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Taxonomic revision of the Brazilian Atlantic Forest *Atractus* (Reptilia: Serpentes: Dipsadidae)

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Abstract

Dipsadine snakes of the genus *Atractus* are endemic to the Neotropical region, occurring from Panama to Argentina. Currently, the taxonomic status of most species of the genus is unclear and previous attempts of taxonomic revisions have been local in scale. In this paper we evaluate the taxonomic status of the Brazilian Atlantic Forest species of *Atractus* based on meristic, morphometric, maxillary dentition, and hemipenis characters. Quantitative and qualitative analyses suggest the recognition of one new species (*A. caete* sp. nov.) from the state of Alagoas, another (*A. francoi* sp. nov.) from the mountain regions of the states of Rio de Janeiro and São Paulo, and the synonymy of *A. kangueryensis* with *A. thalesdelemai*. Specimens previously assigned to *A. taeniatus* in Argentina and Brazil are here considered *A. paraguayensis*. A key to the Atlantic Forest *Atractus* is provided and three new species groups are proposed for some cis-Andean *Atractus*, mainly on the basis of hemipenial morphology: the *A. emmeli*, *A. maculatus*, and *A. pantostictus* species groups.

Key words: *Atractus*, Atlantic Forest, South America, Morphology, Geographical variation, Taxonomy

Resumo

As serpentes dipsadíneas do gênero *Atractus* são endêmicas da região Neotropical, ocorrendo do Panamá à Argentina. Atualmente, o posicionamento taxonômico da maioria das espécies do gênero é confuso e as tentativas de revisões taxonômicas foram limitadas à escala regional. Neste trabalho, nós avaliamos o posicionamento taxonômico das espécies de *Atractus* da Floresta Atlântica brasileira por meio de caracteres merísticos, morfométricos, de dentição maxilar e morfologia do hemipênis. Análises quantitativas e qualitativas sugerem o reconhecimento de uma nova espécie (*A. caete* sp. nov.) do estado de Alagoas e outra (*A. francoi* sp. nov.) da região serrana dos estados do Rio de Janeiro e São Paulo e a

sinonimização de *A. kangueryensis* com *A. thalesdelemai*. Ademais, os espécimes previamente assinalados a *A. taeniatus* na Argentina e Brasil são aqui considerados *A. paraguayensis*. Uma chave é fornecida para as *Atractus* da Floresta Atlântica e três novos grupos de espécies são propostos para algumas *Atractus* cisandinas, baseado principalmente na morfologia do hemipênis: os grupo de espécies de *A. emmeli*, *A. maculatus* e *A. pantostictus*.

Palavras-chave: *Atractus*, Floresta Atlântica, América do Sul, Morfologia, Variação geográfica, Taxonomia

Introduction

The dipsadine genus *Atractus* is endemic of the Neotropical region, occurring primarily on the mainland from 11° North to 35° South, from sea level to 4,500 meters elevation, in almost all South American biomes (Passos 2008). The genus comprises small to moderate-sized snakes, having secretive (semi-fossorial or cryptozoic) lifestyles and feeding on earthworms, arthropods, and mollusks (Cunha & Nascimento 1993; Martins & Oliveira 1993, 1999; Cisneros-Heredia 2005). *Atractus* is a diverse genus of snakes closely related to *Adelphicos* and *Geophis* (Savage 1960; Downs 1967; Fernandes 1995b; Passos 2008), including about 130 valid species, many of them known only from their type specimens and sometimes having restricted distributions (Passos & Fernandes 2008; Prudente & Passos 2008; Passos & Arredondo 2009; Passos *et al.* 2009a,b,c,d,e,f). To date, the taxonomic status of several species remains unclear, and all attempts of taxonomic revisions have been limited to a local scale (Savage 1960; Roze 1961; Cunha & Nascimento 1993; Martins & Oliveira 1993; Giraud & Scrocchi 2000; Myers 2003; Silva 2004; Esqueda & La Marca 2005). The major problem with *Atractus* taxonomy is that geographical variability data as well as sexual and/or ontogenetic variations are unknown for most currently recognized taxa (Passos *et al.* 2009 a,c,e). Lack of comparative specimens and poor knowledge of intraspecific variation led some authors to recognize new taxa on the basis of slight nuances in colour pattern and/or meristic characters (e.g., Scrocchi & Ceï 1991; Alvarez *et al.* 1992; Bernal-Carol & Roze 1996). These taxa, in many cases, were shown to not be diagnosable from previous recognized species after the examination of large series of specimens (e.g., Passos *et al.* 2009d; Fernandes 1996; Passos *et al.* 2009c).

The Brazilian Atlantic Forest is one of the most diverse and threatened ecosystems on Earth, with only about 7% of its original coverage remaining (Morellato & Haddad; Oliveira-Filho & Fontes 2000). Its remarkable diversity has been attributed to the presence of a rich flora with unique physiological adaptations to unusual biophysical characteristics (Pessenda *et al.* 2009). The biome is composed of two major vegetation types, the coastal forest or Atlantic Rainforest (*sensu strictu*) and the tropical seasonal forest or Atlantic Semi-deciduous forest (Morellato & Haddad 2000). The Atlantic Rainforest covers mostly low to medium elevations (≤ 1000 m) of the eastern slopes of the mountain chain that runs subparallel and close to the coastline from southern to northeastern Brazil; the Atlantic Semi-deciduous forest extends across the plateau (usually > 600 m) in the centre and southeastern interior of the country (Morellato & Haddad 2000). The Atlantic Rainforest experiences warm and wet climate without a well defined dry season, while a seasonal climate with relative severe dry season (generally from April to September) predominates over the distribution of the Atlantic Semi-deciduous forest (Morellato & Haddad 2000). The biome lies almost entirely within Brazil, with a small portion extending to northeastern Argentina and southeastern Paraguay (Oliveira-Filho & Fontes 2000). Currently, 11 species of Atlantic Forest *Atractus* are recognized (*A. guentheri*, *A. kangueryensis*, *A. maculatus*, *A. paraguayensis*, *A. potschi*, *A. ronnie*, *A. serranus*, "*A. taeniatus*", *A. thalesdelemai*, *A. trihedrurus*, and *A. zebrinus*), and two other are distributed on transitional zones between Atlantic Forest and general open formations in central and southern Brazil (*A. pantostictus* and *A. reticulatus*) (Fernandes 1996; Passos *et al.* 2005b; Cacciali *et al.* 2007; Passos *et al.* 2007b).

The aim of this study is to provide a comprehensive revision of the Atlantic Forest *Atractus* in order to evaluate the validity of the currently know taxa, and to present accurate diagnostic characters and data on intraspecific and interspecific variation for all recognized species in the area.

Material and Methods

Material and Techniques

We examined more than 1,500 specimens housed in the following institutions: Argentina—Universidad Nacional del Nordeste (UNNEC), Corrientes; Austria—Naturhistorisches Museum Wien (NMW), Vienna; Brazil—Coleção Zoológica Gregório Bondar (CZGB), Centro de Pesquisas do Cacau, Ilhéus, BA; Departamento de Zoologia da Universidade Federal do Rio Grande do Sul (DZURGS), Porto Alegre, RS; Instituto Butantan (IBSP), São Paulo, SP; Museu de Zoologia da Universidade de São Paulo (MZUSP), São Paulo, SP; Instituto Vital Brazil (IVB), Niterói, RJ; Departamento de Zoologia da Universidade Federal do Rio de Janeiro (DZUFRJ), Rio de Janeiro, RJ; Laboratório de Zoologia dos Vertebrados, Universidade Federal de Ouro Preto (LZVUFOP), Ouro Preto, MG; Museu de Ciência e Tecnologia da Pontifícia Universidade Católica do Rio Grande do Sul (MCP), Porto Alegre, RS; Museu de Ciências Naturais da Fundação Zoobotânica do Rio Grande do Sul (MCN), Porto Alegre, RS; Museu de Ciências Naturais da Pontifícia Universidade Católica de Minas Gerais (MCNR), Belo Horizonte, MG; Museu de História Natural Capão da Imbuia (MHNCI), Curitiba, PR; Museu de Zoologia da Universidade Estadual de Feira de Santana (MZUEFS), Feira de Santana, BA; Museu de Zoologia da Universidade Estadual de Santa Cruz (MZUESC), Ilhéus, BA; Museu de Zoologia da Universidade Federal da Bahia (MZUFBA), Salvador, BA; Museu de Zoologia da Universidade Federal de Alagoas (MUFAL), Maceió, AL; Museu de Zoologia da Universidade Federal do Ceará (CHUFC), Fortaleza, CE; Museu Nacional, Universidade Federal do Rio de Janeiro (MNRJ), Rio de Janeiro, RJ; Museu Zoológico Augusto Ruschi, Universidade de Passo Fundo (CRUPF), Passo Fundo, RS; Germany—Museum für Naturkunde, Universität Humboldt (ZMB), Berlin; UK—Natural History Museum (BMNH), London; and USA—Museum of Zoology, University of Michigan (UMMZ), Ann Arbor. Specimens and localities are listed in Appendix I, and include all Atlantic Forest species of *Atractus*. Type series of all Atlantic Forest species of *Atractus* were examined, except for *Atractus kangueryensis* and *A. zebrinus* (the latter was seemingly destroyed in the Second World War), which were not available to us.

Diagnostic characters used here are based on meristics, morphometrics, maxillary dentition, and hemipenis morphology. Terminology for *Atractus* cephalic shields follows Savage (1960), whereas the method of counting ventral scales follows Dowling (1951). Terms used to describe the condition of the loreal scale follow Passos *et al.* (2007b). Sex was determined by the presence or absence of hemipenes through a ventral incision at the base of the tail. Measurements were taken with a dial caliper to the nearest 0.1 millimeter under an optical stereoscope, except for snout-vent (SVL) and caudal lengths (CL), which were taken with a flexible ruler to the nearest millimeter. Body and caudal size terminology follow Passos *et al.* (2009f). Measurements for paired cephalic shields were taken only on the right side of the head. Terminology for hemipenis descriptions follow Dowling and Savage (1960), Myers and Campbell (1981), and Zaher (1999). Techniques for hemipenis eversion from preserved specimens follow Pesantes (1994), Myers and Cadle (2003), and Dowling (2004). Maxillae were examined *in situ* by a narrow latero-medial incision between supralabials and the maxillary arch. Tissues covering the maxillary arch were removed and teeth as well as empty sockets were counted. Terminology for teeth and maxillary conditions follow Passos *et al.* (2009f). Females having flaccid oviducts, oviductal eggs, and/or ovarian follicles > 1 mm (modified from Shine 1988), and males having opaque and convoluted testes (Shine 1994) were considered mature.

Statistical Analyses

We used multivariate statistical methods, in order to quantitatively assess variation within and between defined groups and across the whole sample. We defined each group based on the currently recognized species that show sufficient samples according to assumptions of normality and homoscedasticity. When sample sizes were adequate we partitioned groups (= currently recognized species) into geographically defined subpopulations, with the explicit purpose of evaluating geographical distinctiveness. On the other hand, due to the large number of *Atractus* species and in the face of robust diagnostic characters (e.g., 15 or 17 dorsal scale

rows; banded, striped or uniform colour pattern; capitate or non-capitate hemipenis), the multivariate analyses were performed considering putative closely related (most similar) taxa or geographically nearest populations only. We performed multivariate statistical analyses in all species for which we had an adequate sample. However, we present results only for the few species in which these analyses were actually important to understand the morphological variation patterns.

We verified secondary sexually dimorphic characters through univariate analysis of variance (see below) to each group. Nevertheless, although the samples size for some groups was limited, we decided to always consider sexes separately because of the presence of strong sexual dimorphism in meristic and morphometric characters in most species of this genus (Savage 1960; Passos *et al.* 2005; Passos *et al.* 2007b). We evaluated the assumptions normality and homoskedasticity with Kolmogorov-Smirnov and Levene's tests respectively (Zar 1999).

We used univariate (ANOVA) and multivariate (MANOVA) variance analyses to evaluate differences among group centroids (Zar 1999). We performed planned comparisons through Tukey test for unequal sample sizes (Spjøtvoll & Stoline 1973), in order to determine which original variables discriminate groups (Sokal & Rohlf 1995). We performed a discriminant function analysis (DFA) in order to segregate groups defined *a priori*, and a principal component analysis (PCA) when groups were not earlier established. Both techniques have been widely used in snake taxonomy with satisfactory results (e.g., Fernandes *et al.* 2004; Passos *et al.* 2005; Henderson *et al.* 2009; Passos & Fernandes 2009).

We projected the first two discriminant functions onto orthogonal axes and computed 95% confidence regions from the simulation of 1,000 pseudoreplicate data matrices obtained by parametric bootstrap (Efron 1979). Because DFA requires assumption of equivalency in covariance matrices, as well as normality in the data distribution within each group (Manly 2000), we used the bootstrap method to access the variance bias, as well as for assessing robustness of the obtained results. All discriminant function loadings are portrayed as vector correlations (directional cosines), which are estimated for each character by correlations with projection scores across individuals (Wright 1954; Strauss 1985).

All statistical inference was performed with a significance level of 5% ($\alpha = 0.05$). We performed discriminant analyses with MATLAB 4.2c for Windows (MathWorks 1994), and variance analyses, assumption tests, and graphics with STATISTICA 6.1 for Windows (StatSoft 2002). We estimated missing data with the *estgroup* function in MATLAB 4.2c (MathWorks 1994), in which empty cells are computed based on a variance/covariance matrix for each group. We excluded individuals or variables having 30% or more missing data. Characters that violated the normality assumption were excluded from the analyses.

We used the following non-transformed variables on statistical inference: number of ventral scales (**VENT**); number of subcaudal scales (**SBCD**); number of supralabial scales (**SUPR**); number of infralabial scales (**INFR**), number of infralabials contacting chinshields (**IFCH**), number of gular scale rows (**GULA**), number of prefrontals (**PREV**), SVL/CL ratio (**SVCLr**), SVL/body diameter ratio (**SVLD**); and number of maxillary teeth (**MATH**).

Scope and Style of the Study

The Atlantic Forest as understood here follows mostly the morphoclimatic domains of Ab'Sáber (1977), and the floristic composition as defined and discussed by Oliveira-Filho and Fontes (2000). Most of the previously forested areas of the region have been transformed into cultivated or pasture fields, or in open formations. Consequently, *Atractus* species previously occurring in transitional zones and/or along Pampas, Campos Sulinos, and Cerrado core areas have expanded their distribution into Atlantic Forest limits (e.g. *A. reticulatus* and *A. pantostictus*). Moreover, Semi-deciduous Forests and Cerrado biome share several elements to each other, particularly at generic and familial levels of floristic composition (Oliveira-Filho & Fontes 2000). We therefore included these two taxa in the present study.

For ease of comparison, species accounts mostly follow traditional taxonomic revisions of snakes (e.g., Peters 1960; Savage 1960; Downs 1967; Myers 1974). The subheading “Variation” concerns meristic and morphometric data only. Nevertheless, we extend the range of variation for characters recently reported in the literature (Cacciali *et al.* 2007 and Loebman *et al.* 2009) in diagnosis. Other character variation is discussed in appropriate subheadings (e.g., colour pattern, maxillary dentition, hemipenis morphology). The subheading “Diagnosis” reports mostly data within our main examined sample taken from preserved specimens, and colour in life is reported here only when relevant to diagnosis of a species. In the case of ontogenetic variation in colour pattern, we describe juvenile colouration under a separate subheading. Where necessary, statistical results are discussed in “Remarks”, where taxonomic history and other relevant data on the species are also commented. Taxa are treated in alphabetical order and lists of synonyms refer only to changes, nomenclatural acts carried out, and/or important references for a given species, so that they do not represent a comprehensive list of the names cited in the literature.

Species Accounts

Atractus caete sp. nov.

Figs. 1, 2A, 3A–B

Holotype: Adult female, MNRJ 16936 (formerly IVB 2983), collected on 1986 by A. R. Melgarejo, municipality of Quebrângulo (09°19'S, 36°28'W, ca. 360 m), state of Alagoas, Brazil.

Diagnosis: *Atractus caete* is distinguished from all congeners by the following combination of characters: (1) 17/17/17 smooth dorsal scale rows; (2) two postoculars; (3) long loreal; (4) temporals 1+2; (5) usually six supralabials, third and fourth contacting orbit; (6) seven infralabials, first four contacting chinshields; (7) seven maxillary teeth; (8) three gular scale rows; (9) four preventrals; (10) 160 ventrals in the single female; (11) 16?–19 subcaudals; (12) dorsum uniformly black; (13) venter beige anteriorly, becoming gradually brown from the 15th ventral in adults, and cream marked with brown laterally in sub-adults; (14) moderate body size, female reaching 376 mm SVL; (15) small tail size on female (8.5% SVL).

Comparisons: Among all congeners, *A. caete* shares 17 dorsal scale rows, dorsal colour pattern uniformly black, and at least the posterior region of the venter of adults dark brown with posterior margin of ventral scales having pale (beige) pigmentation only with *A. duidensis*, *A. serranus*, *A. steyermarki*, and *A. trihedrurus*. *Atractus caete* differs from these four species by having six supralabials and seven maxillary teeth (vs. seven supralabials in *A. serranus*, *A. steyermarki*, and *A. trihedrurus*, five maxillary teeth in *A. steyermarki* and eight to ten in *A. duidensis*, *A. serranus*, and *A. trihedrurus*).

Regarding sympatric or parapatric species, *A. caete* differs from *A. maculatus* and *A. potschi* by having dorsum uniformly black in juveniles and adults, belly with lateral margins of ventrals marked with brown in juveniles and almost uniform brown in adults, and six supralabials (vs. dorsal ground colour cream with black transversal bands, blotches, or dots in juveniles and adults, venter uniformly creamish white, and seven supralabials in both species). *Atractus caete* is somewhat similar to the central Brazilian *A. albuquerquei* and *A. edioi*, in which the supralabials are reduced to five or six (apparently by fusion of the third and fourth scales), the dorsum mostly brown or black, and having three gular scale rows. However, the new species differs from both by having 17 dorsal scale rows, seven infralabials with first four contacting chinshields, single postdiastemal tooth, and lateral maxillary process poorly developed (vs. 15 dorsals, six infralabials with first three contacting chinshields, two postdiastemal teeth in both species, and lateral process moderately developed in *A. edioi* and well developed in *A. albuquerquei*).

Description of the holotype: Adult female, SVL 376 mm, CL 32 mm (8.5% SVL); body diameter 6.4 mm (1.7 % SVL); head length 13.4 mm (3.6% SVL); head width 6.3 mm (47% head length); interorbital distance 4.5 mm; rostro-orbital distance 4.1 mm (90% interorbital distance); naso-orbital distance 3.2 mm; cervi-

cal constriction barely distinct; head slightly arched in lateral view, round in dorsal view; snout truncate in lateral view, round in dorsal view; rostral sub-triangular in frontal view, 2.0 mm wide, 1.1 mm high, barely visible in dorsal view; internasal 0.8 mm long, as long as wide; internasal suture sinistral with respect to prefrontal suture; prefrontal 3.0 mm long, 2.6 mm wide; supraocular sub-trapezoidal, 1.0 mm long, about as long as wide; frontal triangular, 3.1 mm long, 3.8 mm wide; parietal 4.6 mm long, twice as long as wide; nasal divided; nostril located between prenasal and postnasal; postnasal 0.8 mm high, twice higher than long; loreal

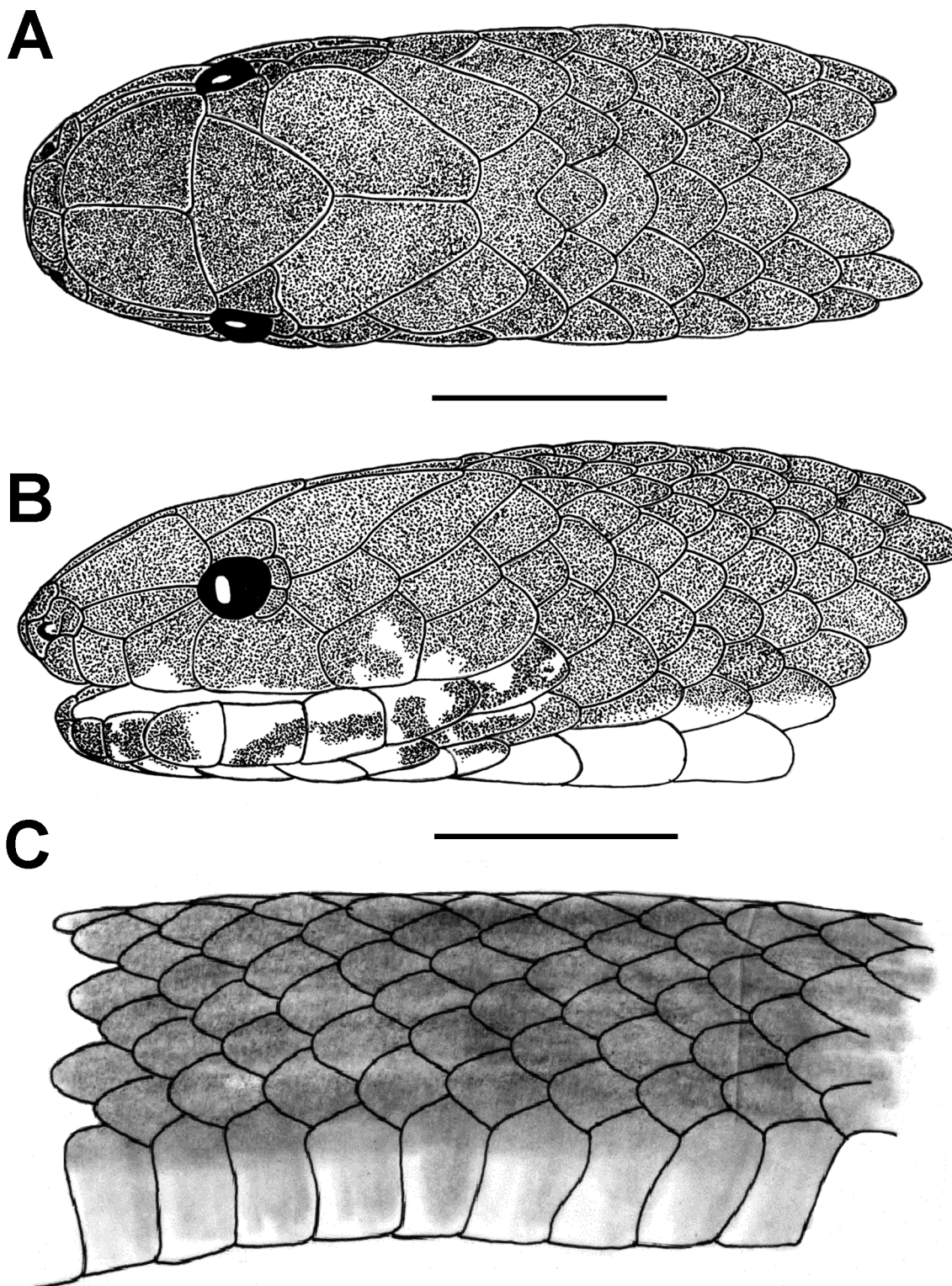


FIGURE 1. Dorsal (A) and lateral (B) views of head, and lateral view of body (C) of the holotype of *Atractus caete* sp. nov. (MNRJ 16936). Scale = 5 mm.

2.6 mm long, 0.6 mm high, contacting second and third supralabials; eye diameter 1.2 mm; pupil subelliptical; two postoculars; upper postocular slightly higher (0.5 mm) and longer (0.4 mm) than lower postocular; temporals 1+2; anterior temporal 2.1 mm long, twice as long as high; upper posterior temporal elongate (3.6 mm), three times longer than wide; six supralabials, third and fourth contacting orbit; second supralabial higher than first and lower than third; sixth supralabial higher and longer than remaining supralabials; symphyisial triangular, 1.9 mm wide, about three times broader than long; seven infralabials, first four contacting chinshields; first pair of infralabials in contact behind symphyisial, preventing symphyisial/chinshield contact; chinshields 3.7 mm long, about three times longer than wide; three gular scale rows; four preventrals; 160 ventrals; 19 (left side) and 20 (right side) subcaudals; 17/17/17 smooth dorsal scale rows; dorsals lacking apical pits, supra-anal tubercles, and keels; midbody diameter 5.7 mm; 10 dorsal scale rows at the level of second subcaudal; anal gland four subcaudals long; caudal spine short, robust, and rhomboid (Fig. 1).

Maxillary arch: Arched in dorsal view, with six prediastemal and one postdiastemal teeth; prediastemal teeth large, well spaced, of similar size, curved posteriorly, angular in cross section, robust at base, narrower on the apices; maxillary diastema moderately long; postdiastemal teeth half size of prediastemal teeth; lateral process of maxilla poorly developed, lacking posterior projections.

Colour in preservative: Dorsum of head dark brown, except for pale brown spots on distal portion of prefrontals; head dark brown, except for irregular pale brown dots covering anterior portion of loreal and fourth to sixth supralabials; head uniformly black; symphyisial and first three infralabials spotted with brown, remaining infralabials, chinshields, and preventrals beige; gulars with dark brown dots; venter uniform beige anteriorly, with brown blotches on lateral portions of ventrals from 15th scale; lateral blotches increase progressively in size, collapsing at the level of 20th ventral; posterior to this point venter becomes uniform brown, only with posterior ventral margin pale (creamish brown) pigmented; tail brown with beige dots on posterior suture of subcaudals; dorsum of body uniformly dark brown (Fig. 2A).

Juvenile colouration in life: An immature female (MUFAL not catalogued) has a distinctive juvenile colouration. Dorsum of head uniformly black; ventral margin of supralabials grayish white; gular region uniformly creamish white; venter mostly creamish white, with lateral margin of ventrals dark brown; tail mostly creamish white, with dark brown pigmentation restricted to subcaudal sutures; first four dorsal scales rows dark brown and remaining seven rows uniformly black (Fig. 3A-B).

Etymology: The specific epithet caeté is a Tupi indigenous name, here employed as a noun in apposition alluding to the Atlantic Rainforest remnants (caá = forest; etê = true) where *A. caete* was found. The Tupi word caeté is also the denomination for the extinct anthropophagous group of Brazilian Indians native to the region of the type locality. Portuguese colonizers later exterminated the “Caetés” after the natives captured and devoured Dom Pero Fernandes Sardinha, first bishop of Brazil on July 16 1556.

Distribution: Known only from the municipalities of Quebrângulo (09°19'S, 36°28'W) and Chã Preta (09°15'S, 36°18'W), state of Alagoas, Brazil. *Atractus caete* apparently inhabits small remnant patches of Submontane Rainforest between 300–500 m elevation (Fig. 4).

Remarks: In the course of this study we examined photographs of a second known specimen of *A. caete* (Figs. 3A-B). That individual (MUFAL not catalogued) was collected November 2008 in the municipality of Chã Preta (09°15'S, 36°18'W, ca. 500 m), state of Alagoas, Brazil. Because we had access only to photographs of that specimen we decided to not designate it as paratype of the new species. On the basis of available photographs it is possible to determine that the specimen (probably an immature female) has seven/six (left/right, respectively) supralabials and about 16 subcaudals.

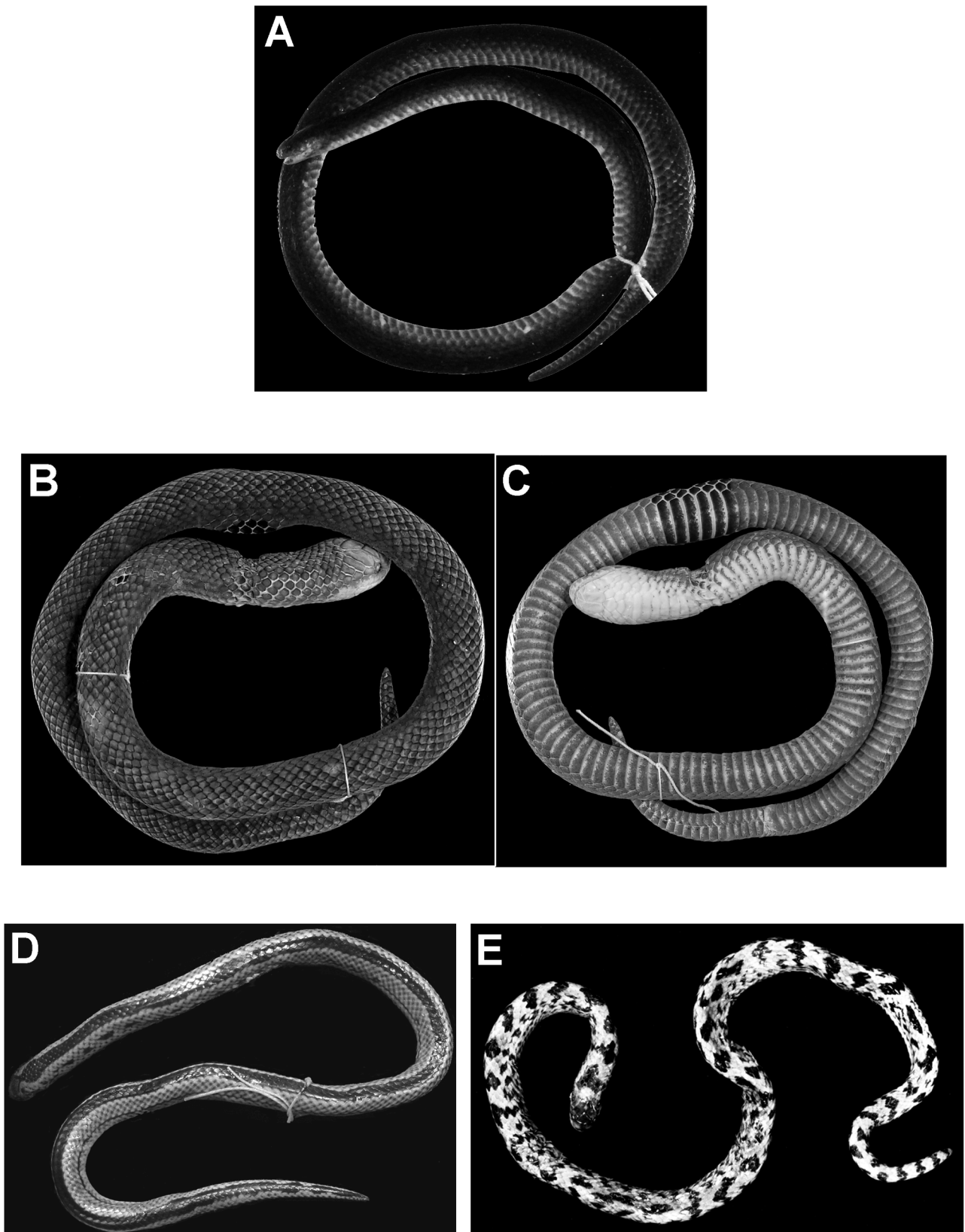


FIGURE 2. General view of the holotypes of (A) *Atractus caete* sp. nov. (MNRJ 16936), (B, C) *A. francoi* sp. nov. (MNRJ 17537), (D) *A. guentheri* (BMNH 1946.1.1.76), and (E) *A. maculatus* (BMNH 1946.1.6.46).

