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GROUNDSNAKES OF THE LOST WORLD: A REVIEW OF *ATRACTUS* (SERPENTES: DIPSADIDAE) FROM THE PANTEPUI REGION, NORTHERN SOUTH AMERICA

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Abstract: We review the taxonomic status of the snakes belonging to the genus *Atractus* from the Pantepui region on the basis of morphological characters (meristic, morphometric, color pattern, and hemipenis). We redescribe and illustrate the holotype of *A. insipidus*, correcting the elevation of the type locality and providing its exact coordinates. We report the third known specimen of *A. riveroi* on the basis of an individual collected in the Sierra Parima close to the Venezuela/Brazil border. We report the geographical variation of *A. steyermarki*, expanding its known distribution on the basis of specimens collected in Guyanese tepuis, and consider the species a senior synonym of *A. guerreroi*. We also report the geographical variation in meristic, morphometric, color pattern, and hemipenial characters of *A. tamessari* on the basis of the discovery of new specimens. Finally, we provide a key to the *Atractus* of the Guiana Shield and discuss on the evolution of some particular features of hemipenial morphology in the genus.

Resumen: Se revisó el estado taxonómico de las serpientes pertenecientes al género *Atractus* del Pantepui, a través de caracteres morfológicos (merísticos, morfométricos, patrón de coloración y hemipene). Se redescribe e ilustra el holotipo de *A. insipidus* y se detalla la ubicación y altitud de la localidad tipo. Se registra el tercer ejemplar conocido de *Atractus riveroi* a través de un individuo proveniente de la Sierra de Parima, cerca a la frontera Venezuela/Brasil. *Atractus steyermarki* se considera un sinónimo senior de *A. guerreroi.* Se amplía la distribución y variación geográfica de esta especie, a través de ejemplares capturados en tepuis de Guyana. Se describe también la variación geográfica en los caractéres merísticos, morfometricos, patrón de coloración y hemipene de *A. tamessari,* basado en el hallazgo de nuevos individuos. Por último, se presenta una clave para los *Atractus* del Escudo de Guayana y se discute la evolución de algunas características particulares de la morfología del hemipene en el género.

Key words: Gran Sabana; Guiana Shield; Hemipenis morphology; Highland *Atractus*; Pantepui

Sir Arthur Conan Doyle coined the expression "The Lost World" in the title of his famous novel published in 1912, in which he depicts an expedition to an isolated tepui in the middle of the tropical jungle of northern South America in search of dinosaur-like creatures and a forgotten civilization (Doyle, 1912). Doyle was largely inspired by the account of an expedition of the Royal Geographical Society of London on the summit of Mount Roraima led in 1884 by Sir Everard im Thurn (McDiarmid and Donnelly, 2005).

The Guiana Shield Highlands that inspired Doyle cover an area of high biological diversity and endemism and were later referred to as the Pantepui region (Mayr and Phelps, 1967; McDiarmid and Donnelly, 2005; Kok et al., 2012; Kok, 2013). As understood here, Pantepui refers to the complex of mountains (the sandstone flat-topped mountains, called "tepuis," and the faunistically related granitic mountains) and the intervening lowlands and uplands mostly located in southern Venezuela, west-central Guyana, and northern Brazil (Huber, 1987; McDiarmid and Donnelly, 2005). Pantepui is sometimes limited to the upper slopes and summits of the Guiana Shield Highlands, covering a total surface of about 5000 km^2 with an altitudinal range of 1500–3014 m above sea level (asl; Mayr and Phelps, 1967;

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Rull and Nogué, 2007). Nonetheless, Steyermark (1982), followed by Kok et al. (2012) and Kok (2013), expanded the original definition of Pantepui to include also the intervening lowlands and uplands (>200 m asl), which better reflects the biogeography and the past and current biotic interactions in the area (see Kok, 2013).

The zoogeography of the Guiana Shield Highlands has been a recent topic of interest, with several sources of published data (McDiarmid and Donnelly, 2005, and references therein) and ongoing works by one of us (PJRK). It has been recently demonstrated that despite their current unique geomorphology the tepuis were insufficient barriers to local (i.e., within Pantepui) gene flow, leading to a low genetic diversity among tepui summit amphibians and reptiles (Kok et al., 2012). Although several herpetological expeditions have been carried out on isolated tepuis (Roze, 1958a,b; Donnelly and Myers, 1991; Gorzula, 1992; Myers, 1997; McDiarmid and Paolillo, 1998; Myers and Donnelly, 1996, 1997, 2001, 2008; MacCulloch et al., 2007; Kok, 2008, 2009, 2010, 2013; Kok and Rivas, 2011) and also in the uplands of the Gran Sabana in Venezuela (Duellman, 1997; Gorzula and Señaris, 1999), species of *Atractus* were reported only by Roze (1958b), Gorzula and Señaris (1999), and Myers and Donnelly (2008) from Chimantá and Auyán Massifs, respectively. A few additional papers have described *Atractus* specimens from tepuis (Roze, 1961) or from the uplands of the Guiana Shield (Prudente and Passos, 2008).

The cryptozoic snake genus *Atractus* Wagler, 1828 is widely distributed in the Neotropical region, occurring from Panama to Argentina (Giraudo and Scrocchi, 2000; Myers, 2003). *Atractus* is the most speciose snake genus, with about 140 recognized species, most of them with relatively restricted distribution (Passos and Fernandes, 2008; Passos et al., 2009a,b,c,d,e). The taxonomic status of many species remains unclear, with several taxa misidentified in herpetological collections (Passos et al., 2005, 2007a,b, 2009a,b,c,d,e).

The major problem in *Atractus* taxonomy is that several species are still known only from the type specimen(s), and their geographical, ontogenetic, and sexual variation cannot be properly assessed (Passos et al., 2010a,b,c, 2012; Passos and Lynch, 2011). A comprehensive revision of *Atractus* is still lacking, and despite several recent publications focusing on the genus additional efforts are needed to address problems of morphological variation, geographic ranges, and species boundaries among many recognized species (Passos et al., 2010a,b,c, 2013a,b; Passos and Lynch, 2011), notably those from poorly sampled regions like the Guiana Shield Highlands.

The most comprehensive revision of *Atractus* of the Guiana Shield was provided by Hoogmoed (1980), in which that author recognized nine distinct taxa from Suriname. To date, the following species have been formally added to the Guiana Shield herpetofauna (sensu Hoogmoed, 1979): *A. alphonsehogei* Cunha and Nascimento, 1983; *A. badius* (Boie, 1827); *A. duidensis* Roze, 1961; *A. elaps* (Günther, 1858), *A. favae* (Filippi, 1840); *A. flammigerus* (Boie, 1827); *A. guerreroi* Myers and Donnelly, 2008; *A. insipidus* Roze, 1961; *A. latifrons* (Günther, 1868); *A. major* Boulenger, 1894; *A. poeppigi* (Jan, 1862); *A. riveroi* Roze, 1961; *A. schach* (Boie, 1827); *A. snethlageae* Cunha and Nascimento, 1983; *A. steyermarki* Roze, 1958b; *A. surucucu* Prudente and Passos, 2008; *A. tamessari* Kok, 2006; *A. torquatus* (Duméril, Bibron, and Duméril, 1854); *A. trilineatus* Wagler, 1828; *A.* cf. *univittatus* (Jan, 1862; sensu Hoogmoed, 1980, who expressed doubts about the correctness of the locality and identification of this specimen), and *A. zidoki* Gasc and Rodrigues, 1979 (Avila-Pires, 2005; Kok, 2006; Myers and Donnelly, 2008; Prudente and Passos, 2008).

Although the alpha-taxonomy of most of *Atractus* species from the lowlands (below 400 m asl) of the Guiana Shield is remarkably stable and still well supported since Hoogmoed's revision (Cunha and Nascimento, 1983, 1993; Kok, 2006; Prudente and Passos, 2010), available data on the taxa from the highlands of the area are scarce and sometimes restricted to brief or inaccurate original species descriptions (most of them also lacking species' illustrations and detailed descriptions; e.g., Roze, 1961). Therefore, we aim to present a taxonomic revision of *Atractus* from the Guiana Shield Highlands and provide new data on morphological variation and distribution of poorly known species of the genus, including a key to all known *Atractus* species from the Guiana Shield.

Materials and Methods

Material Examined

Institutional abbreviations are those listed by Sabaj Pérez (2013). Data from additional specimens of *Atractus* examined are found in Passos et al. (2005, 2007a,b, 2009a,b,c,d,e, 2010a,b,c, 2012, 2013a,b), Passos and Fernandes (2008), Prudente and Passos (2008, 2010), Passos and Arredondo (2009), Passos and Lynch (2011), and Passos and Prudente (2012).

Study Area

From a topographical point of view Pantepui is marked by extensive uplands (400–1500 m asl), isolated highlands (>1500 m asl), and peripheral lowlands (200–400 m asl) that occur along the rivers and coastal plain (Kok, 2013). This study focuses on *Atractus* species from the Pantepui uplands and highlands as defined by Steyermark (1982) and refined by Kok (2013), which thus also includes the Gran Sabana of Venezuela and most intervening areas below 1500 m asl (contra Mayr and Phelps, 1967; Rull and Nogué, 2007). As demonstrated below, Steyermark's arguments (on the basis of floral elements) to expand the concept of Pantepui (sensu Mayr and Phelps, 1967) are also valid for the genus *Atractus*. Indeed, some highland species of *Atractus* occur between 400 and 2200 m asl (e.g., *A. steyermaki* and *A. tamessari*), which is not in favor of arbitrarily limiting the Pantepui region to areas above 1500 m asl. Furthermore, all other species of *Atractus* from the Guiana Shield region have elevation ranges below 400 m asl (i.e., all species included in Hoogmoed, 1980).

Geographical Data

Coordinates of localities were acquired in the field by using global positioning system devices (referenced to map datum WGS84), and by consulting data in museum's catalogues, databases, geographical gazetteers (Paynter, 1982; Stephens and Traylor, 1985), or official documentation (PCDL, 1952). We refined, when possible, the coordinates obtained from the literature by using the software Google Earth 6.0 (Google, 2005).

Characters, Techniques, and Style

Terminology for cephalic shields follows Savage (1960), whereas ventral counts follow Dowling (1951). Description of the shape of the loreal scale follows Passos et al. (2007b). Measurements were taken with a dial caliper to the nearest 0.1 mm, except for snout–vent length (SVL) and tail length (TL), which were measured to the nearest 1 mm with a flexible ruler. Measurements and descriptions of paired cephalic scales were taken and are provided from the right side. Sex was determined by the presence or absence of hemipenes through a ventral incision at the base of the tail. Terminology for hemipenis description follows Dowling and Savage (1960), as augmented by Myers and Campbell (1981) and Zaher (1999). Method for preparation of preserved hemipenis was modified from Pesantes (1994) in replacing KOH by distilled water. To stain the ornamenting calcareous structures, before the inflation with solution of paraffin and vaseline, we left one of the organs from *A. steyermarki* (MHNLS 11004) 20 min in an alcoholic solution of alizarin red according to modifications proposed by Harvey and Embert (2009) and Nunes et al. (2012) from the original procedures used by Uzzell (1973). We follow Passos et al. (2009e, 2010c) with respect to conditions of the morphological characters, as well as the general format of the species account. In this way, the subheadings for unavailable data are omitted (e.g., color in life). Some of our countings and measurements differed somewhat from the original species descriptions; in such cases we present the original data between brackets. We draw the dorsal and lateral views of head of the holotypes of *A. insipidus*, *A. duidensis*, and *A. riveroi* on the basis of digital photographs, whereas we refer to the drawings of the holotypes of *A. steyermarki*, *A. surucucu*, and *A. tamessari* provided by Myers and Donnelly (2008), Prudente and Passos (2008), and Kok (2006), respectively.

Taxonomic Account

Atractus duidensis *Roze, 1961*
(Figs. 1–3A)

Holotype.—Adult male, AMNH 36609, collected on 28 January 1929 by members of the Tyler-Duida expedition, Cerro Duida

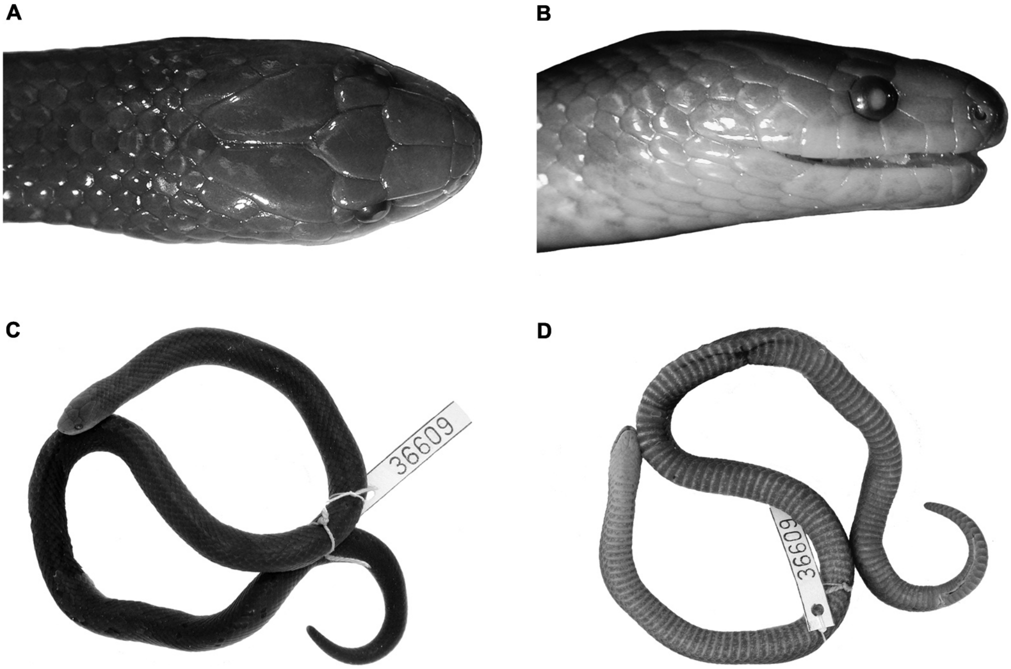

FIG. 1.—Dorsal (A) and lateral (B) views of head, and dorsal (C) and ventral (D) views of body of the holotype of *Atractus duidensis* (AMNH 36609).

(03°25′N, 65°40′W; ca. 2050 m asl), Amazonas, Venezuela.

Paratype.—Adult female, AMNH 36607, collected on 25 January 1929 by members of the Tyler–Duida expedition, Cerro Duida (03°25′N, 65°40′W; ca. 2150 m asl), Amazonas, Venezuela.

Material examined.—AMNH 36607, AMNH 36609.

Diagnosis.—*Atractus duidensis* can be distinguished from all congeners by the following combination of characters (data between brackets are those of Roze, 1961): (1) smooth dorsal scale rows 17/17/17; (2) postoculars two; (3) loreal long; (4) temporals 1 + 2; (5) supralabials seven, third and fourth contacting orbit; (6) infralabials seven, first three contacting chin shields; (7) maxillary teeth eight or nine; (8) gular scale rows three; (9) preventrals two or three; (10) ventrals 171 [173] and 156 in the single female and male, respectively; (11) subcaudals 36 [35] in the single female, male tail incomplete; (12) in preservation, dorsum uniform grayish brown to black in adults; (13) in preservation, venter creamish yellow anteriorly, gradually invaded by brown dots, becoming uniform brown posteriorly in adults; (14) body size moderate, female reaching 400 mm [415] and male 306 mm [315] SVL; (15) tail moderate in female (13.7% [11.7] SVL).

