

Molecular phylogeny of the tribe Philodryadini Cope, 1886 (Dipsadidae: Xenodontinae): Rediscovering the diversity of the South American Racers

Juan Camilo Arredondo^{1,6}; Felipe G. Grazziotin²; Gustavo J. Scrocchi³; Miguel Trefaut Rodrigues⁴; Sandro Luís Bonatto⁵ & Hussam Zaher^{6,7}

¹ Universidad CES, Facultad de Ciencias y Biotecnología, Colecciones Biológicas Universidad CES (CBUGES). Medellín, Antioquia, Colombia. ORCID: <http://orcid.org/0000-0003-1925-4556>. E-mail: jcas36@gmail.com

² Instituto Butantan, Laboratório Especial de Coleções Zoológicas (LEZ). São Paulo, SP, Brasil. ORCID: <http://orcid.org/0000-0001-9896-9722>. E-mail: fgrazziotin@gmail.com

³ Fundación Miguel Lillo, Unidad Ejecutora Lillo (CONICET-UDEL). San Miguel de Tucumán, Tucumán, Argentina. ORCID: <http://orcid.org/0000-0002-8924-8808>. E-mail: gustavo.scrocchi@gmail.com

⁴ Universidade de São Paulo (USP), Instituto de Biociências (IB-USP), Departamento de Zoologia. São Paulo, SP, Brasil. ORCID: <http://orcid.org/0000-0003-3958-9919>. E-mail: mturodri@gmail.com

⁵ Pontifícia Universidade Católica do Rio Grande do Sul (PUC-RS), Escola de Ciências da Saúde e da Vida, Laboratório de Biologia Genômica e Molecular. ORCID: <http://orcid.org/0000-0002-0064-467X>. E-mail: slbonatto@puccrs.br

⁶ Universidade de São Paulo (USP), Museu de Zoologia (MZUSP). São Paulo, SP, Brasil.

⁷ ORCID: <http://orcid.org/0000-0002-6994-489X>. E-mail: hussam.zaher@gmail.com (corresponding author)

Abstract. South American racers of the tribe Philodryadini are a widespread and diverse group of Neotropical snakes with a complex taxonomic and systematic history. Recent studies failed to present a robust phylogenetic hypothesis for the tribe, mainly due to incomplete taxon sampling. Here we provide the most extensive molecular phylogenetic analysis of Philodryadini available so far, including 20 species (83% of the known diversity) from which six were not sampled previously. Our results reveal that Philodryadini is not monophyletic, but instead includes a central Andean clade formed by *Philodryas simonsii*, *P. tachymenoides*, and *P. amarum*, and a southern and cis-Andean clade including all remaining philodryadines. This discovery requires resurrection of two genera as well as erection of a new tribe of Xenodontinae for the central Andean clade. Within the southern and cis-Andean radiation, our analyses resolve a basal dichotomy separating two main lineages: Clade A, containing the Common Green Racers *P. laticeps* and *P. viridissima* and the South American Vine snakes *P. georgeboulengeri* and *P. argentea*; and Clade B, including the remaining species of *Philodryas sensu stricto*. We resurrect the genera *Chlorosoma* and *Xenoxybelis* to better represent the monophyly of lineages within the southern and cis-Andean clade.

Key-Words. *Philodryas*; *Chlorosoma*; *Xenoxybelis*; Andean Endemism; New Tribe; Hemipenial morphology.

INTRODUCTION

The South American racers of the tribe Philodryadini Cope 1886 are a diverse and widespread group of snakes with a wide variety of morphologies and ecological roles, ranging from large, semiarboreal, and generalist species to small, secretive, and diet specialist species (Greene & Jaksic, 1992; Hartmann & Marques, 2005; Marques *et al.*, 2006). Most of this diversity occurs along the cis-Andean portion of South America (Table 1). Twenty species are distributed from Colombia to Argentina, while only four species inhabit the trans-Andean parts of Ecuador,

Peru, and Chile (Cacciali *et al.*, 2016; Grazziotin *et al.*, 2012; Zaher *et al.*, 2014). Because of their diversity, broad distribution, and variety in ecomorphological traits, the species have a long history of taxonomic instability and uncertainty (Thomas, 1976; Zaher *et al.*, 2008; Wallach *et al.*, 2014).

The unpublished PhD thesis of Robert A. Thomas (1976) was the first large taxonomic review of the genus *Philodryas*, and several of his conclusions are currently accepted and followed by most researchers. Subsequent taxonomic studies that changed significantly the composition and diversity of the genus were made by Thomas and colleagues (Thomas, 1977; Thomas & Dixon,

Pap. Avulsos Zool., 2020; v.60: e20206053

<http://doi.org/10.11606/1807-0205/2020.60.53>

<http://www.revistas.usp.br/paz>

<http://www.scielo.br/paz>

Edited by: Carlos José Einicker Lamas

Received: 07/10/2020

Accepted: 14/10/2020

Published: 20/10/2020

ISSN On-Line: 1807-0205

ISSN Printed: 0031-1049

ISNI: 0000-0004-0384-1825

<http://zoobank.org/30684314-ABD0-4952-96E4-B6A864D1CDE3>



Table 1. Species diversity and geographical distribution of the members of the tribe Philodryadini (*sensu lato*). CE = Central, E = East, NO = North, NE = Northeastern, NW = Northwestern, SO = South, SE = Southeastern, SW = Southwestern, W = West, Ar = Argentina, Co = Colombia, Ch = Chile, Bo = Bolivia, Br = Brazil, Ec = Ecuador, Gu = Guianas, Pa = Paraguay, Pe = Peru, Su = Suriname, Ve = Venezuela, and Ur = Uruguay.

Species	Geographical Distribution	Andes related Distribution
<i>Ditaxodon taeniatus</i> (Peters, 1868)	SE Br	cis-Andean
<i>Philodryas aestiva</i> (Duméril, Bibron & Duméril, 1854)	NW Ar, Bo, SW-SE-SO Br, Pa, and Ur	cis-Andean
<i>Philodryas agassizii</i> (Jan, 1863)	Ar, SW-SO Br, Pa, and Ur	cis-Andean
<i>Philodryas amaru</i> Zaher et al., 2014	CE-SO Ec	trans-Andean
<i>Philodryas argentea</i> (Daudin, 1803)	SO Co, Bo, CE-NO-NE-NW Br, E Ec, Gu, E Pe, and SO Ve	cis-Andean
<i>Philodryas arnaldoi</i> (Amaral, 1932)	SW Br	cis-Andean
<i>Philodryas boliviana</i> Boulenger, 1896	CE Bo	cis-Andean
<i>Philodryas baroni</i> Berg, 1895	NO Ar, W Bo, SW Br, and Pa	cis-Andean
<i>Philodryas chamissonis</i> (Wiegmann, 1835)	CE-W Ch	trans-Andean
<i>Philodryas cordata</i> Donnelly & Myers, 1991	SO Ve	cis-Andean
<i>Philodryas erlandi</i> Lönnberg, 1902	NO Ar, Bo, and Pa	cis-Andean
<i>Philodryas georgeboulengeri</i> (Grazziotin et al., 2012)	Bo, CE-NO-NW Br, and E Pe	cis-Andean
<i>Philodryas laticeps</i> Werner, 1900	CE Bo and SE Br	cis-Andean
<i>Philodryas livida</i> (Amaral, 1923)	SW Br and NO Pa	cis-Andean
<i>Philodryas mattogrossensis</i> Koslowsky, 1898	SW Br	cis-Andean
<i>Philodryas nattereri</i> Steindachner, 1870	SW-CE-NE Br and NO Pa	cis-Andean
<i>Philodryas olfersii</i> (Lichtenstein, 1823)	CE-NO Ar, SO Co, Bo, Br, E Ec, Gu, Pa, E Pe, Su, SO Ve, and Ur	cis-Andean
<i>Philodryas patagoniensis</i> (Girard, 1858)	SO-CE-NO Ar, Bo, SO-SE-CE-NE Br, Pa, and Ur	cis-Andean
<i>Philodryas psammophidea</i> Günther, 1872	NW Ar and SW Br	cis-Andean
<i>Philodryas simonsii</i> Boulenger, 1900	CE-SO Ec and Pe	trans-Andean
<i>Philodryas tachymenoides</i> (Schmidt & Walker, 1943)	CE-SO Pe	trans-Andean
<i>Philodryas trilineata</i> (Burmeister, 1861)	NO Ar	cis-Andean
<i>Philodryas varia</i> (Jan, 1863)	NW Ar and W Bo	cis-Andean
<i>Philodryas viridissima</i> (Linnaeus, 1758)	SO Co, Bo, NW-NO-NE-CE-SE Br, E Ec, Gu, E Pe, Su, and SO Ve	cis-Andean

1977; Thomas & Fernandes, 1996; Thomas & Johnson, 1984; Thomas & Di-Bernardo, 2001), D'Agostini (1998), Barrio et al. (1977), and Zaher (Zaher, 1999; Zaher et al., 2008, 2009, 2014). Nonetheless, a number of widely distributed and taxonomically complex entities with poorly assessed morphological variation await investigation, including, for example, *P. aestiva*, *P. olfersii*, *P. patagoniensis*, and *P. psammophidea* (Arredondo, 2012; Thomas, 1976; Zaher et al., 2008).

