

A new and threatened species of *Listrura* (Siluriformes: Trichomycteridae), a rare catfish from an Atlantic Forest continental island



Correspondence:
Lucas Silva de Medeiros
lucasmedeiros0@hotmail.com

Lucas Silva de Medeiros^{1,2}, Laura Modesti Donin³, Juliano Ferrer⁴,
 Sergio Maia Queiroz Lima² and Mário de Pinna³

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Listrura is a genus of small pencil catfishes of Trichomycteridae that currently comprises 12 valid species in coastal drainages of Southern and Southeastern Brazil, all with fossorial dwelling habitats and eel-like morphology. Here, we describe a new species of *Listrura* known from only two specimens collected in an interval of 24 years in order to make it taxonomically available for biodiversity inventories and conservation decisions. The new species is morphologically distinguished from its congeners by the combination of features, as pectoral-fin rays counts, number of free vertebrae, number caudal-fin procurent rays, interopercular odontodes counts and the anterior-most position of dorsal and anal fin. Partial sequences of the mitochondrial gene *cox1* were used to infer the phylogenetic relationships and biogeography of the new species and its congeners. The new species is the first freshwater fish endemic to a continental island in the Atlantic Forest Biome, and only the second trichomycterid endemic of an island.

Keywords: Conservation, Insular ichthyofauna, Microcambevinae, Santa Catarina Island, Taxonomy.

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¹ Programa de Pós-Graduação em Sistemática e Evolução, Centro de Biociências, Universidade Federal do Rio Grande do Norte, Av. Senador Salgado Filho, 3000, 59064-741 Natal, RN, Brazil. (LSM) lucasmedeiros0@hotmail.com (corresponding author).

² Laboratório de Ictiologia Sistemática e Evolutiva, Departamento de Botânica e Zoologia, Centro de Biociências, Universidade Federal do Rio Grande do Norte, Av. Senador Salgado Filho, 3000, 59064-741 Natal, RN, Brazil. (SMQL) smaialima@gmail.com.

³ Seção de Peixes, Museu de Zoologia da Universidade de São Paulo, Av. Nazaré, 481, Ipiranga, 04263-000 São Paulo, SP, Brazil. (LMD) lauramdonin@usp.br; (MP) pinna@ib.usp.br.

⁴ Programa de Pós-Graduação em Biologia Animal, Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, Av. Bento Gonçalves, 9090, 91540-000 Porto Alegre, RS, Brazil. (JF) julianoferrer@gmail.com.

Listrura é um gênero de pequenos bagres da família Trichomycteridae, que compreende 12 espécies válidas ocorrendo em drenagens costeiras do Sul e Sudeste do Brasil, todas com hábitos fossoriais e morfologia anguiliforme. Aqui é descrita uma nova espécie de *Listrura* conhecida de apenas dois exemplares coletados em um intervalo de 24 anos, a fim de torná-la taxonomicamente disponível para inventários de biodiversidade e decisões de conservação. A nova espécie é morfologicamente distinguível de suas congêneres pela combinação do número de raios da nadadeira peitoral, número de vértebras livres, número de raios procorrentes caudais, número de odontódeos interoperculares e pela posição anterior das nadadeiras dorsal e anal. Sequências parciais do gene mitocondrial *cox1* foram utilizadas para inferir as relações filogenéticas e a biogeografia da nova espécie e de suas congêneres. A nova espécie é o primeiro peixe de água doce endêmico de uma ilha continental do Bioma da Mata Atlântica, e o segundo tricomictérido endêmico de uma ilha.

Palavras-chave: Conservação, Ictiofauna insular, Ilha de Santa Catarina, Microcambevinæ, Taxonomia.

INTRODUCTION

The Atlantic Forest (AF) is recognized as one of the five biodiversity hotspots in the world due to the outstanding number of species and elevated endemism, presently severely impacted by habitat loss and degradation (Myers *et al.*, 2000; Brooks *et al.*, 2002; Mittermeier *et al.*, 2011). Current estimates indicate that about 70% of its original forests were lost (Rezende *et al.*, 2018), the remaining fragments are small, isolated, and facing heavy environmental pressures (Brooks *et al.*, 2002). The AF aquatic ecosystems are strongly affected by deforestation, mainly in the riparian zones, as well as by pollution and introduction of exotic species (Menezes *et al.*, 2007; Castro, Polaz, 2020; Dala-Corte *et al.*, 2020). The eastern coastal drainages of Brazil exhibit a remarkable diversity of small-sized fish species associated to AF aquatic habitats, such as small streams, ponds, and marshes, which are dependent on the riparian vegetation (Oyakawa *et al.*, 2006; Menezes *et al.*, 2007; Abilhoa *et al.*, 2011; Albert *et al.*, 2011; Castro, Polaz, 2020). At the same time, the AF also harbors the highest number of threatened freshwater fishes among the Brazilian biomes according to a recent assessment (ICMBio, 2023).

Trichomycteridae encompasses nearly 400 species (Fricke *et al.*, 2023), distributed in the Neotropics, from rivers at sea level to high altitudes in the Andes (de Pinna, 1998; Ochoa *et al.*, 2020; Reis, de Pinna, 2022). *Listrura* de Pinna, 1988 currently includes 12 interstitial species (Fricke *et al.*, 2023), most of them described in the last 20 years (Tab. 1). Species of this genus possess a restricted distribution, usually limited to one or a few localities in specific biotopes, such as shallow marginal water bodies with leaf litter and/or sandy substrate separated from main river (de Pinna, 1988; Nico, de Pinna, 1996; Villa-Verde *et al.*, 2013; 2022). Most of these species are found in small and medium coastal river basins in the AF biome that drain from Serra do Mar and Serra Geral (large, partly adjacent, mountain ranges along in southeastern and southern Brazil), except

L. depinnai Villa-Verde, Ferrer & Malabarba, 2014, which occurs in a transition zone between the AF and the Pampa biome (Villa-Verde *et al.*, 2014).

The genus *Listrura* was proposed to include two species, *L. nematopteryx* de Pinna, 1998 and *L. camposae* (Miranda-Ribeiro, 1957), the latter previously included in the genus *Eremophilus* Humboldt, 1805, and was initially assigned to the Glanapteryginae subfamily due to a set of morphological traits shared with these Amazonian trichomycterids (de Pinna, 1988). More recently, Costa *et al.* (2020), based on molecular phylogeny and a few morphological synapomorphies, transferred *Listrura* from Glanapteryginae and *Microcambeva* Costa & Bockmann, 1994 from Sarcoglanidinae (see de Pinna, 1988; Costa, Bockmann, 1994) to the subfamily, Microcambevinae. Species of *Listrura* are easily distinguished by their singular morphology, presenting a minute and elongate body, absence of pelvic fins, and the caudal fin continuous dorsally and ventrally with a prominent membrane in the caudal peduncle supported by numerous procurrent rays (de Pinna, 1988; Villa-Verde *et al.*, 2013, 2022). The presence of *Listrura* in Santa Catarina Island, in Southern Brazil has been reported for a long time, but their taxonomic status has been uncertain (Nico, de Pinna, 1996; Villa-Verde, 2008; Villa-Verde *et al.*, 2013; Costa, Katz, 2021).

Non-destructive three-dimensional imaging techniques have offered new perspectives to taxonomy by providing rapid and detailed access to the internal anatomy of museum specimens (Faulwetter *et al.*, 2013). Micro-computed tomography or microtomography (microCT) has been widely applied to describe the osteology of several trichomycterid catfishes (*e.g.*, Cleason *et al.*, 2008; Schaefer, Fernández, 2009; Adriaens *et al.*, 2010; de Pinna *et al.*, 2018a,b, 2020; Reis *et al.*, 2019; Medeiros *et al.*, 2020; Henschel *et al.*, 2020, 2022; de Pinna, Dagosta, 2022; Bockmann *et al.*, 2023; Datovo *et al.*, 2023). This technique is especially valuable for taxa with limited comparative material, which is the case of the *Listrura* from Santa Catarina Island. We analyzed two specimens using molecular and morphological analyses, including 3D skeleton reconstructions using microCT, and concluded that they represent a new species, as previously suggested by other authors (Villa-Verde, 2008; Villa-Verde *et al.*, 2013; Costa, Katz, 2021), which is herein described. The new species is the first freshwater fish endemic of a continental island inserted in the AF biome, and the second trichomycterid restricted to an Island, along with *Trichomycterus gorgona* Fernández & Schaefer, 2005 from Gorgona island in the Pacific Ocean, in Colombia (Fernández, Schaefer, 2005).

TABLE 1 | Chronological list of *Listrura* species and their respective drainages and states.

