

Northwestern, Cordillera Central, and Atlantic Lowland areas: 22, 13, and 13%, respectively. The Southwestern area has a lower but essentially equal value, 10%. The absence of endemics from the two Meseta Central faunal areas suggests that their recognition as discrete units is suspect.

GENERAL PATTERNS

The analysis above indicates that three general patterns of distribution reflect different histories for groups in the faunal areas. It should not be surprising that the autochthonous Middle American Element and Central American Component are major contributors to most of these faunas. The robust representation of South American Element taxa emphasizes the role of the isthmian region as an area of fairly recent, geologically speaking, mixing of tropical Middle American and South American biotas.

The three patterns are as follows:

- I. Faunal areas in which a combination of Middle American and South American elements make up 65% or more of the herpetofauna (SW, A)
- II. Faunal areas in which a combination of Middle American Element and Central American Component taxa make up 65% or more of their composition, with Middle American genera predominating (PS, AS, CC)
- III. A faunal area where Middle American Element and Central American component genera are nearly equal in contribution (NW)

The areas constituting the Meseta Central Occidental and Meseta Central Oriental are anomalous as the only putative areas in which Central American genera (40:30%) substantially outnumber Middle American (30:28%) ones. They also resemble the NW area in having relatively low numbers of South American Element representatives.

The Cordillera de Talamanca area is unique and ambiguous as to placement, since it could be referred to pattern I (MA = 43% + SA = 28% = 71%) or pattern II (MA = 43% + CA = 23% = 66%).

The degree of species endemism within these areas sheds further light on the situation. The high degree of endemism combined with its unique combination of taxa strongly suggests a long-term isolation of the NW fauna from the others. The relatively high level of endemism in SW, A, and CT faunal areas seems to indicate separate histories within a single pattern (I).

Within pattern II, there appears to be no basis for separating out PS and AS as distinctive faunal areas, since they are similar in generic composition and proportional representation of historical units. The Cordillera Central is not supported as a separate faunal area but appears to be at one end of a gradient in historical unit contributions from

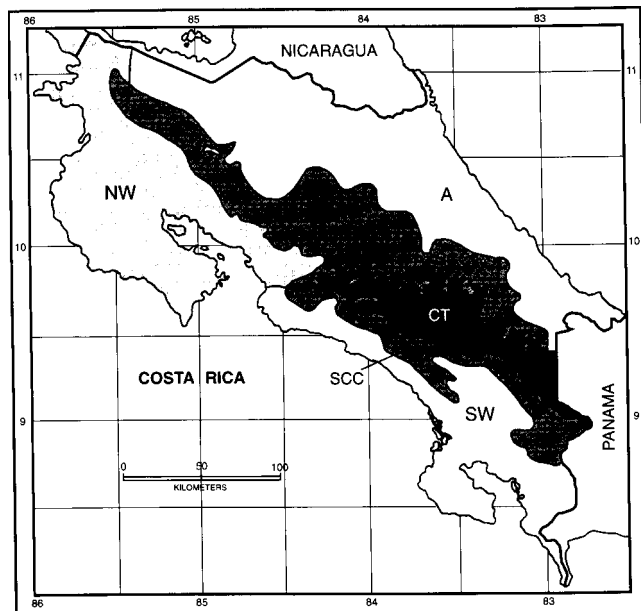


Figure 15.7. Faunal areas for the Costa Rican herpetofauna.

PS + AS + MOC - MOC - CC. If PS + AS + CC are combined the level of species endemism is 15%, similar to that for other recognizable faunal areas.

The Meseta Central Occidental (MOC) and Meseta Central Oriental (MOR) have no endemic species and most closely resemble NW in generic composition. As Scott (1969) pointed out long ago, they appear to form a geographic transitional area between patterns III (MA = 34% + CA = 36% = 70%) and II, that is, the NW and upland areas. The Meseta Central Occidental more closely resembles the Northwest region in proportions of historical contributions (MA = 30% + CA = 40% = 70%) and the Meseta Central Oriental (MA = 28% + CA = 38% = 66%) the uplands (PS = AS + CC): an balance both Meseta faunas are best regarded as part of the Upland Fauna because of the greater similarity in generic composition compared with that of the Northwestern region.

In summary, the following discrete recognizable faunal areas (fig. 15.7) appear to have had separate histories and are the biogeographic areas whose history will be traced in chapter 16:

- Lowland
- Pacific Northwest (NW)
 - Southwest (SW)
 - Atlantic (A)
- Upland/Highland
- Montane Slopes and Cordillera Central (SCC)
 - Highland
 - Cordillera de Talamanca (CT)

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Development of the Herpetofauna

CENTRAL AMERICA as a land-positive region has a long and complex geologic and climatological history spanning some 90 million years from the Late Cretaceous to the present (fig. 16.1). To explain the evolution of the Costa Rican herpetofauna it is first necessary to describe something of this broader history in order to establish the context. The following paragraphs highlight the most important events in earth's history that shaped the region and in turn are responsible for the patterns of distribution described in chapters 14 and 15.

PALEOGEOGRAPHIC BACKGROUND

Mobile Plates, Blocks, and Island Arcs

Among the most exciting scientific discoveries of the second half of the nineteenth century was the realization that the earth's outer layer consists of a number of rigid, mobile plates riding on a deeper elastic, nearly liquid plastic layer. The plates underlying the oceans are about 65 km deep, and those making up the continents are as deep as 140 km (box 16.1). The uppermost portion of the plates forms the earth's rocklike crust. Oceanic crust is very dense, highly magnetized, and relatively thin, about 5 km thick. Continental crust is much lighter, less magnetized, and much thicker than oceanic crust—about 35 to 40 km thick. The two kinds of crust are also composed of different kinds of rocks. In the course of geologic history continental and oceanic crust have maintained their integrity, and interactions between the various plates at their boundaries produced many of the most prominent features of the earth's geography. In addition, the plates have not remained static in position through time; in the Permian what we now recognize as continents formed a single continent, Pangaea, whose constituent plates have separated and drifted apart over the intervening 225 million years.

The geography of Central America is the result of a complex geologic development over the past 75 million years involving the interactions of five of these mobile tectonic plates (fig. 16.2). The current structure of the land portions of the area consists of four primary crustal blocks:

1. Mayan block: mostly continental crust with its southern border at the Motagua fault system in Guatemala

2. Chortis block: mostly continental crust with its southern boundary at the Santa Elena fault in northern Costa Rica
3. Chorotega block: accretionary crust, with its southeastern border at the Gattin fault
4. Chocö block: accretionary crust with its boundary with the South American plate at the Romerol fault

The Mayan, Chortis, and Chorotega blocks are bordered on the Pacific margins by the Middle American trench, where oceanic crust is being subducted under the lighter continental and accretionary crust. The Chocö block is similarly bordered on the Pacific by the Colombia trench subduction zone (box 16.2). It should be noted that before about 25 million years ago (Ma) the Cocos and Nazca plates were part of the Farallon plate (Atwater 1989).

The following paragraphs and accompanying figures (figs. 16.3 to 16.6) present a summary of the major geologic events affecting the origins of the extant herpetofauna, based primarily on a synthesis of data from Coates and Obando (1996), Donnelly et al. (1990), Escalante (1990), Frisch, Meschede, and Sick (1992), Kerr and Iturralde (1999), Lucas (1986), Mann (1995), Marshall and Sempre (1993), Pindell and Barrett (1990), Rage (1978, 1981, 1986, 1995), and Savage (1982).

The initial fragmentation of the supercontinent Pangaea into a northern land mass, Laurasia, and a southern one, Gondwanaland, was essentially completed by the middle of the Jurassic epoch, about 160 Ma (Barron et al. 1981).

Box 16.1

Principal Types of Crusts Forming Upper Layers of Earth's Surface

- Oceanic: formed mainly at midoceanic ridges and hot spots
- Continental: formed by mantle differentiation, magmatism, sedimentation, and metamorphism; mostly ancient Precambrian crystalline rock
- Accretionary: formed from a mixture of rock types principally at a subduction zones

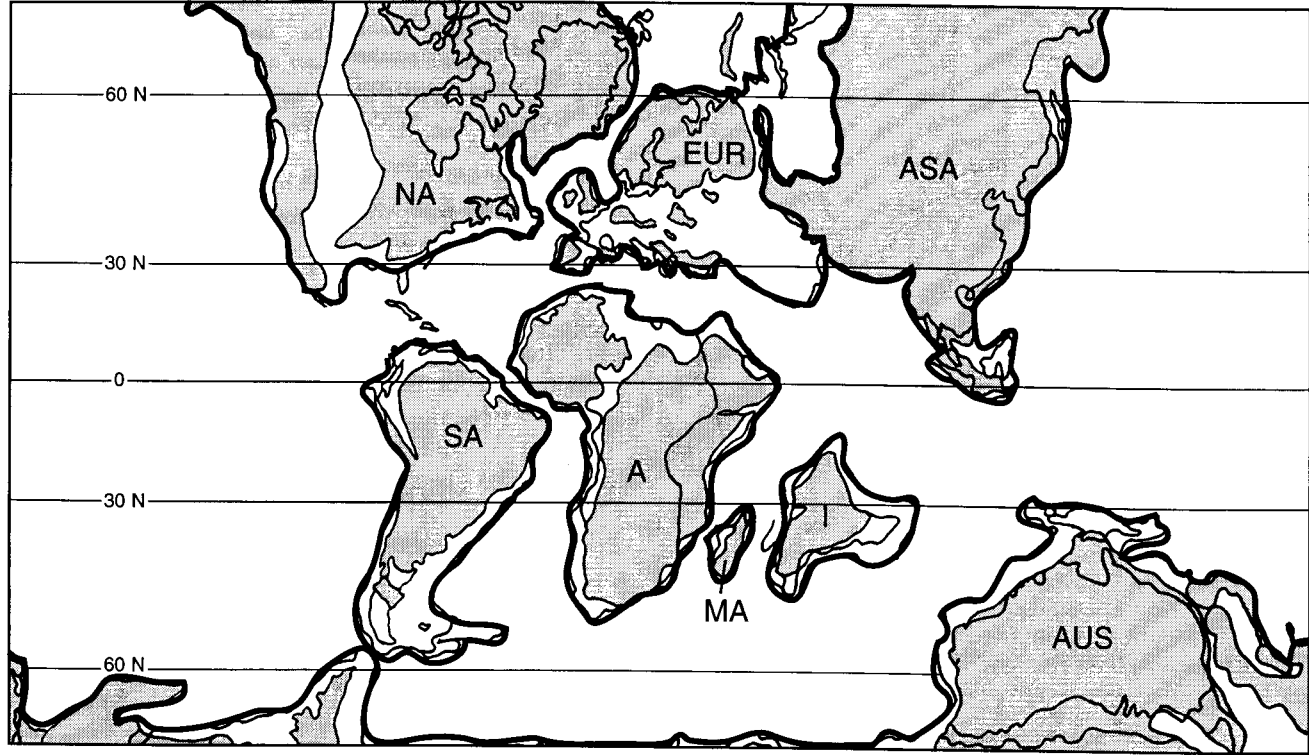


Figure 16.3. Relationships of continents approximately 80 Ma; shading indicates land-positive areas. Note complete isolation of South America.

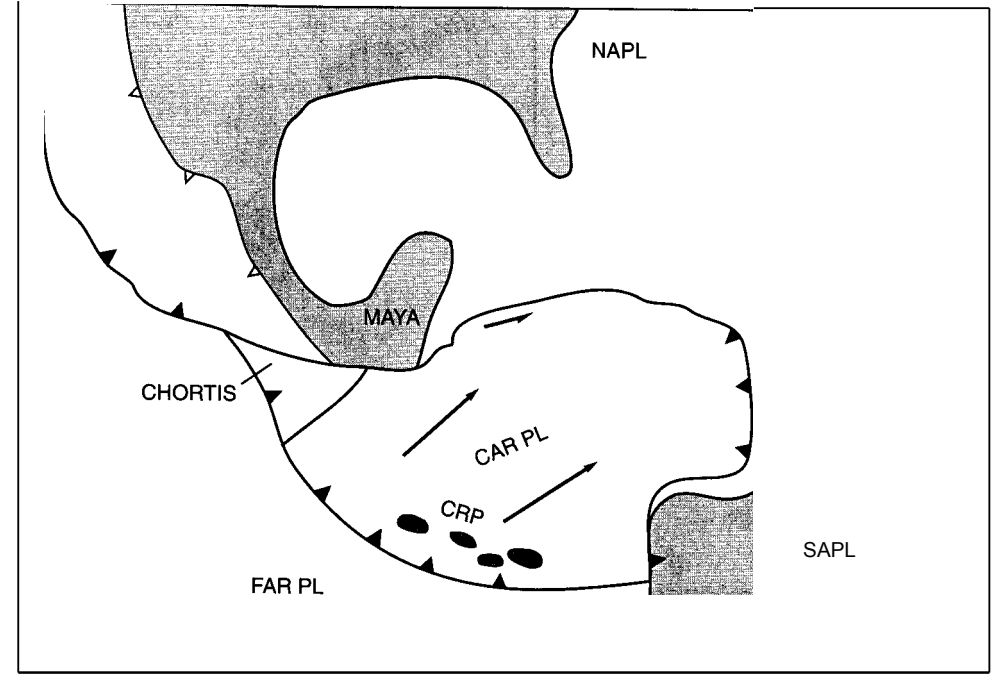


Figure 16.5. Mesoamerican region in the Eocene. Abbreviations as in figure 16.4.

