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Author(s): Paulo Passos, Angele Martins and Daniela Pinto-Coelho
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Population Morphological Variation and Natural History of *Atractus potschi* (Serpentes: Dipsadidae) in Northeastern Brazil

***Paulo Passos*[1,*], *Angele Martins*[1], *Daniela Pinto-Coelho*[2]**

[1] *Departamento de Vertebrados, Museu Nacional, Universidade Federal do Rio de Janeiro.*
Quinta da Boa Vista, Rio de Janeiro, CEP 20940-040, Rio de Janeiro, Brazil.
[2] *Departamento de Zoologia, Universidade Federal da Bahia, CEP 40170-290 Salvador, Bahia, Brazil.*
* *Corresponding author. Email: atractus@gmail.com*

Abstract. *Atractus potschi* was described based on 12 specimens from the Brazilian states of Alagoas and Sergipe, and later knowledge of its morphological variation (meristic, morphometric, and color pattern data) was augmented on the basis of nine additional individuals from additional localities in northeastern Brazil. Based on the examination of collections and fieldwork, we found more than 70 additional specimens of *Atractus potschi,* 60 of them obtained during a single collecting event. In this paper, we report new data on intra-population morphological variation (external morphology, hemipenis, osteology, cephalic glands, and soft anatomy) and natural history for the species. We associate the variation displayed in some characters with sex or age. We relate most of the variation observed in the shape of the hemipenis with preparation artifacts at the moment of preserving specimens. Our results reveal a high level of population polychromatism, supplanting the geographical variability exhibited by this system, while other complexes of morphological characters are relatively conserved both within and among populations. Although this polychromatic pattern seems to be retained in several lineages of *Atractus,* this phenomenon might be related to distinct life history constrains of the species. On the basis of anecdoctal field data, we discuss the possibility of post-parturition aggregation of juveniles in *Atractus potschi*. Despite being based on a single observation, this report is significant, since such post-birth interactions in nature (other than reproductive ones) have only been documented previously in temperate regions.

Keywords. Cephalic glands; Cranial osteology; External morphology; Hemipenis; Neonate aggregation; Polychromatism; Visceral anatomy.

Resumo. *Atractus potschi* foi descrita baseado em 12 espécimes provenientes dos estados brasileiros de Alagoas e Sergipe, depois sua variação morfológica (dados merísticos, morfométricos e padrões de coloração) foi incrementada a partir de nove indivíduos de outras localidades do nordeste do Brasil. Por meio do exame de coleções e a condução de trabalhos de campo, foram examinados mais do que 70 exemplares adicionais de *Atractus potschi,* 60 destes obtidos durante um único evento de coleta. No presente estudo, reportamos novos dados sobre a variação morfológica de natureza populacional (morfologia externa, hemipenes, osteologia, glândulas cefálicas e anatomia visceral) e de história natural para a espécie. Associamos a variação observada em alguns caracteres com o sexo e maturidade dos exemplares. A maior parte da variação observada na forma dos hemipenes foi relacionada à artefatos de preparação no momento de preservação dos espécimes. Nossos resultados revelaram um alto grau de policromatismo intrapopulacional, suplantando a variação geográfica observada neste sistema, enquanto outros complexos de caracteres morfológicos são relativamente conservados em ambos níveis, intra- e interpopulacionais. Embora este padrão policromático seja aparentemente retido em diversas linhagens de *Atractus,* este fenômeno pode estar relacionados com às diferentes restrições de histórias de vida das espécies. A partir de dados de campo de cunho anedótico, discutimos a possibilidade de agregação de juvenis pós-parturição em *Atractus potschi.* Ainda que pautada em observações pontuais, acreditamos que este registro é muito significativo, dado que interações após o nascimento na natureza (outras que os agregados reprodutivos) somente são documentados para as regiões temperadas.

INTRODUCTION

Dipsadid species of the genus *Atractus* Wagler, 1828 include small- to moderate-sized snakes that have secretive habits and feed on annelids and molluscs (Martins and Oliveira, 1999; Cisneros-Heredia, 2005; Balestrin et al., 2007). The genus is widely distributed in the New World, occurring from Panama to Argentina, primarily on mainland, from sea level to nearly 4,000 meters elevation above sea level, along almost all South American ecoregions (Passos et al., 2010a). *Atractus* is a species-rich and highly diversified genus closely related to *Geophis* Wagler, 1830 (Savage, 1960; Downs, 1961; Grazziotin et al., 2012), comprising 143 valid species to date, many of them known only from small series and usually with restricted distributions (Passos and Fernandes, 2008; Prudente and Passos, 2008, 2010; Passos et al., 2009a, b, c, d, e, 2013a, b). As a result, sometimes the scarcity of geographical samples might indirectly contribute to the status of threats to the conservation of some of these species of *Atractus* (see Brasil, 2014).

On the other hand, the taxonomy of the genus is in a state of flux with frequent resurrections (Passos et al., 2010b), rediscoveries (Passos et al., 2012), synonymizations (Passos et al., 2013a), descriptions of new taxa (Salazar-Valenzuela et al., 2014), and studies testing the taxonomic validity of distinct morphotypes (Almeida et al., 2014). In synthesis, the taxonomic status of several poorly known or previously poorly diagnosed congeners has been much improved on the light of new samples

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studied within a comparative framework through reproducible methodological approaches (Passos and Prudente, 2012; Passos et al., 2016). With the elucidation of the taxonomic status of many congeners, it is now possible to appropriately delineate relevant questions about the natural history of some species with large samples in collections.

Fernandes (1995) described *Atractus potschi* on the basis of 12 specimens from the states of Alagoas and Sergipe, Brazil. More recently, Passos et al. (2010a) reported on morphological variation (meristic, morphometric, and colour pattern) based on nine additional individuals from localities of the northeast region of Brazil. Thus, although we are acquainted with some aspects of the geographical variation in external morphology, nothing is known about its intra-population level of variability or variation in characters of the hemipenis, osteology, cephalic glands, or soft anatomy. Surprisingly, in view of the large number of congeners, the variability inherent in these last three morphological complexes has not been evaluated for any congener to date. As a general rule, data on population variation for all these morphological characters systems are still elusive for most Neotropical snakes. To date, most available studies have focused on the population level in Tropical snakes are, as far as we know, restricted to external morphological characters traditionally employed in snake systematics (e.g., Hardy and Cole, 1968), ecomorphological phenotypic traits (e.g., Natush and Lyons, 2014), and population dynamics (e.g., Guimarães et al., 2014) or population genetics (e.g., McCartney-Melstad et al., 2012).

In the course of examining collections and conducting fieldwork in northeast Brazil, we found more than 70 additional specimens of *Atractus potschi,* 60 of which were obtained during a single collection event. In this paper, we report new data on intra-population morphological variation and natural history for the species and briefly discuss on the main patterns of morphological variation and post-birth aggregation in the genus *Atractus.*

MATERIALS AND METHODS

Data collection

We examined 90 specimens of *Atractus potschi* (see Appendix). In addition to specimens preserved in natural history collections we include a few new distribution records (Fig. 1) based only on our photographic records (Fig. 2A–B, D–E). We used unpublished data kindly provided by V. Wallach on visceral anatomy from 33 species of *Atractus* for comparison. Terminology for cephalic shields follows Savage (1960) and ventral and subcaudal counts follow Dowling (1951). Condition of the scales in the loreal region follows Passos et al. (2007) and gular scale row counts follow Passos et al. (2005). The sex of each specimen was determined through a ventral incision at the base of the tail in order to check for the presence of the hemipenis. We defined mature individuals through inspection of convoluted deferent ducts in males and occurrence of vitellogenic follicles (at least 5 mm in length; Resende and Nascimento, 2015), eggs or pleated glandular uterus in females (Shine, 1988a, 1994).

We obtained morphometric measurements with an analog calliper (Mitutoyo®) to the nearest 0.1 mm under an Olympus SZX7 stereomicroscope, except for snout–vent length (SVL) and tail length (TLL), which we measured with a flexible ruler to the nearest 1 mm. We measured cephalic shields on the right side of the head. We prepared hemipenes according to procedures described in Pesantes (1994) but using distilled water instead of KOH (Passos et al., 2013b, c). We immersed the everted and fully expanded hemipenis inside an alcoholic solution saturated with Alizarin Red for approximately 15 min in order to stain calcified structures (Uzzell, 1973; Nunes et al., 2012). We inflated the organs with a mixed solution of green paraffin and liquid petroleum jelly to obtain contrast for photographs. Terminology for hemipenis descriptions follows Dowling and Savage (1960), as augmented by Zaher (1999).

We selected five specimens from each sex in order to study cephalic glands and skull variability, since this requires more destructive procedures. We removed the skin of the head until reaching the first vertebrae and performed dissections with the aid of forceps under a stereomicroscope. After removal of the head, we exposed the glands from both sides of the head to assess bilateral asymmetry and took photographs with a digital camera (Olympus DP25) connected to a stereomicroscope (see above). Fourteen specimens were selected in order to study visceral topology and gross morphology, using also the partially damaged specimens (see below). For this

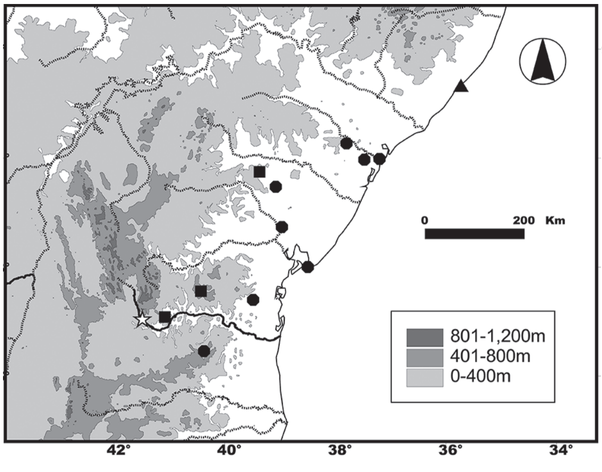

Figure 1. Known distribution of *Atractus potschi.* Closed triangle = type-locality of *A. potschi;* closed octagons = voucher specimens reported previously in literature; closed squares = new records; and open star = study site (Barragem de Cristalândia). Dotted lines represent tributaries of the São Francisco River Basin; continuous line highlights the Rio de Contas.

purpose, a ventral incision was made to expose all visceral organs. Terminology of cephalic glands follows Taub (1966), Kochva (1978), and Zaher (1997). Subsequently, we prepared the skulls following Hangay and Dingley's (1985) protocol, whereby muscles were manually removed with the aid of sodium hypochlorite (NaClO) and subsequently immersed approximately 5 min in hydrogen peroxide (H_2O_2) for clearing. One head removed from an immature specimen was cleared and stained according to a protocol modified from Taylor and Van Dyke (1985) with adaptations from Song and Parenti (1995). Terminology for the skull follows Cundall and Irish (2008) and for soft anatomy follows Perry (1998) and Wallach (1998) to the pulmonary system, Farrel et al. (1998) to the cardiovascular system, Schaffner (1998) to the hepatic system, and Tanaka (1998) to the spleen.

Figure 2. Polychromatism in *Atractus potschi* as evidenced by following populations: **(A)** Maracás, **(B, D–E)** Santaluz, **(C)** Barragem de Cristalândia, and **(F)** Feira de Santana, all from the state of Bahia, Brazil. Photos A–E by R. Abreu, F by M. Freitas.

Table 1. Samples obtained during fieldwork at Barragem de Cristalândia, Brumado, Bahia, Brazil. The "morning" here considered extends from 8:00–11:59 h, whereas "afternoon" extends from 14:00–18:00 h. Coordinates are given toward South/West hemispheres.

Location	*n*	Date	Activity pattern	Time of day	Method of capture	Efforts person-hours	Coordinates
1	2	September 22	On the ground	Morning	Active search	20	13.950296/41.483552
2	1	September 22	On the ground	Morning	Active search	20	13.951202/41.483349
3	3	September 23	On the ground	Two in the morning and one at afternoon	Active search	20	13.950618/41.484785
4	3	September 24	On the ground	Afternoon	Active search	20	13.952001/41.489139
5	2	September 25	On the ground	Morning	Active search	20	13.951240/41.487586
6	2	September 25	On the ground	Afternoon	Active search	20	13.948838/41.48657
7	24	September 28	16 morning e 8 afternoon	Afternoon	Tractor excavation	10	13.947765/41.489935
8	25	September 29	Runaway from underground	Morning	Tractor excavation	10	13.948604/41.490046
9	0	September 29	–	–	Active search	10	13.948923/41.491474
10	20	September 29	Runaway from underground	Afternoon	Tractor excavation	10	13.947719/41.491738
11	1	October 01	On the ground	Afternoon	Active search	10	13.954025/41.476709

Study area

We collected *Atractus postchi* specimens from 22 September–01 October 2009, as part of a faunal rescue for the construction of a dam at Rio de Contas in the locality of Cristalândia (locally denominated "Barragem de Cristalândia"; hereafter BC), municipality of Brumado, state of Bahia, Brazil (Fig. 1). This region is included in the semi-arid domain of the Caatingas (*sensu* Ab'Sáber, 1974, 1977), which presents a variable floristic composition (shrubs and small trees) depending on the amount of rainfall as well as the local edaphic conditions (Eiten, 1992). The climate of the Brumado Municipality is dry, with an annual average rainfall around 600 mm. The average monthly rainfall in the rainy season (October–April) is 80 mm, with December being the wettest month (~ 130 mm). The montly average in the dry season (May–September) is < 5 mm, with August being the driest month (~ 2 mm). The average temperature in the rainy season is 19.3°C and 30.3°C (minimal and maximum, respectively), with October being the hottest month (~ 31.6°C), whereas in the dry season the average temperature is 16.2°C and 28°C (minimal and maximum, respectively) and July is the coldest month (~ 15.1°C).

