

## REVISION OF THE *EPICRATES CENCHRIA* COMPLEX (SERPENTES: BOIDAE)

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**ABSTRACT:** The *Epicrates cenchria* complex is endemic to the Neotropical region, occurring in mainland portions of Central and South America. The taxonomic status of the nine currently recognized subspecies (*E. c. alvarezi*, *E. c. assisi*, *E. c. barbouri*, *E. c. cenchria*, *E. c. crassus*, *E. c. gaigei*, *E. c. hygrophilus*, *E. c. maurus*, and *E. c. polylepis*), were evaluated based on external morphology, osteology, and hemipenis characters. Results obtained through quantitative and qualitative analyses support the recognition of *E. alvarezi*, *E. assisi*, *E. cenchria*, *E. crassus*, and *E. maurus* as distinct species based on statistically robust delimitation of species boundaries.

**Key words:** Boinae; *Epicrates cenchria* complex; Morphological variation; Morphometry; Species boundaries; Taxonomy.

THE boid genus *Epicrates* Wagler is currently recognized as a paraphyletic group with respect to *Eunectes* Wagler, owing to recent studies those found mainland *Epicrates* in a sister relationship group with *Eunectes* (Burbrink, 2005; Noonan and Chippindale, 2006). The genus is endemic to the Neotropical region, and contains ten species (Kluge, 1989; McDiarmid et al., 1999) comprising two monophyletic groups (Burbrink, 2005; Kluge, 1989; Noonan & Chippindale, 2006; Passos, 2003). An insular group distributed in the West Indian islands contains 21 taxa (Henderson and Powell, 2007), whereas the continental endemic *Epicrates cenchria* (Linnaeus) has nine currently recognized subspecies (McDiarmid et al., 1999), but see below.

The *Epicrates cenchria* complex (*sensu* McDiarmid et al., 1999) is a monophyletic group (Passos 2003), ranging from mainland portions of Nicaragua to Argentina, and at Trinidad & Tobago and Margarita continental islands (Köhler, 2003; McDiarmid et al., 1999). Although the taxonomic status of the Caribbean taxa has been partially resolved (see Schwartz and Henderson, 1988; Sheplan and Schwartz, 1974; Tolson and Henderson, 1993), continental species of *Epicrates* remain poorly known (Duellman, 2005). The mainland group contains customarily the following recognized subspecies: *E. cenchria cenchria* occurring in the east of the Andes at Amazon

Forest from Venezuela south to Bolivia, eastern to French Guyana, and southeastern to Brazil; *E. c. maurus* Gray occurring in the Savannas or Dry Forest of the Nicaragua to northern Brazil; *E. c. crassus* Cope occurring in the open formations from Brazil, Bolivia, and Argentina; *E. c. barbouri* Stull occurring in the Savannas from Marajó Island at Brazilian state of Pará; *E. c. gaigei* Stull occurring in the Amazon Forest from Peru and Bolivia; *E. c. assisi* Machado occurring in the Caatinga from Brazilian States of Paraíba to northern Minas Gerais; *E. c. hygrophilus* Amaral occurring in the Atlantic Rainforest from east Brazil, from the States of Alagoas to Rio de Janeiro; *E. c. polylepis* Amaral occurring in the Cerrado from Brazilian States of Goiás and Minas Gerais; *E. c. alvarezi* Abaloz, Baez & Nader occurring in the Chaco from southeastern Bolivia to northern Argentina (McDiarmid et al., 1999; Passos, 2003). Nevertheless, recently Matz (2004) considered *E. c. maurus* as a full species and described two new subspecies for it, restricting the distribution of the nominal species to eastern and western Venezuela and Margarita Island; proposed *E. m. colombianus* on the basis of four specimens from Atlantic coast of the Colombia and Panama, extending their distributional range from Nicaragua to north Venezuela; and named *E. c. guayanensis* based on three individuals from Atlantic coast of French Guyana, expanding their distribution to Surinam as well.

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Since the original description by Linnaeus (1758), few studies have addressed problems regarding the morphological variation, geographic ranges, and species boundaries among continental populations of *Epicrates*. In previous studies of *Epicrates*, most authors used small sample sizes, inadequate coverage of the literature, and failed to examine type series (Amaral, 1929, 1935, 1954; Boulenger, 1896; Chippaux, 1986; Gorzula and Señaris, 1999; Lema, 2002; Matz, 2004; Stull, 1935, 1938). The single revision of the continental complex was provided by Amaral (1954), however, he did not examine either the types or any additional specimen of some subspecies (e.g., *E. c. barbouri* and *E. c. gagei*). Moreover, Amaral (1954) based his conclusions on a small sample size (e.g., *E. c. polylepis*), a subjective criterion (e.g., *E. c. hygrophilus*), or on inadequate coverage of the literature (e.g., *E. c. xerophilus* = *E. c. assisi*) to recognize some taxa. Despite the current taxonomic shortcomings, some subspecies have greater differentiation in color pattern and pholidosis characters (Duellman, 2005), indicating a divergence that might be sufficient to consider them into the specific rank (Frost and Hillis, 1990; Frost et al., 1992). On the other hand, there are subspecies currently recognized that may be an artifact of the hypothetical diagnosis corresponding nothing more than clinal or ontogenetic variation in the meristic and color pattern characters (Amaral, 1954; Matz, 2004).

The use of an *a priori* diagnostic criterion to test the boundaries among species as a hypothesis that could be empirically accepted or rejected (Jorge da Silva and Sites; Sites and Crandall, 1997; Wiens and Servedio, 2000) was never applied in previous studies focusing the taxonomy of the *Epicrates cenchria* complex. Therefore, earlier papers shed little light on the species limits between putative diagnosable taxa. The extensive samples now available in museum collections allowed us to adequately describe the morphological variation in meristic, morphometric, color pattern, osteological, and hemipenial characters for all currently recognized taxa in order to evaluate the status of the *Epicrates cenchria* complex. Our goal in this study is to test the validity of each race of continental *Epicrates*

on the basis of morphological characters and to propose a new taxonomy that better represents the evolutionary relationships among these taxa.

#### HISTORICAL RÉSUMÉ

A comprehensive synonymy list to the *Epicrates cenchria* complex is provided by Stimson (1969), and augmented by McDiarmid et al. (1999). Nonetheless, among the recent taxonomic changes not mentioned in these papers, Chippaux (1986) elevated *Epicrates cenchria cenchria* and *E. c. maurus* to specific rank without an extensive comparative study, examination of the type series, or use of appropriate literature. This author distinguished *E. c. maurus* from the nominal subspecies on the basis of morphological features, such as number of ventrals, subcaudals, supralabials, and position of loreal plate. However, Pérez-Santos and Moreno (1988) preferred to recognize these taxa as subspecies. Later Gorzula and Señaris (1999) following Chippaux (1986), recognized *E. c. maurus* as a full species on the basis of segmental scale counts, color pattern, and adult body size. However, McDiarmid et al. (1999) preferred to maintain this taxon at the subspecific rank awaiting a comprehensive revision of this assemblage. Lema (2002) elevated *E. c. crassus* to specific level without further comments on his decision. Matz (2004), following Chippaux (1986), recognized *E. maurus* as a distinct species from the *E. cenchria* complex, and described *E. m. colombianus* and *E. m. guayanensis*. Matz (2004) have not cited any specimens other than his own new taxa and relied in the literature to compare them to the nominal species. Matz's (2004) paper includes very short descriptions and lack any comparative effort or conceptual background to recognize the new races of *E. maurus*. Tipton (2005) followed McDiarmid et al. (1999) and considered *E. maurus* as subspecies from *E. cenchria*, and did not listed *E. m. colombianus* and *E. m. guayanensis* as valid taxa. Henderson and Powell (2007) listed *E. cenchria* with eight subspecies and *E. maurus* comprising three subspecies, recognizing the Matz's arrangement.

## MATERIAL AND METHODS

*Material Examined*

We examined more than 650 specimens of *Epicrates* deposited in the following collections: Colección Boliviana de Fauna, La Paz, Bolivia (CBF), Escuela Politécnica Nacional, Quito, Ecuador (EPN), Fundación Miguel Lillo, San Miguel de Tucumán, Argentina (FML), Instituto Alexander von Humbolt, Villa de Leyva, Colombia (IAvH), Instituto Butantan São Paulo, Brazil (IBSP), Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá D.C. (ICN), Museo de Historia Natural de Cochabamba, Bolivia (MHNC), Museo de Historia Natural La Salle, Fundación La Salle, Caracas D.F. (MHNLA), Museo de Biología de la Universidad Central de Venezuela, Caracas D.F. (MBUCV), Museo de Historia Natural, Universidad Mayor de San Marcos, Lima, Peru (MHNSM), Museo La Salle, Universidad de La Salle, Bogotá D.C. (MLS), Museo de Historia Natural Noel Kempff Mercado, Santa Cruz de la Sierra, Bolivia (MNKR), Museu de Biologia Prof. Mello Leitão, Santa Teresa, Brazil (MBML), Museu Nacional da Universidade Federal do Rio de Janeiro, Brazil (MNRJ), Museu Paraense Emílio Goeldi, Belém, Brazil (MPEG), Museu de Zoologia da Universidade de São Paulo, Brazil (MZUSP), Natural History Museum, London, U.K. (NHM), Pontificia Universidad Católica del Ecuador, Quito (QCAZ). Specimens and localities are listed in Appendix I.

For a few taxa we could only exam the photographs of the types specimens sent to us by courtesy of curators and staff of the following Institutions: Naturhistoriska Riksmuseet, Stockholm, Sweden (NRS), Museum of Comparative Zoology, Harvard University, Cambridge, U.S.A. (MCZ), University of Michigan Museum of Zoology, Ann Arbor, U.S.A. (UMMZ), United States National Museum, Smithsonian Institution, Washington D.C. (USNM).

*Meristic, Morphometric, and Color Pattern Characters*

Terminology for most *Epicrates* cephalic shields follows Sheplan and Schwartz (1974), whereas the method of ventral counting follows Dowling (1951). Measurements were

taken with a dial caliper to the nearest 0.1 mm, except to snout-vent (SVL) and tail (TL) lengths, which were taken with a flexible ruler to the nearest 1.0 mm. Sex was determined through a ventral incision on the base of tail. We examined the following external quantitative characters for each specimen: number of anterior dorsal scales rows, counted one head of distance behind the neck (ADORS), number of midbody dorsal scales rows (MDORS), number of posterior dorsal scales rows, counted one head of distance previous to anal plate (PDORS), number of dorsal scales rows in the level of the second subcaudal (TDORS), number of ventral scales (VENT), number of subcaudal scales (SUBC), number of supralabials scales (SUPRA), number of infralabials scales (INFRA), number of infralabials contacting chinshields (INFRG), number of lorilabial scales (LORIL), number of scales forming the mental groove (SULK), number of scales between supraoculars shields (INTS), number of interriectals, corresponding to scales between last supralabial from both sides of head (INTRC), number of gular scales, corresponding to scales between the last infralabial and pre-ventrals (GULAR), number of pre-ventral scales (PVENT), number of dorsal rings, counted from the neck to cloacae, the collapsed rings were counted only one time (RING), number of ocelli, counted from the neck to cloacae, the collapsed ocelli were counted only one time, and interruptions in the lateral stripe were not considered to the count (OCEL). In the species accounts, means  $\pm$  standard deviation then and sample size follow the range in parenthesis.

*Cranial Osteology*

Terminology for osteological description follows Frazzetta (1959, 1966, 1975), and Kluge (1989, 1991). Description of the cranium was based on the examination of at least five skulls for each taxon (juveniles and adults from both sexes), except to *E. c. alvarezi* ( $n = 3$ ), as this taxon is poorly represented in the museum collections examined. As the cranium of the type species of the genus *Epicrates* (*E. c. cenchria*) was described in detail by Frazzetta (1959), we report only

the variable or diagnostic features found in the remainder taxa of *E. cenchria* complex.

#### *Hemipenial Morphology*

Hemipenis terminology follows Dowling and Savage (1960), as augmented by Myers and Campbell (1981), Branch (1981), and Zaher (1999). Descriptions of the hemipenis are based on the examination of at least five everted organs for each taxon, except to *E. c. alvarezii* ( $n = 1$ ), as explained above. When necessary, inverted organs were prepared following the procedures proposed by Pesantes (1994) and recommendations from Dowling (2004) and Myers and Cadle (2003). Because of the similarities in hemipenial morphology among *Epicrates cenchria* complex members, we preferred to represent and to describe the features of the type species of the genus and report only the differences in the remainder taxa.

#### *Statistical Analysis*

We employed an analysis of variance (ANOVA) using segmental counts to test for sexual dimorphism within each group and within the whole sample, and performed descriptive analyses to summarize the morphometric and meristic variation within the sample.

All groups were analyzed by two distinct treatments. In a first approach, discriminant function analysis (DFA; Manly, 2000) and multivariate analysis of the variance (MANOVA; Zar, 1999) were employed to verify morphological variation between and within each subspecies of *Epicrates cenchria* in order to evaluate the taxonomic status of these categories. Each subspecies currently recognized (*sensu* McDiarmid et al, 1999) was used as a distinct group in this first treatment. We preferred to consider *E. maurus* as a monotypic group part of the *E. cenchria* complex not considering Matz (2004) proposal (see remarks of the *E. maurus* for justification to this procedure).

A second DFA was performed with redefined groups based on results of the previous analysis, when some groups could be not discriminated. In a second approach, principal component analysis (PCA; Manly, 2000) was performed in order to evaluate the distribution of individuals (both applied to currently recog-

nized subspecies, as well as from redefined groups) in multivariate space without *a priori* definition of group. This procedure allows checking if the groups discriminated by DFA correspond to those found in PCA. The recognition of very discordant patterns between these two approaches might imply necessitate of the reconfiguration of some groups.

Due to discrepancies in the sample size between groups we performed the posterior comparisons of MANOVA by the Tukey test for unequal samples (Spjøtvoll and Stoline, 1973). Still, the assumption concerning both analyses (PCA and DFA) require equivalency in covariance matrices, as well as normality in the data distribution within each group (Manly, 2000), we used the bootstrap method (Efron, 1979) with 1000 pseudo-replications to access the variance bias, as well as for robustness test of the obtained results. Assumptions of univariate normality and homocedasticity were evaluated with the Kolmogorov-Smirnov's and Levene's test, respectively (Zar, 1999). We estimated the missing values for DFA and PCA analyses through a *missing* function from MATLAB software, but in the remaining analyses the missing values were not computed. Individuals or variables with missing data above 30% were not considered in the statistical analysis.

All statistical inferences were performed with MATLAB 4.2c1 (MATHWORKS, 1994), except for MANOVA, classificatory matrixes, and normality and homocedasticity tests, which were performed with STATISTICA 5.1 (STATISOFT, 1995). Some characters were not used in the statistical analysis because they showed insufficient variation to justify the assumption of normality. The following characters were employed in the statistical analyses: ADORS, MDORS, PDORS, TDORS, VENT, SBCD, SUPRA, INFRA, INTSP, INTRC, PVENT, GULAR, RING, and OCEL.

#### *Species Concept and Diagnosis Criteria*

Species concepts have been a controversial point of discussion in the systematic literature of the last century (see Wheeler and Meyer, 2001 for a detailed review). Recently, De Queiroz (1998) pointed out those differences among species concepts are often rooted uniquely in divergent ontological views. Hence

in this study, we followed the general lineage species concept according to De Queiroz (1998, 1999). In spite of the considerable focus on the species concepts, methodological aspects of testing species boundaries has received little attention by most taxonomists (Benavides et al., 2002; Wiens and Servedio, 2000). From an operational perspective, some authors have emphasized that greater clarity would be achieved if investigators provide an *a priori* criteria by which species boundaries may be tested as a hypothesis and empirically accepted or rejected (Benavides et al., 2002; Sites and Crandall, 1997). In the present study, we consider the presence of one or more diagnostic characters that distinguish a given taxon from others, as species delimitation criteria (Davis and Nixon, 1992; Wiens and Servedio, 2000).

