

TRANSACTIONS OF THE 12TH CARIBBEAN GEOLOGICAL CONFERENCE

ST. CROIX, U.S. VIRGIN ISLANDS

August 7th - 11th, 1989



12me Conference Geologique de Caraibes

Edited by

David K. Larue

Department of Geology, University of Puerto Rico
Mayagüez, PR 00708, Puerto Rico

and

Grenville Draper

Department of Geology, Florida International University
Miami, FL 33199
U.S.A.

Additional copies of this book may be purchased from



Miami Geological Society
P.O. Box 431552
South Miami, FL 33243, U.S.A.

December 1990

Origin of the Eastern Caribbean: Data from Reptiles and Amphibians

Jonathan Roughgarden

Departments of Biological Sciences and Geophysics
Stanford University

Abstract

Data on the ecology, systematics, and biogeography of *Anolis* lizards, combined with that on other reptiles and amphibians in the eastern Caribbean, suggest that:

1. The northeastern and southeastern Caribbean have had distinct geologic histories. The line separating these provinces starts between Dominica and Martinique and extends southwest to between Curacao and Bonaire.
2. Within the northeastern province, material in the Guadeloupe-Dominica region has split off from Puerto Rico. The fauna of Guadeloupe and Dominica has had a primarily vicariant origin (i.e., consists of the descendants of populations that were on Proto-Guadeloupe at the time of its original fragmentation from Puerto Rico). This region has then served as a biological source for the younger islands north of Guadeloupe up to the Anegada Passage. Propagules have come north from Guadeloupe by over-water dispersal, in accordance with the prevailing currents.
3. Within the southeastern province, St. Lucia, La Blanquilla and Bonaire seem to be members of a former island arc that was "upstream" of the eastward-moving Caribbean plate. Collision with this island arc resulted in the insertion of St. Lucia between Martinique and St. Vincent, while La Blanquilla and Bonaire were pushed down onto the Venezuelan shelf. The oceanic islands of the southeastern province thus consist of at least four classes of terrains: Curacao—related perhaps to Grand Cayman; Bonaire and La Blanquilla—related to St. Lucia; the triplet consisting of Martinique, St. Vincent, and Grenada; and Barbados—exposed accretionary prism that has formed *in situ* and been colonized recently through local over-water dispersal.

The colorful and small arboreal lizards of the genus *Anolis* found on all the islands of the Caribbean and in Central America may serve as "living strata." Here, information about eastern Caribbean anoles is offered to help in reconstructing the origin of the Lesser Antillean Island Arc in relation to Puerto Rico and the Netherlands-Venezuelan Antilles. A preliminary account has appeared in Roughgarden et. al. (1987).

For a biological population to mark a geologic entity, such as an island or island bank, it must be a ready colonist; it must re-buff subsequent colonizations from adjacent geological entities, for otherwise the labels would mix; and it must not be prone to extinction. Anoles are hardy survivors on tropical cays; ecological competition between anoles for limiting resources retards cross invasion between adjacent islands, and prevents cross invasion altogether between species of the same body size; and the huge population size on a Lesser Antillean island (estimated at 10^8 for a 400 km² island assuming 0.25 lizards per m²) precludes chance extinction and increases the likelihood of contributing a propagule to newly opened habitat. Also, anoles are diverse, and thereby provide many labels. There are over 300 species of *Anolis*, about half of which are in the West Indies, and half in Central and northern South America. The genus is one of the largest of all vertebrate genera, and comprises about 5–10% of all lizard species in the world today.

Moreover, anoles have been in the Caribbean theater for a long time. A complete fossil *Anolis* encased in early Miocene amber (ca. 20–23 my BP) has been found in the Cordillera Septentrional of the Dominican Republic (Rieppel 1980). It may be even older than originally reported, lower Oligocene or upper Eocene (35–40 my BP), according to Poiner and Cannatella (1987). The specimen is a juvenile lizard indistinguishable from the green anoles now living in Hispaniola, *A. chlorocyanus* and *A. aliniger*. Skin fragments from another fossil anole have been described from Chiapas, Mexico; its amber has been dated as late Oligocene to early Miocene (Lazell 1965). Finally, the lineage (clade) consisting of the Iguanidae (including *Anolis*) is old, splitting from a sister lineage consisting of the Agamidae and Chamaeleonidae in the middle Jurassic (175 Ma) (Estes 1983). In contrast, old rock strata in the Caribbean are scarce, as Jurassic and Cretaceous materials have been lost to subduction or covered by more recent magmatic activity. Thus, anoles have been in place as the Caribbean itself has formed, and the systematics, ecology, and biogeography of these lizards may therefore provide sorely needed clues about the origin of the Caribbean to supplement geologic data.

The key conclusions offered here are:

- The northeastern and southeastern Caribbean have had separate geologic histories. The line separating these provinces starts between Dominica and Martinique and extends southwest to between Curacao and Bonaire, demarking a triangle at the southeastern corner of the Caribbean Plate.

- Within the northeastern Caribbean, material in the Guadeloupe-Dominica region split off from Puerto Rico. The fauna of this region has had a primarily vicariant origin (i.e., it consists of the descendents of populations that were on Proto-Guadeloupe at the time of its original fragmentation from Puerto Rico). The Guadeloupe region has itself served as the source for the biota on the younger islands north of Guadeloupe up to the Anegada Passage, and the propagules have come north from Guadeloupe by over-water dispersal, in accordance with the prevailing currents.
- Within the southeastern triangle of the Caribbean, St. Lucia, La Blanquilla and Bonaire are members of a former island arc that was upstream of the eastward-moving Caribbean plate. Collision with this island arc resulted in the addition of St. Lucia between Martinique and St. Vincent, and pushed La Blanquilla and Bonaire down onto the Venezuelan shelf.

The oceanic islands of the southeastern Caribbean thus consist of at least four classes of terranes: (1) Curacao—perhaps related to Grand Cayman; (2) Bonaire and La Blanquilla—related to St. Lucia; (3) the triplet consisting of Martinique, St. Vincent, and Grenada; and (4) Barbados—an exposed piece of accretionary prism that has formed in situ and has been colonized solely through over-water dispersal.

Also, biological data are consistent with speculation that some geologic material presently in the West Indies was in the neighborhood of nuclear Central America and northern South America during the Cretaceous, all of which comprised an archipelago in the Pacific. The southeastern triangle may have been sutured to the Caribbean plate.

1 Biological Data

We now review the main facts about the systematics, ecology, and biogeography of *Anolis* lizards, and of reptiles and amphibians in general, for the eastern Caribbean.

1.1 Systematics

1.1.1 Early Research on *Anolis*

Using squamation characters (number, size, shape, texture and arrangement of scales), Underwood (1959) proposed that the anoles of the eastern Caribbean comprise three sets having the relationship diagrammed in Figure 1.

The northern Lesser Antilles (Figure 2), from the Anguilla Bank through Dominica, are populated by the "bimaculatus group," which itself contains two series, the "wattsii series" and the "bimaculatus series."

The wattsii series are small brown lizards that typically perch near the ground and on the leaf litter. Each population from this series co-occurs with a population from the bimaculatus series; no population of the wattsii series occurs alone on an island.

The bimaculatus series consists of colorful large- and medium-sized lizards that are relatively arboreal. Some bimaculatus populations are alone on an island and others co-occur with a member of the wattsii series. Underwood (1959) envisaged that each of these series represented a separate invasion from Puerto Rico, and that the wattsii series was the more recent invasion.

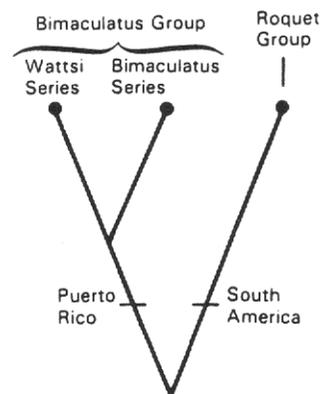


Figure 1. Relationship among eastern Caribbean *Anolis* from early systematic research. The wattsii and bimaculatus series of the northern Lesser Antilles were presumed to represent separate waves of invasion from Puerto Rico, with the wattsii series being the more recent invasion. The roquet series of the southern Lesser Antilles was presumed to be derived from South America.

The southern Lesser Antilles (Figure 2), from Martinique through Grenada, are populated by the "roquet group;" today it is also known that the anoles on Bonaire in the Netherlands Antilles and La Blanquilla in the Venezuelan Antilles are also members of this group. The roquet group was presumed to have colonized from South America.

1.1.2 Contemporary Studies of *Anolis*

Systematic research since the species were originally described has clarified the phylogenetic relationships of the species, and corroborates the early definitions of species groups based on squamation. The new data consist of karyotypes (descriptions of chromosomes), the immunological analysis of blood albumins, and the electrophoresis of proteins from over 20 loci (Gorman and Atkins 1969, Gorman 1973, Paull et al. 1976, Yang et al. 1974, Gorman and Kim 1976, Gorman et al. 1980, 1983, Shochat and Dessauer 1981).

Figure 3 offers my synthesis of the phylogenetic relationships entailed by this recent work (see also the extensive notes accompanying the figure). The taxa being classified are the populations on each of the island banks in the Lesser Antilles, together with all the Puerto Rican anoles. Geographically differentiated varieties (subspecies) are diagrammed as horizontal lines with vertical tick marks to indicate each named variety. Notice that the islands in the center of the arc, Guadeloupe, Dominica, and Martinique have species with geographical variation (i.e., multiple subspecies); the species on the other islands show little internal differentiation. The major branches express a strict consensus among the morphological, karyotypic, and biochemical data.

The most important new findings are: (1) the distinction between the bimaculatus and roquet groups reflects a deeply different chromosomal makeup, and great biochemical dissimilarity in blood albumins; (2) the bimaculatus group is sister to the cristatellus group of Puerto Rico, and both belong to a lineage termed the Central Caribbean Complex by Shochat and Dessauer (1981); (3) the genetic distances among the populations in the wattsii series are as great or greater than those

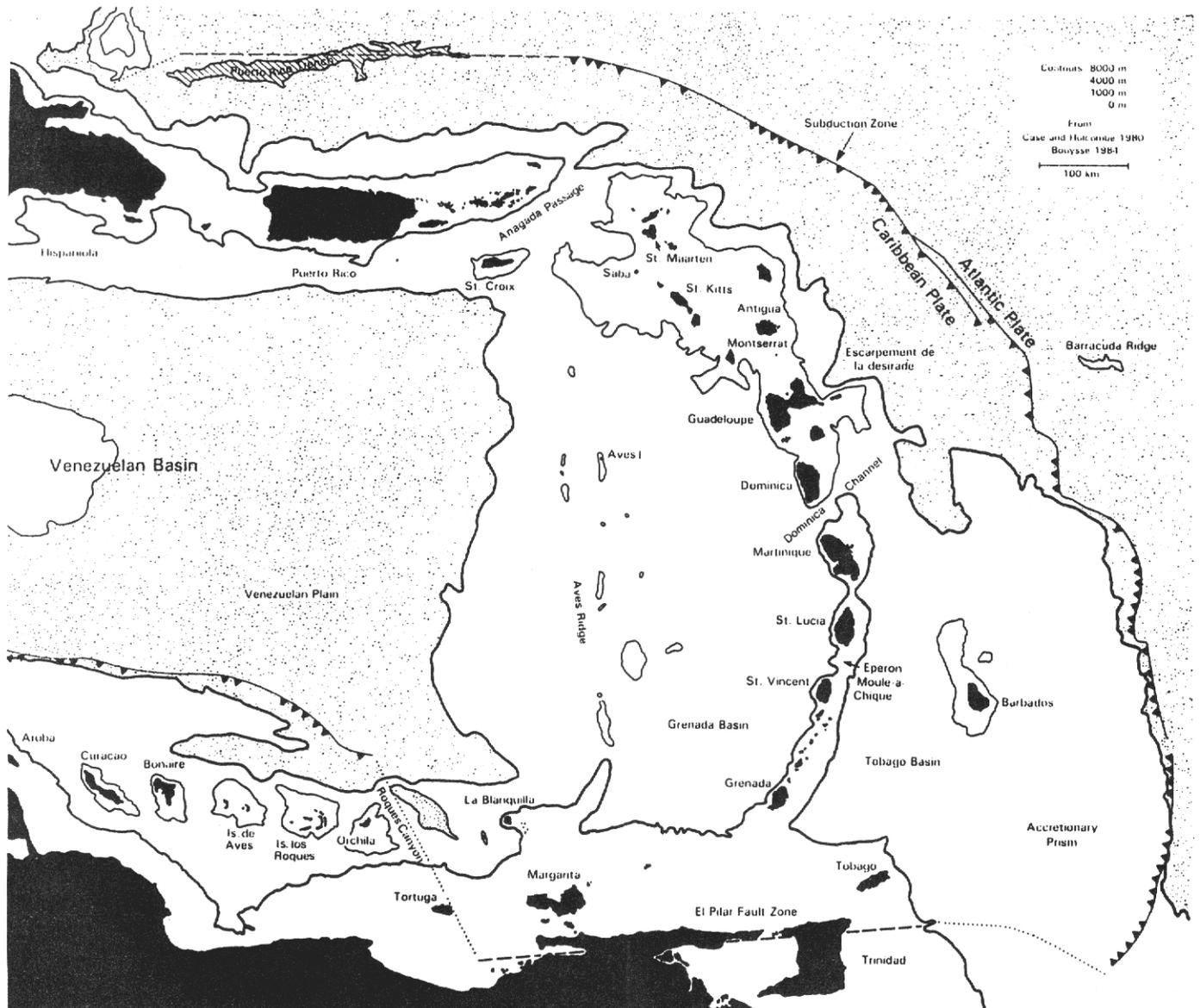


Figure 2. Tectonic map of Lesser Antilles. In the North, the Guadeloupe area has deposits as old as the oldest in the Greater Antilles. It is also a center of endemism for the bimaculatus

in the bimaculatus series; and (4) the roquet group subdivides into a "roquet" series and a "luciae" series, with the luciae series comprising the populations on St. Lucia, La Blanquilla, and Bonaire.