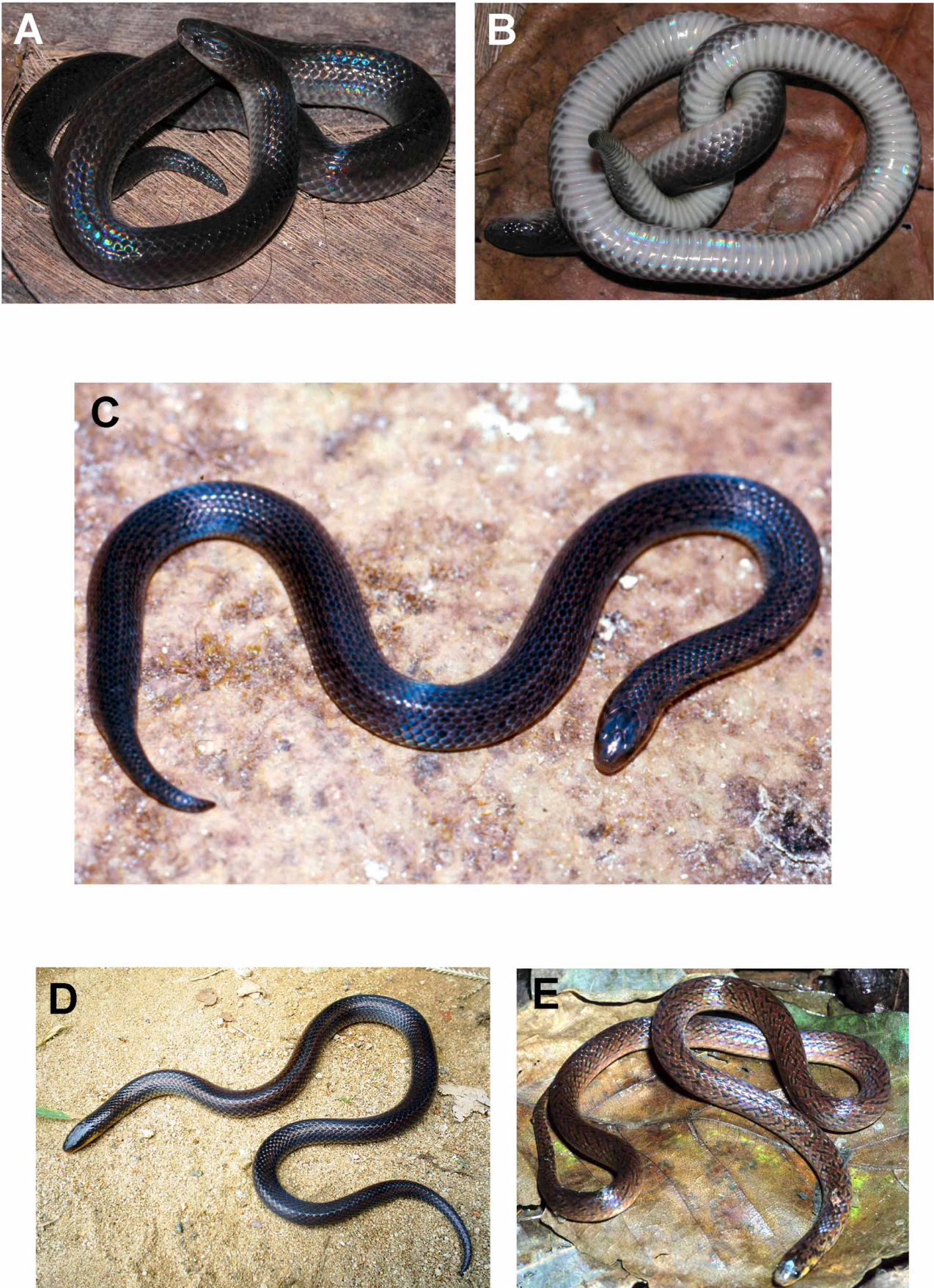


FIGURE 3. General view in life of (A, B) *Atractus caete* sp. nov. from Chã Preta, state of Alagoas, photo by G. Skuk, (C) *A. francoi* sp. nov. from Santa Virgínia, state of São Paulo, photo by P. Hartmann, (D) *A. guentheri* from Ilhéus, state of Bahia, photo by A.J.S. Argôlo, and (E) *A. pantostictus* from Palmas, state of Tocantís, photo by O.A.V. Marques.

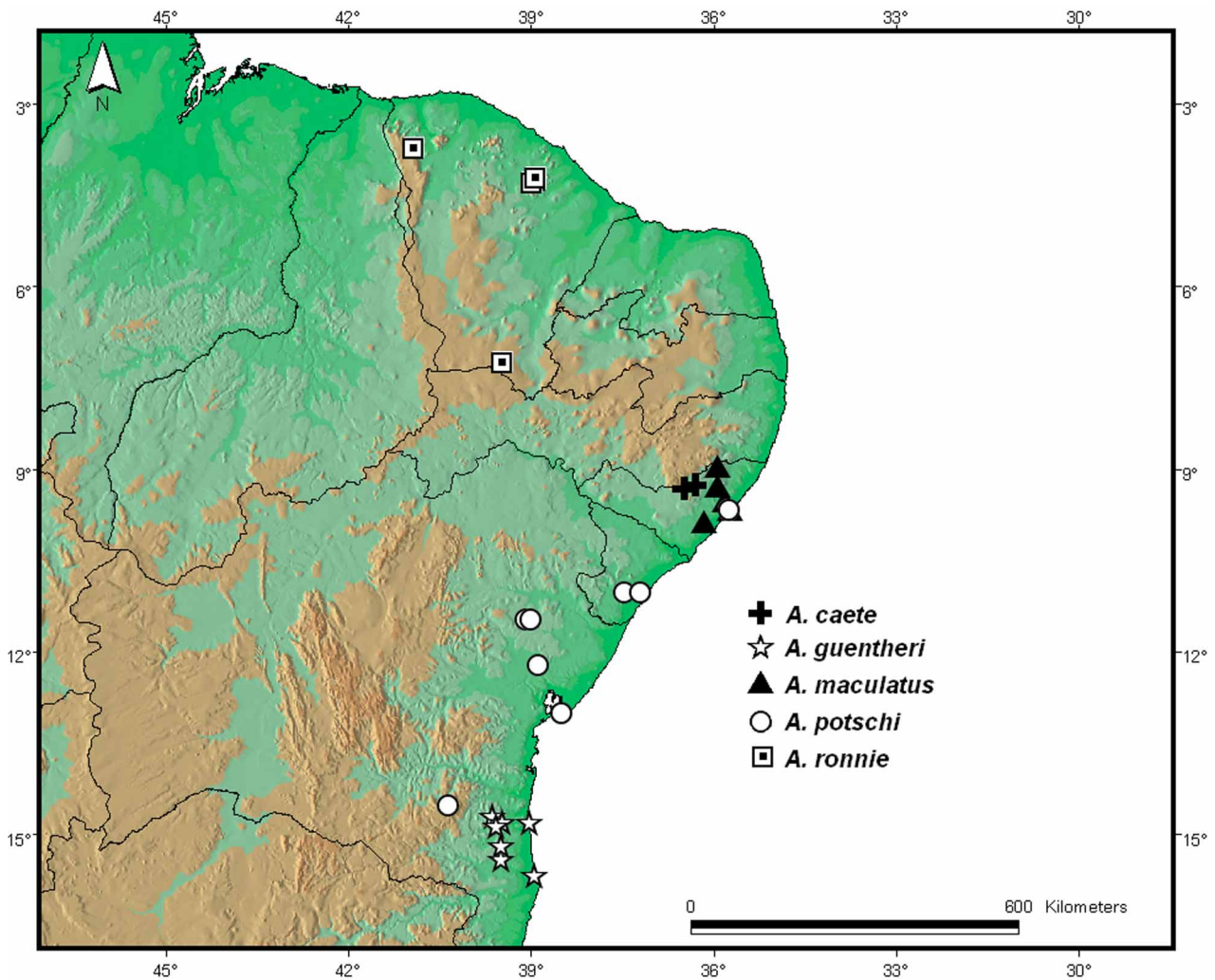


FIGURE 4. Geographical distribution of *Atractus caete*, *A. guentheri*, *A. maculatus*, *A. potschi*, and *A. ronnie*.

Atractus francoi sp. nov.

Figs. 2B–C, 3C, 5

Atractus sp. – Marques, Eterovic & Sazima, 2004; Snakes of the Brazilian Atlantic Forest: An Illustrate Field Guide for the Serra do Mar. Holos, Ribeirão Preto, 1–205:69.

Holotype: Adult male, MNRJ 17537 (formerly DZUFRJ 1742), collected 17 July 2006 by M. C. Carlo, locality Fazenda Recanto, Serra do Piloto (22°50'S, 44°03'W, ca. 600 m), municipality of Mangaratiba, state of Rio de Janeiro, Brazil.

Paratypes:Sixn specimens: adult male (IBSP 72654), municipality of São José do Barreiro (22°38'S, 44°35'W, ca. 600 m), state of São Paulo; an adult male (IBSP 74724), two juvenile females (IBSP 53924, 74723), and adult female (IBSP 74648), collected by P. A. Hartmann, Núcleo SantaVirgínia, Parque Estadual da Serra do Mar, municipality of São Luís de Paraitinga (23°14'S, 45°20'W, ca. 770 m), state of São Paulo; adult female (MNRJ 17536), collected on September 1989 by R. Schasse, municipality of Nova Friburgo (22°16'S, 42°32'W, ca. 915 m), state of Rio de Janeiro.

Diagnosis: *Atractus francoi* is distinguished from all known congeners by the following combination of characters: (1) 17/17/17 smooth dorsal scale rows; (2) two postoculars; (3) moderate loreal; (4) temporals 1+2; (5) usually seven supralabials (six in one side), third and fourth contacting orbit; (6) seven infralabials,

first four contacting chinshields; (7) eight or nine maxillary teeth; (8) two to four gular scale rows; (9) three or four preventrals; (10) 156–164 ventrals in females and 162–164 in males; (11) 14–19 subcaudals in females and 25–30 in males; (12) dorsum uniformly black in adults and brown with scattered small black dots in juveniles; (13) venter beige anteriorly, becoming gradually black after 15th ventral in juveniles and adults; (14) moderate body size, females reaching 473 mm SVL and males 420 mm SVL; (15) tail short in females (6.3–8.6% SVL) and moderate (12.6–13.6% SVL) in males; (16) moderately bilobed, semicapitate, and semicalyculate hemipenis.

Comparisons: Among congeners, *A. francoi* shares 17 dorsal scale rows, dorsal colour pattern uniformly black in adults, venter dark with posterior margin of ventral scales with pale (beige) pigmentation, seven to ten maxillary teeth, and semicapitate and semicalyculate hemipenis [unknown in *A. caete*] only with *A. caete*, *A. serranus*, and *A. trihedrurus*. *Atractus francoi* differs from *A. caete* by usually having seven supralabials (six in one side of one specimen), eight or nine maxillary teeth, and juveniles dark brown with small black dots dorsally and having venter mostly brown (vs. usually six supralabials, seven maxillary teeth, and juvenile with dorsum uniformly black and venter mostly cream); from *A. serranus* and *A. trihedrurus* by having females attain maturity below 500 mm SVL, 152–154 ventrals in males and 162–164 in females, hemipenial lobes smaller than remaining capitulum, asulcate capitulum lacking medial and lobular crests, sulcus spermaticus narrow, basal region of hemipenis lacking moderate hooked spines, and barely distinct ontogenetic change of dorsal colouration (vs. mature females always more than 500 mm SVL, 141–147 ventrals in males and 150–163 in females of *A. serranus* and 136–150 in males and 146–159 in females of *A. trihedrurus*, hemipenial lobes longer than remaining capitulum, asulcate capitulum with conspicuous medial and lobular crests, sulcus spermaticus expanded laterally, basal region of hemipenial with moderate hooked spines, and juveniles of *A. trihedrurus* with banded colour pattern).

Atractus francoi occurs sympatrically with *A. zebrinus* along the coastal mountains of the states of Rio de Janeiro and São Paulo, but differs from it by having the dorsum and venter mostly black (vs. dorsum beige to creamish red with wide transversal black blotches, venter immaculate creamish white).

Description of the holotype: Adult male, SVL 420 mm, CL 53 mm (12.6% SVL); body diameter 9.0 mm (2% SVL); head length 18.2 mm (4.3% SVL); head width 10.8 mm (59.3% head length); interorbital distance 6.9 mm; rostro-orbital distance 4.9 mm (70% interorbital distance); naso-orbital distance 3.7 mm; cervical constriction barely distinct; head slightly arched in lateral view, round in dorsal view; snout truncate in lateral view, round in dorsal view; rostral sub-triangular in frontal view, 3.0 mm wide, 1.0 mm high, little visible in dorsal view; internasal 1.3 mm long, as long as wide; internasal suture sinistral with respect to prefrontal suture; prefrontal 2.2 mm long, 3.5 mm wide; supraocular sub-rectangular, 1.9 mm long, 1.3 mm wide; frontal sub-pentagonal, 4.2 mm long, 4.4 mm wide; parietal 7.1 mm long, 4.0 mm wide; nasal divided; nostril located between prenasal and postnasal; prenasal 1.2 mm high, 0.6 mm long; postnasal 1.5 mm high, 0.9 mm long; loreal 2.5 mm long, 1.0 mm high, contacting second and third supralabials; eye diameter 2.0 mm; pupil subelliptical; two postoculars; upper postocular 1.1 mm high, 0.9 mm long, similar in height and slightly longer than lower postocular; temporals 1+2; anterior temporal 3.5 mm long, 1.3 mm high; upper posterior temporal fragmented into small occipital-like scales and elongate (on the left side), 5.1 mm long, 1.9 mm wide; six (left) and seven (right) supralabials, third and fourth contacting orbit; second supralabial higher than first and lower than third; sixth supralabial higher and seventh longer than remaining supralabials; symphyisial triangular, 2.6 mm wide, 1.2 mm long; seven infralabials, first four contacting chinshields; first pair of infralabials in contact behind symphyisial, preventing symphyisial/chinshield contact; chinshields 5.1 mm long, 2.1 mm wide; two (left) and three (right) gular scale rows; two preventrals; 152 ventrals; 29 (left) and 30 (right) subcaudals; 17/17/17 smooth dorsal scale rows; dorsals lacking apical pits, supra-anal tubercles, and keels; eight dorsal scale rows at the level of second subcaudal; anal gland three subcaudals long; caudal spine short, robust, and rhomboid; retracted hemipenis extends to the level of 11th and bifurcates at 10th subcaudal; six prediastemal and two postdiastemal teeth; maxillary diastema moderate (Fig. 5).

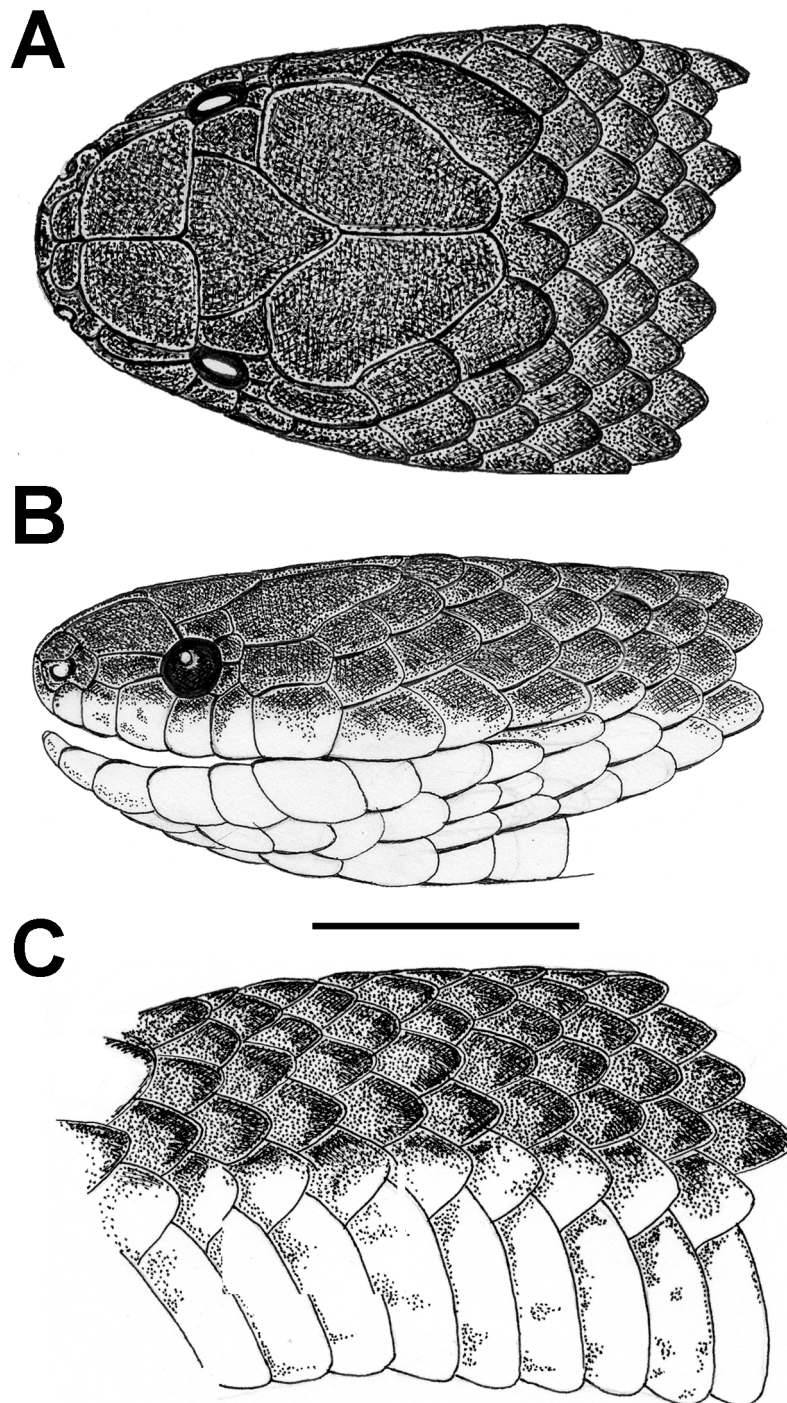


FIGURE 5. Dorsal (A) and lateral (B) views of head, and lateral view of body (C) of the holotype of *Atractus francoi* sp. nov. (MNRJ 17535). Scale = 5 mm.

Maxillary arch: Arched in dorsal view, with six prediastemal and two postdiastemal teeth; prediastemal teeth large, similar in size, curved posteriorly, angular in cross section, robust at base, narrower on the apices; first five teeth generally closely spaced, space between fifth and sixth tooth moderate; maxillary diastema moderate; postdiastemal teeth about half size of prediastemal teeth; lateral process of maxilla moderately developed, lacking posterior projections.

Colour in preservative: Dorsum of head dark brown, except for pale brown spots on distal portion of prefrontals; head dark brown, except for irregular pale brown dots covering anterior portion of loreal and fourth to sixth supralabials; symphyseal and first three infralabials spotted with brown, remaining infralabials,

chinshields, and preventrals beige coloured; gulars with dark brown dots; venter uniform beige anteriorly, with brown blotches on lateral portions of ventrals from 15th scale; lateral blotches increase progressively in size, collapsing at level of 20th ventral; posterior to this point venter becomes uniform brown, with only the posterior margin pale (creamish brown); tail brown with beige dots on posterior suture of subcaudals; dorsum of body uniformly dark brown (Fig. 2B).

Juvenile colouration in preservative: Dorsum of body dark brown with small (one scale long) black dots concentrated on paravertebral region, occasionally in a fragmented barely distinct vertebral black line; first four scale rows lacking marks on both sides of body; venter similar to adults with slightly paler colour.

Juvenile colouration in life: Dorsum of head almost black, with reddish brown blotches concentrated on anterolateral portion of prefrontals and temporal region; lower margins of supralabials beige; dorsal ground colour of body and tail dark reddish brown with small fragmented black dots (Fig. 3C).

Hemipenis morphology (everted organs $n = 2$): Retracted organ bifurcates at level of eighth and extends to level of ninth subcaudal. Everted hemipenis moderately bilobed, semicapitate, semicalyculate; lobes distinct and restricted to distal portion of capitulum; lobes sub-cylindrical, of similar size, with round apices; lobes slightly centrifugally oriented, with length similar to remaining capitulum; lobes and capitulum covered with small papillate calyces; vertical walls of calyces well defined, not arranged in distinct calyculate flounces on both sides of organ; asulcate side of capitulum with irregular calyces lacking lobular and medial crests; capitular groove indistinct on the sulcate side and well defined on the asulcate side of hemipenis; capitulum located just above sulcus spermaticus bifurcation and slightly smaller than hemipenial body; sulcus spermaticus bifurcates at about middle of organ; sulcus spermaticus branches centrifugally oriented, running to tip of lobes; margins of sulcus spermaticus stout and narrow, bordered with papillae from the base to the apices of lobes; hemipenial body sub-cylindrical, covered with moderate hooked spines on laterodistal region of the sulcate side of hemipenis; basal portion of the hemipenial body with small spines only, lacking moderate hooked spines; basal naked pocket restricted to basal portion of hemipenial body; proximal region of hemipenis with an evident constriction with uniformly scattered longitudinal plicae and diffuse spinules (Fig. 6A).

Variation: Largest male 420 mm SVL, 53 mm CL; largest female 475 mm SVL, 40 mm CL; tail 12.6–13.6% ($n = 2$) SVL in males, 6.3–8.6% ($\bar{x} = 7.6$; $SD = 3.5$; $n = 4$) SVL in females; 152–154 ($n = 2$) ventrals in males, 162–164 ($\bar{x} = 161$; $SD = 1$; $n = 3$) in females; 25–30 ($\bar{x} = 27.2$; $SD = 2.1$; $n = 3$) subcaudals in males, 14–19 ($\bar{x} = 16.9$; $SD = 2.1$; $n = 4$) in females; 6 ($n = 1$ side) or 7 ($n = 13$ sides) supralabials; 2 ($n = 2$ sides), 3 ($n = 8$ sides), or 4 ($n = 3$ sides) gular scale rows; 2 ($n = 1$) or 3 ($n = 6$) preventrals; 8 ($n = 6$ sides) or 9 ($n = 2$ sides) maxillary teeth; 8–10 ($\bar{x} = 8.9$; $SD = 0.7$; $n = 14$ sides) dorsal scale rows at the level of second subcaudal; 7.2–9.2 mm ($\bar{x} = 8.6$; $SD = 0.9$; $n = 4$) body diameter; hemipenis bifurcates at level of seventh to 10th and extends to level of eighth to 11th ($n = 2$) subcaudal.

Etymology: This species is dedicated to our friend Dr. Francisco Luís Franco, Curator of Herpetology at Instituto Butantan in Brazil, for his contribution to the systematics of South American snakes, and also for calling our attention to this undescribed species.

Distribution: Highlands of the Serra da Bocaina and Serra dos Órgãos, in Southeastern Brazil between the states of Rio de Janeiro and São Paulo, ranging from Nova Friburgo to São Luís do Paraitinga. *Atractus francoi* inhabits Lower Montane Rainforest between 600–1000 m elevation (Fig. 7).

Remarks: Marques *et al.* (2004) identified and illustrate a juvenile female of *A. francoi* (IBSP 74723, actually paratype) as possibly an undescribed species (= *Atractus* sp.). A female (MNRJ 17536, 473 mm SVL, CL 30 mm) layed six eggs in captivity (R. Fernandes pers. observ.), which corroborates that females of *A. francoi* attain maturity below 500 mm SVL.

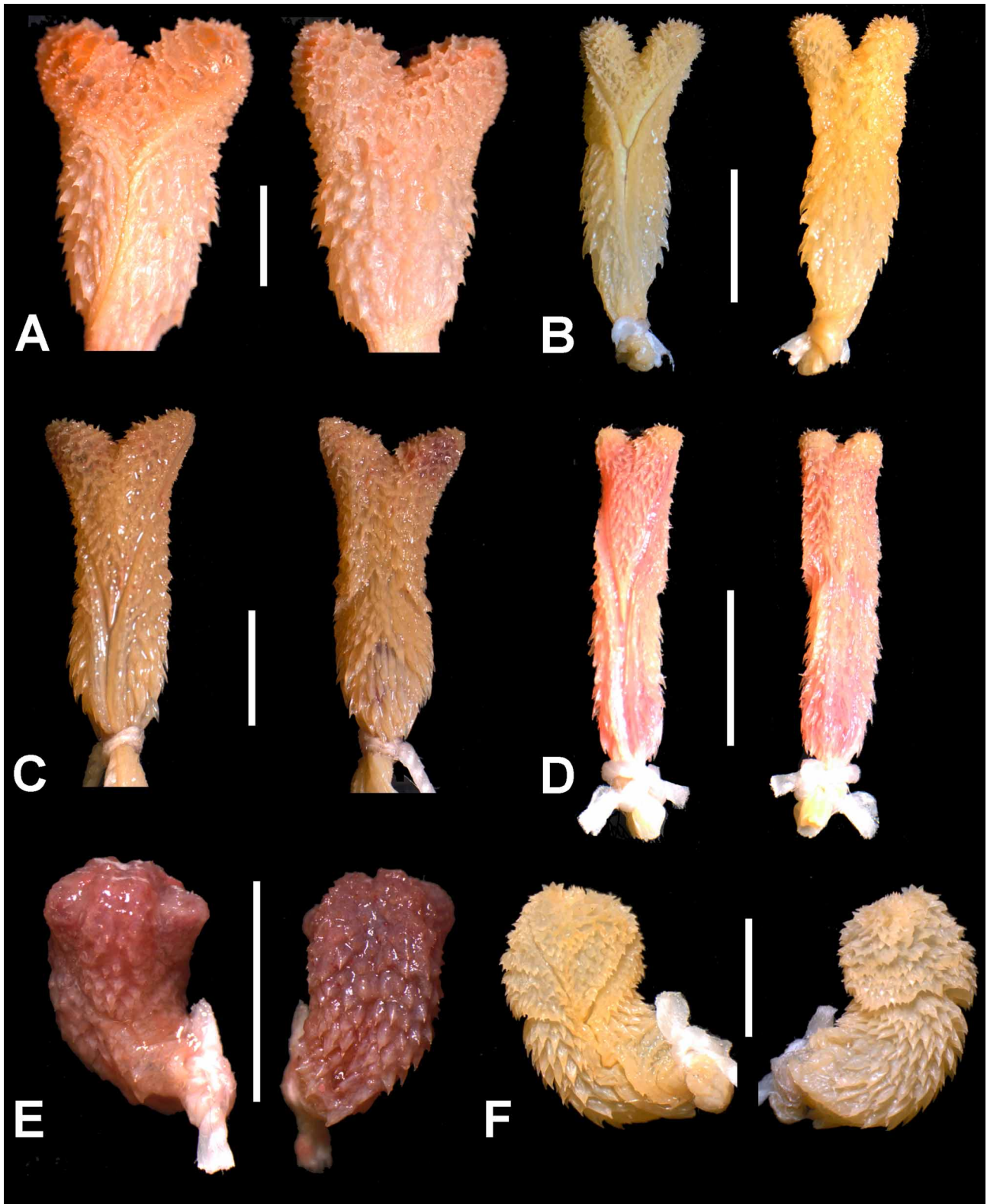


FIGURE 6. Sulcate (left) and asulcate (right) sides of the hemipenis of (A) *Atractus francoi* (IBSP 72654), (B) *A. guentheri* (MNRJ 6710), (C) *A. maculatus* (MNRJ 14197), (D) *A. potschi* (MZUEFS 682), (E) *A. pantostictus* (MNRJ 13195), and (F) *A. paraguayensis* (MNRJ 10123). Scale = 5 mm.

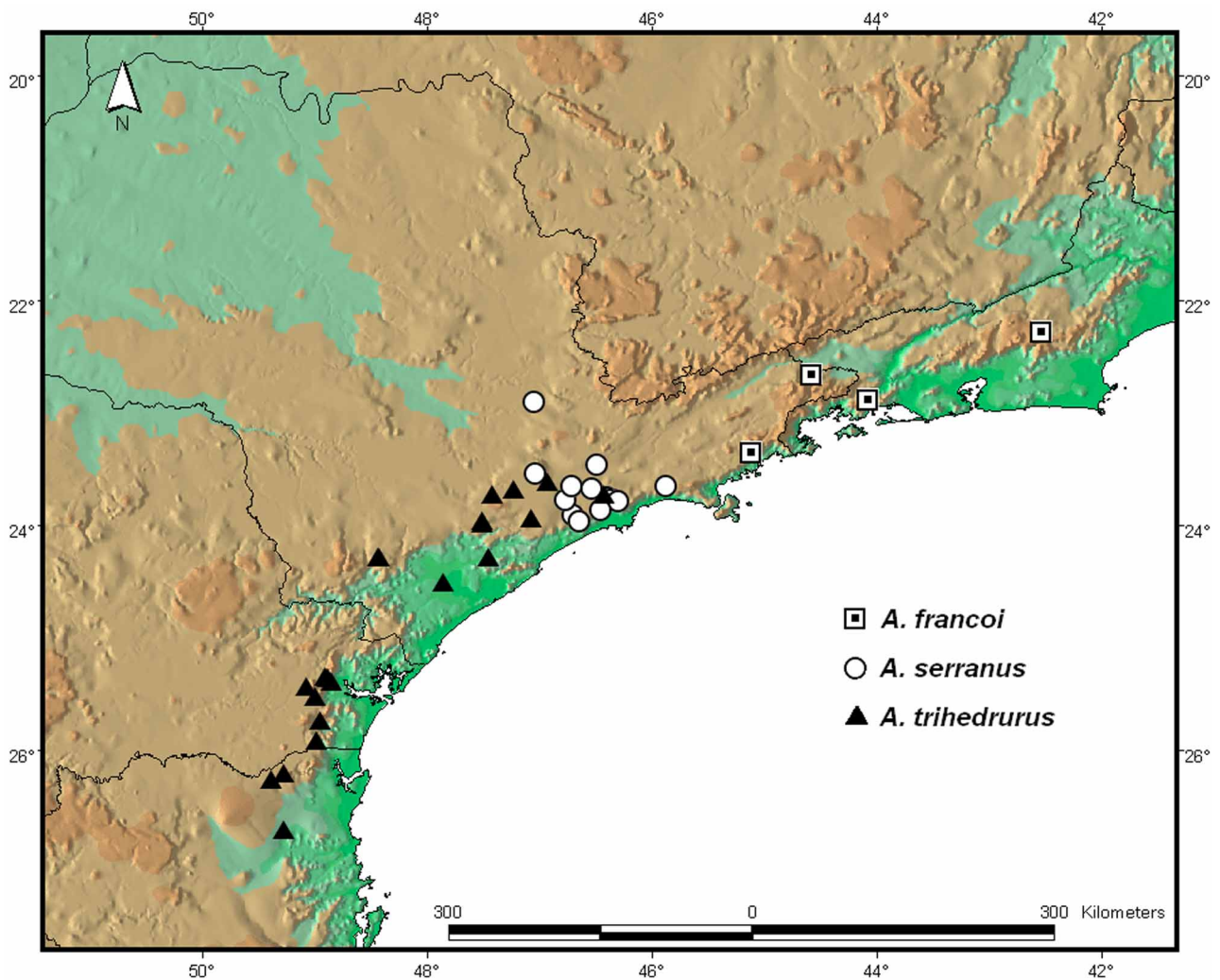


FIGURE 7. Geographical distribution of *Atractus francoi*, *A. serranus*, and *A. trihedrurus*.

***Atractus guentheri* (Wucherer, 1861)**

Figs. 2D, 3D

Geophis Güntheri Wucherer, 1861; Proc. Zool. Soc. London 1861:115.

Atractus guentheri – Boulenger, 1894; Catalogue of the Snakes in the British Museum 2:305. (part.).

Atractus guentheri – Roze, 1961; Acta Biol. Venez. 3:117

Atractus guentheri – Peters & Orejas-Miranda 1970; U.S. Nat. Mus. Bull. 297:29. (part).