Several molecular phylogenetic studies incorporated a limited number of representatives of Philodryadini, and obtained conflicting hypotheses of relationships for the tribe (Cadle, 1984a, b, c; Grazziotin et al., 2012; Jenner & Dowling, 1985; Machado, 1993; Maglio, 1970; Zaher, 1999; Zaher et al., 2009). Cadle (1984a) found that *Philodryas* was not related to *Alsophis*, as previously stated by Maglio (1970), but rather was more closely related to the South American genus *Xenodon*. Machado (1993), based on hemipenial evidence, allocated *Oxybelis argenteus* (Daudin, 1803) to the new xenodontine genus *Xenoxybelis* which, along with *Pseudablables agassizii* (Jan, 1863), were considered by Zaher (1999) to share hemipenial characteristics with *Philodryas*. Lobo & Scrocchi (1994) provided the first osteological phylogenetic analysis of *Philodryas*, based on representatives of 11 species. Thomas & Fernandes (1996) further revised the morphological definition of *Philodryas* by including monotypic *Platyinion* Amaral, 1923 in the synonymy of *Philodryas*. According to Zaher (1999), *Philodryas* was paraphyletic and could be divided in two distinct lineages defined by their hemipenial morphology: the *olfersii*-group including *Xenoxybelis*; and the *chamisso-*

nis-group. More recently, a series of molecularly oriented studies allowed a better understanding of supra-generic relationships within New World colubroid snakes, corroborating many of Zaher's (1999) previous morphological conclusions for that group (Vidal et al., 2000, 2010; Zaher et al., 2009). Subsequent molecular assessments that included species of the tribe Philodryadini invariably recovered the tribe as a monophyletic assemblage (Grazziotin et al., 2012; Pyron et al., 2011, 2013; Vidal et al., 2010; Zaher et al., 2018, 2019). Nevertheless, the sampled diversity of Philodryadini in these studies never exceeded slightly more than half of the known species of the tribe (Table 2).

Here, we provide a phylogenetic analysis based on a multilocus molecular dataset that incorporates representatives of 83% of all known species of Philodryadini. Our assessment requires a taxonomic revision to maintain monophyletic lineages.

MATERIAL AND METHODS

Taxon sampling, DNA extraction, and sequencing

We based our analyses on a molecular dataset comprising 33 terminals previously classified as Philodryadini and 59 additional colubroidean terminal taxa (Extended Data S1; see Supplementary Information at Figshare <http://doi.org/10.6084/m9.figshare.13061516>). We included representatives of the following five families (number of terminals in parenthesis): Colubridae (3), Sibynophiidae (2), Grayiidae (1), Natricidae (4) and

Table 2. Species of Philodryadini (*sensu lato*) employed by the most recent molecular phylogenetic studies. X^A = Species sampled for the first time in a molecular study.

Species	Zaher et al. (2009)	Vidal et al. (2010)	Pyron et al. (2011)	Grazziotin et al. (2012)	Figueroa et al. (2016)	Zaher et al. (2018)	Zaher et al. (2019)	This study	Distribution
<i>P. aestiva</i>	X	X		X	X	X	X	X	cis-Andean
<i>P. agassizii</i>	X	X	X	X	X	X	X	X	cis-Andean
<i>P. argentea</i>	X	X		X	X	X	X	X	cis-Andean
<i>P. arnaldoi</i>								X ^A	cis-Andean
<i>P. baroni</i>		X	X	X	X	X	X	X	cis-Andean
<i>P. georgeboulengeri</i>			X		X	X	X	X	cis-Andean
<i>P. chamissonis</i>					X			X ^A	trans-Andean
<i>P. erlandi</i>								X ^A	cis-Andean
<i>P. laticeps</i>								X ^A	cis-Andean
<i>P. livida</i>							X	X	cis-Andean
<i>P. mattogrossensis</i>	X	X		X	X	X	X	X	cis-Andean
<i>P. nattereri</i>			X	X	X	X	X	X	cis-Andean
<i>P. olfersii</i>		X	X	X	X	X	X	X	cis-Andean
<i>P. patagoniensis</i>	X	X	X	X	X	X	X	X	cis-Andean
<i>P. psammophidea</i>		X		X	X	X	X	X	cis-Andean
<i>P. simonsii</i>								X ^A	trans-Andean
<i>P. tachymenoides</i>								X ^A	trans-Andean
<i>P. trilineata</i>					X	X	X	X	cis-Andean
<i>P. varia</i>							X	X	cis-Andean
<i>P. viridissima</i>		X	X	X	X	X	X	X	cis-Andean
Total	5	9	7	10	13	12	14	20	

Dipsadidae (49). In order to provide a proper test for the monophyly of Philodryadini, we densely sampled within Dipsadidae by including representatives of the 12 tribes of Xenodontinae (31), of the subfamilies Carphophiinae (5) and Dipsadinae (11), and of the Asian genera *Thermophis* (1) and *Stichophanes* (1). Our sample of the genus *Philodryas* comprised all known species, with the exception of *P. amaru* Zaher et al., 2014, *P. boliviana* Boulenger, 1896, and *P. cordata* Donnelly & Myers, 1991, which are known from only a few type specimens (Donnelly & Myers, 1991; Wallach et al., 2014; Zaher et al., 2014). We did not obtain sequences from *Ditaxodon* Hoge 1958, the other genus of Philodryadini, also known from only a few specimens (Thomas et al., 2006). We rooted our resulting trees on Natricidae, following the topology presented in Zaher et al. (2019).

We extracted DNA from liver, muscle, scales, or shed skins, using Phenol-Chloroform method or PureLink® Genomic DNA kit (ThermoFisher, MA, USA). We amplified fragments via polymerase chain reaction (PCR) for three nuclear (*bdnf*, *c-mos* and *nt3*) and three mitochondrial (*12S*, *cox1* and *cytb*) genes. The primer sets and protocols used in the PCR were based in the following studies: Noonan & Chippindale (2006) for *bdnf* and *nt3*; Zaher et al. (2009) for *12S* and *c-mos*; Grazziotin et al. (2012) for *cytb*; Graboski et al. (2018) for *cox1*.

We used standard PCR protocols with modifications to improve the efficiency as follows: adding 10% of Trehalose 100 for *12S*, *cytb*, and *cox1*, and 0.4% of Triton 100 for *cmos*, *bdnf*, and *nt3*. We amplified both strands and employed an annealing temperature of 54°C for *12S*, 56°C for *bdnf* and *cmos*, a touch down cycle of 58-46°C with final annealing of 48°C for *nt3*, and a touch down cycle of 60-50°C with final annealing of 54°C for *cytb* and *cox1*. All PCR products were purified with the Exo-Sap

(exonuclease and shrimp alkaline phosphatase) protocol and the sequences were processed at the Laboratório de Biologia Genômica e Molecular from the Pontifícia Universidade Católica do Rio Grande do Sul (PUCRS), Laboratório de Toxinologia Aplicada (LETA) from Instituto Butantan, and Macrogen (Seoul, Korea). We sequenced and checked both strands, and when necessary the chromatographs were edited manually. We performed the assembly and generated the consensus sequences using Geneious 6.1.8 (<http://www.geneious.com>, Kearse et al., 2012).

Phylogenetic analyses

We generated 179 new sequences and obtained other 300 sequences from GenBank to build our molecular matrices (Extended Table S1). Our concatenated dataset comprised a total of 4,433 base pairs of aligned sequences, including 510 from *12S*, 1,107 from *cox1*, 997 from *cytb*, 710 from *bdnf*, 586 from *cmos*, and 523 from *nt3* (Extended Data S1).

We used MAFFT 1.3.6 (Katoh et al., 2005), as implemented in Geneious, to align all sequences. The rRNA gene *12S* was aligned under the E-INS-i algorithm, while the protein-coding genes *bdnf*, *c-mos*, *cox1*, *cytb*, and *nt3* were aligned under the G-INS-i algorithm. We used default parameters for gap opening and extension. All protein-coding genes were visually checked using Geneious to verify if all sequences follow the correct reading frame. We concatenated our sequences using Sequence Matrix 1.8 (Vaidya et al., 2011).

We used PartitionFinder 2 (Lanfear et al., 2016) to choose the models of molecular evolution for our database and employed two different analyses. In the

first analysis, we used the Akaike Information Criterion with correction (AICc), allowing the selection of models of molecular evolution implemented in RAxML 8.2.3 (Stamatakis, 2014), using unlinked branch lengths and the greedy search option. We only allowed PartitionFinder to select GTR model with or without GAMMA, preventing models with correction for proportion of invariant sites, as suggested in the RAxML manual. In the second analysis, we used the Bayesian Information Criterion (BIC), allowing selection of all models of molecular evolution implemented in MrBayes 3.2.5 (Ronquist *et al.*, 2012). We preliminarily defined 16 partitions for our concatenated matrix, treating the rRNA gene (12S) as a separate partition and partitioning all five protein-coding genes by their codon positions. The results of PartitionFinder are provided in Extended Table S2.

We conducted a maximum likelihood (ML) analysis in RAxML using the algorithm that conducts a rapid bootstrap analysis and searches for best scoring ML tree in the same run (option *-f a*), and defined 1,000 bootstrap iterations to estimate branch support (BS). We also conducted a Bayesian Inference phylogenetic analysis (BI) in MrBayes 3.2.5 with four independent runs, 20 million generations, sampling trees every 1,000 generations. We used Tracer 1.7.1 (Rambaut *et al.*, 2018) to check the effective sample size (ESS) and trace convergence to set the burn-in. We estimated Bayesian posterior probability (PP) after burn-in. Both ML and BI phylogenetic analyses were carried out on the CIPRES Science Gateway (<http://www.phylo.org>, Miller *et al.*, 2010). Robustness of clades were checked using both BS and PP support values.

When defining and naming evolutionary lineages retrieved in our analyses, we followed the Taxon Naming Criteria (TNCs) suggested by Vences *et al.* (2013), avoiding taxonomic instability and inadequate classification schemes of non-monophyletic groups.

RESULTS

The ML and BI tree topologies showed very similar higher-level relationships, with Colubridae, Natricidae, Sibynophiidae, and Dipsadidae being all recovered as monophyletic lineages with robust to unambiguous support values (Fig. 1; Extended Figs. S1-S2). Only the position of Grayiidae varied, being retrieved with ambiguous support as the sister group of Colubridae in the ML tree and as the sister group of a clade formed by Colubridae and Sibynophiidae in the BI tree (Fig. 1; Extended Fig. S2). Within Dipsadidae, the Asian *Thermophis baileyi* and *Sticophanes ningshaanensis* were retrieved as two successive sister taxa to the New World dipsadids in both ML and BI topologies (Fig. 1). Within the New World radiation, North American Carphophiinae was retrieved as monophyletic only in the ML tree, with no statistical support. Subfamilies Dipsadinae and Xenodontinae as well as tribes Imantodini and Dipsadini were retrieved as robustly supported clades in both ML and BI topologies (Fig. 1; Extended Fig. S2).

