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A new species of cat-eyed snake (Serpentes: Dipsadinae: Leptodeirini) from the Andes of southern Ecuador

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Abstract

Leptodeira is one of the most widespread and taxonomically problematic snake taxa in the Americas. Here we describe a new species of *Leptodeira* from the Andes of southern Ecuador based on morphological and molecular data. The new species is geographically close and morphologically similar to *L. ornata* and *L. larcorum*, from which it can be distinguished by having smaller dorsal body blotches, a longer tail, and shorter spines on the hemipenial body. The shortest genetic distances between the new species and its congeners are 0.02 (*16S*), 0.05 (*cytb*), and 0.18 (*ND4*). The new species is restricted to the Jubones River Basin in southern Ecuador, an area of endemism for other reptile species. Our phylogenetic analysis based on mitochondrial and nuclear DNA sequence data also supports recognition of the names *L. larcorum* (restricted to Peru) for "*L. septentrionalis larcorum*", and *L. ornata* for populations of "*L. s. ornata*" from central and eastern Panama, western Colombia, and western Ecuador. However, some samples of "*L. s. ornata*" from Panama and Costa Rica, as well as the new species described herein, are not included within or more closely related to *L. ornata*, which is sister to the clade (*L. bakeri*, *L. ashmeadii*).

Key words: Andes; color pattern; hemipenial morphology; *Leptodeira ornata*; *Leptodeira larcorum*; *Leptodeira septentrionalis*; molecular phylogeny

Resumen

Leptodeira es uno de los taxones de serpientes más ampliamente distribuidos y problemáticos de América. Aquí describimos una especie nueva de *Leptodeira* de los Andes de Ecuador en base a datos morfológicos y moleculares. La especie nueva es similar en morfología y está geográficamente cerca de *L. ornata* y *L. larcorum*, de las cuales se distingue por poseer manchas dorsales más pequeñas, una cola más larga, y el cuerpo del hemipene con espinas más cortas. Las distancias genéticas más cortas entre la especie nueva y sus congéneres son 0.02 (*16S*), 0.05 (*cytb*), y 0.18 (*ND4*). La especie nueva está restringida a la cuenca del río Jubones al sur del Ecuador, un área de endemismo para otras especies de reptiles. Nuestro análisis filogenético, basado en secuencias de ADN mitocondriales y nucleares, respalda el reconocimiento de los nombres *L. larcorum* (restringida al Perú) para "*L. septentrionalis larcorum*", y *L. ornata* para las poblaciones de "*L. s. ornata*" del centro y este de Panamá, occidente de Colombia y occidente de Ecuador. Sin embargo, algunas muestras de "*L. s. ornata*" de Panamá y Costa Rica, así como la especie nueva descrita aquí, no están incluidas ni más cercanamente emparentadas a *L. ornata*, la cual es hermana del clado (*L. bakeri*, *L. ashmeadii*).

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Palabras clave: Andes; filogenia molecular; *Leptodeira ornata*; *Leptodeira larcorum*; *Leptodeira septentrionalis*; morfología hemipenial; patrón de coloración

Introduction

Cat-eyed snakes traditionally ranked as the genus *Leptodeira* Fitzinger 1843 are one of the most common and widespread squamate taxa in the Americas, occurring from southern Sonora in Mexico and Rio Grande in Texas to northern Argentina and Paraguay, as well as in Aruba, Margarita, and Trinidad and Tobago in the West Indies (Duellman 1958). They are nocturnal snakes with elliptical pupils, and feed primarily upon anurans and lizards. Despite their broad distribution range, the diversity of cat-eyed snakes as currently recognized is relatively low, with 12 species described mostly during the 19th century: *Leptodeira annulata* (Linnaeus 1758); *L. bakeri* Ruthven 1936; *L. frenata* (Cope 1886); *L. maculata* (Hallowell 1861); *L. nigrofasciata* Günther 1868; *L. polysticta* Günther 1885; *L. punctata* (Peters 1866); *L. rhombifera* Günther 1872; *L. rubricata* (Cope 1893); *L. septentrionalis* (Kennicott [in Baird 1859]); *L. splendida* Günther 1885; *L. uribei* (Bautista & Smith 1992). Cat-eyed snakes and vine snakes (*Imantodes* Duméril 1853) are closely related (Cadle 1984), forming a clade that has been named Imantodini (Myers 2011) or Leptodeirini (Mulcahy *et al.* 2011).

The most widespread species—*L. septentrionalis* and *L. annulata*—are paraphyletic as revealed by molecular phylogenetic analyses (Daza *et al.* 2009; Mulcahy 2007), suggesting that the diversity of cat-eyed snakes is currently underestimated. In fact, four subspecies of *L. septentrionalis* and five of *L. annulata* were proposed more than 60 years ago (Duellman 1958) to reflect geographical variation in morphology. Of these, *L. septentrionalis polysticta* and *L. annulata rhombifera* were subsequently elevated to full species status (Campbell 1998; McCranie 2011, respectively). These taxonomic changes are supported by the comprehensive phylogenetic study of Daza *et al.* (2009), who also synonymized *L. annulata cussiliris* Duellman 1958 with *L. maculata*. More recently, however, *L. s. ornata* (Bocourt 1884), *L. s. larcorum* Schmidt & Walker 1943, and *L. a. ashmeadii* (Hallowell 1845) were also elevated to full species (Barrio-Amorós 2019) without or even against (i.e., recognizing paraphyletic groups as species) phylogenetic evidence. Of the three subspecies of *L. septentrionalis* elevated to species, *L. s. ornata* is paraphyletic (Daza *et al.* 2009), and both *L. s. septentrionalis* and *L. s. larcorum* have never been included in a phylogenetic analysis.

Leptodeira septentrionalis and *L. annulata* are also the only two species of *Leptodeira* known from Ecuador, west and east of the Andes, respectively (Torres-Carvajal *et al.* 2019). Duellman (1958) reported *L. a. annulata* and *L. s. ornata* for this country and suggested that populations from southwestern Ecuador were intergrades between *L. s. ornata* and *L. s. larcorum*, although he recorded no specimens of *L. s. larcorum* from southwestern Ecuador or nearby localities in Peru. Subsequently, several authors have reported *L. s. larcorum* in Ecuador (Peters 1960; Pérez Santos & Moreno 1991; Almendáriz & Carr 2012). Based on the first collections of *Leptodeira* along the Jubones River Basin in southwestern Ecuador, here we describe a new species of *Leptodeira* using morphological and phylogenetic evidence. We also present an updated phylogenetic analysis of *Leptodeira* including for the first time samples of *L. s. larcorum* from Peru, a dense sampling of *L. s. ornata* from western Ecuador, and the candidate species. Finally, we use phylogenetic evidence to comment on the current taxonomy of *Leptodeira septentrionalis*.

Material and methods

Fieldwork and data sampling. A total of four specimens of the candidate species were collected during several field trips to different localities along the Jubones River Basin in southwestern Ecuador between 2015–2018. Altitudes and geographic coordinates were recorded with a GPS (Garmin) using the geodetic datum WGS84. After lethal anesthetization of voucher specimens with an intracelomic injection of benzocaine (2%), muscle and liver tissue samples were extracted for DNA analyses. Specimens were then fixated in 10% formalin and stored in 70% ethanol in the herpetological collections at MZUA-RE (RE = reptile collection) and QCAZ; institutional abbreviations follow Sabaj (2020). We also examined 111 specimens of *Leptodeira septentrionalis ornata* from western Ecuador deposited at QCAZ, and 22 specimens of *Leptodeira s. larcorum* from Peru (including the holotype and five paratypes) deposited at FMNH, CORBIDI, MUSA, and ZFMK (Appendix). Some of these specimens were

collected in a previous survey along the northern Peruvian dry forest (Koch *et al.* 2018). We used QGIS v3 (QGIS Development Team 2019) to generate a distribution map based exclusively on locality data of examined specimens obtained from Bioweb (Torres-Carvajal *et al.* 2020), Koch et al. (2018), and Venegas (2005). Holotype and paratype localities of *Leptodeira s. larcorum* were georeferenced in Google Maps based on the information provided in the original description.

Snout–vent length (SVL) and tail length (TL) measurements were recorded with tape measure. All other measurements were made with digital calipers and recorded to the nearest 0.01 mm. Dorsal dark blotches (i.e., dark mark larger than one scale) were counted separately on body (from neck to level of vent) and tail (from vent to tip of tail); if possible, collapsed blotches were counted individually (e.g., a zig-zag mark clearly composed of four blotches was counted as four). Sex was determined by noting the presence of everted hemipenes or by gonad inspection (testes and ovaries) through dissection. Hemipenes of the new species described here, as well as of *L. s. ornata* and *L. s. larcorum* were prepared from fixed specimens following standard techniques (Pesantes 1994). Morphological terminology follows that of Duellman (1958).

Phylogenetic analyses.

We assembled a data matrix of 148 terminals and 3,532 characters with nucleotide sequences of three mitochondrial genes, small subunit ribosomal RNA (*16S*, 537 aligned sites), cytochrome b (*cytb*, 1,043), subunit IV of NADH dehydrogenase (*ND4*, 681), as well as two nuclear genes, neurotrophin 3 (*NT3*, 528) and dynein axonemal heavy chain 3 (*DNAH3*, 743). We generated novel DNA sequences from 19 specimens of *Leptodeira septentrionalis ornata* from western Ecuador, five of *L. s. larcorum* from Peru, and four specimens of the candidate species (Table 1). We followed the PCR amplification protocols presented by Daza *et al*. (2009). In addition, we obtained sequences of 120 specimens from GenBank representing 12 additional species of *Leptodeira*, *Imantodes cenchoa* (Linnaeus), *I. inornatus* (Boulenger), and *Dipsas pratti* (Boulenger), which was used to root the trees (Mulcahy *et al.* 2011).

