Article

Species delimitations in the *Atractus collaris* complex (Serpentes: Dipsadidae)

PAULO PASSOS[1,5], ANA L. C. PRUDENTE[2], LUCIANA O. RAMOS[1], JOSÉ RANCES CAICEDO-PORTILLA[3] & JOHN D. LYNCH[4]

[1]*Departamento de Vertebrados, Museu Nacional, Universidade Federal do Rio de Janeiro, Quinta da Boa Vista, Rio de Janeiro, RJ 20940-040, Brazil.*
[2]*Laboratório de Herpetologia, Coordenação de Zoologia, Museu Paraense Emílio Goeldi, PB 399, Belém, PA 66040-170, Brazil.*
[3]*Instituto Amazónico de Investigaciones Científicas-Sinchi, Sede principal, Av. Vásquez Cobo, Leticia, Amazonas, Colombia.*
[4]*Laboratorio de anfibios, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Apartado 1495, Bogot DC, Colombia.*
[5]*Corresponding author. E-mail: atractus@gmail.com*

Abstract

We reassessed the taxonomic status of the species in the *Atractus collaris* complex (*A. alphonsehogei*, *A. collaris*, *A. limitaneus*, and *A. gaigeae*) on the basis of congruence between quantitative and qualitative morphological characters (meristic, morphometric, color pattern, hemipenis, and scale microdermatoglyphics) along its wide geographical distribution. Our results support the recognition of three species with apparently fixed diagnostic characters. We propose the synonymization of *Atractus limitaneus* with *A. collaris* based on the wide overlap of all morphological character systems here analyzed, as well as on the basis of examination of the holotype and two topotypes of *A. limitaneus*. Finally, we discuss the geographical variation and morphological distinction of *A. alphonsehogei*, *A. collaris* and *A. gaigeae*. Furthermore, we provide a dichotomous key for all recognized species in the *A. collaris* species group.

Key words: *Atractus gaigeae*, *Atractus limitaneus*, *Atractus alphonsehogei*, species boundaries, color patterns, morphometry, microdermatoglyphics, hemipenis, Amazonia

Introduction

The cryptozoic snakes of the genus *Atractus* Wagler, 1828 accommodates about 150 currently recognized species, occurring from Panama to Argentina (Giraudo & Scrocchi 2000; Myers 2003). Despite being the most diverse snake genus in the world, several *Atractus* species are still known from small series with relatively restricted distributions (Passos & Fernandes 2008; Prudente & Passos 2008, 2010; Passos *et al*. 2009b,e; Passos *et al*. 2013d; Köhler & Kieckebuch 2014; Arteaga *et al*. 2017). Although many of these instances of distributional restriction may reflect insufficient sampling of particular regions (Passos et al. 2009d; De Fraga et al. 2017) or the taxonomic complexity of some species groups (Passos & Prudente 2012; Passos et al. 2012), some of them may indeed represent rare and, eventually, threatened micro-endemic taxa (e.g., *A. caete* Passos, Fernandes, Bérnils & Moura-Leite, 2010 and *A. hoogmoedi* Prudente & Passos, 2010; Brazil 2014). In addition, other factors such as the logistic difficulties to access remote areas and security problems in certain portions of the Amazonia, Chocó in Colombia, and Llanos of Venezuela and Colombia (Passos *et al*. 2016b), affected the unbalanced level of samples and—consequently to a certain level—taxonomic accuracy in the species delimitation across the entire genus.

However, this scenario has been gradually changing with a series of studies based on the faunal elements of countries (Savage 1960; Myers 2003), biogeographic provinces from trans-Andean (Passos & Lynch 2011; Passos *et al*. 2009e) or cis-Andean portions of South America (Passos *et al*. 2013b), broad ecoregions (Passos *et al*. 2010c), as well as directed toward to certain species complex (Passos & Prudente 2012). As an expected result, old taxa poorly characterized in the past were resurrected (Passos *et al*. 2010b), rediscovered as misidentified specimens in scientific collections (Cisneros 2005; Passos & Arredondo 2009; Passos & Lynch 2011; Passos *et al*. 2013d) or obtained through fieldwork carried out in poorly sampled regions (Passos *et al*. 2009a, 2010a; Vanegas-

Guerrero *et al.* 2014). On other hand, evaluation of many recently described species has revealed an astonishing amount of junior synonymies (Kok et al. 2007; Passos *et al.* 2009a,d; Passos *et al.* 2010c; Passos & Prudente 2012; Passos *et al.* 2012; Passos *et al.* 2013d), adding more difficulties to the already challenging task towards achieving the taxonomic accuracy in the genus *Atractus* (Passos *et al.* 2016b).

In this paper, we evaluate the taxonomic status of the snakes from the *Atractus collaris* species complex [i.e., *A. alphonsehogei* Cunha & Nascimento 1983; *A. collaris* Peracca 1897; *A. gaigeae* Savage 1955; and *A. limitaneus* (Amaral 1935)] on the basis of concordance between qualitative (color patterns, micro-ornamentation of dorsal scales, and hemipenes) and quantitative (meristics and morphometrics) analyses of putatively independent morphological characters. As remaining taxa placed in the *A. collaris* species group (i.e., *A. zidoki* Gasc & Rodrigues 1979, *A. caxiuana* Prudente & Santos-Costa 2006, *A. surucucu* Prudente & Passos 2008, and *A. hoogmoedi* Prudente & Passos 2010) were recently evaluated (see section below), the present study concludes the reappraisal of the alpha taxonomy from this characteristic and very distinctive assemblage of *Atractus*.

Historical résume

Bocourt (1883) described *Rhabdosoma maculatum* based on two specimens from Ecuador. Boulenger (1894) transferred *R. maculatum* to the genus *Atractus*, creating a secondary homonymy with respect to *Isoscelis maculata* Günther 1858. Boulenger (1894) established the composite nature of the type-series of *R. maculatum* Bocourt 1883, identifying (but not including in the type-series) one of the syntypes as part of his new species, *A. bocourti*. Boulenger (1894) also proposed the synonymy of *R. maculatum* with *A. badius* (Boie 1827). Boulenger (1896) reported on four additional specimens of *A. bocourti* (two from Yurimahuas, higher Huallaga River in the Peruvian Andes and two others from Canelos and Paitanga in the Ecuadorian Amazonia). Peracca (1897) described *Atractus collaris* on the basis of a specimen collected in the Cononaco River, province of Pastaza in the Ecuadorian Amazonia. Amaral (1935) proposed *Leptocalamus limitaneus* on the basis of a single individual from La Pedrera, department of Amazonas, Colombia. Savage (1955) described *Atractus gaigeae* based on seven specimens from Tungurahua and Pastaza Provinces in the Ecuadorian Amazonia, recognizing that this species was originally described as part of *Rhabdosoma maculatum* Bocourt 1883 (which had a composite type-series) and also included in this species the specimens from the east of Andes (Canelos and Paitanga) previously referred to as *A. bocourti* by Boulenger (1894, 1896). Savage (1955) highlighted the morphological similarities between *A. gaigeae* and *A. collaris,* but distinguished both species by the presence of a vertebral stripe and 189–198 ventral scales in males and 207–213 in females of *A. gaigeae* (vs. lacking of vertebral stripe, 163 and 175 ventrals in the single male and female of *A. collaris*, respectively). Savage (1960) transferred *Leptocalamus limitaneus* to the genus *Atractus* based on its original description and reported three additional specimens of *A. gaigeae* from Ecuador. Dixon & Soini (1977) pointed out that the material they studied from Santa Maria (from Iquitos region of Peru) was "intermediary between *A. collaris* and *A. gaigeae* and considered the latter taxon a subspecies of the former species. According to Dixon & Soini (1977), these specimens have seven longitudinal lines and 191 and 212 ventrals plus subcaudals (= sum of ventrals and subcaudals) in the male and female specimens, respectively (Dixon & Soini 1977 *op. cit.*).

Gasc & Rodrigues (1979) described *Atractus zidoki* based on two specimens from Oyapock in French Guiana. Hoogmoed (1980) reported on seven new specimens of *A. zidoki* in French Guiana (Sepanguy) and Surinam (Brokopondo and Marowijne). Cunha & Nascimento (1983) proposed *Atractus alphonsehogei* based on fourteen specimens (strictly compared with *A. zidoki*) from localities along eastern portions of the state of Pará (Bela Vista, Santo Antônio do Tauá, Parada Bom Jesus, Santa Rosa, Fazenda Cacoal, and Colônia Nova) and western part of the state of Maranhão (Nova Vida and Santa Inês) in the east of Brazilian Amazonia. Cunha & Nascimento (1984) reported on two additional specimens of *A. zidoki* from Capitão Poço in the east of the state of Pará in Brazilian Amazonia (these specimens were later included in the type series of *Atractus hoogmoedi*). Martins & Oliveira (1993) reported a new specimen supposedly of *A. alphonsehogei* from Presidente Figueiredo, state of Amazonas, Brazil. Carrillo & Icochea (1995) treated *A. collaris* and *A. gaigeae* as full species in their list of reptiles from Peru without any considerations regarding the system of Dixon & Soini (1977). Lehr (2002) followed Carrillo & Icochea (1995) in not recognizing both subspecies, listing *Atractus collaris* (without subspecific rank) in his account of Peruvian reptiles. Silva (2004) reported on four additional specimens of *A. zidoki* from Colombian

Amazonia, two of them from Leticia and other two from La Pedrera both localities, in the department of Amazonas. However, Passos *et al*. (2007b) re-identified such specimens from Leticia as *A. snethlageae* Cunha & Nascimento 1983. More recently, a series of papers have addressed the status of species closely related to *Atractus collaris* and its allies (see Prudente & Santos-Costa 2006; Prudente & Passos 2008, 2010; Passos *et al*. 2013b), dismissing a new reassessment of their taxonomy. Although Prudente & Passos (2008, 2010) refer to unique states of characters (e.g., presence of apical pits and supracloacal tubercles on dorsal scales) shared by this assemblage of snakes, the proposal of the species group to these cluster of species was made only in Passos *et al*. (2013b).

Material and methods

Material and presentation style. Institutional abbreviations follows Sabaj Pérez (2016), except for SINCHI-R (Instituto Amazónico de Investigaciones Científicas Sinchi, Leticia, Colombia) and UAM (Museo de Historia Natural, Universidad de la Amazonia, Florencia, Colombia) not included in this source. Data from additional specimens of *Atractus* previously examined by the senior author are available in: De Fraga *et al*. (2017), Prudente & Santos-Costa (2006), Passos *et al*. (2005), Passos *et al*. (2007a,b), Passos & Fernandes (2008), Passos & Arredondo (2009), Passos *et al*. (2009a,b,c,d,e), Passos *et al*. (2010a,b,c), Passos & Lynch (2011), Passos & Prudente (2012), Passos *et al*. (2012), Prudente & Passos (2008, 2010), Passos *et al*. (2013a,b,c,d), Almeida *et al*. (2014), Schargel *et al*. (2013), Salazar-Valenzuela *et al*. (2014), Passos *et al*. (2016a,b), and Passos *et al*. (2017). Nonetheless, we list all specimens examined of the *Atractus collaris* species group in the Appendix in order to facilitate future comparisons and references. The rationale along the species account follows a chronological order of descriptions, with the specific subheadings synthetizing all information for each character system according with Passos *et al*. (2013b). We follow Passos *et al*. (2009e) and Passos *et al*. (2010c) regarding the conditions of the morphological characters used in diagnosis and descriptions.

Geographical data. We retrieved coordinates of localities from museum catalogues or databases, as well as in geographical gazetteers (Savage 1960; Stephens & Traylor 1983, 1985; Paynter & Traylor 1991; Paynter 1993, 1997; IBGE 2011). Whenever possible, we refined the coordinates of localities not associated with precise geographic data with the aid of software Google Earth Pro 7.1.2 (Google 2005). We also include in the map geographic records based on the photographs of specimens in life but not associated with collected vouchers (Figs. 2–3).

Techniques. Terminology for cephalic shields follows Savage (1960) and Peters (1964), whereas ventral and subcaudal counts follow Dowling (1951). Condition of the loreal scale follows Passos *et al*. (2007b). We took measurements with a dial caliper (Mitutoyo) to the nearest 0.1 mm, except for snout–vent length (SVL) and caudal length (CL), for which used a ruler to the nearest 1 mm. Measurements and descriptions of paired cephalic scales are strictly based on the right side of head. We examined maxillae of all specimens in situ under a Stemi 2000C (Zeiss) stereoscope, through a narrow lateromedial incision between the supralabials and the maxillary arch. After removing tissues covering the maxillary bone, we counted teeth and empty sockets.

Terminology for micro-ornamentation descriptions follows Price (1982) and Price & Kelly (1989). We collected samples of the superficial layers of the dorsal scales of the specimens at mid-body. We removed layers with forceps and separately stored the samples in 70% ethylic alcohol. We affixed the samples with double-faced carbon tape in metal plates (stubs), submitted then to metallization using an ELMITECH K550 metallizer. After metallization, we took high resolutions photographs on a JEOL JSM 6460LV scanning electron microscope (SEM) under 500x–10.000x magnifications and 20kV at Scanning Electron Microscopy laboratory at Museu Nacional/ UFRJ. We investigated two portions of the scales were investigated (basal and mid-apical) and each of them displayed their own features.

Terminology for hemipenial descriptions follows Dowling & Savage (1960) and Zaher (1999) with a few minor adaptations based on Passos *et al*. (2013b,d). We employed the method for preparation of preserved hemipenis modified from Pesantes (1994) in replacing the KOH solution by distilled water according (Passos *et al*. 2016a). Prior to the inflation with petroleum jelly, the organs remained 15–20 min in an alcohol solution of Alizarin red in order to stain the ornamented calcareous structures to adaptations from original procedures used by Uzzell (1973).

Species concept and diagnosis criteria. In this study, we followed the general lineage species concept according de Queiroz (1998). We consider the presence of one or more exclusive, apparently fixed diagnostic character, which distinguishes a putative taxon from the others in the *A. collaris* complex, as species delimitation criteria. However, when the limited sample did not allow statistical confidence from qualitative characters in many populations (sensu Wiens & Servedio 2000), we alternatively recurred for concordance between the discrete and continuous characters (Passos *et al*. 2010a; Passos & Prudente 2012). Since some features such as color pattern, morphometric characters, hemipenial morphology, and microdermatoglyphs are likely uncorrelated with each other, the correspondence between these data sources might represent independent evidence for robust species boundaries (see Passos & Fernandes 2009).

Operational analytical unities. We considered putative natural barriers (e.g., rivers) and geographical proximity of the available sample to evaluate level of distinction among populations through of a strictly exploratory approach. We used the major tributaries from the banks of the right (from east to west: Tocantis, Xingu, Tapajós, Madeira, Purus, Juruá, and Ucayali) and left (from east to west: Negro, Japurá, Putumayo, Napo, and Pastaza) banks of the Amazonas River as presumed barriers to dispersion along the Amazonian populations.

We divided the sample into three groups (Fig. 1), reflecting the current taxonomy and considering the type-localities, disjointed geographical distribution and/or morphological similarities of each taxa. Group 1 included specimens from eastern portions of Brazilian Amazonia from the east of the Tocantins River, attributed to be *A. alphonsehogei*. Group 2 included specimens from Amazon Basin, between west of the Negro and east of the Pastaza rivers, attributed to as *Atractus collaris*, including two topotypes of *A. limitaneus*. We grouped *A. collaris* and *A. limitaneus* in a single operational group because there are no qualitative differences and no apparent geographical disjunction between them. Group 3 included specimens from Amazon Basin with vertebral strip and higher number of segmental counts, diagnostic features of *A. gaigeae* (sensu Savage 1955, 1960).
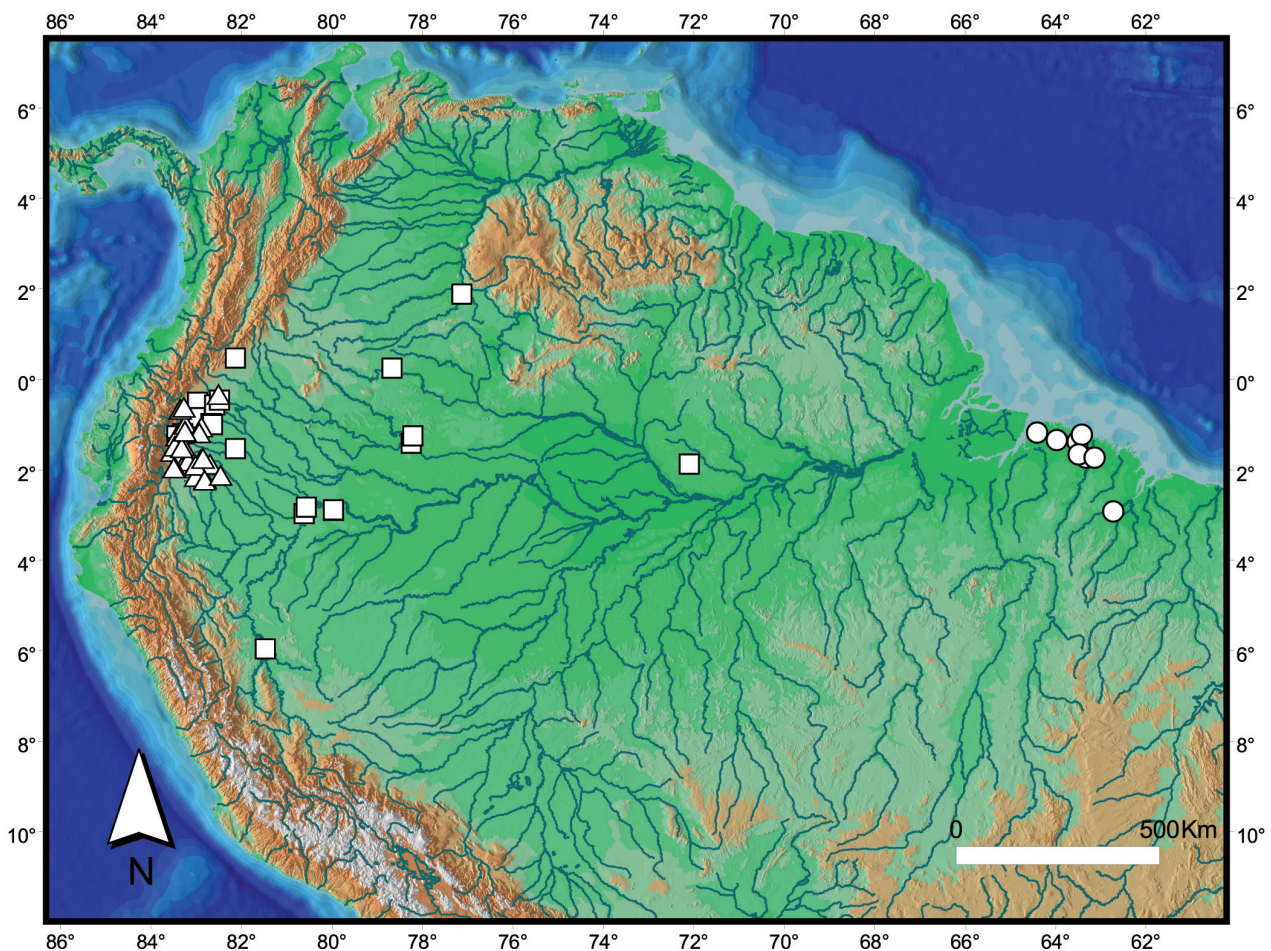

FIGURE 1. Distribution of *Atractus alphonsehogei* (circles), *A. collaris* (squares) and *A. gaigeae* (triangles).

