Rediscovery and redescription of the rare Andean snake *Atractus modestus*

Paulo Passos[1], Diego F. Cisneros-Heredia[2] & David Salazar-V.[3]

[1]*Departamento de Vertebrados, Museu Nacional/UFRJ, Rio de Janeiro, Brazil*

[2]*College of Biological and Environmental Sciences, Universidad San Francisco de Quito, Quito, Ecuador*

[3]*Museo de Zoología, Centro de Biodiversidad y Ambiente, Escuela de Biología, Pontificia Universidad Católica del Ecuador, Quito, Ecuador*

Atractus modestus was described based on a single specimen from western Ecuador, and since its original description there have been no further records for this species. During the examination of Ecuadorian collections, we found additional specimens of this poorly known snake. In this paper, we redescribe the holotype of *A. modestus*, describe the hemipenis and report new specimens, localities, and data on meristic and morphometric variation in the species. We also compare and diagnose this species from all others members of this highly diverse genus.

Key words: Colubridae, Dipsadinae, hemipenis, taxonomy

INTRODUCTION

The fossorial snake genus *Atractus* Wagler, 1828, is distributed widely throughout South America, occurring from Panamá to northern Argentina (Giraudo & Scrocchi, 2000; Myers, 2003). This genus is closely related to *Adelphicos* Jan, 1862 and *Geophis* Wagler, 1830 (Downs, 1967; Savage, 1960; Fernandes, 1995a,b; Zaher, 1999), and comprises nearly 100 species, most of them described based on small type series with highly restricted distribution (Fernandes, 1995a,b; Passos et al., 2005). Currently, the taxonomic status of several species is chaotic, and there are many misidentified specimens in herpetological collections (Fernandes & Puorto, 1993). While examining Ecuadorian collections, we found some specimens of a rare Andean species, *Atractus modestus* Boulenger, 1894. This species was described based on a single specimen from "Western Ecuador", and since its original description, there have been no further records for the species. Herein, we redescribe the holotype of *A. modestus*, describe the hemipenis and report new specimens, localities, and data on meristic and morphometric variation for the species. In addition, comparisons between *A. modestus* and all members of this highly diverse genus are provided.

MATERIALS AND METHODS

Specimens examined are listed in the appendix and are deposited in the following collections: Colección Boliviana de Fauna (CBF), La Paz, Bolivia; DFCH collection, Universidad San Francisco de Quito (DFCH–USFQ), Quito, Ecuador; Escuela Politécnica Nacional (EPN), Quito, Ecuador; Fundación Herpetológica G. Orcés (FHGO), Quito, Ecuador; Instituto Butantan (IBSP), São Paulo, Brazil; Museo Noel Kempff Mercado (MNKR), Santa Cruz de La Sierra, Bolivia; Museo de la Universidad Major de San Marcos (MHNSM), Lima, Peru; Museo de Zoología, Pontificia Universidad Católica del Ecuador (QCAZ), Quito, Ecuador; Museu Nacional, Universidade Federal do Rio de Janeiro (MNRJ), Rio de Janeiro, Brazil; Natural History Museum (NHM), London, UK.

Terminology for *Atractus* cephalic shields follows Savage (1960), while the method of counting ventral scales follows Dowling (1951). Regarding the condition of the loreal scale we recognize three states: short – when the length of scale is approximately equal to the height, with anterior and posterior margins the same height; moderate – when the scale is slightly (less than two times) longer than high, with anterior and posterior margins approximately the same height; long – when the length of the scale is twice (or more) as long as high, with the anterior margin higher than the posterior. Terminology for hemipenis description follows Dowling & Savage (1960), as augmented by Myers & Campbell (1981) and Zaher (1999). Techniques for hemipenis preparation follow Pesantes (1994). Sex was determined by the presence or absence of hemipenes through a ventral incision at the base of the tail. Measurements were taken with an ocular micrometer to the nearest 0.1 mm in a Zeiss (Stemi SV8) stereoscope, except for snout–vent (SVL) and caudal lengths (CL), which were taken with a flexible ruler to the nearest millimetre.