Considering both ML and BI analyses, only the tribes Philodryadini and Echinantherini within Xenodontinae were not recovered as monophyletic groups. All other tribes represented by more than one terminal were recovered with strong to unambiguous support values in both analyses, but relationships between them were not supported by high values of support, with the BI tree resulting in a large polytomy (Fig. 1; Extended Fig. S2).

The traditionally recognized tribe Philodryadini was split into two monophyletic lineages in both analyses—a central Andean clade and a southern and cis-Andean clade—with Tropicodryadini nested between them, robustly positioned in both analyses as the sister group of the southern and cis-Andean radiation of Philodryadini (Fig. 1; Extended Figs. S1-S2). The central Andean clade was retrieved as the sister group of the clade formed by Tropicodryadini + southern and cis-Andean Philodryadini only in the ML analysis, with low values of BS, while in the BI analysis it was recovered in a polytomy along with several other clades (Fig. 2).

The central Andean clade was composed by the strictly Andean species *Philodryas simonsii* and *Philodryas tachymenoides*. These represented a distinct evolutionary lineage from the southern and cis-Andean clade of Philodryadini. Phylogenetic affinities exhibited within southern and cis-Andean radiation were the same in both ML and BI topologies (Extended Figs. S1-S2).

Phylogenetic relationship within the southern and cis-Andean radiation revealed the presence of two main evolutionary lineages: Clades A and B in Fig. 2. Clade A was recovered with low values of support, and contained the Common Green Racer *P. viridissima* and the rare *P. laticeps* forming Subclade A1, and the South American Vine Snakes *P. argentea* and *P. georgeboulengeri* composing Subclade A2, both with robust and unambiguous support values (Fig. 2). The remaining species of *Philodryas* grouped in the robustly supported Clade B, with *P. nattereri* placed as the sister group of five successive, robustly to unambiguously supported subclades, as follow: Subclade B2 composed by *P. mattogrossensis* and *P. erlandi*; Subclade B3 including the Southern Andean *P. chamissonis* as sister of the Argentinian species *P. baroni* and *P. trilineata*; Subclade B4 formed by the South American Green Racers *P. offersii* and *P. arnaldoi*; Subclade B5 composed only by the Brazilian Green Racer *P. aestiva*; and Subclade B6 formed by the “patagoniensis group” composed by *P. agassizii*, *P. livida*, *P. patagoniensis*, *P. psammophidea*, and *P. varia* (Fig. 2). Within the “patagoniensis group”, *P. varia* and *P. patagoniensis* on the one hand, and *P. psammophidea* nested with *P. livida* + *P. agassizii*, on the other hand, grouped together as sister clades, the former lacking statistical support values while the latter was robustly supported.

Our results indicate that the traditional taxonomic arrangement for Philodryadini does not reflect the topology of the phylogenetic tree. To determine a more accurate classification based on monophyletic groups, we propose below a revised classification for the tribe based on our phylogenetic results and on a diagnostic set of morphological characters.

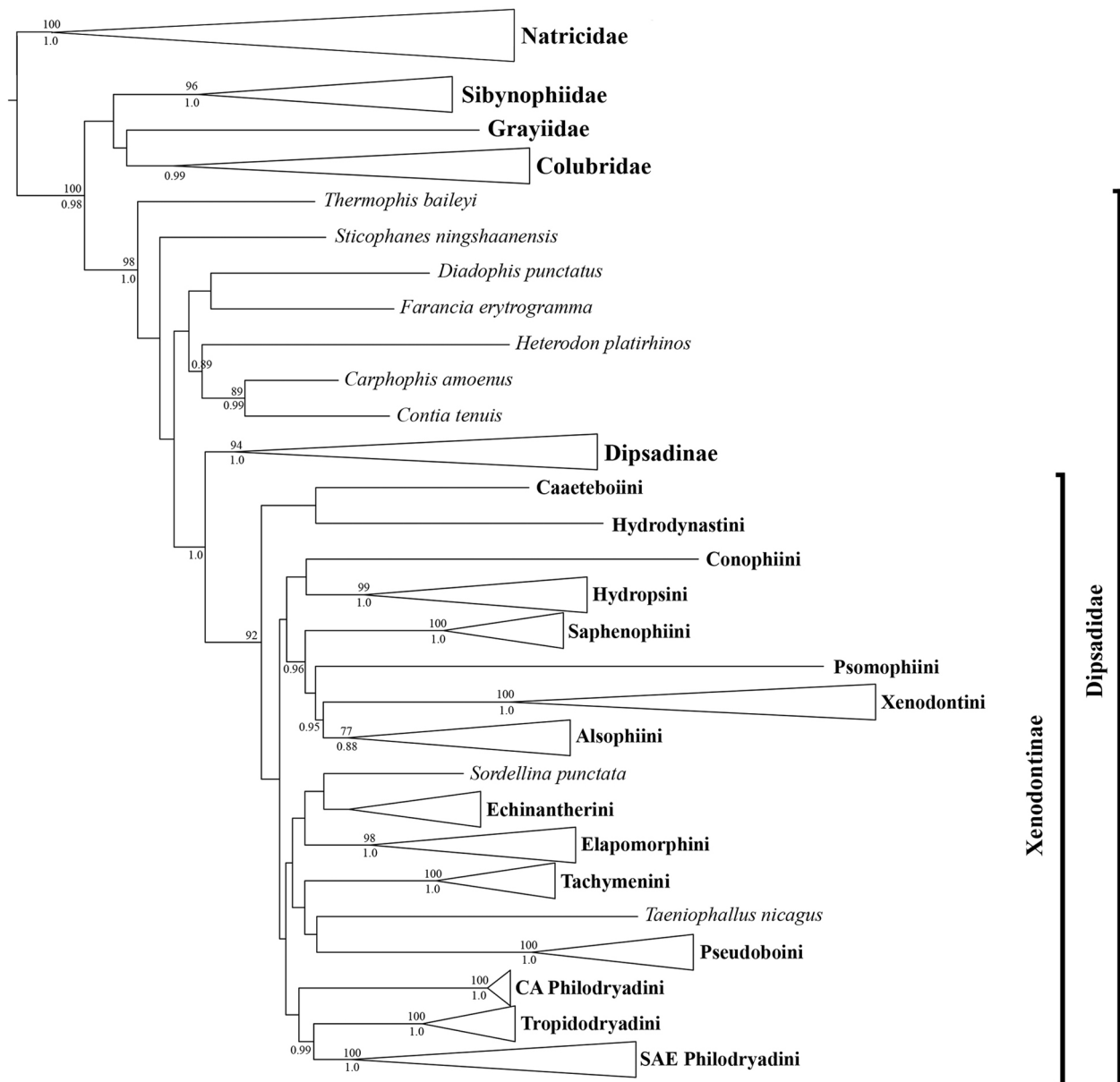


Figure 1. Maximum likelihood (ML) tree of Dipsadidae estimated using RAXML. Summary tree with collapsed terminals showing higher-level relationships. Numbers above and below branches indicate bootstrap and posterior probability support values, respectively. Bootstrap values below 70% and posterior probabilities below 85% are not shown. Abbreviations: CA = central Andean; SAE = southern and cis-Andean.

Systematic Account

Tribe Philodryadini Cope, 1886

Type-genus: *Philodryas* Wagler, 1930 by original designation and monotypy.

Type species: *Coluber olfersii* Lichtenstein, 1823.

Content: *Chlorosoma* Wagler, 1830 resurrected; *Ditaxodon* Hoge, 1958; *Philodryas* Wagler, 1830; *Xenoxybelis* Machado, 1993 resurrected.

Diagnosis: Members of the tribe Philodryadini can be distinguished from the other xenodontine genera by the following combination of characters: hemipenis bilobed, semicalyculate and semicapitate; large body calyces cov-

ering both medial and distal portions of the asulcate side of the hemipenial body and lobes (Figs. 3–4); maxillary dentition diacranterian and opisthoglyphous, with a deep groove that opens laterally.

Geographical distribution: most of the Cis-Andean portion of South America, from southern Colombia, Venezuela, Guianas, Ecuador, Peru, Brazil, Bolivia, Paraguay, Uruguay, and Argentina, and in the Trans-Andean portion of the southern Andes in Chile.

Genus *Philodryas* Wagler, 1930

Type species: *Coluber olfersii* Lichtenstein, 1823.

Synonyms: See Wallach *et al.* (2014) for a complete list of generic synonyms.

Content (16 species): *Philodryas aestiva* (Duméril, Bibron & Duméril, 1854), *Philodryas agassizii* (Jan, 1863), *Philodryas arnaldoi* (Amaral, 1932), *Philodryas boliviana* Boulenger, 1896, *Philodryas baroni* Berg, 1895, *Philodryas chamissonis* (Wiegmann, 1835), *Philodryas cordata* Donnelly & Myers, 1991, *Philodryas erlandi* Lönnberg, 1902, *Philodryas livida* (Amaral, 1923), *Philodryas mattogrossensis* Koslowsky, 1898, *Philodryas nattereri* Steindachner, 1870, *Philodryas olfersii* (Lichtenstein, 1823), *Philodryas patagoniensis* (Girard, 1858), *Philodryas psammophidea* Günther, 1872, *Philodryas trilineata* (Burmeister, 1861), and *Philodryas varia* (Jan, 1863).

Diagnosis: *Philodryas* can be distinguished from the other Philodryadini genera by the following combination of characters: Hemipenial body much longer than the lobes (more than twice the length), with the asulcate side of the hemipenial body covered with two parallel rows of

enlarged body calyces on most or all its surface (Figs. 3-4); dentary teeth equal in size (significantly enlarged dentary teeth in *Ditaxodon*); ventral scales smooth (keeled in *Chlorosoma*); buccal epithelium cream or white.

