

Geographic Variation in the Emerald Treeboa, *Corallus caninus* (Squamata: Boidae)

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The arboreal boa *Corallus caninus* is widely distributed across northern South America (the Guianas and Amazonia). We examined geographic variation based on examination of 192 specimens from throughout the range, and revised its taxonomy on the basis of quantitative and qualitative analyses of morphological characters (meristics, morphometrics, and color patterns). Based on the high number of lateral blotches on the body and the high number of scales across the snout, populations south of the Rio Amazonas and west of the Rio Negro are identified as a species (or, potentially, a species complex) separate from *C. caninus*, and the name *Corallus batesii* is resurrected for those populations. The distribution of *Corallus caninus* is restricted to the Guiana Shield (north of the Rio Amazonas and east of the Rio Negro).

La boa arbórea *Corallus caninus* presenta una distribución amplia en el norte de América del Sur (las Guayanas y la Amazonia). Obtuvimos datos de la variación geográfica utilizando 192 especímenes procedentes de varias localidades a los largo de su distribución. Revisamos su taxonomía utilizando caracteres morfológicos cuantitativos y cualitativos (merísticos, morfometría y patrones de coloración). Las poblaciones distribuidas al sur del Río Amazonas y al occidente del Río Negro fueron identificadas como una especie aparte de *C. caninus*, esto basándonos en una alto número de manchas laterales del cuerpo y de escamas del hocico. Se resucitó el nombre *Corallus batesii* para estas poblaciones. La distribución de *Corallus caninus* queda restringida al escudo de las Guayanas (al norte de Río Amazonas y al oriente del Río Negro).

THE boid snake genus *Corallus* is currently comprised of eight species with a combined distribution from Guatemala to southern Brazil. *Corallus annulatus* occurs in Guatemala, south to northern Colombia west of the Andes; *Corallus blombergi* in Ecuador west of the Andes, and possibly extreme southwestern Colombia; *Corallus caninus* in the Guiana Shield and the Amazon basin; *C. cookii* only on St. Vincent, West Indies; *C. cropanii* in southeastern Brazil; *C. grenadensis* on the Grenada Bank, West Indies; *C. hortulanus* in the Guianas, Amazon Basin, and Brazil's Atlantic forest; and *C. ruschenbergerii* in southern Central America, northern Colombia and Venezuela, including associated islands. With the exception of *C. hortulanus*, *C. caninus* has the broadest distribution of any member of the genus (and is widely sympatric with *C. hortulanus*). In South America it occurs throughout the Guianas, much of the Amazon basin, and in areas west of the Andes in northwestern Colombia (Renjifo and Lundberg, 1999; Daza and Henderson, 2005). It is largely confined to lowland rainforest habitat, but may also be found in forested areas of Cerrado and gallery forests associated with seasonally flooded grasslands (Henderson et al., 1995; W. W. Lamar, pers. comm.). Its latitudinal distribution is from approximately 08°11'N in northwestern Colombia to approximately 15°35'S in Brazil; elevational distribution is from sea level to about 1000 m in Peru (Lehr, 2001). *Corallus caninus* is almost exclusively arboreal, nocturnally active, and a predator of lizards (as a neonate), birds (J. Lemm, in litt.), rodents (Henderson, 1993), and marsupials (Pough et al., 1998). As an adult, *C. caninus* is almost invariably green, but neonates are usually red-orange (rarely green).

Commonly referred to as the "Emerald Treeboa" in English-speaking countries, *Corallus caninus* was described

250 years ago by Linnaeus (1758) and, since then, it has maintained remarkable taxonomic stability. Although other "emeralds" were described, all were subsequently relegated to the synonymy of *C. caninus* (at least two, *Boa aurantiaca* and *Chrysensia batesii*, were based on specimens exhibiting juvenile dorsal coloration and, therefore, superficially appearing very different from *C. caninus*; see McDiarmid et al., 1999, for a comprehensive synonymy). *Chrysensia batesii* Gray (1860) was the last to be described, and Boulenger (1893) placed it into the synonymy of *C. caninus*. Since then, the species has received surprisingly little attention despite its enigmatic juvenile coloration, its spectacular adult coloration, and its popularity in zoos and among herpetoculturists (where it may command prices in excess of US \$5,000). Recently, Vidal et al. (2005) examined phylogenetic relationships in *C. caninus* with DNA samples from five geographically disparate localities from across the species' range. Sequence divergence ranged from 1.7 ± 0.3 between Guyana and Venezuela to 16.2 ± 0.9 between Peru and the remaining samples. As a complement to the work of Vidal et al. (2005), and as part of an ongoing review of geographic variation in species of *Corallus* (Henderson, 1997; Henderson et al., 2001), we here present the results of an analysis of geographic variation in *C. caninus*, one of the most easily identified snake species in the world.

MATERIALS AND METHODS

Techniques and characters.—Measurements were taken with a dial caliper to the nearest 0.1 mm, except for snout–vent (SVL) and tail (TL) lengths, which were taken with a flexible ruler to the nearest 1.0 mm. Sex was determined by dissection. We examined the following external quantitative

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characters for each specimen: number of anterior dorsal scales rows, counted at the level of 10% of the ventral scales (ADORS), number of mid-body dorsal scales rows, counted at the level of 50% of the ventral scales (MDORS), number of posterior dorsal scales rows, counted at the level of 100% of the ventral scales (PDORS), number of ventral scales (VENT), number of subcaudal scales (SUBC), number of supralabial scales (SUPRA), number of scales across the snout at the level of suture between the third and fourth supralabials (SNOUT), number of infralabial scales (INFRA), number of lateral blotches in the left side of body (LATBL), and number of pattern triangles on the left side of mid-body (TRIMD).

We were able to examine diagnostic characters via digital images of type specimens, including the holotypes of *Boa canina* in the Naturhistoriska Riksmuseet and of *Chrysenis batesii* in the Natural History Museum (London). These images and the descriptions in Andersson (1899) and data provided by C. McCarthy (NHM) allowed us to produce abbreviated descriptions of the holotypes of *B. canina* and *C. batesii*, respectively.

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. In order to evaluate the taxonomic status of currently recognized *Corallus caninus*, we partitioned the sample into three groups on the basis of geographic proximity, the presence of putative barriers to gene flow, and population discontinuities. Group 1 included specimens from the Guiana Shield (*vide* Hoogmoed, 1979), north of the Rio Amazonas and east of the Rio Negro. Group 2 included specimens from localities in the Amazon basin, south of the Rio Amazonas and east of the Rio Tapajós. Group 3 included specimens from the Amazon Basin, west of the Rio Negro and west of the Rio Tapajós.

We performed a multivariate analysis of variance (Manly, 2000) and size-free discriminant function analysis (DFA; Strauss, 1985) at group level to evaluate meristic and color pattern differentiation between defined groups (Manly, 2000). We performed comparisons on the basis of Tukey's test for unequal samples (Spjøtvoll and Stolone, 1973) at the group level to evaluate discrimination between groups with *a priori* definition (Manly, 2000). We projected the first two discriminant functions of size-free analyses onto orthogonal axes and computed 95% confidence regions from the simulation of 1000 pseudoreplicate data matrices obtained by parametric bootstrapping (Efron, 1979). All discriminant function loadings are portrayed as vector correlations (directional cosines), which are estimated for each variable by correlations with projection scores across individuals (Wright, 1954).

