



Morphological variation and affinities of the poorly known snake *Atractus caxiuana* (Serpentes: Dipsadidae)

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Abstract

Atractus caxiuana was recently described based on three specimens (two males and one female) from the Floresta Nacional de Caxiuana, municipality of Melgaço, state of Pará, in the eastern portion of the Brazilian Amazon. Apart from the type series, no additional samples are known for the species. In this study, we report new specimens of *A. caxiuana*, providing new morphological data (meristic, morphometric, pholidosis, colour pattern, and hemipenis) and localities. We relate the variability displayed by the characters analyzed to sexual dimorphism, geographic variation, and ontogeny. Additionally, we provide detailed comparisons with *A. collaris* and putative sister species, and propose a new species group to accommodate this distinct and possible monophyletic assemblage.

Key words: Hemipenial morphology; sexual, ontogenetic and geographic variation; *Atractus collaris* species group

Resumo

Atractus caxiuana foi descrita recentemente a partir de três exemplares (dois machos e uma fêmea) oriundos da Floresta Nacional de Caxiuana, município de Melgaço, estado do Pará, na porção oriental da Amazônia brasileira. Além da série-tipo, nenhuma amostra adicional é conhecida para a espécie. Neste estudo reportamos novos espécimes de *A. caxiuana*, fornecendo novos dados morfológicos (merísticos, morfométricos, foliose, padrão de coloração e hemipênis) e localidades. Nós relacionamos a variabilidade observada nestes caracteres analisados com fenômenos de variação sexual, ontogenética e geográfica. Adicionalmente, fornecemos comparações detalhadas deste táxon com *A. collaris* e possíveis espécies afins e propomos um novo grupo de espécies para acomodar esta assembleia distinta e possivelmente monofilética.

Palavras-chave: Morfologia hemipeniana; variação sexual, ontogenética e geográfica; grupo de espécies afins a *Atractus collaris*

Introduction

The dipsadid snake genus *Atractus* Wagler, 1828 comprises small to moderate-sized snakes, which have secretive lifestyles (semi-fossorial or cryptozoic) and feed on earthworms, arthropods and molluscs (Martins & Oliveira 1999; Cisneros-Heredia 2005a; Balestrin *et al.* 2007; Oliveira *et al.* 2008). The genus is widely distributed in the Neotropical region, occurring from Panama to Argentina, primarily on mainland portions from sea level to about 4,000 meters elevation, along most of South American biomes (Passos *et al.* 2010c). *Atractus* is a highly speciose genus closely related to *Geophis* Wagler, 1830 (Savage 1960; Downs 1967; Graziotin *et al.* 2012) that comprises about 140 valid species, most of them known only from their type specimens (Passos & Fernandes 2008; Prudente & Passos 2008; Passos *et al.* 2009a,b,c,d,e; Passos & Lynch 2011; Passos *et al.* 2013b).

Although the genus is often well represented in relevant New World herpetological collections, the taxonomic

status of many species of *Atractus* is currently in a state of flux, resulting in a high number of specimens misidentified in collection (Passos *et al.* 2005; Passos *et al.* 2007a,b; Passos & Arredondo 2009; Passos *et al.* 2009a,b,c,d,e). Additionally, the large number of species that are known only from type-series hampers any attempt to assess intraspecific variability with confidence (Passos *et al.* 2009c; Passos *et al.* 2010a,c; Passos & Lynch 2011). As a result, many of the recently described taxa are, in fact, junior synonyms of poorly known, but valid species (Passos *et al.* 2009a; Passos *et al.* 2010c; Passos *et al.* 2012; Passos & Prudente 2012).

More recently, a number of contributions defined more accurately the specific boundaries within several species complexes in the genus, revealing relatively widespread distributions of highly variable species instead of high levels of endemism in the genus (Passos *et al.* 2009a,b; Passos *et al.* 2012; Passos & Prudente 2012; Passos *et al.* in press). Consequently, we consider that any taxonomic study within *Atractus* should rely heavily on large, geographically representative samples and thorough comparisons with related species and their type material (cf. Passos 2008). Within such a taxonomically complex scenario, Prudente & Santos-Costa (2006) described *Atractus caxiuana* based on three specimens from Floresta Nacional de Caxiuana, municipality of Melgaço, state of Pará, in the eastern portion of the Brazilian Amazon. To date the species is still known only from its type series.

Here, we report additional information on the morphological variation (meristic, morphometric, pholidosis, colour pattern, and hemipenis) of the species based on four specimens of *A. caxiuana* obtained in the western and eastern Amazonian portions of Brazil and Colombia, respectively. We also provide detailed comparisons with *A. collaris* and other putatively related species, suggesting a new species group to accommodate *A. caxiuana* and its related species.

Materials and methods

We examined specimens housed in the following institutions: National Museum of Natural History, Smithsonian Institution, Washington (USNM); Museo de Historia Natural, Universidad de La Salle, Bogotá (MLS); Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá (ICN); Museo de Historia Natural, Escuela Politécnica Nacional, Quito (MEPN); Museo de Zoología, Pontificia Universidad Católica del Ecuador, Quito (QCAZ); Instituto Butantan, São Paulo (IBSP); Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro (MNRJ); Museu Paraense Emílio Goeldi, Belém (MPEG); Museu de Zoologia da Universidade de São Paulo, São Paulo (MZUSP); Museo de Historia Natural, Universidad Mayor de San Marcos, Lima (MHNSM). Specimens examined are listed in the Appendix I.