The distinction between the roquet and bimaculatus groups has proved so significant that Guyer and Savage (1986) recently suggested elevating the roquet group to generic status, and suggested the generic name, *Dactyloa* for the roquet group anoles.

Locating continental relatives of Caribbean anoles is difficult, even though over 150 species occur in Central and South America. The continental anoles are only distantly related to Caribbean anoles.

The closest known relative of an anole from the northeastern Caribbean, *A. evermanni* from Puerto Rico, is *A. gadovi*, from the Pacific versant [sic] of tropical Mexico. *A. gadovi* is itself a member of a cluster of rather closely related species in western Mexico, called the *gadovi* group. The albumin distance

group of *Anolis* lizards, a sister lineage of the cristatellus group of the Puerto Rico bank. In the South, the anoles come from the roquet group, and are not closely related to those in the North.

of the Puerto Rican anole to this Mexican anole is 29 units, a value far less than, for example, the typical albumin distance of about 55–60 units between a bimaculatus and roquet anole (Gorman 1984). (See notes to Figure 3 for other known albumin distances.) The karyotype of *A. gadovi* also includes sex chromosomes, which may be considered a derived characteristic shared with the eastern Caribbean anoles, all of which also have sex chromosomes (Lieb 1981).

Perhaps even more surprising, the closest known non-West Indian relative of an anole from the southeastern Caribbean is *A. agassizi* on the isolated island of Malpelo in the Pacific south of Panama and west of Columbia (Graham 1975). Shochat and Dessauer (1981) report an albumin distance of 40 units between *A. extremus* of Barbados (itself nearly identical to *A. roquet* of Martinique) and *A. agassizi* of Malpelo, and unpublished data of Gorman (personal communication) show an even closer relationship. The distance of *A. extremus* to a typical anole of

1986), whereas dispersal from Puerto Rico down into the Lesser Antilles is contrary to those currents.

Finally, the biochemical differentiation among the bimaculatus populations is appreciably less than that among the cristatellus populations or among the roquet populations, suggesting that the bimaculatus series is younger than the cristatellus or roquet series.

1.2 Ecology

1.2.1 Population Dynamics

Long-term monitoring of *Anolis* populations on St. Maarten has revealed a remarkable stability in the population dynamics of *Anolis* on a tropical island. Roughgarden and coworkers have censused two sites on St. Maarten once or twice a year from 1977–1987. Year after year the same cyclic pattern recurs even though two hurricanes passed the sites and the annual rainfall may vary by a factor of up to 2 in consecutive years. The abundance is lowest during the summer when the abundance is typically 0.5 lizards per m² and more than doubles during the winter with the production of juveniles. The between-year variation in abundance compared at the same point in the seasonal cycle is less than the within-year variation, and the summer abundance has been essentially constant (within 10%) at the two sites during 11 years. This abundance is what makes anoles likely colonists of new habitat as it forms, and makes chance population extinction unlikely.

1.2.2 Resource Limitation

Experimental studies point to food, and not space, as the principal limiting resource. Removal of lizards from experimental enclosures leads to a doubling of insect abundance on the forest floor and to a 10- to 30-fold increase in the quantity of spiders in the vegetation (Pacala and Roughgarden 1984, Schoener and Spiller 1987). Also, food augmentation increases lizard growth rates in nature (Licht 1974, Stamps 1977). In contrast, experimentally increasing the spatial overlap in perch positions of the two species on St. Eustatius produces little effect (Rummel and Roughgarden 1985) and interspecific territoriality cannot be detected except between animals of nearly identical body sizes (Bohlen 1983). The existence of food as a limiting resource is what underlies the existence of competition between lizard species.

1.2.3 Competition between Species

Experiments in which anoles were introduced to an offshore cay and to 12m × 12m enclosures experiments proved the existence of strong present-day competition between the two species on St. Maarten (where the body sizes of the two species are nearly the same) and also that competition between the two species on St. Eustatius (where the lizard species differ in size by a factor of nearly two) is weak and barely detectable (Roughgarden et al. 1984, Pacala and Roughgarden 1985, Rummel and Roughgarden 1985). This competition is what prevents islands from simply accumulating species without limit; it ensures that a species on an island becomes, in time, a unique label for that island.

1.2.4 Invasion

The record of recently introduced anoles supplies more evidence of interspecific competition. To aid the biological control of the fruit fly, *Ceratitidis capitata*, in 1905 the Director of Agriculture of Bermuda liberated 71 individuals of *A. grahmi* in public gardens (Wingate 1965). *A. grahmi* is a medium sized lizard; it was collected from the Kingston area of Jamaica. By 1940 *A. grahmi* was abundantly distributed throughout Bermuda. About 1940 the large anole from Antigua, *A. bimaculatus leachi*, first appeared. The species is now established in the center of Bermuda (Warwick area), primarily in woods. The spread of this large anole has taken place on territory already occupied by the medium sized anole. Finally, the solitary-sized anole, *A. extremus* from Barbados was noted in 1953 at the western end of Bermuda (Somerset and Ireland areas) where it still has a patchy distribution.

Hispaniola provides two well-documented instances of "enclaves" of introduced anoles; these typically form when natural habitat is cleared and replaced with plantings (Williams 1977). The Cuban green anole, *A. porcatius*, has been known since 1970 from a few city blocks in Santo Domingo at the site of former trade fairs. Its range has remained static through 1977 and is surrounded by the native green anole, *A. chlorocyanus*. The Puerto Rican trunk-ground anole, *A. cristatellus*, has been known since 1956 to be abundant in gardens in the port city of La Romana in the Dominican Republic. The town is the site of a sugar mill constructed by a Puerto Rican based company. The range of the anole has been static for over 20 years and is surrounded by the native trunk-ground anole, *A. cybotes*. Schoener and Schoener (1983a) also produced enclaves in the Bahamas with experimental introductions to tiny cays that were already inhabited by an anole. In contrast, introductions to empty cays large enough to support anoles invariably produced a population explosion of the introduced species.

Introduced small anoles evidently do not form enclaves when surrounded by larger anoles. A population of *A. watsi* known from the botanical garden in St. Lucia has become extinct (Underwood 1959, Williams 1977). *Anolis watsi* was introduced four times to a cay near Anguilla where *A. gingivinus* was already living and *A. watsi* eventually became extinct each time. The waiting time to extinction could be doubled simply by removing half of the *A. gingivinus* at the site prior to the introduction (Roughgarden et al. 1984).

Thus, a large anole can become established in the presence of a smaller anole, an anole introduced to newly opened habitat can form a virtually static enclave in the range of another anole with similar size and habits, and a small anole evidently cannot be introduced successfully in the presence of a larger anole. Thus, competition between species ensures that the species, considered as labels for islands, remain as faithful markers of geologic structures.

1.2.5 Extinction

The tiny cays on the Puerto Rico Bank (British Virgin Islands) demonstrate how a complex herpetofauna responds to habitat fragmentation. These keys reveal that the species lists for a sequence of islands of decreasing area comprise, approximately, a sequence of nested subsets. The cays are not random subsets of some larger fauna. Specifically, all the cays with only one species of amphibian or reptile have precisely *A. cristatellus*, those with two species have both *A. cristatellus* and a gecko

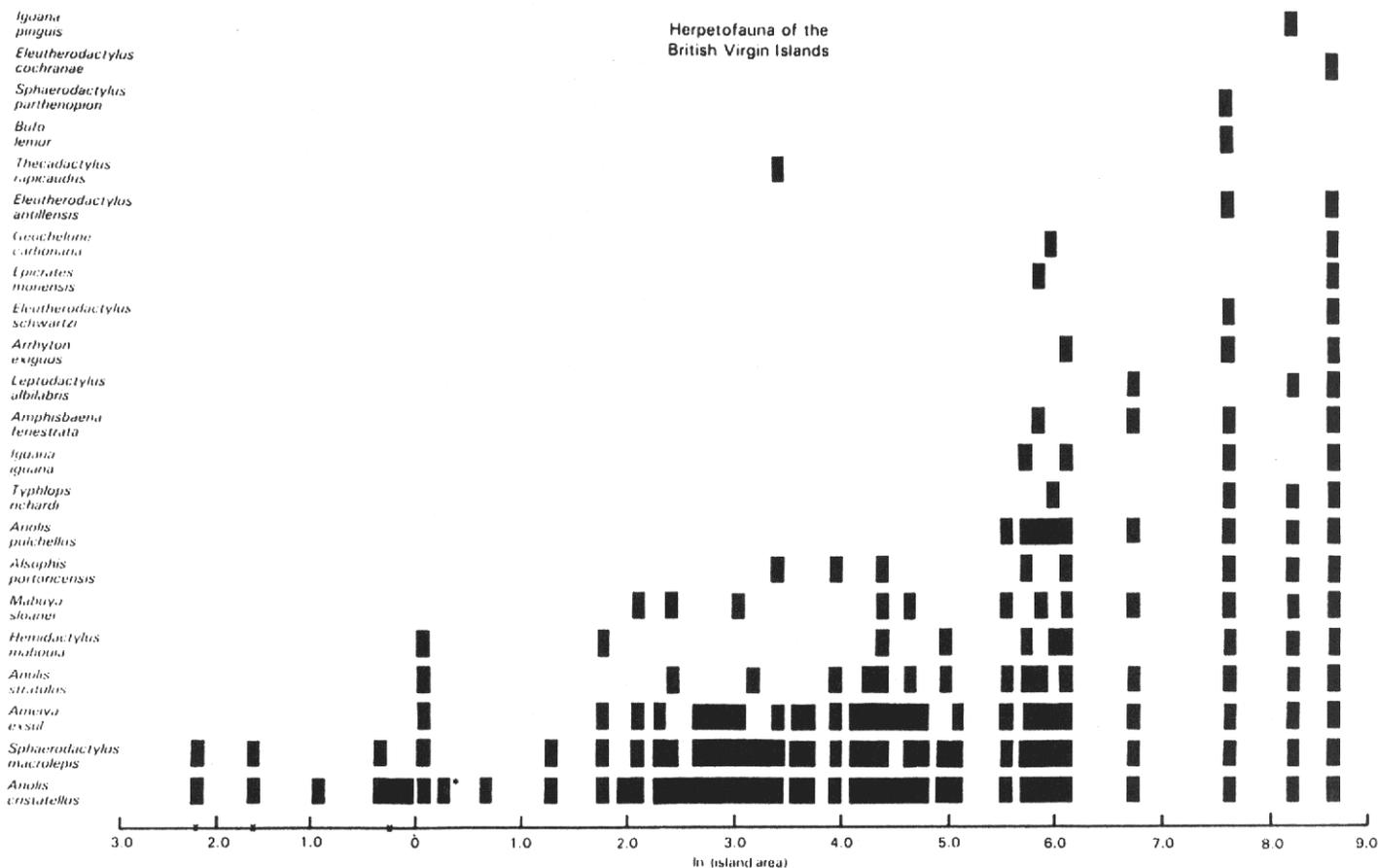


Figure 4. Nested subset pattern for the relation between island area and species occurrence for amphibians and reptiles in the British Virgin Islands. Notice that *Anolis cristatellus* is the species that can survive on the smallest cay; it has the

Sphaerodactylus macrolepis, those with three or more species have these plus certain others—each species seems to have a minimum island area at which it is first found, and is present on all islands larger than its minimum area. Thus, the islands with only one species do not possess random species, nor do islands with only two species possess random pairs, drawn, as it were, from some urn of all species in the region. Figure 4 presents the data from Lazell (1983) for the British Virgin Islands. Schoener and Schoener (1983b) discovered that the lizards on cays of the Bahama Bank also form nested subsets.