Because segmental counts are known to be sexually dimorphic in *Atractus* (see Savage, 1960; Passos et al., 2005) we used Mann–Whitney *U*-tests to look for statistical differences between sexes. A non-parametric test was used because the data violated the assumptions of univariate normality and homoscedasticity (Zar, 1999). These assumptions were evaluated using Kolmogorov–Smirnov tests and Levene's test, respectively (Zar, 1999). The following characters were employed in the statistical analysis: number of ventrals, number of subcaudals and snout–vent length.

RESULTS

Atractus modestus showed significant sexual dimorphism in the number of ventral ($U_{-2.5}$=0; P<0.05, n=12), subcaudal

Correspondence: Paulo Passos, Departamento de Vertebrados, Museu Nacional/UFRJ, Quinta da Boa Vista, Rio de Janeiro, RJ 20940-040, Brazil. *E-mail:* ppassos@mn.ufrj.br

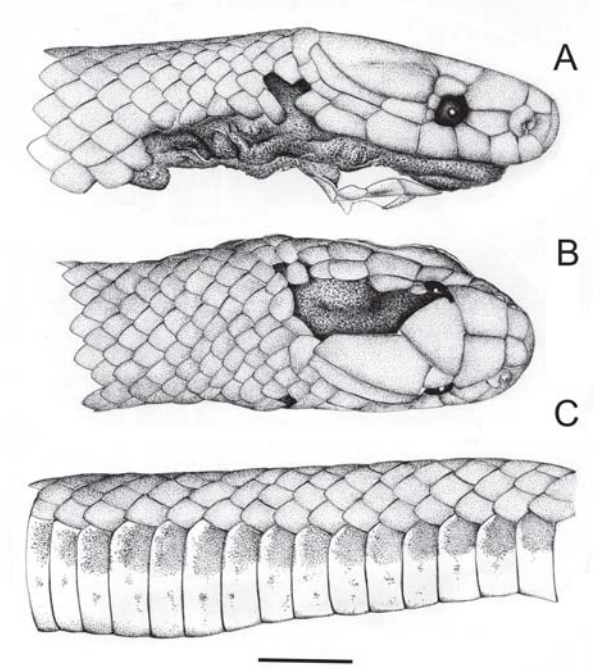

Fig. 1. *Atractus modestus* (holotype, NHM 1946.1.6.30): A) dorsal and B) lateral views of the head, and C) lateral view of the midbody. Scale bar = 5 mm.

($U_{2.5}$=3, P<0.05, n=12) scales, and caudal length ($U_{2.1}$=0; P<0.05; n=10). Therefore, these data are presented separately for males and females.

Atractus modestus Boulenger, 1894 (Figs 1 and 2)

Atractus modestus Boulenger, 1894

Atractus modestus Savage, 1960

Holotype. NHM 1946.1.6.30, adult male specimen, collected by Mr Fraser in western Ecuador. The holotype is poorly preserved; head, neck, and gular region are crushed, showing some darker and shrivelled muscles; dorsal portion of head is lacking the left parietal shield; body and tail (dorsally and ventrally) with small, shrivelled areas lacking the correspondent scales.

Diagnosis. *Atractus modestus* can be distinguished from all species of the genus by the following combination of characters: 1) 17 dorsal scale rows; 2) moderate loreal; 3) 5–8 maxillary teeth; 4) six supralabials; 5) seven infralabials, first four contacting chin shields; 6) nasal completely divided; 7) two postoculars; 8) 155–173 ventral scale rows in males and 174–185 in females; 9) 34–41 subcaudals in males and 26–31 in females; 10) total segmental counts 191–202 in males and 202–216 in females; 11) moderate size, reaching a maximum SVL of 273 mm in males and 328 mm in females; 12) moderate tail (15.5–21.4% SVL in males and 11–12.5% SVL in females); 13) dorsal pattern uniformly chocolate to dark brown with a light nuchal collar and a white paraventral stripe in juveniles.

