ORIGINAL ARTICLE

# From the inside out: Discovery of a new genus of threadsnakes based on anatomical and molecular data, with discussion of the leptotyphlopid hemipenial morphology

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## Abstract

The systematics of Leptotyphlopidae is historically controversial mostly due to their conserved external morphology in comparison with other snakes. However, recent studies have stressed that anatomical data might be informative for clarifying the leptotyphlopid taxonomy and evolution. We erect a new genus to accommodate *Leptotyphlops collaris* based on evidence from osteology, hemipenial morphology, and molecular data. We also provide expanded data regarding the intraspecific variation based on additional specimens collected in field trips and literature data, performing detailed comparisons among the new genus and all other New World leptotyphlopids. The new genus is distinguished from other leptotyphlopids by its unique hemipenial morphology and its exclusive combination of osteological and external morphology characters, with molecular data also supporting the new generic arrangement. We also provide a comprehensive discussion of the hemipenial morphology for the sub-family Epictinae based on literature and novel data gathered herein.

**KEYWORDS**
Guiana Shield, hemipenis, molecular phylogeny, osteology, Scolecophidia

## 1 | INTRODUCTION

The threadsnakes of the family Leptotyphlopidae Stejneger, 1892, are represented by about 140 currently recognized species (Adalsteinsson, Branch, Trape, Vitt, & Hedges, 2009; Uetz, Freed, & Hošek, 2018), divided into two subfamilies: Epictinae and Leptotyphlopinae. The 52 species of Leptotyphlopinae inhabit the sub-Saharan Africa, the Arabian Peninsula and southwest Asia, while the subfamily Epictinae contains about 90 species allocated in nine recognized genera (Uetz et al., 2018) that occur in the New

World (Americas and Antilles: *Rena* Baird & Girard, 1853, *Trilepida* Hedges, 2011, *Mitophis* Hedges, Adalsteinsson & Branch, 2009, *Tetracheilostoma* Jan, 1861, *Siagonodon* Peters, 1881, and *Mitophis* Hedges, Adalsteinsson & Branch, 2009) and in Africa (*Tricheilostoma* Jan, 1860, *Rhinoleptus* Orejas-Miranda, Roux-Estève, and Guibé, 1970, and *Rhinoguinea* Trape, 2014). Most of these genera have been proposed with basis on a molecular phylogeny that did not provide compelling phenotypic evidence for their recognition (Adalsteinsson et al., 2009). Despite the ancient cladogenesis event and the separation between the two main lineages of the family (Leptotyphlopinae and Epictinae; Adalsteinsson et al., 2009), all living species present an entirely fossorial or semifossorial lifestyle, actively eating on larvae or adults of social insects (Cundall & Greene, 2000; Greene, 1997; Webb, Shine, Branch, & Harlow, 2000).

The leptotyphlopid external morphology is very conserved in comparison with other snakes, and therefore, other evidence such as anatomical and molecular data is needed to clarify relationships among close-related genera (Martins, Passos, & Pinto, 2018; Passos, Caramaschi, & Pinto, 2005,2006; Pinto & Curcio, 2011). Internal anatomical characters have proven to be useful in snakes' systematics for both inferring phylogenetic relationships (Lee, Hugall, Lawson, & Scanlon, 2007; Lee & Scanlon, 2002; Underwood, 1967), as well as in the delineation of close-related species (Myers & McDowell, 2014). Some previous studies on the leptotyphlopid visceral anatomy, skull, and/or hemipenial morphology (e.g., Bailey & Carvalho, 1946; Broadley & Wallach, 2007, 1997; Passos, Caramaschi, & Pinto, 2006; Pinto & Fernandes, 2012,2017) have reinforced the value of such characters for the systematics of this group. However, considering the anatomy of leptotyphlopids is still unexplored, additional studies might reveal several diagnostic features that can be directly applied for their systematics (Martins et al., 2018).

Herein, we propose a new genus of Leptotyphlopidae based on anatomical data (mostly skull and hemipenial morphologies), which is also supported by new molecular data. We also provide novel data on hemipenial morphology of Epictinae with a comprehensive discussion on its comparative morphology.

## 2 | MATERIAL AND METHODS

### 2.1 | Taxon sampling and data acquisition

We examined specimens housed in the following institutions: Instituto Butantan, São Paulo, Brazil (IBSP); Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil (MNRJ); Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (MZUSP); Museu Paraense Emílio Goeldi, Belém, Brazil (MPEG); Universidade Federal de Mato Grosso, Cuiabá, Brazil (UFMT); Fundación Miguel Lillo, Tucuman, Argentina (FML); Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá DC, Colombia (ICN); Coleção Herpetológica da Universidade de Brasília, Brasilia, Brazil (CHUNB); Laboratório de Zoologia de Vertebrados, Universidade Federal de Ouro Preto, Ouro Preto, Brazil (LZV-UFOP); Museo de Zoología de la Pontificia

Universidad Católica del Ecuador, Quito, Ecuador (QCAZ); Field Museum of Natural History, Chicago, USA (FMNH); Natural History Museum, University of Kansas, Lawrence, USA (KU); Museum of Comparative Zoology, Cambridge, USA (MCZ); Los Angeles County Museum, Los Angeles, USA (LACM); American Museum of Natural History, New York, USA (AMNH); United States National Museum, Smithsonian Institution, Washington DC, USA (USNM); Illinois Museum of Natural History, Illinois, USA (UIMNH); Sam Noble Oklahoma Museum of Natural History, Oklahoma, USA (OMNH); San Diego Natural History Museum, San Diego, USA (SDNHM); and Muséum National d'Histoire Naturelle, Paris, France (MNHN). We provide information on the specimens and localities in the Appendix 1. We follow Passos et al. (2006), Broadley and Wallach (2007), and Pinto and Curcio (2011) for meristic and pholidosis terminologies. We consider the total number of middorsal scales by excluding the rostral scale and caudal spine, and the number of subcaudals by excluding the caudal spine. Terminology for hemipenial morphology follows Dowling and Savage (1960), as augmented by Myers and Campbell (1981) and Branch (1986). Techniques for hemipenis preparations follow Pesantes (1994), except when examined in situ. Measurements were taken with a digital caliper to the nearest 0.1 mm, except for total length (TL) and caudal length (CL), which were taken with a flexible ruler to the nearest 1.0 mm. Sex was determined through a ventral incision at the base of the tail. External morphology characters of other Neotropical leptotyphlopids are based on data from: Francisco, Pinto, and Fernandes (2012); Francisco, Pinto, and Fernandes (2018); Adalsteinsson et al. (2009); Passos, Caramaschi, and Pinto (2005), Passos et al. (2006); Pinto, Passos, Portilla, Arredondo, and Fernandes (2015), Pinto et al. (2015); Pinto and Curcio (2011); and Pinto and Fernandes (2012). Comparisons of skull, lower jaw, and cervical vertebrae for *Trilepida* spp. and *Rena* spp. are based on Kley (2006); Rieppel, Kley, and Maisano (2009); Martins (2016); Pinto et al. (2015); Salazar-Valenzuela, Martins, Amador-Oyola, and Torres-Carvajal (2015); and Martins, Koch, Pinto, and Passos (in prep; see Material examined). The head and cloacal regions of each specimen were X-rayed in 3D using a high-resolution micro-CT scanner (Bruker SkyScan 1,173) at ZFMK. The head and cloacal region were CT-scanned in 180° degrees at rotation steps of 0.3° or 0.4° degrees with a tube voltage of 40 kV and a tube current of 200 uA without the use of a filter, and at an image resolution of 8.4 μm. The CT-dataset was reconstructed using N-Recon software (Bruker MicroCT) and rendered in three dimensions through the aid of CTVox for Windows 64 bits version 2.6 (Bruker MicroCT). Comparisons with the skulls of *Siagonodon*, *Tetracheilostoma*, and *Mitophis* are based on Martins (2016). Comparisons of hemipenial morphology are based on Bailey and Carvalho (1946), Orejas-Miranda (1962), Thomas (1965), Peters and Orejas-Miranda (1970), Fabrezi, Marcus, and Scrocchi (1985), Branch (1986), Scrocchi (1990), Cei (1993), Savage (2002), Passos et al. (2005), Passos et al. (2006), Pinto et al. (2015), Pinto and Curcio (2011), and Pinto and Fernandes (2012). Coloration in life follows Köhler (2012).

## 2.2 | Molecular data and phylogenetic analysis

Aiming to assess the phylogenetic position of *Epictia collaris* (current species allocation; sensu Adalsteinsson et al., 2009) within Leptotyphlopidae, we included representatives of all genera currently included in Epictinae (except for the African genera *Rhinoguinea* and *Epacrophis*), and representatives of two other basal snake families (Boidae and Typhlopidae). We selected specific out-group terminals trying to maximize character coverage (i.e., homologous sequences available from GenBank) and phylogenetic structure according to the trees of the two most densely sampled leptotyphlopid phylogenies (Adalsteinsson et al., 2009; McCranie & Hedges, 2016). We compiled the complete or partial sequences of 10 genes: mitochondrial genes for *tRNAPhe*, *12S rRNA* (12S), *tRNAVal*, *16S rRNA* (16S), *cytochrome b* (*cytb*); nuclear genes for *amelogenin* (*AMEL*), *brain-derived neurotrophic factor* (*BDNF*), *oocyte maturation factor* (*c-mos*), *recombination activating gene 1* (*RAG1*), and *neurotrophin 3* (*NT3*). Information of the specimens and GenBank accession numbers used in this study is given in the Appendix 2.

We collected DNA sequence data for three mitochondrial gene segments (*12S rRNA*, *16S rRNA*, and *cytb*) and three nuclear gene segments (*BDNF*, *c-mos*, and *NT3*). We performed PCRs using a PCR Master Mix and a pair of primers for each segment (Table S1Supporting Information): BDNF-forward and BDNF-reverse, NTF3_f1, and NTF3_r1 (Townsend, Alegre, Kelley, Wiens, & Reeder, 2008); c-mos S77 and c-mos S78, 12S L1091mod, and 12S H1557mod, 16sar, and 16Sbr (Zaher et al., 2009); cytb 703Botp and cytb MVZ16p (Grazziotin et al., 2012).

Thermocycling for DNA amplification for the first partition began with a denaturation at 94°C (5 min), followed by 40 cycles of denaturation at 94°C (30 s), annealing at 43–48°C (30 s), extension at 70°C (1 min), and a final step at 72°C after the final cycle (7 min). PCR products were visualized in 1% agarose gels and sent to Macrogen Inc. (Seoul, Republic of Korea) for purification and sequencing reactions. Resulting electropherograms for both DNA strands were analyzed using Geneious v8.1.7 (Kearse et al., 2012), adjusted manually to generate consensus sequences for each specimen. Sequences were checked with basic local alignment search tool (Altschul et al., 1997) against the GenBank nucleotide database to ensure that the amplified product was correct and not contaminated.

In order to incorporate all sequences into similarity-alignment analysis in MAFFT version 7 (Katoh, Misawa, Kuma, & Miyata, 2002), each of the mitochondrial markers *tRNAPhe*, *12S*, *tRNAVal*, and *16S* had to be independently prealigned and divided into putatively homologous sections of sequences according to individual alignments with the *Rena humilis* mitochondrial genome (GenBank: AB079597) in ClustalW (Thompson, Higgins, & Gibson, 1994). Then, these sequences were aligned using MAFFT, with a gap opening penalty of 1.53 and an offset value of 0.0. Parameters for *cytb*, *AMEL*, *BDNF*, *c-mos*, *RAG1*, and *NT3* were left at their default settings (L-INS-i model) and parameters for *tRNAPhe*, *12S*, *tRNAVal*, and *16S* were set to the G-INS-i model. We aligned each segment separately (Alignment S1), and segments were concatenated using Mesquite 3.10, to a total of 6,353 bp. We selected appropriate models of the DNA sequences using the software

jModeltest 2.17 (Posada, 2008) based on the Akaike information criterion or AIC (Akaike, 1974). Obtained models were HKY + G for *c-mos*, GTR + G for *AMEL* and *RAG1*, K80 + G for *NT3*, SYM + I for *tRNAPhe*, GTR + G + I for *cytb*, *BDNF*, *12S*, *tRNAVal*, and *16S*.

We performed partitioned Bayesian Inference (BI) using MrBayes 3.2.2 (Ronquist & Huesenbeck, 2003) through the portal CIPRES Science Gateway (Miller, Pfeiffer, & Schwartz, 2010) using the concatenated dataset and the partition models described. Each analysis included two independent runs of 20,000,000 generations with four chains of Markov and Monte Carlo. Parameters and trees were sampled every 5,000 generations. We considered convergence of the runs when the standard deviation of the frequency splits was lower than 0.05 and by observing ESS values above 300 in Tracer v1.4 (Rambaut & Drummond, 2007). The first 25% of samples were discarded as burn-in. Branch support was assessed by posterior probability, and nodes with posterior probabilities $p > 0.95$ were considered strongly supported (Matiolli & Fernandes, 2012).

## 3 | RESULTS

Order Squamata Oppel, 1811

    Family Leptotyphlopidae

    Subfamily Epictinae

    *Leptotyphlops collaris* (Hoogmoed, 1977), Zoologische Mededelingen, 51 (7):99–125.

    *Epictia collaris* – (Adalsteinsson et al., 2009). Zootaxa, 2244:1–50.

