



## Morphological variation and taxonomy of *Atractus latifrons* (Günther, 1868) (Serpentes: Dipsadidae)

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### Abstract

As currently understood *Atractus latifrons* is widely distributed in South America, occurring from Suriname to the east of the Andes in Bolivia. Throughout this widespread distribution, at least three distinct color patterns were previously reported in the literature. Here, we test whether quantitative variation and qualitative distribution of morphological characters are correlated with any color pattern displayed by the species along its range. We recognize three aposematic color patterns (bicolor in monads, tricolor in dyads, and tricolor in tetrads) for *A. latifrons*. We found no obvious correspondence between these patterns and any character systems analyzed herein. Additionally, we redescribe the holotype of *A. latifrons* and report on morphological variability (meristics, morphometrics, color patterns, and hemipenis) and geographical distribution (extending its distribution to the state Roraima, Brazil) of the species.

**Key words:** Amazon Basin, Morphometry, Polychromatism, Aposematic color patterns, Mimeticism

### Introduction

The cryptozoic snake genus *Atractus* Wagler, 1828 is distributed widely in the Neotropical region, occurring from Panama to Argentina (Giraudo & Scrocchi 2000; Myers 2003). *Atractus* is the most speciose snake genus comprising about 140 species, but several taxa are still known from small series near their type localities (Passos & Lynch 2011; Passos *et al.* 2013b). Despite recent studies focusing on its taxonomy (Passos & Fernandes 2008; Passos & Arredondo 2009; Passos *et al.* 2009a,b,c,d,e; Passos *et al.* 2010a,b,c; Prudente & Passos 2008, 2010; Passos *et al.* 2013a,b,c,d; Schargel *et al.* 2013), additional efforts must be made to address instances of morphological variation, geographic range, sexual dimorphism, and ontogenetic change of coloration (Passos *et al.* 2010a,b,c). Clarifying these aspects will help solve the taxonomic status for many species within this genus (Passos & Lynch 2011; Passos *et al.* 2012). As currently understood, *Atractus latifrons* is widely distributed in South America, occurring in the Amazonian lowlands of Colombia, Venezuela, French Guiana, Suriname, Brazil, and Peru (Peters & Orejas-Miranda 1970; Gasc & Rodrigues 1980; Hoogmoed 1980; Cunha & Nascimento 1983, 1993; Martins & Oliveira 1993; Passos & Fernandes 2008; Prudente & Passos 2008). This species is found in the forest litter of primary and secondary rainforests as well as cultivation fields along the Amazon Basin (Dixon & Soini 1977, 1986; Hoogmoed 1980; Martins & Oliveira 1993, 1999; Silva 2004).

Günther (1868) described *Geophis latifrons* on the basis of a single specimen from the municipality of Pebas, department of Loreto, in the northeastern portion of Peruvian Amazon. Boulenger (1894) redefined the genus *Geophis* Wagler, 1828 and transferred *G. latifrons* to *Atractus*. Ahl (1927) described *Elaps herthae* through a specimen from the locality of Munducuru, along the Manacapuru River near Manaus, in Brazil. Savage (1960) proposed to allocate *A. elaps* and *A. latifrons* in the *A. elaps* species group, characterized by an aposematic coloration and unusual head scale pattern, maxillary dentition, and hemipenial morphology. Peters & Orejas-Miranda (1970) placed *Elaps herthae* in the synonymy of *A. latifrons*. Dixon & Soini (1977, 1986) reported on the

external morphological variation of *A. latifrons*, and identified two very distinct color patterns based on specimens collected in the Iquitos region of Peru. Hoogmoed (1980) described the hemipenial morphology of *A. latifrons* through its inverted organs and extended the species distribution to Suriname. Cunha & Nascimento (1983) described another aposematic color pattern of *A. latifrons* (tricolor in dyads), suggesting a possible mimicry between *A. latifrons* and some species of the coral snake genus *Micrurus* Wagler, 1824. Savage & Slowinski (1992) recognized three distinct chromatic patterns of *A. latifrons* (tricolor in dyads, tricolor in triads and tricolor in tetrads), highlighting its apparent mimicry with some species of the genus *Micrurus*.

To date, authors associated some color morphs of *A. latifrons* with several species of the genus *Micrurus* (*M. albicinctus*, *M. annelatus*, *M. hemprichii ortonii*, *M. filiformis*, *M. lemniscatus lemniscatus*, *M. l. diutus*, *M. l. helleri*, *M. mipartitus*, and *M. putumayensis*) or *Erythrolampus aesculapii* (Cunha & Nascimento 1983, 1993; Martins & Oliveira 1993, 1999; Silva Jr. 1993). Here, we test if quantitative variation and qualitative distribution of morphological characters are correlated with any color pattern recognized in *A. latifrons*. We also provide a redescription of the holotype of *A. latifrons*.

## Material and methods

We examined 143 specimens housed in the following institutions: Brazil-Centro de Estudos e Pesquisas Biológicas da Pontifícia Universidade Católica de Goiás (CEPB), Goiânia; Coleção Herpetológica, Universidade Federal do Ceará (CHUFC), Fortaleza; Fundação de Medicina Tropical (FMT), Manaus; Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus; Instituto Butantan (IBSP), São Paulo; Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo; Museu Paraense Emílio Goeldi (MPEG), Belém; Universidade Federal do Mato Grosso (UFMT), Cuiabá; Museu Nacional, Universidade Federal do Rio de Janeiro (MNRJ), Rio de Janeiro. Bolivia-Museo Noel Kempff Mercado (MNKR), Santa Cruz de La Serra. Colombia-Instituto Alexander von Humboldt (IAvH), Villa de Leyva; Museo de la Universidad La Salle (MLS), Bogotá; Universidad Nacional de Colombia (ICN), Bogotá. England-British Museum of Natural History (BMNH), London. Germany-Zoologisches Museum zu Berlin (ZMB), Berlin. Peru-Museo de Historia Natural de la Universidad Mayor de San Marcos (MHNSM), Lima. Specimens and localities are listed in Appendix 1.

Terminology for *Atractus* cephalic shields follows Savage (1960). The method of counting ventral scales follows Dowling (1951). Nomenclature regarding the loreal condition follows Passos *et al.* (2007). Nomenclature for other measurements and discrete characters follows Passos *et al.* (2009e). The style of the chromatic patterns follows Savage & Slowinski (1992). Techniques for hemipenis preparation follow Pesantes (1994) as modified by Zaher & Prudente (2003). Terminology for hemipenis description follows Dowling & Savage (1960) and Zaher (1999). We determined sex by subcaudal incision. Measurements were taken with a digital caliper to the nearest 0.1 mm under a stereoscope, except for snout-vent (SVL) and caudal lengths (CL) that were taken with a flexible ruler to the nearest 1 mm.

**Qualitative morphological analyses.** We defined *a priori* three distinct color patterns for the chromatic variability of *Atractus latifrons* (see chromatic variability). These were based on number, extension, and combination of black, white (or yellow) and red rings along the body and tail. We performed a discrete analysis of these patterns based on the frequency of occurrence of each one throughout the species distribution. We considered putative natural barriers (e.g., rivers) and geographic proximity of available samples as parameters to define these groups. Seven population groups were defined: 1) Eastern Amazon (including eastern Pará and western Maranhão, Brazil), 2) North of the Amazon River (comprising eastern Negro River and central Amazon, Brazil), 3) Southwest Amazon Basin (including the towns of municipality of Benjamin Constant, Porto Urucu, and nearby localities in the state of Amazonas, Brazil), 4) Southeast of the Amazon Basin (including the states of Rondônia and Mato Grosso, Brazil), 5) northern Bolivia (including the departments of Santa Cruz and Beni, Bolivia); 6) southern Colombia (including the departments of Caquetá, Vaupés, and Amazonas, Colombia), and 7) northern Peru (including the department of Loreto and Amazonas, Peru and state of Acre, Brazil).

On the basis of the frequency of distribution, we investigated if each of the patterns here defined have any geographical basis. Independently, we searched for a correspondence between the patterns recognized herein and hemipenial morphology.

**Quantitative morphological analyses.** 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

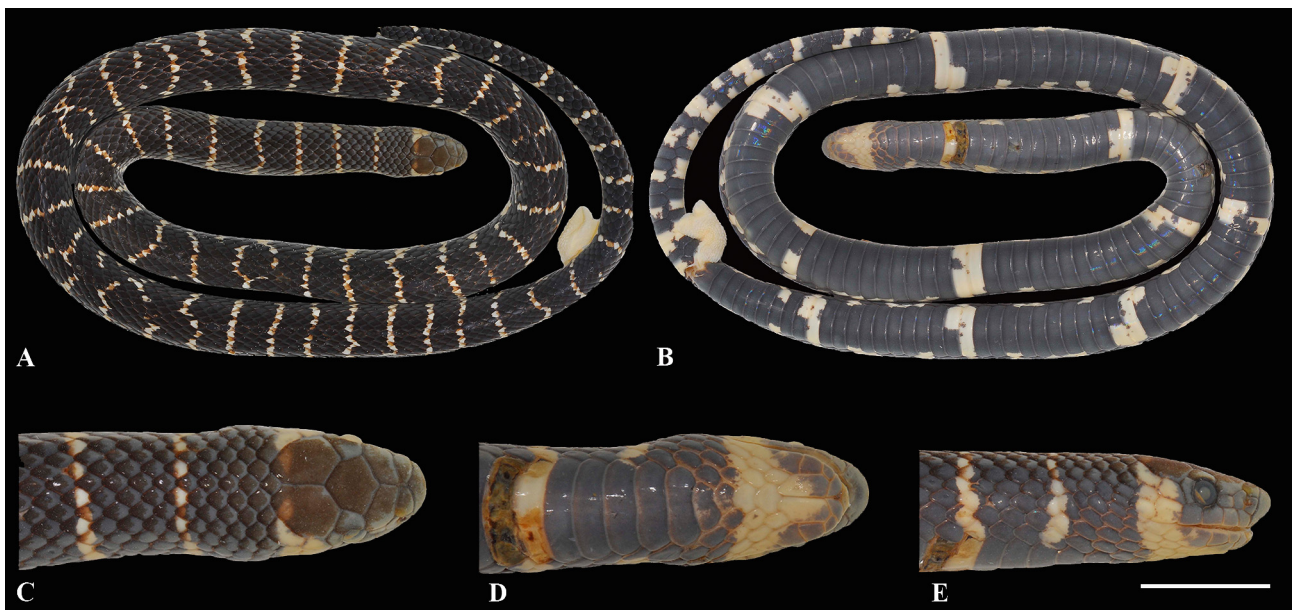
evaluated the assumptions of univariate normality and homoscedasticity with the Kolmogorov-Smirnov's and Levene's tests, respectively (Zar 1999). In cases where characters showed insufficient variation to justify these assumptions, we performed non-parametric tests, such as Kruskal-Wallis (Zar 1999). We performed a discriminant analysis (DFA) for males and females separately in order to evaluate differentiation between chromatic patterns with *a priori* definition (Manly 2000). We used the following characters in the statistical analyses: number of ventral scales, subcaudal scales, SVL, CL, and SVL/CL ratio. We performed all analyses using the software STATISTICA 7 (Statsoft 1998).

