

# Reassessing the systematics of *Leptodeira* (Serpentes, Dipsadidae) with emphasis in the South American species

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## Abstract

Within the diverse subfamily Dipsadinae, Imantodini represents one of the few groups distributed in North, Central and South America. The tribe comprises the genera *Leptodeira* and *Imantodes*, from which *Leptodeira* is the most diverse, including 15 species and 11 subspecies, distributed from southern USA to central Argentina. Taxonomy and affinities among these taxa are poorly resolved, and the phylogenetic relationships among the South American diversity were never properly assessed before. Here, we investigate the phylogenetic relationships and the taxonomic status of *Leptodeira* spp. based on a comprehensive multilocus dataset with emphasis in the South American radiation. Besides assessing the phylogenetic relationship and species cohesion, we also evaluate the morphological variation among the South American diversity of *Leptodeira*. Our results support the monophyly of Imantodini and *Leptodeira*, while indicating that several individuals classified as *Leptodeira annulata* and *L. septentrionalis* do not cluster together within their respective species. Moreover, specimens identified as belonging to the subspecies *L. a. annulata*, *L. a. cussiliris*, *L. s. ornata* and *L. s. polysticta* do not group together suggesting the current classification includes non-natural groups. The analysis of morphological evidence also supports the phylogenetics results, indicating that several clades can be recognized as evolutionary units presenting distinct phenotypes. To equate the taxonomy to our results, we propose a new taxonomic arrangement for *Leptodeira* in which we are: (1) redefining the composition of *L. annulata* and *L. septentrionalis*; (2) elevating five subspecies to species level; (3) revalidating one species; (4) recognizing four species complexes; and (5) indicating the presence of hidden diversity (probably four undescribed species). Finally, we describe a new species (*Leptodeira tarairiu* sp. nov.) from the open formations of South America (Cerrado and Caatinga), and we provide detailed redescrptions for all South American species of *Leptodeira*.

## KEYWORDS

imantodini, morphology, phylogeny, taxonomy

## 1 | INTRODUCTION

The snake family Dipsadidae (*sensu* Zaher et al., 2009) is one of the largest radiations of squamates, assembling more than 750 species mostly endemic to the Neotropics, with two relictual groups occurring in Asia and North America (Grazziotin et al., 2012; Sun et al., 2011; Wang & Messenger, 2014; Zaher et al., 2018). The Neotropical radiation of dipsadids includes two monophyletic groups, allocated in the subfamilies Dipsadinae and Xenodontinae (Cadle, 1984; Grazziotin et al., 2012; Vidal et al., 2007; Vidal & Hedges, 2002; Zaher et al., 2009, 2014, 2019).

Dipsadinae (*sensu* Zaher et al., 2009) differs from Xenodontinae by a number of immunological, morphological and molecular characters (Cadle, 1984; Dowling & Jenner, 1987; Kraus & Brown, 1998; Myers & Cadle, 1994; Pinou et al., 2004; Slowinski & Lawson, 2002; Zaher, 1999). Although Dipsadinae represents a mainly Central American radiation (Cadle, 1984, 1985), typical dipsadine genera such as *Atractus*, *Dipsas*, *Leptodeira* and *Imantodes* (Cadle, 1985) are also known to be widely distributed throughout South America. *Leptodeira* and *Imantodes* are mainly nocturnal, arboreal snakes that are long known to be more closely related to each other than to any other dipsadine (Daza et al., 2009; Duellman, 1958; Mulcahy, 2007; Mulcahy et al., 2011) and, for this reason, were formally allocated in the tribe Imantodini (Myers, 2011).

Duellman (1958) provided the first taxonomic, and until now the more complete revision of *Leptodeira* (cat-eyed snakes). Based on a comprehensive morphological analysis of a broad geographical sampling he considered valid the following taxa: (1) *Leptodeira annulata annulata* Linnaeus, 1758, *Leptodeira annulata ashmeadii* Hallowell, 1845, *Leptodeira annulata cussiliris* Duellman, 1958, *Leptodeira annulata pulchriceps* Duellman, 1958, and *Leptodeira annulata rhombifera* Günther, 1872; (2) *Leptodeira septentrionalis septentrionalis* Kennicott, 1859, *Leptodeira septentrionalis larcorum* Schmidt & Walker, 1943, *Leptodeira septentrionalis ornata* Bocourt, 1884, and *Leptodeira septentrionalis polysticta* Günther, 1885; (3) *Leptodeira bakeri* Ruthven, 1936; (4) *Leptodeira frenata frenata* Cope, 1886, *Leptodeira frenata malleisi* Dunn & Stuart, 1935, and *Leptodeira frenata yucatanensis* Cope, 1886; (5) *Leptodeira latifasciata* Günther, 1894; (6) *Leptodeira maculata* Hallowell, 1861; (7) *Leptodeira nigrofasciata* Günther, 1885; (8) *Leptodeira punctata* Peters, 1866; and (9) *Leptodeira splendida splendida* Günther, 1885, *Leptodeira splendida bressoni* Taylor, 1938, and *Leptodeira splendida ehippiata* Smith & Tanner, 1944. He also proposed four morphological groups to accommodate these taxa: (1) *annulata* group, comprising *L. annulata*, *L. bakeri*, *L. frenata*, and *L. maculata*; (2) *septentrionalis* group, formed by *L. septentrionalis* and *L. splendida*; (3)

*nigrofasciata* group, composed by *L. nigrofasciata* and *L. latifasciata*; and (4) the *punctata* group for *L. punctata*.

Shannon and Humphrey (1964) removed *L. latifasciata* from *Leptodeira*, allocating it in *Pseudoleptodeira* Taylor, 1938. After being synonymized with *Leptodeira* by Duellman (1966) and resurrected by Dowling and Jenner (1987), recently Reyes-Velasco and Mulcahy (2010) confirmed the taxonomic proposal of Shannon and Humphrey through a molecular phylogenetic analysis. They also indicated that the former *Pseudoleptodeira uribei* Ramírez-Bautista & Smith, 1992 is in reality a species of *Leptodeira*, suggesting that *L. uribei* is closed allied to *L. frenata*.

Despite the inclusion of *L. uribei* and the removal of *L. latifasciata* from *Leptodeira*, the current composition of the genus is mainly based on the groups proposed by Duellman (1958). In his study, Duellman classified most of the taxonomic units within the genus as subspecies of *L. annulata* and *L. septentrionalis*. Both species are distributed throughout the Neotropical realm and the geographic distribution of their subspecies (*sensu* Duellman, 1958) can be summarized as follows: *L. a. annulata*, distributed in the Amazon forest, Cerrado and on the Brazilian Atlantic coast; *L. a. ashmeadii*, occurring on the Caribbean coast and in the Llanos of Venezuela and Colombia; *L. a. cussiliris*, distributed on the Atlantic and Pacific versant of Mexico; *L. a. pulchriceps*, restrict to the Pantanal and Chaco regions; *L. a. rhombifera*, distributed in Central America, from Guatemala to Panama; *L. s. larcorum*, occurring in the Marañon Valle and on the Pacific versant of Peru, and southern coast of Ecuador; *L. s. ornata*, distributed from Costa Rica to the northern coast of Ecuador, occurring also in the Cauca and Magdalena valleys in Colombia; *L. s. polysticta*, distributed from Mexico to Costa Rica; and *L. s. septentrionalis* that occurs from southeastern Texas to Mexico, through the Gulf of Mexico coast. In addition to these subspecies, Duellman (1958) identified three morphologically distinct Brazilian populations of *L. a. annulata*, one present along the banks of the São Francisco River, and two others distributed allopatrically throughout northeastern and southeastern coasts of Brazil.

The morphological polymorphism and wide distribution of *Leptodeira* entail a complex evolutionary history, which has been a long-time challenge for systematists, and only recently started to be unravelled through phylogenetic methods (Daza et al., 2009; Mulcahy, 2007; Mulcahy et al., 2011; Torres-Carvajal et al., 2020). Recent analyses using molecular evidence retrieved a monophyletic *Leptodeira* (including *L. uribei*) but did not support all species group proposed by Duellman (Daza et al., 2009; Mulcahy, 2007). Mulcahy (2007) recognized *L. s. polysticta* and *L. a. cussiliris* as distinct species. He also indicated that *L. septentrionalis* and *L. annulata* were paraphyletic

with respect to each other, although he did not take further taxonomic decisions and allocated these species in a clade named as '*L. annulata* complex'.