Comparisons.—Among all congeners, *A. duidensis* shares 17 dorsal scale rows, a uniformly brown or black dorsum, and a mostly brown or black venter at least after the mid-body region, with light posterior margin on each ventral noted only on *A. caete* Passos, Fernandes, Bérnils, and Moura-Leite, 2010; *A. francoi* Passos, Fernandes, Bérnils, and Moura-Leite, 2010; *A. matthewi* Markezith and Barrio-Amorós, 2004; *A. serranus* Amaral, 1930, *A. steyermarki*, and *A. trihedrurus* Amaral, 1926. *Atractus duidensis* differs from *A. caete* and *A. steyermarki* by having eight or nine maxillary teeth and 36 subcaudals in the single female known (vs. seven, 16–19 in *A. caete* and five or six, 27–33 in *A. steyermarki*, respectively); from *A. matthewi* by having 36 subcaudals in the single female known (vs. 20–25); from *A.*

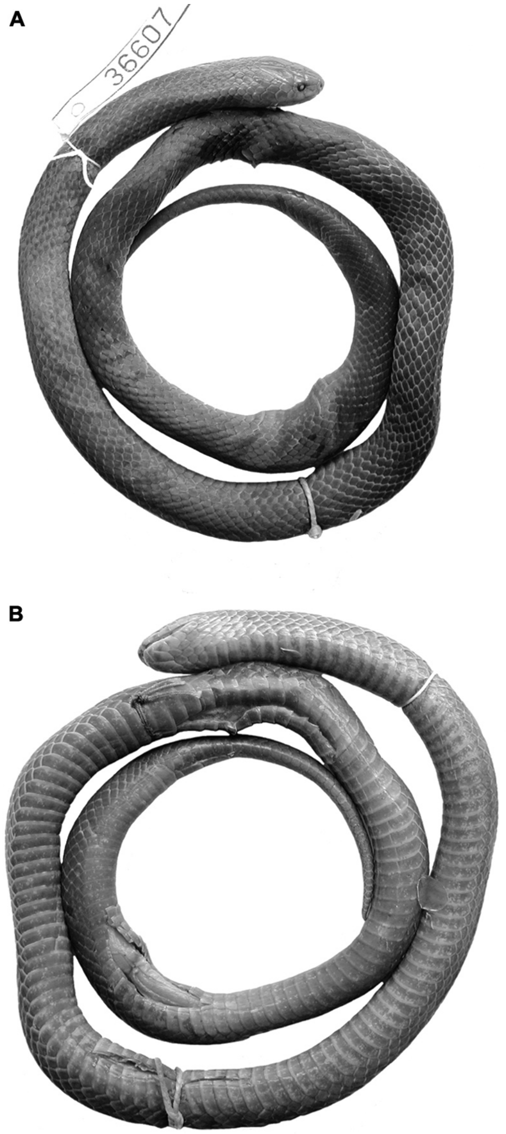

Fig. 2.—Dorsal (A) and ventral (B) views of the paratype of *Atractus duidensis* (AMNH 36607).

francoi, A. serranus, and *A. trihedrurus* in having the first three infralabials in contact with chin shields (vs. first four infralabials). Morphologically, *A. duidensis* is most similar to *A. steyermarki* in sharing the following characters: 17 dorsal scale rows, brown or black dorsal color pattern, venter with dark markings, seven supralabials, seven infralabials, and a moderate tail in females. *Atractus duidensis* further differs from *A. steyermarki* by having 171 and 156 ventrals in the single female and male, respectively (vs. 177 in females and 160–167 in males).

Description.—Head slightly distinct from body, about twice as long as wide, flattened in lateral view and rounded in dorsal view; snout truncate in lateral view, and rounded in dorsal view; rostral wide, subtriangular in frontal view, barely visible in dorsal view; internasal wider than long; internasal suture sinistral to prefrontal medial suture; prefrontal as long as wide; supraocular subrectangular in dorsal view, about twice as long as wide; frontal subpentagonal in dorsal view, as long or slightly longer than wide; parietals about twice as long as wide; nasal divided; nostril almost restricted to prenasal; prenasal two or three times higher than long; postnasal about twice as high as long, contacting second and third supralabials; loreal long, contacting second and third supralabials; pupil subelliptical; two postoculars similar in size; temporals 1 + 2; anterior temporal about twice as long as high; upper posterior temporals not fused; supralabials seven, third and fourth contacting orbit; first two supralabials similar in height and smaller than third supralabial; sixth supralabial higher and seventh longer than remaining supralabials; symphysial subtriangular, about three times as wide as long; infralabials seven, first three contacting chin shields; first pair of infralabials in contact behind symphysial, preventing symphysial–chin-shields contact; chin shields about twice as long as wide; gular scale rows three; preventrals two or three; dorsal scale rows 17/17/17, lacking apical pits and supra-anal tubercles; caudal spine moderate, conical, and acuminate (Figs. 1, 3A).

Adult color in preservative.—Dorsum of head brown or reddish brown, with faint cream spots on prefrontals and parietals; head brown laterally extending to dorsal edges of supralabials; lower surface of supralabials mostly cream, occasionally brown pigment reaching median portion of sixth and seventh supralabials; infralabials, chin shields, gular region, and preventrals predominantly cream; gular region occasionally presenting brown dots concentrated on symphysial, first two pairs of infralabials, and anterior region of chin shields; first ventrals mostly cream, sometimes with brown dots concentrated on

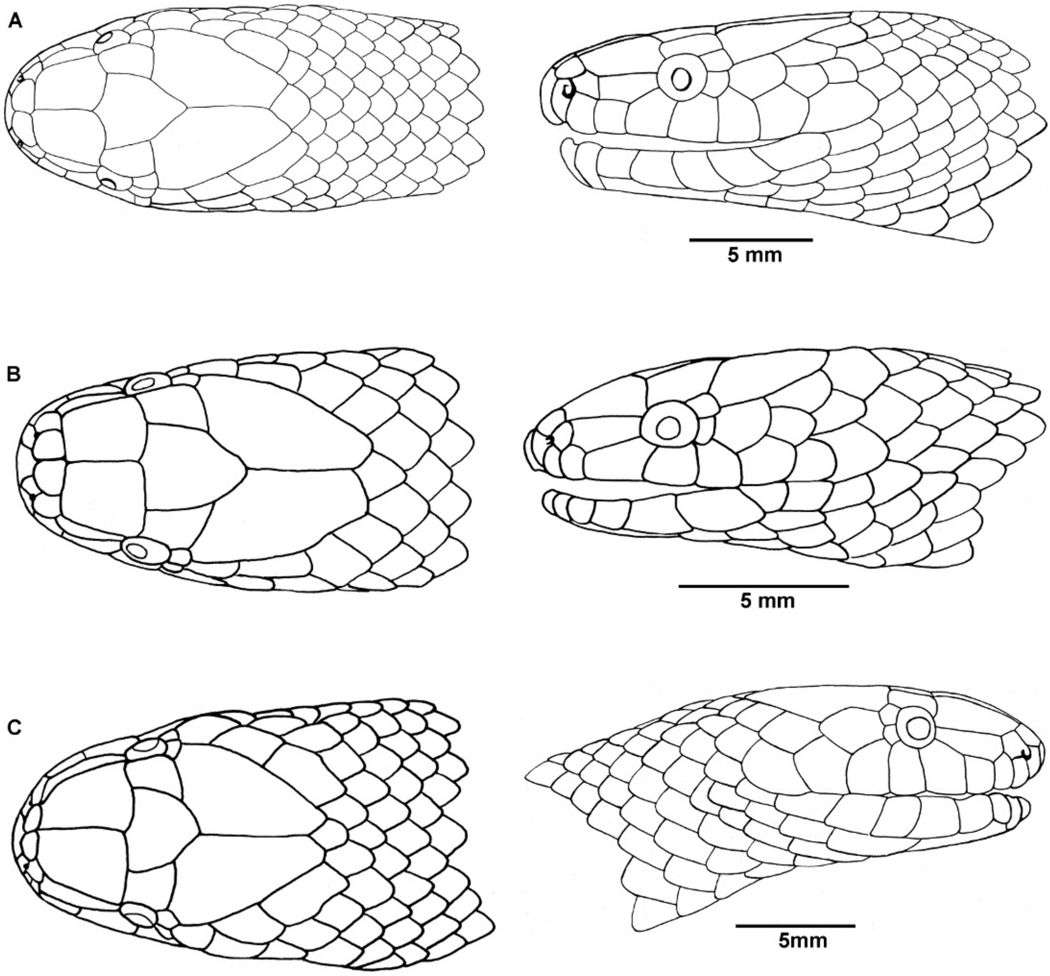

FIG. 3.—Dorsal (left) and lateral (right) views of head of the holotypes of *Atractus duidensis* (A–AMNH 36609), *A. insipidus* (B–MBUCV 3957), and *A. riveroi* (C–AMNH 36615).

anterior region of each ventral; venter posterior to fifth ventral mostly brown, with posterior surface cream; ventral portion of tail uniformly dark brown; dorsal ground color uniformly grayish brown to black (Figs. 1, 2).

Quantitative variation.—Male 306 mm SVL, 37 mm TL (tail incomplete); female 400 mm SVL, 55 mm TL; tail 13.7% SVL in female; ventrals 156 in male, 171 in female; subcaudals 26 in male (tail incomplete), 36 in female; preventrals 2–4 ($n = 2$); dorsal scale rows at the level of second subcaudal 9–10 ($n = 2$); prediastemal teeth six or seven ($n = 2$) and two additional postdiastemal teeth.

Distribution and habitat.—Only reported between 2050–2150 m asl on Cerro Duida, a tepui reaching a maximum elevation of 2358 m, located west of the Rio Caroní, in the Duida-Marahuaka Massif, Amazonas State, Venezuela (Fig. 4). According to McDiarmid and Donnelly (2005), the vegetation on the summit of Cerro Duida is composed of "broad-leaved, shrubby highland meadows on peat; broad-leaved, shrubby high-tepui meadows on peat and rock; low to tall upland and high-tepui scrub; low evergreen high-tepui forest."

Remarks.—Roze (1961) described *A. duidensis* on the basis of two specimens from Cerro de Duida in Venezuela. Roze compared *A. duidensis* with *A. modestus* Boulenger, 1894 (a species restricted to the Ecuadorian

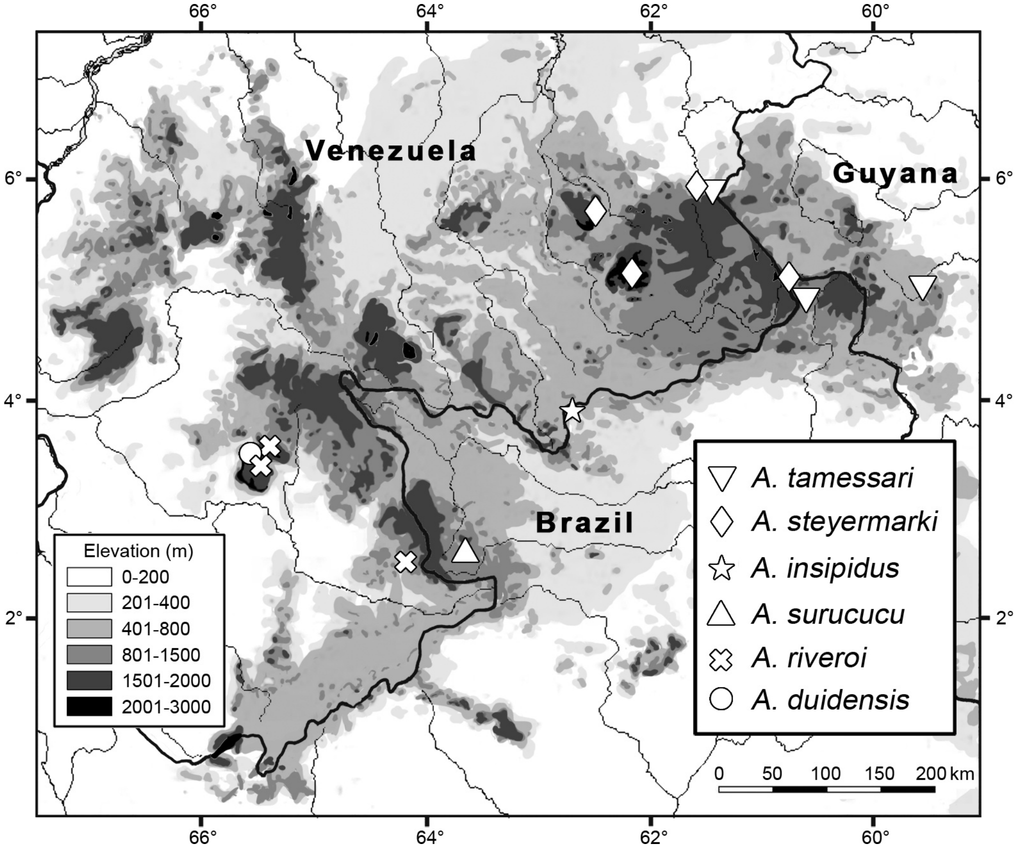

FIG. 4.—Geographical distribution of species of the genus *Atractus* in the Pantepui region.

Andes; Passos et al., 2007a), differentiating both taxa by the number of supralabials (seven in *A. duidensis* vs. six in *A. modestus*). Interestingly, Roze (1961) described the hemipenis of *A. duidensis* (retracted organ; N. Albuquerque, personal observation) as undifferentiated (sensu Savage, 1960) and bilobed with a proximal region nude, longitudinal plicae, and spines of the hemipenial body decreasing in size toward apices of the lobes. As noted in previous studies of *Atractus* (Schargel and Castoe, 2003; Passos et al., 2007a, 2013a; Prudente and Passos, 2010), the hemipenis descriptions based only on the retracted organ may not reveal certain hemipenial features (see discussion). Hence, we highlight the need that the bilobed and noncalyculated conditions reported for the hemipenis of *A. duidensis* should be confirmed by complete preparation or dissection of the organ.

Atractus insipidus *Roze, 1961*
(Fig. 5, 3B)

Holotype.—Male, probably subadult, MBUCV 3957, collected on February 1952 during the delimitation of the boundary between Brazil and Venezuela by the "Comissão Mista Brasileiro-Venezuelana Demarcadora de Limites" and later donated to Universidad Central de Venezuela by Georges Pantchenko ["Panchenco" as stated by Roze, 1961], Poste M-1 landmark (04°01′08″N, 62°33′14″W; 952 m asl [ca. 400 m as stated by Roze, 1961]), Serra (or Sierra in Spanish) de Pacaraima, between headwaters of Rio Uraricapará (= Uraricaá in indigenous language) on the Brazilian side and Río Paraguamusi (= Parauamuxi in indigenous language) on the Venezuelan side (see remarks).

Material examined.—MBUCV 3957.

Diagnosis.—*Atractus insipidus* can be distinguished from all congeners by the following

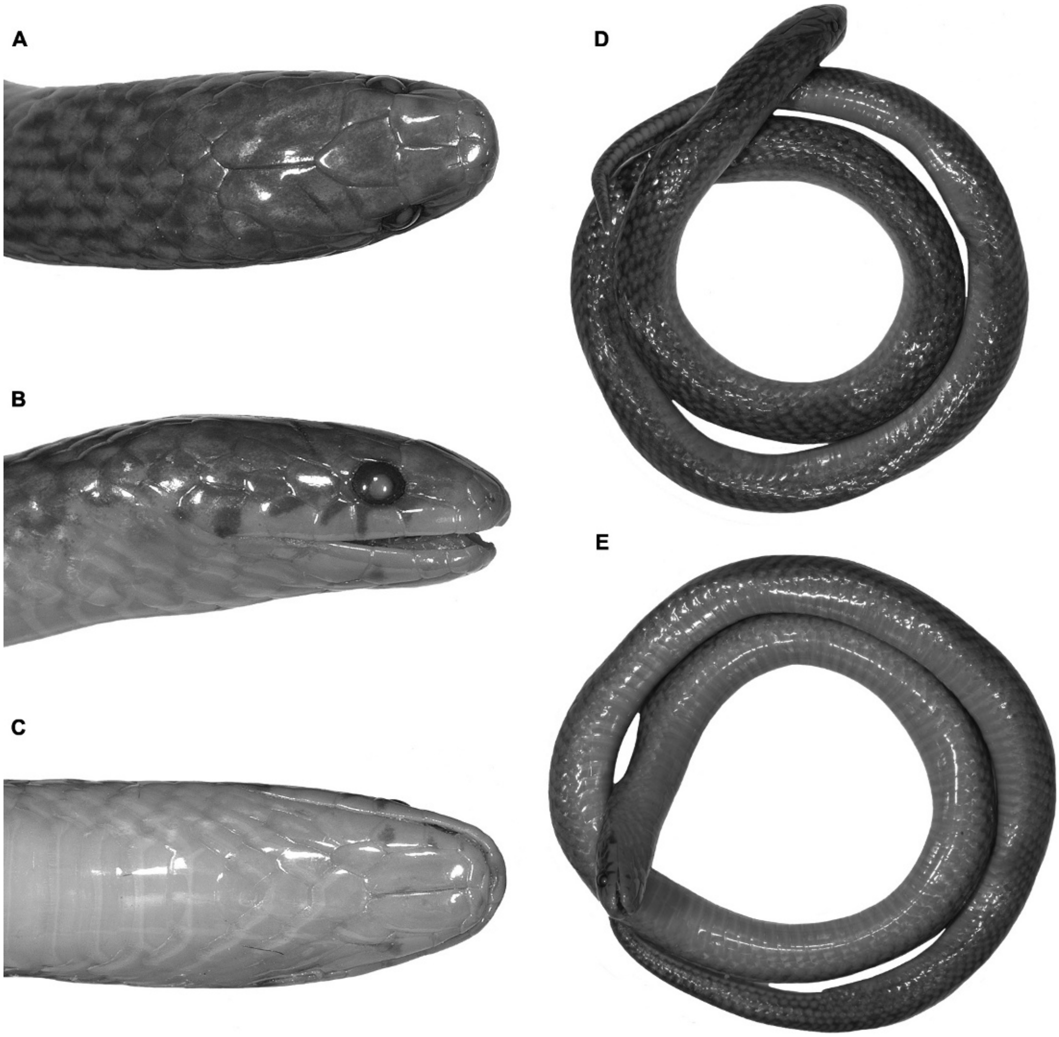

FIG. 5.—Dorsal (A), lateral (B), ventral (C) views of head, and dorsal (D) and ventral (E) views of body of the holotype of *Atractus insipidus* (MBUCV 3957).

combination of characters (data between brackets are those of Roze, 1961): (1) smooth dorsal scale rows 15/15/15; (2) postoculars two; (3) loreal long; (4) temporals 1 + 2; (5) supralabials seven, third and fourth contacting orbit; (6) infralabials seven, first four contacting chin shields; (7) maxillary teeth seven; (8) gular scale rows three; (9) preventrals three; (10) ventrals 157 in the single male; (11) subcaudals 34 [36] in the single male; (12) in preservation, dorsum light brown with irregular dark brown spots concentrated on vertebral and paravertebral regions; (13) in preservation, venter immaculate cream; (14) body size small in male, 206 mm SVL [205]; (15) tail moderate in male (13.6% [14.6] SVL); (16) hemipenis moderately bilobed and semicalyculate.

