

Taxonomic status of *Atractus sanctaemartae* and *Atractus nebularis*, and description of a new *Atractus* from the Atlantic coast of Colombia

Paulo Passos¹, John D. Lynch² & Ronaldo Fernandes¹

¹Departamento de Vertebrados, Universidade Federal do Rio de Janeiro, Brazil

²Laboratório de Anfíbios, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, Colombia

The taxonomic status of *Atractus sanctaemartae* and *A. nebularis* is revised on the basis of quantitative and qualitative analyses of morphological characters (meristics, morphometrics, colour pattern and hemipenis). Characters used previously for diagnosing *Atractus nebularis* from *A. sanctaemartae* are demystified, and the synonymy of these species is proposed. Colour pattern, meristic, morphometrical and scale ornamentation differences originally employed in recognizing both taxa are explained as sexually dimorphic characters, which hold no geographic or phylogenetic basis. Additionally, a new species closely related to *Atractus sanctaemartae* is described from the Atlantic coast of Colombia. It is distinguished from *A. sanctaemartae* mainly by having two gular scale rows, slender (62% of body diameter) and acuminate head, snout acuminate in lateral view, dorsum uniformly reddish brown and venter cream with a series of rhomboidal blotches arranged linearly on the lateral portion of the ventral scales. We also discuss putative affinities of the new species and *A. sanctaemartae* on the basis of shared similarity characters, and comment on the occurrence of strong sexually dichromatic coloration in *A. sanctaemartae*, unique within the genus.

Key words: geographical variation, sexual dichromatism, Sierra Nevada de Santa Marta, taxonomy

INTRODUCTION

The cryptozoic snake genus *Atractus* Wagler is widely distributed throughout the neotropical region, occurring from Panama to northern Argentina (Giraud & Scrocchi, 2000; Myers, 2003). *Atractus* is the most diverse Alethinophidian snake genus in the world, currently containing 120 valid species, most of them known only from their type localities (Passos, 2008). Despite many recent works focusing on this genus (Myers & Schargel, 2006; Passos et al., 2007a,b; Myers & Donnelly, 2008; Prudente & Passos, 2008; Passos & Fernandes, 2008; Passos & Arredondo, 2009), additional efforts must be made to further understand geographic variation, ontogenetic changes in coloration, sexual dimorphism and species boundaries among most *Atractus* species.

The isolated triangular massif of the Sierra Nevada de Santa Marta ranges apart from the Andean mountain belts of Colombia (Western, Central and Eastern Cordilleras), on the Atlantic coastline of the country 50 kilometres from the Caribbean sea. The Sierra Nevada mountain system is the highest point of Colombia, reaching 5800 metres and attaining higher elevations than any other coastal mountain range on earth. Transition from mountainous to lowland terrain occurs abruptly across the Oca fault, the Santa Marta–Bucaramanga fault and the Cesar lineament (Aleman & Ramos, 2003). The Sierra Nevada comprises a large number of ecoregions, which vary mainly through altitude (see Ruthven, 1922). Tectonic

and stratigraphic evidence suggests that the Sierra Nevada uplift is associated with underthrusting of the Caribbean plate and that it has probably evolved in isolation from the remaining Andean geodynamics since the Eocene (Aleman & Ramos, 2003).

With regard to *Atractus*, Griffin (1916) identified two specimens from Sierra Nevada de Santa Marta as *Atractus badius*. Subsequently, Ruthven (1922) used the name *Atractus iridescens* with reference to ten specimens also from the Sierra Nevada de Santa Marta. Dunn (1946) examined Griffin's and Ruthven's specimens, as well as additional material from the Santa Marta region, establishing that these individuals represented an undescribed species for which the name *Atractus sanctaemartae* was proposed. Dunn (1946) emphasized the enormous colour pattern variation shown by this species, and interpreted the extreme limits in its variation simply as inversion of background colour rather than a change in the general pattern of coloration (Dunn, 1946, p. 5). Bernal-Carol & Roze (1997) analysed most of the previously reported specimens as well as 14 new ones from the Sierra Nevada and concluded that Dunn's (1946) specimens represented two distinct species. Bernal-Carol & Roze (1997) proposed *Atractus nebularis* for specimens having a dark dorsum with light bands, a lower number of ventrals (144–149 in males and 145–149 in females), a higher number of subcaudals (29–35 in males and 22–29 in females), and small supra-anal tubercles in males. Although Bernal-Carol & Roze (1997) found two syntopic areas for *A.*

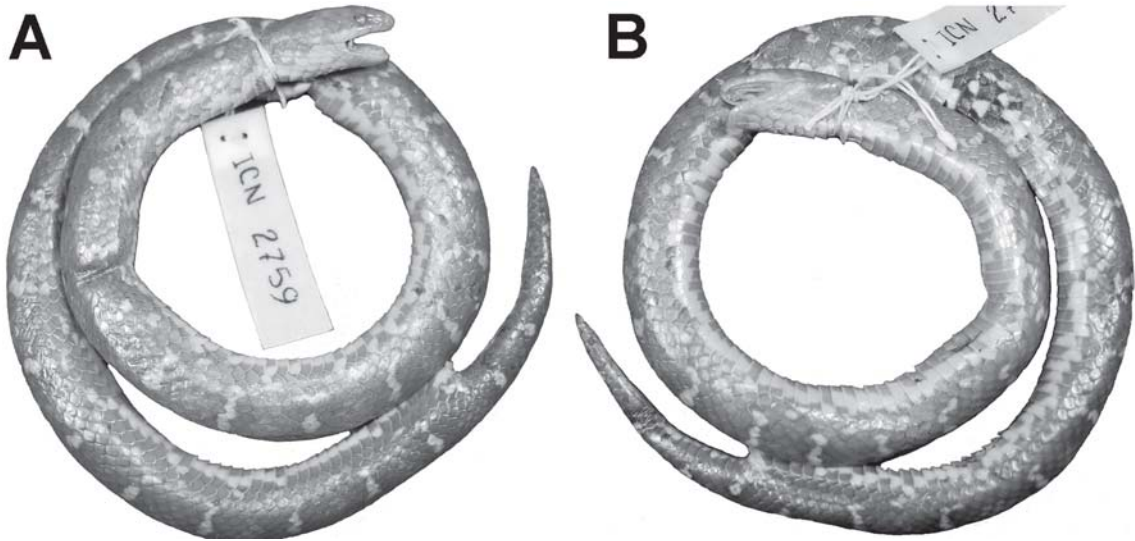


Fig. 1. Dorsal (A) and ventral (B) view of the paratype of *Atractus nebularis* (ICN 2759), from San Lorenzo, Sierra Nevada de Santa Marta, Colombia.

nebularis and *A. sanctaemartae*, they suggested that syntopic specimens of *A. nebularis* were smaller than the *A. sanctaemartae* individuals.

In this paper we evaluate the taxonomic status of the currently recognized *Atractus sanctaemartae* and *A. nebularis* on the basis of qualitative and quantitative analyses of meristic, morphometric, colour pattern and hemipenial characters. In addition, we describe a new species apparently closely related to *Atractus sanctaemartae*.

MATERIALS AND METHODS

We examined *Atractus* specimens in the following collections:

Venezuela. Colección de Vertebrados de la Universidad de Los Andes (CVULA), Mérida; Estación Biológica Rancho Grande (EBRG), Maracaibo; Museo de Historia Natural, Fundación La Salle (MHNLS), Caracas D.C.; Colección Herpetologica del Laboratorio de Biogeografía de la Universidad de Los Andes (ULABG), Mérida; Museo de Biología, Universidad Central de Venezuela (MBUCV), Caracas D.C.

Colombia. Colección Herpetologica de la Universidad de Quindío (UQC), Arménia, Quindío; Colección Zoológica de la Universidad de Tolima (CZUT-R), Ibagué, Tolima; Instituto Alexander von Humboldt (IAvH), Villa de Leyva, Boyacá; Instituto de Ciencias Naturales, Universidad Nacional de Colombia (ICN), Bogotá D.C.; Museo de Herpetología, Universidad de Antioquia (MHUA), Medellín, Antioquia; Museo de la Universidad La Salle (MLS), Bogotá D.C.; Museo de Zoología de la Universidad Javeriana (MUJ), Bogotá, D.C.; Museo de Historia Natural de Universidad Industrial de Santander

(UIS), Bucaramanga, Santander; Colección Herpetológica de la Universidad del Valle (UV-C), Cali, Valle del Cauca.

Ecuador. Escuela Politecnica Nacional (EPN), Quito; Museo de Zoología, Pontificia Universidad Católica de Ecuador (QCAZ), Quito.

