



Morphological variation in *Xenoxybelis boulengeri* (Procter, 1923) (Serpentes, Xenodontinae, Philodryadini)

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Abstract

The genus *Xenoxybelis* contains two species, *X. argenteus* and *X. boulengeri*, characterized by semi-arboreal habits and an extremely thin rostral area, classified in the subfamily Xenodontinae (Colubridae). *Xenoxybelis boulengeri* is considered a rare species and is poorly represented in scientific collections. Its external morphology is known only from the original description and seven other specimens. In this study, twenty additional specimens were examined from the Brazilian states of Acre, Amazonas and Rondônia. Variation in meristic and morphometric characters are described, and new characters are incorporated in a revised diagnosis of the species. Illustrations and a description of the hemipenes of *X. boulengeri* are presented for the first time. Analysis of morphological and molecular characters permit allocation of *Xenoxybelis* to the tribe Philodryadini, together with *Ditaxodon*, *Philodryas*, *Pseudablakes* and *Tropidodryas*.

Key words: *Xenoxybelis boulengeri*; morphology; hemipenis, Philodryadini

Introduction

The genus *Xenoxybelis* Machado, 1993 contains two species: *X. argenteus* (Daudin, 1803) and *X. boulengeri* (Procter, 1923). Prior to Machado's study (1993), these species were allocated to the genus *Oxybelis* Wagler, 1830, together with *O. aeneus* (Wagler, 1824), *O. brevirostris* (Cope, 1861) and *O. fulgidus* (Daudin, 1803), traditionally included in the Colubrinae Opper, 1811 (Ferrarezzi, 1994). Machado (1993) observed that *Oxybelis* (*sensu* Keiser, 1974; 1989) was polyphyletic, proposing the genus *Xenoxybelis* for *X. argenteus* and *X. boulengeri*, based on hemipenial structure (semicapitate and bilobed, with a forked sulcus spermaticus). Machado removed *Xenoxybelis* from Colubrinae, and allocated it to the subfamily Xenodontinae Bonaparte, 1845 (tribe Alsophiini Fitzinger, 1843). Zaher (1999) described the hemipenes of *X. argenteus* and affirmed that this species shares a common hemipenial pattern with other Xenodontinae related to species of *Philodryas* Wagler, 1830 of the "olfersii" group (*P. olfersii* Lichtenstein [1823], *P. viridissimus* Linnaeus [1758] and *P. cordata* Donnelly and Myers [1991]).

Xenoxybelis argenteus was described by Daudin (1803) as *Coluber argenteus* Linnaeus, 1758, being later transferred by Boulenger (1896) to *Oxybelis*. This species occurs in the humid forests of Venezuela, Guyana, Ecuador, Colombia, Peru, Bolivia, Paraguay and in Brazil, where it is found in the Amazonian region (Keiser, 1974; Cunha & Nascimento, 1978, 1993; Machado, 1993; Cisneros-Heredia, 2007). According to Martins & Oliveira (1999), *X. argenteus* is semi-arboreal, occurring mainly in primary forests. *Xenoxybelis boulengeri*

was described by Procter (1923) (as *Oxybelis boulengeri*), based on a single specimen from Trinidad, Mamoré River, Bolivia.

Amaral (1930) examined the holotype of *O. boulengeri*, and suggested that the divided cloacal plate and the uniform coloration of the gular area represented individual variation of *O. argenteus*, considering these taxa to be synonymous. Keiser (1974), in his identification key for the species of *Oxybelis*, suggested that *O. boulengeri* (at that time treated as a junior synonym of *O. argenteus*) might be a distinct and valid species. Subsequently, Keiser (1989) examined the holotype and seven additional specimens (six of them from an area in the influence of the Madeira River Basin, including southeastern Peru, northeastern Bolivia and high Amazonas River in Brazil), recognizing *O. boulengeri* and increasing the range of known variation.

