

## REDESCRIPTION AND MORPHOLOGICAL VARIATION OF *OXYRHOPUS CLATHRATUS* DUMÉRIL, BIBRON AND DUMÉRIL, 1854 (SERPENTES: DIPSADIDAE: XENODONTINAE)

PEDRO HENRIQUE BERNARDO<sup>1,2,5</sup>, FABIO A. MACHADO<sup>1,4</sup>, ROBERT W. MURPHY<sup>2,3</sup>, AND HUSSAM ZAHER<sup>1</sup>

<sup>1</sup> Museu de Zoologia da Universidade de São Paulo, Avenida Nazaré, 481, CEP 04263-000, São Paulo, SP, Brazil.

<sup>2</sup> Centre for Biodiversity and Conservation Biology, Royal Ontario Museum, 100 Queen's Park, Toronto, ON M5S 2C6, Canada.

<sup>3</sup> Key Laboratory of Genetic Resources and Evolution, Kunming Institute of Zoology, Chinese Academy of Sciences, Kunming 650223, China.

<sup>4</sup> Departamento de Genética e Biologia Evolutiva, IB-USP, Rua do Matão, travessa 14, nº 227, CEP 05422-970, São Paulo, SP, Brasil.

<sup>5</sup> E-mail corresponding author: bernardoph@gmail.com

**ABSTRACT.** The snake *Oxyrhopus clathratus*, which has a restricted distribution within the Atlantic Forest Domain, exhibits great variability in color pattern, shape of the hemipenis, and scalation. The extent of variation has resulted in substantial taxonomic confusion. To date, identification and recognition are problematic, and this is reflected in the synonymy of the species. We examine the type series and specimens from throughout the species' distribution to assess intraspecific morphological variation. Morphological variability is correlated with geographical distribution and elevation. Further, we explore whether the morphological data support recognition of more than one species or not. The results suggest that *O. clathratus* is a single species that exhibits considerable variation in morphology, including three distinct patterns of coloration (melanistic, melanistic with inconspicuous narrow light bands, and with conspicuous dark and light bands alternating along the body) that overlap geographically. The morphology of the ornamented hemipenes varies between "T-shape" and "Y-shape" forms, which occur without any meaningful or elevational structuring. The loreals are usually absent. Based on our results we designate a lectotype for the species.

**KEYWORDS.** Taxonomy; External morphology; Hemipenis; Geographic Variation; Morphometric Analyses; Polychromatism.

### INTRODUCTION

The taxonomy and phylogenetic relationships of advanced snakes (Serpentes, Caenophidia) have experienced great changes in recent years (Vidal *et al.*, 2007, 2008, 2010; Zaher *et al.*, 2009). Currently, the species *Oxyrhopus clathratus* Duméril, Bibron and Duméril, 1854 is allocated to the family Dipsadidae, subfamily Xenodontinae and tribe Pseudoboini. This tribe is considered a monophyletic assemblage (Zaher, 1994; Zaher, 1999; Zaher *et al.*, 2009; Vidal *et al.*, 2010) comprised of the genera *Boiruna*, *Clelia*, *Drepanoides*, *Mussurana*, *Oxyrhopus*, *Phimophis*, *Pseudoboa*, *Rhachidelus*, and *Siphlophis*.

Among pseudoboines, the genus *Oxyrhopus* retains a history of substantial nomenclatorial instability. Until modern definition of the pseudoboin genera (Bailey, 1970; Zaher, 1996), some species were allocated within *Clelia* and *Pseudoboa* (Boulenger, 1896; Stejneger, 1901; Gomes, 1918; Amaral, 1926; Bailey, 1967, 1970). Currently, the genus is considered to be a polyphyletic group (Zaher, 1994) consisting of 14 species (Zaher and Caramaschi, 2000; Lynch, 2009) that occur from southern Mexico to northern Argentina (Bailey, 1970; Lynch, 2009). The taxonomy is well resolved for some species, such as *O. guibei* Hoge and Romano 1977 (Zaher and Caramaschi, 1992) but is still problematic for many others, such as *O. clathratus*.

*Oxyrhopus clathratus* is restricted to the Atlantic Forest Domain (Ab'Sáber, 1977) of southeastern South America (Bailey, 1970) and was described based on specimens possessing a banded coloration pattern and no loreal scales (Duméril *et al.*, 1854). Posteriorly, Werner (1903) and Müller (1923) described *O. doliatus* var. *viperina* and *Clelia clathrata pulcherrima*, respectively. Amaral (1930) transferred *O. clathratus* to the genus *Pseudoboa* Schneider, 1801, and considered the last two species as junior synonyms of *Pseudoboa clathrata*. Differing from Amaral (1930), Prado (1945) placed the species in the genus *Clelia*. Taxonomic chaos decreased after Bailey (1967) reviewed all three genera, and three years later (Bailey, 1970) recognized *Oxyrhopus clathratus*. However, problems with intraspecific variation persist. The extent of morphological diversity throughout the geographic range of *O. clathratus* remains to be investigated. Morato (2005) first documented melanistic variation in *O. clathratus*, suggesting a relationship between this character and altitudinal elevation. He suggested that some populations should be recognized as new species. Bernardo and Pires (2005) agreed with Morato (2005) and also suggested a correlation occurs between melanistic individuals and high elevations.

Herein, we examine variation in several morphological characters involving color, shape of the hemipenes and presence of loreal scales in *O. clathratus*

from specimens collected throughout the geographic range of the species. Our main objectives are to verify the existence of distinct spatial patterns and to correlate these patterns with geographic and elevational gradients, testing if the currently recognized species is polytypic. To this end, we employ our analyses to delimit the geographic distribution of the species and to revise the species' diagnosis.

## MATERIAL AND METHODS

### Material

We visited the following museums and analyzed 233 specimens of *O. clathratus*, which covered the entire geographic range of the species (Fig. 1; Appendix I): Argentina – Museo Argentino de Ciencias Naturales “Bernardino Rivadavia” (MACN), Buenos Aires; Brazil – Instituto Butantan (IBSP), São Paulo, SP; Laboratório de Zoologia dos Vertebrados da Universidade Federal de Ouro Preto (LZV-UFOP), Ouro Preto, MG; Museu Biológico Mello Leitão (MBML), Santa Teresa, ES; Museu de Ciência e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul (MCP), Porto Alegre, RS; Museu Nacional, Universidade Federal do Rio de Janeiro (MNRJ), Rio de Janeiro, RJ; Museu de Zoologia “João Moogen” da Universidade Federal de Viçosa (MZUFV), Viçosa, MG; Museu de Zoologia da Universidade Estadual

Santa Cruz (MZUESC), Ilhéus, BA; Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, SP; Museu de Zoologia da Universidade Estadual de Campinas (ZUEC), Campinas, SP; and France – Muséum National d'histoire Naturelle (MNHN), Paris.

Our morphological assessment examined scutellation, meristic, coloration, and hemipenial morphology. Terminology for ventral scales followed Dowling (1951), whereas the terminology of the remaining scales followed Vanzolini *et al.* (1980). Measurements of specimens were made using a string stretched over the ventral surface then stretched over a measuring tape with 1 mm precision and a digital caliper with 0.01 mm precision. To improve the accuracy of small measurements (head length and head width), we used the morphometric software TPSDig2 version 2.1.4 (Rohlf, 2009) with high definition images acquired by using a Pentax K10D digital camera. A total of 48 hemipenes were analyzed. The preparation method followed Pesantes (1994) as modified by Zaher and Prudente (2003), and the terminology for hemipenial morphology followed Zaher (1999).

### Geographical variation

We employed spatial analysis of morphometric and meristic variables in order to identify the presence of any patterning of morphological variation.

