

Narrow Endemism or Insufficient Sampling? Geographic Range Extension and Morphological Variation of the Poorly Known *Atractus riveroi* Roze, 1961 (Serpentes: Dipsadidae)

The cryptozoic ground snakes of the genus *Atractus* Wagler, 1928 are widely distributed in the Neotropics, ranging from the Isthmus of Panama to northern Argentina (Giraud and Scrocchi 2000; Myers 2003). Despite the high *Atractus* species diversity (ca. 140 species), the low availability of samples constrains our knowledge about morphological variation, ecology, natural history, and geographic distribution of many *Atractus* species (see Passos et al. 2013a). In addition, because several *Atractus* species have been found only in their type localities and

vicinities (Passos and Lynch 2011; Passos et al. 2012; Salazar-Valenzuela et al. 2014), the taxonomic status of some of them has been unclear (Schargel et al. 2013) or controversial (Silva 2004; Passos et al. 2012; Passos and Prudente 2012). This is particularly critical for species from areas with difficult access, such as the Pantepui region in the Guiana Shield (see Passos et al. 2016 for similar examples from lowlands). The Pantepui region covers mostly the flat-top sandstone mountains in northern Brazil and southern Venezuela, but it also includes granitic mountains that are similar in faunal composition and the lowlands connecting the disjunctive mountain chains (Kok et al. 2012; Kok 2013).

Atractus riveroi (Rivero's Ground Snake) was originally described on the basis of two specimens from Cerro Duida (1800 m above sea level; hereafter asl) and Cerro Marauaka (1300 m asl) in Venezuela (Roze 1961). Fifty-one years after the original description, the species was redescribed based on the type series and an additional specimen from Sierra Parima (980 m asl) in Venezuela (Passos et al. 2013b). Here we report a range extension of *A. riveroi* based on six specimens from the Amazon rainforest on the Brazilian side of the Pantepui region, in extreme northern portion of Brazil. In addition, we present new data on variation in color, morphometrics, and meristic characters.

MATERIALS AND METHODS

Sampling.—We present data from two independent expeditions to the Pantepui region, in the extreme northern portion of Brazil. The study area comprises a region of an ancient massive

RAFAEL DE FRAGA

Instituto Nacional de Pesquisas da Amazônia -
 Coordenação de Biodiversidade, Av. Efigênio Sales 2239,
 69060-020, Manaus, Amazonas, Brazil;
 e-mail: r.defraga@gmail.com

ALEXANDRE PINHEIRO DE ALMEIDA

Universidade Federal do Amazonas -
 Programa de Pós-Graduação em Zoologia,
 Av. General Rodrigo Octávio Jordão Ramos 3000,
 69077-000, Manaus, Amazonas, Brazil;
 e-mail: alexandre.dealmeida@hotmail.com

LEANDRO JOÃO CARNEIRO DE LIMA MORAES

Instituto Nacional de Pesquisas da Amazônia -
 Coordenação de Biodiversidade, Av. Efigênio Sales 2239,
 69060-020, Manaus, Amazonas, Brazil;
 e-mail: leandro.jclm@gmail.com

MARCELO GORDO

Universidade Federal do Amazonas -
 Laboratório de Ecologia, Departamento de Biologia,
 Av. General Rodrigo Octávio Jordão Ramos 3000, 69077-000,
 Manaus, Amazonas, Brazil; e-mail: projetosauim@gmail.com

RENATA PIRANI

Instituto Nacional de Pesquisas da Amazônia -
 Coordenação de Biodiversidade, Av. Efigênio Sales 2239,
 69060-020, Manaus, Amazonas, Brazil;
 e-mail: renatampirani@gmail.com

ROBERTO ROJAS ZAMORA

Universidade Federal do Amazonas -
 Laboratório de Evolução e Genética Animal, Departamento de Biologia,
 Av. General Rodrigo Octávio Jordão Ramos 3000, 69077-000,
 Manaus, Amazonas, Brazil; e-mail: rrojaszamora@gmail.com

VINÍCIUS TADEU DE CARVALHO

Universidade Federal do Amazonas -
 Laboratório de Evolução e Genética Animal, Departamento de Biologia,
 Av. General Rodrigo Octávio Jordão Ramos 3000, 69077-000,
 Manaus, Amazonas, Brazil; e-mail: anfibios.repteis@gmail.com