Some authors have suggested that the issue of deciding which characters are truly “fixed” is the most relevant question in the alpha taxonomic studies (e.g., Davis and Nixon, 1992; Wiens, 1999). Although some authors (Nixon and Wheeler, 1990; Davis and Nixon, 1992) advocated that only fixed characters are appropriate to infer species boundaries, Wiens and Servedio (2000) pointed out that fixation might be simply an artifactual result caused by small sample size. For that reason, these authors proposed a more realistic procedure, which recognize characters as diagnostic for species if they attain a certain cutoff frequency with a high degree of statistical confidence. We employ this approach, using a character frequency cutoff of 10%, with a 5% confidence interval (Wiens and Servedio, 2000). Therefore, we explicitly diagnose taxa as species if they attain the cutoff frequency for putative “fixed” diagnostic characters in the Wiens-Servedio test (WST). The WST test was employed after we performed the morphometrical framework, searching by concordance between quantitative and qualitative characters support of the species boundaries.

## RESULTS

### *Conservative Morphological Features among Continental Epicrates*

All continental *Epicrates* are characterized by, at least in juvenile stage, a conspicuous

color pattern with dark rings dorsally and ocelli laterally. All taxa of the study group have relatively conservative external morphology that is generally in agreement with the following characteristics: head well distinct from neck; rostral broader than high, well visible in dorsal view; internasals as wide as long; nasal divided in prenasal and postnasal; nostril located between pre- and postnasal; prenasal contacting rostral anteriorly, internasal dorsally, and first supralabial ventrally; postnasal contacting prefrontal dorsally, second supralabial ventrally, and loreal posteriorly; posterior to internasals there are two large prefrontals generally with “V” arrangement, diverging posteriorly, about twice longer than wide; frontal slightly longer than wide, generally with hexagonal shape in dorsal view; supraoculars generally twice longer than wide; preoculars as high as wide; loreals rectangular, twice longer than high, placed between nasals and preoculars; distance between eye and border of mouth less than eye diameter; pupil vertical or sub-elliptical; postoculars generally four, upper in contact with supraoculars and lower with supralabials; upper and lower labials with distinct shallow pits or impressions between them; dorsal scales smooth without apical pits, keels or supra-anal tubercles; anal plate entire; body rounded and robust; tail moderate and cylindrical; caudal spine short, robust, conical, and rhomboidal.

The general osteological features agree well with described by Frazzetta (1959), but we observed a few conservative traits discordant or not commented in that paper as: septomaxillary and nasal bones considerably shorter than those figured on that paper (Fig. 1A); dorsally to alary processes of vomers, there are two other processes (*process palatine*) of vomers, both curled upward and oriented directly to parasphenoid process of palatine (Fig. 1B); *processus medialis* of maxillary bone is poorly developed, compared to Frazzetta’s picture (Fig. 1C–D).

All continental *Epicrates* have hemipenes strongly bilobed, bifurcating for about one third of the hemipenial body; proximal half of basal portion of hemipenial body nude and the distal half encircled by fleshy transverse flounces; just bellow of first flounce there is a

stout basal papilla; spermatic sulk with centrolineal orientation running medially to about lobes tips; branches completely encircled by several papillate rows more or less conspicuous.

### *Morphometrical Analyses*

Results of a multivariate analysis of variance were unable to find significant sexual dimorphism in all analyzed groups despite the large sample for each taxon. Therefore, males and females were treated together in all subsequent analyses. In the first approach, MANOVA showed significant differences ( $W = 0.0074$ ;  $P < 0.001$ ;  $n = 455$ ) among all groups. Posterior comparisons using the Tukey test for unequal samples (Spjotvoll and Stoline, 1973) have also revealed significant differences between each group. Despite these results, the great discrepancy in sample size among some groups (e.g., *E. c. crassus*  $n = 135$  vs. *E. c. alvarezi*  $n = 24$ ) violated the assumptions of these tests and may generate a type I error (see Zar, 1999). Furthermore, homogeneity of variance-covariance matrices is not supported by the Levene's test to some groups. Consequently, the results of the DFA and PCA, with bootstrap of the 1000 pseudo-replications, should be preferred (Manly, 2000; Benavides et al., 2002).

Discriminant analysis showed significant differences for some groups, both in the classificatory function (Tab. 1) and in the plot of the canonical scores (Fig. 2). Orthogonal comparisons of DFA differentiate some groups through the first two axes, which correspond to 73–90% of the entire variation, and were significantly correlated, based on the plot of directional cosines (data not shown), to following variables: OCEL, RING, SUBCD, and VENT. The combination of the third discriminant function, with the first or second functions, showed no satisfactory discrimination of the groups. *Epicrates cenchria gaigei* and *E. c. hygrophilus* attained no sufficient discrimination in relation to *E. c. cenchria*, *E. c. polylepis* could not be distinguished from *E. c. crassus*, and *E. c. barbouri* was not differentiated from *E. c. maurus*. In spite of the partial overlapping in the orthogonal comparisons, *E. c. assisi* and *E. c. maurus* were considered as distinct groups for the next

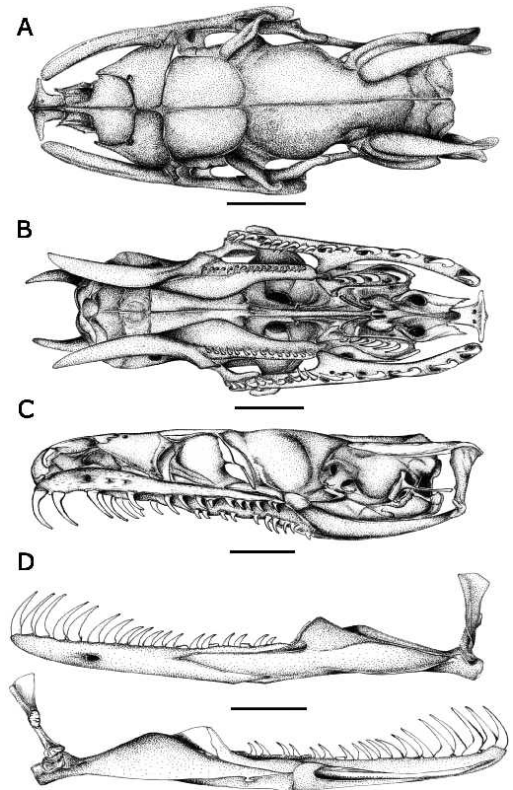


FIG. 1.—Dorsal (A), ventral (B), and lateral (C) views of the skull, and lateral and medial (D) views of the mandible of *Epicrates cenchria* (MNRJ 1447). Ruler equals to 5 mm.

analysis based on the values above 90% of correct allocation by classificatory function (Table 1), and through qualitative characters that diagnose them from all other members of the complex (see below session). Based on the results above, the major groups defined to the second analysis were *E. c. cenchria* (including *E. c. gaigei* and *E. c. hygrophilus*), *E. c. crassus* (including *E. c. polylepis*), *E. c. maurus* (including *E. c. barbouri*), *E. c. alvarezi*, and *E. c. assisi*.

In the second analysis, DFA achieved significant differences for every group defined in the previous analysis, both in orthogonal comparisons (Figs. 3–4) and classificatory function (Table 2). The first two axes correspond to 78–95% of the entire variation, and were heavily correlated to the same original variables as found in the previous analysis. Although first two axes from DFA could not

TABLE 1.—Classificatory matrix from DFA analysis to all subspecies of *Epicrates cenchria* (sensu McDiarmid et al., 1999), showing the individuals correctly allocated based on the classification by Jackknife. Level of significance ( $\alpha$ ) to correct allocations is  $P \leq 0.1$ . The numbers in the row heading correspond to the taxa at first column.

Taxon	% correct allocation	1	2	3	4	5	6	7	8	9
		$P = 0.10$	$P = 0.28$	$P = 0.19$	$P = 0.08$	$P = 0.18$	$P = 0.09$	$P = 0.05$	$P = 0.06$	$P = 0.07$
<i>E. c. cenchria</i> (1)	79.7	59	0	2	10	0	0	0	0	3
<i>E. c. crassus</i> (2)	95.0	0	129	2	0	0	0	0	4	1
<i>E. c. assisi</i> (3)	97.0	1	0	89	0	0	0	0	1	1
<i>E. c. hygrophilus</i> (4)	75	9	0	1	30	0	0	0	0	0
<i>E. c. barbouri</i> (5)	62.5	0	0	0	0	5	3	0	0	0
<i>E. c. maurus</i> (6)	93.0	0	0	0	0	3	39	0	0	0
<i>E. c. alvarezii</i> (7)	100	0	0	0	0	0	0	25	0	0
<i>E. c. polylepis</i> (8)	68.0	0	6	3	0	0	0	0	19	0
<i>E. c. gaigei</i> (9)	78.1	2	0	1	3	0	1	0	0	25
Total	88.0	71	135	98	43	8	43	25	24	30

discriminate significantly *Epicrates c. alvarezii* from *E. c. maurus* (including *E. c. barbouri*) groups (Fig. 3A), combination of first with third axis differentiates entirely both groups (Fig. 3B). The third axis was much correlated, based on the directional cosines (data not shown), with the following variables: ADORS, MDORS, INTRC, and VENT. The MANOVA (Table 3) for these redefined groups entirely corroborated DFA results. Although in the second approach there were some overlapping groups regarding the DFA, PCA find a similar pattern of distribution for those groups in the multivariate space (Fig. 4, Tables 4–5) supporting the redefined groups.

#### Geographical Variation and Diagnosis of *Epicrates cenchria* Complex

Few morphological features that can diagnose some currently recognized subspecies of *Epicrates cenchria* exhibit no true population-level fixation or overlap a continuous range of

variation among conspecifics. *Epicrates cenchria hygrophilus* has one supralabial scale contacting the orbit, which distinguishes this taxon from all other continental *Epicrates* populations. Nevertheless, this character shows a high level of polymorphism, with 40% of the Atlantic Rainforest specimens showing the alternate state (two scales contacting the orbit). Another distinctive feature of this taxon is a lighter dorsal ground color, varying from pale to yellow reddish. Even so, either Atlantic or Amazon populations show considerable variation in dorsal ground color, with a color gradient occurring along specimens from the Atlantic Rainforest population. Amaral (1954) described *E. c. hygrophilus* from the Brazilian state of Espírito Santo on the basis of pholidosis characters (number of ventrals, subcaudals, supralabials, and infra-labials scales). However, the author did not comment that variation of *E. c. hygrophilus* completely overlapped with *E. c. cenchria* (see table IV in Amaral, 1954). Apparently, Amaral (1954) considered this disjunct pattern of distribution as a sufficient evidence to recognize a new taxon in subspecific rank (see Discussion). In our study *E. c. hygrophilus* showed no significant discrimination in all statistical tests relative to the Amazon Forest population *E. c. cenchria* (Fig. 2 and 4A). Besides, the analysis of qualitative characters, as well as augmented to the examination of the types showed no differences between them. Therefore, *E. c. hygrophilus* is herein synonymized with the nominal subspecies *E. c. cenchria*.

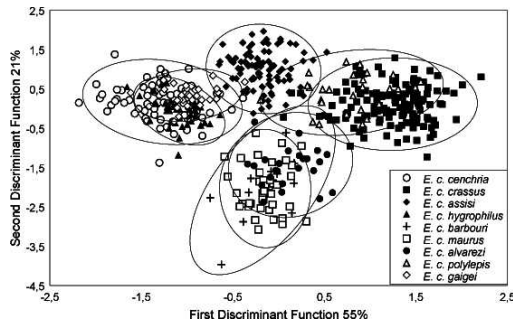


FIG. 2.—Bivariate plot with 95% confidence regions for the first two axes derived from scores of DFA analysis for all subspecies of *Epicrates cenchria*.

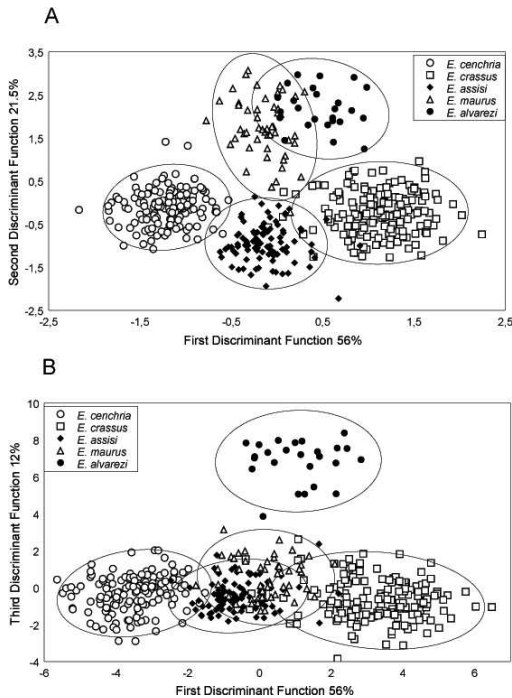


FIG. 3.—Bivariate plot with 95% confidence regions for the first two axes (A) and (B) for first and third axis derived from scores of DFA analysis for redefined groups (see Material and Methods for explanations) of *Epicrates cenchria*.

Similar to *Epicrates cenchria hygrophilus* individuals, about 50% of the *E. c. gaigei* specimens have eight gular scales, which differentiate this taxon from other continental *Epicrates*. Furthermore, this subspecies attained no significant discrimination in all statistical analyses performed from *E. c. cenchria* (Fig. 2A and 4A). Stull (1938) distinguished the Bolivian subspecies *E. c. gaigei* from the *E. c. cenchria* based on the fewer number of dorsal scales rows (40–43 vs. 47–51). We found this diagnostic character to be an artifact from a small sample size ( $n = 8$  in Stull, 1938), because it is within the known variation of nominal subspecies (see below). Moreover, our quantitative and qualitative analyses, including the examination of the type series, revealed that the meristic and color pattern characters of the *E. c. gaigei* are indistinguishable from *E. c. cenchria* (Fig. 2A and 4A). Additionally, the known distribution of *E. c. gaigei* is contiguous to the range of *E. c. cenchria* in the Amazon Basin, and some

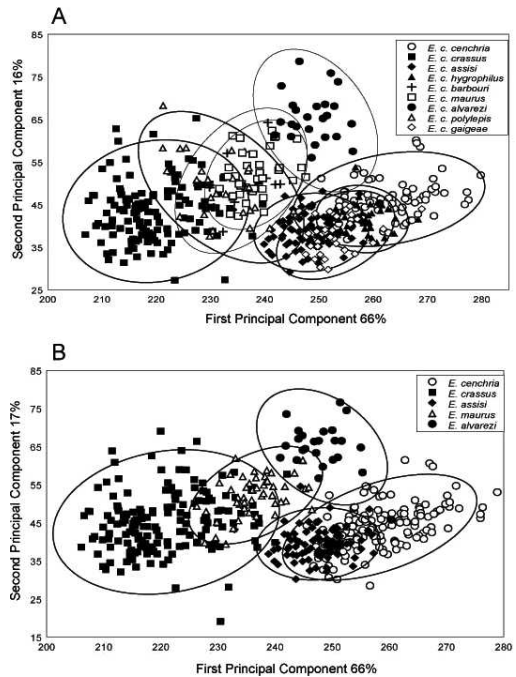


FIG. 4.—Bivariate plot with 95% confidence regions for the first two axes derived from scores of PCA analysis for all subspecies of *Epicrates cenchria* (A), and (B) to redefined groups (see Material and Methods for explanations).

authors have noticed the occurrence of both in the same region (Dixon and Soini, 1977; Fugler and Cabot, 1995). Our results suggest that *Epicrates cenchria* (including *E. c. gaigei* and *E. c. hygrophilus*) comprises a uniform group distributed along Equatorial Forest of the South America, with an isolated population in the Atlantic Rainforest of Brazil (see Discussion). Therefore, according to the priority of Linnaeus's description we relegated *E. c. gaigei* also for synonymy of *E. c. cenchria*.

Two other subspecies achieved no significant discrimination in the morphometrical analyses (*Epicrates cenchria barbouri* and *E. c. polylepis*) and could not be distinguished through any qualitative characters (seeming fixed or not). Stull (1938) described *Epicrates cenchria barbouri* from Marajó Island, State of Pará, northern Brazil, based on the fewer number of dorsal scales of midbody and lower supralabials scales (45 and 11, respectively;  $n = 1$ ; Stull, 1938). Nevertheless, the distribution of these characters completely overlaps



TABLE 2.—Classificatory matrix from DFA analysis to the five reconfigured groups, showing the individuals correctly allocated based on the classification by Jackknife. Level of significance ( $\alpha$ ) to correct allocations is  $P \leq 0.1$ . The numbers in the row heading correspond to the taxa at first column.

