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A new giant *Atractus* (Serpentes: Dipsadidae) from Ecuador, with notes on some other large Amazonian congeners

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Abstract

We describe a new species of *Atractus* from Cordillera de los Guacamayos in the Andes of Ecuador. This new species is the largest known species of *Atractus*, reaching almost 120 cm in total length with a robust habitus. We also use multivariate statistical analyses of morphometric data to look into the taxonomic confusion involving other large, banded/blotched, species of *Atractus* in Western Amazonia. We show that *A. snethlageae* has a widespread distribution in Amazonia and has been repeatedly confused with *A. major* in Ecuador owing to its color polymorphism. Our multivariate statistical analyses support previous suggestions to recognize *A. snethlageae* as a distinct species relative to *A. flammigerus*. Taxonomic accounts are provided for both *A. major* and *A. snethlageae* including detailed color pattern descriptions. We also find that there are no valid morphological differences to support recognizing *A. arangoi* as a separate species from *A. major*; consequently we synonymize the former name with the latter.

Key words: Atractus major, Atractus snethlageae, Atractus touzeti, Cordillera de Los Guacamayos, rainforest, reptiles, snakes

Introduction

The genus *Atractus* consists of generally small, semi-fossorial or cryptozoic snakes that feed mostly on earthworms and other small invertebrates (Martins & Oliveira 1993, 1999). The genus is distributed from central Panama (Myers 2003) to northeastern Argentina (Giraudo & Scrocchi 2000); ranging across a wide variety of habitats from lowland rainforest and Neotropical savannas to cloud forest and páramos in the Andes and even inhabiting the summits of some tepuis (the table-top mountains in the Guayana Region). Currently more than 130 species are recognized in *Atractus* (Passos et al. 2012), which makes it the most species-rich genus of snakes in the world. The taxonomy of this genus, however, remains in a confused state especially in regard to species boundaries. Several factors have made taxonomic studies of *Atractus* a difficult task. The main problem seems to be the scarcity of specimens in collections, which may reflect the difficulty of collecting these snakes because of their secretive habits (Downs 1967; Myers 2003). Consequently, many species of *Atractus* are known from only a few specimens. To complicate matters, the original descriptions of many of the species in this genus are basic and lack a proper diagnosis. Regrettably, most of the work done so far to expand our knowledge on the variation of these species covers only a fraction of the genus.

The first modern taxonomic review of Atractus was undertaken by Savage (1960) for Ecuador. This work

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remains one of the most important contributions to the taxonomy of the genus. Savage (1960) described the variation for the 16 species that were known in Ecuador; he also proposed three putatively monophyletic groups within the genus and provided an account of all the names (including synonyms) that were available at the time. Subsequently, other reviews have been published for Venezuela (Roze 1961), Suriname (Hoogmoed 1980), Panama (Myers 2003), northeastern Argentina (Giraudo & Scrocchi 2000) and particular regions of Brazil (Cunha & Nascimento 1983; Martins & Oliveira 1993; Passos et al. 2010c) and Colombia (Silva Haad 2004; Passos et al. 2009b; Passos & Lynch 2011). The fact that many of these reviews have been restricted to politically defined areas (e.g. country, state), which in some cases are relatively small, has posed limitations to the definition of species boundaries, especially in widespread species complexes (e.g. Amazon species of *Atractus*). Therefore, a complete taxonomic review of *Atractus* is still warranted.

Although the great majority of species of *Atractus* are quite small, rarely exceeding 40 cm, a few have been found that approximate or even exceed one meter in total length (e.g. *A. gigas, A. obesus* and *A. trihedrurus*). These so called "giant" *Atractus* tend to also have a robust habitus and in some cases are known from only a handful of specimens. In this study we report on yet another giant species of *Atractus* known from specimens collected in the Cordillera de los Guacamayos in Ecuador. This species, although extremely large in size relative to other *Atractus*, has a color pattern (brown background with transverse bands) and scalation similar to other relatively large species of *Atractus* that have been found in cis-Andean Ecuador as well as other regions of Amazonia. Several species names have been used to refer to these species in Western Amazonia, including *A. badius*, *A. flammigerus*, *A. major* and *A. snethlageae*. While examining specimens and the literature concerning these other species we realized that much confusion still persists about their taxonomy. In this study we use statistical analyses of morphological data to clarify the confusion regarding these species, as well as to provide support for the new giant species of *Atractus*.

Material and methods

Although we have collectively examined a vast number of specimens of *Atractus*, belonging to many different species, we list in the appendix only those specimens that were used for the purpose of statistical analyses and/or for documenting morphological variation reported in the species accounts. These specimens are deposited in the following collections: UNITED STATES: American Museum of Natural History (AMNH); California Academy of Sciences (CAS); Carnegie Museum of Natural History (CM); Field Museum of Natural History (FMNH); Florida Museum of Natural History (UF); Louisiana Museum of Natural History (LSUMZ); Museum of Comparative Zoology (MCZ), Museum of Vertebrate Zoology (MVZ); Natural History Museum of Los Angeles County (LACM); National Museum of Natural History (USNM); Museum of Zoology University of Michigan (UMMZ); University of Kansas (KU); The University of Texas at Arlington (UTA); Texas Cooperative Wildlife Collection (TCWC). COLOMBIA: Museo de Historia Natural, Universidad de La Salle (MLS), Bogotá D.C. VENEZUELA: Colección de Vertebrados de la Universidad de Los Andes (CVULA), Mérida; Museo de Ciencias Naturales de Guanare (MCNG), Guanare. ECUADOR: Fundación Herpetológica Gustavo Orcés (FHGO); Museo de Zoología, Pontificia Universidad Católica del Ecuador (QCAZ), Museo Ecuatoriano de Ciencias Naturales (MECN). NETHERLANDS: National Natuurhistorisch Museum in Leiden (RMNH).

For the purpose of statistical analysis we recorded for each specimen data for 18 quantitative external morphology variables, which included the following body and head plate measurements (abbreviations in parenthesis): Total length (TL), head length (HL), head width (HW), frontal length (FL), frontal width (FW), prefrontal suture length (PREFS), loreal length (LORL), loreal height (LORH), parietal length (PARL), parietal width (PARW), rostral height (ROSTH), rostral width (ROSTW), Internasal width (INW), internasal suture (INS), chinshield length (CHINL), eye diameter (EYED), eye-nostril distance (EYENOS) and supraocular length (SUPRAOC). Total length was measured to the nearest millimeter by stretching the specimens along a metric ruler. All other measurements were taken with a dial caliper to the nearest 0.1 millimeter and with the aid of a dissecting scope. Paired head plates were all measured only on the right side. Morphological differentiation between operational taxonomic units was examined by conducting principal component analyses (PCA) using the correlation matrix of the data. PCA has the advantage over other statistical techniques in that it condenses the information contained in a large number of original variables into a smaller set of new composite dimensions,

while making no *a priori* assumptions about groupings in the data (McGarigal et al. 2000). The results of the PCA were examined by making scatterplots using the principal components (PC) recovered and grouping the specimens' values by other putatively diagnostic characters (e.g. coloration) not included in the data matrix. Many, possibly all, species of *Atractus* are sexually dimorphic in relative tail size and segmental counts (ventral and subcaudal scales) examined separately. However, there seems to be little or no sexual dimorphism in the total segmental count (the sum of ventral and subcaudal scales), which might indicate that the sexual difference in relative tail size is mostly accounted by the position of the vent on the body instead of a difference in tail size relative to all other measurements. Based on this observation we decided to use TL instead of having snout-vent length (SVL) and tail length as two separate measurements in the analyses. The purpose of doing so was to reduce the effect of sexual dimorphism while maximizing sample size by combining males and females together in the statistical analyses. To assess whether this was a valid decision we examined grouping specimens within species by sex when plotting the principal components in analyses in which TL was used versus SVL and tail length. As suspected, gender did not have an obvious effect in the analyses (i.e. males and females did not separate in multivariate space) whenever TL was used, whereas separation by gender was observed whenever SVL and tail length were included together. All statistical analyses were performed on SYSTAT 11 (SPSS Inc.).