Peru. Museo de Historia Natural de la Universidad Mayor de San Marcos (MHNSM), Lima; Museo de Historia Natural de Universidad Nacional de Arequipa (MUSA), Arequipa.

Brazil. Instituto Butantan (IBSP), São Paulo, SP; Museu Nacional, Universidade Federal do Rio de Janeiro (MNRJ), Rio de Janeiro; Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo.

UK. Natural History Museum (NHM), London.

Germany. Zoologisches Museum Hamburg (ZMH), Hamburg.

The specimens cited correspond to all trans-Andean species of *Atractus* examined. Specimens and localities are listed in the Appendix.

The characters observed are from meristic, morphometric, dentition and hemipenis data. Terminology for *Atractus* cephalic shields follows Savage (1960), whereas the method of counting ventral scales follows Dowling (1951). The condition for loreal scale follows Passos et al. (2007b). Hemipenis terminology follows Dowling & Savage (1960), Myers & Campbell (1981) and Zaher (1999). Techniques for hemipenis preparation follow Pesantes (1994) and Myers & Cadle (2003). Sex was determined by the presence or absence of a hemipenis through a ventral incision at the base of the tail. Measurements were taken with an analogue calliper to the nearest 0.1 mm under a stereoscope, except for snout–vent (SVL) and caudal lengths (CL), which were taken with a flexible ruler to the nearest millimetre.

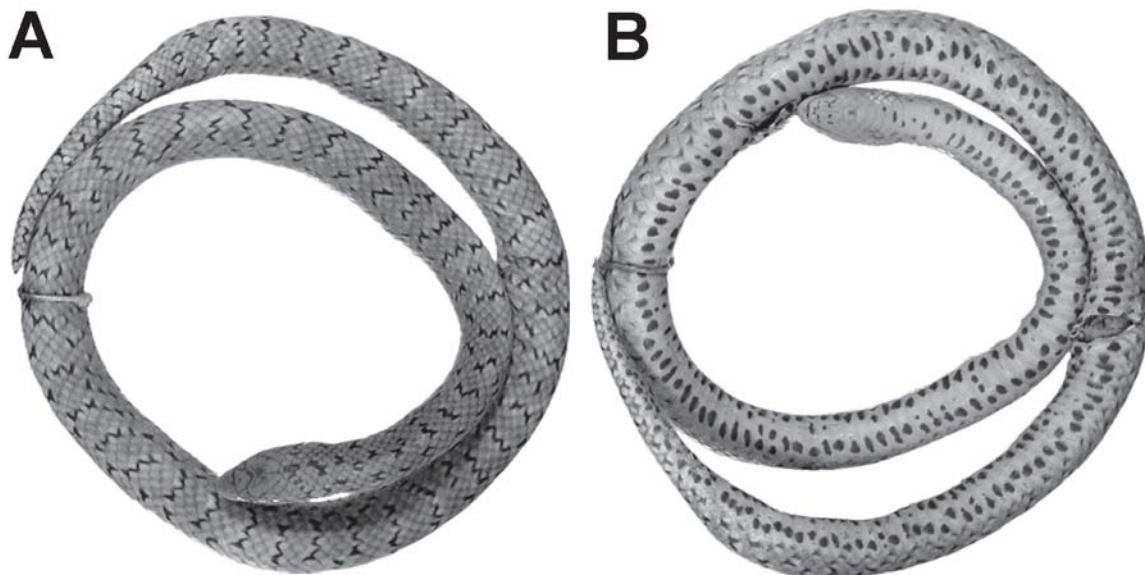


Fig. 2. Dorsal (A) and ventral (B) views of the paratype of *Atractus sanctaemartae* (MCZ 6531), from San Sebastian de Rábago, Sierra Nevada de Santa Marta, Colombia.

Analysis of variance (ANOVA) using segmental counts (ventral and subcaudal scales) and measurements (CL/SVL ratio) were employed in order to assess the presence or absence of sexual dimorphism within each taxon, except when the sample sizes were too small to allow the use of statistical tests. Assumptions of univariate normality and homoscedasticity were evaluated using the Kolmogorov–Smirnov test and Levene’s test, respectively (Zar, 1999). In cases where characters did not show sufficient variation to justify such assumptions, or when the sample size was too small, non-parametric tests (Mann–Whitney *U*-test and Fisher two-tailed exact test) were performed (Zar, 1999). The following characters were employed in the statistical analysis: number of ventral, subcaudal, supralabial and infralabial scales, snout–vent and caudal lengths and colour pattern.

RESULTS

Groups showed significant sexual dimorphism in the number of ventral ($U_{2,34}=24$; $P<0.1$; $n=23$) and subcaudal scales ($U_{3,6}=0.5$; $P<0.001$; $n=23$), and in SVL ($U_{3,7}=0.1$; $P<0.001$; $n=23$). The sample of the type series of *Atractus nebularis* was increased with 10 additional specimens and reveals that the colour pattern characters of *A. nebularis* (darker ground colour; Fig. 1) and *A. sanctaemartae* (light ground colour; Fig. 2) are strongly associated with our male and female samples, respectively ($Q=14.56$; $P<0.001$; $n=23$). Hence, differences in segmental counts for distinct patterns obtained by Bernal-Carol & Roze (1997) could be expected (but see below), if colour patterns previously associated with each species occur almost exclusively within a given sex. This fact perfectly explains why syntopic specimens of both species mentioned by Bernal-Carol & Roze (1997) differ in total body size. As a rule, in *Atractus* there is strong

sexual dimorphism in snout–vent and caudal lengths, which is also reflected in segmental counts (Savage, 1960; Passos et al., 2005). Consequently, size discrepancies reported by Bernal-Carol & Roze (1997), according to our sample, merely reflect the usual sexual dimorphism in size between males and females.

Moreover, new specimens with a dark colour pattern (= *A. nebularis sensu* Bernal-Carol & Roze, 1997) reported here considerably extend the range of variation in segmental counts for *A. nebularis* (145–157 ventrals in males, 148–162 in females, and 29–37 subcaudals in males, 24–29 in females). This degree of variation of the dark pattern falls within the range of variation of the light pattern previously referred to as *A. sanctaemartae* (see Bernal-Carol & Roze, 1997). Furthermore, based on the new records, it is possible to see that both patterns occur syntopically along the whole range of the species’ distribution (e.g. Nabusímaque, Cienega, Minca, Serrania San Lorenzo). Although the study of the type series of *A. nebularis* corroborated the occurrence of the supra-anal tubercles (cited as a diagnostic character for *A. nebularis* by Bernal-Carol & Roze, 1997), we found supra-anal tubercles only in male individuals. As the occurrence of supra-anal tubercles also appears to be a secondary sexual character apparently restricted to male specimens of some *Atractus* species (Prudente & Passos, 2008), the absence of it is unsurprising in the colour pattern here associated mainly with females.

For the reasons outlined above, *A. nebularis* is relegated herein to the synonymy of *A. sanctaemartae*. Additionally, while examining material for this study, we found one specimen from an isolated locality on the Atlantic coast of Colombia, near the Sierra Nevada massif, that did not match any previously described species of the genus. Therefore, we also provide below a description of this new species and comment on its possible affinities.

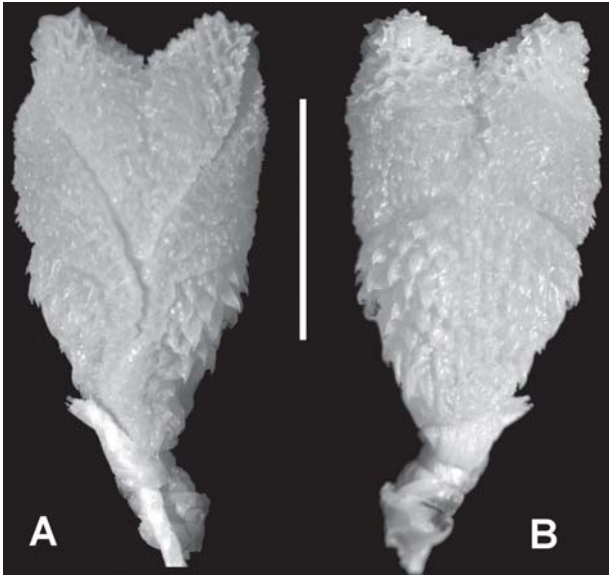


Fig. 3. Sulcate (A) and asulcate (B) sides of the hemipenis (ICN 10809) of *Atractus sanctaemartae*.

SPECIES ACCOUNTS

Atractus sanctaemartae Dunn, 1946 (Figs. 1–2)

Atractus badius Griffin, 1916; Mem. Carnegie Mus. 7:172 (part.).