PAULO PASSOS

Universidade Federal do Rio de Janeiro - Departamento de Vertebrados,
 Museu Nacional, Quinta da Boa Vista, 20940-040, Rio de Janeiro,
 Rio de Janeiro, Brazil; e-mail: attractus@gmail.com

FERNANDA P. WERNECK

Instituto Nacional de Pesquisas da Amazônia -
 Coordenação de Biodiversidade, Av. Efigênio Sales 2239, 69060-020,
 Manaus, Amazonas, Brazil; e-mail: fewerneck@gmail.com

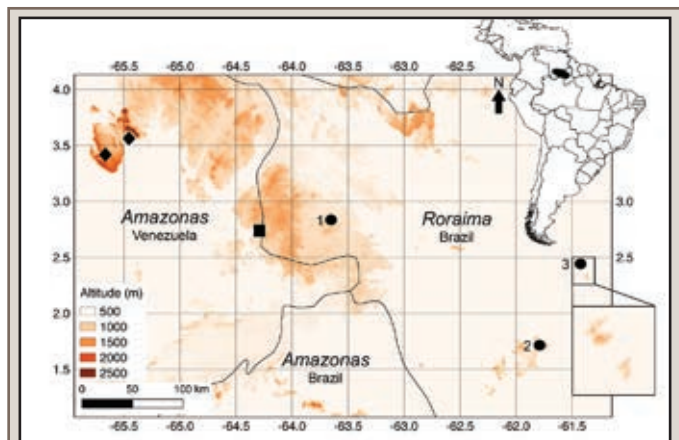


FIG. 1. Geographic range of *Atractus riveroi* in the Pantepui region. Diamonds: type-series from Cerro Duida and Cerro Marauaka, Amazonas, Venezuela (Roze, 1961). Square: Sierra Parima, Amazonas, Venezuela (Passos et al. 2013b). Circles: Serra dos Surucucus (1), Serra da Mocidade (2), and Serra do Apiaú (3), Roraima, Brazil. The rectangle on the bottom right zooms in on isolated mountains.

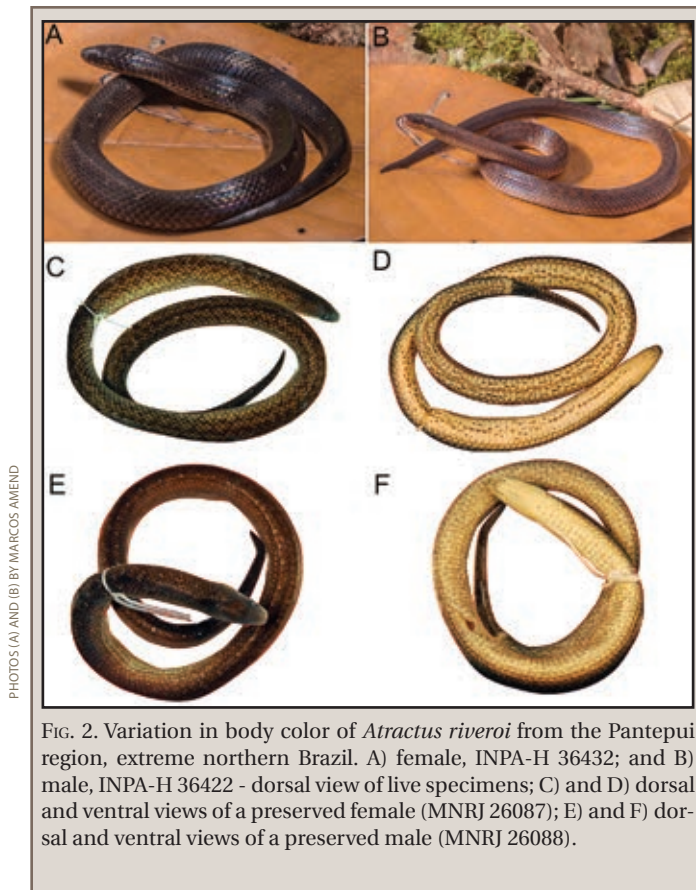


FIG. 2. Variation in body color of *Atractus riveroi* from the Pantepui region, extreme northern Brazil. A) female, INPA-H 36432; and B) male, INPA-H 36422 - dorsal view of live specimens; C) and D) dorsal and ventral views of a preserved female (MNRJ 26087); E) and F) dorsal and ventral views of a preserved male (MNRJ 26088).

complex of sedimentary, metamorphic and magmatic rocks (1.8–2.5 billion years old), mostly covered by dense montane forest or dominated by shrubby vegetation and patches of moss forest, depending on the elevation (Mayr and Phelps 1967). Five specimens (MNRJ 26087, MNRJ 26088 and INPA-H 36422, 36432, 36451) were collected in pitfall traps in primary dense montane forest. Additionally, we analyzed a misidentified specimen from a collection (MZUSP 10366). Our data include adults and juveniles of both sexes, and general information about the analyzed specimens is summarized in the Table 1.