Terminology for cephalic shields in *Atractus* followed Savage (1960). Method for counting ventral scales followed Dowling (1951). Nomenclature regarding the loreal condition followed Passos *et al.* (2007b). Nomenclature for measurements and other discrete characters followed Passos *et al.* (2009e). Techniques for hemipenial preparation followed Pesantes (1994) and Zaher & Prudente (2003). Terminology for hemipenial description followed Dowling and Savage (1960) and Zaher (1999). We determined sex by subcaudal incision. Measurements were taken under a stereoscope with an analogical caliper to the nearest 0.1 mm, except for snout-vent (SVL) and caudal lengths (CL), which were taken with a flexible ruler to the nearest 1 mm.

Coordinates of localities were obtained in museum databases and geographical gazetteers (IBGE 2011, Paynter 1993, 1997; Paynter & Traylor 1991; Stephens & Traylor 1983, 1985). When possible, we corrected the coordinates obtained from literature with the aid of the software *Google Earth 6.0*.

Results

Atractus caxiuana Prudente & Santos-Costa, 2006; *Zootaxa* 1285:22.

Figs. 1–3, Tab. 1

Holotype. An adult male, MPEG 19964, from Estação Ecológica Ferreira Penna, Floresta Nacional de Caxiuana (01°42'S, 51°32'W; ca. sea level), municipality of Melgaço, state of Pará, Brazil.

Paratypes. Two specimens from the same locality as the holotype. An adult female, MPEG 19657, collected by J. Bernardi at September 1999, and a poorly preserved adult male, MPEG 20128, collected by M.C. Santos-Costa at 27 January 2002.

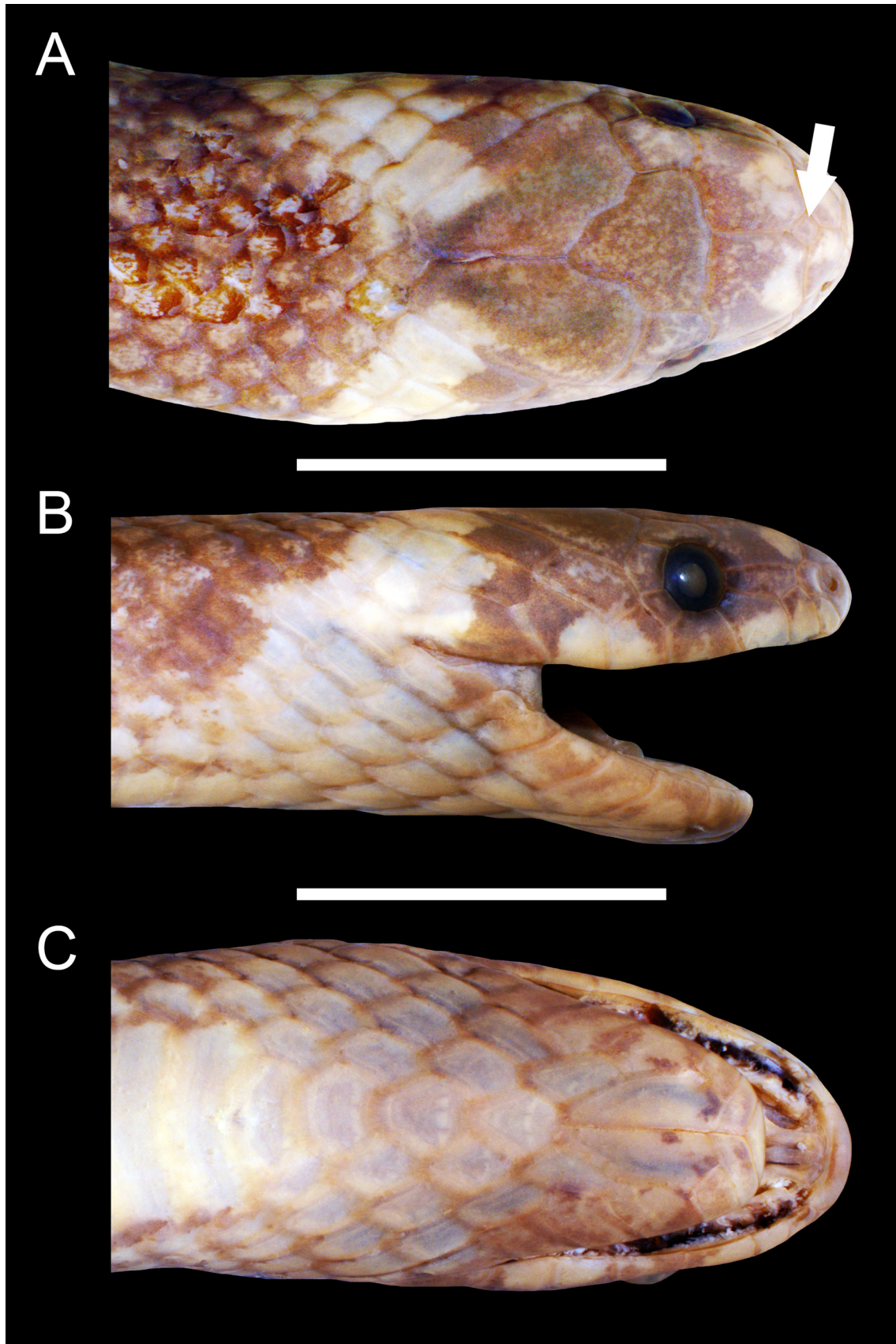


FIGURE 1. Dorsal (A), lateral (B) and ventral (C) views of the head of *Atractus caxiuana* from Vila Cachoeira do Samuel, municipality of Porto Velho, state of Rondônia, Brazil (MNRJ 3026). The arrow indicates the azygous scale located between the internasal shields. Scale bar = 5 mm.