Results

The banded Atractus species confusion in the Amazonian Andean slopes. The first analysis was to evaluate the identity of the species involved in what previous authors have referred to A. badius, A. flammigerus, A. major and A. snethlageae in the upper Amazon Basin. Three distinctive color pattern types (Fig. 1) were observed on specimens for which these four names have been applied in the literature. The typical A. major color pattern type (I) is a pale to medium brown dorsum with dark brown blotches or bands edged by pale coloration, and agrees with the pattern stated by Boulenger (1894) when he described the species, as well as with patterns A and B and perhaps also C defined by Savage (1960) for A. major. Specimens with this color pattern type have also been called A. badius at least one time relatively recently in the literature (see remarks under A. major). In the second color pattern type (II) the dorsum is dark brown or dark grey with pale (cream or buff in preservative) bands usually edged by black, and it agrees with pattern D described by Savage (1960) for A. major. The names A. badius and A. flammigerus have also been applied to specimens with this color pattern in Peru (see species account for A. snethlageae). Passos et al. (2010b) also indicated that Savage (1960) included specimens of A. gigas under the pattern D of A. major. In the third color pattern (III) the dorsum is pale brown to buff with dark brown blotches not edged by pale coloration, and it seems to agree with pattern E, and maybe also C, described by Savage (1960) for A. major as well as with the picture provided by Duellman (1978) for A. major. A PCA of specimens with these three color patterns shows that the first two principal components explained 81.9% and 6.1% of the variance in the sample, respectively. Because all other components explained independently very little of the variance (<3%) and did not seem to discriminate between groups, we present results only on the first two components. A scatterplot with the factor scores for the first two PCs is shown in Figure 2 and the component loadings are shown on Table 1. The scatterplot shows that specimens with color patterns II and III widely overlap in multivariate space but specimens with color pattern I form a well-defined cluster that barely overlaps with specimens of the other two color patterns. Separation of specimens with color pattern I from those with color patterns II and III occurs mostly along the second principal component axis, with EYED and SUPRAOC being the two variables that had the higher loadings on PC2. The first principal component does not seem to contribute to the separation observed. However, when using morphometric data in a PCA the first principal component is generally considered a "size factor" (Humphries et al. 1981). A plot of TL against the first principal component scores shows that there is indeed a strong linear relationship between size and the first principal component. Therefore, the differences observed in the confidence ellipses of color pattern B and C can be mostly explained by the fact that the three largest specimens between these two groups have color pattern C. In addition to the results of the PCA it was noted that specimens with color pattern I always have three infralabials in contact with the chinshields on each side whereas specimens with color pattern II and III always have four. These observations suggest that two species are involved, one of which is A. major and clearly corresponds with color pattern I.



FIGURE 1. Specimens of large banded/blotched *Atractus* from the Amazon Basin grouped into three color pattern types (I: top row, II: middle, III: bottom). Extremes of variation within each color pattern type are shown.

TABLE 1. Component loadings for the first two principal components of a multivariate analysis that included specimens of *Atractus* grouped into three different color patterns.

Variable	PC1	PC2
TL	0.946	-0.064
HL	0.983	-0.096
HW	0.919	0.001
FL	0.903	-0.282
FW	0.947	0.174
PREFS	0.963	0.010
PARL	0.965	0.021
PARW	0.944	0.018
LORL	0.965	0.109
LORH	0.769	0.528
ROSTH	0.901	0.063
ROSTW	0.935	0.067
INS	0.780	0.129
INW	0.914	0.011
CHINL	0.892	0.269
EYED	0.736	-0.528
EYENOS	0.978	0.040
SUPRAOC	0.790	-0.548

TABLE 2. Component loadings for the first two principal components of a multivariate analysis that included specimens of *Atractus badius*, *A. flammigerus* and *A. snethlageae*.

Variable	PC1	PC2
TL	0.946	0.141
FL	0.927	-0.105
FW	0.923	0.309
PARL	0.955	0.206
LORH	0.908	0.188
ROSTW	0.933	0.135
INS	0.888	-0.240
CHINL	0.964	0.170
EYED	0.855	-0.351
SUPRAOC	0.726	-0.639

The species represented by color patterns II and III is assigned in this work to A. snethlageae because it agrees well with this species in aspects of coloration (pattern II agrees with the description of the holotype of A. snethlageae) and meristics. However, the status of A. snethlageae itself has to be reassessed owing to its nomenclatural history. This taxon was first proposed by Cunha & Nascimento (1983) as a subspecies of A. flammigerus, in a description based on specimens from Pará, northeastern Brazil. Only three years before the description of A. snethlageae, Hoogmoed (1980) resurrected A. flammigerus, which at the time was considered a synonym of A. badius. Hoogmoed's definition of A. flammigerus included specimens from the Guiana Shield (A. flammigerus sensu stricto) as well as from Peru (herein A. snethlageae). Vanzolini (1986) elevated A. snethlageae to full species status but without providing a justification for this decision. Subsequent to these works, the names A. badius and A. flammigerus have been applied (see species account for A. snethlageae) in western Amazonia to

what we herein consider to be *A. snethlageae*. In light of this confusion we decided to conduct a PCA (Table 2) of the morphometric dataset comparing the specimens we refer to *A. snethlageae* with specimens of both *A. badius* and *A. flammigerus* (sensu stricto). Because of the concern of having a small number of specimens relative to the number of variables included, we reduced to original dataset to only ten variables following the same procedure as in the previous analysis. A scatterplot (Fig. 2) of the first two PC (which explain 81.9% and 8.4% of the variance, respectively) shows that the specimens of *A. snethlageae* do not overlap in multivariate space with either *A. badius* or the two specimens examined of *A. flammigerus* sensu stricto. These results further support Vanzolini's (1986) decision to elevate *A. snethlageae* to full species status. Other aspects of morphology that distinguish *A. snethlageae* from *A. flammigerus* are discussed under the account for the former species.

