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Morphological variation in *Siphlophis worontzowi* (Squamata: Serpentes: Dipsadidae) from the Brazilian Amazon

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Abstract. The Neotropical snake *Siphlophis worontzowi* was described based on a single specimen from Rio Amanã, Amazonas state in the western portion of the Brazilian Amazon, but has subsequently become known from Bolivia and Peru as well. Here, we report a new morphological data set of *S. worontzowi* (meristic, morphometric, pholidosis, colour pattern, and hemipenial characters) and new geographic localities. Geographical variation and sexual polymorphism are analysed and described. *Siphlophis worontzowi* can be distinguished from its congeners by the combination of the following characters: dorsal scale rows 19–19–15, dorsals with two apical pits; undifferentiated vertebral scales; 3 postoculars; long loreal; 2+3temporals; 8 supralabials, with the third, fourth and fifth contacting the orbit; 9 infralabials, first four pairs contacting chin shields; 14–17 prediastemal and 2 postdiastemal maxillary teeth; 21 mandibular teeth, with 4–5 larger than others; 2 or 3 preventrals; 221–243 ventrals; 93–119 subcaudals; body black with 12–22 conspicuous yellowish or reddish vertebral spots, and black head with one or two conspicuous reddish or orange nuchal spots when alive; hemipenis with Y-shaped and T-shaped conditions; intrasulcar surface with a row of three enlarged spines in the proximal region of each lobe. Additionally, we provide detailed descriptions of the hemipenis, and discuss its polymorphic condition in the genus *Siphlophis*.

Key words. Hemipenis, morphology, Neotropics, taxonomy.

Introduction

The genus *Siphlophis* currently comprises seven species of semi-arboreal snakes from forested areas of Panama, Colombia, Venezuela, Ecuador, Guyana, Suriname, Guyana, Trinidad and Tobago, Bolivia, Brazil, and Paraguay (Boulenger 1896, Dunn 1944, Peters & Orejas-Miranda 1970, Amaral 1977, Cunha & Nascimento 1978, 1993, Lema 1987, 1994, Nascimento et al. 1987, Sazima & Argôlo 1994, Barrio et al. 1998, Barreto Guedes et al. 2011, Sheehy et al. 2014). *Siphlophis ayauma* is present on the Amazonian slopes of the Ecuadorian Andes (Sheehy et al. 2014); *S. cervinus* throughout a wide area of the Amazon basin in northern South America (Bailey 1970, Cunha & Nascimento 1993); *S. compressus* is found from Costa Rica to southeastern South America (Bailey 1970, Marques et al. 2001, Savage 2002); *S. leucocephalus* occurs in southeastern and central Brazil (Argôlo 2004); *S. longicaudatus* and *S. pulcher* are found in forested areas of southeastern and southern Brazil (Prudente & Feio 2001, Lema 2002, Di-Bernado et al. 2004); and *S. worontzowi* is known from Amazonian Brazil, Bolivia, and Peru (Zaher & Prudente 1999, Moravec et al. 2009, Costa et al. 2010, Dal Vechio et al. 2015). These species are considered forest dwellers with semi-arboreal and nocturnal habits, feeding mainly upon lizards (Prudente et al. 1998, Marques et al. 2001, Gaiarsa et al. 2013, Dal Vechio et al. 2015).

According to Zaher (1994) and Zaher & Prudente (1999), the species of *Siphlophis* share four unambiguous synapomorphies within the Pseudoboinae radiation, including: maxillary process of the prefrontal bone reduced or absent; Meckelin canal closed from the anterior region of the splenial to the tip of the dentary; posteroventral region of the nasal gland sharp-edged; and dorsal region of the maxilla with a well-developed *adductor mandibulae externus superficialis* muscle. Zaher & Prudente (1999) described the intraspecific hemipenial variation of all species of *Siphlophis*, with each showing two distinctly different hemipenial forms (Y- and T-shaped). These authors suggested that this hemipenial polymorphism represented a feature that has never been fixed in any of the species.

Siphlophis worontzowi is an exclusively Amazonian species with a wide distribution ranging from the locality of Estreito, Municipality of Babaçulândia, Tocantins state in Brazil to Tinkanari in the department of Cuzco in Peru. In Brazil, the species has been recorded in the states of Acre, Amazonas, Pará, Rondônia, Mato Grosso, Mato Grosso do Sul, and Tocantins (Prado 1940, Silva Jr. 1993, Prudente et al. 1998, Zaher & Prudente 1999, Santos-Jr et al. 2003, Frota et al. 2005, Costa et al. 2010, Kawashita-Ribeiro et al. 2011, Matos & Melo-Sampaio 2013, Dal Vechio et al. 2015). It has also been recorded in Bolivia and Peru (Moravec et al. 2009). Like its congeners, the species is nocturnal, has semi-arboreal habits, and feeds mainly on lizards and occasionally on frogs and other snakes (Prudente et al. 1998, Dal Vechio et al. 2015).

Siphlophis worontzowi was first described by Prado (1940) within the genus *Alleidophis*, based on one specimen from the Rio Amanã, Amazonas state, Brazil. The description included illustrations of the anterior part of the body, meristic and morphometric data, colour pattern, and mentioned the number of teeth. Amaral (1944) recognized *A. worontzowi* as synonymous with *Siphlophis cervinus* based on the similarity of the colour pattern. Hoge (1964), however, revalidated *Alleidophis* based on differences in pupil shape and colour pattern of body and head, as compared to the other species of *Siphlophis*. Later, Bailey (1970) reaffirmed *S. worontzowi* as a valid species with the following diagnostic characters: black body, nuchal mark, 16–19 lateral spots, dark belly, 16–19 maxillary teeth, 3 postoculars, and 15 dorsal scale rows anterior to the cloaca. Re-evaluating the characters used by Zaher (1998), Prudente (1998), included further morphological characters and proposed a phylogenetic hypothesis for *Siphlophis,* where *S. worontzowi* was sister to *S. cervinus*, sharing the presence of a well-developed *adductor mandibulae externus superficialis* muscle, and the Harder gland being visible only in the anterior region.

