyllopezus* **sp. nov. 1** is characterized by the following combination of character states: (1) Mental scales in sub-triangular shaped, with similar length and width and posterior margin not exceeding the second infralabial; (2) Postmental scales increased, in hexagonal shaped, twice as long as wide, with broad contact each other and previously separated by about 1/3 of its length by the mental scale; (3) Up to two scales in contact with the ventral margin of first infralabial; (4) Presence of increased scales that surround and separate the postmental scales from the granules of the gular region; (5) Six to seven infralabial scales; (6) Presence of granular scales in the distal region of mandible, juxtaposed, and may present as tubercles of different sizes; (7) Presence of increased dorsal tubercles, corresponding to about six granular scales, elongated and keeled; (8) Developed prepolex; (9) Cycloid or triangular scales around the auditory meatus, little bristly; (10) Homogeneous scales of the same size in the region of the labial commissure; (11) Many tubercles in the angular region between the upper and lower edges of the opening of the auditory meatus and eyes; (12) Postcloacal pores always present in males and females; and (13) large sized, SVL 76.41 – 96.25 mm in males, and 72.38 – 82.36 mm in females. See Comparison with congeners section for more individual diagnosis with other genus species.

Description of holotype. Adult female, SVL 96.25, fully regenerated tail, DBL 37.97, TBW 10.12, HL 27.75, HW 19.17, HD 8.73, SL 11.01, NSD 2.42, ESD 8.82, ED 6.94, IOD 8.87, IND 3.27, LH 21.04, LF 13.13, LT 22.02, LTB 15.41, WM 4.41, LM 4.28, WR 4.05, LR 2.16, R 1, PR 3, SN 2, SL 7, IL 7, M 1, PM 2, SSP 7, VLR 59, DT 45, L4F 10, L4T 14, TP 3, and CP 1. Head large (SVL/HL = 3.43), distinct from neck. Mental large (HW/WM = 4.3 and HL/LM = 6.4), sub-triangular, slightly wide than longer (WM/LM = 1.03), bordered by the 1st infralabial and in broad contact with two postmentals. A pair of postmental, large, hexagonal-shaped, juxtaposed, longer than wide, separated for mental by one third of length, flanked by seven large scales with differentiated sizes, which are replaced by granules juxtaposed that extend to the level of the labial commissure and are gradually replaced by similar small scales, smooth and imbricate, similar to ventral scales. First five infralabials rhomboid; the first largest, in broad contact with the postmental pair and a group of seven large, smooth, variable-shaped scales that isolate the postmentals from the granules of the

gular region. These are succeeded by small scales that undergo abrupt reduction in size until become granules in the beginning of the gular region. 1st infralabial smaller than 2nd, and from 2nd decrease in size towards the labial commissure, the commissure area with granules. 1st to 4th infralabial scales rhomboid-shaped. From the 2nd infralabial, there is a group of small, elongated scales that border the infralabial row to near of the labial commissure, which also isolates them from the granules of the gular region. Ventral scales smooth and imbricate, cycloid-shaped, arranged in longitudinal rows. Large rostral (HW/WR = 4.7 and HL/LR = 12.8), wider than long (WR/LR = 1.8), triangular-shaped, visible in dorsal view, with a fissure extending from the region in contact with the nasal to half of the rostral, and a perforation in the upper left side. A pair of post-rostrals protruding, separated by two tiny scales and in contact with the one of postnasals. Large supralabials, longer than wide, decreasing in size to the end of the labial commissure. First supralabial in broad contact with the rostral and one of the postnasals, involving part of the nostril. Posterior snout region and concave interorbital region. Dorsal and lateral surfaces of the head covered with granular juxtaposed scales, with scattered tubercles on the upper surface starting at the level of interorbital region. Granules in the snout larger than those of the occipital region. Eighteen small granules between the postnasals and anterior ocular margin. The granules surrounding the ocular region are tiny and more spaced than those of the snout and the dorsum. Postnasals swelling, elongated and bordering 1/4 of the nostril. The border of the auditory meatus is surrounded by small scales and granules. In the auditory meatus, the scales are small and smooth. Dorsal region of the body covered by granular scales and larger tubercles almost equidistant, conical-shaped and anteroposteriorly elongated, arranged in 10 to 14 irregular lines, reaching the level of the hindlimbs posterior region (before the tail insertion). Postcloacal tubercles present, three on each side, easily perceived. Postcloacal pores present, one on each side. Regenerated tail, presenting smaller overlapping cycloid scales in the dorsal region and increasing in size in the lateral region. A row of smooth, elongated medial scales in the ventral region of the tail, two or three times wider than long, covering to half of the ventral region of tail. Dorsal surface of the forelimbs and hindlimbs different of the dorsum of the body, with medium scales smooth and imbricate, tubercles absent. Palmar and plantar regions with small granules is replaced in the forearms by smooth, cycloid, and imbricated scales. The infradigital lamellae on the fourth finger of the forelimbs and hindlimbs are wider than long, wider than high, almost straight and two distal lamellae in open V-shaped falanges. Claws bordered by smooth and

imbricate scales, composed of five scales in the ventral region, five dorsal scales. Side of the claws formed by two rows of scales with five each. Presence of sheath with three scales.

Coloration in life (Fig. 6). XX

Coloration in preservative (Fig. 5). XX

Intraspecific variation. All diagnostic characteristics for the new species are seen in all specimens analyzed. The JC1180 specimen did not present postcloacal tubercles. The JC1176 specimen did not present postrostral scale. Morphometric variation and the scale count range among specimens are provided in Table 1.

Distribution, habitat, and natural history. XX

***Phyllopezus* sp. nov. 2**

(Figs. 7, 8, 9E – H, 10F – J, 11H)

[http://zoobank.org/urn:lsid:zoobank.org:act: *Incluido no momento da publicação*]

Hemidactylus mabouia: Roberto *et al.* (2015: part, p. 715, fig. 7)

Phyllopezus sp.: Gonçalves & Palmeira (2016)

Phyllopezus sp.2 (aff. *pollicaris*): Dubeux *et al.* (*present study*)

Holotype. MUFAL 13481, an adult female (original field number UGS 702) from Cariri da Prensa Farm (9.694722ºS, 36.204444ºW; DATUM WGS84; 83 m a.s.l.), in municipality of Boca da Mata, Alagoas state, Brazil, collected by U. Gançalves and C. Palmeira on 15 January 2014.

Paratypes. Adult females (MUFAL 13482, 13482, 13485) and an adult male (MUFAL 13486) from the same locality of holotype (topotypes), collected on XX; adult male (MUFAL 12401) and juvenile unsexed (MUFAL XXXX) from municipality of Quebrangulo, Alagoas state, Brazil, collected by MJMD, on XX (9.241111ºS, 36.420278ºW; 813 m a.s.l.); adult females (MUFAL 12166, 12170, 12169, 12196, 12198, 12398) and adult males (MUFAL 12167, 12168, 12172, 12396, 12197, 12397, 12400) from municipality of Limoeiro de Anadia, Alagoas state, Brazil, collected on XX (9.784722ºS, 36.467777ºW; 117 m a.s.l.); adult female (MUFAL 12449) and adult male (MUFAL 12128) from municipality of Coruripe, Alagoas state, Brazil, collected by on XX (10.054761ºS, 36.275761ºW; 68 m a.s.l.); adult females (MUFAL 10200, 12201, 12202) from municipality of Igaci, Alagoas state,

Brazil, collected on XX (9.533392ºS, 36.612003ºW; 269 m a.s.l.). All paratypes were collected by U. Gançalves and C. Palmeira.

Etymology. *Removido do texto.*

Diagnosis. *Phyllopezus* **sp. nov. 2** is characterized by the following combination of character states: (1) Mental scales in bell shaped, with concave margins and a slight strangulation in its half, similar length and width and posterior margin not exceeding the second infralabial; (2) Postmental scales increased, in hexagonal shaped, twice as long as wide, with broad contact each other and previously separated by about 1/5 of its length by the mental scale; (3) Up to two scales in contact with the ventral margin of first infralabial; (4) Presence of increased scales that surround and separate the postmental scales from the granules of the gular region; (5) Six to seven infralabial scales; (6) Precense of cycloid scales, imbricated, of similar size in distal region of mandible; (7) Presence of increased dorsal tubercles, corresponding to about six granular scales, elongated and slightly keeled; (8) Developed prepolex; (9) Cycloid or triangular scales around the auditory meatus, little bristly; (10) Homogeneous scales of the same size in the region of the labial commissure; (11) Up to two tubercles or tubercles absents in the angular region between the upper and lower edges of the opening of the auditory meatus and eyes; (12) Cloacal pores not always present; and (13) large sized, SVL 89.2 – 100.24 mm in males, and 83.5 – 99.47 mm in females. See Comparison with congeners section for more individual diagnosis with other genus species.

Description of holotype. Adult female, SVL 99.47 mm, fully regenerated tail, DBL 42.82 mm, TBW 12.31 mm, HL 27.02 mm, HW 19.53 mm, HD 9.2 mm, SL 11.08 mm, NSD 2.73 mm, ESD 8.29 mm, ED 6.09 mm, IOD 8.42 mm, IND 3.79 mm, LH 20.11 mm, LF 12.23 mm, LT 20.88 mm, LTB 15.3 mm, WM 4.64 mm, LM 4.98 mm, WR 4.54 mm, LR 2.3 mm, R 1, PR 2, SN 2, SL 8, IL 7, M 1, PM 2, SSP 7, VLR 51, DT 43, L4F 14, L4T 13, TP 2, and CP 0. Head large (SVL/HL = 3.68), distinct from neck. Mental large (HW/WM = 4.2 and HL/LM = 5.4), bell-shaped, slightly longer than wide (WM/LM = 0.93), narrower posteriorly and with a slight strangulation in its half, bordered by the 1st infralabial and in broad contact with two postmentals that isolated it from others infralabial and gular scales. A pair of postmental, large, hexagonal-shape, juxtaposed, longer than wide, and flanked by seven large scales with differentiated sizes, which are replaced by small scales, smooth and imbricate, similar to ventral scales. First, 2nd and 3rd infralabials in rhomboid format; 1st the largest, in contact with the postmental pair, and a group of five large, smooth and variable in shape scales that isolate the pair of postmentals from scales in the gular region. The infralabials

decrease in size towards the labial commissure; commissure area with granules. From the 2nd infralabial, there is a group of small, elongated scales that border the infralabial row near of the labial commissure, which also isolates them from the granules of the gular region. Ventral scales smooth and imbricate, cycloid-shaped, arranged in longitudinal rows. Large rostral (HW/WR = 4.3 and HL/LR = 11.74), wide than longer (WR/LR = 1.97), triangular-shaped, with a median depression at the top where there is a fissure extending from the region in contact with the nasal to half of the rostral. Large supralabials, longer than wide, decreasing in size to the end of the labial commissure. First supralabial in broad contact with the rostral and one of the postnasals, involving part of the nostril. Dorsal and lateral surfaces of the head covered with granular juxtaposed scales, with scattered tubercles on the upper surface starting at the level of interorbital region. Granules in the snout four to five times larger than those of the occipital region. Fifteen small granules between the postnasals and anterior ocular margin. The granules surrounding the ocular region are tiny and more spaced than those of the snout or the dorsum. The supranasal region involves half of the nasal fossa. Postnasals swelling, elongated and bordering 1/3 of anterior portion of the nostril. The border of the auditory meatus is surrounded by small granules. In the auditory meatus, the scales are erect and acicular, of triangular-shape, being smooth and imbricate. Dorsal region of the body covered by granular scales and larger tubercles almost equidistant, conical-shaped and elongated anteroposteriorly, arranged in 11 to 14 irregular lines, reaching the level of the posterior region of the hindlimbs (before the tail insertion). Postcloacal tubercles present, a pair on each side, very conspicuous. Postcloacal pores absent. Regenerated tail, presenting smaller overlapping cycloid scales in the dorsal region and increasing in size in the lateral region. A row of smooth, elongated medial scales in the ventral region of the tail, three or four times wider than long, covering almost the entire ventral region. Dorsal surface of the forelimbs and hindlimbs different of the dorsum of the body, with medium scales smooth and imbricate, tubercles absent. The small granules in the palmar and plantar regions are replaced by smooth, cycloid, and imbricated scales in the forearms. The infradigital lamellae on the fourth finger and fourth toe are wider than long, wider than high, slightly arched and becoming straighter in the distal portions. Claws bordered by smooth and imbricate scales, composed of five scales in the ventral region, five dorsal scales. Side of the claws formed by two rows of scales with five each. Presence of sheath with three scales.

Coloration in life (Fig. 8). Body with background color Raw Umber (22). The dorsum with semicontinuous longitudinal bands, on sides beginning in the postnasal region and

extending towards the base of the tail; band near the dorsal midline begins in the nuchal region; these bands show irregular dashes in the Dusky Brown (285) surrounded by Sayal Brown (41) tones. Small irregular spots in the Pale Horn Color (11) tones distributed along the dorsum of the body and limbs. A lateral band in the head beginning in the labial commissure (rather than dashes), Dusky Brown (285) color, that extends until the hindlimbs. Limbs in Raw Umber (22) pattern with irregular spots in Dusky Brown (285) and Sayal Brown (41) up to the claws. Head Raw Umber (22), superimposed by irregular spots Dusky Brown (285). Snout with a triangular-shaped Army Brown (46) spot, surrounded by Dusky Brown (285). Irregular Dusky Brown (285) spots between the eyes and the auditory meatus. Tail with well-defined transverse bands alternating between Raw Umber (22) and Sayal Brown (41) with Dusky Brown (285) spots. In the beginning of the tail, there is a Dusky Brown (285) triangular-shaped spot. The regenerated segment of the tail is a Raw Umber (22) color that is overlaid by Sayal Brown (41) spots that do not form a distinguishable pattern. Ventral region Pale Horn Color (11), without spot pattern. Infradigital lamellae Pale Mauve (204).

Coloration in preservative (Fig. 7). the color pattern is similar with alive specimens. The background color becomes similar to Belge (254), tending to a more grayish tone. The longitudinal bands retain their color; however, they lose the Sayal Brown color (41) that surrounds them in life, becoming more prominent in relation to the background. On the dorsal surface of the limbs and in the regenerated portion of the tail, the Sayal Brown color (41) becomes Fawn Color (258) and the ventral region becomes Pale Horn Color (11) slightly darker.

Intraspecific variation. All diagnostic characteristics used for describing the new taxon are present in all specimens analyzed. However, different patterns of dorsal background coloration in life were observed, depending on the time and type of the substrate of capture, ranging from Raw Umber (22) to Drab [19]. Ontogenetic variations of color were also observed, with juvenile individual (MUFAL XXX) presenting a more demarcated dark bars and more light color background (Pale Buff [1]). Morphometric and meristic variation are provided in Table 1.

