

CHAPTER 18

Biogeography

The most striking feature of past and present distributions [of amphibians] is the fundamental and consistent association of distributions of each group with either Laurasia or Gondwanaland, and those supercontinent's Cretaceous fragments that by continental drift have come to form today's major land areas.

Jay M. Savage (1973)

Few scientific discoveries have influenced historical biogeography so significantly as the accumulating data on plate tectonics beginning in the early 1960s. Most syntheses of historical biogeography before the late 1960s were influenced by the arguments of Matthew (1915) that the evolution and distribution of mammals could be explained adequately by continental isostasy. Among Matthew's many influential disciples was Noble, who, in a series of papers culminating in his synthesis of amphibian biology (1931b), attempted to explain the distribution of families of amphibians by dispersal between static continents. With the advent of extensive geophysical evidence in support of continental drift, biogeographers began to reexamine earlier biogeographic arrangements. The results have been striking changes in biogeographic interpretations.

In order to address the biogeographic problems, one must formulate working principles and review the geologic and climatic changes that have taken place since the time of the origin of amphibians. This chapter discusses these subjects and then analyzes the historical and modern distributions of the three living orders of amphibians.

BIOGEOGRAPHIC PRINCIPLES

The documentation of the distribution of organisms in space and time is the raw material for biogeographic analysis. Although each taxon has its individual distri-

bution because of its unique evolutionary history and particular ecological requirements, it is possible to determine patterns (generalized tracks) of coincident distributions of many monophyletic groups. This is the first step in biogeographic analysis. Second, it is necessary to determine disjunct clusters of distributions within the overall distribution of an inclusive taxonomic unit. These clusters commonly define the geographic limits of major modern biotas, have a high degree of endemism, and constitute centers of adaptive radiation. Third, it is desirable to identify the historical source units that contributed to the modern biotas, for the biota in any given region may have been derived from several historical source units at different times.

A major revitalization of historical biogeography has taken place in recent years with the formulation of vicariance biogeography (see G. Nelson and Platnick, 1981, and G. Nelson and D. Rosen, 1981, for reviews). Considerable controversy exists between adherents of the dispersal theory and the proponents of the vicariance theory, who argue that the vicariance approach provides testable hypotheses, whereas the dispersalist approach is untestable. J. Savage (1982) took a balanced view and outlined the conceptual framework of each approach, as given below.

Dispersal Theory

1. A monophyletic group arises at a center of origin.

2. Each group disperses from this center.
3. A generalized track corresponds to a dispersal route.
4. Each modern biota represents an assemblage derived from one to several historical source units.
5. Direction of dispersal may be deduced from tracks, evolutionary relationships, and past geologic and climatic history.
6. Climatic and/or physiographic change provides the major impetus and/or opportunity for dispersal.
7. Biotas are constituted by dispersal across barriers and subsequent evolution in isolation.
8. Dispersal is the key to explain modern patterns; related groups separated by barriers have dispersed across them when the barriers were absent or relatively ineffective, or less commonly by passing over or through existing barriers.
9. Dispersal is of primary significance in understanding current patterns; dispersal preceded barrier formation and vicariance, and occurs again when barriers subsequently are removed or become ineffective.

Vicariance Theory

1. Vicariants (allopatric taxa) arise after barriers separate parts of a formerly continuous population.
2. Substantial numbers of monophyletic groups are affected simultaneously by the same vicariating events (geographic barrier formation).
3. A generalized track estimates the biotic composition and geographic distribution of an ancestral biota before it subdivided (vicariated) into descendant biotas.
4. Vicariance after geographic subdivision produced modern biotas.
5. Each generalized track represents a historic source unit.
6. Sympatry of generalized tracks reflects geographic overlap of different biotas owing to dispersal.
7. The primary vicariating events are change in world geography that subdivided ancestral biotas.
8. Biotas evolve in isolation after barriers arise.
9. Vicariance is of primary importance in understanding modern patterns; related groups separated by barriers were fragmented by the appearances of barriers.

These two approaches differ mainly in their emphases. In the dispersal model, geographically associated taxa dispersed together so as to form a common pattern. In the vicariance model, original distributions are frag-

mented and the geographically associated taxa in each fragment evolved together.

The major patterns of amphibian distribution at the familial and subfamilial levels can be explained best by vicariance biogeography. Some facets of peripheral distributions definitely are the result of dispersal, but these are relatively minor in comparison with the overall distribution patterns, except for some widespread genera, such as *Bufo*, *Hyla*, and *Rana*, in which both phenomena seem to have been important. Any biogeographic scenario is only as good as the understanding of the phylogenetic relationships of the organisms involved. Unresolved phylogenetic relationships of many amphibian groups, especially some anurans, make some aspects of the biogeographic analysis tenuous at best.

Ideally, all biogeographic syntheses should be based on phylogenetic analyses of component taxa. This has not been the case, nor is it likely that this ever will be a reality. Instead, the methodology suggested by J. Savage (1982) has been used to a great extent, especially with the anurans. This method uses events in the history of the earth to predict general patterns of phylogenetic relationship. This approach implies a reciprocal relationship between the history of the earth and the history of the biota.

However, even this approach presents some problems, especially in the anurans, a group in which familial assignments of many taxa are open to question (see Chapter 17). Many assumptions are made in the following discussion, and in some cases alternatives are offered. Moreover, if the scenarios depicted are correct, many groups as now recognized are paraphyletic. These include the families Caeciliidae, Myobatrachidae, Leptodactylidae, Bufonidae, Hylidae, and Ranidae, the subfamily Microhylinae, and the genera *Eleutherodactylus*, *Bufo*, *Hyla*, and *Rana*.

The application of times of divergences of lineages derived from biochemical studies provides a data set independent of the phylogenies based on morphology and biogeography based solely on earth history. Although the evolutionary clock hypothesis of albumen changes has been criticized by some workers (see Chapter 16), the results are encouraging. In most cases in which phylogenetic analyses and earth history agree, there also is congruence of the molecular data.

The fossil record and the biochemical information emphasize the antiquity of many lineages of lissamphibians. As gaps are filled in the fossil record, more molecular data accumulated, and more cladistic studies completed, the biogeographic picture of amphibians should improve.

HISTORICAL SETTING

The fossil record of modern groups of amphibians extends back to the early Triassic (Table 18-1). Therefore, in order to interpret the distributional histories of the living groups, it is necessary to project the hypothesized phylogenetic relationships of each of the orders (see

Figure 18-1. Major Geologic and Climatic Events Affecting the Distribution of Amphibians

Period or epoch ^a	Geologic events	Climatic events	Earliest known appearance of amphibian families ^b
Triassic, 220 m.y.	At Permo-Triassic boundary, east Asia consisted of several separate blocks south and east of major Asian continent. Otherwise, most if not all continents united in single land mass—Pangaea.	High-latitude humid belts separated from tropical humid belt by midlatitude arid zones; expansion of northern in Late Triassic.	Protobatrachidae
Triassic, 190 m.y.	East Asian blocks unite with Pangaea. Breakup of Pangaea initiated about 180 m.y. when North America and Africa began to separate. By 160 m.y., Tethys Sea separated east Laurasia from east Gondwanaland; epeiric seas probably connected Tethys Sea with North Atlantic and possibly with East Pacific via Caribbean Basin. At about 140 m.y., Gondwanaland fragmented into three major blocks—South America—Africa, Antarctica—Australia, Madagascar—India.	Contraction of arid zones and expansion of high latitude and especially tropical humid belts.	Karauridae (U) Prosirenidae (M) Leiopelmatidae (L) Discoglossidae (U) Palaeobatrachidae (U)
Cretaceous, 135 m.y.	Turgai Sea separated east and west Eurasia. Midcontinental Sea separated east and west North America 100 to 75 m.y. Kolyma Block united with Asia 120 m.y. South Atlantic Ocean separated South America and Africa (± 100 m.y.). Madagascar separated from Indian—Seychellean Plate. New Zealand separated from Australia. Possible connection between Central and South America in Late Cretaceous.	Temperate humid zones discontinuous in high latitudes. Tropical and subtropical climates dominating most land masses; arid zones small and discontinuous.	Sirenidae (U) Amphiumidae (U) Scapherpetontidae (U) Batrachosauroididae (U) Pipidae (L) Pelobatidae (L)
Eocene, 65 m.y.	Turgai Sea separated east and west Eurasia. Seychelles separated from Indian Plate. Australia separated from Antarctica. Formation of Greater Antilles. DeGeer passage between Europe and North America. Beringia intermittent. Brief connection of South America with Central America.	Equable tropical and subtropical.	Cryptobranchidae Proteidae Dicamptodontidae Caeciliidae Rhinophrynidae Bufonidae Hylidae
Oligocene, 54 m.y.	Turgai Sea separated east and west Eurasia. Thule connection of Europe and North America. Beringia intermittent.	Equable tropical and subtropical.	Salamandridae Pelodytidae Myobatrachidae
Pliocene, 36 m.y.	Turgai Sea subsided. Indian Plate collided with Asia. Japanese Archipelago separated from Asia. Southern edge of Oriental Plate formed proto-East Indies. Beringia intermittent.	Polar cooling and latitudinal zonation of climates.	Ambystomatidae Leptodactylidae Ranidae
Pliocene, 23 m.y.	Australian Plate collided with Oriental Plate. Lesser Antilles began to form. Africa briefly connected with Eurasia. Beringia intermittent. Uplift of Andes and Sierra Nevada ranges.	Continued cooling; elimination of tropics in North America and Eurasia. Expansion of arid climates.	Plethodontidae Microhylidae
Pliocene, 10 m.y.	South America connected with Central America. Beringia submerged.	Continued polar cooling, latitudinal zonation, and aridity.	