Species	Year	River basin	State	References
<i>Listrura camposae</i> (Miranda-Ribeiro, 1957)	1957	Ribeira de Iguape	São Paulo	Villa-Verde <i>et al.</i> (2013)
<i>Listrura nematopteryx</i> de Pinna, 1988	1988	Estrela	Rio de Janeiro	de Pinna (1988)
<i>Listrura tetradactyla</i> Landim & Costa, 2002	2002	Ibiciuíba	Rio de Janeiro	Landim, Costa (2002)
<i>Listrura boticario</i> de Pinna & Wosiacki, 2002	2003	Guaraqueçaba	Paraná	de Pinna, Wosiacki (2002)
<i>Listrura pinguabae</i> Villa-Verde & Costa, 2006	2006	Fazenda	São Paulo	Villa-Verde, Costa (2006)
<i>Listrura costai</i> Villa-Verde, Lazzarotto & Lima, 2012	2012	Jurumirim	Rio de Janeiro	Villa-Verde <i>et al.</i> (2012)
<i>Listrura depinnai</i> Villa-Verde, Ferrer & Malabarba, 2014	2014	Gravataí	Rio Grande do Sul	Villa-Verde <i>et al.</i> (2014)
<i>Listrura macaensis</i> Costa & Katz, 2021	2021	Macaé	Rio de Janeiro	Costa, Katz (2021)
<i>Listrura macacuensis</i> Costa & Katz, 2021	2021	Guapi-Macacu	Rio de Janeiro	Costa, Katz (2021)
<i>Listrura menezesi</i> Villa-Verde, de Pinna, Reis & Oyakawa, 2022	2022	São João	Rio de Janeiro	Villa-Verde <i>et al.</i> (2022)
<i>Listrura gyrinura</i> Costa, Feltrin & Katz, 2023	2023	Madre	Santa Catarina	Costa <i>et al.</i> (2023)
<i>Listrura urussanga</i> Costa, Feltrin & Katz, 2023	2023	Urusanga	Santa Catarina	Costa <i>et al.</i> (2023)

MATERIAL AND METHODS

Morphological data. Counts and measurements follow de Pinna (1988). Measurements are presented as percentages of standard length (SL), except for subunits of the head, which are expressed as percentages of head length (HL). Measurements were taken with digital calipers, calibrated to the nearest tenth-millimeter under binocular stereomicroscope. Fin ray counts were obtained from the ethanol-preserved specimens using transmitted light under a binocular stereomicroscope. The counts include all rays, including small procurrent rays and principal rays, of dorsal and anal fins. Osteology was examined in 3D reconstructed models of two specimens scanned using a Phoenix v|tome|x M equipment (General Electric Company) Museu de Zoologia da Universidade de São Paulo, with following parameters: voxel size X= 0.2395892, number of images 4400, voltage 60kV, and current 220mA. The 3D visualization and analysis of the reconstructed osteology were performed using VGStudio MAX2.2.3 64-bit (Volume Graphics GmbH, Heidelberg, Germany). Counts of pre-caudal, caudal and total vertebrae, procurrent caudal-fin rays, branchiostegal rays, pleural ribs, opercular and interopercular odontodes, and jaw teeth were also taken from the images of X-rays and 3D-reconstructed models. Osteological nomenclature followed de Pinna (1989) and Adriaens *et al.* (2010), except the bones of the orbital region, named barbular and lacrimal-antorbital, following de Pinna *et al.* (2020). Terminology of the external anatomical structures of the opercular apparatus, followed de Pinna, Dagosta (2022). Vertebrae with complete hemal arch are referred to as caudal vertebrae, while those lacking a complete arch are termed as pre-caudal vertebrae. Morphological, meristic and osteological data of *L. macaensis*, *L. macacuensis*, *L. gyrynura*, and *L. urussanga* were obtained from their original descriptions (Costa, Katz; 2021; Costa *et al.*, 2023). Institutional abbreviations follow Sabaj (2020).

Molecular data and phylogenetic analysis. DNA extractions from ethanol-preserved tissues samples followed the protocol described in Bruford *et al.* (1992). Partial sequences of mitochondrial gene cytochrome c oxidase sub-unit I (*cox1*) (Hebert *et al.*, 2003) with 655 bp were amplified by PCR using the primers L5698-ASN (5'-AGG CCT CGA TCC TAC AAA GKT TTA GTT AAC -3') (Inoue *et al.*, 2001) and H7271-COI (5'-GTG GTG GGC TCA TAC AAT AAA -3') (Villa-Verde *et al.*, 2013). The amplicons were purified using 1µL of Exosap for every 10µL of PCR product. The PCR amplifications and sequencing of *cox1* followed Villa-Verde *et al.* (2013). The purified PCR products were sequenced in both directions at Macrogen Inc (Seoul, South Korea). DNA sequences were aligned using the ClustalW algorithm (Chenna *et al.*, 2003) in MEGA-X (Kumar *et al.*, 2018). To estimate genetic distances between species, we used the Kimura 2-parameter model (Kimura, 1980) in MEGA X. Ingroup species included almost all *Listrura* species, except for *L. gyrynura* and *L. urussanga*. The outgroups were the glanapterygine *Pygidianops amphioxus* de Pinna & Kirovsky, 2011, and two *Microcambeva* species, *M. barbata* Costa & Bockmann, 1994 and *M. jucuiensis* Costa, Katz, Mattos & Rangel-Pereira, 2019 (Tab. 2). Bayesian Inference (BI) analyses were performed using BEAST 2.5 (Bouckaert *et al.*, 2019), and GTR+G+I as nucleotide substitution models under the Akaike criteria in jmodeltest 2 (Darriba *et al.*, 2012). In BI we used a strict clock lognormal model a tree model set to yule model,

TABLE 2 | Terminal taxa used for molecular analysis, with their respective voucher numbers and GenBank accession codes.

Species	Voucher number	Accession number
<i>Listrura</i> sp.n.	UFRGS 22874	PP891549
<i>Listrura depinnai</i>	UFRGS 19536	PP886156
<i>Listrura boticario</i>	MNRJ 32442	PP886152
<i>Listrura camposae</i>	MNRJ 37023	HM245417
<i>Listrura costai</i>	MNRJ 39620	HM245412
<i>Listrura nematopteryx</i>	MNRJ 37022	HM245417
<i>Listrura macacuensis</i>	UFRJ 9268	MN385802
<i>Listrura menezesi</i>	MNRJ 32026	JN830897
<i>Listrura macaensis</i>	UFRJ 9693	OK144133
<i>Listrura picinguabae</i>	LBP 3864	HM245415
<i>Listrura tetradradiata</i>	UFRJ 11399	JQ231083
<i>Microcambeva barbata</i>	UFRJ 12185	MN385804
<i>Microcambeva mucuriensis</i>	UFRJ 11028	MN385806
<i>Pygidianops amphioxus</i>	UFRJ 11248	MN385801

and the remaining parameters were set as default. Length of the Markov Chain Monte Carlo (MCMC) was 10 million runs with sampling every 1,000 runs. ESS (> 200) values were checked using Tracer 1.7.2 (Rambaut *et al.*, 2018). The first one million trees were discarded as burn-in periods (approximately 10%), and a final consensus tree and posterior probabilities were reconstructed using the software TreeAnnotator v. 1.10.4 and, edited using the software TreeViewer (Bianchi, Sánchez-Baracaldo, 2023).

RESULTS

Listrura bernunssa, new species

urn:lsid:zoobank.org:act:97BDD7D5-661A-4B67-AF21-96AEF999DEA3

(Figs. 1–8; Tab. 3)

Listrura camposi (non-Miranda Ribeiro, 1957). —Nico, de Pinna, 1996:29 (distribution map indicated by “7”, habitat notes). —de Pinna, Wosiacki, 2003:275 (checklist, comparative material examined). —Wosiacki, de Pinna, 2007:74 (checklist, comparative material examined, conservation status).

Listrura sp. —Villa-Verde, 2008:20, 21, 23–42, 43–59, 93, 96, 103 (sampling site, color pattern, external morphology, osteology, character matrix, distribution map indicated by “15”, photographed specimen). —Villa-Verde *et al.*, 2013:61–62 (distribution map, osteological traits).

Listrura sp.1 —Costa, Katz, 2021:318, 319, 338, 341 (molecular phylogeny, distribution map, comparative material examined, character matrix).

Holotype. UFRGS 22874, 36.5 mm SL, Brazil, Santa Catarina State, Santa Catarina Island, Florianópolis, Córrego Grande stream at Parque Natural Municipal do Maciço da Costeira, 27° 36'37”S 48° 30'24”W, 30 May 2017, J. Ferrer, L. Donin, N. Pio & T. P. Carvalho. Tissue sample number: TEC 7338.

