

A NEW SPECIES OF *ATRACTUS* (SERPENTES: DIPSADIDAE) FROM THE ANDES OF ECUADOR

DAVID SALAZAR-VALENZUELA^{1,2,4}, OMAR TORRES-CARVAJAL², AND PAULO PASSOS³

¹ Department of Evolution, Ecology, and Organismal Biology, The Ohio State University, 300 Aronoff Laboratory, 318 West 12th Avenue, Columbus, OH 43210, USA

² Escuela de Biología, Pontificia Universidad Católica del Ecuador, Avenida 12 de Octubre y Roca, Apartado 17-01-2184, Quito, Ecuador

³ Departamento de Vertebrados, Museu Nacional, Quinta da Boa Vista, Universidade Federal do Rio de Janeiro, Rio de Janeiro, RJ, 20940-040, Brasil

ABSTRACT: A new species of *Atractus* is described from cloud forests of the extreme northern Ecuadorian Andes, Tulcán County, Carchi Province. *Atractus savagei* sp. nov. is distinguished from all congeners by the combination of 17 dorsal scale rows, long loreal, six supralabials (third and fourth contacting orbit), seven infralabials (first four contacting chinshields), 5–8 maxillary teeth, 161–165 ventrals in females and 149–154 in males, 23–26 subcaudals in females and 28–33 in males, a brown dorsum with black specks on the margins of scales, two black longitudinal stripes on each side of the body, yellow ventral color of head gradually changing to orange and red toward the back of the body, venter with lateral and median series of black blotches arranged in conspicuous longitudinal stripes, moderate body size, a long tail in males, and a moderately bilobed, barely capitate, and slightly calyculate hemipenis. Based on shared morphological characters, especially hemipenial features, we propose to tentatively allocate the new species to the *A. paucidens* group.

RESUMEN: Se describe una nueva especie de *Atractus* de los bosques nublados del extremo norte de los Andes ecuatorianos, Cantón Tulcán, Provincia de Carchi. *Atractus savagei* sp. nov. se distingue de otras especies del género por la combinación de 17 filas de escamas dorsales, loreal larga, 6 supralabiales (tercera y cuarta contactando la órbita), 7 infralabiales (primeras cuatro en contacto con las geneiales), 5–8 dientes maxilares, 161–165 ventrales en hembras y 149–154 en machos, 23–26 subcaudales en hembras y 28–33 en machos, dorso café con manchas negras en los márgenes de las escamas, dos líneas longitudinales negras en cada lado del cuerpo, color ventral de la cabeza amarillo que cambia gradualmente a naranja y rojo hacia atrás del cuerpo, vientre con series laterales y medias de manchas negras dispuestas en líneas longitudinales conspicuas, tamaño del cuerpo moderado, cola larga en machos, y un hemípene moderadamente bilobular, muy poco capitado y un poco caliculado. Con base en caracteres morfológicos compartidos, especialmente asociados a los hemipenes, se propone incluir tentativamente a esta nueva especie en el grupo *A. paucidens*.

Key words: *Atractus paucidens* species group; *Atractus savagei* sp. nov.; Cloud forest; Groundsnake; Hemipenis; Morphological variation

THE CRYPTOZOIC snake genus *Atractus* Wägler, 1828, is distributed widely in the Neotropical region, occurring from central Panama to northeastern Argentina (Giraldo and Scrocchi, 2000; Myers, 2003). Totalling about 140 recognized species so far, *Atractus* is the richest snake genus (Passos et al., 2010b,c), with most of this diversity concentrated in the northern Andes (Colombia, Venezuela, and Ecuador; Schargel and García-Pérez, 2002; Passos, 2008). Probably owing to their secretive habits, altitudinal endemism, and lack of proper identification in herpetological collections, most species are known from only a few specimens and localities, which in turn has made the

taxonomic delimitation within the genus historically challenging (Myers, 2003; Passos et al., 2007a). One of the early strategies adopted by researchers (Savage, 1960; Roze, 1961; Hoogmoed, 1980; Cunha and Nascimento, 1983; Martins and Oliveira, 1993) to deal with this bewildering diversity was to focus their studies on small geographical regions: countries or biogeographical provinces (Schargel et al., 2013). Although not ideal because it precludes the analysis of intra- and interspecific variation across the whole distribution of a species or group, such an approach has been extensively replicated over the last decade (Myers, 2003; Silva-Haad, 2004; Esqueda and La Marca, 2005; Passos et al., 2009e, 2010c; Passos and Lynch, 2010; Schargel et al., 2013). These studies have increased our understanding of the morpho-

⁴ CORRESPONDENCE: e-mail, salazar-valenzue.1@osu.edu

logical variation present in *Atractus*, and a comprehensive taxonomic review of the entire genus is likely a more feasible future achievement, especially with the addition of molecular approaches.

Savage (1960) published a taxonomic revision of Ecuadorian *Atractus* in which he recognized 16 species for the country, provided comparable diagnoses, and described their morphological variation (meristic, morphometric, color pattern, and hemipenis characters). After Savage's (1960) influential and comprehensive work, Cisneros-Heredia (2005) and Passos et al. (2007a, 2012) reported the morphological variation for *A. dunnii*, *A. modestus*, and *A. microrhynchus*, respectively, three species previously known exclusively from Ecuadorian holotypes (Savage, 1955, 1960; Passos et al., 2009e). Myers and Schargel (2006) described *A. gigas* on the basis of a single specimen from Bosque Protector Río Guajalito, Pichincha, Ecuador, and Tolhurst et al. (2010) and Passos et al. (2010b) reported morphological variation (meristic, morphometric, and color pattern characters) of this species based on additional samples. A revision of *A. duboisi*, *A. occipitotuberculatus*, and *A. orcesi*, species with a distribution that mainly includes eastern Ecuador, was provided by Passos et al. (2010a). More recently, the variation present in *A. carrioni*, *A. major*, and *A. snethlageae* was reviewed, as well as the description of *A. touzeti* for the eastern cloud forests of the country (Passos et al., 2013a; Schargel et al., 2013). Currently, 23 *Atractus* species are reported for Ecuador (Torres-Carvajal et al., 2014).

In the course of examining Ecuadorian collections and conducting fieldwork in the cloud forests of the northern Andes of the country, we identified specimens of an undescribed species of the *Atractus paucidens* group, which we describe herein.

MATERIALS AND METHODS

Material Examined

Specimens examined are housed in institutions in Colombia, Ecuador, Peru, Brazil, Switzerland, and the United States. Data from additional specimens of *Atractus* are found in Passos et al. (2005, 2007a,b, 2009a,b,c,d,e,

2010a,b,c, 2012, 2013a,b,c,d), Passos and Fernandes (2008), Prudente and Passos (2008, 2010), Passos and Arredondo (2009), Passos and Lynch (2010), and Passos and Prudente (2012).

Techniques and Characters

Terminology for cephalic shields follows Savage (1960), whereas ventral and subcaudal counts follow Dowling (1951). Loreal scale character states follow Passos et al. (2007a). Measurements were taken with a dial caliper (± 0.1 mm), except for snout–vent length (SVL) and caudal length (CL), which were measured with a ruler (± 1 mm); values are reported as means ± 1 SD. Paired cephalic scales were described and measured on the right side. Sex was determined by the presence or absence of hemipenes through a ventral incision at the base of the tail. We examined maxillae in situ under a Zeiss Stemi 2000-C stereoscope through a narrow lateromedial incision between the supralabials and the maxillary arch. After removing tissues covering the maxillary arch, we counted teeth and empty sockets. The method for preparation of preserved hemipenes was modified from Pesantes (1994) in replacing KOH with water. Hemipenes were immersed for 6 h in an alcoholic solution of Alizarin Red to dye the calcareous ornaments (e.g., spines) according to modifications by Nunes et al. (2012) from original procedures used by Uzzell (1973). Terminology for hemipenis description follows Dowling and Savage (1960), as augmented by Myers and Campbell (1981) and Zaher (1999). We follow Passos et al. (2009b, 2010c) with respect to conditions of the morphological characters used in the diagnosis and description.