As the assumption concerning both analyses 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 assess the variance bias, as well as for robustness test of the results. Assumptions of univariate normality and homoscedasticity were evaluated with the Kolmogorov-Smirnov and Levene's test, respectively (Zar, 1999). We estimated the missing values for both analyses through an *estgroup* function from MATLAB software. Individuals or variables with missing data above 30% were not considered in the statistical analysis.

Table 1. Tukey Test for Three Defined Groups of *Corallus*. Statistical significance is denoted in bold. Alpha level = 0.05. Group 1 = populations north of the Rio Amazonas and east of Rio Negro (*C. caninus*); group 2 = populations south of the Rio Amazonas and east of the Rio Tapajós (*C. batesii*); group 3 = populations south of the Rio Amazonas, west of the Rio Negro, and west of the Rio Tapajós (*C. batesii*).

	Group 1	Group 2	Group 3
Group 1		<i>P</i> < 0.001	<i>P</i> < 0.001
Group 2	<i>P</i> < 0.001		<i>P</i> = 0.09
Group 3	<i>P</i> < 0.001	<i>P</i> = 0.09	

All statistical inferences were performed with MATLAB 4.2c1 (MathWorks, Matlab for Windows 4.2c1. Mathworks, Inc., Natick, Massachusetts, 1994), except for MANOVA, classificatory matrixes, and normality and homoscedasticity tests, which were performed with STATISTICA 5.1 (StatSoft, Statistica for Windows. Version 5.1. Tulsa, Oklahoma, 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, VENT, SNOUT, LATBL TRIMD, and SVL.

Institutional abbreviations are as listed at <http://www.asih.org/codons.pdf>, except the following institutions that were not included in this source: Venezuela—Museo de Historia Natural, Fundación La Salle (MHNLS), Caracas D.C.; Colombia—Museo Universitario de la Universidad de Antioquia, Colección de Reptiles, Medellín (MUAREP).

RESULTS

Multivariate analysis of variance did not find significant sexual dimorphism despite the large sample for each group assessed. Therefore, males and females were treated together in all subsequent analyses. In the first approach, MANOVA showed significant differences ($W_{14,174} = 21.0$; $P < 0.001$) among all groups. Posterior comparisons using the Tukey test for unequal samples have also revealed significant differences between first and remaining groups (Table 1).

Discriminant analysis also indicated significant differences between the first group compared to the other two groups in the classificatory function (Table 2), and considerable differentiation in the plot of the canonical scores (Fig. 1A). Orthogonal comparisons of DFA partially segregate group 1 through the first two axes, which correspond to 80–97% of the entire variation, and were significantly correlated, based on the plot of directional cosines to SNOUT and LATBL (Fig. 1B). The combination of the third discriminant function, with the first or second functions, showed no satisfactory discrimination of the groups. Groups 2 and 3 exhibited no significant differences with respect to each other. In spite of the partial overlapping in the orthogonal comparisons, group 1 was considered distinct based on the MANOVA (Table 1), and 100% of values were correctly allocated by classificatory function (Table 2). We infer from the above results that currently recognized *C. caninus* includes two diagnosable and apparently geographically isolated species.

On the basis of qualitative characters, group 1 differs from the other two groups previously defined by having the number of scales across the snout reduced (Figs. 2, 3) and

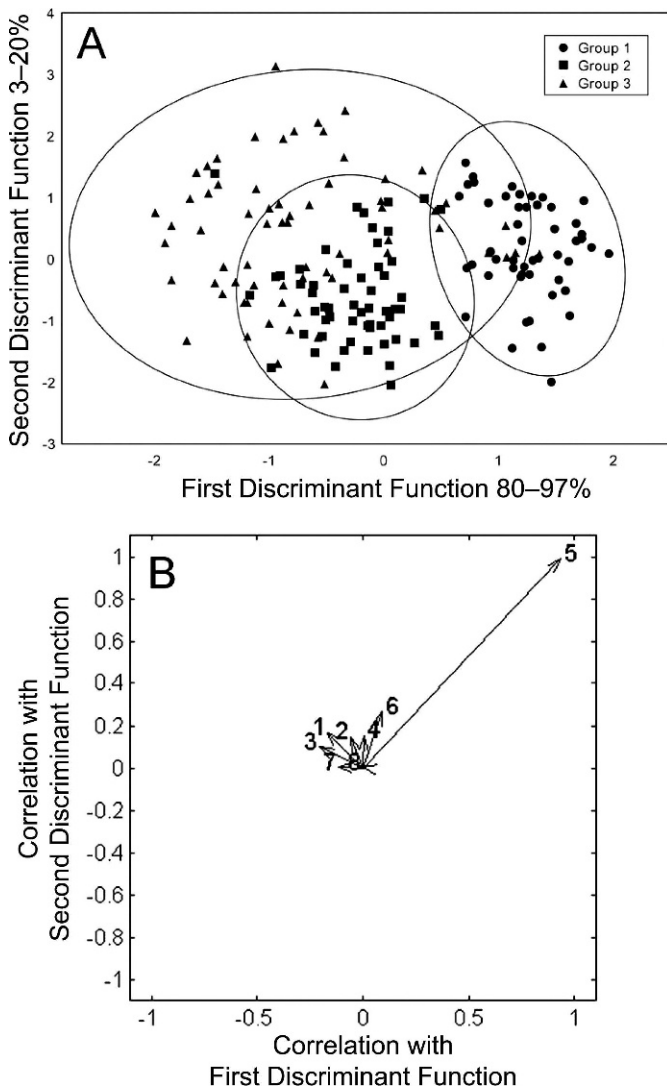


Fig. 1. Bivariate plot with 95% confidence regions (ellipses) for the first two axes derived from scores of discriminant size-free analysis for three *a priori* defined groups of *Corallus caninus* (A) and correlations of meristic characters with corresponding first discriminant functions (directional cosines) (B). Group 1 = populations north of the Rio Amazonas and east of the Rio Negro (i.e., *C. caninus* populations); Group 2 = populations south of the Rio Amazonas and east of the Rio Tapajós (*C. batesii*); Group 3 = populations south of the Rio Amazonas, west of the Rio Negro, and west of the Rio Tapajós (*C. batesii*). Variables represented in the directional cosines graph correspond respectively to: 1 = ADORS, 2 = MDORS, 3 = PDORS, 4 = VENT, 5 = SNOUT, 6 = LATBL, 7 = TRIMD, 8 = SVL.

with few lateral body blotches or their complete absence (Fig. 3). *Chrysenis batesii* is an available name for the species occurring in the Amazon Basin south of the Rio Amazonas and west of the Rio Negro and Rio Tapajós (groups 2 and 3). Therefore, herein we propose the resurrection of Gray's species under the new combination *Corallus batesii*.

Corallus caninus (Linnaeus, 1758)

Figure 4D

Boa canina Linnaeus, 1758:215. Type locality: America.
Boa hipnale Linnaeus, 1758:215. Type locality: Asia.
Boa thalassina Laurenti, 1768:89 (substitute name for *Boa canina* Linnaeus).
Boa aurantiaca Laurenti, 1768:89. Type locality: America.

Boa exigua Laurenti, 1768:89 (substitute name for *Boa canina* Linnaeus).

Xiphosoma aramboya Wagler, 1824:45. Type locality: Rio Negro, Amazonas State, Brazil.

Xiphosoma caninum.—Fitzinger, 1826:54.

Corallus caninus.—Boulenger, 1893:102.