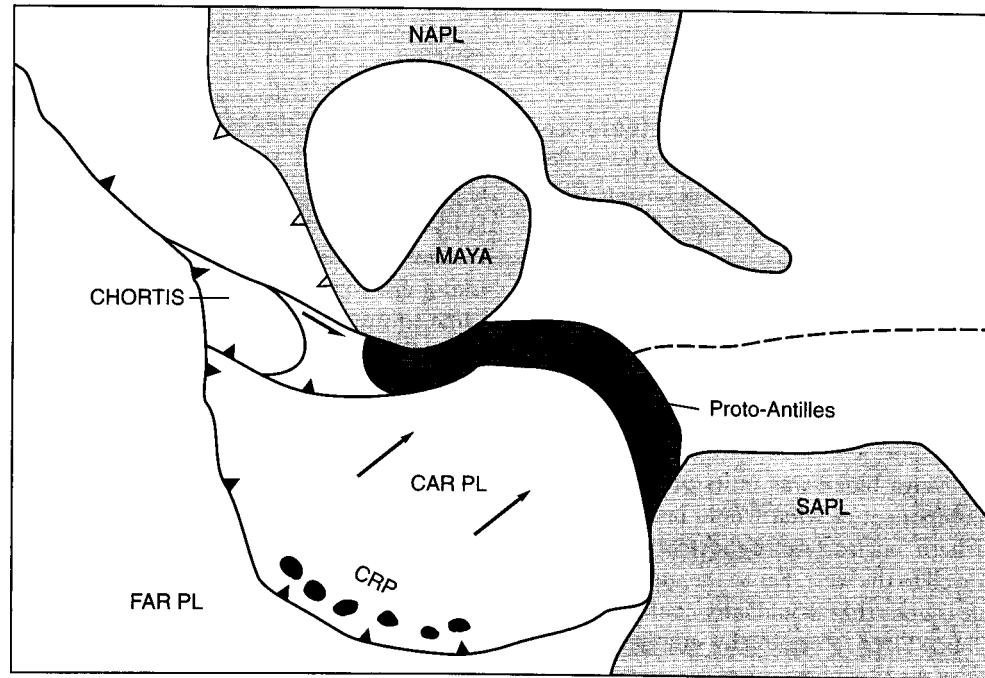


Figure 16.4. Mesoamerican region in the Late Cretaceous-early Paleocene. Plates (PL): CAR = Caribbean, FAR = Farallon, NA = North American, SA = South American. Location of Chortis and Maya blocks. CRP = magmatic arc forming part of present-day Costa Rica and Panama. Dotted line equals approximate boundary between NAPL and SAPL.

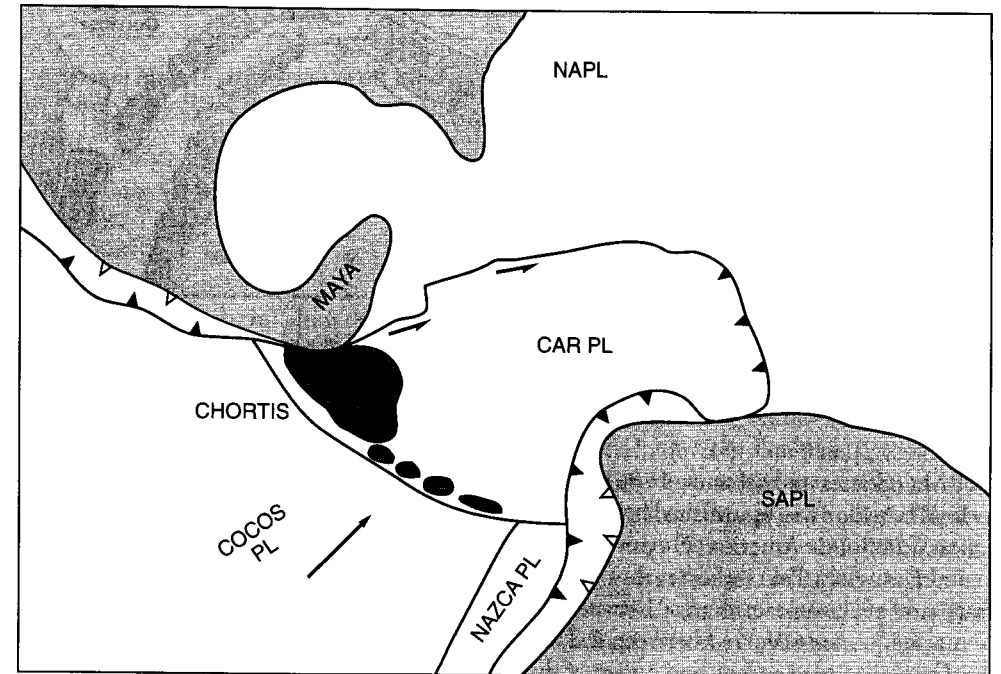


Figure 16.6. Mesoamerican region in the early Miocene. Abbreviations as in figure 16.4.

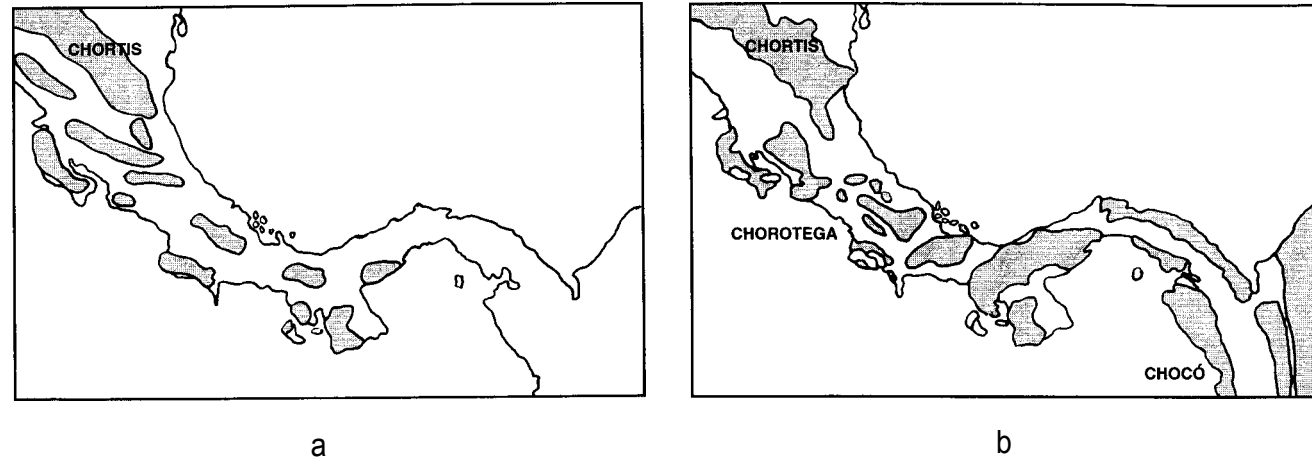


Figure 16.7. Isthmian Link area in the middle (a) and late (b) Miocene.

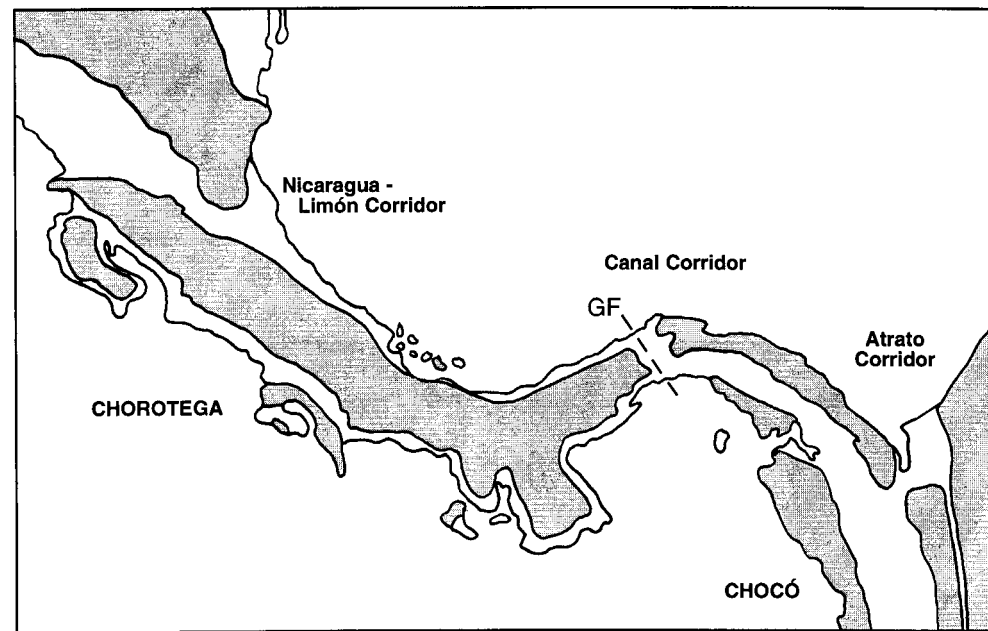


Figure 16.8. Isthmian Link area in the Pliocene. Chorotega and Chocó blocks sutured at Gatün fault (GF); principal marine barriers indicated.

Pliocene, 3.4 to 3.1 Ma (Coates and Obando 1996). At this time a continuous land corridor was established between the Chortis block region and South America. However, other evidence (Cronin and Dowsett 1996) indicates that the closure was temporary and that some exchange between Atlantic and Pacific marine faunas occurred between 2.8 and 2.5 Ma. This would explain the apparent two pulses of dispersal of northern terrestrial forms into South America and South American forms into lower Central America in late Pliocene and Pleistocene times as discussed below.

Uplands, Mountains, and Volcanoes

The Mesoamerican region is characterized by a complex series of elevated areas. Many of these support endemic taxa in their herpetofaunas. They are also often invoked as dispersal routes for various faunal components. Thus the distribution and timing of uplift and possible previous connections of these highlands with other areas are basic to understanding current faunal distribution patterns (Cserna 1989; Ferrusquía 1993; Ortega, Sedlock, and Speed 1994

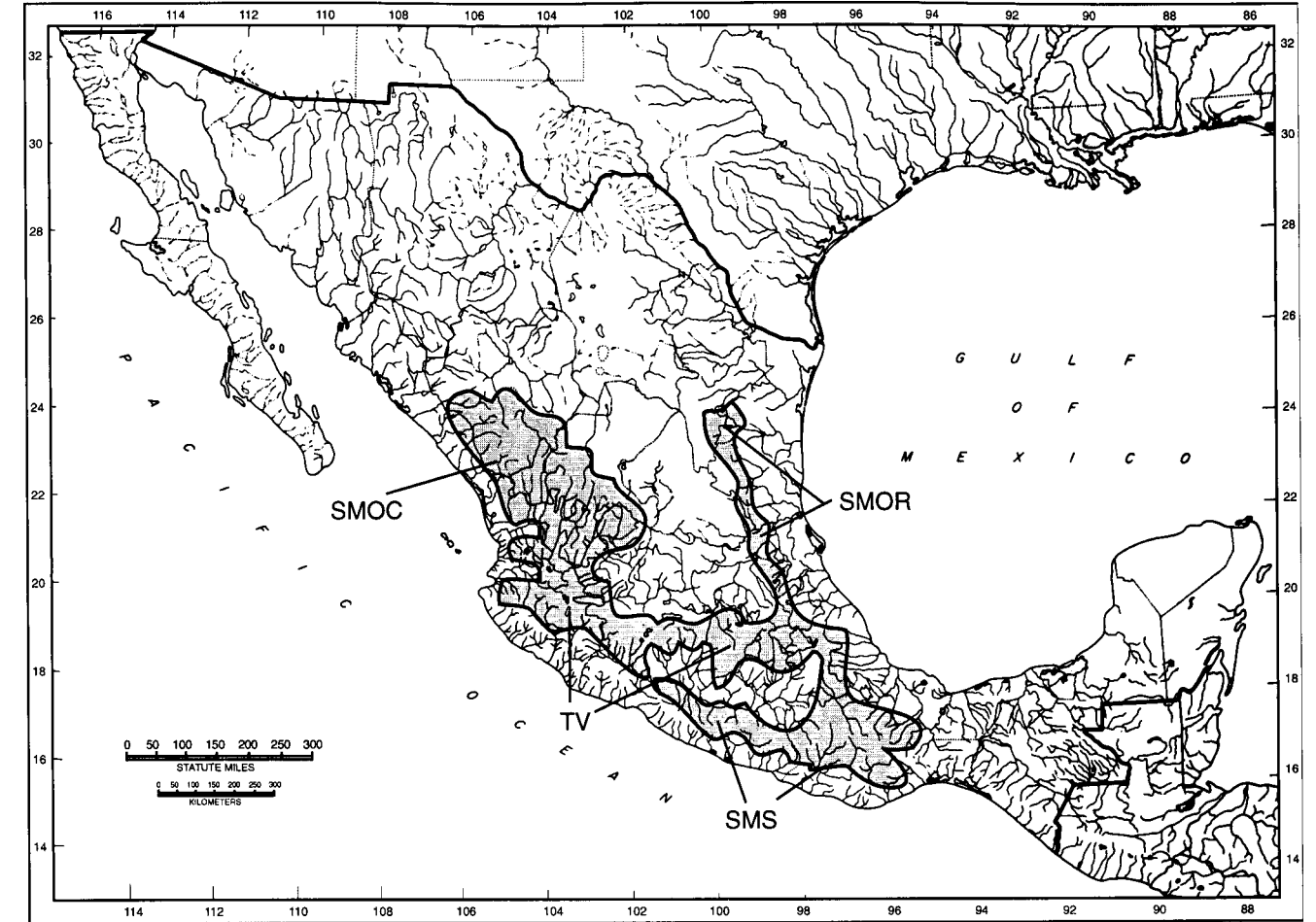


Figure 16.9. Upland areas of tropical Mexico, east of the Isthmus of Tehuantepec: SMOC = Sierra Madre Occidental, SMOR = Sierra Madre Oriental, SMS = Sierra Madre del Sur, TV = Transverse Volcanic Range.

for Mexico; Weyl, 1980 for Central America) (figs. 16.9 and 16.10).

