



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.

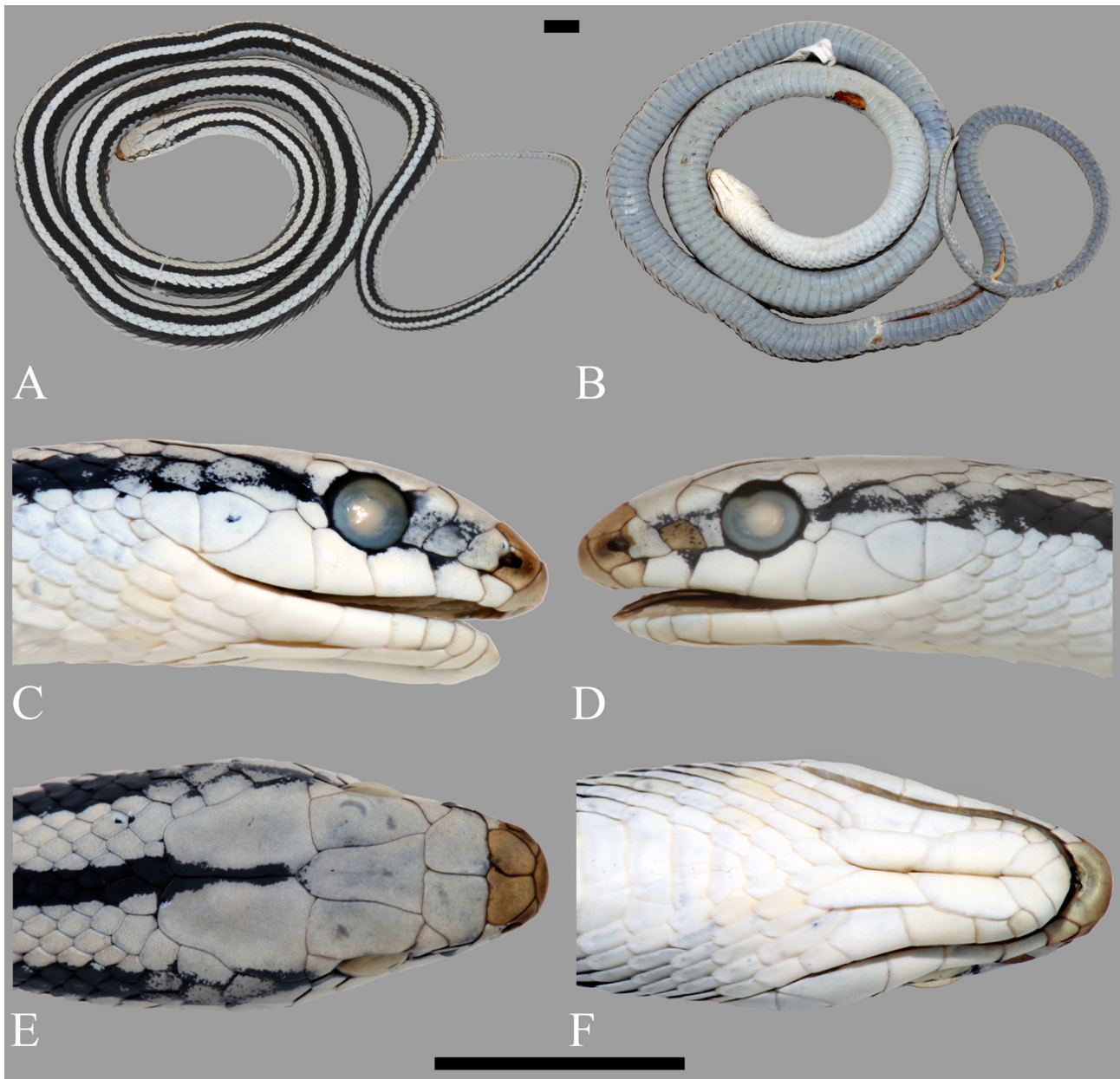


FIGURE 1. Holotype of *Philodryas amaru* (FHGO 4749) in dorsal (A) and ventral (B) views. Head of the holotype in right lateral (C), left lateral (D), dorsal (E), and ventral (F) views. Scale length = 10 mm.