Our examination of twenty specimens of *Xenoxybelis boulengeri* deposited in the Museu Paraense Emílio Goeldi, from the states of Acre, Amazonas and Rondônia, Brazil, has contributed to the knowledge of this species, mainly with regard to external features and hemipenial morphology, resulting in its allocation to the tribe Philodryadini of the colubrid subfamily Xenodontinae.

Material and methods

Twenty specimens of *Xenoxybelis boulengeri* and 78 of *X. argenteus* were examined in the collection of the Museu Paraense Emílio Goeldi (MPEG), Belém, Pará (Appendix). For analysis of meristic and morphometric characters, the approaches of Peters (1964) and Prudente (1998) were followed. Ventral scales were counted according to Dowling (1951). Measurements of the specimens are presented in millimeters, and were made using a measuring tape and digital calipers.

Three everted hemipenes of *Xenoxybelis argenteus* (MPEG 2631, 19356 and 19979) and one everted hemipenis of *X. boulengeri* (MPEG 18226) were available for examination. Preparation of the hemipenes involved fixation in 10% formaldehyde, following Manzani & Abe (1998). For recently preserved animals, we followed the methodology of Pesantes (1994), with modifications proposed by Zaher & Prudente (2003). The terminology describing hemipenes follows Dowling & Savage (1960), Myers & Cadle (1994), and Zaher (1999). The illustrations were produced using a stereomicroscope.

Xenoxybelis boulengeri (Procter, 1923)

Oxybelis boulengeri: Procter, 1923: 1062. Type Locality: Rio Mamoré, Trinidad, Bolívia.

Oxybelis argenteus: Amaral, 1930: 45.

Oxybelis boulengeri: Keiser, 1989: 764.

Xenoxybelis boulengeri: Machado, 1993: 99.

Revised diagnosis. *Xenoxybelis boulengeri* is distinguished from *X. argenteus* by: loreal present (*vs.* absent); divided cloacal plate (*vs.* single); absence of dark spots on ventral side of head (*vs.* presence); presence of wide dark green band on median side of vent (*vs.* absence); presence of median dark green band on subcaudals (*vs.* absence); dark green dorsum (*vs.* dorsum with dark vertebral band); moderately long hemipenes, three times longer than wide (*vs.* string-like, about two times longer than wide); profoundly bilobed (*vs.* slightly bilobed), with two to four rows of lateral spines on each side, that extend from the sulcate to asulcate site, without any distinct rows larger than others (*vs.* two to four rows of lateral spines on each side, with one row larger than others).

Description. Smooth dorsal scales most frequently in 17/17/15 rows ($n = 18$), ranging from 17/17/13 ($n = 1$) to 15/17/13 ($n = 1$), without apical pits. Ventrals: 189–202 ($n = 10$) in males; 190–207 ($n = 6$) in females. Subcaudals divided: 174–198 ($n = 10$) in males; 180–209 ($n = 6$) in females. Divided cloacal plate. Cloacal

glands of males and females reach the 4th and 5th subcaudals, respectively. Snout-vent length ranging from 561–721mm (\bar{x} = 632.4; SD = 55.1; n = 10) in males; 592–790mm (\bar{x} = 695.5; SD = 78.0; n = 7) in females. Tail length ranging from 330–472mm (\bar{x} = 410.5; SD = 62.6; n = 10) in males; 424–508mm (\bar{x} = 467.1; SD = 40; n = 7) in females. Elongate head, distinctly wider than neck, head length ranging from 20.3–25.2mm (\bar{x} = 22; SD = 1.6; n = 9) in males; 24.7–30.0mm (\bar{x} = 26.2; SD = 2.2; n = 7) in females. Distance from the eye to anterior of rostral plate ranging from 6.7–8.3mm (\bar{x} = 7.43; SD = 0.57; n = 9) in males; 8.3–10.3mm (\bar{x} = 8.8; SD = 0.76; n = 7) in females. Head width ranging from 6.6–7.9mm (\bar{x} = 7.2; SD = 0.5; n = 7) in males; 8.2–9.23mm (\bar{x} = 8.7; SD = 0.6; n = 7) in females. Head height ranging from 5.6–7.6mm (\bar{x} = 6.6; SD = 0.61; n = 7) in males; 6.5–9.2mm (\bar{x} = 7.9; SD = 0.9; n = 7) in females. Eye width corresponding, on average, to 15.5% of the head length and eye height on average about 42.5% of the head height. One preocular, three postoculars. Temporals 1+2. Six supralabials, fourth larger than others and in contact with eye (n = 19). Eight infralabials (n = 15), rarely seven (n = 4). Two pairs of chin shields, posterior pair larger than anterior pair. Nasal single. Loreal longer than high. Rostral wider than high. Pentagonal frontal longer than wide, length on average about 24.6% of the head length.

