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PHYLOGENETICS OF THE BOID SNAKE GENUS *EPICRATES* AND CARIBBEAN VICARIANCE THEORY

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ABSTRACT.—*Tolson, Peter J, 1987. Phylogenetics of the boid snake genus* Epicrates *and Caribbean vicariance theory. Occ. Pap. Mus. Zool. Univ. Michigan, 715:1-00, figs. 1-26.* Skin and scent gland secretion lipids from the ten species of the boid snake genus *Epicrates* were fractionated using silicic acid column chromatography and thin-layer chromatography. The fractionated lipids were coded according to their relative mobilities and combined with a set of morphological characters. Polarity was determined using outgroup comparisons. A single most parsimonious cladogram was generated from the combined data set and was used to test the phylogenetic hypothesis of Sheplan and Schwartz for *Epicrates*. The genus forms a monophyletic group; so do the Antillean species. Nested within the Antillean group is another monophyletic assemblage: *E. fordii, E. gracilis,* and *E. monensis*. Sister species relationships are suggested for *E. chrysogaster* and *E. exsul, E. fordii* and *E. monensis,* and *E. inornatus* and *E. subflavus*. The most primitive member of the Antillean group appears to be *E. angulifer*. In addition, the phylogenetic cladogram was compared to a current geological area cladogram of the Greater Antilles, area cladograms derived from current mobilist theory, and distributions of other genera of Antillean amphibians and reptiles in an attempt to discover possible vicariant patterns shared with *Epicrates,* and in order to test the Greater Antilles vicariance model of Rosen and the dispersalist biogeography of Sheplan and Schwartz. These comparisons suggest that the snakes reached the islands by linear dispersal after a single initial invasion of Cuba, rather than by vicariance.

Key words: Epicrates, *Caribbean, vicariance,* boa.

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INTRODUCTION

The geographic origin of the herpetofauna of the Greater Antilles has engendered heated debate for over half a century. Early biogeographers were certain that the presence of a rich and varied fauna on those islands precluded overwater dispersal from the continents, and they postulated the existence of land bridges to account for the distributions (Stejneger, 1904; Barbour, 1916; Scharff, 1922). Such a view was embraced by the only reviewer of the geology of the region at that time (Schuchert, 1935).

The land bridge hypotheses finally collapsed under the weight of the arguments for overwater dispersal as the most plausible explanation for the origin of the Greater Antillean fauna (Matthew, 1939; Darlington, 1938; Simpson, 1956). The dispersal hypothesis was accepted for nearly 25 years until Rosen (1975), citing new geological interpretations of the region (Malfait and Dinkleman, 1972) and using the vicariance biogeographic method of Croizat (1958; 1964), reexamined the distributions and affinities of the Caribbean biota. According to Croizat's method, the distributions of monophyletic groups of plants and animals of the region are examined for coincident "tracks" of distribution. Several such tracks, including the mainland and the Greater Antilles, for example, are considered evidence of a former, more widespread, parent biota that was subsequently fragmented, or vicariated, with the origin of the islands. After he examined numerous tracks, Rosen concluded that the flora and fauna of the Greater Antilles represented a vicariated biota, transferred *en masse* from Nuclear Central America to its present position by the movement of a proto-Antillean archipelago on which it resided. Rosen considered that the proto-Antilles originated from a point close to the present Isthmus of Panama and moved eastward hundreds of kilometers to the position now occupied by the Greater Antilles. This eastward movement was hypothesized to have begun in the early Mesozoic and been essentially completed by the Eocene (Malfait and Dinkleman, 1972).

Two major problems attend Caribbean vicariance studies: (1) much of the biota has no fossil history earlier than the Pleistocene, and (2) corroborated phylogenetic hypotheses are nearly nonexistent. The boid genus *Epicrates* is one of the few island-continental faunal elements thought to be ancient enough to have been affected by the date set for Greater Antilles vicariance (Underwood, 1953). In addition, unlike many other ancient Antillean reptile elements (*Chamaeleolis, Cricosaura, Aristelliger*; Underwood, 1953), *Epicrates* has living representatives on several islands so that vicariance hypotheses within the

archipelago may be profitably investigated. When I undertook this study I was especially hopeful that vicariance theory would provide an explanation for the origin of the puzzling set of disjunct distributions exemplified by *Epicrates*.

While *E. cenchria* is widely distributed in Central and South America from Costa Rica to Argentina, all other congeners are restricted to the Greater Antilles and Bahamas (Table 1; Figs. 1-3). *Epicrates angulifer*, the largest species in the genus, is endemic to Cuba and the Isla de Piños, where it occurs in a variety of habitats. *Epicrates subflavus* is endemic to Jamaica and the species most phenotypically similar to it, *Epicrates inornatus*, is confined to Puerto Rico. *Epicrates fordii* and *E. gracilis* are Hispaniolan endemics, the former confined to dry lowland areas and the latter to more mesic forested habitats. Three species inhabit the Bahamas. *Epicrates chrysogaster* is endemic to the southern Bahamas, south of the Crooked Island Passage, while *E. exsul* is confined to the Little Bahama Bank. These two forms are similar, but the islands of the Great Bahama Bank, those between the Little Bahama Bank and the southern Bahamas, are populated by a subspecies of *E. striatus*. The nominate form of *E. striatus* is locally macrosympatric with *E. gracilis* and *E. fordii* on Hispaniola. The remaining island species, *E. monensis*, occurs on Isla Mona, between Hispaniola and Puerto Rico, and on St. Thomas and Tortola of the Virgin Islands. Photographs of each species are presented in Figs. 4-8.

Now that the complex taxonomic and nomenclatural snarls associated with *Epicrates* have been substantially settled by Sheplan and Schwartz (1974), the way is open to attempt to deduce a well-corroborated phylogenetic hypothesis. Sheplan and Schwartz showed that meristic scale characters are extremely variable in the genus, so I chose to emphasize scent gland and skin lipid characters in my analysis of phylogenetic relationships. Unlike the assays for most biochemical characters, these required no sacrifice of living material. This is an important consideration in a study of *Epicrates* because of the rarity of some species. Also, Oldak (1976) showed that lipid secretions from the scent glands of snakes were useful as diagnostic characters. Other recent workers have indicated that lipids play an integral part in species recognition (Devine, 1977; Crews, 1980) as well as other aspects of snake physiology, such as the control of evaporative water loss (Roberts and Lillywhite, 1980). I hypothesized that if lipoidal chemical cues were responsible for species recognition, the chromatography of skin lipid extracts would show species differences, perhaps even more so than extracts from scent glands. These lipoidal characters, along with selected scale characters gleaned from Sheplan and Schwartz

TABLE 1
PRESENT RANGES OF EXTANT SPECIES OF *Epicrates* IN THE BAHAMAS AND THE GREATER ANTILLES

Species	Range
angulifer	Cuba and the Isle of Pines
chrysogaster	Caicos Islands, Acklins Island, Great Inagua and Crooked Island
exsul	Abaco Islands; possibly on Grand Bahama
fordii	Cul-de-Sac and Valle de Neiba Plains of Hispaniola Isolated populations on the west and north coasts of Haiti and western Dominican Republic
gracilis	Mesic areas of Hispaniola
inornatus	Puerto Rico
monensis	Isla Mona, St. Thomas, and Tortola of the Virgin Islands; possibly on Guana Island
striatus	Widely distributed on Hispaniola and the Bahama Islands north of the Crooked Island Passage, except the Little Bahama Bank
subflavus	Jamaica

(1974), were subjected to analysis by phylogenetic inference. For this purpose, I have used the method of inference promulgated by Hennig (1966), phylogenetic systematics, along with a battery of technical refinements (Kluge and Farris, 1969; Farris, 1970; Farris et al., 1970; Swofford, 1985).

I have critically examined three major propositions: (1) the phylogenetic hypothesis of Sheplan and Schwartz (1974); (2) the Greater Antilles vicariance model of Rosen (1975); and (3) the dispersalist biogeography hypothesis of Sheplan and Schwartz (1974). In addition, I compared the area cladogram derived from current mobilist geological theory with the distributions of other genera of Antillean amphibians and reptiles.

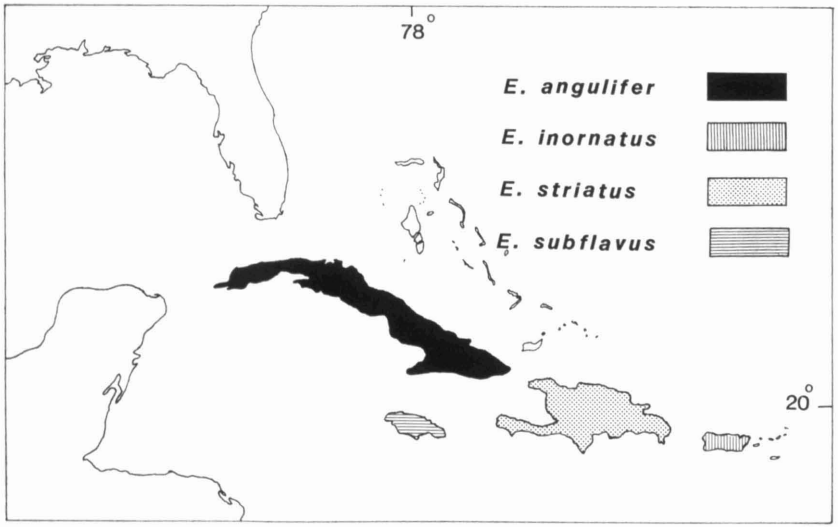

FIG. 1. Distribution of the large species of Greater Antillean *Epicrates*.

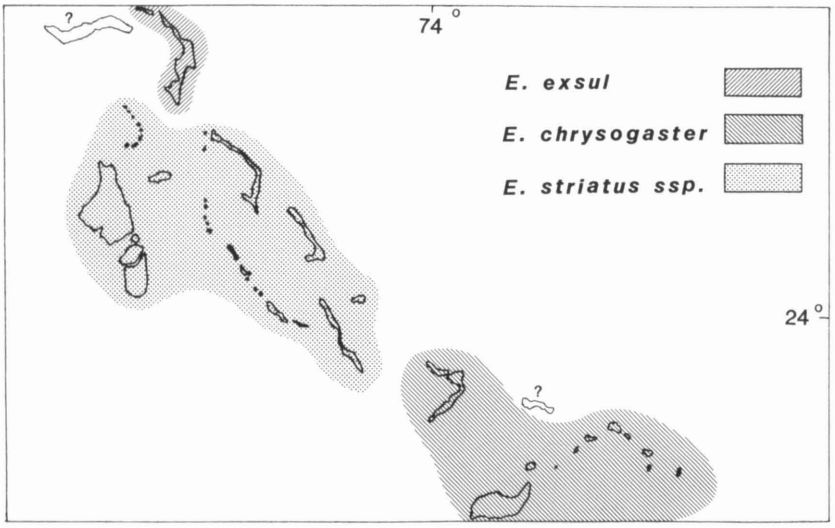

FIG. 2. Distribution of the Bahamian species of *Epicrates*.

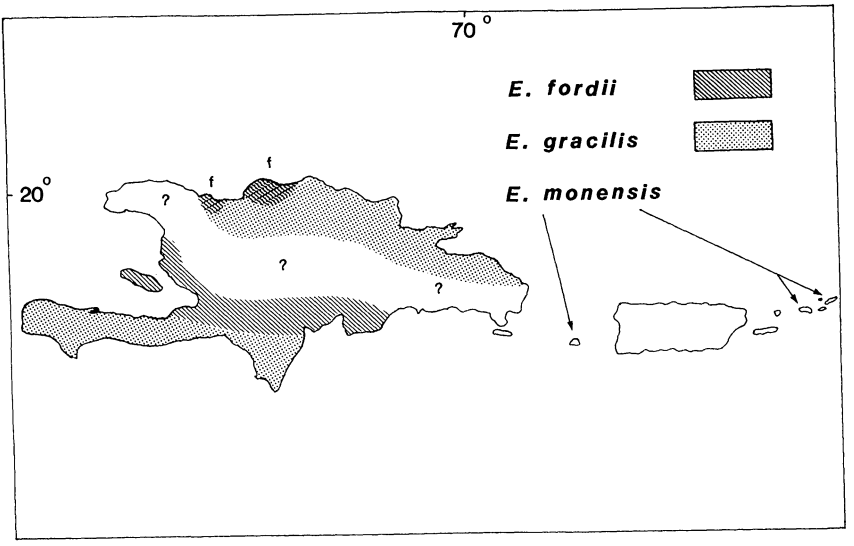

FIG. 3. Distribution of the small species of Greater Antillean *Epicrates*.

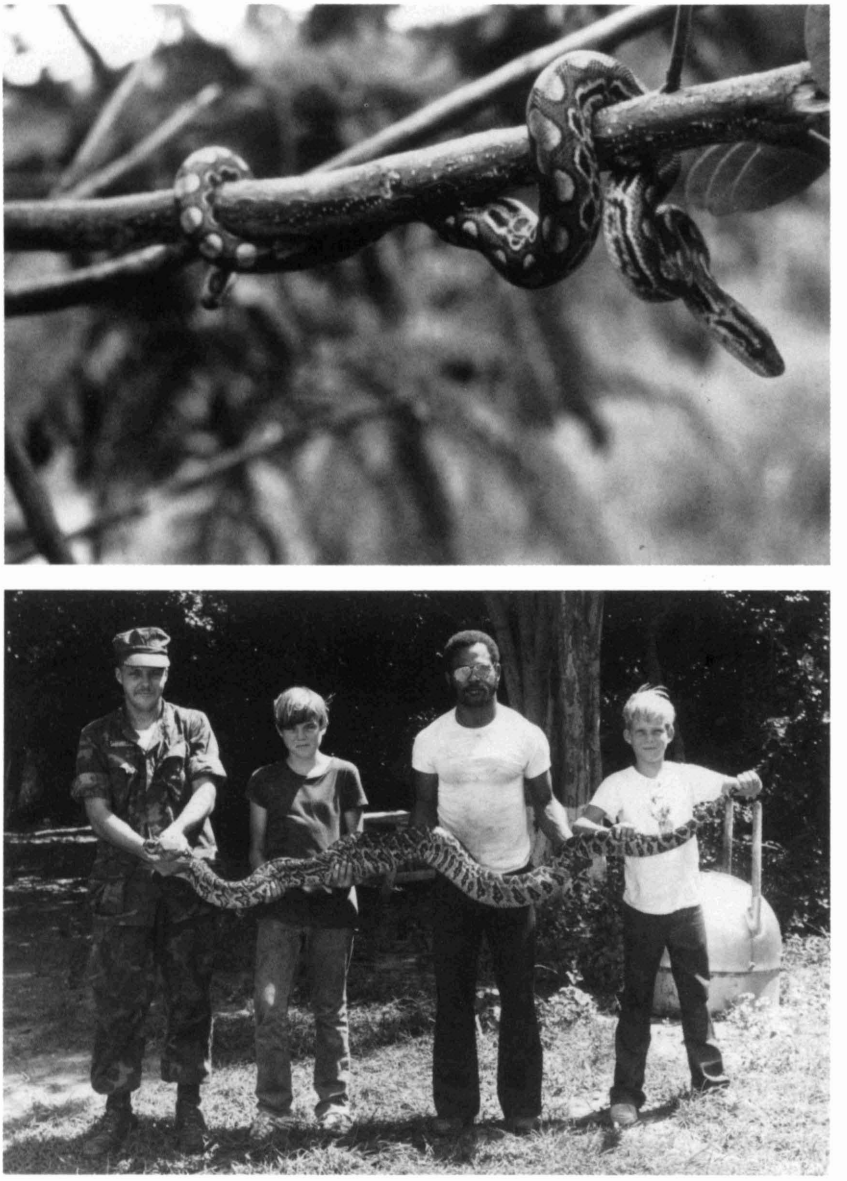

FIG. 4. Above: *Epicrates cenchria*, Exu,Pernambuco, Brazil. Below: *Epicrates angulifer*, U. S. Naval Base, Guantanamo Bay, Cuba.

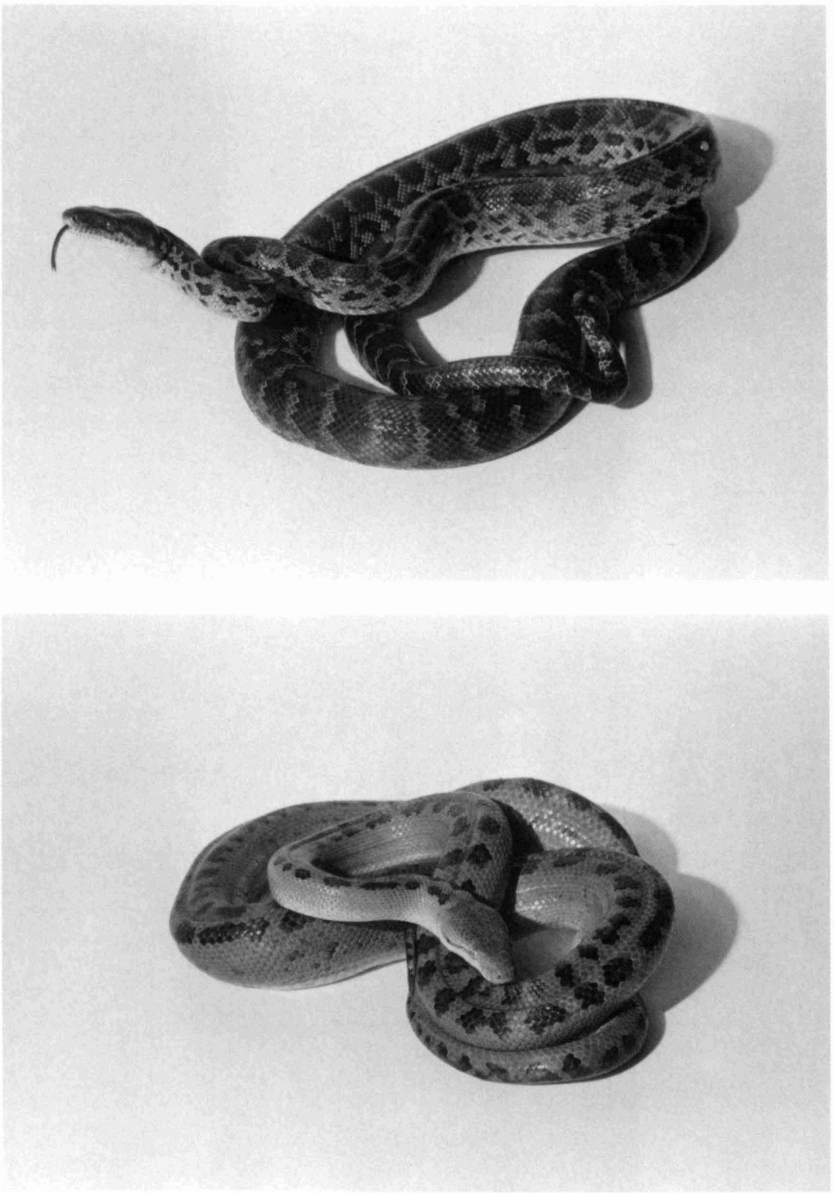

FIG. 5. Above: *Epicrates striatus*, near Limbe, Dept. du Nord, Republic du Haiti. Below: *Epicrates chrysogaster*, near Kew, North Caicos Island, Turks and Caicos Islands.

