New Polychromatic Species of Atractus (Serpentes: Dipsadidae) from the Eastern Portion of the Colombian Andes

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We describe herein a new polychromatic species of the snake genus Atractus from the cloud forests of the northeastern Andes of Colombia. The new species is distinguished from all congeners by having an exclusive combination of phenotypic characters, such as: dorsal scale rows 17, loreal long, seven to ten maxillary teeth, ventrals 156-174 in females and 153-169 in males, subcaudals 20–30 in females and 23–30 in males, dorsum with variable coloration, changing from dark green to orange or red with a black nuchal band (three to four scales long) connected to a black vertebral line and two black dorsolateral continuous stripes from the occipital region to tip of the tail, venter with irregular black blotches, relatively small body size, small tail length in females and moderately long in males, hemipenis moderately bilobed, semicapitate and semicalyculate. We compared the new species with all congeners occurring along the Cordillera Oriental in Colombia, Sierra de Perijá in the Colombia/Venezuela frontier and Cordillera de Mérida in Venezuela. We discussed aspects related to polychromatism and its implication toward a robust taxonomy for the genus Atractus.

Describimos una nueva especie de serpiente policromática del género Atractus para los bosques nublados del noreste de los Andes de Colombia. La nueva especie se distingue de todos los congéneres por tener una combinación exclusiva de caracteres fenotípicos, como: escamas dorsales en 17 hileras, loreales largas, siete a diez dientes maxilares, ventrales 156-174 en hembras y 153-169 en machos, subcaudales 20-30 en hembras y 23-30 en machos, dorso con coloración variable, cambiando de verde oscuro a naranja o rojo con una banda nucal negra (largo de tres o cuatro escamas) conectada a una línea vertebral negra y dos franjas continuas dorsolaterales negras desde la región occipital hasta la punta de la cola, superficie ventral del cuerpo con manchas irregulares negras, tamaño corporal relativamente pequeño, longitud de la cola pequeña en las hembras y moderadamente larga en los machos, hemipene moderadamente bilobado, semicapitado y semicaliculado. Comparamos las nuevas especies con todos los congéneres que ocurren a lo largo de la Cordillera Oriental en Colombia, Sierra de Perijá en la frontera de Colombia/Venezuela y la Cordillera de Mérida en Venezuela. Discutimos aspectos relacionados con el policromatismo y su implicación hacia una taxonomía sólida para el género Atractus.

HE cryptozoic snake genus *Atractus* is widely distributed in the Neotropical region, occurring from central Panama to northeastern Argentina (Giraudo and Scrocchi, 2000; Myers, 2003). Atractus comprises 140 currently recognized species making it the most species-rich extant snake genus (Passos et al., 2018a), with the highest number of currently recognized taxa in the trans-Andean region of Colombia (Passos et al., 2009a). However, factors such as the small body size and cryptozoic lifestyle may be responsible for the relative paucity of samples for some species available in collections (Schargel and García-Pérez, 2002; Myers, 2003; Myers and Donnelly, 2008; Prudente and Passos, 2010). On the other hand, there are a lot of specimens currently misidentified in collections and public repositories (Passos et al., in press). To date, 25 species in Atractus are recognized to occur in the highlands of the Cordillera Oriental, Serranía de Perijá, Cordillera de Mérida in the Colombia and Venezuela boundary, but many of them still remain with uncertain taxonomic status. Although a comprehensive review for the species of this region is underway, we anticipate herein the formal description of a new polychromatic Atractus from the western slopes of the Cordillera Oriental of Colombia.

MATERIALS AND METHODS

Specimens examined of the new species are housed in the herpetological collection of the Universidad Industrial de Santander, department of Santander, Colombia (MHN-UIS),

and comparative material is listed in the Material Examined. Data from additional specimens of *Atractus* previously examined by PP can be found in: Passos et al. (2005, 2007a, 2007b, 2009a, 2009b, 2009c, 2009d "2008", 2009e, 2010a "2009", 2010b, 2010c, 2012, 2013a, 2013b, 2013c, 2013d, 2016a, 2016b, 2017, 2018a, 2018b, 2018c), Passos and Fernandes (2008), Passos and Arredondo (2009), Passos and Lynch (2011 "2010"), Passos and Prudente (2012), Prudente and Passos (2008, 2010), Schargel et al. (2013), Almeida et al. (2014), Salazar-Valenzuela et al. (2014), and de Fraga et al. (2017).

Measurements were taken with a dial caliper to the nearest 0.1 mm under a stereomicroscope, except for snout-vent length (SVL) and caudal length (CL), which were taken with a flexible ruler to the nearest 1.0 mm. Terminology for cephalic shields in Atractus follows Savage (1960), except for the loreal that follows the proposal of Passos et al. (2007b). Method of counting ventral and subcaudal scales follows follows Dowling (1951). Condition of the loreal scale follows Passos et al. (2007b). Measurements and descriptions of paired cephalic scales are strictly based on the right side of head. We describe the color pattern of the new species based on live specimens or on its digital photographs taken directly in the field, since several specimens were released after the measurement of general biometric data. Sex was determined based on presence or absence of hemipenes verified through a ventral incision at the base of the tail. We examined maxillae in situ under a Nikon C-LEDS stereomicroscope through a narrow lateral-medial incision between the supra-

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labials and the maxillary arch. After removing tissues covering the maxillary bone, we counted teeth and empty sockets. The method for preparation of preserved hemipenis was modified from Pesantes (1994) in replacing potassium hydroxide (KOH) with distilled water (see Passos et al., 2016a), observing precautions highlighted by Zaher and Prudente (2003). Prior to inflation with petroleum jelly, the organs remained 15–20 min in a 70% ethanol solution with Alizarin red to stain the ornamented calcareous structures according to Uzzel (1973), with adaptations from Harvey and Embert (2008) and Nunes et al. (2012). Terminology for hemipenial descriptions follows Dowling and Savage (1960) and Zaher (1999) with a few minor adaptations. We follow Passos et al. (2009e) and Passos et al. (2010a "2009") with respect to conditions of the morphological characters used in diagnosis and description.

Because scales counts are known to be sexually dimorphic in Atractus (Savage, 1960; Passos et al., 2005), we used the Mann-Whitney U-test to evaluate statistical differences between sexes. Previously, we evaluated the assumptions of univariate normality and homoscedasticity with the Kolmogorov-Smirnov's and Levene's tests, respectively (Zar, 1999). We used the following characters in the statistical analysis: number of ventral scales, subcaudal scales, snout-vent length (SVL), tail length (TL), and SVL/CL ratio. Additionally, we performed a discriminant function analysis (DFA) for males and females separately to evaluate differentiation between chromatic patterns with an *a priori* definition of operational groups based on each morphotype (Manly, 2005). We used a cross-validation matrix to obtain the posterior classification probabilities in which each individual is allocated to its own group. For this analysis, meristic and morphometric data were used for adult males and females. The minimal body size for sexually mature individuals was based on the study of Gualdrón-Durán et al. (in press). We used the packages "MASS" (Ripley et al., 2016) and "ellipse" (Murdoch and Chow, 2013) for performing statistical analysis. We used the packages "ggplot2" (Wickham, 2009) and "colorspace" (Ihaka et al., 2013) for producing the graphics. All these packages are in the R software (R Core Team, 2018).

