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Original Article

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Morphology and molecular systematics support a new species of *Pseudogonatodes* (Squamata: Gekkota: Sphaerodactylidae) from Venezuela with a remarkable telescoped skull

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ABSTRACT

We describe a new species of miniaturized gecko (genus *Pseudogonatodes*) from the Peninsula de Paria in northeastern Venezuela. Externally, the new species resembles *Pseudogonatodes furvus* and *Pseudogonatodes manessi*, from the Sierra Nevada de Santa Marta in Colombia and the Central Coastal Range in Venezuela, respectively; however, it differs from these species in terms of molecular genetic data (12S rRNA, 16S rRNA, and *c-mos*), osteological characters, and scale counts. The new species is unique in skull osteology, and we adopt the term 'telescoped' from the literature to describe the overlap of bones in the snout, in particular the premaxilla fully separating the nasal bones and contacting the frontal bone. The new species is also the only known species of *Pseudogonatodes* with fused parietal bones. Using molecular data, we present the first phylogeny of *Pseudogonatodes*, including six of the nine species in the genus. The new species is sister to *P. manessi*, which is consistent with biogeographical patterns in the mountainous areas of northern Venezuela. The phylogenetic results also indicate that *Pseudogonatodes guianensis* is non-monophyletic and raise the possibility of resurrecting the name *Pseudogonatodes amazonicus*. However, large sampling gaps in Amazonia prevent us from rigorously assessing species limits and proposing a taxonomic change.

Keywords: gecko; micro-computed tomography scan; montane forests; Peninsula de Paria; reptile; skeleton; sphaerodactyl; taxonomy

INTRODUCTION

Within Neotropical geckos (Gekkota), those in the sphaerodactyl clade (*sensu* Kluge 1995) of the family Sphaerodactylidae have received the most attention in terms of their morphology and systematics (Kluge 1995, Daza *et al.* 2008, Gamble *et al.* 2008a, 2011a, b, Schargel *et al.* 2010, Batista *et al.* 2015, Bauer *et al.* 2018, Montes-Correa *et al.* 2021), and they continue to be the main source of new taxonomic discoveries for geckos in the

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region (Rivas *et al.* 2013, Batista *et al.* 2015, Schargel *et al.* 2017, Carvajal-Cogollo *et al.* 2020, Meneses-Pelayo and Ramírez 2020, Díaz-Lameiro *et al.* 2022). This group includes six genera, with *Pseudogonatodes* Ruthven, 1915 perhaps having received the least taxonomic attention so far. Currently, there are eight described species in the genus, most of which are known from a small number of specimens and have seemingly restricted geographical distributions (Rojas-Runjaic *et al.* 2024, Uetz *et al.* 2024). This genus is distributed in northern and central South America, including Colombia, Venezuela, the Guianas, Ecuador, Peru, Bolivia, and Brazil. Known species are cryptozoic and are found mostly in humid forests from the lowlands of the Amazon Basin and Guiana shield, in addition to the mid-elevations of mountain ranges in the region, including the Andes, the Sierra Nevada de Santa Marta, and the Venezuelan Coastal Mountain Range.

Recent dedicated contributions to the systematics of *Pseudogonatodes* are limited to the description of a new species, *Pseudogonatodes quihuai* Rojas-Runjaic, Koch, Castroviejo-Fisher & Prudente, 2024, from Venezuela (Rojas-Runjaic *et al.* 2024), and the expansion of our knowledge of the morphological variation and distribution for the type species of the genus, *Pseudogonatodes furvus* Ruthven, 1915 and the Venezuelan endemic *Pseudogonatodes lunulatus* Roux, 1927 (Esqueda *et al.* 2016, Montes-Correa *et al.* 2021). Additionally, a detailed bone-by-bone description of the skull of *Pseudogonatodes barbouri* (Noble, 1921) has been published (Bauer *et al.* 2018), which opened a window into exploring comparative osteology and its systematic value in the genus (Montes-Correa *et al.* 2021, Rojas-Runjaic *et al.* 2024). Some phylogenetic studies (Gamble *et al.* 2008a, 2011a, b, Schargel *et al.* 2010, Pyron *et al.* 2013) based on molecular data have included up to three species of *Pseudogonatodes* as terminals. As such, we are still lacking phylogenetic hypotheses for interspecific relationships within *Pseudogonatodes*, and even the phylogenetic position of the genus within sphaerodactyl geckos remains unclear. One objective of this article is to present the first phylogenetic hypothesis of relationships within *Pseudogonatodes*. Our main goal, however, is to provide a new species description for a seemingly isolated population of *Pseudogonatodes* from northeastern Venezuela. An account of the genus in Venezuela and the discovery of the new species is presented below.

In Venezuela, four species of *Pseudogonatodes* have been recorded: *Pseudogonatodes guianensis* Parker, 1935 is found in the lowlands of the Venezuelan Guayana, whereas *P. lunulatus*, *P. quihuai*, and *Pseudogonatodes manessi* Avila-Pires & Hoogmoed, 2000 are found associated with montane areas north of the Orinoco River, including the Andes and Coastal Mountain Range. The Venezuelan Coastal Mountain Range extends along the Caribbean coast of Venezuela and on the northern portion of Trinidad Island (Republic of Trinidad and Tobago). In mainland Venezuela, the Coastal Mountain Range is divided into the Central Coastal Range and the Eastern Coastal Range, the latter itself subdivided into the Turimiquire massif and the Paria Range (*sensu* Rivas *et al.* 2021), and has been an area of important herpetological discoveries in the last three decades (Ayarzagüena and Señaris 1996, Rivas *et al.* 1999, 2005, Mijares-Urrutia *et al.* 2000, Schargel *et al.* 2005, Barrio-Amorós *et al.* 2006, Manzanilla *et al.* 2007, Kaiser *et al.* 2015).

On 19 July 2002, while collecting specimens in an evergreen premontane forest in the Paria Range, Venezuela (Fig. 1), one of us (G.A.R.), spotted a tiny lizard that immediately disappeared within the abundant leaf litter associated with tree roots. However, a few seconds later, this specimen was caught after sorting the mass of leaf litter where it had initially been observed. Unfortunately, the specimen was a small subadult that had lost part of its skin and was identified initially as *P. manessi* (Rivas *et al.* 2006). In August 2014, two of us (G.A.R. and M.D.F.), walking in the same patch of forest visited in 2002, were able to secure three additional specimens of this presumably isolated population of *Pseudogonatodes*. Because the Paria Range is an area of endemism (Rivas *et al.* 2021), especially for humid forest montane species, we were motivated to evaluate the taxonomic status of these specimens. In doing so, we have used several lines of evidence, including external morphology, micro-computed tomography data of the skeleton, and molecular data. Because the species of *Pseudogonatodes* from Paria Range has distinctive skull morphology, we discuss the variation of relevant skull characters in the genus and at the family level.

MATERIALS AND METHODS

Morphological analysis

Specimens of the genus *Pseudogonatodes* available for this study (Appendices 1 and 2) are housed in the following collections: Museum of Natural History, University of Kansas (KU; Lawrence, KS, USA); Amphibian and Reptile Diversity Research Center, The Division of Amphibians and Reptiles, United States National Museum of Natural History (USNM; Washington, DC, USA); The University of Texas at Arlington (UTA; Arlington, TX, USA); Museum of Comparative Zoology, Harvard University (MCZ; Cambridge, MA, USA); California Academy of Sciences (CAS, San Francisco, CA. USA); Instituto de Ciencias Naturales, Universidad Nacional de Colombia (ICN; Bogotá, Colombia); Centro de Colecciones Científicas, Universidad del Magdalena (CBUMAG; Santa Marta, Colombia); Museo de la Estación Biológica de Rancho Grande (EBRG; El Limón, Venezuela); Museo de Biología, La Universidad del Zulia (MBLUZ; Maracaibo, Venezuela); and Museo de Historia Natural La Salle (MHNLS; Caracas, Venezuela).

We follow Avila-Pires (1995) and Avila-Pires and Hoogmoed (2000) for general morphological characters and lepidosis. Measurements were taken with digital Vernier callipers (0.01 mm precision). The following abbreviations were used: SVL, snout–vent length; TL, tail length; AXG, axilla–groin distance; HL, head length from posterior margin of ear opening to tip of the snout; HW, head width measure at widest section posterior to the eyes; HD, head depth measured at deepest section posterior to the eyes; EYN, eye–nostril distance; EYE, eye diameter longitudinally; SAM, number of scales around midbody; VFH, ventral scales from anterior level of hindlimbs to anterior level of forelimbs; VFC, ventral scales from anterior level of hind limbs to cloaca; PR, number of postrostrals; PN, number of postnasals; LOR, number of loreal scales counted along the shortest straight line between the postnasals and the eye socket; SUPL, number of supralabials counted up to the level below the center of the eye; INFL, number of infralabials counted up to the level below

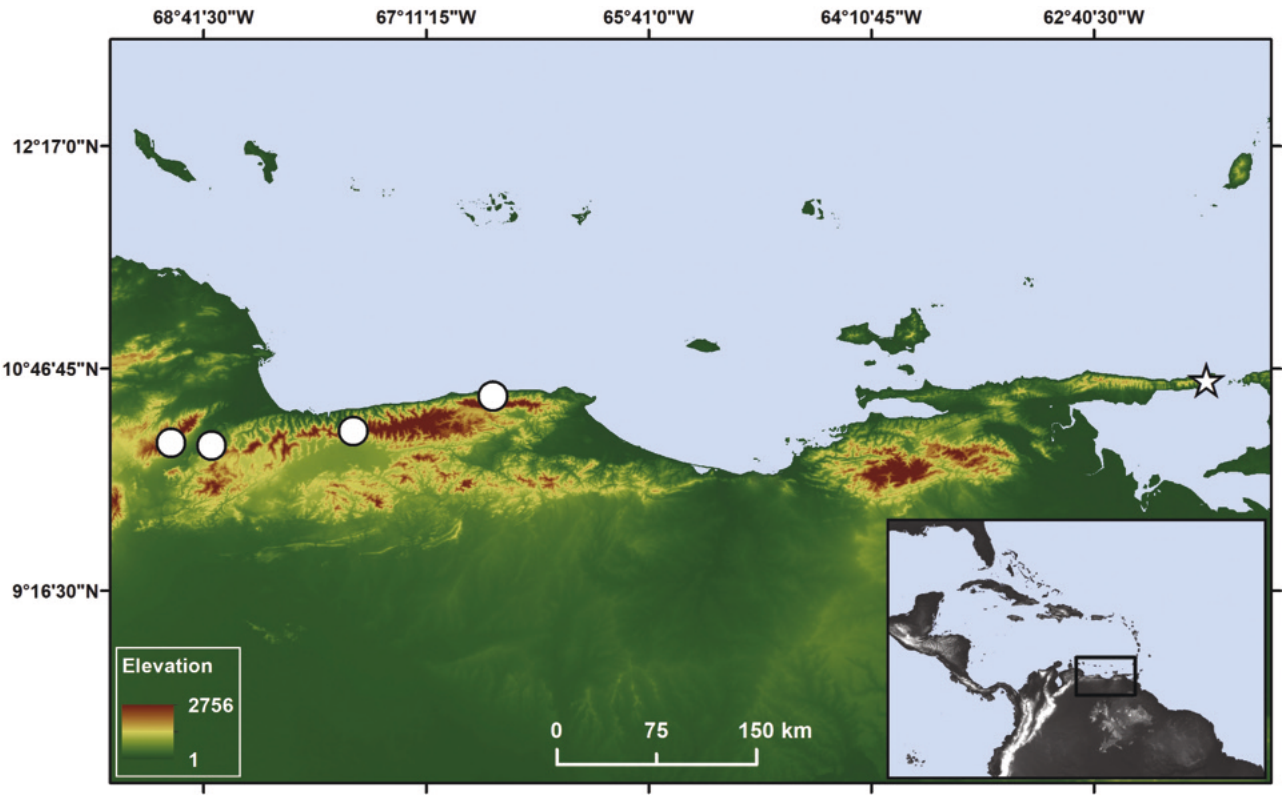

Figure 1. Map of northern Venezuela, showing the geographical distribution of ***Pseudogonatodes fuscofortunatus*** (star) and its sister species *Pseudogonatodes manessi* (circles).

the center of the eye; PM, number of postmental scales; LFF, number of lamellae under the fourth finger; and LFT, number of lamellae under the fourth toe.