Qualitative analyses of morphology. We performed a discrete analysis of qualitative characters (pholidosis, color pattern, micro-ornamentation of scales, and hemipenial morphology) based on the frequency of occurrence to each state throughout the distribution of the *Atractus collaris* complex. Independently, we searched for correspondence between the above groups as well as the current taxonomy (including *A. alphonsehogei*, *A. collaris*, *A. gaigeae* and *A. limitaneus*) and unique qualitative features apparently fixed on population level.

Quantitative analyses of morphology. We employed an analysis of variance (ANOVA) using segmental counts to assess the presence or absence of sexual dimorphism within each group and the whole sample. We evaluated the assumptions of univariate normality and homocedasticity with the aid of the Kolmogorov-Smirnov's and Levene's tests, respectively (Zar 1999). In cases where characters showed insufficient variation to justify these assumptions, we performed non-parametric tests (Zar 1999). We performed a discriminant analysis (DFA), with an exploratory proposal, and a Mann-Whitney test at group level for males and females separately (see below) to evaluate differentiation between the groups with *a priori* definition (Manly 2005). We projected the first two discriminant functions onto orthogonal axes and computed 95% confidence regions from the simulation of 1000 pseudoreplicate data matrices obtained by parametric bootstrap (Efron 1979).

We used the following characters in statistical analyses: dorsal scales at the level of second subcaudal, number of ventrals, subcaudals, supralabials, infralabials, postoculars, maxillary teeth, and SVL/CL ratio. Several variables were excluded due to showing low or no variance, such as the number of supralabials, infralabials, preventrals, tempral, and gular scale rows. We report descriptive statistics as minimum–maximum (mean, SD and n = sample size). We performed all computations using the software MATLAB 4.2c1 (MathWorks 1994), except normality and homocedasticity tests, for which we used STATISTICA 5.1 (Statsoft 1995).

Results

Qualitative analyses. Color pattern. Savage (1955, 1960) uses the vertebral line typical of *Atractus gaigeae* to distinguish it from *A. collaris* (apparently lacking this trait). Although features such as vertebral line and paravertebral spots may become obscured in melanistic and old preserved specimens, they are detectable when already present, even after preservation when specimens are immersed in alcohol (P. Passos pers. observ.). Our data corroborated the early impression from Dixon & Soini (1977) regarding the presence of individuals with (Fig. 2) and without (Fig. 3A–C) a conspicuous vertebrate stripe in the Iquitos region. However, in contrast with their conclusion, we interpreted this phenomenon as polychromatism of *A. collaris* with respect to the presence of vertebral line rather than an evidence for intergradation of the first with *A. gaigeae*, because there is no overlap in the ventral and subcaudal scale counts of both taxa and there is no specimens presenting one postocular in all samples of *A. collaris* (a nearly fixed trait for females of *A. gaigeae*; see discussion). Besides *A. collaris*, we found that the vertebral line also occurs in some individuals of *A. caxiuana* (see fig. 2A from Passos *et al*. 2013b), and is being apparently absent in all other species of the *A. collaris* species group (*A. alphonsehogei*, *A. hoogmoedi*, *A. limitaneus*, *A. surucucu* and *A. zidoki*). Although we did not examine Dixon and Soini's (1977) material housed at TCWC (nine individuals), the new data suggest that *A. collaris* at least at the Santa Maria and Madre Selva localities in the Iquitos region of Peru, may occasionally exhibit a vertebral line (Fig. 2), corroborating the early observation of Dixon & Soini (1977). Unfortunately, we only had access to one specimen from the Iquitos region and it is undoubtedly a female of *Atractus collaris* (MUSM 2310). Therefore, the vertebral stripe of *A. gaigeae* apparently represents an ambiguous diagnostic feature with respect to some other members of the *A. collaris* species group. Furthermore, we found other unique coloration features displaying a geographic tendency or apparent fixation to *A. collaris* (e.g., dorsum of body with spots white bordered on the paravertebral region, supralabials yellow, and a red iris; Fig. 3A–C), *A. gaigeae* (e.g., dorsum of body without spots with white borders on the paravertebral region, cream supralabials and black iris; Fig. 3D), and *A. alphonsehogei* (e.g., dorsum of head and body nearly uniformly dark brown lacking conspicuous spots in the snout and paravertebral region, cream supralabials, and iris coloration in life unknown).

Pholidosis characters. In the *Atractus collaris* species group there are apparently two distinct conditions with respect to the arrangement of some cephalic shields (i.e., internasals, loreal, postnasals, and supralabials). While the *A. collaris* complex (*A. alphonsehogei*, *A. collaris*, *A. limitaneus* and *A. gaigeae*) displayed the contact between first supralabial and loreal (Figs. 3–8), in remaining species of the *A. collaris* species group (*A. caxiuana*, *A. hoogmoedi*, *A. surucucu* and *A. zidoki*) the loreal is separate from the first supralabial by the postnasal, contacting

only the second and third supralabials (Prudente & Passos 2008, 2010; Passos *et al*. 2013b). However, Passos *et al*. (2013b) reported some level of variation in the arrangement of snout scales with respect to *Atractus caxiuana*, with one specimen exhibiting the contact between first supralabial and loreal (see discussion). Our results confirm that all populations sampled here display a moderately long loreal in contact with the first three supralabials as previously suggested (but see below).

Despite the original description of *Atractus limitaneus* suggesting that the first supralabial is isolated from loreal by a large postnasal scale (Fig. 6B with black arrow), the examination of the two topotypes revealed that one of the specimens has this condition, whereas the other exhibited the first supralabial in contact with the loreal. Unfortunately, the head of the holotype of *A. limitaneus* is completely damaged precluding the verification of the condition on the loreal region. To complicate matters, Amaral (1935) mislabelled the dorsal view of the holotype of *A. limitaneus* (his figure 5) with *Apostolepis niceforoi* (his figure 2). It is evident on the inspection of both holotypes (P. Passos pers. observ.) and checking the original drawings for the presence of entire nasal shield and a supralabial–parietal contact depicted in figure 2 from Amaral (1935). Although no species of *Atractus* have such features, both represent common external traits of snakes of the Tribe Elapomorphini (Ferrarezzi 1994) and we assume that Amaral's figures were changed before going to press. Consequently, we cannot establish if the original picture is also accurate regarding the loreal condition of *A. limitaneus* or, as denoted by the topotypes, where there is certain level of polymorphism comprising this feature within La Pedrera population. In any case, such feature cannot unambiguously diagnose *A. limitaneus*.

Microdermatoglyphics. The analyses of the scale micro-ornamentation show some differences for each species in the *Atractus collaris* complex. However, the general pattern found for each portion was very similar among the populations sampled, with only minor differences among them. Those specific differences are described following for *A. alphonsehogei, A. collaris* and *A. gaigeae*. Due to the poor conditions of preservation, we could not take scale samples of the holotype of *A. limitaneus* and their topotypes (all very old and poorly preserved specimens). All populations studied, in general, have a basal portion of the scales with lamellate and imbricate cells (overlapping the adjacent cells) and denticulation at cell borders, which vary in shape and size. Small pores, when present, compose micro-ornamentation at the surface of the cells. Cells on the mid-apical portion of the scales are lamellate and imbricate with borders very close to each other, showing denticulations in the form of narrow and long spinules, which fit at the adjacent border. Since cell borders at this portion are too close to each other, it is not possible to visualize the patterns of the surface of these cells.

The differences between *A. collaris* and *A. alphonsehogei* occur at the basal portion in which *A. alphonsehogei* has a more triangular denticulations and micro-ornamentations not visible, at cell surface under magnifications up to 10.000x; while *A. gaigeae* differs from *A. alphonsehogei* and *A. collaris* in having cell borders closer to each other at mid-apical portion (rarely exceeding a distance of 2.5 µm) and more conspicuous pores at cell surface (Fig. 9).

Hemipenial morphology. The analyses of hemipenial variation, although based on a relatively small sample ($n = 6$), reveal potentially diagnostic features among some populations of the *Atractus collaris* complex. The differences refer to the level of development of the basal expansion of the alary spines (sensu Passos *et al*. 2013d), orientation of the sulcus spermaticus and lobes and, more significantly, to the condition of the spines on the hemipenial body and their level of calcification. The organ of *A. collaris* differs in the number of the alary spines on the distal region of the asulcate face and with respect to depth and lateral expansion of sulcus spermaticus (Fig. 10; see discussion). Concerning to the level of calcification of the hemipenes it may be expected differences in specimens preserved in distinct levels of formalin concentration with decades of time interval among collections (see Passos *et al*. 2013c; Passos *et al*. 2016a), but it is not apparently the case. The hemipenis that was distinct in this respect (lacking calcified spines) is from the most recently collected specimen from those with organ prepared by us, *A. collaris* (MNRJ 24959 collected around 2000's) compared to the other individuals, one from *A. alphonsehogei* (MPEG 10874, collected in 1975) and other from *A. gaigeae* (USNM 217627, collected in 1955). The hemipenial morphology of *A. gaigeae* and *A. alphonsehogei* was briefly approached in both original descriptions based on retracted organs (Savage 1955; Cunha & Nascimento 1983), preventing the detection of the aforementioned ornamentation details (Passos *et al*. 2007a). Herein, our fully everted and almost completely expanded organs revealed highly similar shape and ornamentation patterns between *A. alphonsehogei* and *A. gaigeae*, while the hemipenis of *A. collaris* differs substantially from the those of both previous taxa, and also from *A. caxiuana* (Passos *et al*. 2013b), *A. hoogmoedi* and *A. zidoki* (Prudente & Passos 2010).
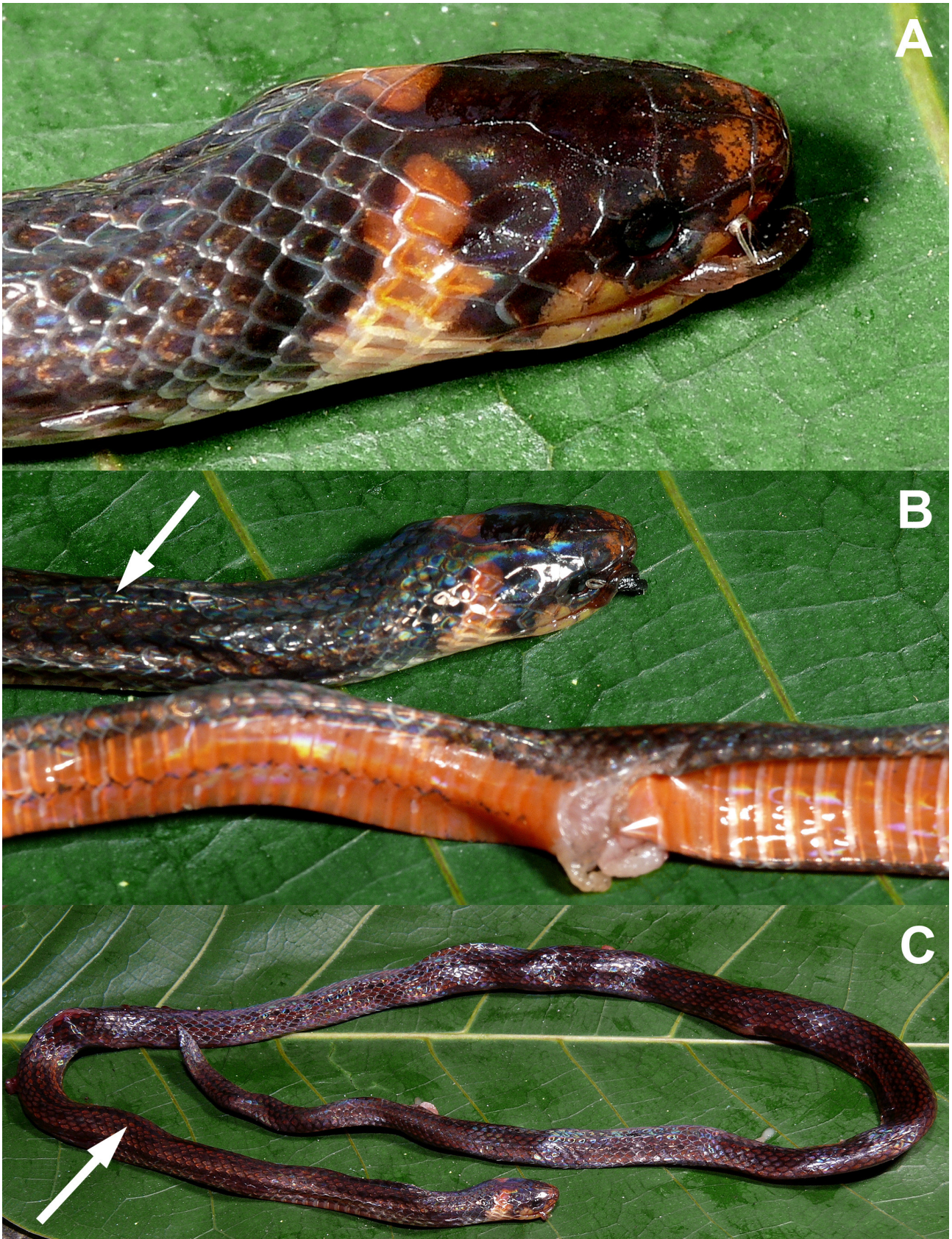
FIGURE 2. Uncollected specimen of *Atractus collaris* from Nauta-Iquitos road, in Loreto, Peru, exhibiting a distinct vertebral stripe (absent in other specimens from the region), demonstrating local polymorphism of this feature in the species. Photos by Konrad Mebert.

FIGURE 3. General view in life of *Atractus collaris* (A–B) both specimens from Madre Selva, Orosa River and a third individual (C) from Santa Cruz, Mazan River, both localities in the Iquitos region, department of Loreto, Peru; and *Atractus gaigeae* (D, QCAZ 8339) from Comunidad Tarangaro, Campo Villano, province of Pastaza, Ecuador. Photos A–C by Mattew Cage (specimens not preserved in scientific collections) and photo D by Diego Paucar and ReptiliaWebEcuador.

Quantitative analyses. *Atractus collaris* complex shows significant sexual dimorphism at least in the number of ventral scales ($F_{1,72}$ = 54.6; $p < 0.001$) and, therefore, we treated separately each sex in all subsequent analyses. Among all measured variables, only three (number of ventral and subcaudal scales, and CL/SVL ratio) approaches from a normal distribution but were heteroscedastic due to the differences in the sample size for each group. We found that the number of ventrals (H_2 = 33.8; $p < 0.001$), subcaudals (H_2 = 35; $p < 0.001$) and CL/SLV (H_2 = 12,7; $p < 0.01$) in males; and ventrals (H_2 = 18.9; $p < 0.001$), subcaudals (H_2 = 14.6; $p < 0.001$), CL/SLV (H_2 = 10.5; $p < 0.01$) and postoculars (H_2 = 19.3; $p< 0,001$) were significantly distinct among the groups. However, the projections of the bivariate plots based on the scores of discriminant analyses for males (Fig. 11A) and females (Fig. 11B) were unable to entirely discriminate the two groups in *a priori* fashion. Nonetheless, the group represented by *Atractus gaigeae* obtained good distinction for both sexes (Fig. 11), with reduced overlapping with respect to the other two groups. The group *a priori* defined as *A. gaigeae* obtained 100% of correct allocation in the classification matrix of discriminant analyses for males and females, while the groups represented by *A. alphonsehogei* and *A. collaris* presented values of correct allocation lower than 80% for both, males and females. The major discrimination occurred mainly in the first discriminant function axis, which was strongly correlated with the number of ventrals and SVL/CL ratio for males and with the number of ventral and postocular scales for females (data not show).