The total area of the study site described above comprises 11 collection points covering about 260 ha (Table 1), but the locality where most of the sample was collected (*n* = 62) includes about ~ 2000 m^2 covered by xerophytes and deciduous or semi-deciduous herbaceous or low and medium-size shrubs and trees interspersed by areas with shallow litosoil and exposed boulders. DPC and the field team collected the BC samples by hand while a tractor exposed the superficial layer of the soil (eutrophic red latosoil; ERL hereafter) and revealed shallow underground tunnels and chambers in which specimens were housed on (Fig. 3). However, several individuals were damaged during this process, while others escaped intact to the ground surface (Fig. 3A).

Qualitative analyses

First, we conducted a discrete analysis based on external (color pattern, meristic, and morphometric variables) and internal (skull, cephalic glands, hemipenis, and soft anatomy) morphological characters in order to assess the frequencies of each character state in *Atractus potschi* BC population.

Quantitative analyses

We performed an analysis of variance (ANOVA) in order to assess the presence of sexual dimorphism within the sample. The assumptions of homoscedasticity and normality were evaluated through Levene and Komolgorov-Smirnov tests, respectively (Zar, 1999). In cases where characters showed insufficient variation to justify such assumptions, or when the sample size was too small, nonparametric tests (Mann-Whitney *U*-test) were performed (Zar, 1999). The following variables were employed in the statistical analysis: number of ventral and subcaudal scales; snout–vent length; tail length. We performed all statistical using the software Statistica 5.1 (Statsoft, 1996).

RESULTS

Natural history

Our results suggest that *Atractus postchi* attains sexual maturity at ca. 235 mm SVL in males and 250 mm

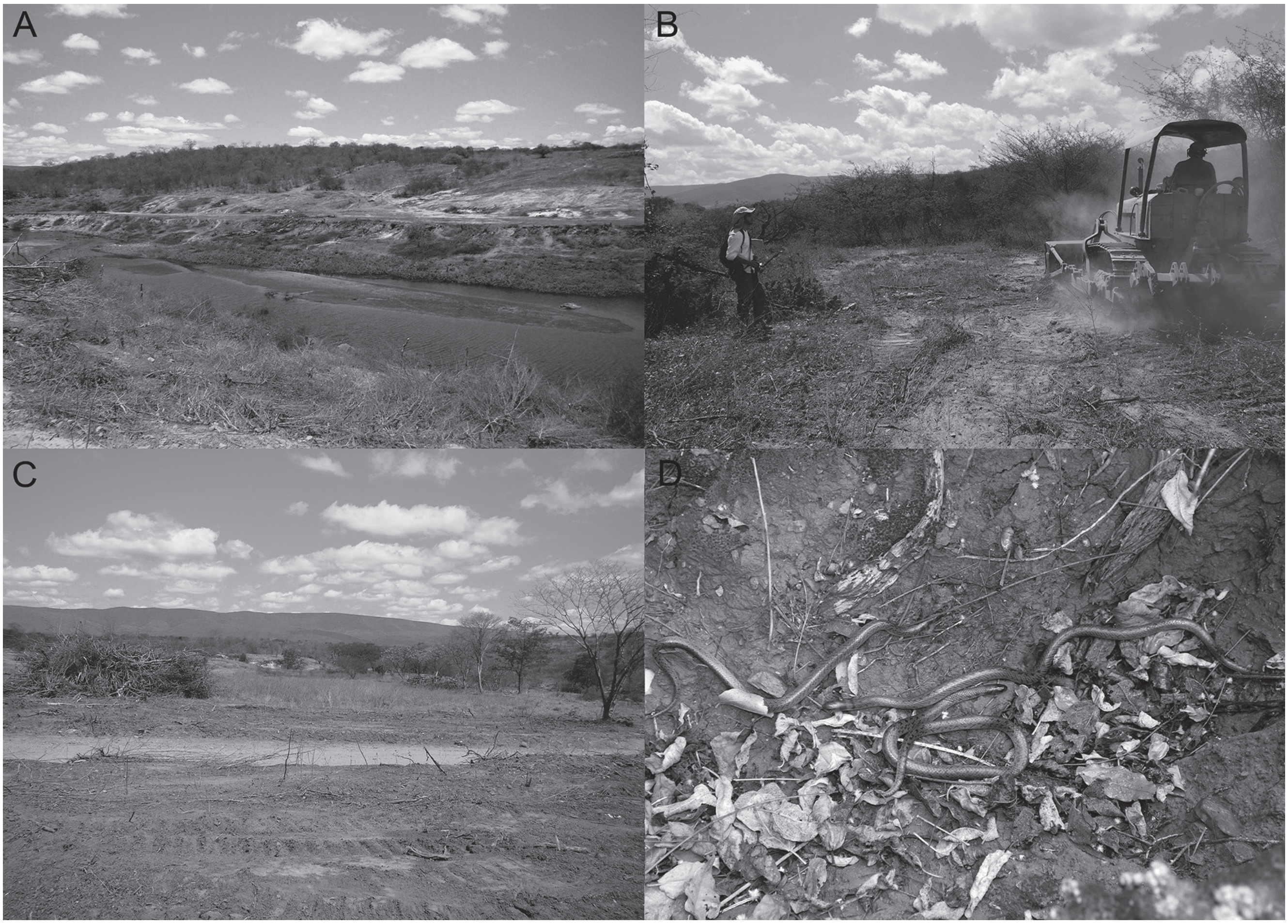

Figure 3. (A) Landscape view of the region of study in the Barragem de Cristalândia, **(B)** during and **(C)** after excavation. **(D)** Specimens that were exposed undamaged along the excavation process. All photos by R. Abreu.

in females (defined on the basis of specimens displaying pleated glandular uterus). Sex ratio was slightly skewed towards males (55%) compared to females (42%), with two damaged individuals of unidentifiable sex. We did not find any female with eggs or secondary follicles and even newborns (individuals with umbilical scars) in the BC sample. Since there were no neonates and the number of juveniles ($n = 31$) was only slightly greater than the number of mature specimens ($n = 29$), we suspect the immature specimens hatched in the previous rainy season (see Discussion). However, this conclusion must be tempered by the possibility of bias in the data collection because 21 specimens (from unpredictable sex but with equivalent number of juveniles and adults individuals) were released in adjacent areas to the study site. During all fieldwork, specimens of *A. potschi* were only found on the ERL soils (not compressed), whereas other species of reptiles with secretive lifestyles (e.g., *Amphisbaena vermicularis* Wagler, 1824) were also abundant in the sandier soils (Fig. 3). At collection point 7 we found underground chambers (20–50 cm deep and ca. 40 cm diameter) 2 m apart, with 3–5 juveniles observed in each chamber (Fig. 4). Although no adult was observed sheltered at underground chambers, it is likely that the tractor had driven their escape by displacement because we found many adults very damaged in the field, while most (but not all) immature specimens were intact.

Some patterns of coloration were restricted almost entirely to the immature individuals (Fig. 4), such as the occipital region being pigmented conspicuously white. This white band is lost in sexually mature specimens, regardless of their geographic origin (Fig. 2), and represents a putative synapomorphy shared by species (in juvenile stages) of the *Atractus paraguayensis* species group (see Discussion). On the basis of the large sample now available for all age classes of *A. potschi,* we do not corroborate the previous suggestion of ontogenetic changes on the size of dorsal marks (Passos et al., 2010a). We found secondary sexual dimorphism only in adult caudal length ($U_{1,15} = 7.0$; $P < 0.01$), and the number of ventral ($F_{1,35} = 46.91$; $P < 0.001$) and subcaudal ($F_{1,62} = 101.38$; $P < 0.001$) scales. Dimorphism in the juvenile and adult SVL and juvenile for TLL were not significant, but several specimens in the sample could not be included in the

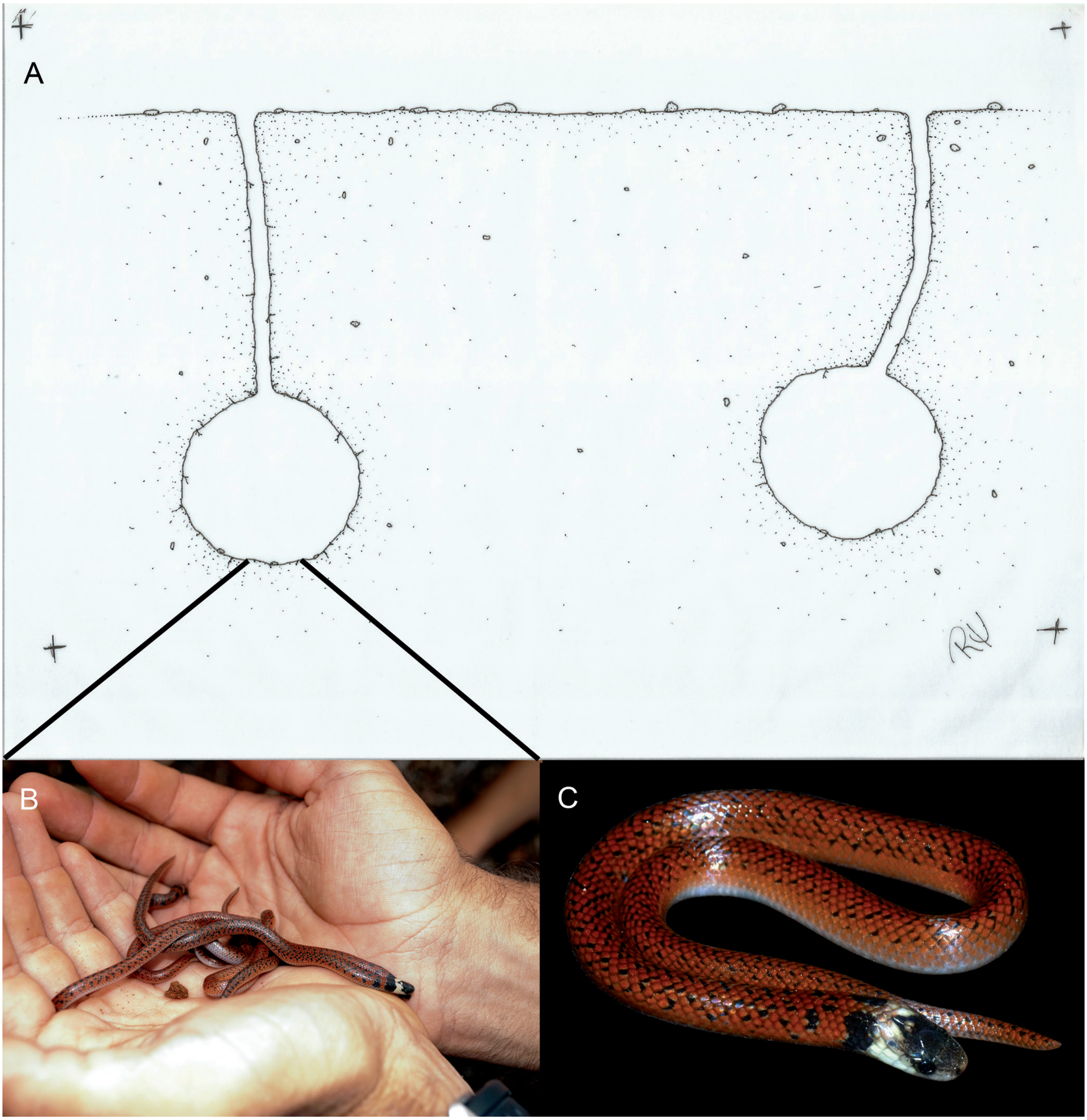

Figure 4. (A) Schematic drawings of the underground nests of young *Atractus potschi* found in the Barragem de Cristalândia, with **(B)** the litter collected at underground chambers. **(C)** General view of juvenile (MNRJ 21012) from Contendas do Sincorá, showing a conspicuous white occipital band. A–B: R. Abreu. C: H. Greene.

statistical analyses due to damage caused by the collection method (see above).

