Systematics of the genus *Erythrolamprus* Boie 1826 (Serpentes: Dipsadidae) based on morphological and molecular data

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Dissertação apresentada ao Museu de Zoologia da Universidade de São Paulo, para a obtenção do título de mestre em ciências, no programa de Sistemática, Taxonomia Animal e Biodiversidade.

Orientador: Prof. Dr. Hussam Zaher

São Paulo

2016

FICHA CATALOGRÁFICA

Hurtado-Gomes, Juan Pablo

Systematics of the genus *Erythrolampus* Boie 1826 (Serpentes: Dipsadidae) based in morphological and molecular evidence / Juan Pablo Hurtado-Gómez; orientador Hussam El Dine Zaher. – São Paulo, SP: 2016.

62 p.

Dissertação (Mestrado) – Programa de Pós-graduação em Sistemática, Taxonomia Animal e Biodiversidade, Museu de Zoologia, Universidade de São Paulo, 2016.

1. Dipsadidae - Systematics. 2. *Erythrolampus* - morphology. 3. *Erythrolampus* – molecular. I. Zaher, Hussam. II. Título.

Banca examinadora

Prof. Dr._____ Instituição: _____

Julgamento: _____ Assinatura: _____

Prof. Dr._____ Instituição: _____

Julgamento: _____ Assinatura: _____

Prof. Dr. Hussam Zaher (Orientador)

Julgamento: _____ Assinatura: _____

Agradecimientos

Formais.

A CAPES, pela bolsa.

Pela doação de tecidos e empréstimo de material, agradeço ao M.T. Rodrigues (IB,USP); A.LC. Prudente (Museu Paraense Elimio Goeldi, Pará); P. Passos (Museu Nacional do Rio de Janeiro); B. Noonan and A.M Snyder (Mississippi University, USA), G. Watkins-Colwell (Yale Peabody Museum of Natural History); D. Blackburn and J. Vindum (California Academy of Sciences); R. Murphy and A. Lathrop (Royal Ontario Museum). Ao J. M. Daza (Museo de Herpetología de la Universidad de Antioquia), pelo acesso ao laboratório de molecular e tecidos. .

Não Formais

Primeiro, quero agradecer ao Hussam por abrir as portas do laboratório, pela orientação e apoio durante este trabalho.

Ao pessoal da Herpetologia, Dona Zina, Beto, Chico e Andre, pela ajuda com o material da coleção e a parceria.

Ao pessoal da biblioteca, Dione, Marta e Ricardo, pela grande ajuda com a bibliografia.

A Jaqueline pela ajuda e paciência durante o meu trabalho no laboratório da Molecular.

Quero agradecer especialmente a Isabel e o Juan Camilo por ter aberto as portas da sua casa para me aguentar tantas vezes. Muito, muito obrigado.

Ao Sergio pela parceria, apoio e por não dar problema.

Aos companheiros dessa viagem que têm sido maestros, amigos e colaboradores. O Felipe, Gringo, Juan Camilo, Leo, Fausto (papi), Beta, Vivian, Giovanna, Dani coleguinha, Hana, Paola, Natalia, Dani França, Paulo, Ana, Leo Malagoli, Paolo e Scott; sem as muitas conversas e as muitas brejas, não teria aprendido tanto nem teria curtido tanto a minha estadia no Brasil.

Aos meus velhos amigos, Ale, Jhon, foram um grande apoio fora de casa.

Finalmente, quero agradecer a minha família, pelo apoio incondicional na distância.

Abstract

The genus *Erythrolamprus* currently groups 50 species that have traditionally been allocated in the genera *Erythrolamprus*, *Liophis* and *Umbrivaga*. Although synonymization of these three genera with *Erythrolamprus* finds support in all molecular studies, the systematic value of such nomenclatural act is still under debate, mainly because of the lack of morphological synapomorphies and dense taxonomic sampling for the group. Within *Erythrolamprus*, 13 taxonomic groups may be recognized based in a traditional taxonomic arrangement, but its monophyly has never been tested. The present study analyzed 78 morphological characters, from cranial osteology and hemipenis, and six genes, three mitochondrial (coi, 12s, cytb) and three nuclear (bdnf, cmos, nt3), in 27 species representing all previously recognized taxonomic groups, in order to test the monophyly of the genus and of its constituent parts. We performed parsimony, bayesian and maximum likelihood analyses for the molecular data, and parsimony analyses for morphological and combined matrices (morphology and molecules). Our results retrieved a monophyletic genus *Erythrolamprus* as currently accepted, composed by nine main clades that are, for most of them, supported by morphological synapomorphies. On the other hand, only four of the traditional taxonomic groups were retrieved as monophyletic. *Erythrolamprus sagittifer* was found to be nested within *Lygophis* and is reallocated in that genus. Additionally, we resurrected the genus *Leimadophis* for the clade formed by *E. almadensis, E. atraventer, E. carajasensis, E. jaegeri, E.maryellenae,* and *E. viridis*, since it was recovered as the sister group of a clade composed by all the other species of the genus *Erythtorlamprus*.

Resumo

O gênero *Erythrolamprus* atualmente agrupa 50 espécies que têm sido incluídas tradicionalmente nos gêneros *Erythrolamprus, Liophis* e *Umbrivaga*. Embora a recente sinonimização tem sido suportada em todas as análises moleculares, ainda existe debate, devido ao baixo número de espécies incluídas e a falta de sinapomorfías morfológicas. Dentro de *Erythrolamprus*, podem se reconhecer 13 grupos com base nos arranjos taxonômicos tradicionais, mas a monofilia desses grupos nunca tem sido testada. Utilizando 78 caracteres de osteologia craniana e hemipênis, e seis genes: três mitocondriais (coi, 12s, cytb) e três nucleares (bdnf, cmos, nt3); para 27 espécies, testamos a monofilia do gênero, dos grupos taxonômicos e das espécies, além do relações internas. Realizamos analises de parcimônia, bayesianos e de máxima verossimilhança para os dados moleculares; enquanto que para as matrizes morfológica e combinada (morfologia e molecular) só foi utilizada analise de parcimônia. Os nossos resultados recuperaram monofilético *Erythrolamprus* como atualmente aceito, nove clados principais dentro do gênero, sendo que para a maioria deles propomos sinapomorfias morfologicas. Só quatro dos grupos taxonômicos tradicionais foram recuperados monofileticos. *Erythrolamprus sagittifer* foi encontrada aninhada dentro de *Lygophis* e é realocada neste gênero. Adicionalmente, para o clado conformado por *E. almadensis, E. atraventer, E. carajasensis, E. jaegeri, E.maryellenae, E. viridis* ressuscitamos o gênero *Leimadophis*, dado que foi recuperado como irmão de todas as outras espécies do clado *Erythrolamprus*.

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Introduction

The dipsadid tribe Xenodontini Bonaparte 1845, is a Central and South American group that contains around 70 species currently grouped in three genera: *Erythrolamprus* Boie 1826, *Lygophis* Fitzinger 1843, and *Xenodon* Boie 1826 (Zaher et al. 2009, Grazziotin et al. 2012). Monophyly of the tribe is supported by the presence of a bilobed, non-capitate and non-calyculate hemipenis with lobes ending in apical disks (Myers 1986, Zaher 1999, Moura-Leite 2001, Masiero 2006, Zaher et al. 2009) and by molecular evidence (Myers 1986, Zaher et al. 2009, Vidal et al. 2010, Grazziotin et al. 2012, Pyron et al. 2013a, 2015) (but see Pyron et al. 2013b). Within the tribe, the most diverse genus is *Erythrolamprus* with approximately 50 currently recognized species, and reaching 84 taxa when accounting for subspecies (Dixon 1989, Grazziotin et al. 2012, Uetz and Hosek 2015). Currently, the genus includes species traditionally allocated in the genus *Erythrolamprus sensu stricto* (the coral snake mimics; from now on *Erythrolamprus s. st.*), *Liophis* Wagler, 1830, and *Umbrivaga* Roze, 1964 (Zaher et al., 2009; Grazziotin *et al.* 2012). *Erythrolamprus sensu lato* (*Erythrolamprus s. st.* + *Liophis* + *Umbrivaga*, hereafter *Erythrolamprus s. lat.*) is distributed through Central and South America, occurring in all biomes, except for the Southern part of the Andes (Dixon 1989). *Erythrolamprus s. lat.* is strongly supported by molecular evidence, but no morphological synapomorphies are currently known for the genus (Zaher et al. 2009, Vidal et al. 2010, Grazziotin et al. 2012, Jowers et al. 2013, Pyron et al. 2013a).

The taxonomic history of *Erythrolamprus s. lat.* is rather chaotic, mainly for species formerly included in *Liophis* (including *Lygophis*). During most of the 20th century, *Liophis* had species separated in several different genera (i.e. *Dromicus*, *Leimadophis*) and grouped together with taxa currently in the genera *Rhadinaea* and *Saphenophis*. It was mainly the work of Dixon (1980) that brought some order to the group by redefining *Liophis*, which he characterized mainly as having ungrooved postdiastemal maxillary teeth, more than eight maxillary teeth, an anterolateral expansion of the frontal bone and lack of complete rings in body color. Later works by Dixon and collaborators (Dixon 1980, 1983a, 1983b, 1983c, 1983d, 1985a, 1987, 1991, 2000, Dixon and Thomas 1982, Michaud and Dixon 1987, Dixon and Michaud 1992, Dixon and Markezich 1992) and other authors (Fernandes et al. 2002, Giraudo et al. 2006, Rivas et al. 2012) resulted in the recognition of approximately 40 species and 12 artificial groups

in the genus *Liophis* (Dixon 1989) (Table 1). Nevertheless, taxonomy of this group is far from being resolved given the vague taxonomic limits and complex geographic variation within and among many of the taxons currently recognized.

Table 1. Grouping of the species included in the genus *Erythrolamprus sensu lato* and *Lygophis* showing current allocation (after Zaher et al. 2009 and Grazziotin et al. 2012), and Dixon's groupings for former *Liophis* (see text for references). *Erythrolamprus sensu stricto*, follows Curcio *et al.* (2009b, 2015), Hardy & Boos (1995) and Peters & Orejas-Miranda (1970). Names in bold are species included for the first time in phylogenetic analyses.[1]Species sampled for morphology; [2] Species sampled for molecular data.

Current genus	Former genus	Dixon's groups	Sampled	Not Sampled
Erythrolamprus sensu lato	*Umbrivaga*	-	***pyburni***[1], *pygmaeus*[1,2]	*mertensi,*
	Erythrolamprus sensu stricto	-	*aesculapii*[1,2], *mimus*[1,2], ***ocellatus***[2], ***pseudocorallus***[1,2], ***bizona***[1,2]	*guentheri*
	Liophis	*almadensis*	*almadensis*, ***carajasensis***	
		cobella	*breviceps*[1,2], ***frenatus***[1,2], ***taeniogaster***[1,2]	*cobella, ingeri, longiventris, torrenicola, trebbaui*
		cursor/Caribbean	*juliae*[1,2], *cursor*[2]	*ornatus, perfuscus*
		miliaris	*miliaris*[1,2], ***mossoroensis***[1,2]	*semiaureus*
		poecilogyrus	*poecilogyrus*[1,2], *ceii*[2]*	
		reginae	*epinephelus*[1,2], ***oligolepis***[1,2], *reginae*[1,2]	*andinus, dorsocorallinus, williamsi, zweifeli*
		taeniurus		*festae, janaleeae, taeniurus, vitti*
		typhlus/ green	***maryellenae***[1,2], ***viridis***[1,2], *atraventer*[1,2], *jaegeri*[1,2], ***typhlus***[1,2]	*albertguentheri*
		Not assigned	***melanotus***[1,2], ***triscalis***[2], ***sagittifer***[1]	
		insertae sedis		*leucogaster, problematicus, subocularis*
Lygophis		*anomalus*	*anomalus, elegantissimus*	*vanzolinii*
		lineatus	*flavifrenatus, lineatus, meridionalis, paucidens*	*dilepis*

*Species originally grouped with *E. almadensis* by Dixon (1991), but later associated with *E. poecilogyrus* by Cei (1993).

The taxonomy of the genera *Erythrolamprus s. st.* and *Umbrivaga* (Table 1), to the contrary, faced only minor changes through history. Despite some intrageneric controversies and rearrangements (Cunha and Nascimento 1980, Hardy and Boos 1995, Curcio et al. 2009a, 2009b, 2015), the group has six currently accepted species (Curcio et al. 2015); and the concept of *Erythrolamprus s. st.* as a genus has remained stable for at least the last century, being diagnosed by its coral color pattern and opistoglyph dentition. On the other hand, *Umbrivaga* was erected by Roze (1964) for *E. mertensi*, based in the reduced number of maxillary teeth, lance-shaped post-diastemal teeth, and a shelf-like

premaxilla. Later, Markezich and Dixon (1979) added two species to the genus, however they doubted the validity of the genus given the similarities of diagnostic characters with species of *Liophis*..

The first cladistic work that studied the systematics of taxa currently included within *Erythrolamprus s. lat.* was that of Vidal *et al.* (2000), based on two mitochondrial genes (12S and 16S), found that *Erythrolamprus s. st.* positioned within *Liophis*. Nevertheless, even though the clade was highly supported, Vidal *et al.* (2000) argued that no nomenclatural actions were taken because of the small sample included.

Later, Moura-Leite (2001) while studying the systematics of the tribe Xenodontini using morphological evidence, found *Liophis* to be polyphyletic by including *L. amarali* and species of the *Liophis lineatus* and *L. anomalus* groups (*sensu* Dixon 1985a, Michaud and Dixon 1987) along with *L. sagittifer*. Additionally, Moura-Leite (2001) also found *Liophis* to be paraphyletic regarding to *Erythrolamprus*. This author suggested that a new genus should be erected for *L. amarali* and revalidated *Lygophis* Fitzinger 1843 including the species of the *L. lineatus* group and *L. anomalus*. However, no taxonomic changes were suggested regarding *Erythrolamprus*.

Afterwards, Zaher *et al.*(2009), in a phylogenetic analysis based on molecular evidence of two mitochondrial (12S and 16S) and one nuclear (c-mos) markers, had very similar results than those of Moura-Leite (2001). Zaher *et al.*(2009) recognized *Lygophis* for all species of the *L. anomalus* and *L. lineatus* groups (*sensu* Dixon 1985a, Michaud and Dixon 1987), and described a new tribe and genus, *Caaeteboini* and *Caaeteboia*, respectively, for *Liophis amarali*. Additionally, Zaher *et al.*(2009) further found *Liophis* to be paraphyletic with respect to *Erythrolamprus s. st.* and synonymized the later within the former.

Shortly after, in a reply to Zaher *et al.*(2009), Curcio *et al.* (2009a) highlighted the priority of the name *Erythrolamprus* Boie, 1826 over *Liophis* Wagler, 1830, and questioned the changes made by Zaher *et al.*(2009) regarding *Erythrolamprus*, *Liophis* and *Lygophis* because of the reduced sample size, lack of morphological synapomorphies and for not including the generic type species. Curcio *et al.* (2009a) also challenged the validity of the name *Erythrolamprus* Boie, 1826, since the type species of the genus, *Coluber venustissimus* Wied-Neuwied, 1821, was a subspecies of *E. aesculapii* and needed redefinition. Nevertheless, later Curcio *et al.* (2015) suggested that *E. a.*

venustissimus (Wied-Neuwied, 1821) may be assignable to *E. aesculapii* populations of the Brazilian Atlantic forest, but clarification is still needed.

Vidal *et al.* (2010) in a study of the systematics of the family Dipsadidae using two mithochondrial markers (12S and 16S), with a larger taxonomic sample, including for the first time a sample of *Umbrivaga*, found that *Liophis* (excluding *Lygophis* and *Caaeteboia*) was paraphyletic regarding both *Erythrolamprus s. st.* and *Umbrivaga.* The authors did not follow earlier synonymization by Zaher *et al.*(2009) of *Erythrolamprus s. st.* within *Liophis*, but highlighted the inadequacy of the taxonomic arrangement used to date. These authors pointed out some possible scenarios, but no taxonomic changes were proposed.

Recently, Grazziotin *et al.* (2012) published a phylogeny with an improved taxonomic and genetic sampling with five mitochondrial (12S, 16S, cytb, nd2, nd4) and three nuclear (bdnf, c-mos, rag2) markers. Results of Grazziotin *et al.* (2012) were highly consistent with Zaher *et al.* (2009), with *Erythrolamprus s. st.* and *Umbrivaga* species embedded within *Liophis*. In order to reflect a monophyletic classification, Grazziotin *et al.* (2012) kept the taxonomic rearrangements made by. Zaher *et al.*(2009), corrected the generic name to *Erythrolamprus*, and included *Umbrivaga* species within the genus.

Shortly after, Jowers *et al.* (2013) using three mitochondrial genes (12s, 16s and COI), studied the phylogenetic position of *E. cursor*, finding it as sister to *E. juliae*, suggesting the Caribbean group as monophyletic. Otherwise, results of Jowers *et al.* (2013) were similar to those of Grazziotin *et al.* (2012). Other recent molecular analyses also retrieved a monophyletic *Erythrolamprus s. lat.* and relationships within the group have varied slightly depending on the methodological and taxonomical approaches (Pyron et al. 2013b, 2013a, 2015), but no new taxa or data have been included for the genus.

Despite *Erythrolamprus s. lat.* as defined by Zaher *et al.*(2009) and Grazziotin *et al.*(2012) being well supported by molecular evidence, there is still some debate about the synonymization, and some authors still recognize *Liophis*, *Erythrolamprus s. st.* and *Umbrivaga* (Curcio et al. 2009a, 2015, Wallach et al. 2014), mainly because the last two genera have a very divergent morphology when compared with *Liophis*, and no single morphological synapomorphy is so far known for *Erythrolamprus s. lat.* (Myers 2011, Lynch 2015).

All phylogenetic studies of *Erythrolamprus s. lat.* include morphological (Moura-Leite 2001) or molecular data (Vidal et al. 2000, 2010, Zaher et al. 2009, Grazziotin et al. 2012, Jowers et al. 2013, Pyron et al. 2015), but none have combined these two bulks of evidence. A combined analysis may well lead to more consistent results and reveal additional morphological synapomorphies. Taxonomic sampling of *Erythrolamprus s. lat.* in phylogenetic studies reached only around 30% of the species diversity of the group (Moura-Leite 2001, Grazziotin et al. 2012, Jowers et al. 2013, Pyron et al. 2015), which seems scarce for such a highly diverse and complex group. Furthermore, none of the former studies focused on solving the systematics of *Erythrolamprus s. lat.* nor testing the monophyly of the taxonomic groups within the genus.

The present study attempts to evaluate the phylogenetic relationships within the genus *Erythrolamprus s. lat.* by using an extensive taxonomic sampling, integrating morphological and molecular evidence, and comparing different phylogenetic methodologies.

Materials and Methods

Taxonomy and Taxonomic sampling

In order to describe and compare our data with previous results, we used the following terms: "*Erythrolamprus s. lat.*" for the genus as defined by Zaher *et al.* (2009) and Grazziotin *et al.* (2012); "*Erythrolamprus s. st.*" for the coral mimics species as recognized by Peters & Orejas-Miranda (1970), Wallach *et al.* (2014) and Curcio *et al.* (2015); "*Liophis*" as defined by Dixon (1989) for the species formerly included in that genus, but excluding *Lygophis* and *Caaeteboia*; and "*Umbrivaga*" for the species formerly included in that genus (Markezich and Dixon 1979). Given the lack of clarity in the nomenclature and delimitation of subspecies belonging to *E. aesculapii*, we recognize three groups in our sample: *E. a. aeculapii*, as defined by Curcio *et al.* (2015); and the southwestern Brazilian populations with monad and dyad patterns, as recognized by Barbo *et al.* (2011).