## Results

### Chromatic variability

Were analyzed 143 individuals (total frequency 100%). Color patterns were as follow ( $n= 140$ ; total frequency 97.90%): bicolor in monads (Fig. 1), tricolor in dyads (Figs. 2–4), and tricolor in tetrads (Fig. 5). The tricolor pattern in triads, described by Savage & Slowinski (1992) for *A. latifrons*, was not observed in any of the analyzed specimens. As a rule, specimens displayed a more conspicuous dorsal pattern, while ventral coloration showed spurious variation sometimes. We did not find any association of the patterns recognized here with sex or age class. Nevertheless, some individuals ( $n = 3$ ; total frequency 2.10%) showed some discrepancies with respect to shape, number, position and combination of black, red, white or yellow rings on the body and tail (see undefined pattern). Therefore, we considered these specimens aberrant and to classify them within one of the undefined patterns.

**Bicolor in monads ( $n = 26$ ; total frequency 18.18%).** Head uniformly black; background of head black, except for the 5–6th supralabials and temporals white; symphyseal, first five infralabials, and anterior region of chinshields black; dorsum with 26–50 black rings (2–8 dorsal and 2–4 ventral scales long), bordered by 25–50 white rings (0.5–1.0 dorsal and 1–3 ventral scales long), and 1–13 black rings (2–4 dorsal and 1–2 ventral scales long) bordered by 3–10 white rings (0.5–1.0 dorsal and 1–4 ventral scales long) on the tail (Fig. 1). White rings occasionally interrupted ventrally by irregular blotches.



**FIGURE 1.** “Bicolor in monads” pattern in *Atractus latifrons*. Dorsal (A) and ventral (B) views of body; and dorsal (C), ventral (D), and lateral (E) views of head of the specimen (MPEG 20363) from Parque Estadual Guarajá Mirim, municipality of Espigão d’ Oeste, state of Rondônia, Brazil. Scale = 10 mm.

**Tricolor in dyads ( $n = 103$ ; total frequency 72.03%).** Dorsum of head with black cephalic cap, extending from rostral to posterior region of parietals; cephalic cap followed by a white band covering the posterior region of parietals and temporals; lateral region of the head black until postocular region, except for white blotch usually

covering both nasals and first two supralabials; eventually white blotch extends dorsally into prefrontals, giving an impression of an incomplete ring dorsally; symphyseal, anterior region of chinshields and first four infralabials black; posterior region of chinshields and anterior gulars white; first black ring incomplete ventrally, presenting black dots on the posterior gulars and preventrals; 7–14 dyads on the body and 1–3 on the tail; 16–30 black rings (3–7 dorsal and 2–5 ventral scales long) on the body and 2–9 (3–7 dorsal and 2–5 ventral scales long) on the tail; 8–25 white rings (1–3 dorsal and 1–4 ventral scales long) on the body and 1–4 (0.5–2 dorsal and 1–3 ventral scales long) on the tail; 8–15 red rings (3–20 dorsal and 2–17 ventral scales long) on the body and 1–5 on the tail (4–10 dorsal and 3–10 ventral scales long) (Fig. 2).

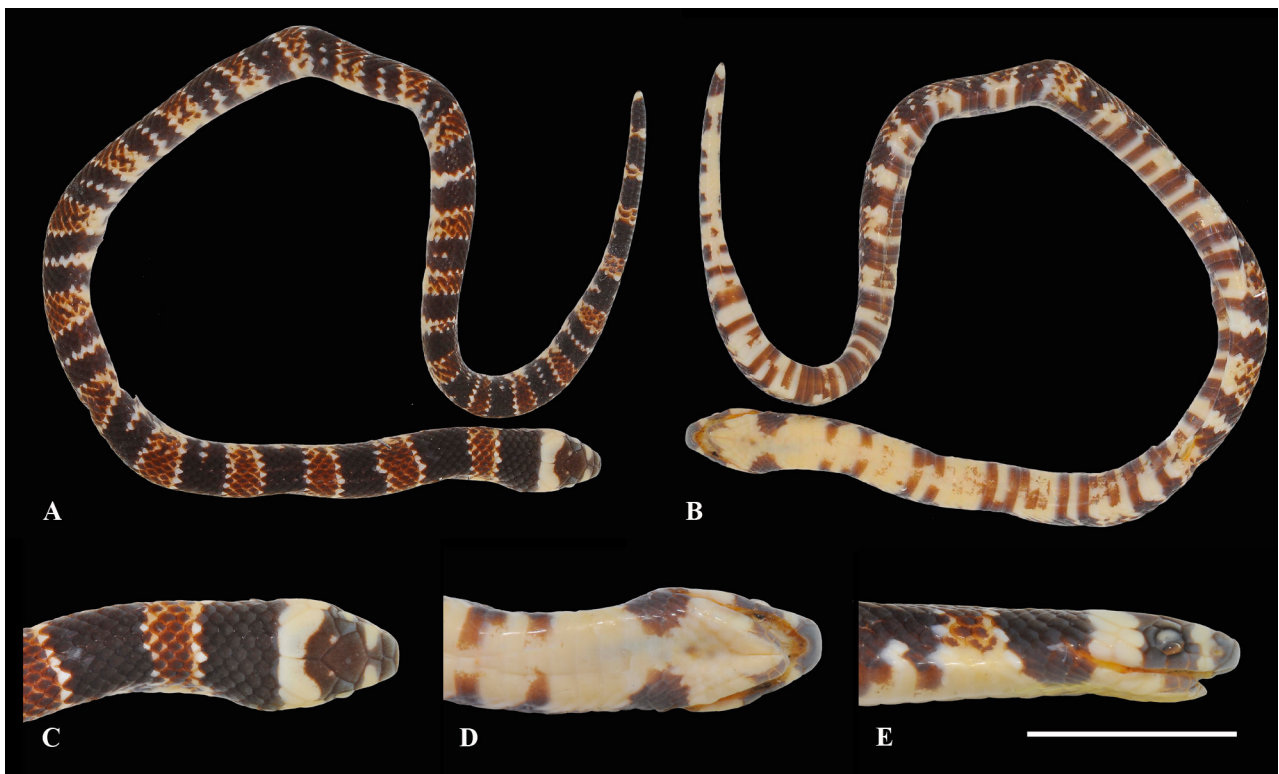


**FIGURE 2.** “Tricolor in dyads” pattern in *Atractus latifrons*. Dorsal (A) and ventral (B) views of body; and dorsal (C), ventral (D), and lateral (E) views of head of the specimen (MZUSP 6594) from Jurupá River, state of Amazonas, Brazil. Scale = 10 mm.

Melanistic specimens were more common in this pattern ( $n = 13$ ). Melanistic specimens with this pattern had a darker dorsal color, although the black, red, and white rings were more easily observed on the ventral side. Some specimens with this pattern exhibited variation in color ( $n = 15$ ). Central and posterior regions of chinshields, gulars, and preventrals white; first black ring of body usually interrupted ventrally. Based on the length of the red rings, two morphs are recognized within this pattern: 8–10 monads on the body and usually 1–3 on the tail, and red rings covering 10–20 dorsals and 9–17 ventrals on the body and 5–8 dorsals, and 1–2 ventrals on the tail ( $n = 8$ ) (Fig. 3); 11–16 monads on the body and usually 1–4 on the tail, and red rings covering 2–3 dorsals and 1–3 ventrals on the body and 1–2 ventrals on the tail ( $n = 7$ ) (Fig. 4).