Principal Upland Areas

Sierra Madre Oriental (Mexico): paralleling the Gulf coast, originally uplifted during the Laramide orogeny under influence of the now extinct Farallon-North American subduction zone; minimal Cenozoic volcanism; most recent uplift Miocene-Pliocene

Sierra Madre del Sur (Mexico): originally formed in the early Paleogene and probably related to subduction in the extinct Farallon-North American subduction zone; minimal Cenozoic volcanism; most recent uplift in the Miocene-Pliocene

North Central American Sierras: a series of subparallel ranges forming an arc open to the north extending from Chiapas, Mexico, across Guatemala and Honduras to northern Nicaragua; probably originally formed during suturing of the Chortis block to the Mayan block and

transfer of the former to the Caribbean plate; minimal Cenozoic volcanism; Pliocene uplift.

Tertiary Volcanics

Sierra Madre Occidental (Mexico): originally formed above former Farallon-North American plate subduction zone; extensive Tertiary volcanism; Miocene uplift

Central American: lying eastward of the Quaternary volcanic chain from Guatemala to southern Nicaragua; related to movements of the Chortis block; extensive volcanism from Miocene through Pliocene; Pliocene uplift

Costa Rica-Panama: mountains from central Costa Rica to eastern Panama originally formed as an island arc at Cocos-Caribbean subduction zone; extensive volcanism through Miocene; Miocene uplift

Quaternary Volcanics

Pacific Volcanic Chain: from Mexico-Guatemala border along Pacific versant to central Costa Rica; formed by

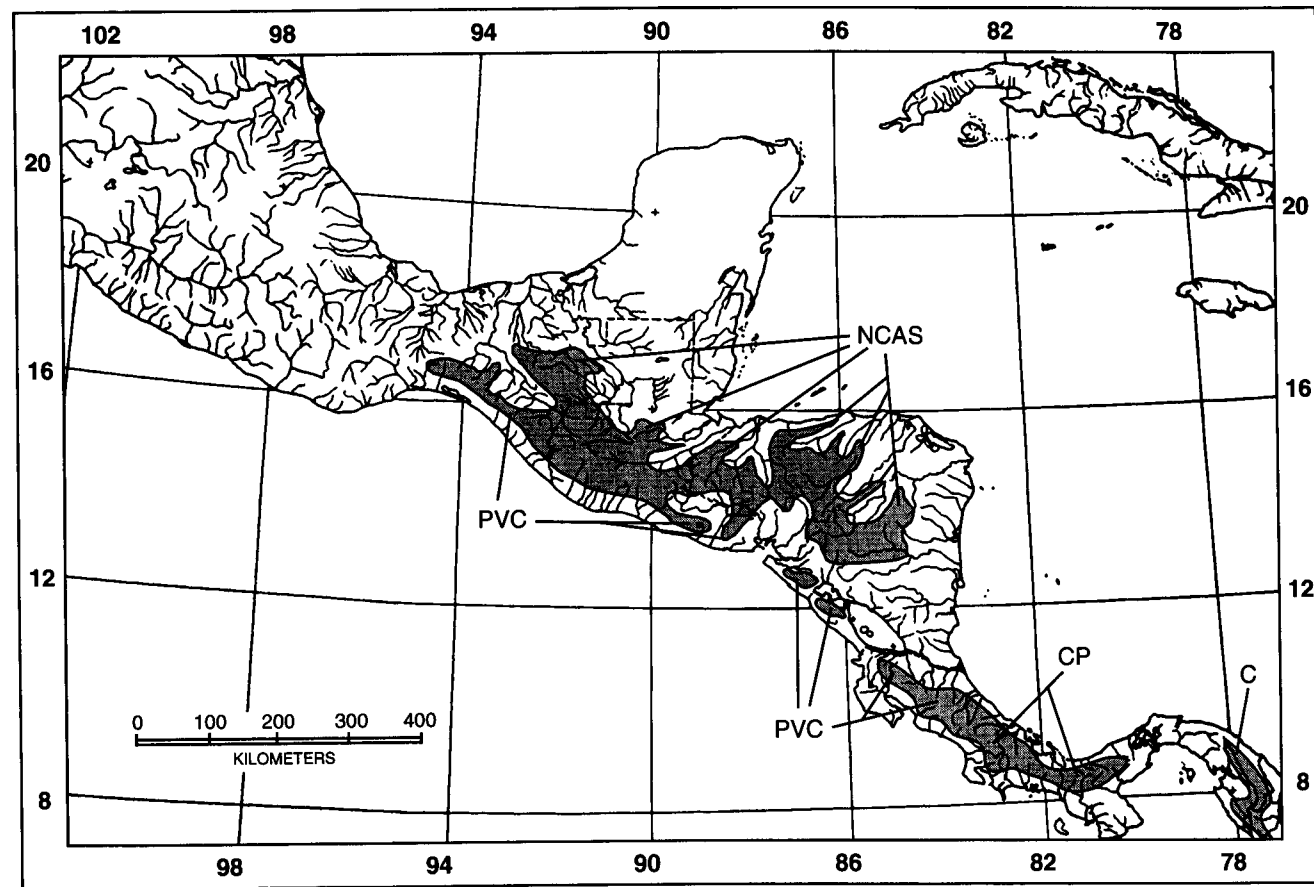


Figure 16.10. Upland areas of Central America: CPC = Costa Rica-Panama cordilleras, NCAS = Northern Central American sierras, PVC = Pacific volcanic chain. The Central American Quaternary volcanic chain lies generally to the east of the PVC and partially underlies it.

subduction at Middle American trench; many still active volcanoes often sitting on top of earlier volcanic ranges; uplift continuing today
 Transverse Volcanic Belt (Mexico): formed by subduction of Cocos plate under North American plate; many still active volcanoes; uplift continuing today

PALEOCLIMATES AND VEGETATION

In addition to drifting landmasses and the uplift of mountain masses, the current distribution of the herpetofaunas has been shaped by changing climatic factors through the Cenozoic. Estimates of past climates are based principally on analyses of oxygen and carbon isotope composition, fossil faunal (especially marine) assemblages, fossil pollen profiles, and fossil plant assemblages (Frakes, Francis, and Syktus 1992; Graham 1994, 1996, 1997, 1999a,b,c; Burnham and Graham 1999). Terrestrial angiosperm foliar physiognomy reflects to a substantial extent climatic conditions, so fossil floras are invaluable indicators of climate, regardless

of taxonomic composition, and palynofloras often provide the only estimates of past climate as reflected by vegetation. In this section I will briefly review the major climatic shifts that have affected the herpetofauna and describe in broad strokes the changes in vegetation that occurred in our area of study. Frakes, Francis, and Syktus (1992) recognized two climate modes, periods during which similar climates prevail, as characteristic of Phanerozoic times. Cool modes are periods of global refrigeration, ranging from those in which glaciation occurs to those where ice is formed at high latitudes only during the winter. Warm modes are periods when climates are globally warm with little or no polar ice. Late Cretaceous and Paleocene times were among the very warmest and most humid of times in earth's history (fig. 16.11). The polar regions were free of ice, with temperatures warm enough to allow forests and associated reptile and amphibian faunas to live there. Mean global temperatures were 6°C higher than today. Sea levels were high in the Tate Cretaceous, about 200 m above current levels, and large areas of the continents were covered by extensive seaways (Vail, Mitchum,

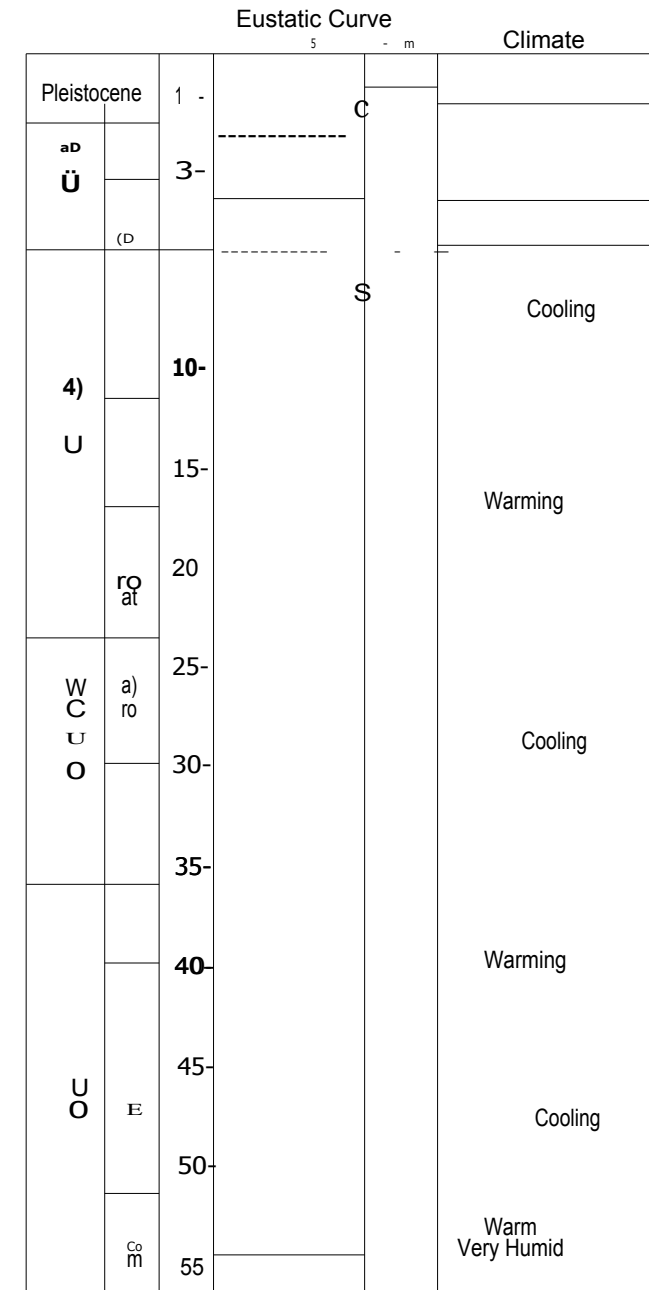


Figure 16.11. General pattern of climatic and sea level fluctuations, Eocene to present.

and Thompson 1977). By the Paleocene the seaways had gradually receded. Vegetation over most of what is now the Americas consisted of tropical and subtropical broadleaf evergreen forests (rainforest). Temperate forests including broadleaf evergreen and deciduous formations grew surrounding the poles. The tropical assemblage and the north temperate one have been recognized as the Neotropical Tertiary and Arcto-Tertiary geofloras, respectively (Axelrod 1958; Axelrod and Ting 1960).

By the time the Proto-Antillean Isthmus began to break up in the Tate Paleocene, tropical and subtropical evergreen forests ranged north to 60 to 65°, temperate broadleaf forests to 70°, and a previously minor component of the Arcto-Tertiary geoflora, conifer forest, began developing around the pole (fig. 16.12a).

The onset of the overall cooling trend for the rest of the Cenozoic began in the Eocene at about 50 to 55 Ma. This early cool period saw displacement of the vegetational belts southward, and a number of temperate forests components ranged even farther southward along the developing uplands of western North America and eastern Mexico. At lower elevations a transitional zone appears to have been present between subtropical evergreen and temperate evergreen forests at about 50°N (fig. 16.12b). Although there were later warm modes in the Cenozoic with some shifting north and south of climate-vegetation zones, tropical and subtropical vegetation became displaced farther and farther south throughout the rest of the era (fig. 16.12c) (Wolfe 1985).

Superimposed on the cooling trend was a drying trend that was associated with the mountain building of the western North American cordilleras and the increasing continentalization of climate. The drying trend is already noticeable in the Oligocene, since broadleaf deciduous forests dominated eastern North America and subtropical deciduous vegetation covered most of what is now the southwestern United States and adjacent Mexico (fig. 16.13a). The latter vegetation corresponds to the Madre-Tertiary geoflora of Axelrod (1958).