Boa canina.—Amaral, 1925:8.

Corallus caninus.—Peters and Donoso-Barros, 1970:72.

Holotype.—NRM Linnaean 8 from "Americae".

Diagnosis.—Distinguishable from all other species of *Corallus* (except *C. batesii*) based on its green dorsal ground color with enamel-white markings on the dorsum (dorsum occasionally immaculate green, devoid of any white markings); juveniles usually red-orange (rarely green) with enamel-white markings (other species of *Corallus* have dorsal ground colors of various shades of gray, brown, red, and yellow as adults, always with patterns consisting of more than just white markings). It differs from *C. batesii* by reduced number of scales across snout at level of the suture between third and fourth supralabials (2–6, mean = 3.4 ± 1.1 in *C. caninus*; 3–12, mean = 6.9 ± 1.6 in *C. batesii*), absence of mid-dorsal longitudinal stripe (present or absent in *C. batesii*), and absence or near-absence of lateral blotches (0–11, mean = 1.3 ± 2.7 in *C. caninus*; 0–38, mean = 18.1 ± 8.2 in *C. batesii*). Juvenile dorsal coloration (in alcohol) pale yellow to beige (in life, red-orange) in specimens 380–516 mm SVL. Mitochondrial DNA sequence differences between Guiana Shield samples (*C. caninus*) and those from Amazonia (*C. batesii*) ranged from 3.1–16.2% (Vidal et al., 2005).

Description of holotype.—Adult. SVL 1290 mm. Dorsal scale rows at mid-body 66. Ventrals 203. Scales across snout at level of suture between third and fourth supralabials two. Dorsal ground color green with white mid-dorsal triangles. Mid-dorsal stripe absent. Lateral blotches absent. Venter dingy pale yellow.

Variation.—Maximum SVL in our sample 1820 mm (female from French Guiana). Maximum total length in a captive female 2108 mm (J. Polanco, in litt.). ADORS 43–56 (mean = 50.1 ± 2.4). MDORS 58–73 (mean = 65.9 ± 3.0). PDORS 32–42 (mean = 38.5 ± 2.0). VENT 191–212 (mean = 202.5 ± 4.5). SNOUT 2–6 (mean = 3.4 ± 1.1). Dorsal ground color in adults various shades of green, often with dark blue-green or black stippling on dorsals, sometimes very dense and widely dispersed (e.g., IBSP 52193, female from Presidente Figueiredo, UHE Balbina) often bordering white markings. Zero–40 (mean = 24.9 ± 8.6) enamel-white triangle-like markings on mid-dorsum (with base of triangle on dorsal midline) of body; triangles on either side of midline may be unconnected, in contact but offset, or more or less mirror images (base to base, forming a mid-dorsal diamond); triangles longest near MDORS (1–14 scales long), but narrower (1–5 scales wide at base) than at ADORS (1–6 scales wide at base) or PDORS (1–8 scales wide at base); triangles often absent from region around ADORS; anteriormost triangles occasionally tinged with green, and in RMNH 36029 from Sipaliwini, Suriname MDORS triangles heavily suffused with green. Lateral white blotches generally absent (0–11, mean = 1.3 ± 2.7), if present tend to occur towards mid-body, are vertically oriented, and encompass few scales (1–2 scales

Table 2. Classification Matrix from the Discriminant Analysis Showing the Correct Allocation for Three *a priori* Defined Groups of *Corallus caninus*. Group 1 = populations north of the Rio Amazonas and east of the Rio Negro (*C. caninus*); Group 2 = populations south of the Rio Amazonas and east of the Rio Tapajós (*C. batesii*); Group 3 = populations south of the Rio Amazonas, west of Rio Negro, and west of the Rio Tapajós (*C. batesii*).

	Percent correct	Group 1	Group 2	Group 3
Group 1	100	49	0	0
Group 2	72.5	2	37	12
Group 3	76.3	7	7	45
Total	82.4	58	44	57

wide and up to five scales long); some individuals lack white markings (e.g., SMF 73517, a female from Linden, West Demerara, Guyana; MNHN 1997.2017 from Petit Saut, French Guiana lacks white markings on body, but with four triangles on tail; IB 40216 from Itacoatiara, Amazonas, Brazil, lacks blotches on right side, but has two on left side); white triangles occur on tail. Top of head usually immaculate green, but in some cases heavily stippled with dark blue-green (e.g., IBSP 52193, female from Presidente Figueiredo, Amazonas, Brazil). Supralabials and infralabials some shade of yellow (may sometimes be lime green), and often suffused with pale green. Ventral coloration ranges from dingy white or off-white, to pale or moderately bright yellow; venter usually immaculate, but some light to moderate flecking or smudging may occur posteriorly. Underside of head immaculate yellow or yellow washed or stippled with pale green. Yellowish coloration of venter encroaches onto dorsal scales, most heavily at or near ADORS (4–12 dorsal scale rows), fewer at MDORS (1–10 rows), and at PDORS (1–7 rows); dorsal encroachment of yellow almost invariably flecked with green. Subcaudals tend to be colored as ventrals. Mental groove usually white to gray, rarely black. Juvenile dorsal coloration (in alcohol) pale yellow to beige (in life, red-orange) in specimens 380–516 mm SVL.

Distribution.—Guyana, Suriname, French Guiana, eastern and southern Venezuela (states of Bolívar and Amazonas), and northeastern Brazil north of the Rio Amazonas and north and east of the Rio Negro (in the states of Amapá, Pará, Roraima, and Amazonas); elevational distribution from sea level to about 200 m (Fig. 5).

***Corallus batesii* (Gray, 1860)**

Figure 4A–C

Chrysenis batesii Gray, 1860:132. Type locality: Upper Amazon.

Corallus caninus.—Boulenger, 1893:102.

Boa canina.—Amaral, 1925:8.

Corallus caninus.—Peters and Donoso-Barros, 1970:72.

Holotype.—NHM 1859.12.28.12. A juvenile from the “Upper Amazons”; as Bates’s collecting activities were restricted to Brazil, we assume the locality from which the snake originated was the upper Amazon of Brazil. Based on the map in Bates (1864), the “Upper Amazons” was the area along the Rio Amazonas west of the Rio Negro.

