

Juan Camilo Arredondo Salgar

**Phylogenetic systematics and
taxonomic review of the snakes of the
tribe Philodryadini Cope, 1886
(Dipsadidae: Xenodontinae)**

**Sistemática filogenética e revisão taxonômica das
serpentes da tribo Philodryadini Cope, 1886
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Museu de Zoologia da Universidade de São Paulo to
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Advisor: Prof. Hussam El Dine Zaher, PhD

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A mis chicas Isa y Elena y a mi chico Ben

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Abstract

The tribe Philodryadini is constituted by a rich group of neotropical snakes that are highly diverse ecologically and morphologically. Currently, 24 species compose the tribe, and are recognized as common components of the ophidian diversity in several regions of South America. The species of Philodryadini exhibit two great geographical distribution patterns, with most species occurring in the lowlands of the cis-Andean region of the American continent, while another not so diverse group is distributed in the trans-Andean region of the central and southern Andes, in Ecuador, Peru and Chile. The richness of the tribe and its evolutionary relationships has varied greatly in recent years, mainly due to the recent formulation of diverse phylogenetic hypotheses based on molecular evidence. In the same way, in recent years many taxonomic complexes have been studied and the taxonomic status of several species has been clarified. However, many questions about the status of some complexes and phylogenetic relationships within the tribe are still unknown. To understand the evolutionary relationships between Philodryadini and the other Xenodontinae tribes we performed a phylogenetic analysis including molecular evidence of a representative sample of all tribes of the subfamily. Simultaneously, we evaluated the relationships within Philodryadini using DNA sequences from the vast majority of the species of the tribe described so far. Likewise, we performed a taxonomic revision of the tribe species, using a combination of morphological and molecular evidence. Our phylogenetic analyzes revealed that the tribe Philodryadini is a non-monophyletic group, and is currently composed of two different lineages of unrelated xenodontine snakes. To provide a phylogenetic structure that reflected the relations of the tribes in the interior of the subfamily, we erected a new tribe and a new genus to accommodate the group of species that constituted a completely different radiation of xenodontine snakes from the Andes. Within Philodryadini (*sensu stricto*), we recognize a particular pattern of diversification, with a first clade, composed of two groups, closely related to the clade that contains the type species of Philodryadini. To best represent the pattern of evolutionary diversification within the tribe, we restructured its generic composition by resurrecting the genera *Chlorosoma* and *Xenoxybelis*. Additionally, with our taxonomic revision we resolve the taxonomic status of three species complexes and recognize four taxa previously located in the synonymy of *Philodryas*. With our study,

the relationships within Philodryadini are now better understood and their diversity is currently consisted of three genera and 24 species.

Keywords: *Philodryas*, Species Complex, Morphology, Molecular Systematics, Hemipenis.

Resumo

A tribo Philodryadini é composta por um rico grupo de serpentes neotropicais altamente diversas ecológica e morfologicamente. Na atualidade, 24 espécies fazem parte da tribo, sendo amplamente reconhecidas como um dos componentes comuns da diversidade de ofídio-fauna de América do Sul. As espécies que fazem parte de Philodryadini apresentam dois grandes padrões de distribuição geográfica, sendo que a grande maioria das espécies ocorrem nas terras baixas da região cis-Andina do continente americano, enquanto que um outro grupo não tão diverso distribui-se na região trans-Andina dos Andes centrais e do Sul, no Equador, Peru e Chile. O conhecimento da diversidade da tribo e das suas relações evolutivas tem variado muito nos últimos anos, principalmente pela recente formulação de diversas hipóteses filogenéticas baseadas em evidência de biologia molecular. Do mesmo jeito, muitos complexos taxonômicos têm sido abordados recentemente e o status taxonômico de várias espécies esclarecido. No entanto, ainda se desconhecem muitas questões sobre o status de alguns complexos e as relações filogenéticas do interior da tribo. Para entender as relações evolutivas entre Philodryadini e as demais tribos de Xenodontinae realizamos uma análise filogenética incluindo evidência molecular de uma amostra representativa de todas as tribos da subfamília. Simultaneamente, avaliamos as relações ao interior de Philodryadini empregando sequências de ADN da grande maioria das espécies da tribo descritas até o momento. De igual forma, realizamos uma revisão taxonômica das espécies da tribo, empregando uma combinação de variáveis morfológicas e moleculares. As nossas análises filogenéticas mostraram que a tribo Philodryadini é um grupo não monofilético, estando na atualidade composto por duas linhagens diferentes de serpentes xenodontineas não relacionadas. Para fornecer uma estrutura filogenética que refletisse as relações das tribos no interior da subfamília, erigimos uma nova tribo e um gênero novo para acomodar o grupo de espécies que constituem uma radiação completamente diferente de serpentes xenodontineas dos Andes. Já no interior de Philodryadini (*sensu stricto*), reconhecemos um padrão de diversificação particular, com um primeiro clado, composto por dois grupos (as cobras cipó e as cobras de focinho afiado da Amazônia), estreitamente relacionado com o clado que contem a espécie tipo de Philodryadini. Pra melhor representar o padrão de diversificação evolutivo no interior da tribo, reestruturamos a sua composição genérica ao ressuscitar os gêneros *Chlorosoma* e

Xenoxybelis. Adicionalmente, com a nossa revisão taxonômica reconhecemos o status taxonômico de três complexos de espécies e reconhecemos a validade de quatro táxons previamente localizadas na sinonímia de *Philodryas*. Com o nosso estudo, as relações no interior da tribo Philodryadini ficaram melhor resolvidas e a sua diversidade ficou constituída por três gêneros e 24 espécies.

Palavras-chave: *Philodryas*, Complexo de Especies, Morfologia, Sistemática Molecular, Hemipenes.

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General Introduction

Neotropical snakes of the family Dipsadidae Bonaparte, 1838 are one of the most diverse groups of snakes in the planet (> 700 spp.). Although its monophyly is largely supported by both molecular and morphological evidence (Grazziotin *et al.*, 2012; Zaher *et al.*, 1999, 2009, 2019), interrelationships within the family are still controversial (Pinou *et al.*, 2004; Vidal *et al.*, 2010; Zaher *et al.*, 2009, 2019). Three subfamilies are commonly recognized within Dipsadidae: Carphophiinae Zaher *et al.*, 2009, Dipsadinae Bonaparte, 1838, and Xendontinae Bonaparte, 1845 (Pinou *et al.*, 2004; Vidal *et al.*, 2007; 2010; Zaher *et al.*, 2009). The subfamily Xenodontinae, currently with more than 350 species, presents a distributional pattern with most of its diversity occurring in South America, with a few genera and species inhabiting Central and North America (Wallach, Williams & Boundy, 2014). Xenodontine snakes exhibit a wide ecological diversity, with terrestrial, arboreal, fossorial and aquatic species, occurring in all available habitats in the tropical Americas. Likewise, members of this subfamily show a wide morphological diversity, with a variety of forms, sizes and color patterns (Cadle 1985, Cadle & Greene, 1994).

Phylogenetic relationships within Xenodontinae have been studied intensively in recent years (Figuroa *et al.*, 2016; Grazziotin *et al.*, 2012; Pyron *et al.*, 2011; Vidal *et al.*, 2007; 2010 Zaher *et al.*, 2009, 2019), and currently it is composed by 15 tribes, which are: Alsophiini, Amnesteophiini, Caaeteboiini, Conophiini, Echinantherini, Elapomorphini, Hydrodynastini, Hydropsini, Philodryadini, Pseudoboini, Psomophiini, Saphenophiini, Tachymenini, Tropidodryadini and Xenodontini (Myers, 2011; Grazziotin *et al.*, 2012; Zaher *et al.*, 2009; 2018; 2019). Our study group is focused in the South American Racers, tribe Philodryadini Cope, 1886. Originally, the tribe Philodryadini was erected to contain the species of the genera *Bucephalus*, *Callirhinus*, *Chrysopelea*, *Dromophis*, *Ichthyocyphus*, *Jaltris*, *Malpolon*, *Philodryas*, and *Tropidodryas* (Cope, 1886). Nevertheless, the composition of this tribe varied notoriously through time (Cadle, 1984; Jenner & Dowling, 1985; Machado, 1993; Maglio, 1970), until recently, when Zaher *et al.* (2009) and Grazziotin *et al.* (2012)

redefined the tribe to contain only the genera *Ditaxodon* Hoge, 1958 and *Philodryas* Wagler, 1830, synonymizing *Pseudablabe*s Boulenger, 1896 and *Xenoxybelis* Machado, 1993 under *Philodryas*.

Philodryadini is currently composed by 24 species, with the monotypic *Ditaxodon taeniatus* (Peters, 1868) and the diverse *Philodryas*, which comprise *Philodryas aestiva* (Duméril, Bibron & Duméril, 1854), *Philodryas agassizii* (Jan, 1863), *Philodryas amaru* (Zaher et al. 2014), *Philodryas argentea* (Daudin, 1803), *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 georgeboulengeri* (Procter, 1923), *Philodryas laticeps* (Werner, 1900), *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 simonsii* (Boulenger, 1900), *Philodryas tachymenoides* (Schmidt & Walker, 1943), *Philodryas trilineata* (Burmeister, 1861), *Philodryas varia* (Jan, 1863), and *Philodryas viridissima* (Linnaeus, 1758). Members of the tribe Philodryadini constitute a common faunistic element in South America, with most species being widely distributed and covering most of the Biomes throughout the continent (Thomas, 1976). Species of Philodryadini are highly diverse ecologically and morphologically, inhabiting a broad variety of environments and Biomes through its distribution (Greene & Jaksic, 1992; Hartmann & Marques, 2005; Marques et al., 2006; Prudente *et al.*, 2008).

At the moment, there is not a single known character that characterizes and diagnoses the tribe Philodryadini (Grazziotin *et al.*, 2012). This is probably a product of the high levels of convergence present in the diagnostic characters typically employed in South American snakes, that led members of Philodryadini, a group with a wide diversity in ecology, physiology and morphology, to be related to different snake genera (*i.e.* species of *Alsophis*, *Conophis*, *Dromicus*, *Rhadinaea*, *Thamnodynastes*, *Tomodon*, and *Tropidodryas*; Cadle 1984). Additionally, many species of the tribe Philodryadini are currently involved in complicated taxonomic scenarios, mainly as species complexes with several subspecies (Arredondo 2012; Thomas, 1976; 1977). Recent taxonomical studies have resolved and clarified the apparently hidden diversity in several species complexes (Cacciali *et al.*, 2016; D'Agostini, 1998; Zaher *et al.*, 2008),

however, many of species with wide distributions in South America (*i.e.* *Philodryas offersii*) still await taxonomic review, since most are currently re defined as polytypic species (Thomas, 1976; Zaher *et al.*, 2008).

Herein, we present an extensive review of the systematics and taxonomy of a complex of the species belonging to the tribe Philodryadini. We use using both morphological and molecular evidence to disclose the actual diversity in the tribe. We revalidate three genera and a new tribe of Xenodontinae to allocate three species previously considered as *Philodryas*. Additionally, we resurrect and describe four species previously considered to be synonyms of several species of *Philodryas*.

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Chapter 1

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

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

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Abstract

South American racers, tribe Philodryadini, are a widespread, morphologically diverse and species-rich group of neotropical snakes with a large and obscure taxonomical and systematical history. Recent systematic studies of have not find congruent results on the understanding of the evolutionary history and the phylogenetic relationship among the members of Philodryadini, mainly because of lack of a representative sampling of its whole diversity. We presented the most complete phylogenetic analysis for Philodryadini, including evidence for 20 species (83 % of the total diversity), which six were not previously sampled for molecular sequences. We found that Philodryadini is not a monophyletic group, as it was composed by two different and unrelated lineages. We erected a new genus and tribe to accommodate the group of species that

constituted a completely different radiation of xenodontine Andean snakes. Within Philodryadini (*sensu stricto*) we retrieved a particular lineage diversification pattern, with two well supported clades (Common Green Racers and South American Sharpnose snakes) nested along the main lineage that contained the type species of *Philodryas*. In order to better represent the diversity of lineages inside the Philodryadini (*sensu stricto*), we restructure the generic composition of the tribe by resurrecting the genus *Chlorosoma* to accommodate *P. viridissima* and *P. laticeps* and the genus *Xenoxybelis*, with *P. argentea* and *P. georgeboulengeri* inside it. Philodryadini, as we redefined it, is composed by three genera and 20 species, mostly distributed in the cis-Andean portion of South America, except for *P. chamissonis* that occurs in trans-Andean portion of Chile.

Introduction

The South American racers, tribe Philodryadini Cope 1886, are a diverse and widespread group of snakes with an extensive variety of morphologies and ecological roles, from large, semiarboreal, and generalist species to small, secretive, and diet specialist species (Greene & Jaksic, 1992; Hartmann & Marques, 2005; Marques *et al.*, 2006). The diversity of this tribe (Table 1) is better represented on the cis-Andean portion of South America, with 20 species distributed from Colombia to Argentina, while only four species inhabiting the trans-Andean portions of Ecuador, Peru and Chile (Cacciali *et al.*, 2016, Graziotin *et al.*, 2012, Zaher *et al.*, 2014). The species of the genus *Philodryas* are relevant members of snake communities of most biomes of South America, since several species exhibit wide distributions and relative high abundances, and by the its medical importance related with snakebite envenoming (Assakura *et al.*, 1992; Da Rocha *et al.*, 2006; Nickerson & Henderson, 1976). As a result of its high diversity of species, varied morphologies, broad distributions and a variety of ecologies, the members of the tribe Philodryadini exhibit a large history of taxonomical confusion, evidenced as an extensive nomenclatural inflation for most of its species (Thomas, 1976, Zaher *et al.*, 2008, Wallach, Williams & Boundy, 2014).

The unpublished PhD thesis of Robert A. Thomas (1976) was the first large taxonomical review made for 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 *Philodryas* were made by Thomas (Thomas, 1977; Thomas & Dixon, 1977; Thomas & Di-Bernardo, 2001; Thomas & Fernandes, 1996; Thomas & Johnson, 1984) and several other authors (D'Agostini, 1998; Barrio *et al.*, 1977; Zaher *et al.*, 2008). Despite these relevant contributions on the taxonomy of the species of *Philodryas*, currently there are several taxonomic complex mainly involving species with wide distribution or without enough knowledge on their geographical and morphological variation (*e.i.* *P. aestiva*, *P. offersii*, *P. patagoniensis*, and *P. psammophidea*) (Thomas, 1976, Zaher *et al.*, 2008)

In the last decade, several authors included a few or several species of Philodryadini in their systematic studies, with miscellaneous results about the relationship of the tribe with the other members of Xenodontinae (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 with *Alsophis*, as previously stated by Maglio (1970), and according to his results *Philodryas* was more closely related with the South American genus *Xenodon*. Machado (1993), based on hemipenial evidence, allocated *Oxybelis argenteus* (Daudin, 1803) to a new xenodontine genus, *Xenoxybelis*; which along with *Pseudablabe agassizii* (Jan, 1863) were considered by Zaher (1999) to shared hemipenial characteristics with *Philodryas*, suggesting that this genus (as defined by Thomas & Fernandes, 1996) was paraphyletic respecting the first two genera. The first proposal that investigated the evolutionary relationships within the genus *Philodryas*, based on osteological data and including a representative number of species (11 in total), was made by Lobo & Scrocchi (1994). They recovered a sister relationship between *P. mattogrossensis* and *P. varia* as well as between *P. baroni* and *P. [trilineata] burmeisteri*. Thomas and Fernandes (1996), defined the genus *Philodryas* based on a set of morphological traits, and placed the name *Platyinon* (Amaral, 1923) under the synonymy of *Philodryas*, including in it the species *P. livida*. As described by Zaher (1999), *Philodryas* content included two groups defined by hemipenial characters, the *offersii*-group and the *chamissonis*-group. More recently, molecular data allowed a better understanding of supra-generic relationships within new world colubroid snakes, where the proposal of Zaher *et al.* (2009) was the first to brought new insights on the natural subfamily and tribal ensembles of the South American dipsadids. This study, along with several posterior phylogenetic studies that included species of the tribe Philodryadini,

recovered it as a monophyletic and valid lineage (Grazziotin *et al.*, 2012; Pyron *et al.*, 2011; 2013; Vidal, Dewynter & Gower, 2010; Zaher *et al.*, 2009; 2018; 2019). Nevertheless, the sampled diversity of Philodryadini in these studies did not exceed the 55 % of the known species of the tribe (Table 3), and the systematic relationship of all members inside this tribe remains unresolved (e.g., Thomas 1996; Zaher 1999; Zaher *et al.*, 2008; 2009).

Here, we provide a phylogenetic analysis based on a multilocus molecular database of an extensive sample of the species of the tribe Philodryadini (83 % of the known diversity). Additionally, we test the monophyly of the tribe by including in our analyses a significant sample of species of Dipsadidae, with representatives of 14 of the 15 recognized Xenodontinae tribes. We finally revalidate three genera and a new tribe of Xenodontinae snakes for several species previously considered as *Philodryas*.

Material and Methods

Taxon sampling, DNA extraction and sequencing

We based our analysis on a molecular dataset composed by 33 terminals in the ingroup and 59 terminals in the outgroup (Appendix 1). Our sampling for members of genus *Philodryas* (*sensu* Grazziotin *et al.*, 2012) comprised all species but three, *Philodryas amaru* Zaher *et al.*, 2014, *Philodryas boliviana* Boulenger, 1896, *Philodryas cordata* Donnelly & Myers 1991, which are only known by a few specimens of each respective type series (Donnelly & Myers, 1991; Wallach, Williams & Boundy, 2014; Zaher *et al.*, 2014). Unfortunately, we did not obtain sequences from the other genus of Philodryadini, *Ditaxodon* Hoge 1958. We used Natricidae (*Afronatrix anoscopus*, *Amphiesma stolatum*, *Natrix natrix*, and *Thamnophis sirtalis*) as an outgroup to root our trees.

We extracted DNA from liver, muscle, scales, or shed skins, using Phenol-Chloroform method or PureLink® Genomic DNA kit (ThermoFisher, MA, USA). The sequence fragments were amplified via polymerase chain reaction (PCR) using the primers bdnf and nt3 as described by Noonan and Chippindale (2006), 12S and c-mos as described

by Zaher *et al.* (2009); *cytb* as described by Graziotin *et al.* (2012), and *cox1* as described by Graboski *et al.* (2018).

We employed standard protocols in the elaboration of PCRs, with minimal modifications or adjustments to improve the efficiency of the amplifications as follows: adding 10% of Trehalose 100 for 12S, *cytb* and COI, 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 ExoSap protocol - shrimp alkaline phosphatase and exonuclease I- (GE healthcare, Piscataway, NJ) and the sequences were processed using the DYEnamic ET Dye Terminator Cycle Sequencing Kit in a MegaBACE 1000 automated sequencer (GE healthcare) following manufacturer's protocols. We checked forward and reverse strands, and when necessary the chromatographs were edited manually. We performed the assemble and generated the consensus sequences using Geneious 6.1.8 (<http://www.geneious.com>, Kearse *et al.* 2012).

Sequence and phylogenetic analyses

We used MAFFT 1.3.6 (Kato 2013), as implemented in Geneious, to align all sequences. The rRNA gen 12S was aligned under the E-INS-i algorithm, while the protein-coding genes *bdnf*, *cmos*, *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 (Vaidya, Lohman & Meier, 2011).

We used PartitionFinder 2 (Lanfear *et al.*, 2016) to choose the models of molecular evolution for our database and employed two different analysis to comparing models. The first analysis employed the Akaike Information Criterion with correction (AICc) allowing the selection of models of molecular evolution implemented in RAxML 8.2.3 (Stamatakis 2014) without any correction for proportion of invariant sites and defined the branch lengths as unlinked and the greedy search option. In the second analysis we employed the Bayesian Information Criterion (BIC), allowing the selection using the

models of molecular evolution implemented in MrBayes 3.1.2, and defined the branch lengths as linked and the greedy search option. We divided our molecular data set in 16 partitions, treating the rRNA gene (12S) as a separate partition and partitioned all five protein-coding genes by codon positions.

We conducted a maximum likelihood (ML) analysis using RAxML 8.2.3 (Stamatakis 2014) 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 one thousand bootstrap iterations to estimate branch support (BS). We also conduct a Bayesian Inference phylogenetic analysis (BI) using MrBayes 3.2.5 (Ronquist *et al.*, 2011) with four independent runs, 20 millions of generations and sampling trees every 1000 generations. We estimated the maximum clade credibility tree (MCT) and branch support as values of Bayesian posterior probability (PP) after discarding a sample of trees (burn-in), which along with the check of the effective sample size (ESS) of parameters were evaluated in Tracer 1.7.1 (Rambaut *et al.* 2014). Both ML and BI phylogenetic analysis were carried out on the CIPRES Science Gateway (<http://www.phylo.org>, Miller *et al.* 2010). Our phylogenetic analyses were rooted in *Natrix natrix* (Linnaeus 1758), a species of Natricidae (Bonaparte 1838). In order represent robustness of the evaluated clades in the phylogenies obtained, we categorized the bootstrap and posterior probability values of support in four different categories: maximal support, with BS of 100% and PP of 1; strongly supported with BS between 80 and 99 % and PP values higher than 0.90; moderately supported with BS between 70 and 80 % and PP values between 0.8 and 0.90; and weakly supported with BS and PP values lower than 70 % and 0.8, respectively. We avoid taxonomic instability and inadequate classification schemes of non-natural groups, when defining, describing and naming evolutionary lineages revealed in our analyses, by following the Taxon Naming Criteria (TNCs) of Vences *et al.* (2013).