Daza et al. (2009) extended considerably the geographic and taxonomic sampling present in Mulcahy's study. In their phylogenetic analysis they also recovered the paraphyly between *L. septentrionalis* and *L. annulata* and referred to this composed clade as '*L. annulata-septentrionalis* complex'. Daza et al. (2009) also identify two main clades within the complex: (1) a northern clade, distributed from the southern Sonora region in Mexico to northern Panama [composed and phylogenetically structured as: (*L. s. polysticta*, ((*L. rubricata*, *L. a. rhombifera*), ((*L. a. cussiliris*, *L. maculata*), *L. a. cussiliris*))]]; and (2) a southern clade, ranging from southern Costa Rica through all South America, reaching central Argentina and Paraguay [composed and phylogenetically structured as: ((*L. s. ornata*, *L. a. annulata*), (*L. s. ornata*, (*L. bakeri*, (*L. a. ashmeadii*, *L. a. annulata*)))). However, Daza et al. (2009) did not provide further evaluation of the South American taxa (particularly the diversity distributed in the cis-Andean region of South America), since they concentrated the sampling effort on Central America and the central region of Colombia (regions of Cauca and the Magdalena River Valley).

In 2019, Barrio-Amorós promoted several taxonomic acts regarding the composition of *Leptodeira* (Barrio-Amorós, 2019). Based mainly on the phylogenetic results of Mulcahy (2007) and Daza et al. (2009), and comments about the morphological analyses of Duellman (1958), Savage (2002) and Solórzano (2004) he elevated, synonymized and revalidated several taxa. Since Barrio-Amorós (2019) did not provide enough information about the methods and datasets used, his taxonomic proposal leaves room for formal tests and proper taxonomic description (see further comments in "Material and methods" and "Discussion").

More recently, Torres-Carvajal et al. (2020) provided a more comprehensive phylogenetic analysis of *Leptodeira*, and described a new Peruvian species belonging to the *L. annulata-septentrionalis* complex, *Leptodeira misinawui* Torres-Carvajal et al. (2020). Although they agreed with Barrio-Amorós (2019) in recognizing the subspecies *L. s. larcorum* as a valid species, their proposed taxonomic scheme is different when considering the composition of '*L. s. ornata*'. Torres-Carvajal et al. (2020) elevated *L. s. ornata* to species level but restricted its definition to only include the well-supported clade composed by samples from central and eastern Panama, western Colombia, and western Ecuador. The unrelated clade formed by populations of '*L. s. ornata*' from Costa Rica and northern Panama were referred by these authors as *Leptodeira* sp., pending further analysis to access its taxonomic identity.

Therefore, despite recent advances, phylogenetic affinities within the *L. annulata-septentrionalis* complex are still poorly resolved, and the systematics of the South American populations (particularly the cis-Andean region) was never accessed before. Moreover, the taxonomy proposed by recent studies did not provide thorough descriptions of species limits and the geographic distributions of most taxa were poorly defined. Here, we re-evaluate the systematics of *Leptodeira* using comparative morphological approaches and phylogenetic analyses based on a multilocus dataset. We mainly focused our phylogenetic analyses on the South American radiation of *Leptodeira*, and we generated new sequences for key populations sampled in Argentina, Brazil, Colombia and Peru, increasing the geographical sampling in more than 3.5 million km<sup>2</sup> when compared to previous studies. Based on our phylogenetic results and comparative morphological analyses we describe a new South American species for *Leptodeira*, and we propose a provisional taxonomic scheme for the genus.

## 2 | MATERIAL AND METHODS

### 2.1 | Taxonomic background

The abundance of recent taxonomic schemes for *Leptodeira* turns into a difficult task to unambiguously refer to some species without explicitly stating their definition and limits (e.g. *Leptodeira ornata sensu* Barrio-Amorós, 2019 or *Leptodeira ornata sensu* Torres-Carvajal et al., 2020). Therefore, we are preliminarily following Duellman's (1958) classical taxonomic proposal for *Leptodeira*, only accepting the inclusion of *L. urbei* (Reyes-Velasco & Mulcahy, 2010) and the new species described by Torres-Carvajal et al. (2020), *L. misinawui*. Additionally, we are following Daza et al. (2009) and we are preliminary considering the phylogenetic unit of the '*annulata-septentrionalis* complex', which includes the entire diversity of *L. annulata*, *L. septentrionalis*, *L. bakeri* and *L. maculata*.

Duellman (1958) was the last comprehensive taxonomic revision for the genus, which was based on morphological evidence, proper taxonomic description, and appropriate information about geographic distribution (see above). Although we refrain from initially following some recent taxonomic changes we are not assuming that such proposals are unfounded [e.g. the revalidation of *L. rubricata* by Savage (2002); synonymization of *L. a. cussiliris* with *L. maculata* by Daza et al. (2009); elevation of *L. s. larcorum* and redefinition of *L. ornata* by Torres-Carvajal et al. (2020), and the broad taxonomic rearrangement of Barrio-Amorós (2019)]. Our return to

Duellman's classical taxonomic units is based on our understanding of the strengths of his broader view of the whole morphological diversity included in *Leptodeira*, and as a formal strategy to properly test the recently proposed taxonomic hypotheses.

## 2.2 | Taxon sampling for DNA sequencing

We sequenced a total of 146 DNA fragments, from 33 specimens of *Leptodeira* – *L. a. annulata*, *L. a. ashmeadii*, *L. a. pulchriceps*, *L. maculata*, *L. s. ornata*, *L. s. polysticta*, *L. s. septentrionalis* and *L. uribei* (Table S1), for five genes, including three mitochondrial (*cytb*, *nd4* and *cox1*) and two nuclear (*dnah3* and *nt3*), as follows: 29 samples for *cox1* (cytochrome c oxidase subunit I), 30 for *cytb* (cytochrome b), 26 for *nd4* (NADH dehydrogenase subunit 4), 30 for *dnah3* (dynein, axonemal, heavy chain 3) and 31 for *nt3* (neurotrophin 3). We also sampled throughout the tribe Imantodini by including other 297 additional GenBank sequences for the diversity of *Leptodeira* (Table S2) and for two species of *Imantodes* (*Imantodes cenchoa* and *I. inornatus*). Aiming to provide further outgroups to our phylogenetic analysis, we additionally included a reduced version of Zaher et al. (2018) and Zaher et al. (2019) molecular matrix (Table S2). We root our phylogenetic tree in Boinae, by using *Eryx conicus* and *Boa constrictor*.

## 2.3 | DNA sequencing and alignment

DNA was extracted from scales, liver, muscle or heart tissue using the PureLink® commercial extraction kit (Invitrogen), following the manufacturer's protocol. The following primers were used for PCR amplification: to amplify the fragment for *cox1* we used a modified version of primer MLepF1 (5' GCA TTY CCA CGA ATA AAT AAY ATR AG 3') from Hajibabaei et al. (2006) and COI\_r928 (5' CCT GTT GGA AYT GCR ATR ATT AT 3') from Graboski et al. (2018); for *cytb* we used 703Botp.mod and MVZ16p.mod from Grazziotin et al. (2012); for *dnah3* we used the primers DNAH-f1 and DNAH-r6 (Townsend et al., 2008); for *nd4* we used NAD4 and Leu (Arevalo et al., 1994); and for *nt3* we used the primers NT3F3 and NT3R4 (Noonan & Chippindale, 2006). To amplify the gene fragments, we followed the protocols described by Grazziotin et al. (2012). Both strands of the PCR amplification products were sequenced using the MacroGen Sequencing Service (MacroGen Inc.).

The chromatograms were quality checked, and when necessary, edited manually. The consensus of both strands was generated using Geneious 7.1.8 ([\[ous.com\]\(http://www.genei.com\), Kearse et al., 2012\). Alignments were carried out in MAFFT v7.017 \(Katoh & Standley, 2013\), we use the alignment algorithm G-INS-i for the coding genes and the E-INS-i algorithm for the tRNA sequences. We used the program Sequencing Matrix v1.7.8 \(Vaidya et al., 2011\) to concatenate all genes and generate the files for the subsequent analyses.](http://www.genei</a></p>
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## 2.4 | Phylogenetic inference

We performed maximum likelihood (ML) analyses using RAxML 8.2.3 (Stamatakis, 2014). We used PartitionFinder 2 (Lanfear et al., 2016) to choose the combined sets of partitioning schemes and models of molecular evolution. We divided our concatenated matrix into 15 initial partitions (each coding genes were partitioned by codon positions), and we performed a search using the *greedy* option. We performed a run allowing the program to select using Akaike Information Criterion with correction (AIC) only the models of molecular evolution implemented in RAxML (models GTR and GTR + G).