Comparisons.The only other species of *Atractus* that share a relatively short loreal scale with *A. modestus* are *A. favae* (Filippi, 1846), *A. zidoki* Gasc & Rodrigues, 1979, and the *Atractus elaps* species group, which includes the following currently recognized species: *A. charitoae* Silva, 2004, *A. elaps* (Günther, 1858), *A. franciscopaivai* Silva, 2004, *A. latifrons* (Günther, 1868) and *A. poeppigi* (Jan, 1862). *Atractus modestus* can be distinguished from all these species by having a uniform dark brown dorsal colour pattern reaching the lateral portions of the ventral scales (vs. coral colour pattern with black and white bands ventrally in the *A. elaps* species group and *A. favae*, and with dark white bordered paired dots dorsally in *A. zidoki*).

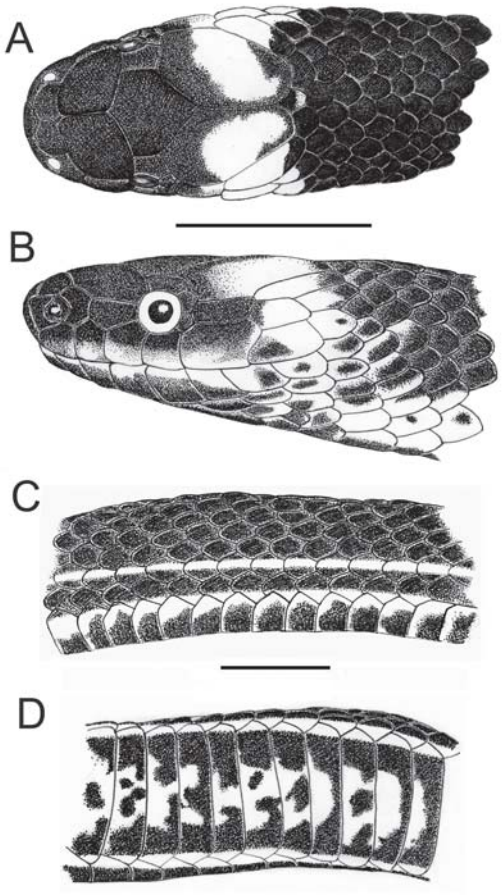

Fig. 2. Juvenile specimen of *Atractus modestus* (QCAZ 1167): A) dorsal and B) lateral views of the head, and C) lateral and D) ventral views of midbody. Scale bar = 5 mm.

Redescription of the holotype. An adult male, SVL 328 mm; CL 51 mm (15.5% SVL); head length 12.3 mm (3.7% SVL) from tip of snout to rictus of mouth; head width 7.1 mm (57.9% head length) at the broadest point; interocular distance 3.9 mm; snout–orbit distance 3.4 mm; head slightly distinct from body; rostral 2.6 mm wide, about one time broader than high, visible from above; internasals 1.2 mm wide, slightly broader than long; internasal suture sinistral relative to prefrontal suture; prefrontals 2 mm wide, slightly broader than long; frontal 3.2 mm wide, slightly broader than long, with a triangular shape in dorsal view; parietals 4.7 mm wide, about twice as long as wide; nasal completely divided; loreal 1.5 mm long, about 1.4 times higher than long; eye diameter 1.2 mm; pupil

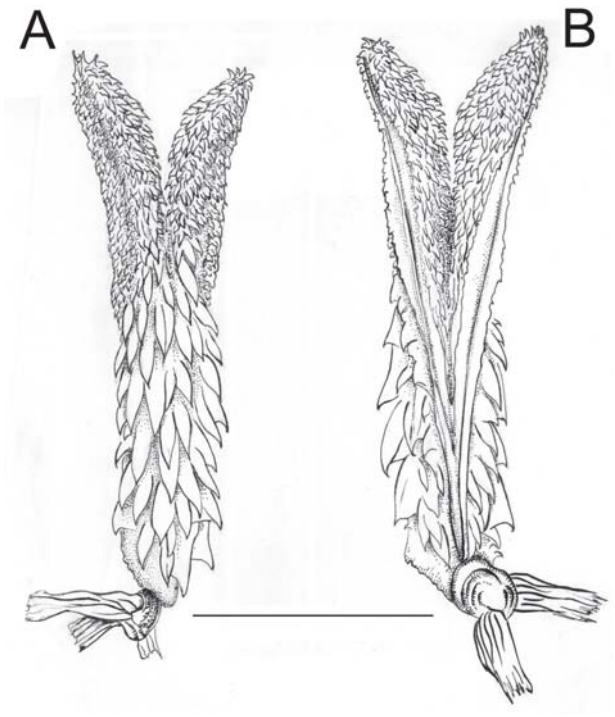

Fig. 3. A) Sulcate and B) asulcate sides of the hemipenis of *Atractus modestus* from Las Pampas, Cotopaxi Province, Ecuador (QCAZ 2100). Scale bar = 5 mm.