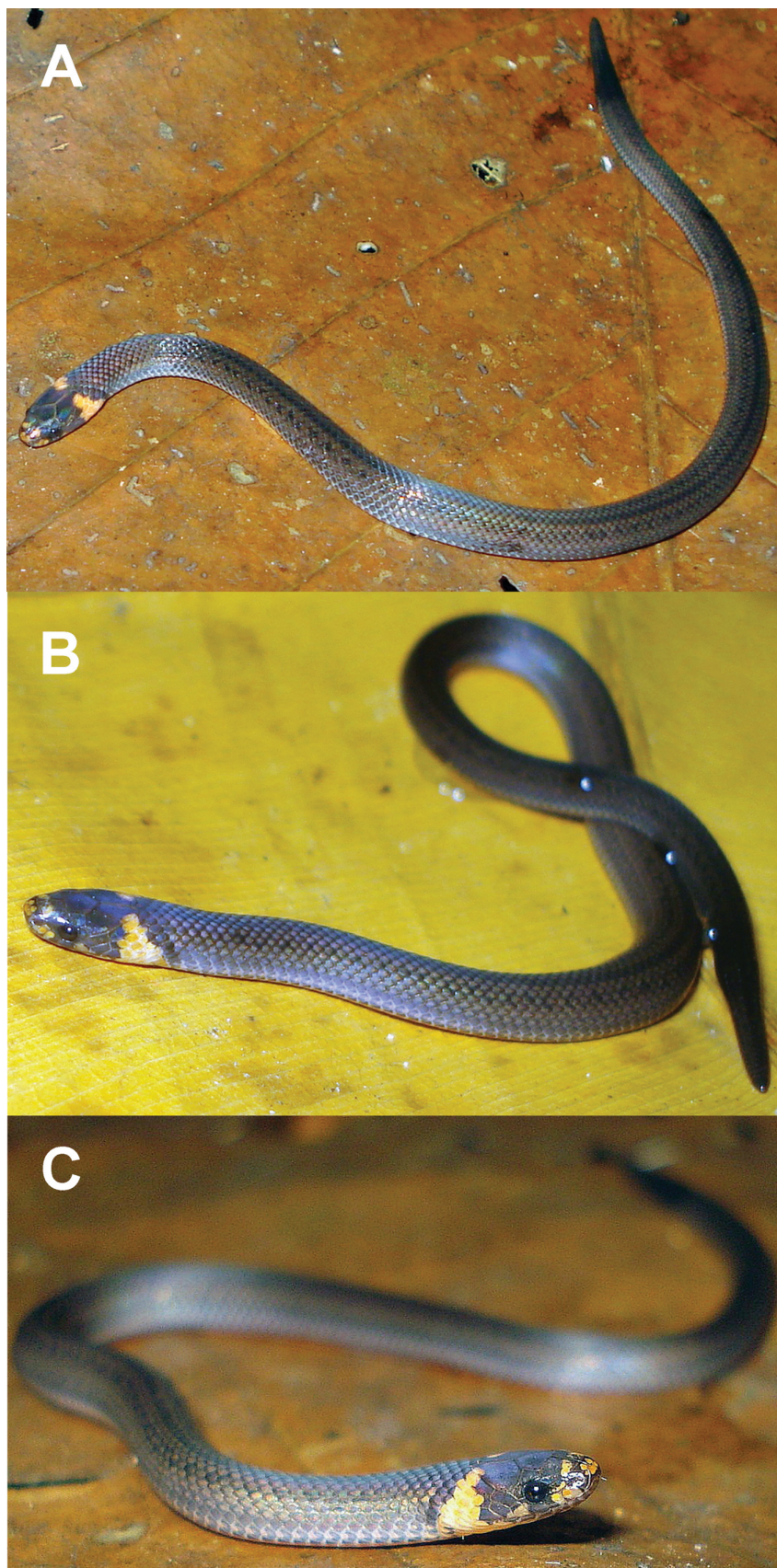


FIGURE 2. Dorsal (A), dorsolateral (B) and lateral (C) views of a juvenile specimen of *Atractus caxiuana* in life from the right bank of the Rio Madeira, municipality of Porto Velho, state of Rondônia, Brazil (MZUSP 18892). Photos by Renato Gaiga.



FIGURE 3. Dorsal (A) and ventral (B) views of an adult preserved specimen of *Atractus caxiuana* from Taraira, department of Vaupés, Colombia (ICN 10114). Scale bar = 10 mm.

Diagnosis. *Atractus caxiuana* is distinguished from all other congeners by the following combination of characters: loreal contacting the internasal (but see below); 17/17/17 dorsal scale rows with paired apical pits in both sexes and supra-anal tubercles present only in males; one or two postoculars; loreal moderately long; temporals 1+2; seven supralabials, third and fourth contacting orbit; seven infralabials, first three contacting chinshields; five or six maxillary teeth; four gular scale rows; four preventrals; 171–184 ventrals in females, 160–162 in males; 18–24 subcaudals in females, 25–30 in males; dorsum mostly dark brown, except for dispersed beige blotches on snout, a creamy incomplete collar covering the parietal, occipital and temporal regions of the head, and two pale brown longitudinal stripes covering the centre of first two dorsal scale rows of the body; belly creamy with lateral portion of the ventral scales dark brown, forming paraventral stripes; small body size, females reaching 265 mm SVL, males 261 mm SVL; small tail length in females (9.0–9.2% SVL), moderately long in males (9.2–13.2% SVL); hemipenis slightly bilobed, non-capitate and non-calyculate.