    *Habrophallos collaris* – **New Genus.**

    **Genus *Habrophallos*** Martins, Koch, Pinto, Folly & Passos **New Genus.**

    **Type-species**: *Habrophallos collaris* (Hoogmoed, 1977) by original designation.

    **Etymology:** The generic name is derived from the Greek "*habros*" (pretty, graceful, delicate) + the Greek "*phallos*," used herein in reference to the small, delicate, and diagnostic hemipenial morphology of the new genus.

    **Definition and diagnosis:** *Habrophallos* is a small leptotyphlopid snake genus characterized by the following unique combination of characters: hemipenis unilobed, with two flattened areas (one basal and another on the apex); hemipenis with a large lateral flounce with folding at one side and a hook-shaped process on the other side; apex of the hemipenis with a double projection lateroproximally oriented; skull with paired nasal bones; parietal bone not fused to any other skull element; parietal fontanelle absent, internal pillars of parietal bone present; supraoccipitals fused into a single unit, moderate statolithic mass present in *cavum vestibuli*, otooccipitals prevent the basioccipital on forming the foramen magnum; distinct eye; midbody scale rows 14, midtail scale rows 10; 151–163 middorsal scales, 13–15 subcaudals, 1 + 1 supralabials; 92–120 mm maximum total length in adults, a body shape of 31–41 (total length/width), a relative tail length of 8.5%–9.7%, a relation of tail length/diameter of 3.3–4.7; supraocular scale present; terminal spine present; no striped pattern (although some lighter

pigmentation in the tip of scales might suggest a striped pattern), brown dorsal color, and light brown venter; yellow blotch on rostral region present; ultimate part of tail including spine yellow; yellow nuchal collar present.

**Comparisons with other Neotropical leptotyphlopid genera (conditions for other genera in brackets):** The genus *Habrophallos* is distinguished from *Epictia* by the presence of a fused supraoccipital bone (vs. paired), absence of the posterior process of quadrate (vs. presence), hemipenis with a large hook-like lateral process at one side and an enlarged flounce with folds on the other side (vs. organ usually without enlarged flounce and hook-like process), and presence of a double process in the apex of the hemipenis (vs. absence). It differs from *Trilepida* by the presence of yellow coloration on the rostral region and at the end of the tail (vs. absence), by the otooccipital bones excluding the basioccipital of forming the foramen magnum (vs. basioccipital participates in the formation of the foramen magnum) and absence of an enlarged hemipenial apex (vs. wide apex). The new genus differs from *Siagonodon* by the presence of a supraocular scale (vs. absence), although such character may be subject to variation in *S. septemstriatus* (Schneider, 1801), presence of a terminal spine (vs. absence), number of middorsal scales ranging from 151 to 163 (vs. 163–299), eye large and distinct, not covered by ocular scale (vs. usually very reduced as a black spot or indistinct and covered by ocular scale), rostral scale pyramidal, longer than wide (vs. rectangular, wider than long), rounded snout in dorsal view (vs. straight), absence of anterior or lateral expansion of the snout bones (vs. snout bones conspicuously anteriorly elongated in *S. cupinensis* (Bailey & Carvalho, 1946) and laterally expanded in *S. septemstriatus*), premaxilla forms a short anteroventral cover of the snout (vs. conspicuously expanded posteriorly, comprising the ventral limits of the snout), dentary teeth short (vs. long), coronoid bone as wide as tall (vs. distinctively dorsally elongated, two or three times taller than wide). The genus *Habrophallos* differs from *Mitophis* by its low number of 151–163 middorsal scales (vs. 262–414), presence of two supralabials (vs. four), brown dorsum with a yellow blotch on the rostral scale and a yellow end of the tail (vs. pale brown or unpigmented dorsum without yellow blotches on rostral scale and tail), and presence of supraoccipitals not participating on the formation of the foramen magnum (vs. a posterior extension to participate in the formation of the foramen magnum). The new genus differs from *Tetracheilostoma* by the presence of two supralabials (vs. four) and distinct (vs. indistinct) supraoccipital bones. The genus *Habrophallos* distinguishes from *Rena* by its lower number of 151–163 middorsal scales (vs. 168–312), presence of yellow blotches on the rostral scale and end of the tail (vs. absence), otooccipitals excluding the basioccipital on forming the foramen magnum (vs. basioccipital participates in the formation of the foramen magnum), fused supraoccipital bone (vs. paired), and paired nasal bones (vs. fused).

**Color in life (**Figure 1**):** Coloration in life based on a photograph of a presumably adult individual (MNHN2019.0003). General dorsal background color medium brown (Hazel, Color 26), with scales bordered by dark brown (Warm sepia, Color 40) outlines. Rostral spot, nuchal collar, and tip of tail (including terminal spine) medium yellow



**FIGURE 1** General view of *Habrophallos collaris* gen nov. (MNHN2019.0003) in life

(Cream yellow, Color 82). Additional color descriptions from individuals in life may be found in Hoogmoed and Lima (2018).

**Color variation in preservative (**Figures 2–5**):** Body uniformly dark brown or medium brown in dorsum and venter, with scale limits bordered by dark brown color. Yellow coloration changes to cream or white on rostral, nuchal collar, and on the tail.

**Skull (**Figures 6 and 7**;** *n* = 3**).** Premaxilla not visible in dorsal view, roughly rectangular in frontal and ventral views, edentulous, pierced by six foramina; transversal process of premaxilla absent and vomerian process double with distinct medial concavity exposing the nasal septum in ventral view (*n* = 1) or single without ventral exposition (*n* = 2); nasals paired, approximately rectangular in dorsal view, each bearing a medial projection toward the premaxilla; loose contact between nasal–prefrontal–frontal, with triangular gap in dorsal view (*n* = 1) or not (*n* = 2); *apicalis nasi* opening formed by the nasal and prefrontal; nasal septum descending as medial vertical flanges; schizartrotic contact between nasals and frontals with regular transverse suture; nostril anterolateral, being delimited by the premaxilla, septomaxilla, maxilla, and nasals; prefrontals paired, subtriangular in dorsal view, in contact with septomaxilla and nasal anteriorly, maxilla ventrally and frontal posteromedially; prefrontal recess present to accommodate the nasal gland anteroventrally; septomaxillae paired, complex in shape, expanding dorsally into the naris; conchal invagination of premaxilla absent; ascending process of premaxilla pierced by single large foramen; vomers paired, located midventral to vomeronasal cupola, bearing transversal arms, and with short posterior and lateral arms, the former overlapped by palatines (in ventral view); frontals paired, nearly rectangular in dorsal view, without anterolateral projections to attach to prefrontals; frontal pillars absent; optic nerve foramen restricted to the posterior third of the lateral descending surface of frontals; maxilla edentulous, irregular in shape, pierced by one large foramen that opens medially into two large foramen (anterior and posterior); no distinct foramina (*n* = 1), one (*n* = 1) or two (*n* = 1) distinct foramina in dentigerous process of maxilla, although concavities are noticeable in this region for the former condition; posterior process of maxilla does not reach the optic
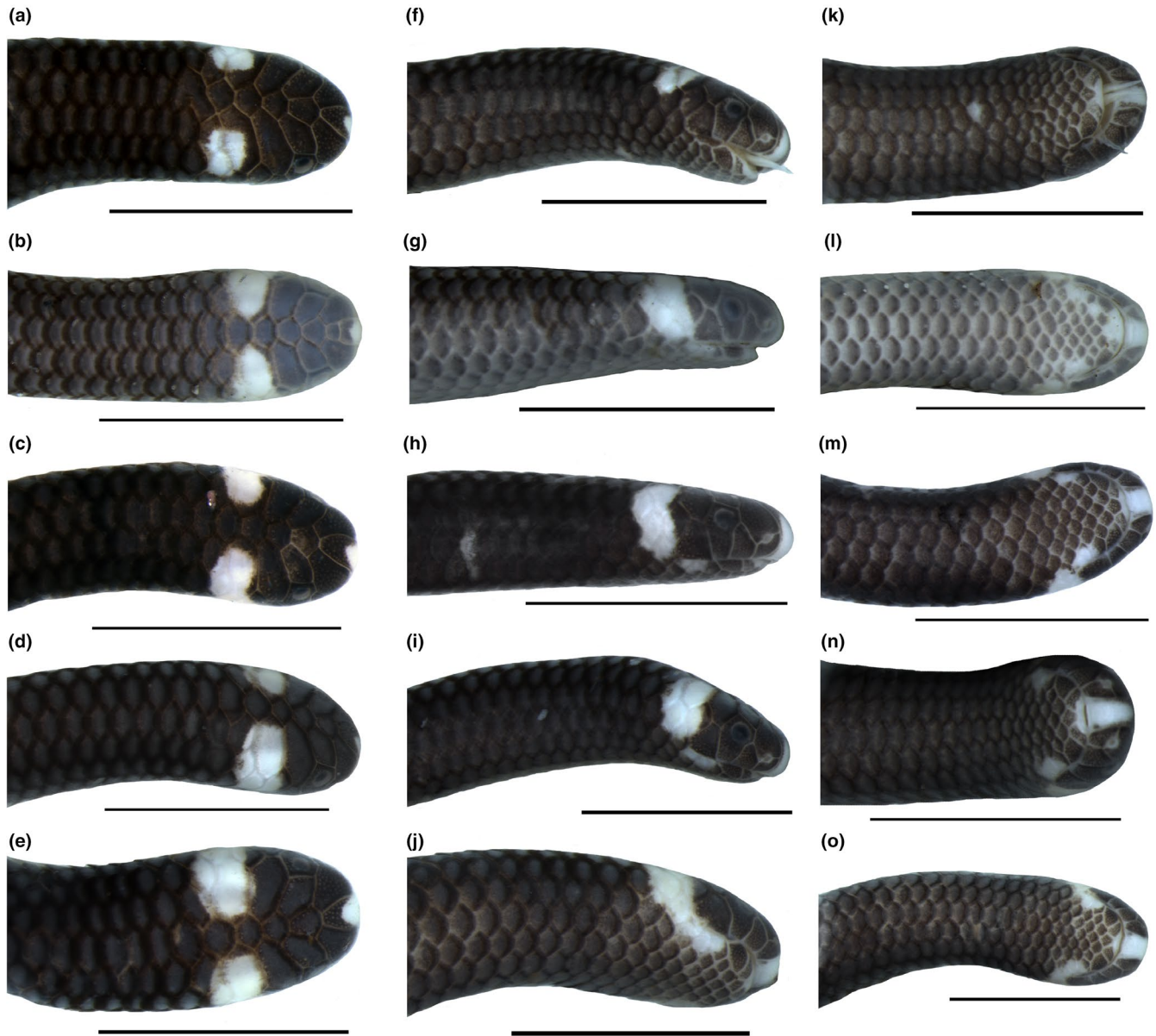
**FIGURE 2** Comparisons of the dorsal (a–e), lateral (f–j), and ventral (k–o) views of the heads of *Habrophallos collaris* gen nov. MNRJ27144 (a, f, k), MNHN2019.0001 (b, g, l), MNRJ27145 (c, h, m), MNHN2019.0002 (d, i, n), MNHN2019.0003 (e, j, o). Scale 5 mm

nerve foramen in lateral view; posterior orbital element absent; parietal single, wide, representing the largest bone of braincase, without fontanelle; internal pillars of parietal (sensu Martins, 2016) present; concavities for the insertion of the *Musculus spinalis et semispinalis capitis* absent in the parietal dorsal lamina; parietal participates in the formation of the exit for the palatine branch on the facial nerve together with the parabasisphenoid; parabasisphenoid arrow-like, with tapered anterior tip lying below palatine (ventral view), and fitting in medial line of vomeronasal cupola; parabasisphenoid with shallow pituitary fossa; anterior opening to the palatine artery and its sulcus absent; loose contact between parabasisphenoid–parietal–frontal; basioccipital single and approximately triangular; supraoccipitals fused into a single unit, approximately triangular; prootics paired and subellipsoidal in lateral view; moderate statolithic mass present in

cavum vestibuli; stapedial footplate apparently not co-ossified with prootic; otooccipitals paired and L-shaped in dorsal view, descending ventrally excluding basioccipital from the formation of foramen magnum; otooccipitals pierced by a wide vagus nerve foramen posteriorly; acoustic nerves paired; perilymphatic foramen present; palatines paired, triradiate, and contacting medially to each other; anterior margin of maxillary process slightly ventrally projected, contacting both prefrontals and maxilla dorsally; pterygoids slender and rod-like, not contacting quadrate posteriorly, and not reaching the posterior limit of parabasisphenoid; ectopterygoid indistinct.