round; supraoculars 1.2 mm long, slightly longer than wide; two postoculars, upper slightly higher and broader than lower; temporals 1+2, upper posterior temporal elongate, about six times longer than high, and twice as long as first temporal; six supralabials, 3rd–4th contacting orbit; symphisial 2 mm wide, about twice as broad as long, separated from chin shields by first pair of infralabials; six infralabials, 1st–4th contacting chin shields; anterior chin shields about twice as long as broad; posterior chin shields absent; three series of gular scales; dorsal scales 17/17/17 rows, smooth without apical pits; preventrals 4; ventrals 173; anal plate single; paired subcaudals 37 on the left and 38 on the right side; hemipenis (in situ) extends to the level of 11th and bifurcates at ninth subcaudal.

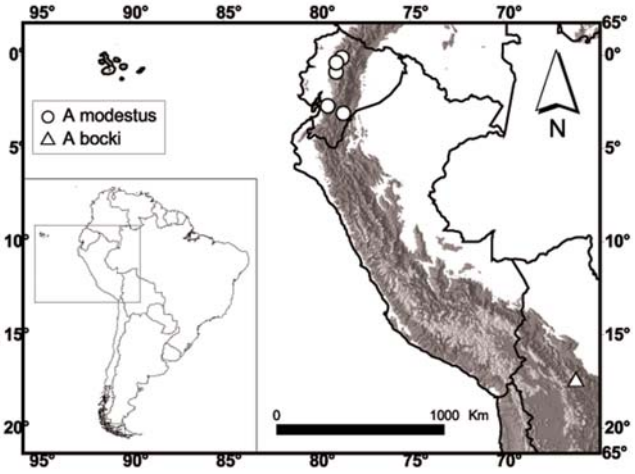

Fig. 4. Geographic distribution of *Atractus bocki* and *Atractus modestus*.

Colour of the holotype in preservative (Fig. 1). Uniformly brown dorsally; this colour extends downward to lateral portion of ventral scales. Gular region and median region of ventral scales uniformly creamish white. Underside of tail entirely black.

Colour of juvenile specimens in preservative (Fig. 2). Dorsal ground colour of head uniformly dark brown, except for a large light (creamish white) collar on the middle of the parietals and the occipital region; dorsum and sides of head dark brown, with ventral portion of supralabials light (creamish white); dorsal ground colour of body uniformly dark brown, except for a regular lateral stripe, between the third and fourth dorsal scale rows, generally half a scale wide; infralabials and gular region spotted with dark brown blotches, mostly on the anterior portion of each scale; ventral scales usually uniformly dark brown, with a light stripe between the first dorsal scale row and the edge of ventrals; ventrals generally with light centre, which forms a barely-defined and irregular middle ventral stripe; venter sometimes entirely black, with a pair of lateral stripes in the paraventral region.

*Hemipenis [everted organ, n=1] (Fig. 3).*The inverted organ extends to the level of the 13th subcaudal, and bifurcates at the level of the 11th; organ non-capitate and strongly bilobed, lobes distinct from the base and exhibiting an attenuate form; each lobe narrowing in the apices, displaying a series of spinules; apices of lobes with distinct spinules projecting upward; margins of sulcus spermaticus stout, bordered by spinules, bifurcating at half of the hemipenial body; branches have centrifugal orientation running medially to the tip of each lobe; hemipenial body covered by enlarged hooked spines, concentrated on asulcate side; spines on sulcate side concentrated laterally; most basal portion of hemipenial body devoid of spines.