TABLE 1. Vouchers, locality data, and GenBank accession numbers of taxa and gene regions sequenced in this study. CORBIDI: Centro de Ornitología y Biodiversidad, Lima, Peru; MZUA-RE: Colección de Reptiles, Museo de Zoología, Universidad del Azuay, Cuenca, Ecuador; QCAZ: Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito; ZFMK: Zoologisches Forschungsmuseum Alexander Koenig, Bonn, Germany.

Taxon	Voucher and locality	Coordinates		Genbank accession number				
		Lat	Long	*16S*	*ND4*	*cytb*	*DNAH3*	*NT3*
Leptodeira larcorum	**CORBIDI 1865**. PERU: Cajamarca: Bellavista.	-5.633	-78.650	MW208456	—	—	—	—
Leptodeira larcorum	**CORBIDI 5643**. PERU: Amazonas: Pangueico creek, Zapatalgo.	-6.092	-78.497	MW208457	—	—	MW208505	MW208519
Leptodeira larcorum	**CORBIDI 7664**. PERU: Cajamarca: Bellavista.	-5.633	-78.650	—	MW208483	—	MW208506	MW208517
Leptodeira larcorum	**ZFMK 90929**. PERU: Cajamarca: Pucará.	-6.032	-79.127	MW208458	MW208484	—	MW208507	MW208520
Leptodeira larcorum	**ZFMK 91794**. PERU: La Libertad: Calemar.	-7.520	-77.722	MW208459	MW208485	—	MW208508	MW208518

...Continued onthe next page

TABLE 1. (Continued)

Taxon	Voucher and locality	Coordinates		Genbank accession number				
		Lat	Long	*16S*	*ND4*	*cytb*	*DNAH3*	*NT3*
Leptodeira misinawui sp. nov.	**MZUA-RE 0252**. ECUADOR: Azuay: Poetate.	-3.417	-79.227	MW208450	MW208501	MW208464	MW208513	MW208524
Leptodeira misinawui sp. nov.	**MZUA-RE 0253**. ECUADOR: Azuay: Poetate.	-3.417	-79.227	MW208451	MW208502	MW208465	MW208514	MW208523
Leptodeira misinawui sp. nov.	**QCAZ 16510**. ECUADOR: Azuay: road Santa Isabel-Pasaje.	-3.300	-79.340	MW208452	MW208503	MW208466	MW208515	MW208522
Leptodeira misinawui sp. nov.	**QCAZ 16511**. ECUADOR: Azuay: road Santa Isabel-Pasaje.	-3.320	-79.353	MW208453	MW208504	MW208467	MW208516	MW208521
Leptodeira ornata	**QCAZ 4469**. ECUADOR: Los Ríos: Pedro Franco Dávila Reserve.	-1.246	-79.660	—	—	MW208468	—	—
Leptodeira ornata	**QCAZ 6387**. ECUADOR: Manabí: Canoas, 3 km on road to San Vicente.	-0.465	-80.427	MW208454	MW208486	MW208460	MW208509	MW208528
Leptodeira ornata	**QCAZ 6392**. ECUADOR: Loja: 14 km N Alamor.	-3.949	-80.026	—	—	MW208469	—	—
Leptodeira ornata	**QCAZ 8020**. ECUADOR: Esmeraldas: Durango, 2 km on road to San Francisco river.	1.047	-78.618	MW208455	MW208487	MW208461	MW208510	MW208527
Leptodeira ornata	**QCAZ 8431**. ECUADOR: Los Ríos: Finca Zoila Emiliana, Baba River dam.	-0.661	-79.424	—	MW208490	MW208470	—	—
Leptodeira ornata	**QCAZ 8777**. ECUADOR: Guayas: Manglares Churute Reserve.	-2.395	-79.630	—	MW208491	MW208471	—	—

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TABLE 1. (Continued)

Taxon	Voucher and locality	Coordinates		Genbank accession number				
		Lat	Long	*16S*	*ND4*	*cytb*	*DNAH3*	*NT3*
Leptodeira ornata	**QCAZ 9837**. ECUADOR: Esmeraldas: near Caimito.	0.705	-80.089	—	MW208492	MW208472	—	—
Leptodeira ornata	**QCAZ 10198**. ECUADOR: Los Ríos: Río Palenque Field Station.	-0.588	-79.362	—	MW208493	MW208473	—	—
Leptodeira ornata	**QCAZ 10344**. ECUADOR: Loja: El Faique creek.	-4.337	-80.275	MW208448	MW208488	MW208462	MW208511	MW208526
Leptodeira ornata	**QCAZ 10371**. ECUADOR: Loja: Zapotillo, Garzareal.	-4.286	-80.232	—	MW208494	MW208474	—	—
Leptodeira ornata	**QCAZ 10550**. ECUADOR: Esmeraldas: Caimito.	0.695	-80.090	MW208449	MW208489	MW208463	MW208512	MW208525
Leptodeira ornata	**QCAZ 10597**. ECUADOR: Manabí: El Aromo.	-1.046	-80.832	—	MW208495	MW208475	—	—
Leptodeira ornata	**QCAZ 11773**. ECUADOR: Manabí: Flavio Alfaro, Río Javier community.	-0.695	-80.012	—	MW208496	MW208476	—	—
Leptodeira ornata	**QCAZ 11775**. ECUADOR: Manabí: Pedernales, Santa Rosa community.	-0.206	-80.124	—	MW208497	MW208477	—	—
Leptodeira ornata	**QCAZ 12459**. ECUADOR: Santa Elena: El Rincón del Tigre, 1 km from Dos Mangas.	-1.826	-80.655	—	MW208498	MW208478	—	—
Leptodeira ornata	**QCAZ 12571**. ECUADOR: Loja: Zapotillo, Cazaderos Natural Reserve.	-4.024	-80.447	—	MW208499	MW208479	—	—
Leptodeira ornata	**QCAZ 14040**. ECUADOR: El Oro: Arenillas Ecological Reserve.	-3.510	-80.123	—	—	MW208480	—	—

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TABLE 1. (Continued)

Taxon	Voucher and locality	Coordinates		Genbank accession number				
		Lat	Long	*16S*	*ND4*	*cytb*	*DNAH3*	*NT3*
Leptodeira ornata	**QCAZ 14044**. ECUADOR: El Oro: Arenillas Ecological Reserve.	-3.566	-80.142	—	—	MW208481	—	—
Leptodeira ornata	**QCAZ 14180**. ECUADOR: Guayas: Cerro Blanco Protected Forest.	-2.177	-80.022	—	MW208500	MW208482	—	—

Data were assembled and aligned in Geneious v7.1.5 (Kearse *et al.* 2012) under default settings for MAFFT (Algorithm: Auto, Scoring Matrix: 200PAM/k=2, Gap open penalty: 1.53, Offset value: 0.123; Katoh & Standley 2013). Sequences were translated into amino acids for confirmation of alignment. After partitioning the concatenated dataset by codon position for each gene, we chose the best partitioning scheme using PartitionFinder v2 (Guindon *et al.* 2010; Lanfear *et al.* 2017) under the Bayesian Information Criterion (BIC). The "greedy" algorithm (Lanfear *et al.* 2012) was used with branch lengths of alternative partitions "linked" to search for the best-fit scheme.

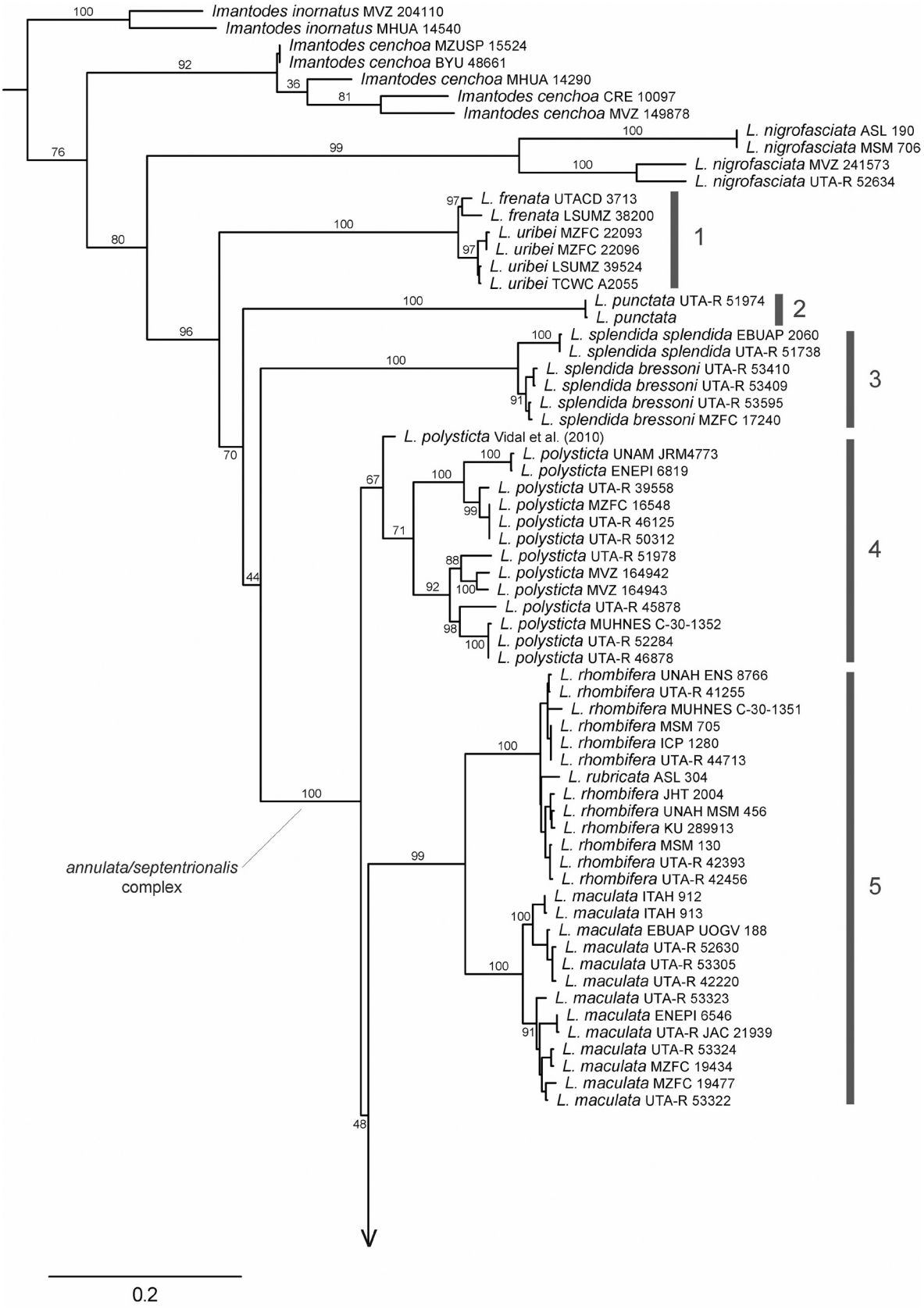
A maximum likelihood inference method was used to obtain the optimal tree topology of the combined, partitioned dataset using the program RAxML v8.2.10 (Stamatakis 2014). This analysis was performed under the GTRGAMMA model, with 1,000 rapid bootstrap inferences followed by a thorough ML search. Nodal support (BS) was assessed with the rapid bootstrapping algorithm (Stamatakis *et al.* 2008) under the MRE-based Bootstopping criterion (150 replicates). Additionally, uncorrected genetic distances among species were calculated in MEGA v7 (Kumar *et al.* 2016) for all mitochondrial genes.