Atractus iridescens Ruthven, 1922; Misc. Publ. Mus. Zool. Univ. Michigan 8:66 (part.).

Atractus sanctaemartae Dunn, 1946; Occ. Pap. Mus. Zool. Univ. Michigan 493:2.

Atractus nebularis Bernal-Carol & Roze, 1987; Bull. Maryland Herp. Soc. 33(4):165. *New synonymy*.

Holotype. Female, UMMZ 48298, from San Sebastián, Sierra Nevada de Santa Marta, Department of Magdalena, Colombia, collected in 1899 by W. Brown (photos examined).

Paratypes. Fifteen specimens (municipalities in parenthesis): six males, CM 201 (Minca), MCZ 6533 (San Sebastian de Rábago), UMMZ 47739–41 (Serrania San Lorenzo), UMMZ 54946 (Taqua), UMMZ 55675, and eight females, CM 215 (El Líbano), MCZ 6525 and 6531–32 (San Sebastian de Rábago), MCZ 32766 and UMMZ 54945 (Serrania San Lorenzo), UMMZ 63774 (Vista Nieve), UMMZ 85595 (San Sebastian de Rábago). All specimens are from Sierra Nevada de Santa Marta, Magdalena Department, Colombia (photos from CM 201, 215, MCZ 6533 examined).

Diagnosis. *Atractus sanctaemartae* is distinguished from all congeners by having: 1) 17/17/17 dorsal scale rows with supra-anal tubercles in males; 2) generally two postoculars; 3) loreal long; 4) temporal 1+2; 5) seven supralabials, third and fourth contacting orbit; 6) seven infralabials, first three contacting chinshields; 7) six to eight maxillary teeth; 8) three or four gular scale rows; 9)

three or four preventrals; 10) 145–165 ventrals in females, 142–150 in males; 11) 19–27 subcaudals in females and 27–37 in males; 12) dorsal colour pattern with males having black dorsum and alternate light transversal bands, and females otherwise generally having creamish yellow dorsum with alternate black bands; 13) venter creamish white with round dark brown blotches frequently arranged linearly constituting irregular wide stripes; 14) large body size in females (maximum SVL 650 mm) and moderate in males (maximum SVL 376 mm); 15) moderate tail length in females (10.9–12.3% of SVL) and moderate to long tail (13.3–18.7% of SVL) in males; 16) slightly bilobed, semicapitate and semicalyculate hemipenis.

Comparisons. Among all congeners, *Atractus sanctaemartae* shares only with *Atractus crassicaudatus* 17 dorsal scale rows, seven upper and lower labials, first three infralabials contacting chinshields, 7–11 maxillary teeth, maxillary diastema present, dorsum light with dark or dark with light alternate transversal bands, hemipenis slightly bilobed, semicapitate and semicalyculate. *Atractus sanctaemartae* differs from *A. crassicaudatus* in having ventral round blotches arranged linearly forming wide irregular stripes (vs ventral blotches variable but never forming conspicuous stripes).

Description. Head twice as long as wide, flattened or slightly arched in lateral view, sub-triangular in dorsal view; snout truncate in lateral view, round in dorsal view; canthus rostralis well defined in lateral view; cervical constriction indistinct; rostral twice as wide as high, sub-triangular in frontal view, well visible in dorsal view; internasal as long as wide; internasal suture sinistral with respect to prefrontal suture; prefrontal longer than wide; supraocular sub-trapezoidal, longer than wide; frontal sub-triangular, wider than long; parietal twice as long as wide; nasal divided; nostril restricted to prenasal; prenasal twice as high as long; postnasal slightly higher than long; moderately long loreal, contacting second and third supralabials; loreal occasionally reduced posteriorly, with prefrontals contacting third supralabial; pupil round; two postoculars with similar length; lower postocular generally twice as high as upper postocular; temporals 1+2; first temporal 0.6 times longer than high; upper posterior temporal elongate, four times as long as wide; seven supralabials, third and fourth contacting orbit; first two supralabials similar in size and lower than third one; sixth higher and seventh longer than remaining supralabials; symphyisial sub-triangular, twice as wide as long; seven infralabials, generally first three contacting chinshields; first pair of supralabials in contact behind symphyisial, preventing symphyisial/chinshield contact; chinshields about four times as long as wide; three or four gular scale rows; generally three or four preventrals; 17/17/17 dorsal scale rows; dorsals lacking apical pits and keels, and with supra-anal tubercles in males; caudal spine moderately conical, and acuminate; maxillary arched in dorsal view, with five to six prediastemal teeth and one or two postdiastemal ones; first two prediastemal teeth slightly smaller and little spaced, remaining teeth moderately spaced and higher than first two; prediastemal teeth curved posteriorly, angular in cross

section, robust at the base, and narrower on the apices; maxillary diastema moderately spaced; postdiastemal teeth slight smaller than last prediastemal tooth; lateral process poorly developed, lacking posterior projection.

Male colour pattern (Fig. 1). Dorsum of head black or dark brown, with brown blotches eventually above internasals, anterior portion of prefrontals, parietals and temporals; background of head black or dark brown, extending to dorsal margins of supralabials; supralabials creamish yellow, except last supralabial generally uniformly black; mental region cream with dispersed dark brown dots concentrated above proximal portion of infralabials and chinshields; prefrontals generally cream; venter cream with a series of lateral dark brown blotches, frequently collapsed forming broad irregular stripes; venter occasionally uniformly black; black tail with cream small dots concentrated on median suture of subcaudals; dorsal ground colour of body dark brown or black, with alternate transversal cream bands (one scale wide); bands frequently black bordered and not contacting opposite one above vertebral region; body occasionally uniform dark brown or black, lacking light bands.

Female colour pattern (Fig. 2). Dorsum of head yellowish brown or light brown, occasionally with creamish yellow blotches on lateral portion of parietals; background of head yellowish brown or light brown, extending to dorsal margins of supralabials; orbital region and dorsal edges of third to seventh supralabial frequently pigmented dark brown, forming a conspicuous postorbital stripe; supralabials predominantly cream; mental region cream, generally scattered with dark brown dots or blotches concentrated on anterior portion of chinshields and at first infralabials; venter creamish white with dark brown rounded blotches concentrated on lateral portion of ventrals, constituting wide irregular stripes; in juvenile specimens lateral blotches frequently collapsed laterally, forming two broad regular stripes separated from one another by a light median line; tail cream with dispersed dark brown dots; dorsum of body with a black vertebral line (one scale wide) above ten first dorsal scale rows; dorsal ground colour yellowish brown or light brown, with a series of transversal black wide (one or two scales wide) or tiny (half scale wide) bands white bordered; dorsal bands rarely contact the opposite one above vertebral region; dorsum occasionally irregular, having diffuse small black dots along body. ICN 2759–60, 5664, and MCZ 6525 have colour pattern most frequent in male specimens (see below).

Hemipenis morphology (everted organs $n=5$). Retracted organ bifurcates and extends to the level of ninth subcaudals. Organ slightly bilobed, semicapitate and semicalyculate; lobes poorly distinct from and restricted to distal portion of *capitulum*; lobes barely clavate, with a laterodistal depression on the apices; lobes and *capitulum* uniformly covered with spinulate calyces, arranged in irregular transverse flounces; vertical walls of calyces forming poorly distinct longitudinal crests on sulcate side of *capitulum*; asulcate side of *capitulum* with more concentrated and irregular calyces; capitular groove well marked on both sides of *capitulum*; *capitulum* situated

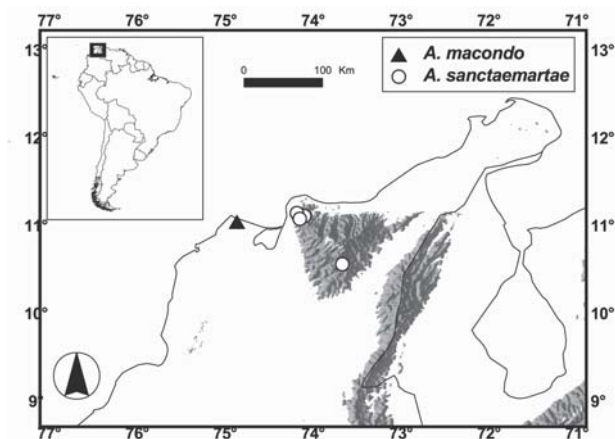


Fig. 4. Geographical distribution of *Atractus sanctaemartae* and *Atractus macondo*.

on the level of bifurcation of *sulcus spermaticus*; *sulcus spermaticus* divides in the middle of the organ; branches of *sulcus spermaticus* with centrifugal orientation, running to the tips of lobes; *sulcus spermaticus* stout and narrow; margins of *sulcus spermaticus* bordered with spinules all along their extension; hemipenial body sub-cylindrical, uniformly scattered with hooked spines with base moderately expanded; hemipenial body similar in size to *capitulum*; basal naked pocket restricted to basal portion of hemipenial body; proximal portion of hemipenis with longitudinal plicae and disperse spinules (Fig. 3).