Morphological and morphometric data.—We analyzed variation in body color in life and after preservation in 10% formalin. For a better contrast, coloration was described from specimens immersed in ethanol. We also counted scales and used a digital calliper (0.01 mm) to measure amplitudes of variation in morphometric characters that are relevant for taxonomy of ground snakes. Sex was determined by the presence or absence of a hemipenis.

RESULTS

Geographic range.—Our new records extend the known geographic range of *A. riveroi* about 320 km SE (straight line) from Sierra Parima (Fig. 1), the easternmost locality in the previously known range. We also present the first record of *A. riveroi* in Brazil, and the first morphological data from females.

Variation in body color.—Dorsal background color of body and tail blackish brown (Fig. 2A) or brownish red with irregular dark brown marks (Fig. 2B) or black usually covered with a series of yellowish cream spots (one scale long and wide) or transversal narrow bands (one scale long and two scales wide); lighter spots

sometimes indistinct after preservation (Fig. 2E); first dorsal scale row usually with the ventral region or midportion of scales lighter, creamish brown in a paler background or greyish black in a black background (Fig. 2B); dorsum occasionally darkened with blotches almost indistinct or only distinguishable after ethanol immersion (Fig. 2A); most rarely dorsum pale brown to brown with irregular dark brown dots concentrated along vertebral region, becoming an irregular vertebral stripe or with marks forming irregular alternated bands across body (Fig. 2C; see also figure 7 in Passos et al. 2013b). Background of head brown or black up to dorsal edges of supralabials (Fig. 2B); snout region occasionally yellowish orange, black or brown pigments covering most of nasals, dorsal margins of first three supralabials and anterior-ventral portion of loreal scales; supralabials mostly yellow, except for dorsal edges dark brown to black; dark pigmentation frequently covers the posterior region of supralabials, giving impression of a denticulate margin in lateral view; last supralabial (usually eighth) entirely covered by brown or black pigments; remaining portions of supralabials yellowish cream to yellowish orange; infralabials, symphyisial, and chinshields yellowish cream usually with dispersed dark brown marks concentrated on posterior-lateral edges of supralabials or anteriorly on scales of gular region (symphyisial and chinshields); occasionally, gular region heavily marked with irregular dark brown blotches; ventral surface of body creamish yellow heavily marked with rectangular or rhomboidal brown blotches (Fig. 2F) or arranged as two or three irregular longitudinal stripes (Fig. 2D); belly sometimes scattered with brown dots between irregular blotches more concentrated at midline on posterior regions of body (Fig. 2D); ventral surface of tail mostly brown with few irregular cream to beige spots laterally disposed; tail occasionally uniformly brown to dark brown (Figs. 2D and 2F).

We did not detect any conspicuous variation in body color associated with geography, sex, or age of the specimens. Each of the two main patterns (black with light marks [Fig. 2A] and pale brown with dark marks [Fig. 2B]) is found on both sexes at the same locality (Fig. 2). Younger specimens (e.g., MNRJ 26087–26088) may have dorsum dark brown with irregular stripes or indistinct light spots.

Meristic and morphometric variation.—Intraspecific variation of the main diagnostic characters is shown in Table 2. Data from INPA-H 36451 were not included in the general variation (except by counting scales), because this specimen was found dead and dehydrated. A detailed description of morphological variation is presented below.