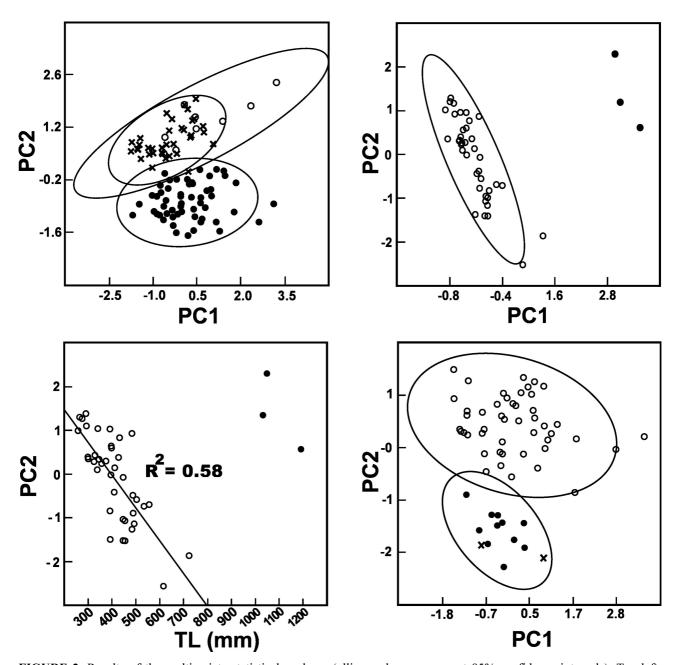


FIGURE 2. Results of the multivariate statistical analyses (ellipses always represent 95% confidence intervals). Top left: Scatterplot of the first two PC of an analysis grouping specimens into color patterns types I (solid dots), II (Xs), and III (open dots). Top right: Scatterplot of the first two PC of an analysis including specimens of *A. snethlageae* (open dots) and *A. touzeti* (solid dots). Bottom left: scatterplot of TL vs. PC2 in specimens of *A. snethlageae* (open dots) and *A. touzeti* (solid dots); fitted straight line and squared correlation coefficient are for the first species. Bottom right: Scatterplot of the first two PC of an analysis including specimens of *A. badius* (solid dots), *A. flammigerus* (Xs), and *A. snethlageae* (open dots).

Taxonomic evaluation of a new giant *Atractus*. The new giant species of *Atractus* is known from only three large (>1000 mm in TL) and robust specimens collected from cloud forests (>2000 m) in the Cordillera de los Guacamayos in Ecuador. The largest specimen in this small series is 1195 mm in TL and represents a size record for Atractus. The size and robustness of this species is only paralleled by Atractus serranus and A. trihedrurus from Atlantic Rainforest of southeastern Brazil (see Passos et al. 2010c), and Atractus gigas (Myers & Schargel 2006; Passos et al. 2010b) from western Ecuador, which was until now the largest species of *Atractus*, exceeding 1000 mm in SVL.Because the new giant species is most similar in coloration to A. snethlageae, which occurs in close geographic proximity but at lower elevations, we made an exhaustive comparison between these two species. A PCA (Table 3) of the new giant species and A. snethlageae shows that the first two PC explain 95.9% and 2.0% of the variance, respectively. A scatterplot of the first two PC (Fig. 2) shows that the two species included in the analysis have a large separation in the first PC. However, this was expected because, as mentioned before, the first PC is highly correlated with size. The difference in size between the two species is quite obvious considering that the largest specimen of A. snethlageae is 718 mm in TL, but only four of all the specimens examined and reported in the literature (n= 85; Cunha & Nascimento 1983; Martins & Oliveira, 1993) exceed 500 mm, whereas all three specimens of the new species exceed 1000 mm in TL. In terms of the second PC there is overlap in factor scores between the two species yet there seem to be allometric differences between them. For A. snethlageae there is a strong inverse relationship between the first (a size factor) and second PC, that is, factor scores in the second PC have the tendency to become smaller as individuals get larger. Although it is not known whether this allometric relationship is also characteristic of the new species, the three specimens in the analysis have factor scores on the second PC that are comparable to small specimens of A. snethlageae (Fig. 2). We believe this is strong evidence supporting the distinctiveness of the new species relative to A. snethlageae; that is, if the specimens of the new species were just very large individuals of A. snethlageae we would have expected them to have small factor scores on the second PC consistent with the allometric relationship found in A. snethlageae.

TABLE 3. Component loadings for the first two principal components of a multivariate analysis that included specimens of *A. snethlageae* and *A. touzeti* **sp. nov.**

Variable	PC1	PC2	
TL	0.990	0.008	
HW	0.979	0.132	
FL	0.975	0.176	
PREFS	0.964	-0.233	
PARW	0.987	0.110	
LORL	0.980	-0.165	
LORH	0.970	-0.105	
INW	0.989	0.065	
EYENOS	0.984	-0.139	
SUPRAOC	0.970	0.148	

The two species also differ in other morphological aspects. The new species has a proportionally much wider head (HW/HL= 97–112%) than *A. snethlageae* (HW/HL= 55–89%). In the new species the frontal scale is always longer than wide (FL/FW = 1.01–1.17) whereas in *A. snethlageae* the frontal scale is usually wider than long and rarely as wide as long (FL/FW = 0.75–1.0). All three specimens of the new species have 8/8 supralabials whereas only two out of 85 specimens (including data from Cunha & Nascimento 1983, and Martins & Oliveira 1993) of *A. snethlageae* have 8/8 supralabials, and an additional five specimens have 7/8 or 8/7 supralabials. To assess the significance of the observed difference in the frequency of supralabials we used the binomial equation to obtain the probability that three specimens randomly drawn from pooling the data of the two species in question would all have 8/8 supralabials. Even being conservative (specimens with asymmetry in number of supralabials counted as having 8/8) the probability of obtaining three specimens with 8/8 supralabials is so low (p<0.001) that we are confident our data reflect taxon-specific differences in supralabials.

Species accounts

Atractus major Boulenger, 1894

Figs. 1, 3 and 4

Rhabdosoma maculatum—Günther, 1859: 411 (in part).

Rhabdosoma badium—Jan 1862: 13 (in part); Jan & Sordelli 1865: Plate 1, Fig. 1

Atractus major Boulenger 1894: 307; Amaral 1930b: 61; Savage 1960: 47 (in part, see remarks. Lectotype designated); Roze 1961: 114, 1966: 84; Duellman 1978: 229 (in part, see remarks); Dixon & Soini 1986: 95; Pérez-Santos & Moreno 1991: 94 (in part, see remarks); Martins & Oliveira 1993: 28, 1999: 96; Silva Haad 2004: 435; Duellman 2005: 367; Esqueda & La Marca 2005: 7; Passos et al. 2010b: 76.

Atractus arangoi Prado 1939: 1. Holotype: female, "Colombia" (MLS 136). Daniel 1949: 314 (distribution restricted to Puerto Asís). [new synonymy, see remarks]

Atractus badius (F. Boie)—Peréz-Santos & Moreno 1988: 68 (in part, pictures 17 and 18 on plate 10).

Lectotype and type locality. Juvenile male, BMNH 1946.9.7.27 (formerly BMNH 80.12.8.129; Fig. 4), collected by Buckley at locality of Canelos (01°36'S, 77°48'W; *ca.* 520 m), Province of Pastaza, Ecuador. The lectotype was designated by Savage (1960), restricting the type locality from eastern Ecuador to "Canelos, Ecuador."

Diagnosis. A species of *Atractus* with 17 midbody dorsal scales rows, differing from all congeners by the following combination of characters: (1) large size, adults reaching almost 800 mm in TL; (2) loreal long (about three times longer than high); (3) generally seven (rarely six) supralabials with third and fourth in contact with eye; (4) generally seven (rarely six) infralabials with first three in contact with chinshields; (5) five to seven maxillary teeth, usually with a single postdiastemal teeth; (6) 163–185 ventral scales in females and 150–173 in males; (7) 27–37 subcaudal scales in females and 29–53 in males; (8) tail of moderate length: Tail/TL 9.4–12.5% in females and 11.6–18.8% in males; (9) dorsal color pattern consisting of dark brown blotches or bands edged by yellow or cream on a pale to medium brown ground color.