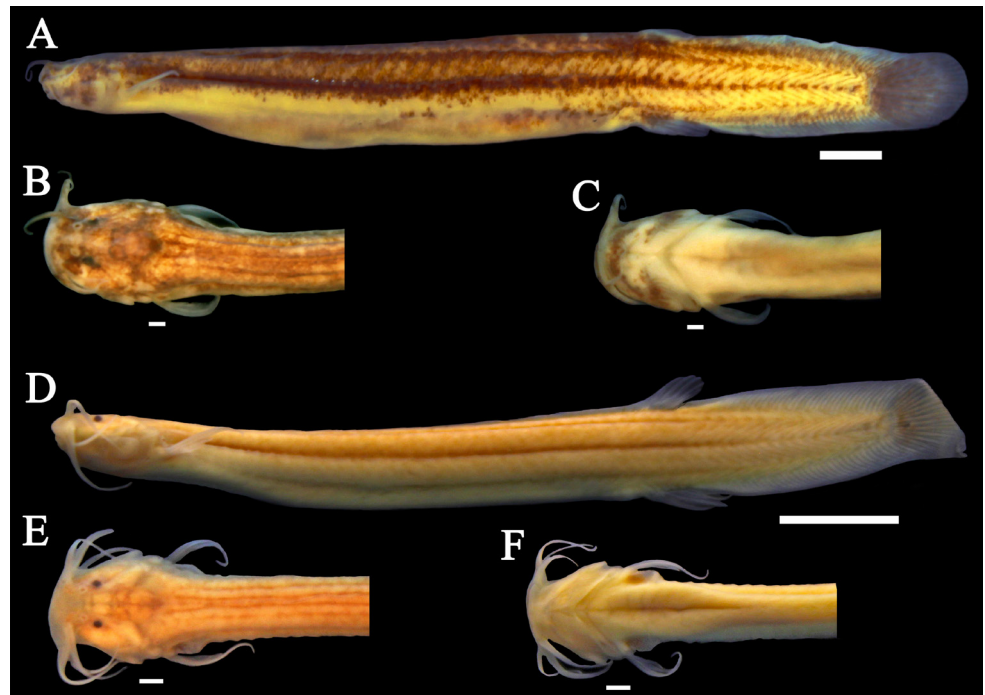


FIGURE 1 | *Listrura bernunssa*, holotype, **A**, **B** and **C**, UFRGS 22874, 36.5 mm SL, Córrego Grande mountain stream in the Parque Natural Municipal do Maciço da Costeira, Santa Catarina Island, Florianópolis, Santa Catarina State, Brazil; paratype, **D**, **E** and **F**, MZUSP 63440, 37.9 mm SL, Ribeirão da Ilha, Santa Catarina Island, Santa Catarina State, Brazil. **A** and **D**. left lateral view; **B** and **E**. dorsal view; **C** and **F**. ventral view. Scales bars: **A** and **D** = 5.0 mm; **B**, **C**, **E** and **F** = 1.0 mm.

Paratype. MZUSP 63440, 1, 37.9 mm SL, Brazil, Santa Catarina State, Santa Catarina Island, Florianópolis, Ribeirão da Ilha district, shallow water pool continuous with a mountain stream, ca. 27° 42'S 48° 32'W, 23 Mar 1993, M. Gomes, O. Peixoto, R. Schasse & S. Potsch Carvalho e Silva.

Diagnosis. The new species is distinguished from all congeners, except *L. camposae*, *L. urussanga* and *L. gyrinura*, by the number of pectoral-fin rays (three *vs.* one in *L. nematopteryx*, *L. picinguabae*, *L. costai*, *L. macaensis*, *L. macacuensis* and *L. menezesi*; two in *L. boticario* and *L. depinmai*; four in *L. tetradradiata*). *Listrura bernunssa* is further distinguished from all congeners with the both anal and dorsal fins, except *L. costai* and *L. urussanga* by the position of the dorsal and anal fin relative to the vertebral column: the first pterygiophores of the dorsal and anal fin is located anterior to the neural spine of the 29th free vertebra (*vs.* first pterygiophore of the dorsal and anal fin is located anterior to the neural spine of the 30th free vertebra more). *Listrura bernunssa* is further distinguished from *L. camposae* by the absence of a depression at the dorsal margin of the quadrate (*vs.* presence) and by the absence of a vestigial neural arch at the compound caudal centrum (*vs.* presence). *Listrura bernunssa* differs from *L. gyrinura* by having 47 free vertebrae (*vs.* 51–52) and six anal fin-rays (*vs.* eight). *Listrura bernunssa* differs from *L. urussanga* by having nine or 10 interopercular odontodes (*vs.* 6–8) and fewer dorsal (32–33) and ventral (30–31) procurent caudal-fin rays (*vs.* 38–39 and 35–36, respectively).

TABLE 3 | Morphometric data of the holotype (UFRGS 22874) and paratype (MZUSP 63440) of *Listrura bernunssa*.

	Holotype	Paratype
	36.5 mm SL	37.9 mm SL
Percentage of standard length		
Body depth	12.2	11.8
Caudal peduncle depth	11.1	13.0
Body width	5.0	5.6
Caudal peduncle width	3.1	2.5
Caudal peduncle length	21.9	25.9
Dorsal-fin base length	3.2	3.6
Anal-fin base length	5.5	6.4
Pectoral-fin length	8.9	11.3
Pre-dorsal length	77.7	71.0
Pre-anal length	77.3	80.3
Head length	14.3	14.2
Percentage of head length		
Head depth	48.7	51.0
Head width	86.2	97.0
Interorbital width	28.9	26.9
Preorbital length	20.1	31.7
Eye diameter	18.9	8.5
Mouth width	39.6	42.3
Internarinal width	16.9	17.8

Description. Morphometric data for holotype and paratype given in Tab. 2. Body elongated, head wider than trunk in dorsal view (Figs. 1A, D). Cross section of body cylindrical posterior to head, gradually more compressed to anal-fin insertion, tapering to caudal. In lateral view, lowest body depth posterior to head and deepest approximately at origin of dorsal fin. Dorsal body profile almost straight from tip of snout to dorsal-fin origin; slightly convex at dorsal-keel (*i.e.*, the skin-fold partly supported by dorsal-fin procurrent rays), confluent with caudal-fin. Ventral head profile slightly concave. Ventral body profile convex from gular region to insertion of anal fin; mostly straight from anus to caudal peduncle; concave at ventral-keel (the skin-fold supported by ventral procurrent rays) and confluent with caudal fin. Dorsal keel extending anteriorly beyond dorsal fin as low rayless middorsal cutaneous fold.

Head small, depressed, trapezoid in dorsal view, less deep than body, dorsal surface flat (Figs. 1B, E). Mouth subterminal, wide; upper jaw slightly longer than lower (Figs. 1C, F). Anterior margin of upper lip gently convex and continuous laterally with maxillary-barbels base. Lower lip thinner than upper one, nearly straight at anterior margin and continuous laterally with rictal-barbel base. Snout long; anterior profile mostly straight in dorsal view. Anterior nostril small and round, positioned closer to upper lip than to anterior margin of eye, surrounded by short tube of integument continuous posterolaterally with nasal barbel. Posterior nostril round and larger than anterior one; located slightly closer to eye than to anterior nostril, surrounded by low rim of integument. Barbels large; similar to each other in general aspect, their internal cores visible by transparency (Figs. 1B, E). Maxillary barbel wide at base, gradually tapering to fine distal tip reaching anterior portion of interopercle, and to posterior portion of opercle

in paratype. Rictal barbel originating laterally at lower lip reaching to posterior margin of interopercular patch of odontodes in holotype and base of pectoral fin in paratype. Nasal barbel originating at latero-median portion of anterior nostril, wide at base and tapering distally, reaching to posterior region of posterior nostril in holotype and posterior region of opercle in paratype. Eye round, small, located dorsoventrally on head, with well-differentiated lenses and covered with thin transparent integument. Inter-orbital distance nearly four and half times longitudinal size of eye. Opercular odontodophore small, oval, surrounded by fleshy periodontodal fold. Interopercular odontodophore hyaline and ellipsoid, larger compared with opercular one, twice and half times larger than opercular one. Odontodes weakly visible in ventral and lateral views. Branchiostegal membranes narrowly joined to isthmus; six branchiostegal rays visible by transparency in ventral view. Three pleural ribs. Free vertebrae, 47 (40 caudal vertebrae and seven pre-caudal; Fig. 2).

Pectoral-fin rays, three, all rays unbranched and segmented; first ray modified into long filament, approximately 50% longer than the other rays, around half of HL, second and third rays small, approximately two-third and one-third length of first one (Fig. 1). Axillary gland small, located posterior to pectoral-fin insertion. Dorsal fin small, originating at vertical through 30th vertebrae, subtriangular, with six unbranched rays, first one not segmented and remaining one segmented (i+5). Anal fin larger than dorsal fin, originating at same line as dorsal fin, subtriangular, with seven unbranched rays, first one not segmented remaining one segmented (i+6). Pelvic fin and girdle absent. Caudal fin elongated, posterior margin round; with 14 principal fin rays (ii+8+iv). Dorsal procurrent caudal-fin rays 32 in holotype and paratype, ventral procurrent caudal-fin rays 30 in holotype and 31 paratype (Fig. 2).

