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# Morphological variation, polymorphism, and Taxonomy of the *Atractus torquatus* complex (Serpentes: Dipsadidae)

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## Abstract

The taxonomic status of *Atractus torquatus* is revised on the basis of concordance between quantitative and qualitative analyses of morphological characters (meristic, morphometric, colour pattern, and hemipenis) throughout its geographical distribution. We propose the synonymy of *Atractus davidhardi, A. janethae*, and *A. lucilae* based on wide overlap of morphological characters (qualitative and quantitative). Despite some differences in the frequency of the number of supralabials, infralabials and maxillary teeth among *A. torquatus* populations, we find that these characters exhibit a high level of polymorphism and therefore cannot unambiguously diagnose Guiana Shield and Amazon Basin populations. Additionally, we discuss the polymorphism and geographical variation in *A. torquatus* and its appropriateness for hypotheses of landscape evolution in Amazonia.

**Key words:** *Atractus davidhardi*, *Atractus janethae, Atractus lucilae,* Morphological variation, Polychromatism

## Introduction

The cryptozoic snake genus *Atractus* Wagler is widely distributed in the Neotropics, occurring from Panama to Argentina (Giraudo & Scrocchi 2000; Myers 2003). *Atractus* is the most speciose Alethinophidian snake genus, with about 130 valid species, most of them known only from few specimens and localities (Passos *et al*. 2010c). Despite several studies focusing on the taxonomy of the genus in the past five years (Kok, 2006; Myers & Schargel 2006; Prudente & Santos-Costa 2006; Passos *et al*. 2007 a,b; Passos & Fernandes 2008; Prudente & Passos 2008, 2010; Passos & Arredondo 2009; Passos *et al*. 2009a,b,c,d,e), additional efforts must be made to address problems of morphological variation, geographic ranges, polymorphism, sexual dimorphism, and ontogenetic change of coloration for most *Atractus* species (Passos *et al*. 2010 a,b,c). Consequently, only studying in detail all these aspects may shed more light on the species diversity of this complex and poorly known genus (Passos *et al*. 2010a; Passos & Lynch 2011).

Boie (1827) described *Brachyorrhos torquatum*, but as he did not present a formal description of the species, this combination became a *nomen nudum* (Hoogmoed 1980). Schlegel (1837) proposed to synonymize *B. torquatum* with *Calamaria badia* (Boie). Duméril *et al*. (1854) revalidated *B. torquatum* Boie as *Rabdosoma torquatum*, and reported eight individuals for the species. Seven specimens are from Surinam and one from Santa Cruz de La Sierra in Bolivia. All belong to the series of syntypes of *R. torquatum* (Hoogmoed 1980). Jan (1862) described *R. varium*, apparently on the basis of one of the syntypes of *R. torquatum* (RMNH 114; Hoogmoed 1980). Boulenger (1894) transferred *R. torquatum* to the genus *Atractus* and synonymized *R. varium* with the former species. Savage (1960) designated the specimen from Santa Cruz de La Sierra in Bolivia as the lectotype of *A. torquatus.* Dixon & Soini (1977) reported a series of specimens of *A. torquatus* as *Atractus* sp. from Iquitos region in Peru. Later, Dixon & Soini (1986) identified these specimens as *A. torquatus*.

Hoogmoed (1980) rediscovered seven of the syntypes of *R. torquatum* and pointed out that Savage's (1960) designation of a lectotype was an invalid action (see Hoogmoed 1980 for details). Hoogmoed (1980) designated

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RMNH 114 as lectotype of *R. torquatum* Duméril, Bibron and Duméril, and restricted the type locality of the species to Paramaribo in Suriname. Hoogmoed (1980) corroborated the synonymy of *R. varium* with *A. torquatus* that was previously proposed by Boulenger (1894). More recently, Silva (2004) described *A. davidhardi* from the locality of Muniyamena, municipality of Leticia, *A. janethae* and *A. lucilae* from the localities of La Chorrera and La Pedrera, municipality of Puerto Córdoba, respectively. All these localities are situated in the department of Amazonas, in the eastern portion of Colombian Amazonia. Curiously, Silva (2004) identified a specimen of *Atractus torquatus* from the locality of Mitú, department of Vaupés, which is very similar to *A. janethae* and *A. lucilae*. This locality also resides in the eastern portion of Colombian Amazonia.

In this paper we evaluate the taxonomic status of the currently recognized *Atractus torquatus* complex, including the recently described *A. davidhardi*, *A. janethae*, and *A. lucilae*, on the basis of concordance between qualitative and quantitative analyses of morphological characters.

## Material and methods

**Material and techniques.** We examined 71 specimens of *A. torquatus* housed in the following institutions: Brazil—Instituto Butantan (IBSP), São Paulo, SP; Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, AM; Fundação de Medicina Tropical do Amazonas (FMT), Manaus, AM; Museu Nacional, Universidade Federal do Rio de Janeiro (MNRJ), Rio de Janeiro, RJ; Museu Paraense Emílio Goeldi (MPEG), Belém, PA; Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, SP. Colombia—Instituto Alexander Von Humboldt (IAvH), Villa de Leyva, Boyacá; Instituto de Ciencias Naturales (ICN), Universidad Nacional de Colombia, Bogotá, D.C. Venezuela—Museo de Biología de la Universidad Central de Venezuela (MBUCV), Caracas, D.F.; Museo de Biología de la Universidad de Los Andes (CV-ULA), Mérida, Mérida; Museo de Historia Natural de la Fundación La Salle (MHNLS), Caracas D.F. All examined specimens are listed in Appendix I.

The terminology for *Atractus* cephalic shields followed Savage (1960), and the method of counting ventral scales followed Dowling (1951). Nomenclature regarding the loreal condition followed Passos *et al.* (2007b). Nomenclature for the other measurements and discrete characters followed Passos *et al*. (2009e). Techniques for hemipenis preparation followed Pesantes (1994) and Zaher & Prudente (2003). Terminology for hemipenis description followed Dowling & Savage (1960) as augmented by Zaher (1999). We verified the sex of each specimen through an incision in the first subcaudal scales. Measurements were taken with an analogical caliper to the nearest 0.1 mm under stereoscope, except for snout-vent (SVL) and caudal lengths (CL), which were taken with a flexible ruler to the nearest 1 mm. SVL was measured from the tip of the rostral scale to the posterior region of the anal plate, and CL from the anterior edge of first subcaudal to the end of the terminal spine. The concept of Guiana Shield here adopted followed Hoogmoed (1979).

**Species concept and diagnosis criteria.** In this study, we followed the general lineage species concept according De Queiroz (1998). We consider the presence of one or more exclusive, apparently fixed diagnostic character, which distinguishes a putative taxon from the others in the *A. torquatus* complex, as species delimitation criteria. However, the limited sample size did not allow statistical confidence from qualitative characters for some populations (see Wiens & Servedio 2000), we alternatively looked for concordance between the discrete and continuous characters. Since these features are likely uncorrelated, the correspondence between these kinds of data might represent independent evidence of species boundaries (see Passos & Fernandes 2009; Passos *et al*. 2010a).

**Qualitative analyses of morphology.** We performed a discrete analysis of qualitative characters based on the frequency of occurrence to each state throughout the distribution of the *Atractus torquatus* complex (see below). We considered putative natural barriers (e.g., rivers) and geographical proximity of the available sample to define these operational groups. We used the Rio Amazonas and Rio Negro as supposed barriers to dispersion of Guiana Shield and Amazon Basin population (see Henderson *et al*. 2009 for similar procedure). On the basis of frequency of distribution of characters we investigated if each group has any geographical basis. Independently, we searched for correspondence between the above groups as well as the current taxonomy (including *A. davidhardi*, *A. janethae* and *A. lucilae*) and hemipenial morphology.

**Quantitative analyses of morphology.** We employed an analysis of variance (ANOVA) using segmental counts to assess the presence or absence of sexual dimorphism within each group and the whole sample. We evaluated the assumptions of univariate normality and homocedasticity with the Kolmogorov-Smirnov's and Levene's tests, respectively (Zar 1999). In cases where characters showed insufficient variation to justify these assumptions we performed non-parametric tests such as Mann-Whitney and Kruskal-Wallis (Zar 1999). We performed a principal component analysis (PCA) at group level (see below) to males and females separately to evaluate differentiation between the groups without *a priori* definition (Manly 2000). We projected the first two principal components onto orthogonal axes and computed 95% confidence regions from the simulation of 1000 pseudoreplicate data matrices obtained by parametric bootstrap (Efron 1979).

We labelled, *a posteriori* of the PCA analyses, the sample into three groups, reflecting the current taxonomy and considering disjointed geographical distribution and/or morphological similarities of each valid taxa. Group 1 included specimens from Guyana Shield, north to Rio Amazonas and east to Rio Negro, considered like *A. torquatus* sensu stricto. Group 2 included specimens from Amazon Basin, west to Rio Negro, formally *A. janethae* and *A. lucilae*. Group 3 comprise the holotype of *A. davidhardi*. We grouped *A. janethae* and *A. lucilae* in a single operational group because there is no morphological difference and geographical disjunction between these species, while *A. davidhardi* display an apparently distinct colour pattern (but see results). We used the following characters in statistical analyses: number of ventral, preventral, subcaudal, postocular, supralabial, infralabial, gular scales; number of maxillary teeth; SVL/CL and SVL/midbody diameter ratios.

We performed all computations using the software MATLAB 4.2c1 (MathWorks 1994), except normality and homocedasticity tests, for which we used STATISTICA 5.1 (Statsoft 1995).

## Results

### Qualitative analyses

**Colour pattern.** Silva (2004) identified a specimen from Mitú (ICN 10111) as *A. torquatus* (Silva 2004; Figs. 48–49). After examining this specimen (Fig. 1), we found the colour pattern very similar to the types of *A. janethae* and *A. lucilae* (Figs. 2–3), differing from them with respect to segmental counts because it is a male, whereas the type series of the last two species are only females. A possible explanation to the Silva's identification was the lack of black nuchal collar in the Mitú specimen (see Fig. 48 from Silva 2004; and Fig. 1), but the presence of conspicuous black collar is extremely variable among populations of *A. torquatus* (Fig. 4), and apparently does not show any geographical and/or phylogenetic signal. Furthermore, the state conditions for other coloration features examined in the types of *A. janethae* and *A. lucilae* entirely overlaps the pattern of the population of *A. torquatus* previously reported by Dixon & Soini (1977, 1986), Hoogmoed (1980), Martins & Oliveira (1993), and from the present study (Figs. 1–5). However, *Atractus davidhardi* displays an alternate banded pattern that was not described in the previous studies, but for which we found a gradual (apparently non-clinal, see below) increase of the transversal flecks turning conspicuous bands (Figs. 6–7). However, on the basis of available samples this colour pattern does not show any geographical structure. Indeed, this colour pattern also occurs in the Guiana Shield populations closer to the type locality of *A. torquatus* (Fig. 7).

**Meristic characters.** Throughout the distributional range of *A. torquatus* there are some meristic characters (number of supralabials, infralabials, and maxillary teeth) with slight differences in their states of occurrence. In order to properly evaluate the geographical structure of variation of these characters we performed ~~a~~ qualitative analyses considering Guiana Shield and Amazon Basin populations as distinct operational groups (see material and methods). The frequency analyses revealed a tendency among populations from the Amazon Basin in exhibiting a smaller (six or seven vs. eight or nine) number of supra- (81%) and infralabial (52%) scales and maxillary teeth (81%) compared to the proportion observed in the Guyana Shield populations (02%, 02% and 04% respectively). Despite distinct frequencies in character states, we found a high level of polymorphism in the Amazon Basin population (Fig. 8). On the other hand, the Guiana Shield showed that those characters were nearly fixed for each state (Fig. 8).