For the species groups, we follow mainly Dixon's proposals, as described in Table 1. For species identification and species ranges, we follow Curcio *et al.* (2009b, 2015), Hardy & Boos (1995) and Peters & Orejas-Miranda (1970) for *Erythrolamprus s. st.* (Table 1); for species formerly included in the genus *Liophis*, we use the arrangements

advanced by Dixon (1989) and some subsequent proposals (i.e. Fernandes et al. 2002, Giraudo et al. 2006, Rivas et al. 2012); and Markezich & Dixon (1979) for the species formerly allocated in the genus *Umbrivaga*.

Our sample includes five species of *Erythrolamprus s. st.*, two of *Umbrivaga* and 22 species of *Liophis*, including terminals representing all taxonomic groups (see Table 1), except the *'taeniurus'* group for which no material was made available for this study.

Morphological data

We obtained morphological data for 25 species of *Erythrolamprus s. lat.*, reaching 50% of the genus diversity and duplicating the sample size in previous morphological works (Moura-Leite 2001). As outgroups, we codified morphological characters for 18 species, from which eight belonged to the tribe Xenodontini (*Lygophis* and *Xenodon*), nine to other tribes of the family Dipsadidae and one to Colubridae. Taxa and specimens examined are listed in Appendix 1.

For the osteological data, we used skulls skeletonized with larvae of dermestid beetles and cleared and stained specimens prepared following Dingerkus & Uhler's (1977) technique. Osteological terminology follows Cundall & Irish (2008). Hemipenes were prepared following Zaher & Prudente (2003) and calcified structures were stained using an ethanol 70%/alizarin red solution (Curcio et al. 2011).Terminology for hemipenis follows Zaher (1999).

Characters were codified following Sereno (2007) and the matrix was created in the program MESQUITE (Maddison and Maddison 2015). A total of 78 morphological characters were included in the analysis, from which 29 were hemipenial and the remaining 49 were osteological. Several characters were taken from Masiero (2006) and Moura-Leite (2001), but modified and reinterpreted in order to fit into the new evidence. Characters are described in Appendix 2, and the character matrix is provided in Appendix 3.

Molecular data

The molecular dataset included three mitochondrial (12s, coi, cytb) and three nuclear (bdnf, cmos, nt3) genes from 57 terminal taxa for the ingroup, from which 28 belong to *Erythrolamprus s. lat*. Sequences for 41 terminals representing 15 distinct species are new in this analysis (See Appendix 4). We obtained DNA from multiple tissue sources (liver,

muscle, scales) using DNeasyTissue extraction kit (Qiagen Inc.), following the manufacturer's protocol. Amplification of the genes were made through polymerase chain reaction (PCR), using the primers and protocols previously described for snakes (Pook et al. 2000, Noonan and Chippindale 2006, Zaher et al. 2009, Grazziotin et al. 2012); except for the COI, for which we used four different primers, one designed by Arevalo *et al.* (2009) and the three others designed for this work (Table 2). Purification and sequencing was carried out at the Macrogen facilities in Korea (Macrogen, Inc.).

Table 2. Name and sequence of the primers used for gene amplification and size of the amplified fragment for each gen used.

Gene	Name	Primer Sequences	Base pairs
12S	L1091mod	5’ CAAACTAGGATTAGATACCCTACTAT 3’	386
	H1557mod	5’ GTACRCTTACCWTGTTACGACTT 3’	
cyt *b*	703Botp.mod	5’ TCAAAYATCTCAACCTGATGAAAYTTYGG 3’	758
	MVZ16p.mod	5’ GGCAAATAGGAAGTATCAYTCTGGYTT 3’	
COX 1	COI_r928	5’ CCTGTTGGAAYTGCRATRATTAT 3’	650
COX 1 New	Cox1_36_F	5' AACCACAAAGAYATYGGAMCC 3	963
	Cox1_1302_R	5' AAGTGTTGTGGRAAGAATGT 3	
c-mos	S77	5’ CATGGACTGGGATCAGTTATG 3’	570
	S78	5’ CCTTGGGTGTGATTTTCTCACCT 3’	
BDNF	BDNFF	5’ GACCATCCTTTTCCTKACTATGGTTATTTCATACTT 3’	671
	BDNFR	5’ CTATCTTCCCCTTTTAATGGTCAGTGTACAAAC 3’	
NT3	NT3F3	5’ ATATTTCTGGCTTTTCTCTGTGGC 3’	498
	NT3R4	5’ GCGTTTCATAAAAATATTGTTTGACCGG 3’	

Additional sequences for both outgroup and ingroup taxa were obtained from GenBank. Sequences for ingroup taxa were only included when the voucher specimen and taxonomic identity could be comfirmed. Outgroup sampling included 103 terminals, and aimed to sample most genera within Dipsadidae, and members of the different clades of the caenophidian and booid radiations (Appendix 4).

Sequences were assembled and aligned using Geneious v. 6.1.8 (Kearse et al. 2012), with MAFFT default settings (Katoh and Toh 2010). Codifying genes (COI, cytb, cmos, bdnf, nt3) were translated to amino acid sequences in order to check the alignment for stopping codons. The combined dataset for all genes was assembled with the software Sequence Matrix (Vaidya et al. 2011).

Phylogenetic analyses

Two sets of evidence, molecular and morphological, were used in phylogenetic inferences and arranged in three different ways: (i) molecular only, (ii) morphology only and (iii) combined. The molecular matrix was analyzed through maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI) approaches. Morphology only and combined evidence matrices were analyzed using MP. The molecular data was partitioned by gene and codon position and the best partition scheme was evaluated in the software PartitionFinder v 1.1.1 (Lanfear et al. 2012) using the Akaike information criterion for ML analyses, and the Bayesian information criterion for de BI analyses. *Coluber constrictor* was used as outgroup in the morphological analysis, whereas *Boa constrictor* was used for both molecular and combined analyses.

In order to reduce the number of missing entries in the combined matrix, only outgroup terminals that were coded for both sources of evidence were retained in the analysis (i.e. morphology and molecular). On the other hand, all ingroup terminals were kept in the combined matrix. Additionally, ingroup terminals with more than one molecular sample in the combined matrix, we repeated the morphological data for each terminal.

In order to find morphological synapomorphies, the morphological characters were optimized in the combined tree in MESQUITE (Maddison and Maddison 2015).

Maximum parsimony

All three datasets (molecular, morphology and combined) were analyzed with equally weighted parsimony using the software TNT v. 1.1 (Goloboff et al. 2008). A heuristic tree search strategy was conducted using the New Technology searches provided by TNT (command xmult= consense 5) until the consensus was stabilized five times. The best trees obtained at the end of the replicates were subjected to a final round of TBR branch swapping. Zero length branches were collapsed if they lacked support under any of the most parsimonious reconstructions. Measures of node support were calculated performing 1000 pseudoreplicates of jackknife resampling of characters. Jackknife supports were considered to be high above 90%, moderate between 70-89%, and weak below 70%. Low values of node support (<70%) are not reported throughout the text.

Maximum Likelihood

The ML analysis was conducted in RAxML v8.2.4 (Stamatakis 2014) in the CIPRES portal (Miller et al. 2010). Five partitions were used, all of them using the GTRGAMMA (GTR + Γ) model, as inferred in PartitionFinder. Node support was obtained under the partitioned rapid bootstrapping with GTRCAT model, for 1000 non-parametric bootstrap replicates. Clades with values over 90% were considered as highly supported, values between 70 and 89% were considered as moderately supported, while values below 70% were considered to be weak and are not reported in figures throughout the text.

Bayesian inference

Bayesian analyses were performed in MrBayes v3.2.6 (Huelsenbeck and Ronquist 2001) in the CIPRES portal (Miller et al. 2010). Four simultaneous chains (one cold, three heated) were run for $20x10^6$ generations, sampling every 1.000. Stability parameters and burn-in value were checked in Tracer v1.6 (Rambaut and Drummond 2007). A consensus tree with posterior probability (PP) indices was summarized in TreeAnnotator utility of BEAST v2.3.1 (Drummond et al. 2012), discarding trees sampled prior to stationary as burn-in. Clades with posterior probability values above 0.95 were considered as highly supported, between 0.80 and 0.94 as moderately supported, and below 0.80 as weakly supported.

Results

Our multiple alignment of the molecular dataset resulted in a total of 4341 characters, and the combined molecular and morphological dataset had a total of 4419 characters. Below are described the clades for each dataset that were recovered in at least two of the three distinct analyses performed here (MP, ML, and BI). For each clade, support values for the three separate analyses were given as follows: jackknife (JS), bootstrap (BS), and posterior probability (PP). Support values for each given method are provided in parenthesis as follows (JS/BS/PP). When a specific clade was not recovered in one of the analyses, only the remaining two support values were provided in the same order of appearance defined above.

Molecular analyses

(Figure 1, Appendix 5)

The MP molecular analysis recovered 20 trees of 18367 steps (consistency index = 0.194; retention index =0.521), while ML score was –lnL= -78449.2141. The resulting MP and ML molecluar trees with their respective supports are shown in Figure 1; BI tree is shown in Appendix 5 .

Higher level relationships

Higher level relationships from our molecular data are nearly identical to previously published phylogenies (Zaher et al. 2009, Vidal et al. 2010, Grazziotin et al. 2012, Pyron et al. 2013a, 2015). Xenodontini was recovered with high support values as monophyletic (100/100/1), sister to a clade of the polyphyletic Alsophini, forming a highly supported clade in ML and BI (100/1); whereas in the MP tree *Conophis lineatus*, was sister to Xenodontini, forming a clade with weak support (<70).

Within Xenodontini, *Lygophis* was found monophyletic with moderate to high support (6/95/99/1) and sister to a moderately to highly supported clade (99/100/1) formed by *Erythrolamprus s. lat.* and *Xenodon*. *Erythrolamprus s. lat.* (100/100/1) and *Xenodon* (99/100/1) were also recovered with moderate to high support.

Species groups and internal relationships

Five taxonomic groups within *Erythrolamprus s. lat.* were recovered as monophyletic in all analyses; these are: *Erythrolamprus s. st.*, the '*almadensis*' group, the '*cobella*' group, the '*cursor*' group, and the '*poecilogyrus*' group. Although several species sampled with multiple terminals were recovered as monophyletic, seven were retrieved either as polyphyletic or paraphyletic (i.e., *E. epinephelus*, *E. aesculapii*, *E. breviceps*, *E. miliaris*, *E. taeniogaster*, *E. frenatus*, *E. maryellenae*).

Erythrolamprus s. st. was recovered as monophyletic with high support values (99/100/1). Within this clade, two highly to moderately supported clades were obtained, one formed by *E. bizona* and *E. pseudocorallus* (98/94/1) and another by the remaining taxa (71/91/0.95). *Erythrolamprus aesculapii*, with five terminals, was recovered as polyphyletic, forming three different groups. One of those, with two terminals assigned to *E. a. aesculapii*, was recovered with moderate to high support (76/89/1) in both ML and BI analyses (but not in the MP analysis) as the sister group to a weakly supported

branch that included the remaining *E. aesculapii* terminals plus *E. mimus* and *E. ocellatus*. In the MP analysis, the same latter group excluded *E. ocellatus*. The other two groups of *E. aesculapii* were included in a weakly supported clade (<70/<70/<0.80), where *E. mimus* and the terminal of *E. aesculapii* with a dyadal pattern formed a clade with weak support (<70/<70/<0.80) that was thesister group to a moderately to weakly supported clade (<70/78/<0.80) containing the two terminals of *E. aesculapii* with a monadal pattern.

The '*cobella*' group was retrieved as monophyletic with high support values (92/93/0.99), but the species within were not. One of the terminals of *E. breviceps* was always recovered as sister to the moderately supported clade (-/<70/85) containing all other terminals of the group. In this clade, only a group formed by the two other terminals of *E. breviceps* was found in all analyses with high support values (96/100/1); whereas the relationships of the remaining clades were variable and with weak support.

The '*reginae*' species group was recovered as polyphyletic, with only the terminals of *E. reginae* being recovered together with high support (99/100/1). Terminals of *E. epinephelus*, *E. melanotus* and *E. pygmaeus* formed a highly supported clade in both MP and BI analyses (85/1), but without support in MP (-), where two out of three terminals of *E. pygmaeus* were found associated to the '*poecilogyrus*' group. In this clade, *E. e. epinephelus* and *E. e. pseudocobella* formed a clade with high support values (99/100/1) and *E. melanotus* formed a monophyletic group with high support values (100/100/1); both groups forming a weakly supported clade in MP and BI (<70/<0.80). In ML and BI, terminals of *E. pygmaeus* formed a clade with *E. e. bimaculatus* and *E. e. lamonae* with weak and high support values (<70/0.99), respectively. The only sample of *E. oligolepis* that was included had no stable position in any of the three analyses, but was never associated with the other species of the '*reginae*' group.

The '*miliaris*' group was retrieved as polyphyletic, given that *Erythrolamprus miliaris miliaris* did not form a clade with the other terminals of the group. *Erythrolamprus m. miliaris* was recovered as the sister group to *Erythrolamprus s. st.*, forming a clade with low support values in MP and ML while moderate in BI (<70/<70/94). The terminals of *E. mossoroensis* and *E. miliaris orinus* were grouped in a highly supported clade (98/97/1), where *E. m. orinus* was found to form a monophyletic group with high support values (100/100/1). *Erythrolamprus triscalis*, a species never

associated to this group, was retrieved as the sister group to thelatter group, forming a highly supported clade (99/100/1).

The '*typhlus*/green' species group was recovered as polyphyletic. Terminals of *Erythrolamprus typhlus* were retrieved forming a weakly supported clade in all trees (<70/<70/<0.80), and two clades that correspond to two distinct subspecies were recovered: *E. t. brachyurus* with high support (99/98/1) and *E. t. typhlus* with weak support (-/<70/<0.80). The remaining species of the '*typhlus*' group with *E. almadensis* were recovered forming a clade that was moderately supported in MP and highly supported in ML and BI (78/100/1). Inside the latter clade, *E. atraventer* was found to be the sister group to the highly supported clade (99/99/0.99) containing the remaining species within this clade. In the MP tree, *E. almadensis*, *E. jaegeri*, *E. maryellenae* and *E. viridis*, formed a polytomy, but in ML and BI trees, terminals of *E. jaegei*, *E. maryellenae* and *E. viridis* formed a clade with high and moderate supports, respectively (99/76), with *E. almadensis* as their sister taxon. *Eythrolamprus atraventer* and *E. almadensis* were recovered as monophyletic with high support values (99/100/1 and 100/100/1, respectively), while terminals of *E. maryellenae* never formed a monophyletic group, and their relationships with *E. jaegeri* and *E. viridis* varied among the methodological approaches.

The '*poecilogyrus*' group was recovered as monophyletic with high support values (96/91/1). In MP, *Erythrolamprus ceii* was found to be the sister group to a monophyletic but weakly supported *E. poecilogyrus* (<70), where terminals of *E. poecilogyrus schotti* formed a highly supported clade (98) that was the sister taxon to *E. p. sublineatus*. In both ML and BI, two highly supported sister clades were recovered, one formed by the two terminals of *E. p. schotti* (95/1) and the other by *E. ceii* and *E. p. sublineatus* (84/1), rendering *E. poecilogyrus* non-monophyletic.

Species of the '*cursor*' group formed a weakly supported clade in all trees (-/<70/<80).

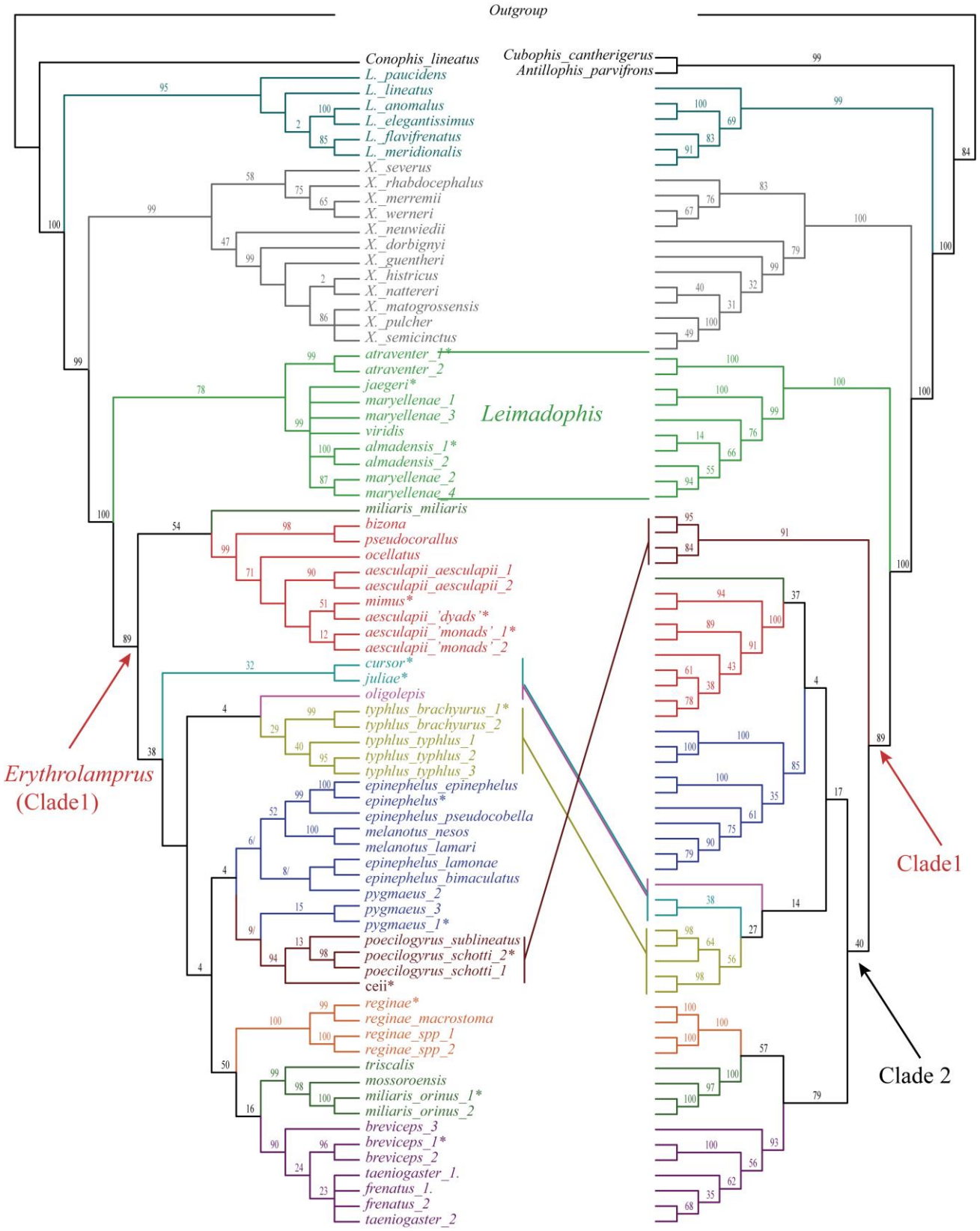


Figure 1. Maximum parsimony (left) and Maximum likelihood (right) trees obtained from the analysis of the molecular data. Values in the branches indicate Jackknife support, in the MP tree; and bootstrap in ML. The order in the ML clades is not necessarily the same as in the MP tree. Asterisks indicate terminals previously published.

