# 15 Geographic Distribution

## Historical Units, Faunal Areas, Endemism, and General Patterns

THE HERPETOFAUNA of Costa Rica lives between two continents and between two great seas that were connected by a broad seaway through most of Cenozoic times. The Isthmian Link between North and South America, formed mostly by present-day Costa Rica and Panama, has only recently been established to allow a mixing of major faunal elements from the two continents. Present patterns of distribution, however, are not simply products of the development of the recent land bridge, since a much earlier one connected the continents during the beginning of the Cenozoic, with effects still reflected in the composition of the isthmian herpetofauna.

For these reasons, any attempt to explain the biogeography of amphibians and reptiles in the region must recognize that the Costa Rican herpetofauna is embedded within a broader Tropical Mesoamerican faunal unit. This fauna formerly ranged much farther to the north but has become restricted to more southern latitudes by cooling and drying trends from the Oligocene onward and today is found in the tropical lowlands and premontane slopes from Tamaulipas and Sinaloa, Mexico, southward over southern Mexico and all of Central America. In addition, it mixes in a complex fashion with representatives of the northern or Nearctic herpetofauna an the slopes of the mountains bordering the central plateau of Mexico and with that of South America, principally in northern and northwestern areas of that continent.

## COMPOSITION OF THE HERPETOFAUNA

The herpetofauna of the Tropical Mesoamerican unit comprises the following numbers of families and genera (tables 15.2, 15.3): Caecilians 1/4, salamanders 1/13, anurans 9/43, lizards 16/47, snakes 9/97, turtles 5/9, crocodilians 1/2; total 42/215. The numbers of families and genera of amphibians and reptiles living in Central America are caecilians 1/4, salamanders 1/8, anurans 9/38, lizards 14/41, snakes 11/79, turtles 5/9, crocodilians 1/2; total 40/18 1.

The genera of the Tropical Mesoamerican unit may be placed into one of four major groupings based an their 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
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 shown in table 15.1.

These data demonstrate that the Central American herpetofauna is composed primarily of genera with one of two major distribution patterns. The first (I) includes those genera with a tropical Middle American distribution that predominate an the lowlands and slopes in Mexico from Sinaloa and Tamaulipas southward and at all elevations east of the Isthmus of Tehuantepec to central Panama. The other (II) comprises genera with a South American distribution pattern and is most fully represented in the Central American region in Panama. Of the 215 genera in tropical Mesoamerica, 55% have their distribution centered there, 29% are South American, and 10% are extratropical (Nearctic) in pattern. North of Costa Rica only 21 genera (10%) are South American groups, while in eastern Panama 62 genera are South American (55% of the herpetofauna in the area). These data and the distribution of the 65 families of American amphibians and reptiles (table 15.2) are the basis (Savage 1966a,1982) for recognizing the Middle American tropical assemblage as a biogeographic unit equivalent to the Nearctic and Neotropical units of traditional biogeography (Darlington 1957).

Within the tropical Middle America region seven major herpetofaunal assemblages may be recognized:

1. Eastern and Western Lowland Herpetofauna: a wide-ranging fauna, the most diverse and the richest in species composition in the region, 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 an the Pacific lowlands of southwestern Costa Rica and extreme western Panama.



Table 15.1. Distribution of Tropical Mesoamerican Genera of Living Amphibians and Reptiles

| | |
|---|---|
| **1. Widespread Tropical (8)** | |
| *Eleutherodactylus* | *Mabuya* |
| *Bufo* | *Leptotyphlops* |
| *Phrynohyas* | *Micrurus* |
| *Hyla* | *Bothrops* |
| **2. South American (62)** | |
| A. Northern Limit of Range in Panama (22) | |
| *Caecilia* | *Echinosaura* |
| *Protopipa* | *Prionodactylus* |
| *Rhamphophryne* | *Amphisbaena* |
| *Epipedobates* | *Trachyboa* |
| *Minyobates* | *Atractus* |
| *Chiasmocleis* | *Diaphorolepis* |
| *Elachistocleis* | *Phimophis* |
| *Hemiphractus* | *Pseudoboa* |
| *Pleurodema* | *Siphliophis* |
| *Morunasaurus* | *Bothriopsis* |
| *Enyalioides* | *Chelonoides* |
| B. Northern Limit of Range in Costa Rica (19) | |
| *Oscaecilia* | *Neusticurus* |
| *Gastrotheca* | *Anadia* |
| *Nelsonophryne* | *Anomalepis* |
| *Phyllobates* | *Helminthiophis* |
| *Colostethus* | *Liotyphlops* |
| *Phyllomedusa* | *Epicrates* |
| *Atelopus* | *Liophis* |
| *Dactyloa* | *Tripanurgos* |
| *Bachia* | *Ptychoglossus* |
| *Leposoma* | |
| C. Northern Limit of Range Between Costa Rica and Guatemala (9) | |
| *Centrolenella* | *Corallus* |
| *Cochranella* | *Erythrolamprus* |
| *Dendrobates* | *Nothopsis* |
| *Polychrus* | *Lachesis* |
| *Diploglossus* * | |
| D. Northern Limit of Range in Mexico (12) | |
| *Leptodactylus*** | *Gymnophthalmus* |
| *Physalaemus* | *Typhlops* |
| *Scinax* | *Clelia* |
| *Hyalinobatrachium* | *Oxyrhopus* |
| *Ameiva* | *Xenodon* |
| *Gonatodes* | *Caiman* |
| **3. Tropical Middle American (119)** | |
| A. Endemics (44) | |
| *Gymnopis* | *Anotheca* |
| *Bradytriton* | *Abronia* |
| *Cryptotriton* | *Coloptychon* |
| *Dendrotriton* | *Loxocemus* |
| *Ixalotriton* | *Adelphicos* |
| *Nototriton* | *Amastridium* |
| *Nyctanolis* | *Chapinophis* |
| *Pseudoeurycea* | *Crisantophis* |
| *Atelophryniscus* | *Conophis* |
| *Crepidophyrne* | *Hydromorphus* |
| *Duellmanohyla* | *Leptodrymus* |
| *Plectrohyla* | *Scolecophis* |
| *Ptychohyla* | *Symphimus* |
| *Triprion* | *Tantillita* |
| *Corytophanes* | *Trimetopon* |
| *Aristelliger* | *Tropidodipsas* |
| *Laemanctus* | *Atropoides* |
| *Ctenosaura* | *Cerrophidium* |
| *Lepidophyma* | *Porthidium* |
| *Celestus* * | *Claudius* |
| *Mesaspis* | *Staurotypus* |
| *Xenosaurus* | *Dermatemys* |
| B. Northern Limit of Range in Extratropical North America (19) | |
| *Rhinophrynus* | *Drymarchon* |
| *Hypopachus* | *Drymobius* |
| *Gastrophryne* | *Ficimia* |
| *Syrrhophus* | *Oxybelis* |
| *Coleonyx* | *Leptodeira* |
| *Phyllodactylus* | *Rhadinaea* |
| *Heloderma* | *Tantilla* |
| *Cnemidophorus* | *Trimorphodon* |
| *Gerrhonotus* | *Kinosternon* |
| *Coniophanes* | |
| C. Southern Limit of Range in Northern andlor Northwestern South America (21) | |
| *Dermophis* | *Ninia* |
| *Oedipina* | *Rhinobothryum* |
| *Agalychnis* | *Scaphiodontophis* |
| *Smilisca* | *Sibon* |
| *Basiliscus* | *Stenorrhina* |
| *Lepidoblepharis* | *Tretanorhinus* |
| *Thecadactylus* | *Urotheca* |
| *Ungaliophis* | *Bothriechis* |
| *Dendrophidion* | *Rhinoclemmys* |
| *Enulius* | *Crocodylus* |
| *Geophis* | |
| D. Southern Limit of Range in Amazon Basin or Farther South (12) | |
| *Bolitoglossa* | *Chironius* |
| *Norops* | *Imantodes* |
| *Iguana* | *Leptophis* |
| *Sphaerodactylus* | *Mastigodryas* |
| *Boa* | *Pseustes* |
| *Dipsas* | *Spilotes* |
| E. Endemic Genera in Tropical to Subtropical Mexico (23) | |
| *Chiropterotriton* | *Adelophis* |
| *Lineatriton* | *Chersodromus* |
| *Parvimolge* | *Cryophis* |
| *Thorius* | *Conopsis* |
| *Hylactophryne**** | *Geagras* |
| *Pachymedusa* | *Manolepis* |
| *Pternohyla* * * * | *Pseudoficimia* |
| *Anelytropsis* | *Rhadinophanes* |
| *Barisia* | *Sympholis* |
| *Bipes* | *Tantalophis* |
| *Exiliboa* | *Toluca* |
| *Ophryacus* | |
| **4. Extratropical North American (34)** | |
| A. Southern Limit of Range in Tropical Mexico (18) | |
| 1) Southern Limit of Range in Central or Southern Mexico (10) | |
| *Scaphiopus* | *Gyalopion* |
| *Sisturus* | *Hypsiglena* |
| *Phrynosoma* | *Rhinocheilus* |
| *Urosaurus* | *Sonora* |
| *Ophisaurus* | *Salvadora* |
| 2) Southern Limit of Range Marginally Tropical (8) * * * * | |
| *Siren* | *Holbrookia* |
| *Notophthalmus* | *Anolis* |
| *Callisaurus* | *Arizona* |
| *Dipsosaurus* | *Micruroides* |
| B. Southern Limit of Range in Central America (10) | |
| *Terrapene* | *Storeria* |
| *Sceloporus* | *Nerodia* |
| *Eumeces* | *Elaphe* |
| *Sphenomorphus* | *Thamnophis* |
| *Pituophis* | *Agkistrodon* |
| C. Southern Limit of Range in South America (6) | |
| *Rana* | *Crotalus* |
| *Coluber* | *Chelydra* |
| *Lampropeltis* | *Chrysemys*"*** |

*Note:* The lizard genus *Phyllodactylus* and the snake genera *Coniophanes* and *Drymobius* range south to Western Peru; the lizard genus *Cnemidophorus* and the snake genera *Drymarchon, Leptodeira, Oxybelis,* and *Tantilla* range to the Amazon basin or farther south.

* Also in Antilles

* * Also in Antilles and reaches southern United States.

Occurs in southern United States

"* The eight genera below are not treated further in this book and have been included here only for the sake of completeness.