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).

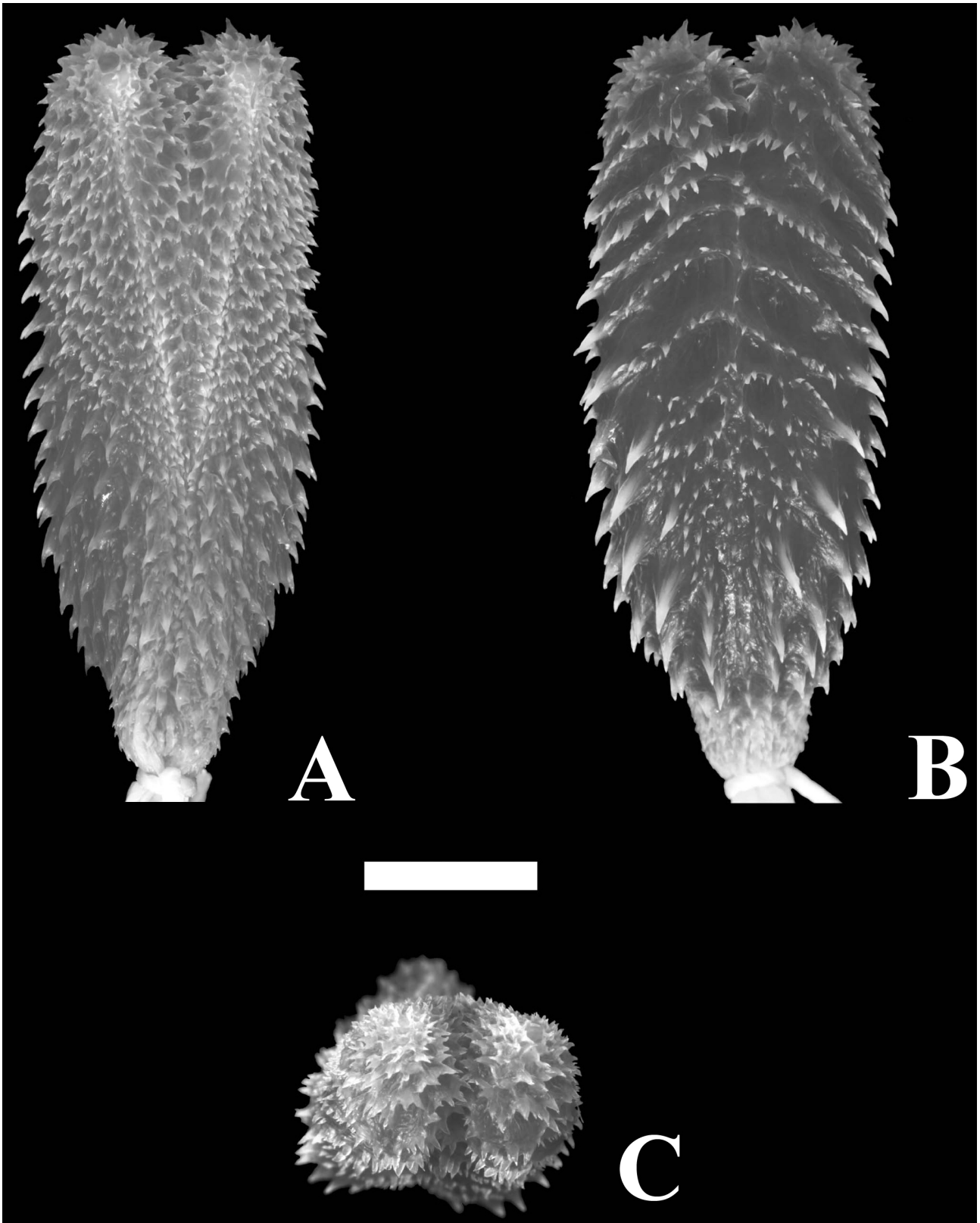


FIGURE 3. Hemipenis of the holotype of *Philodryas amaru* (FHGO 4749) in sulcate (A), asulcate (B), and top (C) views. Scale length = 5 mm.