**Lower jaw** (Figure 8; *n* = 3). Quadrate long and slender, about 50% of skull length; ventroposterior process of quadrate absent; anterior foramen of quadrate absent; dentary supports a series of five (*n* = 5 sides) or six (*n* = 1 sides) teeth ankylosed to the inner surface
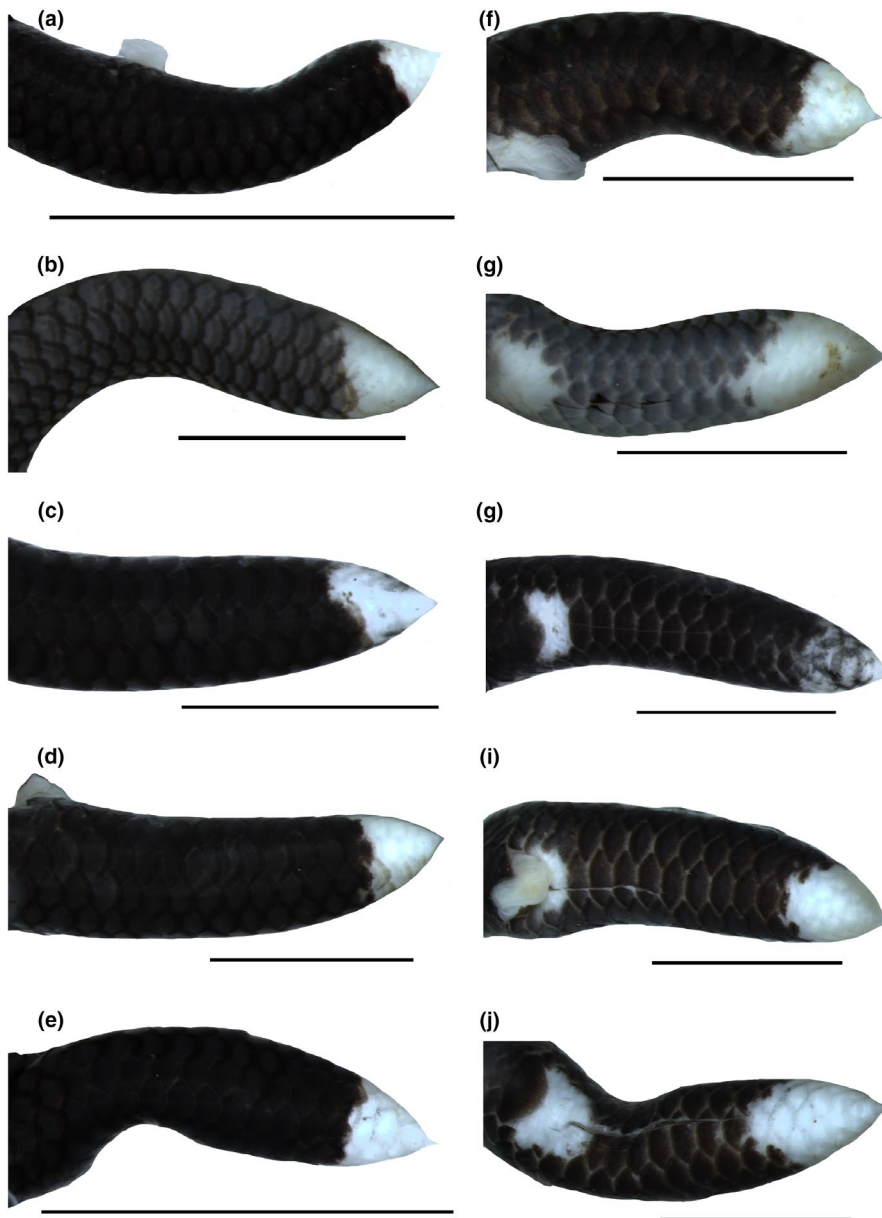
**FIGURE 3** Comparison of dorsal (a–e) and ventral (f–j) views of the tail of *Habrophallos collaris* gen. nov. MNRJ27144 (a, f), MNHN2019.0001 (b, g), MNRJ27145 (c, h), MNHN2019.0002 (d, i), MNHN2019.0003 (e, j). Scale 5 mm

of the anterolateral margin of the dental concha; mental foramen nearly under the fourth (*n* = 2) or fifth (*n* = 1) tooth; splenial conical, representing smallest bone in lower jaw, visible in lateral view, with anterior limit reaching the level of fifth tooth; anterior mylohyoid foramen absent on splenial; posterior mylohyoid foramen on the ventral surface of angular; angular conical; compound bone pierced by two foramina in the surangular lamina, posterior surangular foramen large and anterior to the articular portion of the compound bone, anterior surangular foramen located anterior to the coronoid; foramen for the hyomandibular ramus of facial nerve VII present; coronoid rests on the compound bone; prearticular process of coronoid present; dorsal process of coronoid single (*n* = 2) or double (*n* = 1).

**Cervical vertebrae (*n* = 3).** Atlas composed by neural arches not fused dorsally or ventrally; a ventral element (intercentrum I sensu Holman, 2000) is absent; short lateral projections of the atlas are present. Axis with short spinal process projected dorsally; lateral

foramina of axis indistinct or absent; short lateral processes present. Odontoid process of axis osseous and sutured to axis, approximately losangular in anterior view, with an anterior tapered process; intercentra II and III ventral, compressed laterally, bearing fused and pointed hypapophyses in lateral view (sensu Holman, 2000).

**Pelvic girdle (Figure 9; *n* = 1).** Composed by four non-fused bones: ilium, ischium, femur, and pubis. Ilium, ischium, and pubis rod-like; ilium represents the longest bone of the pelvic girdle, twice as long as pubis; femur stout, approximately triangular. Pelvic girdle located at the level of the last three trunk vertebrae (*n* = 1, 20%), last two trunk vertebrae and first cloacal vertebrae (*n* = 2, 40%), or last trunk vertebrae and first cloacal vertebrae (*n* = 2, 40%).

**Postcranial quantitative variation.** Precloacal vertebrae 132–144 (x̄ = 137.6 ± 4.5, *n* = 5); cloacal vertebrae 3–4 (x̄ = 3.2 ± 0.4, *n* = 8); caudal vertebrae 14–17 (x̄ = 15.9 ± 1, *n* = 7), the last vertebrae representing a fusion of two vertebrae (*n* = 2). Correlation (*n* = 5)

**FIGURE 4** Comparison of dorsal views of the body of *Habrophallos collaris*. MNRJ27144 (a), MNHN2019.0001 (b), MNRJ27145 (c), MNHN2019.0002 (d), MNHN2019.0003 (e), MNHN1977.49 (f), MNHN 1996.4580 (g), MNHN1999.8309 (h). Scale 5 mm

between middorsal scales and precloacal vertebrae (1:0.8), between midventral scales and precloacal vertebrae (1:0.9), and between subcaudal scales and caudal vertebrae (0.9:1).

**Hyoid (*n* = 4).** Hyoid Y-shaped, extending from the 9–15th (MNHN2019.0002), 10–16th (MNHN2019.0003), 11–15th (MNRJ 27,145), or 11–17th (MNRJ 27,144) vertebrae. Cornua typically longer than the lingual process.

**Hemipenial morphology (**Figure 10**; Fully everted, examined ex situ; *n* = 1).** Organ unilobed, slightly broadened on the base, followed by a short tapered area that posteriorly widens to taper again at
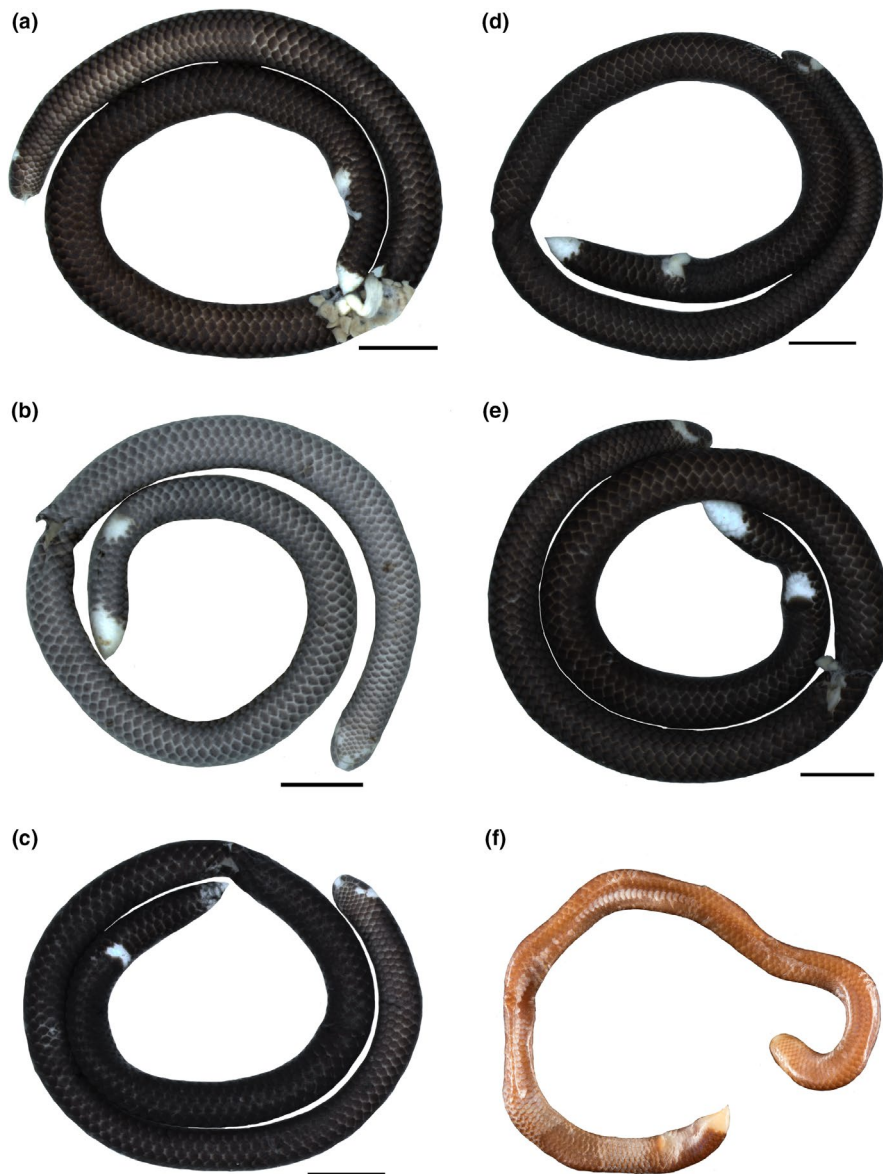
**FIGURE 5** Comparison of ventral views of the body of *Habrophallos collaris*. MNRJ27144 (a), MNHN2019.0001 (b), MNRJ27145 (c), MNHN2019.0002 (d), MNHN2019.0003 (e), MNHN1977.49 (f). Scale 5mm

apex; basal portion with a large lateral hook-like process at one side and a large flounce with folding on the other side; hemipenial body wide, with no ornamentation on either the sulcate or the asulcate sides on its first distal half; sulcus spermaticus single, entering the organ on the basal surface and extending toward the apex of the organ; sulcal folds raised and not ornamented; distal half of hemipenial body covered by discrete longitudinal flounces; organ apex convex and covered by several papillae arranged in two rows that surround the apex; paired projection develops from the apex of the asulcate side being lateral-proximally oriented.

**Molecular analysis (**Figure 11**).** The topology recovered on the basis of BI shows that the genus *Epictia* (so far known) is paraphyletic, supporting the recognition of the new genus. *Habrophallos* is strongly supported (pp > 0.95) as the sister-group of the genus *Siagonodon* and this clade represents the sister-group of *Epictia*, restoring the monophyly of Epictina. Furthermore, the monophyly of four tribes (Epictini Hedges, Adalsteinsson, & Branch,

2009, Leptotyphlopini Hedges, Adalsteinsson, & Branch, 2009, and Myriopholini and Rhinoleptini Hedges, Adalsteinsson, & Branch, 2009) is also recovered. All aforementioned relationships are supported by high posterior probabilities.

**Distribution (**Figure 12**).** *Habrophallos collaris* occurs in moderate uplands and lowland rainforests of the Eastern Guiana Shield and surrounding areas from the sea level to 830 m above sea level, in Suriname, French Guiana, and Brazil. After the species description in 1977, new records were provided by Gasc and Rodrigues (1980), Blanc and Dewynter (2005) and Starace (2013), and a few online records (Groot, 2006; Szpigel, 2014; Brusini, s.d.). A comprehensive map synthetizing the species distribution as well as detailed novel data on habitat is provided by Hoogmoed and Lima (2018).

**Remarks**. Hoogmoed (1977) described *Leptotyphlops collaris* based on a sample of nine specimens from Suriname and French Guiana. The author allocated *Leptotyphlops collaris* in

the *Leptotyphlops albifrons* species group based on meristic data from Orejas-Miranda (1967). Adalsteinsson et al. (2009) allocated *Leptotyphlops collaris* in the genus *Epictia* based on external morphology characters but without testing for the phylogenetic position or relationships.