High-resolution X-ray computed tomography scans were obtained at The University of Texas High-resolution X-ray Computed Tomography Facility, using a Zeiss Xradia 620 Versa scanner. Tomograms were imported to the data visualization software AvizoLite v.2019.1 (Thermo Fisher Scientific). Bones from the snout were digitally separated and rendered using volume rendering and/or the isosurface option. In the case of the surface models, they were smoothed and colourized using a colour palette visible by persons with colour vision deficiency (Tol 2021). Scans were obtained for the type series of the new species (see below: http://zoobank.org/References/6521D183-40B4-4422-8833-D9963DED99DA), one specimen of *P. manessi* (KU 182740), and one specimen of *P. lunulatus* (KU 117078). New high-resolution X-ray computed tomography scans are available at https://www.morphosource.org: *Pseudogonatodes fuscofortunatus* (Media ID 000634333, ark:/87602/m4/634333); and *Pseudogonatodes manessi* (Media ID 000634418, ark:/87602/m4/634418). The osteology of these species was compared with available published descriptions of *Pseudogonatodes* (Daza *et al.* 2008, Bauer *et al.* 2018, Montes-Correa *et al.* 2021). We explore two character transformations related to the telescoped skull condition:

1. Premaxillary nasal process overlaps nasals: (0) one-quarter of their length; (1) one-half of their length; (2) entire length.
2. Premaxilla–frontal contact: (0) absent; (1) present.

Character definition follows Kluge (1976) and Kearney (2003). These characters were mapped over the topology resulting from the combination of the hypothesis of the relationships at genus level (Gamble *et al.* 2015) and the hypothesis of the relationships within *Pseudogonatodes* obtained by us (see below). Terminals were selected considering the previous cranial descriptions by Daza *et al.* (2008). The character mapping was made using the function 'plotTree.datamatrix' of the R package 'phytools' (Revell 2024).

Molecular analysis

Genomic DNA was extracted from *Pseudogonatodes* tail and liver tissue using standard laboratory protocols. PCR was used to amplify sequences for two mitochondrial gene fragments (12S rRNA and 16S rRNA) and one nuclear gene (*c-mos*). Primers detailed by Gamble *et al.* (2008a, b, 2011a) and Schargel *et al.* (2010) were used for *c-mos* and 12S rRNA, respectively. A new 16S rRNA primer pair was developed for this study (Table 1). PCR purification and sequencing were conducted by Psomagen, Inc. (Rockville, MD, USA). GenBank accessions can be found in Table 2. Sequences were assembled and quality checked in Geneious Prime (v.2022.2.2; Kearse *et al.* 2012). Publicly available data for additional *Pseudogonatodes* sequences and two outgroup taxa, *Sphaerodactylus townsendi* Grant, 1931 and *Coleodactylus brachystoma* (Amaral, 1935), were acquired from GenBank to supplement the new sequences for analyses (Gamble *et al.* 2008a, 2011a, Geurgas *et al.* 2008, Schargel *et al.*

Table 1. Primers used for PCR and DNA sequencing.

Gene	Size (bp)	Primer sequences	Reference
Oocyte maturation factor mos (*c-mos*)	435	FU-F [5′-TTTGGTTCKGTCTACAAGGCTAC-3′] FU-R [5′-AGGGAACATCCAAAGTCTCCAAT-3′]	Gamble *et al.* (2008a)
Mitochondrial ribosomal subunit 16S	516	16S GEKF [5′-GTTTACCAAAAACATRGCCTTTAG-3′] 16S GEKR [5′-GGTCTGAACTCAGATCACCTAGGA-3′]	This paper
Mitochondrial ribosomal subunit 12S	368	12a [5′-CTGGGATTAGATACCCCACTA-3′] 12b [5′-TGAGGAGGGTGACGGGCGGT-3′]	Pellegrino *et al.* (2010)

Table 2. GenBank accessions for terminals of phylogenetic analysis. Outgroups are *Coleodactylus brachystoma* and *Sphaerodactylus townsendi*.

Specimen	Locality	12S	*c-mos*	16S
Pseudogonatodes barbouri TG00314	Forest near Bagua, Amazonas, Peru		PP101637.1	PP101639.1
Pseudogonatodes guianensis AMCC106916	Berbice River, Guyana		HQ426571.1	PP101640.1
Pseudogonatodes guianensis KU222142	Loreto, Peru	PP101641.1	EF534908.1	PP101642.1
Pseudogonatodes guianensis LSUMZ13583	Rio Jurura, Acre, Brazil		HQ426572.1	PP101643.1
Pseudogonatodes guianensis MTR09893	Rio Preto da Eva, Amazonas, Brazil		EU435260.1	EU435275.1
Pseudogonatodes guianensis MTR09894	Rio Preto da Eva, Amazonas, Brazil		EU435261.1	EU435276.1
Pseudogonatodes furvus CBUMAG:REP:00763	Bella Vista (type locality), Santa Marta, Magdalena, Colombia	PP193844.1		PP193830.1
Pseudogonatodes fuscofortunatus MBLUZ1294	Cerro El Olvido, Sucre state, Venezuela	PP193845.1	PP133044.1	PP193831.1
Pseudogonatodes lunulatus MBLUZ1460	Cuyagua, Aragua, Venezuela	PP101646.1		PP101647.1
Pseudogonatodes lunulatus MHNLS17481	Bahía de Cata, Aragua, Venezuela	GU139951.1	GU139844.1	PP101644.1
Pseudogonatodes manessi MHNLS17984	Rancho Grande, Aragua, Venezuela	GU139952.1	GU139845.1	PP101649.1
Coleodactylus brachystoma IAH020	Serra do Amolar, Mato Grasso do Sul, Brazil		EU435238.1	EU435268.1
Sphaerodactylus townsendi ST-P-2 and TG3112	Puerto Rico	KC840514.1	MK337609.1	KC840608.1

2010, Díaz-Lameiro *et al.* 2013, Pinto *et al.* 2019). Sequences for each individual gene were aligned using MUSCLE with the default PPP algorithm, two refinement iterations, a gap open penalty of 12, and gap extension penalty of 3 (Edgar 2004) implemented in Geneious Prime (v.2022.2.2; Kearse *et al.* 2012), with minor subsequent manual adjustments to remove gaps and trim ends.

Phylogenetic inference

We used IQ-TREE 2 (Minh *et al.* 2020) for maximum likelihood phylogenetic reconstruction with the partitioned dataset. The three partial genes were analysed in three assemblages for phylogenetic tree building: one for concatenated mitochondrial loci, one for the *c-mos*, and one for concatenated mitochondrial plus nuclear loci. The two mitochondrial genes (mtDNA) were partitioned separately from *c-mos*. ModelFinder (Kalyaanamoorthy *et al.* 2017) selected best substitution models for each partition followed by partition modelling (Chernomor *et al.* 2016) to determine whether partitions could be merged using the -m -TESTMERGE option and -p option for edge-linked branch lengths with different evolutionary rates between partitions. IQ-TREE 2 ran with default tree search settings, including generation of a set of 100 maximum parsimony starting trees. Node support was assessed with 1000 ultrafast bootstrap replicates (Hoang *et al.* 2018), where support is strong at values ≥95 (Minh *et al.* 2013), and the SH-like approximate likelihood ratio test (SH-aLRT) (Guindon *et al.* 2010), where support is strong at values ≥80. Bootstrap trees were optimized using the nearest neighbour interchange search option -bnni to reduce risk of overestimating branch support. We calculated the pairwise genetic distance between all individuals for each mitochondrial gene using MEGA11 (Stecher *et al.* 2020, Tamura *et al.* 2021).

All calculated p-distances used uniform rates, with ambiguous sites between pairs deleted.

RESULTS

Phylogenetic analysis and molecular divergences

A concatenated maximum likelihood tree was constructed with a total of 13 individuals, 11 in *Pseudogonatodes* and two outgroup taxa, with 1307 total sites. The mitochondrial genes (12S and 16S) were partitioned separately from *c-mos* according to the partition finder results, and ModelFinder found best-fitting models according to the Bayesian information criterion of GTR+F+G4 and Kimura two-parameter for the mitochondrial and nuclear partition, respectively. The mitochondrial, *c-mos*, and concatenated maximum likelihood trees (Fig. 2) show a congruent sister relationship between the population of *Pseudogonatodes* from the Paria Range and *P. manessi* from the Central Coastal Range. This clade is sister to all other *Pseudogonatodes* included in the analysis. In mitochondrial and concatenated trees, *P. furvus* (the type species), for which nuclear data are missing, is the sister taxon to a clade containing all species with an expanded third subdigital lamella in the fourth toe: *P lunulatus*, *P. barbouri*, and *P. guianensis*. Although the relationships within this clade differ slightly for each tree, with varying node support values, the widespread *P. guianensis* was recovered as non-monophyletic in all analyses. In the concatenated tree, the samples of *P. guianensis* from central Amazonia (Amazonas, Brazil) and Guyana form a clade sister to *P. lunulatus*, whereas the samples of *P. guianensis* from western Amazonia [Brazil (Acre) and Peru] form a clade sister to *P. barbouri*. In the mitochondrial tree, the only difference is that *P. barbouri* is sister to the remaining species in this clade instead of being sister to *P. guianensis* from western Amazonia. In the *c-mos* tree, the interspecific relationships within the clade of species with the third expanded lamella are not fully resolved, and nodal support is low, but this tree still supports a non-monophyletic *P. guianensis*.