RESULTS

Atractus savagei sp. nov. (Figs. 1–3, Table 1)

Holotype.—Adult female, QCAZ (Museo de Zoología, Pontificia Universidad Católica del Ecuador) 8713 collected on 25 February 2009 by Omar Torres-Carvajal, Silvia Aldás-Alarcón, and Elicio E. Tapia, surroundings of Chilmá Bajo on the way to Tres Marías waterfall

($0^{\circ}51'53.82''N$, $78^{\circ}2'59.23''W$; datum = WGS84; 2071 m above sea level [asl]), Tucán County, Carchi Province, Ecuador.

Paratypes.—Twelve specimens with same locality data as holotype: two adult females (QCAZ 8714 and 8691), four adult males [QCAZ 8692, 8715, 8716 and MNRJ (Museu Nacional, Universidade Federal do Rio de Janeiro) 23267], and one juvenile male (QCAZ 8722) collected 23–26 February 2009 by same collectors as the holotype. Two adult females (QCAZ 5774 and 5777), one adult male (QCAZ 57767), one juvenile male (QCAZ 5773), and one juvenile female (QCAZ 5775) collected on 21 February 2013 by David Salazar-Valenzuela, Henry Pozo, Arnulfo Chapapud, and David Males. An adult male (QCAZ 7504) collected on 10 June 1989 by Luis A. Coloma, 26.9 km east of Maldonado on the road to Tucán ($0^{\circ}48'28.8''N$, $78^{\circ}1'8.4''W$; datum = WGS84; 2420 m asl), Tucán County, Carchi Province, Ecuador.

Diagnosis.—*Atractus savagei* is distinguished from all congeners by the following combination of characters: (1) 17–17–17 smooth dorsal scale rows; (2) two postoculars; (3) long loreal; (4) temporals 1 + 2; (5) six supralabials, third and fourth contacting orbit; (6) seven infralabials, first four contacting chinshields; (7) 5–8 maxillary teeth; (8) four gular scale rows; (9) four preventrals; (10) 161–165 ventrals in females, 149–154 in males; (11) 23–26 subcaudals in females, 28–33 in males; (12) brown dorsum with black specks on the margins of the scales and two black longitudinal stripes on each side of the body: one occupying the upper and lower half of the first and second dorsal scale rows, respectively, and a second stripe present on the upper margin of the fourth dorsal scale row; (13) ventral ground color of head yellow, gradually changing to orange and red toward the back of the body, with two lateral and two medial series of round to rhomboidal black blotches arranged into four conspicuous longitudinal stripes; (14) moderate body size (females and males reaching 335 and 297 mm SVL, respectively); (15) long tail in males (14.4–18.2% SVL), moderate (11.3–12.5% SVL) in females; (16) hemipenis moderately bilobed, barely capitate, and slightly calyculate.



FIG. 1.—Dorsal (A), lateral (B), and ventral (C) views of the head of the holotype of *Atractus savagei* sp. nov. (QCAZ 8713). Eye diameter = 1.5 mm. Photographs by D. Quiroga.

Comparisons.—Among all congeners, *Atractus savagei* is unique in having a ventral coloration in preservative consisting of a cream-colored background with three or four black longitudinal stripes (two conspicuous stripes are always present on the sides of the venter and one or two irregular stripes are located on the center). Other *Atractus* species with 17 dorsal scale rows, a dark brown or black dorsum, and a cream venter with black blotches arranged in linear series are *A. chthonius*, *A. macondo*, and melanistic specimens of *A. lancingii* or *A. ayeush*. *Atractus savagei* differs from all of these by having two regular and one or two irregular stripes on venter (vs. generally one median stripe in *A. chthonius*, *A. lancingii*, and *A. ayeush* and two

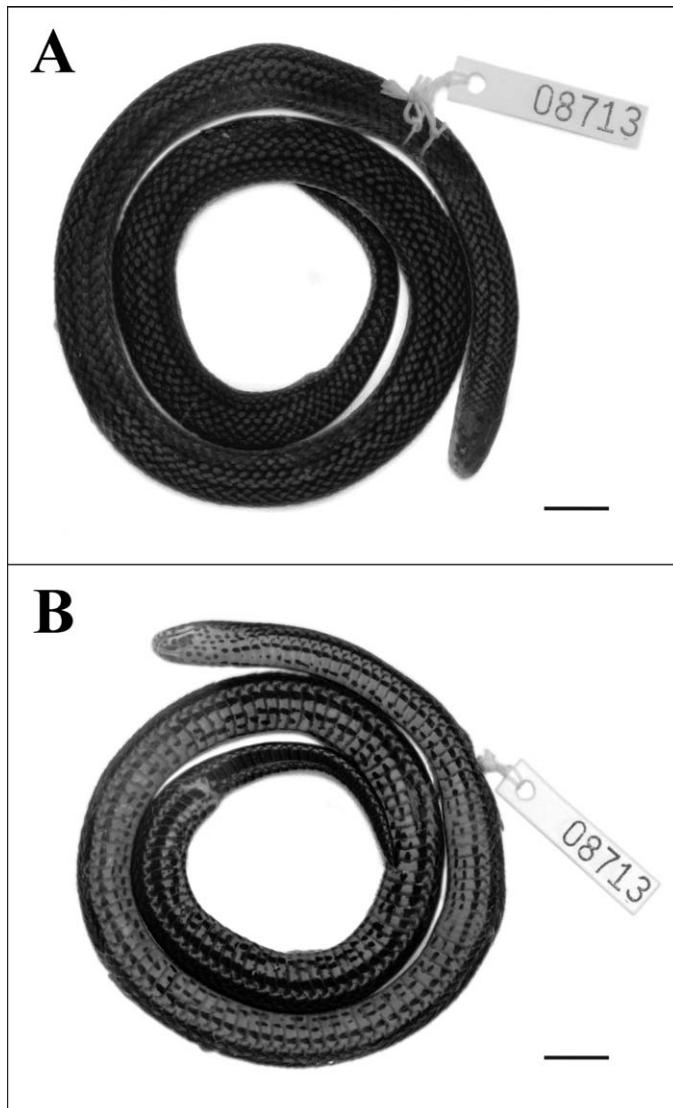


FIG. 2.—Dorsal (A) and ventral (B) views of the holotype of *Atractus savagei* sp. nov. (QCAZ 8713). Scale bar = 1 cm. Photographs by D. Quirola.

lateral irregular stripes in *A. macondo*), six supralabials (vs. seven supralabials in *A. ayeush*, *A. chthonius*, and *A. macondo* and seven or eight in *A. lencinii*), and 5–8 maxillary teeth (vs. ≥ 9 in *A. chthonius* and *A. macondo*). Moreover, it differs from *A. chthonius*, *A. lencinii*, and *A. ayeush* by having 149–154 ventrals in males, 161–165 ventrals in females, and 28–33 subcaudals in males (vs. 138–146, 137–148, and 20–21, respectively, in