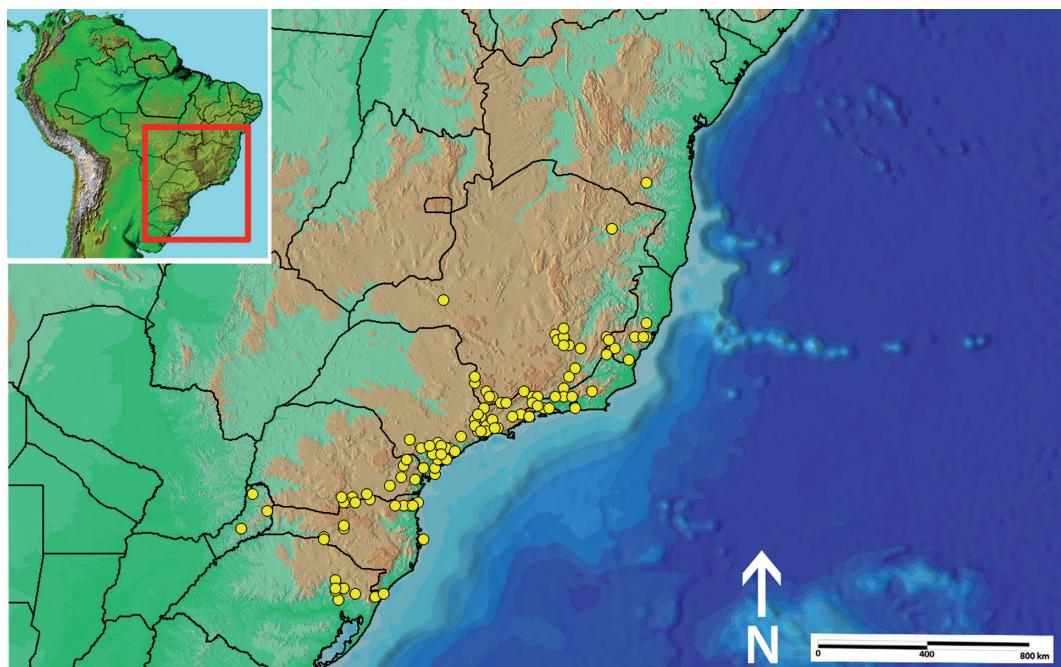


FIGURE 1. Specimens analyzed and geographic distribution map of *Oxyrhopus clathratus*.

Our analysis used the following meristic variables: mid-dorsal scale rows (MDR), ventral scales (VENT), subcaudals scales (SC), bands on the body (BBD), and bands on the tail (TBD). Continuous characters included the following: head length (HL), head width (HW), tail length (TL), and snout vent length (SVL). These measurements were log-transformed and corrected for ontogenetic allometry using Common Principal Component Analysis and Burnaby's back-projection method (Burnaby, 1966). The variance-covariance matrix necessary for this analysis was estimated pooling both sexes together while after correcting for mean differences between them (see Results). Residuals of this analysis and meristic variables were used as two different datasets. Even though some variables showed no clear deviance from normality in a quantile-quantile plot, we opted to analyze them using non-parametric methods, because each dataset contained at least one non-normal variable.

The geographical variation of these characters was investigated using geographical coordinates of the sampling site of each specimen. In order to account for spatial autocorrelation between observations, we employed a Principal Coordinate Analysis of Neighbors Matrices filtering method (PCNM; Dray *et al.*, 2006), which produced independent geographical vectors that were used as variables in other statistical analyses. We calculated the Moran's I associated with each PCNM vector and tested its significance through a parametric test in order to obtain the relevant vectors for analysis.

The presence of sexual dimorphism in each dataset was investigated using a non-parametric multivariate analysis of variance (NP-MANOVA), which allowed control of variation from confounding factors (Anderson, 2001), such as geography (PCNM) and altitude. The NP-MANOVA used morphological distances between specimens to test hypotheses. To test for the presence of sexual dimorphism in meristic characters, we used a Gower distance among observations to control differences in magnitude between variables. For size-controlled continuous variables, we used Euclidian distances between individuals because the variables were already log-transformed and size-corrected. Significance of the NP-MANOVA was calculated through permutations.

To evaluate the presence of geographical patterning of morphological variation, we performed a Canonical Trend Surface Analysis (CTSA; Wartenberg, 1985) using significant PCNM vectors as geographical variables and both morphological datasets

separately. The significance of the CTSA was accessed through a permutation procedure.

To investigate geographic variation in discrete variables related to coloration and shape of hemipenes, we analyzed differences in the geographical distribution of individuals with different character states using the NP-MANOVA method as described above. We employed Mann-Whitney tests to evaluate elevational variation associated with these characters. We performed pair-wise tests of color variation for both geographical and elevational variation and *p*-values were adjusted for repeated tests with a Bonferroni correction.

All statistical analyses were performed using the software R v. 2.14.2 (R Development Core Team, 2012). The significance of non-parametric methods was accessed through 999 permutations, and empirical *p*-values were evaluated at  $\alpha = 0.05$  (Manly, 1997). The back-projection size correction was done with the "cpcbp" package v. 0.3.2 (McCoy *et al.*, 2006); PCNM analysis was performed with the PCNM package v. 2.1-2/r106 (Legendre *et al.*, 2012); NP-MANOVA and CTSA were implemented in the package "vegan" v. 2.0-3 (Oksanen *et al.*, 2010).

## RESULTS

The PCNM analysis yielded 21 significant axes. These were used as geographical variables ( $p < 0.047$  for all axes, see online appendix for more details). The NP-MANOVAs detected significant deviations from random for the count-variables dataset associated with sexual dimorphism ( $p = 0.001$ ) after controlling for geography and elevation. Sexual dimorphism explained approximately 11.52% of the overall variation. Females tended to have larger values for MDR, VENT, and BBD than males; males had larger values of SC and TBD than females. Analysis of allometrically corrected quantitative traits detected significant sexual dimorphism ( $p = 0.002$ ) after controlling for geography and altitude, but explained only 2.9% of the total variation; females had larger bodies and heads (SVL, HL, and HW) and males had larger tails (TL). To correct for sexual dimorphism, we computed the difference in means and medians of the morphometric and meristic variables, respectively, and added the difference to all male individuals. Reanalyzes of sexual dimorphism based on the corrected dataset did not differentiate the sexes ( $p > 0.239$ ).

Only the count dataset showed a significant correlation with elevation (count:  $p = 0.035$ ; continuous:

$p = 0.335$ ) after controlling for geographical variation. However, this explained only 1.2% of the total variation in meristic characters.

The CTSA was significant for both datasets ( $p > 0.002$ ). The adjusted  $R^2$  coefficients showed high spatial structuring of meristic variables (42.9%), but the morphometric variables showed a lower value (8.94%). The weights of each variable on the canonical axes showed a trend for meristic characters to increase in BBD and TBD from the southwest to the northeast (Fig. 2A). Variation in morphometric variables was subtler, but we noticed a moderate increase in SVL and TL and an associated decrease in HL and HW on the same geographical gradient (Table 1, Fig. 2B). This may be related to an increase in overall size.

The NP-MANOVA obtained a significant difference between geographic distribution and the different shapes of hemipenes ( $p = 0.024$ ). T-shaped hemipenes tended to occur more to the southwest, the Y-shaped more in the northeast (Fig. 2C). Regardless, a considerable geographic overlap of the types of hemipenes occurred (Fig. 2C; Fig. 3). The pair-wise comparison of geographical variation of individual color showed a distinction only between the distributions of banded and melanic individuals (*adjusted-p* = 0.017). Banded-melanic individuals showed no difference when compared to both other color morphs (*adjusted-p* > 0.05). Regardless, inspection of the geographical distributions (Fig. 2D) showed that these differences were mainly related to samples