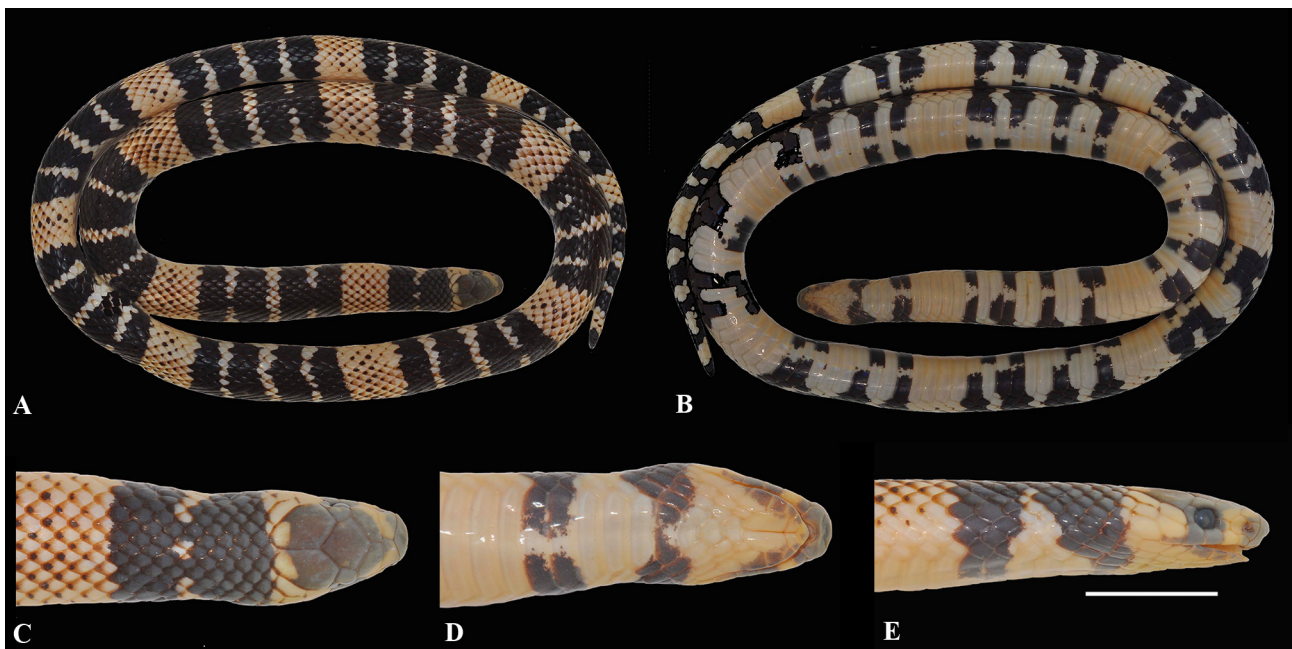


**FIGURE 3.** Variation of “tricolor in dyads” pattern in *Atractus latifrons*. Dorsal (A) and ventral (B) views of body; and dorsal (C), ventral (D), and lateral (E) views of head of the specimen (MPEG 17460) from Balbina Plant Hydroelectric, municipality of Presidente Figueiredo, state of Amazonas, Brazil. Scale = 10 mm.



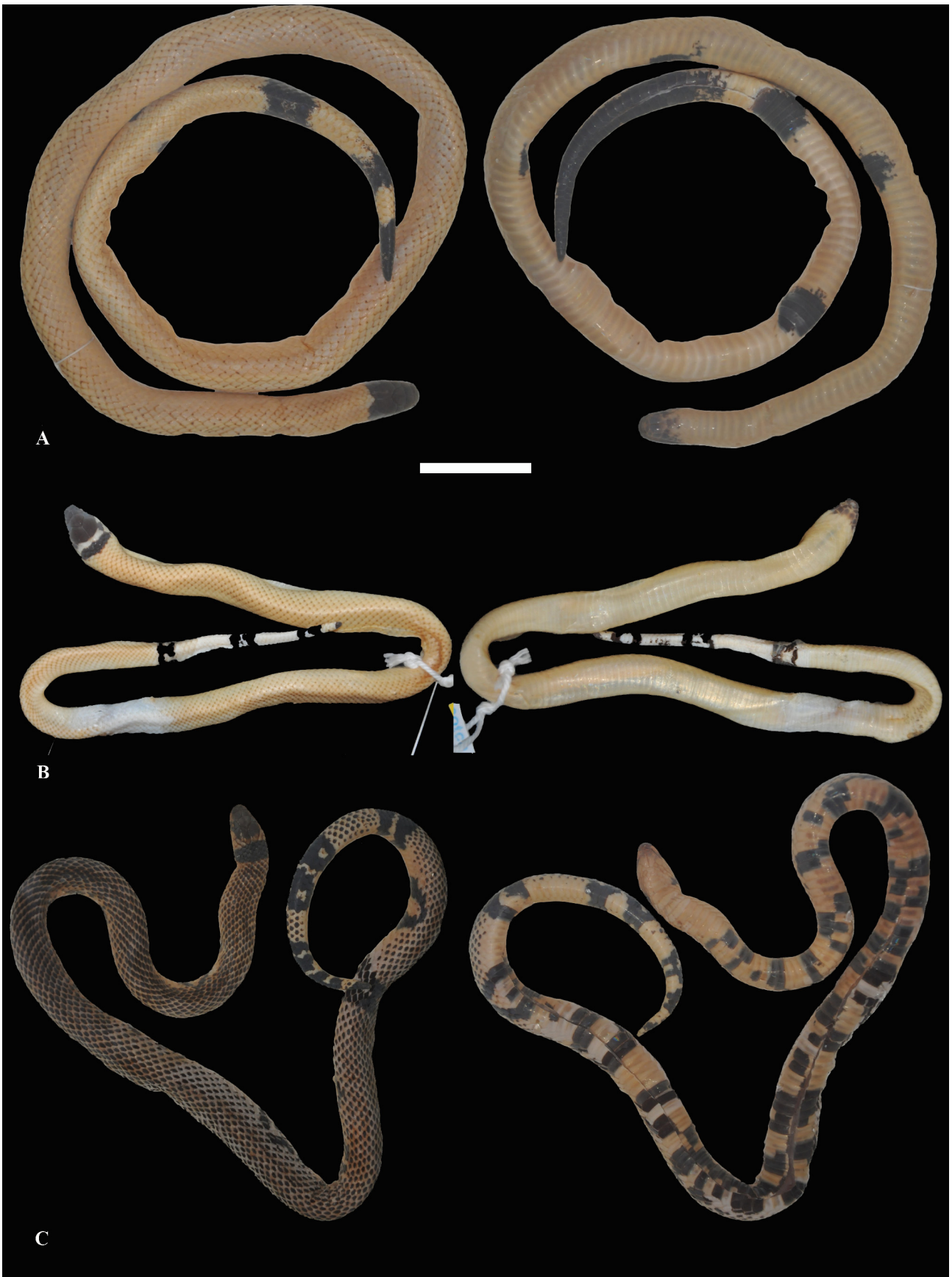
**FIGURE 4.** Variation of “tricolor in dyads” pattern in *Atractus latifrons*. Dorsal (A) and ventral (B) views of body; and dorsal (C), ventral (D), and lateral (E) views of head of the specimen (MPEG 19261) from municipality of Porto Urucu, state of Amazonas, Brazil. Scale = 10 mm.

**Tricolor in tetrads ( $n = 11$ ; total frequency 7.69%).** Dorsum of head with black cephalic cap, extending from rostral to posterior region of parietals; cephalic cap interrupted by white bands situated on the internasals anteriorly and posterior region of parietals and temporals posteriorly; lateral region of the head black with a white blotch covering internasals, nasal and first two supralabials; white blotches usually in contact medially, completing anterior white band dorsally; symphyseal, anterior region of chinshields and first four or five infralabials usually black; posterior region of chinshields, gulars, and preventrals white; first black ring of the body generally complete ventrally after preventrals; 8–11 tetrads on the body and 1–3 on the tail; 18–45 black rings (2–7 dorsal and 1–4 ventral scales long) on the body and 3–10 (2–3 dorsal and 1–2 ventral scales long) on the tail; 8–34 white rings (1–2 dorsal and 1–3 ventral scales long) on the body and 2–7 (1–2 dorsal and 1–2 ventral scales long) on the tail; 8–11 red rings (3–8 dorsal and 4–9 ventral scale long) on the body and 1–3 (3–4 dorsal and 3–4 ventral scale long) on the tail (Fig. 5). In one specimen (MPEG 17499) red rings are narrower and tetrads can be best observed on the lateral and posterior region of the body.



**FIGURE 5.** “Tricolor in tetrads” pattern in *Atractus latifrons*. Dorsal (A) and ventral (B) views of body; and dorsal (C), ventral (D), and lateral (E) views of head of the specimen (MPEG 17548) from Balbina Power Plant Hydroelectric, municipality of Presidente Figueiredo, state of Amazonas, Brazil. Scale = 10 mm.