Distribution, habitat, and natural history. *Phyllopezus* **sp nov. 2** is a nocturnal species found in rocky outcrops and trees up 10 meters high. In the daytime, specimens were found sheltering either under tree bark, clumps of epiphytes or bromeliad roots in early evening where it was found foraging. Specimens were found in the border and in the interior

of forested sites near rivers with rocky bed, where also it was found foraging. The species was also recorded sharing bromeliads with *P. lutzae*. When specimens were captured manually, it twisted the body using the movement to turn quickly to the sides, in the attempt to bite producing an agonistic sound. The distribution of the species is only known for the state of Alagoas, with altitudes ranging from 68 m a.s.l. in the municipality of Coruripe at 813 m at the top of the rock formation of Pedra Talhada, municipality of Quebrangulo (Fig. 1).

Comparison with congeners

Phyllopezus **sp. nov. 1** and *Phyllopezus* **sp. nov. 2** are morphologically more similar to each other than to the other representatives in the genus and together are distinguished from the congeners mainly by characters in the gular region (Fig. 11). Both new species (Fig. 11G – H) differ from *P. periosus* (Fig. 11A) by the presence of increased scales separating the postmentals granules in the gular region (versus absent in *P. periosus*), posterior margin of the mental scale not exceeding the anterior margin of the second infralabial scale (versus exceeding the anterior margin of the second infralabial in *P. periosus*) and postmental scales in direct contact (versus separated by the mental scale in *P. periosus*). Both new species differ from *P. lutzae* (Fig. 11B) by presenting a long mental scale, with similar length and width (versus short mental with a length corresponding to half the width in *P. lutzae*), posterior margin of the posmental scales exceeding half of the second infralabial (versus not reaching the second infralabial in *P. lutzae*) and up to two scales in contact with the first infralabial (versus three to four scales in contact with the ventral margin of the first infralabial in *P. lutzae*). Both new species differ from *P. maranjonensis* (Fig. 11C) in having the central pair of postmentals distinctly larger than the scales that surround them and in contact with the first infralabial (versus almost the same size and separated from the first infralabial by one or two scales in *P. maranjonensis*). Both new species differ from *P. maranjonensis* and *P. heuteri* in having six or seven infralabial scales (versus 7 **–** 10 in *P. maranjonensis* and eight – nine in *P. heuteri*). Both new species differ from *P. maranjonensis*, *P. heuteri (*Fig. 11F), *P. pollicaris* stricto sensu (Fig. 11D) and *P. przewalskii* (Fig. 11E) in having postmental scales twice longer than wide (versus postsmentals with similar width and length in *P. maranjonensis, P. heuteri, P. pollicaris* and *P. przewalskii*).

In relation to other morphological characters, the two new species can also be distinguished from *P. periosus* in having a color pattern in longitudinal or transverse dark irregular dorsal

bars (versus 6 to 7 well-defined light-colored transverse bands limited anteriorly and posteriorly by bars dark in *P. periosus*). The two new species can be distinguished from *P. lutzae* in being distinctly larger (72.38 – 96.25 mm in *Phyllopezus* **sp. nov. 1** and 83.50 – 100.24 mm in *Phyllopezus* **sp. nov. 2** versus a maximum of 62.77 mm in *P. lutzae*), in having a staining pattern in irregular longitudinal or transverse dorsal dark bars (versus homogeneous orange marbled pattern in *P. lutzae*). Both new species can be distinguished from *P. lutzae* and *P. maranjonensis* in having increased dorsal tubercles, corresponding to about six granules (indistinct dorsal tubercles in *P. lutzae* and few slightly enlarged tubers on the back, rarely forming rows on *P. maranjonensis*). Both new species can be distinguished from *P. lutzae* in having developed prepolex (versus absent or poorly developed in *P. lutzae*). The two new species can be easily distinguished from *P. maranjonensis* in having a pattern of staining in irregular longitudinal or transverse dorsal dark colored bars (versus four regular dark colored cross bars between the neck and vent in *P. maranjonensis*), and six to eight supralabial scales (versus 8 – 10 in *P. maranjonensis*). Both new species can be distinguished from *P. heuteri* in being cycloid or triangular scales around the auditory meatus, little bristly (versus spiny and bristling scales in *P. heuteri*).

Regarding the two new species described here, *Phyllopezus* **sp. nov. 1** can be differentiated from *Phyllopezus* **sp. nov. 2** due to the presence of granular scales of the distal region of mandible, juxtaposed, and may present tubercles of different sizes (versus cycloid scales, imbricated, of similar size in *Phyllopezus* **sp. nov. 2**), mental scale with triangular-shape and almost straight lateral edges (versus bell-shaped with concave margins and a slight strangulation in its half in *Phyllopezus* **sp. nov. 2**; Fig. 9), and anterior portion of the postmental scales separated by almost 1/3 of the length by the mental scale (versus separated by 1/5 in *Phyllopezus* **sp. nov. 2**; Fig. 9), dorsal coloration pattern in dark transverse bands interrupted by a light cervical band (dark bands arranged in well-defined or transverse longitudinal rows showing interruptions, light cervical band absent or not evident in *Phyllopezus* **sp. nov. 2**; Figs. 5-8), four to six tubercles in the angular region between the upper and lower edges of the opening of the auditory meatus and eyes (up to two tubercles or tubercles absents in this region in *Phyllopezus* **sp. nov. 2**; Fig. 10A and F), homogeneous scales of the same size in the region of the labial commissure (increased scales on the upper and lower sides of the labial commissure in *Phyllopezus* **sp. nov. 2**; Fig. 10A and f), and a pair of postcloacal pores is always present (not always present in *Phyllopezus* **sp. nov. 2**, Fig.

10B and G). Morphometric variations and the scale counts range among specimens analyzed are provided in Table 1.

Discussion

In addition to the cryptic diversity already recognized for the *Phyllopezus pollicaris* complex (Gamble *et al.* 2012; Werneck *et al.* 2012; Cacciali *et al.* 2018), the loss of the lectotype (ZSM 2510/0; Michael Franzen *comm. pers.* in Cacciali *et al.* 2018) have hampered taxonomic arrangements involving the group. *Phyllopezus* (*Thecadactylus*) *pollicaris* was described by Spix (1825) almost 200 years ago, to accommodate a population in the interior of the state of Bahia ("*sylvis interioris Bahiae campestribus*"), with no further locality data (Spix 1825; Vanzolini 1953). In Bahia state, a high diversity of lineages belonging to the *P. pollicaris* complex were found, some of them are not closely related (*Phyllopezus* **sp. nov. 1** and *P. pollicaris* Clades III, VI and VIII; Werneck *et al.* 2012; Cacciali *et al.* 2018; present study).

All the diagnostic characters for the both new species and the comparisons with congeners were based on the photographs of the paralectotypes of *P. pollicaris* [ZSM 165/0/1–2; according to Müller & Brongersma (1933) those specimens were in the original type series], in the detailed description of these provided by Müller & Brongersma (1933) and Cacciali *et al.* (2018), and in the original description by Spix (1825). We observed that the *P. pollicaris* paralectotypes are morphologically similar to lineages belonging to Group B (*P. heuteri* + *P. przewalskii* + *P. pollicaris* Clades IV and VI – VIII). They share characteristics such as number, size, format and disposition of the gular scales and its small size (see Taxonomic Implications and Comparison with Congeners Sessions). Although the municipality of Mucugê is located in Bahia, the same Brazilian state where the type-locality of *P. pollicaris* sensu stricto is located, based on the morphological comparisons explicated above we are confident that the new species is not the same phylogenetic lineage of *P. pollicaris* of Spix. The 16SrRNA was the most conservative mitochondrial gene in the delimitation of genetic clusters of *Phyllopezus* (Cacciali *et al.* 2018) and recovered the monophyletic reciprocity of *Phyllopezus* **sp. nov. 1** and *Phyllopezus* **sp. nov. 2.** In addition, it was efficient in recovering the phylogenetic relationships of the *Phyllopezus* lineages even among the more recent diversifications, as already identified in previous studies (Gamble *et al.* 2012; Cacciali *et al.* 2018).

The high cutoff point for the transition between intra and interspecific variation identified by the analysis of Local Minima (5.73%) and reinforced by ABGD is probably the result of the long and complex evolutionary history of the genus (Werneck *et al.* 2012). According to Werneck *et al.* (2012) the populations of the municipality of Mucugê (Bahia) (*Phyllopezus* **sp. nov. 1**), together with those of the municipalities of São Geraldo do Araguaia (Pará state) and Barra do Garça (Mato Grosso state) (Clade II; not included in the present study), and now also the lineage of *Phyllopezus* **sp. nov. 2** for Alagoas state (present study), correspond to the sister clade to all the remaining representatives of the *P. pollicaris* complex, highly distinct from the other congeners and that diverged early (~11.5 Ma). Although related, the lineages within this clade have a widely disjunct distribution and are surrounded by areas of occurrence of other lineages belonging to the complex (Werneck *et al.* 2012). Such a scenario may represent a sampling deficit in some regions or a wide historical extinction of these lineages in the intermediate regions, which may be key to understanding the diversification and current distribution of the oldest lineages of *P. pollicaris* complex.

The type locality of ***Phyllopezus*** **sp. nov. 1** is located in the septentrional portion of the mountain range of *Serra do Espinhaço*, a region of "*campos rupestres*" at more than 1,000 meters of elevation. Such regions with high elevation are characterized by unique phytophysiognomies and a high index of endemism (see below). The establishment of these mountain ranges may have been related with regional events that potentialized the divergence of lineages of the *P. pollicaris* complex, as has already been reported to of frogs (Lugli & Haddad 2006a, b; Cassimiro *et al.* 2008; Faivovich *et al.* 2009; Pombal-jr *et al.* 2012; Leite *et al.* 2012; Carvalho *et al.* 2013; Trevisan *et al.* 2020), lizards (Rodrigues *et al*. 2006; Cassimiro & Rodrigues 2009; Rodrigues *et al.* 2009a, b; Rodrigues *et al.* 2017), and amphisbaenans (Mott *et al.* 2008).

For *Phyllopezus* **sp. nov. 2**, although it is known for a wide latitudinal gradient in the state of Alagoas, it is likely that its area of occurrence is still underestimated, since the state still has a high level of Wallacean deficit (lack of knowledge of the geographic distribution of species; Whittaker *et al.* 2005). Almost all areas of registration of the species are associated with the Coruripe River basin, obtained in one of the few herpetofauna inventories carried out in the *Agreste* region of the state (Gonçalves & Palmeira 2016).

Although we are far from resolving the taxonomy of *P. pollicaris* species complex, the present work brings diagnostic morphological characters and the formal description of two species. One of them was considered as the candidate species by Werneck *et al.* (2012) and

the other was not included in previous studies. It is the beginning of a long journey to describe the morphological diversity in the genus neglected for decades.

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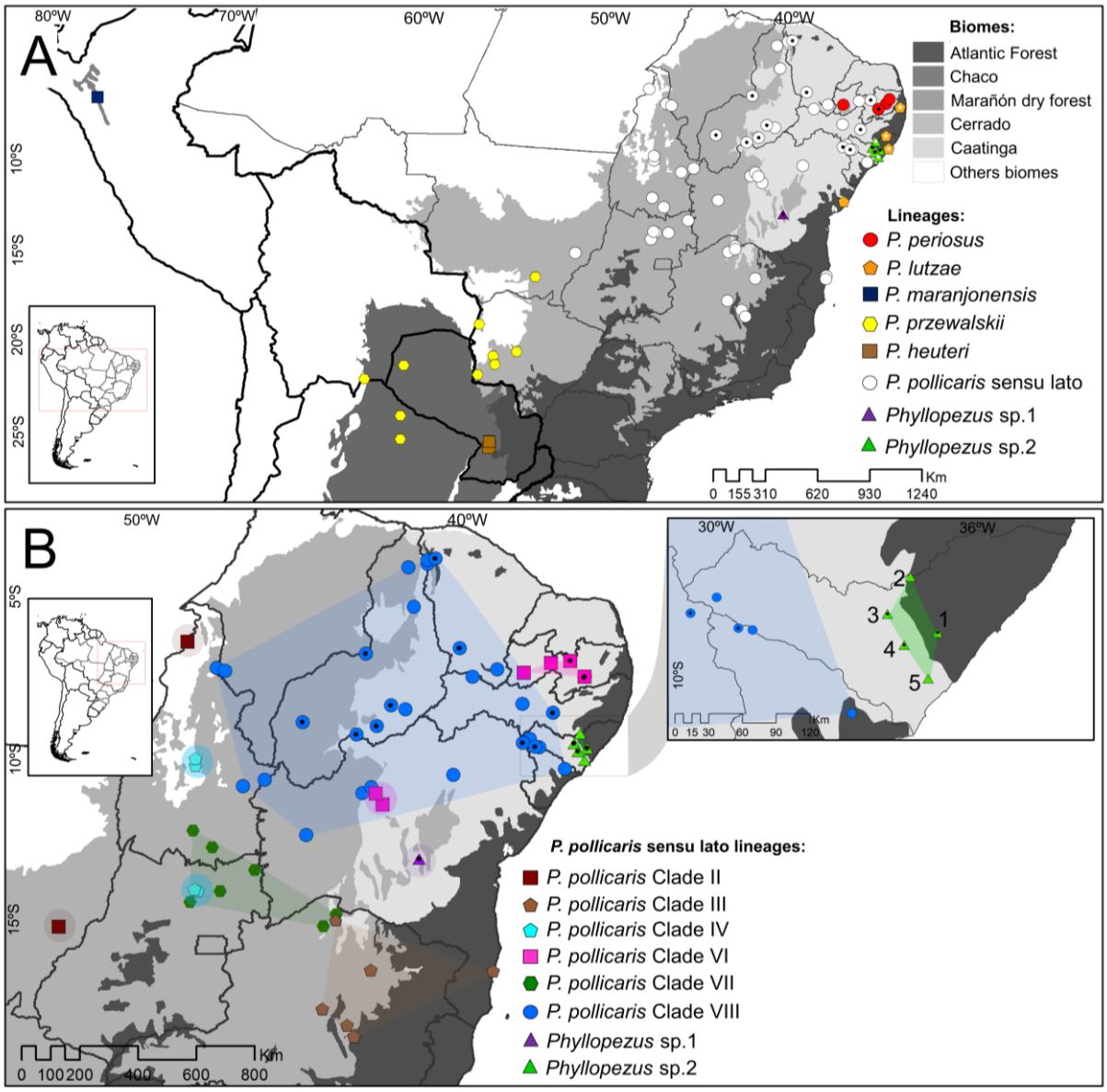

FIGURE 1. Geographic distribution of genetic and morphological vouchers analyzed in this study. (A) *Phyllopezus* nominal species and (B) only of the lineages belonging to the *P. pollicaris* sensu lato following Werneck *et al.* 2012. Black dots denote the localities with molecular and morphological samples. White dots denote the localities with only morphological samples. Locations without points denote only molecular samples. Inset map: South America.