Results

We produced 179 DNA sequences for six genes for 20 species of Philodryadini and two of Tropicodryadini (*sensu* Grazziotin *et al.* 2012 and Zaher *et al.* 2009, respectively), which 92 sequences were from three mitochondrial genes (12s, cytb, and cox1) and 87 sequences were from three nuclear genes (bdnf, cmos, and nt3)

(Appendix 1). Additionally, we include a total of 300 sequences from GenBank for the six genes (Appendix 1), of which 243 were from Dipsadidae and 57 were from members of four closely related colubroid families (Colubridae, Grayiidae, Natricidae, and Sibynophiidae). Within Dipsadidae, 31 sequences were from basal members of the family (*Carphophis amoenus*, *Contia tenuis*, *Diadophis punctatus*, *Farancia erytrogramma*, *Heterodon platirhinos*, *Sticophanes ningshaanensis*, and *Thermophis baileyi*), 64 sequences were from Dipsadinae, and 148 sequences were from a significant sample (26 genera and 30 species) of 12 tribes of Xenodontinae (sensu Graziotin *et al.*, 2012) (Appendix 1). Our dataset comprised a concatenated matrix of 4433 base pairs of aligned sequences, which 510 were from 12S, 1107 from cox1, 997 from cytb, 710 from bdnf, 586 from cmos, and 523 from nt3. We obtained 14 partitions with PartitionFinder for the RAxML analysis and 12 partitions for the MrBayes analysis; these partitions along with the chosen model for each partition are presented in the Table 2.

The topologies of the best scoring ML tree and the MCT were very similar at the higher-level relationships, with Colubridae, Natricidae, Sibynophiidae, and Grayiidae recovered as monophyletic lineages (Appendix 2A-C, Figure 1). However, the position of Grayiidae varied between ML and BI topologies, placed as sister of Colubridae in the first and as sister of the clade formed for Colubridae and Sibynophiidae in the latter (Appendix 2C, Figure 1). Within Dipsadidae, *Thermophis baileyi* and *Sticophanes ningshaanensis* were retrieved as the successive sister groups of the all members of Dipsadidae, in both ML and BI topologies (Figure 1). Nevertheless, our phylogenetic analyses of ML and BI showed different arrangements in the remain dipsadid lineages. A clade formed by *Contia tenuis* and *Carphophis amoenus* was strongly supported in both topologies. This clade has *Heterodon platirhinos* as its sister group, however its support was moderate in BI and weak in ML (Appendix 2C, Figure 1). *Diadophis punctatus* and *Farancia erytrogramma* were nested in a clade weakly supported in the ML tree, but these species were not closely related in the BI tree, with *F. erytrogramma* being part of a polytomy with the clade formed by *Co. tenuis*, *Ca. amoenus*, and *H. platirhinos*, and a clade formed by *D. punctatus* and the remain dipsadids. The sister group relationship between *D. punctatus* and the other dipsadids is weakly supported. In both topologies, the two larger subfamilies of Dipsadidae, Dipsadinae and Xenodontinae, were retrieved forming a strongly supported sister group relationship.

Several nodes inside Dipsadinae were maximal or strongly supported and the relationship patterns exhibited in the ML and BI topologies were equal (Appendix 2C, Figure 1).

Higher-level relationship of Xenodontinae

Considering both phylogenetic analyses, most Xenodontinae tribes, except Philodryadini and Echinantherini, were recovered as monophyletic (Appendix 2C, Figure 1). A partial Echinantherini (without *Sordellina*) was found as monophyletic with low support by the BI, since *Taeniophallus nicagus* was retrieved as sister of the tribe Pseudoboini in the ML topology. The relationship pattern of the tribes inside Xenodontinae was completely different between the two phylogenetic analyses employed, where the BI tree had Caateboini nested to a large polytomy of nine clades containing the remain 13 tribes (Appendix 2C), and the ML tree had the clade Caateboini + Hydrodynastini nested to an arrangement of two large clades encompassing the remain 12 tribes (Figure 1). The nine clades (or terminals representing a single tribe) retrieved as a polytomy in the BI topology were: 1) Conophiini; 2) Hydrodynastini; 3) Pseudoboini; 4) Hydropsini; 5) Central Andes Philodryadini (CA Philodryadini); 6) Tachymenini; 7) a polytomy of *Sordellina punctata*, Elapomorphini, and Echinantherini; 8) a clade with Saphenophiini and Psomophiini as consecutive sister groups of Xenodontini + Alsophiini; and 9) Trepidodryadini + Southern Andes and Eastern Philodryadini (SAE Philodryadini) (Appendix 2C). On the other hand, the two large clades retrieved in the ML analysis were: 1) Conophiini + Hydropsini as sister group of the clade 8) recovered by the BI analysis; and 2) CA Philodryadini nested to Trepidodryadini + SAE Philodryadini, which formed a sister group to the clade composed by two additional small sister clades, part of Echinantherini nested to Elapomorphini, and Pseudoboini + *Taeniophallus nicagus* nested to Tachymenini. In both ML and BI analysis, the relationships between most of the tribes of Xenodontinae were weakly supported, with the exception of the clade formed by Trepidodryadini + SAE Philodryadini with 80 % of BS and 0.99 of PP (Figure 1).

Systematics of Philodryadini

Our analyses (ML and BI) retrieved the tribe Philodryadini as a non-natural group, with a clade composed by a couple of species (*Philodryas simonsii* and *Philodryas tachymenoides*) representing a different evolutionary lineage from a Central Andean radiation of Xenodontinae snakes. Without considering the Central Andean Philodryadini, the arrangement pattern and evolutionary relationships exhibited by the remain species of *Philodryas* (SAE Philodryadini) were exactly the same between the ML and BI topologies., thus the Figure 2 represents a pruned version of the ML topology that only shows a detailed relationships within the clades CA Philodryadini and SAE Philodryadini + Tropicodryadini.

The higher-level phylogenetic relationship inside the SAE Philodryadini clade revealed the presence of two large evolutionary lineages (Clades A and B in the Figure 2) related with a maximal support in both ML and BI analyses. The clade A contained the Common Green Racers, *P. viridissima* and *P. laticeps* (subclade A1, Figure 2), and the South American Sharpnose snakes, *P. argentea* and *P. georgeboulengeri* (subclade A2, Figure 2). Within the clade A, *P. viridissima* and *P. laticeps*, as well as, *P. argentea* and *P. georgeboulengeri* formed two subclades with maximal support each, however the relationship between them was weakly supported in both trees (Appendix 2B, Figure 2). On the other hand, the clade B was formed by the remaining species of *Philodryas*, with *P. nattereri* as the sister of a group composed by five different subclades, which we described as follows: the subclade B1 was composed by the sister species *P. mattogrossensis* + *P. erlandi*; the subclade B2 that included the Long-tailed Snake from Southern Andes, *P. chamissonis*, as sister of the subclade composed by the Argentinian species, *P. baroni* + *P. trilineata*; the subclade B3 formed by the South American Green Racers, *P. offersii* and *P. arnaldoi*; the subclade B4 formed by the Brazilian Green Racer, *P. aestiva*, as the sister group of the subclade B5, the “patagoniensis group”, which was composed by *P. agassizii*, *P. livida*, *P. patagoniensis*, *P. psammphidea*, and *P. varia*. Within the “patagoniensis group”, *P. varia* and *P. patagoniensis* grouped together (weakly supported) and were the sister of the subclade composed by *P. psammphidea* nested with *P. livida* + *P. agassizii*.

The arrangement of the consecutive basal sister groups (*P. nattereri* and *P. mattogrossensis* + *P. erlandi*) in the clade B were strongly supported in the BI topology, however, in the ML analysis the relationship of *P. nattereri* was strongly supported and

the subclade B1 was moderately supported. We also found a weakly supported relationship between the subclade B2 and the clade composed by the subclades B3, B4, and B5, as well as, between subclades B3 and the clade containing the subclades B4 and B5. We retrieved a maximal support between the subclades B4 and B5 and among the species within the subclades B1, B2 (strong support between *P. chamissonis* and *P. baroni* + *P. trilineata* in the ML tree), B3 and part of B5 in the BI analysis. Inside the subclade B5 (“*patagoniensis* group”), the subclades of *P. varia* + *P. patagoniensis* and *P. livida* + *P. agassizii* were weakly supported in the ML analysis, whereas the latter was strongly supported in the BI tree (Appendix 2B, Figure 2).

Among the results we produced in our phylogenetic analyses of the members traditionally associated to Philodryadini, three different clades required a new classification arrangement: 1) the clade of the Central Andes species (CA Philodryadini), currently assigned to *Philodryas*, do not constitute a closely related lineage to Philodryadini, and in order to correctly represent its phylogenetic position a different genus and tribe must be erected to accommodate it; and 2) the Southern Andes and Eastern members of tribe (SAE Philodryadini) showed a diversification pattern that reflects two additional evolutionary lineages (subclades A1 and A2), which must be named separately to represent a stable, adequate, and informative classification frame of the known diversity inside the tribe. All new lineages considered by us as candidates to bearing new names followed the three criteria of Vences et al. (2013) of monophyly, clade stability and phenotypic diagnosability.

Systematic Accounts

Tribe Philodryadini Cope, 1886.

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

Type species: *Coluber offersii* Lichtenstein, 1823.

Content: *Chlorosoma* Wagler, 1830 **resurrected**, *Ditaxodon* Hoge, 1958, *Philodryas* Wagler, 1830, and *Xenoxylbelis* Machado, 1993 **resurrected**.

Diagnosis: hemipenis bilobed, semicalyculated, semicapitate or noncapitate, body calyces covering medial and distal portions of the asulcate side of the hemipenial body and lobes; enlarged lateral spines extending distally, entering into the lobes;

diacranterian maxillae; opisthoglyphous dentition, with a deep groove that opens laterally; canthus rostralis extended laterally over the eye, denoting an expression of a frown of disgust.

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.

Comment: a clade with high support values in both phylogenetic inferences (98 % of BS and 1 of PP). Zaher *et al.* (2009) delimited the tribe phylogenetically and diagnosed it by having the “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” (Zaher *et al.* 2009:145).

Genus *Philodryas* Wagler, 1930

Type species: *Coluber offersii* Lichtenstein, 1823.

Synonyms: See Wallach, Williams and Boundy (2014) to a complete list of genus 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 offersii* (Lichtenstein, 1823), *Philodryas patagoniensis* (Girard, 1858), *Philodryas psammophidea* Günther, 1872, *Philodryas trilineata* (Burmeister, 1861), and *Philodryas varia* (Jan, 1863).

Diagnosis: The genus *Philodryas* can be diagnosed from all xenodontine genera by the combination of the following characteristics: dentary teeth equal in size, without notoriously enlarged teeth; ventral scales smooth; buccal epithelium cream to white; anterior projection of the snout only composed by soft tissues, not bones; and reduction

of the number of longitudinal rows of dorsal scales in the posterior portion of the body (except *P. agassizii*).

Geographical distribution: Same as the tribe.

Etymology: Donnelly and Myers (1991:46) revealed the correct etymology of the generic name *Philodryas*, as a feminine name product of the combination of the Greek words *Philos-* (noun, φίλος) that means “friend or friendly” and *-Dryas* (noun, Δρυάς) that means “tree nymph”, which in combination literally means “friendly tree nymph”.

Comment: a clade with maximal support values in both BI and ML trees (Figure 2). Due to the morphological similarity found among the members of Philodryadini and a large amount of species of snakes from Central and South America (*i.e.* species of *Alsophis*, *Conophis*, *Dromicus*, *Rhadinaea*, *Saphenophis*, *Thamnodynastes*, *Tomodon*, and *Tropidodryas*), a generalized confusion on the taxonomic and systematics have historically increased around the genus *Philodryas* and most of its species (Cadle 1984a). In fact, a significative number of taxa (ca. 600) have been described or related to *Philodryas*, even species from other continents (Thomas, 1976a; Thomas *et al.*, 2001). Currently, many of these names have already been placed in other genera, are synonyms, or belong to taxonomic complexes (Arredondo 2012; Thomas & Dixon, 1977; Zaher *et al.*, 2008).

Genus *Chlorosoma* Wagler, 1830 **resurrected**.

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

Synonyms: *Philodryas* Wagler, 1830.

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

Diagnosis: Ventral and subcaudal scales strongly angulated laterally (keeled). Ontogenetic change in color pattern, where juveniles exhibit dark chevrons thorough the body dorsum and adults lost this condition and present a dorsum homogeneously green. Adults with the gular region (excluding infralabial scales) along with the first ventral scales (up to 30) yellow, white or cream, and the remain ventral surface body and tail green.

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 disjunctive 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 and is a combination of the ancient Greek words *Chloros-* (adjective, χλωρός) that means “bright green” and *-soma* (noun, σῶμα) that means “body”, in reference to the bright green coloration covering most of the body of these species.

Comment: a clade that was recovered in both our trees (BI and ML) with the maximal support values (Figure 2). Wagler (1830), in the same scientific publication, erected the genera *Chlorosoma* and *Philodryas* to include the species *Coluber viridissimus* Linnaeus 1758 and *Coluber olfersii* Liechtenstein 1823, respectively. Shortly after, Günther (1858: xvi, 123-125), redefined the genus *Philodryas* to contain *Philodryas aestivus*, *Philodryas [altris] dorsalis*, *Philodryas [Ithycyphus] goudotii*, *Philodryas olfersii*, *Philodryas [Tropidodryas] serra*, *Philodryas schottii [patagoniensis]*, and *Philodryas viridissimus*. Considering that Wagler (1830: 185) in the same publication described first *Chlorosoma* and later *Philodryas*, Amaral (1929a; b; 1932) applied the Principle of Priority and assigned all species known in that time as *Philodryas* in 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, under the principle of the First Reviser (Art. 24.2.2, ICZN 1999) the Günther’s (1858) generic classification had priority and the genus-group name for these species was until now *Philodryas* (also see Parker, 1932). Our study recovered an evolutionary lineage that included *Philodryas viridissima*, the type of the genus *Chlorosoma*, which allow us to resurrect this name.

The gender of the name *Chlorosoma* is grammatically neuter (as implemented by Amaral 1929a; b; c; 1932), since the meaning that Wagler (1830) gave it simply refers to a “green snake”. According to that, the correct spelling for the type species of the genus is *Chlorosoma viridissimum*.

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: All structures (scales, muscles, bones, etc.) of the anterior region of the head markedly elongated, delineating the shape of the head as acuminate and sharp. Large number of prediastemal maxillary teeth (16-21), followed by one or two grooved postdiastemal teeth. Hemipenes with a well-defined longitudinal crest that runs medially in the asulcate surface, covered with papillae and slightly larger spines and bordered by two to four rows of spinulate body calyces (Figure 3).

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

Etymology: The generic name *Xenoxybelis* is composed by the ancient Greek words *Xenos-* (adjective, ξένος) that means “different”, *-oxy-* (adjective, οξύς) that means “sharp”, and *-belos* (noun, βέλος) that means “dart”. The meaning of the generic name make reference to a different group of snakes with similar sharp rostrum to the species of the genus *Oxybelis* Wagler, 1830.

Comment: a clade with maximal support values in both BI and ML inferences (Figure 2). Zaher *et al.*, (2009) found *Philodryas* paraphyletic respect to *Xenoxybelis* and place all the species of the latter one under the synonymy of the first one. Posteriorly, Grazziotin *et al.*, (2012) redefined the genus *Philodryas* and formally placed *Xenoxybelis* and *Pseudablades* under its synonymy. These authors faced a nomenclatural conflict with the synonymization of these genera, since moving *Xenoxybelis boulengeri* (Procter, 1923) to *Philodryas* resulted in creating a secondary homonym of *Philodryas boulengeri* Werner, 1909, a junior synonym of *Philodryas mattogrossensis* Koslowsky, 1898. The solution of Grazziotin *et al.*, (2012) was assigned the species name *georgeboulengeri* to *Philodryas boulengeri* (Procter, 1923).

According to our phylogenetic results, placing *Philodryas georgeboulengeri* (Procter, 1923) back to the genus *Xenoxybelis* does not produce conflicting names or homonyms, thus we revalidated the status of the species name and recovered *Xenoxybelis boulengeri* (Procter, 1923) as a valid name.

Tribe Incaspidini, Arredondo, Zaher, Grazziotin, and Scrocchi **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: diacranterian maxillae; opisthodont dentition, with an ungrooved postdiastemal teeth in the maxilla. Hemipenes significantly longer than wide (up to 3.5 times), with a well-defined constriction in the basal portion of the hemipenes body (Figure 4).

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*, thus the correct spelling of the new tribe is Incaspidini.

Comment: a clade with maximal support values in both BI and ML inferences (Figure 2). See genus comments.

Genus *Incaspis* Donoso-Barros, 1974, **resurrected**.

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

Synonyms: *Leimadophis* Parker, 1932; *Dromicus* Schmith & Walker 1943; *Liophis* Dixon, 1980.

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) that means royalty, and the Greek word *-aspis* (noun, ἄσπις) that means venomous snake. The meaning of *Incaspis* is associated to the region where these group of snakes occurs, the Andean mountains where the Inca empire were historically established.

Comment: Originally, 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 samples to obtain molecular evidence were available from *I. amaru*, we included this species in the genus *Incaspis* since it shares all diagnostic characters with the species we sampled (*I. simonsii* and *I. tachymenoides*), occurs in the same biogeographical region (Central Andes), and show an overall morphological similarity (pholidosis, coloration, and hemipenial anatomy) with the other two species of *Incaspis*.

Discussion

The highly diverse family Dipsadidae was retrieved, with strong support, as monophyletic in our results, as previously documented by recent systematic studies (Figueroa *et al.*, 2016; Grazziotin *et al.*, 2012; Pyron *et al.*, 2011; Vidal, Dewynter, & Gower, 2010; Zaher *et al.*, 2009; 2018; 2019). Likewise, we could not recover a structured and resolved evolutionary relationships within Dipsadidae. However, our topologies (ML and BI) showed that the most of the previously hypothesized xenodontine tribes (except Philodryadini and Echinantherini) were recovered as monophyletic groups (Grazziotin *et al.*, 2012; Zaher *et al.*, 2009). We found a highly supported sister group relationship between Philodryadini (*sensu stricto*) and Tropicodryadini in our analyses (Figures 1 and 2). Unfortunately, we were not able to establish the phylogenetic position of this clade (Philodryadini+Tropicodryadini) inside Dipsadidae.

Historically, a close relationship has been considered to occur between the members of the tribes Philodryadini and Tropicodryadini (Amaral 1937; Dowling & Duellman, 1978; Ferrarezzi, 1994; Günther, 1858) and several authors had presented topologies supporting a sister relationship (Lobo & Scrocchi, 1994; Pyron *et al.*, 2011; Vidal, Dewynter, & Gower, 2010; Zaher *et al.*, 2018; 2019), while others did not found such association (Grazziotin *et al.*, 2012; Zaher *et al.*, 2009). According to our results, the previous documentation of the close relationship between Philodryadini and Tropicodryadini is supported and more evidence will be necessary In order to evaluate the common evolutionary history between these lineages.

Our molecular dataset for members of the tribe Philodryadini (*sensu lato*) constituted 35 % of our whole matrix and is the most complete used for systematics until now (83 % of its total diversity) accounting for 20 species of Philodryadini (*sensu lato*). The samples used in the previous most complete systematic study on caenophidian snakes (Zaher *et al.*, 2019) only account for 58 % (14 species) of the diversity of Philodryadini. Other recent phylogenetic hypotheses about neotropical snakes obtained contrasting results in terms of the monophyly of the tribe and its internal relationships, mainly because were included half or even less species of Philodryadini (*sensu lato*) (Table 3). Pyron *et al.* (2011), retrieved a non-monophyletic Philodryadini, with *P. viridissima* grouped with *Tomodon* and *Hydropsini* inside an unsupported clade, and the remaining species formed a separated clade, also without support, grouped with Tropicodryadini. Figueroa *et al.* (2016) also found a non-monophyletic Philodryadini, recovering a highly supported clade with *P. chamissonis* and *P. trilineata* related to *Xenopholis*, *Hydrodynastini*, and *Caateboini*, and a poorly supported clade with the remaining species of *Philodryas* grouped with *Sordelina punctata* and *Echinantherini*. The results of Figueroa *et al.* (2016) were a product of the lack of homology between the molecular markers sampled, as they only used sequences of NAHD4 for *P. chamissonis* and *P. trilineata*, and a combination of 12S, 16S, *bdnf*, *cmos*, and *cytb* for the remain species of *Philodryas* they sampled (Table 3).

We found that Philodryadini is not a monophyletic group and that the species previously placed in this tribe actually comprise two different and unrelated lineages within the South American Xenodontinae (Figure 1). According to that, the tribe Philodryadini (*sensu stricto*) is a lineage composed mostly by cis-Andean species (except for the trans-Andean *P. chamissonis*, that occurs in the Southern Andes), and

the tribe Incaspidini is constituted by a separate radiation of snakes from Central Andes, which are only found in the highlands of the Andes of Ecuador and Peru. Historically, certain confusion has existed around the systematics of the species here allocated in the tribe Incaspidini, mainly due to the characteristic condition of ungrooved postdiastemal maxillary teeth, which had led several authors to associated them with the genera *Alsophis*, *Dromicus*, *Leimadophis* and *Philodryas* (Amaral, 1929a; b; c; Parker, 1932; Peters, 1960; Thomas, 1977). By placing the species *amaru*, *simonsii* and *tachymenoides* into a different genus and tribe, we resolve its systematic status and help to understand a relevant portion of the classification of the South American lineages inside Xenodontinae.

Recently, *Philodryas erlandi* Lönnberg, 1902 was extracted, mostly based on coloration differences, from the synonymy of *Philodryas mattogrossensis* Koslowsky, 1898 and revalidated as valid species by Cacciali *et al.* (2016). These species, as expected, group together in our topologies, and constituted an clade with a particular biogeographical pattern, with *P. mattogrossensis* mostly occurring in the Cerrado biome in Southern Brazil and eastern Paraguay, while *P. erlandi* inhabits the norther region of the Chaco biome in Argentina, Paraguay and Bolivia (Cacciali *et al.*, 2016). These species (subclade 1, Figure 5) are characterized by their coloration, with a unique pattern of gradually change from green or yellow in the anterior portion of the body, to reddish brown from the middle to the tail (Cacciali *et al.*, 2016; Thomas 1976), which could represent a synapomorphic trait for this group of species.