Comparisons.—Among all congeners, *A. insipidus* shares 15 dorsal scale rows, seven supralabials, seven infralabials, three gular scale rows, two or three preventrals, six to eight maxillary teeth, dorsum with light brown ground color and dark brown spots, and venter with creamish white ground color only with *A. punctiventris* Amaral, 1933. *Atractus* *insipidus* differs from *A. punctiventris* by having small-dispersed dorsal blotches and an immaculate creamish white venter (vs. broad dorsal blotches generally more than two scales wide and venter creamish white with a median line comprised of round brown blotches in the center of each ventral scale).

Redescription of the holotype.—Male, SVL 206 mm, TL 28 mm (13.6% SVL); head length 10.1 mm (4.9% SVL); head width 4.8 mm (47% head length); interorbital distance 3.4 mm; rostro-orbital distance 2.6 mm (80% interorbital distance); naso-orbital distance 2.2 mm; cervical constriction barely evident; head slightly arched in lateral view, rounded in dorsal view; snout truncate in lateral view, rounded in dorsal view; rostral subtriangular in frontal view, barely visible in dorsal view, 1.3 mm wide, 0.7 mm high; internasal 0.7 mm long, 0.6 mm wide; internasal suture sinistral to prefrontal medial suture; prefrontal 1.6 mm long, as long as wide; supraocular subtrapezoidal in dorsal view, 1.5 mm long, 0.8 mm wide; frontal subtriangular, 2.5 mm long, 1.8 mm wide; parietal 3.7 mm long, 2.1 mm wide; nasal divided; nostril almost restricted to prenasal; prenasal 0.4 mm high, about twice as high as long; postnasal 0.5 mm high, as high as long; loreal 1.4 mm long, 0.3 mm high, contacting second and third supralabials; eye diameter 1.2 mm; pupil subelliptical; two postoculars; lower postocular 0.4 mm high, as high as long; upper postocular slightly higher and longer than lower postocular; temporals 1 + 2; anterior temporal 1.1 mm long, 0.7 mm high; upper posterior temporals not fused; supralabials seven, third and fourth contacting orbit; first two supralabials similar in height, slightly smaller than third supralabial; sixth higher and seventh longer than remaining supralabials; symphysial triangular, 1.1 mm wide, 0.3 mm long; infralabials seven, first four contacting chin shields; first pair of infralabials in contact behind symphysial, preventing symphysial–chin shields contact; chin shields 2.6 mm long, 0.7 mm wide; gular scale rows three; preventrals three; ventrals 157; subcaudals 34; dorsal scale rows 15/15/15, lacking apical pits and supra-anal tubercles; body diameter 4.2 mm (2.0% SVL); retracted hemipenis six subcaudals long; anal gland four subcaudals long; caudal spine long, conical, robust, and acuminate. Maxillary arched in dorsal view, with six prediastemal teeth and one postdiastemal tooth; prediastemal teeth large, moderately spaced, similar in size, curved, angular in cross-section, robust at base, narrower at apices; diastema moderately long; postdiastemal tooth slightly smaller than the last prediastemal one (Figs. 3B, 5).

Color of holotype in preservative.—Dorsum of head brown, except snout region (rostral, internasals, and anterior portion of prefrontals) and margins of frontal and parietals beige; lateral surface of head brown until dorsal edges of supralabials, except for beige pigmentation of snout region (rostral, nasals, and anterior portion of loreals); supralabials mostly cream above dorsal margins of each scale; third to sixth supralabials with dark brown blotches on posterior region of scales, reaching labial margin of fourth scale; dark brown blotches covering almost the posterior one-third margin of seventh supralabial; four infralabials predominantly cream with covering slightly of brown pigment the region adjacent to chin shields; chin shields, gular, preventrals, and venter immaculate creamish white; ventral surface of tail creamish white with central brown stripe on median sutures of subcaudals; dorsal ground color, except for scale of first dorsal row, light brown with irregular dark brown spots concentrated on vertebral and paravertebral region (above sixth scale row); first dorsal scale rows uniformly creamish white; small dark markings unevenly dispersed on edges of dorsal scales, making a poorly defined reticulated pattern along dorsum of body and tail (Fig. 5).

Hemipenial morphology.—Retracted and nondissected organ bifurcated and extending to the level of sixth subcaudal; hemipenis apparently moderately bilobed; lobes restricted to distal portion of hemipenial body; sulcus spermaticus divides on distal third of organ.

Distribution and habitat.—Known only from the type locality, Poste M-1 landmark (04°01′08″N, 62°33′14″W; 952 m asl), between headwaters of Uraricapará (= Rio Uraricaá) and Paraguamusi (= Parauamuxi) Rivers, Serra (or Sierra in Spanish) de Pacaraima on the Brazil/Venezuela boundary. Nothing is known about the habitat of this species, but according to the type locality, it seems to occur in submontane forest (Fig. 4).

Remarks.—Roze (1961) described *A. insipidus* on the basis of a single specimen from Poste M-1, near Rio Uraricapará (= Rio Uraricaá), supposedly about 400 m asl on the Brazil/Venezuela boundary. We contacted the First Brazilian Commission for Boundaries Delimitations of the "Ministério das Relações Exteriores" of the Brazilian government and found that the elevation of the type locality as stated by Roze is incorrect (see PCDL, 1952). "The Brazilian Subsecretaria Geral do Serviço Exterior" published a map showing the type locality (Poste M-1 landmark; available at http://sistemas.mre.gov.br/kitweb/datafiles/Pcdl/pt-br/file/Fronteiras/Venezuela/Carta%2002.pdf. Archived by WebCite at http://www.webcitation.org/6Ikjp6UIR on 9 August 2013).

Roze (1961) compared *A. insipidus* with *A. reticulatus* Boulenger, 1885 (a species occurring in southern Brazil, northeastern Argentina, western Uruguay, and eastern Paraguay; Passos et al., 2010c), and distinguished the two species on the basis of different color patterns. Cunha and Nascimento (1983) identified a female from the municipality of Carolina in the state of Maranhão, Brazil as *A. insipidus.* Cunha and Nascimento (1983) stated that their specimen agrees with Roze's description, and suggested that disjunct populations of *A. insipidus* might occur in the Brazilian Cerrado as well as in savannahs of the Guiana Shield. However, 10 yr later, Cunha and Nascimento (1993) did not include *A. insipidus* in their account of the snakes from the eastern part of the state of Pará and western Maranhão in Brazilian Amazonia and thus apparently reconsidered their previous identification of *A. insipidus.* This seems to be the case since one of us (PP) found other specimens previously identified as *A. "insipidus"* in the MPEG collection that were not included in Cunha and Nascimento (1993). Similarily, Jorge da Silva (1993) and Jorge da Silva et al. (2005) identified *Atractus* specimens from the state of Rondônia, Brazil as *A.* cf. *insipidus* and *A. insipidus*, respectively. Comparisons between the holotype of *A. insipidus* and the aforementioned specimen reported by Cunha and Nascimento (1983) with additional samples from the same region in state of Rondônia previously sampled by Jorge da Silva (1993) and Jorge da Silva et al. (2005) revealed that individuals occurring in the southern Amazon River differ significantly from the holotype of *A. insipidus* (P. Passos, personal observation). The status of those specimens will be discussed elsewhere. Finally, Schargel and García-Pérez (2002) listed a specimen identified as *A. insipidus* from "Piedra de la Virgen" in the Canaima National Park, state of Bolívar, Venezuela, but we reidentified it as *A. tamessari* (see remarks on *A. tamessari*).

Atractus riveroi *Roze, 1961*
(Figs. 3C, 6, 7)

Holotype.—Adult male, AMNH 36615, collected on 20 April 1929 by members of the Tyler–Duida expedition, Cerro Duida (03°25′N, 65°40′W; ca. 1800 m asl), Amazonas, Venezuela.

Paratype.—Adult male, MBUCV 7175 (formerly UPR 49/R-20), collected by J.A. Rivero, Cerro Marahuaka (03°34′N, 65°27′W; ca. 1300 m asl), Amazonas, Venezuela.

Material examined.—AMNH 36615, MBUCV 7175, MHNLS 12889 ("Parima 8" [02°44′24″N, 64°17′02″W; ca. 980 m asl], Alto Orinoco, Sierra Parima, Amazonas,Venezuela/Brazil border); no females are known.

Diagnosis.—*Atractus riveroi* can be distinguished from all congeners by the following combination of characters: (1) smooth dorsal scale rows 17/17/17; (2) postoculars two; (3) loreal long; (4) temporals 1 + 2; (5) supralabials eight, fourth and fifth contacting orbit; (6) infralabials eight, first four contacting chin shields; (7) maxillary teeth seven; (8) gular scale rows three or four; (9) preventrals three or four; (10) ventrals 152–161 in males; (11) subcaudals 34–41 in males; (12) in preservation, dorsum variable, ground color beige with dark brown transversal bands or ground color black with light transversal bands; (13) in preservation, venter cream with rhomboidal dark brown blotches linearly arranged forming irregular stripes; (14) body size moderate, males reaching 415 mm SVL; (15) tail relatively long in males (16.2–18.2% SVL); (16) hemipenis moderately bilobed, semicapitate, semicalyculate.

Comparisons.—Among all congeners, *A. riveroi* shares 17 dorsal scale rows, eight supralabials, eigth infralabials, first four infra-

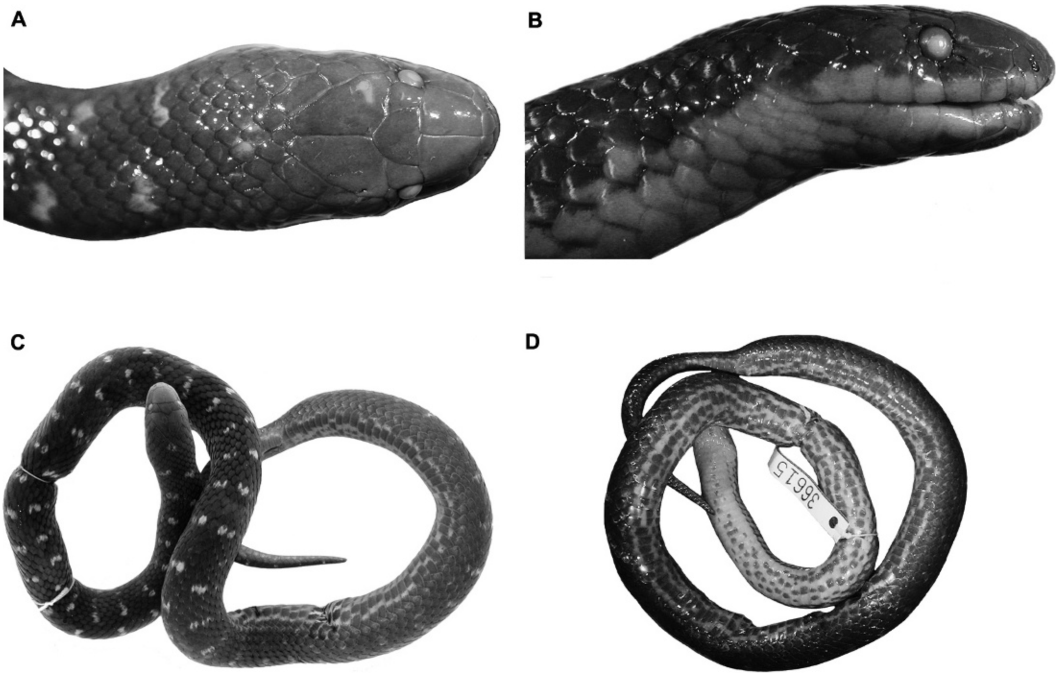

FIG. 6.—Dorsal (A) and lateral (B) views of head, and dorsal (C) and ventral (D) views of body of the holotype of *Atractus riveroi* (AMNH 36615).

labials contacting chin shields, relatively long tail in males, dorsum sometimes black with light transversal blotches, and venter with brown blotches making irregular broken stripes only with *A. lancinii* Roze, 1961. *Atractus riveroi* differs from *A. lancinii* by having seven maxillary teeth and a single postdiastemal tooth (vs. eight or nine maxillary teeth with two postdiastemal teeth). Some individuals of *A. riveroi* show an inversion of background coloration (i.e., light with dark transversal blotches instead of dark with light transversal blotches), which is also reported in *A. erythromelas* Boulenger, 1903 (Passos, 2008) and *A. sanctaemartae* Dunn, 1946 (Passos et al., 2009d). *Atractus riveroi* differs from these two species by having eight supralabials and eight infralabials (vs. seven supra- and seven infralabials in *A. erythromelas* and *A. sanctaemartae*).

Description.—Head twice as long as wide, arched in lateral view, round in dorsal view; cervical constriction barely distinct; snout truncate in lateral view, rounded in dorsal view; canthus rostralis well marked in lateral view; rostral subtriangular in frontal view, wider than high, barely visible in dorsal view; internasal as long as wide; internasal suture sinistral to prefrontal medial suture; prefrontal longer than wide; supraocular subtrapezoidal, twice as long as wide; frontal subpentagonal, as long as wide; parietal about twice as long as wide; nasal divided; nostril almost restricted to prenasal; prenasal slightly higher than long; postnasal about as high as long; loreal long, contacting second, third, and fourth supralabials; pupil round; two postoculars similar in height; upper postocular longer than lower postocular; temporals 1 + 2; anterior temporal about twice as long as high; upper posterior temporals not fused; supralabials eight, fourth and fifth in contact with orbit; first three supralabials similar in height and slightly shorter than fourth supralabial; seventh and eighth supralabials respectively higher and longer than remaining supralabials; symphysial subtriangular, twice as wide as long; infralabials eight, first four contacting chin shields; first pair of infralabials in contact behind symphysial, preventing symphysial–chin-shields contact; chin shields about three times as long as wide; gular scale rows

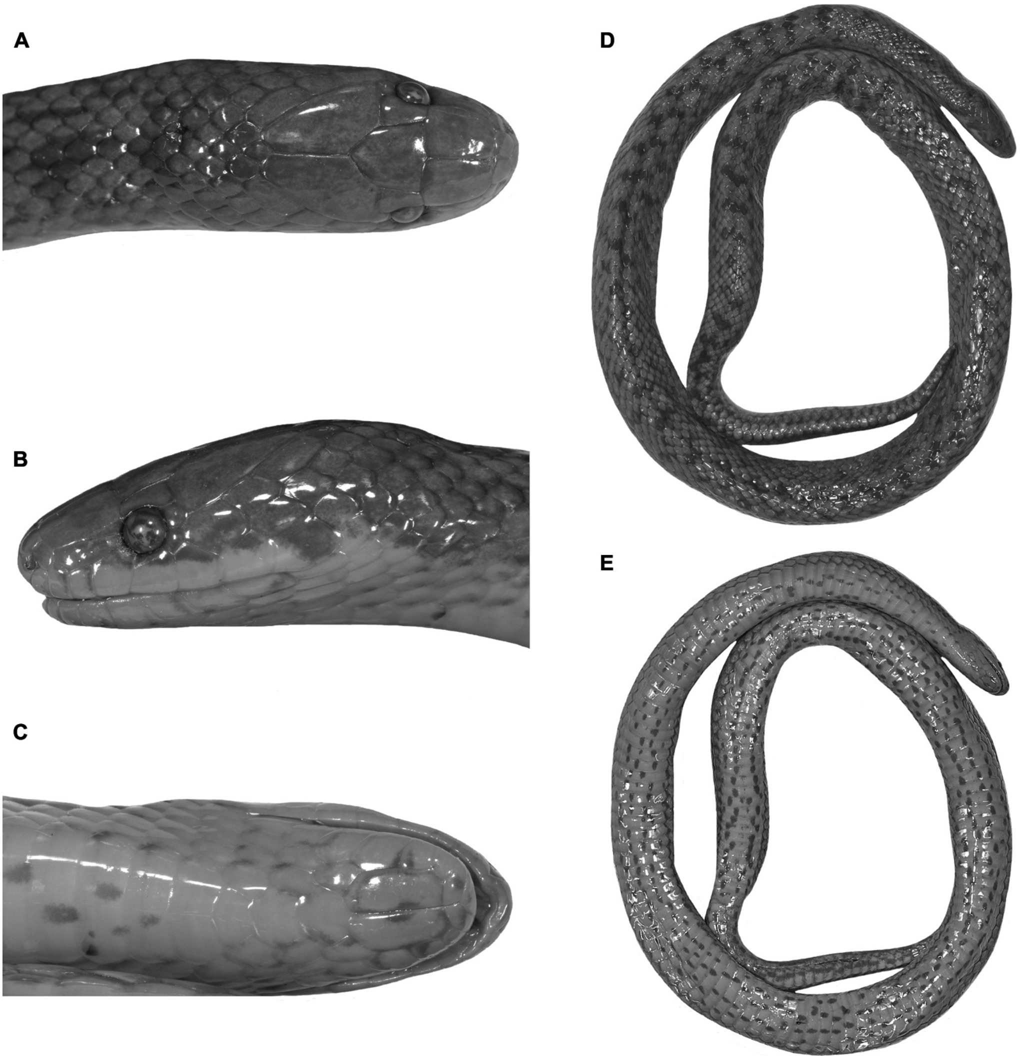

FIG. 7.—Dorsal (A), lateral (B), ventral (C) views of head, and dorsal (D) and ventral (E) views of body of the paratype of *Atractus riveroi* (MBUCV 7175).

generally three; preventrals three; dorsal scale rows 17/17/17, lacking apical pits and supra-anal tubercles; caudal spine moderately long, rhomboid, and acuminate. Maxillary arched in dorsal view, with six prediastemal and one postdiastemal teeth; prediastemal teeth moderately spaced, curved, angular in cross-section, robust at base, and narrower at apices; diastema moderately long; postdiastemal tooth significantly shorter than last prediastemal ones (Figs. 3C, 6, 7).