**Hemipenis morphology.** The analysis of hemipenial variation did not show any fixed morphological diagnostic characteristic among all populations of the *Atractus torquatus* sampled. The differences here observed (Fig. 9) may be expected for a species having widespread distribution and is in accordance to previous findings reported for this genus (see Prudente & Passos 2010). The hemipenial morphology of *A. davidhardi* is almost identical to the morphology previously described for *A. torquatus* (Schargel & Castoe 2003) and illustrated by our extensive sample herein (*n* = 12). However, our sample differed from earlier studies mainly with respect to the lobular ornamentation.

Silva (2004) and Schargel & Castoe (2003) described and illustrated the hemipenis of *A. torquatus* with a completely nude lobular region. Although we found some variation in calycular distribution and/or level of development (see below), our results suggest that the lobular region of the organ is never entirely nude. The tips of the organs can be completely nude, but the intrasulcar region of the lobes always displays some ornamentation (e.g., spines). The basal portion of lobes varied from barely defined and sparse calyces to conspicuous and concentrated calyces. We examined (*in situ*) the hemipenes of the holotype of *A. davidhardi* and confirmed the presence of slight lobular calyces. A possible explanation of discrepancies in our findings with regard to previous studies is the preparation artefacts because the hemipenis of *A. davidhardi* is not fully everted or maximally expanded (Silva, 2004; Fig. 6b). Effectively, calyces are sometimes difficult to observe in everted hemipenes that are not maximally expanded (Fig. 9b) (compare with Fig. 9a, which corresponds to a fully everted and maximally expanded organ). Finally, we interpreted the hemipenis illustration of *A. davidhardi* provided by Silva (2004) as being inaccurate.

## Quantitative analyses

*Atractus torquatus* (*sensu* Hoogmoed 1980) shows significant sexual dimorphism in the number of ventral scales ($F_{1,56} = 37.5$; $p < 0.0001$; *n* = 71), subcaudal scales ($F_{1,57} = 38.8$; $p < 0.0001$; *n* = 66) and SVL/CL ratio ($F_{1,57} = 88.3$; $p < 0.0001$; *n* = 66), and therefore these characters were treated separately for each sex in all subsequent analyses. Among all measured variables, only three (number of ventral and subcaudal scales, and CL/SVL ratio) approaches a normal distribution but were heteroscedastic due to the differences in the sample size for each group. Our sample from the Guiana Shield populations was about five times greater than the Amazon Basin populations for males and females. As the assumption of normality and/or homocedastycity were violated we refrained to perform nonparametrics analyses of variance and we preferred to carry out a principal component analyses just as an exploratory purpose (Manly 2000). The projections of the bivariate plots based on scores of principal component analyses for males (Fig. 10a) and females (Fig. 10b) were unable to entirely discriminate the two groups in *a posteriori* fashion. A slight discrimination occurred mainly in the first principal component axis, which was strongly correlated with the number of ventrals and SVL/CL ratio.

## Taxonomic decision

Despite qualitative analyses of morphological characters demonstrating that the populations of the Amazon Basin differ from Guiana Shield in the frequency of distribution of some characters, these characters are polymorphic in both populations. The polymorphic traits were nearly fixed (above 95% frequency) in the Guiana Shield, thus the name *Atractus torquatus* is applicable just to these populations (see Hoogmoed 1980). Therefore, we conclude that Amazon Basin populations displayed a high level of polymorphism with respect to the discrete characters here analysed. Moreover, the exploratory morphometric analyses corroborate that both groups also cannot be distinct by the principal components of variation, which were correlated with size (SVL/CL ratio) and form (number of ventral). For these reasons, the qualitative and quantitative analyses of *A. torquatus* along with its distribution are congruent in suggesting that the taxa proposed by Silva (2004) are co-specific with *A. torquatus* (see discussion). Therefore, we propose here to place *A. davidhardi*, *A. janethae* and *A. lucilae* in the synonymy of *A. torquatus.*

## Taxonomy

### *Atractus torquatus* (Duméril, Bibron & Duméril, 1854)

Figs. 1–7, 11–12.

*Brachyorrhos torquatum* F. Boie, 1827; Isis Von Oken:540. (*nomen nudum*).
*Calamaria badia* —Schlegel, 1837; Essai sur la Physignomie des Serpens:35. (*part.*)
*Rabdosoma torquatum* Duméril, Bibron & Duméril, 1854; Erpétologie Générale:101.

*Rabdosoma varium* Jan, 1862; Arch. Zool. Anat. Fis. 2:18.
*Atractus torquatus* – Boulenger, 1894; Catalogue of the Snakes in the British Museum 2:309.
*Atractus* sp. A – Dixon & Soini, 1977; Contr. Biol. Geol. Milwalke Publ. Mus. 12:37.
*Atractus torquatus* – Dixon & Soini, 1986; The Reptiles of Upper Amazon Basin, Iquitos, Peru. 2nd ed. Milwaukee, Wisconsin Milwaukee Public Museum 154:96.
*Atractus davidhardi* Silva, 2004; Rev. Acad. Col. Cien. Exat. Fis. Nat. 108:418. **New synonymy**.
*Atractus janethae* Siva, 2004; Rev. Acad. Col. Cien. Exat. Fis. Nat. 108:429. **New synonymy**.
*Atractus lucilae* Silva, 2004; Rev. Acad. Col. Cien. Exat. Fis. Nat. 108:434. **New synonymy**.

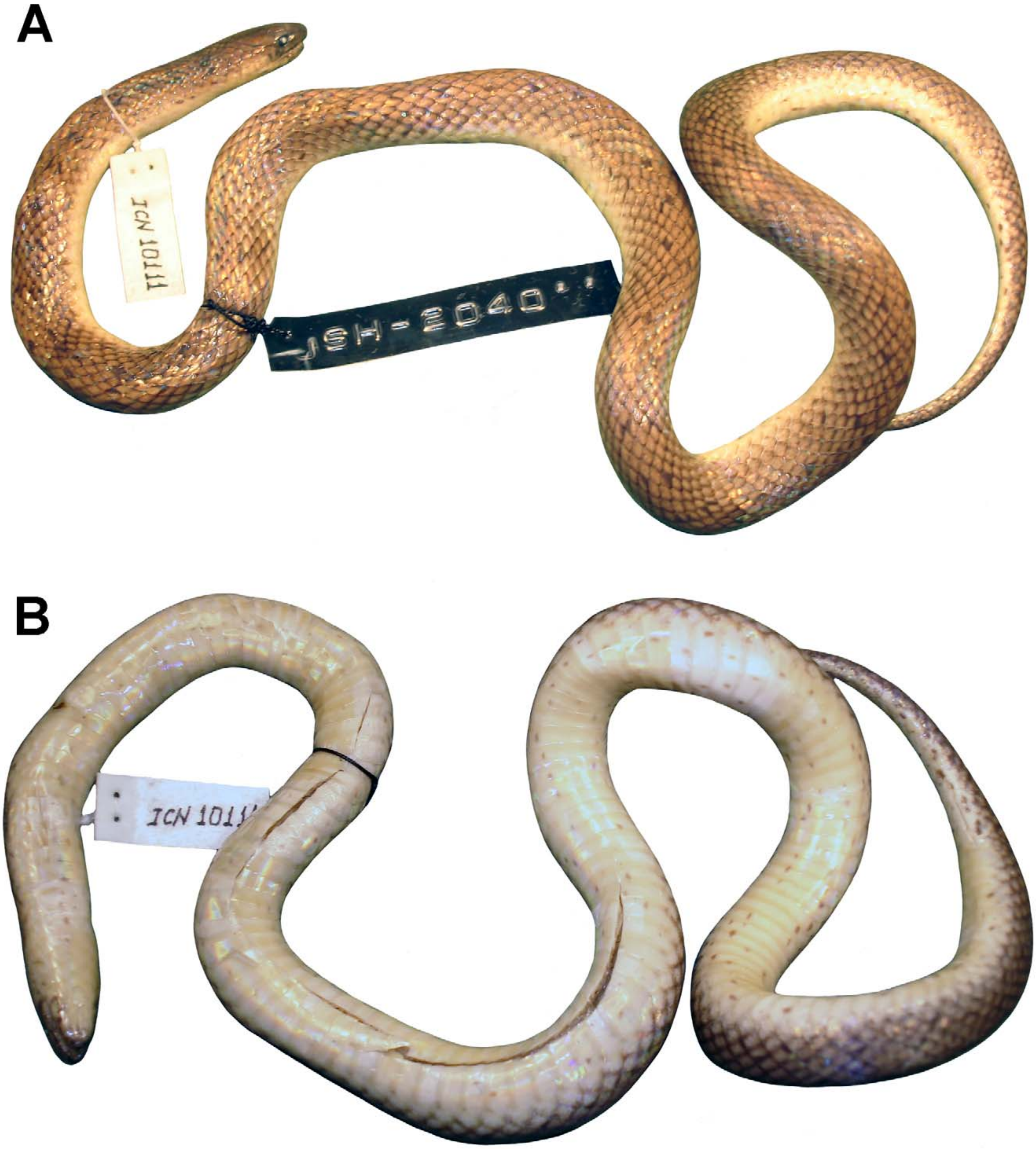

**FIGURE 1.** Dorsal (A) and ventral (B) views of body of the specimen of *Atractus torquatus* (ICN 10111) from municipality of Mitú, department of Vaupés, Colombia.

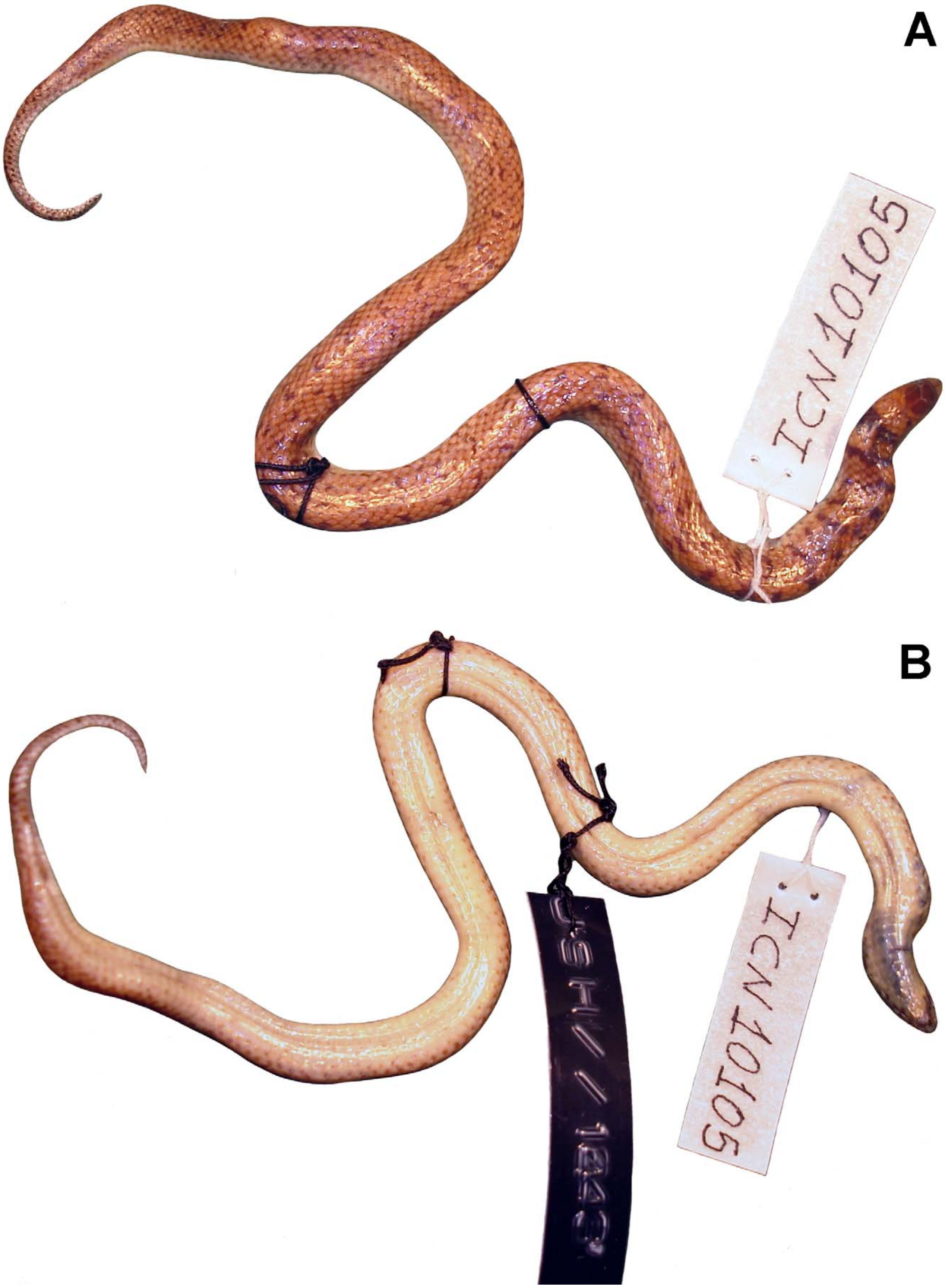

**FIGURE 2.** Dorsal (A) and ventral (B) views of body of the holotype of *Atractus lucilae* (ICN 10105) from La Pedrera, municipality of Puerto Córdoba, department of Amazonas, Colombia.