Taxon	% Correct allocation	1	2	3	4	5
		$P = 0.3$	$P = 0.3$	$P = 0.3$	$P = 0.1$	$P = 0.05$
<i>E. c. cenchria</i> (1)	97.3	142	0	4	0	0
<i>E. c. crassus</i> (2)	96.0	0	157	7	0	0
<i>E. c. assisi</i> (3)	95.0	4	1	87	0	0
<i>E. c. maurus</i> (4)	100	0	0	0	50	0
<i>E. c. alvarezi</i> (5)	100	0	0	0	0	25
Total	97.0	146	158	98	50	25

with the range of *E. c. maurus*, according to our study. Both holotypes are similar in all morphological characters except by a distinct color pattern, which probably lead the last authors (Amaral, 1954; Chippaux, 1986; Cunha and Nascimento, 1993; Stimson, 1969; Stull, 1938) to recognize the two taxa as well. In effect, this species has an ontogenetic change in coloration that was only recently noted (Savage, 2003). The type specimens showed the extremes phases of variation in color pattern characters, with *E. c. barboursi* showing a juvenile and *E. c. maurus* showing an adult pattern (Figs. 9, 10). Consequently, *E. c. barboursi* is synonymized with *E. c. maurus*.

*Epicrates c. polylepis* obtained a poorly discrimination from *E. c. crassus* in all analyses performed (Fig. 2A and 4A). Despite of some meristic characters (e.g., number of ventral and subcaudals) show slightly differences in their averages, there is a large overlapping in the total range of variation presented by these taxa. Amaral (1954) described *E. c. polylepis* based on four

specimens from a region between the States of Goiás and Minas Gerais in Brazil. He distinguished *E. c. polylepis* from *E. c. crassus* on the basis of high number of dorsal (47–55 vs. 40–46) and subcaudal scales (46–54 vs. 34–43). However, Amaral's (1954) characters, after examination of a large sample, including the types series, fails to discriminate either, and a south/north cline is apparent on the scale counts (see DISCUSSION). Therefore, we synonymize *E. c. polylepis* with *E. c. crassus*.

The other two taxa, *Epicrates cenchria assisi* and *E. c. alvarezi*, are recognized based on the results of morphometrical (Fig. 3A) and qualitative analyses (see below). *E. c. assisi* obtained significant discrimination from all other taxa from *E. cenchria* complex in the morphometric analysis. Additionally, the hemipenis of *E. c. assisi* along with the organ of *E. c. alvarezi* are remarkably different from all other continental *Epicrates* (see SYSTEMATIC ACCOUNTS). As the general hemipenial morphology is very conservative in the genus (see Sheplan and Schuwartz, 1974; Branch, 1981), this differentiation corrobo-

TABLE 3.—MANOVA with non planned comparisons based on the Tukey test for unequal sample (Spjøtvoll and Stolene, 1973) between the five reconfigured groups (see Material and Methods for explanation). The groups are: 1 = *E. c. cenchria*; 2 = *E. c. crassus*; 3 = *E. c. assisi*; 4 = *E. c. maurus*; 5 = *E. c. alvarezi*. Values in bold represent  $\alpha$  level below 95% ( $P \leq 0.05$ ).

Contrast	ADORS	MDORS	PDORS	TDORS	VENT	SUBCD	SUPRA	INFRA	INTSP	INTRC	RING	OCEL
1 × 2	<b>0.01</b>	<b>0.01</b>	0.5	<b>0.01</b>	<b>0.01</b>	<b>0.01</b>	0.1	0.2	1	<b>0.05</b>	<b>0.01</b>	<b>0.01</b>
1 × 3	<b>0.01</b>	<b>0.01</b>	0.2	<b>0.05</b>	<b>0.01</b>	<b>0.05</b>	<b>0.01</b>	<b>0.01</b>	<b>0.01</b>	<b>0.01</b>	1	<b>0.01</b>
1 × 4	0.09	0.19	0.3	0.2	<b>0.01</b>	0.2	<b>0.05</b>	0.9	1	0.9	0.7	0.4
1 × 5	<b>0.01</b>	<b>0.01</b>	<b>0.01</b>	<b>0.01</b>	<b>0.01</b>	<b>0.01</b>	0.2	<b>0.05</b>	<b>0.01</b>	<b>0.01</b>	<b>0.01</b>	<b>0.01</b>
2 × 3	<b>0.01</b>	<b>0.01</b>	<b>0.05</b>	<b>0.01</b>	<b>0.01</b>	<b>0.01</b>	<b>0.01</b>	<b>0.01</b>	<b>0.01</b>	<b>0.01</b>	<b>0.01</b>	0.9
2 × 4	0.8	<b>0.01</b>	0.1	<b>0.01</b>	<b>0.05</b>	<b>0.01</b>	<b>0.01</b>	1	0.8	1	0.7	<b>0.01</b>
2 × 5	<b>0.01</b>	<b>0.01</b>	<b>0.01</b>	<b>0.01</b>	<b>0.01</b>	<b>0.01</b>	0.7	<b>0.01</b>	<b>0.01</b>	<b>0.01</b>	0.4	<b>0.01</b>
3 × 4	0.6	0.6	0.9	1	<b>0.01</b>	1	<b>0.01</b>	<b>0.05</b>	<b>0.01</b>	<b>0.01</b>	0.6	<b>0.01</b>
3 × 5	<b>0.01</b>	<b>0.01</b>	<b>0.01</b>	<b>0.01</b>	0.8	<b>0.01</b>	<b>0.01</b>	1	<b>0.01</b>	<b>0.01</b>	<b>0.01</b>	<b>0.01</b>

TABLE 4.—Eigenvectors, eigenvalues, and percent variance explained for the first three axes of principal component analysis of non-transformed data for all subspecies of *Epicrates cenchria* (sensu McDiarmid et. al, 1999). Loadings in bold font correspond to the original variables heavily correlated with the respective principal components.

Variable	PC I	PC II	PC III
ADORS	0.0666	<b>0.1438</b>	0.0011
MDORS	0.0932	<b>0.1698</b>	0.0167
PDORS	0.0275	0.0769	-0.0341
VENT	<b>0.8487</b>	-0.1152	<b>0.3777</b>
SUBC	<b>0.4209</b>	-0.0515	<b>-0.1806</b>
SUPRA	0.0072	-0.0164	0.0609
INFRA	0.0184	0.0192	0.0169
INTSP	0.0029	0.0103	0.0184
INTRC	0.0360	0.0862	0.0312
TDORS	0.0268	0.0450	-0.0088
RING	<b>-0.1242</b>	<b>0.6994</b>	<b>0.6400</b>
OCEL	<b>0.2660</b>	<b>0.6521</b>	<b>-0.6239</b>
Eigenvalues	287.04	69.29	31.57
Percent of variance	66.36	16.02	7.30

rates the morphometrical results supporting recognition of both. Furthermore, *E. c. alvarezi* is the most distinct taxa among the continental *Epicrates*, showing several exclusive morphological features (see below).

The application of WST test for discrete characters (Table 6) entirely corroborates, except for comparisons between *Epicrates c. assisi* and *E. c. crassus* (but see below), the results of morphometric analyses. Nonetheless, the test does not identify which characters for each taxon are above the cutoff level (Wiens and Servedio, 2000). Although *Epicrates c.*

*assisi* and *E. c. crassus* not attained the cutoff level for all characters considered in the WST test, these taxa were significantly discriminate in all morphometrical analyses performed, and have very distinct hemipenial features (see Systematic Account). Nevertheless, hemipenis characters were not considered to WST test (see DISCUSSION). Finally, based on the morphometrical analyses in accordance to WST results the following taxa are here recognized as full species among continental *Epicrates*: *E. cenchria*; *E. maurus*; *E. crassus*; *E. assisi*; *E. alvarezi*.

TABLE 5.—Eigenvectors, eigenvalues, and percent variance explained for the first three axes of principal component analysis of non-transformed data for reconfigured groups of *Epicrates cenchria* (see Material and Methods for explanation). Loadings in bold font correspond to the original variables heavily correlated with the respective principal components.

Variable	PC I	PC II	PC III
ADORS	0.0699	<b>0.1369</b>	-0.0062
MDORS	0.0933	<b>0.1605</b>	-0.0079
VENT	0.0271	0.0728	-0.0409
SUBC	<b>0.8462</b>	-0.1149	0.4011
SUPRA	<b>0.4197</b>	-0.0284	<b>-0.2062</b>
SUPRA	0.0070	-0.0144	0.0601
INFRA	0.0185	0.0212	0.0121
PVENT	0.0150	0.0047	0.0169
SULK	-0.0036	0.0025	0.0001
INTSUP	0.0032	0.0103	0.0171
INTRC	0.0351	0.0848	0.0192
GULAR	0.0014	0.0506	-0.0041
TDORS	0.0243	0.0234	0.0024
RING	<b>-0.1339</b>	<b>0.7104</b>	<b>0.6323</b>
OCEL	<b>0.2700</b>	<b>0.6461</b>	<b>-0.6230</b>
Eigenvalues	287.22	70.29	29.68
Percent of variance	66.4	16.1	6.9

SYSTEMATIC ACCOUNTS

***Epicrates cenchria*** (Linnaeus, 1758)  
(revalidated status)  
(Fig. 5, 6A)

[*Boa*] *cenchria* Linnaeus, 1758; Syst. Nat. 10th ed. 1:215. *Terra typica*: Surinam. Holotype: NRS Lin. 6.

*Coluber tamachia* Scopoli, 1788; Delic. Flor. Faun. Insubr. 3:28. *Terra typica*: Brazil. Holotype: not traced.

*Boa cenchris* Gmelin, 1788; Syst. Nat. 13th ed. 1:1083. (New spelling to *Boa cenchria* Linnaeus).

*Boa aboma* Daudin, 1803; Hist. nat. Rept. 5:132 (*nomen substitutum* for *Boa cenchria* Linnaeus).

*Boa ternatea* Daudin, 1803; Hist. nat. Rept. 5:153. *Terra typica*: "Moluques". Holotype: presumed lost.

*Boa annulifer* Daudin, 1803; Hist. nat. Rept. 5:202. *Terra typica*: South América. Holotype: presumed lost.

[*Epicrates*] *cenchria* — Wagler, 1830; Nat. Syst. Amph.:168.

*Epicrates cenchris* — Duméril & Bibron, 1844; Erp. Génér. 6:555.

*Epicrates cenchria cenchria* — Amaral, 1930 [1929]; Mem. Inst. Butantan 4:140.

*Epicrates cenchria gaigei* Stull, 1938; Occ. Pap. Boston Soc. nat. Hist. 8:300. *Terra typica*: Buena Vista, Santa Cruz, Bolivia. Holotype: UMMZ 77236. **New synonymy.**

*Epicrates cenchria hygrophilus* Amaral, 1954; Mem. Inst. Butantan 26:239. *Terra typica*: Baixo Guandu, Rio Doce, Espírito Santo, Brazil. Holotype: IBSP 8445. **New synonymy.**

*Epicrates cenchria* — Chippaux, 1986; Fauna Trop. 27: 36.

*Epicrates cenchria cenchria* — Pérez-Santos & Moreno, 1988; Mus. Reg. Sci. Nat. 7:43. *Holotype*.—Adult specimen housed at NRS under number 6 Lin., from Surinam. Anderson (1899) listed this as number 322 (specimen photographs examined).

*Diagnosis*.—Distinguished from all continental species of *Epicrates* by having: (1) non-collapsed lateral ocelli, (2) dorsal ground color pale to yellow reddish, (3) SVL > 1500 mm, (4) lateral process of surangular much expanded latero-posteriorly. Additionally, *E. cenchria* differ from *E. crassus*, *E. maurus*,

TABLE 6.—Discrete putative fixed diagnostic characters used in the WST test for previous discriminated subspecies of *Epicrates cenchria*. The cut-off frequency adopted is the 10% and 5% confidence interval. Abbreviations correspond to: Dg = dorsal ground color gray; Db = dorsal ground color brown; Dr = dorsal ground color reddish; Dyb = dorsal ground color yellow (juveniles) or uniform brown (adults); Dt = number of dentary teeth > 21; FRa = frontal plate absent or reduced; FRt = frontal plate typical; HSp = head stripe parallel at the neck; HSt = head stripes arranged in a trident shape like; Ld = loreal plate divided; Le = loreal plate entire; LSa = lateral body stripe absent; LSp = lateral body stripe present; Or = regular ocelli; Oi = irregular ocelli; PFj = prefrontal plates juxtaposed; PFD = prefrontal divergent; SCc = symphyisial-chinshield contact; SCs = symphyisial-chinshield separated by the first pair of infralabials; SVLh = maximum snout-vent length superior to 1500 mm, SVLl = maximum snout-vent length inferior to 1500 mm.

Taxa	1	2	3	4	5
<i>E. c. albarezi</i> (1) <i>P</i> < 0.05		Dg, FRa, HSp, Ld, LSa, PFj, SCc,	Dg, FRa, HSp, Ld, PFj, SCc	Dg, FRa, Ld, LSa, PFj, SCc	Dg, FRa, HSp, Ld, LSa, PFj, SCc
<i>E. c. assisi</i> (2) <i>P</i> < 0.05	Db, FRt, Le, LSp, PFd, SCs		Db, HSp, LSp, SVLl	—	Db, HSp, Oi
<i>E. c. cenchria</i> (3) <i>P</i> < 0.01	Dr, Dt, HSt, MSVLh	Dr, HSt, LSa, MSVLh		Dr, HSt, LSa, MSVh	Dr, LSa, Or, MSVh,
<i>E. c. crassus</i> (4) <i>P</i> < 0.05	Db, FRt, Le, LSp, PFd, SCs	—	Db, HSp, LSp, SVLl		Db, HSp, Oi
<i>E. c. maurus</i> (5) <i>P</i> < 0.05	Dyb, Dt, FRt, HSt, Le, LSp, Oi, PFD, SCs	Dyb, HSt, Oi	Dyb, LSp, Oi	Dyb, HSt, Oi	

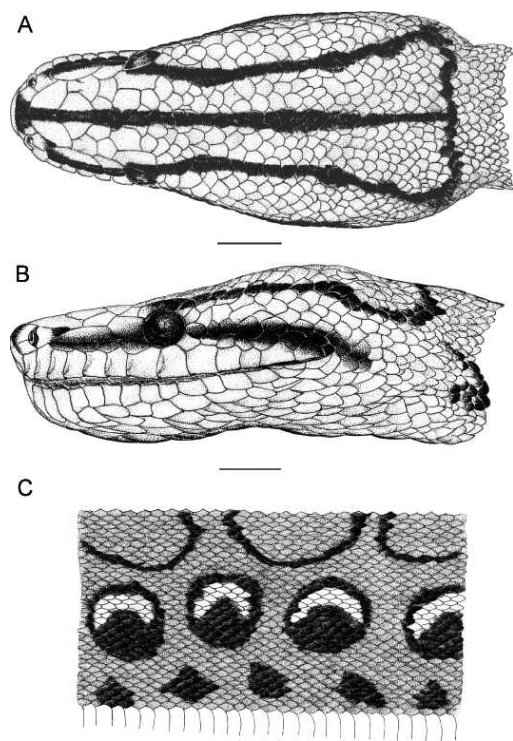


FIG. 5.—Dorsal (A), lateral (B), and midbody (C) views of the head and body, respectively of *Epicrates cenchria* (MNRJ 3038). Ruler equals to 5 mm.

and *E. assisi* by having alary process of vomer laterally expanded; from *E. crassus* and *E. maurus*, by having ventral scales > 245; from *E. crassus* by having subcaudal scales generally > 45; from *E. alvarezii* by having inverted hemipenis bifurcates at fifth and extends to the level of tenth subcaudal. Refer to Tables 6–7 for additional diagnostic features of the continental *Epicrates*.

**Meristic and morphometric variation.**—Largest specimen SVL 1850 mm, TL 255 mm, TL/SVL 14.0; maximum head length 62.0 mm and width 30.6 mm, head width/length 5.0; INTSP 2–4 (3.1, 0.4, 145); INTRC 17–24 (19.9, 1.4, 141); LORIL 3–6 (3.9, 0.3, 146); postoculars generally four, upper contacting supraoculars and lower 8–9<sup>th</sup> supralabials; SUPRA 11–15 (13, 0.6, 146), generally 7–8<sup>th</sup> (195 sides) contacting orbit; INFRA 13–18 (15.5, 0.8, 146), first two or three pairs contacting anterior chinshields; generally first pair of infralabials in contact

behind symphysial; GULAR 7–10 (8.7, 0.7, 144); SULK 3–6 (4.8, 0.7, 145); PVENT 3–7 (4.4, 0.8, 138); ADORS 30–40 (34.9, 2.1, 145); MDORS 39–54 (45.8, 3.3, 145); TDORS 22–30 (25.8, 1.6, 145); VENT 246–279 (259.5, 6.7, 143); SUBCD 45–68 (57.5, 3.5, 138).

