

A Taxonomic Review of the *Corallus hortulanus* Complex of Neotropical Tree Boas

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ABSTRACT.—The arboreal boa *Corallus hortulanus* has a wide geographic and ecological distribution on the Neotropical mainland and several continental and oceanic islands. Through examination of over 600 specimens of *C. hortulanus* from throughout its range utilizing characters of scalation, size, color, and pattern, coupled with analysis of mtDNA sequences from several critical areas, it was determined that *C. hortulanus* is a complex of four species: *Corallus hortulanus* (Linnaeus) (the Guianas, throughout Amazonia, and into southeastern Brazil), *C. ruschenbergerii* (Cope) (southern Costa Rica, Panama and associated islands, northern Colombia, northern Venezuela including Isla Margarita, and Trinidad and Tobago), *C. cooki* Gray (St. Vincent), and *C. grenadensis* (Barbour) (Grenada Bank).

RESUMEN.—La boa arborícola *Corallus hortulanus* tiene una amplia distribución ecológica y geográfica en áreas continentales neotropicales y en varias islas oceánicas o continentales. Mediante el estudio de más de 600 ejemplares de *C. hortulanus* colectados a lo largo de su área de distribución, y usando caracteres de escamas, tamaño, color, y patrón, además de análisis de secuencias de mtDNA de varias áreas críticas, se determinó que *C. hortulanus* es un complejo de cuatro especies: *Corallus hortulanus* (Linnaeus) (Guyanas, a lo largo de Amazonia hasta el sur de Brasil), *C. ruschenbergerii* (Cope) (sur de Costa Rica, Panamá e islas asociadas, norte de Colombia, norte de Venezuela incluyendo Isla Margarita y Trinidad y Tobago), *C. cooki* Gray (San Vicente), y *C. grenadensis* (Barbour) (banco de Grenada).

INTRODUCTION

Species in the boid genus *Corallus* are conspicuous members of the Neotropical snake fauna, and with the exception of the rare and enigmatic *C. cropanii*, are easily identified by their laterally compressed bodies, chunky heads, slender necks, and prominent labial pits. Four species are currently recognized: *C. annulatus*, *C. caninus*, *C. cropanii*, and *C. hortulanus*. Formerly, the taxon *cropanii* belonged to the monotypic genus *Xenoboa* (see Kluge, 1991), and *C. hortulanus* was until recently usually referred to as *C. enydris* (see McDiarmid et al., 1996). Members of the genus occur from northern Central America to southeastern Brazil (just south of the Tropic of Capricorn), and on oceanic (St. Vincent, Grenada Bank) and continental islands (off Panama, Venezuela, and Brazil). Three of the four species occur in northern South America.

Corallus hortulanus is the most widespread member of the genus, and it has one of the broadest ranges (geographically and

ecologically) of any Neotropical snake (Henderson et al., 1995). It is a common species in some lowland snake communities. Throughout much of its wide range the species exhibits an amazing variety of dorsal colors and patterns, and this has led to taxonomic confusion with new species being described solely on the basis of color or pattern. Two subspecies are currently recognized: *C. h. hortulanus* occurs throughout the Guianas, Amazonia, and into southeastern Brazil just south of the Tropic of Capricorn; and *C. h. cooki* occurs in southern Central America, northern Colombia and Venezuela, Trinidad and Tobago, and the southern Windward Islands (St. Vincent and the Grenada Bank).

Here, based on examination of more than 600 specimens from throughout the range, I present a new taxonomic arrangement for the *hortulanus* complex. Not presented here is a detailed analysis of geographic variation in color pattern. One of my primary goals at the inception of this project was to

attempt to determine if there was ecological content in the seemingly bewildering variety of color pattern varieties. I have demonstrated that on Grenada predominant dorsal color is correlated with ecological factors (Henderson, 1990, 1996), but even there, where color and pattern variability reach their apex, considerable refinement of the data is possible. That aspect of the project will be addressed in a future publication.

METHODS

Six hundred and thirty-eight specimens of *Corallus hortulanus* (*sensu stricto*) from throughout its range were examined, but 616 provided most of the data (some specimens were severely damaged or had incomplete locality data). Up to 30 characters were recorded for each specimen, but nine were the most informative regarding geographic variation. They are: *size*: (1) snout-vent length (SVL); *scale characters*: (2) ventrals, (3) subcaudals, (4) infralorals (Fig. 1), (5) circumorbitals, (6) scales between supraoculars (Fig. 1), (7) maximum number of dorsal scale rows; and *color and pattern*: (8) dorsal ground color, (9) shape of primary element in dorsal pattern (recorded at midbody).

Statistical procedures were done using the Statistical Analysis System (SAS Institute, 1990), and a significance level of $\alpha = 0.05$ was used on all statistical tests. Tests of geographic variation used analysis of variance (ANOVA) with Tukey's studentized range test on all main effect means, and principal component analysis (PCA). ANOVA was used to determine if significant sexual differences in meristic characters occurred.

For analysis of geographic variation, 33 Operational Taxonomic Units (OTUs) were defined based primarily on political boundaries (Table 1); only Colombia, Venezuela, Peru, and Brazil were subdivided into 2–5 additional units based on geographic features. A second group of 13 OTUs based on the morphoclimatic domains of Ab'Saber (1977) was used for material from South America, and provided an ecological perspective. Since Ab'Saber's work did not include Central America, the West Indies, or

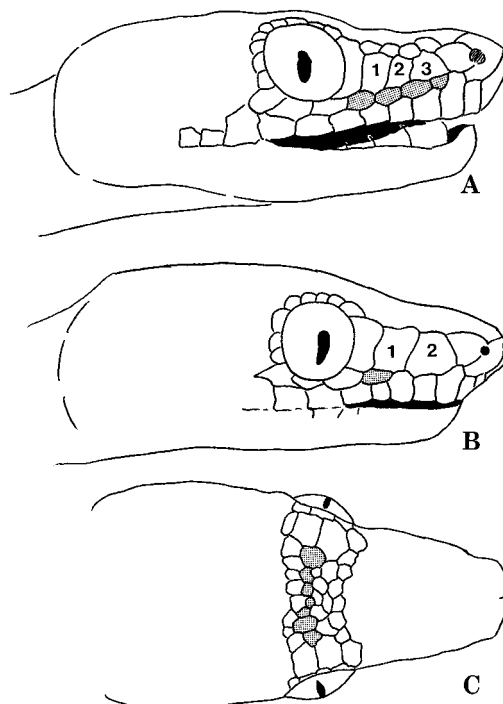


FIG. 1. Schematic drawings illustrating scale counts. A and B. Loreal region depicting fragmentation of scales in A (1, 2, 3) compared to B (1, 2), and in infralorals (shaded scales). Infralorals border the large scales between the eye and nostril, the supraorbitals, the nasals, and the circumorbitals, but are never included in any of those counts. C. Scales between supraorbitals (= intersupraorbitals or intersupraoculars). The snake depicted in A and C is MZUSP 8356 from Brazil, and that in B is MPM 27955 from Grenada.

Trinidad and Tobago, material from those areas was omitted from that analysis.

There is great variation in predominant dorsal ground color and major element in the dorsal pattern at midbody across the wide geographic range of *Corallus hortulanus*. To facilitate working with this variation, predominant dorsal color was divided into only three categories: (1) taupe (including gray and many shades of brown), (2) yellow brown (including yellow, tan, khaki, beige; in reality still shades of brown), and (3) orange. Snakes that are orange in life lose the color quickly in preservative, and it is likely that this color is under represented in the sample, especially from mainland South America. There is some collecting bias in regards to predominant dorsal ground col-

TABLE 1. Operational Taxonomic Units (OTUs) and the sample size for each used in preliminary statistical analysis of variation in the *Corallus hortulanus* complex.

| OTU | N |
|--|-----|
| West Indies | |
| 1. St. Vincent | 50 |
| 2. Bequia | 14 |
| 3. Ile Quatre | 4 |
| 4. Baliceaux Island | 2 |
| 5. Mustique | 3 |
| 6. Canouan | 11 |
| 7. Mayreau | 8 |
| 8. Union Island | 15 |
| 9. Petite Martinique | 1 |
| 10. Carriacou | 6 |
| 11. Grenada | 130 |
| Central America | |
| 12. Costa Rica | 5 |
| 13. Panama | 41 |
| 14. Islands off Panama | 6 |
| South America (including continental islands) | |
| 15. Northern Colombia | 11 |
| 16. Southern Colombia | 6 |
| 17. Tobago | 7 |
| 18. Trinidad | 36 |
| 19. Northern Venezuela (including Isla Margarita) | 11 |
| 20. Orinoco Delta (Venezuela) | 9 |
| 21. Southern Venezuela | 10 |
| 22. Guyana | 22 |
| 23. Suriname | 20 |
| 24. French Guiana | 7 |
| 25. Ecuador | 10 |
| 26. Northern Peru | 48 |
| 27. Southern Peru | 24 |
| 28. Bolivia | 28 |
| Brazil | |
| 29. Northern (north of Rio Amazonas) | 16 |
| 30. Western Amazonia | 11 |
| 31. Central and Eastern Amazonia | 29 |
| 32. Atlantic Forest | 10 |
| 33. Ilha Grande | 6 |

or. Based on personal experience, I know that in areas where tree boas are common, not all of the snakes encountered are collected. Instead, "unusual" colors are taken over the more prevalent taupe. At least on Grenada, the most commonly occurring dorsal ground color changes from locality to locality, depending on climatic conditions. So collecting sites can also be another source of bias.

The major element in the dorsal pattern at midbody was even more difficult to evalu-

ate, but seven character states were identified (Fig. 2): (1) ellipse (dorsoventrally oriented and usually with the dorsalmost portion wider than the ventralmost portion), (2) rhomb, (3) hourglass (usually with sharp angles rather than soft curves), (4) spade (with the spade shape oriented dorsally; with either soft or sharp angles), (5) free edge of dorsals edged with black or dark brown, (6) flecks (small flecks 1–2 scales wide and only occurring on snakes with a yellow dorsal ground color), (7) patternless (only occurred

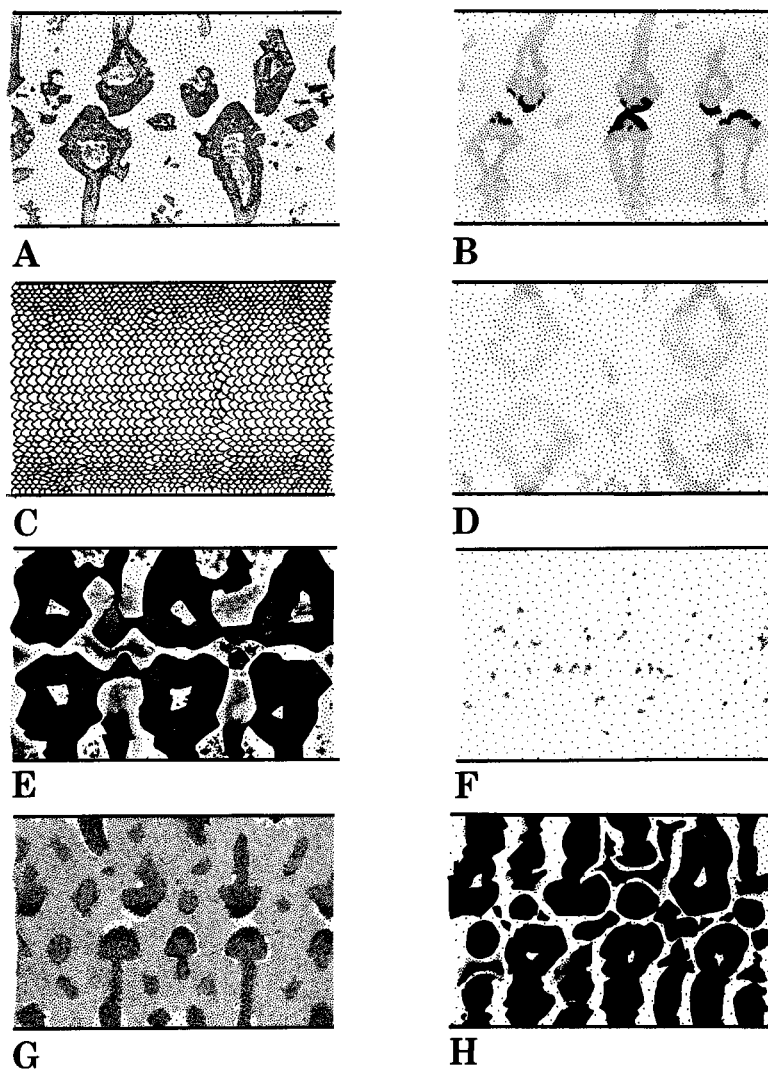


FIG. 2. Schematic representations of dorsal color patterns in members of the *Corallus hortulanus* complex. A. Bolivia (CMNH 2756), B. Guyana (USNM 145463), C. Trinidad (AMNH 73097), D. Costa Rica (UMMZ 131314), E. St. Vincent (MPM 23302), F. Guyana (USNM 145470), G. Grenada (USNM 167398), H. Grenada (USNM 67233).

in snakes with a yellow dorsal ground color), and (8) "other" (any pattern that could not easily be scored 1–7 and was extremely rare in the sample). The pattern on the dorsal surface of the head is also extremely variable, but not diagnostic; a sample of the variation appears in Fig. 3.