The early Miocene (fig. 16.13b) was a period of warming and increasing aridity. This coupled with uplift of the Sierra Madres in Mexico completed the isolation of tropical Mesoamerica and its highlands from biotas to the north by the development of semiarid to desert vegetation across America west of the Mississippi and south through central Mexico. The Tate Miocene and earliest Pliocene (6 to 4.8 Ma) formed a period of severe cyclic glaciations in which average annual temperatures in Middle America were depressed as much as 6°C below present ones. Continuing drying trends, however, prevented any substantial movement southward of temperate forests, so that they came to be compressed between the taiga and scrubland-grassland belt (fig. 16.14).

After a brief interval of warming and a rise in sea level, the rest of Pliocene, from the initial closure of the Panamanian seaway (3.1 Ma) throughout the Quaternary, saw repeated cooling and warming episodes as polar glaciers waxed and waned. Interglacial periods in tropical Mesoamerica would have climate and vegetation patterns similar to those at present. Glacial periods saw temperature depressions of 5 to 6°C so that upland vegetation was displaced downward and mixed with lowland communities. Contrary to earlier authors (Clapperton 1993; Haffer 1969; Webb 1985), in lower Central America and the Amazon at least,

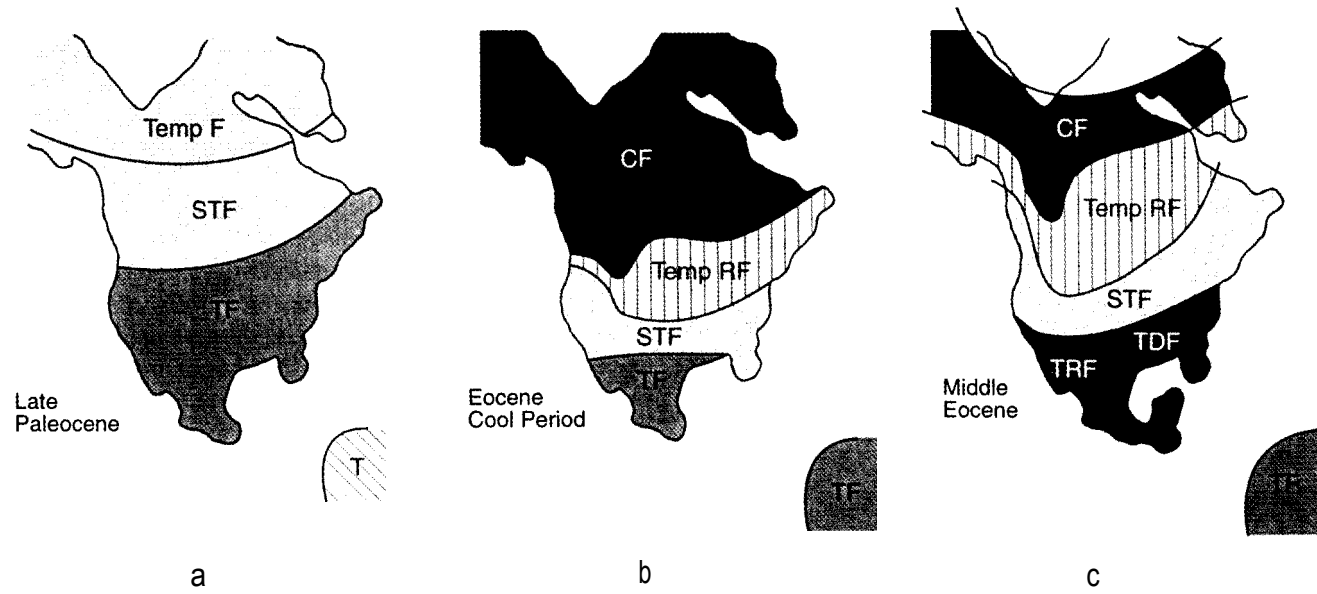


Figure 16.12. General distribution for forest vegetation in the early Paleocene to middle Eocene: CF = conifer forest, STF = subtropical rainforest, TDF = tropical deciduous forest, TF = tropical rainforest, Temp F = temperate forest, Temp RF = temperate rainforest.

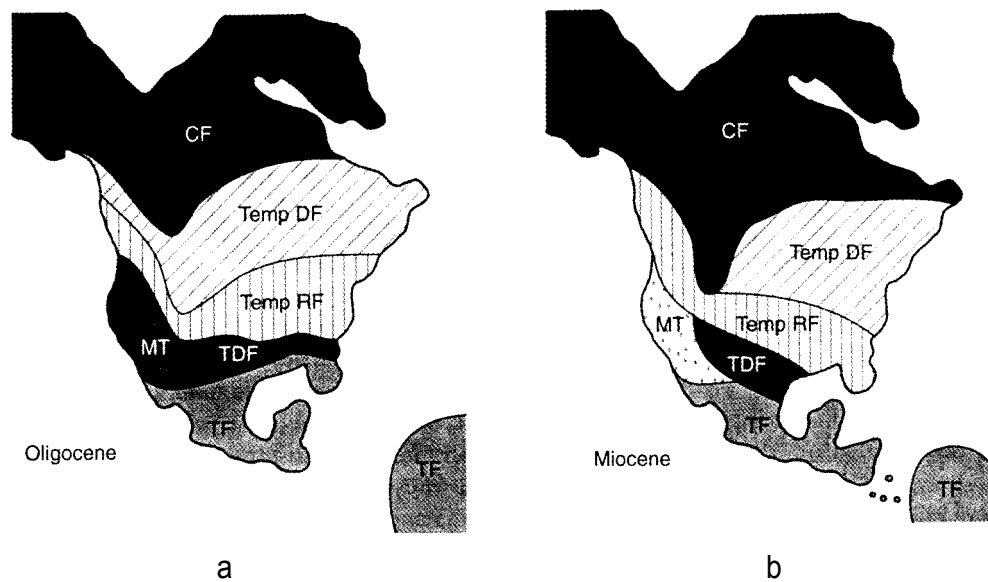


Figure 16.13. General distribution of vegetation, Oligocene to Miocene. Abbreviations as in figure 16.12. Temp DF = temperate deciduous forest. Subtropical vegetation, not shown because of scale, forms transition between tropical and temperate formations. MT = Madro-Tertiary woodland, chaparral, and scrub vegetation.

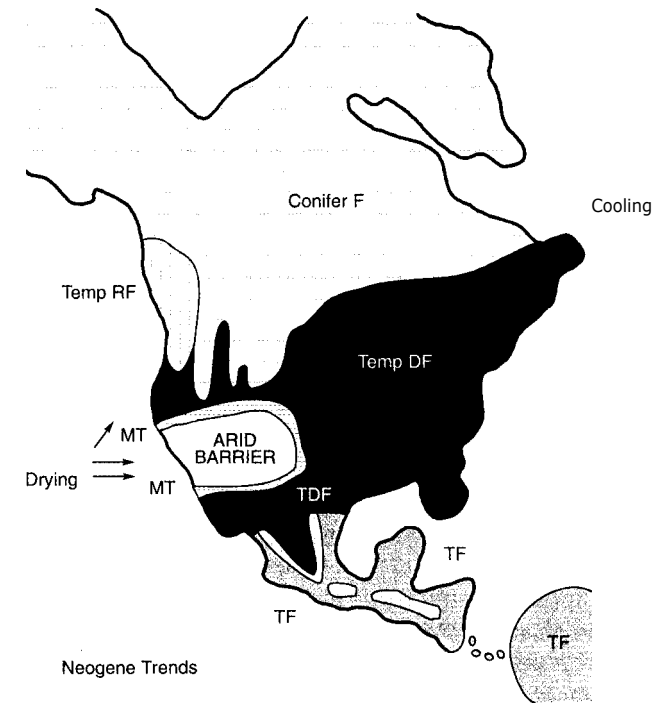


Figure 16.14. Neogene trends in vegetation produced by increased cooling and drying and continentalization of climates. Abbreviations as in figures 16.12 and 16.13.

interglacial intervals were not periods of increased dryness (Colinvaux 1993, 1996). I will return to this matter later in the discussion of the biogeographic patterns for montane amphibians and reptiles.

DISPERSALS, VICARIANCE, AND FAUNAL ASSEMBLAGE: THE BIG PICTURE

The history of the Tropical Mesoamerican herpetofauna includes a series of concordant dispersal events interspersed with periods of fragmentation of formerly continuous ranges followed by diversification within the now separate areas (vicariance). The earliest major vicariance to affect the present-day fauna was the gradual fragmentation of Pangaea into northern (Laurasia) and southern (Gondwanaland) landmasses in the middle Jurassic (about 160 Ma). During this period of separation all extant families of amphibians and reptiles probably evolved as further fragmentation led to the present pattern of continental units (table 16.1). For this discussion, that initial separation is called vicariance V_0 .

Sometime in the late Cretaceous the accretionary island arc described above came to lie between North and South America and through uplift formed an isthmian connection between the two continents (the Proto-Antilles). This connection lasted 5 to 10 million years and mediated a major

Table 16.1. Historical Sources for Suprageneric Groups of the Mesoamerican Herpetofauna

Group	Laurasian	Pangaean	Gondwanan
Caecilians			Caeciliidae
Salamanders	Plethodontidae		Pipidae
Frogs and Toads	Rhinophrynidae		Bufoinae
	Ranidae		Leptodactylidae
			Hylidae
			Centrolenidae
			Dendrobatidae
			Microhylidae
Lizards	Phrynosomatidae		Corytophanidae
	Eublepharidae		Iguanidae
	Gekkoninae (pt.)		Hoplocercidae
	Xantusiidae		Polychrotidae
	Scincidae (pt.)		Sphaerodactylinae
	Dibamidae		Gymnophthalmidae
	Teiidae		Gekkoninae (pt.)
	Bipedidae		Scincidae (pt.)
	Anguinae		Amphisbaenidae
	Xenosauridae		
	Helodermatidae		
Snakes	Loxocemidae	Typhlopidae	Anomalepididae
	Ungaliophiidae	Leptotyphlopidae	Boidae
	Colubridae (pt.)		Tropidophiidae
	Elapidae		Colubridae (pt.)
	Viperidae		
Turtles	Kinosternidae		
	Dermatemydidae		
	Chelydridae		
	Emydidae		
Crocodylians	Crocodylidae (pt.)		Crocodylidae (pt.)

dispersal event (D_1) with apparent extensive faunal exchange between the two continents. All evidence points to an ancient continuity and essential similarity of a generalized tropical herpetofauna that ranged over tropical North, Middle, and South America in the Late Cretaceous-Paleocene times. Descendants of this assemblage are represented today by the South and Middle American Elements defined in chapter 15. These elements are associated with the Neotropical-Tertiary geoflora defined above, which at this time ranged far to the north (70°), and its derivatives throughout the Cenozoic. To the north of this fauna ranged a temperate, Laurasian-derived unit associated with the Arcto-Tertiary geoflora, now represented by Old Northern Element herpetofaunal taxa.

By the end of the Paleocene the Proto-Antillean Isthmus became fragmented as the Caribbean plate moved north-eastward to separate the continents and isolated northern and southern fragments of the generalized tropical herpetofauna in North and South America to constitute a second major vicariance event (V_1). Differentiation in situ within the two fragments during the next 54 million years created the distinctive tropical elements of the two herpetofaunas that became intermixed with the establishment of the new Isthmian Link in the Pliocene. Phylogenetic analysis of several groups of xenodontine snakes (Cadle 1985), the coral snakes of the genus *Micrurus* (Slowinski 1991, 1995), the Frogs of the genus *Eleutherodactylus* (Lynch 1986; Savage 1987), and the anole lizards (Guyer and Savage 1992) strongly support the significance of this vicariance (fig. 16.15).

In the Eocene, probably related to the Eocene cool pe-

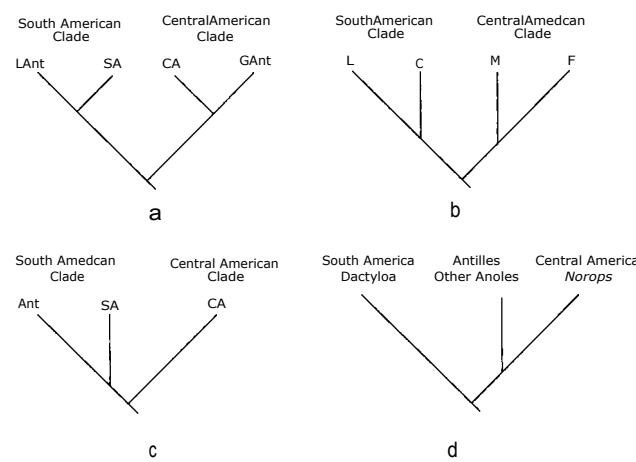


Figure 16.15. Phylogenetic relationships reflecting separation of North and South America in the early Paleogene: (a) xenodontine snakes; (b) venomous coral snakes (genus *Micrurus*): C = *collaris* group, F = *fulvus* group, L = *lemniscatus* group, M = *mipartitus* group; (c) frogs of the genus *Eleutherodactylus*; (d) anole lizards. Ant = Antilles, G = Greater, L = Lesser.