Adult color in preservative.—Dorsum of head light to dark brown; head laterally brown until dorsal margin of supralabials; supralabials cream, except for last scale, which is mostly brown; first five pairs of infralabials cream with dark brown spots on region adjacent to chin shields; genials, chin shields, and preventrals with dispersed dark brown spots; venter cream with one to three series of round or rhomboidal dark brown blotches linearly disposed, making irregular broken stripes; ventral blotches concentrated on anterior part of body; ventral surface of tail with brown blotches restricted to subcaudal edges or with dark brown pigments concentrated on lateral margin of subcaudals; dorsal ground color of body light to dark brown; when light, with about 60 wide black blotches (one scale long and three scales wide) on paravertebral region and black spots (smaller than one scale wide) along interspaces of flanks or connected dorsally to paravertebral blotches; when dark, with about 80 paired narrow creamish yellow transversal bands (one scale long and two or three scales wide) on the flanks that never contact each other on vertebral region (Figs. 6, 7).

Hemipenial morphology.—Retracted and nondissected hemipenis (MBUCV 7175, both organs) bifurcates on 10–11th and extends to the level of 12–13th subcaudal. Partially everted and not fully expanded hemipenis (MHNLS 12889, both organs) moderately bilobed, semicapitate, and semicalyculate; lobes distinct, longer than remaining capitulum; capitulum located just above sulcus spermaticus bifurcation; capitular groove distinct on sulcate side of hemipenis; hemipenial body covered with moderately hooked spines; basal portion of hemipenis with longitudinal plicae and dispersed spinules.

Quantitative variation.—Largest male 415 mm SVL, 70 mm TL; tail 16.2–18.2% (mean = 17.1; SD = 1; n = 3) SVL in males; ventrals 152–161 (mean = 155.3; SD = 4.9; n = 3) in males; subcaudals 34–41 (mean = 37.5; SD = 3.3; n = 3) in males; gular scale rows three (n = 4 sides) or four (n = 2 sides); dorsal scale rows at the level of second subcaudal 8–10 (mean = 8.7; SD = 1; n = 4 sides); body diameter 7.1–9.4 mm.

Distribution and habitat.—Reported between 1300 and 1800 m elevation on the slopes of Cerro Duida, Cerro Marahuaka, and from the Alto Orinoco Sierra Parima (02°44′24″N, 64°17′02″W; ca. 980 m asl) in the state of Amazonas, Venezuela. According to the original description, the holotype was collected in "subparamo" savannah. McDiarmid and Donnelly (2005) described the vegetation on the summit and slopes of these locations as being composed of "broad-leaved, shrubby highland meadows on peat; broad-leaved, shrubby high-tepui meadows on peat and rock; low to tall upland and high-tepui scrub; low evergreen high-tepui forest" (Fig. 4).

Remarks.—Roze (1961) described *Atractus riveroi* on the basis of two specimens from Cerro Duida and Cerro Marahuaka in Venezuela. We report herein the third known individual of *A. riveroi* from the Sierra Parima close to the Venezuela/Brazil border. This new record suggests that the species may be more widely distributed than expected and may also occur in Brazil. This specimen has a semi-everted hemipenis, but we were not allowed to dissect and prepare the organs.

Atractus steyermarki *Roze, 1958*
(Figs. 8–12)

Atractus zidoki Means, 2007. [Misidentification].
Atractus guerreroi Myers and Donnelly, 2008. [New synonymy].

Holotype.—Adult male, FMNH 69920, collected on 09 April 1953 by C. Griffin, on Chimantá Tepui (05°18′N, 62°10′W; ca. 1430 m), Bolívar, Venezuela.

Paratype.—FMNH 74036, adult female, collected on 14 February 1955 by J. Steyermark and J. Wurdack, on Chimantá Tepui (05°18′N, 62°10′W; Tirica River, ca. 2160 m asl), Bolívar, Venezuela.

Material examined.—FMNH 69920, FMNH 74036, BMNH 1976.348 (Mount Roraima, Cuyuni-Mazaruni District, Guyana), HA 701 (upper slope of Mount Roraima, Guyana), MHNLS 11004 (south of Churi-Tepui, Chimantá massif, Bolívar, Venezuela), MBUCV 3872 (109 km south of El Dorado, Bolívar, Venezuela), IRSNB 18091 (Wei Assipu Tepui, 2244 m elevation, Cuyuni-Mazaruni District, Guyana), EBRG 3403 (holotype of *A. guerreroi* from Auyantepui, Bolívar, Venezuela), EBRG 5197 (Sierra de Lema, La Escalera, Bolívar, Venezuela).

Diagnosis.—*Atractus steyermarki* can be distinguished from all congeners by the following combination of characters: (1) smooth dorsal scale rows 17/17/17; (2) postoculars usually two; (3) loreal moderately long; (4) temporals 1 + 2; (5) supralabials six or seven, third and fourth contacting orbit; (6) infralabials seven, first three contacting chin shields; (7) maxillary teeth five or six; (8) gular scale rows four; (9) preventrals four or five; (10) ventrals 177–183 in females, 160–167 in males; (11) subcaudals 27–33 in females, 37–44 in males; (12) in preservation, dorsum

A

B

C

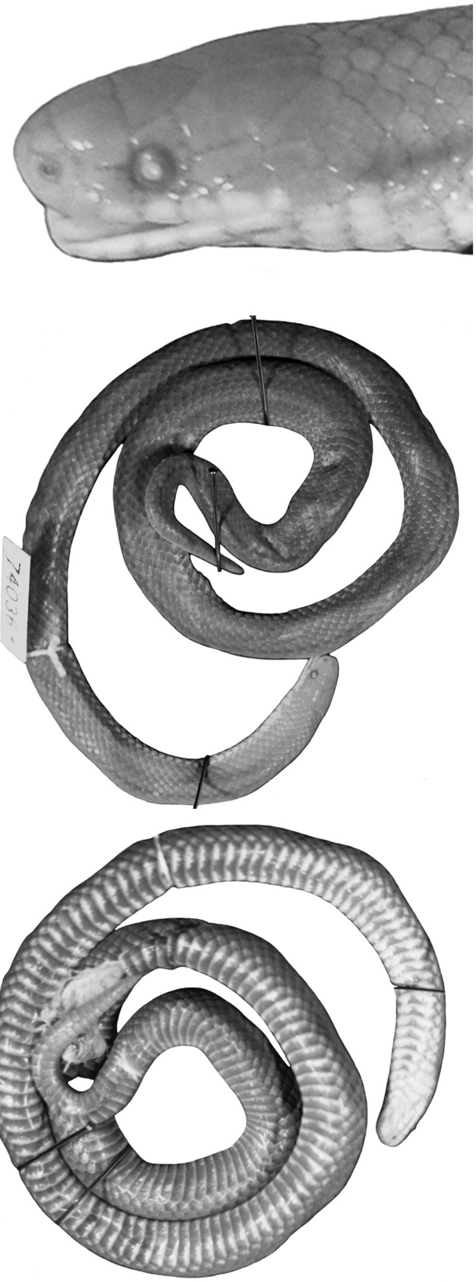

FIG. 8.—Dorsal (A) and view of head and dorsal (B) and ventral (C) views of body of the paratype of *Atractus steyermarki* (FMNH 74036). Photos by A. Resetar.

dark brown to black, usually with a dark vertebral stripe and sometimes with barely defined dark brown dorsolateral stripes; (13) in preservation, venter of juveniles predominantly cream generally with a midventral stripe at least in the posterior region of the body, venter of adults similar, but with broader and more conspicuous midventral stripe; (14) body size moderate, females reaching 373 mm SVL, males 348 mm SVL; (15) tail size moderate in females (11.1–13.4% SVL) and relatively long (16.1–20.1% SVL) in males; (16) hemipenis unilobed with bifurcate sulcus spermaticus, organ noncapitate and noncalyculate.

Comparisons.—Among all congeners, *A. steyermarki* shares a unilobed (sensu Prudente and Passos, 2010) hemipenis only with *A. hoogmoedi* Prudente and Passos, 2008 and *A. zidoki* Gasc and Rodrigues, 1979. *Atractus steyermarki* differs from both by having dorsal scales lacking apical pits and supra-anal tubercles (vs. dorsals with apical pits and supra-anal tubercles in males of both species). Among species having 17 dorsal scale rows, *A. steyermarki* superficially resembles *A. duidensis* and *A. matthewi*, from which it differs by the peculiar hemipenial morphology and by having 160–167 ventrals in males and 177–184 in females, 37–44 subcaudals in males, 27–33 in females, and five to six maxillary teeth (vs. 156 and 171 ventrals, respectively, in the male and the female, 36 subcaudals in female, and eight to nine maxillary teeth in *A. duidensis*; 157–161 ventrals in males, 158–171 in females, 25–28 subcaudals in males, 20–25 in females, and nine to 10 maxillary teeth in *A. matthewi*).

Description.—Head twice as long as wide, sligthly arched in lateral view, round in dorsal view; snout truncated in lateral view, rounded in dorsal view; rostral subtriangular in frontal view, barely visible in dorsal view, wider than high; internasal as long as wide; internasal suture sinistral to prefrontal medial suture; prefrontal wider than long; supraocular subrectangular, longer than wide; frontal pentagonal, as long as wide; parietal about twice as long as wide; nasal divided; nostril located between prenasal and postnasal; prenasal twice as high as long; postnasal as long as high; loreal moderate to long, contacting second and third supralabials; pupil round; generally two postoculars similar in length; upper postocular slightly higher than lower postocular; upper postocular rarely very reduced in size or fused with lower postocular

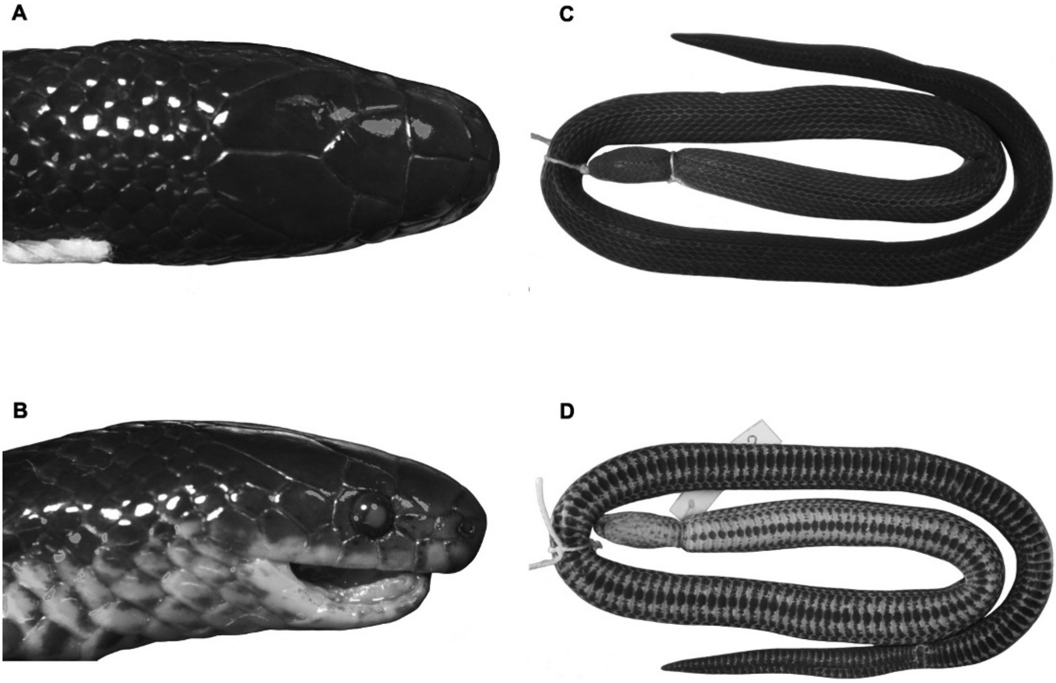

FIG. 9.—Dorsal (A) and lateral (B) views of head, and dorsal (C) and ventral (D) views of body of *Atractus steyermarki* from Churi-Tepui, Venezuela (MHNLS 11004).

(n = 2); temporals 1 + 2; anterior temporal twice as long as high; upper posterior temporals fused, about three times as long as wide; supralabials six to seven, third and fourth contacting orbit; first two supralabials similar in height and smaller than third supralabial; sixth higher and seventh longer than remaining supralabials; symphysial subtriangular, about three times as wide as long; infralabials seven, first three contact chin shields; first pair of supralabials in contact behind symphysial, preventing symphysial–chin-shields contact; chin shields three times as long as wide; gular scale rows four; preventrals four; dorsal scale rows 17/17/17, lacking apical pits and supra-anal tubercles; caudal spine long, robust, and rounded. Maxillary arched in dorsal view, with usually five prediastemal teeth and one postdiastemal tooth; first prediastemal tooth slightly smaller than remaining teeth, which are similar in size; prediastemal teeth well spaced, curved posteriorly, angular in cross-section, robust at base, slightly narrower at apices; diastema moderately long; postdiastemal tooth slightly smaller than last prediastemal one; lateral process of maxilla well developed, lacking posterior projection (Figs. 8, 9).

Juvenile color in preservative.—Dorsum of head brown; head laterally brown until dorsal margin of supralabials; supralabials mostly cream; mental region cream with few brown spots concentrated on symphysial, first pair of infralabials and anterior portion of chin shields; venter cream with rhomboidal black blotches in center of each ventral scale, forming a conspicuous stripe; central blotches gradually wider, covering half width of venter posteriorly; ventral surface of tail mostly black, with lateral or posterior region of subcaudals cream to beige; dorsum grayish brown with barely defined longitudinal black stripes (one or one half scale wide); distinct vertebral stripe and two dorsolateral lines (one on each side), covering second to third and third to fourth scale rows (counting from vertebral line).

Adult color in preservative.—Dorsum of head brown to dark brown; head laterally brown until dorsal margins of supralabials; supralabials mostly cream, with brown pigment on scale sutures occasionally reaching

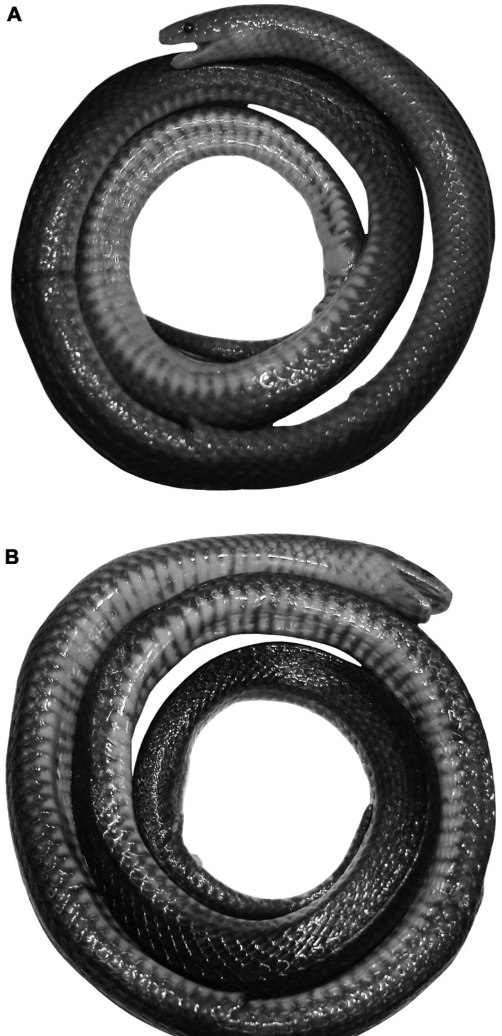

FIG. 10.—Dorsal (A) and ventral (B) views of body of *Atractus steyermarki* from the La Escalera region, Venezuela (MBUCV 3872).

