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

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## 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 *Erythrolamprus*.

## 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 sinapomorfias 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 análises de parcimônia, bayesianos e de máxima verossimilhança para os dados moleculares; enquanto que para as matrizes morfológica e combinada (morfológica e molecular) só foi utilizada análise 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 morfológicas. 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* resuscitamos o gênero *Leimadophis*, dado que foi recuperado como irmão de todas as outras espécies do clado *Erythrolamprus*.

## 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.<sup>1</sup>Species sampled for morphology; <sup>2</sup> Species sampled for molecular data.

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

\*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 opisthognath 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, *Caeteboini* and *Caeteboia*, 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 mitochondrial 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.

## 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.

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