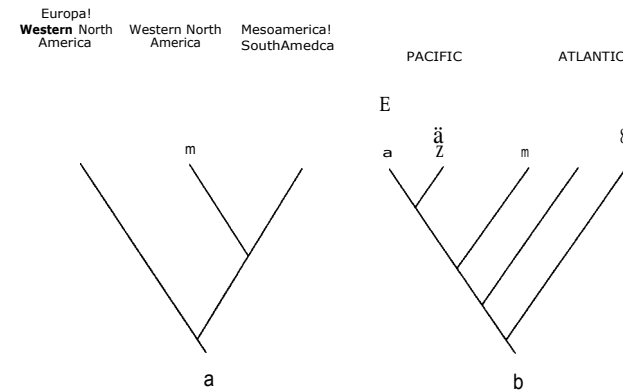


Figure 16.16. Phylogenetic relationships: (a) bolitoglossine salamanders illustrating incorporation of one lineage (BOL = *Bolitoglossa* plus twelve genera) into the Central American biogeographic component (after Wake and Larson 1987); (b) Mesoamerican batugarine turtles of the genus *Rhinolemmys* showing vicariance event V_3 .

riod and emerging uplands in western North America and Mexico, a substantial number of Old Northern groups became integrated with tropical taxa in Mexico (dispersal event D_2). Most prominent among these organisms were plethodontid Salamanders and colubrine snakes, but several freshwater turtles and a variety of lizards are also represented (table 15.9). As the former continuity between the region and what is now the eastern and far western United States was affected by mountain building and the subsequent cooling and drying trends for the rest of the Cenozoic, these components became disjunct in Mexico (Axelrod 1975; Graham 1997). This disjunction (Rosen 1978) allowed differentiation of the Central American Component of the Old Northern Element (fig. 16.16a), which from the Oligocene onward evolved in association with the Middle American Element.

Thus the initial organization of what was to become the Mesoamerica herpetofauna involved a pair of vicariance events: complete geographic isolation from South America and fragmentation and isolation of the Central American Component from its northern congeners, by a combination of physiographic and climatic factors. By the Oligocene, most of the genera or their ancestors, which now form the Old Northern and Middle American Elements (table 15.9), were present in the region.

A momentous physiographic development, the uplift of the main mountain axis of Mexico and Central America, created one major dispersal event (D_3) and 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 beginning in the Oligocene, and the highlands of Nuclear Central America developing in the Miocene. The final sequence of uplift was in lower Central America leading to the closure of the Panamanian Portal

in the Pliocene. As the uplift proceeded, Middle American Element and Central American Component taxa dispersed southward (D_3) over the emerging landmass. A primary vicariance effect of the uplift was to gradually fragment what was a rather homogeneous Mesoamerican herpetofauna into several geographic assemblages, most notably in the lowlands, where the orogenic effects and the northeast trade winds produced a partial rain shadow along the Pacific versant from Sinaloa, Mexico, to Costa Rica. This process led to the replacement of humid conditions and evergreen vegetation by subhumid to semiarid climates and deciduous and thorn forest formations. As pointed out in chapter 14, many species and most genera of lowland groups in Central America are found on both the Pacific and Caribbean coastal strips. Duellman (1966b, 1988) and I (Savage 1966a, 1982) also emphasized the relative homogeneity of the herpetofauna on each lowland versant. Nevertheless, a considerable number of sister species pairs reflect the impact of the mountain barrier. An example supporting the significance of this vicariance event (V_3) is provided by the turtle genus *Rhinolemmys* (fig. 16.16b) based on the study of Lahanas (1992).

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 constituting the backbone of Middle America. This fragmentation has led in some cases to the development of endemic montane isolates from ancestors with a formerly continuous north-to-south range. However, this explanation does not seem satisfactory in all cases, and I will return to the problem of montane speciation in a later section.

The final major factor in shaping the herpetofauna of Central America was the complete emergence of the Panamanian Isthmus in the Pliocene to directly connect North and South America. Reconnection led to the dispersal (D_4) of many South American Element genera northward and permitted immigration into South America by Old Northern and many Middle American stocks. Concordant dispersal events (D_4), have brought sixty-five living generic-level taxa of clearly South American origin across the Isthmus to contribute to the Central American herpetofauna (table 15.9). 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 Old Northern and Middle American generic level taxa and species are found in northwestern South America, but many range southward to the Amazon basin or beyond.

The recent herpetofaunas of Central America, except those in eastern Panama, are based on a fundamental core of autochthonous Middle American groups whose history in the region goes back at least to the early Tertiary. Coexisting with this unit throughout the region are a series of en-

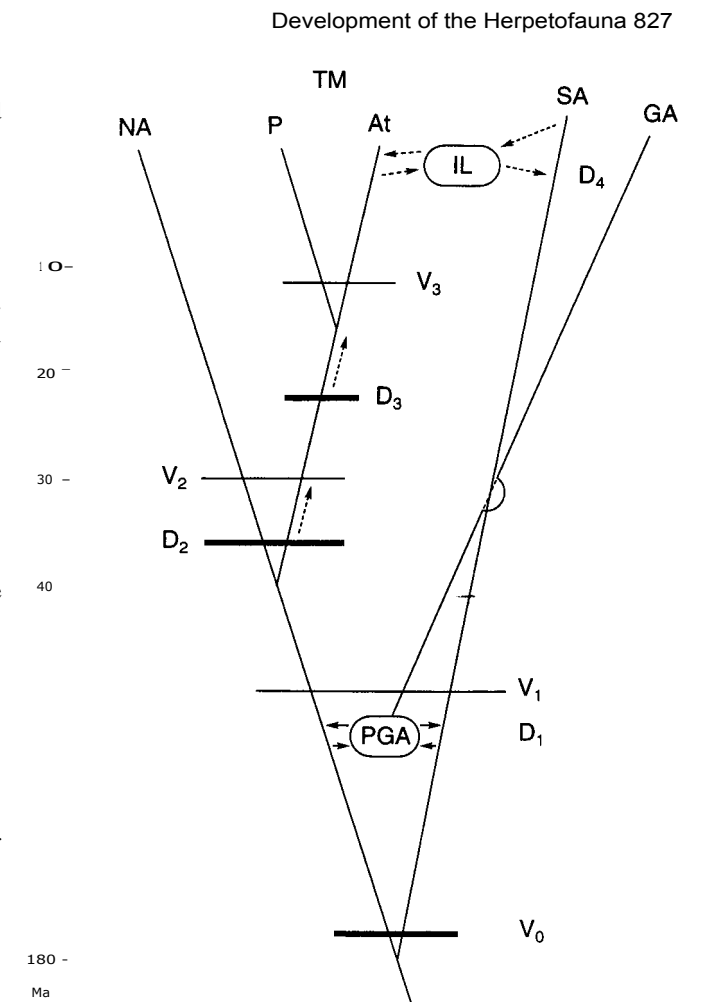


Figure 16.17. Area cladogram showing sequence of major vicariance (V) and dispersal (D) events responsible for present biogeographic patterns for the terrestrial herpetofauna: At = Atlantic, GA = Greater Antilles, IL = Isthmian Link, NA = North America, P = Pacific, PGA = Proto-Greater Antilles, TM = Tropical Mesoamerica.

demically derivative stocks of Old Northern relationships that have been in the region from Eocene-Oligocene times onward. Only in Panama and Costa Rica do South American Element taxa contribute significantly to the fauna and predominate in eastern Panama.

To summarize, the events leading to the present pattern for Mesoamerica are as follows (figs. 16.17 and 16.18):

Vicariance (V_0): breakup of Pangaea

Dispersal (D_1): from the south over the Proto-Antillean Isthmus

Vicariance (V_1): breakup of the Proto-Antillean Isthmus

Dispersal (D_2): invasion and integration of Old Northern fauna with the tropical herpetofauna

Vicariance (V_2): climate changes introducing a semiarid to arid barrier between temperate North America and tropical Mesoamerica

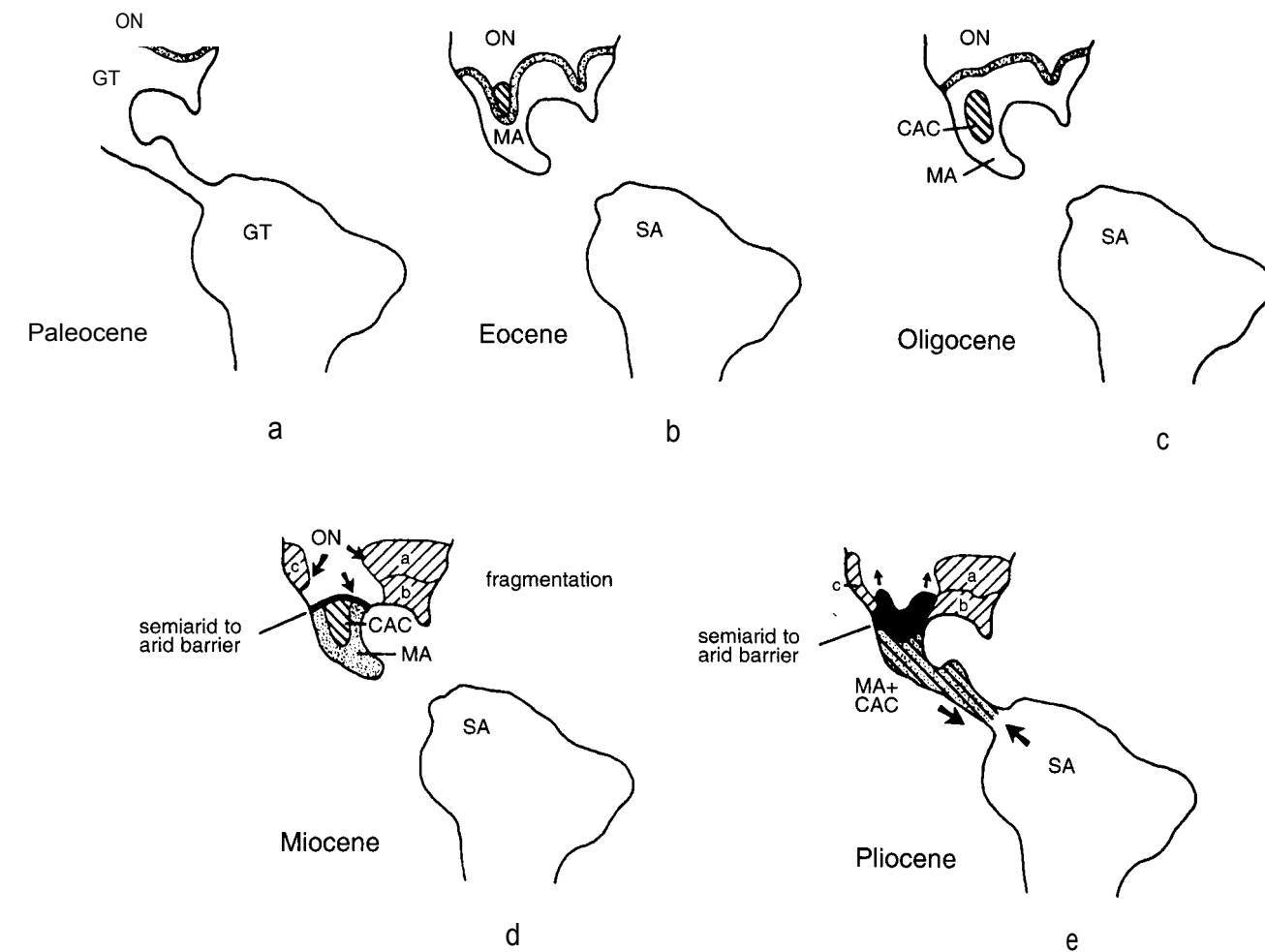


Figure 16.18. Evolution of the Tropical Mesoamerican herpetofauna showing distribution of historical source units over time: CAC = Central American Component, GT = Generalized Tropical Fauna, MA = Middle American Element, ON = Old Northern Element, SA = South American Element.

Dispersal (D_3): concordant population of the emerging Isthmian Link by Mesoamerican and Central American faunal units from the north

Vicariance (V_3): uplift of Mesoamerican highlands

Dispersal (D_4): from the south after emergence of the Panamanian Isthmus; this event subsumes two pulses that occurred about 1 million years apart

The Costa Rican Herpetofauna and the Closure of the Panamanian Portal

By the end of the Paleogene the land-positive portions of the Maya and Chortis blocks were populated by a variety of Mesoamerican Element and Central American Component genera, many shared with tropical Mexico. The continuing east-northeastward movement of the Caribbean plate by this time had brought the Costa Rica-Panama island arcs into

approximately their present locations. Uplift of a series of gradually emerging islands characterized this period for the Chorotega block, but the islands were widely separated from South America by a deep and wide seaway (fig. 16.7). The earliest of these islands are represented today by a series of Pacific versant peninsulas: Santa Elena, Nicoya, Herradura, Osa, Burica, Soná, and Azuero.

At this same time, although the Chortis and Chorotega blocks were sutured together at their margins, the contiguous Nicaragua depression and the Tempisque, San Carlos, and northern Limón basins formed a significant marine barrier to dispersal onto the islands from the north. Coates and Obando (1996) suggested that this barrier continued as an elongated marine connection between the Pacific Ocean and Caribbean Sea into the Pliocene (3 Ma). Other reconstructions (Van Andel et al. 1971; Donnelly 1989; Iturralde and MacPhee 1999; Perfit and Williams 1989; Pindell and Bar-

rett 1990) indicate a land-positive connection between the Chortis and Chorotega blocks in the Tate Miocene (10 Ma). It seems likely that the connection was completed at the earlier time, as indicated by the late Miocene (6 Ma) mammal fossils of strictly northern affinities from central Panama (Whitmore and Stewart 1965). However, eustatic fluctuations may have opened and closed this and other interoceanic connections at various times before final closure of the Isthmian Portal.