## 2.5 | Specimens analysed, meristic counts and measures

In our morphological comparison, we analysed the South American diversity of *Leptodeira*, and we included samples of two species and five subspecies as follows (see Appendix S1 for a list of analysed material): *L. annulata* (*L. a. annulata*, *L. a. ashmeadii* and *L. a. pulchriceps*) and *L. septentrionalis* (*L. s. ornata* and *L. s. septentrionalis*). For taxonomic comparison with *L. misinawi* and *L. larcorum*, we used the information available in Torres-Carvajal et al. (2020).

Terminology for cephalic shields followed Dixon (1983), and the method of counting ventral and subcaudal scales followed Dowling (1951). Measurements of specimens were taken under a stereoscope with a dial calliper to the nearest 0.1 mm, except for total length (TTL), snout-vent length (SVL), and tail length (TL), which were measured to the nearest 1.0 mm with a flexible ruler. Counts and measurements of paired structures are given as right/left. Dorsal scales are given as anterior body/mid-body/posterior body. Generalized colouration summaries were derived directly from live specimens or indirectly from photos of live specimens. We codify the colour pattern of the head, body and tail in dorsal, lateral and ventral views according to Duellman (1958). Herein, the term 'blotch' refers to broad (two or more scales long and wide) dorsal markings located in the vertebral and paravertebral regions, the term 'spot' refers to smaller (between one and

two scales long and wide) markings on dorsum or venter, and 'dot' refers to any marking smaller than a single scale.

Sex was determined by conducting a longitudinal incision at the base of the tail to check for the presence of a hemipenis. Preserved hemipenes were prepared following Pesantes (1994), observing the precautions highlighted by Zaher and Prudente (2003). Terminology for hemipenial descriptions followed Dowling and Savage (1960) and Zaher (1999). We dissected the specimens of the new species at the ventral portion nearest to the cloacal plate to observe the condition of the epididymis, and we preliminarily infer maturity by considering the presence of convoluted epididymis (Shine, 1977, 1982).

### 3 | RESULTS

#### 3.1 | Phylogenetic relationships

Our concatenated alignment for extended dataset totalized in 3669 base pairs (1089 bp for *cytb*, 643 bp for *cox1*, 681 bp for *nd4*, 737 bp for *dnh3* and 519 bp for *nt3*) for 206 terminals. PartitionFinder selected 12 partitions with GTR + G model for ML analysis.

The tribe Imantodini was recovered as monophyletic in the ML analyses, with high values of BS (96%) and was positioned as a sister group of the clade formed by *Atractus trihedrurus* and *Dipsas catesbyi*, with high values of BS (89%). *Imantodes* and *Leptodeira* were recovered as monophyletic, showing low values of BS (60%) and high values of BS (81%), respectively. Our phylogenetic analyses recovered the two species of *Imantodes* as monophyletic, with high values of clade support (Figure S1). *Imantodes inornatus* (BS values of 97%) was retrieved as the sister group of a clade composed by *Imantodes cenchoa* (BS values of 76%).

Within *Leptodeira*, our analyses recovered five well-supported main clades (Figure 1a-c), as follows: clade C1 (100%), composed only by samples of *L. nigrofasciata*; clade C2 (100%), composed by *L. frenata* and *L. uribei*; clade C3 (100%) formed by *L. punctata* only; clade C4 (100%), composed by *L. splendida* and *L. bressoni*; and clade C5 (88%), which includes all samples from the '*L. annulata-septentrionalis* complex'. These five clades were recovered as successive sister groups (Figure 1a-c).

Within clade C5 our phylogenetic trees show six well-supported main subclades (Figure 1a-c). These subclades were named as follows: subclade A (98%) composed by *L. s. septentrionalis* and *L. s. polysticta*; subclade B (99%) composed of *L. a. cussiliris*, *L. maculata*, *L. a. rhombifera* and *L. a. rubricata*; subclade C (100%) composed by *L. misinawui*; subclade D (100%) composed by specimens of *L. s. ornata* from Costa Rica and Panama (*L. s. ornata*

lineage L3 in Figure 1b); subclade E (100%) comprising specimens of *L. a. annulata* and *L. a. pulchriceps*; subclade F (97%) composed by *L. larcorum*; subclade G (99%) formed by individuals of *L. bakeri* and *L. a. ashmeadii*; and subclade H (96%) composed by individuals of *L. s. ornata* from South America (*L. s. ornata* lineages L1 and L2). Subclade A and B were recovered as the successive sister groups (76%) of a strongly supported clade (95%) composed by all other subclades. The subclade C was recovered as the successive sister group of a low supported clade (39%) composed by the remaining subclades. The subclades D and E grouped together with moderate support (70%), and the subclades F, G and H grouped together with strong support (95%).

The species *L. annulata* and *L. septentrionalis* were not recovered as monophyletic in our phylogenetic analysis, as well as the subspecies *L. a. annulata*, *L. a. cussiliris*, *L. s. polysticta*, and *L. s. ornata*. All the other species and subspecies of *Leptodeira*, with more than one sampled individual, were retrieved as monophyletic (Figure 1a-c; Figure S1).

The nominal subspecies *L. s. septentrionalis* was positioned in subclade A, nested inside the lineages of *L. s. polysticta* (Figure 1a). The diversity of *L. s. polysticta* was structured in three different lineages, represented by the following three well-supported clades: *L. s. polysticta* L1 (82%), formed by samples distributed in the Atlantic coast of Mexico; *L. s. polysticta* L2 (100%), including individuals from the Atlantic coast of Central America; and *L. s. polysticta* L3 (99%) comprising samples from the Pacific coast of Mexico, Guatemala, and El Salvador. *Leptodeira s. polysticta* L3 and *Leptodeira s. polysticta* L2 were recovered as successive sister groups (98%) of a clade composed by *L. s. septentrionalis* and *L. s. polysticta* 1 (98%).

Within subclade B, two main clades sister clades were recovered, one including samples of *L. a. rhombifera* and the only sampled individual of *L. a. rubricata* (51%); and the second formed by individuals of *L. a. cussiliris* and *L. maculata* (100%).

*Leptodeira maculata* was positioned nested inside the lineages of *L. a. cussiliris* and the non-monophyletic *L. a. cussiliris* presented the following two lineages: *L. a. cussiliris* L1 (100%), composed by individuals from the Atlantic coast of Mexico, Isthmus of Tehuantepec, and the Pacific coast of Guatemala; *L. a. cussiliris* L2 (100%), formed by individuals from the Pacific coast of Mexico. The clade composed by individuals of *L. maculata* was retrieved with strong BS support (87%).

The subclade C comprises of *L. misinawui* from Ecuador, with a strong BS support (100%). The subclade D (100%) only comprises samples of *L. s. ornata* (*L. s. ornata* L3 in Figure 1b) from Costa Rica and northern Panama

and is the sister group of subclade E (100%) that includes samples of *L. a. annulata* and *L. a. pulchriceps*.

*Leptodeira annulata annulata* is not monophyletic in our phylogenetic trees and the following three main lineages were recovered for this subspecies: *L. a. annulata* L1 (100%), composed by specimens from Ecuador; *L. a. annulata* L2 (95%), composed by individuals from the open areas of the central and northeastern Brazil (Caatinga and Cerrado); and *L. a. annulata* L3 (99%), comprising specimens from Amazonia, Atlantic forest, highland forest fragments in the northeastern Brazil (Brejos de Altitude), and from the ecotonal regions of the central-western and northeastern Brazil. *Leptodeira annulata annulata* L2 and *L. a. annulata* L3 formed a highly supported clade (99%) that is sister to the sampled individuals of *L. a. pulchriceps* (100%). *Leptodeira annulata annulata* L1 was recovered as the basal lineage in this subclade sister to a clade formed by *L. a. pulchriceps*, *L. a. annulata* L2 and *L. a. annulata* L3 (100%).