TABLE 1. Summary of quantitative morphological variation for the known specimens of *Atractus caxiuana*. We use “|” when the counts were different from the right to the left sides, otherwise this character is represented by a single value. The measures and scores marked with - were not taken due to the poor state of preservation of the specimen.

Variables	MPEG 19964	MPEG 19657	MPEG 20128	MNRJ 3026	ICN 10114	ICN 10115	MZUSP 18892
Sex	Male	Female	Male	Male	Male	Female	Female
Tail dorsal rows	9	9	-	9	9 8	8 9	8
Ventral scales	162	171	-	162	160	184	171
Subcaudal scales	29 30	24	-	27	24 25	24 25	20
Postocular scales	2 2	2 2	1 1	2 2	2 2	2 2	2 2
SVL (mm)	261	265	-	208	165	223	101
CL (mm)	24	24	-	24	21	21	8.5
Maxillary teeth	5	5	5	5	-	6	5

Comparisons. *Atractus caxiuana* is distinguished from all other congeners by usually having the internasal shields in contact with loreal scales. Occasionally, when the postnasal scale prevents this contact, there is an azygous scale between internasals modifying the orientation of the scales (Fig. 1) or a slight separation between the internasal and loreal by increasing the height of the postnasal (Fig. 2C). Nonetheless, the lateral expansion and relative width of the internasals (with respect to the prefrontal shields) remains an autapomorphic character state of this species (see discussion). Besides the relative widening of the internasals, *A. caxiuana* shares a unique suite of morphological characters (e.g., presence of apical pits and supra-anal tubercles) only with *A. collaris* and allied species (see discussion). *Atractus caxiuana* differs from all of them (except *A. surucucu*) in having an uniformly dark brown dorsum in adults and dark brown ventral side of the tail in juvenile and adult specimens. *Atractus caxiuana* differs from *A. surucucu* by having 171–184 ventral in females (vs. 200–207 in *A. surucucu*, known only from female specimens).

Description. Head twice as long as wide, slightly arched in lateral view, round in dorsal view; cervical constriction barely distinct; snout truncate in lateral view, round in dorsal view; rostral subtriangular in frontal view, wider than high, barely visible in dorsal view; internasal about twice as wide as long; posterior portion of internasal usually contacting loreal; occasionally postnasal preventing internasal/loreal contact; suture dextral or sinister with respect to prefrontal midline suture; prefrontal as wide as long; supraocular subtrapezoidal, slightly longer than wide; frontal subtriangular, as long as wide; parietal twice as long as wide; nasal completely divided; nostril situated between prenasal and postnasal; prenasal twice as high as postnasal; postnasal slightly higher than long, as long as prenasal; loreal moderately long, contacting second and third supralabials ventrally and internasal anteriorly; pupil round; usually two postoculars slightly higher than long; upper postocular generally higher and longer than lower postocular; temporals 1+2; first temporal three times as long as high; upper posterior temporals fused, about four times as long as wide; seven supralabials, third and fourth contacting orbit; first supralabial approximately half the height of second; second and third supralabials with similar height; second supralabial higher than seventh and longer than remaining supralabials; symphyisial semi-circular, three or four times broader than long; usually seven infralabials, first three in contact with chinshields; first pair of infralabials in contact behind symphyisial, preventing symphyisial/chinshields contact; chinshields about four times longer than wide; four gular scale rows; four preventrals; 17/17/17 dorsal scale rows with paired apical pits in both sexes and supra-anal

tubercles only in males; dorsal scales lacking keels; caudal spine long, conical and acuminate. Maxillary arch straight in dorsal view, with four to five prediastemal teeth and one postdiastemal tooth; prediastemal teeth decreasing in size and increasing the curvature angle posteriorly (approximately 40°); prediastemal teeth well spaced, angular in cross section, robust on their bases and narrower at apices; maxillary diastema moderately long; lateral process of maxillary bone well developed and projected posteriorly (Fig. 1).



FIGURE 4. Sulcate (A) and asulcate (B) sides of the hemipenis of *Atractus caxiuana* from Vila Cachoeira do Samuel, municipality of Porto Velho, state of Rondônia, Brazil (MNRJ 3026). Scale bar = 1 mm.

Juvenile coloration in life. Dorsum of head dark brown; snout region with creamish yellow blotches above internasals, prefrontals, and second and third supralabials; a beige blotch covering the fifth and eventually sixth supralabials; incomplete creamish yellow collar covering the temporal and occipital regions; dorsum of body,

above second dorsal scale row, brown with a barely defined dark brown vertebral line (one scale wide) and paravertebral small blotches (half scale wide) on the sixth row of scales; first two rows of dorsal scales brownish gray, with the first series having posterior region cream; gular region and venter uniformly cream; ventral side of tail dark brown (Fig. 2).