In the Middle Miocene (ca. 15 Ma) the Panama portion of the arc began to be compressed by the South American plate, at which time the Chocó block was formed and a series of land-positive areas emerged in the diminishing gap between South America and the Chorotega block. These areas formed islands, continuing the isthmian archipelago southward, and today are represented by the Serranias San Blas-Darien and Maje of western Panama, the Serranía Sapobaudo of western Panama and northwestern Colombia, and the Dabeiba region of the Sierra Occidental of Colombia.

In addition, beginning about 5 Ma, the Cocos ridge began to subduct under the central portion of the Chorotega block to uplift the Cordillera de Talamanca. Thus by the early Pliocene a continuous land connection formed a dispersal corridor between the southern portion of nuclear Central America and what is now Costa Rica and western Panama. These events provided a landscape of coastal lowlands with a rapidly rising upland region that ultimately formed a continuous montane barrier 2,000 m in altitude across the Isthmus. Paleobotanical and paleoclimatic data (Graham 1987a,b, 1999a,b,c; Savin 1977; Savin and Douglas 1985) indicate that mid-Miocene climates were much the same as today at these latitudes (ca. 10° N), and the principal vegetation present was humid evergreen forests. However, Graham (1987a) noted that a substantial number of genera represented groups now found in midaltitude situations. These facts suggest that the basic habitats used by the modern herpetofauna were in place, except for the dry forest component, by the mid-Miocene (5 to 10 Ma). It is little wonder then that Mesoamerican Element and Central American Component taxa dominate all areas on the Chorotega and Chocó blocks, since they had the earliest and exclusive opportunity to invade the emerging Isthmus from the north.

The final chapters in this process involved complete closure of the seaway by further uplift of the Chocó block. The first such episode occurred in the Pliocene, when sea level was 100 m lower than today (Vail and Hardenbol 1979), about 3.4 to 3 Ma. This event led to the concordant dispersal of South American Element taxa into lower Central America. These earliest invaders are probably represented by the few genera of this unit now ranging north to Guatemala or beyond.

Later, warming temperatures and rising sea level appear to have again connected the Caribbean Sea and the Pacific

via the Atrato region for a time, with final closure dated at about 2 Ma (Cronin and Dowsett 1996). This resulted in a second pulse of dispersal that continues to this day. Although I have included them within dispersal event D_4 (fig. 16.17), they may be thought of as D_{4a} and D_{4b} . It is these dispersals that are responsible for the substantial representation of South American taxa in Costa Rican faunal areas other than the northwest region.

The temporary opening and final closure of the seaway in the Pliocene also may explain a puzzling aspect of South American biogeography. Many Mesoamerican and Central American unit genera have relatively few South American representatives, and their distributions are restricted to northern South America. Others, however, have wider distributions and considerable species richness on the continent (e.g., *Bolitoglossa*, *Norops*, and *Botrops*). It appears that there were also two pulses of dispersal southward, mirroring those just described for South American genera dispersing northward across the Isthmus. Middle American genera showing wide distributions and considerable speciation in South America probably represent the first wave of migrants across the Isthmus—for example, the salamanders of the genus *Bolitoglossa* (Hanken and Wake 1985) and some colubrine snakes (*Atractus* and *Sibynomorphus*, Cadle 1985), and perhaps the pitvipers of the genus *Botrops*. Those with more restricted ranges and less diversity would have arrived in the second, more recent pulse after the second and final closure of the seaway.

The two-step closure model would also explain the frequent occurrence of endemic species of Mesoamerican Element and Central American Component genera in the Chocó region of western Colombia or northern South America (e.g., the lizards of the genus *Basiliscus* and turtles of the genus *Rhinoclemmys*). The ancestors of such forms would have migrated across the first Pliocene land connection and become isolated from Central American populations. During separation, allopatric speciation occurred to produce the South American form(s). In some cases, after the final Pliocene closure, dispersal has brought the descendant species into sympatry. Examples include *Basiliscus basiliscus* of Central America and northern South America and *B. galeritus* of the Chocó and *Rhinoclemmys annulata* and *R. nautica*, with the latter species in the Chocó. In other cases they may continue to be allopatric: *Kinosternon angustipons* (Atlantic slope Costa Rica and western Panama) and *K. dunnii*. The South American genus *Phyllobates* mirrors this situation in reverse with allopatric species in Costa Rica and Panama (*Phyllobates lugubris* and *P. vittatus*) and their sister species (*P. aurotaenia*) in the Chocó. All are probably isolated fragments of an ancestor that crossed over the first Pliocene land bridge.

Several authors have argued that the presence and diversity of Middle American taxa in South America, here asso-

ciated with the first Pliocene dispersal pulse, shows they must have arrived there by island hopping along the magmatic arc before the emergence of the Isthmian Link in the Pliocene. Hanken and Wake (1985) proposed that salamanders of the genus *Bolitoglossa* made such a journey in the middle Miocene about 18 Ma based on a molecular clock derived from genetic distances. Zamudio and Greene (1997) evoke a similar scenario for colubrine snakes and *Lachesis*. Using mtDNA data, they established a molecular clock that estimated the time of divergence between Central American and South American *Lachesis* as 6 to 18 Ma, again before completion of the Isthmian Link. Given the unreliability of molecular clock estimates (Scherer 1990; Avise et al. 1992; Avise 1994; Gaut 1998), the evidence for island hopping dispersal raises the issue whether dispersal could have occurred before the Pliocene by successive, sporadic connections of islands in the arc. The two-closure model of the portal also needs further verification to satisfactorily explain these and other distribution patterns.

By the late Pliocene most components of the present herpetofauna of Costa Rica and western Panama were in place. Mesoamerican Element and Central American stocks had arrived from the north during the Miocene to inhabit the emerging Isthmian Link as it gradually extended toward South America. Uplift of the Talamanca massif had provided an upland center for differentiation of these same lineages. Simultaneously, it split the lowland area into Pacific and Atlantic regions, where unique faunal assemblages would develop. Final closure of the Panamanian seaway had led to the migration of South American Element taxa northward to contribute eventually to herpetofaunal differentiation on both Pacific and Atlantic versants and in the uplands as well.

The Problem of Tropical Montane Herpetofaunas

Three principal upland areas occur in tropical Middle America: the Mexican Sierra Madres, the highlands of nuclear Central America, and the highlands of Costa Rica and western Panama. The first two are separated from one another by the low-lying Isthmus of Tehuantepec and the last two by the Nicaragua depression. No evidence suggests that these regions were ever connected by montane corridors at any time in their histories, yet closely related taxa and sometimes disjunct populations of arguably the same species occur on two or more of these highlands.

Three principal hypotheses have been proposed to account for these patterns:

At times of maximum Ice Age cooling, a temperature depression of about 6°C would allow dispersal through the lowlands from one upland area to another

The upland taxa are derivatives of widespread lowland taxa that independently invaded each upland area from below. The ancestral taxa were originally widespread lowland ones

that were carried upward and fragmented as each highland was uplifted

Recent studies on fossil pollen profiles by Colinvaux (1993, 1996) have clarified the issue at least as it relates to climate and vegetation in the Quaternary of Lower Central America. His principal conclusions are:

During glacial periods temperatures were depressed by 6 to 8°C from Guatemala through Panama, and glaciers formed at the highest elevations in the Cordillera de Talamanca

During these periods there was not a simple downward depression of the vegetational zones by 800 m, a condition that would have eliminated all components of lowland vegetation

Rather, the distributions of upland genera were compressed downward, where they became mixed with lowland taxa. The lowlands of the region were covered during glacial periods by these humid forests, with no indication of Ice Age increase in aridity

During interglacial periods the upland taxa were sorted out by moving back up the cordilleras as temperatures returned to levels equivalent to those at present

There have been repeated cycles of these events in Quaternary times

Although this pattern is documented for the Quaternary, an earlier period of severe glaciation cycles that occurred in latest Miocene to earliest Pliocene times (6 to 4.8 Ma) probably showed a similar sequence of events. One may assume that, like the flora, herpetofaunal assemblages responded to long-term temperature changes.

It therefore seems likely that the populating of the mountains of nuclear Central America by upland genera from the Sierras of Mexico occurred during a late Miocene to early Pliocene glacial period. Upland taxa became mixed with lowland ones at this time and were able to disperse across the Isthmus of Tehuantepec. During a subsequent warming period the upland genera were sorted out of the mixed fauna by moving into the newly available montane habitats. An example of the result of such a process is the distribution of the lizard genus *Abronia* (fig. 16.19).

Similar subsequent cycles would lead to a sequential invasion from north to south of more southern uplands throughout the Pliocene. An example of this pattern is the distribution of the snakes of the *Rhadinaea godmani* group (fig. 16.20).

The formation of the Quaternary volcanic chain in Central America would expedite this process during the several cooling and warming cycles. A general model for montane speciation in the region (fig. 16.21) requires an initial dispersion event followed by cycles of temperature depression (glacial periods) and release (interglacial periods). The initial period of such a sequence is probably responsible for the

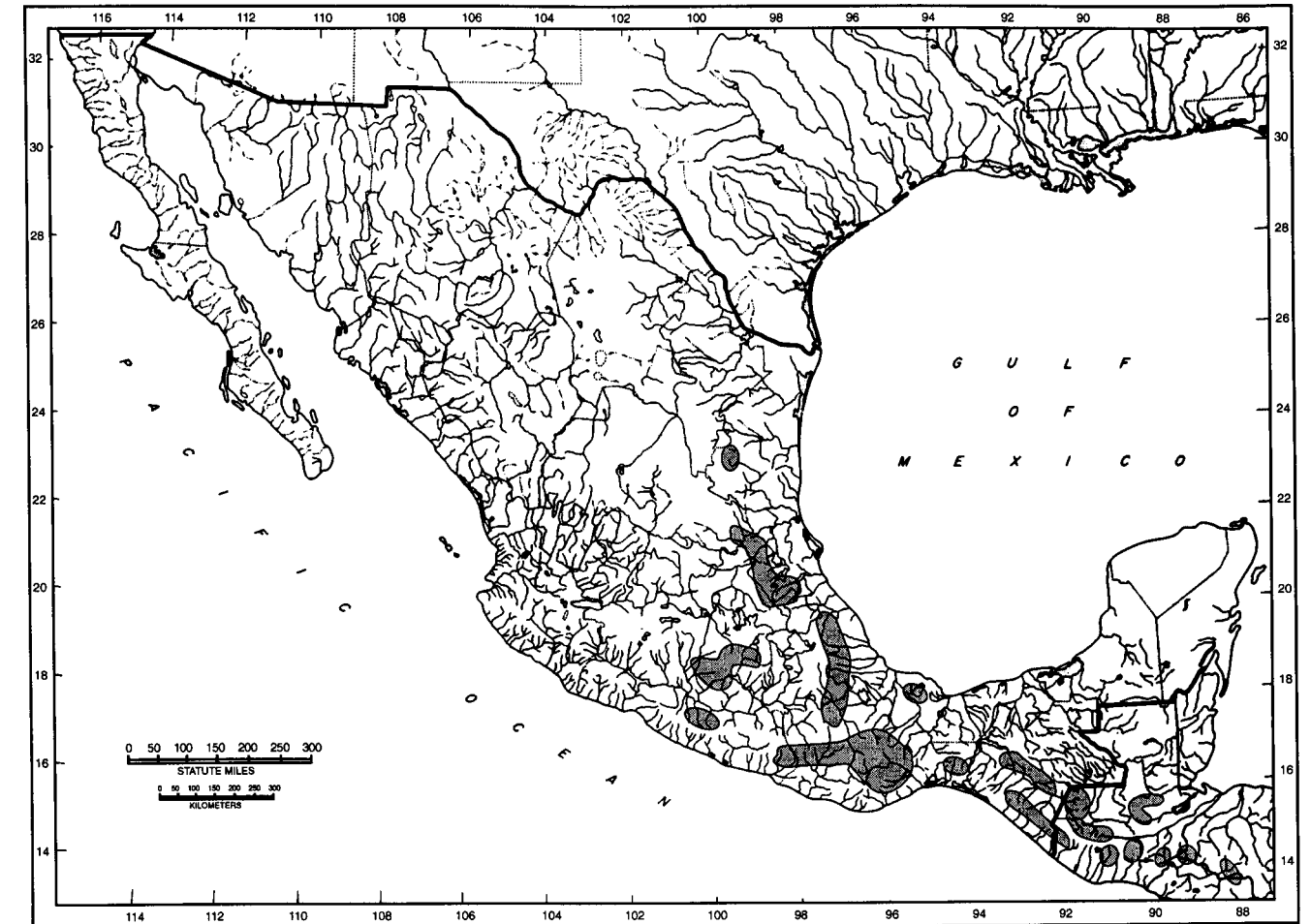


Figure 16.19. Distribution of the lizard genus *Abronia*.

differentiation of sister species in isolated ranges such as the Cordillera Central and Cordillera de Talamanca. An example of this process is the genus *Nototriton* in Costa Rica (fig. 16.22).