A. chthonius; 153–172, 159–182, and 32–40, respectively, in *A. lencinii*; and 155 ventrals in females of *A. ayeush*).

Regarding Ecuadorian species of *Atractus* with an Andean distribution, besides its distinct color pattern, *A. savagei* differs from *A. carrióni* by having a loreal scale (vs. lacking loreal); from *A. duboisi* by having 17 dorsal scale rows, six supralabials, 28–33 subcaudals in males and 23–26 in females (vs. 15 dorsal

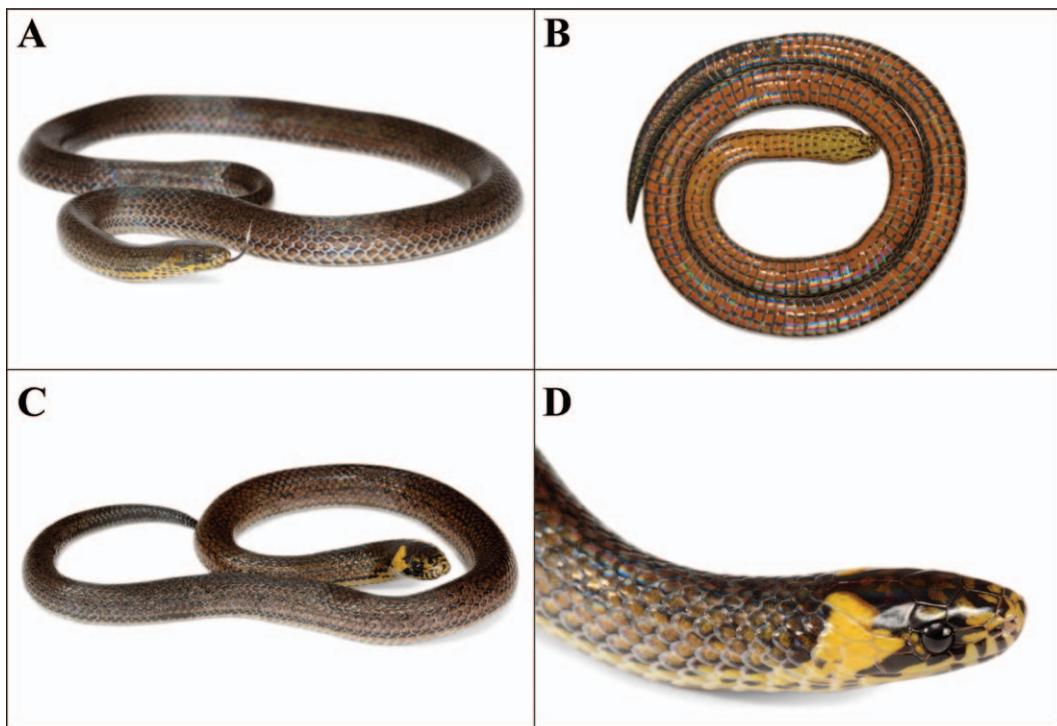


FIG. 3.—*Atractus savagei* sp. nov. in life. Lateral (A) and ventral (B) views of adult male individuals (QCAZ 5776 and 8716, respectively); lateral (C) view and head detail (D) of a juvenile male (QCAZ 5773). (A color version of this figure is available online.)

scale rows, eight supralabials, 23–26 subcaudals in males and 13–21 in females); from *A. dunni* by having four gular scale rows, 149–154 ventrals in males and 161–165 in females (vs. usually three gular scales row, 125–144 ventrals in males and 137–157 in females); from *A. ecuadorensis* by having six supra-

labials, seven infralabials, four gular series, and 28–33 subcaudals in males (vs. seven supralabials, five infralabials, three gular series, and 40 subcaudals in the single male known); from *A. gigas* by having four gular scale rows and four preventrals, 149–154 ventrals in males and 161–165 in females,

TABLE 1.—Morphometric (measurements in mm) and meristic data for the type series of *Atractus savagei* sp. nov. Abbreviations: SVL = snout-vent length, CL = caudal length, BD = body diameter, HL = head length, HW = head width, ED = eye diameter.

Character	Adults		Juveniles		Adult males		Adult females	
	(n = 11)	Range	(n = 3)	Range	(n = 6)	Range	(n = 5)	Range
SVL	280.9	236–335	165.3	147–187	270	236–297	294	236–335
CL	41.1	29–50	22.7	19–27	46	40–50	35.2	29–42
CL/SVL × 100	14.7	11.3–18.2	13.7	11.7–15	17.1	16–18.2	12	11.3–12.5
BD	7.6	5.4–8.6	5.3	4.4–6.7	7.8	6.8–8.4	7.4	5.4–8.6
HL	9.2	8.4–10.2	7.6	7.3–7.9	9	8.4–9.8	9.3	8.4–10.1
HW	5.9	5.2–6.9	5.1	4.5–5.6	5.8	5.4–6.1	5.9	5.2–6.9
ED	1.5	1.3–1.7	1.3	1.1–1.4	1.5	1.3–1.7	1.5	1.5–1.6
Ventrals	155.7	149–165	155	152–161	150.2	149–154	162.4	161–165
Subcaudals	28.1	23–33	28.7	25–33	31.3	30–33	24.2	23–26

28–33 subcaudals in males and 23–26 in females (vs. three gular scales and three preventrals, 155–164 ventrals in males and 166–177 in females, 42–46 subcaudals in males and 25–37 in females); from *A. lehmanni* by having 149–154 ventrals in males, 161–165 ventrals in females, and 28–33 subcaudals in males (vs. 141–144 ventrals in males, 148–153 ventrals in females, and 23–29 subcaudals in males); from *A. microrhynchus* by having six supralabials, four gular scale rows and four preventrals (vs. seven supralabials, three gular scales, and three preventrals); from *A. modestus* by having 149–154 ventrals in males and 161–165 in females (vs. 155–173 ventrals in males and 174–185 in females); from *A. occidentalis* by having six supralabials, seven infralabials, four gular scale rows, and 28–33 subcaudals in males (vs. seven supralabials, six infralabials, three gular scale rows, and 39 subcaudals in the single male known); from *A. orcesi* by having 17 dorsal scale rows, six supralabials, 161–165 ventrals and 23–26 subcaudals in females (vs. 15 dorsal scales rows, eight supralabials, 142–158 ventrals and 13–22 subcaudals in females); and from *A. roulei* by having 17 dorsal scale rows, 5–8 maxillary teeth, 149–154 ventrals in males and 161–165 in females, 28–33 subcaudals in males and 23–26 in females (vs. 15 dorsal scales rows, 10–11 maxillary teeth, 137–145 ventrals in males and 145–149 in females, 20–26 subcaudals in males and 14–23 in females).