Atractus guentheri – Vanzolini, 1986; Adenda and Corrigenda Part 1 Snakes, Catalogue of Neotropical Squamata:3.

Atractus guentheri – Fernandes & Argôlo, 1999; Bol. Mus. Nac. Nov. Ser. Zool. 397:2.

Holotype: Adult male, BMNH 1946.1.1.76 (formerly BMNH 61.3.23.16), municipality of Canavieiras (15°41'S, 38°57'W, sea level), state of Bahia, Brazil (specimen examined).

Diagnosis: *Atractus guentheri* is distinguished from all congeners by the following combination of characters: (1) 17/17/17 smooth dorsal scale rows; (2) two postoculars; (3) moderate to long loreal; (4) temporals 1+2; (5) seven supralabials, third and fourth contacting orbit; (6) seven infralabials, first four contacting chinshields; (7) seven to eight maxillary teeth; (8) three gular scale rows; (9) three preventrals; (10) 147–149 ventrals in females, 136–145 in males; (11) 20–23 subcaudals in females, 29–32 in males; (12) dorsum beige or brown, with a dark brown vertebral (three scales wide) and two dorsolateral lines (one scale wide); (13) venter uniform creamish white in preserved and creamish red to pink in living specimens; (14) moderate body size,

females reaching 437 mm SVL and males 313 mm SVL; (15) moderate tail size in females (9.6–11.1% SVL) and long (16.9–18.1% SVL) in males; (16) moderately bilobed, semicapitate, and semicalyculate hemipenis.

Comparisons: Among all congeners, *A. guentheri* shares 17 dorsal scale rows and dorsum with three conspicuous longitudinal stripes only with *A. emigdioi*. *Atractus guentheri* differs from *A. emigdioi* by having seven to eight maxillary teeth (vs. 10–14).

Description: Head twice as long as wide, flattened in lateral view, round in dorsal view; cervical constriction indistinct; snout truncate in lateral view, round in dorsal view; rostral sub-triangular in frontal view, about twice as broad as high, poorly visible in dorsal view; internasal as long as wide; internasal suture sinistral with respect to prefrontal suture; prefrontal about as long as wide; supraocular sub-rectangular, about twice as long as wide; frontal sub-triangular or pentagonal, broader than long; parietal twice as long as wide; nasal divided; nostril located between prenasal and postnasal; prenasal twice as high as long; postnasal twice as high as long; loreal moderate or long, contacting second and third supralabials; pupil round; usually two postoculars of similar size; upper postocular slightly longer than lower postocular; temporals 1+2; anterior temporal twice as long as high; upper posterior temporal elongate, four times as long as wide; seven supralabials, third and fourth contacting orbit; second supralabial higher than first and shorter than third; sixth higher and seventh longer than remaining supralabials; symphisial triangular, twice as broad as long; usually seven infralabials, first four contacting chinshields; first pair of infralabials in contact behind symphisial, preventing symphisial/chinshield contact; chinshields three times longer than wide; three gular scale rows; three prementals; 17/17/17 smooth dorsal scale rows; dorsals lacking apical pits, supra-anal tubercles, and keels; caudal spine moderate, conical, and acuminate.

Maxillary arch: Arched in dorsal view, with five to six prediastemal and two postdiastemal teeth; first two prediastemal teeth slightly smaller and closely spaced, remaining prediastemal teeth large and moderately spaced; prediastemal teeth curved posteriorly, angular in cross section, robust at base, and narrower on the apices; maxillary diastema moderate spaced; postdiastemal teeth smaller than last prediastemal tooth; lateral process of maxilla poorly developed, lacking posterior projection.

Colour in preservative: Dorsum of head generally dark brown or black; head occasionally beige, with dark brown lateral stripes on posterior region of parietals, connected posteriorly on the mid portion, forming anterior end of the vertebral line; lateral of head brown anteriorly to mid portion of supralabials, frequently with brown covering last three supralabials; lower margin of supralabials, infralabials, chinshields, gular region, and prementals creamish white scattered with small brown dots; venter uniformly creamish white; venter occasionally with dark brown dots concentrated medially; tail creamish white, with small dark brown dots on lateral margins of subcaudals; dorsal ground colour beige or brown reticulated with small dark brown dots; dark pigment concentrated on lateral margins or restricted to anterior part of dorsals; dorsum with three or five longitudinal stripes; vertebral line (three scales wide) black or dark brown, extending from posterior region of parietals to tip of the tail; dorsolateral stripes (one scale wide) black or dark brown above third and fourth scale rows; occasionally there are two additional longitudinal stripes above fifth and sixth scale rows; longitudinal stripes indistinct on melanic specimens (Fig. 2D).

Juvenile colouration in preservative: Juveniles and sub-adults have a beige dorsal ground colour with distinct dorsolateral dark brown longitudinal stripes.

Colour in life: Dorsal ground colour reddish brown or red, with black longitudinal lines; ventral edge of supralabials and mental region creamish yellow or creamish red; venter and tail creamish red, with small black dots on lateral portion of ventrals (Fig. 3D).

Hemipenis morphology (everted organ $n = 1$): Retracted organ bifurcates at level of ninth and extends to the level of 10th subcaudal. Hemipenis moderately bilobed, semicapitate, and semicalyculate; lobes subcylindrical, similar in size, and with slightly centrifugal orientation; lobes restricted to distal portion and slightly smaller than remaining capitulum; capitular groove poorly distinct on the sulcate side and well marked on the asulcate side of hemipenis; capitulum located just above sulcus spermaticus bifurcation; capitulum distinct, of

similar size to hemipenial body; lobes and capitulum uniformly covered with spinulate calyces; calyces arranged transversely forming well-defined transversal flounces on the asulcate side of capitulum; sulcate side of capitulum with irregular and concentrated calyces; sulcus spermaticus divides at middle of organ; sulcus spermaticus with centrifugal orientation, branches running to apices of lobes; sulcus spermaticus margins stout and moderately wide, bordered with spinules from the base to the tip of lobes; hemipenial body subcylindrical, covered with moderate hooked spines; basal naked pocket extends to middle of hemipenial body; basal region of hemipenis with longitudinal plicae and diffuse spinules (Fig. 6B).

Variation: Largest male 313 mm SVL, 55 mm CL; largest female 437 mm SVL, 42 mm CL; tail 16.9–18.1% (\bar{x} = 17.4; SD = 0.5; n = 4) SVL in males, 9.6–11.1% (\bar{x} = 10.1; SD = 0.8; n = 3) SVL in females; 136–145 (\bar{x} = 139.7; SD = 3.8; n = 4) ventrals in males, 147–149 (\bar{x} = 148; SD = 1; n = 3) in females; 29–32 (\bar{x} = 31; SD = 1.5; n = 4) subcaudals in males, 20–23 (\bar{x} = 22; SD = 1.2; n = 4) in females; 6 (n = 2 sides) or 7 (n = 14 sides) infralabials; 1 (n = 1 sides) or 2 (n = 15 sides) postoculars; 6 (n = 4 sides) or 7 (n = 9 sides) maxillary teeth; 8–10 (\bar{x} = 8.9; SD = 0.7; n = 16 sides) dorsal scale rows on the level of second subcaudal; 4.3–11.3 mm (\bar{x} = 7.7; SD = 2.5; n = 7) body diameter; hemipenis bifurcates level with seventh (n = 1) to ninth (n = 1) and extends to the level of 10th (n = 1) or 11th (n = 2) subcaudal.

Distribution: A small portion of coastal Atlantic Rainforest in the southeast of the state of Bahia in Brazil, from Almadina (14°48'S, 39°38'W) eastward to Ilhéus (14°47'S, 39°02'W) and southeastward to Canavieiras (15°41'S, 38°57'W), between Contas and Pardo rivers. *Atractus guentheri* inhabits Lowland Rainforest between 0–300 m elevation (Fig. 4).

Remarks: Wucherer (1861) described *Geophis guentheri* based on a specimen from Canavieiras in southeastern Bahia, Brazil. Boulenger (1894) synonymized *G. guentheri* with *Rhabdosoma univittatum* Jan (described from Caracas, Venezuela), and associate with this species additional material from Rio de Janeiro previously referred to *R. maculatum* by Günther (1858, pp. 241). Subsequent authors (e.g., Amaral 1930a,b) followed Boulenger's concept of *A. univittatus*. Roze (1961) removed *A. guentheri* from the synonymy of *A. univittatus*. Subsequent authors reported *A. guentheri* as a widespread South American species, occurring in the Andes, Amazon forest, and Cerrado (Peters & Orejas-Miranda 1970; Amaral 1978; Pérez-Santos & Moreno 1988). Vanzolini (1986) suggested that *A. guentheri* was probably restricted to forest in eastern Brazil. Fernandes and Puerto (1993) examined the holotype of *A. guentheri* and considered that specimens from the Brazilian Cerrado belong to an undescribed taxon for which they proposed the name *A. pantostictus* (see below). Fernandes and Argôlo (1999) redescribed the holotype of *A. guentheri* and reported new specimens and localities from southeastern Bahia. Fernandes and Argôlo (1999) restricted the concept of *A. guentheri* to striped specimens occurring in the southeast of the state of Bahia of Brazil, which we corroborate herein.

Atractus maculatus (Günther, 1858)

Fig. 2E

Isoscelis maculata Günther, 1858; Catalogue of the Colubrine Snakes in the British Museum: 204.

Rhabdosoma maculatum – Günther, 1858; Catalogue of the Colubrine Snakes in the British Museum: 241. (part).

Atractus maculatus – Boulenger, 1894; Catalogue of the Snakes in the British Museum 2: 306. (part).

Atractus maculatus – Fernandes, Freire & Puerto, 2000; Bol. Mus. Nac. Nov. Ser. Zool. 419:2.

Holotype: Adult male, BMNH 1946.1.6.46 (formerly BMNH 51.3.12.151), without data according to Günther (1858). Boulenger (1894) and Fernandes *et al.* (2000) reported the specimen as from “Brazil?”, according to the original specimen label (specimen examined).

Diagnosis: *Atractus maculatus* is distinguished from all congeners by the following combination of characters: (1) 17/17/17 smooth dorsal scale rows; (2) two postoculars; (3) long loreal; (4) temporals 1+2; (5) seven supralabials, third and fourth contacting orbit; (6) seven infralabials, first four contacting chinshields;

(7) six to eight maxillary teeth; (8) three gular scale rows; (9) usually three prementals; (10) 165 ventrals in the single female, 146–151 in males; (11) 19 subcaudals in female, 27–30 in males; (12) dorsum creamish yellow with wide transverse black blotches, occasionally fragmented into small dots; (13) venter uniformly creamish white; (14) moderate body size, female 284 mm SVL, males reaching 360 mm SVL; (15) tail small in female (8.1% SVL), moderate (11.3–15.6% SVL) in males; (16) hemipenis moderately bilobed, semicapitate, and semicalyculate.

Comparisons: Among all congeners, *A. maculatus* shares 17 dorsal scale rows, transverse wide blotches on a pale dorsum, and venter immaculate creamish white only with *A. zebrinus*. *Atractus maculatus* differs from *A. zebrinus* by having dorsum creamish yellow with dark blotches lacking white border, and capitulum longer than hemipenial body (vs. dorsum creamish red and dark blotches with white border and capitulum shorter than hemipenial body). *Atractus maculatus* occasionally shares with *A. pantostictus*, *A. potschi*, and *A. ronnie* dorsal colour pattern with blotches fragmented into small dots or thin transverse bands. *Atractus maculatus* differ from *A. pantostictus* by having hemipenis moderately bilobed and semicalyculate (vs. slightly bilobed and non-calyculate); from *A. potschi* by having 17 dorsal scale rows (vs. 15 dorsals); from *A. ronnie* by having 146–151 ventrals and 27–30 subcaudals in males, generally eight maxillary teeth, and hemipenis moderate bilobed and semicapitate (vs. 134–144 ventrals, 20–25 subcaudals in males, hemipenis slightly bilobed, non-capitate).

Description: Head twice as long as wide, arched in lateral view, round in dorsal view; snout truncate in lateral view, round in dorsal view; canthus rostralis well marked in lateral view; cervical constriction indistinct; rostral sub-triangular in frontal view, about twice as broad as high, poorly visible in dorsal view; internasal as long as wide; internasal suture sinistral with respect to prefrontal suture; prefrontal as long as wide; supraocular sub-trapezoidal, twice as long as wide; frontal pentagonal, as long as wide; parietal twice as long as wide; nasal divided; nostril located between prenasal and postnasal; prenasal twice as high as long; postnasal as long as wide; loreal long, contacting second and third supralabials; pupil round; two postoculars similar in size; upper postocular slightly longer than lower postocular; temporals 1+2; anterior temporal twice as long as high; upper posterior temporal elongate, about three times as long as wide; seven supralabials, third and fourth contacting orbit; second supralabial higher than first and smaller than third; sixth higher and seventh longer than remaining supralabials; symphyisial triangular, three times longer than wide; seven infralabials, first four contacting chinshields; first pair of infralabials in contact behind symphyisial, preventing symphyisial/chinshield contact; chinshields twice as long as wide; three gular scale rows; usually two prementals; 17/17/17 smooth dorsal scale rows; dorsals lacking apical pits, supra-anal tubercles, and keels; caudal spine short, conical, and slightly acuminate.

Maxillary arch: Arched in dorsal view, with five or six prediastemal and two or three postdiastemal teeth; prediastemal teeth large, moderately spaced, similar in size, curved posteriorly, angular in cross section, robust at base, and narrower on the apices; maxillary diastema moderate; postdiastemal teeth half size of last prediastemal tooth; lateral process well developed, lacking posterior projection.

Colour in preservative: Dorsum of head creamish yellow, with dark brown or black irregular blotches on cephalic shields; head laterally creamish yellow, with dark brown blotches concentrated on orbital and occipital regions; supralabials uniform creamish white; infralabials, chinshields, gular region, and prementals creamish white; venter and tail immaculate creamish white; dorsal ground colour of body creamish yellow, with dark brown or black transverse blotches; transverse blotches wide (six to ten scales wide and two or three scales long), equivalent to pale interspaces on vertebral region; anterior blotches rhomboid, extending to the level of fourth scale rows; posterior blotches narrower than anterior ones, diagonally oriented, and occasionally connected above vertebral region; posterior blotches reaching second dorsal scale rows; first dorsal scale rows uniformly creamish white; second and third scale rows with small black spots (half to one scale wide) placed on pale interspaces between dorsal dark blotches; spots frequently connected ventrally to wide blotches, forming barely defined irregular longitudinal stripes above dorsal margin of second or third scale

rows; tail dorsally similar to body; transverse blotches occasionally fragmented into small black dots or tiny bands arranged linearly on anterior region of body. (Fig. 2E).

Juvenile colouration in preservative: Juveniles and sub-adults with dorsal ground colour creamish yellow, uniformly scattered with small black dots (one scale long), usually not merged into transverse cross-bands.

Hemipenis morphology (everted organ $n = 1$): Retracted organ bifurcates at level of ninth and extends to level of 10th subcaudal. Hemipenis moderately bilobed, semicapitate, and semicalyculate; lobes distinct and restricted to distal portion of capitulum; lobes attenuate, centrifugally oriented, and of similar size; lobes and capitulum uniformly covered with spinulate calyces; calyces in subtransverse rows, forming well defined flounces on lateral portion of sulcate and on asulcate sides of capitulum; capitular groove well marked laterally on the asulcate side, and indistinct on the sulcate side of hemipenis; capitulum distinct, located just above sulcus spermaticus bifurcation, and about twice longer than hemipenial body; sulcus spermaticus bifurcates on the basal third of hemipenial body; branches of sulcus spermaticus with centrifugal orientation, running to apices of lobes; margins of sulcus spermaticus narrow and stout, bordered with spinules from the base of organ to tip of lobes; hemipenial body subcylindrical, uniformly covered with moderate hooked spines; basal naked pocket restricted to basal portion of hemipenial body; basal region of hemipenis with longitudinal plicae and disperse spinules (Fig. 6C).

Variation: Largest male 360 mm SVL, 55 mm CL, largest female 284 mm SVL, 23 mm CL; tail 11.3–15.6% ($\bar{x} = 14.5$; SD = 1.4; $n = 3$) SVL in males, 8.1% SVL in female; 146–151 ($\bar{x} = 149.5$; SD = 2.3; $n = 6$) ventrals in males, 165 in female; 27–30 ($\bar{x} = 28.3$; SD = 1.2; $n = 6$) subcaudals in males, 19 in female; 1 ($n = 1$), 2 ($n = 1$), or 3 ($n = 6$) prefrontals; 8–10 ($\bar{x} = 8.8$; SD = 1; $n = 14$ sides) dorsal scales on the level of second subcaudal; 6 ($n = 2$ sides), 7 ($n = 2$ sides) or 8 ($n = 4$ sides) maxillary teeth.

Distribution: Atlantic Forest remnants in the states of Alagoas and Pernambuco, from Serra Talhada (07°59'S, 38°18'W) southeastward to São Miguel dos Campos (09°47'S, 36°05'W). *Atractus maculatus* inhabits Lowland to Submontane and Montane Rainforest between 0–500 m elevation (Fig. 4).

Remarks: Günther (1858) described the genus *Isoscelis* to accommodate *I. maculata*, diagnosing the genus by the large size of the anteriormost compared with remaining maxillary teeth. In the appendices of the same book, Günther corrected his earlier observation, proposing the synonymy of *Isoscelis* with *Rhabdosoma*. Boulenger (1894) transferred *Rhabdosoma maculatum* to *Atractus* and synonymized *R. zebrinum* with *A. maculatus*. Fernandes *et al.* (2000) found two allopatric and diagnosable populations under the name *Atractus maculatus*, revalidating *Rhabdosoma zebrinum* Jan (as *A. zebrinus*) for the populations distributed from southern Bahia to Santa Catarina and restricting *A. maculatus* to the species occurring in the state of Alagoas, Brazil. Besides differences in colour pattern between *A. maculatus* and *A. zebrinus* previously stressed by Fernandes *et al.* (2000), we found both species strongly differing in hemipenial morphology. *Atractus maculatus* has a hemipenis with a capitulum twice as long as the hemipenial body, whereas *A. zebrinus* has lobes similar in size to the hemipenial body (see Figs. 6C and 11F).

***Atractus pantostictus* Fernandes & Puerto, 1993**

(Figs. 3E, 8A)

Atractus guentheri – Amaral, 1937; Comptes Rendus 12th Congress Internat. Zool. Lisbon, vol. 3:1751. (part).

Atractus guentheri – Peters & Orejas-Miranda 1970; U.S. Nat. Mus. Bull. 297:29. (part).

Atractus pantostictus Fernandes & Puerto 1993; Mem. Inst. Butantan 55:8.

Holotype: Adult male, IBSP 54844, collected on 30 June 1992 by M. S. Santos, municipality of Franco da Rocha (23°20'S, 46°43'W, ca. 800 m), state of São Paulo, Brazil (specimen examined).

Paratypes: Three specimens, all from Brazil: adult female (IBSP 54237), collected on 15 February 1991 by M. Sacioto, municipality of Jundiaí (23°11'S, 46°52'W, ca. 1070 m), state of São Paulo; adult female (MNRJ 4459), collected on November 1987 by M. Porto and G. Kisteumacher, locality Fazenda Triângulo Formoso, municipality of Pirapora (17°21'S, 44°56'W, ca. 540 m), state of Minas Gerais; adult female (MZUSP 3158), collected on June 1956 by J. Pinto, municipality of Boracéia (22°10'S, 48°45'W, ca. 440 m), state of São Paulo.

Diagnosis: *Atractus pantostictus* is distinguished from all congeners by the following combination of characters: (1) 17 smooth dorsal scale rows at midbody; (2) two postoculars; (3) moderate loreal; (4) temporals 1+2; (5) seven supralabials, third and fourth contacting chinshields; (6) usually seven infralabials, first four contacting chinshields; (7) six to eight maxillary teeth; (8) three gular scale rows; (9) usually three pre-ventrals; (10) 154–170 ventrals in females, 145–166 in males; (11) 19–28 subcaudals in females, 22–33 in males; (12) dorsal ground colour creamish yellow to brown uniformly scattered with small black dots; (13) venter immaculate creamish white; (14) moderate body size, females reaching 390 mm SVL, males 322 mm SVL; (15) tail short to moderate in females (6.4–13.2% SVL) and short to long (8.0–17.6% SVL) in males; (16) hemipenis slightly bilobed, slightly semicapitate, and semicalyculate.

Comparisons: Among all congeners, *A. pantostictus* shares seven upper and lower labials, seven to eight maxillary teeth, dorsum pale to pale brown uniformly scattered with small black dots, venter immaculate creamish white only with *A. maculatus*, *A. potschi*, and *A. ronnie*. *Atractus pantostictus* differs from *A. maculatus* by having slightly bilobed hemipenis with lateral projections of lobes (vs. hemipenis moderately bilobed lacking lateral projections); from *A. potschi* by having 17 dorsal scale rows on midbody, dots on dorsum never fused to form crossbands or blotches, hemipenis slightly bilobed with lateral lobes projections (vs. 15 dorsal scale rows, dots frequently fused forming tiny crossbands or transverse blotches, hemipenis moderately bilobed lacking lobe projections); from *A. ronnie* by having black collar capitular crotch indistinct on asulcate side of hemipenis, and lateral tip projections on lobes (vs. lacking black collar on neck and lateral tip projections, and capitular crotch evident).

Description: Head twice as long as wide, flattened in lateral view, round in dorsal view; snout truncate in lateral view, round in dorsal view; cervical constriction indistinct; rostral sub-triangular in frontal view, poorly visible in dorsal view; internasal as long as wide; internasal suture sinistral with respect to prefrontal suture; prefrontal as long as wide; supraocular sub-rectangular, twice as long as wide; frontal pentagonal, longer than wide; parietal twice as long as wide; nasal divided; nostril located between prenasal and postnasal; prenasal twice as high as long; postnasal slightly higher than long; loreal moderate, contacting second and third supralabials; pupil round; two postoculars; upper postocular higher and longer than lower postocular; temporals 1+2; anterior temporal twice as long as high; upper posterior temporal elongate, three times as long as wide; seven supralabials, third and fourth contacting orbit; second supralabial slightly higher than first and similar in size to third; sixth supralabial higher and seventh longer than remaining supralabials; symphyisial sub-triangular, twice broader than long; seven (rarely six) infralabials, first four contacting chinshields; first pair of infralabials in contact behind symphyisial, preventing symphyisial/chinshields contact; chinshields twice as long as wide; three gular scale rows; usually three pre-ventrals; usually 17/17/17 smooth dorsal scale rows; dorsals lacking apical pits, supra-anal tubercles, and keels; caudal spine moderate, conical, and slightly acuminate.

Maxillary arch: Flattened in dorsal view, with four to six prediastemal and two postdiastemal teeth; first three prediastemal teeth closely spaced, remaining moderately spaced, similar in size, curved posteriorly, angular in cross section, robust at base, narrower on the apices; maxillary diastema moderate; postdiastemal teeth half size of last prediastemal tooth; lateral process well developed, lacking posterior projection.

Colour in preservative: Dorsum of head uniformly brown or occasionally beige with diffuse grayish brown blotches above cephalic plates; head brown laterally down to dorsal margins of supralabials; frequently with a dark brown blotch covering anterior portion of posterior temporals downward to seventh supralabial;

supralabials mostly creamish white, except for black upper margin of third, fourth, and seventh scales; symphyisial and infralabials creamish white with dark brown spots on anterior region of each scale; chinshields, gular region, preventrals, venter, and tail immaculate creamish white; dorsal ground colour creamish yellow to brown uniformly scattered with small black dots (one or two scales wide/long); neck region frequently with a black collar (two or three scales long); first dorsal scale row usually uniform creamish white; black dots poorly visible in melanic specimens (Fig. 8A).

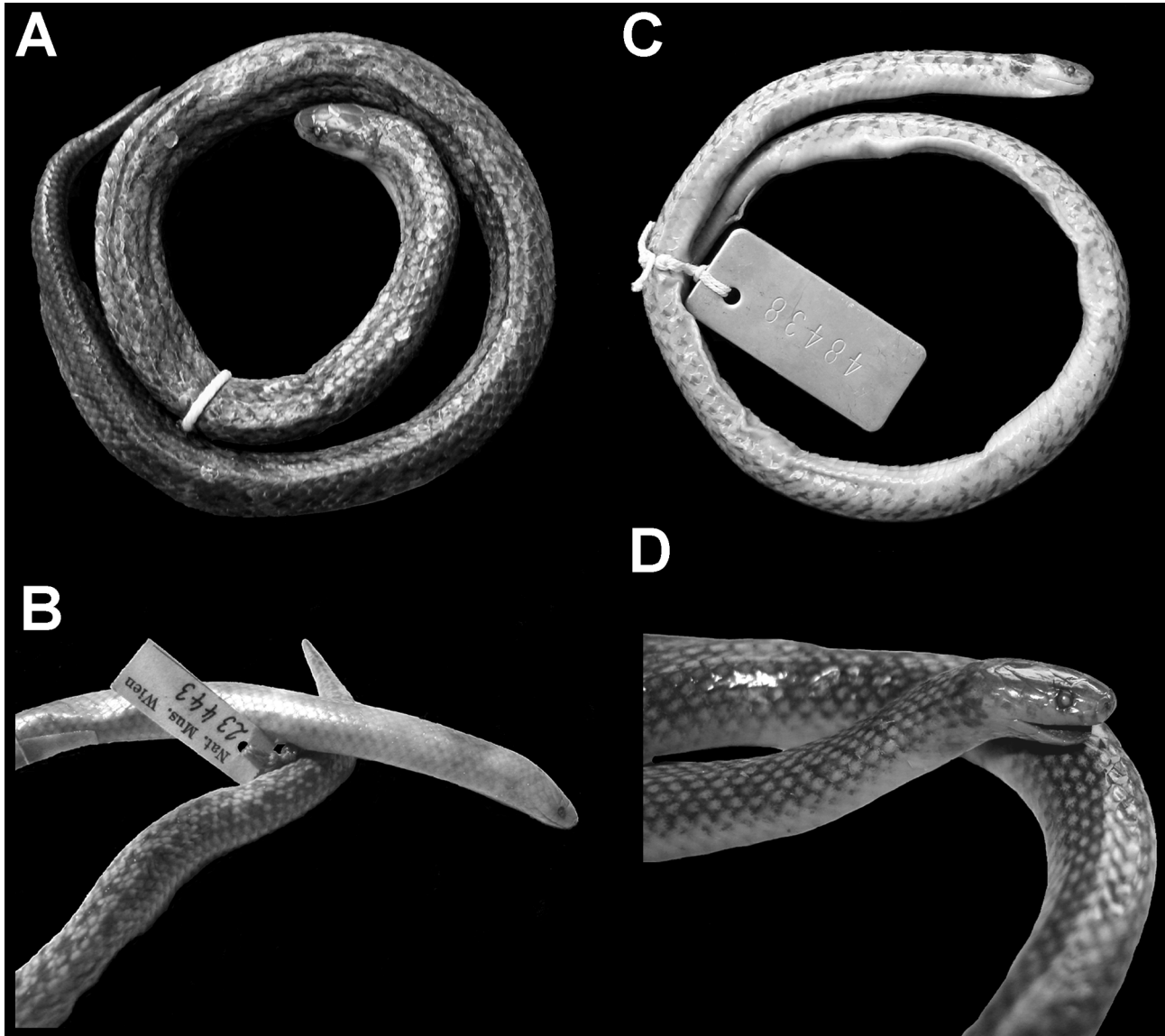


FIGURE 8. General view of the holotypes of (A) *Atractus pantostictus* (IBSP 54844), (B) *A. paraguayensis* (NMW 23443), (C) *A. potschi* (IBSP 48438), and (D) *A. reticulatus* (BMNH 1946.1.2.7).

Juvenile coloration in preservative: Juveniles and sub-adults with dorsal ground colour creamish yellow with uniformly scattered small black dots (one scale long); black collar barely defined or absent.

Colour in life: Dorsum of head brown, with some yellowish brown blotches concentrated on the snout region; lower margin of temporal region and supralabials yellow; mental region creamish yellow with some brown spots at anterior infralabials; venter and tail creamish yellow; dorsal ground colour of body reddish brown uniformly scattered with black dots; dots occasionally with yellow borders on flanks (Fig. 3E).

Hemipenis morphology (everted organs $n = 5$): Retracted organ bifurcates and extends to the level of seventh subcaudal. Hemipenis slightly bilobed, slightly semicapitate, and semicalyculate; lobes poorly dis-

tinct and restricted to the distal portion of the poorly defined capitulum; lobes with lateral projection covered with small papillate calyces; depressions on the basis of lobes delimiting lateral projections; lateral projections of lobes attenuated and centrifugally oriented; intrasulcar region and medial portion of the asulcate side of capitulum thick, covered with moderate alary spines and spinulate calyces barely distinct; spinules progressively replaced with papillae toward apices of lobular projections, forming barely defined spinulate flounces; capitular groove poorly defined on the asulcate and poorly distinct on the sulcate side of capitulum; capitular groove located just above sulcus spermaticus bifurcation; capitulum longer on the sulcate side and similar in size to hemipenial body on the asulcate side; sulcus spermaticus divides on the basal third of hemipenial body; sulcus spermaticus branches centrifugally oriented, running to the apices of lobular projections; margins of sulcus spermaticus stout and narrow, bordered with spinules from the base of the organ to tip of lobes; hemipenial body subcylindrical, narrower than capitulum, uniformly covered with moderate hooked spines; basal naked pocket restricted to basal portion of hemipenial body; basal region of hemipenis with longitudinal plicae and disperse spinules (Fig. 6E).

Variation: Largest male 322 mm SVL, 35 mm CL, largest female 390 mm SVL, 40 mm CL; tail 8.0–17.6% (\bar{x} = 13.6; SD = 2.1; n = 29) SVL in males, 6.4–13.2% (\bar{x} = 10.3; SD = 1.1; n = 34) SVL in females; 145–166 (\bar{x} = 150.3; SD = 3.9; n = 31) ventrals in males, 154–170 (\bar{x} = 163.3; SD = 3.3; n = 34) in females; 22–33 (\bar{x} = 27.8; SD = 1.8; n = 30) subcaudals in males, 19–28 (\bar{x} = 22.5; SD = 1.7; n = 34) in females; 6 (n = 3 sides) or 7 (n = 127 sides) infralabials; 3 (n = 2 sides) or 4 (n = 128 sides) infralabials contacting chinshields; 1 (n = 1), 2 (n = 3) or 3 (n = 61) preentrals; 15/17/17 (n = 1), 17/17/15 (n = 5), 16/17/15 (n = 1), 16/17/17 (n = 1), 17/17/15 (n = 5), 17/17/16 (n = 7), or 17/17/17 (n = 50) dorsal scale rows; 6–10 (\bar{x} = 8.1; SD = 1; n = 124 sides) dorsal scale rows on the level of second subcaudal; 6 (n = 3 sides), 7 (n = 95 sides) or 8 (n = 4 sides) maxillary teeth; retracted hemipenis bifurcates and extends to the level of fifth to ninth subcaudal (n = 11).

Distribution: Central and Southeastern Brazil, from Lajeado (09°45'S, 48°22'W) in the state of Tocantins southward to Itapeccerica da Serra (23°43'S, 46°51'W) and Paranapiacaba (23°47'S, 46°18'W), both in the state of São Paulo. *Atractus pantostictus* inhabits Cerrado and Cerrado/Submontane to Lower Montane Semi-deciduous Forest transition zones between 200–1200 m elevation (Fig. 9).