During the Pleistocene 15000 years ago, the Puerto Rico Bank extending to Anegada was above water (Heatwole and MacKenzie 1967). As the glaciers melted slight hilltops became the tiny cays of the British Virgin Islands today. The lizards on these cays presumably did not have to disperse there, they were there to begin with. The fauna on the cays consists of special species that have the property of not becoming extinct when the size of their habitat shrinks. They have, so to speak, a good "bottle-necking" ability—colonizing ability is probably irrelevant to their presence on the cays of the Puerto Rico Bank.

It is important to observe that *A. cristatellus*, the particular lizard that is retained on even the smallest of the Virgin Island cays, is the sister taxon to the bimaculatus group of the northern Lesser Antilles. This fact supports a hypothesis that the fauna in the northern Lesser Antilles is a differentiated fragment extracted from the Puerto Rican fauna.

best "bottle-necking" ability, and presumably for this reason is the parental lineage to the bimaculatus group centered in the Northern Lesser Antilles, as noted in Figure 2.

1.3 Biogeography

1.3.1 Distribution of Amphibians and Reptiles

Table I presents all the amphibians and reptiles of the Lesser Antilles today compiled from the checklist of Schwartz and Thomas (1975) and the magnificent field guide of Schwartz and Henderson (1985).

The faunal break at Dominica marking the end of the bimaculatus group of anoles in the Lesser Antilles is observed by *Ameiva* ground lizards, *Typhlops* blind snakes, and *Alsophis* snakes. The *Ameiva* in St. Vincent and Grenada is South American, and the *Liophis* snakes of the southern islands are a South American genus.

Also, Dominica is the southern end of the *Sphaerodactylus fantasticus* complex, and the *S. vincenti* complex begins in the adjacent Martinique where seven subspecies are found. It would be useful to know if the *S. vincenti* complex is very distantly related to the *S. fantasticus* complex as are the anoles on these adjacent islands. Perhaps a difference between the *S. fantasticus* and *S. vincenti* complex is as great as that between the bimaculatus and roquet groups, and a test of this proposition would be very significant.

The Guadeloupe archipelago is unique among the northern islands in having a great endemic differentiation of anoles, *Sphaerodactylus* geckoes, *Alsophis* snakes and *Eleutherodactylus* frogs. *A. mormonatus* is recognized as one species having 12

Table Ia. Herpetofauna of Northern Lesser Antilles

	ANGUILLA	SABA	ST. KITTS <i>marinus</i> ^A	ANTIGUA <i>marinus</i>	MONTERRAT <i>marinus</i>	GUADELOUPE <i>marinus</i>	DOMINICA
<i>Bufo</i>							
<i>Hyla</i>							
<i>Leptodactylus</i>			<i>fallax</i> ^C		<i>fallax</i>	<i>fallax</i>	<i>fallax</i>
<i>Eleutherodactylus</i>	<i>johnstoni</i> ^E	<i>johnstoni</i>	<i>johnstoni</i>	<i>johnstoni</i> <i>martinicensis</i> ^F	<i>johnstoni</i>	<i>johnstoni</i> <i>martinicensis</i> <i>barlagnei</i> ^G <i>pinchoni</i> ^H	<i>martinicensis</i>
<i>Mabuya</i>	<i>mabouya</i> ^K						
<i>Diploglossus</i>							
<i>Ameiva</i>	<i>corvina</i> ^M <i>pleei</i> ^N		<i>erythrocephala</i> ^O	<i>griswoldi</i> ^P	<i>mabouya</i> <i>montisserrati</i> ^L <i>pluvianotata</i> ^Q	<i>mabouya</i>	<i>mabouya</i>
<i>Cnemidophorus</i>						<i>cineracea</i> ^R	<i>fuscata</i> ^S
<i>Bachia</i>							
<i>Kentropyx</i>							
<i>Gymnophthalmus</i>							
<i>Thecadactylus</i>	<i>rapicauda</i> ¹	<i>rapicauda</i>	<i>rapicauda</i>	<i>rapicauda</i>		<i>underwoodi</i> ^X	
<i>Hemidactylus</i>	<i>mabouia</i> ²	<i>mabouia</i>	<i>mabouia</i>	<i>mabouia</i>	<i>rapicauda</i>	<i>rapicauda</i>	<i>rapicauda</i>
<i>Phyllodactylus</i>					<i>mabouia</i>	<i>mabouia</i>	<i>mabouia</i>
<i>Sphaerodactylus</i>	<i>sputator</i> ⁵ <i>macrolepis</i> ⁶ <i>delicatissima</i> ^c	<i>sabanus</i> ⁷	<i>sputator</i> <i>sabanus</i> <i>delicatissima</i>	<i>elegantulus</i> ⁸	<i>fantasticus</i>	<i>fantasticus</i> spp. ⁹	<i>fantasticus</i>
<i>Iguana</i>		<i>iguana</i> ^d				<i>delicatissima</i>	<i>delicatissima</i>
<i>Anolis</i>	<i>gingivinus</i> ^e <i>wattsii</i> ^f	<i>sabanus</i> ⁸	<i>bimaculatus</i> ^h <i>wattsii</i> ^g <i>monastus</i> ^v	<i>bimaculatus</i> ^j <i>wattsii</i> spp. ^k <i>monastus</i>	<i>iguana</i> <i>lividus</i> ^l <i>monastus</i> ^m	<i>iguana</i> <i>marmoratus</i> spp. ^m <i>dominicana</i> ^x	<i>oculatus</i> spp. ⁿ <i>dominicana</i> ^y
<i>Typhlops</i>							
<i>Leptotyphlops</i>							
<i>Bothrops</i>							
<i>Boa</i>							<i>constrictor</i> ^{dd}
<i>Corallus</i>							
<i>Alsophis</i>	<i>rijersmaii</i> ^{ss}	<i>rufiventris</i> ^{hh}	<i>rufiventris</i>	<i>antillensis</i>	<i>antillensis</i>	<i>antillensis</i> spp. ⁱⁱ <i>juliae</i> spp. ^{jj}	<i>antillensis</i> <i>juliae</i>
<i>Liophus</i>							
<i>Chironius</i>							
<i>Clelia</i>							<i>clelia</i> ^{pp}
<i>Mastigodryas</i>							
<i>Pseudoboa</i>							

Table Ib. Herpetofauna of Southern Lesser Antilles

	MARTINIQUE	ST. LUCIA	ST. VINCENT	GRENADA	BARBADOS
<i>Bufo</i>	<i>marinus</i>	<i>marinus</i>	<i>marinus</i>	<i>marinus</i>	<i>marinus</i>
<i>Hyla</i>		<i>rubra</i> ^B			
<i>Leptodactylus</i>		<i>fallax</i>	<i>wagneri</i> ^D	<i>wagneri</i>	
<i>Eleutherodactylus</i>	<i>johnstoni</i> <i>martinicensis</i>	<i>johnstoni</i> <i>mabouya</i>	<i>johnstoni</i> <i>urichi</i> ^I <i>mabouya</i>	<i>johnstoni</i> <i>urichi</i> ^J <i>mabouya</i>	<i>johnstoni</i> <i>mabouya</i>
<i>Mabuya</i>			<i>ameiva</i> ^T	<i>ameiva</i>	
<i>Diploglossus</i>		<i>vanzoi</i> ^U			
<i>Ameiva</i>				<i>heteropus</i> ^V	
<i>Cnemidophorus</i>					<i>copei</i> ^W
<i>Bachia</i>		<i>pleei</i> spp. ^Z	<i>underwoodi</i>		<i>underwoodi</i>
<i>Kentropyx</i>		<i>rapicauda</i>	<i>rapicauda</i>	<i>rapicauda</i>	
<i>Gymnophthalmus</i>	<i>pleei</i> ^Y	<i>mabouia</i>	<i>mabouia</i>	<i>mabouia</i>	
<i>Thecadactylus</i>	<i>rapicauda</i>	<i>palaichthus</i> ³			
<i>Hemidactylus</i>	<i>mabouia</i>				<i>pulcher</i> ⁴
<i>Phyllodactylus</i>		<i>microlepis</i> spp. ^b			
<i>Sphaerodactylus</i>		<i>vincenti</i>	<i>vincenti</i>		
<i>Iguana</i>	<i>vincenti</i> spp. ^a <i>delicatissima</i>	<i>iguana</i> <i>luciae</i> ^P	<i>iguana</i> <i>griseus</i> ^Q <i>trinatis</i> ^R	<i>iguana</i> <i>richardi</i> ⁸ <i>aeneus</i> ^t <i>tasymicris</i> ²	<i>extremus</i> ^u
<i>Anolis</i>	<i>roquet</i> spp. ^o				
<i>Typhlops</i>					
<i>Leptotyphlops</i>	<i>bilineata</i> ^{aa}	<i>bilineata</i>			<i>bilineata</i>
<i>Bothrops</i>	<i>lanceolata</i> ^{bb}	<i>caribbaea</i> ^{cc}			
<i>Boa</i>		<i>constrictor</i> ^{ee}			
<i>Corallus</i>			<i>enydris</i> ^{ff}	<i>enydris</i>	
<i>Alsophis</i>					
<i>Liophus</i>	<i>cursor</i> ^{kk}	<i>ornatus</i> ^{ll}		<i>melanotus</i> ^{mm}	<i>perfuscus</i> ⁿⁿ
<i>Chironius</i>			<i>vincenti</i> ^{oo}		
<i>Clelia</i>		<i>clelia</i>		<i>clelia</i>	
<i>Mastigodryas</i>			<i>bruesi</i> ^{qq}	<i>bruesi</i>	
<i>Pseudoboa</i>				<i>neuwiedii</i> ^{rr}	

subspecies on Guadeloupe and the nearby islands, including the Ile de Saintes and Marie Galante. The species on Montserrat and Dominica are very close to *A. mormoratus*. Similarly, the *Sphaerodactylus* is recognized as one species having seven subspecies on Guadeloupe and nearby islands, together with subspecies on Montserrat and Dominica. The *Alsophis* is recognized as one species having two subspecies on Guadeloupe and nearby islands, together with subspecies on the Antigua bank, Montserrat, and Dominica. The *Eleutherodactylus* is recognized as four species including two species that occur only in middle elevation forest on Basse-Terre in Guadeloupe.

St. Lucia is as anomalous for other components of the herpetofauna as it is for *Anolis*. The closest relatives of *A. luciae* are the anoles of Bonaire and La Blanquilla near the coast of Venezuela, not the anoles from adjacent islands. St. Lucia is also anomalous in having the only hylid frog of the Lesser Antilles, *Hyla rubra* from South America; the only *Cnemidophorus* lizard of the Lesser Antilles, *C. vanzoi* similar to the widespread *C. lemniscatus* of South America; a South American gecko, *Hemidactylus palaichthus*; and a fere-de-lance, *Bothrops caribbaea*, nearly identical to the widespread South American *Bothrops atrox*.

Competition appears related to body size in some other lizards as it is in *Anolis*. The two species of *Iguana* having the same body size show a perfect checkerboard distribution. Every island has an iguana, but the two species do not co-occur anywhere. Even on Guadeloupe *I. delicatissima* occurs on Grand Terre while *I. iguana* is on Basse Terre. Similarly, no habitat has two species of *Ameiva* all of which have about the same body size in the Lesser Antilles. *Ameiva polops* is endemic to Sombrero and *A. corvina* occurs throughout the rest of the Anguilla bank. Yet on Hispaniola, where there are four species, the two extremes in body size coexist in the same habitat.

The Puerto Rico bank has five species of *Amphisbaena* burrowing lizards. One species is found today in the British Virgin Islands on cays larger than 300 ha. None, however, is found in the Lesser Antilles. The Puerto Rico bank also has four species of *Typhlops* blind snakes, and one occurs in the British Virgin islands on cays larger than 350 ha. The Lesser Antilles do have a *Typhlops* on the St. Kitts and Antigua banks through to Dominica.

1.3.2 Distribution of Other Groups

While it is beyond the scope of this article to review all known distributions of plants and animals in the Caribbean, the following paragraphs should help to place the data on amphibians and reptiles in perspective.