Description of the holotype.—Adult female, 335 mm SVL, 42 mm CL (12.5% SVL); head rounded in dorsal view, flattened in lateral view, 10.1 mm long (3.0% SVL), 6.9 mm wide (68.3% head length); cervical constriction indistinct; snout rounded in dorsal view, truncated in lateral view; rostrum–orbit distance 4.2 mm (41.6% head length); nasal–orbit distance 2.9 mm (28.7% head length); intraorbital distance 4.4 mm (63.8% head wide); body subcylindrical, body diameter 8 mm (2.4% SVL); belly flattened; tail moderately long, with terminal spine moderately long and acuminate; rostral subtriangular in frontal view, wider (2.3 mm) than high (1.5 mm), visible from above; internasal slightly wider (1.2 mm) than long (1.1 mm); internasal suture (2.1 mm long) sinistral to prefrontal

median suture; prefrontal slightly wider (2.4 mm) than long (2.3 mm); frontal subtriangular, about as wide (3.2 mm) as long; supracocular subtrapezoidal, longer (2.0 mm) than wide (1.5 mm); parietal about twice as long (4.8 mm) as wide (2.9 mm); nasal divided; prenasal about as high (1.2 mm) as long (1.0 mm), contacting rostral, internasal, first supralabial, and postnasal; postnasal about as high (0.9 mm) as long (1.1 mm), contacting prenasal, prefrontals, loreal, and first and second pair of supralabials; long loreal (2.1 mm long, 0.9 mm high); loreal contacting eyes, prefrontals, nasals, and second to third supralabials; eye diameter 1.5 mm; pupil round; two postoculars, upper postocular higher (0.9 mm) and longer (0.8 mm) than lower postocular (0.8 mm high, 0.5 mm long); upper postocular contacting eye, lower postocular, supraocular, parietal, and anterior temporal; lower postocular contacting eye, upper postocular, fourth and fifth supralabial, and anterior temporal; temporals 1 + 2; anterior temporal twice as long (2.0 mm) as high (1.0 mm), contacting parietal, fifth supralabial, postoculars, and posterior temporals; upper posterior temporal elongate (3.4 mm long, 1.0 mm high), about three times as long as wide; lower posterior temporals similar in size and shape to anterior temporal (1.8 mm long, 0.9 mm high); six supralabials, third and fourth contacting orbit; second supralabial higher than first and lower than third; fifth supralabial (2.5 mm long, 1.8 mm high) higher and sixth (2.6 mm long, 1.4 mm high) longer than remaining supralabials; symphysis subtriangular, twice as wide (2.0 mm) as long (1.0 mm); seven infralabials, first four pairs contacting chinshields; first pair of infralabials in contact behind symphysis, preventing symphysis/chinshield contact; chinshields about three times as long (3.2 mm) as wide (1.2 mm); 17–17–17 smooth dorsal scales rows, lacking apical pits and supra-anal tubercles; four gular scale rows between last supralabial and preventral; four preventral scales; 161 ventral scales; anal plate single; 25/24 (left/right) subcaudal scales. Maxilla arched anteriorly in dorsal view and flattened on median to posterior portion; maxillary arch with four prediastemal and two postdiastemal teeth; prediastemal teeth angular in cross section,

robust at base, narrower at apices, curved posteriorly; first two teeth large, moderately spaced and similar in size; third and fourth prediastemal teeth reduced in size; maxillary diastema moderate, with space equivalent to distance between third and fourth teeth; postdiastemal teeth slightly smaller than fourth prediastemal one; lateral process of maxilla moderately developed.

Coloration in preservative of the holotype (Figs. 1, 2).—Dorsum of head brown, with dark brown spots dispersed over rostral, internasals, prefrontals, frontal, and supraoculars; parietals brown with variegate dark brown blotches concentrated around interparietal suture, from anterolateral region to medial portion of parietal shields; lateral surface of head brown up to the dorsal edges of supralabials, with black spots irregularly dispersed over posterior region of postnasal and along loreal; rostral and mental creamish white with black spots on the margins; black postocular stripe descending, covering postoculars, anterior portion of first temporal, and posterior and anterior halves of fifth and sixth supralabials, respectively; supralabials mostly creamy, with invasion of black pigment on posterior suture between scales and below eye; posterior part of sixth supralabial brown; temporal and occipital regions brown scattered with black dots; first two infralabials (on each side) black, with region adjacent to chinshields creamish white; third infralabial creamish white anteriorly and above with a conspicuous black spot posteriorly; fourth infralabial white above and black below, and vice versa on sixth infralabial; fifth and seventh infralabials black anteriorly and white posteriorly; mental region cream with black dots on anterior portion of chinshields; gular series and preventrals with dark brown blotches. Dorsal ground color brown with black specks present on margins of the scales and not displaying any characteristic pattern, except for two black longitudinal stripes on each side of the body; the first stripe is more conspicuous and occupies the upper and lower half of the first and second dorsal scale rows, respectively, the second stripe is faint and occupies the upper margin of the fourth dorsal scale row; black dots on each dorsal scale are more concentrated on the distal part

of the tail; lower half of the first dorsal scale row cream along the body and tail. Ventral background cream (orange hue on posterior half of body) with scattered dark brown marks; first 25 ventrals predominantly cream with dark brown irregular dots positioned in the middle and toward the lateral margins of the scales, forming three conspicuous stripes; posterior to that point the central stripe divides and four lines are evident: two along the center of the ventrals and two near the margins; lateralmost edge of ventrals creamy colored; dark brown dots concentrated toward posterior region of body; underside of tail dark brown suffused with few creamy dots concentrated on margins of subcaudals, in the sutures between them, and in the extreme tip of the tail.

Color variation in preservative.—Dorsal ground color of body similar in all specimens; some individuals have a light brown vertebral band that includes the medial half of each of two dorsal rows; this band is bordered laterally by black stripes that are each half a scale wide; in some specimens both dorsolateral black stripes are conspicuous with the space between them cream; disposition of black bars on infralabials is variable with respect to holotype; orange hue of venter is lost in some specimens and the presence of the four black ventral stripes is variable, with some individuals showing them markedly, while in others the two medial stripes fuse into one intermittently, and still others possess one medial and two wide paraventral stripes. Ontogenetic variation is present in juveniles by the occurrence of cream and black blotches dispersed over loreal, postnasals, prefrontals, and supraoculars. They also possess an incomplete cream nuchal band that does not meet on the interparietal suture.

Color in life (Fig. 3).—The following description is based on analysis of color photographs and recently collected female, male, and juvenile individuals (QCAZ 5773–5777, QCAZ 8692, and QCAZ 8716). Dorsum brown with black specks on the margins of the scales, except on the two paraventral dorsal rows on each side of the body; first dorsal scale row light brown ventrally and black on the upper half; second dorsal scale row black on lower half and gray on the upper half; black

coloration forms a longitudinal stripe on the upper and lower half of the first and second dorsal scale rows, respectively; another black stripe present on the edge of the fourth dorsal scale row; tail with two paravertebral black stripes and a reddish brown band between them. Iris dark brown and black tongue with white tips. Ventral portion of head, preventrals, rostral, and supralabials yellow with black markings; around 20 of the anteriormost ventral scutes are orange and the rest of the venter is red; two lateral and two median black longitudinal stripes along ventral surface of body; underside of tail black on the edges, with a red band medially. Light marks on the front of the head and nuchal band of juveniles is yellow.

Quantitative variation.—Largest male 297 mm SVL, 49 mm CL; largest female 335 mm SVL, 42 mm CL; tail 14.4–18.2% SVL ($\bar{X} = 16.5 \pm 1.3\%; n = 8$) in males, 11.3–12.5% SVL ($\bar{X} = 11.9 \pm 0.5\%; n = 6$) in females; 149–154 ($\bar{X} = 151 \pm 1.9; n = 8$) ventrals in males, 161–165 ($\bar{X} = 162 \pm 1.8; n = 6$) in females; 28–33 ($\bar{X} = 31 \pm 1.6; n = 8$) subcaudals in males, 23–26 ($\bar{X} = 24 \pm 1.2; n = 6$) in females; body diameter 5.4–8.6 mm ($\bar{X} = 7.6 \pm 0.6$ mm; $n = 10$) in adults, 4.4–6.7 mm ($\bar{X} = 5.3 \pm 1.2$ mm; $n = 3$) in juveniles (Table 1); five ($n = 4$ sides), six ($n = 9$ sides), seven ($n = 9$ sides), or eight ($n = 5$ sides) maxillary teeth.