*Leptodeira larcorum*, in subclade F, is the sister group of a highly supported clade (95%) composed by subclade G (99%) and H (96%). *Leptodeira bakeri* (100%) grouped with *L. a. ashmeadii* (99%) in subclade G. The following two different lineages of *L. s. ornata* were recovered in subclade H: *L. s. ornata* L1 (<70%) from Ecuador and *L. s. ornata* L2 from Cauca and Magdalena River Valley in Colombia and north Ecuador (97%).

### 3.2 | New taxonomic arrangement for *Leptodeira*

Based on the topology of our phylogenetic tree and on the available morphological evidence, we present below a reassessed taxonomic arrangement for *Leptodeira*. We avoid changing taxa that were not properly evaluated here (see Appendix S2) or in any recent study. For these we preserve the classical definition of Duellman (1958), only transferring or elevating subspecies or geographically restricted populations to keep a cohesive taxonomy on the species level. We are also explicitly implementing the use of 'open nomenclature' (Bengtson, 1988; Sigovini et al., 2016) to express remarks about taxa redefined here. Particularly, we use the abbreviation aff. (*affinis*) to indicate that a specific lineage or population has some morphological

affinity to a known species, but it seems not to represent the same taxonomic unit, and likely belongs to a new and undescribed species (Bengtson, 1988).

Although we concur that evolutionary lineages are better expressed as full species, which should preferentially represent the essential taxonomic units in a classification system, we are keeping here the subspecific level for some apparently well recognized genetic lineages or geographically restricted population. We opted for maintaining the traditional subspecific level for some lineages aiming to be conservative, and/or because we were not able to access enough data to properly test alternative taxonomic hypotheses.

We propose here the following taxonomic changes for *Leptodeira*:

1. Redefinition of *Leptodeira septentrionalis* by restricting its definition to include the diversity of two subspecies, *L. s. septentrionalis*, and *L. s. polysticta*, distributed from southern USA to El Salvador (clade A; Figure 1a; Figure S1). Our results do not support the elevation of *L. s. polysticta* (sensu Duellman, 1958) to species level as suggested by Campbell (1998), and we argue that keeping the subspecific level to both morphotypes represents a more conservative approach (see extended justification in the Discussion section).
2. Redefinition of *L. maculata* (sensu Barrio-Amorós, 2019) to comprise *L. m. maculata* ('*L. maculata*' as defined by Duellman, 1958) and *L. m. cussiliris* ('*L. a. cussiliris*' sensu Duellman, 1958), thus transferring the subspecies *L. a. cussiliris* from *L. annulata* to *L. maculata* (justification for this taxonomic proposal is described in the Discussion section).
3. We consider *L. a. rubricata* and *L. a. rhombifera* as valid species in order to keep a cohesive taxonomy on the species level. Therefore, we acknowledge the taxonomic proposal of Savage (2002) and Barrio-Amorós (2019) and we remove the morphological diversity of *L. a. rubricata* and *L. a. rhombifera* from the redescription of *L. annulata* (extended justification in the Discussion section).
4. We redefine *L. ornata* (sensu Barrio-Amorós, 2019) as only comprising the populations distributed in Colombia and southern Panama (supporting the taxonomic scheme proposed by Torres-Carvajal et al.,

**FIGURE 1** Maximum Likelihood tree zoomed-in *Leptodeira* resulting from the RAxML analysis. Numbers on branches represent bootstrap values of RAxML (>75%). The color of branches and tip labels represents the previous taxonomy for the genus. Black bars represent the taxonomy proposed in this study. Underline tip labels represent samples sequenced in this study. A) Maximum Likelihood tree zoomed-in *Leptodeira nigrofasciata*, *L. frenata*, *L. uribei*, *L. punctata*, *L. sp. splendida*, *L. sp. bressoni*, *L. se. septentrionalis*, *L. se. polysticta* L1, *L. se. polysticta* L2, and *L. se. polysticta* L3 clades. B) Maximum Likelihood tree zoomed-in *Leptodeira an. rubricata*, *L. an. rhombifera*, *L. an. cussiliris* L1, *L. an. cussiliris* L2, *L. maculata*, *L. misinawui*, *L. se. ornata* L3, *L. an. annulata* L1, *L. an. pulchriceps*, and *L. an. annulata* L2 clades. C) Maximum Likelihood tree zoomed-in *L. an. annulata* L3, *L. se. larcorum*, *L. se. bakeri*, *L. an. ashmeadii*, *L. se. ornata* L2, and *L. se. ornata* L1 clades



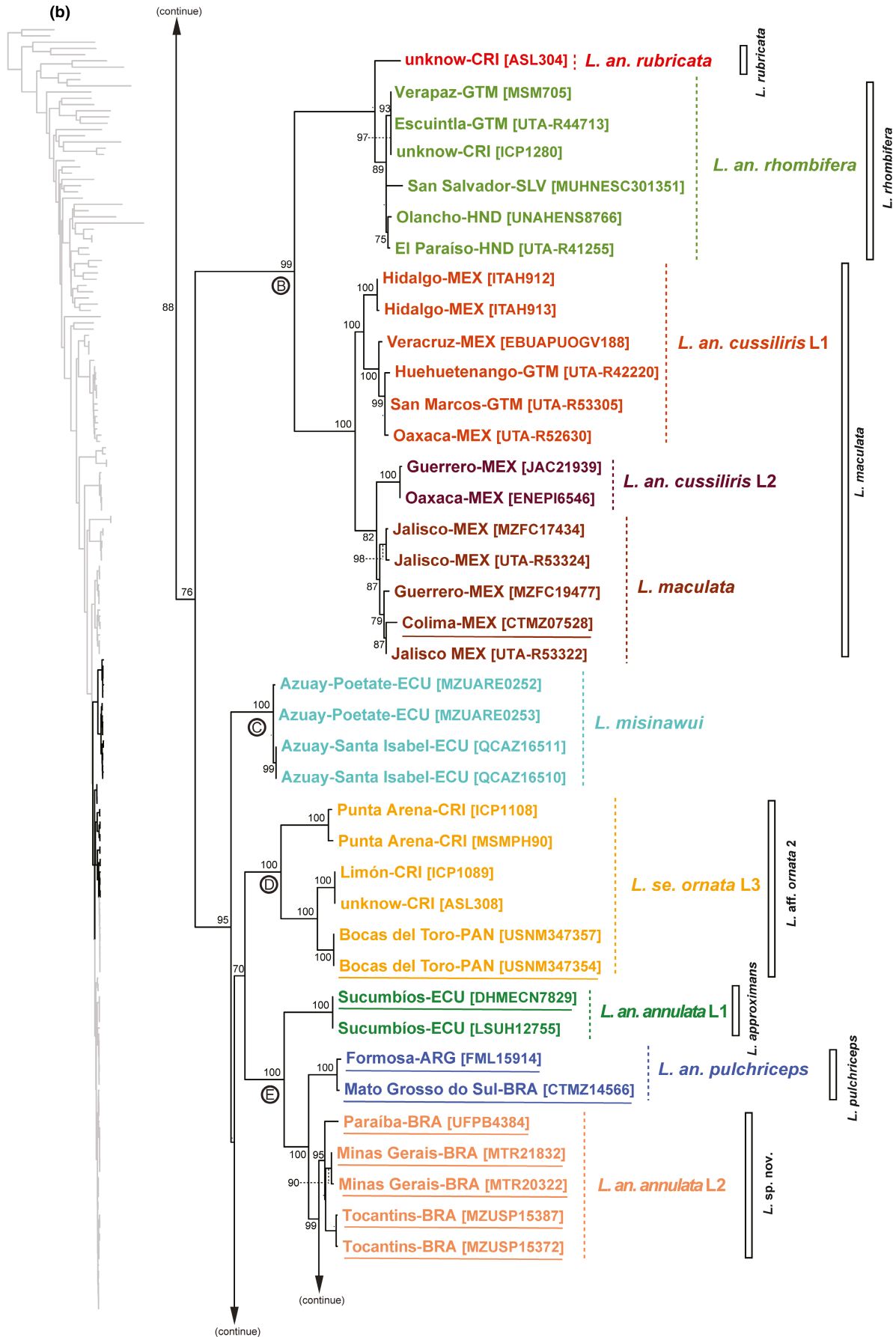


FIGURE 1 (Continued)



FIGURE 1 (Continued)

2020), represented as *L. s. ornata* L2 in our phylogeny (Figure 1b; Figure S1). The redescription of *L. ornata* can be found in Appendix S2. The Central American lineage represented as *L. s. ornata* L3 in our phylogeny (Figure 1b; Figure S1) is considered here as a putative undescribed species *L. aff. ornata* 2 restricted to Costa Rica and northern Panama (Appendix S2; Figure 12). The South American lineage represented as *L. s. ornata* L1 in our phylogeny (Figure 1c) is also considered here as a probable undescribed species *L. aff. ornata* 1 restricted to southwestern Ecuador and northwestern Peru (Appendix S2; Figure 12). We refrain to describe here these lineages as new species because we did not have access to a comprehensive geographical sampling to allow comparative morphological analyses able to properly identify the specific limits (justifications for our taxonomic proposal are fully described in the Discussion section).