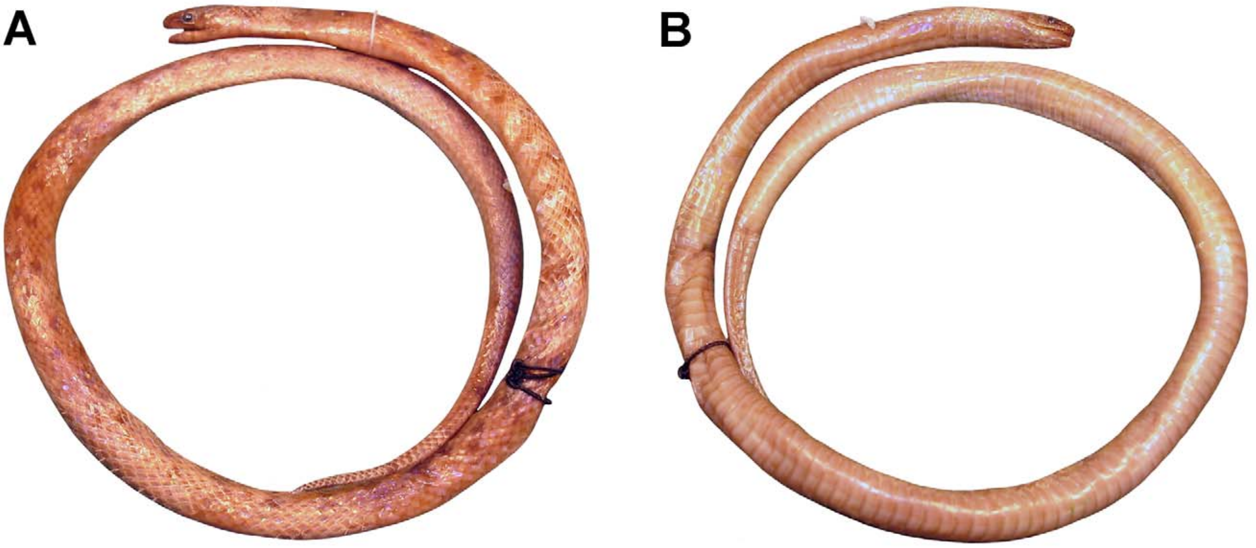

**FIGURE 3.** Dorsal (A) and ventral (B) views of body of the holotype of *Atractus janethae* (ICN 10104) from La Chorera, municipality of Puerto Córdoba, department of Amazonas, Colombia.

**Lectotype:** Adult male, RMNH 114, collected by H. Dieperink in Guyana. Hoogmoed (1980) designated the lectotype and restricted the type locality to Paramaribo (05º50'N, 55º10'W, sea level) in Suriname (specimen photograph examined; Fig. 12). It specimen is also the holotype of *Rabdosoma varium* (Fig. 11).

**Paralectotypes:** RMNH 115, adult female, same data as lectotype; RMNH 117a,b,c,d,e, originally from "Gabinet Hendrix" lacking additional data, these specimens were later donated to RMNH (Hoogmoed 1980); Muséum national d'Histore naturelle (MNHN 0.437), from Santa Cruz de La Sierra (17º48'S, 63º10'W; ca. 440 m), department of Santa Cruz, Bolivia.

**Diagnosis.** *Atractus torquatus* can be distinguished from all congeners by the combination of the following characters: (1) 17 smooth dorsal scale rows; (2) usually a single postocular; (3) long loreal; (4) temporals 1+2; (5) usually eight supralabials, third and fourth or fourth and fifth contacting orbit; (6) usually eight infralabials, first four contacting chinshields; (7) six to nine maxillary teeth; (8) three or four gular scale rows; (9) three or four preventrals; (10) 151–172 ventrals in females, 144–166 in males; (11) 34–47 subcaudals in females, 35–53 in males; (12) dorsum in preservative dull red to reddish brown, uniform coloured or presenting since paravertebral black dots until transversal alternated blotches reaching paraventral region; (13) venter in preservative uniformly cream or presenting disperse dark brown dots along the body; (14) large body size, females reaching 683 mm SVL, males 525 mm SVL; (15) moderate to long tail length in females (12.4–18.7% SVL), long tail length (15.6–20.9% SVL) in males; (16) hemipenis moderately bilobed, semicapitate and semicalyculate.

**Comparisons.** Among all congeners, *Atractus torquatus* shared 17 dorsal scale rows at midbody, large maximum body size (> 500 mm in both sexes), long tail (generally > 15% SVL in both sexes) and dorsal ground colour red to reddish brown covered by black bands only with *A. badius*. *Atractus torquatus* differs from *A. badius* by having usually a single postocular, generally infralabial, first four infralabials contacting chinshields, and blotches or bands never forming diads (vs. two postoculars, seven infralabials, first three infralabials contacting chinshields and dorsal bands forming conspicuous diads on anterior portion of body).

**Description.** Head twice as long as wide, slightly arched in lateral view, sub-triangular in dorsal view; snout slightly acuminate in lateral view, round in dorsal view; conspicuous canthus rostralis in lateral view; cervical constriction indistinct; rostral about twice as wide as high, subtriangular in frontal view, poorly visible in dorsal; internasal as wide as long; internasal suture sinistral with respect to prefrontal suture; prefrontal longer than wide; supraocular sub-trapezoidal, about twice as long as wide; frontal pentagonal, longer than wide; parietal about twice as long as wide; nasal divided; nostril located between prenasal and postnasal; prenasal twice as high as long; postnasal as high as long; loreal moderately long, contacting second, third and fourth supralabials; pupil subelliptical or rounded; usually a single postocular as high as long; eventually two postocular, similar in size; temporals 1+2; first temporal about 60–70% times longer than high; upper posterior temporals usually non fused; usually eight supralabials

bials, fourth and fifth contacting orbit; first two or three supralabials with similar high and smaller than fourth supralabial; sixth or seventh supralabials higher and seventh or eighth longer than remaining supralabials; symphysial sub-triangular, two or three times as wide as long; first pair of infralabials contacting behind symphysial, perventing symphysial/chinchields contact; usually eight infralabials, first four contacting chinshields; chinshields about three times as long as wide; three or four gular scale rows; three or four preventrals; 17 smooth dorsal scale rows on midbody, lacking apical pits, supra-anal tubercles, and keels; caudal spine moderately long, conical, and acuminate.

**Maxillary arch.** Arched in dorsal view, with five to seven prediastemal and one to three postdiastemal teeth; prediastemal teeth with similar size, large, moderately spaced, curved, angular in cross section, robust at base, and narrower on the apices; maxillary diastema short; postdiastemal teeth smaller than last prediastemal one; lateral process of maxilla poorly developed, lacking posterior projection.

**Colour pattern in preservative.** Dorsum of head pale brown to dark brown, reaching posterior region of parietals; frequently anterior region of snout darker than posterior cephalic scales and body; background of head reddish to dark brown, region around orbit eventually black; supralabials most cream with dorsal edge dark brown; ventral margins of supralabials usually cream; last two supralabials eventually covered with brown pigment; mental region cream with dark brown dots or blotches covering symphysial, first pair of infralabials, and anterior portion of chinshields; mental region of second to fourth pair of infralabials eventually covered by dark brown blotches; preventrals uniformly cream; belly uniformly cream or pale brown, frequently covered by small disperse dark brown dots; belly eventually heavy pigmented by irregular dark brown dots or well defined squared or rhomboid blotches; underside of tail usually cream with irregular dark brown dots; sometimes tail most brown with lighter centre; rarely tail uniform cream; dorsal ground colour of body red to reddish brown, with black collar on neck (one to four scales long); black collar located on second to fourth dorsal rows; eventually the medial portion of collar discontinuous or absent; dorsum of body usually with disperse paravertebral black spots (one or least of one scale long), alternate transversal flecks (one or two scales long) or bands (two or three scales long), covering paravertebral region and sometimes reaching lateral portion of flanks; dorsum with large anterior transversal flecks or bands generally connecting disperse paraventral spots; eventually dorsal flecks or bands decreasing in size posteriorly, becoming disperse spots or small blotches restricted to paravertebral region; transversal flecks or bands eventually keep it size of anterior ones along the body (three or four scales long); banded pattern with 25–50 alternated blotches, connecting the opposite one above vertebral region; bands usually twice as long as interspaces; eventually alternate bands connected above vertebral region constituting a zig-zag pattern, more conspicuous on posterior third of body. Melanism tendency rarely noted in individuals, with dorsum of head black and dorsal ground colour pale brown to brown covered by alternate black bands (Figs. 1–4, 6–7, 11–12). The melanic individuals occur in low frequency along the species distribution and did not show any geographic structure.

**Colour in life.** Dorsum and background of head uniformly red to reddish brown; dorsal ground colour of body dull red to reddish brown with black dots, flecks, or bands; ventral portion of supralabials, mental region, and belly cream to creamish yellow; belly frequently covered by dark brown dots or blotches; underside of tail cream to creamish yellow, with dark brown to black dots; eye brown to red (Fig. 5).

**Hemipenis morphology.** Inverted organ bifurcates in the level of seventh and extends to ninth subcaudal. Hemipenis slightly to moderate bilobed, semicapitate, and semicalyculate; lobes sub-cylindrical with rounded apices, similar size and oriented centripically; capitular crotch evident but incomplete on asulcate (median portion covered by moderated spines) and sulcate (region adjacent to bifurcation of sulcus spermaticus branches); capitulum define basal region of lobes on both sides of organ; lobes covered by spinulate calyces in it basal portion and papillate calyces at apical region; tip of lobes usually nude and sometimes scattered by papillate calyces; sulcus spermaticus divides on distal portion of hemipenial body below to capitular crotch; intrasulcar region with moderate hooked spines; sulcus spermaticus branches centrifugally oriented running to tip of lobes; margins of sulcus spermaticus stout and bordered by spinules on basal to most of distal portion of lobes; sulcus spermaticus expanded at apices of lobes; hemipenial body subelliptical, narrower than lobular region of organ; hemipenial body covered by spines on both sides of organ; distal region of hemipenial body barely defined by transversal series of largest spines connected at the base; transversal series of spines delimited basal region of hemipenial body; proximal region of hemipenis scattered with small disperse spines; lateral portion of hemipenial body covered with naked pocket (Fig. 9).