Color pattern in 70% alcohol (Fig. 1). Dorsal side of the body and head ranging from olive-green to brown. Lateral dark brown band begins on rostral area and extends along body as far as cloacal plate. This lateral band divides the dorsal coloration into two stripes: a dark green vertebral stripe and pale green lateral one. Pale green supralabials. Pale green ventral side of the head, without spots. Ventrals pale cream, with a wide median dark green band, beginning on first ventral and extending as far as end of the tail. Discrete, narrow, pale cream line in center of green band, beginning on first ventral and extending as far as the vent, absent on subcaudals.

Hemipenis morphology (Fig. 2). MPEG 18226, right organ removed for illustration. Organ bilobed, semicalyculate and semicapitate, about three times longer than wide at the level of the sulcus spermaticus division. Slightly divergent lobes, about 20% of the total length. On the sulcate side, there is a deep capitular sulcus delimitating the capitula, which is equal to about two-thirds of hemipenis size. Both capitula are almost totally confluent in broad intrasulcar region, forming an uninterrupted calyculate area restricted to sulcate side of the organ. Calyculate area occupying two-thirds of the sulcate side of organ. The sulcus spermaticus divides at the base of the capitulum, with centrolinal branches terminating on distal tip of lobes. The basal third of organ, on the sulcate side, with large lateral spines arranged in two to four longitudinal lateral rows. Lateral spines hook-like, decreasing in size toward apical region, being slightly larger in central area of the organ. Lateral spines increasing in size from sulcate to asulcate side, lacking row or rows of spines conspicuously larger than the others. Asulcate surface ornamented with two longitudinal and six parallel rows of papillate body calyces extending from the tip of the lobes to the base of the hemipenial body. Papillate crest runs on middle of asulcate surface between two rows of body calyces, covered with longitudinal row of small spines.

Geographic distribution (Fig. 3). *Xenoxylis boulengeri* occurs in Amazon Forest, from southeast Peru and northeast Bolivia to northern Brazil, in the states of Amazonas, Acre and Rondônia (Procter, 1923; Cunha & Nascimento, 1978; 1993; Keiser, 1989; Machado, 1993).

Discussion

Comparison of hemipenis morphology of *Xenoxylis argenteus* and *X. boulengeri*. The description and illustration of the hemipenis of *Xenoxylis argenteus* provided by Machado (1993) does not emphasize some important details, and the organ is a little longer than that figured in Zaher (1999), possibly as an artifact of the different methods of preparation. Because the photographs presented by Zaher (1999) show maximally inflated organs, comparisons can be made with the hemipenis of *X. boulengeri* prepared here.