5. We are considering *L. a. ashmeadii* as full species, supporting recent taxonomical proposal (Barrio-Amorós, 2019). Its detailed redescription can be found in Appendix S2 and an extended analysis of the recent elevation of this species by Barrio-Amorós (2019) can be found in the Discussion section.
6. We revalidate *Leptodeira approximans* Günther, 1872 to include the lineage represented as *L. a. annulata* L1 in our phylogenetic tree (Figure 1b; Figure S1). This species is restricted to the western portion of the Amazon Forest (see Appendix S2; Figure 6) and its complete redescription can be found in Appendix S2.
7. We elevate *L. a. pulchriceps* to species level to include the populations of *Leptodeira* from the South American Pantanal and Chaco ecoregions (see Appendix S2; Figure 15). The redescription of this taxon can be found in Appendix S2.
8. We describe below a new species for the lineage represented as *L. a. annulata* L2 in our phylogenetic tree (Figure 1b; Figure S1). This new species is restricted to the Brazilian open areas of Cerrado and Caatinga.
9. We redefine and elevate *L. a. annulata* to include only the morphotype represented by the lineage *L. a. annulata* L3 (Figure 1c; Figure S1) distributed in the Amazonia and Brazilian Atlantic Forest (see Appendix S2; Figure 3). The redescription of this taxon can be found in Appendix S2.

We provide an extended description for the new species (Appendix S3) and a summary of quantitative external features and high-quality illustrations of type specimens and hemipenis for *L. annulata* (Linnaeus, 1758), *L. approximans* (Günther, 1872), *L. ashmeadii* (Hallowell, 1845), *Leptodeira ornata* (Bocourt, 1884), and *Leptodeira pulchriceps* (Duellman, 1958) (see Appendix S2).

### 3.3 | Description of the new species

*Leptodeira tarairiu* sp. nov.

(<https://www.urn:lsid:zoobank.org:act:C58BB3F0-EE29-4C9E-9DE3-1F3049741DF8>).

(Description of new taxa in Appendix S3). Holotype: CHUFPB 447

## 4 | DISCUSSION

### 4.1 | Phylogenetic relationships within Dipsadinae and the monophyly of Imantodini

The monophyly of Imantodini has been repeatedly supported by several studies (Daza et al., 2009; Graziotin et al., 2012; Mulcahy, 2007; Mulcahy et al., 2011; Pyron et al., 2015; Zaher et al., 2009, 2014, 2019), although Vidal et al. (2010) recovered it as non-monophyletic because *Nothopsis* was sister to *Leptodeira*. In our analyses Imantodini is monophyletic and *Nothopsis* is its sister group (Figure S1). So far, the most complete analysis of Dipsadinae was performed by Pyron et al. (2015) which analysed four mitochondrial genes (*12S*, *16S*, *cytb* and *nd4*) and one nuclear locus (*c-mos*) for a comprehensive taxon sampling within the subfamily. In that study, the authors redefined the tribes Nothopsini (restricted to *Nothopsis rugosus*) and Diaphorolepidini (*Diaphorolepis*, *Emmochliophis* and *Synophis*), and recovered the monophyly of Imantodini with high support value. Their phylogenetic tree supports a sister-group relationship between Nothopsini and Imantodini that was corroborated by our ML analysis.

### 4.2 | Monophyly of *Leptodeira* and the basal relationships within the genus

We recovered a monophyletic *Leptodeira*, corroborating all previous studies using DNA sequences (Daza et al., 2009; Graziotin et al., 2012; Mulcahy, 2007; Mulcahy et al., 2011; Pyron et al., 2015; Zaher et al., 2014). Similarly, our results also support Mulcahy (2007) and Daza et al. (2009) revision of most of Duellman's morphological groups (Duellman, 1958).

The general topology within *Leptodeira* is very similar to the results presented by Mulcahy (2007) and Daza et al. (2009). The following parenthetical tree summarizes most of the concordant topology among these studies (*L. nigrofasciata*, ((*L. frenata*, *L. uribei*), ((*L. punctata*, ((*L. splendida*, *L. bressoni*), '*L. annulata-septentrionalis* complex')))). However, for Mulcahy (2007) and Daza et al. (2009) *L. splendida* is the sister group of *L. punctata*.

The successive sister groups position of *L. splendida* and *L. punctata* in relation to the ‘*L. annulata-septentrionalis* complex’ was poorly supported in our analysis (Figure 1a-c; Figure S1) but corroborates the results of Pyron et al. (2015).

### 4.3 | The Central and South American radiation of the ‘*Leptodeira annulata-septentrionalis* complex’

To facilitate the discussion of distinct combinations and taxonomic schemes used for the *annulata-septentrionalis* complex by successive authors in the last century, we are using quotes to identify any taxon name that is a homonym to a species or subspecies defined in our reclassification (see ‘Results’) but represent a distinct combination. For all such homonyms we explicitly indicate—each first time it appears in a paragraph—the author from whom the name's sense is derived.

The *annulata-septentrionalis* complex as defined by Daza et al. (2009) is no longer a meaningful combination of evolutionary units. This complex represents the entire clade C5 in our phylogeny (Figure 1a-c) and by considering the results and taxonomic proposal presented here (also suggested by Barrio-Amorós, 2019) the current understanding about the composition of *L. annulata* and *L. septentrionalis* has changed completely. We define below the species complexes and group of species we recognize for *Leptodeira*, discussing and justifying our taxonomic proposal.

### 4.4 | The polysticta/septentrionalis complex of species (here defined as including *L. s. septentrionalis* and *L. s. polysticta*)

Our study represents the first phylogenetic analysis to include a sample of *L. s. septentrionalis*—collected near the type-locality in southern Texas, USA. We justified our taxonomic proposal for *L. septentrionalis* mainly based on the unexpected phylogenetic positioning of this sample (subclade A, Figure 1a; Figure S1) and on the geographic distribution of the remaining lineages (as described by Daza et al., 2009 and Duellman, 1958). Duellman (1958) considered ‘*L. septentrionalis*’ as composed by the following four subspecies: ‘*L. s. septentrionalis*’, ‘*L. s. polysticta*’, ‘*L. s. ornata*’ and ‘*L. s. larcorum*’. The subspecies ‘*L. s. polysticta*’ was elevated to the species level (‘*L. polysticta*’) based on morphological evidence by Campbell (1998). Campbell's taxonomic act was supported by Mulcahy (2007) and Daza et al. (2009), which stated that their

molecular phylogenetic trees corroborated Campbell's claims of distinctiveness and validity of ‘*L. s. polysticta*’ and ‘*L. s. septentrionalis*’ as full species. Mulcahy (2007) and Daza et al. (2009) also suggested that ‘*L. s. ornata*’ was a different species, but since they did not sample the nominal subspecies, *L. s. septentrionalis*, they avoided changing the taxonomy of ‘*L. s. ornata*’. Taking a less conservative approach, Barrio-Amorós (2019), based on the results of Mulcahy (2007) and Daza et al. (2009), elevated not only ‘*L. s. septentrionalis*’ and ‘*L. s. polysticta*’ to the species level, but also ‘*L. s. ornata*’ and ‘*L. s. larcorum*’ (see further comments below).

The elevation of ‘*L. s. polysticta*’ (*sensu* Duellman, 1958) to the species level by Campbell (1998) was contested by Lee (2000) and Savage (2002) because of the lack of presented data. The corroboration of Campbell's ‘*L. polysticta*’ by Mulcahy (2007) and Daza et al. (2009) also lacks phylogenetic grounds, since their taxonomic sampling precludes any formal test about the cohesion of *L. s. polysticta* in relation to *L. s. septentrionalis* (not sampled in their analyses).