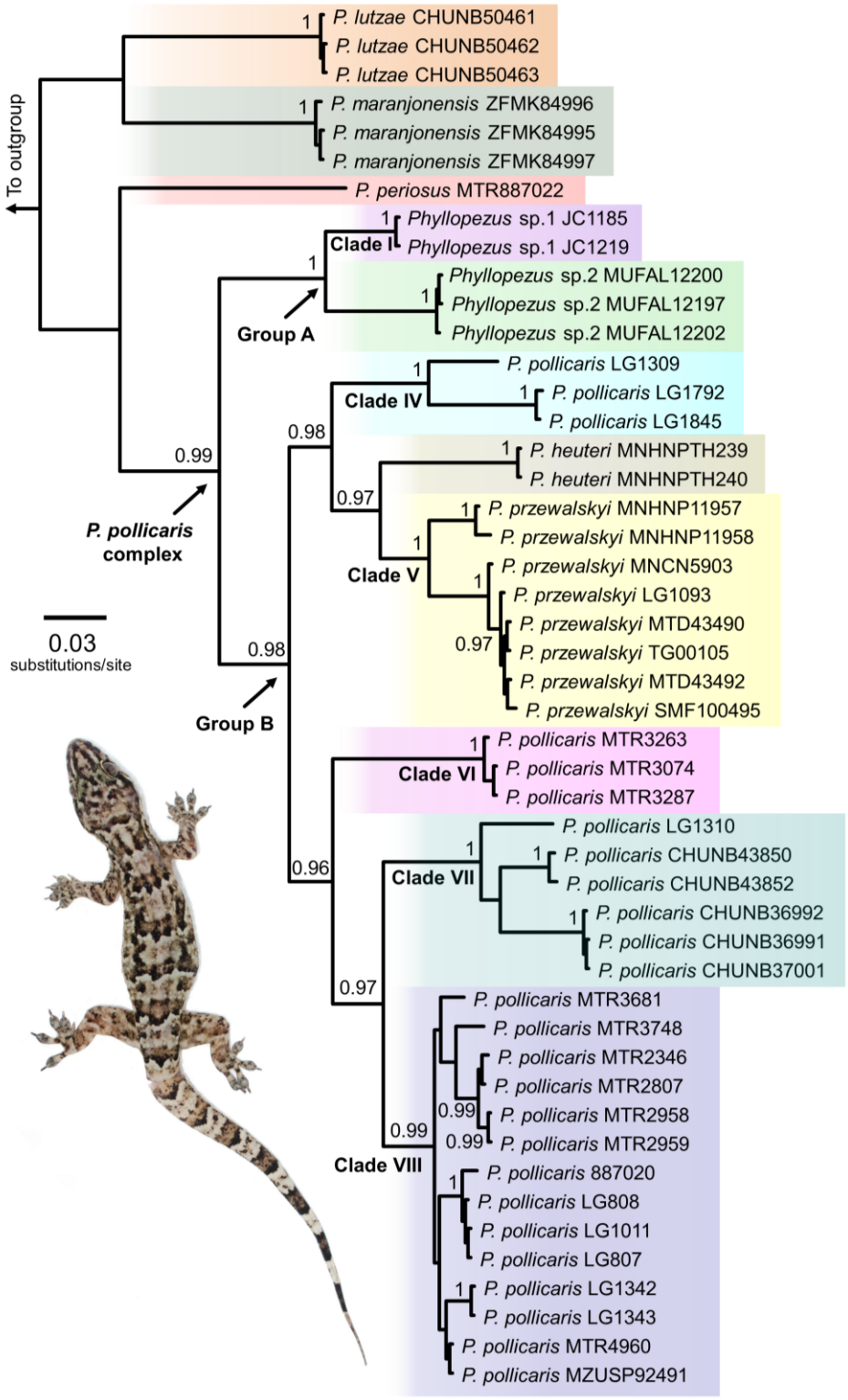

FIGURE 2. Phylogram obtained by the Bayesian Inference of the16SrRNA mitochondrial gene fragment (486 pb) of *Phyllopezus*. Values in nodes indicate Bayesian posterior probabilities. *Phyllopezus pollicaris* Clades I and IV – VIII follow the definitions by Werneck *et al.* (2012). No representatives of the Clades II and III were included due to the lack of 16SrRNA sequences.

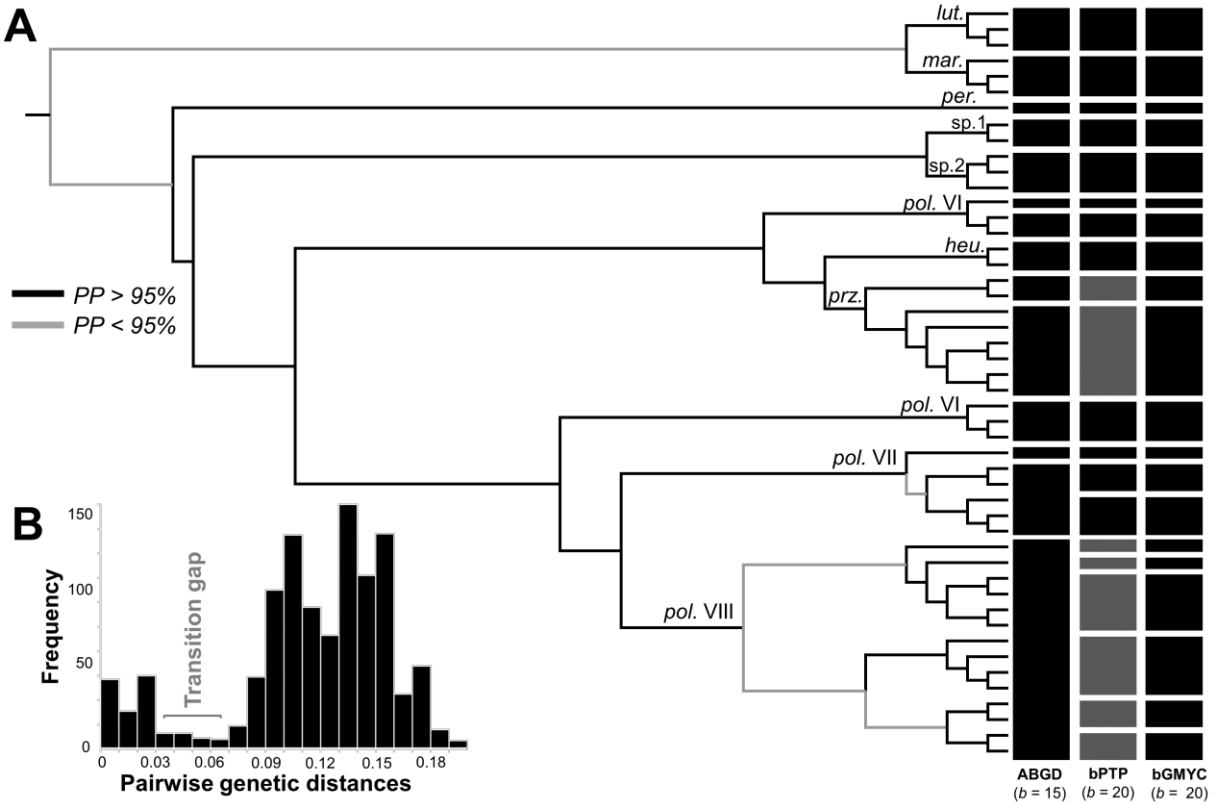

FIGURE 3. (A) Summary results of *Phyllopezus* species delimitations based on 16SrRNA mitochondrial gene fragment using ABGD, bPTP and bGMYC models, respectively. Total genetic breaks found in each model. Abbreviations above nodes: lut. = *P. lutzae*, mar. = *P. maranjonensis*, per. = *P. periosus*, sp.1 = *Phyllopezus* sp.1, sp.2 = *Phyllopezus* sp.2, pol. VI = *P. pollicaris* VI, heu. = *P. heuteri*, prz. = *P. przewalskii*, pol. VI = *P. pollicaris* VI, pol. VII = *P. pollicaris* VII, and pol. VIII = *P. pollicaris* VIII. (B) Most likely transition gap between intraspecific (left) and interspecific (right) genetic distances of *Phyllopezus* sequeces using 347 bp of 16SrRNA mitochondrial gene fragment. *Phyllopezus pollicaris* Clades follow Werneck *et al.* (2012).

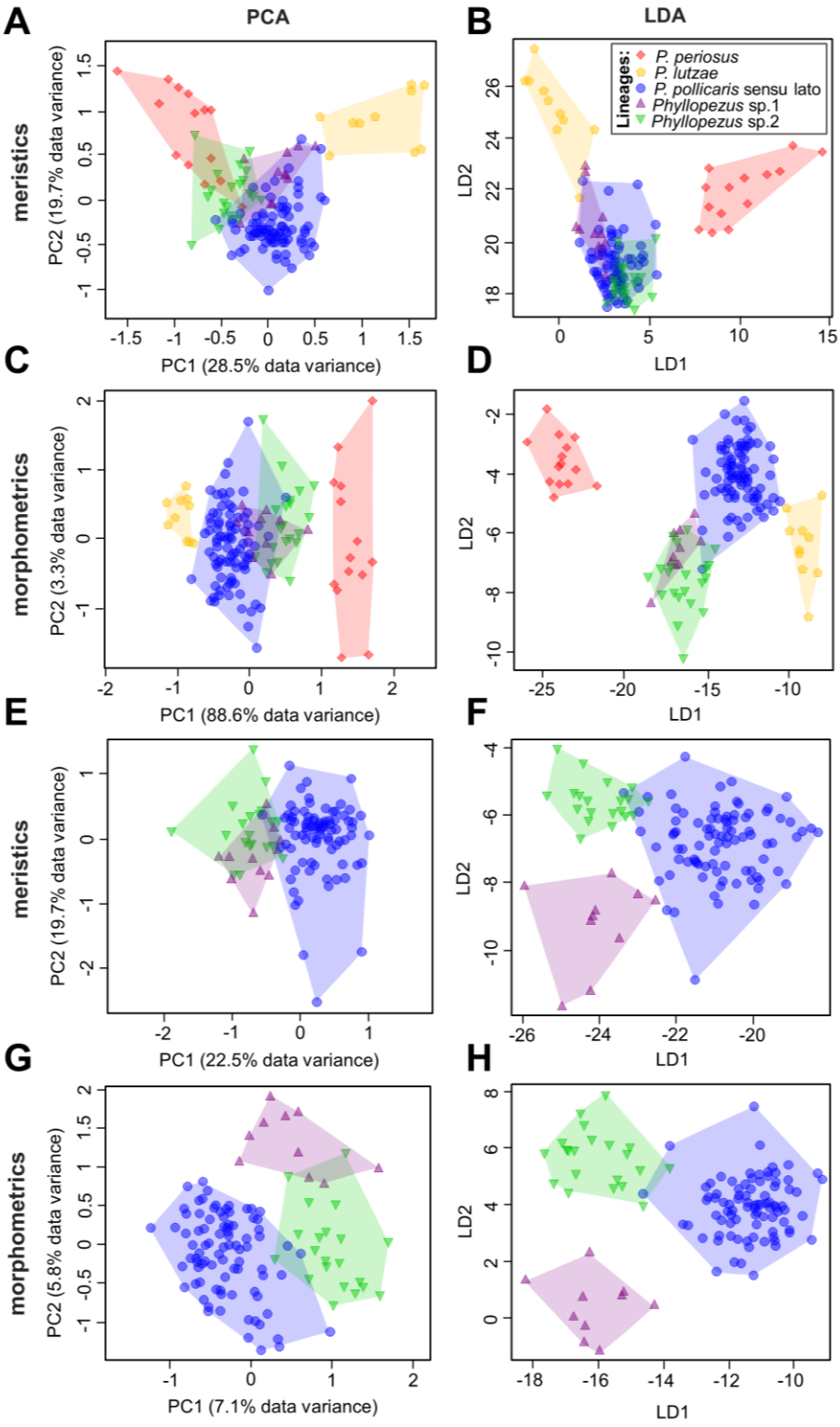

FIGURE 4. Principal Component Analysis (PCA; left) and Discriminant Function Analyzes (DFA; right) based on 13 meristic and 20 morphometric characteristics independently for (A – D) all lineages of *Phyllopezus* and (E – H) only the lineages of *P. pollicaris* complex occurring in northeastern Brazil.

FIGURE 5. Holotype of *Phyllopezus* **sp. nov. 1** *(*JC1234, adult female, SVL = 96.25 mm). Scale bar = 10 mm.

FIGURE 6. Coloration in life of *Phyllopezus* **sp. nov. 1**.

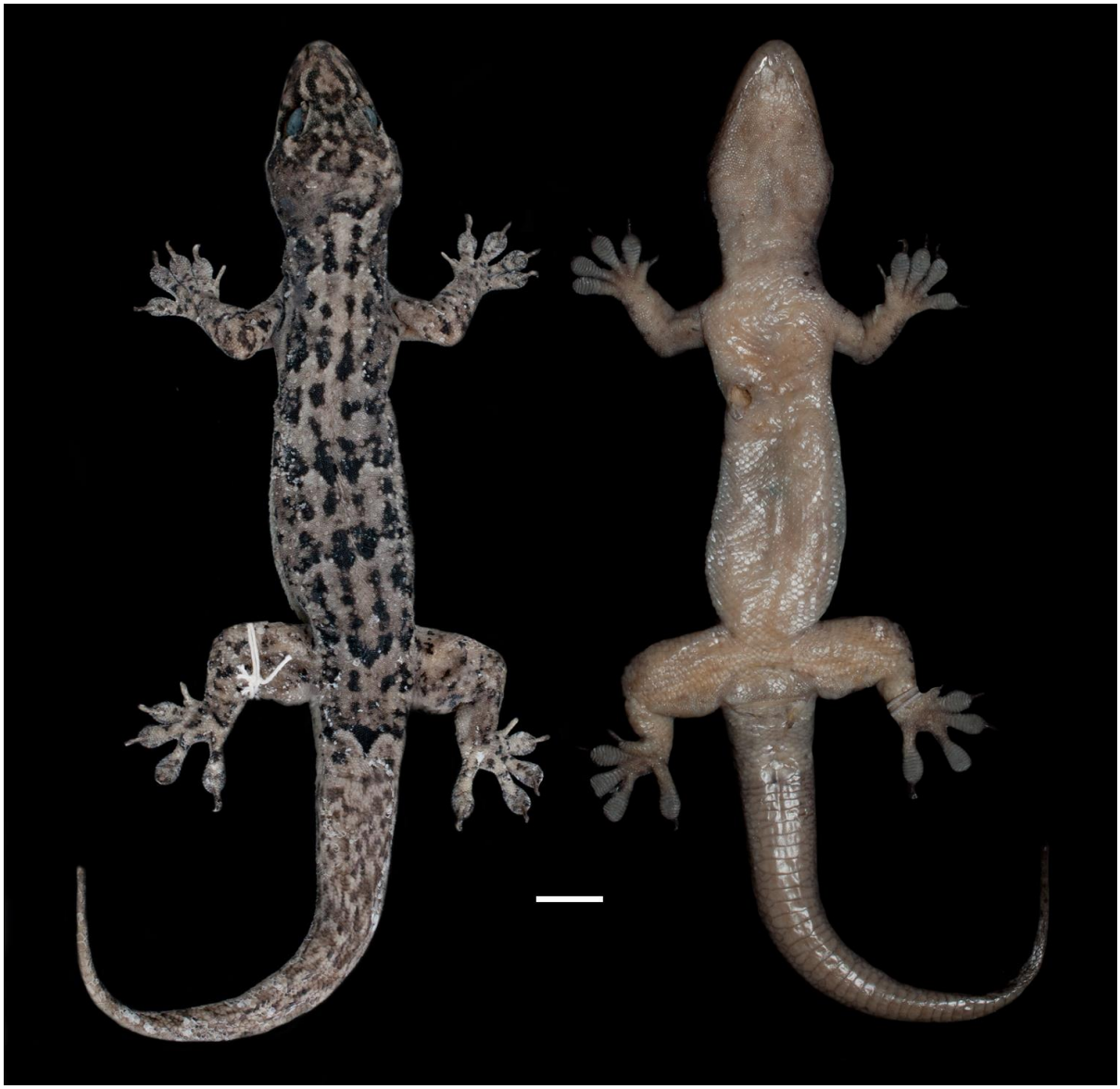

FIGURE 7. Holotype of *Phyllopezus* **sp. nov. 2** *(*MUFAL 13481, adult female, SVL = 99.47 mm). Scale bar = 10 mm.