Variation. Largest male SVL 273 mm, tail length 51 mm; largest female SVL 328 mm, tail length 51 mm; tail 15.5–21.4% of the SVL in males and 11–12.5% of the SVL in females; six supralabials (*n*=24 sides); ventrals 155–173 (mean=161.1; SD=5.7; *n*=9) in males, 174–185 (mean=180; SD=5.7; *n*=3) in females; subcaudals 34–41 (mean=37.8; SD=2.3; *n*=9) in males, 26–31 (mean=28.3; SD=2.5; *n*=3) in females; dorsal scales of the tail 8–11 (mean=9.87; SD=0.64; *n*=12) in both sexes; temporal formula 1+1 (*n*=3 sides) and 1+2 (*n*=19 sides); hemipenis (inverted organ, *n*=3) extends to 11–13th , and bifurcates at ninth to 11th subcaudal scales; maxillary teeth 5–8 (mean=5.9; SD=1.3; *n*=20, both sides). All remaining characters examined, except for juvenile colour pattern (Fig. 2), were identical to the condition of the holotype.

Distribution (Fig. 4). Atractus modestus was described from the general type locality "Western Ecuador" (Boulenger, 1894). Savage (1960) pointed out the poor reliability of Fraser's localities. However, herein, we confirmed that the species inhabits the Pacific versant of the Andes of Ecuador at altitudes between 2400 (at Pilaló) and 2560 m (Molleturo) and probably lower elevations

(see Cisneros-Heredia & Touzet, 2004), with records in the provinces of Pichincha, Cotopaxi and Azuay. There is one specimen from Plan de Milagro at Morona-Santiago Province, but in our opinion, additional specimens are required in order to confirm the occurrence of *A. modestus* on the Atlantic versant of the Andes of Ecuador. This species inhabits plant formations associated with Mountain Cloud forests (*sensu* Sierra, 1999) in the temperate zoogeographic zone (*sensu* Albuja et al., 1980).

Remarks. Amaral (1929) examined the holotype of *Atractus bocki* Werner, 1909 housed in the Zoologisches Museum, Universität Hamburg, and suggested that the taxon was a junior synonym of *A. modestus*. However, Peters & Orejas-Miranda (1970) did not follow Amaral's assertion and listed *A. bocki* as a valid species. Regrettably the holotype of *A. bocki* was destroyed during the Second World War (J. Hallermann, pers. comm.), and new specimens are needed to clarify the status of this species. However, the original description of *A. bocki* mentions a spotted dorsal pattern and 50 subcaudal scales, which differ strongly from the uniformly greyish-brown dorsal pattern and 26–41 subcaudal scales in both sexes of *A. modestus*. Furthermore, *A. bocki* is known only from the type locality (Cochabamba, Bolivia), which is very distant from the range of *A. modestus* (see Fig. 3). Therefore, in the absence of detailed information on *A. bocki* and based on its original description, we prefer to recognize this as a valid species.

DISCUSSION

Savage (1960) suggested that *Atractus modestus* is unique among the Ecuadorian *Atractus*, along with the *Atractus elaps* group, in bearing a relative short loreal scale. However, our reanalysis of loreal condition in the genus reveals that reduced loreals are also found in the *Atractus trilineatus* species group (*sensu* Savage, 1960). At least two more species included in the *Atractus trilineatus* group (*A. favae* and *A. zidoki*; see Hoogmoed, 1980) and *A. modestus* (allocated here to that group, see below) exhibit this condition. As the reduction of the loreal scale is an apomorphic state in the phylogeny of *Atractus*, shared with the putatively monophyletic *A. elaps* species group (Fernandes, 1995b), we hypothesize that this character state may have evolved more than once in *Atractus*.