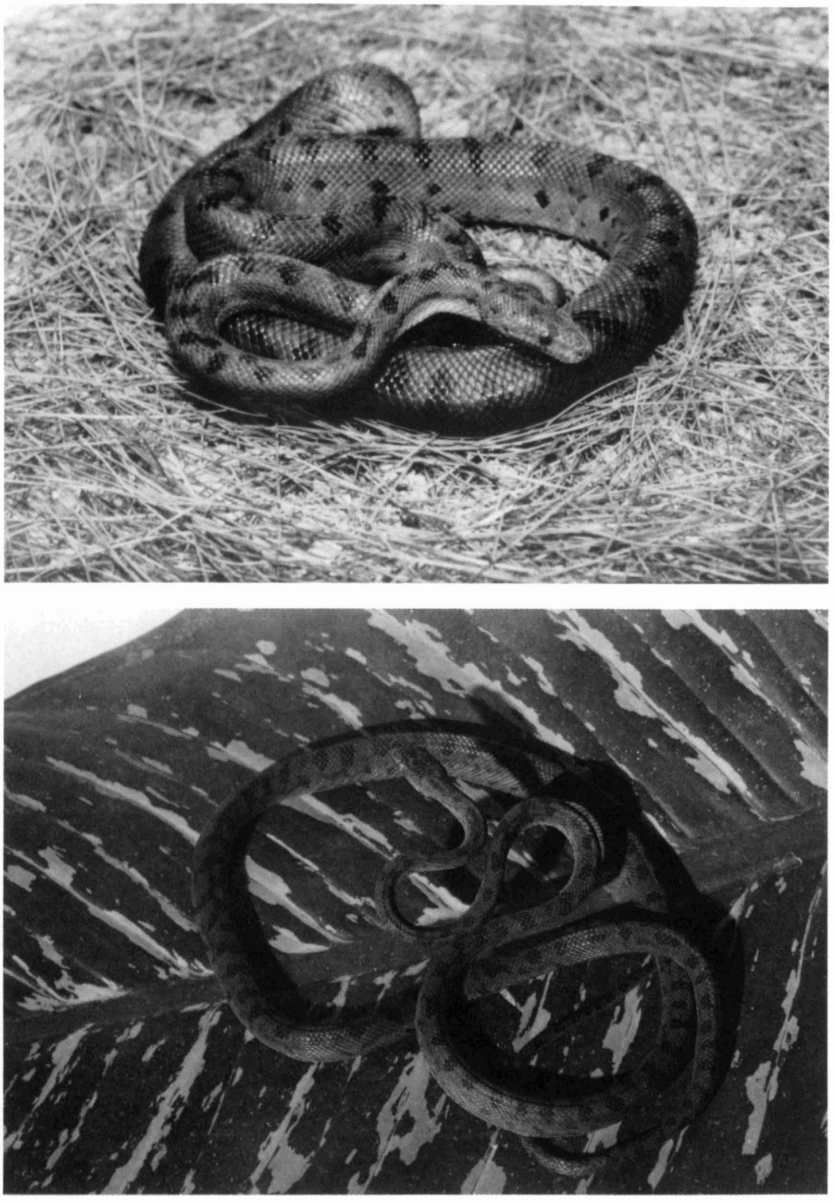

FIG. 6. Above: *Epicrates exsul*, near Hopetown, Elbow Cay, Bahama Islands. Below: *Epicrates gracilis*, near Limbe, Dept. du Nord, Republic du Haiti.

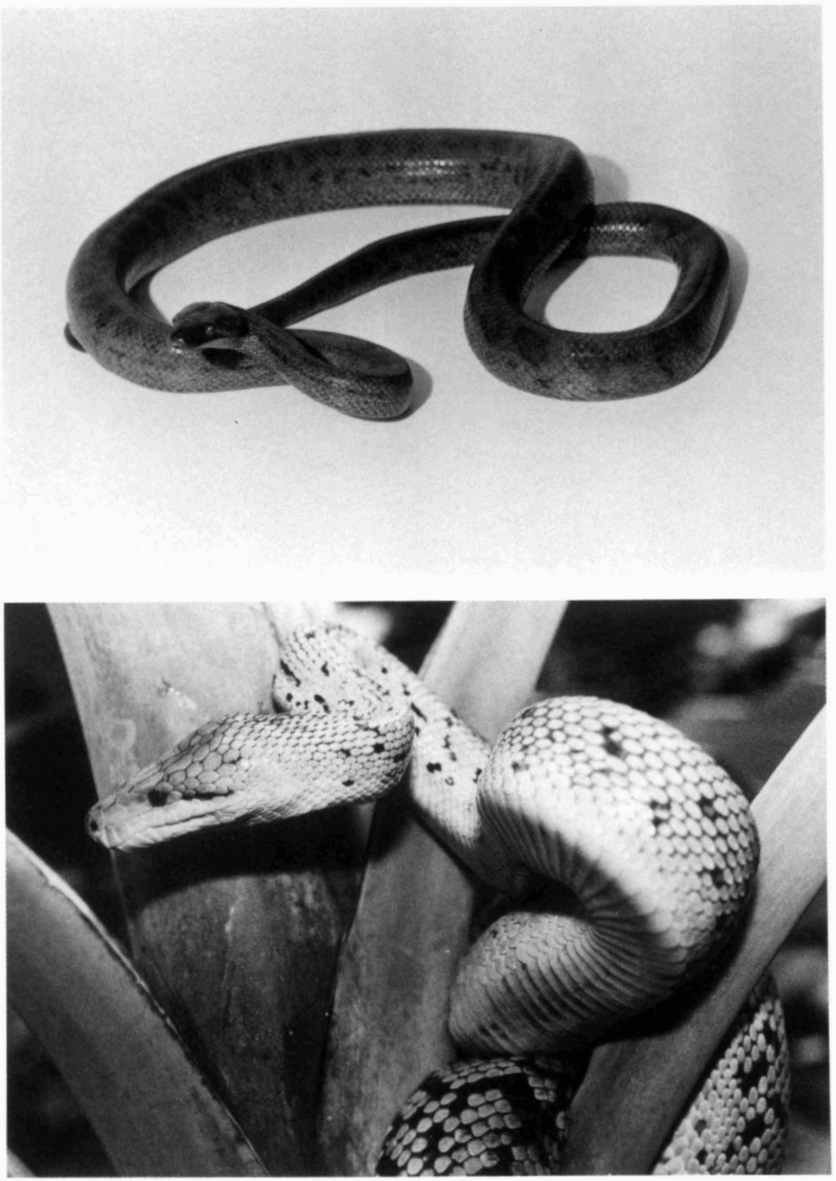

FIG. 7. Above: *Epicrates inornatus*, Puerto Rico. Below: *Epicrates subflavus*, Jamaica.

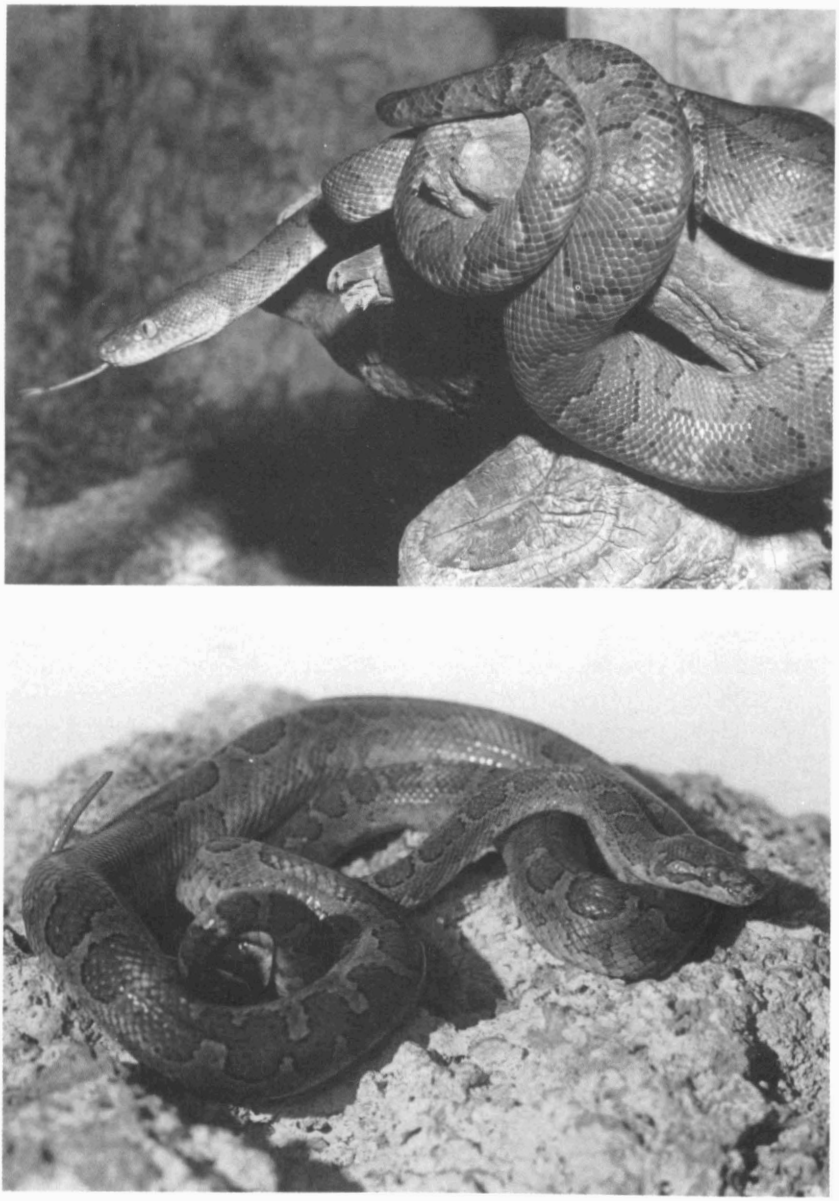

FIG. 8. Above: *Epicrates monensis granti*, Cayo Diablo, Puerto Rico. Below: *Epicrates fordii*, near Manneville, Dept. L'Ouest, Republic du Haiti.

MATERIALS AND METHODS

Abbreviations

The following abbreviations are used in the text, figures, and tables. For lipid standards (STD): CH = cholesterol; CA = cholesteryl acetate; CAR = cholesteryl arachidate; CP = cholesteryl palmitate; PA = palmitic acid; PAR = palmitoyl arachidate; PE = phosphatidyl ethanolamine; PG = phosphatidyl glycerol; PI = phosphatidyl inositol; PS = phosphatidyl serine; SPH = sphingomyelin; TM = trimyristin. For the solvent systems: 80:20:2 = hexane:ethyl ether:acetic acid 80:20:2 v/v/v; 96:4 = carbon tetrachloride:hexane 96:4 v/v; 30:20:18:9:6 = chloroform:2-propanol:triethylamine:methanol:0.25% KCl v/v/v/v/v. For the species examined: ANG = *E. angulifer*; CEN = *E. cenchria*; CHR = *E. chrysogaster*; EXS = *E. exsul*; FOR = *E. fordii*; GRA = *E. gracilis*; INO = *E. inornatus*; MON = *E. monensis*; SUB = *E. subflavus*; STR = *E. striatus*; COR = *Corallus*; ANN = *C. annulata*; ENH = *C. enydris*; CAN = *C. canina*. For the collections utilized: GK, collection of George Kratsas; PJT, author's collection; RBF, Reptile Breeding Foundation, Picton, Ontario, Canada; TZS, Toledo Zoological Society; UMMZ, The University of Michigan Museum of Zoology; VH, collection of Valerie Hornyak. For place-names: C AMER = Central America; CUB = Cuba; HISP = Hispaniola; JAM = Jamaica; PR = Puerto Rico; VI = Virgin Islands.

The Lipids

Collection of Samples and Their Storage.—Scent gland secretions were collected with a modification of the technique used by Oldak (1976). Snakes were grasped anterior to the cloaca using the left hand, with the thumb placed firmly over the vent to prevent defecation. The cloacal area was cleaned with a damp cotton swab, and then the snake was held venter up while the other thumb provided firm, gentle pressure at the base of the tail. The exuded waxy secretion was collected on a clean glass petri dish. The secretion was transferred to a clean tared screw-cap vial with a teflon cap liner. The vial was flooded with N_2 prior to sealing. Lipids were stored dessicated at -20°C until extraction. All glassware used in this study had been washed twice in $CHCl_3$:methanol 2:1 v/v after normal washes of tap and distilled water.

Lipids extracted from shed skins were treated as follows. Snakes were transferred to clean glass aquaria prior to shedding (when the snakes were opaque). The freshly shed skins were collected as soon as possible

after shedding and stored in plastic zip-lock bags at -20°C until extraction. Portions of skin contaminated with uric acid or fecal material were excised and discarded, as were the portions of skin adjacent to the scent glands and cloaca.

EXTRACTION PROCEDURES.—Scent gland secretions were dissolved in a mixture of $CHCl_3$ and methanol, 2:1 v/v. One ml of solvent was used for each 50 mg of secretion. Lumps of secretion were broken up while in the solvent with several up and down strokes of a teflon-glass homogenizer. A modification of the technique used by Folch et al. (1957) was followed for extraction. After the addition of the $CHCl_3$: methanol solution, the mixture was allowed to sit until the denatured protein was precipitated. The mixture was filtered through a pyrex sintered glass filter into a clean separatory funnel. A volume of glass-distilled water equal to one-quarter of the total volume of the $CHCl_3$: methanol extract was acidified to pH 2.0 with concentrated HCl and then added to the funnel. The funnel was shaken vigorously until mixing of the two phases was complete. The separatory funnel was allowed to sit until the two phases were resolved. The aqueous upper layer was decanted and replaced with a fresh aliquot of Folch upper phase ($CHCl_3$:methanol:H_2O, 36:576:564 v/v/v) acidified to pH 2.0. The funnel was again shaken and the layers were allowed to resolve as before. Replacement of the upper layer, shaking, and resolution was repeated a final time, after which the bottom organic layer was decanted, then evaporated to near dryness under a stream of N_2. The dry product was transferred to a tared glass vial, and the solvent was evaporated entirely. The residue was placed under vacuum over anhydrous $CaCl_2$ overnight to remove traces of solvent and H_2O before weighing.

Freshly-shed skins were weighed, cut into 1 cm^2 pieces, and immersed in $CHCl_3$:methanol 2:1 v/v using 40 ml of solvent for each 1.0 g of skin. The high volume to weight ratio of solvent to skin was necessary in order to completely immerse the skins. This mixture was sealed in an Ehrlenmeyer flask under N_2 and periodically agitated for at least 48 hours. The extracted pieces of skin were discarded and the solvent filtered through a pyrex sintered glass filter to remove small fragments of the remaining skin. The solvent was then extracted, evaporated, and weighed as above.

FRACTIONATION: COLUMN CHROMATOGRAPHY.—Lipid samples were fractionated using silicic acid column chromatography after Hirsch and Ahrens (1958). Clean chromatography columns with teflon stop-

cocks were packed with #50 mesh silicic acid (Chromosorb, Clarkson Chemical Company) using 60 times the weight of the extracted lipid. The silicic acid was activated at 110° C for 24 hours, mixed with technical grade petroleum hydrocarbon b/p. 60-80° C, and applied to the column as a slurry. A glass wool plug washed with $CHCl_3$:methanol 2:1 v/v prevented the slurry from washing off the column through the hole in the stopcock as the packing progressed. The column was charged by adding the lipid sample dissolved in 1 ml or less of hexane. The undissolved polar lipids had to be carefully washed onto the column with hexane in those samples with high phospholipid levels. The phospholipids remained undissolved at the head of the column until the more polar washes dissolved them. After charging, a small circle of washed Whatman filter paper, the size of the inside diameter of the column, was placed on the column head to prevent disturbance of the head during solvent changes.

Lipids were eluted from the column according to scheme B of Hirsch and Ahrens (1958). The hydrocarbons, wax esters, and cholesterol esters (fraction I) were eluted by 350 ml of 1% ethyl ether in hexane followed by 60 ml of ethyl ether. The neutral lipids (fraction II) were eluted by 300 ml of ethyl ether, and 200 ml of absolute methanol eluted the polar lipids (fraction III). Each of these fractions was collected in a clean 500 ml round-bottomed boiling flask and evaporated to complete dryness using a rotary evaporator. The lipids were transferred from the flasks with two washes of 1 ml hexane (fractions I and II) or 1 ml of absolute methanol (fraction III). The washes were pooled and collected in tared screw-cap vials with teflon cap liners and evaporated to dryness under a stream of N_2. The samples were further dried overnight under vacuum in a dessicator with anhydrous $CaCl_2$ to remove all traces of solvent. The fractions were then weighed.

The more complicated elution scheme A of Hirsch and Ahrens (1958) for separating the major classes was used in preliminary studies to help determine the solvent volumes necessary to elute the major classes of lipids. I determined that all polar lipids in all species of *Epicrates* were eluted from the column after adding only 200 ml of methanol, so this volume was used in subsequent fractionations. The large eluate volumes described above were used to fractionate lipid samples over 30 mg in weight. Columns were constructed using clean pipettes, prepared exactly like the larger columns, for smaller samples (usually under 20 mg) of lipid collected from individuals of the smaller species (e.g. *E. exsul, E. gracilis, E. fordii,* and *E. monensis*). The use of the small-bore columns allowed a better column height to packing-weight ratio and enhanced resolution of fraction I from fraction II lipids.

Although the ratio of column packing to lipid weight remained fixed for columns of all lengths, much smaller eluate volumes were possible with the smaller columns. Fraction I lipids were eluted using 100 ml of straight hexane, fraction II lipids were eluted with 100 ml of ethyl ether, and fraction III lipids were eluted with 100 ml of absolute methanol. Test mixtures of known weights of mixed lipid standards (2 mg cholesterol, 2 mg trimyristin, 2 mg palmitic acid, 2 mg cholesteryl palmitate and 2 mg phosphatidyl choline) resulted in virtually 100% recovery of the sample applied to the column.

THIN-LAYER CHROMATOGRAPHY.—Pre-activated commercially prepared thin-layer chromatography plates were used. One dimensional separations of fraction I and fraction II lipids were accomplished using Whatman LQ6DF plates in 19 channel 20 x 20 cm, and 4 channel 5 x 20 cm, sizes. Using a micropipette, 10-25 μl of 0.1-1.0% solutions of lipid samples were applied to the plates. Spot sizes were carefully controlled and not allowed to exceed 5 mm in diameter. Spots of lipid samples were dried under a stream of N_2 between applications and before the placement of plates in the developing tank. In general, the chromatographic techniques used were those suggested by Mangold (1961). Neutral lipid standards and fraction I and fraction II lipids were applied to the plates using hexane as the solvent. Polar lipid standards and fraction III lipids were applied using $CHCl_3$:methanol 1:1 v/v as the solvent. Whatman LK5DF 19 channel 20 x 20 cm plates were used for chromatography of polar lipids.

THE SOLVENT SYSTEMS.—Fraction I lipids were resolved using a solvent system of carbon tetrachloride:chloroform 96:4 v/v (Waldi, 1962). One dimensional separations of fraction II lipids were performed using a solvent system of hexane:diethyl ether:acetic acid 80:20:2 v/v/v. Fraction III lipids were resolved using a solvent system of chloroform:2-propanol:triethylamine:methanol:0.25% KCl 30:20:18:9:6 v/v/v/v/v (Touchstone et al., 1980).