Comparisons. Atractus major is widely sympatric with A. snethlageae and these two species have been repeatedly confused with each other. In terms of color pattern A. major has brown crossbands which are darker than the background coloration and are also edged by yellow or cream. In A. snethlageae the crossbands are typically paler than the background coloration and are edged by black; less frequently the background color is pale brown with dark crossbands/blotches, but these are never edged by a different color as in A. major. When confusion persists, the best way to distinguish between the two species is examining the number of infralabials on each side in contact with the chinshields and the number of postdiastemal teeth (three infralabials contacting chinshields and a single postdiastemal tooth in A. major vs. four infralabials and two postsiastemal teeth in A. snethlageae). With respect to other Amazonian species of Atractus having 17 dorsal scale rows, A. major is similar in aspects of color pattern and size to A. schach, and A. torquatus. Atractus major differs from A. torquatus by having blotches/ crossbands edged by a pale color (no pale edges on the bloches/crossbands in A. torquatus) and having two postoculars (as opposed to one postocular). Atractus schach is sympatric with A. major in northcentral Amazonia but this species lacks pale edges on the dark dorsal blotches/crossbands and it also has four infralabials in contact with the chinshields and two postdiastemal teeth. Atractus natans is sympatric with A. major in western Amazonia and specimens of this species oftentimes have pale-edged dark blotches; however, A. natans is a much smaller species with adults rarely exceeding 400 mm in TL, which, as opposed to A. major, has a mostly dark (dark grayish brown to black) venter (mostly cream in A. major) and four infralabials in contact with the chinshields.

Color pattern. The dorsal ground color is pale to medium brown or grayish brown, with irregular or ellipsoidal dark brown, primary blotches or crossbands narrowly edged by pale coloration, which can be pale brown, cream or yellow. The first dorsal blotch is usually elongated forming a short middorsal stripe on the neck, with separate, irregular blotches on the sides. The size, shape, extent on the lateral regions, and distance between the blotches/crossbands is variable but they generally expand longitudinally on the middorsal region. Typically the blotches/crossbands occupy a smaller area than the interspace between them, but the two specimens examined from Bolívar State, Guayana region of Venezuela, are notable exceptions in which the bands are at least twice as large as the interspace between them. In some specimens the blotches are in series of two and do not contact each other either because they do not reach the vertebral scale row (typical condition in specimens from Táchira, Venezuela) or, if they do, they do not coincide with each other. Most individuals also have smaller, irregular secondary blotches on the lower half of the sides. These secondary blotches are the same color as the primary blotches and

might alternate with them or they might appear as broken continuations of the primary blotches on the sides. The first two scales rows are typically paler than the dorsal background coloration but they are often also overlaid with small, irregular dark spots and mottling. The head is usually darker than the dorsal background color. The venter is also variable in color pattern, but generally the background color is cream with brown spots and/or blotches. In some specimens the blotches are located contiguously across scales forming broken ventral stripes, in which case the most common pattern is a single midventral stripe.



FIGURE 3. Photographs of individuals in life of *A. major* (top left: Amazonas, Venezuela; top right: Bolívar, Venezuela; bottom left: Ecuador) and *A. snethlageae* (bottom right: Ecuador).



FIGURE 4. Lectotype (BMNH 1946.9.7.27) of *A. major*.

Distribution. Amazon Rainforests of Ecuador, Colombia, Peru, Venezuela, and Brazil.

Remarks. Savage (1960) redescribed *A. major* based on a significant number of specimens from Ecuador; however, he erroneously included many specimens of *A. snethlageae* as *A. major* in his work. Color pattern D, and most likely color pattern E, as well as some of the specimens allocated to color pattern B, described by Savage (1960) for *A. major*, represent specimens of *A. snethlageae*. Duellman (1978) & Pérez-Santos & Moreno (1991) committed the same mistake apparently following Savage (1960); that is, their accounts for *A. major* include specimens of *A. snethlageae*. Moreover, the pictures referred as *A. major* in Duellman (1978), figure 138, page 229, and in Pérez-Santos & Moreno (1991), Photo 59, page 484, are indeed *A. snethlageae*. Duellman (2005) later realized his mistake and indicated that he had included specimens of *A. flammigerus* (= *A. snethlageae*) in his earlier account of *A. major* in Amazonian Ecuador (Duellman 1978).

Prado (1939) described *A. arangoi* from Colombia without specifying the type locality. Daniel (1949) mentioned that this species is known from Puerto Asís, Department of Putumayo, southeastern Colombia. Prado (1939) only compared *A. arangoi* with *A. major*, which he indicated was related, but in his view *A. arangoi* differed in color pattern, having a smaller size, and fewer ventrals and subcaudals. However, all the putative diagnostic characters for *A. arangoi* fall within the variation in *A. major* as herein defined. The examination of the holotype of *A. arangoi* (Fig. 5) by one of us (PP) has confirmed an agreement with *A. major* in all other examined morphological features that were not reported in the original description of the species. The holotype of *A. arangoi* is a female (MLS 136), 373 mm in TL, tail is 15.5% of TL. The variation is standard meristic characters is: 161 ventrals, two preventrals, three gulars separating chinshields from first preventral, 32 subcaudals, 6/7 supralabials, seven infralabials (first three in contact with chinshields), 6/5 maxillary teeth. The dorsal color pattern consists of 36 dorsal, pale bordered, dark brown blotches on the body and 10 on the tail. Based on all the evidence at hand we consider *A. arangoi* to be a junior synonym of *A. major*.



FIGURE 5. Holotype (MLS 136) of *A. arangoi*.

Atractus snethlageae Cunha & Nascimento 1983

Figs. 1 and 3

Atractus badius (F. Boie)—Amaral 1930a: 93 (in part), 1930b: 59 (in part); Carrillo & Icochea 1995: 13; Doan & Arizábal 2000: 116.

Atractus major Boulenger—Savage 1960: 47 (in part, see remarks); Duellman 1978: 229 (in part, see remarks); Pérez-Santos & Moreno 1991: 94 (in part, see remarks)

Atractus sp. B—Dixon & Soini 1977: 37.

Atractus flammigerus (F. Boie)—Hoogmoed 1980: 20 (in part, specimen from Peru); Dixon & Soini 1986: 93; Duellman & Salas 1991: 9; Duellman 2005: 366.

Atractus flammigerus snethlageae Cunha & Nascimento 1983: 19.

Atractus snethlageae—Vanzolini 1986: 25; Martins & Oliveira 1993: 34; Martins & Oliveira 1999: 97; Giraudo & Scrocchi 2000: 82.

Holotype and type locality. Adult male, MPEG 10131, collected in October 03, 1976, at locality of Colônia Nova (01°26'S, 47°32'W), Rio Gurupi, Rodovia BR-316, State of Pará, Brazil.

Diagnosis. A species of *Atractus* with 17 dorsal scales rows, differing from all congeners by the following combination of characters: (1) large size, adults reaching about 700 mm in TL; (2) loreal long (about three times longer than high); (3) generally seven (rarely eight) supralabials with third and fourth (fourth and fifth whenever eight supralabials are present) in contact with eye; (4) generally eight (rarely seven) infralabials with first four in contact with chinshields; (5) six to seven maxillary teeth; (6) 151–180 ventral scales in females and 137–165 in males; (7) 19–28 subcaudal scales in females and 27–45 in females; (8) tail of moderate length: Tail/TL 6.9–17.6%; (9) dorsal color pattern of dark gray/brown ground coloration with pale crossbands or blotches usually edged in black, or dorsal ground color pale brown with dark brown or black blotches.