Taxonomic decision. The combination of qualitative and quantitative (in part) analyses of the *Atractus collaris* complex allows the unambiguously recognition of three species on the basis of phenotypic traits here evaluated. While one of the putative lineages is more widespread in Amazonia, the two others displayed relatively restricted distribution. Savage (1955, 1960) and Cunha & Nascimento (1983) recognized such assemblages based on the meristic and color pattern features respectively, and our exploratory morphometric analyses corroborate two of the three groups labeled *a priori* (Fig. 11). Although morphometric data do not allow one to distinguish the groups represented by *A. collaris* and *A. alphonsehogei*, both groups present unique qualitative diagnostic differences and have allopatric distribution. In contrast, the number of maxillary teeth (another continuous variable) is currently polymorphic among the studied populations and, therefore, does not allow ensure any groups recognition. On the other hand, complementing and partially corroborating the quantitative approach, the qualitative analyses of frequencies reveled that unique features of coloration, microdermatoglyphics and hemipenial morphology are congruent in supporting the recognition of three distinct species.

Herein, we associated the widespread group of populations with the oldest name in the group, *Atractus collaris* Peracca 1827, characterized by exclusive features of hemipenial morphology and color pattern. While the other two names available represent more restricted and diagnosable taxa, we recognize as *A. gaigeae* Savage 1955 the Ecuadorian populations distinguishable by meristic, hemipenis and color pattern characters, and as *A. alphonsehogei* Cunha & Nascimento 1983 the populations from the eastern portion of the Brazilian Amazonia defined by the unique micro-ornamentation of dorsal scales combined with hemipenis and color pattern features. Although it is possible that within this broad region there are some level of divergence among geographically distant populations of *A. collaris* (see discussion), neither condition of the morphological systems studied here unambiguously diagnoses any subpopulations. For that reason, we propose to place *A. limitaneus* in the synonymy of the *A. collaris*, since the La Pedrera populations were not diagnosable from the nominal species as here recognized.

Species account

Atractus collaris Peracca, 1897
Figures 2, 3A–C, 4–6

Atractus collaris Peracca 1897: 4 (Cononaco River, Pastaza, Ecuador).
Leptocalamus limitaneus Amaral 1935: 219 (La Pedrera, Amazonas, Colombia; IBSP 9196). **New synonymy.**
[*Atractus*] *limitaneus*—Savage 1960: 81.
Atractus collaris collaris—Dixon & Soini 1977: 34 (in part).
Atractus alphonsehogei—Martins & Oliveira 1993: 24 (FMT 450, a male specimen).
Atractus collaris—Carrillo & Icochea 1995: 13.

Holotype. Adult male housed in the Museo Regionali di Scienza Naturali di Torino (MRSNT) from Cononaco

River (c.a., 01°31'S, 75°36'W; 190m asl), province of Pastaza, Ecuador. Specimen apparently lost (see Andreaone & Gavetti 2007) (Fig. 4).
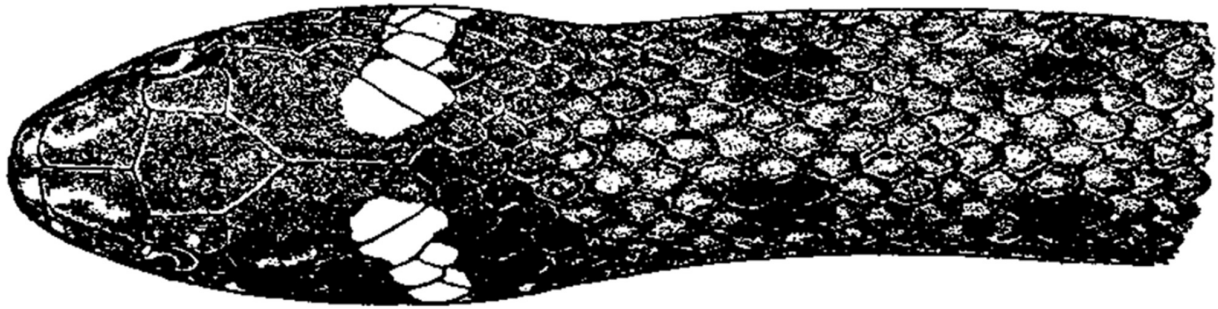

FIGURE 4. Dorsal view of the anterior portion of body of the holotype of *Atractus collaris* from the Cononaco River, Ecuador. Picture modified from Peracca (1897).

Diagnosis. *Atractus collaris* is distinguished from all congeners, except for those species of the *A. collaris* species group by having one (usually) or two (rarely) apical pits on dorsal scales from both sexes and supracloacal tubercles in the cloacal region of mature males (Passos *et al.* 2013b). Additionally, the following combination of morphological characters is unique of the species and distinguishes it from any other species of *Atractus*: (1) dorsal scale rows 17/17/17 with apical pits in both sexes and supracloacal tubercles in males; (2) postoculars two; (3) moderately long loreal, contacting first three supralabials; (4) temporals 1+2; (5) seven supralabials, third and fourth contacting eye; (6) seven infralabials, first three contacting chinshields; (7) five (rarely) or six maxillary teeth; (8) gular scale rows in four series; (9) preventrals usually four; (10) ventrals 167–186 in females, 145–178 in males; (11) subcaudals 18–24 in females, 22–33 in males; (12) in preservative, dorsum brown to grayish black, with cream occipital collar incomplete and small paired black spots usually cream bordered along the body, first dorsal scale rows with lighter center and brown lateral lines; (13) in preservative, venter cream except for two lines (one from each side of belly) in the lateral margins of ventral scales (paraventral region); (14) small body size, females reaching 300 mm SVL, males 218 mm; (15) moderately tail length in females (8.2–10.9.3% SVL) and males (10.9–14.5% SVL); (16) hemipenis moderately bilobed, non-capitate, and non-calyculate.

Comparisons. *Atractus collaris* differs from all members of the *A. collaris* species group, except *A. alphonsenhogei* and *A. gaigeae,* in having first supralabial contacting loreal (vs. first supralabial not contacting loreal in *A. caxiuana*, *A. hoogmoedi*, *A. surucucu*, and *A. zidoki*). *Atractus collaris* differs from *A. alphonsehogei* in having descalcified alary spines and hemipenial lobes centrolineally oriented, dorsum with conspicuous spots, and yellow supralabials (vs. calcified alary spines and hemipenial lobes centrifugally oriented, dorsum uniformly dark brown or black lacking spots, and cream supralabials; from *A. gaigeae* in having 167–186 ventrals in females, 146–178 in males and lacking the vertebral line (vs. 200–214 ventrals in females, 184–198 in males).

Description. Head slightly distinct from body, twice as long as wide, and arched in lateral view; snout rounded in dorsal view and truncated in lateral view; rostrum-orbit distance about half of head length; nostril-orbit distance as long as prefrontal length; interorbital distance as lon as parietal length; rostral subpyramidal in frontal view, wider than high, and barely visible in dorsal view; internasals as wide as long; internasal suture sinistral with respect to prefrontal suture; prefrontal as wide as long; supraocular subtrapezoidal in dorsal view, about three times as long as wide; frontal subpyramidal, as long as wide; parietal about twice as long as wide; nasal divided; nostril between prenasal and postnasal; prenasal about twice as high as long; postnasal shorter than prenasal, as high as long; loreal long, contacting first three supralabials; pupil round; two postoculars similar in height; upper postocular slightly longer than lower postocular; temporals 1+2; first temporal about three times as long as high; upper posterior temporals usually fused in a single shield, about five times as long as wide; supralabials seven, third and fourth contacting eye; first four supralabials nearly equal in height; sixth supralabial taller and seventh supralabial longer than remaining supralabials; symphysial semicircular, about three times as wide as long; fist pair of infralabials preventing symphysial/chinshields contact; infralabials seven, first three contacting chinshields; chinshields three times as long as wide; gular scales in four series; preventrals usually four; dorsal scale rows 17/17/17; dorsal scales usually with one apical pit (rarely two) on both sexes and supracloacal tubercles in mature males; terminal spine large (longer than last subcaudal), approximately robust and conical.
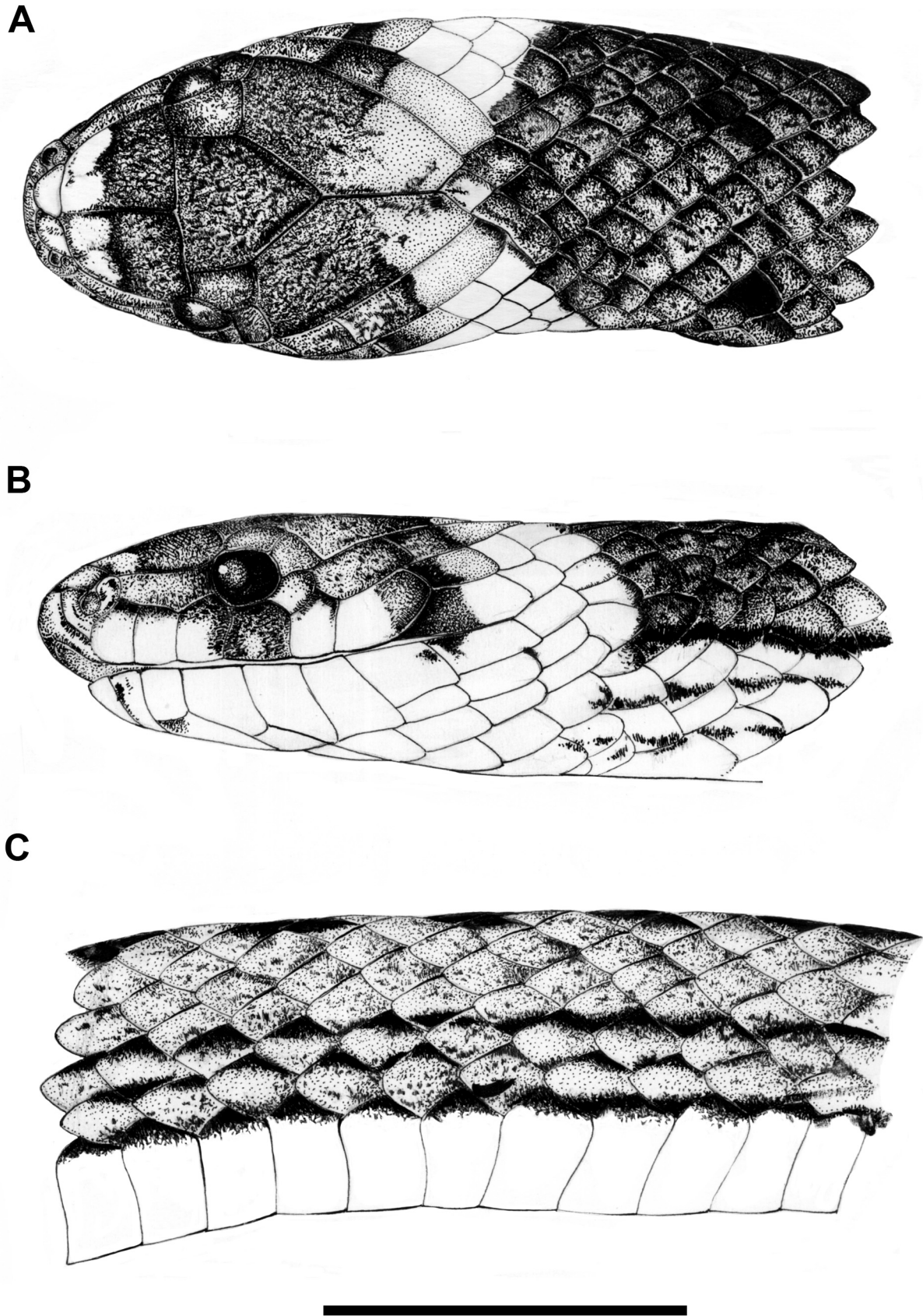
FIGURE 5. Dorsal (A) and lateral (B) views of head and lateral view of body (C) of the *Atractus collaris* (MNRJ 24959) from Laguna Grande Scientific Station, municipality of Cuyabeno, Sucumbíos, Ecuador. Scale bar = 5 mm.
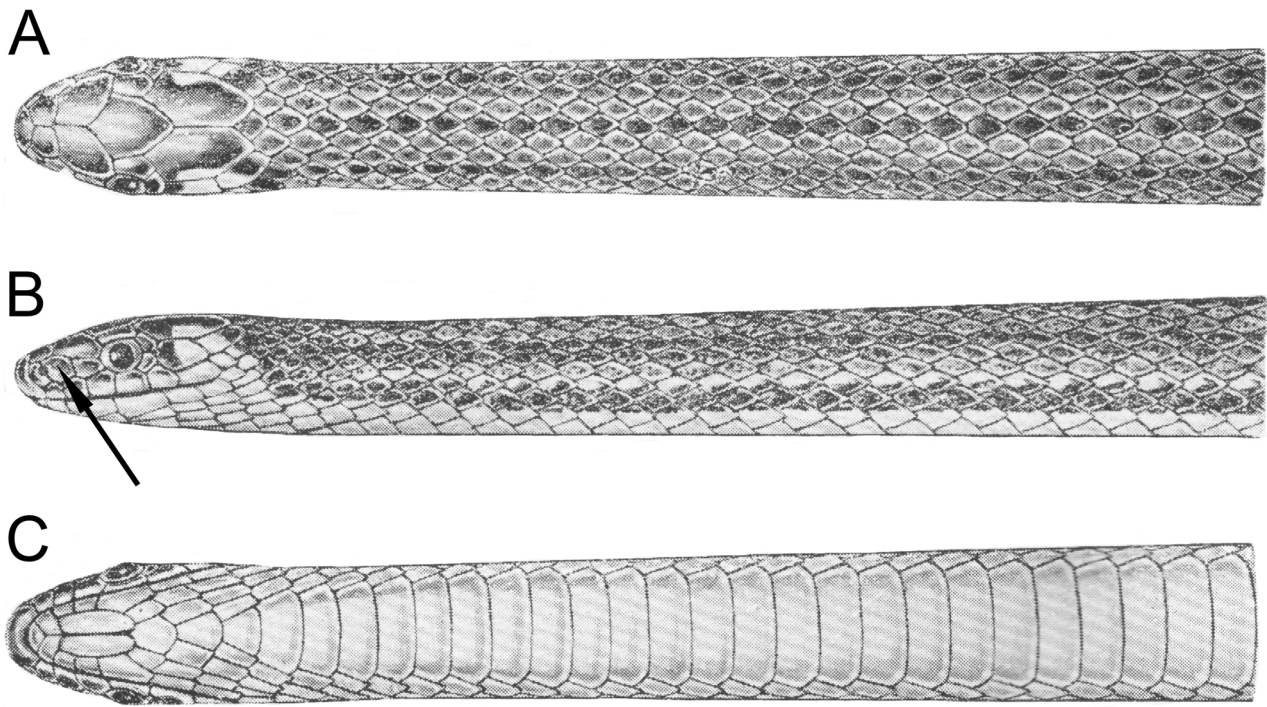
FIGURE 6. Dorsal (A), lateral (B) and ventral (C) views of body of the holotype of *Leptocalamus limitaneus* (IBSP 9196) from La Pedrera, municipality of Puerto Córdoba, department of Amazonas, Colombia. Picture modified from Amaral (1935). Arrow shows a distinct postnasal scale (see text for details).

Maxilla arched in dorsal view with usually with four prediastemal teeth and one postdiastemal tooth; first two teeth moderately spaced (smaller than tooth size, measure taken from the base of the tooth to its apex); spaces among each one of third and fourth teeth longer (similar to the tooth size); prediastemal teeth, posteriorly curved, angulars, robust at base and narrowed in the apices; teeth decreasing posteriorly in size; diastema longer than size of postdiastemal tooth; postdiastemal tooth half-sized of predistemal ones; lateral maxillary process little developed lacking posterior projection.