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^aTime since beginning; m.y. = million years.^bL = lower, M = middle, U = upper.

Chapter 17) on the patterns of changing continental configurations and climates during the past 200 million years. The continental configurations used here in reconstructing the biogeography of amphibians were taken from the paleogeographic maps prepared by Barron et al. (1981). The distribution of paleoclimates was synthesized from various sources, principally Axelrod (1960) and P. Robinson (1973). All dates are given in millions of years before the present (my).

Triassic

The earliest period of the Mesozoic extended from about 20 to 190 my.

Geologic Events. At the Permo-Triassic boundary, eastern Asia consisted of several separate blocks south and east of the major Asian land mass. Otherwise, most, if not all, continental masses were united into a single land mass—Pangaea.

Climatic Events. Latitudinal zonation of climates existed. A tropical (equatorial) humid zone was bordered by midlatitude arid belts. Humid temperate conditions existed at high latitudes. Toward the end of the Triassic, the northern humid zone expanded westward across central and western Laurasia.

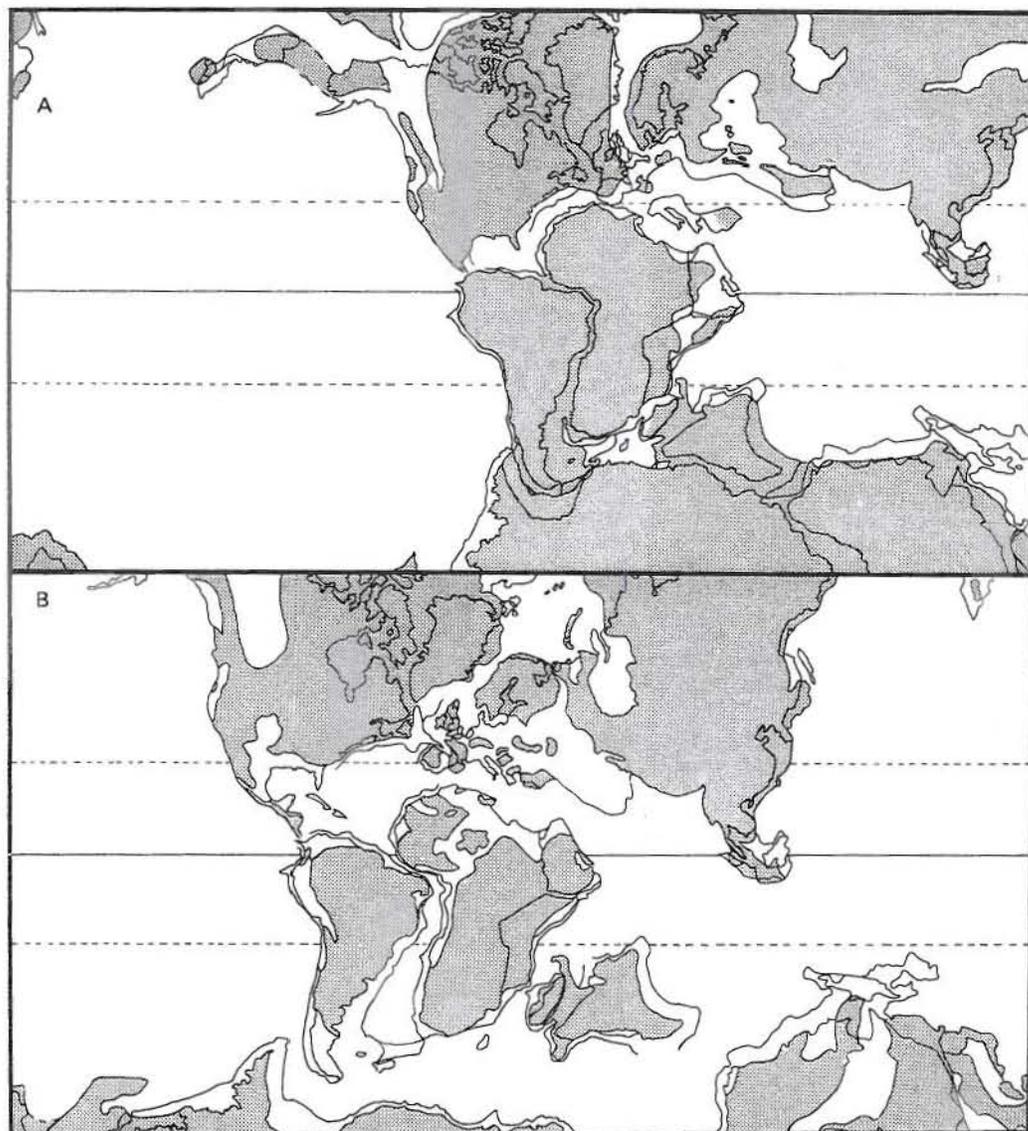


Figure 18-1. Paleogeographic maps depicting continental movements. **A.** Middle Jurassic (160 m.y.). **B.** Middle Cretaceous (100 m.y.). Edges of continental crusts are outlined. Shaded areas are emergent land. Adapted from Mercator projections of Barron et al. (1981).

Jurassic

The initial breakup of Pangaea was in this period, 190 to 135 my (Fig. 18-1A).

Geologic Events. At the beginning of the Jurassic the east Asian blocks united with Pangaea, the breakup of which was initiated at about 180 my by the opening of the North Atlantic Ocean and separation of North America from Africa. One plate (the Kolyma Block) rifted from northwestern North America about 180 my and drifted westward. By 160 my, the Tethys Sea separated eastern Laurasia to the north from eastern Gondwanaland to the

south. Epeiric seas probably connected the Tethys Sea with the North Atlantic Ocean and possibly, by way of the Caribbean Basin, with the eastern Pacific Ocean. Extensive epeiric seas inundated North America and Eurasia from the Arctic Ocean and Asia from the Tethys Sea. By 140 my, that epeiric sea (now called the Turgai Sea) fragmented southern Europe and southwestern Asia into many large islands, and separated Europe from Asia. At about 140 my, the breakup of Gondwanaland also was initiated by fragmentation into three major land masses—South America-Africa, Antarctica-Australia, and Madagascar-Seychelles-India.

Climatic Events. Climatic zonation became less distinctive with an expansion of the humid zones, especially in the tropics, with resulting contraction of mid-latitude arid zones.

Cretaceous

This is the longest period in the Mesozoic, 135 to 65 my.