Atractus marthae, new species

urn:lsid:zoobank.org:act:E7B6E8EB-0183-4624-B46F-9E51B2CD7E64 Martha's Groundsnake Culebras Tierreras de Martha Figures 1–6, Table 1

Holotype.—UIS-R 3027, adult male, Colombia, department of Santander, municipality of Santa Bárbara, Vereda Esparta, 07°01′5.38″N, 72°53′43.04″W, ca. 2400 m above sea level (hereafter asl), E. Meneses-Pelayo, 23 October 2014.

Paratypes.—(111 specimens, all collected or legated by first author from the department of Santander, Colombia): Reserva el Diviso, 07°03′6.16″N, 72°59′11.97″W, ca. 2400 m asl, municipality of Piedecuesta: UIS-R 1734, 5 May 2007; Vereda Potrero Grande, 06°50′46.96″N, 72°51′20.67″W, ca. 2220 m asl, municipality of Guaca: UIS-R 3248–49, 20 November 2015; Vereda Esparta, 07°01′5.38″N, 72°53′43.04″W, ca. 2400 m asl, municipality of Santa Bárbara: IAvH 9046 (formerly UIS-R 3021), IAvH-R 9045 (formerly UIS-R 3020), IUCN-R 13168 (formerly UIS-R 3022), IUCN-R 13169 (formerly UIS-R 3024), MHUA 15283–84 (formerly UIS-R 3018–19), UIS-R 3017, UIS-R 3023, UIS-R 3025–26, UIS-R 3028–35, UIS-R 3054, 23 October 2014; UIS-R 3038–44, UIS-R 3053, UIS-R 3055, 20 December 2014; UIS-R 3061–74, 22 February 2015; UIS-R 3090–98, UIS-R 3100, UIS-R 3262–63, 14 March 2015; UIS-R 3108–14, UIS-R 3120–25, 25 April 2015; UIS-R 3138–44, 23 May 2015; UIS-R 3148–54, UIS-R 3156, 28 June 2015; UIS-R 3172–78, UIS-R 3193, 25 July 2015; UIS-R 3194–97, 29 August 2015; UIS-R 3198–3205, 19 September 2015; UIS-R 3251–55, 20 November 2015.

Diagnosis.—Atractus marthae is distinguished from all congeners by unique combination of the following characters: (1) dorsal scale rows smooth in 17/17/17; (2) postoculars two; (3) long loreal; (4) temporals usually 1+2; (5) supralabials usually seven, third and fourth contacting the orbit; (6) infralabials usually seven, first three contacting chinshields; (7) maxillary teeth seven to ten; (8) gular scale rows usually four; (9) preventrals usually four; (10) ventrals 156-174 in females, 153-169 in males; (11) subcaudals 20-30 in females, 23-30 in males; (12) dorsum with variable coloration and pattern, presenting green to red ground color with broad black vertebral line (four scales wide) or narrow vertebral line (one scale wide) and two dorsolateral bands; (13) ventral ground color varying from cream with irregular black spots to belly mostly black with a few cream blotches anteriorly, usually posterior region of body and ventral surface of tail uniformly black; (14) moderately long body size, females reaching 346 mm SVL, males 307 mm; (15) small tail length in females (7.9–10.2% of SVL), small to moderately long in males (8.1-14.4% SVL); (16) hemipenis moderately bilobed (lobe size equivalent to the capitulum length), semicapitated and semicalyculated.

Comparisons .- Among all currently recognized species of Atractus from the Cordillera Oriental of Colombia, Sierra de Perijá in the Colombia/Venezuela frontier and Cordillera de Mérida in Venezuela, the new species shared conspicuous and regular longitudinal stripes (lacking paravertebral connections with spots and/or transversal blotches) only with Venezuelan species A. emigdioi, A. mariselae, and A. taphorni. Atractus marthae differs from A. taphorni by having 17/17/17 dorsal scale rows and two dorsal-lateral stripes (vs. 15/15/15 rows of dorsal scales and absence of dorsal-lateral lines in A. taphorni); differs from A. mariselae by having three longitudinal stripes, 20-30 subcaudals in females and 23-30 in males (vs. reticulated brown dorsal coloration with two narrow dorsolateral lines; 31-33 subcaudals in females and 36–39 in males); differs from A. emigdioi by having belly mostly black with irregularly distributed and few dispersed square cream spots and hemipenis moderately bilobed, semicapitated and semicalyculated (vs. belly with a broad black central stripe with cream lateral lines on the paraventral region or with midline divided in two black longitudinal stripes cream bordered; hemipenis slightly bilobed, non-capitated and non-calyculated).

Considering the congeners with overlapping ranges of distribution, *Atractus marthae* occur sympatrically or parapatrically only with *A. pamplonensis, A. variegatus,* and *A. wagleri* along the Cordillera Oriental of Colombia. The new species differs from all of them by having dorsum with three continuous and conspicuous dorsal-lateral stripes from the neck to the tip of the tail (vs. variable color pattern but lacking longitudinal lines or stripes in *A. pamplonensis, A. variegatus,* and *A. variegatus,* and *A. variegatus,* and *A. wagleri*).



Fig. 1. General view of the holotype of *Atractus marthae*, new species (UIS-R 3027) in life.



Fig. 2. Lateral (A), dorsal (B), and ventral (C) views of head, and dorsal (D) and ventral (E) views of body of the holotype of *Atractus marthae* (UIS-R 3027) preserved in 70% ethanol.



Fig. 3. General view in life of the four distinctive color patterns of Atractus marthae observed in the type-locality.

Description of the holotype.—Adult male, SVL 277 mm, TL 29 mm (10.5% SVL); head rounded in dorsal view, flattened in lateral view, 8.8 mm long (3.2% SVL), 5.6 mm wide (63.6% head length); cervical constriction indistinct; body subcylindrical, body diameter 6 mm (2.2% SVL); belly flattened; tail moderately long, with terminal spine moderately long and acuminate; snout rounded in dorsal view, truncated in lateral view; rostrum-orbit distance 3.1 mm (35.2% head length); nasal-orbit distance 2.3 mm (26.1% head length); intraorbital distance 3.5 mm (62.4% head width); rostral subtriangular in frontal view, twice as wide (1.9 mm) as high (0.9 mm), visible dorsally; internasal slightly wider (1.3 mm) than long (1.0 mm); internasal suture (0.9 mm long) sinister with respect to prefrontal median suture; prefrontal 2.2 mm long, 1.9 mm wide; frontal subtriangular, as wide (2.6 mm) as long (2.6 mm); supraocular subtrapezoidal, slightly longer (1.5 mm) than wide (1.2 mm); parietal about twice as long

(4.0 mm) as wide (2.4 mm); nasal divided; prenasal 0.9 mm high, 0.6 mm long, contacting rostral, internasal, first supralabial, and postnasal; postnasal slightly higher (1.0 mm) than long (0.7 mm), contacting prenasal, prefrontal, loreal, and first and second pair of supralabials; loreal twice as long (1.6 mm) as high (0.8 mm); loreal contacting eyes, prefrontals, nasals, and second and third supralabials; eve diameter 1.3 mm; pupil round; two postoculars, upper postocular about as high (0.9 mm) as long (0.7 mm); lower postocular twice as high (0.9 mm) as long (0.4 mm); upper postocular contacting eye, lower postocular, supraocular, parietal, and anterior temporal; lower postocular contacting eye, fourth and fifth supralabials, and anterior temporal; temporal formula 1+2; anterior temporal twice as long (1.6 mm) as high (0.8 mm), contacting parietal, fifth supralabial, sixth supralabial, postocular, and posterior temporal; posterior superior temporal about three times as long (3.4 mm) as



