THE ENIGMA OF THE CENTRAL AMERICAN HERPETOFAUNA: DISPERSALS OR VICARIANCE?[1]

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Some years ago, I essayed to elucidate the biogeographic history of the amphibians and reptiles of Central America, based upon the then available facts of distribution, understandings of phylogenetic relationships and climatic and geologic correlates (Savage, 1966). In subsequent biogeographic studies on the role of the region in the evolution of world frog faunas (Savage, 1973) and of neotropical mammals (Savage, 1974), I alluded to confirming and contradictory new evidence that affected my earlier interpretation.

The essential conclusions reached in 1966 were that: 1) the recent herpetofaunas of Central America are based upon a fundamental core of autochthonous groups whose history in the region goes back to Eocene-Oligocene times; 2) coexisting and evolving in association with the autochthonous groups throughout the region is a series of groups derived from northern sources; 3) the contribution of South American groups to the herpetofauna is minimal, except in extreme eastern Panama, and reflects Pliocene to Recent dispersal across the newly emergent Isthmian link between northwestern South America and lower Central America; 4) the autochthonous Central American groups had an ancient common ancestry with the South American stocks, but the two had undergone independent evolution in isolation in Central America and South America, respectively, during most of the Tertiary; and that 5) the relationship between the autochthonous and South American groups reflects a previous land connection between the two regions prior to Eocene times.

While no one has directly addressed these conclusions nor attempted to refute them, the studies of Savage (1974), Webb (1977, 1978), and Marshall et al. (1981) on mammals, Raven and Axelrod (1974) for angiosperms, and Bussing (1976) for freshwater fishes are not concordant with them. More importantly, recent interpretations of the geology of the Isthmian region (Malfait & Dinkelman, 1972; Marshall et al., 1979) raise doubts regarding the age of the pre-Eocene land connection between North and South America and place it so far back in time (100 m.y. B.P.) as to antedate seemingly the origin of most extant Central American groups. In addition, Rosen (1976, 1978) has developed a powerful explanatory

model of Central American biogeography based upon a number of major animal groups, which does not seem to support my ideas of 15 years ago. Duellman (1979), without directly acknowledging Rosen as his source, presented a brief explanation of the possible interchange of herpetofaunal components between North and South America, based upon Rosen's (1976) model.

For these reasons, and because our knowledge of distributions, fossil history, and phylogenetic relations for the amphibians and reptiles of Central America have substantially increased in the interim, the time seems ripe for a reconsideration of their biogeography. That the period since the appearance of my original paper has seen a major revolution in geological thinking associated with the theory of continental drift and the new tectonics (Uyeda, 1978) and the subsequent emergence of a new model for biogeographic explanation (Croizat et al., 1974; Nelson & Rosen, 1981), provides further stimulus for preparation of the present report.

It is not my purpose in the present study to reconstitute the entire data base nor recapitulate in detail the arguments and explanation of herpetofaunal history developed in my earlier paper (Savage, 1966). I have attempted to provide a revised summary of basic distributional data for Central America as part of this study. Otherwise, I have avoided repetition of materials and ideas presented in the 1966 report, particularly where there seems no reason to re-examine or modify major points or conclusions. This is especially the case with regard to characterization of subdivisions of the Mesoamerican herpetofauna, the recognition of relationship between post-Eocene events of physiographic and climate changes and concordant distribution patterns and the epigenetic influences (sensu Rosen, 1978) of Pleistocene-Recent climatic and vegetational fluctuations.

COMPOSITION AND DISTRIBUTION OF THE HERPETOFAUNA

Although the focus of the present report is on Central America, as will be seen below, reference to adjacent tropical lands and physiographic subdivisions is necessary throughout. The following terminology is consistently employed for present land areas:

North America—the continental land mass lying west and north of the Isthmus of Tehuantepec

South America—the southern continental land mass extending east and south from eastern Panama

Central America—the region running southeast from the Isthmus of Tehuantepec to northwestern South America, including the Isthmus of Panama

Mesoamerica or Middle America—Mexico and Central America

Nuclear or upper Central America—the northern portion of Central America extending from the Isthmus of Tehuantepec to the uplands of northern Nicaragua; land positive throughout Cenozoic

Isthmian Link or lower Central America—the southern portion of Central America lying between southern Nicaragua and Colombia; submerged through much of Tertiary.

Wauchope and West (1964) and Stuart (1966) have outlined the major physiographic, hydrographic, climatologic, and vegetational aspects of the region. Duellman (1966, 1979), Savage (1966), and Rosen (1978) provide additional in-

formation as it relates to faunal distribution. Stuart (1966), Dengo (1968), Malfait and Dinkelman (1972), and Rosen (1976) provide much data on geologic features and their evolution.

The distributional data forming the basis for this account include the sources cited in my earlier work (Savage, 1966) and a host of more recent works, especially Duellman (1970, 1979), Henderson and Hoevers (1975), Lee (1980), Meyer and Wilson (1971, 1973), Villa (1972), Savage (1980a, 1980b), Wake and Lynch (1976), and the primary taxonomic literature cited in these reports.

The herpetofauna of Central America is comprised of nearly 700 species of amphibians and reptiles grouped by genera as follows: caecilians (4), salamanders (5), frogs and toads (33), turtles (9), lizards (40), snakes (76), and crocodilians (2), for a total of 42 amphibians and 127 reptiles (grand total 169). It forms the major portion of a somewhat more extensive tropical herpetofauna that ranges westward and northward from the Isthmus of Tehuantepec along the lowlands and premontane slopes of Mexico to about the level of Tamaulipas on the Atlantic and Sinaloa on the Pacific versant; in addition, it intermixes in a complex fashion with representatives of the northern or Nearctic herpetofauna in the mountains bordering the central plateau of Mexico on the east, west, and south. For purposes of this paper, the combined fauna of 197 genera, caecilians (4), salamanders (9), frogs and toads (37), turtles (9), lizards (45), snakes (91), and crocodilians (2), of the area is considered as a single unit, the Tropical Mesoamerican herpetofauna.

These genera may be placed into one of four major groupings based upon distribution: 1) widespread tropical—tropical genera found throughout the Middle and South American tropics with equally strong species differentiation in both regions; 2) South American—genera with centers of distribution and differentiation in South America; 3) Tropical Middle American—genera with centers of distribution and differentiation in tropical Mexico and Central America; and 4) Extratropical North American—genera with centers of distribution and differentiation in extratropical Mexico or the United States. A number of distinctive patterns of distribution within the four major groupings are evident and provide a basis for evaluating the composition of the Central American herpetofaunas as follows:

1. WIDESPREAD TROPICAL (11)

Eleutherodactylus	*Leptotyphlops*
Bufo	*Drymarchon*
Phrynohyas	*Drymobius*
Hyla	*Spilotes*
Mabuya	*Micrurus*
	Bothrops

2. SOUTH AMERICAN (60)

A. Northern Limit of Range in Panama (22)

Caecilia	*Enyalioides*
Oscaecilia	*Echinosaura*

Protopipa
Rhamphophryne
Chiasmocleis
Elachistocleis
Relictivomer
Gastrotheca
Hemiphractus
Pleurodema
Chelonoides
Morunasaurus

Amphisbaena
Trachyboa
Atractus
Diaphorolepis
Lygophis
Phimophis
Pseudoboa
Siphlophis
Bothriopsis

B. Northern Limit of Range in Costa Rica (20)

Glossostoma
Phyllobates
Colostethus
Phyllomedusa
Atelopus
*Anolis**
Polychrus
Bachia
Leposoma
Ptychoglossus

Neusticurus
Anadia
Anomalepis
Helminthophis
Liotyphlops
Epicrates
Helicops
Leimadophis
Nothopsis
Tripanurgos

* *Anolis* reaches southern United States via the West Indies.

C. Northern Limit of Range Between Costa Rica and Guatemala (6)

Dendrobates
Corallus
Chironius

Erythrolamprus
Rhinobothryum
Lachesis

D. Northern Limit of Range in Mexico (11)

*Leptodactylus**
Physalaemus
Centrolenella
Ameiva
Gonatodes
Gymnophthalmus

Typhlops
Clelia
Oxyrhopus
Xenodon
Caiman

* Reaches southern United States.

3. TROPICAL MIDDLE AMERICAN (105)

A. Endemics (32)

Bolitoglossa B
Pseudoeurycea
Chiropterotriton B
Triprion

Plectrohyla
Ptychohyla
Anotheca
Coloptychon

Claudius
Staurotypus
Dermatemys
Corytophanes
*Aristelliger**
Laemanctus
Ctenosaura
Enyaliosaurus
Lepidophyma
*Celestus**
Xenosaurus
Crepidophryne

Loxocemus
Adelphicos
Amastridium
Crisantophis
Conophis
Hydromorphus
Leptodrymus
Scolecophis
Symphimus
Tantillita
Trimorphodon
Crocodylus

* Also in Antilles.

B. Northern Limit of Range in Extratropical North America (17)

Rhinophrynus
Hypopachus
Gastrophryne
Syrrhophus
Kinosternon
Coleonyx
Phyllodactylus
Heloderma
Cnemidophorus

Coniophanes
Ficimia
Oxybelis
Leptodeira
Rhadinaea
Tantilla
Trimorphodon
Crocodylus

C. Southern Limit of Range in Northern and/or Northwestern South America (21)

Dermophis
Gymnopis
Oedipina
Smilisca
Rhinoclemmys
Basiliscus
Lepidoblepharis
Thecadactylus
Ungaliophis
Coniophanes
Dendrophidion

Enulius
Geophis
Ninia
Pliocercus
Scaphiodontophis
Sibon
Stenorrhina
Tretanorhinus
Bothriechis
Crocodylus

D. Southern Limit of Range in Amazon Basin or Farther South (17)

Bolitoglossa A
Norops
Iguana
Sphaerodactylus
Phyllodactylus
Cnemidophorus

Dipsas
Imantodes
Leptodeira
Leptophis
Mastigodryas
Oxybelis

Diploglossus
Boa

Pseustes
Rhadinaea
Tantilla

E. Endemic Genera in Tropical Mexico (19)

Chiropterotriton A
Lineatriton
Parvimolge
Thorius
Hylactophryne*
Tomodactylus
Pternohyla*
Anelytropsis
Bipes
Exiliboa

Chersodromus
Cryophis
Geagras
Manolepis
Pseudoficimia
Rhadinophanes
Sympholis
Tantalophis
Toluca

* Occurs in southern United States.

4. EXTRATROPICAL NORTH AMERICAN (33)

A. Southern Limit of Range in Tropical Mexico (15)

1) Southern Limit of Range in Central or Southern Mexico (9)

Phrynosoma
Urosaurus
Ophisaurus
Gyalopion
Hypsiglena

Rhinocheilus
Sonora
Salvadora
Scaphiopus

2) Southern Limit of Range Marginally Tropical (6)

Notophthalmus
Callisaurus
Dipsosaurus

Holbrookia
Arizona
Micruroides

The latter six genera are not treated further in this report and have been included here only for the sake of completeness.

B. Southern Limit of Range in Central America (12)

Terrapene
Sceloporus
Eumeces
Sphenomorphus
Pituophis
Storeria

Abronia
Gerrhonotus
Nerodia
Elaphe
Thamnophis
Agkistrodon

C. Southern Limit of Range in South America (6)

Rana
Chelydra
Chrysemys*

Coluber
Lampropeltis
Crotalus

* Includes Pseudemys.

These data demonstrate that the recent Central American herpetofauna is composed primarily of genera with one of two major distribution patterns. One group includes genera with a tropical Middle American distribution pattern that predominate in Central America at all elevations from the Isthmus of Tehuantepec to central Panama and in the lowlands on both coasts of Mexico, to the limits of tropical conditions. The second group includes genera with a South American distribution pattern and is fully represented in the region only in Panama. Of the 197 genera in tropical Mesoamerica, 53% are centered essentially there, 30% are South American, and 17% are extratropical North American (Nearctic) in distribution. North of Costa Rica only 18 genera (9%) are South American groups, while in eastern Panama around 60% of the genera are South American. These data and the distribution of the 55 New World families of amphibians and reptiles (Table 1) support the idea developed in my 1966 paper that the tropical Mesoamerican herpetofauna is a distinctive assemblage only distantly related to that of South America and even less so to that of extratropical North America.

General faunal relationships between tropical Middle America and South America is suggested by family distributions. Only seven families found in Central America do not range into South America and only 10 are conversely found in South America but not in tropical Middle America. Nevertheless, the herpetofaunas of the two regions each stands as an unique combination of families, subfamilies, genera, and species groups. A comparison at the generic level will suffice to emphasize the degree of faunal difference. Of the 169 genera in the herpetofauna of Central America, 32 are endemic to the area and 21 others are essentially restricted to the region. Only 16 rather wide-ranging South American genera occur in Central America north of Costa Rica, while the South American continent supports about 200 endemic genera that are not known from north of Colombia. A sample of the Neotropical endemics is provided in the list below, with emphasis on tropical groups:

Gymnophiona: *Rhinatrema, Siphonops, Typhlonectes.*

Anura: *Pipa, Adenomera, Ceratophrys, Crossodactylus, Cycloramphus, Hylodes, Eupsophus, Odontophrynus, Pseudis, Pseudopaludicola, Thoropa, Zachaenus, Dendrophryniscus, Melanophryniscus, Brachycephalus, Amphignathodon, Aparasphenodon, Cryptobatrachus, Nototheca, Osteocephalus, Tetraprion, Ctenophryne, Dermatonotus, Elachistocleis, Synapturanus.*

Testudinata: *Podocnemis, Batrachemys, Chelys, Hydromedusa, Phrynops.*

Sauria: *Aptycholaemus, Hoplocercus, Liolaemus, Ophryoessoides, Plica, Stenocercus, Tropidurus, Urocentron, Coleodactylus, Homonota, Dicrodon, Dracaena, Euspondylus, Kentropyx, Proctoporus, Tupinambis, Leposternon.*

Serpentes: *Anilius, Eunectes, Apostolepis, Drepanoides, Drymoluber, Elapomorphus, Hydrops, Liophis, Lystrophis, Philodryas, Sibynomorphus, Thamnodynastes.*

Crocodilia: *Melanosuchus, Paleosuchus.*

The facts of distribution reinforce the concept of the Middle American tropical assemblage as a distinctive unit, more or less equivalent to the Nearctic and Neotropical units. It must be emphasized that the Mesoamerican herpetofauna is not transitional between the Nearctic and Neotropical assemblages as proposed by Darlington (1957) but is comprised primarily of endemic genera, species groups,

TABLE 1.   Distribution of New World families of amphibians and reptiles.

I. Restricted to One Geographic Region		
Nearctic (9)	Tropical Mesoamerica (5)	South America (9)
		Rhinatrematidae
		Typhlonectidae
Cryptobranchidae		
Sirenidae		
Proteidae		
Amphiumidae		
Ambystomatidae		
Salamandridae		
Ascaphidae	Rhinophrynidae	Pipidae*
Pelobatidae		Rhinodermatidae
		Brachycephalidae
		Pseudidae
Trionychidae	Dermatemydidae	Pelomedusidae
	Dibamidae	
	Xenosauridae	Chelidae
	Loxocemidae	Aniliidae

II. Occurring in Two Regions		
Nearctic-Tropical Mesoamerica (2)	South America-Nearctic (1)	Tropical Mesoamerica-South America (6)
Xantusiidae	Testudinidae*	Caeciliidae
Helodermatidae		Dendrobatidae
		Centrolenidae
		Gymnophthalmidae
		Anomalepididae
		Typhlopidae

III. Occurring in All Three Regions (22)		
Plethodontidae	Iguanidae	Micruridae
Microhylidae	Gekkonidae	Viperidae
Leptodactylidae	Teiidae	Crocodylidae
Bufonidae	Scincidae	
Hylidae	Anguidae	
Ranidae	Amphisbaenidae	
Kinosternidae	Leptotyphlopidae	
Chelydridae	Boidae	
Emydidae	Trophidophiidae	
	Colubridae	

* Reaching Eastern Panama.

and species, with a small representation of Nearctic forms and a somewhat larger sampling of groups with Neotropical affinities.

Six major herpetofaunal assemblages may be recognized in the Central American area (Fig. 1 and Table 2):

1. **Eastern and Western Lowland Herpetofauna**—a wide-ranging fauna, the most diverse and richest in species composition of the Central American assemblages, found along the Atlantic lowlands from Tamaulipas, Mexico, to central Panama; with more or less isolated segments at moderate elevations along the Pacific slopes of Guatemala and in the Golfo Dulce region in the Pacific lowlands of southwestern Costa Rica and extreme western Panama.

2. **Western Lowland Herpetofauna**—a fauna associated with semiarid to sub-

humid climatic conditions, ranging along the Pacific lowlands from northern Sinaloa in Mexico, to the Golfo de Nicoya region and Meseta Central of Costa Rica; including the subhumid and semiarid assemblages of Atlantic drainage valleys in Chiapas, Mexico, and Guatemala and the uplands of Honduras and Nicaragua; characterized by a predominance of lizard and snake species and virtual absence of salamanders.

3. **Guatemalan Highland Herpetofauna**—an assemblage restricted to the cool moist habitats of the Chiapas and Guatemala highlands.

4. **Talamancan Herpetofauna**—a fauna with a well-developed amphibian complement, occurring in the humid environments of highland Costa Rica and western Panama.

5. **Panamanian Herpetofauna**—a fauna associated with disjunct subhumid lowland habitats from eastern Panama, along the Pacific versant, to the Chiriqui region of western Panama; showing closest affinities to the herpetofaunas of northern lowland Colombia and Venezuela that are associated with subhumid to arid conditions along the Caribbean lowlands.

6. **Chocoan Herpetofauna**—a South American fauna, extremely rich in species composition, found along the Pacific lowlands from northern Ecuador through Colombia and barely entering eastern Panama, where it is found in the Darien region along the Caribbean versant.

THE FOSSIL RECORD

The fossil record for amphibians and reptiles in Central America is meager with only one tortoise genus ? *Chelonoides* recorded from Oligocene to Miocene in Costa Rica and a few Pleistocene examples of modern genera. The general fossil record for recent Central and South American families is summarized (Table 3) and commented on below.

It should be noted that the following extant families were represented in America north of Mexico as well: Salamanders—Cryptobranchidae (Cretaceous), Proteidae (Cretaceous, Eocene), Sirenidae (Cretaceous, Eocene), Amphiumidae (Cretaceous, Paleocene), Salamandridae (Cretaceous), and Pelobatidae (Pliocene-R). Two extant lizard families—Agamidae (Eocene), Varanidae (Cretaceous-Oligocene)—are also represented, but do not occur in the Americas at present.

The ancient, but contemporary turtle family Trionychidae occurs in North America as far back as Cretaceous and in the Pliocene of South America.

ORIGINS AND HISTORY OF THE HERPETOFAUNA:
A REVIEW OF THE PROBLEM

In my earlier paper (1966), I concluded from an analysis of the distributional data, geologic, climatological, and vegetational correlates and changes, together with an assessment of phylogenetic relationships, that three major and one minor historical source units had contributed to the Central American herpetofauna.

The most important unit (the Middle American Element) is comprised of genera that are primarily tropical Mesoamerican in distribution and have their closest allies either in the region or in South America, but are mostly endemic to Central

FIGURE 1.   Major herpetofaunas of Central America. See text for description of assemblages denoted by numbers.

America and Mexico. Available evidence indicates that members of this unit and/ or their ancestors had a more extensive range in North America in early Tertiary when humid warm climates occurred as far north as the region of what is now Montana, Wyoming, Utah, Colorado, and the Dakotas, but became restricted southward by climatic change in late Cenozoic to tropical Mesoamerica.

A second unit (the Old Northern Element) contains a series of genera that are primarily extratropical in distribution in Eurasia and/or North America, but are represented by several tropical forms in the Americas. These groups and/or their ancestors were distributed more or less continuously and circumpolarly in early Tertiary, but were forced southward and fragmented into distinct geographic isolates by the results of increased cooling and acidity through Cenozoic. Included in this stock is a unique Mesoamerican component of endemic families and genera that has evolved with the autochthonous Middle American unit from Eocene onward.

The third major group (the South American Element) is principally South American in distribution and relationships but occurs to various distances onto the Isthmian Link and northward. This stock obviously underwent evolution on the South American land-mass during most of Cenozoic and must be interpreted as a recent contributor to Central American faunal diversity.

The fourth minor unit (the Young Northern Element) in terms of the region under study is represented by a few genera that are primarily extratropical in distribution and associated with the semiarid to arid regions of the southwestern

TABLE 2. Distribution of Central American genera of amphibians and reptiles.

| | Mesoamerican | | | | South American | |
	Humid E and W Lowland	Western Lowland	Guate-malan Highland	Tala-mancan Highland	Pana-manian	Chocoan
GYMNOPHIONA (4)						
Caecilia	X					X
Oscaecilia					X	X
Gymnopis	X					
Dermophis	X	X				X
CAUDATA (5)						
Bolitoglossa A	X		X	X		X
Bolitoglossa B			X	X		
Pseudoeurycea			X			
Chiropterotriton B			X	X		
Oedipina	X	X	X	X		X
ANURA (33)						
Protopipa					X	
Rhinophrynus	X	X				
Leptodactylus	X	X			X	X
Pleurodema					X	
Physalaemus	X	X			X	
Eleutherodactylus	X	X	X	X		X
Syrrhophus	X	X				
Dendrobates	X					X
Phyllobates	X					X
Colostethus	X					X
Centrolenella	X			X		X
Bufo	X	X	X	X	X	X
Crepidophryne				X		
Rhamphophryne						X
Atelopus				X		X
Smilisca	X	X		X	X	X
Phrynohyas	X	X			X	
Hyla	X	X	X	X	X	X
Plectrohyla			X			
Ptychohyla			X			
Hemiphractus	X					X
Gastrotheca	X					X
Anotheca	X					
Triprion	X					
Agalychnis	X					X
Phyllomedusa	X					X
Chiasmocleis					X	
Elachistocleis					X	
Relictivomer					X	
Glossostoma				X		
Gastrophryne	X	X				
Hypopachus	X	X	X			
Rana	X	X	X	X		X
TESTUDINATA (9)						
Kinosternon	X	X			X	X
Chelydra	X	X				X
Claudius	X					
Staurotypus	X	X				
Dermatemys	X					
Terrapene	X					

TABLE 2. Continued.

	Mesoamerican				South American	
	Humid E and W Lowland	Western Lowland	Guate-malan Highland	Tala-mancan Highland	Pana-manian	Chocoan
Chrysemys	X	X			X	X
Rhinoclemmys	X	X				X
Chelonoides					X	
SAURIA (40)						
Anolis					X	X
Norops	X	X	X	X		
Polychrus	X					X
Basiliscus	X	X		X	X	X
Corytophanes	X					X
Laemanctus	X					
Morunasaurus	X					
Enyalioides						X
Sceloporus	X	X	X	X		
Ctenosaura	X	X			X	
Enyaliosaurus	X	X				
Iguana	X	X			X	X
Coleonyx	X	X				
Sphaerodactylus	X	X				
Lepidoblepharis	X					X
Gonatodes	X	X			X	X
Aristelliger	X					
Thecadactylus	X					X
Phyllodactylus	X	X				
Lepidophyma	X	X				
Eumeces	X	X				
Sphenomorphus	X		X			
Mabuya	X	X			X	X
Ameiva	X	X			X	X
Cnemidophorus	X	X			X	
Bachia	X				X	
Gymnophthalmus		X	X		X	
Leposoma	X					X
Echinosaura	X					X
Ptychoglossus	X					X
Neusticurus	X					
Anadia	X					X
Amphisbaena						X
Abronia			X			
Gerrhonotus			X	X		
Coloptychon	X			X		
Celestus	X			X		
Diploglossus	X					X
Xenosaurus			X			
Heloderma		X				
SERPENTES (76)						
Helminthophis				X		
Liotyphlops	X				X	X
Anomalepis	X					
Typhlops	X			X		
Leptotyphlops	X	X			X	
Boa	X	X			X	X
Corallus	X				X	X
Epicrates	X	X			X	

TABLE 2. Continued.

| | Mesoamerican | | | | South American | |
	Humid E and W Lowland	Western Lowland	Guate-malan Highland	Tala-mancan Highland	Pana-manian	Chocoan
Loxocemus		X				
Trachyboa						X
Ungaliophis	X	X				
Adelphicos	X		X			
Amastridium	X			X		
Atractus						X
Chironius	X	X			X	X
Clelia	X	X		X	X	X
Coluber	X	X			X	
Coniophanes	X	X				X
Conophis	X	X				
Crisantophis		X				
Dendrophidion	X				X	X
Diaphorolepis						X
Dipsas	X	X			X	X
Drymarchon	X	X			X	X
Drymobius	X	X			X	X
Elaphe	X	X				
Enulius	X	X			X	X
Erythrolamprus	X	X			X	X
Ficimia	X	X				
Geophis	X		X	X		
Helicops				X		
Hydromorphus	X			X		
Imantodes	X	X			X	X
Lampropeltis	X	X		X	X	X
Leimadophis	X			X	X	X
Leptodeira	X	X			X	X
Leptodrymus		X				
Leptophis	X	X			X	X
Lygophis	X					X
Mastigodryas	X				X	X
Nerodia	X					
Ninia	X	X	X	X	X	X
Nothopsis	X					X
Oxybelis	X	X			X	X
Oxyrhopus	X				X	X
Phimophis					X	
Pituophis			X			
Pliocercus	X					X
Pseudoboa					X	
Pseustes	X	X			X	X
Rhadinaea	X		X	X		X
Rhinobothryum	X					X
Scaphiodontophis	X	X			X	
Scolecophis		X				
Sibon	X	X				X
Siphlophis					X	X
Spilotes	X	X			X	X
Stenorrhina	X	X				X
Storeria	X					
Symphimus	X	X				
Tantilla	X	X		X		X
Tantillita	X					

TABLE 2. Continued.

	Mesoamerican				South American	
	Humid E and W Lowland	Western Lowland	Guate-malan Highland	Tala-mancan Highland	Pana-manian	Chocoan
Thamnophis	X	X	X			
Tretanorhinus	X	X			X	X
Trimetopon	X	X		X		
Trimorphodon		X				
Tropidodipsas	X	X	X			
Tripanurgos	X					X
Xenodon	X	X			X	X
Micrurus	X	X			X	X
Agkistrodon	X	X				
Bothriechis	X	X	X	X	X	X
Bothriopsis						X
Bothrops	X	X	X	X	X	X
Lachesis	X					X
Crotalus	X	X				
CROCODILIA (2)						
Caiman	X	X			X	X
Crocodylus	X	X			X	X
Totals (169)	130	82	28	34	61	87

United States and adjacent Mexico. This unit contains many distinctive genera outside of Central America to form a significant component of the North American herpetofauna (Savage, 1960, 1966) and seems to have evolved *in situ* in response to increasing acidity and cooling trends in the latter portion of the Cenozoic.

It appeared that in early Cenozoic, the Americas (Fig. 2) were dominated by two major herpetofaunal units. In subtropical and tropical America, to at least 40°N latitude, a generalized tropical herpetofauna occurred. To the north were representatives of ancestral Old Northern groups. It was proposed, based upon correlation with geologic data (Vinson & Brineman, 1963), that the continuity of the generalized tropical herpetofauna was interrupted by the inundation of the Isthmian Link in late Paleocene. With the establishment of the open marine portal across the region from Nicaragua to Colombia, the two fragments of the generalized tropical unit underwent independent evolution to the north and south of the portal during most of the rest of the Tertiary. The distinctive Middle American and South American Elements were believed to have been the result of this fragmentation.

Apparently, certain representatives of the Old Northern Element (the Central American component) reached Middle America in Eocene and evolved in association with the Middle American Element for the remainder of Cenozoic. Subsequently, the events of mountain building and the drying and cooling trends that were initiated in Oligocene led to a southward latitudinal depression of tropical and subtropical conditions and with the resultant compression of the descendant species of the two stocks into the Middle American Peninsula. By the middle of

TABLE 3. Fossil records for extant families of the Central (X) and South American (*) herpetofaunas.

	Recent	Pleisto-cene	Pliocene	Miocene	Oligo-cene	Eocene	Paleo-cene	Creta-ceous
Rhinatrematidae	*							
Caeciliidae	*						*	
Typhlonectidae	*							
Plethodonidae	*							
	X	X	X	X				
Pipidae	*						*	*
Rhinophrynidae	X				X	X		
Microhylidae	*							
	X	X		X				
Leptodactylidae	*	*	*	*	*	*	*	
Bufonidae	*	*	*	*				
	X	X	X					
Rhinodermatidae	*							
Brachycephalidae	*							
Dendrobatidae	*							
Pseudidae	*							
Centrolenidae	*							
Hylidae	*							
	X	X	X	X				
Ranidae	X	X	X					
Pelomedusidae	*	*	*	*		*	*	*
				X				X
Chelidae	*	*	*	*	*	*		
Kinosternidae	*							
	X	X	X					
Dermatemydidae	X					X	X	X
Chelydridae	X	X		X	X			
Emydidae	*	*						
	X	X	X	X	X	X	X	X
Testudinidae	*	*	*	*	*	*		
	X	X	X	X	X			
Iguanidae	*			*			*	*
	X	X	X	X	X	X		
Teiidae	*	*	*	*			*	
	X	X	X					X
Gekkonidae	*							
	X							
Scincidae	*							
	X	X	X	X	X	X	X	X
Gymnophthalmidae	*							
Dibamidae	X							
Xantusiidae	X	X				X	X	
Xenosauridae	X				X	X	X	X
Anguidae	*							
	X			X	X	X		
Helodermatidae	X				X			
Amphisbaenidae	*	*						
	X				X	X		
Anomalepididae	*							
	X							
Typhlopidae	*							
	X							
Leptotyphlopidae	*							
	X							

TABLE 3. Continued.