Geologic Events. Epeiric seas fragmented many continents. Although parts of southern Europe and southwestern Asia were united temporarily with the rest of Europe about 120 my, and northern Europe with northwestern Asia about 100 my, the Turgai Sea persisted throughout the Cretaceous (Fig. 18-1B). The Midcontinental Sea separated eastern and western North America in the mid- to late Cretaceous (100 to 75 my), a time when epeiric seas fragmented northwestern Africa into at least two large islands and separated the western part of Australia from the Antarctic-Australian continent. The Kolyma Block collided with northeastern Asia about 120 my. The South Atlantic Ocean began to form between Africa and South America at about 125 my; during the ensuing 20 my, South America drifted westward, and the Atlantic Ocean became continuous. Volcanic activity in the Central American region may have provided an intermittent land connection between North and South America (Donnelly, 1985); this probably lasted into the Paleocene. At about 100 my, Madagascar terminated its northeastward drift, whereas the Seychelles-Indian continent continued drifting. The separation of the land mass now represented by New Zealand occurred at about 74 my.

Climatic Events. The climates throughout most of the Cretaceous were equable and tropical or subtropical. Temperate humid zones were discontinuous in the far north; arid zones were small and discontinuous.

Cenozoic

During the last 65 my the continents moved to their present positions and modern climatic patterns became established.

Geologic Events. The Turgai Sea persisted intermittently throughout the first half of the Cenozoic; continuous land connection between Europe and Asia has persisted since the end of the Eocene, about 35 my (Fig. 18-2). The Seychelles broke off from the Indian continent about 64 my, and India continued its northeastward arc to collide with Asia in the Oligocene (about 35 my). The collision resulted in the orogenic uplift of the Himalayas, which in time effectively separated the Indian subcontinent from the rest of Asia; an extensive embayment in Assam and Burma provided a barrier between India and southeastern Asia for much of the later Cenozoic. The land mass now represented by the Japanese Archipelago seems to have broken off from Asia at the Oligocene-Miocene boundary (23 my). The southern and eastern edge of the Oriental Plate became a series of islands in the Oligocene and Miocene. Australia separated from Antarctica about 55 my (late Paleocene). The northeastward arc of the Australian Plate resulted in its collision with the Oriental Plate in the Miocene with the consequent orogeny of the mountains of New Guinea. South America continued to drift westward and finally estab-

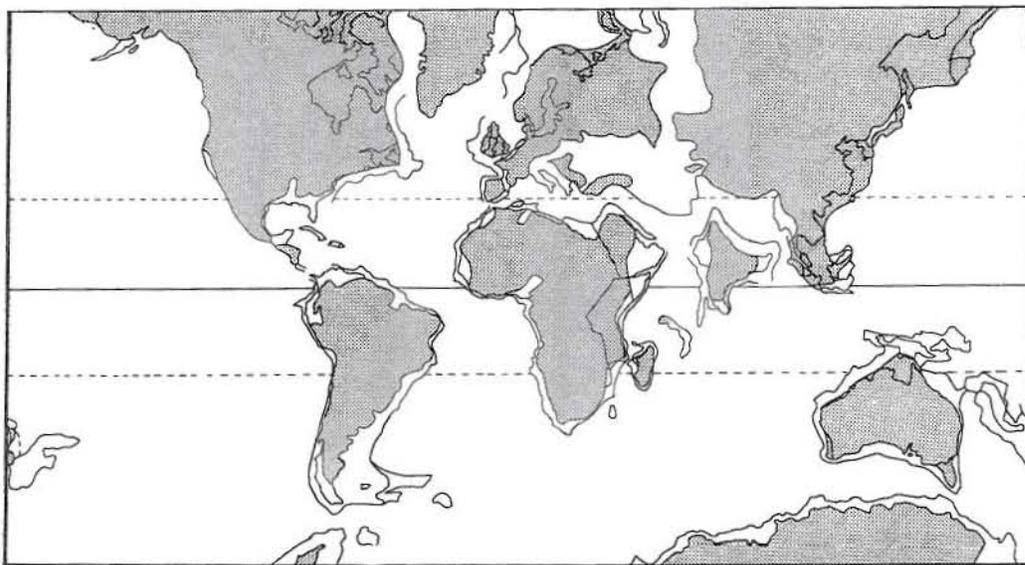


Figure 18-2. Paleogeographic map depicting the arrangement of the continents in the late Eocene (40 m.y.). Edges of continental crusts are outlined. Shaded areas are emergent land. Adapted from Mercator projections of Barron et al. (1981).

lished contact with the Central American appendage of North America in the Pliocene (3–6 my). Nuclear Central America was variously connected and separated from North America throughout most of the Cenozoic. The opposing movements of the Caribbean Plate (eastward) with respect to North America and South America (westward) resulted in the formation of the Greater Antilles, perhaps as early as the Cretaceous but certainly by the Paleocene (54–65 my), possibly with a continuous land connection with Central America. Beginning in the Miocene, the Lesser Antilles began to arise as oceanic islands along the arc of the Caribbean Plate to form the chain of islands between South America and the Greater Antilles. Africa had a restricted connection with Eurasia via Arabia from the late Miocene (about 8–10 my); with the rifting of the Red Sea this is now restricted to the Sinai region. Also in the late Miocene and/or early Pliocene there was a connection between Africa and the Iberian Peninsula. In the Northern Hemisphere there were two intermittent connections between Eurasia and North America. The Beringia land connection between North America and Asia was intermittent throughout most of the Cenozoic and finally submerged in the Pliocene (3–5 my). In the Paleocene-Eocene (50–60 my), two intermittent connections have been postulated to have existed between northern Europe and North America (McKenna, 1975)—(1) the DeGeer passage via Spitzbergen, northern Greenland, and Ellesmere Island, and (2) the Thule route via southern Greenland and Ellesmere Island.

Climatic Events. At the beginning of the Cenozoic most of the land masses of the world were under equable or subtropical climates; temperate climates existed only at high latitudes. Beginning in the Oligocene, polar cooling brought about a more distinctive latitudinal zonation of climates with a gradual elimination of tropical conditions and vegetation in North America and Eurasia, and with the restriction of tropical groups to the southern paleopeninsulas (Malay-Indonesian region of southeastern Asia and Central America) by the Miocene. Concomitant with the restriction of the tropics, there was an expansion of temperate climates into the lower latitudes of North America and Eurasia. During the northeastward drift of Australia in the Cenozoic, the continent changed latitudinal positions with the consequence that the climate changed from moist temperate to arid and semiarid over much of the continent in the latter part of the Cenozoic. Also at this time, most terrestrial life was eliminated from Antarctica. From the Miocene onward, there was an expansion of the arid and semiarid climates and vegetation over southwestern North America, southwestern Asia, western South America, and northern Africa. The development of arid conditions on western sides of continents was caused by cooling of high-latitude oceans and the patterns of cold currents from high to low latitudes along the west sides of continents. Also tectonic processes of the continental crusts of North and South America resulted in orogenies producing high mountains along the

western edges of the continents; the Andes and Sierra Nevada chains uplifted at various times during the Cenozoic, and by the time of the major uplifts in the Miocene and Pliocene they interrupted moisture-laden onshore winds and created rain shadows to the east. During the last 2 my, Pleistocene climatic fluctuations resulted in four or more major advances of polar and montane glaciers with concomitant latitudinal and altitudinal shifts in temperature belts and the restriction of humid tropical conditions during glacial phases and restrictions of the arid tropics during interglacials.

LISSAMPHIBIA

The fossil record of early lissamphibians is too poor to provide any meaningful information on the early distribution of the group. J. Savage (1973) emphasized that the early history of salamanders was associated with Laurasia, whereas caecilians and most anurans were restricted to Gondwanaland. If P. Robinson's (1973) interpretation of Permo-Triassic climatic zonation is correct, the distribution of lissamphibians at that time may have been divided by the midlatitude arid belt that isolated prosalamanders in the high-latitude humid zone and procaecilians and proanurans in the equatorial humid zone.

CAUDATA

The fossil history of the salamanders extends back to the Middle Jurassic, so the evolutionary geography of these amphibians is closely correlated with the breakup of Pangaea, especially Laurasia (essentially all fossil and living salamanders are associated with Laurasian land masses). Milner (1983) provided a geologically well-documented model for the biogeography of salamanders, but her phylogenetic arrangement is notably different from that proposed here (Chapter 17). Although Milner's emphasis on Laurasian cosmopolitanism of salamanders by the Middle Jurassic is correct, some of the details of the model do not fit the phylogenetic history.