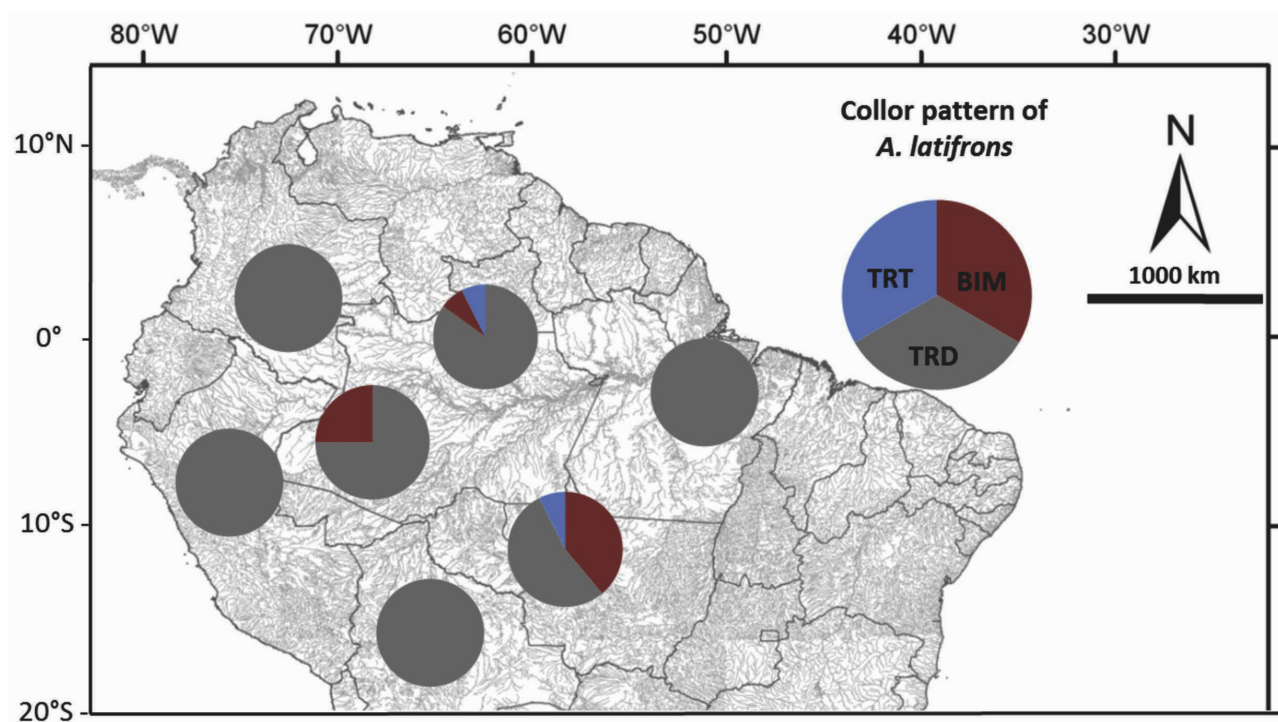
**Undefined Pattern ( $n = 3$ ; total frequency 2.10%).** Color pattern in some individuals were impossible to group in any color pattern described in this study and, therefore, were included under this subheading. We observed one major patterns of variation, as follow was: (1) Body red ( $n = 3$ ): presence of a black cephalic cap ending at the level of parietals, and tail with black rings or bands (FMT 2162, FMT 1249, and MZUSP 8462); simple nuchal collar (FMT 1249 and FMT 2162); red body, no black spots (MZUSP 8462, Fig. 6A) or two black bands (5–6 scales) in the posterior region (FMT 1249, Fig. 6B) or with three dyad arrangements (FMT 2162, Fig. 6C).



**FIGURE 6.** Dorsal and ventral views of the specimens with undefined patterns. Red body, no black spots (MZUSP 8462) (A), red body with two black bands in posterior region (FMT 1249) (B), and red body with three triads arrangements (FMT 2162) (C).

## Geographic frequency of distribution within chromatic patterns

*Atractus latifrons* showed a wide distribution of the three chromatic patterns along the Amazon region. In more specific cases, chromatic patterns co-occurred or dominated in some of the populations studied, being possible to observe the following trend: (1) Chromatic patterns co-occurred: chromatic patterns present in a single location as the municipality of Presidente Figueiredo, Amazonas and the municipality of Cláudia, Mato Grosso; (2) Frequency occurred: chromatic patterns present along all the geographic distribution, as the tricolor in dyads pattern is more frequent and widely distributed, being recorded in all populations studied; and (3) Restrict distribution: pattern present in restricted areas such as the pattern bicolor in monads (showed in populations of the states of Amazonas and Rondônia) and the pattern tricolor in tetrads (showed in populations of the central Amazon) (Fig. 7).

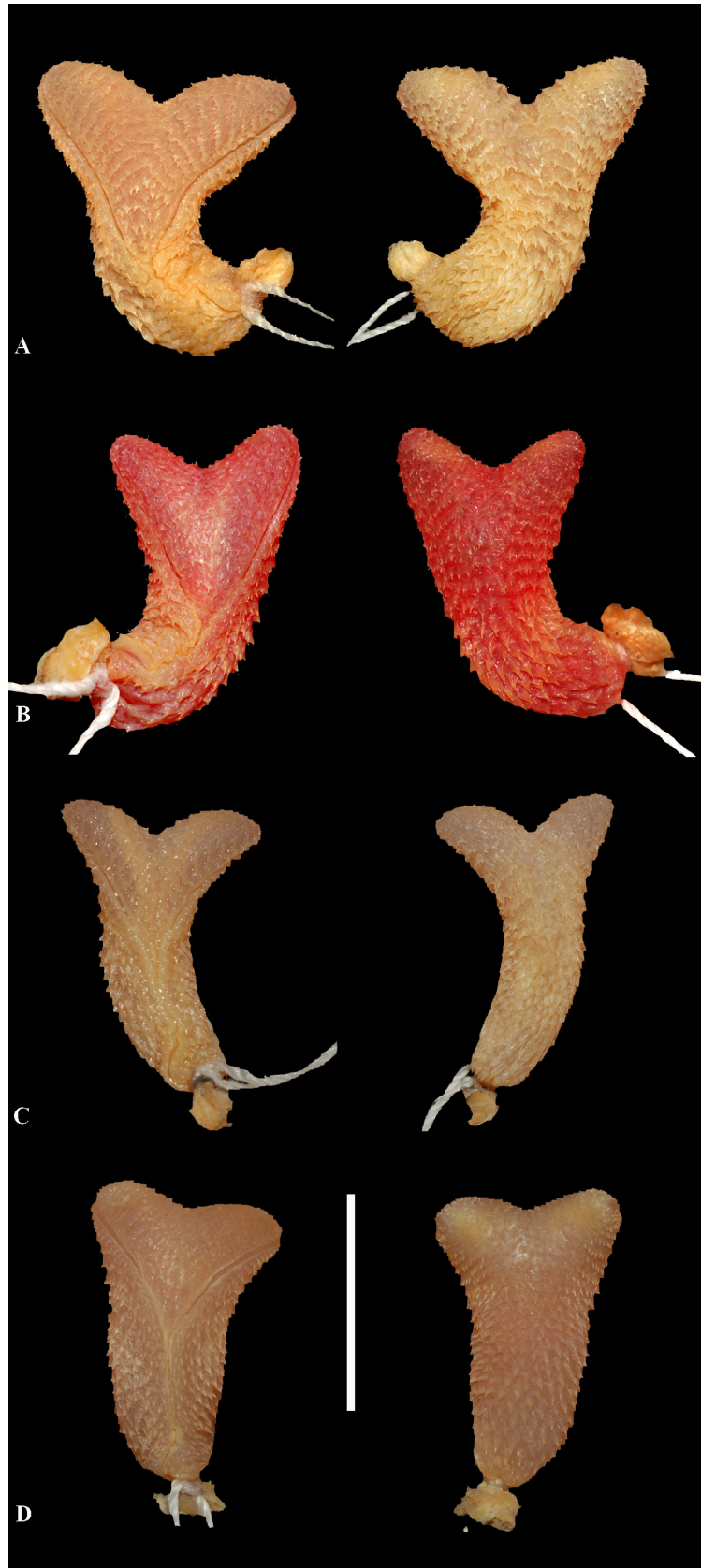


**FIGURE 7.** Geographical frequency distribution of color patterns in *Atractus latifrons*. TRD = tricolor in dyads; TRT = tricolor in tetrads; and BIM = bicolor in monads.

## Hemipenial morphology

The hemipenis observed in all populations of *Atractus latifrons* are bilobed with lobes evident to slightly evident; the sulcus spermaticus bifurcates in the basal ( $n=7$ ), or medial region ( $n=4$ ) of the hemipenial body; the lateral portion of the hemipenial body can be ornamented with basal naked pocket (tree specimens from Amazonas, Rondônia and Mato Grosso) or this structure are slightly evident. The organs showed some little variation, but not significant for this group. This observed variation was not geographically structured and could not be associated with a single chromatic pattern (Fig. 8).