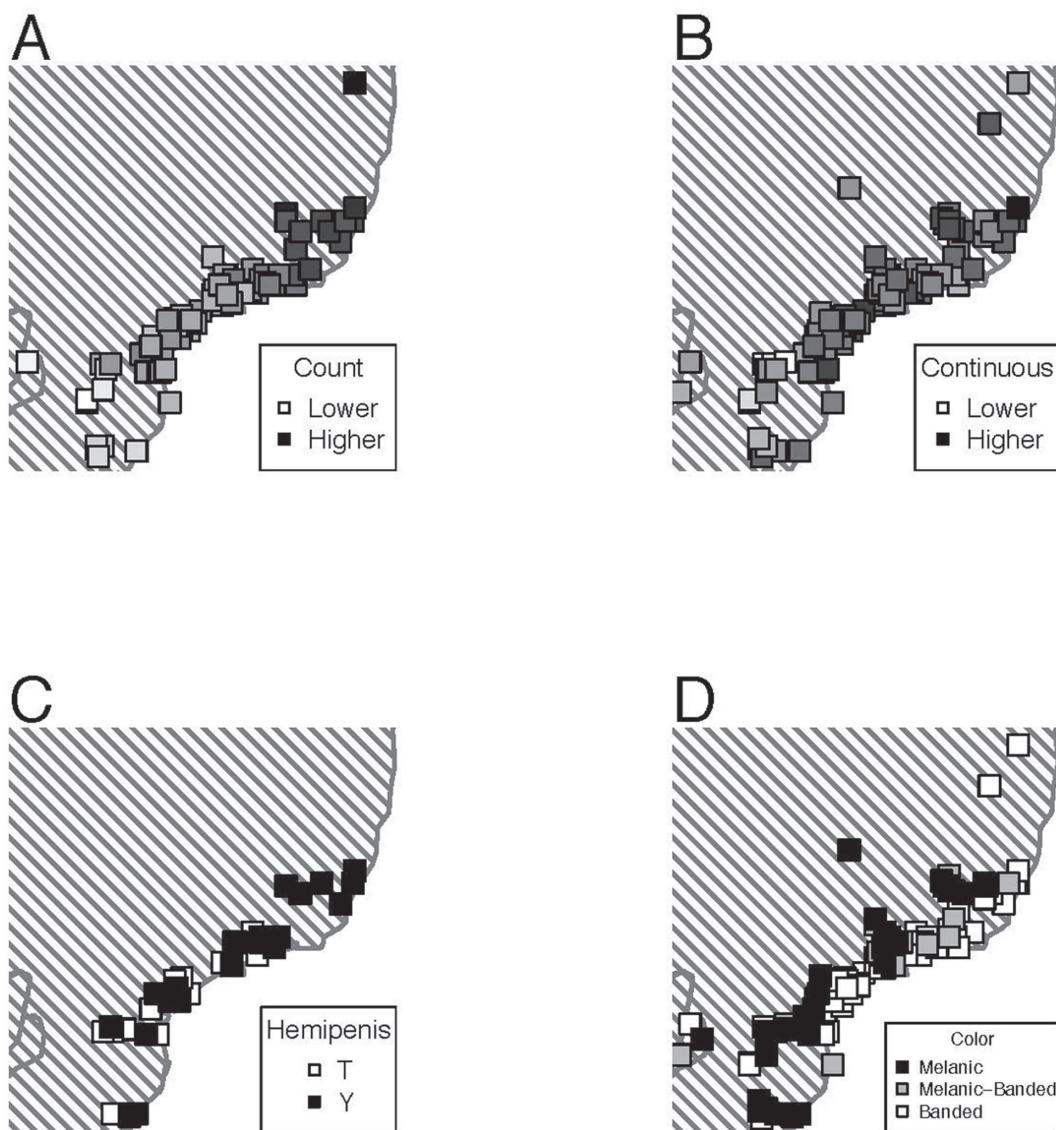


FIGURE 2. Geographic variation of *Oxyrhopus clathratus*. Darker symbols indicates higher values and whiter ones indicates lower values for A and B. A: First Canonical Axis of meristic variation; B: First Canonical Axis of morphometric variation; C: Geographic distribution of Hemipenis shape; D: Geographic distribution of the different color morphs.

TABLE 1. Table of weights of Canonical Trend Surface Analyses.

	CanAxis 1	CanAxis 2	CanAxis 3	CanAxis 4	CanAxis 5
MDR	0.115	0.640	-0.529	-0.096	0.536
VENT	0.124	0.811	0.025	0.385	0.422
SC	0.212	0.641	0.117	-0.478	-0.550
BBD	0.984	0.023	-0.072	0.146	-0.060
TBD	0.933	0.091	0.247	-0.243	0.018
	CanAxis 1	CanAxis 2	CanAxis 3		
SVL	0.403	0.783	0.474		
TL	0.692	-0.615	0.378		
HL	-0.741	0.321	0.590		
HW	-0.387	0.258	-0.885		

taken from the northern edges of the distribution, and the correlation could have been affected by sampling bias. Thus, a NP-MANOVA performed on all color morphs simultaneously indicated that, despite

significant ( $p\text{-value} = 0.017$ ), these differences were negligible (2.5% of the total geographic variation).

The analysis of elevation with respect to coloration detected the co-occurrence of melanistic and melanistic-banded specimens ( $\text{adjusted-}p = 0.462$ ), and that banded individuals tended to be found at lower elevations ( $\text{adjusted-}p = 0.0307$  and  $0.00046$  for melanistic and melanistic-banded specimens, respectively). Despite the large elevational superposition detected between color morphs, melanistic individuals (either fully melanistic or partially banded) were associated with higher elevations.

There is no significant correlations between shape of hemipenis and elevation, nor between the presence of the loreal scale in relation to elevation and geographic distribution ( $p\text{-value} > 0.7718$  for all analyses).

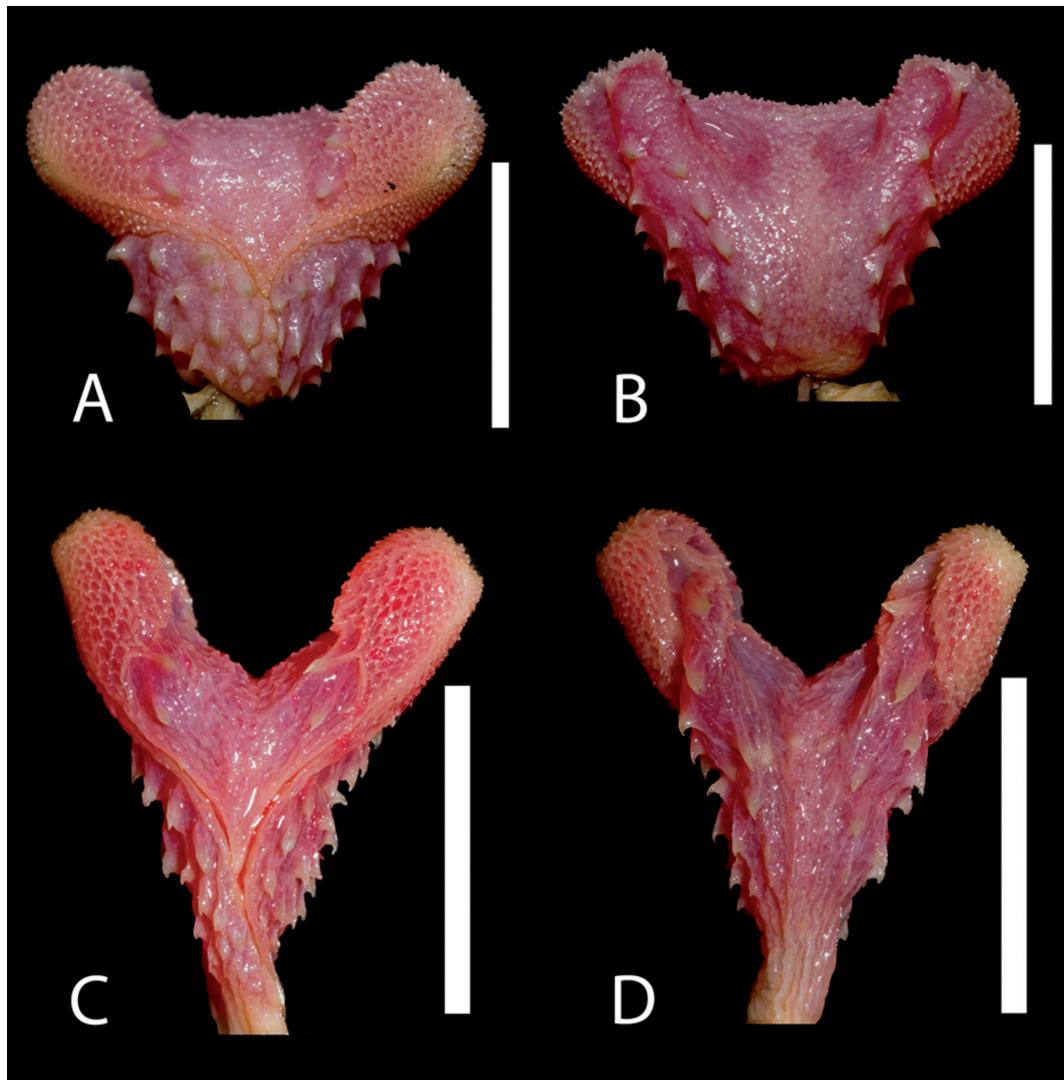


FIGURE 3. Fully everted and maximally inflated hemipenes of *Oxyrhopus clathratus*. Hemipenis in T-shape (MZUSP 2848) in (A) sulcate and (B) asulcate view. Hemipenis in Y-shape (MZUSP 4111) in (A) sulcate and (B) asulcate view. Both specimens collected at the Biological Station of Boracéia, Salesópolis, São Paulo, Brazil. Scale = 10 mm.

Overall, morphological variation in *O. clathratus* was correlated with geographic distance. No distinct break in morphology was found, indicating a gradual transition. No evidence served to reject the null hypothesis of conspecificity, *i.e.*, one species. Thus, *O. clathratus* was assumed to be a highly polymorphic species.

*Oxyrhopus clathratus* Duméril, Bibron et Duméril, 1854

*Oxyrhopus clathratus* Duméril, Bibron et Duméril, 1854. Erp. gén., 7:1026. Type locality: Brazil.

*Oxyrhopus doliatus* var. *viperina* Werner, 1903. Zool. Anz. 26:250. Type locality: Brazil.

*Clelia clathrata pulcherrima* Müller, 1923. Zool. Anz. 57:153. Type locality: Humboldt, Santa Catarina, Brazil.