**Color pattern in preservative** (Fig. 6A).—Dorsum of head uniformly pale reddish, except by three black longitudinal stripes arranged with trident form; central stripe (generally two scales wider) extending from snout to neck, and lateral stripes (generally one scale wider) extending from supraoculars to neck, both contacting central stripe posteriorly; head laterally with black stripe (two scales wider), originates on snout and extends through orbit to mouth articulation angle; supralabials and infralabials generally pale reddish, eventually darker in adult specimens; mental region uniformly creamish white; dorsal ground color of body pale to yellow reddish, with 20–44 (43.8, 5.6, 144) black rings; black rings with light center, occasionally collapsed at anterior and posterior portions of body; body with 36–52 (42.6, 3.5, 143) dark lateral ocelli; each ocelli having dorsal portion white bordered (generally three scales wider), resembling last quarter moon; ventrally to ocelli, there are several irregular dark brown blotches arranged among interspaces; paraventral region with small diffuse dark brown blotches, eventually overlapping lateral edges of ventral scales; ventral ground color mostly creamish white; occasionally lateral blotches overlaps belly posteriorly.

**Hemipenis** (Fig. 7A).—Inverted hemipenis bifurcates at 6–7<sup>th</sup> (6.2, 0.4, 5) and extends to the level of 10–13<sup>th</sup> (11, 1.2, 5) subcaudal. Everted organ deeply bilobed; lobes slightly smaller than hemipenial body, approximately twice longer than wide, and with clavate form in frontal view; proximal half of basal portion of hemipenial body nude; distal half encircled transversely by six overlapping fleshy flouces; on the asulcate side, below to first flounce, there is stout basal papilla; margins of spermatic sulks stout; spermatic sulks bifurcating approximately between third and fourth flouces; branches running almost to tips of lobes, with centrolinal orientation; each lobe covered by series of large papillae in the sulcate and asulcate sides.

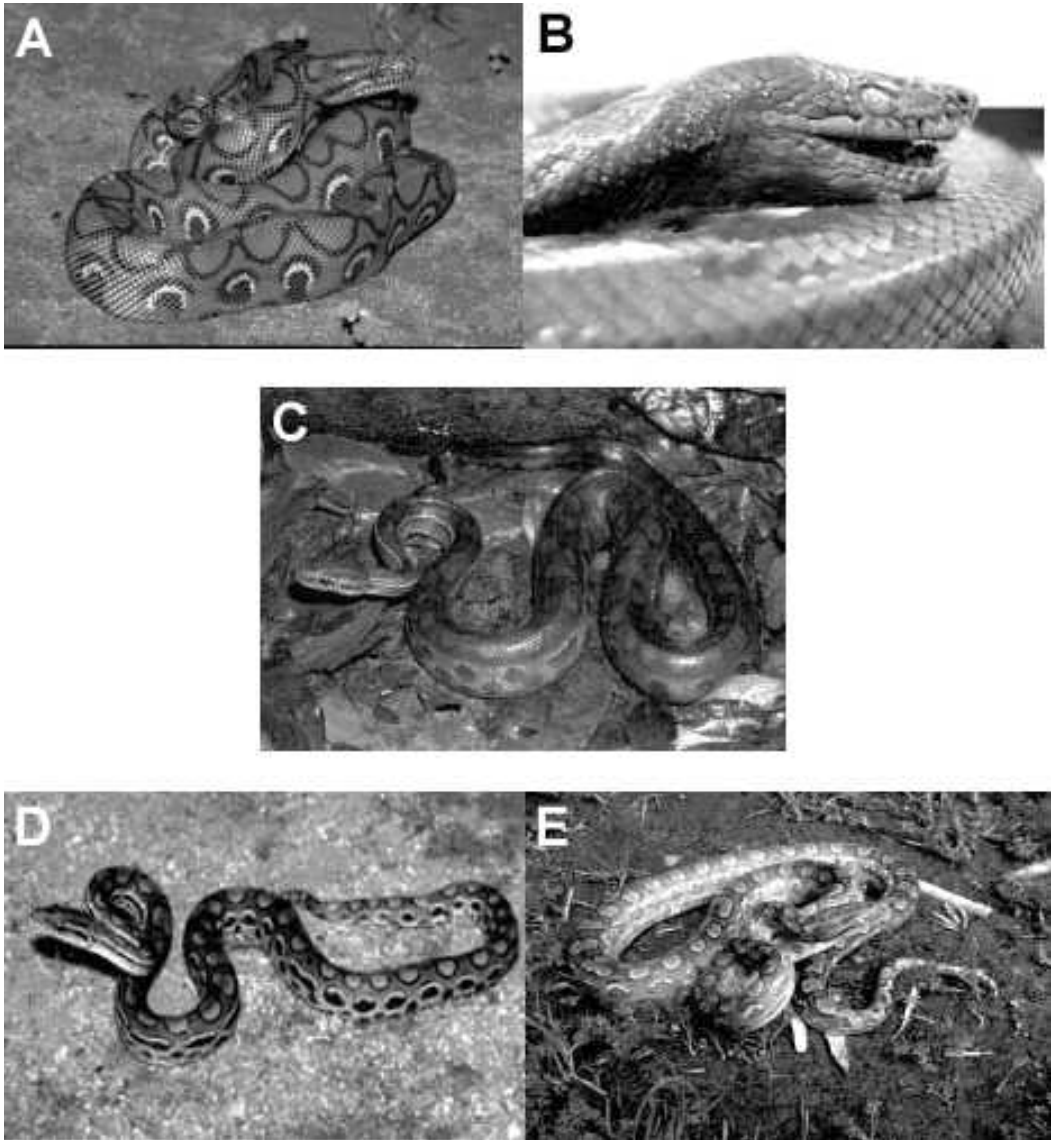


FIG. 6.—General view of *Epicrates cenchria* (A), *Epicrates maurus* [holotype] (B), *Epicrates crassus* (C), *Epicrates assisi* (D), and *Epicrates alvarezii* (E).

*Cranium* (Fig. 1).—Alary process of vomers and parietal crest strongly developed; supra-temporals with cranial portion attached next to parietal crest and either caudal portion diverging to about  $45^\circ$  posteriorly; lateral process of surangular strongly developed caudally; maxillary 20–24 (22.2, 1.3, 10); dentary teeth 21–24 (21.9, 1.3, 10); palatine bones with five teeth ( $n = 10$ ).

*Distribution* (Fig. 8).—Forested Amazon Basin of Colombia, Ecuador, Peru, Bolivia, Venezuela, Guyana, Suriname, French Guyana, and Brazil. There is a disjunct population in Atlantic Forest of Brazil from the States of Alagoas to Rio de Janeiro. This species inhabits Amazonian and Atlantic rain-forest plant formations, and are not found in syntopy with anyone congener. Even so, it

TABLE 7.—Comparative table based on selected continuous characters among the recognized mainland species of *Epicrates*. The values for each quantitative variable correspond to mean,  $\pm$  standard deviation, and range in parenthesis. Characters abbreviations are identical to the statistical analysis, except for: VENT+SUBC = ventral plus subcaudal scales; MAXt = maxillary teeth; DT = dentary teeth; HEML = hemipenis length for inverted organs.

Characters	<i>E. altarezi</i>	<i>E. assisi</i>	<i>E. cenchria</i>	<i>E. crassus</i>	<i>E. maurus</i>
ADORS	43.2 $\pm$ 1.2 (37–46)	36.3 $\pm$ 2.5 (31–42)	34.9 $\pm$ 2.1 (30–40)	33.5 $\pm$ 2.1 (26–39)	35.5 $\pm$ 2.0 (30–39)
MDORS	55.2 $\pm$ 2.2 (50–59)	49.3 $\pm$ 2.9 (42–56)	45.8 $\pm$ 3.3 (39–54)	44.3 $\pm$ 2.9 (32–54)	48.3 $\pm$ 2.4 (43–53)
VENT	248.3 $\pm$ 4.6 (241–260)	251 $\pm$ 4.4 (240–260)	259.6 $\pm$ 6.6 (246–279)	228.4 $\pm$ 7.2 (214–247)	235.3 $\pm$ 3.9 (228–246)
VENT+SBC	296 $\pm$ 5.5 (290–309)	305.7 $\pm$ 6.0 (282–318)	316.9 $\pm$ 9.2 (300–342)	269.2 $\pm$ 12.6 (186–312)	289.5 $\pm$ 5.7 (278–303)
SBCD	49.9 $\pm$ 2.9 (44–56)	54.7 $\pm$ 3.4 (40–60)	57.5 $\pm$ 3.5 (45–68)	41.3 $\pm$ 3.9 (33–52)	54.2 $\pm$ 2.7 (49–61)
SUPRA	13.5 $\pm$ 0.7 (11–15)	14.1 $\pm$ 0.4 (13–16)	13 $\pm$ 0.6 (11–16)	13.2 $\pm$ 0.7 (11–16)	12.1 $\pm$ 0.5 (11–14)
INFRA	16.5 $\pm$ 1.0 (14–18)	16 $\pm$ 0.7 (14–18)	15.5 $\pm$ 0.8 (13–18)	15.1 $\pm$ 0.8 (13–18)	15.6 $\pm$ 0.9 (13–18)
INFMC	1.7 $\pm$ 0.4 (1–2)	2.3 $\pm$ 0.5 (2–4)	2.6 $\pm$ 0.4 (2–3)	2.4 $\pm$ 0.4 (2–3)	2.2 $\pm$ 0.4 (2–3)
LORL	4.7 $\pm$ 0.4 (4–5)	4.0 $\pm$ 0.3 (3–5)	3.9 $\pm$ 0.3 (3–6)	3.5 $\pm$ 0.5 (2–5)	3.1 $\pm$ 0.4 (2–4)
INTRC	25.4 $\pm$ 1.4 (23–29)	21.5 $\pm$ 1.8 (17–26)	19.9 $\pm$ 1.4 (17–24)	19.4 $\pm$ 1.5 (17–24)	19.9 $\pm$ 1.4 (18–23)
GULAR	11.8 $\pm$ 0.6 (10–13)	9.1 $\pm$ 0.4 (8–10)	8.7 $\pm$ 0.7 (7–10)	9.0 $\pm$ 0.6 (7–11)	9.1 $\pm$ 0.7 (7–10)
RING	56.6 $\pm$ 7.1 (34–67)	43.8 $\pm$ 4.2 (36–58)	43.8 $\pm$ 5.6 (20–62)	50.8 $\pm$ 8.3 (32–83)	48.1 $\pm$ 4.5 (42–59)
OCEL	52.7 $\pm$ 4.2 (46–66)	31.7 $\pm$ 4.2 (22–42)	42.5 $\pm$ 3.5 (36–52)	31.4 $\pm$ 4.7 (22–45)	46.7 $\pm$ 6.5 (33–59)
MAXt	19.7 $\pm$ 0.6 (19–20)	20.7 $\pm$ 0.5 (20–21)	22.2 $\pm$ 1.3 (20–24)	20.7 $\pm$ 1.6 (18–22)	21.5 $\pm$ 1.7 (20–24)
MAnt	19.3 $\pm$ 0.6 (19–20)	21.2 $\pm$ 1.0 (20–22)	21.9 $\pm$ 1.3 (21–24)	20.5 $\pm$ 1.0 (18–22)	22.7 $\pm$ 1.3 (21–24)
HEML	6	9.3 $\pm$ 0.9 (8–11)	11 $\pm$ 1.2 (10–13)	12.7 $\pm$ 1.5 (11–15)	14.5 $\pm$ 0.6 (14–15)

occurs in sympatry with *E. maurus* in Venezuela, Colombia, Guyana, Suriname, French Guyana, and in the States of Roraima, Amapá, and Pará in Brazil; with *E. crassus* in Bolivia and in the Brazilian States of Mato Grosso, Goiás, Tocantins, and Minas Gerais; with *E. assisi* in Brazilian States of Alagoas, Bahia, and Pernambuco.

*Remarks.*—The controversy about the correct spelling of *Epicrates cenchria* begins with Gmelin (1789), who corrected “*cenchría*” to “*cenchrís*”. Posterior authors employed both forms indiscriminately (e.g., Amaral, 1929, 1935; Boulenger, 1896; Duméril and Bibron, 1844). Amaral (1954) established that the original form “*cenchría*” should be preferred following the recommendations of the International Code of Zoological Nomenclature. In fact, as Linnaeus (1758) used the combination *Boa cenchria*, being *Boa* a neuter genus, he apparently preferred to employ the feminine substantive “*cenchría*” (= an eagle from the Greek mythology). According to ICNZ (1999) and anterior editions, the original intention of the author should be maintained, and therefore we sustain the original spelling.

***Epicrates maurus* Gray, 1849**  
(Figs. 6B, 9, 10)

*Epicrates maurus* Gray, 1849; Cat. Snakes Brit. Mus.:96. *Terra typica*: Venezuela. Holotype: NHM 1946.1.10.40.

*Cliftia fusca* Gray, 1849; Cat. Snakes Brit. Mus.:99. *Terra typica*: “India”. Holotype: presumed lost.

*Epicarsius cupreus* Fischer, 1856; Abh. Geb. Naturwiss. Hamburg 3:96. *Terra typica*: Puerto Cabello, Apure, Venezuela.

*Epicrates cupreus* var. *concolor* Jan, 1864; Elenco sist. Ofidi:24. *Terra typica*: Costa Rica. Holotype: not traced.

*Epicrates cenchria* var. *fusca* — Griffin, 1916; Mem. Carnegie Mus. 7:168.

*Epicrates cenchria maurus* — Stull, 1935; Proc. Boston Soc. nat. Hist. 40:238.

*Epicrates cenchria barbouri* Stull, 1938; Occ. Pap. Boston Soc. nat. Hist.: 300. *Terra typica*: Ilha do Marajó, Pará, Brazil. Holotype: MCZ 22442. **New synonymy.**

*Epicrates maurus* — Chippaux, 1986; Fauna Tropic. 27:37.

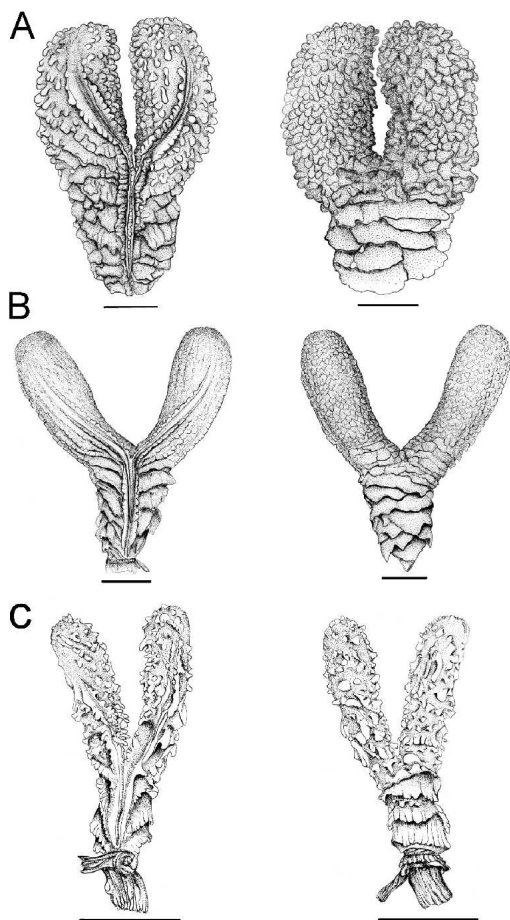


FIG. 7.—Sulcate and asulcate sides of the hemipenis of (A) *Epicrates cenchria* (MNRJ 1447), (B) *Epicrates assisi* (MNRJ 8338), and (C) *Epicrates alvarezii* (IBSP 9073). Ruler equals to 5 mm.

*Epicrates cenchria maurus* — Pérez-Santos & Moreno, 1988; Mus. Reg. Sci. Nat. 7:44.

*Epicrates maurus* — Gorzula & Señaris, 1998; Scientia Naturae 8:159.

*Epicrates cenchria maurus* — McDiarmid, Campbell & Touré, 1999; Snakes Spec. World 1:194.

*Epicrates maurus maurus* — Matz, 2004; Situla 10:4.