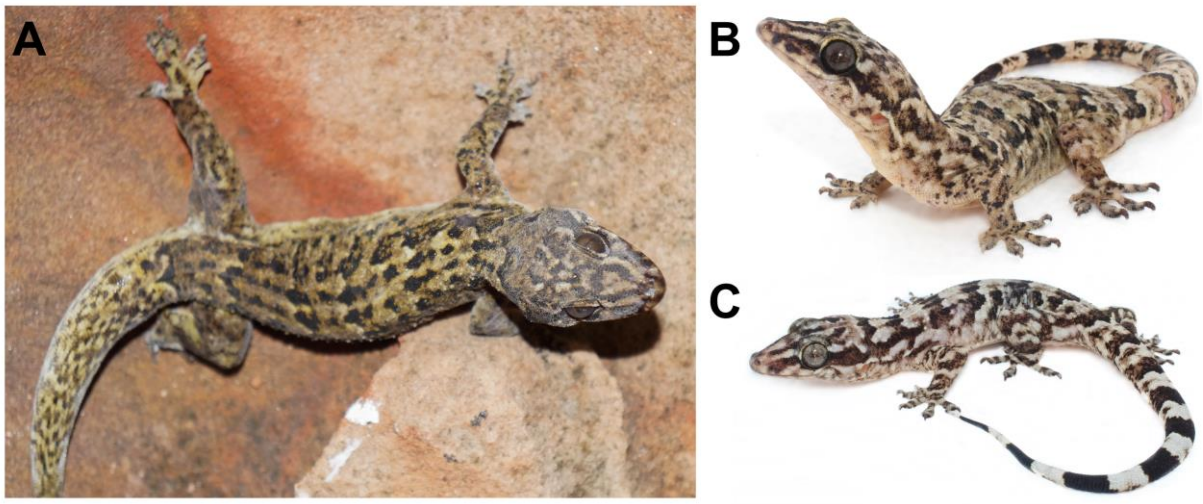

FIGURE 8. Coloration in life of *Phyllopezus* **sp. nov. 2**. **(**A) Holotype [MUFAL 13481], (B and C) paratypes [MUFAL XXX and MUFAL XXX, respectively], (C) variation of juvenile coloration.

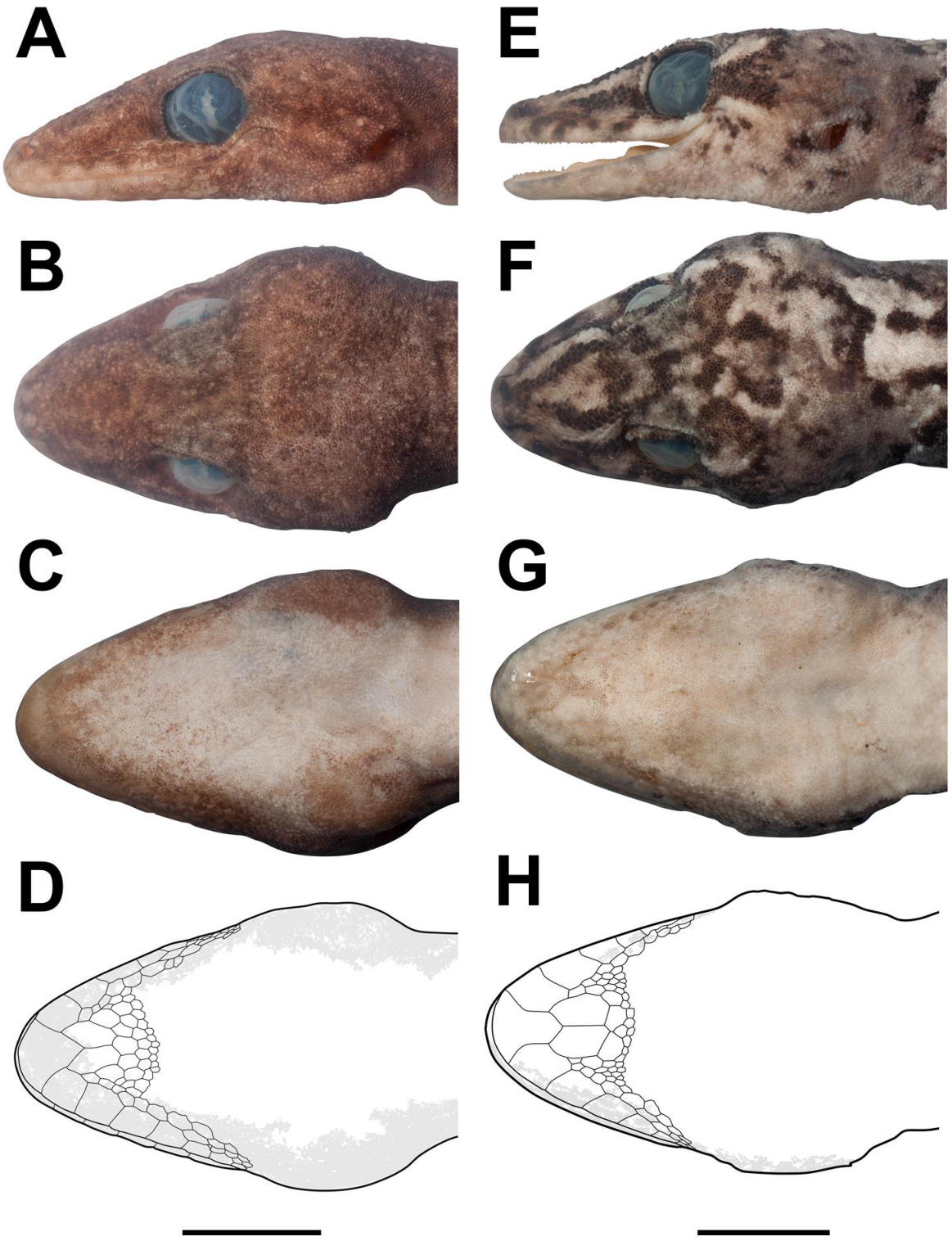

FIGURE 9. Details of head in lateral, dorsal and ventral views and scheme of scales limits in gular region of holotypes of *Phyllopezus* **sp. nov. 1** *(*A – D) and *Phyllopezus* **sp. nov. 2** *(*E – H). Scale bars = 10 mm.

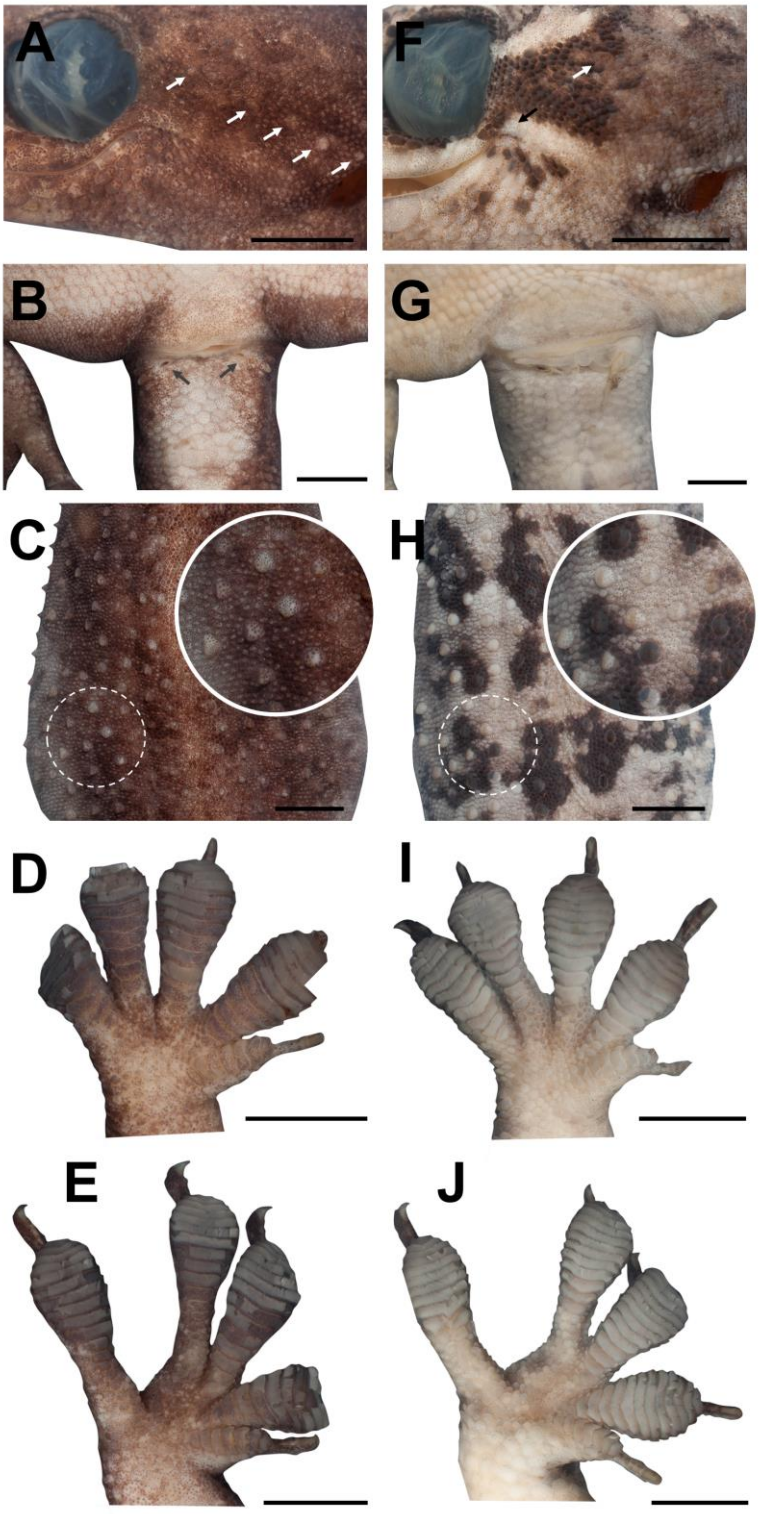

FIGURE 10. Details of diagnostical characters between *Phyllopezus* **sp. nov. 1** *(*A – E) and *Phyllopezus* **sp. nov. 2** *(*F – J). Angular region between the ocular and auditory meatus region [white arrows highlight enlarged tubercles, black arrow highlights enlarged scales in the region of the labial commissure]; cloacal region [grey arrows highlight the postcloacals pores]; dorsal region of the body highlight the dorsal tubercles; palm of hand; and sole of foot. Scale bars = 5 mm.

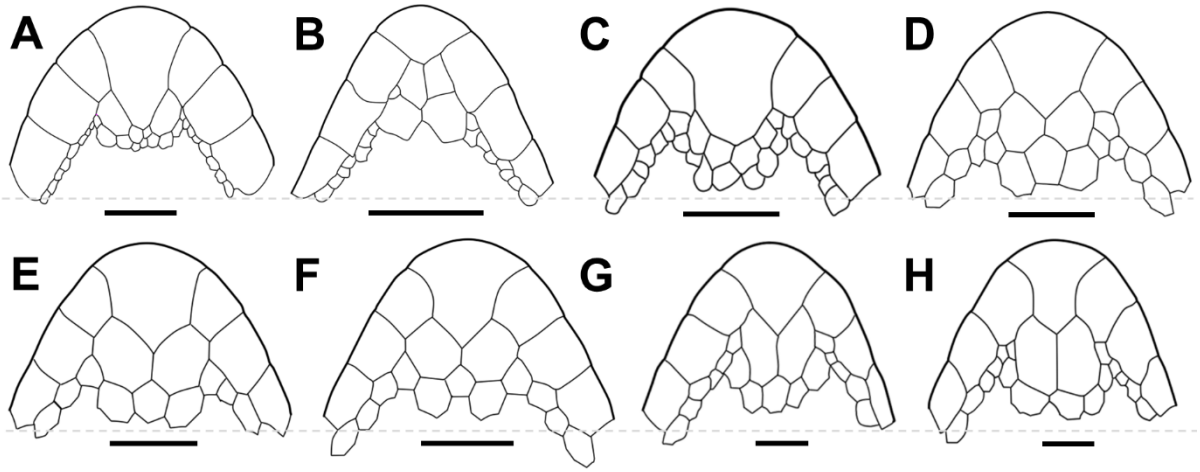

FIGURE 11. Scheme of the arrangement of scales in the gular region of *Phyllopezus* species. (A) *P. periosus* [based on CHUFPB 1936], (B) *P. lutzae* [based on CHUFPB 19518], (C) *P. maranjonensis* [based on ZFMK 84997], (D) *P. pollicaris* stricto sensu [ZSM 165/0/1, paralectotype], (E) *P. przewalskii* [based on SMF 100496], (F) *P. heuteri* [based on SMF 100494], (G) *Phyllopezus* **sp. nov. 1** [based on JC 1234] and (H) *Phyllopezus* **sp. nov. 2** [based on MUFAL 13481]. Figures D – F adapted of the photographs provided by Cacciali *et al.* (2018). Horizontal dashed gray line marks the posterior margin of the third infralabial scale. Scale bars = 3mm.