Contrarily to these studies, our results indicate that *L. s. septentrionalis* from the USA is positioned nested inside the clade of ‘*L. s. polysticta*’ (*sensu* Duellman, 1958). This clade represents almost the complete morphological and geographical diversity of the current composition of ‘*L. polysticta*’ (*sensu* Campbell, 1998; supported by Barrio-Amorós, 2019). Particularly, *L. s. septentrionalis* from the USA is genetically close to the lineage *L. s. polysticta* L1 (Figure 1a) from eastern Oaxaca (Mexico). We presume the latter is also present in Veracruz (Mexico) and probably represents the westernmost part of the distribution of a lineage that includes the former subspecies *L. annulata taylori* Smith, 1941, which was synonymized with ‘*L. s. polysticta*’ by Duellman (1958). Although Duellman has supported synonymizing Smith's subspecies based on morphological similarities, he noticed that the specimens from northern and central Veracruz have intermediate morphology between *polysticta* and *septentrionalis*. Shannon and Humphrey (1964) contested Duellman's act by commenting about the differences between *L. a. taylori* and ‘*L. s. polysticta*’ and indicated the possible integration between populations of *L. a. taylori* from lowland and coastal Veracruz with ‘*L. s. septentrionalis*’ (*sensu* Duellman, 1958). We suppose that both studies, Duellman (1958) and Shannon and Humphrey (1964), were in reality describing the morphological similarity of different local populations of *L. s. septentrionalis*. These populations are in fact morphologically and genetically different from ‘*L. s. polysticta*’ from Belize and the Atlantic portions of southern Mexico, Guatemala, and Honduras (see Duellman, 1958). Consequently, *Leptodeira s. polysticta* is only represented by the lineage *L. s. polysticta* L2 in our

phylogeny tree, which is distributed on the surrounding areas of the type locality of *L. s. polysticta* (Belize; Smith & Taylor, 1950). On the other hand, *L. s. polysticta* L1 may represent a population of *L. s. septentrionalis* and *L. s. polysticta* L3 a putative undescribed taxon.

Therefore, our results suggest that Campbell's understanding of '*L. polysticta*' (also supported by Barrio-Amorós, 2019) includes at least four different entities: (1) a lineage representing the nominal subspecies *L. s. septentrionalis* (*L. s. septentrionalis* and *L. s. polysticta* L1 in Figure 1a) that occurs from the southern USA to Oaxaca province in Mexico, through the coastal and semi-arid Atlantic plains in the Mexican provinces of Tamaulipas and Veracruz, and on the borders of Sierra Madre Oriental; (2) *L. s. polysticta* (*L. s. polysticta* L2 in Figure 1a) distributed throughout the southeastern portion of Mexico (Veracruz, Tabasco and the Yucatan peninsula), Guatemala, Honduras and Belize; (3) the morphologically and genetically distinct lineage *L. s. polysticta* L3 (Figure 1), distributed from northwestern Mexico to El Salvador, through the Pacific coast; and (4) the morphologically different population of *L. s. polysticta* distributed from Nicaragua and Costa Rica (Duellman, 1958).

The latter population comprises the individuals of '*L. polysticta*' (*sensu* Campbell, 1998) from Nicaragua and Costa Rica that have never been included in a phylogenetic analysis so far. We also did not have access to complementary evidence for this population to test its taxonomic status, although Duellman (1958) commented that specimens from this region have fewer ventral scales and body blotches than other populations of '*L. polysticta*' from Mexico, Guatemala, Honduras or Belize. He also suggested that this population could be intergrading with '*L. s. ornata*' (*sensu* Duellman, 1958) in Costa Rica because they share some morphological characteristics.

Our tentative proposal of keeping the subspecific level for *L. s. septentrionalis* and *L. s. polysticta*, and explicitly indicating the probable existence of two undescribed taxa, is arguably the least impacting taxonomic act possible given our current phylogenetic knowledge. The alternative option is to only synonymize '*L. polysticta*' (*sensu* Campbell, 1998) into *L. septentrionalis* (since the latter has priority over the former), without identifying the genetic and morphological distinction among the populations as found in Duellman (1958). In our opinion, this option creates a highly diverse taxon and a less informative taxonomic scheme.

Although acknowledging that our proposal does not represent a conclusive taxonomic solution for the complex, besides keeping an undesirable non-monophyletic *L. s. polysticta*, the recognition of four evolutionary entities within *L. septentrionalis* adequately mirror our understanding about the diversity of this group. As stated

before, only a thorough analysis concerning the morphological and genetic structure along the complex can shed light on the validity of these taxa. We tend to suppose that after a proper analysis, both subspecies and the two undescribed taxa will be recognized as full species, having their descriptions, distribution and diagnose revised. But since we do not know the morphological limits of these taxonomic units, and we did not have access to enough specimens to proceed with a desirable phylogenetic analysis, we argue that our suggested taxonomic scheme is the best preliminary solution to set bases for further advances concerning the systematics of this complex. We did not include in this study extensive descriptions or formal delimitations for any redefined subspecies. The description for *L. s. septentrionalis* and *L. s. polysticta* can be found in Duellman (1958), as well as the description of the morphological differences/similarities of the populations represented by the phylogenetic lineages *L. s. polysticta* L1, *L. s. polysticta* L2, and *L. s. polysticta* L3.

#### 4.5 | The maculata/cussiliris complex of species (here defined as including only *L. maculata*)

Duellman (1958) considered '*L. maculata*' as a full species, restricting its distribution to the Pacific coastal lowlands and the slopes of Sierra Madre Occidental, from the southern portions of the Mexican province of Sinaloa to the province of Guerrero. He commented about the morphological similarities between '*L. maculata*' and '*L. a. cussiliris*' (*sensu* Duellman, 1958), remarking that the northern populations of '*L. a. cussiliris*' resembles '*L. maculata*' also in colour. The distribution of '*L. a. cussiliris*' provided by Duellman (1958) presents two distinct geographical groups, separated by a sampling gap. There is a population distributed on the Atlantic coastal lowlands and low slopes of Sierra Madre Oriental, from the Mexican state of Tamaulipas to the Isthmus of Tehuantepec, where the distribution follows to west, through the Pacific coastal lowlands of the province of Oaxaca and towards south until the province of Chiapas. The second population is isolated in the Mexican province of Guerrero and the extreme north of Oaxaca. Duellman (1958) indicated that the individuals of '*L. a. cussiliris*' from this latter region present some morphological variability, and many specimens are strikingly different from the general morphology found in other parts of the subspecies' distribution.

Mulcahy (2007) genetically differentiated '*L. a. cussiliris*' (*sensu* Duellman, 1958) from '*L. annulata*' (*sensu* Duellman, 1958) elevating the former to species level without further comments. In the phylogenetic study of

Daza et al. (2009), they disregarded Mulcahy's taxonomic proposal, and sampled both populations of '*L. a. cussiliris*' (*sensu* Duellman, 1958), as well as '*L. maculata*' (*sensu* Duellman, 1958). Their result showed that '*L. maculata*' is nested within the diversity of '*L. a. cussiliris*', with '*L. maculata*' clustering together with individuals of '*L. a. cussiliris*' from Guerrero and from the extreme north of Oaxaca. Based on this result, they mistakenly synonymized '*L. maculata*' into '*L. a. cussiliris*' (Daza et al., 2009), without any formal description of this new combination. Barrio-Amorós (2019) corrected this mistake by revalidating '*L. maculata*'—since *L. maculata* has priority over *L. cussiliris*. Following Barrio-Amorós (2019), *L. maculata* includes the diversity of '*L. a. cussiliris*' (*sensu* Duellman, 1958), although the study did not present any formal re-description of '*L. maculata*'.

Our result for the *maculata/cussiliris* complex is completely based on the sequences produced by Mulcahy (2007) and Daza et al. (2009), although our phylogenetic interpretation and taxonomic proposal are different from these previous studies, giving partial support to the taxonomic scheme presented by Barrio-Amorós (2019). Like in Daza et al. (2009), our phylogenetic analysis indicates *L. maculata* as sister to lineage *L. a. cussiliris* L2 (Figure 1; Figure S1), which comprises the populations of '*L. a. cussiliris*' (*sensu* Duellman, 1958) with a distribution restricted to the Mexican provinces of Guerrero and northern Oaxaca. We suppose lineage *L. a. cussiliris* L2 represent a different evolutionary unit when compared to the populations of '*L. a. cussiliris*' (*sensu* Duellman, 1958) distributed in the Mexican Atlantic coast, Isthmus of Tehuantepec, and southern Oaxaca to Chiapas through the Pacific coast. Alternatively, *L. a. cussiliris* L2 could be interpreted as representing a local population of *L. maculata* based on Duellman (1958) description of their similar morphology.