## 3.1 | Key to Genera of New World Leptotyphlopidae

1.  Ocular scale separated from lip border by continuous row of supralabials; supralabials normally four (rarely three)..................................................................................**2**
    Ocular scale forms part of the lip border; supralabials two (1+1) or three (2+1) .......**3**
2.  Middorsal scale rows > 200; midtail scale rows 12; no striped pattern (except for *M. pyrites*); extremely thin body; pale brown or unpigmented dorsum...............***Mitophis***
    Middorsal scale rows < 200; midtail scale rows usually 10 (rarely 11 or 12 in *T. bilineata*); striped pattern; stouter body diameter; dark brown dorsum ..............................................................................................***Tetracheilostoma***
3.  Supraoccipital bones fused...............................................................................**4**
    Supraoccipital bones paired ............................................................................**6**
4.  Supraocular scale usually absent......................................................................**5**
    Supraocular scale present ...............................................................................**7**
5.  Supralabials two (1+1); non-fused caudals on tip of tail; frontal subcircular and enlarged; rostral scale moderately to distinctly enlarged at nostril level...***Siagonodon***
    Supralabials mostly three (2+1); fused caudals on tip of tail; frontal scale subrectangular and not enlarged; rostral scale not enlarged at nostril level .. ***Trilepida brasiliensis***
6.  Supraocular scale present, distinctly larger than frontal or postfrontal; two (1+1) supralabials; rostral scale and tip of tail usually pigmented in distinct color from the body.....................................................................................................***Epictia***
    Supraocular scale absent or small, but not or hardly larger than frontal or postfrontal; two (1+1) or three (2+1) supralabials; no striped pattern, brown dorsal color .....***Rena***
7.  Rostral and tip of the tail pigmented in yellow (color in life) or creamish white (preserved in alcohol); yellow (color in life) or white (preserved in alcohol) neck collar; hemipenis with double process at apex; hemipenis base with a lateral hook-like process and an enlarged flounce; basioccipital bone does not form the foramen magnum.............................................................................................***Habrophallos***
    Rostral and tip of tail same color as body; neck collar absent; hemipenis mace-shaped without process at apex; basioccipital forms the posterior–inferior margin of the foramen magnum ............................................................................... ***Trilepida***

## 3.2 | Hemipenial morphology of the Subfamily Epictinae

*Mitophis leptepileptus* (Thomas, McDiarmid & Thompson, 1985) (Figure 13c; *n* = 1). Fully everted and almost maximally expanded organ (examined in situ). Organ unilobed slightly broadened at base, slightly tapering toward ventral area of the apical disk. Basal portion and hemipenial body not ornamented; sulcus spermaticus single, counterclockwise around the organ; sulcal lips not elevated and not ornamented; apex with apical disk projecting ventrally into a process on the asulcate side of the organ; apical disk bears a central mound with shallow lateral sulcus, and with expanded and unornamented lateral borders.

*Rena dugesii* (Bocourt, 1881) (*n* = 1). Partially everted organ (apex not fully everted), examined in situ. Organ unilobed, wide at base, tapering toward the apex, inverted apex; basal portion bearing two lateral flounces; hemipenial body naked, without ornamentation, except for three lateral flounces in the proximal half of the hemipenial body; sulcus spermaticus single, crossing the organ from its base toward the apex; sulcal lips elevated and not ornamented.

*Rena dulcis* Baird & Girard, 1853 (Figure 13a; *n* = 2). Fully everted and almost maximally expanded organ (examined in situ). Organ unilobed wide at base and tapered from half hemipenial body extension until the apex; hemipenial body naked without ornamentation; basal
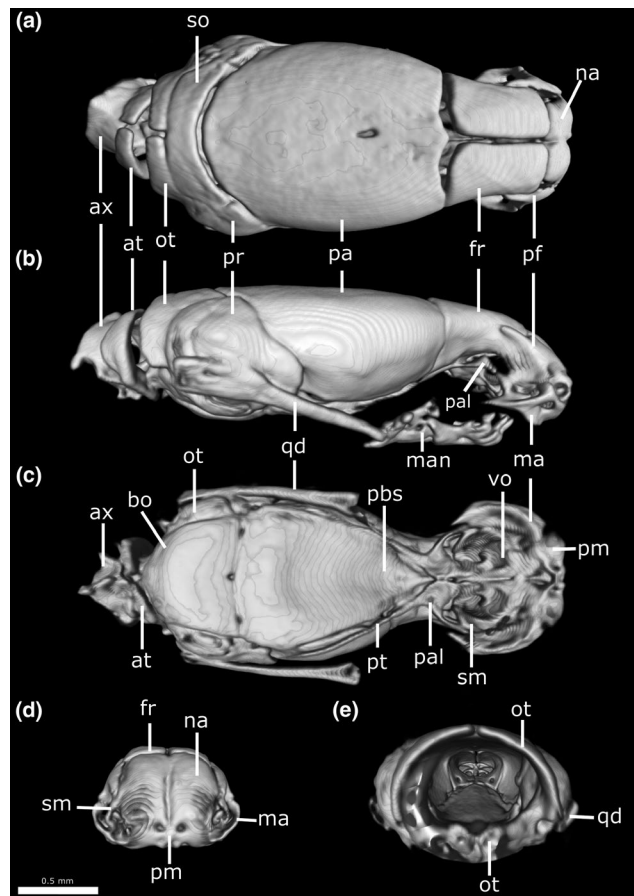


**FIGURE 6** Three-dimensional reconstruction of the skull of *Habrophallos collaris* based on μ-CT data of the paratype (MNHN 1977.49). Dorsal (a), lateral (b), ventral (c), anterior (d), and posterior (e) views. Abbreviations are as follow: at, atlas; ax, axis; bo, basioccipital; fr, frontal; ma, maxilla; man, mandible; na, nasal; ot, otooccipital; pa, parietal; pal, palatine; pbs, parabasisphenoid; pf, prefrontal; pm, premaxilla; pr, prootic; pt, pterygoid; qd, quadrate; sm, septomaxilla; so, supraoccipital; vo, vomer

portion covered by a single wide flounce on each side; sulcus spermaticus single, entering the organ at its basal surface and extending toward the apex; sulcal lips elevated and not ornamented; apex bearing an apical disk slightly lateralized toward the sulcate side, covered by small spines at disk border.

*Rena segrega* (Klauber, 1939) (Figure 13b; *n* = 1). Fully everted and almost maximally expanded organ (examined in situ). Organ unilobed, wide at base, and tapering gradually toward the apex until the region ventral to the apical disk; basal portion with two flounces on each lateral surface of the hemipenis; hemipenial body not ornamented covered by superficial folds; sulcus spermaticus single, entering the organ on its basal surface, lateralizing at half the hemipenial body extension, reaching the opposite side; sulcal lips expanded and not ornamented, extending from the basal portion toward the apex; hemipenial apex bearing an apical disk that projects proximally over the asulcate side of the hemipenis; apical disk with central mound, bearing shallow lateral sulcus and with expanded border bearing reduced spines.
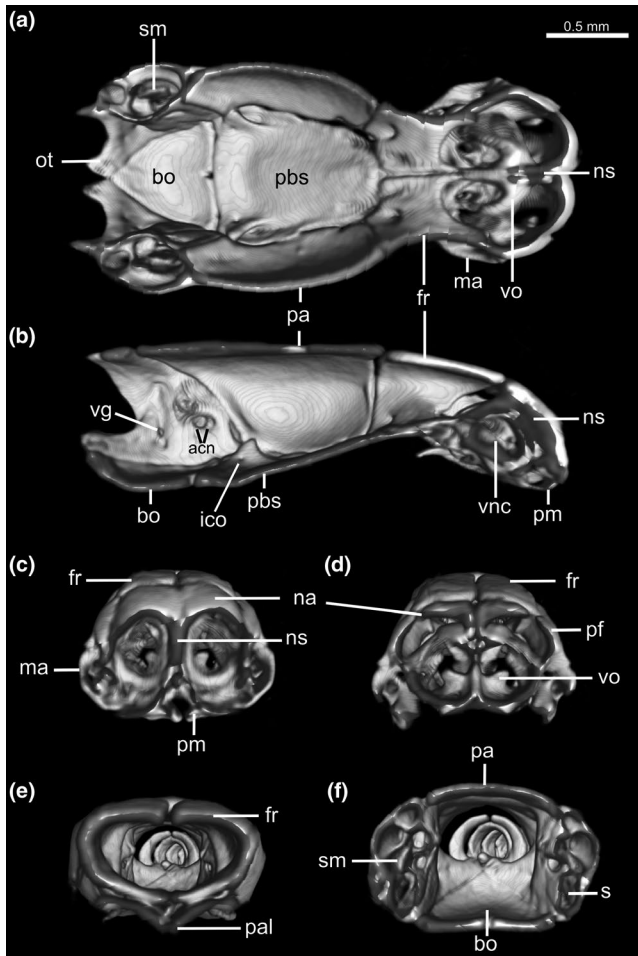
**FIGURE 7** Three-dimensional cutaway views along the frontal (a), sagittal (b), and transverse (c–f) axis of the skull of *Habrophallos collaris* based on μ-CT data of the paratype (MNHN 1977.49). Abbreviations are as follow: acn, acoustic nerve; bo, basioccipital; fr, frontal; ico, internal carotid opening; ma, maxilla; na, nasal; ns, nasal septum; ot, otooccipital; pa, parietal; pal, palatine; pbs, parabasisphenoid; pf, prefrontal; pm, premaxilla; s, stapes; sm, statolithic mass; vg, vagus nerve foramen; vnc, vomeronasal cupola; vo, vomer

*Rena unguirostris* (Boulenger, 1902) (*n* = 1). Fully everted and almost expanded organ (examined in situ). Organ unilobed, extremely dried out, wide at base, and tapered in half the apex extension; hemipenial body naked without ornamentation; sulcus spermaticus single, crossing the organ from its base toward the apex.

*Trilepida koppesi* (Amaral, 1955) (*n* = 2). Fully everted and almost expanded organ (examined in situ). Organ unilobed, mace-shaped, narrow at base, and wide at apex; hemipenial body ornamented with longitudinal flounces, two of them well developed that cover both the asulcate and sulcate side; basal portion bearing two reduced flounces; sulcus spermaticus following a straight line until the apex; sulcal lips slightly elevated and not ornamented; apex slightly concave, covered by several well-developed papillae.

*Trilepida macrolepis* (Peters, 1858) (Figure 13d; *n* = 1). Fully everted and almost maximally expanded organ (examined in situ).

Organ unilobed, long, mace-shaped, slightly wider at apex; basal portion narrow, bearing a wide flounce that extends from the asulcate side distally to the sulcate side; four additional transversal flounces are present in the hemipenial body; sulcus spermaticus single, following a straight line until the apex; sulcal lips slightly elevated; apex slightly convex, bearing a transversal flounce.

## 4 | DISCUSSION

### 4.1 | Systematics

By combining distinct lines of evidence such as phenotype (meristics, osteology, and hemipenis) and molecular data (mitochondrial and nuclear genes), we provide strong theoretical basis to justify the proposition of a new supraspecific taxon within Leptotyphlopidae. Although the proposition/erection of new genera for neotropical snakes is not uncommon, most studies are based exclusively on molecular data. Several recent papers have addressed the systematics of Scolecophidia (sensu strictu Miralles et al., 2018), expanding the knowledge on the systematics of the group in several regions of the world (e.g., Adalsteinsson et al., 2009; Vidal et al., 2010; Marin et al., 2013; Kornilios et al., 2012; Hedges, Marion, Lipp, Marin, & Vidal, 2014; Pyron & Wallach, 2014; Nagy et al., 2015, Wallach, 2016). However, most studies focus on the superfamily Typhlopoidea (e.g., Vidal et al., 2010; Marin et al., 2013a,b; Kornilios et al., 2012; Hedges et al., 2014; Pyron & Wallach, 2014; Nagy et al., 2015), compared with a few systematic studies on the family Leptotyphlopidae (i.e., Adalsteinsson et al., 2009; McCranie & Hedges, 2016; Wallach, 2016). Adalsteinsson et al. (2009) proposed a new classification for the family Leptotyphlopidae considering a phylogenetic hypothesis based on molecular data, with a few genera (e.g., *Siagonodon*, *Trilepida*, and *Tricheilostoma*) proposed with only a single terminal sampled. Additionally, the allocation of other congeners was exclusively based on similarity to groups previously proposed by Orejas-Miranda (1967) or Peters and Orejas-Miranda (1970). In this classification scheme, *Leptotyphlops collaris* was allocated to the genus *Epictia* without any justification or additional information. The diagnosis of *Epictia* (sensu Adalsteinsson et al., 2009) was based uniquely on meristics and color pattern features, most of them invariable or widely overlapping along Neotropical genera of Epictinae (e.g., *Rena* and *Trilepida*). This is an aftermath of a common pattern found in threadsnakes related to their relatively conserved external morphology (Martins et al., 2018; Passos et al., 2006, 2005; Pinto & Curcio, 2011; Pinto et al., 2015). In view of the extreme relevance of including anatomical datasets for threadsnake's systematics (present study), we reinforce the need of integration of various data sources (sensu Padial, Miralles, De la Riva, & Vences, 2010) for the classification of this group.