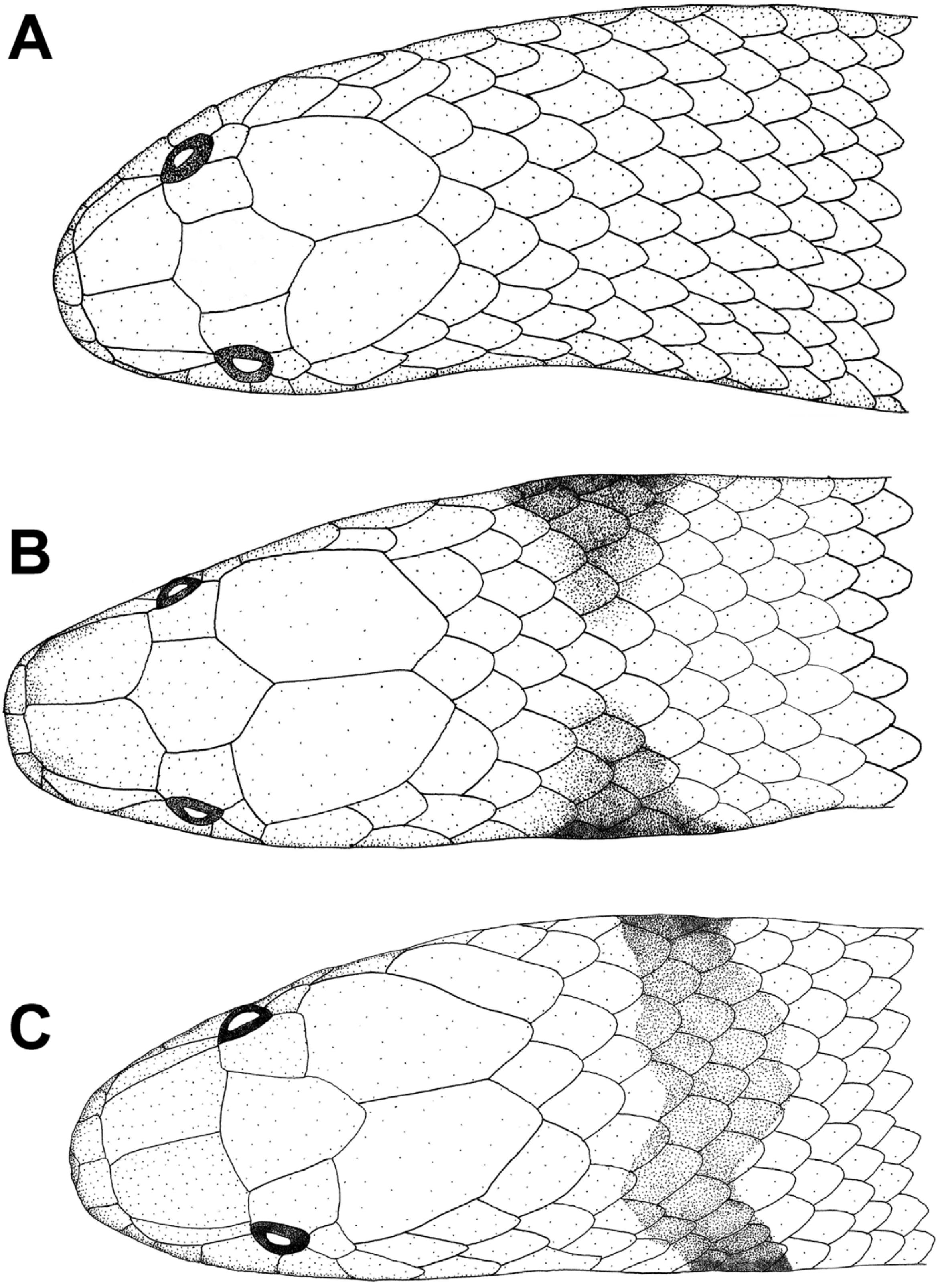

**FIGURE 4.** Variation of the blotch condition on the nuchal region to the specimens of the *Atractus torquatus* from Balbina Hydroelectric Plant, municipality of Presidente Figueredo (FMT 1358) (A), municipality of Manaus (FMT 338) (B) and municipality of São Miguel da Cachoeira (INPA 15760) (C). All specimens come from localities in the state of Amazonas in Brazil and they are part of Guiana Shield populations.

**FIGURE 5.** General view in life of *Atractus torquatus* from Reserva Ducke, municipality of Manaus, state of Amazonas, Brazil, photo by M. Martins (a); Moiobamba, Rio Purus, Arumã district, municipality of Beruri, state of Amazonas, Brazil, photo by M. Senna (b); Balbina Hydroelectric Plant, municipality of Presidente Figueiredo, state of Amazonas, Brazil, photo by M. Martins (c); Parque Nacional do Pico da Neblina, municipality of São Grabriel da Cachoeira, state of Amazonas, Brazil, photo by V. Carvalho (d); Rio Madeira, Abunã district, Porto Velho, state of Rondônia, Brazil, photo by M. Senna (e); Moiobamba, Rio Purus, Arumã district, municipality of Beruri, state of Amazonas, Brazil, photo by M. Senna (g); Río Uey, middle basin of Río Cuyuní, state of Bolívar, Venezuela, photo by C. Barrio-Amorós (g–h).

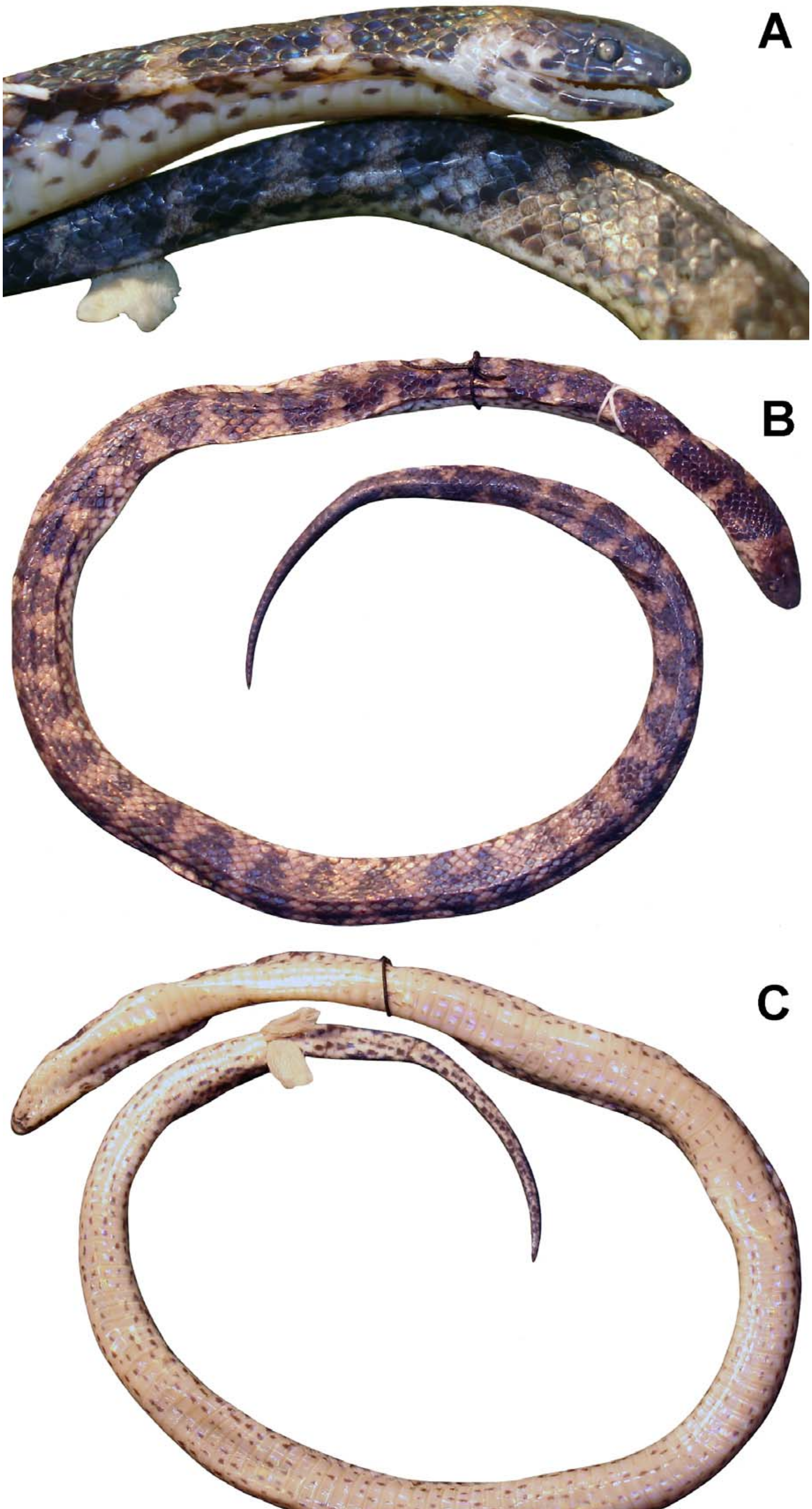

**FIGURE 6.** Lateral view of head (A) and dorsal (B) and ventral (C) views of body of the holotype of *Atractus davidhardi* (ICN 10096) from Muniyamena, municipality of Leticia, department of Amazonas, Colombia.