Evolution of the Lowland Dry Forest Herpetofauna

The northwestern region of Costa Rica forms the southern terminus of a continuous corridor of thorn woodland and semiarid, deciduous, and semideciduous forests and patches of savanna that extends from Sinaloa, Mexico, southward along the Pacific coast. The Meseta Central Occidental represents a transitional zone between the Lowland Dry Forest of Guanacaste and northern Puntarenas Provinces and more humid formations. Climates and vegetation similar to those found along the Pacific coastal plain also occur on the outer portion of the Yucatán Peninsula and in the rain shadow valleys on the Atlantic versant of nuclear Central America (fig. 16.23).

The disjunct distribution of several amphibians and rep-

tiles in the separate portions of these habitats suggests former continuity. An example is the distribution of the spiny-tailed iguanas of the *Ctenosaura quinquecarinatus* group (fig. 16.24).

Elements of these vegetational formations are of Neotropical-Tertiary geoflora types, but this complex probably represents a transition between the increasingly drier and cooler core of the Madro-Tertiary flora and tropical evergreen formations (Axelrod 1958). By late Oligocene times the relation between these might be visualized as a broad belt of tropical evergreen forest bordered on the north by tropical deciduous forest. The latter in turn was bordered by the horseshoe-shaped enclave of developing Madro-Tertiary vegetation in what is now northern Mexico and the southwestern United States (fig. 16.14). This element would continue to expand over western North America for the rest of Cenozoic to produce the familiar semiarid live oak-conifer woodland, chaparral, arid subtropical scrub, desert grasslands, and subdesert and desert formations.

In the Miocene the northern limits of tropical conditions

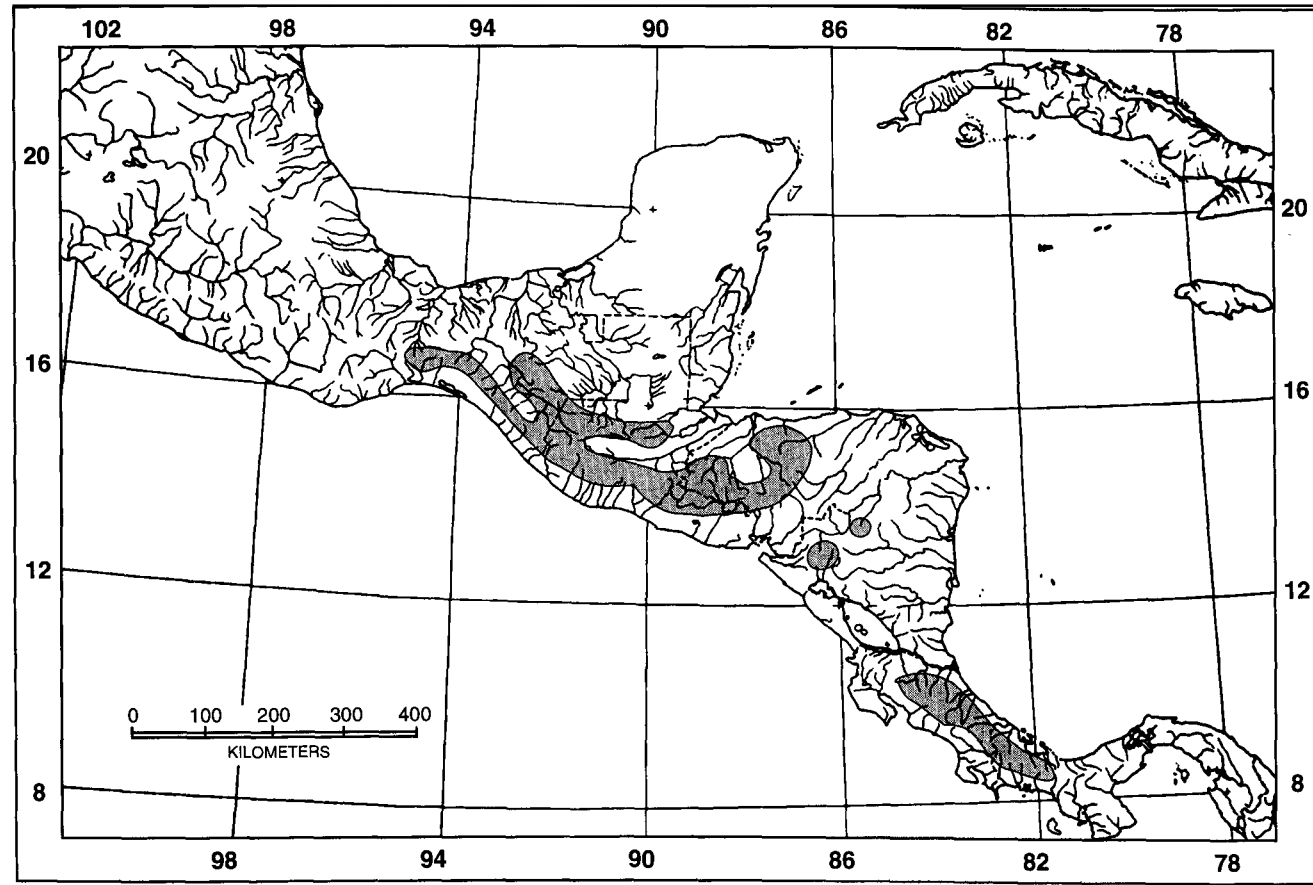


Figure 16.20. Distribution of the snakes of the *Rhadinaea godmani* group.



Figure 16.22. Distribution of the salamanders of the genera *Cryptotriton* and *Nototriton*: triangles = *Cryptotriton*; shading = *Nototriton*; cross = sympatry between the two genera.

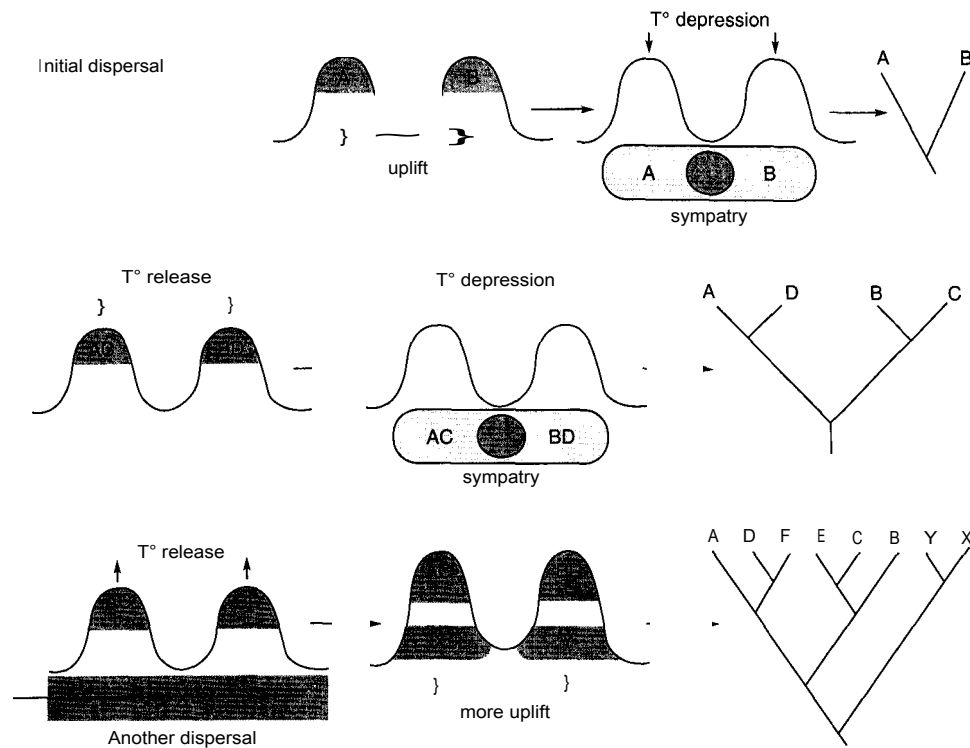


Figure 16.21. Model for montane speciation involving cycles of temperature depression and release beginning in the Pliocene; letters indicate species, cladograms indicate phylogenetic results.

were being restricted farther and farther south. At the same time the uplift of the Mexican Sierra Madres Oriental and Occidental and the Mexican Plateau drove an upland wedge southward that by the mid-Pliocene fragmented the lowland region into Pacific and Atlantic sections connected only across the Isthmus of Tehuantepec.

Herpetofaunal associates of the tropical deciduous forest belt were isolated at this time in three areas: along the western margin of the Gulf of Mexico; the outer margin of the Yucatán Peninsula, but doubtless extending more to the south than now; and western coastal Mexico. An example of a clade now found disjunctly in all three areas are the cantils *Agkistrodon bilineatus* and *A. taylori* (fig. 16.25).

During the rest of Neogene times the rain shadow effect of the rising nuclear Central American mountains combined with the Pacific climatic regimen saw the expansion southward of the subhumid to semiarid formations to replace humid ones for the most part in the western lowlands, producing considerable endemism over time. The herpetofauna of this corridor is more strongly influenced by members of the Central American Component than any other represented in Costa Rica. This fauna probably reached Costa Rica rel-

atively recently, during the time of Quaternary volcanism and after the uplift of the Nicaragua depression just to the north.

The distribution of this fauna in the Atlantic slope rain shadow valleys also appears to represent late Neogene fragmentation of once continuous ranges. Stuart (1954) long ago proposed a subhumid corridor involving dispersal across intermediate pine-oak forest barriers from the Pacific lowlands at the Isthmus of Tehuantepec through the Grijalva valley of Chiapas, Mexico, in the Atlantic drainage and into the semiarid Rio Negro and Rio Motagua valleys of Atlantic slope Guatemala (see also Wilson and McCranie 1998).

Another explanation seems more parsimonious. It is likely that these four areas and the dry Sula and Aguan valleys of Honduras were part of a more or less continuous corridor during glacial maxima in the Pliocene. Subsequent uplift of the Sierra Madre of Chiapas, the transverse ranges of Guatemala, and the Sierra de Oma and Sierra de Sulaco in Honduras appear to have fragmented this corridor into its present components and allowed differentiation of some endemic taxa.

The other isolated dry valleys of more southern Honduras

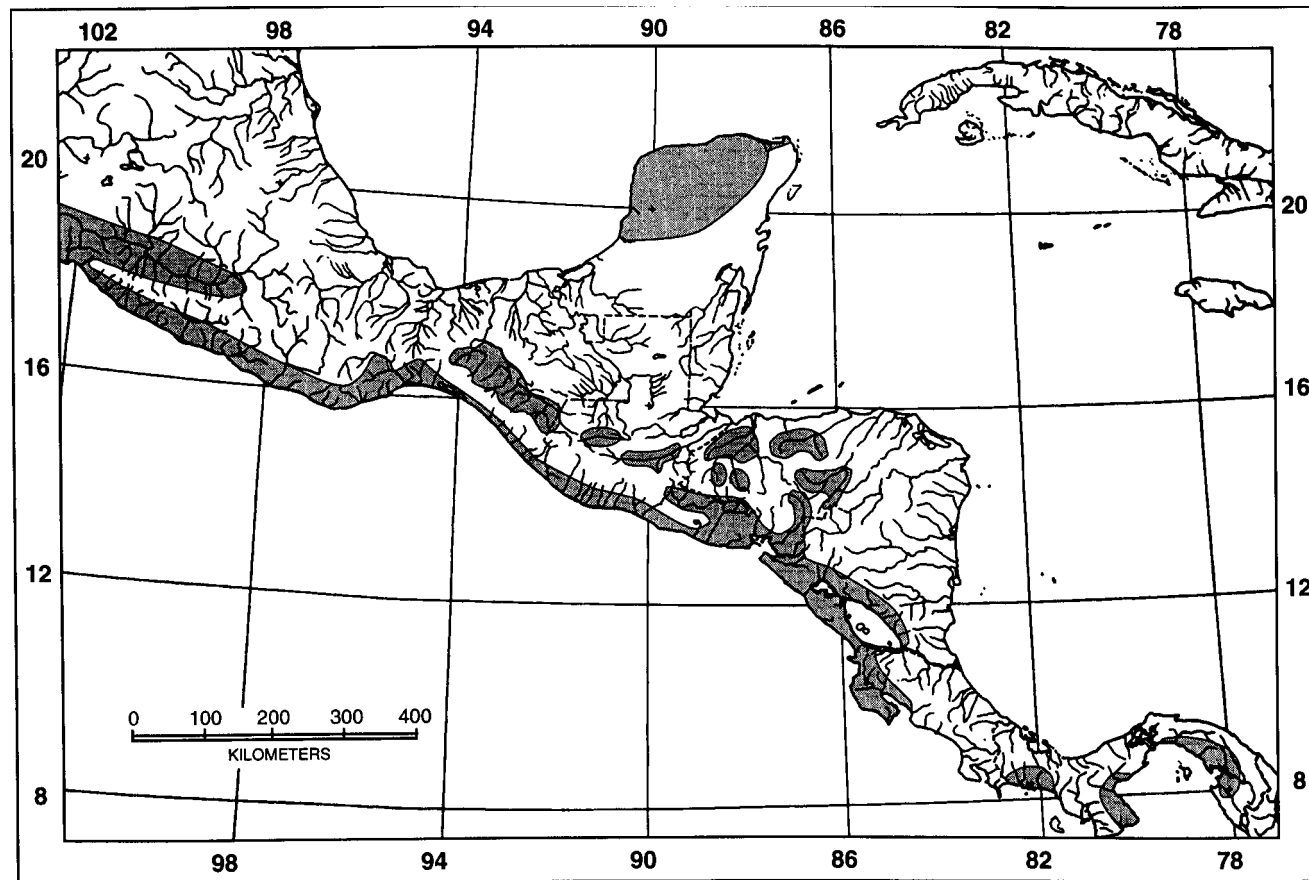


Figure 16.23. Distribution of subhumid to arid climatic conditions in tropical Mesoamerica supporting deciduous forests, thorn forests, thorn woodlands, and savanna. Areas of these types in Panama show little faunal similarity to those from Costa Rica northward.

were probably connected across the low early Pliocene continental divide with the Pacific slope dry corridor. Again Pliocene orogeny, reinforced by Quaternary volcanism, would have isolated the Atlantic sector from the Pacific sector. Although there clearly were considerable expansions of dry forest conditions into areas where evergreen forest now predominates in upper Central America during the Pleistocene, it is unlikely that the various isolated valleys were relinked as in their Pliocene continuities.