Philodryadini, as defined here, is a group that contain species with high relevance in public health (Sánchez *et al.*, 2014; Weinstein *et al.*, 2011), with records of envenomation from several species, and even lethal cases on humans (Da Rocha *et al.*, 2006; Weinstein *et al.*, 2013). With opisthoglyphous dentition, a venom delivery apparatus, and gland secretions containing diverse venomous proteins and toxins (Modahl *et al.*, 2016; Urra *et al.*, 2015), *Philodryas* spp. constitute one of the principal group of snakes that cause most of the non-front fanged envenomation in South America (Oliveira *et al.*, 2017). Most studies focused on venom and envenomation of *Philodryas* has been developed without an evolutionary context (Acosta *et al.*, 2003; da Rocha *et al.*, 2006), bypassing issues on intra and inter specific variation and phylogenetic structure among groups of species. Our phylogenetic hypothesis of the relationship among the members of Philodryadini provides an evolutionary framework

that will help to understand variation and diversification on venom and associated structures, that can be applied to envenoming treatment and pharmacological development.

Our results represent a great advance in understanding the diversity and the evolutionary patterns of a relevant component of South American dipsadid snakes.

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Figure Captions

Figure 1. Best scoring maximum likelihood (ML) tree estimated using RAxML, as implemented in the CIPRES Science Gateway. Terminals collapsed on family, subfamily and tribe hierarchical levels to show higher-level relationships. Numbers in the nodes correspond to Bootstrap support values.

Figure 2. Best scoring maximum likelihood (ML) tree estimated using RAxML, as implemented in the CIPRES Science Gateway. Pruned version that only shows the relationships within the clades SAE Philodryadini and Tropicodryadini. Numbers in the nodes correspond to Bootstrap support values.

Figure 3. Hemipenial morphology of *Xenoxybelis argenteus* (BMNH 1994.7000) in A) sulcate and B) asulcate views. Scale bar 5 mm.

Figure 4. Hemipenial morphology of *Incaspis amaru* (BMNH 1994.7000) in A) sulcate and B) asulcate views. Scale bar 5 mm.

Figure 1. Best scoring maximum likelihood (ML) tree estimated using RAxML, as implemented in the CIPRES Science Gateway. Terminals collapsed on family, subfamily and tribe hierarchical levels to show higher-level relationships. Numbers in the nodes correspond to Bootstrap support values.

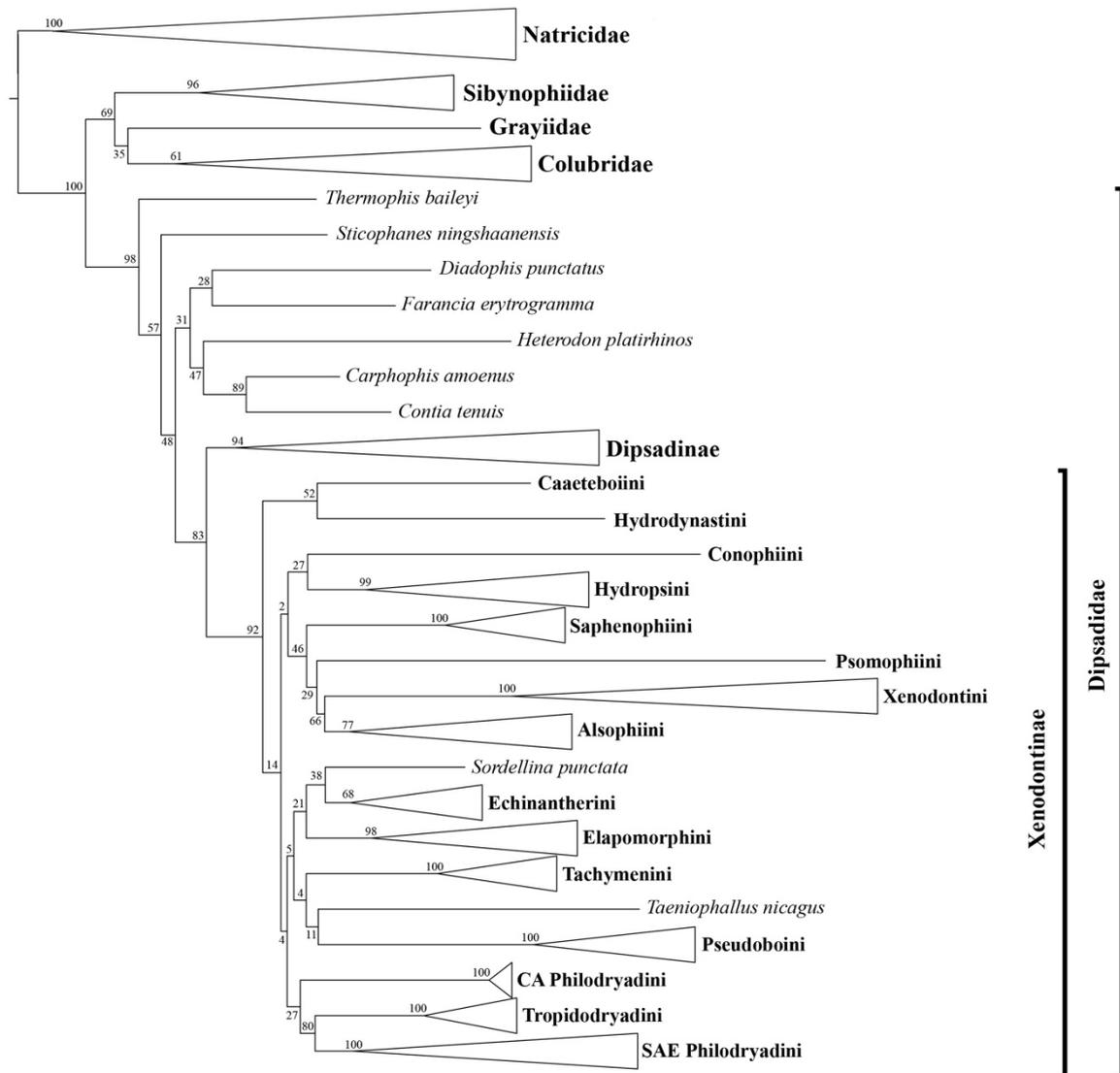


Figure 2. Best scoring maximum likelihood (ML) tree estimated using RAxML, as implemented in the CIPRES Science Gateway. Pruned version that only shows the relationships within the clades SAE Philodryadini and Tropidodryadini. Numbers in the nodes correspond to Bootstrap support values.

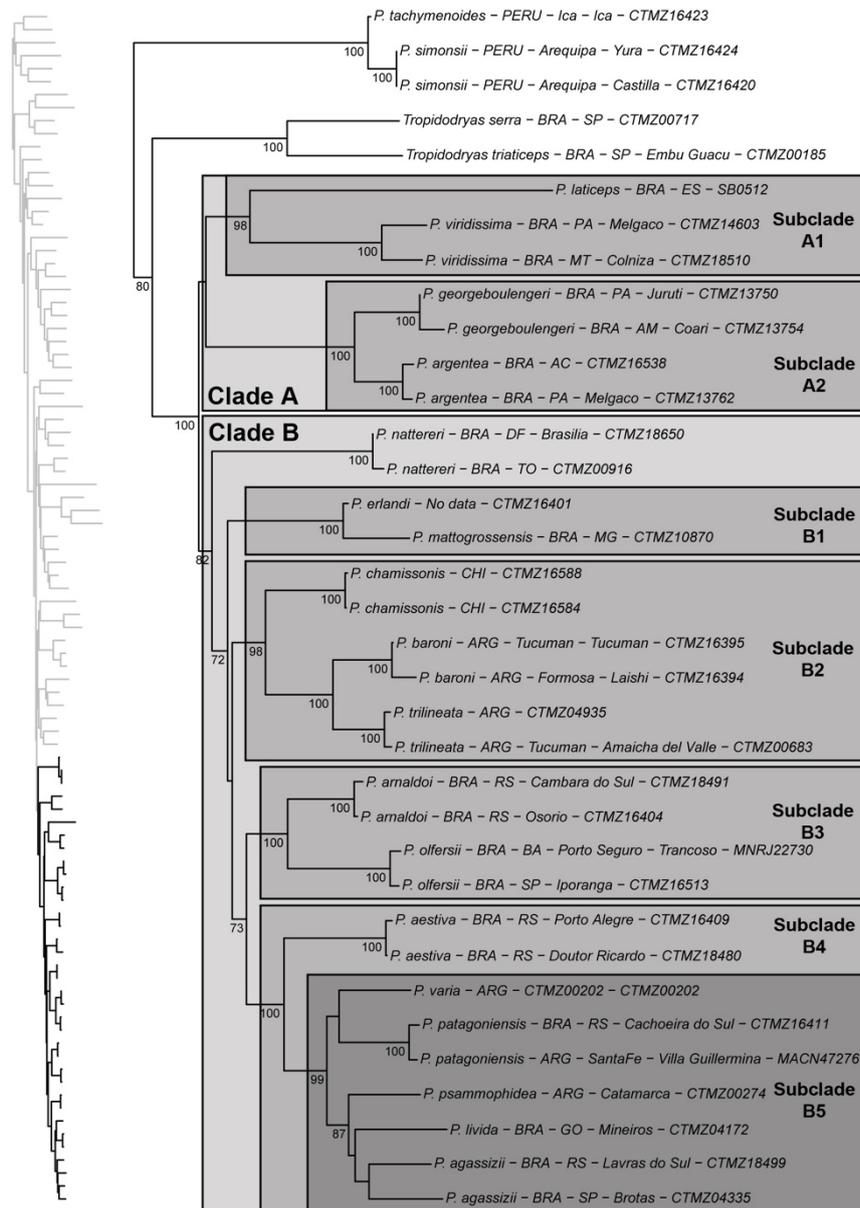
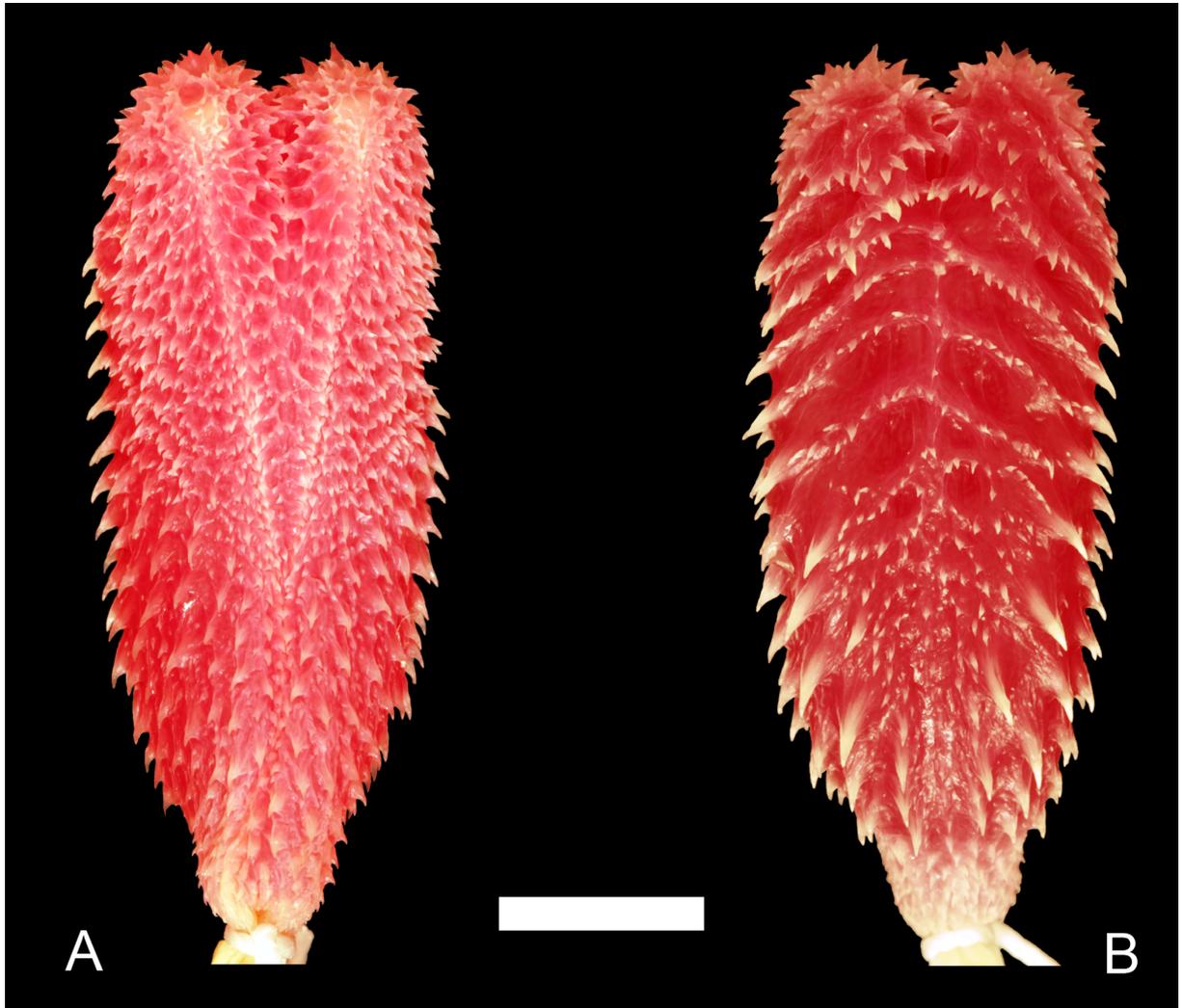


Figure 3. Hemipenial morphology of *Xenoxybelis argenteus* (BMNH 1994.7000) in A) sulcate and B) asulcate views. Scale bar 5 mm.



Figure 4. Hemipenial morphology of *Incaspis amaru* (FHGO 4749 Holotype) in A) sulcate and B) asulcate views. Scale bar 5 mm.



Tables

Table 1. Species diversity and geographical distribution of the members of the tribe Philodryadini. 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> (Procter, 1923)	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 offersii</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

Table 2. The partitions of the mitochondrial and nuclear genome sequences identified by Partition Finder for analysis run in MrBayes and RaxML

Method	Partition	Best Model	Subset Partitions	Subset Sites
MrBayes	p1	GTR+I+G	12s	1-510
	p2	K80+I	bdnf (p2), bdnf (p1)	512-1220\3, 511-1220\3
	p3	K80+I+G	bdnf (p3)	513-1220\3
	p4	HKY+G	cmos (p1)	1221-1806\3
	p5	K80+I+G	nt3 (p3), nt3 (p2), cmos (p2), cmos (p3)	3913-4433\3, 3912-4433\3, 1222-1806\3, 1223-1806\3
	p6	F81+I+G	coi (p1)	1807-2913\3
	p7	GTR+G	coi (p2)	1808-2913\3
	p8	SYM+I+G	coi (p3)	1809-2913\3
	p9	GTR+G	cytb (p1)	2914-3910\3
	p10	GTR+G	cytb (p2)	2915-3910\3
	p11	HKY+G	cytb (p3)	2916-3910\3
	p12	HKY+G	nt3 (p1)	3911-4433\3
RAxML	p1	GTR+G	12s	1-510
	p2	GTR+G	bdnf (1)	511-1220\3
	p3	GTR+G	bdnf (2), cmos (3)	512-1220\3, 1223-1806\3
	p4	GTR+G	bdnf (3)	513-1220\3
	p5	GTR+G	cmos (1)	1221-1806\3
	p6	GTR+G	cmos (2), nt3 (3)	1222-1806\3, 3913-4433\3
	p7	GTR+G	coi (1)	1807-2913\3
	p8	GTR+G	coi (2)	1808-2913\3
	p9	GTR+G	coi (3)	1809-2913\3
	p10	GTR+G	cytb (1)	2914-3910\3
	p11	GTR+G	cytb (2)	2915-3910\3
	p12	GTR+G	cytb (3)	2916-3910\3
	p13	GTR+G	nt3 (1)	3911-4433\3
	P14	GTR+G	nt3 (2)	3912-4433\3

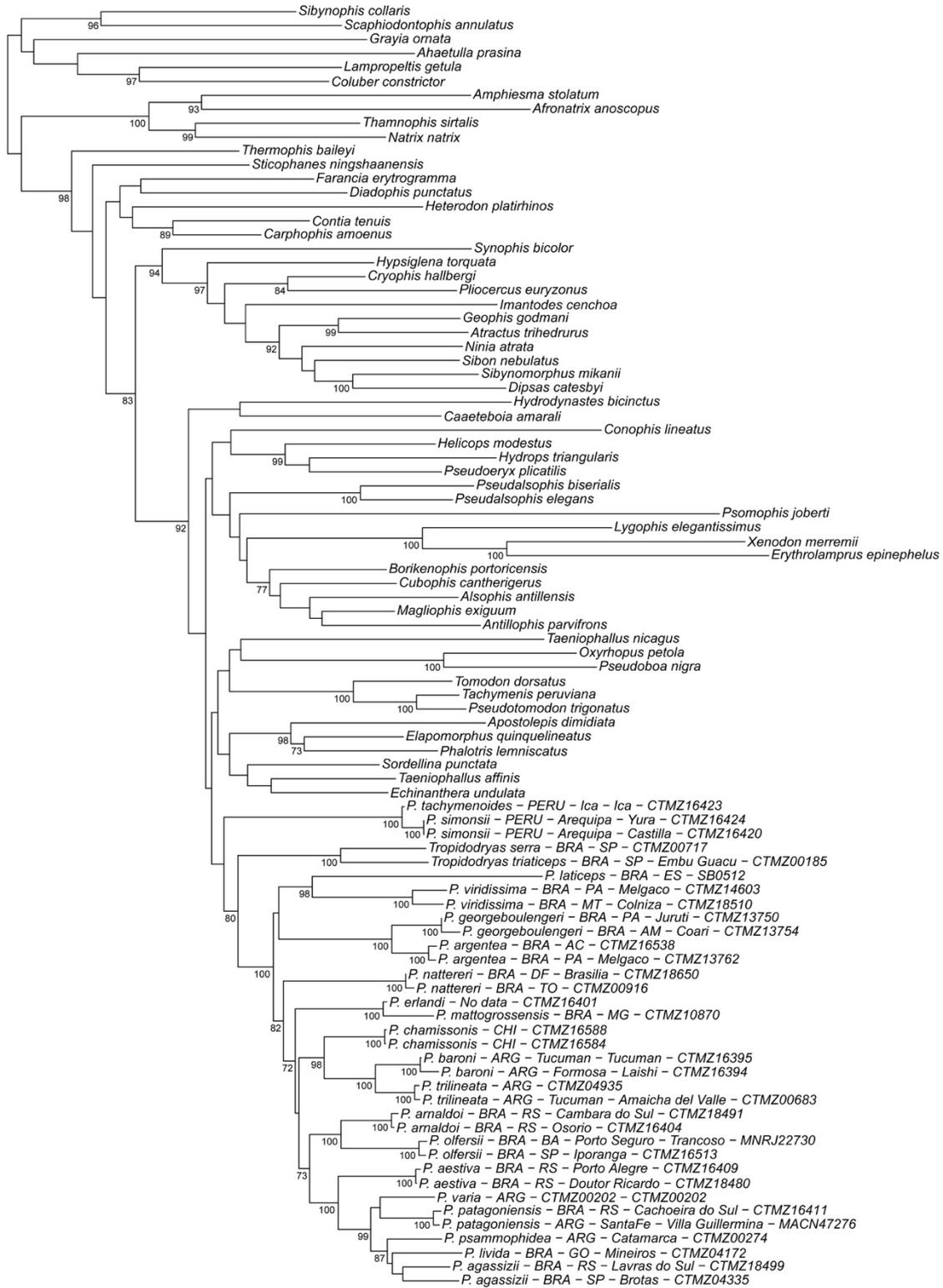
Table 3: Species of Philodryadini (*sensu lato*) employed by the most recent molecular phylogenetic studies. X^A: Species for first time sampled for traditional molecular markers used for most systematic studies.