Genetic p-distances between the *Pseudogonatodes* from the Paria Range and its sister species, *P. manessi*, are 12.1% and 10.7% for 12S and 16S, respectively (Table 3). The highest interspecific genetic distances within *Pseudogonatodes* are 23.1% for 12S (between *P. lunulatus* and *P. manessi*) and 19.5% for 16S (between *P. furvus* and *P. manessi*). The 16S distance between the two clades recovered for *P. guianensis* range between 13.6% and 15.0%, whereas the distance within clades ranges between 0.0% and 8.0%.

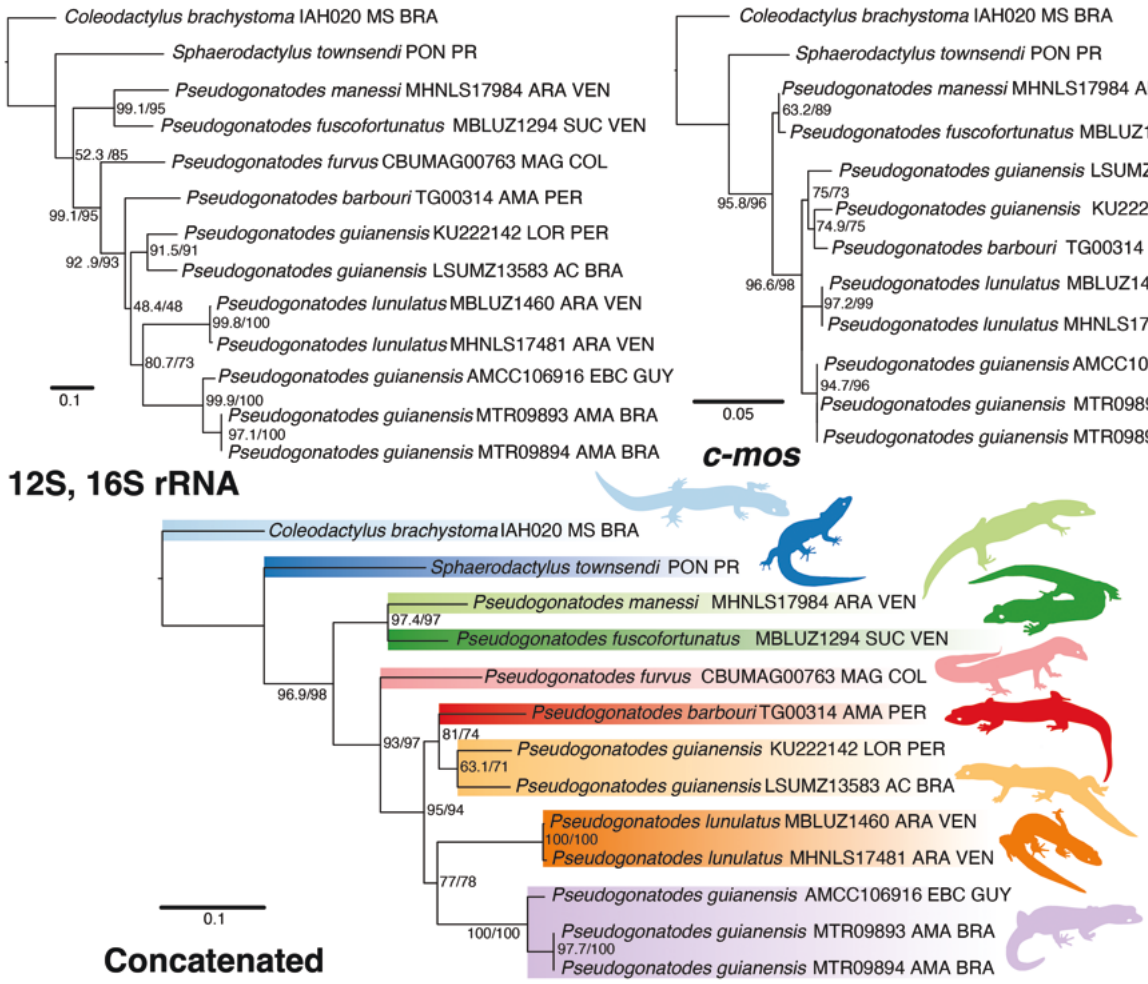

Figure 2. Maximum likelihood phylogeny reconstructed with the mitochondrial, *c-mos*, and concatenated datasets. Nodal support values include results from 1000 ultrafast bootstrap replicates and the SH-like approximate likelihood ratio test. Numbers at nodes are the SH-aLRT support (%)/ultrafast bootstrap support (%).

Table 3. Genetic p-distances among specimens of *Pseudogonatodes* and outgroups *Coleodactylus brachystoma* and *Sphaerodactylus townsendi* for 12S (above the diagonal) and 16S (below the diagonal).

	1	2	3	4	5	6	7	8	9	10	11	12	13
1. ***P. fuscofortunatus*** MBLUZ1294		0.12069				0.21902	0.2219	0.17765	0.21012	0.20952			0.22989
2. *P. manessi* MHNLS17984	0.10722					0.22767	0.23055	0.19253	0.19844	0.18471			0.23919
3. *P. guianensis* MTR09893	0.16150	0.17026											
4. *P. guianensis* MTR09894	0.16150	0.17026	0.00000										
5. *P. guianensis* AMCC106916	0.16029	0.16977	0.04328	0.04328									
6. *P. lunulatus* MHNLS 17481	0.14382	0.14751	0.13823	0.13823	0.13953		0.00568	0.19658	0.15385	0.13651			0.24355
7. *P. lunulatus* MBLUZ1460	0.14382	0.14935	0.13793	0.13793	0.13921	0.00423		0.19943	0.15385	0.13968			0.24355
8. *P. furvus* CBUMAG:REP:00763	0.16990	0.19524	0.17703	0.17703	0.18391	0.14146	0.14146		0.18251	0.17035			0.22663
9. *P. barbouri* TG00314	0.17355	0.17251	0.15259	0.15259	0.15217	0.12568	0.12295	0.13971		0.11673			0.24906
10. *P. guianensis* KU222142	0.16746	0.16512	0.14351	0.14351	0.13636	0.11395	0.11833	0.14368	0.11413				0.21656
11. *P. guianensis* LSUMZ13583	0.16268	0.17209	0.15034	0.15034	0.14318	0.12326	0.12297	0.15517	0.09783	0.07955			
12. *C. brachystoma*	0.13115	0.16063	0.17007	0.17007	0.17676	0.15945	0.15909	0.17021	0.17529	0.14528	0.15496		
13. *S. townsendi*	0.15385	0.16798	0.19789	0.19789	0.19737	0.17942	0.17895	0.25000	0.17816	0.18421	0.17895	0.15119	

TAXONOMIC ACCOUNT

***Pseudogonatodes fuscofortunatus* sp. nov.**

(Figs 3A, 4–7)

Pseudogonatodes manessi: Rivas *et al.* 2006: 107.

Pseudogonatodes sp: Rivas *et al.* 2021: supporting information, table S3.

Holotype: MBLUZ 1292, an adult male, collected from a footpath between Macuro and Los Chorros (Cerro El Olvido, 10°41′33″N, 61°57′47″W), at ~500 m elevation, Península de Paria, Sucre state, Venezuela; one of three specimens collected on 13 August 2014 by Gilson A. Rivas and Mayke De Freitas.

Paratypes: MBLUZ 1293–1294; two specimens with the same collection data as the holotype.

Referred specimen: MHNLS 16202, a subadult specimen in poor condition (a piece of skin is missing on the body) from the same locality as the type series, but collected by Gilson Rivas and César Barrio-Amorós on 19 July 2002.

Diagnosis: Pseudogonatodes fuscofortunatus can be distinguished from all its congeners by the following combination of characters: (1) maximum SVL of 39.2 mm; (2) dorsal scales granular, roughly homogeneous in size, subconical but somewhat flattened and inclined posteriorly, larger than scales on top of head; (3) 98–106 scales around midbody; (4) rostral with posterior median cleft, bordered posteriorly by four postrostrals; (5) four supralabials; (6) three infralabials; (7) eight or nine loreals; (8) posterior edge of mental scale without conspicuous median clefts; (9) five or six postmentals, which are equal to subequal in size compared with subsequent scales; (10) 37–41 ventrals in a straight line between anterior level of forelimbs and border of cloaca, (11) 31–33 ventrals between anterior levels of forelimbs and hindlimbs; (12) long digits lacking expanded subdigital third lamella; (13) eight or nine subdigital lamellae under finger IV; (14) 10 subdigital lamellae under toe IV; (15) subcaudal scales with an inconspicuous medial row of larger scales in contact with three scales laterally alternating with smaller scales in contact with two scales laterally; (16) long snout, with an elongated ascending nasal process of the premaxilla separating the nasal bones; and (17) fused parietal bones in adults.

Comparisons: Pseudogonatodes fuscofortunatus is distinguished from *P. barbouri*, *P. guianensis*, and *P. lunulatus* by lacking an enlarged third subdigital lamella on the fourth toe (for a discussion of this character, see Huey and Dixon 1970). It also differs from those three species by its larger size, with adults of *P. fuscofortunatus* reaching a maximum SVL of 39.2 mm and the smallest specimen known (a juvenile) with an SVL of 32.2 mm, whereas the maximum SVL reported is 25.6 mm for *P. barbouri*, 30.0 mm for *P. guianensis*, and 29.9 mm for *P. lunulatus*. *Pseudogonatodes fuscofortunatus* further differs from *P. guianensis* and *P. lunulatus* by having a higher number of lamellae under the fourth finger (eight or nine vs. four to seven) and fourth toe (10 vs. five to seven), and from *P. barbouri* and by having dorsal scales that are granular and subconical as opposed to being flat and imbricated.