Hemipenial morphology.—The following description is based on the left hemipenis of MNRJ 23267. Retracted organ bifurcates at sixth and extends to the level of 11th subcaudal. Fully everted and almost maximally expanded hemipenis rendered a bilobed, barely captiate, and semicalyculate organ. Lobes with similar size, right lobe slightly longer than left, clavate at base and attenuated in the apices; lobes centrifugally oriented, with rounded apices; terminal portion of lobes with slight constriction, just below the apices and in lateral portion of inner sides of lobes; lobes clearly distinct from barely defined capitulum, as long as hemipenial body on sulcate side, and about half the length of the hemipenial body on asulcate side; lobes covered with moderate alary spines on basal portion and spinulate calyces from the basis increasing toward apices of lobes; calyces poorly developed on sulcate side and more

conspicuous on asulcate side; vertical walls of calyces connected at lobular portion of capitulum; spinulate calyces on both sides of organ replaced by papillae toward distal portion of lobes; tip of lobes with large papillae vertically oriented; capitular groove indistinct on sides of organ; capitulum located above bifurcation of sulcus spermaticus; intrasulcar region of capitulum with spines enlarged in their base disposed on longitudinal series similar to alary spines previously reported in the genus (see Passos et al., 2013d); sulcus spermaticus bifurcates on basal portion of hemipenial body; branches of sulcus spermaticus centrifugally oriented, running to tips of lobes; sulcus spermaticus margins narrow, bordered with spinules from basal portion of organ to lobular region; spinules replaced by papillae on distal region of lobes; hemipenial body subelliptical, uniformly covered with moderate hooked spines; large hooked spines concentrated on lateral region of sulcate side and homogeneously distributed on asulcate side; basal naked pocket located on the left area of basal portion on sulcate side of organ; basal portion of hemipenis uniformly covered with longitudinal plicae (Fig. 4). The left everted hemipenis of QCAZ 8715 is very similar to that of MNRJ 23267.

Etymology.—The specific epithet is a noun in the genitive case, in honor of Professor Jay M. Savage for his lifetime of fruitful work with the New World herpetofauna (Donnelly, 2013), and also as a tribute to his seminal monograph on Ecuadorian *Atractus* (Donnelly, 2013). Proposed standard English and Spanish names: Savage's Groundsnakes; Culebras Tiereras de Savage.

Distribution and natural history.—*Atractus savagei* is known from the western versant of the Cordillera Occidental of the extreme northern Ecuadorian Andes in Tulcán County, Carchi Province. *Atractus savagei* occurs at two montane cloud forest (Valencia et al., 1999) localities between 2071 and 2420 m asl (Fig. 5). Some of the specimens collected in the type locality were found below mounds of dirt, stones, and moss in conjunction with eggs of *Liophis vitti* (Curcio et al., 2009) and a specimen of an undescribed species of slender blindsnake of the genus *Trilepida* (D. Salazar-



FIG. 4.—Sulcate (A) and asulcate (B) views of the hemipenis of *Atractus savagei* sp. nov. (left organ from MNRJ 23267) from Chilmá Bajo, Carchi Province, Ecuador. Scale bar = 5 mm.

Valenzuela and O. Torres-Carvajal, personal observations). The rest were found below stones located in areas of pasture or on the side of the road.

DISCUSSION

Passos et al. (2009e) proposed the *Atractus paucidens* species group to accommodate Pacific lowland species of *Atractus* sharing a unique combination of morphological characters. The authors indicated that at least some of these features might constitute derived characters in the evolution of the subfamily Dipsadinae (e.g., presence of a lateral projection on the proximal region of the hemipenis), most specifically to the unnamed clade from Grazziotin et al. (2012). In terms of external

morphological characteristics (meristic, morphometric, and color pattern characters), *A. savagei* is most similar to the members of the *A. paucidens* group, sharing the following features: dorsum in preservative dark brown or black, belly in preservative heavily pigmented with dark brown blotches or dots on the lateral portion of ventrals, and long tail in females and males. The only external features of *A. savagei* that do not fit the definition of the *A. paucidens* group are the total number of infralabials (seven and six, respectively) and number of infralabial scales contacting chin shields (four and three, respectively). Both characters are frequently correlated, however, and might occur individually or in some combination in several other species or

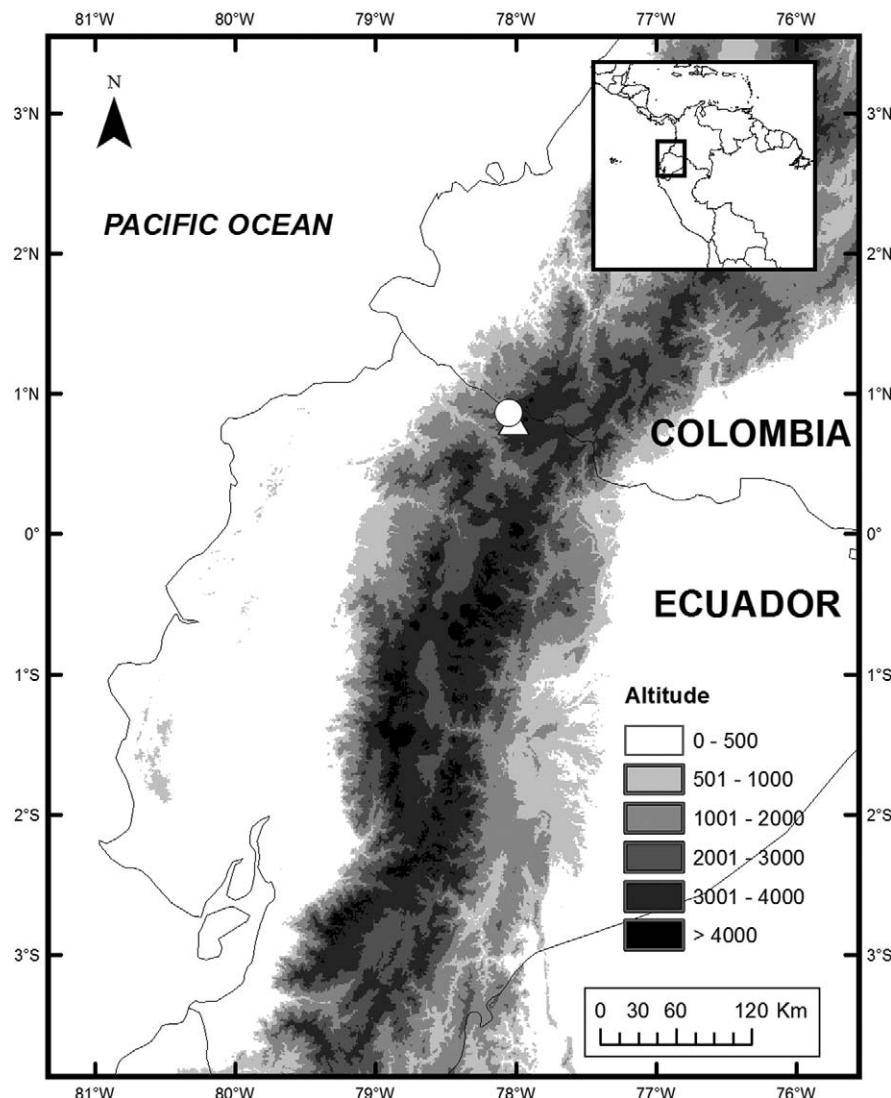


FIG. 5.—Geographic distribution of *Atractus savagei* sp. nov. in northwestern Ecuador. Circle represents type locality; triangle indicates the other locality where individuals have been collected.

species groups in the genus (Passos et al., 2012).