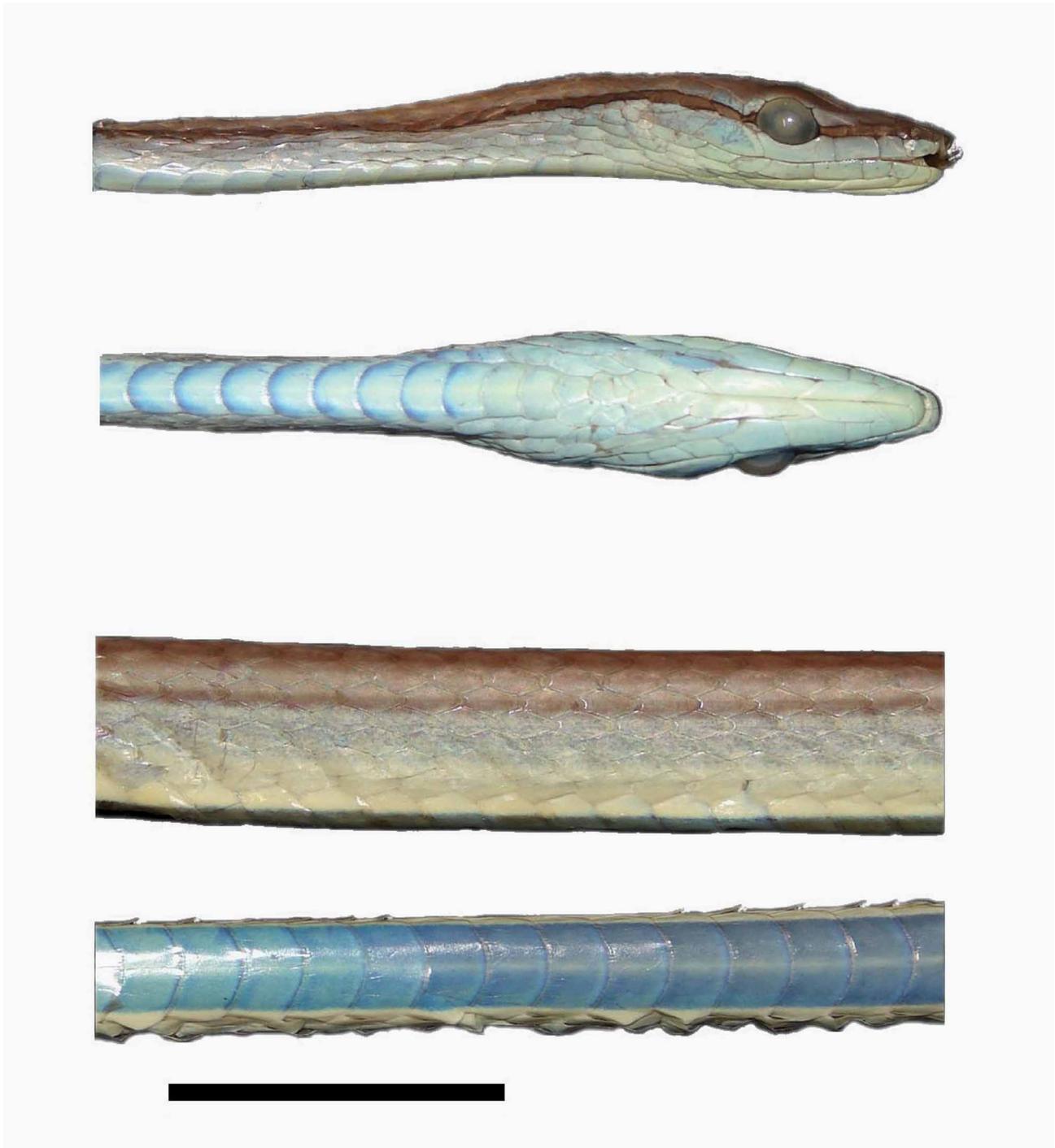


FIGURE 1. Color pattern of *Xenoxybelis boulengeri* (MPEG 19537, Careiro da Várzea, Amazonas, Brazil). Lateral (A) and ventral (B) views of the head; lateral (C) and ventral (D) views of the body. Scale bar 20 mm

The hemipenes of *Xenoxybelis argenteus* and *X. boulengeri* resemble one another in many features. Both are bilobed, semicalyculate and semicapitate, with the capitulum restricted to the sulcate side of the organ and the apical region of the lobes, and the sulcus spermaticus dividing on the base of the capitulum. Rows of large lateral spines are present, and the capitulum is ornamented with papillate calyces. However, the hemipenes of these species present some diagnostic differences that are summarized as follows.