Color pattern variation in preservative. Dorsum of head dark brown to black with cream spots usually covering snout region (rostral, internasals and anterior portion of prefrontals) and displaying an incomplete occipital collar; incomplete occipital collar extending from posterior area of parietals to lower temporal region, frequently connected with wide cream gular region; lateral surface of head brown to dorsal edges of supralabials; supralabials cream except for dorsal area of third and fourth supralabials mostly dark brown; eventually fourth supralabial entirely dark brown; posterior region of sixth and fully seventh supralabials usually dark brown; infralabials, chinshields, gular region and preventrals usually uniformly cream; occasionally, suture region among infralabials, symphysial, chinshields and other scales from mental region with dispersed and irregular dark brown dots or spots; ventral surface of body and tail uniformly cream, except for dark brown to black lateral margins of ventral scales; lateral pigmentation of ventrals longitudinally arranged forming paraventral lines; occasionally, ventral surface of tail with irregular brown dots or spots; dorsal background of body brown to dark brown, usually with a series of small paired black spots (one scale long and one to two scale wide) along paravertebral region (seventh to eighth scales rows) and continuous dorsolateral black stripes covering dorsal edges of first two or three scale rows; more rarely, individuals displaying a conspicuous vertebral stripe; paired black spots edged anteriorly, laterally (sometimes) and posteriorly by light (pale brown or beige) spots (one scale long and wide); stripes usually located on the dorsal edges of first three scale rows but sometimes restricted to first two scale row; lower half of first two scales rows sometimes light pigmented given an impression of a light stripe due to the contrast with the dark brown dorsolateral stripes; central portion of first dorsal scale row usually cream pigmented contrasting sharply with paraventral and dorsolateral dark lines on the first three scale rows. Paravertebral spots and dorsolateral lines are usually barely distinct from brown background in old preserved or melanistic specimens.

Color pattern variation in life. Dorsum of head dark brown with cream to orange spots covering snout region; eye with red to reddish brown iris; center of supralabials and infralabials cream to yellow pigmented;

incomplete occipital collar cream to creamish red; belly salmon to red colored, except for lateral margins of ventral scales black pigmented; ventral surface of tail salmon to red with dispersed black dots or spots, sometimes concentrated on the scales sutures; dorsal background of body red to dark brown, with black spots and stripes; paravertebral spots bordered by cream to creamish red; light dorsolateral stripes cream to beige (Fig. 3A–C).

Microdermatoglyphics. Apical borders of basal portion cells 2–4 μm apart from each other; borders of denticulations slightly triangular not exceeding 1 μm high; cells surface composed by small and barely conspicuous pores; at midapical portion, spinules from cell borders longitudinally narrow with 1.5–2.0 μm height. Microdermatoglyphic pattern at this portion of the scale is, essentially, the same for the *A. alphonsehogei* and *A. gaigeae* (Fig. 9A).

Hemipenis morphology. Retracted organ extends at level of seventh to eighth subcaudal and bifurcates at level of sixth to seventh subcaudal ($n = 2$). Fully everted and almost maximally expanded hemipenis ($n = 1$, MNRJ 24959) renders a moderately bilobed, non-capitate and non-calyculate; lobes barely centrifugally oriented distally and slightly distinct from hemipenial body; distal portion of lobes clavate with nearly attenuated apices; lobular region is not distinct from the hemipenial body, both in ornamentation and by lacking the capitular groove; lobes and hemipenial body uniformly covered by alary spines (sensu Passos *et al*. 2013d), except for lobular portion on the asulcate side with scarce and spaced spines; alary spines with reduced size above lobular region, forming irregular barely defined flounces at distal portion of hemipenial body on the asulcate side; alary spines spaced widely at their bases on the intrasulcar region and at medial portion of hemipenial body; sulcus spermaticus bifurcates on the proximal third of organ; each sulcus spermaticus branch with centrolinear orientation, extending to lobe apices; sulcus spermaticus moderately laterally expanded before division and narrowed after bifurcation; margins bordered lacking spinules along almost all entire extension; basal naked pocket indistinct; basal region of hemipenis with longitudinal plicae and small spinules irregularly distributed (Fig. 10A).

Meristic and morphometric variation. Largest male SVL 218 mm, TL 26 mm; largest female SVL 300 mm, TL 25 mm; tail 10.9–14.2% SVL (mean = 12.3; SD = 0.4; $n = 21$) in males, 8.2–10.9% SVL (mean = 9.0; SD = 1.0; $n = 6$) in females; ventrals 145–178 (mean = 158.7; SD = 10.6; $n = 21$) in males, 167–186 (mean = 176.2; SD = 7.2; $n = 9$) in females; subcaudals 22–35 (mean = 27.5; SD = 3.1; $n = 21$) in males, 20–26 (mean = 22.5; SD = 2.4; $n = 8$) in females; dorsals at the level of second subcaudal 7–9 (mean = 8.5; SD = 0.6; $n = 60$ sides); midbody diameter 2.0–4.4 mm (mean = 3.6; SD = 0.8; $n = 9$); maxillary teeth 5 ($n = 8$ sides) or 6 ($n = 28$ sides).

Distribution. Amazon rainforest eastern of the Andes from Inírida (03°48'N, 67°50'W), department of Guainía, Colombia, south to Coronel Portillo (08°23'S, 74°35'W) department of Ucayali, Peru; and east to Urucú River (ca. 04°31'S, 64°23'W), state of Amazonas, Brazil. *Atractus collaris* occurs from 100–700 m elevation (Fig. 12). Martins & Oliveira (1993) report a specimen of *A. alphonsehogei* from Presidente Figueiredo (01°26'S, 60°01'W), state of Amazonas, Brazil. Although this specimen (a male, FMT 405) was not available to us, we have examined other specimen from Presidente Prudente (MPEG 17545) and confirmed its identification as *Atractus collaris*. Therefore, based on the data available in the Martins & Oliveira (1993) and also on the above species record, we tentatively consider FMT 405 as *A. collaris*.

Remarks. Recently, Wallach *et al*. (2014) pointed out that the holotype of *Leptocalamus limitaneus*—as well as many other types of Neotropical snakes taxa—was lost in the tragic fire accident that consumed most of the herpetological collection of the Instituto Butantan (see Kumar 2010; Warrel *et al*. 2010; Franco 2012). However, this and other types of *Atractus* remain intact and available to examination because such specimens were loaned to the senior author when the accident happened. In addition, we emphasize that other type specimens kept on the metallic cabinets survived (with some degree of damage) from the fire due to oxygen consumption inside the compacted racks (P. Passos pers. observ.). Therefore, authors of future studies must make sure to consult the curator in charge of the Instituto Butantan collection regarding the whereabouts of the types of interest for comparisons before proposing neotype designations based on the provisions of ICZN (1999).

***Atractus gaigeae* Savage, 1955**
Figures 3D, 7

Rhabdosoma maculatum Bocourti 1883: 540. [ZMB lectotype from Ecuador; see Savage (1955, 1960)] (in part).
Atractus bocourti—Boulenger 1896:645 (in part).
Atractus gaigeae Savage, 1955:12.

Atractus collaris gaigeae—Dixon & Soini 1977:34.
Atractus gaigeae—Lehr 2002:204 [indirectly, by restoring the specific rank for the former species, *Atractus collaris*].

Holotype. Adult male (UMMZ 82887) collected by Clarence Altenberg and Bancroft G. Buttler on 1935 without a precise location in the province of Zamora-Chinchipe (formerly Santiago-Zamora), Ecuador. The specimen has a midventral incision exposing some viscera (Fig. 7).

Paratypes. All specimens from the provinces of Napo and Pastaza, Ecuador: male (AMNH 35891) from a locality between Baños (01°25'S, 78°33'W) and Canelos; female (CAS-SU 15619) and male (CAS-SU 15620) from Canelos (01°35'S, 77°45'W; ca. 490 m); male (CAS-SU 15621) from headwaters of Bobonaza River (01°28'S, 53°40'W; ca. 250 m); male EPN 8693 (formerly EPN 48) from Bobonaza River, Sarayacu (01°44'S, 77°29'W; ca. 400 m); and EPN female 5272 (formerly EPN 46) from Bobonaza River, Chichirota (02°32'S; 76°39'W; ca. 250 m).

Diagnosis. *Atractus gaigeae* is distinguished from all congeners, except for those species of the *A. collaris* species group (see below the distinction among these members), by having one (usually) or two (rarely) apical pits on dorsal scales of both sexes and supracloacal tubercles on cloacal region of mature males (Passos *et al.* 2013b). Additionally, the following combination of morphological characters is unique from the species and also distinguishes it from any other species of *Atractus*: (1) dorsal scale rows 17/17/17 with apical pits on both sexes and supracloacal tubercles in mature males; (2) postoculars usually one in female and two in males; (3) loreal moderately long, contacting first three supralabials (4) temporals 1+2; (5) seven supralabials, third and fourth contacting eye; (6) infralabials six or seven, first three contacting chinshield; (7) maxillary teeth usually five or six; (8) gular scale rows usually four; (9) preventrals four; (10) ventrals 200–214 in females, 184–198 in males; (11) subcaudals 23–28 in females, 33–40 in males; (12) dorsum of head dark brown with an incomplete occipital light collar, dorsal ground color of body brown with paired paravertebral black spots and longitudinal stripes (rarely with vertebral but usually with dorsolateral lines); (13) belly almost immaculate cream, except for lateral edges of ventral scales dark brown forming paraventral lines; (14) small body size, females reaching 295 mm SVL, males 266 mm SVL; (15) small tail length in females (7.1–12.5% SVL), moderately long in males (11.7–15.9% SVL); (16) hemipenis moderately bilobed, non-capitate and non-calyculated.

Comparisons. *Atractus gaigeae* differs from all members of the *A. collaris* species group, except for *A. alphonsenhogei* and *A. collaris,* in having first supralabial contacting loreal (vs. first supralabial not contacting loreal in *A. caxiuana*, *A. hoogmoedi*, *A. surucucu*, and *A. zidoki*). *A. gaigeae* differs from both species in having 200–214 ventrals in females, 184–198 in males (vs. 163–176 in females, 150–162 in males of *A. alphonsehogei*; and 167–186 in females, 145–178 in males of *A. collaris*).

Description. Head slightly distinct from body, twice as long as wide, and arched in lateral view; snout rounded in dorsal view and truncated in lateral view; rostrum-orbit distance about half of head length; nostril-orbit distance equivalent to pre-frontal length; interorbital distance equivalent to parietal length; rostral subpyramidal in frontal view, wider than high, and visible in dorsal view; internasals slightly wider than long; internasal suture sinistral with respect to prefrontal suture; prefrontal as wide as long; supraocular subtrapezoidal in dorsal view, about two times as long as wide; frontal subpyramidal, as long as wide; parietal about twice as long as wide; nasal divided; nostril between prenasal and postnasal; prenasal about twice as high as long; postnasal shorter than prenasal, as high as long; loreal long, contacting first three supralabials; pupil round; usually one postocular (73% on both sides and 91% only on one side) in females (*n* = 22 sides) and two postoculars (< 80%) similar in height in males (*n* = 38 sides); upper postocular slightly longer than lower postocular; temporals 1+2; first temporal about two times as long as high; upper posterior temporals usually fused in a single shield, about five times as long as wide; supralabials seven, third and fourth contacting eye; first four supralabials similar in height; sixth supralabial taller and seventh supralabial longer than remaining supralabials; symphysial subtriangular, about three times as wide as long; fist pair of infralabials preventing symphysial/chinshields contact; infralabials seven, first three contacting chinshields; chinshields three times longer than wide; gular scales in four series; preventrals usually four; dorsal scale rows 17/17/17; dorsal scales usually with one apical pit (rarely two) on both sexes and supracloacal tubercles in mature males; terminal spine large (longer than last subcaudal), robust and slightly acuminate.

Maxilla arched in dorsal view with five or four prediastemal teeth and one postdiastemal tooth; first two teeth moderately spaced (smaller than teeth size); spaces among each one of third and fourth teeth longer (similar to the teeth size); prediastemal teeth, posteriorly curved, angular, robust at base and narrowed in the apices; teeth decreasing posteriorly in size; diastema longer than size of postdiastemal tooth; postdiastemal tooth half-sized of predistemal ones; lateral maxillary process little developed, lacking posterior projection.

FIGURE 7. Dorsal (A), lateral (B) and ventral (C) views of head, and dorsal (D) and lateral (E) views of body of the holotype of *Atractus gaigeae* (UMMZ 82887) from the province of Zamora-Chinchipe, Ecuador without precise location.

Color pattern variation in preservative. Dorsum of head dark brown, usually with darker pigments restricted to the suture of cephalic shields and snout region, rostral, internasals and anterior prefrontals cream colored; cream spots or irregular blotches restricted to the center of each scale/shield or covering mostly of snout dorsally; posterior region of head with an incomplete conspicuous cream collar (two scales long); light collar extends from occipital region to lateroposterior end of parietals; parietals mostly dark borwn, precluding contact between each branch of the incomplete cream collar; lateral surface of head dark brown to dorsal edge of supralabials; supralabials mostly cream, except for posterior region of third and anterior region of fourth and anterior portion of sixth and seventh supralabials almost entirely dark brown; occasionally, suture between each supralabial scale dark brown with its central portion cream; temporal and occipital regions covered by cream collar, decreasing in length towards parietals; symphysial and infralabials with cream ground color sometimes covered with dark brown spots concentrated on the posterior regions of infralabials and anterior portion of chinshields; symphysial and infralabials rarely almost entirely brown pigmented; chinshields and gular region uniformly cream or with a few dark brown dots; ventral surface of body cream with conspicuous black spots on the lateral margins of ventral and subcaudal scales; black spots forming a conspicuous longitudinal stripe on the paraventral region of body; dorsum of body with dark brown to black band on neck (usually three scales long) forming an inverted "V" shaped collar; more rarely, dark collar discontinuous with each branch separate above vertebral region; dorsal ground color brown with a black vertebral line (one scale wide), paired black paravertebral spots (one or two scales long and wide), and dorsolateral stripes; paired spots located between sixth and seventh scales rows and dorsolateral stripes (one scale wide) covering second scale rows and, eventually, above ventral portion of third scale row between both series of scales; paraventral line originating from lateral margins of ventral scales usually extending dorsally to ventral edge of first scale row (half-scale wide); first scale row usually lighter (pale brown), contrasting among both dark lateral stripes.

Color pattern variation in life. Dorsum of head dark brown with cream to creamish red spots covering snout region; eye with brown to black iris; center of supralabials and infralabials cream; belly cream colored, except for black pigmented lateral margins of ventral scales; ventral surface of tail cream with dispersed black dots or spots, sometimes concentrated on the scales sutures; dorsal background of body brown, with black spots and stripes; paravertebral spots not bordered by light pigments; light dorsolateral stripes beige (Fig 3D).

Microdematoglyphics. Scales of *Atractus gaigeae* presents cell borders at midapical portion closer to each other (rarely exceeding 2.5 μm of distance) and more conspicuous pores at cell surface compared to *A. collaris* (Fig. 9B).

Hemipenis morphology. Retracted organ extends at level of eighth to ninth subcaudal and bifurcates at level of seventh to eighth subcaudal ($n = 3$). Fully everted and almost maximally expanded hemipenis ($n = 1$, USNM 217627) renders a moderately bilobed, non-capitate and non-calyculate; lobes centrolinearly oriented distally and slightly distinct from hemipenial body; distal portion of lobes clavate with nearly rounded apices; lobular region do not distinct from the hemipenial body (similar ornamentation and capitular groove absent); lobes and hemipenial body uniformly covered by alary spines (sensu Passos *et al.* 2013d); alary spines increasing in size below lobular region, forming irregular barely defined flounces at distal portion of hemipenial body on the asulcate side; alary spines irregular on the intrasulcar region and at medial portion of hemipenial body; sulcus spermaticus centrolinear, bifurcating at half length of organ and extending to lobe apices; sulcus spermaticus wide laterally expanded along all its extension; margins lacking spinules along almost all its extension; basal naked pocket indistinct; basal region of hemipenis with longitudinal plicae and small spinules irregularly distributed (Figs. 10B).

Meristic and morphometric variation. Largest male 266 mm SVL, 34 mm CL; largest female 295 mm SVL, 21 mm CL; tail 11.7–15.9% SVL(mean = 14.0; SD = 1.3; $n = 15$) in males, 7.1–12.5% SVL (mean = 9.0; SD = 1.5; $n = 10$) in females; ventrals 184–198 (mean = 189.3; SD = 3.7; $n = 18$) in males, 200–214 (mean = 204.8; SD = 4.5; $n = 10$) in females; subcaudals in males 33–40 (mean = 36.1; SD = 1.7; $n = 4$), 23–28 (mean = 25.8; SD = 1.4; $n = 10$) in females; gular scale rows 3 ($n = 3$ sides) or 4 ($n = 56$ sides); postocular 1 ($n = 7$ sides) or 2 ($n = 39$ sides) in males, 1 ($n = 14$ sides) or 2 ($n = 6$ sides) in females; dorsal scale rows at level of second subcaudal 8–10 ($x̄ = 8.9$; SD = 0.5; $n = 58$ sides); midbody diameter 2.0–5.7 mm (mean = 3.6; SD = 0.8; $n = 25$); maxillary teeth 5 ($n = 26$ sides), 6 ($n = 26$ sides) or 7 ($n = 2$).

Distribution. From Cuyabeno (ca., 00°25'27''S, 76°06'09''W), province of Subumbíos, southeast to Chichirota (0232'S, 7638'W), and southwest to Taisha (02°09'53''S, 77°39'32''W) provence of Morona Santiago, along the Amazonian versant of Ecuador. *Atractus gaigeae* occurs between 200–750 m asl (Fig. 12).

Atractus alphonsehogei Cunha & Nascimento, 1983
Fig. 8

Atractus alphonsehogei Cunha & Nascimento, 1983:25 (Fig. 2 pp. 27).

Holotype. Adult male (MPEG 14928) collected by O. Cunha and F. Nascimento on August 01 1978 at Bela Vista, Km 75 of the PA-242 road near municipality Nova Timboetuba (ca., 01°12'47''S, 47°23'18''W; 30 m asl), state of Pará, Brazil (Fig. 8).