*Epicrates maurus colombianus* Matz, 2004; Situla 10:4. *Terra typica*: Barranquilla, Atlántico Department, Colombia. Holotype: MNHN 2000.4319. **New synonymy.**

*Epicrates maurus guayanensis* Matz, 2004; Situla 10:5. *Terra typica*: Mana, French

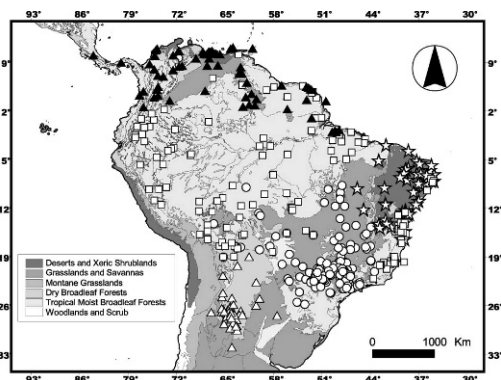


FIG. 8.—Geographical distribution of continental *Epicrates*. □ = *Epicrates cenchria*; ○ = *Epicrates crassus*; ▲ = *Epicrates maurus*; ☆ = *Epicrates assisi*; ▽ = *Epicrates alvarezii*.

Guyana. Holotype: MNHN 2000.4291.

#### **New synonymy.**

*Holotype*.—Adult male, NHM 1946.1.10.40 (formerly BMNH 46.7.23. 2a + vi.6.3a), from Venezuela (specimen examined).

*Diagnosis*.—Distinguished from all continental species of *Epicrates* by having: (1) lateral stripe of the body with four scales width, (2) irregular lateral ocelli in juvenile and indistinct in adults specimens, (3) dorsal ground color yellow to light brown in juveniles and uniform brown in adults, with noticeable ontogenetic change of coloration. Additionally, *E. maurus* differ from *E. cenchria*, *E. assisi*, and *E. alvarezii* by having hemipenis length (*in situ*) > 13 subcaudal scales long; from *E. cenchria* and *E. alvarezii*, by having barely conspicuous parietal crest and reduced alary process of vomer; from *E. cenchria*, by having ventral scales < 245; from *E. crassus*, by having subcaudal scales generally > 50. Refer to Tables 6–7 for additional diagnostic features of the continental *Epicrates*.

*Redescription of the holotype* (Figs. 6B and 9).—Head well distinct from neck, head length 38.0 mm, head width 23.4, head width/length 0.54; SVL 1045 mm, TL 164 mm, TL/SVL 0.12; rostral broader than high, well visible in dorsal view; internasals as wide as long; nasal divided in prenasal and postnasal; nostril located between pre- and postnasal; prenasal contacting rostral anteriorly, internasal dorsally, and first supralabial ventrally; postnasal contacting prefrontal dorsally, sec-

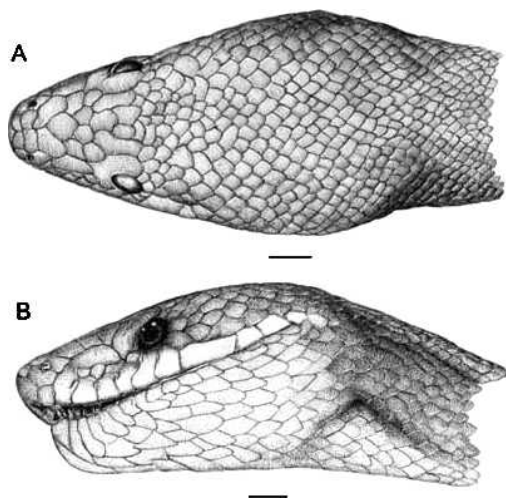


FIG. 9.—Dorsal (A) and lateral (B) views of the head of the holotype of *Epicrates maurus* (BMNH 1946.1.10.40). Ruler equals to 5 mm.

ond supralabial ventrally, and loreal posteriorly; posterior to internasals there are two large prefrontals arranged in “V” form; prefrontals about twice longer than wide, in broad contact with frontal; frontal slightly longer than wide, with approximately hexagonal shape in dorsal view; right supraocular twice longer than wide; left supraocular fused to preocular; intersupraoculars 3/4/4; interrials 20; preoculars as high as wide; loreals rectangular, about twice longer than high; three lorilabials in right and four in left side; four postoculars; upper postocular contacting supraoculars and lower contacting 7–8th supralabials; supralabials 11 in right and 10 in left side, 6–8th and 7–8th contacting orbit, respectively; infralabials 15 in right and 16 in left side, first two pairs contacting anterior chinshields; first pair of infralabials in contact behind symphyisial scale, preventing symphyisial-chinshields contact; mental groove with five scales long; gular scales with nine rows in right and ten in left side; five preventrals; dorsal scales smooth, without apical pits, keels or supra-anal tubercles; dorsal scale rows 38/48/28; dorsal scales at level of second subcaudal 15; ventral scales 236; subcaudal scales 55; maxillary teeth 20 on both sides.

*Meristic and morphometrical variation.*—Largest specimen SVL 1280 mm, TL 161 mm, TL/SVL 0.12; maximum head length 49.0 mm and width 26.7, head width/length

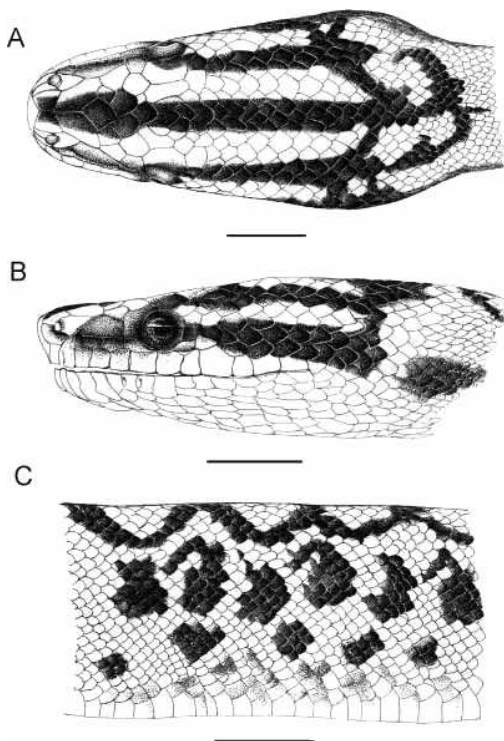


FIG. 10.—Dorsal (A), lateral (B), and midbody (C) views of the head and body, respectively, of *Epicrates maurus* (MPEG 18192). Ruler equals to 5 mm.

0.54 mm; INTSP 2–5 (3.1, 0.5, 49); INTRC 17–24 (19.9, 1.4, 50); LORIL 2–4 (3.1, 0.4, 49); postoculars generally four, upper contacting supraoculars and lower generally 7–8th supralabials; SUPRA 11–14 (12.1, 0.5, 50), 6th (4 sides), 6–7th (89 sides) or 7–8th (9 sides) contacting orbit; INFRA 13–18 (15.6, 0.9, 49), first two, occasionally three, pairs contacting anterior chinshields; generally first pair in contact behind symphyisial; SULK 4–6 (5.1, 0.5, 50); GULAR 7–11 (9.1, 0.7, 50); PVENT 4–7 (5.2, 0.7, 50); ADORS 30–39 (35.5, 2.0, 50); MDORS 43–53 (48.3, 2.4, 49); PDORS 24–31 (27.6, 1.5, 49); VENT 228–246 (235.3, 3.9, 49); SUBCD 49–61 (54.2, 2.7, 45).

*Color pattern in preservative of the holotype* (Figs. 6B, 9).—Dorsal ground color of head and body uniformly brown without distinct dorsal stripes or rings; lateral portion of body with indistinct lateral ocelli; dorsal coloration overlaps paraventral region extending until mid portion of ventral scales.



*Juvenile color pattern in preservative* (Fig. 10).—Dorsum of head yellow to light brown, except by three dark brow longitudinal stripes (two scales width), arranged in trident form; central stripe extending from snout to neck; lateral stripe extends from supraoculars to neck, contacting central stripe posteriorly; head with a dark brown stripe (two scales wide) in lateral view, originates on snout and extends through orbit, connecting posteriorly dorsolateral stripes; supralabials, infralabials, and mental region predominantly creamish white; dorsal ground color of body yellow to light brown above lateral ocelli and grayish white below them; body dorsally with 48–59 (48.6, 4.7, 32) dark brown rings (two scales wide); dark brown rings with light brown center frequently collapsed anteriorly; body having series of irregular dark brow lateral ocelli, with their dorsal portion frequently white bordered (one scale border width); anterior ocelli collapsed forming a stripe that extends approximately to midbody; below to ventral edge of lateral stripe (or ocelli), there are rounded lateral dark brown blotches; paraventral region with several diffuse brown blotches, generally overlapping ventral scales; ventral ground color creamish white anteriorly; posteriorly lateral blotches overlap subcaudal scales.

*Ontogenetic color variation* (Figs. 9, 10).—Adults become uniformly brown, with indistinct blotches, rings, ocelli, or stripe at head and body; paraventral region often brown, overlapping lateral edges of ventrals.

*Hemipenis*.—General features are similar to the *E. cenchria*, differing from that by having inverted hemipenis bifurcation at 9th ( $n = 5$ ) and extending to the level of 14–15th subcaudals (14.5, 0.6, 5).

*Cranium*.—General osteology features are similar to *E. cenchria*, differing that by having non conspicuous parietal crest; maxillary teeth 20–24 (21.5, 1.7, 5); dentary teeth 21–24 (22.7, 1.3, 5); pterygoid teeth 15–20 (17.7, 2.2, 5).

*Distribution* (Fig. 8).—Dry forest and open plant formations in Central and South America from Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Guyana, Suriname, French Guyana, and northern Brazil; occurring also in the islands of Trinidad and Tobago and Margarita. This species inhabits enclaves of Neotropical Savanna plant formation in

Central to northern South America, and may occur syntopically with *E. cenchria*.

*Remarks*.—Chippaux (1986), Gorzula and Señaris (1999), and more recently Matz (2004) considered *E. maurus* as a distinct species from the *E. cenchria* complex. Despite the real distinctiveness of *E. maurus*, these arrangements have enforced the *Epicrates cenchria* complex to be paraphyletic, because *Epicrates assisi* and *E. crassus* have a closer phylogenetic relationship to *E. maurus* than *E. cenchria* (Passos, 2003). Nonetheless, with the present comprehensive review of the all continental *Epicrates* we can rank *E. maurus* as a full species without turning the *E. cenchria* complex paraphyletic.

Matz (2004) described *E. maurus colombianus* on the basis of four specimens from the Atlantic coastal regions of Colombia and Panama, distinguishing it from nominal race by having 11–12 supralabials, 14 infralabials, two or three lorilabials (from the present study), larger total length, more robustness, and 236 ventrals. Matz (2004) described also *E. m. guayanensis* based on three individuals from Mana Municipality in the French Guyana, and diagnosed it from *E. m. maurus* and *E. m. colombianus* by having smallest total length, 43–47 dorsal scales, 227–235 ventrals, 47–53 subcaudals, and yellowish lateral stripe. However, all characters employed by Matz (2004) to differentiate the proposed subspecies fall within the range of variation of the nominal species (see above). Surprisingly, the range of variation from *E. m. colombianus* and *E. m. guayanensis* presented by Matz (2004, Table 4) completely overlaps the reported to nominal subspecies. In fact, the differences noted by Matz (2004) reflect merely his small sample size and/or phases of the ontogenetic variation in color pattern and body proportions of the species. Therefore, *E. m. colombianus* and *E. m. guayanensis* are formally place herein in the synonymy of *E. maurus*, and we decide to furnish a redescription of the holotype of *E. maurus* in order to easy any future comparisons. Moreover, if Matz (2004) suggestions are to be accepted by subsequent authors, *Cliftia fusca* Gray and *Epicrates concolor* Jan have priority with respect to *E. m. guayanensis* and *E. m. colombianus*, respectively.

***Epicrates crassus*** Cope, 1862  
(revalidated status)  
(Figs. 6C, 11)

*Epicrates crassus* Cope, 1862; Proc. Acad. nat. Sci. Philadelphia 14:349. *Terra typica*: Cadosa, Paraná River, Paraguay. Holotype: USNM 12413.

*Epicrates cenchria crassus* — Amaral, 1929 [1930]; Mem. Inst. Butantan 4:140.

*E[picrates]. cenchria polylepis* Amaral, 1935; Mem. Inst. Butantan 9:236. *Terra typica*: Rio Pandeiro, Minas Gerais, Brazil. Holotype: IBSP 9165. **New synonymy**

*Epicrates crassus* — Lema, 2002; Répt. Rio Grande do Sul:51.

*Holotype*.—Adult specimen, USNM 12413 (formerly 5409 according to Stimson, 1969), from Cadosa, Paraná River [Paraguay]. Corrected to Gardosa, Rio Paraná, Paraguay, by Williams and Francini (1991) [specimen photographs examined].

*Diagnosis*.—Distinguished from *Epicrates cenchria*, *E. maurus*, and *E. alvarezii* by having dorsal ground color light to dark brown in juveniles and adults, number of subcaudal < 45 scales. Distinguished from *E. cenchria* and *E. alvarezii* by having barely conspicuous parietal crest, and reduced alary process of vomer; from *E. alvarezii* by having inverted hemipenis bifurcates after 7th subcaudal; from *E. assisi* by having lobes slightly smaller than hemipenial body, approximately twice longer than wide, lobes slightly clavate, ventrals generally < 245 scales. Refer to Tables 6–7 for additional diagnostic features of the continental *Epicrates*.

*Meristic and morphometric variation*.—Largest specimen SVL 1320 mm, TL 143 mm, TL/SVL 0.11; maximum head length 56.2 mm and width 30.6, head width/length 0.54; INTSP 2–6 (3.2, 0.6, 158); INTRC 17–24 (19.4, 1.5, 157); LORIL 2–5 (3.5, 0.5, 162); postoculars generally four, upper contacting supraocular and lower 8–9th supralabials; SUPRA 11–16 (13.2, 0.7, 162), 6–7th (111 sides) or 7–8th (196 sides) contacting orbit; INFRA 13–18 (15.1, 0.8, 162), first two or three pairs contacting anterior chinshields; generally first pair in contact behind symphyseal; SULK 4–7 (5.1, 0.6, 159); GULAR 7–11 (9.0, 0.6, 160); PVENT 3–7 (4.8, = 0.7, 157); ADORS 26–39 (33.5, 2.1, 163); MDORS

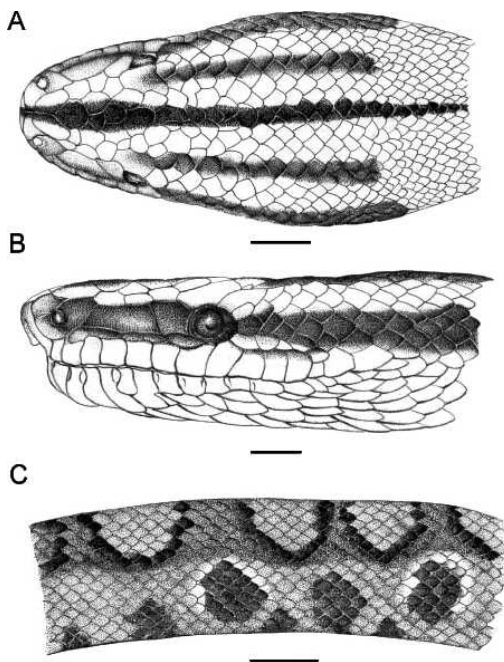


FIG. 11.—Dorsal (A), lateral (B), and midbody (C) views of the head and body, respectively, of *Epicrates crassus* (MNRJ 1368). Scale bar = 5 mm.

32–54 (44.3, 2.9, 163); PDORS 22–31 (25.5, 1.5, 162); VENT 214–247 (228.4, 7.7, 162); SUBCD 33–52 (41.3, 3.9, 158).

*Color pattern in preservative* (Figs. 6C and 11).—Dorsum of head uniformly pale to dark brown except by three dark brown longitudinal stripes (generally two scales wider); central stripe extends from the snout to neck, and ill-defined lateral stripes from supraoculars to rictual region; head laterally with dark brown stripe, originates on snout and extends often along body; supralabials generally pale brown in dorsal margins and grayish below; infralabials and mental region creamish white; dorsal ground color of body pale to dark brown above lateral ocelli and grayish brown below them; body dorsally with 32–83 (50.8, 8.3, 157) dark brown or black rings; rings generally with light (pale brown) center, eventually collapsed along body; lateral portion of body with 22–45 (31.4, 4.7, 160) dark brown or black lateral ocelli; ocelli with dorsal portion generally white bordered (one scale border width), and collapsed at anterior portion of body, forming a lateral stripe extending approximately to first third of body;

among ocelli there are irregular lateral dark brown blotches in lower portion of flanks; paraventral region with several diffuse brown blotches generally not overlapping ventral scales; ventral ground color creamish white, with lateral blotches eventually overlapping subcaudal scales posteriorly.