	Recent	Pleisto-cene	Pliocene	Miocene	Oligo-cene	Eocene	Paleo-cene	Creta-ceous
Loxocemidae	X							
Aniliidae	*			*				
				X			X	X
Boidae	*	*	*	*		*	*	
	X			X	X	X	X	
Tropidophiidae	X							
Colubridae	*	*		*				
	X	X	X	X				
Micruridae	*							
	X	X	X					
Viperidae	*	*						
	X	X	X					
Crocodylidae								
Crocodylinae	*	*	*	*	*	*	*	
Alligatorinae	*	*	*	*	*	*	*	

Oligocene, the tropical Mesoamerican region was isolated on the north by a temperate semiarid to arid climatic barrier that increased in extent throughout the remainder of the Cenozoic. The two isolating factors of the marine portal to the south and the climatic barrier to the north allowed for the *in situ* development of much of the typical tropical Mesoamerican herpetofauna during most of the Cenozoic.

When the Panamanian Isthmus was reformed in Pliocene, some South American groups dispersed into lower Central America and some Middle American and associated Central American stocks into South America. Nevertheless, tropical Mesoamerica, except in eastern Panama, is dominated by the autochthonous Middle American Element that indicates the long and independent *in situ* evolution of the herpetofauna. A summary diagram (Fig. 2) illustrates the principal features of this explanation.

Although there can be little argument regarding the distinctive nature of the core tropical Mesoamerican herpetofauna or that its major element has an ancient relationship to South American stocks, new geologic and biotic evidence and its interpretation raise into question my earlier explanation of how the observed patterns developed. The new evidence and its impact are discussed below in terms of geologic history, distributional data for other groups, and theoretical considerations.

A central feature of my attempt to explain the distinctiveness of the core Mesoamerican herpetofauna relates to the history of intercontinental land connections between Central and South America. Most recent geologic studies concur with the view of Dietz and Holden (1970), Malfait and Dinkelman (1972), and Ladd (1976), that there was no direct land connection between North America plus Nuclear Central America and South America, throughout most or all of Cretaceous and Cenozoic. Only with the establishment of the Isthmian Link, at
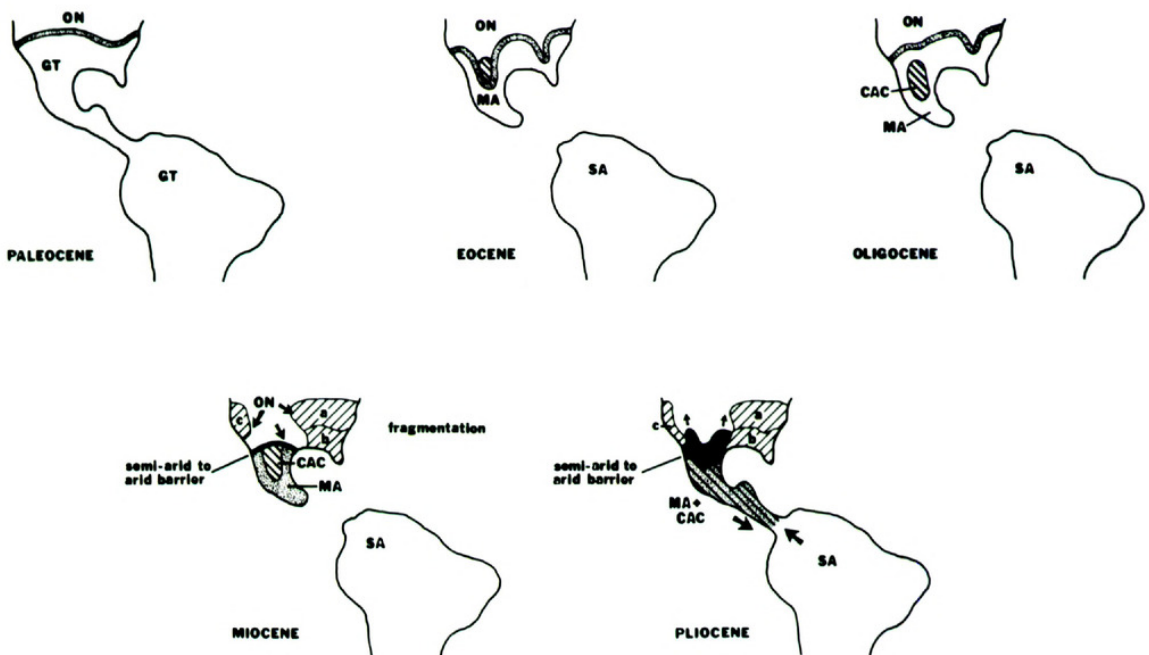
FIGURE 2.   Origins and history of the Mesoamerican herpetofauna according to model of Savage (1966). See text for description of history of Old Northern (ON), Generalized Tropical (GT), Middle American (MA), South American (SA), and Central American Components (CAC).

the beginning of the Pliocene (Raven & Axelrod, 1974; Savage, 1974), about 5.2 m.y. B.P. or late Pliocene (3 m.y. B.P.) according to others (Simpson, 1950, 1969; Patterson & Pascual, 1968; Webb, 1977, 1978; Marshall et al., 1979) was there an opportunity for overland immigration between Central and South America. While there is a suggestion of a mid-Cretaceous connection of Nuclear Central America and South America (Smith & Briden, 1977), available data indicate a minimum period of separation between the two regions for about 100,000 m.y. During about half of that time interval, South America was an isolated island continent because direct land connections to Africa were eliminated by late Jurassic (140 m.y. B.P.) and with Antarctica-Australia by Eocene or Oligocene (50 m.y. B.P.).

A number of workers have suggested that a series of island arcs developed in the general area between Nuclear Central America and South America during late Cretaceous and early to late Tertiary. Dengo (1968, 1973) proposed that a volcanic chain extended across the portal region, somewhat south of the present isthmus from Cretaceous to Eocene. A second volcanic arc, the precursor of the present isthmus, appeared by the Oligocene at the level of present-day Costa Rica and Panama. Rosen (1976), on the basis of his interpretation of the work of Holden and Dietz (1972), and Malfait and Dinkelman (1972), hypothesized the presence of a late Cretaceous-Pliocene island arc (the proto-Antilles) in the portal region, that later became displaced far to the east by tectonic events associated with movements of the Caribbean plate.

Another group of workers (Owen, 1976; Carey, 1976; Shields, 1979), advocates of the expanding earth hypothesis, indicated that a land bridge or a series of closely proximate islands connected the region of present day Venezuela, the

Greater Antilles, the Nicaragua Plateau, and Nuclear Central America in late Cretaceous-Paleocene, with a possible connection between Cuba and Florida, as well. Carey (1976) further regarded the Panamanian Portal to have been open but only transitorily in Cenozoic and stated (p. 393), "and at no time from the Paleozoic to the present has there been any substantial marine barrier separating North and South America."

Lillegraven et al. (1979) developed a somewhat similar idea of an eastern archipelago in addition to those described by Dengo (1968, 1973) in the Panamanian Portal zone, perhaps influenced by the views of Carey (1976) and Shields (1979). The proposed archipelago probably persisted from late Cretaceous to Eocene and was formed by volcanic islands of the Aves Arc, which originally were located about 200 km further west than their submerged present day remnant, and the volcanic islands that were the predecessors of the Greater Antilles. The latter series terminated in close proximity to the now submerged Nicaragua Plateau, which was probably land positive and connected to Nuclear Central America (Perfit & Heezen, 1978).

These conflicting ideas and recent geologic studies on sea-floor and tectonic features in the region (Bowin, 1976; Christofferson, 1976; Hey et al., 1977; Londsdale & Klitgord, 1978) confirm the complexity of its history and the likelihood of the substantial uncertainties in interpretation for sometime to come. Nevertheless, the majority opinion rejects the notion of a continuous land connection between Central and South America for all of Cretaceous to Pliocene time. Therefore, the hypothesis of 1) a Paleocene land connection that existed in the region of the present Isthmian Link and permitted the wide distribution of a generalized tropical herpetofauna and 2) the fragmentation of that herpetofauna into Middle American and South American Elements by submergence of the land bridge, is brought into serious doubt. If, indeed, the tropical Mesoamerican and South American herpetofaunas are as distinctive as I claimed them to be in 1966, some other progenetic model for their differentiation needs to be found

Biogeography is based upon the recognition of concordant distribution patterns and attempts to explain their congruence. If the patterns I recognized for herpetofaunal distributions in 1966 have general significance, they should show concordance with the distributions of other organisms. In addition, the common patterns should provide clues to the cause of the observed congruence. Several major studies on the biogeography of Central America have appeared in the 15 years since my theory was published, especially Raven and Axelrod (1974) for seed-plants; Savage (1974), Webb (1977, 1978), Ferrusquia-Villafranca (1978), and Marshall et al. (1979) for mammals; Bussing (1976) for freshwater fishes; and Duellman (1979) for the South American herpetofauna. In the following paragraphs, the degree to which this paper recognizes patterns that are concordant or discordant with herpetofaunal ones is briefly explored.

Raven and Axelrod (1974) compared the situation among angiosperms in Central America to that in Australasia. In the latter region, the typical tropical Asian vertebrate fauna occurs eastward along the Indo-Malayan island chain to near the region of Wallace's Line (Darlington, 1957). East of this area through New Guinea, Australia, and associated islands, a markedly different fauna is present. Unlike the vertebrates, the flora is essentially similar from southern Asia, through
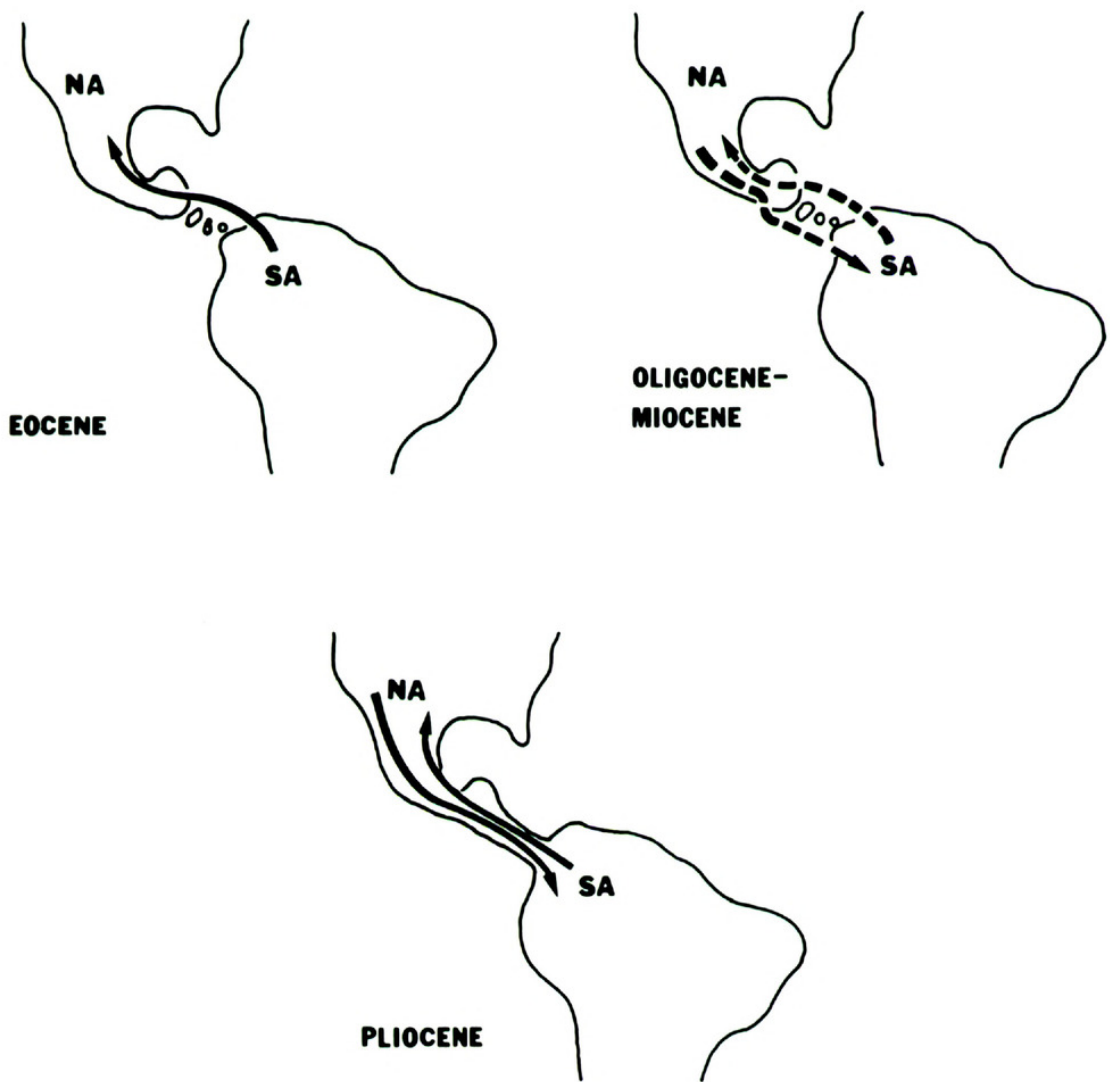
FIGURE 3.   Origins and history of the Mesoamerican angiosperm flora, according to the model of Raven and Axelrod (1974). See text for description of history of North (NA) and South American (SA) derivatives.

New Guinea, northern Australia, and eastward to Fiji. According to Raven and Axelrod, the Central American vertebrate fauna has retained a level of distinctiveness. They argue that these differences have to do with the better powers of plants for overwater and waif dispersal. They suggest that until the Isthmian Link was established, the faunas on either side were distinctive and well-differentiated (as if on either side of Wallace's Line), while the flora north of the marine portal was not, and corresponded to the flora east of Wallace's Line. The subsequent blurring of the differences between faunas by overland immigration in both directions across the link has led to the current resemblances among the biotas throughout tropical America.

In essence, Raven and Axelrod proposed that Central America was populated by many plant families from South America through overwater and/or island-hopping dispersal in Eocene-Oligocene times. These groups joined a substantial suite of North American families. Subsequently, dispersals in both directions,
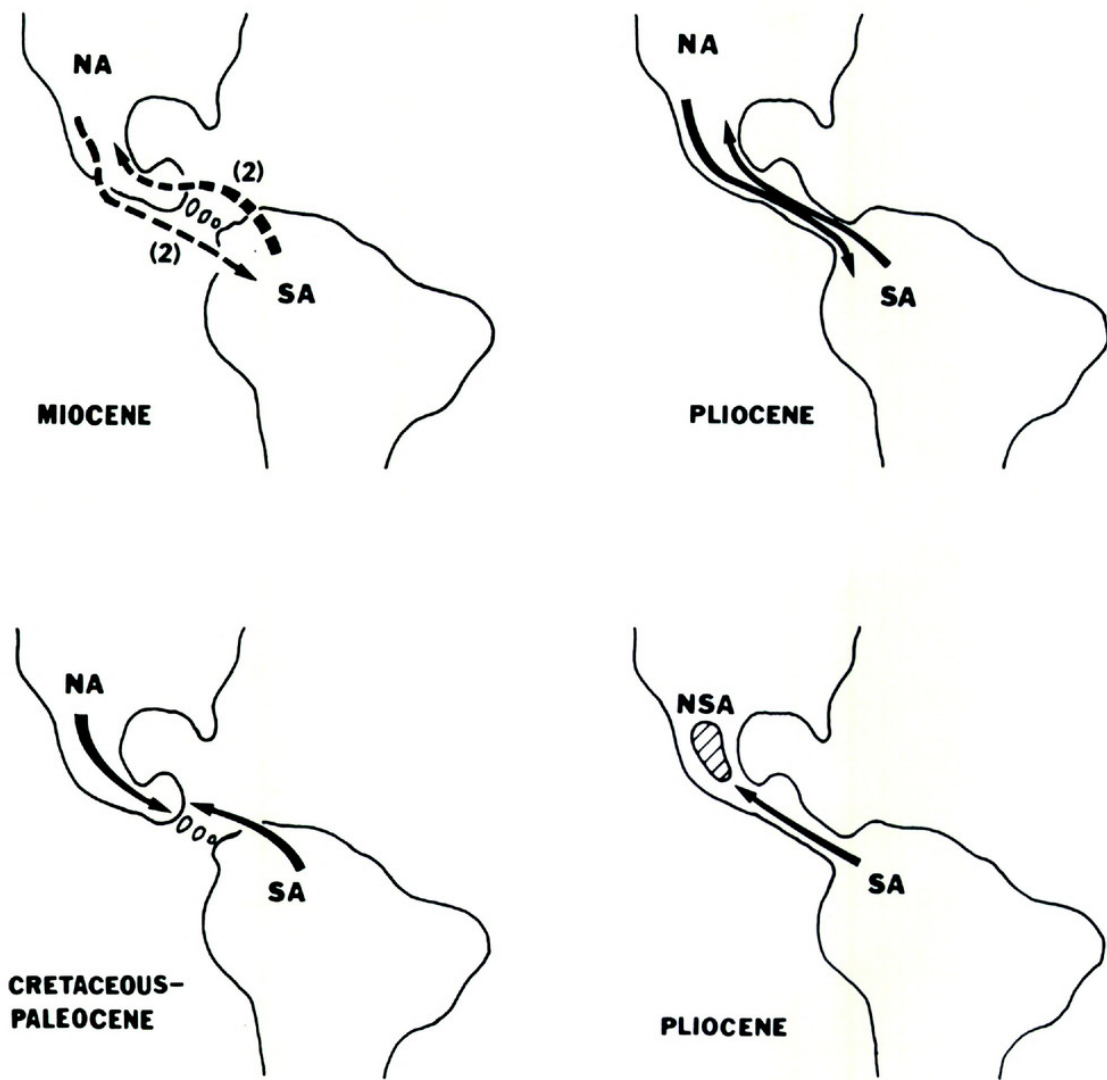
FIGURE 4.   Origins and history of the Mesoamerican mammal fauna (upper) and freshwater fish fauna (lower), according to Marshall et al. (1979) and Bussing (1976), respectively. See text for explanation of history of North (NA) and South American (SA) and endemic Middle American (NSA) components.

first across the Central American archipelago and later across the emergent land connection, added to the floras of both Central and South America. These ideas on plant dispersal patterns are presented in a summary figure (Fig. 3).

Savage (1974), Webb (1977, 1978), Ferrusquia-Villafranca (1978), and Marshall et al. (1979) have reviewed the history of the relationships of Central and South American mammal faunas. These studies up-date the earlier treatments of Simpson (1950, 1969), Hershkovitz (1966, 1969), and Patterson and Pascual (1968). While differing, to some degree, the first group of authors agree that the Central and South American regions were essentially isolated from one another by the Panamanian Portal for most of Cretaceous and Tertiary. Minor dispersals from the south to the north (two families of ground sloths) and north to south (a genus to raccoon and the ancestor of a series of endemic cricetid mouse genera) occurred in Miocene. An extensive and balanced exchange took place over the

Isthmian Link in Pliocene-Recent times. The idea that the ancestors of cavio-morph rodents and South American primates arrived by overwater dispersal from North America earlier in the Tertiary is not now generally accepted. In conse-quence, the mammal fauna of tropical Middle America was almost exclusively northern in its relationships until the Isthmian Link appeared and allowed a mix-ing with southern elements (Fig. 4).

Bussing (1976) reviewed the freshwater fish data for the region, with emphasis on island-hopping dispersal of South American groups in late Mesozoic and/or early Tertiary times. These groups underwent development *in situ* until the emer-gence of the Isthmian Link. Some groups of northern relations were also in the region. Subsequent to the establishment of the land connection to South America, additional southern stocks invaded Central America, but the endemic Central American lines did not re-invade South America (Fig. 4).

Duellman (1979), in the introductory chapter of a major symposium on the biogeography of the South American herpetofauna, briefly reviewed the problem of Central American relationships. While accepting the overall validity of my 1966 study, he recognized the difficulty presented by the geologic evidence for no land connection between the two areas over most of Cretaceous and Tertiary. As a result, he followed Bussing's (1976) and Rosen's (1976, paper to be discussed below) ideas of a dispersal route across the early proto-Antilles (late Cretaceous-Paleocene) and later Central American archipelago as a modus for producing major aspects of present patterns. Duellman's explanation requires a minimum of 17 dispersals at the family unit level (family or subfamily or tribe) in this fashion. He, of course, regards the emergent Isthmian Link as a dispersal route in both directions for previously isolated components in Central and South Amer-ica, while confirming my conclusion that the influence of the southern immigrants on the herpetofauna of Middle America is minimal north of Panama.

These biological data sets, as interpreted above, are somewhat at variance with my 1966 conclusions, based upon herpetofaunal evidence. First, all of the mentioned authors favor overwater, island-hopping and/or waif dispersal as pro-viding the principal source of extensive (plants, amphibians, and reptiles), mod-erate (freshwater fishes), or slight (mammals) South American group contribu-tions to Central America prior to the final emergence of the Isthmian Link. Second, no distinctive Middle American component is recognizable for mammals. Third, Raven and Axelrod (1974) believed that angiosperms agree with the mammal pattern in lacking a recognizable Middle American component, except that they believed that dispersal from South America occurred over much of Cenozoic, while most South American mammals reached the area only in Pliocene to Ho-locene times.

In contrast, the data for freshwater fishes (Bussing, 1976) are more congruent with herpetofaunal patterns than are those for mammals and plants. Bussing recognized the distinctiveness of a Middle American component of the ichthyo-fauna, which is of South American origin, but which underwent evolution in isolation from the latter during much of Tertiary. Duellman (1979) concurred with my recognition of allied, but distinctive Middle and South American Elements in the herpetofauna.

The apparent non-congruence of the several sets of distributional data, if the data are accepted at face value, suggests that a) the history of plants and mammals in the region was substantially different than for fishes, amphibians, and reptiles, b) that some major differences in mode of interpretation of the data exist among students of the different groups, or c) that some mixture of these two alternates is involved. These latter two points lead directly to a consideration of theoretical issues which contribute to the problem in biogeographic interpretation as it applies to Central America.

During the last decade, a resurgence of interest in biogeographic theory has been engendered by the wide acceptance of continental drift and a new approach to attacking biogeographic problems (Nelson & Rosen, 1981). Prior to 1970, almost all biogeographic studies accepted the overall position of continental and ocean basin stability and dispersal as the major guide-posts for theory construction. In the 1970s, a new school of biogeographers, led by Gareth Nelson (1973, 1975) in association with his colleagues, Donn Rosen and Norman Platnick, invented vicariance biogeography. Although paying homage to Leon Croizat as the group's founder (Croizat, Nelson & Rosen, 1974) and later discovering an intellectual precursor in de Candolle (Nelson, 1978; Nelson & Platnick, 1981), the framework of ideas and the vigor and relative rigor of biogeographic hypothesis-testing developed by this group is original with them. They characterized the approach of earlier workers (Darwin, 1859; Wallace, 1876; but especially Matthew, 1915; Simpson in many papers republished as a book in 1965) as dispersal biogeography. Since the presumed differences between the two views, enumerated as a bill of particulars by the vicariance school (Croizat, Nelson & Rosen, 1974; Platnick & Nelson, 1978; Nelson & Platnick, 1981) against their rivals, are significant, they will be discussed in more detail in a later section. At this point, however, consideration must be given to the vicariance model of Central American biogeography developed by Rosen (1976, 1978) as it affects the problem of herpetofaunal history.

Rosen's (1976) study was aimed at a broad goal, the interpretation of the terrestrial, freshwater, and marine biogeography of the Caribbean region from the viewpoint of vicariance theory. In fact, his paper is the only precise exposition of the vicariance biogeographic method for a substantial geographic region. Because both the methodology and conclusions were innovative, the study is already considered a classic despite recent evidence (Patterson, 1981; Pregill, 1981) that the geological interpretations need revision. Although Rosen's theory of Caribbean biogeography also dealt with the history of marine groups and the Antilles, the following discussion is directed primarily to his ideas as they relate to the Central American biota. The essence of his vicariance model is summarized below:

1) a late Cretaceous proto-Antillean archipelago, lying in the region of the Panamanian portal, allowed for dispersal of South American groups into Nuclear Central America and for North American stocks into the archipelago (dispersal)

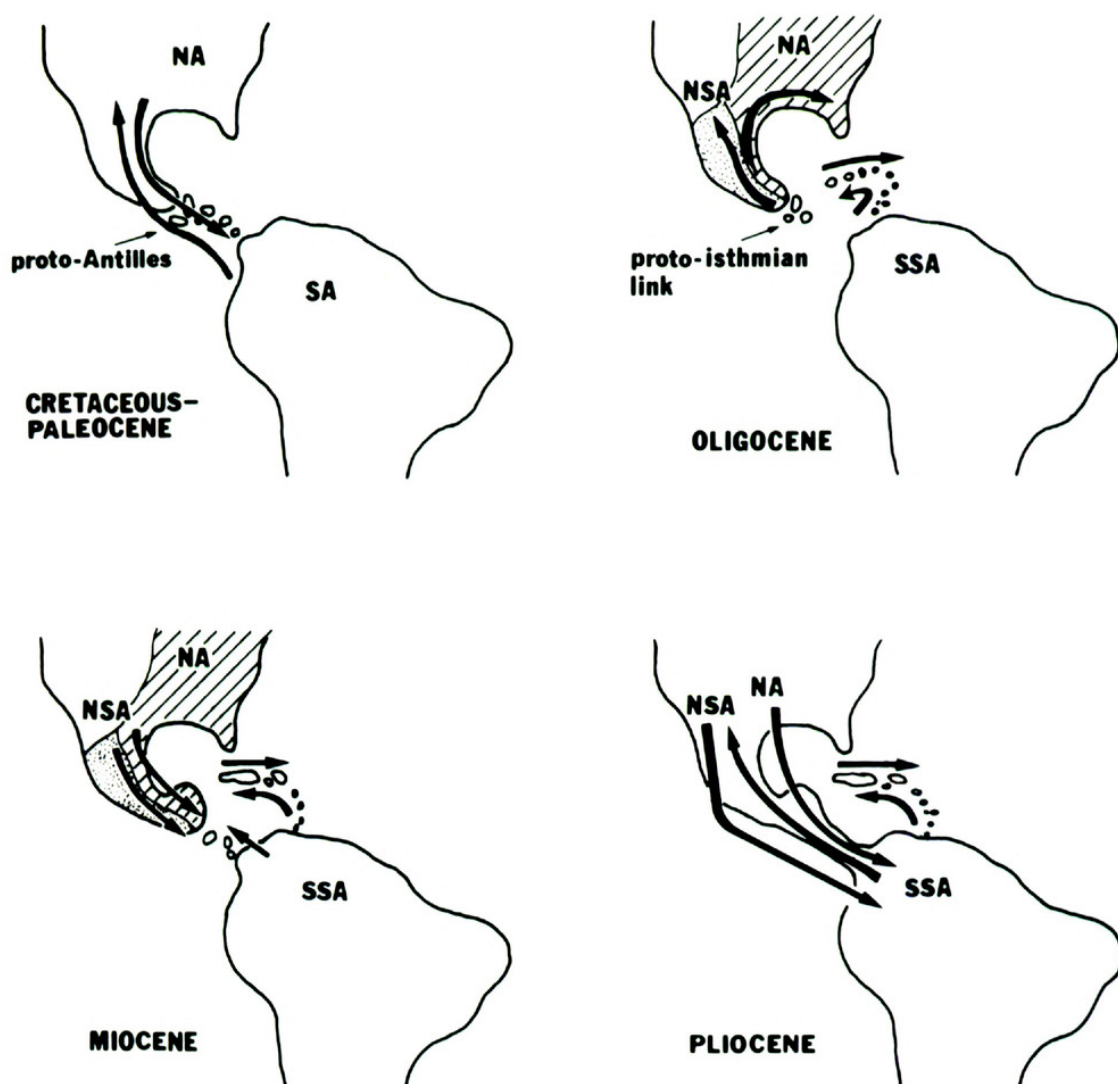2) the movement of the proto-Antilles eastward created the Panamanian portal

FIGURE 5.   A vicariance model of Caribbean biogeography, according to Rosen (1976). See text for explanation; NA = North American, SA = South American, SSA = Southern South American, NSA = Central American stocks.

of early Tertiary that isolated North America from South America and allowed North American (NA) and South American derivatives (NSA) in Central America to evolve in isolation from stocks (SSA) in the southern island continent (vicariance)

3) the emergence of the Panamanian Isthmus in late Tertiary created a route for dispersal of South American groups (SSA) into Central America and Central American groups (NA + NSA) into South America (dispersal).

Two points are to be emphasized from this summary. First, Rosen indicated that South American groups reached Central America over the proto-Antilles archipelago, but contrary to Patterson's (1981) interpretation, North American groups dispersed no further than the archipelago. Second, Rosen recognized the distinctive nature of the Middle American fauna (isopods, onychophorans, spiders, butterflies, frogs and toads, lizards, snakes, birds, bats, monkeys, hystricomorph rodents, and particularly freshwater fishes), but included it as part of

his South American-Caribbean unit (track) to emphasize the presumed ancient continuity of distribution (Fig. 5).

The above review indicates the several areas of discordance with my 1966 model for herpetofaunal history in Central America. One is the conflicting geological evidence that centers on a consensus that there was no land connection between Central and South America for most of Cretaceous and Tertiary. Second is the apparently conflicting data from the distribution of other groups (plants, mammals, and freshwater fishes). Finally, the use of the newly developed theory and methodology of vicariance biogeography as applied to a wide variety of organisms in the development of a model of Caribbean biogeography, apparently, does not produce results congruent with my 1966 report.

For these reasons, it seems appropriate to re-evaluate the distributional data, the apparent patterns of distributional congruence, the interpretation of the patterns, and the model I developed in 1966 to explain the origins and history of the herpetofauna of the region. This resynthesis will include a consideration of the central theoretical problem of biogeography (dispersal versus vicariance); a re-analysis of the data of distribution using a different methodology in order to determine historical source units; development of a biogeographic model for the Central American herpetofauna; and comparison of the model to the distributional data for other groups and with geologic events.

THE CENTRAL THEORETICAL PROBLEM:
DISPERSAL VERSUS VICARIANCE

The raw data of historical biogeography are the distributions (or tracks) of individual species in space (geographical ecology) and time. Because each species has its own set of peculiar ecological requirements and its own unique evolutionary history, each species has a discrete non-random ecogeographic distribution. As a consequence, no species is universally present and many species have very small or unique tracks.