The earliest known fossil salamander is the prosirenid *Albanerpeton* from the Middle Jurassic of Europe. If the hypothesized phylogeny of salamanders is correct, the four suborders were extant by the Middle Jurassic. However, the fossil record of early salamanders provides only limited support for this idea. The Karauroidea is known only from the Upper Jurassic of Asia, and the Sirenoidea and Salamandroidea (other than prosirenids) are unknown before the Late Cretaceous. Furthermore, the Cryptobranchoidea is unknown before the Paleocene. Nevertheless, the changing continental configurations and climates in the Mesozoic provide a basis for a biogeographic interpretation of the phylogenetic model.

If protosalamanders were distributed throughout the northern humid zone at the beginning of the Jurassic, the earliest fragmentation of Laurasia would have played an important role in their early evolution. Moreover, only

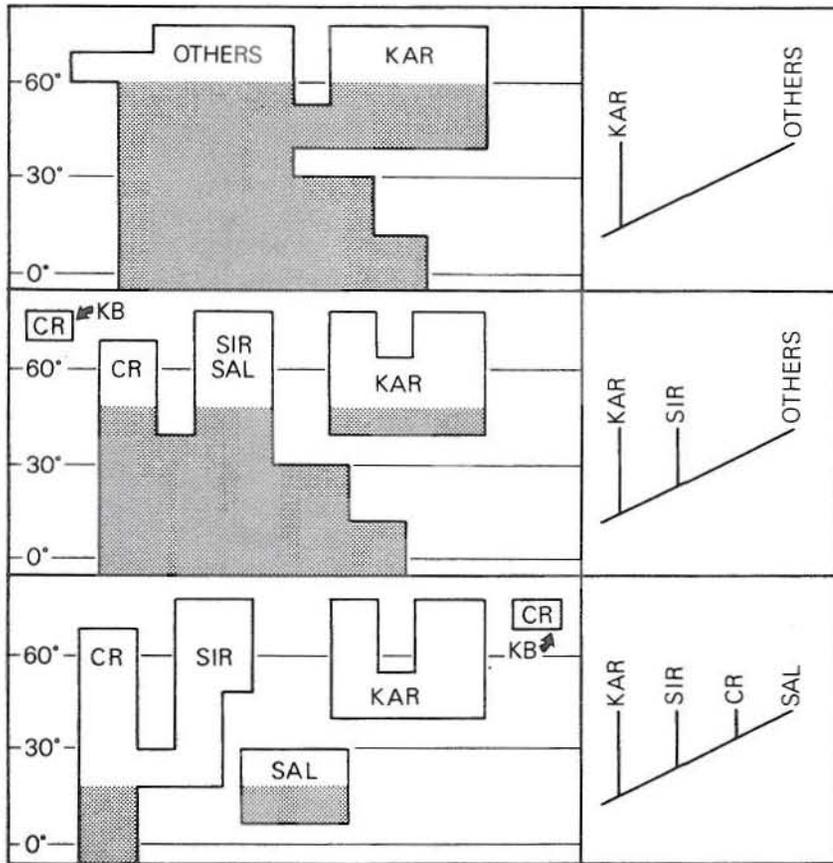


Figure 18-3. Diagrammatic representation of the sequential breakup of Laurasia in the Early and Middle Jurassic and corresponding vicariance events of the suborders of salamanders. Cross-hatched regions have unsuitable climates for salamanders. Abbreviations: CR = Cryptobranchoidea, KAR = Karauroidea, KB = Kolyma Block, SAL = Salamandroidea, SIR = Sirenoidea.

the northern fragmentation would have affected salamanders, because they were excluded from the middle and lower latitudes by the arid midlatitude climates. The combination of continental fragmentation (drift and epeiric seas) and expanding humid climates resulted in a series of vicariance events that could have given rise to the four suborders of salamanders by the Middle Jurassic. These geological and vicariance events are (Fig. 18-3):

1. Opening of the North Atlantic Ocean in the Early Jurassic (180 my) resulting in the separation of ancestral salamanders into two stocks along the northern margins of Asia and Euramerica. The stock in Asia gave rise to the Karauroidea and the one in Euramerica was the stock for all other salamanders.
2. Separation of the northern part of Euramerica by the Midcontinental Sea (160 my) resulting in the separation of sirenoids in aquatic habitats in eastern North America and cryptobranchoids and salamandroids in terrestrial habitats in western and eastern Euramerica, respectively. Cryptobranchoids also were present on the Kolyma Block, which subsequently rifted from western North America.
3. Fragmentation of Euramerica (150 my) resulting in the Sirenoidea surviving only in eastern North America and the Salamandroidea surviving only in Europe (then completely separated from Asia by the Turgai Sea).

Thus, by the Middle Jurassic, four stocks of salamanders were present on at least five land masses. From this point in time, the biogeography of each of the suborders can be treated separately.

The Karauroidea may have existed in parts of Asia east of the Turgai Sea until sometime in the Cenozoic, but the absence of fossils (other than the type) of this extinct suborder precludes any definitive biogeographic statements.

According to the vicariance events that isolated the suborders on separate continental blocks, the Sirenoidea was widespread east of the Midcontinental Sea in North America in the Upper Cretaceous and early Cenozoic. Presumably, limblessness and aquatic habits evolved early in the history of the suborder. Concomitant with the zonation of climates beginning in the Oligocene, the distribution of sirenoids became restricted to southeastern North America.

Early in its history, the Cryptobranchoidea was re-



stricted to North America. In the Early Jurassic, cryptobranchoids probably resembled hynobiids; such a stock remained relatively unchanged on the Kolyma Block as it drifted westward from North America and collided with eastern Asia in the Early Cretaceous (120 my), thereby introducing cryptobranchoids into Asia. This was the ancestral stock of the hynobiids. These salamanders probably did not reach their easternmost distribution until the Himalayan Orogeny and the disappearance of the Turgai Sea in the Oligocene. However, they probably were on the land mass that became the Japanese Archipelago before that block separated from Asia in the late Oligocene or early Miocene. The patterns of distribution of the living hynobiids suggest that lineages were isolated in the mesic montane areas by continental desiccation in the middle and late Cenozoic. The cryptobranchoid stock that remained in North America evolved through arrested development to become obligate neotenes, the cryptobranchids. Presumably, these aquatic salamanders were widespread throughout North America and Eurasia (via the DeGeer Passage) in the early Cenozoic. Latitudinal climatic zonation and continental desiccation in the Cenozoic resulted in the distributional relicts of *Cryptobranchus* in southeastern North America and *Andrias* in southeastern China and Japan.

The fragmentation of what now is Europe and southwestern Asia by the Tethys Sea probably resulted in salamandroids on several small land masses. Contraction of midlatitude arid zones in the Late Jurassic and Early Cretaceous would have allowed the expansion of the range of salamandroids into North America before the complete separation of Europe and North America in the early Cenozoic. The stocks of salamandroids that gave rise to the prosirenid-batrachosauroidid-proteid lineage, to the dicamptodontid-scapherpetontid lineage, and possibly to the amphiumids must have differentiated prior to the Late Cretaceous. All of these families are known from late Mesozoic or early Cenozoic deposits in both Europe and North America, except amphiumids and scapherpetontids, which are known only from North America. Therefore, the differentiation of these lineages of salamandroids seems to be associated with the complex fragmentation of Euramerica in the Middle Jurassic.

The prosirenids, batrachosauroidids, and scapherpetontids are extinct. Proteids survive as the subterranean *Proteus* in southern Europe and as five species of *Necturus* in eastern North America. The only living dicamptodontids are *Dicamptodon* and *Rhyacotriton* living in cold streams in northwestern North America. The only surviving amphiumid is *Amphiuma* in southeastern North America. All of these living salamanders are relicts of formerly more diverse and widespread groups of salamanders. The vicariance of the salamandrid and the ambystomatid-plethodontid lineage also may have occurred toward the end of the Mesozoic, when the last major land connections between Europe and North America were broken. According to Özeti and D. Wake (1969), there

are three groups of salamandrids. *Pleurodeles* in Europe and *Tylostotriton* and *Echinotriton* in eastern Asia show primitive characters and may represent relicts of a formerly widely distributed group of primitive salamandrids. *Salamandra* and its relatives are restricted to western Eurasia and presumably never existed east of the Turgai Sea; *Salamandra* is known in the fossil record of Europe since the late Eocene. The so-called *Triturus* group is holarctic in distribution. This group underwent its early differentiation in western Eurasia in the Cenozoic (for *Triturus* known as early as the Eocene in Europe) and apparently did not disperse into eastern Eurasia until subsidence of the Turgai Sea at the beginning of the Oligocene. This timing is in accordance with this group reaching eastern Asia prior to the separation of the land mass that was destined to be the Japanese Archipelago and also for the dispersal of salamandrids into North America via Beringia (the first salamandrid fossils in North America are from the late Oligocene).