*Hemipenis*.—Hemipenial features similar to *E. cenchria*, except by having inverted hemipenis bifurcation at 7–8th (7.2, 1.0, 6) and extending to the level of 11–14 (12.3, 1.2, 6) subcaudal.

*Cranium*.—General osteology features similar to *E. cenchria* except by having barely conspicuous parietal crest; small alary processes of vomer; maxillary teeth 18–22 (20.7, 1.0, 15); dentary teeth 18–22 (20.5, 1.0, 15); pterygoid teeth 13–19 (16.4, 1.5, 16); occasionally palatine bones with six teeth 5–6 (5.4, 0.5, 15).

*Distribution* (Fig. 8).—Open formations in the Andean slopes of Bolivia, grasslands of Argentina and Paraguay, and Brazilian Cerrado in the States of Rondônia, Pará, Mato Grosso, Tocantins, Goiás, Minas Gerais, São Paulo, and grassland of Mato Grosso do Sul, Paraná, and Rio Grande do Sul. This species is sympatric but not syntopic with *E. cenchria* in Bolivia and in Brazilian States of Mato Grosso, Tocantins, and Goiás.

*Remarks*.—Lema (2002) considered *Epicrates cenchria crassus* as full species without further comments for his decision, leaving the remaining continental *Epicrates* paraphyletic (see above in the *E. maurus* remarks). However, with entire revision of the *E. cenchria* complex this problem is surpassed.

***Epicrates assisi* Machado, 1945 (new status)**  
(Figs. 6D and 12)

*Epicrates cenchria assisi* Machado, 1945; Bol. Inst. Vital Brazil 5:61. *Terra typica*: Campina Grande, Paraíba, Brazil. Holotype: presumed lost.

*Epicrates cenchria xerophilus* Amaral, 1954; Mem. Inst. Butantan 26:237. *Terra typica*: Rio Branco, Pernambuco, Brazil. Holotype: IBSP 9252.

*Epicrates cenchria xerophilus* — Peters & Orejas–Miranda, 1970; Bull. U.S. Nat. Mus. Bull. 297(1):108.

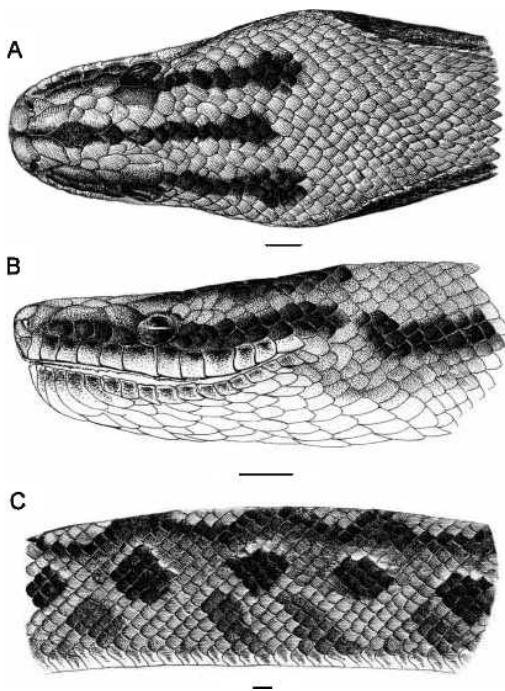


FIG. 12.—Dorsal (A), lateral (B), and midbody (C) views of the head and body, respectively, of the neotype of *Epicrates assisi* (IBSP 55463). Ruler equals to 5 mm.

*Holotype*.—Adult male, housed in Instituto Vital Brazil (IVB) not numbered, from Campina Grande, State of Paraíba, Brazil, collected by Arlindo de Assis. The type specimen is presumed to be lost (A. Melgarejo, pers. comm.).

*Diagnosis*.—Distinguished from all continental *Epicrates* by having sub-cylindrical, hemipenial lobes long (about three times longer than wide), with reduced papillate rows. Additionally, differ from *E. cenchria*, *E. maurus*, and *E. alvarezi* by having dorsal ground color pale to dark brown in juveniles and adults; from *E. crassus* and *E. maurus*, by having ventrals generally > 245; from *E. maurus*, by having inverted hemipenis < 12 subcaudal scales long. Refer to Tables 6 and 7 for additional diagnostic features of the continental *Epicrates*.

*Meristic and morphometrical variation*.—Largest specimen SVL 1420 mm, TL 190 mm, TL/SVL 0.13; maximum head length 55.0 mm and width 31.0 mm, head width/length 0.5; INTSP 3–5 (3.8, 0.4, 59); INTRC 17–26 (21.5, 1.8, 59); LORIL 3–5 (4.0, 0.3, 93); postoculars generally four, upper contacting supraocular

and lower 8–9th supralabials; SUPRA 13–16 (14.1, 0.45, 93), 7–8th (154 sides) or 8–9th (19 sides) contacting orbit; INFRA 14–18 (16.0, 0.7, 93), first two or three pairs contacting anterior chinshields; generally first pair in contact behind symphyseal; SULK 4–7 (5.4, 0.6, 90); GULAR 8–10 (9.1, 0.1, 60); PVENT 4–7 (4.9, 0.8, 14); ADORS 31–42 (36.4, 2.5, 93); MDORS 42–56 (49.4, 2.3, 93); PDORS 24–30 (27.0, 1.4, 93); VENT 240–260 (251.0, 4.4, 93) SUBCD 40–62 (54.7, 3.5, 91).

*Color pattern in preservative* (Fig. 12).—Dorsum of head uniformly pale to dark brown except by three longitudinal black stripes (two scales wide); central stripe extends from snout to posterior end of head; lateral stripes extends from supraoculars to posterior end of head; head laterally with black stripe extending from snout to posterior edge of mouth, not contacting lateral stripe of body; supralabials brown at dorsal margins and grayish white below; infralabials and mental region creamish white; dorsal ground color of body pale to dark brown above lateral ocelli and grayish brown below them; body dorsally with 36–58 ( $\bar{x}$  = 45.4, SD = 4.3,  $n$  = 47) dark brown rings; rings generally with pale brow center, collapsed mainly at anterior portion of body; body laterally with 24–42 ( $\bar{x}$  = 34.1, SD = 4.5,  $n$  = 14) dark brown ocelli; ocelli with their dorsal portion white bordered (generally one scale border width), and collapsed at anterior portion of body forming stripe that extends approximately to midbody; among ocelli there are rounded lateral dark brown blotches; paraventral region with several diffuse brown blotches, generally not overlapping ventral scales; ventral ground color creamish white, with lateral blotches overlapping subcaudal scales posteriorly.

*Hemipenis* (Fig. 7B).—Inverted hemipenis bifurcates at 4–6th (4.6, 0.8, 7) and extends to the level of 8–11th (9.3, 0.9, 7) subcaudal. Everted organ deeply bilobed; lobes slightly longer than hemipenial body, approximately three times longer than wide, and with sub-cylindrical form; proximal half of the basal portion nude and distal half encircled transversally by six overlapping fleshy flounces; margins of spermathecal sulcus stout for two third of branches; spermathecal sulcus bifurcates at level of fourth flounce; branches with centrolateral

orientation, not running to tips of lobes; lobes covered with about 15 weakly defined rows of coarse papillae in both sides; sulcate side with papillary series slightly scarce on tip.

*Cranium*.—General osteology features similar to *E. cenchria* except by having barely conspicuous parietal crest; small alary processes of vomer; maxillary teeth 20–21 (20.7, 0.5, 6); dentary teeth 20–22 (21.2, 1.0, 6); pterygoid teeth 14–18 (16.0, 1.4, 6); and occasionally palatine bones with six teeth 5–6 (5.5, 0.5, 6).

*Distribution* (Fig. 8).—Restrict to Caatinga domain (*sensu* Ab'Sáber, 1977a), from the States of Piauí to southern Bahia and north of Minas Gerais in Brazil. This species is sympatric but not syntopic with *E. cenchria*, the latter being restricted to Atlantic Rainforest in Northeastern Brazil. Even so, *E. assisi* may occur in syntopy with *E. crassus* in the southwestern of the State of Bahia to northern Minas Gerais (see below).

*Remarks*.—According to our sample there are at least two possible syntopic zones for *Epicrates assisi* and *E. crassus*, one of them in the western of the Bahia state and eastern state of Tocantins, and another between southwestern Bahia and northwestern of the state of Minas Gerais in Brazil. These areas constitute ecotones between Cerrado and Caatinga domains (Ab'Sáber, 1977a,b), and are difficult to define phytogeographically and morphoclimatically (Eiten, 1978; Rizinni, 1997). Even so, in these areas, both species show certain differences in color pattern features, which can suggest character displacement, which also simplify specific identification. Populations of *E. assisi* generally have a brown ground color at latitudes above 13° south, but exhibit a light brown coloration in latitudes below 10° south. On the other hand, populations of *E. crassus* have a pale brown ground color along most of their dispersal range, but display a very dark brown coloration at eastern of the state of Tocantins.

*Epicrates alvarezii* Abaloz, Baez & Nader,  
1964 (new status)  
(Figs. 6, 13)

*Epicrates cenchria alvarezii* Abaloz, Baez & Nader, 1964;

*Holotype*.—Adult female, housed at “Instituto de Animales Venenosos Jorge Washington Abaloz” (collection number not given), from Forres, Robles Department, Santiago Del Estero, Argentina, collected on July 1, 1959 by Cástulo Salvatierra (specimen not examined).

*Diagnosis*.—Distinguished from all continental *Epicrates* by having: (1) anterior dorsal scales rows > 40, (2) interrials > 24, (3) gular scale rows > 10, (4) loreal divided, (5) juxtaposed prefrontals, (6) frontal reduced or absent, (7) symphyisial-chinshields contact; (8) maximum length of inverted hemipenis six subcaudals long, (9) inverted hemipenis bifurcates at 4th subcaudal, (10) dorsal ground color gray to grayish brown, (11) anterior portion of nasal bone short. Refer to Tables 6–7 for additional diagnostic features of the continental *Epicrates*.

*Meristic and morphometrical variation*.—Largest specimen SVL 1443 mm, TL 170 mm, TL/SVL 0.11; maximum head length 51.0 mm, width 26.6, head width/length 0.54; internasals as wide as long, frequently separated by ascending portion of rostral scale; behind internasals there are two juxtaposed prefrontals, as long as wide; frontal reduced or absent; INTSP 3–6 (4.4, 0.8, 24); INTRC 23–29 (25.4, 1.4, 25); loreals fragmented in at least two scales; anterior loreal scale reduced, as long as high, and similar to the first lorilabial; second loreal large, about twice longer than right; LORIL 4–5 (4.7, 0.4, 25); four postoculars, upper contacting supraoculars and lower generally 7–8th supralabials; SUPRA 11–15 (13.5, 0.7, 25), 6–7th (15 sides) or 7–8th (29 sides) contacting orbit; INFRA 14–18 (16.5, 1.1, 25), generally two pairs contacting anterior chinshields; first pair of infralabials not in contact behind symphyisial; symphyisial-chinshields contact; SULK 5–7 (5.8, 0.5, 25); GULAR 10–13 (11.8, 0.6, 24); PVENT 4–8 (6, 1.0, 25); ADORS 37–46 (43.2, 1.9, 24); MDORS 50–59 (55.2, 2.2, 23); PDORS 28–31 (29.5, 0.9, 23); VENT 241–260 (248.3, 4.6, 24); SUBCD 44–56 (49.9, 2.9, 20).

*Color pattern in preservative* (Fig. 13).—Head ground color gray, with three grayish brown longitudinal stripes (generally three scales width); sometimes these stripes are diffused in irregular blotches; central stripe

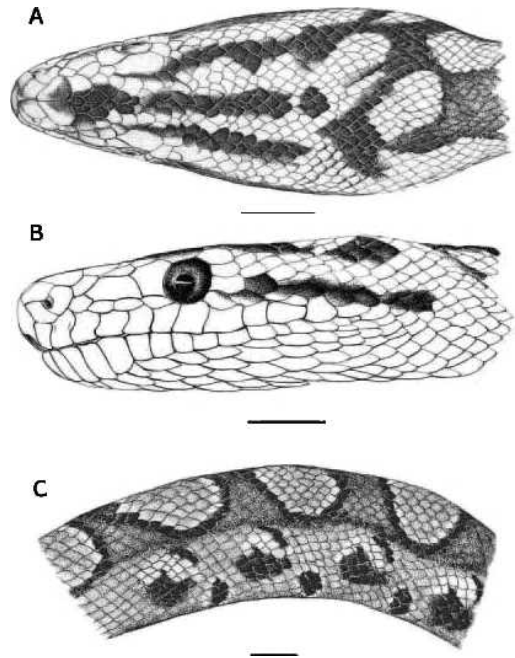


FIG. 13.—Dorsal (A), lateral (B), and midbody (C) views of the head and body, respectively, of *Epicrates alvarezii* (IBSP 57486). Ruler equals to 5 mm.

generally extends from snout to end of head; lateral stripes extends from supraoculars to posterior region of head; head laterally with grayish brown stripe, originates behind supraoculars and extends to mouth corner; supralabials generally gray at dorsal margins and grayish white below; infralabials and mental region creamish white; dorsal ground color of body gray to grayish brown above lateral ocelli and grayish white below them; body dorsally with 56–61 (65.6, 7.1, 23) dark brown rings; rings with light (grayish brown) center, and collapsed along body; body with 46–66 (52.7, 4.2, 22) grayish brown white bordered (two scale width) lateral ocelli; ocelli collapsed, only in the anteriormost portion of body, rarely forming a little and non conspicuous stripe; among ocelli in lower portion of flanks there are rounded lateral grayish brown blotches; eventually blotches overlap edge of ventral scales; ventral ground color creamish white, with lateral blotches sometimes overlapping posterior subcaudals.

*Hemipenis* (Fig. 7C).—Inverted hemipenis bifurcates at fourth and extends to the level of sixth subcaudal ( $n = 2$ ). Everted organ deeply

bilobed; lobes slightly longer than hemipenial body, approximately three times longer than wide, and with slightly sub-cylindrical form; proximal half of basal portion of hemipenial body nude and distal half encircled transversally by fourth overlapping fleshy flounces; margins of spermatic sulc stout and irregular for two third of branches; spermatic sulc bifurcates approximately to the level of forth flounce; branches with centrolinal orientation, not running to tips of lobes; Lobes covered with enlarged and diffused coarse papillae in both sides; sulcate side with papillary series slightly scarce on tip.

*Cranium*.—General osteology features similar to *E. cenchria* except by having parietal crest least developed; anterior portion of nasal bones shorter; supratemporals approximately the same size as quadrate; maxillary teeth 19–20 (19.7, 0.6, 3); dentary teeth 19–20 (19.3, 0.6, 3); pterygoid teeth 12–16 (14.7, 3.8, 3).

*Distribution* (Fig. 8).—Chaco region between southeastern Bolivia, western Paraguay, and northern to northeastern Argentine. This species is sympatric with *E. crassus* in northwestern of Paraguay and northern of Argentina, but there no syntopic records between them.

#### KEY TO CONTINENTAL SPECIES OF *EPICRATES*

1. Lateral stripe formed by the union of ocelli present at least in the anterior portion of the body ..... 2  
Lateral stripe absent; dorsal ground color pale to yellow reddish ..... *E. cenchria*
2. Anterior dorsal scales < 40; number of interrials < 24; loreal single; prefrontal scales with "V" arrangement; frontal scale as long as wide; first pair of infralabials preventing contact between symphyisial and chinshields ..... 3  
Anterior dorsal scales rows > 40; number of interrials > 24; loreal divided; prefrontal scales coupled; frontal scale reduced or absent; symphyisial-chinshields contact ..... *E. alvarezii*
3. Lateral ocelli of the body with uniform shape (Figs. 11C, 12C, and 13C); lateral stripe of the body with less than four scales width; color in juvenile and adults brown or dark brown, without ontogenetic change ..... 4  
Lateral ocelli of the body with irregular shape (Fig. 10C); lateral stripe of body with four scales width; juvenile ground color light brown; adults become uniformly

- brown generally without rings, ocelli, or stripe ..... *E. maurus*
4. Number of ventral scales generally > 245; sub-cylindrical hemipenis, with thin lobes (about three times longer than wide), and coarse papillate rows ..... *E. assisi*  
Number of ventral scales generally < 245; clavate hemipenis, with robust lobes (about two times longer than wide), and large papillate rows ..... *E. crassus*.