Variation. Largest male SVL 376 mm, CL 50 mm, largest female SVL 650 mm, 60 mm; tail 13.3–18.7% (mean=16.1; SD=1.3; $n=15$) of SVL in males, 10.9–12.3% (mean=11.9; SD=1.7; $n=7$) of SVL in females; 142–150 (mean=147.1; SD=3.4; $n=15$) ventrals in males, 145–165 (mean=155.2; SD=7.8; $n=8$) in females; 27–37 (mean=32.1; SD=2.5; $n=14$) subcaudals in males, 19–27 (mean=23.4; SD=2.7; $n=7$) in females; seven ($n=45$ sides) or eight ($n=3$ sides) infralabials; three ($n=44$ sides) or four ($n=2$ sides) first infralabials contacting chinshields; one ($n=1$), two ($n=15$), three ($n=1$) or four ($n=6$) prefrontals; three ($n=32$ sides) or four ($n=14$ sides) gular scale rows; two ($n=45$ sides) or three ($n=1$ side) postoculars; 8–12 (mean=9.2; SD=0.7; $n=46$ sides) dorsal scale rows on the level of second subcaudals; 3.6–8.4 mm (mean=6.3; SD=1.9; $n=7$) body diameter; six ($n=2$ sides), seven ($n=2$ sides) or eight ($n=39$ sides) maxillary teeth; retracted organ extends to the level of ninth subcaudals ($n=2$).

Distribution (Fig. 4). North, western and south versants of Sierra Nevada de Santa Marta massif of Colombia, from Minca (11°09'N, 74°07'W) in the Department of Magdalena to the locality of Nabusímaque, municipality of Valledupar (10°29'N, 73°15'W) in the Department of Cesar. *Atractus sanctaemartae* occurs in cloud forest between 1200 and 2500 m. Although there are specimens labelled as being from lowland portions of the Sierra Ne-

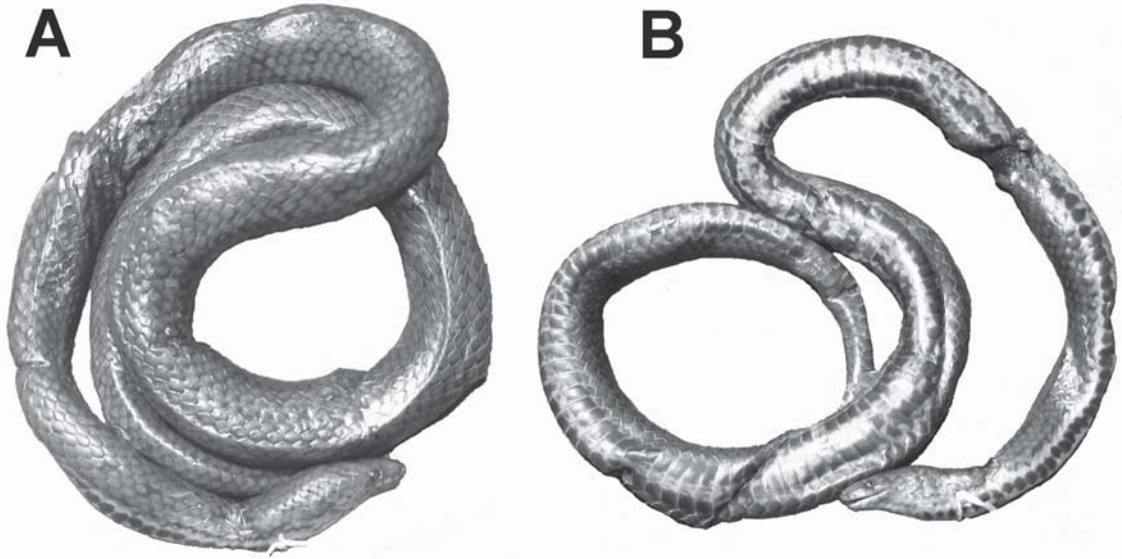


Fig. 5. Dorsal (A) and ventral (B) views of the holotype of *Atractus macondo* (IAvH 15). From Parque Nacional Natural Isla de Salamanca, municipality of Sitionuevo, Colombia.

vada de Santa Marta, as earlier pointed out by Dunn (1946) and Bernal-Carol & Roze (1997), numerous specimens from the Santa Marta region having no specific collection data or precise coordinates could not be traced. To complicate matters, several localities in the Santa Marta region have a deep altitudinal gradient, ranging abruptly from sea level to 1500 m in elevation (see Ruthven, 1922). Consequently, most specimens labelled from lowland administrative localities (e.g. Santa Marta and Rio Frío; see Dunn, 1946) should come from elevated portions of each municipality.

Atractus macondo sp. nov. (Fig. 5)

Holotype. Adult male, IAvH 15 (formally IND-R 15), from Parque Nacional Natural Isla de Salamanca (10°58'N, 74°30'W, approximately 3 m), municipality of Sitionuevo, Department of Magdalena, Colombia, collected by G. Toro.

Diagnosis. *Atractus macondo* distinguished from all congeners by the combination of the following characters: 1) 17/17/17 smooth dorsal scale rows; 2) two postoculars; 3) long loreal; 4) temporals 1+2; 5) seven supralabials, third and fourth contacting orbit; 6) seven infralabials, first three contacting chinshields; 7) nine maxillary teeth; 8) two gular scale rows; 9) two preventrals; 10) 151 ventrals in the single male; 11) 29 subcaudals; 12) dorsum uniformly reddish brown; 13) venter cream with a series of rhomboidal blotches arranged linearly on lateral portion of ventral scales, forming irregular stripes; 14) moderate body size, the only male reaching 334 mm SVL; 15) moderate tail in male (14.7% of SVL).

Comparisons. Of all congeners, *Atractus macondo* shares only with *A. sanctaemartae* 17 dorsal scale rows, seven upper and lower labials, first three infralabials in contact with chinshields, eight to nine maxillary teeth, diastema present, occasionally dorsum with uniform pattern, venter cream with round blotches arranged lin-

early on lateral portion of ventral scales. *Atractus macondo* differs from *Atractus sanctaemartae* in having nine maxillary teeth, two gular scale rows, slender (62% of body diameter) and acuminate head, snout acuminate in lateral view, and dorsal colour pattern reddish brown, vs eight maxillary teeth, three to four gular scale rows, head round and broad (equal or broader than body diameter), snout truncate in lateral view, black with light bands or yellowish brown with black bands in *A. sanctaemartae*.

Description of holotype. Adult male, SVL 334 mm, CL 49 mm (14.7% of SVL); body diameter 9.2 mm (2.7% of SVL); head length 12.6 mm (3.8% of SVL); head width 5.7 mm (45% head length); head slender (62% of body diameter), arched in lateral view, acuminate in dorsal view; snout acuminate in lateral view, round in dorsal view; rostral sub-triangular in frontal view, 2.0 mm wide, 1.4 mm high, visible in dorsal view; internasal 1.1 mm long, 1.2 mm wide; internasal suture sinistral with respect to prefrontal suture; prefrontal 3.0 mm long, 2.7 mm wide; supraocular sub-rectangular 1.7 mm long, 1.1 mm wide; frontal sub-triangular, 2.9 mm long, 3.2 mm wide; parietal 5.4 mm long, 2.9 mm wide; nasal divided; nostril restricted to prenasal; prenasal 0.9 mm high, about twice as high as long; post-nasal as high (0.7 mm) as long; loreal 2.6 mm long, 0.6 mm high, contacting second and third supralabial; eye diameter 1.4 mm; pupil round; two postoculars similar in length (0.6 mm); lower postocular (0.9 mm) slightly higher than upper postocular; temporals 1+2; first temporal 2.5 mm long, about twice as long as high; upper posterior temporal elongate (5.0 mm), three times as long as wide; seven supralabials, third and fourth contacting orbit; second supralabial higher than first and similar in size to third one; sixth higher and seventh longer than remaining supralabials; symphyial triangular, 1.4 mm wide, 0.9 mm long; seven infralabials, first three contacting chinshield; first pair of supralabials in contact behind symphyial, preventing symphyial/chinshield contact; chinshields

3.3 mm long, 1.1 mm wide; two gular scale rows; two prefrontals; 151 ventrals; 30 (on right side) and 29 (on left side) subcaudals; 17/17/17 smooth dorsal scale rows; dorsals lacking apical pits, supra-anal tubercles and keels; caudal spine short, conical and rhomboid; maxillary arched in dorsal view, with seven prediastemal and two postdiastemal teeth; prediastemal teeth large, little spaced and of similar size; prediastemal teeth curved posteriorly, angular in cross section, robust at base, narrower on the apices; postdiastemal teeth half the size of the last prediastemal tooth; maxillary diastema moderate.