If the cladistic arrangement of the ambystomatids and plethodontids is correct, there is no major geologic event that could have separated these groups in North America after the Cretaceous, at which time the ancestral stock might have been split by the Midcontinental Sea. Ambystomatids do not appear in the fossil record until the Oligocene, and plethodontids are unknown as fossils prior to the Miocene. However, ages of separation of groups of plethodontids suggested by immunological distances are much older; some are placed in the Paleocene (Maxson et al., 1979). These data suggest that the separation of ambystomatids and plethodontids in the Cretaceous is reasonable. Ambystomatids seem to have adapted to subhumid climates better than any other North American salamanders. Their major centers of differentiation are in southeastern North America and along the southern edge of the Mexican Plateau.

The evolution of the plethodontids seems to have been associated with the Appalachian uplands of eastern North America. Generic differentiation between *Plethodon* and *Ensatina* took place in the Paleocene, and differentiation between the eastern and western groups of *Plethodon* occurred in the Eocene (dating based on immunological distances given by Maxson et al., 1979). Presumably *Plethodon* became separated into eastern and western groups as the result of climatic desiccation in midcontinental North America beginning in the Oligocene. The dispersal of the plethodontid genus *Hydromantes* from North America to Eurasia presumably took place via Beringia in the Oligocene; dating is based on immunological data (D. Wake et al., 1979). On the basis of that data it can be assumed that plethodontines of the tribe Ectoglossini evolved prior to the Oligocene.

The supergenus *Bolitoglossa* contains 11 genera and 140 species in the tropical lowlands and the mountains of Mexico and Central America; two genera (*Bolitoglossa* and *Oedipina*) have representatives in South America (see section: Inter-American Interchange under Anura).

According to dates suggested by genic differentiation, *Bolitoglossa* entered South America in the late Miocene, prior to the establishment of the present continuous land connection in the Pliocene (Hanken and D. Wake, 1982). The greatest differentiation of genera of bolitoglossines is in the mountains of southern Mexico, and the greatest differentiation of species is in the highlands of southeastern Mexico (Oaxaca and Veracruz) and nuclear Central America (Guatemala and Chiapas, Mexico) and the highlands of Costa Rica and adjacent Panama (D. Wake and J. F. Lynch, 1976; D. Wake and P. Elias, 1983).

It might be expected that the differentiation of bolitoglossines in Mexico and Central America occurred in association with the orogenic events that took place principally in the Miocene and Pliocene. Immunological distances provide possible dates for differentiation of species of *Pseudoeurycea* from the Eocene to the Pliocene (8–50 my); differentiation of the genera *Chiropterotriton*, *Dendrotriton*, and *Pseudoeurycea* occurred in the Paleocene and Eocene according to immunological data (Maxson and D. Wake, 1981).

GYMNOPHIONA

With the exception of a few caeciliids in Central America and Mexico and a few ichthyophiids in southeastern Asia, all living caecilians occur on Gondwanan land masses. Moreover, the single fossil caecilian is from the Paleocene of Brazil. Therefore, the evolutionary history of caecilians must be associated with the history of the southern continents.

If the phylogeny proposed here (Fig. 17-2) is correct, the major vicariance events of the families of caecilians must have occurred prior to the breakup of Gondwanaland. The most primitive caecilians, the rhinatrematids, presently are restricted to the northern Andes and Guiana Shield in South America. Presumably rhinatrematids are relicts of a group that was widespread in Gondwanaland prior to the breakup of the continents in the Late Jurassic. Also, the ichthyophiids that survived on the Indian Plate as it drifted from Africa to Asia are relicts of a formerly more widely distributed group. Possibly the uraeotyphlids and scolecomorphids evolved in situ in peninsular India and tropical Africa, respectively. The caeciliids have a classic Gondwanan pattern—South America, Africa, and India, including the Seychelles Islands. The aquatic typhlonectids presumably evolved in situ in South America from a caeciliid-like ancestor.

The distributional data, in combination with the phylogenetic arrangement of caecilians, dictate an early divergence of most of the families—prior to the Late Jurassic, except for typhlonectids. The drift of the Indian Plate must have carried ichthyophiids, uraeotyphlids, and caeciliids to Asia; of these, only the ichthyophiids have extended beyond the Indian subcontinent. The presence of caeciliids on the India-Madagascar-Seychelles Plate is obvious because of their presence today in peninsular

India and on the Seychelles. But why are there no caecilians on Madagascar?

The spread of ichthyophiids into southeastern Asia and adjacent islands must have occurred after the collision of the Indian Plate with Asia in Oligocene. Some caeciliids (*Dermophis* and *Gymnopsis*) dispersed from South America into Central America during a brief connection in the Paleocene. Others (e.g., *Caecilia* and *Oscaecilia*) dispersed northward only after the closure of the Panamanian Portal in the Pliocene.

This hypothesized history of caecilians is supported (in part) by immunological data (Case and M. Wake, 1977). An estimated divergence time of *Dermophis* from *Caecilia* of 57 my coincides with the Paleocene separation of South and Central America. Estimated times of divergence of African (*Boulengerula* and *Geotrypetes*) and neotropical (*Dermophis*) caeciliids of 99 and 120 my are consistent with the separation of Africa and South America. An immunological distance of 210 units between *Ichthyophis* and *Dermophis* suggests an ancient separation of these taxa, but the limits of accurate measurement of immunological distance is at about 200 units. Thus it is possible to suggest only that divergence occurred more than 120 my.

ANURA

J. Savage (1973) provided a lengthy discussion of the distribution of anurans, in which he showed that the histories of the family groups were intimately associated with the histories of the land masses that they occupied in the Mesozoic and Cenozoic. In some cases, Savage took unwarranted liberties with the classification of anurans. For example, he eliminated the distributional enigma of a dyscophine microhylid in the Oriental Region by assigning the genus *Calluella* to the Asterophryinae; otherwise, the Dyscophinae is restricted to Madagascar. Also, he split the melanobatrachine microhylids and placed *Melanobatrachus* in the Microhylinae and recognized the African genera in the Hoplophryinae. Moreover, he considered the Australo-Papuan hylids to be a separate family, the Pelodryadidae, having a history independent from the neotropical Hylidae. Savage's rearrangements make perfectly good sense biogeographically, and he may be correct evolutionarily; existing phylogenetic evidence neither supports nor refutes his changes. Savage's phylogeny of the suborders of anurans was based on P. Starrett's (1973) suggestion that the pipoid and microhylid frogs were primitive sister groups. This idea was based on her interpretation of the evolution of larval characters. Starrett's phylogeny has been disputed by evidence from larvae provided by Sokol (1975) and Wassersug (1984).

As emphasized by J. Savage (1973), the historical biogeography of anurans is associated mainly with Gondwanaland. However, limited fossil evidence and present distributions of some families of anurans indicate that differentiation of some anuran stocks was associated with

the initial breakup of Pangaea in the Early Jurassic (160–180 my). The Triassic *Triadobatrachus* from Madagascar generally is considered to be an early frog. The earliest known fossil that unquestionably is a frog is *Vieraella* from the Lower Jurassic of Argentina. By the Late Jurassic there are diverse anuran fossils from Europe, North America, and South America, so it may be assumed that frogs became widespread in the world during the Jurassic.