Adult coloration in preservative. Dorsum of head uniformly dark brown, except for snout region (internasals and prefrontals) with disperse creamy or beige (in melanistic specimens) blotches, and incomplete creamy or beige collar on neck (covering occipitals, temporals and latero-posterior region of parietals); nuchal collar (two scales long) interrupted near interparietal suture; cephalic-cap dark brown, except for creamy or beige areas covering ventral portions of second, third, fifth and sixth supralabials; seventh supralabial with posterior region creamy; infralabials and anterior third of chinshields dark brown; mid-posterior area of chinshields, gulars and preventrals creamish yellow; venter uniformly creamish yellow, except occasionally for a barely defined brown median line; lateral edge of ventral scales dark brown, forming two conspicuous paraventral lines; undersides of tail uniformly dark brown or black; dorsum of body dark brown, except for two pale brown longitudinal stripes, covering the centre of first two dorsal scale rows (Fig. 3).

Hemipenial morphology (everted organ $N = 2$). Retracted organ (MNRJ 3026) bifurcates and extends to the level of eighth subcaudal. Fully everted and almost maximally expanded hemipenis (Fig. 4) rendered a slightly bilobed, non-capitate and non-calyculate organ; lobes distinct and restricted to distal portion of hemipenial body; lobes conical, centrifugally oriented and uniformly scattered with moderate alary spines with a broad base, except for the tips of the lobes, which are covered by papillae; sulcus spermaticus divides at about half of hemipenial body; sulcus spermaticus branches with centrolinear orientation, reaching apices of lobes; margins of sulcus spermaticus stout and expanded laterally along sulcus spermaticus extension; sulcus spermaticus bordered by spinules from basal region to the tips of the organ; hemipenial body uniformly scattered with moderate hooked spines; basal naked pocket located at the right side and extending to basal region of hemipenial body; proximal region of hemipenis with longitudinal plicae and dispersed small spines. A further analysis on the hemipenis of the holotype (MPEG 19964; Fig. 3 in Prudente & Santos-Costa 2006), indicates that its lobes are not completely everted, presenting nearly flattened tips and an apparent asymmetry (the right lobe is slightly longer and wider than the left one). This organ also seems to be only partially expanded, mainly at the lobular crotch and at the bases of the lobes in its sulcate side, which hampers the observation of the spinules located at this region.

Variation. Largest male 261 mm SVL, 24 mm CL, largest female 265 mm SVL, 24 mm CL; tail 9.2–13.2% SVL ($\bar{x} = 11.1$; $SD = 2.7$; $n = 3$) in males, 8.4–9.2% SVL ($\bar{x} = 8.9$; $SD = 0.4$; $n = 3$) in females; 160–162 ($\bar{x} = 161.3$; $SD = 1.5$; $n = 3$) ventrals in males, 171–184 ($\bar{x} = 175.3$; $SD = 7.5$; $n = 3$) in females; 25–30 ($\bar{x} = 27$; $SD = 2.5$; $n = 3$) subcaudals in males, 18–24 ($\bar{x} = 20.7$; $SD = 3.0$; $n = 3$) in females; 1 ($n = 3$ sides) or 2 ($n = 11$ sides) postoculars; 8 ($n = 7$) or 9 ($n = 6$) dorsal scales rows around tail in the level of second subcaudal; 5 ($n = 9$ sides) or 6 ($n = 2$ sides) maxillary teeth; 3.3–5.0 mm body diameter. Both paratypes have dextral internasal suture with respect to prefrontal suture, while the holotype and additional specimens reported here present sinistral orientation of the internasal suture with respect to prefrontal one. The paratype MPEG 19964 has first pair of infralabials shorter, allowing a slightly contact between symphyisial and chinshields. The specimen MNRJ 3026 has an azygous scale located between internasals, promoting the re-orientation of postnasal that prevents contact between internasal and loreal (Fig. 1). The specimen MZUSP 18892 has a post-nasal scale barely preventing the contact between loreal and internasals, lacking the azygous internasal (Fig. 2).

Distribution. *Atractus caxiuana* is distributed from Taraira (00°30'N, 69°40'W), department of Vaupés, Colombia; southeast to Melgaço (01°42'S, 51°32'W), state of Pará, Brazil. *Atractus caxiuana* occurs in rainforest environments between 0–200 m above sea level. The species' range of distribution extends more than 2,000 Km (airline) with the new records presented here, including areas above Rio Amazonas in the east of Colombian Amazonia (Fig. 5).

Remarks. With respect to the possible ontogenetic change of coloration in *Atractus caxiuana* (Figs. 2–3), although the color pattern of MZUSP 18892 (juvenile) is still evident after preservation, this specimen was recently collected (2010), while adult specimens (which do not present the paravertebral blotches) were preserved a long time ago (between 1940–1980). Therefore, we cannot establish with certainty if only immature specimens display a barely defined vertebral line and paravertebral blotches or if these features are also present in adult specimens.