Species	Zaher <i>et al.</i> (2009)	Vidal <i>et al.</i> (2010)	Pyron <i>et al.</i> (2011)	Grazziotin <i>et al.</i> (2012)	Figueroa <i>et al.</i> (2016)	Zaher <i>et al.</i> (2018)	Zaher <i>et al.</i> (2019)	<i>This study</i>
<i>P. aestiva</i>	X	X		X	X	X	X	X
<i>P. agassizii</i>	X	X	X	X	X	X	X	X
<i>P. amaru</i>								
<i>P. argentea</i>	X	X		X	X	X	X	X
<i>P. amaldoi</i>								X ^A
<i>P. baroni</i>		X	X	X	X	X	X	X
<i>P. boliviana</i>								
<i>P. boulengeri</i>			X		X	X	X	X
<i>P. chamissonis</i>					X			X ^A
<i>P. cordata</i>								
<i>P. erlandi</i>								X ^A
<i>P. laticeps</i>								X ^A
<i>P. livida</i>							X	X
<i>P. mattogrossensis</i>	X	X		X	X	X	X	X
<i>P. nattereri</i>			X	X	X	X	X	X
<i>P. olfersii</i>		X	X	X	X	X	X	X
<i>P. patagoniensis</i>	X	X	X	X	X	X	X	X
<i>P. psammophidea</i>		X		X	X	X	X	X
<i>P. simonsii</i>								X ^A
<i>P. tachymenoides</i>								X ^A
<i>P. trilineata</i>					X	X	X	X
<i>P. varia</i>							X	X
<i>P. viridissima</i>		X	X	X	X	X	X	X
<i>D. taeniatus</i>								
24	5	9	7	10	13	12	14	20

Family	Subfamily	Tribe	Taxon	12s	BDNF	CMOS	CyT-b	NT3	COI
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas agassizii</i> CTMZ18499	CTMZ18499	CTMZ18499	CTMZ18499	CTMZ18499	CTMZ18499	CTMZ18499
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas agassizii</i> CTMZ18650	CTMZ18650	CTMZ18650	CTMZ18650	CTMZ18650	CTMZ18650	CTMZ18650
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas argentea</i> CTMZ16538	CTMZ16538	CTMZ16538	CTMZ16538	CTMZ16538	CTMZ16538	CTMZ16538
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas argentea</i> CTMZ13762	CTMZ13762	CTMZ13762	CTMZ13762	CTMZ13762	CTMZ13762	-
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas arnaldoi</i> CTMZ18491	CTMZ18491	CTMZ18491	CTMZ18491	CTMZ18491	CTMZ18491	CTMZ18491
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas arnaldoi</i> CTMZ16404	CTMZ16404	CTMZ16404	CTMZ16404	CTMZ16404	CTMZ16404	CTMZ16404
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas baroni</i> CTMZ16394	CTMZ16394	CTMZ16394	CTMZ16394	CTMZ16394	CTMZ16394	CTMZ16394
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas baroni</i> CTMZ16395	CTMZ16395	CTMZ16395	CTMZ16395	CTMZ16395	CTMZ16395	CTMZ16395
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas chamissonis</i> CTMZ16584	CTMZ16584	CTMZ16584	CTMZ16584	CTMZ16584	CTMZ16584	CTMZ16584
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas chamissonis</i> CTMZ16588	CTMZ16588	CTMZ16588	CTMZ16588	CTMZ16588	CTMZ16588	CTMZ16588
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas georgeboulengeri</i> CTMZ13754	CTMZ13754	CTMZ13754	CTMZ13754	CTMZ13754	CTMZ13754	CTMZ13754
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas georgeboulengeri</i> CTMZ13750	CTMZ13750	CTMZ13750	CTMZ13750	CTMZ13750	CTMZ13750	CTMZ13750
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas laticeps</i> SB0512	SB0512	-	-	SB0512	SB0512	SB0512
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas livida</i> CTMZ04172	CTMZ04172	CTMZ04172	CTMZ04172	CTMZ04172	CTMZ04172	CTMZ04172
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas mattogrossensis</i> CTMZ10870	CTMZ10870	CTMZ10870	CTMZ10870	CTMZ10870	CTMZ10870	CTMZ10870
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas erlandi</i> CTMZ16401	CTMZ16401	CTMZ16401	CTMZ16401	CTMZ16401	CTMZ16401	CTMZ16401
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas nattereri</i> CTMZ00916	CTMZ00916	CTMZ00916	CTMZ00916	CTMZ00916	CTMZ00916	CTMZ00916
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas nattereri</i>	JQ598829	CBGM00220	JQ598992	AF236806	CBGM00220	CBGM00220
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas olfersii</i> MNRJ22730	MNRJ22730	MNRJ22732	MNRJ22733	MNRJ22734	MNRJ22735	MNRJ22735
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas olfersii</i> CTMZ16513	CTMZ16513	CTMZ16515	CTMZ16516	CTMZ16517	CTMZ16518	CTMZ16518
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas patagoniensis</i> MACN47276	MACN47276	MACN47278	MACN47279	MACN47280	MACN47281	MACN47281
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas patagoniensis</i> CTMZ16411	CTMZ16411	CTMZ16411	CTMZ16411	CTMZ16411	CTMZ16411	CTMZ16411
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas psammophidea</i> CTMZ00274	CTMZ00274	CTMZ00274	CTMZ00274	CTMZ00274	CTMZ00274	CTMZ00274
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas simonsii</i> CTMZ16420	CTMZ16420	CTMZ16420	CTMZ16420	CTMZ16420	CTMZ16420	CTMZ16420
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas simonsii</i> CTMZ16424	CTMZ16424	CTMZ16424	CTMZ16424	CTMZ16424	CTMZ16424	CTMZ16424
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas tachymenoides</i> CTMZ16423	CTMZ16423	CTMZ16423	CTMZ16423	CTMZ16423	CTMZ16423	CTMZ16423
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas trilineata</i> CTMZ00683	CTMZ00683	CTMZ00683	CTMZ00683	CTMZ00683	CTMZ00683	CTMZ00683
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas trilineata</i> CTMZ04935	CTMZ04935	CTMZ04935	CTMZ04935	CTMZ04935	CTMZ04935	CTMZ04935
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas varia</i> CTMZ00202	CTMZ00202	CTMZ00202	CTMZ00202	CTMZ00202	CTMZ00202	CTMZ00202
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas viridissima</i> CTMZ18510	CTMZ18510	CTMZ18510	CTMZ18510	CTMZ18510	CTMZ18510	CTMZ18510
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas viridissima</i> CTMZ14603	CTMZ14603	CTMZ14603	CTMZ14603	CTMZ14603	CTMZ14603	CTMZ14603
Dipsadidae	Xenodontinae	Pseudoboini	<i>Oxyrhopus petola</i>	OXPE001	CBGM00149	OXPE001	GQ334554	GQ334684	CBGM00149
Dipsadidae	Xenodontinae	Pseudoboini	<i>Pseudoboia nigra</i>	GQ457825	JQ599043	GQ457885	JQ598948	CTMZ00036	CTMZ00036
Dipsadidae	Xenodontinae	Psomophiini	<i>Psomophis joberti</i>	GQ457829	JQ599046	GQ457889	JQ598950	KX695043	CBGM 01444
Dipsadidae	Xenodontinae	Saphenophiini	<i>Pseudalsophis biserialis</i>	CTMZ4659	CTMZ4659	CTMZ4659	CTMZ4659	CTMZ4659	CTMZ4659
Dipsadidae	Xenodontinae	Saphenophiini	<i>Pseudalsophis elegans</i>	CTMZ7428	CTMZ7428	CTMZ7428	CTMZ7428	CTMZ7428	-
Dipsadidae	Xenodontinae	Tachymenini	<i>Pseudotomodon trigonatus</i>	GQ457827	-	GQ457887	-	CTMZ00238	CTMZ00238

Family	Subfamily	Tribe	Taxon	12s	BDNF	CMOS	CyT-b	NT3	COI
Dipsadidae	Xenodontinae	Tachymenini	<i>Tachymenis peruviana</i>	GQ457835	JQ599054	GQ457895	-	CBGM00063	CBGM00063
Dipsadidae	Xenodontinae	Tachymenini	<i>Tomodon dorsatus</i>	GQ457838	JQ599059	GQ457897	JQ598960	KX695055	KX695055
Dipsadidae	Xenodontinae	Tropidodrydini	<i>Tropidodryas serra</i>	CTMZ00717	CTMZ00717	CTMZ00717	CTMZ00717	CTMZ00717	CTMZ00717
Dipsadidae	Xenodontinae	Tropidodrydini	<i>Tropidodryas striaticeps</i>	CTMZ00185	CTMZ00185	CTMZ00185	CTMZ00185	CTMZ00185	CTMZ00185
Dipsadidae	Xenodontinae	Xenodontini	<i>Erythrolamprus epinephelus</i>	MHUAT0694	MHUAT0694	MHUAT0694	-	MHUAT0694	MHUAT0694
Dipsadidae	Xenodontinae	Xenodontini	<i>Lygophis elegantissimus</i>	GQ457808	CBGM00055	GQ457868	CBGM00055	CBGM00055	CBGM00055
Dipsadidae	Xenodontinae	Xenodontini	<i>Xenodon merremii</i>	GQ457840	JQ599062	CBGM00178	JQ598963	YPX150	CBGM00178

Appendix 2. A) Best Scoring Maximum Likelihood Tree, estimated using RAXML as implemented in CIPRES Science Gateway. Values in the nodes correspond to Bootstrap support values.



Appendix 2. B) Maximum Clade Credibility Tree estimated using MrBayes, as implemented in the CIPRES Science Gateway. Numbers in the nodes correspond to posterior probability support.



Chapter 2

An integrative approach for species delimitation in the *Philodryas psammophidea* complex (Serpentes, Xenodontinae, Dipsadidae).

An integrative approach for species delimitation in the *Philodryas psammophidea* complex (Serpentes, Xenodontinae, Dipsadidae).

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Abstract

Philodryas psammophidea is a common species in northern Argentina, Paraguay, Bolivia and central and southwestern Brazil. Currently this species includes three subspecies, *Philodryas psammophidea psammophidea*, *Philodryas p. andensis*, and *Philodryas p. lativittata*. Additionally, *P. lineatus* is traditionally referred to its synonymy. Here, we present morphological and molecular evidence supporting the recognition of *P. psammophidea lativittata* as a distinct species while *P. p. andensis* could not be distinguished morphologically and should thus be rejected as a distinct taxon. We further present evidence that *Philodryas lineatus* does not belong to the genus *Philodryas* and should be rather reallocated in the genus *Lygophis* of Xenodontini.

Introduction

The South American racers of the tribe Philodryadini Cope, 1886, are a diverse and widespread monophyletic group of snakes composed by the genera *Philodryas* Wagler, 1830, *Chlorosoma* Wagler, 1839, *Xenoxybelis* Machado, 1993, and the rare and monotypic *Ditaxodon* Hoge 1958 (Arredondo *et al.*, *In Prep*; Zaher 1999, Zaher *et al.*, 2009, Grazziotin *et al.*, 2012). The genus *Philodryas* is the most speciose, with 14 species distributed in the cis-Andean portion of South America, from Colombia to Argentina, and with a single species inhabiting the trans-Andean region of Chile (Wallach, Williams & Boundy, 2014; Zaher *et al.*, 2014). Despite significant advances in our taxonomic knowledge of *Philodryas* in the last few years, a number of polytypic species complexes still persist within the genus, requiring extensive additional research and revision (Cacciali *et al.*, 2016; Zaher *et al.*, 2008; 2014). Currently, the most comprehensive review of *Philodryas* was given by Thomas (1976), with many of his taxonomic arrangements being retained since (Wallach, Williams & Boundy, 2014).

Among those species complex, one that still persists is *Philodryas psammophidea* Günther, 1872, a common and abundant species that occurs in central and southwestern Brazil, central and northeastern Argentina, Bolivia, and Paraguay (Kacoliris, Berkunsky, & Williams, 2006; Leynaud, Gerardo & Bucher, 1999). This species exhibits considerable morphological variation in its coloration and body size throughout its extensive distribution, which includes different biomes and physiognomies (Ceï, 1993; Scrocchi, Moreta, & Kretzschmar, 2006). Since its original description by Günther in 1872, several names have been associated with populations believed to belong to *Philodryas psammophidea*, thus increasing taxonomic uncertainty and obscuring the possibility of generating a stable taxonomic arrangement for this species complex (Thomas 1976, Zaher *et al.* 2008).

Philodryas psammophidea was described from a single specimen, collected in the province of Tucumán, northwestern Argentina, and purchased by the British Museum between 1868 and 1872 (Günther, 1872). Several populations possibly closely related or belonging to *P. psammophidea* were named as distinct species since its original description, including *Dirrhox lativittatus* Cope, 1887, *Liophis trifasciatus* Werner, 1899, *Philodryas lineatus* Werner 1909, *Philodryas weneri* Müller, 1926, and *Philodryas*

pallidus Werner, 1927 (Wallach, Williams & Boundy, 2014). The latter three were posteriorly allocated into distinct genera and remain valid, while *Dirrhox lativittatus* Cope, 1887 was considered a junior synonym of *P. psammophidea* (Boulenger 1896). Thomas (1976) and Thomas *et al.* (1977, 2001) further clarified the taxonomic status of three of these names by placing *Philodryas weneri* Müller, 1926 under the synonymy of *Philodryas varia* (Jan, 1863), and reallocating *Liophis trifasciatus* Werner, 1899 and *Philodryas pallidus* Werner, 1927 into distinct genera. As it stands, the names *Dirrhox lativittatus* Cope, 1887 and *Philodryas lineatus* Werner 1909, presently considered as junior synonyms of *P. psammophidea* (Boulenger 1896), are still in need of taxonomic clarification. Additionally, Thomas (1976) recognized three subspecies of *P. psammophidea*: *P. psammophidea andensis*, *P. psammophidea lativittata*, and *P. psammophidea psammophidea*. He distinguished them uniquely through their coloration as follows: *P. p. andensis* presents dorsal dark blotches on the nape and a white spot restricted to the preocular scale, *P. p. lativittata* retains three well defined dark stripes in the dorsum and the preocular without white spot, and *P. p. psammophidea* retains a continuous dark stripe on the dorsum that reaches the parietal scales and a small white band covering the preocular, loreal and nasal scales (Thomas, 1976). Additionally, Thomas (1976: 195) included a fourth category of coloration in this complex, denominated as “integrades” or *P. p. psammophidea X andensis*, which were defined by sharing diagnostic characteristics between *P. p. psammophidea* and *P. p. andensis*. Since Thomas’ (1976) work, no attempt was made to further clarify the validity of these populations.

Herein, we review the taxonomic status of these snakes by testing species boundaries along their distribution through an integrative approach combining both morphological and molecular evidence.

Material and Methods

Specimens examined and morphological comparisons

We reviewed a total of 423 specimens belonging to the *Philodryas psammophidea* complex from 17 collections of natural history (Appendix 1). Museum abbreviations follow Frost (2019), except for the following institutions: Museo de Historia Natural de San Rafael, Mendoza, Argentina (MSRH); Instituto Butantan, São Paulo, Brazil (IBSP);

Universidade Federal do Mato-Grosso, Cuiabá, Brazil (UFMT-R); and private collections of Dirk Embert (MSR, BIOD). Ventral scales were counted following Dowling (1951). Snout-vent length (SVL) and tail length (TL) were measured with a flexible ruler to the nearest 1.0 mm. Head length (HL) was measured to the nearest 0.1 mm with the aid of a digital caliper. Methods for hemipenial preparation and terminology follow Zaher (1999) and Zaher and Prudente (2003). We reviewed the type specimens of *Philodryas psammophideus* (BMNH 1946.1.2.79), *Dirrhox lativittatus* (ANSP 11200), *Philodryas lineatus* (ZMH 4403, now ZMH R04767), the holotype (UF 33363) and four paratypes and *Philodryas psammophideus andensis*. Coloration morphs of the three subspecies and their “Integrades” described by Thomas (1976) were employed to define the groups used in the quantitative comparisons, which account for a total of 250 individuals. We used descriptive statistics and parametric tests (t-Student and ANOVA) and a non-parametric test (Kruskal & Wallis) when need in the quantitative comparisons of the groups. We used the Tukey and Dunn test as post-hoc analysis to evaluate the differences among the groups. We made all the quantitative comparisons using R (R Core Team, 2019).

Recognition of separate evolutionary entities follows the Taxon Naming Criteria (TNCs) defined by Vences *et al.* (2013), to avoid taxonomic instability and inadequate classification schemes of non-natural groups.

Taxon sampling, DNA extraction and sequencing

We sampled 26 terminals in total, including 15 ingroup and 11 outgroup taxa (Appendix 2). Our ingroup sample was composed of 11 species of *Philodryas*, including five individuals of two subspecies (*P. p. psammophideus* and *P. p. lativittatus*) the complex of *P. psammophidea*, while the outgroup sample included a single terminal of the families Viperidae, Colubridae and Natricidae, and 23 Dipsadidae, including one Dipsadinae and 24 Xenodontinae. We rooted our phylogenetic analysis in the viperid *Crotalus durissus*.

We extracted DNA from liver, muscle, scales, or shed skins, using Phenol-Chloroform method or PureLink® Genomic DNA kit (ThermoFisher, MA, USA). The sequence fragments were amplified via polymerase chain reaction (PCR) using the primers bdnf and nt3 as described by Noonan and Chippindale (2006), 12S and c-mos as described

by Zaher *et al.* (2009); *cytb* as described by Graziotin *et al.* (2012), and *cox1* as described by Graboski *et al.* (2018). We used the PCR protocol modifications described by Arredondo *et al.* (*In Prep*) for all six molecular markers we sampled. All PCR products were purified with the ExoSap protocol-shrimp alkaline phosphatase and exonuclease I- (GE healthcare, Piscataway, NJ) and the sequences were processed using the DYEnamic ET Dye Terminator Cycle Sequencing Kit in a MegaBACE 1000 automated sequencer (GE healthcare) following manufacturer's protocols. We checked forward and reverse 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).

Sequence edition and phylogenetic analyses

We used MAFFT 1.3.6 (Kato 2013), as implemented in Geneious, to align all sequences. The rRNA gen 12S was aligned under the E-INS-i algorithm, while the protein-coding genes *bdnf*, *cmos*, *cox1*, *cytb*, and *nt3* were aligned under the G-INS-i algorithm. We used default parameters for gap opening and extension. The correct reading frame for the protein-coding genes was visually checked using Geneious. We concatenated our sequences using Sequence Matrix (Vaidya, Lohman & Meier, 2011).

We used PartitionFinder 2 (Lanfear *et al.*, 2016) to choose the models of molecular evolution for our molecular database. We selected the Akaike Information Criterion with correction (AICc) allowing the selection of models of molecular evolution implemented in RAxML 8.2.3 (Stamatakis 2014) without any correction for proportion of invariant sites and defined the branch lengths as unlinked and the greedy search option. We divided our molecular data set in 16 partitions, treating the rRNA gene (12S) as a separate partition and partitioned all five protein-coding genes by codon positions.

We conducted a maximum likelihood (ML) analysis using RAxML 8.2.3 (Stamatakis 2014) 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 one thousand bootstrap iterations to estimate branch support (BS). Our ML phylogenetic analysis was carried out on the CIPRES Science Gateway (<http://www.phylo.org>, Miller *et al.* 2010).

Results

On the validity of *Philodryas lineatus* Werner, 1909

Amaral (1929) reviewed two specimens deposited in the Zoological Museum of Hamburg (CeNak), the type (ZMH 4230), collected in Argentina, and an additional individual labeled as ZMH 4403 (now ZMH R04767) with “Brazil” as procedence. Unfortunately, the type specimen was lost during World War II (J. Hallermann *pers. comm.*), but the second specimen of *P. lineatus* is still present in ZMH’s collection, and agrees in all details with Werner’s description (Figure 1). This specimen more closely resembles species of the genus *Lygophis* Fitzinger, 1843 rather than *Philodryas*, since *Lygophis* retains a well-defined dorsal striped pattern that runs from the snout or the canthus rostralis to the tip of the tail (Michaud & Dixon, 1987), while species of *Philodryas* that exhibit in some way a dorsal striped pattern (*P. chamissonis*, *P. nattereri*, and *P. psammophidea*) always retain an irregular pattern not similar to the one present in ZMH R04767 (see Figure 6). Additionally, the specimen of *P. lineatus* has a lower ventral count (157 vs 176-223 from Michaud & Dixon, 1987) and two apical pits (one in *P. psammophidea*). Therefore, the specimen ZMH R04767 is not a member of the genus *Philodryas*.

Morphological and geographical analyses

The morphological datamatrix was composed by 137 females and 113 males, including the holotypes of *Philodryas psammophideus andensis* (UF 33363), *Dirrhox lativittatus* (ANSP 11200) and *Philodryas psammophideus* (BMNH 1946.1.2.79). Into our sample we identified the four coloration morphs described by Thomas (1976), including a total of 76 individuals that meet the description of “Intergrades” (*P. p. psammophidea* X *andensis*). In terms of morphological diversity, we found a similar pattern of variation in the meristic (ventrals and subcaudals) characters in both sexes between all the groups of the complex (Tables 1 and 2, Figure 2). Pairwise comparisons that showed a more representative and significative difference were all associated with *P. p. lativittata* (Table 2) since, even with a small sample, this group showed differences at some level with all the remaining groups of the complex. Only the subcaudal scales of females were different between *P. p. psammophidea* and the “Intergrades”. All

remaining comparisons did not show any difference between *P. p. psammophidea*, *P. p. andensis* and the “Intergrades” (Table 2).

The color pattern in *P. p. lativittata* is unique to this population, showing no overlap with “Intergrades” or any other population from the other groups (Figure 7). On the other hand, the pattern of dorsal coloration in *P. p. psammophidea* and *P. p. andensis* is highly variable, as evidenced by the large number of “Intergrades” registered. Hemipenial morphology is very similar between *P. p. andensis*, *P. p. psammophidea* and the “Intergrades”. However, the body calyces in the asulcate side varied in our sample, with *P. p. andensis* presenting a few shallow body calyces, the “Intergrades” exhibiting several deep body calyces, and *P. p. psammophidea* showing more calyces than *P. p. andensis* but less than *P. p. lativittata* (Figures 3 and 8).

The geographical pattern shown (Figure 4) along the continuous distribution of populations pertaining to *P. p. andensis* and *P. p. psammophidea* evidenced a latitudinal continuous gradient of variation in coloration, with the former occurring in the extreme north of the distribution of the complex while the latter appears to occupy the central and southern ranges of their general distribution. Moreover, the distribution of the “Intergrades” is concentrated in the central and northern regions of the distribution, connecting the southern *P. p. psammophidea* with the northern *P. p. andensis* (Figure 4). On the other hand, *P. p. lativittata* is isolated from the other groups of the complex and is restricted to the western margin of the Cerrado Biome in Mato Grosso, Brazil. There is an actual geographical barrier, the Pantanal and the Chiquitano dry forest, that separates *P. p. lativittata* from the southern groups of the *P. p. psammophidea* complex.

Molecular analyses

Our molecular database comprised 4161 base pairs of aligned and concatenated sequences. We obtained eight subsets with PartitionFinder for the RAxML analysis, which are presented in Appendix 3, along with the chosen model for each partition. Our phylogenetic hypothesis (best scoring Maximum Likelihood tree) recovered the tribe Phylodryadini as a well-supported monophyletic group (Figure 5). We obtained a topology that supports the lineage separation between populations of the extreme northwestern (Mato Grosso, Brazil) and southern distributions (northern Argentina) of

the *P. psammophidea* complex (Figures 4 and 5). The external morphology and coloration of the specimens belonging to the Brazilian subclade were concordant with the variation described by Thomas (1976:196) for *P. p. lativittatus* and the description of *Dirrhox lativittatus* of Cope (1887) while specimens from the Argentinean subclade corresponded to the typical morphology and coloration of the populations of *P. psammophidea* present in northern Argentina (Figures 6 and 7).

Systematic accounts

Based on the evidence gathered from morphological, molecular, and geographical data, we concluded that the *P. psammophidea* complex can be separated in only two distinct lineages: the first one corresponding to the type species of *Philodryas psammophidea* Günther, 1872, and the second one to *Dirrhox lativittatus* Cope, 1887. We further demonstrated that the population described as *P. p. andensis* falls into the morphological range of variation described for *P. p. psammophidea* and does not represent a geographically distinct entity. We also concluded that *Philodryas lineatus* Werner, 1909 should be removed from the genus *Philodryas* and tentatively reallocated into *Lygophis*. Consequently, we present below a redescription of *P. psammophidea* that excludes the recognition of distinct subspecies and resurrect *P. lativittata* as a valid species.