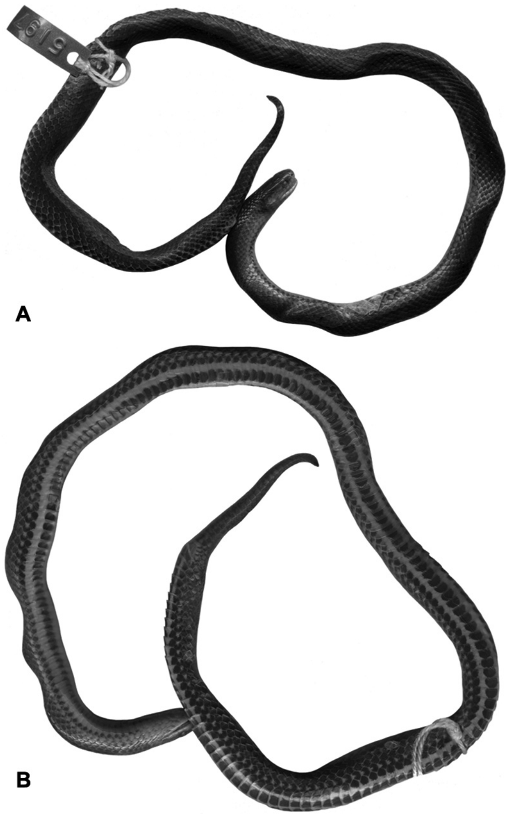

FIG. 11.—Dorsal (A) and ventral (B) views of body of *Atractus steyermarki* from the Sierra de Lema, La Escalera region, Venezuela (EBRG 5197).

lower margin of scales; mental region cream with brown spots concentrated above symphysial, first pair of infralabials and anterior part of chin shields; posterior region of infralabials, chin shields, gulars and preventral scales cream with small brown dots; anterior part of venter cream with central (wide, rhomboidal) and lateral (small, irregular) dark brown spots or blotches; these blotches are connected or almost connected in the middle, forming a more or less continuous stripe; venter gradually becomes almost uniformly dark brown because of the presence of central blotches; posterior edges of ventral scales generally lighter (beige); ventral surface of tail mostly dark brown, with beige spots above posterior subcaudal sutures; dorsal ground color brown to dark brown, usually with a darker middorsal (vertebral) stripe bordered by a lighter stripe on each side (these markings are more evident when the specimen is immersed in preservative), sometimes with ill-defined dark lateral stripes (Figs. 8–12).

Adult color in life.—Dorsally shiny black with two ill-defined reddish brown paravertebral stripes extending roughly from occipital region to base of tail; posterior border of flank scales usually slightly peppered with dark brown pigment; scales of first dorsal row black anteriorly, yellow posteriorly, forming an ill-defined low lateral stripe; supralabials

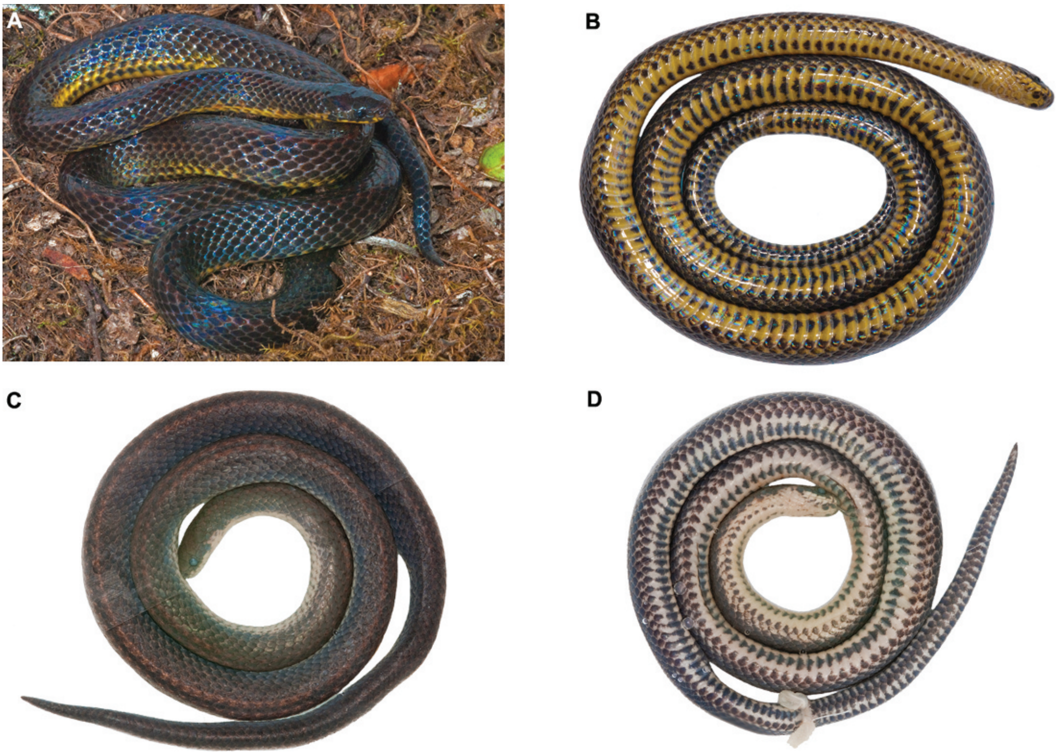

FIG. 12.—Dorsolateral (A) and ventral (B) views in life of *Atractus steyemarki* from Wei-Assipu Tepui (IRSBN 18091), and dorsal (C) and ventral (D) views of the same specimen in preservative. Photos by P.J.R. Kok.

black dorsally and yellow ventrally; iris dark brown; infralabials yellow dorsally, black ventrally; each chin shield with distinctive lateral black spot; ventral scales yellow, with black medial blotch and a black blotch on each side; medial black blotches start as small spots on the first ventrals changing into half-moon markings that gradually increase in size posteriorly, forming a discontinuous median line; subcaudal scales yellow, each pair of subcaudal with a black blotch on each side making the subcaudal pattern similar to ventral pattern until mid-tail, but blotches fuse into a distinctive cohesive stripe; from mid-tail, posterior subcaudals almost completely black (Fig. 12A,B).

Hemipenial morphology.—Organ unilobed, noncapitate, and noncalyculate; hemipenis arched, clavate, and slightly attenuate on the apices; basal portion of organ broader and longer than apical region; hemipenis covered by small to moderate hooked spines and papillae; apical portion of hemipenis with robust papillae and longitudinal crests derived from lateral spines; sulcus spermaticus bifurcates on distal third of organ; sulcus spermaticus branches centrolinearly oriented, running toward apex of organ; asulcate side of hemipenis with well-distinct median longitudinal crest on organs partially expanded and slightly distinct on fully expanded organs; median intrasulcar crest situated just above sulcus spermaticus bifurcation; sulcus spermaticus margins stout at basal portion of hemipenis and moderately expanded before division of sulcus spermaticus; hemipenial body covered by small and dispersed hooked spines; basal naked pocket extending through first third of the asulcate side of hemipenis; proximal region of hemipenis with longitudinal plicae and dispersed spinules (Fig. 13).

Quantitative variation.—Largest female 373 mm SVL, 47 mm TL; largest male 348 mm SVL, 70 mm TL; tail 11.1–13.4% (mean = 12.1; SD = 1.1; n = 4) SVL in females, 16.1–20.1 (mean = 17.7; SD = 1.7;

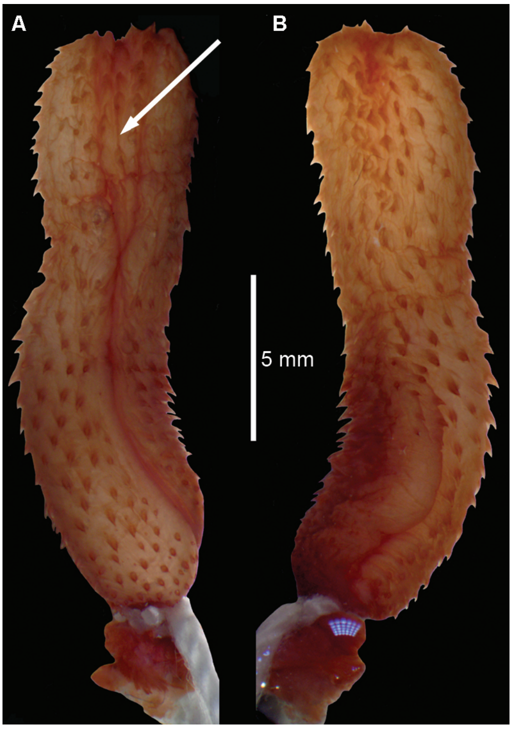

FIG. 13.—Sulcate (left) and asulcate (right) sides of the hemipenis of *Atractus steyermarki* (MHNLS 11004). White arrow indicates longitudinal medial crest on sulcate side.

n = 5) in males; ventrals 177–183 (mean = 178.7; SD = 2.9; *n* = 4) in females, 160–167 (mean = 164; SD = 2.9; *n* = 5) in males; subcaudals 27–33 (mean = 29.2; SD = 2.9; *n* = 4) in females, 37–44 (mean = 40; SD = 2.7; *n* = 5) in males; supralabials six (*n* = 1 side) or seven (*n* = 17 sides); preventrals four (*n* = 8) or five (*n* = 1); scale rows at the level of second subcaudal eight (*n* = 1 side), nine (*n* = 1 side), 10 (*n* = 2 sides), or 11 (*n* = 6 sides); maxillary teeth five (*n* = 2 sides) or six (*n* = 9 sides); body diameter 4.3–7.6 mm; retracted hemipenis extends to the level of eighth subcaudal (*n* = 2 sides). Specimen MHNLS 11004 has the upper postocular very reduced in size (lower postocular three times higher than upper postocular) on the right side, and postoculars entirely fused on the left side of the head.

Distribution and habitat.—Pantepui region, from Auyantepui and Chimantá Tepui, state of Bolívar, Venezuela to Wei Assipu tepui, Cuyuni-Mazaruni District, Guyana. *Atractus steyermarki* occurs in open formations like savannahs and tepui meadows as well as cloud forests between 500 and 2244 m asl (Fig. 4).

Remarks.—Roze (1958a) described *A. steyermarki* on the basis of two specimens from Chimantá Tepui, Bolívar, and compared it with *A. boettgeri* Boulenger, 1896 and *A. modestus* Boulenger, 1894 (both species sharing 17 dorsal scale rows and uniformly brown to black coloration). Subsequently, Roze (1961, 1966) cited a third individual from the region of the municipality of El Dorado, also in Bolívar state. To date, this record remains unverified (see Myers and Donnelly, 2008). Gorzula (1992) reported the fourth known specimen of *A. steyermarki* from Churi Tepui in the Chimantá Massif. This specimen was briefly described by Gorzula and Señaris (1999) who stated that, on the basis of the available evidence, *A. steyermarki* is endemic to the summits of the Chimantá Massif. Apparently, Gorzula and Señaris (1999) did not agree with the identification of the specimen from El Dorado. In the course of a revision of the genus *Atractus*, the senior author examined the El Dorado specimen (MBUCV 3872, Fig. 10) and confirmed its identification as *A. steyermarki*. Means (2007) reported *A. zidoki* from ca. 2090-m elevation on the talus slope of Mount Roraima, in Guyana. One of us (PJRK) was informed by C. J. Cole (personal observation)—who examined photographs of that specimen—that it is not an *A. zidoki*, but an *A. steyermarki* specimen. During a visit to the University of Guyana PJRK examined the specimen (HA 701) and confirmed its identification as *A. steyermarki* (see also Cole et al., 2013). The examination of these individuals, as well as the specimen reported by Gorzula (1992) from the Chimantá Massif (MHNLS 11004) and four additional specimens from the Sierra de Lema (also in the La Escalera region of Venezuela, EBRG 5195–97; Fig. 11) and Mount Roraima (BMNH 1976.348), provided new insights in the pattern of variation and distribution of *A. steyermarki*.

Myers and Donnelly (2008) described *A. guerreroi* on the basis of a single specimen from Auyantepui (ca. 2100 m asl). These authors stated that although *A. guerreroi*

TABLE 1.—Measurements (mm) for some specimens of *Atractus steyermarki*. The measurements of the holotypes of *A. guerreroi* and *A. steyermarki* are from Myers and Donnelly (2008), and these were based on the species descriptions provided by them. Our absolute measurements are according with Myers and Donnelly definitions. Values to the right of percentages are measurements in the numerator of each ratio.

Variables	Holotype of *A. guerreroi*		Holotype of *A. steyermarki*		MHNLS 11004	
Total length	250		257		360	
Snout–vent length (SVL)	215		219		308	
Tail length/SVL	14%	35	14.8%	38	14.4%	52
Head length/SVL	3.5%	7.6	4.2%	9.2	3.5%	10.8
Snout–parietal distance/head length	90.8%	6.9	85%	7.8	87%	9.4
Head width/head length	63%	4.8	53%	4.9	53%	5.7
Body width/SVL	2.8%	6	2.5%	5.5	1.9%	7.0
Body height/SVL	2.8%	6	2.5%	5.5	1.9%	7.0
Snout eye distance/head length	29%	2.2	27.2%	2.5	29.6%	3.2
Eye length/head length	14.5%	1.1	13%	1.2	11.1%	1.2
Eye-to-lip distance/head width	16.5%	0.8	14.3%	0.7	14%	0.8
Nasal length/snout–eye distance	63.6%	1.4	60%	1.5	56.2%	1.8
Loreal length/snout–eye distance	36.3%	0.8	44%	1.1	34%	1.1
Loreal height/head width	10.4%	0.5	12.2%	0.6	12.3%	0.7
Internasal length/head length	11.8%	0.9	8.7%	0.8	8.3%	0.9
Internasal width/head width	20.8%	1.0	22.4%	1.1	21%	1.2
Internasal suture length/internasal length	40%	0.4	72.7%	0.8	50%	0.6
Prefrontal length/head length	27.6%	2.1	19.5%	1.8	19.4%	2.1
Prefrontal width/head width	35.4%	1.7	36.7%	1.8	38.6%	2.2
Prefrontal suture/prefrontal length	76.2%	1.6	83.3%	1.5	86.4%	1.9
Frontal length/head length	23.7%	1.8	27.2%	2.5	25%	2.7
Frontal width/head width	45.8%	2.2	53%	2.6	47.3%	2.7
Supraocular length/head length	15.8%	1.2	15.2%	1.4	13.9%	1.5
Supraocular width/head width	16.7%	0.8	32.6%	1.6	19.3%	1.1
Parietal length/head length	47.4%	3.6	42.4%	3.9	42.6%	4.6
Interparietal suture length/parietal length	63.9%	2.3	60%	2.3	58.7%	2.7
Chin-shield length/head length	31.6%	2.4	25%	2.3	31.5%	3.4
Chin-shield width/head width	18.7%	0.9	20.4%	1.0	15.8%	0.9

shares multiple similar morphological characters with *A. steyermarki*, their new species could be distinguished from the latter on the basis of different color pattern and reduced head size (including cephalic scales measurements). They provided detailed comparisons and illustrations of the head of both species to diagnose them (pp. 118–121 in Myers and Donnelly, 2008). Even so, they pointed out that, although their limited data suggests divergence of the evolutionary course of *A. steyermarki* and *A. guerreroi* with respect to coloration and head size, their hypothesis needed larger sampling to be accurately tested. According to Myers and Donnelly (2008), *A. guerreroi* has a relatively reduced head and a tendency to be uniformly colored (not necessarily melanistic as suggested by the authors). We made the same observations while examining additional specimens of *A. steyermarki* (Figs. 8–12) and found overlap in most measurements of the cephalic scales between the specimens of *A. steyermarki* and *A. guerreroi* (Table 1). As such, the morphometric diagnostic characters used by Myers and Donnelly (2008; loreal, frontal, and supraocular length and supraocular width) cannot be used to distinguish these two species from each other. Strong variation in cephalic scale proportions and color pattern are well documented in the genus *Atractus* (Savage, 1960; Dixon et al., 1976; Passos et al., 2010c; Passos and Prudente, 2012). We interpret the minor differences in color pattern between the holotypes of *A. guerreroi* and *A. steyermarki* (see Myers and Donnelly, 2008) as an expected result of geographic or ontogenetic variation (which is still not clear on the basis of the available sample). Myers and Donnelly (2008) attributed the stripped pattern of the holotype of *A. steyermarki* to a faded ground color possibly as a result of preservation. However, it could also represent the juvenile color pattern of the species since