Here, we report additional information on the morphological variation (meristics, morphometrics, pholidosis, colour pattern, and hemipenial morphology) of *S. worontzowi* obtained in the western and eastern portions of the Brazilian Amazon region. Additionally, we present a compilation of the known geographical distribution information on *S. worontzowi* based on the literature and new records, and provide a detailed morphological comparison with other species of *Siphlophis*.

Material and methods

We analysed specimens of *Siphlophis* (*S. cervinus, S. compressus*, *S. leucocephalus*, *S. longicaudatus, S. pulcher*, and *S. worontzowi*) housed in the following institutions (acronyms in parentheses) in Brazil: Coleção Zoológica Gregório Bondar (CZGB) da Comissão Executiva do Plano da Lavoura Cacaueira (CEPEC/CEPLAC), Ilhéus, Bahia; Coleção Zoológica da Universidade Federal do Mato Grosso (UFMT), Cuiabá, Mato Grosso; Instituto Butantan (IBSP), São Paulo; Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, Amazonas; Museu de História Natural Capão da Imbuia (MHNCI), Curitiba, Paraná; Museu Nacional do Rio de Janeiro (MNRJ), Rio de Janeiro; Museu de Zoologia da Universidade Estadual de Londrina (MZUEL), Londrina, Paraná; and Museu Paraense Emílio Goeldi (MPEG), Belém, Pará (Appendice 1). Additional information used for comparisons was taken from Costa et al. (2010), Moravec et al. (2009) and Dal Vechio et al. (2015). Comparative data of *S. ayauma* were obtained from Sheehy et al. (2014).

Measurements of specimens were taken under a stereoscope with a dial calliper to the nearest 0.1 mm, except for total length (TL), snout–vent length (SVL), and tail length (TAL), which were measured to the nearest 1.0 mm with a flexible ruler. Cephalic measurements were taken point-to-point on the right side of the specimen following Missassi & Prudente (2015). Our morphological description and scale counts follow Savage (1960) and Dowling (1951), respectively. Generalized coloration summaries were derived directly from live specimens or indirectly from photos of live specimens. Within the standardized colour descriptions of selected individuals, the colours and colour codes (in parentheses) follow Smithe (1975–1981).

Sexing was conducted by a longitudinal incision at the base of the tail to check for the presence of a hemipenis. Techniques for hemipenial preparation followed Pesantes (1994), Manzani & Abe (1998), and Zaher & Prudente (1999, 2003). The terminology used to describe the hemipenis follows Dowling & Savage (1960), Myers & Cadle (1994), and Zaher (1999). Techniques for skull preparations and osteological nomenclature followed Passos & Fernandes (2005).

In addition to the distinct morphological characters that distinguish *S. worontzowi* from the others species of *Siphlophis*, we used univariate statistics on the morphometric and meristic data set. This included all available specimens (n=41) and literature data (n=15) of *S. worontzowi* (Appendix 1). A Student t-test was performed to test for the presence of sexual dimorphism in relation to the morphometric and meristic data sets. All data had normality and homogeneity of variance. In all tests for sexual dimorphism, only data from sexually mature females and males were considered (25 females and 29 males), four juveniles were not considered (MZUFV 1734, UFMT 5364, UFMT 6268, MZUSP 11323). Descriptive statistics and Student t-tests were carried out with Statistica 6.0 (StatSoft 2003). Data on variation includes number of specimens (N), mean ($\bar{x}$), and standard deviation (SD). Statistical comparisons were considered significant if $p \leq 0.05$.

We analysed specimens along the distribution range to identify any possible morphological variation in coloration and shape of the hemipenis, considering extremes of the distribution. Illustrations were obtained using a stereomicroscope. Coordinates for localities were obtained from museum databases and geographical gazettes (IBGE 2011). Where possible, we corrected coordinates obtained from the literature using GoogleEarth 6.0.

Results

Siphlophis worontzowi (Prado, 1940)

Figs 1–6, Table 1

Alleidophis worontzowi Prado 1940. Mem. Inst. Butantan, 13. Type locality: Rio Amanã, Amazonas state, Brazil.
Siphlophis cervinus cervinus – Amaral 1944. Papéis Av. Zool., 5 (9): 65–74.
Alleidophis worontzowi – Hoge 1964. Mem. Inst. Butantan, 30: 35–50.
Siphlophis worontzowi – Bailey 1970. In: Peters & Orejas-Miranda (eds): Catalogue of the Neotropical Squamata. Pt. I: Snakes. Washington: Smithson. Inst. Press.

Holotype: An adult male, IBSP 10.062, from Rio Amanã, Amazonas state, Brazil (4.400°S, 57.5833°W).

Diagnosis: *Siphlophis worontzowi* can be distinguished from all congeners by the combination of the following characters: dorsal scale rows 19–19–15, dorsals with two apical pits; undifferentiated vertebral scales; postoculars 3; long loreal; temporals 2+3; supralabials 8, with third, fourth and fifth contacting orbit; infralabials 9, first four pairs contacting chin shields; 14–17 prediastemal and 2 postdiastemal maxillary teeth; preventrals 2 or three; ventrals 221–243 (221–239 in females, 225–243 in males); subcaudals 93–119 (93–109 in females, 102–119 in males); body black, with 12–22 conspicuous yellowish or reddish vertebral spots, and head black with one or two conspicuous reddish or orange nuchal spots when alive; hemipenis Y- or T-shaped; intrasulcar surface with a row of three enlarged spines in the proximal region of each lobe.