    Paratypes. Thirteen specimens, eleven of them from the state of Pará and the other two from the state of Maranhão, all of them collected by O. Cunha, F. Nascimento or by both in the same fieldtrip: female (MPEG 2221) collected on September 20 1972 on road PA-140 from Santo Antônio do Tauá (ca., 01°08'S, 48°07'W; 20m asl) toward municipality of Vigia (00°51'S, 48°08'W; 10m asl); male (MPEG 8573) collected on March 02 1975 and female (MPEG 8667) collected on October 07 1974 on Parada Bom Jesus on the PA-242 road, 11 Km to municipality of Bragança (01°03'13''S, 46°45'56''W; 10m asl); male (MPEG 12593) collected on September 17 1976 at PA-140 road in the locality of Santa Rosa da Vigia 12 Km (airline) from the municipality of Vigia; female (MPEG 9949) collected on June 26 1975 at Cacoal Farm, Arari road a confluence of PA-242 27 Km from the municipality of Bragança; two males (MPEG 2976) and (MPEG 10130) collected on March 14 and 10 1976, respectively and three females (MPEG 6408) collected on March 27 1974, and (MPEG 10129) and (MPEG 10132) both collected on March 10 1976 at locality of Colônia Nova, Km 264 of the BR-316 highway near to Rio Gurupi (ca., 01°49'S, 48°24'W; 30m asl); female (MPEG 10093) collected on June 23 1975 at Km 224 of the BR-316 highway; and two other males from the state of Maranhão: (MPEG 10874) collected on November 02 1975 on BR-316 highway 25 Km before Rio Gurupi (ca., 01°49'S, 46°06'W; 46m asl), Nova Vida, and (MPEG 11145) collected on February 23 1976 at São Raimundo ca. 8 Km from Santa Inês (03°39'S, 45°23'W; 30m asl).

    Diagnosis. *Atractus alphonsehogei* is distinguished from all congeners, except for those species of the *A. collaris* species group by having one (usually) or two (rarely) apical pits on dorsal scales of both sexes and supracloacal tubercles in the cloacal region of mature males (Passos *et al.* 2013b). Additionally, the following unique combination of morphological characters is unique from the species and also distinguishes it from any species of *Atractus*: (1) dorsal scale rows 17/17/17 with apical pits and supracloacal tubercles in males; (2) postoculars two; (3) moderately long loreal, contacting first three supralabials; (4) temporals 1+2; (5) seven supralabials, third and fourth contacting eye; (6) seven infralabials, first three contacting chinshields; (7) six maxillary teeth; (8) gular scale rows in four series; (9) preventrals usually four; (10) ventrals 163–176 in females, 150–162 in males; (11) subcaudals 17–21 in females, 23–26 in males; (12) in preservative, dorsum brown to grayish black, with cream occipital collar incomplete, first dorsal scale rows with lighter center limited dorsally by dark brown lateral lines on the second and third scale rows, and two barely conspicuous brown dorsolateral lines on the sixth to seventh scale rows on each side of body; (13) in preservative, venter cream except for two lines (one from each side of belly) on the lateral margins of ventral scales (paraventral region); (14) small body size, females reaching 284 mm SVL, males 218 mm; (15) moderate tail length in females (8.0–11.4% SVL) and males (12.3–13.1% SVL); (16) hemipenis moderately bilobed, non-capitate, and non-calyculate.

    Comparisons. *Atractus alphonsehogei* differs from all members of the *A. collaris* species group, except *A. collaris* and *A. gaigeae,* by having first supralabial contacting loreal (vs. first supralabial not contacting loreal in *A. caxiuana*, *A. hoogmoedi*, *A. surucucu*, and *A. zidoki*). *Atractus alphonsehogei* differs from *A. collaris* in having calcified alary spines and hemipenial lobes centrifugally oriented, dorsum uniformly dark brown or black lacking spots, and cream supralabials (vs. alary spines lacking calcification and lobes centrolinearly oriented, dorsum with conspicuous spots, and yellow supralabials); from *A. gaigeae* in having 163–176 ventrals in females, 150–162 in males, six maxillary teeth, and lacking the vertebral line (vs. 200–214 ventrals in females, 184–198 in males; usually five maxillary teeth, and conspicuous vertebral line).

    Description. Head indistinct from body, neraly twice as long as wide, and slightly flattened in lateral view; snout rounded in dorsal view and truncated in lateral view; head length about twice as long as wide; rostrum-orbit distance about one-third of head length; nostril-orbit distance equivalent to pre-frontal length; interorbital distance slightly smaller than parietal length; rostral subpyramidal in frontal view, wider than high, and visible in dorsal view; internasals slightly wider than long; internasal suture sinistral with respect to prefrontal suture; prefrontal as wider as long; supraocular subtrapezoidal in dorsal view, about twice as long as wide; frontal subpyramidal, as long

as wide; parietal about twice as long as wide; nasal divided; nostril between prenasal and postnasal; prenasal about twice as high as long; postnasal shorter than prenasal, as high as long; loreal long, contacting first three supralabials; pupil round; two postoculars; upper postocular higher and longer than lower postocular; temporals 1+2; first temporal about twice as long as high; upper posterior temporals usually not fused in a single shield, about three times as long as wide; supralabials seven, third and fourth contacting eye; first four supralabials nearly similar in height; sixth supralabial usually taller and seventh supralabial longer than remaining supralabials; symphysial subtringular, about three times as wide as long; fist pair of infralabials preventing symphysial/chinshields contact; infralabials seven, first three contacting chinshields; chinshields three times as long as wide; gular scales in four series; preventrals usually four; dorsal scale rows 17/17/17; dorsal scales usually with one apical pit on both sexes and supracloacal tubercles in mature males; terminal spine large (longer than last subcaudal), conical and slightly acuminate.

Maxilla arched in dorsal view with usually with four prediastemal teeth and two postdiastemal teeth; first two teeth moderately spaced (smaller than teeth size); spaces among each one of third and fourth teeth longer (similar to the teeth size); prediastemal teeth, posteriorly curved, angular, robust at base and narrowed at the apices; teeth decreasing posteriorly in size; diastema longer than size of postdiastemal tooth; postdiastemal tooth half-size of predistemal ones; lateral maxillary process little developed lacking posterior projection.

Color pattern variation in preservative. Dorsum of head usually uniformly dark brown to black, displaying an usually incomplete (rarely complete; MPEG 8667) occipital light collar (one to two scales long) extending from parietal tip to lower temporal region; anterior portion of snout (rostral, internasal, and anterior portion of prefrontals) occasionally cream colored (MPEG 8667, 9949); more rarely, both collar parts connected on the medial region (MPEG 8667); occipital collar extends from end of parietal to lower temporal region; lateral surface of head brown to nearly to mid-ventral region of supralabials; supralabials with cream spots except for third and fourth supralabials contacting the eye almost entirely dark brown; posterior region of sixth and fully seventh supralabials usually dark brown; infralabials cream with dark brown spots; spots generally covering first two infralabials, anterior chinshields, and posterior region of third to sixth infralabials; gular region and preventrals usually uniformly cream; ventral surface of body and tail uniformly cream, except for lateral margins of ventral scales dark brown to black; lateral pigmentation of ventral scales longitudinally arranged forming paraventral lines; dorsal background of body brown to dark brown, usually with continuous dorsolateral black stripes above the sixth scale row (one scale wide); stripes occasionally located on the dorsal edges of first three scale rows but sometimes restricted to first two scale rows; lower half of first two scale rows sometimes light pigmented creating the impression of a light stripe due to the contrast between the dark brown lines dorsally; central portion of first dorsal scale row usually cream pigmented contrasting sharply with paraventral and dorsoslateral dark lines on the first three scale rows.

Color pattern variation in life. Species known only from the type-series and two additional topotypes, lacking any information regarding coloration in life.

Microdermatoglyphics. At basal portion of scales, *A. alphonsehogei* differs from *A. collaris* by presenting more triangular denticulations and by not presenting visible micro-ornamentations at cell surface under magnifications up to 10.000x (Fig. 9C).

Hemipenis morphology. Retracted organ extends at level of sixth to eighth subcaudal and bifurcates at level of fifth to seventh subcaudal ($n = 2$). Fully everted and almost maximally expanded hemipenes ($n = 2$, MPEG 10874, 11145) render a moderately bilobed, non-capitate and non-calyculate; lobes barely centrifugally oriented distally and slightly distinct from hemipenial body; distal portion of lobes clavate with nearly attenuated apices; lobular region do not distinct from the hemipenial body, both in ornamentation and lacking the capitular groove; lobes and hemipenial body uniformly covered by alary spines (sensu Passos *et al*. 2013d); alary spines with reduced size on the lobular region, forming irregular and barely defined flounces at distal portion of hemipenial body on the asulcate side; alary spines with widely basal region above lobular region on both sides of organ; sulcus spermaticus deeper until its division, bifurcating to the half-length of organ; branches of sulcus spermaticus centrifugally oriented, running to tip of each lobe; margins of sulcus spermaticus laterally expanded along all sulcus spermaticus extension, lacking spinules; hemipenial body sub-cylindrical scattered with larger alary spines, concentrated on the median region of asulcate side of organ; basal naked pocket indistinct; basalmost region of hemipenis with longitudinal plicae and dispersed spinules (Fig. 10C).
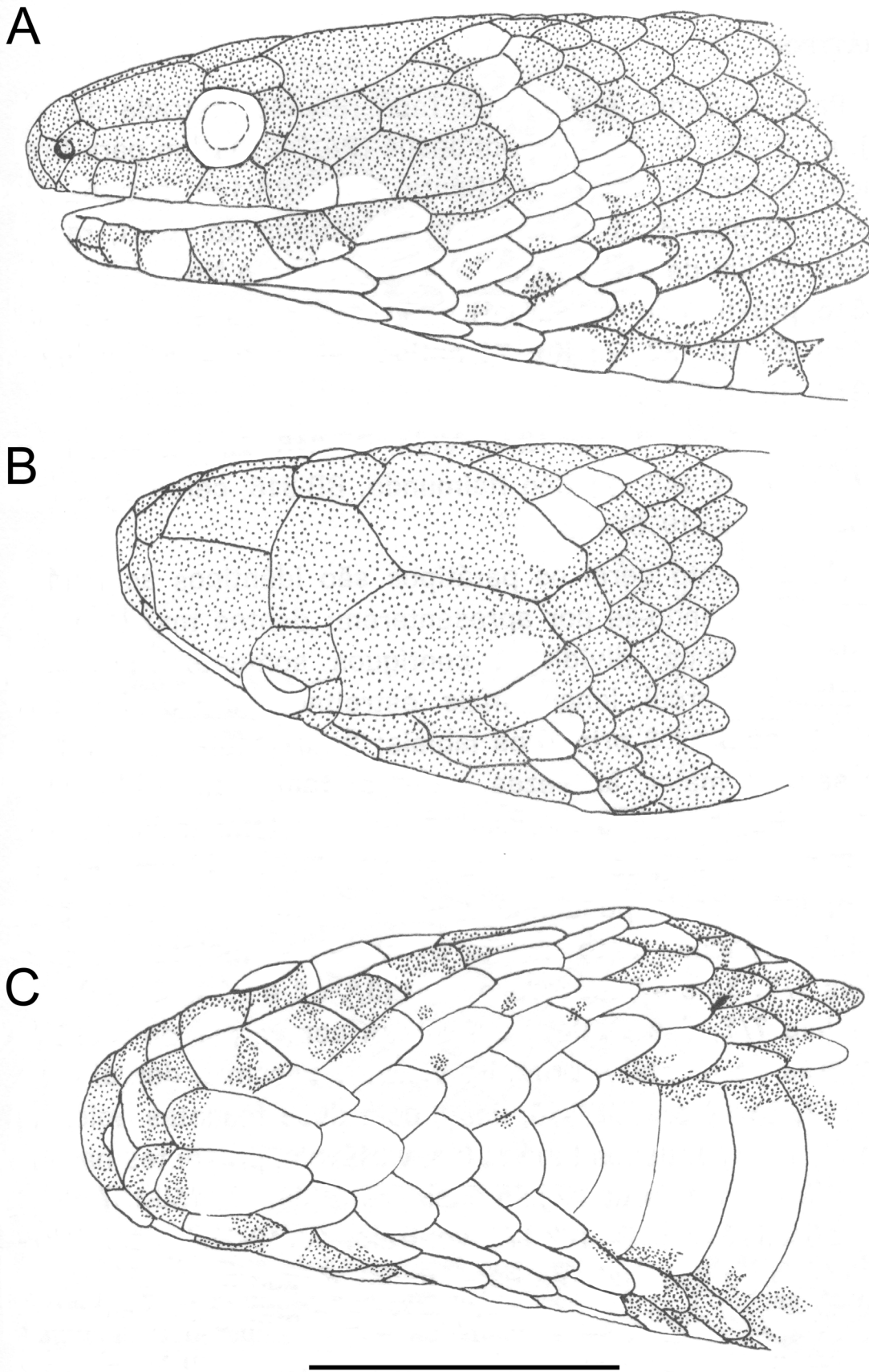
FIGURE 8. Dorsal (A), lateral (B) and ventral (C) views of head of the holotype of *Atractus alphonsehogei* (MPEG 14928) from Bela Vista, Km 75 PA-242 road, state of Pará, Brazil. Picture modified from Cunha and Nascimento (1983). Scale bar = 4 mm.
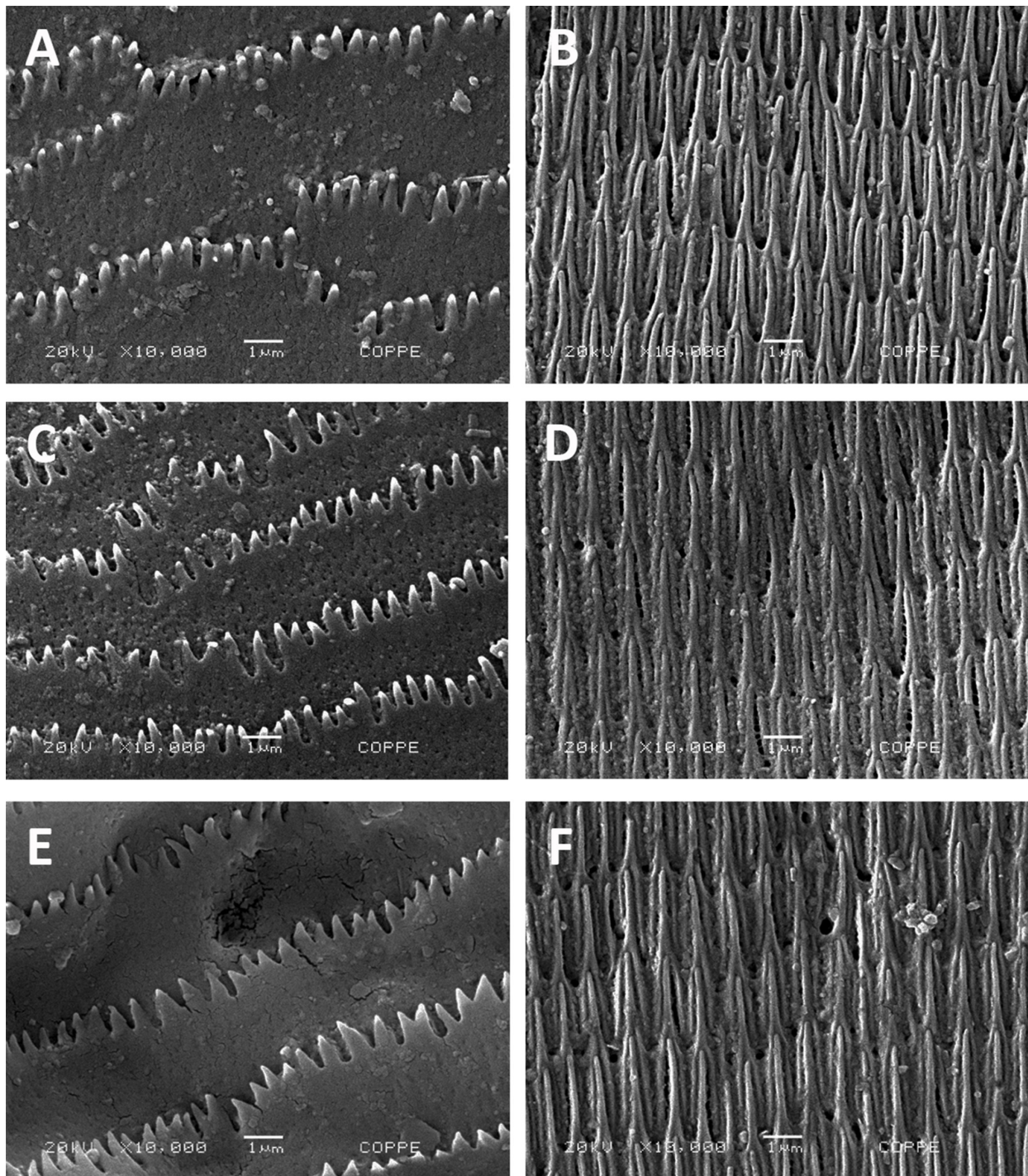
FIGURE 9. Microdermatoglyphics of the dorsal scales of *Atractus collaris* (A–B, MNRJ 24959) from Laguna Grande Scientific Station, municipality of Cuyabeno, Sucumbíos, Ecuador; *Atractus gaigeae* (C–D, USNM 217623) from municipality of Montalvo, province of Pastaza, Ecuador; and *Atractus alphonsehogei* (E–F, MPEG 10874) from São Raimundo, 8 Km from municipality of Santa Inês, state of Maranhão, Brazil. Each scale region was photographed from basal portion (left side) and apical portion (right side).