*Oxyrhopus clathratus*: Werner, 1925. Arch. Berlin 90:127

*Cloelia clathrata pulcherrima*: Werner, 1929. Zoo. Jahrb. Jena. Syst. 57:182

*Pseudoboa formosa clathrata*: Amaral, 1930. Mem. Inst. But. 4:37

*Cloelia clathrata*: Prado, 1945. Serp. Bras.: 83

*Pseudoboa clathrata*: Anthony, 1955. Ann. Des. Nat. Zool. 11:10

*Oxyrhopus clathratus*: Bailey, 1970. in Peters and Orejas-Miranda Cat. Neot. Squa. Part I: 231

**Type series:** Following the International Code of Zoological Nomenclature (ICZN, 1999) and the comparative analysis of the syntypes, MNHN 3791 and MNHN 3792, we designed specimen MNHN 3791 as the Lectotype for the following reasons: (1) the original description states that the loreal scale is almost always absent, as in specimen MNHN 3791; (2) the dorsal coloration of MNHN 3791 better fits the original description as translated from French into English as follows: "The front and upper back of the body and tail are blackish-brown or uniform olive. On the flanks there are shades of yellow that in juveniles vary from 70 to 100 bands or vertical bars. With age, these yellow bands narrow forming little triangular patches" (Duméril *et al.*, 1854:1027). Specimen MNHN 3791 clearly displays these bands, while MNHN 3792 is melanistic, with a few almost imperceptible bands; and (3) MNHN 3791 is in better condition than MNHN 3792.

**Description of the lectotype MNHN 3791 (Fig. 4):** Adult male, SVL = 752 mm, TL = 192 mm. Head

almost twice longer than wide (HL = 22.4 mm; HW = 11.7 mm). Rostral wider than high, two internasals, nasal divided, two prefrontals, which touch the supraocular separating the frontal from the preocular. Loreal absent. One preocular; two postoculars; temporal 2 + 3; 8 supralabials on each side, the 4<sup>th</sup> and 5<sup>th</sup> touching eye; 9 infralabials on each side, first four scales touching anterior genial. Dorsal scales smooth, with two apical pits, arranged in 19:19:17 rows. The reduction of dorsal rows occurs through the merger of the 3<sup>rd</sup> and 4<sup>th</sup> rows on both sides at the level of 133 ventral scale on the left and 134 on the right. Ventral scales 203. Anal plate single and 69 paired subcaudals. The lectotype has conspicuous dark and light bands alternating along the body, but because it is a very old specimen some parts of the body are discolored and we were unable to count the side bands. Bands are joined dorsally, forming a uniform blackish brown dorsum (Duméril *et al.*, 1854). Laterally the alternating dark and light bands are clearly visible (Fig. 2E) and invade the edges of ventrals along the entire body. The anterior portion of belly is pale brown, with few darker spots, which increase in intensity posteriorly (Duméril *et al.*, 1854).

**Diagnosis:** *Oxyrhopus clathratus* can be distinguished from the sympatric species *O. formosus*, *O. rhombifer*, and *O. guibei* by the following combination of characters: preocular does not touch frontal (preocular in contact with frontal in *O. rhombifer* and *O. guibei*); the head is uniformly black (the head is uniformly red or orange-red in *O. formosus*); non-melanistic specimens possess a banded dorsal pattern of coloration with black and white/red/brown bands uniformly distributed throughout the dorsum (black bands are disposed in triads in *O. guibei*); the ventral edge of the black bands invade the ventral scales (black bands never invade the ventrals in *O. rhombifer* and form complete rings throughout the ventrals in *O. formosus*); the hemipenis lacks a naked area on the tip of the lobes (*O. guibei* and *O. rhombifer* possess a conspicuous nude area on the tip of the lobes).

#### Morphological Variation

**Pholidosis:** Loreal either present ( $n = 150$ ), or absent or fused to the pre-frontal ( $n = 60$ ), occasionally present on one side only ( $n = 16$ ). Anterior temporal scales range from 1 to 3, with 99.13% of the observed individuals ( $n = 228$ ) possessing 2 scales; posterior temporal scales range from 2 to 3, with 99.13% of the observed

individuals ( $n = 228$ ) possessing 3 scales. Number of supralabials ranges between 7 and 9, with 97.3% of the observed individuals ( $n = 216$ ) showing 8 supralabials. The 4<sup>th</sup> and 5<sup>th</sup> supralabials usually touch the orbit (98.2%;  $n = 218$ ). Number of infralabials ranges from 8 to 10 with 78.4% of the observed individuals ( $n = 171$ ) with 9 infralabials. Usually with two anterior and two posterior genials, and the first four infralabials usually contact the anterior genial (92%;  $n = 207$ ). Dorsal scales smooth with two apical pits, arranged in rows of 19:19:17 ( $n = 220$ ), 19:19:15 ( $n = 7$ ), or 19:21:17 ( $n = 3$ ). Reduction of dorsal rows similar on both sides of the body, the left side reduction mainly involving the merger of the third and fourth scale rows (83.3%,  $n = 176$ ) at the position of between the 115 and 158 ventral ( $\bar{x} = 132$ ;  $sd = 6.8$ ;  $n = 210$ ). Likewise,

reduction on the right side usually involves fusion of the third and fourth rows (93.3%,  $n = 181$ ) and the reduction occurs between the ventrals 111 and 156 ( $\bar{x} = 132$ ;  $sd = 6.9$ ;  $n = 194$ ). Number of ventrals ranges from 183 to 212 in males ( $\bar{x} = 197.86$ ;  $sd = 4.89$ ;  $n = 115$ ) and 190 and 221 in females ( $\bar{x} = 203.41$ ;  $sd = 5.57$ ;  $n = 107$ ). Paired subcaudals range between 46 and 88 in males ( $\bar{x} = 77$ ;  $sd = 7$ ;  $n = 111$ ) and 59 and 85 in females ( $\bar{x} = 68$ ;  $sd = 5$ ;  $n = 96$ ). MDR ranges from 193 to 220 in males ( $\bar{x} = 205.92$ ;  $sd = 4.98$ ;  $n = 106$ ) and 194 to 231 in females ( $\bar{x} = 210.64$ ;  $sd = 6.4$ ;  $n = 105$ ).

**Morphometrics:** A medium size snake, the largest male measures 904 mm SVL and 246 mm TL, and the largest female measures 1008 mm SVL and 196 mm TL. The smallest specimens are a series of neonates,



FIGURE 4. *Oxyrhopus clathratus*, MNHN 3791 (Lectotype) head in (A) dorsal, (B) ventral, (C) right view, (D) left view, and mid-body in (E) left view. Scale = 10 mm.

with one still inside the egg (MZUFV 709A-709D) with SVL ranging from 195 to 215 mm ( $\bar{x} = 205$ ;  $sd = 8.52$ ;  $n = 4$ ) and TL ranging from 50 to 52 mm ( $\bar{x} = 51$ ;  $sd = 1.15$ ;  $n = 4$ ).

**Hemipenial morphology:** The hemipenes of *O. clathratus* may be T- or Y-shaped. They are deeply bilobed, bicalculate, bicapitate and have four rows of well-developed enlarged lateral spines that originate on the sulcate surface and extend to the lateral sides of the organ until the asulcate surface (Fig. 3). The sulcus spermaticus divides midway on the hemipenial body and each branch extends to the lateral sides of the organ in centrifugal orientation. The lobes do not have a nude area at the tip and are fully ornamented with papillate calyces that tend to be spinulate on the edges of the capitulum. The intrasulcar region is expanded and has two rows of spines adjacent to each capitulum. Lobular crests are present but without spines and covered with spinules as in the entire body of the hemipenis. Nude pockets on the lobular crotch are present and very evident.

**Coloration in preservation:** Preserved juveniles and adults exhibit one of the following three different dorsal patterns (Fig. 5): 1) body uniformly black (melanic), with no visible bands ( $n = 43$ ); 2) body with alternating light and black bands, but with some degree of melanism that makes it difficult to count the black bands ( $n = 25$ ); 3) body with a series of clearly visible black bands ( $n = 164$ ) alternating with light cream bands. In the latter condition, the number of black dorsal body bands varies between 29 and 94 in males ( $\bar{x} = 50.99$ ;  $sd = 14.34$ ;  $n = 96$ ) and between 31 and 100 in females ( $\bar{x} = 63.43$ ;  $sd = 18.5$ ;  $n = 68$ ). Black dorsal tail bands range from 11 to 35 in males ( $\bar{x} = 19.83$ ;  $sd = 5.41$ ;  $n = 93$ ) and 10 to 33 in females ( $\bar{x} = 19.21$ ;  $sd = 5.69$ ;  $n = 63$ ). In all non-melanistic specimens, black dorsal bands fuse mid-dorsally and invade the edges of ventrals ventrally. In all specimens, the belly is yellowish throughout the body, with scattered black spots that increase in number from the anterior to the posterior two-thirds of the belly, while the tail is either banded or uniformly black.

**Coloration in life:** Live individuals of *Oxyrhopus clathratus* show significant polymorphism in body coloration (Fig. 6), ranging from completely melanic to strongly banded specimens. The dorsal coloration can be all black (melanic specimens), banded (black bands alternated with lighter bands) or banded with the posterior part of the body melanic.