Perhaps the most intriguing biogeographic reference relative to today's tectonic setting is Alexander Agassiz's (1835-1910) "demonstration that the deep-water animals of the Caribbean Sea are more nearly related to those of the Pacific depths than they are to those of the Atlantic."—quoted from Singer (1931, p.255). Agassiz concluded that the Caribbean was once a bay of the Pacific that since the Cretaceous has been cut off from the Pacific by the uplift of the Isthmus of Panama. Today, of course, this observation would be taken as consistent with the hypothesis that much of the Caribbean sea floor was in the Pacific during the Cretaceous. The most recent analysis of tectonic implications for marine biogeography is offered by Durham (1985).

Howard (1973) noted 10 genera of plants from the Greater Antilles that reach the northern Lesser Antilles (Table VI, p. 23). Of these, five terminate at Guadeloupe and the rest north of

Guadeloupe; that is, Guadeloupe is as far south as these genera reach.

Schwartz (1978) reviewed the distribution of amphibians and reptiles throughout the Greater and Lesser Antilles. Table I for the Lesser Antilles is drawn from this and his later work. For the Greater Antilles, highlights include the existence of endemic satellite genera to the anoles: *Chamaeleolis* with three species on Cuba, and *Chamaelinorops* from the south island of Hispaniola. Cuba also has an endemic genus of burrowing lizard, *Cadea*, with two species. And of special interest, Cuba has an endemic genus *Cricosaura* of the family Xantusiidae, the night lizards. The other three genera of this family occur in the southwestern United States, on the Channel Islands off southern California, and in central Mexico and Central America.

West Indian mammal and bird fossils come primarily from the Pleistocene and Holocene (Olson 1978). Extinct faunas in the Greater Antilles are generally rodents, insectivores, and edentates, together with raptorial birds, often of great size that presumably evolved in response to the lack of mammalian predators. Moreover, a dramatic bear sized-rodent *Anblyrhiza inundata* in an endemic Antillean family, Heptaxodontidae, was excavated from mines on Anguilla (Cope 1883). Still, Olson concludes that this fauna is the result of multiple overwater colonizations in the Oligocene and later, with the mammals having stronger affinities with South America and the birds with North America. These data indicate the limited value of mammals for tectonic reconstruction of the Caribbean. Mammals have only been available as colonists since the mid Tertiary after much of the tectonic events that created the Caribbean had already occurred.

For bats, as with reptiles and amphibians, Guadeloupe is a center of endemism—six of 10 bat species are endemic to the Antilles (Baker and Genoways 1978) a significance to over water dispersal seems obvious. In contrast with anoles, 11 species in the southern Lesser Antilles show a classic distance effect with respect to South America, as illustrated in Baker and Genoways' Figure 2 (p. 77).

The freshwater fish of the Greater Antilles are "secondary" meaning that they are derived from salt water ancestors (Briggs 1984). Also, the diversity of endemic genera and species of fresh water fishes is highest in Cuba and declines progressively eastward. No endemic freshwater fish occur in the Lesser Antilles, and therefore can contribute limited information about the origin of the eastern Caribbean.

A suborder (Auchenorrhyncha) of the Homoptera that includes cicadas, treehoppers, spittlebugs, planthoppers, and leafhoppers for the Greater Antilles. is derived primarily from Central America and Mexico, with little or no affinity to North or South America (Ramos 1988). Ramos emphasized agreement with Metcalf (1947) who proposed defining a zoogeographic region, "the Caribbean", to include the West Indies, Mexico and Central America, and distinguished from the Neotropical region.

The Scaritinae, an old and cosmopolitan group of Carabid burrowing ground beetles that consists of over 1500 species throughout the world has single island endemics in the Greater Antilles, Guadeloupe and Martinique (Nichols 1988). There is also an endemic genus, *Antilliscaris*, found on Puerto Rico and Hispaniola. The presence of three species in this genus on Puerto Rico, together with a 38% endemism in the fauna on Puerto Rico, led Nichols to suggest that Puerto Rico is the oldest emergent land mass in the West Indies.

Another large group of Carabid beetles, the genus *Platynus*, has over 300 species in Mexico and Central America and 1000

or more worldwide. Most are found at elevations >300m. Many endemic species are found in the Greater Antilles although, curiously, none occur in Puerto Rico (Liebherr 1988). Five endemic species occur on Guadeloupe, four on Dominica, and one each on Martinique, St. Lucia, and St. Vincent.

Fifty eight species of drosophilid flies are endemic to the Antilles (Grimaldi 1988). Also, an endemic genus of drosophilid in the Caribbean is *Mayagueza*—it has only one species and is endemic to Puerto Rico. Moreover, the *Drosophila repleta* group that feeds primarily on decaying cactus has *D. peninsularis* endemic in the Greater Antilles; it is related to Central American stocks.

The classic power law of island biogeography relating number of species to island area is valid in the West Indies for ant species (Wilson 1988). Curiously, no endemics are reported for the northern Lesser Antilles including Guadeloupe and Martinique, but endemic species are reported from St. Lucia, St. Vincent, Grenada, and Barbados—this suggests the need for further collection and analysis in the Lesser Antilles. On the Greater Antilles a wealth of fossil ants are preserved in Tertiary amber from the Dominican Republic. The late Tertiary fauna of the Greater Antilles is more characteristic of a continental fauna. Several genera were present on Hispaniola, including army ants, that are now absent from the West Indies but that remain abundant on the continent.

Other insect groups recently reviewed include the Lygaeidae where overwater dispersal is of primary importance (Slater 1988). There is limited endemism in the Lesser Antilles (only one in about 40 species on each of St. Kitts, Dominica, St. Vincent and Grenada) and a distance effect with respect to South America. Although the Lygaeids are a Lower Cretaceous group, their biogeography in the Lesser Antilles seems rather recent. In the Greater Antilles, however, 119 species are endemic to the islands, including four endemic genera two of which are in Cuba, one in Hispaniola, and the other more widely distributed in the West Indies. Similarly, the sweat bees (Halictidae) have also been interpreted primarily in terms of overwater dispersal in the Lesser Antilles (Eickwort 1988). Both these groups seem to accord with the butterflies, which have long been interpreted in terms of overwater dispersal (Brown 1978).

As a generalization then, Cuba and perhaps to a lesser extent, Puerto Rico, are old biologically as evidenced by the endemic genera on these islands. Also, the central islands of the Lesser Antilles are places of endemism at the specific and subspecific level in many groups.

Finally, the Antilles have long been conjectured as possibly providing land bridges between North and South America while they were west of their present positions closer to the continents. This issue is explored in detail in a marvelous volume edited by Stehli and Webb (1985a). Recently, Perfit and Williams (1989) have concluded that an isthmus of continuous dry land did not exist between North and South America during the latest Cretaceous and earliest Tertiary (Paleocene) based on mammalian data. Stehli and Webb (1985b), however, document substantial evidence from mammals, reptiles, nonmarine mollusks, and angiosperm plants that filtered in both directions between North and South America at this time. They envision island-arc stepping stones as the route of dispersal. Yet Perfit and Williams note the absence of mammalian evidence in the Antilles themselves for this dispersal. Again, the suitability of mammals for the reconstruction of late Cretaceous events is called into question.

Thus, this paper differs from previous biogeographic studies in focussing on a specific group, the anoles, that have enough antiquity to be relevant to Cretaceous as well as later events, that have desirable ecological characteristics to support their use as labels for tectonic units, and whose species relationships are nearly fully worked out for the eastern Caribbean. Also, this paper is as much concerned with the geologic origin of the Caribbean itself as it is with the origin of the Caribbean's biota.

2 Synthesis with Geologic Data

The phylogenetic tree of *Anolis* shows a major dichotomy between the cristellus-bimaculatus lineage of the northeastern Caribbean from Puerto Rico through Dominica versus the roquet group of the southeastern triangle of the Caribbean from Martinique through Bonaire.

At the top of the southeastern triangle, between Dominica and Martinique, Tomblin (1975), Vierbuchen (1979), and Dorel (1981) have noted the deepest seismicity of the Lesser Antilles; the seismicity occurs there with an East-West trend and Stein et al. (1982) show that strike slip faulting occurs there at depth. This fault is labeled as the "Dominica Fault" in Figure 2.

A line extending southwest from the fault between Dominica and Martinique to some point between Bonaire and Curacao appears to coincide with a major difference in the crustal structure of the ocean floor in the Venezuelan Basin. Biju-Duval et al. (1978) discovered three parallel faults trending east-northeast that they termed the "central Venezuelan Basin fault zone." Diebold et al. (1981) confirmed this discovery and characterized the very different crustal structure on opposite sides of this fault zone. West of the central Venezuelan Basin fault the so-called "B" reflecting layer is smooth, as characteristic of most of the Caribbean, whereas it is described as rough east of this fault in the southeastern corner of the Caribbean. Moreover, this southeastern corner is a magnetically quiet zone, in contrast to the rest of the Venezuelan Basin where northeast-southwest trending magnetic anomalies parallel the central Venezuelan Basin Fault (Ghosh et al. 1984).

Although differing somewhat from the hypothesis offered here, Bouysse (1984) has suggested that the northern Lesser Antilles has developed separately from the southern Lesser Antilles, and Speed (1985) has alluded to a similar possibility. The data on *Anolis* strongly support this kind of hypothesis. Presumably, this southeastern triangle, that harbors the roquet group of *Anolis*, is a small separate plate or a piece of the South American plate that has become sutured to the present-day eastward-moving Caribbean plate.

Now focus on the northeastern part of Lesser Antilles. La Desirade, on the Guadeloupe archipelago, has Jurassic rock (Fink 1972). After repeated study, no doubt remains as to its magmatic origin, similar in appearance, chemical composition, and mineralogy to the basal units of the Greater Antilles, and especially Puerto Rico. (Bouysse et al. 1983). Although a tiny sliver of land on an aerial map (ca 30 km²), La Desirade is the tip of an "iceberg" marking the edge of a cliff that drops 5000m to the ocean floor in less than 10 km horizontal distance, and is the site of a distinct local positive gravity anomaly (Bourguier anomaly). Tomblin (1975, p. 471) wrote "... in view of the long time interval between these and the next oldest rocks in the Lesser Antilles and the large horizontal movements which undoubtedly took place in the region during this interval ... it

is possible that the crust now exposed in Desirade represents a small block which was much closer to the Virgin Islands in Late Jurassic time and which subsequently separated from this area and moved relatively eastward." Alternatively, basement as old as that exposed on La Desirade may underly all the northern Lesser Antilles, but simply not be exposed between the Guadeloupe region and Puerto Rico. Many authors, including Bouysse (1979, 1984), Speed (1985), and Donnelly (1985), have referred to the origin of the northern Lesser Antilles as occurring together, in some way, with Puerto Rico.

The phylogenetic tree of *Anolis* supports an hypothesis that the Guadeloupe region has moved apart from the Puerto Rico bank because the bimaculatus group of the northern Lesser Antilles is sister to the cristatellus group of Puerto Rico. The bifurcation in the phylogenetic tree where these lineages split would seem to coincide with the movement of a small block representing proto-Guadeloupe away from the Puerto Rican area. This block would carry on it the ancestor of *A. cristatellus*, just as the small cays of the Puerto Rico bank today retain *A. cristatellus* itself. This ancestor of Puerto Rico's *A. cristatellus* developed in isolation on proto-Guadeloupe to become the present-day *A. marmoratus*. And this *A. marmoratus*, in turn, spawned propagules that dispersed north, with the prevailing currents, to islands younger than Guadeloupe as they surfaced. In fact, the entire range of the bimaculatus group coincides exactly with the geologic entity bounded by the 1000m depth contour encompassing the area from the Anegada passage to the passage between Dominica and Martinique.

The Anagada passage between the Virgin Islands and the northern Lesser Antilles is an extensional basin today (cf. Speed, this conference) and perhaps this type of expansion has occurred before. Alternatively, the Aves Ridge, when more exposed than at present, may have provided a stepping stone path for dispersal from Puerto Rico to Guadeloupe, assuming Guadeloupe was emergent before the islands north of it. This alternative would not require an expansion of the arc between Guadeloupe and Puerto Rico and would be consistent with common Jurassic basement to all the northern Lesser Antilles. Still, there is no evidence of a Jurassic basement common to the northern Lesser Antilles and the Puerto Rico bank; migration down an exposed Aves Ridge to Guadeloupe would run counter to the ocean currents; and such migration would have had to involve many species to account for the large fauna on Guadeloupe today. Thus, I feel the weight of the data favors an expansion of the arc between Guadeloupe and Puerto Rico.