Therefore, the *maculata/cussiliris* complex is composed by three genetic lineages (Subclade B, Figure 1b; Figure S1) that we tentatively considered as representing three different evolutionary units (see below). These three lineages can be associated with three different populations that were morphologically identified by Duellman (1958), who explicitly indicated the distinctiveness among them. These three populations also show an almost allopatric distribution, with a possible overlap only in the Mexican province of Guerrero between *L. maculata* and the population represented by lineage *L. a. cussiliris* L2.

We chose to not formally identify these three populations as different species within the complex because we did not evaluate a comprehensive sampling that covers the whole geographic distribution. However these tree populations/lineages can be broadly defined, as follows: (1) *L. maculata*, as described by Duellman (1958); (2) lineage *L. a. cussiliris* L2 (Figure 1b; Figure S1) that represents the

Mexican populations of '*L. a. cussiliris*' (*sensu* Duellman, 1958) from Guerrero and north of Oaxaca; and (3) lineage *L. a. cussiliris* L1 (Figure 1b; Figure S1), described by Duellman (1958) as '*L. a. cussiliris*', but from which we should remove the morphological variation found in the population of *L. a. cussiliris* from Guerrero and north of Oaxaca. Therefore, based on the exposed reasoning, we are preliminarily following Barrio-Amorós (2019) regarding the recognition of *L. maculata*, although we are moving the subspecies *L. a. cussiliris* (*sensu* Duellman, 1958) from *L. annulata* to *L. maculata*, but keeping its subspecific composition as described in Duellman (1958). We argue that our proposal represents a more conservative taxonomic scheme until further studies can bring a better understanding about the hidden diversity within *L. maculata*.

#### 4.6 | The rhombifera/rubricata complex of species (here defined as including *L. rubricata* and *L. rhombifera*)

The short branch length supporting the clade formed by individuals of *L. rhombifera* from Honduras, San Salvador, Guatemala and Costa Rica raises doubts about the recognition of *L. rubricata* as a full species (Subclade B, Figure 1b; Figure S1). However, our sampling of *L. rubricata* is restricted to the single individual sequenced by Daza et al. (2009), and we did not have access to morphological data for this species. As claimed by Daza et al. (2009) this lack of information about these species precludes any proper conclusion about the validity of *L. rubricata* based on genetic data. Savage (2002), Solórzano (2004) and Barrio-Amorós (2019) on the other hand recognized *L. rubricata* as a valid species based on morphological evidence. The later species, despite of its strikingly different colour, was synonymized to '*L. annulata*' (*lato sensu*) by Dunn (1936) and to '*L. a. rhombifera*' (*sensu* Duellman, 1958) by Duellman (1958). Dunn (1936) and Duellman (1958) are the only two studies that properly analysed and presented morphological evidence of the *rhombifera/rubricata* complex. All other studies based their opinions on Savage's accounts for the species. It is noteworthy that Savage, on the other hand, based his taxonomic proposal on the brief suggestion of distinctiveness regarding the type-species made by Taylor (1951), and most of the morphological data for *L. rubricata* presented in his book was derived from an unpublished analysis of Floyd Downs and Douglas C. Robinson that on Savage's opinion '... convincingly establishes *L. rubricata* as a valid species.' (Savage, 2002; pg. 613). Such analysis by Floyd Downs and Douglas C. Robinson was never completely published. Duellman (1958), on the contrary, stated that the

type-species of *L. rubricata* (AMNH 17367) is in reality ‘...an unusual variant of *L. a. rhombifera*.’ (Duellman, 1958; pg. 42), but with general number of scales falling into the variation of *L. a. rhombifera*. He also included number and pattern of body blotches presented in *L. rubricata* within the clinal variation of ‘*L. a. rhombifera*’, suggesting that the *L. rubricata* is nothing more than a geographical variant of a widespread ‘*L. a. rhombifera*’.

Because we did not have access to any new evidence for this complex, we are following Savage (2002) and Barrio-Amorós (2019) in considering *L. rubricata* and *L. rhombifera* as valid species (taxonomic scheme also acknowledged by Torres-Carvajal et al., 2020), but we recommend taking this taxonomic scheme as a preliminary attempt until a genetic/morphological revision of the *rhombifera/rubricata* complex can be carried out.

#### 4.7 | The ornata complex of species (here defined as including *L. ornata* and the undescribed taxa *L. aff. ornata 1* and *L. aff. ornata 2*)

Mulcahy (2007) was the first to show the polyphyletic condition of ‘*L. s. ornata*’ (*sensu* Duellman, 1958), although he did not take any taxonomic conclusion since his analysis and sampling design was focused on the high-level relationship within Imantodini. Daza et al. (2009) also retrieved ‘*L. s. ornata*’ (*sensu* Duellman, 1958) as polyphyletic, presenting two clades, one from Colombia and Ecuador, and other from Costa Rica. Similar to Mulcahy (2007), they also did not suggest any taxonomic act regarding ‘*L. s. ornata*’ (*sensu* Duellman, 1958), justifying that the lack of proper sampling precluded any compelling conclusion. Contrastingly, Barrio-Amorós (2019) elevated ‘*L. s. ornata*’ (*sensu* Duellman, 1958) to full species, without any new evidence or analysis. His taxonomic proposal is based on generalized assessments of the species morphological diversity, the phylogeny presented by Daza et al. (2009) and photographs published on websites. By doing that, Barrio-Amorós (2019) created a polyphyletic new combination for ‘*L. ornata*’, which phylogenetically encompass four other distant species recognized in his own study (*L. bakeri*, *L. ashmeadii*, *L. larcorum*, and *L. anulata*). In parallel to this taxonomic act, Barrio-Amorós (2019)—also without any new data, analysis or proper description—elevated ‘*L. s. larcorum*’ (*sensu* Duellman, 1958) by simply stating ‘I have no doubt that *L. larcorum* deserves specific status, as it inhabits a completely different habitat that is separated from that occupied by the southern *L. ornata*...’ (Barrio-Amorós, 2019; pg. 7). He also stated that ‘*L. s. larcorum*’ (*sensu* Duellman, 1958)

has a distinctive pattern, pointing to the set of photos included in his study, but without properly describing any aspect to support the distinctiveness.

Torres-Carvajal et al. (2012) brought some stability to the polyphyletic *L. ornata* created by Barrio-Amorós (2019). In their study, Torres-Carvajal et al. (2012) sequenced new individuals of *L. s. ornata* and *L. s. larcorum* from Ecuador and Peru and through a reanalysis of all the molecular evidence available at GenBank, they defined monophyletic groups and properly elevated *L. s. ornata* and *L. s. larcorum* to the species level. Their *L. ornata* is defined as restricted to populations from western Ecuador, western Colombia, as well as central and eastern Panama. Although representing an improvement over the proposal of Barrio-Amorós (2019), the tree topology presented by Torres-Carvajal et al. (2012) prevented the authors to solve the relationship of some populations of *L. ornata* from Panama and Colombia.

The non-monophyletic condition of ‘*L. s. ornata*’ (*sensu* Duellman, 1958) was also observed in our tree topology (Subclades D and H, Figure 1b-c; Figure S1), indicating the subspecies is composed by at least three different taxonomic units: (1) *L. ornata* (*L. s. ornata* L2 in our phylogeny, Figure 1c; Figure S1), distributed in Colombia, southern Panama (Appendix S2; Figure 12); (2) *L. aff. ornata 2* (*L. s. ornata* L3 in our phylogeny), distributed in Costa Rica and northern Panama (Appendix S2; Figure 12); and (3) *L. aff. ornata 1* (*L. s. ornata* L1 in our phylogeny), distributed in Ecuador and Peru (Appendix S2; Figure 12).