Coloration of holotype (Fig. 5). Dorsum uniformly reddish brown; background of head reddish brown, extends to dorsal margin of supralabials; supralabials with dorsal edges black pigmented, forming a stripe extended to sixth supralabial; ventral margin of supralabials cream anterior to orbit (first three scales), and creamish red posterior to it; seventh supralabial uniformly reddish brown; mental region cream, with dark brown blotches extended for symphyseal, first pair of infralabials, proximal portion of second to fifth infralabials, and chinshields; gular region cream with small dark brown dots; prefrontals cream; venter cream with rhomboidal dark brown blotches concentrated on lateral portion of ventrals, forming barely regular lateral stripes; lateral stripes broad, occupying about 50% of belly; medial region cream covered with diffuse dark brown dots; tail dark brown, with cream dots concentrated on lateral portion of subcaudals; dorsal ground colour of body reddish brown, with a vertebral line (one scale wide) barely distinct above first nine scale rows; first two dorsal scale rows light (orange brown); dorsum with small black dots on edges of dorsal scales, converging to paravertebral region; dorsum of tail with dark brown vertebral line (one scale wide), barely distinct.

Etymology. The specific epithet “*macondo*” is the fictitious name of the village from García-Márquez’ novel *Cien Años de Soledad*. This story was based along and broadly inspired by the Atlantic coast of Colombia. The word *macondo* is used here in apposition, referring to the type locality of the new species, and also honouring the coastal people of Colombia.

Distribution (Fig. 4). Known only from Parque Nacional Natural Isla de Salamanca, municipality of Sitionuevo, Department of Magdalena, Atlantic coast of Colombia. The only specimen of *Atractus macondo* was captured in a mangrove forest near the coast.

DISCUSSION

Atractus macondo appears to be a close relative of and shared only with *A. sanctaemartae* a similar number of ventral and subcaudal counts for males, seven supralabials and infralabials, first three infralabials contacting chinshields, and rhomboidal blotches on venter arranged linearly forming irregular wide stripes. Nevertheless, in addition to apparently robust diagnostic characters distinguishing the new species from *A. sanctaemartae* (see above), *A. macondo* is known only from the Parque Nacional Natural Isla de Salamanca at sea

level on the Colombian coast, whereas *A. sanctaemartae* is endemic to the highlands of the Sierra Nevada de Santa Marta, occurring in cloud forest between 1200 and 2500 m elevation (Fig. 4). Among congeners, *A. sanctaemartae* and *A. macondo* share only with *A. crassicaudatus*, *A. nigriventris*, *A. pamplonensis* and *A. variegatus* 17 dorsal scale rows, seven upper and lower labials, first three infralabials contacting chinshields, seven to twelve moderately spaced maxillary teeth, maxillary diastema present, dorsal colour pattern reticulate, banded or variegate, venter heavily pigmented with black, slightly bilobed, semicapitate and semicalyculate hemipenis, hemipenis with a lateral depression in the lobe apices, *capitulum* broader than hemipenial body. Of all characters considered above, at least the lateral depression in the apices of the hemipenial lobes seems to constitute a synapomorphy within the genus, possibly defining a more inclusive clade in the greatly diverse Andean *Atractus* (Passos, 2008).

Although there is general consensus for a recent uplift of the Santa Marta massif apart from the geodynamics of the Andean Cordilleras (Tschanz et al., 1974; Gregory-Wodzicki, 2000), some geological evidence indicates a much older contact between the Santa Marta region and the terrain currently occupied by the Eastern Cordillera of Colombia. The Santa Marta massif has amphibolite-grade rocks overlain by Silurian phylites and unmetamorphosed Palaeozoic and Mesozoic rocks that are typical of the Eastern Cordillera (Tschanz et al., 1974; Aleman & Ramos, 2003). Additionally, palaeobotanical data also suggest a rapid uplift of the Eastern Cordillera between two and five million years ago at some level due to erosion-driven isostatic rebound rather than only by mean surface uplift (Gregory-Wodzicki, 2000). As all putative closely related taxa of *Atractus sanctaemartae* are endemic to the Eastern Cordillera, we speculate that this assemblage could derive from a common widespread trans-Andean ancestor that split before the orogenic events related to the uplift of the Eastern Cordillera in the Pliocene (Gregory-Wodzicki, 2000; Aleman & Ramos, 2003).

Although snakes do not show coloration as vivid as those seen in many sexually dichromatic lizard species, sex-related colour differences are more common among snakes than has been generally appreciated (Shine, 1993). While most examples of sexual dichromatism in snakes are tenuous and involve minor differences in background coloration, others are more obvious and involve distinct dorsal and ventral colour patterns (see Shine, 1993 for a review). As a rule, in dichromatic species of snakes, males have brighter colour patterns than females (Shine, 1993; Shine & Madsen, 1994; Lindell & Forsman, 1996). The courting male’s bright colour was first interpreted as cryptic, inducing “flicker-fusion” confusion in the visual systems of vertebrate predators through the rapid movement of black-and-white zigzag bands (Shine, 1993; Shine & Madsen, 1994; Lindell & Forsman, 1996). This hypothesis is consistent with greater male mobility with respect to females during the mating season, resulting in distinct selective pressures as a result of predation (Shine & Madsen, 1994; Forsman, 1995; Lindell & Forsman, 1996).

However, Wüster et al. (2004) suggest that sexual dichromatism can alternatively be interpreted as mimicry of dangerous venomous species.

Atractus sanctaemartae is the only species of its genus that shows strong sexual dichromatism (Passos, 2008), but possible coral snake mimicry has been reported at least for *A. poeppigi* (Martins & Oliveira, 1993), *A. elaps* (Roze, 1996) and melanistic (Silva, 1993) and non-melanistic (Martins & Oliveira, 1999) individuals of *A. latifrons*. Nevertheless, in the present study, based on preserved specimens of *A. sanctaemartae*, females have brighter coloration than males (Figs 1–2; pale areas correspond probably to reddish in life). As such, the brighter pattern of the females disagrees in part with both the mimicry and crypsis hypotheses, in which females generally tend to display uniformly coloured or melanistic patterns, apparently reducing predation pressure given the lesser mobility of gravid females (Forsman, 1995; Lindell & Forsman, 1996). Moreover, male and female patterns cannot be unambiguously associated with any dangerous model species occurring in the Sierra Nevada de Santa Marta. Therefore, it is not obvious which selective pressures, if any, are responsible for such bright dichromatic patterns in *A. sanctaemartae*.

ACKNOWLEDGEMENTS

The senior author is grateful to the following people for permission to examine specimens under their care and/or facilities: A. Acosta (MUJ), C. Aguilar and J. Santa-Gadea (MHNSM), A. Almendariz (EPN), M. Bernal (CZUT-R), F. Bisbao (EBRG), R. Casallas and A. Rodríguez (MLS), J. Cobos (UQC), L. Coloma and S. Ron (QCAZ), C. Ferreira (MBUCV), F. Franco (IBSP), J. Hallermann (ZMH), E. La Marca (ULABG), V. Páez (MHUA), A. Pascual (CV-UJA), D. Perico (IAvH), M.P. Ramírez (UIS), C. Señaris and G. Rivas (MHNLS), M. Wilkinson and C. McCarthy (NHM), H. Zaher (MZUSP). We thank A.W.A. Kellner, A.L.C. Prudente, W. Schargel and W. Wüster for helpful comments on the manuscript. Financial support from P. Passos and R. Fernandes was provided by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and Fundação Carlos Chagas de Apoio à Pesquisa do Estado do Rio de Janeiro (FAPERJ). P. Passos thanks Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for a doctoral fellowship in Colombia.