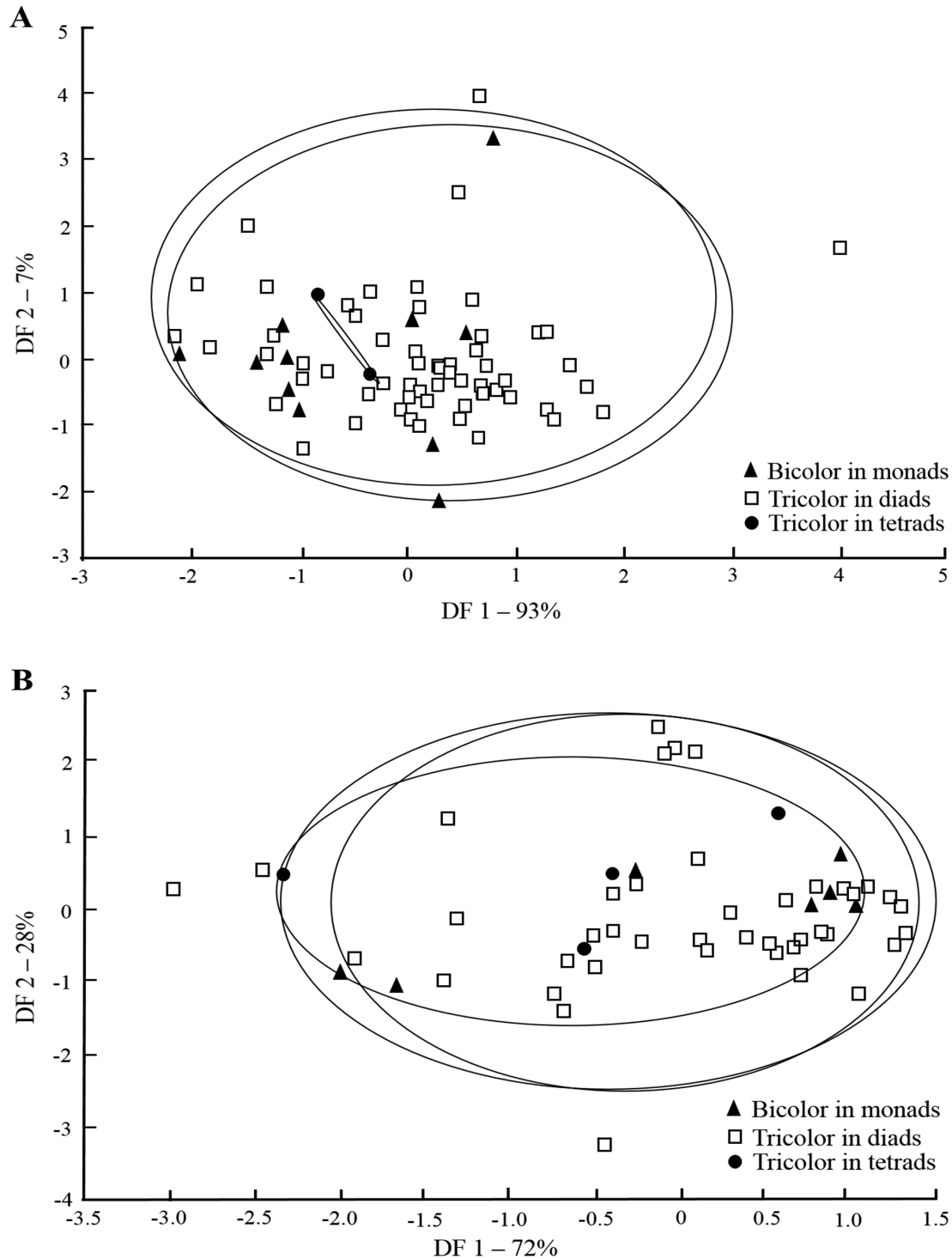




**FIGURE 8.** Sulcate (left) and asulcate (right) views of the hemipenis for all recognized color patterns in *Atractus latifrons*. (A) MPEG 17548, from Balbina Power Plant Hydroelectric, municipality of Presidente Figueiredo, state of Amazonas, Brazil; (B) UFMT 3698, from municipality of Cláudia, state of Mato Grosso, Brazil; (C) MPEG 17564, Balbina Power Plant Hydroelectric, municipality of Presidente Figueiredo, state of Amazonas, Brazil; and (D) MPEG 17837, Samuel Power Plant Hydroelectric, municipality of Porto Velho, Rondônia, Brazil. Scale = 7 mm.

## Morphometric variability

*Atractus latifrons* showed significant sexual dimorphism in the number of ventral scales ( $F = 1.0$ ;  $df = 120$ ;  $p < 0.01$ ;  $n = 142$ ), subcaudal scales ( $F = 2.2$ ;  $df = 120$ ;  $p < 0.01$ ;  $n = 142$ ), and caudal length ( $F = 1.3$ ;  $df = 120$ ;  $p < 0.01$ ;  $n = 142$ ). However, we did not find a significant sexual dimorphism in snout-vent length ( $F = 1.8$ ;  $df = 120$ ;  $p = 0.209$ ;  $n = 142$ ). The principal orthogonal axes from DFA were unable to discriminate the groups based on any of the color patterns of *A. latifrons* (Fig. 9). In synthesis, the observed variation, based on meristic and morphometric variables, was not geographically structured and cannot be associated with a single chromatic pattern.



**FIGURE 9.** Bivariate plots with 95% confidence regions for the first two axes derived from scores of discriminant analyses for males (A) and females (B) of *Atractus latifrons*.

## Taxonomy

Our qualitative and quantitative analyses of morphological characters in *Atractus latifrons* suggest that chromatic variability represents polychromatism within a single species instead of taxonomically distinct units (see discussion). For this reason, we propose an emended diagnosis for *A. latifrons* and redefine its species boundaries accordingly.

### *Atractus latifrons* (Günther, 1868)

*Geophis latifrons* Günther, 1868; Annals Magazine of Natural History 4(1):415.

*Atractus latifrons*—Boulenger, 1894; Catalogue of the Snake in the British Museum 3:303.

*Elaps herthae* Ahl, 1927; Zwei neue Korallenschlangen der Gattung Elaps, *Zoologischer Anzeiger*, 70, 251–252.

*Atractus* sp.—Silva Jr., 1993; Herpetological Natural History 1(1): 54.

**Holotype.** Adult male, BMNH 1946.1.6.52 (formally BMNH 67.9.17.207), collected by Hauswell in the municipality of Pebas (= Pevas, 03°20'S, 71°49'W, ca. 100 m above sea level), department of Loreto, Peru (Figs. 10–11).

**Diagnosis.** *Atractus latifrons* can be distinguished from all its congeners by the following combination of characters: (1) dorsal scale rows 17/17/17; (2) postocular single; (3) loreal short, eventually fused to postnasal; (4) temporals 1+2; (5) supralabials six, third and fourth contacting orbit; (6) infralabials seven ( $n=79$ ), first four contacting chinshields ( $n=80$ ); (7) maxillary teeth five to six, lacking maxillar diastema; (8) gular scale rows three or four; (9) preventrals three or four; (10) ventrals 145–190 in females, 134–178 in males; (11) subcaudals 24–41 in females, 20–42 in males; (12) aposematic coloration, in preservation, with three mainly patterns [bicolor in monads, tricolor in dyads, and tricolor in tetrads] intercalating black and/or white rings separated by red interspaces; (13) ventral coloration, in preservation, similar to dorsum with complete black rings intercalating by red interspaces; (14) body size moderate to large, females reaching 566 mm SVL, males 521 mm SVL; (15) caudal length moderately long in females (10.9–14.6% SVL), moderately long to long in males (13.3–20.0% SVL); (16) hemipenis moderately bilobed, slightly semicapitate, and semicalyculate.

**Comparisons.** Among all congeners, *Atractus latifrons* shares 17 dorsal scale rows at midbody and strict coral color pattern only with *A. badius* and *A. obesus*. *Atractus latifrons* differs from both by having snout acuminate, loreal short, prefrontals large, supralabials six, and maxillary teeth conical, lacking postdiastemal tooth (vs. truncate snout, loreal moderately long to long, prefrontals moderate, postoculars two, usually seven supralabials, and elliptic maxillary teeth with one or two postdiastemal teeth). *Atractus latifrons* differs from *A. elaps*, *A. charitoae*, *A. franciscopaivai*, and *A. poeppigi* by having dorsal scale rows 17 (vs. 15). Additionally, *A. latifrons* differs from *A. franciscopaivai* and *A. poeppigi* by having posterior temporals two, loreal eventually fused to postnasal, and dorsal coloration with black dyads intercalated by white rings and red interspaces (vs. posterior temporal single, loreal never fused to postnasal, and dorsum generally uniform black with rhomboidal blotches covering paraventral region).

**Redescription of the holotype.** Adult male; SVL 227 mm, CL 35.7 mm (15.7% SVL); head length 12.8 mm (5.6% SVL), head width 5.4 mm (42% head length); head height 4.7 mm. Head indistinct from body; head flattened in lateral view and sub-triangular in dorsal view; snout acuminate in lateral view and rounded in dorsal view; rostral large, well visible in dorsal view and rounded in frontal view; internasal as wide as long; internasal suture sinistral with respect to prefrontal suture; prefrontal wider than long; supraocular sub-trapezoidal in dorsal view, about twice longer than wide; frontal sub-pentagonal, longer than wide; parietal about twice longer than wide; nasal divided; nostril almost restricted to prenasal; prenasal and postnasals about twice higher than long; loreal short, about as high as long; loreal contacting second and third supralabials; pupil subelliptical; postocular single, sub-pentagonal, about twice higher than long; temporal 1+2; anterior temporal slightly longer than high; upper posterior temporals fused, about twice longer than high; supralabials six, third and fourth contacting orbit; first two supralabials with equivalent height and smaller than third and fourth supralabials; fifth supralabial higher and sixth longer than remaining supralabials; symphyseal sub-triangular, twice wider than long; first pair of infralabials preventing contact between symphyseal and chin shields; infralabials seven, first four in contact with chin shields; chin shields twice longer than wide; gular scale rows three; preventrals four; ventrals 150; subcaudal 36 in both sides; dorsal scale rows, 17/17/17, smooth and lacking apical pits; caudal spine short, robust, and conical.

Dorsum of head with black cephalic cap extending from rostral to posterior region of parietals, interrupted by a white band covering posterior part of parietals and temporals; lateral view of head black, white band covering fifth to seventh supralabials temporal and occipital scales; first four infralabials and anterior portion of chin shields black; posterior portion of fourth supralabials and two thirds of chin shields white; remaining gular region and preventrals white; body with 10 dyads, comprising 22 black rings (4–9 scales long) separated by 11 tiny white rings (1–2 scales long), broader in ventral view (3–4 scales long); dyads intercalated by 11 red rings (3–7 scales long); tail with two dyads, comprising four black rings (4–6 scales long) separated by two tiny white rings (1–2 scales long), broader in ventral view (3–4 scales long); dyads intercalated by two red rings (5–7 scales long); dorsal and lateral portions of red rings with black pigmentation in the mid–posterior region of each scale (Fig. 10).



**FIGURE 10.** Dorsal (A) and ventral (B) views of body; and dorsal (C), ventral (D), and lateral (E) views of head of the holotype of *Atractus latifrons* (BM 1946.1.6.52). Scale = 10 mm.