The results of a previously published study using mitochondrial DNA sequences are herein reiterated and materials and methods for that analysis can be found in Henderson and Hedges (1995). Although

that study included only seven samples, they were from geographically strategic localities: 1) Canal Zone, Panama; 2) Jonestown, Guyana 3) Reserva Cuzco Amazónico, Madre de Dios, Peru; 4) Iguape, São Paulo, Brazil (Atlantic coastal forest in southeastern Brazil) 5) Trinidad; 6) St. Vincent, West Indies; and 7) Grenada, West Indies. *Corallus caninus* was included for comparison and *Epicrates striatus* (from the Dominican Republic) for the purpose of rooting the tree.

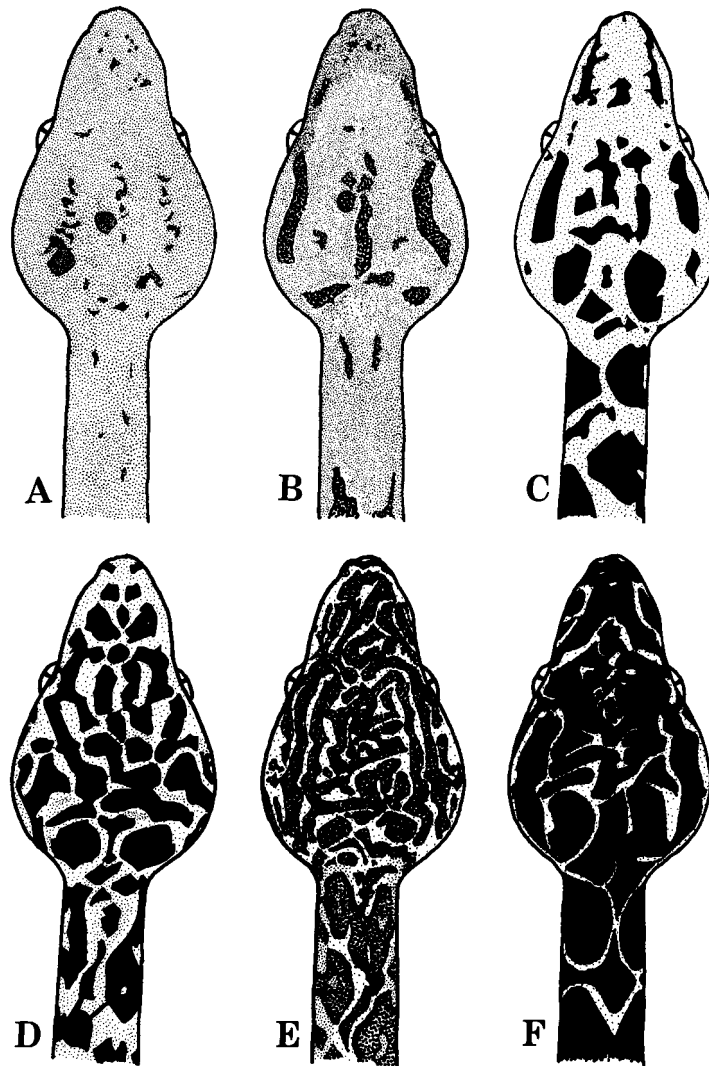


FIG. 3. Schematic representations of dorsal head patterns in members of the *Corallus hortulanus* complex. A. Grenada (MPM 23511), B. Peru (MPM 10430), C. Panama (UMMZ 135365), D. St. Vincent (MPM 23295), E. Suriname (UTACV R15699), F. Grenada (MPM 23487).

RESULTS

DNA Sequences.—A phylogenetic tree (Fig. 4) indicates a major dichotomy between the samples from Panama and Trinidad (79% confidence probability) and those from other areas (98%). The West Indian samples (St. Vincent and Grenada) clustered strongly (98%) with the South American (Guyana, Brazil, Peru) samples rather than with the geographically more proximate Trinidad sample. A maximum parsimony analysis (Fig. 5) showed the

same major dichotomy found in the neighbor-joining analysis (Fig. 4).

Multivariate Analysis.—Multivariate analysis produced equivocal results and they are not fully congruent with DNA sequencing. Six meristic characters were used: ventrals, subcaudals, maximum number of dorsal scale rows, number of scales in circumorbital series, infralorals, and number of scales between supraoculars. The 33 OTUs (540 observations) were compared using PCA. Principal component 1 (Eigenvalue

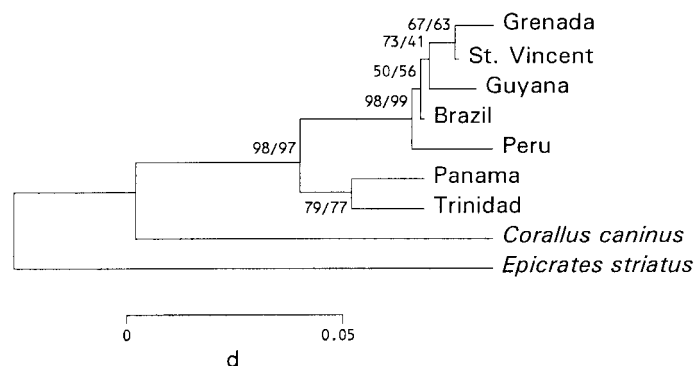


FIG. 4. Phylogenetic relationships of *Corallus hortulanus* from seven widely distributed localities, inferred from a neighbor-joining analysis of DNA sequences (Jukes-Cantor distance) of a portion of the mitochondrial cytochrome b gene. The numbers on the tree are statistical estimates of confidence of each node: the "confidence probability" (Rzhetsky and Nei, 1992; Kumar et al., 1993) derived from the standard error estimate of the branch length (left of slash), and the bootstrap P-value (Felsenstein, 1985) based on 2000 replications (right). The West Indian boine species *Epicrates striatus* was used to root the tree. d = distance. Modified from Henderson and Hedges (1995).

3.7742) separated OTUs on the basis of ventrals, dorsal scale rows, and scales between supraorbitals, and accounted for 62.9% of the variation. Principal component 2 (Eigenvalue 0.8887) showed a high loading for infralorals and accounted for 14.8% of the variation. A plot of the first and second principal components indicated two main clusters: (1) the West Indies, Central America, northern South America, Trinidad, and Tobago; and (2) Amazonian South America, the Guianas, Atlantic forests, Cerrado, Caa-tinga. There was considerable overlap of OTUs within each of the two main clusters. PCA and plot of only the means of each OTU ($n = 33$) clarified the situation (Fig. 6). Snakes from Central America, non-Ama-zonian South America, Trinidad, and To-bago form a cluster separate from snakes

from the Grenada Bank. Material from St. Vincent is more isolated from the other two. "Amazonian" material formed a fairly tight cluster with the exception of material from the Atlantic forest area of Brazil.

Another PCA (PCA2) was run using Ab'Saber's (1977) morphoclimatic domains as the OTUs. Principal component 1 (Eigenvalue 3.23017) separated OTUs on the basis of dorsal scale rows, scales between supraorbitals, and subcaudals, and accounted for 53.8% of the variation. Principal component 2 (Eigenvalue 1.08112) separated OTUs on the basis of infralorals and accounted for 18.0% of the variation. Principal component 3 (Eigenvalue 0.63768) had a high loading for circumorbital scales and accounted for 10.6% of the variation. Morphoclimatic domains do not have political

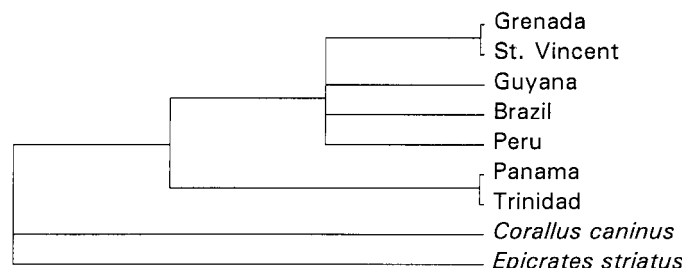


FIG. 5. Phylogenetic relationships of *Corallus hortulanus* inferred from a maximum parsimony analysis (branch-and-bound). The tree is a strict consensus of six most-parsimonious trees, each of length = 41. Modified from Henderson and Hedges (1995).

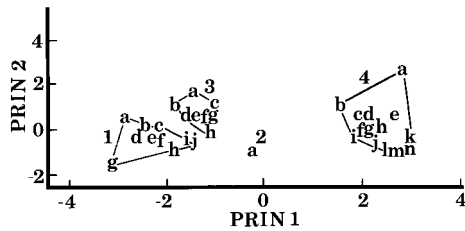


FIG. 6. Means of 33 OTUs used in PCA1. Cluster 1: a. Ile Quatre, b. Baliceaux, c. Bequia, d. Petit Martinique, e. Canouan, f. Grenada, g. Mayreau, h. Union Island, i. Mustique, j. Carriacou; Cluster 2: a. St. Vincent; Cluster 3: a. Trinidad, b. Tobago, c. northern Venezuela (including Isla Margarita), d. Orinoco Delta, e. Panama, f. islands off Panama coasts, g. Costa Rica h. northern Colombia; Cluster 4: a. Atlantic forests of Brazil, b. Ilha Grande, Brazil, c. southern Peru, d. Bolivia, e. western Brazil, f. central and eastern Amazonian Brazil, g. southern Colombia, h. northern Peru, i. Ecuador j. Suriname, k. southern Venezuela, l. Guyana, m. northern Brazil, n. French Guiana.

boundaries, and PCA2 provides an ecological perspective of the same data used in PCA1. There were two virtually non-overlapping clusters, but a single Cerrado domain specimen occurred with material from the more northern localities. To visually clarify the situation, another PCA was run using only the mean values for each domain (Fig. 7).

Color and Pattern.—Snakes with a dorsal ground color of taupe occurred throughout the range of *C. hortulanus*, but snakes from mainland South America south of the Andes and the Río Orinoco, and from St. Vincent exhibited this color more than others (56.5–100%), with Guyana having the lowest incidence. Yellow snakes occurred throughout much of the range, but were especially common in Guyana (43.5%), on the Grenada Bank (primarily Grenada, 43.4%) and in Central America, northernmost South America, and Trinidad and Tobago (39.8%). They were absent from St. Vincent and Ilha Grande, Brazil.

Pattern elements showed a similar distribution. Nearly 90% of the snakes from St. Vincent exhibited an hourglass pattern that was nearly absent elsewhere. An ellipse pattern was very common (64.7%) in snakes from Amazonia, the Guianas, and southern Brazil, but was nearly absent elsewhere (0–5.4%). Rhombs predominated (59.7%) in

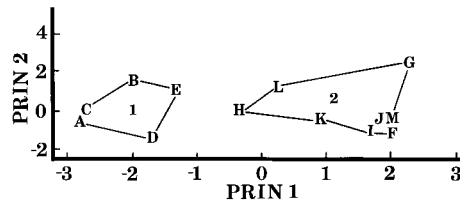


FIG. 7. Morphoclimatic domains (Ab'Saber, 1977) used in principal component analysis (PCA2). Each letter represents the mean of a domain or of a transition zone between domains. A. Equatorial Pacific (Chocó), B. Orinoco Llanos, C. Interandean valleys (Colombia and Venezuela), D. Subequatorial Caribbean-Guajira (Colombia and Venezuela), E. Transition zone between Llanos and Amazonia, F. Amazonia, G. Tropical Atlantic (Atlantic forests of Brazil), H. Brazilian Cerrados, I. Roraima-Guiana, J. Brazilian Caatingas, K. Chaco Central (Bolivia), L. *Araucaria* Plateau (Brazil) M. Transition zone between Amazonia and Chaco Central (Bolivia). Cluster 1 represents domains in the range of *Corallus ruschenbergerii* and cluster 2 represents domains within the range of *C. hortulanus*.