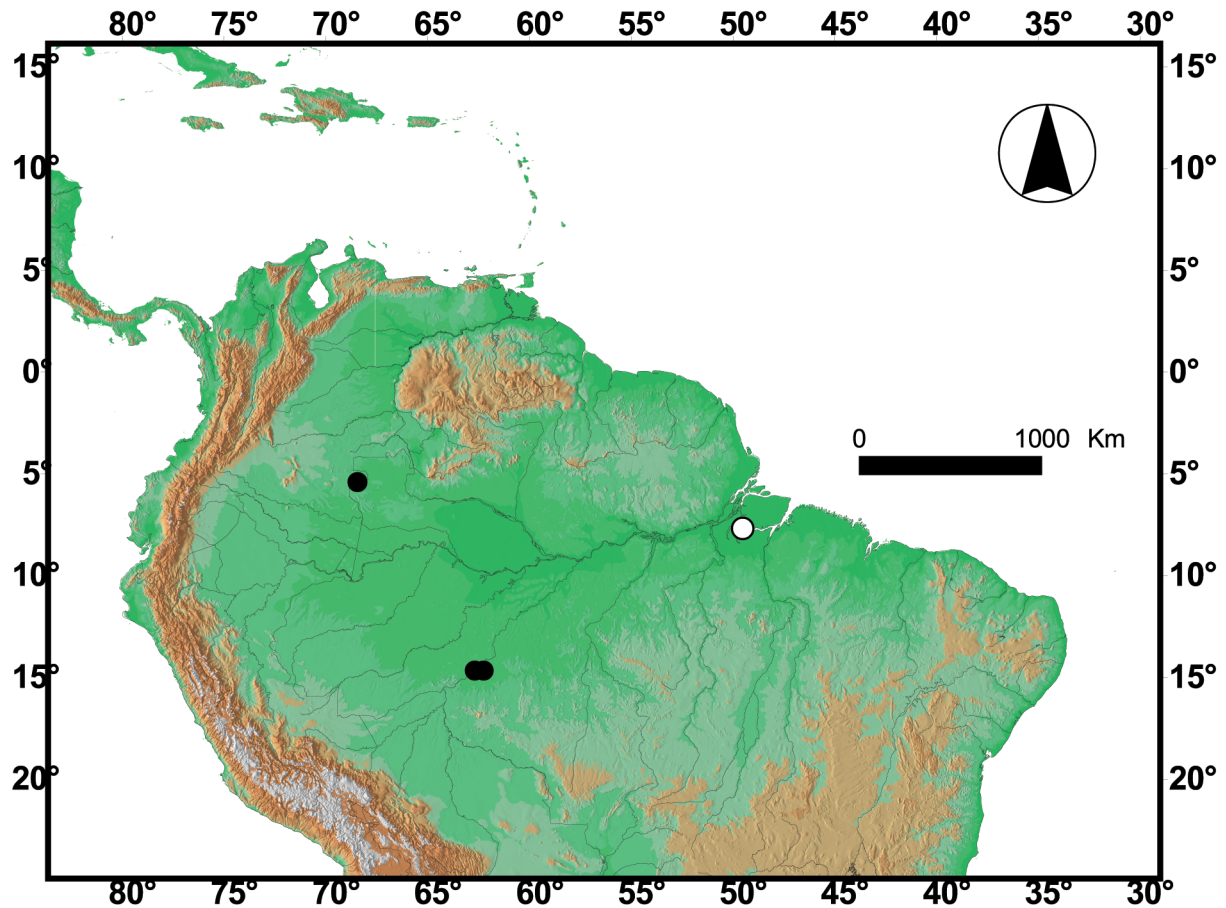


FIGURE 5. Geographical distribution known for *Atractus caxiuana*. The white dot represents the type-locality of the species.

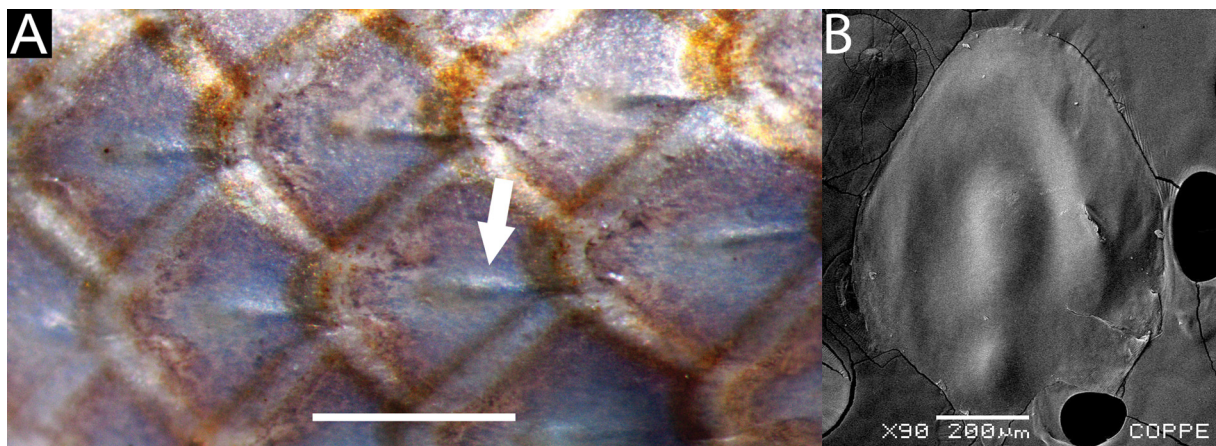


FIGURE 6. Lateral view of posterior region of the body above the cloacae (A) of *Atractus caxiuana* from Taraira, department of Vaupés, Colombia (ICN 10114) and detail of the supra-anal tubercle (B) of *Atractus caxiuana* from Vila Cachoeira do Samuel, municipality of Porto Velho, state of Rondônia, Brazil (MNRJ 3026). The arrow indicates one of the supra-anal tubercles and the scale bar represents 1 mm.