Relationships within the clades

Two highly supported clades within *Erythrolamprus s. lat.* were retrieved in all three methodological approaches: one containing *E. almadensis*, *E. atraventer*, *E. jaegeri*, *E. maryellenae* and *E. viridis*, and the other containing all remaining species (91/89/1). The latter clade will be called herein "Clade 1". Within Clade 1, only *E. miliaris miliaris* and *Erythrolamprus s. st.* clustered together in all three analyses, showing weak support values in MP and ML and moderate in BI (<70/<70/94). Otherwise, the results of ML and BI were highly concordant within Clade 1, but MP results were not.

The following relationships were common to ML and BI trees for Clade 1. The '*poecilogyrus*' group was retrieved as the sister group to the clade containing all remaining taxa with weak and moderate support (<50/ 0.94). This latter clade will be called from now on "Clade 2". Clade 2 contained two main clades: the first, with moderate and high support values (79/0.98), containing the '*cobella*' group as the sister group to the weakly and highly supported (<70/1) clade, containing the terminals of *Erythrolamprus reginae* and the clade formed by *E. triscalis*, *E. mossoroensis* and *E. miliaris orinus*. The second also held two main clades: the first one grouping *E. oligolepis*, *E. typhlus*, and the species of the '*cursor*' group, recovered with weak support in ML and moderate in BI (<70/0.80); and the second one recovered with weak support (<50/<0.80) and containing two clades: *E. epinephelus*, *E. melanotus*, and *E. pygmaeus* on the one hand, and *E. miliaris miliaris* and *Erythrolamprus s.st*. on the other hand.

Clade 1 in the MP tree, on the other hand, showed weak jackknife support (<70) for all the relationships between the main clades. A clade formed by *E. miliaris miliaris* and *Erythrolamprus s. st.* was recovered as sister to the clade with the remaining species. In this latter clade, the '*cursor*' group was retrieved as the sister taxon to a clade with all the other species. The latter contained the following clades: *E. typhlus* + *E. oligolepis*; two terminals of *E. pygmaeus* + the '*poecilogyrus*' group; *E. epinephelus* + *E. melanotus* + one terminal of *E. pygmaeus*; terminals of *E. reginae*; *E. triscalis* + *E. miliaris orinus* + *E. mossoroensis*; and the '*cobella*' group.

Morphological analysis

(Figure 2)

The MP analysis for 78 characters and 50 terminal taxa recovered 180 most parsimonious trees with 448 steps each (consistency index = 0.268; retention index =0.562).

Higher level relationships

Morphological results recovered Xenodontini as non-monophyletic, with its members in a polytomy containing also *Philodryas patagoniensis* and a weakly supported clade (<70) formed by *Psomophis joberti*, *Oxyrhopus guibei, Arryton vittatum* and *Tomodon dorsatus*. *Xenodon* was retrieved as monophyletic, but with weak support (<70). *Lygophis* was retrieved as paraphyletic with respect to *Erythrolamprus sagittifer*, forming a weakly supported clade (<70). *Erythrolamprus s. lat.* was also found to be paraphyletic with respect to *Lygophis*, in a weakly supported clade (<70).

Given that the '*cursor*' and the '*poecilogyrus*' groups were sampled for only one species in the morphology analysis, their monophyly could not be tested.

Species groups and internal relationships

Erythrolamprus s. st. was recovered with moderate support (87), but with no structure within its species. The following clades were also recovered, but with weak support: *E. juliae* + *Erythrolamprus s. st.* (<70); *E. almadensis* + *E. carajasensis* (<70), retrieving the '*almadensis*' group as monophyletic; *E. miliaris* + *E. mossoroensis* (<70), making the '*miliaris*' group monophyletic; *E. breviceps* + *E. frenatus* + *E. taeniogaster* (<70), rendering monophyletic the '*cobella*' group; *E. atraventer* + *E. jaegeri* + *E. maryellenae* + *E. viridis* (<70), retrieving the '*typhlus*' group as non-monophyletic; *E. epinephelus* + *E. melanotus* + *E. pyburni* + *E. pygmaeus* + *E. reginae* (<70), making paraphyletic the '*reginae*' group with respect to *E. melanotus, E. pyburni* and *E. pygmaeus*. *Erythrolamprus oligolepis, E. poecilogyrus* and E. *typhlus* were not found strongly associated to any of the clades listed above.

Relationships between the clades

All above mentioned clades were found to fall in a large polytomy, and therefore no relationships among clades could be described.

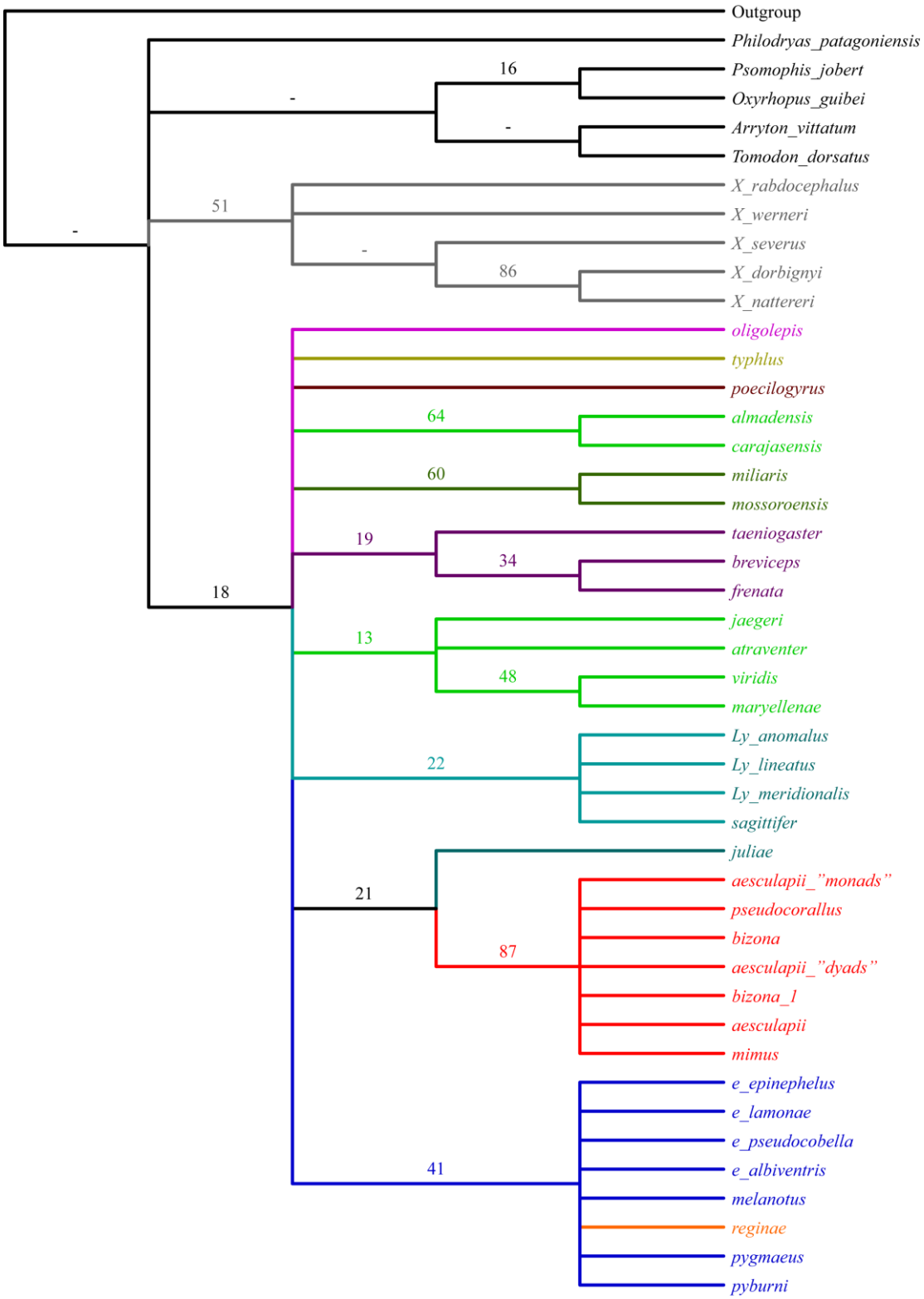


Figure 2. Maximum parsimony tree obtained from the analysis of the morphological data. Values in the branches indicate Jackknife support.

Combined analysis

(Figure 3)

The MP analysis of the combined dataset obtained 100 trees with 18849 steps (consistency index = 0.383; retention index =0.581). Synapomorphies obtained for the clades in TNT are listed in Appendix 6.

Higher level relationships

As in the molecular results, relationships among higher level clades were very similar to those previous studies (Zaher et al. 2009, Vidal et al. 2010, Grazziotin et al. 2012, Pyron et al. 2013a, 2015). Xenodontini was found monophyletic with high support (99), keeping the relationships as in the molecular trees, with *Lygophis* as sister to the highly supported clade (97) grouping *Erythrolamprus s. lat.* and *Xenodon*.

Lygophis was found to be paraphyletic with respect to *Erythrolamprus sagittifer*, but, as in the morphological tree, forming a clade with moderate support (75). Concordant with the molecular and morphological results, *Xenodon* was retrieved as monophyletic, with high jackknife support (99). On the other hand, *Erythrolamprus s. lat.* was found to be polyphyletic with *E. sagittifer* clustering along with the speices of the genus *Lygophis*. The remaining species of *Erythrolamprus s. lat.* formed a clade with high support (97).

Species groups and internal relationships

Within *Erythrolamprus s. lat.*, the same main clades found in the molecular analyses and most of those in the morphological tree were retrieved. *Erythrolamprus s. st.* was retrieved as monophyletic with a high jackknife support (94), but as in the morphological tree, the terminals formed a polytomy. *Erythrolamprus aesculapii* was recovered as non-monophyletic and the same three branches found in the molecular trees for the five terminals were also retrieved here: *E. a. aesculapii* (*sensu* Curcio et al. 2015) with two terminals and with moderate support (87); one clade corresponding to the monads pattern, with two terminals and weakly supported (<70); and one loose terminal assignable to the dyads pattern.

Concordant with the morphological and molecular results, the '*cobella*' group was recovered as monophyletic, with a high jackknife support (94). In the combined tree, *Erythrolamprus taeniogaster* and *E. frenatus* were retrieved as monophyletic with weak (<70) and high support (99) values, respectively, and both species were grouped in a

weakly supported clade (<70). *Erytheolamprus breviceps*, as in the molecular trees, was retrieved as non-monophyletic and its terminals formed a polytomy with the *E. frenatus/taeniogaster* clade.

The '*reginae*' group was polyphyletic, as in the molecular trees. Terminals of *Erythrolamprus reginae* formed a highly supported clade (94). *Erythrolamprus epinephelus* was recovered as paraphyletic with respect to *E. melanotus*, *E. pygmaeus* and *E. pyburni*, forming a weakly supported clade (<70). Within these groups, *E. melanotus* formed a clade with high jackknife support (86), and the terminals of *E. pygmaeus*, unlike in the molecular MP tree, were retrieved as a monophyletic group with weak support (<70). Terminals of the *Umbrivaga* group were found to be non-monophyletic, forming a polytomy with *E. e. lamonae* in a weakly supported clade (<70). *Erythrolamprus melanotus, E. e. epinephelus, E. e. pseudocobella* and *E. e. albiventris* formed a weakly supported clade (<70), where *E. melanotus* was sister to the other terminals. This clade was similar to the one obtained in the molecular analysis, except that it also contains *E. e. albiventris*, a terminal sampled only for morphology. *Erythrolamprus oligolepis* and *E. typhlus* formed a weakly supported clade (<70) that was only distantly related to the other members of the '*reginae*' group.

The '*miliaris*' group was found to be polyphyletic given that the terminal of *Erythrolamprus miliaris miliaris* remained distant to the other terminals, as in the molecular results. *Erythrolamprus miliaris orinus* and *E. mossoroensis* formed a clade with high jackknife support (99), with *E. triscalis* sister to them, forming a highly supported clade (99).

Figure 3. Maximum parsimony tree obtained from the analysis of the combined data. Values in the branches indicate Jackknife supports. One asterisk indicate terminals previously published; two asterisks indicate terminals included only for morphology.

The '*typhlus*' group was polyphyletic, given that *Erythrolamprus typhlus* did not form a clade with the other members of the group. Terminals of *E. typhlus* formed a highly supported clade (85), with two clades corresponding to *E. t. brachyurus* and *E. t. typhlus* showing high (99) and weak supports (<70), respectively. The remaining species of the '*typhlus*' group sampled (*E. atraventer, E. jaegeri, E. maryellenae, E. viridis*) formed a weakly supported clade (<70) with the species of the '*almadensis*' group (*E. almadensis* and *E. carajasensis*). *Erythrolamprus atraventer* was recovered as monophyletic with a high jackknife support (93) and as the sister group to all other species in the clade. *Erythrolamprus almadensis, E. carajasensis, E. jaegeri, E. maryellenae,* and *E. viridis* formed a polytomy in a moderately supported clade (7/78). Contrary to all molecular trees, *E. maryellenae* was retrieved as monophyletic, in a clade with moderate jackknife support (3/84). On the other hand, concordant with the morphological results, the '*almadensis*' group was recovered as monophyletic with moderate support (75), with terminals of *E. almadensis* forming a weakly supported clade (<70).

With high support values, the '*poecilogyrus*' group (98) was retrieved as monophyletic. Monophyly of *Erythrolamprus poecilogyrus* could not be confirmed, since *E. ceii*, *E. p. schotti* and *E. p. sublineatus* formed a polytomy. Nevertheless, *E. p. schotti* formed a highly supported clade (8/99), as in all molecular analyses.

As in the molecular MP, ML and BI trees, the '*cursor*' group was recovered as monophyletic, but with weak support (<70).

Relationships among the clades

As in the molecular approaches, a clade formed by *E. almadensis*, *E. atraventer, E. carajasensis, E. jaegeri, E. maryellenae,* and *E. viridis* was recovered as the sister group to the weakly supported Clade 1 (<70), the clade containing all other species of the group. As in the MP molecular tree, Clade 1 included two main clades, one weakly supported (<70) with *E. miliaris miliaris* as sister to the weakly supported clade (5/<70) containing the '*cursor*' group and *Erythrolamprus s.st*. The other group within Clade 1, contained all the remaining groups, formed a large polytomy.

Discussion

All recent phylogenies recovered a monophyletic Xenodontini with the same main constituent clades: *Lygophis* as the sister group to a strongly supported clade formed by *Xenodon* and *Erythrolamprus s.lat*., with all three genera retrieved as monophyletic with

high support values (Moura-Leite 2001, Zaher et al. 2009, Grazziotin et al. 2012, Jowers et al. 2013, Pyron et al. 2013a, 2015). Our results also recovered these groups in the molecular and combined analyses, but not in the morphological analysis where *Lygophis* was found within the *Erythrolamprus s. lat.* clade, and *Xenodon* did not cluster with this latter clade. The main clades recovered are described below with their morphological synapomorphies (character number and state in parentheses).

The tribe Xenodontini is herein characterized by a non-capitate (9.0) and non-calyculate (7.0) bilobed hemipenis with an apical disk (8.1) on medium (6.0) to short sized lobes (6.1). These characters have been largely recognized as synapomorphies for the tribe (Myers 1986, Zaher 1999, Moura-Leite 2001, Masiero 2006, Zaher et al. 2009). However, some Xenodontini lack these synapomorphies: the hemipenes of *Xenodon rabdocephalus*, *X. werneri* and *X. merremi* have long lobes (6.2), *Lygophis lineatus* is unicaliculated (7.2), and *Erythrolamprus melanotus*, is semicapitated (9.1). Zaher (1999) and Myers (in Myers and McDowell 2014) recently discussed about the validity of the apical disk and lobe length as a generic diagnostic character, stating that the loss of this feature is not enough evidence to erect new genera, as was the case of *Thalesius* Yuki, 1993 and *Waglerophis* Hoge & Romano 1972. Our evidence agrees with these authors, showing that hemipenes with short to medium sized lobes and the presence of apical disks are ancestral states for Xenodontini, with the other states appearing as secondary modifications within the clade.

Dixon & Thomas (1982) suggested that *Erythrolamprus sagittifer* may be associated to species of the *Liophis lineatus* group (sensu Michaud and Dixon 1987) and Moura-Leite (2001) found it in a clade with species currently in *Lygophis*, even if he did not recognize it as a member of that genus in his taxonomic proposal. In our morphology and combined analyses, *E. sagittifer* was found nested ithin the highly supported genus *Lygophis*, and therefore we reallocate it to this genus.

In our combined and morphology trees, *Lygophis* is supported by having a clavate hemipenes (1.1), with short lobes (6.0), small postdiastemal teeth in relation to the last prediastemal tooth (44.0), splenial larger than the angular bone (49.2), and a short frontal process of the prefrontal bone (50.1). The hemipenial characters were previously suggested as synapomorphies for the genus (Moura-Leite 2001, Zaher et al. 2009) and herein we corroborate them in our phylogenetic analysis. Additionally, these characters are shared by *L. sagittifer*, which supports the reallocation of the species in the genus.

The clade formed by *Xenodon* and *Erythrolamprus s. lat.* is supported by having a quadrate-like hemipenis (1.0) with medium sized lobes (6.1), a splenial that is smaller or as large as the angular bone (49.0/1), and a short frontal process of the prefrontal bone (50.0). Hemipenial features are modified in some clades or species, but this will be discussed below (e.g. *X. rabdocephalus*). Despite that this clade was also recovered in the morphological phylogeny of Moura-Leite (2001) and all other subsequent molecular phylogenies, none of them have previously pointed out synapomorphies to support it.

Systematics of the genus *Xenodon* and its hemipenial, osteological and muscular synapomorphies have already been discussed before, along with the modifications in some of its clades (Zaher 1999, Masiero 2006, Zaher et al. 2009). In our analyses, *Xenodon*, formed a highly supported clade characterized by having a hemipenes without inflated areas in the lateral region of the asulcate side (13.0) nor in the proximal region of the sulcate side (14.0), a flat asulcate surface (17.0), presence of a dorso-posterior process in the vomer (38.1), lance-shaped post-diastemal teeth (43.0), a wide quadrate bone head (66.1), anterior extention of the parabasisphenoid aligned with the anterior extention of the frontal bone (69.0) and an anteriorly located transversal process of the basioccipital bone (72.0). Within *Xenodon*, the clade formed by *X. merremi*, *X. rabdocephalus*, and *X. werneri* has extremely large lobes (6.2), which may be considered as modifications of the ancestral form of the genus (medium sized lobes). *Xenodon rabdocephalus* is here sampled for molecular data for the first time. Its retrieved position corroborates the idea of a derived hemipenial morphology in the highly supported clade formed by *X. merremi*/*rapbocephalus*/*werneri* (Zaher 1999, Masiero 2006).

Despite the fact that all recent systematic works recovered *Erythrolamprus s. lat.* as a highly supported clade (Moura-Leite 2001, Zaher et al. 2009, Grazziotin et al. 2012, Jowers et al. 2013, Pyron et al. 2013a, 2015), no single synapomorphy is known for that clade, which generated controversies about current taxonomic arrangements (Curcio et al. 2009a, Myers 2011, Lynch 2015). Our results, in all approaches, recovered *Erythrolamprus s. lat.* as a monophyletic group, with species of *Erythrolamprus s. st.* and *Umbrivaga* rooted within this clade. Monophyly of that clade is supported by a hemipenis with inflated surfaces in the proximal region of the asulcate (13.1) and sulcate (14.1) sides and with a longitudinal concavity in the asulcate side (18.0). This latter character was also found in *X. neuwiedii*, but we consider it a convergence in this species.