Central America, northern South America, Trinidad and Tobago, but were virtually absent elsewhere (0–2.4%). A spade shape predominated on the Grenada Bank (80.0%), but occurred infrequently elsewhere. Black-edged dorsal scales were fairly common (27.1%) in Central America, northernmost South America, and Trinidad and Tobago, but occurred nowhere else. A flecked pattern was rare (0–7.0%), and occurred most often on Grenada. Truly patternless snakes were rare but occurred most often in Trinidad. Snakes devoid of a dorsal pattern invariably had a yellowish dorsal ground color (although W. W. Lamar [in litt.] has observed a patternless example in Peru with a dorsal ground color of pale pink-red), and the venter was often patternless or only lightly patterned.

The most conspicuous difference between juvenile and adult coloration is in the presence of pink, pale orange, pale rose, or salmon color on the juveniles where white or whitish appears on the adults. This coloration usually borders the main pattern elements on the head and dorsum.

Hemipenes.—Differences in hemipenial morphology are minimal. Specimens from Panama, northern Venezuela, and Trinidad have organs that are more conspicuously bilobed than those in specimens from Amazonia and the West Indies, where there is

TABLE 2. Mean \pm SE (range; N) for selected meristic characters in species of the *Corallus hortulanus* complex. None of the species exhibited significant sexual dimorphism in any of the characters (ANOVA, $P > 0.05$).

| | <i>C. hortulanus</i> | <i>C. grenadensis</i> | <i>C. cooki</i> | <i>C. ruschenbergeri</i> |
|-------------------------------------|------------------------------------|------------------------------------|-----------------------------------|------------------------------------|
| Ventrals | 278.6 \pm 0.43 (258–297; 252) | 263.7 \pm 0.30 (251–278; 187) | 268.4 \pm 0.65 (257–278; 42) | 262.9 \pm 0.47 (250–272; 119) |
| Subcaudals | 117.9 \pm 0.37 (105–137; 234) | 109.0 \pm 0.32 (100–119; 174) | 115.2 \pm 0.61 (100–122; 35) | 105.8 \pm 0.35 (94–115; 113) |
| Scales between supraoculars | 10.2 \pm 0.10 (5–14; 252) | 6.3 \pm 0.08 (3–9; 193) | 9.7 \pm 0.25 (7–13; 42) | 6.0 \pm 0.12 (3–10; 125) |
| Subloreal | 3.7 \pm 0.09 (0–9; 257) | 1.8 \pm 0.07 (0–4; 189) | 2.0 \pm 0.17 (0–4; 43) | 2.7 \pm 0.08 (0–6; 126) |
| Circumorbital scales | 14.6 \pm 0.08 (8–17; 249) | 11.5 \pm 0.08 (8–14; 186) | 12.5 \pm 0.17 (10–14; 39) | 13.5 \pm 0.09 (11–16; 122) |
| Maximum number of dorsal scale rows | 55.0 \pm 0.17 (47–63; 255) | 41.0 \pm 0.12 (37–46; 192) | 43.9 \pm 0.34 (39–48; 42) | 43.8 \pm 0.19 (38–48; 123) |

only a subtle hint of bifurcation (= terminal lateral bulges *vide* Branch [1981]). Although Branch (1981) described the hemipenis of a *C. hortulanus* from Venezuela as having three shallow transverse flounces and that of a specimen from Panama as having five well-developed flounces, I have examined the hemipenes of *C. hortulanus* from several localities and the number of flounces has been either four or five. A specimen from northern Venezuela had very shallow transverse flounces (UIMNH 95135), and Branch described the same condition in a specimen (KU 167563) from east central Venezuela. Snakes from Panama, Amazonian Brazil and Peru, and the West Indies had well-developed, scalloped flounces.

Size.—For analysis of size I used four OTUs which correspond to OTUs that cluster in Fig. 6: 1) Grenada Bank, 2) St. Vincent, 3) Central America, northernmost South America, Trinidad, and Tobago, and 4) Guianas, Amazonia, Atlantic forest, and Ilha Grande. The largest specimen in OTU3 has a SVL 230 mm longer than the largest representative of OTU4, 245 mm longer than the largest specimen in OTU1, and 496 mm longer than the largest representative in OTU2. The largest specimen in OTU4 is only 15 mm longer than the largest in OTU1, but 266 mm longer than the largest specimen in OTU2. In summary, tree boas from Central America, northern Colombia, and Venezuela (including Isla Margarita),

Trinidad, and Tobago are the longest; snakes from the West Indies are the shortest and most slender, and those from Amazonia are intermediate.

Based on (1) size (2) color pattern, (3) mitochondrial DNA sequences, (4) scale characters, and (5) geographic and ecological distribution, I recognize four species in the *Corallus hortulanus* complex. In addition to *C. hortulanus*, I elevate *Corallus cooki* to species status, and I resurrect Cope's (1876) *Xiphosoma ruschenbergerii* and Barbour's (1914) *Boa grenadensis*. No subspecies are recognized. Table 2 provides a summary of scale count data for all taxa discussed below, and Table 3 does likewise for color and pattern.

CORALLUS HORTULANUS COMPLEX

Definition and Diagnosis.—Members of the complex usually have nasals in contact (usually not in contact in *C. annulatus*, *C. caninus*, and *C. cropanii*); subcaudals 94–137 (79–87 in *C. annulatus*, 65–74 in *C. caninus*, and less than 60 in *C. cropanii*). Other scale counts include maximum number of dorsal scale rows 37–63, ventrals 251–297, infra-loreal 0–9, and scales between supraorbitals 3–14. In less than 1.0% of samples a supra-labial scale is not separated from the orbit by a circumorbital scale (a diagnostic characteristic of the widely sympatric *Epicrates cenchría*).

Distribution.—Southern Central America

TABLE 3. Summary of predominant color and pattern characteristics in tree boas of the *Corallus hortulanus* complex. All figures are percentages within each species.

| | Species | | | |
|--------------------------|-------------------|--------------|--------------------|------------------------|
| | <i>hortulanus</i> | <i>cooki</i> | <i>grenadensis</i> | <i>ruschenbergerii</i> |
| Dorsal color | | | | |
| Taupe | 80.9 | 100.0 | 64.9 | 60.2 |
| Yellow | 19.1 | 0.0 | 30.4 | 39.8 |
| Orange | 0.0 | 0.0 | 4.6 | 0.0 |
| Pattern | | | | |
| Ellipse | 64.7 | 0.0 | 5.4 | 0.0 |
| Rhomb | 2.4 | 0.0 | 0.0 | 59.7 |
| Hourglass | 2.7 | 87.8 | 1.1 | 0.0 |
| Spade | 9.0 | 2.4 | 80.0 | 0.0 |
| Dorsals edged with black | 0.0 | 0.0 | 0.0 | 27.1 |
| Flecks | 2.0 | 0.0 | 7.0 | 0.0 |
| Patternless | 3.9 | 0.0 | 2.2 | 9.8 |
| Other | 15.3 | 9.8 | 4.3 | 3.4 |

(south of 10° N) and some associated islets, northern South America (including the continental islands Isla Margarita, Trinidad, and Tobago), throughout the Guianas and Amazonia, to southeastern Brazil (Atlantic forests) to at least 26° 08' S; also St. Vincent and the Grenada Bank in the West Indies.

Corallus hortulanus (Linnaeus)

Boa Hortulana Linnaeus, 1758:215.

Boa Enydris Linnaeus, 1758:215

Corallus Hortulanus: Gray, 1842:42

Xiphosoma hortulanum: Dumeril and Bibron, 1844:545

Corallus hortulanus: Boulenger, 1893:101

Boa enydris enydris: Stull, 1935:388

Corallus enydris (part): Forcart, 1951:197

Corallus enydris enydris: Forcart, 1951:197

Corallus hortulanus hortulanus: Stafford and Henderson, 1996:21

Holotype.—Naturhistoriska Riksmuseet, Stockholm (NRS) Lin. 7, collector and date of collection unknown. Type-locality, "America."

Definition.—A species with maximum number of dorsal scale rows 47–63; subcaudals 105–137; scales between supraoculars 5–14; infralocals 0–9; circumorbital scales 8–17. Dorsal ground color variable (yellow, gray, taupe, brown, pink, or reddish), but taupe predominates (71.5% in a sample of 256), and taupe+brown+gray account for

80.9%; yellow-brown (yellow, khaki, beige, brownish yellow) is much less common (19.1% of sample). The main element of the dorsal pattern is usually a dorsoventrally oriented ellipsoid with the dorsal end broader than the ventral end; many minor variations of this shape appear throughout the range. The anteriormost elements of the dorsal pattern are diamond-shaped. Maximum snout-vent length (SVL) is 1640 mm. Color photographs appear in Stafford and Henderson (1996: Plates 23–25 and 27–33).

Diagnosis.—*Corallus hortulanus* is distinguishable from other species in the complex by the maximum number of dorsal scale rows (almost always over 50 in *hortulanus*, always less than 50 in *cooki*, *grenadensis*, and *ruschenbergerii*). Populations of *hortulanus* with less than 50 dorsal scale rows occur in Guyana, Suriname, Bolivia, and Peru. In general, *hortulanus* has higher counts for meristic characters (Table 3) than other members of the complex. The shape of the main element in the dorsal pattern at mid-body is more or less ellipsoidal, whereas it is a ragged hourglass in *cooki* and is usually spade-shaped in *grenadensis* (Table 3).

Variation.—Tree boas with a predominantly taupe dorsal ground color accounted for 70–100% of the samples in OTUs 21, 23–29, and 32–33. Snakes from Guyana (OTU 22), and the western and central Amazon

of Brazil (OTUs 30 and 31) had a higher percentage of "yellow" individuals; Guyana had the highest percentage (43.5%) of yellow snakes. My Bolivia sample (n = 28) contained no yellow snakes, nor did the samples from French Guiana (n = 7; Chipaux [1986], however, describes "beige" snakes from that country) and Ilha Grande (n = 6). There is a great deal of variation in the shape of the main element of the dorsal pattern at midbody, but in general an ellipse-like shape was present. Snakes from southern Venezuela exhibited some *ruschenbergerii* influence, and snakes from the Guianas had more spade shapes than those elsewhere in the range of *C. hortulanus*. Tree boas from Ilha Grande had a uniformly distinctive dorsal pattern, reminiscent of a hot-air balloon. The venter is predominantly dull yellow, but may also be white or cream; it may be immaculate (usually in snakes with a yellowish dorsal ground color) or patterned with a few flecks, scattered spots and blotches, or nearly covered with dark brown. Lateral encroachment of the dorsal pattern onto the ventrals is common. The ventral pattern becomes more densely patterned posteriorly.

Distribution.—The Guianas and Amazonia (southern Colombia, southern Venezuela, Ecuador, Peru, Bolivia, Brazil). The distribution in Brazil also includes Cerrado, mesic enclaves in Caatinga (Puerto and Henderson, 1995), sand dune areas in Caatinga (Rodrigues, 1996), and Atlantic rainforest to about 26° 08' (Puerto and Henderson, 1995), and Ilha Grande (off southeastern Brazil) (Fig. 8). The distribution is widely sympatric (and probably syntopic) with *C. caninus*, sympatric with *C. cropanii*, and marginally sympatric or parapatric with *C. ruschenbergerii* (see below). Altitudinal distribution is from sea level to about 915 m (USNM 60694 from the Río Cosireni, Cuzco, Peru). In general, collection localities above 200–300 m are rare. The record for *C. hortulanus* collected between La Aguadita and Fusagasugá, Cundinamarca, Colombia, at 1900 m (Pérez-Santos and Moreno, 1988) is based on a misidentified *Chironius monticola* (O. Victoria Castaño, in litt.).

Remarks.—McDiarmid et al. (1996) determined that *Corallus hortulanus* is the correct

name for snakes long-referred to as *C. enydris*. Based on the scale counts and inadequate color and pattern description given in Linnaeus (1758) and Andersson (1899), the type of *Boa enydris* is most likely *C. hortulanus*.

The synonymy given here for *Corallus hortulanus* is not complete; most of the names have not been used for the past 100–200 years. Using the synonymy in Henderson (1993d), the following names refer to *Corallus hortulanus*: *Vipera bitis*, *Vipera madaensis*, *Boa Ambleocephala*, *Boa obtusiceps*, *Corallus obtusirostris*, *Xiphosoma ornatum*, *Xiphosoma dorsuale*, *Boa modesta*, and *Corallus maculatus*. McDiarmid et al. (1996) provide extensive documentation and discussion of *Corallus hortulanus* nomenclature.