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 (*Calamagostris 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

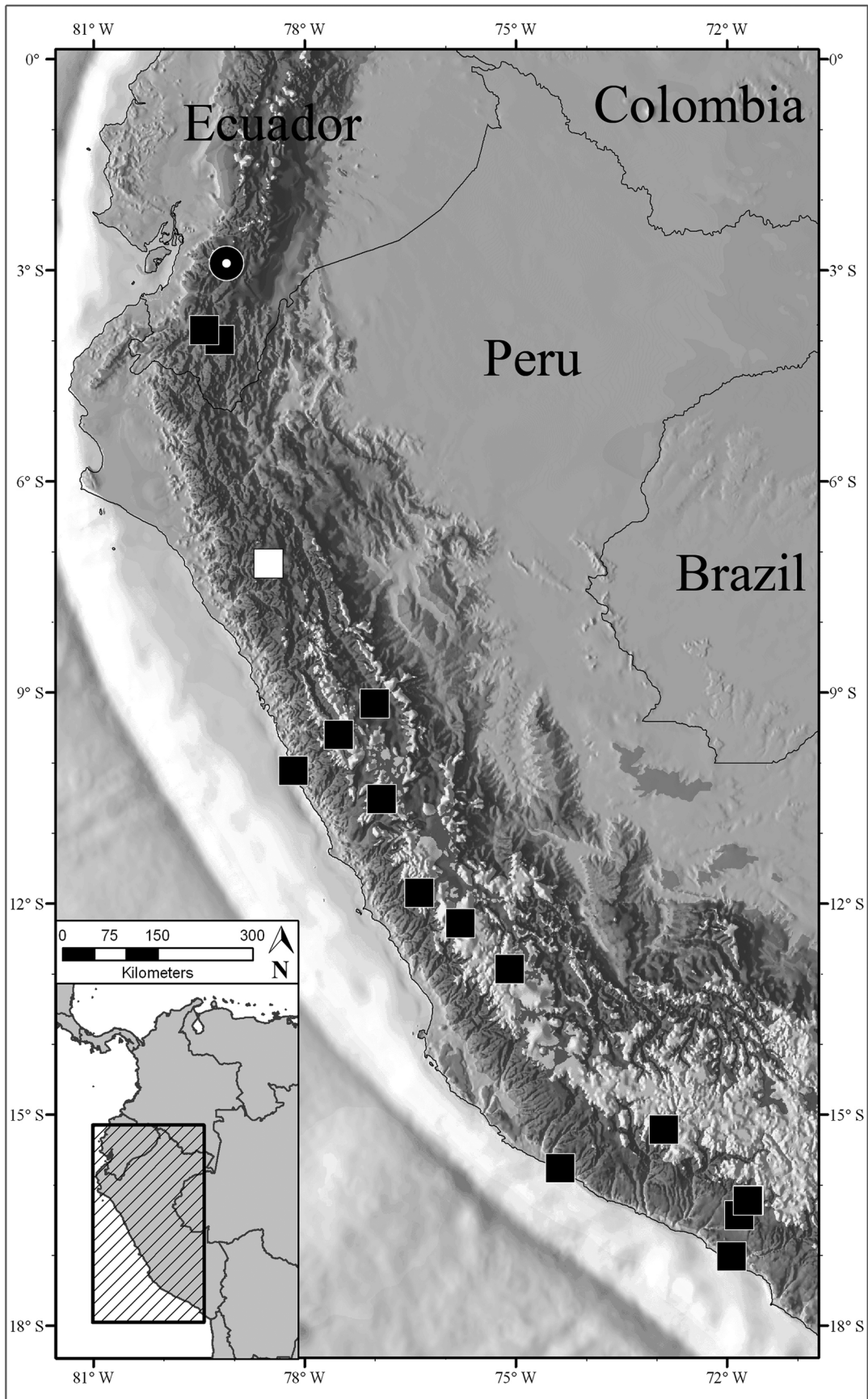


FIGURE 4. Type locality of *Philodryas amaru* (circle with the white dot) and distribution records of *Philodryas simonsii* (squares). The white square corresponds to the type locality of *Philodryas simonsii*.



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.

Acknowledgements

We are grateful to C. Torres and J. Cordova (MUSM), K. Garzón and M. E. Barragán (FHGO), M. Wilkinson and D. Gower (BMNH), R. Santa Cruz and E. López (MUSA), P. Venegas (CORBIDI) for allowing us to examine specimens under their care. We thank A. Vega, L. Ortiz, F. Juella, F. Siavichay, D. Alvarado, J. M. Falcon (Bioparque y Zoológico Amaru), F. Sánchez, F. Buchelli (ETAPA), M. Merchán, and J. Monsalve for fieldwork assistance in the type locality. This research was supported by grants to HZ from Fundação de Amparo Pesquisa do Estado de São Paulo (BIOTA/FAPESP grant number 2011/50206-9) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq grant numbers 565046/2010-1 and 303545/2010-0). JCA was supported by a grant from the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq grant number 2008/52781-5) and a PhD scholarship from the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES). JHV was supported by Fundación Herpetológica Gustavo Orcés (FHGO) and Secretaría Nacional de Ciencia y Tecnología (SENESCYT grant number PIC-08-000047), as part of the project “Inventario y caracterización genética y morfológica de los anfibios, reptiles y aves de los Andes de Ecuador” granted to Pontificia Universidad Católica del Ecuador (QCAZ). EA’s field research was supported by Bioparque y Zoológico Amaru, and ETAPA and their Corporación Municipal Parque Nacional Cajas, through a permit for the project Consultoría Investigación Colúbrido – CMPNC - Biodiversidad 2007.