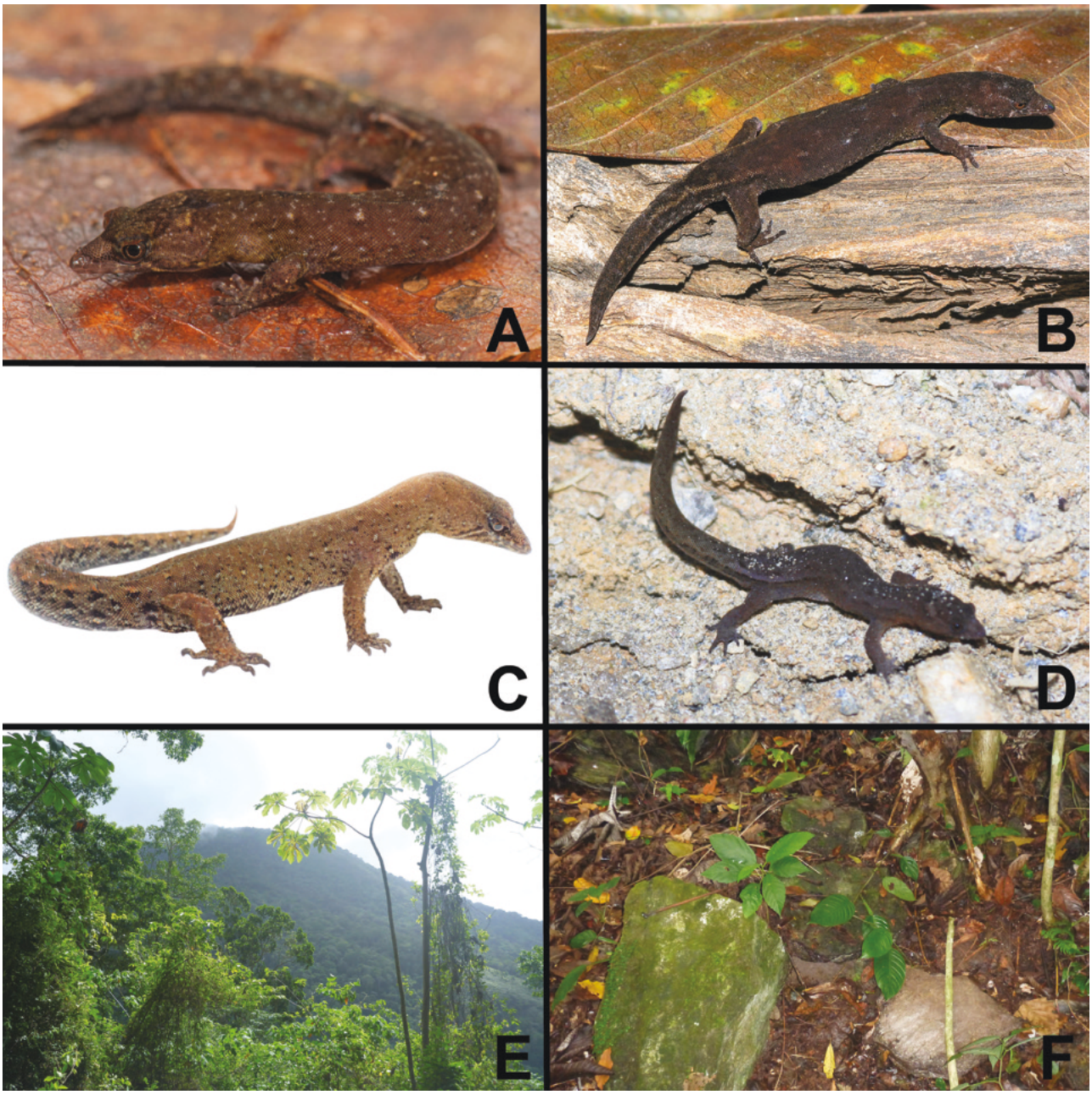

Figure 3. Specimens of *Pseudogonatodes* from northern South America in life. A, ***Pseudogonatodes fuscofortunatus*** female (presumably) paratype (MBLUZ 1293), Cerro El Olvido, Venezuela. B, *Pseudogonatodes manessi*, female, Rancho Grande, Parque Nacional Henri Pittier, Venezuela (MHNLS 17984). C, *Pseudogonatodes furvus*, male topotype, Sierra Nevada de Santa Marta, Colombia (CBUMAG:REP:00767). D, *Pseudogonatodes manessi*, young specimen, from La Cumbre, Municipio Bruzual, Sierra de Aroa, Venezuela; this individual would represent the westernmost limit of the species. E, view of Cerro Azul from Cerro El Olvido, two of the highest mountains with humid forests at the eastern end of the Paria Peninsula, Venezuela. F, undergrowth with abundant decomposing organic matter and rocks, an environment where ***P. fuscofortunatus*** lives. Photographs: Luis A. Rodríguez J. (A), Eric N. Smith (B), Andrés C. Montes-Correa (C), Alberto Navas and Edward Camargo (D), and Gilson Rivas (E, F).

Pseudogonatodes fuscofortunatus shares with *P. furvus*, *Pseudogonatodes gasconi* Avila-Pires & Hoogmoed, 2000, *P. manessi*, *Pseudogonatodes peruvianus* Huey & Dixon, 1970, and *P. quihuai* the lack of an enlarged third lamella on the fourth toe. In comparison to *P. fuscofortunatus*, *P. furvus* seems to be a larger species, with adults exceeding 41 mm in SVL, differing in having fewer postrostrals (three vs. four) and postmentals (two to four vs. five or six), and more lamellae under the fourth finger (10 or 11 vs. eight or nine) and toe (11–15 vs. 10). *Pseudogonatodes gasconi* is a very small species; the only known specimen (holotype) is a gravid female 24 mm in SVL, much smaller than the only juvenile known of *P. fuscofortunatus* (SVL 32.2 mm). The single specimen of *P. gasconi* also has several other differences in comparison to *P. fuscofortunatus*, including more postrostrals (five vs. four), fewer lamellae under the fourth finger (seven vs. eight or nine) and toe (eight vs. 10), tall conical scales as

Figure 4. Laser scanning images from the preserved holotype of ***Pseudogonatodes fuscofortunatus*** (*MBLUZ 1292*) in dorsal and ventral views. Images were obtained using a VR-6000 series KEYENCE 3D Optical Profilometer.

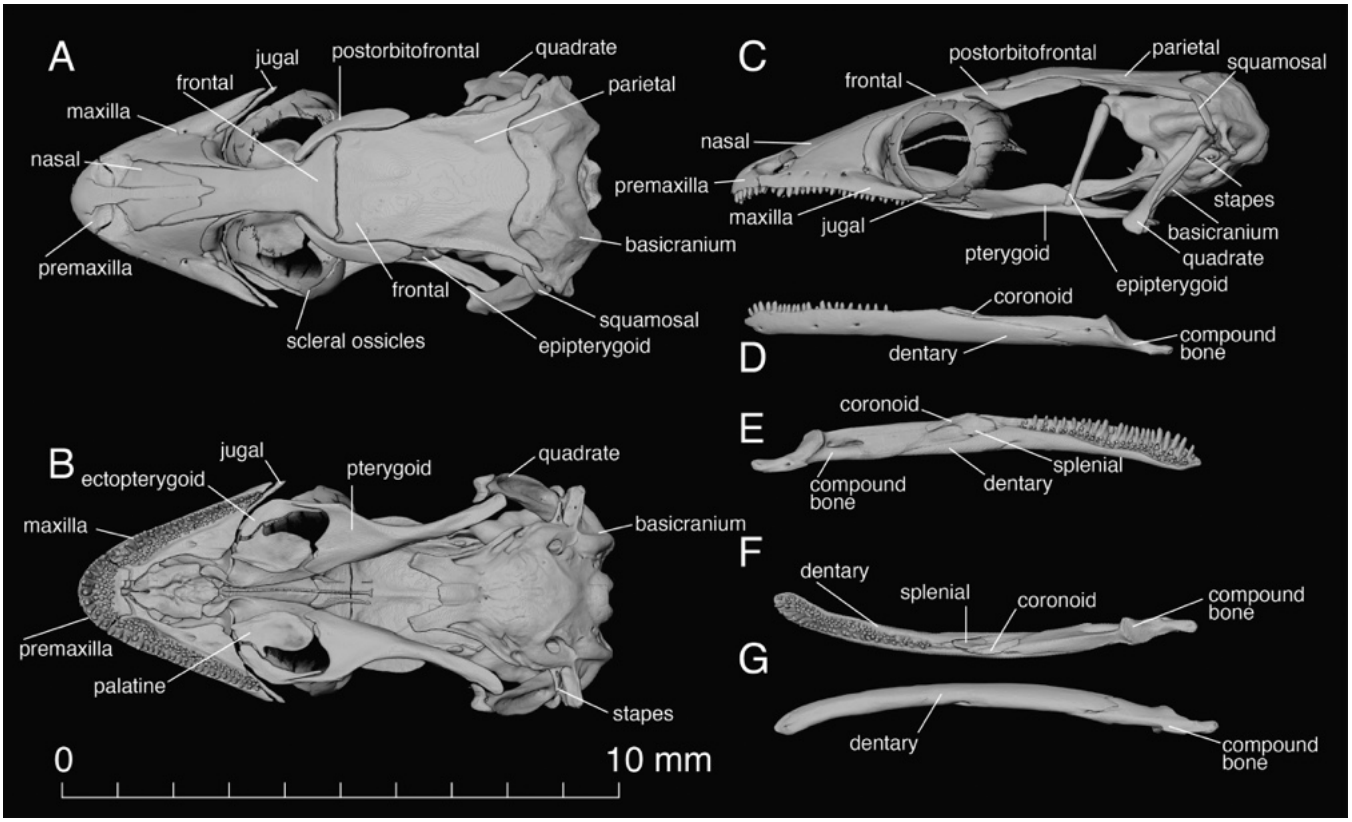

Figure 5. Three-dimensional rendering of the skull of the holotype of ***Pseudogonatodes fuscofortunatus*** (*MBLUZ 1292*). Cranium in dorsal (A), ventral (B), and lateral (C) view, and jaw in lateral (D), medial (E), dorsal (F) and ventral (G) views.

opposed to short subconical scales dorsally, and lacking a medial cleft on the rostral scale, which is present all specimens of *P. fuscofortunatus*. *Pseudogonatodes fuscofortunatus* differs from *P. peruvianus* in being a larger species (largest adult in *P. peruvianus* is 32 mm in SVL) and having more lamellae under the fourth finger (eight or nine vs. six or seven) and toe (10 vs. eight or