#### DISCUSSION

##### *Putative Fixed Diagnostic Characters as a Taxonomic Rule*

The methodological aspect of testing boundaries among species in a morphological framework was little explored in the past (but see Davis and Nixon, 1992 and Wiens and Servedio, 2000) compared to employment of DNA haplotypes (see Avise, 2000). The use of at least one putative fixed diagnostic character in the alpha-taxonomic studies has been the habitually adopted operational criteria, but rarely explained (Nixon and Wheeler, 1990; Sites and Crandal, 1997) by most taxonomists for the last 100 years (Wiens and Servedio, 2000). Recent authors have highlighted that recognition of species should be based in the concordance of two or more diagnostic characters, both in a molecular (Avise and Ball, 1990; Avise and Wollenberg, 1997) or morphological (Jorge da Silva and Sites, 1998) framework. Nonetheless, we judge concordance of two or more features in the characters distribution are not required when a single diagnostic trait is above the cutoff level in the Wiens and Servedio's (2000) test. Since the WST is exceptionally sensible to characters or specimens sample sizes (Wiens and Servedio, 2000), once statistical confidence is attained it refutes the hypothesis of populational intergradation. Otherwise, in the lack of enough sample size to achieve significance, we realize that concordance of two or more characters is a more conservative procedure to diagnosis support.

##### *Species Boundaries and Statistical Test among Continental Epicrates*

On the most inclusive hierarchical level, qualitative and morphometric data provided evidence for diagnostic features to the follow-

ing species: *Epicrates alvarezi*, *E. assisi*, *E. cenchria*, *E. crassus*, and *E. maurus*. In most of taxa (e.g., *E. cenchria* and *E. maurus*) the sample size was adequate to achieve the statistical support for species delimitation, even considering WST sensitivity to sample size (Wiens and Servedio, 2000). On the other hand, even species with relatively small samples (*E. alvarezi*) yielded results within the cutoff frequency of 10% ( $\alpha = 0.05$ ), since these taxa have more putative fixed diagnostic characters. *Epicrates assisi* and *E. crassus* did not attained the cutoff frequency based on the discrete characters, but we did not perform this test with osteological and hemipenial features, which can easily differ them, due to the relative small sample size generally available for these kind of data. We performed WST only with external morphological features that could be observed in every specimen analyzed. Recently, Benavides et al. (2002) performed WST with morphological and allozyme characters, but did not attain the cutoff frequency in most taxa. Based on our results we suggest the use of external morphological characters (frequently employed in alpha taxonomic studies) might obtain better results in WST due to the large sample size generally accessed.

#### *Distribution and Speciation of Continental Epicrates*

Wagler (1830) described the genus *Epicrates* to accommodate the species *Boa cenchria* Linnaeus. Subsequently, many forms of continental *Epicrates* have been placed or described as subspecies of the nominal species. Nonetheless, the authors did not explicitly justify the use of such categories (Abaloz et al., 1964; Amaral, 1929, 1935, 1954; Machado, 1945; Stull, 1935, 1938; Matz, 2004). Frost et al. (1992) pointed out that the use of this category within a historical context of phylogenetic inference is severely restricted, demanding the same kind of evidence (e.g., diagnostic features) needed to recognize a species. Besides in the absence of the fine application this rank in herpetology (see Frost and Hillis, 1990 and Frost et al., 1992), the use of subspecific rank to recognize diagnosable allopatric or parapatric populations of the continental *Epicrates* fails to

reflect the subspecies conceptual framework (Mayr, 1999). Additionally, some sympatric populations are not close related (e.g., *E. cenchria* with *E. crassus*; Passos, 2003) and there is an apparent character displacement phenomenon between peripheral populations in the possible intergradation's zones (e.g., *E. assisi* and *E. crassus*). Based on the above arguments we prefer to recognize the diagnosable continental taxa of *Epicrates* only on the specific level.

*Epicrates cenchria* is a single recognized taxon that occurs in the South American Rainforest, with a disjunct population in the Atlantic Rainforest of eastern Brazil. As the Amazon Forest group has no unambiguous diagnosable characters with respect to the Atlantic Rainforest population, and occurs in adjacent areas in the State of Maranhão eastern Brazil (Cunha and Nascimento, 1993), we interpret that both populations maintained gene flow until Pleistocene (see also Costa, 2003; Fernandes et al., 2004). Some authors postulated a past contact zone between Amazonian and Atlantic Forests during the Quaternary through the region currently occupied by the Caatinga xeric formation (Bigarella and Andrade-Lima, 1982; De Vivo, 1997; Costa, 2003; Wang et al., 2004). Another hypothesis that may explain the disjunct distribution of *E. cenchria* holds that those biomes were connected through Riparian Forest from a large hydrographic basin of the Madeira-Paraná complex rivers (Dixon, 1979). Regardless where was the contact between Amazonian and Atlantic Forest populations, the connection between them is well documented (Damuth and Fairbridge, 1970; Vuilleumier, 1971; Haffer, 1974; Raven and Axelrod, 1975; Bigarella and Andrade-Lima, 1982; Costa, 2003; Wang et al., 2004). As noted by Fernandes et al. (2004), this connection probably allowed some species, which at present have disjunct distributions among these biomes (e.g., mammals, Cerqueira, 1982; birds, Haffer, 1969; lizards, Vanzolini and Williams, 1970; and frogs Cruz et al., 1997), to have contiguous populations during Quaternary, curtailing allopatric speciation.

*Epicrates maurus* was described from Venezuela and occurs in dry forests from

Nicaragua (Köhler, 2003) to northern South America in the state of Pará, Brazil (Passos and Franco, 2002). The physiognomies of these open formations are similar to those found in Marajó Island and adjacent areas from north state of Pará (Eiten, 1992), which suggests the affinity of *E. maurus* with Neotropical Savanna formations of Central and northern South America. Geomorphological and palynological data reinforce the Amazon Basin was subject of regional regressions of forest associated to modifications of floristic composition during alternations of moist/hot and dry/cool eras between 10,000–8000 years ago (Absy and Van Der Hamem, 1976; Liu and Colinvaux, 1988). In this sense, we hypothesize that the actual distribution pattern of *E. maurus* may be caused by the formation of Neotropical Savanna about 10,000 years ago (Absy and Van Der Hamem, 1976; Liu and Colinvaux, 1988).

*Epicrates crassus* is recognized as the single species occurring in the central to southern South American open formations. We found a south/north cline variation among the segmental counts, which may have influenced Amaral (1935) to recognize a different subspecies. This clinal factor increasing the scale counts in smaller latitudes has been well documented to some snakes (Fox, 1948; Fox and Fox, 1961; Hoge et al., 1977, Passos et al., 2005), and as such characters do not have a phylogenetic signal, we prefer to recognize *E. crassus* as single species distributed in South American Cerrado and grassland.

*Epicrates assisi* is endemic to the xerophic Caatinga formation (*sensu* Ab'Sáber, 1977a), which has recently diverged from other open areas of South America, according to some authors (Ab'Sáber, 1959; Vanzolini, 1974, 1976, 1994). Although phytogeographical studies corroborate this assertion (Matos-Filho, 1970), regarding the snake fauna, there are species or subspecies endemic to this domain (e.g., *Bothrops erythromelas*, *Liophis miliaris mossoroensis*). Despite the lack of studies focusing xerophytic adaptations to most Caatinga endemic species, Navas et al. (2002) reported physiological, behavior, and morphological putative adaptations that prevent water loss in the amphibian species *Corythomantis greeningi* Boulenger. Further-

more, phytogeographical and geomorphological evidence suggests this morphoclimatic domain is well defined (Ab'Sáber, 1977a; Rizzini, 1997).

*Epicrates alvarezi* is the most distinct species among the continental *Epicrates*, showing several exclusive morphological features (see results). This allopatric species is endemic of the Argentine/Bolivian Chaco, and probably is the most basal mainland *Epicrates* (Passos, 2003).

RESUMO: O complexo *Epicrates cenchria* é endêmico da região Neotropical, ocorrendo nas porções continentais das Américas Central e do Sul. A posição taxonômica das nove subespécies atualmente reconhecidas (*E. c. alvarezi*, *E. c. assisi*, *E. c. barbouri*, *E. c. cenchria*, *E. c. crassus*, *E. c. gaigei*, *E. c. hygrophilus*, *E. c. maurus* e *E. c. polylepis*), foi avaliada por meio de caracteres de morfologia externa, osteologia e hemipênis. Os resultados obtidos através de análises quantitativas e qualitativas suportam o reconhecimento de *E. alvarezi*, *E. assisi*, *E. cenchria*, *E. crassus* e *E. maurus* como espécies distintas, baseado na delimitação estatística robusta dos limites entre espécies.

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## APPENDIX I

### *Specimens Examined*

(Asterisks correspond to skulls examined)

*Epicrates cenchria* ( $n = 200$ ).—Unknown locality (MNRJ 3337\*). **BOLIVIA**: BENI: Unknown locality (CBF 1949); Ballivian (CBF 1174); COCHABAMBA: Unknown locality (CBGR 66–67, AMS 01); 95 Km from Montero (CBF 1162); LA PAZ: Unknown locality (CBF 259, 452); Inquisivi: Flor de Mayo (CBF 1181–1196); Rio Imieva (CBF 302); SANTA CRUZ DE LA SIERRA: Ichilo: Rio Víbora (MNKR 427), San Carlos (MNKR 339); Ñufllo de Chávez: Cerra a la Mecha (MNKR 1025), Puerto Almacum, Rio Negro (MNKR 374). **BRAZIL**: AMAPÁ: Unknown locality (IBSP 34104); Macapá: UHE Paredão (IBSP 24828–29); Oiapoque (IBSP 14035, 14624, 14626); Serra do Navio (IBSP 19126, 24770, 25425). **AMAZONAS**: Balbina: UHE Presidente Figueiredo (IBSP 51494, 51873); Benjamin Constant (MNRJ 1309\*, 1448); Borba (MNRJ 1447\*); Itacoatiara (IBSP 44169); Iauareté: Uaupés (IBSP 33386); Manaus: Calmon (IBSP 24140). **BAHIA**: Muritiba: Barragem Pedra do Cavallo (IBSP 50982–83). **ESPÍRITO SANTO**: Afonso Cláudio (IBSP 49400, 51084, 51967); Águia Branca (IBSP 25039, 25350, 25940); Baixo Guandu (IBSP 8401, 8718, 8751, 8762, paratypes of the *E. c. hygrophilus*), (IBSP 8845, holotype of the *E. c. hygrophilus*); Caratinga (IBSP 608); Colatina

(IBSP 18257, 33018, 30415, 31665); Fundão (IBSP 32905); Guaiú (IBSP 51765); Itá [currently Baixo Guandu] (IBSP 8948, 8959, 8995–96, 9072, paratypes of the *E. c. hygrophilus*); João Neiva (IBSP 12217–18, paratypes of the *E. c. hygrophilus*); Linhares (MBML 479); Santa Teresa (MNRJ 9805); São Gabriel da Palha (IBSP 49732–33, 51235, 51390, 51391\*, 51392). **MATO GROSSO**: Unknown locality (MNRJ 324); Alta Floresta (IBSP 41463, 41447, 46559, 48155, 51093); Barra do Garas: Serra do Roncador (IBSP 44274, 48156, IBSP 51091); Cuiabá (IBSP 47675); Marcelândia (IBSP 49979); Pontes de Lacerda (IBSP 50900); Rio Aripuanã: north of Mato Grosso (MNRJ 353); Sinop (IBSP 40688, 50052, 51962, 56141); Vera (IBSP 43151, 55245–46); Xingu: Faz. Alto da Mata (IBSP 46592). **MARANHÃO**: Ailândia (IBSP 24484); Mirinzal: Faz. Flechal (IBSP 41275); Nova Vidal: 25 Km from Gurupí (MPEG 15250); Palmerândia (IBSP 21778); Parauá: Br-316 (MPEG 10833); Puraquêú: Br-222 (MPEG 15250). **MINAS GERAIS**: Caratinga (IBSP 608); Raul Soares (IBSP 21989\*); Rio Casca (IBSP 33315). **PARÁ**: Acará (IBSP 14690–91); Belém: Jardim Zoológico (IBSP 14628); Instituto Agro-Norte (IBSP 15028); Cameté: Estrada de Ferro Bragança (IBSP 2206, 14627); Itaituba (IBSP 46479, 46591); Itupiranga (IBSP 32820); Monte Dourado: Projeto Jarí (MNRJ 8137); Rio Cururu: Afluente do Rio Tapajós (IBSP 23942\*); Tomé-Aú (IBSP 14687, 14692, 14694); Tucuruí: Rio Tocantins (IBSP 46410–11, 46662–63, 46880, 46882, 46885). **PERNAMBUCO**: Cabo 24 (IBSP 50622); Ipojuca (IBSP 48811); Nazaré da Mata: Engenho Boa Ventura (IBSP 278); Recife (IBSP 46547). **RONDÔNIA**: Espigão D' Oeste (IBSP 41031, 41037); Guaporé (IBSP 40349); Porto Velho (MNRJ 3038, 49249, 49840, 53122). **COLOMBIA**: Unknown locality (MLS 91, MLS 88a–n). **AMAZONAS**: Aracuaera: Rio Caquetá (IAvH 3277); Letícia (IAvH 63, 990, 2057, 3439, ICN 10066, 10468, 10476, MLS 87). **CAQUETA**: Florencia (MLS 90, 1590); Tres Esquinas (MLS 1591). **META**: La Macarena: Puerto Chamuza: Parque Natural Nacional Los Tinuaguas: Rio Duda (IAvH 4009). **PUTUMAYO**: Unknown locality (MLS 92). **ECUADOR**: NAPO: Rio Coca (QCAZ 188); Rio Napo (QCAZ 437). **MORANA SANTIAGO**: Palora: Aripicos (EPN 8672). **PASTAZA**: Chichirota: Bajo Bobonaza (EPN 8671); Puyo (QCAZ 634); Pozo Misión (EPN 8848); Villano: Curaray: Arajuno (EPN 6879). **SUCUMBÍOS**: Jambeli (QCAZ 1170); Limoncacha (QCAZ 2053); R. P. F. Cayabeno (QCAZ 1015, 3311). **PERU**: **AMAZONAS**: Cordillera del Condor (MHNSM 3349). **HUANUCO**: Gingo Maria (MHNSM 2225, 2425, 2853–54); Iparia (MHNSM 2465). **IQUITOS**: Loreto (MHNSM 2620). **JUNÍN**: Colonia del Perene (MHNSM 2224); Satipo (MHNSM 2154). **MADRE DE DÍOS**: Cosco Amazônico (MHNSM 11798, 11812); Lago Valencia (MHNSM 13370). **UCAYALI**: Hilliges (IBSP 14635\*, 14642). **VENEZUELA**: Unknown locality (IBSP 3811). **BOLIVAR**: Auyantepui (MBUCV 1000); Guayaraca (MBUCV 3075). **MONAGAS**: Garipito (MBUCV 8117).