"* * Includes *Pseudemys* and *Trachemys*

Table 15.2. Distribution of New World Families of Amphihians and Nonmarine Reptiles

| Restricted to One Geographic Region (28) | | |
|---|---|---|
| Nearctic (12) | Tropical Mesoamerica (6) | South America (10) |
| Cryptobranchidae | Rhinophrynidae | Rhinatrematidae |
| Sirenidae | Dibamidae | Typhlonectidae |
| Rhyacotritonidae | Xenosauridae | Pipidae" |
| Proteidae | Loxocemidae | Rhinodermatidae |
| Amphiumidae | Ungaliophiidae | Brachycephalidae |
| Dicamptodontidae | Dermatemydidae | Allophrynidae |
| Salamandridae | | Pseudidae |
| Ambystomatidae | | Aniliidae |
| Ascaphidae | | Pelomedusidae |
| Pelobatidae | | Chelidae |
| Crotaphytidae | | |
| Trionychidae | | |
| **Occurring in Two Region (16)** | | |
| Nearctic-Tropical Mesoamerica (5) | South America-Nearctic (1) | Tropical Mesoamerica-South America (10) |
| Phrynosomatidae | Testudinidae° | Caeciliidae |
| Eublepharidae | | Centrolenidae |
| Bipedidae | | Dendrobatidae |
| Xantusiidae | | Corytophanidae |
| Helodermatidae | | Hoplocercidae |
| | | Gymnophthalmidae |
| | | Amphisbaenidae |
| | | Anomalepididae |
| | | Typhlopidae |
| | | Trophidophiidae" |
| **Occurring in All Three Regions (21)** | | |
| Plethodontidae | Iguanidae | Elapidae |
| Leptodactylidae | Polychrotidae'"° | Viperidae |
| Bufonidae | Gekkonidae | Kinosternidae |
| Hylidae | Teiidae | Chelydridae |
| Michrohylidae | Scincidae | Emydidae |
| Ranidae | Anguidae | Crocodylidae |
| | Leptotyphlopidae | |
| | Boidae | |
| | Colubridae | |

Reaching Eastern Panama from South.

" One Nearctic species.

2. Pacific Lowland Herpetofauna: a fauna associated with semiarid to subhumid climatic conditions, ranging along the Pacific lowlands from northern Sinaloa in Mexico to the Golfo de Nicoya region and Meseta Central of Costa Rica; includes the subhumid and semiarid assemblages of Atlantic drainage valleys in Chiapas, Mexico, Guatemala, and Honduras and the uplands of Honduras and Nicaragua; characterized by a predominance of lizard and snake species and virtual absence of salamanders.
3. Mexican Highland Herpetofauna: an assemblage restricted to the Sierras of tropical Mexico.
4. Nuclear Highland Herpetofauna: an assemblage restricted to the cool, moist habitats of the Chiapas, Guatemala, and Honduras highlands.
5. Talamancan Herpetofauna: a fauna with a well-developed amphibian complement, occurring in the humid environments of highland Costa Rica and western Panama.
6. 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 affinities to the herpetofaunas of northern lowland Colombia and Venezuela that are associated with subhumid to arid conditions along the Caribbean lowlands.
7. Chocoan Herpetofauna: a South American fauna, extremely rich in species composition, found along the Pacific lowlands from northern Ecuador through Colombia and entering eastern Panama, where it is found in the Darien region and along the Caribbean versaut.

The tropical subhumid to semiarid areas of the northern Yucatän Peninsula (Lee 1996) are something of an enigma under this scheme, since they are characterized by a mixture of taxa having affinities to both faunas 1 and 2.

The approximate geographic limits of the assemblages are indicated in figure 15.1. The distribution by genus of all members of the Tropical Mesoamerican herpetofauna is presented in tables 15.3 to 15.7.

Table 15.8 shows the proportion of genera of each major group to the total Tropical Mesoamerican complement of genera in each assemblage and the proportion each makes up within a particular assemblage. The numbers of genera of caecilians, turtles, and crocodilians are so low as to have no significant effect an comparisons. However, rote that turtles and crocodilians are absent from the highland faunas and caecilians are virtually absent.

Other comparisons are somewhat distorted by the unequal number of amphibian genera (60) in relation to reptile genera (155), with a heavy predominance of snake genera (97). Salamanders make their major contribution to the faunas of upland regions. Anurans and lizards contribute nearly equally to all assemblages except that the number of lizard genera is disproportionally greater in the Mexican Highland fauna, with the reverse most striking in the Talamancan Highland fauna. In most faunas the combined proportions of amphibian plus lizard genera are about equal to that of snake genera alone. The most striking exceptions are in the Pacific Lowland assemblage (amphibians plus lizards 39%, snakes 54%), the Mexican Highland assemblage (amphibians plus lizards 44%, snakes 56%), and the Talamancan Highland fauna (amphibians plus lizards 60%, snakes only 40%).

In terms of diversity by taxonomic dass, amphibians reach their zenith in the Talamancan Highland fauna (19 genera, 47% of the assemblage) and reptiles in the humid East and West Lowland assemblage. However the Pacific Lowland, Mexican Highland, and Chocoan faunas also have very high values for the reptile contributions to their faunas, but many

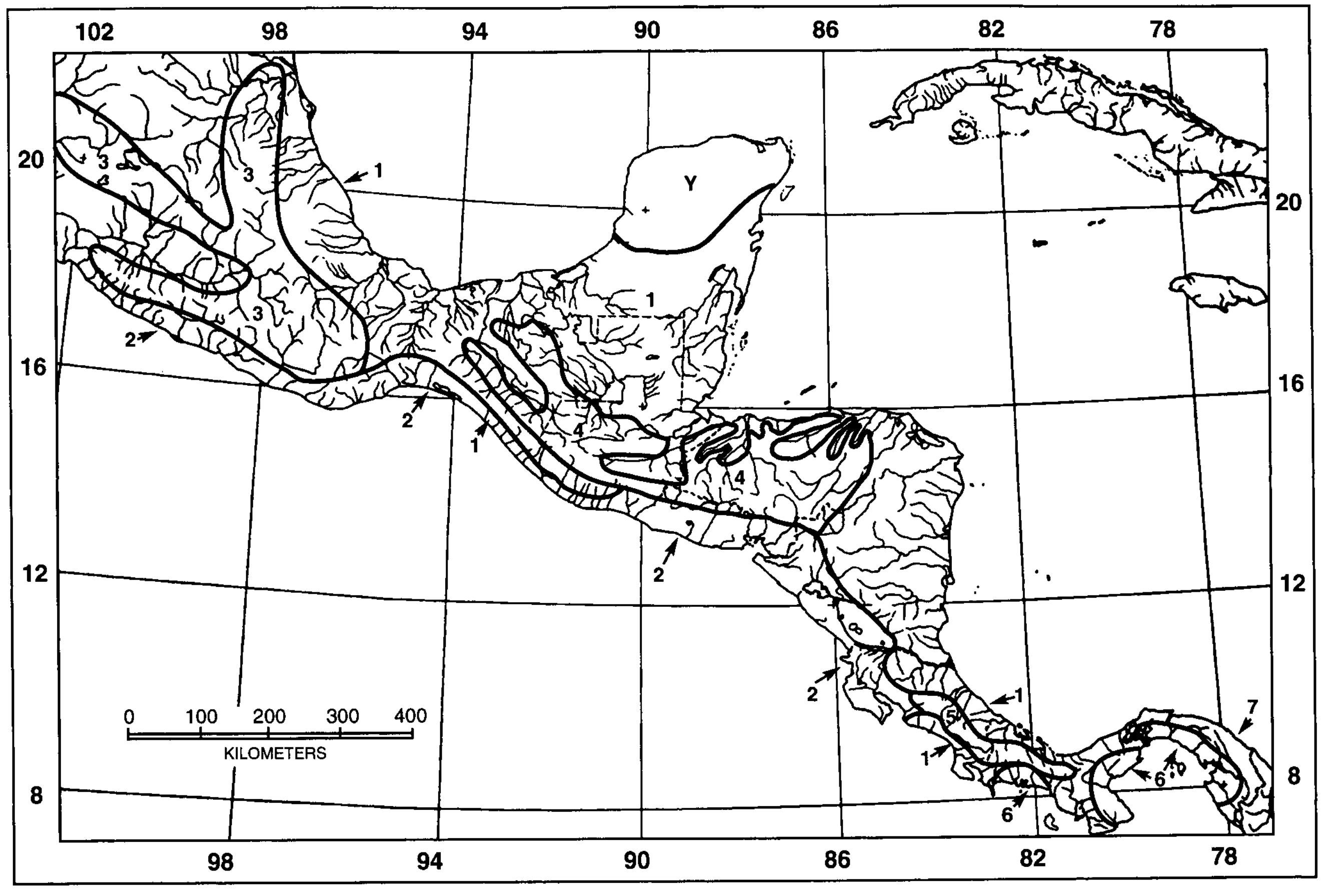


Figure 15.1. Central American herpetofaunas.

Table 15.3. Distribution of Caecilian and Salamander Genera in Tropical Mesoamerica

| | Humid East and West Lowland | Pacific Lowland | Mexican Highland | Nuclear Highland | Talamancan Highland | Panamanian | Chocoan |
|---|---|---|---|---|---|---|---|
| Gymnophiona (4) | | | | | | | |
| *Caecilia* | X | | | | X | | X |
| *Dermophis* | X | X | | | | | X |
| *Gymnopis* | X | | | | | | X |
| *Oscaecilia* | X | | | | | X | X |
| TOTAL | 4 | 1 | | | 1 | 1 | 4 |
| Caudata (13) | | | | | | | |
| *Bolitoglossa* | X | | X | X | X | | X |
| *Bradytriton* | | | | X | | | |
| *Chiropterotriton* | | | X | | | | |
| *Cryptotriton* | | | X | X | | | |
| *Dendrotriton* | | | | X | | | |
| *Ixalotriton* | | | | X | | | |
| *Lineatriton* | | | X | | | | |
| *Nototriton* | | | | | X | | |
| *Nyctanolis* | | | | X | | | |
| *Oedipina* | X | X | | X | X | | X |
| *Parvimolge* | | | X | | | | |
| *Pseudoeurycea* | | | X | | | | |
| *Thorius* | | | X | | | | |
| TOTAL | 2 | 1 | 7 | 7 | 3 | 0 | 2 |

Table 15.4. Distribution of Anuran Genera in Tropical Mesoamerica

| | Humid East and West Lowland | Pacific Lowland | Mexican Highland | Nuclear Highland | Talamancan Highland | Panamanian | Chocoan |
|---|---|---|---|---|---|---|---|
| Anura (43) | | | | | | | |
| *Protopipa* | | | | | | X | |
| *Rhino phrynus* | X | X | | | | X | X |
| *Scaphiopus* | | X | | | | | |
| *Eleutherodactylus* | X | X | X | X | X | | X |
| *Hylactophryne* | | | X | | | | |
| *Leptodactylus* | X | X | | | | | |
| *Physalaemus* | X | X | | | | X | X |
| *Pleurodema* | | | | | | X | |
| *Syrrhopus* | X | X | | | | | |
| *Atelophryniscus* | | | | X | | | |
| *Atelopus* | X | | | | X | | X |
| *Bufo* | X | X | X | X | X | X | X |
| *Crepidophryne* | | | | X | | | |
| *Rhamphophryne* | | | | | | | X |
| *Agalychnis* | X | | | X | X | X | X |
| *Anotheca* | X | | X | | | | |
| *Duellmanohyla* | | | X | X | X | | |
| *Gastrotheca* | X | | | | | | X |
| *Hemiphractus* | X | | | | | | X |
| *Hyla* | X | X | X | X | X | X | X |
| *Pachymedusa* | | X | | | | X | |
| *Phrynohyas* | X | X | | | | | |
| *Phyllomedusa* | | | | | X | | X |
| *Plectrohyla* | | | X | X | | | |
| *Pternohyla* | | X | X | | | | |
| *Ptychohyla* | | | X | X | | | |
| *Scinax* | X | X | | | | X | X |
| *Smilisca* | X | x | | | | X | X |
| *Triprion* | X | x | | | | | |
| *Phyllobates* | X | | | | | | |
| *Centrolenella* | X | | | | x | | X |
| *Cochranella* | X | | | | x | | X |
| *Hyalinobatrachium* | X | | | | x | | X |
| *Colostethus* | X | | | | x | | X |
| *Dendrobates* | X | | | | x | | X |
| *Epipedobates* | | | | | X | | |
| *Minyobates* | X | | | | | | X |
| *Chiasmocleis* | X | | | | | | |
| *Gastrophryne* | X | x | | | | | |
| *Elaschistocleis* | | | | | | X | |
| *Hypopachus* | | X | | x | | | |
| *Nelsonophryne* | X | | | | x | | |
| *Rana* | X | x | x | x | x | x | X |
| TOTAL | 27 | 17 | 10 | 11 | 15 | 12 | 20 |