TABLE 1. Genetic distances between and within species and clades of the *Phyllopezus* genus estimated using Kimura 2-parameters evolutionary model (K2P = bottom right diagonal) and p-distance (p-D = top left diagonal) with complete deletion of gaps in the 16SrRNA mitochondrial gene fragment. The lowest values of genetic distances between species are highlighted in bold. *Intraspecific genetic distances higher than the cutoff point indicated by the Local Minima analysis. *Phyllopezus pollicaris* Clades follow Werneck *et al.* (2012).

Specie/Clade	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**Intraspecific**	
												K2P	**p-D**
1. *P. periosus*	-	0.156	0.169	0.182	0.183	0.181	0.185	0.203	0.187	0.173	0.168	-	-
2. *P. lutzae*	0.177	-	0.135	0.173	0.165	0.176	0.161	0.182	0.154	0.145	0.150	0	0
3. *P. maranjonensis*	0.193	0.150	-	0.181	0.164	0.157	0.170	0.192	0.167	0.156	0.171	0.002	0.002
4. *P. heuteri*	0.211	0.199	0.208	-	**0.089**	0.131	0.129	0.155	0.130	0.139	0.127	0.000	0.000
5. *P. przewalskii*	0.213	0.189	0.186	**0.096**	-	0.112	0.106	0.139	0.110	0.126	0.123	0.023	0.022
6. *P. pollicaris* IV	0.209	0.204	0.177	0.147	0.123	-	0.128	0.155	0.123	0.142	0.148	0.061*	0.057
7. *P. pollicaris* VI	0.214	0.183	0.193	0.144	0.115	0.142	-	0.125	0.097	0.154	0.145	0.004	0.004
8. *P. pollicaris* VII	0.240	0.212	0.224	0.178	0.156	0.177	0.139	-	0.094	0.161	0.154	0.050	0.047
9. *P. pollicaris* VIII	0.217	0.174	0.189	0.145	0.120	0.136	0.105	0.102	-	0.145	0.143	0.021	0.021
10. *Phyllopezus* sp.1	0.198	0.162	0.175	0.155	0.140	0.159	0.174	0.185	0.162	-	**0.087**	0	0
11. *Phyllopezus* sp.2	0.190	0.169	0.194	0.141	0.135	0.168	0.162	0.175	0.160	**0.093**	-	0	0

APPENDIX I. Additional specimens examined

Phyllopezus lutzae: BRAZIL: Paraíba: Pedras de Fogo (CHUFPB 19517, 19518, 19519, 24979); Alagoas: Maceió (UFRN 36, 236; LABI 181, 182, 183); Quebrangulo (LABI 653).
Phyllopezus periosus: BRAZIL: Paraíba: Cabaceiras (Topotypes: CHUFPB 1930, 1931, 1934, 1936, 1939, 1940, 1947); Rio Grande do Norte: Serra Negra do Norte (MUFAL 12426, 12428); Currais Novos (UFRN 5551, 5552).
Phyllopezus pollicaris: BRAZIL: Bahia: Paulo Afonço (CHUFPB 11294, 11295, 11296, 11297, 11298, 11299, 11300, 12058, 22330, 25018, 25111, 25137, 25569); Ceará: Aiuaba (CHUFPB 5145, 5147, 5153, 5159, 5160, 5161, 5162, 5163, 5165, 5324, 5325, 5326, 5327, 5328, 5329, 13767, 13768, 13769, 13778, 13780, 13788); Ubajara (CHUFPB 26129, 26894, 26916); Paraíba: Cabaceiras (CHUFPB 10224, 10225, 10228, 10229, 10230, 10231); Pernambuco: Buíque (CHUFPB 23509, 25026, 25562, 25973; CHUFPE-R CAT272, 391, 271,388, 392); Piauí: Urucuí (CHUFPB 8697); Floriano (CHUFPB 8699); Coronel José Dias (CHUFPB 14603, 14606, 14608, 14611, 14614, 14616, 14617, 14618); Andorinha (CHUFPB 22324, 22349, 22364, 22450, 22473, 22603); São Raimundo Nonato (CHUFPB 25050, 25153); Sergipe: Canindé de São Francisco (CHUFPB 18559, 18562, 18563, 18567, 18568, 18570, 18573, 18581, 18587, 18592, 18594, 18595, 18602, 18605, 18626, 18633).

APPENDIX II. 16SrRNA mitochondrial gene fragment sequences of *Phyllopezus* species used in the study. Clades previously delimited by Werneck *et al.* (2012) are identified by Roman numbers.

Species	Clade	Voucher	Locality	GenBank
Phyllopezus **sp. nov. 1**	I	(MTR) JC 1185	Mucugê, Bahia, Brazil	JN935553
Phyllopezus **sp. nov. 1**	I	(MTR) JC 1219	Mucugê, Bahia, Brazil	JN935554
Phyllopezus **sp. nov. 2**	-	MUFAL 12202	XXX	
Phyllopezus **sp. nov. 2**	-	MUFAL 12200	XXX	
Phyllopezus **sp. nov. 2**	-	MUFAL 12195	XXX	
Phyllopezus pollicaris	IV	LG 1309	Serra da Mesa, Goiás, Brazil	JN935569
Phyllopezus pollicaris	IV	LG 1792	Palmas, Tocantins, Brazil	JN935572
Phyllopezus pollicaris	IV	LG 1845	Lajeado, Tocantins, Brazil	JN935574
Phyllopezus pollicaris	VI	MTR 3074	Santo Inácio, Bahia, Brazil	JN935584
Phyllopezus pollicaris	VI	MTR 3287	Santo Inácio, Bahia, Brazil	JN935586
Phyllopezus pollicaris	VI	MTR 3263	Gentio do Ouro, Bahia, Brazil	JN935585
Phyllopezus pollicaris	VII	LG 1310	Niquelândia Goiás, Brazil	JN935568
Phyllopezus pollicaris	VII	CHUNB 36991	Paranã, Tocantins, Brazil	JN935559
Phyllopezus pollicaris	VII	CHUNB 36992	Paranã, Tocantins, Brazil	JN935560
Phyllopezus pollicaris	VII	CHUNB 37001	Paranã, Tocantins, Brazil	JN935561
Phyllopezus pollicaris	VII	CHUNB 43850	São Domingos, Goiás, Brazil	JN935563
Phyllopezus pollicaris	VII	CHUNB 43852	São Domingos, Goiás, Brazil	JN935564
Phyllopezus pollicaris	VIII	MTR 887020	Cabaceiras, Paraíba, Brazil	JN935558
Phyllopezus pollicaris	VIII	LG 1011	Porto Seguro, Bahia, Brazil	JN935566
Phyllopezus pollicaris	VIII	LG 807	Xingó, Alagoas, Brazil	JN935575
Phyllopezus pollicaris	VIII	LG 808	Xingó, Alagoas, Brazil	JN935576
Phyllopezus pollicaris	VIII	LG 1342	Campo Formoso, Bahia, Brazil	JN935570
Phyllopezus pollicaris	VIII	LG 1343	Campo Formoso, Bahia, Brazil	JN935571
Phyllopezus pollicaris	VIII	MTR 2346	Uruçuí-Una, Piauí, Brazil	JN935580
Phyllopezus pollicaris	VIII	MTR 2807	Uruçuí-Una, Piauí, Brazil	JN935581
Phyllopezus pollicaris	VIII	MTR 2958	Uruçuí-Una, Piauí, Brazil	JN935582
Phyllopezus pollicaris	VIII	MTR 2959	Uruçuí-Una, Piauí, Brazil	JN935583
Phyllopezus pollicaris	VIII	MTR 3681	Ilha do Gado Bravo, Bahia, Brazil	JN935587
Phyllopezus pollicaris	VIII	MTR 3748	Alagoado, Bahia, Brazil	JN935588
Phyllopezus pollicaris	VIII	MTR 4960	Serra das Confusões, Piauí, Brazil	JN935589
Phyllopezus pollicaris	VIII	MZUSP 92491	Serra das Confusões, Piauí, Brazil	JN935590
Phyllopezus przewalskii	V	TG 00105	unknown, Paraguay	JN935565
Phyllopezus przewalskii	V	LG 1093	Fuerte Esperanza, Chaco, Argentina	JN935567
Phyllopezus przewalskii	V	MTD 43490	Fortin Toledo, Boqueron, Paraguay	JN935578
Phyllopezus przewalskii	V	MTD 43492	Fortin Toledo, Boqueron, Paraguay	JN935579
Phyllopezus przewalskii	V	MNCN 5903	Serranía Aguarague, Tarija, Bolivia	JN935577
Phyllopezus przewalskii	-	SMF 100495	Paraguay	MF278834
Phyllopezus przewalskii	-	MNHNP 11957	Paraguay	MH397465
Phyllopezus przewalskii	-	MNHNP 11958	Paraguay	MH397466
Phyllopezus heuteri	-	MNHNP 2 39	Cordillera Department, Paraguay	MH397468
Phyllopezus heuteri	-	MNHNP 2 40	Cordillera Department, Paraguay	MH397467
Phyllopezus lutzae	-	CHUNB 50461	Mata de São João, Bahia, Brazil	JN935548
Phyllopezus lutzae	-	CHUNB 50462	Mata de São João, Bahia, Brazil	JN935549
Phyllopezus lutzae	-	CHUNB 50463	Mata de São João, Bahia, Brazil	JN935550
Phyllopezus periosus	-	MTR 887022	Cabaceiras, Paraíba, Brazil	JN935552
Phyllopezus maranjonensis	-	ZFMK 84995	Balsas, Peru	JN935555
Phyllopezus maranjonensis	-	ZFMK 84997	Balsas, Peru	JN935557
Phyllopezus maranjonensis	-	ZFMK 84996	Balsas, Peru	JN935556
Phyllodactylus xanti	-	ROM 38490	Baja California Sur, Mexico	AY763284

APPENDIX III. Morphometrics (in mm) and meristic data [mean ± standard deviation (range)] of *Phyllopezus* occurring in northeastern Brazil. Details of acronyms of characteristics are mentioned in Material and methods section.