The hemipenis of *Atractus modestus* was described by Savage (1960) as having a differentiated condition, which defines the *Atractus badius* species group (see Savage, 1960). In this account Savage (1960) noticed also that the hemipenial body of *A. modestus* is abruptly demarcated from the distal portion of the organ (= lobes *sensu* Zaher, 1999) by having large spines, while the distal portion is covered with small papillate structures. Although the occurrence of papillae on the distal portion of the hemipenis is in disagreement with our observations, Savage's description was based on the examination of the retracted hemipenis from the holotype of *A. modestus* made by J. C. Battersby (Savage, 1960, p. 54). We examined the retracted hemipenis from the holotype of *A. modestus* and found that the right organ was dissected in its basal and medial portions, showing the enlarged spines. However, the lobes were not dissected and consequently, the distal structures are not evident in the retracted hemipenis of the holotype. Further, as stressed by Schargel & Castoe (2003), the hemipenis descriptions based on the retracted hemipenis may be unable to reveal certain features that are best appreciated on fully everted organs. In this sense, the hemipenis of *A. modestus* fails to conform to the differentiated condition as described by Savage (1960). Therefore, as *Atractus modestus* shares the undifferentiated condition as well as other morphological traits with the *Atractus trilineatus* species group (e.g. colour pattern with paraventral stripe), and because there is no previous phylogenetic hypothesis for the genus, we transferred this taxon to the *Atractus trilineatus* group.

Several authors have noted the apparent rarity in scientific collections of most *Atractus* species (Pérez-Santos & Moreno, 1988; Giraudo & Scrocchi, 2000; Schargel & García-Pérez, 2002; Hoogmoed & Prudente, 2003; Myers, 2003; Jorge da Silva Jr. et al., 2005), which could be related to their secretive habits (e.g. Jorge da Silva Jr. et al., 2005) or to altitudinal endemism (e.g. Schargel & García-Péres, 2002). Despite the apparent rarity of some species, intensive field studies (Martins & Oliveira, 1993; Dixon & Soini, 1977) or the re-examination of collections (Fernandes & Argôlo, 1999; Fernandes et al., 2000, Cisneros-Heredia, 2005), have revealed that some South American *Atractus* may be somewhat common within their distributional range. At the moment, a large number of *Atractus* specimens remain misidentified or unidentified in herpetological collections (P. Passos, pers. obs.). Revision of this material should improve our knowledge on these puzzling snakes, and could better estimate the natural diversity of the genus.

ACKNOWLEDGEMENTS

The authors thank C. McCarthy and M. Wilkinson (NHM), J. Aparício (CBF), F. L. Franco (IBSP), L. Gonzales and R. Montaño (MNKR), A. Almendáriz (EPN), L. Coloma (QCAZ) and J. Santa-Gadea (MHNSM) for allowing the examination of the specimens under their care, and J. Hallermann (ZMH) for information about the holotype of *Atractus bocki*. We are grateful to P.R. Nascimento and A. Chiesse for rendering the line arts and to P.R. Gonçalves for providing us with a topographic basin from Ecuador. We thank D. S. Fernandes, R. Fernandes, J.P. Pombal Jr., A. Markezich and W. Schargel for helpful comments on the manuscript. Financial support to the senior author was provided by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and Coordenação de Aperfeiçoamento de Pessoal de Ensino de Nível Superior (CAPES). D.F.C.H.'s work was financed by Universidad San Francisco de Quito, Ma. E. Heredia and L. Heredia.

REFERENCES

Albuja, L., Ibarra, M., Urgilés, J. & Barriga, R. (1980). *Estudio Preliminar de los Vertebrados Ecuatorianos*. Quito: Escuela Politécnica Nacional Published.

Amaral, A. (1929). Contribuição ao conhecimento dos ophidios do Brasil IV. Lista remissiva dos ophidios do Brasil. *Memórias do Instituto Butantan* 4, 69–126 [dated 1930].

Boulenger, G.A. (1894). *Catalogue of the Snakes in the British Museum (Natural History), Vol. 2*. London: Trustees of the British Museum.

Cisneros-Heredia, D.F. (2005). Rediscovery of the Ecuadorian snake *Atractus dunni* Savage, 1955 (Serpentes: Colubridae). *Èasopis Národního Muzea, Øada pøírodovì dná* 174, 109–116.

Cisneros-Heredia, D.F. & Touzet, J.-M. (2005). Distribution and conservation status of *Bothrops asper* (Garman, 1884) in Ecuador. *Herpetozoa* 17, 135–141.

Dixon, J.R. & Soini, P. (1977). The reptiles of the Upper Amazon Basin, Iquitos region, Peru. Part II. Crocodilians, turtles, and snakes. *Contributions in Biology and Geology of the Milwaukee Public Museum* 12,1–91.