Table 15.5. Distribution of Lizard Genera in Tropical Mesoamerica

| | Humid East and West Lowland | Pacific Lowland | Mexican Highland | Nuclear Highland | Talamancan Highland | Panamanian | Chocoan |
|---|---|---|---|---|---|---|---|
| Sauria (47) | | | | | | | |
| *Basiliscus* | x | x | | | | x | x |
| *Corytophanes* | X | | | | | | X |
| *Laemanctus* | X | | | | | | |
| *Ctenosaura* | X | x | | | | X | |
| *Iguana* | X | x | | | | X | X |
| *Morunasaurus* | X | | | | | | |
| *Enyalioides* | | | | | | | X |
| *Dactyloa* | X | | | | | | X |
| *Norops* | X | x | x | x | x | x | X |
| *Polychrus* | X | | | | | | X |
| *Phrynosoma* | | X | x | | | | |
| *Sceloporus* | | X | x | x | x | | |
| *Urosaurus* | | X | | | | | |
| *Coleonyx* | X | x | | | | | |
| *Aristelliger* | X | | | | | | |
| *Phyllodactylus* | X | x | | | | | |
| *Thecadactylus* | X | | | | | | X |

Table 15.5. continued

| | Humid East and West Lowland | Pacific Lowland | Mexican Highland | Nuclear Highland | Talamancan Highland | Panamanian | Chocoan |
|---|---|---|---|---|---|---|---|
| *Gonatodes* | X | X | | | | X | X |
| *Lepidoblepharis* | X | | | | | | X |
| *Sphaerodactylus* | X | X | | | | X | X |
| *Lepidophyma* | X | X | X | X | | | |
| *Ameiva* | X | X | | X | | X | X |
| *Cnemidophorus* | X | X | X | | | | |
| *Anadia* | | | | | X | | X |
| *Bachia* | X | | | | | X | |
| *Echinosaura* | X | | | | | | X |
| *Gymnophthalmus* | X | X | | | | X | X |
| *Leposoma* | X | | | | | | |
| *Neusticurus* | | | | | | | |
| *Prionodactylus* | | | | | | | X |
| *Ptychoglossus* | X | | | | | | X |
| *Amphibaenea* | X | | | | | X | X |
| *Bipes* | | X | | | | | |
| *Eumeces* | X | X | X | X | | | |
| *Mabuya* | X | X | X | | | X | X |
| *Sphenomorphus* | X | | X | X | | | |
| *Anelytropsis* | X | | X | | | | |
| *Celestus* | X | | X | X | X | | |
| *Diploglossus* | X | | | | | | X |
| *Abronia* | | | X | X | | | |
| *Barisia* | | | X | | | | |
| *Coloptychon* | X | | | | | | |
| *Gerrhonotus* | | | X | | | | |
| *Mesaspis* | | | X | X | X | | |
| *Ophisaurus* | X | | | | | | |
| *Xenosaurus* | | | x | X | | | |
| *Heloderma* | | x | | | | | |
| TOTAL | 34 | 19 | 15 | 10 | 5 | 11 | 20 |

Table 15.6. Distribution of Snake Genera in Tropical Mesoamerica

| | Humid East and West Lowland | Pacific Lowland | Mexican Highland | Nuclear Highland | Talamancan Highland | Panamanian | Chocoan |
|---|---|---|---|---|---|---|---|
| Serpentes (97) | | | | | | | |
| *Anomalepis* | x | | | | | | |
| *Helminthophis* | | | | | | | X |
| *Liotyphlops* | X | | | | | x | |
| *Typhlops* | X | | x | x | x | | |
| *Leptotyphlops* | X | x | x | x | | x | |
| *Loxocemus* | | X | | | | | |
| *Boa* | X | x | | | | x | x |
| *Corallus* | x | | | | | x | x |
| *Epicrates* | X | x | | | | x | x |
| *Trachyboa* | | | | | | | X |
| *Exiliboa* | | | X | | | | |
| *Ungaliophis* | X | x | | | | | |
| *Adelophis* | | X | | | | | |
| *Adelphicas* | | | | X | | | |
| *Amastridium* | X | | | | x | | |
| *Atractus* | | | | | | | X |
| *Chapinophis* | | | | X | | | |
| *Chersodromus* | | | X | | | | |
| *Chironius* | X | | | | | X | |
| *Clelia* | X | x | | x | x | | x |
| *Coluber* | X | x | x | x | | x | |
| *Conio phanes* | X | x | x | | | | X |
| *Conophis* | | X | | | | | |
| *Conopsis* | | | X | | | | |
| *Crisantophis* | | X | | | | | |
| *Cryophis* | | | X | | | | |
| *Dendrophidion* | X | | | | x | | X |
| *Diaphorolepis* | | | | | | | X |
| *Dipsas* | X | x | | | | | X |
| *Drymarchon* | X | x | x | x | | X | x |

continued

Table 15.6. continued

| | Humid East and West Lowland | Pacific Lowland | Mexican Highland | Nuclear Highland | Talamancan Highland | Panamanian | Chocoan |
|---|---|---|---|---|---|---|---|
| *Drymobius* | X | X | X | X | | X | X |
| *Elaphe* | X | | X | X | | | |
| *Enulius* | X | X | | | | X | X |
| *Erythrolamprus* | X | X | | | | | X |
| *Ficimia* | X | X | | | | | |
| *Geargas* | X | | | | | | |
| *Geophis* | X | X | X | X | X | | X |
| *Gyalopion* | | | X | | | | |
| *Hydromorphus* | X | | | | X | | |
| *Hypsiglena* | | X | X | | | | |
| *Imantodes* | X | X | | | | X | X |
| *Lampropeltis* | X | X | X | X | X | X | X |
| *Leptodeira* | X | X | X | | | X | X |
| *Leptodrymus* | | X | | | | | |
| *Leptophis* | X | X | X | X | X | | X |
| *Liophis* | X | | | | X | | X |
| *Manolepis* | | X | X | | | | |
| *Mastigodryas* | X | X | | X | | X | X |
| *Nerodia* | X | | | | | | |
| *Ninia* | X | X | X | X | X | | X |
| *Nothopsis* | X | | | | | | X |
| *Oxybelis* | X | X | X | X | X | X | X |
| *Oxyrhopus* | X | | | | | | X |
| *Phimophis* | | | | | | X | |
| *Pituophis* | | | X | X | | | |
| *Pseudoboa* | | | | | | X | X |
| *Pseudoficimia* | | X | X | | | | |
| *Pseustes* | X | | | | | | X |
| *Rhadinaea* | X | | X | X | X | | X |
| *Rhandinophanes* | | | X | | | | |
| *Rhinobothryum* | x | | | | | | x |
| *Rhinocheilus* | | x | | | | | |
| *Salvadora* | | x | x | | | | |
| *Scaphiodontophis* | x | x | | | | | x |
| *Scolecophis* | | x | | | | | |
| *Sibon* | x | x | | | | x | x |
| *Siphlophis* | | | | | | x | x |
| *Sonora* | | x | x | | | | |
| *Spilotes* | x | x | | | | x | x |
| *Sternorrhina* | x | x | | | | | x |
| *Storeria* | x | | x | | | | |
| *Symphimus* | x | x | | | | | |
| *Sympholis* | x | x | | | | | |
| *Tantalophis* | | x | x | | | | |
| *Tantilla* | x | x | x | | | x | x |
| *Tantillita* | x | x | | | | | |
| *Thamnophis* | x | x | x | x | x | | |
| *Tolnca* | | | x | | | | |
| *Tretanorhinus* | x | | | | | | |
| *Trimetopon* | x | | | | x | | |
| *Trimorphodon* | x | x | x | x | | | |
| *Tripanurgos* | x | | | | | | x |
| *Tropidodipsas* | x | x | x | x | | | |
| *Urotheca* | x | x | | | | | x |
| *Xenodon* | x | x | | | | x | x |
| *Micrurus* | x | x | x | x | | x | x |
| *Agkistrodon* | x | x | | | | | |
| *Atropoides* | x | x | | | x | | x |
| *Bothriechis* | x | | | x | x | | |
| *Bothriopsis* | | x | | | | | x |
| *Bothrops* | x | | | | | x | x |
| *Cerrophidium* | | | x | x | x | | |
| *Crotalus* | x | x | x | x | | | |
| *Lachesis* | x | | | | | | x |
| *Ophryacus* | | | x | | | | |
| *Porthidium* | x | | x | | | x | x |
| *Sisturus* | | | x | | | | |
| TOTAL | 62 | 51 | 41 | 24 | 16 | 25 | 45 |



Table 15.7. Distribution of Turtle and Crocodilian Genera in Tropical Mesoamerica

| | Humid East and West Lowland | Pacific Lowland | Mexican Highland | Nuclear Highland | Talamancan Highland | Panamanian | Chocoan |
|---|---|---|---|---|---|---|---|
| Testudinata (9) | | | | | | | |
| *Claudius* | X | | | | | | |
| *Kinosternon* | X | X | | | | | |
| *Staurotypus* | X | X | | | | | |
| *Dermatemys* | X | | | | | | |
| *Chelydra* | X | | | | | | X |
| *Chrysemys* | X | X | | | | X | X |
| *Rhinoclemmys* | X | X | | | | | X |
| *Terrapene* | X | | | | | | |
| *Chelonoides* | | | | | | X | |
| TOTAL | 8 | 4 | | | | 3 | 4 |
| Crocodilia (2) | | | | | | | |
| *Caiman* | X | X | | | | X | X |
| *Crocodylus* | X | X | | | | X | X |
| TOTAL | 2 | 2 | | | | 2 | 2 |