In melanic individuals, the dorsum is uniformly black (Fig. 6A) while the belly is white with scattered black spots that increase in number from the anterior to the posterior region. Rarely, in strongly melanic specimens, the belly becomes largely invaded with black from the edges to the center, leaving only an uninterrupted white string in the middle of the venter. The ventral part of the tail is always uniformly black.

All non-melanistic specimens have a black head cap from the tip of the snout to the posterior border of the parietals and anterior portion of the temporal region. A strait white, red or brown light collar follows the black head cap. The light collar covers no more than three dorsal scales along the vertebral line. The dorsum is banded with alternating light (white, red or brown) and black bands distributed uniformly throughout the body, while the belly is white throughout the body with the edges of ventral scales always invaded by the black bands and occasional black spots scattered throughout its posterior two-thirds. The ventral surface of the tail is either banded or uniformly black. In some specimens, dorsal bands tend to fuse together in the posterior part of the body.

Light bands in banded specimens can be white, red or brown, showing an ontogenetic color shift from white to red or brown. Light bands are white or light cream in all young individuals (Fig. 6B) whereas in juveniles the white bands are invaded with red or brown, with the white parts being restricted to the lateral and ventral edges of the bands (Figs. 6C and 6D). In large adult specimens, the nuchal collar and all light bands become entirely red or brown (Figs. 6E and 6F).

**Distribution:** *Oxyrhopus clathratus* occurs only in the Atlantic Forest Domain (Fig. 1; Ab'Sáber, 1977). The northern limit for the species is near Barra do Choça, Bahia, Brazil (Argôlo, 2001), with records extending from the states of Minas Gerais and Espírito Santo to Rio Grande do Sul in southern Brazil; and west in forested areas of Misiones, Argentina (Bailey, 1970; Giraudo and Scrocchi, 2002; Argôlo, 2001).

## DISCUSSION

A comparison of the scalation of *O. clathratus* and other species of *Oxyrhopus* is presented in Table 2. With few exceptions, the scalation in *O. clathratus* does not differ from that of the other species. Species of *Oxyrhopus* have usually eight supralabials (with the exception of *O. marcapatae* with seven), nine or

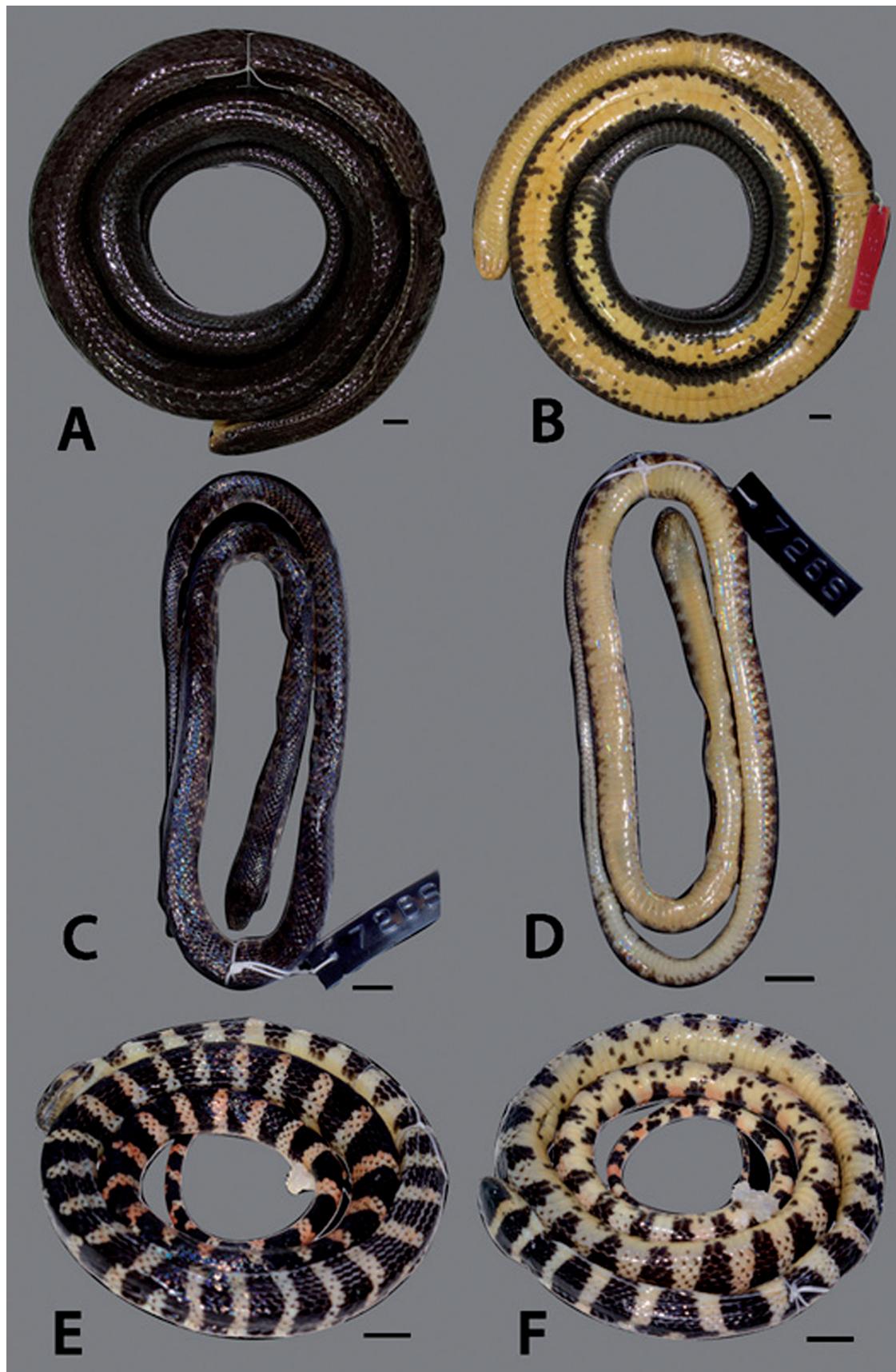


FIGURE 5. Coloration in preserved adult specimens of *Oxyrhopus clathratus*. (A) Dorsal and (B) ventral views of a melanic specimen (MCP 16881); (C) dorsal and (D) ventral views of a partially melanic specimen (LZV-UFOP 726); (D) dorsal and (E) ventral views of a banded specimen (MZUSP 15233). Scale = 10 mm.



FIGURE 6. Coloration in life: (A) Melanic (Arvoredo, Santa Catarina, Brazil); (B) banded with high degree of melanism (Chapecó, Santa Catarina, Brazil); (C) new born banded (MZUSP 15139 from Parque Estadual Jacupiranga, São Paulo, Brazil); (D) juvenile banded (MZUSP 15233 from São Miguel Arcanjo, São Paulo, Brazil); (E) adult “red banded” (Camacan, Bahia, Brazil); and (F) subadult “brown banded” (DZUFRGS 6295 from Praia Grande, Santa Catarina, Brazil).

10 infralabials (with the exception of *O. leucomelas*, which ranges between seven and eight), a single preocular and two postoculars, two anterior genials and two posterior genials, 2 + 3 temporals (except in *O. marcapatae* which has 1 + 2), two apical pits (except for *O. erdisii*, which has none), 19 rows of dorsal scales (with the exceptions of *O. marcapatae* and *O. leucomelas*), a single anal plate, and divided subcaudals.

The contact between the frontal and the preocular is a conspicuous taxonomic character within the genus *Oxyrhopus*. This contact occurs in six species while in the other eight, including *O. clathratus*, the frontal does not touch the preocular. This is one of the main characters that Duméril *et al.* (1854) used in the description of *O. clathratus* and it serves to diagnose the species from two of the three sympatric species

TABLE 2. Comparison of the scalation between species of the genus *Oxyrhopus*.