Remarks: Fernandes and Puerto (1993) clarified the taxonomic status of the Brazilian Cerrado populations previously referred to *A. guentheri* (see Amaral 1937; Peters & Orejas-Miranda 1970), restricting the species to populations of southeastern Bahia (see also *A. guentheri* remarks). Fernandes and Puerto (1993) described *A. pantostictus* on the basis of four specimens from Cerrado regions of the states of Minas Gerais and São Paulo, Brazil, comparing it with *A. guentheri* and *A. reticulatus*. These authors described and illustrated the hemipenis of *A. pantostictus* based on an almost fully everted organ, which lacks lateral lobe projections as described above.

Atractus paraguayensis Werner, 1924

Figs. 8B, 10

Atractus paraguayensis Werner, 1924; Sitz. Akad. Wiss. Wien 133:40.

Atractus reticulatus paraguayensis – Amaral, 1930; Mem. Inst. Butantan 4:27.

Atractus taeniatus – Williams & Gudynas, 1991; Cont. Biol. 15:2.

Atractus paraguayensis – Fernandes, 1996; Comun. Mus. Ciênc. Tecnol. PUCRS, Sér. Zool. 8:39.

Atractus taeniatus – Lema, 1994:106; Fernandes, 1996:51; Moura-Leite, Morato & Bérnils, 1996:216; Giraudo & Scrocchi, 2000:83; Giraudo, 2001:28; Giraudo & Scrocchi, 2002:11; Passos, Fernandes & Zanella, 2005:211; Zaher, Souza, Gower, Hingst-Zaher & Jorge da Silva, 2005:29; Bérnils, Giraudo, Carreira & Cechin, 2007:19.

Atractus reticulatus – Vanzolini, 2000; Pap. Avul. Zool. 41:140.

Atractus paraguayensis – Giraudo & Scrocchi, 2002; Smithsonian Herp. Inform. Serv. 132:10.

Atractus trihedrurus – Lema, 2005; Comun. Mus. Ciênc. Tecnol. PUCRS, Sér. Zool. 18:53.

Atractus paraguayensis – Passos, Fernandes & Borges-Nojosa, 2005:795; Prudente & Passos, 2008:731.

Holotype: Adult female, NMW 23443 (formerly NMW 130), collected by G. Wieninger, Paraguay (specimen examined).

Diagnosis: *Atractus paraguayensis* is distinguished from all congeners by the combination of the following characters: (1) 15/15/15 smooth dorsal scale rows; (2) usually two postoculars; (3) moderate loreal; (4) temporals 1+2; (5) seven supralabials, third and fourth contacting orbit; (6) usually seven infralabials, first four contacting chinshields; (7) eight or nine maxillary teeth; (8) usually three gular scale rows; (10) 147–167 ventrals in females, 136–162 in males; (11) 19–29 subcaudals in females, 21–33 in males; (12) dorsum beige with black paravertebral blotches, a single vertebral line, or both; (13) venter immaculate creamish white; (14) moderate body size, females reaching 490 mm SVL, males 375 mm SVL; (15) tail moderate in females (9.3–14.8% SVL), moderate to long (12.7–18.1 % SVL) in males; (16) slightly bilobed, semicapitate, and semicalyculate hemipenis.

Comparisons: Among all congeners, *A. paraguayensis* shares 15 dorsal scale rows, seven upper and lower labials, first four infralabials contacting chinshields, creamish white occipital band, black collar on the neck, venter immaculate creamish white, and semicapitate and semicalyculate hemipenis only with *A. reticulatus*. *Atractus paraguayensis* differs from *A. reticulatus* by having a conspicuous vertebral line occasionally broken into paravertebral blotches, transverse blotches covering flanks, eight or nine maxillary teeth, and hemipenis slightly bilobed (vs. dorsum dark brown reticulate with pale colour on centre of scales, lacking transverse bands on the flanks, six or seven maxillary teeth, and moderately bilobed hemipenis).

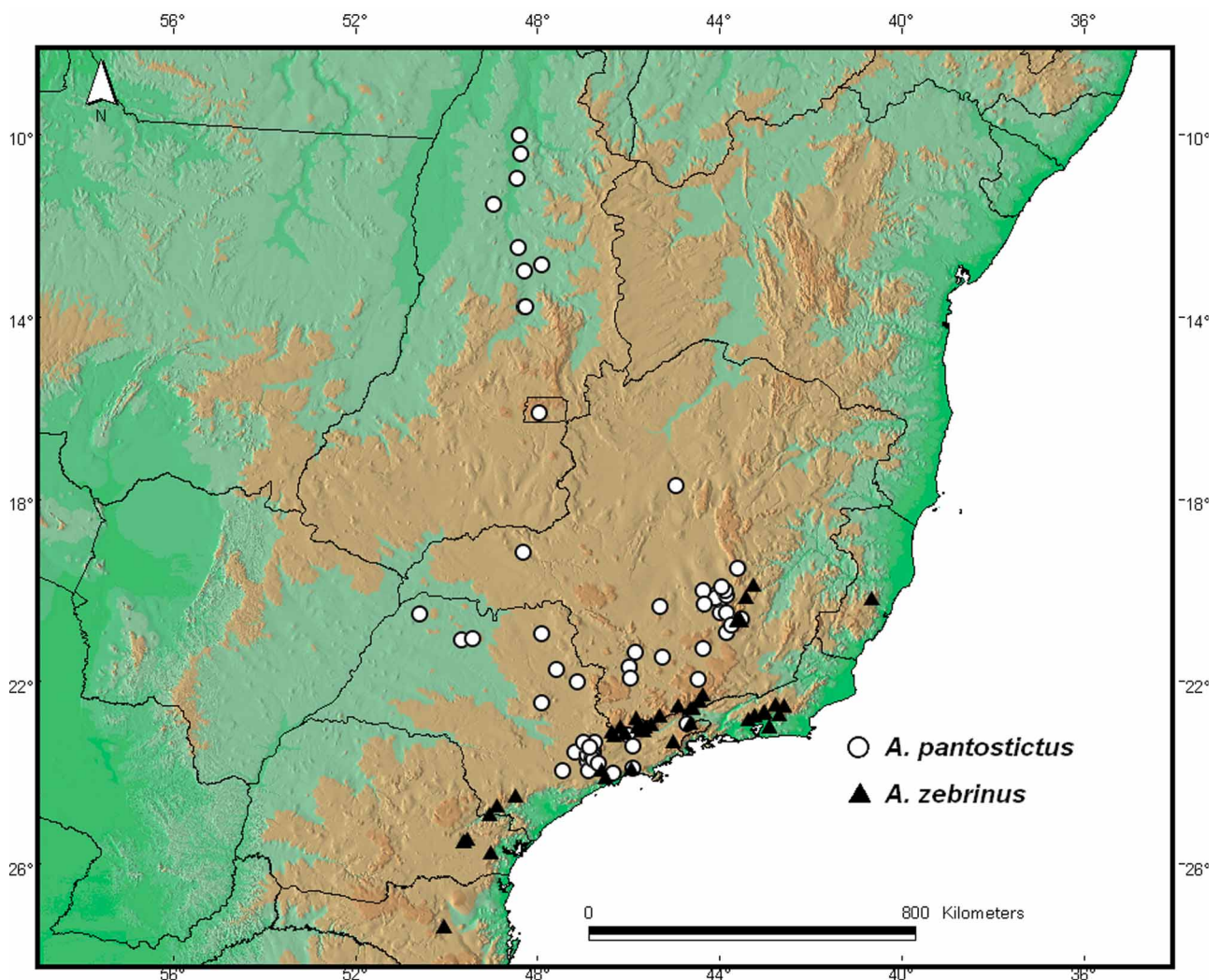


FIGURE 9. Geographical distribution of *Atractus pantostictus* and *A. zebrinus*.

Description: Head twice as long as wide, arched in lateral view, round in dorsal view; snout truncate in lateral view, round in dorsal view; cervical constriction indistinct; rostral sub-triangular, about twice as broad as high, poorly visible in dorsal view; internasal moderate; internasal suture sinistral with respect to prefrontal suture; prefrontal as long as wide; supraocular sub-trapezoidal slightly longer than wide; frontal sub-triangular, broader than long; parietal twice as long as wide; nasal divided; nostril restricted to prenasal; prenasal and postnasal twice as high as long; loreal moderate, contacting second and third supralabials; pupil round or sub-elliptical; one or two postoculars; upper postocular usually slightly higher and longer than lower postocular; temporals 1+2; anterior temporal twice as long as high; upper posterior temporal elongate, twice as long as wide; usually seven supralabials, third and fourth contacting orbit; first two supralabials of similar size and slightly smaller than third; sixth supralabial higher and seventh longer than remaining supralabials; symphisial triangular, twice as broad as long; generally seven infralabials, first four contacting chinshields; first pair of infralabials in contact behind symphisial, preventing symphisial/chinshields contact; chinshields three times longer than wide; generally three gular scale rows; usually three preventrals; 15/15/15 smooth dorsal scale rows; dorsals lacking apical pits, supra-anal tubercles, and keels; caudal spine, long, robust, and rhomboid.

Maxillary arch: Flattened in dorsal view, with five or six prediastemal and two or three postdiastemal teeth; prediastemal teeth large, moderately spaced, similar in size, curved posteriorly, angular in cross section, robust at base, and narrower on the apices; maxillary diastema short; postdiastemal teeth slightly smaller than last prediastemal tooth; lateral process well developed, lacking posterior projection.

Colour in preservative: Dorsum of head with black cap extending from rostral to anterior margin of parietals; occipital band (posterior region of parietal, temporals, and supralabials) creamish white or beige covering region between black cap and black collar; black collar disposed above first dorsal scale rows (two or three scales long), occasionally connected to vertebral body line; head black laterally, extending to middle of supralabials; first six supralabials creamish white with black dorsal edges; seventh supralabial generally uniform creamish white; gular region creamish white, occasionally with brown blotches covering first infralabials; venter and tail immaculate creamish white; dorsal ground colour variable, occasionally adults with vertebral line lacking transverse blotches on the paravertebral region; frequently adults with reddish brown ground colour and irregular vertebral line, sometimes broken into paravertebral blotches; generally paravertebral blotches connected to irregular vertebral line and/or barely defined paravertebral lines, constituting a variegated general pattern; adults occasionally with vertebral line entirely fragmented into transverse black blotches or irregular bands (two or three scales long and three or four scales wide), covering paravertebral region and flanks; sometimes individuals have a combination of latter two colour patterns; frequently first three scale rows are pale (pale brown) and small black dots (one or two scales wide) connected dorsally to transverse blotches (Fig. 8B).

Juvenile colouration in preservative: Juveniles and sub-adults usually with beige ground colour and regular black vertebral line (one or two scales wide); juveniles rarely with vertebral line fragmented into paravertebral spots or transverse bands; sometimes young with irregular vertebral and paravertebral blotches.

Colour in life: Dorsum and lateral region of head (cephalic cap) grayish brown to black, generally with pale (beige) pigmentation concentrated on loreal region; occipital band white to pale brown (in melanic specimens); cephalic cap generally continuous with black collar through mid parietal suture; mental region white with disperse black blotches covering anterior infralabials mainly; venter and tail creamish white to creamish yellow; dorsal ground colour of body red, red orange, or reddish brown; dorsum covered with regular black vertebral line, frequently fragmented on black paravertebral blotches or conspicuous bands; line, blotches, or bands poorly distinct from ground colour on melanic individuals (Fig. 10).

Hemipenis morphology (everted organs $n = 4$): Retracted organ bifurcates and extends to the level of seventh subcaudal. Hemipenis slightly bilobed, semicapitate, and semicalyculate; lobes poorly defined and restricted to distal portion of capitulum; apices of lobes separated from each other by median calycular crest

on distal portion of capitulum, with medial projections directed upward; lobes barely clavate with round tip, having spinules oriented dorsally; lobes and capitulum uniformly covered with spinulate calyces; calyces distributed irregularly on the intrasulcar and asulcate side of capitulum; lateral portion of capitulum on the sulcate side with calyces disposed transversally, forming well defined calyculate flounces; capitulum located just above sulcus spermaticus bifurcation; capitular groove distinct on both sides of hemipenis; capitulum of similar size to hemipenial body; sulcus spermaticus divides at middle of organ, in the distal portion of hemipenial body; branches of sulcus spermaticus with centrifugal orientation, running to tips of lobe projections; sulcus spermaticus margins narrow and stout, bordered with spinules from the base of the organ to tip of lobes; hemipenial body subcylindrical, uniformly covered with moderate hooked spines; large spines located on lateral portion of sulcate side and medial region adjacent to capitulum on the asulcate side; basal naked pocket extending to distal portion of hemipenial body; basal portion of hemipenial body with longitudinal plicae and disperse spinules (Fig. 6F).

Variation: Largest male 375 mm SVL, 54 mm CL, largest female 490 mm SVL, 65 mm CL; tail 8.8–18.1% (\bar{x} = 14.9; SD = 1.4; n = 95) SVL in males, 6.3–14.8% (\bar{x} = 11; SD = 1.3; n = 112) SVL in females; 136–162 (\bar{x} = 145; SD = 3.4; n = 96) ventrals in males, 147–167 (\bar{x} = 159.4; SD = 3.2; n = 123) in females; 21–33 (\bar{x} = 26.7; SD = 2; n = 96) subcaudals in males, 19–29 (\bar{x} = 23; SD = 2; n = 116) in females; 1 (n = 2 sides), or 2 (n = 182 sides) postoculars; 6 (n = 1 side), 7 (n = 410 sides), or 8 (n = 1 side) supralabials; 6 (n = 11 sides), 7 (n = 392 sides), or 8 (n = 4 sides) infralabials; 3 (n = 7 sides), 4 (n = 396 sides) or 5 (n = 3 sides) infralabials contacting chinshields; 2 (n = 5), 3 (n = 31) or 4 (n = 8) prefrontals; 6–10 (\bar{x} = 7.8; SD = 0.8; n = 88 sides) dorsal scale rows on the level of second subcaudal; 8 (n = 25 sides) or 9 (n = 41 sides) maxillary teeth; 9 (n = 2) dentary teeth; retracted organ extends from fifth to ninth subcaudal (n = 20).

Distribution: Forests associated with the Paraná river basin, from Cascavel (24°56'S, 53°27'W) in the state of Paraná, Brazil, southward to Villa Urquiza (31°39'S, 60°22'W) in the province of Entre Rios, Argentina. *Atractus paraguayensis* inhabits riparian to Lower Montane Semi-deciduous Forest between 30–1000 m elevations (Fig. 11).

Remarks: Werner (1924) described *A. paraguayensis* on the basis of a single specimen from Paraguay, collected by George Wieninger but without more detailed data, although Vanzolini (2000) suggested that Wieninger's localities were all near Asunción. Werner (1924) compared *A. paraguayensis* with *A. emmeli* (another *Atractus* species having 15 dorsal scale rows) diagnosing the former by its single postocular (vs. two postoculars in *A. emmeli*). Amaral (1930) considered *A. paraguayensis* to be a subspecies of *A. reticulatus*. Peters and Orejas-Miranda (1970) followed the arrangement proposed by Amaral (1930). Williams and Gudynas (1991) associated specimens of *Atractus* having 15 dorsal scale rows from northwestern Argentina with *A. taeniatus* (species previously synonymized with *A. emmeli* by McCoy 1971). Fernandes (1996) revised the *A. reticulatus* complex (see below) and considered *A. paraguayensis* a valid species, but did not include the Argentinean specimens reported by Williams and Gudynas (1991). Despite Fernandes' (1996) argumentation, Vanzolini (2000) proposed that *A. paraguayensis* is a synonym of *A. reticulatus*, although without inspection of the holotype and examination of additional specimens, or any further justification. Giraudo and Scrocchi (2000) reported new specimens of *A. paraguayensis* from southeastern Paraguay and northeastern Argentina, but they identified specimens from northwestern Argentina as *A. taeniatus*, according with the proposition of Williams and Gudynas (1991). Specimens identified as *A. taeniatus* (*sensu* Williams & Gudynas 1991) were cited again from northeastern Argentina by Giraudo (2001) and also from southern Brazil by Lema (1994), Moura-Leite *et al.* (1996), Passos *et al.* (2005), and Bérnils *et al.* (2007).

Our examination of the holotype of *A. paraguayensis*, as well as photos and data from the holotype of *A. taeniatus*, revealed that Argentinean (e.g., Williams & Gudynas 1991; Giraudo & Scrocchi 2000; Giraudo 2001) and Brazilian (e.g., Lema 1994; Moura-Leite *et al.* 1996; Passos *et al.* 2005) populations previously referred to *A. taeniatus* are in fact *A. paraguayensis*. The results of our quantitative analyses were congruent in placing together populations from Argentina, Brazil, and Paraguay previously associated with *A. taeniatus*

and/or *A. paraguayensis*. The principal orthogonal axes from DFA were unable to discriminate the holotype of *A. paraguayensis* from *A. taeniatus* groups based on any of the colour patterns and/or geographical populations for females as well males (Fig. 12).



FIGURE 10. General view in life of *Atractus paraguayensis*. Specimens from Chapecó, state of Santa Catarina (A, C, and D), photos by F.M. D'Agostini. Specimens from Segredo Hydroelectric Power Plant, Reserva do Iguaçu, state of Paraná (B and F), photos by M.V. Segalla. Specimen from Passo Fundo River, Nanoai, state of Rio Grande do Sul (E), photo by N.R. Albuquerque.

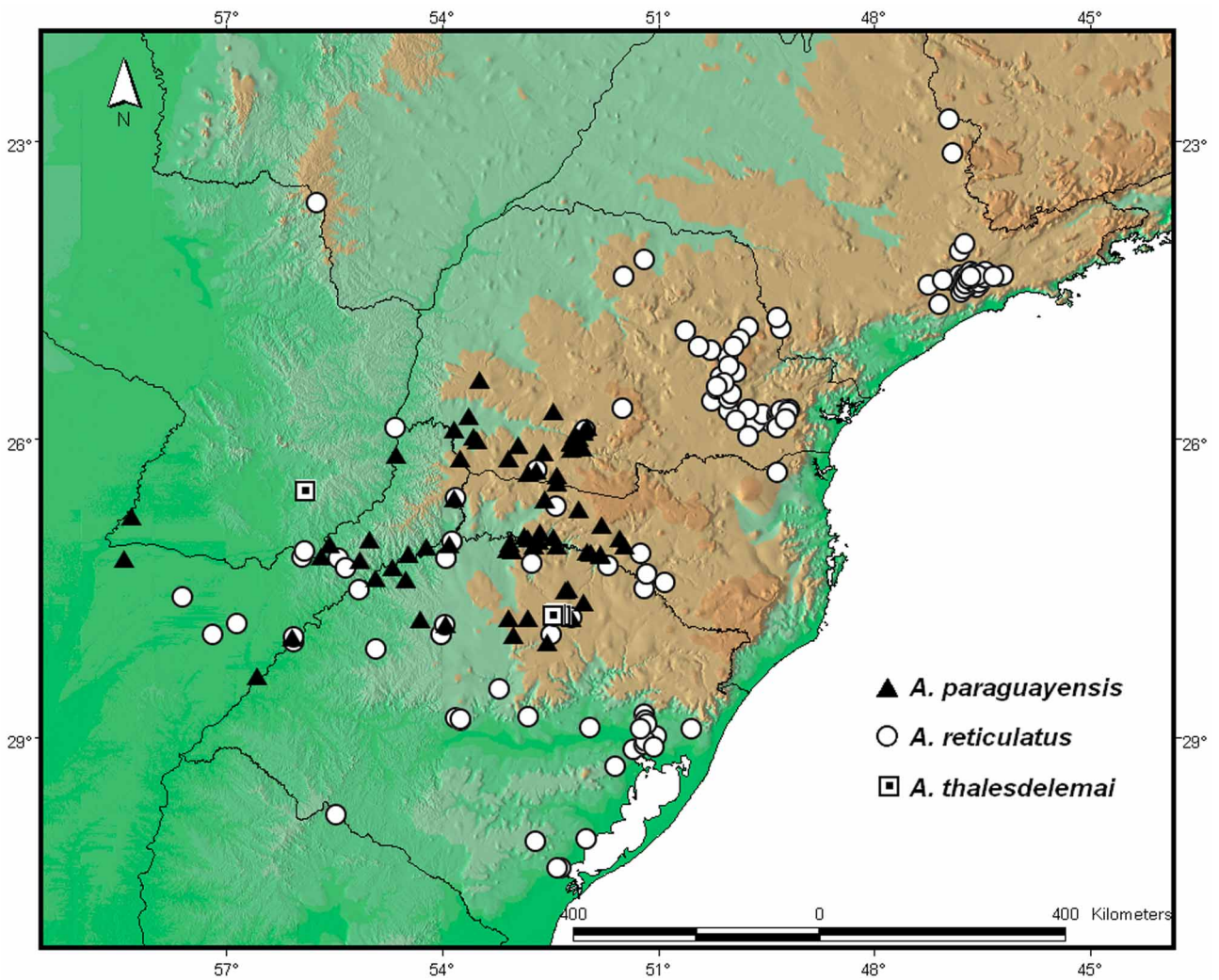


FIGURE 11. Geographical distribution of *Atractus paraguayensis*, *A. reticulatus*, and *A. thalesdelemai*.

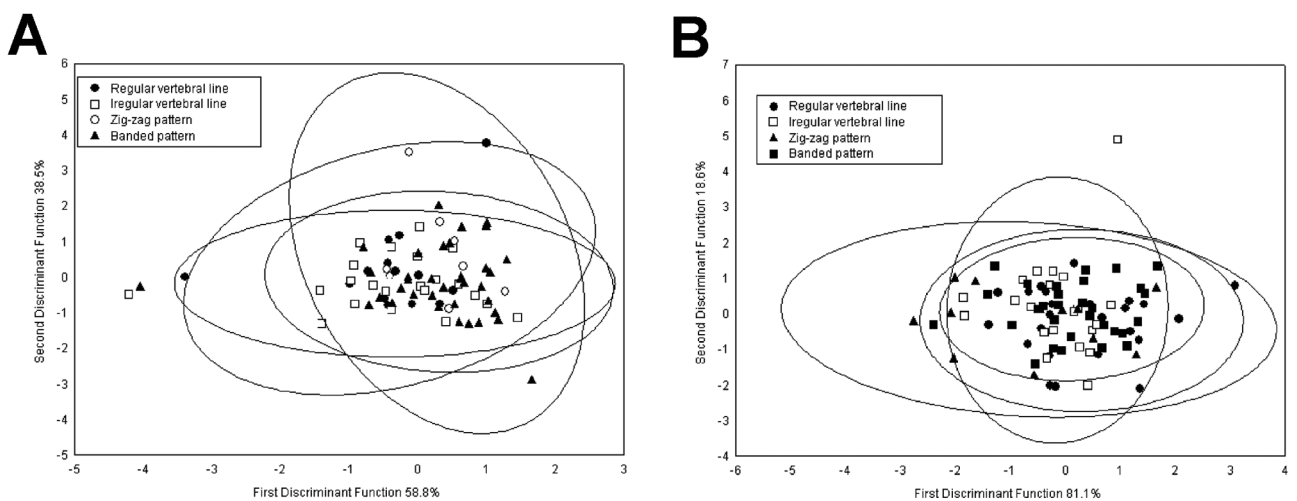


FIGURE 12. Bivariate plots with 95% confidence regions for the first two axes derived from scores of DFA analyses for male (A) and female (B) colour patterns of *Atractus paraguayensis*.

The qualitative analyses of colouration, dentition, and hemipenial characters corroborate the morphometric results. Furthermore, the distribution of *A. paraguayensis*, as herein defined, provided additional insights for considering these populations within a single evolutionary unit associated with semideciduous forests in the Paraná River basin. Therefore, all populations referred to *A. taeniatus* in Brazil and Argentina are herein considered to be *A. paraguayensis*. The type of *A. taeniatus* would more usefully be considered in a study of *A. emmeli* and other similar Amazonian species of *Atractus* (P. Passos unpubl. data).

Finally, an old specimen of *A. paraguayensis* housed at the Instituto Butantan (IBSP 4784, dated from 03 December 1927) is labeled from the municipality of São Carlos, state of São Paulo, about 700 km from the northernmost record for the species (Cascavel, state of Paraná). Due to the improbability of this provenance, as well as that the fact the specimen was obtained at the beginning of the Butantan collection, we believe this may be labeled in error. Therefore, we decide to not include this record in the distribution of *A. paraguayensis*.

***Atractus potschi* Fernandes, 1995**

Figs. 8C, 13A

Atractus potschi Fernandes, 1995; J. Herpetol. 29:417.

Holotype: Adult male, IBSP 48438, collected on 19 July 1985 by A. J. Santos, municipality of Maceió (09°40'S, 35°43'W, sea level), state of Alagoas, Brazil, (specimen examined).

Paratypes: Eleven specimens all from state of Sergipe: adult female (MZUSP 7196) and adult males (MZUSP 7001, 7165, 7197) collected on 29 April 1978 by E. M. X. Freire; adult males (MZUSP 7275–76, 7278, 7280–81) and females (MZUSP 7277, 7279) collected between September and November 1978 by E. M. X. Freire, all from municipality of Salgado (11°02'S, 37°28'W, ca. 150 m).

Diagnosis: *Atractus potschi* is distinguished from all congeners by the combination of the following characters: (1) 15/15/15, smooth dorsal scale rows; (2) two postoculars; (3) loreal long; (4) temporals 1+2; (5) seven supralabials, third and fourth contacting orbit; (6) seven infralabials, first four contacting chinshields; (7) seven maxillary teeth; (8) three gular scale rows; (9) three preventrals; (10) 153–165 ventrals in females, 141–150 in males; (11) 22–25 subcaudals in females, 27–32 in males; (12) dorsal ground colour creamish yellow, with black collar and black dots, occasionally merged to form blotches or crossbands; (13) venter immaculate creamish white; (14) moderate body size, females reaching 370 mm SVL, males 312 mm SVL; (15) tail short in females (8.6–11.4% SVL) and short to moderate (8.8–15.6% SVL) in males; (16) slightly bilobed, semicapitate, and semicalyculate hemipenis.

Comparisons: Among all congeners, *A. potschi* shares 15 dorsal scale rows, seven or eight maxillary teeth, dorsal colour pattern creamish yellow or beige with black spots or blotches, and venter predominantly creamish white only with *A. insipidus* and *A. punctiventris*. *Atractus potschi* differs from *A. insipidus* by having a black collar, dorsal blotches forming thin crossbands, two postdiastemal teeth, and retracted hemipenis as long as 10 subcaudal scales (vs. black collar absent, dorsal colour pattern uniformly scattered with small black dots, single postdiastemal teeth, retracted hemipenis six subcaudal scales long); from *A. punctiventris* by having venter immaculate, creamish white (vs. venter with round dark brown blotches on the middle of ventrals, forming a conspicuous median stripe).

Description: Head twice longer than wide, slightly arched in lateral view, sub-triangular in dorsal view; snout truncate in lateral view, round in dorsal view; cervical constriction indistinct; rostral wider than high, sub-triangular in frontal view, poorly visible in dorsal view; internasal as long as wide; internasal suture sinistral with respect to prefrontal suture; prefrontal as long as wide; supraocular sub-trapezoidal, twice as long as wide; frontal sub-pentagonal or sub-triangular, broader than long; parietal twice as long as wide; nasal

divided; nostril located between prenasal and postnasal; prenasal and postnasal twice as high as long; loreal moderate, contacting second and third supralabials; pupil round; generally two postoculars of similar size; upper postocular occasionally slightly longer than lower and lower postocular higher than upper; temporals 1+2; anterior temporal twice as long as high; upper posterior temporal elongate, three times longer than wide; seven supralabials, third and fourth contacting orbit; second supralabial higher than first and smaller than third; sixth higher and seventh longer than remaining supralabials; symphyial sub-triangular, twice as broad as long; seven infralabials, first four contacting chinshields; first pair of infralabials in contact behind symphyial, preventing symphyial/chinshields contact; chinshields twice as long as wide; three gular scale rows; generally three preventrals; 15/15/15 smooth dorsal scale rows; dorsals lacking apical pits, supra-anal tubercles, and keels; caudal spine moderate, conical, robust, and acuminate.

Maxillary arch: Arched in dorsal view, with five or six prediastemal and two postdiastemal teeth; prediastemal teeth large, moderately spaced, curved and decreasing gradually in size posteriorly, angular in cross section, robust at base, and narrower on the apices; maxillary diastema moderate; postdiastemal teeth slightly smaller than last prediastemal tooth; lateral process moderately developed, lacking posterior projection.

Colour in preservative: Dorsum of head brown to the middle of parietals; posterior region of parietals and temporal area creamish yellow; background of head brown to dorsal edges of supralabials; supralabials, except for dorsal margins, uniformly creamish yellow; mental region immaculate creamish white; venter and tail immaculate creamish white; dorsum of body with a black collar at neck on the third to sixth dorsal scale rows; region between end of parietals and black collar creamish yellow; occasionally there is a second black collar (three scales long) separated from the first by four creamish yellow scale rows; dorsal ground colour creamish yellow, uniformly scattered with small black dots (one scale wide/long); dots frequently arranged transversally, forming tiny (one scale wide) dorsal crossbands; bands extending above flanks to the level of fourth dorsal scale rows; bands occasionally constituting broad transversal blotches (one to three scales long), with size similar to interspaces anteriorly and decreasing posteriorly; first dorsal scale rows creamish white, second with small black dots (half scale wide) covering pale interspaces; dorsal dots or spots rarely merged, and arranged linearly along body (Fig. 8C).

Juvenile colouration in preservative: Juveniles and sub-adults with dorsal ground colour creamish yellow with narrow black dots (one scale long) usually merged into tiny crossbands.

Colour in life: Dorsum of head uniform brown to the level of anterior region of parietals; posterior portion of parietals and occipitals beige, forming a pale band; wide collar black; supralabials creamish yellow, except for brown dorsal margins of third and fourth scales; infralabials and mental region creamish yellow; venter and tail creamish yellow; dorsal ground colour of body reddish, uniformly scattered with small black dots (Fig. 13A).

Hemipenis morphology (everted organ, $n = 1$): Retracted organ bifurcates and extends to the level of seventh subcaudals. Organ slightly bilobed, semicapitate, and semicalyculate; lobes poorly distinct, restricted to distal portion of capitulum; lobes sub-cylindrical with round apices, and smaller than remaining capitulum; lobes and capitulum uniformly covered with spinulate calyces; capitulum located just above sulcus spermaticus bifurcation; capitular groove poorly distinct on sulcate and well marked on the asulcate side of hemipenis; capitulum longer than hemipenial body on both sides of organ; sulcus spermaticus divides on basal third of hemipenial body; sulcus spermaticus branches with centrifugal orientation, running to tips of lobes; margins of sulcus spermaticus stout and moderately broad, bordered with spinules from the base to the end of lobes; hemipenial body sub-cylindrical as broad as capitulum, covered with moderate hooked spines; naked pocket absent; basal portion of hemipenial body with longitudinal plicae and diffuse spinules (Fig. 6D).

Variation: Largest male 312 mm SVL, 46 mm CL, largest female 370 mm SVL, 38 mm CL; tail 8.8–15.6% ($\bar{x} = 13.1$; $SD = 2.2$; $n = 11$) SVL in males, 8.6–11.4% ($\bar{x} = 10.2$; $SD = 1$; $n = 7$) SVL in females; 141–150 ($\bar{x} = 145.3$; $SD = 3.7$; $n = 11$) ventrals in males, 153–165 ($\bar{x} = 157.7$; $SD = 4.9$; $n = 7$) in females; 27–32 ($\bar{x} = 29.4$; $SD = 1.5$; $n = 11$) subcaudals in males, 22–25 ($\bar{x} = 22.3$; $SD = 0.9$; $n = 7$) in females; 7 ($n = 35$ sides) or 8 (n

= 1 side) supralabials; 4 ($n = 35$ sides) or 5 ($n = 1$ side) infralabials contacting chinshields; 2 ($n = 1$), 3 ($n = 4$) or 4 ($n = 1$) preventrals; 8–10 ($\bar{x} = 8.5$; $SD = 0.5$; $n = 12$ sides) dorsal scale rows level with second subcaudal; 7 ($n = 14$ sides) or 8 ($n = 4$ sides) maxillary teeth; retracted hemipenis extends to level of 10th subcaudal ($n = 3$).