**Meristic and morphometric variation.** Largest male 521 mm SVL, 92 mm CL; largest female 566 mm SVL, 83 mm CL; SVL 150–521 ( $\bar{x}$  = 354.6; SD = 82;  $n$  = 75) in males, 150–566 ( $\bar{x}$  = 372; SD = 108;  $n$  = 60) in females; CL 20–92 ( $\bar{x}$  = 60.4; SD = 17.7;  $n$  = 75) in males, 20–83 ( $\bar{x}$  = 50.2; SD = 14.9;  $n$  = 60) in females; ventrals 134–178 ( $\bar{x}$  = 148; SD = 7.2;  $n$  = 75) in males, 145–190 ( $\bar{x}$  = 158.6; SD = 8.8;  $n$  = 60) in females; subcaudals 20–42 ( $\bar{x}$  = 34.8; SD = 3.4;  $n$  = 75) in males, 24–41 ( $\bar{x}$  = 30.9; SD = 4.9) in females; infralabials 7 ( $n$  = 80 sides) or 8 ( $n$  = 8 sides); first infralabials contacting chinshields 3 ( $n$  = 6 sides), 4 ( $n$  = 77 sides) or 5 ( $n$  = 5 sides); gular scale rows 3 ( $n$  = 44 sides) or 4 ( $n$  = 44 sides); preventrals 2–4 ( $\bar{x}$  = 3.5; SD = 0.5;  $n$  = 45); midbody diameter 3.0–10.2 mm ( $\bar{x}$  = 8.4; SD = 1.7;  $n$  = 6); dorsal scale rows in the level of second subcaudal 7–10 ( $\bar{x}$  = 8.4; SD = 0.9;  $n$  = 88 sides); maxillary teeth 5 ( $n$  = 58 sides) or 6 ( $n$  = 13 sides); hemipenis (*in situ*) bifurcates between sixth and ninth and extends at the level of seventh to 11<sup>th</sup> subcaudal ( $n$  = 14). Additional morphometric variation of the *Atractus latifrons* is presented in Table 1.

**TABLE 1.** Morphometric variation of *Atractus latifrons*. Abbreviations are as follow: SD = standard deviation; SVL = snout–vent length; CL = caudal length. Length is given in millimeters.

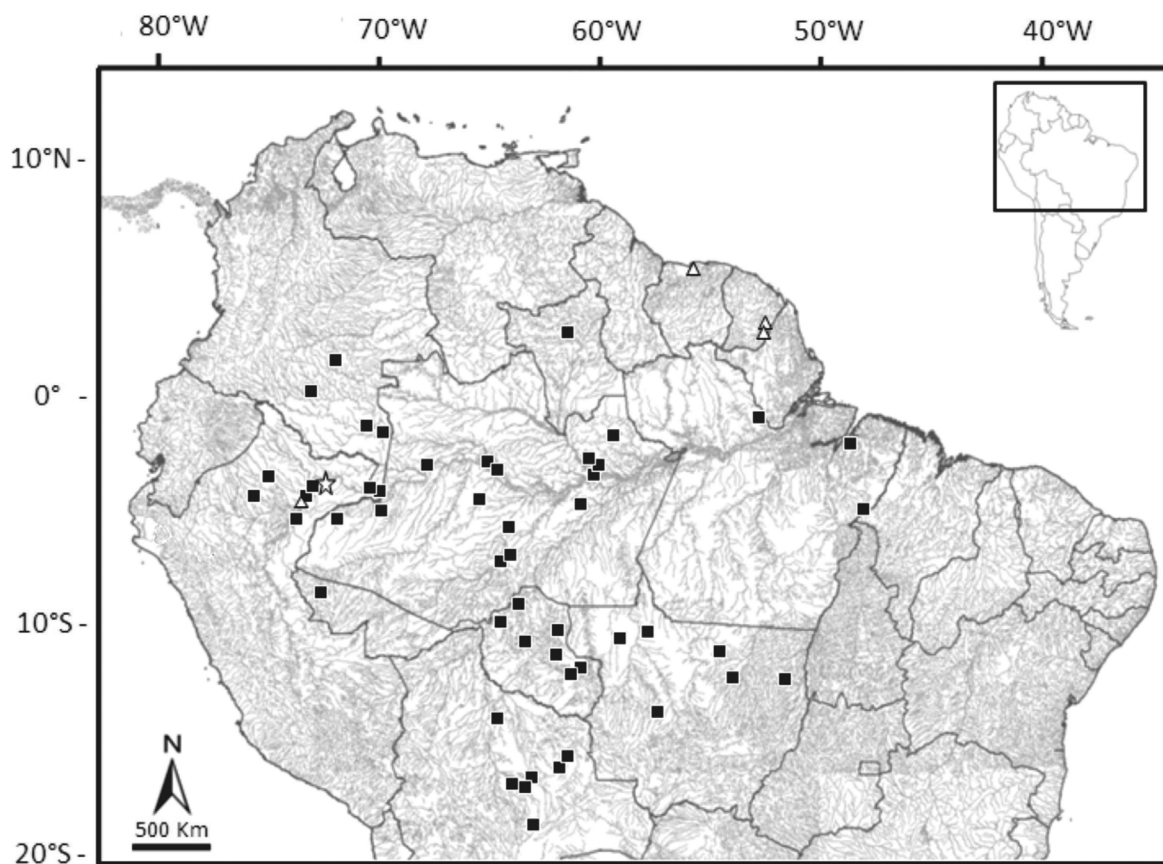
Variables	Males				Females			
	n	Range	Mean	SD	n	Range	Mean	SD
CL/SVL ratio	75	0.06–0.2	0.16	0.02	60	0.08–0.2	0.13	0.02
Ventrals	75	134–178	148	7.2	60	145–190	158.6	8.8
Subcaudals	75	20–42	34.8	3.4	60	24–41	30.9	4.9
SVL	75	150–521	354.6	82	60	150–566	372	108
CL	75	20–92	60.4	17.7	60	20–83	50.2	14.9

.....continued on the next page

**TABLE 1.** (Continued)

Variables	Males				Females			
	n	Range	Mean	SD	n	Range	Mean	SD
Head length	33	5.9–13.6	10.3	1.7	41	7.7–18.6	11.3	2.4
Nostril distance	44	2.8–4.6	3.7	0.5	34	2.5–5.0	3.6	0.6
Head height	46	4.2–9.3	6.2	1.0	40	3.0–11.0	6.1	1.5
Head width	46	3.8–10.2	6.9	1.2	40	5.1–10.1	7.1	1.2
Rostral height	46	1.5–3.4	2.1	0.4	34	1.2–3.0	2.0	0.4
Rostral width	46	2.1–4.5	3.1	0.6	33	1.6–4.2	2.9	0.5
Frontal length	44	2.7–4.4	3.4	0.5	39	2.4–4.9	3.4	0.6
Frontal width	44	3.1–5.0	4.0	0.5	39	2.6–5.1	3.8	0.6
Frontal–eye distance	44	2.3–4.6	3.1	0.5	39	1.2–4.1	3.1	0.5
Parietal length	44	3.8–6.3	5.1	0.6	39	3.2–6.1	4.8	0.8
Parietal width	44	2.8–4.7	3.6	0.4	33	2.5–4.7	3.5	0.6

**Distribution.** *Atractus latifrons* presents a wide distribution in South America east of the Andes, occurring in the Amazonian lowlands of Colombia, Venezuela, French Guiana, Suriname, Brazil, and Peru. This species ranges from Paloemeu River, district of Marowijne in Suriname (03°21'N, 55°26'W), east to Urubichá, department of Santa Cruz in Bolivia (15°23'S, 62°57'W), and southeast to Bela Vista, state of Pará in Brazil (07°33'S, 53°18'W). *Atractus latifrons* occurs on the forest litter of primary Amazon rainforest, as well as secondary forest and cultivation fields (Dixon & Soini 1977, 1986; Hoogmoed 1980; Martins & Oliveira 1993, 1999) from sea level to 300 meters elevation. Given current distribution in the literature, the range of *A. latifrons* is extended here to the state of Roraima in Brazil (Fig. 11).



**FIGURE 11.** Geographical distribution of *Atractus latifrons*. Open triangles correspond to literature records and squares correspond to material examined. Star indicates the type locality. Literature records are from Boulenger (1894), Dixon & Soini (1977), Gasc & Rodrigues (1980), Hoogmoed (1980), and Chippaux (1986).

## Discussion

The hypothesis of rivers as barriers (Wallace 1854; Capparella 1988) has been proposed to explain the pattern of distribution of some snakes and lizards, among other groups of vertebrates, being the Amazon River a barrier for the dispersal of individuals from each species (e.g., *Plica umbra umbra* and *P. u. ochrocollaris*, Avila-Pires 1995; *Atractus zidoki* and *A. hoogmoedi*, Prudente & Passos 2010). However, Passos & Prudente (2012), analyzing the morphological variation of *Atractus torquatus*, noted that, while there is a tendency for populations of the Amazon basin (west of the Negro River and south of the Amazon River) to have low numbers of supralabials, infralabial, and maxillary teeth compared to the population of the Guiana Shield, a large overlap of morphometric characteristics does not allow for the recognition of distinct species. Both qualitative and quantitative analyses of morphological characters of *Atractus latifrons* indicate chromatic variability, such as polychromatism, within a single evolutionary unit. The frequency and distribution of the three color patterns of *A. latifrons* on opposite banks of the Amazon River (Fig. 8) indicate that there is no relationship between polychromatism and major Amazonian rivers. The tricolor triad pattern reported by Savage & Slowinski (1992) for *A. latifrons*, although not observed in this study, is likely to be recorded in additional studies considering the wide range of combinations between black, red, and white rings known in the species.