In our results, nine monophyletic clades were recovered within the genus *Erythrolamprus s. lat.*: (1) *E. almadensis* + *E. atraventer* + *E. carajasensis* + *E. jaegeri* + *E.maryellenae* + *E. viridis*; (2) *Erythrolamprus s. st.*; (3) *E. breviceps* + *E. taeniogaster* + *E. frenatus*; (4) *E. reginae*; (5) *E. epinephelus* + *E. melanotus* + *E. pygmaea* + *E. pyburni*. (6) *E. miliaris* + *E. mossoroensis* + *E. triscalis*; (7) *E. ceii* + *E. poecilogyrus*; (8) *E. cursor* + *E. juliae*; (9) *E. typhlus*.

Dixon & Thomas (1985) initially proposed the '*almadensis*' group as a complex including *E. alberguentheri*, *E. almadensis*, *E. atraventer*, *E. jaegeri*, *E. poecilogyrus*, *E. typhlus* and *E. viridis*. Later, Dixon (1987) revised and proposed the 'green' or '*typhlus*' group for *E. albertguentheri*, *E. atraventer*, *E. jaegeri*, *E. maryellenae*, *E. typhlus* and *E. viridis*, based mainly in the presence in these species of a dorsal green coloration. The remaining species previously included in the '*almadensis*' group, *E. almadensis* and *E. poecilogyrus*, were later treated independently by Dixon (1991) and Dixon & Markezick (1992), respectively. Later, Cei (1993), grouped these two species with *E. cei* in what he denominated the *'poecilogyrus*' group. All recent molecular phylogenies have shown that these arrangements are not monophyletic (Zaher et al. 2009, Vidal et al. 2010, Grazziotin et al. 2012, Jowers et al. 2013, Pyron et al. 2013a, 2015), and our results uphold those findings.

Molecular approaches found a clade formed by *E. almadensis*, *E. atraventer* and *E. jaegeri* as sister to the clade containing all remaining members of *Erythrolamprus s.lat.* (Zaher et al. 2009, Vidal et al. 2010, Grazziotin et al. 2012, Pyron et al. 2013a, 2015). Our molecular and combined results retrieved a highly supported clade grouping these species plus *E. carajasensis*, *E. maryellenae* and *E. viridis*, that is sister to all remaining *Erythrolamprus s.lat.* In the morphology tree, the same clade was found, merged with all other clades within *Erythrolamprus s.lat.*, but without *E. almadensis*. As recovered in the combined analysis, this clade is supported by the following morphological synapomorphies: a high density of spinules in the sulcate side (26.2), a ventral projection of the vomerine process of the premaxilla (36.1), and an anteriorly located transversal process of the supraoccipital (62.0). Two secondary modifications are considered for these characters: in *E. atraventer* the density of spinules in the asulcate side is moderate (26.1) and in *E. almadensis* there is no ventral projection in the vomerine process of the premaxilla (36.0). Given that this clade is highly supported and its position within the Xenodontini and *Erythrolamprus s. lat.* has remained stable, we recognize it as an

independent lineage from and resurrect *Leimadophis* Fitzinger, 1843 to accommodate these species (see systematic account).

Clade 1 (*Erythrolamprus s. lat.* excluding *Leimadophis*) was highly supported in our molecular trees, with moderate support in the combined tree, but was not retrieved in the morphological analysis. Species of this clade sampled in preceding molecular studies retrieved the same grouping, also with high to moderate support (Zaher et al. 2009, Vidal et al. 2010, Grazziotin et al. 2012, Pyron et al. 2013a, 2015). Despite our results showing morphological synapomorphies for most clades within Xenodontini and within Clade 1 (see below), none were found to support this branch. Nevertheless, we recognize this clade as a new combination for the genus *Erythrolamprus* given its high support in our molecular and combined trees, and its stability throughout recent studies.

Previous phylogenies have sampled two species of *Erythrolamprus s. st.* (*E. aesculapii* and *E. mimus*) finding them always forming a highly supported clade, but within the species formerly allocated in the genus *Liophis* (Vidal et al. 2010, Grazziotin et al. 2012, Jowers et al. 2013, Pyron et al. 2013a, 2015). The present study, which includes five out of the six currently recognized species, also recovered *Erythrolamprus s. st.* as a highly supported clade within the *Erythrolamrus s. lat.* in all three results (molecular, morphological and combined). Six morphological synapomorphies are herein recognized for this clade: distal row of enlarged spines not differentiated (19.1); proximal end of the transversal process of the nasal bone sharped (39.0); Transversal process of the nasal bone wider posteriorly (40.2); canal present in the post-diastemal teeth (42.1, i.e. opistoglyph dentition); medial process of the maxillary processes of the ectopterygoid bone projected anteriorly with respect to the lateral process (45.1); and uniradiated parabasisphenoid rostrum (70.0). Within *Erythrolamprus s. lat.*, the non-differentiated condition of the distal row of enlarged spines appears also in four species of *Leimadophis* and in *E. epinephelus pseudocobellus*, but it seems to be a convergence within these distantly related taxa and *Erythrolamprus s. st.*, representing a modification from the ancestral condition within *Erythrolamprus s. lat.* (differentiated distal row of enlarged spines [19.2]). The remaining characters were recovered as unambiguous synapomorphies for the group.

Erythrolamprus aesculapii has four currently accepted subspecies, *E. a. aesculapii*, *E. a. monozona*, *E. a. tetrazana* and *E. venustissimus* (Peters and Orejas-

Miranda 1970, Curcio et al. 2015). Recently, Curcio *et al.* (2015) redefined *E. a. aesculapii* and *E. a. tetrazana* and pointed out the taxonomic and nomenclatural problems related to *E. a. monozona* and *E. venustissimus*, names assigned to populations of southwestern Brazil. For this region, two morphological groups have been recognized based in their color pattern, the monad and dyad patterns (Marques and Puorto 1991, Barbo et al. 2011). In our results, *E. aesculapii* is retrieved as non-monophyletic in all trees, forming three independent groups in the molecular and combined trees. These three separate clusters correspond to *E. a. aesculapii*, the monad and the dyad patterns, respectively, suggesting that these taxa should be recognized as different species. Nevertheless, a more comprehensive approach clarifying the nomenclatural and taxonomic issues within this species must bring clarity to this issue and on the validity of the name *Erythrolamprus* Boie 1826, since *E. a. venustissimus* (=*Coluber venustissimus* Wied-Neuwied, 1821) is the type species of the genus.

The '*cobella*' group is monophyletic in all our trees, being only weakly supported in the morphological analysis. This is the first phylogenetic study where the monophyly of the group is tested, since all former approaches only sampled one species. The '*cobella*' clade is supported by a single synapomorphy: post-diastemal teeth twice the size or less than the pre-diastemal teeth (44.1). This character state was also found in *Lygophis*, in the monad specimens of *Erythrolamprus aesculapii*, and was variable in *E. miliaris*. However, since these taxa are not closely related, it is likely to be a convergence.

The three species of the '*cobella*' group available for this study were sampled for multiple terminals, with only *E. frenatus* and *E. taeniogaster* appearing as monophyletic in the combined tree, with high and moderate supports, respectively. Otherwise, all species were retrieved as non-monophyletic in the molecular trees. The group was revised by Dixon (1983b) and later by Fenandes *et al.* (2002). Nevertheless, our results suggest that a more comprehensive approach is needed in order to have a better understanding of the taxonomic limits and phylogenetic relationships within this clade.

In our molecular and combined results, the '*miliaris*' group appears as polyphyletic since the clade formed by *Erythrolamprus miliaris orinus* and *E. mossoroensis* was found distantly related to the terminal of *E. mi. miliaris*. In our morphological sample the terminal of *E. miliaris*, corresponded to *E. m. orinus*, and formed a weakly supported clade with *E. mossoroensis*. *Erythrolamprus miliaris miliaris*

was found to be sister to the clade containing *Erythrolamprus s. st.* in the molecular results and to the clade containing the '*cursor*' group and *Erythrolamprus s. st.* in the combined results, always with weak support and no morphological synapomorphies to support it. Polyphyly of *Erythrolamprus miliaris* is unexpected and calls into question the results shown here. However, an eventual contamination of our sample seems to be discarded given that our samples were retrieved in in similar positions in the gene trees (data not shown), and never clustered with any other taxa.

On the other hand, the clade containing *Erythrolamprus miliaris orinus* and *E. mossoroensis* was found with high support in the molecular and combined trees and weakly supported in the morphological one. In the molecular and combined analysis, this group forms a highly supported clade with *E. triscalis*, a species previously not associated to any group. Despite high support and concordance between molecular and morphological evidence in our results, no unambiguous synapomorphy was found to support this clade.

Previous phylogenies found the species of the '*reginae*' group (*Erythrolamprus reginae* and *E. epinephelus*) distantly related (Vidal et al. 2010, Grazziotin et al. 2012, Jowers et al. 2013, Pyron et al. 2013a, 2015). Concordant with these phylogenies, results of the molecular and combined trees retrieved the '*reginae*' group as a polyphyletic group, whereas in the morphological tree it was paraphyletic with respect to *E. melanotus*, *E. pygmaeus* and *E. pyburni*. The terminals of *E. reginae* form a highly supported clade in the molecular and the combined trees, but there is no morphological synapomorphy to point out since only one morphological terminal was codified for this clade.

Dixon (1983a) suggested that *Erythrolamprus oligolepis* is a synonym of *E. reginae*, but later, Cunha & Nascimento (1993) revalidated it as a full species. Our molecular and combined analyses retrieved *E. oligolepis* distantly related to the *E. reginae* clade, supporting it as a valid species as recognized in the recent literature (Frota et al. 2004, Zaher et al. 2009, Grazziotin et al. 2012, França et al. 2013).

Erythrolamprus epinephelus, a member of the '*reginae*' group, was found to be paraphyletic with respect to *E. melanotus* and *E. pygmaeus* in the molecular trees, and to *E. melanotus, E. pygmaeus* and *E. pyburni* in the combined phylogeny. Some previous phylogenies found association of *E. pygmaeus* with *E. epinephelus* (Grazziotin et al. 2012, Pyron et al. 2015), forming weakly supported clades, but only one sample of each

species was included and none of *E. melanotus* or *E. pyburni*. Herein, we increased the number of taxa and terminals, and found them forming a highly supported clade in the molecular ML and BI trees and in the combined results. In our combined tree, this group is supported by one unambiguous synapomorphy: low density of spinules in the sulcate side of the hemipenes (26.0). These results corroborate the synonymization of *Umbrivaga* with *Erythrolamprus*, and suggest that the specialized morphology of the species included in this group (e.g. small size, reduced number of maxillary teeth) is a derived condition within *Erythrolamprus s. lat.*

Erythrolamprus epinephelus has eight vaguely defined subspecies (Dixon 1983d). Herein we included evidence for five of them, finding the subspecies grouped in clades with terminals of *E. melanotus E. pygmaeus* and *E. pyburni*, showing that the species is polytypic. Nevertheless, our evidence does not allow us to delimit correctly these taxa, and this issue should be addressed with a better sampling in the future.

The '*poecilogyrus*' and '*cursor*' groups were retrieved as monophyletic in our molecular and combined analyses, with high and weak to moderate supports, respectively. These are the same results obtained in previously published molecular phylogenies (Grazziotin et al. 2012, Jowers et al. 2013, Pyron et al. 2013a, 2015). Likewise, in our molecular and combined trees, *Erythrolamprus typhlus* was found to be monophyletic with moderate to weak support, with the subspecies sampled through multiple terminals (*E. t. typhlus* and *E. t. brachyurus*) also appearing as monophyletic but with variable supports. Though, for each group only one morphological terminal was codified and, therefore, it is not possible to infer morphological synapomorphies for these clades.

Despite *Erythrolamprus* (Clade 1) being recurrently recovered as a monophyletic component with high node support values, relationships within this clade have remained ambiguous since most results found only weak support for the inner groupings. This is also true in all our analyses, despite having increased the taxonomic sampling of both molecular and morphological datasets. Recently, Myers (in Myers and McDowell 2014) suggested the use of subgenera (i.e. retaining *Liophis* and *Erythrolamprus* as subgenera) as a way to maintain nomenclatural stability for this group. However, the lack of phylogenetic evidence to support such nomenclatural act prevents it to represent an effective solution for the group. We therefore prefer to maintain the allocation of species in Clade 1 to the genus *Erythrolamprus* (even if generic names are still available for its

clades) until a better understanding of the relationships within this clade is reached and a more objective taxonomic arrangement could be achieved.

Conclusions

Our results confirm previous higher phylogenetic relationships within Xenodontini and corroborate the monophyly of the tribe. Additionally, our analyses agree with the taxonomic decisions made by Zaher *et al.* (2009) and Grazziotin *et al.* (2012) in merging *Erythrolamprus*, *Liophis* and *Umbrivaga*, supported with molecular and morphological evidence and removing previous doubts (Curcio et al. 2009a, Myers 2011, Lynch 2015). These results suggest that the particular morphological features that lead to the recognition of *Erythrolamprus s. st.* and *Umbrivaga* as different genera are derived within this clade.

Erythrolamprus sagittifer was found nested within *Lygophis*, supported by morphological evidence, and therefore we reallocate the species to this genus.

Nine main clades were recovered within *Erythrolamprus s. lat.*, four of them corresponding to the traditionally recognized taxonomic groups (i.e. *Erythrolamprus s. st.*, '*almadensis'*, '*cobella*', '*cursor*', and '*poecilogyrus*'); whereas remaining groups were recovered as polyphyletic.

Leimadophis Fitzinger, 1843 is resurrected for the highly supported clade that appears as the sister group of *Erythrolamprus*, and contains *Le. almadensis*, *Le. atraventer* new comb., *Le. carajasensis* new comb., *Le. jaegeri* new comb., *Le. maryellenae* new comb., and *Le. viridis* new comb. *Leimadophis guentheri* new comb. is also included in this group due to its in morphological similarities already acknowledged by Dixon (1985b, 1987).

Our results support the monophyly of most species sampled through multiple terminals (e.g. *Erythrolamprus reginae*, *E. typhlus*, *E. melanotus*). Nevertheless, several species were recovered as non-monophyletic (e.g. *E. aesculapii*, *E. breviceps*, *E. epinephelus*). A detailed revisions of the latter is here recommended, including multiple sources of evidence and extensive sampling, in order to elucidate the taxonomic problems within these species.

Systematic account

Erythrolamprus Boie, 1826

Type species: *Coluber venustissimus* Linnaeus Wied-Neuwied, 1821

Diagnosis: No unambiguous synapomorphy is known so far for the current arrangement.

Content: *Erythrolamprus aesculapii* (Linnaeus, 1766); *Erythrolamprus andinus* (Dixon, 1983); *Erythrolamprus bizona* (Jan, 1863); *Erythrolamprus breviceps* (Cope, 1860); *Erythrolamprus ceii* (Dixon, 1991); *Erythrolamprus cobella* (Linnaeus, 1758); *Erythrolamprus cursor* (Lacépède, 1789); *Erythrolamprus dorsocorallinus* (Esqueda, Natera, La Marca and Ilija-Fistar, 2007); *Erythrolamprus epinephelus* (Cope, 1862); *Erythrolamprus festae* (Peracca, 1897); *Erythrolamprus frenatus* (Werner, 1909); *Erythrolamprus guentheri* (Garman, 1883); *Erythrolamprus ingeri* (Roze, 1958); *Erythrolamprus janaleeae* (Dixon, 2000); *Erythrolamprus juliae* (Cope, 1879); *Erythrolamprus leucogaster* (Jan, 1863); *Erythrolamprus longiventris* (Amaral, 1925); *Erythrolamprus melanotus* (Shaw, 1802); *Erythrolamprus mertensi* (Roze, 1964); *Erythrolamprus miliaris* (Linnaeus, 1758); *Erythrolamprus mimus* (Cope, 1868); *Erythrolamprus ocellatus* Peters, 1869; *Erythrolamprus oligolepis* (Boulenger, 1905); *Erythrolamprus ornatus* (Garman, 1887); *Erythrolamprus perfuscus* (Cope, 1862); *Erythrolamprus poecilogyrus* (Wied, 1825); *Erythrolamprus problematicus* (Myers, 1986); *Erythrolamprus pseudocorallus* (Roze, 1959); *Erythrolamprus pyburni* (Markezich and Dixon, 1979); *Erythrolamprus pygmaeus* (Cope, 1868); *Erythrolamprus reginae* (Linnaeus, 1758); *Erythrolamprus semiaureus* (Cope, 1862); *Erythrolamprus subocularis* (Boulenger, 1902); *Erythrolamprus taeniogaster* (Jan, 1863); *Erythrolamprus taeniurus* (Tschudi, 1845); *Erythrolamprus torrenicola* (Donnelly and Myers, 1991); *Erythrolamprus trebbaui* (Roze, 1958); *Erythrolamprus triscalis* (Linnaeus, 1758); *Erythrolamprus typhlus* (Linnaeus, 1758); *Erythrolamprus vitti* (Dixon, 2000); *Erythrolamprus williamsi* (Roze, 1958).

Leimadophis Fitzinger, 1843 **resurrected**

Type species: *Natrix almadensis* Wagler, 1824

Diagnosis: High spinules density in the sulcate side of the hemipenis (modified in *L. atraventer*); a ventral projection of the vomerine process of the premaxilla (modified in *L. almadensis*); transversal process of the supraoccipital located anteriorly.

Content: *Leimadophis almadensis* (Wagler, 1824); *Leimadophis carajasensis* (Cunha, Nascimento and Ávila-Pires, 1985) **new combination**, *Leimadophis guentheri* (Peracca, 1897) **new combination**; *Leimadophis jaegeri* (Gunther, 1958) **new combination**; *Leimadophis atraventer* (Dixon and Thomas, 1985) **new combination**; *Leimadophis maryellenae* (Dixon, 1985) **new combination**; *Leimadophis viridis* (Günther, 1862).

Comments: We include *Leimadophis guentheri* herein following Dixon (1985b, 1987) association with *L. jaegeri*, *L. atraventer*, *L. maryellenae* and *L. viridis*. *Leimadophis guentheri* was formerly changed to *Erythrolamprus alberguentheri* by Grazziotin *et al.* (2012) since it was an homonym of *Erythrolamprus guentheri* Garman, 1883. In the current taxonomic arrangement they are no longer synonyms and the nomenclatural change is reversed.

Lygophis Fitzinger, 1843

Type species: *Coluber lineatus* Linnaeus, 1758.

Diagnosis: Hemipenes clavate, with short lobes; small postdiastemal teeth in relation to the last prediastemal tooth; splenial bone larger than the angular; short frontal process of the prefrontal bone and pattern of dorsal scale microornamentation fasciculate (Moura-Leite 2001); dorsal pattern with different arrangements of longitudinal stripes or tending to striation (Zaher et al. 2009).

Content: *Lygophis anomalus* (Günther, 1858); *Lygophis dilepis* (Cope, 1862); *Lygophis elegantissimus* (Koslowsky, 1896); *Lygophis flavifrenatus* (Cope, 1862); *Lygophis lineatus* (Linnaeus, 1758); *Lygophis meridionalis* (Schenkel, 1902); *Lygophis paucidens* (Hoge, 1953); *Lygophis sagittifer* (Jan, 1863) **new combination**; *Lygophis vanzolinii* (Dixon, 1985).