Head flattened in lateral view, snout moderately elongated (rostral–orbit distance 3.4–3.7 mm), round in dorsal view and truncated in lateral view (nasal–orbit distance 2.3–3.6 mm); canthus rostralis not defined (interorbital distance 3.2–3.9 mm); head length 9.4–12.7 mm (3.7–4.5% SVL); rostral subtriangular in frontal view, 1.0–1.8 mm wide, 0.8–1.1 mm high, little visible in dorsal view; internasals 0.7–0.9 mm long, 0.6–0.8 mm wide; internasal suture sinistral or aligned with prefrontal suture; prefrontal 2.4–2.9 mm long, 1.6–2.0 mm wide; frontal subpyramidal with anterior margin slightly projected medially, 2.7–2.8 mm long, 2.3–2.8 mm wide; supraocular sub-trapezoidal, 1.4–1.6 mm long, 0.8–1.0 mm wide; parietal 4.1–4.5 mm long, 2.1–2.6 mm wide; nasal divided; nostril separates pre- and postnasal; prenasal 0.6–1.0 mm high, 0.3–0.5 mm long; postnasal 0.5–1.0 mm high, 0.7–1.0 mm long; loreal contacting second, third and fourth supralabials, 2.1–2.5 mm long, 0.5–1.0 mm high; eye diameter 1.1–1.5 mm; pupil rounded; postoculars 2/2, upper

TABLE 1. Specimens of *Atractus riveroi* found in the Pantepui region, extreme northern Brazil. Altitude is shown as meters above sea level. MZUSP = Museu de Zoologia, Universidade de São Paulo; MNRJ = Museu Nacional, Universidade Federal do Rio de Janeiro; INPA-H Amphibian and Reptiles Collection, Instituto Nacional de Pesquisas da Amazônia, Manaus.

Voucher	Sex	Locality	Coordinates (WGS84)	Altitude (m)
MZUSP 10366	Female	Serra dos Surucucus	02.833333°N, 63.633333°W	1000
MNRJ 26087	Female	Serra do Apiaú	02.435833°N, 61.415833°W	944
MNRJ 26088	Male	Serra do Apiaú	02.435000°N, 61.417139°W	990
INPA-H 36422	Male	Serra da Mocidade	01.707111°N, 61.785833°W	1061
INPA-H 36432	Female	Serra da Mocidade	01.707111°N, 61.785833°W	1061
INPA-H 36451	Female	Serra da Mocidade	01.707111°N, 61.785833°W	1061

TABLE 2. Meristic and morphometric variation for all known specimens of *Atractus riveroi*. SVL = snout–vent length, CL = caudal length, MD = midbody diameter, DSC = dorsal scale rows in the level of second subcaudal. Distinct values for each side of the specimens are listed separately. Bolded specimens are new specimens described in this study. AMNH 36615 and MBUCV 7175 are the holotype and paratype, respectively. Dashes show unavailable data. AMNH = American Museum of Natural History, New York; MBUCV = Museo de Biología, Universidad Central de Venezuela, Caracas; MZUSP = Museu de Zoologia da Universidade de São Paulo; INPA-H = Herpetological section of the Zoological Collections, Instituto Nacional de Pesquisas da Amazônia, Manaus; MNRJ = Museu Nacional, Universidade Federal do Rio de Janeiro.

Voucher	Sex	SVL (mm)	CL/SVL (ratio)	MD (mm)	DSC	Ventrals	Subcaudals	Supralabials
AMNH 36615	Male	415	16.8	–	8	153	41	8
MBUCV 7175	Male	356	18.2	9.4	8	152	37	8
MHNLS 12889	Male	320	16.5	7.1	9	161	34 / 35	8
MZUSP 10366	Female	254	12.2	6.2	8	153	28 / 29	8
MNRJ 26087	Female	283	10.6	7.6	8	160	28	8
MNRJ 26088	Male	156	15.4	4.2	9	160	39	7 / 8
INPA-H 36422	Male	290	18.8	7.4	10	160	46	8
INPA-H 36432	Female	273	12.4	7.5	8	161	28	8
INPA-H 36451	Female	229	12.3	–	8	161	32	8

postoculars 0.7–0.8 mm high, 0.4–0.7 mm long; lower postocular 0.3–0.6 mm long, 0.3–0.5 mm high; temporals in most of specimens 1+2, 1+3 at right side of INPA-H 36432; first temporal 2.0–2.4 mm long, 0.8–1.8 mm high; second upper temporal equivalent size to dorsal scales; third upper posterior temporal 1.9–2.5 mm long, 1.0–1.3 mm high, supralabials eight, fourth and fifth contacting eye; supralabials seventh higher and eighth longer, or seventh and eighth longer than remaining supralabials; symphyseal semicircular, 1.3–1.9 mm wide, 0.5–0.6 mm long; seven maxillary teeth, eight infralabials, first four contacting chinshields; first pair of infralabials in contact, preventing symphyseal-chinshields contact; chinshields 3.4–4.4 mm long, 1.1–1.3 mm wide; three gular scales; 17/17/17 dorsal scale rows; dorsals smooth, lacking apical pits and keels but, eventually, with supra-cloacal tubercles; caudal spine moderately long (longer than last subcaudal), conical and moderately to very acuminate.