Results

Phylogeny of *Leptodeira*. Selected partitions were (i) *16S*, *ND4*-1st codon position, *cytb*-1st codon position; (ii) *ND4*-2nd codon position, *cytb*-2nd codon position; (iii) *ND4*-3rd codon position, *cytb*-3rd codon position; (iv) *DNAH3*-1st & 2nd codon positions, *NT3*-1st & 2nd codon positions; (v) *DNAH3*-3rd codon position, *NT3*-3rd codon position. The ML tree (Fig. 1) strongly supports (BS=80) monophyly of *Leptodeira*, with *L. nigrofasciata* as sister to all other species. Following branching order (clade numbers as in Fig. 1 in parentheses), the next taxa to split are (1) the maximally supported clade (*L. frenata* Cope, *L. uribei* Bautista & Smith), (2) *L. punctata* Peters, and (3) *L. splendida* Günther as sister taxon to the remaining species, which are nested in a clade (BS=100) corresponding to the *L. annulata*/*septentrionalis* complex (Daza *et al.* 2009). The first lineage to split within this complex is (4) *L. polysticta* Günther, followed by (5) the strongly supported (BS=99) clade (*L. rhombifera* Günther, *L. maculata* Hallowell), which is sister to a larger clade (BS=57) containing all remaining taxa. Although the deeper nodes within this larger clade were poorly supported, the following subclades were moderately to strongly supported: (6) *Leptodeira septentrionalis ornata* Bocourt (*Leptodeira* sp. from here on) from Costa Rica and western Panama (BS=100); (7) *L. annulata annulata* Linnaeus from Ecuador, Peru, Brazil, French Guiana and Suriname (BS=99), (8) *L. septentrionalis ornata* (*Leptodeira* sp. from here on) from central and western Panama (BS=89), (9) *L. annulata* from Panama (BS=98), (10) *L. septentrionalis larcorum* Schmidt & Walker (*L. larcorum* from here on) from Peru (BS=94), (11) *L. bakeri* Ruthven, *L. ashmeadii* Hallowell (BS=94), (12) *L. septentrionalis ornata* (*L. ornata* from here on) from northwestern South America, and both central and eastern (Darien) Panama (BS=83), the clade (11, 12) (BS=73), and the new species described below (BS=99). *Leptodeira* sp. from central and western Panama (clade 8) was recovered as the sister taxon of the species described in this paper, although with low support (BS=52).

Uncorrected p-distances are presented in Tables 2–4, and range from 0.01 (*L. larcorum*/*L. ornata*) to 0.04 (*L. misinawui* **sp. nov.**/*L. polysticta*) for *16S* (X=0.03 ± 0.01 SD; five species); 0.02 (*L. rhombifera*/*L. rubricata*) to 0.20 (*L. nigrofasciata*/*L. maculata*; *L. nigrofasciata*/*L. rhombifera*; *L. nigrofasciata*/*L. polysticta*) for *cytb* (X=0.13

± 0.04 SD; 14 species); and 0.01 (*L. rhombifera*/*L. rubricata*; *L. frenata*/*L. uribei*) to 0.19 (*L. nigrofasciata*/*L. splendida bressoni*) for *ND4* (X=0.12 ± 0.04 SD; 15 species). Genetic distances between the new species described herein and other species of *Leptodeira* (in parentheses) range between 0.02 (*L. larcorum*, *L. ornata*) and 0.04 (*L. polysticta*) for *16S*; 0.05 (*L. ashmeadii*, *L. bakeri*, *L. ornata*) and 0.18 (*L. nigrofasciata*) for *cytb*; 0.04 (*L. larcorum*) and 0.16 (*L. nigrofasciata*) for *ND4*.



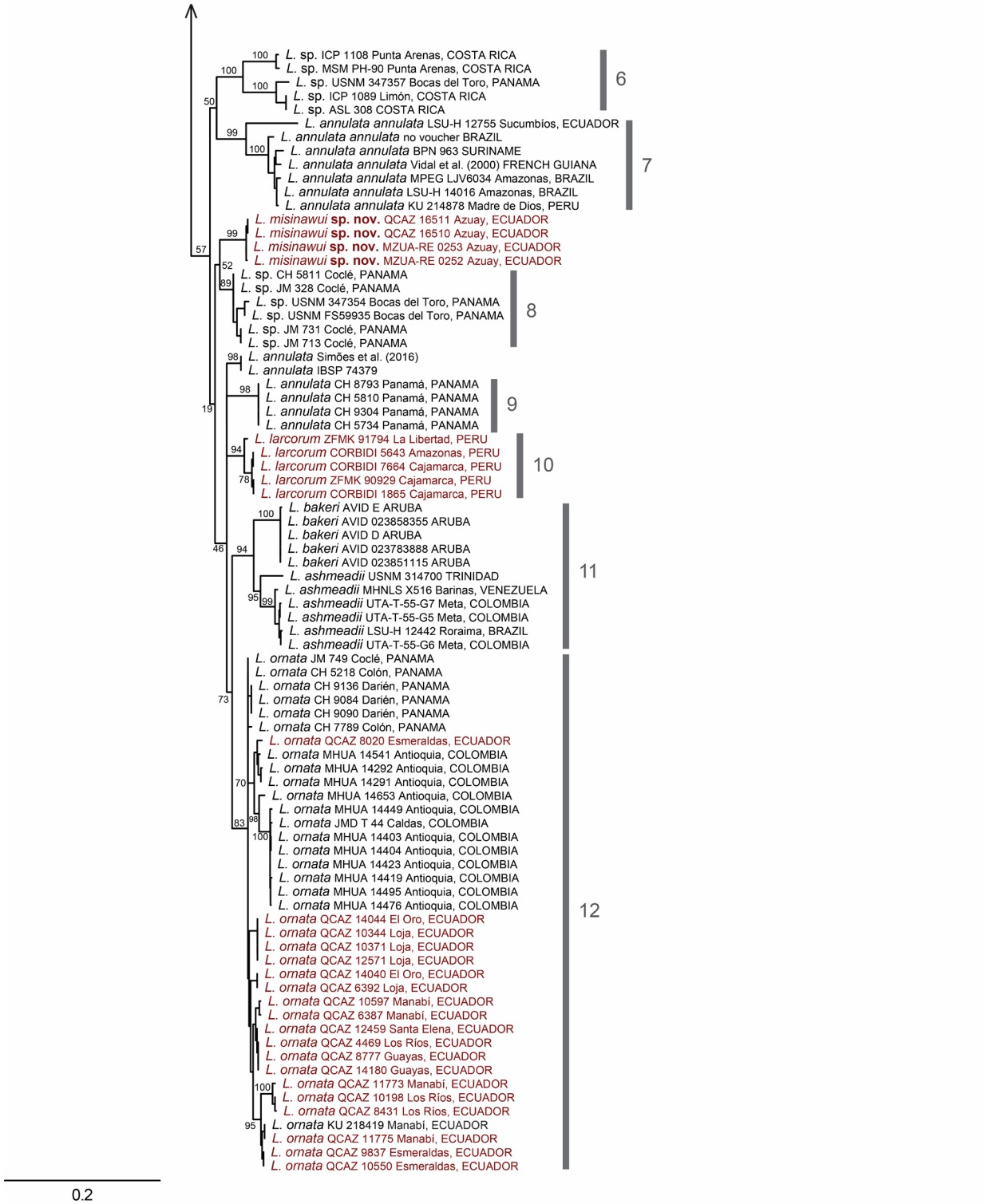


FIGURE 1. Phylogeny of *Leptodeira*. Maximum likelihood tree obtained from a RAXML analysis of three mitochondrial (*16S, cytb*, *ND4*) and two nuclear genes (*NT3*, *DNAH3*). Numbers next to branches are bootstrap support values; for clarity, support values on short branches are not shown. Voucher number is indicated for each terminal. In addition, country (if available) preceded by Department or Province are shown for taxa in the *Leptodeira annulata/septentrionalis* complex except *L. maculata*, *L. rhombifera*, and *L. polysticta*. Clade numbers (see Results) are shown next to vertical bars. Specimens sequenced in this paper are colored in brown. GenBank accession numbers along with more detailed locality data of newly sequenced specimens are presented in Table 1. Outgroup species *Dipsas pratti* is not shown.