Comparisons: *Siphlophis worontzowi* differs from *S. compressus, S. leucocephalus* and *S. longicaudatus* by having 19–19–15 dorsal scale rows, and a black body with red-orange vertebral spots (vs 19–19–17 dorsal scales rows, and brown body without vertebral spots). *S. worontzowi* differs from *S. ayauma* by having 19 dorsal scales rows at midbody (vs 17 dorsal scales rows at midbody), and from *S. longicaudatus* and *S. leucocephalus* by its third and fourth mandibular teeth being larger than the others (vs subequal). It differs from *S. compressus* by having undifferentiated vertebral scales, and black eyes (vs vertebral scales wider than dorsals, and red eyes). It differs from *S. pulcher* by having 12–22 yellowish or reddish vertebral spots and a row of three enlarged spines in the proximal region of each lobe, black eyes, and three intrasulcar spines in the proximal region of each hemipenial lobe (vs 60–72 red diamond-shaped vertebral spots, no enlarged intrasulcar spines, and red eyes). It differs from *S. cervinus* by having three postoculars and a black snout, belly, and long body bands (vs 2 postoculars and brown and cream snout and belly, with bands or spots).

Description of holotype: Adult male, 655 mm in SVL (74.86% of total length) and 220 mm tail length (25.14% of total length), head distinct from body. Rostral shield visible from above, two times wider than its greatest length. Internasals wider than long. Prefrontals as wide as long. Frontal pentagonal, longer than wide. Supraocular pentagonal, longer than wide. Parietals wider than long and wider than frontal. Nasal divided, in contact with the first and second supralabials. Loreal simple, longer than wide, contacting second and third supralabials. Preocular simple, contacting third supralabial. Three postoculars, contacting fifth and sixth supralabials. Temporals 2+3. Supralabials 8, with third, fourth and fifth bordering the orbit. Infralabials 9, first pair in broad contact behind symphysial, first four pairs contacting anterior chin shields, and fourth and fifth contacting posterior chin shields. Dorsals in 19–19–15 rows, smooth, with two apical pits. Vertebral scale rows undifferentiated. Two preventrals, 243 ventrals and 114 subcaudals. Anal scute entire.

Meristic and morphometric variation: Loreal simple (n=26), sometimes divided (n=4). Postoculars three (n=54), rarely two (n=2), contacting fifth and sixth supralabials (n=31). Preoculars contacting third (n=22) or third and fourth supralabials (n=6), rarely not contacting supralabials (n=2). Supralabials eight, with third, fourth and fifth (n=29) or fourth and fifth (n=9) bordering the orbit. Infralabials nine, first four pairs contacting anterior chin shields (n=39), rarely first three pairs (n=1), and fourth and fifth pairs (n=29), or fifth pairs (n=11), contacting posterior chin shields. Two preventrals (n=18), rarely three (n=3). Ventrals more numerous in males (225–243, $\bar{x}$ =233, n=29) than in females (221–239, $\bar{x}$ =228, n=25) (t-value=-4.07; df=52; p=0.0001). Subcaudals divided, more numerous in males (102–119, $\bar{x}$ =110, n=30) than in females (93–117, $\bar{x}$ =104, n=21) (t-value=-4.94; df=49; p=0.000). Female's cloacal gland extends over first five subcaudals. SVL greater in females (226–760 mm, $\bar{x}$ =553.4, n=21) than in males (223–712, $\bar{x}$ =533, n=28), but not statistically significant (t-value=0.64; df=47; p=0.52). Tail length greater in males (104–360 mm, $\bar{x}$ =180.8, n=29) than in females (67–220 mm, $\bar{x}$ =162.4, n=17), but not statistically significant (t-value=-1.36; df=44; p=0.18). Head length greater in females (11.8–21.9 mm, $\bar{x}$ =17.8, n=19) than in males (12.9–20.3 mm, $\bar{x}$ =16.8, n=18), but not statistically significant (t-value=1.10; df=35; p=0.27). Vertical diameter of eyes 1–3 mm (n=56) (Table 1).

Colour pattern in preservative: Head with a black cap from the tip of the snout to the posterior borders of the parietals, including rostral, pre- and postoculars, frontal, internasals, and supralabials. Nuchal region with one pair of orange blotches separated by one row of black occipital scales. These orange blotches cover not more than three occipital scales along the vertebral line and never extend onto the belly as to form a ring. In some specimens, these two blotches are fused in the vertebral region. The eyes are black. Body mostly black with 13–23 white blotches in fe-

Table 1. Morphological variables taken from all available specimens analysed (n=41) and literature data (n=15) of *Siphlophis worontzowi* (Costa et al. 2010, Moravec et al. 2009, Dal Vechio et al. 2015).

Variables	Males mean	Males range	Males n	Females mean	Females range	Females n
Ventrals	233	225–243	29	228	221–239	25
Subcaudals	110	102–119	30	104	93–117	21
Snout–vent length (mm)	533.5	382–712	28	553.4	375–760	21
Tail length (mm)	180.8	118–360	29	162.4	108–220	17
Head length (mm)	16.8	12.9–20.3	18	17.2	13.6–21.9	19
Preoccelars	1	1	31	1	1	25
Postoculars	2–3	2–3	31	2–3	2–3	25
Supralabials	8	7–8	31	8	8	25
Infralabials	9	8–9	31	9	9	25
Body spots	16	12–22	31	18	13–23	25
Tail spots	9	3–15	31	9	4–13	25
Left maxillary teeth	16	14–17	31	15,8	14–17	25

males (n=25) and 12–22 in males (n=31). The first white blotches occur between dorsal scales 10–25, and they can fuse mid-dorsally or be limited to the lateral region of the body. In the vertebral region, there are some small, irregularly distributed, orange spots. The edges of white dorsal scales are black. Ventrally, the white dorsal blotches invade the ventral scales and may form complete rings. Belly otherwise mainly black. Tail black, with 4–13 white blotches in females (n=25), and 3–15 in males (n=31) (Figs 1 and 2).

Figure 1. Colour pattern of the head in dorsal (A), lateral (B), and ventral (C) views of *Siphlophis worontzowi* (MPEG 26134). Scale bar: 5 mm.