References

Arevalo, E.; Davis, S.K. & Sites, J.W.J. 2009. Mitochondrial DNA Sequence Divergence and Phylogenetic Relationships among Eight Chromosome Races of the *Sceloporus grammicus* Complex (Phrynosomatidae) in Central Mexico. **Systematic Bioloy,** 43: 387–418.

Barbo, F.E.; Marques, O.A.V. & Sawaya, R. 2011. Diversity, Natural History, and

Distribution of Snakes in the Municipality of São Paulo. **South American Journal of Herpetology,** 6: 135–160.

Cei, J.M. 1993. **Reptiles del noroeste , nordeste y este de la Argentina: Herpetofauna de las selvas subtropicales, Puna y Pampas**. Torino, Museo Regionale di Scienze Naturali. 949 p. (Monografie, n. 14)

Cundall, D. & Irish, F. 2008. The snake skull. *In*: Gans, C.; Gaunt, A. & Adle, K. (Eds). **Biology of the Reptilia, Vol. 20. The Skull of Lepidosauria**. Ithaca, NY, Society for the Study of Amphibians and Reptiles. p. 349–392.

Cunha, O.R. da & Nascimento, F.D. 1993. Ofídios da Amazônia. As cobras da região leste do Pará. **Boletim do Museu Paraense Emilio Goeldi, Serie Zoologia,** 9: 1–191.

Cunha, O.R. da & Nascimento, F.P. do. 1980. Ofídios da Amazônia. XI. Ofidios de Roraima e notas sobre *Erythrolamprus bauperthrusii* Duméril, Bibron and Duméril, 1854, sinônimo de *Erythrolamprus aesculapii* (Linnaeus, 1758). **Boletim do Museu Paraense Emilio Goeldi, Serie Zoologia,** 102: 1–21.

Curcio, F.F.; Nunes, P.M.S.; Harvey, M.B. & Rodrigues, M.T. 2011. Redescription of Apostolepis longicaudata (Serpentes: Xenodontinae) with Comments on Its Hemipenial Morphology and Natural History. **Herpetologica,** 67: 318–331.

Curcio, F.F.; Piacentini, V.Q. & Fernandes, D.S. 2009a. On the status of the snake genera *Erythrolamprus* Boie, *Liophis* Wagler and *Lygophis* Fitzinger (Serpentes, Xenodontinae). **Zootaxa**, 2173: 66–68.

Curcio, F.F.; Sánchez-Pacheco, S.J.; Mueces-Cisneros, J.J. & Rodrigues, M.T. 2009b. Notes on distribution, variation and characterization of *Erythrolamprus pseudocorallus* Roze, 1959 (Serpentes: Colubridae) with the first records from Colombia. **Zootaxa,** 2045: 33–42.

Curcio, F.F.; Scali, S. & Rodrigues, M.T. 2015. Taxonomic Status of *Erythrolamprus bizona* Jan (1863) (Serpentes, Xenodontinae): Assembling a Puzzle with Many Missing Pieces. **Herpetological Monographs,** 29: 40–64.

Dingerkus, G. & Uhler, L. 1977. Enzyme clearing of alcian blue stained whole small vertebrales for demonstration of cartilage. **Stain Technology,** 52: 229–232.

Dixon, J.R. 1980. The Neotropical colubrid snake genus *Liophis*: the generic concept. **Milwaukee Public Museum Contributions in Biology and Geology** 31: 1–40.

Dixon, J.R. 1983a. Systematics of *Liophis reginae* and *L. williamsi* (Serpentes, Colubridae), with a description of a new species. **Annals of Carnegie Museum** 52, 113–138.

Dixon, J.R. 1983b. Systematics of the Latin American snake, *Liophis epinephelus* (Serpentes: Colubridae). *In*: Rhodin, A.G.J. & Miyata, K. (Eds). **Advances in Herpetology and Evolutionary Biology: Essays in Honor of Ernest E. Williams**. Cambrige, Museum Comparative Zoology. p. 132–149.

Dixon, J.R. 1983c. Taxonomic Status of the South American Snakes *Liophis miliaris, L. amazonicus, L. chrysostomus, L. mossoroensis and L. purpurans* (Colubridae: Serpentes). **Copeia,** 1983: 791–802.

Dixon, J.R. 1983d. The *Liophis cobella* group of the neotropical colubrid snake genus *Liophis*. **Journal of Herpetology** 17: 149–165.

Dixon, J.R. 1985a. A new species of the colubrid snake genus *Liophis* from Brazil. **Proceedings of the Biological Society of Washington,** 98: 295–302.

Dixon, J.R. 1985b. A review of *Liophis anomalus* and *Liophis elegantissimus*, and the description of a new species (Serpentes: Colubridae). **Copeia,** 1985: 565–573.

Dixon, J.R. 1987. Taxonomy and geographic variation of *Liophis typhlus* and related" green" species of South America (Serpentes: Colubridae). **Annals of Carnegie Museum Carnegie Museum,** 56: 173–191.

Dixon, J.R. 1989. A key and checklist to the Neotropical snake genus Liophis with country lists and maps. **Smithsonian Herpetological Information Service**, 79:1-28.

Dixon, J.R. 1991. Geographic variation and taxonomy of *Liophis almadensis* (Wagler)(Serpentes, Colubridae), and description of a New Species of *Liophis* from Argentina and Bolivia. **Texas Journal of Science,** 43: 225–236.

Dixon, J.R. 2000. Ecuadorian, Peruvian, and Bolivian snakes of the *Liophis taeniurus* complex with descriptions of two new species. **Copeia,** 2000: 482–490.

Dixon, J.R. & Markezich, A.L. 1992. Taxonomy and geographic variation of *Liophis poecilogyrus* (Wied) from South America (Serpentes: Colubridae). **Texas Journal of Science** 44: 132–165.

Dixon, J.R. & Michaud, E.J. 1992. Shaw's black-backed snake (*Liophis melanotus*)(Serpentes: Colubridae) of northern South America. **Journal of Herpetology,** 26: 250–259.

Dixon, J.R. & Thomas, R. 1982. The status of the Argentine colubrid snakes *Liophis sagittifer* and *L. trifasciatus*. **Herpetologica,** 38: 389–395.

Dixon, J.R. & Thomas, R. 1985. A new species of South American water snake (genus *Liophis*) from southeastern Brazil. **Herpetologica,** 41: 259–262.

Drummond, A.J.; Suchard, M.A.; Xie, D. & Rambaut, A. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. **Molecular Biology and Evolution,** 29: 1969–1973.

Fernandes, D.S.; Germano, V.J.; Fernandes, R. & Franco, F.L. 2002. Taxonomic status and geographic distribution of the lowland species of the Liophis cobella group with comments on the species from the Venezuelan Tepuis (Serpentes, Colubridae). **Boletim do Museu Nacional, Serie Zoologia**, 1–14.

Giraudo, A.R.; Arzameida, V. & Cacciali, P. 2006. Geographic variation and taxonomic status of the southernmost populations of *Liophis miliaris* (Linnaeus, 1758)(Serpentes: Colubridae). **The Herpetological Journal,** 16: 213–220.

Goloboff, P.A.; Farris, J.S. & Nixon, K.C. 2008. TNT , a free program for phylogenetic analysis. **Cladistics,** 24: 774–786.

Grazziotin, F.G.; Zaher, H.; Murphy, R.W.; Scrocchi, G.J.; Benavides, M.A.; Zhang, Y.P. & Bonatto, S.L. 2012. Molecular phylogeny of the New World Dipsadidae (Serpentes: Colubroidea): a reappraisal. **Cladistics,** 28: 437–459.

Hardy, J.D. & Boos, H.A.E. 1995. Snakes of the genus *Erythrolamprus* (Serpentes:

Colubridae) from Trinidad and Tobago, West Indies. **Bulletin of The Maryland Herpetological Society,** 31: 158–190.

Huelsenbeck, J.P. & Ronquist, F. 2001. MRBAYES: Bayesian inference of phylogenetic trees. **Bioinformatics,** 17: 754–5.

Jowers, M.J., Caut, S. & Garcia-Mudarra, J.L. 2013. Molecular Phylogenetics of the Possibly Extinct Martinique Ground Snake. **Herpetologica,** 69, 227–236.

Katoh, K. & Toh, H. 2010. Parallelization of the MAFFT multiple sequence alignment program. **Bioinformatics,** 26: 1899–1900.

Kearse, M.; Moir, R.; Wilson, A.; Stones-Havas, S.; Cheung, M.; Sturrock, S.; Buxton, S.; Cooper, A.; Markowitz, S.; Duran, C.; Thierer, T.; Ashton, B.; Meintjes, P. & Drummond, A. 2012. Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. **Bioinformatics,** 28: 1647–1649.

Lanfear, R.; Calcott, B.; Ho, S.Y.W. & Guindon, S. 2012. PartitionFinder: Combined selection of partitioning schemes and substitution models for phylogenetic analyses. **Molecular Biology and Evolution,** 29: 1695–1701.

Lynch, J.D. 2015. The role of plantations of the african palm (*Elaeis guineensis* Jacq.) in the conservation of snakes in Colombia. **Caldasia,** 37: 169–182.

Maddison, W.P. & Maddison, D.R. 2015. **Mesquite: a modular system for evolutionary analysis. (Version 3.04) http://mesquiteproject.org.**

Markezich, A.L. & Dixon, J.R. 1979. A new South American species of snake and comments on the genus *Umbrivaga*. **Copeia,** 1979: 698–701.

Marques, O.A. V & Puorto, G. 1991. Padrões cromáticos, distribuição e possível mimetismo em *Erythrolamprus aesculapii* (Serpentes, Colubridae). **Memorias do Instituto Butantan,** 53: 127–134.

Masiero, R.L. 2006. **Filogenia morfológica do gênero *Xenodon* Boie 1827 (Serpentes, Xenodontinae)**. São Paulo, Instituto de Biociencias da Universidade de São Paulo. Dissertaçãode Mestrado.

Michaud, E.J. & Dixon, J.R. 1987. Taxonomic revision of the *Liophis lineatus* complex (Reptilia: Colubridae) of Central and South America. **Contributions in Biology and Geology**, Milwaukee Public Museum**,** 71: 1–26.

Miller, M.A.; Pfeiffer, W. & Schwartz, T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *In*: Gateway Computing Environments Workshop, GCE 2010. **Proceedings of a Meeting**. New Orleans, IEEE.

Moura-Leite, J.C. 2001. **Sistemática e análise filogenética das serpentes da Tribo Xenodontini Bonaparte, 1845 (Colubridae, Xenodontinae)**. Curitiba, Universidade Federal do Paraná. Dissertação de Mestrado.

Myers, C.W. 1986. An enigmatic new snake from the peruvian Andes, with notes on the Xenodontini (Colubridae: Xenodontinae). **American Museum Novitates**, 2853: 1–12.

Myers, C.W. 2011. A New Genus and New Tribe for *Enicognathus melanauchen* Jan, 1863, a Neglected South American Snake (Colubridae: Xenodontinae), with Taxonomic Notes on Some Dipsadinae. **American Museum Novitates,** 3715: 1–33.

Myers, C.W. & McDowell, S.B. 2014. New taxa and cryptic species of neotropical snakes (Xenodontinae), with commentary on hemipenes as generic and specific characters. **Bulletin of the American Museum of Natural History,** 295: 1–112.

Noonan, B.P. & Chippindale, P.T. 2006. Vicariant origin of malagasy reptiles supports late cretaceous antarctic land bridge. **The American Naturalist,** 168: 730–741.

Peters, J.A. & Orejas-Miranda, B.R. 1970. Catalogue of the Neotropical Squamata: Part I. Snakes. **Bulletin. United States National Museum**, 297: 1–347.

Pook, C.E.; Wüster, W. & Thorpe, R.S. 2000. Historical biogeography of the Western Rattlesnake (Serpentes: Viperidae: *Crotalus viridis*), inferred from Mitochondrial DNA sequence information. **Molecular Phylogenetics and Evolution,** 15: 269–282.

Pyron, R.A.; Burbrink, F.T. & Wiens, J.J. 2013a. A phylogeny and revised

classification of Squamata, including 4161 species of lizards and snakes. **BMC Evolutionary Biology,** 13: 93-146.

Pyron, R.A.; Guayasamin, J.; Peñafiel, N.; Bustamante, L. & Arteaga, A. 2015. Systematics of Nothopsini (Serpentes, Dipsadidae), with a new species of *Synophis* from the Pacific Andean slopes of southwestern Ecuador. **ZooKeys,** 541: 109–147.

Pyron, R.A.; Kandambi, H.K.D.; Hendry, C.R.; Pushpamal, V.; Burbrink, F.T. & Somaweera, R. 2013b. Genus-level phylogeny of snakes reveals the origins of species richness in Sri Lanka. **Molecular Phylogenetics and Evolution,** 66: 969–78.

Rambaut, A. & Drummond, A. 2007. **Tracer ver. 1.4**. *Program available at http://beast. bio. ed. ac. uk/Tracer*.

Rivas, G.A.; Molina, C.; Ugueto, G.N.; Barros, T.; Barrio-Amorós, C.L. & Kok, P.J.R. 2012. Reptiles of Venezuela: an updated and commented checklist. **Zootaxa**, 3211: 1–64.

Roze, J.A. 1964. Snakes of the *Leimadophis-Urotheca-Liophis* complex from Parque Nacional Henri Pittier (Rancho Grande), Venezuela, with a description of a new genus. **Senckenbergiana biologica** 45: 533–542.

Sereno, P.C. 2007. Logical basis for morphological characters in phylogenetics. **Cladistics,** 23: 565-587.

Stamatakis, A. 2014. RAxML Version 8 : A tool for Phylogenetic Analysis and Post-Analysis of Large Phylogenies. **Bioinformatics,** 30: 1312–1313.

Uetz, P. & Hosek, J. 2015. **The Reptile Database**. Available from: www.reptile-database.org (January 25, 2015).

Vaidya, G.; Lohman, D.J. & Meier, R. 2011. SequenceMatrix: Concatenation software for the fast assembly of multi-gene datasets with character set and codon information. **Cladistics,** 27: 171–180.

Vidal, N.; Dewynter, M. & Gower, D.J. 2010. Dissecting the major American snake

radiation: A molecular phylogeny of the Dipsadidae Bonaparte (Serpentes, Caenophidia). **Comptes rendus Biologies,** 333: 48–55.

Vidal, N.; Kindl, S.G.; Wong, A. & Hedges, S.B. 2000 Phylogenetic relationships of xenodontine snakes inferred from 12S and 16S ribosomal RNA sequences. **Molecular Phylogenetics and Evolution,** 14: 389–402.

Wallach, V., Williams, K. & Boundy, J. 2014. **Snakes of the World: A Catalogue of living and extinct species**. Boca Raton, Fl., Taylor & Francis Group. 1227p.

Zaher, H. 1999. Hemipenial morphology of the South American xenodontine snakes: with a proposal for a monophyletic Xenodontinae and a reappraisal of colubroid hemipenes. **Bulletin of the American Museum of Natural History,** 240: 1–168.

Zaher, H.; Grazziotin, F.G.; Cadle, J.E.; Murphy, R.W.; Moura-Leite, J.C. de & Bonato, S.L. 2009. Molecular phylogeny of advanced snakes (Serpentes, Caenophidia) with an emphasis on South American Xenodontines: a revised classification and descriptions of new taxa. **Papéis Avulsos de Zoologia** 49: 115–153.

Zaher, H. & Prudente, A.L.D.C. 2003. Hemipenes of *Siphlophis* (Serpentes, Xenodontinae) and techniques of hemipenial preparation in snakes: A response to Dowling. **Herpetological Review,** 34: 302–307.

Appendices

Appendix 1. Taxa and specimens used for morphological data. Institution codes are as follows: AMNH, American Museum of Natural History, New York; BM, Natural History Museum, London; IB, Instituto Butantan, São Paulo, FML, Fundación Miguel Lillo, La Plata KU, Museum of Natural History, Kansas University, Laurence; MCP, Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre; MHNCI, Museu de História Natural Capão da Imbuia, Curitiba; MHUA-R, Museo de Herpetología de la Universidad de Antioquia, Medellín, Colombia; MNHN, Muséum national d'histoire naturelle, Paris; MNRJ, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro; MPEG, Museu Paraense Emílio Goeldi, Belém de Pará; MZUSP, Museu de Zoologia da Universidade de São Paulo, São Paulo; UFRGS, Laboratório de Herpetologia, Universidade Federal do Rio Grande do Sul, Porto Alegre.

Cranial osteology: *Erythrolamprus aesculapii aesculapii*: MPEG 2025; *E. aesculapii* 'dyads': IB 53187; *E. aesculapii* 'monads': IB 54684; *E. bizona*: MHUA-R 14304; *E. breviceps*: MZUSP5503; *E. epinephelus epinephelus*: MHUA-R 14526; *E. epinephelus lamonae*: MHUA-R 14019; *E. epinephelus pseudocobella*: MHUA-R 14882 ; *E. frenatus*: MHNCI 909; *E. juliae*: KU 268639; *E. melanotus*: MHUAR 14457; *E. miliaris*: MZUSP 3627, MZUSP 3670, MZUSP 5874, MZUSP 13108, MZUSP 14011, MZUSP 14137; *E. mimus*: AMNH 13540; *E. mossoroensis*: MZUSP 6742; *E. oligolepis*: MZUSP 3961; *E. poecilogyrus*: MZUSP 4646, MZUSP 6527, MZUSP 11798, MZUSP 13032, MZUSP 13040, MZUSP 13043, MZUSP 13046, MZUSP 13979 ; *E. pseudocorallus*: MHUA-R 14620; *E. pygmaeus*: MPEG, Kawashita-Ribeiro and Carvalho, 2011; *E. reginae*: MZUSP 13054, MZUSP 13996, MZUSP-DID 174; *E. taeniogaster*: MZUSP 3603; *E. typhlus*: MZUSP 2498, MZUSP 3690, MHNCI 7576; *Leimadophis almadensis*: MZUSP 14915; *Le. atraventer*: MZUSP 4480; *Le. jaegeri*: MHNCI 4649, MZUSP 3682 ; *Le. maryellenae*: MZUSP 6609; *Le. viridis*: MZUSP 3450, MZUSP 6695; *Lygophis anomalus*: MCP 3643, MCP 6072; *Ly. lineatus*: IB 25753; *Ly. meridionalis*: MZUSP 3359, MZUSP 3365; *Xenodon dorbignyi*: IB 1807, IB 1832; *X. nattereri*: IB 10410; *X. rabdocephalus*: MHUAR 14534; *X. severus*: IB 40243; *X. werneri*: MNHN 1994.8782; *Arryton vittatum*: AMNH_44839; *Caateboia amarali*: CEPLAC 197, Passos et al. 2012; *Coluber contrictor*: KU 18201; *Conophis pulcher*: KU 183871; *Dipsas indica*: MZUSP 10126; *Helicops modestus*: IB 9752*; Oxyrhopus guibei*: IB 53958; *Philodryas patagoniensis*: MZUSP 14423; *Tomodon dorsatus*: MZUSP 13096.