Polychromatism in snakes has been commonly documented for species displaying aposematic colors (most frequently having a coral color pattern) (Kikuchi & Pfennig 2009; Nascimento 2009). Several authors associate this phenomenon with mimicry of distinct dangerous species (Wickler 1968; Greene & McDiarmid 1981; Pough 1988; Marques & Puerto 1991; Del-Claro & Vasconcelos-Neto 1992; Savage & Slowinski 1992) or with environmental factors (Fraser 1973). Although reports on the polychromatism of *Atractus latifrons* are not new, the lack of any correspondence between color patterns and other morphological complexes of characters evaluated here is, in some way, unexpected, owing to the significant difference between them. In the absence of a phylogenetic signal for distinct color patterns in the species, we must take both environmental factors and mimicry into account as possible explanations for the evolution of the *A. latifrons* coloration. The first hypothesis can be rejected because there are localities (e.g., Presidente Figueiredo Municipality) in which we found all color patterns occurring syntopically (Fig. 8).

The apparent mimicry of distinct species of *Micrurus* by *A. latifrons* may increase the species' fitness regionally (Pfennig *et al.* 2001; Harper & Pfennig 2007; Pfennig *et al.* 2007; Kikuchi & Pfennig 2009), but it is not clear how such phenomenon evolved in a cryptozoic to semi-fossorial group of snakes. Despite of usual association of the polychromatism phenomenon of *A. latifrons* with mimicry, Martins & Oliveira (1999) suggest that those may have evolved as abstract coral snake mimicry (Pough 1988). Such hypothesis does not need *in situ* evolutionary mechanism to explain the polychromatism of the species. Additional studies investigating the correlation between frequencies of mimetic patterns of *A. latifrons* and relative abundance of sympatric species of *Micrurus* may elucidate this question.

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## References

- Ahl, E. (1927) Zwei neue Korallenschlangen der Gattung *Elaps*. *Zoologischer Anzeiger*, 70, 251–252.
- Avila-Pires, T.C.S. (1995) Lizards of the Brazilian Amazonia (Reptilia: Squamata). *Zoologische Verhandlungen*, 299, 1–702.
- Boulenger, G.A. (1894) *Catalogue of the Snakes in the British Museum (Natural History)*, vol. 2. Trustees of the British Museum, London, 466 pp.
- Capparella, A.P. (1988) Genetic variation in neotropical birds: implications for the speciation process. *Acta Congressus Internationalis Ornithologici*, 19, 1658–1673.
- Chippaux, J.P. (1986) *Les Serpents de la Guyane Française*. Orstom, Paris, 165 pp.
- Cunha, O.R. & Nascimento, F.P. (1983) Ofídios da Amazônia XX—As espécies de *Atractus* Wagler, 1828, na Amazônia Oriental e Maranhão. (Ophidia, Colubridae). *Boletim do Museu Paraense Emílio Goeldi, Nova Série, Zoologia*, 123, 1–38.
- Cunha, O.R. & Nascimento, F.P. (1993) Ofídios da Amazônia. As cobras da Região Leste do Pará. *Boletim do Museu Paraense Emílio Goeldi, Nova Série, Zoologia*, 9, 1–191.
- Del-Claro, K. & Vasconcelos-Neto, J. (1992) Os padrões de coloração animal: exemplos na Serra do Japi. In: Morellato, L.P. (Ed.), *História Natural da Serra do Japi. Ecologia e Preservação de uma Área Florestal no Sudeste do Brasil*. Editora da Unicamp/Fapesp, Campinas, pp. 228–308.
- Dixon, J. & Soini, P. (1977) The reptiles of the upper Amazon Basin, Iquitos Region, Peru. *Contributions in Biology and Geology, Milwaukee Public Museum*, 12, 1–91.
- Dixon, J.R. & Soini, P. (1986) *The Reptiles of the Upper Amazon Basin, Iquitos Region, Peru*. Milwaukee Public Museum, Milwaukee, 160 pp.
- Dowling, H.G. (1951) A proposed standard system of counting ventral 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 characteristics. *Zoologica*, 45, 17–27.
- Fraser, D.F. (1973) Variation in the snake *Micrurus diastema*. *Copeia*, 1, 1–17.  
<http://dx.doi.org/10.2307/1442350>
- Gasc, J.P. & Rodrigues, M.T. (1980) Une nouvelle espèce du genre *Atractus* (Colubridae, Serpentes) de la Guyane Française. *Bulletin Muséum national d' Histoire Naturelle*, 4 (1), Section A, 2, 547–557.
- Giraud, A.R. & Scrocchi, G.J. (2000) The genus *Atractus* (Serpentes: Colubridae) in Northeastern Argentina. *Herpetological Journal*, 10, 81–90.
- Greene, H.W. & McDiarmid, R.W. (1981) Coral snake mimicry: does it occur? *Science*, 213, 4513, 1207–1212.  
<http://dx.doi.org/10.1126/science.213.4513.1207>
- Günther, A. (1868) Sixth account of new species of Snakes in the collection of the British Museum. *Annals Magazine of Natural History*, 1, 413–429.  
<http://dx.doi.org/10.1080/00222936808695725>
- Harper, G.R. Jr. & Pfennig, D.W. (2007) Mimicry on the edge: why the mimics vary in resemblance to their model in different parts of their geographical range? *Proceedings of the Royal Society B*, 274, 1955–1961.  
<http://dx.doi.org/10.1098/rspb.2007.0558>
- 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 Verhandlungen*, 175, 1–47.
- Kikuchi, D.W. & Pfennig, D.W. (2009) High model abundance may permit the gradual evolution of the Batesian mimicry: an experimental test. *Proceedings of the Royal Society B*, 1098, 1–8.  
<http://dx.doi.org/10.1098/rspb.2009.2000>
- Manly, B.F. (2000) *Multivariate Statistical Methods. 2<sup>nd</sup> Edition*. Chapman and Hall/CRC, Boca Raton, 224 pp.
- Marques, O.A.V. & Puorto, G. (1991) Padrões cromáticos, distribuição e possível mimetismo em *Erythrolamprus aesculapii* (Serpentes: Colubridae). *Memórias do Instituto Butantan*, 53, 1, 127–134.
- Martins, M. & Oliveira, M.E. (1993) The snakes of the genus *Atractus* Wagler (Reptilia: Squamata: Colubridae) from the Manaus region, central Amazonia, Brazil. *Zoologische. Mededelingen*, 69, 21–40.
- Martins, M. & Oliveira, M.E. (1999) Natural history of snakes in forests of the Manaus region, Central Amazônia, Brazil. *Herpetological Natural History*, 6, 78–150.
- 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.  
[http://dx.doi.org/10.1206/0003-0082\(2003\)391<0001:RSFNSF>2.0.CO;2](http://dx.doi.org/10.1206/0003-0082(2003)391<0001:RSFNSF>2.0.CO;2)
- Nascimento, E.A. (2009) *Estudos de Mimetismo em Lycidae (Insecta: Coleoptera)*. Unpublished Ph.D. Thesis, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo, Ribeirão Preto, 176 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. & Lynch, J.D. (2011) “2010” Revision of *Atractus* from upper and middle Magdalena drainage of Colombia. *Herpetological Monographs*, 24, 149–173.  
<http://dx.doi.org/10.1655/09-041.1>