Fig. 4. Dorsal and ventral views of recently dead specimens (before fixation in formalin solution) of *Atractus marthae* observed in the type-locality.

high (0.9 mm); temporal posterior inferior 1.5 mm long, 0.8 mm high; seven supralabials, third and fourth contacting orbit; second supralabial higher than first and lower than third; fifth and sixth supralabials with similar height, seventh taller (1.4 mm) and longer (2.3 mm) than anterior supralabials; symphysial subtriangular, twice as wide (1.6 mm) as long (0.7 mm); seven infralabials, first three pairs contacting chinshields; first pair of infralabials in contact behind symphysial, avoiding symphysial-chinshields contact; chinshields more than twice as long (2.5 mm) as wide (1 mm); dorsal scale rows smooth, in 17/17/17 series; four rows of gular scales between last supralabial and preventrals; four preventrals; 163 ventrals; 26/25 (left/right) subcaudals. Maxillary bone arched anteriorly in dorsal view and flattened on the middle toward its end; maxilla with ten teeth arranged linearly; teeth angular in cross section, robust at



Fig. 5. Sulcate (left) and asulcate (right) sides of the hemipenis of *Atractus marthae* (UIS-R 3110). Scale bar = 5 mm.

the base, narrower at the apex, curved $45-60^{\circ}$ posteriorly; first tooth anteriorly projected and more spaced from the other first five teeth; four subsequent teeth similar in size and slightly spaced; sixth to tenth teeth gradually decreasing in size but increasing the spacing among teeth; no apparent diastema: jaw with a lateral process strongly developed (Fig. 6).

After 17 months of storage in 70% ethanol after fixation in 10% formalin solution, dorsum of head dark brown with pale brown spots covering medial-posterior portion of internasals, prefrontals, supraoculars, and lateral-posterior area of parietals; lateral surface of head dark brown to dorsal edges of supralabials, except irregular cream spots on the prenasal and postnasal; rostral with dark irregular spots dorsally; dark



Fig. 6. Morphology of the maxillary arch of *Atractus marthae* (UIS-R 3061) in labial (top), ventral (middle), and lateral (bottom) views. Scale bar = 1 mm.

Juvenile males (n = 7)		Juvenile females $(n = 12)$		Adult males (<i>n</i> = 32)		Adult females $(n = 37)$	
115.5	103-137	136.2	100-216	264.8	197–307	276.7	216–346
13.4	11-15	13	10-16	31.4	22-35	24.2	19–29
11.6	9.5-14.3	9.7	7.8-14	11.2	8.1-14.4	8.8	7.9-10.2
3.9	3.0-5.2	4.2	3.4-4.9	6.4	5.1-7.7	6.37	4.6-7.9
6.3	5.8-6.7	6.4	6.0-6.9	8.0	7.0-9.0	7.9	6.3-9.3
4.2	3.5-4.7	4.2	3.7-4.8	5.4	4.1-6.3	5.4	4.2-6.8
1.0	0.8-1.1	0.9	0.8-1.0	1.2	0.9-1.4	1.2	0.9-1.4
160.1	157-162	164.4	157-171	160.4	153-169	169.3	166–174
27.6	26–29	22.4	20–28	26.6	23–30	21.7	20-27
	Juver (r Mean 115.5 13.4 11.6 3.9 6.3 4.2 1.0 160.1 27.6	Juvenile males $(n = 7)$ MeanRange115.5103–13713.411–1511.69.5–14.33.93.0–5.26.35.8–6.74.23.5–4.71.00.8–1.1160.1157–16227.626–29	Juvenile malesJuvenile $(n = 7)$ $(n = 7)$ MeanRangeMean115.5103–137136.213.411–151311.69.5–14.39.73.93.0–5.24.26.35.8–6.76.44.23.5–4.74.21.00.8–1.10.9160.1157–162164.427.626–2922.4	Juvenile malesJuvenile females $(n = 7)$ $(n = 12)$ MeanRangeMeanRange115.5103–137136.2100–21613.411–151310–1611.69.5–14.39.77.8–143.93.0–5.24.23.4–4.96.35.8–6.76.46.0–6.94.23.5–4.74.23.7–4.81.00.8–1.10.90.8–1.0160.1157–162164.4157–17127.626–2922.420–28	Juvenile malesJuvenile femalesAdu $(n = 7)$ $(n = 12)$ $(n$ MeanRangeMeanRangeMean115.5 $103-137$ 136.2 $100-216$ 264.8 13.4 $11-15$ 13 $10-16$ 31.4 11.6 $9.5-14.3$ 9.7 $7.8-14$ 11.2 3.9 $3.0-5.2$ 4.2 $3.4-4.9$ 6.4 6.3 $5.8-6.7$ 6.4 $6.0-6.9$ 8.0 4.2 $3.5-4.7$ 4.2 $3.7-4.8$ 5.4 1.0 $0.8-1.1$ 0.9 $0.8-1.0$ 1.2 160.1 $157-162$ 164.4 $157-171$ 160.4 27.6 $26-29$ 22.4 $20-28$ 26.6	Juvenile malesJuvenile femalesAdult males $(n = 7)$ $(n = 12)$ $(n = 32)$ MeanRangeMeanRangeMeanRange115.5103-137136.2100-216264.8197-30713.411-151310-1631.422-3511.69.5-14.39.77.8-1411.28.1-14.43.93.0-5.24.23.4-4.96.45.1-7.76.35.8-6.76.46.0-6.98.07.0-9.04.23.5-4.74.23.7-4.85.44.1-6.31.00.8-1.10.90.8-1.01.20.9-1.4160.1157-162164.4157-171160.4153-16927.626-2922.420-2826.623-30	Juvenile malesJuvenile femalesAdult malesAdult $(n = 7)$ $(n = 12)$ $(n = 32)$ $(n = 32)$ MeanRangeMeanRangeMeanRange115.5103-137136.2100-216264.8197-307276.713.411-151310-1631.422-3524.211.69.5-14.39.77.8-1411.28.1-14.48.83.93.0-5.24.23.4-4.96.45.1-7.76.376.35.8-6.76.46.0-6.98.07.0-9.07.94.23.5-4.74.23.7-4.85.44.1-6.35.41.00.8-1.10.90.8-1.01.20.9-1.41.2160.1157-162164.4157-171160.4153-169169.327.626-2922.420-2826.623-3021.7

 Table 1.
 Meristic and morphometric variation from the type-series of Atractus marthae. Abbreviations are as follow: SVL = snout-vent length, TL = tail length, BD = body diameter, HL = head length, HW = head width, and ED = eye diameter.

brown descending postocular stripe covering two postoculars, anterior-ventral portion of anterior temporal, posterior half of fifth supralabial to anteriormost border of seventh supralabial; remaining supralabials mostly cream, with upper edges adjacent to orbit dark brown pigmented; cream temporal region adjacent to descending postocular stripe; temporal area scattered with diffuse brown dots, extending from mid-posterior portion of anterior temporal to upper and lower posterior temporals including immaculate seventh supralabial; occipital region uniformly dark brown connected dorsally to nuchal band (two to three scales long); gular region cream with few dispersed brown dots covering first pair of infralabials near chinshields suture, lateral portions of second and third pairs of supralabials, and anterior chinshields; preventrals almost uniformly cream; ventral ground color anteriorly (to the level of 17th) mostly cream with few irregular black spots; from the 18th ventral belly mostly black with a few square cream spots diffuse along body, except for cream lateral portion of ventrals; cream spots concentrated on the posterior region of body near the cloacal region; ventral surface of tail mostly cream with lateral-anterior areas of subcaudals pigmented with black, leaving the mid-ventral suture region uniformly cream colored until 17th subcaudal; posterior portion of tail cream with irregular black spots; dorsal ground color of body light brown with dark brown nuchal band connected to three dark brown dorsal-lateral continuous stripes extending to tip of tail; vertebral line (one scale wide) and two dorsal-lateral narrow stripe pigmenting the suture between fourth and fifth scale rows (Fig. 2).