Hemipenes: *Erythrolamprus aesculapii* aesculapii: IB 59990, IB 69416, MZUSP 9273, MZUSP 11218, MNHN 1990.4326; *E. aesculapii* 'dyads': MZUSP 19598; *E. aesculapii* 'monads': MZUSP 13219, MZUSP 10314; *E. bizona*: MHUA-R 14304, MHUA-R 14012, AMNH 35576, MZUSP 8085; *E. breviceps*: MZUSP 5505, MZUSP 6116; *E. epinephelus albiventris*: MZUSP 8369, KU 164214; *E. epinephelus epinephelus*: MHUA-R 14332; *E. epinephelus lamonae*: MHUA-R 14019, MHUA-R 14031, MHUA-R 14219; *E. epinephelus pseudocobella*: MHUA-R 14882, MHUA-R 14884, MHUA-R 14907; *E. frenatus*: HF 324, HF 85, HF 326, HF 327; *E. juliae*: MNHN1997.1617A, KU 268640; *E. melanotus*: MHUA-R 14457, MHUA-R w/o number, MZUSP 7823; *E. miliaris*: MZUSP 9445, MZUSP 12735, MZUSP 13977 ; *E. mimus*: AMNH 12697; *E. mossoroensis*: MZUSP 6500, MZUSP 19615; *E. oligolepis*: MZUSP 20010; *E. poecilogyrus*: HF 325, MNHN 1993.1624, MZUSP 13043, MZUSP 13046, MZUSP 13144; *E. pseudocorallus*: MHUA-R ; *E. pyburni*: AMNH 143811; *E. pygmaeus*: MPEG; *E. reginae*: HF 324, MHUA-R 14747, MZUSP 11500, MZUSP 13323, MZUSP 13996, MZUSP 20522; *E. taeniogaster*: MZUSP 19104; *E. typhlus*: MZUSP 15284, MZUSP 20871, MZUSP 20896; *Leimadophis almadensis*: MZUSP 799, MZUSP 2415, MZUSP 18497, MZUSP 18497, IB 53445, MZUSP 2007, MZUSP 17821, MZUSP 5347, MZUSP 14915; *Leimadophis atraventer*: MZUSP 4912; *Le. carajasensis*: MPEG 16506, MPEG 16600; Leimadophis jaegeri: MZUSP 2960, MZUSP 3355, MZUSP 5742, MZUSP 7524, MZUSP 15011, MZUSP 20790; Leimadophis maryellenae: MZUSP 15120, CHUNB 59001; *Le. viridis*: MZUSP 15120, CHUNB 59001; *Lygophis anomalus*: MZUSP 1133, MZUSP 1134, MZUSP 1193, MZUSP 7463, MZUSP 21265; *Ly. dilepis*: MZUSP 2315, MZUSP 7125, MZUSP 7129, MZUSP 7130, MZUSP 20511; *Ly. flavifrenatus*: UFRGS 0730, UFRGS 2022, UFRGS 6150; *Ly. lineatus*: MZUSP 10398; *Ly. meridionalis*: MZUSP 14762, MZUSP 14579, MZUSP 19850; *Ly. sagittifer*: MZUSP 14578, JW 1708; *Xenodon dorbignyi*: IB 33914, IB 40277, UFRGS 7365; *X. nattereri*: IB 14570; *X. rabdocephalus*: AMNH 140265, IB 54934, MHUA-R 14534; *X. severus*: IB 33382, IB 51997; *X. werneri*: Yuki (1993); *Arryton vittatum*: AMNH 46727; *Caateboia amarali*: CEPLAC 197; *Oxyrhopus guibei*: KU 140401; *Coluber constrictor*: AMNH 133458; *Conophis pulcher*: MNHN 5981; *Dipsas indica*: MZUSP 10126; *Helicops modestus*: IB 56130; *Philodryas trilineata*: FML 02263-B; *Psomophis joberti*: MZUSP 20496.

Appendix 2. Characters used for the morphological analyses.

Hemipenial morphology

1. Hemipenes shape in frontal/ventral view: (0) Quadrangular like, with the distal and basal portion with around the same width and flattened; (1) clavate; (2) cylindrical.
2. Hemipenial base shape: (0) Smaller than the body, with an abrupt reduction; (1) Funnel shaped, gradually reducing in size.
3. Basal pocket size: (0) very small; (1) not exceeding the height of the sulcus spermatius; (2) big, with the asulcate margin markedly pronounced.
4. Basal Pocket: (0) absent; (1) present.
5. Lobation: (0) unilobated; (1) bilobated; (2) semibilobated.
6. Lobe length: (0) short, lobes less than 20% of the hemipenes length; (1) medium sized, the length of the body is at least 20% of the hemipenes length, but never more than half of the length; (2) extremely large, with the length of the lobes much longer than the length of the body.
7. Type of calyculation on capitulum: (0) non-calyculate; (1) unicalyculate; (2) semicalyculate; (3) bicaliculate.
8. Apical disk: (0) absent; (1) present.
9. Capitation: (0) non capitate; (1) semicapitate; (2) capitate; (3) bicapitate.
10. Sulcus spermaticus trajectory: (0) centrolineal; (1) centrifugal; (2) sinusoidal.
11. Position of the division of the Sulcus spermaticus: (0) Proximal, under 33% of the hemipenes length; (1) Medial, between 33-66% of the hemipenes length; (2) Distal, above 66% of the hemipenes length.
12. Body Calyces on the asulcate surface of the hemipenes: (0) Absent; (1) Present.
13. Inflated surfaces in the lateral sections of the proximal region of the asulcate side of the hemipenial body: (0) Absent; (1) Present.
14. Inflated surfaces in the proximal region of the sulcate side of the hemipenial body: (0) Absent; (1) Present.
15. Lobular crotch: (0) Naked; (1) Ornamented.
16. Intrasulcal ornamentation: (0) With spines equal or subequal in size; (1) With spines markedly enlarged; (2) With papillae flounces or calyces; (3) With spinulate flounces or calyces.
17. Concavity in the asulcate side of the hemipenes: (0) Absent; (1) Present.
18. Spines in the medial portion of the lobes: (0) Very few or absent; (1) Present, numerous.
19. Distal row of enlarged spines: (0) Absent; (1) Non-differentiated; (2) Present.
20. Proximal row of enlarged scales: (0) Absent; (1) Non-differentiated; (2) Present.
21. Origin of spines in the proximal row of enlarged spines: (0) In the lobes; (1) Near the crotch level; (2) Below the crotch level.
22. Spines in the region over the proximal row of enlarged spines, and when present below the distal row of enlarged spines: (0) small, very few; (1) Smaller than the spines in the subcapitular arch; (2) Homogenously covered with large spines.
23. Lobe spines (ornamentation) in the asulcate side: (0) Absent; (1) With naked areas; (2) Homogenously covered.
24. Spines in the mid-line in the asulcate side of the hemipenial body: (0) Naked, Without spines; (1) Homogeneously covered with spines of around the same size; (2) Homogeneously covered with spines with a group of enlarged ones; (3) Only with enlarged spines organized in the midline, with few or none surrounding smaller ones; (4) Covered with spines of different sizes.
25. Size of the enlarged lateral spines of the body: (0) Small, equal or less than three times the size of the spines in the lobes; (1) Big, three or more times the spines in the lobes.
26. Spinules density in the sulcate side: (0) Low; (1) High; (2) Very High.
27. Enlarged spines density in the lateral area: (0) Low; (1) High; (2) Very High.
28. Distribution of the spines through the asulcate region: (0) homogeneously; (1) Disperse; (2) Organized in other patterns.
29. Transversal row of enlarged spines at the base in the asulcate side: (0) Absent, spinules instead; (1) Present; (2) Absent.

Cranial osteology

30. Transverse process of the premaxilla, length in relation to the length of the vomerine process of the premaxilla: (0) equal or subequal in size; (1) smaller; (2) larger.
31. Posterior projection of the transverse process of the premaxilla: (0) Absent; (1) Present.
32. Vomerine process of the premaxilla, Shape: (0) Unique; (1) Bifurcated.
33. Point of bifurcation of the vomerine processes of the premaxillae: (0) Basally; (1) Distally.
34. Separation of the vomerine processes: (0) Separated; (1) Attached.
35. Basal angulated widening of the vomerine process of the premaxilla: (0) Absent; (1) Present.
36. Ventral projection of the vomerine process of the premaxilla: (0) Absent; (1) Present.

37. Shelf-like projection coming out anterior to the premaxila: (0) Absent; (1) Present.
38. Dorso-posterior process of the vomer: (0) Absent; (1) Present.
39. Proximal end of the transversal process of the nasal: (0) Fine and sharped, markedly thinner than the posterior process; (1) Nearly or as wide as the frontal process of the nasal..
40. Widest part of the transversal process of the nasal bone: (0) Anteriorly; (1) Medially; (2) Posteriorly.
41. Post-diastemal maxillary teeth: (0) Absent; (1) Present.
42. Post diastemal teeth, canal: (0) Absent (Aglyph); (1) Present (opisthoglyph).
43. Post-Diastemal maxillary teeth, shape: (0) Lance-shaped (flattened laterally); (1) Rounded.
44. Post-diastemal teeth, relative size in relation to the last pre-diastemal tooth: (0) More than twice the size; (1) Around twice the size or less.
45. Maxillary processes of the ectopterygoid bone, Anterior extent: (0) Aligned or nearly so; (1) Medial process projected anteriorly.
46. Pterygoid, posterior fossa: (0) One without division; (1) Dorsal crest separating the postero-dorsal fossa from the pterygoid in a groove in the latero-dorsal region.
47. Medial-ventral process of the compound bone, projection, Where a branch of the adductor mandubulae posterior, pars profundus inserts: (0) Soft, projected ventro-medialy; (1) Marked, projected medially; (2) Marked, projected dorso-medialy, creating a concavity.; (3) absent.
48. Retroarticular process, size in relation to the width of the articulation o: (0) Short; (1) Long.
49. Splenial, Size in relation to the angular bone: (0) Shorter; (1) Around the same size; (2) Larger.
50. Frontal process of the prefrontal bone: (0) Short, covering half or less of the anterior margin of the frontal; (1) Long, overpassing half of the anterior margin of the frontal; ; 51. Anterior process of the prefrontal bone: (0) Absent or reduced; (1) Present, long; (2) Present, short; (3) Very large.
52. Postero-ventral process of the prefrontal bone: (0) Reduced; (1) Small; (2) Long.
53. Lacrimal forame size: (0) Small; (1) Large; (2) Reduced.
54. Medio ventral process of the prefrontal: (0) Small; (1) Large; (2) Reduced.
55. Foramen in the lateral lamina of the prefrontal: (0) Absent; (1) Present.
56. Parietal process of the post-orbital bone: (0) In contact with the parietal and frontal bone; (1) In contact only with the parietal bone.
57. Size of the maxillary process of the postorbital bone: (0) Short, covering less than half of the posterior border orbital margin; (1) Large, Covering most of the posterior border of the orbital margin.
58. Dorso-lateral crest of the parietal bone: (0) Absent; (1) Present.
59. Dorso-lateral crest of the parietal bone, border: (0) Only sharped in part of its margin; (1) Sharped in its entire margin.
60. Dorso-lateral crests of the parietal bone, end: (0) Converging in one crest; (1) End parallel.
61. Posteiorend of the parietal bone: (0) Ends aligned with the lateral margins; (1) Enter in the supraoccipital bone.
62. Depression within the posterior portion of the parietal and the antero-lateral portions of the supraoccipital: (0) Marquedly depressed; (1) Slightly depressed.
63. Transversal process of the supraoccipital, position of the posterior end: (0) Anterior; (1) Posterior.
64. Supratemporal shape: (0) Straight or nearly so; (1) Markedly curved.
65. Supratemporal extension: (0) Exceeding the supraoccipital; (1) Barely or not exceeding the supraoccipital.
66. Quadrate head: (0) Wide; (1) Short.
67. Antero-Dorsal process of the quadrate, point shape: (0) Reduced; (1) Truncated; (2) Rounded; (3) Sharped.
68. Dorso-posterior process of the quadrate: (0) Reduced; (1) Truncated; (2) Rounded; (3) Sharped.
69. Parabasisphenoid, anterior extension in relation to the frontal: (0) Aligned with the anterior end of the frontal; (1) Posterior to the anterior end of the frontal.
70. Parabasisphenoid rostrum: (0) Uniradiated; (1) Biradiated; (2) Triradiated.
71. Transversal process of the basioccipital: (0) Absent; (1) Present.
72. Transversal process of the basioccipital, position: (0) Anterior; (1) Posterior.
73. Longitudinal process of the basioccipital: (0) Absent; (1) Present.
74. Shape of the frontal bone: (0) Wider than long; (1) Longer than wide.
75. Optical foramne, size: (0) Small; (1) Medium sized; (2) Large.
76. Separation between the V3 foramen and the Fenestra ovalis: (0) Wide; (1) Short.
77. Oval window, position: (0) Lateral; (1) Postero-lateral; (2) Posterior.
78. Contact between the prootic and tuberalis cristas in the ventral margin of the fenestra ovalis: (0) Contacting from the oval window to the basioccipital; (1) Contacting only dorsally; (2) Contacting only ventrally; (3) With no contact, separated by the "shoe" of the crista interfenestralis.

Appendix 3. Morphological matrix codified for the phylogenetic analysis. Interrogation (?) correspond to missing data; line (-) mean non-aplicable.

	Hemipenial morphology																												
Taxon/Character number	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**
aesculapii_monads	0	0	1	1	1	1	0	1	0	1	1	0	1	1	0	0	1	0	1	1	1	2	2	2	0	1	1	1	0
pseudocorallus	0	0	0	1	1	1	0	1	0	1	1	0	1	1	0	0	1	0	1	1	1	2	2	2	0	1	1	1	0
bizona_andina	0	0	0	1	1	1	0	1	0	1	1	0	1	1	0	0	1	0	1	1	1	2	2	2	1	1	1	1	0
aesculapii_dyads	0	0	0	1	1	1	0	1	0	1	0	0	1	1	0	0	1	0	1	1	1	2	2	2	1	1	1	1	0
bizona_cisandina	0	0	0	1	1	1	0	1	0	1	1	0	1	1	0	0	1	0	1	1	1	2	2	2	1	1	1	1	0&1
aesculapii	0	0	1	1	1	1	0	1	0	1	1	0	1	1	0	0	1	0	1	1	1	2	2	2	1	1	1	1	0
mimus_micrurus	0	0	?	?	1	1	0	1	0	1	1	0	1	1	0	0	1	0	1	1	1	2	1	3	1	1	1	1	0
e_epinephelus	0	0	1	1	1	1	0	1	0	1	0	0	1	1	0	1	1	0	2	2	1	0	1	3	1	0	0	1	0
e_lamonae	0	0	1	1	1	1	0	1	0	1	1	0	0	1	0	1	1	0	2	1	1	0	1	3	0	0	0	1	0
e_pseudocobella	0	0	1	1	1	1	0	1	0	1	0	0	1	1	0	1	1	0	1	1	0	0	2	2	1	0	0	1	0
e_albiventris	0	0	1	1	1	1	0	1	?	1	0	0	1	1	0	1	1	0	2	2	0	0	1	3	1	0	0	1	0
melanotus	0	0	1	1	1	1	0	1	1	1	0	0	1	1	0	1	1	0	2	2	1	0	1	3	1	0	0	1	0
reginae	0	0	1	1	1	1	0	1	0	1	0	0	1	1	0	1	1	0	2	2	1	0	1	2	1	1	0	1	0
oligolepis	0	0	1	1	1	1	0	1	0	1	0	0	1	1	0	1	1	0	2	2	1	1	1	1	1	1	0	0	0
typhlus	0	0	2	1	1	1	0	1	0	1	0	0	1	1	0	1	1	0	2	2	0	0	1	1	1	1	0	0	0
viridis	0	0	2	1	1	1	0	1	0	1	1	0	1	1	0	1	1	0	1	1	0	?	2	1	1	2	1	0	0
jaegeri	0	0	2	1	1	1	0	1	0	1	1	0	1	1	0	1	1	0	2	1	1	1	1	1&2	1	2	1	0	0
maryellenae	0	0	2	1	1	1	0	1	0	1	1	0	1	1	0	1	1	0	1	1	1	1	2	1	0	2	1	0	0
atraventer	0	0	2	1	1	1	0	1	0	1	1	0	1	1	0	1	1	0	2	1	1	0	1	2	1	1	1	0	0
almadensis	0	0	1	1	1	1	0	1	0	1	0	0	1	1	0	0	1	0	1	1	0	1	1	2	1	2	2	0	0
carajasensis	0	0	0	1	1	1	0	1	0	1	0	0	1	1	0	0	1	0	1	1	0	1	1	2	1	2	1	0	0
poecilogyrus	0	0	1	1	1	1	0	1	0	1	0	0	1	1	0	1	1	0	2	1	1	1&2	2	1	1	2	1	0	0
taeniogaster	0	0	1	1	1	1	0	1	0	1	1	0	1	1	0	1	1	0	2	1	1	1	2	2	1	1	1	2	0
breviceps	0	0	1	1	1	1	0	1	0	1	0	0	1	1	0	0	1	0	2	2	1	0	2	1	0	1	1	2	0
frenatus	0	0	0	1	1	1	0	1	1	1	0	0	1	1	0	1	1	0	2	1	0	0	1	2	1	1	1	2	0
miliaris	0	0	1	1	1	1	0	1	0	1	0	0	1	1	0	1	1	0	2	2	1	1	1&2	1	1	2	0&1	0	0
mossoroensis	0	0	1	1	1	1	0	1	0	1	0	0	1	1	0	1	1	0	2	2	0&1	1	2	1	1	2	0&1	0	0
juliae	0	0	?	?	1	1	0	1	0	1	1	0	1	1	0	0	1	0	2	2	1	1	1	1	1	1	1	0	0
pygmaeus	0	0	?	?	1	1	0	1	0	1	1	0	1	1	0	1	?	0	2	2	1	0	2	2	1	0	0	0&1	0&1
pyburni	0	0	1	1	1	1	0	1	0	1	1	0	1	1	0	1	1	0	2	1	1	0	1	2	1	0	0	0&1	0&1
Ly._anomalus	1	0	2	1	1	0	0	1	0	1	0	0	1	1	0	1	0	0	2	2	1	1	2	1	1	2	0	0	1
Ly._lineatus	1	0	-	0	1	0	1	1	0	1	0	0	0	0	1	1	0	1	2	2	2	1	2	1	1	2	0	2	1

Appendix 3. continued

	Hemipenial morphology																												
Taxon/Character number	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	**27**	**28**	**29**
Ly._meridionalis	1	0	1	1	1	0	0	1	0	1	0	0	0	1	1	1	0	1	2	2	2	1	2	1	1	2	0	0	1
Ly._sagittifer	1	0	2	1	1	0	0	1	0	1	0	0	1	1	0	1	0	0	2	1	2	1	2	1	1	2	0	0	1
X._rabdocephalus	2	0	-	0	1	2	0	1	0	1	0	0	0	0	1	1	0	1	2	2	0	0	2	0	0	0	0	1	2
X._werneri	2	0	-	0	1	2	0	0	0	1	0	0	0	0	1	1	0	1	2	2	0	?	2	?	1	?	?	?	2
X._severus	0	0	-	0	1	1	0	1	0	1	0	0	0	0	1	0	0	1	1	1	1	1	1	1	1	1	0	0	1
X._dorbignyi	0	0	0	1	1	1	0	1	0	1	0	0	0	0	1	1	0	1	2	2	0	1	2	1	1	1	0	0	1
X._nattereri	0	0	0	1	1	1	0	1	0	1	0	0	0	0	1	1	0	1	2	2	1	1	1	1	1	1	0	0	1
Psomophis_jobert	1	?	?	?	1	1	3	0	3	1	0	0	0	0	1	2	0	0	2	2	2	1	1	1	1	1	0	-	2
Conophis_pulcher	0	0	?	?	1	1	2	0	0	0	1	0	1	0	1	3	0	1	0	0	-	-	2	1	1	1	1	0	2
Haitiophis_anomalus	1	0	1	1	1	1	2	0	3	1	0	1	0	0	1	3	?	1	2	2	2	2	?	0	1	1	1	0	?
Arryton_vittatum	1	?	?	?	1	1	2	0	1	0	0	0	0	0	1	3	0	1	2	2	2	2	2	1	1	1	0	0	1
Philodryas_patagoniensis	1	2	1	1	1	1	2	0	0	1	0	1	0	0	1	2	0	?	2	2	1	1	-	1	1	2	?	0	0
Tomodon_dorsatus	2	2	-	0	1	0	2	0	0	0	2	1	0	0	1	3	0	1	0	0	-	-	2	1	-	0	?	2	1
Dipsas_indica	2	2	1	1	2	0	1	0	1	1	1	0	0	0	1	3	0	-	?	?	-	-	-	1	-	2	?	0	0
Oxyrhopus_guibei	1	?	?	?	1	1	3	0	3	1	0	0	0	0	0	1	0	0	2	2	2	2	0	1	1	2	0	0	?
Caaeteboia_amarali	1	1	1	1	1	1	2	0	1	0	1	0	0	0	1	3	0	1	2	2	1	?	1	4	1	1	?	2	2
Helicops_modestus	1	1	-	0	1	0	0	0	0	1	1	0	0	0	1	0	0	1	0	0	-	-	1	1	-	1	-	0	0
Coluber_contrictor	2	0	?	?	0	-	1	0	0	2	-	0	0	0	-	-	0	-	0	0	-	-	-	1	1	0	1	2	0