Solvent depths in the developing tank were limited to 0.5 cm. Equilibrium of the liquid solvent with the vapor phase was achieved by pouring the solvent system over a piece of filter paper placed against one side of the tank. The tank was then closed and allowed to equilibrate for 5 minutes prior to the introduction of the plate. Plates were air-dried in a hood for 5 minutes after development, and then oven-dried at 100° C for an additional 5 minutes prior to visualization.

VISUALIZATION.—Plates were first viewed under ultraviolet light and the locations of fluorescing lipid spots noted. The plates were then exposed to iodine vapors to visualize unsaturated lipids (Mangold, 1961). The iodine was sublimed from the plates by placing them under a hood for 5 minutes, then into a drying oven at 100° C for an additional 5 minutes. The general detection system used for neutral lipids (fraction I and II) was 0.5% phosphomolybdic acid in isopropanol, and saturated $K_2Cr_2O_7$ in 50% sulphuric acid was used as a general detection reagent for polar lipids (fraction III).

Specialized detection systems were used for certain fractions. Cholesterol esters and cholesterol were detected in chromatograms of neutral lipid fractions by spraying them with Liebermann-Burchard reagent (30% H_2SO_4 in acetic anhydride) and heating in a drying oven at 100° C for 10 minutes. Rhodamine B, 0.05% in ethanol, was used to detect glycerides in neutral lipid fractions. After the initial spraying with the rhodamine B solution, the plates were allowed to sit for 3 minutes and then sprayed with 10N KOH to enhance the colors of the glyceride spots. Free fatty acids were localized in neutral lipid chromatograms with a spray of bromocresol green, 0.2% in N-butanol:aqueous acetic acid 95:5 v/v. Nitrogenous phospholipids were visualized in polar lipid chromatograms with a spray of ninhydrin solution 0.1% in 99.5% ethanol. After spraying, the chromatograms were assessed for differences in lipid patterns resulting from individual or geographic variation, and species differences.

All of the above detection reagents were purchased from Sigma Chemical Company, St. Louis, Missouri, as were the following lipid standards used during the thin-layer chromatography: cholesterol, cholesteryl arachidate, cholesteryl palmitate, cholesteryl acetate, palmitic acid, trimyristin, phosphatidyl glycerol, phosphatidyl inositol, phosphatidyl serine, lysolecithin, and sphingomyelin. Solvents used in the thin-layer chromatography were glass distilled and obtained from Burdick and Jackson Laboratories, Inc., Muskegon, Michigan.

LIPID VARIATION WITHIN SPECIES.—Only fall and summer samples were used to assess interspecific variation of lipids. Antillean *Epicrates* are more likely to be non-reproductive at these times. Variable intensities of the same lipid spots in different individuals strongly suggested that there were quantitative differences in certain lipids. Quantitative distinctions were not assessed because the systematic analysis rested on the qualitative differences of lipids in these snakes.

METHOD OF COMPARISON.—Interspecific comparisons were based on the relative R_fs of the lipid components extracted from each species. The R_f is a measure of the relative mobility of a lipid in a given solvent system.

$$R_f = \frac{\text{migration distance of lipid from origin}}{\text{migration distance of solvent front from origin}}$$

Use of R_f values as an index of mobility allowed me to standardize the data. Commercially prepared silica gel plates were used for the thin-layer chromatography to enhance reproducibility, but the R_f of a particular compound in a thin-layer system is dependent on a number of variables: purity of solvents, temperature, humidity, etc. (Mangold, 1961). As such, it was not realistic to expect constant R_f values for a particular compound for each and every chromatography run carried out during a study lasting several months. Because interspecific comparisons were carried out in a single run, however, differences in R_f values between species were due solely to phylogenetic differences in the mobility of the lipids, not the experimental conditions.

I compared 19 different samples in a single run using the Whatman plates. My sample size for species of *Epicrates* ranged from 4 specimens of *E. cenchria* to 21 specimens of *E. striatus*. I assessed individual variation in each species in a single run for any given solvent system. A representative sample was then chosen from this series and later chromatographed with the samples representing the other species. With this approach, I was able to compare lipid extracts from all the species of *Epicrates* in a single run. Moreover, the interspecific R_fs were truly comparable because the conditions during chromatography were the same. The only variables were the mobilities of the particular lipid compounds contained within the skin or scent gland extracts.

Samples from both males and females were utilized in the runs assessing individual variation. Summer and fall samples (June through November) were used for the species comparisons because variation due to reproductive state was less likely. Most *Epicrates* mate from December through May, although out-of-season matings occur occasionally in captive populations. Captive individuals were kept on light cycles and temperature regimes similar to those experienced by wild populations of Antillean *Epicrates*, and out of season mating behavior was not observed. Sexes were housed separately except for those individuals placed together for captive propagation.

While lipid characters did not present the problem of intraspecific variability associated with scale characters, there are other problems

TABLE 2
DETECTION REAGENTS USED IN THIN-LAYER CHROMATOGRAPHY

Reagent	Lipids Detected	Fraction
20% concentrated H_2SO_4 in acetic anhydride	Cholesterol and cholesterol esters	Fractions I and II
0.5% phosphomolybdic acid in isopropanol	Neutral lipids	Fractions I and II
0.1% bromcresol green in 99.5% ethanol	Free fatty acids	Fraction II
Saturated $K_2Cr_2O_7$ in 50% H_2SO_4	Polar lipids	Fraction III
0.2% ninhydrin in N-butanol-acetic acid 10% 95:5 v/v	Aminophosphatides	Fraction III
2 mg/ml orcinol in H_2SO_4-H_2O 3:1 v/v	Glycolipids	Fraction III
Iodine vapors	Unsaturated lipids	All Fractions
0.05% rhodamine B in 96% ethanol	Glycerides	Fraction II

involved with their use. In most molecular systematic studies, comparisons are made on the basis of primary gene products, e.g. enzymes or other proteins or gene sequences corresponding to lengths of DNA. In the case of lipid comparisons, I had to deal with the absence or presence of a secondary product which may be the result of several enzymes acting in concert. In this regard, lipids are like morphological characters—they are the result of many different biochemical reactions involving numerous unknown enzymatic participants.

A major criticism of electrophoretic studies is that the patterns produced may have hidden heterogeneity (Johnson, 1977). Electrophoretic bands with the same migration rate in an electric field may be different molecular entities, distinguishable only by more complicated methods of analysis like isoelectric focusing. The most tenuous assumption made in this study is that lipid compounds with identical R_fs are the same. For purposes of my analysis, the assumption is conditional on: (1) there being no differences in mobility when compared in several different solvent systems, and (2) their reactions being identical with the various indicators used. Table 2 lists the solvent systems and

the indicators employed in these comparisons. Lipid pattern analysis might be subject to criticism, as the lipid bands with the same R_f on a thin-layer chromatogram are assumed to represent the same type of lipid. I tried to detect hidden heterogeneity in the chromatograms by utilizing several solvent systems of widely different polarities on the same lipid samples and watching for changes in the number of lipid bands. This, plus the use of two-dimensional chromatography and numerous different indicator systems, has allowed me to be fairly certain that my comparisons were free of major undetectable variation or heterogeneity.

Although a greater level of resolution could have been obtained with the use of a coupled gas-liquid chomatography-mass spectrometry system, this process would have been far too time-consuming and costly given the large number of lipid samples processed. It would be analogous to a systematic study which utilized protein sequencing for several different proteins or enzymes.

CHARACTER CODING

The chromatograms of lipids from all species of *Epicrates* were examined and compared to each other and to those in the sister genus *Corallus*. Differences in lipid composition were reflected in the presence or absence of lipid bands at a particular R_f in a given chromatography system.

Once the presence or absence of a particular lipid was verified for a given species, the lipid characters were given a binary value—0 if the character state was considered primitive, and 1 if derived.

Character state polarity was deduced using the outgroup comparison (Wiley, 1981). The boine genus *Corallus* was chosen as the outgroup because independent studies by Underwood (1970) and Hoffstetter and Rage (1972) established that *Corallus* and *Epicrates* share a more recent common ancestor than either does with any other boid. After I had analyzed the lipids of a number of different boids, including *Acrantophis, Boa,* and *Corallus,* it became apparent that the Antillean *Epicrates* had undergone a considerable amount of evolution in scent gland lipids. While other boine genera, like *Boa* and *Corallus,* have relatively few lipid components in their scent gland lipids, Antillean *Epicrates* may have upwards of 20 different components. The continental *E. cenchria,* like most other boines, has few lipid components in its scent gland secretion. With few exceptions, such as cholesterol or phosphatidyl choline, the primitive condition of a particular lipid

character was absence of that component from the extract. It seems certain that new or different lipids were added to the scent gland secretion as the species evolved on the islands. Thus, the presence of a lipid band shared by two or more species of *Epicrates,* but not the sister group, was considered a synapomorphy. It was not possible to trace a transformation series of lipid characters such as state 0 to state 1 to state 2, and the primitive or derived designations were based only on the presence or absence of a lipid band at a particular R_f.

Scale data were taken from Sheplan and Schwartz (1974). Following them, I used modal species values as the states of each scale character. Scale characters, like lipid characters, were recoded in binary form, 0 representing the primitive condition and 1 the derived condition (Table 3). *Corallus* was used as the outgroup.

DELETION OF VARIABLE CHARACTERS

Characters with high intraspecific variability were deleted; they included a series of presumed wax esters from skin that was extremely variable in all species examined and a lipid band running at the same R_f as lysolecithin in the polar lipid fraction of skin extracts. At least some individuals of all species of *Epicrates* possessed this band.

I considered three of the characters used by Sheplan and Schwartz (1974) too variable for use in my phylogenetic analysis. They were either bimodal or had significant interspecific overlap. They included: (1) scales in the circumorbital series; 8-10 in *E. angulifer* with bimodes of 8 and 9; 8-14 in *E. striatus* with bimodes of 9 and 10; 9-13 in *E. chrysogaster* with modes of 10, 11, 12, and 13; 7-10 in *E. inornatus* with a mode of 8; 10-12 in *E. monensis* with a mode of 11; 8-13 in *E. fordii* with a mode of 10; 9-14 in *E. gracilis* with a mode of 11; 10-11 in *E. exsul* with a mode of 10; (2) number of loreals; 1-3 in *E. fordii* with a mode of 2; 1-2 in *E. exsul, E. monensis, E. gracilis,* and *E. inornatus* with a mode of 1; 1-2 in *E. chrysogaster* with a mode of 2; (3) number of ventrals; 271-292 in *E. angulifer,* 266-299 in *E. striatus,* 245-275 in *E. chrysogaster,* 258-273 in *E. inornatus,* 261-296 in *E. monensis,* 231-261 in *E. fordii,* 271-304 in *E. gracilis,* 305-326 in *E. exsul.*

TABLE 3
DATA MATRIX[a]

Character	COR	CEN	ANG	STR	CHR	EXS	SUB	INO	MON	FOR	GRA
						Lipids					
1	0	1	1	1	1	1	1	1	1	1	1
2	0	0	1	1	1	1	1	1	1	1	1
3	0	0	1	1	1	1	1	1	1	1	1
4	0	0	0	0	1	1	0	0	0	0	0
5	0	0	0	0	1	1	0	0	0	0	0
6	0	0	0	1	0	0	0	0	0	1	0
7	0	0	0	0	1	0	1	1	1	1	1
8	0	0	1	1	1	1	1	1	1	1	1
9	0	0	0	0	0	0	0	0	1	1	0
10	0	0	0	0	0	0	0	0	1	1	1
11	0	0	0	0	0	0	0	0	1	1	1
12	0	0	0	0	0	0	0	0	1	1	1
13	0	0	0	0	0	0	1	1	0	0	0
14	0	0	1	1	1	1	1	1	1	1	1
15	0	0	0	0	0	0	0	1	1	1	1
16	0	0	0	0	0	0	0	0	1	1	1
17	0	0	0	0	0	0	0	0	1	1	1
18	0	0	0	1	1	1	1	1	1	1	1
19	0	0	0	1	1	1	1	1	1	1	1
20	0	0	0	1	0	0	0	0	1	1	0
21	0	0	0	0	1	1	0	0	0	0	0
22	0	0	0	0	1	1	0	0	0	0	0
23	0	0	0	0	1	1	0	0	0	0	0
24	0	0	0	0	1	1	0	0	0	0	0
						Morphology					
25	0	0	0	1	1	1	1	1	1	1	1
26	0	0	0	0	0	0	0	0	1	1	0
27	0	0	0	0	0	0	0	0	1	1	1
28	0	0	0	1	1	1	1	1	1	1	1
29	0	0	0	0	1	1	1	1	1	1	1
30	0	0	0	1	1	1	2	2	2	2	2
31	0	0	0	0	1	1	1	1	1	1	1
32	0	0	0	0	0	0	1	1	0	0	0
33	0	0	0	0	1	1	1	1	1	1	1

[a] 0 = primitive, 1 = derived, 2 = derived from 1.

DESCRIPTION AND SCORING OF CHARACTERS

Lipids

1. Skin diglyceride, 80:20:2. 0 = absent; 1 = present.
2. Skin free fatty acid, 80:20:2. 0 = absent; 1 = present.
3. Skin free fatty acid, 80:20:2. 0 = present; 1 = absent.
4. Skin neutral, 96:4. 0 = absent; 1 = present.
5. Skin neutral, 96:4. 0 = absent; 1 = present.
6. Skin neutral, 96:4. 0 = absent; 1 = present.
7. Skin neutral, 96:4. 0 = present; 1 = absent.
8. Skin polar, 30:20:18:9:6. 0 = absent; 1 = present.
9. Skin polar, 30:20:18:9:6. 0 = absent; 1 = present.
10. Scent free fatty acid, 80:20:2. 0 = present; 1 = absent.
11. Scent free fatty acid, 80:20:2. 0 = absent; 1 = present.
12. Scent neutral, 80:20:2. 0 = present; 1 = absent.
13. Scent neutral, 80:20:2. 0 = absent; 1 = present.
14. Scent neutral, 80:20:2. 0 = absent; 1 = present.
15. Scent neutral, 80:20:2. 0 = absent; 1 = present.
16. Scent neutral fluorescent, 96:4. 0 = absent; 1 = present.
17. Scent neutral fluorescent, 96:4. 0 = absent; 1 = present.
18. Scent polar, 30:20:18:9:6. 0 = absent; 1 = present.
19. Scent polar, 30:20:18:9:6. 0 = absent; 1 = present.
20. Scent polar, 30:20:18:9:6. 0 = absent; 1 = present.
21. Scent polar, 30:20:18:9:6. 0 = present; 1 = absent.
22. Scent polar, 30:20:18:9:6. 0 = absent; 1 = present.
23. Scent polar, 30:20:18:9:6. 0 = present; 1 = absent.
24. Scent polar, 30:20:18:9:6. 0 = absent; 1 = present.

Morphology

25. Labial pits. 0 = present; 1 = absent.
26. Juvenile coloration. 0 = reddish or orange-brown; 1 = gray or gray-brown.
27. Adult snout-vent length. 0 = greater than 1 m; 1 = less than 1 m.
28. Number of subcaudal scales. 0 = fewer than 55; 1 = greater than 75.
29. Lorilabial scale row. 0 = present; 1 = absent.
30. Modal number of intersupraocular scales. 0 = 3 or greater; 1 = 2; 2 = 1.
31. Number of scale rows at midbody. 0 = greater than 50 rows; 1 = fewer than 50 rows.

32. Modal number of supralabial scales. 0 = greater than 12; 1 = fewer than 12.
33. Modal number of infralabial scales. 0 = greater than 16; 1 = fewer than 16.

PHYLOGENETIC INFERENCE

I analyzed the above data set with a computerized Wagner tree algorithm, WAGNER 78 (Farris, 1970). That Wagner tree algorithm was used to formulate a phylogenetic hypothesis because it accepts ordered character states, produces a best fit to all data, makes no assumptions about evolutionary rates, and allows character state reversals. The *Epicrates* cladogram provided by WAGNER 78 formed the basis for examining Rosen's (1975) vicariance model of the Greater Antilles. The data were run later through D.L. Swofford's PAUP (Phylogenetic Analysis Using Parsimony) version 2.3, using the branch and bound option, a method implementing the Hendy-Penny (1982) algorithm for finding shortest trees. Only one tree—the same tree generated by WAGNER 78—was found.

RESULTS

Neutral Skin Lipids

Thin-Layer Chromatography.—Thin-layer chromatography revealed an apparent lack of cholesterol esters in the skin of every species of boid examined. The three cholesterol ester standards, cholesteryl acetate, cholesteryl arachidate, and cholesteryl palmitate, were visualized easily with the Leibermann-Burchard reagent. Usually 400 μg of lipid was spotted per lane. When no skin cholesterol esters were visualized the sample was increased to 800 μg per lane with the same results. In control runs, 10 μg of standard showed up very strongly.

Roberts and Lillywhite (1980) reported that cholesterol esters were present in chloroform-methanol 2:1 v/v extracts from the skin of the black rat snake, *Elaphe obsoleta,* but they did not state how the presence of these compounds was confirmed. They used a solvent system for their thin-layer chromatography similar to mine—hexane: diethyl ether:formic acid 80:20:2 versus my system of hexane:diethyl ether:acetic acid 80:20:2 v/v/v. My wax ester standard, palmitoyl arachidate, ran with the same mobility as cholesteryl palmitate in this system.

SPECIES DIFFERENCES.—The neutral skin lipids were remarkably similar in all species of *Epicrates* (Figs. 9-10). In the 80:20:2 system, each species had a large amount of cholesterol present and a large diglyceride component running at an R_f only slightly lower than that of cholesterol. There were also significant amounts of free fatty acids in these fractions. Four bands appeared at R_fs .133, .169, .197, and .225 in Antillean *Epicrates* and .133, .186, .197, and .225 in *E. cenchria* and *Corallus*. This was the only significant difference between any of the *Epicrates* in this system, but it was clear cut and not subject to individual variation. All *Epicrates* and *Corallus* had a band at R_f .408, running just below the triglyceride standard. A glyceride running at .126 was present in all *Epicrates,* but absent in *Corallus.*

Faster-running neutrals in the 96:4 system showed more differences. Significant lipids in this system ran between a band of wax esters at R_f .966 and the cholesterol standard. The wax esters ran above the cholesterol ester standards of cholesteryl arachidate and cholesteryl palmitate and the wax ester standard of palmitoyl arachidate. I predict that they are probably long chain branched waxes, given the relative mobilities of these compounds. No doubt gas-liquid chromatography and mass spectrometry would resolve their identity. A number of unidentified lipids also ran immediately below the cholesteryl palmitate standard. These compounds were present in all species of *Epicrates* and *Corallus* and are probably integumentary waxes.

Epicrates striatus had a band at R_f .392 and *E. fordii* had one at R_f .379. Differences in the mobilities of these compounds were considered to be due to edge effects. Significantly, *E. exsul* and *E. cenchria* shared two bands, one at R_f .301 and another at R_f .353. These bands were not present in any other species. The bands described for *E. fordii* and *E. striatus* were absent in all the other species examined. *Epicrates cenchria, E. angulifer,* and *E. striatus* had very similar bands at approximately R_f .638; *E. fordii* at .587; *E. gracilis* at .571; *E. subflavus, E. monensis,* and *E. inornatus* at .539, and *E. exsul* at .569. These bands were so diffuse that the calculated R_fs are very questionable. They were not used as characters.

INDIVIDUAL VARIATION.—Although the bands in the 80:20:2 system did not reveal many uniquely derived character states, they were the most invariant lipid components within any species studied. I detected no chromatographic differences between individuals of any species analyzed.