References

- Amaral, A. (1929) Valor systemático de varias formas de ophidios neotropicos. *Memórias do Instituto Butantan*, 4, 3–68.
- Arbeláez, E. & Vega, A. (2008) *Guía de Anfibios, Reptiles y Peces del Parque Nacional Cajas*. Corporación Municipal Parque Nacional Cajas, ETAPA, Cuenca, Ecuador, 161 pp.
- Donoso-Barros, R. (1974) Descripción de una Culebra del Perú. Neotropica. *Notas Zoológicas Sudamericanas*, 20, 14–16.
- Dowling, H.G. (1951) A proposed standard system of counting ventrals in snakes. *British Journal of Herpetology*, 1, 97–99.
- Grazziotin, F.G., Zaher, H., Murphy, R.W., Scrocchi, G., Benavides, M.A., Zhang, Y.-P. & Bonatto, S.L. (2012) Molecular phylogeny of the New World Dipsadidae (Serpentes: Colubroidea): a reappraisal. *Cladistics*, 28, 437–459.
<http://dx.doi.org/10.1111/j.1096-0031.2012.00393.x>
- Lobo, F. & Scrocchi, G.J. (1994) Osteología craneal del género *Philodryas* (Serpentes: Colubridae). *Cuadernos de Herpetología*, 8, 104–111.
- Maglio, V.J. (1970) West Indian xenodontine colubrid snakes: their probable origin, phylogeny, and zoogeography. *Bulletin of the Museum of Comparative Zoology*, 141, 1–54.
- Myers, C.W. & Cadle, J.E. (2003) On the snake hemipenis, with notes on *Psomophis* and techniques of eversion: a response to Dowling. *Herpetological Review*, 34, 295–302.
- Parker, H.W. (1932) Some new or rare reptiles and amphibians from southern Ecuador. *Annals and Magazine of Natural History*, Series 10, 9 (49), 21–26.
<http://dx.doi.org/10.1080/00222933208673460>
- Peters, A.J. & Orejas-Miranda, B. (1970) Catalogue of the Neotropical Squamata. Part I: Snakes. *Bulletin United States National Museum*, 297, 1–347.
<http://dx.doi.org/10.5479/si.03629236.297.1>
- Prudente, A.L.C., Da Silva, M.A.A., Da Rocha, W.A. & Franco, F.L. (2008) Morphological variation in *Xenoxybelis boulengeri* (Procter, 1923) (Serpentes, Xenodontinae, Philodryadini). *Zootaxa*, 1743, 53–61.
- Pyron, R.A., Burbrink, F.T. & Wiens, J.J. (2013) A phylogeny and revised classification of Squamata, including 4161 species of lizards and snakes. *BMC Evolutionary Biology*, 13, 93.
<http://dx.doi.org/10.1186/1471-2148-13-93>
- Sallaberry-Pincheira, N., Garin, C.F., González-Acuña, D., Sallaberry, M.A. & Vianna, J.A. (2011) Genetic divergence of Chilean long-tailed snake (*Philodryas chamissonis*) across latitudes: conservation threats for different lineages. *Diversity and Distributions*, 17, 152–162.
<http://dx.doi.org/10.1111/j.1472-4642.2010.00729.x>
- Schmidt, K.P. & Walker, W. (1943) Snakes of the Peruvian coastal region. *Zoological Series of Field Museum of Natural History*, 24, 297–324.
- Tipton, B.L. (2005) *Snakes of the Americas: Checklist and Lexicon*. Krieger Publishing Company, Melbourne, Florida, U.S.A., 175 pp.
- Thomas, R.A. (1976) *A Revision of the South American Colubrid Snake Genus Philodryas Wagler, 1830*. PhD Thesis, Texas A & M University, 378 pp.
- Thomas, R.A. (1977) A new generic arrangement for *Incaspis* and mainland South American *Alsophis* and the status of two additional Peruvian species. *Copeia*, 1977 (4), 648–652.

<http://dx.doi.org/10.2307/1443163>

- Thomas, R.A. & Fernandes, R. (1996) The Systematic Status of *Platyinion lividum* Amaral, 1923 (Serpentes: Colubridae: Xenodontinae). *Herpetologica*, 52, 271–275.
- Thomas, R.A. (1997) Galapagos terrestrial snakes: biogeography and systematics. *Herpetological Natural History*, 5, 19–40.
- Zaher, H. (1999) Hemipenial Morphology of the South American Xenodontine snakes, with a proposal for a monophyletic Xenodontinae and a reappraisal of Colubroid hemipenes. *Bulletin of the American Museum of Natural History*, 240, 1–168.
- Zaher, H. & Prudente, A.L.C. (2003) Hemipenes of *Siphlophis* (Serpentes, Xenodontinae) and techniques of hemipenial preparation in snakes: a response to Dowling. *Herpetological Review*, 34, 302–307.
- Zaher, H., Scrocchi, G. & Masiero, R. (2008) Rediscovery and redescription of the type of *Philodryas laticeps* Werner, 1900 and the taxonomic status of *P. oligolepis* Gomes, 1921 (Serpentes, Colubridae). *Zootaxa*, 1940, 25–40.
- Zaher, H., Grazziotin, F.G., Cadle, J.E., Murphy, R.W., Moura-Leite, J.C. & Bonatto, S.L. (2009) Molecular phylogeny of advanced snakes (Serpentes, Caenophidia) with an emphasis on South American Xenodontines: a revised classification and descriptions of new taxa. *Papéis Avulsos de Zoologia*, 49, 115–153.
- <http://dx.doi.org/10.1590/s0031-10492009001100001>

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).