TABLE 2. Uncorrected p-distances among five species of *Leptodeira* for the *16S* gene region. Taxonomy is based on the phylogenetic tree in Figure 1.

	L. ornata	*L. misinawui*	*L. annulata*	*L. larcorum*
L. ornata				
L. misinawui	0.02			
L. annulata	0.02	0.03		
L. larcorum	0.01	0.02	0.02	
L. polysticta	0.03	0.04	0.03	0.03

TABLE 3. Uncorrected p-distances between 14 species of *Leptodeira* for the *cytb* gene region. Taxonomy is based on the phylogenetic tree in Figure 1.

	L. annulata	*L. ashmeadii*	*L. maculata*	*L. rhombifera*	*L. bakeri*	*L. frenata*	*L. nigrofasciata*	*L. polysticta*	*L. punctata*	*L. rubricata*	*L. ornata*	*L. misinawui*	*L. splendida bressoni*	*L. s splendida*
L. annulata														
L. ashmeadii	0.08													
L. maculata	0.12	0.10												
L. rhombifera	0.10	0.10	0.07											
L. bakeri	0.06	0.04	0.10	0.09										
L. frenata	0.15	0.15	0.16	0.16	0.14									
L. nigrofasciata	0.19	0.19	0.20	0.20	0.18	0.19								
L. polysticta	0.10	0.08	0.11	0.10	0.08	0.15	0.20							
L. punctata	0.15	0.16	0.16	0.16	0.15	0.16	0.18	0.15						
L. rubricata	0.10	0.10	0.06	0.02	0.09	0.15	0.19	0.09	0.17					
L. ornata	0.07	0.05	0.10	0.09	0.04	0.15	0.18	0.08	0.15	0.09				
L. misinawui	0.06	0.05	0.09	0.08	0.05	0.14	0.18	0.08	0.16	0.08	0.05			
L. splendida bressoni	0.16	0.14	0.15	0.15	0.14	0.15	0.19	0.14	0.15	0.15	0.14	0.13		
L. s. splendida	0.16	0.14	0.15	0.15	0.13	0.16	0.18	0.15	0.16	0.15	0.14	0.14	0.03	
L. uribei	0.16	0.16	0.16	0.16	0.14	0.03	0.19	0.15	0.17	0.16	0.15	0.14	0.15	0.15

Taxonomic decision

The taxonomic conclusions of this study are based on the study of external morphology, including color pattern and color tones, as well as inferred phylogenetic divergences. We consider this information as species delimitation criteria following the unified species concept (de Queiroz 2007).

Leptodeira misinawui sp. nov.

(Figs. 2–3)

Holotype. An adult male, MZUA-RE 0253, collected on 22 April 2015 by Elvis Celi in Poetate (-3.417S, -79.227W, 2,734 m above sea level; hereafter asl), cantón Susudel, Azuay province, Ecuador.

Paratypes (N=3). ECUADOR: Azuay: adult female, MZUA-RE 0252, with the same collection data as the holotype; adult male, QCAZ 16510, collected on 18 March 2018 by Diego Almeida on the road Santa Isabel-Pasaje (-3.30S, -79.340W, 971 m asl); juvenile, QCAZ 16511, collected on 20 March 2018 by Diego Almeida on the road Santa Isabel-Pasaje (-3.320S, -79.353W, 950 m asl).

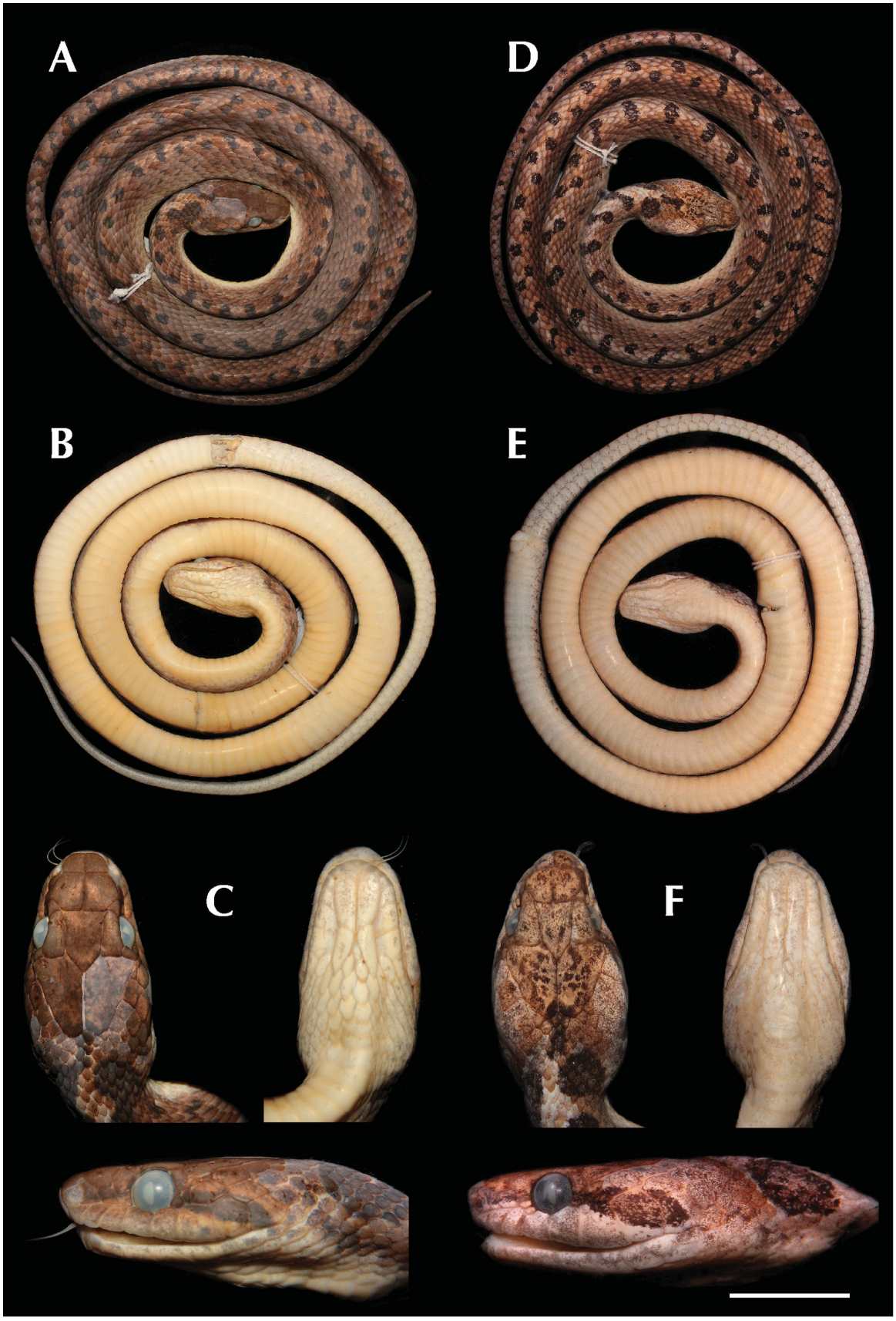


FIGURE 2. Male holotype (MZUA-RE 0253) and female paratype (MZUA-RE 0252) of *Leptodeira misinawui* **sp. nov.** in preservative. Dorsal (A) and ventral (B) views of body, and dorsal, ventral and lateral views of head (C) of the holotype. Dorsal (D) and ventral (E) views of body, and dorsal, ventral and lateral views of head (F) of the paratype. Photographs by J.C. Sánchez. Scale bar (C, F) = 10 mm.



FIGURE 3. General view of *Leptodeira misinawui* **sp. nov.** in life. Top: holotype (MZUA-RE 0253); bottom: paratype (QCAZ 16510), adult male from Azuay province, road Santa Isabel-Pasaje. Photographs by E. Celi (top) and G. Pazmiño (bottom).

Diagnosis. *Leptodeira misinawui* can be distinguished from other congeners by unique combination of the following characters: 19 (25%) or 21 (75%) midbody dorsal scale rows, reducing to 16 (25%) or 17 (75%) posteriorly; 2–3 preoculars (usually 2); vertebral and paravertebral rows not enlarged; single nape bar; faint intercalary spots; and 54–72 (average 63.25 ± 7.89 SD) body blotches rarely forming a continuous zig-zag stripe, 2–3 dorsal scales in length, half the length of light interspaces, and extending laterally onto scale rows 7–8.

The new species differs from *Leptodeira ornata* (in parentheses) from western Ecuador in having 54–72 dorsal blotches along body (vs. 30–47), and tail length/body length 0.30 in females, 0.36–0.39 in males (vs. 0.21–0.26 in females, 0.23–0.30 in males). Similarly, *L. misinawui* has more dorsal blotches along body than *L. larcorum* (42–54). The dorsal blotches of *L. misinawui* are noticeably smaller (usually < 2 scales long and < 5 scales wide) than those of *L. ornata* and *L. larcorum* (usually > 2 scales long and > 10 scales wide). Although similar in morphology, the hemipenis of *L. misinawui* differs from those of *L. larcorum* and *L. ornata* in having shorter spines, with an average spine length/spine base-width ratio of 1.6 (vs. 3.3 and 2.2, respectively). A comparison of scutellation and size between *Leptodeira misinawui*, *L. ornata* from western Ecuador, and *L. larcorum* is presented in Table 5.