The most significant individual variation occurred in *E. striatus* in the 80:20:2 system. Four individuals, PJT STR 013, 014, 017, and 026, lacked lipid bands at R_f .337 and .387. These were present in all of the

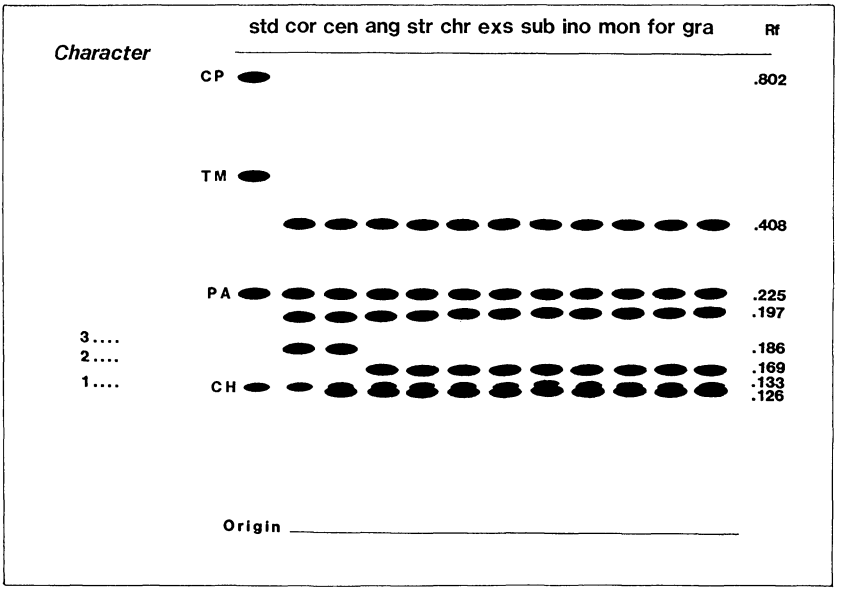

FIG. 9. Schematic representation of thin-layer chromatogram illustrating species comparisons of skin neutral lipids, 80:20:2 system. For abbreviations, see Materials and Methods section.

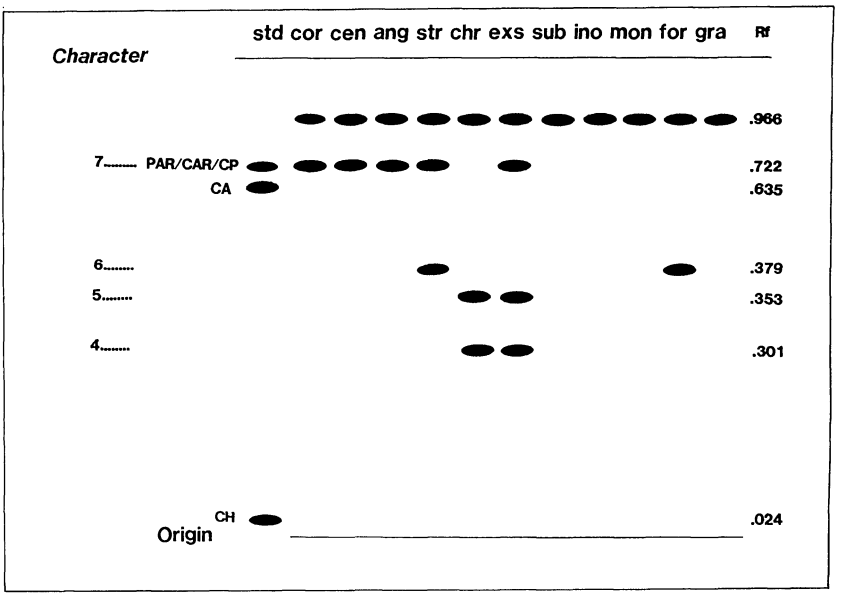

FIG. 10. Schematic representation of thin-layer chromatogram illustrating species comparisons of skin neutral lipids, 96:4 system. For abbreviations, see Materials and Methods section.

other *E. striatus* examined. Individuals STR 013 and 014 are *E. s. fosteri* from Bimini, Bahamas. The other *E. striatus*, including 017 and 026, were all the nominate form from Hispaniola. Variation in *E. striatus* is shown in Fig. 11.

Qualitatively, *E. exsul* and *E. cenchria* do not vary intraspecifically, but the densities of certain lipid bands at R_f .337 and .387 tend to differ between individuals of these species. Individual variation was not detectable in the other species. I faced one problem evaluating lipids running in the 96:4 system. The bands tended to be more diffuse than the tight bands produced by the other systems. This may indicate that several different lipids make up one band on the chromatogram, or that there may be some degradation of these lipids. In any case, while the bands were diffuse, the R_fs were essentially the same within any given species. These characters were not used as data for phylogenetic inference.

Polar Skin Lipids

Species Differences.—Skin polar lipids were the least informative of any of the lipids chromatographed. All boid species analyzed had at least six lipid bands running below the cholesterol standard (Fig. 11). All species had two bands with R_fs identical to those of phosphatidyl choline (PC) and sphingomyelin (SPH), which ran at R_fs .312 and .223, respectively. A third band ran between these two standards at R_f .255. A fourth band ran slightly below the phosphatidyl ethanolamine (PE) standard at R_f .484. All species had two bands running slightly below the solvent front close to phosphatidyl glycerol (PG), one at the same R_f of .841, and another about 1 cm below at .828. *Epicrates monensis* and *E. fordii* shared a unique band at R_f .529 between PE and PI. *Epicrates cenchria* lacked a band between PC and SPH.

Seasonal variation occurred in a single polar lipid component in *E. angulifer, E. cenchria, E. exsul,* and *E. striatus*. This lipid, running at R_f .255, was present in winter and spring samples taken from these species. This is immediately prior to and including the mating season. The chromatography runs were made at different times, with different solvent lots and with zero sample control lanes. I doubt that they are artifacts. A puzzling feature of this lipid is that the seasonal changes occurred in both males and females. The significance of this variation is completely unknown; it may be significant in some aspect of courtship or reproduction.

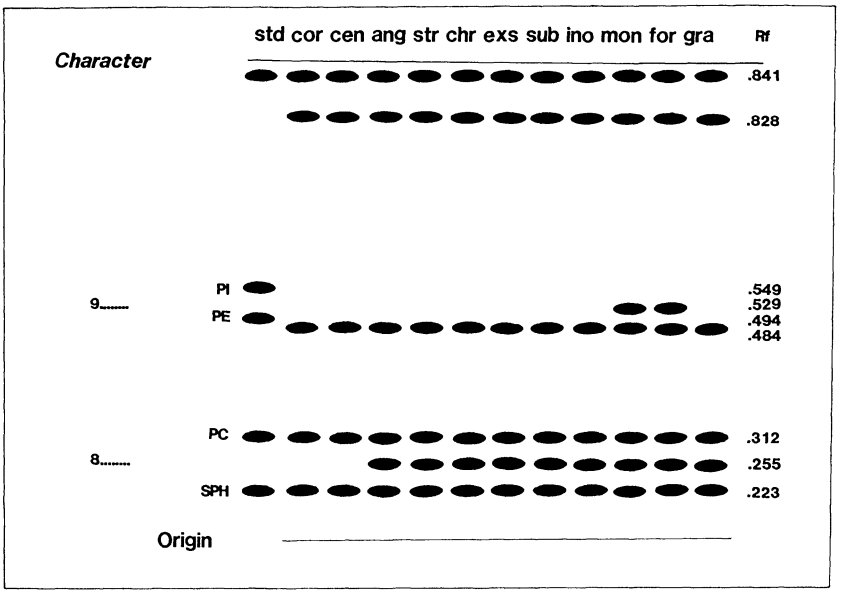

FIG. 11. Schematic representation of thin-layer chromatogram illustrating species comparisons of skin polar lipids. For abbreviations, see Materials and Methods section.

INDIVIDUAL VARIATION.—There was no detectable individual variation in any of the *E. cenchria* examined for these lipids. *Epicrates angulifer* was free of qualitative differences but ANG 036 had a stronger band at R_f .798 than at .761. The reverse was true for the other individuals of *E. angulifer* examined. The most significant variation in *E. chrysogaster, E. exsul,* and *E. striatus* also occurred near the solvent front. STR 021 and 026 had a strong band at R_f .728 that was lacking in the other *E. striatus.* This band was present in three individuals of *E. exsul* (044, 045, and 046). It also appeared to be absent in *E. chrysogaster.* INO 285, 212, and 276 had a band at R_f .207 which was absent in the other individuals of *E. inornatus,* and INO 824 and 827 lacked the band at R_f .123 which was present in all other *E. inornatus.* Specimens SUB 422 and 424 possessed an extra band at R_f .239 which was absent in other *E. subflavus.* No variation was observed in the species of *Corallus* examined, but only small sample sizes were available.

Neutral Scent Gland Lipids

Thin-Layer Chromatography.—In contrast to the skin lipids, there was even less individual variation and greater species differences in the lipids extracted from scent glands. In the 80:20:2 system, *Corallus* and all the *Epicrates* shared a band at R_f .379, which proved to be cholesterol. *Epicrates angulifer, E. striatus, E. chrysogaster, E. exsul, E. inornatus,* and *E. subflavus* shared two bands with *E. cenchria* and *Corallus* at R_fs .458 and .541. This band was absent in *E. fordii, E. gracilis,* and *E. monensis,* but these species had a shared lipid which ran at .515. All the Antillean species shared a band at R_f .754. *Epicrates inornatus* and *E. striatus* had a unique band at R_f .581. All *Epicrates* and *Corallus* also shared bands at .936 and .980. *Epicrates inornatus, E. fordii,* E. *gracilis,* and *E. monensis* shared a band at an approximate R_f of .854. This band was very diffuse and only present when the sample lipid charge exceeded 800 μg. Its use may be questionable. The patterns described above are illustrated in schematic form in Fig. 12.

In the 96:4 system, no major differences were apparent among the Antillean *Epicrates* with phosphomolybdic acid as the detection reagent (there were over ten bands shared by all species between R_f .284 and .529). When the chromatogram was viewed under ultraviolet light, however, *E. fordii, E. gracilis,* and *E. monensis* were found to share two brightly fluorescing yellow bands at R_fs .153 and .822 (Fig. 13). *Epicrates exsul* possessed yellow fluorescing bands at R_fs .242, .287, and .796. These bands were considered apomorphies but further analytical work may change this assessment. *Epicrates striatus* possessed a single fluorescent band at R_f 1.0. All species of *Epicrates* shared three non-fluorescent bands in this system with R_fs of .790, .879, and .924, significantly above the cholesteryl palmitate and cholesteryl arachidate standards which ran at R_fs of .605 and .631, respectively. These bands are not illustrated.

Individual Variation.—Lipids were without variation within the larger species in the 80:20:2 system. I could find no significant variation in *E. cenchria, E. angulifer, E. chrysogaster, E. exsul, E. inornatus, E. striatus,* and *E. subflavus.* There was some variation in *E. fordii, E. monensis,* and *E. gracilis.* Specimen FOR 032 lacked the two bands at R_f .371 and .475 that surfaced in the other *E. fordii.* Most *E. gracilis* had bands at R_fs .438, .475, .481, and .881. The bands at R_fs .475 and .881 were absent in the sample from GRA 017. Bands at R_fs .438 and .481 were absent in the sample from GRA 022. Bands at R_fs .400 and .500, present in most *E. monensis,* were not visible in the chromatogram of MON 053.

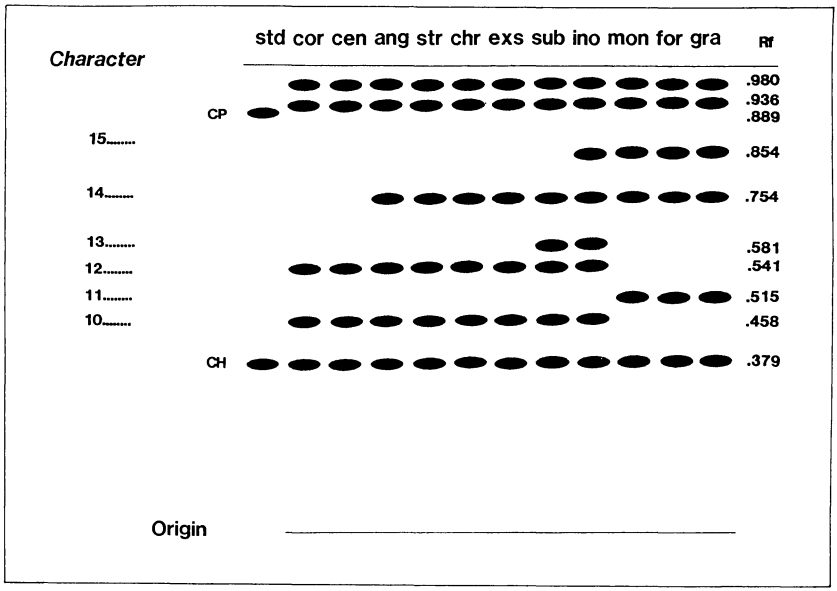

FIG. 12. Schematic representation of thin-layer chromatogram illustrating species comparisons of scent gland neutral lipids, 80:20:2 system. For abbreviations, see Materials and Methods section.

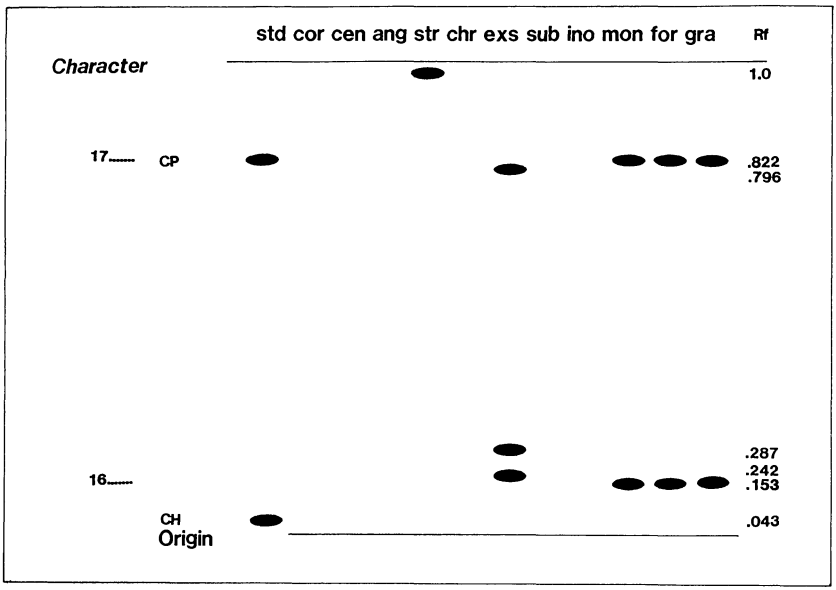

FIG. 13. Schematic illustration of thin-layer chromatogram illustrating species comparisons of scent gland neutral lipids, 96:4 system. For abbreviations, see Materials and Methods section.

Like 80:20:2, the 96:4 system showed no significant variation with any given species of *Epicrates*. Some variation was present in *E. subflavus*. Specimens SUB 737, 738, and 740 lacked a band running at the same R_f as the cholesteryl palmitate standard (R_f .583), while SUB 003, 095, and 290 possessed a band at this R_f. Individual *E. inornatus* showed no variation in this system. No band was found in FOR 030 at R_f .460. This may be a qualitative difference; all other *E. fordii* had a band at this R_f. Specimens GRA 019 and 022 had a band running just below the solvent front at R_f .798. This band was absent in the sample from GRA 022, while GRA 017 did not have the R_f .908 band found in the other *E. gracilis*. Specimen MON 054 had a band at R_f .908 as well, but it was not visible in chromatograms of the other *E. monensis*. No variation was detectable in *Acrantophis*, *E. cenchria*, or *Corallus*; they had few scent gland lipids to begin with.

Polar Scent Gland Lipids

Species Differences.—While skin lipids lacked cholesterol esters, the scent gland lipids had low levels of polar components. To adequately visualize polar scent gland lipids, 800 μg of sample had to be spotted in each lane. Despite the relatively low concentrations of certain components, these characters were often highly informative.

The Antillean *Epicrates*, exclusive of *E. angulifer*, shared two bands at R_fs .201 and .223 in the polar lipid fractions. The upper band is probably PC; the lower ran just above the SPH standard at R_f .145. *Epicrates striatus*, *E. monensis*, and *E. fordii* shared a band at R_f .440, just between the PE and PI standards which ran at R_fs of .497 and .403, respectively. *Corallus* and all species of *Epicrates*, exclusive of *E. exsul* and *E. cenchria*, had bands at R_f .679 and .780. The bands shared by *E. exsul* and *E. cenchria* at R_fs .704 and .793 are probably similar compounds. These differences are illustrated in Fig. 14.

Individual Variation.—No detectable differences were found in individuals of *E. angulifer*, *E. inornatus*, *E. gracilis*, *E. monensis*, or *E. subflavus*. Virtually no individual variation was evident in the specimens of *E. exsul* and *E. striatus* examined. Specimen CHR 296 had no bands at R_fs .115, .127, and .248. This was probably a quantitative difference from other *E. chrysogaster*. Specimen FOR 030 did not have the bands at R_fs .537 and .568 found in the other *E. fordii* examined. Individual samples from all three species of *Corallus* were indistinguishable.

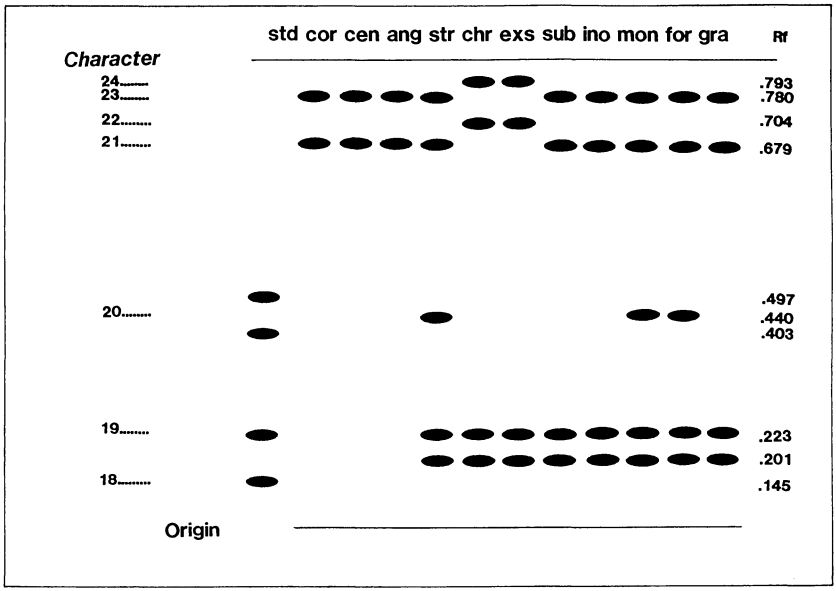

FIG. 14. Schematic representation of thin-layer chromatogram illustrating species comparisons of scent gland polar lipids. For abbreviations, see Materials and Methods section.

DISCUSSION AND SUMMARY

Thin-layer chromatography of lipids from skin and scent gland extracts showed that there was little individual variation in the samples tested, and furthermore, that there were trenchant species differences when several members of the genus were compared. These findings corroborated Oldak's (1976) conclusions that patterns produced by thin-layer chromatography of scent gland secretion lipids were species-specific (for several taxa of colubrid snakes) and that these patterns were not subject to much individual variation.