Xenoxybelis boulengeri has a relatively longer organ (3x longer than wide) than *X. argenteus* (2x longer), lacking a heart-shaped condition. The lobes of *X. boulengeri* are larger than those of *X. argenteus*, with the proximal part of the lobes somewhat constricted, a condition that is absent in *X. argenteus*. This character

reinforces the absence of the heart-shaped condition in *X. boulengeri*. In both species, the sulcus spermaticus divides in the distal portion of the calyculate area of the capitulum. According to Zaher (1999), the divided condition of the sulcus spermaticus in the capitulum area is a product of the smaller size of the organ, not as a reflection of the Dipsadinae pattern. Because the hemipenis of *X. boulengeri* is not as short as that of *X. argenteus* and presents the same pattern of sulcus division, it may be hypothesized that sulcus division has evolved independently from the shortening of the hemipenis in *X. argenteus*. The branches of the sulcus spermaticus in *X. boulengeri* are centrolinear. Machado (1993) described this condition of the sulcus branches as semi-centrifugal and Zaher (1999) considered them centrolinear in *X. argenteus*. In both species, two to four rows of enlarged lateral spines of moderate size are arranged on the sulcate and lateral surfaces. In *X. boulengeri* there is no evident size variation in the spine rows as in *X. argenteus*, and the spines increase progressively in size from the sulcate side toward the asulcate one, invading the lateral sides of the asulcate region in a more conspicuous way than in *X. argenteus*. In both species, there is a papillate crest in the middle of the asulcate side between the two rows of body calyces, which are larger and more numerous in *X. boulengeri*.

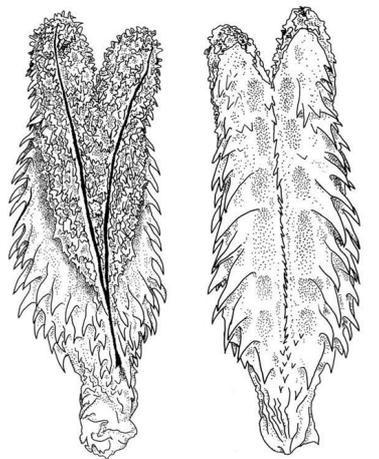


FIGURE 2. Hemipenes of *Xenoxybelis boulengeri* (MPEG 18226). Sulcate (A) and asulcate (B) views. Scale bar 5mm.

Phylogenetic relationships of *Xenoxybelis* and *Philodryas*. Machado (1993), describing the hemipeneal morphology of the species of *Oxybelis* (*sensu* Keiser, 1974; 1989, containing *O. fulgidus*, *O. aeneus* and *O. brevirostris*, *O. argenteus* and *O. boulengeri*), suggested the polyphyly of this genus, with the inclusion of members from the Colubrinae and Xenodontinae. Machado (1993) affirmed that *Oxybelis argenteus* and *O. boulengeri* presented a typically Xenodontinae hemipenis, while the other species possessed the typical pattern of colubrids (mono or bilobed, with simple and asymmetric sulcus spermaticus). Thus, Machado (1993) proposed that the species *O. argenteus* and *O. boulengeri* should be transferred to the genus *Xenoxybelis* in the subfamily Xenodontinae, tribe Alsophiini. This taxonomic reallocation was based on the classification of Dowling & Duellman (1978) and Jenner (1981), which emphasizes characters of hemipeneal morphology, although Dowling & Duellman (1978) omitted the genus *Oxybelis* in their classification.

Machado (1993) described the hemipenis of *Xenoxybelis argenteus* and *X. boulengeri* as bilobed, with semi-centrifugal sulcus spermaticus, and semicapitated, with proximal spines and distal spinulate calyces on the sulcate surface, with the asulcate side almost naked with two median sulcus and two lateral rows of large spines. Jenner (1981) diagnosed the Xenodontinae as taxa with hemipenes with some form of capitation or apical disc, generally a divided sulcus spermaticus, and most species having basal spines and apical calyces. Jenner (1981) further diagnosed the Alsophiini as species with a bilobed and semicapitate hemipenis, basal spines, apical calyces, and divided sulcus (below the semi-capitation). Thus, the generic reallocation of Machado (1993) was consistent with the available information at that time.