Description of the holotype. Male, SVL= 445 mm, TL= 173 mm. Head distinct from neck; rostral barely visible from above; head two times longer than broad and almost 2.4 times longer than deep. Eye slightly protuberant, occupying 16.5% of length of head, with elliptical pupil visible from anterior, lateral, dorsal, and ventral aspects; rostral 1.8 times wider than high, concave in anterior view, and narrowly visible from above. Prefrontals hexagonal,

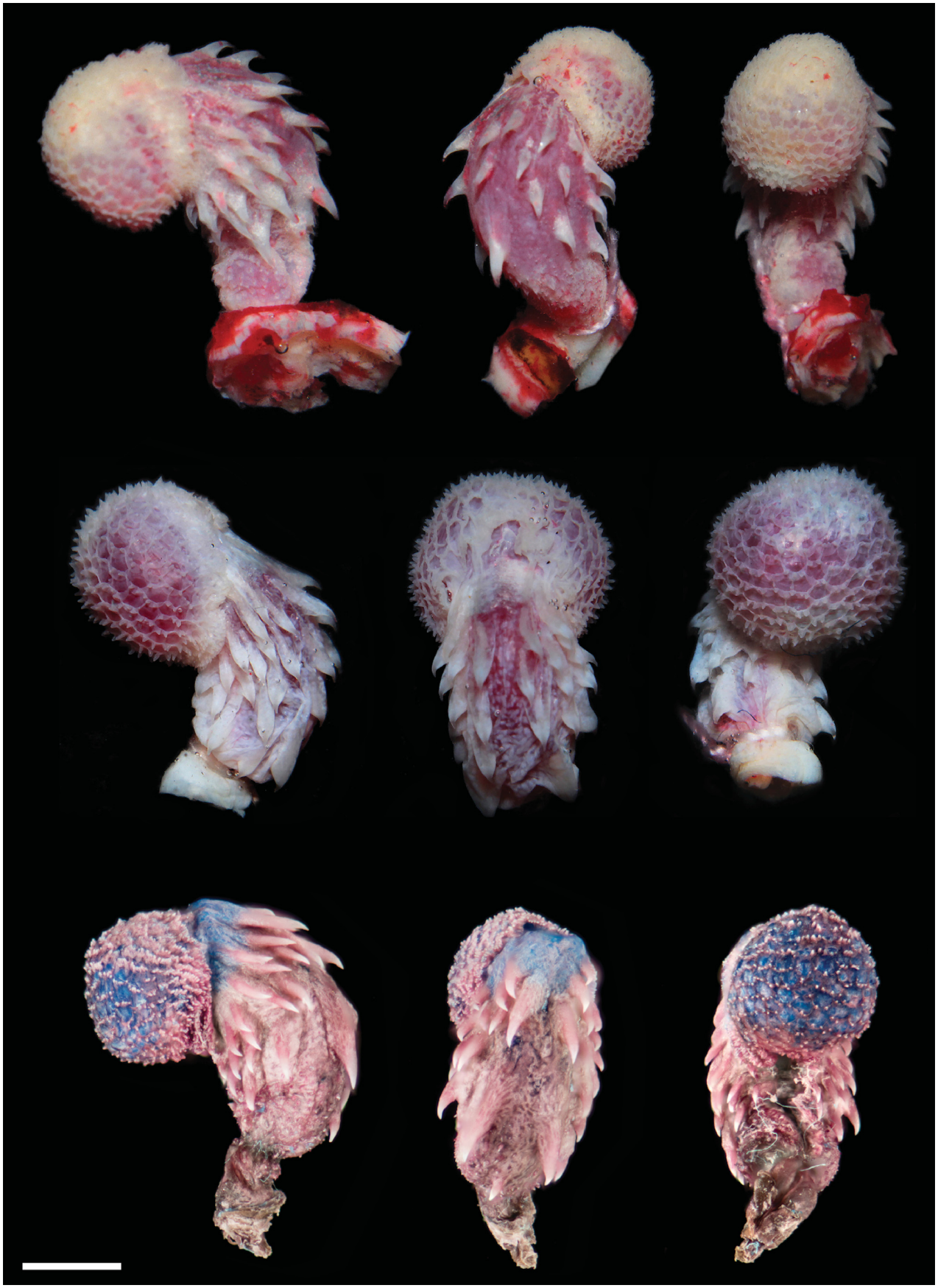


FIGURE 4. Hemipenes of *Leptodeira misinawui* **sp. nov.** (top, MZUA-RE 0253, holotype), *L. ornata* (middle, MZUA-RE 0173), and *L. larcorum* (bottom, ZFMK 91794). Views from left to right: lateral, asulcate, and sulcate. Photographs by J.C. Sánchez and M. Flecks. Scale bar = 5 mm.

TABLE 4. Uncorrected p-distances between 15 species of *Leptodeira* for the *ND4* gene region. Taxonomy is based on the phylogenetic tree in Figure 1.

	L. annulata	*L. ashmeadii*	*L. maculata*	*L. rhombifera*	*L. bakeri*	*L. frenata*	*L. larcorum*	*L. nigrofasciata*	*L. polysticta*	*L. punctata*	*L. rubricata*	*L. ornata*	*L. misinawui*	*L. splendida bressoni*	*L. s. splendida*
L. annulata															
L. ashmeadii	0.08														
L. maculata	0.10	0.09													
L. rhombifera	0.10	0.08	0.07												
L. bakeri	0.08	0.03	0.08	0.09											
L. frenata	0.15	0.14	0.15	0.13	0.14										
L. larcorum	0.07	0.04	0.09	0.09	0.04	0.13									
L. nigrofasciata	0.17	0.16	0.17	0.15	0.18	0.17	0.17								
L. polysticta	0.10	0.08	0.10	0.10	0.09	0.14	0.08	0.16							
L. punctata	0.15	0.15	0.15	0.15	0.14	0.15	0.14	0.18	0.14						
L. rubricata	0.10	0.09	0.07	0.01	0.09	0.13	0.09	0.15	0.10	0.15					
L. ornata	0.07	0.04	0.08	0.08	0.05	0.14	0.04	0.17	0.08	0.13	0.08				
L. misinawui	0.06	0.05	0.08	0.07	0.06	0.13	0.04	0.16	0.08	0.14	0.08	0.05			
L. splendida bressoni	0.13	0.13	0.14	0.13	0.14	0.13	0.13	0.19	0.13	0.14	0.13	0.11	0.12		
L. s. splendida	0.14	0.13	0.14	0.13	0.14	0.15	0.13	0.18	0.14	0.15	0.13	0.12	0.13	0.03	
L. uribei	0.15	0.13	0.14	0.14	0.14	0.01	0.13	0.17	0.13	0.14	0.14	0.14	0.13	0.14	0.15

slightly longer than broad, twice the length of internasals, each in contact with its mate and with frontal posteriorly, supraocular (left only) posterolaterally, preocular posterolaterally, nasal anterolaterally, internasal anteriorly, and loreal laterally; frontal approximately pentagonal, 1.3 times longer than wide (greatest width), and its length about the same distance from its anterior edge to tip of snout. Supraocular longer than wide, in contact with frontal medially, preocular anteriorly, eye laterally, postocular posterolaterally, and parietal posteriorly; frontal slightly shorter than suture between parietals; broad parietals, about 2 times longer than wide; interparietal suture 1.1 times shorter than distance from frontal to tip of snout; nasal plate single, centrally pierced by large naris (1.17 mm in diameter), in contact with rostral anteriorly, internasal dorsally, prefrontal posterodorsally, loreal posteriorly, and first and second supralabials ventrally; preoculars two, the ventral one hexagonal and much smaller than the dorsalmost; postoculars two (an extra tiny scale between postoculars on left side), the lower less than half the size of the upper one; temporals 1+2 (the upper second temporal broken into two small scales on left side); supralabials eight, first and second in contact with nasal, second and third in contact with loreal, third and fourth in contact with preocular, fourth and fifth bordering the orbit; infralabials 10, with first to fifth in contact with anterior genial, and fifth and sixth touching posterior genial; first pair of infralabials in contact medially behind mental; genials in two pairs of similar length (Fig. 2C). Body higher than wide, rounded ventrolaterally; dorsal scales 19–21–17, smooth, juxtaposed or subimbricate, with paired apical pits; scales of vertebral row similar in size to adjacent rows; ventrals 180; anal plate divided; subcaudals divided, 90 (Fig. 2A,B).

Dorsal background light brown, with a longitudinal series (~67 on body and ~38 on tail) of dark brown paravertebral blotches on each side, some of which are fused with the corresponding opposite blotch, but never forming a zig-zag line. Paravertebral blotches on body 2–3 dorsal scales in length, half the length of dorsal light interspaces, extending laterally onto scale rows 7–8, and becoming smaller towards the tip of the tail. Faint intercalary spots on dorsal row 4, or between rows 4 and 5. Ventral surface of body cream with minute dark brown dots, more numerous at lateral ends of ventral scales, head (ventrally), and margins of subcaudals. Dark brown postocular stripe from eye to corner of mouth, extending from postoculars across ventral edges of primary and secondary temporals, dorsal edge of supralabial VI, upper half of supralabial VII, and anterior half of supralabial VIII; another dark stripe from

nostril across loreal and upper preocular to orbit. Infralabials cream, densely marked with tiny dark dots. Head background same as dorsum, with irregular dark brown marks that are denser on parietals. Longitudinal nape bar extending from posterior margins of parietals to about third middorsal row; two short longitudinally elongated blotches on nape, the left one fused with nape bar. Iris bronze (Fig. 3).