Distribution: Northeastern Brazil, from São Cristovão (11°01'S, 37°12'W) in the state of Sergipe south-westward to Poções (14°32'S, 40°22'W) in the state of Bahia. *Atractus potschi* inhabits rainforest remnants in transitional areas amongst Lowland to Lower Montane Semi-deciduous Forest between 0–800 m elevation (Fig. 4).

Remarks: Fernandes (1995) described *A. potschi* on the basis of 12 specimens from the states of Alagoas and Sergipe, Brazil. Lima *et al.* (2000) extended species distribution southern to Feira de Santana, in the state of Bahia. We report herein nine additional specimens of *A. potschi*, extending the species range of distribution for five new localities on northeastern Brazil (see Fig. 4).

Atractus reticulatus (Boulenger, 1885)

Figs. 8D, 13B

Geophis reticulatus Boulenger, 1885; Ann. Mag. Nat. Hist. 16(5):87.

Atractus reticulatus – Boulenger, 1894; Catalogue of the Snakes in the British Museum 2:311.

Atractus reticulatus scrochii Alvarez, Rey & Cei, 1992; Boll. Mus. Reg. Sci. Nat. Torino 10(2):250.

Atractus reticulatus – Fernandes, 1996; Comun. Mus. Cienc. Tecnol. PUCRS, Sér. Zool. 8:41.

Holotype: Adult female, BMNH 1946.1.2.7 (formerly BMNH 85.6.26.10), collected by R. von Ihering, municipality of São Lourenço do Sul (31°22'S, 51°59'W, sea level), state of Rio Grande do Sul, Brazil, (specimen examined).

Diagnosis: *Atractus reticulatus* is distinguished from all congeners by the following combination of characters: (1) 15/15/15 smooth dorsal scale rows; (2) two postoculars; (3) loreal moderate; (4) temporals 1+2; (5) seven supralabials, third and fourth contacting orbit; (6) six or seven infralabials, first four contacting chinshields; (7) six to eight maxillary teeth; (8) usually three gular scale rows; (9) usually three preventrals; (10) 149–165 ventrals in females, 130–151 in males; (11) 19–30 subcaudals in females, 24–34 in males; (12) dorsum ground colour dark grayish brown or black, reticulating with pale colour; (13) venter immaculate creamish white; (14) moderate body size, females reaching 390 mm SVL, males 279 mm SVL; (15) tail short to moderate in females (7.8–13.5% SVL), short to long (7.9–17.1% SVL) in males; (16) moderately bilobed, semicapitate, and semicalyculate hemipenis.

Comparisons: Among all congeners, *A. reticulatus* shares 15 dorsal scales rows, first four infralabials contacting chinshields, six or seven maxillary teeth, pale occipital band at least on juveniles, dorsum dark brown or black, hemipenis semicapitate, semicalyculate only with *A. emmeli*. *Atractus reticulatus* differs from *A. emmeli* by having two or three gular scale rows, 149–163 ventrals in females and 130–151 in males, and venter immaculate creamish white (vs. four gular scale rows, 154–185 ventrals in females and 151–165 in males, and venter generally black). *Atractus reticulatus* is apparently close relative and occurs sympatrically with *A. paraguayensis*, but is easily distinguished from this species by having a moderately bilobed hemipenis and dorsal colour pattern reticulate grayish brown to black, lacking paravertebral blotches in preserved adults (vs. slightly bilobed hemipenis and dorsal colour pattern beige to pale brown usually scattered with paravertebral blotches in adults).

Description: Head twice as long as wide, slightly arched in lateral view, round in dorsal view; snout truncate in lateral view, round in dorsal view; cervical constriction indistinct; rostral sub-triangular in frontal view, broader than high, poorly visible in dorsal view; internasal moderate; internasal suture sinistral with respect to prefrontal suture; prefrontal as long as wide; supraocular sub-trapezoidal, twice as long as wide; frontal sub-pentagonal or sub-triangular, broader than long; parietal twice as long as wide; nasal divided; nostril located

between prenasal and postnasal; prenasal and postnasal twice as high as long; loreal moderate, contacting second and third supralabials; pupil round; generally two postoculars of similar size; upper postocular occasionally longer than lower and lower higher than upper postocular; temporals 1+2; anterior temporal twice as long as wide; upper posterior temporals, three times as long as wide; seven supralabials, third and fourth contacting orbit; first two supralabials of similar size and slightly smaller than third; sixth higher and seventh supralabial longer than others; symphyisial triangular, slightly broader than long; seven infralabials, first four contacting chinshields; first pair of infralabials in contact behind symphyisial, preventing symphyisial/chinshields contact; chinshields twice longer than wide; three gular scale rows; generally three preventrals; 15/15/15 smooth dorsal scale rows; dorsals lacking apical pits, supra-anal tubercles, and keels; caudal spine moderate, conical, and acuminate.

Maxillary arch: Arched in dorsal view, with six prediastemal and two postdiastemal teeth; prediastemal teeth large, closely spaced, of similar size, curved posteriorly, angular in cross section, robust at base, narrower on the apices; maxillary diastema short; postdiastemal teeth slightly smaller than last postdiastemal tooth; lateral process poorly developed, lacking posterior projection.

Colour in preservative: Dorsum of head uniformly dark brown; background of head dark brown, extending to the dorsal edges of supralabials; occasionally, dark pigment extends to labial margin through anterior edges of supralabials; mental region immaculate creamish white; venter and tail immaculate, creamish white; dorsum of body with black collar (two to four scales long); dorsal ground colour brown to dark brown, reticulating with pale brown spots; pale brown reticulations (beige or grayish brown) concentrated on the centre of each dorsal scale, with dark colour restricted to scale borders; first two dorsal scale rows generally creamish white; dorsum frequently with a dark brown vertebral line (one scale wide) along body (Fig. 8D).

Juvenile colouration in preservative: Juveniles with a pale (beige) occipital band, extending generally from parietal shield to black collar.

Colour in life: Dorsum of head uniformly black; supralabials, mental region, venter, and tail creamish red; dorsal of body reticulate with creamish white to reddish brown spots (bordered with black) on the centre of scales (Fig. 13B).

Hemipenis morphology (everted organs, $n = 4$): Retracted organ bifurcates and extends to the level of seventh subcaudal. Hemipenis moderately bilobed, semicapitate, and semicalyculate; lobes distinct and restricted to distal portion of capitulum; lobes cylindrical, with round apices; lobes generally similar in size, longer than remaining portion of capitulum; lobes and capitulum uniformly covered with spinulate calyces; calyces arranged in transverse series, constituting well defined spinulate flounces; capitulum located just at the level of sulcus spermaticus bifurcation; capitular groove well evident on the asulcate side and barely distinct on the sulcate side; capitulum of similar size to hemipenial body; sulcus spermaticus divides for about middle of organ; branches of sulcus spermaticus with centrifugal orientation, running to tip of lobes; sulcus spermaticus margins stout and narrow, bordered with spinules from the base of organ to tip of lobes; hemipenial body subcylindrical, uniformly covered with moderate hooked spines; large spines restricted to lateral portion of sulcate side of hemipenis; basal naked pocket restricted to proximal region of hemipenial body; basal portion of hemipenis with longitudinal plicae and disperse spinules (Fig. 14A).

Variation: Largest male 279 mm SVL, 42 mm CL, largest female 390 mm SVL, 47 mm CC; cauda 7.9–17.0% ($\bar{x} = 14.3$; $SD = 1.8$; $n = 90$) SVL in males, 7.0–13.5% ($\bar{x} = 11.2$; $SD = 1.4$; $n = 53$) SVL in females; 130–151 ($\bar{x} = 142.5$; $SD = 4.3$; $n = 98$) ventrals in males, 149–163 ($\bar{x} = 157$; $SD = 3.1$; $n = 57$) in females; 24–34 ($\bar{x} = 28.7$; $SD = 2.1$; $n = 95$) subcaudals in males, 19–30 ($\bar{x} = 24.1$; $SD = 2.5$; $n = 57$) in females; 3 ($n = 6$ sides) or 4 ($n = 55$ sides) infralabials contacting chinshields; 2 ($n = 10$ sides) or 3 ($n = 50$ sides) gular scale rows; 2 ($n = 3$), 3 ($n = 24$), or 4 ($n = 3$) preventrals; 7–10 ($\bar{x} = 8.1$; $SD = 0.6$; $n = 62$ sides) dorsal scale rows on the level of second subcaudal; 6 ($n = 1$ side) or 7 ($n = 24$ sides) maxillary teeth; retracted hemipenis bifurcates and extends to the level of seventh to ninth subcaudal ($n = 7$).

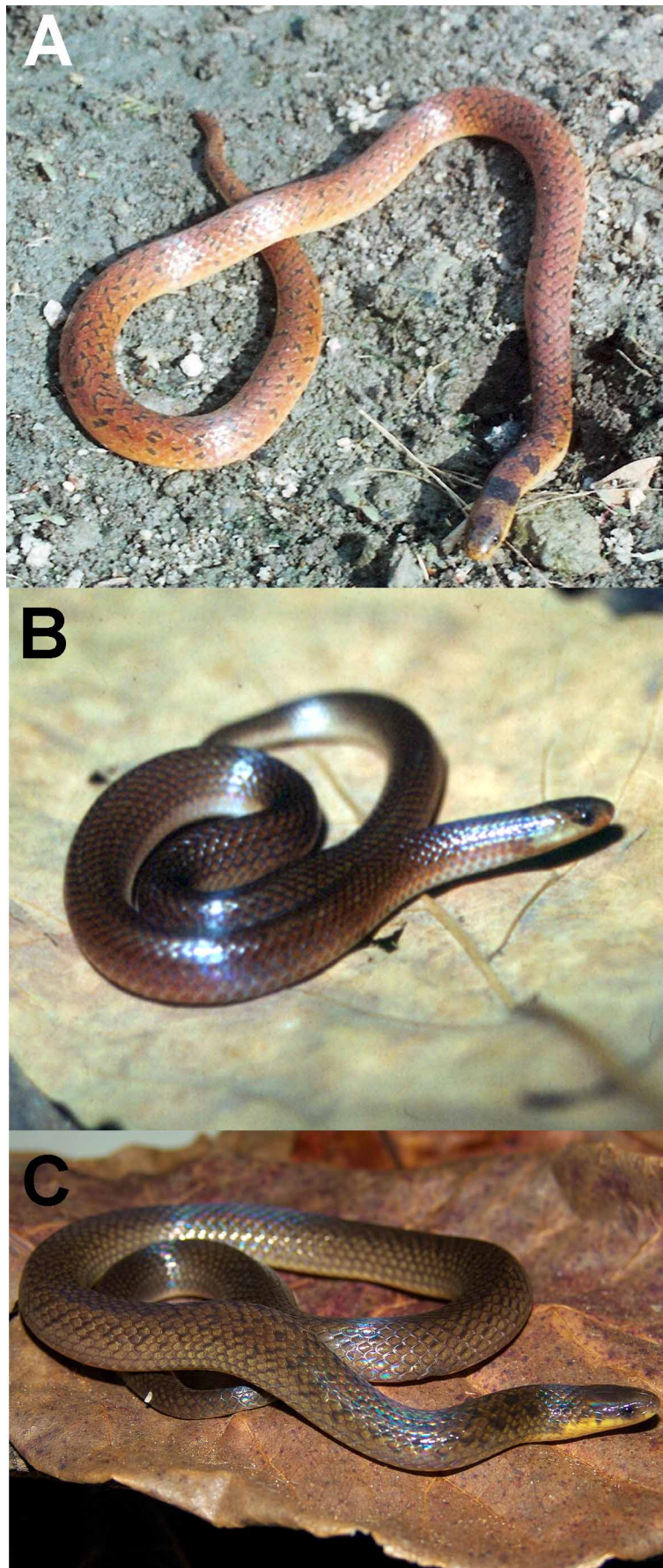


FIGURE 13. General view in life of (A) *Atractus potschi* from Feira de Santana, state of Bahia, photo by M.A. Freitas, (B) *A. reticulatus* from Ferraz de Vasconcelos, state of São Paulo, photo by M.R. Duarte, and (C) *A. ronnie* from Tianguá, state of Ceará, photo by D. Loebmann.

Distribution: From Arceburgo (21°22'S, 46°56'W) in the state of Minas Gerais, Brazil, southeastward to Colonia Carlos Pellegrini, San Martín (28°32'S, 57°10'W) in the province of Corrientes, Argentina (Giraudó 2001), and southward to Establecimiento Trinidad (31°02'S, 55°27'W) in the department of Rivera, Uruguay (Carreira *et al.* 2004; 2005). *Atractus reticulatus* inhabits Pampas, Campos, southern Cerrado, and transitional zones between these vegetation types and Lowland to Lower Montane Semi-deciduous Forest between 0–1100 m elevation (Fig. 11).

Remarks: Boulenger (1885) described *Geophis reticulatus* based on a specimen from “S. Lourenço” (currently São Lourenço do Sul, 31°22'S, 51°58'W) in the state of Rio Grande do Sul, Brazil. Boulenger (1894) transferred this species to the genus *Atractus*. Amaral (1930a) considered *A. paraguayensis* to be a subspecies of *A. reticulatus*, without discussion. Amaral (1930b) extended the range of distribution of *A. r. reticulatus* to Colombia, without citing any voucher specimens to support this statement. Several subsequent authors followed Amaral (1930b) in considering *A. reticulatus* native to Colombia (Nicéforo-Maria 1942; Prado 1945; Daniel 1949). Peters and Orejas-Miranda (1970) restricted the distribution of *A. reticulatus* to Paraguay and southern Brazil. Nevertheless, Pérez-Santos and Moreno (1988) still considered *A. reticulatus* in the Colombian fauna.

Alvarez *et al.* (1992) described *A. reticulatus scrocchi* based on 10 specimens from Santa Maria, state of Rio Grande do Sul, Brazil and San Miguel, province of Corrientes, Argentina. Alvarez *et al.* (1992) distinguished *A. r. scrocchi* from the nominal form by having a pale occipital band and more contrasting colour pattern (vs. lacking occipital band and with a less contrasting reticulate pattern in *A. r. reticulatus*). Fernandes (1996) revised the *A. reticulatus* complex (*A. r. reticulatus*, *A. r. paraguayensis*, and *A. r. scrocchi*), considering *A. paraguayensis* as a full species and synonymizing *A. r. scrocchi* with the nominal species. Fernandes (1996) diagnosed *A. paraguayensis* from *A. reticulatus* by the holotype of the former having 165 ventrals compared to 149–163 in his sample of *A. reticulatus*. Fernandes (1996) established that characters employed previously to diagnose *A. r. scrocchi* fall within the range of ontogenetic colour variation of *A. r. reticulatus*. The same author restricted again the concept of *A. reticulatus* to the populations from southern South America, stressing that AMNH material (from Colombia) referred to *A. reticulatus* by Pérez-Santos and Moreno (1988) were in fact *A. nicefori*.

Based on additional specimens examined here, we corroborate all decisions proposed by Fernandes (1996). Although the range of ventrals in both sexes of *A. paraguayensis* and *A. reticulatus* broadly overlap, these species are easily diagnosed by dorsal colour pattern, number of maxillary teeth, and hemipenis morphology (see above and under remarks for *A. paraguayensis*). A distinct feature reported here with respect to the study of Fernandes (1996) is hemipenial morphology. We found that the organ of *A. reticulatus* described and illustrated by Fernandes (1996) was only partially everted, and that this species has in fact a moderately bilobed hemipenis (see Fig. 14A).

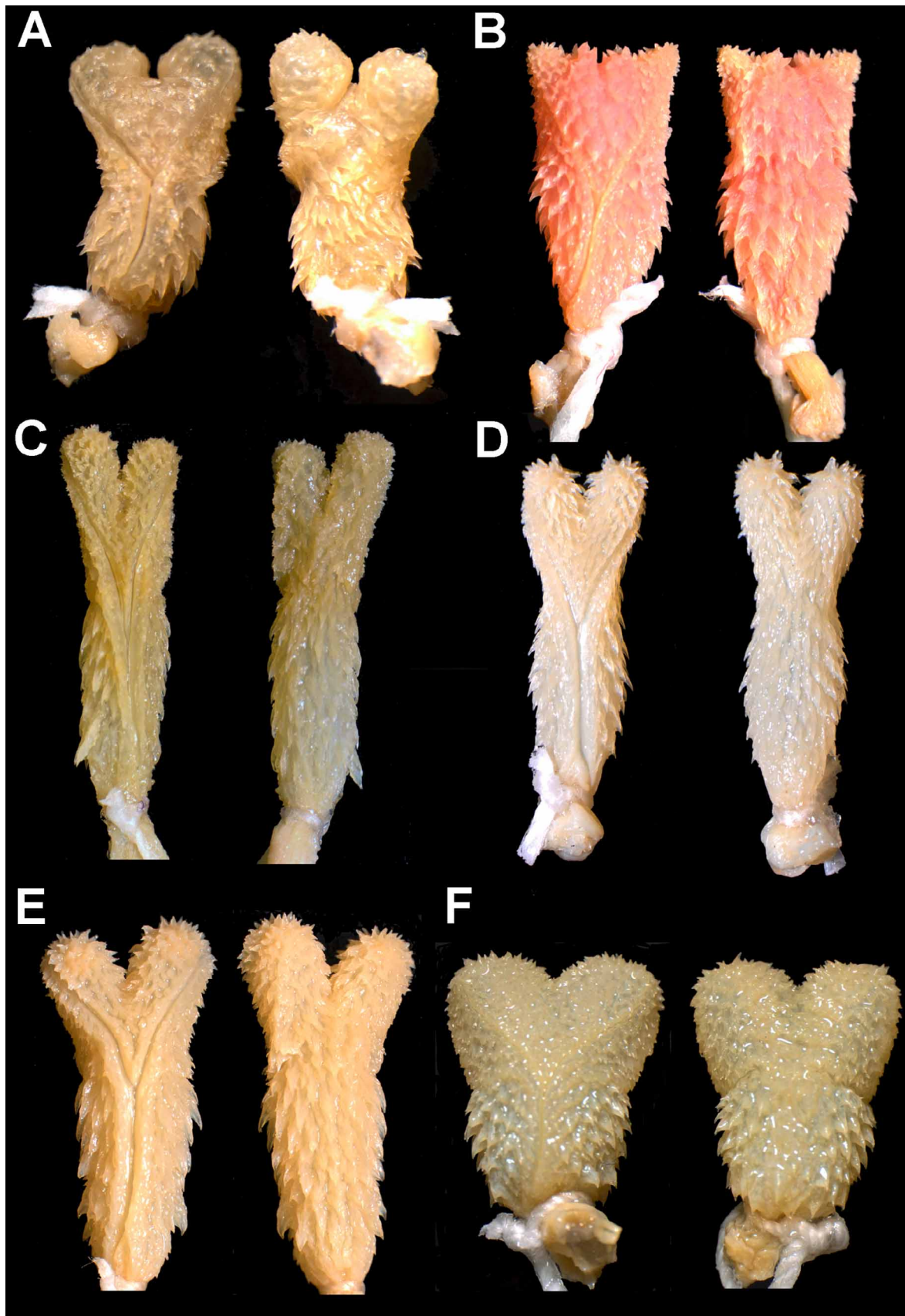


FIGURE 14. Sulcate (left) and asulcate (right) sides of the hemipenis of (A) *Atractus reticulatus* (MNRJ 1524), (B) *A. ronnie* (MNRJ 14194), (C) *A. serranus* (IBSP 9076), (D) *A. thalesdelemai* (MNRJ 10052), (E) *A. trihedrurus* (IBSP 55698), and (F) *A. zebrinus* (MNRJ 4470). Scale = 5 mm.

***Atractus ronnie* Passos, Fernandes & Borges-Nojosa, 2007**

Figs. 13C, 15A

Atractus ronnie Passos, Fernandes & Borges-Nojosa, 2007; Copeia 2007:789.*Atractus ronnie* – Loebmann, Ribeiro, Sales & Almeida, 2009; Biotemas 22:170.

Holotype: Adult female, MNRJ 14194, from Serra de Baturité (04°10'S, 38°55'W, ca. 800 m), municipality of Pacoti in the state of Ceará, Brazil, collected on 10 April 1998 by D. M. Borges-Nojosa (specimen examined).

Paratypes: Twenty-four specimens, all from Serra do Baturité, state of Ceará: municipality of Pacoti (CHUFC 1396, MNRJ 14195), collected on 17 July 1989 by L. W. Lima-Verde; (CHUFC 2646), 18 December 1997 by D. M. Borges-Nojosa; (CHUFC 2648), 11 January 1998 by D. M. Borges-Nojosa; (CHUFC 2658), 09 December 2005 by D. M. Borges-Nojosa, J. C. L. Melo, and M. J. B. Leite, locality of Sítio Olho d'água dos Tangarás; (CHUFC 2481, 3500), 23 February 1989 by D. M. Borges-Nojosa, locality of Monguba; (CHUFC 3502), 03 April 1990 by D. M. Borges-Nojosa, locality of Sítio São José; (MNRJ 14196–97), 16 February 1999 and 10 April 1998, respectively by D. M. Borges-Nojosa, locality of Granja; (CHUFC 2641, 2647), 02 November 1997 by D. M. Borges-Nojosa, locality of Sítio Pau do Alho; (CHUFC 25980), 28 April 2005 by W. C. M. Luz, locality of Sítio Xangrilá; (CHUFC 2652–24), 2005 December by W. C. M. Luz, locality of Cidade Pacoti; (CHUFC 2675–76, 2678), between 17 February and 02 March 2006 by W. C. M. Luz, locality of Cidade Pacoti; (CHUFC 2733), 04 April 1990 by D. M. Borges-Nojosa, district of Santana. Municipality of Baturité: (CHUFC 2578), 11 February 2005 by D. M. Borges-Nojosa, P. Cascon, and J. C. L. Melo, locality of Sítio Escuro. Municipality of Mulungu: (CHUFC 2645), 1991 by D. M. Borges-Nojosa and S. M. Cornélio. Municipality of Guaramiranga: (CHUFC 2649), 15 August 1998 by D. M. Borges-Nojosa, locality of Linha da Serra; (CHUFC 2651), 6 June 2005 by D. M. Borges-Nojosa, P. Cascon, and J. C. L. Melo, locality of Sítio Guaramiranga.

Diagnosis: *Atractus ronnie* is distinguished from all congeners by the combination of the following characters (1) 17 smooth dorsal scale rows; (2) two postoculars; (3) moderate loreal; (4) temporals generally 1+2; (5) seven supralabials, third and fourth contacting orbit; (6) seven infralabials, first four contacting chinshields; (7) seven or eight maxillary teeth; (8) three gular scale rows; (9) generally three preventrals; (10) 146–163 ventrals in females, 129–151 in males; (11) 16–23 subcaudals in females, 20–25 in males; (12) dorsum creamish yellow uniformly scattered with black dots; (13) venter immaculate creamish white; (14) body size moderate in females (maximum 391 mm SVL), small in males (248 mm SVL); (15) tail short in females (8.1–10.5% SVL), moderate (11.4–15.5% SVL) in males; (16) hemipenis slightly bilobed, slightly semicapitate, and semicalyculate.

Comparisons: Among all congeners, *A. ronnie* shares 17 dorsal scale rows, seven upper and lower labials, first four infralabials infralabials contacting chinshields, generally three gular scale rows, seven maxillary teeth, dorsum creamish yellow uniformly scattered with black dots, venter and tail immaculate creamish white, hemipenis slightly bilobed, semicapitate, semicalyculate, and lateral projections on the lobes only with *A. pantostictus*. *Atractus ronnie* differs from *A. pantostictus* by lacking a black collar and lateral tip projections on lobes (vs. conspicuous black collar and lateral tip projections on lobes).

Description: Head longer than wide, flattened in lateral view, round in dorsal view; snout truncate in lateral view, round in dorsal view; canthus rostralis well marked in lateral view; cervical constriction indistinct; rostral sub-triangular in frontal view, broader than high, poorly visible in dorsal view; internasal as long as wide; internasal suture sinistral with respect to prefrontal suture; prefrontal as long as wide; supraocular sub-trapezoidal, slightly longer than wide; frontal sub-pentagonal, as long as wide; parietal twice as long as wide; nasal divided; nostril located between prenasal and postnasal; prenasal twice as high as long; postnasal slightly higher than long; loreal moderate, contacting second and third supralabial; pupil subelliptical; generally two postoculars of similar size; lower postocular occasionally longer than upper postocular; temporal

generally 1+2; anterior temporal twice as long as high; upper posterior temporal elongate, about four times as long as wide; seven supralabials, third and fourth contacting orbit; first two supralabials of similar size and slightly smaller than third; sixth higher and seventh longer than remaining supralabials; symphyial sub-triangular, twice broader than long; seven infralabials, first four contacting chinshields; first pair of supralabials in contact behind symphyial, preventing symphyial/chinshields contact; chinshields twice as long as wide; generally three gular scale rows; generally three prementals; 17 smooth dorsal scale rows; dorsals lacking apical pits, supra-anal tubercles, and keels; caudal spine long, conical, robust, and acuminate.

Maxillary arch: Flattened in dorsal view, with five prediastemal and two postdiastemal teeth; prediastemal teeth large, moderately spaced, of similar size, curved posteriorly, angular in cross section, robust at base, narrower on the apices; maxillary diastema short; postdiastemal teeth slightly smaller than last prediastemal tooth; lateral process absent or poorly developed.

Colour in preservative: Dorsum and background of head grayish brown, except for snout region (rostral, nasals, internasals, loreal, and anterior portion of prefrontals) creamish white coloured; supralabials creamish white, except for dorsal edges of third and fourth supralabials dark brown; mental region and paraventals creamish white; venter and tail generally immaculate creamish white; venter rarely with dark brown spots concentrated on the centre of ventral and subcaudals scales; dorsal ground colour creamish yellow uniformly scattered with black dots (one or two scales wide), arranged in three longitudinal series anteriorly to the level of 11th ventral scale (Fig. 15A).

Juvenile colouration in preservative: Juveniles and sub-adults with dorsal ground colour creamish yellow with uniformly scattered small black dots (one or two scales long), frequently arranged in longitudinal series.

Colour in life: Dorsum of head uniform brown; supralabials creamish yellow, except for brown dorsal margins of third and fourth scales; infralabials and mental region creamish yellow; venter and tail creamish yellow; dorsal ground colour of body reddish brown to brown uniformly scattered with black dots (Fig. 13C).

Hemipenis morphology (everted organ $n = 1$): Retracted organ bifurcates and extends to the level of 10th subcaudal. Hemipenis slightly bilobed, semicapitate, and slightly semicalyculate; lobes poorly distinct and restricted to distal portion of capitulum; lobes with lateral projections on the apices, well marked by lateral depressions on their bases, covered with spinulate calyces; spinulate calyces concentrated on lateral portions on both sides of capitulum; weakly defined capitulum located just above sulcus spermaticus bifurcation; capitular groove indistinct on sulcate side and clearly visible on asulcate side of hemipenis; intrasulcar region and asulcate side of capitulum covered with alary spines; median portion of capitulum thick compared to hemipenial body; capitulum similar in size to hemipenial body on sulcate side and smaller than hemipenial body on asulcate side; sulcus spermaticus bifurcates on the middle of the organ; branches of the sulcus spermaticus with centrifugal orientation, running to lobes projections; sulcus spermaticus margins stout and narrow, bordered with spinules from the base of organ to tips of lobes; hemipenial body similar in width to capitulum, covered with large hooked spines; basal naked pocket absent; basal portion of hemipenis with longitudinal plicae and disperse spinules (Fig. 14B).

Variation: Largest male SVL 248 mm, CL 37 mm; largest female SVL 312 mm, CL 30 mm; tail 11.4–15.5% ($\bar{x} = 13.4$; SD= 1.2; $n = 13$) SVL in males, 8.1–10.4% ($\bar{x} = 9.4$; SD= 0.6; $n = 11$) SVL in females; 133–144 ($\bar{x} = 140.3$; SD= 3.3; $n = 14$) ventrals in males, 154–160 ($\bar{x} = 157.4$; SD = 1.6; $n = 11$) in females; 20–25 ($\bar{x} = 23.1$; SD = 1.7; $n = 14$) subcaudals in males, 17–20 ($\bar{x} = 18.9$; SD = 1.1; $n = 11$) in females; 2 ($n = 2$), 3 ($n = 24$), or 4 ($n = 1$) prementals; 3 ($n = 3$ sides) or 4 ($n = 47$ sides) first infralabials contacting chinshields; 1 ($n = 2$ sides) or 2 ($n = 48$ sides) postoculars; 1+2 ($n = 45$ sides) or 2+2 ($n = 5$ sides) temporals; 17 ($n = 10$), 16 ($n = 7$), or 15 ($n = 8$) anterior dorsal scale rows; 8–10 ($\bar{x} = 8.7$; SD = 0.6; $n = 52$ sides) dorsal scale rows level with the second subcaudal; 7 ($n = 19$) or 8 ($n = 1$) maxillary teeth; retracted hemipenis extends to the level of seventh ($n = 1$), eighth ($n = 4$) or ninth ($n = 1$) subcaudal.

Distribution: Initially known only from Serra do Baturité Mountains in the state of Ceará on northeastern Brazil (Passos *et al.* 2007b), *A. ronnie* was reported recently from two other mountainous areas in the state of Ceará, the Ararípe (07°15' S, 39°28' W) and Ibiapaba (03°43' S, 40°56' W) plateaus (Loebmann *et al.* 2009). This species inhabits Lower Montane Rainforest above 600 m elevation (Fig. 4).

Remarks: Passos *et al.* (2007b) described *A. ronnie* based on 25 specimens and suggested this species was closely related to *A. pantostictus*. The close similarity between these two species is here reinforced based on the analysis of additional characters (see above), and consistent with the suggestion that these species are closely related to Amazonian *A. altagratiae*, *A. insipidus*, and *A. punctiventris* (Passos & Fernandes 2008).