Our topology for the family Leptotyphlopidae is congruent with the previous phylogenetic hypotheses in recovering two major sister clades (Leptotyphlopinae and Epictinae) (Figure 11; see
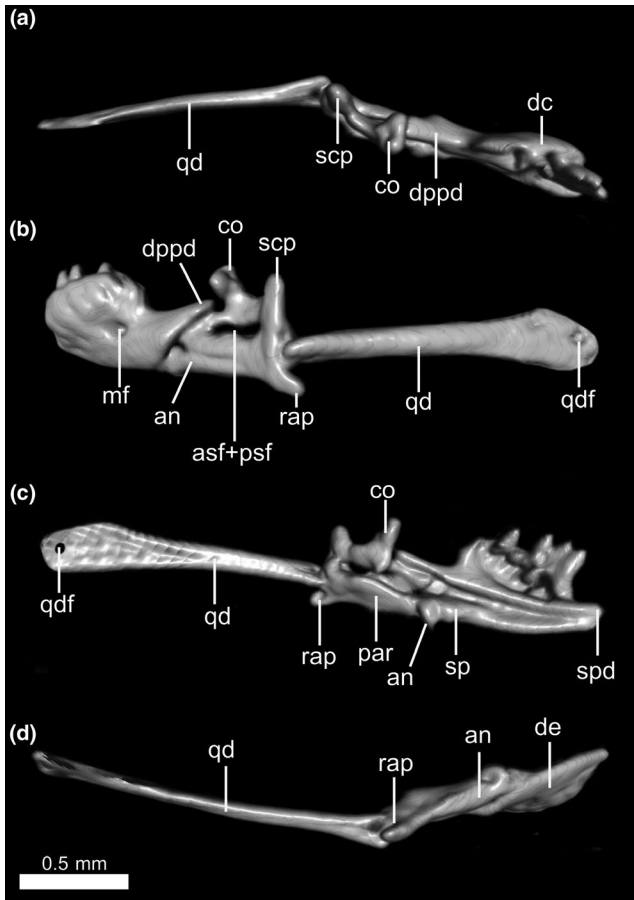
**FIGURE 8** Three-dimensional reconstruction of the suspensorium (quadrate + lower jaw) of *Habrophallos collaris* based on μ-CT data of the paratype (MNHN 1977.49). Dorsal (a), lateral (b), medial (c), and ventral (d) views. Abbreviations are as follow: an, angular; asf, anterior surangular foramen; co, coronoid; dc, dental concha; de, dentary; dppd, dorsoposterior process of dentary; mf, mental foramen; par, prearticular lamina of compound bone; psf, posterior surangular foramen; qd, quadrate; qdf, quadrate foramen; rap, retroarticular process; scp, supracotylar process of surangular; sp, splenial; spd, symphyseal process of dentary



**FIGURE 9** Three-dimensional reconstruction of the pelvic girdle of *Habrophallos collaris* based on μ-CT data of MNHN1999.8309. Lateral view of the posterior thoracolumbar + caudal area (a) and pelvic girdle digitally isolated in lateral view (b). Abbreviations are as follows: fe, femur; il, ilium; is, ischium; pu, pubis



**FIGURE 10** Sulcate (a), lateral (b), and asulcate (c) sides of the hemipenis of *Habrophallos collaris* MNHN2019.0002

Adalsteinsson et al., 2009; Vidal et al., 2010). Within Epictinae, two tribes are recovered as also seen in previous analyses (Adalsteinsson et al., 2009; Vidal et al., 2010). *Rhinoleptus* and *Tricheilostoma* are allocated within Rhinoleptini, and other Epictinae (*Epictia*, *Mitophis*, *Rena*, *Siagonodon*, *Tetracheilostoma*, and *Trilepida*) are recovered within Epictini. The monophyly of all Epictini subtribes (Epictina, Renina, and Tetracheilostomina) was also recovered, as seen in Adalsteinsson et al. (2009). However, relationships of *Siagonodon* and *Epictia* (as a reciprocal sister clade in Adalsteinsson et al., 2009) are not recovered (see Figure 1 of Vidal et al., 2010). Additionally, with the inclusion of *Habrophallos collaris* (present study), the topology resulted in a relationship of *Habrophallos* and *Siagonodon* as a sister clade of *Epictia*. Although *Habrophallos* is related to *Siagonodon* in the topology recovered, several external morphological and anatomical evidences support the recognition of this
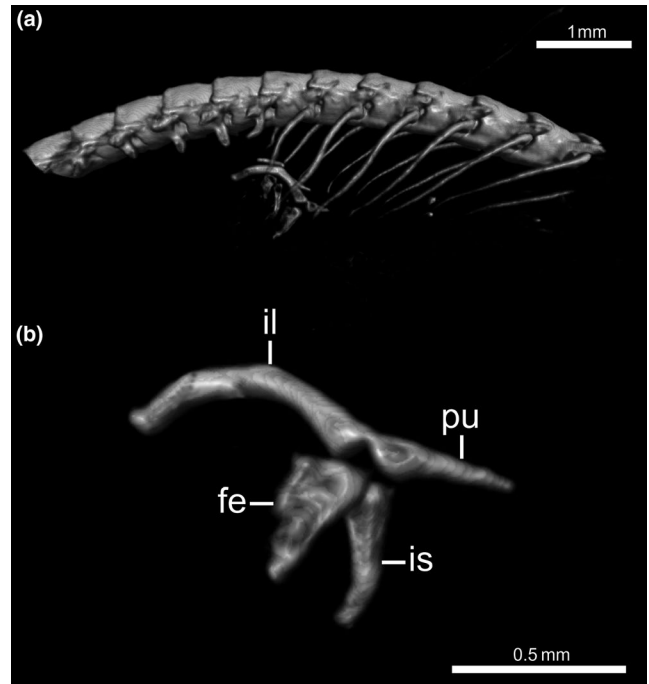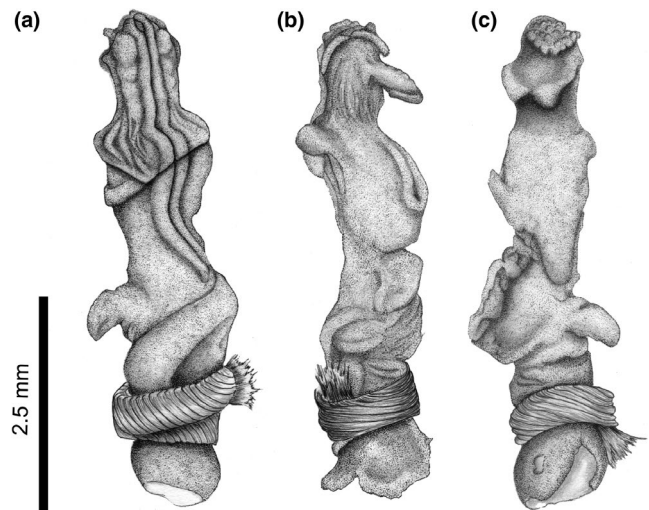
taxon as a new and distinct genus. Such proposition also preserves the diagnosis of *Siagonodon*, which is based on fairly well-established external and internal morphological characters. Finally, our topology showed that the inclusion of *Habrophallos* (previously assigned to *Epictia*) recovered a paraphyletic *Epictia*, reinforcing that the current taxonomy of threadsnakes is problematic and should be revised. *Epictia* currently represents the most speciose genus
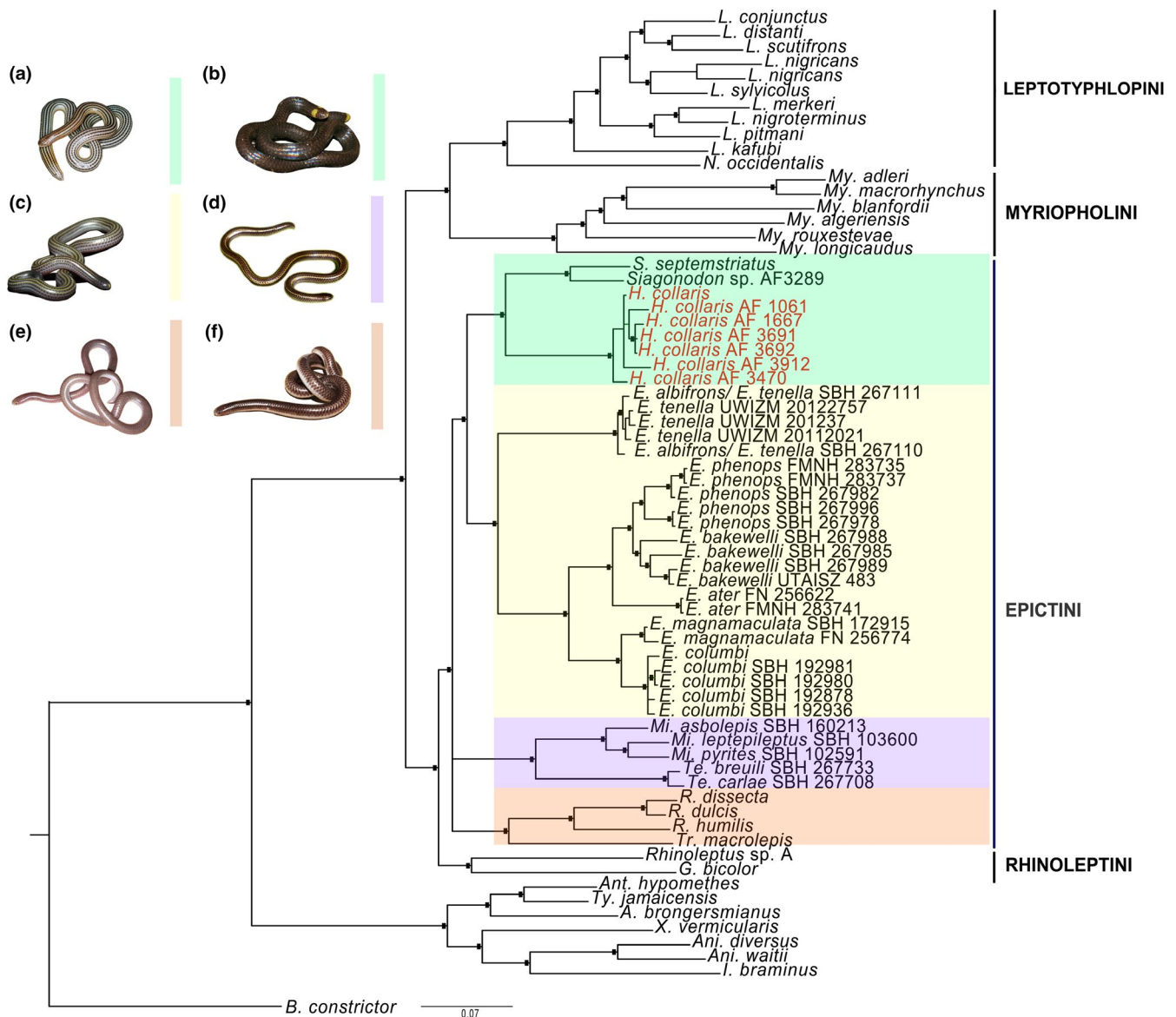
**FIGURE 11** Phylogenetic relationships of Leptotyphlopidae estimated under a Bayesian framework based on 10 molecular markers. Only posterior probabilities above 0.95 are shown for clarity. *Siagonodon septemstriatus* (a), *Habrophallos collaris* (b), *Epictia munoai* (c), *Tetracheilostoma bilineatum* (d), *Rena humilis* (e), *Trilepida brasiliensis* (f). Photos: L. Vitt (a), M. Dewynter (b), C. Rosa (c), C. Anderson, (d), S. Orlof (e), A. Cerqueira (f)

of Leptotyphlopidae, and even if recent studies have addressed their systematics based on both molecular and morphological data (e.g., McCranie & Hedges, 2016; Wallach, 2016), several taxonomic issues still remain. Additional integrative studies addressing the anatomy of the aforementioned genus might reveal new taxa yet to be described, especially for species with distribution in South America.

The description of *Habrophallos* increases to 14 the number of genera included in the family Leptotyphlopidae, ten of which pertaining to the subfamily Epictinae. *Habrophallos collaris* is presumably endemic to the Eastern Guiana Shield, occurring in both disturbed and not disturbed environments from lowlands to 800 m altitude (Hoogmoed & Lima, 2018).

## 4.2 | Comments on the hemipenial morphology of Epictinae

The hemipenial morphology has been widely applied in snake systematics (Dowling & Duellman, 1978; Zaher, 1999) mostly due to its usefulness in species delimitation (Arnold, 1986; Dowling & Savage, 1960) and distinction of cryptic species (Arnold, 1986; Eberhard, 1985, 2009; Passos, Prudente, Ramos, Caicedo-Portilla, & Lynch, 2018). Although studies on the hemipenial morphology have proven its usefulness in snake's systematics, leptoyphlopids still account for very few descriptive studies. Many of the available studies focus on New World taxa (Bailey & Carvalho, 1946; Orejas-Miranda, 1962; Peters & Orejas-Miranda, 1970; Thomas, 1965, 1975; Fabrezi et al.,
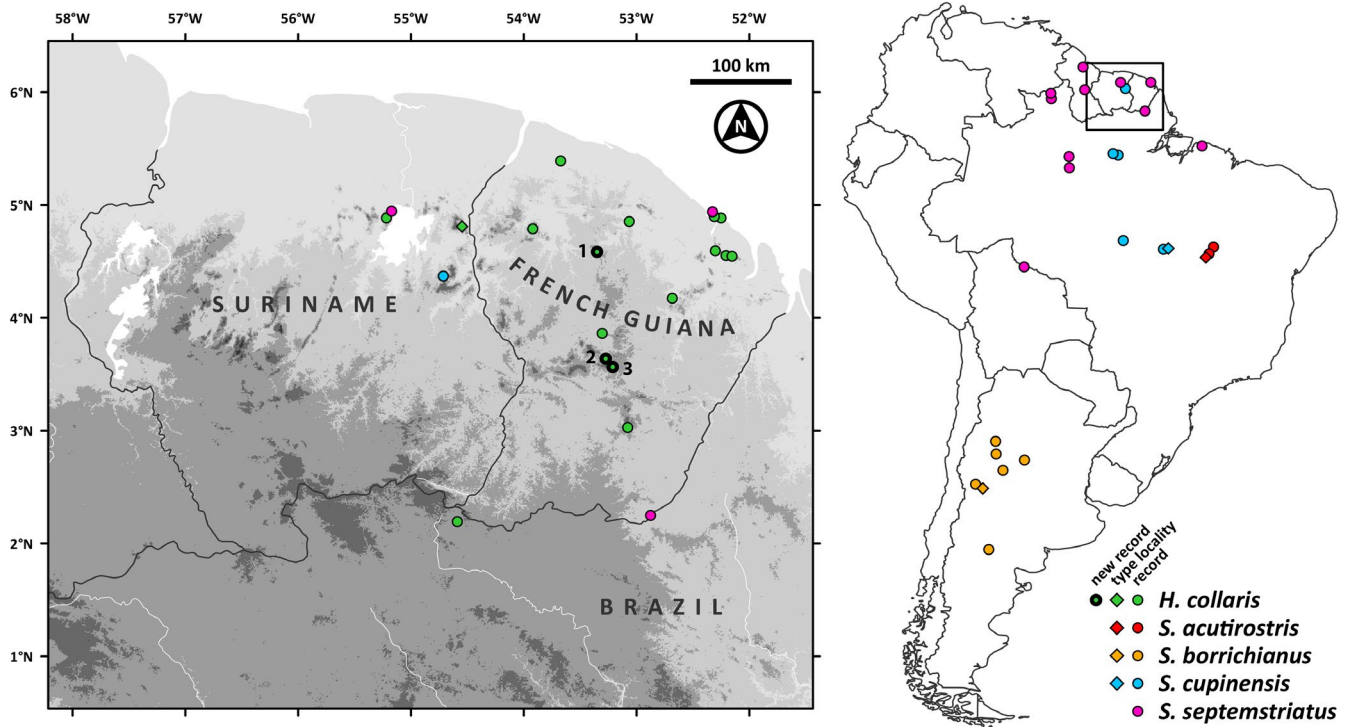
**FIGURE 12** Distribution map of *Habrophallos collaris* and the sister clade *Siagonodon*. Locality data are based on recent literature (*Siagonodon*: Francisco et al., 2018; *H. collaris*: Hoogmoed & Lima, 2018), and new records (for *H. collaris*): 1. Trinité (MNRJ 27145), 2. Nouragues Pararé (MNRJ 27144), 3. Saul Limonade (MNHN2019.0001). The type locality of *S. septemstriatus* is unknown but was designated as Suriname fide Hoogmoed (1977)