A hatchling male (MNRJ 26088) differed from adults by having shorter snout (rostral–orbit distance 2.2 mm); longer head (5.7% SVL); rostral bell-shaped in frontal view; loreal contacting second and third supralabials in the right side of the head and supralabials seven in the right side of the head.

DISCUSSION

We presented new information for a rarely sampled species, from a remote region of the Amazon which had never been sampled. In a broader view, our findings represent a novel contribution for the understanding of diversity and biogeography

patterns in the isolated Amazonian highlands in Brazil and also a new snake record to be considered on the official lists relevant for conservation assessments.

An interesting fact about MZUSP 10366 (female) is the presence of supra-cloacal tubercles on the dorsal scales, a character otherwise known only for male specimens of the *Atractus collaris* species-group. However, different from the members of this group, *A. riveroi* does not have apical pits covering most of dorsal scales (see Passos et al. 2013c).

Taxonomic uncertainty involving many *Atractus* species has often been related to scarcity of samples covering wide geographic scales. Lack of samples may be explained by the secretive habits of ground snakes or altitudinal range restriction in some species (Schargel and García-Peréz 2002; Myers 2003; Myers and Schargel 2006). For the latter, revealing *Atractus* species diversity associated with narrow endemism and its specificity in establishing populations at high altitudes depends on sampling not only on the highlands of the Pantepuis region, but also in the lowlands connecting disjunctive mountain ranges. Additionally, *Atractus* diversity in high altitudes has been underestimated by misidentification, mainly because many species are polychromatic (Passos et al. 2009; Passos et al. 2010; Passos and Prudente 2012; Passos et al. 2016). For example, one of the *A. riveroi* specimens reported here (MZUSP 10366) remained misidentified as *Atractus major* for 25 years (see Schargel et al. 2013).

Despite not knowing if gene flow in *A. riveroi* occurs through the lowlands connecting the isolated mountains in the Pantepui

region, our species occurrence data show that altitudinal isolation does not necessarily cause narrow endemism. Although the species occurrence is apparently restricted to altitudes higher than 940 m, the geographic range covers more than 40,000 km². This finding is consistent with a previous study, which found the lowlands of Pantepui are not effective barriers to gene flow in reptiles from the highlands (Kok et al. 2012), although the entire region is considered to have high species diversity and endemism rates (Kok et al. 2012; Kok 2013). We encourage collection of new samples to identify mechanisms driving the establishment of populations in high altitudes, especially because dispersal in *Atractus* snakes is often limited by its cryptozoic habits.

Acknowledgments.—We are grateful to the following persons for allowing us to examine specimens under their care: C. Ferreira (MBUCV), D. Frost and D. Kizirian (AMNH), G. Rivas and C. Señares (MHNLS), A. A. Silva, R. Vogt (INPA-H), and H. Zaher (MZUSP). We thank the Instituto Chico Mendes de Conservação da Biodiversidade for collection permissions (ICMBio, processes 52206-1 and 44832-1). M. Amend provided photos of live specimens, and Mariah Kenney reviewed the English. The Biodiversity of the Serra da Mocidade Expedition resulted from a collaboration among Instituto Nacional de Pesquisas da Amazônia (INPA), Instituto Chico Mendes de Conservação da Biodiversidade (ICMBio), Comando Militar da Amazônia (CMA), and Grifa Filmes. We are deeply indebted to S. Marques (USP) and A. Prudente (MPEG) for providing photos and data for the specimen MZUSP 10366. RF and LJCLM thank Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for scholarship. FPW was supported by CNPq (proc. 475559/2013-4) and Fundação de Amparo à Pesquisa do Amazonas (FAPEAM, proc. 062.00665/2015). PP was supported by CNPq (processes 8256995713198058, 482086/2012-2, and 306227/2015-0) and Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ processes E-26/110.434/2012 and E-26/111.636/2012).