***Philodryas psammophidea* Günther, 1872**

Philodryas psammophideus andensis Thomas, 1976.

Philodryas lineatus Günther, 1872

Type: Holotype, BMNH 1946.1.2.79. Female (Figure 6).

Type locality: “Tucuman”, Northwester of Argentina.

Diagnosis and comparisons: *Philodryas psammophidea* can be easily diagnose from *P. laticeps*, *P. viridissima*, *P. aestiva* and *P. olfersii* by the body coloration (striped irregular vs homogeneously green). *Philodryas agassizii* has a lower dorsal count at midbody (13 vs 19), *P. arnaldoi*, *P. livida*, *P. patagoniensis*, and *P. agassizii* have different dorsal pattern (vertebral stripe absent vs irregular stripe in the vertebral

region). *Philodryas varia* exhibits a dorsal pattern with paired blotches on the dorsum (stripes irregularly organized in the vertebral region). *Philodryas baroni* and *P. aestiva* have anterior projections of soft tissue in the snout (snout normal in *P. psammophidea*). *Philodryas trilineata*, *P. laticeps*, and *P. viridissima* have ontogenetic shift of coloration (no ontogenetic shift of coloration in *P. psammophidea*). *Philodryas amaru*, *P. simonsii*, and *P. tachymenoides* have ungrooved postdiastemal teeth (grooved teeth in *P. psammophidea*). *Philodryas varia* has a lower count of rows dorsal scales at midbody (17 vs 19 in *P. psammophidea*). The Amazonian species *Philodryas argentea* and *Philodryas georgeboulengeri* differs notoriously of *P. psammophidea* by its head anatomy and the general semi-amboreal habit. *Philodryas mattogrossensis* and *P. erlandi* have a regular striped pattern, while in *P. psammophidea* the stripes are irregular.

Description: Large snake, maximum SVL = 1445 mm in females and 1190 mm in males; maximum TL = 350 mm in females and 350 mm in males; maximum HL = 33 mm in females and 32 mm in males. Dorsal, lateral and ventral cephalic scales following the colubroid pattern. Supralabial scales 7-10, with usually the fourth and fifth in the orbit, infralabial scales 8-12, with usually five or six contacting the shin shields. Generally, a single preocular, two postoculars and 1+2 temporals most of the time. Ventral, subcaudals and selected morphometric variables are detailed in the table 1.

Coloration: Coloration of the dorsum in preservative is brownish to grayish with most specimens showing a striped pattern. The venter is mostly cream with only the lateral border of each ventral scale striped with a thin dark line that form a dark longitudinal stripe on each side of the specimen. The dorsal surface of the head is uniform brown or variably marked by irregular dark pigmentation. The brownish cap extends to the dorsal lateral surface of the head. A distinct cream or white preocular stripe extends from the posterior border of the nasal to the preocular, loreal and preocular, or is confined only to the preocular. Either a thin dark postocular line or a brown postocular stripe, bordered dorsally and ventrally by a thin dark line, and extending through the postocular and temporal areas. When present, the postocular stripe tends to vanish on the neck, and the dark lines that border it tends to fuse and extend through the lateral side of the dorsum, running ventrally to each lighter paravertebral band. More rarely, the postocular stripe extends as a brown band through the lateral side of the dorsum of the body. Supralabials are mostly light cream to yellowish, being variably pigmented

with dark spots and dorsally invaded by a slightly darker grayish color. Infralabials and chin shields are also light cream to yellowish and pigmented with irregular dark spots. In dorsal view, the body shows a conspicuous striped pattern formed by one large brownish vertebral band bordered by two lighter grayish paravertebral bands. The vertebral band extends from the nape to the tip of the tail and occupies two to five scales in width. Scales composing the vertebral band are variably pigmented with brown and dark with, in some cases, light borders, resulting in a highly variable pattern that includes continuous lines and a variety of broken lines. When the vertebral band is well defined, a dark line is formed along its border separating it from the lighter adjacent paravertebral bands. Scales forming the vertebral band may be more densely pigmented, resulting in a darker vertebral band with a reticulated pattern. The vertebral band may be broken in a series of small dark dots or two parallel series of larger dots that merge posteriorly on the body to form an uninterrupted vertebral band. Some heavily pigmented specimens might retain only small, completely dark dots instead of a vertebral band. Larger dots formed by an inner brownish surface lined by an outer dark edge whereas. The two paravertebral bands are always lighter than the vertebral band, being silver, grayish, or yellowish to light brown. As already mentioned above, paravertebral bands are generally well defined ventrally by a dark line that extends from the postocular stripe. The lateral side of the dorsum below the dark paravertebral stripe is almost uniform darker brown or grayish with a thin light stripe that, when present, is visible on the lower lateral surface of the dorsum from the neck to the vent. The darker lateral coloration ends abruptly in the upper part of the first dorsal scale row contacting the ventral scales. The lower surface of the last dorsal scale row and the lateral border of the ventral scales are uniform light cream or yellowish, forming a conspicuous light stripe that extends along the area of contact between dorsal and ventral scales. This light paraventral stripe is always lighter than the belly and is bordered below by a thin dark line that may be continuous or interrupted between each ventral scale. It may or may not be also bordered dorsally by another dark line. Ventral surfaces of the head, belly, and tail are uniformly creamish to yellowish, except for the lower dark lines bordering each paraventral stripe and a series of dark dots ornamenting the chin, preventral, and first ventral scales.

Hemipenes: Large and thin, semycalculated and semicapitate, calyculated lobes restricted to the distal portion of the organ. Large lobes covered with papillate calyces.

On the intrasulcar region, the calyces extending proximally, very close to the base of the organ. The calyculated region on the sulcate surface begin around the base of the hemipenial body. Body calyces on the asulcate surface papillated, larger distally. The sulcus spermaticus runs centrolineally and divides near the base of the hemipenis. Larger lateral enlarged spines, less than six per side.

***Philodryas lativittata* (Cope, 1887) resurrected**

Dirrhox lativittatus Cope, 1887

Type: ANSP 11200. Adult Male (Figure 7).

Type locality: “Cuyabá, Chupada” = Cuiabá, Chapada, Mato Grosso, Brazil.

Diagnosis and comparisons: *Philodryas lativittata* differs from *P. laticeps*, *P. cordata*, *P. olfersii*, and *P. viridissima* by the presence of a long hemipenis, with the capitulum representing less than half the length of the organ (the capitulum extends to half or more of the sulcate surface of the organ in the latter species). This species differs from *P. amaru*, *P. tachymenoides*, and *P. simonsi*, by having postdiastemal grooved teeth (absent in these species). *P. lativittata* differs from *P. varia* and *P. boliviana* by its count of dorsal rows at midbody (17 vs 19 in *P. lativittata*). *P. mattogrossensis* and *P. erlandi* exhibit a particular pattern of dorsal coloration (regular stripes in *P. lativittata* vs lateral clear stripes that changed posteriorly). *P. nattereri* has white bands on the canthus rostralis (absent in *P. lativittata*). Differs from *Philodryas psammophidea* molecularly, and morphologically by the presence of a cream venter variably smudged with dark brown (overall cream venter in *P. psammophidea*), by the presence of three regular stripes on the dorsum (irregular dorsum stripes in *P. psammophidea*), and several scale counts (Table 1). Differs from *P. aestiva*, *P. arnaldoi*, *P. baroni*, *P. cordata*, *P. livida*, *P. mattogrossensis*, *P. nattereri*, *P. olfersii*, *P. patagoniensis*, *P. varia*, and *P. viridissima* by the striped pattern (not striped in the other species); from *P. trilineata* and *P. boliviana* by the number of dorsal scale rows at midbody (19 in *P. lativittata* versus 17 in *P. boliviana* and 23 or more in *P. trilineata*).

Description: Maximum SVL = 827 mm in females and 503 mm in males; maximum TL = 210 mm in females and 197 mm in males; Dorsal, lateral and ventral cephalic scales following the colubroid pattern. Supralabial scales 8, with the fourth and fifth in the

orbit, infralabial scales 9-11. A single preocular, two postoculars and usually 1+2 temporals. Ventral, subcaudals and selected morphometric variables are detailed in the table 1.

Coloration – In preservative, the coloration of the dorsum is brownish with four conspicuous light brown or bright gray stripes that run from the neck to the tip of the tail. Venter variably smudged with dark brown or black markings on a cream ground color. In most specimens the darker smudging invades ventrals and subcaudals from the neck to the tip of the tail. However, the anterior one-third of the venter is always slightly more cream than the rest of the body, being mostly marked by black dots in some specimens (e.g., IB 31109). Ventrals and subcaudals normally retain a lateral margin cream.

Hemipenis – (Figure 8) Hemipenial morphology is very similar to the found in *P. psammophidea*.

Discussion

Until recently, *Philodryas psammophidea* was known to include three distinct subspecies and a number of forms with questionable taxonomic status under its synonymy. Despite its long-standing taxonomic instability, several questions still persist, including the validity of the three subspecies recognized by Thomas (1876) and of *P. lineatus* included in the synonymy of *P. psammophidea*. We tackled these issues in the present study.

Werner (1909: 234) described *Philodryas lineatus* from a single specimen harbored in the Natural History Museum of Hamburg (Today Center for Natural History –CeNak– Hamburg University), and used the condition of three supralabials in contact with the orbit to diagnose it from the other members of the genus. This specimen does not belong to the genus *Philodryas* and thus should not be included in the synonymy of *P. psammophidea*. According to the morphological evidence at hand, *Philodryas lineatus* should be rather allocated in the genus *Lygophis*.

Philodryas lativittata was originally described by Cope (1887), as *Dirrhox lativittatus*, from a single specimen collected in The Chapada near Cuiabá, Mato Grosso state,

Brazil. Shortly after, Boulenger (1896) synonymized it with *Philodryas psammophidea*, without an explanation or reason for this nomenclatural act. Since then, this species was just considered as another synonym of *P. psammophidea*. It was Thomas (1976) who first revised the status of *D. lativittatus*, suggesting it should be recognized as a valid subspecies of *P. psammophidea*. Here we found, based on an extensive analysis of 423 specimens, that several individuals from a well-defined region in Brazil agree with the description Cope's (1896) of *Dirrhox lativittatus*, differing from *P. psammophideus* both morphologically and molecularly, thus supporting its recognition as a valid species. *P. lativittatus* occurs in the western margin of the Brazilian Cerrado, completely isolated from *P. psammophidea* as they are separated by the Pantanal ecoregion.

The case of *P. p. andensis* represents a more complicated scenario, since the morphological evidence shows a clear cline (South to North) where the distributional extremes exhibit different patterns of variation in coloration. Some possible phenomena could explain this variation pattern, including among them: i) a simple geographical cline associated with differential use of resources or habitats; ii) a possible incipient sympatric speciation emerging along the distribution of the species complex, fixing polymorphism as a result of ecological differentiation (Meyer, 1990). At the moment, it is difficult to define if *andensis* represents a valid species since the evidence at hand is not conclusive.

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Appendix 1.

List of specimens examined.

Philodryas p. andensis.

(N = 9). WITHOUT LOCALITY: (FML322, MACNBB 1533) ARGENTINA: Jujuy, Dto. Santa Barbara, El Fuerte (FML 25538). BOLIVIA: Sucre (IBSP 24553); SANTA CRUZ: Florida, Laguna de Becerro (MNKR 1443); Florida, Zanjón (MNKR 1882); DTO. CHUQUISACA: Valle de la Prov. Del Acero (IBSP 18075); Yamparuez 2.800m de altura (IBSP 18074); Chimoré (FML 78).

Philodryas p. psammophidea.

(N = 315). WITHOUT LOCALITY: (FML 17292, MSRH 1313, MACN 10110[38660], MNKR 3527, MNKR 690, MNKR 3525, MNKR 3501, FS 118, GC5). ARGENTINA: (MLP-JW 1591, MLP-JW 506, MACN7975); BUENOS AIRES: Dto. Campana, Campana (MACN 7871); CATAMARCA: Dto. Ambato, Ruta Rodeo-Las Juntas, EL Manchao (1300 m) (FML 1152); Dto. Andalgalá, Alrededores de Villa Vil (FML 1409); Dto. Andalgalá, Capillitas (FML 1342); Dto. Belén, Puerta San José (FML 19875); Dto. Pomán, Finca Celum, Ruta Prov. 46, Km 45 (FML16129); Dto. Pomán, Puesto Río Blanco - 30 km al S de Andalgalá (FML 1640); Dto. Santa María, Famabalasto (FML 16976, FML 16987); Dto. Tinogasta, Ruta Nacional 60 - 4 km de Río La Punta, camino a Tinogasta (FML1639); Dto. Tinogasta, Tinogasta (1100m) (FML 1578); Agua Colorada (FML 700); Campo el Arenal, Cto. Andalgalá (FML 16175); Farayon Negro (MLP-JW 1556); La Guardia, ramal Recreo a Chumbicha (MACN 336); Tinogasta (MACN 10111); CHACO: Chaco, Quitilipi (CENAI 1350); Coronel DuGraty (CENAI 1287); Pampa del Infierno (CENAI 2846); CÓRDOBA: (MLP- JW 843); Dto. Calamuchita, El Sauce (MACN 7995, MACN7996); Dto. Colón, Villa Allende (MACN 38655); Dto. Cruz del Eje, Dique Nivelador a 55 km SE de Cruz del Eje (FML 6612); Dto. Cruz del Eje, El Brete (FML 2715-1, FML 2715-2, FML 2715-3); Dto. Ischilín, Dean Funes (MZUSP 14580); Dto. Pocho, Chancani (FML 26135, FML2499); Dto. Pocho, Tala Cañada (MACN 19572 MACN 19573); Dto. Punilla, Capilla del Monte (FML 2732, FML 2734); Dto. Punilla, Tanti (FML 2596); Dto. Río Cuarto, El Cano, Alpa Corral, Campus de la Universidad (FML 19877); Dto. Río Primero, La Puerta (MZUSP 8365); Dto. Río Primero, Obispo Trejo (MACN 38659); Dto. San Alberto, Panaholma (MACN

29161); Dto. San Justo, Sanat6rio G. Rawson, Miramar (MZUSP 14575); Dto. Sobremonte, Los Hoyos (MACN 19492, MACN19493); San Alberto, San Lorenzo: A 8 Km de mina Clavero (MLP-JW 564); Bialeto -Masse (MACN 2276); Dean Funes (CENAI 1543 CENAI 1976, CENAI 1977); La Posta (MLP- JW 842, MLP-JW848); Lucio V. Mansilla (CENAI 1093, CENAI 1097); Miramar (CENAI 3286, CENAI 3287); Tanti Viejo (MLP-JW656, MLP-JW657); Valle de los Reartes (MACN 4319); Valle del Rio Cruz Grande, cerca de ruta 38 (MACN 17913); Villa Allende (CENAI 1633); CORRIENTES: Dto Ituzaing6, Ituzaing6 (FML 289); ENTRE RIOS: Concordia (CENAI 2507); JUJUY: (MACN 5779); Dto. Ischill6n, Dean Funes (MACN 24456); Dto. Tilcara, Huacalera (FML 716); LA PAMPA: (MACN 5657, MACN 5658, MACN 609-A, MACN 609-B); Dto. Chadileo, Santa Isabel (FML 26171); Santa Isabel (MLP-R5935); LA RIOJA: Dto. Arauco, Aimogasta (MACN 9357); Dto. Arauco, Aimogasta, Sierra del Velasco, Finca Asch6 (MACN 24984, MACN 24985); Dto. Capital, Ruta Nac. 38 Km 498 (FML 9390); Dto. Castro Barros, 6 km E de Anillaco (FML7806); Dto. Castro Barros, Anillaco (FML 26151); Dto. Castro Barros, Ruta Nac. 75 - Los Molinos - 28o45`S; 66o54`W (FML 9209); Dto. Chilecito, Chilecito (FML 2595); Dto. Coronel Felipe Varela, Aicu6a (FML 18554); Dto. Famatina, El Barrial (10 km E de Pituil) - Ruta Prov. 11 (FML 2220); Dto. Independencia, Patqu6a, Guayapa, Estancia de Breyer (MACN22173); Dto. Rosario Vera Pe6aloza, Ruta Provincial 29 (frente Alisca) 30o57`48,5"S; 66o45`56,3"W (FML7805); Chepes (CENAI 3308); Chilecito (MLP-JW1966); Destacamento Chamental (MACN 46792); Patquia (CENAI 2263, CENAI 2481, CENAI 2482); MENDOZA: Dto. Capital, Colonia Papagaios (MACN 36065); Dto. San Rafael, Alrededores de la ciudad, San Rafael (MSRH 543); Dto. San Rafael, Balneario El Rinc6n, Ca66n del Atuel, Valle Grande (MSRH 859); Dto. San Rafael, Isla R6o Diamante, ciudad (MSRH 854); Dto. San Rafael, La Resolana, Colonia Espa6ola, Cuadro Nacional (MSRH 579); Dto. San Rafael, Lomas de la Sepultura, Pampa del Diamante, Cuadro Benegas (MSRH 285); Dto. San Rafael, San Rafael (FML 2733, FML 9627, MSRH 903); Mendoza (MSRH 1156); Quebrada R6o Papagayo (FML 686); NEUQUEN: (MACN72a); SALTA: Dto. Anta, Finca Los Colorados, 100 Km NE de Joaqu6n V. Gonzalez (FML 8242); Dto. Cafayate, Cafayate (FML 1206); Dto. Capital, Cachapoyas (CENAI 1089); Dto. General Jos6 de San Mart6n, Coronel Cornejo (MACN 38658); Dto. General Jos6 de San Mart6n, Hickmann (FML 20, FML 23); Dto. Gral Martin Miguel de G6emes, Cabeza de Buey (FML 936); Dto. La Poma, La Paya (FML 16176); Dto. Molinos, Laguna Brealito (FML 2170); Dto. Or6n, Urundel (FML 56); Dto. San Carlos, Angastaco (FML

24108); Lumbreras (CENAI 2051); Metan (CENAI 1793); Rosario de la Frontera (MLP-JW 687); SAN JUAN: Dto. Valle Fértil, Los Baldecitos (MLP-R 5610); San Carlos (FML 432); Valle Fértil (MLP-R 5270); SAN LUIS: (MACN 4822); 34°46'20.4"S 65°33'51.9"W (MLP-R 5558); Alto Pencoso (MLP- JW 1698); Arizona (CENAI 2321); Bagual (FENS) (MACN3642-A, MACN3642-B); Ruta Prov. 27, próx. Batavia, 34°28'20.9"S 65°48'0.2"W (MLP-R 5280); Ruta Prov. 27, próx. Batavia, General Padernera, 34°38'21.7"S 65°40'10.5"W (MLP-R 5338); SANTA FE: Tostado a Pinedo (CENAI 2255); SANTIAGO DEL ESTERO: (FML 715, MLP-JW 847, MLP-JW 872); Dto. Copo, Chaco Santiagueño, entre Urutaú y Pampa de los Guanacos (FML 584); Dto. Figueroa, Caspi Corral (FML 1263, FML 1271); Dto. Figueroa, Km 0 - Bañado de Figueroa (FML 2576); Dto. General Taboada, desvío km 511 (MACN 27856, MACN 27857); Dto. Loreto, Estación Loreto (FML 2324); Dto. Moreno, Girardet (MLP-JW 102); Dto. Pellegrini, Alrededores de Nueva Esperanza (FML 2129); Dto. Río Hondo, Dique El Frontal, Termas de Río Hondo (FML 2141); Dto. Robles, Turena (MLP-JW 443); Colonia Dora (CENAI 1092, MLP-JW 1687); Frías (CENAI 3493); Guardia Escolta (CENAI 2591, CENAI 3500); km 1343 (CENAI 1091); La Banda (CENAI 1101, CENAI 1662); Los Tigres (CENAI 1090); Lugones (CENAI 1965); Malbrán (MACN 34573); Ojo de Agua (MACN 26519); Otumpa (CENAI 1384); Puente Negro (FML 2); San José de la Dormida (CENAI 3298); Santiago del Estero (MSRH 1216); Sumampa (CENAI 3220); Tiun Punco (CENAI 2485); TUCUMÁN: Dto. Capital, San Miguel de Tucumán (FML 12541); Dto. Cruz Alta, Alderetes (FML 24712); Dto. Leales, Santa Rosa de Leales (FML 139); Dto. Trancas, Potrero Grande (FML 1023); Dto. Trancas, Tapia (FML 16391); Dto. Yerba Buena, Cerro San Javier (FML 2438); Leales (FML 19). BOLIVIA: CHUQUISACA: (CBF 00968, CBF 01827); Vale de la Prov. Camargo (IBSP 18073); COCHABAMBA: Cercado, Laguna Alalay (BIODIV_DE 16, MNKR 3028); SANTA CRUZ: Andrés Ibañez, Santa Cruz, Campus Universitario (MNKR 22); Cordillera, San Antonio de Parapetí (MACN 36350); Caballero, San Juan de Portrero (MNKR509); Cordillera, Campamento Cerro cortado (MNKR 1829); Cordillera, Cerro Colorado (MNKR 2872, MNKR 2873); Cordillera, Isiporenda (MNKR 1413); Cordillera Izozog, Izozog, Kopere Brecha (MNKR 3132); Florida, Aguaclara (MNKR 888, MNKR 1982, MNKR 1543, MNKR 614, MNKR 616, MNKR 3292); Florida, Algodonal (MNKR 1050, MNKR 860); Florida, Angostura (MNKR 1535, MNKR 1536); Barrio chaqueno (MNKR 679); Becerro (MNKR 1610, MNKR2446, MNKR 2333); Bermejo (MNKR 1604); C.R.E. (MNKR 1497); Campeche (MNKR 1889, MNKR 1205); Caraparial

(MNKR 602); El Millu (MNKRDE 072, ZFMKDE 036); La Challita (MNKR 2679); La Hoyada (MNKR 1529, MNKR 1540, ZFMKDE 024, MNKR 3024); La Laguna (MNKR 3392, MNKR 1890); Laguna de Becerro (MNKR 1700); Los Gallos (MNKR 1521, MNKR 1541); Los Negros (MNKR 2267, MNKR 3296); Los Negros, Barrionuevo (MNKR 615, MNKR 2951); Mairana (MNKR 592, MNKR 2377, MNKR 2378); Mataral (MNKR 1439, MNKR 1701, MNKR 1976, MNKR 1272, MNKR 1367, MNKR 2273, MNKR 3239, MNKR 1528); Nogal (MNKR 1206); Pacay (MNKR 1633); Palmasola (MNKR 1860, ZFMKoderMNKRDE 059, MNKR 2381); Florida, Pampagrande (MNKR 623, MNKR 680, MNKR 877, MNKR 954, MNKR 955, MNKR 956, MNKR 975, MNKR 1214, MNKR 1274, MNKR 1493, MNKR 1513, MNKR 1702, MNKR 1715, MNKR 1961 MNKR 1966, MNKR 1985, MNKR 2002, MNKR 2240, MNK R2467, MNKR 2513, ZFMKDE 078, ZFMKDE 056, MNKR 759, MNKR 864, MNKR 953, MNKR 1362, MNKR 1522, MNKR 1526, MNKR 1527, MNKR 1542, MNKR 1548, MNKR 1592, MNKR 1871, MNKR 1992, MNKR 2618, MNKR 3229, MNKR 3408, MNKR 606, MNKR 761, MNKR 1215, MNKR 1615, MNKR 2415, MNKR 2216, ZFMKDE 058, MNKR 597, MNKR 716, MNKR 937, MNKR 2159, MNKR 2451, MNKR 3329); Florida, Potzillo (MNKR 2328); Florida, Pozuelo (MNKR 574); Florida, Samaipata (MNKR732, F.Sagot); Florida, Santa Rosa de Lima (ZFMKDE 008 ZFMKDE 099, ZFMKDE 101); Florida, Valle hermoso (MNKR 1027); Florida, Venadillo (MNKR 2423); Florida, Villa Merced (MNKR 3069, MNKR 1570, MNKR 3477, MNKR 1226, MNKR 2681); Florida, Zanjón (MNKR 1061, MNKR 1879, MNKR 1892, MNKR 2005, MNKR 2017, MNKR 2164, MNKR 1496, MNKR 1898, MNKR 1222); Florida (MNKR 2895).