With respect to hemipenial morphology, *Atractus savagei* revealed an intermediate hemipenial condition presenting a basal bifurcation of the sulcus spermaticus similar to the members of the *A. multicinctus* group and lacking the capitulation structures like the members of the *A. paucidens* group (Passos et al., 2009e). The hemipenis of *A. savagei* differs from that of most members of the *A.*

paucidens group in lacking a lateral projection on the proximal region, and in having well-developed lobular calyces (Fig. 4). Nonetheless, such features are apparently restricted to a few lowland species (e.g., *A. iridescens* and *A. typhon*) and might represent synapomorphies in a less inclusive level within the *A. paucidens* species group. We propose to tentatively allocate *A. savagei* to the *A. paucidens* group based on the aforementioned shared external and hemipenial characters.

We recognize that we are not testing homologies, however, and only a robust phylogenetic analysis will help clarify evolutionary relationships among species of *Atractus*.

Localities in cloud forests of extreme northwestern Ecuador, where *Atractus savagei* individuals have been registered, belong to an area still in need of exploration. Most snake species described from Ecuador in recent decades have been found in cloud forests or midelevation localities of the Andes (Hillis, 1990; Freire-Lascano, 1991; Dixon, 2000; Myers and Schargel, 2006; Schargel et al., 2013). These forests are cradles of diversity for amphibians and reptiles, showing high species richness and endemism (Duellman, 1979; Hutter et al., 2013; Pincheira-Donoso et al., 2013). Additionally, distributional data and climatic models for some vertebrate groups point to the existence of a transition between northern and central parts of the Chocó bioregion (western Colombia and northwestern Ecuador) and communities found farther south along the Pacific coast and adjacent Andean slopes of Ecuador (Anderson and Jarrín-V., 2002; Anderson and Martínez-Meyer, 2004; Cisneros-Heredia, 2006). The recent description of snake species from the Colombia–Ecuador border (Passos et al., 2009e; Torres-Carvajal et al., 2012) provides support for these observations and demands a greater focus of surveys on these areas.

Acknowledgments.—We thank the following curators and their staff for allowing us to examine specimens under their care: C. Aguilar and J. Santa-Cadea (Universidad Mayor de San Marcos), A. Almendáriz (Escuela Politécnica Nacional), M. Bernal (Universidad de Tolima), R. Casallas and A. Rodrigues (Universidad de La Salle), F. Castro (Universidad del Valle), F.L. Franco and A. Germano (Instituto Butantan), K. de Queiroz and R. Wilson (National Museum of Natural History), S. Fisch-Muller and A. Schmitz (Muséum d'Histoire Naturelle de la Ville de Genève), J.M. Guayasamín (Universidad Tecnológica Indoamérica), A. Leviton (California Academy of Sciences), J.D. Lynch and M. Calderón (Instituto de Ciencias Naturales), C. McCarthy (Natural History Museum), D. Pericó (Instituto Alexander Von Humboldt), L. Trueb (University of Kansas), P. Venegas (Centro de Ornitología y Biodiversidad), and A. Zamudio (Colegio San José). We are grateful to E. Levy, A. Pozo, and the Chilimá Bajo community for assistance with logistics in the field. S. Aldás, G. Buitrón, P. Piedrahita, and E. Tapia provided assistance in the field. We thank A. Carvajal for improving the distribution map and P. Santiana for help with figure editing. L. Bustamante and A. Arteaga kindly shared information on *Atractus dunnii* and *A. occidentalis*.

Reviews by W.E. Schargel, M.L. Holding, and an anonymous reviewer substantially improved the manuscript. The specimens were collected under collection permit 008–09 IC-FAU-DNB/MA and were deposited at Museo de Zoología (QCAZ), Pontificia Universidad Católica del Ecuador. DSV received a travel grant from the Muséum d'Histoire Naturelle de la Ville de Genève. OTC received support from Secretaría Nacional de Ciencia y Tecnología del Ecuador, project PIC-08-0000470. Financial support for PP was provided by Conselho Nacional de Desenvolvimento Científico e Tecnológico, Pró-Reitoria de Pós-Graduação e Pesquisa da Universidade Federal do Rio de Janeiro (PR-2/UFRJ), Fundação de Amparo à Pesquisa do Estado de São Paulo (process 2011/50313-0), and Fundação Carlos Chagas de Amparo à Pesquisa do Estado do Rio de Janeiro (processes E-26/110.434/2012 and E-26/111.636/2012).

LITERATURE CITED

- Anderson, R.P., and P. Jarrín-V. 2002. A new species of spiny pocket mouse (Heteromyidae: *Heteromys*) endemic to western Ecuador. American Museum Novitates 3382:1–26.
- Anderson, R.P., and E. Martínez-Meyer. 2004. Modeling species' geographic distributions for preliminary conservation assessments: an implementation with the spiny pocket mice (*Heteromys*) of Ecuador. Biological Conservation 116:167–179.
- Cisneros-Heredia, D.F. 2005. Rediscovery of the Ecuadorian snake *Atractus dunnii* Savage, 1955 (Serpentes: Colubridae). Journal of the National Museum (Prague), Natural History Series 174:87–94.
- Cisneros-Heredia, D.F. 2006. Distribution and ecology of the western Ecuador frog *Leptodactylus labrosus* (Amphibia: Anura: Leptodactylidae). Zoological Research 27:225–234.
- Cunha, O.R., and F.P. Nascimento. 1983. Ofídios da Amazônia. XX. As espécies de *Atractus* Wagler, 1928 na Amazônia oriental e Maranhão (Ophidia: Colubridae). Boletim do Museu Paraense Emílio Goeldi, Nova série, Zoológia 128:1–39.
- Curcio, F.F., V.d.Q. Piacentini, and D.S. Fernandes. 2009. On the status of the snake genera *Erythrolamprus* Boie, *Liophis* Wagler and *Lygophis* Fitzinger (Serpentes, Xenodontinae). Zootaxa 2173:66–68.
- Dixon, J.R. 2000. Ecuadorian, Peruvian, and Bolivian snakes of the *Liophis taeniurus* complex with descriptions of two new species. Copeia 2000:482–490.
- Donnelly, M.A. 2013. Jay M. Savage. Copeia 2013:757–767.
- 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.
- Duellman, W.E. 1979. The herpetofauna of the Andes: Patterns of distribution, origin, differentiation, and present communities. Pp. 371–459 In W.E. Duellman (Ed.), The South American Herpetofauna: Its Origin, Evolution, and Dispersal. University of Kansas Museum of Natural History Monograph, USA.