Colour in life: Live individuals *Siphlophis worontzowi* have a Jet Black (colour 89) head cap from the tip of the snout to the posterior border of the parietals (MPEG 24427, MPEG 24966, MPEG 25353, MPEG 26134, and MPEG 26145). A distinct pair of bright Chrome Orange (16) blotches (or a single fused blotch) follows the black head cap. Eyes are Jet Black (89). The dorsum and venter are alternatingly banded white or Light Cream (54) and black distributed irregularly throughout the body in all adults analysed thus (n=5). In three specimens, the dorsal light bands tend to fuse at the vertebral line or are limited to the lateral region of the body. In the vertebral region, there are some small, irregularly distributed, Chrome Orange (16) spots. The ventral face of the tail is banded like the body (Fig. 3).

Dentition: Maxillary arch curved in dorsal view, with 14–17 prediastemal and 2 postdiastemal teeth (n=34). Prediastemal teeth decrease in size posteriorly, moderately spaced, curved, angular in cross section, robust at base, and narrower on the apices. Maxillary diastema short. Two postdiastemal teeth larger than last prediastemal one. Pterygoid slightly concave, with 18 conical teeth; palatine with 12 teeth; mandible with 21 teeth, with teeth 4–5 being larger than the others (MHNCI 7350 and MZUEL 631; Fig. 4).

Hemipenial morphology: Inverted, the organ reaches subcaudals 8–10. The fully everted and expanded hemipenis is deeply bilobed, bicapitated, and bicalyculated (everted organs, n=4). The hemipenis may have long Y-shaped lobes (MHNCI 7350) or short T-shaped lobes (MZUEL 631, MPEG 23638, MPEG 24225, and UFMT 8208). If Y-shaped, the body, lobes, and capitulum are elongated, and sulcus spermaticus is deeply bifurcated at about mid-body, and its branches are parallel to the centrifugal orientation. If T-shaped, the lobes and body are much shorter, the capitulum is rounded, and the sulcus spermaticus branches diverge.

In both configurations of the organ, the capitulum is ornamented with papillate calyces, which tend to be spinu-

Figure 2. Colour pattern of the body in dorsal (A), lateral (B), and ventral (C) views of *Siphlophis worontzowi* (MPEG 26134). Scale bar: 10 mm.

late on the edges of the capitulum. The upper face of each lobular crotch contains a pair of nude pockets that are separated by an inflated crest, which begins at the base of the capitulum on the asulcate side and terminates at the upper and proximal face of each lobe. Lobular crests covered by spinules. The intrasulcar surface is covered with spinules, and there is a row of three enlarged spines on the proximal region of each lobe. There are three or four rows of well-developed enlarged spines on the body of the organ, which originate on the sulcate side and extend to the lateral sides of the organ and the lobular crests on the asulcate side. These spines decrease in size toward base of the organ. The proximal region of the body bears irregularly scattered with small spines, which gradually increase in size proximally and distally. The asulcate side is covered with irregularly arranged spinules as is the entire body of the hemipenis (Fig. 5)

Natural history: *Siphlophis worontzowi* is considered a nocturnal, semi-arboreal forest dweller that inhabits primary or disturbed forests and open areas. This species is usually found climbing or resting on vegetation at night, with one record of an individual being active during twilight hours (Silva Jr. 1993, Bernarde & Abe 2006, Moravec et al. 2009, Costa et al. 2010, Gaiarsa et al. 2013, Dal Vecchio et al. 2015). Although *S. worontzowi* occasionally feeds on frogs, this species predates primarily upon lizards (Prudente et al. 1998, Bernarde & Abe 2006, Gaiarsa et al. 2013, Dal Vecchio et al. 2015). Four species of lizards have been recorded as prey: *Iphisa elegans*, *Gonatodes humeralis*, *Hemidactylus mabouia*, and *Copeoglossum nigropunctata*. We recorded one *Copeoglossum nigropunctata* in the intestine of one specimen (MPEG 26124). We also found eight eggs in the oviduct of another specimen of *S. worontzowi* (MHNCI 7350).

Distribution: *Siphlophis worontzowi* occurs only in the Amazon Forest Domain (Ab'Saber 1977) in Bolivia, Peru (Moravec et al. 2009), and Brazil. In Brazil, the species occurs in the states of Acre (Matos & Melo-Sampaio 2013), Amazonas (type locality, Prado 1940), Mato Grosso (Freitas 2003, Costa et al. 2010, Kawashita-Ribeiro et al. 2011, Dal Vechio et al. 2015), Pará (Santos-Jr et al. 2003, Frota et al. 2005), Rondônia (Silva Jr. 1993, Prudente et al. 1998, Zaher & Prudente 1999, Zaher & Prudente 2003, Bernarde & Abe 2006, Dal Vechio et al. 2015), and Tocantins (Dal Vechio et al. 2015). We confirmed the identification of IBSP 29074 as *S. worontzowi*, which we analysed before the fire in May of 2010 that destroyed most of the specimens housed in the herpetological collection of the Instituto Butantan, São Paulo, Brazil. However, we believe that the record from Mato Grosso do Sul in Brazil is erroneous, considering that *S. worontzowi* appears restricted to the Amazon region east of the Purus and south of the Amazon rivers (Fig. 6).

Discussion

Siphlophis worontzowi is easily identified using morphometric and meristic characters and colour pattern, even though it exhibits some geographical variation and sexual polymorphism. The species is dimorphic, with males having more ventrals and subcaudals than females. The variation in pho-

Figure 3. Dorsal view of *Siphlophis worontzowi* in life (MPEG 26134), from the Municipality of Juruti, state of Pará, Brazil (SVL 435 mm and TAL 142 mm). Photo: A. Dourado.