1985; Scrocchi, 1990; Cei, 1993; Savage, 2002; Passos et al., 2005, 2006; Pinto & Curcio, 2011; Pinto & Fernandes, 2012; Wallach, 2016), whereas knowledge on the hemipenial morphology of Old World leptotyphlopids remains elusive (Branch, 1986). As general rule, almost all available studies are focused on *Trilepida* spp. and *Epictia* spp., with very few studies on other leptotyphlopid genera. Prior to this study, no information on hemipenial morphology was available for *Mitophis* (provided in this study), *Tetracheilostoma*, *Tricheilostoma*, *Rhinoleptus*, and *Siagonodon* among Epictinae; and *Epacrophis*, *Myriopholis*, and *Namibiana* for Leptotyphlopinae. Difficulties on the description of leptotyphlopid hemipenis include the following: (a) too low representativeness of specimens from several species in collections to allow a moderately destructive approach, and (b) in the case of available material, the eversion process is almost impossible due to the reduced organ's size as well as its fragility (Francisco et al., 2012; present study). Therefore, most available descriptions of the hemipenial morphology are based on the organs fully or partially everted in the field. However, eversion of the leptotyphlopid hemipenis from entirely retracted organs remains a delicate task, and therefore, such procedure should be conducted with extreme caution.

We provide novel hemipenial descriptions and comparisons in this study, and a comprehensive comparison of major variation in hemipenial morphology and ornamentation for Epictinae is provided in Table 1. New information provided herein generate
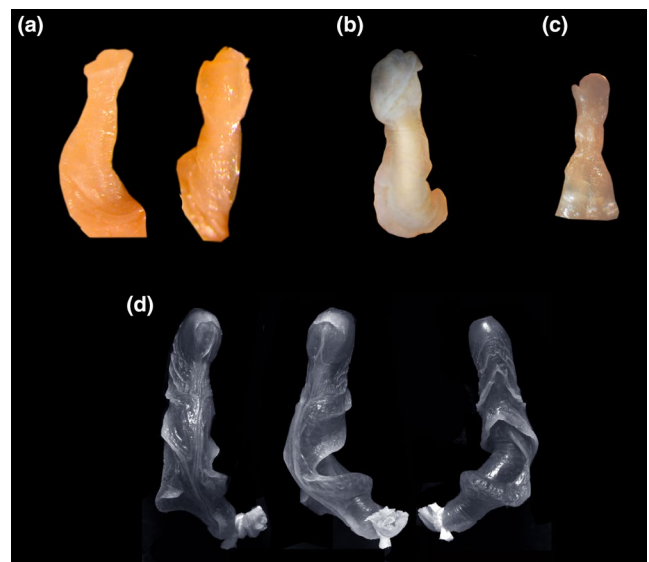


**FIGURE 13** Hemipenial morphology of some Epictinae (Leptotyphlopidae) species: *Rena dulcis* USNM 299,642 (a), *Rena segrega* LACM 2154 (b), *Mitophis leptepileptus* KU 275562 (c), and *Trilepida macrolepis* ICN 7677 (d)

relevant data on possible morphological patterns for previously proposed genera and species groups, which therefore might represent synapomorphies in more or less inclusive levels. Considering the hemipenial morphology of Epictinae, the hemipenes of *Rena*

**TABLE 1** Comparative morphology of the hemipenial structure along Epictinae (Leptotyphlopidae, Scolecophidia) based on literature and novel data provided here. "?" is used when data are unknown

| Species | Base general feature | Basal ornamentation | Body ornamentation | Apex general feature | Apex ornamentation | Source of data |
|---|---|---|---|---|---|---|
| *Epictia albipuncta* (= *Leptotyphlops albipuncta* and *E. weyrauchi* in Fabrezi, 1985) | Narrow | Not ornamented | Not ornamented | ? | ? | a |
| *Epictia ater* | Narrow | Not ornamented | Calyces | ? | Papillae | b; c |
| *Epictia australis* | Wide | Not ornamented | Not ornamented | Narrow and tapered | Not ornamented | d |
| *Epictia bakewelli* | Narrow | Not ornamented | ? | ? | ? | c |
| *Epictia magnamaculata* | Wide | Not ornamented | Calyces | Flat | Not ornamented | c; e |
| *Epictia martinezi* | Narrow | Not ornamented | Calyces | ? | ? | c |
| *Epictia munoai* | Wide | Not ornamented | Not ornamented | Narrow and tapered | Not ornamented | f |
| *Epictia tenella* | Slightly broadened | Not ornamented | Not ornamented | Apical disk with mound | Not ornamented | g; **p.s.** |
| *Epictia diaplocia* (= *Leptotyphlops tenella* in Thomas, 1975) | Wide | Not ornamented | Flounces | Apical disk with central mound | Intercepta | h |
| *Epictia pauldwyeri* | Wide | Not ornamented | Not ornamented | Narrow and tapered | Not ornamented | c |
| *Epictia phenops* | Wide | Not ornamented | Papillae | Convex | Papillae | e |
| *Epictia striatula* (=*Leptotyphlops melanotermus* in source) | Narrow | Nor ornamented | Flanges | ? | ? | e |
| *Epictia wynni* | Wide | Not ornamented | Not ornamented | Narrow and tapered | Not ornamented | c |
| **Habrophallos collaris** | Slightly broadened | Flounce and hook-like projection | Not ornamented | Apical disk double, projected proximally | Papillae | **p.s.** |
| *Mitophis lepitepileptus* | Slightly broadened | Not ornamented | Not ornamented | Apical disk projected proximally | Not ornamented | **p.s.** |
| *Rena dulcis* | Wide | Flounce | Not ornamented | Apical disk projected distally | Spines at disk border | **p.s.** |
| *Rena dugesii* | Wide | Flounce | Not ornamented | ? | ? | **p.s.** |
| *Rena segrega* | Wide | Flounces | Not ornamented | Apical disk projecting proximally | Spines at disk border | **p.s.** |
| *Rena unguirostris* | Wide | Not ornamented | Not ornamented | ? | ? | **p.s.** |
| *Trilepida brasiliensis* | Narrow | Flounces | Flounces | Concave | Papillae | i |
| *Trilepida fuliginosa* | Narrow | Not ornamented | Flounces | Concave | Calyces | j |
| *Trilepida jani* | Narrow | Flounce | Flounces | Concave | Papillae | l |
| *Trilepida macrolepis* | Narrow | Flounce | Flounces | Convex | Flounce | **p.s.** |
| *Trilepida koppesi* | Narrow | Flounces | Flounces | Concave | Papillae | **p.s.** |
| *Trilepida salgueiroi* | Narrow | Not ornamented | Flounces | Convex | Calyces | m |

*Note:* a: Fabrezi et al. (1985); b: Savage (2002); c: Wallach (2016); d: Scrocchi (1990); e: Peters and Orejas-Miranda (1970); f: Orejas-Miranda (1962); g: Bailey and Carvalho (1946); h: Thomas (1975); i: Pinto and Curcio (2011); j: Passos et al. (2006); l: Pinto and Fernandes (2012); m: Passos et al. (2005); p.s.: present study
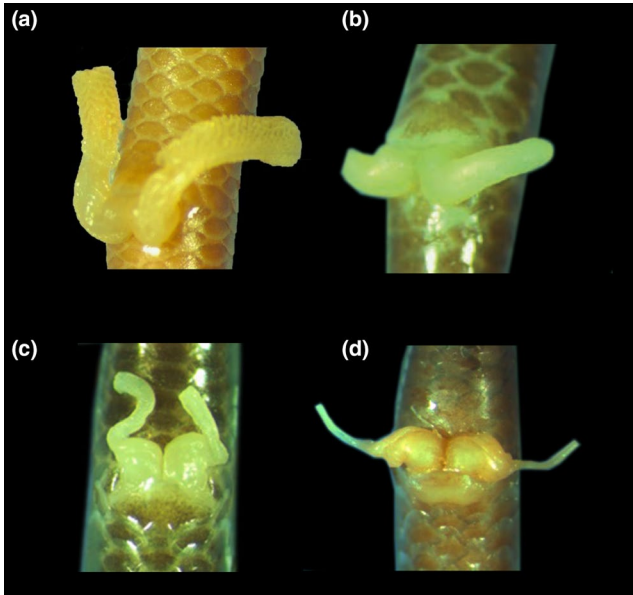
**FIGURE 14** Hemipenial morphology of *Epictia* spp., showing the impressive variation in the genus. *Epictia ater* KU 174119 (a), *E. magnamaculata* LACM 127623 (b), *E. wynni* TCWC 45530 (c), and *E. pauldwyeri* KU 125032 (d). Photos by Van Wallach

spp. (*R. dulcis*, *R. dugesii*, *R. segrega*, and *R. unguirostris*) and *Mitophis leptepileptus* exhibit a wide basal portion, tapering toward the apical portion, bearing an apical disk and lacking ornamentation along the hemipenial body. The general pattern found in *Rena* is distinct by the presence of a hemipenial body with same width as the basal portion, bearing flounces and with an apex bearing a central mound ornamented with papillae (Passos et al., 2005, 2006; Pinto & Curcio, 2011; Pinto & Fernandes, 2012; present study). Passos et al. (2006) previously suggested the general hemipenial morphology and ornamentation of Renina (*Trilepida* and *Rena*) were potential synapomorphies for the *Leptotyphlops dulcis* species group (sensu Orejas-Miranda, 1970 = almost all species currently allocated in the genus *Trilepida*). The analysis of additional species of Renina reinforces this assumption in such a way that the general morphology and ornamentation of both genera are distinct and therefore should be used as relevant sources of character for the systematics of threadsnakes (e.g., Passos et al., 2005, 2006; Pinto & Fernandes, 2012; present study).

The hemipenial morphology of *Epictia* spp. is highly variable among its congeners (Figures 10, 13, and 14; Table 1), such as: unornamented hemipenial bodies, except for the presence of vertical flounces along its extension, and the presence of an apical disk in *E. albipuncta* (Burmeister, 1861) (Fabrezi et al., 1985); hemipenial body ornamented with a series of papillae and calyces, slightly expanding toward distal tip (Savage, 2002; Wallach, 2016), but none of them bearing an apical disk; and hemipenial body and medial regions expanded, distinct by the presence of a constriction followed by a tapered and long apical region in *E. australis* (Freiberg & Orejas-Miranda, 1968) and *E. munoai* (Orejas-Miranda, 1961;

Orejas-Miranda, 1962; Scrocchi, 1990). On the other hand, the hemipenial morphology can provide solid evidence for the recognition of cryptic species of the genus *Epictia*. For example, there is an evident difference between the hemipenial morphology of *E. tenella* (Klauber, 1939) from Bailey and Carvalho (1946) with respect to the specimen from Peru described by Thomas (1975). According to Thomas (1975), the hemipenis of *E. tenella* exhibits a narrow base, expanding distally, with the presence of an apical disk with a central mound. This projection is confluent with the *sulcus spermaticus*, which enters the central region by crossing a rim consisting of two concentric fleshy walls interconnected by about 13 evenly spaced septa. The hemipenial morphology observed herein of *E. tenella* is similar to that described by Bailey and Carvalho (1946), with a narrow base and body without ornamentation. Differences between the hemipenial morphology of the specimens examined by Thomas (1975) from the specimens assessed by Bailey and Carvalho (1946) reinforce the need of further studies on the *E. tenella* population in Peru. According to Franco and Pinto (2009), *E. tenella* should be limited to populations of the east Amazon and, therefore, the specimens examined by Thomas (1975) possibly represent a distinct taxon, and *Epictia diaplocia* (Orejas-Miranda, 1969) may be a name applicable to this population (R.R. Pinto, unpubl. data). Furthermore, general similarities in the hemipenial morphology of *Mitophis* and *Rena* must be investigated with major details, considering the isolation of Caribbean islands from the North and Central American mainland. In case, such similarities represent true synapomorphies (=secondary synapomorphies), and they might favor an ancient vicariant scenario from the Antilles conformation contra the neo-dispersalist wave in biogeography (see Ebach, 2017).