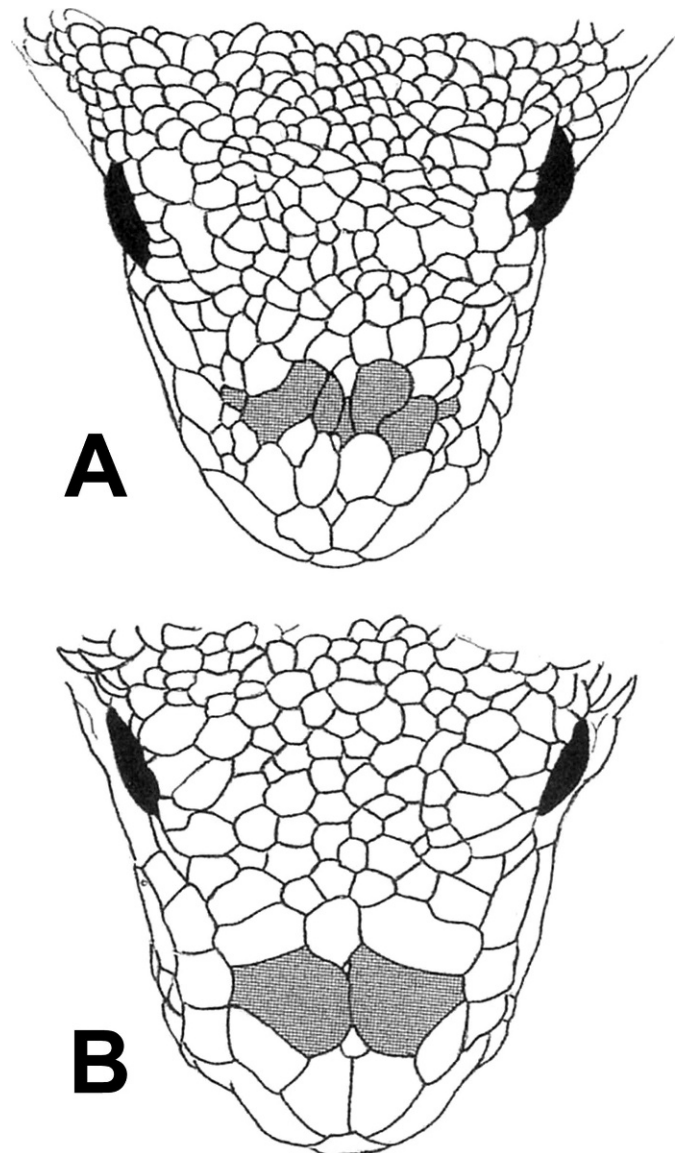


Fig. 2. Scales across the top of the snout at the level of the suture between the third and fourth supralabials. (A) *Corallus batesii* from Montalvo, Pastaza, Ecuador (USNM 204089); (B) *C. caninus* from Moengo, Marowijne, Suriname (USNM 64623).

Diagnosis.—Distinguishable from all other species of *Corallus* (except *C. caninus*) based on its green dorsal ground color (rarely black or nearly so) with enamel-white markings on the dorsum (never immaculate green). Juveniles are usually red-orange with enamel-white markings (other species of *Corallus* are various shades of gray, brown, red, and yellow as adults, always with patterns consisting of more than just white markings). Differs from *C. caninus* by the number of scales across snout at level of suture between the third and fourth supralabials (3–12, mean = 6.9 ± 1.6 in *C. batesii*; 2–6, mean = 3.4 ± 1.1 in *C. caninus*), presence or absence of mid-dorsal longitudinal stripe (absent in *C. caninus*), and lateral blotches rarely absent (0–38, mean = 18.1 ± 8.2 in *C. batesii*; 0–11, mean = 1.3 ± 2.7 in *C. caninus*). Mitochondrial DNA sequence differences between Amazonia samples (*C. batesii*) and those from the Guiana Shield (*C. caninus*) ranged from 3.1–16.2% (Vidal et al., 2005).

Description of holotype.—Juvenile. Dorsal ground color of pale brown to beige (in alcohol). Dorsal scale rows at level of

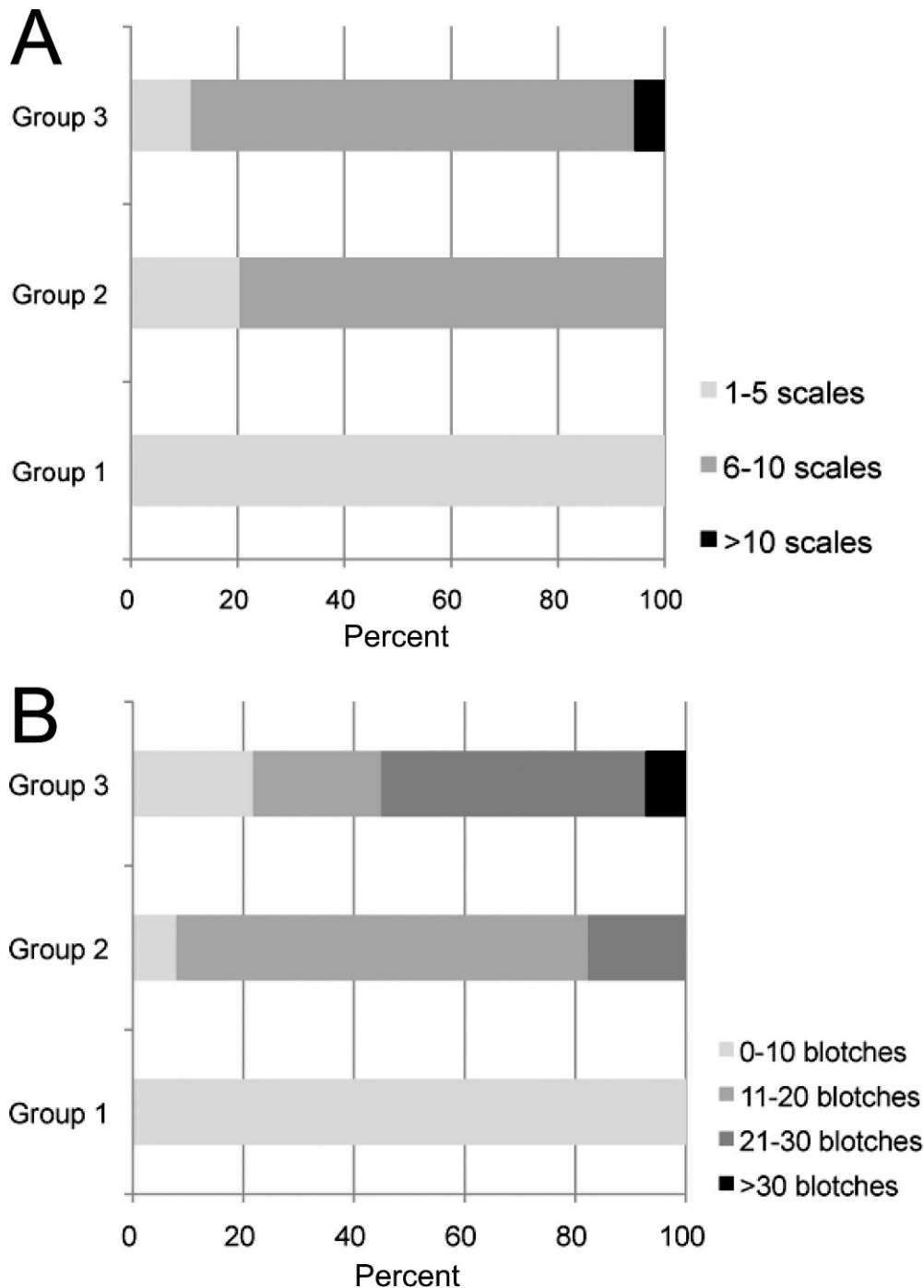


Fig. 3. Frequency plots of the polymorphic diagnostic characters for groups of *Corallus caninus*: (A) The number of scales across the snout at the level of the suture between the third and fourth supralabials; (B) the number of lateral blotches on the left side of the body. Group 1 = populations north of the Rio Amazonas and east of the Rio Negro (i.e., *C. caninus* populations); Group 2 = populations south of the Rio Amazonas and east of the Rio Tapajós (*C. batesii*); Group 3 = populations south of the Rio Amazonas, west of the Rio Negro, and west of the Rio Tapajós (*C. batesii*).

MDORS 70. Ventrals 214. SNOUT eight or nine. Dorsal pattern of triangles edged in dark brown or black. Middorsal stripe absent. Left-side lateral blotches approximately 12.