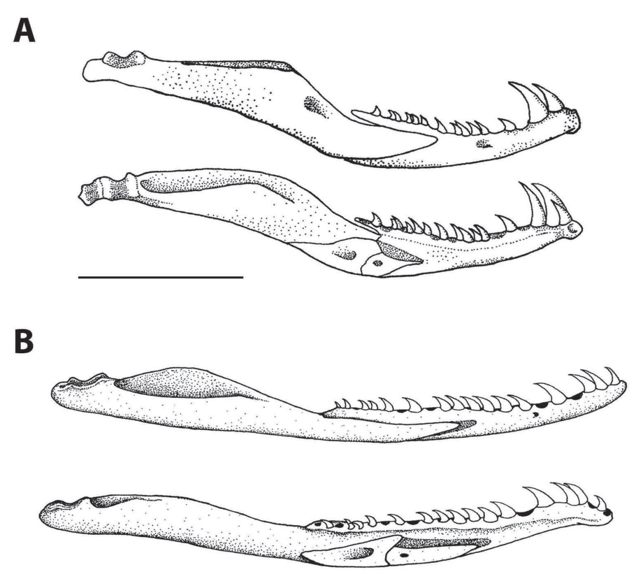

Figure 4. Lateral views of the mandible of *Siphlophis worontzowi* (A) and *S. longicaudatus* (B). Scale bars: 5 mm.

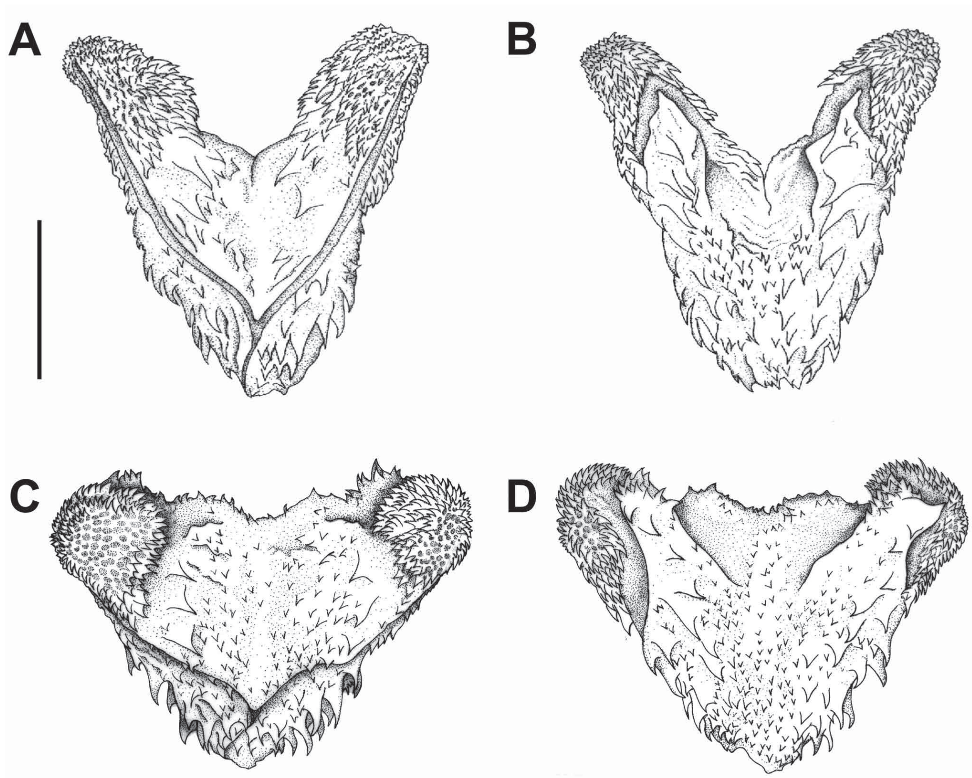

Figure 5. Hemipenis of *Siphlophis worontzowi*, in "Y-shape" (MHNCI 7350), sulcate (A) and asulcate (B) views, and in "T-shape" (MZUEL 631), sulcate (C) and asulcate (D) views. Scale bar: 5 mm.