Leiopelmatids generally are considered to be the most primitive living anurans. The Jurassic *Vieraella* and *Notobatrachus* in Argentina and the living *Ascaphus* in North America and *Leiopelma* in New Zealand provide evidence that the primitive frogs grouped in the Leiopelmatidae were widely distributed prior to the breakup of Pangaea and that the living genera are relicts of this ancient group of anurans. The histories of the other families of anurans (with the possible exception of the pipids) are associated with either Laurasia or Gondwanaland.

Laurasia. Laurasian groups include the Discoglossidae, Palaeobatrachidae, Rhinophrynidae, Pelobatidae, and Pelodytidae.

Discoglossids presumably were associated with the humid temperate climates of Laurasia; the earliest fossils of the family are from the Late Jurassic of Europe and the Late Cretaceous of North America. Therefore, it seems likely that discoglossids evolved prior to the breakup of Laurasia in the Jurassic. Discoglossids seem to have diversified in Eurasia west of the Turgai Sea, where four genera survive. Subsequent to the subsidence of the Turgai Sea in the Oligocene, the European *Bombina* dispersed eastward. Ages of differentiation of species of *Bombina* determined from immunological distances by Maxson and Szymura (1979) show that the eastern Asian species *B. orientalis* differentiated in the Miocene, whereas *B. bombina* and *B. variegata* are late Pliocene or Pleistocene vicariants. Climatic deterioration in midcontinental Eurasia in the late Cenozoic and/or Pleistocene climatic fluctuations resulted in great discontinuities in the distribution of *Bombina*. However, *Barbourula* presumably was in Asia, where it became adapted to tropical conditions. As climatic cooling restricted tropical organisms to the Indo-Malay region, *Barbourula* survived in Borneo and dispersed to the Philippines.

Assuming that their unique larvae evolved only once, the pipoids (Rhinophrynidae, Palaeobatrachidae, and Pipidae) can be considered a natural group. Early fossil remains exist from Laurasia and Gondwanaland, and pipoids now occur in tropical North America, South America, and Africa. The palaeobatrachids are known from the uppermost Jurassic through the Pliocene of Europe, and from the late Cretaceous of North America. Rhinophrynids are known from the late Paleocene through the Oligocene of North America; the single living species is restricted to Mexico and Central America. Pipids are known from the Lower Cretaceous of Israel, Upper Cretaceous

of South America, and various Cenozoic ages in Africa and South America; living pipids occur in tropical South America and sub-Saharan Africa.

Protopipoids apparently were widely distributed in the humid tropical zone in Pangaea. The vicariance of rhinophrynids from other pipoids may have resulted from their isolation in North America after the initial opening of the North Atlantic Ocean in the early Jurassic (180 my). Subsequently, the vicariance of palaeobatrachids and pipids could have been associated with the separation of western Laurasia from western Gondwanaland by the Tethys Sea in the mid-Jurassic (160 my). Palaeobatrachids still had access to North America until the Eocene. In Europe at least, this family seems to have been the Laurasian counterpart to the Gondwanan pipids. The palaeobatrachids were widespread and diverse in Europe; their disappearance at the end of the Pliocene possibly was caused by the cold climates and glaciation in the Pleistocene. The history of the Pipidae is associated with the separation of Africa and South America and is discussed in the following section on Gondwanaland.

The pelobatoids include the pelobatids (Eopelobatinae, Pelobatinae, and Megophryinae) and the pelodytids in Laurasia. Estes (1970) considered the eopelobatines, which are known from the Late Cretaceous of North America and Asia, to be the most primitive group. Pelobatines are well represented in the fossil record beginning in the Eocene of Europe and in the Oligocene of North America; however, immunological dating of the living European *Pelobates* and North American *Scaphiopus* indicates divergence in the Cretaceous (Sage et al., 1982). Pelodytids first appear in the mid-Eocene of Europe, where the living *Pelodytes* survives; they also are known from the Miocene of North America, where the family is extinct. Living and fossil pelobatines have greatly enlarged metatarsal tubercles, and living species are fossorial. *Eopelobates* has only slightly enlarged metatarsal tubercles and may be a grade in the evolution of the fossorial pelobatines. Possibly these anurans evolved in the Laurasian arid zone and dispersed throughout xeric habitats in Laurasia prior to the separation of North America and Eurasia in the Early Jurassic and prior to the contraction of the arid zones in the Mid- and Late Cretaceous. The megophryines inhabit humid tropical and subtropical regions in southeastern Asia and adjacent archipelagos, and some taxa in the Himalayas; there are no fossils. Presumably they evolved from an eopelobatine-like ancestor (Estes, 1970). If pelodytids are a historical reality, they must have diverged from propelobatids prior to the mid-Jurassic; however, there is no fossil evidence for such an early vicariance.

Gondwanaland. The vicariance of the other family groups of anurans is associated primarily with the breakup of Gondwanaland. It is safe to assume that an ancestral stock of arciferous anurans was in Gondwanaland prior to the separation of that southern land mass from Laurasia

Table 18-2. Families of Anurans and Their Association with Gondwanan Continents in the Late Jurassic

Africa— South America	Madagascar— Seychelles-India	Australia— Antarctica
Leiopelmatidae	Myobatrachidae?	Leiopelmatidae
Pipidae	Bufoidea?	Myobatrachidae
Leptodactylidae	Microhylidae	Hylidae
Hylidae	Ranidae	
Bufoidea	Hyperoliidae	
Microhylidae	Rhacophoridae	
Ranidae		
Hyperoliidae		
Rhacophoridae		

in the mid-Jurassic. At that time, this group of anurans shared Gondwanaland with leiopelmatids and pipids. Prior to the initial breakup of Gondwanaland in the late Jurassic (140 my), this ancestral stock differentiated into three major groups that can be referred to as the bufonoids, ranoids, and microhylids. The association of different lineages of these three major groups with different Gondwanan continents necessitates further differentiation within each group prior to the fragmentation of the continents (Table 18-2). The initial breakup of Gondwanaland resulted in three continental masses; the histories of the anuran faunas associated with each are discussed separately.

Antarctica-Australia.—The anuran fauna of the Antarctica-Australian continent definitely was composed of leiopelmatids and myobatrachids, and probably hylids. J. Savage (1973) suggested that microhylids reached the Oriental Region by being on Antarctica-Australia. As emphasized by Tyler (1979), there is no evidence for the presence of microhylids in Australia until the late Cenozoic, when a few species reached northern Australia from New Guinea. If the Australo-Papuan hylids represent a lineage independent from the neotropical hylids, the Hylidae (sensu stricto) was not present on Antarctica-Australia.

This continent had temperate and tropical climates; leiopelmatids apparently became restricted to the former and myobatrachids to the latter. In the Late Cretaceous, the land mass destined to become New Zealand fragmented from the temperate part of the continent. Leiopelmatid frogs survived as the only anurans on New Zealand and became extinct on Antarctica-Australia. Biochemical evidence suggests that the three species of *Leiopelma* diverged in the Miocene and Pliocene (Daugherty et al., 1981). Antarctica and Australia split apart in the Paleocene (55 my). Antarctica remained in its polar position and beginning in the Oligocene was subjected to extreme cold; the extensive polar icecap now conceals the fossils of the former biota. Australia drifted northeastward and late in the Cenozoic became increasingly arid.

According to dates derived from immunological data (Daugherty and Maxson, 1982), the differentiation of many

myobatrachine genera occurred in the mid-Cretaceous (*Assa*) or Late Cretaceous (*Arenophryne*, *Geocrinia*, *Myobatrachus*, *Paracrinia*, *Rheobatrachus*, and *Taudactylus* from *Crinia*); *Uperoleia* presumably diverged from *Crinia* in the late Eocene. On the other hand, hylid differentiation is a Cenozoic phenomenon (Maxson et al., 1982). In this view divergence of the *Cyclorana-Litoria aurea* lineage from other *Litoria* occurred in the late Eocene, and *Cyclorana* and the *Litoria aurea* group vicaried in the late Oligocene. Therefore, it is possible that most, if not all, of the autochthonous genera of Australian frogs, as well as some species groups, were in existence before Australia made contact with the Oriental Region.