The first level of generalization in biogeography is based on the recognition that in spite of the unique nature of individual species distributions, many individual tracks are concordant to show a common pattern. Determination of the patterns (generalized tracks) involving the coincident distribution of many species or several monophyletic groups (genera, families, etc.) of species is the fundamental first step in biogeographic analysis.

The second level of generalization in this process is to recognize the several disjunct adjoining or distant clusters of distributions that form nodes or track components within the generalized track. These components may be regarded as defining the geographic limits of major modern biotas, characterized by a high degree of endemism.

A third level of generalization attempts to tentatively identify the historical source units (ancestral biotas) that contributed to the modern biotas. In any given region, the biota may have been derived from several historical source units at different times, but usually the dominant source unit has developed *in situ* and is a component of a major generalized track.

In the remainder of this section, I will discuss the essential conceptual features of the two major current competing theoretical constructs that attempt to interpret

the recurrent coincident distribution patterns (generalized and component tracks) to produce explanations of biogeographic history.

As mentioned above, the field of historical biogeography has undergone a major revitalization during the last decade through the development of an original approach to biogeographic thinking, the vicariance theory, which seems to fit very well with the facts of continental drift and the new tectonics. The chief architects and proponents of vicariance (Croizat et al., 1974; Rosen, 1974: 321, 1976, 1978; Nelson & Rosen, 1981; Nelson & Platnick, 1981) maintain that their approach is superior to all others as a general explanation of pattern, primarily because it is more rigorously analytical and establishes historical hypotheses that may be independently tested by phylogenetic and/or geologic evidence. Ball (1976), McDowell (1978), and Pielou (1981), and to a lesser extent, Patterson (1981), have effectively countered this claim, without seriously weakening the fundamental strengths of vicariance biogeographic analysis, especially as it has evolved in its latest phases (Rosen, 1978; Platnick & Nelson, 1978; Morse & White, 1979), through association with cladistic studies of phylogenetic relationships.

The adherents of vicariance theory (vicariists à la Pielou, 1981) lump, willy-nilly, a host of alternate biogeographic explanations, methods, and analyses of distribution under the rubric of dispersal biogeography as an alternative, but essentially unscientific approach with which they take issue on every ground (Croizat et al., 1974; Platnick & Nelson, 1981). Unfortunately, to date, the only formulation of dispersal theory, in this context, has been by the vicariists, who have attributed all kinds of errors of procedure, philosophy, fact, and concept to the opposition. In this sense, dispersal biogeography is not a coherent set of concepts, but is a straw-man set up by vicariists, to emphasize the strengths of their own approach against a diffuse set of ideas attributed to dispersalists. Viewpoints as diverse and contradictory as: northern origin of groups and southward dispersal over stable continents (Matthew, 1915, and Simpson, 1965); Asian tropical origin of groups and radiation over stable continents to elsewhere (Darlington, 1957); dispersals by drifting continents (Raven & Axelrod, 1974; Savage, 1974); so-called island biogeography (MacArthur & Wilson, 1967); dynamic biogeography (Udvardy, 1969); and "phylogenetic" (= cladistic) biogeography, combining dispersal and vicariance (Hennig, 1966; Brundin, 1972, 1981) among others are placed within the dispersalist orb by vicariists.

Superficially, the dichotomy in biogeographic thought between dispersalists and vicariists seems to be one of emphasis. The former emphasize the active or passive dispersion of organisms as the principal agent responsible for patterns. The latter regard dispersal as relatively unimportant in producing present patterns and regard movement and fragmentation of land masses and the general immobility of plants and animals as major factors. The differences between the two viewpoints are more pronounced and complicated than suggested by this comparison (Nelson & Rosen, 1981; Pielou, 1981). It therefore seems important to clearly distinguish between the conceptual basis of the two theories and, for what I believe to be the first time, to present an outline of dispersal theory that fairly contrasts it to vicariance dogma. The fact that only vicariists have defined the limits of dispersal theory during the past decade has seriously distorted most biologists' concept of dispersal. Even such a perceptive scientist as Pielou (1981)

uncritically accepted the vicariists' terms for evaluation of dispersal theory, by following their lead in defining it as based upon long-distance dispersals that occur separately and independently in individual taxa. Perhaps some dispersalists (island biogeographers?) would concur. Most of those studying historical biogeography will not!

Some colleagues may question my qualifications for undertaking a balanced comparison of the alternate views, since my 1966 study of the Central American herpetofauna has a strong vicariance aspect (Fig. 2). Hopefully, their concerns may be laid to rest, since Croizat (1976) and Nelson (1977), commanders for the vicariists, characterize me as an ardent, but junior grade officer in the dispersalist army, who has dabbled in Neotropical biogeography. In any event, neither group is likely to be satisfied with my summarization of the central concepts of their preferred theory; the vicariists, because dispersal theory is shown to be very different from the distorted model they have created of it; the dispersalists, because of their diffuse variety of positions and general lack of parsimonious hypotheses for testing.

Both approaches to biogeographic theory construction recognize the occurrence of dispersal and vicariance events. Both are based upon recognizing and interpreting recurrent distribution patterns of many clusters of distantly related groups or organisms. Both have an evolutionary basis and are concerned with historical (phylogenetic) similarity. Both provide scientific models for the understanding of biogeography by addressing the following key elements: 1) recognizing congruent patterns of distribution; 2) analyzing these patterns to determine common ecologic, geologic, and/or evolutionary processes that produced the patterns; 3) using the patterns and processes to predict: a) patterns for yet unstudied groups and b) as yet undiscovered geographic and evolutionary events. The central conceptual framework of each approach is given below (Fig. 6):

Dispersal Theory:

A monophyletic group arises at a center of origin.

Each group disperses from this center.

Substantial numbers of monophyletic groups followed the same dispersal route at about the same time to contribute to the composition of a modern biota.

A generalized track corresponds to a dispersal route.

Each modern biota represents an assemblage derived from one to several historical source units.

Direction of dispersal may be deduced from tracks, evolutionary relations, and past geodynamic and climatic history.

Climate and/or physiographic change provide the major impetus and/or opportunity for dispersal.

Biotas shaped by dispersal across barriers and subsequent evolution in isolation.

Dispersal is the key to explaining modern patterns: related groups separated by barriers have dispersed across them: a) when the barriers were absent or relatively ineffective; b) less commonly by passing over or through existing barriers.
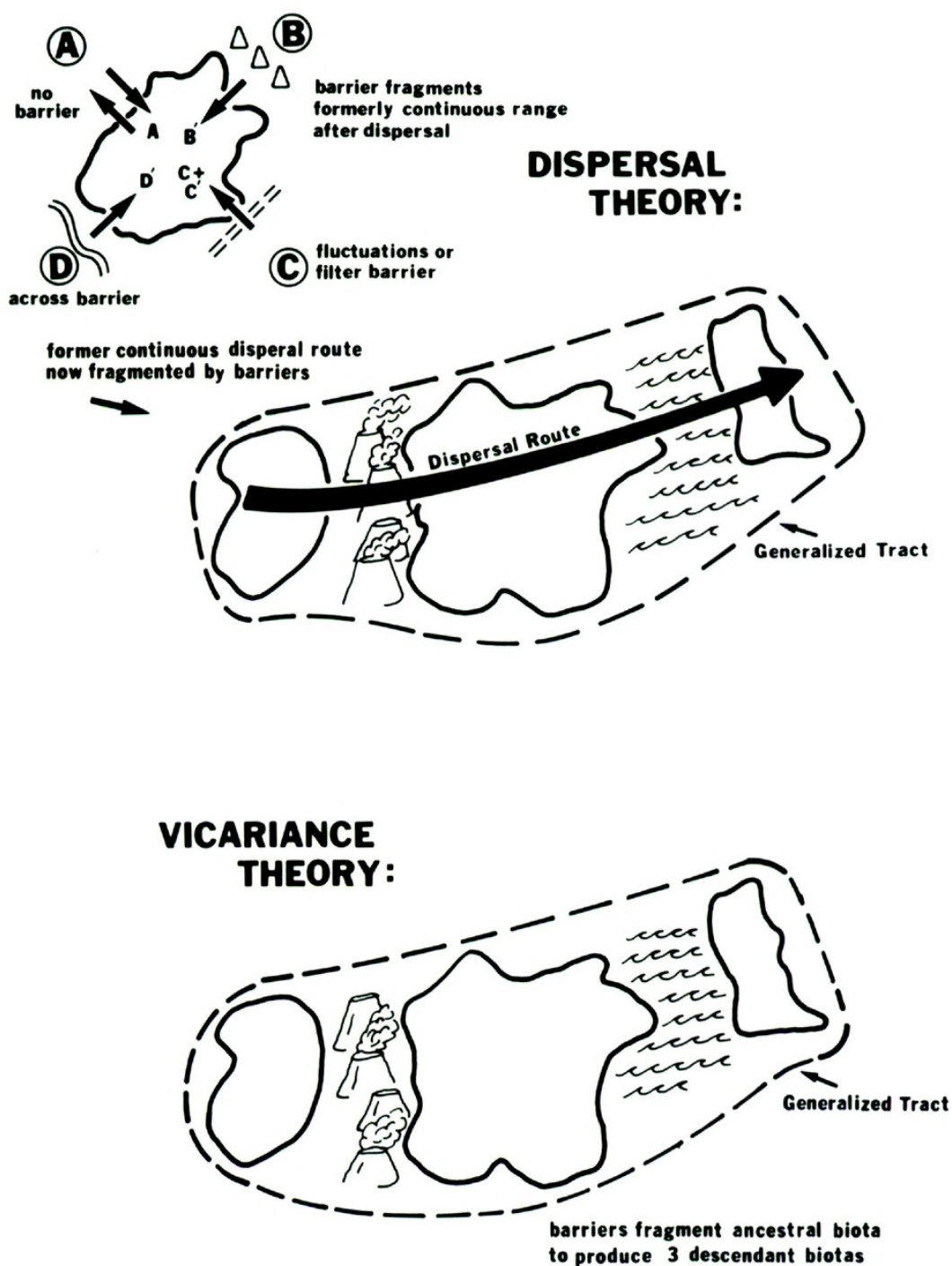
FIGURE 6.   Essential features of dispersal and vicariance theories of biogeography.

Dispersal is of primary significance in understanding current patterns: dispersal precedes barrier formation and vicariance and again occurs when barriers are subsequently removed or become ineffective.

Vicariance Theory:

Vicariants (allopatric species) arise after barriers separate parts of a formerly continuous population.

Substantial numbers of monophyletic groups are simultaneously affected by the same vicariating events (geographic barrier formation).

A generalized track estimates the biotic composition and geographic distribution of an ancestral biota before it subdivided (vicariated) into descendant biotas.

Vicariance after geographic subdivision produced modern biotas.

Each generalized track represents a historical source unit.

Sympatry of generalized tracks reflects geographic overlap of different biotas due to dispersal.

The primary vicariating events are changes in world geography (geodynamics) that subdivide ancestral biotas.

Biotas evolve in isolation after barriers arise.

Vicariance is of primary significance in understanding modern patterns: related groups separated by barriers were fragmented by the appearance of the barriers.

The two approaches differ essentially in their emphases. In the dispersal model, associated organisms dispersed together to form the recurrent patterns. In the vicariance model, the original distributions are fragmented and the associated organisms in each fragment evolve together. Other key differences include:

Dispersal	*Vicariance*
1. Each monophyletic group has a center of origin from which it dispersed.	1. The ancestors of each monophyletic group originally occurred in the areas where the group occurs today and the descendant taxa now present evolved in place; center of origin not a valid concept (Croizat et al., 1974).
2. Concordant dispersal of many groups leads to patterns.	2. Concordant vicariance of many groups produce patterns.
3. Generalized track = dispersal route, used by a historical source unit.	3. Generalized track = ancestral biota (historical source unit).
4. Direction of dispersal deduced from track, phylogenetic relations, geodynamic and climatic relations.	4. Geological or geographical change causes biotic fragmentation.
5. Fossils very important; aid in locating center of origin and direction of dispersal; can contradict Recent distributions.	5. Fossils cannot contradict evidence from Recent distributions (Patterson, 1981); have no special role (Parenti, 1981).
6. Fossils aid in determining extinctions and phylogenetic age.	6. Fossils have no special role, since they do not invariably document ancestral biotas even when documenting extinctions (Parenti, 1981).

7. Discovery of new fossils tests biogeographic hypotheses.

7. Discovery of new fossils adds to track, but does not test or corroborate biogeographic hypotheses (Patterson, 1981).

8. Relative age of groups important in explanation; fossils important.

8. Age of group determined by vicariance pattern; fossils not necessary.

9. Ecologic valance and associates significant in analysis.

9. Ecologic valance and associates of little significance because they will correlate with ecologic and physiographic conditions of modern landscapes (Rosen, 1978).

10. Concordant dispersal occurs before establishment of barriers; isolation occurs after barrier formation ("Vicariance in disguise," Nelson & Platnick, 1978).

10. A primitive wide-ranging biota is fragmented by establishment of barriers.

11. Spatial (allopatry, parapatry, and sympatry) relations ambiguous.

11. Sympatry indicates dispersal; allopatry and parapatry indicate vicariance (Rosen, 1976).

12. Progenetic events involve concordant dispersal, and subsequent vicariance; epigenetic influences often equated with progenetic ones.

12. Progenetic events lead to fragmentation; epigenetic events produce details of current distributions (Rosen, 1978).

13. Ideas influenced by concept of constancy of ocean basins and permanency of continents: land and ocean areas stable, organisms dispersed.

13. Ideas strongly influenced by the new continental drift and (plate) tectonics: continents move, organisms carried passively with them.

14. Biotas dispersed along ecogeographic corridors with no or ineffective barriers or when barriers are removed.

14. Biotas carried on crustal plates or other geologic subdivisions; pattern reflects fragmentation brought about by origin of barriers.

15. Ideas influenced by mammal data as interpreted by Matthew and Simpson: dispersal from northern continents to southern ones.

15. Ideas influenced by data for fishes as interpreted by Nelson and Rosen: fish groups are old enough to have been affected by the breakup of Pangaea.

16. Often a heavy emphasis on Quaternary events as sufficient to explain patterns through ecologic correlations (Müller, 1973; Haffer,

16. Major patterns represent ancient (Mesozoic onward) disjunctions; speciation events generally pre-Quaternary.

1981); sometimes even shorter time frame emphasized (MacArthur & Wilson, 1967; Simberloff, 1974; Cody & Diamond, 1975).

17. Components (nodes) in generalized track equal minimum number of dispersal events.

18. Hypotheses tested adding additional individual tracks; corroborated if conform to dispersal routes; falsified if incongruent.

19. Lack of conformity with well-documented generalized and/or component tracks: a) individual track represents dispersal of another historical source unit; b) the individual track reflects independent long-distance dispersal; c) the individual track is based on a non-monophyletic group.

20. Hypotheses tested by comparing proposed number of major dispersals with geologic, physiographic, ecologic, and climatic changes.

21. Predicts some geologic, physiographic, and climatic events, but these are usually highly correlated with recent conditions; does not distinguish among effects.

22. Predicts patterns for unstudied groups of same age.

23. Need some initial notion of age of groups, timing of geologic and climatic events and centers of origin.

24. Eclectic analytical method: equal weight to original historical patterns, dispersals, climatic effects, evolution *in situ* and interrelationships; final arbiter, paleontology (Keast, 1977).

17. Components (nodes) in generalized tracks equal minimum number of vicariance events.

18. Hypotheses tested by adding additional individual tracks; corroborated by congruence; falsified by incongruence.

19. Lack of conformity with well-documented generalized and/or component tracks: a) the individual track belongs to another generalized track; b) the members of the individual track have broken away from the parent biota and have independently dispersed; c) the individual track is based on a non-monophyletic group.

20. Hypotheses tested by comparing proposed number of vicariance events with geologic history.

21. Predicts geologic history (Rosen, 1976, 1978).

22. Predicts patterns for unstudied groups.

23. No prior judgement of former history of dispersals or geologic ages of distributional events; these discovered by the analysis.

24. Robust analytical method: construct cladograms of areas that are tested by cladograms of relationships for individual taxa; geologic history is final arbiter (Rosen, 1978; Nelson & Platnick, 1978).

As shown by the wide range of evidence and explanation in the Vicariance Biogeography Symposium held in New York City in 1979 (Nelson & Rosen, 1981), the debate between and among dispersalists and vicariists goes on (Pielou, 1981) and will probably continue to do so for sometime. The vicariists show some tendency to back away from earlier rigid theoretical formulations through: a) recognition that generalized tracks are phenetic measurements of overall similarity between disjunct or adjoining biotas; b) consideration by implication of the possibility for the existence of second order vicariance events besides those caused by the major forces of earth history, i.e. sea-floor spreading and drifting tectonic plates (Rosen, 1978; Platnick & Nelson, 1978); c) recognition that cladistic analyses of the interrelationships of areas does not equivocally distinguish between vicariance and concordant dispersal (Morse & White, 1979); d) concession that fossils are useful in documenting extinctions and giving minimum ages for occupation of areas (Patterson, 1981); and e) realization that dispersal events and differential extinctions obscure the picture established through vicariance (Patterson, 1981). The dispersalists, on the other hand, remain in disarray, since in most cases, their narrative explanations tend to be overly complicated (non-parsimonious) and rarely subjected to rigorous analysis. In other words, most dispersal hypotheses treat individual cases and do not provide a general explanation of pattern.

Probably the most important recent trend in vicariance biogeography has been the concentration on development of a methodology to evaluate the interrelationships among areas (see item 23 above), since distributional data seem insufficient to resolve whether dispersal or vicariance is the cause of particular disjunct or adjoining patterns of distribution. The methodology, as proposed by Platnick and Nelson (1978), generalized by Morse and White (1979) and utilized by Rosen (1978) and Patterson (1981) requires a detailed cladistic analysis of a number of monophyletic groups for a particular region. These hypotheses of interrelationships among taxa are then converted to a cladogram of areas that expresses a hypothesis concerning the interrelationships between biotas. Additional congruent taxon cladograms may corroborate the general pattern of area relations. In that event, a review of the geologic history of the region may allow specification of a sequence of events that correlates with the interconnections and subsequent sequential isolation of areas. If additional taxon cladograms are non-congruent with the original hypothesis of area relations (because of non-concordant dispersal or the presence of another general pattern of area relations), a new hypothesis or hypotheses need to be formulated for further testing (Fig. 7).

The method is further restrictive as emphasized by Nelson and Platnick (1979) in that the only informative taxa are those with endemic representatives in each of three or more areas. Widespread taxa (i.e. those found in two or more areas) are regarded as the equivalents of shared primitive characters in systematics (non-informative). Congruent cladograms of individual taxa occupying the areas are equivalent to shared derived features in systematics and I suppose that unique endemic taxa are analogous to unique features.

If the comparison to cladistic systematics is extended, this biogeographical method aims at interpreting the geographic distribution of "sister groups" parsimoniously (Patterson, 1981). It asks whether there is a single cladogram of areas
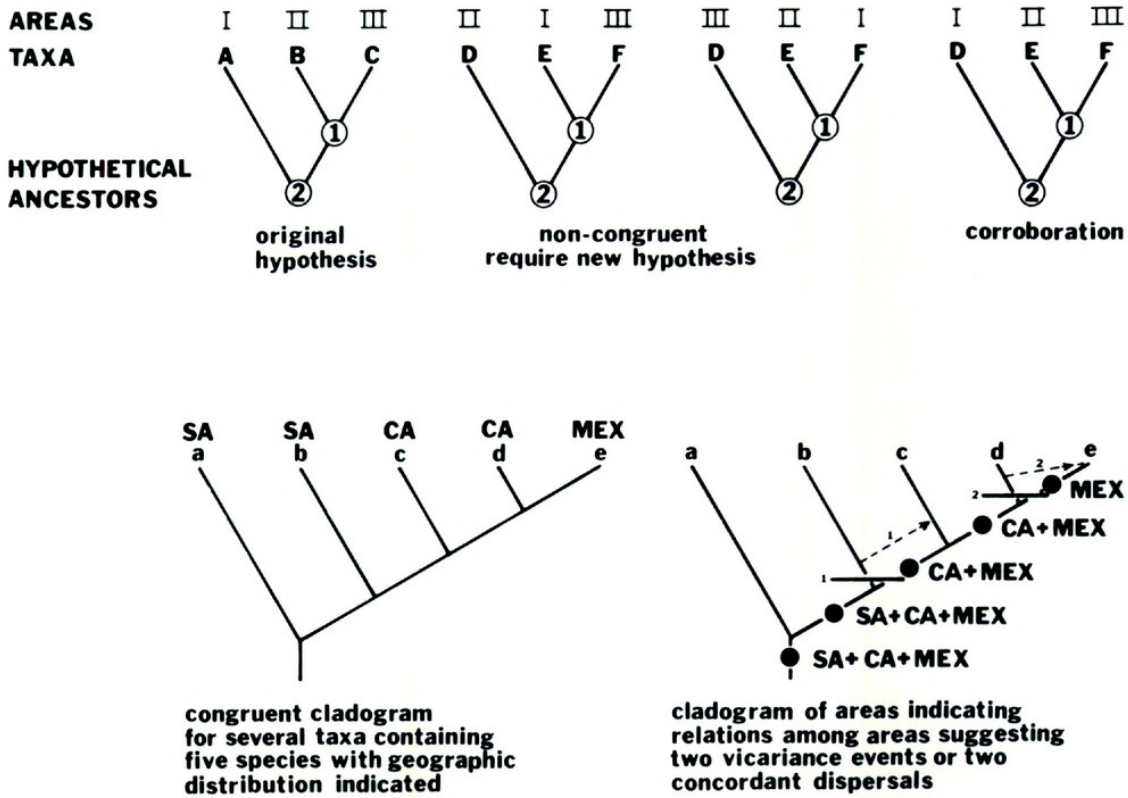
FIGURE 7. Evaluation of interrelationships among areas. Upper, phylogenetic relationships form a hypothesis of area (I, II, III) relationships to be tested by additional phylograms; arabic numbers (1–2) denote hypothetical ancestors and/or ancestral distributions. Lower, phylogenetic relationships form a hypothesis of geographic interrelationships; dispersal theory requires two dispersals for explanation, vicariance theory assumes a single widespread ancestor in South America (SA), Central America (CA), and Mexico (MEX) fragmented by two major vicariance events.

(or more than one) that summarizes the interrelationships of endemic taxa of the groups found in a region. If the intra-group relationships of the distributions of a number of taxa are congruent, then a general explanation is sought. If the relationships are non-congruent, independent long-distance dispersal seems likely. If two or more congruent patterns emerge, then there are two or more general explanations that must be correlated among known geological, geographical, and ecological events to assess actual causal relations. Contrary to the expectation of Patterson (1981), discovery of a general congruence of distributions cannot discriminate by itself concordant dispersal from vicariance (Morse & White, 1979).

This method has been applied in actual cases only to upper Mesoamerica (Rosen, 1978) and marsupials (Patterson, 1981), although several other studies of its application are in preparation. Although Pielou (1981) questions its effectiveness and scientific rigor, it appears to have great potential when sufficient cladistic analyses of taxa are available for a region. At the present time, we may conclude that the method has not been proven by adequate testing and that its restriction to a three or more endemic taxa comparison, the elimination of wide-spread taxa from consideration, the subsidiary use of fossils, and the failure to specify how to distinguish concordant dispersal from vicariance without reference to geologic history, limit its applicability, since it only resolves the pattern of interconnec-

tions among areas. A general pattern of area relations may, however, be ascribed to dispersal or vicariance by the use of the independent test of earth history (Platnick & Nelson, 1978). The absence of a sufficient number of cladistic analyses of taxa for Central America, especially, forces me to utilize another approach in the analysis and synthesis present in the subsequent sections of the paper. The method of Platnick and Nelson (1978) and Rosen (1978) should be an effective test of my conclusions as more cladistic analyses become available.

HISTORICAL UNITS OF THE HERPETOFAUNA

In my 1966 report, I utilized what are now called by vicariists traditional and/ or conventional methods of correlative evaluation of present distribution, ecologic associations, the meager fossil record, phylogenetic relationships, and the association of herpetofaunal units with geofloral history to develop a narrative (sensu Ball, 1976) theory of herpetofaunal development. Essential to that theory were the recognition of herpetofaunal source units using the method described in an earlier study (Savage, 1960). The narrative theory consisted of a description of the *in situ* development in, or the concordant dispersal into, Central America of the taxa belonging to each unit.

As outlined in the immediately preceding section, the generalized track method (Croizat, 1976; Rosen, 1976) may be used as a basis for estimating patterns, regardless of biogeographic theory. Since this method was not used in my earlier study, it seemed that it might be applied to the herpetological data to see if it produces independently similar or distinctly different results than previously obtained. This seems an especially good idea because of questions raised concerning my interpretation of herpetofaunal distribution for the region as outlined in an earlier section (A Review of the Problem).

The generalized track method as used in vicariance biogeography is described in detail by Rosen (1978: 432–433). In summary, the method consists of outlining the distribution of disjunct or adjoining taxa of several to many monophyletic groups on a map and linking the distributional areas of each group by an all-encompassing circle or a line (track). Where commonality of distribution occurs, lines that repeatedly link sister groups will form a single massed pathway called a generalized track. Distinct clusters of distributions (nodes) within the generalized tracks form component tracks tied together by the more general pattern. Although claimed by vicariists to be a significantly different method of pattern recognition, construction of tracks differs in no significant way from the methods used by conventional biogeographers, i.e. overlaying the distribution maps of many groups, to establish patterns.

In vicariance biogeography, generalized tracks are assumed to link two or more vicariant fragments of an ancestral biota. It is further assumed that there is a general explanation of the congruence of the distributions of taxa within a track. The congruence is then explained by correlative or causal relations between earth history and the fragmentations.

The tracks seen by most dispersalists correspond to corridors of present or past concordant dispersal, whose directionality may be estimated from the phylogeny of the groups, and a knowledge of climatic, ecologic, and geologic rela-

tionships. In essence, the dispersalists take the generalized track of the vicariists and put an arrow at one or both ends to indicate the directionality of dispersal.

Ball (1976), McDowell (1978), Patterson (1981), and Pielou (1981) are critical of the value of the use of the generalized track method in vicariance theory because it is phenetic. By that, they mean that a generalized track measures overall similarity in distribution but obscures evolutionarily based similarities through the biogeographic equivalents of convergences (recent and/or long-distance dispersals by individual taxa). As such, they argue that generalized tracks cannot point to a single general explanation of coincident distributions. Why is this so? Tracks tend to follow current physiographic and ecologic trends. For many groups of organisms, the tracks represent an ancient relationship that may indeed be interpreted in terms of vicariance events and an association with the areas involved that predates current physiography and ecology. In other cases, this ancient pattern may be overlain by group distributions that appear to conform to the same general track but represent a more recent concordant dispersal event. Finally, rather recent individual dispersal events may add a distribution to the track that appears to conform to the ancient pattern.

Within the context of dispersal theory, generalized tracks correspond to dispersal routes. Since modern biotas are regarded in this view as derived from several source units (not as a single fragment of one track), the biotas are phenetic units equivalent to overlapping nodes representing several different generalized tracks. In this regard, dispersalists believe that different source units may have utilized more or less the same dispersal route at different times in geologic history depending upon barrier relationships. Dispersalists, generally speaking, see a modern biota as comprised of the components of several historical units, derived at different times from several sources, but usually dominated by a source unit that has developed *in situ* (Fig. 8).

It should be mentioned that Rosen (1976), in his analysis of Caribbean biogeography, breaks with orthodox vicariance dogma to suggest that several generalized tracks with temporally different histories have contributed to the modern Central American and Antillean biotas.

A final set of problems with the use of generalized tracks by vicariists, as pointed out by McDowell (1978) and Pielou (1981), lies with the reliability of the method of track construction and at what point sufficient congruent individual tracks are accumulated to recognize a generalized one. For example, if one looks at Rosen's (1976) carefully researched and documented South American-Caribbean track, it can immediately be extended by additional groups that conform to the track, but are distributed well to the north. Similarly, the track may be substantially extended to the south, to make the track cover most of the Americas (Fig. 9). Very likely by judicious choice of monophyletic groups, the generalized track could be extended to Africa and elsewhere. By the same token, while many monophyletic groups of taxa will fit the originally proposed track, some others do not. Despite the claims of Croizat et al. (1974) and others, the mere coincidence of a number of tracks does not test the reality of the track. Coincidence merely corroborates the hypothesis that a track exists. The vicariist track then is an empirical construct of pattern that invites explanation and cannot provide an explanation, itself.
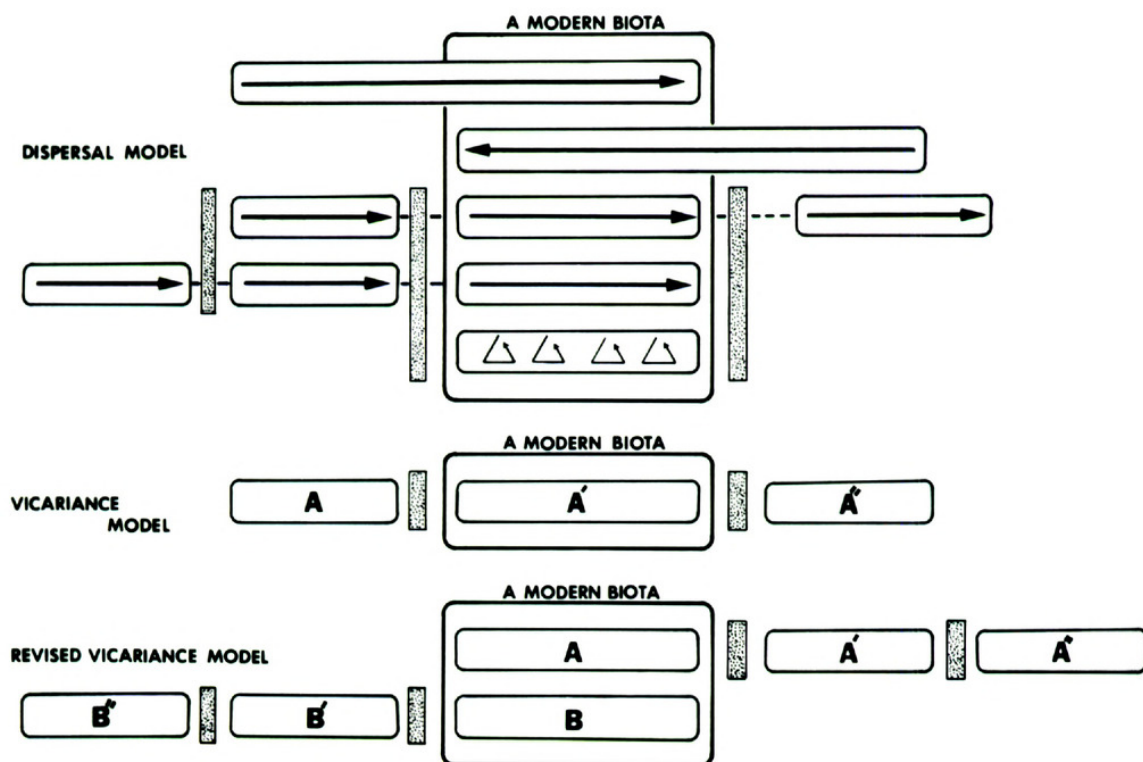
MODERN BIOTAS AND GENERALIZED TRACKS

FIGURE 8. Generalized tracks and biotas. Upper, dispersal theory, with several tracks (= dispersal tracks) or historical units contributing to a biota. Lower, vicariance models. Stippled bars represent barriers, small arrows *in situ* differentiation.