Well-corroborated monophyletic groups within *Epicrates* can be discerned with congruent scent gland synapomorphies. In contrast, the skin lipids were extremely similar in all the species studied. Sex differences were not apparent. Probably, the level of resolution is not high enough in thin-layer chromatography to resolve sex differences. I interpret the similarities in skin lipid makeup to be a reflection of the importance of these compounds in slowing evaporative water loss. The same classes of lipids which were extracted from skins of *Epicrates* were

present in *Elaphe obsoleta,* and they are know to decrease water loss (Roberts and Lillywhite, 1980). This may explain the high phospholipid content of skin. Cholesterol is another common membrane component found in the skin lipid extracts. The importance of the triglycerides and free fatty acids is unknown. The seasonal differences found in the polar lipids of the large *Epicrates* may provide a prospective mate with sensory information on reproductive condition. Both sexes undergo phospholipid changes with the onset of the breeding season.

The fact that the species of *Corallus* and *E. cenchria* show few lipid components in their scent gland secretions suggests the Antillean *Epicrates* (and possibly their continental ancestors) evolved the capability of synthesizing large amounts of widely divergent lipid species in their scent glands. The behavior of the Antillean species when captured leaves little doubt that the scent glands play a major role in defense. When grasped, a snake will coil in such a way that it is possible for the tail to spread the expelled waxy secretion over large portions of the snake's body. The secretion is often combined with uric acid and runny mucous excretions expelled from the cloaca. Captive individuals that are not often handled usually expel musk when any attempt is made to restrain them, no matter how gentle. Fractionation of this secretion showed large amounts of free and esterified unsaturated fatty acids. After exposing the developed chromatograms to iodine vapors, it was discovered that nearly every lipid class had at least some unsaturated fatty acids. The unsaturated fatty acids rancidified quickly after exposure to air. These compounds are toxic and have an unpleasant odor, and they may decrease palatability of *Epicrates* to potential predators. The waxy consistency of the secretion prevents it from being easily removed from a surface upon which it has been spread.

These types of defensive compounds might be expected to exhibit a great degree of parallelism, especially in island forms occupying similar habitats and presumably exposed to the same types of predators. Wax esters, triglycerides, diglycerides, monoglycerides, cholesterol, free fatty acids, and phosphatides are present in all individuals. Species do differ, however, in the chain length and degree of unsaturation of the fatty acid moieties of esterified lipids. Perhaps as these species of *Epicrates* evolved in isolation, there was a fine-tuning of the scent gland products to match the predators encountered. Why certain classes of compounds are found within this secretion is unknown. The presence of cholesterol, for example, may be due to a role as a precursor

to cholesterol esters. Scent gland secretions may also play a role in species or sex recognition. Huff (1979) reported that male *Epicrates* engaging in combat release musk. I have seen this phenomenon only once—in a combat encounter between two male *E. inornatus*. Scent trails left by individuals could also be helpful in finding prospective mates in a widely scattered population.

THE CLADOGRAM

The phylogenetic hypotheses illustrated in Figs. 15 and 16 were produced from an analysis of the lipid and morphological data sets, respectively (Table 3). The lipid cladogram has a total length of 28; there are four extra steps (homoplasies) and the consistency index is .86. The morphology hypothesis (Fig. 16) has a total length of 10, there are no extra steps, and its consistency index of 1.0 reflects a perfect fit to data. These two hypotheses are perfectly consistent, and the lipid data resolved the two trichotomies on the morphology cladogram. The lipid and morphological data were combined and analyzed as a single data set to produce the cladogram illustrated in Fig. 17.

ROBUSTNESS OF THE CLADOGRAM

The cladogram (Fig. 17) is quite robust. The total length of the tree is 38, there are only four extra steps predicted, and the consistency index is .895. Almost all branching points within the West Indian species of the genus are corroborated by at least two synapomorphies, and seven of the nine monophyletic groups are diagnosed by both lipid and morphological characters. In one of those two cases where no morphological characters reinforced determination of branching points, four lipid synapomorphies diagnose the group. The following are particularly strongly supported monophyletic groups: the Antillean + Bahamian species (diagnosed by characters 2, 3, 8, and 14), the Antillean + Bahamian species, exclusive of *Epicrates angulifer* (characters 18, 19, 25, 28, and 30), the Bahamian endemics, *E. exsul* and *E. chrysogaster,* (characters 4, 5, 21, 22, 23, and 24), and the small *Epicrates, E. fordii, E. gracilis,* and *E. monensis,* (characters 10, 11, 12, 16, 17, and 27). The *E. inornatus—E. subflavus* sister species relationship is only weakly corroborated.

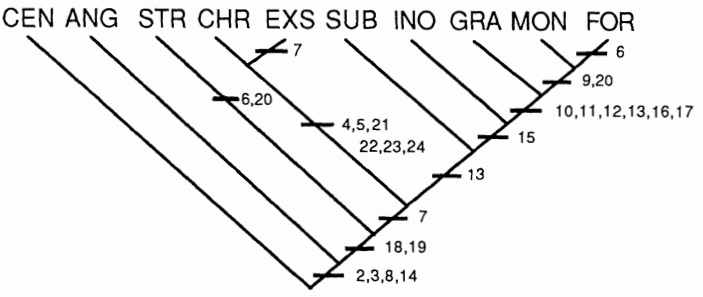

FIG. 15. The best-fitting cladogram based on the lipid data, using WAGNER 78. Characters 7 and 13 show hypothesized reversals; characters 6 and 20 are hypothesized parallelisms. For abbreviations, see Materials and Methods section.

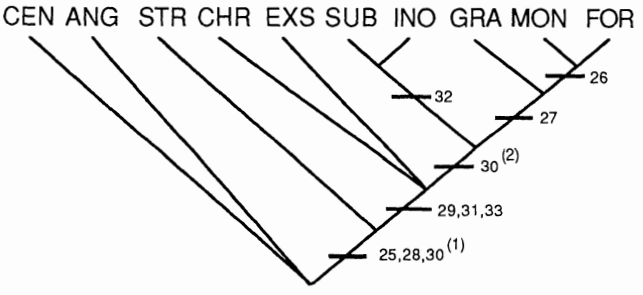

FIG. 16. The best-fitting cladogram based on the morphological data, using WAGNER 78. Superscripts represent states of the multi-state character. For abbreviations, see Materials and Methods section.

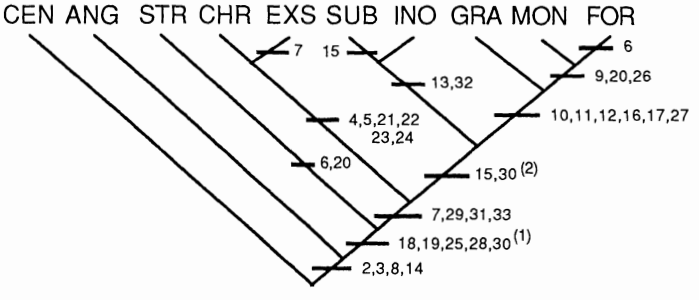

FIG. 17. The best-fitting cladogram based on the lipid and morphological data combined, using WAGNER 78 and PAUP. Superscripts represent states of the multi-state character. Characters 7 and 15 show hypothesized reversals; characters 6 and 20 are hypothesized parallelisms. For abbreviations, see Materials and Methods section.

HOMOPLASY

Homoplasy is predicted for only four lipid characters in the cladogram (Fig. 17): 6, 7, 15, and 20. Characters 7 and 15 are hypothesized reversals, characters 6 and 20 parallelisms. No homoplastic characters appear to be present in the morphological data set, but it must be remembered that several scale characters used by Sheplan and Schwartz were discarded from my analysis because they were highly variable. Had the variable characters been included, I am sure that some morphological homoplasies would have been predicted.

CONGRUENCE AMONG PHYLOGENETIC HYPOTHESES

No phylogenetic hypotheses were proposed for *Epicrates* prior to Sheplan and Schwartz (1974), but several associations within the genus were implied by taxonomic revisions. For example, Amaral (1929) synonymized *E. striatus* with *E. angulifer, E. monensis* with *E. fordii,* and *E. subflavus* with *E. inornatus.* Stull (1935) considered *E. monensis* a subspecies of *E. gracilis, E. chrysogaster* a subspecies of *E. striatus,* and *E. fordii* and *E. inornatus granti* (now synonymized with *E. monensis*) subspecies of *E. inornatus.* There was little or no rationale given for these taxonomic manipulations and they will not be mentioned further.

Sheplan and Schwartz (1974:122-127) were the first to present a phylogeny for *Epicrates* reasoned directly from empirical observations, and I have corroborated many of their hypothesized species associations with the lipid data (Fig. 15). Specifically (1974:122), they postulated that Antillean *Epicrates* were derived from a population of *E. cenchria* in Central America. On page 123 they stated "... it is fairly certain that *Epicrates angulifer* is the basic stock for West Indian *Epicrates.*" Later, on the same page, they elaborated further: "Assuming that *Epicrates angulifer* is the primitive Antillean member of the genus, we derive two series of large species from it: *inornatus-subflavus* and *striatus-chrysogaster.*" These statements imply that Antillean *Epicrates* form a monophyletic group: however, that seems to be contradicted when one reads on (p. 124): "... we interpret *subflavus* as an early insular invader from the mainland, which later dispersed to Puerto Rico (with differentiation there) but did not reach Hispaniola. The alternative explanation, that *subflavus and inornatus are independent derivatives of angulifer* [italics mine] seem less reasonable." In view of these conflicting statements, I have represented *E. angulifer, E.*

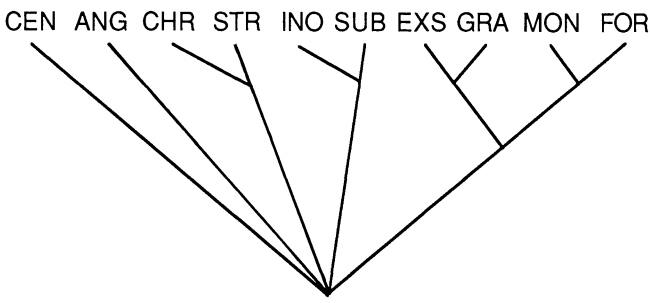

FIG. 18. The phylogenetic hypothesis of Sheplan and Schwartz (1974). For abbreviations, see Materials and Methods section.

cenchria, E. striatus + *E. chrysogaster,* and *E. inornatus* + *E. subflavus* relationships as an unresolved polychotomy (Fig. 18). *Epicrates exsul, E. fordii, E. gracilis,* and *E. monensis* are interpreted as "an old sidebranch of *Epicrates,* specializing in small size and arboreality" (p. 126). *Epicrates exsul* and *E. gracilis* are hypothesized to "represent one line of smaller boa radiation" while "*monensis* and *fordii* represent another" (p. 127)—all sharing a common ancestor sometime in their history. The cladogram in Fig. 18 conveys the essence of Sheplan's and Schwartz's conclusions.

There are several branching points common to the phylogenetic hypothesis of Sheplan and Schwartz (1974) and the cladogram presented here as Fig. 17. *Epicrates angulifer* appears as an early offshoot from an ancestral Central American stock in both cases, and both lipid and morphological data corroborate the existence of an *E. inornatus* + *E. subflavus* monophyletic group. The *E. monensis* + *E. fordii* association appears to be confirmed; so is the common ancestry between those two species and *E. gracilis.*

Two major differences exist between my cladogram (Fig. 17) and the hypothesis of Sheplan and Schwartz (1974) (Fig. 18). My analysis groups *E. exsul* with *E. chrysogaster,* not *E. gracilis.* I view *E. exsul* and *E. chrysogaster* as an early radiation of Bahamian *Epicrates,* evolved from an ancient Hispaniolan stock which ultimately gave rise to *E. inornatus, E. subflavus, E. striatus,* and the small *Epicrates* (*E. fordii, E. gracilis,* and *E. monensis*) as well. I also hypothesize that the Antillean species are the result of a single stock which dispersed or vicariated from the mainland. Aside from these few differences, the consistency between Figs. 17 and 18 is remarkable.

I conclude that *Epicrates* is a monophyletic group. Aside from lipid character 1, the genus is weakly defined osteologically by the arrange-

ment of the prefrontal bones (Boulenger, 1893), but stands out from the other boines in general habitus and coloration. They are not nearly as laterally compressed as *Corallus* nor as stout as *Acrantophis, Boa,* and *Eunectes.* Nested within *Epicrates* is another large monophyletic group—the Antillean complex. This finding has much significance for the patterns of dispersal previously hypothesized for the genus and will be further discussed below. The Antillean and Bahamian *Epicrates,* exclusive of *Epicrates angulifer,* are distinguished by their longer tails, lack of labial pits, and several lipid characters. In addition, these *Epicrates* differ from *E. cenchria* and *E. angulifer* in their reproductive strategies. *Epicrates angulifer* and *E. cenchria* give birth to large young with masses ranging from 25 g to well over 100 g (*E. angulifer* only). In contrast, all the other *Epicrates,* including large adult *E. striatus, E. inornatus,* and *E. subflavus,* give birth to young weighing under 15 g. The close association of *E. angulifer* and *E. striatus* postulated by Sheplan and Schwartz (1974:124-125) is not corroborated by this marked dichotomy of birth weights. The superficial similarities of these two species are more likely due to symplesiomorphy than synapomorphy.

Within the genus *Epicrates, E. angulifer* stands alone as the only truly large species, with adults reaching sizes in excess of 3 m (Gundlach, 1880; Tolson, 1982). In contrast, *E. fordii, E. gracilis,* and *E. monensis* are conspicuously smaller than their congeners. It seems reasonable to conclude that the smaller taxa must have evolved from one of the larger boa lineages, as both *E. cenchria* and *E. angulifer,* the primitive members of the genus, are fairly large, robust forms. The largest adult males and females of *E. fordii, E. gracilis,* and *E. monensis* rarely exceed 1 m in total body length and 100 g in weight. I consider small size to be a unique, shared derived character in the genus uniting *E. fordii, E. gracilis,* and *E. monensis* as a monophyletic group.

Of all the species of *Epicrates, E. gracilis,* with its elongate, laterally compressed body, blunt head, and large eyes, stands out as the most morphologically distinct boid in the Bahamas and Greater Antilles. *Epicrates monensis* shows a small amount of lateral compression, but not nearly as great as *E. gracilis. Epicrates fordii* and *E. monensis* resemble each other to a much greater degree. Adult color patterns of *E. fordii, E. monensis,* and *E. gracilis* are each unique, but *E. fordii* and *E. monensis* are both boldly patterned snakes with a series of single or confluent chain-like blotches extending down the midline. These blotches have chocolate brown centers bordered by dark brown in adult *E. fordii,* and have reddish-brown or light brown centers bordered by

dark brown or black in adult *E. monensis*. *Epicrates fordii* and *E. monensis* are the only neonate *Epicrates* born with gray or grayish-brown ground color. Neonate color is interpreted as a shared derived character state uniting the *E. fordii* + *E. monensis* natural assemblage. Other neonate *Epicrates* and *Corallus* are reddish colored. Interestingly, the gray-brown juvenile *E. monensis* eventually develop a reddish-brown adult coloration in later life. The lipid and morphological data, and the phylogenetic hypothesis of Sheplan and Schwartz, all predict a sister species relationship for *E. fordii* and *E. monensis*.

A larger monophyletic group, which includes *E. inornatus, E. subflavus, E. fordii, E. gracilis,* and *E. monensis,* is depicted in Fig. 17. These species are set apart from their congeners by the presence of a single intersupraocular scale (character 30). This is an interesting character because it allies the small *Epicrates* with a particularly well-diagnosed subset of large *Epicrates*. Under one hypothesis of character state evolution, lipid character 15, although homoplasious, corroborates that association.

Epicrates subflavus of Jamaica and *E. inornatus* of Puerto Rico appear to be sister species, although their disjunct distribution may suggest otherwise. Their common ancestry is indicated by single lipid and scale synapomorphies in this analysis. The two species were long considered conspecific before being separated by Stejneger (1901). Sheplan and Schwartz noted a suite of characters shared by *E. inornatus* and *E. subflavus*: modal numbers of dorsal scale rows at midbody (38-42 in *E. inornatus,* 38-44 in *E. subflavus*), head scale formulae of 2-1-2, supralabial number six below eye (shared also with *E. gracilis*), and a similar number of infralabials and supralabials. As adults, *E. subflavus* and *E. inornatus* differ considerably in pattern coloration. Adult *E. inornatus* are dark brown with a much faded pattern of small solid blotches, while adult *E. subflavus* are yellow or yellow-brown with reddish scales dispersed at various intervals and a fragmented black body and tail pattern. Despite these differences in adult pattern and coloration between *E. inornatus* and *E. subflavus,* neonates of both species appear similar in pattern. This could be a symplesiomorphy, as *E. fordii* and *E. monensis,* another hypothesized sister species pair, have similarly colored neonates. All data considered, I view *E. inornatus* and *E. subflavus* as sister species.

A sister species association is also suggested for the Bahamian *E. chrysogaster* and *E. exsul*. The striking resemblance between these two taxa was noted by Netting and Goin (1944) in their original description of *E. exsul*. These two species share six unique lipid synapomorphies (4, 5, 21, 22, 23, 24; see Table 3) and both show a similar pattern of

ontogenetic color change, from reddish or orange-brown babies to a gray or gray-brown adult coloration. Nominate *E. striatus* share a two-intersupraocular condition with *E. exsul* and *E. chrysogaster*. Bahamian *E. striatus* usually have only one intersupraocular[1]. Two apomorphic fluorescent lipids of *E. exsul* (characters 16 and 17; Fig. 13) may be the same fluorescent compounds found in *E. fordii, E. gracilis,* and *E. monensis*. Their R_fs, however, are different and I have recorded them as such in Table 3. The weight of all evidence (Fig. 17) suggests that they are not homologues.

BIOGEOGRAPHY

The Vicariance Model

The cornerstone of Rosen's approach (1978) requires that the geographic coincidence of plant and animal distributions are historically related to each other through geographic history, and that these historical connections can be revealed by comparing biological cladograms to models of paleogeographic events. Congruence of the biological cladograms with a geological area cladogram allows one to assume at a high confidence level that a specific series of paleogeographic events are responsible for the current distributions of the taxa under study. Vicariance biogeography assumes that fragmentation of a landmass is reflected in the patterns of distribution of the fragmented biota left in the wake of the shifting landmasses. The more taxa that share common patterns of distribution, the greater the probability that similar historical processes shaped the evolution of such species. Thus, in an exercise of this sort, one first searches for coincident patterns of distribution, and then compares these patterns with a model of paleogeographic history (preferably expressed as a geological area cladogram) in a search for congruence.

I used this approach to discover possible vicariant patterns in Antillean *Epicrates*. The distributions of amphibian taxa and reptile taxa (Tables 4 and 5) taken from Thomas and Schwartz (1975) were first examined to discover congruent patterns, or tracks. In this part of the

[1]Embryo and neonate individuals of *E. striatus, E. fordii, E. inornatus, E. subflavus,* and *E. monensis* examined by me often exhibit a broken pattern of head shields early in ontogeny. Subsequent scale fusion reduces the number of intersupraocular scales as the snakes age. This ontogenetic pattern (Nelson, 1978) further reinforces the hypothesis that a high number of intersupraocular scales (three or more) is primitive in this genus.

study I was only interested in correlations of distributions within the Greater Antilles (which would indicate a particular configuration of proto-Antillean island masses).