Table 15.8. Generic Composition of the Tropical Mesoamerican Herpetofaunas

| | Humid East and West Lowland | Pacific Lowland | Mexican Highland | Nuclear Highland | Talamancan Highland | Panamanian | Chocoan |
|---|---|---|---|---|---|---|---|
| Caecilians (4) | | | | | | | |
| • total herpetofauna | 2 | <1 | 0 | 0 | <1 | <1 | 2 |
| • assemblage | 3 | 1 | 0 | 0 | 3 | 2 | 4 |
| Salamanders (13) | | | | | | | |
| • total herpetofauna | <1 | <1 | 3 | 3 | 1 | 0 | <1 |
| % assemblage | 1 | 1 | 10 | 14 | 8 | 0 | 2 |
| Anurans (43) | | | | | | | |
| % total herpetofauna | 13 | 8 | 5 | 5 | 7 | 6 | 10 |
| % assemblage | 19 | 17 | 14 | 21 | 38 | 22 | 21 |
| Lizards (47) | | | | | | | |
| • total herpetofauna | 16 | 9 | 7 | 5 | 2 | 5 | 9 |
| assemblage | 23 | 20 | 21 | 20 | 13 | 20 | 21 |
| Snakes(97) | | | | | | | |
| total herpetofauna | 29 | 24 | 19 | 11 | 8 | 12 | 21 |
| • assemblage | 45 | 54 | 56 | 49 | 40 | 46 | 47 |
| Turtles (9) | | | | | | | |
| total herpetofauna | 4 | 2 | 0 | 0 | 0 | 1.5 | 2 |
| % assemblage | 6 | 4 | 0 | 0 | 0 | 6 | 2 |
| Crocodilians (2) | | | | | | | |
| • total herpetofauna | <1 | <1 | 0 | 0 | 0 | <1 | <1 |
| % assemblage | 1 | 2 | 0 | 0 | 0 | 4 | 2 |
| Total amphibians | | | | | | | |
| *N* (60) | 33 | 19 | 17 | 18 | 19 | 13 | 26 |
| • total herpetofauna | 16 | 9 | 8 | 8 | 9 | 6 | 12 |
| % assemblage | 24 | 19 | 23 | 35 | 47 | 24 | 27 |
| Total reptiles | | | | | | | |
| *N* (155) | 106 | 76 | 56 | 34 | 21 | 41 | 71 |
| • total herpetofauna | 50 | 36 | 26 | 16 | 10 | 19 | 34 |
| • assemblage | 76 | 81 | 77 | 65 | 53 | 76 | 73 |
| Grand total | | | | | | | |
| *N* (215) | 139 | 95 | 73 | 52 | 40 | 54 | 97 |
| • total herpetofauna | 66 | 44 | 34 | 24 | 19 | 26 | 46 |

fewer genera. Amphibians contribute the least to the Pacific Lowland assemblage (19%) and reptiles the least to the Talamancan Highland fauna (40%).

The herpetofauna of Costa Rica is the meeting ground of three of these assemblages: The Eastern and Western Lowland fauna, the Pacific Lowland fauna, and the Talamancan fauna. The first ranges over the Atlantic lowlands and the Pacific lowlands of southwestern Costa Rica. The second is found an the lowlands of the northwestern region. The third lives in the Cordillera Central and the Cordillera de Talamanca. These major units have distributions broadly correlated with physiographic and climatic parameters and contain a mixture of genera with different histories. Therefore comparisons of the composition of these contemporary units cannot by themselves elucidate the process by which they were assembled over time.

## GENERALIZED TRACKS AND HISTORICAL SOURCE UNITS

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 nonrandom ecogeographic distribution. As a consequence, no species is universally present, and mang species have very small or unique tracks.

The first level of generalization in biogeography is based an the recognition that in spite of the unique nature of individual species distributions, many individual tracks are concordant and Show a common pattern. Determining 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 is to recognize the several disjunct adjoining or distant clusters of distributions that form nodes or track components along 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 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 my 1982 paper an the biogeography of Central American herpetofauna I was able to discern three major general tracks for tropical Mesoamerica based an track analysis:

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. 15.2a). 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. 15.2b). 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. 15.2c). The portions of this track that extend to Ecuador and southern Brazil represent post-Miocene dispersal across the Isthmian Link.

A fourth track, the Western North American-Central American track, is a generalized track including western North America, Mexico, and Central America north of Panama (fig. 15.2d). 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. This track is represented by only a few taxa of reptiles in the tropical Mesoamerican region.

Each of these tracks is characterized by two features. First, they are composed of a string of components (areas of endemism) that represent a once more wide-ranging generalized fauna that has been fragmented by vicariance events and differentiated in situ. Second, they also reflect the recent emergence of the isthmian land connection between Central and South America that provided a corridor for concordant dispersal of many taxa from south to north and north to south in what has been called the great American biotic interchange (Marshall et al. 1982; Stehli and Webb 1985).

An analysis of distributional data, geologic, climatological, and vegetational correlates and changes, together with an assessment of phylogenetic relationships, led me (Savage 1982) to conclude that the four general tracks described above correspond to four historical herpetofaunal source units whose taxa have had an ancient and continuing association with one another. Genera and a few subgeneric groups whose distributions coincide with a particular track were grouped together as a primary historical unit or element. In the present context the following three elements are recognized as having made significant contributions to the Tropical Mesoamerican herpetofauna:

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 the late Cenozoic. This unit comprises taxa having long-term Laurasian affinities. Typical members of this element, including the "hanging" Middle American relicts, the Trog family Rhinophrynidae, the turtle family Dermatemydidae, and the lizard families Xantusiidae, Xenosauridae, and Helodermatidae, were widespread over much of North America to 40° N in the early Tertiary. As I pointed out in 1966 and as 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 times and 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 the Cenozoic and must be considered a recent contributor to Middle American faunal diversity. The affinities of this unit are Gondwanan.

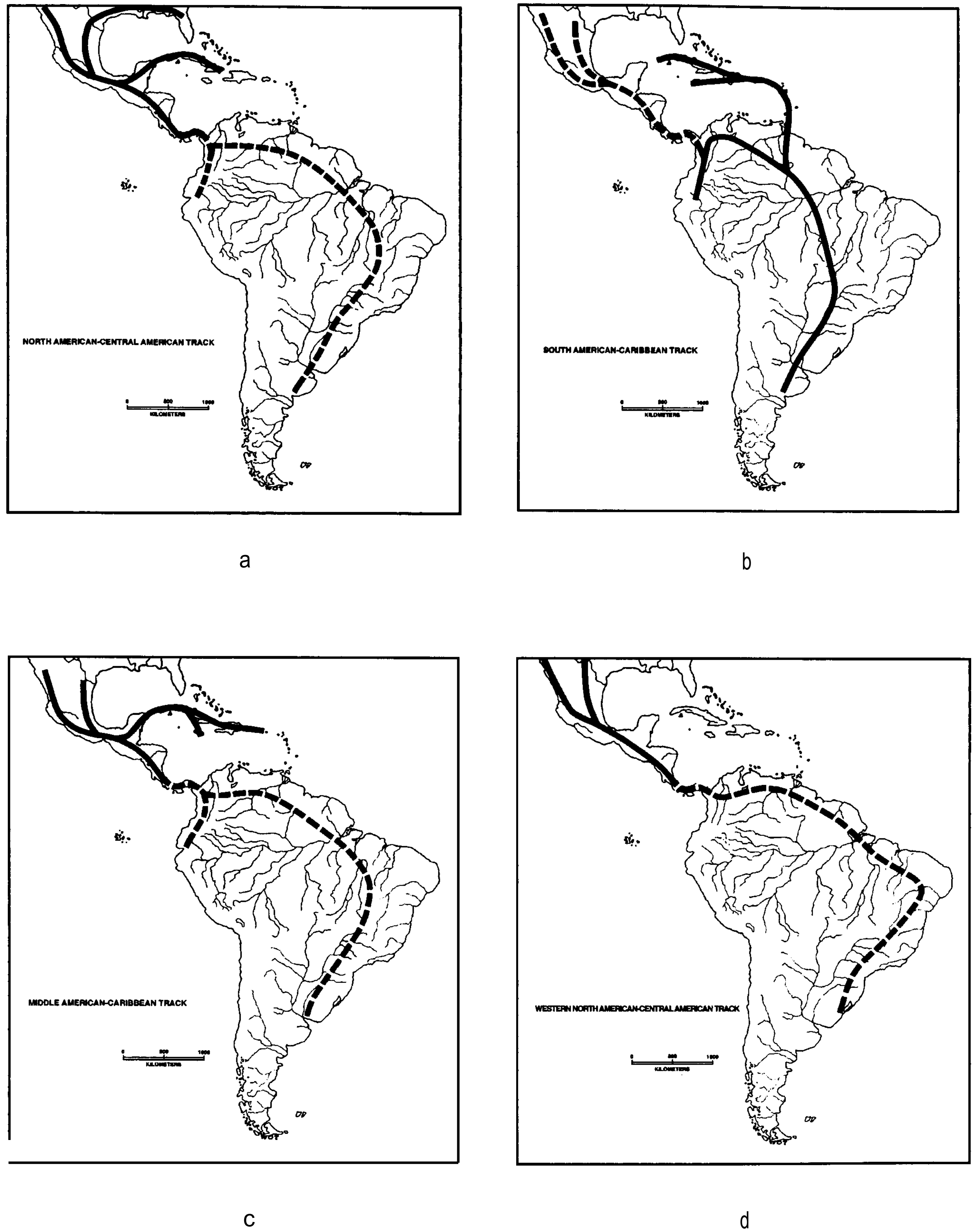


Figure 15.2. General tracks (historical source units) in the Tropical Mesoamerican region: (a) North American-Central American; (b) South American-Caribbean; (c) Middle American-Caribbean; (d) Western North American-Central American.

Table 15.9. Component Genera of Principal Historical Units of the Tropical Mesoamerican Herpetofauna