Finally, the hemipenial morphology of *Habrophallos* is unique among Leptotyphlopidae with the combination of a wide basal portion bearing a hook-like process at one side and a large flounce at the other, and also by the presence of paired projections on the apex. As far as we know, the possession of such characters might represent putative autapomorphies of *Habrophallos collaris*. Unfortunately, we were not able to evert the hemipenis of *Siagonodon* in order to provide detailed comparisons with *H. collaris*, a task that should be addressed in the near future. In fact, with the relatively conservative external morphology of threadsnakes, data on hemipenial morphology (and also other phenotype internal systems) are more important than ever to clarify the systematic position of supraspecific taxa in the family Leptotyphlopidae.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Table S1.** Primer sequences, amplicon lengths and length of the final alignments.

**Alignment S1.** Final alignments for each gene 12S, Phe, Val, 16S, cytb, AMEL, BNDF, C-mos, NT3, RAG1, respectively.

## APPENDIX 1

### Material examined

\* Hemipenis and \*\* Skull

*Epictia ater* (*n* = 8): **EL SALVADOR**: SAN MIGUEL: KU 183846\*\*; **NICARAGUA**: CHINANDEGA: *Volcan Chongo*: KU 194336, 200596; ESTELLI: KU

174119, 174120, 174121, 174134, 174135.

*Epictia goudotii* (*n* = 1). **VENEZUELA**: ARAGUA: *Girardot: Cuyagua*: USNM 258148\*\*.

*Epictia magnamaculata* (*n* = 1). **HONDURAS**: ISLAS DE LA BAHÍA: *Isla de Utila*: USNM 54760.

*Epictia munoai* (*n* = 1).**URUGUAY**: TACUAREMBO: *Tambores: Pozo Hondo:* USNM 163506.

*Epictia phenops* (*n* = 4). **MEXICO**: YUCATÁN: FMNH 20606\*\*, 36345\*\*, OAXACA: FMNH 111477\*\*, 111481; QUINTANA ROO: *Isla Cozumel*: LACM 127814\*\*.

*Epictia rufidorsa* (*n* = 1). **PERU**: LIMA: *Rimac Valley*: USNM 49993.

*Epictia tenella* (*n* = 13). **BRAZIL**: AMAZONAS: *Urucá*: MNRJ 18831; PARÁ: *Oriximiná: Porto Trombetas*: MNRJ 16827\*\*,16828\*\*; **TRINIDAD AND TOBAGO**: TRINIDAD: *Arima*: USNM 536525\*\*; *Guayagueyare*: MCZ 60801; *Mathura*: MCZ 96538, 96539; *Mazanilla Beach*: MCZ160087\*\*; *Parrylands*: MCZ160088;*Port of Spain City Corporation*: MCZ 79785, 79786; *San Juan-Laventille Regional Corporation*: MCZ 28208; *Trinity Hills*: MCZ 38660.

*Epictia tricolor* (*n* = 1). **PERU**: ANCASH: *Huyalas: Yunca Pampa*: USNM 195853.

*Habrophallos collaris* (*n* = 9). **FRENCH GUIANA**. *Itoupe*: MNHN2019.0002 -3; *No locality*: MNHN 1977.49\*\*, MNHN 1996.4580\*\*; *Nouragues Pararé*:MNRJ27144; *Saül*: MNHN 1999.8309\*\*; *Saul Limonade*: MNHN2019.0001; *Trinité*: MNRJ 27145; **SURINAME**: *Brownsberg*: AF 3912.

*Mitophis asbolepis* (*n* = 1). **DOMINICAN REPUBLIC**: BARAHONA: *Loma del Aguacate*: USNM 236660.

*Mitophis calypso* (*n* = 2). **DOMINICAN REPUBLIC**: SAMANA: *Las Galeras*: USNM 236658, 236659.

*Mitophis leptepileptus* (*n* = 8). **HAITI**: SUD-EST: *Soliette*: KU 275542, 275543, 275548, 275549, 275562\*,\*\*, 275567, USNM 576217\*\*; *Fond Verettes*: USNM 236661.

*Mitophis pyrites* (*n* = 2). **DOMINICAN REPUBLIC**: PERDENALES: *Perdernales*: MCZ 77239, USNM 152452.

*Rena dulcis* (*n* = 23) **UNITED STATES OF AMERICA**: FLORIDA: USNM 15466; OKLAHOMA: *Comanche*: OMNH 35564\*\*, 35580\*\*; *Marshall*: USNM 258213, 258214, 258217, 258218; *Seminole*: USNM 198022, 198023, USNM 258197; TEXAS: *Bell*: USNM 198036; *Frio*: LACM 162021\*\*; *Hays*: AMNH 160152\*\*, LACM 162022\*\*; *Hidalgo*: USNM 299630, 299642\*; *McLennan Co*: FMNH 40957\*\*, USNM 198037, 198042, 258186, 258188; *Pecos*: USNM 7296; *Travis Austin*: USNM 161288.

*Rena humilis* (*n* = 42): **MEXICO**: BAJA CALIFORNIA: AMNH 5576; JALISCO: AMNH 94866; NAYARIT: AMNH 75587, 87584, 96616, USNM 240693, 240879; SINALOA: AMNH 90761, 90762; SONORA: *Navojoa*: 141978, *Bahia Kino*: USNM 214128; without locality: AMNH 66170\*\*, USNM 26140; **UNITED STATES OF AMERICA**: ARIZONA: *Graham*: AMNH 63458; Maricopa: USNM 246639; *Pima*: AMNH 73716\*\*; *Yuma*: USNM 26289\*\*; CALIFORNIA: *Imperial*: USNM 139916\*\*, 139917\*\*, 222794\*\*; *Riverside*: AMNH 84309; *San Bernardino*: AMNH 131165; *San Diego*: FMNH 77599\*\*, SDNHM 2956, 9347, 24273, 24407, 24408, 33950\*\*, 34302\*\*, 42772, 61052, 61055, 61057, 61059, 61060, 61062, 61068, 61088, USNM 193023, 196570, UIMNH 84591.

*Rena maxima* (*n* = 1). **MEXICO**: GUERRERO: *Chilpancinga*: MCZ 33606\*\*.

*Rena myopica* (*n* = 3). **UNITED STATES OF AMERICA**: NEW MEXICO: *Eddy: Malaga*: USNM 125131\*\*; **MEXICO**: SAN LUIS POTOSÍ: AMNH 172551\*\*; TAMAULIPAS: *Gomez Farias*: 248499\*\*.

*Rena segrega* (*n* = 1). **UNITED STATES OF AMERICA**: NEW MEXICO: *Doña Ana*: LACM 2154\*.

*Rena segrega* (*n* = 12). **MEXICO**: COAHUILA: *Torreon*: USNM 193593\*\*; **UNITED STATES OF AMERICA**: ARIZONA: without locality: AMNH 43439; *Pima*: USNM 16952; NOVO MÉXICO: *Doña Ana*: AMNH 172545,172546, LACM 2154, 134007\*\*, 134009\*\*; TEXAS: *Val Verde*: AMNH 172548; *Brewster*: USNM 103670; without locality: AMNH 112249.

*Rena unguirostris* (*n* = 2). **ARGENTINA**: *Poman Puesto Rio Blanco*: FML 1399\*; TINOGASTA: *Palo Blanco*: FML 1773\*\*.

*Siagonodon cupinensis* (*n* = 1). **BRAZIL**: MATO GROSSO: *Barra do Tapirapés: Guarantã do Norte*: UFMT 5627\*\*.

*Siagonodon septemstriatus* (*n* = 1). **BRAZIL**: AMAZONAS: *Presidente Figueiredo*: IBSP 51897\*\*.

*Siagonodon* sp. (*n* = 1). **FRENCH GUIANA:** MITARAKA (AF 3299).

*Tetracheilostoma billineatum* (n =4) **MARTINIQUE**: LE LAMENTIN: without locality: USNM 564808\*\*, 564809\*; **SAINT LUCIA**: SAINT LUCIA: *Anse-La- Raye*: USNM 222954; without locality: MCZ 10693.

*Tetracheilostoma breuili* (n = 8). **SAINT LUCIA**: ILHAS MARIA: *Ilha Maria Major*: USNM 564810–17.

*Tetracheilostoma carlae* (*n* = 2). **BARBADOS**: SAINT JOSEPH: *Bonwell*: USNM 564818–19.

*Tricheilostoma bicolor* (*n* = 2). **GHANA**: SOMANYA: *Krobo*: MCZ 55388, MCZ 55383.

*Tricheilostoma sundewalli* (*n* = 1). **GHANA**: SOMANYA: *Krobo*: MCZ 55396\*\*.

*Trilepida brasiliensis* (*n* = 7). **BRAZIL**: MATO GROSSO DO SUL: *Corumbá*: UFMT 683, 1159\*\*, 1160, 1162, 1163\*\*, 1169; *Rosário d'Oeste*: MNRJ 24334\*\*.

*Trilepida dimidiata* (*n* = 3). **BRAZIL**: RORAIMA: *Boa Vista*: MZUSP 10090\*\*, 10120\*\*; **GUYANA**: LETHEM: *Karanamboo Ranch*: USNM 566291.

*Trilepida fuliginosa* (*n* = 6). **BRAZIL**: GOIÁS: *Colinas do Sul*: MNRJ 19223; *Luziânia*: CHUNB 40847\*\*, 408486; *Minaçú*: MZUSP 11019; Ouvidor: MNRJ 19221; MINAS GERAIS: *Unaí*:

MNRJ 24400.

*Trilepida jani* (n = 2). **BRAZIL:** MINAS GERAIS: *Ouro Preto*: LZV 813S\*\*; *Ouro Branco*: 778S1; without locality: MNRJ 16990\*.

*Trilepida joshuai* (*n* = 1). **COLOMBIA:** ANTIOQUIA: *Jericó*: IBSP 8919\*\*.

*Trilepida koppesi* (*n* = 6). **BRAZIL:** GOIÁS: *Caldas Novas*: MZUSP 11111\*; *Aporé*: MNRJ 24715\*\*, 24716\*\*; *Luiziânia*: CHUNB 40788\*\*; *Mineiros*: CHUNB 25714\*\*; TOCATINS: *Porto Alegre do Tocantins*: CHUNB 38928\*.

*Trilepida macrolepis* (*n* = 7). **BRAZIL**: PARÁ: *Paraupebas*: Floresta Nacional de Carajás: MPEG 23017\*\*; **COLOMBIA**: VALE DEL CAUCA: *Buenaventura*: USNM 154031, 267261; CÓRDOBA: *Pueblo Nuevo*: ICN 7677\*; **ECUADOR**: ESMERALDAS: *Durango*: QCAZ 12494\*\*; **VENEZUELA**: CARABOBOS: *Caracas*: USNM 62205, 107891.

*Trilepida salgueiroi* (*n* = 1). **BRAZIL:** BAHIA: *São José do Macuco (currently São José da Vitória)*: MZUSP 9098. ESPÍRITO SANTO: *Governador Lindemberg*: MNRJ 12132, *Itá (currently Baixo Guandu)* IB 8876, holotype; *Aracruz*: MNRJ 4856; *Campinho* (MNRJ 1925); *Governador Lindemberg* (MNRJ 12131-12132); *Linhares, Goytacazes* (MNRJ 1926); *Linhares, Sooretama* (MZUSP 2463). MINAS GERAIS: *Aimorés* (MCNR 1468\*\*-1469, MNRJ 12239), *Muriaé*: MZUFV 1519\*\*; *Recreio* (MNRJ 7856). RIO DE JANEIRO: *Cambuci*: MNRJ 14487\*\*; *Itaipu, Niterói*: MNRJ 13124\*\*,15422\*\*.

*Trilepida pastusa* (*n* = 1). **ECUADOR:** CARCHI: *Tulcán*: QCAZ 5778\*\*.