At least several of the reptile species appear to have ancient relict distributions (Underwood, 1953): *Aristelliger* (two species on Hispaniola and one species on Jamaica), *Chamaelinorops* (two species on Hispaniola), *Chamaeleolis* (two species on Cuba) and *Cricosauria* (one species on Cuba). There are not enough surviving congeners of these species to make any meaningful assessments of the historical distributions. However, when the distributions of other Greater Antillean amphibians and reptiles are assessed, several patterns emerge. The most common of these is one in which a genus had at least one species occupying each of the Greater Antilles *exclusive* of Jamaica. *Ameiva, Amphisbaena, Hemidactylus, Leiocephalus,* and *Peltophryne* exhibit this pattern. A second pattern, in which a genus has representatives on all the Greater Antilles, is also present. *Alsophis, Chrysemys, Cyclura, Diploglossus,* and *Eleutherodactylus,* along with *Epicrates,* are distributed in this way. These two possible generalized tracks are compatible if one were to assume that dispersals are responsible for the presence of the genera listed above on Jamaica.

After the patterns were diagnosed, they were compared with the hypothesized sister group relationships within *Epicrates* in an attempt to correlate probable vicariant events with the postulated speciational history of the genus. The taxonomic cladogram of *Epicrates* was based on the combined morphological and lipid data generated by this study. The result was that the distributions of certain amphibian and reptilian genera matched the vicariant pattern illustrated in Fig. 19.

Rosen (1975) concluded that vicariance was responsible for some, if not most, of the Antillean biotic diversity. He argued that the basic geological event responsible for the wholesale transfer of species to the Antilles was the eastward movement of a proto-Antillean archipelago from the vicinity of the present day Panamanian Isthmus. Rosen illustrated the phylogeny of a group of hypothetical taxa that owed its origin to this type of vicariant event (1975, fig. 20), and *Epicrates* fits this predicted pattern (Fig. 19). The Central American and South American *Epicrates* share a more recent common ancestry than either does with any Antillean *Epicrates* (Central and South American *Epicrates* are at best subspecifically distinct (Peters and Donoso-Barros, 1970)).

TABLE 4
DISTRIBUTIONAL PATTERNS OF THE AMPHIBIAN GENERA OF THE GREATER ANTILLES[a]

Genus	Cuba	Jamaica	Hispaniola	Puerto Rico
Calyptahyla	0	2	0	0
Eleutherodactylus	29	13	43	17
Hyla	0	2	3	0
Leptodactylus	0	0	1	1
Osteopilus	1	1	1	0
Peltophryne	6	0	2	1

[a]Numbers refer to the number of species inhabiting a particular island.

TABLE 5
DISTRIBUTIONAL PATTERNS OF OTHER REPTILIAN GENERA OF THE GREATER ANTILLES[a]

Genus	Cuba	Jamaica	Hispaniola	Puerto Rico
Alsophis	1	1	2	1
Ameiva	1	0	4	2
Amphisbaena	1	0	4	5
Antillophis	1	0	1	0
Aristelliger	0	1	1	0
Arrhyton	3	2	0	1
Cadea	2	0	0	0
Chaelinorops	0	0	2	0
Chameleolis	2	0	0	0
Chrysemys	1	1	1	0
Cricosaura	1	0	0	0
Cyclura	1	1	2	1[b]
Darlingtonia	0	0	1	0
Diploglossus	1	7	7	1
Hemidactylus	2	0	2	2
Hypsirynchis	0	0	1	0
Ialtris	0	0	2	0
Leiocephalus	6	0	8	1[b]
Mabuya	0	0	1	1
Tropidophis	11	1	1	0
Typhlops	2	1	4	3
Uromacer	0	0	3	0
Wetmorena	0	0	0	1

[a]Numbers refer to the number of species inhabiting a particular island.
[b]Extinct.

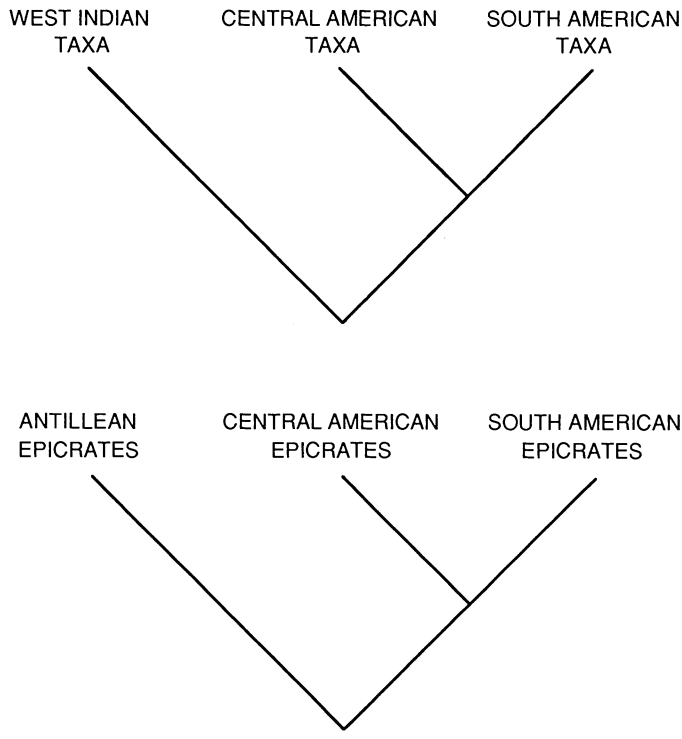

FIG. 19. Three-taxon cladogram (above) and *Epicrates* cladogram (below) representing a Caribbean vicariance pattern according to Rosen (1975).

Because of this congruence between distributional tracks of certain Antillean reptiles and amphibians with that of *Epicrates,* several geophysical models were examined to search for a likely geological area cladogram which would most parsimoniously interpret the tracks. The competing models used are summarized below.

Pregill (1981) seems to be the first to discover that several of Rosen's (1975, fig. 7) interpretations of the geological history of the Caribbean Basin bore little resemblance to the Malfait and Dinkleman (1972) model that he cited. Pregill's main objection to Rosen's hypothesis was that the late Cretaceous-early Tertiary position of the proto-Antilles was essentially no closer to the continents than the modern Antilles are today, and that any colonizations of those islands during that time were more likely due to dispersal. Malfait's and Dinkelman's (1972) fig. 1 clearly shows that the proto-Antilles were already well-removed from

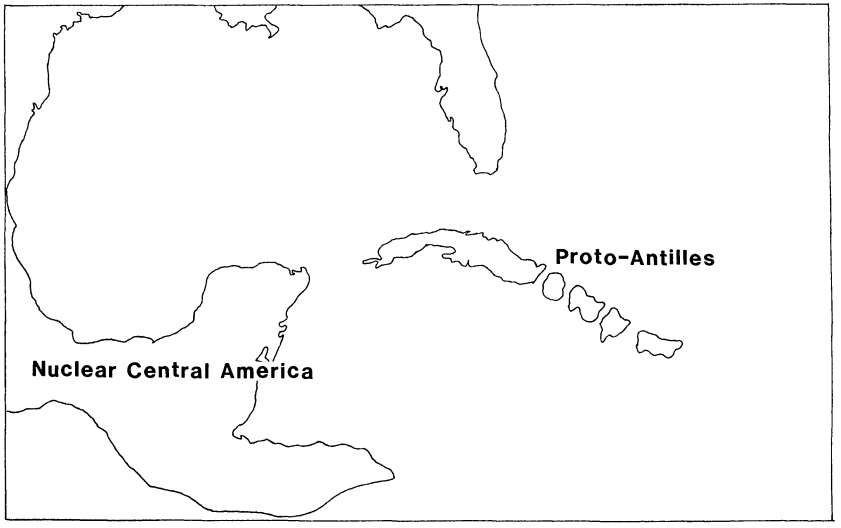

FIG. 20. The proto-Antillean reconstruction of Malfait and Dinkleman (1972); late Cretaceous.

Central America by the late Cretaceous[2] (this stage in their model is illustrated in my Fig. 20). In fact, a common feature of nearly all current geological models for the Caribbean is that the proto-Antilles are well to the east of the Central American coastline by the Cretaceous.

It must be mentioned, however, that since the publication of Rosen's (1975) paper other models have surfaced which postulate the origin of the Greater Antilles in the Isthmian region of Central America. These include Dickenson and Coney (1980), Pindell and Dewey (1982), Sykes et al. (1982), and, more recently, Burke et al. (1984). While these models differ in significant details, they each provide a framework upon which a hypothesis of Caribbean vicariance could be constructed. The Pindell and Dewey (1982), Dickenson and Coney (1982), and Burke et al. (1984) paleoreconstructions agree in one important aspect: the presence of a Greater Antillean magmatic arc as a single landmass in the Isthmian region at 80 mybp. Perhaps most significant is the Sykes et al. (1982, fig. 9, p. 10666) contention that the proto-Antilles existed in a close-packed conformation close to Nuclear Central America as late as 48 mybp. Their reconstruction (Fig. 21) resembles the proto-Antillean reconstruction of Rosen (Fig. 22), and, if correct, negates Pregill's main criticism of Rosen's (1975) vicariance model.

[2]The lone exception in this case might be Jamaica, which, along with the rest of the Nicaragua Rise, was hypothesized by Malfait and Dinkleman (1972) to be crustal material rafted in from southern Mexico.

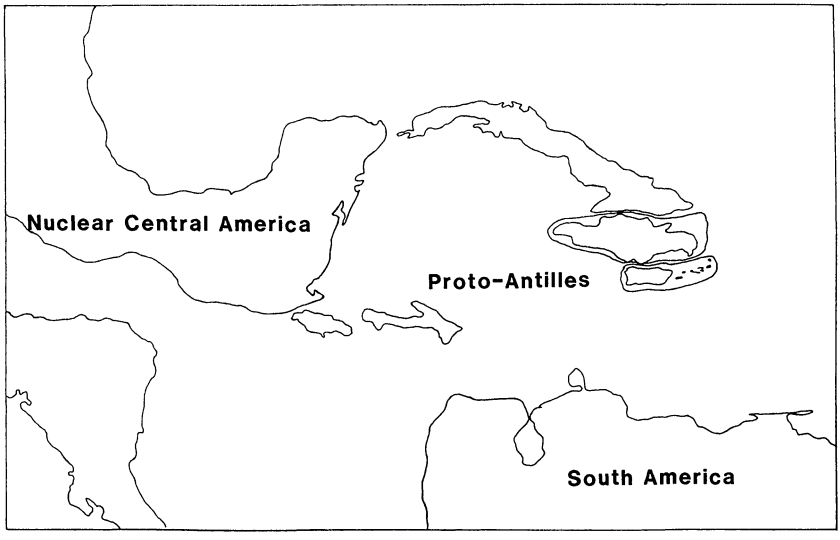

FIG. 21. The proto-Antillean reconstruction of Sykes et al. (1982).

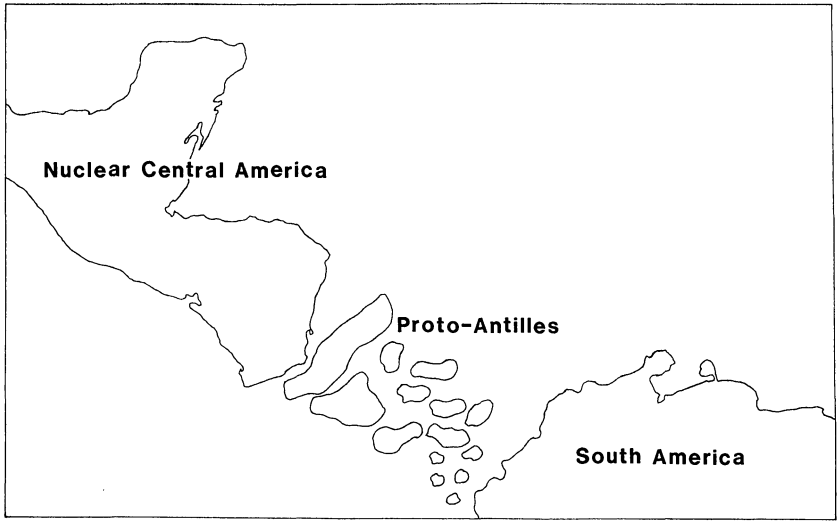

FIG. 22. The proto-Antillean reconstruction of Rosen (1975).

Tectonic Models of the Caribbean

The Gulf of Mexico and the Caribbean Basin are characterized by a wealth of structural complexity. The vast carbonate provinces, salt diapirs, uplifts, and valleys of the Greater Antillean Geosyncline, island arcs of the Aves Ridge and the Lesser Antilles, and the complex system of troughs, rises, and ridges that delineate the modern boundaries of the Caribbean Plate have created the most diverse topography found in the Atlantic Basin (Uchupi, 1975). The accumulated geophysical data, including seismic velocity profiles, indicates that crustal thicknesses of the Caribbean Basin vary from 12 to 15 km, compared to the thickness of approximately 7 km usually found in the main ocean basins. In addition, the magnetic anomalies usually associated with sea floor spreading centers and newly-generated oceanic crust are generally absent (Officer et al., 1959; Ewing et al., 1960).

This diverse and often puzzling geology includes a wide variety of sedimentary and igneous rocks of various ages (Donnelly, 1975), often emplaced in unlikely localities. Various workers have attempted to use these rocks in rather speculative reconstructions of the geological evolution of the area. Controversy surrounding these interpretations has led to the formation of two opposing camps. Stabilists view Middle America, the Caribbean, and the Gulf of Mexico as ancient physiographic features, largely unaffected by plate movements or cratonic rotations (Khudoley and Meyerhoff, 1971; Meyerhoff and Meyerhoff, 1972). Mobilists, in contrast, interpret Caribbean geological evolution in the context of plate-plate interactions and sea-floor spreading. In recent years, the mobilists' thesis has become widely accepted, despite the equivocal nature of some of the evidence, and there has been a proliferation of tectonic models interpreting the geology of the region. The vicariance biogeographers' hypotheses are often founded on mobilist theory. Although not dependent on particular models, they require evidence of changing geography, regardless of the process involved.

Some tectonic models posit the evolution of the Caribbean in terms of fragmentation and rotation of large blocks (Freeland and Dietz, 1972a; Perfit and Heetzen, 1978), and intrusion and subsequent uncoupling of an extension of an East Pacific Plate through the area which is now occupied by the Panamanian Isthmus (Wilson, 1966; Malfait and Dinkleman, 1972; Pindell and Dewey, 1982; Sykes et al., 1982). Rosen (1975) largely used the Malfait and Dinkleman model to explain the origin and present distribution of the Caribbean biota, mainly because one of its basic features, an eastward moving proto-

Antillean archipelago, fit his conception of Caribbean biogeographic events in the Tertiary. In addition, both Freeland and Dietz (1972a) and Perfit and Heetzen (1978) offered reconstructions of the Caribbean which involve large eastward displacements of the Greater Antilles. These models differ considerably, however, in their interpretations of Caribbean geological features and in their hypotheses of subsequent Greater Antilles evolution, as the following review documents.

Malfait and Dinkleman (1972) believed that the westward drift of North America and South America and their subsequent collision with the East Pacific Plate resulted in the subduction of Pacific crust beneath the two continents and the formation of two faults which now define the northern and southern borders of the Caribbean Plate. The plate itself, formed when a tongue-like extension of the East Pacific Plate wedged itself between North and South America, was later sheared off and became an independent tectonic unit. The northern plate border was at first an eastward extension of the Southern Mexico Trench in the late Cretaceous, and later evolved into a complicated trench system which now includes the Montagua fault zone, the Cayman Trough, and the Puerto Rico Trench. Although present-day Cuba is well removed from the Caribbean Plate boundary, the southwest to northeast-trending basement faults in Cuba (Skvor, 1969) were interpreted as remnants of a series of transform faults created when the boundary between North America and the Caribbean was displaced sequentially to the east. Portions of the Caribbean lithosphere are hypothesized to have been transferred and later welded to the North American Plate. This would in part help to explain the marked differences in the tectonic fabric of Cuba when compared to the rest of the Greater Antilles.

According to the Malfait and Dinkleman (1972) interpretation, the Cayman Trough intersected the Cuban Trench and terminated the underthrusting of oceanic crust surrounding Cuba and western Hispaniola during the late Eocene or early Oligocene. Eastward movement of the Caribbean Plate began by the Oligocene and the subduction zone once present in the Puerto Rico Trench later became a transform fault. Decoupling of the Caribbean Plate from the East Pacific Plate was claimed to be essentially complete by the Oligocene. The Nicaragua Rise, including Jamaica, was interpreted as a portion of non-oceanic crust rafted in from southern Mexico. The Laramide orogenic and intrusive activities of the Antilles were considered a result of the lithospheric underthrusting of the nascent North American Plate by the Caribbean Plate beneath Cuba and Hispaniola and overthrusting of the North American Plate by the Caribbean Plate to the east beneath

northern Puerto Rico. Peculiar distributions of sedimentary facies in the Antilles were thought to have resulted from the same processes. The Beata Ridge was believed to be the result of orogenic activity along a hypothesized Beata Fault which acted as a hinge fault permitting the change from underthrusting to overthrusting described above. Malfait and Dinkleman (1972) further hypothesized that by the Eocene, after the intersection of the Cayman Trough and the Cuban Trench, relative motion had changed from a northeasterly movement to an easterly movement. Continued eastward movement of the Caribbean Plate since the Eocene accounts for a left lateral displacement of the Greater Antilles of approximately 180-200 km. Figure 20 shows the Antilles in the late Cretaceous according to Malfait and Dinkleman (1972).

Freeland and Dietz (1972a) assumed that the lack of magnetic anomalies in the region was due to opening of the Gulf during a magnetic quiet time and later to the slow chilling of pillow lavas generated when new ocean floor was produced. The slower chilling of the lavas was postulated to have occurred because of rapid sedimentation into the rift zones. Furthermore, these authors hypothesized that the rotation of Yucatan and Honduras occurred as a single unit until about a point near the Isthmus of Panama (Fig. 23). This large block later split and resulted in the emplacement of the Yucatan and Nicaragua-Honduras blocks in their present positions. Freeland and Dietz (1972a) also proposed that a Jurassic sedimentary accretionary wedge within the Gulf of Honduras split away from the Nicaraguan block on both sides of the proto-Cayman Trough to form proto-Cuba and proto-Hispaniola. According to their theory, additional spreading centers south of the Cayman Trough split proto-Hispaniola into the sub-blocks of Jamaica, Hispaniola, and Puerto Rico and the Virgin Islands by the end of the middle Eocene.

The Pindell and Dewey (1982) paleogeographic reconstruction is in some ways a hybrid of the Malfait and Dinkleman (1972) and the Freeland and Dietz (1972a) models. Like Freeland and Dietz, these authors hypothesize that there was a complete closure of the proto-Atlantic Ocean between North America and South America, with the Yucatan and possibly Chortis blocks situated between these two continents. In addition, they hypothesize that the Caribbean Plate is an extension of Pacific crust which entered into the Isthmian region at approximately 125 mybp.