Meristic and morphometric variations. Largest male SVL 218 mm, TL 26 mm; largest female SVL 284 mm, TL 22 mm; tail 12.3–13.1% SVL (mean = 12.7; SD = 0.3; $n = 7$) in males, 8.0–11.4% SVL (mean = 8.9; SD = 1.2; $n = 7$) in females; ventrals 150–162 (mean = 155.7; SD = 4.5; $n = 7$) in males, 163–176 (mean = 168.1; SD = 5.1; $n = 7$) in females; subcaudals 23–26 (mean = 25.4; SD = 1.1; $n = 7$) in males, 17–21 (mean = 19.1; SD = 1.5; $n = 7$) in females; preventrals 3 ($n = 1$) or 4 ($n = 13$); dorsals at level of second subcaudal 8–9 (mean = 8.3; SD = 0.3; $n = 18$ sides); midbody diameter 3.6–4.0 mm ($n = 2$).
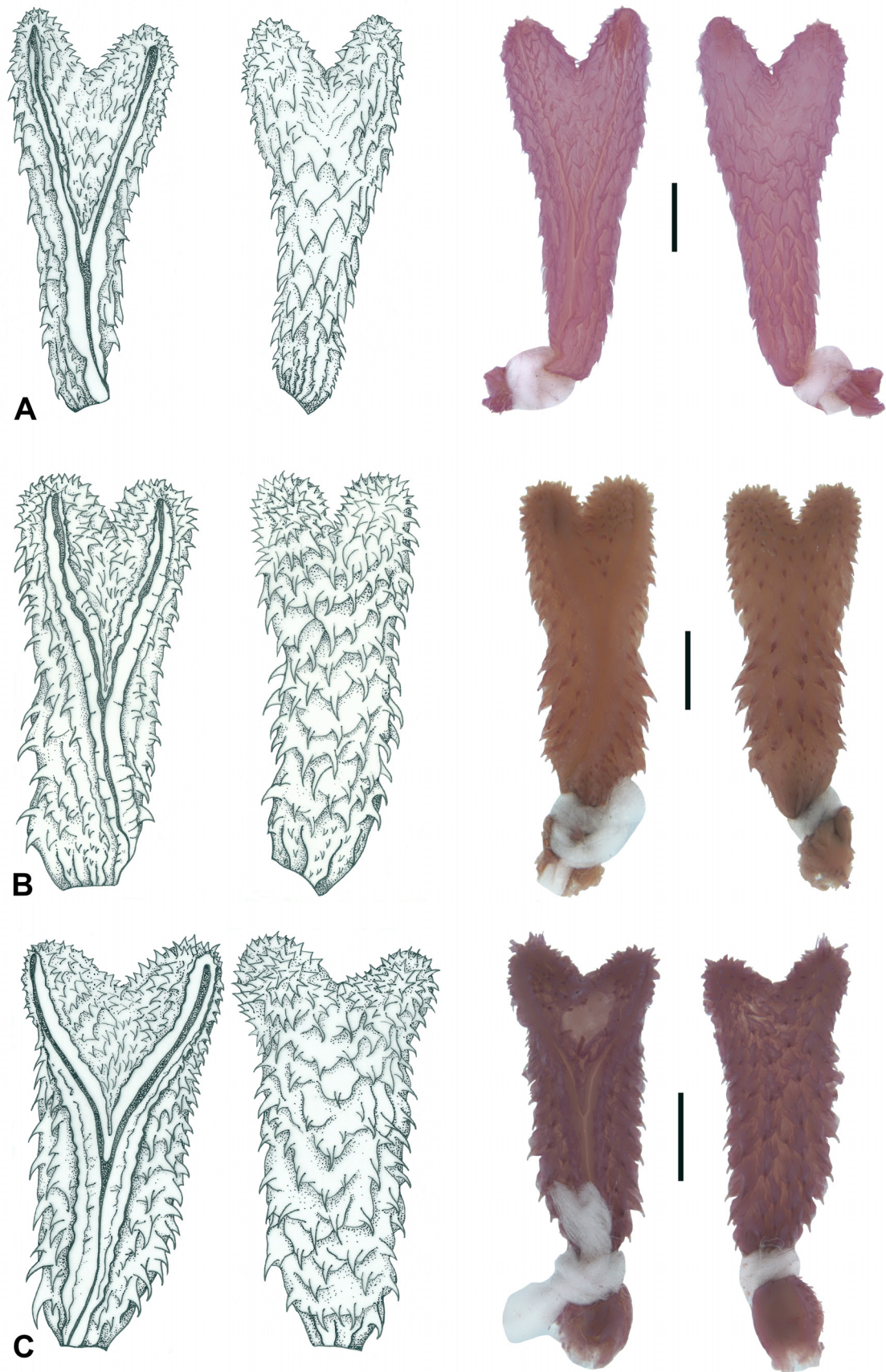
FIGURE 10. Hemipenial morphology (detailed line arts on the left and photographs on the right) of *Atractus collaris* (A, MNRJ 24959) from Laguna Grande Scientific Station, municipality of Cuyabeno, Sucumbíos, Ecuador; *Atractus gaigeae* (B, USNM 217627) from municipality of Montalvo, province of Pastaza, Ecuador; and *Atractus alphonsehogei* (C, MPEG 10874) from São Raimundo, 8 Km from municipality of Santa Inês, state of Maranhão, Brazil. Scale bar = 1 mm.
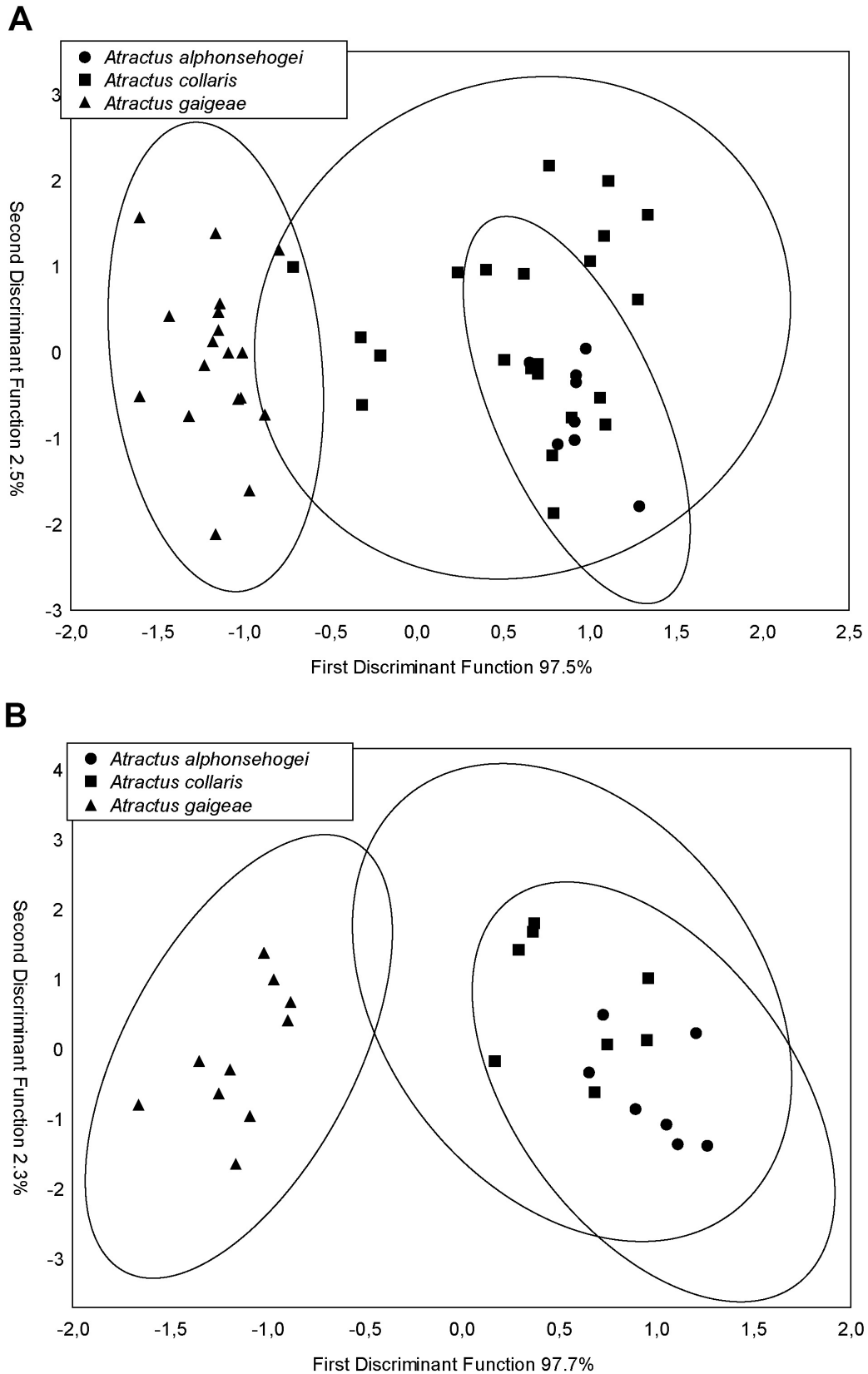
FIGURE 11. Bivariate plots with 95% confidence regions for the first two axes derived from scores of discriminant analyses (DFA) with 1,000 replicates of bootstrap for males (A) and females (B) from the *Atractus collaris* complex. The direct cosines display the variables more related with the discriminant functions.
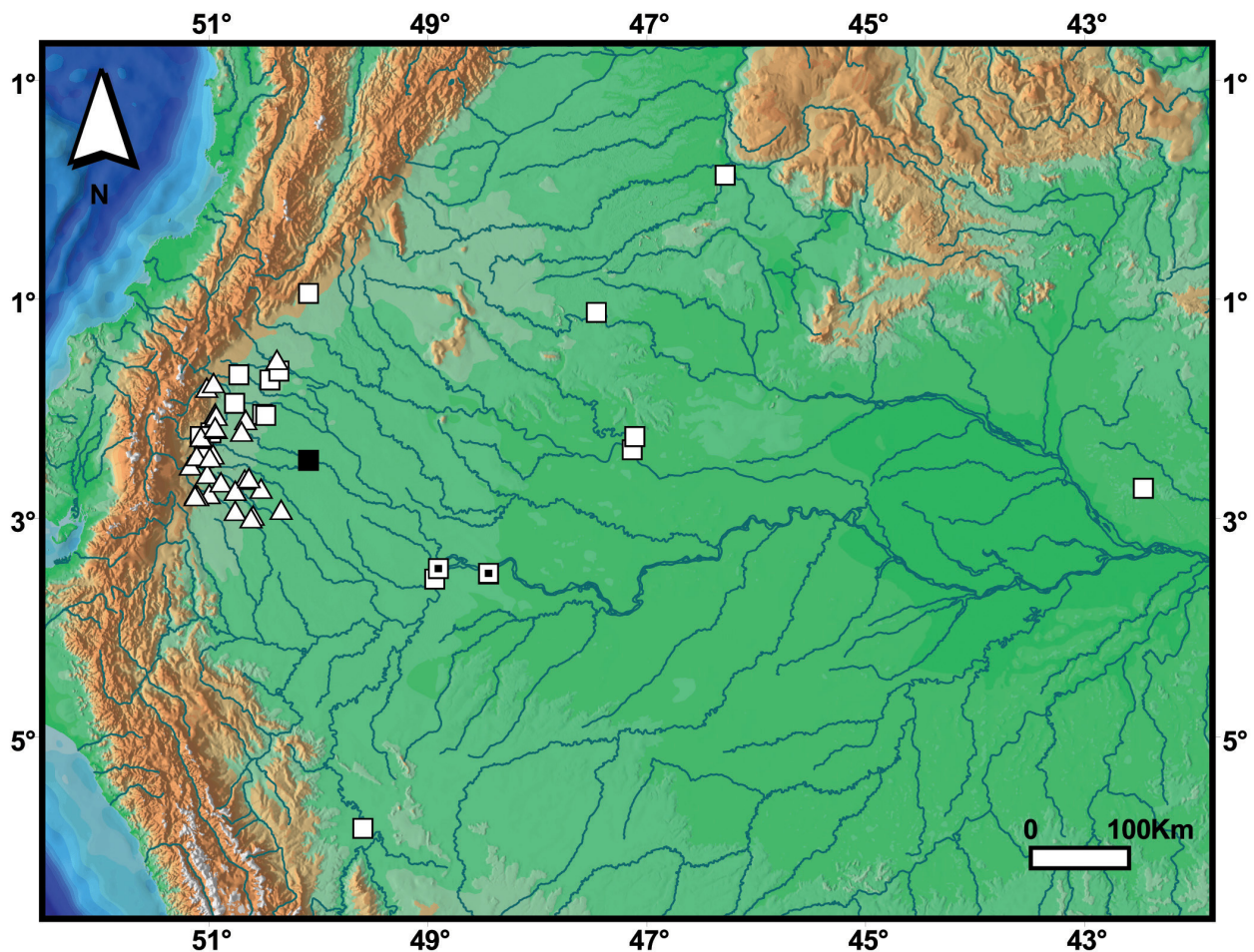
FIGURE 12. Distribution of *Atractus collaris* (squares) *A. gaigeae* (triangles). We use records based on the specimens preserved at scientific collection as well as the photographic records with detailed provenance data (white squares with central dots). The black symbol square represents the type-locality of *A. collaris*.

Distribution. Apparently restricted to easternmost portions of the Brazilian Amazonia near the Atlantic coast, from Vigia (00°51'S, 48°08'W), state of Pará southeast to Santa Inês (03°40'S, 45°22'W), state of Maranhão. *Atractus alphonsehogei* occurs from sea level up to 50 m elevation (Fig. 13).

Remarks. *Atractus alphonsehogei* is known to date only from the original type series (14 individuals) and two additional topotypes (MPEG 13907–08), all which collected between 1972 and 1978. The absence of additional samples in almost 40 years, as well as its relatively restricted range may represent substantial evidence of rarity and endemism. Such combination of factors would render *A. alphonsehogei* a rare and highly threatened taxon in view of the broad deforestation in this region of Amazonia during the last three decades. Considering that the area harbors other endemic taxa (e.g., *Atractus hoogmoedi*—Prudente & Passos 2010) our data provide further support to the proposition of a conservation unit in the coastal region of the Brazilian Amazon rainforest.

Key to the known species of the *Atractus collaris* species group

In order to simplify field and laboratory identification, this key is mainly based on external morphology but we must employ a few traits also from internal morphology (e.g., maxillary dentition) or sexually dimorphic characters (e.g., hemipenial morphology). However, whenever we use more restricted (or of difficult observation) characters they are in combination with other externally discernible characteristics. In general, the use of more than one character in all of key steps improves the reliability of the identifications. Finally, we highlighted that this key was conceived on the basis of available sample, which may underestimate taxa polymorphism and, therefore, we recommend to it be complementary to species diagnoses.