	P. lutzae		***P. periosus***		***P. pollicaris* sensu lato**		***Phyllopezus* sp. nov. 1**		***Phyllopezus* sp. nov. 2**	
	Male(n = 3)	Female(n = 7)	Male(n = 10)	Female(n = 4)	Male(n = 43)	Female(n = 44)	Male(n = 6)	Female(n = 4)	Male(n = 9)	Female(n = 12)
SVL	61 ±1.61 (59.61–62.77)	56.93 ±2.85 (53.2–60)	107.23 ±4.27 (101.34–113.62)	104.03 ±4.21 (97.28–108.38)	73.31 ±4.94 (65.12–85.6)	70.78 ±4.96 (63.65–87.11)	84.66 ±6.7 (76.41–96.25)	76.67 ±4 (72.38–82.36)	93.59 ±3.68 (89.2–100.24)	92.06 ±5.61 (83.5–99.47)
DBL	26.12 ±1.1 (25.36–27.38)	24.06 ±1.92 (20.94–26.2)	46.3 ±2.91 (41.56–50.43)	45.68 ±2.26 (42.1–47.69)	31.7 ±2.42 (28.53–38.8)	30.75 ±2.84 (25.51–37.37)	35.55 ±2.87 (32.07–39.06)	31.45 ±2.44 (28.09–34.07)	41.28 ±1.35 (38.6–43.05)	40.53 ±1.49 (38.61–42.82)
TBW	6.95 ±0.44 (6.58–7.44)	6.91 ±1.81 (5.35–10.84)	13.36 ±1.43 (11.63–15.43)	10.45 ±1.94 (8.36–13.64)	9.03 ±1.41 (7.27–13.07)	8.49 ±1.18 (5.5–11.58)	8.46 ±1.2 (6.56–10.12)	6.87 ±0.47 (6.36–7.49)	11.2 ±0.58 (10.34–11.91)	9.91 ±1.08 (9.02–12.31)
HL	17.58 ±0.67 (16.99–18.3)	14.9 ±3.41 (7.35–17.49)	29.98 ±1.65 (27–32.4)	30 ±1.52 (27.38–31.21)	20.67 ±1.41 (18.49–25.3)	19.79 ±1.44 (17.42–23.46)	24.1 ±2.05 (21.46–27.75)	22.12 ±1.1 (21.08–23.93)	25.22 ±0.59 (24.41–26.21)	24.87 ±1.37 (22.88–27.02)
HW	11.6 ±0.45 (11.1–11.96)	11.76 ±2.26 (10.31–16.76)	22 ±1.17 (19.81–23.67)	21.09 ±1.46 (19–23.11)	15.32 ±1.04 (13.61–18.3)	14.25 ±1.11 (12.32–17.46)	16.45 ±1.84 (13.47–19.17)	14.29 ±0.73 (13.16–14.89)	18.33 ±0.94 (17.4–20.23)	17.72 ±0.97 (16.18–19.53)
HD	6.1 ±0.43 (5.83–6.59)	5.76 ±0.65 (4.63–6.72)	12.55 ±1.12 (11.28–14.2)	12.51 ±1.18 (11.38–13.8)	8.19 ±0.9 (6.22–10.43)	7.95 ±0.86 (6.36–9.65)	8.07 ±0.73 (7.3–9.06)	7.22 ±0.4 (6.55–7.55)	9.86 ±0.82 (8.89–10.97)	8.62 ±0.66 (7.47–9.54)
SL	7.33 ±0.13 (7.2–7.45)	6.96 ±0.34 (6.32–7.37)	12.84 ±0.62 (11.68–13.83)	12.75 ±0.38 (12.1–13.08)	8.24 ±0.59 (7.17–10.32)	7.87 ±0.59 (6.99–9.33)	9.98 ±0.71 (8.93–11.01)	8.98 ±0.46 (8.5–9.69)	10.22 ±0.44 (9.68–10.99)	10.15 ±0.49 (9.48–11.08)
NSD	1.65 ±0.22 (1.39–1.79)	1.7 ±0.17 (1.46–1.96)	2.48 ±0.4 (2–3.22)	2.94 ±0.24 (2.74–3.3)	1.94 ±0.31 (1.4–3.08)	1.77 ±0.25 (1.25–2.29)	2.08 ±0.19 (1.9–2.42)	1.92 ±0.08 (1.83–2.02)	2.28 ±0.2 (1.95–2.53)	2.27 ±0.37 (1.75–2.75)
ESD	5.43 ±0.2 (5.2–5.59)	5.34 ±0.44 (4.57–5.78)	10.32 ±0.66 (8.87–10.89)	9.79 ±0.64 (8.67–10.24)	6.48 ±0.41 (5.53–7.49)	6.23 ±0.58 (5.25–7.79)	7.76 ±0.72 (6.76–8.82)	6.99 ±0.29 (6.75–7.32)	7.71 ±0.53 (6.94–8.41)	7.79 ±0.35 (7.38–8.29)
ED	3.34 ±0.22 (3.09–3.49)	3.27 ±0.29 (2.92–3.54)	6.09 ±0.45 (5.4–6.66)	6.06 ±0.26 (5.66–6.35)	4.36 ±0.41 (3.52–5.46)	4.27 ±0.36 (3.29–5.32)	5.24 ±1.11 (3.72–6.94)	4.66 ±0.52 (4.11–5.16)	5.08 ±0.3 (4.56–5.39)	5.19 ±0.49 (4.76–6.09)
IOD	5.91 ±0.3 (5.62–6.21)	5.44 ±0.66 (4.78–6.78)	9.9 ±0.53 (9.17–10.84)	8.95 ±0.21 (8.68–9.17)	7.2 ±0.66 (5.56–8.41)	6.86 ±0.61 (5.84–8.73)	7.48 ±0.79 (6.65–8.87)	6.39 ±0.7 (5.65–7.08)	8.58 ±0.63 (7.55–9.28)	8.34 ±0.51 (7.73–9.39)
IND	2.48 ±0.07 (2.4–2.54)	2.2 ±0.18 (1.94–2.38)	3.87 ±0.49 (3.34–4.88)	3.81 ±0.16 (3.71–4.09)	2.69 ±0.3 (2–3.46)	2.61 ±0.29 (1.98–3.32)	2.98 ±0.35 (2.64–3.38)	2.77 ±0.31 (2.47–3.24)	3.37 ±0.32 (3.12–3.98)	3.27 ±0.28 (2.77–3.79)
LH	11.49 ±0.8 (10.58–12.06)	10.76 ±0.57 (9.99–11.71)	23.26 ±1.94 (21.22–26.73)	20.09 ±0.86 (19.26–21.46)	15.09 ±1.27 (13.12–18.03)	14.43 ±1.33 (11.8–18.37)	18.07 ±1.64 (16.37–21.04)	16.11 ±0.51 (15.65–16.72)	18.38 ±1.44 (17.04–20.84)	18.54 ±0.88 (17.36–20.11)
LF	7.09 ±0.44 (6.59–7.4)	6.84 ±0.39 (6.12–7.41)	14.82 ±0.6 (13.92–15.78)	14.18 ±0.69 (13.27–15.09)	9.65 ±0.78 (7.59–11.29)	9.07 ±0.72 (7.76–11)	11.89 ±0.72 (10.91–13.13)	10.94 ±0.48 (10.35–11.36)	11.75 ±0.71 (10.67–12.81)	11.28 ±0.57 (10.34–12.23)
LT	12.24 ±0.51 (11.69–12.7)	11.91 ±0.34 (11.49–12.39)	25.68 ±1.06 (24.26–27.75)	25.39 ±1.61 (23.04–27.15)	16.12 ±1.25 (13.79–19.76)	15.54 ±1.23 (13.08–18.13)	20.24 ±1.24 (18.32–22.02)	18.44 ±1.06 (17.28–19.58)	21.02 ±1.78 (19.25–24.12)	19.97 ±1.21 (18.06–21.23)
LTB	8.51 ±0.18 (8.31–8.63)	8.18 ±0.48 (7.27–8.7)	18.63 ±1.15 (15.73–19.86)	17.67 ±0.84 (16.51–18.48)	11.58 ±0.9 (10.23–14.3)	11.05 ±0.8 (9.51–13.12)	14.06 ±0.91 (12.57–15.41)	13.1 ±0.72 (12.16–13.94)	14.46 ±0.7 (13.51–15.4)	14.07 ±0.73 (13.04–15.3)
WM	2.46 ±0.02 (2.44–2.48)	2.32 ±0.21 (2.06–2.67)	5.09 ±1.61 (3.85–8.8)	4.54 ±0.26 (4.21–4.85)	3.08 ±0.32 (2.49–4.14)	2.93 ±0.26 (2.27–3.58)	3.76 ±0.21 (3.56–4.05)	3.43 ±0.24 (3.14–3.76)	3.87 ±0.3 (3.39–4.23)	4.03 ±0.38 (3.54–4.54)
LM	1.19 ±0.15 (1.03–1.32)	0.96 ±0.11 (0.8–1.17)	2.49 ±0.45 (1.84–3.2)	2.16 ±0.27 (1.79–2.48)	1.56 ±0.19 (1.15–1.93)	1.48 ±0.18 (1.15–1.95)	1.93 ±0.19 (1.6–2.16)	1.58 ±0.18 (1.39–1.85)	2.11 ±0.2 (1.82–2.33)	2.02 ±0.23 (1.52–2.3)
WR	2.68 ±0.05 (2.64–2.74)	2.48 ±0.32 (2.06–2.96)	4.69 ±0.36 (4.26–5.28)	4.63 ±0.26 (4.35–4.96)	3.3 ±0.28 (2.83–4.12)	3.08 ±0.33 (2.1–3.92)	4.38 ±0.41 (3.65–4.77)	3.74 ±0.44 (3.13–4.23)	4.03 ±0.19 (3.82–4.32)	4.26 ±0.37 (3.53–4.64)
LR	1.55 ±0.16 (1.37–1.66)	1.64 ±0.22 (1.33–1.97)	6.34 ±0.44 (5.36–6.81)	6.28 ±0.54 (5.74–7.19)	3.47 ±0.43 (2.54–4.27)	3.33 ±0.48 (2.53–4.8)	4.07 ±0.32 (3.67–4.58)	3.34 ±0.36 (2.82–3.74)	4.03 ±0.38 (3.51–4.46)	4.15 ±0.46 (3.57–4.98)
R	1 ±0(1–1)	1 ±0(1–1)	1 ±0(1–1)	1 ±0(1–1)	1 ±0(1–1)	1 ±0(1–1)	1 ±0(1–1)	1 ±0(1–1)	1 ±0(1–1)	1 ±0(1–1)
PR	3 ±1(2–3)	3 ±0(2–3)	2 ±0(2–2)	2 ±0(2–2)	2 ±0(2–3)	2 ±0(2–3)	2 ±1(2–3)	2 ±0(2–2)	2 ±0(2–2)	2 ±0(2–2)
PN	2 ±0(2–2)	2 ±0(2–3)	3 ±1(2–3)	2 ±1(2–3)	2 ±0(2–2)	2 ±0(2–2)	2 ±0(2–2)	2 ±0(2–2)	2 ±0(2–3)	2 ±0(2–2)
SL	8 ±1(8–9)	8 ±1(8–9)	8 ±1(7–9)	7 ±0(7–7)	7 ±0(6–8)	7 ±0(6–8)	7 ±0(6–7)	7 ±0(7–7)	7 ±0(6–7)	7 ±0(7–8)
IL	7 ±1(7–8)	7 ±1(7–8)	7 ±1(6–8)	6 ±1(6–7)	6 ±0(5–7)	6 ±0(6–7)	7 ±0(6–7)	7 ±1(6–7)	6 ±1(6–7)	7 ±0(6–7)
SSP	2 ±1(1–2)	2 ±0(1–2)	5 ±1(4–7)	5 ±1(4–7)	2 ±0(2–4)	2 ±0(2–4)	2 ±0(2–2)	2 ±0(2–2)	2 ±0(2–2)	2 ±0(2–2)
VLR	59 ±4(56–63)	60 ±3(56–64)	43 ±3(38–48)	44 ±1(42–46)	47 ±4(40–60)	45 ±3(39–55)	56 ±3(51–59)	55 ±2(52–57)	46 ±1(44–48)	46 ±2(45–51)
DT	31 ±11(20–42)	33 ±8(20–43)	45 ±4(37–49)	43 ±4(40–50)	38 ±4(34–47)	37 ±4(30–49)	45 ±5(38–52)	47 ±3(43–50)	45 ±2(41–47)	44 ±1(42–46)
L4F	10 ±1(9–10)	10 ±1(9–11)	14 ±1(13–15)	13 ±1(12–14)	11 ±1(10–14)	11 ±1(10–14)	12 ±1(11–13)	12 ±1(11–13)	13 ±1(12–14)	13 ±1(11–14)
L4T	11 ±2(9–12)	11 ±1(9–12)	14 ±1(13–16)	14 ±0(13–14)	12 ±1(10–13)	11 ±1(10–13)	13 ±1(12–14)	13 ±1(12–14)	14 ±1(13–15)	13 ±1(12–14)
TP	0 ±0(0–0)	0 ±0(0–0)	2 ±1(2–3)	2 ±1(1–2)	3 ±1(0–5)	2 ±1(0–4)	2 ±0(2–3)	2 ±0(2–2)	2 ±0(2–3)	2 ±1(0–3)
CP	0 ±1(0–1)	0 ±1(0–1)	1 ±0(1–1)	1 ±0(1–1)	0 ±0(0–1)	0 ±1(0–1)	1 ±0(1–1)	1 ±0(1–1)	0 ±0(0–0)	0 ±0(0–0)

4 CONCLUSÃO

Os resultados parciais obtidos até o momento trazem importantes avanços acerca da variação morfológica das populações de *Phyllopezus* ocorrentes no Nordeste brasileiro. Mesmo com a reduzida representatividade taxonômica (em relação as linhagens putativas previamente propostas; Werneck et al., 2012) uma diversidade morfológica ímpar foi identificada entre populações de *P. pollicaris* analisadas. Esses morfogrupos e morfotipos apresentaram certa congruência em relação a distribuição geográfica, e corroboram, em parte, as linhagens recuperadas com os dados moleculares. No entanto, ainda há grandes lacunas ou completa ausência de dados genéticos para a maioria deles. As primeiras descrições de morfologia hemipeniana para o gênero já indicam que tais características podem vir a ser informativas na diagnose das linhagens, apresentando substancial variação entre as espécies e morfotipos caracterizados. Com as novas propostas taxonômicas e descrições de novas espécies (ver Capítulo II), avançamos em um de nossos principais objetivos e, embora representem avanços importantes na taxonomia do grupo, estão longe de resolver a instabilidade taxonômica do gênero. Por fim, a diversidade molecular já identificada, agora sob a luz de uma elevada variação morfológica e hemipeniana, deixa clara a necessidade da continuação desse estudo, com a ampliação geográfica e taxonômica das populações analisadas. Desse modo, espera-se fornecer uma revisão sistemática e detalhada elucidando questões taxonômicas que por décadas permeiam o gênero *Phyllopezus*.

Como perspectivas futuras, a inclusão de novas amostras permitirá uma análise mais refinada da variação morfológica em relação a distribuição geográfica das linhagens e populações. Assim, por meio de visitas técnicas ou empréstimos que já foram ou serão realizados, esperamos ampliar a amostragem morfológica em escala geográfica e taxonômica. Para as novas amostras genéticas aqui obtidas, temos também já disponíveis sequências de 11 genes nucleares de rápida evolução que serão incluídas nas análises em breve, assim como a obtenção de um novo conjunto amplo de amostras visando preencher lacunas geográficas na amostragem atual. A adição de análises de delimitação de espécies uni e multilocus serão realizadas. Diante da morfologia críptica presente em muitas das linhagens, novas fontes de evidência também serão empregadas como, por exemplo, morfometria geométrica escutelar e craniana e osteologia.

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ANEXO 1 – ARTIGO 3 – ON THE ATLANTIC FOREST ROCK OUTCROPS: THE FIRST RECORD OF *Phyllopezus pollicaris* (SPIX, 1825) (SQUAMATA: PHYLLODACTYLIDAE) IN THE STATE OF ESPÍRITO SANTO, BRAZIL

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On the Atlantic Forest rock outcrops: the first record of *Phyllopezus pollicaris (*Spix, 1825) (Squamata: Phyllodactylidae) in the state of Espírito Santo, southeastern Brazil

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Abstract

We present the first record of *Phyllopezus pollicaris* from the state of Espírito Santo, southeastern Brazil, at the Atlantic Forest rock outcrops of the *Pedra do Elefante* – an inselberg area located at the municipality of Nova Venécia. We discuss the first state record for the genus, the geographic distribution range for this species, and the records outside the seasonally dry forest biomes, in which the species rarely occurs.

Key words

Distribution, Gekkota, Inselbergs, Lizard, Rock Gecko

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Introduction

The South America gecko *Phyllopezus pollicaris (*Spix, 1825) is a nocturnal, saxicolous and/or arboreal species, widespread distributed, predominantly occurring in the Cerrado and Caatinga biomes (Gamble et al., 2012; Werneck et al., 2012; Cacciali et al., 2018). Although rare, few occurrence records of *P. pollicaris* are known for the Atlantic Forest (municipaly of Porto Seguro, state of Bahia, northeastern Brazil) and Amazon (municipality of São Geraldo do Araguaia, state of Pará, northern Brazil; Werneck et al., 2012).

Molecular studies considered the nominal taxon *P. pollicaris* as a complex of cryptic lineages, with population genetic structure concordant with the geographic limits of the dry open biomes, represented by the Caatinga, Cerrado, and Chaco (Pennington et al., 2006; Werneck et al., 2012). Populations from Chaco biome and from the southern limit of the Cerrado were afterwards designated as *P. przewalskii* and *P. heuteri*, taxonomic proposal that made *P. pollicaris* a paraphyletic taxon (Cacciali et al., 2018). Lineage differentiation in this species complex in three major clusters was related to historical events happening since the Neogene (Werneck et al., 2012). In the Cerrado, the historical geomorphological rearrangements of the landscapes in ancient plateaus and young valleys have likely shaped the populations genetic structure (Werneck et al., 2012). Therefore, the current distribution of the species should be associated with stable landscapes of the rock outcrops at the Cerrado, and possibly also at the Atlantic Forest, during the last 11.5 Ma (Miocene) – time of initial diversification of the species, according to Werneck *et al*. (2012). *Phyllopezus pollicaris* occupy a wide range of microhabitats across its distribution, including rocky habitats, either on granitic, gneissic or quartzite sandstones (Rodrigues, 1986; Cei, 1993; Vitt, 1995; Werneck et al., 2009; Recoder et al., 2012). The rock outcrops, besides experiencing a great gradient of temperatures for lizard's thermoregulation, comprises distinct refuge microhabitats, presenting suitable conditions for this nocturnal opportunistic predator (Recoder et al., 2012).

The landscape of southeastern Brazil, particularly the state of Espírito Santo, is covered by inselbergs (granitic or gneissic rock outcrops abruptly rising within the Atlantic Forest landscape) varying in area and degrees of connectivity (Safford & Martinelli 2000; de Paula et al., 2020b). Except for *Gymnodactylus darwinii (*Gray, 1845) *(*Phyllodactylidae) and the exotic species *Hemidactylus mabouia* (Moreau-de-Jonnès, 1818) (Gekkonidae), no other gecko was previously recorded for the state (Costa & Bernils, 2018). We herein present the

first state record of the genus and address the occurrence of *Phyllopezus pollicaris* in the Atlantic Forest rock outcrops.