Color pattern variation in life.—(n = 112) Dorsum of head and body with green, yellow, orange, red, or reddish brown ground color; background coloration with continuous black longitudinal stripes, constituted by vertebral (one to four scales wide) and two dorsal-lateral lines (half-scale to two scales wide); sometimes black stripes tenuously bordered with yellow pigment; paraventral region (first three scales rows) frequently with contrasting (lighter, Fig. 3A-B or darker, Fig. 3C, F) background with respect to paravertebral area; lower part of supralabials, gular region, and ventral portion of head cream to yellow; belly frequently mostly black scattered with square creamish yellow, orange, or red spots or blotches; sometimes belly predominantly cream, yellow, or red with few black spots or blotches; ventral marks (lighter or darker) restricted to a single or a series of ventrals or even to lateral region of each scale; usually anterior third of body predominantly lighter (cream, yellow, or red) with

few black spots laterally concentrated; ventral surface of tail almost entirely lighter (cream, yellow, or red) with a few black dispersed spots to entirely black (Figs. 3–4).

Chromatic variability of the adult specimens.—(n = 92) A total of 92 specimens (100%) were analyzed and grouped into color categories as follows: Pattern A: back with thin, black vertebral band (1–2 scales wide) and background greenish to almost yellow (Fig. 3C, E, n = 36, frequency = 39.1%); Pattern B: back with wide, black vertebral band (3–4 scales wide) and greenish to almost yellow background (Fig. 3F, n = 15, frequency = 16.3%); Pattern C: back with thin, black vertebral band (1–2 scales wide) and orange-red background (Fig. 3D, n = 29, frequency = 31.5%); Pattern D: back with wide, black vertebral band (3–4 scales wide) and orange-red background (Fig. 3A, B, n = 12, frequency = 13%). We performed a discriminant analysis for each pattern and the results for males and females do not show any structuration with respect to *a priori* labels.

Sexual dimorphism.—We found significant differences in body size (t = -2.76, df = 30, P < 0.01), with females presenting larger SVL (mean = 276.7 ± 30.2 , n = 37) than males (mean = 265.6 ± 24.7 , n = 32), and males presenting larger tail size (t = 10.34; df = 31; P < 0.0001; mean = 31.4 ± 3.2 , n = 32) than females (mean = 24.4 ± 2.6 , n = 32). Similarly, in the meristic data we found that the males had a lower number of ventral scales than the females ($U_{-6.7} = 33.5$, P < 0.0001), while females have lower numbers of subcaudal scales than males ($U_{-6.9} = 16.5$, P < 0.0001).

Hemipenial morphology.—(*n* = 7) Organ *in situ* (fully retracted) extends and bifurcates at level of seventh to eighth subcaudals; fully everted and maximally expanded hemipenis renders a moderately bilobed, semicapitate, and semicalyculate organ; lobes clavate with flattened tips; lobes with similar size and moderately distinct from capitulum; lobes with higher concentration of non-calcified calyces arranged in transverse series; capitulum located at the level of spermatic sulcus bifurcation; capitular groove well defined on the asulcate side and indistinct on the sulcate side of hemipenis; capitulum of equal size of hemipenial body on both sides of organ; sulcus spermaticus bifurcates on the middle part of organ with each branch centrifugally oriented, running to tip of lobes; sulcus spermaticus margins well defined and narrow, bordered by spinules from its base to apices of lobes; hemipenial body uniformly covered by

calcified hooked spines; large spines restricted to lateral sides of organ; basal portion with longitudinal plicae and dispersed spinules (Fig. 5).

Meristic and morphometric variation.—(n = 69) Largest male 307 mm SVL, 35 mm TL; largest female 346 mm SVL, 29 mm TL; adult midbody diameter 2.5-2.6% (mean = 2.55, SD = 0.69, n = 30) SVL in males, 2.2–2.3% (mean = 2.25, SD = 0.48, n = 36) SVL in females; tail 8.1–14.4% (mean = 11.9, SD = 1.12, n = 30) SVL in males, 7.9–10.2% (mean = 8.7, SD = 0.6, n = 36) SVL in females; ventrals 153–169 (mean = 160.4, SD = 5.43, n = 32) in males, 166–174 (mean = 169.3, SD = 2.99, n =37) in females; subcaudals 23–30 (mean = 26.6, SD = 1.4, n =32) in males, 20–26 (mean = 21.7, SD = 2.04, n = 37) in females; preventrals 3–5 (mean = 4, SD = 0.37, n = 69); rows of gular scales 3–5 (mean = 3.9, SD = 0.31, n = 69); supralabials 6 (n = 3), 7 (n = 65), or 8 (n = 1); infralabials 6 (n = 1) or 7 (n = 68); infralabials contacting chinshields 3 (n =68) or 4 (n = 1); rows of dorsal scales at the level of the second subcaudal 7–10 (mean = 8.4, SD = 0.8, n = 62); midbody diameter 4.6–7.9 mm (mean = 6.4, SD = 0.8; n = 69); maxillary teeth 6 (n=2), 7 (n=3), 8 (n=25), 9 (n=27), or 10 (n = 12; Table 1).

Etymology.—The new species is named herein in honor of Martha Patricia Ramírez-Pinilla for her invaluable contribution to the knowledge of the biology of Colombian amphibians and reptiles. Furthermore, we would like to acknowledge her dedicated vocation as a professor at the Universidad Industrial de Santander, during which she has contributed to the formation of many generations of herpetologists.

Distribution and natural history.—*Atractus marthae* is known from three localities in the western slope of Cordillera Oriental, department of Santander, Colombia. These regions are covered by cloud forest between 1990–2400 m asl (Fig. 7). We found specimens under rocks in wide areas of paddocks both in the type locality and in the southernmost locality in the path Potrero Grande (Fig. 8A), municipality of Guaca. One specimen was collected near the Cerro de la Judía, Regional Natural Park in the municipality of Florida-blanca. Many individuals at the type locality were found crossing trails of well-conserved forested areas dominated by *Quercus humboldtii* (Fig. 8B), in pastures of short grasses (savannas) with high density of rocks, very humid soils, and little arborization (Fig. 8C), as well as in areas of blackberry crops.

Atractus marthae was found active during crepuscular periods between 1700-1830 hrs, generally associated with non-compacted soils with high humidity and with the presence of abundant earthworms that could constitute their main diet, as reported for other species of Atractus (Balestrin et al., 2007). In periods of inactivity, the specimens are found generally under rocks and underground until 30 cm of depth; in such microhabitats were also found litters of 3-5 eggs (Fig. 8D-E). These eggs were collected and monitored in the laboratory under controlled conditions until their hatching (temperature between 15-18°C, relative humidity between 80-100%). Neonates did not vary in coloration with respect to adults (n = 12), and within the same litter there were neonates with different coloration patterns, displaying A-D morphotypes. We observed reproductive behaviors in April with four males and five females found under a rock forming a "mating ball"; when the rock was lifted, the snakes freed from the ball and hid themselves underground. Males attained maturity at a smaller size (137 mm SVL, n = 7) than females (216 mm SVL, n = 12; Gualdrón-Durán et al., in press), as reported for other congeners (Balestrin et al., 2005; Resende and Nascimento, 2015; Passos et al., 2016a).