Geographical distribution: Same as the tribe.

Etymology: Donnelly & Myers (1991: 46) argued convincingly that the meaning of the generic name *Philodryas* is “friendly tree nymph,” being a feminine gender resulting from the combination of the Greek words *Philos-* (noun, φίλος, meaning “friend or friendly”) and *-Dryas* (noun, Δρῦᾶς, meaning “tree nymph”).

Genus *Chlorosoma* Wagler, 1830 resurrected

Type species: *Coluber viridissimus* Linnaeus, 1758, by original designation and monotypy.

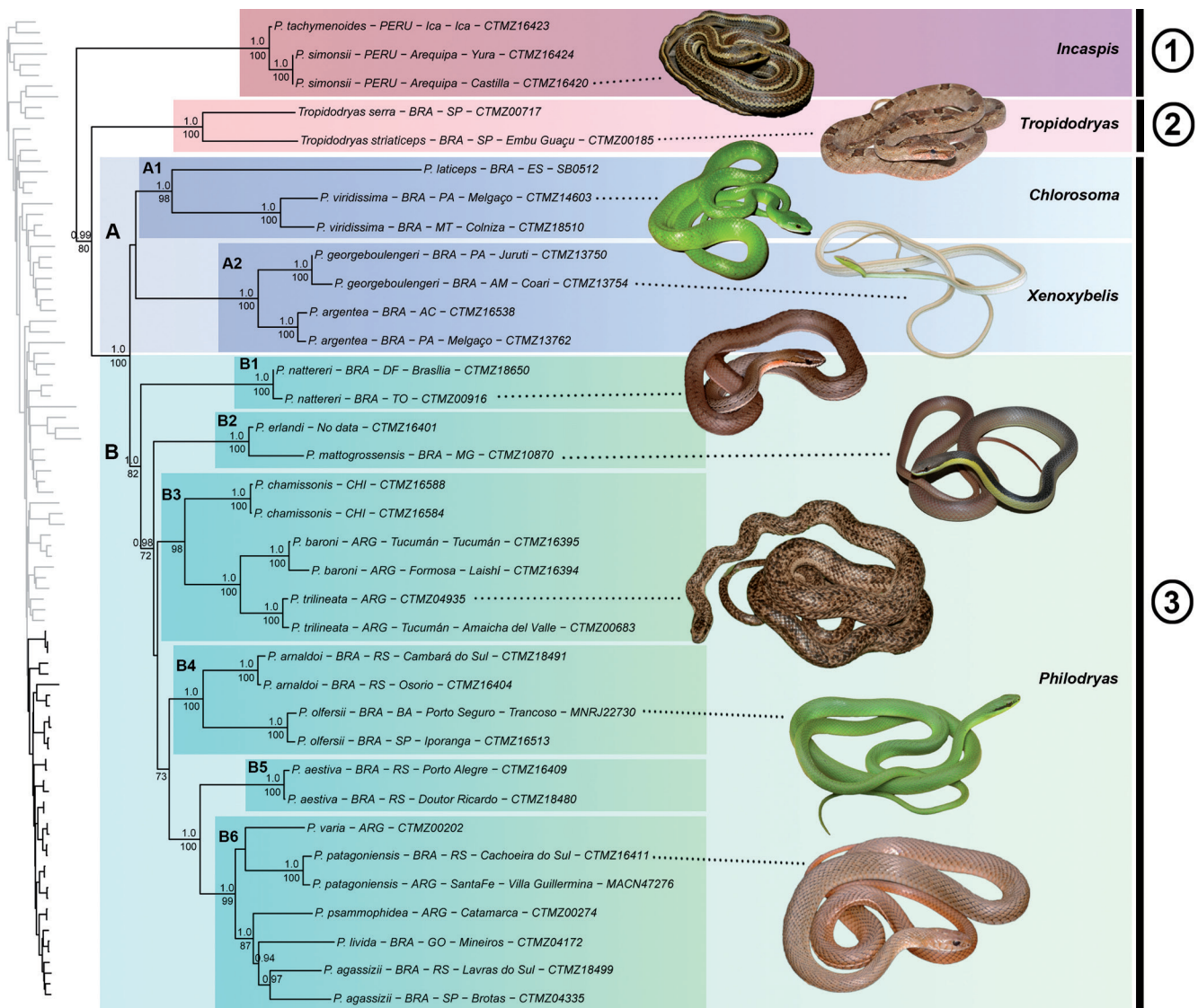


Figure 2. Maximum likelihood (ML) tree estimated using RAXML, showing only the relationships of Incaspini (1), Tropidodryadini (2), and Philodryadini (3). Terminal names on the left are presented following nomenclature in current literature, while generic and tribal arrangements on the right show our changes in the classification of Philodryadini. Numbers above and below branches indicate posterior probability and bootstrap support values, respectively. Bootstrap values below 70% and posterior probabilities below 85% are not shown.

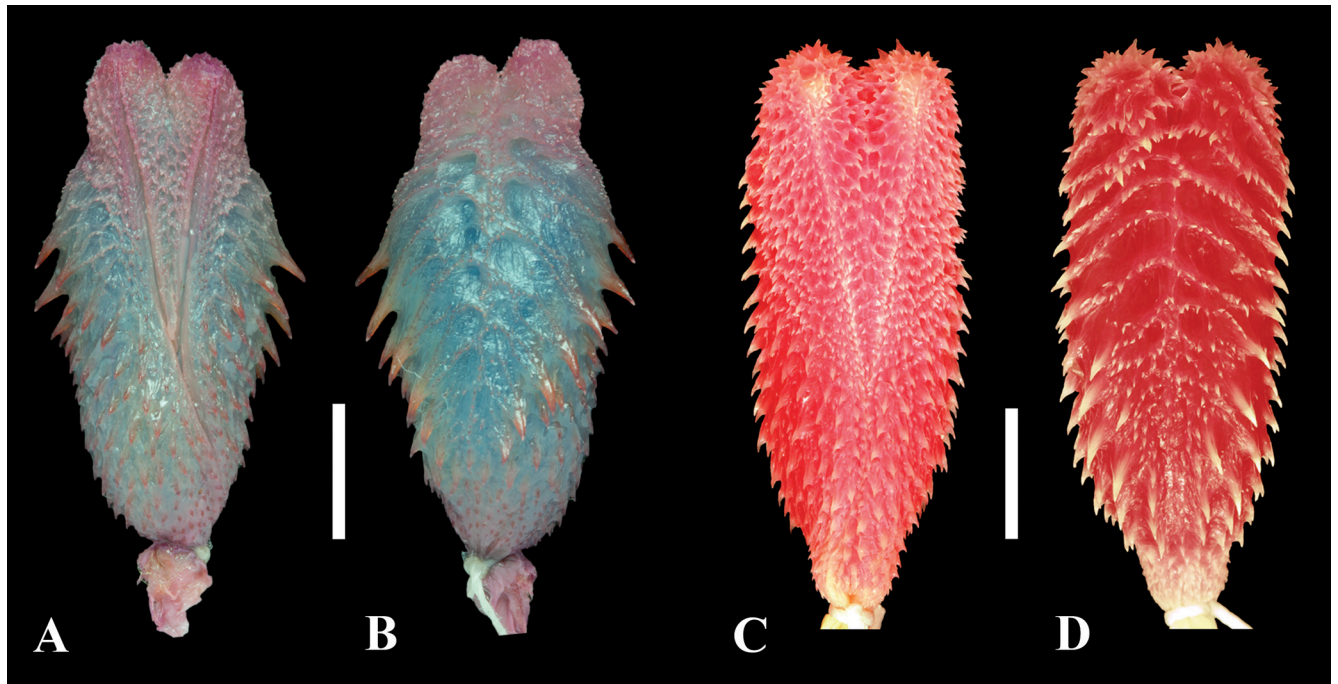


Figure 3. Hemipenes of *Chlorosoma viridissimum* (MUSM 2403) in A and B, and *Incaspis amarum* (FHGO 4749) in C and D. Photographs in A and C are in sulcate views, and photographs in B and D are in asulcate views. Scale bars: 5 mm.

Content: (two species) *Chlorosoma laticeps* (Werner, 1900) new combination; *Chlorosoma viridissimum* (Linnaeus, 1758).

Diagnosis: *Chlorosoma* can be distinguished from the other genera of Philodryadini by the following combination of characters: ventral and subcaudal scales strongly

angulated laterally (keeled); ontogenetic change in color pattern, with juveniles exhibiting dark chevrons throughout the body dorsum and adults changing to a homogeneously green dorsum; ventral surface with a yellow, white or cream gular region (excluding infralabial scales) and green venter and tail; short hemipenes with reduced lateral enlarged spines.