Variation.—Maximum SVL in our sample 1524 mm (female from Pará, Brazil). Maximum SVL in Pizzatto and Marques (2007) 1710 mm. Maximum total length in captive female 2235 mm (J. Polanco, in litt.). ADORS 46–61 (mean = 53.1 ± 2.8). MDORS 61–88 (mean = 70.8 ± 4.3). PDORS 29–54 (mean = 40.2 ± 3.2). VENT 186–218 (mean = 200.3 ± 7.4).

SNOUT 3–12 (mean = 6.9 ± 1.6). Dorsal ground color in adults various shades of green, often with dark blue-green or black stippling on dorsals, often bordering white markings, sometimes heavily; with or without middorsal longitudinal stripe. Middorsal stripe presence most consistent in specimens from state of Pará, Brazil, south of the Rio Amazonas; stripe may be present or absent in specimens from same locality (e.g., two females, stripe present in IBSP 46477 and absent in IBSP 46753 from Tucuruí, Pará, Brazil). Middorsal stripe usually narrow (1–2 scales wide), but may be as wide as

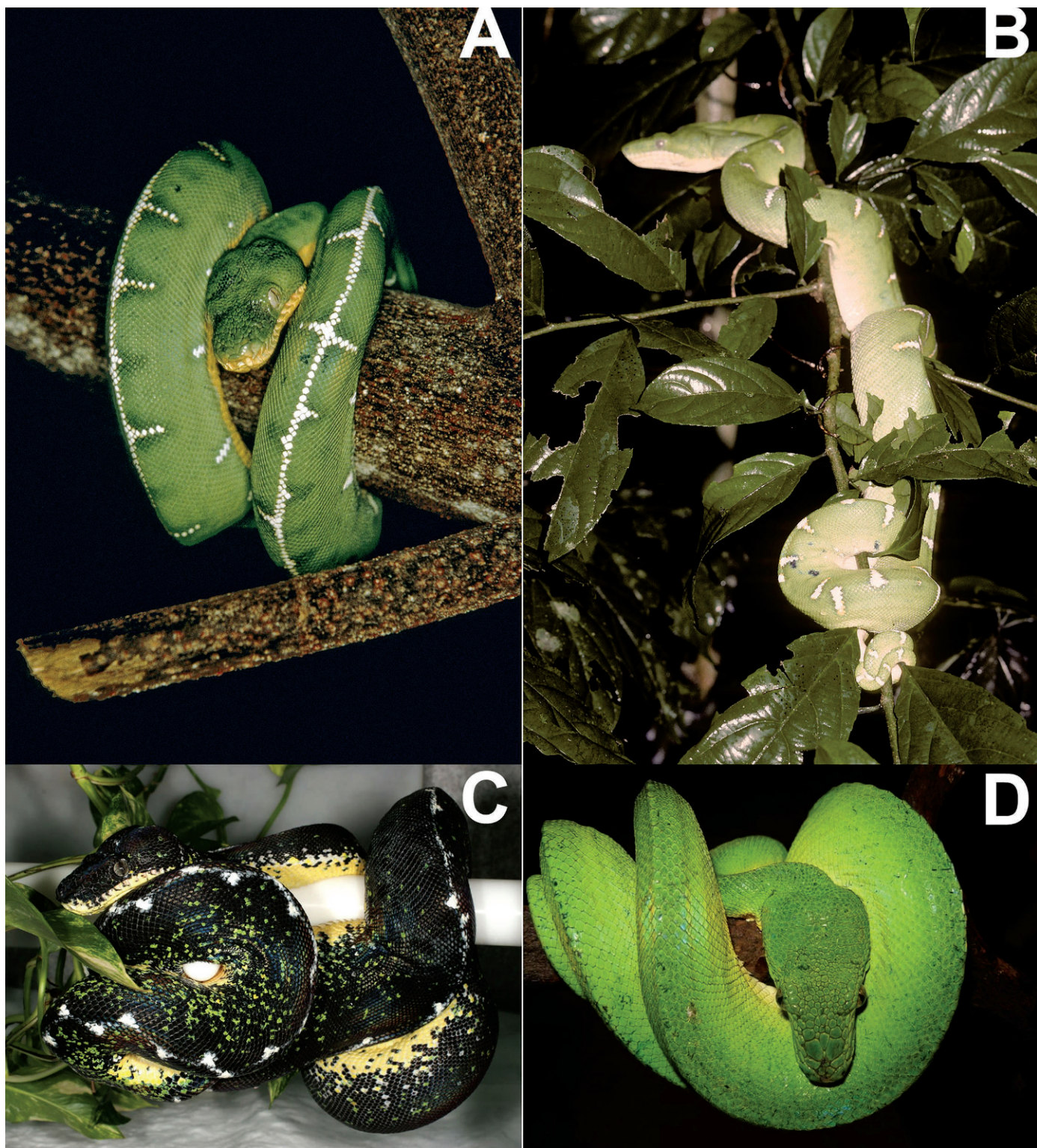


Fig. 4. (A) *Corallus batesii* from Santa Cecilia, Sucumbios, Ecuador (KU 121833); (B) *C. batesii* from Ariquemes, Rondônia, Brazil; (C) *C. cf. batesii* from an unknown locality; (D) *C. caninus* from Santa Elena de Uairen, Bolívar, Venezuela.

3–4 scales (female, MZUSP 4253 from Canindé, Pará, Brazil). Seven to 44 (mean = 29.3 ± 6.7) enamel-white triangle-like markings on mid-dorsum (with base of triangle on dorsal midline) of body. Triangles on either side of midline may be unconnected, in contact but offset, or more or less mirror images (base to base, forming mid-dorsal diamond). Triangles longest near MDORS (1–13 scales long), often absent at ADORS (but, if present, shorter than at MDORS), and

shortest at PDORS (0–9). Some specimens with portion of body with stripe only and other portion with stripe and triangles (e.g., AMNH 53424 from Pampa Hermosa, Loreto, Peru). Triangle pattern continues onto tail. Some specimens with only middorsal stripe and no triangular markings. Lateral white blotches present in most specimens 0–38 (mean = 18.1 ± 8.2), in specimens from Mato Grosso and Rondônia absent or reduced (2–12); two specimens from