The Australian Plate contacted the Oriental Plate in the Miocene and caused the complex uplift of New Guinea. This contact provided the first opportunity for interchange of biotas that had been separated for 120 million years since the initial fragmentation of Gondwanaland. At this time, hylids and myobatrachids from Australia became associated with Oriental microhylids in New Guinea, and one stock of Papuan hylids evolved into *Nyctimystes*. Although there have been brief periods of continuous land connection between New Guinea and Australia via the Torres Strait as recently as the Pleistocene, few Papuan taxa have dispersed southward into Australia. These include a few species of *Nyctimystes*, several species of two genera of microhylids (*Cophixalus* and *Sphenophryne*), and one species of *Rana*.

Madagascar-Seychelles-Australia.—The anuran fauna of the Madagascar-Seychelles-Indian continent that rifted from the rest of Gondwanaland about 140 million years ago contained only tropical groups. Present on this continent were ranids, hyperoliids, rhacophorids, and microhylids. Myobatrachids also are presumed to have been present, and probably bufonids were present. The ranids consisted of ranines and the stock that gave rise to the mantellines. The microhylids minimally consisted of melanobatrachines, microhylines, and a stock, perhaps much like living scaphiophrynines, that was to give rise to five subfamilies. If the Eocene *Indobatrachus* is indeed a myobatrachid, that family must have been represented on the continent. Also, the presence of myobatrachids is supported by evidence that myobatrachids and sooglossids are related. J. Savage (1973) suggested that the radiation of bufonids in southeastern Asia was a late Cenozoic event following the dispersal of *Bufo* into that region from North America via Beringia. The diversity of bufonid genera (e.g., *Ansonia* and *Pedostibes*) in southeastern Asia and adjacent islands strongly suggests an earlier arrival of a bufonid stock. This arrival could have been via the drifting continent. Unfortunately, there is no fossil evidence whatsoever. Savage also suggested that rhacophorids dispersed from Africa to Madagascar by waiving and to southeastern Asia by terrestrial dispersal via southwestern Asia, and that hyperoliids dispersed from Africa to Madagascar and the Seychelles. If these groups of

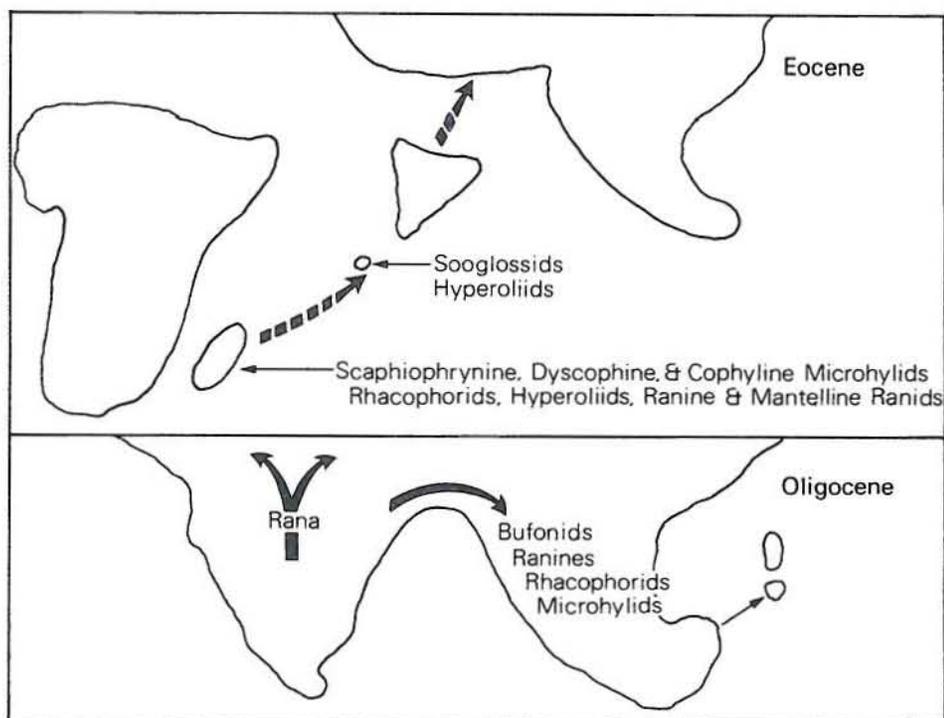


Figure 18-4. Sequential tectonic movements of India and associated land masses during the early and middle Cenozoic, showing (top) the consequent isolation of anuran taxa on Madagascar and the Seychelles Islands and (bottom) the dispersal of taxa from India to Asia.

anurans were present on the drifting continent, these independent long-distance dispersals are not necessary.

During its drift from western Gondwanaland, the Madagascar-Seychelles-Indian continent fragmented. Madagascar split away from the rest of the continent in the mid-Cretaceous (100 my) and moved northward to its present position off the coast of Africa. As the Indian continent continued in its arc toward Asia, the small land mass that later became known as the Seychelles Islands broke off in the early Paleocene (64 my). India finally collided with Asia in the Oligocene (35 my). This drifting land mass provided transportation for several groups of Gondwanan anurans to the Oriental Region and resulted in the isolation of various groups of anurans on fragments left along its path.

The major part of the anuran fauna of Madagascar consists of scaphiophrynine, dyscophyne, and cophyline microhylids, mantelline ranids, rhacophorids, and hyperoliids. Ranines are represented by one species of *Tomopterna*, a genus that also has species in Africa and India. With the exception of *Tomopterna* and the dyscophine genus *Calluela*, which occurs in southeastern Asia and adjacent islands, all of the subfamilies of ranids and microhylids on Madagascar are endemic, as are the rhacophorid genera *Aglyptodactylus* and *Boophis*, and the hyperoliid genus *Heterixalus*. The subfamilies endemic to Madagascar presumably evolved in situ after the separation of the island from the rest of the drifting continent, which carried with it *Tomopterna* and an ancestor to *Calluela* (Fig. 18-4).

The Seychelles Islands have a small but significant anuran fauna. Except for *Ptychadena mascariensis*, a waif from Africa via Madagascar, the anuran fauna consists of three species of the endemic family Sooglossidae and the monotypic hyperoliid genus *Tachycnemis*. If sooglossids indeed are related to myobatrachids, as suggested by J. D. Lynch (1973) and Nussbaum (1979b), sooglossids can be viewed as isolated relicts, perhaps derivatives of an ancient lineage that is represented only by *Indobatrachus* from the Eocene of India. Most likely the anuran fauna of the Seychelles was much more diverse in the early Cenozoic than it is now. There is no reason to assume that microhylines, ranines, and rhacophorids did not exist there; those groups presumably met the fate of many island populations—extinction.

When India collided with Asia in the Oligocene, the subcontinent contained *Tomopterna* (also present today in Madagascar and Africa), *Melanobatrachus* (other melanobatrachine microhylids in Africa), ranines, rhacophorids, bufonids, microhylines, and an ancestor to the dyscophine *Calluela*. Once the land connection was effected, these groups (with the exception of *Tomopterna* and *Melanobatrachus*) dispersed eastward and thence southward into the area that fragmented in the late Oligocene and Miocene into the Greater Sunda Islands (Fig. 18-4). Most of this dispersal occurred prior to the marine transgression into the Assam-Burma region in the late Cenozoic. Bufonids, rhacophorids, and microhylids apparently waived to the Philippines, which arose in the Oligocene.

The ancestral *Calluella* (Microhylidae) dispersed through this now insular region and differentiated into a stock that gave rise to the Genyophryinae, represented today by the widespread lowland genera *Cophixalus*, *Oreophryne*, and *Sphenophryne*. With the uplift of New Guinea resulting from the collision of the Australian Plate with the southern edge of the Oriental Plate in the Miocene, this microhylid stock differentiated into the diversity of genyophryine and asterophryine microhylids known there today.

The early ranines in the Oriental Region probably were the stocks that gave rise to two groups of ranids. One of these differentiated into several Oriental genera (e.g., *Amolops* and *Occidozyga*) that are distributed on the mainland (some in peninsular India) and in some cases also in the Greater Sunda Islands and the Philippines. The other group is the so-called platymantine ranids (*Batrachylodes*, *Ceratobatrachus*, *Discodeles*, *Palmatorappia*, and *Platymantis*). This group is widely distributed from the Philippines to Fiji but does not occur on the mainland; the greatest diversity is in the Solomon Islands. The genus *Rana* seems to have arrived in the Indo-Malayan region more recently.