1.   Loreal scale generally in contact with the first surpalabial scale, usually six maxillary teeth 5
-       Loreal scale isolated from the first supralabial by postnasal scale, usually four or five maxillary teeth 2
2.   Hemipenis bilobed, dorsum lacking conspicuous paravertebral spots in preservative, and CL/SVL ≤ 9.2 in females and < 14.0 in males 3
-       Hemipenis unilobed, dorsum with paravertebral spots in preservative, and CL/SVL ≥ 9.2 in females and 14.0 in males 4
3.   Ventral scales > 199 in females, internasal separated from loreal scale by postnasal scale, dorsum uniformly black in preservative, and CL/SVL < 9 in females. . . . . A. surucucu.
-       Ventral scales < 190 in females, internasal usually in contact with loreal scale, dorsum with barely defined paravertebral spots and occasionally vertebral line in preservative, and CL/SVL ≥ 9.0 . . . . A. caxiuana.
4.   Hemipenis with sulcus spermaticus divided distally, ventral scales > 173 in males and > 195 in females . . . . A. zidoki.
-       Hemipenis with sulcus spermaticus undivided, ventral scales < 172 in males and < 181 in females . . . . A. hoogmoedi.
5.   Ventral scales ≥ 200 in females and > 184 in males, and subcaudal scales > 35 in males and ≥ 24 in females, single postocular in females, presence of vertebral line, and females with a single postocular scale at least on the one side of the head . . . . A. gaigeae.
-       Ventral scales < 200 in females and < 184 in males, and subcaudal scales < 35 in males and ≤ 24 in females, two postocular in both sexes, usually lacking vertebral line, and females with tow postocular scales . . . . 6.
6.   Hemipenis with calcified alary spines, hemipenial lobes and sulcus spermaticus centrifugally oriented, and dorsum uniformly dark brown or black usually lacking spots in preservative . . . . A. alphonsehogei.
-       Hemipenis with alary spines lacking calcification, lobes and sulcus spermaticus centrolinearly oriented, and dorsum with conspicuous white bordered spots in preservative . . . . A. collaris.
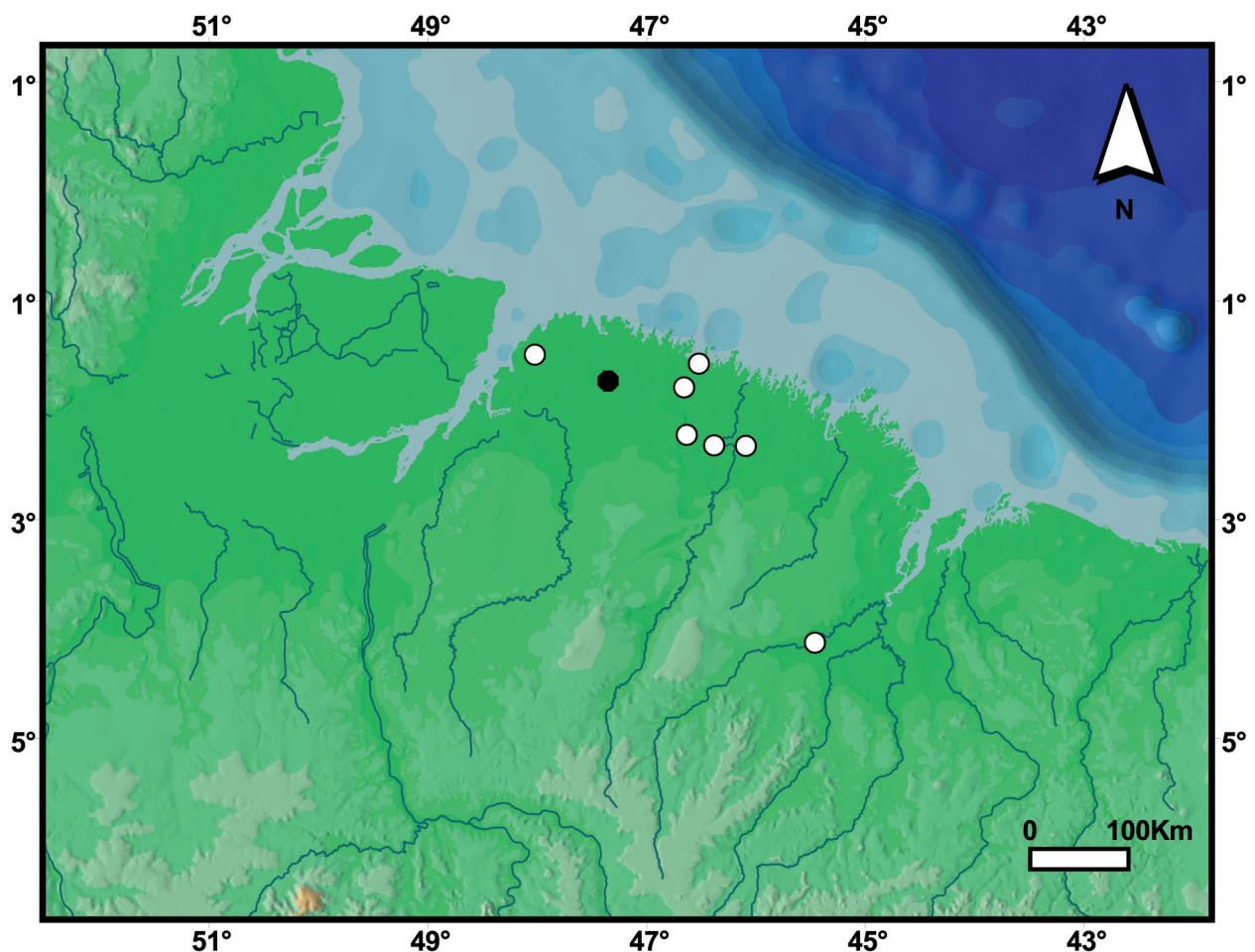

FIGURE 13. Distribution of *Atractus alphonsehogei.* The black circle represents the type-locality.

Discussion

We examined all available types of the *Atractus collaris* complex increased with more than 70 additional specimens from some geographically representative samples across the Amazonia of Brazil, Colombia, Ecuador

and Peru (including all known topotypes for *A. alphonsehogei* and *A. limitaneus*). The results of our qualitative and quantitative (in part) analyses of morphological characters are congruent in support the recognition of three distinct species in this group. Despite the fact that the holotype of *A. collaris* has been apparently lost (Andreaone & Gavetti 2007) and there is no notice of any topotypic material, the quality of original description ensures the association of specimens from Brazil, Colombia, Ecuador and Peru with the former species (but see below). The other two species those here distinguished on the basis of quantitative and qualitative traits have more restricted and allopatric distribution in the western (*A. gaigeae*) and eastern (*A. alphonsehogei*) areas of the Amazonia. In contrast, we failed to find any objective distinction between *A. limitaneus* and *A. collaris*, supporting our decision to synonymize both names, recognizing the priority of the latter.

Dixon & Soini (1977) pointed out that the specimens in the Iquitos region of Peru are variable regarding the occurrence of the vertebral line. They considered the possibility of intergradation between *A. collaris* and *A. gaigeae* in this area and, for that reason, relegated the last taxon as a subspecies of the former. However, it became evident that this interpretation was apparently misguided, since there is no apparent overlap of ventral and subcaudal scales between *A. collaris* and *A. gaigeae.* It is possible that the use of the sum of values from ventral plus subcaudal scales by Dixon & Soini (1977) obscured the differences between each one of the species range. Such usage with sum of segmental counts was relatively common in the past literature for some taxonomic groups of snakes (e.g., Savage 1960), but it generally brings confusion in associating two features with distinct selection regimes (Lindell 1994). Moreover, nearly all (> 90% *n* = 22 sides) females of *A. gaigeae* have one postocular, at least on the one side of the head, in combination with higher scales counts and presence of a conspicuous vertebral line. On the other hand, all specimens from the Iquitos region present lower values of segmental counts within the range of variation of *A. collaris* and the specimens always have two postoculars (*n* = 48 sides). Therefore, our meristic data reinforce our interpretation of the variation regarding the presence/absence of a vertebral stripe as a local instance polychromatism of *A. collaris* in the Iquitos region.

With respect to the occurrence of a vertebral line in other taxa in the *Atractus collaris* species group, we noted that the only other species sharing such a feature is *A. caxiuana* (see fig. 2 in Passos *et al*. 2013b). Nonetheless, the fact that the Colombian records for *A. caxiuana* do not show the vertebral line and also exhibit polymorphism with respect to the contact between internasal and loreal scales may indicate the existence of a putative undescribed species in Colombia. Unfortunately, the geographically limited sample and the absence of male individuals with hemipenis feasible to be prepared and the lack of data from coloration in life of the available specimens precluded a more robust conclusion regarding its taxonomic status. Similarly, the northern (Inírida, Colombia) and southern (Coronel Portillo, Peru) extremes limits of distribution of the *A. collaris* (as defined herein), both displayed higher counts of scales considering the female range of variation (increasing the standard deviation of this variable). Thus, perhaps new geographically representative samples, including material from both sexes, allow the future inference of more robust boundaries among the populations currently attributable to *A. collaris* in the north of Colombia and south Peru.

As a rule, in the *Atractus* taxonomy, employing phenotypic characters based on hemipenial morphology is crucial for the recognition and/or corroboration of many species, both for distinction (Passos 2010b,c) or synonymy (Passos & Prudente 2012; Passos *et al*. 2013b). Hemipenial characters are important especially when other character systems are not available (e.g., coloration in life), display continuous variation overlapping the ranges of putative closely related taxa (e.g., meristics and morphometrics), or show reduced variability in the intraspecific level (e.g., microdermatoglyphics and maxillary dentition). Accordingly, in *A. collaris* complex, some hemipenial features were decisive in corroborating the validity of species also distinguished by other morphological traits. In this particular group, the species *A. alphonsehogei* and *A. gaigeae* have the most similar hemipenial structure, although representing the most geographically distant lineages (Fig. 1). These organs differed in minor aspect of shape (lobes and sulcus spermaticus orientation) and ornamentation (level of development of basal wall of the alary spines), while the organ of *A. collaris* was the most divergent in both aspects (Fig. 10B). Such facts suggest directions for future efforts of sampling and investigation, in which the preparations of more hemipenes from other populations may reveal additional characters helping to distinguish cryptic taxa, as in the case of *A. hoogmoedi* (see Prudente & Passos 2010). Finally, we highlight to the fact of most of the species from *A. collaris* species group, except the former taxon and *A. caxiuana*, display very restricted distributional ranges, encouraging future investigations on the possible existence of additional cryptic lineages under both names.

Acknowledgments

References

Amaral, A. (1935) Estudos sobre ophidios neotropicos. XXXIII. Novas espécies de ophidios da Colômbia *Memórias do Instituto Butantan*, 9, 219–223.

Almeida, P.C., Passos, P., Feitosa, D.T. & Prudente, A.L.C. (2014) Morphological variation and taxonomy of the *Atractus latifrons* (Günther, 1868) (Serpentes: Dipsadidae). *Zootaxa*, 3860 (1), 64–80.
https://doi.org/10.11646/zootaxa.3860.1.3

Andreone, F. & Gavetti, E. (2007) *The life and Herpetological Contribution of Mario Giacinto Peracca 1861-1923.* Facsimile published by Society of Study of Amphibians and Reptiles, Salt Lake City, 570 pp.

Arteaga, A., Mebert, K., Valencia, J.H. Cisneros-Heredia, D., Peñafiel, N., Reyes-Puig, C., Vieira-Fernandes, J.L. & Guayasamin, J.M. (2017) Molecular phylogeny of *Atractus* (Serpentes: Dipsadidae), with emphasis on Ecuadorian species and description of three species. *Zookeys*, 661, 91–123.
https://doi.org/10.3897/zookeys.661.11224

Bocourt, W. (1883) *Mission scientifique au Mexique et dans l'Amérique Centrale. Recherches zoologiques. Troisième partie. Première Section. Études sur les Reptiles.* Imprimeire Nationale, Paris, 1012 pp.

Boulenger, G.A. (1894) *Catalogue of the Snakes in the British Museum (Natural History). Vol. 2.* Trustees of the British Museum, London, 448 pp.

Boulenger, G.A. (1896) *Catalogue of the Snakes in the British Museum (Natural History). Vol. 3.* Trustees of the British Museum, London, 727 pp.

BRAZIL. (2014) *Diário Oficial da União. Sessão 1. Portaria 444.* Available from: http://www.jusbrasil.com.br/diarios/82544531/dou-secao-1-18-12-2014-pg-121 (accessed 20 April 2017)

Carrillo, N.E. & Icochea, J. (1995) Lista taxonómica preliminar de los reptiles vivientes del Perú. *Publicaciones del Museo de Historia Natural de la Universidad Mayor de San Marcos, serie Zoología*, 49, 1–27.

Cisneros-Heredia, D.F. (2005) Rediscovery of the Ecuadorian snake *Atractus dunni* Savage, 1955 (Serpentes: Colubridae). *Řada Přírodovědná*, 174, 87–114.

Cunha, O.R. & Nascimento, F.P. (1983) Ofídios da Amazônia XX—As espécies de *Atractus* Wagler, 1828 na Amazônia oriental e Maranhão. (Ophidia, Colubridae). *Boletim do Museu Paraense Emílio Goeldi*, Nova Série, 123, 1–37.

Cunha, O.R. & Nascimento, F.P. (1984) Ofídios da Amazônia XXI—*Atractus zidoki* no leste do Pará e notas sobre *A. alphonsehogei* e *A. schach.* (Ophidia, Colubridae). *Boletim do Museu Paraense Emílio Goeldi, Zoologia*, 1, 219–228.

de Fraga, R., Almeida, A.P., Moraes, L.J.C.L., Gordo, M., Pirani, R., Zamora, R.R., Carvalho, V.T., Passos, P. & Werneck, F.P. (2017) Narrow endemism or insufficient sampling? Geographic range extension and morphological variation of the poorly known *Atractus riveroi* Roze, 1961 (Serpentes: Dipsadidae). *Herpetological Review*, 48 (2), 281–284.

de Queiroz, K. (1998) The general concept of species, species criteria, and the process of speciation: a conceptual unification and terminological recommendations. *In*: Howard, D. & Berlocher, S.H. (Eds.), *Endless Forms: Species and Speciation.* Oxford University Press, Oxford, pp. 57–75.

Dixon, J.R. & Soini, P. (1977) The reptiles of the upper Amazon basin, Iquitos region, Peru. *Contributions in Biology and Geology of the Milwaukee Public Museum*, 12, 1–91.

Dowling, H.G. (1951) A proposed standard system of counting ventrals in snakes. *British Journal of Herpetology*, 1, 97–99.

Dowling, H.G. & Savage, J.M. (1960) A guide to the snake hemipenis: a survey of basic structure and systematic characters. *Zoologica*, 45, 17–28.

Efron, B. (1979) Bootstrap methods: another look at the Jackknife. *Annals of Statistics*, 7, 1–26.
https://doi.org/10.1214/aos/1176344552

Ferrarezzi, H. (1994) Uma sinopse dos gêneros e classificação das serpentes (Squamata): II família Colubridae. *In*: Nascimento, L.B., Bernardes, A.T. & Cotta, G.A. (Eds.), *Herpetologia no Brasil*. Published by PUC-MG, Fundação Biodiversitas & Fundação Ezequiel Dias, Belo Horizonte, pp. 81–91.

Franco, F.L. (2012) A coleção herpetológica do Instituto Butantan: da sua origem ao incêndio ocorrido em 15 de maio de 2010. *Herpetologia Brasileira*, 1, 22–31.

Gasc, J.P. & Rodrigues, M.T. (1979) Une nouvelle espèce du genre *Atractus* (Colubridae, Serpentes) de la Guyane française. *Bulletin du Muséum national d'Histoire naturelle*, 4 (1), Section A, 545–557.

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

Google (2005) http://www.google.com/about/corporate/company/history.html#2005 (Accessed 20 April 2017)

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

ICZN (International Commission on Zoological Nomenclature) (1999) *International Code of Zoological Nomenclature Adopted by the International Union of Biological Sciences.* International Trust for Zoological Nomenclature, London, 306 pp.

IBGE (Instituto Brasileiro de Geografia e Estatística). (2011) *Índice de Nomes Geográficos, Vol. 1. escala 1:100.000, Base Geográfica Continua do Brasil ao Milionésimo—BCIM*. Ministério do Planejamento, Orçamento & Gestão, Brasília, 388 pp.

Köhler, G. & Kieckbusch, M. (2014) Two new species of *Atractus* from Colombia (Reptilia: Squamata: Dipsadidae). *Zootaxa*, 3872 (3), 291–300.
https://doi.org/10.11646/zootaxa.3872.3.5

Kok, P.J.R., Rivas, G.A.F. & Pauwels, O.S.G. (2007) The taxonomic status of the Venezuelan snake *Atractus matthewi* and *A. nororientalis* (Serpentes, Colubridae). *Zootaxa*, 1493, 66–68.

Kumar, A. (2010) A tragic loss: fire at Instituto Butantan, Brazil. *Toxicon*, 1528–1529.
https://doi.org/10.1016/j.toxicon.2010.07.002

Lehr, E. (2002) *Amphibien und Reptilien in Peru*. NTV Wissenschaft Publisher, Münster, 206 pp.

Lindell, L.E. (1994) The evolution of vertebral number and body size in snakes. *Functional Ecology*, 8, 708–719.
https://doi.org/10.2307/2390230

Manly, B.F.J. (2005) *Multivariate Statistical Methods: A Primer*. Chapman & Hall/CRC Press, Boca Raton, 224 pp.

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

MathWorks, Inc. (1994) *Matlab for Windows Versio*n *4.2c1.* The MathWorks, Texas Tech University, Abilene. [software]

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

Passos, P. & Arredondo, J.C. (2009) Rediscovery and redescription of the Andean earth-snake *Atractus wagleri* (Reptilia: Serpentes: Colubridae). *Zootaxa*, 1969, 59–68.

Passos, P. & Fernandes, R. (2008) A new species of the colubrid snake genus *Atractus* (Reptilia: Serpentes) from the central Amazon of Brazil. *Zootaxa*, 1849, 59–66.

Passos, P. & Fernandes, R. (2009) 2008 Revision of the *Epicrates cenchria* complex (Serpentes: Boidae). *Herpetological Monographs,* 22, 1–30.
https://doi.org/10.1655/06-003.1

Passos, P. & Lynch, J.D. (2011) 2010 Revision of *Atractus* from upper and middle Magdalena drainage of Colombia. *Herpetological Monographs*, 24, 149–173. https://doi.org/10.1655/09-041.1

Passos, P. & Prudente, A.L.C. (2012) Morphological variation, polymorphism and taxonomy of the *Atractus torquatus* complex (Serpentes: Dipsadidae). *Zootaxa*, 3407, 1–21.

Passos P., Fernandes, R. & Zanella N. (2005) A new species of *Atractus* (Serpentes: Colubridae) from Southern Brazil. *Herpetologica*, 61, 209–218.
https://doi.org/10.1655/03-91

Passos, P., Cisneros-Heredia, D.F. & Salazar-V., D. (2007a) Rediscovery and redescription of the rare Andean snake *Atractus modestus*. *Herpetological Journal*, 17, 1–6.