**APPENDIX 2**

**Vouchers, species, and GenBank accession numbers of samples used in molecular analyses. See Material and Methods sections for museum acronyms.**

| Taxons | SBH | Voucher | Mitochondrial | | | |
| --- | --- | --- | --- | --- | --- | --- |
| | | | Phe | 12S | Val | 16S |
| *Epictia* | | | | | | |
| *E. albifrons* | 267110 | ROM 20503 | GQ469223 | GQ469223 | GQ469223 | GQ469223 |
| *E. albifrons* | 267111 | ROM 22487 | GQ469224 | GQ469224 | GQ469224 | GQ469224 |
| *E. ater* | | FMNH 283741 | — | KP171710 | — | |
| *E. ater* | | FN 256622 | — | KP171711 | — | |
| *E. bakewelli* | | UTAISZ 483 | — | KP171712 | — | |
| *E. collaris* | | | — | — | KR815892 | KR815892 |
| *E. columbi* | | | | | | |
| *E. columbi* | 192878 | USNM 576215 | GQ469212 | GQ469212 | GQ469212 | GQ469212 |
| *E. columbi* | 192936 | | GQ469211 | GQ469211 | GQ469211 | GQ469211 |
| *E. columbi* | 192980 | | GQ469214 | GQ469214 | GQ469214 | GQ469214 |
| *E. columbi* | 192981 | | GQ469215 | GQ469215 | GQ469215 | GQ469215 |
| *E. goudotii* | 267978 | UTA R-42208 | — | GQ469218 | GQ469218 | GQ469218 |
| *E. goudotii* | 267982 | UTA R-52658 | — | GQ469219 | GQ469219 | GQ469219 |
| *E. goudotii* | 267985 | UTA R-54554 | GQ469220 | GQ469220 | GQ469220 | GQ469220 |
| *E. goudotii* | 267988 | UTA R-57498 | GQ469221 | GQ469221 | GQ469221 | GQ469221 |
| *E. goudotii* | 267989 | UTA R-53657 | GQ469217 | GQ469217 | GQ469217 | GQ469217 |
| *E. goudotii* | 267996 | ENEPI 6752 | GQ469222 | GQ469222 | GQ469222 | GQ469222 |
| *E. magnamaculata* | | FN 256774 | — | KP171714 | — | |
| *E. magnamaculata* | 172915 | | GQ469216 | GQ469216 | GQ469216 | GQ469216 |
| *E. phenops* | | FMNH 283737 | — | KP171715 | — | |
| *E. phenops* | | FMNH 283735 | — | KP171716 | — | |
| *E. tenella* | | UWIZM.2011.20.21 | — | KX446890 | — | KX446893 |
| *E. tenella* | | UWIZM.2012.27.57 | — | KX446891 | — | KX446894 |
| *Habrophallos* | | | | | | |
| *H. collaris* | | MNRJ 27144 | — | MK734164 | — | MK736932 |
| *H. collaris* | | MNRJ 27145 | —– | MK734167 | — | MK736935 |
| *H. collaris* | | MNHN2019.0001 | — | MK734165 | — | MK736933 |
| *H. collaris* | | MNHN2019.0002 | — | — | — | MK736936 |
| *H. collaris* | | MNHN2019.0003 | — | MK734168 | — | MK736937 |
| *H. collaris* | | AF 3912 | — | MK734169 | — | MK736938 |
| *Leptotyplops* | | | | | | |
| *L. merkeri* | 268226 | PEM R17862 | GQ469260 | GQ469260 | GQ469260 | GQ469260 |
| *L. nigricans* | 268047 | PEM R 12556 | — | GQ469235 | GQ469235 | GQ469235 |
| *L. nigroterminus* | 268067 | PEM R17346 | GQ469257 | GQ469257 | GQ469257 | GQ469257 |
| *L. pitmani* | 268223 | PEM R5577 | GQ469255 | GQ469255 | GQ469255 | GQ469255 |
| *L. scutifrons* | 268045 | MCZ R184538 | GQ469270 | GQ469270 | GQ469270 | GQ469270 |
| *L. sylvicolus* | 268079 | PEM R17343b | GQ469272 | GQ469272 | GQ469272 | GQ469272 |
| *Mitophis* | | | | | | |
| *M. asbolepis* | 160213 | | GQ469210 | GQ469210 | GQ469210 | GQ469210 |
| *M. leptepileptus* | 103600 | USNM 564820 | GQ469197 | GQ469197 | GQ469197 | GQ469197 |
| *M. pyrites* | 102591 | | GQ469194 | GQ469194 | GQ469194 | GQ469194 |

| cytb | Nuclear | | | | | References |
|---|---|---|---|---|---|---|
| cytb | RAG1 | AMEL | C-mos | BDNF | NT3 | References |
| GQ469096 | — | — | — | — | — | a |
| GQ469097 | GQ469043 | GQ468997 | GQ469065 | GQ469180 | GQ469020 | a |
| KP171718 | — | — | — | — | — | b |
| — | — | — | — | — | — | b |
| — | — | — | — | — | — | b |
| — | — | — | — | — | — | c |
| AF544671 | AY487383 | FJ434036 | AF544718 | FJ433957 | FJ434063 | d |
| GQ469089 | — | — | — | — | — | a |
| GQ469090 | GQ469041 | GQ468995 | GQ469063 | GQ469178 | GQ469018 | a |
| GQ469092 | — | — | — | — | — | a |
| GQ469093 | — | — | — | — | — | a |
| GQ469117 | — | — | — | — | — | a |
| GQ469119 | — | — | — | — | — | a |
| GQ469121 | — | — | — | — | — | a |
| GQ469122 | — | — | — | — | — | a |
| GQ469123 | — | — | — | — | — | a |
| GQ469124 | — | — | — | — | — | a |
| KP171719 | — | — | — | — | — | b |
| GQ469094 | — | — | — | — | — | a |
| KP171720 | — | — | — | — | — | b |
| KP171721 | — | — | — | — | — | b |
| KX446896 | — | — | — | — | — | e |
| KX446897 | — | — | — | — | — | e |
| | | | | | | |
| MK764736 | — | — | MK764740 | MK764729 | MK764746 | p.s. |
| — | — | — | MK764742 | MK764732 | MK764749 | p.s. |
| — | — | — | MK764741 | MK764 | MK764747 | p.s. |
| MK764737 | — | — | MK764743 | MK764733 | MK764750 | p.s. |
| MK764738 | — | — | MK764744 | MK764734 | MK764751 | p.s. |
| MK764739 | — | — | MK764745 | MK764735 | MK764752 | p.s. |
| | | | | | | |
| GQ469164 | — | — | — | — | — | a |
| GQ469128 | — | — | — | — | — | a |
| GQ469140 | GQ469050 | GQ469005 | GQ469073 | GQ469188 | GQ469027 | a |
| GQ469163 | — | — | — | — | — | a |
| GQ469127 | — | — | — | — | — | a |
| GQ469150 | GQ469054 | GQ469009 | GQ469077 | GQ469192 | GQ469031 | a |
| | | | | | | |
| GQ469088 | GQ469037 | GQ468991 | GQ469059 | GQ469174 | GQ469015 | a |
| GQ469081 | GQ469047 | GQ469002 | GQ469070 | GQ469185 | GQ469024 | a |
| GQ469079 | GQ469033 | GQ468987 | GQ469056 | GQ469170 | GQ469011 | a |

(Continues)

**APPENDIX 2** (Continued)

| Taxons | SBH | Voucher | Mitochondrial | | | |
|---|---|---|---|---|---|---|
| | | | Phe | 12S | Val | 16S |
| M. adleri | 268179 | TR 7750 | — | GQ469246 | GQ469246 | GQ469246 |
| Myriopholis | | | | | | |
| M. algeriensis | 268122 | TR 115 | GQ469243 | GQ469243 | GQ469243 | GQ469243 |
| M. blanfordii | 267164 | MVZ 236621 | GQ469241 | GQ469241 | GQ469241 | GQ469241 |
| M. rouxestevae | 268180 | TR 7760 | — | GQ469247 | GQ469247 | GQ469247 |
| M. longicaudus | 268050 | MCZ R184447 | — | GQ469244 | GQ469244 | GQ469244 |
| M. macrorhynchus | 267894 | LSUMZ H-20102 | GQ469245 | GQ469245 | GQ469245 | GQ469245 |
| Namibiana | | | | | | |
| N. occidentalis | 268052 | PEM R11915 | GQ469251 | GQ469251 | GQ469251 | GQ469251 |
| Rena | | | | | | |
| R. dissecta | 267891 | LSUMZ H-9314 | GQ469230 | GQ469230 | GQ469230 | GQ469230 |
| R. dulcis | 267165 | MVZ 230602 | GQ469229 | GQ469229 | GQ469229 | GQ469229 |
| R. humilis | 267112 | ROM 45259 + SDSU 3939 + CAS:HERP:190589 | GQ469228 | GQ469228 | GQ469228 | GQ469228 |
| Rhinoleptus spA | 2010 | TR 7757 | — | GQ469242 | GQ469242 | GQ469242 |
| Siagonodon | | | | | | |
| S. septemstriatus | 267895 | LSUMZ H-12312 | GQ469232 | GQ469232 | GQ469232 | GQ469232 |
| Siagonodon sp. | | AF 3299 | MK734166 | — | — | MK736934 |
| Tetracheilostoma | | | | | | |
| T. breuili | 267733 | USNM 564812 | GQ469205 | GQ469205 | GQ469205 | GQ469205 |
| T. carlae | 267708 | USNM 564819 | GQ469204 | GQ469204 | GQ469204 | GQ469204 |
| Trilepida | | | | | | |
| T. macrolepis | 267113 | ROM 28367 | GQ469225 | GQ469225 | GQ469225 | GQ469225 |
| Outgroup | | | | | | |
| Amerotyphlops | | | | | | |
| A. brongersmianus | 267135 | AMNH-R140972 | — | KF993138 | — | KR815889 |
| Anilios | | | | | | |
| A. diversus | 268481 | WAM-R166605 + WAM-R112027 | — | KF992980 | — | KF993067 |
| A. waitii | 268472 | WAM-R166874 + WAM-R165022 | — | KF993035 | — | KF993125 |
| Antillotyphlops | | | | | | |
| A. hypomethes | 172182 | USNM 300584 + USNM 300581 | — | AF366717 | — | AF366786 |
| Boa constrictor | | | — | KF576870 | — | KF576910 |
| Indotyplops | | | | | | |
| I. braminus | 268766 | NV + ZCMV 2290 | — | KT316430 | — | KJ783475 |
| Typhlops | | | | | | |
| T. jamaicensis | 172445 + 172446 | USNM 328408 (SBH 172446) | — | KF993158 | — | KF993206 |
| Xerotyphlops | | | | | | |
| X. vermicularis | | CAS 228715-x | — | JQ045196 | — | — |

a: Adalsteinsson et al. (2009); b: McCranie & Hedges (2016); c: Simões et al. (2015); d: Vidal, Rage, Couloux, and Hedges (1946); e: Murphy, Rutherford, and Jowers (2009); f: Slowinski and Lawnson (1997); g: Wiens et al. (2008); h: Vidal et al. (2010); i: Hedges et al. (2014); j: Simoes et al. (1974); l: Nagy et al. (2015); m: Hedges et al. (2001); n: Suarez-Atilano, Burnrink, and Vazquez-Dominguez (1986); o: Vidal and Hedges (2003); p: Kornilios et al. (2012); p.s. – present study.

| cytb | Nuclear | | | | | References |
|------|---------|------|-------|------|-----|------------|
| | RAG1 | AMEL | C-mos | BDNF | NT3 | |
| GQ469155 | GQ469035 | GQ468989 | GQ469058 | GQ469172 | GQ469013 | a |
| | | | | | | |
| GQ469151 | GQ469036 | GQ468990 | — | GQ469173 | GQ469014 | a |
| GQ469104 | GQ469039 | GQ468993 | GQ469061 | GQ469176 | — | a |
| GQ469156 | GQ469052 | GQ469007 | GQ469075 | GQ469190 | GQ469029 | a |
| GQ469131 | GQ469048 | GQ469003 | GQ469071 | GQ469186 | GQ469025 | a |
| GQ469115 | GQ469049 | GQ469004 | GQ469072 | GQ469187 | GQ469026 | a |
| | | | | | | |
| GQ469133 | GQ469051 | GQ469006 | GQ469074 | GQ469189 | GQ469028 | a |
| | | | | | | |
| GQ469112 | — | — | — | — | — | a |
| GQ469105 | GQ469045 | GQ468999 | GQ469067 | GQ469182 | GQ469022 | a |
| GQ469098 | — | — | AY099979 | EU402648 | — | a; f; g |
| | | | | | | |
| GQ469158 | GQ469055 | — | GQ469078 | GQ469193 | GQ469032 | a |
| | | | | | | |
| GQ469116 | GQ469053 | GQ469008 | GQ469076 | GQ469191 | GQ469030 | a |
| — | — | — | — | MK764731 | MK764748 | p.s. |
| | | | | | | |
| GQ469108 | — | — | — | — | — | a |
| GQ469107 | — | — | — | — | — | a |
| | | | | | | |
| GQ469099 | — | — | — | — | — | a |
| | | | | | | |
| | | | | | | |
| KF993239 | GU902640 | GU902313 | — | GU902390 | GU902563 | h; i; j |
| | | | | | | |
| KT316487 | GU902661 | GU902333 | — | GU902411 | GU902582 | h; i; l |
| | | | | | | |
| KT316499 | GU902652 | GU902324 | — | GU902402 | GU902573 | h; i; l |
| | | | | | | |
| KF993258 | GU902679 | GU902351 | — | GU902431 | GU902601 | h; i; m |
| | | | | | | |
| KJ621420 | — | FJ434054 | AF471115 | KF576914 | — | h; i; m; n |
| | | | | | | |
| GQ469118 | GU902633 | GU902306 | — | GU902383 | GU902556 | h; l; n |
| | | | | | | |
| KF993158 | AY487387 | GU902352 | AF544733 | GU902432 | GU902602 | h; i; m; o |
| | | | | | | |
| KT316552 | GU902647 | GU902320 | — | GU902397 | GU902569 | h; l; p |