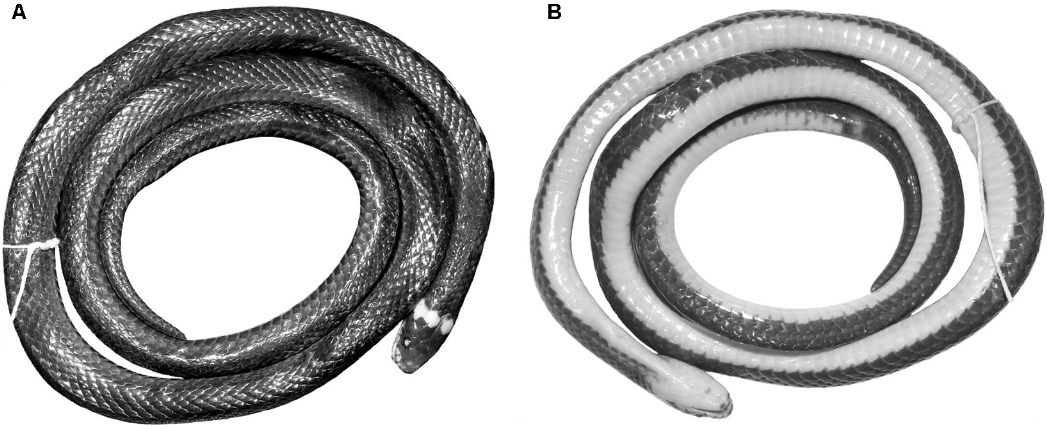

FIG. 14.—Dorsal (A) and ventral (B) views of body of the holotype of *Atractus surucucu* from Serra das Surucucus, Brazil (MPEG 19146). Photos by A. Prudente.

both holotypes are relatively "small" and more similar to each other in coloration than the remaining known specimens of *A. steyermarki* (see figs. 67 and 70 in Myers and Donnelly, 2008, and Figs. 8–12 of the present study). The dorsal color pattern of the paratype of *A. steyermarki* is more similar to the El Dorado specimen, whereas the latter shows the ventral pattern observed in the holotypes of *A. guerreroi* and *A. steyermarki* (Figs. 8–12). Although the ontogenetic change consisting of the darkening of the dorsal coloration is common in the genus *Atractus* (Savage, 1960; Passos et al., 2010a, 2013a), melanistic individuals of polychromatic species are more rarely found (e.g., *A. zebrinus*; Passos et al., 2010c). Finally, the hemipenis of *A. steyermarki* is very similar to that of *A. guerreroi* (Myers and Donnelly, 2008, pp. 117–118) and the only major difference between both hemipenial descriptions is the terminology used, not the general morphology (compare Fig. 13 of this paper with fig. 69 in Myers and Donnelly, 2008). Although Myers and Donnelly (2008) described the hemipenis of *A. guerreroi* as weakly bilobed, we consider the organs to be unilobed. The occurrence of the sulcus spermaticus bifurcation is independent of bilobation in some species of *Atractus* and putative closely related genera, like *Geophis* (Downs, 1967; see also the discussion for more details). In conclusion, and for the reasons mentioned above, we herein synonymize *A. guerreroi* with *A. steyermarki*.

Atractus surucucu *Prudente and Passos, 2008* *(Fig. 14)*

Holotype.—Adult female, MPEG 19146, collected on 12 November 1996 by the Comissão Mista Brasileiro-Venezuelana Demarcadora de Limites and later donated to MPEG by J. B. F. Silva, from Serra das Surucucus (alternative spelling of the "Serra do Surucucu;" 02°47′N, 63°40′W, ca.1000 m asl), municipality of Alto Alegre, state of Roraima, Brazil.

Paratypes.—Subadult females, MPEG 18436 and 18437, collected at the type locality on 19 November 1991 by Comissão Mista Brasileiro-Venezuelana Demarcadora de Limites and later donated to MPEG by S. Almeida.

Material examined.—MPEG 19164 and MPEG 18436–37.

Diagnosis.—*Atractus surucucu* can be distinguished from all congeners by the following combination of characters: (1) smooth dorsal scale rows 17/17/17; (2) postoculars two; (3) loreal moderate; (4) temporals 1 + 2; (5) supralabials seven, third and fourth contacting orbit; (6) infralabials seven, first three contacting chin shields; (7) maxillary teeth five; (8) gular scale rows three or four; (9) preventrals four; (10) ventrals 200–207 in females; (11) subcaudals 25–26 in females; (12) in preservation, dorsal ground color uniform chocolate to dark brown, with two creamish white stripes on the paraventral region, and incomplete cream occipital collar;

(13) in preservation, venter immaculate creamish white and ventral suface of tail entirely black; (14) body size moderate, females reach 388 mm of SVL; (15) tail short in females (7.7–8.8% SVL).

Comparisons.—Among all congeners, *A. surucucu* shares an atypical suite of characters with *A. alphonsehogei* Cunha and Nascimento, 1983; *A. caxiuana* Prudente and Santos-Costa, 2006; *A. collaris* Peracca, 1896; *A. gaigeae* Savage, 1955; *A. hoogmoedi* Prudente and Passos, 2010; *A. limitaneus* Amaral, 1935; and *A. zidoki* (see Prudente and Passos, 2008, 2010). *Atractus surucucu* differs from *A. collaris, A. gaigeae, A. hoogmoedi, A. limitaneus,* and *A. zidoki* by having a dorsal color pattern uniformly dark brown and the tail entirely black (vs. dorsal color pattern with white-bordered paired spots on paravertebral region, longitudinal stripes on the vertebral area, in the paravertebral region or on the flanks, and ventral surface of tail never entirely black). Compared with the above species in which some individuals may present a uniform color pattern, *A. surucucu* differs from *A. alphonsehogei* by having a higher number of ventral scales (200–208) in females and uniformly black subcaudals (vs. 163–175 in females and white subcaudals); it differs from *A. caxiuana* by having the loreal not contacting the internasals (vs. in contact).

Description.—Head about twice as long as wide, flattened in lateral view, round in dorsal view; snout truncated in lateral view, rounded in dorsal view; rostral subtriangular in frontal view, visible in dorsal view, about twice as wide as high; internasal longer than wide; internasal suture dextral or sinistral with respect to prefrontal medial suture; prefrontal wider than long; supraocular subrectangular, longer than wide; frontal pentagonal, as long as wide; parietal about twice as long as wide; nasal divided; nostril situated between prenasal and postnasal; prenasal twice as high as long; postnasal as long as high; loreal moderate to long, contacting second and third supralabials; pupil round; two postoculars similar in size; temporals 1 + 2; anterior temporal twice as long as high; upper posterior temporals fused, about three times as long as wide; supralabials seven, third and fourth contacting orbit; first two supralabials similar in height and smaller than third supralabial; sixth higher and seventh longer than remaining supralabials; symphysial subtriangular, about three times as wide as long; infralabials seven, first three contact chin shields; first pair of supralabials in contact behind symphysial, preventing symphysial–chin-shields contact; chin shields three times as long as wide; gular scale rows four; preventrals four; dorsal scale rows 17/17/17, lacking apical pits and supra-anal tubercles in the known females (but see Prudente and Passos, 2008 for comments in this regard); caudal spine long, robust, and rounded. Maxillary arched in dorsal view, with usually four prediastemal teeth and one postdiastemal tooth; first prediastemal tooth slightly smaller than remaining teeth, which are similar in size; prediastemal teeth well spaced, curved posteriorly, angular in cross-section, robust at base, slightly narrower at apices; diastema moderately long; postdiastemal tooth slightly smaller than last prediastemal one; lateral process of maxilla well developed, lacking posterior projection.

Adult color in preservative.—Dorsum of head dark brown, with most cephalic shields having small cream spots toward the center; anterior part of first six pairs of supralabial scales cream; posterior part of head with two large cream blotches on each side, not in contact medially, forming an incomplete occipital collar that covers posterior part of parietals, most of temporal region, and posterior part of seventh supralabial; infralabials and gular region uniformly cream white; anterior region of the first pair of infralabials, lateral portions of symphysial, and medial portion of gular scales black pigmented; dorsal ground color of body uniformly dark brown except for two light rows on paraventral region forming conspicuous longitudinal lines; lateral margins of ventral scales black, remaining scale areas uniform creamish white; cloacal plate and subcaudals uniform black (Fig. 14).

Quantitative variation.—Largest female 388 mm SVL, 30 mm TL; tail 7.7–8.8% (mean = 8.2; SD = 0.5; n = 3) SVL in females; ventrals 200–207 (mean = 204.3; SD = 3.8; n = 3) in females; subcaudals 25–26 (mean = 25.3; SD = 0.6; n = 3) in females.

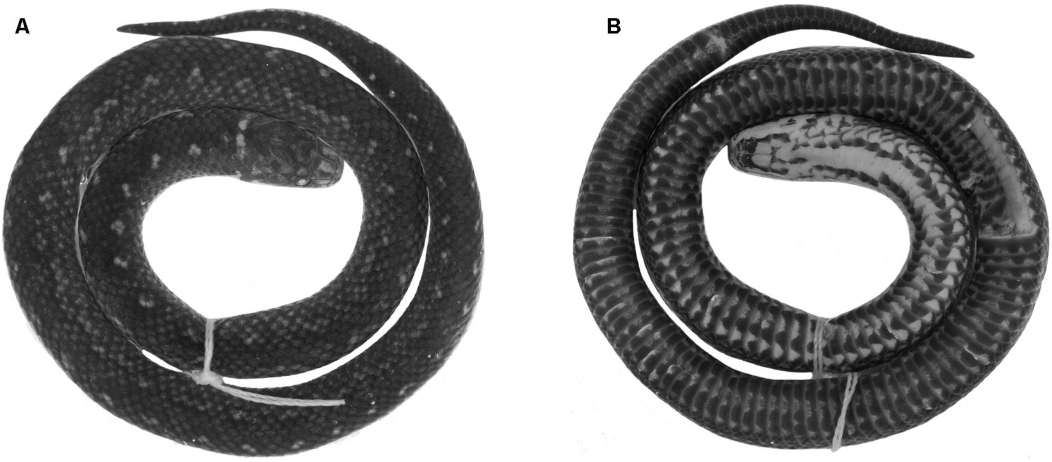

FIG. 15.—Dorsal (A) and ventral (B) views of a preserved juvenile of *Atractus tamessari* from Kaieteur National Park (IRSNB 18082).

Distribution and habitat.—Known only from 1000-m elevation in the Serra do Surucucu, a mountain range that predominantly harbors an altitudinal savanna-type vegetation (Fig. 4).

Remarks.—More detailed data and description of the type series of *A. surucucu* are found in Prudente and Passos (2008).

Atractus tamessari *Kok, 2006*
(Figs. 15–19)

Atractus insipidus (Schargel and García-Pérez, 2002). [Misidentification.]

Atractus tamessari (Prudente and Passos, 2008).

Holotype.—Adult male, IRSNB 2640, collected on 23 March 2006 by P.J.R. Kok, P. Benjamin, and G. Seegobin along a tributary of Elinkwa River, ESE Kaieteur National Park (05°08′09″N, 59°25′28″W, ca. 500 m asl), Potaro-Siparuni district, Guyana.

Paratypes.—Subadult (IRSNB 2641) and adult (IRSNB 2642) females; same data as the holotype.

Material examined.—IRSNB 2640 and IRSNB 2641–42; EBRG 1964, EBRG 5182–83 (Sierra de Lema, La Escalera region, Bolívar, Venezuela); MHNLS 5950 (km 126 on the road El Dorado-Santa Elena de Uairén, Canaima National Park, Bolívar, Venezuela), MHNLS 15124 (Uei-Tepui, Bolívar, Venezuela), MCNG-R 1865 (Piedra de la Virgen, Canaima National Park, Bolívar, Venezuela), IRSNB 18068, 18082, 18154–55, 18309–10 (Kaieteur National Park, Guyana).

Diagnosis.—*Atractus tamessari* can be distinguished from all congeners by the following combination of characters: (1) smooth dorsal scale rows 15/15/15; (2) postoculars usually two; (3) loreal long; (4) temporals 1 + 2; (5) supralabials usually eight, fourth or fifth contacting orbit; (6) infralabials usually eight, first four contacting chin shields; (7) maxillary teeth six or seven; (8) gular scale rows three or four; (9) preventrals usually three or four; (10) ventrals 155–163 in females, 149–158 in males; (11) subcaudals 24–32 in females, 31–37 in males; (12) dorsum brown to dark brown, sometimes scattered with red irregular marks on flanks; (13) venter usually mostly dark brown with posterior part of each ventral paler (beige), rarely predominantly cream with black pigment concentrated on the posterior margin of ventral scales or ill-defined dark brown rhomboidal blotches on the center of ventral scales; (14) body size moderate, females reaching 420 mm SVL, males 346 mm SVL; (15) tail size moderate in females (10.5–14.9% SVL) and males (14.4–16.7% SVL); (16) hemipenis slightly to moderately bilobed, noncapitate to semicapitate, and semicalyculated.

Comparisons.—Among all congeners, *A. tamessari* shares 15 dorsal scale rows, first four infralabials generally contacting chin shields, and equivalent segmental counts in males only with *A. insipidus*, from which it differs by usually having eight supralabials

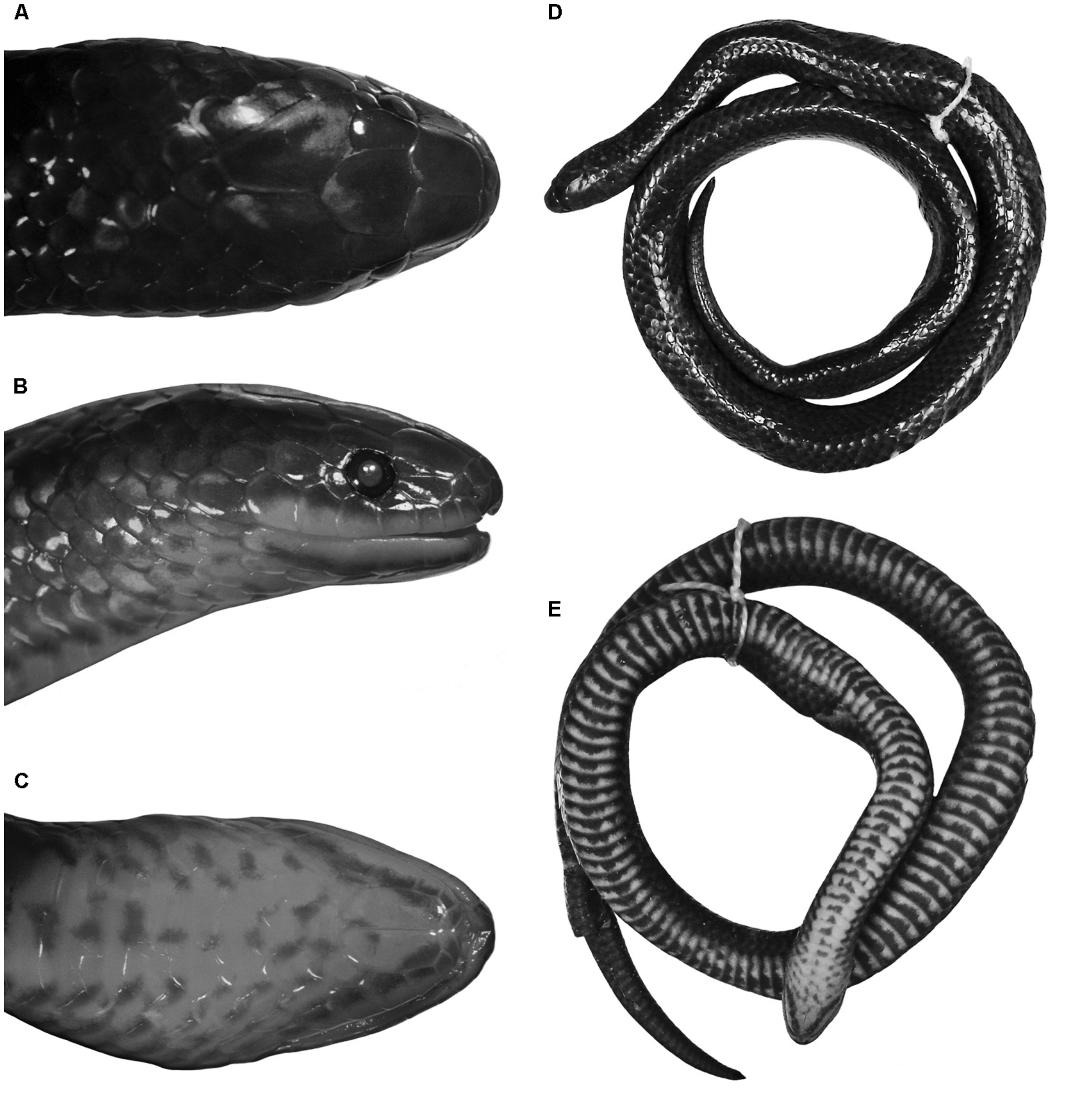

FIG. 16.—Dorsal (A), lateral (B), and ventral (C) views of head, and dorsal (D) and ventral (E) view of body of *Atractus tamessari* from the La Escalera region, Venezuela (MHNLS 5950).

and eight infralabials, brown to dark brown dorsum sometimes scattered with reddish irregular spots, venter heavily pigmented with black, and black subcaudals (vs. seven supralabials and seven infralabials, dorsum light brown with irregular dark brown spots unevenly dispersed on edges of dorsal scales forming a poorly defined reticulated pattern, venter immaculate creamish white, and white subcaudals).