With the realization that generalized track analysis was founded on a phenetic basis, vicariance theoreticians shifted ground to identifying areas of endemism as the basis for analytical study of patterns (Rosen, 1978; Platnick & Nelson, 1978). In doing so, they raised four important questions that are to be asked in the biogeographic analysis of a region: 1) What are the areas of endemism (we already known that they are geographically non-random)? 2) Do the interrelationships of the endemic taxa form a geographically non-random pattern(s)? 3) Does the pattern(s) correlate with geologic history? 4) If the answer to 3 is yes, can a causal hypothesis be established? (Nelson & Platnick, 1978). The method for undertaking this analysis has been outlined in an earlier section of the present paper.

This approach requires a reversal of traditional biogeographic analysis, where much emphasis has been placed upon taxa shared in common. The conventional wisdom is that biotas that have the most taxa in common are most closely related to one another (Vuilleumier, 1975). As an example, comparison between biotas I, II, and III might result in the conclusion that II and III are more closely related to one another than either is to I, because they share more taxa in common than either does with I (Fig. 10). It is easy to accept what is accurately perceived by the vicariists, that wide-ranging taxa, those shared by all areas (three in this case) in a region provide little information on interrelationships of biotas. Essentially, widespread or shared taxa inform us only that there *is* a relationship among the
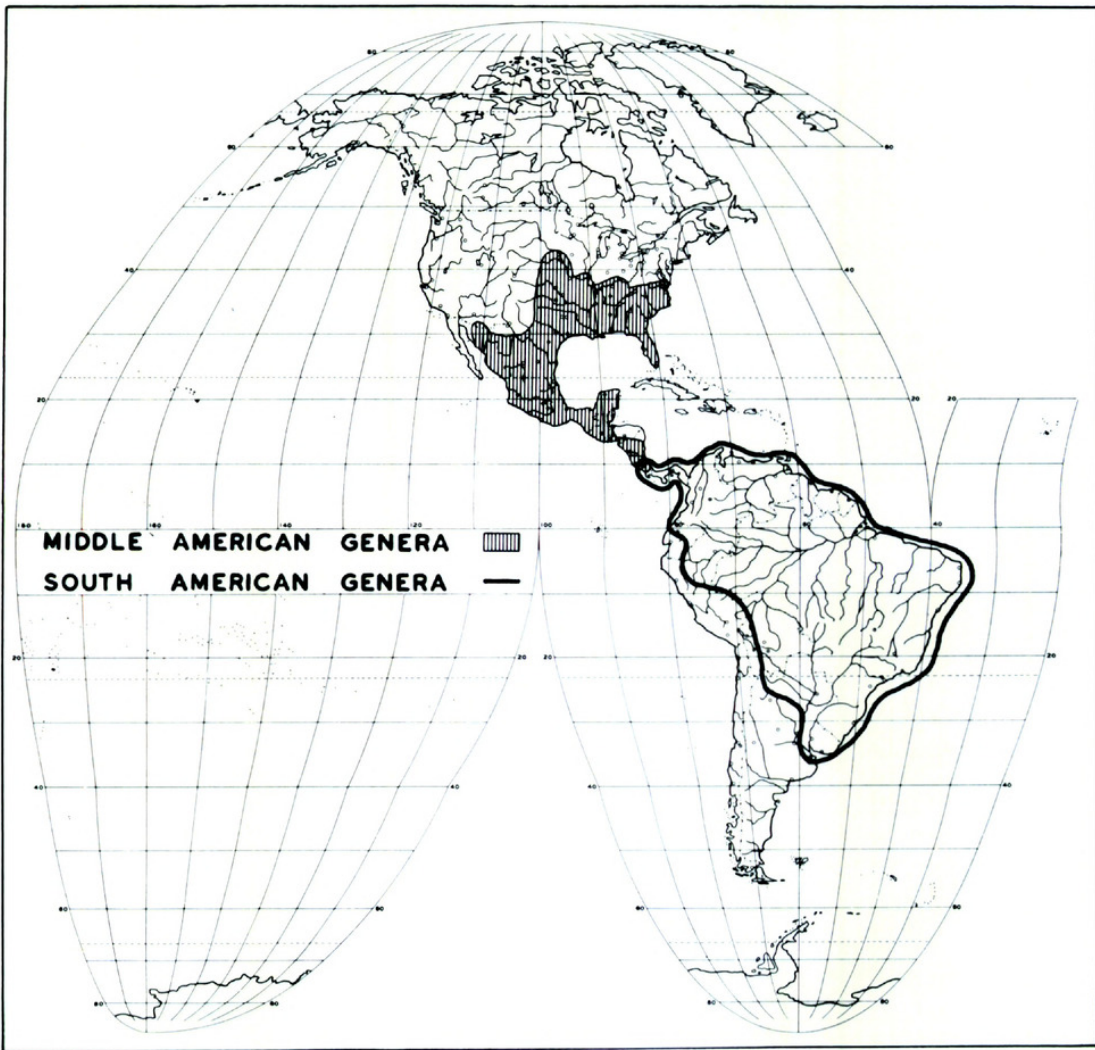
FIGURE 9.   Distribution of microhylid frogs in the Americas, showing discreteness of northern and southern fragments and correspondence with the extension of Rosen's (1976) South American-Caribbean generalized track.

areas, since they correspond to primitive shared characters in evolutionary analysis. What is not so easy to see is the vicariists' brilliant insight that taxa shared by any two of three areas are equally irrevelant to the question of interrelationships, since the same two historical events may produce a situation where any two taxa may be shared by any pair of the three areas (Fig. 11). It is for this reason that a minimum of three areas of endemism, each characterized by an endemic species, are required for vicariance analysis at this level. As pointed out earlier (Fig. 7), an initial hypothesis relating to interconnections or dispersals between the areas may be generated when two (or more) sets of endemic taxa are found to be area congruent in their phylogenetic relationships.

What then of the criticism that this methodology discards important or significant data, the distribution patterns of widespread forms? A widespread taxon in the region, under study, can be utilized as an endemic when the region is compared to two or more other areas having endemic sister taxa and will con-

tribute to understanding the hierarchial pattern of regional relationships. As in cladistic analysis of the interrelationships of taxa, what is a shared primitive character at one level of analysis of the hierarchial pattern of evolutionary novelties, must represent a shared derived feature for another more-encompassing unit.

Because of the emphasis in the vicariists' approach on areas of endemism, most dispersalists will be surprised to learn that comparisons of the relative number of endemics among areas provides little information on their interrelationships (Nelson & Platnick, 1981: 398–409, for a stunning *denouncement* of this old idea). Indeed, it sometimes turns out that two endemics out of a hundred are more informative than 82 endemics out of a hundred (Fig. 10).

GENERALIZED TRACKS AND AREAS OF ENDEMISM

With the difficulties of generalized track analysis and the enhanced significance of areas of endemism in mind, we may now turn to a review of these matters as discerned in the Central American herpetofauna. My concept of generalized tracks is of a pattern of distribution giving initial phenetic clues as to past distributional events. Metaphorically, a generalized track is a trace marked on the earth's surface of ancient dispersal and vicariance events. As mentioned above, track analysis may be obscured by coincidence with the track of several different concordant dispersals in different time frames, rather recent individual dispersal events, and overlapping of two or more generalized tracks. Nevertheless, track analysis seems to afford a method for proposing initial hypotheses regarding the historical source units in a region.

Areas of endemism may be regarded as indicators of significant vicariance events that fragmented previously continuous ranges or as the products of concordant dispersal followed by vicariant evolution. Areas of endemism form nodes of differentiation connected by generalized tracks. Metaphorically, generalized tracks may be thought of as a string of pearls, with the centers of endemism represented by the pearls and the record of past events by the connecting string. The pearls may be closely packed, widely spaced, or of mixed pattern, but they hang together because of the string. Just as several strings of pearls of similar or different length may be worn at the same time, several generalized tracks may overlap. In the final analysis, the richness of the effect or the biota is the result of the total visual impact or the general pattern, respectively, produced by the juxtaposition of the strands of pearls.

For purposes of this study, individual tracks of all genera and a few subgeneric groups that occur in tropical Mesoamerica were constructed. Component generalized tracks within the region were recognized as repeated nodes of congruent distributions. Whenever monophyletic allies of Mesoamerican groups were known to occur elsewhere, their ranges were plotted and joined in a generalized track, including regional and extraregional components. An initial assumption was made that congruent distributions represented a shared history of concordant dispersal or vicariance.

It was expected that, because of the complex history of the region, a single generalized track might simultaneously contain an overlay of recent dispersal
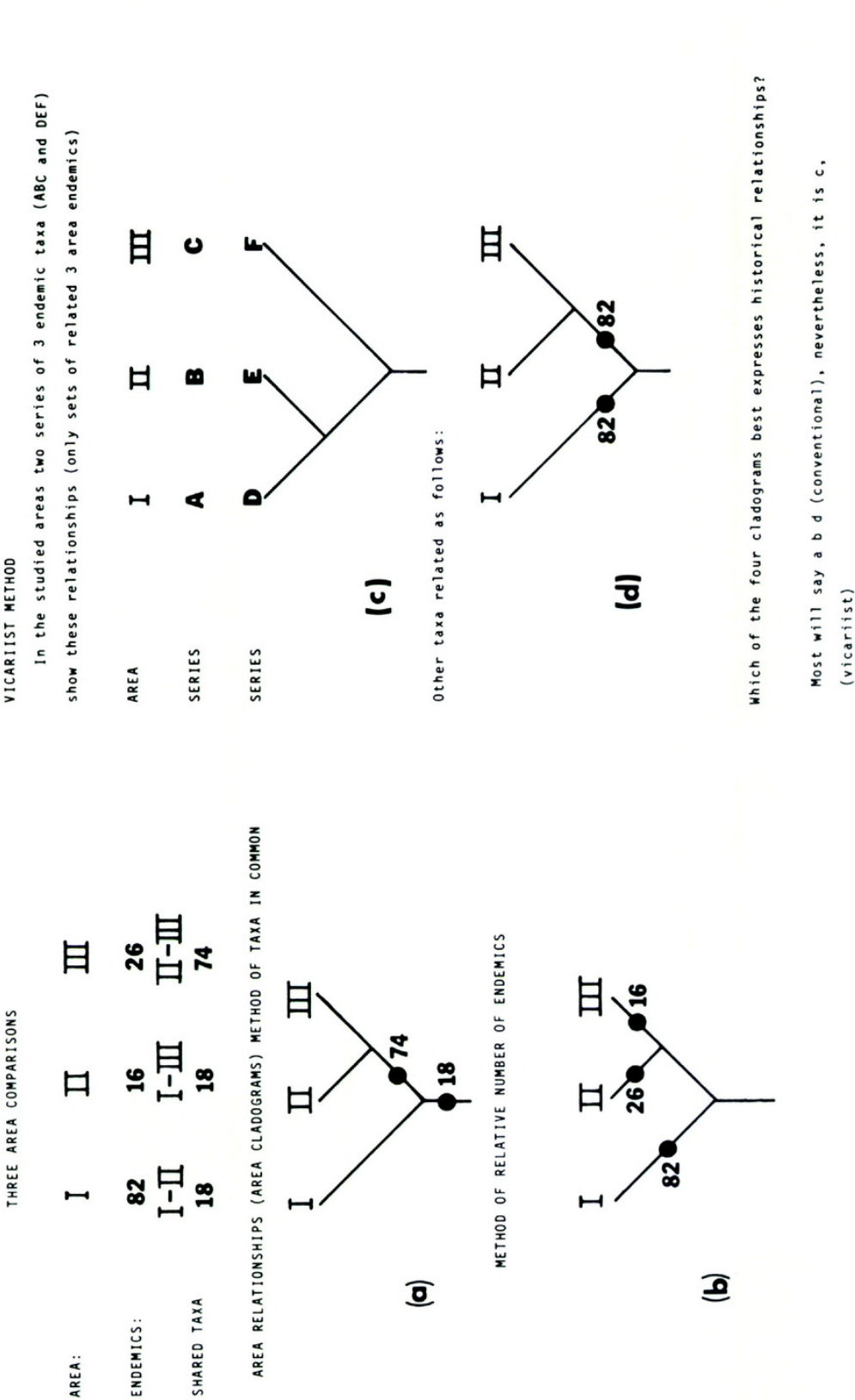
FIGURE 10. Why biotas with the most taxa in common are not necessarily the most closely related (a). Why the relative number of endemics among areas (b) provides little information on area relationships. Why phylogenetic relationships of three endemics in three areas (c) are more significant than relationships among 82 other taxa (d).
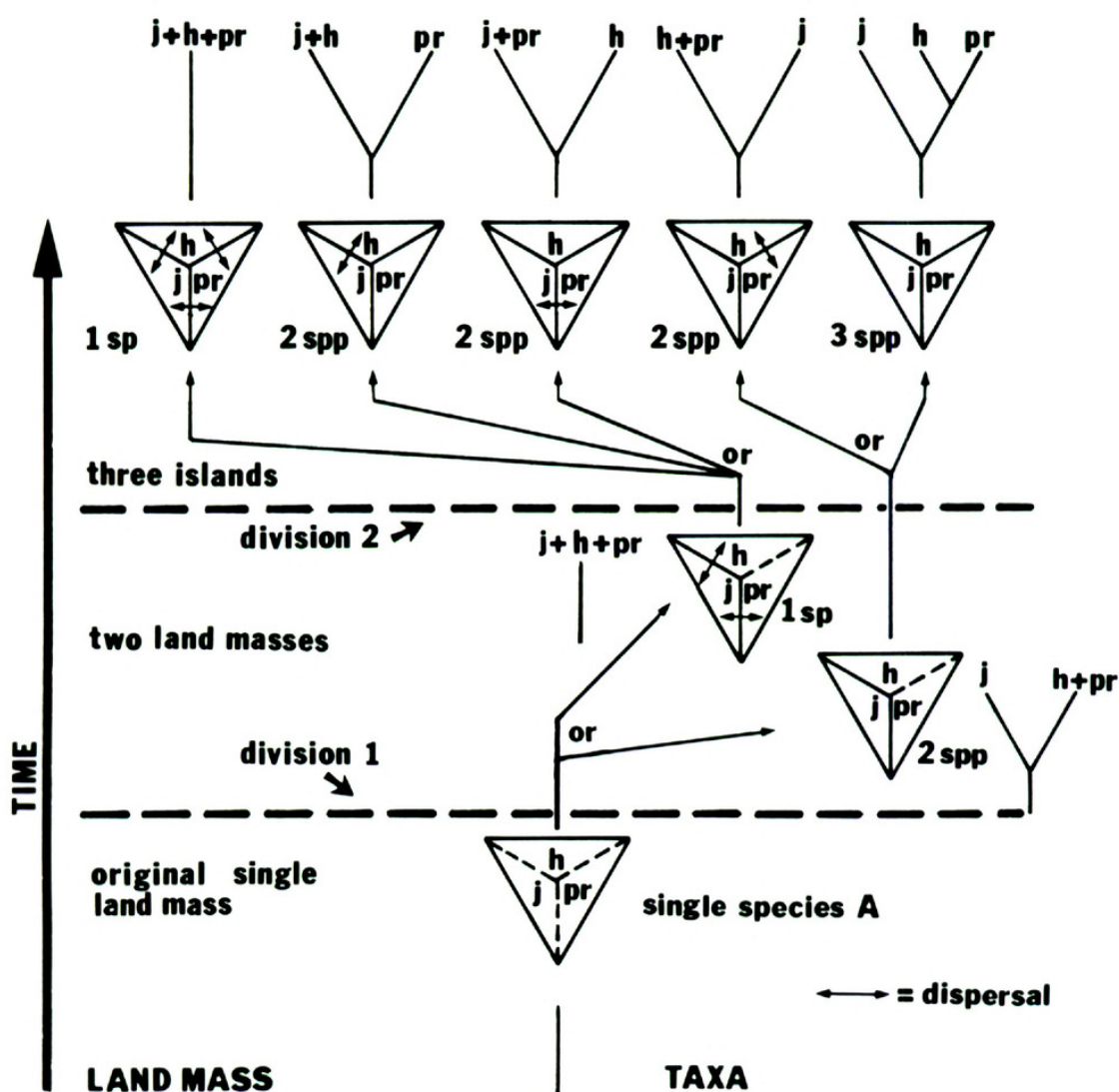
FIGURE 11.   Explanation of why taxa shared by two areas in a three area comparison are relatively uninformative concerning area interrelationships. In this example there are three different ways in which two of three islands may share the same species; only when each area has an endemic (3) can area relationships be determined.

events and evidence of an ancient interconnection between components, which would obscure the patristic biogeographic relationships. Since dispersal events are of two general types, individual and concordant, both possibilities needed to be considered and eliminated from construction of the generalized tracks. The following paragraphs introduce a method for these purposes. The method does not eliminate the possibility of long-distance dispersal by individual taxa joining and sharing a track. However, it does eliminate them from the process of track construction.

The method is as follows:

1. Any species that had a more or less continuous distribution involving a substantial area in extratropical North, Central, and South America was
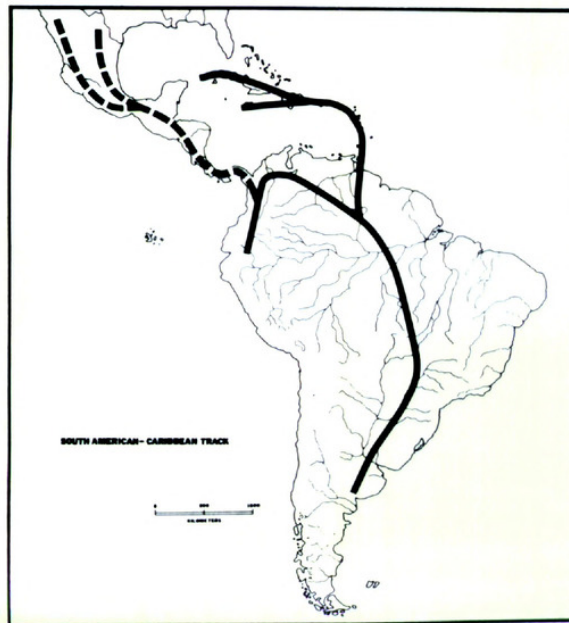
FIGURE 12. Generalized North American-Central American Track; dotted portion indicates post-Miocene dispersal across Isthmian Link.

eliminated from initial analysis (e.g. the indigo snake *Drymarchon corais*, which ranges from Florida to Uruguay).

2. Where a group has an area of differentiation in South America and one or two wide-ranging forms with more or less continuous geographic ranges extending a limited distance into Central America, or vice versa, this was interpreted tentatively as dispersal across the Isthmian Link during its pe-

FIGURE 13. Generalized South American-Caribbean Track; dotted portion indicates post-Miocene dispersal across Isthmian Link.
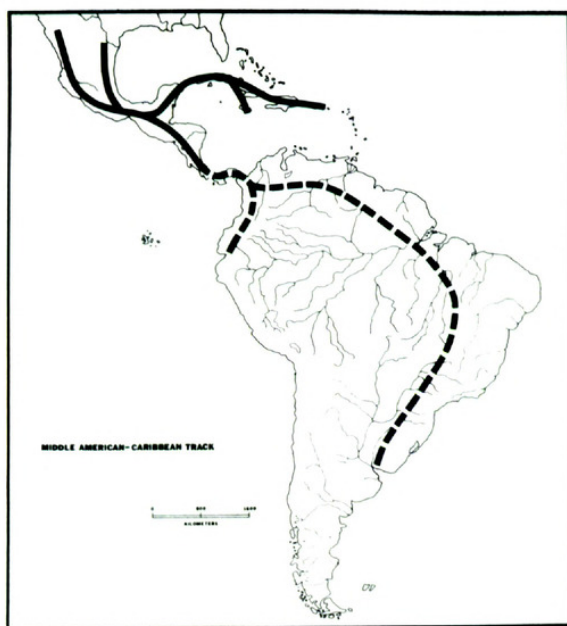
FIGURE 14.   Generalized Middle American-Caribbean Track; dotted portion indicates post-Miocene dispersal across Isthmian Link.

riod of emergence (the past 5–3 million years); these groups were eliminated from establishing the track (e.g. the family Dendrobatidae, which is primarily South American, but ranges north to southern Nicaragua).
3. Whenever possible, the fossil record of group history was used to test the tentative decision from 2, since the presence of the group or a close ally in both North and South America prior to the formation of the Isthmian
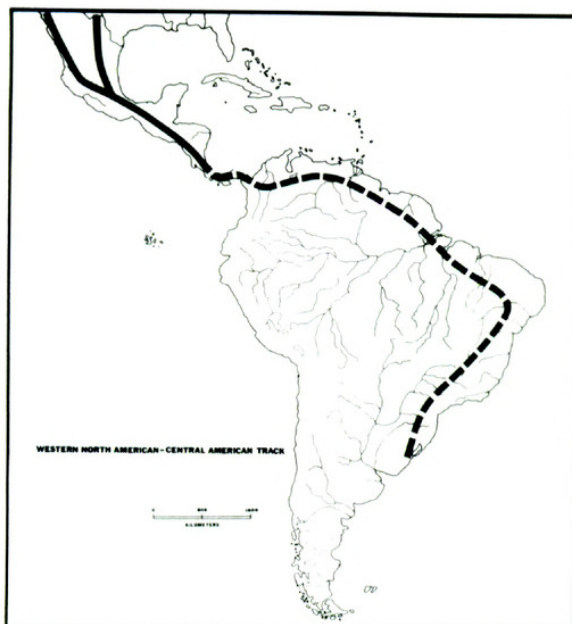

FIGURE 15.   Generalized Western North American-Central American Track; dotted portion indicates post-Miocene dispersal across Isthmian Link.

Link would falsify the conclusion that the group had dispersed across the present Isthmus; the group and its fossil allies could then be added to a track; the contrary situation where the group and/or its fossil allies are known from one region (e.g. North America), but not the other (South America), would support the initial hypothesis of post-Miocene dispersal (e.g. the iguanine lizard *Iguana* in both Central and South America, all other mainland genera in the group have fossils from North and Central America).

4. The appearance of several sympatric generalized tracks in the analysis will disclose potential concordant dispersal events.

5. Groups originally eliminated from the process of establishing tracks may be identified with a track by subsequent comparison of phylogenetic relationships and fossil data (e.g. *Drymarchon* is a member of an essentially North American stock of colubrid snakes, unknown in the fossil record of South America).

Based upon a review of the distributions of the genera of amphibians and reptiles in Central America, according to these principles, three major and one minor (comprised of a relatively few taxa) tracks may be recognized:

1. The North American-Central American track is a generalized track that includes North America, the Mexican lowlands and montane uplands, Central America, and the Greater Antilles (Fig. 12). South American portions of this track extend to Ecuador and Argentina but represent dispersal after the reconnection of Central and South America in the Tertiary.

2. The South American-Caribbean track is a generalized track including South America, the Greater and Lesser Antilles and the Bahamas (Fig. 13). Mexican and Central American portions of this track represent dispersal from South America after establishment of the Isthmian Link in the Pliocene.

3. The Middle American-Caribbean track is a generalized track including the lowlands of Mexico, Central America and the Greater Antilles and the Bahamas (Fig. 14). The portions of this track that extend to Ecuador and southern Brazil represent post-Miocene dispersal across the Isthmian Link.

4. The Western North American-Central American track is a generalized track including western North America, Mexico and Central America, north of Panama (Fig. 15). A portion of this track, extending into South America, represents the dispersal of two genera (*Cnemidophorus* and *Crotalus*) across the Isthmian Link in late Cenozoic, followed by differentiation into a few species, each.

Descriptive and phenetic, generalized tracks represent empirical repetitive patterns of distribution that need biogeographic explanation. In both dispersal and vicariance biogeography, the patterns require that we seek explanations that are concordant with the phylogenies of the taxa and with earth history. Identification of areas of high endemism forms a further useful aspect of perceiving patterns, since the interrelationships among endemic taxa from such areas can provide testable hypotheses of biogeographic history.

In Central America, 10 major areas of herpetofaunal endemism are recognizable (Duellman, 1966; Savage, 1966; Müller, 1973) (Fig. 16):
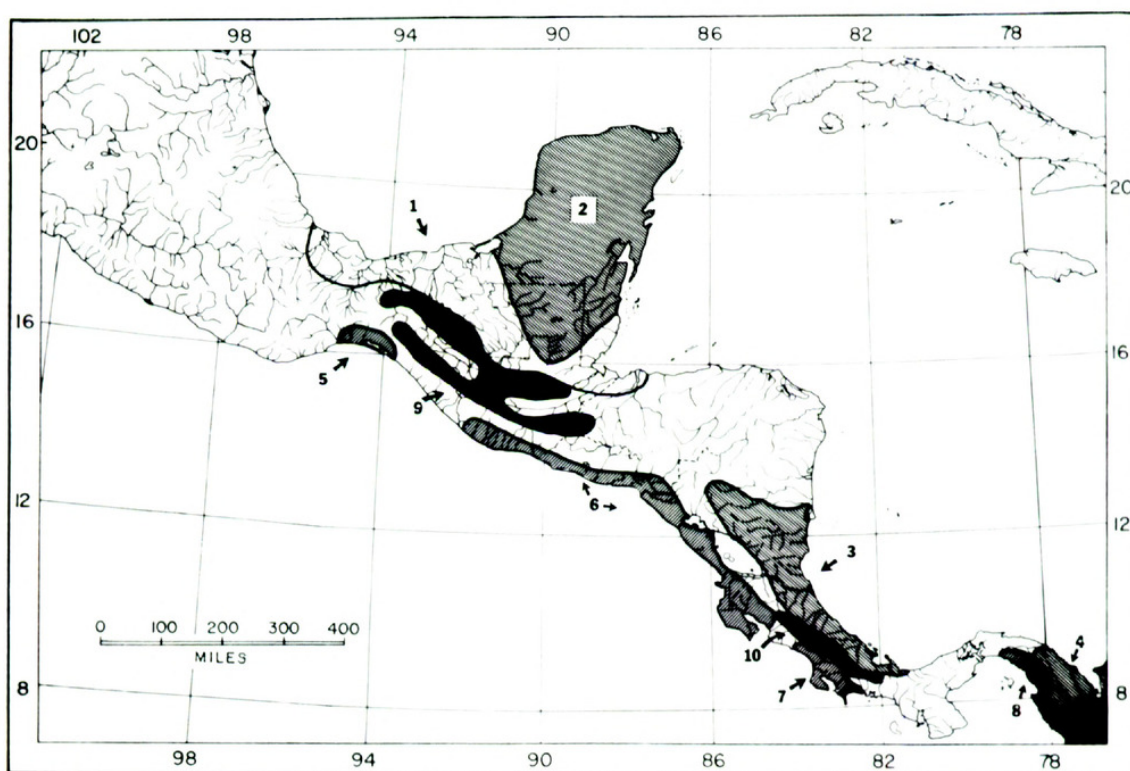
FIGURE 16. Principal Central American areas of herpetofaunal endemism; see text for description of numbered areas.

I. Lowland-Foothill Areas (0–±1,500 m).
    A. Atlantic Versant
        1. Northern—southeastern Mexico to western Honduras
        2. Yucatan—Yucatan Peninsula
        3. Southern—southern Nicaragua to northwestern Panama
        4. Chocoan—eastern Panama and Colombia
    B. Pacific Versant
        5. Tehuantepec—Plains of the Isthmus of Tehuantepec
        6. Southern—El Salvador to northwestern Costa Rica
        7. Golfo Dulcean—southwestern Costa Rica and adjacent Panama
        8. Savannas of eastern Panama
II. Highland Areas (1,500–   ).
        9. Nuclear—highlands of Chiapas, Mexico, Guatemala, El Salvador and Honduras
       10. Talamancan—highlands of Costa Rica and western Panama

As pointed out by Duellman (1966) and confirmed in the present analysis, the principal differences between lowland herpetofaunas in Central America involve east-west separation between Atlantic and Pacific areas. Along either coast, change in faunal composition is minimal in a northwest-southeast direction, except on the plains of Tehuantepec, the Yucatan Peninsula, around the Golfo Dulce, and in eastern Panama. The latter is empirically true, but only because eastern Panama contains wide-ranging forms from the Chocoan and northern South American areas of endemism.

The situation for the two highland areas is much different. They share few species in common and have a very high number of endemics. As will be seen below, they show considerable affinity to the endemic areas of the highlands of southern Mexico (Oaxaca and Guerrero) and these, in turn, are related to the Sierra Oriental and Occidental areas of endemism further northward in Mexico.