Discussion

The new specimens of *Atractus caxiuana* reported here from Brazil and Colombia agree in all respects with the holotype of the species, except for the polymorphism shown by the contact between internasal/loreal (50% of new

individuals). However, if we interpret this feature as the result of two distinct, but apparently correlated processes (lateral expansion of internasals concomitant with shortening of post-nasals), it may still be interpreted as an autapomorphy for the species (Passos 2008). The discovery of additional specimens of *A. caxiuana* so distant from the type locality (ca. 2,000 km in a straight line) is not surprising since most Amazonian congeners have widespread distributions (Cunha & Nascimento 1983, 1984; Martins & Oliveira 1993; Passos & Prudente 2012; Passos *et al.* 2012). The occurrence of *A. caxiuana* northwest to the Rio Amazonas is in accordance with the pattern reported for other species of *Atractus* (Almeida *et al.* in press). As a general rule, in its western course, the Rio Amazonas is a less effective barrier for the dispersal of many vertebrate groups (Colwell 2000), including species of *Atractus* (Passos & Prudente 2012). In fact, much of the apparent regional endemism attributed to the genus is often the result of examination of restricted samples (e.g., Silva 2004), incomplete bibliographic revision (e.g., Esqueda *et al.* 2007), insufficient comparative efforts with the relevant type material (e.g., Esqueda & La Marca 2005), and incomplete knowledge of the variability of certain morphological characters (e.g., Bernal-Carol & Roze 1997). Therefore, with the increase of available specimens we anticipate that many poorly represented species of *Atractus*, known only from their type material, will have their taxonomic status revised and their distributional range extended (e.g., Cisneros-Heredia 2005b, Passos & Arredondo 2009, Passos *et al.* 2007b, 2009a,d, 2010b, 2012).

TABLE 2. Occurrence of apical pits and/or supra-anal tubercles in the dorsal scales for the members of the unnamed clade from Grazziotin *et al.* (2012), comprising the genera *Atractus* and *Geophis*. We consider apical pits and supra-anal tubercles present in the groups when most of its members had unequivocally these structures.

Species group	Apical pits	Supra-anal tubercles	Group definition
<i>Atractus badius</i>	Absent	Absent	Savage 1960
<i>Atractus collaris</i>	Present	Present	This study
<i>Atractus elaps</i>	Absent	Absent	Savage 1960
<i>Atractus emmeli</i>	Absent	Absent	Passos <i>et al.</i> 2010c
<i>Atractus maculatus</i>	Absent	Absent	Passos <i>et al.</i> 2010c
<i>Atractus multicinctus</i>	Absent	Absent	Passos <i>et al.</i> 2009e
<i>Atractus pantostictus</i>	Absent	Absent	Passos <i>et al.</i> 2010c
<i>Atractus paraguayensis</i>	Absent	Absent	Passos <i>et al.</i> 2013b
<i>Atractus paucidens</i>	Absent	Absent	Passos <i>et al.</i> 2009e
<i>Atractus roulei</i>	Absent	Absent	Passos <i>et al.</i> 2013a
<i>Atractus trilineatus</i>	Absent	Absent	Savage, 1960
<i>Geophis chalybeus</i>	Absent	Absent	Downs 1967
<i>Geophis championi</i>	Present	Present	Downs 1967
<i>Geophis dubius</i>	Present	Present	Downs 1967
<i>Geophis latifrontalis</i>	Absent	Absent	Downs 1967
<i>Geophis omiltemanus</i>	Absent	Present	Downs 1967
<i>Geophis semidoliatus</i>	Present	Present	Downs 1967
<i>Geophis sieboldi</i>	Present	Present	Downs 1967

Savage (1960) proposed the *Atractus trilineatus* species group to accommodate taxa that share an undifferentiated condition of the hemipenis (= non-calculated organs; Savage, 1960: 70, tab. 6), and placed *A. collaris* and *A. gaigeae* in this group. However, Savage's observations were based only on the examination of retracted (inverted) hemipenes, which may fail to reveal certain key features (e.g., a capitular groove) that are better appreciated only on fully everted and maximally expanded organs (Schargel & Castoe 2003; Passos *et al.* 2007b; Prudente & Passos 2010). In fact, hemipenial variation in the genus *Atractus* seems to be much more complex than previously thought, with the most common condition being a semicapitate and semicalyculate organ (Hoogmoed & Prudente 2003; Passos *et al.* 2005; Zaher *et al.* 2005; Passos *et al.* 2007a,b; Passos & Fernandes 2008; Passos & Arredondo 2009; Passos *et al.* 2009a; Passos *et al.* 2013a). Actually, hemipenes of several species allocated in the *A. trilineatus* group (including *A. trilineatus* itself) present the differentiated condition (Passos 2008; Passos *et al.* 2009e; Passos *et al.* 2012; Passos *et al.* 2013a). Therefore, the *A. trilineatus* group should be entirely redefined. For this reason, many of the Ecuadorian *Atractus* formerly placed in the *A. trilineatus* group

have recently been transferred to their own new groups (Passos *et al.* 2009e, 2013a) or to previously described ones (Passos *et al.* 2012). Furthermore, other species allocated by Savage (1960) in the *A. trilineatus* group (*A. ecuadoriensis*, *A. lehmanni*, *A. occidentalis*, and *A. resplesdens*) are apparently more closely related to members of the *A. paucidens* group, although further taxonomic and phylogenetic studies are necessary to clarify this issue (Passos *et al.* 2012).