Morphological variation

Since some morphological sources of characters are relatively conserved (e.g., cephalic pholidosis; Fernandes, 1995) or were previously described in detail in the literature (e.g., hemipenis; Passos et al., 2010a), we only report population variation observed in these character systems. Nonetheless, in the case of less known morphological complexes of characters, at least for the genus *Atractus* (skull, cephalic glands, and soft anatomy), we took the opportunity to provide detailed descriptions followed by a summary on the intrapopulation variability. However, in the case of meristic characters, the BC sample augmented slightly the variability previously reported in the literature (Fernandes, 1995; Passos et al., 2010a) and we report it here to increase the range of the aforementioned characters in the species' diagnosis.

Pholidosis

Loreal moderate (*n* = 32; 82%) or long (*n* = 7; 18%); prefrontal suture with respect to internasal suture, continuous (*n* = 8; 21%), directed to the left side (*n* = 2; 5.3%) or to the right side (*n* = 28; 73.7%); supraocular wider than long (*n* = 2; 5.3%), longer than wide (*n* = 5; 13.1%), or approximately as high as large (*n* = 31; 81.6%). Ventrals 140–160 (148 ± 4.64; *n* = 21) in males, 147–166 (159.1 ± 6.8; *n* = 13) in females; subcaudals 24–31 (27.3 ± 1.5; *n* = 33) in males, 19–25 (22.6 ± 0.9; *n* = 26) in females; 6 (*n* = 1 side; 1.1%) or 7 (*n* = 88 sides; 98.9%) supralabials; 1–4 (2.8 ± 0.73; *n* = 43) preventrals; 2–4 (2.8 ± 0.4; *n* = 72 sides) gular rows; 6–10 (8 ± 0.5; *n* = 61) dorsals around the tail.

Hemipenes (Fig. 5)

Retracted organ extends to the level of 6th (*n* = 5; 26.3%), 7th (*n* = 6; 31.6%), 8th (*n* = 6; 31.6%) or 10th (*n* = 2; 10.5%) subcaudal scales; fully everted and almost maximally expanded organs with basal portion of the hemipenial body without spinules (*n* = 3; 30%) or with diffuse spinules (*n* = 7; 70%); spines in lateral portion of capitulum irregularly distributed (*n* = 6; 60%) or transversally organized in regular lines (*n* = 4; 40%); capitular groove moderately evident on asulcate side (*n* = 9; 90%) or well defined (*n* = 1; 10%); lobes covered with irregularly distributed spines (*n* = 8; 80%) or arranged transversally in lines (*n* = 2; 20%); hemipenis shape clavate (*n* = 9; 90%) or with conspicuous constriction on lobular region (*n* = 1; 10%). Much of the variability observed on hemipenial shape (Fig. 5C) was due to preparation artifacts (see discussion for details).

Color patterns (Figs. 6–7)

Dorsum of head dark brown with cephalic-cap extending to middle of parietals (*n* = 27; 79.4%) or reaching posterior half of parietals (*n* = 7; 20.6%); posterior region of cephalic-cap with projections and white spot (*n* = 9; 21%), divided (*n* = 17; 39.5%) or undulated (*n* = 17; 39.5%); occasionally dorsum of head light brown with conspicuous brown spot in parietals (*n* = 8; 18.2%); tapered and divided pattern with (*n* = 13; 76.4%) or without (*n* = 4; 23.6%) small white spot at posterior end; undulated cephalic-cap with rounded white spot posteriorly (*n* = 2; 11.9%), black triangular spot posterior to cap (*n* = 9; 52.9%) or undulated (*n* = 6; 35.2%); region between parietals and first collar generally darker (*n* = 16; 43.2%), with same color (*n* = 10; 27%) or lighter (*n* = 11; 29.8%) than dorsum; supralabials creamish yellow, often scattered by slightly brown dots (*n* = 13; 37.2%) or pigmented only on dorsal margins close to eye (*n* = 22; 62.8%); infralabials generally immaculate (*n* = 22; 64.7%) or scattered with slightly brown dots (*n* = 12; 35.3%); gular region immaculate (*n* = 31; 83.8%) or with few disperse dots (*n* = 6; 16.2%); dorsal ground color of body creamish yellow (*n* = 24; 43.6%) or light brown (*n* = 31; 56.4%); dorsum with black collar on neck starting at level of first (*n* = 6; 13.6%), second (*n* = 30; 68.2%) or third (*n* = 8; 18.2%) scale rows; collar with two (*n* = 7; 15.9%), three (*n* = 24; 54.5%) or four (*n* = 13; 29.5%) scales of width; presence (*n* = 21; 55.2%) or absence (*n* = 17; 44.7%) of second black collar; when present, second collar with two (*n* = 19; 82.6%) or (*n* = 4; 17.4%) three scales long and with two (*n* = 5; 22.7%), three (*n* = 12; 54.5%), four (*n* = 2; 9%) or five (*n* = 3; 13.6%) scales distant of first collar; second collar complete (*n* = 10; 47.6%), slightly interrupted (*n* = 7; 33.3%) or entirely interrupted (*n* = 4; 19.1%); dorsum uniformly scattered with black dots with one scale or less (*n* = 30; 60%), spots with two (*n* = 14; 28%) or blotches (*n* = 6; 12%) with three or more scales long; dorsal marks concentrated (*n* = 32; 61.5%) or dispersed (*n* = 20; 38.5%); blotches transversally arranged forming tiny crossbands (*n* = 5; 11.4%), with conspicuous bands on flanks (*n* = 18; 40.9%) or irregularly dispersed marks (*n* = 21; 47.7%), sometimes larger on vertebral region than flanks (*n* = 3; 6.4%).

Atractus potschi shows an ontogenetic variation of coloration with juveniles displaying occipital region conspicuously white pigmented (Fig. 4), which becomes reddish to dark brown in mature individuals (Fig. 2).

Cephalic glands (Fig. 8)

Premaxillar gland: small and triangular located almost entirely over anterior lamina of premaxillar bone, not touching supralabial glands laterally and slightly exceeding internal limits of nostril in lateral view. Nasal glands: trapezoidal, filling most of area between nostril and eye; each nasal gland limited anteriorly by nostril, posteriorly by eye, medially by frontals, and laterally by maxillar roof; dorsolateral region of nasal glands concave and with its dorsal-anterior margin projecting slightly over nostril. Supralabial glands: thin, not in contact with premaxillar gland anteriorly, extending from anterior tip of nostril through maxilla until reaching anterior portion of Musculus adductor mandibulae externus superficialis. Harderian glands: robust with orbital portion concave, filling most of posterior half of eye, and with posterior end triangular; each gland visible between eye and anteriormost limits of Musculus levator anguli oris and ventrally limited by supralabial gland; after removal of muscles M. levator angularis oris, M. aductor mandibulae externus superficialis and eye, glands become totally exposed;

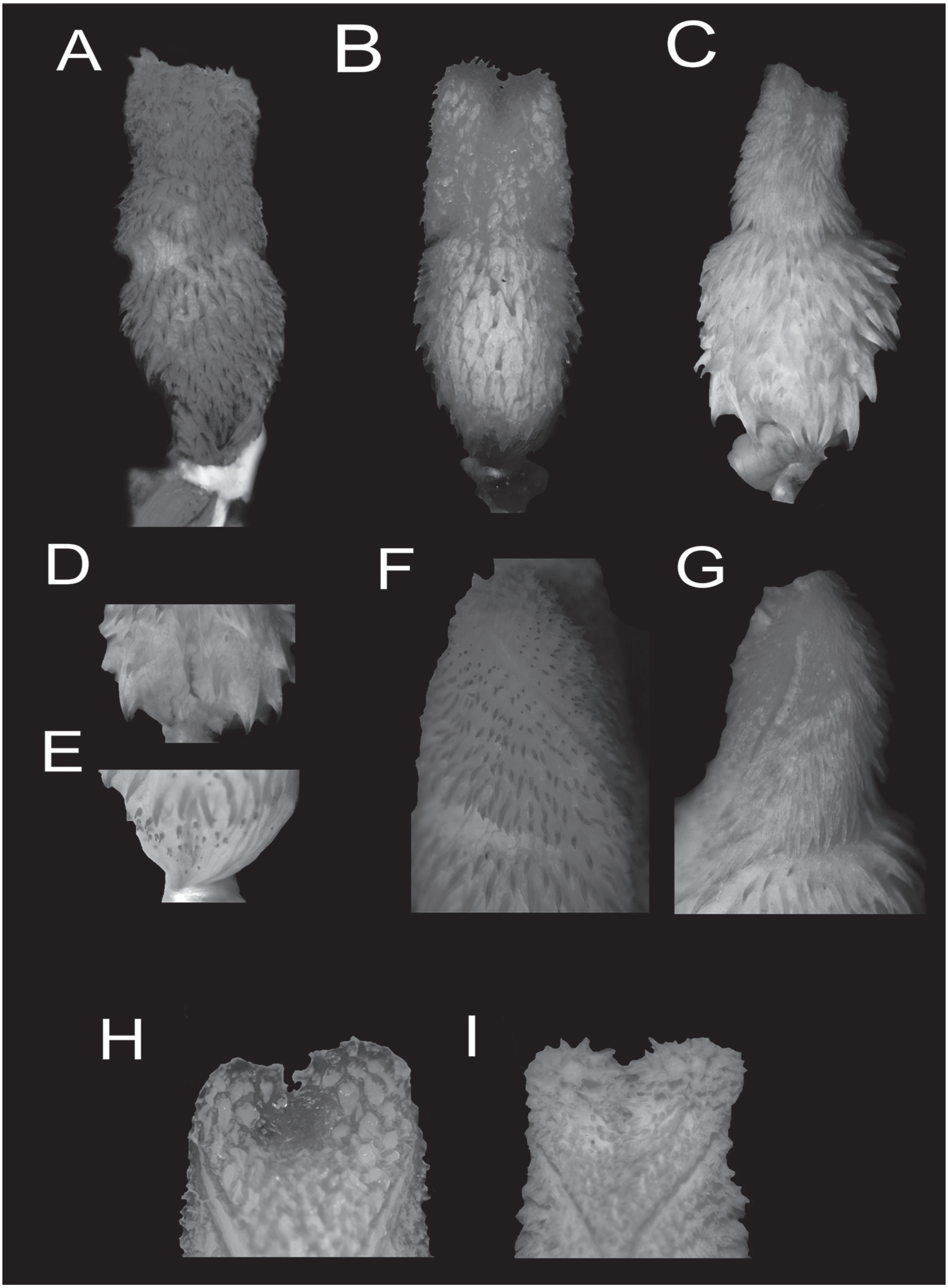

Figure 5. Variation of the hemipenial morphology based on the organs **(A)** completely everted in the field (MZUFBA 2081), **(B)** preserved entirely retracted (UEFS 682), and **(C)** partially everted in the field (CMZUFBA 1591). Details of the proximal region of the hemipenes showing variation with respect to **(D)** extension and size (MZUFBA 1591) and **(E)** calcification (MZUFBA 2045) of basal spines; **(F–G)** lateral view of the capitulum displaying the level of development of the capitular groove (F: MZUFBA 2195; G: MZUFBA 1591); and distal portion of capitulum on the sulcate side of the organ showing **(H)** asymmetry (MZUFBA 2081) and **(I)** symmetry of the lobes (MUZUFBA 2088).