Appendix 3. continued

	Cranial osteology																														
Taxon/Character number	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**	**59**
aesculapii_monads	2	1	1	1	0	0	0	1	0	0	0	1	1	1	1	1	1	1	0	0	0	1	1	1	0	1	1	1	1	1
pseudocorallus	2	1	1	1	0	0	0	1	0	0	0	1	1	1	0	1	1	1	1	1	1	1	2	1	0	1	1	1	1	1
bizona_andina	2	1	1	0	0	1	0	1	0	0	0	1	1	1	0	1	1	1	1	0	1	1	2	1	1	1	1	1	1	1
aesculapii_dyads	?	?	1	1	0	0	0	1	0	0	0	1	1	1	0	0	1	1	1	0	0	1	2	1	0	1	1	1	1	1
bizona_cisandina	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
aesculapii	2	1	1	1	0	0	0	0	0	0	0	1	1	1	0	1	1	1	0	0	1	1	2	1	0	1	1	1	1	1
mimus_micrurus	0	1	1	1	0	0	0	1	0	0	0	1	1	1	0	1	1	1	1	0	0	1	2	1	0	1	1	1	1	1
e_epinephelus	2	1	1	1	0	0	0	0	0	1	1	1	0	1	0	0	1	1	1	1	0	1	1	1	1	0	1	1	1	0
e_lamonae	2	1	1	1	0	0	0	1	0	1	1	1	0	1	0	0	1	1	1	0	0	1	1	1	1	0	1	1	1	0
e_pseudocobella	2	1	1	1	0	0	0	1	0	0	1	1	0	1	0	0	1	1	1	0	0	1	1	1	1	0	1	1	1	0
e_albiventris	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
melanotus	2	1	1	0	0	0	0	1	0	1	1	1	0	1	0	0	1	1	1	1	0	1	1	1	1	0	1	1	1	1
reginae	2	1	1	1&2	0&1	1	0	1	0	1	1	1	0	1	0	0	1	2	1	0	0	1	1	1	1	0	1	1	1	0
oligolepis	0	0	1	1	0	0	0	1	0	1	1	1	0	1	0	0	1	1	1	0	0	1	1	1	1	0	1	1	1	0
typhlus	0	1	1	1	0	0	0	1	0	1	1	1	0	1	0	0	1	1	0	0	0	1	2	1	1	1	1	1	1	1
viridis	0&2	1	1	1	0	0	0	0	0	1	1	1	0	1	0	0	1	0	1	1	0	1	1	1	1	0	1	1	1	1
jaegeri	2	1	0	-	?	1	1	1	0	1	1	1	0	1	0	0	1	1	1	1	0	1	2	1	1	0	1	1	1	1
maryellenae	0	1	1	1	0	0	1	1	0	1	1	1	0	1	0	0	1	1	1	?	0	1	1	1	?	0	1	1	1	1
atraventer	0	1	1	1	0	0	1	1	0	1	1	1	0	1	0	0	1	1	1	0	0	1	1	1	?	0	1	1	1	1
almadensis	2	1	1	1	0	0	0	1	0	1	1	1	0	1	0	0	1	2	1	0	0	1	1	1	1	0	1	1	1	1
carajasensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
poecilogyrus	0	0&1	1	0	0	0&1	0	1	0	1	1	1	0	1	0	0&1	1	1	0	0	0	1	1	1	1	0	1	1	1	0&1
taeniogaster	0	1	1	1	0	0	1	1	0	1	1	1	0	1	1	0	1	1	0	0	0	1	1	?	1	0	1	1	1	1
breviceps	2	0	1	0	0	0	0	1	0	1	1	1	0	1	1	0	1	1	0	1	0	1	1	1	1	0	1	1	1	1
frenata	0	0	1	1	0	0	0	1	0	1	1	1	0	1	1	0	1	1	0	1	0	1	1	0	1	0	1	1	1	1
miliaris	2	1	1	0	0	0	0	0	0	1	1	1	0	1	0&1	0	0&1	2	0	0	0	1	1	1	1	0&1	1	1	1	1
mossoroensis	2	1	1	1	0	0	0	0	0	1	1	1	0	1	0	0	1	1	0	0	0	1	1	1	1	1	1	1	1	1
juliae	2	1	1	1	0	0	0	1	0	0	1	1	0	1	0	0	1	1	1	1	0	1	1	1	0	1	1	1	1	1
pygmaeus	?	?	?	?	?	?	?	?	?	?	?	1	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
pyburni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

Appendix 3. continued

	Cranial osteology																														
Taxon/Character number	**30**	**31**	**32**	**33**	**34**	**35**	**36**	**37**	**38**	**39**	**40**	**41**	**42**	**43**	**44**	**45**	**46**	**47**	**48**	**49**	**50**	**51**	**52**	**53**	**54**	**55**	**56**	**57**	**58**	**59**
Ly._anomalus	1	1	1	1	0	0	0	0	0	1	1	1	0	1	1	1	1	1	0	2	1	2	1	1	1	1	1	1	1	1
Ly._lineatus	2	1	1	1	0	0	0	0	0	0	1	1	0	?	?	1	1	1	1	2	1	1	1	1	1	0	1	1	1	0
Ly._meridionalis	1	1	1	0	0	1	0	0	0	1	1	1	0	1	1	0&1	1	0	1	1&2	1	1	1	1	?	1	1	1	1	1
Ly._sagittifer	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
X._rabdocephalus	2	1	1	1	0	0	0	1	1	0	1	1	0	0	0	?	1	1	1	0	0	2	2	1	1	1	1	1	1	1
X._werneri	2	1	1	1	0	0	0	1	1	1	1	1	0	1	0	1	1	0	1	0	0	2	2	1	1	1	1	1	1	1
X._severus	2	1	1	1	0	0	0	1	1	0	1	1	0	0	0	1	1	0	1	0	0	2	2	1	1	0	1	1	1	1
X._dorbignyi	1	1	1	2	1	0	0	0	0	0	2	1	0	0	0	0	1	0	0	0	0	1	1	1	?	0	1	1	0	-
X._nattereri	1	1	0	-	-	0	0	0	1	0	2	1	0	0	0	1	1	1	0	1	0	2	1	1	?	0	1	0	0	-
Psomophis_jobert	2	0	?	2	?	0	0	0	0	1	1	1	1	0	0	0	1	0	1	2	0	1	0	0	1	1	1	0	1	0
Conophis_pulcher	2	1	1	1	1	0	0	0	0	1	1	1	1	0	0	1	0	0	1	0	0	1	1	1	1	1	1	1	1	1
Haitiophis_anomalus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Arryton_vittatum	0	0	1	1	0	0	0	0	0	-	2	1	0	0	1	1	1	1	0	0	2	1	1	1	1	1	0	1	0	-
Philodryas_patagoniensis	2	1	1	0	0	1	0	1	1	1	1	1	0	0	0	0	?	1	1	1	0	1	2	1	1	1	1	1	1	1
Tomodon_dorsatus	0	0	1	1	0	1	0	0	1	1	1	1	0	1	0	1	1	0	1	0	1	1	2	1	1	1	1	1	1	1
Dipsas_indica	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Oxyrhopus_guibei	0	0	1	1	0	1	0	0	1	0	2	1	1	1	1	0	1	0	0	1	0	3	0	1	1	0	1	0	1	1
Caaeteboia_amarali	?	?	?	?	?	?	?	0	1	1	1	1	0	1	0	0	0	0	1	2	0	1	1	1	1	1	1	0	1	1
Helicops_modestus	2	1	1	1	0	0	0	0	0	0	2	1	0	1	1	0	1	2	1	0	0	0	1	1	0	1	1	1	1	1
Coluber_contrictor	1	1	1	1	0	0	0	0	1	1	1	0	-	-	-	0	0	3	1	1	0	3	1	0	1	1	0	1	1	1

Appendix 3. continued

Taxon/Character number	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78
aesculapii_monads	1	0	0	0	0	0	0	2	1	0	0	1	1	1	1	1	1	0	3
pseudocorallus	1	0	0	0	0	0	0	1	1	0	0	1	1	1	1	1	1	0	?
bizona_andina	1	1	0	1	0	0	0	3	3	0	0	1	1	1	1	1	1	0	3
aesculapii_dyads	1	1	0	1	0	0	0	2	1	0	0	1	1	1	1	2	1	0	3
bizona_cisandina	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
aesculapii	1	0	0	0	0	0	0	1	1	0	0	1	1	1	1	1	1	0	3
mimus_micrurus	1	0	0	0	0	0	0	2	1	0	0	1	1	1	1	2	1	0	3
e_epinephelus	-	1	1	1	0	0	0	2	1	0	2	1	1	1	1	1	1	0	?
e_lamonae	-	1	1	1	0	0	0	2	2	0	2	1	1	1	1	1	1	0	3
e_pseudocobella	-	1	1	1	0	0	0	1	1	0	1	1	1	1	1	1	1	0	?
e_albiventris	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
melanotus	1	1	1	1	0	0	0	2	1	0	2	1	1	1	1	1	1	0	?
reginae	-	1	1	1	0	0	0	1	1	0	1	1	1	1	1	1	1	0	3
oligolepis	-	1	0	0	0	0	0	1	1	0	?	1	1	1	1	2	1	0	?
typhlus	0	1	0	1	0	0	0	2	1	0	2	1	1	1	1	2	1	0	1
viridis	1	1	0	0	0	0	0	2	1	0	2	1	1	1	1	1	1	1	2&3
jaegeri	1	1	0	0	0	0	0	2	1	0	1	1	1	1	1	1	1	0	1
maryellenae	1	1	0	0	0	0	0	2	1	0	2	1	1	1	1	2	1	1	2
atraventer	1	1	0	0	0	0	0	2	1	0	?	1	1	1	1	2	1	1	1
almadensis	1	0	0	0	0	0	0	1	1	0	2	1	1	1	1	1	1	0	?
carajasensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
poecilogyrus	1	0	0	1	0	0	0	2	2	0	2	1	0	1	1	1	1	0	?
taeniogaster	0	1	0	1	0	0	0	2	1	0	2	1	1	1	1	1	1	0	0
breviceps	1	1	1	1	0	0	0	1	3	0	2	1	1	1	1	0	1	0	?
frenata	1	1	0	0	0	0	0	2	0	0	2	1	1	1	1	0	1	1	?
miliaris	0	1	0	1	0	0	0	3	1	0	2	1	1	1	1	1	1	1	1
mossoroensis	0	1	0	1	0	0	0	3	1	0	2	1	1	1	1	1	1	1	1
juliae	1	0	1	1	0	0	0	2	1	0	1	1	1	1	1	2	1	1	3
pygmaeus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
pyburni	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Ly._anomalus	1	0	0	1	?	0	0	3	0	?	2	1	0	1	1	1	0	0	?

Appendix 3. continued

Taxon/Character number	60	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78
Ly._lineatus	-	1	0	1	?	0	0	1	1	?	?	1	1	1	1	?	1	1	?
Ly._meridionalis	1	0	0	1	?	0	0	1	1	?	2	1	1	1	1	2	1	1	1
Ly._sagittifer	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
X._rabdocephalus	1	0	0	0	?	0	1	1	1	0	2	1	1	1	1	1	0	0	?
X._werneri	1	1	0	0	?	1	1	0	1	0	2	1	0	1	1	2	1	0	3
X._severus	1	1	0	0	?	0	1	0	1	1	2	1	0	1	0	1	1	0	3
X._dorbignyi	-	0	-	0	?	1	1	1	0	1	2	1	0	1	0	0	1	0	3
X._nattereri	-	0	-	0	?	1	1	1	2	1	2	1	0	1	0	0	1	1	3
Psomophis_jobert	-	1	0	1	?	1	1	1	2	0	1	1	1	0	1	0	0	1	?
Conophis_pulcher	0	1	0	1	?	0	0	3	1	1	2	1	0	1	1	0	1	1	3
Haitiophis_anomalus	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Arryton_vittatum	-	1	1	1	0	1	0	0	2	1	0	1	1	1	1	0	1	0	?
Philodryas_patagoniensis	1	1	1	1	0	0	0	2	1	0	2	1	0	1	1	2	1	1	1
Tomodon_dorsatus	1	0	1	1	?	1	0	2	0	?	?	1	1	1	1	2	0	0	?
Dipsas_indica	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?
Oxyrhopus_guibei	0	1	1	1	1	0	0	2	1	1	0	1	1	1	1	0	0	0	3
Caaeteboia_amarali	1	0	1	1	?	?	1	3	1	?	2	0	-	1	1	1	1	1	0
Helicops_modestus	0	1	0	-	?	0	0	3	3	1	0	1	1	1	0	1	1	1	3
Coluber_contrictor	0	1	0	1	?	0	1	0	1	1	2	1	0	1	1	0	1	1	3

Appendix 4. Taxa and genes sampled for the molecular dataset. Voucher codes are as follows: MZUSP, Museu de Zoologia da Universidade de São Paulo; CAS, California Academy of Sciences; MTR, M. T. Rorigues, Field Number; MHUAR, Museo de Hepetología de la Universidad de Antioquia; YPMR, Yale Peabody Museum; AMS, Andrew Sneyder, field seires; WLSV; W. L. Silva.

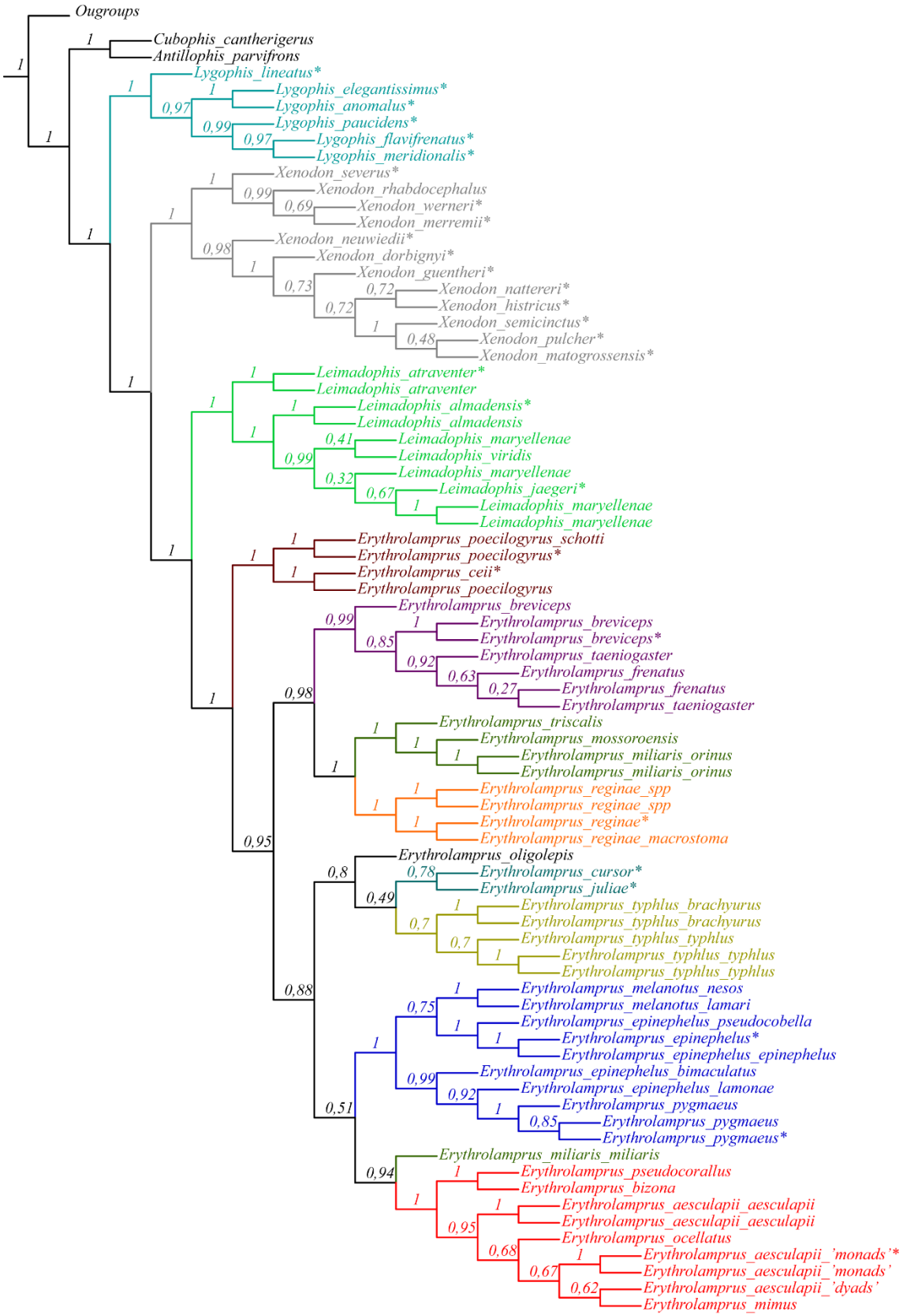
Taxon	Voucher	12s	coi	cytb	bdnf	cmos	nt3
Erythrolamprus aesculapii aesculapii 1	MZUSP20213	X	X	X	X	X	X
Erythrolamprus aesculapii aesculapii 2	AMS550	X	X	-	X	X	X
Erythrolamprus aesculapii 'dyads'	MZUSP19598	X	X	X	X	X	X
Erythrolamprus aesculapii 'monads'	MZUSP17930	X	X	X	X	X	X
*Erythrolamprus aesculapii 'monads'**		GQ457795	-	X-	**JQ599024**	GQ457856	-
*Erythrolamprus almadensis 1**		**JQ598808**	-	-	X	**JQ598979**	X
Erythrolamprus almadensis 2	MZUSP16794	X	X	X	X	X	X
*Erythrolamprus atraventer_1**		**JQ598809**	-	-	X	**JQ598980**	X
Erythrolamprus atraventer_2	MTR21628	X	X	-	X	X	X
Erythrolamprus bizona	MHUAR14801	X	X	-	X	X	X
Erythrolamprus breviceps_1		AF158464	-	-	-	-	-
Erythrolamprus breviceps_2	BPN758	X	X	X	X	X	X
Erythrolamprus breviceps_3	MZUSP17446		X	-	-	-	X
Erythrolamprus ceii		**JQ598810**	X	-	X	**JQ598981**	X
Erythrolamprus cursor		JX905306	-	-	-	-	-
Erythrolamprus epinephelus		GU018158	-	-	X	X	X
Erythrolamprus epinephelus bimaculatus	MHUAR14949	X	X	-	X	X	X
Erythrolamprus epinephelus epinephelus	MHUAR14526	X	-	X	X	X	X
Erythrolamprus epinephelus lamonae	MHUAR14799	X	-	X	-	-	-
Erythrolamprus epinephelus pseudocobella	MHUAR14434	X	-	X	X	X	X
Erythrolamprus frenatus_1	CTMZ004914	X	-	-	-	-	-
Erythrolamprus frenatus_2	MTR169	X	X	-	X	X	X
Erythrolamprus jaegeri		GQ457809	-	-	X	GQ457869	X
Erythrolamprus juliae		AF158464	-	-	-	-	-
Erythrolamprus maryellenae 1	CTMZ00291	X	-	-	-	-	-
Erythrolamprus maryellenae 2	MZUSP14346	X	X	-	X	X	X
Erythrolamprus maryellenae 3	MZUSP6609	X	-	-	X	-	-
Erythrolamprus maryellenae 4	MNRJ19817	X	-	-	X	X	X
Erythrolamprus melanotus lamari	MHUAR14609	X	-	-	X	X	X
Erythrolamprus melanotus nesos	CAS245401	X	X	X	X	X	X
Erythrolamprus miliaris miliaris	AMS448	X	X	X	X	X	X
*Erythrolamprus miliaris orinus 1**		**JQ598811**	X	**JQ598931**	**JQ599025**	**JQ598982**	X
Erythrolamprus miliaris orinus 2	MZUSP17277	X	X	X	X	X	X
Erythrolamprus mimus		GU018157	-	-	-	-	-
Erythrolamprus mossoroensis	MZUSP19615	X	X	X	X	X	X
Erythrolamprus ocellatus	CAS245326	X	X	X	X	X	X
Erythrolamprus oligolepis	MZUSP20795	X	X	X	X	X	X