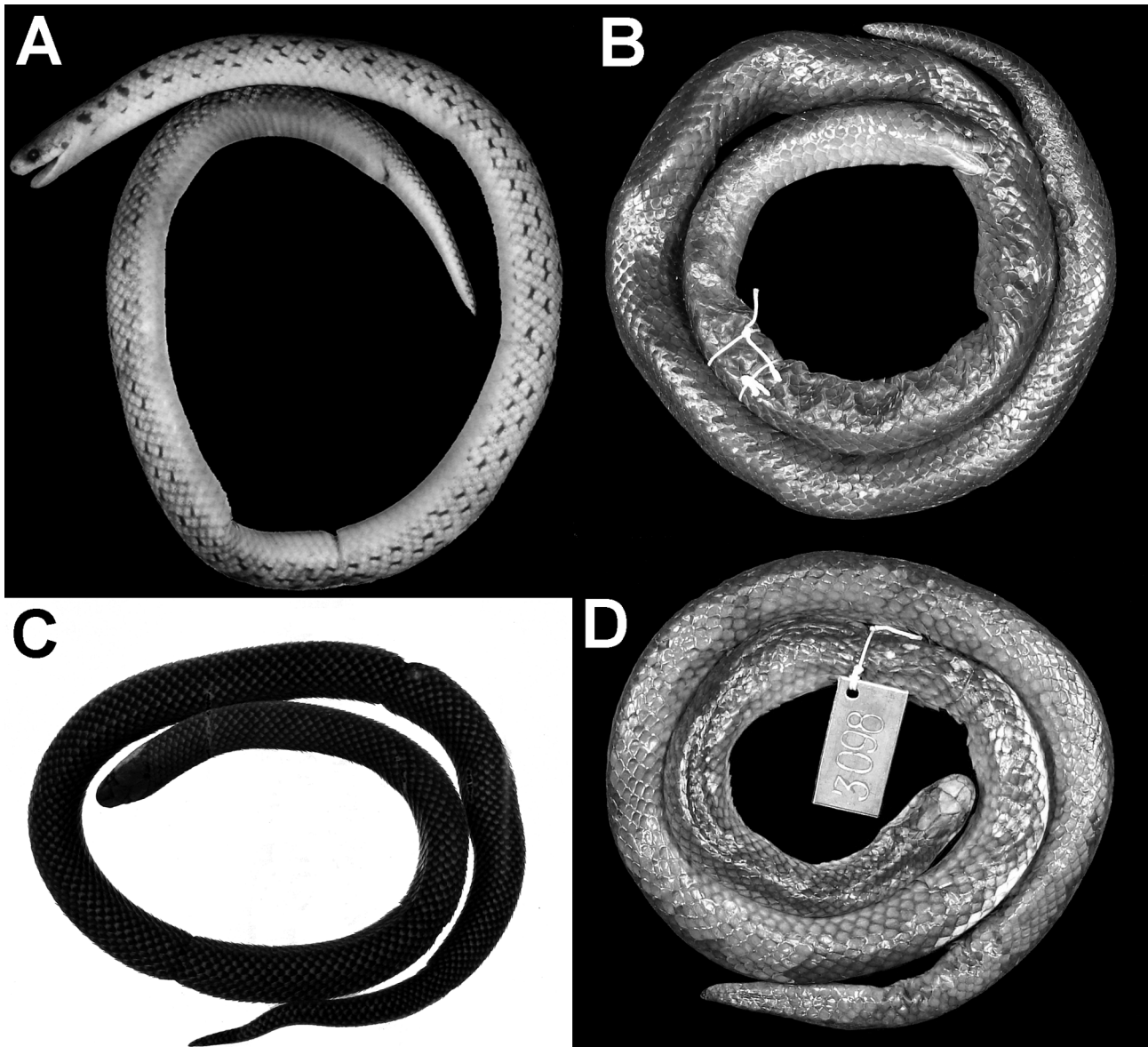


FIGURE 15. General view of the holotypes of (A) *Atractus ronnie* (MNRJ 14134), (B) *A. serranus* (IBSP 7239), (C) *A. thalesdelemai* (MNRJ 10051), and (D) *A. trihedrurus* (IBSP 3098).

Atractus serranus Amaral, 1930

Figs. 15B, 16A,C

Atractus serranus Amaral, 1930; Bull. Antivenin Inst. Amer. 4:65.

Holotype: Adult female, IBSP 7238 (not 5315, as reported in the original description), from an uncertain point at the northernmost section of the Serra de Paranapiacaba (between the municipalities of São Paulo and São Vicente), state of São Paulo, Brazil, collected on 17 August 1930 by "men working in the construction of the railway between Mayrink and Santos" (*sensu* Amaral 1930d) (specimen examined).

Diagnosis: *Atractus serranus* is distinguished from all congeners by the following combination of characters: (1) 17/17/17 smooth dorsal scale rows; (2) generally two postoculars; (3) loreal moderate to long; (4) temporals 1+2; (5) generally seven supralabials, third and fourth contacting chinshields; (6) seven infralabials, first four contacting chinshields; (7) eight to ten maxillary teeth; (8) generally three gular scale rows; (9) generally three preventrals; (10) 150–163 ventrals in females, 141–147 in males; (11) 18–23 subcaudals in females, 26–29 in males; (12) dorsum uniformly black in adults and reddish brown to black scattered with irregular dorsal blotches in juveniles; (13) venter uniformly black in adults and usually paler in juveniles; (14) large body size in females (790 mm SVL) and males (515 mm SVL); (15) tail short in females (7.9–10.2% SVL), moderate in males (9.2–14.6% SVL); (16) hemipenis moderately bilobed, semicapitate, and semicalyculate.

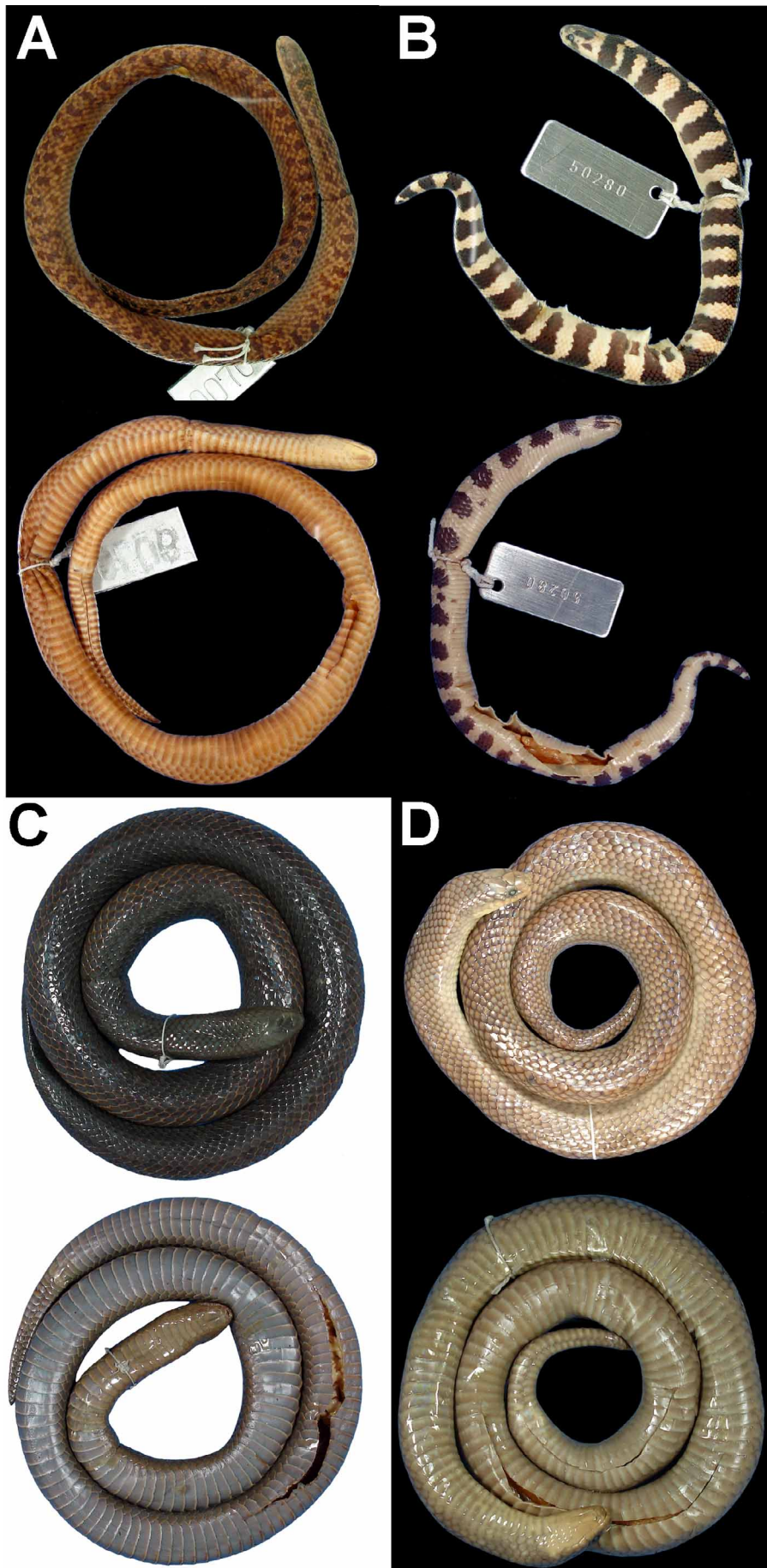
Comparisons: Among all congeners, *A. serranus* shares 17 dorsal scale rows at midbody, large body (> 500 mm in mature females), and black colour on the belly only with *A. gigas* and *A. trihedrusus*. *Atractus serranus* differs from *A. gigas* by having four infralabials contacting chinshields, 18–23 subcaudals in females and 26–29 in males (vs. two or three infralabials contacting chinshields, 31–37 subcaudals in females and 42–46 in males); from *A. trihedrusus* by having juvenile colouration red or reddish dark brown uniformly scattered with black irregular blotches or fragmented dots, belly uniformly black after 15th ventral, 141–147 ventrals in males and 150–163 in females, maximum SLV 370 mm in males and 790 mm in females (vs. juveniles red or reddish brown with wide transverse bands reaching the paraventral region, 136–150 ventrals in males and 146–159 in females, maximum SVL 735 mm in males and 1010 mm in females).

Description: Head longer than wide, arched in lateral view, sub-triangular in dorsal view; snout truncate in lateral view, round in dorsal view; canthus rostralis well marked in lateral view; cervical constriction barely distinct; rostral broader than high, sub-triangular in frontal view, poorly visible in dorsal view; internasal as long as wide; internasal suture sinistral with respect to prefrontal suture; prefrontal broader than long; supraocular sub-rectangular, longer than wide; frontal sub-triangular, as long as wide; parietal twice longer than wide; nasal divided; nostril generally restricted to prenasal; prenasal and postnasal twice as high as long; moderate to long loreal, contacting second and third supralabials; pupil sub-elliptical; generally two postoculars; upper postocular slightly higher and longer than lower postocular; temporals 1+2; anterior temporal twice longer than high; upper posterior temporal elongate, three times longer than wide; generally seven supralabials, third and fourth contacting orbit; second supralabial higher than first and smaller than third; sixth higher and seventh longer than remaining supralabials; symphyisial triangular, twice broader than long; seven infralabials, first four contacting chinshields; first pair of supralabials in contact behind symphyisial, preventing symphyisial/chinshields contact; chinshields twice longer than wide; generally three gular scale rows; generally three preventrals; 17/17/17 smooth dorsal scale rows; dorsals lacking apical pits, supra-anal tubercles, and keels; caudal spine long, robust, and rhomboid.

FIGURE 16. Dorsal and ventral views of juveniles (A, B) and adults (C, D) specimens of *Atractus serranus* (left) and *A. trihedrusus* (right).

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Maxillary arch: Slightly arched in dorsal view, with six to eight prediastemal and two or three postdiastemal teeth; prediastemal teeth large, moderately spaced, of similar size, curved posteriorly, angular in cross section, robust at base, narrower on the apices; diastema short; postdiastemal teeth smaller than prediastemal tooth; lateral process poorly developed, lacking posterior projection.

Colour in preservative: Dorsum of head black; background of head black to dorsal edges of supralabials; supralabials creamish white, pale brown, or beige; mental region beige, brown or black; mental region, if beige, with dark brown blotches concentrated on symphyseal, first pair of infralabials, and anterior portion of chinshields; venter pale brown in the first 15th scales and uniformly black after; venter occasionally with posterior margin of each ventral scales paler (beige); tail black, occasionally with posterior margins of each subcaudal beige; dorsal ground colour generally uniformly black; occasionally adults maintain poorly distinct black dots along body (Fig. 14B, 16C).

Juvenile colouration in preservative: Juveniles and sub-adults with dorsum of head reddish brown to dark brown; dorsum of head frequently with black dots along sutures or centre of cephalic plates; ventral ground colour brown (juveniles) or dark brown to black (sub-adults); dorsal ground colour of body reddish brown, with irregular black blotches (two or three scales long) above paravertebral region; blotches frequently fragmented as irregular dots (one or two scales long) on the flanks and paraventral region; small dots frequently connected dorsally to irregular blotches (Fig. 16A).

Hemipenis morphology (everted organs $n = 3$): Retracted organ bifurcates on eighth and extends to the level of 10th subcaudal. Hemipenis moderately bilobed, semicapitate, semicalyculate; lobes distinct and restricted to distal portion of capitulum; lobes sub-cylindrical generally of similar size and with round apices; lobes considerably longer than remaining capitulum; lobes and capitulum covered with small spinulate calyces; horizontal walls of calyces forming well defined calyculate flounces on lateral portion of the sulcate side of hemipenis; spinules replaced by papillae toward lobe apices; asulcate side of capitulum with irregular calyces, forming conspicuous medial and lobular crests; capitular groove slightly distinct on the sulcate side and well defined (except above median crest) on the asulcate side of hemipenis; capitulum located just above sulcus spermaticus bifurcation and slightly smaller than hemipenial body; sulcus spermaticus bifurcates on the middle of organ; sulcus spermaticus branches centrifugally oriented, running to tip of lobes; margins of sulcus spermaticus stout and laterally expanded, bordered with spinules from the base to the apices of lobes; hemipenial body subcylindrical, covered with moderate hooked spines along length; large spines concentrated on lateral portion of the sulcate side of hemipenis; basal naked pocket restricted to basal portion of hemipenial body; basal region of hemipenis with longitudinal plicae and diffuse spinules (Fig. 14C).

Variation: Largest male 515 mm SVL, 68 mm CL, largest female 790 mm, SVL, 65 mm CL; tail 9.2–14.6% ($\bar{x} = 12.6$; $SD = 1.8$; $n = 6$) SVL in males, 7.9–10.2% ($\bar{x} = 8.8$; $SD = 0.6$; $n = 20$) SVL in females; 141–147 ($\bar{x} = 145.7$; $SD = 2.3$; $n = 6$) ventrals in males, 150–163 ($\bar{x} = 157.7$; $SD = 3.1$; $n = 20$) in females; 26–29 ($\bar{x} = 27.6$; $SD = 1.3$; $n = 6$) subcaudals in males, 18–23 ($\bar{x} = 20.3$; $SD = 1.3$; $n = 20$) in females; 6 ($n = 1$ side), 7 ($n = 50$ sides), or 8 ($n = 1$ side) supralabials; 6 ($n = 1$ side), or 7 ($n = 51$ sides) infralabials; 3 ($n = 4$ sides) or 4 ($n = 48$ sides) first infralabials contacting chinshields; 3 ($n = 51$ sides), or 4 ($n = 1$ side) gular scale rows; 1 ($n = 1$), 2 ($n = 4$), or 3 ($n = 21$) prementals; 1 ($n = 1$ side), or 2 ($n = 49$ sides) postoculars; 1+1 ($n = 2$ sides), 1+2 ($n = 48$ sides), or 2+2 ($n = 2$ sides); 8–10 ($\bar{x} = 8.9$; $SD = 0.5$ $n = 26$) dorsal scale rows on the level of second subcaudal; 8 ($n = 4$ sides), 9 ($n = 35$ sides), or 10 ($n = 2$ sides) maxillary teeth; 4.1–25.2 mm body diameter; retracted hemipenis bifurcates on seventh to eighth and extends from ninth to 10th subcaudal ($n = 3$).

Distribution: Serra de Paranapiacaba and Tietê Valley, from Salesópolis (22°16'S, 42°32'W) westward to Campinas (22°54'S, 47°05') and southward to Cubatão (24°56'S, 47°58'W) in the state of São Paulo, Brazil. *Atractus serranus* inhabits Lower Montane Rainforest between 700–1000 m elevation (Fig. 7). The Cubatão record is based probably on the label from the municipality's headquarters, without other data sources, and we suppose it was collected from high elevations in the foothills of the Serra do Mar.

Remarks: Amaral (1930d) described *A. serranus* on the basis of one individual from Serra de Paranapiacaba, a mountain range near São Paulo city, southeastern Brazil. Subsequently, several Brazilian herpetologists (including ourselves) in the last two decades have placed the taxonomic status of *A. serranus* in doubt with respect to *A. trihedrurus* (see Marques *et al.* 2001: 171). In order to test the morphometric discrimination of these two species and the similar *A. francoi*, we performed a DFA with all available samples of these nominal taxa. We labeled individuals according to similarity of colour pattern to the type series of *A. serranus* and *A. trihedrurus*, as well as considering the geographical proximity among subpopulations of each taxon. Thus the juveniles with wide dorsal bands and adults with dorsum pale to grayish brown and venter pale brown were labeled as *A. trihedrurus*; juveniles having irregular blotches and adults with dark brown to black dorsum and venter were labeled as *A. serranus*; juveniles and adults with a nearly uniform black dorsum and venter were labeled as *A. francoi*. Although the first two axes from DFA were insufficient to entirely discriminate *A. serranus* and *A. trihedrurus*, the female population of *A. francoi* was distinguished (Fig. 17). The first principal orthogonal axis corresponds to about 78.6% of intergroup variance and is strongly correlated with the number of ventral scales and CL/SVL ratio, whereas the second DFA function corresponds to about 21.4% of variance and was strongly correlated with the number of subcaudals (Table 1). Nevertheless, qualitative (juvenile colour patterns) character analyses distinguish the populations previously labeled as *A. serranus* from the populations attributed to *A. trihedrurus*. Furthermore, the classificatory matrix from the DFA (based only on quantitative characters) resulted in more than 90% correct allocations of individuals into *A. serranus* and *A. trihedrurus* based on colour patterns (Table 2).

TABLE 1. Classificatory matrix from discriminant analysis for females of *Atractus francoi*, *A. serranus*, and *A. trihedrurus*, showing individuals correctly allocated based on the classification by Jackknife.

| Groups | Frequency of correct classification | <i>A. serranus</i> | <i>A. trihedrurus</i> | <i>A. francoi</i> |
|-----------------------|-------------------------------------|--------------------|-----------------------|-------------------|
| <i>A. serranus</i> | 90% | 18 | 1 | 1 |
| <i>A. trihedrurus</i> | 90.5% | 2 | 19 | 0 |
| <i>A. francoi</i> | 100% | 0 | 0 | 4 |
| Total | 91% | 20 | 20 | 5 |

TABLE 2. Eigenvectors, eigenvalues, and percent variance explained for the first two axes of discriminant analysis of non-transformed data for females of *Atractus francoi*, *A. serranus*, and *A. trihedrurus*. Loadings in bold font correspond to the original variables heavily correlated with the respective discriminant functions.

| Variable | DF I | DF II |
|---------------------|-----------------|-----------------|
| DORC | 0.29523 | 0.031261 |
| VENT | -1.03028 | -0.03963 |
| SUBC | 0.36587 | -1.02971 |
| CHIN | -0.22852 | 0.33786 |
| GULA | 0.37797 | -0.18651 |
| SVL/CL | -0.10411 | 0.40218 |
| MATH | 0.53824 | -0.32475 |
| Eigenvalues | 2.50025 | 0.68041 |
| Percent of variance | 78.6 | 21.4 |

Additionally, we found that colour patterns of adult *A. serranus* and *A. trihedrurus* do not have a latitudinal or altitudinal cline in variation such as occurs in some other species of *Atractus* (Passos 2008). In fact, the colour pattern of adult *A. serranus* is most similar to darker individuals from the extreme south of the distribution of *A. trihedrurus* (Brazilian states of Paraná and Santa Catarina). This pattern is consistent with character displacement in which geographically closer populations of the two species (sympatric populations from vicinities of São Paulo city) have very different colour patterns (Fig. 16), while subpopulations from non-overlapping extremes of their distribution are, in general, most similar in colour. Therefore, despite difficulties in distinguishing adult specimens from some localities, we interpreted this as crypsis between *A. serranus* and *A. trihedrurus* rather than evidence for disparate intrapopulational variation in juveniles and adults of a single species.

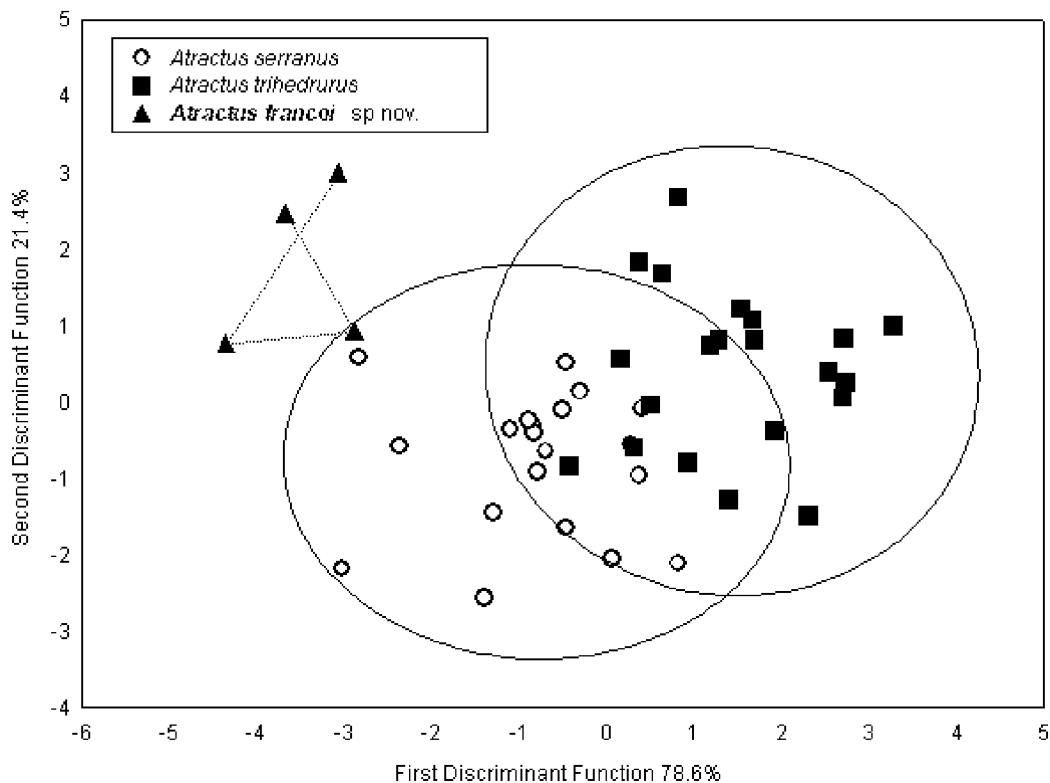


FIGURE 17. Bivariate plot with 95% confidence regions for the first two axes derived from scores of DFA analyses for females of *Atractus francoi* sp. nov., *A. serranus*, and *A. trihedrurus*.

Atractus thalesdelemai Passos, Fernandes & Zanella, 2005

Fig. 15C

Atractus thalesdelemai Passos, Fernandes & Zanella, 2005; Herpetologica 61:210.

Atractus kangueryensis Cacciali, Villalba & Yanoski, 2007; South Amer. J. Herpetol. 2:84. **New synonymy.**

Holotype: Adult male, MNRJ 10052, from Fazenda Corporação da Brigada Militar, municipality of Passo Fundo (28°14'S, 52°21'W, ca. 625 m), state of Rio Grande do Sul, Brazil, collected on 30 January 2001 by N. Zanella (specimen examined).

Paratypes: Seven specimens, all from the municipality of Passo Fundo, state of Rio Grande do Sul: adult females (MNRJ 10053–54), collected on 26–30 November 2001 by Noeli Zanella in pitfall traps, locality Fazenda Corporação da Brigada Militar; juvenile and adult males (MNRJ 10080–81) collected on 15 August

2001 and 25 August 2002, respectively by Noeli Zanella in pitfall traps, locality Fazenda Corporação da Brigada Militar; adult female (CRUPF 172), collected on 5 August 1994 by L. Portilho, locality Jardim Botânico; adult female (CRUPF 405), collected on 12 October 1998 by R. Bibiano, locality Vera Cruz; adult male (CRUPF 801), collected on 12 February 2001 by Nicolau Pot, locality Jardim Botânico.

Diagnosis: *Atractus thalesdelemai* is distinguished from all congeners by the combination of the following characters: (1) 17/17/17 smooth dorsal scale rows; (2) single postocular; (3) loreal moderate; (4) temporals 1+2; (5) six supralabials, third and fourth contacting orbit; (6) six infralabials, first three contacting chinshields; (7) generally six maxillary teeth; (8) three gular scale rows; (9) generally three preventrals; (10) 165–169 ventrals in females, 149–154 in males; (11) 22–26 subcaudals in females, 26–30 in males; (12) dorsum grayish brown, except for first two dorsal scale rows creamish white; (13) venter and tail immaculate creamish white; (14) body size moderate in females (maximum SVL 381 mm), small in males (maximum SVL 265 mm); (15) tail small in females (9.1–10.8% SVL), moderate (13.1–14.3% SVL) in males; (16) hemipenis moderately bilobed, semicapitate, and semicalyculate.

Comparisons: Among all congeners, *A. thalesdelemai* shares 17 dorsal scale rows, six upper and lower labials, single postocular, dorsum uniformly grayish or pale brown, and venter creamish white only with *A. balzani*. *Atractus thalesdelemai* differs from *A. balzani* by having maximum tail length 38 mm, 149–154 ventrals in males and 165–169 in females, 26–30 subcaudals in males and 22–26 in females, dorsum with scales paler in the posterior edges, and homogeneously creamish white venter (vs. tail length 50 mm, 159 ventrals, 32 subcaudals, dorsum with scales paler in the centre, and venter yellowish speckled with brown in *A. balzani*).

Description: Head twice as long as wide, flattened in lateral view, round in dorsal view; snout truncate in lateral view, round in dorsal view; cervical constriction indistinct; rostral sub-triangular in frontal view, wider than long, poorly visible in dorsal view; internasal moderate; internasal suture sinistral with respect to prefrontal suture; prefrontal longer than wide; supraocular sub-trapezoidal, twice as long as wide; frontal sub-triangular, as long as wide; parietal twice as long as wide; nasal divided; nostril located between prenasal and postnasal; prenasal and postnasal twice as high as long; loreal moderate, contacting second and third supralabials; pupil round; single postocular twice as high as long; temporals 1+2; anterior temporal twice as long as high; upper posterior temporals generally not fused into a single plate; six supralabials, third and fourth contacting chinshields; second supralabial slightly higher than first and similar in size to third; fourth supralabial higher and sixth longer than remaining supralabials; symphyisial sub-triangular, twice broader than long; generally six infralabials, first three contacting chinshields; first pair of infralabials in contact behind symphyisial, preventing symphyisial/chinshields contact; chinshields twice longer than wide; three gular scale rows; generally three preventrals; 17/17/17 smooth dorsal scale rows; dorsals lacking apical pits, supra-anal tubercles, and keels; caudal spine moderate, robust, conical, and acuminate.

Maxillary arch: Arched in dorsal view, with five or six prediastemal and one or two postdiastemal teeth; first three teeth large, angular in cross section, robust at base, slightly narrower on the apices, curved posteriorly, of similar size, tightly spaced; remaining prediastemal teeth moderately spaced, decreasing gradually in size posteriorly; maxillary diastema moderate; postdiastemal teeth slightly smaller than last prediastemal tooth; lateral process well developed, projected posteriorly.

Colour in preservative: Dorsum of head uniformly grayish brown; background of head grayish brown to dorsal edges of supralabials; ventral margins of nasals and lower temporals occasionally creamish white; supralabials creamish white; mental region, preventrals, belly, and tail immaculate creamish white; dorsum reticulated grayish brown with pale spots, except for two first scale rows creamish white; dorsal ground colour reticulations composed by grayish brown anterior and grayish white posterior from each scale (Fig. 15C).

Colour in life: Like colouration in preservative, but with first dorsal scale rows reddish white coloured.

Hemipenis morphology (everted organ, $n = 2$): Retracted organ bifurcates at 10th and extends to the level of 11th subcaudal. Hemipenis moderately bilobed, semicapitate, semicalyculate; lobes distinct and restricted to distal portion of capitulum; lobes clavate, centrifugally oriented with round apices; lobes and capitulum cov-

ered with small spinulate calyces; calyces progressively replaced with papillae toward lobe apices; capitulum with irregular calyces; horizontal walls of calyces originate calyculate flounces, occasionally restricted to lateral of sulcate side of capitulum; asulcate side of capitulum with conspicuous lobular and medial crests; capitular groove indistinct on the sulcate and slightly to well marked on the asulcate side of hemipenis; capitulum located just above sulcus spermaticus bifurcation and taller than hemipenial body; sulcus spermaticus bifurcates on the middle of the organ; sulcus spermaticus branches centrifugally oriented, running to tips of lobes; margins of sulcus spermaticus stout and narrow, bordered with spinules from the base to the lobe apices; hemipenial body sub-cylindrical, covered with moderate hooked spines; large spines concentrated on lateral portion of sulcate and distal region of asulcate side; basal naked pocket extends to distal portion of hemipenial body; basal region of with longitudinal plicae and diffuse spinules (Fig. 14D).

Variation: Largest male 265 mm SVL, 38 mm CL, largest female 381 mm SVL, 38 mm CL; tail 13.1–14.3% ($n = 2$) SVL in males, 6.9–10.8 % ($\bar{x} = 9.1$; $SD = 1.4$; $n = 4$) SVL in females; 149–154 ($\bar{x} = 151$; $SD = 2.2$; $n = 4$) ventrals in males, 165–169 ($\bar{x} = 166.5$; $SD = 1.0$; $n = 4$) in females; 26–30 ($\bar{x} = 28.2$; $SD = 1.7$; $n = 2$) subcaudals in males, 22–26 ($\bar{x} = 23.5$; $SD = 1.8$; $n = 4$) in females; 6 ($n = 16$ sides) or 4 ($n = 2$ sides) infralabials; 3 ($n = 16$ sides) or 4 ($n = 4$ sides) infralabials contacting chinshields; 1 ($n = 1$), 2 ($n = 1$), 3 ($n = 6$), or 4 ($n = 1$) preventrals; 9–11 ($\bar{x} = 9.9$; $SD = 0.6$; $n = 8$) dorsal scale rows on the level of second subcaudal; 6 ($n = 13$ sides) or 7 ($n = 3$ sides) maxillary teeth; 6 ($n = 9$ sides) or 7 ($n = 5$ sides) dentary teeth; retracted hemipenis bifurcates at level of eighth to 10th and extends to ninth to 11th subcaudal ($\bar{x} = 9$; $SD = 1.25$; $n = 4$).

Distribution: From Estancia San Isidro (26°31'S, 55°52'W) in the department of Itapúa, Paraguay, south-eastward to Passo Fundo (28°14'S, 52°21') in the state of Rio Grande do Sul, Brazil. *Atractus thalesdelemai* inhabits plant formations composed of Campos in transition zones with Submontane Semi-deciduous and riparian forests between 100–700 m elevation (Fig. 11).

Remarks: Passos *et al.* (2005b) described *A. thalesdelemai* based on eight specimens from the municipality of Passo Fundo in the Brazilian state of Rio Grande do Sul. Recently, Cacciali *et al.* (2007) described *A. kangueryensis* based on three individuals from Kangüery, department of Itapúa, Paraguay. Cacciali *et al.* (2007) distinguished *A. kangueryensis* from *A. thalesdelemai* on the basis of the number of ventral scales and colour pattern nuances, and pointed out that in contrast with *A. thalesdelemai*, *A. kangueryensis* undergoes an ontogenetic colour change. Although the type-series of *A. kangueryensis* could not be examined in the course of this study, the characters used by Cacciali *et al.* (2007) to differentiate their new species from *A. thalesdelemai* are insufficient to recognize *A. kangueryensis* as distinct from the former species. First, we strongly disagree with Cacciali *et al.* (2007) that the species differ in number of ventral scales because the range for *A. kangueryensis* (165–169) overlaps that for *A. thalesdelemai* (151–167). Furthermore, all colouration characters used by Cacciali *et al.* (2007) for diagnosing *A. kangueryensis* (temporal region grey, only first dorsal scale rows creamish white or pink, specimens uniformly grayish brown) from *A. thalesdelemai* (vs. temporal region creamish white, first two dorsal scale rows creamish white, specimens uniformly reticulate with pale colour posteriorly) are encompassed by variation occurring in adults and juveniles of *A. thalesdelemai* (see above).