Fully everted hemipenis (Fig. 4) longer (11.3 mm) than wide (5.5 mm), extending to fifth/sixth subcaudal in situ, unilobed, unicapitate; capitulum rounded and finely crenulate, with a deep fold at the base; hemipenial body with small spinules at its base and large spines distally, which are more numerous laterally; sulcus spermaticus unforked.

Variation. Intraspecific variation of *Leptodeira misinawui* in scutellational and meristic characters is presented in Table 5. Paratypes are generally similar to holotype in color patterns. Paratype MZUA-RE 0252 has less elongated blotches on nape (circular right, ovoid left) and the nape stripe is not fused to the first body blotches (Fig. 2). In paratype QCAZ 16511, the longitudinal nape bar is fused to the right nape blotch, whereas in QCAZ 16510 both nape blotches are fused to the nape bar forming a butterfly-shaped mark (Fig. 3). The two examined males have more subcaudals and a longer tail than the female (Table 5).

Etymology. The specific epithet "*misinawui*" derives from the Quechua-Cañari words "*misi*" meaning cat, and "*ñawui*" meaning eye, and refers to the similarity of the eye of the new species to the eye of a cat. This epithet honors the Quechua-Cañari culture from southern Ecuador. We propose the Standard English Name: Jubones Cat-Eyed Snakes and the Standard Spanish Name: Serpientes Ojo de Gato del Jubones.

Distribution and natural history. *Leptodeira misinawui* is known from upper basin of Jubones River, Azuay Province, at elevations between 950–2,734 m asl (Fig. 5). This area corresponds to Evergreen Montane Forest of the southern Ecuadorian Andes and is characterized by a series of small isolated mountains within an inter-Andean valley (Ministerio del Ambiente del Ecuador 2012). Habitat at the type locality is characterized by medium size shrubs < 2m high, with scattered herbaceous vegetation that usually accumulate water (Fig. 6). Individuals of *L. misinawui* were encountered active at night near roots of shrubs, near trails, and in a small water pool.

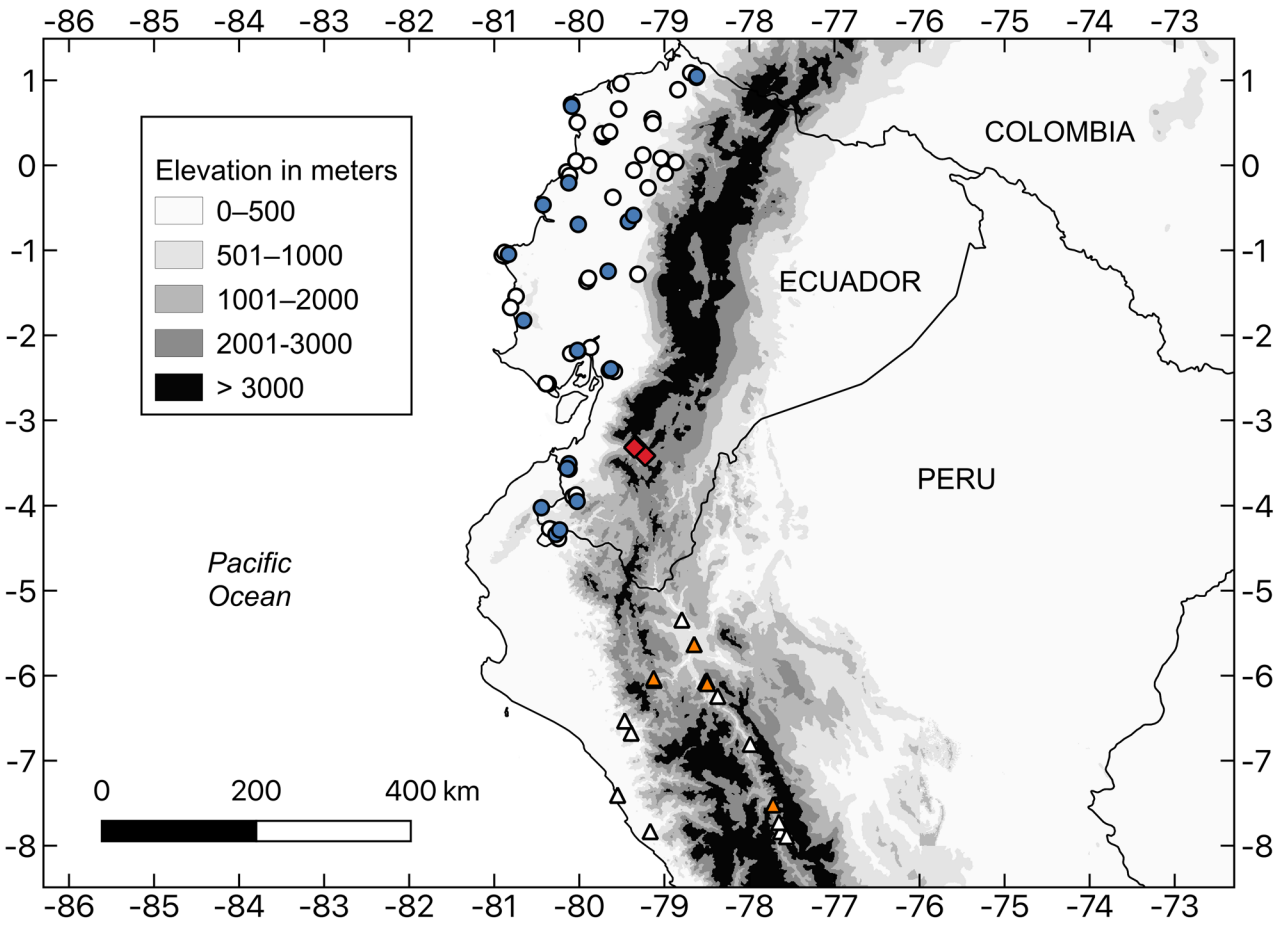


FIGURE 5. Known distribution of *Leptodeira misinawui* (diamonds), *L. ornata* in western Ecuador (circles), and *L. larcorum* (triangles). Filled symbols represent specimens sequenced in this study.



FIGURE 6. Landscape view of Jubones River Basin in southern Ecuador (A), and close-up of the type-locality habitat of *Leptodeira misinawui* (B). Photographs by S.R. Ron (A) and E. Celi (B).

TABLE 5. Selected meristic and morphometric characters for *Leptodeira misinawui*, *L. ornata* from western Ecuador, and *L. larcorum* from Peru. Range (first line) and mean ± SD (second line) are presented when appropriate.

Character	*L. misinawui* ECUADOR N=4	*L. ornata* ECUADOR N=61	*L. larcorum* PERU N= 21
Dorsal scale rows on neck	19 (75%) 21 (25%)	17 (1.7%) 19 (53.3%) 20 (6.6%) 21 (33.3%) 22 (3.4%) 23 (1.7%)	(N=20) 15 (5%) 17 (5%) 19 (60%) 20 (30%)
Dorsal scale rows at midbody	21 (75%) 19 (25%)	19 (13.1%) 21 (65.6%) 22 (1.6%) 23 (19.7%)	(N=20) 17 (5%) 19 (10%) 20 (25%) 21 (60%)
Dorsal scale rows anterior to cloaca	17 (75%) 16 (25%)	13 (1.6%) 14 (1.6%) 15 (54.2%) 16 (16.4%) 17 (26.2%)	(N=20) 14 (5%) 15 (60%) 16 (15%) 17 (15%) 18 (5%)
Ventrals in males	180–181 (N=2) 180.5 ± 0.71	176–197 (N=37) 187.49 ± 5.19	186–196 (N=10) 189 ± 3.56
Ventrals in females	183	177–198 (N=19) 187.21 ± 6.55	176–199 (N=5) 190 ± 8.86
Subcaudals in males	89–90 89.5 ± 0.71	83–107 (N=31) 94.65 ± 6.21	87–92 (N=7) 89.7 ± 1.8
Subcaudals in females	76	72–93 (N=16) 83.38 ± 6.11	77–94 (N=4) 85.25 ± 8.5
Preoculars	2–3 usually 2	1–3 usually 2	1–3 (N=17) usually 1
Postoculars	2	2–4 usually 2	2–3 (N=11) usually 2
Supralabials	8	8	7–9 (N=20) usually 8
Supralabials entering orbit	4–5	3–4–5, 4–5, 4–5–6 usually 4–5	3–4–5, 4–5, 4–5–6 usually 4–5
Infralabials	10	9–12 usually 10	8–12 (N=20) usually 10
Temporal formula	1+1, 1+2, 2+1 usually 1+2	1+1, 1+2, 1+3, 2+2 usually 1+2	1+2, 2+2 (N=10) usually 1+2
Dorsal body blotches	54–72 63.25 ± 7.89	30–47* 38.8	42–54 (N=5) 49.6 ± 5.37
Maximum SVL in females	523 mm	648 mm	630 mm (N=5)
Maximum SVL in males	445 mm	639 mm	443 mm (N=10)
Tail length/body length in females	0.30 (N=1)	0.21–0.26 (N=15) 0.24 ± 0.02	0.3–0.36 (N=4) 0.34 ± 0.03
Tail length/body length in males	0.36–0.39 (N=2) 0.37 ± 0.02	0.23–0.30 (N=28) 0.27 ± 0.02	0.3–0.48 (N=7) 0.37 ± 0.05

* Data from Duellman (1958) for specimens of "*Leptodeira septentrionalis ornata"* from western Ecuador.