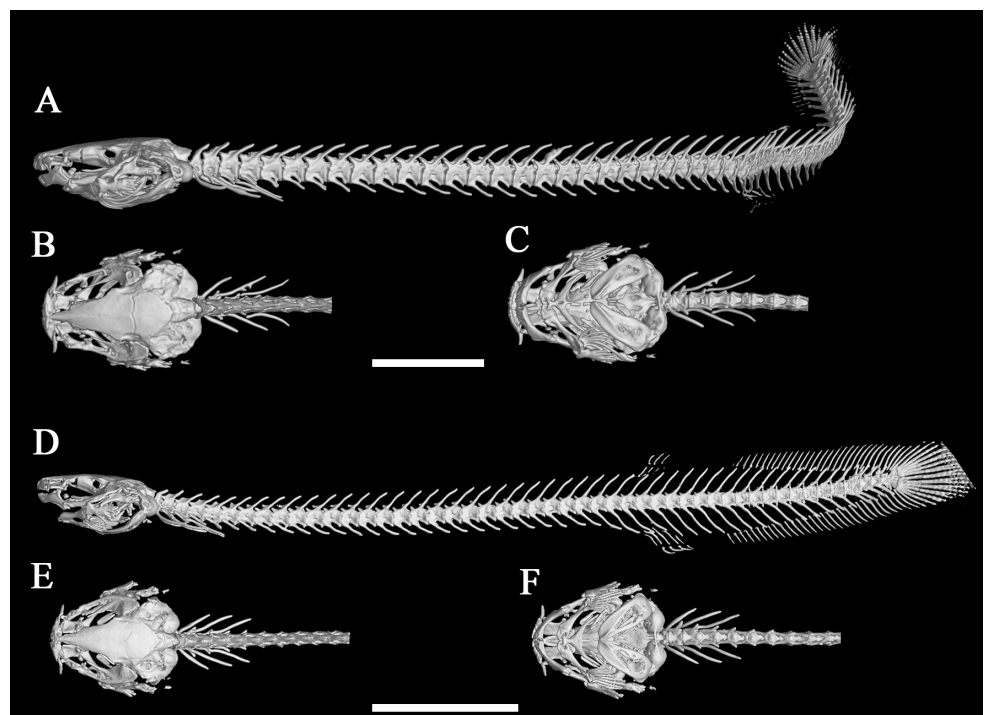


FIGURE 2 | 3-D reconstructed CT-images of the skeleton of *Listrura bernunssa*, holotype (A, B and C, UFRGS 22874, 36.5 mm SL), and paratype (D, E and F, MZUSP 63440, 37.9 mm SL). A and D, lateral view; B and E, dorsal view of the head; C and F, ventral view of the head. Scale bars = 5.0 mm.

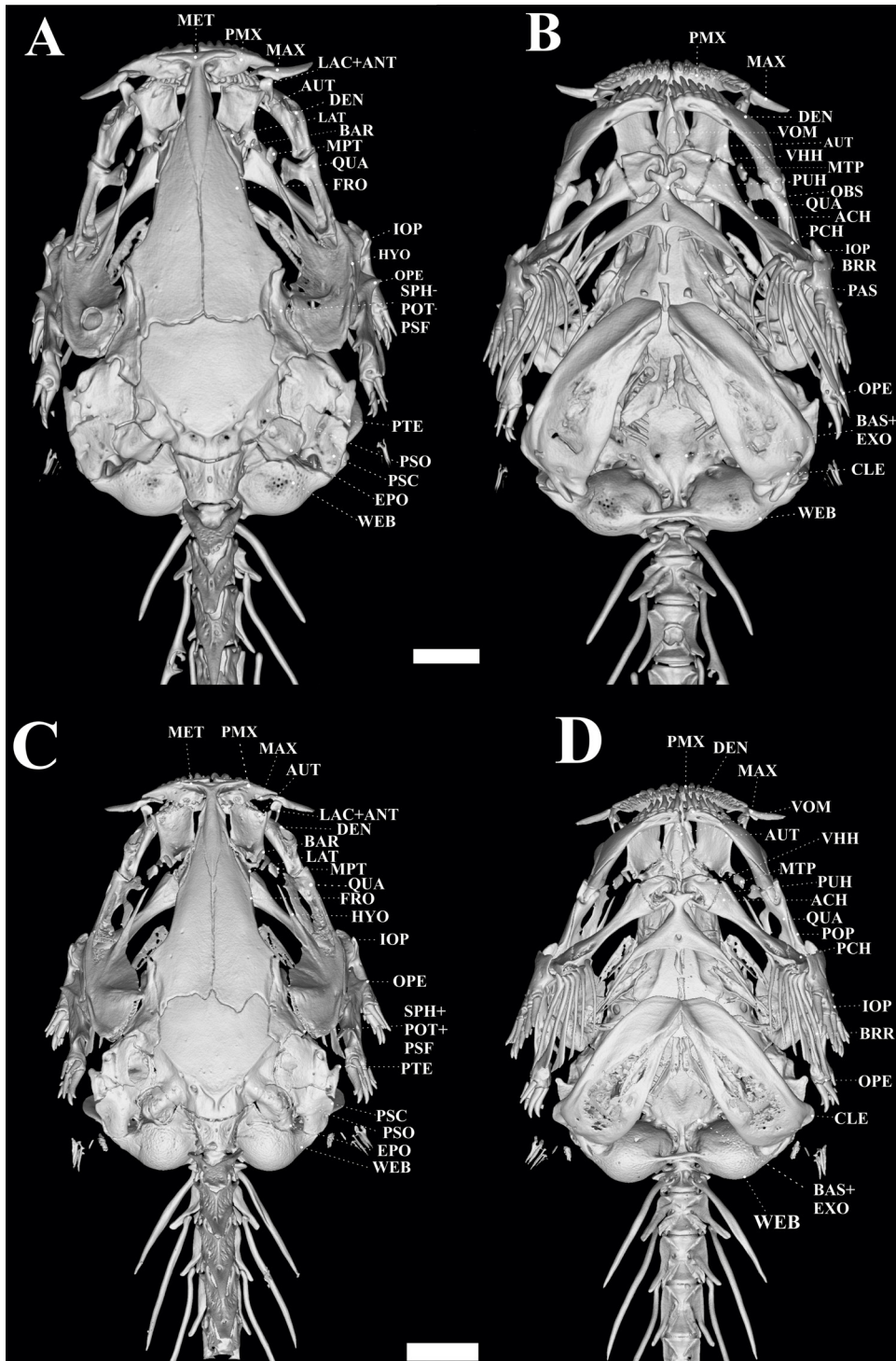


FIGURE 3 | Skull, hyoid arch, jaws, opercular apparatus, pectoral fin and girdle, suspensorium, anterior vertebrae and Weberian complex of *Listrura bernunssa*, holotype (A and B, UFRGS 22874, 36.5 mm SL), and paratype (C and D, MZUSP 63440, 37.9 mm SL), in dorsal (A and C) and ventral view (B and D). Abbreviations: ACH: Anterior ceratohyal; AUT: Autopalatine; BAR: Barbular; BAS+EXO: Basioccipital-exoccipital bone; BRR: Branchiostegal rays; CLE: Cleithrum; DEN: Dentary; EPO: Epioccipital; FRO: Frontal; HYO: Hyomandibula; IOP: Interopercle; LAC+ANT: Lacrimal-antorbital; LAT: Lateral ethmoid; MAX: Maxilla; MET: Mesethmoid; MPT: Metapterygoid; OBS: Orbitosphenoid; OPE: Opercle; PCH: Posterior ceratohyal; PMX: Premaxilla; PSC: Posttemporo-supracleithrum; PSO: Parieto-supraoccipital; PTE: Pterotic; PUH: Parurohyal; QUA: Quadrate; SPH+POT+PSF: Sphenotic + Prootic + Pterosphenoid complex; VHH: Ventral hypohyal; VOM: Vomer; WEB: Weberian capsule. Scale bar = 1.0 mm.

Mesethmoid narrow just posterior to cornua and widening from posteriorly to that point, its main axis and anterior margin mostly straight, overlain postero-dorsally by frontal (Figs. 3A, C). Mesethmoid cornua short and straight. Lateral ethmoid with distinctive sub-cylindrical process at posteromedian margin (condition present only on right side of paratype, Fig. 4). Frontal roughly triangular, with small triangular projection at corner. Parieto-supraoccipital roughly pentagonal. Frontal and parieto-supraoccipital sutured; cranial fontanel absent. Sphenotic, pterosphenoic and prootic fused into slender and trapezoid-like complex. Pterotic squarish with laminar lateral process. Epioccipital squarish. Posttemporo-supracleithrum rectangular. Vomer short and 'bottle-shaped', with distinct posterior process and lateral constriction on anterior portion (Fig. 5). Basisoccipital fused with exoccipital and with Weberian complex posteriorly.

Premaxilla triangular, with conspicuous protuberance on dorsal surface at posteromedial region, lateral to narrow part of mesethmoid cornua. Two rows of conical premaxillary teeth: 23 on left and 20 on right side of the holotype, 17 on left and 16 on right side of paratype (Figs. 3A, B). Maxilla, narrow, elongate, with pointed tips, slightly shorter than premaxilla. Autopalatine squarish; ending postero-laterally in straight small process dorso-medially directed, its mesial margin almost straight its lateral margin with pronounced concavity. Articular autopalatine process conspicuous, with distinctive dorsal process. Lacrimal-antorbital short and club-shaped. Barbular extremely reduced and cylindrical. Dentary triangular, with two rows of small conical teeth, 19 in inner and outer rows on both sides of the holotype, 17 in inner row and 18 in outer row in paratype.