Methods

In October 2019 we conducted an exploratory visit to the surroungdings of the *Pedra do Elefante*, an inselberg area, located at the municipality of Nova Venécia, state of Espírito Santo, southeastern Brazil. A single specimen of *P. pollicaris* was found and collected under the permits of Ministério do Meio Ambiente (MMA/SISBIO #56580) and Instituto Estadual do Meio Ambiente (IEMA #76433846). Voucher is deposited at the Reptile Collection of Museu de Biologia Professor Mello Leitão (MBML), municipality of Santa Teresa, state of Espírito Santo, Brazil. The geographic coordinates and elevation record were taken with a Garmin 64SX GPS, using Datum WGS84, and the altimeter manually calibrated at the sea level. Morphometric measurements of the specimen were taken with a digital caliper (precision of 0.1 mm). Its taxonomic identity was confirmed by morphological analysis under the stereomicroscope, and further comparisons with related taxa literature (Koslowsky, 1895; Müller & Brongersma, 1933; Loveridge, 1941; Vanzolini, 1953; Rodrigues, 1986; Koch et al., 2006; Cacciali et al., 2018).

The geographic distribution map was built in ArcMap (ESRI, 2020), considering the new record and distribution records of *Phyllopezus pollicaris* from literature (Werneck et al., 2012; Cacciali et al., 2018). We also checked records from *P. pollicaris* deposited at Museu de Biologia Professor Mello Leitão (MBML), Instituto Nacional da Mata Atlântica (INMA), Santa Teresa, state of Espírito Santo, to ensure no other specimen was previously collected at the state of Espírito Santo. This included the manual search for possible misidentified specimens of *P. pollicaris* among the deposited material of *Hemidactylus mabouia* and *Gymnodactylus darwinii*. A single specimen of *P. pollicaris* from Porto Seguro, state of Bahia, northeastern Brazil (MBML 1160) was found among the examined material identified as *H. mabouia*.

Results

Phyllopezus pollicaris (Spix, 1825)

New record (Fig. 1). BRAZIL – **state of Espírito Santo •** municipality of Nova Venécia; Área de Proteção Ambiental Pedra do Elefante (APAPE); 18°46'08"S, 40°27'24"W; 601 meters elev.; 17.X.2019; 07 p.m.; Thais H. Condez, Juliane P. Ribeiro, Paulo. M. Gonella, Claudio N. Fraga, and Dayvid Couto leg.; observed on the floor at the exposed rock surface, but immediately collected hidden at the bromeliad roots [*Alcantarea trepida* Versieux & Wand.]; snout-vent length = 58.35 mm, tail length = 63.20 mm, head length = 12.18 mm, head width = 18.59, nares-eye distance = 5.64 mm, interorbital distance = 6.85 mm, internarial distance = 1.83 mm, humerus length = 7.36 mm, radio length = 8.36 mm, thigh length = 12.42 mm, tibia length = 8.64 mm; 01 ♂ *Phyllopezus pollicaris*; MBML XXXX [Field Number TC 524] (Fig. 2).

Identification. The specimen was identified by the combination of the following characters: thin skin with small granular scales and modified scales in equidistant larger tubercles, absence of differentiated scales on the tail, a single series of digital lamellae (not cloven), the two distal phalanges of all fingers narrowed towards the claw, central pair of posmentals scales in direct contact, developed dorsal tubercles and pollex (Müller & Brongersma, 1933; Loveridge, 1941; Vanzolini, 1953; Rodrigues, 1986; Kock et al., 2009; Cacciali et al., 2018). Additionally, the specimen can be distinguished from others two described species of *P. pollicaris* complex (restricted to Chaco and southern limit of Cerrado; Cacciali et al., 2018) by present homogeneous scales at the mouth commissure (presence of two to three larger scales in tubercle-shaped in *P. heuteri*), one tubercle between eye and ear opening (five to eight in *P. heuteri*), 11 and 12 lamellae under the fourth toe (9 to 11 in *P. przewalskii*) and presence of three postcloacal tubercles in each side (not always present in adults of *P. przewalskii*) (Vanzolini, 1953; Cacciali et al., 2018).

Discussion

Our finding represents the first record for the genus *Phyllopezus* at the state of Espírito Santo, expand 272 km south (municipality of Porto Seguro [district of Trancoso], Bahia state)

and 312 km east (municipality of Serro, Minas Gerais state) the known distribution of *P. pollicaris* (Fig. 1). The area where the specimen was found is a legally protected area (APAPE) that encompasses several granitic/gneissic inselbergs immersed on a matrix of forest fragments and human-modified landscape. The locality where we found the specimen is characterized as a natural open formation surrounded by montane semideciduous forests (Fig. 3).

This remarkable record for a relatively well-known species at the Atlantic Forest rock outcrops reinforces the importance of herpetological surveys in sampling gaps, such as the inselbergs at southeastern Brazil (Almeida et al., 2010). These areas configure neglected ecosystems in comparison with the coastal forests of southeastern Brazil, with potential to harbor exceptional diversity and endemism (Safford & Martinelli, 2000; Porembski, 2007). Despite this, inselbergs might act as natural refuges for reptiles in surrounding areas of human-modified landscapes (Michael et al., 2008). Not always included in conservation plans, inselbergs are directly threatened by mining activities, besides being very susceptible to fire, biological invasions, and ornamental plant illegal extraction (Martinelli, 2007).

Neotropical inselbergs are geomorphological stable and isolated habitats, forming phytophysiognomic "islands", completely distinct of the surrounding landscape in terms of its edaphic and microclimatic characteristics (Porembski, 2007; de Paula et al., 2020a). Inselbergs' exclusive environmental conditions, such as the higher air temperature, lower air relative humidity, windy and severe insolation conditions relatively to the surroundings, might limit the occurrence of forest-adapted species, and favor the occurrence of specialized taxa in open and relatively drier habitats (Porembski, 2007). Also, the slope and the lack of soil in tropical inselbergs contribute for the rainwater run-off; being the water a seasonable resource scarcely stored in rock depressions or vegetation (Porembski, 2007). In addition to the desiccation-tolerant and well-adapted plants, the saxicolous frog *Thoropa miliaris (*Spix, 1824), and the bromeligenous treefrog *Scinax arduous* Peixoto, 2002, are examples of amphibian specialists, commonly observed in southeastern Brazil inselbergs (Teixeira et al., 2006).

Other records for *Phyllopezus pollicaris* in the Atlantic Forest are known for municipalities of Porto Seguro and Trancoso, both at the state of Bahia, northeastern Brazil (Werneck et al., 2012). The available molecular evidence suggests these populations might be distinct candidate species, despite being only 29 km apart from each other. The Porto Seguro population is associated to the northeastern cluster (Caatinga) while the Trancoso population

is associated to the central cluster (Cerrado; Werneck et al., 2012). Further investigation is crucial to include this newly discovered population from Espírito Santo in molecular studies aiming to determine their phylogenetic relationships with the putative lineages of this species complex.

Additionally, the occurrence of *Phyllopezus pollicaris* in the Atlantic Forest rock outcrops of Espírito Santo, southeastern Brazil, a species with origin and diversification associated with the South American Dry Diagonal biomes (Werneck et al., 2012), might add important information for the study of the diversification this taxon and the diversification of the herpetofauna associated with of the Atlantic Forest inselbergs.

Acknowledgements

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Authors’ Contributions

THC and JPR collected the specimen during the fieldwork expedition. THC provided the photographs, morphometric measurements, and checked records in scientific collections. MJMD prepared the figures and produced the map. All the authors (THC, MJMD, JFRT, and JPR) wrote the manuscript.

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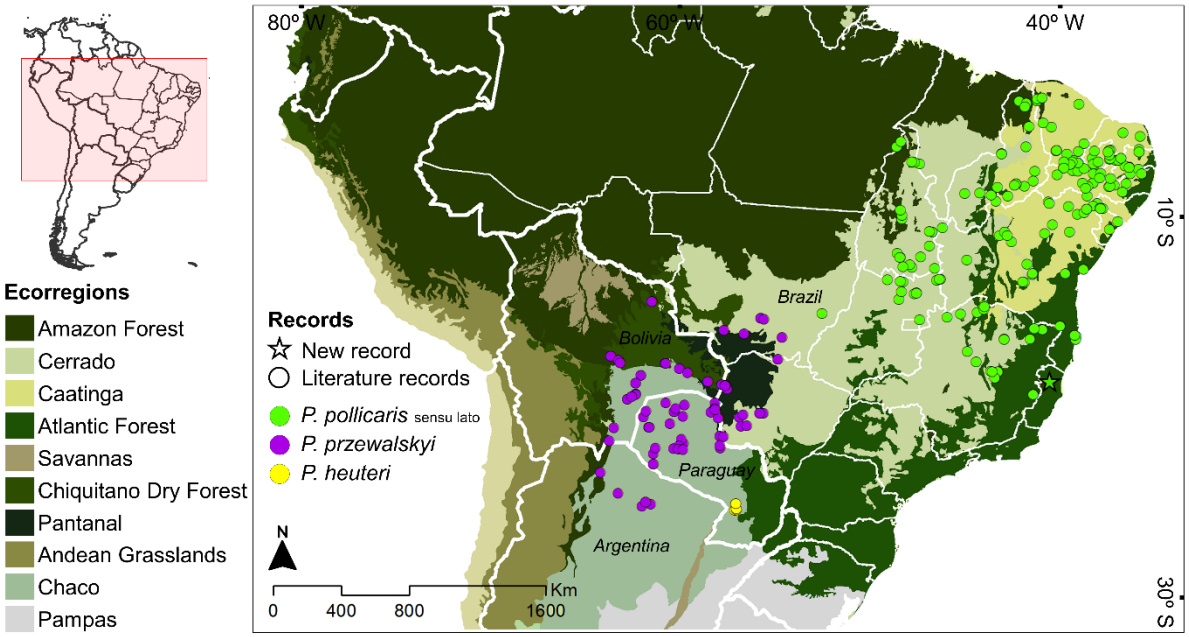

Figure 1. Geographic distribution of *Phyllopezus pollicaris* species complex. *Phyllopezus pollicaris* senso lato (green circles) and *P. przewalskii* (purple circles) and *P. heuteri* (yellow circles). Green star represents the new occurrence record. Inset map: South America.

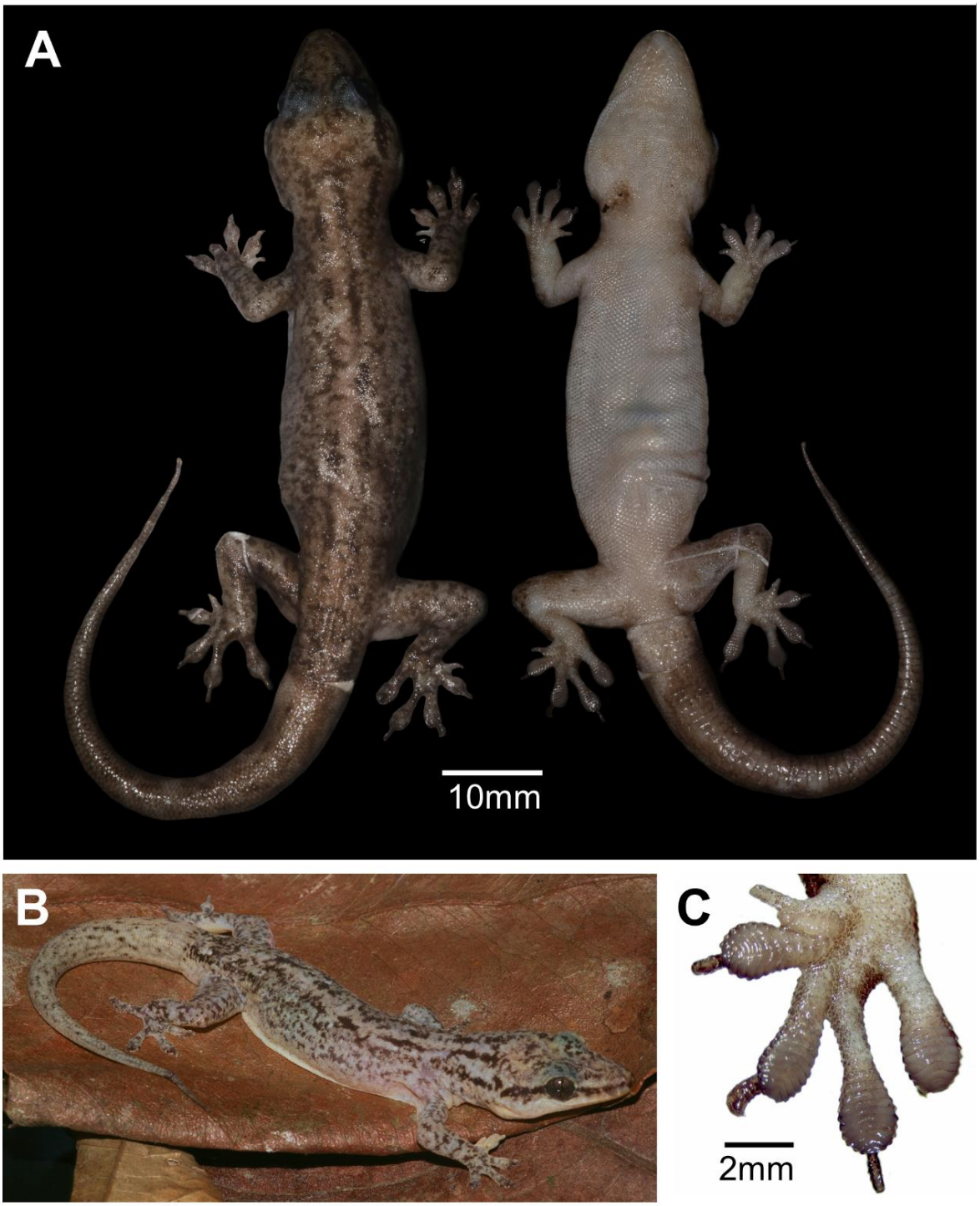

Figure 2. Specimen of *Phyllopezus pollicaris* [MBML XXXX] collected in Área de Proteção Ambiental Pedra do Elefante (APAPE), municipality of Nova Venécia, state of Espírito Santo, Southeastern Brazil. **A.** Dorsal and ventral view of specimen in preservative. **B.** Dorsolateral view of specimen in life. **C.** Detail of the toe digital lamellae.