Discussion

Over six decades ago, Duellman (1958) used morphology to recognize *Leptodeira septentrionalis* as a widespread species, with four subspecies occurring from southern Texas to northern Peru: *L. s. septentrionalis*, *L. s. ornata*, *L. s. polysticta*, and *L. s. larcorum*. While monophyly of *L. septentrionalis* as conceived by Duellman was later rejected by molecular phylogenetic evidence (Mulcahy 2007; Daza *et al.* 2009), recognition of *L. septentrionalis polysticta* as a distinct species (Campbell 1998) was supported. In contrast, monophyly of *L. s. ornata* was rejected, while neither *L. s. septentrionalis* nor *L. s. larcorum* were evaluated. More recently, *L. s. septentrionalis*, *L. s. ornata*, and *L. s. larcorum* were also elevated to full species without phylogenetic evidence (Barrio-Amorós 2019). Although a comprehensive revision of the *Leptodeira annulata/septentrionalis* complex is out of the scope of this paper, we increased sampling of *L. s. ornata* and included for the first time samples of *L. s. larcorum* because these taxa are geographically close to *L. misinawui*. Reciprocal monophyly and genetic distances (Tables 2–4) support recognition of *L. misinawui*, *L. ornata* and *L. larcorum* as distinct species, although the composition of *L. ornata* is different from the proposal by Barrio-Amorós (2019). We restrict the name *L. ornata* to a well-supported clade containing samples from western Ecuador, western Colombia, as well as central and eastern Panama (D. Mulcahy unpubl. data), including the Darien Mountain Slope, which is the type locality of *L. ornata* (Fig. 1). According to our analysis, *L. ornata* is supported as sister to the clade *L. bakeri* (Aruba) + *L. ashmeadii* (northern South America east of the Andes). We highlight, however, that other samples of "*L. s. ornata"* from central and western Panama are nested in two separate, well-supported clades, one of which (Costa Rica + Panama) was already reported in previous studies (Daza *et al*. 2009). For the sake of taxonomic stability, we refer to these clades as *Leptodeira* sp., and recognize that their taxonomic identity should be addressed with further sampling (both taxa and characters). Similarly, solving the relationships among species within the *Leptodeira annulata/septentrionalis* complex needs further comprehensive study.

Schmidt & Walker (1943) described *Leptodeira larcorum* from "Northern coastal Peru, extending into the arid parts of the Marañon Valley", with Chiclin (coast) in department of La Libertad as the type locality. Because our phylogeny only includes samples from the Marañon Valley, we recommend inclusion of samples from the coast nearby the type locality to confirm the taxonomic identity of populations from the Marañon Valley currently assigned to *L. larcorum*. This species was soon regarded as a subspecies of *L. rhombifera* (Shreve 1947) first, and *L. septentrionalis* later (Duellman 1958; Peters 1960), until it was recently recognized again as a species (Barrio-Amorós 2019; this study). Duellman (1958) also suggested that populations from southwestern Ecuador were intergrades between *L. s. ornata* and *L. s. larcorum*, although he recorded no specimens of *L. s. larcorum* from southwestern Ecuador or nearby localities in Peru. Nevertheless, subsequent authors misinterpreted Duellman and recorded *L. s. larcorum* in Ecuador with no reference to vouchers (Peters 1960; Pérez Santos & Moreno 1991). Characters behind these taxonomic conclusions include the degree of compression of the body (cylindrical or compressed), enlargement of vertebral and paravertebral scale rows, a stripe or a butterfly-shaped mark on the neck, number of scale rows around midbody, and number of ventral scales. Our examination of a large sample of *L. ornata* from western Ecuador and *L. larcorum* from Peru shows that the aforementioned characters are intraspecifically variable, convergent, and taxonomically misleading. For example, in disagreement with previous authors, we found several specimens of *L. ornata* from western Ecuador with a dark nape stripe (Fig. 7), a character that was supposed to be present in *L. larcorum* and absent in *L. ornata* (see Peters 1960). Similarly, most specimens of *L. ornata* examined in this study lack enlarged vertebral or paravertebral scale rows, and their dorsal scale counts at midbody are not restricted to 21 (Table 5; *contra* Pérez Santos & Moreno 1991). These characters have led to misidentifications of *L. ornata* as *L. larcorum*. For example, Almendáriz & Carr (2012) reported *L. larcorum* (indentified as *L. septentrionalis larcorum*) from Machalilla National Park in Manabí Province, Ecuador; however, all specimens from this area included in our phylogeny belong to *L. ornata* (see terminals from Manabí Province in Figure 1). Based on morphological and phylogenetic evidence, with a large geographical sampling of *L. ornata* from western Ecuador and *L. larcorum* (Fig. 5; Appendix), we conclude that *L. larcorum* is apparently restricted to Peru. In addition, despite variation in color patterns in *L. ornata* and *L. larcorum*, both species can be readily distinguished from *L. misinawui* in having larger blotches along the body (Figs 3, 7).

Species of *Leptodeira* occur at low to moderate elevations, usually not exceeding 2,000 m asl (Duellman 1958, Koch *et al*. 2018). The authors of this paper have intensively sampled lowland areas close to the known distribution range of the new species herein described; therefore, *L. misinawui* seems to be different from other conspecifics in



Photo: M. Rivera/Bioweb

Leptodeira ornata, juvenile, SVL 165, QCAZ 16969. ECUADOR: Esmeraldas



Photo: D. Quirola/Bioweb

Leptodeira ornata, adult male, SVL 477, QCAZ 15015. ECUADOR: Esmeraldas



Photo: G. Pazmiño/Bioweb

Leptodeira ornata, adult male, SVL 505, QCAZ 15548. ECUADOR: Manabí



Photo: G. Pazmiño/Bioweb

Leptodeira ornata, adult male, SVL 509, QCAZ 15549. ECUADOR: Manabí



Photo: D. Núñez/Bioweb

Leptodeira ornata, juvenile, SVL 188, QCAZ 16047. ECUADOR: Guayas



Photo: D. Núñez/Bioweb

Leptodeira ornata, adult male, SVL 532, QCAZ 16338. ECUADOR: Guayas



Photo: D. Núñez/Bioweb

Leptodeira ornata, SVL 395, QCAZ 15546. ECUADOR: Pichincha



Photo: D. Salazar/Bioweb

Leptodeira ornata, adult female, SVL 315, QCAZ 4469. ECUADOR: Los Ríos



Photo: D.Núñez/Bioweb

Leptodeira ornata, adult, SVL 579, QCAZ 17101.
ECUADOR: El Oro



Photo: D. Quirola/Bioweb

Leptodeira ornata, juvenile, SVL 266, QCAZ 15104.
ECUADOR: Loja

Photo: D.Núñez/Bioweb



Leptodeira ornata, adult female, SVL 549, QCAZ 15105.
ECUADOR: Loja



Photo: D. Quirola/Bioweb

Leptodeira ornata, adult male, SVL 438, QCAZ 15106.
ECUADOR: Loja



Photo: C. Koch

Leptodeira larcorum, adult female, SVL 535, ZFMK 90930.
PERU: Cajamarca



Photo: C. Koch

Leptodeira larcorum, adult female, SVL 605, ZFMK 91793.
PERU: La Libertad



Photo: C. Koch

Leptodeira larcorum, adult male, SVL 335, CORBIDI 1865.
PERU: Cajamarca



Photo: C. Koch

Leptodeira larcorum, juvenile, SVL 228, CORBIDI 7666.
PERU: La Libertad

FIGURE 7. General view in life of specimens of *Leptodeira ornata* from western Ecuador and *L. larcorum* from Peru, showing variation in color patterns.

having a higher altitudinal distribution (950–2,734 m). The only other species of *Leptodeira* from western Ecuador is *L. ornata* (see taxonomic comments above). From a geographically widespread sample of 110 individuals of *L. s. ornata* from Ecuador housed at the QCAZ collection, 98% were collected at elevations below 700 m asl, and the rest below 1,120 m asl. Therefore, *L. misinawui* and *L. ornata* from Ecuador seem to be allopatrically distributed.

Leptodeira misinawui is apparently restricted to the Jubones River Basin, which extends from the Pacific coast to the Andes in southern Ecuador (0–4,000 m asl) and covers an area of 4,361 km^2 (Ochoa *et al.* 2014). Given that other snakes and lizards are restricted to this area—*Holcosus orcesi* (Peters)*, Phyllodactylus leoni* Torres-Carvajal *et al., Stenocercus rhodomelas* (Boulenger)*, Tantilla insulamontana* Wilson & Mena (Torres-Carvajal *et al.* 2020), and possibly an undescribed species of *Bothrops* (Salazar-Valenzuela *et al.* 2019)—, we conclude that the Jubones River Basin is an important area of endemism for squamate reptiles. This basin represents the northern limit of the Amotape-Huancabamba zone, which has long been recognized as a biologically diverse area with important levels of endemism for animals and plants (Koch *et al.* 2013; Torres-Carvajal 2007; Weigend 2004), as well as a major biogeographic barrier for some Andean organisms (Cadle 1991; Duellman 1979; Vuilleumier 1969), and a migration corridor for others (Quintana *et al.* 2017). Unfortunately, anthropogenic activities have considerably reduced natural ecosystems in southwestern Ecuador, one of the areas where reptiles are most threatened (Reyes-Puig *et al.* 2017). The area where *Leptodeira misinawui* was found is represented by forests < 60 km^2 in the highest and steepest regions. The surroundings show strong processes of change in land use, mainly by paddocks, numerous secondary roads, and deforestation by extraction of firewood. In fact, the lizard *Holcosus orcesi* has not been found in the last few decades despite many collecting efforts, suggesting that this species is critically endangered or extinct. Therefore, we recommend considering all species of reptiles endemic to the Jubones River Basin as endangered.