REFERENCES

- Aleman, A. & Ramos, V.A. (2000). Northern Andes. In *Tectonic Evolution of South America*, 453–480. Cordani, U.G., Milani, E.J., Thomaz-Filho, A. & Campos, D.A. (eds). Rio de Janeiro: Brazilian Academy of Science Press.
- Bernal-Carol, A. & Roze, J.A. (1997). Snake genus *Atractus* (Colubridae) from Sierra Nevada de Santa Marta, Colombia, with a description of a new species. *Bulletin of the Maryland Herpetological Society* 33, 165–170.
- Dowling, H.G. (1951). A proposed standard system of counting ventrals in snakes. *British Journal of Herpetology* 1, 97–99.
- Dowling, H.G. & Savage, J.M. (1960). A guide to the snake hemipenis: a survey of basic structure and systematic characteristics. *Zoologica* 45, 17–28.
- Dunn, E.R. (1946). *Atractus sanctaemartae*, a new species of snake from the Sierra Nevada de Santa Marta, Colombia. *Occasional Papers of the Museum of Zoology, University of Michigan* 493, 1–6.
- Forsman, A. (1995). Opposing fitness consequences of colour pattern in male and female snakes. *Journal of Evolutionary Biology* 8, 53–70.
- Giraud, A.R. & Scrocchi, G.J. (2000). The genus *Atractus* (Serpentes: Colubridae) in north-eastern Argentina. *Herpetological Journal* 10, 81–90.
- Gregory-Wodzicki, K.M. (2000). Uplift history of the central and northern Andes: a review. *Geological Society of America Bulletin* 112, 1091–1105.
- Griffin, L.E. (1916). A catalog of the ophidia from South America at present (June, 1916) contained in the Carnegie Museum, with descriptions of some new species. *Memoirs of the Carnegie Museum* 7, 163–277.
- Lindell, L.E. & Forsman, A. (1996). Sexual dichromatism in snakes: support for the flicker-fusion hypothesis. *Canadian Journal of Zoology* 74, 2254–2256.
- Martins, M. & Oliveira, M.E. (1993). The snakes of the genus *Atractus* Wagler (Reptilia: Squamata: Colubridae) from the Manaus region, central Amazônia, Brazil. *Zoologische Mededelingen* 69, 21–40.
- Martins, M. & Oliveira, M.E. (1999). Natural history of snakes in forests of the Manaus region, Central Amazônia, Brazil. *Herpetological Natural History* 6, 78–150.
- Myers, C.W. (2003). Rare snakes – five new species from eastern Panama: reviews of northern *Atractus* and southern *Geophis* (Colubridae: Dipsadinae). *American Museum Novitates* 3391, 1–47.
- Myers, C.W. & Cadle, J.E. (2003). On the snake hemipenis, with notes on *Psomophis* and techniques of eversion: a response to Dowling. *Herpetological Review* 34, 295–302.
- Myers, C.W. & Campbell, J.A. (1981). A new genus and species of colubrid snake from the Sierra Madre del Sur of Guerrero, Mexico. *American Museum Novitates* 2708, 1–20.
- Myers, C.W. & Donnelly, M.A. (2008). The summit herpetofauna of Auyantepui, Venezuela: report from the Robert G. Goelt American Museum – Terramar expedition. *Bulletin of the American Museum of Natural History* 308, 1–147.
- Myers, C.W. & Schargel, W.E. (2006). Morphological extremes – two new snakes of the genus *Atractus* from northwestern South America (Colubridae: Dipsadinae). *American Museum Novitates* 3532, 1–13.
- Passos, P. (2008). *Revisão Taxonômica do Gênero Atractus Wagler, 1828 (Serpentes: Colubridae: Dipsadinae)*. Ph.D. thesis. Rio de Janeiro: Museu Nacional, Universidade Federal do Rio de Janeiro.
- Passos, P. & Arredondo, J.C. (2009). Rediscovery and redescription of the Andean earth-snake *Atractus wagleri* (Reptilia: Serpentes: Colubridae). *Zootaxa* 1969, 59–68.
- Passos, P., Cisneros-Heredia, D.F. & Salazar-V., D. (2007a).

- Rediscovery and redescription of the rare Andean snake *Atractus modestus*. *Herpetological Journal* 17, 1–6.
- Passos, P., Fernandes, D.S. & Borges-Nojosa D.M. (2007b). A new species of *Atractus* (Serpentes: Dipsadinae) from a relictual forest in northeastern Brazil. *Copeia* 2007, 788–797.
- Passos, P. & Fernandes, R. (2008). A new species of the colubrid snake genus *Atractus* (Reptilia: Serpentes) from the central Amazon of Brazil. *Zootaxa* 1849, 59–66.
- Passos, P., Fernandes, R. & Zanella, N. (2005). A new species of *Atractus* (Serpentes: Colubridae) from south Brazil. *Herpetologica* 61, 209–218.
- Pesantes, O. (1994). A method for preparing hemipenis of preserved snakes. *Journal of Herpetology* 28, 93–95.
- Prudente, A.L.C. & Passos, P. (2008). A new species of *Atractus* Wagler, 1828 (Serpentes: Dipsadinae) from Guyana plateau in northern Brazil. *Journal of Herpetology* 42, 723–732.
- Roze, J.A. (1996). *Coral Snakes of the Americas: Biology, Identification, and Venoms*. Malabar: Krieger Publishing Company.
- Ruthven, A. (1922). The amphibians and reptiles of the Sierra Nevada de Santa Marta, Colombia. *Miscellaneous Publications, Museum of Zoology, University of Michigan* 8, 1–69.
- Savage, J.M. (1960). A revision of the Ecuadorian snakes of the colubrid genus *Atractus*. *Miscellaneous Publications, Museum of Zoology, University of Michigan* 112, 1–86.
- Shine, R.S. (1993). Sexual dimorphism in snakes. In *Snakes: Ecology and Behaviour*, 49–86. Seigel, R.A. & Collins, J.T. (eds). New York: McGraw-Hill.
- Shine, R. & Madsen, T. (1994). Sexual dichromatism in snakes of the genus *Vipera*: a review and a new evolutionary hypothesis. *Journal of Herpetology* 28, 114–117.
- Silva, N.J. (1993). The snakes from Samuel hydroelectric power plant and vicinity, Rondônia, Brazil. *Herpetological Natural History* 1, 37–86.
- Tschanz, C.M., Marvin, R.F., Cruz, J.B., Mehnert, H.H. & Cebula, G.T. (1974). Geologic evolution of the Sierra Nevada de Santa Marta, northeastern Colombia. *Geological Society of America Bulletin* 75, 273–284.
- Wüster, W., Allum, C.S.E., Bjargardóffir, B.I., Bailey, K.L., Dawson, K.J., Guenioni, J., McGurk, J., Moore, A.G., Miskanen, M. & Pollard, C.P. (2004). Do aposematism and Batesian mimicry require bright colours? A test using European viper markings. *Proceeding of the Royal Society of London B* 271, 2495–2499.
- Zaher, H. (1999). Hemipenial morphology of the South American xenodontine snakes, with a proposal for a monophyletic Xenodontinae and a reappraisal of colubroid hemipenes. *Bulletin of the American Museum of Natural History* 240, 1–168.
- Zar, J.H. (1999). *Biostatistical Analysis*. New Jersey: Prentice Hall.

Accepted: 8 January 2009

APPENDIX

Specimens examined

Atractus andinus. Colombia, Antioquia, Andes: (formerly CSJ 231, now CSJ 516 holotype).

Atractus biseriatus. Colombia, Caldas, Villamaria: (MLS 145 holotype).

Atractus bocourti. Peru, Huánuco, Acomayo: (NHM 1946. 1.2.24 holotype, MHNSM 2801), Chaglla: (MHNSM 20041–43), Huancapallac: (MHNSM 20036), Molino-Panao, Pachitea: (MHNSM 3001, 3064), Panao: (MHNSM 20044).

Atractus boulengerii. Colombia, Valle Del Cauca, Anchicayá, Bajo Anchicayá: (UV-C 6591).

Atractus carrioni. Ecuador, Loja, Loja: (EPN 8673–74, QCAZ 793, 1081–82, 1217–19, 2100), Jardín Botánico: (QCAZ 6445–46), Yangana: (QCAZ 6550), Río Molacatus: (QCAZ 6533–34).

Atractus clarki. Colombia, Antioquia, Anorí: (MHUA 14000), Chocó: Andagoya: (MLS 1213), Istmina: (MLS 1214), Valle del Cauca: Restrepo: (ICN 10826).