Perfit and Heetzen (1978) constructed still another view of Caribbean geophysical evolution, which was corroborated by Burke et al., (1984) on the basis of additional observations. Perfit and Heetzen (1978) agreed with Freeland and Dietz (1972a) that there was extensive

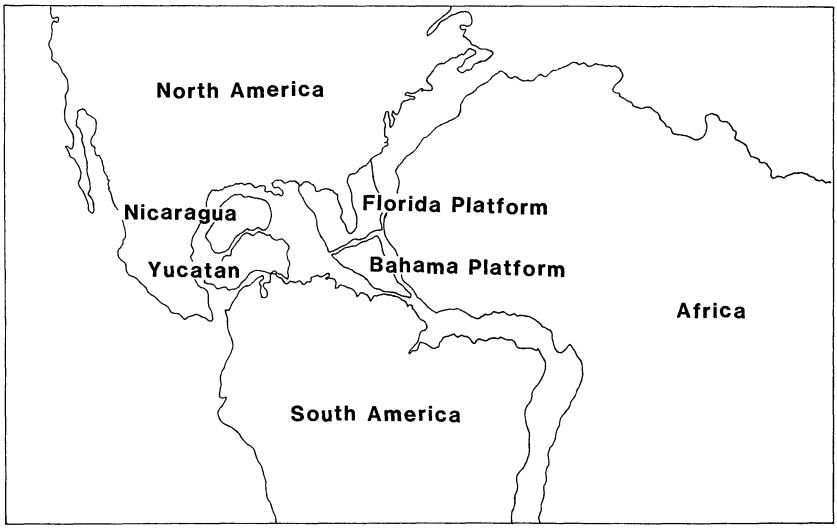

FIG. 23. The continental fit of Freeland and Dietz (1972a); late Triassic.

reorganization of Central America during the Mesozoic, and both sets of authors noted that most Mesozoic pre-drift constructions (like the Bullard fit; Bullard et al., 1965) require an unlikely overlap of pre-Jurassic crustal elements in the region of Central America. Perfit and Heetzen (1978) hypothesized that the Cayman Ridge and the Nicaragua Rise were a single structural unit extending east of Honduras. Like Malfait and Dinkleman (1972), they hypothesized a change in relative plate motions since the early Cretaceous. The clockwise rotation of South America was believed to have caused compression at the northern plate boundaries that resulted in the subduction of oceanic lithosphere beneath Central America and the Nicaraguan Plateau-Cayman Ridge. Arden (1975) also favored this hypothesis. According to Perfit and Heetzen (1978), this subduction led to the development of a volcanic arc above the Benioff zone which evolved into the Cayman Ridge, Nicaraguan Plateau, and elements of the Greater Antilles, including Jamaica, southern Cuba, and western Hispaniola. Additional subduction to the south or southwest was believed to have resulted in the formation of the older Laramide volcanic complexes in Cuba, eastern Hispaniola, and Puerto Rico. Subduction north of Cuba in the late Cretaceous resulted in the collision of Cuba and the Bahama Carbonate Platform. At the end of the Eocene all readily subductible crust had been consumed according to Burke et al. (1984). This marked

the end of the underthrusting on the northern and southern boundaries of the plate. Shortly afterward, the Central American subduction zone joined with the Puerto Rico Trench, forming the west-to-east series of transform faults present in the Caribbean today. The Perfit and Heetzen model, in which southern and northern Cuba evolved as part of different volcanic complexes, eliminates the need for the complicated system of transform faults proposed by Malfait and Dinkleman (1972). The ultimate closure of the subduction zones and the relative eastward movement of the Caribbean Plate is reflected in diminished volcanic activity in the region since the early Tertiary. The tension along the plate boundaries caused by the rotation of South America is hypothesized to have led to the essentially confluent grabens of the Montagua Valley of Guatemala, the Cauto Basin in Cuba, the Enriquillo-Cul-de-Sac Plain of Hispaniola, the Wagwater Trough in Jamaica, and the proto-Cayman Trough. Lateral movements of the Caribbean Plate are believed to have occurred along a complex series of faults parallel to or including the above features.

Perfit and Heetzen (1978) further concluded that the strike-slip motion along the plate boundaries (which now included the Cayman Trough), along with continued plate divergence, resulted in the formation of a spreading center in the Trough. This caused the rifting of the Cayman Ridge and southern Cuba from the volcanic arc which included the Nicaragua Plateau and the rest of the Greater Antilles. Extensive left-lateral movement of the Greater Antilles since the Eocene is also a feature of their model (Fig. 24). Ironically, some of the crustal features of the Caribbean Basin used to justify an intrusion of an East Pacific Plate into the area, e.g. the lack of a defined fracture zone pattern and the absence of a magnetic anomaly in the region, were invoked by stabilists to argue against a mobilist view of Caribbean geological evolution (see Khudoley and Meyerhoff, 1971).

Attempts to penetrate ocean basement in the region have provided some ideas as to why the crustal properties of the Caribbean are not like other ocean basins. Around 80 mybp a tremendous basaltic intrusion known as the "great basalt flood event" deposited several km of additional crustal material over the original basement (Donnelly, 1975). The flood event explains the absence of a coherent fracture zone pattern and the shallow depths of the Caribbean Basin, and it may be a major reason why subduction at the northern and southern boundaries ceased in the Eocene. The buoyancy of the newly formed crustal material was so great that further subduction was impossible (Fox and Heetzen, 1975; Burke et al., 1984).

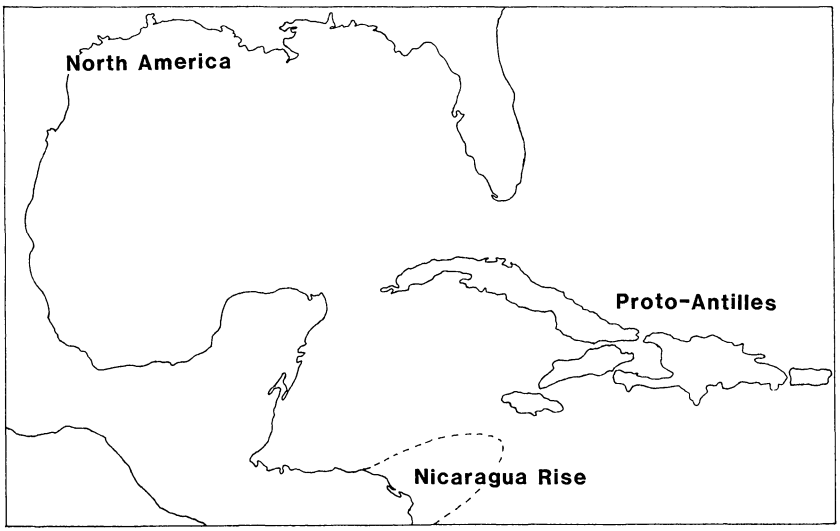

FIG. 24. The proto-Antillean reconstruction of Perfit and Heetzen (1978); early Eocene.

METHOD OF ANALYSIS

As the above summaries indicate, there is no shortage of models attempting to explain the geological evolution of the Caribbean. What I attempted to look for in the geological literature was a model that could be used to produce a geological area cladogram that would fit an area cladogram for *Epicrates*. *Epicrates* is appropriate for such an exercise because there are several well-corroborated, nested subgroups containing a minimum of three endemic taxa (Fig. 17) which could have been the result of vicariant events, and the high degree of island endemism of *Epicrates* limited the type of geological occurrences which would have resulted in allopatric speciation to fragmentation of larger landmasses (all islands) into smaller ones. This is the only process likely to have resulted in the widely separated populations. A major difficulty in interpreting these patterns is attempting to distinguish a distributional pattern resulting from west to east linear dispersal (*sensu* Darlington, 1938) from one produced by the fragmentation of an island mass, where satellite islands are split off sequentially from the west side of an original block as it moves toward the east. I cannot distinguish between these two competing possibilities using the data presented here.

The method of analysis worked as follows. Several species are hypothesized to share a common ancestor, for example, *E. striatus*

(Hispaniola), *E. subflavus* (Jamaica), and *E. inornatus* (Puerto Rico). Their area cladogram (Hispaniola + (Jamaica + Puerto Rico)) was compared to the geological cladogram of those same islands to determine if vicariance was a likely factor in their evolution. While attempting to determine the origins of Antillean *Epicrates* the following questions posed by Platnick and Nelson (1978) were addressed: (1) Are the geographic centers of endemism non-random? (2) Are the relationships of endemic taxa non-random, and if so, what is the pattern produced? (3) How does the pattern, if any, correlate with the geological history of the region? Because the majority of *Epicrates* species are endemic to a particular bank or island, the null hypothesis is that each pair of sister taxa are produced by a vicariant event. If none of the current geological models suggested a hierarchic pattern of landmass fragmentation corresponding to the area cladogram of *Epicrates,* then the hypothesis of vicariance was considered falsified and dispersal was assumed.

Dispersal vs. Vicariance of *Epicrates*

The probable evolutionary history of each subgroup within *Epicrates* was examined with an eye to the possible influence of vicariant events. The co-occurence of two or more species of *Epicrates* on a single island mass or bank was taken as unequivocal evidence of dispersal of at least one of the sympatric taxa. The presence of *Epicrates* on islands known to have been completely submerged sometime since the Pleistocene was also viewed as undeniable evidence of dispersal.

The Continental Species: *E. cenchria*

Making a convincing case for a particular "mainland point of origin" for the ancestral stock of Antillean *Epicrates* is difficult. Most workers assumed that Antillean *Epicrates* evolved from a South American lineage (Savage, 1966; Sheplan and Schwartz, 1974; Rosen, 1975), but two lines of evidence support a North American or Nuclear Central American origin: (1) The only fossil forms presumably similar to *Epicrates* are found in North America, where they are widely separated, and (2) the relatively undifferentiated state of Central and South American *E. cenchria* suggests that this species is a relatively recent arrival in South America. It is not clear why *E. cenchria* is absent from northern Central America, where a variety of suitable habitats exist.

Hecht (1959) described *Paraepicrates* from the Elk River Formation in Wyoming, a late Eocene locality. Hecht found these vertebrae to be

more similar to those of *E. cenchria* than *E. striatus*. The vertebral similarities which ally the Eocene boid with *E. cenchria* could be interpreted as evidence that the group was around by at least the Eocene, thus making them possible candidates for vicariance. Unfortunately, to complicate matters, Kluge (pers. comm.) has recently examined both *Pseudepicrates* and *Paraepicrates* and believes they may not be boines at all.

If *Epicrates* had been an early Tertiary arrival in South America, I would expect at least some evidence of speciation in that region, judging from the considerable divergence that has occurred in other South American boids. Amaral (1954) was able to identify only a few Central American and South American populations of *E. cenchria* as subspecies, thus implying minimal differentiation. In contrast, multiple speciation has occurred in the closely related genera *Corallus* (three species) and *Eunectes* (three species; see Duellman, 1979 for a review). I suppose it could be argued that *E. cenchria* survives unchanged in many different South American environments, including forest edge, rainforest, and savannah and other open vegetation (Dixon, 1979; Hoogmed, 1979; Rivero-Blanco and Dixon, 1979), because gene flow is so great that it has overcome any tendency to speciate. The boas that have speciated are by and large restricted to mesic forest habitats. At any rate, the phylogenetic cladogram (Fig. 17) indicates clearly that *E. cenchria* shares a common ancestor with all of the extant Antillean species.

The Larger Species of *Epicrates*

Vicariant events may have been responsible for at least some of the speciations that produced the Antillean *Epicrates*. The sequence of branching events that resulted in the large species (Fig. 17), *E. angulifer, E. inornatus, E. striatus,* and *E. subflavus,* seems to parallel the historical geographic associations among the Greater Antilles hypothesized by Freeland and Dietz (1972a), and to a large extent Sykes et al. (1982).

Freeland and Dietz believed that the islands of Jamaica, Hispaniola, and Puerto Rico were once combined in a single proto-Hispaniolan landmass. Earlier, both Bowin (1975) and Donnelly (1975) noted the geological similarities between eastern Hispaniola and western Puerto Rico. Sykes et al. (1982) had Jamaica and the Tiburon Peninsula of Haiti associated with the Nicaragua Rise and proto-Cuba with Hispaniola and the Puerto Rican Bank. Hess and Maxwell (1953) and others further stressed the coherence of the Greater Antilles as a single

tectonic element, and Kaye (1959a) noted that sea level lowering of only 600 m would result in dry land connections between Cuba, Jamaica, Hispaniola, and Puerto Rico.

I consider *E. angulifer* to be the oldest divergent lineage from the stock that originally colonized the Greater Antilles (Fig. 17). For dispersal or vicariance, Cuba seems a plausible point of entry from either North America or Central America. Its size and position, stretching for over 1000 km immediately northeast of the Nicaragua Rise and less than 200 km south of the Florida Platform, are excellent with respect to receiving waifs from the mainland, and its position as the island closest to Nuclear Central America makes it an excellent candidate for the first island to separate from a eastward-moving proto-Antillean landmass.

Arden (1975) reported that the emergence of the Nicaragua Rise and Jamaica was at a mimimum until the late Oligocene or Miocene. A dry land environment for at least part of the Rise, exclusive of Jamaica, is indicated by the Miocene red beds of the northeastern portion of the Rise, now occupied by the Gorda Bank (Arden, 1975). Submergence is indicated later in the Tertiary and in the Quaternary by the preponderance of mixed carbonates in the strata corresponding to those ages. Lopez-Ramos (1975) reconstructed the paleogeographic history for the Yucatan Peninsula and indicated that it had a similar history, with emergence likely in the Tertiary (since the Miocene), and widespread submergence at other times. Either of these continental projections (or the Florida Platform for that matter) could have served as a point of departure to the islands. Conversely, Rosen (1975) noted that there are concentrations of old northern elements in Cuba, which might have been derived from stocks vicariated from Nuclear Central America. *Epicrates angulifer* could be one of those species. Its presence in Cuba, however, could just as well be the result of an early colonization overwater from Central America. Cuba has had a longer geological history relative to the other Antilles and its position north of a major trench system may have provided it with long term stability.

Epicrates striatus occupies various islands of the Great Bahama Bank and Hispaniola and its satellites. It has been divided into several populations of subspecific rank by Sheplan and Schwartz (1974), with the "North Island" *E. striatus, sensu* Williams (1961), designated as the nominate form. Although not strictly endemic, nominate *E. striatus* have probably resided in Hispaniola since the Tertiary and so may be examined with the Hispaniolan endemics to see how they might have been affected by Caribbean vicariance (like *E. exsul* and *E. chrysogaster,* the Bahamian populations of *E. striatus* are most likely

Pleistocene arrivals and would not figure in an early Tertiary vicariance model). It is assumed that isolation of populations and subsequent speciation would have occurred after some geological or isostatic event.

The several apomorphies shared by Hispaniolan *E. striatus* and all other, more derived, Antillean *Epicrates* (Fig. 17) indicate that *E. striatus* is probably not a later derivative of Cuban *E. angulifer* as suggested by Sheplan and Schwartz (1974). However, the presence of *E. striatus* on Hispaniola between the ranges of two closely related endemics, *E. subflavus* of Jamaica and *E. inornatus* of Puerto Rico, is remarkable. Sheplan and Schwartz (1974) suggested that *E. subflavus* + *E. inornatus* kinship was the result of: (1) a separate invasion of Jamaica from the mainland by some proto-*E. subflavus* + *E. inornatus* stock, and (2) dispersal of the lineage from Jamaica to Puerto Rico directly, without the use of Hispaniola as a steppingstone. The evidence, whether biochemical or morphological, does not support the hypothesis of two separate invasions of the Greater Antilles, and clearly shows that the Antillean *Epicrates* form a monophyletic group. Figure 17 predicts that the common ancestor of *E. angulifer* and other Antillean *Epicrates* originally colonized Hispaniola from Cuba, and then dispersed or vicariated independently to Jamaica and Puerto Rico. All of the Greater Antilles were emergent during the time period hypothesized for these events (Arden, 1975; Bowin, 1975; Pardo, 1975; Kaye, 1959b; Woodring, 1954). I would predict that the *E. striatus* + (*E. subflavus* + *E. inornatus*) dichotomy occurred on Hispaniola, and the complex tectonic movements which resulted in the present topography of Hispaniola could certainly have been a major factor in the speciation of this complex (Sykes et al., 1982).

If the *E. angulifer* + (*E. striatus* + *E. inornatus* + *E. subflavus* + *E. gracilis* + *E. monensis* + *E. fordii*) divergence predicted by the final cladogram (Fig. 17) was the result of a vicariant event then one would expect to find evidence for a corresponding geological cladogram, e.g. Cuba + (Hispaniola + (Jamaica + Puerto Rico)). Furthermore, as *E. subflavus* and *E. inornatus* are corroborated sister species (Fig. 17), vicariance theory predicts that Jamaica and Puerto Rico shared a connection more recent than either had with Hispaniola. In the latter case, it seems reasonable to suggest that if Jamaica and Puerto Rico were ever joined, the juncture must have included Hispaniola, due to the geological similarities shared between the eastern coast of Hispaniola and the western coast of Puerto Rico and the fact that Hispaniola is situated between Jamaica and Puerto Rico. It is possible,

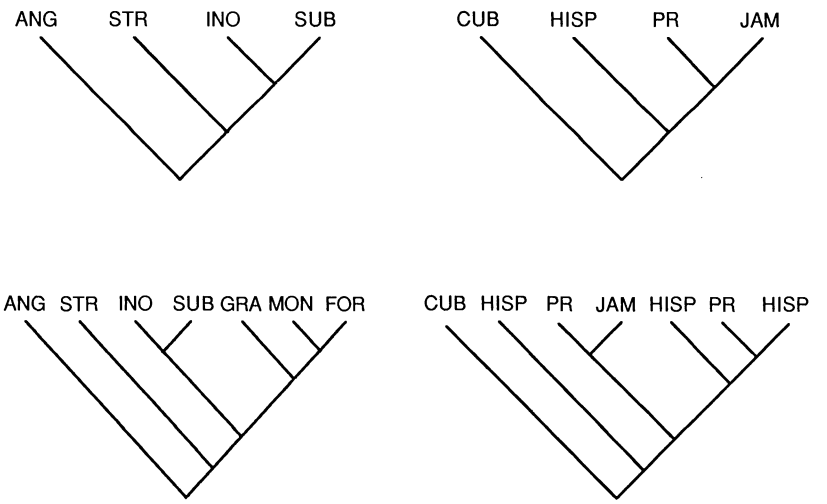

FIG. 25. Congruence between taxon cladograms (left) and geological cladograms (right) of selected species of *Epicrates*. For abbreviations, see Materials and Methods section.

however, that if the islands were ever in a configuration such as that suggested by Rosen (1975, fig. 8), in the later Cretaceous or early Eocene, juxtaposition of proto-Jamaica and proto-Puerto Rico would not be impossible. In a scheme of vicariance speciation (Fig. 25) that would produce an *E. angulifer* + (*E. striatus* + (*E. inornatus* + *E. subflavus*)) array of sister lineages there would have been a series of vicariant events separating (1) Cuba from a landmass that included (Hispaniola + Puerto Rico + Jamaica), followed by (2) Hispaniola separating from (Jamaica + Puerto Rico), which in turn was followed by the breakup of the landmass consisting of the latter two islands.

This type of insular fragmentation (Fig. 26) is plausible within the framework of a vicariance model, but difficulties arise when one examines the hypothesis closely. While *E. subflavus* and *E. inornatus* are well-documented sister species, there is no plausible geological model that would unite Jamaica and Puerto Rico exclusive of Hispaniola at any time in the Tertiary. Jamaica is an eastern extension of the Nicaragua Rise with a history of total submergence until the Miocene (Arden, 1975), while Puerto Rico rests on its own bank far to the east, on the other side of Hispaniola. The structure of the Greater Antilles Geosyncline precludes a strong geological association between Puerto Rico and Jamaica.