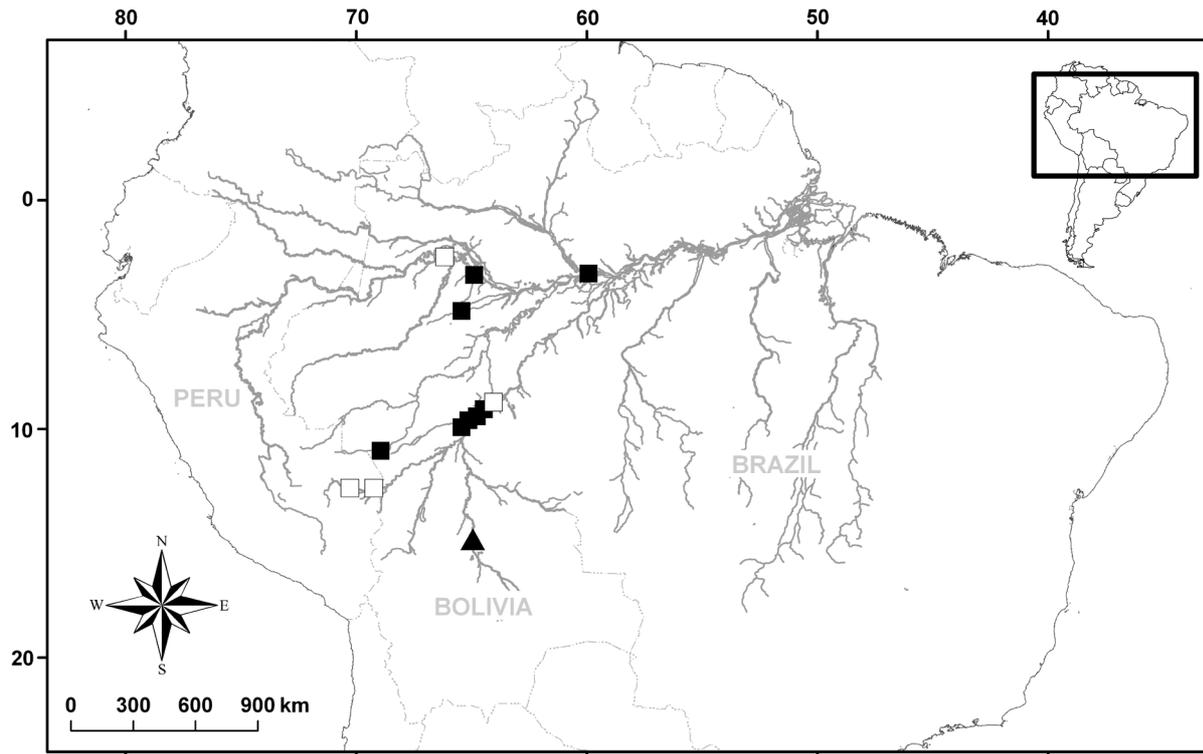


FIGURE 3. Distribution of *Xenoxybelis boulengeri* (closed square – material examined; open square – literature records; closed triangle – type locality). Materials examined are listed in the Appendix.

Zaher (1999) described the hemipenis of *Xenoxybelis argenteus*, indicating its resemblance with the hemipenis of the 'green group' of *Philodryas* (*P. olfersii*, *P. viridissimus* and *P. coronata*). Zaher hypothesized a clade formed by *Xenoxybelis* and the three species of *Philodryas* based on the following synapomorphies: developed body calyces on practically all the hemipenis surface, extending from the top of the lobes to the base of the asulcate side of the hemipenis; heart-shaped organ, with the capitulum of each lobe restricted to the sulcate surface of the organ.