Comparisons. The comparisons and confusions in the literature involving A. snethlageae and A. major are discussed in the previous species account and will not be repeated here. With respect to Amazonian species with 17 dorsal scales, the frequent color morph of A. snethlageae is rather unique in having well-defined pale crossbands, typically edged in black, on a dark background. Some specimens of A. latifrons are somewhat similar in color pattern, but they can be easily distinguished from A. snethlageae in having one postocular (as opposed to two), a loreal that is less than twice as long as wide (as opposed to twice as long as wide), and typically having six supralabials (as opposed to typically having seven). Juvenile specimens of A. gigas have a color pattern similar to A. snethlageae but the two species differ in the number of infralabials in contact with the chinshields (three in A. gigas, four in A. snethlageae). The less common color pattern, a pale brown background with dark blotches, is similar to A. schach (see remarks) and A. torquatus. Attractus torquatus has one postocular (as opposed to two in A. snethlageae) without reported exceptions. Atractus snethlageae is most similar to A. flammigerus (character states in parenthesis) but differs from this species in lacking keels on dorsal scales (adults have keels on dorsal scales at the level of the vent), typically seven supralabials (typically eight), and a venter with tiny dark spots forming irregular diffuse markings (spots are solid, regular, about the size of a dorsal scale and which tend to form longitudinal stripes). According to the statistical analysis A. snethlageae and A. flammigerus also differ morphometrically (Fig. 2) with a large separation in PC2. Because SUPRAOC had the highest component loadings on PC2 we looked into this variable to see if it could be helpful for discriminating the two species. Indeed A. flammigerus has longer supraoculars than A. snethlageae and this character, for the purpose of being used as diagnostic, can be presented as SUPRAOC/HL ratio. In A. flammigerus this ratio is 0.182-0.188 whereas in A. snethlageae it is 0.093-0.152.

Color pattern. Two different color pattern types occur in this species with considerable variation within them. The most common pattern (pattern II in statistical analyses) consists of a dark brown or dark grayish brown ground coloration with cream or buff yellow dorsal crossbands that extend down to the second or third dorsal scale row on the sides. The dorsal bands typically expand longitudinally into one or two dorsal scales and are edged by black, but in some specimens the bands are irregular and form blotches that may expand longitudinally more than two dorsal scales. Rarely the black edges are inconspicuous. The crossbands may be complete across the dorsum, interrupted in the vertebral region or alternating on the sides. The interspace between crossbands is longer than the crossbands themselves, encompassing two to seven dorsal scales but with variation within individuals. The first two dorsal scales have an irregular pattern of dark and pale mottling and solid cream spots might also be present at that level. A large white or cream nuchal band is present in juveniles and small adults but gradually darkens and

disappears as individuals get larger. In adults the top of the head is either the same color as the background color of the body or slightly paler. Irregular and inconspicous dark spots or mottling are frequently observed on the head. In the other, less common color pattern type (pattern III in statistical analyses) the dorsal background coloration is pale brown or creamy brown (in preservative) with a series of irregular paired dark brown blotches that may or may not contact each other middorsally. A dark brown nuchal band is usually present with the head usually darker than the dorsal background. The ventral coloration in both color pattern types is creamy with varying levels of dark brown pigmentation in the form of tiny dark spots that may form diffuse blotches. In some specimens the dark markings can form a broken midventral stripe. Rarely the venter is so heavily pigmented that it is almost uniform dark brown.

Distribution. Attractus snethlageae as currently defined is a widespread species occurring in northern Brazil, and the most part of the upper Amazon Basin in Colombia, Ecuador, Peru, Bolivia and Gran Chaco in northern Argentina (Giraudo and Scrocchi, 2000; Passos 2008). This species inhabits lowland and lower montane rainforests, from sea level up to 1800 m.

Remarks. As stated above, *A. snethlageae* has been repeatedly confused with *A. major* in Ecuador (e.g. Savage 1960; Duellman 1978; Pérez-Santos & Moreno 1991). We think that part of this confusion stems from the great amount of intraspecific color pattern variation in *A. snethlageae*, especially the fact that two distinct color morphs are found in this species, one of which (pattern III in this study) is similar in general aspects to the color pattern observed in *A. major*. Discrete polymorphism in color pattern as documented here for *A. snethlageae*, although rare in snakes, has been found in other species of *Atractus* (Fajardo 2000; Passos & Prudente 2012; Schargel, unpublished observations) and will likely become a more common observation as we obtain larger samples of poorly known species and a better understanding of the taxonomy of the genus.

The name *A. badius* has also been used for specimens of *A. snethlageae* from Argentina, Bolivia, Brazil, Ecuador and Peru in the literature or on a significant number of museum specimens that we have examined. This has been the case in the literature (e.g. Carrillo & Icochea 1995; Doan & Arizábal 2000) even after Hoogmoed (1980) had redescribed *A. badius* and resurrected *A. flammigerus* (which at the time included *A. snethlageae*) from its synonymy. As a matter of fact, the name *A. badius* has historically been a "dumping ground" for several different species of *Atractus* having crossbands. Our current understanding of the species together with the examination of material and records misidentified as *A. badius* seems to indicate that this species is endemic to the Guiana Region as delimited by Hoogmoed (1979). Although *A. badius* likely occurs in southeastern Venezuela, records of this species for this country in the Coastal and the Mérida Mountain Ranges represent misidentifications of *A. lancini*, *A. univittatus*, and *A. meridensis*.

Comparisons between A. snethlageae and A. schach are currently problematic. The color pattern III of A. snethlageae is similar to the color pattern that has been reported in A. schach. Atractus schach was originally described from Suriname and, just like A. flammigerus, had long been considered a synonym of A. badius (see Hoogmoed 1980). The few works (Cunha & Nascimento 1983, 1993; Martins & Oliveira 1993, 1999) that have provided taxonomic accounts for both A. schach and A. snethlageae have separated these two species solely on color pattern. As a matter of fact, before Hoogmoed (1980) resurrected A. schach, Cunha and Nascimeno (1978) had considered specimens that they examined and which they later referred to A. schach and A. flammigerus snethlageae (Cunha and Nascimento 1983) as conspecific and under the name A. badius. At this point we have no evidence from our meristic or morphometric data that would support recognizing the two color patterns that we have assigned to A. snethlageae in western Amazonia as two different species. However, without a more comprehensive sampling we cannot establish whether what has been referred to A. snethlageae and A. schach from Brazil are conspecific or not. If specimens referred to A. schach in Brazil prove to be a different species from A. snethlageae it would still be necessary to determine whether those specimens are indeed conspecific with topotypic material of A. schach. As such, we are aware that Atractus snethlageae as herein defined might represent a species complex and a more in depth taxonomic examination of this species is in progress (Passos in prep.)

Atractus touzeti sp. nov.

Figs. 6 and 7

Holotype. Adult female, FHGO 517, collected dead on road on 16 August 1992 by Peter Pearman at Cosanga—Archidona road (00°37'S, 77°48'W; 2200 m) in the Cordillera de Los Guacamayos, Province of Napo, Ecuador.

Paratypes. Two adult females, FHGO 2035 and FHGO 2036, collected dead on road on 5 April 1998 by Felipe Campos at La Virgen (ca. 2000 m) in the Cordillera de Los Guacamayos, Province of Napo, Ecuador.