I term the structure that contains the present-day islands of the Anguilla Bank down through Dominica as the "NLA platform." A "taxon cycle" involving an invasion, coevolution, and extinction of *Anolis* species seems to be occurring on the Anguilla, Antigua, and St. Kitts banks toward the northern part of this platform as a result of dispersal from the Guadeloupe Archipelago (Roughgarden and Pacala 1989). The dispersal of the bimaculatus series followed that of the wattsi series. The interval between these distinct waves of invasion from Guadeloupe north might represent the time needed for Guadeloupe to grow large enough in area and elevation for a subspecies of the anole there to evolve in montane habitat—such an anole is sufficiently different from a wattsi-series anole to invade successfully.

Turning now to the southeastern triangle of the Caribbean there is further heterogeneity. The coast of Venezuela, including the Netherlands-Venezuelan Antilles, appears to be the remnant of an island arc that collided with the coast of South America in

the late Cretaceous (Maresch 1974). Curacao and Bonaire have different basements, formed at a mid-ocean spreading ridge and at a subduction zone respectively (Beets and MacGillavry 1977, Beets et al. 1984), and the anoles on these adjacent islands are not at all closely related. Also, in the Lesser Antilles, the chemical composition of the rocks on St. Lucia differ markedly from those of its neighbors (Figure 2 in Tomblin 1975) just as St. Lucia's anole is not closely related to those of its neighbors.

Bucher (1952) suggested that the motion of the Caribbean plate between the North and South American plates is analogous to the motion of a glacier in a valley. The analogy explains the opposite asymmetry of pull-apart basins with the strike-slip motion at faults in the north and south boundary zones of the Caribbean plate (Mann and Burke 1984). Perhaps the analogy can be extended by viewing the southern Lesser Antilles as the "terminal moraine" at the southern half of the leading edge of the Caribbean Plate. As this part of the Caribbean plate has moved eastward, it may have accumulated some islands in its path. The magmatic activity at the subduction zone adds an enormous amount of material tending to mask nuclei that may have both heterogeneous origins and times of entry into the island arc moraine. Specifically, St. Lucia (perhaps near Eperon Moule-a-Chique) may have a different geologic origin from its present-day neighbors of Martinique and St. Vincent, and instead, may have originated with Bonaire and La Blanquilla both of which are now lodged on the Venezuelan coast.

Figure 5 presents a reconstruction of the geologic origin of the eastern Caribbean that takes into account the points raised above. The two halves of the Lesser Antilles are hypothesized to develop separately. In the north, Puerto Rico and Desirade split. As they move apart, the NLA platform, containing the present-day Anguilla, Antigua, and St. Kitts banks, grows in area. Thereafter the *A. wattsi* lineage, and then the *A. bimaculatus* lineage colonize the exposed areas on the platform by overwater dispersal. In the south matters are more complex. An island arc consisting of basal elements of Bonaire, La Blanquilla, and St. Lucia is hypothesized to lie in the path of the material that contributes to Martinique and St. Vincent-Grenada. As the Caribbean plates moves east, it pushes the islands presently between Bonaire and La Blanquilla onto the Venezuelan shelf, and picks up St. Lucia.

3 Discussion

3.1 The Lesser Antilles—Not Homogeneous and Not Tertiary

Panoramic plate-tectonic reconstructions of the origin of the Caribbean generally view the Lesser Antillean island arc as a homogeneous grouping of islands that formed during the Tertiary (e.g. Pindell and Dewey 1982). Yet new discoveries point to an older age for the basement of the Lesser Antilles than previously believed. In 1975, the oldest material known in the Lesser Antilles, apart from the Aves Ridge and the then-controversial La Desirade find, was Eocene (ca 50 my BP), with large deposits on the NLA platform, and on the Grenada Bank. These facts contributed to the acceptance of a Tertiary origin for the Lesser Antilles. Now, Upper Cretaceous (ca 70 my BP) basement material has been obtained from both slopes of the Anegada Passage (Speed et al. 1979, Bouysse et al. 1980, 1985), and on Union Island in the Grenadines (Westercamp et al. 1985). Similarly,

the endemic vertebrate fauna of the Lesser Antilles primarily involves amphibians and reptiles, forms that were abundant and successful during the Cretaceous. These data are all consistent with the hypothesis that the Lesser Antillean island arc is Cretaceous, not Tertiary, and has been available as a terrestrial habitat since that time.

Furthermore, the geologic data reviewed above are not consistent with the view that the Lesser Antillean island arc is a homogeneous grouping of islands. The isolated occurrence of Jurassic material in La Desirade is one example of heterogeneity. The difference in earthquake frequencies between the northern and southern halves of the arc, the occurrence of distinctive ocean floor in the southeast corner of the Caribbean, the difference between the basements of Curacao and Bonaire, together with suggestions of a different lithic chemistry on St. Lucia, offer other examples. Biologically, the contrast between the bimaculatus anoles of the northern Lesser Antilles and the roquet anoles of the southern Lesser Antilles is stark, and the difference between the lineages of the anole on Curacao and that on the adjacent island of Bonaire is almost as dramatic. Thus, many data point to a heterogeneous history for the structures that are now aligned at the edge of the Caribbean plate.

3.2 A Pacific Archipelago

Vertebrate paleontology and biogeography in Central America have focussed on the study of mammals as indicators of when the isthmus of Panama closed. This application of biogeography relies on the fact that mammal faunas of North and South America are distinctive, while Central American mammals are essentially a North American fauna. The closure of the isthmus is then indicated by dispersal of South American forms northward into Central and then North America, and North American forms into South America. This entire investigation has, however, diverted attention away a fundamental clue offered by the biogeography of other vertebrate groups. For amphibians, reptiles, and fresh water fish, Central America is a faunal province of its own, with many endemic genera, that have southern, not northern, affinity (Bussing 1976; Duellman 1966, 1979; Miller 1966; Savage 1966). To quote from Savage (1982),

"The distributions of recent and fossil mammals for the region have been extensively reviewed by several workers, most recently by Savage (1974), Ferrusquia-Villafranca (1978), and Marshall et al. (1979). These studies all confirm that the South American mammal fauna was isolated from that of Central America until Pliocene; that no distinctive Middle American mammal fauna can be recognized; that no cluster of taxa of southern relationships, equivalent to the Middle American unit seen in the freshwater fishes and herpetofauna, can be distinguished; and that the region was dominated by groups of northern affinity until the interchange with South America."

Similarly, the Antillean herpetofauna is generally allied with Central America, and to some extent South America; for example, it does not contain the North American forms readily observed in the southwestern U. S.

These considerations led Savage (1982) to propose that

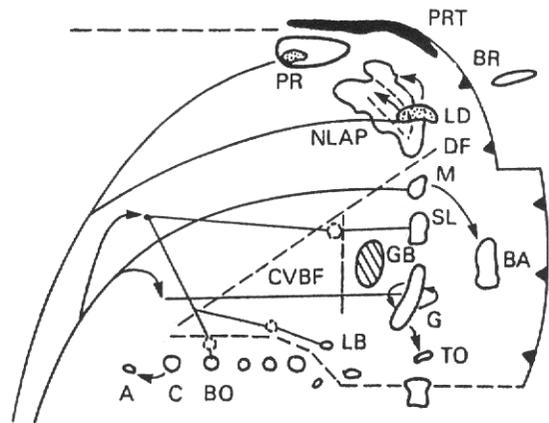


Figure 5. Schematic for proposed geologic origin of the eastern Caribbean. Abbreviations are: PR, Puerto Rico; PRT, Puerto Rico Trench; BR, Barracuda Ridge; LD, La Desirade; NLAP, Northern Lesser Antilles Platform; DF, Dominica Fault; M, Martinique; SL, St. Lucia; BA, Barbados; GB, Grenada Basin; G, Grenada-ST. Vincent; TO, Tobago; CVBF, Central Venezuelan Basin Fault; LB, La Blanquilla; BO, Bonaire; C, Curacao; A, Aruba. Lines ending in an arrow indicate overwater dispersal by anoles. Lines without arrows indicate the path traced by *Anolis* populations as they occupied basal elements of geologic structures that today are in the eastern Caribbean.

"There was a continuous land connection or series of proximate islands extending from northern South America to the area of Nicaragua in late Mesozoic and/or early Tertiary. This land connection or island archipelago seems to have included the future Greater Antilles that were closely associated with the Nicaraguan region."

While this proposal may, of course, not be correct in detail, it is important to appreciate the point it is intended to convey—there has been a lot of evolutionary action in Central America by the very vertebrate groups that were abundant and successful during the Cretaceous (the so-called Age of Reptiles). In contrast, mammals are primarily creatures of the Tertiary (the so-called Age of Mammals) and they have not figured prominently in Central America. So, mammals apparently arrived in Central America with too little time for much evolution to occur. Hence, some material now in Central America and the Antilles appears to have been available to amphibians and reptiles during the Cretaceous before mammals became successful.

The evidence of interchange between North and South America at approximately the upper Cretaceous-Paleocene boundary argues that islands were present in the gap between North and South America at that time. Before that time this material had to be further west out in the Pacific. But was it exposed and available as habitat earlier in the Cretaceous? Quite possibly, in view of the relatives of *crisatellus-bimaculatus* anoles in western Mexico and roquet anoles on Malpalo off Columbia, the Pacific distribution of the relatives of the xantusid lizard of Cuba, and the extensive development of endemism in the Central American/Antillean province that Savage has emphasized in the quotations above. The suture of the southeastern corner of

the Caribbean plate also seems to have taken place in the Pacific because the Central Venezuelan Basin Fault separates smooth from rough B" material. This material that characterizes the Caribbean sea floor (Burke et al. 1978) was produced by an off-ridge episode of volcanism, called the B" event by Burke (1988), and the flood basalt event by Donnelly (1985), about 80 Ma. It appears to mark the initiation of the Galapagos hot spot (Duncan and Hargraves 1984) when the Caribbean ocean floor was in the Pacific. Given that both sides of the CVBF have B" material, both must have originated in the Pacific, even though they are not identical. The smooth B" sea floor may have been more northern, closer to the Nicaraguan block. The rough B" floor, with islands containing the roquet group of anoles, may have come more from the south, perhaps with affinity to the Cretaceous island arc now part of the Western Cordillera of Columbia and Ecuador (Bourgeois et al. 1987, Lebras et al. 1987.)

The existence of a Cretaceous archipelago in the Pacific near South America as a theatre where small reptiles evolved and diversified might also be relevant to two of the classic mysteries of herpetology: the occurrence of *Tropidurus* and iguanine lizards on the Galapagos (Wright 1984) and the iguanine *Brachylophus* of Fiji (Gibbons 1985). Such an archipelago would be well positioned to contribute fauna to both the Galapagos and the Fiji's.

3.3 A Grand Scenario

The preceding facts invite a conjecture—a grand scenario for how the origin of the eastern Caribbean might be spliced into the context of the origin of Central America. During the Cretaceous an archipelago formed west of the Americas, closer to South America than to North America. As North and South America moved westward, and while this archipelago was still in the Pacific, a piece of ocean floor containing the basement of the southern Lesser Antilles becomes sutured to the southeastern margin of the Caribbean plate. As the Caribbean plate moved between the Americas, some of the material remained at the gap between the Americas, to be incorporated into Central America, while other material continued through the gap to become the Antilles. As the Antillean material moved eastward relative to the Americas, it sent propagules to become the Jamaican radiation of anoles. Thereafter, the eastern margin of the Caribbean plate developed whereby the Guadeloupe region moved apart from Puerto Rico in the north, and in the south the Netherlands-Venezuelan Antilles are pushed onto the Venezuelan shelf while St. Lucia became lodged between Martinique and St. Vincent, as previously discussed.

3.4 Further Exploration and Dating

On a more empirical note, the reptile and amphibian faunas of Central and northern South America, and of Cuba and Hispaniola, need much more exploration. What is especially needed is collection and systematic study using modern molecular biology techniques. While conventional morphological analysis suffices for naming and identifying species, determining lineage relationships requires molecular information. The molecular data for anoles is based solely on blood albumins. DNA hybridization studies would be even better. It cannot be over-emphasized that the lineage relationships combined with species range maps are what is needed to address geological processes using biological data. While most species of Caribbean, Central, and South American amphibians and reptiles have been collected

and described, their lineage relationships have not been worked out. The data presented here for the eastern Caribbean is most of what is presently known about the lineage relationships of anoles. I believe that a large effort devoted to determining the species relationships of Caribbean, Central and South American anoles using molecular biology methods could quickly provide data of great relevance to reconstructing their plate tectonic origin.