FIGURE 4 | Anterior portion of skull of *Listrura bernunssa* holotype (UFRGS 22874, 36.5 mm SL), with lateral ethmoid in evidence, showing the distinctive subcylindrical process at its median-posterior margin (red circle). Abbreviations as in Fig. 3. Scale bar = 1.0 mm.

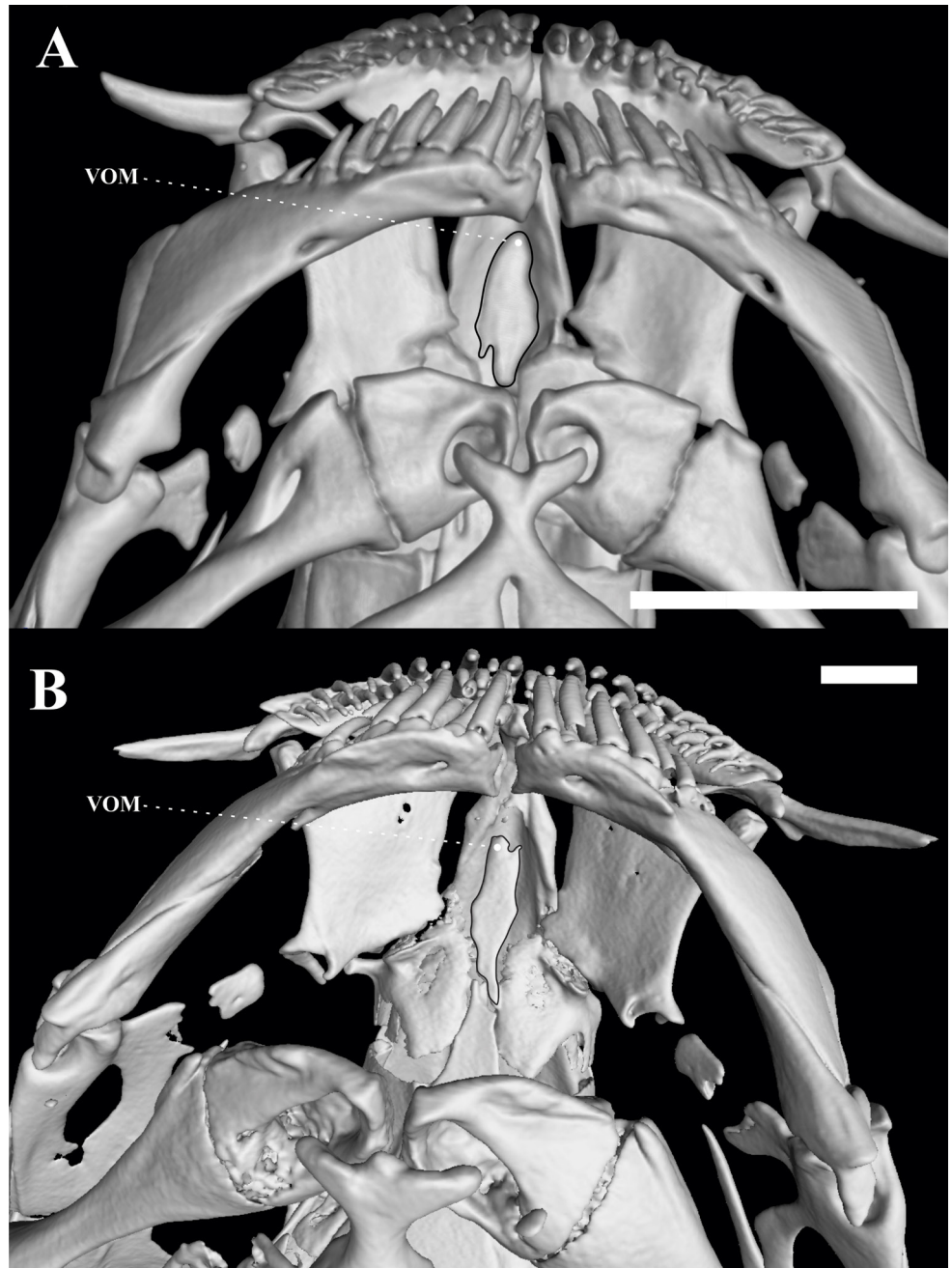


FIGURE 5 | Anterior portion of skull of *Listrura bernunssa*, holotype (A, UFRGS 22874, 36.5 mm SL) and paratype (B, MZUSP 63440, 37.9 mm SL), in ventral view. The vomer (VOM), with its distinct, short posterior process and its lateral constriction on the anterior portion, is highlighted. Scale bars = 1.0 mm.

Hyomandibula long with narrow, pointed and elongate anterior process, ventrally-curved at anterodorsal portion, its anterior tip reaching vertical through anterior tip of preopercle (Figs. 6A, B). Metapterygoid reduced, triangular and articulating by large synchondrosis with anterodorsal portion of quadrate. Quadrate elongate, with narrow laminar process extending anterodorsally from anterior tip; dorsal margin almost straight. Preopercle straight and tapering anteriorly, posterior edge rounded. Interopercle thin,

with nine or 10 side conical odontodes disposed obliquely on posterior portion, arranged in two irregular longitudinal rows. Interopercular anterior process well developed. Opercle slender, with dorsomedial concavity and elongated pointed process dorsally, and bifid process ventrally. Opercle articulating dorsally with hyomandibula via small condyles at anterior process; with seven conic odontodes arranged obliquely in three irregular rows disposed vertically on posterior region.

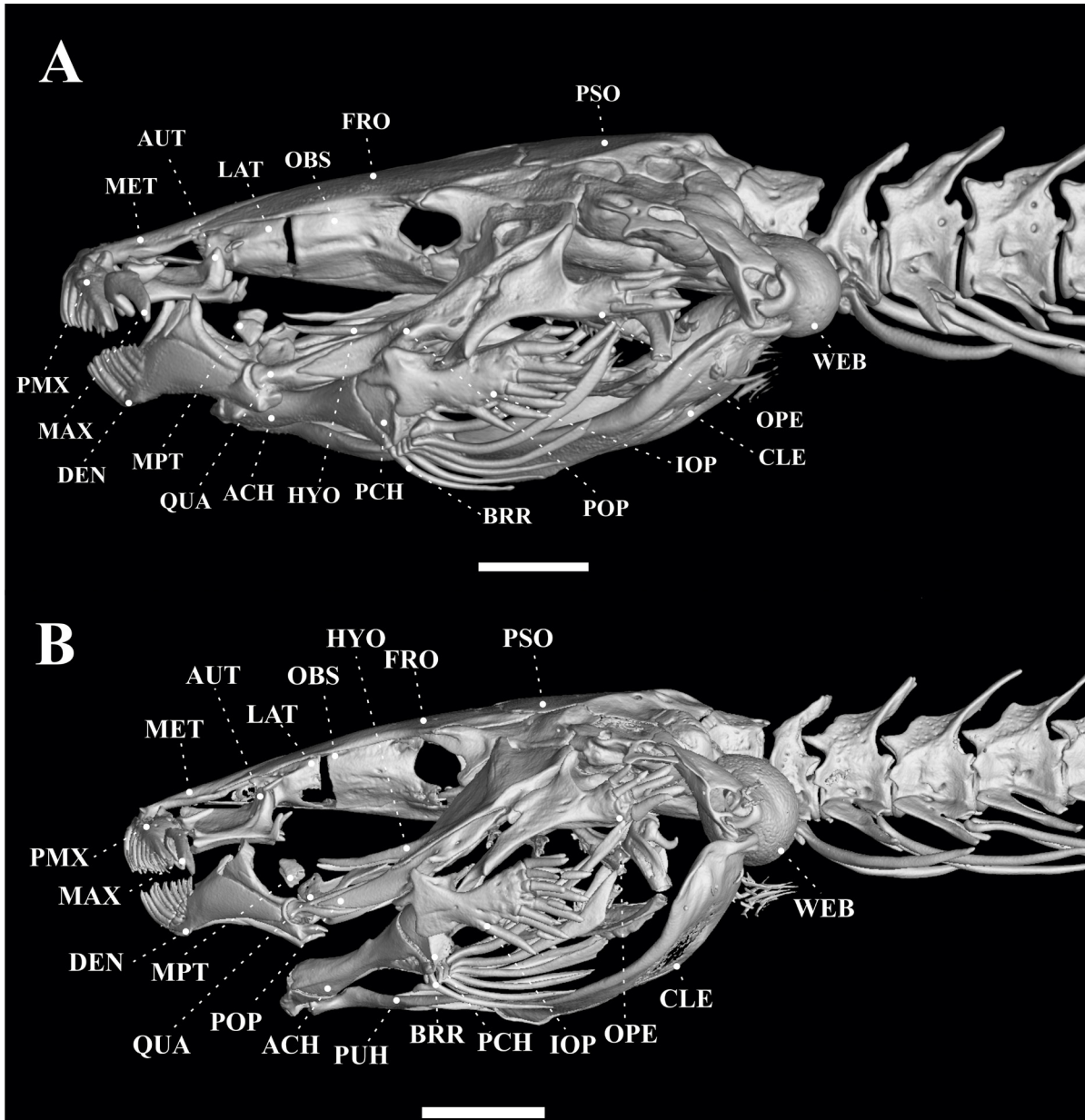


FIGURE 6 | Skull and anterior portion of vertebral column of *Listrura bernunssa*, holotype (A, UFRGS 22874, 36.5 mm SL), and paratype (B, MZUSP 63440, 37.9 mm SL), in left lateral view. Abbreviations: ACH: Anterior ceratohyal; AUT: Autopalatine; BRR: Branchiostegal rays; CLE: Cleithrum; DEN: Dentary; HYO: Hyomandibula; IOP: Interopercle; LAT: Lateral ethmoid; MAX: Maxilla; MET: Mesethmoid; MPT: Metapterygoid; OPE: Opercle; OBS: Orbitosphenoid; PCH: Posterior ceratohyal; PMX: Premaxilla; POP: Preopercle; PUH: Parurohyal; QUA: Quadrato. Scale bars = 1.0 mm.