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 characters. *Zoologica* 45, 17–28.

Downs, F.L. (1967). Intrageneric relationships among colubrid snakes of the genus *Geophis* Wagler. *Miscellaneous Publications, Museum of Zoology, University of Michigan* 131,1–193.

Fernandes, R. (1995a). A new species of snake in the genus *Atractus* (Colubridae: Xenodontinae) from northeastern Brazil. *Journal of Herpetology* 29, 416–419.

Fernandes, R. (1995b). *Phylogeny of the Dipsadine Snakes*. Ph.D. dissertation. Arlington: University of Texas.

Fernandes, R. & Argôlo, J.S. (1999). Rediscovery of *Atractus guentheri* (Wücherer, 1861) (Serpentes, Colubridae). *Boletim do Museu Nacional, (N.S.), Zoologia* 397, 1–5.

Fernandes, R., Freire, E.M.X. & Puorto, G. (2000). Geographic variation of the Brazilian Atlantic rain forest snake *Atractus maculatus* (Günther, 1858), with revalidation of *Rhabdosoma zebrinum* Jan, 1862 (Serpentes: Colubridae). *Boletim do Museu Nacional, (N.S.), Zoologia* 419,1–8.

Fernandes, R. & Puorto, G. (1993). A new species of *Atractus* from Brazil and the status of *A. guentheri* (Serpentes: Colubridae). *Memórias do Instituto Butantan* 55, 7–14.

Giraudo, A.R. & Scrocchi, G.J. (2000). The genus *Atractus* (Serpentes: Colubridae) in north-eastern Argentina. *Herpetological Journal* 10, 81–90.

Hoogmoed, M.S. (1980). Revision of the genus *Atractus* in Surinam, with the resurrection of two species (Colubridae, Reptilia). Notes on the herpetofauna of Surinam VII. *Zoologische Verhandelingen* 175, 1–47.

Hoogmoed, M.S. & Prudente, A.L.C. (2003). A new species of *Atractus* (Reptilia: Ophidia: Colubridae: Dipsadinae) from the Amazon forest region in Brazil. *Zoologische Mededelingen* 77, 425–439.

Jorge da Silva Jr., N., Silva, H.R.L., Ribeiro, R.S., Souza, I. & Souza, C.A. (2005). Uma nova espécie do gênero *Atractus* Wagler, 1928 (Colubridae: Dipsadinae) do cerrado do Brasil central. *Papéis Avulsos de Zoologia* 45, 33–39.

Martins, M. & Oliveira, M.E. (1993). The snakes of genus *Atractus* Wagler (Reptilia: Squamata: Colubridae) from the Manaus region, central Amazonia, Brazil. *Zoologische Mededelingen* 67, 21–40.

Myers, C.W. (2003). Rare snakes – five new species from eastern Panama: reviews of northern *Atractus* and southern *Geophis* (Colubridae: Dipsadinae). *American Museum Novitates* 3391,1–47.

Myers, C.W. & 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.

Passos, P., Fernandes, R. & Zanella, N. (2005). A new species of *Atractus* (Serpentes: Colubridae) from south Brazil. *Herpetologica* 61, 209–218.

Pérez-Santos, C. & Moreno, A.G. (1988). Ofidios de Colombia. *Museo Regionale di Scienze Naturali, Monografie* 6, 6–512.

Pesantes, O. (1994). A method for preparing hemipenis of preserved snakes. *Journal of Herpetology* 28, 93–95.

Peters, J.A. & Orejas-Miranda, B. (1970). Catalog of the neotropical Squamata. Part 1. Snakes. *Bulletin United States National Museum* 297, 1–347.

Savage, J.M. (1960). A revision of the Ecuadorian snakes of the colubrid genus *Atractus. Miscellaneous Publications, Museum of Zoology, University of Michigan* 112,1–86.

Schargel, W.E. & Catoe, T.A. (2003). The hemipenis of some snakes of the semifossorial genus *Atractus* with comments on variation in the genus. *Journal of Herpetology* 37, 718–720.