- Esqueda, L.F., and E. La Marca. 2005. Revisión taxonómica y biogeográfica (con descripción de cinco nuevas especies) de serpientes del género *Atractus* (Colubridae: Dipsadinae) en los Andes de Venezuela. *Herpetotropicos* 2:1–32.
- Freire-Lascano, A. 1991. Dos nuevas especies de *Bothrops* en el Ecuador. Universidad Técnica de Machala, Publicaciones de Trabajos Científicos del Ecuador:1–11.
- Giraldo, A.R., and G.J. Scrocchi. 2000. The genus *Atractus* (Serpentes: Colubridae) in north-eastern Argentina. *Herpetological Journal* 10:81–90.
- Graziotin, F.G., H. Zaher, R.W. Murphy, G. Scrocchi, M.A. Benavides, Y. Zhang, and S.L. Bonatto. 2012. Molecular phylogeny of the New World Dipsadidae (Serpentes: Colubroidea): a reappraisal. *Cladistics* 28:437–459.
- Hillis, D.M. 1990. A new species of Xenodontine colubrid snake of the genus *Synophis* from Ecuador and the phylogeny of the genera *Synophis* and *Emmochliophis*. *Ocassional Papers of the Museum of Natural History*. The University of Kansas, Lawrence, Kansas 135:1–9.
- 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 Verhandelingen* 175:1–47.
- Hutter, C.R., J.M. Guayasamin, and J.J. Wiens. 2013. Explaining Andean megadiversity: The evolutionary and ecological causes of glassfrog elevational richness patterns. *Ecology Letters* 16:1135–1144.
- Martins, M., and M.E. Oliveira. 1993. The snakes of the genus *Atractus* Wagler (Reptilia: Squamata: Colubridae) from the Manaus region, Central Amazonia, Brazil. *Zoologische Mededelingen* 67:21–40.
- 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 J.A. Campbell. 1981. A new genus and species of colubrid snake from Sierra Madre del Sur of Guerrero, Mexico. *American Museum Novitates* 2708:1–20.
- Myers, C.W., and W.E. Schargel. 2006. Morphological extremes—two new snakes of the genus *Atractus* from northwestern South America (Colubridae: Dipsadinae). *American Museum Novitates* 3532:1–13.
- 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. 2008. Revisão Taxonômica do Gênero *Atractus* Wagler, 1828 (Serpentes: Colubridae: Dipsadinae). Ph.D. Dissertation, Universidade Federal do Rio de Janeiro, Brazil.
- 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., and R. Fernandes. 2008. A new species of colubrid snake genus *Atractus* (Reptilia: Serpentes) from central Amazon. *Zootaxa* 1849:59–66.
- Passos, P., and J.D. Lynch. 2010. Revision of *Atractus* (Serpentes: Disadidae) from middle and upper Magdalena drainage of Colombia. *Herpetological Monographs* 24:149–173.
- 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., R. Fernandes, and N. Zanella. 2005. A new species of *Atractus* (Serpentes: Colubridae) from southern Brazil. *Herpetologica* 61:209–218.
- 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., 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. Aguayo, and G. Scrocchi. 2009a. Rediscovery of the rare *Atractus bocki*, with assessment of the taxonomic status of *A. canedi* (Serpentes: Colubridae: Dipsadinae). *Journal of Herpetology* 43:710–715.
- Passos, P., J.C. Arredondo, R. Fernandes, and J.D. Lynch. 2009b. Three new *Atractus* (Serpentes: Colubridae) from the Andes of Colombia. *Copeia* 2009:425–436.
- Passos, P., G.R. Fuennmayor, 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., J.D. Lynch, and R. Fernandes. 2009d. 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., J.J. Mueses-Cisneros, J.D. Lynch, and R. Fernandes. 2009e. Pacific lowland snakes of the genus *Atractus* (Serpentes: Dipsadidae), with description of three new species. *Zootaxa* 2293:1–34.
- Passos, P., A. Chiesse, O. Torres-Carvajal, and J.M. Savage. 2010a. Testing species boundaries within the *Atractus occipitoalbus* complex (Serpentes: Dipsadidae). *Herpetologica* 65:384–403.
- Passos, P., M. Dobiey, and P.J. Venegas. 2010b. Variation and natural history notes on giant groundsnares, *Atractus gigas* (Serpentes: Dipsadidae). *South American Journal of Herpetology* 5:73–82.
- Passos, P., R. Fernandes, R.S. Bérnuls, and J.C. Moura-Leite. 2010c. Revision of the Atlantic Forest *Atractus* (Reptilia: Serpentes: Dipsadidae). *Zootaxa* 2364:1–63.
- Passos, P., D. 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., L.Y. Echevarría, and P.J. Venegas. 2013a. Morphological variation of *Atractus carrióni* (Serpentes: Dipsadidae). *South American Journal of Herpetology* 8:109–120.
- Passos, P., P.R.J. Kok, N.R. Albuquerque, and G.F. 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., L.O. Ramos, P.H. Pinna, and A.L.C. Prudente. 2013c. Morphological variation and affinities of the

- poorly known snake *Atractus caxiuanus* (Serpentes: Dipsadidae). Zootaxa 3745:35–48.
- Passos, P., M. Teixeira-Junior, R.S. Recoder, M.A. De Sena, F. Dal Vechio, H.B. Pinto, S.H.S.T. Mendonça, J. Cassimiro, and M.T. Rodrigues. 2013d. A new species of *Atractus* (Serpentes: Dipsadidae) from Serra de Cipó, Espinhaço Range, southeastern Brazil, with proposition of a new species group to the genus. Papéis Avulsos de Zoologia (São Paulo) 53:75–85.
- Pesantes, O. 1994. A method for preparing hemipenes of preserved snakes. Journal of Herpetology 28:93–95.
- Pincheira-Donoso, D., A.M. Bauer, S. Meiri, and P. Uetz. 2013. Global taxonomic diversity of living reptiles. PLoS ONE 8:e59741.
- Prudente, A.L.C., 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.C., and P. Passos. 2010. New cryptic species of *Atractus* (Serpentes: Dipsadidae) from Brazilian Amazonia. Copeia 2010:397–404.
- Roze, J.A. 1961. El género *Atractus* (Serpentes: Colubridae) en Venezuela. Acta Biológica Venezolana 3:103–119.
- Savage, J.M. 1955. Descriptions of new colubrid snakes, genus *Atractus*, from Ecuador. Proceedings of the Biological Society of Washington 68:11–20.
- Savage, J.M. 1960. A revision of the Ecuadorian snakes of the genus *Atractus*. Miscellaneous Publications of the Museum of Zoology, University of Michigan 112:1–86.
- Schargel, W.E., 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.
- Silva-Haad, J.J. 2004. Las serpientes colombianas del género *Atractus* Wagler, 1828 (Colubridae, Xenodontinae) en la Amazonía Colombiana. Revista de la Academia Colombiana de Ciencias Físicas, Exactas y Naturales 28:409–446.
- Tolhurst, B., M. Peck, J.N. Morales, T. Cane, and I. Recchio. 2010. Extended distribution of a recently described dipsadine colubrid snake: *Atractus gigas*. Herpetology Notes 3:73–75.
- Torres-Carvajal, O., D. Salazar-Valenzuela, and A. Merino-Viteri. 2014. ReptiliaWebEcuador, Version 2014.0. Available at <http://zoología.puce.edu.ec/Vertebrados/reptiles/ReptilesEcuador/>. Archived by WebCite at <http://webcitation.org/6QipH1fUS> on 30 June 2014.
- Torres-Carvajal, O., M.H. Yáñez-Muñoz, D. Quirola, E.N. Smith, and A. Almendáriz. 2012. A new species of blunt-headed vine snake (Colubridae, *Imantodes*) from the Chocó region of Ecuador. Zookeys 244:91–110.
- 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.
- Valencia, R., C. Cerón, W. Palacios, and R. Sierra. 1999. Las formaciones naturales de la Sierra del Ecuador. Pp. 79–108 In R. Sierra (Ed.), Propuesta Preliminar de un Sistema de Clasificación de Vegetación para el Ecuador Continental. Proyecto INEFAN/GERF-BIRF y Eco-ciencia, Ecuador.
- Wagler, J.G. 1828. Auszüge aus seinem Systema Amphibiorum. Isis von Oken 21:740–744.
- 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.