In either dispersal or vicariance theory, the areas of endemism represent isolates fragmented by vicariance events. Thus, these areas are presumed to have been isolated by physiographic or other environmental changes and tell us about the history of the region and its biota. Dispersalists tend to regard the endemic areas as milestones (or kilometer posts) along an old highway of dispersal that is now interrupted by barriers. The new super highways are more recent, ecologically fit corridors that are characterized by taxa in common or gradual changes in biotic composition along a gradient. Vicariists regard endemic areas as time capsules that contain data marking the timing of geologic and phylogenetic events. There is something to be said for both views. In many cases, disjunct areas of endemism on continental land masses appear to have been produced by an initial concordant dispersal, followed by a set of vicariance events that allowed for differentiation in isolation. The interrelations among areas of endemism may, thus, provide evidence for the timing and directionality of dispersal. Most vicariists (Rosen, 1976; Patterson, 1981) acknowledge that Central American generalized tracks represent two initial major dispersal events by two historical source units (a northern and a southern one) while claiming that concordant dispersal does not occur. On the other hand, much of the differentiation in any geographic region occurs *in situ* after an initial dispersal. In this sense, areas of endemism reflect vicariance events and form the units for evaluating interrelationships among areas. Recurrent concordance of biological and geological area-cladograms for these areas provides the basis for explaining causes of the patterns.

The matter of the interrelationships among areas of endemism in Central America will be discussed in another section. However, the following descriptive (phenetic) points need to be made:

* Each area, except 7, has endemic representatives of at least two tracks.

* North American-Central American and Middle American-Caribbean tracks have congruent endemism in areas 1, 2, 5, 6, 9.

* Middle American-Caribbean and South American-Caribbean tracks have congruent endemism in area 7.

* North American-Central American and South American-Caribbean tracks have congruent endemism in area 4.

* All three of these tracks have congruent endemism in areas 3 and 10.

To a very substantial degree, the generalized tracks and areas of endemism described above conform to patterns recognized in my earlier analysis. The generalized tracks appear to represent four historical source units whose constituent taxa have had an ancient and continuing association together. That association is reflected in the coincident distribution of diverse stocks of amphibians and reptiles along the tracks and coincident patterns of evolution that are correlated with major events in earth and environmental history. Genera and a few subgeneric groups whose distributions coincide with a particular track may be grouped together as a primary historical unit or Element. The four Elements recognized here correspond to the units discussed in my earlier papers (Savage, 1960, 1963,

TABLE 4. Component genera of principal historical units of the tropical Mesoamerican herpetofauna.

Old Northern (67)	Middle American (60)	South American (65)	Young Northern (7)
Salamanders: (9)	Caecilians: (2)	Caecilians: (2)	
Bolitoglossa A	*Dermophis*	*Caecilia*	
Bolitoglossa B	*Gymnopis*	*Oscaecilia*	
Chiropterotriton A			
Chiropterotriton B			
Lineatriton			
Oedipina			
Parvimolge			
Pseudoeurycea			
Thorius			
Frogs and Toads: (3)	Frogs and Toads: (14)	Frogs and Toads: (21)	
Rhinophrynus	*Gastrophryne*	*Protopipa*	
Scaphiopus	*Hypopachus*	*Chiasmocleis*	
Rana	*Bufo* (pt.)	*Relictivomer*	
	Crepidophryne	*Glossostoma*	
	Eleutherodactylus (pt.)	*Eleutherodactylus* (pt.)	
	Hylactophryne	*Leptodactylus*	
	Syrrhophus	*Physalaemus*	
	Tomodactylus	*Pleurodema*	
	Agalychnis	*Atelopus*	
	Hyla (pt.)	*Bufo* (pt.)	
	Plectrohyla	*Rhamphophryne*	
	Pternohyla	*Dendrobates*	
	Ptychohyla	*Phyllobates*	
	Triprion	*Prostherapis*	
		Centrolenella	
		Anotheca	
		Gastrotheca	
		Hemiphractus	
		Hyla (pt.)	
		Phrynohyas	
		Phyllomedusa	

TABLE 4. Continued.

Old Northern (67)	Middle American (60)	South American (65)	Young Northern (7)
Turtles: (8)		**Turtles: (1)**	
Claudius		*Chelonoides*	
Kinosternon			
Staurotypus			
Dermatemys			
Chelydra			
Chrysemys			
Rhinoclemmys			
Terrapene			
Lizards: (14)	**Lizards: (11)**	**Lizards: (16)**	**Lizards: (4)**
Coleonyx	*Basiliscus*	*Anolis*	*Phrynosoma*
Lepidophyma	*Corytophanes*	*Enyalioides*	*Sceloporus*
Anelytropsis	*Ctenosaura*	*Morunasaurus*	*Urosaurus*
Eumeces	*Enyaliosaurus*	*Polychrus*	
Mabuya	*Iguana*	*Lepidoblepharis*	
Sphenomorphus	*Laemanctus*	*Phyllodactylus* (pt.)	
Abronia	*Norops*	*Thecadactylus*	
Celestus	*Phyllodactylus* (pt.)	*Ameiva*	*Cnemidophorus*
Coloptychon	*Gonatodes*	*Anadia*	
Gerrhonotus	*Sphaerodactylus*	*Bachia*	
Ophisaurus	*Aristelliger*	*Echinosaura*	
Heloderma		*Gymnophthalmus*	
Xenosaurus		*Leposoma*	
Bipes		*Neusticurus*	
		Ptychoglossus	
		Diploglossus	
Snakes: (33)	**Snakes: (32)**	**Snakes: (24)**	**Snakes: (3)**
Loxocemus	*Boa*	*Anomalepis*	*Leptotyphlops* (pt.)
Chironius	*Exiliboa*	*Helminthophis*	*Hypsiglena*
Coluber	*Ungaliophis*	*Liotyphlops*	*Crotalus*
Dendrophidion	*Adelphicos*	*Typhlops*	
Drymarchon	*Amastridium*	*Leptotyphlops* (pt.)	
Drymobius	*Atractus*	*Corallus*	
Elaphe	*Chersodromus*	*Epicrates*	

TABLE 4. Continued.

Old Northern (67)	Middle American (60)	South American (65)	Young Northern (7)
Ficimia	*Coniophanes*	*Trachyboa*	
Gyalopion	*Conophis*	*Clelia*	
Lampropeltis	*Crisantophis*	*Enulius*	
Leptodrymus	*Cryophis*	*Erythrolamprus*	
Leptophis	*Diaphorolepis*	*Leimadophis*	
Mastigodryas	*Dipsas*	*Lygophis*	
Nerodia	*Geagras*	*Manolepis*	
Oxybelis	*Geophis*	*Oxyrhopus*	
Pituophis	*Hydromorphus*	*Phimophis*	
Pseudoficimia	*Imantodes*	*Pseudoboa*	
Pseustes	*Leptodeira*	*Rhadinaea* (pt.)	
Rhinobothryum	*Ninia*	*Siphlophis*	
Rhinocheilus	*Nothopsis*	*Tripanurgos*	
Salvadora	*Pliocercus*	*Xenodon*	
Scaphiodontophis	*Rhadinaea* (pt.)	*Micrurus* (pt.)	
Sonora	*Rhadinophanes*	*Bothriopsis*	
Spilotes	*Scolecophis*	*Bothrops*	
Stenorrhina	*Sibon*		
Storeria	*Tantalophis*		
Symphimus	*Tretanorhinus*		
Sympholis	*Trimetopon*		
Tantilla	*Tropidodipsas*		
Tantillita	*Micrurus* (pt.)		
Thamnophis	*Agkistrodon*		
Toluca	*Bothriechis*		
Trimorphodon			
	Crocodilians: (1)	Crocodilians: (1)	
	Crocodylus	*Caiman*	

1966), but with substantial revision in content, based upon new findings on phylogenetic relationships, especially for snakes (Table 4).

Old Northern Element—derivative stocks of originally extratropical (subtropical-warm temperate) groups distributed more or less continuously and circumpolarly in early Tertiary, but forced southward and fragmented into several more or less disjunct components as a result of increased cooling and aridity trends and mountain building in late Cenozoic. This unit is comprised of taxa having long-term Laurasian affinities. Typical members of this element, including the "hanging" Middle American relicts, the frog family Rhinophrynidae, the turtle family Dermatemydidae, the lizard families Xantusiidae, Xenosauridae, and Helodermatidae, were widespread over much of North America to 40°N in early Tertiary. As I pointed out in 1966 and was confirmed by Rosen (1978), the Central American component of this stock has been disjunct from other components for most of later Tertiary and Quaternary time and has evolved *in situ* in Middle America.

South American Element—derivatives of a generalized tropical American biota that evolved *in situ* in isolation in South America during most of Cenozoic. The affinities of this unit are Gondwanian.

Middle American Element—derivative groups of a generalized tropical American biota isolated in tropical North and Central America during most of Cenozoic; developed *in situ* north of the Panamanian Portal and restricted by mountain building and climatic change in late Cenozoic to Middle America. Savage (1966) established the relationship of this unit to the South American Element and argued that a major vicariance event, the inundation of a putative Paleocene land bridge between Central and South America, led to their differentiation. Some workers believe groups placed here dispersed from South America across the proto-Antilles (Rosen, 1978) or the proto-Antilles and a later island archipelago, both located in the Panamanian Portal Zone (Duellman, 1979); subsequent differentiation has led to the distinctive aspects of this series of descendant groups.

Young Northern Element—derivatives from the generalized tropical American biota of early Tertiary that responded to the challenge of physiographic and climatic revolution in the middle latitudes of western North America and Mexico; essentially an *in situ* extratropical xeric derivative of the Middle American Element.

In my earlier discussion, I designated a number of subdivisions within the primary elements as "complexes." While these are still recognizable geographic patterns, since they correspond to components of a generalized track, they will be called components here. The most distinctive components of the tracks are represented by the nodes of endemic areas discussed above.

Development of the Herpetofauna

The principal contributions of vicariance theory to the field of historical biogeography do not come from the emphasis on vicariance events as primal modalities in shaping distribution patterns nor from the recognition that the patterns represent a trace on the earth's surface of ancient distributional events. Both of these ideas are part of conventional (dispersal) theory. Instead, it is the insistence

in vicariance theory on the search for general patterns and the rigorous testing of their generality that is distinctive. In the search for general pattern, vicariance biogeography proposes that the separate components of the pattern are historically linked to one another and to climatic, physiographic or tectonically induced changes in geography. A general pattern requires concordant dispersal and/or vicariance by many groups. Long-distance or random dispersal, by individual taxa, are stochastic events and are unlikely to produce general patterns. Nevertheless, distributional data alone rarely are sufficient to resolve the question of whether a particular general pattern has resulted from individual dispersal, concordant dispersal, and/or vicariance events. Instead, vicariance biogeography, in its latest formulation, initially seeks evidence, not as to the cause of the pattern, but as to whether the systematic relationships among related taxa in the geographic components of the pattern have a generality. The hypotheses of phylogenetic interrelationships among two or more taxa (each containing a minimum of three endemics) are transformed into one concerning interrelationships among areas. Comparisons with additional taxa test the hypothesis of area relations. The result is then compared for congruence with geologic and climatic history as a means to specify possible causes for the pattern in terms of a general explanation (Morse & White, 1979; and Fig. 7).

Application of this approach (Rosen, 1978) implies that the earth and life have evolved together, that paleogeographic and paleoclimatologic changes on the planet have produced the biological patterns, and that while most of the observed patterns will be specified by events in earth history, some (individual dispersals) will not. It further implies that a knowledge of the evolutionary relationships among taxa will allow for prediction of previously undetected events in earth history. Conversely, a knowledge of earth history must provide a basis for predicting the interrelationships among taxa, a point not mentioned by the vicariists, but implicit in their argument. We will return to this latter point below.

ALTERNATIVE HYPOTHESES

At the present time there are three conflicting theoretical explanations of the biogeography of the Central American herpetofauna (Savage, 1966; Rosen, 1976; Duellman, 1979). Each of these explanations shows some correlation with ideas on the distribution of other groups of organisms in the region (i.e. plants, freshwater fishes, and mammals), so that there appears to be several repetitive general patterns. Presumably, the best explanation of the history of amphibians and reptiles in Central America should provide a basis for explaining the pattern shown in other groups as well.

In the following paragraphs, I will briefly outline the major features of each distributional theory; review each theory in the light of the revised data set, generalized track analysis, and historical source unit assignment provided in the present paper; propose a revised theory to explain the herpetofaunal pattern; and compare these results to patterns for other groups.

The essential features of the three principal theories proposed to explain the origin and history of the Central American herpetofauna are summarized below (Figs. 2–5):

1. Savage (1966)—a major vicariance event in early Tertiary, the inundation of the original Isthmian Link, fragmented an ancestral tropical American herpetofauna into two isolated elements, one in Middle America and one in South America, that underwent differentiation *in situ* for most of the remainder of the Tertiary. A second vicariance event associated with mountain building and climatic changes from Eocene onward led to the isolation of a number of stocks of northern affinities (the Central American component) in Mesoamerica, where they underwent *in situ* differentiation in association with Middle American groups of southern affinities. Upon re-establishment of the Isthmian Link in Pliocene, some South American groups dispersed northward and some stock of the autochthonous Middle American element and associated, originally, northern taxa dispersed southward, to obscure the formerly complete distinction between Mesoamerican and South American herpetofaunas.

2. Rosen (1976)—a major vicariance event in early Tertiary caused by the eastward drift of the proto-Antilles from their position between Nuclear Central America and South America fragmented a formerly more or less continuous biota to isolate Middle American, Antillean, and South American components. The same process fragmented a northern unit of the biota into Middle American and Antillean components. Subsequent mountain building and climatic change in the region of northern Mexico essentially isolated both northern and southern elements in Middle America from Eocene to Pliocene (Axelrod, 1975; Rosen, 1978). Establishment of the Isthmian Link in Pliocene led to limited dispersal between Central and South America, in both directions.

3. Duellman (1979)—island-hopping dispersal events involving the proto-Antilles in early Tertiary and a later Middle American archipelago allowed a number of familial level groups (13–14) to immigrate from South America to Central America and vice versa (4–6). On establishment of the Isthmian Link, in Pliocene, many additional groups dispersed in both directions.

A fourth alternative, not seriously proposed by anyone, might be to attribute the current patterns of distribution in Central America to a primarily post-Miocene dispersal of South American groups into the region, with subsequent rapid differentiation in endemic Middle American taxa.

As may be seen from this summary, the primary differences among the conflicting theories center on the nature of biotic relations, geologic events, and dispersals involving South America and Nuclear Central America. The interpretations of Savage and Rosen, relative to the incorporation of a northern component into the biota of Middle America, due to mountain building and climatic change, that isolated these groups from their allies in eastern North America by Oligocene, are essentially similar. While Duellman does not address this matter directly, since his concern is principally with Central and South American interrelationships, he (p. 16) appears to concur with my 1966 views. Other subsidiary problems involve the composition and time of arrival of northern groups in Central America, the differentiation of lowland areas of endemism, and the origin of montane isolates. Each of these problem areas will be addressed below.

Ideally, the best way to proceed in the analyses of alternative hypotheses would be to employ the method of Morse and White (1979) to discern if there are repetitive patterns of phylogenetic relationships that can be transformed into
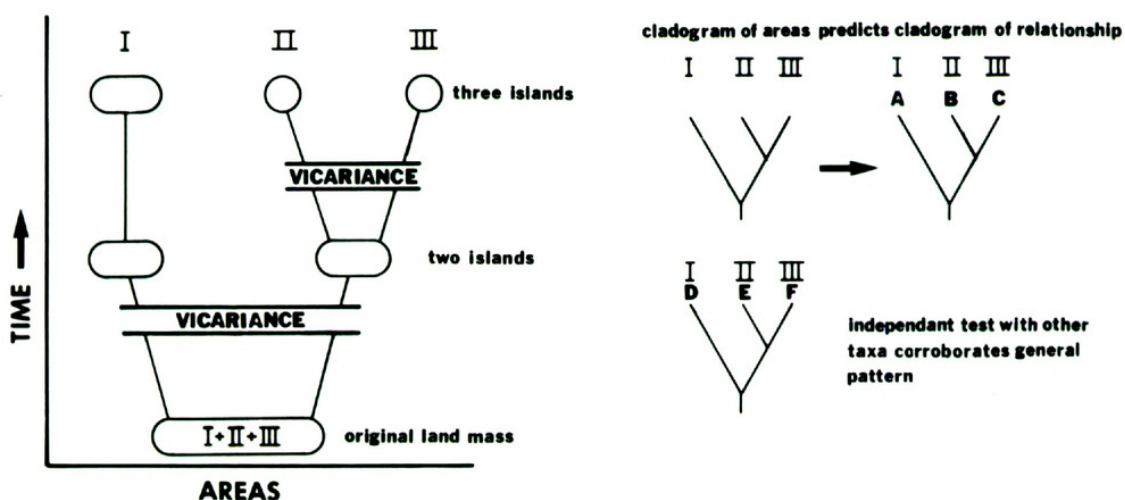
FIGURE 17. Prediction and testing of phylograms from area cladogram based on known geologic history.

general patterns of area relationships. These could then be compared with alternate theories, to test congruence between phylogeny and geography. Unfortunately, the constraints of the cladistic-vicariistic analytical method make this alternative unfeasible in application, first, because there are not a sufficient number of cladistic analyses available for the study area. For this reason, it is not possible to posit sequences of geography events based upon the branching sequences of area cladograms constructed. If one accepts the underlying concept of this approach, i.e. that earth and life have evolved together, and that general patterns of biotic distributions reflect earth history, another method may be used to estimate or test the validity of a biogeographic hypothesis. This method simply reverses the procedure of area-cladogram construction to use events in earth history to predict general recurrent patterns of phylogenetic relationship. Obviously, this approach implies a reciprocal relationship between earth history and the history of life and means that the statement:

pattern of paleogeographic and paleoclimatic change → phylogenetic change,

may be read from either direction. Thus, if we know something about patterns of earth history, it is possible to predict hypothetical phylogenetic patterns that can be tested against actual patterns. For example, if we know in some detail the history of a region which has been fragmented by a pair of vicariance events at known times, we should be able to predict three taxa—three area cladograms of relationships that can then be tested by actual phylogenetic analyses (Fig. 17). In areas for which geologic history is well known, this method provides interesting promise.

Unfortunately, the Central American region is among the most geologically complicated and controversial regions in the world. It remains impossible to obtain the necessary consensus of geologic opinion that would allow construction of a cladistic statement of geologic history, especially as it affects the Nuclear Central American-South American interconnection. The cladistic-vicariist method does, however, offer another way to attack the problem in many cases. This
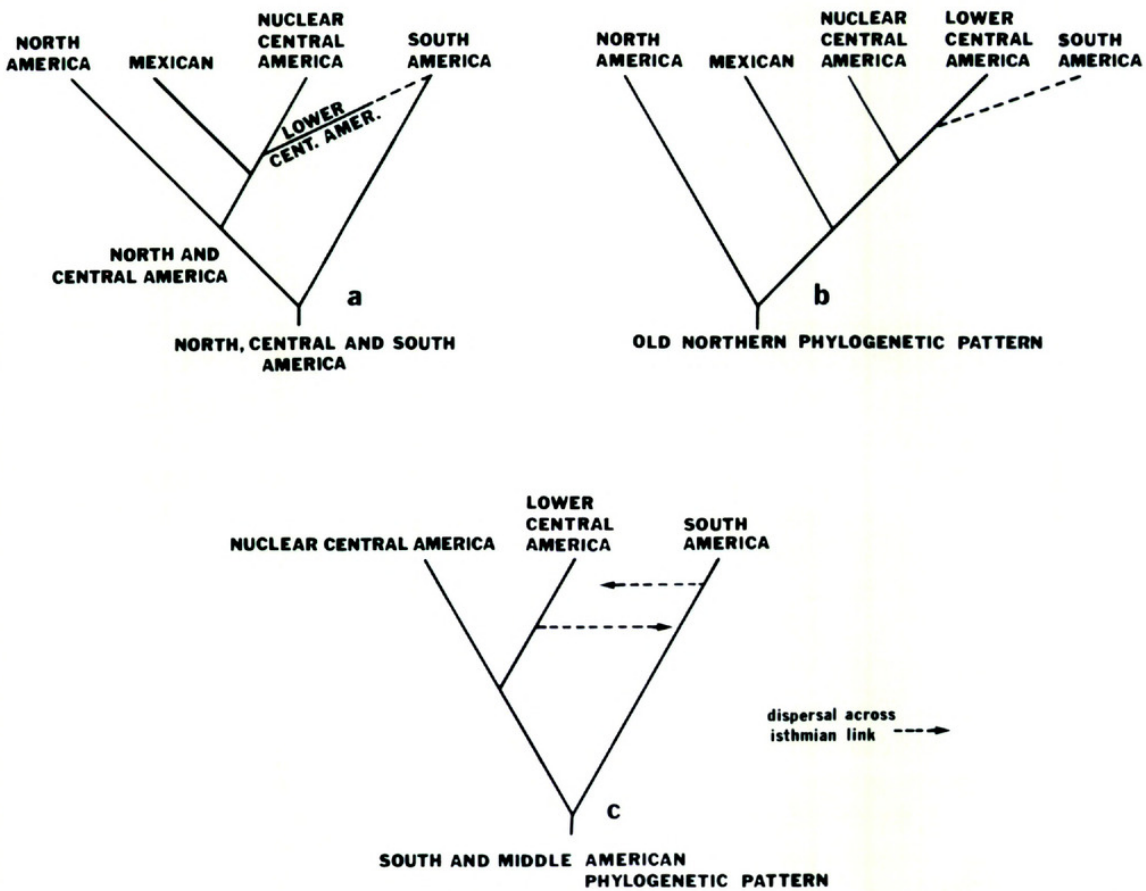
FIGURE 18. Cladogram of areas for the Americas based upon known geologic events (a). Predicted phylograms for major historical units of the herpetofauna, Old Northern (b), and South and Middle American (c).

is simply to transform the key elements of a biogeographic theory into a general cladogram of areas and use it to predict a general pattern of phylogenetic relationships. This hypothesis of pattern may then be tested by cladistic analysis of actual patterns for different taxa. Repeated congruence of relationship could then be interpreted as corroborating the theory. Substantial discongruence will suggest that aspects of the proposed theory are incorrect. Modifications of the theory may then be tested against the biological cladograms. In essence, this is what Rosen (1976) did when he constructed a model of Caribbean geological history (Pregill, 1981) and predicted phylogenetic patterns for northern and southern elements of the biota of Central America, the Antilles, and South America (Fig. 5).

In the present instance, I attempted to utilize the same method to distinguish among the several alternate hypotheses of Central American biogeography. It was thought that the several hypotheses would contain unique aspects that, when reduced to hypothetical area cladograms, would predict differences for phylogenetic pattern. This is not the case. All three hypotheses predict the same phylogenetic patterns (Fig. 18) as related to Central America. The reason again lies in the complex and unique history of the region, which forms a zone of mixing between two formerly isolated biotas now in contact over an emergent land connection, and the fact that all three views agree that Nuclear Central America

clearly was populated by a whole host of groups from South America in the distant past and remained isolated from South America for millions of years. In other words, the three hypotheses predict the same phylogenetic patterns; they disagree as to process.

The Duellman model involves multiple, independent, long-distance dispersals by individual taxa across the Panamanian portal at different times during Tertiary, but primarily, in the direction from South to Central America. Since this view requires an individual explanation for each taxon involved, no general pattern can be expected to emerge. The model is further complicated by Duellman's estimate of 18–20 dispersals southward and 23–25 northward, across the Isthmian Link. As pointed out by the vicariists, dispersal theories such as this are difficult to test. Since dispersal is invoked *a priori* as an explanation, each complication in interpretation is explained by another individual dispersal event, and no real decision can be made that parsimoniously minimizes the number of separate assumptions entailed in the explanation. Any parsimony decision only becomes possible when distribution patterns can be shown to have some significant generality, i.e. they occur in a number of different monophyletic groups. These factors mitigate against or make impossible testing of most theories of this kind. For this reason, theories of this kind may be called special dispersal theories since each dispersal is a unique event. Three features usually characterize long-distance dispersal by individual taxa when the presumed dispersed taxa are grouped as a unit: 1) they constitute a relatively small proportion of their respective biotas; 2) they appear to be a relatively random sample of groups from the presumed source area; and 3) they do not fit a general pattern of concordant distribution.

With these points in mind, let us review Duellman's theory of Central and South American relationships for south to north overwater dispersals prior to the Pliocene. Included groups are: ancestors of Central American Caeciliidae, *Eleutherodactylus, Agalychnis,* Hylidae, Microhylidae, Gekkonidae, primitive Iguanidae, anolines (Iguanidae), Teiidae, Leptotyphlopidae, Typhlopidae, Colubridae (Xenodontinae), and Micruridae (?). These groups comprise an important component in the Middle American herpetofauna; they are a major sample of South American stocks and they conform to the generalized track, congruent with that of other Middle American unit groups. In most cases, they are the endemic sister taxa of endemic South American groups as well. There seems no reason to regard any of these groups as special cases of dispersal, since they conform to the general pattern of vicariance discussed below.

Similarly, while not an issue here, the presumed north to south overwater dispersers identified by Duellman seem to conform to general patterns and do not seem to require special dispersals; they include: Testudinidae, iguanines (Iguanidae), Anguidae, Crocodylidae and, questionably, Colubridae and Viperidae (Table 4). Both the Savage (1966) and Rosen (1976) theories for the biogeography of the region depend upon major vicariance events, although I emphasized then more than I would now, aspects of Plio-Pleistocene dispersals to explain some features of the distribution patterns. Both emphasize 1) an ancient (Cretaceous-Paleocene) major concordant dispersal of southern stocks into Central America; 2) subsequent isolation of the two stocks by a major vicariance event,

the formation of the Panamanian portal region; 3) differentiation *in situ* both north and south of the portal to produce the distinctive components that now are sympatric in the Isthmian region; 4) association of a series of northern groups with the Middle American component during much of Cenozoic; 5) isolation of Middle American and their northern associates (the Central American component) from the areas occupied by the latter's cognates in eastern North America, through the impact of the vicariance events of mountain building and climatic compression, from Oligocene onward.

Based upon my earlier study and the re-analysis undertaken here, I wish to point out those areas of the Rosen (1976) dispersal-vicariance model that do not fit the herpetological data. It should be noted as well, that although Rosen (pp. 445–446) inveighs against the concept of concordant dispersal, he, of course, evokes it to explain (p. 453) the invasion of Nuclear Central America by northern and southern groups. Clearly, his vicariance theory (and all others), is based upon initial concordant dispersal of many groups, followed by fragmentation. When the geographic source of the original concordant dispersal is identified, even in such broad terms as Gondwanian or Southern, as in Rosen's study, the vicariists are, in effect, using the much despised (Croizat et al.) center of origin concept in theory construction. Directionality of the concordant dispersals, one from the north and one from the south, forms an essential ingredient in Rosen's vicariance theory.

Rosen's theory was developed primarily to explain Caribbean biogeographic patterns. For this reason, he did not fully treat nor consider the Pacific lowlands and highlands of Central America in his account. In addition, one of his major focuses was on the relationships of the Antillean biota with reference to other American land masses. Partially, for these reasons, Rosen did not emphasize the marked distinctiveness in group distributions and relationships for the taxa subsumed in his South American-Caribbean track, which have led me to distinguish South and Middle American Elements. Failure to do so is a reflection of the inability of vicariance theory to sort out relatively recent dispersal events in which, as in this case, a major distributional barrier (the marine portal) has been removed. A review of the taxa lying on Rosen's South American-Caribbean track shows that many of those now found in Central America represent Pliocene to Recent dispersal across the Isthmian Link. This pattern overlays the ancient track produced by concordant dispersal prior to the complete separation of Central and South American biota much earlier in Tertiary. For this reason, I prefer to emphasize the autochthonous Middle American and South American tracks as distinct units, in order to reduce the contamination by relatively recent dispersal from south to north and vice versa that tend to obscure the general pattern produced by the major vicariance event.

Finally, I find no evidence that would support the idea that northern taxa (Old Northern Element) were in Nuclear Central America in substantial numbers during Cretaceous, when, according to Rosen's model, they dispersed southward onto the proto-Antilles (Fig. 5). Indeed, one wonders why, if northern taxa were present, did they not have a major dispersal across the proto-Antilles southward? This is especially puzzling, if one accepts Rosen's idea that at the same time

southern groups dispersed northward across the proto-Antilles. As will be pointed out below, a number of Middle American Element taxa were included with his northern (North American-Caribbean) track to inadvertently confuse this issue. These stocks are clearly of southern relations.

Recently, Pregill (1981), utilizing the geological data of Perfit and Heezen (1978), and a dispersalist approach to explaining recent and fossil vertebrate distributions in the Antilles, severely criticized Rosen's model. This eventuality was predicted by Patterson (1981), as noted in an earlier section of the present paper. The key element in Pregill's exposition is the conclusion that there were no proto-Antilles in the Panamanian portal region at any time and that the Greater and Lesser Antilles have had an entirely different history from that proposed by Rosen and from one another. While it is difficult to select from among the several geological models proposed for the Antilles, since Rosen's paper appeared (Owen, 1976; Carey, 1976; Shields, 1979; Lillegraven et al., 1979; Melville, 1981), not all of these support Pregill's contention that the Antilles are essentially oceanic islands populated by overwater dispersal. In any event, I join Patterson (1981) in concluding that the new discoveries in Caribbean geology in no way falsify Rosen's empirical evidence, which still demands explanation. Review of that evidence (Table 5 and Figs. 12–15) indicates that the herpetofauna of the Antilles consists of Old Northern, Middle American, and South American Elements. The former two tend to be concentrated in the Greater Antilles, especially on Cuba, and the latter in the Lesser Antilles. How these patterns may have come to be formed, whether by dispersal or vicariance, will be returned to below.

A Revised Model of Herpetofaunal History

My revised model is essentially a vicariance one. It recognizes the concepts of concordant dispersal, historical source unit, and area of origin (concepts that arch-vicariists may decry) as useful devices for biogeographic theory construction. It emphasizes the relationship between these concepts and the evidence of congruent distribution patterns as seen in generalized and component tracks. It accepts the notion that the model's validity will be tested by cladistic analysis of interrelationships transformed to area cladograms and by new findings in paleogeography and paleoclimatology.

