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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 (Dipsadidae: Xenodontinae)

Corrected Version

Thesis presented to the Post-Graduate Program of the Museu de Zoologia da Universidade de São Paulo to obtain the degree of Doctor of Science (Systematics, Animal Taxonomy and Biodiversity).

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São Paulo

2019

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 contém 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, Morfología, Sistemática Molecular, Hemipênes.

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 (Figueroa *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*, *Ichthycyphus*, *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 *Pseudablabes* 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* (Boulenguer, 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 olfersii*) 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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Conclusion

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.

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 (Olveira *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.

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.