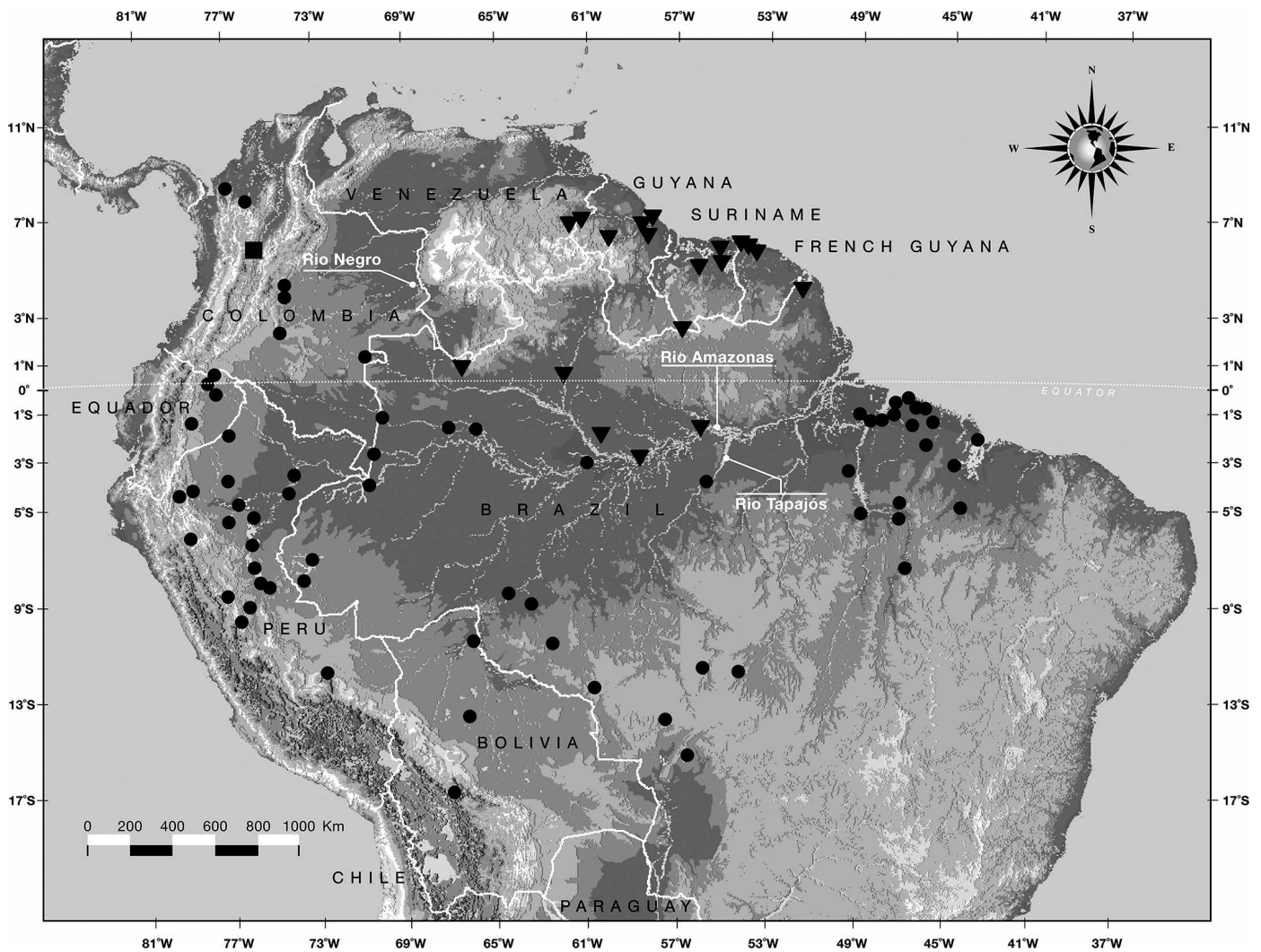


Fig. 5. Geographic distribution of *Corallus caninus* and *Corallus batesii*. Triangles = *C. caninus*, circles = *C. batesii*, square = recent record from the Rio Magdalena valley.

Bolivia with low numbers of lateral blotches (if from eastern Bolivia, may occur in an area contiguous with Rondônia): AMNH 3027 (no data) has 12 left side blotches localized at mid-body; in AMNH 6769 from "Cochabamba," (presumably not the major Andean city of Cochabamba that is situated at an elevation of ~2500 m, unless it was a point from which specimens were shipped; another Cochabamba is situated close to the Brazilian border near Rondônia) ten left side blotches. Blotches are generally narrow (1–3 scales wide) and vertically oriented, often absent anteriorly (around ADORS), longest near MDORS (3–13 scales long), sometimes absent posteriorly, when present shorter (3–8 scales long) than those at mid-body; blotches occasionally round or square-like (e.g., IBSP 26243 from Imperatriz, Maranhão, Brazil; KU 107037 from Santa Cecilia, Sucumbíos, Ecuador). Top of the head usually immaculate green, but sometimes with dense, dark blue-green to black stippling (e.g., IBSP 46752 from Tucuruí, Para, Brazil), or suffused with patches of yellow (live individual from Pacaya-Samiria Reserve, Yarinacocha, Loreto, Peru; in litt. and photograph from W. W. Lamar, 24 September 2008). Labials yellow, sometimes with wash of pale green. Under-side of head white, cream, or a shade of yellow, often immaculate but sometimes stippled or suffused with green.

Ventral color white, cream, beige, or some shade of yellow; white/cream ventral color more prevalent in western Amazon, bright yellow more common in eastern Amazon. Venter usually devoid of markings, but, if present, restricted to the posterior portion. Lateral edges of some ventrals occasionally with suffusion of pale green (rarely dark green; e.g., LACM 75170 from Limoncocha, Sucumbíos, Ecuador). Ventral color encroaches onto adjacent dorsal scale rows: at ADORS from 2–13 scale rows, at MDORS 2–9 scale rows, and at PDORS 2–6 scale rows; encroaching scales are flecked with green. Mental groove usually black, sometimes gray, and rarely white. Some specimens from unknown localities with black dorsal ground color, green flecks, mid-dorsal stripe and associated triangles, bright yellow venter, underside of head yellow, and labials yellow (Fig. 4). Juvenile dorsal coloration (in alcohol) pale yellow to beige (in life, red-orange) in specimens 389–590 mm SVL.

Distribution.—Widely distributed in the Amazon basin. In Brazil north and south of the Rio Amazonas west of the Rio Negro, also in Amazonian Colombia, Ecuador, Peru, and Bolivia, as well as in northwestern Colombia north of the Andes. Elevational distribution 0–1000 m (Fig. 5).

Etymology.—The epithet, a Latinized noun, honors Henry Walter Bates (1825–1892), the British naturalist who spent 11 years in Brazilian Amazonia collecting and studying its flora and fauna.

DISCUSSION

Several Neotropical boid species were previously considered to have wide geographic distributions in Central and South America (e.g., *Boa constrictor*, *Corallus hortulanus*, *Epicrates cenchria*, *Eunectes murinus*; McDiarmid et al., 1999). Recent studies based on large samples and/or employing a robust statistical framework on morphological or molecular data have revealed such taxa to represent species complexes (Henderson, 1997; Vidal et al., 2005; Bonny, 2007; Passos and Fernandes, “2008” 2009). Amazonia is a patchwork of forest/vegetation types intersected by a system of rivers of varying lengths and widths that has undergone a complex history of climatic change; that a widely distributed taxon such as *C. caninus* comprises more than one species is, therefore, not surprising.

Despite the low frequency polymorphism for morphologically discrete gap-based characters (SNOUT and LATBL) among *Corallus batesii* populations, *C. caninus* populations appear to be fixed for both states, and the morphometric results show quantitative characters that were supported above 95% confidence limits for recognition of *C. caninus* and *C. batesii* as distinct species. On the basis of morphological evidence, the only specimens of *C. batesii* having no or few white lateral blotches came from the states of Mato Grosso and adjacent Rondônia in the western Amazon of Brazil, while the eastern populations harbor a few individuals having a reduced number of scales across the snout as in *C. caninus*. Therefore, we interpreted the low polymorphism scale for distinct traits between eastern (referable to group 2) and western (referable to group 3) populations as evidence of a primary vicariance episode splitting the ancestral Guiana Shield stock from the remaining populations, while the Rio Amazonas is an inadequate barrier to consistently prevent gene flow between populations of *C. caninus* and *C. batesii*.