Atractus crassicaudatus. Colombia, without locality: (IBSP 2443, ICN 8505, 8508–25, 8922–25, MLS 139, 152, 156, 293, 2640, MUJ 92, 355), Boyacá, Badohondo: (ICN 10693), Belén: (ICN 10709), Chiquinquirá: (MLS 2577), Coper: (MLS 2578–79), Duitama: (ICN 10700–07), Garagoa: (ICN 10627, MUJ 315–22, 398–99, 509), Guayatá: (IAvH 864–65), Pajarito: (IAvH 1059, ICN 2608–11, 2831–33), Pesca: (IAvH 1880), Río Tectino: (IAvH 799), Sogomoso: (MLS 282, 2751–52), Tunja: (MUJ 04), Ventaquemada: (MLS 2243), Villa de Leyva: (IAvH 2172–73, 3039, 3189, 4788, 4811–20, 4852, 4878, 4889, 4892–93, 4912, 4960, 4976, ICN 2792, 8332–33, 9016–19, 9027, MLS 2021, 2564–65, 2918–20), Zetaquirá: (MUJ 05), Cundinamarca, without locality: (MUJ 482), Aguadita: (MLS 169), Albán: (IAvH 4749, ICN 10626), Bogotá: (IAvH 129, 204, 2478, ICN 1394–426, 1455, 1460–61, 2588, 2623, 2633, 2641, 3377, 4217, 4240, 6209, 6236, 6340, 6449, 6490–91, 6504–05, 6509, 7100, 7102, 8260, 10806, IBSP 226, 7216–17, 10164–67, 42945, MLS 153, 164–65, 167 172, 178, 2546, 2607–09, 2614–15, 2617, 2644–45, MUJ 03, 07, 09–10, 17, 22, 24, 151, 180, 206–09, 211, 400, 609–10, 692), Arrachal: (MLS 265, 2805–13), Cerro de Suba, La Conejera: (ICN 6336, 6577–79, 6580–81, 10692), Codazzi: (MLS 2386), San Joaquín: (MLS 2964–65), Santana: (IAvH 4964), Cajicá: (IAvH 500), Chia: (ICN 7101, MLS 2373–77, 2382–83, 2600, 2622–23, 2830–93, 2900–08, 2935–36, MLS without number, MUJ 18, 477), Cogua: (MLS 163, 185), Cota: (MUJ 164), Facatativa: (MUJ 264, 461–62), Fontinbón: (MUJ 25), Fuquené: (MUJ 16, 20–21), Fusagasuga: (MLS 2634, MUJ 92), Guachancipá: (ICN 8261), Guachetá: (MLS 2263), Guaduas: (MUJ 01), Guasca: (MLS 2626, MUJ 203–05, 215), La Calera: (MUJ 298), La Unión: (MLS 157), Machetá: (MLS 2568–70, 2653, 2921–22, 2927, 2931), Mosquera: (ICN 1453–54, 1456, 1458–59), Laguna Herrera: (IAvH 3815, ICN 859, 1277, 1457), Nemocón: (ICN 7041), Pacho: (MLS 154, 2611–12, 2616, 2923–30, MUJ 550), Pasca: (ICN 485–86, MLS 2602–04), Quetame: (ICN 4477), Represa del Sisga: (IAvH 08),

Reserva Carpanta: (MLS 26), San Antonio del Tequendama: (IAvH 3038–39, MLS 150–51, 200), Sesquilá: (MLS 2571), Sibaté: (MLS 175–76, 295), Sopo: (MLS 2624), Suesca: (MUJ 214, 649), Sumapaz: (MLS 168), Sutatenza: (MLS 283–84, 288, 292, 1860–63, 2493–94), Tabio: (MLS 1898), Tausa (MUJ 142), Tena: (MUJ 12, 19), Une: (MLS 160, 177, 2709–10), Usaquén: (MLS 2378–79, 2381, 2894–99, MUJ 13), Villapinzón: (ICN 2816, MLS 299), Villeta: (IAvH 1587), Meta, Cañon La Curia: (MLS 06), Lomalinda: (IAvH 967), Santander, without locality: (MUJ 212), Bolívar: (MLS 162), Jesús María: (MLS 2246–48), Puente Nacional: (MLS 2629), Santa Rita: (MLS 2630). Locality probably in error: Meta, Puerto Lopez: (ICN 6500, MUJ 15).

Atractus duboisi. Ecuador, Napo, without locality: (EPN four not cataloged specimens, QCAZ 2797), Baeza: (QCAZ 1234–1241, 2103, 2759, 4110, 4156), Cantón Quijos: (EPN 1281–89, 3121), Cordillera de Guacamayos (EPN 6875, QCAZ 3707–08, 3290), Cosanga: (QCAZ 906, 2098, 2106–07, 2759, 2798–2806, 5469), Baeza–Quito road: (QCAZ 4195, 4201), Río Hollin, Loreto road: (QCAZ 2104), Las Palmas: (QCAZ 3347–3350, 6593–95).

Atractus dunni. Ecuador, without locality: (QCAZ 219, 2884), Cotopaxi: without locality (IBSP 54328), Galapagos: (QCAZ 1092), San Francisco de Las Pampas: (QCAZ 163, 240–47, 670, 1077, 1231–33, 1685–86, 2108–10), Reserva Otonga, Cañon Signos: (QCAZ 4036), El Oro, Buenaventura: (EPN not cataloged), Loja, Olmedo: (QCAZ 1219), Pichincha, CERG: (QCAZ 2094), Chiriboqua: (32127–28), Mindo: (QCAZ 4151), Nanegalito: (QCAZ 638), Tandayapa: (QCAZ 872, 1667, 2102, 2111). Localities probably in error: Piso Tropical Oriental: (EPN 8703), Pastaza: Río Bobonaza: (EPN 8733).

Atractus emigdioi. Venezuela, Lara: Moran, La Palma, Páramo El Jábon: (MHNLS 9299), Trujillo, Boconó, Valera–Trujillo road: (ULABG 3791), Parque Nacional Guaramacal: (MHNLS 16209), Trujillo: (ULABG 4473).

Atractus eriki. Venezuela, Táchira: (CV-ULA 6117); Trujillo, Escuche: (ULABG 6710 paratype), Trujillo: (ULABG 6694 paratype), Valera: (ULABG 6693 holotype), ZULIA, Sierra de Perijá: (MBUCV not cataloged).

Atractus erythromelas. Venezuela, Mérida, Libertador: (MHNLS 902), Mérida: (NHM 1.716–17 paratypes of *A. erythromelas*), Mucurubá: (MHNLS 276–78, 630, 902).

Atractus gigas. Ecuador, Cotopaxi, Chiribogua: (QCAZ 01), Palmeras: (QCAZ 2099), Reserva Otonga: (QCAZ 3266), San Francisco de Las Pampas: (QCAZ 175, 179, 443, 647, 662). Locality probably in error: Piso Tropical Oriental: (EPN 8706).

Atractus indistinctus. Colombia, Norte de Santander, Ocaña: (MLS 166 holotype, MLS 261–62, 264, 2695–96).

Atractus iridescens. Colombia, Antioquia: San Pedro de Arama: (CSJ 563), Chocó, Nuquí: (IAvH 4539), Río San Juan: (MLS 1212); Nariño, Barbacoas, El Diviso, Vereda Berlin, Reserva Natural Biotopo Selva Húmeda: (ICN 10901–02).