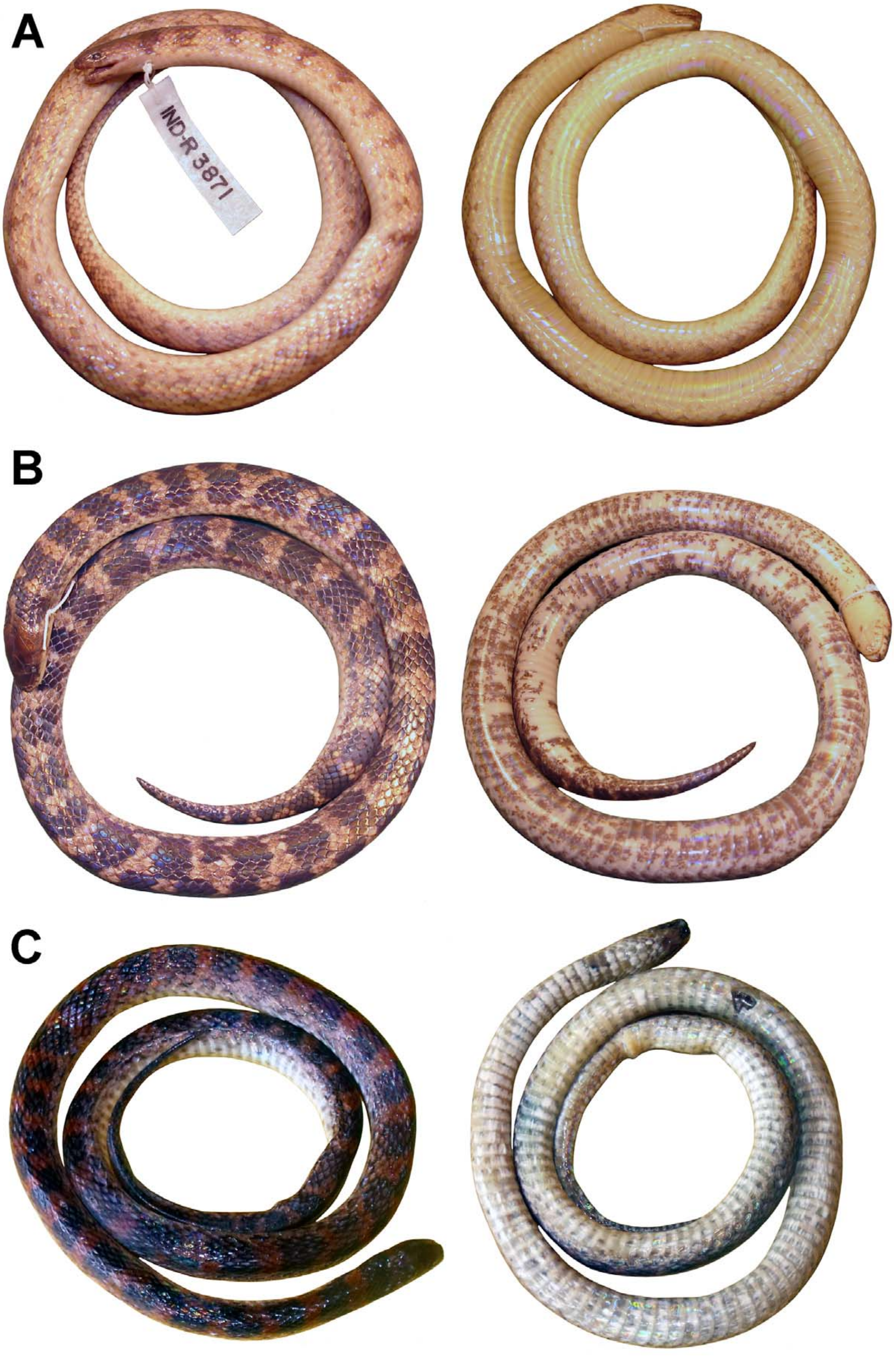

**FIGURE 7.** Dorsal (left) and ventral (right) views of preserved specimens of *Atractus torquatum* from Parque Nacional de Amacayacu, municipality of Leticia, department of Amazonas, Colombia (A–B) and km 38 of the El Dorado–Santa Elena de Uairén road, state of Bolívar, Venezuela, photo by D. Calcaño (C).

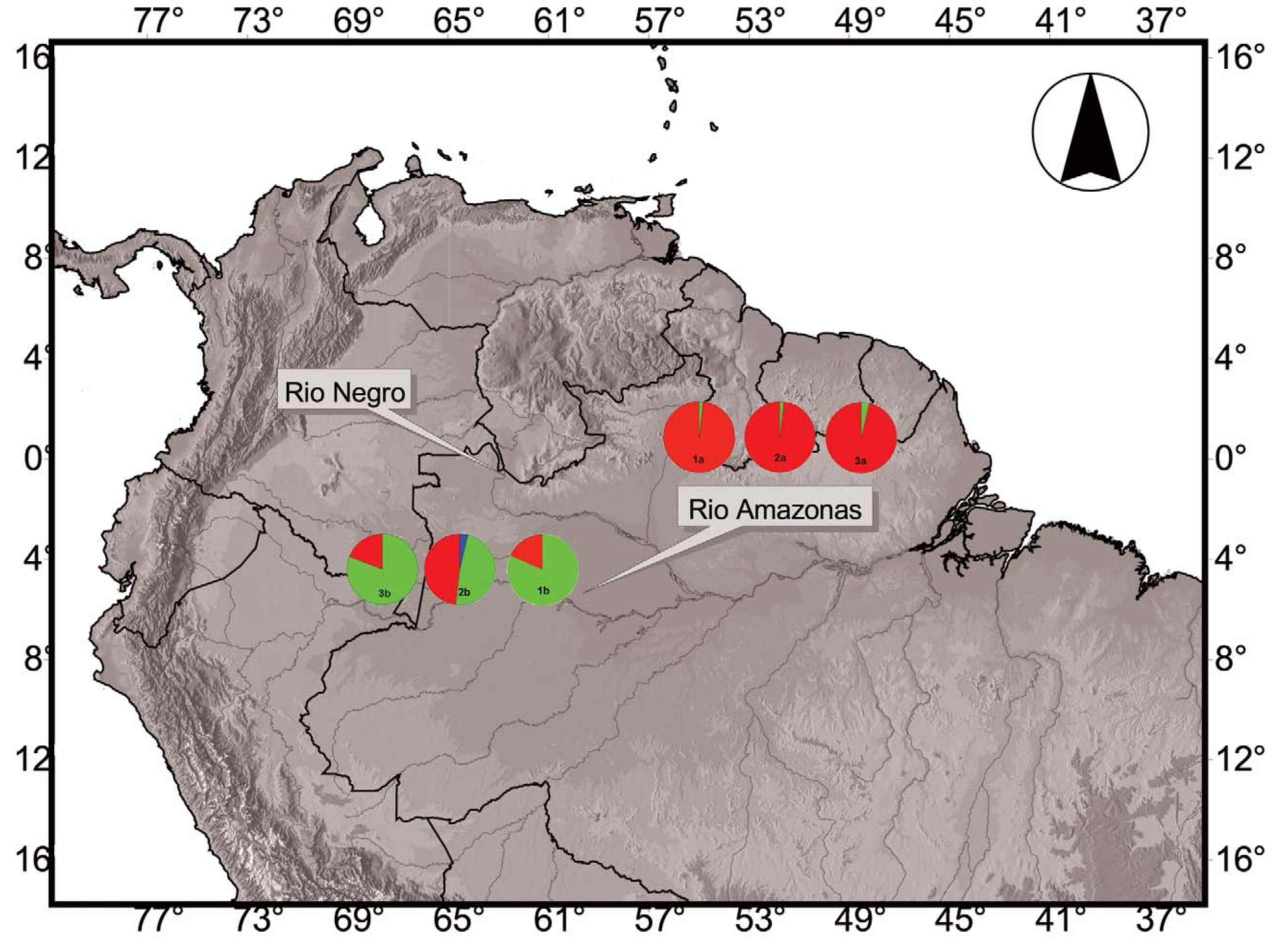

**FIGURE 8.** Pattern of the geographic variation for polymorphic qualitative character along of the *Atractus torquatus* complex. The number of supralabials = 1, number of infralabials = 2 and number of maxillary teeth = 3. The colour represents the frequency for each state of characters: blue correspond to six; green correspond to seven and red correspond to eight. The frequencies of the character states are from our own sample plus from the Dixon & Soini (1986). The total sample comprises 81 individuals and the traits were counted in both sides for each specimen.

**Meristic and morphometric variation.** Large male SVL 525 mm, CL 94 mm; large female SVL 683 mm, CL 96 mm; midbody diameter 1.4–4.8% ($\bar{x}$= 2.5; SD = 0.6; *n* = 31) SVL in males, 1.9–4.6% ($\bar{x}$= 2.7; SD = 0.5; *n* = 29) SVL in females; tail 15.6–20.9% ($\bar{x}$= 18.2; SD = 1.2; *n* = 32) SVL in males, 12.4–18.7% ($\bar{x}$= 15; SD = 1.2; *n* = 33) SVL in females; 144–166 ($\bar{x}$= 154.7; SD = 4.7; *n* = 35) ventrals in males, 151–172 ($\bar{x}$= 161.4; SD = 5.5; *n* = 36) in females; 35–53 ($\bar{x}$= 45.9; SD = 4.1; *n* = 33) subcaudals in males, 34–47 ($\bar{x}$= 40.2; SD = 3.5; *n* = 34) in females; 3–4 ($\bar{x}$= 3.7; SD = 0.5;*n* = 74) preventrals; 3–4 ($\bar{x}$= 3.7; SD = 0.4; *n* = 72) gular scale rows; 7 (*n* = 22 sides) or 8 (*n* = 124 sides) supralabials; 7 (*n* = 18 sides) or 8 (*n*= 128 sides) infralabials; 3 (*n* = 18 sides) or 4 (*n* = 130 sides) first infralabials contacting chinshields; 1 (*n*= 135 sides) or 2 (*n*= 11 sides) postoculars; 15/17/15 (*n*= 1), 15/17/17 (*n* =1) 16/17/16 (*n* = 1) or 17/17/17 (*n*= 25) dorsal scale rows; 7–10 ($\bar{x}$= 8.5; SD = 0.6; *n* = 50 sides) dorsal scale rows in the level of second subcaudal; 3.8–18.6 mm ($\bar{x}$= 9.5; SD = 3.8; *n* = 63) midbody diameter; 6 (*n* = 3 sides), 7 (*n* = 23 sides), 8 (*n* = 100 sides) or 9 (*n* = 11 sides) maxillary teeth; anal gland extends from third to fourth subcaudal (*n* = 4).

**Distribution.** The distribution of *Atractus torquatus* is known to include the Guiana Shield and Amazon Basin (without known records in the eastern portion of the Amazonia), occurring from Paramaribo (5º50'N, 55º10'W) in Suriname southwestern to Iquitos (3º44'53''S, 73º14'50''W) in Peru. We place in doubt the record of *Atractus torquatus* from Santa Cruz de La Sierra in Bolivia, since there is no additional report of the species based on voucher specimen below department of Loreto in north of the Peruvian Amazonia (Hoogmoed 1980; Passos 2008). *Atractus torquatus* inhabits lowlands portions of Neotropical Savanah and Amazon Rainforest from 0–500 m altitude (Fig. 13).