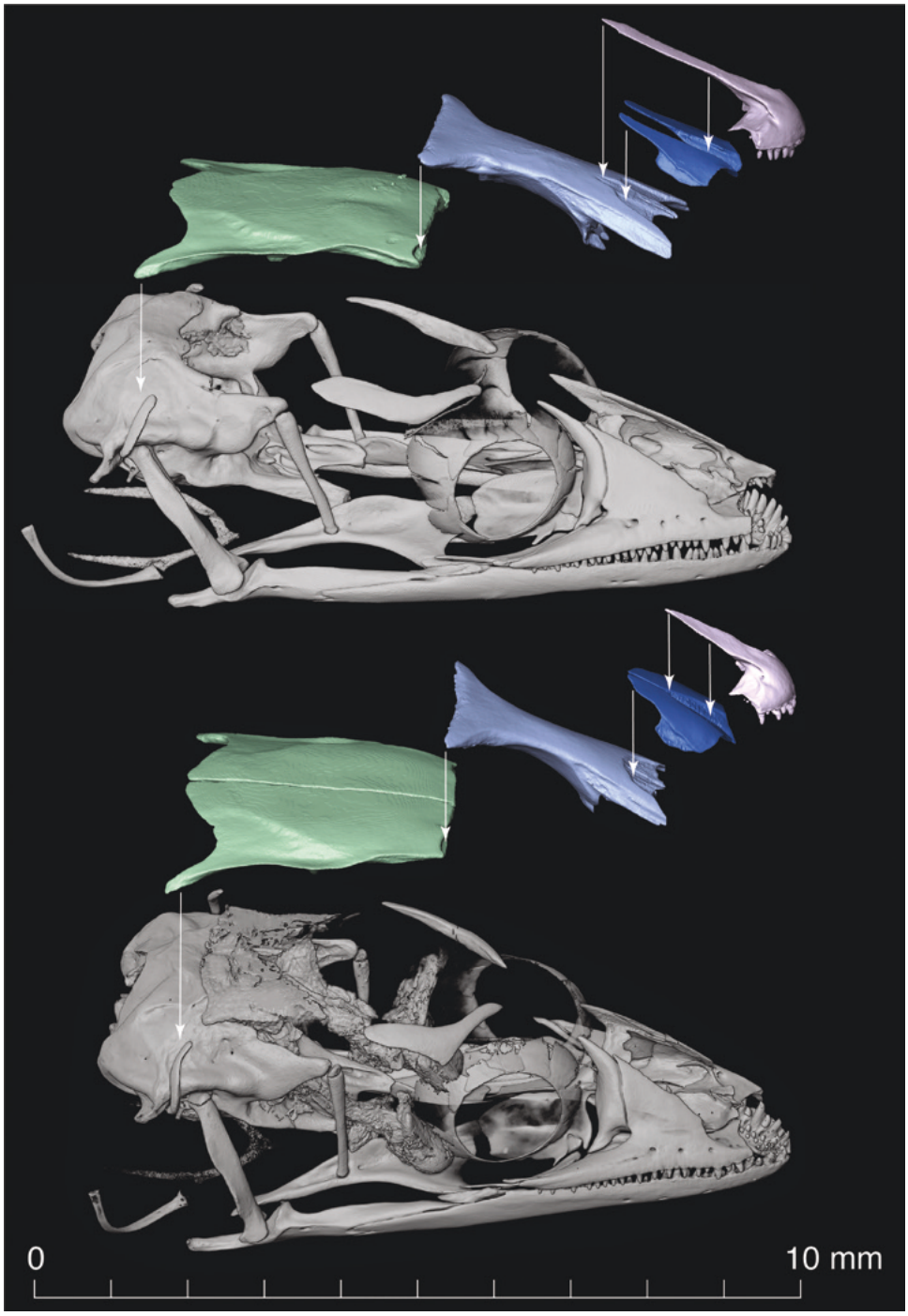

Figure 6. Telescoped pattern of the skull of ***Pseudogonatodes fuscofortunatus*** (*MBLUZ 1292*, top), compared with *Pseudogonatodes manessi* (KU 182740, bottom). Arrows indicate the facets that support each dorsal bone. Colours are as follows: purple, premaxilla; cobalt blue, nasal; light blue, frontal; green, parietal .

nine). It differs from *P. quihuai* in having four postrostrals as opposed to three and having higher numbers of loreal scales (eight or nine vs. five or six) and scales around the midbody (98–106 vs. 85–91). *Pseudogonatodes fuscofortunatus* is both most phenotypically similar and most closely related to *P. manessi*, but it differs from this species in having four postrostrals as opposed to three and in aspects of cranial osteology, as discussed below. Among species of *Pseudogonatodes* for which cranial osteological data are available (*P. barbouri*, *P. furvus*, *P. fuscofortunatus*, *P. guianensis*, *P. lunulatus*, *P. manessi*, and *P. quihuai*), *P. fuscofortunatus* is unique in having fused parietals and a long ascending nasal process that completely separates the nasal bones.

Description of holotype: An adult male (SVL 39.2 mm) with fully regenerated tail (TL 27.8 mm) in a state of good preservation. Morphometric and meristic data are included in Table 4. Head cone-shaped, long, and pointed. Rostral large, visible from above, with a posterior medial cleft extending anteriorly

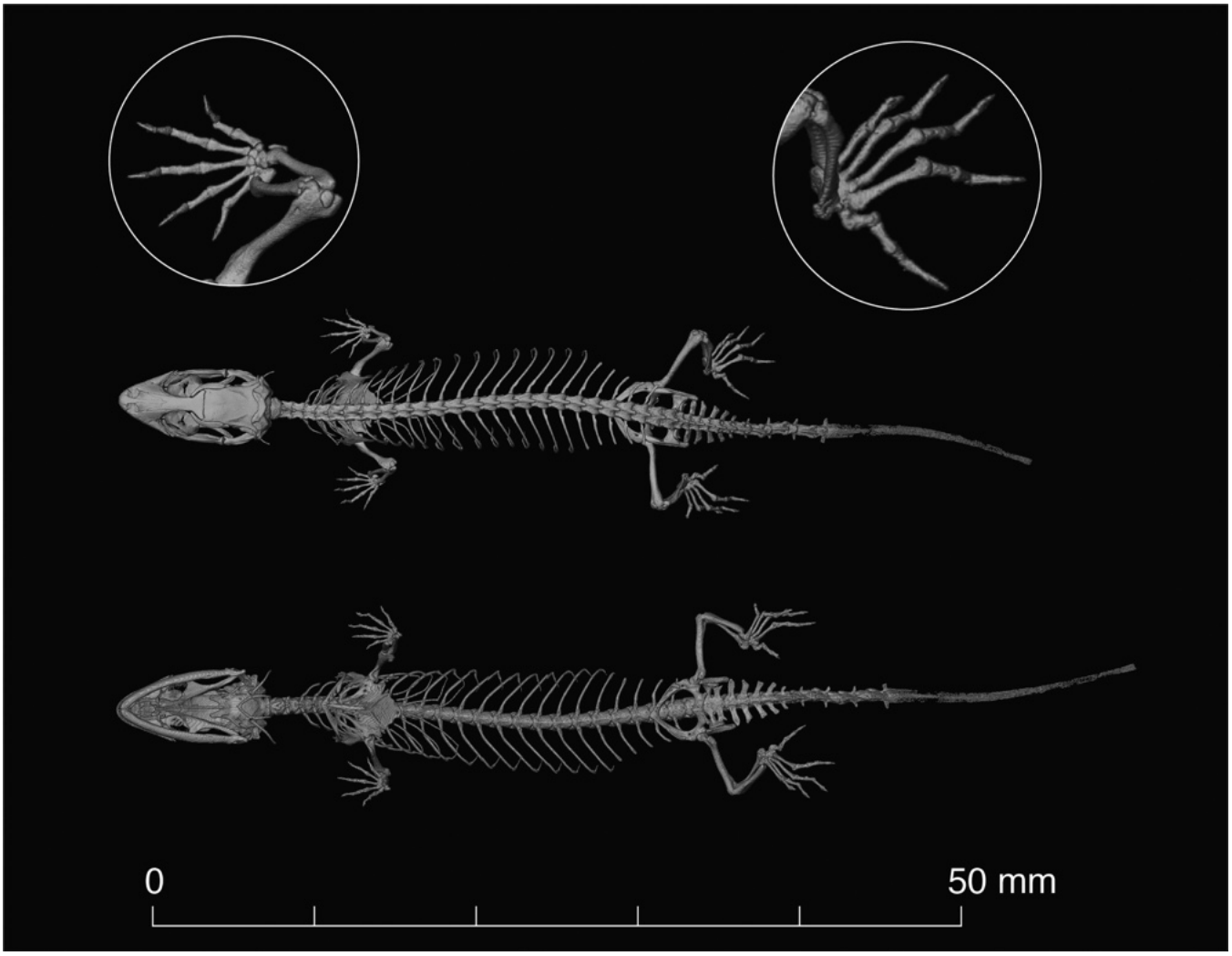

Figure 7. Complete skeleton of ***Pseudogonatodes fuscofortunatus*** (*MBLUZ 1292*) in dorsal and ventral view, and insets with close-up for the right manus and pes.

more than half the length of the rostral. Four postrostrals, the two medial ones indenting the rostral and about half of the size of the two laterals (= supranasals). Nostrils and surrounding scales slightly protruding from snout, each bordered by rostral, supranasal, one (left) or two (right) postnasals, and first supralabial. Postnasals about the same size as loreal scales. Scales on snout and loreal region gradually transitioning from flat, polygonal, and juxtaposed, anteriorly, to conical and subimbricate, posteriorly. Nine loreal scales counted in the shortest straight line between postnasals and eye socket. Scales on supraorbital region subconical and subimbricate, slightly larger than adjacent scales. Anterodorsal ocular scales form a supraciliary flap, with the two anteriormost in dorsal view significantly larger than adjacent scales. Four supralabials, first three subequal in length, but first and second significantly taller than third; fourth supralabial below middle of eye, much smaller than the first three and followed posteriorly by granular scales similar in size to scales on adjacent temporal region. Scales on the temporal and parietal region small, granular to subconical, juxtaposed. Ear opening small and oval, located at a distance from orbit about twice as long as the distance between orbit and nostril.

Mental large, without posterior clefts. Posterior border of mental resembles a half hexagon, with a transverse straight suture and two divergent oblique sutures. Six asymmetrically arranged postmentals, the first two in contact with right oblique suture, the second to fourth in contact with transverse suture, and fourth to sixth with left oblique suture of mental. Postmentals about same size as scales of chin, which are granular and subimbricate. Three infralabials, the first very long, almost reaching anterior level of orbit and more than twice as long as the second infralabial; third infralabial small, below midlevel of orbit, followed posteriorly by four or five small, elongated scales to rictus of mouth. Scales on upper part and sides of neck granular, like dorsals. Anterior scales of the throat granular, rounded, and juxtaposed, gradually transitioning posteriorly to larger, subimbricate granules, to flat, imbricated ventral scales.

Dorsal scales granular, rounded in lateral and dorsal view, slightly inclined posteriorly. Dorsal granules slightly larger than those on parietal region. Ventral scales distinctly larger than dorsals, flat, smooth, imbricate, more or less rhomboidal, with rounded corners; 33 scales in a midventral line between anterior levels of fore- and hindlimbs, 41 until vent. A single row of small

irregular scales borders the vent anteriorly, two rows posteriorly. A narrow transitional zone between dorsals and ventrals. Longitudinal scale rows around midbody 100, of which ~15 are well-defined ventrals. Escutcheon absent.

On the base of tail, supracaudal scales are similar in size and shape to trunk dorsals, abruptly transitioning into large, flat, subimbricate scales on the second sixth of the tail. Tail regenerated at the beginning of the third sixth of tail. Original tail segment has an inconspicuous midventral row of larger scales in contact with three scales laterally alternating with smaller scales in contact with two scales laterally. Dorsal region of the regenerated portion of tail with flat, oval-shaped, imbricate scales, slightly smaller than scales on unregenerated portion. Subcaudal scales on regenerated portion of tail irregular in shape and size, but flat and imbricate.

Scales on anterior part of forelimbs flat, smooth, and imbricate; elsewhere on the forelimbs granular and subimbricate to juxtaposed. Scales on forelimbs flat, smooth, and imbricate except posteriorly, where they are granular and juxtaposed. Ventral surfaces of manus and pes with heterogeneous squamation in shape and size. Lamellae under fourth finger eight, under fourth toe 10. Lamellae under digits subequal in size. Claws enclosed by an ungual sheath comprising five scales, as is characteristic for the genus.