The essential framework of the model differs in no great way from that proposed 15 years ago, and the summary given below will not be detailed.

All evidence points to an ancient contiguity and essential similarity of a generalized tropical herpetofauna that ranged over tropical North, Middle, and most of South America in Cretaceous-Paleocene times. Descendants of this fauna are represented today by the South and Middle American tracks (Elements). To the north of this fauna ranged a subtropical-temperate Laurasian derived unit, today represented by the Old Northern Element (track). By Eocene, northern and southern fragments of the generalized tropical units had become isolated in Middle and South America, respectively. Differentiation *in situ* until Pliocene produced the distinctive herpetofaunas that became intermixed with the establishment of the Isthmian Link (Fig. 2).

By Eocene a substantial number of Old Northern groups became associated

TABLE 5.   Distribution of the genera of amphibians and reptiles on major island groups.

Greater Antilles				Lesser Antilles	Galapagos
Bufonidae:					
Peltophryne	C	H	PR		
Hylidae:					
Calyptahyla	J				
Hyla	H	J		*Hyla*	
Osteopilus	C	H	J		
Leptodactylidae:					
Eleutherodactylus	C H J	PR		*Eleutherodactylus*	
Leptodactylus	H PR			*Leptodactylus*	
Sminthillus	C				
Emydidae:					
Chrysemys	C H J	PR			
Testudinidae:					
Chelonoides	C*			*Chelonoides**	*Chelonoides*
*Monochelys***					
Iguanidae:					
Anolis	C H PR			*Anolis*	
Chamaeleolis	C				
Chamaelinorops	H				
Cyclura	C H J	PR*		*Cyclura*	*Amblyrhynchus*
				Iguana	*Conolopus*
Leiocephalus	C H J	PR*		*Leiocephalus*	*Tropidurus*
Norops	C J				
Gekkonidae:					
Aristelliger	H J				
Gonatodes	C H J				
Hemidactylus	C H PR			*Hemidactylus*	
Phyllodactylus	H PR			*Phyllodactylus*	*Phyllodactylus*
Sphaerodactylus	C H J	PR		*Sphaerodactylus*	
Tarentola	C			*Thecadactylus*	
Gymnophthalmidae:				*Bachia*	
				Gymnophthalmus	
Teiidae:					
Ameiva	C H J	PR		*Ameiva*	
				Kentropyx	
Scincidae:					
Mabuya	H J	PR		*Mabuya*	
Xantusiidae:					
Cricosaura	C				
Anguidae:					
Celestus	H J				
Diploglossus	C H	PR		*Diploglossus*	
Sauresia	H				
Wetmorea	H				
Amphisbaenidae:					
Amphisbaena	C H PR			*Amphisbaena*	
Cadea	C				
Typhlopidae:					
Typhlops	C H J	PR		*Typhlops*	

TABLE 5. Continued.

Greater Antilles					Lesser Antilles	Galapagos
Leptotyphlopidae:						
Leptotyphlops	H				*Leptotyphlops*	
Boidae:						
					Boa	
					Corallus	
Epicrates	C	H	J	PR	*Epicrates*	
Tropidophiidae:						
Tropidophis	C	H	J			
Colubridae:						
Alsophis	C	H	J	PR	*Alsophis*	
Antillophis	C	H				
Arrhyton	C	J	PR		*Arrhyton*	
					Chironius	
Darlingtonia	H				*Clelia*	
Hypsirhynchus	H				*Dromicus*	*Dromicus*
Ialtris	H				*Mastigodryas*	
Nerodia	C				*Pseudoboa*	
Tretanorhinus	C					
Uromacer	H					
Viperidae:						
					Bothrops	
Crocodylidae:						
Crocodylus	C	H	J		*Crocodylus*	

C = Cuba.   * Fossil.
H = Hispaniola.   ** Fossil on Mona Island between Jamaica and Puerto Rico.
J = Jamaica.
PR = Puerto Rico.

with Middle American stocks in Mexico. As the former continuity between that region and what is now the eastern United States was affected by mountain building and subsequent (Oligocene-Pliocene) climatic change, these components became disjunct (Axelrod, 1975). This disjunction (Rosen, 1978) allowed differentiation of what I have continued to call the Central American Component of the Old Northern Element, which evolved in association with the Middle American Element for the remainder of Cenozoic. Thus, the initial organization of what was to become the Meso-American herpetofauna involved a pair of vicariance events: 1) complete geographic isolation from South America and 2) fragmentation and isolation of the Central American Component from its northern congeners, by a combination of physiographic and climatic factors. By Oligocene, most of the genera or their ancestors, which now form the Old Northern and Middle American Elements (Table 4), were present in the region.

A major physiographic development, the uplift of the main mountain axis of Mexico and Central America, created two important additional vicariance events. This process seems to have had a north to south sequence, with the Sierra Madres of Mexico present as upland areas in Oligocene, and the highlands of Nuclear Central America developing in Miocene. The final sequence of uplift was in lower Central America leading to the closure of the Panamanian Portal in Pliocene. A

primary vicariance effect of the uplift was to gradually fragment what was a rather homogeneous Mesoamerican herpetofauna into three groups: a) an eastern lowland, b) a western lowland, and c) an upland assemblage. Although I previously emphasized climatic differences between eastern (humid, evergreen forests) and western lowland (subhumid-semiarid, deciduous, and thorn forests) areas to explain the two lowland patterns of distribution, it now seems that the important phylogenetic factor (progenetic) was the vicariance effect of mountain building. As pointed out, many species and most genera of lowland groups in Central America are found on both Pacific and Caribbean coastal strips. Duellman (1966) and I have also pointed out the relative homogeneity of the herpetofauna on each lowland versant, with most genera and species widely distributed. Examples suggesting the effect of this vicariance event include (Figs. 19–20):

A. Endemic Genera

Atlantic	Pacific
*Gymnopis**	*Loxocemus*
Anotheca	*Crisantophis*
	Leptodrymus
	Scolecophis

B. Endemic Genera With Endemic Species on Both Versants

Triprion
Basiliscus
Enyaliosaurus
Symphimus

C. Species Pairs

Atlantic	Pacific
Bufo valliceps	*Bufo luetkenii*
Dendrobates pumilio	*Dendrobates granuliferus*
Phyllobates lugubris	*Phyllobates vittatus*
*Hyla microcephala**	*Hyla robertmertensi*
Eumeces schwartzei	*Eumeces managuae*
Rhinoclemmys annulata	*Rhinoclemmys pulcherrima*
Bothriechis annectans	*Bothriechis ophryomegas*

* On Pacific versant in lower Central America.

As the mountains were uplifted, the distributions of certain other groups, perhaps originally associated with the low uplands of earlier times, became fragmented onto the three major highland areas today comprising the backbone of Middle America. This fragmentation has led to the development of endemic montane isolates from ancestors with a formerly continuous north to south range. I previously had considered dispersal from one highland to the other as a significant factor responsible for distributions corresponding to this pattern among the several salamander lines; in several groups of montane tree-frogs (Fig. 21); a number of lizards: *Norops, Sceloporus,* and *Gerrhonotus* (Figs. 22–23); and some snakes
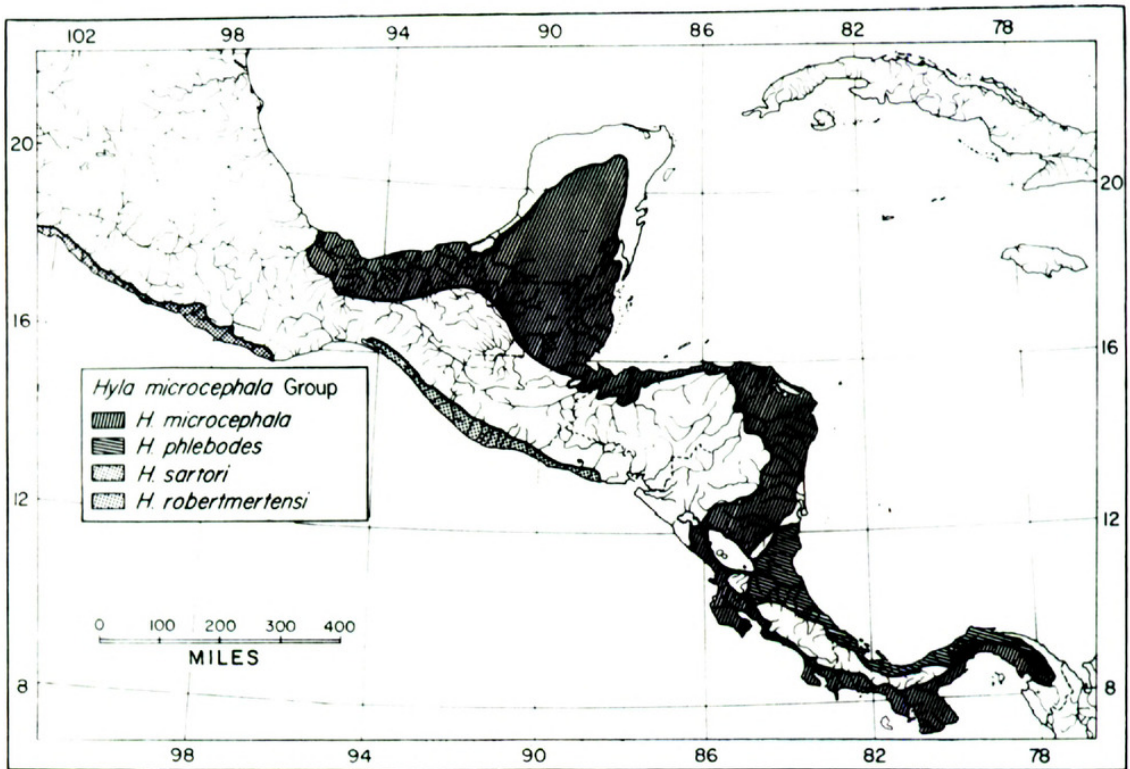
FIGURE 19.   Distribution of tree-frogs of the *Hyla microcephala* stocks, showing Atlantic-Pacific fragmentation produced by uplift of the main mountain axis of Mexico and Central America.

of the genera *Geophis, Ninia, Rhadinaea,* and *Bothriechis*. I now believe that the distinctive montane herpetofaunas of the southern Sierras of Mexico, Nuclear Central America, and the Talamanca area developed more or less *in situ* from ancestors that "rode" the uplifted areas and evolved with them. Each endemic montane area then represents an uplifted island biota vicariated from a more or less similar sea of widely distributed ancestors.

This conclusion was anticipated in my 1966 account (p. 763), where I pointed out the striking differences among the herpetofaunas of the highlands of southern Mexico, Guatemala, and the Talamanca region. As noted then, "It must be stated emphatically that both the northern and southern highland areas of Central America have indigenous faunas drawn, for the most part, from mesic lowland ancestors in the two regions and differing, strikingly, from one another in almost every facet of herpetofaunal composition."

The minor role of Young Northern Element groups in Central America was emphasized in my previous paper and with the discovery that many genera previously included with this unit belong with the Old Northern component (Table 4), that role is even further reduced. Only the lizard genera *Sceloporus* and *Cnemidophorus* and the snake genus *Crotalus* (Table 4) contribute to the region. *Cnemidophorus* and *Crotalus,* and a number of *Sceloporus,* are generally associated with dry formations. One group of *Sceloporus* is montane in distribution, suggesting that the ancestor of this stock was widely spread over the lowlands and fragmented into isolates by riding the emergent separate highlands (Fig. 22).
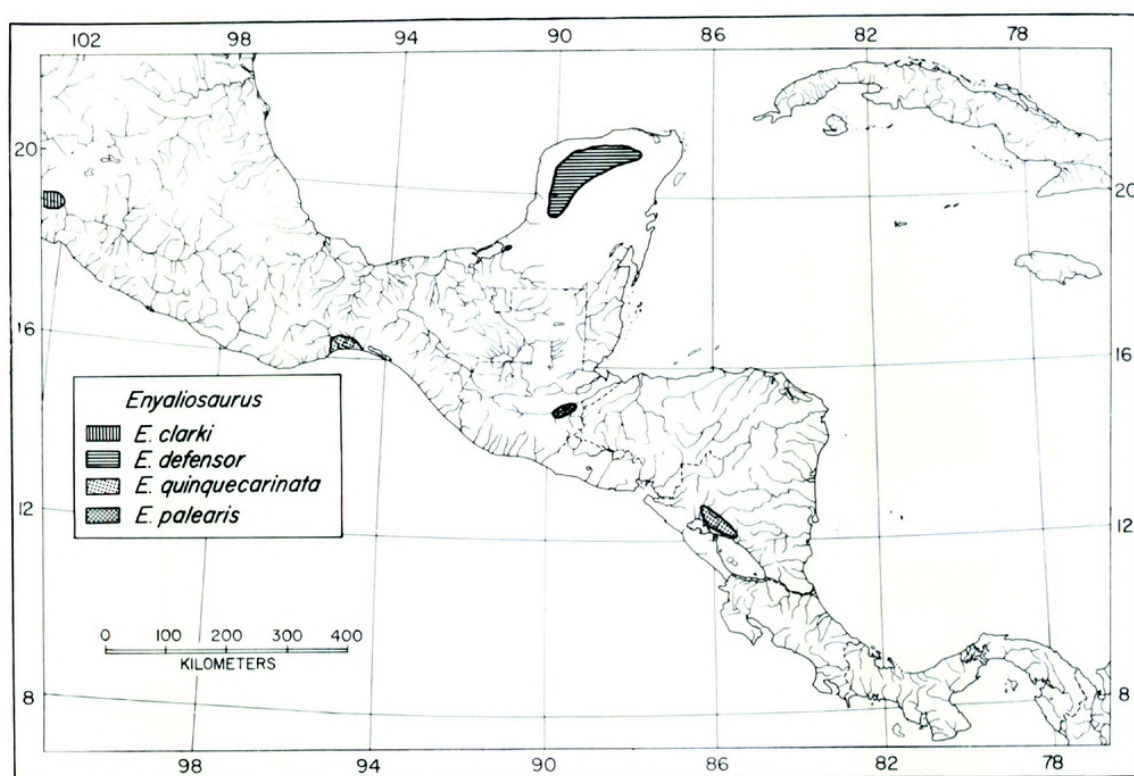
FIGURE 20.   Distribution of the iguanid lizard genus *Enyaliosaurus*, illustrative of the fragmentation of lowland groups into Atlantic and Pacific components by the uplift of the main mountain axis of Mexico and Central America.

The final major factor in shaping the herpetofauna of Central America was the complete emergence of the Panamanian Isthmus in Pliocene to directly connect North and South America. While there remains some question as to whether the connection was completed in early Pliocene (Savage, 1974; Raven & Axelrod, 1974) or late Pliocene (Webb, 1977; Marshall et al., 1979), a difference between 5.7 or 3 m.y. B.P., respectively, the exact dating does not affect our story. The reconnection led to the dispersal of many South American Element genera northward and permitted immigration by some Old Northern and many Middle American stocks into South America. These concordant dispersal events, also well documented for other major groups and fully confirmed by the mammal fossil record (Marshall et al., 1979), conclusively demonstrate that dispersal of this kind cannot be discounted in biogeographic theory as vicariists attempt to do. In any event, 64 living generic level taxa of clearly South American origin have dispersed across the Isthmus to contribute to the Central American herpetofauna (Figs. 2, 13). Most of these groups are restricted to the region from eastern Panama to Costa Rica, so that the South American influence is minimal over most of Mesoamerica. Similarly, the greatest number of Middle American generic level taxa and species is found in northwestern South America.

The recent herpetofaunas of Central America, except those in eastern Panama, are based upon a fundamental core of autochthonous Middle American groups whose history in the region goes back at least to early Tertiary. Coexisting with
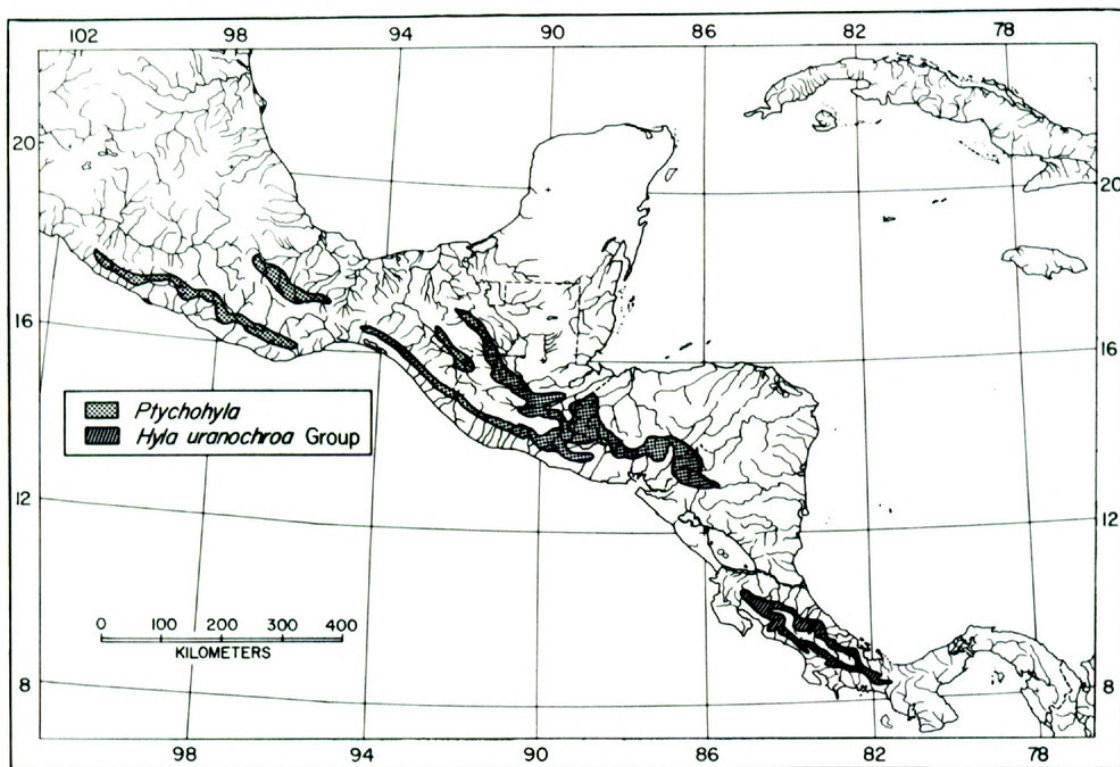
FIGURE 21.   Distribution of the tree-frogs of the genus *Ptychohyla* and *Hyla uranochroa* group, showing the fragmentation of once continuous ranges by the gradual uplift of the Mesoamerican montane regions.

this unit throughout the region are a series of autochthonous derivative stocks of Old Northern relationships that have been in the region from Eocene-Oligocene times onward.

Uplift of the highland regions of Mexico, Nuclear Central America, and the Talamanca region carried with them groups of mesic lowland derivation from both Middle and Northern units. These stocks have produced minor evolutionary radiations in the two Central American highland zones, which differ markedly from one another and the Sierras of Mexico. The impact of this process of mountain building fragmented the lowland herpetofauna into eastern and western components as well. The effects of climatic changes toward more xeric conditions along the Pacific coastal lowlands from Pliocene onward seem to have sorted out a relatively small number of taxa from an originally more diverse fauna. The highland and western lowland herpetofaunas include a representation of Young Northern groups, which may also occur in subhumid to xeric situations on the Atlantic versant, but this component is relatively insignificant. In Panama and Costa Rica, particularly, South American Element taxa contribute significantly to the fauna and predominate in eastern Panama.

DISTRIBUTIONAL EVIDENCE FROM OTHER MAJOR GROUPS

The most interesting aspects of the model outlined in the preceding section remain: 1) the distinction by some kind of vicariance event of the Middle Amer-
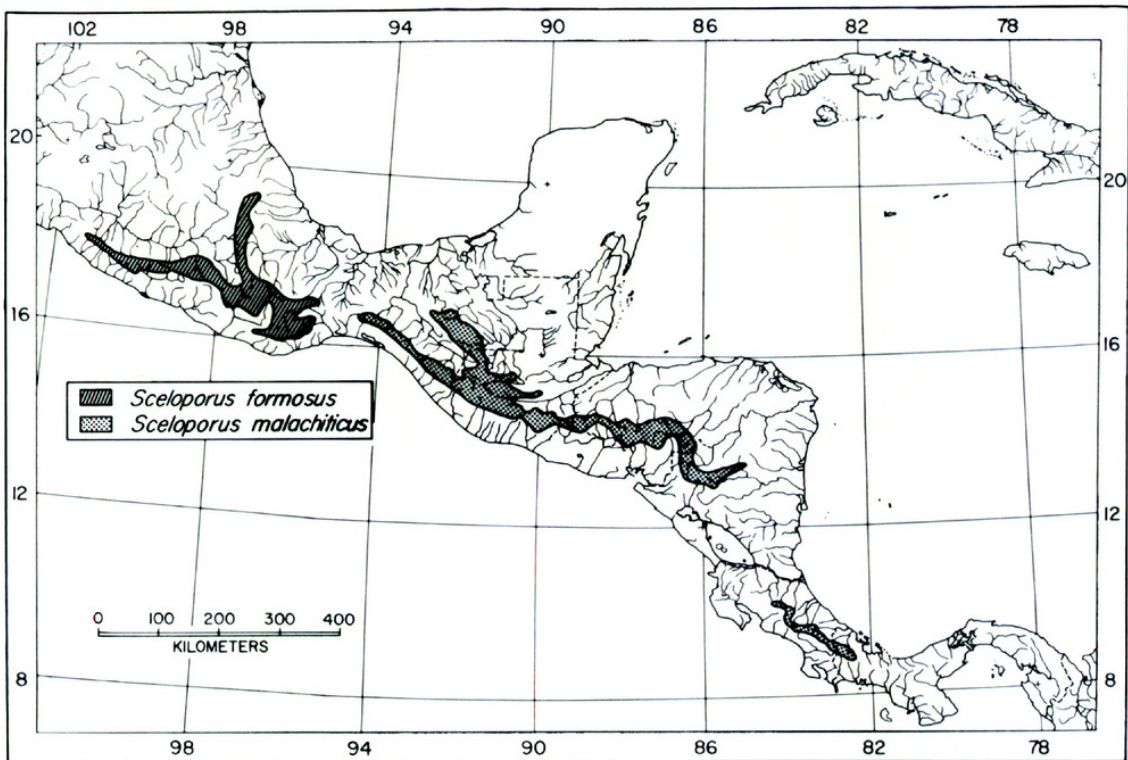
FIGURE 22.   Distribution of the spiny lizard of the *Sceloporus formosus* group, illustrating fragmentation by uplift of the Mesoamerican montane regions.

ican and South American source units prior to Eocene time and, 2) the coexistence of co-differentiation of disjunct Old Northern (Central American Component) taxa along with the Middle American stocks. The question that I will attempt to answer here is: Do other major groups of organisms show similar patterns of distribution and relationships? An answer of "yes" would corroborate the herpetofaunal model as having generality. An answer of "no" would require modification or rejection of the concept.

Raven and Axelrod (1974) presented a strongly dispersalist interpretation of the relationship of South and Central American angiosperms. Their conclusions are summarized (Fig. 3). While it is not possible to analyze their data at the level undertaken for amphibians and reptiles, it seems clear that the pattern for angiosperm distribution is remarkably similar. In my opinion, a detailed analysis of generic distributions for the area would provide even stronger confirmation for my re-interpretation of their data as outlined below.

Raven and Axelrod (1974: 627–630) recognized several components in the Central American flora: 1) a group of 51 families of clear South American affinities, many of which were in North America by Eocene times, but others that were Isthmian Link dispersers; 2) a series of 9 southern families thought to have been present in North America by early Tertiary; 3) a group of 54 families of northern origin, about 40 of which range south, at least to Panama; 4) a group of 25–30 families of apparently northern affinities that dispersed across the Isthmian Link, southward in Pliocene to Recent times; and 5) a group of 11 families of
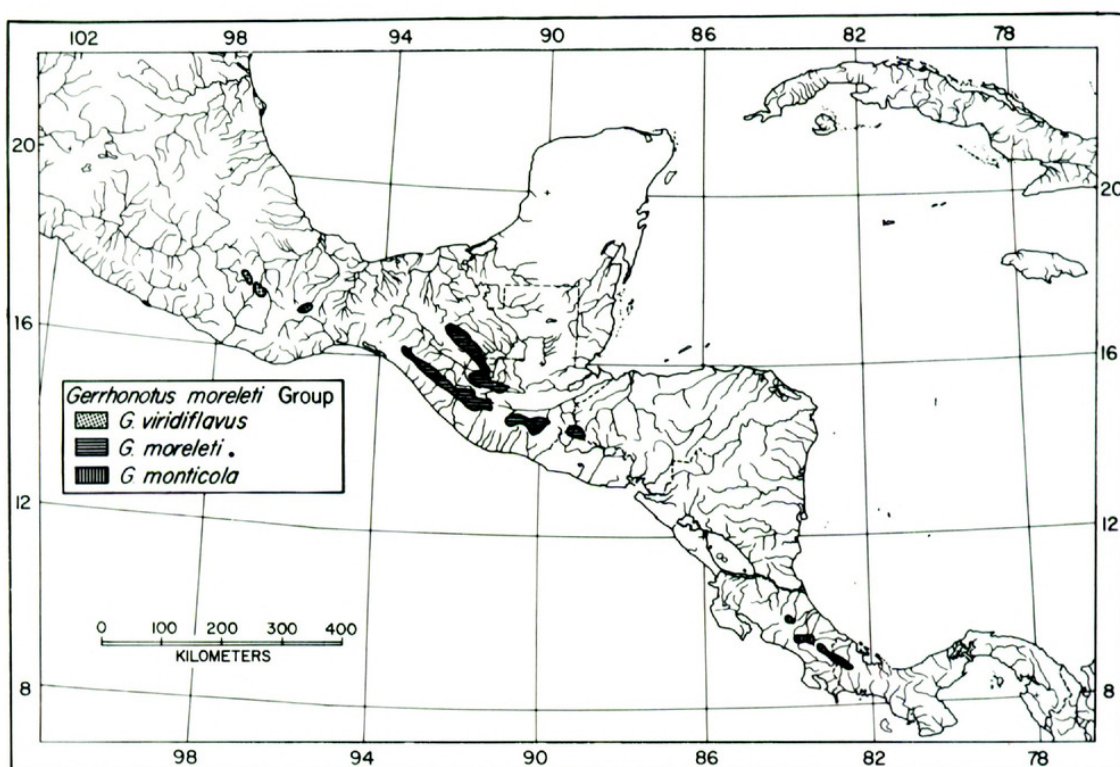
FIGURE 23.   Distribution of the alligator lizards allied to *Gerrhonotus moreleti*, showing fragmentation of once continuous range by uplift of the Mesoamerican montane regions.

northern origin that seemed to have arrived in South America prior to the appearance of the Link. In addition, they list a group of 14 families endemic chiefly to semiarid to arid regions of North and Mesoamerica. The latter two components are uninformative to the problem at hand and will not be discussed further.

Although the various groupings proposed by Raven and Axelrod are ambiguous, they are informative. The data indicate, clearly, that Central America contains angiosperm stocks of both northern and southern affinities. A major cluster of southern families (many in group 1 and all in group 2) were in Central America by Oligocene, where they underwent differentiation in isolation from their sister groups in South America. The picture presented by Raven and Axelrod, for these groups, is obscured somewhat by their failure to sort out post-Miocene dispersers that reached Central America and South America across the Isthmian Link and those that had arrived earlier. Nevertheless, these families conform exactly in distribution to the South American-Caribbean track (for the sister taxa isolated in South America) and the Middle American-Caribbean track (for those isolated in America north of the Panamanian Portal during most of Tertiary); i.e. they correspond to the South American and Middle American herpetofaunal elements described above.

It will be no surprise to the reader that components 3 and 4 are interpreted as equivalent to the Old Northern Element of the herpetofauna, since they conform to the North American-Central American track (Fig. 12). In addition, Axelrod (1975) has conclusively demonstrated the reality of, and explained the his-

tory for, the floral equivalent of the Central American herpetofaunal component of this northern element, which includes such genera as *Acer, Carpinus, Carya, Cornus, Fagus, Ilex, Liquidambar, Myrica, Nyssa, Prunus,* and *Tilia.*

Bussing (1976) briefly reviewed the distribution and history of the freshwater fishes of Middle America, with major emphasis on the San Juan province (Fig. 4). He recognized two major distribution patterns for Central America: 1) Old Southern: a diverse series of genera most closely allied to South American sister groups, thought by Bussing to have been isolated in Central America from Eocene onward; and 2) Young Southern: recent trans-Isthmian dispersers from South America. In addition, he refers to a single Old Northern taxon, the gar, *Lepisosteus.*

It is apparent that the Old Southern Element of Bussing corresponds directly to the Middle American Element and track recognized for the herpetofauna (Fig. 14) and that the Young Southern Element represents the South American-Caribbean track (Fig. 13). Northern freshwater fishes are poorly represented in Central America, but *Lepisosteus* and several other genera conform to the North American-Central American track (Fig. 3).

An analysis of the data for the Mesoamerican region contained in Miller (1966), Martin (1972), Bussing (1976), and Rosen (1976) makes it possible to identify the component freshwater fish genera of each of the three Central American Elements (Table 6). Martin, Bussing, Rosen, and I agree that the somewhat artificial categorization of freshwater fish families into primary (not entering saltwater) and secondary (some members occasionally entering brackish or ocean waters) divisions is inappropriate primarily because some representatives of the former division are now known to have considerable salt tolerance. In addition, almost all species of the secondary division are restricted to freshwater and their patterns of distribution conform to those for primary division taxa. Obviously, marine fishes that frequently migrate or immigrate into freshwater (peripheral division) are not included in the analysis.