Philodryas p. psammophidea X andensis

(N = 76). WITHOUT LOCALITY: (MSRH 1224, MNKR 1748). ARGENTINA: CATAMARCA: Dto. Alto, Guayamba - Depto. Alto – Catamarca (FML 997); CHACO: Reserva Loro Hablador (MLP-R 5176); JUJUY: Dto. Gral. Manuel Belgrano, San Salvador de Jujuy (MACN 22262); Dto. Tumbaya, Sobre Ruta de entrada a Purmamarca a medio camino desde ruta nac 9 (FML 6530); Cazadores de los Andes (CENAI 3255); San Salvador de Jujuy (CENAI 3203); LA PAMPA: Dto. Curacó, 32 km al W Puelches Ruta Nac. 28 - 38o08'29"S; 66o17'35"W (FML8359, FML8360); Dto. Curacó, 38 km NE Casa de Piedra, cruce ruta nac 28 y ruta prov 19 - 38o08'52" S; 66o45'06" W (FML 8378); Dto. Lihuel Calel, 6 km S de Lihuel Calel (MACN 36355);

Dto. Lihuel Calel, Parque Nacional Lihué Calel (MACN 34792); Dto. Limay Mahuida, RP 20, 54 Km SO Chacharramendi (MLP-R 5754); Dto. Puelén, 19 km N de Puelén - Ruta Nac 151 (km 208) 37°12'24"S; 67°34'28"W (FML 8357); Dto. Puelén, Cochicó, Altos de Cochicó (MACN 22075); Ruta Conquista del Desierto, entre Venticinco de Mayo y la Reforma, Km 368 (MLP-R 5712); MENDOZA: Dto. San Rafael, Puesto Agua de la Mula, Malvinas Sur (MSRH 1069); NEUQUEN: Añelo (MLP-R 5267); Aniello (MLP-JW 945); Portezuelo Grande (CENAI 2758); RIO NEGRO: Dto. General Roca, RN 151, 88 Km S Cnia 25 de Mayo (MLP-R 5755); Coronel Juan José Gómez (MACN 9475); General Roca (CENAI 1554). SALTA: Dto. Anta, Entre Esteco y El Bordo (FML 2525); Dto. Anta, Finca Los Colorados (FML 2431); Dto. Anta, Finca Los Colorados, 100 Km NE de Joaquín V. Gonzalez (FML 2361, FML 2481-1, FML 2481-2, FML 2481-3, FML 2484, FML 6532, FML 6587, FML 6588); Dto. Anta, Los Colorados (FML 2273); Dto. General José de San Martín, Coronel Cornejo (MACN 38656, MACN 38657); Dto. La Candelaria, La Candelaria (FML 978); Dto. La Candelaria, Ruta Prov. 6, entre el Tala y El Jardín (FML 25340); Lumbreras (CENAI2105); Rosario de la Frontera (MLP-JW638); SANTIAGO DEL ESTERO: (MLP-JW 873, MLP-R 6013); Dto. Banda, 30 km antes de La Chejchila (FML1625-1, FML1625-2); Dto. Copo, El Caburé (MACN27242); Dto. Copo, Monte Quemado (MACN 27241); Dto. Copo, Pampa de los Guanacos (MACN 27243); Dto. Figueroa, Caspi Corral (FML 1428); Dto. Pellegrini, Alrededores de Nueva Esperanza (FML 2254-1, FML 2254-2); Dto. Pellegrini, Alrededores de Nueva Esperanza, Guardia Escolta (CENAI 1334); TUCUMÁN: Dto. Tafi del Valle, Amaicha del Valle, Los Corpitos (MACN 32274); Dto. Tafi Viejo, Camino a El Cadillal (FML 1134); Dto. Tafi Viejo, Km 21, Racó, (1200 msnm) (FML 16195); Dto. Trancas, Choromoro (FML 2455); BOLIVIA: Dto. Tarija, 1 mi N Tarija (UF/FSM33363); SANTA CRUZ: Florida, La Laguna (MNKR 1646); Florida, Laguna de Becerro (MNKR 2893, MNKR 2683); Florida, Los Negros (MNKR 1270); Florida, Los Negros, Barrionuevo (MNKR 1514); Florida, Pampagrande (MNKR 1263, MNKR 1714, MNKR 2332, MNKR 2358, MNKR 977, MNKR 1204, MNKR 1208, MNKR 624); Florida, Tasajo, Zanjon (MNKR 2633); Florida, Villa Merced (MNKR 2396); Comarapa (MNKR 1955); Cordillera, San Antonio de Parapetí (MACN 43070); COCHABAMBA: Chimoré (FML 76); SANTA CRUZ DE LA SIERRA: (AMNHR-141360).

Philodryas lativittata (N = 17). BRAZIL: GOIÁS: Anápolis (Not Collected); MATO GROSSO: "Cuyabá, Chupada" = Cuiabá, Chapada (ANSP 11200 Holotype); Cuiabá,

Chapada dos Guimaraes (CHUNB 5881, CHUNB5883, CHUNB 5882); Cuiabá, 9o Batalhão de Engenharia e Construção (IBSP 46104); Aquidauana (IBSP 16428); Cuiaba, Chapada dos Guimaraes, APM Manso (UFMT-R489); Cuiaba, Chapada dos Guimaraes (UFMT-R3641); Paranatinga, PCH Paranatinga (UFMT- R9861); Tangará da Serra, Tangará da Serra (CTMZ 5554); Vicinity of Chapada (BMNH1972.439-40); Chapada (ANSP 11200); MATO GROSSO DO SUL: Bodoquena (IBSP 25323, IBSP 16966); Miranda, Guaicurus railroad station, near Duque Estrada and Miranda (IBSP 31109); Aquidauana (IBSP 15709).

Appendix 2. Accession and voucher numbers for the sequences of the taxa analyzed in this study. Codes in bold correspond to new sequences.

Family	Subfamily	Tribe	Taxon	12s	BDNF	CMOS	CyT-b	NT3	COI
Colubridae			<i>Coluber constrictor</i>	U96794	JQ599015	YPX528	EU180486	YPX528	New
Dipsadidae	Dipsadinae		<i>Imantodes cenchoa</i>	GQ457805	JQ599033	GQ457865	EU728586	KX695022	New
Dipsadidae	Xenodontinae	Echinantherini	<i>Taeniophallus nicagus</i>	JQ598845	KX694766	JQ599001	KX694886	KX695053	New
Dipsadidae	Xenodontinae	Elapomorphini	<i>Apostolepis albicollaris</i>	JQ598793	CBGM00201	JQ598965	CBGM00201	CBGM00201	New
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas aestiva</i> CTMZ 18480	CTMZ 18480	CTMZ 18480	CTMZ 18480	CTMZ 18480	CTMZ 18480	New
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas agassizii</i>	GQ457823	CBGM00080	GQ457883	GQ895883	CBGM00080	New
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas argentea</i> CTMZ 16538	CTMZ 16538	CTMZ 16538	CTMZ 16538	CTMZ 16538		New
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas baroni</i> CTMZ 16395	CTMZ 16395	New				
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas georgeboulengeri</i> CTMZ 13754	CTMZ 13754	CTMZ 13754	CTMZ 13754	CTMZ 13754		New
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas mattogrossensis</i> CTMZ 10870	CTMZ 10870	New				
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas nattereri</i> CTMZ 00916	CTMZ 00916	New				
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas offersii</i> CTMZ 18489	CTMZ 18489	New				
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas patagoniensis</i> CTMZ 16411	CTMZ 16411	New				
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas psammophidea</i> CTMZ 00274	CTMZ 00274	New				
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas psammophidea</i> CTMZ 00257	CTMZ 00257	CTMZ 00257		CTMZ 00257	CTMZ 00257	New
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas psammophidea</i> CTMZ 18511	CTMZ 18511	New				
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas psammophidea</i> CTMZ 05554	CTMZ 05554	New				
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas psammophidea</i> CTMZ 14007	CTMZ 14007			CTMZ 14007		New
Dipsadidae	Xenodontinae	Philodryadini	<i>Philodryas viridissima</i> CTMZ 14603	CTMZ 14603	CTMZ 14603	CTMZ 14603	CTMZ 14603		New
Dipsadidae	Xenodontinae	Pseudoboini	<i>Oxyrhopus petola</i>	OXPE001	CBGM00149	OXPE001	GQ334554	GQ334684	New
Dipsadidae	Xenodontinae	Psomophiini	<i>Psomophis joberti</i>	GQ457829	JQ599046	GQ457889	JQ598950	KX695043	New
Dipsadidae	Xenodontinae	Tachymenini	<i>Tomodon dorsatus</i>	GQ457838	JQ599059	GQ457897	JQ598960	KX695055	New
Dipsadidae	Xenodontinae	Xenodontini	<i>Erythrolamprus miliaris</i>	JQ598811	JQ599025	JQ598982	JQ598931	KX695016	New
Dipsadidae		Hydropsini	<i>Hydrops triangularis</i>	GQ457804	JQ599032	GQ457864	AF471039	YPX126	New
Natricidae			<i>Natrix natrix</i>	YPX538	JQ599036	AF471121	AY866541	KF234022	New
Viperidae	Crotalinae		<i>Crotalus durissus</i>	YPX791	YPX791	YPX791	AY196653	YPX415	New

Appendix 3

The partitions of the mitochondrial and nuclear genome sequences identified by Partition Finder for analysis run in RAxML

Partition	Best Model	Subset Partitions	Subset Sites
p1	GTR+G	cytb (p2), 12s	2903-3635\3, 1-498
p2	GTR+G	bdnf (p1), bdnf (p2)	499-1205\3, 500-1205\3
p3	GTR+G	bdnf (p3), nt3 (p2), cmos (p2), nt3 (p3), cmos (p3)	501-1205\3, 3637-4161\3, 1207-1794\3, 3638-4161\3, 1208-1794\3
p4	GTR+G	cmos (p1)	1206-1794\3
p5	GTR+G	coi (p1), cytb (p3)	1795-2901\3, 2904-3635\3
p6	GTR+G	cytb (p1), coi (p2)	2902-3635\3, 1796-2901\3
p7	GTR+G	coi (p3)	1797-2901\3
p8	GTR+G	nt3 (p1)	3636-4161\3

Table 1. Variation from selected meristic characters of the members of the *Philodryas psammophidea* complex. SVL: snout-vent length; TL: tail length; HL: head length. Values in parenthesis correspond to sample size. Morphometric characters in mm.

	<i>P.p.psammophideus</i>	<i>P.p.andensis</i>	<i>P.p.psammophideus</i> X <i>andensis</i>	<i>P.p.lattivitatus</i>
Dosals	17-17-13/21-21-15 ♂ (131)	19-19-15 ♂ (5)	17-17-15 19-19-15 ♂ (24)	19-19-15 ♂ (4)
	17-17-13/19-19-15 ♀ (9)	19-19-15 ♀ (9)	17-19-15/19/19/15 ♀ (41)	19-19-15 ♀ (10)
Ventrals	176–215 ♂ (130)	197–208 ♂ (4)	176–209 ♂ (25)	181–187♂ (4)
	183–218 ♀ (127)	204–212 ♀ (9)	179–214 ♀ (38)	185–207 ♀ (10)
Subcaudals	76–150 ♂ (106)	117–112 ♂ (4)	80–116 ♂ (22)	93–99 ♂ (4)
	73–117 ♀ (97)	73–103 ♀ (8)	71–106 ♀ (32)	72–97 ♀ (9)
Supralabials	7–10 ♂ (125)	8 ♂ (4)	8 ♂ (25)	8 ♂ (4)
	8–9 ♀ (122)	8–9 ♀ (9)	7–9 ♀ (40)	8 ♀ (10)
Infralabials	8–12 ♂ (124)	10–12 ♂ (4)	9–12 ♂ (25)	10 ♂ (4)
	8–12 ♀ (123)	10–12 ♀ (8)	9–12 ♀ (39)	9.5–11 ♀ (5)
SVL	190–1190 ♂ (131)	205–555 ♂ (5)	228–615 ♂ (23)	282–503 ♂ (4)
	198– 1410 ♀ (116)	440– 1260 ♀ (9)	222– 1445 ♀ (39)	201– 827 ♀ (9)
TL	75–350 ♂ (114)	76–216 ♂ (4)	83–299 ♂ (23)	102–197 ♂ (4)
	24– 345 ♀ (97)	133– 305 ♀ (8)	101– 310 ♀ (31)	61– 210 ♀ (8)
HL	10–28 ♂ (79)	12–27.7 ♂ (5)	12.57–31.36 ♂ (23)	15–21 ♂ (4)
	11–33 ♀ (77)	25 ♀ (2)	11.76–32.68 ♀ (29)	12–27 ♀ (7)

Table 2. Pairwise comparisons of groups defined for the *P. psammophidea* complex. Males were compared using non-parametric Kruskal & Wallis and Dunn's Test, while females were compared with ANOVA and Tukey test. **NS** (Not significant) and **S** (Significant) refers to p-values higher and lower than 0.05, respectively.

	Males		Females	
	Ventrals	Subcaudals	Ventrals	Subcaudals
<i>P. p. lativittatus</i> vs <i>P. p. andensis</i>	S	S	S	NS
<i>P. p. psammophideus</i> vs <i>P. p. andensis</i>	NS	NS	NS	NS
Integrades vs <i>P. p. andensis</i>	NS	NS	NS	NS
<i>P. p. psammophideus</i> vs <i>P. p. lativittatus</i>	NS	NS	NS	S
Integrades vs <i>P. p. lativittatus</i>	S	NS	S	NS
Integrades vs <i>P. p. psammophideus</i>	NS	NS	NS	S

Figure Captions

Figure 1. General aspect of *Philodryas lineatus* (ZMH R04767). A) Lateral and B) dorsal views of the head, and C) dorsal and D) ventral views of the body.

Figure 2. Box-plot chart of the Ventrals and Subcaudals for sex and by group.

Figure 3. Hemipenial morphology of A) *P. p. andensis* (IB 18075), B) *P. p. psammophidea X andensis* (MLP-R 6013), and *P. p. psammophidea* (MLP-R 5558). Scale bar 5 mm.

Figure 4. Distribution map of the taxa of the *P. psammophidea* complex. Circles correspond to *P. p. psammophidea*, triangles to *P. p. andensis*, inverted triangles to *P. p. psammophidea X andensis*, and squares to *P. p. lativittata*. White symbols correspond to specimens reviewed by Thomas (1976). Question marks are doubtful locality records.

Figure 5. Best scoring maximum likelihood (ML) tree estimated using RAxML, as implemented in the CIPRES Science Gateway. Numbers in the nodes correspond to Bootstrap support values.

Figure 6. A) dorsal view and B) ventral view of the holotype of *Philodryas psammophideus* Günther, 1872 (BMNH 1946.1.2.79).

Figure 7. A) dorsal view and B) ventral view of the holotype of *Dirrhox lativittatus* Cope, 1887 (ANSP 11200).

Figure 8. Hemipenis of *P. lativittata* (CHUNB 5881) in A) sulcate and B) asulcate views. Scale bar 5 mm.

Figure 1. General aspect of *Philodryas lineatus* (ZMH R04767). A) Lateral and B) dorsal views of the head, and C) dorsal and D) ventral views of the body.



Figure 2. Box-plot chart of the Ventrals and Subcaudals for sex and by group.

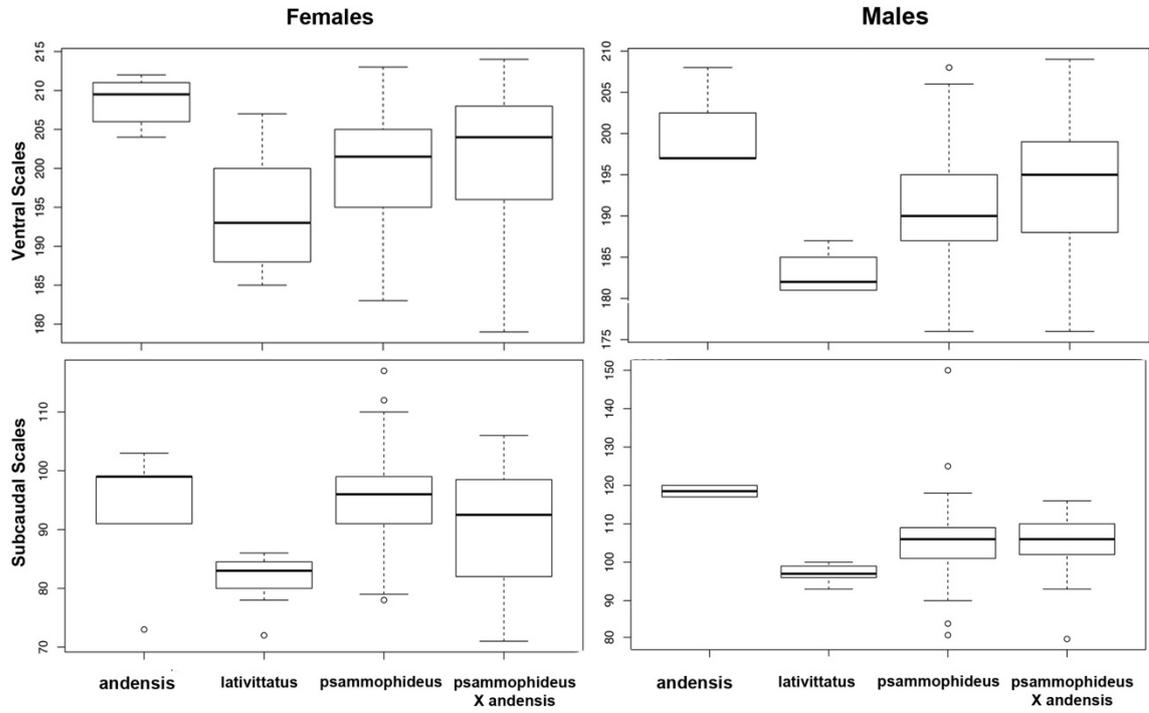


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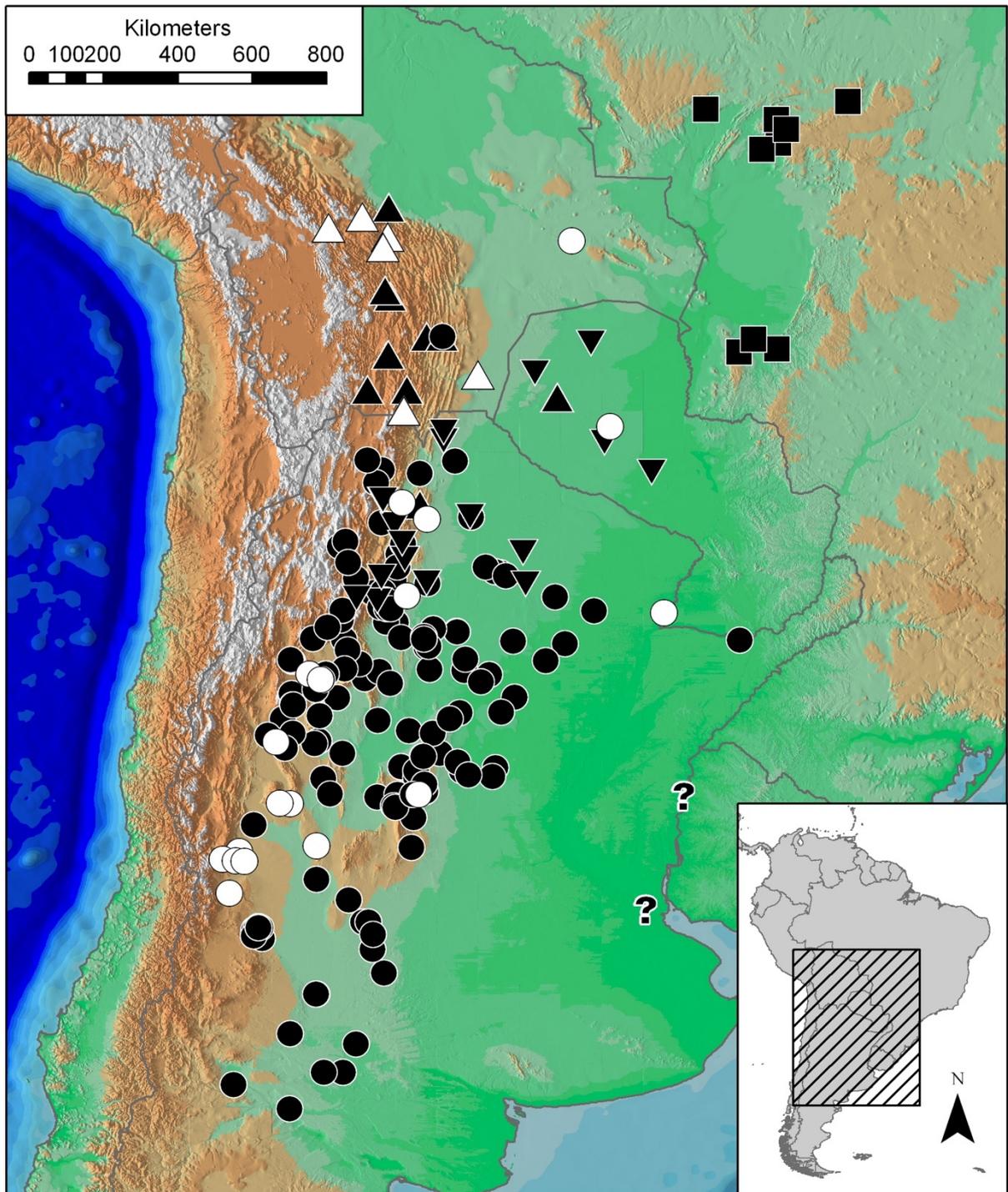


Figure 5. Best scoring maximum likelihood (ML) tree estimated using RAxML, as implemented in the CIPRES Science Gateway. Numbers in the nodes correspond to Bootstrap support values.