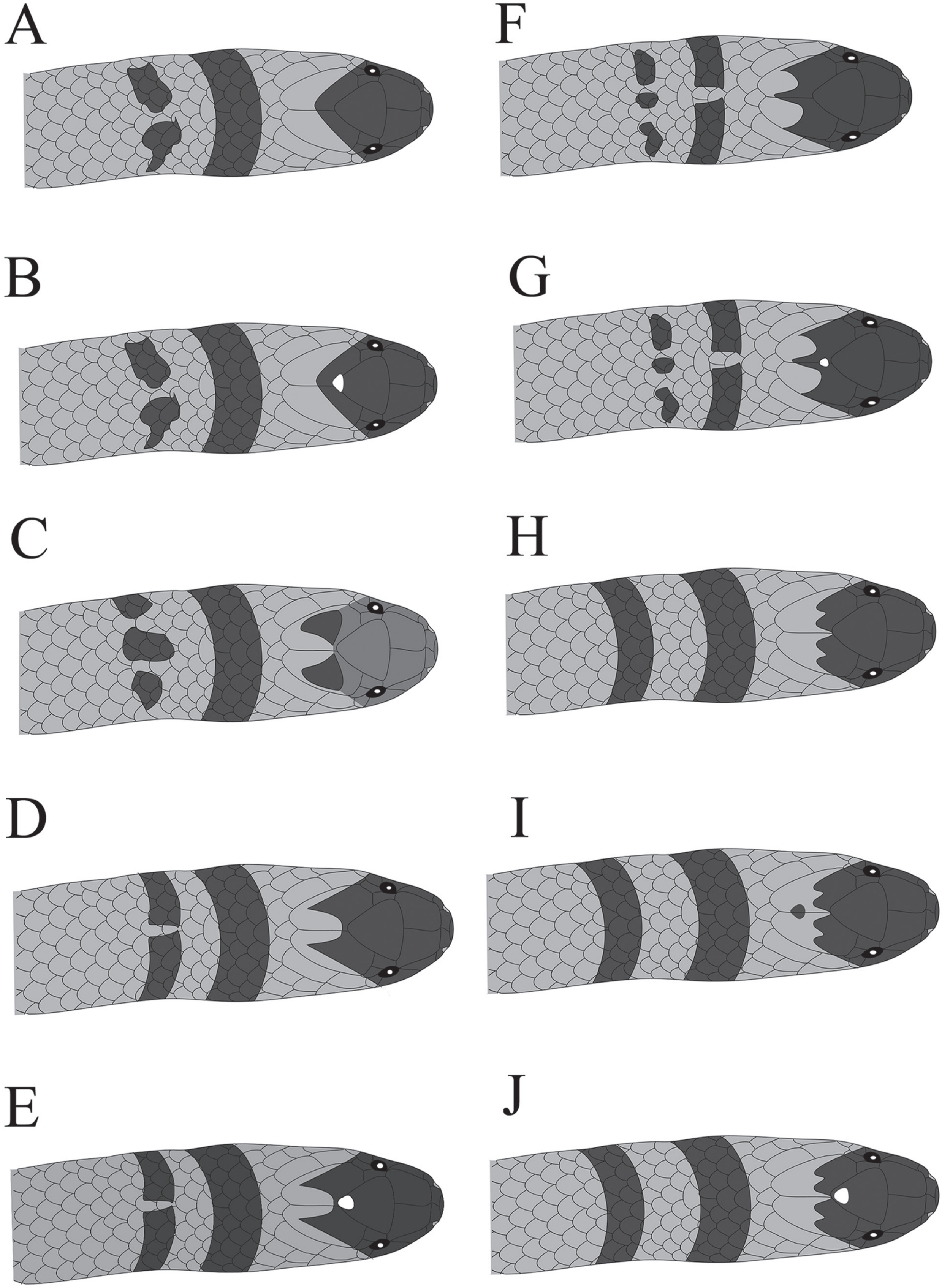

Figure 6. (A–J) Schematic drawings of the head of *Atractus potschi,* summarizing the variation observed in the cephalic-cap, first and second black nuchal collars from specimens of the Barragem de Cristalândia, Brumado, Brazil.

posterior portion of Harderian gland (out of orbit) tapered posteriorly until reaching half of parietal bone. Duvernoy and rictal glands: indistinct or absent. Infralabial glands: in contact with each other at anteriormost portion on symphysial region of lower jaw; each gland enlarging gradually toward rictal region and cover external,

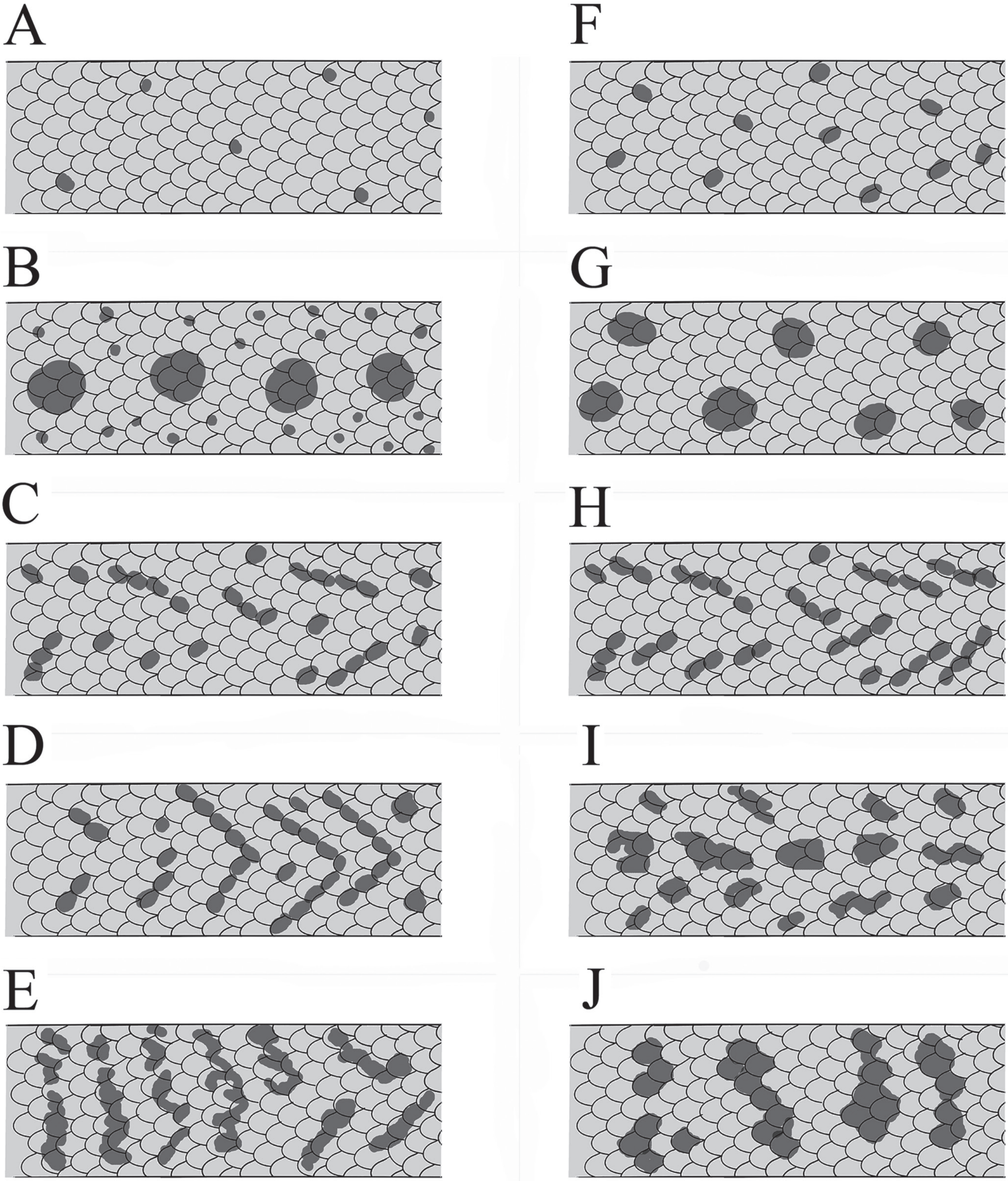

Figure 7. (A–J) Schematic drawings of the midbody region of *Atractus potschi,* summarizing the variation observed in the dorsal marks (spots, blotches or tiny transversal flecks) from specimens of the Barragem de Cristalândia, Brumado, Brazil.

lateral, and ventral portions of lower jaw; infralabial glands enlarge posteriorly until reaching anteriormost border of M. aductor mandibulae externus superficialis. Sublingual gland: consist of medial part and paired lateral components; medial portion elongate, located ventrally to tongue and connected to lateral components anteriorly; medial part of sublingual gland extends nearly at level of posterior limits of Harderian gland; lateral components of sublingual gland drop shaped, fused to each one on anteriormost portion and barely directed to sides of head. Orbital lobe of Harderian gland covering posterior half of eye (*n* = 3; 50%) or both anterior and posterior regions

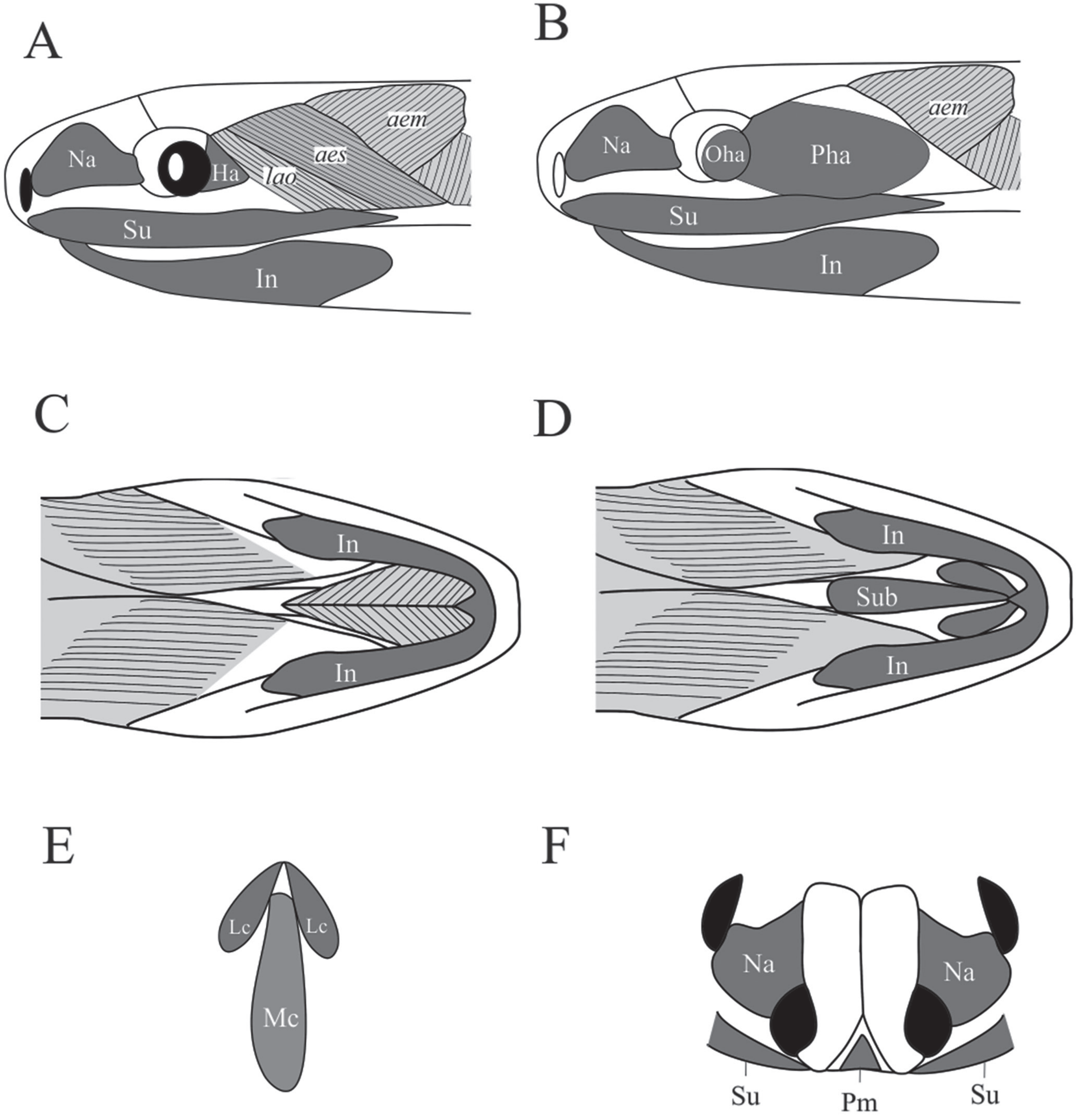

Figure 8. Schematic drawings of the dissected heads of *Atractus potschi,* synthesizing variation observed in lateral **(A–B)** and ventral views **(C–D)** of specimens from Barragem de Cristândia, Brumado, Brazil. Details of sublingual gland **(E)** and snout region of the head **(F)**. Na = Nasal glands, Ha = Harderian gland, Su = Supralabial gland, In = Infralabial gland, Oha = Orbital segment of the Harderian gland, Pha = Posterior segment of the Harderian gland, Sub = Sublingual gland, Me = Medial portion of the sublingual gland, Lc = Lateral components of sublingual gland, lao = Musculus levator anguli oris, aes = Musculus adductor mandibulae externus superficialis, aem = Musculus adductor mandibulae externus medialis.

(*n* = 3; 50%); anterior portion of infralabial glands not enlarged, increasing gradually in size posteriorly (*n* = 3; 60%) or with anterior portion more robust and only slightly enlarged posteriorly (*n* = 2; 40%); supralabial glands not in contact (*n* = 4; 80%) or contacting nasal glands anteriorly (*n* = 1; 20%).