Among the of hemipenial variation in the *Xenoxybelis* species, the one that deserves to be emphasized is the lack of a heart-shaped organ in *X. boulengeri*, but found in *X. argenteus*. This is mainly a result of the longer hemipenis and larger, and more constricted lobes in *X. boulengeri*. Although Zaher (1999) has included the heart-shaped condition of the hemipenis of *X. argenteus* as a probable synapomorphy of the group of 'green' *Philodryas* + *Xenoxybelis*, it does not invalidate the monophyly of the group, because there are other characters that support it. Thus, the diagnosis of the group presented by Zaher (1999) is upheld, excluding only this character. Recently, sequence analysis of mitochondrial ribosomal genes (12S and 16S) of Colubridae, Xenodontinae and Dipsadinae from the Americas, have confirmed a close relationship between *Xenoxybelis* and *Philodryas* (Vidal *et al.*, 2000; Pinou *et al.*, 2004). Vidal *et al.*'s (2000) maximum parsimony analysis recovered the following topology ((*Xenoxybelis argenteus*, *Philodryas viridissimus*) (*P. olfersii*, *P. baroni*)), with this clade as the sister group to *Hydrodynastes* + *Pseudoboini sensu* Bailey (1967). Vidal *et al.* (2000) also conducted a neighbor-joining analysis, which corroborated the *Philodryas* + *Xenoxybelis* clade (and internal relationships) but recovered this as sister to the West Indian Xenodontinae. Pinou *et al.* (2004), using Bayesian analysis, inferred a sister-group relationship between *Philodryas olfersii* (the single representative of the genus in their analyses) and *Xenoxybelis argenteus*, corroborating the results of Vidal *et al.* (2000). In Pinou *et al.*'s tree, the *Philodryas* + *Xenoxybelis* clade is sister group to a clade comprising Xeno-

dontini (*Liophis*, *Xenodon* and *Erythrolamprus*) and the West Indian Xenodontinae. *Hydrodynastes* + *Pseudoboini* are sister to this assemblage. Vidal *et al.* (2000) and Pinou *et al.* (2004) agree on the very close relationship between *Xenoxybelis* and *Philodryas*, and they also corroborate the morphological data that suggest the inclusion of this group within Xenodontinae (= Xenodontidae *sensu* Pinou *et al.* 2004). However there is no consensus between these studies regarding the relationship of *Xenoxybelis*-*Philodryas* with other Xenodontinae. Although there is some strong evidence supporting the inclusion of *Xenoxybelis* species within the genus *Philodryas*, thereby requiring synonymy of these genera, we here follow Zaher (1999) in waiting for a more robust and complete phylogeny of *Philodryas* and related genera.

Tribal Allocation of *Xenoxybelis*. Jenner (1981) defined the tribe Philodryini (= Philodryadini) by the presence of simple or bilobed hemipenes, non-capitate, with bifurcated sulcus spermaticus, proximal spines and distal calyces. Sixteen genera were included in this tribe: *Amastridium*, *Apostolepis*, *Calamodontophis*, *Carphophis*, *Contia*, *Diadophis*, *Hydrops*, *Manolepis*, *Nothopis*, *Philodryas*, *Pseudablables*, *Synophis*, *Tachymenis*, *Thamnodynastes*, *Tomodon* and *Xenopholis*.

Ferrarezzi (1994) restricted the Philodryadini to the genera *Philodryas*, *Pseudablables*, *Ditaxodon*, *Tropidodryas* and *Platyinon* (= *Philodryas sensu* Thomas & Fernandes, 1996), diagnosing the group on the basis of the following characters: opisthognathic teeth; Meckel's canal usually closed anteriorly; bilobed hemipenis, semicapitate (sometimes without distinct capitulation), with dorsolateral spine rows, calyculate apex (bicalyculate in *Tropidodryas*); generally with two distinct rows of wide calyces, similar to pleats on the asulcate side, centrolateral sulcus spermaticus, proximally divided, among other features. Although Ferrarezzi (1994) considered Philodryadini as a non-monophyletic group, hemipenis morphology (Machado, 1993; Ferrarezzi, 1994; Zaher, 1999) and molecular (Vidal *et al.*, 2000; Pinou *et al.*, 2004) evidence support the inclusion of *Xenoxybelis* in the tribe Philodryadini.