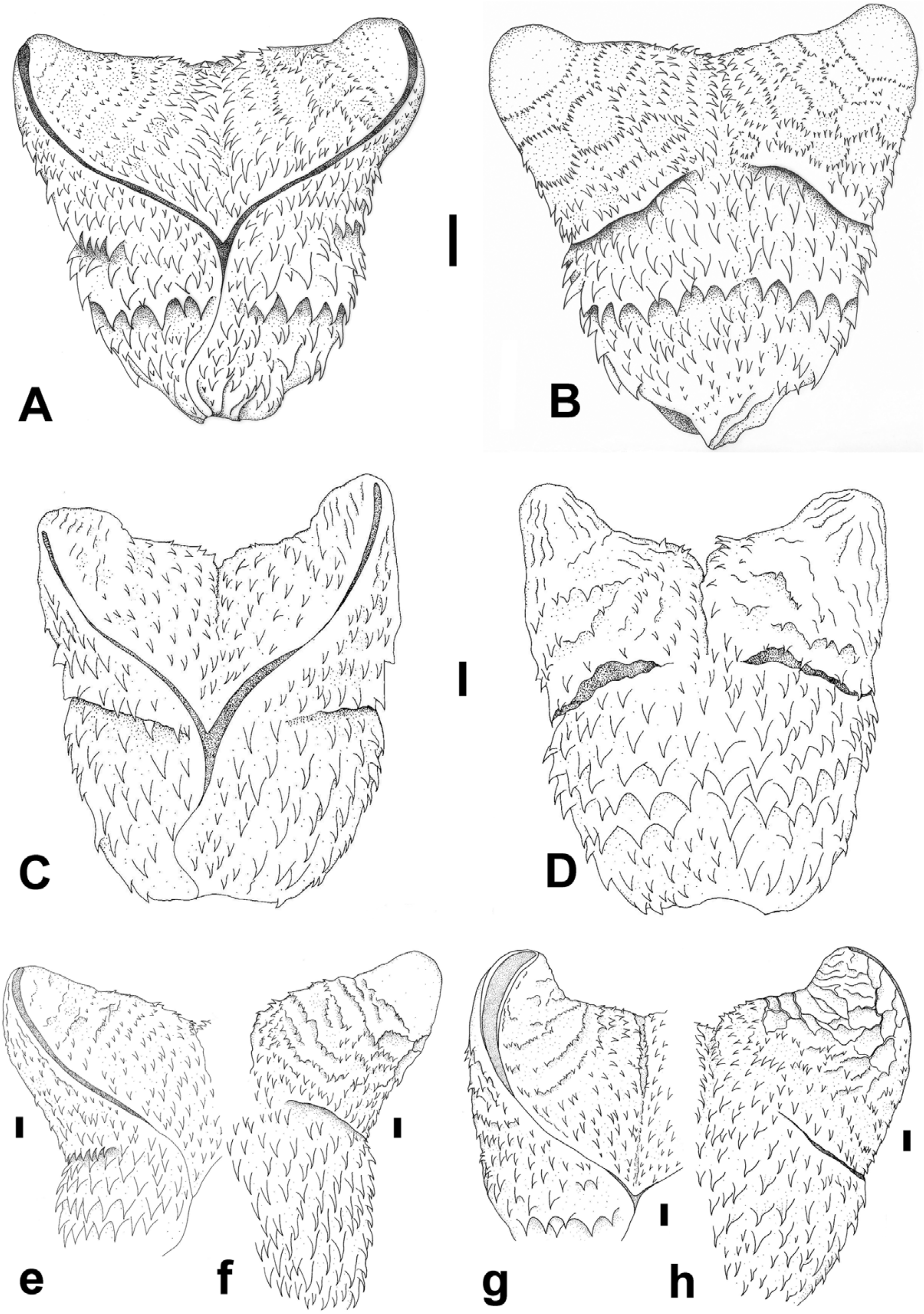

**FIGURE 9.** Morphological variation in the hemipenial morphology along the *Atractus torquatus* populations. Sulcate (left) and asulcate (right) sides of the organ of FMT 1286 from municipality of Manaus, state of Amazonas, Brazil (A–B); INPA 14670 from Lago Ayapuá, Rio Purus, municipality of Beruri, state of Amazonas, Brazil (C–D); FMT 1201 from municipality of Manaus, state of Amazonas, Brazil (e–f); and MPEG 23684 from Serra do Acari, municipality of Oriximiná, state of Pará, Brazil (g–h). Scale = 5 mm.

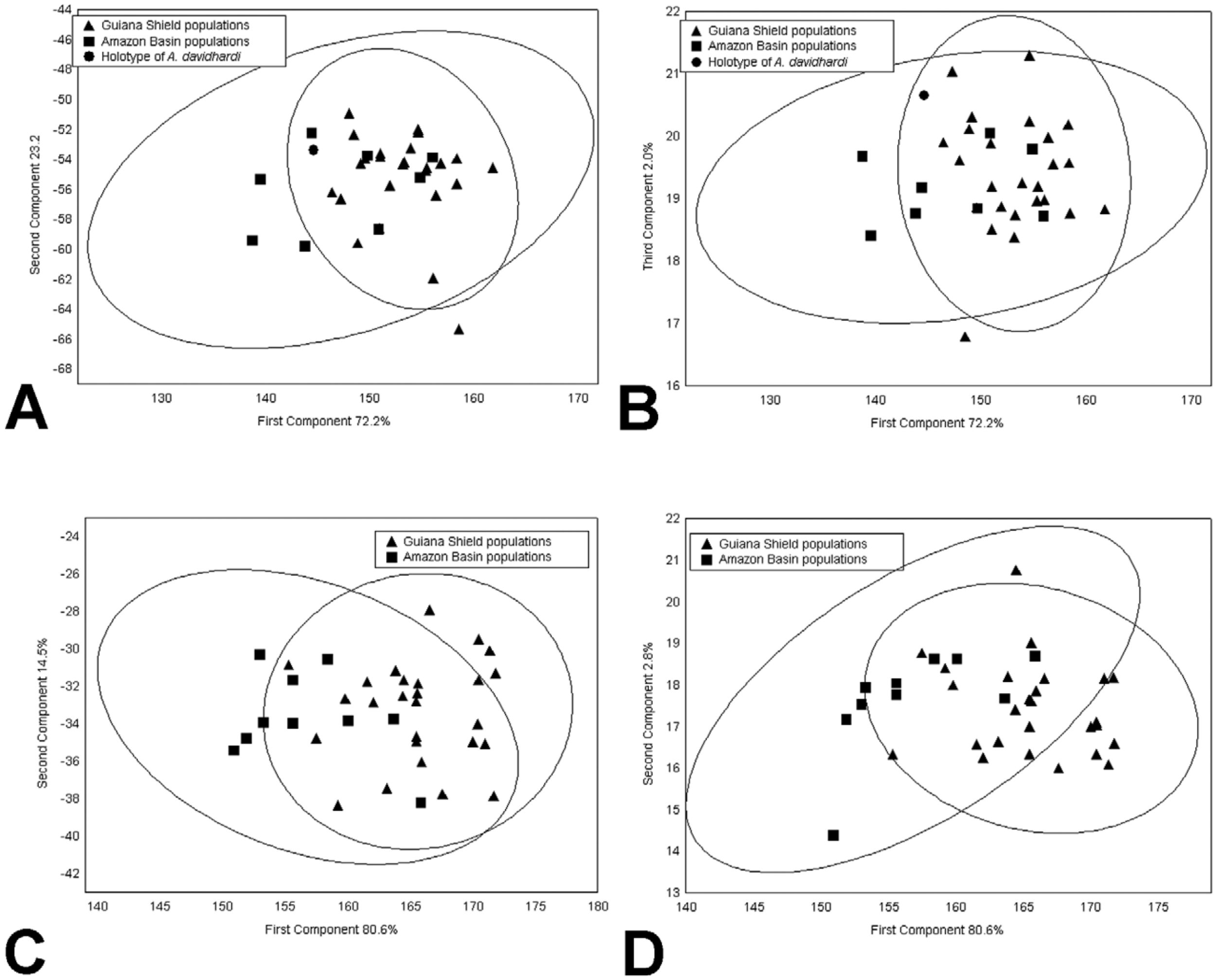

**FIGURE 10.** Bivariate plots with 95% confidence regions for the first two axes derived from scores of PCA analyses for male (A–B) and female (C–D) of *Atractus torquatus* complex.