Species	Supralabials	Infralabials	Genials	Dorsals	Frontal contacting preocular	Loreal present	References
<i>O. clathratus</i>	8 (4,5)	9 or 10	2,2-5	19:19:17	no	yes or no	4,8
<i>O. doliatus</i>	8 (4,5)	9	2,2-4	19	no	yes	2,3,9,18,20
<i>O. erdisii</i>	8 (4,5)	9	2,2-4	19:19:15	no	yes	3
<i>O. fitzingeri</i>	8	9	2,2-4,5	19	no	yes	2,4,16
<i>O. formosus</i>	8 (4,5)	9	2,2-4	19	no	yes	1,4,6,7
<i>O. guibei</i>	8 (4,5)	10	2,2-5	19:19:17	yes	yes	8,11,19
<i>O. leucomelas</i>	7 or 8	7 or 8	2,2-4,5	17:17:15	no	yes	12
<i>O. marcapatae</i>	7 (3,4)	8	2,2-4	15	no	yes	2,5
<i>O. melanogenys</i>	8 (4,5)	10	2,2-4	19:19:17	yes	yes	2,14
<i>O. occipitalis</i>	8 (4,5)	9	2,2-5	19:19:17	no	yes	10,12,13,18
<i>O. petolarius</i>	8 (4,5)	10	2,2-5	19:19:17	yes	yes	9,8,12,15
<i>O. rhombifer</i>	8 (4,5)	9 or 10	2,2-4	19:19:17	yes	yes	8,9
<i>O. trigeminus</i>	8 (4,5)	10	2,2-4	19:19:17	yes	yes	9,19
<i>O. vanidicus</i>	8 (4,5)	10	2,2-4	19:19:17	yes	yes	12

References: (1) Amaral, 1948; (2) Bailey, 1970; (3) Barbour, 1913; (4) Boulenger, 1896; (5) Boulenger, 1902; (6) Cunha and Nascimento, 1983; (7) Gasc and Rodrigues, 1980; (8) Giraudo, 2001; (9) Griffin, 1916; (10) Hoge *et al.*, 1973; (11) Hoge and Romano, 1977; (12) Lynch, 2009; (13) MacCulloch *et al.*, 2009; (14) Nascimento *et al.*, 1987; (15) Roze, 1957; (16) Schmidt and Walker-Jr., 1943; (17) Stejenger, 1901; (18) Wagler, 1824; (19) Zaher and Caramaschi, 1992; (20) Zaher and Caramaschi, 2000.

(*O. guibei* and *O. rhombifer*). Another conspicuous character is the presence or absence of a loreal. *Oxyrhopus clathratus* is the only species within the genus that shows significant polymorphism in this character. However, the presence or absence of the loreal within *O. clathratus* is not correlated with any of the tested variables.

The absence of a loreal and substantial color variation are responsible for much taxonomic confusion in *O. clathratus*. Sometimes these characters lead to misidentification. This confusion is partly due to the species having three types of dorsal patterns and ontogenetic color changes that overlap geographically. Regardless, our statistical analyses show that melanic individuals tend to concentrate in the higher regions, while banded individuals tend to occur in lower elevations. Additionally, the geographic analysis revealed that there are some differences in the distribution of both melanic and banded morphs, with melanic individuals being more abundant in the southwestern portion of the distribution while banded individuals are more widespread throughout the distribution of the species. Banded individuals show a clear reduction in the number of bands in the southwestern part of the species' range, suggesting a correlation between topography (high elevations) and/or geography (southern provenance) with the overall "darkness" of an individual.

Our analyses include four melanic juveniles, and this suggests that melanism does not appear ontogenetically from a banded pattern; the extent of melanism seems to be both determined before birth and

independent from processes that influence the number of bands.

Differently from the black bands, light dorsal bands in *Oxyrhopus clathratus* undergo extensive ontogenetic color change from white to red or brown throughout life. Newly born and young individuals have invariably white bands that are progressively invaded with red or brown in juvenile specimens, turning into completely red or brown bands in large adult individuals. Color replacement tends to advance from the mid dorsal region of the band towards its edges. Both nuchal collar and light dorsal bands of large adult specimens become entirely red or brown in the later stages of ontogenetic color shift. Observations of live adult specimens suggest that individuals with light brown bands tend to occur in higher altitude areas, while specimens from low altitude areas tend to have red bands instead. However, this hypothesis could not be tested statistically since our sampling is mainly composed of preserved specimens in which coloration of lighter bands is not retained.

Intraspecific geographic variation in coloration occurs in many species of snakes (e.g., King, 1988; Forsman and Aberg, 2008; Boback and Siefferman, 2010) and some evidence indicates that distribution and habitat usage are significantly increased in species of non-avian reptiles that display coloration polymorphisms (Forsman and Aberg, 2008). This ecological diversification can result from the sympatric segregation of color morphs and subsequent adaptation to different niches (Forsman *et al.*, 2008; Mckinnon and Pierotti, 2010). However, given that

coloration in *O. clathratus* neither shows clear geographic structuring nor is associated with other morphological polymorphisms, melanism is more likely to be associated with local adaptation to different thermal niches.

*Oxyrhopus clathratus* is sexually dimorphic for both qualitative and quantitative characters. Females tend to have a larger SVL and a greater number of ventrals than males. Rocha-Barbosa *et al.*, (2000) report this dimorphism in *O. guibei* and attribute this difference to the storage of fat for vitellogenesis and egg carrying. Males have longer tails and a greater number of subcaudal scales than females, which is explained by the presence of the hemipenes and the retractor muscle (Rocha-Barbosa *et al.*, 2000).

Hemipenial morphology also varies in *O. clathratus*. Dowling (1967) justified the use of hemipenial characters in taxonomy (macroevolution) because there is no direct relationship between this structure and ecology, feeding habits, and locomotion. Considering the importance of this organ, but disagreeing with the greater importance of these characters in relation to others, Zaher and Prudente (1999) documented intraspecific variation in hemipenial characters for *Siphlophis*. They first described intraspecific variation in the hemipenial morphology of *O. clathratus* and noted the T- and Y-shapes on snakes of the genus *Siphlophis*, indicating that both conditions also occur in *O. clathratus*. Zaher (1999) described the T-shaped hemipenis of *O. clathratus* but did not comment on intraspecific variation. Dowling (2002) criticized these results claiming that the variation found in *Siphlophis* was an artifact of preparation. Zaher and Prudente (2003) countered the criticism by detailing their preparation of the hemipenes and illustrating that it was not an artifact of preparation. As with *Siphlophis*, the hemipenes of *O. clathratus* varies between the T- and Y-shapes, thus confirming that intraspecific variability is possible (Zaher and Prudente, 1999) and seems to be more widespread in Pseudoboini than previously thought.

## RESUMO

A serpente *Oxyrhopus clathratus*, que apresenta distribuição restrita ao Domínio Tropical Atlântico, apresenta grande variação no padrão de coloração, forma do hemipênis e folídose. A existência destas variações resulta em uma confusão taxonômica significativa. Até agora, o reconhecimento e identificação tem sido problemáticos, o que reflete nos sinônimos

desta espécie. Nós examinamos a série tipo e espécimes de toda área de ocorrência da espécies a fim de analisar a variação morfológica intraespecífica. As variações morfológicas foram correlacionadas com a distribuição geográfica e altitude. Além disso, nós avaliamos se os dados morfológicos suportam o reconhecimento de mais de uma espécie ou não. Os resultados sugerem que *O. clathratus* é uma espécie única que apresenta uma variação morfológica significativa, incluindo três padrões distintos de coloração (melânico, melânico com bandas claras finas e inconstantes, e com bandas clara e escuras conspicuas ao longo do corpo) que se sobrepõem geograficamente. A morfologia hemipeniana apresenta um padrão geral de ornamentação, mas com variação frequente entre as formas "T" e "Y", que ocorrem sem estruturação geográfica expressiva ou de altitude. A escama loreal está predominantemente ausente. Baseados nos nossos resultados nós designamos neste trabalho o lectótipo da espécie.

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## LITERATURE CITED

- Ab'saber, A. N. 1977. Os domínios morfoclimáticos na América do Sul. Primeira aproximação. *Geomorfologia*, 52:1-21.
- Amaral, A. 1926. Notas de Ophiologia: Da preferência do nome genérico *Pseudoboa* Schneider 1801 a *Clelia* Fitzinger, 1826 e *Oxyrhopus* Wagler, 1830. *Revista do Museu Paulista*, 14:10-16.
- Amaral, A. 1930. Estudo sobre Ophidios neotropicais. *Memórias do Instituto Butantan*, 4:3-68.