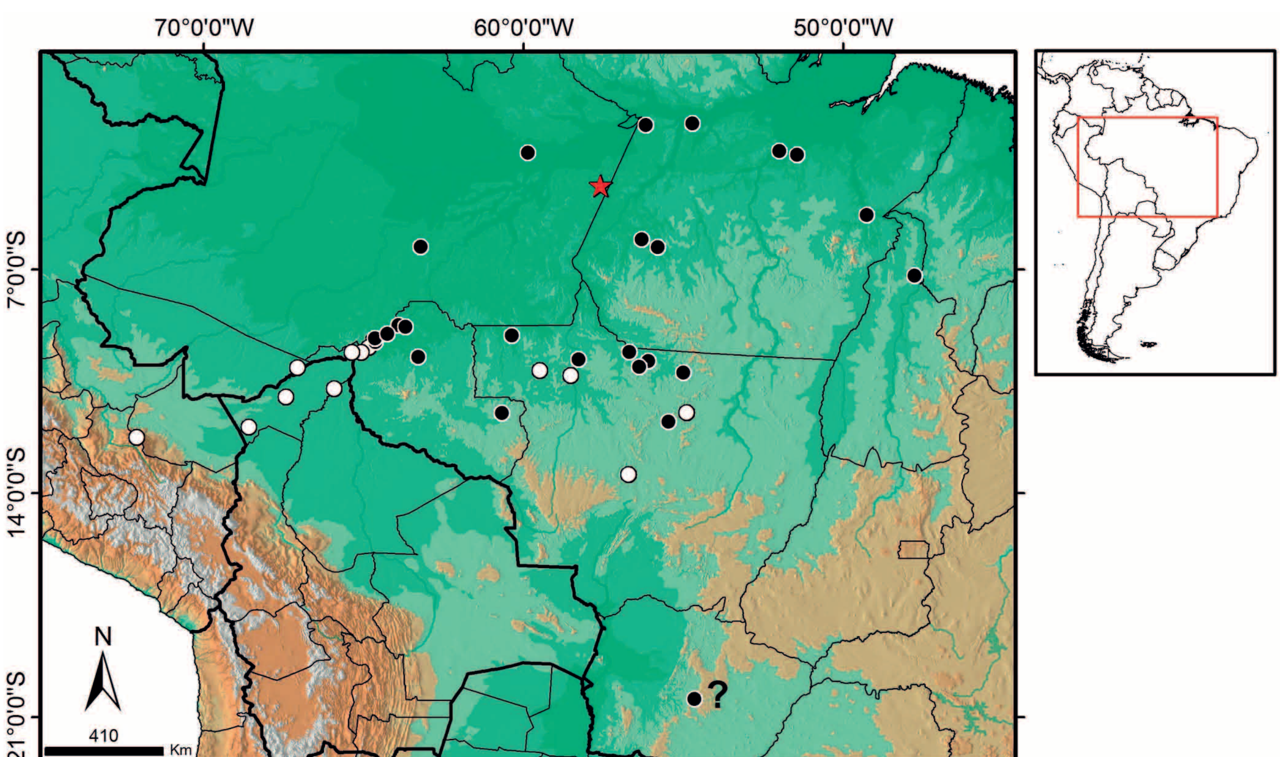

Figure 6. Geographic distribution of *Siphlophis worontzowi*. Black circles refer to specimens examined, white circles to literature records, and the star to the type locality. ? = questionable record.

lidosis as mentioned by some authors (Prado 1940, Silva-Jr 1993, Costa et al. 2010, Dal Vechio et al. 2015) could be considered intraspecific as is observed in other species of snakes. The wide discrepancy between the number of maxillary teeth presented here (14–17+2) and the data presented by Prado (1940) (22+3), as well as discrepancies noted in the size of mandibular teeth (third and fourth larger than the others vs third, fourth and fifth larger than the others, according to Prado 1940) are probably the result of the counting methods employed. We used skulls prepared specifically for dental counting, which allows for more accurate data collection and more precise identification of teeth and dental alveoles. The absence of juveniles in our sample did not permit an assessment of ontogenetic colour pattern variation. Because age-dependent differences in coloration have been observed in other Pseudoboini (Bernardo et al. 2012, Sheehy et al. 2014), it would be important to collect and analyse additional *S. worontzowi* of different age classes to find out whether these also occur in this species. Prado (1940) described the holotype as having a green-bronze head, body and belly, which is possibly a result of its preservation.

Intraspecific variation with respect to hemipenial size, shape, and micro-ornamentation has been reported for some species of snakes (Keiser 1974, Mcdowell 1979, Cole & Hardy 1981, Shine et al. 2000, Schargel & Castoe 2003). Hemipenial polymorphism has been noted in other species of *Siphlophis*, too, and each species exhibited the same two distinctly different types of hemipenes, i.e., Y- and T-shaped (Zaher & Prudente 1999, Sheehy et al. 2014). The Y-shape, which is considered the plesiomorphic state, is found in all Pseudoboini, whereas the T-shape is otherwise also observed in *Oxyrhopus clathratus* and probably represents a synapomorphy of a more inclusive clade within the Pseudoboini (Zaher & Prudente 1999). Zaher & Prudente (2003) provided a guideline for preparing hemipenes from museum specimens and demonstrated that the T-shaped condition was not a result of the preparation technique, as had been suggested by Dowling (2002). Both hemipenial conditions (Y- and T-shaped) are found in different individuals in *S. worontzowi* from the same locality (e.g., municipality of Espigão do Oeste, Rondônia state, Brazil). These observations corroborate the findings of Zaher & Prudente (1999) in that such variation neither leads to population isolation nor does it represent the extreme of a cline.

Rivers have been suggested to play an important role in explaining the patterns of ecological and genetic variation for many Amazonian species and communities (Wallace 1854, Capparella 1988, Gascon et al. 2000, Ribas et al. 2012, Fernandes et al. 2012). The rivers Amazon and Madeira are barriers for the dispersal of several groups of vertebrates, including squamates (Zaher & Caramaschi 1992, Haffer 1992, 2008, Avila-Pires 1995, Henderson et al. 2009, Prudente & Passos 2010). However, locality data indicate that *S. worontzowi* is widely distributed yet restricted to the southern tributaries of the Amazon River. It is found on both the east and west banks of the Madeira River and to the west of the Tocantins River.

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Appendix 1

Morphometric and meristic data from all *Siphlophis worontzowi* individuals included in this study (n=56). Legend: F: female; M: male; SVL: snout-vent length; TL: tail length; HL: head length; PrO: preoculars; PsO: postoculars; SL: supralabials; IL: infralabials; Lo: loreals (e: entire, d: divided); BSp = transversal dorsal spots; TSp = transversal tail spots; Max: maxillary teeth. Localities: AM: Amazonas; MS: Mato Grosso do Sul; MT: Mato Grosso; PA: Pará; RO: Rondônia; TO: Tocantins; BRA: Brazil; BOL: Bolívia. *Holotype, [1] Moravec et al. 2009, [2] Costa et al. 2010, [3] Dal Vechio et al. 2015.