Holotype coloration: In life, the background dorsal coloration of the head, body, limbs, and tail is chocolate brown overlaid with irregular dark brown mottling. A longitudinal and nearly mid-dorsal series of nine small pale cream dots extends from the level of the forelimbs to the midbody level and continues with three additional dots immediately anterior to the level of the hindlimbs. These pale dots are small, encompassing two to four scales, and are separated by three to four scales. There are also slightly larger pale spots dorsolaterally, but much more interspersed, three on each side of the body. The top of the head has inconspicuous pale dots not forming a discernible pattern. The labial region also has inconspicuous pale markings, especially around the sutures between the supralabials and infralabials, respectively. The top of the tail has short irregular and broken cream and brown dorsolateral stripes that extend only from the level of the hindlimbs to the anterior sixth portion of the tail. The venter is pinkish brown. The gular area is cream coloured, with some brown suffusions around the postmentals and posteriorly, where there is the colour transition to the venter. Subcaudal coloration same as dorsum except anteriorly, where it is suffused with pinkish brown. The preserved specimen has not changed much in colour, with only the pink hue in the ventral area fading.

Variation: Morphometric and meristic data for the type series is presented in Table 4. Sexing of the holotype and the largest paratype (MBLUZ 1293) is tentative. These two specimens have differences in the subcaudal region adjacent to the vent. In the holotype, presumably a male, there are two inconspicuous bulges ventrolaterally that might correspond to the presence of hemipenes. In MBLUZ 1293, presumably a female, the tail is constricted and regenerated shortly behind the vent, and there does not seem to be enough space for hemipenes. This specimen also has a noticeable swollen and decoloured area on the left side of the neck (observable in Fig. 3A), which might correspond to an extracranial endolymphatic sac, but computed tomography scans do not show extracranial calcium deposits in the endolymphatic sacs in any of the three type specimens. In geckos, it has been demonstrated that females have larger endolymphatic sacs than males, e.g. in *Gonatodes antillensis* (de Jeude, 1887) (Lamb *et al.* 2017) and *Gekko gecko* (Linnaeus, 1758) (Laver *et al.* 2019), but unfortunately the lack of visible extracranial calcium deposits in MBLUZ 1293 precludes us from using this structure to help determine the sex of specimens.

Table 4. Measurements (in millimetres) and scale counts for the type series ***Pseudogonatodes fuscofortunatus***. Definitions and abbreviations for all measurements are in the Materials and Methods section. A forward slash is used when there is left/right side variation.

Character	*MBLUZ 1292*	MBLUZ 1293	MBLUZ 1294
Sex	Male	Female	?
Measurements			
SVL	39.2	34.4	32.2
TL	27.8	22.4	Broken
AXG	19.2	16.6	14.9
HL	8.9	7.8	7.6
HW	5.2	4.7	4.0
HD	3.5	3.0	2.8
EYN	2.3	2.2	2.1
EYE	1.6	1.4	1.4
Scale counts			
SAM	100	98	106
VFH	33	31	33
VFC	41	37	40
PR	4	4	4
PN	½	2	1/2
LOR	9	9	8
SUPL	4	4	4
INFL	3	3	3
PM	6	5	6
LFF	8	9	9
LFT	10	10	10

There is noteworthy colour variation in the type series. Both MBLUZ 1293 and 1294 lack a well-defined series of mid-dorsal pale dots as observed in the holotype. MBLUZ 1293 has many more pale markings than the other two types, as described in the next few lines. The dorsolateral pale dots are more conspicuous and frequent, five as opposed to three on each side, compared with the holotype. These dots seem to have dark markings suffused around them, forming poorly defined ocelli. There is an additional series of smaller (encompassing two scales) pale cream dots laterally, about eight on each side. The rest of the pale markings are small and do not seem to form any pattern. MBLUZ 1293 also has a creamish yellow, roughly W-shaped marking on the parietal area that is not observed in the two other types. MBLUZ 1294 has dark suffusions in the gular area that form three diffuse and incomplete slanted stripes on each side of the head that extend posteromedially from the infralabials and, except for the anteriormost, do not contact each other medially. It is possible that these stripes fade ontogenetically, because they are not observed in the two adult specimens.

Etymology: The specific epithet *fuscofortunatus* is a combination of the words *fusco* (from *fuscus*, a noun in Latin), referring to the general brown colour of this species of lizard, and *fortunatus* (Latin adjective meaning lucky or fortunate), and is formed as a compound noun in apposition. It is in reference to the lucky occasion of the discovery of this small brown gecko, which had gone unnoticed by other naturalists and explorers who visited these mountains over the previous century. The name was selected from a list of names proposed at the OroVerde office.

Cranial anatomy: Typically, the skull (Figs 5–7) is lightly built, as in other sphaerodactyls (i.e. *Chatogekko*, *Coleodactylus*, *Gonatodes*, *Lepidoblepharis*, and *Sphaerodactylus*); however, it is unique in being slender, having an elongated snout, and having a distinctive overlap of the premaxilla, nasals, and frontal. The nasals are completely separated from one another by the premaxilla; the frontal width is almost constant along most of the bone length and expands significantly and abruptly only in the posterior quarter. There is only a slight interorbital constriction of the frontal, which is unique among congeners. The frontal also has two long and well-defined anterolateral processes. Each eye has 14 scleral ossicles. The premaxilla has 11 tooth loci, the maxilla 25 tooth loci, and there are four supralabial foramina. The parietals are fused, and the frontoparietal suture is braced by the postorbitofrontal, which has a curved lateral margin. The braincase is not globular as in many other miniaturized sphaerodactyls. The vomer is fused; the palatine has a deep ventral choanal groove. The pterygoid braces the ectopterygoid as in other *Pseudogonatodes*.

The crista prootica extends to the base of the basipterygoid process; the posterior opening of the vidian canal is entirely ventral; the lateral aperture of the recessus scalae tympani is visible ventrally and the spheno-occipital tubercle is reduced. A stapedial foramen is present. The jaw is formed by the dentary, coronoid, splenial, and compound bone. The dentary extends laterally almost to the level of the posterior surangular foramen and bifurcates posteriorly into angular and surangular processes. There are three mental foramina and 30 tooth loci. The compound bone has a moderate retroarticular process, not expanded or excavated dorsally; the foramen for the chorda tympani opens medially.

Postcranial anatomy: The skeleton (Fig. 7) of *P. fuscofortunatus* has 26 presacral vertebrae; the atlas has fused neural arches and bifurcated hypaphophyses. MBLUZ 1293 has a total of nine caudal vertebrae, five in the pygal series, and four with autotomy planes. It has a regenerated axial rod beginning at the level of the ninth caudal. The specimen has no clavicular fenestra; the interclavicle has no lateral processes; and there are four pairs of ribs attached to the presternum, one via the mesosternum.

There are four phalanges in the 4th digit of manus and pes. Four phalanges are also present in the manual digit IV in *Coleodactylus* and *Chatogekko*, but this character is unique in the pedal digit IV of *Pseudogonatodes* (Kluge 1995, Gamble *et al.* 2011a, Bauer *et al.* 2018, Montes-Correa *et al.* 2021). Using a combination of X-rays and micro-computed tomography data, this character was confirmed in 28 specimens, belonging to six species (including *P. fuscofortunatus*). Pedal digit IV looks long in *P. quihuai*, but no osteological data are available to corroborate the reduction in the number of phalanxes. *Pseudogonatodes quihuai* is also differentiated from all other *Pseudogonatodes* in having paired frontals, a character reported before only in *Coleodactylus*, *Teratoscincus*, and *Saurodactylus* (Daza and Bauer, 2012), but in recent analyses this species was confirmed as member of *Pseudogonatodes* (F.M.J. Rojas-Runjaic, personal communication to W.E. Schargel).

Natural history and conservation: All type specimens were collected on a trail that goes from Macuro to Los Chorros, along the eastern flank of Cerro El Olvido, at an elevation of ~500 m a.s.l. The individuals were active on the ground when captured at ~11.00 h. The species appeared to be common at that time, because eight individuals in addition to those collected were observed in 2 h. The first individual of this species was captured on 19 July 2002 (Rivas *et al.* 2006). It was active at the base of a large tree located along the same trail where the type series was collected, but at ~15.00 h. It is important to note that at this elevation (500 m a.s.l.), there is a noticeable and abrupt transition in temperature and vegetation, changing from a warm lower level of deciduous vegetation to a cooler evergreen forest with medium-sized and larger trees. The soil is more humid, with abundant organic matter and rocky outcrops, producing a substrate with many suitable hiding places for these tiny lizards.

A particular feature of the Peninsula de Paria is that, owing to the Massenerhebung effect, Tropical Montane Humid Forest and Tropical Montane Cloud Forests are encountered at lower elevation than in the rest of Northern Venezuela. This phenomenon is particularly pronounced at the very end of the Peninsula, because the Trade Winds or Easterlies are prevalent and strong and carry seasonally high levels of moisture that are then pushed up by the mountain mass. The trade winds, moving from east to west, will encounter land at the easternmost side of the peninsula, offloading a higher amount of humidity at lower elevation. As they move westwards, the remaining humidity will be available at higher elevations, such as the surroundings of Cerro Humo, the highest peak of the Paria Range.

The Paria Range is composed of two geographically distinct sections (western and eastern) demarcated by a low pass (<200 m in elevation) at Mejillones Cove. This lowland region is reputed to break up the continuity of the evergreen forest, and it might represent a significant barrier to the dispersal of animal populations in recent times between both sections, although the barrier might have become established too recently to have allowed speciation to occur. However, there seem to be some differences in species composition between eastern and western Paria based on the significant fieldwork conducted by G.A.R. and M.D.F. in the region. *Pseudogonatodes fuscofortunatus* has been collected only in the eastern section of Paria, despite considerable field effort in the western section. Another example is *Oreosaurus rhodogaster* (Rivas, Schargel & Meik, 2005; Gymnophthalmidae), which appears to be common in the forest understorey of the western section, mainly in the surroundings of Cerro Humo and the village of Las Melenas, whereas it has not been observed in similar habitats in the eastern mountains around Macuro. This does not necessarily mean non-existence, but potentially that local conditions vary and significantly affect the abundances of these two species. It is well known that many amphibians have been observed at much lower elevations in the eastern section, around Macuro, than in the western ridges of Cerro Humo. Some

amphibians and reptiles observed in Macuro and its surrounding mountains, El Olvido and Cerro Azul, are *Mannophryne riveroi* (Donoso-Barros, 1956), *Mannophryne venezuelensis* Manzanilla, Jowers, La Marca, & García-Paris, 2007, *Hyalinobatrachium orientale* (Rivero, 1968), *Vitreorana castroviejoi* (Ayarzaguena & Señaris 1997), *Phyllomedusa trinitatis* Mertens, 1926, *Scinax ruber* (Laurenti, 1768), *Flectonotus fitzgeraldi* (Parker, 1934), *Leptodactylus turimiquensis* Heyer, 2005, *Gonatodes ceciliae* Donoso-Barros, 1966, *Hemidactylus palaichthus* Kluge, 1969, *Phyllodactylus ventralis* O'Shaughnessy, 1875, *Thecadactylus rapicauda* (Houttuyn, 1782), *Ninia atrata* (Hallowell, 1845), *Tantilla melanocephala* (Linnaeus, 1758), and *Bothrops* aff. *venezuelensis* Sandner-Montilla, 1952. Ramón Urbano, as cited by Phelps and Phelps (1948), additionally mentioned the presence of the bushmaster (*Lachesis muta*) as very abundant in the upper slopes of the mountains surrounding Macuro.