- Amaral, A. 1948. Ofídios do Mato Grosso (Contribuição II para o conhecimento dos ofídios do Brasil). Publicações. Comissão de Linhas Telegráficas Estratégicas de Mato Grosso ao Amazonas, 84:1-43.
- Anderson, M. 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, 26:32-46.
- Argôlo, A. J. S. 2001. *Oxyrhopus clathratus* – Geographic Distribution. *Herpetological Review*, 32:61.
- Bailey, J. R. 1967. The synthetic approach to colubrid classification. *Herpetologica*, 23:155-161.
- Bailey, J. R. 1970. *Oxyrhopus*; pp. 229-235. In: J. A. Peters and B. Orejas-Miranda (Eds.), Catalogue of the Neotropical Squamata. Part I: Snakes. Smithsonian Institution Press, Washington.
- Barbour, T. 1913. Reptiles Collected by the Yale Peruvian Expedition of 1912. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 65:506-507.
- Bernardo, P. H. and M. R. S. Pires. 2005. *Estudo Taxonômico de Oxyrhopus clathratus Duméril, Bibron e Duméril, 1854 (Serpentes, Xenodontinae)*. In: 13º Seminário de Iniciação Científica da Universidade Federal de Ouro Preto, Ouro Preto, Minas Gerais, Brasil, 1 pp.
- Boback, S. and L. Siefferman. 2010. Variation in color and color change in island and mainland boas (*Boa constrictor*). *Journal of Herpetology*, 44:506-515.
- Boulenger, G. A. 1896. Catalogue of the Snakes in the British Museum (Natural History). British Museum (Natural History), London, 727 pp.
- Boulenger, G. A. 1902. Descriptions of new batrachians and reptiles from the Andes of Peru and Bolivia. *Annals and Magazine of Natural History*, 7:401-402.
- Burnaby, T. 1966. Growth-invariant discriminant functions and generalized distances. *Biometrics*, 22:96-110.
- Cunha, O. R. and F. P. Nascimento. 1983. Ofídios da Amazônia: As espécies de *Oxyrhopus Wagler*, com uma subespécie nova, e *Pseudoboa Schneider*, na Amazônia oriental e Maranhão (Ophididae, Colubridae). *Boletim do Museu Paraense Emílio Goeldi*, 122:1-47.
- Dowling, H. G. 1951. A proposed standard system of counting ventrals in snakes. *British Journal of Herpetology*, 1:97-99.
- Dowling, H. G. 1967. Hemipenis and other characters in colubrid classification. *Herpetologica*, 23:138-142.
- Dowling, H. G. 2002. "Intraspecific variation of the hemipenis" a correction, with comments on other erroneous descriptions. *Herpetological Review*, 33:12-14.
- Dray, S., P. Legendre, and P. R. Peres-Neto. 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecological Modelling*, 196:483-493.
- Duméril, A. M. C., G. Bibron, and A. Duméril. 1854. Erpétologie générale, 7:1026.
- Forsman, A. and V. Åberg. 2008. Associations of variable coloration with niche breadth and conservation status among Australian reptiles. *Ecology*, 89:1201-1207.
- Forsman, A., J. Ahnesjö, S. Caesar, and M. Karlsoon. 2008. A model of ecological and evolutionary consequences of color polymorphism. *Ecology*, 89:34-40.
- Gasc, J. P. and M. T. Rodrigues. 1980. Liste préliminaire des Serpents de la Guyane française. *Bulletin de Muséum National d'histoire Naturelle*, Ser. 4, 2:559-598.
- Giraldo, A. R. 2001. Serpientes de la Selva Paranaense y del Chaco Húmedo. L. O. L. A., Buenos Aires, Argentina, 328 pp.
- Giraldo, A. R. and G. J. Scrocchi. 2002. Argentinian snakes: an annotated checklist. *Smithsonian Herpetological Information*, 132:1-53.
- Gomes, J. F. 1918. Contribuição para o conhecimento dos ofídios do Brasil. II. Ophidios do Museu Rocha (Ceará). *Revista do Museu Paulista*, 10:505-527.
- Griffin, L. E. 1916. A catalog of the Ophidia from South America at present (June 1916) contained in the Carnegie Museum with descriptions of some new species. *Memories of Carnegie Museum*, 7:163-277.
- Hoge, A. R., N. P. Santos, C. Heitor, L. A. Lopes, and I. M. Souza. 1973. Serpentes coletadas pelo projeto Rondon VII em Iauaretê, Brasil. *Memórias do Instituto Butantan*, 36:221-232.
- Hoge, A. R., S. Alma, and S. A. Romano. 1977. Description of a new subsp. of *Oxyrhopus Wagler* (Serpentes, Coluridae). *Memórias do Instituto Butantan*, 40/41:55-62.
- ICZN [International Commission on Zoological Nomenclature]. 1999. International Code of Zoological Nomenclature. The International Trust for Zoological Nomenclature, Padova, 306 pp.
- King, R. 1988. Polymorphic populations of the garter snake *Thamnophis sirtalis* near Lake Erie. *Herpetologica*, 44:451-458.
- Legendre, P., D. Borcard, F. G. Blanchet, and S. Dray. 2012. PCNM: MEM spatial eigenfunction and principal coordinate analyses. R package version 2.1-2/r106. <http://R-Forge.R-project.org/projects/sedan>.
- Lynch, J. D. 2009. Snakes of the genus *Oxyrhopus* (Colubridae: Squamata) in Colombia: taxonomy and geographic variation. *Papéis Avulsos de Zoologia*, 49:319-337.
- MacCulloch, R. D., A. Lathrop, P. J. R. Kok, R. Ernst, and M. Kalamandeen. 2009. The genus *Oxyrhopus* (Serpentes: Dipsadidae: Xenodontinae) in Guyana: morphology, distributions and comments on taxonomy *Papéis Avulsos de Zoologia*, 49:487-495.
- Manly, B. F. J. 1997. Randomization, Bootstrap and Monte Carlo Methods in Biology. London, Chapman and Hall, 461 p.
- McCoy, M., B. Bolker, C. Osenberg, B. Miner, and J. Vonesh. 2006. Size correction: comparing morphological traits among populations and environments. *Oecologia*, 148:547-554.
- Mckinnon, J. and M. Pierotti. 2010. Colour polymorphism and correlated characters: genetic mechanisms and evolution. *Molecular Ecology*, 19:5101-5125.
- Morato, S. A. A. 2005. Serpentes da Região Atlântica do estado do Paraná, Brasil: Diversidade, Distribuição e Ecologia. Ph.D dissertation, Universidade Federal do Paraná, Curitiba, Paraná, 165 pp.
- Müller, L. 1923. Neue order seltene Reptilien und Batrachier der Zoologischen Sammlung des bayrischen Staates. *Zoologischer Anzeiger*, 57:153-154.
- Nascimento, F. P., T. C. Ávila-Pires, and O. R. Cunha. 1987. Os répteis de Carajás, Pará, Brasil (Squamata) II. *Boletim do Museu Paraense Emílio Goeldi*, 3:33-65.
- Oksanen J., F. G. Blanchet, R. Kindt, P. Legendre, R. B. O'Hara, G. L. Simpson, P. Solymos, M. Henry, H. Stevens, and H. Wagner. 2010. Package Vegan: Community Ecology Package. <http://CRAN.R-project.org/package=vegan>.
- Pesantes, O. S. 1994. A method for preparing the hemipenis of preserved snakes. *Journal of Herpetology*, 28:93-95.
- Prado, A. 1945. Serpentes do Brasil. Editora Sítios & Fazendas, São Paulo, Brazil, 134 pp.
- R Development Core Team. 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [www.R-project.org](http://www.R-project.org).
- Rocha-Barbosa, O., M. G. Salomão, G. Puerto, I. L. Ferreira, and C. Mandarim-De-Lacerda. 2000. Allometry and ecology of the *Oxyrhopus guibei* Hoge and Romano, 1977 (Serpentes; Colubridae). *Biomedical Research*, 11:259-264.