Webb (1977, 1978) and Webb and Rancy (1996) proposed that a continuous "savanna" corridor extended through Central America and across the emerging Isthmian Link and served as a major pathway for movements of fauna, as indicated by mammalian fossils, between the Americas in the late Pliocene to mid-Pleistocene. Their concept of "savanna" was broad and was applied to all subhumid to semiarid habitats now represented in Central America, including those discussed in the previous paragraphs. Colinvaux (1996) recently has demonstrated that such a corridor could develop only during glacial periods but found no support in the fossil plant record that one could have existed. All evidence

from herpetofaunal distributions indicates that the Pacific lowland subhumid-semiarid corridor never extended farther south than its present location near 10° N in Costa Rica.

Colinvaux (1993, 1996) has further discredited the notion, first proposed by Haffer (1969), that at times of glacial maxima in the Quaternary lowland evergreen forests and their faunas were replaced in tropical America, except in a few refugia, by dry-adapted formations. According to Haffer and others (Whitmore and Prance 1987), present-day dry forests and related associations have contracted ranges that will expand and reconnect during the next glacial expansion. The Pleistocene alternation of rainforest (interglacial) and dry forest (glacial) expansion and contractions was postulated as being responsible for numerous speciation events. As described above, the distribution of dry forest habitats and their faunal associates are the result of long-term changes in the physiography and climate of Central America in the Neogene, not slight Pleistocene fluctuations. Most important in this regard was the uplift of the central mountain backbone of the region that emphasized the rain shadow effect on the Pacific slope and fragmented Atlantic



Figure 16.24. Distribution of the lizards of the *Ctenosaura quinquecarinatus* group.

dry forest habitats from those on the Pacific and from one another. The strong evidence for these vicariant processes as primary for dry forest development adds support to Colinvaux's refutation of the refugium hypothesis.

WHY THERE ARE SO MANY SPECIES BETWEEN TWO CONTINENTS, BETWEEN TWO SEAS

The present Isthmian Link is relatively recent geologically, having its initial connection to the southern end of the Chortis block between 6 and 10 Ma. Its final emergence as a continuous landmass between North and South America was not permanently effected until the late Pliocene, as recently as 2 Ma. Most of the species in the herpetofauna of Costa Rica and Panama or their ancestors could have migrated onto the link no sooner than 6 or 7 Ma from the north and no more than 3 Ma from the south. Subsequent rapid speciation must have occurred to produce the astonishing diversity characteristic of the region today (table 16.2).

It is not surprising that at the species level the greatest diversity is represented by the representatives of the autochthonous Mesoamerican Element and the coevolving Cen-

tral American Component that developed in situ in tropical Middle America throughout the Tertiary (table 16.3). Fully 70% of the species found in Costa Rica and elsewhere on the Link are derivatives of these historical units. There may have been some minimal overwater dispersal to the island precursors of the Isthmus in the early Miocene, but it is clear that the central core of the herpetofauna dispersed from nuclear Central America after the island chain became connected via the Chortis block. Without question, the availability of the many unoccupied ecological niches for amphibians and reptiles led to substantial differentiation. Within the Central American herpetofauna 156 species are endemic to Costa Rica and western Panama. Of these endemics, 54% are Mesoamerican Element species and 29% are Central American Component representatives. Of the total Costa Rican-western Panamanian herpetofauna, Mesoamerican Element forms endemics make up 20% and Central American Component 11% of the species.

The second principal factor contributing to differentiation was the continuing uplift and volcanic activity on the emerging Isthmus (Gardner et al. 1987). These processes opened new habitats and fragmented old ones. Volcanic eruptions and Lava flows constantly modified topography

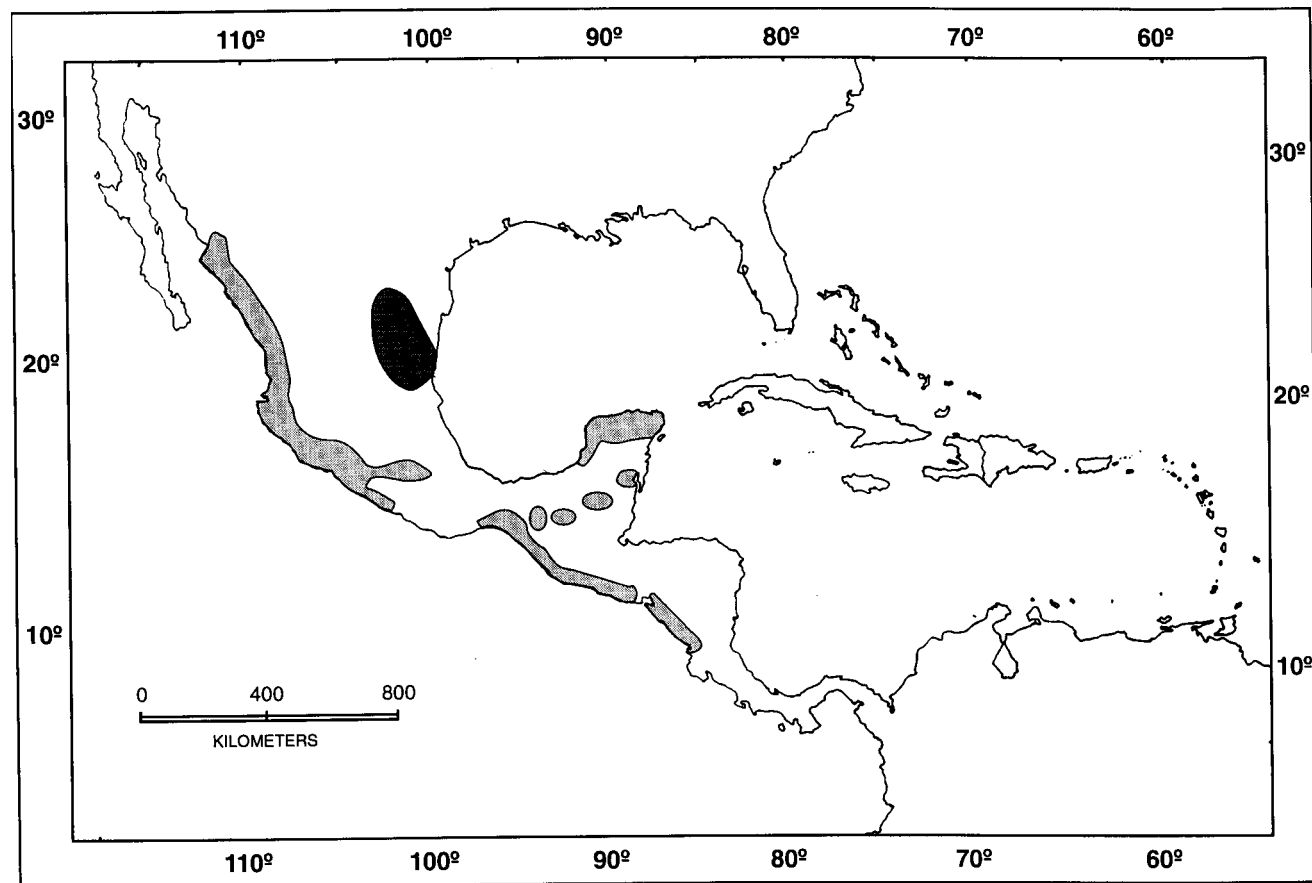


Figure 16.25. Distribution of the cantils *Agkistrodon bilineatus* and *A. taylori*, light and darker shading, respectively.

Table 16.2. Comparison of Species Numbers and Relative Species Richness (ISR) for Selected Geographit Areas

Geographit Unit	N	Area (km ²)	ISR
United States	547	7,828,080	0.0007
Mexico	997	1,972,545	0.0005
California	126	441,015	0.03
Florida	122	151,670	0.08
Cuba	158	114,524	0.13
Guatemala	325	108,889	0.29
Oaxaca	355	95,364	0.37
Panama	399	75,474	0.53
Costa Rica	383	50,900	0.75

Introduced and marine species not included.

Index of Species Richness (ISR) = $N/kma \times 100$.

and produced a constantly changing mosaic of isolated areas where speciation could occur. The orogenic influence cannot be overemphasized as a factor in the diversification of the many upland endemics in the region.

The fluctuations of cooling and warming cycles in the latter part of the Cenozoic, in association with the continued uplift of the cordilleras, provided additional impetus for speciation. At times of glacial maximum the compression of

altitudinal zones produced environments in the lowlands most closely resembling those of midelevation forests (500 to 1,600 m) at present. This situation allowed cool-adapted members of the herpetofauna to migrate between separate mountain masses and volcanoes, where during times of warmer conditions the corridor was broken and each allopatric montane population had the opportunity for differentiation. The several glacial cycles created multiple opportunities for this process to be repeated, with potential for further speciation events (fig. 16.21).

A fourth factor in the assemblage of the diverse Costa Rican herpetofauna was the reconnection of Central America to South America by the completed Isthmian Link. This resulted in the invasion of Central America by South American Element taxa long isolated from any relatives to the north. In Costa Rica and western Panama, endemics derived from this source make up 12% of the endemics and 4% of the total species in the herpetofauna. Some of these species doubtless are descendants of ancestors that crossed the first bridge that closed the seaway, and others probably arrived after the second closure proposed by Cronin and Dowsett (1996). In either case they arrived after the Mesoamerican

Table 16.3. Numbers (Upper Figure) of Species and Percentage (Lower Figure) of Total Costa Rican Herpetofauna by Historical Source Unit

Group	Old Northern			Mesoamerican	South American	Totals
	CAC	EAC	WAC			
Caecilians				3	1	4
				0.7	0.25	1
Salamanders	37			—		37
	10			0		9
Anurans	4	2		66	59	131
	1	0.5		17	15	34
Total amphibians	41	2		69	60	172
	10	0.5		18	15	45
Lizards	8	—	4	36	21	69
	2		1	9	6	18
Snakes	51	4	1	60	6	133
	13	1	0.25	16	4	35
Turtles		2				8
	1.6	0.5				2
Crocodylians				1	1	2
				0.25	0.25	0.5
Total reptiles	65	6	5	97	38	211
	17	1.6	1.3	26	10	55
Grant total	106	8	5	166	98	383
	28	2.1	1.3	43	26	100

Seven marine species and six introduced species not included.

Element and Central American Component units were well in place and make up a significant but smaller percentage (26%) of the total species in the fauna.

The final act, bringing our story to its dose, was the rather recent movement of dry forest taxa into northwestern Costa Rica and onto the Meseta Central. Late Quaternary volcanism was the principal factor in reducing the effects of the northeast trade winds on the Pacific slope. Increasingly xeric conditions in the northwest, unmitigated by monsoonal flow from the Southern Hemisphere, created an opportunity for northern forms to penetrate the formerly humid lowlands. The recency of these events is demonstrated by the absence of any species strictly endemic to this region of Costa Rica and the dose resemblance of its herpetofauna to that of the subhumid to semiarid lowlands from Guatemala south.

The population of the Meseta Central Occidental by dry forest species may imply a recent ongoing dispersal event. On the other hand, both mesetas may have been covered by dry forest earlier in history, and perhaps their continuing uplift has merely carried dry forest taxa upward in the process.

The former hypothesis suggests that the Subset of dry forest amphibians and reptiles on the Meseta are good dispersers with more to follow. The second hypothesis is that they are holdovers and are gradually slipping off the Pacific side from the Meseta Central Occidental as uplift continues, a process that will ultimately lead to their extinction on the Meseta Central Oriental.

Documentation of herpetofaunal diversity for Costa Rica remains incomplete. Recognition and description of species new to science by several authors is ongoing, and some of these works will doubtless appear while this book is in press. Still other species will be discovered in the future in underexplored areas of the republic as access increases and habitat destruction accelerates. *Vaya bien* to all of you searchers on this rich coast. May you too emerge from the forest of interlocking opposites on the Pass of Desengafio while following the trail of the golden frog to new and exciting discoveries. ; *Pura vida!*