| Old Northern (90) | Middle American (66) | South American (64) |
|---|---|---|
| Salamanders (13) | Caecilians (2) | Caecilians (2) |
| *Bolitoglossa* | *Dermophis* | *Caecilia* |
| *Bradytriton* | *Gymnopis* | *Oscaecilia* |
| *Chiropterotriton* | | |
| *Cryptotriton* | | |
| *Dendotriton* | | |
| *Ixalotriton* | | |
| *Lineatriton* | | |
| *Notrotriton* | | |
| *Nyctanolis* | | |
| *Oedipina* | | |
| *Paravimolge* | | |
| *Pseudoeurycea* | | |
| *Thorius* | | |
| Frogs and Toads (3) | Frogs and Toads (18) | Frogs and Toads (24) |
| *Rhinophrynus* | *Atelophrynisus* | *Protoptpa* |
| *Scaphiopus* | *Bufo (pt.)* | *Atelopus* |
| *Rana* | *Crepidophryne* | *Bufo (pt.)* |
| | *Eleutherodactylus* | *Rhamphophryne* |
| | *(Craugaster)* | *Eleutherodactylus* |
| | *Hylactophyrne* | *Leptodactylus* |
| | *Syrrhophus* | *Physalaemus* |
| | *Agalychnis* | *Pleurodema* |
| | *Pachymedusa* | *Gastrotheca* |
| | *Anotheca* | *Hemiphractus* |
| | *Duellmanohyla* | *Hyla (pt.)* |
| | *Hyla (pt.)* | *Phrynohyas* |
| | *Plectrohyla* | *Phyllomedusa* |
| | *Pternohyla* | *Scinax* |
| | *Ptychohyla* | *Gentrolenella* |
| | *Triprion* | *Cochranella* |
| | *Gastrophryne* | *Hyalinbatrachium* |
| | *Hypopachus* | *Dendrobates* |
| | *Nelsonophryne* | *Epipedabates* |
| | | *Colostethus* |
| | | *Minyobates* |
| | | *Phyllobates* |
| | | *Chiasmocleis* |
| | | *Elachistocleis* |
| Lizards (19) | Lizards (11) | Lizards (18) |
| *Phrynosoma* | *Basiliscus* | *Dactyloa* |
| *Sceloporus* | *Coryto phanes* | *Enyalioides* |
| *Urosaurus* | *Ctenosaura* | *Morunasaurus* |
| *Coleonyx* | *Iguana* | *Polychrus* |
| *Lepidophyma* | *Laemanctus* | *Lepidoblepharis* |
| *Cnemidophorus* | *Norops* | *Phyllodactylus (pt.)* |
| *Bipes* | *Phyllodactylus (pt.)* | *Thecadactylus* |
| *Eumeces* | *Gonatodes* | *Amevia* |
| *Mabuya* | *Sphaerodactylus* | *Anadia* |
| *Sphenomorphus* | *Aristelliger* | *Bachia* |
| *Anelytropsis* | *Celestus* | *Echinosaura* |
| *Abronia* | | *Gymnophthalmus* |
| *Barisia* | | *Leposoma* |
| *Coloptychon* | | *Neusticurus* |
| *Gerrhonotus* | | *Ptychoglossus* |
| *Mesaspis* | | *Prionodactylus* |
| *Ophisaurus* | | *Amphisbaena* |
| *Heloderma* | | *Diploglossus* |
| *Xenosaurus* | | |
| Snakes (47) | Snakes (34) | Snakes(18) |
| *Leptotyphlops (pt.)* | *Boa* | *Anomalepis* |
| *Loxocemus* | *Exiliboa* | *Helminthophis* |
| *Adelophis* | *Ungaliophis* | *Liotyphlops* |
| *Chironius* | *Adelphicos* | *Typhlops* |
| *Coluber* | *Amastridium* | *Leptotyphlops (pt.)* |
| *Conopsis* | *Atractus* | *Corallus* |
| *Dendrophidion* | *Chapinophis* | *Epicrates* |
| *Drymarchon* | *Chersodromus* | *Trachyboa* |
| *Drymobius* | *Coniophanes* | *Clelia* |
| *Elaphe* | *Conophis* | *Erythrolamprus* |
| *Ficimia* | *Crisantophis* | *Liophis* |
| *Gyalopion* | *Cryophis* | *Oxyrhopus* |
| *Lampropeltis* | *Diaphorolepis* | *Phimophis* |
| *Leptodrymus* | *Dipsas* | *Pseudoboa* |
| *Leptophis* | *Enulius* | *Siphlophis* |
| *Mastigodryas* | *Geagras* | *Tripanurgos* |
| *Nerodia* | *Geophis* | *Xenodon* |
| *Oxybelis* | *Hydromorphus* | *Micrurus (pt.)* |
| *Pituophis* | *Hypsiglena* | |
| *Pseudoficimia* | *Imantodes* | |
| *Pseustes* | *Leptodeira* | |
| *Rhinobothryum* | *Manolepis* | |
| *Rhinocheilus* | *Ninia* | |
| *Salvadora* | *Nothopsis* | |
| *Scaphiodontophis* | *Rhadinaea* | |
| *Sonora* | *Rhadinophanes* | |
| *Spilotes* | *Scolecophis* | |
| *Stenorrhina* | *Sibon* | |
| *Storeria* | *Tantalophis* | |
| *Symphimus* | *Tretanorhinus* | |
| *Sympholis* | *Trimetopon* | |
| *Tantilla* | *Tropidodipsas* | |
| *Tantillita* | *Urotheca* | |
| *Thamnophis* | *Micrurus (pt.)* | |
| *Toluca* | | |
| *Trimorphodon* | | |
| *Agkistrodon* | | |
| *Atropoides* | | |
| *Bothriechis* | | |
| *Bothriopsis* | | |
| *Bothrops* | | |
| *Cerrophidium* | | |
| *Crotalus* | | |
| *Lachesis* | | |
| *Ophryacus* | | |
| *Porthidium* | | |
| *Sisturus* | | |
| Turtles (8) | | Turtles (1) |
| *Claudius* | | *Chelonoides* |
| *Kinosternon* | | |
| *Staurotypus* | | |
| *Dermatemys* | | |
| *Chelydra* | | |
| *Chrysemys* | | |
| *Rhinoclemmys* | | |
| *Terrapene* | | |
| | Crocodilians (1) | Crocodilians (1) |
| | *Crocodylus* | *Caiman* |

Middle American Element: derivative groups of a generalized tropical American biota isolated in tropical North and Central America during most of the Cenozoic; developed in situ north of the Panamanian Portal and restricted by mountain building and climatic change in the late Cenozoic to Middle America. This element comprises genera that are primarily tropical Mesoamerican in distribution and haue their closest allies either in the region or in South America but are mostly endemic to Central America and Mexico. Available evidence indicates that members of this unit or their ancestors had a more extensive range in North America in the 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 to tropical Mesoamerica by climatic change in the Tate Cenozoic.

These units correspond to those 1 discussed earlier (Savage 1982), but with substantial revision in generic content (table 15.9) based an the most recent findings an phylogenetic relationships, especially for "iguanid" lizards (Frost and Etheridge 1989) and colubrid snakes (Jener 1981;

Cadle 1984c, 1987; Zaher 1999). As well as more clearly defining the several elements, these studies have led me to abandon the idea of a separate Young Northern Element. The taxa formerly placed in that unit have proved to be a subset of the Old Northern Element that developed in response to the challenge of physiographic and climatic revolution in the middle latitudes of western North America and Mexico from the Oligocene to the present.

As now understood, the Old Northern Element is represented by four principal components in the Americas: Eastern North American, Western North American, Southwestern North American, and Central American. The Central American Component consists of derivatives of the Old Northern Element taxa that became associated with tropical conditions and isolated from the ancestral unit by cooling and drying trends from the Oligocene onward. Members of this component evolved in situ in Mesoamerica with the autochthonous Middle American Element during the rest of the Cenozoic.

The Southwestern North American Component contains most of the genera previously placed in the Young Northern Element (Savage 1966a, 1982). These genera are derivatives of Old Northern lineages that evolved in the southwest as a result of the orogenic and climatic drying trends in post-Oligocene times that produced the semiarid to desert environments of the region. Only a few tropical Mesoamerican taxa are distributionally associated with this component.

## GEOGRAPHIC PATTERNS IN COSTA RICA

As 1 pointed out earlier (Savage 1975) and as was confirmed by Lynch and Duellman (1997), the Holdridge (1967) system is too sophisticated for sketching broad geographic correlates of animal distribution. Although this system, as discussed in chapter 2, is without peer in defining major tropical bioclimates, most species of amphibians and reptiles tend to occur over wider geographic areas that usually encompass two or more bioclimates/plant formations (tables 14.1 to 14.5).

A preliminary analysis of geographic distribution for Costa Rica, influenced in part by the unpublished manuscripts of Norman J. Scott Jr. (1969) for snakes and Marvalee H. Wake *(1964)* for lizards, identified nine putative geographic areas as high centers of diversity differing from the others in herpetofaunal composition. These faunal areas and their humidity province(s), representative plant Formations, and approximate altitudinal limits are listed below:

Lowlands
- Northwest Pacific (NW): subhumid: Dry Forest; 0 to 600 m.
- Southwest Pacific (SW): humid and perhumid: Lowland Moist and Wet Forests; 0 to 600 m
- Atlantic (A): humid and perhumid: Lowland Moist and Wet Forests; 0 to 500 m

Foothills and uplands
- Pacific Slope (PS): perhumid and superhumid: Premontane Wet and Rainforests; 600 to 1,600 m
- Meseta Central Occidental (MOC): humid: Premontane Moist Forest; 600 to 1,500 m
- Meseta Central Oriental (MOR): humid: Premontane Moist Forest; 500 to 1,500 m
- Atlantic Slope (AS): perhumid and superhumid: Premontane Wet Forest and Rainforest; 500 to 1,500 m

Highlands
- Cordillera Central (CC): humid, perhumid, and superhumid: Lower Montane and Montane Moist and Wer Forest and Rainforest; about 1,500 to 3,343 m
- Cordillera de Talamanca (CT): humid, perhumid, and superhumid: Montane Moist and Wet Forests and Rainforest and Subalpine Pluvial Paramo; about 1,500 to 3,840 m

These geographic units are mapped (fig. 15.3) and are used as the basis for evaluating the history of the Costa Rican herpetofauna. The abbreviations listed above are used throughout an appropriate tables and figures. Table 15.10 summarize species distributional data by major systematic group from tables 14.1 to 14.6 for each faunal area.

Not surprisingly, the distribution patterns by faunal area (figs. 15.4 and 15.5) reflect the Same ecological trends discussed in chapter 14. The greatest overall diversity is found in humid lowland and slope areas. The number of reptile species in the subhumid Northwest Pacific area is three times that for amphibians. The number of amphibians species exceeds that for reptiles at higher elevations (Cordillera Central and Cordillera de Talamanca areas).

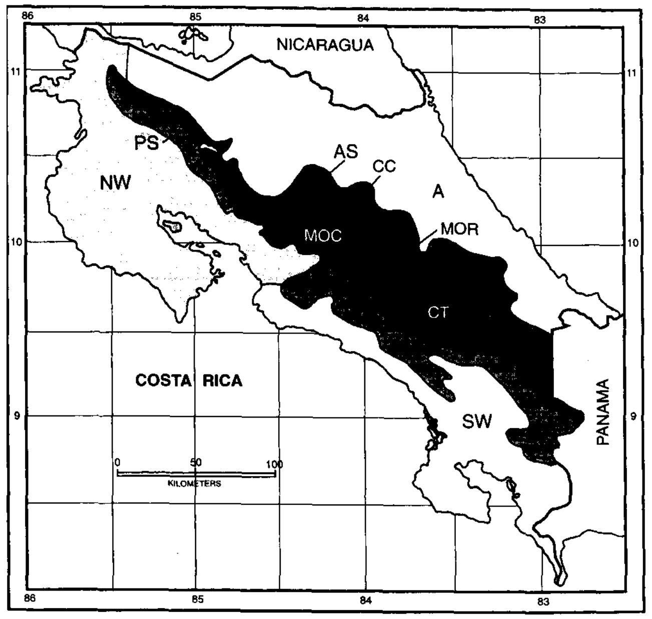


Figure 15.3. Putative faunal areas for the Costa Rican herpetofauna.