Skulls (Fig. 9)

Deeply ossified with elongated aspect; limited anteriorly by premaxilla, anterolaterally by maxillaries and posteriorly by exoccipitals; in lateral view, skull height slightly increases towards posterior end of parietal, where it slightly descends until reaching exoccipitals; pallatomaxillary arc and snout elements visible ventrally; maxillary, lower jaw, palatine, and pterygoid with teeth arranged in longitudinal rows. Premaxilla: small, toothless, and situated on anterior edge of skull; slightly triangular anteriorly with concave edges expanding dorsally forming nasal process attached to anterior-dorsal tip of nasals; laterally, ascending process bears two foramina and expands towards maxillary constituting maxillary processes of premaxilla; in ventral view, premaxilla displaying two foramina and expands posteriorly, comprising septomaxillary processes, but not in contact with vomer. Septomaxillaries: located between nasals and vomers, forming floor of nasal cavity; its anterior edge fits internal angle of nasal process of premaxilla; septomaxillaries dorsally projected comprising short conchal process, approximately rectangular and not touching nasals or prefrontals dorsally; septomaxillar attaches to frontals dorsally, being only connection of prokinetic joint attaching to braincase. Nasals: trapezoidal, located anteriorly in skull between premaxilla and frontals, covering nasal cavity dorsally; nasal septum situated vertically to longitudinal line of contact between nasals, forming inner wall of nasal cavity; in dorsal view, anterior and posterior edges of nasals narrowing; medial anterior edges contact nasal processes of premaxilla and posterior margins contact frontals ventrally in lateral view; nasals with convex dorsal surface partially overlapping the prefrontals through process originated on its posterior-lateral edges; nasals not

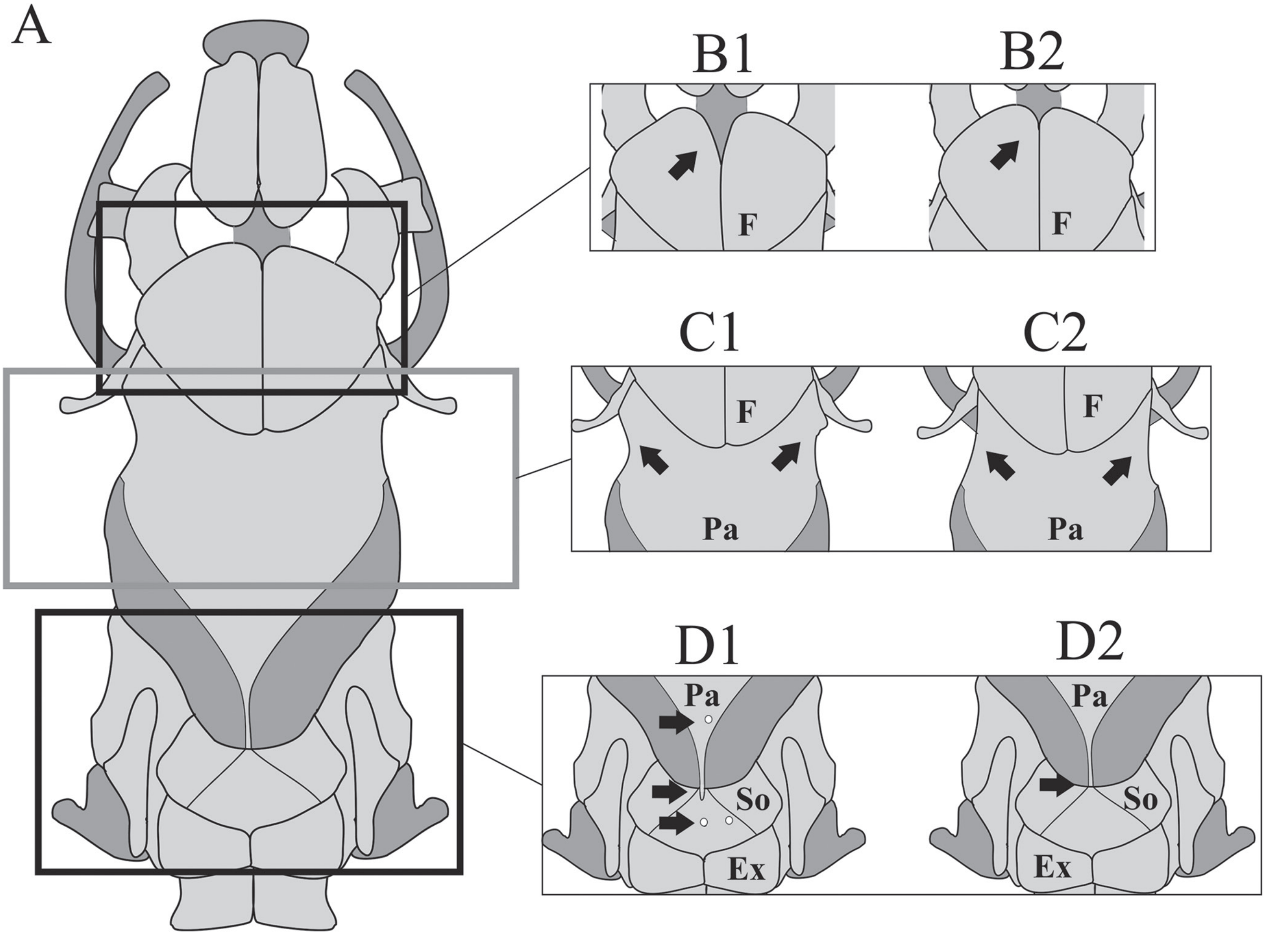

Figure 9. Schematic drawings of **(A)** the skull of *Atractus potschi,* summarizing the variation observed in the **(B)** anterior, **(C)** medial, and **(D)** posterior portions of the crania of specimens of the Barragem de Cristalândia, Brumado, Brazil. F = Frontal, Pa = Parietal, So = Supraoccipital, Ex = Exoccipital.

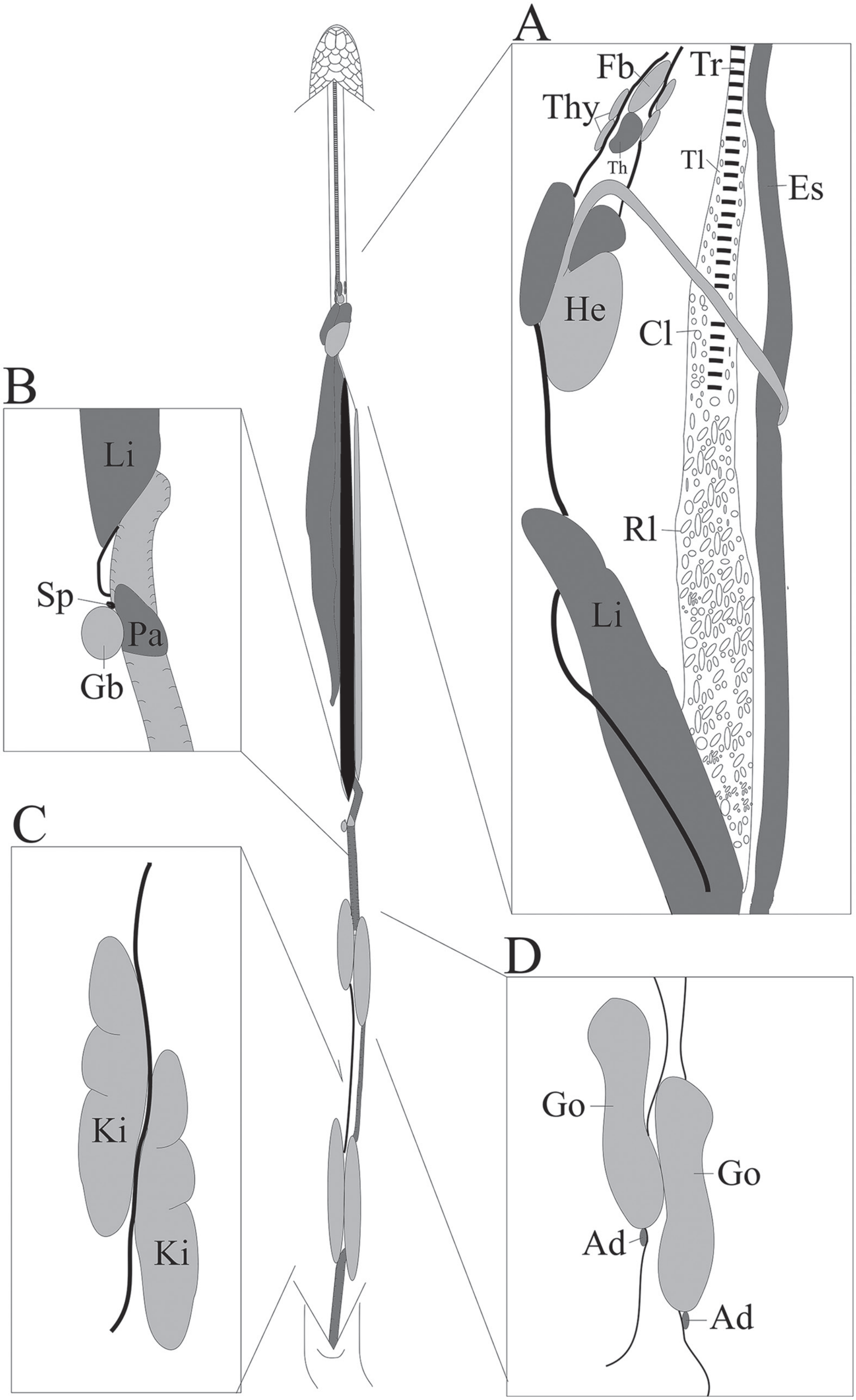

Figure 10. Schematic drawings of the soft anatomy of *Atractus potschi,* summarizing the variation on the visceral morphology and topology observed in the **(A)** anterior, **(B–C)** medial, and **(D)** posterior portions of the body of specimens of the Barragem de Cristalândia, Brumado, Brazil. Li = Liver, Ki = Kidney, Thy = Thymus, Ad = Adrenal gland, Rl = Right lung, Cl = Cardiac lung, Es = Esophagus, He = Heart, Th = Thyroid gland, Fb = Fat body, Sp = Spleen, Gb = Gall bladder, Pa = Pancreas, Tl = Tracheal lung, Tr = Trachea, Go = Gonad.