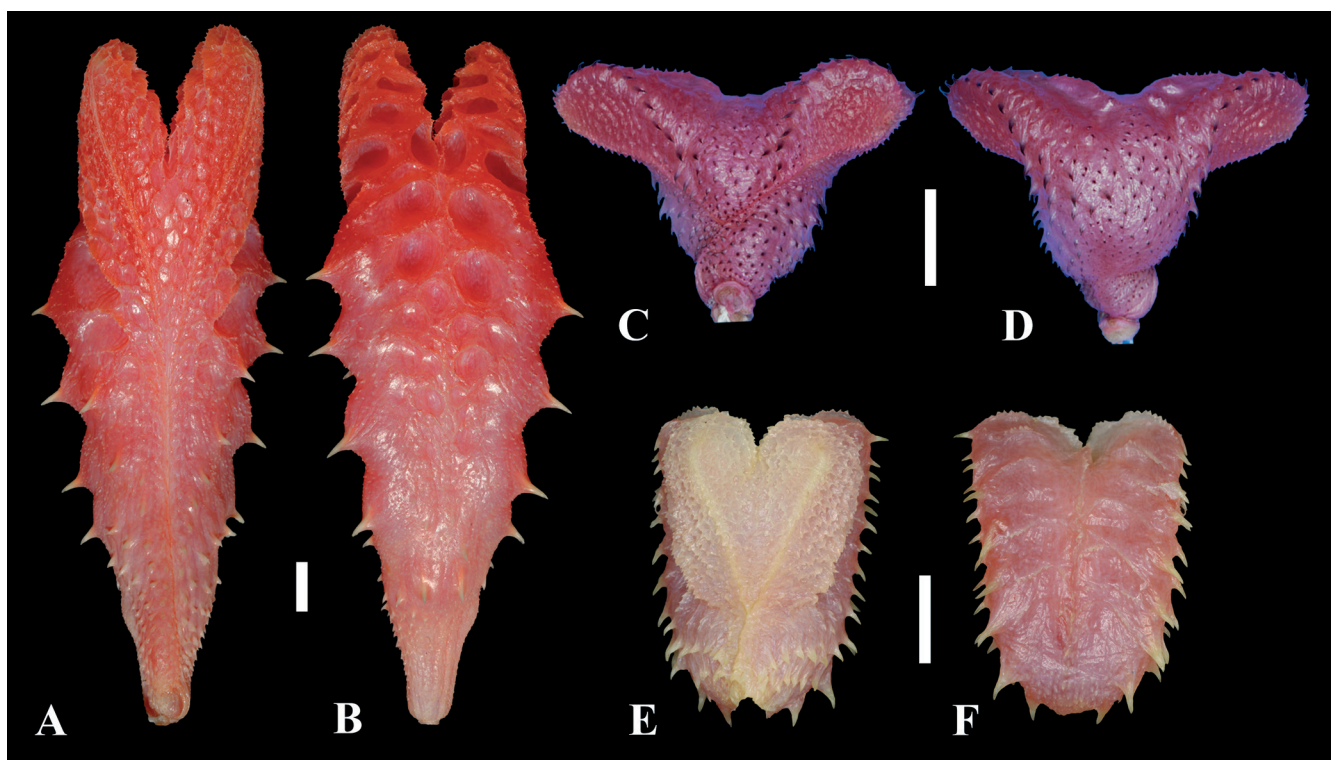


Figure 4. Hemipenis of *Philodryas chamissonis* (MNHN 3807) in A and B, *Tropidodryas serra* (MNRI 7354) in C and D, and *Xenoxybelis argenteus* (BMNH 1994.7000) in E and F. Photographs in A, C, and E are in sulcate views, and photographs in B, D, and F are in asulcate views. Scale bars: 5 mm.

Geographical distribution: *Chlorosoma viridissimum* occurs in the eastern lowlands of northern and central South America, including Amazonian forests of Colombia, Venezuela, Suriname, Guyanas, Ecuador, Peru, Brazil, and Bolivia. In Brazil this species also inhabits the ecotone between Amazonian and Cerrado biomes, and a single population is present in the lowland forest of the Atlantic coast of the Bahia state. *Chlorosoma laticeps* shows a disjunct distribution pattern, with records from central Bolivia in Santa Cruz and Cochabamba departments, and Southeastern Brazil in Espírito Santo, Minas Gerais and Santa Catarina states (Zaher et al., 2008).

Etymology: The generic name is neuter, being a combination of the Greek words *Chloros-* (adjective, χλωρός, meaning "bright green") and *-soma* (noun, σῶμα, meaning "body"), in reference to the overall bright green coloration of the body in these species. The gender of the name *Chlorosoma* is grammatically neuter (Amaral 1929a, b, c, 1932) since the meaning given by Wagler (1830) was of a "green snake." Therefore, the correct spelling for the type species of the genus is *Chlorosoma viridissimum*.

Comment: Wagler (1830) used the same contribution to erect the genera *Chlorosoma* and *Philodryas* for the species *Coluber viridissimus* Linnaeus 1758 and *Coluber olfersii* Liechtenstein 1823, respectively. Shortly after, Günther (1858), redefined the genus *Philodryas* to allocate *P. aestivus*, *P. dorsalis* (= *laltris*), *P. goudotii* (= *Ithycyphus*), *P. olfersii*, *P. serra* (= *Tropidodryas*), *Philodryas schottii* (= *patagoniensis*), and *Philodryas viridissimus*. Considering that Wagler (1830) described *Chlorosoma* before *Philodryas* on page 185, Amaral (1929a, b, 1932) decided to apply the Principle of Priority and assigned all species of *Philodryas* known at the time to the genus *Chlorosoma* (i.e., *C. aestivum*, *C. arnaldoi*, *C. burmeisteri* (= *trilineata*), *C. mattogrossense*, *C. olfersii*, *C. schottii* (= *patagoniensis*), *C. psammophideum*, and *C. viridissimum*). However, Parker (1932) pointed out that Günther's (1858) generic classification using the name *Philodryas* for these species had priority under the Principle of the First Reviser (Art. 24.2.2, ICZN 1999). Thus, the genus *Chlorosoma* is available for the recovered evolutionary lineage including *Philodryas viridissima* and *Philodryas laticeps*.

Genus *Xenoxybelis* Machado, 1993 resurrected

Type species: *Coluber argenteus* Daudin, 1803, by original designation.

Synonyms: *Oxybelis* Wagler, 1830; *Philodryas* Wagler, 1830.

Content: (two species) *Xenoxybelis argenteus* (Daudin, 1803); *Xenoxybelis boulengeri* (Procter, 1923) species name revalidated.

Diagnosis: *Xenoxybelis* can be distinguished from the other genera of Philodryadini by the following combination of characters: markedly elongated snout, forming

an acuminate and sharp head shape; large number of prediastemal maxillary teeth (16-21), followed by one or two grooved postdiastemal teeth; short heart-shaped hemipenes with a well-defined papillate longitudinal crest, formed by the confluence of the body calyces, that runs medially in the asulcate surface; lateral surfaces of hemipenes covered with two to four rows of well-developed enlarged lateral spines (Fig. 4).

Geographical distribution: Both species occur in the Amazonian region, from Colombia and Guianas to Bolivia and Paraguay (Cunha & Nascimento, 1978; Prudente et al., 2008).

Etymology: The generic name of the South American Vine snake *Xenoxybelis* is formed by the Greek words *Xenos-* (adjective, ξένος, meaning "different"), *-oxy-* (adjective, οξύς, meaning "sharp"), and *-belos* (noun, βέλος, meaning "dart"), in reference to their external similarity with the unrelated Neotropical Vine snake genus *Oxybelis* Wagler, 1830.

Comment: Zaher et al. (2009) and Grazziotin et al. (2012) placed *Xenoxybelis* and *Pseudablades* under the synonymy of *Philodryas*. With this nomenclatural act, *Philodryas boulengeri* Werner, 1909 and *Philodryas boulengeri* (Procter, 1923) became secondary homonyms (Grazziotin et al., 2012), resulting in the proposition of the new replacement name *georgeboulengeri* for the latter species. According to our phylogenetic results, returning *Philodryas georgeboulengeri* (Procter, 1923) to the revalidated genus *Xenoxybelis* eliminates the homonymy. Therefore, we revalidate the species name *Xenoxybelis boulengeri* (Procter, 1923).

Tribe Incaspidini, New tribe

Type-genus: *Incaspis* Donoso-Barros, 1974, by original designation, resurrected.

Type species: *Philodryas simonsii* Boulenger, 1900, by original designation.

Content: *Incaspis* Donoso-Barros, 1974, resurrected.

Diagnosis: Members of the tribe Incaspidini can be distinguished from the other genera of Xenodontinae by the following combination of characters: maxillae diacranterian and opisthodont, with ungrooved postdiastemal teeth; hemipenes significantly longer than wide (up to 3.5 times), with large shallow body calyces on upper half of the asulcate region, numerous small-sized lateral enlarged spines, and a well-defined constriction in the proximal region of the hemipenial body (Fig. 3).

Geographical distribution: Andean region in Southern Ecuador, Peru and possibly northern Chile.

Etymology: The singular of the genitive case of the second part of the tribe name (*aspis*) is *aspides*. Therefore, the correct spelling of the new tribe is Incaspidini.

Genus *Incaspis* Donoso-Barros, 1974, resurrected

Type species: *Philodryas simonsii* Boulenger, 1900, by original designation.

Content: (three species) *Incaspis amaru* (Zaher, Arredondo, Valencia, Arbeláez, Rodrigues & Altamirano-Benavides, 2014) new combination; *Incaspis simonsii* (Boulenger, 1900) new combination; *Incaspis tachymenoides* (Schmidt & Walker, 1943) new combination.

Diagnosis: Same as the tribe.

Geographical distribution: Same as the tribe.

Etymology: The genus name is a combination of the Quechua word *Inca* (adjective, meaning royalty) and the Greek word *-aspis* (noun, ἀσπίς, meaning venomous snake), in reference to the Andean region where the Inca Empire was established.

Comment: The generic name *Incaspis* was erected by Donoso-Barros (1974) to describe *Incaspis cercostropha*, which, along with *Dromicus angustilineatus* Schmidt & Walker, 1943 and *Dromicus inca* Schmidt & Walker, 1943, were shortly after placed under the synonymy of *Philodryas simonsii* Boulenger, 1900 by Thomas (1977). Although no tissue samples were available from *Incaspis amaru*, we allocate this species in the genus *Incaspis* since it shares all the diagnostic features listed above for the genus and the tribe. The occurrence of *I. amaru* in the same biogeographical region as *I. simonsii* and *I. tachymenoides* also supports its allocation in the tribe, which seems to be an endemic component of Central Andes.