DISCUSSION

Of the 140 currently recognized species of Atractus, almost a half (~70) occur in the northern Andes (Ecuador, Colombia, and Venezuela), this being a major diversification zone for the genus (Passos et al., 2009b). Of this great Andean diversity and species richness, approximately 14% of the species (10 spp.) are restricted (=endemic) to the Cordillera Oriental of Colombia from the south of the Sumapaz highland (03°52'N, 74°25'W) north to the municipality of Ocaña (08°14'N, 73°21'W), department of Norte Santander, Colombia. Atractus marthae occur sympatrically or parapatrically with A. pamplonensis, A. variegatus, and A. wagleri. However, the new species is easily distinguished from these congeners by having a very distinctive coloration consisting of dorsum of body with three continuous and conspicuous dorsal-lateral stripes from the neck to the tip of the tail (vs. variable color pattern but lacking longitudinal stripes in A. pamplonensis, A. variegatus, and A. wagleri).

The systematized study of polychromatism has been elusive for the genus Atractus and directed to species with large series available in collections mostly from the cis-Andean lowlands, such as: Amazonia (Passos and Prudente, 2012; Almeida et al., 2014; Passos et al., 2016b), Atlantic Forest (Passos et al., 2010c), Cerrado (Passos et al., in press), or Caatinga (Passos et al., 2016a). In many instances, the available samples for Andean taxa do not allow us to access reasonably the interspecific variation, making it difficult to infer species boundaries among many hypothesized taxa (cf. Esqueda and Lamarca, 2005). In contrast, the huge variability displayed by several congeners has greatly impacted the taxonomy of Atractus, with recognition of several junior synonyms based essentially on color morphs or ontogenetic phases inside of a given species (see Passos et al., 2009d "2008", 2018a, 2018c; Passos and Prudente, 2012).

Recently, Passos et al. (2016a) carried out an exhaustive analysis of the variation in different phenotypic axes for Atractus postchi and discussed some scenarios for the evolution of the chromatic polymorphism in the genus. In the case of the A. marthae, all color morphs occur in the same population sampled from the type locality and such variability does not show any sexual or ontogenetic basis. These patterns are characterized mainly by continuous longitudinal lines that vary in thickness, the patterns with thin longitudinal lines being the most common (Pattern A = 39.1% and Pattern C = 31.5%; see Results), followed by those with broad stripes (Pattern B = 16.3% and Pattern D = 13%). Despite the selective pressure involved in the maintenance of polychromatism among several species of Atractus and the paucity of detailed studies on this topic, it is clear that color variance must be taken seriously into account before any taxonomic decisions are made. As a rule for the genus, all species with large series show great color variation, and the studies based on a few specimens should compare them in detail at least with all morphologically similar and sympatric species.





MATERIAL EXAMINED

Atractus acheronius: (n = 1) Venezuela: Zulia: Machiques de Perijá: Río Negro Valley: MHNLS 398 (holotype of *A. acheronius*).

Atractus crassicaudatus: (n = 455) Colombia: without locality: IBSP 2443, ICN 8505, 8508-25, 8922-25, MLS 139, 152, 156, 293, 2640, MUJ 92, 355; Boyacá: Badohondo: ICN 10693, Belén: ICN 10709*, Chiquinquirá: MLS 2577, Coper: MLS 2578-79, Duitama: ICN 10700-07, Garagoa: ICN 10627, MUJ 315-22, 398-99, 509, Guayatá: IAvH 864-65, Pajarito: IAvH 1059, ICN 2608-11, 2831-33, Pesca: IAvH 1880, Río Tectino: IAvH 799, Sogomoso: MLS 282, 2751-52, Tunja: MUJ 04, Ventaquemada: MLS 2243, Villa de Leyva: IAvH 2172-73, 3039, 3189, 4788, 4811-20, 4852, 4878, 4889, 4892-93, 4912, 4960, 4976, ICN 2792*, 8332-33, 9016-19, 9027, MLS 2021, 2564-65, 2918-20, Zipaquirá: MUJ 05; Cundinamarca: without locality: MUJ 482; Aguadita: MLS 169, Albán: IAvH 4749, ICN 10626, Bogotá: IAvH 129, 204, 2478, ICN 1394-426*, 1455, 1460-61, 2588, 2623, 2633, 2641, 3377, 4217, 4240, 6209, 6236, 6340, 6449, 6490-91, 6504-05, 6509, 7100, 7102, 8260, 10806*, IBSP 226, 7216-17, 10164-67, 42945, MLS 153, 164-65, 167, 172, 178, 2546, 2607-09, 2614-15, 2617, 2644-45, MUJ 03, 07, 09-10, 17, 22, 24, 151, 180, 206-09, 211, 400, 609-10, 692, Arrachal: MLS 265, 2805-13, Cerro de Suba: La Conejera: ICN 6336, 6577-79, 6580-81, 10692, Codazzi: MLS 2386, San Joaquín: MLS 2964-65, Santana: IAvH 4964, Cajicá: IAvH 500, Chia: ICN 7101, MLS 2373-77, 2382-83, 2600, 2622-23, 2830-93, 2900-08, 2935-36, MLS not catalogued, MUJ 18, 477, Chocontá: MLS 174 (holotype of A. colombianus), 155 (paratype of A. colombianus), 159, 2620, Cogua: MLS 163, 185, Cota: MUJ 164, Facatativa: MUJ 264, 461-62, Fontinbón: MUJ 25, Fuquené: MUJ 16, 20-21, Fusagasuga: MLS 2634, MUJ 92, Guachancipá: ICN 8261, Guachetá: MLS 2263, Guaduas: MUJ 01, Guasca: MLS 2626, MUJ 203-05, 215, La Calera: MUJ 298, La Union: MLS 157, Machetá: MLS 2568-70, 2653, 2921-

22, 2927, 2931, Mosquera: ICN 1453-54, 1456, 1458-59, Laguna Herrera: IAvH 3815, ICN 859, 1277, 1457, Nemocón: ICN 7041, Pacho: MLS 170 (holotype of A. longimaculatus), 154, 2611-12, 2616, 2923-30, MUJ 550, Pasca: ICN 485-86, MLS 2602-04, Quetame: between Quetame and Guayabetal: ICN 4477, Sisga dam: IAvH 08, Reserva Carpanta: MLS 26, San Antonio del Tequendama: IAvH 3038-39, MLS 150-51, 200, Sesquilá: MLS 2571, Sibaté: MLS 175-76, 295, Sopo: MLS 2624, Suesca: MUJ 214, 649, Sumapaz: MLS 168, Sutatenza: MLS 283-84, 288, 292, 1860-63, 2493-94, Tabio: MLS 1898, Tausa: MUJ 142, Tena: MUJ 12, 19, Une: MLS 160, 177, 2709-10, Usaquén: MLS 2378-79, 2381, 2894-99, MUJ 13, Villapinzón: ICN 2816, MLS 299, Villeta: IAvH 1587; Meta: Cañon La Curia: MLS 06, Lomalinda: IAvH 967; Santander: without locality: MUJ 212, Bolívar: MLS 162, Jesús Maria: MLS 2246-48, Puente Nacional: MLS 2629, Santa Rita: MLS 2630. Localities likely incorrectly labeled: Meta: Puerto Lopez: ICN 6500, MUJ 15; Santander: Encino: MUJ 267.