reaching lateral processes of prefontrals and with narrow descending lamina. Vomers: located midventrally in skull; premaxillary process of each vomer slightly expands anteriorly, delimiting anterior edge of olfactory capsule; premaxillary processes contact each other and septomaxillary anteriorly but do not contact premaxilla; caudal processes of vomer expanded posteriorly in medial line, constituting exochoanal fenestra. Frontals: trapezoidal in dorsal view, located anterior-medially in skull, contributing to dorsal roof and covering ventral and lateral edges of neurocranium; laterally, it forms dorsal edge and inner wall of eye socket; frontals contacting prefrontals anterolaterally, nasals anterior-medially, parietal posteriorly, and postorbital lateral-ventrally; orbital lamina descending and converging medially to form narrow subolfactory process that rests on medial keel of parabasisphenoid; frontals ventrally expanded anteriorly into well developed septomaxillary process. Parietal: pentagonal in dorsal view, representing largest bone of braincase; anterior edge of parietal concave, sutured to frontals, which may or may not have slightly small projection that fits into frontals; parietal with small anterolateral projections articulating with postorbital bone and, usually, exceeding their lateral limits in dorsal view; posteriorly, parietal sutured to supraoccipitals and posteriolaterally to prootics; dorsal surface of parietal smooth with two parietal crests, which converge posteriorly until reaching anterior edge of supraoccipitals; dorsal-posterior region under crests deeply concave, descending laterally to contact prootics and supraoccipital. Supraoccipitals: fused, pentagonal, located in dorsal-posterior region of skull; supraoccipilitals contacting parietal anteriorly, prootics laterally, and exoccipitals posteriorly; anterior edge of supraoccipitals concave and irregular and its posterior edge angles tapered posteriorly; lateral margins contacting supratemporal edge medially; dorsally, supraoccipitals with two connected oblique crests and slight longitudinal crest along its medial line; crests split each supraoccipital in distinct regions: lozenge central portion contacting exoccipitals posteriorly and lateral trapezoidal-like portion contacting prootics laterally, which may or may not display foramina. Exoccipitals: trapezoidal in dorsal view and located in posterior edge of skull, comprising dorsal edge of *foramen magnum;* each exoccipital contacting basioccipital ventrally and prootic laterally; exoccipitals presenting crests continuous to supraoccipital crests anterior-laterally and pierced by foramen in its dorsal surface which may occur exclusively to one or both exoccipitals. Basioccipital: hexagonal and located in middle of posterior portion of braincase; basioccipital contributing to posterior portion of braincase floor, as well as median portion of occipital condyle; anteriorly, basioccipital contact parabasisphenoid complex, prootics and exoccipitals laterally, and atlas posteriorly, where it composes ventral edge of *foramen magnum.* Parabasisphenoid: triangular and located midventrally in skull, contacting frontals dorsal-anteriorly, parietal and prootic laterally, and basioccipital posteriorly; posteriorly, after prootics suture, parabasisphenoid with two foramina corresponding to posterior opening for Vidian nerve. Prootics: irregular and contacting parietal dorsally and anterolateral, basisphenoid and basioccipital ventrally, supraoccipital dorsal-posteriorly, and exoccipital lateral-posteriorly; prootic with slight crest in its dorsal region, approaching to contact region with supratemporal; each prootic pierced by two or three foramina at ventral lamina, giving passage to distinct branches of trigeminal nerve; prootics, in dorsolateral surface, with two foramina under supratemporal; posterior region of prootics with small enlargement to insertion of *columella auris.* Prefrontals: irregular, contacting frontal in its posterior-lateral portion and maxillar and palatine ventrally; lateral edge of prefrontal convex in dorsal view and concave on medial margin with elongate aspect; lateral descending lamina of prefrontal enlarged dorsally, with reduction of size in its ventral half; ventrally, prefrontal with enlarged process supported by palatine; internal surface of prefrontal pierced by lacrimal foramen. Postorbitals: small and slender, delimiting orbital cavity posteriorly; postorbitals with lateral surface concave and posterior region slightly convex; postorbitals contacting frontal and anterolateral processes of parietal. *Columella auris:* small and paired bone inserted in *fenestra ovalis,* composed by prootics and exoocipitals; columella auris crosses the *fenestra ovalis* towards quadrate, attaching to processes located at its medial portion. Maxillaries: curved bones located at marginal line of skull, limiting lateral edge of anterior and medial portion of skull; each maxilla extends from septomaxillary processes of premaxilla until reaching ectopetrygoid at level of palatine and pterygoid contact; medial surface of each maxilla concave, exhibiting two processes, with first (palatine process) located medially; ectopterygoid process represent second maxillary process, located on its posterior portion; lateral surface of maxillary bone, which supports supralabial glands, concave and pierced by single foramina; ventrolateral margins of maxilla with seven to nine teeth curved posteriorly and short diastema (equivalent to penultimate tooth) between antepenultimate and last two teeth; last two teeth gradually reduced in size compared to prediastemal teeth. Palatines: each bone approximately as long as maxilla, contacting prefrontal anteriorly and pterygoid posteriorly; anteriormost portion of palatine extends until half of vomer, while its posterior end extends until contacting pterygoid; maxillary process of palatine located laterally not contacting palatine process of maxilla, and supporting ventral portion of prefrontal bone; ventral surface palatine with longitudinal series of five to seven teeth not extending until posterior portion of bone; palatine ventrally present two foramina posterior to third and fourth teeth; choanal process of palatine absent or indistinct. Ectopterygoids: triradiated bones, connecting posterior end of maxilla to medial region of pterygoid; anterior region of ectopterygoid broad, flattened, and forked attached to ectopterygoid process of maxilla; ectopterygoid edges exceed end of maxillary row of teeth, generally reaching 7th tooth; dorsally it attaches to posterior process of pterygoid. Pterygoids: elongated bones extending through over half of skull total length; each pterygoid located posterior to palatine with its posterior end about two times larger than anterior one; ventral surface of pterygoid curved laterally and with 13–15 teeth; pterygoidal teeth slightly smaller than palatine ones; ectopterygoid fits to pterygoid approximately in gap between 3rd and 4th pterygoid's teeth and extending at level of 6th tooth. Supratemporals: elliptical bones placed posterolaterally to braincase; supratemporals extending over most of prootic extension, being slightly directed ventrally to extend over supraoccipital bone. Quadrates: mace shaped bones, articulating obliquely to skull; proximal portion of quadrate enlarged, articulating with supratemporal; distal end of quadrates slightly enlarged and articulating with glenoid cavity of retroarticular process, forming quadrate-articular articulation; medial surface of each quadrate concave and its posterior edge with short process directed oblique to bone. Dentaries: located at anterior portion of mandible, each curving medially in its anterior end towards opposite dentary; midposterior end of dentary contacts anterodorsal portion of angular and splenial posteriorly; dorsal edge of dentary with row of eight to nine teeth; teeth approximately subequal until mentonian foramen (fifth tooth), reducing gradually in size after that point, slightly curved posteriorly; in lateral view, posterior region of dentary forked, projecting dorsally and ventrally, with ventral expansion slightly longer than dorsal; anterior end of the compound bone fits onto such processes, reaching level of sixth tooth; medial surface of dentary anteriorly concave, with anterior-ventral bend at level of third tooth, which runs through all dentary towards its posterior end, resulting in terminal opening of Meckel's groove; dentary comprises roof of Meckel's groove, while splenial ventrally limits it. Splenials: triangular, located at medial surface of mandible with mesoventral orientation with respect to articulation between dentary and angular; anterior end of splenial fits in dentary through long and tapering process, until reaching fifth tooth, while its posterior end contacts angular; posterior region of splenial pierced by milohyoid foramen. Angulars: triangular and located at medial surface of mandible, with long and tapering projection directed posteriorly and dorsal process that extends above splenial until reaching dentary dorsally; dorsal process of angular originates at level of seventh or eighth tooth; anterior half of angular pierced by milohyoid foramen. Compound bone: elongated bone comprised by coronoid, surangular and articular, representing largest bone of mandible (about two thirds of mandibular length). Compound bone positioned at posterior end of the mandible, being connected to skull through the glenoid cavity in its posterior end; anterior portion of compound bone projected as tapering process, which inserts into dentary and extends until level of sixth tooth of dentary; ventral surface of compound bone concave, and its midventral portion contacts angular; posterior-ventral crest of compound bone with moderated size; in posterior end of compound bone, anterior to glenoid cavity, surangular crest forms mandibular fossa on its medial portion; retroarticular process short and pierced by foramen on its ventral lamina.

Medial contact between frontals at dorsal-anterior edges may occur more anteriorly (*n* = 1; 20%) or centrally (*n* = 4; 80%); lateral-anterior projections of parietal generally exceeding lateral limits of parietal dorsally (*n* = 4; 80%) or not exceeding (*n* = 1; 20%); dorsal-posterior edge of parietal with (*n* = 1; 20%) or without (*n* = 4; 80%) crest overlapping supraoccipital anteriorly; parietal without (*n* = 3; 60%) or with one (*n* = 1; 20%) or two (*n* = 1; 20%) foramina; lateral portion of supraoccipitals without foramen (*n* = 1; 20%) or pierced by one (*n* = 2; 40%), two (*n* = 1; 20%) or three (*n* = 1; 20%) foramina; exoccipitals pierced by foramen in its dorsal surface occurring only in one (*n* = 2; 40%) or on both exoccipitals (*n* = 3; 60%); mesolateral margin of maxilla with seven (*n* = 2 sides; 12.6%), eight (*n* = 5 sides; 31.2%) or nine (*n* = 9 sides; 56.2%) teeth; palatine with five (*n* = 1 side; 10%), six (*n* = 7; 70% sides) or seven (*n* = 2 sides; 20%) teeth; pterygoid with 13 (*n* = 1 side; 20%), 14 (*n* = 3 sides; 60%) or 15 teeth (*n* = 1 side; 20%); dentary with eight (*n* = 2 sides; 22.2%) or nine (*n* = 7 sides; 77.8%) teeth.

Soft anatomy (Fig. 10)

Heart: located in midventral cavity of body, posteriorly on first quarter of body length, being relatively small in size; right atrium approximately twice longer than left, projecting posteriorly over lateral border of ventricle; left atrium limited posteriorly by anteriormost border of ventricle; ventricle elongated, tapering at its posterior end, usually smaller than right atrium; caudal end of ventricle slightly directed to right side of body. Thyroid gland: short, ellipsoidal or rounded, located immediately anterior to heart; yellowish ellipsoidal fat body usually covers thyroid gland partially or totally, extending anteriorly to exceed anterior limits of left pair of thymus. Thymus paired, located anterolateral to thyroid; left pair of thymus situated anteriormost, usually anterior to thyroid gland, while right pair usually lies lateral to it; both pair of thymus creamish white and small in size. Tracheal lung: present, extending to distance close to anterior portion of heart and bearing edicular parenchyma. Right lung: unicameral, bearing edicular parenchyma (sensu Wallach, 1998), originating dorsal and posterior to heart with short anterior lobe; right lung mostly in right side of body cavity, enlarging posterior to heart; right lung accommodated to dorsolateral (right) surface of liver from their anterior extension until its posterior edge; edicular parenchyma reduces caudally as lungs tapers until becoming saccular lung, not reaching posteriormost border of liver; left lung absent. Liver: longest organ of body, extending over approximately one third of SVL; liver light red and located on right side of body cavity, separated from heart by short gap; vena cava embedded in ventrolateral surface of liver and follows straight path until leaving liver surface posteriorly; fat bodies extended posterior to caudal tip of liver, surrounding viscera until reaching cloaca. Pancreas: small, oval and creamish white, attached to anterior end of duodenum. Gall bladder: oval and lies anterior to pancreas, in contact with spleen laterally and to pancreas posteriorly; pancreas, spleen, and gall bladder located in anterior portion of second half of body. Gonads: located in anterior part of last third of body cavity, separated from gall bladder by relatively long gap; either testes or ovaries lie slightly anterior to kidney and right organ always lies anterior to left one. Testes: ellipsoidal, either separate or not by short gap. Ovaries: juxtaposed (usually when not bearing follicles) or separate by short gap. Adrenals: small, light orange, and slightly elongated usually located posterior to each gonad (testes or ovaries). Kidneys: last paired organs of body cavity located on posterior third of body, ellipsoidal, deeply lobed and elongated; left kidney usually longer than right and right kidney located anterior to left one; right and left kidney juxtaposed or separate by gap; medial surface is slightly concave; Rectal caecum: indistinct or absent.

Fat body anterior to heart overlaps thyroid gland (71.5%; *n* = 5) or anterior to thyroid, not overlapping it (28.5%; *n* = 2); thyroid gland usually rounded (62.5%; *n* = 5) or ellipsoidal (37.5%; *n* = 3); right adrenal usually posterior to right testis (71.5%; *n* = 5) or dorsal to gonad midpoint (28.5%; *n* = 2); kidneys separate by short gap (60%; *n* = 9) or juxtaposed (40%; *n* = 6); testis usually separate from kidney by gap (71.5%; *n* = 5) or juxtaposed (28.5%; *n* = 2). Quantitative variation: lengths expressed in percentage of SVL or regarding other visceral organs; heart length 2.5–4.1% (3.2 ± 0.5; *n* = 7) in females, 2.4–3.5 (3.1 ± 0.5; *n* = 7) in males; right atrium/heart length 60–83% (73 ± 8.5; *n* = 7) in females, 58–77% (63 ± 6.5; *n* = 7) in males; left atrium/heart length 38–52% (43.2 ± 4.6; *n* = 7) in females, 27–41% (32.5 ± 4.6; *n* = 7) in males; ventricle/heart length 45–63% (57 ± 6.3; *n* = 7) in females, 52–71% (60 ± 5.9; *n* = 7) in males; fat body anterior to the heart 0.8–2.5% (1.8 ± 0.7; *n* = 4) in females, 1.5–2.7 (2 ± 0.6; *n* = 3) in males; heart midpoint 17.4–24.4% (21.2 ± 2.5; *n* = 7) in females, 18.3–23% (20.6 ± 1.6; *n* = 7) in males; thyroid gland length 0.5–1.2% (0.8 ± 0.2; *n* = 7) in females, 0.5–1.2 (0.9 ± 0.2; *n* = 4) in males; thyroid gland midpoint 14–24% (18 ± 3.5; *n* = 7) in females, 16–20% (18 ± 1.6; *n* = 5) in males; anterior right thymus length 0.6–1.1% (0.8 ± 0.2; *n* = 7) in females, 0.6–0.8 (0.7 ± 0.1; *n* = 5) in males; anterior left thymus length 0.7–0.9% (0.8 ± 0.07; *n* = 7) in females, 0.6–1.2 (0.8 ± 0.2; *n* = 6) in males; right thymus midpoint 13.8–21% (17.3 ± 2.6; *n* = 7) in females, 14.6–18.3% (16.3 ± 1.6; *n* = 6) in males; left thymus midpoint 13.8–19.6% (16.3 ± 2.2; *n* = 6) in females, 15.5–16.8 (16 ± 0.5; *n* = 5) in males; heart–liver gap 4.9–7.9% (6.2 ± 1.1; *n* = 7) in females, 4.2–6.4 (5.2 ± 0.9; *n* = 7) in males; liver length 20–29.4% (25.2 ± 3.35; *n* = 8) in female, 25.8–32% (29.8 ± 2; *n* = 7) in males; liver–gall bladder gap 5–13% (9 ± 2.5; *n* = 8) in females, 6–16% (9.6 ± 4; *n* = 7) in males; liver–kidney gap 20–38.5% (31 ± 5.8; *n* = 8) in females, 26.7–33.7 (30 ± 2.2; *n* = 7) in males; gall bladder at midpoint 57–71.4% (63 ± 4.7; *n* = 8) in females, 58.5–71.1% (66.2 ± 4.4; *n* = 7) in males; gall bladder–gonad gap 1.2–8.4% (4.4 ± 2; *n* = 8) in females, 1.6–9.6% (6 ± 2.8; *n* = 7) in males; gall bladder–kidney gap 11.2–32.8% (22.5 ± 8; *n* = 8) in females, 18.4–25.3% (20.1 ± 2.4; *n* = 7) in males; right ovary midpoint 67.5–75.7% (73.3 ± 2.8; *n* = 8), left ovary midpoint 69.2–85% (78 ± 5.3; *n* = 8); total ovaries midpoint 68.4–80% (75 ± 3.9; *n* = 8); right testis midpoint 63–83% (75.6 ± 6.4; *n* = 7) and left testis midpoint 71.7–86.4% (80 ± 5.1; *n* = 7); total testis midpoint 67.6–84.7% (78 ± 5.7; *n* = 7); right testis length 2.4–4% (3.3 ± 0.6; *n* = 7) and left testis length 1.9–4.9% (3 ± 1.2; *n* = 7); right adrenal midpoint 53.3–56.7% (55 ± 2.4; *n* = 8) in females, 63–86% (77.6 ± 7.5; *n* = 7) in males; left adrenal midpoint 77–91% (82 ± 4.6; *n* = 8) in females, 73–89.4% (81 ± 5.7; *n* = 7) in males; adrenal midpoint 76.2–87.6% (80.6 ± 3.9; *n* = 8) in females, 68.3–87.8% (79.5 ± 6.44; *n* = 8) in males; total kidney midpoint 83.1–94.2% (86.9 ± 3.9; *n* = 8) in females, 85.7–94% (90.5 ± 3.4; *n* = 7) in males; right kidney midpoint 81.2–92% (84.8 ± 3.9; *n* = 8) in females, 75.7–92.7% (87.5 ± 6.1; *n* = 7); left kidney midpoint 84.9–96.3% (88.9 ± 3.9; *n* = 8) in females, 87.2–99% (93.6 ± 4; *n* = 7); right kidney length 2.55–6% (4.2 ± 1.2; *n* = 8) in females, 4.8–6.7% (5.4 ± 0.6; *n* = 7) in males; left kidney length 2.55–6.9% (4.88 ± 1.5; *n* = 8) in females, 4.5–7.5% (6 ± 1.1; *n* = 7) in males; kidney–vent gap 6.8–28% (10.8 ± 7; *n* = 8) in females, 5.4–11.1% (7.6 ± 1.8; *n* = 7) in males; kidney gap, when present, 1.1–1.2% (1.1 ± 0.08; *n* = 3) in females, 2.5–3.6% (3.2 ± 0.7; *n* = 3) in males; ovary–kidney gap 0.66–4% (2.4 ± 1.1; *n* = 8); testis–kidney gap (when present) 1.05–5% (2.9 ± 1.4; *n* = 5); right lung length 16–30% (17 ± 4; *n* = 7) in females, 14–31% (20.5 ± 8; *n* = 6) in males; tracheal lung length 0.3–0.92% (0.8% ± 0.2; *n* = 7) in females, 0.2–1 (0.5% ± 0.2; *n* = 4) in males.