DISCUSSION

As in most recent systematic studies, our analyses retrieve the highly diverse family Dipsadidae with strong support (Figueroa et al., 2016; Grazziotin et al., 2012; Pyron et al., 2011; Vidal et al., 2010; Zaher et al., 2009, 2018, 2019). Notwithstanding, our results from both ML and BI support the monophyly of most previously hypothesized xenodontine tribes (Zaher et al., 2009; Grazziotin et al., 2012), but do not recover well-established relationships between them (Fig. 1). One notable exception is the robustly supported clade formed by the Tropicodryadini and the redefined tribe Philodryadini (Figs. 1–2). Historically, a close relationship between members of the tribes Philodryadini and Tropicodryadini has already been advocated by several authors (Amaral, 1937; Dowling & Duellman, 1978; Ferrarezzi, 1994; Günther, 1858; Lobo & Scrocchi, 1994; Pyron et al., 2011; Vidal et al., 2010; Zaher et al., 2012, 2018, 2019; but see Grazziotin et al., 2012 and Pyron et al., 2013). However, none of these studies had adequate taxon sampling within *Philodryas*, reaching only a maximum of 58% of the known diversity of the tribe Philodryadini and lacking representation

of the Central Andean species (e.g., Pyron et al., 2011; Figueroa et al., 2016) (Table 2). Consequently, Pyron et al. (2011) retrieved a non-monophyletic Philodryadini, with *P. viridissima* clustering with *Tomodon* and *Hydropsini* instead of the other species of *Philodryas*. In contrast, Figueroa et al. (2016) recovered a highly supported clade composed by *P. chamissonis*, *P. trilineata*, and the genera *Xenopholis*, *Hydrodynastes*, and *Caeteboia*, while the remaining species of *Philodryas* grouped with *Sordellina punctata* and the Echinantherini. As pointed out by these authors, their topology most likely resulted from the absence of homologous molecular markers for these lineages, as they only used sequences for the mitochondrial gene *nd4* for *P. chamissonis* and *P. trilineata*, and a combination of *12S*, *16S*, *bdnf*, *cmos*, and *cytb* for the remaining species of *Philodryas*.

Pyron et al.'s (2011) and Figueroa et al.'s (2016) unexpected phylogenetic results highlight the necessity of a comprehensive taxon sampling to resolve the phylogenetic affinities within this group. Here, we expand both gene and taxon samplings for the group, reaching 83% of the known diversity of the former composition of Philodryadini. We also added for the first time critical central and Southern Andean lineages of *Philodryas* and the rare species *C. laticeps* (Table 2). Surprisingly, our results reveal that the central Andean species—represented by *Incaspis simonsii*, *I. tachymenoides*, and *I. amaru*—are a distinct lineage of Andean endemics while the genus *Tropicodryas* appears in a robustly supported clade as the sister group of all other southern and cis-Andean species of *Philodryas* (Fig. 2). Resurrection of *Incaspis* for the central Andean species, with its allocation in the new tribe Incaspidini, reflects their distinctiveness and uncertainties regarding their phylogenetic relationships within Xenodontinae, while highlighting the closer affinities revealed by the Tropicodryadini and the southern and cis-andean *Philodryas* (Fig. 1; Extended Fig. S2). Therefore, our results restrict Philodryadini to a widespread lineage of mostly lowland cis-Andean species, except for the trans-Andean *P. chamissonis*, which occurs in both low and high elevations throughout southern Andean region (Sallaberry-Pincheira et al., 2011). Further, Incaspidini represents a distinct lineage of endemic species mainly found in highlands of the central Andes of Ecuador and Peru.

Historically, a certain confusion has existed around the systematics of the species here allocated in the tribe Incaspidini, mainly because their characteristic ungrooved postdiastemal maxillary teeth led several authors to associate them with the opisthodont genera *Alsophis*, *Dromicus*, and *Leimadophis* (Amaral, 1929a, b, c; Parker, 1932; Peters, 1960; Thomas, 1977). Additionally, *P. chamissonis* also retains ungrooved postdiastemal (opisthodont) maxillary teeth, although its hemipenial morphology characterized by a very long hemipenial body and moderately long lobes closely approaches the one of the larger mainland cis-andean species *P. nattereri*, *P. psammophidea*, *P. baroni*, and *P. trilineata* (Zaher, 1999). *Philodryas chamissonis* was viewed accordingly as a morphological intermediate between the central Andean

opisthodont and the cis-Andean opisthoglyph species of *Philodryas* (Thomas, 1976; Lobo & Scrocchi, 1994; Zaher, 1999). However, our results show that the opisthodont condition found in the Incaspidini and in *P. chamissonis* owes to convergence rather than being a shared derived characteristic (Zaher et al., 2014).

The southern and cis-Andean radiation is recovered in our analyses as two sister Clades A and B (Fig. 2). The topology provides the basis for the resurrection of *Chlorosoma* and *Xenoxybelis*, for the Common Green Racers and South American Vine snakes, respectively. *Xenoxybelis* corresponds to a genus of highly specialized arboreal snakes that have been traditionally considered to be morphologically distinct from all the other Philodryadini. However, their uncertain position within the group led to its synonymization with the latter as a way to reinstate a monophyletic definition for the group (Grazziotin et al., 2012). Our expanded taxonomic coverage recovers a more stable phylogenetic hypothesis that allows the recognition of its morphological differences. Similarly, *Chlorosoma* corresponds to a vestigial clade of arboreal snakes that also harbors morphological differences from *Philodryas* (Clade B), including a short hemipenes and laterally keeled ventral scales.

The redefined genus *Philodryas* includes now 14 species that are retrieved in our analyses in six strongly supported subclades (Subclades B1 to B6 in Fig. 2). Subclades B1 and B2 include *Philodryas nattereri* and *P. erlandi* + *P. mattogrossensis*, respectively, two successive sister groups to the remaining Subclades B3-B6. Subclades B1 and B2 include species that occur throughout the open biomes of Brazil, Bolivia, Paraguay, and Argentina (Nogueira et al., 2019), reinforcing the view that cis-Andean Racers of the genus *Philodryas* originated in open areas in South America and only later occupied forested biomes, such as the Atlantic and Amazonian forests. Species from Subclade B2 have a unique coloration pattern of gradual change from anterior green or yellow to reddish brown in the rest of the body and tail (Cacciali et al., 2016; Thomas, 1976). This appears to represent a synapomorphic trait for this subclade.

Subclade B3 includes *P. chamissonis*, *P. baroni*, and *P. trilineata*, and it corresponds to a group of racers restricted to the southern part of the continent, with *P. chamissonis* reaching as a single dispersal event the eastern part of southern Andes. According to Thomas (1976) and Lobo & Scrocchi (1994), *P. baroni*, and *P. trilineata* are sister species, a hypothesis corroborated in our analysis.

Subclades B4, B5, and B6 include the commonest species of the genus, and these occur mostly in open and forested areas of the continent, east of the Andes and south of the Amazonian basin. The only exception is *P. olfersii*, whose range extends to parts of the Amazonian biome. Subclades B4 and B5 include the southern and southeastern Atlantic forest endemics *P. aestiva* and *P. arnaldoi*, and widespread *P. olfersii*; all three occur mainly in forested areas in South America.

Species in Subclade B6 inhabit both forested and open biomes. In this subclade, *P. varia* occurs in northern Argentina and Bolivia, while *P. patagoniensis* inhabits the southern and eastern parts of the continent, from northern Pará and Tocantins to Chubut in southern Argentina. In contrast, *P. psammophidea*, *P. livida*, and *P. agassizi* occur in the open biomes throughout the central and southern parts of the continent.

Redefined Philodryadini contains species with high relevance in public health (Sánchez et al., 2014; Weinstein et al., 2011). Records of envenomation exist for several species, including lethal cases for humans (Da Rocha et al., 2006; Weinstein et al., 2013). *Philodryas* has opisthoglyphous dentition, a venom delivery apparatus, and gland secretions containing venomous proteins and toxins (Modahl et al., 2016; Urra et al., 2015). This genus of South American opisthoglyphous snakes is responsible for most of the non-front fanged envenomations (Oliveira et al., 2017). Because most studies focusing on venom and envenomation of *Philodryas* were developed without a robust evolutionary context (Acosta et al., 2003; Da Rocha et al., 2006), they likely bypassed issues on intra and inter-specific variation and phylogenetic structure within species groups. Our phylogenetic hypothesis provides a more accurate evolutionary framework that will lead to a better understanding of venom variation and diversification in that group.

AUTHORS' CONTRIBUTIONS

JCA and HZ conceived the research project. JCA gathered the molecular data and performed the analyses; FGG contributed to the molecular analyses; JCA, HZ, and FGG wrote the manuscript; GJS, MTR, and SLB contributed intellectually to the project, revised and discussed the text; HZ funded and supervised the research project.

ACKNOWLEDGMENTS

We are in debt with the curators and institutions staff who granted us access to the samples for obtention of molecular evidence. We thank J. Battilana for her help during acquisition of molecular data. We thank F. Curcio and L.J. Vitt for providing photographs of *P. nattereri*, *X. boulengeri* and *P. olfersii* used in Fig. 2. We are grateful for the comments from two reviewers whose suggestions improved this manuscript. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001. FGG was supported by FAPESP (grants 2012/08661-3 and 2016/13469-5). HZ, MTR, and SLB are grateful to Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for continuing financial support. SLB and MTR were supported by FAPERGS and FAPESP (grants 2003/10335-8 and 2011/50146-6), respectively. This study was funded by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP grants 2011/50206-9 and 2016/50127-5) to HZ.