Parurohyal with small posterior process lateral and arms reaching posterior portion of anterior ceratohyal. Central parurohyal foramen oval (Figs. 3B, D). Ventral hypohyal trapezoid, with deep fossa on ventral surface for articulation with parurohyal condyle. Anterior ceratohyal rod-like and constricted at middle. Posterior ceratohyal subtriangular. Cleithrum flat, triangular. Caudal skeleton largely consolidated. Ventral plate formed by fusion of parahypural plus hypurals 1–2; dorsal plate formed by fusion of hypurals 3–5. Dorsal and ventral plates not fused. Uroneural spine elongate, fused to compound centrum but not to dorsal plate (Figs. 7A, B).

Coloration in alcohol. Dorsum with faint middorsal dark stripe over light brown background originating just posterior to head, narrowing posteriorly to fade at posterior region of caudal peduncle (Fig. 2). Dorsolateral region of body with two longitudinal dark brown stripes separated by wider stripe gradually paler towards caudal peduncle. Mid-lateral stripe, with ventral margin, originating immediately dorsal to pectoral fin, wide anteriorly and narrowing towards caudal peduncle. Ventrolateral region of body pale yellowish with few sparse dark brownish spots, more concentrated between dorsal

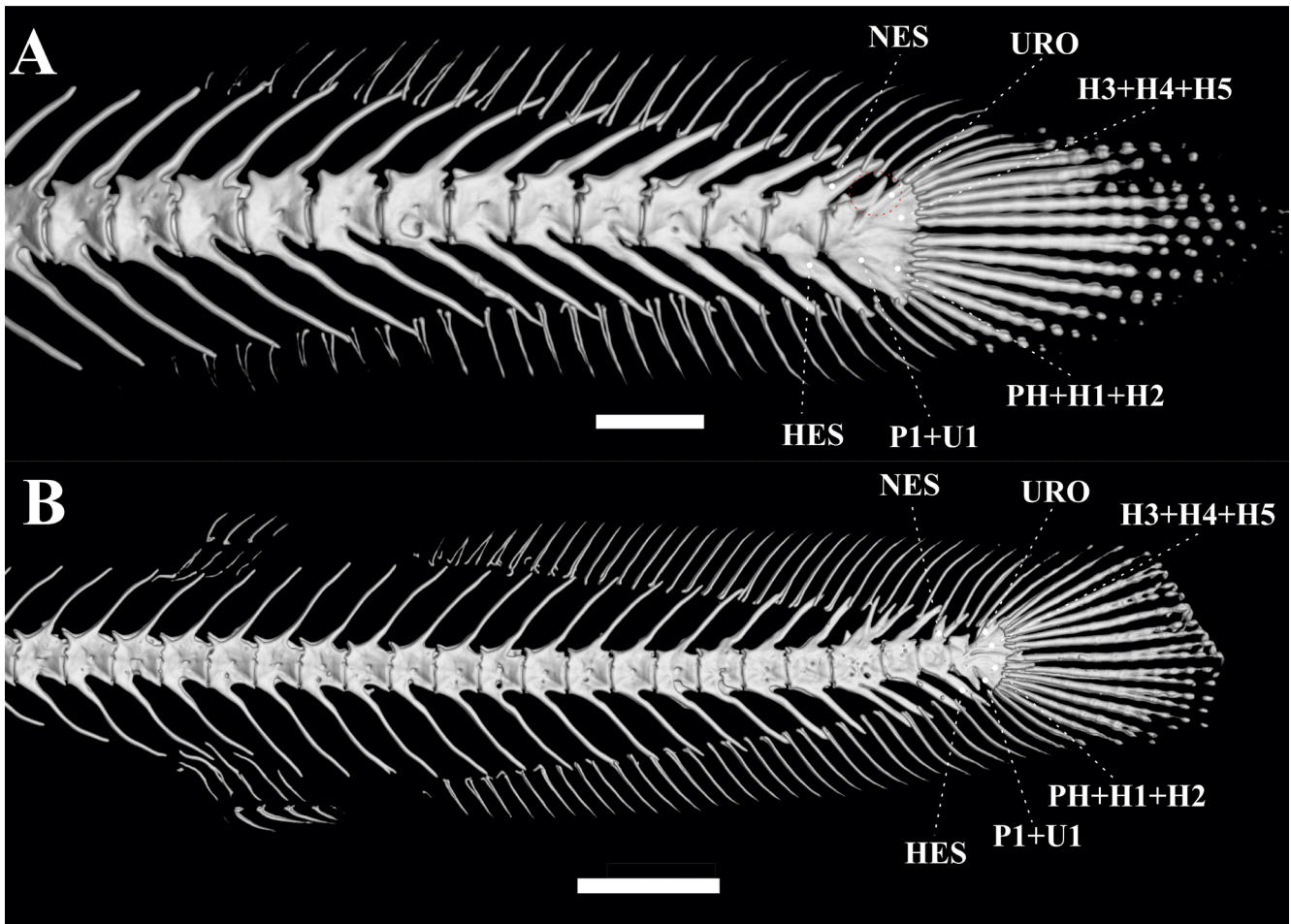


FIGURE 7 | Caudal skeleton of *Listrura bernunssa*, holotype (A, UFRGS 22874, 36.5 mm SL), and paratype (B, MZUSP 63440, 37.9 mm SL) in left lateral view. Abbreviations: HES: Hemal spine; PH+H1+H2: Hypurals plate 1–2 plus parahypural; HYP 3+4+5: Hypural plates 3+4+5 fused; NES: Neural spine; URO: Uroneural. Scale bars = 1.0 mm.

and anal fins. Myomeres on caudal peduncle outlined by irregular and faint dark marks forming v-shaped pattern. Dorsal and ventral skin-folds in caudal peduncle whitish with sparse dark brown spots at base. Dorsal and lateral parts of head mottled, darkest over supraoccipital, around nares and eyes, and on cheeks. Ventral surface of head pale yellow with light brown blotches, mainly on chin. Pectoral fin hyaline. Dorsal and anal fins hyaline with faint brown markings along bases. Caudal fin with large hexagonal brown spot, and hyaline margin.

Coloration in life. Dorsum and sides of body almost dark brown; abdomen pale light brown, reddish on branchial region due to blood seen by transparency (Fig. 8). Dorsal and lateral surfaces of head predominantly brown, yellowish areas on ventrolateral region of maxillary barbel and at posterior portion of opercular and interopercular odontodophores, with their bases brownish. Eyes and iris black. All barbels white to hyaline. Dark brown lateral midline along flanks, originating posterior to pectoral fin and vanishing on caudal peduncle, with randomly scattered brownish spots. Pectoral fin hyaline. Dorsal and anal fins hyaline with brown markings at base. Region of procurrent caudal-fin rays hyaline with sparse small dark brown spots concentrated basally. Caudal fin with brownish triangular spot over hypural plate, extending to the middle of principal caudal fin rays.

Geographical distribution. *Listrura bernunssa* is so far known only from two localities on the Santa Catarina Island, a continental island in Santa Catarina State, Southern Brazil (Fig. 9). The Córrego Grande stream originates in a dense and preserved fragment of Atlantic Forest adjacent to the city of Florianópolis. Soon after, the stream runs to the north along the urban area of Florianópolis up to its mouth in the Itacorubi mangrove, in the western coast of the Santa Catarina island. The second locality is a flooded area in the Ribeirão da Ilha district associated with a stream that drains from a southern mountain chain and runs to the west coast of the Santa Catarina Island.

Ecological notes. Since the 16th century, the Santa Catarina Island has served as a refuge and point of supply of wood, water and food for expeditionary travelers in the region of the Prata River (Saint-Hilarie, 1978). Four centuries of disorderly occupation on the Santa Catarina Island led to drastic changes on its insular fragment of the AF, with approximately 75% of the original vegetation deforested, and the rest reduced to small fragments in montane areas (Caruso, 1990). Throughout the 20th century, all lowland



FIGURE 8 | Live specimen of *Listrura bernunssa*, holotype, UFRGS 22874, 36.5 mm SL, Córrego Grande mountain stream in the Parque Natural Municipal do Maciço da Costeira, Santa Catarina Island, Florianópolis, Santa Catarina State, Brazil. Photo by Tiago P. Carvalho. Scale bar = 1 mm.