DISCUSSION

Natural history

Although the only quantitative studies regarding reproductive cycles in the genus *Atractus* suggest that females attain sexual maturity about 30% larger than males

(*A. reticulatus* Boulenger, 1885, Balestrin and Di-Bernardo, 2005; *A. pantostictus* Fernandes and Puorto, 1993, Resende and Nascimento, 2015), we found that females of *A. potschi* attain maturity just 10% larger than mature males in the BC sample. Since Darwin (1859), late sexual maturity has been considered an adaptive advantage for allowing females to reach a larger body size before driving energy to reproduction (but see Shine, 1988b). Nevertheless, the sample examined by Balestrin and Di-Bernardo (2005) and Resende and Nascimento (2015) came from higher latitudes in the south and southeast regions of Brazil with low average temperatures mainly in the winter. Despite the possibility of phylogenetic inertia in the growth rates for the genus, we suspect that the maturation phase of the latter species may be delayed by the shortening of its activity pattern for only a few months of the year. Both species displayed seasonal reproductive cycles of females with vitellogenic follicles being found from August–December in *A. reticulatus* (Balestrin and Di-Bernardo, 2005) and from September–April in *A. pantostictus* (Resende and Nascimento, 2015). Based on our findings (absence of secondary follicles, eggs, and neonates) and also considering the rainfall rate along the species distribution in the semiarid Caatinga (see Fig. 1), it is possible that the reproductive cycle of *A. potschi* may be seasonal, with secondary vitellogenesis, pregnancy, oviposition and recruitment restricted to the rainy season (October–April).

In many lineages of animals, individuals cluster together in response to a variety of cues (e.g., thermal, hydric, nutritional, reproductive) and derive a corresponding diverse array of potential benefits from such aggregative behaviour (Aubret and Shine, 2009). Snakes have been viewed as a quintessentially asocial lineage apart from antagonistic territorial interactions and mating behaviours (Wilson, 1975), but many species aggregate with conspecifics during key stages in their life cycle (reviewed in Graves and Duvall, 1995). Although such aggregations often appear to be caused by local availability of a determined physical resource, some entail mutually beneficial behaviours with conspecifics (Gregory, 1984) or even kin (Clark et al., 2012), such as reduced rate of water loss in shedding snakes (Duvall et al., 1985) or thermoregulation (Graves and Duvall, 1987; Aubret and Shine, 2009; Clark et al., 2012). We are not aware of any post-parturition aggregation reported other than antagonistic territorial interactions and reproductive mating in Neotropical snakes. Reports on post-mating aggregation in the Neotropics are frequently related with communal egg-laying, which has been recorded for a few species (Graves and Duvall, 1995; Albuquerque and Ferrarezzi, 2004; James and Henderson, 2004; Braz et al., 2008). Thus, communal nests have been reported not only at high-latitude (e.g.,Vaz-Ferreira et al., 1970) and high-altitude (Cadle and Chuna, 1995), but also at disturbed sites with apparent scarcity of suitable nesting sites (Albuquerque and Ferrarezzi, 2004; James and Henderson, 2004; Braz et al., 2008).

We observed an aggregation of immature individuals in the study area (Fig. 3A), which apparently hatched in the previous rainy season (inferred based on absence of umbilical scars and size of the juveniles), as well as some adults outside of the underground chambers (Fig. 4D). Unfortunately, tissue samples were not preserved for molecular study, so it is not possible to infer the paternity relationships among young and adult specimens obtained during fieldwork at each site. Recently, Clark et al. (2012) found that juvenile and pregnant timber rattlesnakes (*Crotalus horridus* Linnaeus, 1758) in the field preferentially aggregate with kin, but other clustering show no kin preferences in the referred study. This seems not to be the case in our study, since there is no reproductive female (= displaying secondary follicles) in the BC sample and the aggregation observed was juveniles-based. Aubret and Shine (2009) report that a neonate litter of *Notechis scutatus* (Peters, 1861) exhibited aggregation under laboratory conditions, especially when subject to rapid cooling. These authors pointed out that post-birth aggregation retards cooling rates, facilitated neonatal locomotor performance, and anti-predator tactics. As there is no scarcity of suitable nesting sites or apparent differences in the local availability of physical resource in the study area, and considering the low relative humidity along the dry season, plausibly the aggregation phenomenon observed in *Atractus potschi* may be due to reduction of evaporation rates. One of us (DPC) noted several (~ 20) dead or dying specimens of *Atractus* as well as other small species of fossorial squamates [e.g., *Epictia borapeliotes* (Vanzolini, 1996), *Amphisbaena vermicularis, Leposternon polystegum* Duméril, 1851] during the fieldwork for this study when those were exposed to direct sunlight on the ground from the mid-morning to mid-afternoon. Benefits related to hydration may be more important for smaller snakes because of increased surface area to volume ratios (Clark et al., 2012). On the other hand, another possible explanation for clustering could be seasonal aggregation, like the communal denning characteristic of several snakes from temperate regions (reviewed in Gibbons and Semlitsch, 1987). In this regard, Atwood (1918) related the absence of fat bodies ventral to thyroid and thymus with periods of starvation in *Thamnophis sirtalis* Linnaeus, 1758, which undergoes seasonal cycles of hibernation related to endogenous factors as well as non-endogenous components (Joy and Crews, 1987). However, only 30% of the specimens of *A. potschi* from BC sample do not have the fat body ventral to thyroid and thymus, suggesting that this species should not hibernate. Moreover, basic data on the natural history (e.g., activity pattern) for members of the genus *Atractus* are still elusive not supporting the assumption of such a pattern of activity with hibernacula during winter.

Morphological variation

Each morphological complex here studied displays a certain level of polymorphism, but most of them (pholidosis, cephalic glands, and osteology) were in agreement with previous studies performed with other congeners (see Passos et al, 2010a; Oliveira et al., 2008; Cundall and Irish, 2008; respectively) in showing reduced intraspecific variability (e.g., Figs. 8–9). On the other hand, some character system depicted considerable variation probably related to distinct selective regime (Figs. 6–7, see below) or even by the way that data were collected (Fig. 5). While we note that much of the variation seen in the hemipenial morphology was likely due to preparation "artifacts" affecting the general shape of the organs, population variation observed in color pattern surpasses even the geographical variation previously reported in the literature (Figs. 2, 6–7).

The variation in the shape of the hemipenis was mostly influenced by its previous condition of preservation. Many aspects of the bias on hemipenis shape and ornamentation were thoroughly discussed in literature, so we will not repeat these arguments here (see Dowling, 2004 and references therein). Such alterations in form are apparently related to differences comprising examination *in situ* or based on fully everted organs (Myers and Cadle, 1994, 2003), specific techniques for eversion of retracted hemipenis (Manzani and Abe, 1988; Pesantes, 1994; Dowling, 2002), concentration and time in which hemipenes were left in formalin solution (Prudente and Passos, 2010), and level of filling the organs (Passos et al., 2013a, c). Myers and Cadle (2003) emphasized that the examination of the organs in retracted and everted conditions [from a given individual or species] are complementary and, therefore, increase the number of potentially taxonomically useful characters. Zaher and Prudente (2003) pointed out that organs that are partially everted in the field are easier to completely prepare in the laboratory than entirely retracted organs. We agree with all these points but, in cases in which eversion was incompletely performed in the field (= mainly organs everted up to a third or halfway of its entire length), we were unable to completely eliminate the median constriction caused by partial eversion of the organs (Fig. 5C), compared to preparation based on organs completely everted in the field (Fig. 5A) or preserved in an entirely retracted condition (Fig. 5B). Hence, as pointed out by Myers and Cadle (2003), we reinforce that the best procedure is the eversion of only one of the organs being sure that the distal portion of each lobe is completely released. Moreover, we recommend caution in the use of KOH solution (regardless of concentration and time of emersion) to soften tissues to reduce artifactual changes, because often this procedure does not show good results and the processes of tissue demineralization is irreversible, causing permanent damage to the organs. Therefore, in the case of fragile and small hemipenes (entirely or partially retracted), like those found in species of *Atractus,* we strongly suggest researchers to evaluate the possibility of using distilled water in the place of KOH. The use of water in the preparation of hemipenis previously stored in 70% ethanol rehydrates the tissue and enables its complete eversion without greater risks of damaging the organ (i.e., Passos et al., 2013a, b, c).

So far, this is the first study to provide a general description of the entire soft anatomy and its intraspecific variation in any species of *Atractus.* Visceral organs in snakes have been understudied when compared to the other "more traditional" source of characters, such as cranial osteology (e.g., Cundall and Irish, 2008) and hemipenis morphology (e.g., Zaher, 1999). Most published studies have focused on viscera from a morphofunctional point of view (e.g., anterior esophagus, Cundall et al., 2014; heart, Jensen et al., 2014) and, less commonly, there are a few comparative studies addressing multiple taxa (e.g., urogenital, Fox, 1965; and pulmonary, Wallach, 1998) or aimed at individuals within a population (Keogh and Wallach, 1999) in certain systems. The majority of the quantitative approaches on visceral organs are in agreement, reporting a low degree of interspecific variation among closely related taxa (e.g., Rossman et al., 1982). Nonetheless, Wallach (1998) provided substantial data on lung and trachea morphology for "38 species" *Atractus* (we reidentified these as the 33 taxa listed in Table 2) and found that the presence of the left lung and tracheal lung are variable within the genus (Wallach, 1998; Table 2 of present study). The lung data reported herein for *A. potschi* do not differ from those gathered by Wallach (1998), except for the shorter tracheal lung when compared to most congeners (Table 2). Analysing the interspecific variation of the visceral organs, it seems obvious that much of the observed variability was concentrated on the level of development of the left and tracheal lungs. Among species of *Atractus,* the left lung can be reduced (either faveolate or non-faveolate) or totally obliterated and there is no obvious correlation with the presence of a tracheal lung. Nevertheless, the complete obliteration of the left lung apparently does not occur simultaneously with the absence of a tracheal lung (see below). Van Soldt et al. (2015) pointed out that the complete obliteration of the left lung represents stepwise heterochronic changes in the developmental mechanisms from basal macrostomatans (shorter left lung) to more advanced snakes (truncation followed by failure to faveolate and complete obliteration). However, species of *Atractus* display almost the entire spectrum of variation in the development of the left lung as reported for snakes in general (Wallach, 1998). The development of a tracheal lung in the species where a left lung is lost or non-faveolate might be triggered by the need for enhanced ventilation, especially when the oxygen available

Table 2. Summary of intraspecific variation in *Atractus potschi* and interspecific variability of visceral organs in the genus *Atractus*. Data from all species except *A. potschi* (in **bold**) were kindly provided by Van Wallach. We confirmed species identification on the basis of Wallach's notes on external morphology (meristic, morphometric, and color pattern data) and digital photographs of each specimen. HM = heart midpoint; TLiL = total liver length; TLuL = tracheal lung length; RLL = right lung length; LL = left lung; TKM = total kidney midpoint; KL = total kidney length (mean of right and left kidneys); KA = kidney asymmetry (right kidney length/left kidney length); TGM = total gonad midpoint (mean of right and left gonad midpoint); GBM = gall bladder midpoint. All measurements are given as percentage of snout–vent length. Numbers in parentheses represent the number of specimens examined for each sex and "–" for TGM indicates missing data.