Atractus elaps: (n = 89) Brazil: without locality: ZMH-R 4421 (holotype of Rabdosoma brevifrenum), IBSP 20314; Amazonas: Borba: MNRJ 1523. Colombia: without locality: MLS 182; Amazonas: Parque Natural Nacional Amacayacu: IAvH 3211; Boyacá: Macanal: MLS 2637; Caquetá: without locality: MLS 183, Florencia: MLS 185, 187, 195, 197, 1316-18, 1322-23, 1326-27, 1739, 2730, 2733-39; Cauca: Puerto Bello: ICN 8240*, Santa Rosa: El Carmen: IAvH 4410; Cundinamarca: Guaicarano: IBSP 5314 (holotype of A. elaps tetrazonus), Paratebueno: MLS 188, Medina: MLS 192, Sasaima: MLS 2527; Meta: Acacias: MLS 191, Cubarral: ICN 7266, Piñalito: ICN 7099, San Juan de Arama: IAvH 929, Villaviciencio: ICN 8313, MLS 179, 189, 193, 196, 266, 1396, 2054-55; Río Ocoa, S Villavicencio: MLS 190; Putumayo: without locality: MLS 180. Ecuador: E Ecuador, without locality: EPN 6892, EPN not catalogued; NAPO: upper Río Napo: EPN 6856, 8686, Archidona: QCAZ 2101; Río Huataracu: EPN 8687; Orellana: Balsayacu: Parque Sumaco: QCAZ 6502, Fuerte: EPN 7324; Loreto: El Tená: EPN 8688, Parque Nacional Yasuní: EPN



Fig. 8. Landscape views of the type locality of Atractus marthae along the Vereda Esparta, municipality of Santa Bárbara, department of Santander, Colombia. General habitat (A), microhabitats (B, C), oviposition site (D), egg orientation in situ (E).

2536, QCAZ 3249, 3959, Río Coca: QCAZ 440; Pastaza: Mera: EPN 1175, Montalvo: Andoas: EPN 758, Nueva Vida: Misión Agua Santa: QCAZ 3450, Puyo: QCAZ 1277, Río Bobonaza: EPN 8678–83, Río Tallín: upper Río Bobonaza: EPN 8675–77, Sarayacu-Pucayacu: EPN 8685; Sucumbíos: Lagartococha: EPN 8689, Lago Ágrio: EPN 5781, Shushufindi: QCAZ 3303. Peru: Amazonas: Bagua: MHNSM 2447; Huánuco: Poncio Prado: MHNSM 2082; Loreto: Maynas: MHNSM 2513; San Martín: San Martín: MHNSM 3133, 3337, Tarapoto: MHNSM 3278. Localities likely incorrectly labeled: Pichincha: Ocidente: EPN 8692; El Oro: Santa Rosa: EPN 8690–91.

Atractus emigdioi: (n = 4) Venezuela: Lara: Moran: La Palma: Páramo El Jábon: MHNLS 9299; Trujillo: Boconó: Valera-

Trujillo road: ULABG 3791, Parque Nacional Guaramacal: N versant: MHNLS 16209, Trujillo: ULABG 4473.

Atractus eriki: (n = 4) Venezuela: Tujillo: Escuche: ULABG 6710 (paratype of *A. eriki*), Trujillo: ULABG 6694 paratype of *A. eriki*), Valera: ULABG 6693 (holotype of *A. eriki*), CV-ULA one specimen not catalogued.

Atractus erythromelas: (n = 31) Venezuela: Mérida: Jaji: CV-ULA two specimens not catalogued, La Mucuy: CV-ULA two specimens not catalogued, La Vega: CV-ULA one specimen not catalogued, Libertador: MHNLS 902, CBA one specimen not catalogued, Los Guaimaros: CV-ULA one specimen not catalogued, Manzano Alto: CV-ULA nine specimens not catalogued, Mérida: BMNH 1.716–17 (paratypes of *A. erythromelas*), CV-ULA four specimens not catalogued, CSJ 519, Mucurubá: MHNLS 276–78*, 630, 902, Santo Domingo: CV-ULA one specimen not catalogued; Táchira: Uribante: CV-ULA one specimen not catalogued.

Atractus indistinctus: (n = 10) Colombia: Cesar: Río de Oro: ICN 11487; Norte de Santander: Ocaña: MLS 166 (holotype of *A. indistinctus*), 261–62, 264, 2695–96. Venezuela: Mérida: La Azulita: El Hato: CV-ULA one specimen not catalogued; Táchira: CV-ULA 6117; Zulia: Sierra de Perijá: Cerro de Las Tetas: MBUCV not catalogued*.

Atractus meridensis: (n = 10) Venezuela: Mérida: Libertador: ULABG 4090–91, 4408, 4941 (paratypes of *A. meridensis*), Mérida: ULABG 4154 (paratype of *A. meridensis*), Las Piedras: Río Pueblo Llano: ULABG 4341 (holotype of *A. meridensis*), Parque Chorros: ULABG 2533 (paratype of *A. meridensis*), Santo Domingo: ULABG 4694–96 (paratypes of *A. meridensis*).

Atractus mijaresi: (n = 11) Venezuela: Mérida: La Carvonera: CBA 01–10, Mucurubá: Rangel: ULABG 4697 holotype of *A. mijaresi*).

Atractus multidentatus: (n = 1) Venezuela: Mérida: La Vega: El Parasiso: CV-ULA 7080 (holotype of *A. multidentatus*).

Atractus ochrosetrus: (n = 2) Venezuela: Mérida: Tovar: ULABG 4698 (holotype of *A. ochrosetrus*); Tovar-Guaraque road: ULABG 4696 (paratype of *A. ochrosetrus*).

Atractus pamplonensis: (n = 94) Colombia: Norte de Santander: Bochalema: MHNLS not catalogued, Chinacotá: MLS 2338– 39; Chitagá: Chucarima: MLS 273–74, 248, 287, 300; Cutilla: MHUA 14163–64; El Diamante: MLS 1920; Labateca: ICN 10715–18*; La Donjuana: MLS 248: Ocaña: MLS 277; Pamplona: IBSP 9192 (holotype of *A. pamplonensis*), 9190– 91, 9040, 9021 (paratypes of *A. pamplonensis*), MLS 241–44, 247, 250–52, 276, 2001–02, 2364, 2369–71, 2458–60, 2688– 94, 2711–15, 2753–69, MLS not catalogued, ICN 10 specimens not catalogued; Alto de la Lejía: ICN 10719–24*; Toledo: MLS 249, 253, 2700–03.

Atractus tamaensis: (n = 6) Venezuela: Táchira: Junin: Betania: MHNLS 8307 (holotype of *A. tamaensis*), 8301, 8303–06* (paratypes of *A. tamaensis*).

Atractus taphorni: (n = 5) Venezuela: without locality: IBSP 25785; Mérida: without locality: CV-ULA not catalogued, El

Chorotal: La Azulita road: CV-ULA 1838, La Carbonera: CV-ULA 6417, Libertador: ULABG 3909.

Atractus turikensis: (n = 1) Venezuela: Zulia: Sierra de Perijá: Mesa Turik base: MBLUZ 302 (paratype of *A. turikensis*).