Erythrolamprus poecilogyrus schotti_1	MZUSP14633	X	X	X	X	X	X
*Erythrolamprus poecilogyrus schotti_2**		**JQ598812**	-	-	X	X	X
Erythrolamprus poecilogyrus sublineatus	MTR72	X	X	X	X	X	X
Erythrolamprus pseudocorallus	MHUAR14620	X	X	X	X	-	X
*Erythrolamprus pygmaeus_1**		GU018154	-	-	-	-	-
Erythrolamprus pygmaeus_2	MZUSP20783	X	X	X	X	X	X
Erythrolamprus pygmaeus_3	MNRJ17979	X	X	X	X	X	X
Erythrolamprus reginae		**JQ598813**	-	-	X	**JQ598983**	X
Erythrolamprus reginae macrostoma	MZUSP18639	X	X	X	X	X	X
Erythrolamprus reginae_spp_1	YPMR16083	X	X	X	X	X	X
Erythrolamprus reginae_spp_2	CAS245114	X	X	X	X	X	X
Erythrolamprus taeniogaster_1	MZUSP11314	X	-	X	X	X	X
Erythrolamprus taeniogaster_2	CTMZ06526	X	-	-	X	X	X
Erythrolamprus triscalis	YPMR18159	X	X	X	X	X	X
*Erythrolamprus typhlus brachyurus 1**		GQ457811	X	-	X	GQ457871	X
Erythrolamprus typhlus brachyurus 2	MZUSP13022	X	X	X	X	X	X
Erythrolamprus typhlus typhlus 1	MUSM22289		X	X	X	X	X
Erythrolamprus typhlus typhlus 2	MZUSP20896	X	X	X	X	X	X
Erythrolamprus typhlus typhlus 3	AMS472	X	X	X	X	X	X
Erythrolamprus viridis	WLSV 3391	X	X	-	X	X	X
Lygophis anomalus		**JQ598817**	X	-	X	X	X
Lygophis elegantissimus		GQ457808	X	X	X	GQ457868	X
Lygophis flavifrenatus		**JQ598818**	-	-	-	-	-
Lygophis lineatus			-	-	X	X	X
Lygophis meridionalis		GQ457810	-	-	X	GQ457870	X
Lygophis paucidens		**JQ598819**	-	-	-	**JQ598987**	-
Xenodon dorbignyi		GQ457812	-	-	X	X	X
Xenodon guentheri		**JQ598849**	-	-	X	X	X
Xenodon histricus		GQ457813	-	**JQ598962**	**JQ599061**	-	X
Xenodon matogrossensis		**JQ598850**	-	-	X	X	X
Xenodon merremii		X	X	X	X	X	X
Xenodon nattereri		**JQ598851**	-	-	X	X	X
Xenodon neuwiedii		GQ457841	X	AF236814	X	X	X
Xenodon pulcher		**JQ598852**	-	-	X	-	X
Xenodon rhabdocephalus	MHUAR14807	X	X	X	X	-	X
Xenodon semicinctus		GU018156	-	X-	-	-	-
Xenodon severus		**JQ598853**	-	**JQ598964**	**JQ599063**	-	X
Xenodon werneri		AF158468	-	-	-	-	-
Achalinus rufescens		X	X	X	X	-	X
Acrochordus javanicus		AF512745	X	X	X	HM234058	AY988053
Afronatrix anoscopus		X	X	X-	EU402622	AF471123	X
Agkistrodon piscivorus		AF259225	X	EU483451	**JQ599004**	AF471096	X

Ahaetulla prasina	X	X	KC010339	X	KC010300	X
Antillophis parvifrons	AF158441	X	FJ416740	**JQ599006**	-	X
Aparallactus capensis	FJ404129	X	AY188006	-	AY187967	-
Aplopeltura boa	AF544761	-	X-	FJ433984	AF544715	X
Apostolepis albicollaris	**JQ598793**	X	X	X	**JQ598965**	X
Apostolepis dimidiata	GQ457782	X	**JQ598917**	**JQ599008**	GQ457844	X
Atractus reticulatus	**JQ598798**	-	-	X	**JQ598970**	-
Atractus trihedrurus	GQ457784	X	**JQ598919**	**JQ599010**	GQ457846	X
Azemiops feae	AF512748	X	AY352747	EU402628	AF544695	X
Bitis gabonica	X	X	X	X	X	X
Boa constrictor	AB177354	X	AY575035	AY988030	AF544676	X
Boiruna maculata	GQ457785	X	**JQ598920**	**JQ599011**	GQ457847	X
Bungarus fasciatus	U96793	X	AJ749349	**JQ599013**	AY058924	X
Calamaria pavimentata	X	-	AF471081	**JQ599014**	AF471103	X
Calamaria yunnanensis	**JQ598801**	X	**JQ598922**	X	X	X
Coluber constrictor	AY122819	X	EU180347	**JQ599015**	AY486938	X
Conophis lineatus	GQ457788	X	**JQ598924**	**JQ599016**	**JQ598975**	-
Contia tenuis	AY577021	-	AF471095	GU112361	AF471134	-
Crotalus durissus	X	X	X	X	X	X
Cubophis cantherigerus	X	-	X	X	X	X
Diadophis punctatus	AY577015	X	EU193670	**JQ599017**	AF471122	X
Dipsas catesbyi	**JQ598805**	X	**JQ598926**	**JQ599021**	**JQ598977**	X
Dipsas indica	GQ457789	X	-	X	GQ457850	X
Drepanoides anomalus	GQ457791	X	**JQ598927**	X	GQ457852	X
Duberria lutrix	X	X	X-	X	X	X
Echinanthera undulata	**JQ598807**	-	**JQ598929**	**JQ599022**	**JQ598978**	-
Elapomorphus quinquelineatus	GQ457794	X	**JQ598930**	**JQ599023**	GQ457855	X
Enhydris bocourti	AF499285	X	EF395904	X	AF544699	X
Eryx conicus	X	X	X	X	X	X
Gonionotophis capensis	X	X	X-	X	X	X
Grayia ornata	X	X	X	X	X	X
Helicops angulatus	GQ457797	-	AF471037	**JQ599027**	GQ457857	-
Helicops hagmanni	**JQ598816**	-	-	-	**JQ598985**	-
Helicops modestus	X	X	-	X	X	X
Heterodon nasicus	GQ457801	-	-	X	GQ457861	X
Heterodon platirhinos	AY577019	-	**JQ598934**	**JQ599028**	**JQ598986**	X
Homalopsis buccata	AF499288	-	EF395917	X	AF544701	X
Homoroselaps lacteus	FJ404135	X	AF217833	**JQ599029**	AY611901	X
Hydrops triangularis	GQ457804	X	AF471039	**JQ599032**	GQ457864	X
Imantodes cenchoa	GQ457805	X	EF078505	**JQ599033**	GQ457865	X
Lampropeltis getula	AY122681	X	DQ486339	X	FJ387204	X

Leptodeira annulata	GQ457806	X	FJ416713	FJ433998	GQ457866	X
Macrovipera lebetina	X	X	X	X	X	X
Manolepis putnami	**JQ598820**	-	**JQ598936**	**JQ599035**	**JQ598988**	-
Mussurana bicolor	X	X	-	X	X	X
Naja atra	X	X	X-	X	X	X
Natrix natrix	AY122682	X	AY866540	**JQ599036**	AF471121	X
Ninia atrata	GQ457814	X	**JQ598937**	**JQ599037**	GQ457874	X
Oxyrhopus clathratus	GQ457815	X	-	X	GQ457875	X
Oxyrhopus guibei	**JQ598822**	-	**JQ598938**	**JQ599038**	**JQ598989**	X
Oxyrhopus petola	GU018150	X	X	X	X	X
Pareas hamptoni	X	X	X	X	X	X
Phalotris lativittatus	**JQ598825**	X	-	X	**JQ598991**	X
Phalotris tricolor	X	X	-	X	X	-
Philodryas nattereri	**JQ598829**	X	AF236806	X	**JQ598992**	X
Philodryas olfersii	**JQ598830**	-	**JQ598945**	**JQ599041**	**JQ598993**	X
Philodryas patagoniensis	GQ457821	-	AF236808	-	GQ457881	-
Phimophis guerini	GQ457822	X	-	-	GQ457882	-
Psammodynastes pulverulentus	X	X	X-	X	X	X
Pseudalsophis biserialis	X	X	X	-	X	X
Pseudalsophis elegans	X	-	X	X	X	-
Pseudoboa coronata	GQ457824	X	-	-	GQ457884	X
Pseudoboa nigra	GQ457825	X	**JQ598948**	**JQ599043**	GQ457885	X
Pseudotomodon trigonatus	GQ457827	X	-	-	GQ457887	X
Pseudoxenodon bambusicola	**JQ598833**	X	-	**JQ599044**	**JQ598996**	X
Pseudoxenodon karlschmidti	**JQ598834**	X	AF471080	**JQ599045**	AF471102	-
Rhamphiophis oxyrhynchus	Z46443	X	**JQ598953**	**JQ599049**	AF544710	X
Sibynomorphus mikanii	GQ457832	X	**JQ598954**	**JQ599050**	GQ457892	X
Sibynophis collaris	X	X	X-	X	X	-
Siphlophis cervinus	**JQ598841**	X	X-	X	**JQ598998**	X
Siphlophis pulcher	GQ457834	X	**JQ598955**	**JQ599051**	GQ457894	-
Sordellina punctata	**JQ598843**	-	**JQ598956**	**JQ599052**	**JQ599000**	X
Spalerosophis diadema	X	X	X-	X	X	X
Stoliczkia borneensis	X	-	-	X	X	X
Tachymenis peruviana	GQ457835	X	-	**JQ599054**	GQ457895	X
Taeniophallus affinis	**JQ598845**	-	X	X	**JQ599001**	-
Thamnodynastes strigatus	**JQ598847**	X	**JQ598959**	**JQ599057**	-	X
Thamnophis sirtalis	AF402646	X	X-	**JQ599058**	DQ902094	X
Tomodon dorsatus	GQ457838	X	**JQ598960**	**JQ599059**	GQ457897	X
Tropidodryas striaticeps	GQ457839	X	AF236811	**JQ599060**	X	X

Appendix 5. Bayesian tree obtained with the molecular data. Number above branches indicate posterior probability values. Asterisks indicate sequences previously published.



Appendix 6. Consensus tree of the combined analysis showing clade numbers, and list of morphological synapomorphies obtained in TNT (command: apo-;).

Appendix 6. Cuntinued

Node 89 :
No synapomorphies
Node 90 :
No synapomorphies
Node 91 :
No synapomorphies
Node 92 :
Char. 2: 0 --> 1
Char. 36: 1 --> 0
Char. 47: 1 --> 0
Char. 49: 0 --> 1
Char. 66: 2 --> 1
Node 93 :
Char. 18: 2 --> 1
Char. 19: 2 --> 1
Char. 21: 1 --> 2
Char. 22: 1 --> 2
Char. 23: 1 --> 2
Char. 27: 0 --> 1
Char. 39: 1 --> 0
Char. 41: 0 --> 1
Char. 44: 0 --> 1
Char. 51: 1 --> 2
Char. 62: 1 --> 0
Char. 76: 1 --> 0
Node 94 :
Char. 10: 0 --> 1
Char. 15: 1 --> 0
Char. 38: 1 --> 0
Char. 53: 1 --> 0
Char. 60: 1 --> 0
Char. 77: 1 --> 3
Node 95 :
No synapomorphies
Node 96 :
No synapomorphies
Node 97 :
Char. 12: 0 --> 1
Char. 13: 0 --> 1
Char. 14: 1 --> 0
Char. 16: 0 --> 1
Char. 17: 1 --> 0
Node 98 :
Char. 0: 1 --> 0
Char. 22: 2 --> 1
Char. 25: 2 --> 1
Node 99 :
Char. 7: 0 --> 1
Node 100 :
Char. 18: 0 --> 2
Char. 19: 0 --> 2
Char. 46: 0 --> 1
Char. 59: 0 --> 1
Char. 77: 3 --> 1
Node 101 :
Char. 0: 2 --> 1
Char. 26: 1 --> 0
Char. 45: 0 --> 1
Node 102 :
Char. 26: 1 --> 2
Node 103 :
Char. 10: 1 --> 0
Char. 15: 1 --> 0
Char. 20: 1 --> 0
Char. 23: 1 --> 2
Node 104 :
Char. 18: 2 --> 1
Char. 25: 1 --> 2
Node 105 :
Char. 10: 0 --> 1
Char. 19: 2 --> 1
Node 106 :
Char. 21: 1 --> 0
Char. 23: 1 --> 2
Char. 29: 2 --> 0
Char. 74: 1 --> 2
Node 107 :
Char. 15: 1 --> 0
Char. 24: 1 --> 0
Char. 27: 0 --> 2
Char. 30: 1 --> 0
Char. 43: 0 --> 1
Char. 48: 0 --> 1
Char. 61: 0 --> 1
Char. 66: 2 --> 1
Char. 67: 1 --> 3
Char. 74: 1 --> 0
Node 108 :
Char. 22: 1 --> 2
Char. 26: 0 --> 1
Char. 32: 1 --> 0
Char. 47: 1 --> 0
Node 109 :
Char. 76: 1 --> 0
Node 110 :
Char. 19: 2 --> 1
Char. 29: 2 --> 0
Char. 60: 1 --> 0
Char. 67: 1 --> 2
Char. 71: 1 --> 0
Node 111 :
Char. 10: 0 --> 1
Char. 21: 0 --> 1
Char. 30: 0 --> 1
Char. 35: 0 --> 1
Char. 48: 1 --> 0
Char. 59: 1 --> 0
Char. 74: 0 --> 1
Node 112 :
Char. 15: 0 --> 1
Char. 19: 2 --> 1
Char. 23: 1 --> 2
Char. 24: 0 --> 1
Char. 29: 2 --> 0
Char. 32: 0 --> 1
Char. 61: 1 --> 0
Char. 66: 1 --> 2
Node 113 :
No synapomorphies
Node 114 :
No synapomorphies
Node 115 :
No synapomorphies
Node 116 :
No synapomorphies
Node 117 :
Char. 25: 1 --> 0
Char. 27: 0 --> 1
Char. 61: 0 --> 1
Node 118 :
Char. 10: 0 --> 1
Node 119 :
Char. 20: 1 --> 0
Node 120 :
Char. 2: 1 --> 0
Char. 8: 0 --> 1
Char. 20: 1 --> 0
Char. 22: 2 --> 1
Char. 62: 1 --> 0
Char. 76: 0 --> 1
Node 121 :
No synapomorphies
Node 122 :
Char. 22: 1 --> 2
Char. 24: 1 --> 0
Char. 29: 2 --> 0
Char. 74: 1 --> 2
Node 123 :
No synapomorphies
Node 124 :
Char. 8: 0 --> 1
Char. 32: 1 --> 0
Node 125 :
Char. 46: 1 --> 2
Node 126 :
No synapomorphies
Node 127 :
No synapomorphies
Node 128 :
Char. 29: 2 --> 0
Char. 74: 1 --> 2
Node 129 :
No synapomorphies
Node 130 :
Char. 22: 1 --> 2
Node 131 :
No synapomorphies
Node 132 :
Char. 23: 1 --> 2
Char. 27: 0 --> 1
Char. 34: 0 --> 1
Char. 46: 1 --> 2
Char. 61: 0 --> 1
Char. 66: 2 --> 1
Char. 69: 2 --> 1
Char. 77: 1 --> 3
Node 133 :
No synapomorphies
Node 134 :
No synapomorphies
Node 135 :
Char. 2: 1 --> 2
Char. 20: 1 --> 0
Char. 47: 1 --> 0
Char. 51: 1 --> 2
Char. 54: 0 --> 1
Node 136 :
No synapomorphies
Node 137 :
No synapomorphies
Node 138 :
Char. 2: 0 --> 1
Char. 24: 1 --> 0
Char. 43: 0 --> 1
Char. 47: 1 --> 0
Char. 51: 2 --> 1
Node 139 :
Char. 3: 1 --> 0
Char. 69: 2 --> 0
Node 140 :
No synapomorphies
Node 141 :
Char. 13: 0 --> 1
Char. 14: 1 --> 0
Char. 17: 1 --> 0
Char. 29: 2 --> 1
Char. 60: 1 --> 0
Node 142 :
Char. 48: 0 --> 2
Char. 49: 0 --> 1
Node 143 :
Char. 19: 2 --> 1
Node 144 :
Char. 20: 1 --> 2
Node 145 :
No synapomorphies
Node 146 :
Char. 29: 2 --> 0
Char. 30: 1 --> 0
Char. 34: 0 --> 1
Char. 61: 0 --> 1
Char. 75: 1 --> 0
Char. 76: 1 --> 0
Node 147 :
No synapomorphies
Node 148 :
No synapomorphies
Node 149 :
Char. 38: 1 --> 0
Char. 65: 0 --> 1
Char. 77: 1 --> 3
Node 150 :
Char. 1: 0 --> 1
Char. 10: 0 --> 1
Char. 14: 1 --> 0
Char. 17: 1 --> 0
Node 151 :
No synapomorphies
Node 152 :
Char. 0: 0 --> 2
Char. 5: 1 --> 2
Char. 20: 1 --> 0
Char. 22: 1 --> 2
Char. 25: 1 --> 0
Char. 27: 0 --> 1
Char. 28: 1 --> 2
Char. 54: 0 --> 1
Node 153 :
Char. 3: 1 --> 0
Char. 51: 1 --> 2