A decade ago, the Venezuelan state-owned oil company Petróleos de Venezuela, S. A (PDVSA) commissioned the reopening of the Güiria–Macuro road to facilitate access to the easternmost areas that were going to be developed as part of oil prospecting on the continental platform a few miles off-shore, but only the first phase of ground levelling was carried out. Finishing it could have spelled disaster for the Peninsula, because the road would have allowed easy access to otherwise isolated areas of the Peninsula, such as Patao and Macuro. Immigration would have been another negative aspect of the development of the liquified gas plant in Güiria and other related projects in or near Macuro (such as the underwater pipeline). Such development would have increased the pressure on a town already lacking basic government assistance for decades. However, for various reasons, the Paria liquified gas project collapsed, and a visit carried out by us in 2014 seemed to indicate that people have migrated from the village, abandoning the local crops. Also, most of the villagers are very happy buying food from grocery stores, rather than taking the risk of being bitten by snakes while looking for food on their small farms near forested areas. Most inhabitants in Paria have an almost supernatural fear of snakes, and most of them prefer not to wander in heavily vegetated areas, in order to avoid the risk of snake bites.

The locality where the type series of *P. fuscofortunatus* comes from is protected within the limits of the Paria Peninsula National Park, thanks to a recent presidential decree (Official Gazette 42.182, Decree No. 4547, dated 3 August 2021) that expanded the mountainous area and marine-coastal area of the Paria Peninsula National Park from 37 500 ha at its creation in 1978 to 89 244 ha. In this sense, the lands above 400 m a.s.l. in the extreme east and south of the Peninsula are now protected within the limits of the National Park. This is the product of a wise decision supported by a series of scientific discoveries in recent decades, which have shown that the local biodiversity is greater than had been estimated until a few years ago. Many of the recent findings deal with new species of plants, amphibians, and reptiles, most of which are endemic to the region. This opens more and broader questions about the distribution of plants and animals in northeastern Venezuela.

DISCUSSION

A sister relationship between *P. fuscofortunatus* and *P. manessi* is consistent with the close biological affinity between the Eastern Coastal Mountain Range, which includes the Paria Range, and the Central Coastal Mountain Range, to which *P. manessi* is endemic (Rivas *et al.* 2021). These two ranges share many montane species in common or have endemic species with a close phylogenetic relationship with each other (Barrio-Amorós *et al.* 2006). The Paria Range, specifically, is biogeographically complex, because it also shares a strong affinity with the Northern Mountain Range of Trinidad (Sánchez-Pacheco *et al.* 2017, Rivas *et al.* 2021) and with rain forest in Amazonia and the Guiana Shield (Steyermark 1962, Schargel *et al.* 2005). We note that within the Coastal Mountain Range, *Pseudogonatodes* is conspicuously missing from the Turimiquire Massif, which is the main section of the Eastern Coastal Mountain Range, and it is geographically close to the Peninsula de Paria. It is possible that the range of *P. fuscofortunatus* extends into the Turimiquire Massif or that a closely related species has yet to be found there, as has been reported with other taxa (Rivas *et al.* 2005, 2021).

Contrary to what was suggested by Montes-Correa *et al.* (2021) based on external morphological similarities and biogeographical affinities of the Caribbean Mountain systems of Colombia and Venezuela (Sánchez-Pacheco *et al.* 2017, Rivas *et al.* 2021), *P. furvus* is not the closest relative of *P. manessi*. *Pseudogonatodes furvus* was recovered as sister to a clade of species that have an enlarged third lamella on the fourth toe. This was one of the characters used by Huey and Dixon (1970) to define three putative groups in *Pseudogonatodes*. Of these three groups, two include species with an enlarged third lamella under the fourth toe, and these two groups differ from each other based only on the shape of the dorsal scales. Our phylogenetic analysis includes all three currently recognized species (*P. barbouri*, *P. guianensis*, and *P. lunulatus*) that have an enlarged third lamella under the fourth toe and supports this character state as a synapomorphy for this clade. Huey and Dixon (1970) also grouped together species of *Pseudogonatodes* that lack an enlarged lamella under the fourth toe, but this group is not monophyletic in our analysis, which is consistent with this character state being symplesiomorphic. Several trans-Andean Colombian populations of *Pseudogonatodes* that lack an enlarged third lamella under the fourth toe have been discovered recently (see Appendix I in Montes-Correa *et al.* 2021), but their taxonomic identity and phylogenetic position remain unclear. This observation suggests that the diversity of *Pseudogonatodes* might be grossly underestimated, especially in the northern Andes.

Our molecular phylogenetic results also indicate the possibility that at least two species are currently included under the name *P. guianensis*. Our concatenated analysis recovered two distinct clades of *P. guianensis*. One clade is sister to *P. lunulatus* and is likely to represent *P. guianensis s.s.*, given that at least one of the samples (AMCC106916) in this clade comes from Guyana, relatively close to the type locality of this species (Parker 1935). The other clade contains two samples from western Amazonia and is sister to *P. barbouri*. It is possible that the name *Pseudogonatodes amazonicus* Vanzolini, 1967, which is currently considered a junior synonym of *P. guianensis* (Hoogmoed 1973, Avila-Pires 1995), applies to that clade. However, because of our limited sampling in the context of the extensive geographical distribution of *P. guianensis*, we currently refrain from proposing any taxonomic changes. Avila-Pires (1995) discussed geographical variation in scalation and colour pattern in *P. guianensis* and concluded that there is geographical variation in this species, with

differences found between populations in western Amazonia and those in the Guiana Shield. However, the limited number of specimens examined from central Amazonia presented a mixture of characters, hence no conclusive taxonomic decision could be made.

The cranial osteology of *P. fuscofortunatus* (Fig. 5), including the remarkable telescoped arrangement of the snout bones (Fig. 6), is highly distinctive. Telescoping of the skull is a term that has been used loosely and poorly defined. Roston and Roth (2019) reviewed the use of this term, which refers to the metaphor of a spyglass, which when collapsed becomes shorter owing to the overlap of its parts. Telescoping in cetacean skulls refers to: (1) extensive bone overlap; and (2) extreme proximity of anterior and posterior cranial elements. One important aspect in cetaceans is the transformation of the nares into the blowhole (dorsal nares), which has been linked to telescoping (Romer 1966), but Roston and Roth (2019) specify that the shifting of the nares is not necessary an outcome of the extensive overlap of the frontal by maxillary and/or occipital bones. Following this definition, the snout of *P. fuscofortunatus* is telescoped. Telescoping has also been identified in some other squamates, particularly mosasaurs (especially those with their nares posteriorly displaced; Lingham-Soliar 1995, Polcyn *et al.* 2022) and varanids (Polcyn *et al.* 2022). Among gekkotans,

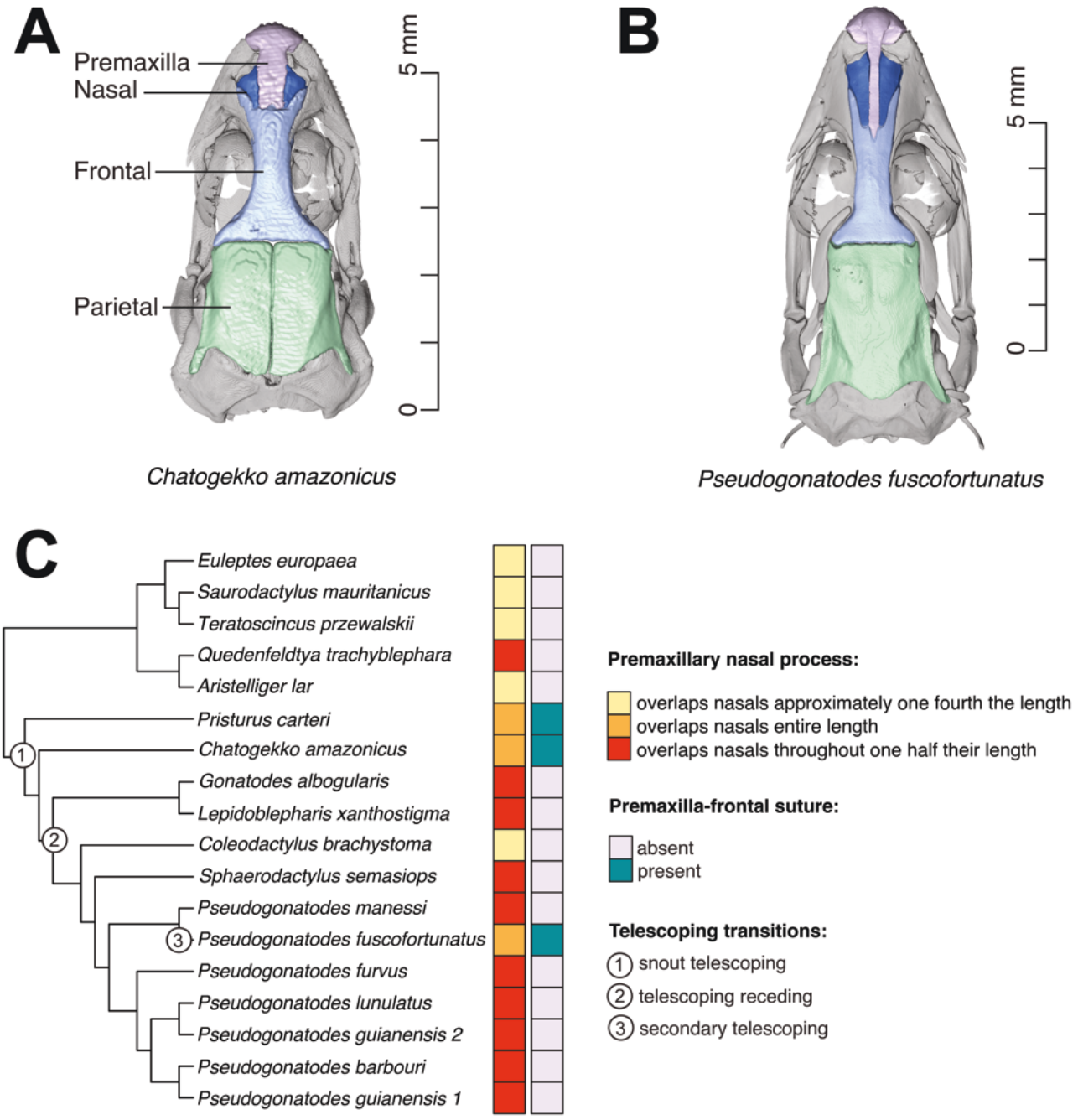

Figure 8. A, dorsal view of *Chatogekko amazonicus*. B, dorsal view of ***Pseudogonatodes fuscofortunatus***. C, overlapping of the premaxilla with the nasals and the premaxilla–frontal contact among sphaerodactylids, mapping of transitions are based on parsimony.

telescoping involving the complete separation of the nasals by the ascending nasal process of the premaxilla, and the contact of the premaxilla with the frontal bone occurs in the pygopod *Pletholax* (Stephenson 1962) and the sphaerodactylid genera *Pristurus* and *Chatogekko* (Daza *et al.* 2008, Gamble *et al.* 2011a), and is reported here for *P. fuscofortunatus*. Mapping of the telescoped skull condition on a phylogenetic hypothesis for the family Sphaerodactylidae (Fig. 8) suggests that this condition has evolved independently at least twice in this group.