Description.—Head twice as long as wide, sligthly flattened in lateral view, round in dorsal view; snout rounded in lateral and dorsal views; rostral subtriangular in frontal view, barely visible in dorsal view, twice as wide as high; internasal as long as wide; internasal suture sinistral to prefrontal medial suture; prefrontal longer than wide; supraocular subrectangular, longer than wide; frontal pentagonal, wider than long; parietal one and half longer than wide; nasal divided; nostril situated between prenasal and postnasal; prenasal twice as high as long; postnasal higher than long; loreal long, three times as

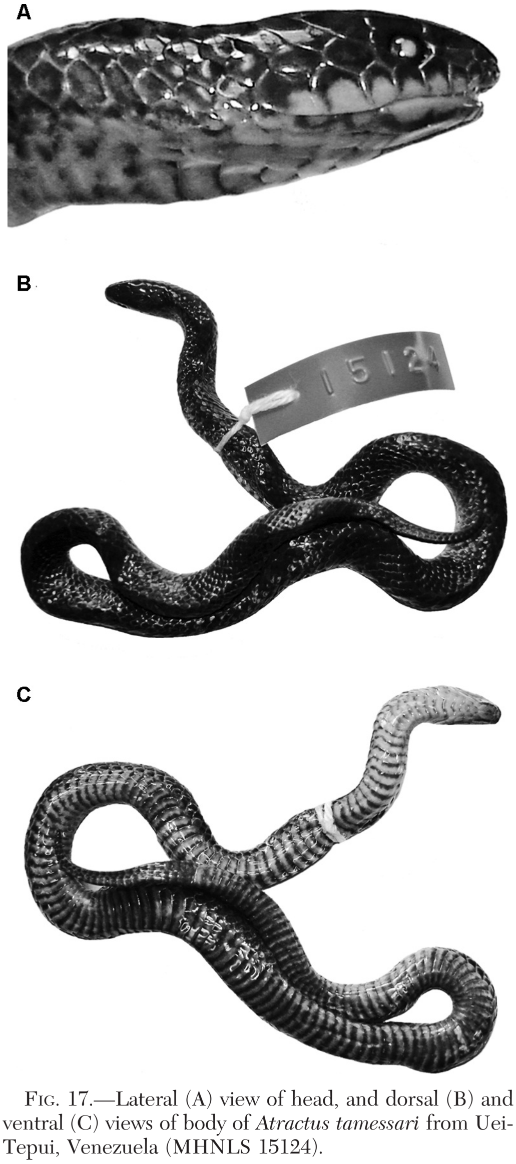

Fig. 17.—Lateral (A) view of head, and dorsal (B) and ventral (C) views of body of *Atractus tamessari* from Uei-Tepui, Venezuela (MHNLS 15124).

long as high, frequently contacting third and fourth supralabials; pupil round; generally two postoculars, upper one usually slightly longer and higher than lower postocular; temporals 1 + 2; anterior temporal twice as long as high; upper posterior temporals usually not fused; supralabials seven to nine, usually eight, third and fourth (rarely) or fourth and fifth (most frequently) contacting orbit; first two supralabials similar in height, smaller than third supralabial or second higher than first and

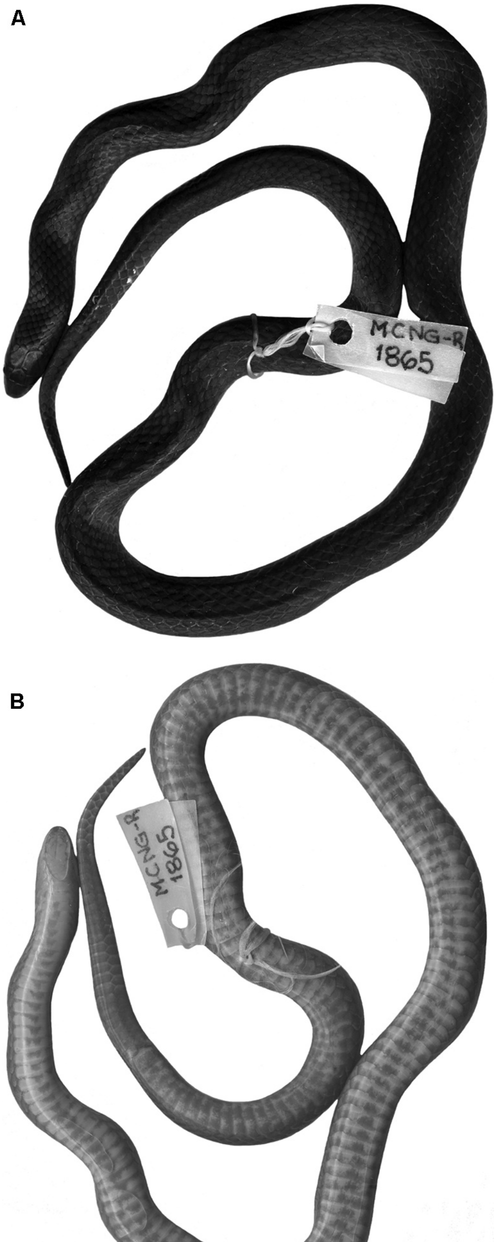

Fig. 18.—Dorsal (A) and ventral (B) views of body of *Atractus tamessari* from "Piedra de la Virgen" in the Canaima National Park, Bolívar, Venezuela (MCNG-R 1865).

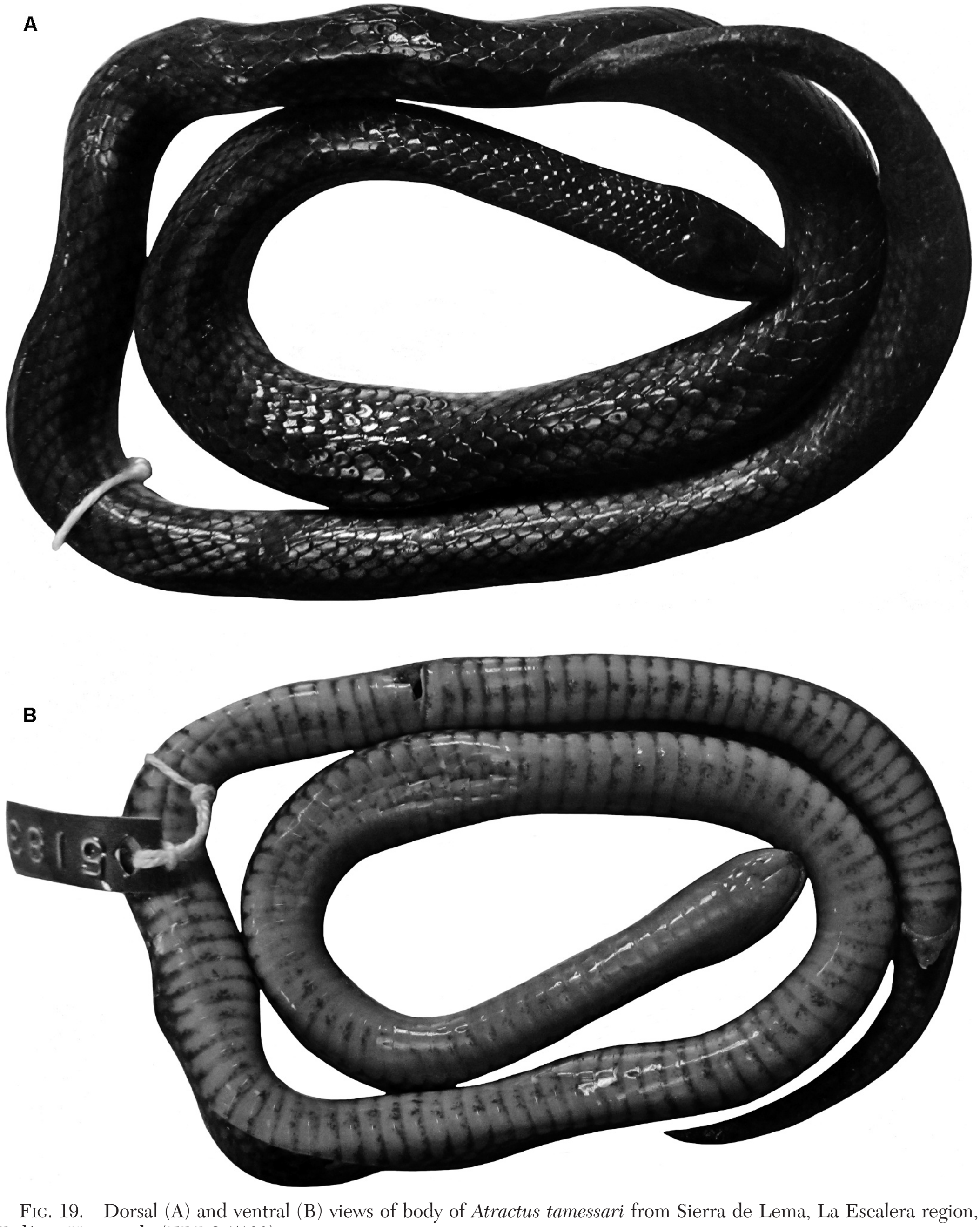

FIG. 19.—Dorsal (A) and ventral (B) views of body of *Atractus tamessari* from Sierra de Lema, La Escalera region, Bolívar, Venezuela (EBRG 5183).

smaller than fourth; sixth or seventh higher and seventh or eighth longer than remaining supralabials; symphysial subtriangular to semicircular, about three times as wide as long; infralabials six to eight, first four contacting chin shields; first pair of supralabials in contact behind symphysial, preventing symphysial–chin-shields contact; chin shields about three times longer than wide; three or four gular scale rows; usually four preventrals;

dorsal scale rows 15/15/15, lacking apical pits and supra-anal tubercles; caudal spine long, robust and round. Maxillary arched in dorsal view, with five prediastemal teeth and one postdiastemal tooth; first prediastemal tooth slightly smaller than remaining teeth, which are similar in size; prediastemal teeth well spaced, curved posteriorly, angular in cross-section, robust at base, slightly narrower at apices; diastema moderately long; postdiastemal tooth slightly smaller than last prediastemal one; lateral process of maxilla well developed, lacking posterior projection (Figs. 16, 17).

Juvenile color in preservative.—Dorsum of head light brown, snout lighter with a slight cream blotch; supralabials and infralabials mostly white; gular region mostly white, with a black blotch anteriorly and black lateral margins; iris dark brown; venter background white, heavily mottled with black, except anteriorly where blotches are few and located on medial and distal parts of the ventral scales; ventral surface of tail black; dorsum of body dark brown, with a light pink collar and regularly distributed paravertebral light pink blotches from occipital region to tip of tail, and few additional smaller irregularly disposed pinkish blotches on flanks (Fig. 15).

Adult color in preservative.—Dorsum of head uniformly dark brown; head background dark brown until upper margin of supralabials; mid- to ventral part of supralabials and upper part of infralabials cream; posterior part of infralabials dark brown; gular region cream with irregular dark brown markings; most of anterior part of venter predominantly cream, scattered with dark brown blotches on posterior margin and sides of each ventral scale; dark brown blotches increase in size posteriorly, sometimes making ventral surface almost completely black; occasionally ventrals with median dark brown rhomboidal blotches; ventral surface of tail predominantly dark brown, with anterior edge of subcaudals cream; dorsum of body uniformly dark brown, sometimes with irregular red markings on flanks (one to two scales wide, sometimes forming an incomplete paravertebral stripe), or two ventrolateral black stripes (Figs. 16–19).

Juvenile color in life.—Color in life similar to that of adult specimen. Dorsum of head dark brown, snout lighter with a slight yellow blotch; supralabials and infralabials mostly yellow; gular region mostly yellow with a dark brown blotch anteriorly and dark brown lateral margins; iris dark brown; venter background yellowish cream, heavily mottled with black, except anteriorly where blotches are few and located on the medial and distal parts of the ventral scales; ventral surface of tail black; dorsum of body very dark brown, almost black with red collar and regularly distributed paravertebral red blotches from occipital region to tip of tail, and few additional smaller, irregularly disposed red blotches on flanks.

Adult color in life.—Dorsum of head brown to dark brown, usually with yellowish snout; ventral pattern less variable, always creamish yellow heavily mottled by irregular black markings; sometimes ventral mottling starts as small black rhomboidal spots on first ventrals; dorsal color in life fairly variable, from medium to dark brown without any conspicuous pattern to medium brown or dark brown with irregular pale reddish brown markings and two ventrolateral black stripes, or irregular bright red markings on a brownish black ground without ventrolateral stripes; bright red markings sometimes form an incomplete dorsolateral stripe (see fig. 2 in Kok, 2006).

Hemipenial morphology.—Hemipenis semicalyculated, varying from slightly bilobed and semicapitate (IRSNB 2640, EBRG 5182, and IRSNB 18309; Fig. 20B) to moderately bilobed and noncapitate (MHNLS 5950; Fig. 20A); lobes distinct from distal region of capitulum; lobes clavate with round or nearly flattened apices; lobes slightly centrifugally oriented, smaller or similar in size to remaining capitulum; lobes and capitulum uniformly densely covered with spinulate calyces; lobular region of capitulum wider than hemipenial body; capitulum covered with irregular calyces, not forming calyculate flounces on both sides of organ; asulcate side of capitulum with lobular crest ranging from barely to well defined and usually with distinct medial crest; capitular groove indistinct on sulcate and barely to well marked laterally and on asulcate side of hemipenis; capitulum located above sulcus spermaticus bifurcation, with length similar to hemipenial body; sulcus spermaticus

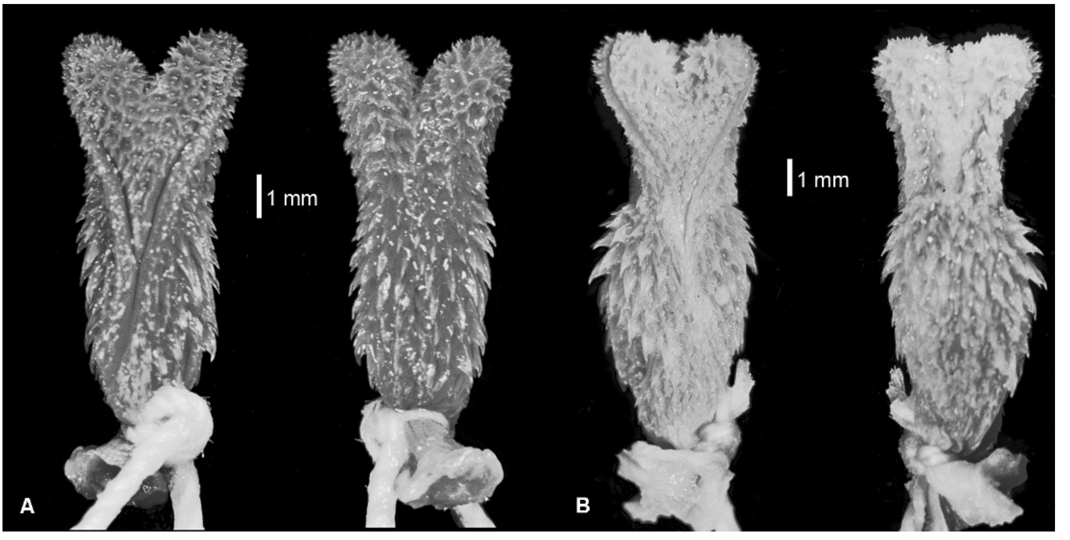

FIG. 20.—Sulcate (left) and asulcate (right) sides of the hemipenis of *Atractus tamessari*, MHNLS 5950 from La Escalera region, Venezuela (A) and IRSNB 18309 from Kaieteur National Park, Guyana (B).

divides in the middle of organ; sulcus spermaticus branches centrifugally oriented, running to tip of lobes; margins of sulcus spermaticus stout and moderately expanded, bordered with spinules along the sulcus spermaticus branches; hemipenial body subcylindrical, covered with moderately hooked spines; larger spines on lateral region of asulcate side of the organ; naked basal pocket extending to basal portion of hemipenial body; proximal region of hemipenis with longitudinal plicae and disperse spinules (Fig. 20).