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APPENDIX

Specimens examined

***Leptodeira larcorum* (N=22).** PERU: **Amazonas:** ZFMK 85030: Chachapoyas: Balsas (-6.807, -77.991, 1,000 m asl); CORBIDI 5643: Utcubamba: Zapatalgo/Chiñuña (-6.092, -78.496, 637 m asl); CORBIDI 5644: Zapatalgo/Chiñuña (-6.059, -78.502, 888 m asl); MUSA 3245: Zapatalgo/Chiñuña (-6.070, -78.517, 503 m asl). **Cajamarca:** CORBIDI 1865, 7664: Jaén: Bellavista (-5.633, -78.65, 410−430 m asl); ZFMK 90929: Pucará (-6.031, -79.127, 1,014 m asl); ZFMK 90930: (-6.053, -79.120, 900 m asl); MUSA 2983: Chota: La Lucma (-6.242, -78.372, 587 m asl); FMNH 232617, FMNH 232618: Rio Zana. **La Libertad:** ZFMK 91794: Bambamarca: Calemar (-7.520, -77.7215, 1,143 m asl); CORBIDI 7665: Pataz: Chagual (-7.834, -77.634, 1,261 m asl); CORBIDI 7666: Vijus (-7.725, -77.653, 1,280 m asl); ZFMK 91793: Pias (-7.892, -77.564, 1,857 m asl); FMNH 34302 (Holotype), FMNH 34306–11 (Paratypes): Chiclin (-7.8, -79.1).

***Leptodeira ornata* (N=111).** ECUADOR: **Bolívar:** QCAZ 5301: Las Naves, Río Suquibi (-1.281, -79.312, 450 m asl). **El Oro:** QCAZ 7386: Puyango Protected Forest, access road (-3.874, -80.038, 315 m asl), QCAZ 14040: Arenillas Ecological Reserve (-3.511, -80.123, 9 m asl), QCAZ 14044: Arenillas Ecological Reserve (-3.567, -80.143, 8 m asl), QCAZ 17101: Arenillas Ecological Reserve, surroundings of Montúfar military base (-3.574, -80.122, 23 m asl). **Esmeraldas:** QCAZ 5255: Caimito (0.698, -80.090, 121 m asl), QCAZ 7335: Caimito surroundings (0.962, -79.513), QCAZ 10550: Caimito, Omar Torres' farm (0.6955, -80.090, 137 m asl), QCAZ 3502: Angostura, Santiago river, Tinajas stream (0.890, -78.842, 110 m asl), QCAZ 7257, 8020: Durango (1.047, -78.618), QCAZ 5421: 3 km on road Durango-San Lorenzo (1.072, -78.651, 158 m asl), QCAZ 2889: Durango surroundings (1.043, -78.624), QCAZ 15379: 20 km airline SE Tundaloma Lodge (1.035, -78.623, 233 m asl), QCAZ 6277, 6422: Estero de Leche (0.505, -80.025), QCAZ 7552: Playón de San Francisco, 2 km E on road to Durango (1.087, -78.690, 63 m asl), QCAZ 16967: Bilsa Biological Station, Dogola river (0.362, -79.717, 488 m asl), QCAZ 16968: Bilsa Biological Station, Dogola river (0.372, -79.732, 464 m asl), QCAZ 16966: Bilsa Biological Station, Verde trail (0.337, -79.721, 516 m asl), QCAZ 16969: Cube lake (0.394, -79.644, 326 m asl), QCAZ 15017: Tesoro Escondido reserve, trail "A" (0.494, -79.136, 686 m asl), QCAZ 15013: Tesoro Escondido reserve, main cabin (0.542, -79.145, 264 m asl), QCAZ 15014: Tesoro Escondido reserve, Camarón river (0.545, -79.139, 244 m asl), QCAZ 15015–16: Tesoro Escondido reserve, Camarón river (0.545, -79.138, 260 m asl), QCAZ 6196: S Quingue (0.716, -80.092), QCAZ 1665, 1668, 1719: Viche (0.661518, -79.53874). **Guayas:** QCAZ 6026: 27 km Las Mercedes-El Naranjal, QCAZ 16052: Parque Lago (-2.214, -80.102, 52 m asl), QCAZ 17102–104: Balzar, Universidad Agraria del Ecuador (-1.364, -79.909, 35 m asl), QCAZ 6388, 9108: Cerro Blanco Protected Forest (-2.182, -80.018, 60 m asl), QCAZ 8730, 9119, 9127: Cerro Blanco Protected Forest (-2.18, -80.020, 237 m asl), QCAZ 14180: Cerro Blanco Protected Forest, Canoa creek (-2.177, -80.022, 66 m asl), QCAZ 4014: Parque Histórico Guayaquil (-2.144, -79.869), QCAZ 17105–107: Quinta Caoba, ~2.5 km NNE Balzar (-1.329, -79.893, 23 m asl), QCAZ 7265, 8776–80: Manglares Churute Ecological Reserve, Cerro Masvale (-2.396, -79.630, 45 m asl), QCAZ 16339–340: Manglares Churute Ecological Reserve, surroundings of El Canclón lake (-2.425, -79.589, 16 m asl), QCAZ 16338: Manglares Churute Ecological Reserve, Cerro Pancho Diablo, Los Aulladores trail (-2.412, -79.648, 185 m asl), QCAZ 16047: San Pablo, Playas military area (-2.571, -80.366, 16 m asl), QCAZ 16048–051: San Pablo, Playas military area (-2.569, -80.392, 30 m asl). **Loja:** QCAZ 6392: 14 km N Alamor (-3.949, -80.027, 666 m asl), QCAZ 4485: Puyango Petrified Forest (-3.893, -80.076, 327 m asl), QCAZ 10344, 10349–350, 10357: El Faique creek (-4.337, -80.275, 256 m asl), QCAZ 10371: El Faique creek, on road to Las Cochas del Almendro (-4.286, -80.232, 257 m asl), QCAZ 15106: La Ceiba-Pilares reserve, El Ñioco creek (-4.272, -80.350, 360 m asl), QCAZ 15103–104: La

Ceiba-Pilares reserve, La Perdida creek (-4.280, -80.326, 413 m asl), QCAZ 15105: La Ceiba-Pilares reserve, La Perdida creek (-4.283, -80.325, 400 m asl), QCAZ 12571: Cazaderos Natural Reserve (-4.024, -80.447, 213 m asl), QCAZ 3070: Zapotillo, Las Lajas creek (-4.387, -80.245, 220 m asl). **Los Ríos:** QCAZ 10198: Río Palenque Scientific Center (-0.589, -79.363, 195 m asl), QCAZ 8429, 8431: El Descanso (-0.661, -79.424), QCAZ 4469: Jauneche (-1.246, -79.661, 71 m asl). **Manabí:** QCAZ 1638: 40 km vía Guabal, QCAZ 15549: Camarones (-0.121, -80.115, 654 m asl), QCAZ 6387: Canoas, 3 km vía a San Vicente (-0.465, -80.427, 8 m asl), QCAZ 11774: Comunidad Cholote (-0.130, -80.117, 46 m asl), QCAZ 11776: Comunidad La Mina (59 m asl), QCAZ 11773: Comunidad Río Javier (-0.695, -80.013, 158 m asl), QCAZ 11775: Comunidad Santa Rosa (-0.206, -80.125, 43 m asl), QCAZ 10597: El Aromo (-1.047, -80.833), QCAZ 7206: 7 km El Carmen-Pita, Rancho RH (400 m asl), QCAZ 11516: Pacoche Lodge & Reserve (-1.067, -80.881, 335 m asl), QCAZ 6418–19: Parque Nacional Machalilla, Agua Blanca (-1.541, -80.744), QCAZ 15547: Playa La Botada (-1.057, -80.907, 16 m asl), QCAZ 15548: Playa Liguiqui (-1.024, -80.881, 2 m asl), QCAZ 4650: Reserva Ecológica Jama Coaque (-0.091, -80.147), QCAZ 16964–965: Reserva Ecológica Mache-Chindul, Estación Biológica Bilsa, Río Rompe Frente y tributarios (0.351, -79.714, 499 m asl), QCAZ 10761, 10763: Reserva Lalo Loor, Sendero Aullador (-0.078, -80.148, 50 m asl), QCAZ 7505: Río Ayampe (-1.673, -80.809, 70 m asl), QCAZ 11453–454: Río Coaque (0.050, -80.039, 33 m asl), QCAZ 7502: Río Coaque, 20 km E Pedernales–El Carmen (-0.001, -79.894, 105 m asl), QCAZ 14496: Zapote (-0.376, -79.606, 154 m asl). **Pichincha:** QCAZ 15546: Ganaderos Orenses (-0.093, -78.990, 707 m asl), QCAZ 17619: Milpe Bird Sanctuary (0.033, -78.869, 1,137 m asl), QCAZ 16231–232: Milpe Bird Sanctuary, Manakin trail (0.0346, -78.867, 1,057 m asl), QCAZ 17593: Monterreal Rainforest Ecolodge, trail to Monterreal waterfall (-0.093, -78.990, 699 m asl), QCAZ 7506–07: 1 km E Pedro Vicente Maldonado (0.083, -79.039, 670 m asl), QCAZ 1204: Puerto Quito (0.122, -79.254, 135 m asl); **Santa Elena:** QCAZ 12459: El Rincón del Tigre, 1 km from Dos Mangas (-1.826, -80.655, 140 m asl); **Santo Domingo de los Tsáchilas:** QCAZ 2041, 7498: La Concordia, Bosque Protector La Perla (-0.057, -79.359, 190 m asl), QCAZ 1612: Santo Domingo de los Tsáchilas (-0.264, -79.192, 518 m asl).