FIGURE 9 | Geographical distribution of *Listrura bernunssa* in Santa Catarina Island. White star: type-locality; white circle, paratype. Dotted lines: conservation units.

areas of the island were occupied (Santiago *et al.*, 2014; IBAM, 2015; Lopes *et al.*, 2020). To mitigate the effects of human occupation, a mosaic of conservation units covering 42% of the island’s total territory were created, preserving small fragments of the AF (Reis, 2010). The freshwater ecosystems of the island of Santa Catarina comprise two lagoons and 15 small river basins (Lopes *et al.*, 2020). The insular freshwater ichthyofauna of the island is composed of 17 species (Bertaco, 2009), including *Listrura bernunssa*.

The holotype of *Listrura bernunssa* was collected in a small mountain stream in the “Maciço da Costeira Municipal Natural Park” conservation area, adjacent to the urban area of the city of Florianópolis. The stream has a substantial slope, rocky bottom, clear and swift running waters, and is surrounded by a dense fragment of AF. A single specimen was collected with a handle net in a small shallow pool among rocks by stirring the submerged roots of plants in the left margin. Rains in the region were intense on the collection day and entire preceding week, increasing the water volume in the stream. The following species were caught in the Córrego Grande stream along with *L. bernunssa*: *Ancistrus multispinis* (Regan, 1912) (Loricariidae), *Cambeva barbosa* Costa, Feltrin & Katz, 2021 (Trichomycteridae), *Hollandichthys multifasciatus* (Eigenmann & Norris, 1900) (Characidae), *Phalloceros maldonadoi* Souto-Santos, Lucinda & Buckup, 2023 (Poeciliidae), and *Rhamdia* sp. (Hepatpteridae). The paratype locality in Ribeirão

da Ilha district was a shallow water pool (no more than 15 cm deep) covered with a dense layer of leaf litter continuous with a swift running rock mountain stream (Sachse, pers. comm. *apud* Nico, de Pinna (1996)). On that occasion, the collectors (who are herpetologists) were searching for amphibians. Urban areas and the International Airport of Florianópolis currently circumscribe this locality, which is not protected by any conservation unit.

Etymology. The species epithet *bernunssa* refers to ‘Bernunça’, a character from the traditional folk manifestation of the coastal region of Santa Catarina. Also known as ‘Boi de Mamão’, it is a legendary creature reminiscent of a dragon, crocodile, or bogeyman, reported for devouring disobedient children. Its origins in Santa Catarina folklore can be traced back to Iberian and Spanish traditions of the Galicia region. A noun in apposition.

Conservation status. *Listrura bernunssa* is endemic to Brazil and has a restricted geographical distribution, known only from two localities in Florianópolis, with an area of occupation (AOO) of less than 100 km². The species is rare and not very abundant, typical of mountain streams with rocky bottoms and clear, fast-moving waters. The species probably occurred continuously along the island of Santa Catarina, and subpopulations may have been lost locally until the current distribution remained. This region is highly altered, mainly due to the rapid rural and urban expansion on the island of Santa Catarina, characterizing a decline in the quality of the remaining habitat. Due to the dynamics of anthropogenic occupation of the species’ natural environments, and its restriction to preserved environments, the severe fragmentation of the population can be inferred. Therefore, the new species was categorized as Endangered (EN) according to the B2ab(ii,iii) criterion (IUCN, 2022).

Molecular analysis. The BI reconstruction (Fig. 10) indicates that the closest relative of the new species *L. depinnai* (PP = 0.99). Interspecific pairwise genetic distances in the *cox1* gene are 2.9% with *L. depinnai*, 3.4% with *L. boticario*, 6.1% with *L. camposae*, 16% with *L. costai*, 17% with *L. nematopteryx*, *L. macacuensis*, *L. macaensis*, *L. pinguabae* and *L. tetradiaata*; and 18% with for *L. menezesi* (Tab. 4).

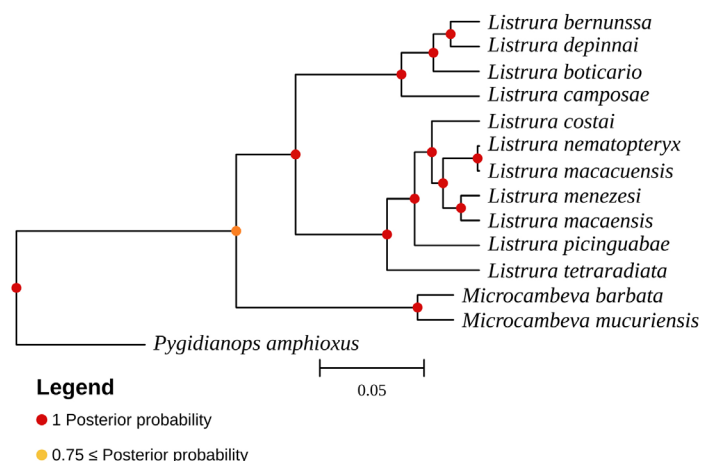


FIGURE 10 | Bayesian inference phylogram including of *Listrura* species (*L. gyrinura* and *L. urussanga* not included) and outgroup taxa based on mitochondrial data of the gene Cytochrome Oxidase sub-unit I (*cox1*). Colored circles in the nodes correspond to posterior probability values.

TABLE 4 | Values of pair-wise mitochondrial DNA genetic distance values for Cytochrome oxidase sub-unit 1 (*cox1*) gene between and within species using a Kimura 2 parameter.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1 – <i>Listrura bernunssa</i>	-													
2 – <i>Listrura depinnai</i>	0.029	-												
3 – <i>Listrura boticario</i>	0.034	0.039	-											
4 – <i>Listrura camposae</i>	0.061	0.065	0.069	-										
5 – <i>Listrura nematopteryx</i>	0.174	0.161	0.170	0.184	-									
6 – <i>Listrura macacuensis</i>	0.174	0.161	0.170	0.184	0.000	-								
7 – <i>Listrura menezesi</i>	0.184	0.165	0.174	0.187	0.036	0.036	-							
8 – <i>Listrura macaensis</i>	0.170	0.162	0.161	0.181	0.034	0.034	0.021	-						
9 – <i>Listrura costai</i>	0.162	0.159	0.173	0.183	0.038	0.038	0.046	0.044	-					
10 – <i>Listrura pinguabae</i>	0.176	0.176	0.165	0.184	0.052	0.052	0.055	0.057	0.057	-				
11 – <i>Listrura tetra radiata</i>	0.167	0.172	0.155	0.170	0.080	0.080	0.086	0.086	0.079	0.082	-			
12 – <i>Microcambeva barbata</i>	0.202	0.216	0.203	0.185	0.200	0.200	0.207	0.196	0.187	0.209	0.215	-		
13 – <i>Microcambeva mucuriensis</i>	0.208	0.213	0.195	0.178	0.187	0.187	0.180	0.170	0.179	0.200	0.221	0.031	-	
14 – <i>Pygidianops amphioxus</i>	0.306	0.307	0.291	0.276	0.275	0.275	0.286	0.278	0.266	0.284	0.291	0.311	0.315	-

DISCUSSION

Correct taxonomic and geographic delimitation of species is fundamental to understanding biodiversity (Mace, 2004; Liu *et al.*, 2022). Describing new species based on few specimens is less than ideal, because intraspecific and ontogenetic variation cannot be properly assessed (de Pinna *et al.*, 2020; Medeiros *et al.*, 2020). However, in certain cases it is necessary to name a species with limited material because there is simply no alternative. Having them reported and characterized helps expanding our knowledge on their systematics and taxonomy, ecology, biogeography, and conservation, particularly for those restricted-range species in highly impacted areas (de Pinna *et al.*, 2020; Medeiros *et al.*, 2020).

Listrura bernunssa has the synapomorphies proposed by Costa *et al.* (2020) for Microcambevinae: (I) a lateral constriction in the antero-median portion of the vomer (Fig. 5), (II) a lateral process in the interopercle accommodating a broad ligament to the lower jaw and posteriorly supporting a ligament connected to the anteroventral process of the opercle (Fig. 6), and (III) a protuberance on the posteromedial region of the dorsal surface of the premaxilla (Fig. 3). It also shares the morphological characters diagnostic for traditional Glanapteryginae (Baskin, 1973; de Pinna, 1988, 1989) and discussion of this controversy is beyond the scope of the present contribution. Still, the new species is a member of the genus *Listrura* based on a combination of synapomorphies proposed by de Pinna (1988) and Costa, Katz (2021): (I) a bottle-shaped vomer (Fig. 5), (II) mesethmoid with lateral widening after anterior cornua (Fig. 3), (III) lacrimal-antorbital club shaped (Fig. 3), (IV) caudal fin with a continuous membrane (dorsal and ventral keels of some authors) (Figs. 2, 8) projected along the dorsal and ventral peduncle, supported by numerous procurrent rays (Figs. 2, 7), and (V) absence of pelvic fin (Figs. 1, 2, 8).