REFERENCES

- Acosta, O.; De Vila, I.I.; Peichoto, M.E.; Maruñak, S.; Ruíz, R.; Teibler, P.; Gay, C. & Rey, I. 2003. Edematogenic and myotoxic activities of the Duvernoy's gland secretion of *Philodryas olfersii* from the north-east region of Argentina. *Biocell*, 27: 363-370.
- Amaral, A. 1929a. Valor systemático de várias formas de ophidios neotropicos. Estudo sobre os ophidios neotropicos XVII. *Memórias do Instituto Butantan*, 4: 3-67.
- Amaral, A. 1929b. Lista remissiva dos ophidios do Brasil. Contribuição ao conhecimento dos ophidios do Brasil IV. *Memórias do Instituto Butantan*, 4: 69-125.
- Amaral, A. 1929c. Lista remissiva dos ophidios da região neotropical. Estudo sobre ophidios neotropicos XVIII. *Memórias do Instituto Butantan*, 4: 127-271.
- Amaral, A. 1932. Contribuição ao conhecimento dos ofídios do Brasil. VI. Uma nova espécie de colubrideo opisthoglypho, do genero *Chlorosoma* Wagler, 1930. *Memórias do Instituto Butantan*, 7: 99-101.
- Amaral, A. 1937. Contribuição do conhecimento dos ophidios do Brasil. 9. Nova especie de colubrideo opisthoglypho confundível com *Philodryas serra* (Schlegel 1837). *Memórias do Instituto Butantan*, 11: 205-212.
- Arredondo, J.C. 2012. *Revisão taxonômica do complexo Philodryas olfersii (Lichtenstein 1823) (Serpentes: Dipsadidae)*. Master Dissertation, Universidade de São Paulo, São Paulo, SP, Brazil.
- Barrio, A.; Laurent, R.F. & Thomas R.A. 1977. The status of *Philodryas subcarinatus* Boulenger (Reptilia, Serpentes, Colubridae). *Journal of Herpetology*, 11(2): 230-231.
- Cacciali, P.; Cabral, H.; Ferreira, V.L. & Köhler, G. 2016. Revision of *Philodryas mattogrossensis* with the revalidation of *P. erlandi* (Reptilia: Squamata: Dipsadidae). *Salamandra*, 52(4): 293-305.
- Cadle, J.E. 1984a. Molecular systematics of Neotropical xenodontine snakes: I. South American xenodontines. *Herpetologica*, 40: 8-20.
- Cadle, J.E. 1984b. Molecular systematics of Neotropical xenodontine snakes: II. Central American xenodontines. *Herpetologica*, 21-30.
- Cadle, J.E. 1984c. Molecular systematics of xenodontine colubrid snakes. III. Overview of xenodontine phylogeny and the history of New World snakes. *Copeia*, 1984: 641-652.
- Cunha, O. & Nascimento, E.F. 1978. Ofídios da Amazonia. X. – As cobras da região leste do Pará. *Publicações Avulsas Museu Paraense Emilio Goeldi*, 31: 1-218.
- Da Rocha, M.; Paixão-Cavalcante, D.; Tambourgi, D.V. & Furtado, E.M. 2006. Duvernoy's gland secretion of *Philodryas olfersii* and *Philodryas patagoniensis* (Colubridae): Neutralization of local and systemic effects by commercial bothropic antivenom (*Bothrops* genus). *Toxicon*, 47: 95-103.
- D'Agostini, F.M. 1998. Variação da foliose de *Philodryas aestivus* (Duméril, Bibron et Duméril, 1854) e a invalidação das subespécies (Serpentes, Colubridae, Xenodontinae, Philodryadini). *Biociências*, 6: 169-182.
- Donnelly, M.A. & Myers, C.W. 1991. Herpetological results of the 1990 Venezuelan expedition to the summit of Cerro Guaiquinima, with new tepui reptiles. *American Museum Novitates*, 3017: 1-54.
- Donoso-Barros, R. 1974. Descripción de una culebra del Perú. *Neotropica*, 20: 14-16.
- Dowling, H.G. & Duellman, W.E. 1978. *Systematic herpetology: a synopsis of families and higher categories*. HISS Publications (privated printed by the senior author). New York.
- Ferrarezzi, H. 1994. Uma sinopse dos gêneros e classificação das Serpentes (Squamata): II. Family Colubridae. Pp. 81-91. In: Nascimento LB, Tristão A, Cotta GA, (Eds.). *Herpetologia do Brasil 1*. Belo Horizonte, MG, Brazil: Fundação Biodiversitas e Fundação Ezequiel Dias.
- Figuroa, A.; McKelvy, A.D.; Grismer, L.L.; Bell, C.D. & Lailvaux, S.P. 2016. A species-level phylogeny of extant snakes with description of a new colubrid subfamily and genus. *PLoS ONE*, 11: 1-31.
- Graboski, R.; Arredondo, J.C.; Grazziotin, F.G.; da Silva, A.A.A.; Prudente, A.L.C.; Rodrigues, M.T.; Bonatto, S.L. & Zaher, H. 2018. Molecular phylogeny and hemipenial diversity of South American species of *Amerotyphlops* (Typhlopidae, Scolecophidia). *Zoologica Scripta*, 48(2): 139-156.
- Grazziotin, F.G.; Zaher, H.; Murphy, R.W.; Scrocchi, G.; Benavides, M.A.; Zhang, Y.P. & Bonatto, S.L. 2012. Molecular phylogeny of the new world Dipsadidae (Serpentes: Colubroidea): a reappraisal. *Cladistics*, 28: 437-59.
- Greene, H.W. & Jaksic, F.M. 1992. The feeding behavior and natural history of two Chilean snakes, *Philodryas chamissonis* and *Tachymenis chilensis* (Colubridae). *Revista Chilena de Historia Natural*, 65: 485-493
- Günther, A. 1858. *Catalogue of Colubrine snakes of the British Museum*. London, I-XVI, 281p.
- Hartmann, P.A. & Marques, O.A.V. 2005. Diet and habitat use of two sympatric species of *Philodryas* (Colubridae) in south Brazil. *Amphibia-Reptilia*, 26: 25-31.
- Jenner, J.V. & Dowling, H.G. 1985. Taxonomy of American xenodontine snakes: the tribe Pseudoboini. *Herpetologica*, 41(2): 161-172.
- Katoh, K.; Kuma, K.; Toh, H. & Miyata, T. 2005. MAFFT version 5: Improvement in accuracy of multiple sequence alignment. *Nucleic Acids Research*, 33: 511-518.
- 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.; Frandsen, P.B.; Wright, A.M.; Senfeld, T. & Calcott, B. 2016. Partition Finder 2: New methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Molecular Biology and Evolution*, 34: 772-773.
- Lobo, F. & Scrocchi, G. 1994. Osteología craneal del género *Philodryas* (Serpentes: Colubridae). *Cuadernos de Herpetología*, 8(1): 104-111.
- Machado, S.R. 1993. A new genus of Amazonian vine snake (Xenodontinae: Alsophiini). *Acta Biologica Leopoldensia*, 15: 99-108.
- Maglio, V.J. 1970. West Indian xenodontine colubrid snakes: their probable origin, phylogeny, and zoogeography. *Bulletin of the Museum of Comparative Zoology*, 141: 1-54.
- Marques, O.A.V.; Sawaya, R.J.; Stender-Oliveira, F. & Franca-Marques, F.G.R. 2006. Ecology of the colubrid snake *Pseudablabe agassizii* in south-eastern South America. *Herpetological Journal*, 16: 37-45
- Miller, M.A.; Pfeiffer, W. & Schwartz, T. 2010. *Creating the CIPRES Science Gateway for inference of large phylogenetic trees*. In: Proceedings of the Gateway Computing Environments Workshop (GCE), New Orleans. DOI
- Modahl, C.M.; Saviola A.J. & Mackessy, S.P. 2016. Venoms of Colubrids. In: Gopalakrishnakone, P.; Calvete, J. (Eds.). *Venom Genomics and Proteomics*. Dordrecht, Springer. p. 51-79. (Toxinology).
- Nogueira, C.C.; Argôlo, A.J.S.; Arzamendia, V.; Azevedo, J.A.; Barbo, F.E.; Bérnills, R.S.; Bolocho, B.E.; Borges-Martins, M.; Brasil-Godinho, M.; Braz, H.; Buononato, M.A.; Cisneros-Heredia, D.F.; Colli, G.R.; Costa, H.C.; Franco, F.L.; Giraud, A.; Gonzalez, R.C.; Guedes, T.; Hoogmoed, M.S.; Marques, O.A.V.; Montingelli, G.G.; Passos, P.; Prudente, A.L.C.; Rivas, G.A.; Sanchez, P.M.; Serrano, F.C.; Silva, N.J.; Strüssmann, C.; Vieira-Alencar, J.P.S.; Zaher, H.; Sawaya, R.J. & Martins, M. 2019. Atlas of Brazilian snakes: verified point-locality maps to mitigate the Wallacean shortfall in a megadiverse snake fauna. *South American Journal of Herpetology*, 14(sp): 1-274.
- Noonan, B.P. & Chippindale, P.T. 2006. Dispersal and vicariance: The complex evolutionary history of boid snakes. *Molecular Phylogenetics and Evolution*, 40: 347-358.