Atractus variegatus: (*n* = 16) Colombia: Boyacá: Boavita: MLS 2484–85, La Uvita: MLS 260 (holotype of *A. variegatus*), 217, 259, 267, 272, 278, 281, 2266, 2268–69, 2271–73, 2697.

Atractus ventrimaculatus: (n = 15) Venezuela: Mérida: Betania: ULABG 2409, Jaji: CV-ULA one specimen not catalogued, La Princesa: ULABG 6701–02, Libertador: El Valle: MHNLS 897–901*; Manzano Alto: CV-ULA two specimens not catalogued, Mérida: BMNH 1946. 1.5.15 (holotype of *A. ventrimaculatus*), La Mucuy: Parque Nacional Sierra Nevada: MBUCV 2016, Pico Humbo: EBRG 4052, Tapa Azul: CV-ULA one specimen not catalogued.

Atractus vertebrolineatus: (n = 1) Colombia: Norte de Santander: Ocaña: MLS 184 (holotype of *A. vertebrolineatus*).

Atractus wagleri: (n = 7) Colombia: Santander: Floridablanca: UIS-R 71, Los Santos: Mesa de los Santos, El Roble Farm, Vereda El Carrizal: UIS-R 1767, Piedecuesta: Conjunto Residencial Pinares de Granada: UIS-R 1716, Guatigurá: Vereda Viricute: UIS-R 281, Mesa de los Santos, El Roble Farm, Vereda El Carrizal: UIS-R 1488–89, San Vicente de Chucuri: MHUA 14504*, Suratá: near Nueva San Luis school: Vereda San Luis: UIS-R 1725.

Atractus werneri: (n = 39) Colombia: without locality: MLS 144, 289, 483; Cundinamarca: El Colégio: IAvH 4327, Fusagasugá: ICN 2727, MLS 2329, 2334, 2345–44, 2427, 2514, 2518, 2523, 2563, 2914–16, 2932–34, MUJ 92, La Mesa: MLS 161, La Vega: IAvH 2068, San Francisco: ICN 5738, 10696*, Santandercito: IAvH 3014, ICN 11207, MLS 1915–16, 2118, 2020, Sasaima: ICN 2612, MLS 236, 238, Silvania: IAvH 145, 823–24, ICN 7268, Vereda Santa Rita: IAvH 17.

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LITERATURE CITED

Almeida, P. C., D. T. Feitosa, P. Passos, and A. L. C. Prudente. 2014. Morphological variation and taxonomy of

Atractus latifrons (Günther, 1868) (Serpentes: Dipsadidae). Zootaxa 3860:64–80.

- **Balestrin, R. L., M. Di-Bernardo, and A. G. Moreno.** 2007. Feeding ecology of neotropical worm snake *Atractus reticulatus* in southern Brazil. Herpetological Journal 17: 62–64.
- de Fraga, R., A. P. Almeida, L. J. C. L. Moraes, M. Gordo, R. Pirani, R. R. Zamora, V. T. Carvalho, P. Passos, and F. P. Werneck. 2017. Narrow endemism or insufficient sampling? Geographic range extension and morphological variation of the poorly known *Atractus riveroi* Roze, 1916 (Serpentes: Dipsadidae). Herpetological Review 48:281– 284.
- **Dowling, H. G.** 1951. A proposed standard system of counting ventrals in snakes. British Journal of Herpetology 1:97–99.
- **Dowling, H. G., and J. M. Savage.** 1960. A guide to the snake hemipenis: a survey of basic structure and systematic characters. Zoologica 45:17–28.
- **Esqueda, L. F., and E. La Marca.** 2005. Revisión taxonómica y biogeoráfica (con descripción de cinco nuevas especies) del género *Atractus* (Colubridae: Dipsadinae) en los Andes de Venezuela. Herpetotropicos 2:1–32.
- Giraudo, A. R., and G. J. Scrocchi. 2000. The genus *Atractus* (Serpentes: Colubridae) in northeastern Argentina. Herpetological Journal 10:81–90.
- Gualdrón-Durán, L. E., M. F. Calvo-Castellanos, and M. P. Ramírez-Pinilla. In press. Annual reproductive activity and morphology of the reproductive system of an Andean population of *Atractus* (Serpentes, Colubridae). South American Journal of Herpetology 13.
- Harvey, M. B., and D. Embert. 2008. Review of Bolivian *Dipsas* (Serpentes: Colubridae), with comments on other South American species. Herpetological Monographs 22: 54–105.
- Ihaka, R., P. Murrell, K. Hornik, J. C. Fisher, and A. Zeileis. 2013. colorspace: Color Space Manipulation. R package version 1.2-2. https://CRAN.R-project.org/package= colorspace
- Manly, B. F. J. 2005. Multivariate Statistical Methods: A Primer. Chapman & Hall/CRC Press, Boca Raton, Florida.
- Murdoch, D., and E. D. Chow. 2013. ellipse: Functions for Drawing Ellipses and Ellipse-Like Confidence Regions. R package version 0.3-8. https://CRAN.R-project.org/ package=ellipse
- 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., and M. A. Donnelly.** 2008. The summit herpetofauna of Auyantepui, Venezuela: report from the Robert G. Goelet Americam Museum–Terramar Expedition. Bulletin of the American Museum of Natural History 308: 1–147.
- Nunes, P. M. S., A. Fouquet, F. F. Curcio, P. J. R. Kok, and M. T. Rodrigues. 2012. Cryptic species in *Iphisa elegans* Gray, 1851 (Squamata: Gymnophthalmidae) revealed by hemipenial morphology and molecular data. Zoological Journal of the Linnean Society 166:361–376.
- **Passos, P., R. Aguayo, and G. Scrocchi.** 2009a. Rediscovery of the rare *Atractus bocki*, with assessment of the taxonomic status of *Atractus canedii* (Serpentes: Colubridae: Dipsadidae). Journal of Herpetology 43:710–715.