- Atractus lancinii*. Venezuela, Aragua, Cumboto road: (EBRG 590), Maracay–Ocumare road: (EBRG 198–99, 291, 407–08, 698), Parque Nacional Pittien, Estación Biológica Rancho Grande: (EBRG 699, 4338); Carabobo, Barbula: (MHNLS 1750); Distrito Capital, Caracas, Parque Nacional El Ávila, Canales del Naigata: (MBUCV 2043a,b, 2044b, MHNLS 11417–18, 11797), Cerro Naigata: (MHNLS 3145), La Guaira: (MBUCV 2044a); Miranda, Guacaipuro: (MHNLS 6848), San Antonio de Los Altos: (MHNLS 2086, 12684), El Amarillo: (MHNLS 15150, 16788), San Diego de Los Altos: (EBRG 1982), Santenejas: (EBRG 4088); Yaracuy, Nirgua, Santa Teresa: (MHNLS 6381).
- Atractus lasallei*. Colombia, without locality: (MLS 301); Antioquia, Bello: (ICN 19621), Bello, San Felix: (MHUA 14060), Belmira: (ICN 10622), El Retiro: (MHUA 14112), Guarne: (MLS 2129), La Ceja: (ICN 10713), Marinilla: (ICN 10714), Medellín: (ICN 10618–20, MHUA 14383, MLS 2944), Medellín, Las Palmas: (ICN 1085), Medellín, San Cristobal: (MHUA 14003), Medellín, Santa Helena: (MHUA 14194, 14221, 114368, MLS 2217), Medellín, Piedras Blancas: (IAvH 970, 1008, 10012–13, 1933, 4857, MLS 204–06, 219, 223, 1782, 2829, 2946, 2958), Medellín, San Antonio de Prado: (MHUA 14028, 14086), Rionegro: (MLS 2077, 2210), San Pedro: (IBSP 5315 holotype, MLS 202–03, 207–09, 280, 1765, 1781, 1783, 1842–43, 1856, 1878, 1941, 2356, 2939, 2941, ICN 10628–31), San Pedro, La Lana: (MLS 2412, 2955), Santa Rosa de Osos: (MLS 1902–04, 1946), Santo Domingo: (MLS 230), Sonsón: (ICN 10697, MLS 135). Locality probably in error: Jericó: (MLS 303).
- Atractus lehmanni*. Colombia, Cauca, Popayán: (ICN 1794, 2590, 2613, 10635–36, MLS 1919), Rio Molina: (MLS 2593), Silvia: (MLS 2595, 2681); Valle Del Cauca, Sevilla: (MHUA 1407).
- Atractus loveridgei*. Colombia, Antioquia, Jardin: (CSJ 566), Jericó: (IBSP 7202, 8908, 8916, 10126, MLS 213–16, 218, 220–22, 224–25, 1205). Locality probably in error: San Pedro: (MLS 2355).
- Atractus manizalensis*. Caldas, Manizales: (IAvH 3309–10, MLS 294), Pacorá: (MLS 2216), Villamaria: (MLS 227 holotype, MLS 228 paratype, MLS 146, 2461, 1999), Salamina: (MLS 173, 226, 1777, 1779–80, 2716); Quindío, Armenia: (UQC 01, 05, 08, three specimens UQC not catalogued).
- Atractus matthewi*. Venezuela, Anzoategui, Macizo de Turimiquire, Cerro El Guamal: (EBRG 3952–54 paratypes of *A. matthewi*, EBRG 4453 holotype of *A. nororientalis*, EBRG 4454 paratype of *A. nororientalis*, MNRJ 8127); Monagas, Caripe: (MBUCV 1669); Sucre, Serrania de Turimiquire: (EBRG 3793).
- Atractus melanogaster*. Colombia, Caldas, without locality: (MLS 296), Pensilvania: (MLS 235, 237); Tolima, Cajamarca, Vereda La Palma: (ICN 10029–34), Ibagué: Ibanasca: (CZUT-R 117), Pastales: (CZUT-R 10), Toche: (CZUT-R 09).
- Atractus melas*. Colombia, Chocó, Quibdo: (MLS 2537); Valle del Cauca: (UV-C 8533).
- Atractus michelae*. Venezuela, Mérida, Canagua, Pueblos del Sur: (ULABG 2672 holotype), Táchira, Uribante, Caparo: (CV-ULA 4445 paratype, CV-ULA 2918).
- Atractus mijaresi*. Venezuela, Mérida, Mucurubá, Rangel: (ULABG 4697 holotype).
- Atractus modestus*. Ecuador, western Ecuador (NHM 1946. 1.6.30, holotype); Azuay, Molleturo: (QCAZ 1167); Cotopaxi, San Francisco de Las Pampas: (QCAZ 002, 201–03, 641, 1216, 2100), Pitaló: (QCAZ 6548); Morona-Santiago, Plan de Milagro: (QCAZ 2013); Pichincha, without locality: (QCAZ 1134).
- Atractus multicinctus*. Colombia: Valle del Cauca, Buenaventura, Queremal: (ICN 7075).
- Atractus nicefori*. Colombia, Antioquia, Jardin: (MLS 2940), Jericó: (MLS 229, MLS 231–33, 239–40, 275, 279, 297, 302, 2635–37), Támesis: (MUJ 02–03).
- Atractus nigricaudus*. Peru, Pasco, Huáchon, Pugmaray: (MHNSM 19175, 19180, 19183, 19194), Oxapampa, San Alberto: (MHNSM 17761), Paucartambo, Agomarca: (MHNSM 18108, 18113, 18192–93, 19047–48), Aquimarca: (MHNSM 17811–12, 17825–27, 17842–44, 17854, 17862, 17867–68, 18015, 18101, 18103, 18050, 18105, 18575), Mayabamba: (MHNSM 18051–54), Santa Isabel (MHNSM 18107, 18427–30), Taurapau: (MHNSM 18571), Uchuhuerta: (MHNSM 18609–10, 19046).
- Atractus nigriventris*. Colombia, Boyacá, Chita: (MLS 234 holotype).
- Atractus obesus*. Colombia: Valle Del Cauca: Cali: Parque Nacional Natural Los Farallones: (ICN 2934). Silvania: (IAvH 145, 823–24, ICN 7268), Vereda Santa Rita: (IAvH 17).
- Atractus obtusirostris*. Colombia, Tolima, Ibagué, Pastales: (CZUT-R 12), Toche: (CZUT-R 11), Icononzo: (ICN 2722, 6497), Juntas: (ICN 5669–71), Rio Combeyma: (ZMH-R 4428 syntype).
- Atractus ochrosetrus*. Venezuela, Mérida, Tovar: (ULABG 4698 holotype), Tovar–Guaraque road: (ULABG 4696 paratype).
- Atractus oculotemporalis*. Colombia, Antioquia, Jericó: (IBSP 6390 holotype).
- Atractus pamplonensis*. Colombia, Norte de Santander, Bochalema: (MHNLS not cataloged), Chinacotá: (MLS 2338–39), Chitagá, Chucarima: (MLS 273–74, 248, 287, 300), Cutilla: (MHUA 14163–64), El Diamante: (MLS 1920), Labateca: (ICN 10715–18), La Donjuana: (MLS 248), Ocaña: (MLS 277), Pamplona: (IBSP 9192 holotype, IBSP 9190–91, 9040, 9021 paratypes, MLS 241–44, 247, 250–52, 276, 2001–02, 2364, 2369–71, 2458–60, 2688–2694, 2711–15, 2753–69, MLS without number, ICN 10719–24), Toledo: (MLS 249, 253, 2700–03).
- Atractus paucidens*. Ecuador, Pichincha, Santo Domingo de Los Colorados: (MZUSP 7703), Finca La Esperanza: (EPN 8729–32).
- Atractus roulei*. Ecuador, Azuay, Hierba Mala: (QCAZ 6256).
- Atractus sanctaemartae*. Colombia: Cesar, Valledupar, Nabusímaque: (ICN 10807–10); Magdalena, Ciudad Perdida: (IAvH 2290), Montes, Cuchilla, Hierbabuena: (ICN 5663–65 paratypes), San Sebastian de Rábago: (ICN 10711), Santa Marta, above San Lorenzo Station: (ICN 10625), Sierra de San Lorenzo: (ICN 2756 holotype, ICN

2757–67 paratypes). Locality in error: Huila, Acevedo, Parque Natural Nacional Cueva de los Guacharos: (IAvH 8302).

Atractus sanguineus. Colombia, Antioquia, Porce: (MLS 2513), San Pedro: (CSJ 518), Yarumal: (formally CSJ 232, now CSJ 517 holotype, MLS 1784–85), Yolombo: (MHUA 1432).

Atractus tamaensis. Venezuela, Táchira, Junin, Betania: (MHNLS 8307 holotype, MHNLS 8301, 8303–06 paratypes).

Atractus taphorni. Venezuela, without locality: (IBSP 25785); Mérida, El Chorotal: La Azulita road: (CV-ULA 1838), La Carbonera: (CV-ULA 6417), Libertador: (ULABG 3909).

Atractus trivittatus. Colombia, Boyacá, Chita: (MLS 258 holotype, MLS 286); Casanare, La Salina: (MLS 257, 290, 2638–39, 2706–07); Norte de Santander, Arboledas: (MLS 269), Gramalote: (MLS 137), La Donjuana: (MLS 245–46).

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

Atractus ventrimaculatus. Venezuela, Mérida, Betania: (ULABG 2409), La Princesa: (ULABG 6701–02), Libertador, El Valle: (MHNLS 897–901), Mérida: (NHM

1946. 1.5.15 holotype), La Mucus, Parque Nacional Sierra Nevada: (MBUCV 2016), Pico Humbo: (EBRG 4052).

Atractus cf. vertebralis. Peru, Cusco, Urubamba, Machu-Pichu: (MHNSM 3100); Huancavelica, Tayacaya: (MHNSM 2849).

Atractus vertebrolineatus. Colombia, Norte de Santander, Ocaña: (MLS 184 holotype).

Atractus vittatus. Venezuela, Aragua, without locality: (IBSP 41082), Colonia Tavor: El Limón road: (EBRG 700, 2959, 4059, 4092); Distrito Capital, Caracas: (MBUCV 703), El Junquito–Colonia Tavor road: (MBUCV 415), El Limón: Las Aguaitas: (MHNLS 5159).

Atractus wagleri. Colombia, Santander, Floridablanca: (UIS-R 71), Piedecuesta, Guatigurá: Vereda Viricute: (UIS-R 281), San Vicente de Chucuri: (MHUA 14504).

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