Table 15.10. Number of Species by Major Taxonomic Group and Percentage Contribution to Each Faunal Area

| | | NW | SW | A | PS | MOC | MOR | AS | CC | CT |
|---|---|---|---|---|---|---|---|---|---|---|
| Caecilians | N | 0 | 4 | 2 | 3 | 2 | 1 | 3 | 0 | 1 |
| | | 0 | 2 | 1 | 2 | 2 | 2 | 2 | 0 | 1 |
| Salamanders | *N* | *0* | 5 | 9 | 19 | 2 | 1 | 24 | 5 | 10 |
| | | 0 | 2 | 4 | 10 | 2 | 2 | 13 | 7 | 15 |
| Anurans | *N* | 18 | 47 | 73 | 66 | 19 | 12 | 63 | 36 | 30 |
| | | 25 | 27 | 36 | 35 | 19 | 25 | 33 | 47 | 45 |
| Subtotal | *N* | 18 | 57 | 84 | 88 | 23 | 14 | 90 | 41 | 40 |
| | % | 25 | 33 | 41 | 46 | 24 | 30 | 48 | 53 | 60 |
| Lizards | *N* | 16 | 41 | 34 | 29 | 14 | 5 | 26 | 9 | 7 |
| | % | 22 | 24 | 17 | 15 | 14 | 11 | 14 | 12 | 10 |
| Snakes | *N* | 33 | 68 | 91 | 75 | 59 | 26 | 70 | 26 | 20 |
| | % | 45 | 40 | 39 | 39 | 60 | 55 | 37 | 34 | 30 |
| Turtles | *N* | 4 | 4 | 5 | 0 | 2 | 2 | 3 | 0 | 0 |
| | | 5 | 2 | 2 | 0 | 2 | 4 | 2 | 0 | 0 |
| Crocodilians | *N* | 2 | 2 | 2 | 0 | 0 | 0 | 0 | 0 | 0 |
| | | 3 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| Subtotal | *N* | 55 | 115 | 122 | 104 | 75 | 33 | 99 | 35 | 27 |
| | | 75 | 67 | 59 | 54 | 76 | 70 | 52 | 46 | 40 |
| Grand total | *N* | 73 | 172 | 206 | 192 | 98 | 47 | 189 | 76 | 67 |

In summary (table 15.10), the total number of species decreases along gradients from humid to drier conditions (e.g., SW to NW areas) and generally from warmer to cooler situations (e.g., AS to CC). The relative proportions change from a predominance of reptiles to amphibians from wetter to drier conditions (e.g., SW, 67:33 to NW, 75:25) and to cooler and wetter situations (e.g., AS, 52:48 to CT, 40:60). Because species distributions so strongly correlate with current ecological parameters, another approach seems required to analyze historical patterns.

As a consequence 1 have chosen to emphasize the contribution of genera and a few subgeneric groups to each of the

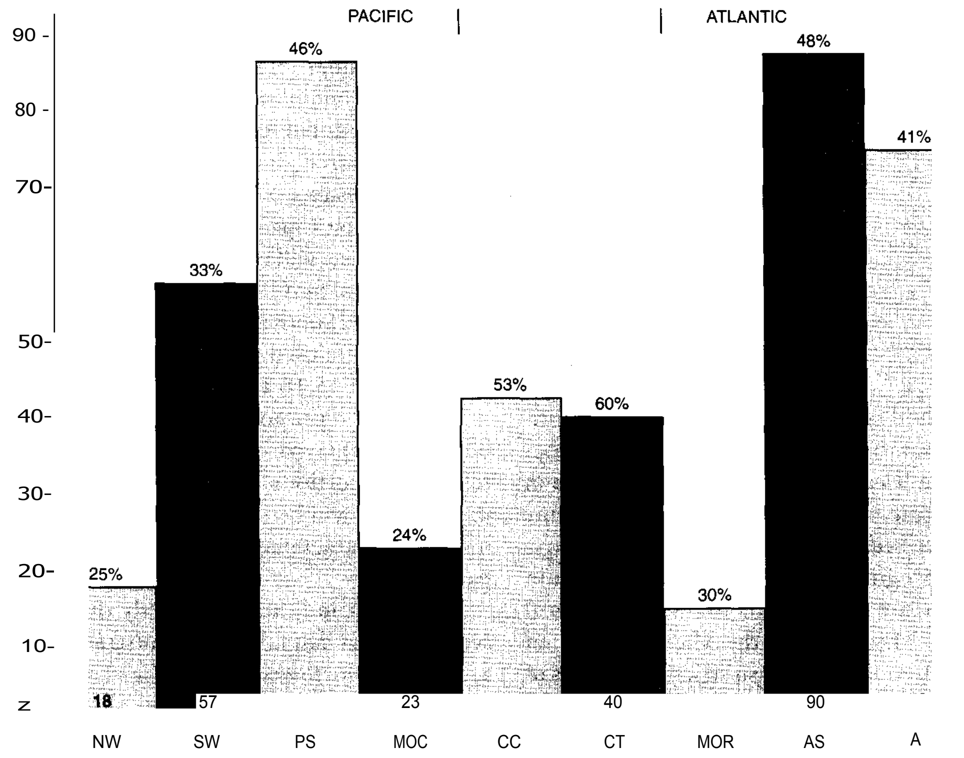


Figure 15.4. Composition by number of species of amphibians in each faunal area; % indicates contribution of amphibians to total herpetofauna of each area.

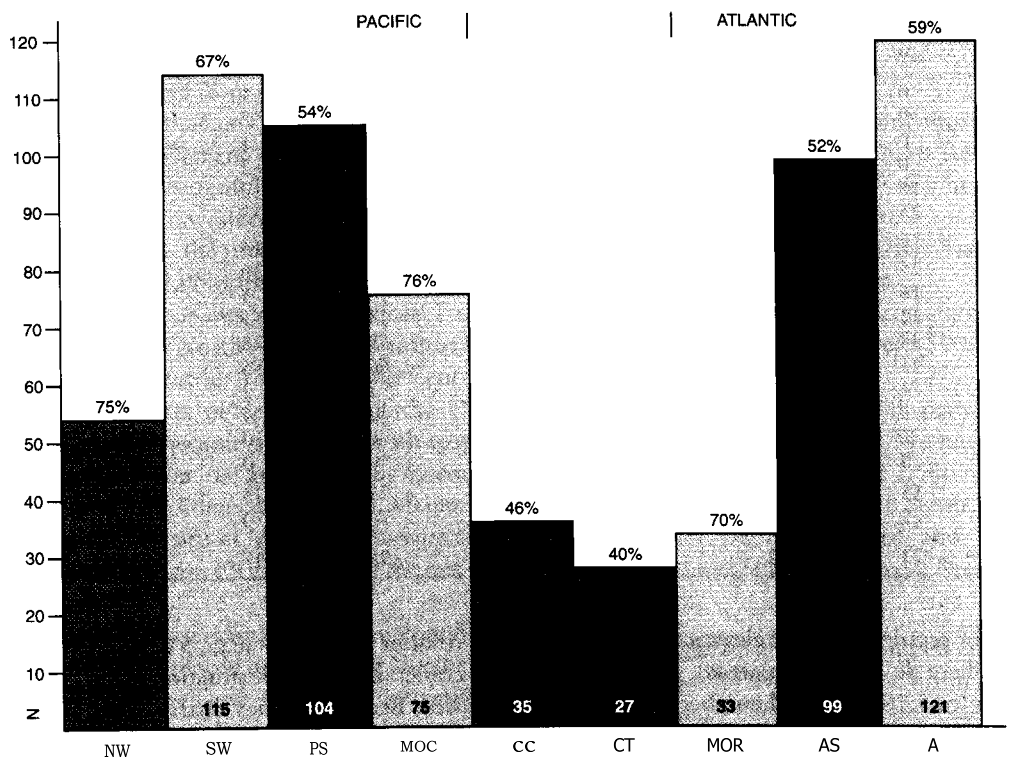


Figure 15.5. Composition by number of species of reptiles in each faunal area; % indicates contribution of reptiles to total herpetofauna of each area.

Table 15.11. Distinctive Mesoamerican Clades of the Anuran Genera *Bufo* and *Hyla*

| Middle American Element | South American Element |
|---|---|
| *Bufo fastidiosus* group | *Bufo guttatus* group |
| *Bufo periglenes* group | *Bufo marinus* group |
| *Bufo valliceps* group | *Hyla albomarginata* group |
| *Hyla godmani* group | *Hyla boans* group |
| *Hyla lancasteri* group | *Hyla leucophyllata* group |
| *Hyla pictipes* group | *Hyla tuberculosa* group |
| *Hyla pseudopuma* group | |
| *Hyla salvadorensis* group | |
| *Hyla zeteki* group | |

faunal areas as a method of establishing the broad historical picture. To carry out this analysis I have plotted the occurrence of each Costa Rica generic or subgeneric group in the faunal areas by their historical source units (elements and components) described earlier in this chapter.

Several currently recognized amphibian genera contain distinctive clades that are assigned to different historical units for this analysis. These include the Middle American (*Craugaster*) and South American (sensu stricto) divisions of the genus *Eleutherodactylus* and Central (*palmipes* group) and Eastern North American (*pipiens* group) components of the genus *Rana*. In addition, the species groups shown in table 15.11 within the composite genera *Bufo* and *Hyla* are treated as separate units.

The distribution of each taxonomic unit (genus or species group) by faunal area is presented in tables 15.12 to 15.15. Table 15.16 summarizes the data for number of genera and their proportional contribution to each faunal area by historical source unit. The contributions of Eastern (E) and Southwestern (SW) Components of the Old Northern Element to the Costa Rican herpetofauna are minimal, so further analysis will emphasize the Central American Component (CA) of the Old Northern Element and Middle American (MA) and South American (SA) Elements. Abbreviations listed above are used for the historical elements and components in table 15.16 and subsequent tables and figures.

The relative proportions (as percentages) of these three units are displayed diagrammatically in figure 15.6. The relative proportions of the predominant historical unit(s) in each area will be used as the basis for determining their historical characteristics and relationships in the following paragraphs.