Accepted: 4 April 2014
Associate Editor: Bryan Stuart

APPENDIX

Specimens Examined

Countries are given in full capitals, states are capitalized, and municipalities are italicized. Specimens examined are housed in the following institutions: COLOMBIA—Colegio San José (CSJ), Medellín, Antioquia; Colección Zoológica de la Universidad de Tolima (CZUT-R), Ibagué, Tolima; Instituto Alexander Von Humboldt (IAvH), Villa de Leyva, Boyacá; Instituto de Ciencias Naturales (ICN), Universidad Nacional de Colombia, Bogotá; Museo de la Universidad de La Salle (MLS), Bogotá; Colección Herpetológica, Universidad del Valle (UV-C), Cali. ECUADOR—Museo de Historia Natural, Escuela Politécnica Nacional (EPN), Quito; Museo de Zoología, Pontificia Universidad Católica del Ecuador (QCAZ), Quito; Museo de Zoología, Universidad Tecnológica Indoamérica (MZUTI), Quito. PERU—Museo de Historia Natural de la Universidad Mayor de San Marcos (MUSM), Lima; Centro de Ornitología y Biodiversidad (CORBIDI), Lima. BRAZIL—Instituto Butantan (IBSP), São Paulo; Museu Nacional, Universidade Federal do Rio de Janeiro (MNRJ), Rio de Janeiro. SWITZERLAND—Muséum d'Histoire Naturelle de la Ville de Genève (MHNG), Geneva. UNITED KINGDOM—Natural History Museum (BMNH), London, England. UNITED STATES—Natural History Museum, University of Kansas (KU), Lawrence; National Museum of Natural History (USNM), Smithsonian Institution, Washington DC.

Atractus chthonius ($n = 11$).—COLOMBIA: between Popayán in the department of Cauca and La Plata in the department of Huila: Santa Leticia: Finca Meremburg (ICN 2288, paratype; ICN 5662, holotype); Huila: La Argentina: Finca Riequito (ICN 11515–11516, paratypes), Vereda Buenos Aires: (CZUTR 171–173, paratypes), Acevedo: Parque Nacional Natural Cueva de Los Guacharos: (IAvH 2062, paratype), Saladoblanco: Cerro Pelado: (ICN 11517, paratype), Corregimiento Morelia: Vereda El Palamar: Finca Quisayá: (ICN 11513–11514, paratypes).

Atractus carrioni ($n = 28$).—ECUADOR: Loja: Loja: without specific locality data (EPN 8673–8674, QCAZ 793, QCAZ 1081–1082, QCAZ 1217–1219, QCAZ 2100),

Jardín Botánico: (QCAZ 6445–6446), *Yangana*: (QCAZ 6550), *Malacatos*: Río Malacatos: (QCAZ 6533–6534). PERU: Piura: *Ayabaca*: Bosque de Chonta: (CORBIDI 11160–11161), Bosque de Cuyas: (CORBIDI 956, 967–972, 1450); *Huancabamba*: Puente Fierro: (CORBIDI 10510–10514).

Atractus Dunnii ($n = 36$).—ECUADOR: without specific locality data: (QCAZ 219, 2884); Cotopaxi: without specific locality data: (IBSP 54328), *Galápagos*: (QCAZ 1092), *San Francisco de Las Pampas*: (QCAZ 163, QCAZ 240–247, QCAZ 670, QCAZ 1077, QCAZ 1231–1233, QCAZ 1685–1686, QCAZ 2108–2110), Reserva Otonga: Cantón Sigchos: (QCAZ 4036); El Oro: *Buenaventura*: (EPN without number); LOJA: *Olmendo*: (QCAZ 1219); Pichincha: Cerg: (QCAZ 2094), *Chiriboga*: (QCAZ 3127–3128), *Mindo*: (QCAZ 4151, MZUTI 1385), *Nanegalito*: (QCAZ 638), *Tandayapa*: (QCAZ 872, 1667, 2102, 2111).

Atractus echidna ($n = 1$).—COLOMBIA: Nariño: Robles: Corregimiento Flor de la Briza: Estero San Antonio: (UV-C 7718, holotype).

Atractus gigas ($n = 25$).—ECUADOR: Cotopaxi: Bosque Integral Otonga: (QCAZ 3266), *San Francisco de Las Pampas*: (QCAZ 175, QCAZ 179, QCAZ 443, QCAZ 647, QCAZ 662, MHNG 2250.31, MHNG 2252.86, MHNG 2397.46–2397.49, MHNG 2441.20, MHNG 2445.30); PICHINCHA: Bosque Protector Río Guajalito (formerly Hacienda Palmeras), between *San Francisco de Las Pampas* and Quito: (QCAZ 2099, MHNG 2309.67, topotypes), *Chiriboga*: (QCAZ 1, MHNG 2250.35), *Manuel Cornejo Astorga* (Tandapi) (QCAZ 3, MHNG 2220.59, MHNG 2269.59), *Peñas Coloradas* (QCAZ 4058), Reserva Bellavista (QCAZ 6526); provenance in error: Piso Tropical Oriental: (EPN 8706). PERU: Cajamarca: *San Ignacio*: Santuario

Nacional Tabaconas Namballe: Alto Lhuama: (CORBIDI 877).

Atractus iridescens ($n = 5$).—COLOMBIA: Antioquia: *San Pedro de Arana*: (CSJ 563); Chocó: *Nuqui*: (IAvH 4539), Rio San Juan: (MLS 1212); Nariño: *Barbacoas*: El Diviso: Reserva Natural Biotopo Selva Húmeda: Vereda Berlin: (ICN 10901–10902).

Atractus macondo ($n = 1$).—COLOMBIA: Magdalena: Sitionuevo: Parque Nacional Natural Isla de Salamanca: (IAvH 15, holotype).

Atractus microrhynchus ($n = 2$).—PERU: Tumbes: Cerros de Amotape National Park: (MUSM 22829–22830).

Atractus modestus ($n = 11$).—ECUADOR: Western Ecuador without specific locality data: (BMNH 1946.1.6.30, holotype); Azuay: *Molleturo*: (QCAZ 1167); Cotopaxi: *San Francisco de Las Pampas*: (QCAZ 002, QCAZ 201–203, QCAZ 641, QCAZ 1216, QCAZ 2100), *Pilaló*: (QCAZ 6548); Morona-Santiago: *Plan de Milagro*: (QCAZ 2013); Pichincha: without specific locality data: (QCAZ 1134).

Atractus orcesi ($n = 40$).—COLOMBIA: Cauca: *Santa Rosa*: Vereda El Cajor: (IAvH 4704); Huila: *Acevedo*: Parque Natural Nacional Cueva de los Guacharos: (IAvH 3105); Putumayo: Valle Sibundoy: *Santiago*: Vereda Balsayaco: (ICN 10803–10804). ECUADOR: Morona-Santiago: between *Chiguaza* and *Macuma*: (USNM 232696), *Gral. Leonidas Plaza Gutiérrez*: (QCAZ 9666, QCAZ 9680); Napo: Upper Río Arajuno: (EPN 8723, USNM 232700), Río Hollín: (QCAZ 6268); Pastaza: Río Villano: (USNM 232702–232704, 232706), Upper Río Bobonaza: (USNM 232699); Sucumbios: *La Bonita*: (QCAZ 2779, USNM 232707–232722), Lago Agrio: (KU 125999–126005).

Atractus roulei ($n = 2$).—ECUADOR: Azuay: *Hierba Mala*: (QCAZ 6256), Chimborazo: (USNM 33861).