Bussing (1976) developed a strong argument for a late Cretaceous land connection between Central and South America that allowed freshwater fishes to invade the former from the south (dispersal). He effectively counters the argument that the ancestors of the Middle American Element could have arrived by swimming through an extensive saltwater barrier. The Middle and South American units were isolated, according to Bussing's concept, by a marine portal (vicariance), during most of Cenozoic, and have now only recently come back into contact along the Isthmian Link. Except for the usage of a different terminology for his historical source units, Bussing's model conforms exactly to that described above for the herpetofauna and suggested for flowering plants. The model includes a single major dispersal of southern taxa into Central America, followed by a major vicariance event to fragment Middle and South American components. Subsequently, northern stocks (in the case of fishes, very few) became associated with the Middle American unit. On the emergence of the Isthmian Link, South American taxa have invaded lower Central America to some degree and there has been a minor reciprocal dispersal of Middle American stocks southward.

TABLE 6.   Component genera of principal historical units of the Central American freshwater fish fauna.

Old Northern (3)	Middle American (32)	South American (42)
Gar:	Characins:	Characins:
Lepisosteus	*Hyphessobrycon* (pt.)	*Apareiodon*
	Gymnotids:	*Astyanax*
Catfishes:	*Gymnotus* (pt.)	*Bramocharax*
Ictiobus		*Brycon*
Ictalurus	Catfishes:	*Bryconamericus*
	Rhamdia (pt.)	*Carlana*
	Killifish:	**Characidium*
	Cyprinodon	**Compsura*
	Floridichthys	**Creagrutus*
	Fundulus	**Ctenolucius*
	Garmanella	**Curimata*
	Oxyzygonectes	**Gasteropelecus*
	Profundulus	**Gephyrocharax*
	Rivulus (pt.)	**Hemibrycon*
		*Hoplias
	Four-eyed Fishes:	**Phenagoniates*
	Anableps	**Piabucina*
	Viviparous Tooth-Carps:	**Pseudocheirodon*
	Alfaro	**Rhoadsia*
	Belonesox	**Roeboides*
	Brachyrhaphis	Gymnotids:
	Carlhubbsia	**Sternopygus*
	Gambusia	**Hypopomus*
	Heterandria	**Eigenmannia*
	Heterophallus	**Apteronotus*
	Neoheterandria	Catfishes:
	Phallichthys	**Trachycorystes*
	Poecilia	**Ageneiosus*
	Poeciliopsis	***Imparales*
	Priapella	**Pimelodus*
	Priapichthys	**Pimelodella*
	Scolichthys	**Pygidium*
	Xenodexia	**Hoplosternum*
	Xiphophorus	**Astroblepus*
	Cichlids:	**Hypostomus*
	Cichlasoma (pt.):	**Chaetostoma*
	Amphilophus	**Ancistrus*
	Archocentrus	**Lasiancistrus*
	Herichthys	**Leptoancistrus*
	Paraneetroplus	**Loricaria*
	Parapetenia	**Sturisoma*
	Theraps	Cichlids:
	Thorichthys	**Aequidens*
	Petenia	**Geophagus*
	Neetroplus	Synbranchids:
	Herotilapia	*Synbranchus*
	Synbranchids:	
	**Ophisternon	

(pt.) = different species group in South America.
   * Restricted to lower Central America.
   ** Same species disjunct in South America.

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 from Miocene onward (Fig. 4).

On the other hand, a cluster of distinctly tropical groups with northern affinities seems to have been established in Central America by the end of Eocene. Some of these represent endemic genera, others were among the first northern invaders across the Isthmian Link when it became emergent. Still others of more temperate affinities remained in Central America or dispersed across the Link to South America (Table 7). The first two groups and possibly the third are equivalent to the Central American Component of the herpetofauna. All four groups lie on the North American-Central American track (Fig. 12).

In addition to his consideration of amphibians, reptiles, and freshwater fishes, Rosen (1976) utilized the distributions of other organisms in the development of his vicariance model of Caribbean biogeography (Figs. 5, 24). As pointed out above, Rosen's South American-Caribbean track is a composite of the isolated fragments (in Middle and South America) of an ancient vicariance event with an overlay of trans-Isthmian dispersal. For example, the distribution of the frog genus *Leptodactylus* (Rosen's fig. 2c) and the fish genus *Synbranchus* (fig. 2f) appear to lie on the same track as the onychophoran genus *Peripatus* (fig. 2b). The former are recent dispersers across the Isthmus; the latter represents an ancient track with endemic Middle and South American components. An additional difficulty with Rosen's data is his confusion of several clearly Middle American stocks (i.e. ones derived from southern sources and affected by the major ancient vicariance event that separated the Americas) with his North American-Caribbean track. He points out the composite nature of this track by referring to an older Laurasian component and a younger Gondwanian one. Review of his examples indicates that the so-called Gondwanian component is comprised of taxa with closest affinities to South American stocks, i.e. they correspond to the Middle American-Caribbean track (Fig. 14) and are equivalent to the Middle American Element described above for freshwater fishes, amphibians, and reptiles. The most important examples of this pattern mentioned by Rosen are cyprinodontid and poeciliid fishes (his specialties). A reordering of Rosen's data, with these points in mind, produces a pattern conforming exactly to that described above for herpetofaunal and freshwater ichthyofaunal development. Rosen's ideas of an ancient major dispersal event from South to Central America, followed by a major vicariance event (the development of the Panamanian Portal) are in complete agreement with herpetofaunal data. In addition, Rosen (1978) further confirms and supports the concept of the incorporation of a distinct Old Northern component into the Mesoamerican biota in Eocene as proposed by Axelrod (1975) and Savage (1966). He agrees that this component became isolated by a disjunc-

TABLE 7. Central American terrestrial mammalian faunal components (bats excluded).

South American	North Tropical	North American

Marsupials:
  Didelphidae
 	
Primates:
  Callithricidae (marmosets)
  Cebidae (monkeys)
 	
Xenarthran edentates:
  Dasypodidae (armadillos)
  **Glyptodontidae
    (glyptodonts)
  **Megalonychidae
    (ground sloths)
  **Megatheriidae
    (ground sloths)
  Bradypodidae (tree sloths)
  **Mylodontidae (mylodonts)
  Myrmecophagidae
    (ant-eaters)
 	
Caviomorph rodents:
  Echimyidae (spiny-rats)
  Dasyproctidae (aguti)
  Cuniculidae (paca)
  Hydrochoeridae (capybara)
  Erethizontidae
    (porcupines)
 	
Sigmodontine mice
  (*Nyctomys, Otonyctomys,*
  Oryzomys, Sigmodon)
	1. Into South America
	  a squirrel (*Sciurillus*)
	  tropical dogs (*Dusicyon,*
	    Chrysocyon, Atelocy-
	    nus, Speothos, Lycalo-
	    pex)
	  spectacled bear (*Tre-*
	    marctos)
	  Procyonids (**Cyonasua, Na-*
	    sua, Potos, Bassari-
	    cyon)
	  Mustelids (*Lyncodon, Galic-*
	    tis, Eira, Pteronura)
	  cats (***Smilodon,* some
	    Felis)
	  **mastodons (Gomphotheriidae)
	
	  **horses (Equidae)
	  tapirs (Tapiridae)
	  deer (*Mazama, Pudu, Hip-*
	    pocamelus, Blastoce-
	    rus, Blastoceros)
	  *camels (*Lama, Vicugna*)
	
	2. Endemic to Central America
	  a squirrel (*Syntheosciurus*)
	  gophers (*Orthogeomys, Het-*
	    erogeomys, Macrogeo-
	    mys)
	  a heteromyid (*Liomys*)
	  a peromyscine mouse (*Sco-*
	    tinomys)
	  a neotomine mouse (*Ototy-*
	    lomys)
		1. Into South America
		  a shrew (*Cryptotis*)
		  rabbits
		  squirrels
		  heteromyids (*Heteromys*)
		  peromyscine mice (*Aporo-*
		    don)
		  a neotomine mouse (*Tylo-*
		    mys)
		  gray fox (*Urocyon*)
		  raccoons (*Procyon*)
		  weasels (*Mustela*)
		  otter (*Lutra*)
		  skunk (*Conepatus*)
		  cats (several *Felis*)
		
		2. In Central America
		  flying squirrel (*Glaucomys*)
		  peromyscine mice (*Baiomys,*
		    Reithrodontomys, Pero-
		    myscus)
		  neotomine mice (*Neotoma*)
		  voles (*Microtus*)
		  coyote (*Canis*)
		  cacomistle (*Bassariscus*)
		  skunks (*Mephitis, Spilogale*)
		  **mastodon (Mammutidae)
		  **mammoth (Elephantidae)
		  **rhinoceros (Rhinocerotidae)
		  **Protoceratidae
		  **oreodonts (Merycoidodonti-
		    dae)
		  *bison (Bovidae)

* Extinct in area.
** Extinct in New World.

tion, across the south-central region of what is now the United States, from its congeners in eastern North America and evolved in coexistence with the Middle American Element. Recent dispersals across the Isthmian Link are responsible in Rosen's theory for sympatry among related taxa in lower Central America and northwestern South America.

To summarize: a reanalysis of data for angiosperms and vertebrates indicates that the major distributional pattern outlined for herpetofaunal development forms a repetitive general pattern for all groups except mammals. That angiosperms, freshwater fishes, amphibians and reptiles are congruent in generalized tracks that seem to have originated through the same series of dispersal and vicariance events is remarkable. That the mammal pattern is different is interesting and suggests strongly that mammals of modern type, except for marsupials, were not present in the Americas at the time when the major vicariance event, isolating Middle from South America, took place.
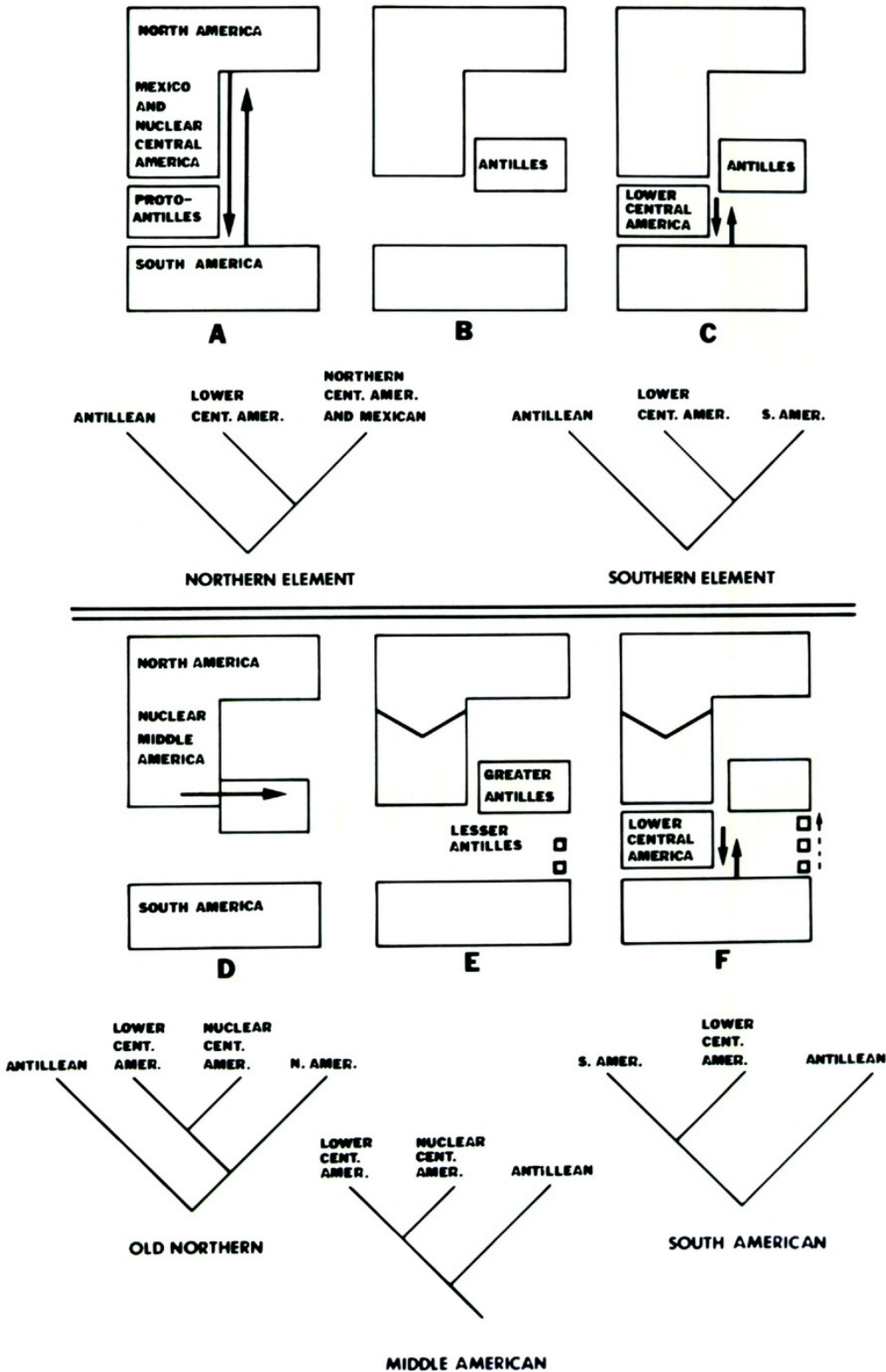
FIGURE 24.   Simplified models of Middle American biogeography. Upper, a vicariance model of Caribbean biogeography, after Rosen (1976); lower, revised model proposed here and described in text. Predicted phylograms for taxa occurring in the indicated areas are indicated below models. Arrows indicate dispersal events.

SPACE, DISPERSAL, VICARIANCE, AND TIME

The first concern of historical biogeography is the search for patterns of phylogenetic relationship that establish connections between biotas in time and space. For the devoted reader who has followed the arguments presented in the preceding sections, it will be a relief and a bemusement to realize that it has taken to this point in the paper to establish the patterns. We may now return to the second concern of biogeography: by what processes were the pattern developed? I wish to state at the outset that I do not believe that it is possible to produce an analysis of process that will explain the distribution of every taxon, nor do I believe that a common distribution pattern is always the product of a single causal event. Neither do I accept *a priori* that the dogma of vicariance or the tenets of revised dispersal theory offer a totally satisfactory means for explaining patterns. Nevertheless, it seems clear that cladistic analysis of relationships for organisms having common distribution patterns can discern repetitive general relationships among areas that will point to common causal events. In general, I expect about 80% of the taxa in a biota to conform to one or the other of several congruent general patterns of phylogenetic-area relationships. These patterns are the ones with common causes that may then be sought in earth and climatic history.

I believe that the account, to this point, has conclusively demonstrated three general patterns of distributional history in Central America. These general patterns require an ancient concordant dispersal event of southern groups into Central America, followed by a major vicariance event that fragmented the original stocks into Middle American and South American units. A second concordant dispersal established northern groups in the region and these groups (and their Middle American associates) were isolated by a second vicariance event from northern congeners. Finally, a late Tertiary reconnection between Central and South America is required to allow for a major dispersal (interchange) of formerly isolated and endemic taxa between the two regions (Figs. 12–15).

These events may be arranged in a chronological order as follows:

Dispersal   I—from south
Vicariance   I—between Central and South America
Dispersal   II—from north
Vicariance II—between tropical Mesoamerica and North America
Dispersal   III—from south

In search for historical processes, the events may be considered in reverse chronological order, since the more recent ones may be less concealed by the modification and distortions produced by time. It is also important to remember that the events cover a range of time, going back to the Cretaceous, when the earliest fossils of almost all the main lineages of amphibians and reptiles in the region make their appearance in the fossil record of North or South America (Table 3). Most of the broad features of Cretaceous to Pliocene historical geology and climate for Middle America have been discussed previously or earlier in the present paper (Savage, 1966; Axelrod, 1975; Bussing, 1976; Rosen, 1978, fig. 15) and the reader is referred to them for background. It is from among these features that the progenetic causes of current patterns will be sought.

Dispersal III is so clearly and unquestionably associated with the emergence of the Isthmian Link in Pliocene that it hardly needs comment. The only question at issue remains the time of the actual final closure of the Bolivar Trough, the most southern and last marine barrier to be uplifted and to complete the land connection. In essence, the Link developed from north to south, beginning in Oligocene, when a series of volcanic islands formed in the Portal Zone. A long narrow peninsula extended continuously from Nuclear Central America to the eastern Panamanian area by late Miocene (Malfait & Dinkelman, 1972). Marshall et al. (1979) claimed that closure was not completed until late Pliocene, about 3 m.y. B.P., on the basis of mammalian fossil correlations. Others (Raven & Axelrod, 1974; Savage, 1974) placed the closure in earliest Miocene, now dated as about 5.7 m.y. B.P.

While the differences in date of closure may be of relatively little importance in the present context, it is significant in any discussion of South American biogeography. The mammal argument is based upon the first appearance of North American groups in temperate zone Argentina, about 3 m.y. B.P. South American groups first appear in the southern United States about 2.5 m.y. B.P. Both United States and Argentine localities are several thousand kilometers from the Isthmian Link. I continue to argue that it would take considerable time for dispersal across the vast intervening areas of tropical America and the diverse ecological settings between the Isthmus and Argentina, Arizona, Texas, or Florida, in order to make possible an occurrence in the fossil record of these places about 3 m.y. B.P. Finally, the records of North American mammal groups, in the late Miocene of Central Panama (Whitmore & Stewart, 1965), further support the idea of closure of the portal at that time to allow 5.7 million years for dispersals across the Isthmus in both directions.

The events of Dispersal II and Vicariance II, which involved dispersal of northern stocks into Middle America and their subsequent disjunction from allied groups in eastern North America and differentiation in isolation, have been reviewed above in several contexts. All evidence (Savage, 1966; Axelrod, 1976; Rosen, 1978) places the dispersal event as prior to Eocene and the vicariance event as associated with mountain building and cooling and drying trends that were instituted in Oligocene. The trends produced a strong climatic barrier of temperate semiarid to arid situations between Middle America and the fragmented northern temperate forest regions by mid-Oligocene (Fig. 2).

Vicariance I seems to be based upon the long isolation of Central and South America prior to the formation of the present Panamanian Isthmus. Evidence from all studied groups, except for placental mammals, strongly supports a relationship between many Middle American stocks and South American taxa, that is prior to and not the result of the most recent dispersal event (III). Dispersal I must have occurred from south to north prior to the differentiation of Middle and South American congeners showing this pattern. The question remains, how did the initial dispersal occur and what event or events led to the fragmentation of Vicariance II?

In 1966, based upon the herpetofaunal evidence and then current ideas on the geology of Central America, I proposed that a Paleocene intercontinental connection existed with South America (Fig. 2). This land connection provided the

route for southern groups to enter Central America (Dispersal I) and its subsidence initiated differentiation (Vicariance I). Most recent geologic studies (Holden & Dietz, 1979; Malfait & Dinkelman, 1972; Ladd, 1976) concur in rejecting any notion of such a connection from early Cretaceous to Pliocene, a time span of over 100,000 m.y.

Rosen (1976) and Duellman (1979) have used the concept of a late Cretaceous-Paleocene series of islands (the proto-Antilles), lying in the region between Nuclear Central America and South America, to explain the distributional phenomena described in this report. Rosen argued for a single concordant dispersal (I) of many southern groups across these islands, which subsequently move eastward with the Caribbean plate to isolate Central and South America (Vicariance I); see Fig. 5. Duellman, on the other hand, advocates numerous dispersals across the proto-Antilles and the later emergent Middle American archipelago, which ultimately became the Isthmian Link. I have dealt, in some detail, with this idea and its rejection in an early section, and so will not repeat it here. Essentially, Rosen's explanation is by vicariance, Duellman's by long-distance dispersal by individual taxa. What concerns us here is not these points, but the reality of the proto-Antilles and their possible role in Dispersal I and Vicariance I.

Pregill (1981), utilizing the data and interpretations of Perfit and Heezen (1978) and a re-reading of Malfait and Dinkelman (1972), concluded that no evidence exists for the presence of any precursors of the Antilles in the Panamanian Portal region at any time. According to this explanation, both Greater and Lesser Antilles are oceanic islands of separate origins and history and cannot be origins significant to the biotic interchanges affecting Middle America. In Pregill's view, as predicted by Patterson (1981) earlier, Rosen's model of vicariance biogeography for the Caribbean, and especially the Antilles, does not stand up to scrutiny in the light of new tectonic and geologic evidence as cited by them and in the earlier section on the nature of this problem in this paper. The result leads to the conclusion that the Panamanian Portal was an open seaway during Paleogene times and only later was a potential dispersal route for island-hopping individual taxa across the Middle American archipelago.

Nevertheless, the evidence of biogeography is incontrovertible in indicating a former ancient continuity between Central and South America, the concordant dispersal (I) of southern groups northward into Central America during this continuity, and the subsequent fragmentation of continuity by a major vicariance event (I). Both dispersal and vicariance obviously occurred prior to Eocene times.

Several groups of earth scientists have proposed alternate configurations of Caribbean geological history that may contribute to resolving this problem. These include traditional (plate-tectonic influenced) workers (Lillegraven et al., 1979; Melville, 1981) and advocates of the expanding earth hypothesis (Owen, 1976; Carey, 1976; Shields, 1979). The first proposed that an archipelago existed from Cretaceous to Eocene that extended from northern Venezuela across the Caribbean Sea to the Nicaraguan Plateau (now submerged) and included the Aves Arc Islands (now submerged) and volcanic islands that were probably the predecessors of the Greater Antilles.

Melville (1981), using the paleomagnetic data from Steinhauser et al. (1972) and Gose and Swartz (1972) rotated the Greater Antilles by about 45° to bring

Cuba and Yucatan into contact and established a continuous connection between Colombia and Central America for Paleocene.

Shields (1979) regarded the Greater Antilles as continental fragments that were originally connected to Nuclear Central American blocks, the Lesser Antilles, and northern South America. In his view, as the Caribbean Sea was formed, beginning in Late Cretaceous (65–75 m.y. B.P.), these several blocks became fractured with the Nicaraguan block and Rise, separating from Venezuela at this time. Separation of the Greater Antilles and Nicaraguan Plateau from one another was probably in Paleocene or even as late as Eocene. Thus, there was a continuous land connection well to the east of the present day Isthmus in late Mesozoic to Paleocene times, which included the Greater Antilles and, possibly, the Lesser Antilles as well. Subsequently, Tertiary events destroyed the connection and further distorted the geographic relations of the insular components into their present configurations.

Coney (1983) in the present symposium argues convincingly for the presence of a proto-Greater Antilles-Aves Arc Island chain lying between Nuclear Central and South America in late Mesozoic-Paleocene time. Subsequently, according to this interpretation, the system moved northeastward, apparently in close proximity to the Guatemala-Yucatan component of Nuclear Central America. The southwestern extension of this system was probably the Aves ridge islands and Cordillera Costeña of northern Venezuela. By Eocene the proto-Greater Antilles had stabilized near their present geographic position with the Lesser Antilles appearing in association with an east-facing subduction zone (Puerto Rican Trench) that began to consume Atlantic Ocean floor. The movement of North and South American plates westward past a nearly stationary Caribbean plate fragmented the Greater Antilles into their present pattern. While this interpretation was not available to me prior to writing the following sections of the present paper, note how well Coney's ideas on Greater Antillean history correspond to the model developed from plant and animal distributions below (Fig. 24).

These references confirm the conflicting ideas concerning the geologic history of the region, but suggest that emerging lines of evidence raise the possibility of a Late Cretaceous-Paleocene land connection between Nuclear Central and South America, lying to the eastward of the present Isthmus. While the evidence for any particular model of the origin and history of such a connection does not seem overwhelming, and since I am unable to evaluate the several conflicting geological interpretations, I will not choose among them. Any of them, however, provides a geographic basis for Dispersal I and Vicariance I.

After reaching this point in the discussion of Central American biogeography, I once again re-evaluated the distributional data to confirm the reality of the patterns and the necessity for a pre-Eocene Dispersal I and Vicariance II to explain them. I was somewhat encouraged by the comments of Melville (1981) that paleontology and plant distributions supported the idea of a Paleocene connection between Central and South America. I was further encouraged by the discovery that Howard's (1973) review of Caribbean plant distributions, which I had overlooked previously, showed patterns similar to those described above for other organisms when generic ranges were studied. He recognized two primary mainland units, a western and a southern continental, that conform closely to the

Middle and South American units, recognized throughout this paper, respectively. After all this, I cannot but conclude that the concordant patterns are generalities requiring explanation and that the explanation requires a pre-Eocene Dispersal I and Vicariance II.

Biogeography, if it is a science, must be able to predict pattern from pattern and estimate process from pattern. In the present case, there remains no recourse but to predict that: 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. Subsidence and reorientation of the components of this connection in late Paleocene were responsible for Vicariance I. Dispersal I occurred across this connection prior to that time. It will be noted that subsidence and distortion of the proposed connection probably occurred from south to north and the final fragmentation involved separation of the Greater Antilles from one another and the other blocks, in early Tertiary.

THE ANTILLES REVISITED, BRIEFLY

When I first began this review of Central American biogeography, it was without any intention of treating the Greater and Lesser Antilles and their relationship to the mainland. My original intention has not been fulfilled for an understanding of the history of the herpetofauna of Central America leads, naturally, to a consideration of Antillean patterns. This is especially so because of Pregill's (1981) critique of Rosen's vicariance model, which attempts to deny the empirical reality of the biotic patterns established above and to invoke a special dispersal theory for the Antilles. Pregill correctly pointed out that some geologic evidence does not support the notion of a proto-Antilles that lay between Nuclear Central America and South America in late Mesozoic-Paleocene times. The presence of these islands and their subsequent movement north and eastward were the cornerstone of Rosen's vicariance model. It was across these stepping-stones that he thought southern taxa had invaded Central America. In addition, because of their relationships to that region and South America, Rosen believed that the northern and southern faunal elements, now found in the Antilles, rode the drifting proto-Antilles as the Caribbean plate moved eastward (Fig. 5 summarizes this model).

Coney (1983) in the present symposium, has effectively countered Pregill's argument and shown that a proto-Greater Antilles-Aves Ridge-northern Venezuela chain of islands doubtless existed in late Mesozoic-Paleocene times. He further demonstrated that this chain lay between the Guatemala-Yucatan portion of Nuclear Central America and northern South America and that the proto-Greater Antilles had a close association with the latter block until middle or late Eocene. He further confirms that the Lesser Antilles are a more recent development of volcanic origin associated with the east-facing subduction zone where Atlantic oceanic crust is consumed along the margin of the Caribbean plate. This interpretation differs from Rosen's (1976) model principally in regarding the Greater

and Lesser Antilles as independent of one another, relating the island chain of Cretaceous-Paleocene times with the Guatemala-Yucatan portion of Central America and having the southern terminus of the arc in what is now Venezuela.

Pregill's other main points against Rosen's proposals are more arguable: 1) that the present fauna of the islands arrived by overwater dispersal from Oligocene onward because many of the Antillean groups are not known prior to that time as fossils in North or South America; 2) that certain major groups, especially of marsupials, carnivores, and ungulate mammals are absent from the islands and unknown as fossils there; a situation that is unlikely, if a land connection or proximate series of islands connected the Antilles to other major land masses; and 3) the current fauna contains remarkably few major (orders, families, and genera) groups and those groups that are present have uneven distributions among islands; again, suggesting overwater dispersal to oceanic islands.

The arguments are all specious. It is clear from accumulating evidence, as emphasized by Rosen (1978), that almost all extant major groups of freshwater fishes, amphibians, and reptiles were present in the Americas by Eocene and that most families go back to Cretaceous. The incomplete fossil record on both the mainland and in the Antilles can only provide us with minimum ages for the presence of groups in these areas and some record of extinctions (Patterson, 1981). It cannot provide direct evidence of mode or time of dispersal, although it may aid in choosing among geological events of different ages that allowed concordant dispersal and created vicariance events. In this regard, I have accepted the view of vicariists that paleogeography and paleoclimatology, not fossils, are arbiters of biogeographic history.

Pregill's second point is also untenable. The absence of groups from the fossil record of an area, especially a lowland tropical one, tells us very little about the history of its biota. There are no fossil records in Central America of marsupials, bats, primates, non-caviomorph rodents, most families of carnivores and ungulates, and almost all families of amphibians and reptiles that occur there today. Does this mean that none of these groups occurred there until very recently? Or tell us at what time they appeared in the region? There are hardly any records of fossil vertebrates from tropical South America, including most families present there today. Does this mean that the missing groups were absent from the region?

In regard to Pregill's final point, it is obvious that the present fauna of the Antilles is not a full-fledged continental one and that some groups may have arrived relatively recently by overwater dispersal. It must also be noted that there is a record of extensive late Pleistocene to Holocene extinctions for the Antilles in which primates and edentates died out along with many other forms (Simpson, 1956; Pregill, 1981). Earlier extinctions cannot, of course, be ruled out as a factor in contributing to the unbalanced nature of the biota, and I must conclude that neither the current decimated fauna nor the fossil record conclusively require a special dispersal theory as proposed by Pregill. He follows the time-honored procedures of conventional biogeography: 1) recognize an individual pattern, 2) elaborate a process (in this case, special dispersal), 3) use the process to explain the pattern, and 4) extend the process to explain other similar patterns (each dispersal by individual taxa).

The vicariance approach, on the other hand, 1) recognizes an individual pat-

tern of phylogenetic-area relationships (Fig. 7), 2) hypothesizes a process, 3) tests the hypothesis with more analyses of phylogenetic-area relationships, 4) accepts or revises the hypothesis, and 5) tests it again with additional phylogenetic-area relationships. This approach is the one advocated by Rosen (1976) and used to test his vicariance model for the Caribbean (Fig. 24). Since the lynchpin of that theory was the proto-Antilles hypothesis and that hypothesis has proven unsound, a brief review of an alternate explanation seems in order.

As discussed in a previous section, Rosen's grouping of the Middle American and South American units of this report on a single track (the South American-Caribbean) and his failure to place the so-called Gondwanian component of his northern track as separate from the Laurasian component obscured the discreteness of the three principal units recognized for Central America, in the present account. Once these units (tracks) have been clearly defined (Figs. 12–14), a coherent explanation of Antillean biogeography emerges (Fig. 24).