As described and illustrated by Passos *et al.* (2005b), the holotype of *A. thalesdelemai* has grayish dorsal margins only on scales of the second dorsal row, temporal region invaded with creamish white, and dorsal scales uniformly reticulate with pale colour. However, re-examination of colour pattern in both sexes and all age classes in the type-series of *A. thalesdelemai*, revealed also the occurrence of features employed by Cacciali *et al.* (2007) to distinguish it from *A. kangueryensis*. Moreover, as found in many *Atractus* species (e.g., *A. reticulatus* and *A. trihedrurus*), the reticulate colour pattern is subject to geographic variation and can be obscured on specimens close to ecdysis or on melanic individuals (e.g., specimens from higher elevations). Furthermore, the pink colour on the first scale rows of the paratypes of *A. kangueryensis*, in our view, represent merely the fresh colour from recently collected specimens rather than an ontogenetic change of colour pattern, and we suspect that live specimens of *A. thalesdelemai* have pink on the first scale rows as is found

also in many congeners (P. Passos pers. observ.). For the reasons expressed above, *A. kangueryensis* is placed herein in the synonymy of *A. thalesdelemai*.

Atractus trihedrurus Amaral, 1926

Figs. 15D, 16B,D, 18A

Atractus trihedrurus Amaral, 1926; Arch. Mus. Nac. 24:105.

Atractus trihedrurus – Peters & Orejas-Miranda; Bull. Nat. Mus. Nat. Hist. 297:327 (*insertae sedis*).

Atractus trihedrurus – Fernandes, 1996; Comun. Mus. Ciênc. Tecnol. PUCRS, Sér. Zool., 8:51.

Holotype: Adult male, IBSP 3098, from São Bento do Sul (26°15'S, 49°23'W, ca. 870 m), state of Santa Catarina, Brazil, collected by J. Naderer on 17 October 1924 (specimen examined).

Paratype: Adult female, IBSP 3067, from Piraquara (25°26'S, 49°04', ca. 910 m), state of Paraná, Brazil, collected by G. Günst on January 27, 1923 (specimen examined).

Diagnosis: *Atractus trihedrurus* is distinguished from all congeners by the following combination of characters: (1) 17/17/17 smooth dorsal scale rows; (2) generally two postoculars; (3) loreal moderate to long; (4) temporals 1+2; (5) generally seven supralabials, third and fourth contacting chinshields; (6) seven infralabials, first four contacting chinshields; (7) eight to ten maxillary teeth; (8) generally three gular scale rows; (9) generally three preventrals; (10) 146–159 ventrals in females, 136–150 in males; (11) 16–23 subcaudals in females, 23–29 in males; (12) dorsum uniformly beige, grayish brown, or black in adults and beige or creamish red with black bands in juveniles and sub-adults; (13) venter creamish brown to uniformly black; (14) large body size, with females reaching 1010 mm SVL and males 735 mm SVL; (15) tail short in females (7.3–10.7% SVL), moderate in males (9.6–15.5% SVL); (16) hemipenis moderately bilobed, semicapitate, and semicalyculate.

Comparisons: Among all congeners, *A. trihedrurus* shares 17 dorsal scale rows on midbody and large body size in both sexes only with *A. gigas*, *A. major*, *A. obesus*, *A. titanicus*, and *A. torquatus*. *Atractus trihedrurus* differs from all of them, except *A. gigas*, by having a grayish brown or black dorsum in adult specimens and maximum female SVL > 1,000 mm. *Atractus trihedrurus* differs from *A. gigas* by having generally four infralabials contacting chinshields, 16–23 subcaudals in females and 23–29 in males (vs. two or three infralabials contacting chinshields, 31–37 subcaudals in females and 42–46 in males).

Description: Head longer than wide, arched in lateral view, sub-triangular in dorsal view; snout truncate in lateral view, round in dorsal view; canthus rostralis well marked in lateral view; cervical constriction barely distinct; rostral broader than high, sub-triangular in frontal view, poorly visible in dorsal view; internasal as long as wide; internasal suture sinistral with respect to prefrontal suture; prefrontal broader than long; supraocular sub-rectangular, longer than wide; frontal sub-triangular, as long as wide; parietal twice longer than wide; nasal divided; nostril generally restricted to prenasal; prenasal and postnasal twice as high as long; moderate to long loreal, contacting second and third supralabials; pupil sub-elliptical; generally two postoculars; upper postocular slightly higher and longer than lower postocular; temporals 1+2; anterior temporal twice longer than high; upper posterior temporal elongate, three times longer than wide; generally seven supralabials, third and fourth contacting orbit; second supralabial higher than first and smaller than third; sixth higher and seventh longer than remaining supralabials; symphyisial triangular, twice broader than long; seven infralabials, first four contacting chinshields; first pair of supralabials in contact behind symphyisial, preventing symphyisial/chinshields contact; chinshields twice longer than wide; generally three gular scale rows; generally three preventrals; 17/17/17 smooth dorsal scale rows; dorsals lacking apical pits, supra-anal tubercles, and keels; caudal spine long, robust, and rhomboid.

Maxillary arch: Slightly arched in dorsal view, with six to eight prediastemal and two or three postdiastemal teeth; prediastemal teeth large, moderately spaced, of similar size, curved posteriorly, angular in cross

section, robust at base, narrower at apices; maxillary diastema short; postdiastemal teeth smaller than prediastemal tooth; lateral process poorly developed, lacking posterior projection.

Colour in preservative: Dorsum of head brown, beige, grayish brown or black; background of head brown or black to dorsal edges of supralabials; supralabials creamish white or pale brown; mental region beige, brown or black; mental region, if beige, with dark brown blotches concentrated on symphyseal, first pair of infralabials, and anterior portion of chinshields; venter pale brown to uniformly black; venter occasionally with posterior margin of each ventral scales paler (beige or cream); tail brown to black, occasionally with posterior margins of each subcaudal beige; dorsal ground colour reticulate pale brown, dark brown, or black; dorsum if creamish or grayish brown, with darker edges of dorsal scales contrasting with pale centres; black bands clearly distinct in the dorsum of sub-adults and barely distinct in the adults (Fig. 15D, 16D).

Juvenile colouration in preservative: Juveniles and sub-adults with dorsum of head uniformly black or black with beige, red, or creamish red blotches along sutures between cephalic plates; dorsum of head occasionally beige, red, or creamish red with variegated black blotches above cephalic plates; ventral ground colour beige (juveniles) to dark brown (sub-adults); dorsal ground colour beige to reddish brown, with black bands on the flanks; dorsum frequently covered with complete bands (three to five scales long), alternated and connected to opposite ones along vertebral region; dorsum occasionally with irregular black blotches (two or three scales long) above paravertebral region and black dots (one or two scales long) fragmented on the flanks and paraventral region; small dots frequently connected dorsally to irregular blotches (Fig. 16B).

Colour in life: Adults with dorsal ground colour pale brown, grayish brown, or dark brown; sub-adults with dorsal ground colour beige to dark reddish covered with more or less evident black bands/blotches; juveniles with dorsal ground colour beige to red and clearly distinct black bands and/or blotches (Fig. 18A).

Hemipenis morphology (everted organs $n = 5$): Retracted organ bifurcates at eighth and extends to the level of 10th subcaudal. Hemipenis moderately bilobed, semicapitate, semicalyculate; lobes distinct and restricted to distal portion of capitulum; lobes sub-cylindrical of similar size, with round apices; lobes considerably longer than remaining capitulum; lobes and capitulum covered with small spinulate calyces; horizontal walls of calyces forming well-defined calyculate flounces on lateral portion of the sulcate side of hemipenis; spinules replaced by papillae toward lobe apices; asulcate side of capitulum with irregular calyces, forming conspicuous medial and lobular crests; capitular groove slightly distinct on the sulcate side and well defined on the asulcate side of hemipenis; capitulum located just above sulcus spermaticus bifurcation and slightly smaller than hemipenial body; sulcus spermaticus bifurcates at the middle of organ; sulcus spermaticus branches centrifugally oriented, running to tip of lobes; margins of sulcus spermaticus stout and laterally expanded, bordered with spinules from the base to the apices of lobes; hemipenial body subcylindrical covered with moderate hooked spines; large spines concentrated on lateral portion of the sulcate side of hemipenis; basal naked pocket restricted to basal portion of hemipenial body; basal region of hemipenis with longitudinal plicae and diffuse spinules (Fig. 14E).

Variation: Largest male 735 mm SVL, 83 mm CL, largest female 1010 mm, SVL, 75 mm CL; tail 9.6–15.5% ($\bar{x} = 12.2$; $SD = 1.3$; $n = 29$) SVL in males, 7.3–10.7% ($\bar{x} = 8.8$; $SD = 1.1$; $n = 20$) SVL in females; 136–150 ($\bar{x} = 143.5$; $SD = 3.9$; $n = 29$) ventrals in males, 146–159 ($\bar{x} = 151$; $SD = 3.1$; $n = 20$) in females; 23–29 ($\bar{x} = 25.2$; $SD = 1.4$; $n = 29$) subcaudals in males, 16–23 ($\bar{x} = 19$; $SD = 1.8$; $n = 20$) in females; 6 ($n = 4$ sides), 7 ($n = 89$ sides), or 8 ($n = 5$ sides) supralabials; 3 ($n = 6$ sides) or 4 ($n = 92$ sides) first infralabials contacting chinshields; 2 ($n = 1$ side), 3 ($n = 84$ sides), or 4 ($n = 24$ sides) gular scale rows; 2 ($n = 4$), 3 ($n = 31$), or 4 ($n = 19$) pre-ventrals; 0 ($n = 1$ side), 1 ($n = 3$ sides), or 2 ($n = 94$ sides) postoculars; 1+2 ($n = 96$ sides), or 2+2 ($n = 2$ sides); 8–12 ($\bar{x} = 8.9$; $SD = 0.6$; $n = 98$ sides) dorsal scale rows on the level of second subcaudal; 8 ($n = 7$ sides), 9 ($n = 68$ sides), or 10 ($n = 9$ sides) maxillary teeth; 5.3–39.4 mm body diameter; retracted hemipenis bifurcates on sixth to 14th and extends from eighth to 16th subcaudal ($n = 8$).

Distribution: A narrow and steep mountain region near the coast in southeast and south Brazil, from Ribeirão Pires (23°43'S, 46°25'W) in the state of São Paulo southward to Rio dos Cedros (26°40'S, 49°16'W)

in the state of Santa Catarina. *Atractus trihedrurus* inhabits Submontane to Upper Montane Rainforest between 500–1400 m (Fig. 7).



FIGURE 18. General view in life of juveniles (above) and adults (below) of *Atractus trihedrurus* (A) and *A. zebrinus* (B). Juvenile of *A. trihedrurus* from São Paulo, state of São Paulo, photo by B. Handam. Juvenile of *A. zebrinus* from Riacho Grande and adult of *A. trihedrurus* from Miracatu both in the state of São Paulo, photos by M.R. Duarte. Adult of *A. zebrinus* from Mananciais da Serra, state of Paraná, photos by H. Garcia.

Remarks: Amaral (1926) described *A. trihedrurus* based on two specimens from the southern part of Serra do Mar, Brazil. Amaral (1930d) proposed *A. serranus* on the basis of one individual from Serra de Paranapiacaba, a mountain range near São Paulo City, southeastern Brazil. Savage (1960) doubted the generic allocation of *A. trihedrurus* based on the original description of the species, in which Amaral (1926) mentioned two pairs of chinshields. Peters and Orejas-Miranda (1970) followed Savage's suspicion, placing *A. trihedrurus* as *incertae sedis*. Fernandes (1996) included *A. trihedrurus* in his key for *Atractus* species from southern portions of South America. Recently, Lema (2005) reported *A. trihedrurus*, without a voucher specimen, from the state of Rio Grande do Sul, but we suspect the specimen could be instead a melanic individual of *A. paraguayensis* because there is no further record of the *A. trihedrurus* for this area.

***Atractus zebrinus* (Jan, 1862)**

Figs. 18B, 19, 20

Rabdosoma zebrinum Jan, 1862; Arch. Zool. Anat. Fis. 2:15.*Rhabdosoma maculatus* – Günther, 1858; Catalogue of the Colubrine Snakes in the British Museum:421. (part.).*Atractus maculatus* – Boulenger, 1894; Catalogue of the Snakes in the British Museum 2:306. (part.).*Atractus guentheri* – Amaral, 1978; Serpentes do Brasil: Iconografia Colorida:114.*Atractus* cf. *guentheri* – Lema, 1994; Comun. Mus. Ciênc. Tecnol. PUCRS, Sér. Zool. 7:105. (part.).*Atractus maculatus* – Moura-Leite, Morato & Bérnils, 1996; Herp. Rev. 27:216.*Atractus zebrinus* – Fernandes, Freire & Puerto, 2000; Bol. Mus. Nac. Nov. Sér. Zool. 419:4.

Holotype: Specimen without defined locality, originally housed at Museo Civico di Storia Naturale di Milano (Jan 1862), believed to have been destroyed during the Second World War (S. Scali pers. comm.).

Diagnosis: *Atractus zebrinus* is distinguished from all congeners by the following combination of characters: (1) 17/17/17 smooth dorsal scale rows; (2) two postoculars; (3) loreal moderate; (4) temporals 1+2; (5) seven supralabials, third and fourth contacting orbit; (6) generally seven infralabials, first four contacting chinshields; (7) eight to ten maxillary teeth; (8) generally three gular scale rows; (9) generally three preventrals; (10) 149–170 ventrals in females, 136–153 in males; (11) 15–27 subcaudals in females, 20–32 in males; (12) dorsum creamish red with irregular transverse black blotches with white borders in adults; (13) venter immaculate creamish white; (14) moderate body size, with females reaching 600 mm SVL and males 457 mm SVL; (15) tail short in females (6.8–11.7% SVL), moderate to long (10.0–16.5% SVL) in males; (16) hemipenis slightly or moderate bilobed, semicapitate, and semicalyculate.

Comparisons: Among all congeners, *A. zebrinus* shares 17 dorsal scale rows, seven upper and lower labials, first four infralabials contacting chinshields, usually three gular scale rows, seven to ten maxillary teeth, preserved specimens having pale dorsum with irregular transverse black blotches, venter creamish white only with *A. maculatus*. *Atractus zebrinus* differs from *A. maculatus* by having blotches with white borders in adults, ground colour creamish red, and capitulum shorter than hemipenial body (vs. blotches lacking white border, dorsal ground colour creamish yellow, and capitulum longer than hemipenial body).

Description: Head twice longer than wide, flattened in lateral view, sub-triangular in dorsal view; snout truncate in lateral view, round in dorsal view; canthus rostralis well marked in lateral view; cervical constriction barely distinct; rostral broader than high, sub-triangular in frontal, clearly visible in dorsal view; internasal as long as wide; internasal suture sinistral with respect to prefrontal suture; prefrontal as long as wide; supraocular sub-trapezoidal, twice longer than wide; frontal sub-triangular, as long as wide; parietal twice as long as wide; nasal divided; nostril restricted to prenasal; prenasal and postnasal about twice as high as long; loreal moderate, contacting second and third supralabials; pupil round; two postoculars of similar size; occasionally upper postocular longer than lower postocular; temporals 1+2; anterior temporal twice as long as high; upper posterior temporal generally elongate, about four times longer than wide; seven supralabials, third and fourth contacting orbit; second supralabial higher than first and smaller than third; sixth higher and seventh longer than remaining supralabials; symphyisial sub-triangular, twice broader than long; seven infralabials, first four contacting chinshields; first pair of supralabials in contact behind symphyisial, preventing symphyisial/chinshields contact; chinshields twice longer than wide; three or four gular scale rows; generally three preventrals; 17/17/17 smooth dorsal scale rows; dorsals lacking apical pits, supra-anal tubercles, and keels; caudal spine moderate, robust, and rhomboid.

Maxillary arch: Slightly arched in dorsal view, with six to eight prediastemal and one or two postdiastemal teeth; prediastemal teeth large, generally of similar size, moderately spaced, curved posteriorly, angular in cross section, robust at base, narrower on the apices; maxillary diastema short; postdiastemal teeth half size of last prediastemal tooth; lacking lateral process.

Colour in preservative: Dorsum of head pale to dark brown with black blotches above frontal and parietals; background of head pale brown to dorsal margins of supralabials; supralabials, except for dorsal edges,

uniformly creamish white; mental region, preventrals, venter, and tail immaculate creamish white; dorsal ground colour creamish red with 29–47 transverse black irregular blotches or bands (one to three scales long); blotches or bands alternated on the flanks, bands frequently connected to opposite one along vertebral region; blotches or bands white bordered, extending to third dorsal scale rows; tail dorsally similar to body pattern, with 4–9 transverse blotches or tiny crossbands. Adults from low latitudes tend to be melanic dorsally, with blotches little distinct from ground colour.

Juvenile colouration in preservative: Juveniles and sub-adults with dorsal ground colour beige to creamish red with narrow transverse blotches or tiny bands (one or two scales long), lacking white pigment on the blotch margins.

Colour in life: Adult dorsum beige to reddish brown to dark brown, covered with black blotches creamish red bordered; juveniles dorsum creamish red to red, covered with black blotches without contrasting border; ventral margins of supralabials and mental region creamish yellow; venter and tail immaculate creamish white (Figs. 18, 20).

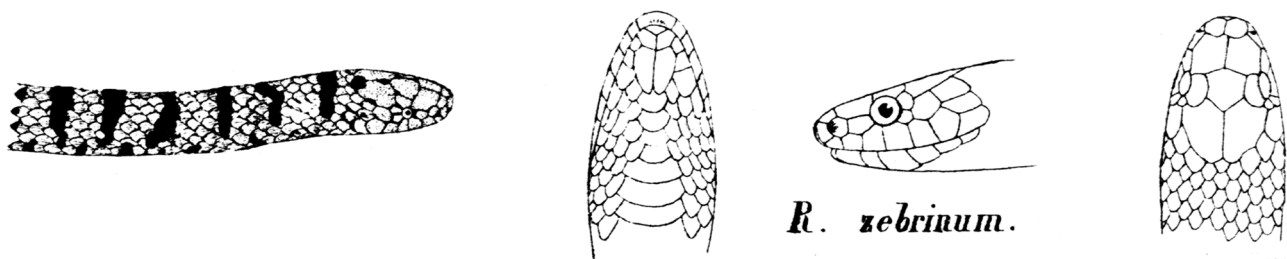


FIGURE 19. Original plate of the holotype of *Rhabdosoma zebrinum*, modified from Jan (1862).

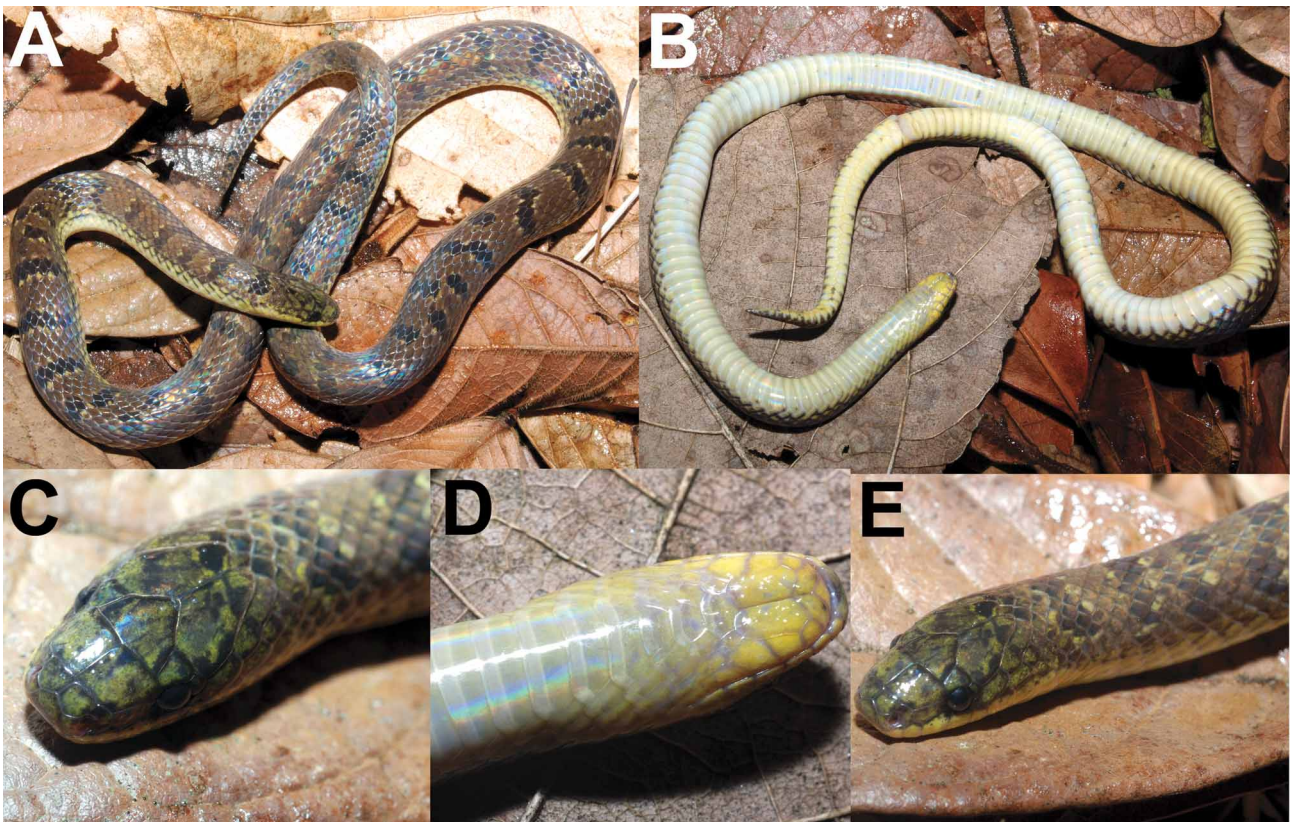


FIGURE 20. Dorsal (A) and ventral (B) views of the body, and dorsal (C), ventral (D), and laterodorsal (E) views of the head of *Atractus zebrinus* from RPPN Serra do Caraça, Catas Altas, state of Minas Gerais, photos by J.P. Pombal Jr.

Hemipenis morphology (everted organs $n = 5$): Retracted organ bifurcates at and extends to the level of eighth subcaudal. Hemipenis slightly moderately bilobed, semicapitate, and semicalyculate; lobes restricted to distal portion and generally weakly distinct from capitulum; lobes clavate and similar in size to remaining capitulum; lobes and capitulum covered with concentrated spinulate calyces; capitular groove evident on both sides of hemipenis; capitulum located at the level of sulcus spermaticus bifurcation; capitulum of similar size to hemipenial body; sulcus spermaticus bifurcates at the middle of organ; sulcus spermaticus oriented centrifugally, running to the tip of lobes; margins of sulcus spermaticus stout and narrow, bordered with spinules from the base of organ to lobes apices; hemipenial body sub-cylindrical uniformly covered with moderate hooked spines; basal naked pocket restricted to basal portion of hemipenial body; basal region of hemipenis with longitudinal plicae and disperse spinules (Fig. 14F).

Variation: Largest male 457 mm SVL, 51 mm CL, largest female 600 mm SVL, 49 mm CL; tail 10.0–16.5% SVL in males, 6.8–11.7% SVL in females; 136–153 ($\bar{x} = 145.4$; $SD = 3.7$; $n = 52$) ventrals in males, 158–174 ($\bar{x} = 155.7$; $SD = 4.1$; $n = 61$) in females; 20–32 ($\bar{x} = 25.1$; $SD = 2.7$; $n = 52$) subcaudals in males, 15–27 ($\bar{x} = 155.7$; $SD = 4.1$; $n = 61$) in females; 6 ($n = 2$ sides) or 7 ($n = 172$ sides) infralabials; 3 ($n = 4$ sides) or 4 ($n = 170$ sides) infralabials contacting chinshield; 2 ($n = 2$ sides), 3 ($n = 153$ sides), or 4 ($n = 17$ sides) gular scale rows; 2 ($n = 4$), 3 ($n = 66$), or 4 ($n = 7$) preentrals; 7–11 ($\bar{x} = 8.9$; $SD = 0.8$; $n = 87$ sides) dorsal scale rows on the level of second subcaudal; 7 ($n = 2$ sides), 8 ($n = 9$ sides), 9 ($n = 9$ sides), or 10 ($n = 3$ sides) maxillary teeth; 3.0–13.0 mm body diameter; retracted hemipenis bifurcates at and extends to seventh to 10th subcaudal ($n = 17$).

Distribution: High mountain chains of southern and southeastern Brazil (Espinhaço, Mantiqueira, Serra dos Órgãos, Serra do Mar, and Paranapiacaba), from Santa Teresa (19°55'S, 40°36'W) in the state of Espírito Santo southward to Peritiba (27°22'S, 51°54'W) in the state of Santa Catarina, and also reaching the state of Minas Gerais up to Itabira (19°37'S, 43°13'W). *Atractus zebrinus* inhabits Submontane to Upper Montane Rainforest and Semi-deciduous forests and Cerrado/Semi-deciduous Forest transition zones between 500–1700 m (Fig. 9). Records of this species for localities below 500 meters are based on specimens labeled only with municipality's headquarters, without other data sources; all these municipalities are located at foothills of high mountains.

Remarks: Jan (1862) described *Rabdosoma zebrinum* on the basis of a specimen from an unknown source. Boulenger (1894) synonymized *R. zebrinum* with *A. maculatus*, and all subsequent authors followed this proposition, except for Amaral (1978) and Lema (1994) who identified specimens of *A. zebrinus* as *A. guentheri*. Fernandes *et al.* (2000) redescribed the holotype and reported additional individuals of *A. maculatus*, restricting the species concept to populations from the Brazilian state of Alagoas. Fernandes *et al.* (2000) resurrected *A. zebrinus* associating it with populations occurring from Bahia southward to Santa Catarina.

We examined nearly 100 specimens of *A. zebrinus* and agree with Fernandes *et al.* (2000) about the distinctness of *A. zebrinus* from *A. maculatus* (see also the remarks section for *A. maculatus* above). However, we could not confirm the identity of the specimen from Porto Seguro, Bahia (IBSP 57202), previously identified as *A. zebrinus* (Fernandes *et al.*, 2000), because this individual is poorly preserved. Although Fernandes *et al.*'s (2000) determination is most probably correct, we choose not to include this record in describing the species' distribution, and prefer to wait for new material to confirm occurrence North of Itabira and Santa Teresa.

Key to the Atlantic Forest species of *Atractus*

Colouration characters refer to adult specimens in preservative, except where we draw attention to distinct juvenile colour pattern. Therefore, this key can be used in the adult and juvenile specimen identification for all considered species.

1. Midbody dorsal scale rows 152
- Midbody dorsal scale rows 17.....4

2. Dorsal ground colour pale with crossbands, transverse blotches, and/or a conspicuous vertebral line; black collar generally present 3
Dorsal ground colour dark reticulated with pale, occasionally with a barely distinct vertebral line, but never with crossbands or irregular blotches; usually lacking black collar *A. reticulatus*
3. Eight to nine maxillary teeth; black cap and occipital pale band..... *A. paraguayensis*
Seven maxillary teeth; lacking black cap and occipital pale band..... *A. potschi*
4. Venter beige anteriorly and dark brown to black posteriorly 5
Venter creamish white at least in juvenile specimens 8
5. Six supralabials; seven maxillary teeth; dorsum black, lacking dorsal ontogenetic change of colouration *A. caete*
Seven supralabials; eight to eleven maxillary teeth; dorsum red to reddish brown with black transverse blotches or small dots in adults and uniformly beige to black in adults..... 6
6. Ventrals 152–154 in males; generally eight maxillary teeth; mature individuals smaller than 500 mm SVL in both sexes; hemipenial lobes smaller than remaining capitulum; asulcate side of hemipenis lacking lobular crests; sulcus spermaticus margin narrow *A. francoi*
Ventrals < 150 in males; generally nine or ten maxillary teeth; mature females > 500 mm SVL; hemipenial lobes longer than rest of capitulum; asulcate side of hemipenis with conspicuous lobular and medial crests; sulcus spermaticus margin laterally expanded..... 7
7. Juveniles and sub-adults red to reddish brown, with wide transverse black bands; mature males reaching > 500 mm SVL; adults with dorsum uniformly beige to grayish brown and venter beige *A. trihedrurus*
Juveniles and sub-adults reddish brown to reddish dark brown, with irregular blotches or small black dots; mature males < 500 mm SVL; adults with dorsum and venter uniformly black..... *A. serranus*
8. Single postocular; six infralabials *A. thalesdelemai*
Two postoculars; seven infralabials 9
9. Dorsum with three to five conspicuous longitudinal stripes (or barely distinct lines in melanic specimens)
..... *A. guentheri*
Dorsum banded, blotched, and/or spotted with black, but never distinctly striped 10
10. Dorsal ground colour creamish red or red with wide transverse back blotches or bands..... 11
Dorsal ground colour creamish red or yellow scattered with small black dots occasionally arranged in tiny transverse lines 12
11. Dorsal black transverse blotches or crossbands white bordered in adults (not in juveniles); maxillary teeth generally seven or eight..... *A. zebrinus*
Juveniles with dorsal black wide transverse crossbands lacking contrasting margins; generally nine to ten maxillary teeth..... *A. trihedrurus*
12. Dorsum creamish yellow with dots arranged in thin transverse lines, occasionally forming irregular blotches; hemipenis moderately bilobed, semicalyculate, lacking lobe projections..... *A. maculatus*
Dorsum with scattered small black dots, never arranged in transverse lines; hemipenis slightly bilobed, slightly semicalyculate, with lateral lobe projections..... 13
13. Black collar; lateral tip projections on lobes narrow and directed upward; 145–166 ventrals in males and 154–170 in females; 22–33 subcaudals in males and 19–28 in females..... *A. pantostictus*
Lacking black collar; lateral tip projections robust and laterally directed; 129–151 ventrals in males and 146–163 in females; 20–25 subcaudals in males and 16–23 in females..... *A. ronnie*

Discussion

Savage (1960) defined three species groups of *Atractus* based on traditional characters (e.g., pholidosis, hemipenis, and colour pattern). Among these groups only the *A. elaps* group appears to constitute a natural assemblage (Fernandes 1995b; Passos 2008). The other two groups (*A. badius* and *A. trilineatus*) were based mainly on hemipenial morphology (see Savage 1960), but both require re-evaluation because they lack unambiguous diagnostic characters (Passos *et al.* 2009f). Due to the great importance of hemipenial morphology in *Atractus* systematics, it is appropriate for us to comment on some aspects of its variation with regard to the taxa studied here.

Savage (1960) recognized two distinct hemipenial conditions for the genus based on the analysis of retracted organs of *Atractus*: a “differentiated state” (for the *A. badius* species group), in which the distal portion of the organ is covered by papillae, calyces, or flounces; and an “undifferentiated state” (for the *A. elaps* and *A. trilineatus* species groups), in which the distal region of the hemipenis is uniformly covered with spines. Most subsequent authors studying *Atractus* examined only the retracted condition of the organ, describing the hemipenis in relation to Savage’s supraspecific classification (e.g., Roze 1961; Gasc & Rodrigues 1979; Hoogmoed 1980; Cunha & Nascimento 1983). As recently stressed by Schargel and Castoe (2003), hemipenis descriptions based exclusively on the retracted condition may overlook some features that are best examined in fully everted organs (e.g., capitulation and calyculature structures; see Passos *et al.* 2007a). In fact, just this type of hemipenial misinterpretation has occurred with respect to the “undifferentiated” condition for some members of the Savage’s *A. trilineatus* species group that actually have the “differentiated” condition (*sensu* Savage 1960), which apparently were overlooked in the examination of retracted organs only (Passos 2008). On the other hand, Savage (1960) determined *A. modestus* as having the “differentiated” condition based on the examination of a retracted hemipenis, Passos *et al.* (2007a) re-examined the holotype and additional specimens of *A. modestus* and pointed out that hemipenis is “undifferentiated”.