Another potential value of lineage relationships based on molecular data is in providing dates for geologic events. The issues are whether the biochemical distance between two population on separate islands increases as a linear function of time since separation, and if so, what the speed of differentiation is. The mathematical formula for the "albumin immunogenetic distance" has been devised according to population-genetic theory in hopes that this distance does increase linearly with time (Wilson and Sarich 1969, Maxson and Wilson 1974, Wilson et al. 1977). Moreover, Shochat and Dessauer (1981) have even suggested that 1.7 units of distance accumulate per 1 million years. This speed is about twice the rate that seems appropriate for the reconstructions that are proposed in this paper. Clearly, more research here would be valuable.

3.5 Historical Ecology of *Anolis*

We return now to the ecology of *Anolis* lizards, the subject that motivated this paper to begin with. Our findings suggest that the composition of *Anolis* communities in the Eastern Caribbean results from the combination of competition, habitat bottlenecking, and plate tectonics. Ecological competition prevents cross colonization by species of the same or very similar body size, but otherwise the strength of competition between anoles is slight. When a geologic fragment splits from a larger unit a very particular set of species is retained on the fragment, those with good "bottle-necking" ability. This special extraction then develops in isolation and need never represent an early stage in the buildup of a complex fauna. Thus, relatively fast-acting ecological interactions such as competition and predation are not sufficient to explain the composition and structure of ecological communities. Instead, ecological communities are fashioned as much by relatively slow geologic processes as by fast species interactions. We have thus come full circle. During the last two decades instances of fast evolution, on an ecological time scale, have been discovered. Now it is also clear that ecological change can itself be very slow, on an evolutionary time scale.

Finally, the explanation for why the eastern Caribbean has been a theater for the evolution of *Anolis* seems to involve a two-part relationship between anoles and birds. I hypothesize that the present-day dominance of anoles as the ground-feeding insectivorous vertebrates in Caribbean communities reflects a competitive superiority of arboreal lizards over birds in the ground-feeding insectivorous niche, provided the temperatures are mild and there is a relative absence of predation. North American birds are continually migrating through the Lesser Antilles, and do not establish there, supporting the idea that the lizards have pre-empted the ground-feeding insectivorous niche in the Lesser Antilles. But larger islands and continental regions support both a higher diversity and a higher abundance of birds of prey. These birds of prey can reduce anole abundance and thereby allow the competitively inferior insectivorous birds to occupy the ground-feeding insectivorous niche. The explanation for the reptile-dominated faunas of the Caribbean, that contrasts markedly

with the avian dominated faunas of the Pacific islands, is that the Caribbean islands are old enough to have accumulated a reptile fauna before birds and mammals diversified. Because the Caribbean islands remained at warm latitudes, and because the islands are small enough to lead to relatively little predation pressure on lizards, the islands today show communities that may resemble ecological communities of the Cretaceous.

4 Acknowledgments

I thank Dave Larue for helpful discussions on this work over a period of several years, and also Fred Nagle for the invitation to attend this wonderful conference. I gratefully acknowledge Joel Cracraft for stimulating this line of research, and for presenting it in my absence at a conference in New Orleans. Finally, I thank my students and colleagues for enjoyable companionship over the years the ecological work reported here has been carried out, and the National Science Foundation (General Ecology Program) for the continued financial support that has made these efforts possible.

5 References

- Baker, R. and H. Genoways. 1978. Zoogeography of Antillean Bats. Pp. 53-97 in: F. B. Gill, ed., *Zoogeography in the Caribbean*, Spec. Pub. No. 13, Academy of Natural Sciences, Philadelphia.
- Beets, D. J. and Mac Gillavry, H. J. 1977. Outline of the Cretaceous and Early Tertiary history of Curacao, Bonaire, and Aruba. Pp. 1-6 in *Guide to Geological Excursions on Curacao, Bonaire, and Aruba*, STINAPA Documentation Series No. 2, Caribbean Marine Biological Institute, Curacao (Also published as GUA Papers of Geology, Ser. 1, No. 10; Stichting GUA, Geologisch Institut, Amsterdam).
- Beets, D. J., Maresch, W. V., Klaver, G. T., Mottana, A., Bocchio, R., Beunk, F. F. and Monen, H. P. 1984. Magmatic rock series and high-pressure metamorphism as constraints on the tectonic history of the southern Caribbean. *Geological Society of America Memoir* 162:95-130.
- Biju-Duval, B., Mascle, A., Montadert, L. and Wannesson, J., 1978. Seismic investigations in the Columbia, Venezuela and Grenada basins, and on the Barbados Ridge for future IPOD drilling. *Geologie en Mijnbouw* 57:105-116.
- Bohlen, C. 1983. Competition for space in the anoles of the island of St. Maarten (Neth. Antilles). Unpublished Master's thesis, Stanford University, Stanford, California.
- Bourgeois, J., J Toussaint, H. Gonzalez, J. Azema, B. Calle, A. Desmet, L. Murcia, A. Acevedo, E. Parra, and J. Tournon. 1987. Geological history of the Cretaceous ophiolitic complexes of Northwestern South America (Columbian Andes). *Tectonophysics* 143:307-327.
- Bouysse, P. 1979. Caracteres morphostructuraux et evolution geodynamique de l'arc insulaire des Petites Antilles. *Bureau de Recherches Géologiques et Minières Bulletin* Section IV, 3/4:185-210.
- Bouysse, P. 1984. The Lesser Antilles island arc: Structure and geodynamic evolution. *Initial Reports, Deep Sea Drilling Project* (United States Government Printing Office) 78A:83-103.
- Bouysse, P., Andreieff, P. and Westercamp, D. 1980. Evolution of the Lesser Antilles island arc, new data from the submarine geology. *Transactions of the 9th. Caribbean Geological Conference* (Santo Domingo, August 1980) pp.75-88.
- Bouysse, P., Andreieff, P., Richard, M., Baubron, J., Mascle, A., Maury, R. and Westercamp, D. 1985. Geologie de la Ride d'Aves et des pentes sous-marines du nord des Petites Antilles et esquisse bathymetrique a 1/1.000.000 de l'Est-Caraibe. *Documents du Bureau de Recherches Géologiques et Minières*93.
- Bouysse, P., Schmidt-Effing, R. and Westercamp, D. 1983. La Desirade island (Lesser Antilles) revisited: Lower Cretaceous radiolarian cherts and arguments against an ophiolitic origin for the basal complex. *Geology* 11:244-247.
- Briggs, J. C. 1984. Freshwater fishes and biogeography of Central America and the Antilles. *Syst. Zool.* 33:428-435.
- Brown, F. M. 1978. The origins of the West Indian butterfly fauna. Pp. 5-30 in: F. B. Gill, ed., *Zoogeography in the Caribbean*, Spec. Pub. No. 13, Academy of Natural Sciences, Philadelphia.
- Bucher, W. H. 1952. Geological structure and orogenic history of Venezuela. *Geological Society of America Memoir* 49.
- Burke, K. 1988. Tectonic evolution of the Caribbean. *Ann. Rev. Earth Planet. Sci.* 16:201-230.
- Burke, K., P. J. Fox, A. Şengör, 1978. Buoyant ocean floor and the evolution of the Caribbean. *J. Geophys. Res.* 83:3949-3954.
- Bussing, W. A. 1976. Geographic distribution of the San Juan ichthyofauna of Central America with remarks on its origin and ecology. In: E. B. Thorson (ed.) *Investigations of the Ichthyofauna of Nicaraguan Lakes*. Univ. Nebraska (10): 157.
- Cope, E. D. 1883. On the contents of a bone cave in the island of Anguilla (West Indies). *Smithson. Cont. Knowl.* 489:1-30.
- Diebold, J. B., Stoffa, P. L., Buhl, P. and Truchan, M. 1981. Venezuela Basin Crustal Structure. *Journal of Geophysical Research* 86:7901-7923.
- Donnelly, T. W. 1985. Mesozoic and Cenozoic plate evolution of the Caribbean region. Pp. 89-121 in: F. G. Stehli and S. D. Webb (eds.) *The Great American Biotic Interchange*, Plenum Press, New York.
- Dorel, J. 1981. Seismicity and seismic gaps in the Lesser Antilles arc and earthquake hazards in Guadeloupe. *Geophysical Journal of the Royal Astronomical Society* 67:679-696.
- Duellman, W. E. 1966. The Central American herpetofauna: an ecology perspective. *Copeia* 1966:700-719.
- Duellman, W. E. 1979. The South American herpetofauna: a panoramic view. *Mus. Nat. Hist. Univ. Kansas. Monogr.* 7:1-28.
- Duncan, R. and R. Hargraves. 1984. Plate tectonic evolution of the Caribbean region in the mantle reference frame. *Geol. Soc. of America, Memoir* 162:81-93.
- Durham, J. W. 1985. Movement of the Caribbean plate and its importance for biogeography in the Caribbean. *Geology* 13:123-125.
- Eickwort, G. C. 1988. Distribution patterns and biology of West Indian sweat bees. Pp. 231-253 in: J. K. Liebherr, ed., *Zoogeography of Caribbean Insects*, Comstock Publishing Associates, Cornell University Press, Ithaca, New York.
- Estes, R. 1983. The fossil record and early distribution of lizards. Pp. 365-398 in: A. G. J. Rhodin and K. Miyata (eds.) *Advances in Herpetology and Evolutionary Biology*, Museum of Comparative Zoology, Harvard University, Cambridge, Mass.
- Ferrusquia-Villafranca, I. 1978. Distribution of Cenozoic vertebrate faunas in Middle and North America and problems of migration between North and South America. *Inst. Geol. Univ. Auto. Mexico. Biol.* 101:193-321.
- Fink, L. K. Jr. 1972. Bathymetric and geologic studies of the Guadeloupe region, Lesser Antilles island arc. *Marine Geology* 12:267-288.
- Ghosh, N., Hall, S. A., and Casey, J. F. 1984. Seafloor spreading magnetic anomalies in the Venezuelan Basin. *Geological Society of America Memoir* 162:65-80.
- Gibbons, J. R. H. 1985. The biogeography and evolution of Pacific island reptiles and amphibians. Pp. 125-142 in: G. Grigg, R. Shine, and H. Ehmann, eds., *Biology of Australasian Frogs and Reptiles*. Royal Zoological Society of New South Wales.
- Gorman, G. C. 1973. The chromosomes of the Reptilia, a cytotaxonomic interpretation. Pp. 349-421 in A. Chiarelli and E. Capanna (eds.) *Cytotaxonomy and Vertebrate Evolution*. Academic Press, London.