Whether or not the Greater Antilles were involved in a land connection between Central and South America, in Cretaceous or Paleocene, it is clear from the geologic evidence cited above that they or their precursors were closely proximate to the Nicaraguan region in early Tertiary, if not physically continuous with it. Volcanic activity, initiated in Cretaceous, was extensive across the region and partially distorts any interpretation of succeeding events. This proximity would allow for the dispersal of Middle American Element taxa onto the peripheral continental fragments that became the Greater Antilles. A few North American Element taxa also reached the Greater Antilles at about the same time, possibly in the Eocene (Shields, 1979), when the Central American component became associated with Middle American taxa on the mainland. These events would explain the closer biotic relationship between the western Greater Antilles, particularly Cuba, and North and Middle America, commented on by Rosen (1976). Subsequently, the several Greater Antillean blocks, including the Nicaragua Rise and Cayman Ridge, were separated or further removed (about 200 km eastward) from proximity to the Nuclear Central American region and affected by the events described by Pregill (1981), as interpreted from Perfit and Heezen (1978), for the post-Oligocene time-frame.

Whatever their possible role in any postulated late Mesozoic-early Tertiary land bridge or archipelago in the region between Central and South America, the Lesser Antilles seem to have had a separate history from the Greater Antilles for most of Tertiary (Malfait & Dinkelman, 1972). The islands are a mostly volcanic arc associated with the zone where Atlantic oceanic crust subducts under the Caribbean plate. As such, they were preceded by the late Cretaceous-Paleogene Aves Arc Islands that originally lay 200 km westward, and that marked an earlier boundary position of the eastward moving Caribbean plate. Dispersal from South America onto the Aves Arc, and then across subsiding stepping stones onto the present Lesser Antilles, as proposed by Rosen and supported by Pregill's discussion, explains the presence of predominately southern groups in these islands.

This model also explains why no northern stocks reached South America in early Tertiary. They simply were not yet in Nuclear Central America. Thus, it avoids the problem of one-way dispersal from south to north required by Rosen's confusion of Middle American and Old Northern Elements on his North Amer-

ican-Caribbean track and his failure to separate Middle American and South American Element tracks from one another. It in no way affects the following conclusions: 1) the Lesser Antilles have been populated by overwater dispersal from the south; 2) the Greater Antilles received the nucleus of their herpetofauna by a single concordant dispersal event from Central America by both Old Northern and Middle American taxa; and 3) other groups of organisms show a similar set of general patterns.

The model described above (Fig. 24) forms my hypothesis of the process responsible for the history of the Caribbean biota. It explains the failure of Old Northern taxa to reach South America early in Tertiary, the presence of Old Northern taxa in the Greater Antilles, the differences between the biotas of the Greater and Lesser Antilles, and the great similarity of the Cuban biota to that of Nuclear Central America. Further, it predicts that 1) the Greater Antillean biota, especially that of Cuba, is older than the lower Central American biota; 2) the Lesser Antilles biota is mostly derived from South American groups and is relatively older than South American representatives in the lower Central American biota; 3) some components of the Greater Antillean biota (Middle American unit) are equal in age to that of Nuclear Central American sister taxa, but younger than their sister groups in South America; and 4) some components of the Greater Antillean biota (Old Northern unit) are older than Nuclear Central American sister taxa, but are equal in age to their sister groups in North America. In other words, if a monophyletic group shows a vicariance pattern in the region, lower Central American taxa will show greater affinity to mainland taxa to the north or south than to Antillean taxa. Greater Antillean taxa will be found to be most closely related to Nuclear Central American taxa or these taxa plus their lower Central American sister groups (Middle American unit) or to North American taxa (Old Northern unit) and their Middle American sister groups. Lesser Antillean taxa will be found to be most closely related to South American taxa or these taxa and their lower Central American sister groups. Comparison of these sets of predicted relationships with Rosen's model summarizes the different concepts (Fig. 24). Predicted cladograms of phylogenetic relationships are included as well.

A review of the cladograms presented by Rosen (1976; fig. 21) is included for comparison with the revised model (Fig. 25). Additional data that aid in evaluating the figures include: A, the closest ally of *Lepisosteus tristoechus* is *L. spatula* of the southeastern United States, but recently discovered to have a disjunct population in lower Central America as well (Wiley, 1976), which, if added to the cladogram, conforms to the proposed model for Old Northern forms. D and E involve cases with an eastern North American form of Central American and/or Antillean affinities, so that the cladograms alone will not resolve their geographic relationships from those of the Old Northerners; since we now know that these groups are anciently related to southern stocks and are part of the Middle American unit, they should fit the Middle American cladogram; D may, E does not, suggesting a possible dispersal event. F appears to conform to a cladogram indicating the ancient interrelationship of a Mesozoic-Paleocene neotropical fauna (Fig. 18) and is compatible with the cladogram for Middle American Element groups (these, too, would ultimately have a South American sister group). The other cladograms (B, C, G) agree with the one for the Middle American unit.
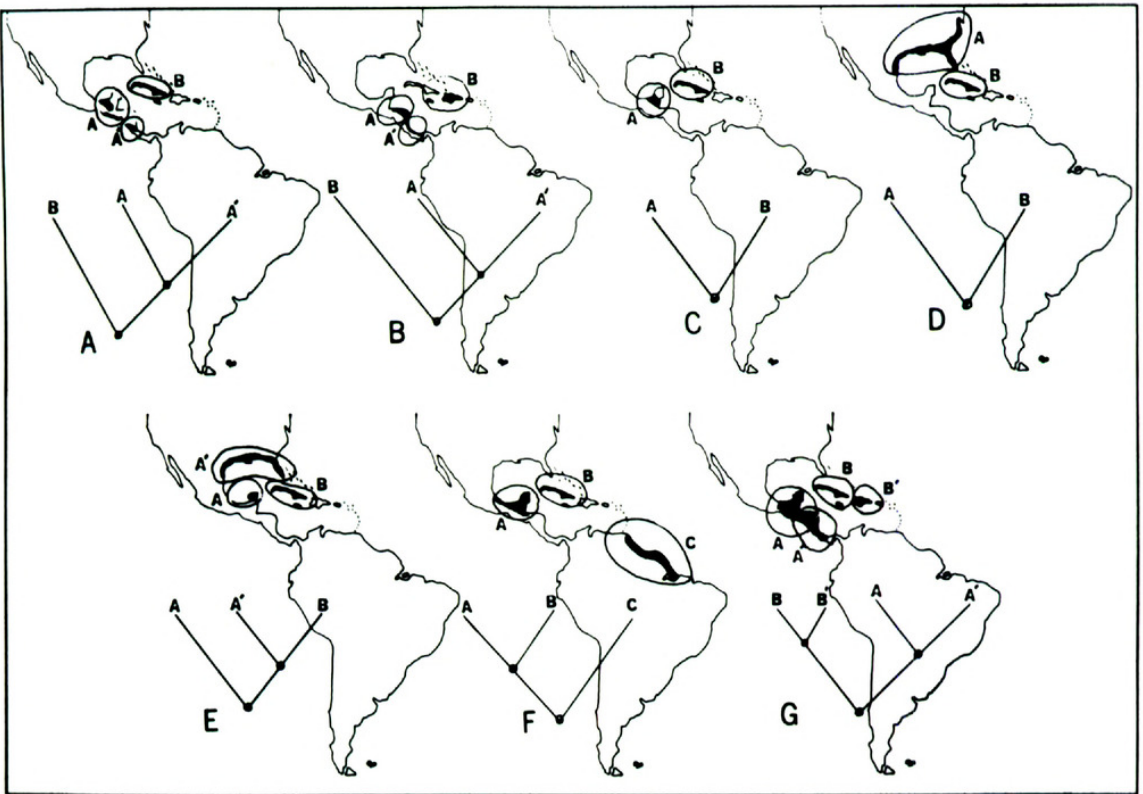
FIGURE 25.   Phylograms of taxa used by Rosen (1976) in support of his vicariance model. A, garfishes, genus *Lepisosteus*; B, viviparous tooth-carps, *Gambusia nicaraguensis* group; C, vivipa-rous tooth-carps, tribe Girardini; D, killifishes, genera *Lucania* and *Cubanichthys*; E, killifishes, genus *Fundulus*; F, the synbranchid eel, *Ophisternon*; G, cichlid fishes, genus *Cichlasoma (Parapetenia)*. See text for revised interpretation of phylograms in relation to biogeography model in Fig. 24 (lower).

It appears from these examples that the model (Fig. 24) has considerable predictive value, explains the patterns and cladograms established by Rosen (1976), and avoids the necessity for positing a pan-Antillean archipelago in the history of the Greater Antilles. It, moreover, predicts that the nucleus of the Greater Antillean biota was present in those areas at least by late Eocene and probably sooner and confirms Rosen's (1978) insight that the observed biological patterns for the region have developed over a great time span, involving geologic events of at least the last 80 million years. Additional testing of the model requires cladistic analysis of the phylogenies of other taxa, especially those with relatives in all five areas, North America, Nuclear Central America, the Greater Antilles, South America, and the Lesser Antilles.

DISPERSALS, VICARIANCE, AND TIME

From the previous review of biogeographic pattern and the paragraphs above, it must now be clear that concordant dispersal and vicariance are two facets of the same process. It is not possible to have one without the other. For example, when the Panamanian Portal was removed as a barrier to terrestrial dispersal and became a land bridge between the Americas, the emergent Isthmian Link became, in turn, a barrier, vicariating the formerly continuous Caribbean-Eastern Pacific

biota. Dispersal to produce a generalized marine biota preceded the vicariant event. Vicariance in Middle and South America preceded the dispersal events that have taken place across the Isthmian Link to produce the great American interchange. The recognition of this point makes much of the argument between dispersal and vicariance biogeography moot.

If we may, then, rephrase the statements of biogeographic principle contrasted earlier (pp. 489–493), it may be possible to provide a basis for a biogeography that combines the best attributes of both approaches.

1–2. Concordant dispersal of many groups at about the same time is followed by vicariance to produce patterns.

3. Generalized source areas = centers of origin (i.e. Gondwanian, South American, Laurasian) may be estimated from track directionality.

4. Directionality of major dispersals may be estimated from generalized tracks, phylogenetic relationships, and paleogeologic and paleoclimatic relations.

5–6. Fossils provide evidence of extinctions, give minimum ages of occupation of areas, and permit a choice among geologic or climatic events of different ages as possible causes of biotic interrelationships.

7. Discovery of new fossils contributes data for testing biogeographic theory by adding new taxa for phylogenetic area analyses.

8. Relative age of groups (times of origin) important in explanation; fossils and their cladistic analysis contribute to estimating age.

9. Ecologic valence and associations relatively insignificant because they are epigenetic and correlate with present ecological and physiographic features (i.e. they are recent epigenetic modifiers of pattern); phylogenetic interrelationships and their relations to geography (past and present) crucial.

10. Concordant dispersal establishes basic pattern, then vicariance fragments continuity and allows differentiation of components of the pattern; random, long-distance, or multiple dispersals by individual taxa produce no repetitive patterns that can be tested.

11. Generally, allopatry indicates vicariance, and sympatry suggests vicariance followed by dispersal; parapatry and some sympatry suggests differentiation *in situ* by genetic means not associated with geographic or climatic barriers; at the time scale of most historical biogeographic studies, the latter events are unimportant.

12. The primary interest in historical biogeography is with progenetic processes.

13. Geologic evidence speaks for itself; continental drift must account for substantial and profound aspects of present patterns.

14. Both concordant dispersal and vicariance involved in patterns and process; plate movements and other geologic and climatic events that create and/or remove barriers contribute to pattern.

15. Individual taxa may show different patterns because of age; i.e. mammal and bird patterns not affected by the initial break-up of Pangaea while fishes, amphibians, and reptiles were.

16. Major patterns represent ancient disjunctions, other patterns represent more recent events; most major groups studied in terrestrial biogeography were present in Mesozoic or early Tertiary and progenetic events producing patterns occurred long before Quaternary.

17. Components (nodes) within tracks reflect the number of vicariance events usually produced by one concordant dispersal event.

18. Hypothesis tested by adding additional tracks, but only in a correlative way.

19. Lack of conformity with a well-documented generalized track suggests: a) the individual track belongs to another generalized track; b) it represents an independent dispersal; c) it is based upon a non-monophyletic group.

20. Hypotheses compared to earth's history to confirm correlations with opportunity for concordant dispersals and geologic and climatic vicariance events.

21. Predicts geologic and/or climatic history.

22. Predicts patterns for unstudied groups of approximately same geologic age; components of older groups may have patterns similar to those found in younger groups.

23. No prior judgement of former history of dispersals or geologic age of distributional events; these are discovered in a cladistic analysis.

24. A preferred method of analysis involves construction of cladograms of area interrelationships from cladograms of phylogenetic relationships (Fig. 7); a hypothesis of process is then constructed from paleogeologic and/or paleoclimatic evidence to conform with the area cladogram; the hypothesis is then tested (Fig. 24) by comparison of the phylogenetic relations for additional groups (Rosen, 1978; Platnick & Nelson, 1978; Morse & White, 1979; Patterson, 1981).

25. These approaches do not, by themselves, distinguish between concordant dispersal and vicariance, since they are so intimately interrelated, it does, however, provide a clear testable hypothesis of area interrelations, which usually will separate long-distance dispersal by individual taxa out from major pattern; knowledge of paleogeology and paleoclimatology may then aid in choosing among alternative dispersal and vicariance sequences and events.

In summary (Fig. 26), biogeographic patterns are produced by: 1) an initial concordant dispersal that establishes what much later may be recognized as a generalized track; 2) followed by the development of geographic or climatic barriers that fragment the original biotas into component parts (component nodes); 3) the vicariance events produced by barrier formation allow for differentiation
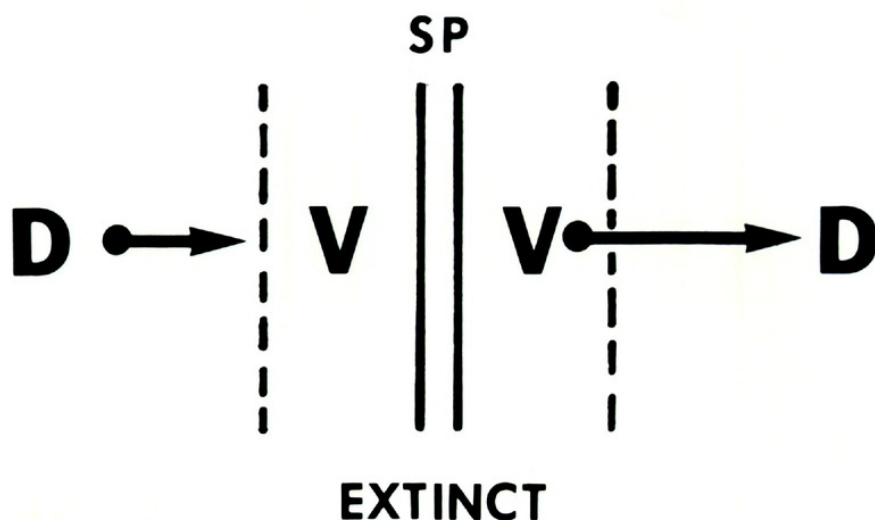
SP

EXTINCT

FIGURE 26.   The biogeographic cycle: pattern produced through interaction of concordant dispersal (D), vicariance (V), differential differentiation (SP), and differential extinction (D). Dotted lines indicate barriers that arose after first dispersal (left) or became ineffective (right) to allow second dispersal. Solid lines represent a continuing barrier that fragmented original stock into two.

of the components; 4) with time, endemic vicariant biotas are formed and their composition becomes molded by differential rates of evolution (initially by speciation) and by differential extinction; and 5) when the barriers are removed or loosened, concordant dispersal will occur again.

While cladistic analyses of phylogenetic-area relationships may provide substantial insight into biogeographic history, the effects of differential rates of evolution, differential extinctions, and subsequent dispersal will cloud the underlying sharpness of pattern produced by the key vicariance events. A final factor that reduces refinement of the pattern is that of time. Ancient patterns can only be ascertained from ancient groups; more recently evolved lineages will have their patterns correlated with more recent events in earth history.

In terms of Central American biogeography, each of the pattern-producing processes summarized above may be recognized: Dispersal I and II from South America and North America, respectively; Vicariance I and II to isolate the Middle American area and its northern and southern derived components; differentiation of the latter *in situ* while vicariant relatives in South America and eastern North America also underwent differentiation and differential extinction; and finally, Dispersal III from South America across the Isthmian Link from early Pliocene onward. In addition, as predicted, the patterns for those ancient major groups, angiosperms, fishes, amphibians, and reptiles (well-differentiated in Mesozoic), confirm the biogeographic history for Cretaceous to Recent. On the other hand, placental mammals (and probably birds), which did not undergo differentiation until into Tertiary times, reveal only the later elements of the story.

The biogeography of the Central American region is now understood in broad outlines.

The processes responsible for its development, the interplay between earth and climatic history and the concordant dispersal and subsequent vicariance of its biota, modified by differential rates of evolution and extinction and the time

of differentiation of major taxa, are also recognizable and may be tested by future cladistic analyses of interrelationship. It seems almost trite to state that this report concurs with the single major tenet of dispersal *and* vicariance biogeography, that the former process produces widespread biotas, which are subsequently fragmented by the latter process into the highly subdivided fractions seen today.

One problem remains, the nature of the geologic event that produced Dispersal I, which, when followed by Vicariance I (obviously, the formation of a marine barrier in the Panamanian region) led to the observed differentiation of Middle American from South American units. Everything in the biotic history of Central America, except the too recently differentiated mammals, demands a land connection or its equivalent, a series of closely proximate islands between Central and South America in late Cretaceous-Paleocene. Geologic evidence for such a connection is absent or ambiguous, as discussed above. Still, it seems that if the tenets of scientific biogeography are sound, then biotic data can predict previously unrecognized geologic patterns. In essence, when in doubt, it is best to let the biota tell one what has occurred. If it is agreed that the fossil record is incomplete, then fossils cannot decisively contradict evidence from Recent distributions (Patterson, 1981) and it follows that if the geologic record is inconclusive, or ambiguous, it cannot contradict the evidence from Recent and past distributions. While it remains tempting to support the argument for the presence of the Cretaceous-Paleocene land connection by manipulating conflicting geologic evidence, especially that from the expanding earth school (Owen, 1976; Carey, 1976; Shields, 1979), I eschew any further attempt to locate the proposed structure. The organisms speak for themselves. Their distributions require the presence of a late Cretaceous-Paleocene intercontinental connection to explain the interrelationships of the biotas of Central and South America and the Greater Antilles (Fig. 24). The biological evidence stands as a challenge to geologists and other biogeographers who doubtless will wish to invalidate the hypothesis. If they undertake that task, it is incumbent upon them to provide a better explanation than mine, based upon a full evaluation of the evidence. I remain convinced that further studies will only enhance the explanatory power of the proposed model and will ultimately confirm the reality of the predicted early intercontinental connection. Hopefully, this challenge will stimulate a resurgence of interest in the biology and geology of the Central American region and that resurgence may lead to a concrete solution of the problem. Until then, I rest my case!

LITERATURE CITED

AXELROD, D. I. 1975. Evolution and biogeography of Madrean-Tethyan sclerophyll vegetation. Ann. Missouri Bot. Gard. 62(2): 280–334.

BALL, I. R. 1976. Nature and formulation of biogeographic hypotheses. Syst. Zool. 24(4): 407–430.

BOWIN, C. 1976. Caribbean gravity field and plate tectonics. Special Pap. Geol. Soc. Amer. 169: 1–79.

BRUNDIN, L. Z. 1972. Phylogenetics and systematics. Syst. Zool. 21: 69–79.

———. 1981. Croizat's panbiogeography versus phylogenetic biogeography. *In* G. Nelson & D. E. Rosen (editors), Vicariance Biogeography: A Critique. Columbia Univ. Press, New York (3): 94–138.

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 (editor), Investigations of the Ichthyofauna of Nicaraguan Lakes. Univ. Nebraska (10): 157.

CAREY, S. W. 1976. The Expanding Earth. Elsevier, Amsterdam, Dev. in Geotectonics 10: 1–488.

CHRISTOFFERSON, E. 1976. Colombian Basin magnetism and Caribbean plate tectonics. Bull. Geol. Soc. Amer. 87: 1255–1258.

CODY, M. L. & J. M. DIAMOND (editors). 1975. Ecology and Evolution of Communities. Harvard Univ. Press, Cambridge. 545 pp.

CONEY, P. J. 1983. Plate tectonic constraints on biogeographic connections between North and South America. Ann. Missouri Bot. Garden 69: 432–443.

CROIZAT, L. 1976. Biogeografia analitica y sintetica ("Panbiogeographia") de las Americas. Bibliog. Acad. Cien. Fis. Mat. Nat. (Caracas) 15–16: 1–890.

———, G. NELSON & D. E. ROSEN. 1974. Centers of origin and related concepts. Syst. Zool. 23: 265–287.

DARLINGTON, P. J. 1957. Zoogeography: The Geographical Distribution of Animals. John Wiley, New York. 675 pp.

DARWIN, C. R. 1859. On the Origin of Species by Means of Natural Selection. J. Murray, London. 440 pp.

DENGO, G. 1968. Estructura geologica, historia tectonica y morfologia de America Central. Cent. Reg. Ayuda Tecn. (AID): 1–50.

———. 1973. Estructura geologia, historia tectonica y morfologia de America Central, ed. 2. Reg. Ayuda Tecn. (AID): 1–52.

DIETZ, R. S. & J. C. HOLDEN. 1970. Reconstruction of Pangaea: breakup and dispersion of continents, Permian to present. J. Geophys. Res. 75: 4939–4956.

DUELLMAN, W. E. 1966. The Central American herpetofauna: an ecology perspective. Copeia 1966: 700–719.

———. 1970. The hylid frogs of Middle America. Mus. Nat. Hist. Univ. Kansas Monogr. 1(2 vols.): xii–754.

———. 1979. The South American herpetofauna: a panoramic view. Mus. Nat. Hist. Univ. Kansas Monogr. 7: 1–28.

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.

GOSE, W. A. & D. G. SWARTZ. 1977. Paleomagnetic results from Cretaceous sediments in Honduras: tectonic implications. Geology (Boulder) 5: 505–508.

HAFFER, J. 1981. Quaternary biogeography of tropical lowland South America. Mus. Nat. Hist. Univ. Kansas Monogr. 7: 107–140.

HENDERSON, R. W. & L. G. HOEVERS. 1975. A checklist and key to the amphibians and reptiles of Belize, Central America. Milwaukee Public Mus. Contr. Biol. Geol. 5: 1–63.

HENNIG, W. 1966. Phylogenetic Systematics. Univ. Illinois Press. 263 pp.

HERSHKOVITZ, P. 1966. Mice, land bridges and Latin American faunal interchange. Pp. 725–751 in R. Wenzel & V. J. Tipton (editors), Ectoparasites of Panama. Field Mus. Nat. Hist.

———. 1969. The recent mammals of the Neotropical Region. Quart. Rev. Biol. 44: 1–70.

HEY, R., G. L. JOHNSON & A. LOWRIE. 1977. Recent plate motions in the Galapagos area. Bull. Geol. Soc. Amer. 88: 1385–1403.

HOLDEN, J. C. & R. S. DIETZ. 1972. Galapagos Gore, NazCoPac Triple Junction and Carnegie/ Cocos Ridges. Nature 235: 266–269.

HOWARD, R. A. 1973. The vegetation of the Antilles. In A. Graham (editor), Vegetation and Vegetational History of Northern Latin America. Elsevier, Amsterdam 1: 1–59.

KEAST, A. 1977. Zoogeography and phylogeny: the theoretical background and methodology to the analysis of mammal and bird faunas. Pp. 249–312 in M. K. Hecht, P. C. Goody & B. M. Hecht, editors, Major Patterns of Vertebrate Evolution. Plenum Press, New York and London.

LADD, J. W. 1976. Relative motion of South America with respect to North America and Caribbean tectonics. Bull. Geol. Soc. Amer. 87: 967–976.

LEE, J. C. 1980. An ecogeographic analysis of the herpetofauna of the Yucatan Peninsula. Misc. Publ. Mus. Nat. Hist. Univ. Kansas 67: 1–75.

LILLEGRAVEN, J. A., M. J. KRAUS & T. M. BROWN. 1979. Paleogeography of the world of the Mesozoic. Pp. 277–308 in J. A. Lillegraven, Z. Kielan-Jaworoska & W. A. Clemmens (editors), Mesozoic Mammals—The First Two-thirds of Mammalian History. Univ. Calif. Press, Berkeley.

LONDSDALE, P. & K. D. KLITGORD. 1978. Structure and tectonic history of the eastern Panama Basin. Bull. Geol. Soc. Amer. 89: 981–999.

MACARTHUR, R. H. & E. O. WILSON. 1967. The theory of island biogeography. Monogr. Pop. Biol. Princeton 1: 1–203.

MALFAIT, B. T. & M. G. DINKELMAN. 1972. Circum-Caribbean tectonic and igneous activity and the evolution of the Caribbean plate. Bull. Geol. Soc. Amer. 83: 251–272.

MARSHALL, L. G., R. F. BUTLER, R. E. DRAKE, G. H. CURTIS & R. H. TEDFORD. 1979. Calibration of the Great American Interchange. Science 204: 272–279.

————, D. G. WEBB, J. J. SEPKOSKI, JR. & D. M. RAUP. 1982. Mammalian evolution and the Great American Interchange. Science 215: 1351–1357.

MARTIN, M. 1972. A biogeographic analysis of the freshwater fishes of Honduras. Ph.D. Dissertation, Univ. So. Calif. 598 pp.

MATTHEW, W. D. 1915. Climate and evolution. Ann. New York Acad. Sci. 24: 171–318.

McDOWELL, R. M. 1978. Generalized tracks and dispersal biogeography. Syst. Zool. 27: 88–104.

MELVILLE, R. 1981. Vicarious plant distributions and paleogeography of the Pacific region. Pp. 238–273 in G. Nelson & D. E. Rosen (editors), Vicariance Biogeography: A Critique. Columbia Univ. Press, New York.

MEYER, J. R. & L. D. WILSON. 1971. A distributional checklist of the amphibians of Honduras. Los Angeles County Mus. Contr. Sci. 218: 1–47.

———— & ————. 1973. A distributional checklist of the turtles, crocodilians and lizards of Honduras. Los Angeles County Mus. Contr. Sci. 244: 1–39.

MILLER, R. R. 1966. Geographical distribution of Central American freshwater fishes. Copeia 1966: 773–802.

MORSE, J. C. & D. F. WHITE, JR. 1979. A technique for analysis of historical biogeography and other characters in comparative biology. Syst. Zool. 28: 356–365.

MÜLLER, P. 1973. The dispersal centres of terrestrial vertebrates in the Neotropical Realm. Biogeographica 2: 1–244.

NELSON, G. 1973. Comments on Leon Croizat's biogeography. Syst. Zool. 22: 312–320.

————. 1975. Historical biogeography: an alternate formalization. Syst. Zool. 23: 555–558.

————. 1977. Review of Biogeographia analitica y sintetica ("Panbiogeografia") de las Americas, by Leon Croizat. Syst. Zool. 26: 449–452.

————. 1978. From Candolle to Croizat: comments on historical biogeography. Syst. Zool. 11: 269–305.

———— & N. I. PLATNICK. 1978. The perils of plesiomorphy: widespread taxa, dispersal and phenetic biogeography. Syst. Zool. 27: 474–477.

———— & ————. 1981. Systematics and Biogeography. Columbia Univ. Press, New York. 567 pp.

———— & D. E. ROSEN (editors). 1981. Vicariance Biogeography: A Critique. Columbia Univ. Press, New York. 593 pp.

OWEN, H. G. 1976. Continental displacement and expansion of the earth during the Mesozoic and Cenozoic. Philos. Trans. 281(A): 223–291.

PARENTI, L. R. 1981. Discussion of C. Patterson, Methods of paleobiogeography. Pp 490–497 in Vicariance Biogeography: A Critique. Columbia Univ. Press, New York.

PATTERSON, B. & R. PASCUAL. 1968. The fossil mammal fauna of South America. Quart. Rev. Biol. 43: 409–451.

PATTERSON, C. 1981. Methods of paleogeography. Pp. 446–489 in G. Nelson & D. E. Rosen (editors), Vicariance Biogeography: A Critique. Columbia Univ. Press, New York.

PERFIT, M. R. & B. C. HEEZEN. 1978. The geology and evolution of the Cayman Trench. Bull. Geol. Soc. Amer. 89: 1155–1174.

PIELOU, E. C. 1981. Crosscurrents in biogeography. Science 213: 324–325.

PLATNICK, N. I. & G. NELSON. 1978. A method of analysis for historical biogeography. Syst. Zool. 27: 1–16.

PREGILL, G. K. 1981. An appraisal of the vicariance hypothesis of Caribbean biogeography and its application to West Indian terrestrial vertebrates. Syst. Zool. 30: 147–155.

RAVEN, P. H. & D. I. AXELROD. 1974. Angiosperm biogeography and past continental movements. Ann. Missouri Bot. Gard. 61: 539–673.

ROSEN, D. E. 1976. A vicariance model of Caribbean biogeography. Syst. Zool. 24: 431–464.

————. 1978. Vicariant patterns and historical explanation in biogeography. Syst. Zool. 27: 159–188.

SAVAGE, J. M. 1960. Evolution of a peninsular herpetofauna. Syst. Zool. 9: 184–212.

————. 1966. The origins and history of the Central American herpetofauna. Copeia 1966: 719–766.

————. 1973. The geographic distribution of frogs: patterns and predictions. In J. L. Vial, editor, Evolutionary Biology of the Anura. Univ. Missouri Press, 13: 349–445.

————. 1974. The Isthmian Link and the evolution of neotropical mammals. Los Angeles County Mus. Contr. Sci. 260: 1–51.

————. 1980a. A Preliminary Handlist of the Herpetofauna of Costa Rica, 3rd ed. Hancock Foundation, Univ. South Calif. 21 pp.

————. 1980b. A Handlist with Preliminary Keys to the Herpetofauna of Costa Rica. Hancock Foundation, Univ. South. Calif. 111 pp.

SHIELDS, O. 1979. Evidence for initial opening of the Pacific Ocean in the Jurassic. Palaeogeogr. Palaeoclimatol. Palaeoecol. 26: 181–220.