Voucher	Sex	Ventrals	Subcaudals	SVL (mm)	TL (mm)	HL (mm)	PrO (SL)	PsO (SL)	SL (O)	IL (MA–MP)	Lo (SL)	BSp	TSp	Max	Locality, State – Country
*IB 10.062	M	243	114	655	220	19.5	1	3	8(3–5)	9(1–4)(4–5)	–	–	–	15	Rio Amanã, AM – BRA
IB 29.074	M	233	112	543	179	15.7	1	3	8(3–5)	9(1–4)(5)	–	16	11	14	Campo Grande, MS – BRA
IB 42.624	F	231	93	760	185	21.4	1	3	8(3–5)	9(1–3)(4–5)	–	13	11	16	Peixoto de Azevedo, MT – BRA
IB 53.604	M	232	107	518.3	105	15	1	3	8	9(1–4)(4–5)	–	12	7	15	UHE Samuel, RO – BRA
IB 55.266	M	237	111	509	157	16.6	1	3	8(3–5)	9(1–4)(4–5)	–	16	9		Alta Floresta, MT – BRA
IB 56.151	F	231	106	412	135	14.8	1	3	8	9(1–4)(4–5)	–	22	9	16	Santarém, PA – BRA
IB 56.550	F	229	107	594	–	19	1	3	8	9(1–4)(4–5)	–	15	7	16	Santarém, PA – BRA
IB 56.561	F	228	Incomplete tail	672	–	21.9	1	3	8(3–5)	9(1–4)(4–5)	–	16	4	16	Alta Floresta, MT – BRA
[1]CBF 2460	M	227	114	590	360	–	1	3	7–8	9	–	–	–	–	Nacebe, Pando – BOL
INPA-H27643	M	238	115	626	209	19.4	1(3)	3(5–6)	8(3–5)	9(1–4)(4–5)	e (2–3)	19	15	16+2	Floresta Tapauá, AM – BRA
INPA-H32121	M	236	113	548	183	17.9	1(3)	3(5–6)	8(3–5)	9(1–4)(4–5)	e (2–3)	16	9	15+2	Porto Velho, RO – BRA
INPA-H32381	F	232	102	520	149	17.5	1(3)	3(5–6)	8(3–5)	9(1–4)(4–5)	e (2–3)	19	8	17+2	Porto Velho, RO – BRA
INPA-H32389	M	243	106	703	214	20.2	1(3)	3(5–6)	8(3–5)	9(1–4)(4–5)	e (2–3)	22	13	15+2	Careiro da Várzea, AM – BRA
MHNCI 7350	M	228	110	–	171	16	1	3	8(3–5)	9(1–4)(4–5)	–	12	9	17+2	Espigão d'Oeste, RO – BRA
MHNCI 7962	F	229	105	–	–	21	1	2	8(4–5)	9(1–4)(5)	–	20	10	–	Espigão d'Oeste, RO – BRA
MPEG 18761	M	230	102	536	175	17	1(3)	3(5–6)	8(3–5)	9(1–4)(4–5)	e (2–3)	14	10	15+2	Candeias do Jamari, RO – BRA
MPEG 21057	F	226	105	540	170	17.5	1(3)	3(5–6)	8(3–5)	9(1–4)(4–5)	e (2–3)	17	10	16+2	Espigão d'Oeste, RO – BRA
MPEG 23638	M	234	112	505	167	16	1(3)	3(5–6)	8(3–5)	9(1–4)(4–5)	e (2–3)	13	9	17+2	Babaçulândia, TO – BRA
MPEG 24225	M	238	112	556	185	–	1(3–4)	3(5–6)	8(4–5)	9(1–4)(4–5)	e (2–3)	18	11	17+2	Porto Velho, RO – BRA
MPEG 24427	F	232	109	670	220	21	1(3–4)	3(5–6)	8(4–5)	9(1–4)(4–5)	e (2–3)	22	13	17+2	Juruti, PA – BRA
MPEG 24966	F	224	107	620	205	20	1(3–4)	3(5–6)	8(4–5)	9(1–4)(4–5)	e (2–3)	20	13	16+2	Juruti, PA – BRA
MPEG 25352	F	224	99	443	129	15	1(3)	3(5–6)	8(3–5)	9(1–4)(4–5)	e (2–3)	17	5	16+2	Marabá, PA – BRA
MPEG 25353	F	223	100	410	127	14	1(3)	3(5–6)	8(3–5)	9(1–4)(4–5)	e (2–3)	15	9	16+2	Itaituba, PA – BRA
MPEG 25864	M	231	102	655	196	19.5	1(3)	2(5–6)	8(4–5)	9(1–4)(4–5)	e (2–3)	17	8	17+2	Itapuã do Oeste, RO – BRA
MPEG 26108	M	233	109	403	126	13.5	1(3)	3(5–6)	8(3–5)	9(1–4)(5)	e (2–3)	17	7	15+2	Porto Velho, RO – BRA
MPEG 26124	F	227	Incomplete tail	601	–	19.8	1(3–4)	3(5–6)	8(4–5)	9(1–4)(5)	e (2–3)	23	–	17+2	Vitória do Xingu, PA – BRA
MPEG 26134	M	228	109	435	142	15.5	1(3)	3(5–6)	8(3–5)	9(1–4)(5)	e (2–3)	16	8	15+2	Juruti, PA – BRA
MPEG 26145	F	225	101	640	197	19	1(3–4)	3(5–6)	8(4–5)	9(1–4)(4–5)	d/e (2–3)	17	9	17+2	Itaituba, PA – BRA
MPEG 26219	F	224	101	375	108	13.6	1(3)	3(5–6)	8(4–5)	9(1–4)(4–5)	e (2–3)	15	6	15+2	Anapu, PA – BRA
MPEG 26220	F	227	107	410	130	13.8	1(3)	3(5–6)	8(3–5)	9(1–4)(4–5)	e (2–3)	20	6	14+2	Vitória do Xingu, PA – BRA