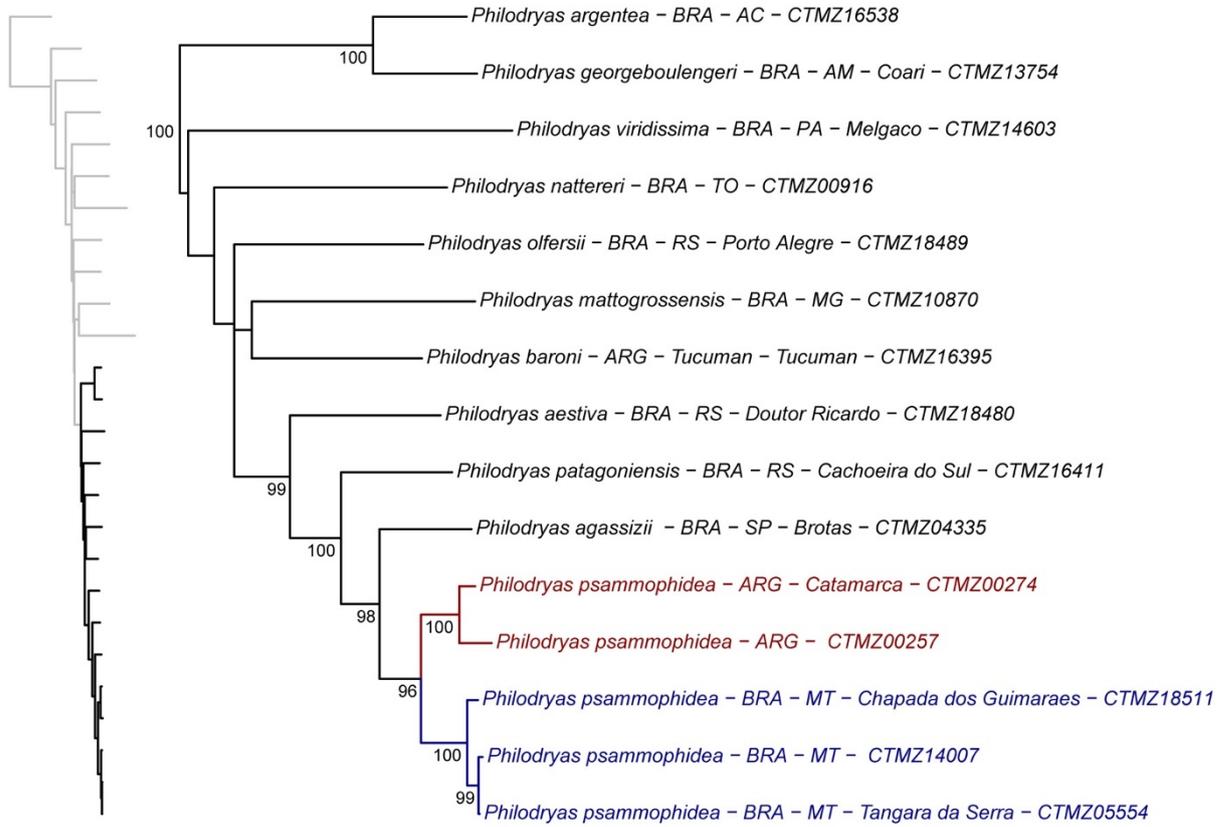


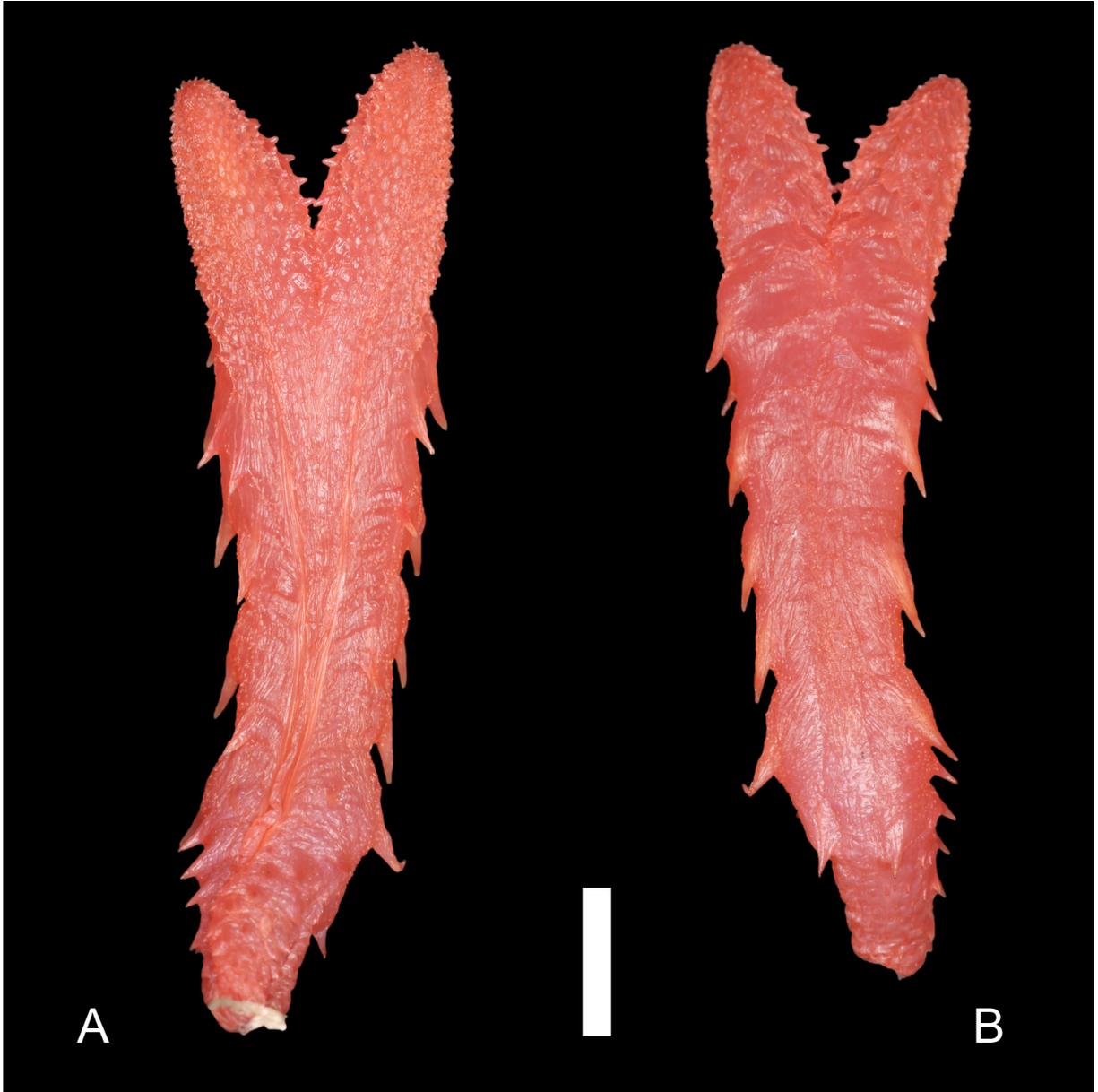
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Chapter 3

A new Andean species of *Philodryas* (Dipsadidae, Xenodontinae) from Ecuador



A new Andean species of *Philodryas* (Dipsadidae, Xenodontinae) from Ecuador

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Abstract

We describe a new species of *Philodryas* from the highlands of southern Ecuador. The new species is distinguished from all known species of *Philodryas* by a unique combination of coloration, scalation, and hemipenial characters. The new species resembles *Philodryas simonsii* in color pattern. However, they differ notoriously by their hemipenial morphology. The three other trans-Andean members of the genus (*Philodryas simonsii*, *Philodryas chamissonis*, and *Philodryas tachymenoides*), along with the new species, compose a probably monophyletic group that may be characterized by the presence of ungrooved postdiastemal teeth in the maxilla. Unlike most species of the genus *Philodryas*, the new species shows a restricted distribution, being apparently endemic to a small region of high-altitude (3150–4450m) grasslands in the southern Andes of Ecuador.

Key words: Andes, Hemipenis, Neotropical Snakes, Philodryadini, taxonomy

Resumen

Describimos una nueva especie de *Philodryas* de las tierras altas del sur de Ecuador. La nueva especie se distingue de todas las especies de *Philodryas* por una combinación única de coloración, escamación y caracteres hemipenianos. La nueva especie se asemeja a *Philodryas simonsii* en el patrón de coloración. Sin embargo, estas especies difieren notoriamente en su morfología hemipeniana. Los otros tres miembros trans-Andinos del género (*Philodryas simonsii*, *Philodryas chamissonis*, y *Philodryas tachymenoides*) junto con la nueva especie componen un grupo probablemente monofilético, que puede ser caracterizado por la presencia de dientes post-diastemales sin surco en el maxilar. A diferencia de la mayoría de las especies del género *Philodryas*, la nueva especie presenta una distribución restringida, aparentemente siendo endémica a una pequeña región de pastizales de gran altitud (3150–4450m) al sur de los Andes de Ecuador.

Palabras Clave: Andes, Hemipenes, Philodryadini, Serpientes Neotropicales, taxonomía

Introduction

Snakes of the genus *Philodryas* Wagler 1830 are large diurnal racers endemic from South America (Thomas 1976; Tipton 2005). Currently, 20 species are known to belong to the genus (Zaher *et al.* 2008, 2009). However, the taxonomic identity of several taxa within *Philodryas* remains obscure (e.g., Thomas 1996; Zaher 1999; Zaher *et al.* 2008, 2009; Grazziotin *et al.* 2012). Most species (17 spp.) inhabit the lowlands of cis-Andean South America, while only three are known to occur along the trans-Andean part of the continent in Chile, Bolivia, Peru, and

Ecuador. These are *P. chamissonis* (Wiegmann 1835), *P. simonsii* Boulenger 1900, and *P. tachymenoides* (Schmidt & Walker 1943) (Sallaberry-Pincheira *et al.* 2011; Thomas 1976, 1977).

Although “western members” of the genus *Philodryas* are currently reduced to three, their composition changed drastically through the last century (Amaral 1929; Maglio 1970; Parker 1932; Thomas 1977; Zaher *et al.* 2008). Most taxonomic changes focused on the generic status of these species, all being apparently closely related Andean banded racers (Amaral 1929; Schmidt & Walker 1943; Parker 1932; Maglio, 1970; Thomas 1976, 1977, 1997; Donoso-Barros 1974; Zaher 1999; Zaher *et al.* 2009). Thomas (1977) clarified for the first time the taxonomic status of several poorly known western racers until then loosely assigned to the genera *Dromicus*, *Leimadophis*, *Alsophis*, and *Philodryas*. This author recognized the continental *Philodryas chamissonis*, *P. elegans*, *P. tachymenoides*, and *P. simonsii* and considered *Alsophis angustilineatus* (Schmidt & Walker 1943), *A. inca* (Schmidt & Walker 1943), and *Incaspis cercostropha* Donoso-Barros 1974 as junior synonyms of *P. simonsii*. More recently, Thomas (1997) recognized *Alsophis hoodensis* (Van Denburgh 1912) as a valid species, and placed it within the genus *Philodryas*. However, Zaher (1999) and Zaher *et al.* (2009) provided morphological evidence for the recognition of a clade formed by the Galápagos species (including *P. hoodensis*) and the mainland *Philodryas elegans* that is only distantly related to the remaining *Philodryas*, erecting the genus *Pseudalsophis* to accommodate them. This hypothesis was partly corroborated by Graziotin *et al.* (2012), who performed a molecular analysis of dipsadid snakes in which two sampled species of *Pseudalsophis* (*Ps. elegans* and *Ps. dorsalis*) formed a strongly supported clade.

Among the three trans-Andean species, *Philodryas simonsii* and *P. tachymenoides* inhabit the Andean highlands of Ecuador and Peru (Thomas 1976, 1977) while *P. chamissonis* is known to occur along the Pacific lowlands of Peru and Chile (Sallaberry-Pincheira *et al.* 2011). Herein, we describe a fourth species of *Philodryas* from the Andean highlands of Ecuador that is closely related to *P. chamissonis*, *P. simonsii*, and *P. tachymenoides*.

Material and methods

Specimens examined are listed in appendix 1. Museum abbreviations are as follow: Centro de Ornitología y Biodiversidad (CORBIDI), Lima, Peru; Fundación Herpetológica Gustavo Orcés (FHGO), Quito, Ecuador; Museo de Historia Natural de la Universidad Nacional de San Agustín de Arequipa (MUSA), Arequipa, Peru; Museo de Historia Natural, Universidad Nacional Mayor de San Marcos (MUSM), Lima, Peru; Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, Brazil; The Natural History Museum (BMNH), London, England. Additional information on the morphological variation of *Philodryas georgeboulengeri*, *P. chamissonis*, *P. simonsii*, and *P. tachymenoides* was taken from Prudente *et al.* (2008), Thomas (1976, 1977) and Zaher (1999).

Head length, cephalic scales, and hemipenial measurements were measured to the nearest 0.1 mm with the aid of a digital caliper. Total length (TTL) and tail length (TL) measurements were taken to the nearest 1 mm by stretching carefully the specimens along a ruler. Ventral scale counting follows Dowling (1951). Hemipenes were prepared following protocols described by Myers & Cadle (2003) and Zaher & Prudente (2003). Hemipenial terminology followed Zaher (1999). Photographs of the hemipenes were taken using a Leica DFC425 digital camera attached to a Leica M205a stereoscopic microscope. Multifocal photographs were composed using the Leica Application Suite software.

Philodryas amaru sp. nov.

Figs. 1–2

Holotype. Adult male (FHGO 4749), collected by Ernesto Arbeláez on 6 June 2006, in the private land owned by Manuel Merchan, Termas de Aguas Calientes-Soldados (2° 55' 55" S, 79° 12' 37" W, ca. 3196 m), Parroquia San Joaquín, Cantón Cuenca, Province of Azuay, Ecuador (Fig. 1).

Paratypes. Two adult females (FHGO 6399 and FHGO 6400) collected along with the holotype.

Diagnosis. A *Philodryas* that differs from all other species of the genus by the following combination of characters: Snout not acuminate anteriorly; maxilla with 14 to 15 prediastemal maxillary teeth and two ungrooved postdiastemal teeth; dorsal pattern with three stripes, one vertebral and two paravertebrals of similar width; ventral

scales 184 in male (N=1) and 200 in females (N=2); subcaudal scales 119 in male and 102–112 in females; supralabial scales 7 or 8; nasal scale completely divided; loreal scale present; infralabial scales 9 or 10; dorsal scale rows 19/19/15; cloacal scale divided; dorsal scales with two apical pits; hemipenial body with a basal constriction and an asulcate surface ornamented by two parallel rows of enlarged body calyces extending from the tip of the lobes to the base of the hemipenial body.

Comparisons. *Philodryas amaru* differs from all cis-Andean congeners by the presence of two ungrooved postdiastemal teeth on the maxilla (vs. grooved postdiastemal teeth present in all cis-Andean species), and from the trans-Andean *P. simonsii*, *P. chamissonis*, and *P. tachymenoides* by the presence of three uniformly dark brown dorsal stripes with two scale rows width (vs. brownish dorsal stripes smaller, with less than one dorsal scale row of width in *P. simonsii*; only one vertebral stripe in *P. chamissonis*; no dorsal stripes in *P. tachymenoides*) and by the presence of two rows of large, shallow body calyces extending along the asulcate surface of the hemipenis from the tip of the lobes to the proximal one third of the hemipenial body (vs. two rows of large and deep body calyces in *P. chamissonis*; more than two rows of smaller and shallow body calyces restricted to the asulcate surface of the lobes and distal portion of the hemipenial body in *P. simonsii*). Furthermore, we refer to Table 1 for additional differences in meristic characters between trans-Andean species of *Philodryas*.

TABLE 1. Variation from selected meristic characters of the four trans-Andean species of *Philodryas*.

	<i>P. amaru</i>	<i>P. chamissonis</i>	<i>P. simonsii</i>	<i>P. tachymenoides</i>
Number of Ventrals	184 ♂ 200 ♀	167–194 ♂ 181–199 ♀	182–205 ♂ 189–215 ♀	185–189 ♂ 200–218 ♀
Subcaudals	119 ♂ 102–112 ♀	96–118 ♂ 93–109 ♀	103–125 ♂ 101–123 ♀	104–105 ♂ 96–108 ♀
Apical Pits	two	One	One	One
Supralabials	7 or 8	8	8	8 or 9
Infralabials	10–11	11	9–11	10–11
Maxillary Teeth	14–15	13–14	10–13	10–12

Description of the holotype. A large male with 622 mm TTL, 206 mm TL (33.1% of TTL), 17.7 mm head length (2.8% of TTL), 9.4 mm head width at broadest point, and 5.4 mm snout length. Head slightly distinct from neck in dorsal view (Fig. 1C); body robust. In lateral view, dorsal margin of the head rounded, with a marked inclination near to the snout (Fig. 1D). Snout rounded in dorsal and lateral views (Fig. 1). Rostral scale subtriangular in frontal view, slightly wider than high (width 3.3 mm, height 2.1 mm), visible in dorsal view, contacting internasals, anterior nasals, and first supralabials. Internasals paired, polygonal, visible in lateral view, in broad medial contact, contacting nasals laterally and prefrontals posteriorly. Prefrontals paired, polygonal, as wide as long, in broad medial contact, with a dextral suture. Prefrontals contact posterior nasals, loreals and preoculars laterally, and preoculars, supraoculars and frontal posteriorly. Supraoculars polygonal, longer than wide, in contact with preoculars and postoculars laterally, with frontal medially, and with parietals posteriorly. Frontal pyramidal, longer than wide (4.8 mm length, 2.9 mm width), in contact with parietals posteriorly. Parietals polygonal, longer than wide, in broad medial contact with each other, contacting postoculars antero-laterally and temporals laterally. Nasal completely divided, with the suture vertical and the nostril mainly positioned in the dorsal region of the anterior nasal. Nasals rectangular, higher than long. Anterior nasals in contact with the first supralabial ventrally. Posterior nasals in contact with first and second supralabials, and loreal posteriorly. Loreal rectangular, slightly longer (1.6 mm) than high (1.3 mm), in contact with second and third supralabials ventrally, and preocular posteriorly. Preoculars nearly polygonal, higher than long, broadly bordering the orbit. Preocular contacting the third and fourth supralabials ventrally. Eye 2.8 mm of diameter, with rounded pupil. Two polygonal postoculars, with the upper one larger than the lower one. The upper postocular contacts the anterior temporal and the parietal posteriorly, while the lower postocular contacts the fourth and fifth supralabials ventrally and the anterior temporal posteriorly. Temporals 1 + 2, arranged in vertical rows. Seven supralabials, increasing in size posteriorly, with third and fourth scales bordering the ventral margin of orbit. Mental triangular, wider than long, and in broad contact with first infralabials laterally. Nine and 10 infralabials on the left and on the right sides, respectively. First pair of infralabials in medial contact. Two pairs of chinshields, with the anterior pair larger than

posterior one. First four infralabials in contact with the first pair of chinshields on the left side and the first five on the right side. Mental groove composed by the first pair of infralabials and the two pairs of chinshields. Gular scales lanceolate, arranged in five diagonal rows. Maxilla with 15 prediastemal teeth and two ungrooved postdiastemal teeth. Dorsal scales smooth, arranged in 19/19/15 rows, with two apical pits in their distal tip. Scale row reduction from 19 to 15 rows along the right side of the dorsum occurs through the loss of the 8th row and the fusion of the 4th and 5th rows at the level of ventral 98. On the left side, scale row reduction from 19 to 17 occurs at the level of ventral 101 through the loss of the 8th row, and from 17 to 15 at the level of ventral 102 through the fusion of the 4th and 5th rows. Ventral scales smooth, with the posterior edge straight. Preventrals four and ventrals 184. Cloacal scale divided, and paired subcaudals 119 plus a terminal spine.