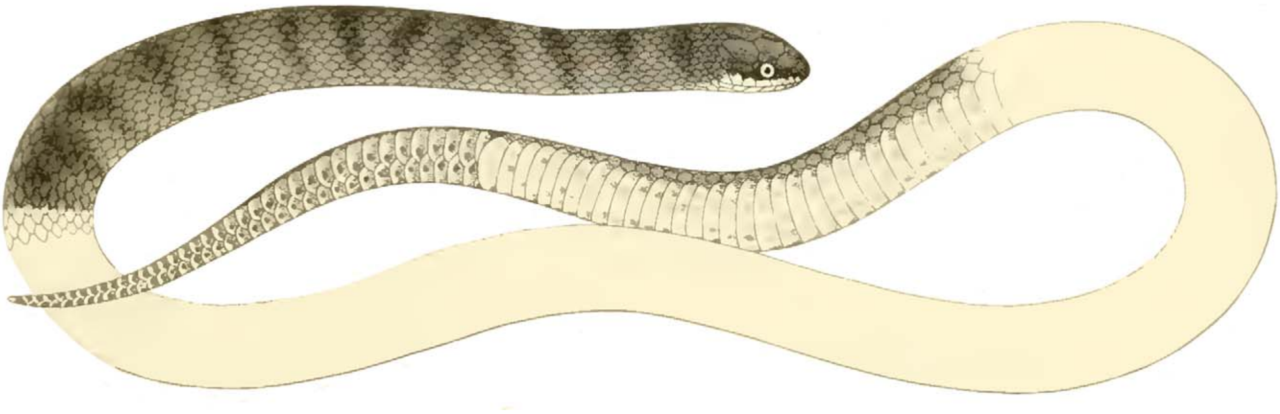

**FIGURE 11.** Original plate of the holotype of *Rabdosoma varium* (RMNH 114), modified from Jan and Sordelli (1865).

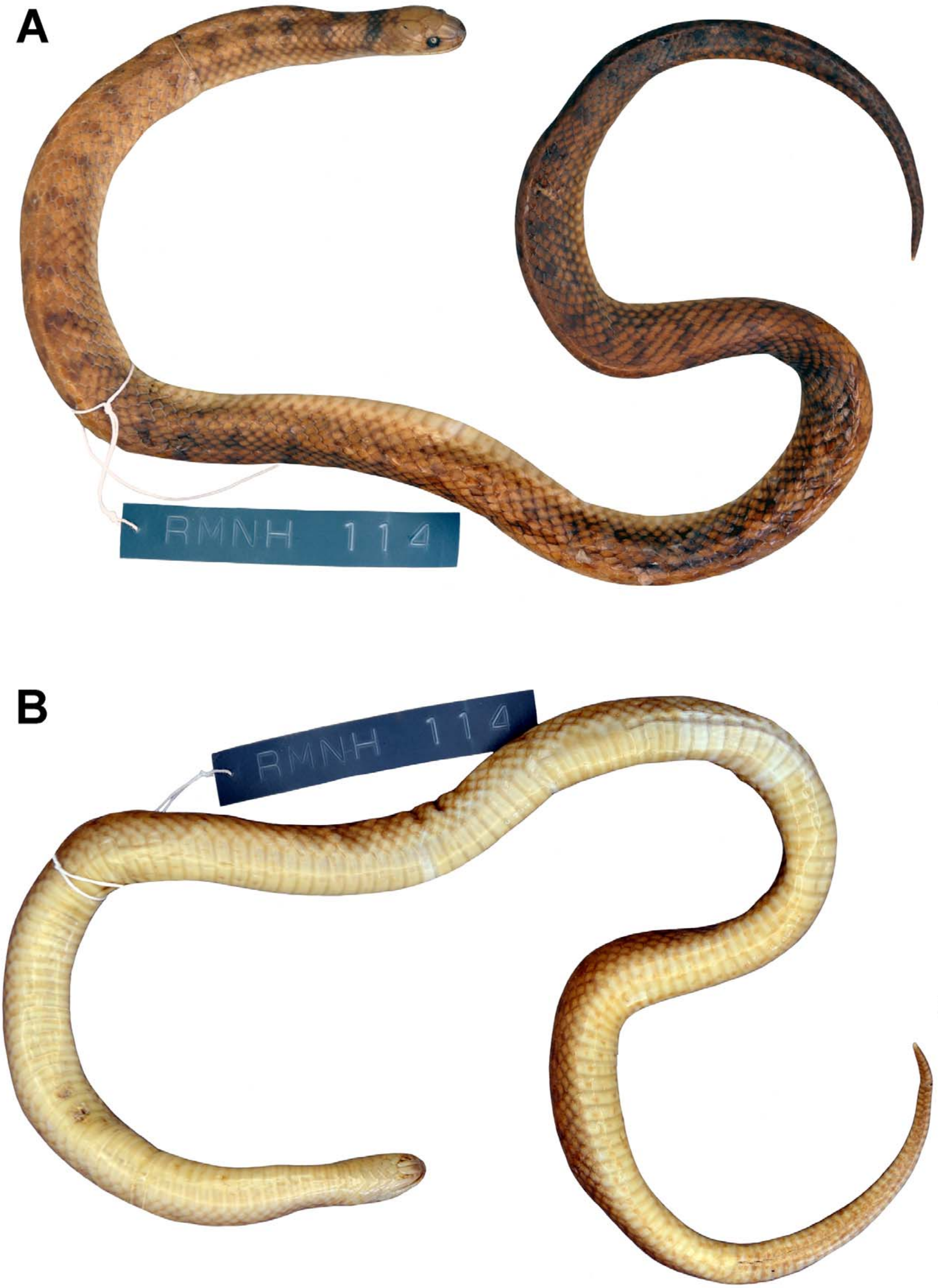

**FIGURE 12.** Dorsal (A) and ventral (B) views of body of the lectotype of *Rabdosoma torquatum* (RMNH 114).

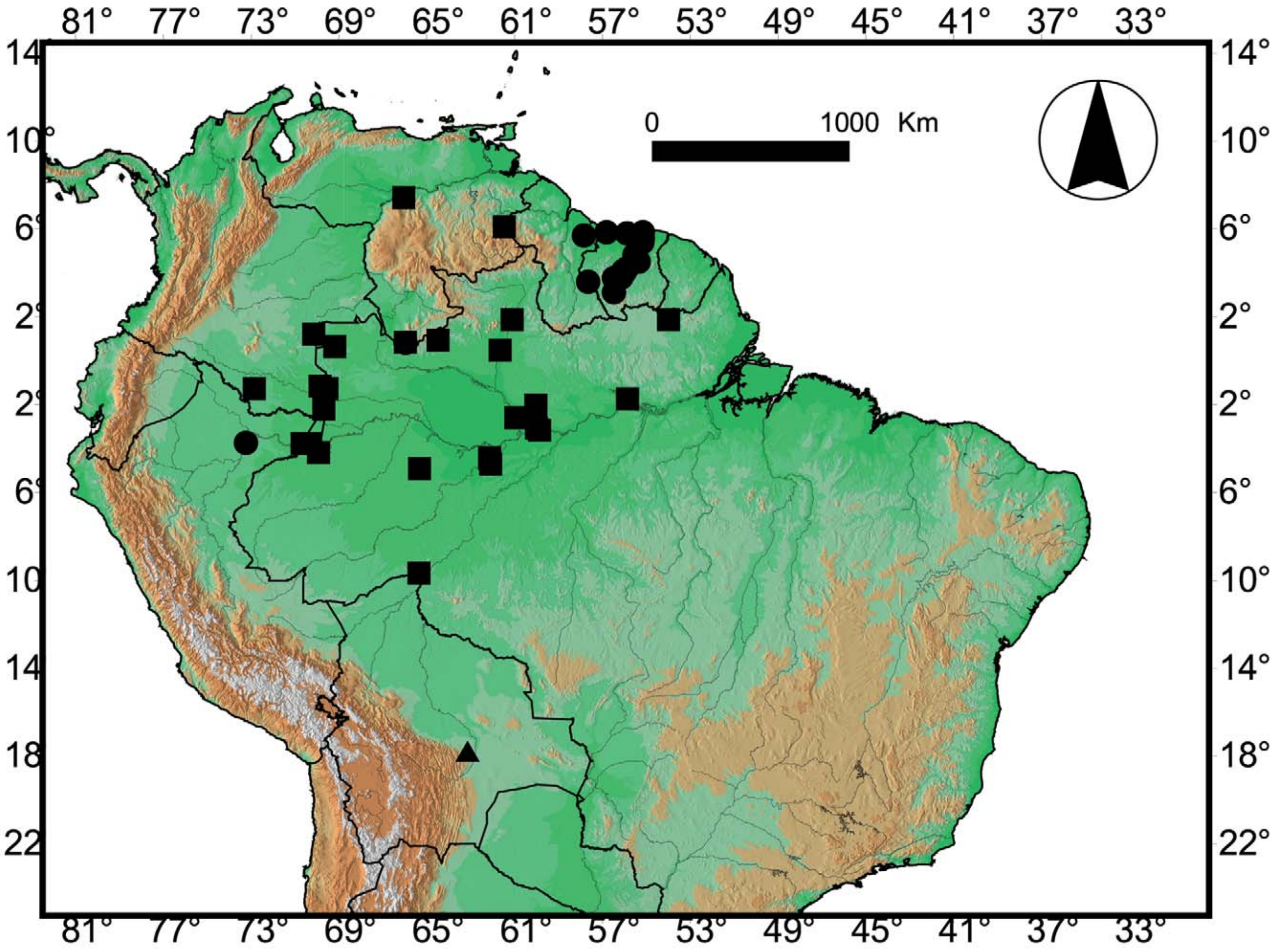

**FIGURE 13.** Geographical distribution of the *Atractus torquatus*. Black triangle corresponds to doubtful and circles to literature records. Literature records were taken from Dixon & Soini (1977, 1986), Hoogmoed (1980) and Abuys (1984).

**Remarks.** The diagnoses provided by Silva (2004), possibly with the exception of *Atractus davidhardi* in which he also included some hemipenial features, were inadequate to distinguish these forms from any other congener. Moreover, many of the characters used by the author were in error (see Tab. 1). Therefore, all putative diagnostic features of the Amazon basin taxa proposed by Silva falls within know morphological variation of the *Atractus torquatus*.

**TABLE 1.** Comparison between meristic and morphometric data of the holotypes of *Atractus davidhardi* (ICN 10096), *A. janethae* (ICN 10104) and *A. lucilae* (ICN 10105) reported by Silva (2004) (without parenthesis) and taken in our study (in parenthesis). We use "—" when our count or measure is the same from Silva (2004). Our morphometric variation is given in millimetre.

| Characters | ICN 10096 | | ICN 10104 | | ICN 10105 | |
|---|---|---|---|---|---|---|
| Dorsal scale rows | 17/17/17 | (—) | 17/17/17 | (16/17/16) | 17/17/17 | (—) |
| Ventrals | 148 | (—) | 156 | (155) | 160 | (153) |
| Subcaudals | 44 | (43/43) | 40 | (36/-) | 38 | (35/36) |
| Supralabials | 7 | (—) | 7 | (—) | 7 | (—) |
| Infralabials | 7 | (—) | 6 | (8) | 6 | (7) |
| Snout-vent length | 310 mm | (302) | 260 mm | (251) | 202 mm | (187) |
| Caudal length | 70 mm | (58) | 40 mm | (37) | 28 mm | (27) |

## Discussion

The Amazonia lowlands contain the richest biome of the world, comprising about 10% of the currently inventoried species in the planet (Silva & Garda 2010). Since Wallace's seminal work (Wallace 1852), many hypotheses were formulated in order to accommodate the plethora of processes responsible by diversification in the Amazonia (review in Haffer 2008). Even so, two historical events (Andean uplift and marine incursions) and two speciation models (riverine barriers and Pleistocene refuges) have usually been taken into account, jointly or separately, to explain the great diversity of the Amazonian biota. According to this complex scenario, the Andes uplift and periodic sea level had a tremendous impact on the formation and/or re-orientation of Amazon drainage and their associated biota in the later Miocene/Pliocene (review in Hoorn *et al*. 2010). While the Brazilian and Guiana shields have been geologically stable for the last 30–50 million of years, the western portion of Amazonia (Amazon Basin concept here adopted) began to take its current conformation only in the last 2,5 million of years ago (Hoorn, *et al*. 1995). As a result, the colonization of this area by lineages of exclusively terrestrial organisms occurred relatively late in the Pleistocene (Hoorn, *et al*. 1995; Aleixo 2004; Borges 2007).

The analysis of morphological variation of *Atractus torquatus* reveals a tendency among populations from the Amazon Basin (west of Rio Negro south to Rio Amazonas) in exhibit a smaller number of supra and infralabial scales (seven) and maxillary teeth (six or seven) compared to Guiana Shield populations (eight supra and infralabial scales and eight or nine maxillary teeth). However, these characters are currently polymorphic within Amazon Basin populations (equal or above 20% for all characters examined, Fig. 8), and probably are not evolutionarily independent traits (Dohm & Garland 1993). In the same way, there is a wide overlap in morphometric features between Amazon Basin and Guiana Shield populations (Fig. 10). Notwithstanding, there is an obvious cline in the meristic characters examined among closer geographical populations from Amazon Basin (Dixon & Soini 1986; Martins & Oliveira 1993). In this sense, a hypothesis of current gene flux between Guiana Shield and Amazon Basin populations of *Atractus torquatus* must be considered (see below). With respect to the colour pattern variation, we observed that all morphotypes identified in the course of this study occur randomly throughout all populations of the *A. torquatus* complex (Figs. 4–7). Therefore the current evidence does not support recognition of Amazon Basin taxa, in which all species proposed by Silva (2004) were based on, as distinct from *A. torquatus*.

On the basis of geographical distribution of morphological characters, the rivers in west Amazonia do not apparently constitute an effective barrier to prevent the contact of subpopulations of *A. torquatus.* As noted before (Colwell 2000; Aleixo 2004), the unsuitability of rivers from western portions of Amazonia as effective barriers is probably explained by its young age compared to Central portions of the Amazon domain (Colwell 2000). Despite differences in the frequencies of characters between Guiana Shield and Amazon Basin, we speculate that the barrier effect of the upper Amazon Rivers is limited and ultimately insufficient to promote complete isolation of *A. torquatus* populations. Another possibility is that gene flow between Guiana Shield and Amazon Basin populations of *A. torquatus* is guided by lateral channel migration responsible for across river transfer of large pieces of land (Colwell 2000). Furthermore, at least one other congener (*A. schach*) displays a pattern of distribution that also includes Guiana Shield and Amazon Basin regions of South America (Martins & Oliveira 1993; Passos 2008). Moreover, we do not discard the possibility that future studies, with more geographical representative samples from southwester Brazilian Amazonia, may demonstrate that the Amazon Basin and Guiana Shield population comprises distinct lineages with some level of current intergradation. In any way, if this panorama is corroborated in the future, we anticipate that it will not be necessary to recognize more than one evolutionary unit for the Amazon Basin populations.

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## References

Abuys, A. (1983) The snakes of Surinam, part VI: subfamily Xenodontinae (general data and genus *Atractus*). *Litteratura Serpentum* 3, 67–81.

Aleixo, A. (2004) Historical diversification of a *Terra-firme* forest bird superspecies: a phylogeographic perspective on the role of different hypotheses of Amazonian diversification. *Evolution*, 58, 1303–1317.

Boie, F. (1827) Ueber Merrem's Versuch eines Systems der Amphibien, Marburg, 1820. Erste Lieferung: Ophidier. *Isis von Oken*, 20, 508–566.

Borges, S. H. (2007) Análise biogeográfica da avifauna da região oeste do baixo Rio Negro, Amazônia brasileira. *Revista Brasileira de Zoologia,* 24, 919–940.

Boulenger, G.A. (1894) *Catalogue of the snakes in the British Museum (Natural History),* vol. 2. Trustees of the British Museum, London, U.K.

Colwell, R.K. (2000) A barrier runs through it… or maybe just a river. *Proceedings of the Natural Academy of Science of the United States of America*, 97, 13470–13472.

De Queiroz, K. (1998) *The general concept of species, species criteria, and the process of speciation: a conceptual unification and terminological recommendations*. Pp. 57–75, *In* Howard, D. & Berlocher, S.H. (Eds.), Endless Forms: Species and Speciation. Oxford University Press, New York, New York, U.S.A.

Dixon, J.R. & Soini, P. (1977) The reptiles of the upper Amazon Basin, Iquitos Region, Peru. Contribuitions in Biology and Geology. *Milwaukee Public Mus*eum, 12, 1–91.

Dixon, J.R. & Soini, P. (1986) *The reptiles of the upper Amazon basin, Iquitos region, Peru*. Second edition, Milwaukee Public Museum, Milwaukee, Wisconsin, U.S.A.

Dohm, M.R. & Garland, T. Jr. (1993) Quantitative genetics of scale counts in the garter snake *Thamnophis sirtalis*. *Copeia*, 4, 987–1002.

Dowling, H.G. (1951) A proposed standard system of counting ventrals in snakes. *British Journal of Herpetology*, 1, 97–99.

Dowling, H.G. & Savage, J.M. (1960) A guide to the snake hemipenis: a survey of basic structure and systematic characters. *Zoologica*, 45,17–28.

Duméril, A.M.C., Bibron G. & Duméril, A. ( 1854) *Erpétologie générale des Ophidiens,* vol. 7 Paris, France.

Efron, B. (1979) Bootstrap methods: another look at the jackknife. *Annals Statistics*, 7, 1–26.