The results of mtDNA analysis, based on samples from five geographically disparate localities throughout the range of *C. caninus* (Vidal et al., 2005), largely parallel the morphological data presented here. Sequence divergence between the Venezuela and Guyana samples (=Guiana Shield) was the smallest (1.7 ± 0.3); between the Guiana Shield and Rondônia was 3.1 ± 0.4 ; and between the Guiana Shield + Rondônia and Pará south of the Rio Amazonas was 6.3 ± 0.5 . What we did not detect in the morphological data was phenotypic concordance with the strong sequence divergence (16.2 ± 0.9) between Peru and the rest of the samples. Assuming additional cryptic diversity in the *C. caninus* complex, additional DNA samples from the Upper Amazon (e.g., state of Amazonas in Brazil, Amazonian Colombia, Ecuador, and Peru) would allow further delineation of potentially discrete ranges. In short, the molecular data support the distinctiveness of *C. caninus*, which is monophyletic. The inclusion of the remaining populations under the name *C. batesii*, which do not comprise a monophyletic group, should be viewed as a preliminary step as that taxon likely includes more than one species.

Documentation of the presence of *C. caninus* in northwestern Colombia was not anticipated. As a trans-Andean dispersal is unlikely, recent evidence indicates possible

dispersal via an Andean corridor between the Cordillera Central and the Cordillera Oriental in the Río Magdalena valley (i.e., a specimen of *C. batesii* was collected and photographed at La Victoria, Depto. Caldas at 800 m asl; it has prominent lateral blotches, but no mid-dorsal stripe connecting dorsal triangles; Sánchez et al., 2009). Although the populations from northwestern Colombia are tentatively assigned to *C. batesii*, it would not surprise us if, should additional specimens and molecular data become available, these populations proved to represent a distinct species. Whether the black *Corallus* from the unknown locality/localities represent a separate species, a color morph that occurs infrequently and sporadically throughout the range of the species, or a localized melanistic enclave is unknown. Three live individuals have varying amounts of black on the dorsum, a mid-dorsal stripe, dorsal triangles, and more than five scales across the snout, and we tentatively assign them to *C. batesii*.

Boids have an ancient distribution in South America, likely since the late Cretaceous (Albino, 1986, 2000, 2007), and all members of the genus *Eunectes* (*E. beniensis*, *E. deschauenseei*, *E. murinus*, *E. notaesus*), five species of *Corallus* (*C. batesii*, *C. caninus*, *C. cropanii*, *C. hortulanus*, *C. ruschenbergerii*), and five species of *Epicrates* (*E. alvarezi*, *E. assisi*, *E. cenchria*, *E. crassus*, *E. maurus*) are endemic to the continent (Henderson, 1997; Dirksen and Böhme, 2005; Passos and Fernandes, “2008” 2009). Distinct from other boine genera, species of *Corallus* are virtually completely arboreal (species will only occasionally descend to the ground), with several exclusive adaptations to an arboreal existence, for example, laterally compressed bodies, relatively long prehensile tails (Pizzatto et al., 2007), and greatly enlarged teeth at the anterior of the upper and lower jaws (in order maintain a secure grasp of prey so that it is not lost to the ground below). In the particular case of *Corallus caninus* and *C. batesii*, the large body-size attained by each species appears to restrict their distribution to sites having broad Amazonian canopy (ca. 15–30 m above ground level; pers. obs.).

Three biogeographic processes in the past 25 million years, including marine incursions in the late Miocene, formation of riverine barriers, and formation of Pleistocene refuges (see Cracraft [1985] and references therein, and Patton and da Silva [1998] and references therein) have been hypothesized to explain Amazonian diversity and may explain diversification of treeboas. According to this complex scenario, periodic sea level rises not necessarily restricted to the Miocene had a tremendous impact on the formation of Amazonian rivers and their associated biota, either by direct inland marine incursions or by formation of large impounded freshwater lakes, especially in the lower Amazon (Räsänen et al., 1995; Irion et al., 1997; Lundberg et al., 1998; Aleixo, 2004). Western Amazonian lowlands were covered extensively by floodplain forest until the Pleistocene (Irion et al., 1997; Lundberg et al., 1998; Aleixo, 2004), and, as a result, colonization of this area by lineages of exclusively terrestrial organisms occurred relatively late (Aleixo, 2004). Given the arboreal habits of *C. batesii* and *C. caninus*, we think those populations may have evolved similarly to most avian and mammalian taxa (Ayres and Clutton-Brock, 1992; Patton et al., 1994; Patton and da Silva, 1998; Aleixo, 2004), when Guiana and Brazilian shield populations experienced a division as a result of reorientation of Amazon drainage between the upper Miocene and the late Pliocene generated by Andean uplift and/or marine

inland incursions (Räsänen et al., 1995; Irion et al., 1997; Lovejoy et al., 1998; Borges, 2007).

The marine incursion model as well as the riverine barrier hypothesis dictates that ancient *Corallus* populations were separated between 5.3 and 25 mya. We speculate that the close relationship between Guiana Shield and Rondônia populations was due to recent dispersal episodes during the Pleistocene through the Vaupes Arch (Lundberg et al., 1998; Borges, 2007). In fact, the putative barriers of the Rio Amazonas and Rio Negro, used herein primarily as an impediment to species contact, apparently do not represent obstacles along all of each watercourse for birds and mammals (Capparela, 1991; Patton and da Silva, 1998; Borges, 2007); therefore, some cross-river dispersal between *C. batesii* and *C. caninus* was likely, mainly in the lower courses of the Rio Negro and Rio Amazonas (Ayres and Clutton-Brock, 1992; Patton and da Silva, 1998; Borges, 2007).