*Epicrates crassus* ( $n = 170$ ).—**ARGENTINA**: MIS- SIONES: Iguazú: Puerto Iguazú (FML 190, 197). **BOLÍVIA**: BENI: Ballivián: Espíritu (CBF 299); SANTA CRUZ DE LA SIERRA: Andrés Ibáñez: Tarebinto (MNKR 966); Ángel Sandoval: Comunidad San Fernando (MNKR 1401); Chiquitos: Finca dos Milanos (MNKR 446, 448); Pailón (MNKR 895). **SUCRE**: Unknown

locality (IBSP 20440\*). **BRASIL:** GOIÁS: Alexânia: Faz. Tiba (IBSP 25667); Aragaras (IBSP 25579); Caldas Novas: Faz. Dois Irmãos (IBSP 40615); Cana Brava (IBSP 9216–17 paratypes of the *E. c. polylepis*); Catalão (IBSP 13670); Goiânia (IBSP 46971); Ipameri (IBSP 44610, 54996); Mambai (IBSP 49448); São João da Aliana: Jatobazinho (MNRJ 3234\*). MATO GROSSO: Barracão Queimado: Br 29 (IBSP); Barra das Garas: São Félix (IBSP 19948, 22441, 22583); Cáceres (IBSP 44350); Cuiabá (IBSP 49993–94); Maroim (IBSP 9335); Mato Verde (IBSP 12057). MATO GROSSO DO SUL: Água Clara (IBSP 54200); Antônio João (IBSP 40267); Corguinho (IBSP 52827); Guaicurus (IBSP 23721, 33227); Ilha Solteira: Rio Paraná (IBSP 38326–27, 38329–34); Nova Andradina (IBSP 20815); Paranaíba (IBSP 46350); Ponta Porã (IBSP 17121\*, 25603, 49977); Promissão (IBSP 15778); Ribas do Rio Pardo: Faz. Monte Alegre (IBSP 27685); Três Lagoas (IBSP 9625, 19493–94, 21650, 21900, 46972); Xavantina (IBSP 25338, 30366). MINAS GERAIS: Arcoverde (IBSP 21122); Campo Florido: Faz. Coibi (IBSP 34404); Confins (IBSP 56567); Engenheiro Dolabela (IBSP 31683–84); Engenheiro Lisboa (IBSP 1127); Fronteira (IBSP 40427, 51838); João Pinheiro (IBSP 45080, MNRJ 13258); Lagoa Santa (MNRJ 1366\*, 1368–69, 1446); Lassance (IBSP 15857, 33931); Manga: Buritizeiro (MNRJ 8136); Paracatu (IBSP 52597; MNRJ 13257); Passos (IBSP 51706); Pedro Leopoldo: Fidalgo (IBSP 43158, 43913, 43915, 51092, 51385); Rio Pandeiro (IBSP 9165, holotype of the *E. c. polylepis*, IBSP 9166 paratype of the *E. c. polylepis*); Sacramento (IBSP 50197); Uberlândia (IBSP 15690); Várzea da Palma (IBSP 45324); Vazante (IBSP 53150); Veríssimo: Faz. Ponta (IBSP 42979). PARÁ: Santana do Araguaia (IBSP 22241). PARANÁ: Unknown locality (IBSP 52281–82, 52369); Arapoti (IBSP 42269); Foz do Iguaçu (IBSP 29113); Guairá (IBSP 32683); Jaguaraiava (IBSP 46965); Londrina (IBSP 46609); Maringá (21694–95); Santo Inácio: Faz. São Pedro (IBSP 43423, 50893); Sarandi (IBSP 53390); Terra Rica (IBSP 19085). RONDÔNIA: Vilhena (IBSP 22288). SÃO PAULO: Altinópolis (IBSP 15679, 22489); Assis (IBSP 47346, 47348); Barretos: Faz. Buracão (IBSP 21919); Boa Esperana do Sul (IBSP 56923); Bofete (IBSP 51837); Brotas (IBSP 51994); Bueno de Andrade (IBSP 10844); Caapava (IBSP 10888); Caiuá (IBSP 7095); Campinas (IBSP 10874); Campos do Jordão (IBSP 19698); Casa Branca (IBSP 1811); Córrego Fundo (IBSP 10994); Cesário Bastos (IBSP 1116); Domingos Vilela (IBSP 698); Embu (IBSP 52012); Engenheiro Paulista (IBSP 1505); Euclides da Cunha Paulista (IBSP 40411); Fortaleza (IBSP 2683); Guaiuvira (IBSP 833); Guararapes (IBSP 28070); Ilha Solteira (IBSP 36717–19, 37859–63); Indiana (IBSP 11023); Indiaporã: UHE Água Vermelha (IBSP 43076, 43749, 46963–64); Iperó (IBSP 33226); Ipiguá (IBSP 57348); Irapuru (IBSP 22783); Itapetinga (IBSP 50248); Itrapiuna (IBSP 27386, 51889); Itu (IBSP 52090, 52555). TOCANTINS: Gurupi (IBSP 46413); Kraó: Indian settlement (IBSP 19084\*); Lajeado: UHE Luiz Eduardo Magalhães (IBSP 65025–30); Natividade (IBSP 32600); Palmas (IBSP 63338); Porto Nacional (IBSP 65426, 65652\*); Santa Isabel: Ilha do Bananal (IBSP 12054).

*Epicrates assisi* ( $n = 93$ ).—**BRASIL:** BAHIA: Barreiras (MNRJ 3072, 3073–74\*, 48154); Brumado (IBSP 32172, 32179, 34456, 40374, 40379, 40384, 40542, 41087, 41145, 44052, 45721, 48584); Castro Alves: Santa Tereza (IBSP 25063); Feira de Santana (IBSP 20914\*); Guanambi (IBSP 50341, 53857); Irecê (IBSP 43890); Itaparica (MNRJ 8338\*); Lapão (IBSP 55304–05); Livramento do Brumado (IBSP 29817–19); Muritiba: Barragem de Cavalo (IB 49309–10, 49333–34, 51119, 52257); Santa Luzia (IBSP 3210); Urandi (IBSP 25883–84). CEARÁ: Unknown locality (IBSP 889, paratype of the *E. c. xerophilus*, IBSP 20207); Fortaleza (MNRJ 9941, 20007, 20257); Icó (IBSP 12101\*, 13078, 13079, 13080, paratypes of the *E. c. xerophilus*), Lima Campos (IBSP 20191); São Vicente (IBSP 1483). PARAÍBA: João Pessoa (IBSP 53724, 54710); Junco do Seridó (IBSP 55463, neotype of the *Epicrates assisi*); Patos (IBSP 33409). PERNAMBUCO: Unknown locality (IBSP 953, paratype of the *E. c. xerophilus*); Alagoinha (IBSP 57844); Cabo 24 (IBSP 50622); Garanhuns (IBSP 51777); Caruaru (IBSP 51954); Glória do Goiatá (IBSP 46973); Pesqueira (IBSP 42896, 42933, 46613); Recife (IBSP 280, 326, paratypes of the *E. c. xerophilus*); Rio Branco (IBSP 9252, holotype of the *E. c. xerophilus*); São José do Belmonte (IBSP 32914). PIAUÍ: Feitosa/Caririá: Serra de São Pedro (IBSP 20296–97); Paranaíba (IBSP 49435); Santa Filomena (IBSP 1690); São Raimundo Nonato (MNRJ 4801, 7598); Teresina (IBSP 49930, 51085). RIO GRANDE DO NORTE: Assú (IBSP 52896, 53107–08); Mossoró (IBSP 51065); Natal (IBSP 44460); Nova Cruz (IBSP 20917). SERGIPE: Aracajú (IBSP 49850, 51083, 53186); Canindé de São Francisco (IBSP 54254); Castro (IBSP 11086).

*Epicrates maurus* ( $n = 171$ ).—**BRAZIL:** AMAPÁ: Marco Zero: Br Amapá–Macapá: Serra do Navio (MNRJ 9105\*). PARÁ: Ilha de Marajó: (IBSP 15224\*), Fazenda Aruã-Soure (MPEG 18130; 18175), Fazenda Tuyuyu: Cachoeira de Arará (MPEG 18164, 18192), Igarapé Taperebá (MZUSP 3599), Tuiuiu (IBSP 17636, 17655); Tiriós Jesuit mission: (IBSP 42745–46). RORAIMA: Alto Alegre (MZUSP 9859); Apiatá (MZUSP 10699); Boa Vista (MZUSP 9107–10, 9745–46, 9851–54, 9960, 10716); Ilha de Maracá (MZUSP 996, 8805, 9268); Mangueira: Maloca (MZUSP 9801); Marco da Fronteira Brasil-Venezuela: BV 8 (MZUSP 9674); Pacaraima (MNRJ 9106\*). **COLOMBIA:** Unknown locality: (MLS 2424). ANTIOQUIA: Cauca: (MLS 2395); Segovia (MLS 94). ARAUCA: Arauca: Estación Biológica El Guafal (IAvH 3191). ATLANTICO: Barranquilla (MLS 86, MZUSP 2116). BOLIVAR: Cartagena (ICN 2681); El Playón: El Viejo (ICN 323); Islas del Rosario (ICN 1890); Laguna de La Conquista: Finca Laguna Roja (MZUSP 6096); Luruaco: Finca El Ceibal (ICN 11227). Santa Rosa (ICN 2724, MZUSP 6299, 6301, 6138–41); Zambrano: Lloresta Monterrey (IAvH 4205–06). CALDAS: La Dorada (IAvH 969). CASANARE: Orocué (ICN 239). CHOCÓ: Ríosucio: Parque Natural Nacional Los Katis (IAvH 2126–27, 2132). CÓRDOBA: Loricá: Hacienda Cubinca (ICN 10199, 10491); Montería: (MLS 80, 2192), Martinica (ICN 10198, 10200); San Bernardo (ICN 1383); Tierras Altas: Los Morrales (ICN 8461–8470). CUNDINAMARCA: Honda (MLS 83, 96); Palanquero (MLS 84, 93, 97). MAGDALENA: Parque Nacional Natural Isla de Salamanca: Km 8 of Barranquilla–Ciénega Highway (IAvH 01), Los Cocos (IAvH 917); Santa Marta: Parque Nacional Natural Tayrona (IAvH 197, 1962, 2152, 2199); Santana: Finca El Recreo (ICN 1882). META: Cunucral (ICN 2726); Peralonzo (ICN 2999); San Martín: Vereda La

Casrañeda (ICN 10788, 10987); Villavicencio (ICN 1384, 1386). NORTE DE SANTANDER: Cucúta: La Rincónada (MLS 108). SANTANDER: Landazuri: Vereda Morro Negro: Finca La Fortuna (ICN 8940). Norte de Girardot (MLS 82); Río Opón (MLS 85). SUCRE: Colosó: Estación Primates (IAVH 3305). TOLIMA: Ambalema: Río Magdalena (MLS 90, 98, 1592, ICN 1475); Armero (ICN 375); Río Magdalena (MLS 2128); Melgar (MLS 1980, 2014); Ortega (MLS 79). VALLE DEL CAUCA: Río Calima (ICN 427). VICHADA: Unknown locality (MZUSP 6120); Río Vichada: Laguna Danta (ICN 2586). **PANAMA:** Unknown locality (FML 861). **TRINIDAD:** Unknown locality (IBSP 185). **VENEZUELA:** Unknown locality (BMNH 1946.1.10.40, holotype of the *Epicrates maurus*; MBUCV 8043, 8118–19.). AMAZONAS: 14 Km de Clarines (MBUCV 8393). ARAGUA: Maracay (IBSP 25725, MBUCV 8114); Turmero (IBSP 18409). BOLIVAR: Republica Guiri (MBUCV 836); Sierra Lema (MBUCV 431). CARABOBO: Valencia: Hacienda Mozanga (MHNLS 4376). DELTA AMACURO: Delta del Orinoco (MHNLS 15180). DISTRITO FEDERAL: Caracas (MBUCV 8104–05, MHNLS 10605), Alta Florida (MBUCV 8407), Caucagua (MHNLS 10707), Country Club (MHNLS 1642), Los dos Caminos (MHNLS 1414, 2207), Parque Natural El Avila (MHNLS 1402, 1709, 1712), Caracas: Universidad Central de Venezuela (MBUCV 412). GUÁRICO: El Sombrero (MBUCV 8109); Espino (IBSP 18408); Veladadero (MBUCV 1073). MIRANDA: Baruta (MHNLS 1435); Caucagua (MHNLS 10707); Cupira (8362); Barlovento: Universidad Simón Bolívar (MBUCV 2191); Maracacuay (MBUCV 367); Santa Teresa (MHNLS 1415); Turgua: Hatillo (MHNLS 1429). NUEVA ESPARTA: Isla Margarita (MHNLS 15202), Boca del Río (MHNLS 4380), Salamanca (MHNLS 4379, 4489–90, 15203). PORTUGUESA: Acarigua (MBUCV 1157). VARGAS: Camurí Chico (IBSP 18406–07, MBUCV 939, 8108, 8110, 8115, MHNLS 4304); Chicheriviche (MBUCV 8303); Macuto (MBUCV 947, 8113); Tacagua: Valle del Muerto (MHNLS 15226). ZULIA: Unknown locality (IBSP 27757; IBSP 18407\*); San Rafael (MBUCV 8116); Sierra de Perija: Kasmera: Caño El Chaparro (IBSP 25724\*); La Trazarenado (IBSP 25723); Maracaybo: Bahía de Turiamo: (MLS 81).

*Epicrates alvarezii* ( $n = 24$ ).—**ARGENTINA:** Unknown locality (IBSP 57486\*, 59073, FML 862). CORRIENTES: Entre Rios: Monte Caseros (IBSP 25587). JUJUI: Unknown locality (IBSP 8250\*). SALTA: Anta (FML 2186), Anta: Finca dos Colorados (FML 2885, 2559). SANTIAGO DEL ESTERO: Unknown locality (FML 618, 1158, 1275); Jimenez: Poso Hondo (FML 1457), Juca Jacu (FML 1881); Pellegrini (FML 2175, 2291); Arredores de Nueva Esperanza (FML 2255–1, 2255–2, 2255–3). SAN MI-

GUEL DE TUCUMÁN: Burruyacu: Ticucho Km 14 (FML 1454); Tinajeros (FML 7245); Capital: Instituto Miguel Lillo (FML 272); Tafi Viejo (FML 430). **BOLIVIA:** SANTA CRUZ DE LA SIERRA: Cordillera: Cerro Colorado (MNKR 1831, 2883).

## APPENDIX II

### Literature records

*Epicrates cenchría*.—**Argôlo (2004):** BRAZIL: Bahia: Almadina; Arataca; Aurelino Leal; Barra do Rocha; Barro Preto; Belmonte; Boa Nova; Buerarema; Canavieiras; Firmino Alves; Gongogi; Guaratinga; Ibicaraí; Ibirapitanga; Ibirataia; Ilhéus; Itacaré; Itamaraju; Ituberá; Jussari; Maraú; Mascote; Pau Brasil; Uruuca. **Boulenger (1893):** PERU: Moyobamba. **Boulenger (1896):** BOLIVIA: Beni: Santa Ana de Movimas, Trinidad; La Paz: Rio Madidi. **Chippaux (1986):** FRENCH GUYANA: Acarouany; Cacao; Roura; Saul. **Fugler (1984):** BOLIVIA: La Paz: Puerto Linares. **Fugler and Cabot (1995):** BOLIVIA: Cochabamba: Locatal: Villa Tunari; Pando: Cobija. **Procter (1921):** BOLIVIA: Beni: Cachuela Esperanza. **Stull (1938):** Santa Cruz de la Sierra: Buenavista.

*Epicrates maurus*.—**Abuys (1989):** SURINAM: Nickerie. **Casado and La Marca (1996):** VENEZUELA: Alcabala de Puente, Victoria region. **Chippaux (1986):** FRENCH GUYANA: Iracoubo; Tonate; Cayenne; Sinnamary; Kouron. **Gozula and Señaris (1999):** VENEZUELA: Bolívar: Danto Manchado; El Manteco. **Roze (1966):** VENEZUELA: Carabobo: Morón; Miranda: Santa Lucía; Yaracuy: Urama. **Staton and Dixon (1977):** VENEZUELA: Guárico: Corozo Pando.

*Epicrates assisi*.—**Machado (1945):** BRAZIL: Paraíba: Campina Grande. **Vitt and Vangilder (1983):** BRAZIL: Pernambuco: Exú.

*Epicrates alvarezii*.—**Abaloz et al. (1964):** ARGENTINA: Santiago del Estero: Dept. Alberdi: Agustina Libarona; Dept. Atamisqui; Dept. Banda: Abra Grande; Ardiles; El Puesto; La Banda; Dept. Capital: Santiago del Estero; Tunas Puncu; Dept. Choya: Frías; Dept. Fernández; Dept. Guasayá; Dept. Jiménez: El Charco; El Paçara; Tacanas; Dept. Matará: Tiun Puncu; Dept. Ojo de Águia: Sol de Julio; Dept. Pellegrini; Dept. Quebrachos: Coronel Fernández; Dept. Robles: Forres; Dept. Salavina: Chilcas Juliana; Los Telares; Dept. San Martín; La Higuera. **Giraud and Scrochii (2002):** Catamarca; Choco; Formosa. **Peracca (1897):** BOLIVIA: Tarija: San Francisco. **Waller and Buongermi (1998):** BOLIVIA: Santa Cruz de La Sierra: San Antonio del Parapeti. **Williams and Francini (1991):** ARGENTINA: Córdoba; Garbosa: Paraná River.