These data indicate a distinctly different history for the Northwestern faunal area compared with other lowland areas. The Northwestern area is characterized by Central and Middle American genera in about equal proportions, 36:34%, respectively. The Southwestern and Atlantic areas are characterized by similar proportions of South American and Middle American taxa, 37:33% and 31:37%, respectively, with South American ones in slightly greater numbers



Table 15.12. Distribution of Genera and Species Groups of the Central American Component (Old Northern Element) by Faunal Area

| | NW | SW | A | PS | MOC | MOR | AS | CC | CT |
|---|---|---|---|---|---|---|---|---|---|
| Salamanders (3) | | | | | | | | | |
| *Bolitoglossa* | | X | X | X | | | X | X | X |
| *Nototriton* | | | | | X | X | X | X | X |
| *Oedipina* | | X | X | X | X | X | X | X | X |
| Subtotal | 0 | 2 | 2 | 2 | 2 | 2 | 3 | 3 | 3 |
| Anurans (2) | | | | | | | | | |
| *Rhinophrynus* | X | | X | | | | | | |
| *Rana palmipes* group | X | X | X | X | X | X | X | X | X |
| Subtotal | 2 | 1 | 2 | 1 | 1 | 1 | 1 | 1 | 1 |
| Total amphibians (5) | 2 | 3 | 4 | 3 | 3 | 3 | 4 | 4 | 4 |
| Lizards (7) | | | | | | | | | |
| *Coleonyx* | X | X | | X | X | X | | | |
| *Lepidophyma* | | X | X | X | X | X | | | |
| *Eumeces* | X | | | | | | | | |
| *Mabuya* | X | X | X | X | | | X | | |
| *Sphenomorphus* | | X | X | X | | | X | | |
| *Coloptychon* | | X | | | | | | | |
| *Mesaspis* | | | | | | | | X | X |
| Subtotal | 3 | 5 | 3 | 4 | 2 | 2 | 2 | 1 | 1 |
| Snakes(25) | | | | | | | | | |
| *Loxocemus* | X | | | | | | | | |
| *Chironius* | | X | X | X | X | | X | | |
| *Dendrophidion* | | X | X | X | | | X | | |
| *Drymarchon* | X | X | X | X | X | X | X | | |
| *Drymobius* | X | X | X | X | X | X | X | | |
| *Elaphe* | X | | | X | X | | X | | |
| *Lampropeltis* | X | X | X | X | X | X | X | X | X |
| *Leptodrymus* | X | | | | X | | | | |
| *Leptophis* | X | X | X | X | X | | X | X | X |
| *Mastigodryas* | X | X | X | X | X | | X | X | |
| *Oxybelis* | X | X | X | X | X | | X | | |
| *Pseustes* | | X | X | X | X | | X | | |
| *Rhinobothryium* | | | X | | | | X | | |
| *Scaphiodontophis* | | X | X | X | | | | | |
| *Scolecophis* | X | | | | X | | | | |
| *Spilotes* | X | X | X | X | X | X | X | | |
| *Stenorrhina* | | X | X | X | X | X | X | | |
| *Tantilla* | X | X | X | X | X | X | X | | |
| *Trimorphodon* | X | | | | | | | | |
| *Atropoides* | | X | X | X | X | | X | X | X |
| *Bothriechis* | | X | X | X | X | X | X | X | X |
| *Bothrops* | X | X | X | X | X | X | X | | |
| *Cerrophidium* | | | | | | | | X | X |
| *Lachesis* | | X | X | X | | | | | |
| *Porthidium* | X | X | X | x | | | x | | |
| Subtotal | 15 | 18 | 19 | 19 | 17 | 8 | 18 | 6 | 5 |
| Turtles (2) | | | | | | | | | |
| *Kinosternon* | X | X | X | x | x | x | x | | |
| *Rhinoclemmys* | X | | X | | x | x | | | |
| Subtotal | 2 | 1 | 2 | 1 | 2 | 2 | 1 | 0 | 0 |
| Total reptiles (34) | 20 | 24 | 24 | 24 | 21 | 12 | 21 | 6 | 5 |
| Grand total (39) | 22 | 27 | 26 | 27 | 24 | 15 | 25 | 10 | 9 |

in the southwest and Middle American ones an the Atlantic. These latter differences may be trivial.

The highland areas are dominated by Middle American taxa (CC = 38%; CT = 43%), with a stronger representation of South American genera (28%) in the Cordillera de Talamanca and of Central American genera (29%) in the Cordillera Central. The two slope faunal areas are similar in having Middle American dominance (PS = 36%; AS = 41%), with considerable Central American influence (PS = 32%; AS = 30%).

The Meseta Central Occidental area is unique in having a high proportion of Central American (40%) to Middle

Table 15.13. Distribution of Genera and Species Group of Eastern and Southwestern North American Components (Old Northern Element) by Faunal Areas

| | NW | SW | A | PS | MOC | MOR | AS | CC | CT |
|---|---|---|---|---|---|---|---|---|---|
| Eastern North American | | | | | | | | | |
| Anurans (1) | | | | | | | | | |
| *Rana pipiens* group | X | | X | X | X | X | X | X | X |
| Subtotal | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Total amphibians (1) | 1 | 0 | 1 | 1 | 1 | 1 | 1 | 1 | 1 |
| Snakes (3) | | | | | | | | | |
| *Coluber* | X | | | | | | | | |
| *Thamnophis* | X | | X | | X | X | | X | |
| *Agkistrodon* | X | | | | | | | | |
| Subtotal | 3 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 |
| Turtles (2) | | | | | | | | | |
| *Chelydra* | X | X | X | X | X | | X | | |
| *Chrysemys* | | X | X | | | | | | |
| Subtotal | 1 | 2 | 2 | 1 | 2 | 0 | 1 | 0 | 0 |
| Total reptiles (5) | 4 | 2 | 3 | 1 | 2 | 1 | 1 | 1 | 0 |
| Grand total (6) | 5 | 2 | 4 | 2 | 3 | 2 | 2 | 2 | 1 |
| Southwestern America | | | | | | | | | |
| Lizards (2) | | | | | | | | | |
| *Sceloporus* | X | | | X | X | X | X | X | X |
| *Cnemidophorus* | X | | | | X | | | | |
| Subtotal | 2 | 0 | 0 | 1 | 2 | 1 | 1 | 1 | 1 |
| Snakes(1) | | | | | | | | | |
| *Crotalus* | X | | | X | X | X | | | |
| Subtotal | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 |
| Total reptiles (3) | 3 | 0 | 0 | 2 | 3 | 1 | 1 | 1 | 1 |
| Grand total (3) | 3 | 0 | 0 | 2 | 3 | 2 | 1 | 1 | 1 |

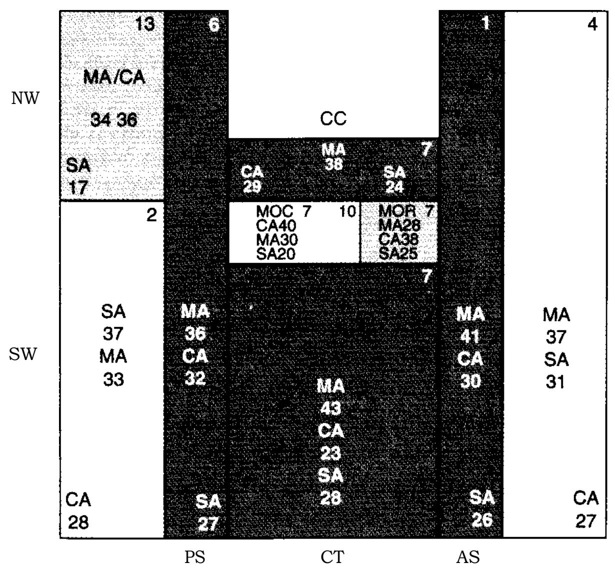


Figure 15.6. Diagram of composition of Costa Rican herpetofauna by percentage of genera of each major historical unit in faunal area; values in upper right hand corner are for E and SW Components (Old Northern Element).

American (30%) and South American genera (20%). The Meseta Central Oriental area is nearly identical to the Meseta Central Occidental area in faunal percentages: MA 28: CA 38: SA 25 and MA 30: CA 40: SA 20, respectively.

## ENDEMISM

Another parameter of history is the degree of endemism each faunal area exhibits. A high level of endemism suggests a Tonger period of isolation for an area than for others with lower levels. Unfortunately the areas of endemism for lower Central America know no political boundaries, so that many species restricted in distribution to one faunal area in Costa Rica may extend into adjacent Panama or Nicaragua or farther to the north.

As 1 pointed out in my earlier paper (Savage 1982), the Northwest Pacific faunal area is the southern portion of a lowland faunal unit that includes lowland areas in western Nicaragua, Honduras, and El Salvador. The Southwest Pacific faunal area is the greater part of an area that includes the lowlands of extreme Western Chiriquf Province, Panama. The Atlantic Lowland faunal area of Costa Rica is the

Table 15.14. Distribution of Genera and Species Groups of the Middle American Element by Faunal Area

| | NW | SW | A | PS | MOC | MOR | AS | CC | CT |
|---|---|---|---|---|---|---|---|---|---|
| Caecilians (2) | | | | | | | | | |
| *Dermophis* | | x | | x | | | x | | x |
| *Gymnopis* | | x | x | x | | | x | | |
| Subtotal | 0 | 2 | 1 | 2 | 0 | 0 | 2 | 0 | 1 |
| Anurans (19) | | | | | | | | | |
| *Bufo fastidiosus* group | | | | x | | | x | x | x |
| *Bufo periglenes* group | | | | | | | | x | |
| *Bufo valliceps* group | x | x | x | x | x | x | | | |
| *Crepidophryne* | | | | x | | | | | x |
| *Eleutherodactylus (Craugaster)* | | x | x | x | x | x | x | x | x |
| *Agalychnis* | | x | x | x | | | x | | x |
| *Anotheca* | | | x | x | | | x | | |
| *Duellmanohyla* | | | | x | | | x | | |
| *Hyla godmani* group | | | x | x | | | x | | |
| *Hyla lancesteri* group | | | x | x | | | | | x |
| *Hyla pictipes* group | | | | x | | | x | x | x |
| *Hyla pseudopuma* group | | | | x | | | x | x | x |
| *Hyla salvadorensis* group | | | | x | | | | | |
| *Hyla zeteki* group | | | | | | | x | x | x |
| *Phrynohyas* | x | x | | | | | | | |
| *Smilisca* | x | x | x | x | x | x | x | | |
| *Gastrophryne* | | | x | | | | | | |
| *Hypopachus* | x | | | | x | x | | | |
| *Nelsonophryne* | | x | x | x | | | x | x | x |
| Subtotal | 3 | 6 | 9 | 14 | 3 | 3 | 12 | 7 | 9 |
| Total amphibians (21) | 3 | 8 | 10 | 16 | 3 | 3 | 17 | 7 | 10 |
| Lizards (9) | | | | | | | | | |
| *Basciliscus* | x | x | x | | | | | | |
| *Corytophanes* | | x | x | x | | | x | | |
| *Ctenosaura* | x | x | x | | | | | | |
| *Iguana* | x | x | x | | | | | | |
| *Norops* | x | x | x | x | x | x | x | x | x |
| *Phyllodactylus* | x | | | | x | | | | |
| *Gonatodes* | x | x | x | | | | | | |
| *Sphaerodactylus* | | x | x | x | | | | | |
| *Celestus* | | | x | x | | | x | x | x |
| Subtotal | 6 | 7 | 8 | 4 | 2 | 1 | 3 | 2 | 2 |
| Snakes (21) | | | | | | | | | |
| *Loxocemus* | x | | | | | | | | |
| *Boa* | x | x | x | x | | | x | | |
| *Ungaliophis* | | x | x | | | | | | |
| *Amastridium* | | x | x | | | | x | | |
| *Coniophanes* | x | x | | x | x | | x | | |
| *Conophis* | x | | | | x | | | | |
| *Crisantophis* | x | | | | x | | | | |
| *Dipsas* | | x | x | | | | | | |
| *Enulius* | x | x | x | | x | | x | | |
| *Geophis* | | x | x | x | x | x | x | x | x |
| *Hydromorphus* | | x | x | x | x | x | | | x |
| *Imantodes* | x | x | x | x | x | x | x | | |
| *Leptodeira* | x | x | x | x | x | | x | | |
| *Ninia* | x | x | x | x | x | x | x | x | x |
| *Nothopsis* | | x | x | | | | x | | |
| *Rhadinaea* | | x | x | | x | x | x | x | x |
| *Sibon* | x | x | x | x | x | x | x | | |
| *Tretanorhinus* | | | x | | | | | | |
| *Trimetopon* | | | x | x | | x | x | x | x |
| *Urotheca* | | x | x | x | x | | x | | |
| *Micrurus* | x | x | x | x | x | x | x | | |
| Subtotal | 11 | 16 | 17 | 11 | 13 | 7 | 15 | 4 | 5 |
| Crocodilians (1) | | | | | | | | | |
| *Crocodylus* | x | x | x | | | | | | |
| Subtotal | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| Total reptiles (31) | 18 | 24 | 26 | 15 | 15 | 8 | 18 | 6 | 7 |
| Grand total (52) | 21 | 32 | 36 | 31 | 18 | 11 | 35 | 13 | 17 |