Diagnosis. A species of *Atractus* with 17 dorsal scales rows differing from all other members of the genus by the following combination of characters: (1) large size and thick body, adults reaching more than 1000 mm in TL; (2) loreal long (about three times longer than high); (3) eight supralabials, four and five in contact with eye; (4) seven or eight infralabials; (5) eight maxillary teeth; (6) 167–170 ventral scales in females; (7) Tail of moderate length Tail/TL 9.5–11.4%; (8) 31 subcaudal scales in females; (9) dorsal color pattern of short pale crossbands edged by black borders that separate the pale color from the brown ground color.

Comparisons. Regarding all known species of Atractus with 17 dorsal scales, only A. gigas, A. latifrons, A. major, A. obesus, A. sanctamartae, A. serranus, A. snethlageae, A. titanicus, A. torquatus, A. trihedrurus, and A. zebrinus attain a TL close to or exceeding 600 mm. Adults of A. serranus and A. trihedrurus have a uniform dorsum, but they also differ from A. touzeti in having fewer ventrals (<164) and subcaudals (<24). In both A. latifrons and A. torquatus there is a single postocular whereas there are two in A. touzeti. Atractus torquatus further differs from the new species in having a cream venter with well-spaced small spots or nearly immaculate whereas in A. touzeti the venter is heavily pigmented with large, roughly rectangular or irregular blotches. Atractus latifrons further differs from A. touzeti in having a color pattern of rings that encircle the whole body. Atractus major, A. obesus, A. sanctamartae, A. titanicus, and A. zebrinus all have seven supralabials. Atractus sanctamartae, A. titanicus and A. zebrinus further differ from A. touzeti in having fewer subcaudals (>28). Atractus major and A. obesus further differ from A. touzeti in aspects of dorsal coloration with A. major having a pattern of pale-edged dark brown blotches or bands, while A. obesus has black rings that encircle the body.

Among the large species of the genus Atractus touzeti is most similar to A. gigas and A. snethlageae. Atractus gigas is the only species in the genus that is really comparable in size and habitus to A. touzeti, but adults of the former species are either uniform or with inconspicuous pale bands dorsally whereas the dorsal crossbands in A. touzeti are conspicuous and well-defined. All three specimens of A. touzeti have eight supralabials whereas specimens of A. gigas typically have six or seven supralabials (see Passos et al. 2010b). The number of infralabials that contact the chinshields on each side is four in the two paratypes of A. touzeti but the holotype is asymmetric and has four on one side and three on the other; all specimens of A. gigas have three infralabials in contact with the chinshields. Atractus snethlageae is a smaller species that is not known to reach a TL of over 718 mm, it has six to seven maxillary teeth (eight in A. touzeti), and typically seven infralabials (eight in A. touzeti). The maximum number of subcaudals observed (including data from Cunha and Nascimento, 1983) in females of A. snethlageae is 28, whereas all three specimens of A. touzeti have 31 subcaudals. Although it is possible that the range of subcaudals of these two species will overlap when more specimens of A. touzeti are obtained, it is obvious that they differ in typical values for this character. These two species also differ in other aspects of morphometrics as explained in the results section; specifically the HW/HL ratio seems to be a useful character for separating them. Among small species of Ecuadorian Atractus (<50 cm TL), all of them except A. multicinctus have dorsal color patterns other than crossbands, usually being striped, spotted or uniformly colored. Atractus multicinctus further differs from A. touzeti by having fewer maxillary teeth (5 or 6) and supralabials (7).

Description of the holotype. An adult female, 1195 mm in TL, tail length 114 mm (9.5% of TL); head slightly distinct from neck, as wide as long (HW: 28.8 mm; HL: 28.6 mm). Snout truncated in dorsal view, rounded in lateral view; eye moderately small (2.9 mm), about same size as the upper postocular, pupil circular; eye-nostril distance 0.29 of HL; 2.8 times eye diameter; rostral bell-shaped, barely visible in dorsal view, 1.6 times broader than high, lingual groove reduced; internasals small, as long as wide, laterally contacting anterior and posterior nasals; prefrontals large, 1.2 times longer than wide, in contact with eye; frontal roughly triangular, 1.2 longer than wide, 1.5 times longer than median suture of prefrontals; parietals 1.6 times longer than wide, median suture of parietals 0.8 times length of frontal. Nasal divided, posterior scale twice the size of the anterior; preocular absent; loreal 2.5 times longer than high, narrowly touching the eye, anterior edge 2.2 times higher than posterior; two postoculars, lower very small, upper 6 times larger; temporals 1 + 2, upper posterior temporals elongated, as large as the frontal; supralabials eight on both sides, first contacting nasals, second contacting posterior nasal and loreal, third and fourth contacting loreal, fourth, fifth and sixth in contact with eye on the right side, fourth and fifth in contact with eye on left side, sixth contacting posterior temporal, seventh contacting anterior and posterior temporals, eighth contacting posterior temporal and dorsals; infralabials eight on the right side seven on the left, four contacting the chinshields on right side, three on left side, first pair short, meeting at ventral midline,

separating mental from chinshields; one pair of chinshields, each 2.3 times longer than wide. Maxillary teeth eight, most teeth bearing a prominent longitudinal ridge on the labial side; palatine teeth large; dorsal scales in 17–17–17 rows, smooth without apical pits; ventrals 170, preventrals four; anal plate single; subcaudals 31, paired.



FIGURE 6. Holotype (FHGO 517) of *A. touzeti*.

Color pattern of the holotype. In preservative (alcohol 70% after formalin), the dorsal ground color is hair brown with dark and cream mottling on dorsal scale rows 1–3; there are 34 dorsal crossbands along the body, seven on the tail, extending laterally to the first dorsal scale row except for the first two which extend to dorsal scale row six (blotches). The crossbands are tawny olive, one dorsal scale long, edged by black borders of about the same length, separated from each other by two to three dorsal scale lengths, they become indistinct and darkly mottled on the first and/or second dorsal scale rows; they alternate with small lateral blotches of the same color that cover partially the first and second dorsal scale rows on each side. The dorsum of the head is olive brown, slightly paler than the dorsum of the body, with some inconspicuous dark brown spots; an incomplete short dark band is present in the nuchal region. Supralabials have cream spots with dark mottling in the lower portion. Infralabials, mental and chinshields are mostly dark brownish olive with cream spots. The venter is cream heavily pigmented with large rectangular and irregular dark brownish olive blotches.

Variation. The two paratypes are adult females with TL of 1050 and 1030 mm, and tail lengths of 120 and 115 mm, respectively comprising 11.4 and 11.2% of TL. The cephalic index (width/length x 100) is 101–120 (mean = 114, n = 3). There are eight supralabials (both sides) with the fourth and fifth entering the orbit in both specimens; infralabials are eight in FHGO 2035 and seven (right side) and eight (left side) in FHGO 2036, with four in contact with the chinshields. In the paratypes the upper posterior temporal is not as large as in the holotype, and is about the same size as the first temporal. The upper postocular is about twice the size of the lower postocular in both specimens. There are 169 and 167 ventrals and 31 subcaudals in the paratypes. Other aspects of lepidosis agree well with the holotype. Both paratypes have eight maxillary teeth on the right side, reducing in size posteriorly. Palatine and pterygoid teeth in FHGO 2035 are seven and five, respectively, on each side. We could not count teeth in the other specimens because of damage to dentigerous bones (FHGO 2036) or the specimen was sufficiently brittle as to preclude opening the mouth without risking breaking the jaw (holotype). The numbers of dorsal crossbands in the paratypes are 34 and 32 along the body, and seven and eight on the tail, respectively. In the holotype the percentage of the venter covered with dark blotches is almost 50%; in the paratypes this percentage is lower, about 35–40%, and the color of the blotches is dark neutral gray.