- Gorman, G. C. and L. Atkins. 1969. The zoogeography of Lesser Antillean *Anolis* lizards - an analysis based upon chromosomes and lactic dehydrogenases. *Bull. Mus. Comp. Zool.* 138:53-80.
- Gorman, G. C., D. G. Buth, M. Soule, and S. Y. Yang. 1983. The relationships of the Puerto Rican *Anolis*: electrophoretic and karyotypic studies. Pp. 626-642 in: A. G. J. Rhodin and K. Miyata (eds.) *Advances in Herpetology and Evolutionary Biology*, Museum of Comparative Zoology, Cambridge, Mass.
- Gorman, G. C., D. G. Buth, and J. S. Wyles. 1980. *Anolis* lizards of the eastern Caribbean: a case study in evolution. III. A cladistic analysis of albumin immunological data, and the definition of species groups. *Syst. Zool.* 29:143-158.
- Gorman, G. C., and Y. J. Kim. 1976. *Anolis* lizards of the eastern Caribbean: a case study in evolution. II. Genetic relationships and genetic variation of the *bimaculatus* group. *Syst. Zool.* 25:62-77.
- Gorman, G. C., C. S. Lieb, and R. H. Harwood. 1984. The relationships of *Anolis gadovi*: albumin immunological evidence. *Carib. J. Sci.* 20:145-152.
- Graham, J. B. 1975. The biological investigations of Malpelo Island, Columbia. *Smithsonian Contributions to Zoology* 176:1-98.
- Guyer, C. and J. Savage. 1986. Cladistic relationships among anoles (Sauria: Iguanidae). *Systematic Zoology* 35:509-531.
- Heatwole, H. and F. MacKenzie. 1967. Herpetogeography of Puerto Rico. IV. Paleogeography, faunal similarity, and endemism. *Evolution* 21:429-438.
- Howard, R. A. 1973. The vegetation of the Antilles. Pp. 1-38 in: A. Graham, ed., *Vegetation and Vegetational History of Northern Latin America*. Elsevier Scientific Publishing Co., Amsterdam.
- Lazell, J. D. Jr. 1965. An *Anolis* (Sauria, Iguanidae) in amber. *J. Paleontology* 39:379-382.
- Lazell, J. D. Jr. 1972. The Anoles (Sauria, Iguanidae) of the Lesser Antilles. *Bull. Mus. Comp. Zool.* 143:1-115.
- Lazell, J. D. Jr. 1983. Biogeography of the herpetofauna of the British Virgin Islands, with description of a new anole (Sauria: Iguanidae). Pp. 99-117 in: A. G. J. Rhodin and K. Miyata (eds.) *Advances in Herpetology and Evolutionary Biology*, Museum of Comparative Zoology, Cambridge, Mass.
- Lebras, M., F. Mégard, C. Dupuy, and J. Dostal. 1987. Geochemistry and tectonic setting of pre-collision Cretaceous and Paleogene volcanic rocks of Ecuador. *Geol. Soc. of Amer. Bull.* 99:569-578.
- Licht, P. 1974. Response of *Anolis* lizards to food supplementation in nature. *Copeia* 1974:215-221.
- Lieb, C. S. 1981. Biochemical and karyological systematics of the Mexican lizards of the *Anolis gadovi* and *A. nebulosus* species groups. Ph. D. Thesis, Department of Biology, University of California-Los Angeles, (University Microfilms, Ann Arbor, Michigan. No. 8113869).
- Liebherr, J. K. 1988. Biogeographic patterns of West Indian *Platynus* Carabid beetles (Coleoptera). Pp. 121-152 in: J. K. Liebherr, ed., *Zoogeography of Caribbean Insects*, Comstock Publishing Associates, Cornell University Press, Ithaca, New York.
- Lister, B. 1976. The nature of niche expansion in West Indian *Anolis* lizards. II. Evolutionary components. *Evolution* 30:677-692.
- MacArthur, R. H. and R. Levins. 1967. The limiting similarity, convergence and divergence of coexisting species. *Amer. Natur.* 101:377-385.
- Mann, P. and Burke, K. 1984. Neotectonics of the Caribbean. *Reviews of Geophysics and Space Physics* 22:309-362.
- Mann, P. and K. Burke. 1984. Neotectonics of the Caribbean. *Rev. Geophys. Space Phys.* 22:309-362.
- Maresch, W. V. 1974. Plate tectonics origin of the Caribbean mountain system of Northern South America: Discussion and proposal. *Geological Society of America Bulletin* 85:669-682.
- Marshall, L. G., R. f. Butler, R. E. Drake, G. H. Curtis, and R. H. Tedford. 1979. Calibration of the Great American Interchange. *Science* 204:272-279.
- Maxson, L. R. and A. C. Wilson. 1975. Albumin evolution and organismal evolution in tree frogs (Hylidae). *Syst. Zool.* 24:1-15.
- Metcalf, Z. P. 1947. The center of origin theory. *Elisha Mitchell Sci. Soc. J.* 62:149-175.
- Nichols, S. W. 1988. Kaleidoscopic biogeography of West Indian Scaritinae (Coleoptera: Carabidae). Pp. 71-120 in: J. K. Liebherr, ed., *Zoogeography of Caribbean Insects*, Comstock Publishing Associates, Cornell University Press, Ithaca, New York.
- Olson, S. L. 1978. A paleontological perspective of West Indian birds and mammals. Pp. 99-117 in: F. B. Gill, ed., *Zoogeography in the Caribbean*, Spec. Pub. No. 13, Academy of Natural Sciences, Philadelphia.
- Pacala, S. W. and J. D. Roughgarden. 1984. Control of arthropod abundance by *Anolis* lizards on St. Eustatius (Neth. Antilles). *Oecologia* 64:160-162.
- Pacala, S. W. and J. D. Roughgarden. 1985. Population experiments with the *Anolis* lizards of St. Maarten and St. Eustatius. *Ecology* 66:129-141.
- Paull, D., E. E. Williams, and W. P. Hall. 1976. Lizard karyotypes from the Galapagos islands: chromosomes in phylogeny and evolution. *Breviora* 441:1-31.
- Perfit, M. R. and E. E. Williams. 1989. Geological constraints and biological retrodictions in the evolution of the Caribbean sea and its islands. Pp. 47-102 in: C. A. Woods, ed., *Biogeography of the West Indies*. Sandhill Crane Press.
- Pindell, J. and Dewey, J. F. 1982. Permo-Triassic reconstruction of western Pangea and the evolution of the Gulf of Mexico/Caribbean region. *Tectonics* 1:179-211.
- Poinar, G. O. Jr. and D. C. Cannatella. 1987. An upper Eocene frog from the Dominican Republic and its implications for Caribbean Biogeography. *Science* 237:1215-1216.
- Ramos, J. A. 1988. Zoogeography of the Auchenorrhynchos Homoptera of the Greater Antilles (Hemiptera). Pp 61-70 in: J. K. Liebherr, ed., *Zoogeography of Caribbean Insects*, Comstock Publishing Associates, Cornell University Press, Ithaca, New York.
- Richardson, P. L., and D. Walsh. 1986. Mapping climatological seasonal variations of surface currents in the tropical Atlantic using ship drifts. *J. Geophys. Res.* 91:10537-10550.
- Rieppel, O. 1980. Green anole in Dominican amber. *Nature* 286:486-487.
- Roughgarden J. and S. W. Pacala. 1989. Taxon cycle among *Anolis* lizard populations: Review of evidence. Pp. 403-432 in: D. Otte and J. Endler, eds., *Speciation and its Consequences*, Sinauer Associates, Sunderland Mass.
- Roughgarden, J. D., S. W. Pacala, and J. D. Rummel. 1984. Strong present-day competition between the *Anolis* lizard populations of St. Maarten (Neth. Antilles). Pp. 203-220 in: B. Shorrocks (ed.) *Evolutionary Ecology*. Blackwell Scientific Publications, London
- Roughgarden, J., S. Gaines, and S. Pacala. 1987. Supply-side ecology: the role of physical transport processes. In: P. Giller and J. Gee (eds.), *Organization of Communities: Past and Present*. Blackwell Scientific Publications. Pp. 459-486.
- Rummel, J. D. and J. D. Roughgarden. 1985. Effects of reduced perch-height separation on competition between two *Anolis* lizards. *Ecology* 66:430-444.
- Savage, J. M. 1966. The origins and history of the Central American herpetofauna. *Copeia* 1966:719-766.
- Savage, J. M. 1974. The Isthmian Link and the evolution of neotropical mammals. *Los Angeles County Mus. Contr. Sci.* 160:1-51.
- Savage, J. M. 1982. The enigma of the Central American herpetofauna: dispersals or vicariance? *Ann. Missouri Bot. Gard.* 69:464-547.
- Schoener, T. W. and A. Schoener. 1983a. The time to extinction of a colonizing propagule of lizards increases with island area. *Nature* 302:332-334.

- Schoener, T. W. and A. Schoener. 1983b. Distribution of vertebrates on some very small islands. II. Patterns in species counts. *J. Anim. Ecol.* 52:237-262.
- Schoener, T. and D. Spiller. 1987. Effect of lizards on spider populations: manipulative reconstruction of a natural experiment. *Science* 236:949-952.
- Schwartz, A. 1978. Some aspects of the herpetogeography of the West Indies. Pp. 31-51 in: F. B. Gill, ed., *Zoogeography in the Caribbean*, Spec. Pub. No. 13, Academy of Natural Sciences, Philadelphia.
- Schwartz, A. and R. Thomas. 1975. A check-list of West Indian amphibians and reptiles. *Carnegie Mus. Nat. Hist. Spec. Publ.* 1:1-216.
- Schwartz, A. and R. W. Henderson. 1985. A Guide to the Identification of the Amphibians and Reptiles of the West Indies exclusive of Hispaniola. Milwaukee Public Museum.
- Shochat, D. and H. C. Dessauer. 1981. Comparative immunological study of albumins of *Anolis* lizards of the Caribbean islands. *Comp. Biochem. Physiol.* 68A:67-73.
- Singer, C. 1931. *A Short History of Biology*. Oxford Clarendon Press.
- Slater, J. A. 1988. Zoogeography of West Indian Lygaeidae (Hemiptera) Pp. 38-60 in: J. K. Liebherr, ed., *Zoogeography of Caribbean Insects*, Comstock Publishing Associates, Cornell University Press, Ithaca, New York.
- Speed, R. C. 1985. Cenozoic collision of the Lesser Antilles arc and continental South America and the origin of the El Pilar Fault. *Tectonics* 4:41-69.
- Speed, R. C., Gerhard, L. C. and McKee, E. H. 1979. Ages of deposition, deformation, and intrusion of Cretaceous rocks, eastern St. Croix, Virgin Islands. *Geological Society of America Bulletin* 1, 90:629-632.
- Stamps, J. A. 1977. Rainfall, moisture, and dry season growth rates in *Anolis aeneus*. *Copeia* 1977:415-419.
- Stehli, F. G. and S. D. Webb. 1985a. eds., *The Great American Biotic Interchange*. Plenum Press, New York.
- Stehli, F. G. and S. D. Webb. 1985b. A kaleidoscope of plates, faunal and floral dispersals, and sea level changes. Pp. 3-16 in: Stehli, F. G. and S. D. Webb. 1985a. eds., *The Great American Biotic Interchange*. Plenum Press, New York.
- Stein, S., Engeln, J., Wiens, D., Fujita, K. and Speed, R. 1982. Subduction seismicity and tectonics in the Lesser Antilles arc. *Journal of Geophysical Research* 87(B10):8642-8664.
- Tomblin, J. F. 1975. The Lesser Antilles and the Aves Ridge. Pp. 467-500 in: Nairn, A. E. M. and Stehli, F. G. (eds.) *The Ocean Basins and Margins*. Vol. 3. The Gulf of Mexico and the Caribbean, Plenum Press, New York.
- Underwood, G. 1959. Revisionary Notes. The anoles of the Eastern Caribbean (Sauria, Iguanidae). Part III. *Bull. Mus. Comp. Zool.* 121:191-226.
- Vierbuchen, R. C. Jr. 1979. *The tectonics of north-eastern Venezuela and the southeastern Caribbean Sea*. Ph. D. thesis. 193 pp. Princeton University. Princeton N. J.
- Westercamp, D., Andreieff, P., Bouysse, P., Mascle, A. and Baubron, J. 1985. Geologie de l'archipel des Grenadines (Petites Antilles meridionales). *Documents du Bureau de Recherches Géologiques et Minières* 92.
- Williams, E. E. 1977. Anoles out of place: introduced anoles. Pp 110-118 in E. E. Williams (ed.) *The Third Anolis Newsletter*. Harvard University.
- Wilson, A. C., S. S. Carlson, and T. J. White, 1977. Biochemical evolution. *Ann. Rev. Biochem.* 46:573-639.
- Wilson, A. C., and V. M. Sarich. 1969. A molecular time scale for human evolution. *Proc. Nat. Acad. Sci. (USA)* 63:1088-1093.
- Wingate, D. 1965. Terrestrial herpetofauna of Bermuda. *Herpetologica* 21:202-218.
- Wright, J. W. 1984. The origin and evolution of the lizards of the Galapagos Islands. *TERRA* March/April 1984:21-27.
- Yang, S. Y., M. Soule, and G. C. Gorman. 1974. *Anolis* lizards of the eastern Caribbean: a case study in evolution. I. Genetic relationships, phylogeny, and colonization sequence of the *roquet* group. *Syst. Zool.* 23:387-399.

6 Notes on Phylogeny

0. Primitive anole karyotype = 12:24:0 (12 macrochromosomes, 24 microchromosomes, 0 sex chromosomes).

1. Twig Anoles. Primitive karyotype, short prehensile tail, reduced lateral exposure of coronoid bone, AID(*evermanni* → *occultus*) = 49, AID(*extremus* → *occultus*) = 51.

2. Giant Anoles. Primitive karyotype, AID(*evermanni* → *cuvieri*) = 45, AID(*extremus* → *cuvieri*) = 53, *A. roosevelti* is recently extinct on Culebra.

3. Central Caribbean Complex. Derived karyotype: 14 or more macrochromosomes and sex chromosomes, AID(*evermanni* → *extremus*) = 59, AID(*cratatellus* → *extremus*) = 54, AID(*bimaculatus* → *extremus*) = 59, AID(*wattsi* → *extremus*) = 54.

4. Cratatellus Group. AID(*evermanni* → *cratatellus*) = 16, AID(*evermanni* → *bimaculatus*) = 33, AID(*cratatellus* → *bimaculatus*) = 41.