Table 15.15. Distribution of Genera and Species Groups of the South American Element by Faunal Area

| | NW | SW | A | PS | MOC | MOR | AS | CC | CT |
|---|---|---|---|---|---|---|---|---|---|
| Caecilians (1) | | | | | | | | | |
| *Oscaecilia* | | x | | | | | | | |
| Subtotal | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Anurans (20) | | | | | | | | | |
| *Atelopus* | | x | | x | x | x | x | x | x |
| *Bufo guttatus* group | | x | x | x | x | x | x | | |
| *Bufo marinus* group | x | x | x | x | x | x | x | | |
| *Eleutherodactylus (s.s.)* | | x | x | x | | | x | x | x |
| *Leptodactylus* | x | x | x | x | | | x | | |
| *Physalaemus* | x | x | | | | | | | |
| *Gastrotheca* | | | | | | | x | | |
| *Hyla albomarginata* group | | x | x | | | | | | |
| *Hyla boans* group | | x | | | | | | | |
| *Hyla bogotensis* group | | | x | | | | | | |
| *Hyla leucophyllata* group | x | x | x | x | | | x | | |
| *Hyla tuberculosa* group | | | x | x | | | x | x | |
| *Phyllomedusa* | | | | x | | | x | x | x |
| *Scinax* | x | x | x | | | | | | |
| *Centrolenella* | | x | x | x | x | x | x | | x |
| *Cochranella* | | x | x | x | | | x | | x |
| *Hyalinobatrachium* | | x | x | x | x | x | x | | x |
| *Colostethus* | | x | x | | | | x | | x |
| *Dendrobates* | | x | x | | | | | | x |
| *Phyllobates* | | x | x | | | | | | |
| Subtotal | 5 | 16 | 15 | 11 | 5 | 5 | 13 | 4 | 8 |
| Total amphibians (21) | 5 | 17 | 15 | 11 | 5 | 5 | 13 | 4 | 8 |
| Lizards (12) | | | | | | | | | |
| *Dactyloa* | | | | | | | | | |
| *Polychrus* | | x | x | x | x | | | | |
| *Lepidoblepharis* | | x | x | x | | | x | | |
| *Thecadactylus* | | x | x | x | x | | | | |
| *Ameiva* | x | x | x | x | | | x | | |
| *Anadia* | | | | x | | | x | x | x |
| *Bachia* | | x | | | | | | | |
| *Gymnophthalamus* | x | x | x | | x | | | | |
| *Leposoma* | | x | x | | | | | | |
| *Neusticurus* | | x | | | | | | | |
| *Ptychoglossus* | | x | x | x | | | x | | x |
| *Diploglossus* | | x | x | x | | x | x | | |
| Subtotal | 2 | 10 | 8 | 8 | 3 | 3 | 5 | 1 | 2 |
| Snakes(13) | | | | | | | | | |
| *Anomalepis* | | | | x | | | | | |
| *Helminithophis* | | | x | | x | x | | | |
| *Liotyphlops* | | | | | | | | | |
| *Leptotyphlops* | x | | | | | | | | |
| *Typhlops* | | | | x | | | | x | |
| *Corallus* | | x | x | | | | | | |
| *Epicrates* | x | x | x | | x | | | | |
| *Clelia* | x | x | x | | | | x | x | |
| *Erythrolamprus* | | x | x | x | x | x | x | | |
| *Liophis* | | x | x | x | x | x | x | x | x |
| *Oxyrhopus* | | x | x | | | | | | |
| *Tripanurgos* | | x | | | | | | | |
| *Xenodon* | | x | x | x | x | | x | | |
| Subtotal | 3 | 8 | 8 | 4 | 4 | 2 | 4 | 3 | 1 |
| Crocodilians (1) | | | | | | | | | |
| *Caiman* | x | x | x | | | | | | |
| Subtotal | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 |
| Total reptiles (26) | 6 | 19 | 17 | 12 | 7 | 5 | 9 | 4 | 3 |
| Grant total (47) | 11 | 36 | 32 | 23 | 12 | 10 | 22 | 8 | 11 |



Table 15.16. Number and Percentage of Assemblage and Percentage of Total Genera and Species Groups by Faunal Area

| Faunal Area | CA | E | SW | MA | SA | Total |
|---|---|---|---|---|---|---|
| NW | | | | | | |
| *N* | 22 | 5 | 3 | 21 | 11 | 62 |
| A | 36 | 8 | 5 | 34 | 17 | 100 |
| T | 15 | 3 | 2 | 14 | 8 | 42 |
| SW | | | | | | |
| N | 27 | 2 | 0 | 32 | 36 | 98 |
| % A | 28 | 2 | 0 | 33 | 37 | 100 |
| % T | 18 | 1.4 | 0 | 22 | 25 | 66 |
| A | | | | | | |
| N | 26 | 4 | 0 | 36 | 32 | 97 |
| A | 27 | 4 | 0 | 37 | 31 | 100 |
| T | 18 | 3 | 0 | 25 | 21 | 67 |
| PS | | | | | | |
| *N* | 27 | 2 | 2 | 31 | 23 | 85 |
| A | 32 | 2 | 2 | 36 | 27 | 100 |
| T | 18 | 1.4 | 1.4 | 21 | 16 | 58 |
| MOC | | | | | | |
| N | 24 | 3 | 3 | 18 | 12 | 60 |
| A | 40 | 5 | 5 | 30 | 20 | 100 |
| T | 17 | 2 | 2 | 12 | 8 | 41 |
| MOR | | | | | | |
| *N* | 15 | 2 | 2 | 11 | 10 | 40 |
| A | 38 | 5 | 5 | 28 | 25 | 100 |
| %T | 10 | 1.4 | 1.4 | 8 | 7 | 27 |
| AS | | | | | | |
| N | 25 | 2 | 1 | 35 | 22 | 85 |
| % A | 30 | 2 | 1.2 | 41 | 26 | 100 |
| %T | 17 | 1.4 | 0.6 | 24 | 15 | 58 |
| CC | | | | | | |
| N | 10 | 2 | 1 | 13 | 8 | 34 |
| A | 29 | 6 | 3 | 38 | 24 | 100 |
| %T | 7 | 1.4 | 0.6 | 9 | 5 | 23 |
| CT | | | | | | |
| *N* | 9 | 1 | 1 | 17 | 11 | 39 |
| A | 23 | 3 | 3 | 43 | 28 | 100 |
| %T | 6 | 0.6 | 0.6 | 12 | 8 | 27 |

A = % of faunal area.

T = % of total herpetofauna.

central part of an area that includes the lowlands of Bocas de Toro Province, Panama, the lowlands of eastern Nicaragua, and extreme northeastern Honduras.

Similarly, the Pacific Slope and Atlantic Slope faunal areas are part of areas that extend along the slopes of Chiriquf and Bocas de Toro Provinces, respectively, in western Panama. The Talamancan Highland faunal area would also include the continuation of the Cordillera de Talamanca into western Panama.

For this reason table 15.17, which summarizes the degree of species endemism in the Costa Rican herpetofauna, gives two values for each faunal area. One indicates the number of species known only for Costa Rica. The second records the number of otherwise Costa Rican species endemic to a particular area, including those portions of a continuous faunal area that extend outside the country.

Species endemism is highest in the Cordillera de Talamanca faunal area (27%), with lower endemism in the

Table 15.17. Degree of Species Endemism in Costa Rican Herpetofauna by Faunal Area

| Faunal Area | *N* in Area | CR *N* | Endemics % | Area *N* | Endemics |
|---|---|---|---|---|---|
| NW | 73 | 0 | 0 | 16 | 22 |
| SW | 172 | 4 | 2.3 | 17 | 10 |
| A | 206 | 8 | 4 | 27 | 13 |
| PS | 192 | 4 | 2.1 | 7 | 3.6 |
| MOC | 98 | 0 | 0 | 0 | 0 |
| MOR | 47 | 0 | 0 | 0 | 0 |
| AS | 189 | 9 | 4.8 | 13 | 7 |
| CC | 76 | 10 | 13 | 10 | 13 |
| CT | 67 | 11 | 16 | 18 | 27 |
| TOTAL *N* + total fauna | 383 | 46 | 12 | 106 | 28 |

*Note:* See text for explanation of Costa Rican versus area endemics.

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:

1. Fauna) areas in which a combination of Middle American and South American elements make up 65% or more of the herpetofauna (SW, A)
II. Fauna) 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 1 (MA = 43% + SA = 28% = 71%) or pattern II ( MA = 43% + CA = 23% = *66%).*

The degree of species endemism within these areas sheds further light an 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 (1).

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

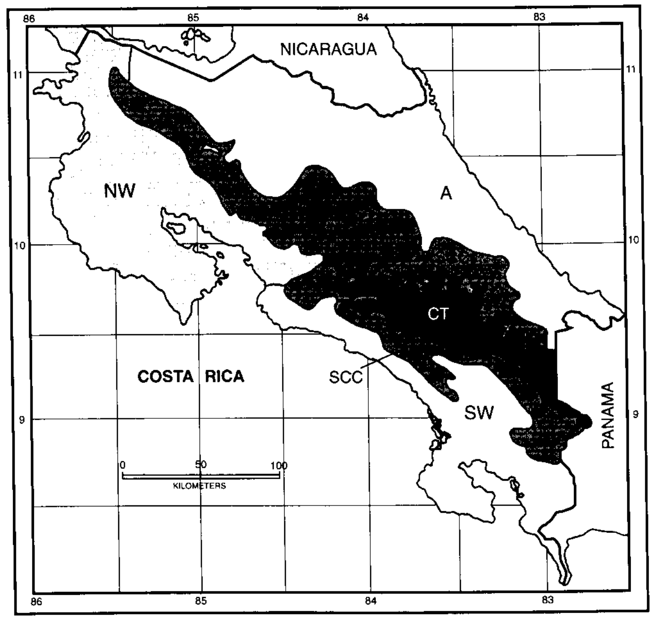


Figure 15.7. Faunal areas for the Costa Rican herpetofauna.

PS + AS -* MOC - MORC - 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)

# 16 Development of the Herpetofauna

CENTRAL AMERICA as a land-positive region has a lang 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 an 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 an 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 an 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 an 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 bot 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