Corallus cooki Gray

Corallus Cookii Gray, 1842:42.

Corallus cookii (part): Boulenger, 1893:99.

Corallus enydris cookii (part): Forcart, 1951:197.

Corallus hortulanus cooki (part): Stafford and Henderson, 1996:21

Holotype.—BMNH 1946.1.1.50, collected by Edward Cooke (date of collection unknown), male, 861 mm SVL. Type-locality "America"; amended to "West Indies" by Gray (1849); here restricted to St. Vincent.

Definition.—A species with maximum number of dorsal scale rows 39–48; ventrals 257–278; subcaudals 100–122; scales between supraoculars 7–13; infralorals 0–4. Dorsal ground color always taupe, gray, or brown. The main element of the dorsal pattern is a ragged hourglass shape in some shade of gray or brown. A color photograph appears in Stafford and Henderson (1996: Plate 10, as *C. hortulanus*)

Diagnosis.—*Corallus cooki* is most easily distinguished from other members of the *C. hortulanus* complex by its color pattern. It lacks the color variation (pale yellow, orange, red, many shades of brown) found in *C. hortulanus* and *C. grenadensis*. Likewise, the main element of the dorsal pattern is relatively constant, and it rarely occurs in populations outside of St. Vincent. The diamond-shape pattern characteristic of *C. ruschenbergerii* does not occur in this spe-

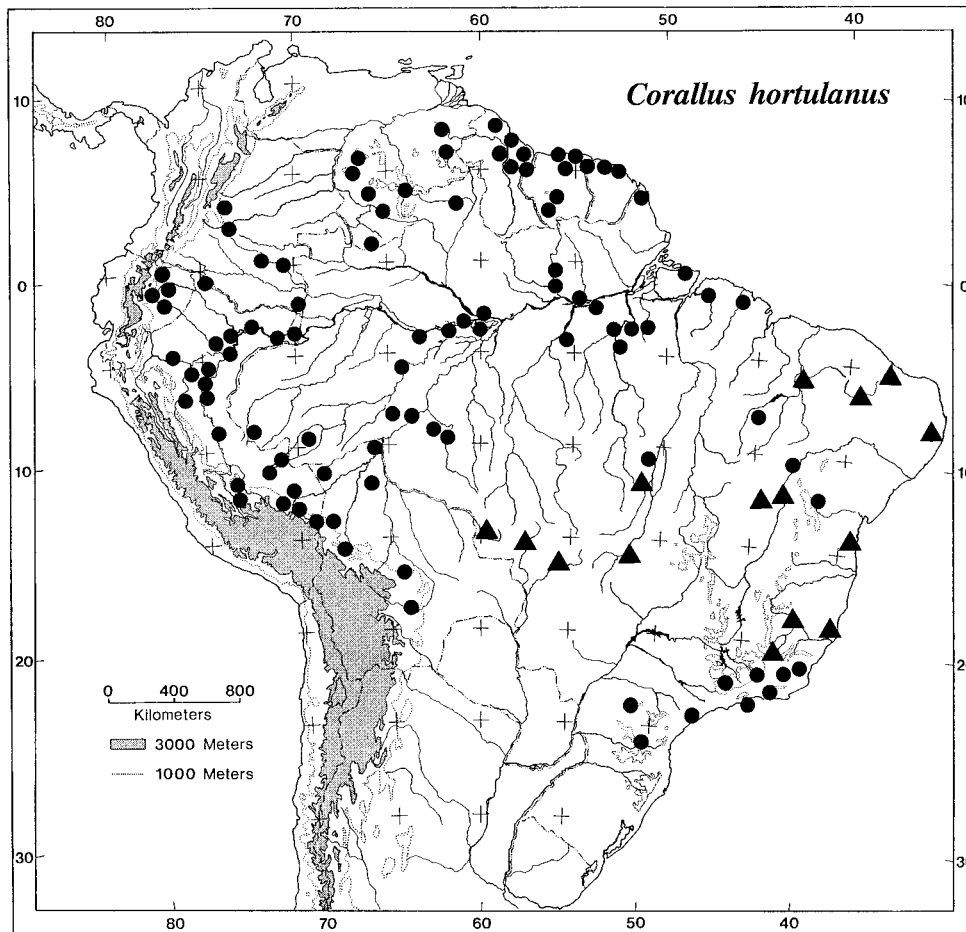


FIG. 8. Distribution of *Corallus hortulanus*. Dots represent specimens examined and triangles represent additional specimens that were not examined but which help delineate the distribution of *C. hortulanus*. Not every specimen that was examined is represented by a dot. Some areas (e.g., Manaus, Pará, Brazil; Iquitos, Loreto, Peru) had so many collecting sites in such close proximity that it was not feasible to map them all.

cies. *Corallus cooki* is distinguishable from *C. hortulanus* by maximum number of dorsal scale rows: invariably less than 50 in *C. cooki* (39–48; $\bar{x} = 43.9 \pm 0.34$) and almost always more than 50 in *C. hortulanus* (47–63; $\bar{x} = 55.0 \pm 0.17$; specimens with less than 50 occur occasionally in Guyana, Suriname, Bolivia, and Peru).

Redescription of Holotype.—A male, 861 mm SVL, tail 226 mm; maximum rows of dorsal scales 48; ventrals 269; subcaudals 119; infralorals 5; circumorbital scales 14; scales between supraoculars 14; head width 15.4 mm, head length 26.2 mm. The dorsal ground color is taupe, and the body has 39 distorted, medium brown, hourglass-

shaped markings; top of head with a somewhat vermiculate pattern; postorbital stripes are interrupted; underside of head off-white with several small taupe smudges; ventrals off-white to pale yellow with scattered medium-brown flecks and smudges over the entire length of body; the dorsal pattern encroaches onto the lateral edges of the ventrals.

Variation.—The dorsal coloration is remarkably uniform considering the variability in *C. hortulanus* and *C. grenadensis*. Out of 47 specimens for which I was able to score dorsal ground color, 41 (87.2%) were taupe and the others were gray or brown. The main element of the dorsal pattern is

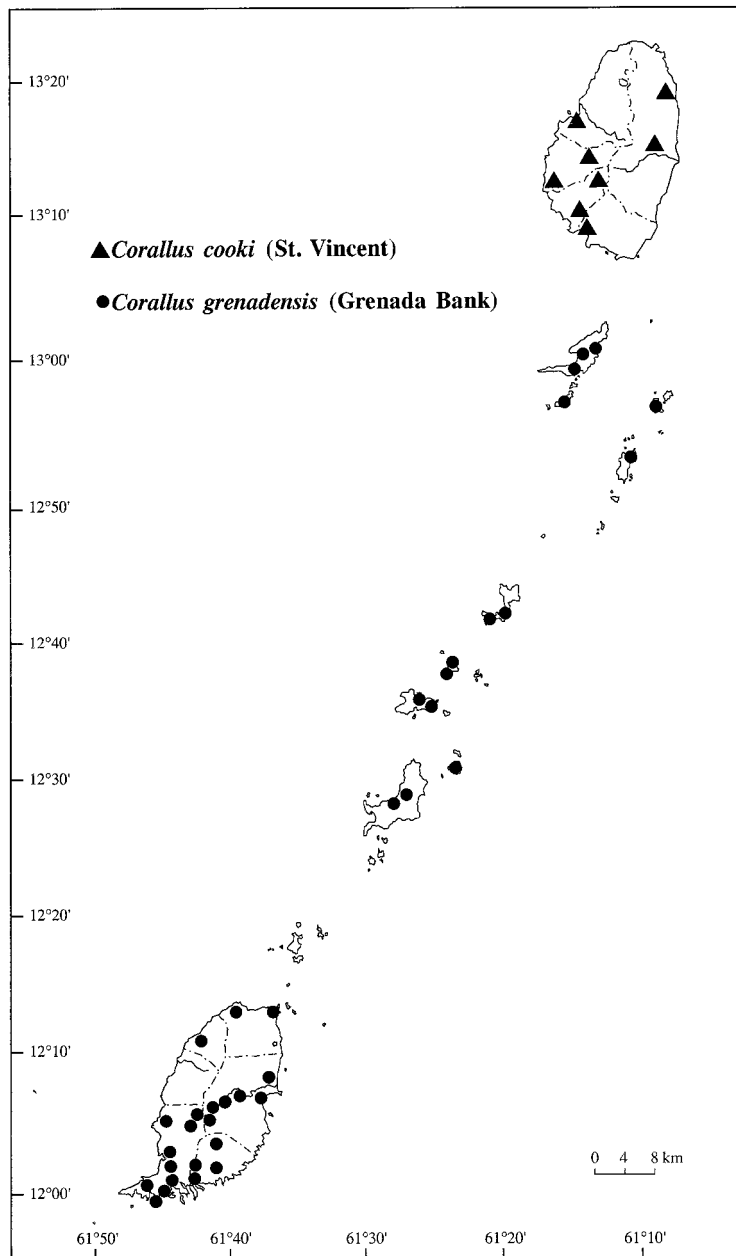


FIG. 9. Distributions of *Corallus cooki* and *C. grenadensis*, based on specimens examined.

best described as an hourglass or dumbbell shape, rarely like a very stout spade; the dorsalmost portion of the shape is hollow. The main elements are usually edged in black, with or without white margins. Between the main elements there is only dorsal ground color, or a dorsoventrally elon-

gated blotch. Unlike other species in the *hortulanus* complex, the anteriormost blotches are not rhomboidal. Near middorsum, the dorsal pattern may become a series of longitudinally elongated blotches with another longitudinally elongated series situated more laterally. Milwaukee Public Museum

(MPM) specimens 23302 and 23304 exhibit fusion of the main pattern elements across their dorsalmost portions, creating a mid-dorsal stripe. MPM 23297 has a taupe ground color with markings similar to *C. hortulanus*, in addition to triangle shapes. The underside of the head is immaculate but the ventrals may be lightly to heavily patterned; lateral encroachment of the dorsal pattern onto the ventrals is common. The top of the head has rounded blotches or a vermiculate pattern. Whereas other *C. hortulanus* complex tree boas usually have well-defined postorbital stripes, in *C. cooki* it is more of a postorbital blotch. Mental and gular regions are white, but marked (often heavily) with brown.

Distribution.—St. Vincent (Fig. 9). Altitudinal distribution is uncertain; there is a record from Kingstown (Museum of Comparative Zoology [MCZ] 140154), but that could be anywhere from sea-level to about 100 m. The highest elevation at which I have encountered *C. cooki* is 425 m (St. Patrick, Hermitage; MPM 26148–49). The distribution does not overlap with that of other *Corallus* species.

Remarks.—This species, long-referred to as Cook's (or, more correctly, Cooke's) tree boa, has posed several problems. The name has usually been applied to populations in the northern portion of the range of *C. hortulanus* (Central America, northernmost South America, Trinidad and Tobago, Isla Margarita, and the West Indies). It was usually characterized by having fewer than 50 dorsal scale rows at midbody.

The type-locality is in question. Gray (1842) gave the type-locality as "Inhabits America," but seven years later (Gray, 1849) he gave it as "West Indies." Andrew Stimson (in litt., 13 Aug 1990) suggested that Gray was uncertain of the place of origin of the specimen and his "Inhabits America" was an informed guess as to the distribution of the species. Stimson (1969) gave the type-locality as West Indies "because that was the information accompanying the specimen" (A. Stimson, in litt., 13 Aug 1990). Peter J. Stafford (in litt., 1996) recently confirmed that the only data accompanying the specimen is "West Indies." Locality data from other material in The Brit-

ish Museum collected by Edward Cooke is not helpful, as it includes specimens collected in Mexico and northern South America. They neither support nor preclude collecting in the West Indies.

The problem is made more difficult because of the more than 600 specimens of *hortulanus* complex tree boas that I have examined, the holotype of *C. cooki* is easily the most enigmatic. Its diagnostic characters are ambiguous. Principal component analysis based on meristic characters puts it between *C. cooki* and *C. hortulanus* populations; color and pattern are typical St. Vincent. If the specimen was collected in the West Indies, it certainly came from St. Vincent. If it was collected on the South American mainland, it would have come from a locality within the range of *C. hortulanus*, thereby placing *C. cooki* as a synonym of *C. hortulanus*.