Osteological data revealed some distinctive characters of the new species. An anteriorly oriented sub-cylindrical process is present on the anterolateral margin of the lateral ethmoid of *L. bernunssa* (Fig. 4). This is also found in the subgenus *Listrura* (Costa, Katz, 2021), even though, according to our molecular analysis (Fig. 10), *L. bernunssa* does not belong to that clade. Such sub-cylindrical process is absent in most other trichomycterid subfamilies. It is present, however, in the basal subfamilies Copionodontinae (where it is posteriorly oriented) and Trichogeninae (laterally oriented) (de Pinna, 1992; de Pinna *et al.*, 2020). The bottle-shaped and short vomer without a posterior process (Fig. 5) is a synapomorphy of *Listrura* as proposed by de Pinna (1988) and Costa, Katz (2021). The new species possess a vomer with an elongated posterior process and a compressed anterior region, fitting that general shape. Within *Listrura*, a small and distinct process in the posterior region of the vomer is also present in *L. pinguabae* (Villa-Verde, Costa, 2006). Finally, an epural (*sensu* Arratia, 1983) is observed in the 3D-reconstruction of the caudal skeleton of *L. bernunssa* (Fig. 7A), representing the first report of this bone in the genus.

The pairwise genetic distances between the new species and its closest relatives are 2.9% for *L. depinnaei*, 3.4% for *L. boticario*, and 6.1% for *L. camposae* are congruent with previously described sister-species (Tab. 4) (Villa-Verde *et al.*, 2012). Our BI analyses of *cox1* gene, indicate that *L. bernunssa* is the closest relative is *L. depinnaei*, with *L. boticario*, and *L. camposae* as successive sister-group. Our topology closely resembles the one by Costa, Katz (2021), which incorporated multigene and morphological data.

The first mention of the genus *Listrura* in the Santa Catarina Island refers to three specimens reported by Nico, de Pinna (1996), one of which is the paratype of *L. bernunssa* (MZUSP 63440). Based on the limited information available, these authors identified these specimens as belonging to a population of *L. camposae*, despite more than 400 km of distance to the type-locality of the latter species at Ribeira de Iguape River basin. Villa-Verde (2008) subsequently provided a brief description of two of those specimens (UFRJ 1278 and UFRJ 1279), proposing them as a putative new species, a hypothesis corroborated in Villa-Verde *et al.* (2013). More recently, Costa, Katz (2021) included these specimens of UFRJ in a phylogenetic analysis and cited them as *Listrura* sp. 1.

Island endemic species evolved separately from continental populations, experiencing a distinctive evolutionary trajectory over time (Barbo *et al.*, 2016), and are often classified as threatened with extinction due to their unique, limited, and usually vulnerable habitats. At least 12 vertebrate species are endemic of the continental islands of South and Southeast Brazil: five species of lancehead snakes [*Bothrops insularis* (Amaral, 1921), *B. alcatraz* Marques, Martins & Sazima, 2002, *B. otavioi* Barbo, Grazziotin, Sazima, Martins & Sawaya, 2012, *B. sazimai* Barbo, Gasparini, Almeida, Zaher, Grazziotin, Gusmão, Ferrarini & Sawaya, 2016 and *B. germanoi* Barbo, Booker, Duarte, Chaluppe, Portes-junior, Franco & Grazziotin, 2022] (Amaral, 1921; Marques *et al.*, 2002; Barbo *et al.*, 2012, 2016, 2022); five species of amphibians [*Ischnocnema manezinho* (Garcia, 1996) – endemic from the Santa Catarina Island –, *Hylodes fredii* Canedo & Pombal, 2007, *Scinax peixotoi* Brasileiro, Haddad, Sawaya & Martins, 2007, *S. faivovichii* Brasileiro, Oyamaguchi & Haddad, 2007 and *Proceratophrys tupinamba* Prado & Pombal, 2008) (Oswald *et al.*, 2023; Canedo, Pombal 2007; Brasileiro *et al.*, 2007a,b; Prado, Pombal, 2008); and two mammal species [*Phyllomys thomasi* (Ihering, 1897) and *Cavia intermedia* Cherm, Olimpio & Ximenez, 1999] (Vivo *et al.*, 2011). In Brazil, *Listrura bernunssa*

is the first freshwater fish endemic of a continental island in the AF, and only second freshwater trichomycterid family of an island (Fernández, Schaefer, 2005).

The Santa Catarina Island has an area of 425 km², and the shortest distance to the mainland is about 500 m of shallow sea. However, the marine oscillations driven by climatic fluctuations, primarily during the Pleistocene (2.580,0117 Mya), connected several islands, along the Brazilian coast, when sea level was 150 m lower (Martin *et al.*, 1986; Thomaz *et al.*, 2015; Leite *et al.*, 2016; Oswald *et al.*, 2023). Some paleorivers on the mainland and on the inland were then connected in their lower courses to the same paleodrainage system (Thomaz, Knowles, 2018). Speciation through population isolation, influenced by pleistocenic oscillations on islands has been hypothesized as the main vicariant agent involved in the speciation of the lancehead snake's *B. jararaca* (Wied-Neuwied, 1824) species complex in the coastal islands of southeastern Brazil (Barbo *et al.*, 2016, 2022) and of the leaf-litter frog *I. manezinho* on Santa Catarina Island (Oswald *et al.*, 2023). The relevance of those factors in the vicariant event between *L. bernunssa* and its closest mainland relative requires further study.

Comparative material examined. Brazil. Ribeira de Iguape basin: *Listrura camposae*: MZUSP 3426, holotype; MZUSP 99624 (1 eth.); MNRJ 37023 (2 eth., 2 cs); MNRJ 33031 (15 eth., 1 cs); MZUSP 95189 (25 eth. 2 cs). **Estrela basin:** *Listrura nematopteryx*: MZUSP 36974, holotype; MZUSP 36975 (12 eth.); MZUSP 37137 (18 eth.); MNRJ 10970 (9 eth.); MNRJ 37022 (1 eth.); MNRJ 9373 (2 eth.); UFRJ 5952 (5 cs). **Guaraqueçaba basin:** *Listrura boticario*: MZUSP 69573, holotype; MNRJ 32444 (21 eth.); MNRJ 32442 (1 eth.). **Jurumirim basin:** *Listrura costai*: MNRJ 31917, holotype; MNRJ 31535 (5 eth., 2 cs); MNRJ 39620 (4 eth.); MNRJ 31918 (5 eth.); UFRJ 7214 (3 eth.); UFRJ 7215 (4 eth.); UFRJ 6577 (3 cs). **São João basin:** *Listrura menezesi*: MZUSP 125906, holotype; MNRJ 32026 (43 eth., 3 cs); MZUSP 93882 (3 eth., 5 cs); MZUSP 125907 (6 eth.). **Gravataí basin:** *Listrura depinmai*: UFRGS 17135, holotype; UFRGS 16383 (1 eth.); UFRGS 19536 (1 eth.); UFRGS 19623 (1 eth.). **Fazenda basin:** *Listrura pinguabae*: UFRJ 6111, holotype; MCP 38921 (2 eth.); UFRJ 5948 (1 eth.); UFRJ 5949 (2 eth.); UFRJ 5950 (15 eth.); UFRJ 5951 (4 cs); UFRJ 5991 (2 eth.); UFRJ 6138 (5 cs); MZUSP 94974 (12 eth.). **Ibicuíba basin:** *Listrura tetraradiata*: MZUSP 52572, holotype; UFRJ 4586 (17 eth.); UFRJ 4588 (6 cs); UFRJ 7587 (17 eth.); UFRJ 4590 (7 eth.); MZUSP 50164 (3 eth.); MNRJ 39068 (6 eth.); MNRJ 19064 (12 eth.); MNRJ 31534 (13 eth., 3 cs). **Madre basin:** *Listrura gyrinura*: UFRJ 6927, holotype; UFRJ 6928 (10 eth.); UFRJ 6929 (4 cs). **Urussanga basin:** *Listrura urussanga*: UFRJ 6914, holotype; UFRJ 6915 (1 eth.); UFRJ 6916 (3 eth.); UFRJ 6917 (1 eth.); UFRJ 6930 (6 eth.); UFRJ 6931 (1 cs). **Macaçu basin:** *Listrura macacuensis*: UFRJ 12669, holotype; UFRJ 9268 (9 eth.); UFRJ 9279 (32 eth.); UFRJ 9691 (3 cs). **Macaé basin:** *Listrura macaensis*: UFRJ 12667, holotype; UFRJ 9065 (1 eth.); UFRJ 9996 (1 cs); UFRJ 9693 (1 eth.); UFRJ 9758 (2 cs).

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AUTHORS' CONTRIBUTION

Lucas Silva de Medeiros: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing-original draft, Writing-review and editing.

Laura Modesti Donin: Conceptualization, Data curation, Formal analysis, Investigation, Methodology.

Juliano Ferrer: Conceptualization, Data curation, Formal analysis, Investigation, Methodology.

Sergio Maia Queiroz Lima: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Supervision, Validation, Writing-original draft, Writing-review and editing.

Mário de Pinna: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Resources, Software, Supervision, Validation, Writing-original draft, Writing-review and editing.

ETHICAL STATEMENT

The specimens were collected with authorizations #9318-1, #9220-1, and #8796-1 from Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio).

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The author declares no competing interests.

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