Color in life. Although we do not have notes about the color in life of the type series of *A. touzeti*, we have received a picture taken *in situ* of a live individual found in the same locality from which the paratypes were obtained. The specimen was found crossing a road and was not collected but its large size and robust habitus are apparent in the picture. The background color of the dorsum is dark brown (darker tone than what was observed in the preserved specimens), becoming almost black towards the middorsal region. The crossbands are conspicuous

and bright yellow on the side but become suffused with brown color towards the middorsal region. The black borders of the crossbands are not distinct in this specimen. There are about 42 crossbands total from neck to tail.

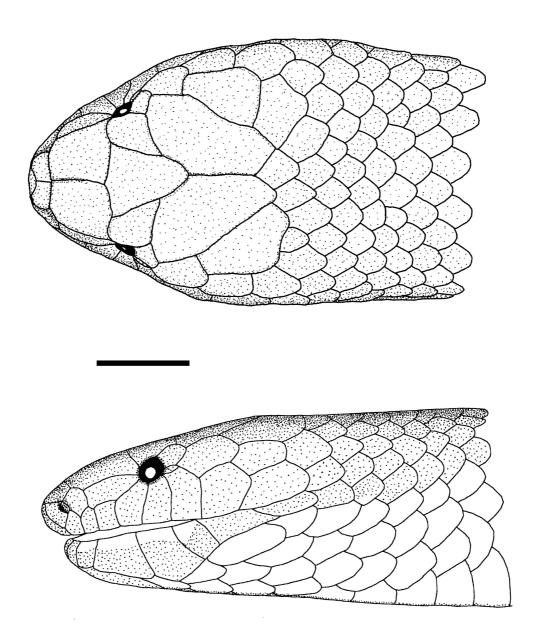


FIGURE 7. Dorsal (top) and lateral (bottom) view illustrations of the head of the holotype (FHGO 517) of A. touzeti.

Etymology. We take great pleasure in naming the new species after Jean-Marc Touzet, an enthusiastic promoter of herpetology in Ecuador and the founder of the Fundación Herpetológica Gustavo Orcés.

Distribution. Known only from the Cordillera de Los Guacamayos in the Eastern Andean range of Ecuador (Fig. 8). According to the recent classification of ecosystems in Ecuador (Ministerio del Ambiente de Ecuador, 2013) the area where the type locality is located is part of the "evergreen montane forest of the north and central Cordillera Oriental of the Andes." The vegetation in this ecosystem is constituted mostly by evergreen forests reaching 20-25 m in height, dominated by Andean species in the families Melastomataceae (*Miconia*), Solanaceae, Myrsinaceae, Aquifoliaceae, Araliaceae, Rubiaceae and several families of ferns. Valencia (1995) studied the composition and structure of a forest near Baeza (2000 m), Napo, Ecuador, which is about 20 km north of the type locality of *A. touzeti* and found that the vegetation was composed of a combination of typical Amazonian and Andean species, with trees reaching 30 m tall and the understory being dominated by the palm tree *Geonoma undata*.

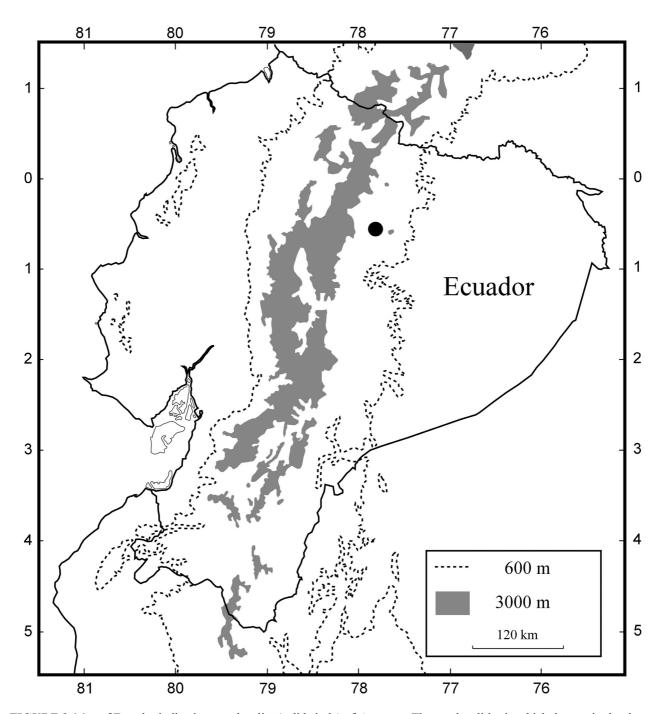


FIGURE 8. Map of Ecuador indicating type locality (solid circle) of *A. touzeti*. The two localities in which the species has been collected are nearby and cannot be separated on the map.

Discussion

Taxonomic research of the genus *Atractus* has been traditionally a difficult task because of the plethora of species described and the fact that many species remain poorly characterized and are known from only a few specimens. To further complicate matters, it is now clear that intraspecific color pattern variation within *Atractus* can be complex and include discrete polymorphism (Fajardo 2000; this work), sexual dimorphism (Passos et al. 2009a) and drastic ontogenetic changes (Passos et al. 2010c; Passos & Prudente 2012). These aspects of color pattern variation have confused taxonomists working with *Atractus* even when relatively large series have been available (e.g. Savage 1960; Bernal-Carlo & Roze 1997). Although color pattern is still an important and useful character system for

taxonomic research in *Atractus*, we stress that it should not be used in isolation to support taxonomic decisions. Because of the generally conservative nature and overlap in traditional meristic and scalation characters within *Atractus* it is important to include alternative morphological characters in taxonomic studies. For example, hemipenial morphology has been shown to be quite variable in the genus (Schargel & Castoe 2003) and informative to establish relatedness and to separate species (Passos et al. 2010a, 2010c; Prudente & Passos 2010). Herein we also show that morphometric data, mostly from the head, used in the context of multivariate statistical analyses (e.g. PCA; see also Schargel 2003) can significantly help support taxonomic decisions. Even if species are closely related, as seems to be the case for *A. flammigerus*, *A. snethlageae* and *A. touzeti*, morphometric data can still be quite informative. The only important limitation that we see for using multivariate statistical techniques on morphometric data to delimit species in *Atractus* is the relatively large sample size required to be able to include several variables in the analyses and to understand intraspecific variation. As mentioned before, many species of *Atractus* remain known from very few specimens.

Atractus touzeti is now the largest known species of Atractus and it is paralleled in size only by A. gigas from western Ecuador. These two species are so large relative to other species in the genus that they almost double the size of species that are considered large (e.g. A. major, A. torquatus) and they quadruple the size of the smaller species in the genus. Interestingly, neither one of these two giant species is atypical in other aspects of external morphology. Not even segmental counts (e.g. ventral scales), which tend to be correlated with size in snakes (Lindell 1994; Head & Polly 2007), are noticeably higher relative to other species in the genus. This observation further supports the notion that gigantism in snakes is achieved by modification of post-somitogenic somatic growth rather than with an increase in somite numbers (i.e. pleomerism; Head & Polly 2007).