Passos, P., Fernandes, D.S. & Borges-Nojosa, D.M. (2007b) A new species of *Atractus* (Serpentes: Dipsadinae) from a relictual forest in Northeasten Brazil. *Copeia*, 2007, 788–797.
https://doi.org/10.1643/0045-8511(2007)7[788:ANSOAS]2.0.CO;2

Passos, P., Aguayo, R. & Scrocchi, G. (2009a) Rediscovery of the rare *Atractus bocki*, with assessment of the taxonomic status of *A. canedii* (Serpentes: Colubridae: Dipsadidae). *Journal of Herpetology*, 43, 710–715.
https://doi.org/10.1670/08-209.1

Passos, P., Arredondo, J.C., Fernandes, R. & Lynch, J.D. (2009b) Three new *Atractus* (Serpentes: Dipsadidae) from Andes of Colombia. *Copeia*, 2009, 425–438.
https://doi.org/10.1643/CH-08-063

Passos, P., Fuenmayor, G.R. & Barrio-Amorós, C. (2009c) Description of two new species from Venezuela in the highly diverse dipsadine genus *Atractus* (Serpentes: Colubridae). *Amphibia-Reptilia*, 30, 233–243.
https://doi.org/10.1163/156853809788201199

Passos, P., Lynch, J.D. & Fernandes, R. (2009d) 2008 Taxonomic status of *Atractus sanctaemartae* and *A. nebularis*, and description of a new species of *Atractus* from Atlantic coast of Colombia. *Herpetological Journal*, 18, 175–186.

Passos, P., Mueses-Cisneros, J.J., Lynch, J.D. & Fernandes, R. (2009e) Pacific lowland snakes of the genus *Atractus* (Reptilia: Serpentes: Dipsadidae), with descriptions of three new species. *Zootaxa*, 2293, 1–34.

Passos, P., Dobiey, M. & Venegas, P.J. (2010a) Variation and natural history notes on giant groundsnakes, *Atractus gigas* (Serpentes: Dipsadidae). *South American Journal of Hepetology*, 5, 73–82.
https://doi.org/10.2994/057.005.0201

Passos, P., Chiesse, A., Torres-Carvajal, O. & Savage, J.M. (2010b) 2009. Testing species boundaries within *Atractus occipitoalbus* complex (Serpentes: Colubridae: Dipsadinae). *Herpetologica*, 65, 384–403.
https://doi.org/10.1655/08-024.1

Passos, P., Fernandes, R., Bérnils, R.S. & Moura-Leite, J.C. (2010c) Taxonomic revision of Atlantic Forest *Atractus* (Serpentes: Dipsadidae). *Zootaxa*, 2364, 1–63.

Passos, P., Cisneros-Heredia, D.F., Rivera, D., Aguilar, C. & Schargel, W.E. (2012) Rediscovery of *Atractus microrhynchus* and reappraisal of the taxonomic status of *A. emersoni* and *A. natans* (Serpentes: Dipsadidae). *Herpetologica*, 68, 375–392.
https://doi.org/10.1655/HERPETOLOGICA-D-11-00078.1

Passos, P., Echevarría, L.Y. & Venegas, P.J. (2013a) Morphological variation of *Atractus carrioni* (Serpentes: Dipsadidae). *South American Journal of Herpetology*, 8, 109–120.
https://doi.org/10.2994/SAJH-D-12-00025.1

Passos, P., Kok, P.J.R., Albuquerque, N.R. & Rivas, G. (2013b) Groundsnakes of the Lost World: a review of *Atractus* (Serpentes: Dipsadidae) from the Pantepui region, northern South America. *Herpetological Monographs*, 27, 52–86.
https://doi.org/10.1655/HERPMONOGRAPHS-D-12-00001R2.1

Passos, P., Ramos, L.O., Pinna, P.H. & Prudente, A.L.C. (2013c). Morphological variation and putative phylogenetic affinities of the poorly known snake *Atractus caxiuana* (Serpentes: Dipsadidae). *Zootaxa*, 3745 (1), 35–48.
https://doi.org/10.11646/zootaxa.3745.1.3

Passos, P., Teixeira-Junior, M., Recoder, R.S., De Sena, M.A., Dal Vechio, F., Pinto, H.B.A., Mendonça, S.H.S.T., Cassimiro, J. & Rodrigues, M.T. (2013d) A new species of *Atractus* (Serpentes: Dipsadidae) from Serra do Cipó, Espinhaço range, Southeastern Brazil, with proposition of a new species group to the genus. *Papéis Avulsos de Zoologia*, 53, 75–85.
https://doi.org/10.1590/S0031-10492013000600001

Passos, P., Martins, A. & Pinto-Coelho, D. (2016a) Population morphological variation and natural history of *Atractus potschi* (Serpentes: Dipsadidae) in Northeastern Brazil. *South American Journal of Herpetology*, 11, 188–211.
https://doi.org/10.2994/SAJH-D-16-00034.1

Passos, P., Prudente, A.L.C. & Lynch, J.D. (2016b) Redescription of *Atractus punctiventris* and description of two new *Atractus* (Serpentes: Dipsadidae) from Brazilian Amazonia. *Herpetological Monographs*, 30, 1–20.
https://doi.org/10.1655/HERPMONOGRAPHS-D-14-00009

Passos, P., Ramos, L.O., Fouquet, A. & Prudente, A.L.C. (2017) Taxonomy, morphology, and distribution of *Atractus flammigerus* Boie 1827 (Serpentes: Dipsadidae). *Herpetologica*, 73 (4), 349–363.
https://doi.org//10.1655/Herpetologica-D-16-00086

Paynter, R.A. Jr. (1993) *Ornithological Gazetteer of Ecuador. Second Edition*. Bird Department, Museum of Comparative Zoology, Harvard University, Cambridge, 247 pp.
https://doi.org/10.5962/bhl.title.14626

Paynter, R.A. Jr. (1997) *Ornithological Gazetteer of Colombia. 2nd Edition*. Bird Department, Museum of Comparative Zoology, Harvard University, Cambridge, 537 pp.
https://doi.org/10.5962/bhl.title.14638

Paynter, R.A. Jr. & Traylor, M.A. Jr. (1991) *Ornithological Gazetteer of Brazil. 2 Vols*. Bird Department, Museum of Comparative Zoology, Harvard University, Cambridge, 788 pp.

Peracca, M.G. (1897) Intorno ad una piccolo raccolta di rettili di Conocacco (Peru Orientale). *Bollettino dei Musei di Zoologia e Anatomia Comparata Della Universita di Torino*, 12 (284), 1–7.

Pesantes, O. (1994) A method for preparing hemipenis of preserved snakes. *Journal of Herpetology*, 28, 93–95.
https://doi.org/10.2307/1564686

Peters, J.A. (1964) *Dictionary of Herpetology*. Hafner Publishing, New York, 426 pp.

Price, R.M. (1982) Dorsal snake scale microdermatoglyphics: ecological indicator or taxonomic tool? *Journal of Herpetology*, 16, 294–306.
https://doi.org/10.2307/1563721

Price, R.M. & Kelly, P. (1989) Microdermatoglyphics: basal patterns and transition zones. *Journal of Herpetology*, 23, 244–261.
https://doi.org/10.2307/1564446

Prudente, A.L.C. & Passos, P. (2008) New species of *Atractus* Wagler, 1828 (Serpentes: Dipsadinae) from Guyana Plateau in Northern Brazil. *Journal of Herpetology*, 42, 723–732.

https://doi.org/10.1670/07-115R3.1

Prudente, A.L.C. & Passos, P. (2010) New cryptic species of *Atractus* (Serpentes: Dipsadidae) from Brazilian Amazonia. *Copeia*, 2010, 397–404.
https://doi.org/10.1643/CH-08-193

Prudente, A.L.C. & Santos-Costa, M.C. (2006) A new species of *Atractus* Wagler, 1828 (Serpentes: Colubridae) from eastern Amazonia, Brazil. *Zootaxa*, 1285, 21–29.

Sabaj Pérez, M.H. (Ed.) (2016) Standard symbolic codes for institutional resource collections in herpetology and ichthyology: An online reference. Version 6.5. American Society of Ichthyologists and Herpetologists, USA. Available from: http://www.asih.org/resources (accessed 3 November 2016)

Salazar-Valenzuela D., Torres-Carvajal, O. & Passos, P. (2014) A new species of *Atractus* (Serpentes: Dipsadidae) from Andes of Ecuador. *Herpetologica*, 70, 350–373.
https://doi.org/10.1655/HERPETOLOGICA-D-13-00045

Savage, J.M. (1955) Descriptions of new colubrid snakes, genus *Atractus*, from Ecuador. *Proceedings of The Biological Society of Washington*, 68, 11–20.

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

Schargel, W.E., Lamar, W.W., Passos, P., Valencia, J.H., Cisneros-Heredia, D.F. & Campbell, J.A. (2013) A new giant *Atractus* (Serpentes: Dipsadidae) from Ecuador, with notes on some other large Amazonian congeners. *Zootaxa*, 3721 (5), 455–474.
https://doi.org/10.11646/zootaxa.3721.5.2

Silva, J.J.H. (2004) Las serpientes del género *Atractus* Wagler, 1828 (Colubridae, Xenodontinae) en la Amazonia Colombiana. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales*, 28 (108), 409–446.

Statisoft INC. (1995) Statistica for Windows Version 5.1. StatSoft Tulsa. [software]

Stephens, L. & Traylor, M.A. Jr. (1983) *Ornithological Gazetteer of Peru*. Bird Department, Museum of Comparative Zoology, Harvard University, Cambridge, 271 pp.

Stephens, L. & Traylor, M.A. Jr. (1985) *Ornithological Gazetteer of the Guianas*. Bird Department, Museum of Comparative Zoology, Harvard University, Cambridge, 121 pp.

Uzzell, T. (1973) A revision of lizards of the genus *Prionodactylus*, with a new genus for *P. leucostictus* and notes on the genus *Euspondylus* (Sauria, Teiidae). *Postilla*, 159, 1–67.
https://doi.org/10.5962/bhl.part.11535

Vanegas-Guerrero, J., Matilla-Castaño, J.C. & Passos, P. (2014) *Atractus titanicus* Passos, Arredondo, Fernandes & Lynch, 2009: filling gaps in its geographical distribution. *Check List*, 10, 672–673.
https://doi.org/10.15560/10.3.672

Wallach, V., Williams, K.L. & Boundy, J. (2014) *Snakes of the World: A Catalog of Living and Extinct Species*. CRC Press, Boca Raton, 1227 pp.
https://doi.org/10.1201/b16901

Warrell, D.A., Theakston, R.D.G. & Wüster, W. (2010) Destruction of the collection of reptiles and arthropods at Butantan Institute: a view from the United Kingdom. *The Journal of Venomous Animals and Toxins including Tropical Diseases*, 16, 534–536.
https://doi.org/10.1590/S1678-91992010000400003

Wiens, J.J. & Servedio, M.R. (2000) Species delimitation in systematics: inferring diagnostic differences between species. *Proceedings of the Royal Society of London, Biological Sciences*, 267, 631–636.
https://doi.org/10.1098/rspb.2000.1049

Zaher, H. (1999) Hemipenial morphology of the South American Xenodontine snakes, with a proposal for a monophyletic Xenodontinae and a reappraisal of Colubroid hemipenes. *Bulletin of the American Museum of Natural History*, 240, 1–168.

Zar J.H. (1999) *Biostatistical Analysis*. 4th Edition. Prentice Hall Press, New Jersey, 123 pp.

Appendix

Material examined

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

Atractus caxiuana (*n* = 7). **BRAZIL:** PARÁ: *Melgaço*: Floresta Nacional de Caxiuanã: (MPEG 19657 holotype, MPEG 19964, 20128 paratypes); RONDÔNIA: *Porto Velho*: right bank of the Madeira River: (MZUSP 18892), Vila Cachoeira do Samuel: (MNRJ 3026*). **COLOMBIA:** VAUPÉS: *Taraira*: Caparú: (ICN 10114–15).

Atractus alphonsehogei (*n* = 16). **BRAZIL:** MARANHÃO: *Junco do Maranhão*: Nova Vida: BR-316 Highway, 25 Km before Gurupi River: (MPEG 11145*, paratype), *Santa Inês*: São Raimundo, 8 Km from Santa Inês: (MPEG 10874*, paratype); PARÁ: *Augusto Correia*: Fazenda Cacoal: Arari road: ramal of the PA-242 road, 27 Km from Bragança: (MPEG 9949, paratype), *Bragança*: PA-242 11 Km from Bragança: Parada Bom Jesus: (MPEG 8573, 8667, paratypes), Km 224 from BR-316 Highway: (MPEG 10093, paratype), *Colônia Nova*: Km 264 from BR-316 Highway, near Gurupi River: (MZUSP 8378 [formerly MPEG 10130], MPEG 2976, 6408, 10129–30, 10132, paratypes), *Santa Rosa*: PA-140: Vigia road: (MPEG 12593 paratype), *Santo Antônio do Tauá*: PA-140: Vigia road: (MPEG 2221, paratype), *Viseu*: (MPEG 13907–08), Bela Vista: Km 75 of the PA-242 in the *Bragança–Viseu* road: (MPEG 14928, holotype).

Atractus collaris (*n* = 35). **BRAZIL:** AMAZONAS: *Presidente Figueiredo*: (MPEG 17545), headwaters of the Urucú River: (MZUSP 10527). **COLOMBIA:** without specific locality: (ICN 9034); AMAZONAS: *La Pedrera*: (IBSP 9196, holotype of *Leptocalamus limitaneus*; ICN 10112–13); CAQUETÁ: *Florencia*: (MLS 1324, 2782, UAM 170–173, 326–27); GUAINÍA: *Inírida*: Caño Vitina Village: (SINCHI-R 252); VAUPÉS: *Mitú*: Bellavista: (SINCHI-R 120), *Taraira*: Caparú Biological Station (ICN 8144, 9034). **ECUADOR:** MORONA SANTIAGO: *Taisha*: Makuma: Centro Shuar Amazonas: (FHGO 4505); NAPO: *Tena:* Chontapunta: Sumak Sacha Village: (QCAZ 7318, 7372); ORELLANA: *Aguarico:* Tibetano: Záparo oil patform: (EPN 10663), Joya de los Sachas: (DHMECN 4984), Yasuni National Park: PUCE Scientific Station: (QCAZ 4044, 5220, 5980, 10837, 10840); SUCUMBÍOS: *Cuyabeno*: Laguna Grande Scientific Station: (MNRJ 24959*, QCAZ 1042); *Nueva Loja*: Lago Agrio: Zábalo oil platform: (EPN 5216), Santa Elena: Dureno: (DHMECN 7817), *Putumayo*: Sansahuari: Singe oil platform: (DHMECN 12837). **PERU:** without specific provenance data: (MUSM 2912); LORETO: *Iquitos*: Maynas: (MUSM 2310); UCAYALI: *Coronel Portillo*: Pucallpa: (MUSM 3083).

Atractus gaigeae (*n* = 29). **ECUADOR:** MORONA SANTIAGO: *Taisha*: Makuma: Centro Shuar Amazonas: (FHGO 4767, 4493, 5567), Centro Shuar Achunts: (FHGO 3969), Centro Shuar Kiim: (FHGO 9831), Centro Shuar Makuma: (FHGO 4463, 5615); NAPO: Jatun Sacha Biological Station: (EPN not catalogued, QCAZ 9832), *Loreto*: (USNM 217621), upper Napo River: (USNM 217622), mouth of the Coca River: (USNM 217623), *Tena*: Ahuano: (DHMECN 3865); ORELLANA: Dicapare Village, oil platform Armadillo: (QCAZ 14144), Yasuní National Park: Pindo, near Tuputini River: (QCAZ 7273); PASTAZA: *Arajuno*: San Elena: (FHGO 8622), Bobonaza River: (EPN 5217), Conambo River: mouth of the Romarizo River: (USNM 217624), mouth of the Shione River: (USNM 217625), Cotopaza: Bobonaza River: (EPN 8693, paratype), Misión: (EPN 752), Rutuno River: tributary of the Bobonaza River: (USNM 217626), *Montalvo*: (USNM 217627), 40Km NE *Montalvo*: (QCAZ 7500), Villano: AGIP oil platform: (QCAZ 8155, 8403), Villano: Tarangaro Village: (QCAZ 8339); SUCUMBÍOS: *Cuyabeno*: Tarapoa: Peñacocha: (FHGO 6374), *Nueva Loja*: Lago Agrio, Santa Elena: Dureno: (DHMECN 7817).

Atractus hoogmoedi (*n* = 3). **BRAZIL:** PAR: *Capitão Poço*: (MPEG 13265–66 paratypes, MPEG 13268*, holotype).

Atractus surucucu (*n* = 3). **BRAZIL:** RORAIMA: *Serra do Surucucu*: (MPEG 18436–37 paratypes, MPEG 19146, holotype)

Atractus zidoki (*n* = 7). **BRAZIL:** AMAPÁ: *Serra do Navio*: (IBSP 24772, 77393, MPEG 16437, MPEG 23227, MZUSP 2840). **FRENCH GUIANA:** without specific provenance data: (MZUSP not catalogued).