Given the inadequacy of the current definition of the *A. trilineatus* group and the lack of any comprehensive phylogenetic analysis of *Atractus*, and as a way to provide a taxonomically useful hypothesis to be tested in the future, we suggest a new putatively natural assemblage within the genus. This assemblage is called here the *Atractus collaris* species group, and includes *A. caxiuana*, *A. alphonsehogei*, *A. collaris*, *A. gaigeae*, *A. hoogmoedi*, *A. limitaneus*, *A. surucucu*, and *A. zidoki*. Species of the *Atractus collaris* species group share the following suite of uncommon characters: presence of two distinct apical pits on the posterior region of dorsal scales (Gasc & Rodrigues 1979: Fig. 3) and supra-anal tubercles in the dorsal scales above the cloacal region of adult males (Fig. 6); midbody diameter ≤ 5 mm; 17 dorsal scale rows; short and curved maxillary bone, with few maxillary teeth (usually five or six) and a well developed and posteriorly expanded lateral process; non-capitate and non-calyculate hemipenis (Fig. 4); dorsal colour pattern brown to dark brown with a light collar on the occipital region, paravertebral blotches (except in adults of *A. caxiuana* and *A. surucucu*), and dark longitudinal stripes intercalated by light paraventral lines; venter with the lateral region of ventral scales dark brown and remaining area of ventral scales cream in preservative (Figs. 1–3).

The presence of apical pits and supra-anal tubercles (= anal ridges of Blanchard 1931 or supracloacal keels of Savage 2002) in dorsal scales are likely to be plesiomorphic for Dipsadinae, being widespread in members of the tribe Imantodini (*sensu* Myers 2011). Nonetheless, within Dipsadinae (Grazziotin *et al.*, 2012), both features are, among the *Atractus* species, unique in the *A. collaris* group, widely distributed in *Geophis* (Tab. 2) and completely absent in the tribe Dipsadini. We consider apical pits and supra-anal tubercles in the *A. collaris* group as being non-homologous to the structures found in basal Dipsadinae. The functional role of apical pits and supra-anal tubercles in snakes remains elusive (Blanchard 1931; Gray 2011). However, Blanchard (1931) found apical pits in higher frequency in reproductively active males of the genera *Natrix* and *Diadophis*. The same condition is present in adult males of the *A. collaris* group (Prudente & Passos 2008, 2010), suggesting that these structures may play a similar role in reproductively active males of *Atractus*.

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Appendix

Material examined

Countries are given in bold capitals, states in plain capitals, municipalities in italics, and localities in plain text.

- Atractus caxiuana* ($n = 7$).—**BRAZIL**: PARÁ: *Melgaço*: Floresta Nacional de Caxiuana: (MPEG 19964 holotype, MPEG 19657, 20128 paratypes); RONDÔNIA: *Porto Velho*: right bank of the Rio Madeira: (MZUSP 18892), Vila Cachoeira do Samuel: (MNRJ 3026). **COLOMBIA**: VAUPÉS: *Taraira*: (ICN 10114–15).
- Atractus alphonsehogei* ($n = 9$).—**BRAZIL**: MARANHÃO: *Santa Inês*: (MPEG 10874); PAR: *Augusto Correia*: Fazenda Cacoal: (MPEG 9949 paratype), *Bragança*: Parada Bom Jesus: (MPEG 2221, 8573, 8667 paratypes), Km 224 from BR 316 highway: (MPEG 10093 paratype), *Colônia Nova*: (MZUSP 8778), *Santa Rosa*: Estrada de Vigia: (MPEG 12593 paratype), *Viseu*: Bela Vista: Km 75 *Bragança/Viseu* road: (MPEG 14928 holotype).
- Atractus collaris* ($n = 10$).—**COLOMBIA**: CAQUETÁ: *Florencia*: (MLS 1324, 2782), Caparú: (ICN 8144). **ECUADOR**: NAPO: oil well Zabalo: (EPN 5216); ORELLANA: *Yasuni*: (QCAZ 5980); SUCUMBÍOS: *Cayabeno*: (QCAZ 983, 986, 1042). **PERU**: LORETO: *Iquitos*: Maynas: (MHNSM 2310); UCAYALI: *Coronel Portillo*: Pucallpa: (MHNSM 3083).
- Atractus gaigeae* ($n = 10$).—**ECUADOR**: NAPO: Sacha Biological Station: (EPN without a number), *Loreto*: (USNM 217621), upper Río Napo: (USNM 217622), mouth of the Río Coca: (USNM 217623); PASTAZA: Río Bobonaza: (EPN 5217), Río Conambo: mouth of the Río Romarizo: (USNM 217624), mouth of the Río Shione: (USNM 217625), Cotopaza: (EPN 8693, paratype), Misión: (EPN 752), Río Rutuno: tributary of the Río Bobonaza, *Montalvo*: (USNM 217627).
- Atractus hoogmoedi* ($n = 3$).—**BRAZIL**: PARÁ: *Capitão Poço*: (MPEG 13265–66 paratypes, 13268, holotype).
- Atractus limitaneus* ($n = 1$).—**COLOMBIA**: AMAZONAS : *La Pedrera*: (IBSP 9196, holotype).
- Atractus zidoki* ($n = 6$).—**BRAZIL**: AMAPÁ: *Serra do Navio*: (IBSP 24772, 77393, MPEG 16437, MPEG without a number, MZUSP 2840). **FRENCH GUIANA**: without locality: (MZUSP without a number).