5. Acutus Series. Karyotype is 14 macrochromosomes but other aspects of the karyotype differ among members of this series: *evermanni* = 14:10:2, *acutus* = 14:10:3, *stratulus* 14:12:3, AID's within the group to *evermanni* = 13-14. The Jamaican anoles also have 14 macrochromosomes; their AID's to *evermanni* = 27-30, to *cratatellus* = 34-41, and to *bimaculatus* = 42-44. Thus the Jamaican anoles appear to be a clade of the Acutus Series. *A. acutus* is on St. Croix.

6. Cratatellus Series. Each has 16 macrochromosomes, 8 to 10 microchromosomes, and 3 sex chromosomes. AID's within group to *cratatellus* = 11-13, Karyotypic, albumin and electrophoretic data corroborate a division into a gundlachi line and a cratatellus line.

7. Grass Anoles.

8. Trunk-ground Anoles. Karyotype = 16:10:3, Western Puerto Rico.

9. Trunk-ground Anoles. Karyotype = 16:8:3, Eastern Puerto Rico.

10. Bimaculatus Group. Karyotype = 18:8:3, except *oculatus* of Dominica = 20:8:3. AID's within group to *bimaculatus* = 10-12.

11. Wattsi Series. Small and brown with ventral scales strongly keeled. Division into wattsi series and bimaculatus series corroborated by electrophoretic data.

12. Genetic distance between *wattsi pogus* and other *wattsi* populations is greater than the distance between *w. schwartzi* and *w. wattsi*.

13. Bimaculatus Series. Large or solitary sized, often colorful, usually with green or grey-green tones. Division into northern and southern lines according to squamation and electrophoretic data.

14. Northern Bimaculatus Line. Ventral scales smooth. Two sublines: the large anoles - *A. bimaculatus bimaculatus* and *A. b. leachi*, frequently in upper canopy, and have large nuchal crests; medium-sized anoles *A. sabanus*, *A. gingivinus*, and *A. nubilus*, females with white lateral flank stripes, all three are electrophoretically closer to each other than are the two large anoles to each other.

15. Southern Bimaculatus Line. Ventral scales faintly keeled in at least some individuals. In spite of extensive differentiation in appearance as recognized by the subspecific nomenclature, electrophoretic distances among these taxa are slight. *A. lividus* from Montserrat and *A. marmoratus* of Guadeloupe are closest electrophoretically, *A. oculatus* of Dominica has karyotype = 20:8:3, and faintly keeled scales. *A. lividus* has the strongest keeling in the line, approaching, in some individuals, that of the wattsi series. The individuals from eastern half of Guadeloupe (Grande Terre) have smooth ventrals, and those from the western half (Basse Terre) are faintly keeled. *A. m. terraaltae* of the Ile des Saintes has smooth scales and some females have white lateral flank stripes. *A. m. alliaceus* from forests on Basse Terre in Guadeloupe is similar in appearance to *A. bimaculatus* and was considered a subspecies of *A. bimaculatus* by Underwood (1959) until

more extensive collections showed it to be conspecific with all the other anoles on Guadeloupe.

16. Roquet Group. Primitive karyotype, AID's to other lineages > 50, derived squamation on snout. Electrophoretic and albumin distances corroborate division into luciae and roquet series. AID's within roquet series to *extremus* = 0-14, and within luciae series to *extremus* = 26-35.

17. Roquet Series. Four unresolved lines according to electrophoretic and albumin distance data. *A. griseus* and *A. richardi* are large while *A. trinatalis* and the roquet line are medium-sized.

18. Roquet Line. Derived karyotype = 12:22:0. Electrophoretic and albumin data corroborate that *extremus* is nearly identical to *roquet*. *A. aeneus* shows extensive clinal variation in appearance but subspecies were not named.

19. Luciae Series. Electrophoretic and albumin data corroborate the relative closeness of *blanquillanus* to *bonairensis*.

20. Lineatus Series. *A. lineatus* has derived transverse processes on autotomic caudal vertebrae as do the anoles of Jamaica. AID(*lineatus* → *evermanni*) = 33, AID(*lineatus* → *crystalinus*) = 34, AID(*lineatus* → *valencienni* of Jamaica) = 22.

7 Notes on Biogeography

A. *Bufo marinus*. Large toad tolerant of brackish conditions; also in Greater Antilles except Cuba (where two large species of *Bufo* are endemic) and Central and South America.

B. *Hyla rubra*. Also Central and South America.

C. *Leptodactylus fallax*. Endemic in Lesser Antilles, recently extinct on St. Kitts, Guadeloupe, and St. Lucia.

D. *Leptodactylus wagneri*. Also South America.

E. *Eleutherodactylus johnstoni*. Endemic in Lesser Antilles.

F. *Eleutherodactylus martinicensis*. Endemic in Lesser Antilles, also on La Desirade, and Ile des Saintes.

G. *Eleutherodactylus barlagnei*. Endemic to Guadeloupe, 600-2100 ft. elevation on Basse Terre.

H. *Eleutherodactylus pinchoni*. Endemic to Guadeloupe, 600-2200 ft. elevation on Basse-Terre.

I. *Eleutherodactylus urichi schrevei*. Subspecies endemic to St. Vincent, *E. u. urichi* in Trinidad and Venezuela.

J. *Eleutherodactylus urichi euphronides*. Subspecies endemic to Grenada.

K. *Mabuya mabouya mabouya*. Also in Trinidad, Tobago, and South America.

L. *Diploglossus montisserrati*. Endemic to Montserrat. Genus occurs on Greater Antilles except Jamaica.

M. *Ameiva corvina*. Endemic to Sombrero.

N. *Ameiva pleei*. Endemic to Anguilla Bank.

O. *Ameiva erythrocephala*. Endemic to St. Kitts Bank.

P. *Ameiva griswoldi*. Endemic to Antigua Bank.

Q. *Ameiva pluvianotata*. Endemic to Lesser Antilles with distinct subspecies on Montserrat and Redonda.

R. *Ameiva cineracea*. Endemic to Guadeloupe, known only from Grand Ilet, off east coast of Basse-Terre, now extinct.

S. *Ameiva fuscata*. Endemic to Dominica. A specimen named "*A. major*" collected in 1839 may represent an extinct population from Martinique.

T. *Ameiva ameiva tobagana*. Subspecies endemic to St. Vincent and Grenada Bank, nominate subspecies occurs in Surinam.

U. *Cnemidophorus vanzoi*. Endemic to Maria Islands off St. Lucia.

V. *Bachia heteropus alleni*. Endemic subspecies to Grenada Bank, other subspecies on Trinidad and Venezuela.

W. *Kentropyx copei*. Endemic to Barbados, only Antillean representative of a genus widespread in South America.

X. *Gymnophthalmus underwoodi*. Also found in Surinam.

Y. *Gymnophthalmus pleei pleei*. Endemic subspecies to Martinique.

Z. *Gymnophthalmus pleei*. Distinct subspecies endemic to St. Lucia and to the Maria Islands off St. Lucia, species endemic to Martinique and St. Lucia.

1. *Thecadactylus rapicauda*. Also in Trinidad, Tobago, South and Central America, not in Greater Antilles, monotypic genus.

2. *Hemidactylus mabouia*. Also in Africa, Madagascar, Eastern South America, Trinidad and Tobago, Greater Antilles and Virgin Islands except Jamaica.

3. *Hemidactylus palaichthus*. On Maria Islands off St. Lucia, also in South and Central America, and Trinidad and Tobago.

4. *Phyllodactylus pulcher*. Endemic to Barbados.

5. *Sphaerodactylus sputator*. Endemic to Anguilla Bank and St. Kitts Bank.

6. *Sphaerodactylus macrolepis parvus*. Subspecies endemic to Anguilla Bank, other subspecies on Puerto Rico Bank.

7. *Sphaerodactylus sabanus*. Endemic to Saba and St. Kitts Bank.

8. *Sphaerodactylus elegantulus*. Endemic to Antigua Bank.

9. *Sphaerodactylus fantasticus*. Nine subspecies in total, two on Basse-Terre and two on Grand Terre in Guadeloupe, and one apiece on Ile des Saintes, Marie Galante, La Desirade, Montserrat, and Dominica.

a. *Sphaerodactylus vincenti*. Nine subspecies in total, seven on Martinique, and one apiece on St. Vincent and St. Lucia.

b. *Sphaerodactylus microlepis*. Endemic to St. Lucia, with distinct subspecies on St. Lucia and the Maria Islands off St. Lucia.

c. *Iguana delicatissima*. Endemic to Lesser Antilles, including Grande Terre in Guadeloupe, La Desirade, and Terre-de-Bas and Terre-de-Haute in the Illes des Saintes.

d. *Iguana iguana*. Also South America, also Lesser Antilles and Virgin Islands including Basse-Terre in Guadeloupe; La Coche, Grand Ilet, Terre-de-Haute, and Ilet a Cabrit in the Illes des Saintes; and the Maria Islands off St. Lucia.

e. *Anolis gingivinus*. Endemic to Anguilla Bank.

f. *Anolis watti pogus*. Subspecies endemic to Anguilla Bank.

g. *Anolis sabanus*. Endemic to Saba.

h. *Anolis bimaculatus bimaculatus*. Subspecies endemic to St. Kitts Bank, species endemic to Lesser Antilles.

i. *Anolis watti schwartzi*. Subspecies endemic to St. Kitts Bank.

j. *Anolis bimaculatus leachi*. Subspecies endemic to Antigua Bank.

k. *Anolis watti*. Species endemic to Lesser Antilles, distinct subspecies on Barbuda and Antigua.

l. *Anolis lividus*. Endemic to Montserrat.

m. *Anolis marmoratus*. Twelve subspecies total, two on Grand Terre and four on Basse-Terre in Guadeloupe, two in the Illes des Saintes, and one apiece on Ilet-a-Kohouanne, La Desirade, Les Iles de la Petite Terre, and Marie Galante.

n. *Anolis oculatus*. Endemic to Dominica with four subspecies.

o. *Anolis roquet*. Endemic to Martinique with six subspecies.

p. *Anolis luciae*. Endemic to St. Lucia.

q. *Anolis griseus*. Endemic to St. Vincent.

- r. *Anolis trinitatis*. Endemic to St. Vincent.
- s. *Anolis richardi*. Endemic to Grenada Bank.
- t. *Anolis aeneus*. Endemic to Grenada Bank.
- u. *Anolis extremus*. Endemic to Barbados.
- v. *Typhlops monastus geotomus*. Subspecies endemic to Antigua and St. Kitts Banks.
- w. *Typhlops monastus monastus*. Species endemic to Lesser Antilles, subspecies endemic to Montserrat.
- x. *Typhlops dominicana guadeloupensis*. Subspecies endemic to Guadeloupe, known only from Grande-Terre.
- y. *Typhlops dominicana dominicana*. Species endemic to Lesser Antilles, subspecies endemic to Dominica.
- z. *Typhlops tasymicris*. Endemic to Grenada Bank, presumed close to South American forms.
- aa. *Leptotyphlops bilineata*. Endemic to Lesser Antilles.
- bb. *Bothrops lanceolata*. Endemic to Martinique, genus widespread in South America.
- cc. *Bothrops caribbaea*. Endemic to St. Lucia, presumed close to *B. atrox* of South America.
- dd. *Boa constrictor nebulosa*. Subspecies endemic to Dominica.
- ee. *Boa constrictor crophias*. Subspecies endemic to St. Lucia.
- ff. *Corallus enydris cooki*. Also South America, nominate subspecies in Amazonian region.
- gg. *Alsophis rijersmai*. Endemic to Anguilla Bank.
- hh. *Alsophis rufiventris*. Endemic to Saba and St. Kitts Bank.
- ii. *Alsophis antillensis*. Five subspecies total, one apiece on the Antigua Bank, Montserrat, Guadeloupe & Marie Galante, Ile des Saintes, and Dominica.
- jj. *Liophus juliae*. Three subspecies total, one apiece on Guadeloupe, Marie Galante, and Dominica.
- kk. *Liophus cursor*. Endemic to Martinique.
- ll. *Liophus ornatus*. Endemic to St. Lucia, collected on Maria Islands off St. Lucia.
- mm. *Liophus melanotus*. Also Trinidad, Tobago, and South America.
- nn. *Liophus perfuscus*. Endemic to Barbados.
- oo. *Chironius vincenti*. Endemic to St. Vincent, a similar form, *C. carinatus* occurs in South and Central America, and Trinidad.
- pp. *Clelia clelia*. Also South and Central America.
- qq. *Mastigodryas bruesi*. Endemic to St. Vincent and Grenada Bank, genus in South America.
- rr. *Pseudoboa newwiedi*. Also in South and Central America.