Since the locality "West Indies" is associated with the holotype, and since the specimen could have originated from St. Vincent, I have retained the name *cooki*, but I have restricted the type-locality to St. Vincent, and the entire range of the species to that island.

Corallus grenadensis (Barbour), new combination

Boa grenadensis Barbour, 1914:327.

Boa enydris cooki (part): Stull, 1935:388.

Corallus enydris cookii (part): Forcart, 1951:197.

Corallus hortulanus cooki (part): Stafford and Henderson, 1996:21.

Holotype.—MCZ 7791, collected 20 August 1910 by G. M. Allen, male, 1170 mm SVL. Type-locality "St. George's, Grenada."

Definition.—A species with maximum number of dorsal scale rows 37–46; ventrals 251–278; subcaudals 100–119; scales between supraoculars 3–9; infralocals 0–4. Dorsal ground color variable (yellowish, orange, gray, taupe, brown), but yellowish (30.4% in a sample of 194) and taupe (64.9%) predominate; collecting sites dictate which color predominates. The main element in the dorsal pattern is usually (80.0%) spade-shaped, either with sharp or rounded edges, but other pattern elements

are more prevalent on the Grenada Bank than elsewhere. The anteriormost pattern elements are diamond-shaped. In the Grenadines, yellow snakes have been collected only on Bequia, but they have been observed on Union Island (J. Daudin, pers. comm.). Color photographs appear in Stafford and Henderson (1996: Plates 6–8, 11, and 13–14, as *C. hortulanus*).

Diagnosis.—*Corallus grenadensis* is distinguished from *C. hortulanus* by maximum rows of dorsal scales (37–46, $\bar{x} = 41.0 \pm 0.12$ in *grenadensis* vs. 47–63, $\bar{x} = 55.0 \pm 0.17$ in *hortulanus*). The primary spade-like element of the dorsal pattern occasionally occurs on the mainland (primarily the Guianas and northeastern Brazil), but not on St. Vincent (*C. cooki*). The rhomb pattern typical of *C. ruschenbergerii* does not occur in *C. grenadensis*.

Redescription of the holotype.—An adult male, 1170 mm SVL, tail 316 mm; maximum rows of dorsal scales 42; ventrals 270; subcaudals 112; infralorals 2; circumorbital scales 10; scales between supraoculars 6; head width 20.3 mm; head length 35.0 mm. The dorsum is pale yellow with taupe flecking and no discernible pattern; top of head with some taupe flecks and small blotches; underside of head immaculate; post-orbital stripes reduced to small blotches near angle of jaw; venter dull yellow, anteriorly immaculate and posteriorly with some taupe flecks.

Variation.—The spade-like element in the dorsal pattern occurs throughout the Grenada Bank, with the greatest variation being whether the spade has sharp angles (53.5%) or is rounded (26.5%). Although the rounded spades may appear in any habitat, they predominate at higher elevations on Grenada. A dorsal ground color of taupe predominates on all of the islands except Mayreau, where orange is predominant (7 of 8 specimens). The primary element in the dorsal pattern in snakes from Mayreau is also consistently different from other populations on the bank (more of a balloon shape rather than a spade; a similar pattern occurs on the other islands on the bank, but not to the exclusion of the more typical spade-shape). The samples from Petit Martinique, Baliceaux, and Mustique are too

small to make a detailed assessment of pattern variation. Based on the examination of living *C. grenadensis*, it appears that dorsal ground color is correlated with iris color and tongue color (i.e., snakes with a yellowish dorsal ground color usually have yellowish irises and a pale-colored tongue; snakes that are taupe to dark brown have very dark irises and dark brown to black tongues). The ventral ground color is usually dull yellow, but it may be white or cream. It may also be immaculate (in snakes with a yellowish dorsal ground color), marked with flecks, spots, large blotches, or almost completely covered with dark brown. The ventral pattern usually becomes denser more posteriorly.

Distribution.—Islands of the Grenada Bank (Fig. 9). It has been collected on Bequia, Ile Quatre, Baliceaux, Mustique, Canouan, Mayreau, Union, Carriacou and Grenada. I suspect it occurs on other islands on the bank, including some that have been unsuccessfully searched for the species (e.g., Prune Island [= Palm Island on some newer maps]). The range of *C. grenadensis* does not overlap with other *Corallus* species. On Grenada, elevational distribution is from sea-level (including branches overhanging the Caribbean) to at least 520 m. It is unlikely that *C. grenadensis* is altitudinally precluded anywhere on the Grenadine Islands. The Grenadines which are known to harbor *C. grenadensis* range in size from 0.7 km² (Petite Martinique) to 32.0 km² (Carriacou); the highest peak is only 305 m (on Union); and annual rainfall ranges from about 900 mm (Mayreau) to about 1880 mm (Bequia) (Howard, 1952). The forests are all secondary, having been cleared for agriculture or in order to make room for the human population (Howard, 1952).

Remarks.—*Corallus grenadensis* on Grenada exhibits the widest range of dorsal ground colors anywhere within the range of the *hortulanus* complex. The predominant dorsal ground color at any locality is correlated with elevation, rainfall, and percent possible sunshine. An initial analysis (Henderson, 1990) was based in part on the collecting whims of myself and others (i.e., selectively collecting certain color morphs and not collecting others). Subsequent ef-

forts have been more objective (e.g., Henderson, 1996) and have confirmed the results of the initial effort.

Corallus ruschenbergerii (Cope), new combination

Xiphosoma ruschenbergerii Cope 1876:129

Corallus cookii (part): Boulenger, 1893:99

Xiphosoma ruschenbergii: Boulenger, 1893:99 [Lapsus]

Corallus cookei var. *ruschenbergii*: Boettger, 1898:10 [Lapsus]

Boa ruschenbergii: Stejneger, 1901 [Lapsus]

Boa salmonidia Briceño Rossi, 1934:1141.

Type locality "Frontera con Colombia en el Río de Oro, y Distrito Colón del Edo Zulia."

Boa enydris cookii (part): Stull, 1935:398

Corallus enydris cookii (part): Forcart, 1951:197.

Corallus hortulanus cooki (part): Stafford and Henderson, 1996:21

Holotype.—ANSP 10325, collected by W. S. W. Ruschenberger, female, 1530 mm SVL. Type-locality "Panama".

Definition.—A very large species (maximum SVL at least 1870 mm; maximum total length at least 2311 mm based on preserved material, but surely reaching at least 2500 mm [the specimen with the longest SVL has a stub tail]). Maximum number of dorsal scale rows 38–48, ventrals 250–272, subcaudals 94–115, infralorals 1–6, circumorbital scales 11–16. The hemipenes are bilobed. The dorsal ground color ranges from yellow brown to deep copper brown; the dorsal pattern may be (1) a series of diamonds (or rhombs) (59.7% in a sample of 134), (2) the free edge of most or all dorsal scales dark brown or black (26.5%), (3) a combination of 1 and 2 (4.1%), or (4) lacking any discernible pattern (9.7%). The ground color of the venter ranges from white to lemon yellow, often without conspicuous markings, but if present more prominent posteriorly. Color photographs appear in Stafford and Henderson (1996: Plates 17 and 19–22 [as *C. hortulanus*]).

Diagnosis.—*Corallus ruschenbergerii* is easily distinguished from all other species of *Corallus* except *C. grenadensis*. The maximum number of dorsal scale rows in *C. cro-*

panii is fewer than 35 (38–48 in *C. ruschenbergerii*). *Corallus annulatus*, the only congener with which there is significant sympatry, has a maximum of 50–57 dorsal scale rows and only 79–87 subcaudals (94–115 in *C. ruschenbergerii*). *Corallus caninus* has a maximum of 63–77 dorsal scale rows, and 186–209 ventrals (250–272 in *C. ruschenbergerii*). With very few exceptions, *C. hortulanus* from mainland South America and Ilha Grande off southeastern Brazil have 50 or more maximum dorsal scale rows (individuals from Guyana, Suriname, Peru, and Bolivia rarely have 47 or 48) and color and pattern are extremely variable.

Corallus from St. Vincent and the Grenada Bank are the shortest and most slender of the Neotropical tree boas, and this can be related to aspects of their ecology (see below). They exhibit great overlap in lepidosis with *C. ruschenbergerii*, but *C. ruschenbergerii* is much larger (maximum SVL in West Indian *Corallus* is 1625 mm), and *C. grenadensis* exhibits tremendous color and pattern variation. Despite the pattern variation in the West Indian populations, none of it duplicates that found in *C. ruschenbergerii*, with the exception of yellow-brown individuals that have no discernible pattern.

Variation.—With the exception of *Corallus cooki*, *C. ruschenbergerii* exhibits less variation in dorsal pattern than other members of the complex. The middorsal rhomb (or diamond-shape) is relatively uniform throughout the range of the species, and it is rarely encountered in other members of the complex (Table 3). The rhomb is especially prevalent in Costa Rica (80.0%) and Panama (90.5%). Tree boas with the free edge of the dorsals edged in black occur only in *C. ruschenbergerii* (Table 3), and this pattern occurs most often in northern Venezuela (32.6%) and on Trinidad (20.5%); it is least common in Panama (7.1%) and northern Colombia (4.2%). The ventral ground color is usually dull yellow, but it may be white or cream. It may also be bright yellow, immaculate, or patterned with a few flecks, scattered spots and blotches, or nearly covered with dark brown to black. The ventral pattern becomes heavier posteriorly.

Redescription of the Holotype.—An adult fe-

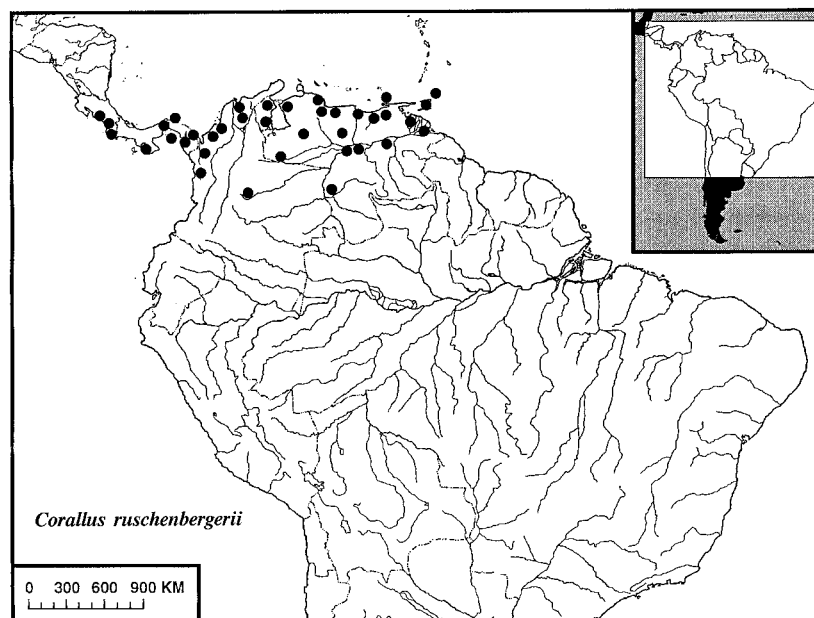


FIG. 10. Distribution of *Corallus ruschenbergerii*, based on specimens examined.

male, 1530 mm SVL, tail 353 mm; maximum rows of dorsal scales 48; ventrals 270; subcaudals 107; infralorals 2; circumorbital scales 14; scales between supraoculars 5; head width 28.2 mm; head length 53.8 mm. Dorsal ground color pale yellow to pale khaki, with about 37 pale taupe to brown rhomboid markings on left side of the laterally compressed body (shapes of the markings are more diamond-like near head and near tail); dorsal markings more prominent on posterior part of body and on tail; top of head with pale smudges posteriorly; underside of head immaculate pale yellow; postorbital stripes pale and ill-defined; ventrals dull yellow, immaculate anteriorly (but with slight lateral encroachment of the dorsal pattern), and with brown blotches appearing near mid-venter and becoming more prominent posteriorly; dull yellow subcaudals moderately to heavily marked with brown.

Distribution.—*Corallus ruschenbergerii* occurs from southern Costa Rica (south of 10° N), through Panama (including the offshore islands of Isla del Rey, Isla Contadora, Isla de Cébaco, and Isla Suscantupu); in Colombia east of the Andes and more-or-less north of the cordilleras Central and Ori-

ental; and in Venezuela north of the Cordillera de Mérida and the Río Orinoco (and on Isla Margarita), and north and west of the Guiana Shield. The eastward edge of the range appears to be the Orinoco Delta. The species also occurs on Trinidad and Tobago (Fig. 10).