The type locality of *L. ornata* is ‘Isthmus of Darién’, southern Panama (see Appendix S2; Figure 12) and although sequences from Darién are available at GenBank for the mitochondrial genes *16S* and *cox1* (see Figure S2A–B), we did not include them in our main phylogenetic analysis to avoid nonrandom missing data (Sanderson et al., 2010). We evaluated the phylogenetic position of these individuals from Panama using a gene-tree approach through the same methods described for our main ML analysis. For both genes, the individuals from Darién grouped together nested in *L. ornata*, supporting our taxonomy for the species (Figure S2A–B). However, samples from the Panamanian departments of Colón and Coclé were positioned in two different clades, within *L. ornata* and *L. aff. ornata 2*. Based on our revised taxonomic understanding of ‘*L. s. ornata*’ (*sensu* Duellman, 1958) we expected these samples could be positioned within *L. aff. ornata 2* with an improved gene sampling.

We did not analyse the morphology for the putative undescribed species *L. aff. ornata 2* from Costa Rica and northern Panama, neither from the population from the region of the Panama Canal (e.g., department of Colón). However, Duellman (1958) provided the grounds for preliminary

comparisons of all lineages identified as '*L. s. ornata*'. He illustrated and compared the means and ranges for ventral and subcaudal scales counts, ratios of tail length by body length, and the number of body blotches for a comprehensive sampling of the morphological variability of '*L. s. ornata*' (*sensu* Duellman, 1958). In this comparison, Duellman suggested that the species can be morphologically divided into the following six populations: (1) Costa Rica and eastern (northern) Panama; (2) region of the Panama Canal; (3) Darien region in Panama; (4) valleys of Colombia; (5) Chocó region in Colombia; and (6) Ecuador.

Our analysis corroborates Duellman's suspicion about the geographical structure for this complex of species. The Ecuadorian population of '*L. s. ornata*' (*sensu* Duellman, 1958) correspond to the putative undescribed species *L. aff. ornata* 1 (*L. s. ornata* L1 in Figure 1c; Figure S1), which is phylogenetically closer to *L. ornata* (*L. s. ornata* L2 in Figure 1c; Figure S1). Although Duellman (1958) has suggested that population of '*L. s. ornata*' (*sensu* Duellman, 1958) from Ecuador and *L. larcorum* can integrate, Torres-Carvajal et al. (2012) and our topology show that *L. larcorum* is a distinct lineage, restrict to Peru, and phylogenetically distant from *L. aff. ornata* 1.

The populations morphologically described by Duellman from the Darien region in Panama (type-locality included) and from the valleys and Chocó region in Colombia are combined in our redefined *L. ornata*, described in Appendix S2. As suggested by Duellman, we also confirmed the morphological contrast between specimens from the valleys of Colombia and the Chocó region, although we did not sample properly the latter for phylogenetic analysis, and we refrain to take any further conclusions about the distinctiveness of these two populations.

The population from Costa Rica and northern Panama are described by Duellman as presenting the highest numbers of ventral scales and body blotches than any other population of '*L. s. ornata*' (*sensu* Duellman, 1958). We consider these populations represent the putative undescribed species *L. aff. ornata* 2, but we refrain to describe it here because we did not have access to proper data to test the morphological limit for the species. Moreover, *L. aff. ornata* 2 is not related to *L. ornata* and *L. aff. ornata* 1, representing a unique and distinct phylogenetic lineage within the diversity of *Leptodeira*, sister to the *L. annulata* group (subclade D, Figure 1b-c; Figure S1). We are tentatively including the population from the region of the Panama Canal in *L. aff. ornata* 2. Duellman (1958) suggests that the individuals from the Panama Canal are more similar to the population from Costa Rica and northern Panama, although our gene-tree analyses (Figure S2A–B) indicate that both species, *L. ornata* and *L. aff. ornata* 2 may be present in the department of Colon, near the Canal.

It is also noteworthy that the distribution of these populations (from the Panama Canal, from Costa Rica and northern Panama, and from Darién and Colombia) suggest the presence of large geographical sampling gaps (Duellman, 1958). Whether these sampling gaps represent a real distributional gap—indicating allopatry among these populations—only a thorough revision of specimens deposited in scientific collections combined with studies in the field can elucidate.

#### 4.8 | The *ashmeadii/bakeri* group of species

Mulcahy (2007) showed for the first time that '*L. a. ashmeadii*' (*sensu* Duellman, 1958) does not cluster with other subspecies of '*L. annulata*' (*sensu* Duellman, 1958), but it is related to populations of *L. ornata* from South America. Daza et al. (2009) using an expanded sampling for '*L. annulata*' showed that specimens of '*L. a. ashmeadii*' from Trinidad and Venezuela were phylogenetically associated with a clade of '*L. a. annulata*' composed by individuals from the Amazon Forest in Brazil and Colombia. The phylogeny of Daza et al. (2009) also indicated that the '*L. a. ashmeadii*' clade includes the population of '*L. a. annulata*' from Amazonia, although they did not take any taxonomic decision about these taxa. On the other hand, Barrios-Amorós (2019) elevated '*L. a. annulata*' and '*L. a. ashmeadii*' to full species. He based his proposal on the very same tree presented by Daza et al. (2009), disregarding the authors claims demanding a proper integrative analysis (morphology and genetics) before any taxonomic decision. Barrios-Amorós also stated that 'Daza et al. (2009) separated *L. annulata* from *L. ashmeadii*' (Barrios-Amorós, 2019, pg. 9), which is not formally present in Daza et al. (2009). On the contrary, Daza et al. (2009) refrained to take any taxonomic decision regarding '*L. a. annulata*' and the associated species (e.g. *L. a. ashmeadii*) since their sampling was not appropriate to sort the conflicting hypotheses apart. The diagnosis provided for *L. ashmeadii* in Barrios-Amorós (2019) is at least inaccurate. Based exclusively on the text presented in Barrios-Amorós (2019) it is not possible to infer whether the individuals of '*L. a. annulata*' from Amazonia are included in *L. ashmeadii* or not.

In our analysis, we improved the sampling for *L. ashmeadii*, and we also examined the Amazonian specimens of '*L. a. annulata*' used by Daza et al. (2009) from the state of Roraima, Brazil, and from the department of Meta in Colombia. We reidentified these individuals as *L. ashmeadii* (see Appendix S2) and they clustered together with the individuals of *L. ashmeadii* collected by us in the state of Roraima, Brazil (Subclade E, Figure 1; Figure S1). This

monophyletic *L. ashmeadii* is the sister group of *L. bakeri* in our analysis, corroborating the result of Daza et al. (2009). This reanalysis of previously sequenced material, together with the inclusion of new samples, provided the basis to support the elevation of '*L. a. ashmeadii*' to full species as proposed by Barrios-Amorós (2019), although different from the latter, here we provided an explicit phylogenetic test and the description of the morphological variability for the species (Appendix S2).

#### 4.9 | The annulata/pulchriceps group of species (here defined as including *L. annulata*, *L. approximans*, *L. pulchriceps*, and *L. tarairiu* sp. nov.)

After removing from '*L. annulata*' (*sensu* Duellman, 1958) the subspecies '*L. a. rubricata*', '*L. a. rhombifera*', '*L. a. cussiliris*' and '*L. a. ashmeadii*', the diversity of "*L. a. annulata*' was still paraphyletic in relation to '*L. a. pulchriceps*' (Subclade E, Figure 1b; Figure S1). To provide a monophyletic taxonomy for *L. annulata*, we revalidated *L. approximans* (*L. a. annulata* L1 in Figure 1b; Figure S1; detailed redescription in Appendix S2), distributed exclusively on western Amazon Forest on the slopes of Andes in Ecuador (Appendix S2; Figure 6), and we described *Leptodeira tarairiu* sp. nov. for the regions of Caatinga and Cerrado in Brazil (*L. a. annulata* L2 in Figure 1b; Figure S1; detailed redescription in Appendix S2). By taking these taxonomic acts it was possible to redefine *L. a. annulata* and elevate the subspecies to the species level (*L. a. annulata* L3 in Figure 1c; Figure S1; detailed redescription in Appendix S2).

Although our dataset represents the most comprehensive sampling for South American species of *Leptodeira*, covering much of the Brazilian territory, our results did not corroborate the three distinct populations of *L. a. annulata* as highlighted by Duellman (1958). On the other hand, our study reveals a different set of lineages, new species and probably hidden species, increasing the knowledge of the morphological and genetic diversity of the South American species of *Leptodeira*.

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