Quantitative variation.—Largest female 420 mm SVL, 52 mm TL; largest male 346 mm SVL, 51 mm TL; tail 10.5–14.9% (mean = 11.8; SD = 1.3; *n* = 9); SVL in females, 14.4–16.7% (mean = 15.1; SD = 0.9; *n* = 6) in males; ventrals 155–163 (mean = 157.9; SD = 3.0; *n* = 9) in females, 149–159 (mean = 154.8; SD = 4.0; *n* = 5) in males; subcaudals 24–32 (mean = 28.1; SD = 2.1; *n* = 9) in females, 31–37 (mean = 33.5; SD = 2.6; *n* = 5) in males; supralabials seven (*n* = 4 sides), eight (*n* = 24 sides), or nine (*n* = 2 sides); infralabials six (*n* = 1 side), seven (*n* = 5 sides), or eight (*n* = 24 sides); infralabials contacting chin shields three (*n* = 1 side) or four (*n* = 23 sides); preventrals one (*n* = 1), two (*n* = 1), three (*n* = 9), or four (*n* = 1); gular scale rows three (*n* = 6 sides) or four (*n* = 2 sides); dorsal scale rows in the level of second subcaudal six (*n* = 1 side), seven (*n* = 2 sides), eight (*n* = 4 sides), nine (*n* = 2), or 11 (*n* = 1 side); maxillary teeth six (*n* = 12 sides) or seven (*n* = 2 sides); body diameter 5.6–7.3 mm; retracted hemipenis bifurcates at seventh to eighth and extends to the level of eighth to ninth subcaudal (*n* = 2).

Distribution and habitat.—Currently known from two localities in Kaieteur National Park, Potaro-Siparuni District in Guyana, Uei-Tepui, state of Bolivar, Venezuela, from km 127 on the road between El Dorado and Santa Elena de Uairén, Canaima National Park, and Sierra de Lema in the La Escalera region, state of Bolivar, Venezuela. *Atractus tamessari* primarily occurs in rainbforest and cloud forest between 500- and 2200-m elevations (Fig. 4).

Remarks.—Schargel and García-Pérez (2002) reported the second known specimen of *A. insipidus* (the specimen previously reported by Cunha and Nascimento from Maranhão in Brazil belongs to another species, see *A. insipidus* remarks) from Piedra de la Virgen, Canaima National Park, Venezuela (MCNG-R 1865). Kok (2006) described *A. tamessari* on the basis of three specimens collected in the Kaieteur National Park, Guyana. The examination of the specimen cited by Schargel and García-Pérez (2002) revealed that it has a uniform brown dorsum and venter cream with a few rhomboidal dark brown central spots anteriorly, which increase gradually in size toward back, almost completely covering the posterior third of the belly, until it becomes entirely brown at underside of the tail (Fig. 18). On the basis of the color pattern briefly described above as well as the meristic and morphometric characters we identified the MCNG-R 1865 as *A. tamessari*. We examined *Atractus* specimens from Sierra de Lema also in the La Escalera region of Venezuela. These are two females (EBRG 1964, 5183) and one male (EBRG 5182), which we identify as *A. tamessari*. Although most of their meristic and morphometric characters fall into the known range of variation of *A. tamessari*, ventrally the female (EBRG 5183) is only slightly dark mottled (vs. heavily mottled in all other specimens), with a completely black tail (Fig. 19). Because of the frequent ontogenetic or geographic variation in color pattern previously reported to the genus *Atractus* (Passos et al., 2009a,b,c, 2010a,b,c; Passos and Prudente, 2012; Almeida et al., in press), we interpreted these differences in coloration as a possible intraspecific chromatic variation of *A. tamessari* (but see Discussion).

Key to the Known Species of *Atractus* in the Guiana Shield

A comprehensive key to the genus in the Guiana Shield is still lacking. Although this study is dealing only with *Atractus* from Pantepui, we propose the first key to identify all *Atractus* species in the area (sensu Hoogmoed, 1979), including additional records made by Avila-Pires (2005). To simplify field and museum identification, the key is mainly based on external morphology and maxillary dentition. We believe that such features are most easily observed in living individuals as well as in most preserved specimens. *Atractus flammigerus* appears in more than one couplet because of the sexual dimorphism in that species. We used more than one character in most of the couplets to improve the reliability of the key, but in the case of fixed characters that are easily assessed (such as the number of dorsal scale rows), we used them as single entries. Although colleagues and students who are not familiar with *Atractus* species have successfully tested this key, it is based on few specimens for some taxa in which the character variation will be underestimated.

1. First pair of infralabials preventing symphysial–chin-shields contact; preocular absent; loreal contacting eye; tail length smaller than 25% SVL 2
   Symphysial in contact with chin shields; preocular usually present, preventing loreal–eye contact; tail length more than 30% SVL .... *A. favae*
2. Dorsal scales with apical pits, supra-anal tubercles or keels at least in males 3
   Dorsal scales smooth, lacking apical pits, supra-anal tubercles or keels 6
3. Dorsal scales with apical pits and supra-anal tubercles in males but never keeled, mid-body diameter of adults ≤ 5 mm; incomplete pale nuchal collar present; five to six maxillary teeth; venter in preservative immaculate cream 4
   Dorsal scales keeled in the cloacal region of males, lacking apical pits or supra-anal tubercles; midbody diameter of adults > 5 mm; nuchal collar absent; eight to nine maxillary teeth; venter with dark brown blotches .... *A. flammigerus*
4. Dorsum uniformly dark brown; underside of the tail dark brown; 200–207 ventrals in females .... *A. surucucu*
   Dorsum generally scattered with small black spots, white bordered on paravertebral region; underside of tail cream in preserved specimens; ventrals ≤ 200 in females 5
5. Loreal moderate; 163–186 ventrals and 17–24 subcaudals in female .... *A. alphonsehogei*
   Loreal short; 196–200 ventrals and 27–32 subcaudals in females .... *A. zidoki*
6. One postocular; six supralabials; rostral as high as wide; loreal short; internasals twice longer than prefrontals; maxillary teeth conical, dorsoventrally compressed and lacking diastema; caudal spine conical and robust; aposematic color pattern consisting of black/red/white rings 7
   Usually two postoculars; generally more than six supralabials; rostral wider than high; internasals less than two times longer than prefrontals; maxillary teeth elliptical, laterally compressed and with posterior diastema; caudal spine rounded to acuminate; color pattern variable but never with complete rings 9
7. Fifteen dorsal scale rows 8
   Seventeen dorsal scale rows .... *A. latifrons*
8. Snout projecting; anterior temporal absent; five to six maxillary teeth; dorsum uniformly black, with rhomboidal rings only laterally and ventrally evident .... *A. poeppigi*

Snout not projecting; anterior temporal generally present; 7 to 10 maxillary teeth; regular rings evident in dorsal, lateral, and ventral views .... *A. elaps*

9. Fifteen dorsal scale rows 10
Seventeen dorsal scale rows 12

10. Dorsal ground color light brown with brown spots or stripes; venter immaculate cream 11
Dorsal ground color dark brown to black scattered with red spots or blotches; venter usually heavily pigmented with black .... *A. tamessari*

11. Dorsum with conspicuous longitudinal lines; eight supra- and infralabials .... *A. trilineatus*
Dorsum with scattered dark brown markings; seven supra- and infralabials .... *A. insipidus*

12. Eight supralabials 13
Seven or six supralabials 15

13. Two postoculars; dorsum variable but never red to reddish brown; venter heavily pigmented with dark brown blotches; moderate body size 14
One postocular in the Guianan populations (see Passos and Prudente, 2012); dorsum reddish brown with black blotches sometimes forming transversal bands; venter cream, sometimes with dispersed black dots on posterior part of the body; large body size .... *A. torquatus*

14. Dorsum light brown with transversal black bands, or dorsal ground color black with transversal cream bands; venter with rhomboidal dark brown blotches arranged in longitudinal series; 152–161 ventrals and 34–41 subcaudals in males; seven maxillary teeth .... *A. riveroi*
Dorsum brown with transversal dark-bordered cream bands; venter scattered with dark brown blotches not arranged in distinct lines; 145–160 ventrals and 26–37 subcaudals in males; eight to nine maxillary teeth .... *A. flammigerus*

15. Dorsum uniformly black or light to dark brown with lines, spots, or bands 16
Dorsum red to reddish brown, with conspicuous diads of black separated from each other by cream pigment at least on anterior portion of the body .... *A. badius*

16. Venter creamish-yellow to beige on anterior part of body with rhomboidal dark brown dots concentrated on anterior part of each ventral, becoming uniformly brown to black posteriorly 17
Venter cream, occasionally with dark brown round spots concentrated on the center of each ventral scale, forming a more or less conspicuous median line 18

17. Five to six maxillary teeth; 160–167 ventrals in males and 177–184 in females; 27–33 subcaudals in females .... *A. steyermarki*
Eight to nine maxillary teeth; 156 ventrals in male and 171 in female; 36 subcaudals in females .... *A. duidensis*

18. Dorsum beige to light brown, with distinct large dark brown blotches or bands alternating along the body 19
Dorsum beige to brown, generally with a conspicuous large dark brown vertebral stripe; sometimes this vertebral stripe is irregular or fragmented on the posterior part of the body; the stripe is rarely absent, in which case the dorsum bears small irregular dark brown spots .... *A. univittatus*

19. Dorsal ground color beige to light brown with dark blotches or bands 20
Dorsal ground color dark brown with light blotches or bands .... *A. snethlageae*

20. Two postdiastemal teeth; generally eight infralabials, first four contacting chin shields; three to four preventrals; dorsal blotches lacking white borders; canthus rostralis rounded; hemipenis lacking transversal flounces .... *A. schach*
Usually one postdiastemal tooth; generally seven infralabials, first three contacting chin shields; one or two preventrals; dorsal blotches white bordered; canthus rostralis angular, well marked; hemipenis with transversal founces .... *A. major.*

Discussion

We opted to discuss certain peculiar and noteworthy features of hemipenial morphology of *Atractus* from the Guiana Highlands because the scope of our study was regional. For this reason, we included those species with apparent phylogenetic affinity (*A. duidensis* and *A. steyermarki*), as well as others distantly related (*A. surucucu* and *A. insipidus*; Passos, 2008). Savage (1960) pointed out that a combination of hemipenial characters (lobular bifurcation, and presence of calyces and basal naked pocket) could be used to distinguish *Atractus* and *Geophis* Wagler, 1830. Later, Downs (1967) noted that Savage's characterization of the hemipenis in *Geophis* does not apply to all congeneric species, as such: the number of chin shields, temporal formulae, or number of supralabials. Traditionally (cf. Boulenger, 1894; Smith, 1942; Savage, 1960), the above combination of external features has been frequently used to diagnose these morphologically similar and apparently closely related genera of dipsadine "goo-eaters" (Grazziotin et al., 2012). For instance, on the basis of external morphology and osteological characters, members of the *G. latifrontalis* Garman, 1883, species group are

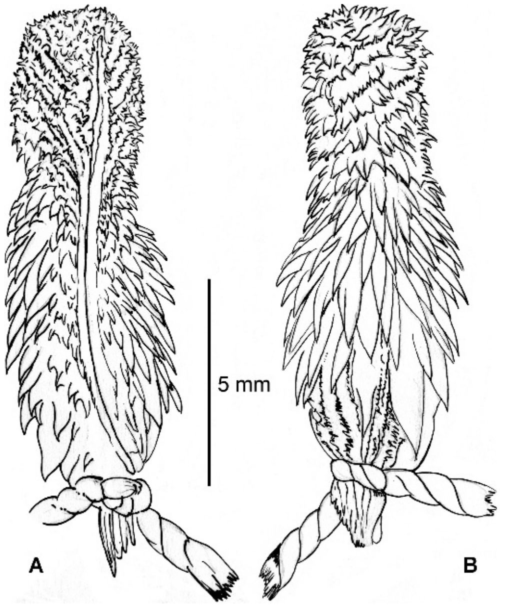

FIG. 21.—Sulcate (A) and asulcate (B) sides of the hemipenis of *Geophis latifrontalis* (IBSP 3879) from Sierra de Alvarez, San Luis de Potosi, Mexico.

extremely similar to *Atractus* species (Downs, 1967). Downs suggested that the most distinctive difference between the *G. latifrontalis* group and *Atractus* is the presence of a unilobed and calyculate hemipenis in the former (Fig. 21), vs. a bilobed and noncalyculate organ in the latter (cf. Savage, 1960). However, the supposed noncalyculated condition for the hemipenis of several species of *Atractus* was much influenced by the examination of retracted organs by Savage (1960). Indeed, some structures like calyces and capitular groove are most likely to be observed on fully everted organs and are usually less evident or indistinct in a retracted hemipenis (Schargel and Castoe, 2003; Passos et al., 2007a; Prudente and Passos, 2010). Variation of hemipenial morphology among *Atractus* species is huge and appears to be very complex (e.g., Schargel and Castoe, 2003; Passos et al., 2009e), with the most common condition in the genus being the semicapitate and semicalyculate organ (Passos et al., 2013a).

Among the approximately 140 species of *Atractus* (Passos et al., 2013b) the unilobed hemipenis is known to occur only in *A. steyermarki*, *A. hoogmoedi*, and *A. zidoki* (Passos, 2008). However, the hemipenis of *A. steyermarki* strongly differs from that of *A. hoogmoedi* and *A. zidoki* (the last two species being members of the *A. collaris* species group; Passos et al., in press), and likely represents an independent reversion to the unilobed condition (Passos, 2008). The hemipenial morphology of *A. zidoki* is similar in many aspects to the pattern observed in some taxa of the *G. latifrontalis* group (Fig. 21). Whereas the organ of *A. steyermarki* has the sulcus spermaticus branches bifurcating in the middle of the hemipenial body and a distinct medial intrasulcar crest on the asulcate side (Fig. 13), the hemipenis of *A. hoogmoedi* has no bifurcation and that of *A. zidoki* has a distal bifurcation of the sulcus spermaticus, with both lacking the medial intrasulcar crest (see fig. 1 from Prudente and Passos, 2010). The unilobed condition of the hemipenis in *A. steyermarki* appears to be derived from a bilobed condition, and the medial intrasulcar crest on the sulcate side (white arrow in Fig. 13) may represent evidence of the secondary fusion of the lobes (Passos, 2008). The apparent reversion to the unilobed condition, the typical character state of the basal radiation of the Dipsadinae goo-eaters (Fernandes, 1995; Zaher, 1999), likely represents an autapomorphy of the *A. steyermarki* (Passos, 2008). On the other hand, the putative homology of the unilobed condition between members of the *A. collaris* and *G. latifrontalis* species groups is not satisfied by these data because all unilobed hemipenis in *Atractus* are noncalyculate and noncapitate; whereas in *Geophis* the unilobed condition of hemipenis is always capitate and calyculate. Beyond these morphological differences (there appears to be a correlation between capitulum and calyces in the genus *Atractus*; P. Passos, personal observation), some members of the *A. collaris* group also have bilobed hemipenises (Prudente and Santos-Costa, 2006; Passos et al., in press). Moreover, the complexity of the *Geophis* hemipenis seems to have been underestimated, at least in the *G. sieboldi* Jan, 1862, group (see Myers, 2003; Savage and Watling, 2008). To conclude, given the speciose nature of *Atractus* and *Geophis* and our little understanding of the phylogenetic relationship between them

(Grazziotin et al., 2012), the primitive hemipenial condition of the genus *Atractus*, at least with respect to bilobation, is not obvious and cannot be established with certainty.

Another relevant finding gathered from this source of morphological characters is the discovery of differences in the hemipenis of *A. tamessari* regarding the level of development of the lobes, capitulation, and lobular crests on the asulcate side of the organ. Although the La Escalera specimen (MHNLS 5950; Fig. 20A) presents a noncapitate organ with relatively larger lobes lacking longitudinal crests, the holotype (IRSNB 2640; fig. 3 in Kok, 2006) and a topotype (IRSNB 18309; Fig. 20B) of *A. tamessari* revealed a semicapitate hemipenis with least developed lobes and conspicuous lobular crests in the asulcate side of the organ. Nonetheless, the Sierra de Lema specimen (EBRG 5182; organ not illustrated), also from the La Escalera region of Venezuela, presents a semicapitate hemipenis with least developed lobes. Interestingly, other characters examined (meristic, morphometric, maxillary dentition, and color pattern) failed to clearly distinguish between these populations. Therefore, recognizing the small sample currently available for the hemipenis ($n = 4$) and by the fact that the geographically close specimen (EBRG 5182) shows a slightly bilobed and semicapitate hemipenial condition, we consider these differences as probably representing intraspecific variation in the hemipenis of *A. tamessari*. Passos and Prudente (2012) recently reported on the variation of the level of completeness of the capitular groove among subpopulations of *A. torquatus*. Although the variability with respect to semicapitate and noncapitate condition of the hemipenis within a single species is here reported for the first time in the genus, the preparation artifacts caused by degree of filling of hemipenis affecting the level of distinction of the lobes or lobular crests on the asulcate side of hemipenis are already known (Myers and Cadle, 2003; Martins, 2012; Passos et al., 2013a). Provisionally, by the reasons discussed, we identify the La Escalera populations as *A. tamessari* until additional specimens from intermediate localities become available to improve our understanding of the hemipenial variation among the populations of *A. tamessari*.

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