The ranges of *Corallus ruschenbergerii* and *C. hortulanus* exhibit a narrow zone of sympatry just south of the Río Orinoco in Venezuela and just east of the Cordillera Oriental in Prov. Meta, Colombia. Altitudinal distribution of *C. ruschenbergerii* is largely under 200 m, but has a limited distribution to at least 600 m asl (above Villavicencio, Meta, Colombia; W. W. Lamar, in litt.). The distribution of *C. ruschenbergerii* largely excludes areas of tropical rainforest on the South American mainland (based on vegetation maps in Hueck and Seibert [1972], Ewel et al. [1976], and Campbell and Lamar [1989]), and on the system of morphoclimatic domains (Ab'Saber, 1977). Instead, it has a wide distribution in lowland dry forest, thorn forest, savanna grassland with woody species (llanos with gallery forests), and lower montane dry forest. On Trinidad and Tobago and in Central America it occurs in tropical moist forest. In contrast, *C.*

caninus is largely restricted to lowland rainforest (although it does occur at altitudes reaching at least 550 m asl [W. W. Lamar, in litt.]) and Cerrado, and *C. hortulanus* has a limited distribution outside of lowland tropical rainforest (with limited distribution in Atlantic forest, Caatinga, Cerrado, and gallery forests in savanna/grassland) (Henderson et al., 1995). Rainfall over most of the range of *C. ruschenbergerii* is depressed: usually 1000–2000 mm annually, although it does occur in areas that receive less than 1000 mm annually. In Central America and the Chocó of Colombia, annual rainfall within its range may reach 4000 mm (Snow, 1976). *Corallus caninus* occurs only in rainfall regimes of 1500–4000 mm annually. The vast majority of the range of *C. hortulanus* occurs in areas that receive annual precipitation of 1500 to 4000 mm; it also has limited distribution in areas that receive less than 1500 mm annually (including areas in Caatinga that receive about 700 mm annually; Rodrigues, 1996).

The ranges of *C. hortulanus* and *C. ruschenbergerii* are roughly paralleled by those of the viperids *Bothrops atrox* and *B. asper* (Campbell and Lamar, 1989), although the range of *B. asper* is more extensive to the north than that of *C. ruschenbergerii*, and that of *C. hortulanus* is more extensive to the south than that of *B. atrox*. The two pairs of species share other similarities; like the two booids, the two viperids: 1) exhibit considerable overlap in scale characters; 2) may be narrowly sympatric in Colombia and Venezuela; and 3) occur in a variety of habitats and often in disturbed situations (Campbell and Lamar, 1989).

Remarks.—The largest *C. ruschenbergerii* SVL is more than 230 mm greater than the largest *C. hortulanus*, and 245 mm larger than the largest *C. cooki* or *C. grenadensis*. Although the available prey in the range of *C. ruschenbergerii* is, in a broad taxonomic sense, essentially the same as for *C. hortulanus* (including high species diversity for lizards, but with population densities much lower than in the West Indies), because of its large size *C. ruschenbergerii* exploits prey species (e.g., *Marmosa*, *Herpestes*) not taken by *C. hortulanus* (Table 4).

TABLE 4. Geographic ranges, mean SVL (in mm) + SE (range of largest 10% of sample, and diet in *Corallus hortulanus*, *C. ruschenbergerii*, *C. cooki*, and *C. grenadensis*.

| | <i>C. ruschenbergerii</i> | <i>C. cooki</i> + <i>C. grenadensis</i> | <i>C. hortulanus</i> |
|----------------------------|---|--|---|
| Range | Costa Rica, Panama, northern Colombia, northern Venezuela plus Isla Margarita, Trinidad, Tobago | West Indies (St. Vincent and the Grenada Bank) | South America (Guianas, Amazonia, Atlantic Forest, Ilha Grande) |
| Mean SVL of largest snakes | 1716.1 ± 23.1 (1630–1870; 128) | 1363.2 ± 21.8 (1215–1625; 248) | 1476.1 ± 18.8 (1357–1640; 226) |
| Diet (%) ¹ | | | |
| Lizards | 18.2 | 67.8 | 0.0 |
| Birds | 27.3 | 4.8 | 32.4 |
| Mammals | 54.5 (marsupials, rodents, bats, carnivores) | 27.4 (rodents, bats ²) | 67.6 (rodents, bats) |
| N | 22 | 62 | 34 |

¹ Based on data in Henderson, 1993a and 1993b.

² Although bats have not been recovered from stomachs of West Indian *Corallus*, attempts to capture bats have been observed in the field.

DISCUSSION

Despite the absence of complete congruence between the DNA and meristic data, I believe that the taxonomic arrangement presented here for the *hortulanus* complex of Neotropical tree boas is tenable. *Corallus ruschenbergerii* populations are distinct from other *hortulanus* complex species on the basis of color and pattern, DNA, size, and in some cases scale characters. Although there is considerable overlap in some meristic variables, especially with *C. grenadensis*, these two species exhibit other differences (color pattern, hemipenis), and their distributions are allopatric (northern South America and Trinidad and Tobago support a reptile fauna very different from that of the Grenada Bank; see Murphy, 1996). Additional collecting is needed, however, in order to define more accurately the geographic boundaries of *C. hortulanus* and *C. ruschenbergerii* in Colombia and Venezuela, and to determine if *C. ruschenbergerii* occurs in northwestern Guyana.

The West Indian taxa exhibit little divergence in mtDNA from *Corallus hortulanus*, but they exhibit differences in scale characters, color, and pattern. Distributions are allopatric. Likewise, although the two West Indian taxa exhibit little divergence from each other in mtDNA, they display differences in meristic characters, dorsal ground color, and dorsal pattern. The ranges of *C. cooki* and *C. grenadensis* occupy different island banks and are completely allopatric, and it is likely that each of the banks was colonized by a separate dispersal event from the South American mainland, probably from the Guianas or northeastern Brazil, via the South Equatorial Current (e.g., Guppy, 1917; Hedges, 1996; Henderson and Hedges, 1995). There is no geological evidence to indicate that the Grenada Bank ever had a continental connection (Maury et al., 1990), and there is no reason to suspect that populations of *cooki*, *grenadensis*, and *hortulanus* will be united. They will, instead, continue to diverge over time. Specimens from Grenada especially appear to have close affinities (based on color, pattern, and meristic data) with material from Guyana.

It is likely that New World tree boas evolved in northern South America. The two species with the largest ranges (*Corallus caninus* and *C. hortulanus*) have largely Amazonian distributions (Henderson, 1993c; Henderson et al., 1995), while all other mainland species (*C. annulatus*, *C. cropanii*, and *C. ruschenbergerii*) are largely peripheral to their ranges (Henderson et al., 1995). It is interesting to note that the two largest (mass, midbody girth, head size) species (*C. caninus* and *C. ruschenbergerii*) have essentially allopatric distributions (they co-occur in marginal habitat [high elevations, gallery forest in llanos]; W. W. Lamar, pers. commun.), but each is sympatric with more slender species. Possibly these size differences allow congeners to co-exist without competing for the same prey species in the same portion of the structural habitat. Conversely, *C. caninus* and *C. ruschenbergerii* are perhaps only marginally sympatric because of their size similarities (i.e., they would compete for the same resources), and *C. ruschenbergerii* may have evolved from prototypic *C. hortulanus* in response to its geographical and ecological isolation from *C. caninus*. Although *C. caninus* does not occur in Brazil's Atlantic rainforest, *C. hortulanus* is there sympatric with *C. cropanii*, a relatively heavy-bodied species of whose natural history we know virtually nothing, and which is the sister species to *C. caninus* (fide Kluge, 1991).

The pattern and color variation in *Corallus hortulanus* and *C. grenadensis* can be best explained by a suite of factors: 1) geographically and/or ecologically widespread (i.e., the species occurs in a wide range of habitats and climatic regimes), 2) large adults sometimes employ a sit-and-wait foraging mode (i.e., rely on cryptic coloration to avoid detection by prey and predators; tree boas in size classes other than the largest are active foragers), and 3) low vagility (i.e., individuals are restricted to a single habitat type and only one climatic regime). Based on these criteria, it is possible that demes of *C. hortulanus* and *C. grenadensis* have responded phenotypically to localized environmental conditions that are selectively advantageous (e.g., crypticity, thermoregulation) for their respective ecologies, but

other characters (e.g., meristic scale characters) are relatively stable. Another factor influencing pattern and color variation are factors that affect rates of gene flow, and these may be natural (e.g., rivers) or human imposed (e.g., agricultural practices). It has been demonstrated that contiguous tree crown vegetation is critical to habitat utilization and/or selection in arboreal boids (Tolson, 1988; Henderson and Winstel, 1995). Anything that interrupts a contiguous crown may have the effect of isolating a localized population of tree boas, thereby interrupting gene flow. Agricultural practices could create permanent or temporary islands of forest, each with a population of tree boas. These isolated (or nearly isolated) demes could in time respond with dorsal ground colors and patterns divergent from other nearby, yet equally isolated, populations (Henderson, 1990). Reuniting previously isolated demes could promote additional color and pattern variations.

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More than 10 years ago Al Schwartz mentioned to me that he believed *Corallus* on St. Vincent was taxonomically distinct from *Corallus* on Grenada, but he did not want to pursue the problem because it would require examining specimens from

outside of the West Indies. So AI, wherever you may be, thanks for the tip.