Schargel, W.E. & García-Pérez, J.E. (2002). A new species and a new record of *Atractus* (Serpentes: Colubridae) from the Andes of Venezuela. *Journal of Herpetology* 36, 398–402.

Sierra, R. (1999). *Propuesta Preliminar de un Sistema de Clasificación de Vegetación para el Ecuador Continental*. Quito: INEFAN/GEF/BIRF & EcoCiencia Published.

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: 21 March 2006

APPENDIX

Specimens Examined

Atractus elaps (*n*=46).

Brazil: Unknown locality: (IBSP 20314). AMAZONAS: Borba: (MNRJ 1523).

Ecuador: Western Ecuador: (NHM 1946.1.6.45, holotype). Eastern Ecuador: Unknown locality: (EPN 6892, EPN not cataloged). MORONA-SANTIAGO: Macas (DFCH-USFQ AA018); Makuma: (FHGO 754, 1913). NAPO: Alto Napo: (EPN 6856, 8686); Archidona: (QCAZ 2101); Río Huataracu: (EPN 8687); Tena (DFCH-USFQ AA009). ORELLANA: Balsayacu, Parque Sumaco (QCAZ 6502); Fuerte: (EPN 7324); Loreto, El Tená: (EPN 8688); Tiputini Biodiversity Station: (DFCH-USFQ AE010-014); Parque Nacional Yasuní: (EPN 2536, QCAZ 3249, 3959); Río Coca (QCAZ 440). PASTAZA: Mera: (EPN 1175); Montalvo, Andoas: (EPN 758); Nueva Vida, Misión Agua Santa: (QCAZ 345); Puyo: (QCAZ 1277); Río Bobonaza (EPN 8678–83); Río Tallín, Alto Bobonaza (EPN 8675–77); Sarayacu–Pucayacu (EPN 8685). SUCUMBíOS: Lagartococha: (EPN 8689); Lago Ágrio: (EPN 5781); Shushufindi: (QCAZ 3303). ZAMORA-CHINCHIPE: Namacuntza vía Nambija (FHGO 675). Erroneous localities: PICHINCHA: Al Occidente: (EPN 8692). EL ORO: Santa Rosa: (EPN 8690–91).

Atractus latifrons (*n*=18).

Brazil: Unknown locality: (MNRJ 20315, IBSP 20315). AMAZONAS: Balbina Hydreletric Plant: (UFC 1367); Benjamin Constant: (MNRJ 729–732, 1289, 1517–20, 1522); Manaus: (MNRJ 726–28). Rio Purus (MNRJ 633). RONDÔNIA: Samuel Hydroeletric Plant: (UFC 1430–32).

Bolivia: BENI: Río San Martin between Río Blanco and Río Negro (MNKR 595). SANTA CRUZ: Guarayos, Urubichá: (MNKR 3436–39), Río San Martin (MNKR 505); Nuflo de Chaves: Oquinquia: Río San Martín: (MNKR 1021); Velasco: (MNKR 218, 520).

Peru: LORETO: Maynas, Iquitos: (MHNSM 2250, 2292), Mishana: Rio Nanay: (MHNSM 2590, 2616); Pebas: (MNRJ 2977, 2979, 2981); Requema (MHNSM 2884).

Atractus modestus (*n*=12).

Ecuador: Western Ecuador (NHM 1946. 1.6.30, holotype). AZUAY: Molleturo [ca 2560 m]: (QCAZ 1167). COTOPAXI: Las Pampas [ca 2100 m]: (QCAZ 002, 201–3, 641, 1216, 2100); Pilaló [ca 2400 m]: (QCAZ 6548). MORONA-SANTIAGO: Plan de Milagro (QCAZ 2013). PICHINCHA: Unknown locality: (QCAZ00 1134).

Atractus poeppigi (*n*=7).

Brazil: AMAZONAS: Alto Rio Negro: (MNRJ 10837).

Peru: AMAZONAS: Bagua: (MHNSM 2380, 2447). PASCO: Cerro de Pasco: Oxapampa: (MHNSM 3485). SAN MARTIN: San Martín: (MHNSM 3133, 3337), Tarapoto: (MHNSM 3278).