Fernandes (1996), based on the examination of fully or semi-everted organs, noticed hemipenis capitulation for the first time in *A. maculatus* (= *A. zebrinus* of this study), *A. reticulatus*, *A. serranus*, *A. taeniatus* (= *A. paraguayensis* of this study), and *A. trihedrurus*; suggesting that the condition represents a plesiomorphic dip-sadine feature shared by a basal grade of the genus (Fernandes 1995b, 1996). Fernandes *et al.* (2000) described the capitular ornamentation in *A. maculatus* (*sensu strictu*) and *A. zebrinus*. Although Schargel and Castoe (2003) found the same condition in *A. univittatus* and *A. ventrimaculatus*, they pointed out that the distal ornamentation was very different from those studied by Fernandes (1996). Later, data on various developments of capitulation structures were reported for several *Atractus* species (e.g., slightly capitate, strongly capitate) and described in different ways (Hoogmoed & Pudente 2003; Passos *et al.* 2005; Zaher *et al.* 2005; Kok 2006; Passos *et al.* 2007b; Myers & Schargel 2006; Passos & Fernandes 2008; Passos & Arredondo 2009; Passos *et al.* 2009b,c,e,f). Passos *et al.* (2007b) suggested that capitular structures likely represent the most widespread condition in *Atractus*, and they might even represent a primitive hemipenial condition retained in many species of the genus (P. Passos unpubl. data).

The species considered in this study comprise three apparently robust and geographically coherent *Atractus* assemblages that can be diagnosed by morphological features, mostly from hemipenial morphology (Passos 2008). Although the capitular and calyculate structures are found in all species studied here, these hemipenes differ in the level of development and orientation of the lobes, presence/absence of a capitular crotch in the sulcate side of capitulum, length and distinction of capitulum with respect to hemipenial body, and level of development of longitudinal walls of calyces. Faced with the unresolved phylogenetic relationships of *Atractus* and the putative close relationship with *Geophis* (Savage 1960; Downs 1967; Fernandes, 1995b), we speculate that specialized ornamentation of the hemipenis herein describe might have evolved from a generalized and widespread moderately bilobed, semicapitate, and semicalyculate condition shared by the most recent common ancestor of the two genera. Under this scenario, the presence of a slightly bilobed organ with well developed capitulum or lateral lobe projections perhaps constitute derived traits for cis-Andean *Atractus* (P. Passos unpubl. data). Even if this is not the case, the groups defined here, in an operational perspective, can facilitate future comparisons between putative closely related species for this speciose and complex genus.

The first group, here named the *A. maculatus* species group, includes the Atlantic Rainforest species of *Atractus*, except for *A. ronnie*, occurring along the eastern Brazilian coast from the state of Alagoas to Santa Catarina. Members of this assemblage share: (1) 17 dorsal scale rows (except *A. potschi*), (2) seven upper and lower labials (except *A. caete*, see below), (3) first four infralabials contacting chinshields, (4) generally three gular scale rows, (5) seven to ten teeth with distinct maxillary diastema, (6) venter immaculate creamish

white, at least in juveniles, (7) moderate to strong ontogenetic colour change, (8) slightly or moderate bilobed, (9) semicapitate, (10) semicalyculate hemipenis, and (11) capitulum wider than hemipenial body. The *A. maculatus* species group is composed of the following species: *A. francoi*, *A. guentheri*, *A. maculatus*, *A. potschi*, *A. serranus*, *A. trihedrurus*, and *A. zebrinus*. Although *A. caete* has six supralabials, we tentatively assigned it to the *A. maculatus* species group because it shares a strong ontogenetic change of colour and a dark belly in adults with *A. francoi*, *A. serranus*, and *A. trihedrurus*. Knowledge of the hemipenial morphology of *A. caete* is needed to decide whether it is more appropriately transferred to the group of species allied with *A. emmeli*.

The second group, here named the *A. pantostictus* species group, comprises cis-Andean species of *Atractus* distributed in Amazonia (*A. altagratiae*), the Atlantic Rainforest (*A. ronnie*), and Neotropical Savannah (*A. pantostictus*), which share the first seven and the 11th characters listed above for the *A. maculatus* group. Nevertheless, the members of this assemblage differ from the former group in having: (8') slightly bilobed, (9') slightly semicapitate, and (10') slightly semicalyculate hemipenis. Furthermore, members of this group have exclusive hemipenial features such as calyculate depressions on the base of lobes delimiting lateral projections. It is possible that the *A. pantostictus* group should also include a couple of Amazonian species (*A. insipidus* and *A. punctiventris*) in which hemipenis morphology is currently unknown (Passos & Fernandes 2008).

The third group, here named the *A. emmeli* species group, contains cis-Andean species distributed in Amazonia (*A. albuquerquei*, *A. emmeli*, *A. paravertebralis*, and *A. taeniatus*) and contiguous Neotropical Savannah or Forest formations (*A. edioi*, *A. balzani*, *A. paraguayensis*, *A. reticulatus*, and *A. thalesdelemai*). The *A. emmeli* group differs from the other groups in having the following state characters: (1') 15 dorsal scale rows (except *A. balzani* and *A. thalesdelemai*), (2') reduction to six upper and lower labials in several species, and (4') four gular scale rows. Members of this assemblage share with the *A. maculatus* group: (8) hemipenis moderately bilobed (except *A. paraguayensis*), (9) semicapitate, (10) semicalyculate, and (11) capitulum wider than hemipenial body. The *A. emmeli* group presents a remarkably different colour pattern (except for *A. paraguayensis*), with uniformly dark brown or black dorsum generally with a pale occipital band. Although we allocate *A. paraguayensis* to the *A. emmeli* group, this species has a slightly bilobed hemipenis like those of the *A. pantostictus* group. Because capitular and calyculature structures in *A. paraguayensis* are very different from those of the *A. pantostictus* group, we interpret the hemipenis of *A. paraguayensis* as secondarily derived from a slightly moderately bilobed condition. Therefore, we tentatively place it in the *A. emmeli* group, until a robust phylogenetic hypothesis is available for the genus.

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Appendix

Material examined

Countries are given in bold capitals, states in plain capitals, municipalities in italics, and localities in plain text. Specimens for which everted hemipenes were examined are indicated with an asterisk.

Atractus caete ($n = 1$). **BRAZIL:** ALAGOAS: *Quebrangulo* (MNRJ 16936 holotype).

Atractus francoi ($n = 7$). **BRAZIL:** RIO DE JANEIRO: *Mangaratiba*, Serra do Piloto (MNRJ 17537* holotype); *Nova Friburgo* (MNRJ 17536 paratype); SÃO PAULO: *São José do Barreiro* (IBSP 72654* paratype); *São Luís do Paraitinga*: Núcleo Santa Virgínia, Parque Estadual da Serra do Mar (IBSP 53924, 74648, 74723–24, paratypes); *Ubatuca*: Núcleo Santa Virgínia, Parque Estadual da Serra do Mar (ZUEC 2114*).

Atractus guentheri ($n = 9$). **BRAZIL:** BAHIA: *Almadina* (CZGB 7563–64); *Barro Preto* (CZGB 823); *Camacã* (CZGB 6094, MNRJ 6710*); *Canavieiras* (BMNH 1946.1.1.76, holotype); *Ibicaraí* (CZGB 6153); *Ilhéus* (CZGB 1584); *Jussari* (CZGB 4896).

Atractus maculatus ($n = 11$). **BRAZIL:** unknown locality (BMNH 1946.1.6.46, holotype); ALAGOAS: *Ibateguara* (CHBEZ 610, MNRJ 14198); *Maceió* (CHBEZ 609, MUFAL 24933, 952242, 952288), Mata do Catolé (MNRJ 14197*); *Murici*: Mata da Bananeira (MUFAL 474–75); *São Miguel dos Campos*: Usina Seresta (MNRJ 3977).

Atractus pantostictus ($n = 325$). **BRAZIL:** DISTRITO FEDERAL: *Brasília*: Zoo Park (MNRJ 4460–66); GOIÁS: *Minaçu* (IBSP 51433–34), *Cana Brava* (IBSP 26711); MINAS GERAIS: *Belo Horizonte* (MHNCI 787, MNRJ 6474, 10909, 13197*, IBSP 40757, 58592, 74498, 74501, MCNR 13, 27, 35, 88, 101, 129, 139, 145–48, 254, 453–54, 459, 516, 726, 929–41); *Campo do Meio* (IBSP 50476); *Conselheiro Lafaiete* (LZVUFOP 501, 614, 627); *Contagem* (IBSP 74496, 74499); *Esmeraldas* (IBSP 7495–96); *Itabirito* (LZVUFOP 118, 158, 274, 282, 331, 426, 466–67, 622); *Machado* (IBSP 57138); *Ouro Branco* (LZVUFOP 421, 579–80); *Ouro Preto* (LZVUFOP 26, 27–29, 33, 56, 82, 382, 425); *Pirapora*: Fazenda Triângulo Formoso (MNRJ 4459 paratype); *Santo Antônio do Monte* (IBSP 75394); *São Vicente de Minas* (IBSP 70244); *Uberlândia* (IBSP 54604–05); *Vespasiano* (IBSP 74500); SÃO PAULO: *Areias*: Fazenda Vargem Grande (IBSP 40404); *Barueri* (IBSP 45208, 55929); *Cabreúva* (IBSP 55125); *Caieiras* (IBSP 56112, 58251, 59320, 62960); *Cajamar* (IBSP 71928; 76520); *Campo Limpo Paulista* (IBSP 9472, 42498, 42500, 44152, 45069, 45225, 49225, 54651, 54896, 55113, 55635, 58744, 61827, 62073, 62075–76, 69746); *Casa Branca* (IBSP 75234); *Francisco Morato* (IBSP 7018–19, 54633–34, 55632, 56123, 64117, 66879, 69296, 69505–06, 70219, 74992); *Franco da Rocha* (IBSP 42093, 44303, 44397, 54844 holotype, 56063, 71533, 73731), Serra dos Cristais (IBSP 27305); *Itapeverica da Serra* (IBSP 54699); *Jales* (MZUSP 4094); *Jarinu* (IBSP 41427, 44752, 62194, 73969); *Jundiá* (MNRJ 6496, IBSP 54235 paratype, IBSP 2728, 10068–69, 42645–47, 42664, 43192, 43684, 44156, 45208, 45624, 46228, 49267, 54235, 54512, 54661, 54910, 55082, 55214, 55957–61, 58712, 58936, 60483, 60485–86, 61217–18, 64675, 64703, 66538–39, 66613–14, 74055); *Louveira* (IBSP 41353); *Neves Paulista* (IBSP 62495); *Orlândia* (IBSP 44537); *Piedade* (IBSP 62827); *Salesópolis*: Boracéia (MZUSP 3157, 3158 parátipo); *Santo André*: Paranapiacaba (MZUSP 2811); *São José do Rio Preto* (IBSP 40028); *São José dos Campos* (IBSP 27231, 27233–34, 29098, 37527, 40355, 44527, 45784, 45802–03, 45807, 59514, 61502–04), São Francisco Xavier (IBSP 55744); *São Paulo* (62469, 63469, 64100, 68679, 74059–60), Jaraguá (IBSP 42404, 55740, 59766, 60694, 60697, 62669), Perus (IBSP 54655, 54886–88, 64675, 64875), Pirituba (IBSP 42485, 53545, 54641, 55639, 59150, 64459, 64733–39, 72428); *São Simão* (IBSP 72767); *Várzea Paulista* (IBSP 9862, 32501, 40855, 40857, 45167); TOCANTINS: *Aliança do Tocantins* (IBSP 43954); *Lajeado*: Luís Eduardo Magalhães Power Plant (IBSP 64494–95, 64507–08, 64522–24, 64696, 65062–63, 65072, 65075, 65124–31); *Palmas* (IBSP 65183–84, 65273–75, 65448–49); *Paraná* (IBSP 74117); *Peixe*: Peixe-Angical Power Plant (IBSP 72250); *Porto Nacional*: Luís Eduardo Magalhães Power Plant (IBSP 64952–5000); *São Salvador do Tocantins* (IBSP 74234, 74237, 74245).

Atractus paraguayensis ($n = 499$). **ARGENTINA:** CORRIENTES: *San Luis del Palmar*: Costa Grande (UNNEC 84); *Santo Tome* (UNNEC 4979). **BRAZIL:** PARANÁ: *Candói*: Fundão Power Plant (MHNCI 12463–67), Santa Clara Power Plant (MHNCI 5156, 11714, 12362–67; 12378–85; 12397–411); *Capanema* (MHNCI 11644–45); *Capitão Leônidas Marques* (IBSP 76890–91); *Cascavel* (MHNCI 4850, 7403, 10351, 11974); *Clevelândia* (MHNCI 10115, 10127–33), Fazenda Tunas (MHNCI 10236); *Coronel Vivida* (MHNCI 10080); *Foz do Jordão* (MHNCI 9773); *Francisco Beltrão* (MHNCI 501); *Guarapuava* (IBSP 33523); *Laranjeiras do Sul* (IBSP 42884); *Mangueirinha* (MHNCI 5106-07), Baixada Schmidt, Iguaçu River (MHNCI 5553, 5556, 5597–601, 5606–08, 5613–14, 5626–27, 5711–21, 5761–63, 9764–65, 9774–75, 9783), Morro Verde River mouth (MHNCI 5555, 5623–25, 5628, 9779); *Pato Branco* (MHNCI 2274, 5914, 9238–39); *Realeza* (MHNCI 12528); *Reserva do Iguaçu*: Jordão River (MCP 7185, 7211, 7364–65, MHNCI 5090), Reserva do Rio dos Touros (MHNCI 5012, 5537–51, 5645, 5743–53), Santa Luzia (MHNCI 8157, 8161), Segredo Power Plant (MHNCI 5492–552, 5557–96, 5602–05, 5615–22, 5629–710, 5722–41, 5743–5756, 5757*, 5758–60, 5764–73, 5779–83, 9766–72, 9780–82), Vila da Copel (MHNCI 5013, 5018–21); *Santa Isabel do Oeste* (MHNCI 5954); *Santo Antônio do Sudoeste* (MHNCI 6351, 7007-08); *Verê* (MHNCI 10540); *Vitorino* (MHNCI 10100); RIO GRANDE DO SUL: *Carazinho* (CRUPF 1180, 76103); *Colorado* (CRUPF 1196); *Derrubadas* (MCP 12387); *Estação* (IBSP 55276–77); *Getúlio Vargas* (CRUPF 64); *Ibiraquitã* (CRUPF 587); *Ijuí* (MCP 13726–32); *Mato Castelhano* (CRUPF 289, 516, 991–92, 1094); *Pinheiro Machado* (CRUPF 257); *Planalto* (MCP 5898–99), Linha Quarta Seção (MCP 5915, 5997); *Porto Mauá* (MCP 11609, 11611, 11623); *Porto Vera Cruz* (MCP 11670); *Santo Ângelo* (MCP 12516–17); *Tapejara* (CRUPF 477, MNRJ 10123*); *Tuparendi* (IBSP 53889, 53919, 54032, 54113); SANTA CATARINA: *Alto Bela Vista*: Entre Rios (MCP 2912); *Caxambu* (MHNCI 12855); *Chapecó* (MCP 14013), Goio-En (MHNCI 12851-2), Marechal Bormann (MHNCI 12853); *Erval Velho* (MHNCI 4092-93); *Guatambu* (MHNCI 12854); *Herval do Oeste* (MHNCI 4967, 6445); *Ipira* (MCP 2913); *Itá*: Itá Power Plant (MHNCI 9880-96); *Nova Teutônia*: Seara (MHNCI 6319); *Peritiba* (IBSP 30129, 30198, 30200, 30285, 30680, 30992, 31634, 32450, 32566, 52571, MCP 2939); *Piratuba* (MCP 2893–94, 2897, 2902); *Vargem Bonita* (MHNCI 4079, 6279–82). **PARAGUAY:** Unknown locality (NMW 23443 holotype).

Atractus potschi ($n = 21$). **BRAZIL:** ALAGOAS: *Maceió* (IBSP 48438 holotype); BAHIA: *Feira de Santana*: Jaíba (MZUEFS 454); *Barrocas*: Fazenda Brasileiro (MZUEFS 682*); *Poçoões* (MZUFBA 1801, 1590–91); *Salvador* (MZUFBA 1589); *Teofilândia* (IBSP 57119); SERGIPE: *Salgado* (MZUSP 7001, 7195–97, 7275–81 paratypes); *São Cristóvão* (MNRJ 14057–58, MZUSP 11074).

Atractus reticulatus ($n = 490$). **ARGENTINA:** CORRIENTE: *San Tomé*: (MNRJ 13393*). **BRAZIL:** MATO GROSSO DO SUL: *Ponta Porã* (IBSP 16236); MINAS GERAIS: *Arceburgo* (IBSP 56023); PARANÁ: Unknown locality (MNRJ 9820); *Apucarana* (MHNCI 3455); *Araucária* (MHNCI 1351, 3707, 4357, 4471, IBSP 4471, 9681, 11979–85, 13033, 18369, 40325); *Balsa Nova* (IBSP 17083); *Campo Largo* (MHNCI 12008); *Carambeí* (IBSP 13637), Boqueirão (IBSP 27561–64); *Castro* (IBSP 4495-97, 4499, 4505, 4511, 4538, 7837, 7876, 8329, 9647, 10307, 10586, 40935), *Caxambu* (MHNCI 604), *Terra Nova* (MCN 7750); *Curitiba* (IBSP 75787, 75870, MCN 3350–52, MCP 3639, MHNCI 259, 262, 296, 299–300, 397–400, 742, 802, 917, 1117, 1320, 1588, 1685, 2183, 2210, 2783, 2833, 3443, 4193, 4588, 4601–02, 4993–94); *Fazenda Rio Grande* (MHNCI 11028); *Foz do Jordão* (MHNCI 10773); *Guarapuava* (MHNCI 3312–13); *Jaguariaíva* (MHNCI 3345); *Lapa* (IBSP 10360, MHNCI 2070); *Palmeira* (IBSP 20723, MHNCI 1184), *Fazenda Santa Rita* (MHNCI 298, 1556–58); *Pato Branco* (MHNCI 1237); *Pinhais* (MHNCI 4356), *Graciosa* (MHNCI 7717); *Piraí do Sul* (IBSP 8981, 9399), *Joaquim Murtinho* (IBSP 13631); *Ponta Grossa* (IBSP 37328, MHNCI 1936, 10341), *Buraco do Padre* (MHNCI 4865), *Guaragi* (IBSP 32943), *Vila Velha* (MHNCI 7417, 10720); *Porto Amazonas* (MHNCI 4553–55, 17519), *Nova Restinga* (IBSP 15007); *São José dos Pinhais* (IBSP 43435, 43633, MHNCI 2379–80, 2451, 2731, MNRJ 9086); *Telêmaco Borba*: *Harmonia* (MHNCI 2388); *Tibagi* (MHNCI 10671), *Guartelá* (MHNCI 8060); RIO GRANDE DO SUL: *Augusto Pestana* (DZURGS 4300); *Bossoroca*: *Fazenda Santa Catarina* (MCN 2842); *Cachoeirinha* (MCP 2009); *Camobi*

(MCP 3873); *Candelária* (MNRJ 1261); *Canguçu* (IBSP 51347, 51350); *Canoas*: Capão do Corvo (MCP 02), Vila Matias (MCP 1281); *Entre Rios do Sul* (CRUPF 309); *Esteio*: Polo Petroquímico (MCN 9438); *General Câmara*: Boca da Picada (MCP 2611); *Gravatá* (MCN 2954, 2999–3001, 1183, 1858), Morro Agudo, Vila Nova (DZURG 138); *Guaíba* (MCP 3241); *Machadinho* (DZURGS 3680–81); *Mariana Pimentel* (MCP 2530, 2538); *Mato Castelhano* (CRUPF 991); *Nicolau Vergueiro* (CRUPF 173, 176); *Passo Fundo* (CRUPF 96, 199, 213, 224–26, 249, 284, 304, 309, 343, 376, 401, 416, 590, 686, 819, 829–30, 1064, 1204); *Pelotas* (IBSP 1647–51), Instituto de Pesquisas Agrárias do Sul (MCN 1329); *Pinhal da Serra* (MCN 16232, 16372); *Porto Alegre* (MCN 03, 416, 1013, 1015–16, 1794, 2766, 3517, 4145, 5405, 5407, 5409, 5411–12, 6060, 6095, 6392, 6489, MCP 01, 06, 886, 1186, 1205, 1304, 1458, 1634–35, 1876, 1907, 2047, 2171, 2470, 2502, 3079, 3479, 3495, 3745, 3921, 4382, 4551, 4663, 4730, 4788–95, 4842); *Porto Xavier* (MCP 3306); *Santa Maria* (MCN 3055, 4039, 7315), Camobi (MCN 3873); *Santo Antônio da Patrulha* (MCP 03–05); *São Borja*: Barreiro (MCP 3144); *São Leopoldo* (MCN 5410), Sítio Laurindo (MZUSP 5054); *São Lourenço do Sul* (BMNH 1946.1.2.7 holotype); *Tenente Portela*: Turvo (MCN 7641–42); *Três Passos* (MCN 8045); *Viamão* (MCN 4096); SANTA CATARINA: *Anita Garibaldi* (MCN 16221–22); *Campos Novos* (MCP 2848–49); *São Bento do Sul*: Rio Vermelho (MZUSP 9417); SÃO PAULO: *Campo Limpo Paulista* (IBSP 59401); *Cotia* (IBSP 69374); *Cubatão*: Piassaguiera (MZUSP 1282, 1856); *Diadema* (IBSP 43390); *Ferraz de Vasconcelos* (IBSP 20599); *Guarujá* (MZUSP 10577); *Ibiúna* (IBSP 40415, 45169, 56395, 56387, 56394, 56996, 68857, 71748); *Itararé* (IBSP 40388, 44094, 45754, 45760, 45762), Fazenda Santa Maria do Espinho (IBSP 40324, 45742); *Jarinu* (MZUSP 9496); *Juquitiba* (IBSP 32556); *Mogi das Cruzes* (IBSP 9452–54, 43400), Jundiapéba (IBSP 48815, 48853); *Osasco* (IBSP 2731); *Poá* (IBSP 1836, 18785–86, 25041–42, 43215); *Santo André* (IBSP 30452, 45738, 61147–48, 69530), Campestre (IBSP 30452); *São Bernardo do Campo* (IBSP 29508, 45678, 59420, 64901, 68103, 69591, 72432, 73195), Rudge Ramos (IBSP 32440); *São Caetano do Sul* (IBSP 4310, 4873); *São Paulo* (IBSP 1012, 1208, 1258, 2790–95, 3506–07, 4807, 5322–23, 5361–67, 5366, 5378–80, 5402–03, 6276, 6892, 7245, 8023, 8614, 9456, 9927, 10371–72, 13168, 20718, 34301, 45674, 52419, 54637, 54663, 60215, 62394–96, 63062, 64071, 64695, 64876, 67351, 72024, 76414, MCN 5406, MNRJ 1524, MZUSP 1226, 1230–34, 1661, 2008, 2624, 2633–34, 2638, 2643, 3159, 4167, 4153, 4164, 4204–05, UMMZ 109058), Brooklin (IBSP 20718), Butantã (IBSP 2716, 3503–07, 54884–85), Campo Belo (IBSP 34301), Chácara Flora (IBSP 55795, 64647), Guaianazes (IBSP 49255, 54914, MZUSP 4096), Guarapiranga (IBSP 50503), Interlagos (IBSP 24465, 43391, 54637, 62884), Itaquera (IBSP 30759, 48312–24, 48416, 50826–7, 50894), Jabaquara (IBSP 55839–40), Jaraguá (IBSP 76756), Jardim Aeroporto (IBSP 32461), Jardim Novo Santo Amaro (IBSP 76413), Jardim Satélite (IBSP 49803), Morumbi (IBSP 52168–72, 54606, 57756), Perdizes (IBSP 31783), Riviera Paulista (IBSP 54572, 55023), Santana (IBSP 7758), Santo Amaro (IBSP 1208, 1219, 1258, 2468, 2686, 2690, 2695–98, 2701–04, 2730, 2736, 2917–18, 2922, 3275, 3365–66, 3418–20, 6577, 20769, 26923, 29649, 54070, 54663, 54817, 54845, 57562), São João Clímaco (IBSP 45674, 45782, 45797, 45800, 45821, 45826), São Mateus (IBSP 68044, 62961–62), São Miguel Paulista (IBSP 27500, 27510–11, 33104, 46530), Sapopemba (IBSP 52712), Vila Carmosina (IBSP 61649–50), Vila Carrão (IBSP 12215), Vila Maria (IBSP 842), Vila Mariana (IBSP 53947, 54535–36), Vila Matilde (IBSP 8023), Vila Nova Conceição (IBSP 12188); *São Vicente* (MZUSP 4582–85); *Suzano* (IBSP 58595–97, 71840, 71890); *Vargem Grande do Sul* (IBSP 41249); *Vargem Grande Paulista* (IBSP 43392, 58745–46).

Atractus ronnie ($n = 26$). **BRAZIL**: CEARÁ: *Guaramiranga*, Serra do Baturité (CHUFC 2649, 2651, paratype); *Mulungu* (CHUFC 2645, paratype); *Pacoti* (MNRJ 14194 holotype, MNRJ 14195–96, CHUFC 1396, 2481, 2578, 2598, 2641, 2646–47, 2652–54, 2658, 2675–76, 2678*, 2733, 3500, 3502, paratypes); *Tianguá* (MNRJ 17326).

Atractus serranus ($n = 32$). **BRAZIL**: unknown locality (IBSP 32857); SÃO PAULO: Serra de Paranapiacaba, Mairinque-Santos railway (IBSP 7238 holotype); *Campinas* (IBSP 50861); *Cubatão* (IBSP 9706); *Guarulhos*: Km 21 Presidente Dutra highway (IBSP 26999, 27147, 27862); *Rio Grande da Serra*: (IBSP 54636, 54974); *Salesópolis*, Estação Biológica da Boracéia (MHNCI 9147*, MZUSP 2193); *Santo André*

(IBSP 53630, 55252), Campo Grande (IBSP 7200), Eletrocloro railway station (IBSP 42947), Paranapiacaba railway station (IBSP 10589, 18645, 23518); *São Paulo*: Engenheiro Marsilac (IBSP 9075–76*, 9088–89), Guaramiranga (MZUSP 1 specimen not catalogued), Rio dos Campos (IBSP 9267, 9431*, 9437–38, 10136), Santo Amaro (IBSP 4852); *São Roque*: São João Novo (IBSP 7002).

Atractus thalesdelemai ($n = 8$). **BRAZIL**: RIO GRANDE DO SUL: *Passo Fundo*: Fazenda Corporação da Brigada Militar (MNRJ 10052* holotype, 10053–54, 10080–81 paratypes), Jardim Botânico (CRUPF 172, 801 paratypes), Vera Cruz (CRUPF 405).

Atractus trihedrurus ($n = 53$). **BRAZIL**: PARANÁ: *Guaratuba*: Guaricana (MHNCI 851); *Morretes*: Recanto Engenho Lacerda (MHNCI 7457), São João da Graciosa, Rio Ipiraguinha (MHNCI 11082*); *Piraquara* (IBSP 3067 paratype of *A. trihedrurus*), Manaciais da Serra (MHNCI 11153*); *Quatro Barras*, Recanto Boa Vista (MHNCI 11426); *Tijucas do Sul*: Araçatuba (MHNCI 6501); SANTA CATARINA: *Campo Alegre* (IBSP 32367, 32369); *Rio dos Cedros* (MHNCI 10543); *São Bento do Sul* (IBSP 3098 holotype of *A. trihedrurus*, IBSP 9111, MZUSP 7569, 9439); SÃO PAULO: *Capão Bonito*, Sítio Guarapiava (IBSP 32664); *Cotia* (IBSP 55698*); *Guapiara*: Parque Estadual Intervales (IBSP 33717, 34360, 34409); *Ibiúna* (IBSP 46476, 46658, 56474, 73816); *Juquitiba* (IBSP 33930, 44676, 46604, 53565, 54703, 57087, 62215, 62860, 68219, 69599, 70036, 72635, 74292, 75041, 76145, 76522, 72900); *Miracatu* (IBSP 58763); *Piedade* (IBSP 49752, 50280, 58413, 73073); *Ribeirão Pires* (IBSP 10136, 31188*, 42906); *Tapiraí* (IBSP 42222, 42963, 46605, 52636, 56938).

Atractus zebrinus ($n = 92$). **BRAZIL**: unknown locality: (IVB 1548); ESPÍRITO SANTO: *Domingos Martins*, Pedra Azul (MNRJ 18684); *Santa Teresa* (MNRJ 733–34*); MINAS GERAIS: *Bocaina de Minas* (IBSP 6463); *Camanducaia* (IBSP 28868–69, 32453, 40106, 41443, 44794, 45431, 45620, 45622, 45691, 46286, 51491, 54818, 67697), Monte Verde (IBSP 33499, 51683, 53839, 60927, 61924); *Catas Altas*, RPPN Serra do Caraça (MNRJ 18717*, 18718); *Delfim Moreira* (IBSP 57476); *Extrema* (IBSP 68962); *Itabira* (IBSP 71376); *Itamonte* (IBSP 43154); *Liberdade* (MNRJ 6497); *Ouro Preto* (LZVUFOP 19, 27, 45, 86, 133, 369); *Paraisópolis* (IBSP 71285); *São Gonçalo do Rio Abaixo*: Peti (MNRJ 9298); *Sapucaí-Mirim* (IBSP 56953, 61385, 62660–61, 66361, 70432); PARANÁ: *Campo Largo*: Três Córregos (MHNCI 4818); *Rio Branco do Sul*: Votuverava (IBSP 12893); RIO DE JANEIRO: *Cachoeiras de Macacu* (MNRJ 7064–65); *Itaboraí* (MHNCI 1295); *Nova Friburgo* (MNRJ 6322, 6498); *Petrópolis* (IVB 1203, 2485, MNRJ 4467–70*, 10091); *Teresópolis* (IBSP 41054, 41059, MNRJ 12899), Parque Nacional da Serra dos Órgãos (MNRJ 6495); *Resende*: Mauá (IBSP 48839); SANTA CATARINA: *Peritiba* (IBSP 44049); SÃO PAULO: *Apiáí*: Serra Formosa (IBSP 52316); *Campos do Jordão* (IBSP 7899, 44190, 50862, 54326*, 68189); *Cubatão* (IBSP 45193); *Cunha* (IBSP 46348); *Guapiara*: Parque Estadual Intervales (IBSP 33717); *Joanópolis* (IBSP 55090, 57017–18, 58310); *Ribeira*: Fazenda Cobalto (IBSP 43733); *Salesópolis*: Estação Ecológica da Boracéia (MZUSP 2194); *Santo Antônio do Pinhal* (IBSP 25020–21, 21949), Eugênio Lefèvre (IBSP 16435); *São Bernardo do Campo* (IBSP 56207); *São José do Barreiro* (IBSP 70789–91, 71018); *São Paulo* (IBSP 4551).