MATERIAL EXAMINED

Corallus batesii (135): Bolivia: unknown locality, AMNH 3027; Cochabamba, AMNH 6769; Beni, NHM 95.11.21.12. Brazil: unknown locality, MNRJ 187, MNRJ 4531–32; Acre, Porto Walter, MZUSP 7392; Amazonas, Lago Amaña-Rio Japura, Mun. de Marã, MPEG 16777; Amazonas, Lomoeiro (Rio Japura), MZUSP 6596; Amazonas, Lago Mamiraua, foz de Japura, MZUSP 8373; Maranhão, Imperatria, IBSP 26243, 26793; Maranhão, Açailandia, IBSP 26892; Maranhão, Gancho do Arari BR-316, Arari, MPEG 13550; Maranhão, Parua, BR-316, MPEG 13551; Maranhão, Aldeia Araçu, Igarapé Gurupi-Una, MZUSP 4311; Mato Grosso, Rio Xingu, IBSP 27228; Mato Grosso, Sinop, IBSP 44370; Mato Grosso, Cuiabá, IBSP 50364; Mato Grosso, Tangara de Serra, IBSP 50585; Pará, Km 16 do Estrada do Acará, MPEG 8063, 10809; Pará, Augusto Correa, Cacoal, MPEG 1978, 9097; Pará, Barcarena, KU 128089; Pará, Belem, MPEG 20, 32, 371; Pará, Casatanhal, Boa Vista/Apeu, MPEG 1560, 4769; Pará, Bom Jesus, Bragança, MPEG 2502; Pará, BR-316, Km 74, PA/MA, MPEG 3553; Pará, Cachoeira do Espelho (Rio Xingu), MCZ 9087; Pará, Caninde, MZUSP 4253; Pará, Colonia Nova, BR 316 (Gurupi), MPEG 10720; Pará, Genipauba, Santa Barbara, MPEG 6953; Pará, Igarape Pirajauara, Estrada do Acará, MPEG 9412; Pará, Maraba, Serra Norte, Est. N1 Caldeirao, MPEG 17038; Pará, Maraba, Serra Norte, area do Manganês, MPEG 17151; Pará, Monte Cristo (Rio Tapajos), MZUSP 1262; Pará, Oriximiná, MNRJ 3433; Pará, Ourem-Faz Gaviao, Patauateua, MPEG 18622; Pará, Pará, MZUSP 2456; Pará, Rio Parajauara, Estrada do Acará, MPEG 10818; Pará, Rodovia Belem-Brasilia, Km 93, MZUSP 3738; Pará, Santo Antonio do Taua, MPEG 6976; Pará, Taperinha, MCZ 2932; Pará, Porto Trombetas, MNRJ 14999, 16455; Pará, Santa Barbara, MPEG 1099; Pará, Santa Barbara, Benevides, MPEG 754, 2645; Pará, Santa Luzia-Capitão Poço, MPEG 1606; Pará, Santarem Novo, Estrada para Salinas, MPEG 29; Pará, Santarem, Agropecuaria Treviso Ltd., MPEG 19099; Pará, Santarem Novo, Rio Jaburu, MPEG 18762; Pará, Sao Pedro, Mun. Capitão Poço, MPEG 10661; Pará, Sitio Bela Vista PA 70, MPEG 12133, 12140, 13383, 14509, 16098; Pará, Tucuruí, IBSP 46477, 46890, MNRJ 4533; Pará, Tucuruí (UHE Tucuruí), IBSP 46752–53; Pará, Vigia, Santa Rosa, MPEG 9305, 11873; Pará, Pará, Viseu, MPEG 1702; Pará, Viseu-Bela Vista, MPEG 8914; Viseu-Fazenda Real, MPEG 1742. Rondônia, Cachoeira Nazaré (Rio Jiparana), MPEG 18972, 18975; Rondônia, Guajará-Mirim, MPEG 19490; Rondônia, Parque

Estadual Guajará-Mirim, MPEG 19453, OMNH 37521; Rondônia, Porto Velho, IBSP 45177, 53748, MNRJ 8863; Rondônia, Santa Barbara, MZUSP 8675; Rondônia, Vilhena, IBSP 34141. Colombia: Amazonas, Tarapaca (Río Putumayo), MCZ 50143; Amazonas, Independencia (Río Aparis), MCZ 53217; Amazonas, Leticia, MPEG 18237. Antioquia, Municipio de Cáceres, MUAREP 001; Córdoba, Tierralta (115 km S of Montería), ICN 8398. Meta, La Macarena (N Caño Guapaza), ICN 1495; Meta, Villavicencio (Col. Teófilo López), ICN 6529; Meta, Villavicencio (Hacienda la Libertad, 22 km E of Villavicencio), ICN 8289; Meta, 50 km E San Martín, MVZ 68687. Vaupés, Wacara, UTACV 22584–85. Ecuador: Pastaza, Coballa Cocha (Río Tigre), AMNH 49154; Pastaza, Canelos (Río Pastaza), MCZ 36952; Pastaza, Montalvo (Río Conambo), USNM 20488–89; Sucumbios, Santa Cecilia, KU 105386, 107037, 112291, 121832–33, 142797, 175394, 179490; Sucumbios, Lago Agrio, KU 148283; Sucumbios, Limoncocha (Río Napo), KU 179490, LACM 75170; Sucumbios, Dureno, MZUSP 8233. Perú: Amazonas, Pongo de Monseriche, MVZ 16908; Amazonas, vicinity of Huampami (Río Cenepa), MVZ 163379; Amazonas, 3 km E Isla Jauma, USNM 306992; Amazonas, vicinity of Sua (Río Cenepa), USNM 316564. Amazonas-Loreto, mouth of Río Santiago-Río Marañon, AMNH 52414, 53017; Huanuco, Pachitea, Monte Alegre (Río Pachitea), AMNH 53044; Huanuco, Pucayacu (marginal highway between Aucayacu and La Morada) (Río Huallaga), USNM 193693. Loreto, Achinamisa (Río Huallaga), AMNH 55910; Loreto, Campo Santa Clara (near Orellana, Río Ucayali), USNM 127121; Loreto, Iquitos, AMNH 52047, 52546, 52846, 53019, 53212, 54023 (Río Itaya), 54061 (Río Itaya), 54926, 55129 (Río Itaya), TCWC 42068 (Río Amazonas); Loreto, Monte Carmelo, Requena, AMNH 55499; Loreto, Río Pacaya-Río Ucayali, NHM 1913.7.28.9–10; Loreto, Pampa Hermosa (Río Cushabatay), AMNH 53424, 55731; Loreto, Río Pisqui, AMNH 52555; Loreto, Roaboya (Río Ucayali), AMNH 54423; Loreto, Santa María (Río Napo), TCWC 42067; Loreto, Yarinacocha (Río Ucayali), FMNH 45630; USNM 127121. Madre de Dios, Manú National Park, MCZ 150254. Pasco, Pozuzo (Yulitunqui), SMF 80017. Ucayali, Río Tamaya, AMNH 52332.

Corallus caninus (57): Brazil: Amapá, Oiapoque, IBSP 14625, 24845; Amazonas, Balbina (Presidente Figueiredo, Rio Uatuma), IBSP 5195; Amazonas, Presidente Figueiredo (UHE Balbina), IBSP 52193, MPEG 18599; Amazonas, Itacoatiara, IBSP 40216, 5195; Amazonas, Manacapuru, MCZ 2554; Roraima, 10 km da Boca do Jundia (Rio Catrimani), MZUSP 6393; French Guiana: unknown locality, MNHN 1997.2330, 1997.2360; Petit Saut, MNHN 1997.2017; Saint-Eugene, MNHN 1997.2018; Piste de Petit Saut, MNHN 1997.2078. Guyana: unknown locality, AMNH 2316, 60835; Demerara River, NHM 1929.7.13.5; East Demerara, Georgetown (Demerara River), MCZ 33384; Mazaruni-Potaro, Kalakun (Mazaruni River), AMNH 8368; Mazaruni-Potaro, Kartabo, AMNH 14133; Mazaruni-Potaro, Kamakusa (Mazaruni River), AMNH 25029; West Demerara, S of Linden, SMF 73509, 73511–20, 73522–23. Suriname: unknown locality, UTACV 26135–37; Brokopondo, near Kabel, RMNH 29779; Brokopondo, Afobaka, 29781; Brokopondo, Brownsberg, 36025; Commewijne, a/d, O-W verb, RMNH 29780; Marowijne, Moengo, RMNH 29762; Marowijne, Mongotapoe, RMNH 36026; Marowijne, Albina, RMNH 36027; Marowijne, Moengo, USNM 64623, 66865; Marowijne, Mongotapoe, UTACV 15697, 16867, 16983,

16986. Para, Saramacca Kreek, RMNH 29778; Sipaliwini, Raleighvallen (Coppename River), RMNH 36028; Sipaliwini, Kwamalasamutu (Sipaliwini River), RMNH 36029, 36976. Wanica, Lelydorp, RMNH 36030. Venezuela: Amazonas, Neblina, USNM 559977; Bolivar: Carretera Santa Elena de Uairen-El Dorado, km 28, MHNLS 1598; Bolivar, Anacoco (Río Cuyuni), MHNLS 8439.

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