The discovery of such a large species of *Atractus* underlines the fact that we are still in a phase of big discoveries with respect to the diversity of this genus. The amount of new species discoveries in *Atractus* as well as the number of more revisionary-oriented taxonomic work has been unprecedented in the last decade. Regardless, it is still clear that a whole lot more work is required before we can obtain a solid taxonomic framework for understating other aspects of the diversification of this genus. Even if several recent efforts have focused on resolving the taxonomic chaos involving some regions (e.g. Andes of Colombia) from which several species were poorly known, our taxonomic approaches are still limited by the fact that pretty much nothing concrete is known about the phylogenetic relationships within *Atractus*. This limitation has prevented those of us working on the taxonomy of this complicated genus from framing our research projects around hypotheses of species relatedness, as opposed to emphasizing our taxonomic revisions on politically defined areas or, at best, biogeographical provinces. The large number of species is certainly intimidating to anyone up to the task of looking into the phylogenetic relationships of *Atractus*, which will likely have to rely largely on molecular data. However, we are reaching a point at which any phylogenetic information of *Atractus*, even if preliminary, would certainly be welcomed and might even have a major impact on taxonomic research if at least major clades can be identified and diagnosed morphologically.

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APPENDIX. Specimens examined.

Atractus badius: BRAZIL: Amapá: Serra do Navio forest: LACM 44686. FRENCH GUIANA: Cayenne: RMNH 12; road between Cayenne and Tonate: CAS 146918. SURINAME: Afobaka: RMNH 13574; Powakka: KU 221545; Brownsberg: UTA 60138; Brownsberg Nature Reserve plateau: MCZ 152691; Djai Creek: RMNH 12860; Nassau Mountains: RMNH 12862; Republiek: RMNH 18677; Paramaribo: RMNH 13773.

Atractus flammigerus.—SURINAME: Nassau Mountains: RMNH 13571, 13572.

Atractus major.—BRAZIL: Rondônia: Rio Formosa: OMNH 37533. COLOMBIA: Amazonas: Ginogoje, Río Apaporis: MCZ 53220; Caquetá: Florencia: MCZ 65384; Putumayo: Puerto Asis: AMNH 53446. ECUADOR: Morona Santiago: Taisha, Makuma: FHGO 788, 815, 890, 959, 2370, 3435, 3814, 4042, 4043, 4046, 4050, 4496, 4517, 4761, 5717; Taisha, Amazonas: FHGO 4762; Taisha, Kiim: FHGO 3963; Taisha Paantim: FHGO 4476; road 45 between Puyo to Macas: QCAZ 10146. Napo: Alto Sindi: QCAZ 3689; Estación Biológica Jatun Sacha: MCZ 178334, 178335, 173886-173889; Tena: (FHGO 7627); Jatun Sacha: FHGO 3495. Orellana: Parque Nacional Yasuní: QCAZ 3079, 6272. Pastaza: -1.12, -76.85: USNM 321108; Arajuno, Villano: QCAZ 8157, 8265, 8379; Charapacocha: FHGO 3813; Mera: KU 98625, 121307, 133527; Mera, Shell, Fábrica Te Zulay: FHGO 4496. Sucumbios: Lago Agrio: KU 125991; Pañacocha: QCAZ 7881, Putumayo, Santa Elena, Bohórquez: MECN 8343; Rio Cotopino: UMMZ 89005, 89006, 92032, 92036, 94068. Santa Cecilia: KU 109830, 109831, 112250, 112251, 121841, 175348, 175399. Zamora Chinchipe: Zamora: FHGO 4496. PERU: Amazonas: Pagaat: USNM 316576; Cuzco: San Martin, 5 km N of Camisea River: KU 538472-538475. Madre de Dios: 15 km E of Puerto Maldonado: KU 207772, 214838-214842; Tambopata Reserve KU 343043. Loreto: Centro Unión: TCWC 42807; Monte Carmelo, Requena: AMNH 55638, 55640; Monte Alegre, Pachitea: AMNH 52780; Pampa Hermosa, Cushabatay: AMNH 55709; Quebrada Grande, near junction between Sucusari River and Napo River: KU 222367. Ucavali: Alto Utuquinia: AMNH 53474; Chiyacu: AMNH 52095; Ollanta: AMNH 52105; Zona Reservada Pucacuro: FHGO 7552. VENEZUELA: Amazonas: road Puerto Ayacucho—Gavilan: CVULA 6560-6566, Bolívar: El Triunfo: CVULA 6567, 6568. Táchira: La Trampa, Uribante-Caparo: CVULA 4317, 4454, 4727, 4280; Presa La Honda, Campamento Siberia: MCNG (1 uncatalogued specimen).

Atractus snethlageae.—BRAZIL: Amazonas: Cuieira River, Between Manaus and Rio Branco: CAS 101607; Manaus: CAS 49797; Presidente Figueiredo: RMNH 26020. BOLIVIA: unknown locality: AMNH 2987. Pando: Ivón: AMNH 28838; Senna, near junction with Río Madre de Dios: UMMZ 59778, 59779. ECUADOR: Morona-Santiago: Chiguaza: USNM 232690, 232691; Méndez: USNM 232692, 232693, 283945, Taisha, Makuma, Tumpaim: FHGO 5614. Napo: 6.5 k, SE of Misahualli: QCAZ 3476, 3477; Archidona, Cotundo, Los Cocodrilos: QCAZ 11075; Cascada de San Rafael: QCAZ 3256, 3257; El Chaco, road to Linares: QCAZ 4047; Estación Biológica Jatun Sacha: MCZ 173870, 173871; San Francisco de Borja, Sardinas: QCAZ 1494, MECN 80; Tena, Sumac Shagcha: FHGO 2178 Orellana: km 10 Maxus road: QCAZ 10614. Pastaza: Abitagua: UMMZ 92033, 94067; Arajuno, Kurintza: QCAZ 8287, Arajuno, Villano: QCAZ 8367; Río Pastaza: UMMZ 89026; Sarayaku: UMMZ 89024. Sucumbios: Lago Agrio: KU 125988-125990, 125992-125998; El Reventador: QCAZ 444; Río Salado, 1 km upstream from Río Coca: KU 164206; Santa Ana: MECN 7873; Santa Cecilia: KU 112249, 125985, 125986, 175397, 175400, MCZ 96674. Tungurahua: San Francisco de Mapoto UMMZ 89023, 89025. Zamora Chinchipe: Yantzaza, Los Encuentros: MECN 8437, PERU: Amazonas; Huampami, Río Cenepa: MVZ 163247, Cuzco: 40 km E of Quincemil, along road to Puerto Maldonado: LSUMZ 48718; Cashiriari, S of Río Camisea: USNM 538466; Pagorini, on Río Camisea: USNM 538467; San Martin, 5 km N of Río Camisea: USNM 538464. Loreto: Paraiso: TCWC 42107; Río Itaya, Iquitos: AMNH 54085, 54257, 54268, 54279, 54368, 54643, 54645, 54667, 54953, 54958; Upper Amazon: FMNH 11180 Madre de Dios: Cuzco Amazónico, 15 km E of Puerto Maldonado: KU 214843, 214905, 220191; Puerto Maldonando: MVZ 247494 Ucavali: Balta, Río Curanja: LSUMZ 14582.