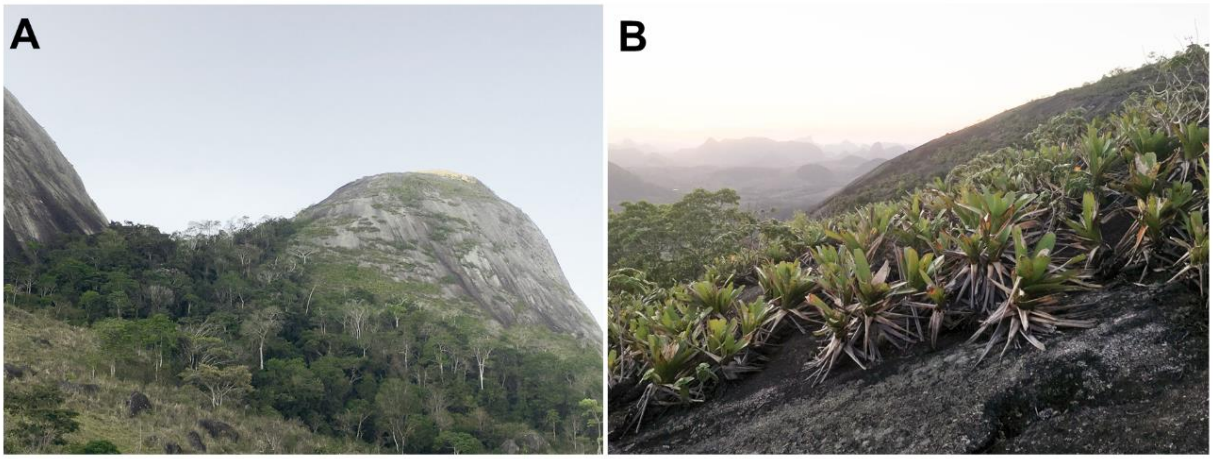

Figure 3. Habitat of *Phyllopezus pollicaris* at Área de Proteção Ambiental Pedra do Elefante (APAPE), municipality of Nova Venécia, state of Espírito Santo, Southeastern Brazil. **A.** External view of the Atlantic Forest inselberg. **B.** Details of the rock outcrop surface where the specimen was found.

ANEXO 2 – INSTRUCTIONS FOR THE AUTHORS – ZOOLOGICAL JOURNAL OF THE LINNEAN SOCIETY

Manuscript format and structure/style

BASIC FORMATTING GUIDE

Authors should aim to communicate ideas and information clearly and concisely, in language suitable for the moderate specialist. Papers in languages other than English are not accepted unless invited. When a paper has joint authorship, one author must accept responsibility for all correspondence; the full postal address, telephone and fax numbers, and e-mail address of the author who is to check proofs should be provided. Authors preparing long texts (20 000 words or more, including references, etc.) should consult the Editor before considering submission. *Please submit your manuscript in an editable format such as .doc, .docx or .rtf, prepared on A4, paginated, double spaced throughout (i.e. including references and quotations), with ample margins. If you submit your manuscript in a non-editable format such as PDF, this will slow the progress of your paper as we will have to contact you to request an editable copy.*

Papers should conform to the following general layout:

Article types

- Original Article
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Title page

This should be uploaded as a separate file, designation 'Title Page'. It should include title, authors, institutions and a short running title. The title should be concise but informative, preferably shorter than 25 words. Catchy titles are encouraged. Where appropriate the title should include mention of family or higher taxon in the form: 'The Evolution of the Brown Rat, *Rattus norvegicus* (Rodentia: Muridae)'. A subtitle may be included. Papers in numbered series are not accepted. Names of new taxa should not be given in titles.

Abstract

Abstracts must be on a separate page and must be concise, clearly written and cover the context of the paper. The abstract is of great importance as it may be reproduced elsewhere and is all that many may see of your work. It should be about 100–200 words long and should

summarize the paper in a form that is intelligible in conjunction with the title. It is advisable to avoid descriptions, lists or jargon if possible. It should not include references. The abstract should be followed by up to ten keywords additional to those in the title (alphabetically arranged and separated by hyphens) identifying the subject matter for retrieval systems. Taxonomic authorities should not be included in the abstract.

Subject matter

The paper should be divided into main sections: INTRODUCTION, MATERIAL AND METHODS, RESULTS, DISCUSSION and CONCLUSION, with the hierarchy of headings below these not exceeding two, except in systematic hierarchies. Results are presented in present tense, whereas previous studies that are discussed need to be presented in past tense. Do not merge results and discussions. Please present your work in clear and concise language, keeping the broad readership in mind. Separate Results and Discussion sections provide a clear distinction between results of the study at hand and discussion of results of other studies, so these separate sections generally should be used.

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Use SI units, and the appropriate symbols (mm, not millimetre; µm, not micron; s, not sec; min for minute; c for circa; Myr for million years, Mya for million years ago; etc.). Use an n-dash (–), not a hyphen (-), for ranges and use the times sign × (not the letter x) for multiplication, dimensions, crosses and hybrids. Use the negative index (m-1, l-1, h-1) except in cases such as 'per plant'). Avoid elaborate tables of original or derived data, long lists of species, etc.; if such data are absolutely essential, consider including them as appendices or as online-only supplementary material. Avoid footnotes and keep cross references by page to an absolute minimum. Please provide a full English translation [in square brackets] for any quoted matter that is not in English.

References

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- **Kamiński MJ, Kanda K, Lumen R, Smith AD, Iwan D. 2019**. Molecular phylogeny of Pedinini (Coleoptera, Tenebrionidae) and its implications for higher-level classification, *Zoological Journal of the Linnean Society* 185: 77–97.
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Tables

Keep these as simple as possible, with few horizontal and, preferably, no vertical rules. When assembling complex tables and data matrices, bear the dimensions of the printed page (225 × 168 mm) in mind; reducing typesize to accommodate a multiplicity of columns will affect legibility.

Illustrations

These normally include (1) half-tones reproduced from photographs, (2) black and white Figs. reproduced from drawings and (3) diagrams. Use one consecutive set of Arabic numbers for all illustrations (do not separate 'Plates' and 'Text-Figs.' - treat all as 'Figs.'). Figs. should be numbered in the order in which they are cited in the text. Use upper case letters for subdivisions (e.g. Fig. 1A-D) of Figs.; all other lettering should be lower case.

Half-tones reproduced from photographs: increasingly, authors' original images are captured digitally rather than by conventional film photography. In these cases, please use settings on your equipment for the highest possible image quality (minimum 300dpi). Desktop technology now allows authors to prepare plates by scanning photographic originals and then labelling them using graphics programs such as Adobe Illustrator. These are acceptable provided:

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- In the case that it is not possible to provide electronic versions, please supply photographic prints with labelling applied to a transparent overlay or to a photocopy.

Grouping and mounting: when grouping photographs, aim to make the dimensions of the group (including guttering of 2 mm between each picture) as close as possible to the page dimensions of 168 × 225 mm, thereby optimizing use of the available space. Remember that grouping photographs of varied contrast can result in poor reproduction. If supplied as photographic prints, the group should be mounted on thin card. Take care to keep the surface of the prints clean and free of adhesive. Always provide overlays to protect the photographs from damage.

Lettering and numbering: If supplied as photographic prints, letters and numbers should be applied in the form of dry-transfer ('Letraset') letters, numbers, arrows and scale bars, but not measurements (values), to transparent overlays in the required positions, rather than to the photographs themselves; this helps to avoid making pressure marks on the delicate surface of the prints, and facilitates relabelling, should this be required. Alternatively, pencilled instructions can be indicated on duplicates or photocopies marked 'FOR LABELLING ONLY'. Self-adhesive labels should be avoided, but if they are used, they should not be attached directly to either photographs or overlays, but to photocopies, to indicate where they are to be positioned. Labelling will be inserted electronically by the typesetter in due course.

Colour: colour is free of charge.

Black and white Figs. reproduced from drawings: these should be scanned at a minimum resolution of 800 dpi and supplied in TIFF, JPEG, or editable PDF format. Lines must be clean and heavy enough to stand reduction; drawings should be no more than twice page size. The maximum dimensions of published Figs. are 168 × 225 mm. Scale bars are the most satisfactory way of indicating magnification. Take account of proposed reduction when lettering drawings.

Diagrams: in most instances the author's electronic versions of diagrams are used and may be re-labelled to conform to journal style. These should be supplied as vector format Encapsulated PostScript (EPS) files. Please note that diagrams or graphs will not reproduce well in the online version of your paper unless they are in vector format due to low maximum screen resolution.

Type legends for Figs. in numerical order on a separate sheet. Where a 'key' is required for abbreviations used in more than one Fig., this should be included as a section of the main text.

Authors wishing to use illustrations already published must obtain written permission from the copyright holder before submitting the manuscript. Authors may, in the first instance, submit good xerox or photographic copies of Figs. rather than the originals.

Upon revision papers should again be submitted in an editable file format (i.e. not PDF) and Figs. must be submitted as separate, high-resolution, uncompressed TIF or EPS files.

Information on Latex files.

You can also send queries about Fig. files to zoolin_oup@newgen.co.

Supporting Information

Submit all material to be considered as Supporting Information online at the same time as the main manuscript. Ensure that the supporting information is referred to in the main manuscript at an appropriate point in the text. Make sure you include a section at the end of the manuscript (after the references) entitled 'SUPPORTING INFORMATION' and listing the titles of the supplementary files. Supplementary Figs. and tables should be numbered 'Fig. S1', 'Table S1', etc. Supporting information will be available online only and will not be copyedited, so it is essential that it is clearly and succinctly presented, and that the style conforms with the rest of the paper. Also ensure that the presentation will work on any Internet browser. It is not recommended for the files to be more than 2 MB each, although exceptions can be made at the editorial office's discretion.

ANEXO 3 – INSTRUCTIONS FOR THE AUTHORS – ZOOTAXA

Manuscript format and structure/style

Preparation of manuscripts

1) *General.* All papers must be in English. Authors whose native language is not English are encouraged to have their manuscripts read by a native English-speaking colleague before submission. Nomenclature must be in agreement with the *International Code of Zoological Nomenclature* (4th edition 1999), which came into force on 1 January 2000. Author (s) of species name must be provided when the scientific name of any animal species is first mentioned (the year of publication needs not be given; if you give it, then provide a full reference of this in the reference list). Authors of plant species names need not be given. Metric systems should be used. If possible, use the common font Times New Roman and use as little formatting as possible (use only **bold** and *italics* where necessary and indentions of paragraphs except the first). Special symbols (e.g. male or female sign) should be avoided because they are likely to be altered when files are read on different machines (Mac versus PC with different language systems). You can code them as m# and f#, which can be replaced during page setting. The style of each author is generally respected but they must follow the following general guidelines.

2) The **title** should be concise and informative. The higher taxa containing the taxa dealt with in the paper should be indicated in parentheses: e.g. A taxonomic revision of the genus *Aus* (Order: family).

3) The **name (s) of all authors** of the paper must be given and should be typed in the upper case (e.g. ADAM SMITH, BRIAN SMITH & CAROL SMITH). The address of each author should be given in *italics* each starting a separate line. E-mail address (es) should be provided if available.

4) The **abstract** should be concise and informative. Any new names or new combinations proposed in the paper should be mentioned. Abstracts in other languages may also be included in addition to English abstract. The abstract should be followed by a list of**key words**that are not present in the title. Abstract and key words are not needed in short correspondence.

5) The arrangement of the **main text** varies with different types of papers (a taxonomic revision, an analysis of characters and phylogeny, a catalogue etc.), but should usually start with an **introduction** and end with a list of **references**. References should be cited in the text

as Smith (1999), Smith & Smith (2000) or Smith *et al.* (2001) (3 or more authors), or alternatively in a parenthesis (Smith 1999; Smith & Smith 2000; Smith *et al*. 2001). All literature cited in the text must be listed in the references in the following format (see a sample page here in PDF).

A) **Journal paper**:

Smith, A. (1999) Title of the paper. *Title of the journal in full*, volume number, issue number if possible & page range.

B) **Book chapter**:

Smith, A. & Smith, B. (2000) Title of the Chapter. *In*: Smith, A, Smith, B. & Smith, C. (Eds), *Title of Book*. Publisher name and location, pp. x–y.

C) **Book**:

Smith, A., Smith, B. & Smith, C. (2001) *Title of Book*. Publisher name and location, xyz pp.

D) **Internet resources**

Author (2002) Title of website, database or other resources, Publisher name and location (if indicated), number of pages (if known). Available from: http://xxx.xxx.xxx/ (Date of access).

Dissertations resulting from graduate studies and non-serial proceedings of conferences/symposia are to be treated as books and cited as such. Papers not cited must not be listed in the references.

Please note that:

(1) **journal titles must be written in full (not abbreviated)**

(2) **journal titles and volume numbers are followed by a ","**

(3) **page ranges are connected by "n dash", not hyphen "-", which is used to connect two words.**

For websites, it is important to include the last date when you see that site, as it can be moved or deleted from that address in the future.

On the use of dashes: (1) Hyphens are used to link words such as personal names, some prefixes and compound adjectives (the last of which vary depending on the style manual in use). (2) En-dash or en-rule (the length of an ‘n’) is used to link spans. In the context of our journal that means numerals mainly, most frequently sizes, dates and page numbers (e.g. 1977–1981; figs 5–7) and also geographic or name associations (Murray–Darling River; a

Federal–State agreement). (3) Em-dash or em-rule (the length of an ‘m’) are used far more infrequently, and are used for breaks in the text or subject, often used much as we used parentheses. In contrast to parentheses an em-dash can be used alone; e.g. What could these results mean—that Niel had discovered the meaning of life? En-dashes and em-dashes should not be spaced.

6) Legends of **illustrations** should be listed after the list of references. Small illustrations should be grouped into plates. When preparing illustrations, authors should bear in mind that the journal has a matter size of 25 cm by 17 cm and is printed on A4 paper. For species illustration, line drawings are preferred, although good quality B&W or colour photographs are also acceptable. See a guide here for detailed information on preparing plates for publication.

7) **Tables**, if any, should be given at the end of the manuscript. Please use the table function in your word processor to build tables so that the cells, rows and columns can remain aligned when font size and width of the table are changed. Please do not use Tab key or space bar to type tables.

8) **Keys** are not easy to typeset. In a typical dichotomous key, each lead of a couplet should be typed simply as a paragraph as in the box below:

1 Seven setae present on tarsus I ; four setae present on tibia I; leg I longer than the body; legs black in color ... Genus A

- Six setae present on tarsus I; three setae present on tibia I; leg I shorter than the body; legs brown in color ... 2

2 Leg II longer than leg I ... Genus B

- Leg II shorter than leg I ... Genus C

Our typesetters can easily convert this to a proper format as in this PDF file.

Deposition of specimens

Whenever possible, authors are advised to deposit type specimens in national or international public museums or collections. Authors are also advised to request registration numbers of deposited material in advance of the acceptance of papers to avoid unnecessary delay of publication. Some countries (e.g. Australia) require that primary type specimens be deposited in collections of the country of origin; authors are advised to take this into consideration.