Taxa	Institution Number	Sex	HM	TLiL	TLuL	RLL	LL	TKM	KL	KA	TGM	GBM
A. bocourti	MCZ 42427	♂	20.5	32.5	3.8	42.6	0.9	88.8	6.1	0.9	79.8	69.7
A. carrioni	MCZ 93585	♂	19.9	34.5	8	42.8	1.1	84.4	10	1.2	77	68
A. collaris	LSUMZ 44597	♂	27.7	27.9	14.83	40	Absent	86.98	7	0.75	–	64.6
A. crassicaudatus	FMNH 82024	♀	22.8	32.24	Absent	40	0.82	87.1	5.3	0.8	–	66.5
A. duboisi	USNM 232552	♂	23.9	25.1	9.02	23.9	1.1	85.8	7.8	1.22	75.2	57.8
A. elaps	MCZ 61158	♂	22.6	25.8	Absent	37.3	0.9	87	4.1	1	76.2	66.7
A. emmeli	ZMH 2850	♀	20.5	36.9	1.83	45.12	Absent	89	5.5	1	–	68.5
A. favae	MCZ 5196	♂	22.5	28.2	12	35.7	0.3	81.5	5	0.9	75.8	67.2
A. gaigeae	MCZ 29298	♂	26.7	28.2	17.2	36.64	Absent	89.6	7.44	0.8	76.5	68.3
A. cf. *iridescens*	MCZ 166571	♂	24	29.8	6.6	39.15	1.94	83.7	7.4	0.9	74.3	65.3
A. latifrons	LSUMZ 43795	♀	20.2	26.7	Absent	39.6	1.1	87.3	4.98	0.9	–	65.7
A. lehmanni	FMNH 54880	♀	22.6	32.8	Absent	37.2	0.34	87.5	6.8	0.7-0.9	–	65.7
A. loveridgei	USNM 86817	♀	23.7	30.7	15	37.1	0.3	87.4	9	2.6	–	63
A. major	MCZ 53220	♀	19.7	26.8	Absent	44.9	1.68	82.5	6.3	0.9	–	65.8
A. mathewi	MCZ 119470	♀	25.3	28.9	Absent	34.87	0.6	84.9	7.9	0.9	–	61.5
A. mariselae	MCZ 152593	♀	26.9	29.9	Absent	40.91	0.6	88.9	6.5	1	74.02	74.6
A. multicinctus	FMNH 11588	♀	21.5	32.8	9.4	43.7	Absent	84.3	5.4	0.9	–	65.5
A. nicefori	USNM 86816	♀	20.5	27	8.8	32.4	0.8	82.9	7.5	1	–	56.7
A. occipitoalbus	MCZ 29293	♂	27.5	34.3	12.5	35.7	0.4	83.9	6	0.9	80.6	70
A. orcesi	USNM 232712	♂	25.4	28.5	7.9	35.3	0.8	81.3	8.4	0.6	71.6	62.4
A. cf. *paisa*	USNM 86817	♀	21.7	31.9	Absent	37.4	0.57	89.1	5.17	2.6	–	–
A. pamplonensis	FMNH 39485	♂	23.5	28.3	Absent	39.86	0.72	85.1	10.5	0.9	76.3	68.4
A. paucidens	MCZ 164423	♂	25	31.9	11.76	37.7	0.98	84.8	5.4	0.8	79.6	69.1
A. potschi	**Material examined**	**♂ (7)**	**18.3–23**	**25.8–32**	**0.2–1**	**14–31**	**Absent**	**85.7–94**	**4.5–7.5**	**0.9**	**67.6–84.7**	**58.5–71.1**
		♀ (8)	**17.4–24.4**	**20–29.4**	**0.3–0.92**	**16–30**	**Absent**	**83.1–94.2**	**2.5–6.9**	**1**	**68.4–80**	**57–71.4**
A. peruvianus	MCZ 8837	♂	21.9	31.9	10.4	32.3	Absent	84.5	8	0.9	76.1	63.5
A. poeppigi	MCZ 48977	♀	21.9	26.4	Absent	36.9	1.1	82.4	6.3	1.08	–	64.9
A. resplendens	MCZ 29295	♀	23.7	30.58	8.3	36.3	0.9	88.5	5	0.86	–	71.8
A. reticulatus	MCZ 142563	♀	18.2	25.1	8.1	33.2	1.1	87.7	6.7	1.3	–	52.9
A. sancataemartae	MCZ 6533	♂	20.6	32.1	3.6	44.5	1.1	86	8	0.9	77.4	–
A. aff. *snethlageae*	MCZ 96674	♀	22.5	31.5	4.4	44.3	0.5	82.9	6.4	1.03	–	69.2
A. torquatus	MCZ 152702	♂	26.8	24.2	13.4	32.1	2.5	79.2	9.5	0.9	70.6	63.6
A. trilineatus	MCZ 49065	♂	24.4	28.9	5.97	37.3	Absent	84.1	7.4	0.9	76.2	64.2
A. univittatus	MCZ 150190	♀	17.3	26.88	5.7	35.08	0.68	80.12	4.9	1.04	–	52.8
A. ventrimaculatus	MCZ 112442	♂	21.5	29	Absent	43.7	0.75	85.6	8.7	0.9	76.4	67.4

in the environment is limited, as observed for taxa with borrowing lifestyles (Wallach, 1998). Although the available data reinforce this hypothesis in finding that both lungs were not "lost" simultaneously in *Atractus,* such assumptions remain incipient even at the genus level and demand further corroboration.

The development and maintenance of polychromatism is one of the great persisting matters in ecology and evolution, in part because it is often unclear whether natural polymorphism constitutes a stable array of forms maintained by frequency-dependent predation or just a pool of alleles resulting from genetic drift and dispersal

(Bond, 2007). Several cases of polychromatism in natural populations, when examined in detail, are closely related to non-selective processes, such as migration and dispersal (King and Lawson, 1995) or genetic drift in local (Brakefield, 1990) or island populations (Bittner and King, 2003). Empirical studies on color polymorphism that exclude stochastic explanations usually invoke apostatic selection by visually oriented predators as the main causal agent (see Bond, 2007). Pizzato and Dubey (2012) demonstrate yet that the presence of intraspecific polychromatism was correlated with the age of each lineage of snakes, with polymorphic species being significantly older than monomorphic ones. Allen et al. (2013) found that the color pattern evolution in snakes is generally phylogenetically conserved and those similar phenotypes are convergent evolving repeatedly along many lineages in response to certain ecological demands. Allen's results correlated species having longitudinally striped pattern with active hunting strategy, blotched pattern with ambush hunting, and spotted pattern with proximity of the ground; while the "flicker-fusion" hypothesis (for the species having crossbands) was evaluated as possible but unlikely. More recently, Titcomb et al. (2014) tested the flicker-fusion hypothesis in two species of coral snake mimics (having alternated rings along the body) and established that these taxa are capable of achieving blurring effect, conferring an additional defence aside from mimicry. Thus, as *Atractus potschi* has a spotted color pattern with anterior nuchal bands it is possible that each region of body will be under different selective regimes within a continuum of defensive mechanisms (sensu Greene, 1994). For example, the spotted pattern may have a disruptive general function at rest (Fig. 3D), whereas the bands on neck perhaps may suggest a putative flicker-fusion effect in motion protecting the head when snakes are in movement. We observed that much of the chromatic variability of *A. potschi* was concentrated on the anterior region of the body where there is ontogenetic variation in the coloration of the occipital region (Fig. 4) and intraspecific variation in the shape of cephalic-cap and second nuchal band (Fig. 6). However, there is expressive interspecific variability in color patterns (Fig. 7) unreported for the species (see below).

The occurrence of a conspicuously white occipital region in juvenile stages, which is lost in adult specimens, represents an exclusive feature (likely a synapomorphy in a less inclusive level) shared by members of the *Atractus paraguayensis* Werner, 1924 species group (Passos et al., 2013d). The contrast enhancement of this feature may be selected in a scenario with differences in the spatial ecology, when juveniles and adults are submitted to distinct selection pressure on warning signalling caused by differential abundance of predators (Valkonen et al., 2012). Interestingly, the presence of a second black band on the neck was not significantly related to either age or sex in *A. potschi* and also did not occur in *A. paraguayensis* (Passos et al, 2010a) or *A. spinalis* (Passos et al., 2013d), the other species of the *A. paraguayensis* species group (sensu Passos et al., 2013b). Therefore, it is not obvious which selective pressures, if any, are responsible for the population pattern of variation in *A. potschi*. Moreover, the chromatic polymorphism seems to be retained in distinct lineages of *Atractus* and related by means of different phenomena: geographic variability (*A. torquatus* [Duméril, Bibron, and Duméril, 1854; Passos and Prudente, 2012), pronounced ontogenetic shifts (*A. gigas* Myers and Schargel, 2006; Passos et al, 2010b; *A. serranus* Amaral, 1930 and *A. trihedrurus* Amaral, 1926; Passos et al., 2010a), sexual dichromatism (*A. sanctaemartae* Dunn, 1946; Passos et al., 2009d), melanism (*A. natans* Hoogmoed and Prudente, 2003; Passos et al., 2012), possible changes on the coral mimetic patterns related to frequencies in the distribution of distinct models [*A. latifrons* (Günther, 1868); Almeida et al., 2014], apparently spurious inversion of background patterns (*A. erythromelas* Boulenger, 1903 and *A. riveroi* Roze, 1961; Passos et al., 2013a), and even by identification of a species complex under certain names (*A. snethlageae* Cunha and Nascimento, 1993; Schargel et al., 2013). Consequently, it would be expected that different factors favor superficially similar color patterns at distinct hierarquical levels (Allen et al., 2013).

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APPENDIX

Specimens examined

Institutional abbreviations are as listed in Sabaj Perez (2014), except for Universidade Federal de Sergipe (UFSE), Aracaju, Sergipe, Brazil. Countries are given in capitals, states in bold, municipalities and localities in plain text, and coordinates in bold face. We provide coordinates for the most accurate locations possible. Specimens for which we examined cephalic glands and soft anatomy or prepared the hemipenis and skull are listed separately from those examined only for external morphology.

External morphology (*n* = 90): BRAZIL: **Alagoas:** Maceió, IBSP 48438 (holotype; **-9.6670, -35.7333**); **Bahia:** Brumado, IBSP 49405, Brumado: Barragem de Cristalândia, MZUFBA 2044–83, 2192–08; **-14.2074, -41.6716**); Barrocas: Fazenda Brasileiro, (MZUEFS 682; **-11.5295, -39.0833**); Contendas do Sincorá: Floresta Nacional de Contendas do Sincorá, (MNRJ 21012; **-13.91667, -41.008333**); Feira de Santana: Jaíba, (MZUEFS 454; **-12.2667, -38.9667**); Poções, (MZUFBA 1801, 1803, 1815, 1590–91; **-14.5444, -40.3786**); Salvador, (MZUFBA 1589; **-13.000, -38.500**); Teofilândia, (IBSP 57119; **-13.6020, -39.4910**); **Sergipe:** Salgado, (MZUSP 7001, 7195–97, 7275–81, paratypes; **-11.0333, -37.4750**); São Cristóvão, (UFSE 1555, UFSE 1606, MNRJ 14057–58, MZUSP 11074); **-11.0167, -37.200;** Simão Dias, (IBSP 77901; **-10.7333, -37.8000**).

Cephalic glands and skulls (*n* = 5): MZUFBA 2054, 2061, 2068, 2080, and 2192.

Soft anatomy (*n* = 14): MZUFBA 2074, 1589, 2048–49, 2051, 2054, 2059, 2061, 2064–65, 2068, 2080, 2082, 2192.

Hemipenes (*n* = 12): MZUEFS 682, MNRJ 14057, MZUFBA 1591, 2088, 2045, 2054, 2063, 2069, 2080-81, 2195, 2200.