LITERATURE CITED

- Ab'Saber, A. N. 1977. Os dominios morfoclimáticos na América do Sul: Primeira aproximação. *Geomorfologia* 52:1–23.
- Andersson, L. G. 1899. Catalogue of Linnean type-specimens of snakes in the Royal Museum in Stockholm. *Handl. Svenska Vet. Akad. Bd. 24, Afd. 4(6):* 1–35.
- Barbour, T. 1914. A contribution to the zoogeography of the West Indies, with especial reference to amphibians and reptiles. *Bull. Mus. Comp. Zool.* 44: 209–359.
- Boettger, O. 1898. Katalog der Reptilien-Sammlung im Museum der senckenbergischen naturforschenden Gesellschaft in Frankfurt am Main. II. Theil (Schlangen). Frankfurt a. M. ix + 160 pp.
- Boulenger, G. A. 1893. Catalogue of snakes in the British Museum (Natural History). Vol. 1., containing the families Typhlopidae, Glauconiidae, Boidae, Ilysiidae, Uropeltidae, Xenopeltidae, and Colubridae aglyphae, part. *British Mus. (Nat. Hist.)*, London.
- Branch, W. R. 1981. Hemipenes of the Madagascan boas *Acrantophis* and *Sanzinia*, with a review of hemipenial morphology in the Boinae. *J. Herpetol.* 15:91–99.
- Briceño Rossi, A. L. 1934. El problema del ofidismo en Venezuela. *Bol. Minist. Salubr. Agric. Cria, Venezuela Año II [Vol. 1] (14):*1079–1177.
- Campbell, J. A., and W. W. Lamar. 1989. The venomous reptiles of Latin America. *Comstock Publ. Assoc., Ithaca, NY.* xiv + 425 pp.
- Chippaux, J-P. 1986. Les serpents de la Guyane française. Ed. ORSTOM, Coll. Faune Trop. 27. Paris, 165 pp.
- Cope, E. D. 1876. Batrachia and Reptilia of Costa Rica. *J. Acad. Nat. Sci. Philadelphia* 2:93–157.
- Duméril, A. M. C., and G. Bibron. 1844. *Erpétologie Générale ou Histoire Naturelle Complète des Reptiles*. Vol. 6. Librairie Encyclopédique de Roret, Paris.
- Ewel, J. J., A. Madriz, and J. A. Tosi, Jr. 1976. Zonas de vida de Venezuela. 2nd ed. Rep. Venezuela Min. Agricult. y Cría, Caracas.
- Felsenstein, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39:783–791.
- Forcart, L. 1951. Nomenclature remarks on some generic names of the snake family Boidae. *Herpetologica* 7:197–199.
- Gray, J. E. 1842. Synopsis of prehensile-tailed snakes, or family Boidae. *Zool. Misc.* 41–46
- . 1849. Catalogue of the specimens of snakes in the collection of the British Museum. *British Mus., London.*
- Guppy, H. B. 1917. Plants, seeds, and currents in the West Indies and Azores. Williams and Norgate, London. 531 pp.
- Hedges, S. B. 1996. The origin of West Indian amphibians and reptiles, pp. 95–128. *In* R. Powell and R. W. Henderson (eds.), *Contributions to West Indian herpetology: A tribute to Albert Schwartz*. Soc. Study Amphib. Rept., Ithaca, New York.
- Henderson, 1990. Correlation of environmental variables and dorsal color in *Corallus enydris* (Serpentes: Boidae) on Grenada: some preliminary results. *Carib. J. Sci.* 26:166–170.
- . 1993a. Foraging and diet in West Indian *Corallus enydris* (Serpentes: Boidae). *J. Herpetol.* 27:24–28.
- . 1993b. On the diets of some arboreal boids. *Herp. Nat. Hist.* 1(1):91–96.
- . 1993c. *Corallus caninus*. *Cat. American Amphib. Rept.* 574.1–574.4.
- . 1993d. *Corallus enydris*. *Cat. American Amphib. Rept.* 576.1–576.6.
- . 1996. Searching for tree boas high, low and in-between. *Lore* 46(1):18–23.
- , and S. B. Hedges. 1995. Origin of West Indian populations of the geographically widespread boa *Corallus enydris* inferred from mitochondrial DNA sequences. *Molec. Phylogen. Evol.* 4:88–92.
- , T. Waller, P. Micucci, G. Puorto, and R. W. Bourgeois. 1995. Ecological correlates and patterns in the distribution of Neotropical boines (Serpentes: Boidae): a preliminary assessment. *Herpetol. Nat. Hist.* 3(1):15–27.
- , and R. A. Winstel. 1995. Aspects of habitat selection by an arboreal boa (*Corallus enydris*) in an area of mixed agriculture on Grenada. *J. Herpetol.* 29:272–275.
- Howard, R. A. 1952. The vegetation of the Grenadines, Windward Islands, British West Indies. *Contrib. Gray Herb., Harvard Univ.* 174:1–129.
- Hueck, K., and P. Seibert. 1972. *Vegetationskarte von Südamerika*. Gustav Fischer Verlag, Stuttgart.
- Kluge, A. G. 1991. Boine snake phylogeny and research cycles. *Misc. Publ., Mus. Zool., Univ. Michigan* 178: iv + 58 pp.
- Kumar, S., K. Tamura, and M. Nei. 1993. MEGA, Molecular Evolutionary Genetic Analysis Software for Microcomputers. *CABIOS* 10:189–191.
- Linnaeus, C. 1758. *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Tomus I. Editio duodecima, Reformata. Laurentii Salvii, Holmiae.
- Maury, R. C., G. K. Westbrook, P. E. Baker, Ph. Bouysse, and D. Westercamp. 1990. Geology of the Lesser Antilles, pp. 141–166. *In* G. Dengo and J. E. Case (eds.), *The Caribbean region*. Geol. Soc. North America, Boulder, Colorado.
- McDiarmid, R. W., T'S. Touré, and J. M. Savage. 1996. The proper name of the Neotropical tree boa often referred to as *Corallus enydris* (Serpentes: Boidae). *J. Herpetol.* 30:320–326.
- Murphy, J. C. 1996. Crossing Bond's Line: The herpetological exchange between the eastern Caribbean and mainland South America, pp. 207–216. *In* R. Powell and R. W. Henderson (eds.), *Contributions to West Indian herpetology: A tribute to Albert Schwartz*. Soc. Study Amphib. Rept., Ithaca, New York.
- Pérez-Santos, C., and A. G. Moreno. 1988. Ofidios de Colombia. *Mus. reg. Sci. nat., Monograf.* 6, Torino.

- Puerto, G., and R. W. Henderson. 1995. Ecologically significant distribution records for the common tree boa (*Corallus enydris*) in Brasil. *Herpetol. Nat. Hist.* 2(2):89–91.
- Rodrigues, M. T. 1996. Lizards, snakes, and amphibians from the Quaternary sand dunes of the middle Rio São Francisco, Bahia, Brazil. *J. Herpetol.* 30:513–523.
- Rzhetsky, A., and M. Nei. 1992. A simple method for estimating and testing minimum- evolution trees. *Molec. Biol. Evol.* 4: 406–425.
- SAS Institute Inc. 1990. SAS/STAT User's Guide, Version 6, 4th ed. SAS Institute, Inc., Cary, NC. 1686 pp.
- Snow, J. W. 1976. The climate of northern South America, pp. 295–478. *In* W. Schwerdtfeger (ed.), *Climates of Central and South America*. Elsevier Scientific Publishing Co., Amsterdam.
- Stafford, P. J., and R. W. Henderson. 1996. Kaleidoscopic tree boas: the genus *Corallus* of tropical America. *Krieger Publ. Co., Malabar, FL.* x + 86 pp.
- Stejneger, L. 1901. An annotated list of batrachians and reptiles collected in the vicinity of La Guaira, Venezuela, with descriptions of two new species of snakes. *Proc. U. S. Natl. Mus.* 24:179–192.
- Stimson, A. F. 1969. Liste der rezenten Amphibien und Reptilien. Boidae (Boinae + Bolyerinae + Loxoceminae + Pythoninae). *Das Tierreich, Berlin* 89: xi + 49 pp.
- Stull, O. G. 1935. A check list of the family Boidae. *Proc. Boston Soc. Nat. Hist.* 40(8):387–408.
- Tolson, P. J. 1988. Critical habitat, predator pressures, and the management of *Epicrates monensis* (Serpentes: Boidae) on the Puerto Rico Bank: a multivariate analysis, pp. 228–238. *In* R. C. Szaro, K. E. Severson, and D. R. Patton (eds.), *Management of amphibians, reptiles, and small mammals in North America*. USDA Forest Serv., Gen. Tech. Rep. RM-166. Ft. Collins, CO.

APPENDIX
SPECIMENS EXAMINED

Corallus hortulanus

BOLIVIA: *Beni*: Vacadiez, Tumi Chucua, USNM 280358–70; Tumupasa, AMNH 22448; *Pando*: 23 km S Cobija, USNM 281762–63; Manoa (extreme NE corner, jct. of Río Abuná and Río Madeira), UMMZ 56865; *Santa Cruz*: no specific locality, BMNH 1904.10.29.37; Buenavista, AMNH 36011, CMNH 2756, UMMZ 60642–43; El Porton (Chiquitos), CMNH 34845; Río Colorado (Sara), CMNH 2950–51; Río San Julian (Chiquitos), CMNH 2755; Santa Cruz, CMNH 2837.

BRAZIL: *Acre*: Alto Purus, MZUSP 2500; Porto Walter, MZUSP 7356; *Amapá*: Aldeia dos Indios Uacá, MZUSP 1962; *Amazonas*: Barreira do Matupiri (Rio Madeira),

MZUSP 5911; Coari, MZUSP 7630; Estrada, MZUSP 7639; Ilha de Marchantaria (Rio Solimoes), MZUSP 7837; Manaus, MNHN 1892–298; Presidente Figueiredo (Usina Hidroeléctrica de Balbina), MCP 2870; Rio Juruá, MZUSP 1333; *Bahia*: no specific locality, BMNH 62.11.23.49; Barreiras Saco (2 leagues below Barreiras), UMMZ 108821; Ibiraba, MZUSP 10036–37; *Mato Grosso*: Barra do Tapirapes, MZUSP 3814; *Pará*: ca. 50 airline mi S Altamira, USNM 303482; Barcarena, KU 128090, KU 129869; Cachoeira do Espelho (Rio Xingu), MZUSP 9049, MZUSP 9088–90; Canindé (Rio Gurupí), MZUSP 4249, MZUSP 4270; Itaituba, MCP 4457; Juruá (Rio Xingu), MZUSP 9310; Lago de Souza (Rio Iriri), MZUSP 9061; Muana, KU 140150; Oriximiná, MZUSP 4795; Rodovia Belem-Brasilia, km 93, MZUSP 3736–37; Santarem, AMNH 2839–40; Taboleiro Leonardo (Rio Trombetas), MZUSP 7416; Taperinha, MZUSP 5186; *Paraná*: no specific locality, USNM 76386–87; *Rio de Janeiro*: Andrade Pinto, IB 4321; Ilha Grande, IB 41213, IB 42565, IB 42579, IB 42595, IB 42604, IB 42670; Miracema, IB 10033; Petropolis, IB 10244; Rio de Janeiro, MZUSP 2729; Rio de Janeiro (Gavea), BMNH 1910.5.4.19; Saco do Anta, IB 44426; *Rondônia*: Alta Paraíso, MZUSP 8356; Cachoeira de Nazare (Rio Machado), MZUSP 9036; Pôrto Velho, MCP 3779; MCP 4271–74; UMMZ 56857; *Roraima*: Cachoeira do Paredao (Rio Mucajaí), MZUSP 9794; Colônia Apiaú, MZUSP 9245–46, MZUSP 9771; Ilha de Maracá, MZUSP 9264–67, MZUSP 9995, USNM 302375; *São Paulo*: Guaratuba, MZUSP 5529; Iguape, IB 55042.

COLOMBIA: *Amazonas*: Leticia, FMNH 81928, FMNH 83603; Tarapuca, CAS 135344; *Caquetá*: Río Macaya, FMNH 69654; *Meta*: Río Guayabero, La Macarena, MZUSP 6110; San Juan de Arama (Los Micos), FMNH 81308–09; *Vaupés*: Wacará, UTACV 3780.

ECUADOR: *Morona-Santiago*: Cusuime (Río Cusuime, 60 airline km SE Macas), AMNH 113638; *Napo*: Limoncocha, KU 98607, UIMNH 61194–95; Santa Cecilia, KU 148282; *Pastaza*: Paracachi, Río Curaray, USNM 204091; Río Pindo (near Río Tigre), USNM 204092; Río Chambrio region of Río Pastaza, AMNH 49136; Río Rutuno (trib.

Río Bobonaza), USNM 204093; Sarayacu (Río Bobonaza), USNM 204090.

FRENCH GUIANA: no specific locality, MNHN 1903–232; MNHN 1955–44; MNHN 1978–2548; MNHN 1986–161, MNHN 1986–574; Acarouany, MNHN 1989–95, Cayenne, MNHN 5548.

GUYANA: Abary River, 50 km above Georgetown, USNM 141763, USNM 145462–72; Atkinson Airport, USNM 166830; Berbice, BMNH 1946.1.10.43; Coomaka Island, Moruca River, UMMZ 55859; Demerara River, BMNH 1929.7.13.6; Dubulay Ranch on Berbice River, AMNH R140232–34; Georgetown vicinity, UF 73141; Kartabo, AMNH 67869, FMNH 14838; Kura-Kura [Kosu Kosu?] Creek, Demerara River, UMMZ 77819; forest near penal settlement, Mazaruni, BMNH 1934.11.1.112.

PERU: *Cuzco*: Río Comerciato (2000 ft.), USNM 60693; Río Coshereni [Cosireni?], 3000 ft., USNM 60694; 102 km E Quincemil on Pto. Maldonado Rd., LSUMZ 27355; *Loreto*: Alto Amazonas, Río Potro, FMNH 109812–13; Balta, Río Curanja, LSUMZ 14583, LSUMZ 26830–32; Centro Unión, TCWC 41404, TCWC 42072, TCWC 44605; Estiron, Río Ampiyacu, MZUSP 4382, MZUSP 4389; Indiana, TCWC 44602; Iquitos, TCWC 41403, TCWC 44603, USNM 197247, USNM 197249; Iquitos, Río Itaya, AMNH 54351; near Iquitos (Río Yanayacu at Río Amazonas), KU 159738; Iquitos, Isla Lupuna, AMNH 56100; Iquitos, Sta. Luisa (Río Nanay), FMNH 109809–11, FMNH 109814; Río Maniti (ca. 50 km below Iquitos), USNM 197251; Mishana, Río Nanay, MPM 10430, TCWC 42075, USNM 197248; Río Momon (tributary of Río Nanay, a few miles above its mouth), USNM 197254; Moropon, TCWC 41398–99, TCWC 42070; Orellana (Reforma), AMNH 54611; Pampa Hermosa, Río Cushabatay, AMNH 53547, AMNH 53583, AMNH 53808, AMNH 55426; Roaboya, Río Ucayali, AMNH 52891, AMNH 53106; Santa María, Río Napo, USNM 197250; Río Ucayali [not mapped], FMNH 4009–10; Yanamono, TCWC 41400–01; Yanayacu (ca. 30 km below Iquitos), TCWC 42069, USNM 197252–53; Yarinacocha (Río Ucayali), FMNH 45632–33, FMNH 56136, LSUMZ 25401; Yurimaguas, BMNH

84.2.18.12; upper Río Ucayali, AMNH 71163 [not mapped]; *Madre de Dios*: NW bank Río Alto Madre de Dios at Salvación (Hacienda Erika), FMNH 224504–05, UC-MVZ 197155–57; Lago Sandoval (Río Madre de Dios), UC-MVZ 173761; extreme W bank of Lago Valencia, UC-MVZ 197160; Pakitza (ca. 57 airline km NW mouth of Río Manu), UC-MVZ 197158–59; 15 km E Pto. Maldonado, KU 204894–95; 30 km SSW Pto. Maldonado (Tambopata Reserve), USNM 222348; Selvas del Río [not mapped], FMNH 40020–21; Zona Boca Amiga, FMNH 81517–18; *San Martín*: Chiparana (Huallaga), AMNH 52224; *Ucayali*: Santa Isabel, FMNH 45634; Yarinacocha, FMNH 45631

SURINAME: Batavia, BMNH 1946.4.4.13; Hanover Savanna, KU 206414; Josikreek (Saramacca), MCZ 154826–33; Kaiserberg Airstrip (Zuid Rivier), FMNH 128781; Moengo, USNM 64624, USNM 66867; Nieuw Grond Plantation (Commewijne Rivier), MCZ 152627; Paramaribo, AMNH 8660, BMNH 1946.4.4.12; Paramaribo (Botanical Garden), AMNH 104607; Sipaliwini (near airstrip), MCZ 152628; Tepoe, UF 73146, UTACV 15698–99; Zanderij, AMNH 130485–86.