- Passos, P. & Prudente, A.L.C. (2012) Morphological variation, polymorphism, and taxonomy of the *Atractus torquatus* complex (Serpentes: Dipsadidae). *Zootaxa*, 3407, 1–21.
- 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.  
<http://dx.doi.org/10.1670/08-209.1>
- Passos, P., Dobiey, M. & Venegas, P.J. (2010a). Variation and natural history notes on giant ground snakes, *Atractus gigas* (Serpentes: Dipsadidae). *South American Journal of Herpetology*, 5, 73–82.  
<http://dx.doi.org/10.2994/057.005.0201>
- Passos, P., Echevarría, L.Y. & Venegas, P.J. (2013a) Morphological variation of *Atractus carrioni* (Serpentes: Dipsadidae). *South American Journal of Herpetology*, 8 (2), 109–120.  
<http://dx.doi.org/10.2994/SAJH-D-12-00025.1>
- Passos, P., Fernandes, D.S. & Borges-Nojosa, D.M. (2007) A new species of *Atractus* (Serpentes: Dipsadinae) from a relictual forest in Northeastern Brazil. *Copeia*, 2007, 788–797.  
[http://dx.doi.org/10.1643/0045-8511\(2007\)7\[788:ANSOAS\]2.0.CO;2](http://dx.doi.org/10.1643/0045-8511(2007)7[788:ANSOAS]2.0.CO;2)
- Passos, P., Fuenmayor, G.R. & Barrio-Amorós, C. (2009b) Description of two new species from Venezuela in the highly diverse dipsadine genus *Atractus* (Serpentes: Colubridae). *Amphibia–Reptilia*, 30, 233–243.  
<http://dx.doi.org/10.1163/156853809788201199>
- Passos, P., Lynch, J.D. & Fernandes, R. (2009c) “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., Arredondo, J.C., Fernandes, R. & Lynch, J.D. (2009d) Three new *Atractus* (Serpentes: Dipsadidae) from Andes of Colombia. *Copeia*, 2009, 425–438.  
<http://dx.doi.org/10.1643/CH-08-063>
- Passos, P., Chiesse, A., Torres-Carvajal, O. & Savage, J.M. (2010b) “2009” Testing species boundaries within *Atractus occipitoalbus* complex (Serpentes: Dipsadidae). *Herpetologica*, 65, 384–403.  
<http://dx.doi.org/10.1655/08-024.1>
- Passos, P., Fernandes, R., Bérnills, R.S. & Moura-Leite, J.C. (2010c) Revision of the Atlantic Forest *Atractus* (Reptilia: Serpentes: Dipsadidae). *Zootaxa*, 2364, 1–63.
- 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.
- Passos, P., Cisneros-Heredia, D., Rivera, D.E., Aguilar, C. & Schargel, W.E. (2012) Rediscovery of *Atractus microrhynchus* and reappraisal of the taxonomic status of *A. emersoni* and *A. natans* (Serpentes: Dipsadidae). *Herpetologica*, 68, 375–392.  
<http://dx.doi.org/10.1655/HERPETOLOGICA-D-11-00078.1>
- Passos, P., Kok, P.J.R., Albuquerque, N.R. & Rivas, G.A. (2013b) Groundsnakes of the Lost World: a review of *Atractus* (Serpentes: Dipsadidae) from Pantepui region, northern South America. *Herpetological Monographs*, 27, 52–86.  
<http://dx.doi.org/10.1655/HERPMONOGRAPHS-D-12-00001R2.1>
- Passos, P., Ramos, R.O., Pinna, P.H. & Prudente, A.L.C. (2013c) Morphological variation and affinities of the poorly known snake *Atractus caxiuana* (Serpentes: Dipsadidae). *Zootaxa*, 3745 (1), 35–48.  
<http://dx.doi.org/10.11646/zootaxa.3745.1.3>
- Passos, P., Teixeira-Junior, M., Recoder, R.S., De Sena, M.A., Dal Vechio, F., Pinto, H.B.A., Mendonça, S.H.S.T. & Rodrigues, M.T. (2013d) A new species of *Atractus* (Serpentes: Dipsadidae) from Serra do Cipó, Espinhaço range, Southeastern Brazil, with proposition of a new species group to the genus. *Papéis Avulsos de Zoologia*, 53, 75–85.
- Pesantes, O.S. (1994) A Method for preparing the hemipenes of preserved snakes. *Journal of Herpetology*, 28, 93–95.  
<http://dx.doi.org/10.2307/1564686>
- Peters, J.A. & Orejas-Miranda, B. (1970) Catalogue of the Neotropical Squamata: Part I. Snakes. *Bulletin of the United States National Museum*, 297, 1–347.  
<http://dx.doi.org/10.5479/si.03629236.297.1>
- Pfennig, D.W., Harcombe, W.R. & Pfennig, K.S. (2001) Frequency-dependent Batesian mimicry. *Nature*, 410, 323.  
<http://dx.doi.org/10.1038/35066628>
- Pfennig, D.W., George Jr., R.H., Brumo, A.F., Harcombe, W.R. & Pfennig, K.S. (2007) Population differences in predation on Batesian mimics in allopatry with their model: selection against mimic is strongest when day are common. *Behavioural Ecology and Sociobiology*, 61, 505–511.  
<http://dx.doi.org/10.1007/s00265-006-0278-x>
- Pough, F.H. (1988) Mimicry of vertebrates: are the rules different? In: Brower, L.P. (Ed.), *Mimicry and the Evolutionary Process*. Chicago University Press, Chicago, pp. 67–102.
- Prudente, A.L.C. & Passos, P. (2008) New species of *Atractus* Wagler (Serpentes: Dipsadinae) from Guyana Plateau in Northern Brazil. *Journal of Herpetology*, 42, 723–732.  
<http://dx.doi.org/10.1670/07-115R3.1>
- Prudente, A.L.C. & Passos, P. (2010) New cryptic species of *Atractus* (Serpentes: Dipsadidae) from Brazilian Amazonia. *Copeia*, 2010, 397–404.  
<http://dx.doi.org/10.1643/CH-08-193>
- Savage, J. (1960) A Revision of the Ecuadorian snakes of the colubrid genus *Atractus*. *Museum of Zoology of the University of Michigan*, 112, 1–86.



- Savage, J.M. & Slowinski, J.B. (1992) The colouration of the venomous coral snakes (Family Elapidae) and their mimics (families Aniliidae and Colubridae). *Biological Journal of the Linnean Society*, 45, 235–254.  
<http://dx.doi.org/10.1111/j.1095-8312.1992.tb00642.x>
- Schargel, W.E., Lamar, W.W., Passos, P., Valencia, J.H., Cisneros-Heredia, D.F. & Campbell, J.A. (2013) A new giant *Atractus* (Serpentes: Dipsadidae) from Ecuador, with notes on other large Amazonian congeners. *Zootaxa*, 3721 (5), 455–474.  
<http://dx.doi.org/10.11646/zootaxa.3721.5.2>
- Silva, N.J. Jr. (1993) The snakes from Samuel hydroelectric power plant and vicinity, Rondônia, Brazil. *Herpetological Natural History*, 1, 37–86.
- Silva, J.J.H. (2004) Las Serpientes del género *Atractus* Wagler, 1828 (Colubridae, Xenodontinae) en la Amazonía Colombiana. *Revista de la Academia Colombiana de Ciencias Fisicas, Exactas y Naturales*, 28, 409–446.
- StatSoft (1998) *Statistica for Windows version 5.1*. Tulsa.
- Wallace, A.R. (1854) On the monkeys of the Amazon. *Annals and Magazine of Natural History*, 14 (84), 451–454.  
<http://dx.doi.org/10.1080/037454809494374>
- Wickler, W. (1968) *Mimicry in Plants and Animals*. McGraw–Hill, New York, 256 pp.
- Zaher, H. (1999) Hemipenial morphology of the South American xenodontine snakes, with a proposal for a monophyletic *Xenodontinae* and a reappraisal of colubroid hemipenes. *Bulletin of the American Museum of Natural History*, 240, 1–168.
- Zaher, H. & Prudente, A.L.C. (2003) Hemipenes of *Siphlophis* (Serpentes, Xenodontinae) and techniques of hemipenial preparation in snakes: a response to Dowling. *Herpetological Review*, 34, 302–307.
- Zar, J.H. (1999) *Biostatistical Analysis*. Prentice–Hall, Inc., New Jersey, 123 pp.

## APPENDIX 1. Specimens examined.

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

***Atractus latifrons* (n = 150).** **BOLIVIA:** BENI: *Ovillas del San Martin River*: Blanco y Negro River: (MNKR 595). SANTA CRUZ: *Guarayos*: Urubichá: (MNKR 3436–39), San Martin River: (MNKR 505); *Nuflo de Chávez*: Oquinquia: San Martin River: (MNKR 1021); *Velasco*: Cruce Moira: Piso Firme: (MNKR 520), Serrania Huauchaca: (MNKR 218). **BRASIL:** without specific locality: (IBSP 20315, MZUSP 3156, 5387, 15580). ACRE: *Porto Walter*: (MZUSP 7353); AMAZONAS: without specific locality: (FMT 851, 943, 946, 1123, 1249, 1339, 1341, 1876, 2114, 2162, 2309, 2922); *Benjamin Constant*: (MNRJ 729–32, 1289, 1517–20, 1522); *Estirão do Equador*: (MPEG 161); *Canutama*: Projeto GEOMA: (INPA 23367); *Presidente Figueiredo*: Balbina Plant Hydroelectric: (MPEG 17395, 17459–60, 17499\*, 17506, 17531, 17548\*, 17556–58, 17562, 17564\*, UFC 1367); *Porto Urucu*: (MPEG 19261); *Serrinha*: Jurupá River: (MZUSP 6594); Purus River: (MNRJ 633); *Carauari*: Comunidade Nova Esperança: (INPA 14043); *Manaus*: Reserva INPA–WWF: (MNRJ 726–28, MZUSP 8658, 8462, 9500); *Mundurucu*: Manacapuru River: (ZMB 30547 holotype of *Elaps hertae*); BR–174 road: Km 80: (MZUSP 8428), KM 15: (MZUSP 7835). PARÁ: *Belém*: (MPEG 256); *Dom Eliseu*: (MPEG 10820); *Marabá*: (MPEG 17039); *Monte Dourado*: (MPEG 17745). RONDÔNIA: *Campo Novo*: Upper River Candeias: (MZUSP 5927); *Nova Brasília*: (MZUSP 8519); *Porto Velho*: Samuel Hydroelectric Plant: (IBSP 40875, 52654, MPEG 17831, 17837\*, 17842, 17901–02, 17904, 17920–21, 17959, 17979, 17990, 18008, 18140, CHUFC 1430–32, CEPB 1703–06, 1708–09, 3077, 3319), Jirau Hydroelectric Plant: (MPEG 23962–64); *Espigão do Oeste*: (MPEG 21059, 21060\*, 21061); Parque Estadual Guajará Mirim: (MPEG 20363); Ribeirão Riachuelo: Afluente Ji–Paraná: (MZUSP 5918). MATO GROSSO: *Alta Floresta*: (MZUSP 10483); *Aripuanã*: (MZUSP 11127); *Campos Novos dos Parecis*: (UFMT 4571, 4572, 4579, 7522); *Cláudia*: (UFMT 3693, 94\*–98\*, 99, 3700–06); *Nova Bandeirantes*: (UFMT 1750); RORAIMA: PARNA Viruá: (INPA 25707); No Material Origin: (ZMB 47765). **COLOMBIA:** AMAZONAS: *La Pedrera*: (MLS 210); Caqueta River: (IAvH 1483); *Leticia*: Los Lagos: (MPEG 18203–05); *Mirití–Paraná*: (MZUSP 6115); *Puerto Nariño*: (MLS 1319–21); Icara–Paraná River: (IAvH 945). CAQUETA: *Caparú*: (ICN 8163). VAUPÉS: *Chiribiquete*: Parque Natural Nacional Cueva de los Guacharos: Corregimiento Miraflores: (IAvH 12, 4264). **PERU:** LORETO: *Pebas*: (BMNH 1946.1.6.52 holotype, MNRJ 2977, 2979, 2981); *Maynas*: (MHNSM 2250, 2292, 2590, 2616); *Urarinas*: (MHNSM 27441); *Tromperos*: (MHNSM 27396); *Requema*: (MHNSM 2884).