- Oliveira, J.S.; Sant'Anna, L.B.; Oliveira Junior, M.C.; Souza, P.R.M.; Andrade Souza, A.S.; Ribeiro, W.; Vieira, R.P.; Hyslop, S. & Cogo, J.C. 2017. Local and hematological alterations induced by *Philodryas olfersii* snake venom in mice. *Toxicon*, 132: 9-17.
- Parker, H.W. 1932. Some new or rare reptiles and amphibians from southern Ecuador. *Annals and Magazine of Natural History*, 9: 21-26.
- Peters, J.A. 1960. The snakes of the subfamily Dipsadinae. *Miscellaneous Publications of the Museum of Zoology, University of Michigan*, 114: 1-224.
- Prudente, A.L.C.; Silva, M.A.A.; Rocha, W.A. & Franco, F.L. 2008. Morphological variation in *Xenoxybelis boulengeri* (Procter, 1923) (Serpentes, Xenodontinae, Philodryadini). *Zootaxa*, 1743: 53-61.
- Pyron, R.A.; Burbrink, F.T. & Wiens, J.J. 2013. A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evolutionary Biology*, 13: 93.
- Pyron, R.A.; Burbrink, F.T.; Colli, G.R.; de Oca, A.N.; Vitt, L.J.; Kuczynski, C.A. & Wiens, J.J. 2011. The phylogeny of advanced snakes (Colubroidea), with discovery of a new subfamily and comparison of support methods for likelihood trees. *Molecular Phylogenetics and Evolution*, 58: 329-342.
- Rambaut, A.; Drummond, A.J.; Xie, D.; Baele, G. & Suchard, M.A. 2018. Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology*, 67(5): 901-904.
- Ronquist, F.; Teslenko, M.; Van der Mark, P.; Ayres, D.L.; Darling, A.; Höhna, S.; Larget, B.; Liu, L.; Suchard, M.A. & Huelsenbeck, J.P. 2012. MrBayes 3.2: Efficient bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, 61: 539-542.
- Sallaberry-Pincheira, N.; Garin, C.F.; González-Acuña, D.; Sallaberry, M.A. & Vianna, J.A. 2011. Genetic divergence of Chilean long-tailed snake (*Philodryas chamissonis*) across latitudes: conservation threats for different lineages. *Diversity and Distributions*, 17, 152-162.
- Sánchez, M.; Timoniuk, A.; Maruñak, S.; Teibler, P.; Acosta, O. & Peichoto, M. 2014. Biochemical and biological analysis of *Philodryas baroni* (Baron's Green Racer; Dipsadidae) venom: Relevance to the findings of human risk assessment. *Human & Experimental Toxicology*, 33: 22-31.
- Stamatakis, A. 2014. RAxML version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, 30: 1312-1313.
- Thomas, R.A. 1976. *A revision of the South American colubrid snake genus Philodryas* Wagler, 1830. Doctoral Thesis, Texas A & M University.
- Thomas, R.A. 1977. A new generic arrangement for *Incaspis* and mainland South American *Alsophis* and the status of two additional Peruvian species. *Copeia*, 1977(4): 648-652.
- Thomas, R.A. & Di Bernardo, M. 2001. *Philodryas pallidus* (Werner, 1926): A synonym of the colubrid snake *Liopholidophis varius* (Fischer, 1884) from Madagascar. *Journal of Herpetology*, 35(1): 120-122.
- Thomas, R.A. & Dixon, J.R. 1977. A new systematic arrangement for *Philodryas serra* (Schlegel) and *Philodryas pseudoserra* Amaral (Serpentes: Colubridae). *Pierce-Sellards Series*, 27: 1-20.
- Thomas, R.A. & Fernandes, R. 1996. The systematic status of *Platyinon lividum* Amaral, 1923 (Serpentes: Colubridae: Xenodontinae). *Herpetologica*, 52(2): 271-275.
- Thomas, R.A. & Johnson, J.D. 1984. *Philodryas varius* (Jan, 1863), a senior synonym of *Philodryas borellii* Peracca (Serpentes: Colubridae). *Journal of Herpetology*, 18(1): 80-81.
- Thomas, R.A.; Bérnills, R.S.; Moura-Leite, J.C. & Morato, S.A.A. 2006. Redescription of *Ditaxodon taeniatus* (Hensel, 1868) (Serpentes, Colubridae, Xenodontinae): variation, relationships, and distribution. *South American Journal of Herpetology*, 1: 94-101.
- Urra, F.A.; Pulgar, R.; Gutiérrez, R.; Hodar, C.; Cambiazo, V. & Labra, A. 2015. Identification and molecular characterization of five putative toxins from the venom gland of the snake *Philodryas chamissonis* (Serpentes: Dipsadidae). *Toxicon*, 108: 19-31.
- Vaidya, G.; Lohman, D.J. & Meier, R. 2011. SequenceMatrix: concatenation software for the fast assembly of multigene datasets with character set and codon information. *Cladistics*, 27: 171-180.
- Vences, M.; Guayasamin, J.M.; Miralles, A. & De la Riva, I. 2013. To name or not to name: criteria to promote economy of change in Linnaean classification schemes. *Zootaxa*, 3636: 201-244.
- 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(1): 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(3): 389-402.
- Wagler, J.G. 1830. *Natürliches System der Amphibien, mit vorangehender Classification der Saugthiere und Vogel. Ein Beitrag zur vergleichenden Zoologie*. München, J.G. Cotta schen Buchhandlung. vi + 354p.
- Wallach, V.; Williams, K.L. & Boundy, J. 2014. *Snakes of the world: a catalogue of living and extinct species*. Boca Raton, CRC Press.
- Weinstein, S.A.; Warrell, D.A.; White, J. & Keyler, D.E. 2011. Medically significant bites by "colubrid" snakes. In: *"Venomous" Bites from Non-Venomous Snakes, a critical Analysis of Risk and Management of "Colubrid" Snake Bites*, Elsevier. p. 33-270.
- Weinstein, S.A.; White, J.; Keyler, D.E. & Warrell, D.A. 2013. Non-front-fanged colubroid snakes: a current evidence-based analysis of medical significance. *Toxicon*, 69: 103-113.
- 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.; Arredondo, J.C.; Valencia, J.; Arbeláez, E.; Rodrigues, M.T. & Altamirano-Benavides, M. 2014. A new Andean species of *Philodryas* (Dipsadidae, Xenodontinae) from Ecuador. *Zootaxa*, 3785: 469-480.
- Zaher, H.; Grazziotin, F.G.; Cadle, J.E.; Murphy, R.W.; Moura-Leite, J.C. & Bonatto, S.L. 2009. Molecular phylogeny of the advanced snakes (Serpentes, Caenophidia), with an emphasis on South American Xenodontines: a revised classification and descriptions of new taxa. *Papéis Avulsos de Zoologia, São Paulo*, 49(11): 115-153.
- Zaher, H.; Grazziotin, F.G.; Graboski, R.; Fuentes, R.G.; Sánchez-Martínez, P.; Montingelli, G.G.; Zhang, Y-P. & Murphy, R.W. 2012. Phylogenetic relationships of the genus *Sibynophis* (Serpentes: Colubroidea). *Papéis Avulsos de Zoologia, São Paulo*, 52(12): 141-149.
- Zaher, H.; Murphy, R.W.; Arredondo, J.C.; Graboski, R.; Machado-Filho, P.R.; Mahlow, K.; Montingelli, G.G.; Bottallo-Quadros, A.; Orlov, N.L.; Wilkinson, M.; Zhang, Y-P. & Grazziotin, F.G. 2019. Large-scale molecular phylogeny, morphology, divergence-time estimation, and the fossil record of advanced caenophidian snakes (Squamata: Serpentes). *PLoS ONE*, 14: e0216148.
- Zaher, H.; Scrocchi, G. & Masiero, R. 2008. Rediscovery and redescription of the type of *Philodryas laticeps* Werner, 1900 and the taxonomic status of *P. oligolepis* Gomes, 1921 (Serpentes, Colubridae). *Zootaxa*, 1940: 25-40.
- Zaher, H.; Yáñez-Muñoz, M.H.; Rodrigues, M.T.; Graboski, R.; Machado, F.A.; Altamirano-Benavides, M.; Bonatto, S.L. & Grazziotin, F.G. 2018. Origin and hidden diversity within the poorly known Galápagos snake radiation (Serpentes: Dipsadidae). *Systematics and Biodiversity*, 1-29.

SUPPLEMENTARY INFORMATION

Available at: Figshare <http://doi.org/10.6084/m9.figshare.13061516>.

Extended Figure S1. Best scoring maximum likelihood (ML) tree estimated using RAxML. Numbers on nodes correspond to Bootstrap values.

Extended Figure S2. Maximum Clade Credibility Tree estimated using MrBayes. Numbers on nodes correspond to posterior probability values.

Extended Table S1. Accession and voucher numbers for the sequences of the taxa analyzed here. Codes in bold correspond to new sequences.

Extended Table S2. The partition schemes and models of evolution for the mitochondrial and nuclear genes as selected by PartitionFinder.

Extended Data S1. Concatenated molecular dataset.

Erratum

In the article “**Molecular phylogeny of the tribe Philodryadini Cope, 1886 (Dipsadidae: Xenodontinae): Rediscovering the diversity of the South American Racers**”, <http://doi.org/10.11606/1807-0205/2020.60.53>, published in the Journal **Papéis Avulsos de Zoologia**, Volume 60: e20206053,

In the Acknowledgments:

Where you read:

We are in dept with the curators and institutions staff who granted us access to the samples for obtention of molecular evidence. We thank J. Battilana for her help during acquisition of molecular data. We thank F. Curcio and L.J. Vitt for providing photographs of *P. nattereri*, *X. boulengeri* and *P. olfersii* used in Fig. 2. We are grateful for the comments from two reviewers whose suggestions improved this manuscript. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001. FGG was supported by FAPESP (grants 2012/08661-3 and 2016/13469-5). HZ, MTR, and SLB are grateful to Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for continuing financial support. SLB and MTR were supported by FAPERGS and FAPESP (grants 2003/10335-8 and 2011/50146-6), respectively. This study was funded by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP grants 2011/50206-9 and 2016/50127-5) to HZ.

Read it:

We are in dept with the curators and institutions staff who granted us access to the samples for obtention of molecular evidence. We thank C. Sarturi (PUCRS), J. Battilana (MZUSP), and N. da Rós (LETA) for their help during the acquisition of molecular data. We thank F. Curcio and L.J. Vitt for providing photographs of *P. nattereri*, *X. boulengeri* and *P. olfersii* used in Fig. 2. We are especially thankful to R. Bernils and R. Rabello-Reis (UFES) for the tissue sample of *Chlorosoma laticeps* (ICMBio/SISBio permit number 57585). We are grateful for the comments from two reviewers whose suggestions improved this manuscript. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001. FGG was supported by FAPESP (grants 2012/08661-3 and 2016/13469-5). HZ, MTR, and SLB are grateful to Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for continuing financial support. SLB and MTR were supported by FAPERGS and FAPESP (grants 2003/10335-8 and 2011/50146-6), respectively. This study was funded by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP grants 2011/50206-9 and 2016/50127-5) to HZ.