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Appendix. Material examined

Xenoxylbelis boulengeri (20) – **BRAZIL - Acre: Brasília** (MPEG 16459). **Amazonas: Careiro da Várzea** (MPEG 19536, MPEG 19537, MPEG 19538); Rio Ituxi (MPEG 20345, MPEG 20346); Coari, Rio Urucu, Porto Urucu (MPEG 18226, MPEG 20680, MPEG 20681, MPEG 20694, MPEG 20706, MPEG 21261, MPEG 21260, MPEG 22276). **Rondônia: Porto Velho**, Abunã, Rio Madeira (MPEG 21093, MPEG 21094, MPEG 21095, MPEG 21101), Morrinho, Rio Madeira (MPEG 21097), Mutum, Rio Madeira (MPEG 21096).

Xenoxylbelis argenteus (78) – **BRAZIL – Acre: Porto Walter**, Rio Juruá (MPEG 20392). **Amazonas: Manaus**, Reserva Ducke (MPEG 18334); **Manicoré**, Fazenda Passo Formoso (MPEG 20851); **Presidente Figueiredo**, Rio Uatumã, UHE Balbina (MPEG 17438, MPEG 17440, MPEG 17484, MPEG 17507, MPEG 17449, MPEG 17502, MPEG 17781, MPEG 17431). **Amapá: Mazagão**, Fazenda Boa Fortuna (MPEG 00153, MPEG 00154), Rio Jarí (MPEG 00062), Rio Camaipé, Cachoeira da Pancada (MPEG 00340). **Maranhão: Ararí**, Gancho do Ararí (MPEG 14856, MPEG 14857). **Pará: Acará** (MPEG 08076); **Augusto Correa**, Cacoal (MPEG 09948); **Barcarena**, Cafezal (MPEG 16453); **Belém** (MPEG19350), Ilha do Mosqueiro (MPEG 00326, MPEG 02051); **Bragança**, Bom Jesus (MPEG 01966, MPEG 02209, MPEG 03039, MPEG 03666, MPEG 05035, MPEG 05126, MPEG 06211, MPEG 06238, MPEG 08241, MPEG 08258, MPEG 11205, MPEG 11286, MPEG 11287, MPEG 12053); **Canaã dos Carajás**, Serra dos Carajás (MPEG 17040, MPEG 19376), FLONA Tapirapé-Aquiri (MPEG 19356, MPEG 19362, MPEG 19363); **Gurupá** (MPEG 15171); **Castanhal**, Apeú, Boa Vista (MPEG 02656, MPEG 04763, MPEG 04763, MPEG 06944); **Dom Eliseu**, Sítio Bela vista (MPEG 12145); **Ilha de Marajó**, Breves (MPEG 17359, MPEG 17360, MPEG 17361, MPEG 17343); **Melgaço**, FLONA Caxiuanã (MPEG 19721, MPEG 19721, MPEG 19746, MPEG 19979, MPEG 20008, MPEG 20199, MPEG 20233, MPEG 20275, MPEG 08318, MPEG 18650, MPEG 19130, MPEG 20439); **Santarém**, Rodovia PA 03 (MPEG 00399, MPEG 00402, MPEG 00403); **São Felix do Xingu**, Garimpo do Rio Grajaú (MPEG 18431); **Viseu** (MPEG 01016). **Rondônia: Guajará-Mirim**, Parque Estadual de Guajará-Mirim (MPEG 19460, MPEG 20353, MPEG 20354, MPEG 20355, MPEG 20356, MPEG 14459); **Ouro Preto do Oeste**, Igarapé Paraíso (MPEG 16862); **Porto Velho**, UHE Samuel, Rio Jamarí (MPEG 17940). **Roraima:** (MPEG 17753).