In all other *Pseudogonatodes* (including *P. manessi*, the sister species of *P. fuscofortunatus*; Fig. 6) the ascending nasal process reaches only about halfway along the length of the nasal bones, partly separating the nasals (Fig. 8). However, *P. manessi* and especially *P. fuscofortunatus* develop proportionally longer snouts. In *P. barbouri*, *P. furvus*, *P. guianensis*, *P. lunulatus*, and *P. quihuai* the snout is shorter, having a short ascending nasal process, as in *Coleodactylus* and the extremely modified *Chatogekko* (Fig. 8). Snout differences in sphaerodactyl geckos might be linked to habitat use, reflecting to some degree an ecomorphological pattern (Daza *et al.* 2008), but without detailed information on the microhabitat used by *P. fuscofortunatus* no functional correlation to its extreme elongated snout can yet be established. A similar elongated snout is also present in *Sphaerodactylus semasiops* Thomas, 1975 from Jamaica (Griffing *et al.* 2018). This gecko is frequently found in bromeliads (Thomas 1975, Vogel 2000), where a long snout might be useful to reach prey in the leaf axils of these plants.

Regarding other aspects of cranial osteology, *P. fuscofortunatus* and geckos in the genus *Aristelliger* are the only members of Sphaerodactylidae with fused parietals (Figs 5–7). The paroccipital process is relatively large, well defined, and diverges posterolaterally, which is atypical of miniaturized geckos, where this structure tends to be very small. The coronoid is very low and not entirely fused to the splenial as in other sphaerodactyls. The basipterygoid process is long, rectangular, and has expanded distally. The teeth are large in the anterior part of the dental arcade, including on the premaxilla, anterior one-quarter of the maxilla, and anterior one-quarter of the dentary. The teeth gradually decrease in size posteriorly, reaching only half the size of the anterior teeth. This species also has a remarkably high number of lingual tooth buds, especially in the anterior part of the tooth arcade.

The separation of the nasal bones in *P. fuscofortunatus* should reflect some differences in the distribution of stress forces in the skull relative to its congeners. It is possible that the separation of nasals might redistribute stress in the snout to the parietal table, resulting in fusion of these elements. Finite element analyses should be used to determine whether the presence of sutures relieves stress locally but produces an increase of stress in other regions (Moazen *et al.* 2009). In other species where the nasals are also separated by the premaxilla, the parietal bones remain separated (i.e. *Chatogekko* and *Pletholax*), which indicates that the distribution of forces in the skull is likely not to be generalizable.

Given that *P. fuscofortunatus* and *P. manessi* are closely related species with hardly any external morphological differences, we were surprised by the major cranial osteological differences between them. This demonstrates that in some cases osteology can be a good source of taxonomic characters in the study of closely related or cryptic species. The availability of non-invasive/non-destructive high-resolution imaging techniques (e.g. computed tomography scans) will facilitate the use of osteological characters in alpha-taxonomic herpetological studies, complementing its already widespread use in higher-level phylogenetic studies.

In recent years, the osteology of the genus *Pseudogonatodes* has received some attention, and currently available information indicates that members of this genus show morphological disparity. Some species in the genus exhibit contrasting morphologies, such as unfused frontals (*P. quihuai*), a telescoped skull and fused parietals (*P. fuscofortunatus*), an elongated snout (*P. fuscofortunatus* and *P. manessi*), and a reduction in the number of phalanges in pedal digit IV (all species). These observations highlight the importance of osteological characters in the study of the evolution of these miniaturized taxa.

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CONFLICT OF INTEREST

None declared.

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DATA AVAILABILITY

The data underlying this article are available in the GenBank Nucleotide Database at https://www.ncbi.nlm.nih.gov/genbank/ and MorphoSource at https://www.morphosource.org/. The unique identifiers and accession numbers are indicated in the text.

APPENDIX 1. SPECIMENS EXAMINED, WITH LOCALITY DATA

- *Aristelliger georgeensis*. BELIZE: Belize District: Caye Caulker Town, CAS 176485.
- *Chatogekko amazonicus*. BRAZIL: Amapá: Serra do Navio, MTR 12682.
- *Coleodactylus brachystoma*. BRAZIL: Bahía: UMMZ 103051.
- *Euleptes europaea*. ITALY: Toscana: Livorno, Isola di Cerboli, MCZ R-4463.
- *Gonatodes albogularis fuscus*. COLOMBIA: Antioquia, FMNH 55929.
- *Lepidoblepharis xanthostigma*. COSTA RICA: Limón, Hwy 9 at Guapiles, CAS 178104.
- *Pseudogonatodes barbouri*. PERÚ: Cajamarca, Bella Vista MCZ R-14385 (paratype).
- *Pseudogonatodes furvus*. COLOMBIA: Magdalena: Santa Marta DTCH, vereda Bellavista (type locality), 1699 m, CBUMAG:REP:00763–68; vereda El Campano, 1420 m, CBUMAG 00295. Municipio de Ciénaga, basin of Río Frío, elevation unknown, MCZ 29700; San Pedro de la Sierra, ~1600 m, ICN 3501–02. Palmor de la Sierra, 1400 m, CBUMAG 00283, 293.
- *Pseudogonatodes guianensis* (eastern). BRAZIL: Amazonas: Santa Isabel do Río Negro, Serra do Tapirapecó, MZUSP 94826; VENEZUELA: Amazonas: Base del Cerro de la Neblina, playa derecha del río Mawarinuma (= Baría), USNM 562609–11, 13–16.
- *Pseudogonatodes guianensis* (western). ECUADOR: Napo: Puerto Napo, Hacienda de George Kiederle, Río Napo, USNM 166138, Tena, Río Misahualli, USNM 234574; Pastaza: Coca, Tiniguo, USNM 321059. PERÚ: Cuzco: San Martín, Cashiriari, río Camisea, USNM 538260–64; Nadre de Dios: Manu, Pakitza, Parque Nacional del Manu, USNM 333018.
- *Pseudogonatodes lunulatus*. VENEZUELA: Aragua: Bahía de Cata, MHNLS 17481; Cuyagua, MBLUZ 1460; Falcón: Distrito de Acosta, El Mené (type locality), MCZ Herp R-48893; Sucre: 7.6 km (by Caripito-Maturín road) South junction of Casanay, KU 117078.
- *Pseudogonatodes manessi*. VENEZUELA: Aragua: Rancho Grande, Parque Nacional Henri Pittier, KU 182740 (paratype), MHNLS 17984.
- *Pseudogonatodes peruvianus*. PERÚ: Amazonas: (X-rays); Shiringa, sobre el río Yutupis (afluente del río Santiago), USNM 343191.
- *Pseudogonatodes* sp. 1. VENEZUELA: Anzoátegui: Quebrada Hoces, 15 km E Puerto Píritu, EBRG 3444, 3525.
- *Pseudogonatodes* sp. 2. COLOMBIA: Meta: Villavicencio, USNM 84970.
- *Quedenfeldtia trachyblepharus*. MOROCCO: Marrakesh–Safi, 3 miles SW Ijoukak, 1160 m, CAS 123275.
- *Saurodactylus fasciatus*. MOROCCO: Rabat-Salé-Kénitra, Tarmilete, CAS 92404.
- *Saurodactylus mauritanicus*. MOROCCO: Souss-Massa, SE of Agadir, 6 miles SE Ait Baba, 775 m, CAS 153743.
- *Sphaerodactylus semasiops*. JAMAICA; Middlesex: Manchester Parish, 2.5 km NW Coleyville, MCZ R-55766.

APPENDIX 2. TYPE OF INFORMATION OBTAINED FROM THE SPECIMENS EXAMINED

Species	Collection number	HRXCT	X-ray	EtOH preserved
Aristelliger georgeensis	CAS 176485	Yes		
Chatogekko amazonicus	MTR 12682A	Yes		
Coleodactylus brachystoma	UMMZ 103051	Yes		
Euleptes europaea	MCZ R-4463	Yes		
Gonatodes albogularis	FMNH 55929	Yes		
Lepidoblepharis xanthostigma	CAS 178104	Yes		
Pseudogonatodes barbouri	MCZ R-14385	Yes		
Pseudogonatodes furvus	CBUMAG 763–768			Yes
Pseudogonatodes furvus	CBUMAG 295			Yes
Pseudogonatodes furvus	MCZ R-29700	Yes		Yes
Pseudogonatodes furvus	ICN 3501, 3502			Yes
Pseudogonatodes furvus	CBUMAG 283, 293			Yes
Pseudogonatodes fuscofortunatus	*MBLUZ 1292*	Yes		Yes
Pseudogonatodes fuscofortunatus	MBLUZ 1293, 1294			Yes
Pseudogonatodes guianensis	MZUSP 94826	Yes		
Pseudogonatodes guianensis	USNM 166138		Yes	
Pseudogonatodes guianensis	USNM 321059		Yes	
Pseudogonatodes guianensis	USNM 538260–538262		Yes	
Pseudogonatodes guianensis	USNM 538263, 538264		Yes	
Pseudogonatodes guianensis	USNM 84970		Yes	
Pseudogonatodes guianensis	USNM 234574		Yes	
Pseudogonatodes guianensis	USNM 333018		Yes	
Pseudogonatodes lunulatus	MHNLS 17481			Yes
Pseudogonatodes lunulatus	MBLUZ 1460			Yes
Pseudogonatodes lunulatus	KU 117078	Yes		
Pseudogonatodes lunulatus	MCZ R-48893			Yes
Pseudogonatodes manessi	KU 182740	Yes		Yes
Pseudogonatodes manessi	MHNLS 17984			Yes
Pseudogonatodes peruvianus	USNM 343191		Yes	
Pseudogonatodes sp.	EBRG 3444			Yes
Pseudogonatodes guianensis	USNM 562609– 562616		Yes	
Quedenfeldtia trachyblepharus	CAS 123275	Yes		
Saurodactylus fasciatus	CAS 92404	Yes		
Saurodactylus mauritanicus	CAS 153743	Yes		
Sphaerodactylus semasiops	MCZ R-55766	Yes		

Abbreviations: HRXCT, high-resolution X-ray computed tomography.

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