Voucher	Sex	Ventrals	Subcaudals	SVL (mm)	TL (mm)	HL (mm)	PrO (SL)	PsO (SL)	SL (O)	IL (MA–MP)	Lo (SL)	BSp	TSp	Max	Locality, State – Country
MPEG 26221	M	–	Incomplete tail	420	–	–	1(3–4)	3(5–6)	8(4–5)	9	e (2–3)	18	3	15+2	Vitória do Xingu, PA – BRA
MZUEL 631	M	235	113	–	171	15	1	3	8(3–5)	9(1–4)(4–5)	–	14	8	–	Espigão d'Oeste, RO – BRA
[2]MZUFV 1692	M	234	110	382	120	–	1	3	8	9	–	–	–	–	Aripuanã, MT – BRA
[2]MZUFV 1734	F	229	109	226	67	–	1	3	8(3–5)	9(1–4)(4–5)	–	–	–	–	Aripuanã, MT – BRA
[3]MZUSP 11251	M	236	114	690	239	–	1	3	8	9	–	–	–	–	Cláudia, MT – BRA
[3]MZUSP 11323	M	230	115	223	104	–	1	3	8	9	–	–	–	–	Jurueana, MT – BRA
[3]MZUSP 11345	F	226	108	497	176	–	1	3	8	9	–	–	–	–	S. José do Rio Claro, MT – BRA
[3]MZUSP 19289	F	238	Incomplete tail	643		–	1	3	8	9	–	–	–	–	Babaçulândia, TO – BRA
[3]MZUSP 19290	M	242	103	630	188	–	1	3	8	9	–	–	–	–	Babaçulândia, TO – BRA
[3]MZUSP 19464	M	225	102	432	132	–	1	3	8	9	–	–	–	–	Porto Velho, RO – BRA
[3]MZUSP 19751	M	232	112	483	161	–	1	3	8	9	–	–	–	–	Porto Velho, RO – BRA
[3]MZUSP 19797	M	231	110	506	171	–	1	3	8	8–9	–	–	–	–	Porto Velho, RO – BRA
[3]MZUSP 20467	M	231	107	511	172	–	1	3	8	9	–	–	–	–	Porto Velho, RO – BRA
[3]MZUSP 20781	M	231	113	401	118	–	1	3	8	9	–	–	–	–	Porto Velho, RO – BRA
[3]MZUSP 20782	F	226	101	651	192	–	1	3	8	9	–	–	–	–	Porto Velho, RO – BRA
[1]NMP6V73610	M	227	113	515	185	–	1	3	8	–	–	–	–	–	Frederico Román, Pando – BOL
UFMT 5364	F	233	Incomplete tail	271	–	11.9	1(3)	3(5–6)	8(3–5)	9(1–4)(4–5)	d (2–3)	21	12	15+2	Alto Paraíso, RO – BRA
UFMT 5480	F	235	101	643	194	18.9	1(3)	3(5–6)	8(3–5)	9(1–4)(5)	e (2–3)	20	11	16+2	Alta Floresta, MT – BRA
UFMT 6268	F	239	117	290	96	11.8	1(0)	3(5–6)	8(3–5)	9(1–4)(5)	e (2–3)	18	13	14+2	Sinop, MT – BRA
UFMT 6532	M	238	119	483	154	15	1(3)	3(5–6)	8(3–5)	9(1–4)(5)	e (2–3)	18	11	16+2	Sinop, MT – BRA
UFMT 6694	M	–	114	712	248	20.3	1(3)	3(5–6)	8(3–5)	9(1–4)(4–5)	d/e(2–3)	18	12	16+2	Cotriguaçu, MT – BRA
UFMT 8208	M	239	108	600	205	18.1	1(0)	3(5–6)	8(3–5)	9(1–4)(5)	d (2–3)	18	13	15+2	Paranaíta, MT – BRA
UFMT 8241	M	240	114	406	131	12.9	1(3)	3(5–6)	8(3–5)	9(1–4)(4–5)	e (2–3)	16	9	15+2	Paranaíta, MT – BRA
UFMT 8518	F	230	106	701	205	21.2	1(3)	3(5–6)	8(3–5)	9(1–4)(4–5)	e (2–3)	18	9	15+2	Paranaíta, MT – BRA
UFMT 8925	F	221	101	431	127	15.3	1(3)	3(5–6)	8(3–5)	9(1–4)(5)	e (2–3)	19	12	15+2	Colniza, MT – BRA
UFMT 10610	F	225	99	390	113	13.7	1(3)	3(5–6)	8(3–5)	9(1–4)(5)	e (2–3)	18	9	16+2	Alto Paraíso, MT – BRA

Appendix 2

Comparative material examined ([1]hemipenis; [2]skull).

Siphlophis cervinus: Brazil: Amazonas: Presidente Figueiredo (MPEG 17737), Mato Grosso: Mato Grosso (MNRJ 369), Pará: Barcarena (MPEG 16431, MPEG 18496), Belém (MPEG 16468, IBSP 17668[1]), Capitão Poço (MPEG 6830), Tucurui (MPEG 16726[1,2]), Viseu (MPEG 10103, MPEG 10104), Rondônia: Porto Velho (IBSP 40874), Samuel - Rio Jamari (MPEG 17887).

Siphlophis compressus: Brazil: Amazonas: Benjamim Constant (MNRJ 1451), Mato Grosso: Mato Grosso (MNRJ 211), Pará: Tucuruí (IBSP 46448, IBSP 47075, IBSP 47617), Rondônia: Espigão do Oeste (IBSP 41233, MHNCI 7963[1,2]), Porto Velho (IBSP 17392[2], IBSP 47.084, LSUMZ 27352[1]).

Siphlophis leucocephalus: Brazil: Bahia: Ilhéus (CEPEC 750[1], CEPEC 993[1], CEPEC 1140, CEPEC 1619, CEPEC 3336, CEPEC 4261), Santa Cruz de Cabrália (CEPEC 5304[2], CEPEC 5360), Goiás: Cana Brava (IBSP 9141).

Siphlophis longicaudatus: Brazil: Espírito Santo: Espírito Santo (IBSP 9727), Goiás: Ipameri (IBSP 55257), Minas Gerais: Mariléia (MHNCI 7961[2], MZV 812). Rio de Janeiro: Alto Teresópolis (IBSP 13179[1]), Teresópolis (IBSP 55702, MNRJ 2881), Rio Grande do Sul: Dom Pedro (IBSP 9985), São Paulo: Campo Limpo (IBSP 5255), Cotia (IBSP 14252, IBSP 23209, IBSP 49206, IBSP 57020), Cubatão (IBSP 19583, IBSP 40725), Sorocaba (IBSP 41183[1]).

Siphlophis pulcher: Brazil: Pará: Tucuruí (IBSP 49849), Rio de Janeiro: Rio de Janeiro (MNRJ 3142, MNRJ 4805, MNRJ 4821), Santa Catarina: Itapoá (MHNCI 334[1], MHNCI 7121[2]), São Paulo: Barra Funda (IBSP 11580), Caraguatatuba (IBSP 54225, IBSP 54973), Guarujá (IBSP 22398[1]).