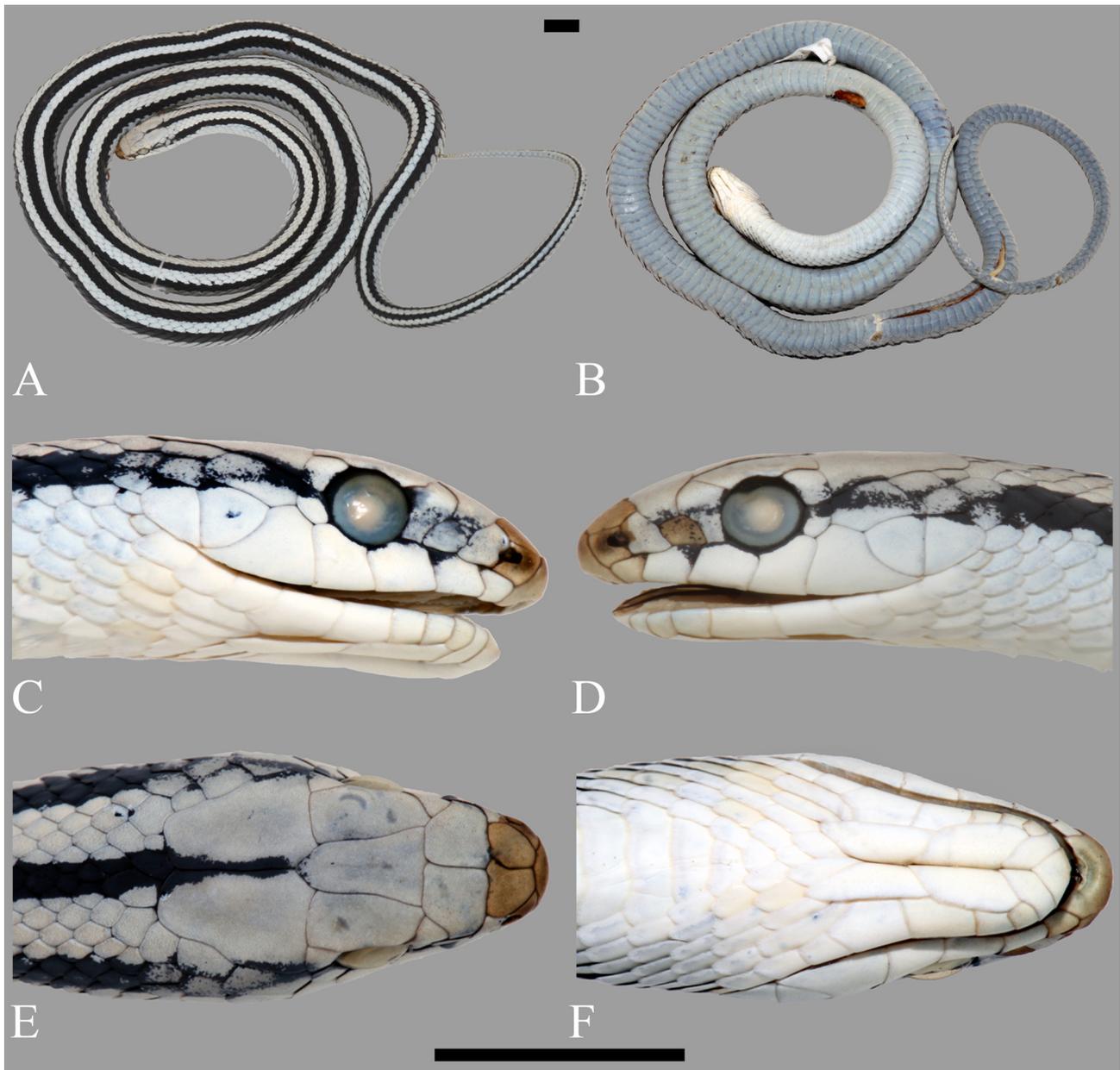


FIGURE 1. Holotype of *Philodryas amaru* (FHGO 4749) in dorsal (A) and ventral (B) views. Head of the holotype in right lateral (C), left lateral (D), dorsal (E), and ventral (F) views. Scale length = 10 mm.



FIGURE 2. Dorsal view of the holotype of *Philodryas amaru* in life (FHGO 4749) from Soldados, San Joaquin, Province of Azuay, Ecuador. Photograph by E. Arbeláez and A. Vega.

Coloration of the holotype in preservative. The dorsal surface of the head is light brownish grey while most of the labial scales and the ventral region of the head are light cream. The dorsum is light bluish grey with three longitudinal uniform black stripes, one vertebral and two paravertebrals. The vertebral stripe runs along the dorsoposterior part of the head and vertebral region, from the anterior tip of the parietal suture to the tip of the tail, occupying two rows of dorsal scales in the first third of the body and three rows posteriorly. The vertebral stripe tapers posteriorly from the level of the cloaca to the tip of the tail. The two paravertebral stripes extend on the lateral surface of the head as irregularly faded lines, on the loreal, uppermost margins of supralabials 2nd, 3rd, 6th, and 7th, postoculars, anterolateral margin of parietals, and temporals. Posterior to the temporal region, the paravertebral stripes turn into uniform black lines that run along the 4th and 5th paravertebral rows along the anterior one-third of the body, enlarging posteriorly to include the 3rd paravertebral row until the level of the cloaca. After the cloacal region, the paravertebral stripes taper posteriorly and fade away before reaching the tip of the tail. The belly is light bluish grey on its anterior one-third, and gradually turns into a darker bluish grey posteriorly, which covers the posterior two-third of the belly and the tail.

Coloration of the holotype in life. In the live specimen, the three vertebral and paravertebral stripes are dark brown while the dorsum is light brown, except for the first and second rows that are yellowish-green. The ventral surface on belly and tail is light yellow-brown to olive green. The head is light brown, while the supralabials and the ventral surface of the head are cream. The first, second, and third supralabials are bordered with dark brown (Fig. 2).

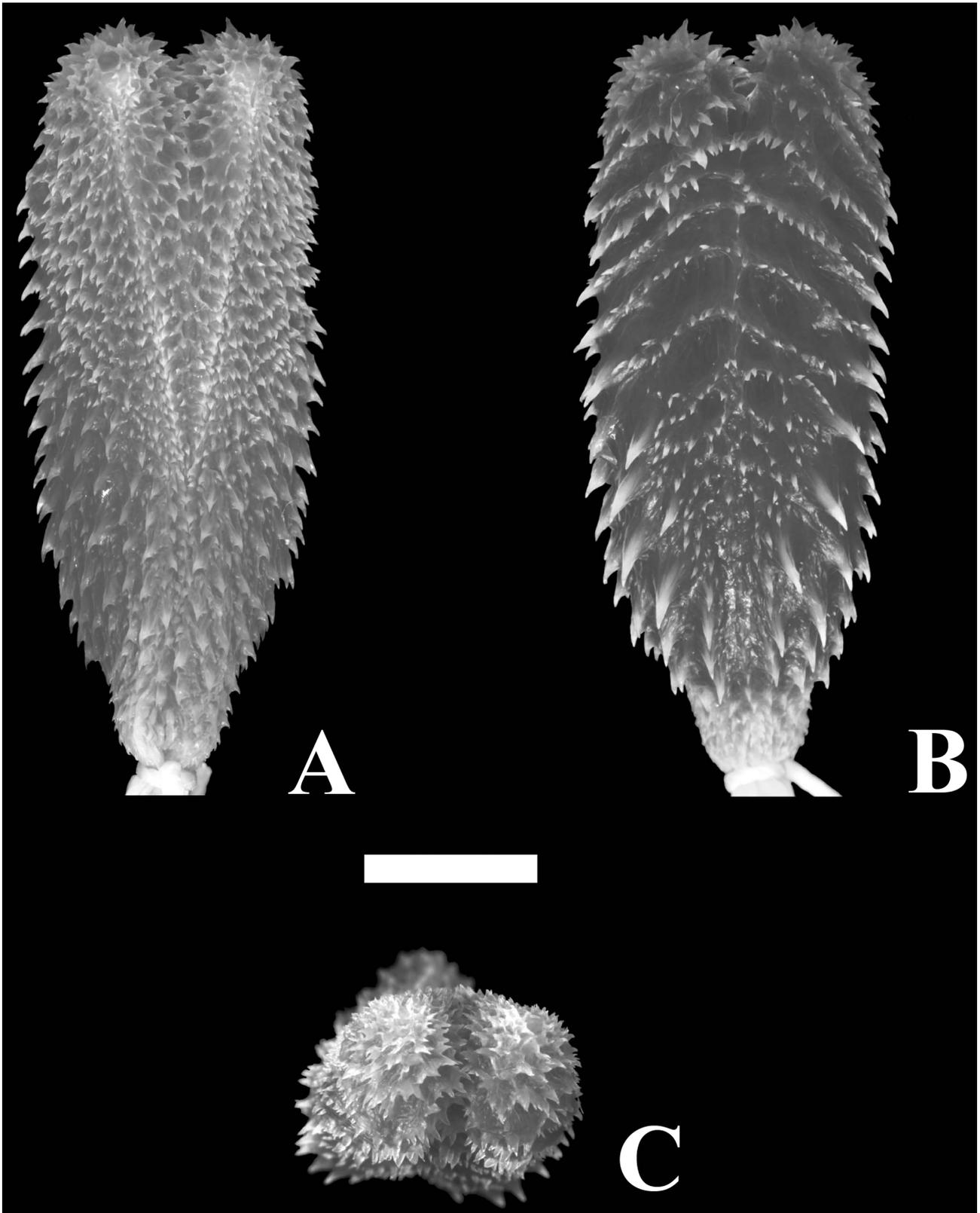


FIGURE 3. Hemipenis of the holotype of *Philodryas amaru* (FHGO 4749) in sulcate (A), asulcate (B), and top (C) views. Scale length = 5 mm.

Hemipenis of the holotype. The hemipenis is fully everted and maximally expanded (Fig. 3), with 21.7 mm of total length, 8.4 mm at the widest point, and lobes with 3.9 mm length (18% of the length of the everted hemipenis). When inverted in the tail, it extends to the level of the 15th subcaudal (inverted hemipenis with 26.1

mm of total length) with the lobes bifurcating at the level of the 13th subcaudal (inverted lobes with 4.4 mm). The organ is flattened in lateral view, with a visible constriction at the base of the hemipenial body. It is semicalyculate, semicapitate, and slightly bilobed, with very short but clearly visible lobes. While the lobes are short, the capitulum covers half of the organ, being only feebly delimited by shallow edges and mostly restricted to the sulcate surface. The capitulum is formed by papillate calyces, which tend to be larger towards the tip of the lobes. The sulcus spermaticus divides on the proximal region of the organ (upper one-third from the base), and both branches extend centripetally along the sulcate surface diverging only slightly from each other to end at the tip of the lobes. The proximal half of the hemipenial body (including the constriction at the base) is covered with rows of small to medium-sized spines in its sulcate surface. Both lateral surfaces of the hemipenis are covered by two to three rows of lateral enlarged spines that converge to the asulcate surface to meet each other proximally on the asulcate surface above the basal constriction. Below the basal constriction, the asulcate surface is covered with small-sized spines. The asulcate surface of the lobes and distal half of the hemipenial body are covered with two rows of large and shallow body calyces that are ornamented by a row of spinulate papillae at their edge and extend from the midline of the hemipenis to the border of the rows of lateral enlarged spines. The spinulate papillae ornamenting the body calyces are large at the level of the lobes and gradually reduce in size towards the proximal half of the hemipenial body. The proximal half of the asulcate surface of the hemipenial body is ornamented with small-sized spines and lateral enlarged spines.

Variation. Differently from the male holotype, the two paratypes (FHGO 6399, 6400) are adult females with eight supralabial scales (with the 4th and 5th entering the orbit). Additionally, FHGO 6399 has 845 mm of TTL, 240 mm of TL (28.4% of TTL), 22.4 mm of head length (2.6% of TTL), three preventrals, 200 ventrals, 112 paired subcaudals, nine infralabials, first pair of chinshields bordered by the first four infralabials and second pair by 4th and 5th, 2 + 2 and 1 + 2 temporals in left and right sides, respectively. FHGO 6400 has 913 mm of TTL, 250 mm of TL (27.3% of TTL), 23.8 mm of head length (2.6% of TTL), three preventrals, 200 ventrals, 102 paired subcaudals, 10 infralabials, first pair of chinshields bordered by the first five infralabials and second pair by 5th and 6th, 1 + 3 temporals. In preservative, the coloration of the two paratypes is quite similar to the condition described for the holotype.

Etymology. The specific epithet *amaru* is derived from the Ecuadorian Kichwa dialect, meaning snake. Along the Andean region of Ecuador, *Amaru* is often known to represent a snake deity related to the economy and vitality of the water that allows the existence of Andean people. Also, “Amaru” or “snake” is considered to represent the first mother of the pre Inca Cañari culture that lived where presently is the city of Cuenca.

Distribution and natural history. The type locality is in the east versant of the inter-Andean valley of the Tomebamba River, in the southern portion of the Andes of Ecuador (Fig. 4). The elevation in this region ranges from 2600 m to 4450 m, and is characterized by complex ecosystems that combine Andean temperate forests, high Andean forests of *Polylepis* (Rosaceae), and high-altitude grasslands called Páramo (Arbeláez & Vega 2008). Vegetational physiognomy at the type locality is dominated by secondary shrub forests called “Andean Chaparro” (*Weimannia* sp. *Ocotea* sp.), medium-size trees, and grasslands (*Calamagostis intermedia*) at higher altitudes (Fig. 5).

We observed 33 individuals alive in the field from 2005 to 2008. All specimens were found active during the day (10:30h to 15:00h) in open grassland areas or between shrubs and water vegetation on the ground, under logs associated to water bodies from natural thermal ponds, streams, and in the border of rivers. Eggs of the *P. amaru* have been found in soil tunnels, galleries and under decaying logs. Three nest groups with 9, 10, and 13 light cream small elliptical eggs, respectively, were found about 150 cm underground. Two specimens that were manipulated regurgitated an Andean lizard (*Stenocercus festae*) and a marsupial frog of the genus *Gastrotheca*, respectively.

Discussion

Unlike most species of *Philodryas* that have large distributional ranges (Thomas 1976, Peters and Orejas-Miranda 1970), *Philodryas amaru* is apparently endemic to a small valley in the Andes of southern Ecuador. *Philodryas amaru*, *P. simonsii*, *P. chamissonis*, and *P. tachymenoides* compose a group of trans-Andean species that is characterized by the presence of ungrooved postdiastemal maxillary teeth. Although this character may represent a

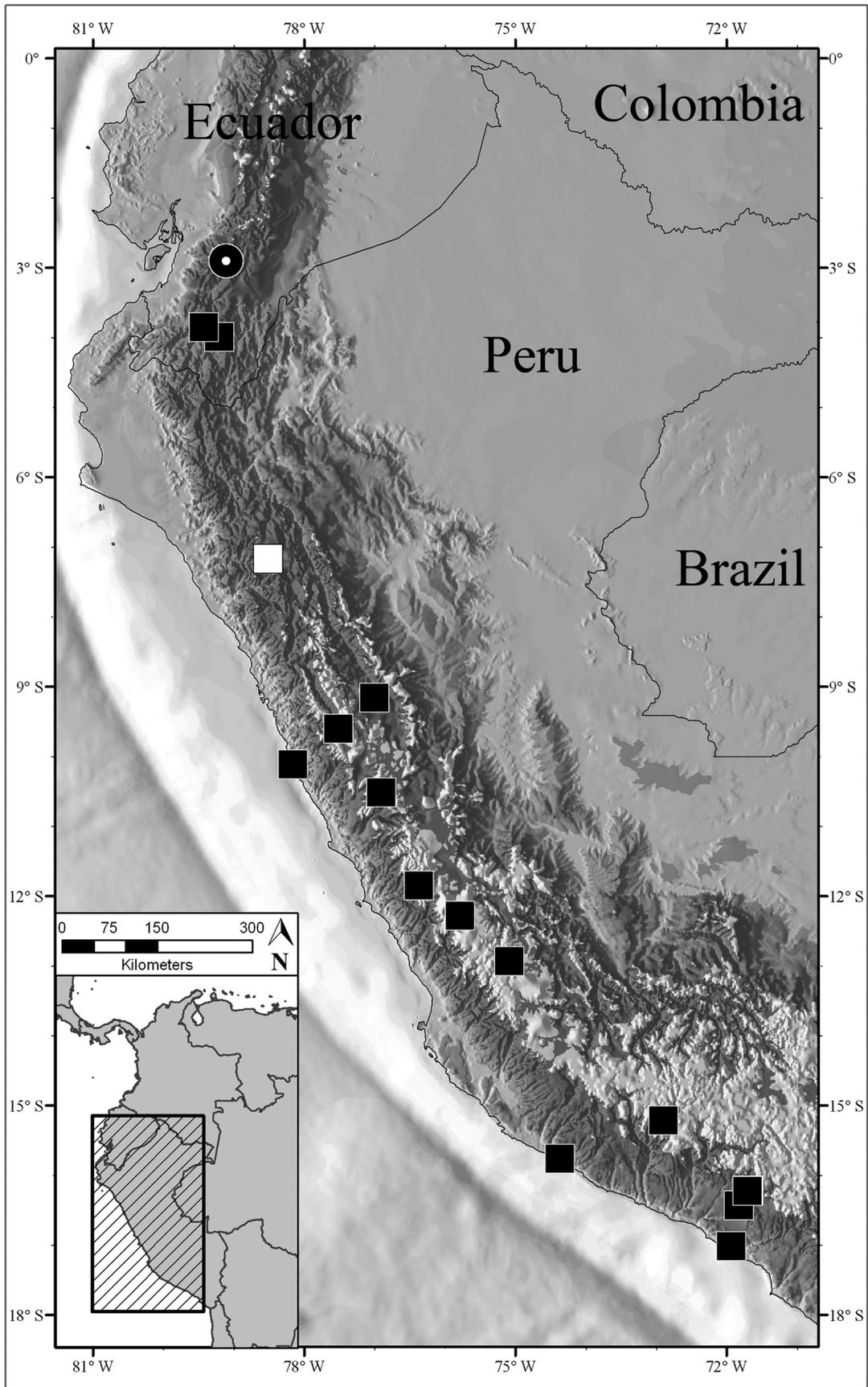


FIGURE 4. Type locality of *Philodryas amaru* (circle with the white dot) and distribution records of *Philodryas simonsii* (squares). The white square corresponds to the type locality of *Philodryas simonsii*.



FIGURE 5. General view of the habitat in the type locality of *Philodryas amaru*, situated in Soldados, San Joaquin, Province of Azuay, Ecuador. Photograph from E. Arbeláez and A. Vega.

synapomorphy for a “western clade” of *Philodryas* geographically separated from all the other species of genus, such hypothesis still need to be tested accurately. The only known morphological phylogeny of the genus suggests a polyphyletic origin for the western group, with *P. simonsii* being retrieved in an unresolved polytomy that does not include *P. chamissonis* (Lobo & Scrocchi 1994). However, these authors did not include in their dataset the postdiastemal teeth conditions found in *Philodryas*, preventing an explicit test of the ungrooved state as a synapomorphy for the western group. Additionally, none of the western species of *Philodryas* were included in recent molecular phylogenetic analyses, precluding any further analysis of their relationships (Zaher *et al.* 2009; Graziotin *et al.* 2012; Pyron *et al.* 2013).

The new species is easily distinguished from *P. chamissonis*, *P. simonsii*, and *P. tachymenoides* by its well-defined dorsal color pattern with three large longitudinal stripes and its hemipenial morphology with a pair of large and shallow body calyces ornamenting the asulcate surface of the lobes and most of the hemipenial body. Among the three western taxa, *P. simonsii* is the species that can be more easily confused with *P. amaru* due to their external similarities. However, the hemipenial morphology of *P. simonsii* is clearly distinct from that of the new species, notably by the presence of smaller irregularly distributed body calyces that are restricted only to the asulcate surface of the lobes and uppermost region of the hemipenial body (Fig. 6).



FIGURE 6. Right hemipenis of the holotype of *Philodryas simonsii* (BMNH 1946.1.4.98), opened through a slit along the sulcus spermaticus and spread flat.

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APPENDIX 1. Specimens examined.

- Philodryas chamissonis* (N = 10).—**CHILE**: ATACAMA: Atacama, Km 700 (MZUSP 8235); BÍO-BÍO: Concepción (MZUSP 14419); Mulchén, Fundo Santa Raquel (MZUSP 8236); Los Angeles (MZUSP 8839); COQUIMBO: Locos (MZUSP 5412); SANTIAGO: No locality data (MZUSP 962); Santiago (MZUSP 4128–4129); Rungue (MZUSP 4135); Cerro San Cristobal (MZUSP 5934).
- Philodryas simonsii* (N = 20).—**PERU**: ANCASH: Malvas (MUSM 20056); Province of Recuay, Chaucayan, (MUSM 24862); Yurayacu (MUSM 3219); AREQUIPA: No locality data (MUSA 3314); Province of Arequipa, Vitor, Vitor (MUSA 902); Province of Caravelí, Atiquipa, Lomas de Atiquipa (MUSA 531, 1063, 1237); Province of Islay, Mejia, Lomas de Mejia (MUSA 527, 1256); Province of La Unión, Cotahuasi, Alrededores de Cotahuasi (MUSA 1300); CAJAMARCA: Cajamarca (BMNH 1946.1.4.98, holotype); LIMA, Province of Alis, Hualaria (CORBIDI 5607); Province of Cajatambo, Cajatambo (MUSM 25347); Province of Huarochiri, Santa Eulalia, 1800 m (CORBIDI 5008); Chacahuaro (MUSM 25315); Province of Oyón, Oyón (MUSM 23480); Tingo Alis (MUSM 23453). **ECUADOR**: LOJA: Loja (BMNH 1931.11.3.16); Catamayo Valley, 4700 m 35 Km N of Loja (BMNH 1935.11.3.93).
- Philodryas tachymenoides* (N = 7).—**PERU**: ANCASH: Bolognesi (MUSM 3029); LIMA: Province of Cajatambo, Cajatambo (MUSM 25351); Province of Yauyos, Alis (MUSM 23454, 23469, 23481–23482); Province of Oyón, Oyón (MUSM 23479).