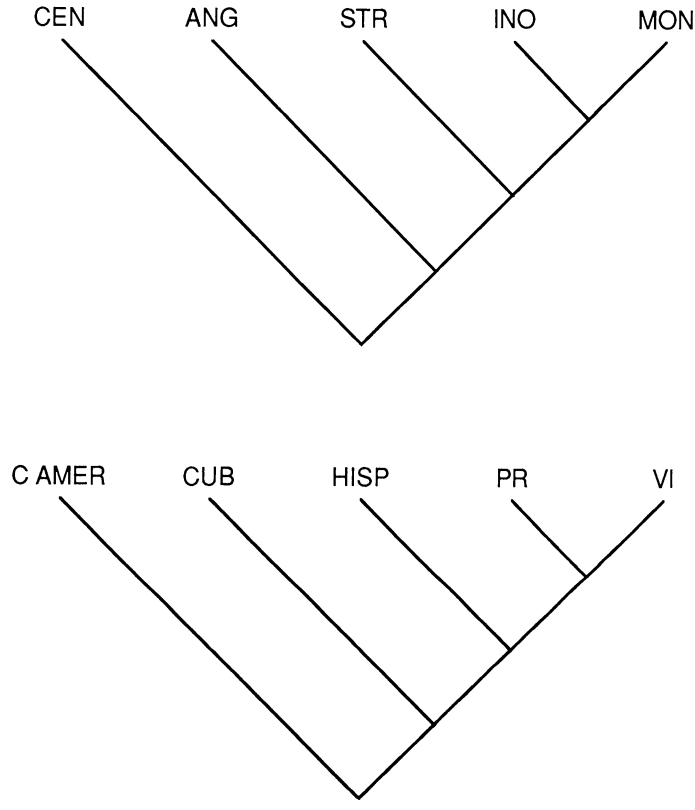

FIG. 26. Phylogenetic cladogram (above) and area cladogram (below) of selected species of *Epicrates*. For abbreviations, see Materials and Methods section.

If one were to ascribe the evolution of the small *Epicrates* to early Tertiary vicariant events, even more serious incongruencies arise. The sympatry of *E. striatus, E. fordii,* and *E. gracilis* on Hispaniola and *E. inornatus* and *E. monensis* on the Puerto Rico Bank provide major inconsistencies which simply do not fit any current geological models. The sympatry of *E. gracilis* and *E. fordii* with *E. striatus* eliminates *E. striatus* from giving rise to the small Hispaniolan species by insular fragmentation. The same type of argument applies to the postulated vicariance between *E. inornatus* and the lineage which led to *E. monensis*. Dispersal must be invoked to explain at least some of this sympatry.

The Smaller Species of *Epicrates*

Several different synapomorphies indicate that the small *Epicrates, E. fordii, E. gracilis,* and *E. monensis,* form a monophyletic group (Fig. 17). Sympatry exists even within this assemblage of snakes: *E. fordii* and *E. gracilis* are both Hispaniolan endemics. Although these species are ecologically separated (*E. gracilis* is a denizen of mesic forest situations, *E. fordii* of xeric habitats), there are areas where the ranges of the two species overlap, particularly on the north coast of Haiti near Cap Haitien, and in the Valle de Cibao, Monte Christi Province, Republica Dominica (Sheplan and Schwartz, 1974). The presence of *E. fordii* and *E. gracilis* on Hispaniola precludes invoking movements of Greater Antillean landmasses as a vicariant event to explain the speciation of these close relatives. In fact, both *E. fordii* and *E. monensis* occur in areas that have emerged since the Pleistocene. *Epicrates monensis* exhibits a disjunct distribution on St. Thomas and Tortola in the Virgin Islands, on Isla Mona, situated in the Mona Passage between Hispaniola and Puerto Rico, and on at least one of the cemented dune satellite islands adjacent to Puerto Rico. The present range suggests a relict distribution. No doubt it once was found on many of the islands of the Puerto Rico Bank which were connected to the main island in the Pleistocene (see paleogeographic maps in Heatwole and Mackenzie, 1967). The apparent absence of the snake from most of the islands of the Virgin Islands chain is possibly the result of mongoose or feral mammal predation, habitat modification, or catastrophic climatic events. *Epicrates monensis* is extremely rare on St. Thomas and Tortola; under 13 specimens have been collected since the Virgin Islands subspecies (*Epicrates monensis granti*) was described by Stull (1933), and their numbers seem to be declining on St. Thomas (A. Damman, pers. comm.). Tortola residents indicate that this boa is rare and may now be close to extinction on the larger British Virgin Islands. I hypothesize that the St. Thomas and Tortola populations of *E. monensis* were isolated by rising sea levels in the Pleistocene; this was followed by extinction of this species on Puerto Rico (Sheplan and Schwartz, 1974). Isla Mona, now capped by Pleistocene marine deposits (Kaye, 1959a), was probably colonized by overwater dispersal from eastern Puerto Rico prior to the extinction of the main island form.

The apomorphies shared by *E. monensis* and *E. fordii* suggest that they are sister species, and imply that the antecedents of *E. fordii* may lie to the east. The Cul-de-Sac/Valle de Neiba Plain area is only lately emergent, judging from the Pleistocene coral reefs present around Lake

Enriquillo and the general Quaternary coastal reef facies predominant in the Llanos Costeros del Seibo of the Dominican Republic. These are the areas where *E. fordii* predominates. Lipid apomorphies shared by *E. fordii, E. gracilis,* and *E. striatus* suggest that the monophyletic group of small *Epicrates* first evolved on Hispaniola. The nearly total restriction of *E. fordii* to recently emergent habitats hints at a late arrival on Hispaniola for this species, but Pregill and Olson (1981) noted that the West Indies were once more xeric than they are today, and that species currently restricted to dry habitats (like *E. fordii*) may have been more widespread. If this is the case, then *E. fordii* may have evolved on Hispaniola prior to the speciation of *E. monensis* on the Puerto Rico Bank. The corroborating synapomorphies between *E. fordii* and *E. monensis* are too many to suggest that *E. fordii* and *E. gracilis* shared a more recent common ancestor than did *E. fordii* and *E. monensis.* I do not believe that an ancestral form colonized Hispaniola from the Puerto Rico Bank or Isla Mona and gave rise to both *E. fordii* and *E. gracilis.* The wide distribution of *E. gracilis* on Hispaniola, both on the "North Island" and the Tiburon Peninsula, suggests that *E. gracilis,* like *E. striatus,* antedates *E. fordii* on Hispaniola.

Perhaps the vertical movements of the islands during the Quaternary (Horsfield, 1975) and the subsequent later isolation of the "North Island" and "South Island" figured in the speciation of the Hispaniolan *Epicrates.* If this is true, it is difficult to reconstruct the events leading to these speciations, for both *E. gracilis* and *E. striatus* are widespread on Hispaniola, and *E. fordii,* although essentially a "North Island" species, has managed to invade the "South Island" (Schwartz, 1980). Because the sister species of *E. fordii* is *E. monensis,* a vicariant event separating Hispaniola from Puerto Rico could be used to explain the origin of these two species, were it not for the great age of the Mona Passage (Kaye, 1959a). Sympatry of *E. inornatus* with *E. monensis* on the Puerto Rico Bank demands that one of these two species reached islands on the bank by dispersal. One other monophyletic group of *Epicrates* also has distributions that are difficult to explain using a speciation model based on the movements of a proto-Antillean archipelago.

The Bahamian Species of *Epicrates*

The origin of the Bahamian and Caicos Banks *Epicrates* is most reasonably explained by dispersal. Although the Bahama Platform was formed prior to the Mesozoic, most, if not all, of the landmasses

presently emergent were submerged sometime in the Pleistocene. The Bahamian boas include *E. chrysogaster* of the Caicos Bank and the Bahamian islands of Crooked, Acklin's, and Great Inagua; *E. exsul* of the Little Bahama Bank; and the populations of *E. striatus* on the Berry Islands, Ragged Islands, Bimini Islands, New Providence, Eleuthera, Andros, and Cat Island.

The Bahamas consist of a group of low-lying islands and cays extending from the southern border of the Florida Platform, on a northwest-to-southeast-trending axis, to a point 150 km off the northern coast of Hispaniola. The islands now exist as a series of banks and dunes which are but the emergent remnants of a vast, fragmented carbonate platform. Similarities in the surface topography and geology conceal the basic historical differences between two distinct provinces: a gravitationally stable platform once part of a large evaporite basin encompassing the main landmass of the Great Bahama Bank and northern Cuba (and extending into the Gulf of Mexico), and a Cretaceous volcanic arc which extends from Great Abaco south to the Navidad Bank off Cabo Cabron of the Republica Dominica (Pardo, 1975; Lee, 1951; Uchupi et al., 1971).

The majority of the species of amphibians and reptiles inhabiting the islands of the Great Bahama Bank are poorly differentiated from their congeners in Cuba and Hispaniola, implying a recent origin (of course it could be argued that the lack of major differentiation is the result of lower evolutionary rates). Others, among them *Alsophis, Chrysemys, Cyclura, Tropidophis,* and *Epicrates,* appear to represent an older "Great Bank Fauna" which have somehow survived the Pliocene and Pleistocene inundations of these islands (Schwartz, 1968). Similarly, islands south of the Crooked Island Passage are populated by an older herpetofauna which differs greatly from related taxa in the Antilles and the "recent southern invaders" which now coexist with them on these islands. This primal southeastern fauna consists of several genera widely distributed elsewhere, including *Aristelliger, Anolis* (*brunneus* and *scriptus*), *Cyclura, Chrysemys, Leiocephalus,* (*arenarius, greenwayi, inaguae, loxogrammus,* and *punctatus*), *Ameiva* (*maynardi*), *Leptotyphlops* (*columbi*), *Sphaerodactylus* (*caicosensis, corticola, inaguae, mariguanae,* and *underwoodi*), *Tropidophis* (*greenwayi*), and again, *Epicrates.*

The historical biogeography of the Bahama Islands and the evolution of the Great Bank and primal southeastern fauna was discussed in detail by Schwartz (1968). The primal assemblage evidently predates the recent fauna which presumably arrived in the Bahamas sometime after the Pleistocene inundations discussed by Rabb and Hayden

(1957). It is not clear why so few Great Bank genera managed to persist on the northern Bahamas while numerous taxa have survived on the southeastern Bahamas. Certainly one possibility is the hypothesis advanced by Pregill (1982) that the northern Bahamas, like certain of the Greater Antilles, underwent a climatic shift from a xeric to a more mesic environment in the Pleistocene which resulted in the mass extinction of many xeric-adapted species. It would seem that a eustatic event catastrophic enough to cause the extinction of small anolines or sphaerodactylines would not spare a larger reptile like *E. exsul*. *Epicrates exsul* may simply have been better able to cope with more mesic environments than the majority of the ancient Little Bank herpetofauna. Alternatively, perhaps modern invaders like *Anolis distichus* and *Sphaerodactylus notatus* are in the process of replacing the older Bahamian stocks, and *E. exsul* and *E. chrysogaster* have remained only because the banks they occupy have not yet been invaded by a more modern competitor, like *E. striatus* (which may have supplanted the original *Epicrates* colonizers of the Great Bahama Bank).

Based on current geological evidence dispersal is the only reasonable explanation for colonization of the Bahamas by *Epicrates* in both cases, even if some of the Bahamas were periodically emergent during the Pliocene and Pleistocene rises in sea level. As Williams (1969) pointed out, many of these banks were more emergent during periods of glaciation during the Pleistocene, and the size of the water gaps between the Bahamas and the Greater Antilles were no doubt considerably less than they are today. The emergence of banks now fully submerged, such as the Navidad and Silver Banks, may have facilitated the colonization of some islands (Schwartz, 1968). Isolation on separate banks may have resulted in the differences which now distinguish *E. chrysogaster* and *E. exsul* from each other.

If the Bahamian *Epicrates* are eliminated from the area cladogram along with *E. fordii* and *E. gracilis* (the two species sympatric with *E. striatus* on Hispaniola), the Isla Mona population of *E. monensis*, and *E. subflavus* of Jamaica, a cladogram similar to Fig. 26 would result. This cladogram includes the remaining species: *E. cenchria, E. angulifer, E. striatus* (Hispaniolan populations only), *E. inornatus* and Virgin Islands *E. monensis*. This group could have arisen by the following scenario of speciation: *E. cenchria* + (*E. angulifer* + (*E. striatus* + (*E. inornatus* + *E. monensis*))), which could have been ultimately caused by the sequential separation of the following landmasses: Central America + (Cuba + (Hispaniola + (Puerto Rico + Virgin Islands))).

Despite this possibility, I believe the available evidence favors dispersal for the origin of West Indian *Epicrates*. The very strong case for dispersal for four of the West Indian species (*E. chrysogaster, E. exsul, E. fordii,* and *E. gracilis*) plus the probable dispersal of several other subspecies in the genus (the Bahamian *E. striatus* and *E. monensis monensis*) makes any case for vicariance as a major speciation force in this genus seem thin and contrived.

This does not mean that proto-Antillean eastward movement had no effect on the evolution of the genus. More than one of the proposed geophysical models shows these islands in close proximity during the Tertiary (Freeland and Dietz, 1972a; Malfait and Dinkleman, 1972; Perfit and Heetzen, 1978; Sykes et al., 1982). A tighter configuration of the islands in the early Tertiary would have significantly decreased the water gaps, not only between the Greater Antilles themselves, but also between the Greater Antilles and the mainland, making dispersal much easier than it is today. Also, I believe this is at least a partial answer to a question posed by Williams (1969) in reference to the mainland anoline fauna of Central and South America: "why have these mainland stocks provided no recent invaders . . . of the larger and more stable island at all?" Moreover, latter day passive dispersals from Central America to the Greater Antilles would be against the path of the prevailing winds and the flow of the Equatorial and Antillean Currents. Darlington (1938) demonstrated that occasional hurricanes crossed from the mainland over the Greater Antilles in the recent past, but by far the majority of these types of storms pass, like the prevailing winds and currents, east to west. *Ameiva, Boa, Corallus* and *Leimadophis* may be representatives of reptilian species which may have colonized the islands or have been distributed within the islands along the flow of the major currents in the area (Lazell, 1964).

What I have attempted to present in this treatise is a biogeographical model that would most parsimoniously interpret the distributions of sister groups of *Epicrates* within the Bahamas and Greater Antilles. Most of these distributions seem unequivocally due to dispersal. Others could be the result of either vicariance or dispersal, and some reduced area cladogram may be yet found that is congruent with patterns of *Epicrates* and other Antillean biological elements—not necessarily amphibians and reptiles. But if vicariance is to be demonstrated, a method must be found to distinguish it from linear dispersal. Herein lies the major problem of this type of analysis (e.g., congruence of several multi-taxon cladograms) applied to the Caribbean: one cannot be certain if a pattern of distribution in the Antilles which includes Cuba, Hispaniola, and Puerto Rico (with more primitive forms in the

west and more advanced forms to the east) was the result of multiple vicariant events trending from west to east or linear dispersal *sensu* Darlington (1938). Recent weather and current patterns in the Caribbean suggest that dispersal might have been an orderly process in this region.

It has been suggested to me (Rosen, pers. comm.) that a way around this difficulty is to examine four-taxon cladistic statements for a wide variety of organisms. There would be a low probability that several groups of organisms of widely differing vagilities would share the same reduced area cladogram. In the Caribbean, however, the faunas are depauperate, and the organisms that predominate are highly vagile. There are few large mammals, fossil or living, and the extant fish faunas are very reduced and salt tolerant. Futhermore, phylogenetic studies of the Antillean fishes can be interpreted to indicate that the present Antillean fish distributions are the result of several invasions from the mainland from the mid-Tertiary to the present (Briggs, 1984). Examination of reduced area cladograms, therefore, may explain nothing. These speculations cannot prove that vicariance was not responsible for the distributions of the herpetofauna in the Greater Antilles, but at present there is no single distributional pattern for the endemic herpetofauna that demands a single causal theory, like vicariance.

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APPENDIX

Specimens Examined

Skin, *Epicrates* spp.:

Epicrates angulifer (total 10) Cuba, U. S. Naval Base, Guantanamo Bay (PJT 034-43).

Epicrates cenchria maurus (total 4) Panama, Canal Zone (PJT 048-9); no data (PJT 007, 050).

Epicrates chrysogaster chrysogaster (total 4) Turks and Caicos Islands, North Caicos, near Kew (PJT 015-6); no data (RBF 292, 444).

Epicrates exsul (total 7) Bahamas, Great Abaco, near Marsh Harbor (PJT 044-7); no data (RBF 536, 749, 765).

Epicrates fordii fordii (total 7) Haiti, near Manneville (PJT 027-31, 033); near Petionville (PJT 032).

Epicrates gracilis (total 6) Haiti, near Port Margot (PJT 017-022).

Epicrates inornatus (total 9) Puerto Rico, no data (PJT 008; RBF 212, 276, 285, 417, 447-8, 824, 827).

Epicrates monensis monensis (total 1) Puerto Rico, Isla Mona, near Pajaros (WHC 1).

Epicrates monensis ssp. (total 6) no data (PJT 051-6).

Epicrates striatus fosteri (total 2) Bahamas, Bimini Islands (PJT 013-4).

Epicrates striatus striatus (total 20) Haiti, near Limbe (PJT 018-9, 023); near Port Margot (PJT 017, 020-2, 024-6); no data (PJT 004-6; seven uncataloged specimens).

Epicrates subflavus (total 4) Jamaica, no data (PJT 001-3; RBF 424).

Skin, *Corallus* spp.:

Corallus canina (total 1) no data (GK, no number).

Corallus enydris (total 5) no data (GK, 2 specimens, no numbers; JLL, 2 specimens, no numbers; VH, 1 specimen, no number).

Scent Glands, *Epicrates* spp.:

Epicrates angulifer (total 10) Cuba, U. S. Naval Base, Guantanamo Bay (PJT 034-43).

Epicrates cenchria maurus (total 2) Panama, Canal Zone (PJT 049); no data (PJT 050).

Epicrates chrysogaster chrysogaster (total 6) Turks and Caicos Islands, North Caicos, near Kew (PJT 015-6); no data (RBF 292, 295-6, 727).

Epicrates chrysogaster reliquus (total 1) Bahamas, Great Inagua, near Matthew Town (RBF 726).

Epicrates exsul (total 7) Bahamas, Great Abaco, near Marsh Harbour (PJT 044-7); no data (RBF 536, 749, 765).

Epicrates fordii fordii (total 7) Haiti, near Manneville (PJT 027-31, 033); near Petionville (PJT 032).

Epicrates gracilis (total 6) Haiti, near Port Margot (PJT 017-22).

Epicrates inornatus (total 6) Puerto Rico, no data (PJT 008; RBF 137, 216-7, 284, 611).

Epicrates monensis ssp. (total 6) no data (PJT 051-6).

Epicrates striatus fosteri (total 5) Bahamas, Bimini Islands (PJT 013-14; RBF 787, 873-4).

Epicrates striatus striatus (total 20) Haiti, near Limbe (PJT 018-9, 023); near Port Margot (PJT 017, 020-2, 024-26); no data (PJT 004-6; seven uncataloged specimens).

Epicrates subflavus (total 7) Jamaica, no data (PJT 001-3, RBF 095, 737-8, 740).

Scent Glands, *Corallus* spp.:

Corallus annulata (total 1) no data (RBF, no number).

Corallus canina (total 1) no data (GK, no number).

Corallus enydris (total 2) no data (GK, 2 specimens, no numbers).