- Passos, P., and J. C. Arredondo. 2009. Rediscovery and redescription of the Andean earth-snake *Atractus wagleri* (Reptilia: Serpentes: Colubridae). Zootaxa 1969:59–68.
- Passos, P., J. C. Arredondo, R. Fernandes, and J. D. Lynch. 2009b. Three new *Atractus* (Serpentes: Dipsadidae) from the Andes of Colombia. Copeia 2009:425–438.
- Passos, P., J. A. R. Azevedo, C. C. Nogueira, R. Fernandes, and R. J. Sawaya. In press. An integrated approach to delimit species in the puzzling *Atractus emmeli* complex (Serpentes: Dipsadidae). Herpetological Monographs.
- Passos, P., A. Chiesse, O. Torres-Carvajal, and J. M. Savage. 2010a "2009". Testing species boundaries within *Atractus occipitoalbus* complex (Serpentes: Dipsadidae). Herpetologica 65:284–403.
- Passos, P., D. F. Cisneros-Heredia, D. E. Rivera, C. Aguilar, and W. E. Schargel. 2012. Rediscovery of *Atractus microrhynchus* and reappraisal of the taxonomic status of *A. emersoni* and *A. natans* (Serpentes: Dipsadidae). Herpetologica 68:375–392.
- **Passos, P., D. F. Cisneros-Heredia, and D. Salazar-V.** 2007a. Rediscovery and redescription of the rare Andean snake *Atractus modestus*. Herpetological Journal 17:1–6.
- Passos, P., M. Dobiey, and P. J. Venegas. 2010b. Variation and natural history notes on Giant Groundsnake, *Atractus gigas* (Serpentes: Dipsadidae). South American Journal of Herpetology 5:73–82.
- **Passos, P., L. Y. Echevarría, and P. J. Venegas.** 2013a. Morphological variation of *Atractus carrioni* (Serpentes: Dipsadidae). South American Journal of Herpetology 8: 109–120.
- Passos, P., and R. Fernandes. 2008. A new species of the colubrid snake genus *Atractus* (Reptilia: Serpentes) from the central Amazon of Brazil. Zootaxa 1849:59–66.
- Passos, P., R. Fernandes, R. S. Bérnils, and J. C. Moura-Leite. 2010c. Taxonomic revision of the Brazilian Atlantic Forest *Atractus* (Reptilia: Serpentes: Dipsadidae). Zootaxa 2364:1–63.
- **Passos, P., D. S. Fernandes, and D. M. Borges-Nojosa.** 2007b. A new species of *Atractus* (Serpentes: Dipsadinae) from a relictual forest in northeastern Brazil. Copeia 2007: 788–797.
- Passos, P., R. Fernandes, and N. Zanella. 2005. A new species of *Atractus* (Serpentes: Colubridae) from southern Brazil. Herpetologica 61:209–218.
- **Passos, P., G. R. Fuenmayor, and C. Barrio-Amorós.** 2009c. Description of two new species from Venezuela in the highly diverse dipsadine genus *Atractus* (Serpentes: Colubridae). Amphibia–Reptilia 30:233–243.
- Passos, P., P. J. Kok, N. R. Albuquerque, and G. A. Rivas. 2013b. Groundsnakes of the lost world: a review of *Atractus* (Serpentes: Dipsadidae) from the Pantepui region, northern South America. Herpetological Monographs 27:52–86.
- **Passos, P., and J. D. Lynch.** 2011 "2010". Revision of *Atractus* from upper and middle Magdalena drainage of Colombia. Herpetological Monographs 24:149–173.
- **Passos, P., J. D. Lynch, and R. Fernandes.** 2009d "2008". Taxonomic status of *Atractus sanctaemartae* and *Atractus nebularis*, and description of a new *Atractus* from the Atlantic coast of Colombia. Herpetological Journal 18:175–186.
- Passos, P., A. Martins, and D. Pinto-Coelho. 2016a. Population morphological variation and natural history of *Atractus potschi* (Serpentes: Dipsadidae) in Northeastern Brazil. South American Journal of Herpetology 11:188–211.

- Passos, P., J. J. Mueses-Cisneros, J. D. Lynch, and R. Fernandes. 2009e. Pacific lowland snakes of the genus *Atractus* (Serpentes: Dipsadidae), with descriptions of three new species. Zootaxa 2293:1–34.
- **Passos, P., and A. L. C. Prudente.** 2012. Morphological variation, polymorphism, and taxonomy of the *Atractus torquatus* complex (Serpentes: Dipsadidae). Zootaxa 3407: 1–21.
- Passos, P., A. L. C. Prudente, and J. D. Lynch. 2016b. Redescription of *Atractus punctiventris* and description of two new *Atractus* (Serpentes: Dipsadidae) from Brazilian Amazonia. Herpetological Monographs 30:1–20.
- Passos, P., A. L. C. Prudente, L. O. Ramos, J. R. Caicedo-Portilla, and J. D. Lynch. 2018a. Species delimitations in the *Atractus collaris* complex (Serpentes: Dipsadidae). Zootaxa 4392:491–520.
- Passos, P., L. O. Ramos, A. Fouquet, and A. L. C. Prudente. 2017. Taxonomy, morphology, and distribution of *Atractus flammigerus* Boie 1827 (Serpentes: Dipsadidae). Herpetologica 73:349–363.
- Passos, P., L. O. Ramos, P. H. Pinna, and A. L. C. Prudente. 2013c. Morphological variation and affinities of the poorly known snake *Atractus caxiuana* (Serpentes: Dipsadidae). Zootaxa 3745:35–48.
- Passos, P., A. Scanferla, P. R. Melo-Sampaio, J. Brito, and A. Almendariz. 2018b. A giant on the ground: another largebodied *Atractus* (Serpentes: Dipsadinae) from Ecuadorian Andes, with comments on the dietary specializations of the goo-eaters snakes. Annals of the Brazilian Academy of Sciences 2018:1–14.
- Passos, P., V. Sudré, G. Doria, and P. D. Campbell. 2018c. The taxonomic status of the "forgotten" Bolivian snakes, *Atractus balzani* Boulenger 1898 and *Atractus maculatus* (sensu Boulenger 1896) (Serpentes: Dipsadidae). Zootaxa 4438:176–182.
- Passos, P., M. Teixeira-Junior, R. S. Recoder, M. A. De Sena, F. Dal Vechio, H. B. A. Pinto, S. H. S. T. Mendonça, J. Cassimiro, and M. T. Rodrigues. 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.** 1994. A method for preparing hemipenis of preserved snakes. Journal of Herpetology 28:93–95.
- Prudente, A. L., and P. Passos. 2008. New species of *Atractus* Wagler, 1828 (Serpentes: Dipsadinae) from Guyana Plateau in Northern Brazil. Journal of Herpetology 42:723–732.
- **Prudente**, **A. L.**, **and P. Passos.** 2010. New cryptic species of *Atractus* (Serpentes: Dipsadidae) from Brazilian Amazonia. Copeia 2010:397–404.

- **R** Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/
- **Resende**, F. C., and L. B. Nascimento. 2015. The female reproductive cycle of the Neotropical snake *Atractus pantostictus* (Fernandes and Puorto, 1993) from south-eastern Brazil. Anatomia Histologia Embryologia 44:225–235.
- Ripley, B., B. Venables, D. M. Bates, K. Hornik, A. Gebhardt, and D. Firth. 2016. MASS: support functions and datasets for Venables and Ripley's MASS.
- Salazar-Valenzuela, D., O. Torres-Carvajal, and P. Passos. 2014. A new species of *Atractus* (Serpentes: Dipsadidae) from the Andes of Ecuador. Herpetologica 70:350–363.
- Sabaj, M. H. 2016. Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an Online Reference. Version 6.5 (16 August 2016). Electronically accessible at http://www.asih.org/, American Society of Ichthyologists and Herpetologists, Washington, D.C.
- Savage, J. M. 1960. A revision of the Ecuadorian snakes of the colubrid genus *Atractus*. Miscellaneous Publications, Museum of Zoology, University of Michigan 112:1–86.
- Schargel, W. E., and J. E. García-Pérez. 2002. A new species and a new record of *Atractus* (Serpentes: Colubridae) from the Andes of Venezuela. Journal of Herpetology 36:398– 402.
- Schargel, W. E., W. W. Lamar, P. Passos, J. H. Valencia, D. F. Cisneros-Heredia, and J. A. Campbell. 2013. A new giant *Atractus* (Serpentes: Dipsadidae) from Ecuador, with notes on some other large Amazonian congeners. Zootaxa 3721: 455–474.
- Uetz, P., P. Freed, and J. Hošek (Eds.). 2018. The Reptile Database. http://www.reptile-database.org (accessed 23 March 2018).
- Uzzell, T. 1973. A revision of lizards of the genus *Prionodactylus*, with a new genus for *P. leucostictus* and notes on the genus *Euspondylus* (Sauria, Teiidae). Postilla 159:1–67.
- Wickham, H. 2009. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York.
- 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., and A. L. C. Prudente. 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. Fourth edition. Prentice-Hall, Upper Saddle River, New Jersey.