Giraudo, A.R. & Scrocchi, G.J. (2000) The genus *Atractus* (Serpentes: Colubridae) in Northeastern Argentina. *Herpetological Journal*, 10, 81–90.

Haffer, J. (2008) Hypothesis to explain the origin of species in Amazonia. *Brazilian Journal of Biology,* 68, 917–947.

Henderson, R.W., Passos, P. & Feitosa, D. (2009) Geographic variation in the emerald treeboa, *Corallus caninus* (Squamata: Boidae). *Copeia*, 2009, 762–772.

Hoogmoed, M.S (1979) Snakes of the Guianan region. *Memórias do Instituto Butantan*, 46, 219–254.

Hoogmoed, M.S. (1980) Revision of the genus *Atractus* in Surinam, with the resurrection of two species (Colubridae, Reptilia). Notes on the herpetofauna of Surinam VII. *Zoologische Verhanderlingen*, 175, 1–47.

Hoorn, C., Guerrero, J., Sarmiento, G.A. & Lorente, M.A. (1995) Andean tectonics as a cause for changing drainage patterns in Miocene northern South America. *Geology*, 23, 237–240.

Hoorn, C., Wesselingh, F.P., ter Steege, H., Bermudez, M.A., Mora, A., Sevink, J., Sanmartín, I., Sanchez-Meseguer, Anderson, C.L., Figueiredo, J.P., Jaramillo, C., Riff, D., Negri, F.R., Hooghiemstra, H., Lundberg, J., Stadler, T., Särkinen, T. & Antonelli, A. (2010) Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science*, 339, 927–931.

Jan, G. (1862) Enumerazione sistematica delle specie d'Ophidi del gruppo Calamaridae. *Archivos di Zoologia, Anatomia e Fisiologia*, 2, 1–76.

Kok, P.J.R. (2006) A new snake genus *Atractus* Wagler, 1828 (Reptilia: Squamata: Colubridae) from Kaieteur National Park, Guyana, northeastern South America. *Zootaxa*, 1378, 19–35.

Manly, B.F.J. (2000) *Multivariate Statistical Methods: A Primer.* 3 edt. Chapmam & Hall, London, UK, 215 pp.

Martins, M. & Oliveira, M.E. (1993) The snakes of the genus *Atractus* Wagler (Reptilia: Squamata: Colubridae) from the

Manaus region, central Amazonia, Brazil. *Zoologische Mededelingem*, 69, 21–40.

Mathworks. (1994) *Matlab for Windows 4.2c1*. Mathworks, Inc., Natick, USA.

Myers, C.W. (2003) Rare snakes–five new species from eastern Panama: reviews of northern *Atractus* and southern *Geophis* (Colubridae: Dipsadinae). *American Museum Novitates*, 3391, 1–47.

Myers, C.W. & Schargel, W.E. (2006) Morphological extremes. Two new snakes of the genus *Atractus* from northwestern South America (Colubridae: Dipsadinae). *American Museum Novitates*, 3532, 1–13.

Passos, P. (2008) *Revisão Taxonômica do Gênero* Atractus *Wagler, 1828 (Serpentes: Colubridae: Dipsadinae)*. Ph.D. Dissertation, Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil, 671 pp.

Passos, P. & Arredondo, J.C. (2009) Rediscovery and redescription of the Andean earth-snake *Atractus wagleri* (Reptilia: Serpentes: Colubridae). *Zootaxa*, 1969, 59–68.

Passos, P. & Fernandes, R. (2008) A new species of the colubrid snake genus *Atractus* (Reptilia: Serpentes) from the central Amazon of Brazil. *Zootaxa*, 1849, 59–66.

Passos, P. & Fernandes, R. (2009) "2008" Revision of the *Epicrates cenchria* complex (Serpentes: Boidae). *Herpetological Monographs*, 22, 1–30.

Passos, P. & Lynch, J.D. (2011) "2010" Revision of Atractus from upper and middle Magdalena drainage of Colombia. *Herpetological Monographs*, 24, 149–173.

Passos, P., Aguayo, R. & Scrocchi, G. (2009a) Rediscovery of the rare *Atractus bocki*, with assessment of the taxonomic status of *A. canedii* (Serpentes: Colubridae: Dipsadidae). *Journal of Herpetology*, 43, 710–715.

Passos, P., Arredondo, J.C., Fernandes, R. & Lynch, J.D. (2009b) Three new *Atractus* (Serpentes: Dipsadidae) from Andes of Colombia. *Copeia*, 2009, 425–438.

Passos, P., Chiesse, A., Torres-Carvajal, O., & Savage, J.M. (2010a) "2009" Testing species boundaries within *Atractus occipitoalbus* complex (Serpentes: Dipsadidae). *Herpetologica*, 65, 284–403.

Passos, P., Cisneros-Heredia, D. F. & Salazar-V., D. (2007a) Rediscovery and redescription of the rare Andean snake *Atractus modestus*. *Herpetological Journal*, 17, 1–6.

Passos, P., Fernandes, R., Bérnils, R.S. & Moura-Leite, J.C. (2010b) Revision of the Atlantic Forest *Atractus* (Reptilia: Serpentes: Dipsadidae). *Zootaxa*, 2364, 1–63.

Passos, P., Fernandes, D. S. & Borges-Nojosa, D.M. (2007b) A new species of *Atractus* (Serpentes: Dipsadinae) from a relictual forest in Northeasten Brazil. *Copeia*, 2007, 788–797.

Passos, P., Fuenmayor, G.R. & Barrio-Amorós, C. (2009c) Description of two new species from Venezuela in the highly diverse dipsadine genus *Atractus* (Serpentes: Colubridae). *Amphibia-Reptilia*, 30, 233–243.

Passos, P., Lynch, J.D. & Fernandes, R. (2009d) "2008" Taxonomic status of *Atractus sanctaemartae* and *A. nebularis*, and description of a new species of *Atractus* from Atlantic coast of Colombia. *Herpetological Journal*, 18, 175–186.

Passos, P., Mueses-Cisneros, J.J., Lynch, J.D. & Fernandes, R. (2009e) Pacific lowland snakes of the genus *Atractus* (Reptilia: Serpentes: Dipsadidae), with descriptions of three new species. *Zootaxa*, 2293, 1–34.

Pesantes, O. (1994) A method for preparing hemipenis of preserved snakes. *Journal of Herpetology*, 28, 93–95.

Prudente, A.L.C. & Passos, P. (2008) New species of *Atractus* Wagelr, 1828 (Serpentes: Dipsadinae) from Guyana Plateau in Northern Brazil. *Journal of Herpetology*, 42, 723–732.

Prudente, A.L.C. & Passos, P. (2010) New cryptic species of *Atractus* (Serpentes: Dipsadidae) from Brazilian Amazonia. *Copeia*, 2010, 397–404.

Prudente, A.L.C. & Santos-Costa, M.C. (2006) A new species of *Atractus* Wagler, 1828 (Serpentes: Colubridae) from esatern Amazonia, Brazil. *Zootaxa*, 1285, 21–29.

Savage, J.M. (1960) A revision of the Ecuadorian snakes of the genus *Atractus. Miscellaneous Publications of the Museum of Zoology, University of Michigan*, 112, 1–86.

Schargel, W.E. & Castoe, T.A. (2003) The hemipenes of some snakes of the semifossorial Genus *Atractus*, with comments on variation in the Genus. *Journal of Herpetology*, 37, 718–721.

Schlegel, H. (1837) *Essai sur la physionomie dês serpens*. Vol. 1: xxvii, 251 pp. Vol.2, 606 + xv pp. Atlas, 21 pls. Text, Amsterdan, Schonekat M.H. Atlas, La haye: J. Kips, J. Hz. Et. W. P. Van Stockum, Nederland.

Silva, J.J.H. (2004) Las serpientes del género *Atractus* Wagler, 1828 (Colubridae, Xenodontinae) en la Amazonia Colombiana. *Revista de la Académia Colombiana de Ciencias Fisicas, Exactas y Naturales*, 28, 409–446.

Silva, J.M.C. & Garda, A.A. (2010) *Padrões e Processos Biogeográficos na Amazônia*. Pp. 189–197, *In* Carvalho, C.J.B. & Almeida, E.A.B. (Eds.), Biogeografia da América do Sul: Padrões e Processos. Ed. São Paulo, Brazil.

Statsoft, INC. (1995) *Statistica for Windows version 5.1*. Tulsa, U.S.A.

Wallace, A.R. (1852) On the monkeys of the Amazon. Proceedings of the Zoological Society of London 20, 107–110.

Wiens, J.J. & Servedio, M.R. (2000) Species delimitation in systematics: inferring diagnostic differences between species. *Proceedings of the Royal Society of London, Biological Sciences*, 267, 631–636.

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) Hemipenis of *Siphlophis* (Serpentes, Xenodontinae) and techniques of hemipenial preparation in snakes: a response to Dowling. *Herpetological Review*, 34, 302–307.

Zar, J.H. (1999) Bioestatistical analysis, Prentice-Hall Press, New Jersey, USA.

## **APPENDIX.** Material examined.

Countries are given in bold capitals, states in plain capitals, municipalities in italics, and localities in plain text. Specimens for which everted hemipenes were examined are indicated with an asterisk.

*Atractus torquatus* (*n* = 71).—**BRAZIL:** AMAPÁ: *Laranjal do Jari*: Parque Nacional do Tumucumaque: (MPEG not catalogued); AMAZONAS: *Beruri*: Rio Purus: Lago Ayapuá: (INPA 14655, 14670*), *Careiro da Varzea*: (MPEG 19551*), *Coari*: Porto Urucu: (MPEG 21143*), *Manaus*: (FMT 338, 536, 1097, 1201*, 1286*, 2025, 2915*), Km 80 BR 174: (INPA 768, 10382, MZUSP 8533–34), Reserva Florestal Adolpho Ducke–INPA: (MZUSP 8455, 9588), Missão Manari: (MZUSP 10405, 14287), *Novo Airão*: (MZUSP 8205), *Presidente Figueredo*: Balbina Hydroelectric Plant: (FMT 1358, 1404, 1424*, 1426, 1457–58, 1529*–30, 1533, 1539, 1555, 1571, 1617): Rio Uatumã: (MPEG 17414, 17462, 17466, 17516, 17560), *São Grabriel da Cachoeira*: Parque Nacional do Pico da Neblina: (INPA 12788, 15760*); PARÁ: *Oriximiná*: Serra do Acarí: (MPEG 23684*–86); RORAIMA: without locality: (MPEG 19021), *Caracaraí*: Parque Nacional do Viruá: (INPA 19245, 25702–05, 25708), Rio Catrimani: (MZUSP 7303). **COLOMBIA:** AMAZONAS: *La Chorrera*: (ICN 10104 holotype of *A. janethae*, ICN 10107 paratype of *A. lucilae*), *Letícia*: Vereda Muniyamena: (ICN 10096* holotype of *A. davidhardi*), *La Pedreira*: Puerto Córdoba: (ICN 10105 holotype and ICN 10106 paratype of *A. lucilae*), *Parque Natural Nacional Amacayacu*: (IAvH 3871); *Rio Muriti-Paraná*: Puerto Bogotano: (IAvH 1914); VAUPÉS: *Lago Taraira*: Rio Apaporis: (IAvH 4093, 4097), *Mitú*: (ICN 10111), *Yavaraté*: (HM 313). **PERU:** LORETO: *Pebas*: Río Ampiyacu: (MZUSP 4380). **VENEZUELA:** (MHNLS two not catalogued specimens); AMAZONAS: Frente 20: (MHNLS 14488); BOLIVAR: *El Dorado*: (MBUCV 1406), Km 38 of the road between *El Dorado* and *Santa Elena de Uairén*: (CVULA not catalogued), Río Uey: middle basin of Río Cuyuní: (MHNLS 18665).