- Rohlf, F. J. 2009. TpsDIG2. Department of Ecology and Evolution, State University of New York at Stony Brook. Available from: <http://life.bio.sunysb.edu/morph> (accessed 15 march 2009).
- Roze, J. A. 1957. Ofidios coleccionados por la Expedicion Franco-Venezolana al Alto Orinoco: 1951 a 1952. *Boletin del Museo de Ciencias Naturales de Caracas*, 1:179-195.
- Schmidt, K. P. and W. F. Walker-Jr. 1943. Snakes of the Peruvian coastal region. *Publications of the Field Museum of Natural History* (Zool. Ser.), 24:312-315.
- Stejneger, L. 1901. An annotated list of batrachians and reptiles collected in the vicinity of La Guaira, Venezuela, with descriptions of two new species of snakes. *Proceedings of the United States National Museum*, 24:179-202.
- Vanzolini, P. E., A. M. M. R. Costa, and L. J. Vitt. 1980. Répteis das Caatingas. Academia Brasileira de Ciências, Rio de Janeiro, Brazil, 181 pp.
- Vidal, N., A. S. Delmas, P. David, C. Cruaud, A. Couloux, and S. B. Hedges. 2007. The phylogeny and classification of caenophidian snakes inferred from seven nuclear protein coding genes. *Comptes Rendus Biologies*, 330:182-187.
- Vidal, N., W. R. Branch, O. S. G. Pauwels, S. B. Hedges, D. G. Broadley, M. Wink, C. Cruaud, U. Joger, and Z. T. Nagy. 2008. Dissecting the major African snake radiation: a molecular phylogeny of the Lamprophiidae Fitzinger (Serpentes, Caenophidia). *Zootaxa*, 1945:51-66.
- Vidal, N., M. Dewynter, and D. Gower. 2010. Dissecting the major American snake radiation: a molecular phylogeny of the Dipsadidae Bonaparte (Serpentes, Caenophidia). *Comptes Rendus Biologies*, 333:48-55.
- Wagler, J. 1824. *Serpentum Brasiliensium species novae ou Histoire Naturelle. Animalia Nova. Monachii: Franc. Seraph. Hubschmann*, 75 pp.
- Wartenberg, D. 1985. Canonical Trend Surface Analysis: A Method for Describing Geographic Patterns. *Systematic Zoology*, 34:259-279.
- Werner, F. 1903. Neue Reptilien und Batrachier aus dem naturhistorischen Museum in Brüssel. *Zoologischer Anzeiger*, 26:246-253.
- Zaher, H. 1994. Phylogénie des Pseudoboini et évolution des Xenodontinae sud-américains (Serpentes, Colubridae). 2 Volumes. Ph.D. dissertation, Muséum National d'Histoire Naturelle, Paris, 205 pp.
- Zaher, H. 1996. A new genus and species of pseudoboin snake, with a revision of the genus Clelia (Serpentes, Xenodontinae). *Bollettino del Museo Regionale di Scienze Naturali*, 14:289-337.
- Zaher, H. 1999. Hemipenial morphology of the South American xenodontine snakes, with a proposal for a monophyletic Xenodontinae and a reappraisal of Colubroid hemipenis. *Bulletin of the American Museum of Natural History*, 240:168.
- Zaher, H. and A. L. C. Prudente. 1999. Intraspecific variation of the hemipenis in *Siphlophis* and *Tripanurgos*. *Journal of Herpetology*, 33:698-702.
- Zaher, H. and A. L. C. Prudente. 2003. Hemipenes of *Siphlophis* (Serpentes, Xenodontinae) and techniques of hemipenal preparation in snakes: a response to Dowling. *Herpetological Review*, 34:302-307.
- Zaher, H. and U. Caramaschi. 1992. Sur le statut taxonomique d'*Oxyrhopus trigeminus* et *O. guibei* (Serpentes, Xenodontinae). *Bulletin de Muséum National d'histoire Naturelle* (ser. 4), 14A:805-827.
- Zaher, H. and U. Caramaschi. 2000. Synonymisation of *Oxyrhopus venezuelanus* Schreve, 1947, with *Oxyrhopus doliatus* Duméril, Bibron e Duméril, 1854, and revalidation of *Oxyrhopus erdisii* (Barbour, 1913) (Serpentes, Colubridae). *Dumerilia*, 4:113-122.
- Zaher, H., F. G. Grazziotin, J. E. Cadle, R. W. Murphy, J. C. Moura-Leite, and S. Bonatto. 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.

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## APPENDIX I

## Material examined

*Oxyrhopus clathratus* ( $n = 233$ ) ARGENTINA – *Misiones*: Cainguás, Dos de Mayo (MACN 3187). *Iguazú*: Arroyo, Uruguaí 30 km E Puerto Bemberg (MACN 12761, 12762). *San Pedro*: Tobuna (MACN 12692). BRAZIL – (MNHN 3791, MNHN 3792). *Bahia*: Barra do Choça (MZUESC 4638, 6666, 7756). *Espírito Santo*: Domingos Martins, Pedra Azul (MBML 510, MNRJ 14342), Domingos Martins (IBSP 49690), Guaçuí (IBSP 50256), Marechal Floriano (MBML 606,747, 748, 773, 781), Santa Teresa (MBML 633, 724, 1740 5012), São Domingos, Vila Araguaia (IBSP 29099). *Minas Gerais*: Andradas (IBSP 42216), Araponga, Parque Estadual da Serra do Brigadeiro (MZUFV 1563), Bueno Brandão (IBSP 56563), Camanducaia (IBSP 31757, 40002, 43622, 60363), Carangola (MZUFV 1290), Cedofeita (IBSP 298), Extrema (IBSP 42799, 5517, 8335, 8372, 7051, 8928, 12328, 73462), Itabirito (LZV-UFOP 475), Itamonte (IBSP 56824), Itinga (MZUSP 10595, 10598), Nova Ponte (MZUFV 777), Ouro Branco (LZV-UFOP 688-90), Ouro Preto (LZV-UFOP 105, 126-127, 725-726, 831), Piranha (LZV-UFOP 112), Poços de Caldas (MZUSP 14070-71), Rio Novo (MZUFV 1060-61), Catas Altas, RPPN Serra do Caraça (MNRJ 16944-46), Sapucai-Mirim (IBSP 57352, 62248, MZUSP 11584, 11687, 12890, 15689), Viçosa (MZUFV 91, 91A, 91B, 369, 445, 525, 709A, 709B, 709C, 709D, 849, 1000, 1202, 1270, 1304, 1351), Alto Caparaó, Parque Nacional da Serra do Caparaó (MZUSP 7722). *Paraná*: Adrianópolis (IBSP 30380), Antonina (IBSP 30193), Balsa Nova (IBSP 16700), Colombo (MCP 5802), Cruz Machado (MCP 16888), Curitiba, km 27 – entre Ribeira e Curitiba (IBSP 30165), Curitiba (IBSP 18049, 18117, 43685), Mallet, Dorizon (MCP 924), Porto Vitória (MCP 16880, 16886), São Matheus do Sul (MCP 16885), União da Vitória (IBSP 18479, 23287, 16252, 16263, 16271, 16878 16881). *Rio de Janeiro*: Rio das Flores, Casal (IBSP 4763), Itatiaia (IBSP 17066, 37258), Lídice (IBSP 7723, 8535), Mangaratiba, Reserva Rio das Pedras (MNRJ 16446), Mendes (IBSP 16848, 33506), Miguel Pereira (IBSP 7860), Natividade (MNRJ 16372), Niterói (ZUEC 1592), Nova Friburgo (IBSP 24168, 22841), Paraty (IBSP 73514), Petrópolis (MZUFV 1079), Resende (IBSP 9856, 69986). *Rio Grande do Sul*: Bento Gonçalves (MCP 945, 12049, 14483), Caí (MZUSP 364), Canela (MCP 5777), Carlos Barbosa (MCP 9005), Caxias do Sul (IBSP 9958, MCP 10394, 12332, 12334), Dom Pedro de Alcântara (MCP 6232, 6482, 6916, 9537, 9548, 15549, 15550), Farroupilha (IBSP 71324), Garibaldi (MCP 9006), Itati (MCP 9731), Marcelino Ramos (MCP 3043), Veranópolis (IBSP 9844). *Santa Catarina*: Corupá (MZUSP 361), Irineópolis (MCP 16876, 16882), Joinville (IBSP 24704, 25968, 33580, 49992, MCP 16259, 16266), Peritiba (MCP 2932), Porto União (MCP 16256, 16258, 16276), São Bento do Sul (MZUSP 7573, 9451-52), São Francisco do Sul (IBSP 17831, 51159), Tangara (IBSP 16070), Três Barras (IBSP 55715, 16877), Videira (IBSP 23131, 27603), Florianópolis, Rio Vermelho (MZUSP 9427). *São Paulo*: Apiaí (IBSP 41531, 27315, 45723), Atibaia, Parque Municipal da Grotta Funda (ZUEC 1626), Bananal, Estação Ecológica de Bananal (MZUSP 13895, 13896, 15181, 15192, 15215-16), Barra do Turvo, Parque Estadual Jacupiranga – Núcleo Cedro (MZUSP 15132, 15139), Bertioga, Parque das Neblinas (MZUSP 17510), Biritiba Mirim (IBSP 70697, 71043, 71570, 72177), Caieiras (IBSP 62848), Cajati (IBSP 52893), Campos do Jordão, Parque Estadual de Campos do Jordão (MZUSP 17294, 12057), Cananéia (IBSP 28022, 55764, 71495, 71982), Capão Bonito (ZUEC 1110), Cunha (IBSP 29261, 45544, 44590, 44594), Despraiado, Estação Ecológica Juréia-Itatins (ZUEC 2144), Eldorado (ZUEC 492), Iguape (MZUSP 362), Itapeva (MZUSP 12440), Juquiá (MNRJ 14033), Juquitiba (MNRJ 10599), Mairiporã (MZUSP 12966), Miracatu (IBSP 34142, 49584), Mogi das Cruzes (IBSP 58475), Parque Açu (IBSP 43907, MNRJ 14032), Registro (MZUSP 16259, ZUEC 2238), Ribeirão Pires (MCP 16278), Salesópolis, Estação Biológica Boracéia (MZUSP 2848, 3479-80, 3709, 4111, 4527, 4666, 5064, 5891, 791), Santo André, Vila de Paranapiacaba (IBSP 29021), São Bento do Sapucaí (MZUSP 13975), São Bernardo do Campo (MNRJ 10017, 10265), São José do Barreiro, Serra da Bocaina (MZUSP 4644), São Luiz do Paraitinga (MCP 8445), São Miguel Arcanjo, Parque Estadual de Carlos Botelho (MZUSP 15233-34), São Paulo (MCP 4806), Sapucai Mirim (IBSP 60088).