LITERATURE CITED

- GIRAUDO, A. R., AND G. J. SCROCCHI. 2000. The genus *Atractus* (Serpentes: Colubridae) in north-eastern Argentina. *Herpetol. J.* 10:81–90.
- KOK, P. J. R. 2013. Islands in the sky: species diversity, evolutionary history, and patterns of endemism of the Pantepui herpetofauna. PhD dissertation, Leiden University, Netherlands.
- , R. D. MACCULLOCH, D. B. MEANS, K. ROELANTS, I. VAN-BOCKLAER, AND F. BOSSUYT. 2012. Low genetic diversity in tepui summit vertebrates. *Curr. Biol.* 22:589–590.
- MAYR, E., AND W. H. PHELPS, JR. 1967. The origin of bird fauna of the south Venezuela highlands. *Bull. Am. Mus. Nat. Hist.* 136:269–328.
- MYERS, C. W. 2003. Rare snakes—five new species from eastern Panama: reviews of northern *Atractus* and southern *Geophis* (Colubridae: Dipsadinae). *Am. Mus. Novit.* 3391:1–47.
- , AND W. E. SCHARGEL. 2006. Morphological extremes—two new snakes of the genus *Atractus* from northwestern South America (Colubridae: Dipsadinae). *Am. Mus. Novit.* 3532:1–13.
- PASSOS, AND J. D. LYNCH. 2011. Revision of *Atractus* (Serpentes: Dipsadidae) from middle and upper Magdalena drainage of Colombia. *Herpetol. Monogr.* 24:149–173.
- , AND A. L. C. PRUDENTE. 2012. Morphological variation, polymorphism, and taxonomy of the *Atractus torquatus* complex (Serpentes: Dipsadidae). *Zootaxa.* 3407:1–21.
- , D. CISNEROS-HEREDIA, D. E. RIVERA, C. AGUILAR, AND W. E. SCHARGEL. 2012. Rediscovery of *Atractus microrhynchus* and *A. natans* (Serpentes: Dipsadidae). *Herpetologica* 68:375–392.
- , L. Y. ECHEVARRÍA, AND P. J. VENEGAS. 2013a. Morphological variation of *Atractus carrioni* (Serpentes: Dipsadidae). *South Am. J. Herpetol.* 8:109–120.
- , R. FERNANDES, R. S. BÉRNILS, AND J. C. MOURA-LEITE. 2010. Taxonomic revision of Atlantic Forest *Atractus* (Serpentes: Dipsadidae). *Zootaxa* 2364:1–63.
- , P. J. R. KOK, N. R. ALBUQUERQUE, AND G. A. RIVAS. 2013b. Ground-snakes of the lost world: a review of *Atractus* (Serpentes: Dipsadidae) from the Pantepui region, northern South America. *Herpetol. Monogr.* 27:52–86.
- , J. D. LYNCH, AND R. FERNANDES. 2009. Taxonomic status of *Atractus sanctaemartae* and *A. nebularis*, and description of a new species of *Atractus* from Atlantic coast of Colombia. *Herpetol. J.* 18:175–186.
- , A. L. C. PRUDENTE, AND J. D. LYNCH. 2016. Redescription of *Atractus punctiventris* and description of two new *Atractus* (Serpentes: Dipsadidae) from Brazilian Amazonia. *Herpetol. Monogr.* 31:1–20.
- , L. O. RAMOS, P. H. PINNA, AND A. L. C. PRUDENTE. 2013b. Morphological variation and putative affinities of the poorly known *Atractus caxiuana* (Serpentes: Dipsadidae). *Zootaxa* 3745:35–48.
- , M. TEIXEIRA-JUNIOR, R. S. RECODER, M. A. DE SENA, F. DAL VECHIO, H. B. A. PINTO, S. H. S. T. MENDONÇA, AND M. T. RODRIGUES. 2013c. 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. *Pap. Avul. Zool.* 53:75–85.
- ROZE, J. A. 1961. El género *Atractus* (Serpentes: Colubridae) en Venezuela. *Acta Biol. Venez.* 3:103–119.
- 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.
- SCHARGEL, W. E., AND J. E. GARCÍA-PÉREZ. 2002. A new species of *Atractus* (Serpentes: Colubridae) from the Andes of Venezuela. *J. Herpetol.* 36:398–402.
- , 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, J. J. H. 2004. Las serpientes del género *Atractus* Wagler, 1828 (Colubridae, Xenodontinae) en la Amazonia Colombiana. *Rev. Acad. Colomb. Ci. Exact.* 28:409–446.