VENEZUELA: *Amazonas*: Esmeralda (56 km NNW Río Cunucunuma, Belen), USNM 217149–52, USNM 217160–61, USNM 217199; 84 km SSE Esmeralda (10 km up Río Mavaca), USNM 217153–54; 32 km S Pto. Ayacucho, USNM 217156, USNM 217164–65; 163 km ESE Pto. Ayacucho (Río Manapiare, San Juan), USNM 217155; Neblina Base Camp on Río Mawarinuma, AMNH 133712, AMNH 133173; Río Pacimani (Marurividi, Estación Climatología), AMNH 127826 [not mapped]; *Bolívar*: 50 km SE El Manteco (Río Supamo), USNM 217158; 56 km SE El Manteco (Río Supamo), USNM 162187; 13 km S, 1 km E Puente Cuyuni, KU 167563;

Corallus cooki

ST. VINCENT: No specific locality; BMNH 91.5.12.8; MCZ 61111, 79105–06, 79761, 100658; USNM 9567 *Charlotte*: 0.4 km WNW Orange Hill, MPM 23600; Upper South Rivers, MPM 26147; *St. Andrew*: Camden Park, MPM 26144–46; *St. David*: 0.2 mi

S Chateaubelair, MPM 23391–92; *St. George*: Kingstown, USNM 140154; *St. Patrick*: Hermitage, MPM 26148–9; 2.0 mi E Layou, ASFS 11296; 2.0 mi ENE Layou, MPM 23291–312, MPM 23386–90, MPM 23596–99; WEST INDIES: BMNH 1946.1.1.50.

Corallus grenadensis

GRENADA: no specific locality: [locality data state Fedon's Camp, but I consider these data bogus], ASFS X7005, ASFS X7044–52, LACM 59140; BMNH 87.6.29.20; BMNH 87.6.29.22; BMNH 87.6.29.25; BMNH 1964.1994; MCZ 6108, MCZ 100622, MCZ 100625; *St. Andrew*: Balthazar Estate, MPM 23483–86, MPM 25365–69, MPM 25372–73; Grand Etang, MPM 23624–25, MPM 25445; 1.0 mi NE Grand Etang, ASFS X6901; 1.0 mi NNE Grand Etang, MPM 23487–88, 23623; 1.5 mi NE Grand Etang, ASFS X7053; Grenville, MPM 23396; near Grenville (0.5 mi NW Paradise), UF 43557–58; Pearls, MPM 23381–82, MPM 23393–94, MPM 25357–64, MPM 27957; Mt. Pleasant, MPM 23508–09, USNM 67233; Mt. Pleasant area, BMNH 97.7.23.49; *St. David*: B Bacolet, MPM 25378–81; 0.5 km N St. David's, MPM 23510–11; Morne Delice Rd., MPM 23513; Mt. William Estate, MPM 26277; 1.0 mi NNW Westerhall Estate, MPM 23513; Westerhall Estate, MPM 25390–95; base of Westerhall Point, ASFS 17618; 3.1 mi [east of?] Woburn, UF 73145; *St. George*: Annandale Falls, MPM 23494, MPM 23512, USNM 167396, USNM 299989; Beausejour, MCZ 79762–65, MCZ 92201–02, MPM 25370–71, MPM 25374, MPM 25376–77; eastern base of l'Anse aux Epines, MPM 23496, MPM 23501; Calvigny Estate, MPM 25382–86, MPM 25388–89; Lower Woburn, MPM 23496–97, MPM 25387; Morne Rouge area of Grande Anse, MPM 23482, MPM 23491–93, MPM 23495; Mt. Hartman Bay, MPM 27955–56; 0.5 km N Prickly Point (l'Anse aux Epines), MPM 23499; *St. George's*, BMNH 87.6.29.21, MCZ 6109–10, MCZ 7790–91, MCZ 8089–91; *St. George's* (Botanic Garden), BMNH 87.6.29.23–24, BMNH 87.6.29.26; True Blue area of Grande Anse, MPM 23489–90, MPM 23506; Vendome, MPM 23395; *St. Mark*: Diamond Estate, MCZ 92200; *St. Patrick*: Mt. Alexander,

ASFS X6995, X7004; Levera Pond, ASFS 11144, ASFS 11146, MPM 21931.

BALICEAUX: near ruins, MPM 26168–69. BEQUIA: No specific locality: BMNH 90.11.25.18, UF 73140, MCZ 100624, 100626; USNM 104228; half-way between Admiralty Bay and Spring Bay, UC-MVZ 84062; Industry Bay area, MPM 23633–35; Parks, ASFS 11352; between Paget Farm and La Pompe area, MPM 26172–75; Port Elizabeth, MPM 23632.

CANOUAN: 0.5 mi NNE Charlestown, MPM 23610–14; Happy Hill, 25629–30; trail to Retreat (outside Charlestown), MPM 26164–65; Riley Hill area, MPM 26166–67.

CARRIACOU: 1.5 km ENE Hillsborough, MPM 23502–05, MPM 23507; between Hillsborough and airport, MPM 23506.

ILE QUATRE: no specific locality: USNM 79097–98; between Lagoon Bay and Mahaut Bay, MPM 26170–71.

MAYREAU: Grand Tarchie, MPM 26161; Old Wall area, MPM 26162; Salt Whistle Bay, MPM 25649; La Souciere area, Saline Bay, MPM 25651; above jetty above La Souciere, MPM 26160; Station Hill area, MPM 25648, 25650, 26163.

MUSTIQUE: Granby Plantation, MPM 23619–20; between Rutland Bay and Lime Kiln Bay, MPM 23618.

PETIT MARTINIQUE: MCZ 6112.

UNION ISLAND: no specific locality: MCZ 79104, MPM 23606–07, MPM 23626; near Belmont Salt Pond, MPM 26157–59; Clifton, MPM 25631–32, MPM 26156; above Richmond Bay, MPM 23608; Salt Pond at Richmond Bay, MPM 23602–05.

Corallus ruschenbergii

COLOMBIA: *Antioquia*: Río Arquia, near Pto. Palacios, LACM 45412; *Bolivar*: Caño Careto, between San Marcos and Los Flores, FMNH 165258; *Cesar*: Río Guaimaral, USNM 117498–99, USNM 117501; *Chocó*: Caño Corazon, Río Tolo, FMNH 73794–95; *Magdalena*: Bonda, UMMZ 63920; *Meta*: Lomalinda, UTACV 2856, UTACV 3779, UTACV 3862; *Norte de Santander*: Rosario de Cucuta (= Villa Rosario), BMNH 89.8.23.3; *Sucre*: 4 km E Tolu, LACM 114656.

COSTA RICA: *Puntarenas*: Palmar Norte, UMMZ 131314; Rincón de Osa, WWL [no number]; near Rincón de Osa, CRE 3155;

vicinity of Rincón de Osa, CRE 6396; 8 km NW Villa Neily, near Río Carcol, CRE 8037.

PANAMA: no specific locality: ANSP 10325, TCWC 33543, UMMZ 65659, USNM 53896; *Canal Zone*: no specific locality, FMNH 31747, MPM 26290; near Fort Clayton Reservation, UIMNH 41808, UIMNH 42230; Fort Kobbe, KU 110259, KU 110273; Palo Seco, KU 110258, USNM 138958; Rodman, KU 110260; *Darién*: Quebrada Portachaque near mouth of Río Tuquesa, UC-MVZ 83431; El Real, KU 80588, KU 107910; KU 110252; near El Real de Santa María [= El Real], USNM 140675; Río Chucunaque opp. Río Canclon, UMMZ 124207–08; Río Chucunaque above Río Chiatí, KU 107624–25; Río Chucunaque, ca. 10 km below Río Subcutí, KU 107626; Río Chucunaque, ca. 7 km above Río Mortí, KU 107627–35; Río Ucurganti, ca. 7 km above mouth, KU 107636–39; Yaviza, UC-MVZ 83433; *Panama*: Altos de Majé, AMNH 109639; Río Bayano (Gorgas Memorial Lab. Field Station), UMMZ 135365; *Pearl Islands*: Isla Contadora, AMNH 108688–90; Isla Rey, FMNH 154316; *San Blas*: Armila, Quebrada Venado, USNM 150129; Camp Sasardí, KU 110255; Isla Suscantupu, KU 110256–57; *Veraguas*: Isla de Cebaco.

TRINIDAD: No specific locality: FMNH 49923, USNM 14675, USNM 17762, USNM 54335; Arima, AMNH 73097; Arima, N of milepost 1.5, USNM 306169; Diego Martin, MCZ 100623; Maracas Valley (0.75 mi N St. Joseph), MCZ 80858; Mt. Harris, FMNH 49915–17, FMNH 49919, FMNH 49921–22; Plaisance Mayero, FMNH 49926; Port-of-Spain, AMNH 73098; between Port-of-Spain and San Fernando, USNM 118048; Quarre

Dam (Hollis Reservoir), MCZ 65491, MPM 23595, MPM 26199–200, MPM 26378, USNM 196370; Sangre Grande (Longstretch), AMNH 85938; Sangre Grande Stretch, AMNH 81480; San Rafael, FMNH 49918, FMNH 49920, FMNH 49924–25; St. Ann's, MPM 26201; Teteron Bay [not located], AMNH 64485; Tucker Valley [not located on map], AMNH 64482; Waller Field, AMNH 73096, AMNH 73099, UF 3638;

TOBAGO: 1.5 mi ENE Charlottesville (hills above Man-of-War Bay), AMNH 108742; ca. 5 km W Charlottesville (near Hermitage), USNM 228020; Hillsborough Dam (east side of lake), USNM 228017–19; west of Roxborough (Roxborough-Bloody Bay road), USNM 306071; Speysise, MCZ 126230.

VENEZUELA: *Amazonas*: 163 km ESE Pto. Ayacucho (Río Manapiare), USNM 217162–63; *Apure*: 29 km SSE Santo Domingo (Selvas de San Camilo, Nulita), USNM 217157; *Barinas*: Hato de la Cruz (Arismendi), UC-MVZ 110723; *Bolívar*: 45 km ESE Caicara, Hato la Florida, USNM 217159; Ciudad Bolívar, USNM 55874; Cuchivero, AMNH 29313; *Carabobo*: NW of Urama, USNM 162836; *Delta Amacuro*: 140 km NE Barrancas, LACM 31474; near mouth of Río Orinoco, BMNH 97.7.23.50; *Guárico*: 50 km S Calabozo, UF 56530; *Miranda*: Río Chico, 100 km E La Guaira, USNM 27832; *Mona-gas*: Caripito, AMNH 65569, AMNH 98224; 42 km SE Maturin, LACM 31472–73; *Nueva Esparta*: 10 km WSW Asuncion, USNM 217166; 1.5 km N San Francisco de Macano, KU 117032; *Sucre*: La Angelita, UIMNH 95135–38; 7 km S Guaraunos, KU 167564–65; El Pilar, CAS 94645.