Africa-South America.—The separation of South America from Africa was initiated in the mid-Cretaceous (100 my), but land connections between the continents may have persisted until 90 million years ago. Prior to the separation of the continents, the anuran fauna consisted of pipids, bufonids, leptodactylids, and microhylids (Fig. 18-5). Additionally, but apparently restricted to the African part of the continent, there were ranids, hyperoliids, and rhacophorids. Assuming that the dendrobatids and petropedetine ranids are sister groups, the immediate ancestor of these groups must have been present before the separation of the continents. Also, if the Australo-Papuan hylids are confamilial with the neotropical hylids, the Hylidae would have had to be present at least in the South American part of the continent.

Once South America and Africa were separated, the anuran faunas diversified independently on the two continents. In Africa, the leiopelmatids (and hylids, if they

were there) became extinct, and the leptodactylid stock survived only as *Heleophryne* in cool streams in South Africa. Prior to the separation of the Madagascar-Seychelles-Indian continent, microhylids in Africa already had differentiated into melanobatrachines and microhylines. The former now is restricted to a few taxa in the mountains of East Africa. The latter differentiated into two lineages—phrynomerines and brevicipitines, both of which presently are widely distributed in sub-Saharan Africa.

In Africa, the pipids differentiated into numerous species; today, *Hymenochirus* and *Pseudhymenochirus* are restricted to tropical West Africa, whereas the more speciose genus *Xenopus* is widespread in sub-Saharan Africa. Among the tree frogs, the hyperoliids have differentiated into an array of 12 genera and nearly 200 species throughout sub-Saharan Africa, whereas the rhacophorids survive only as *Chiromantis* with three species in tropical Africa. Bufonids have diversified into a number of genera, and the genus *Bufo* is represented by many species. The presence of *Bufo* in the Paleocene of Brazil indicates that the genus was in existence before the separation of Africa and South America. Times of divergences based on immunological data corroborate the Cretaceous occurrence of *Bufo* (Maxson, 1981a); furthermore, her data indicated that *Schismaderma* differentiated in the Eocene and at least some species of African *Bufo* are Miocene in origin.

Africa is the site of the major radiation of ranids. A ranid stock represented by the Astylosterninae is restricted to humid habitats in tropical West Africa, and the Petropedetinae is widespread in sub-Saharan Africa. Terrestrial-breeding arthroleptines and fossorial hemisines represent two adaptive types in sub-Saharan Africa. The African ranines are highly diversified in nine genera, of which only *Rana*, *Ptychadena*, and *Tomopterna* occur outside of Africa.

Climatic deterioration in the latter part of the Cenozoic made much of Africa uninhabitable for many kinds of anurans. Humid forest refugia persisted in some lowland areas in West Africa and on ancient mountain masses; many anurans survived the vicissitudes of the Pleistocene

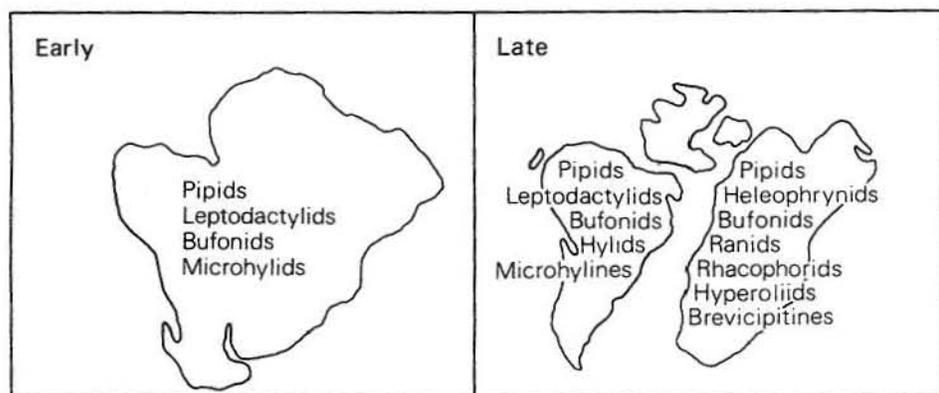


Figure 18-5. Separation of South America and Africa in the Cretaceous. Taxa of anurans listed are those presumed to have inhabited the major part of each continent.

in such refugia. These include bufonids such as *Nectophrynoides*, hyperoliids such as *Chrysobatrachus*, and microhylids such as *Hoplophryne*.

In South America, the leiopelmatids became extinct. Several genera of pipids were extant in South America in the Cretaceous and Paleocene, including *Xenopus* (Estes, 1975). *Xenopus* survives only in Africa, and the only living pipids in South America are members of the genus *Pipa*. The major radiations among South American anurans took place in the leptodactylids and hylids.

Primitive leptodactylids, the telmatobiines, diversified in the southern, humid temperate region, where many primitive telmatobiine genera (e.g., *Caudiverbera* and *Eupsophus*) survive, as does an apparent early derivative, the Rhinodermatidae. Other lineages of leptodactylids differentiated and dispersed throughout South America. These are recognized now as ceratophryines and leptodactylines; the latter are especially diverse in the tropical lowlands east of the Andes. The hylodines are associated with the Brazilian Shield. The largest group of leptodactylids is the Telmatobiinae, which occurs throughout the tropical and subtropical parts of the continent, as well as in the humid temperate region. This subfamily contains diverse genera, such as the stream-dwelling *Telmatobius* in the Andes and the extremely speciose genus *Eleutherodactylus* that occurs throughout the humid tropical part of the continent.

The Hylidae is of unknown origin. Whether the Australo-Papuan hylids are closely related or the neotropical hylids evolved independently from a leptodactylid-like ancestor in South America, the family underwent a tremendous radiation in South America. Fossil hylids are known from the Paleocene of Brazil, but probably before the Late Cretaceous three lineages had differentiated—the arboreal forest-dwelling phyllomedusines, the egg-brooding hemiphractines, and the more generalized hylines. Presumably even earlier, two other groups with intercalary elements evolved from a prohylid ancestor; of these, the pseudids evolved into a specialized lowland aquatic group, and the centrolenids into a principally montane, arboreal group. Maxson's (1976) historical interpretation of immunological data supports an Early Cretaceous divergence of the neotropical subfamilies of hylids; her limited data also indicated smaller immunological distances between neotropical hylines and Australo-Papuan hylids than between neotropical phyllomedusines and hemiphractines.

Within South America, the Bufonidae evolved into various lineages of *Bufo* and some specialized, principally montane groups, recognized as separate genera (e.g., *Atelopus* and *Oreophrynella*). One presumed derivative of a bufonid stock, the Brachycephalidae, survives as two monotypic genera in the forests of eastern Brazil. Microhylines diversified into numerous genera and species; they are distributed throughout tropical South America.

The dendrobatids are widespread in South America but are especially speciose in the northwestern part of the continent, where all four genera occur.

During the Cenozoic, the humid temperate regions and humid tropical regions contracted because of climatic zonation. The elevation of the Andes interrupted wind currents and modified patterns of rainfall. The ancient highland areas—the Brazilian and Guianan shields—harbor presumed relicts of primitive groups (e.g., *Brachycephalus* and elosiines in Brazil, and *Oreophrynella* and *Otophryne* in the Guianas). Late Tertiary and Quaternary climatic changes are thought to have resulted in the contraction of lowland rainforests during arid phases correlated with glacial stages in the Pleistocene and contraction of non-forest habitats during humid phases correlated with interglacial stages. These changing conditions, together with correlated altitudinal fluctuations in climate, are responsible for many of the distributional patterns existing in South America. Also, patterns of speciation in some groups of anurans can be associated with Pleistocene refugia (Duellman, 1982a, 1982b), but the speciation of other groups is much older (Heyer and Maxson, 1982).

Determination of the time of differentiation by immunological distances suggests that many leptodactylid genera (e.g., *Caudiverbera*, *Ceratophrys*, *Cycloramphus*, *Leptodactylus*, *Odontophrynus*, *Proceratophrys*, *Telmatobius*, and *Thoropa*) date back at least to the Eocene (Maxson and Heyer, 1982). Furthermore, speciation in many leptodactylids, especially those associated with the Brazilian Shield, took place in the Paleocene to Miocene (Heyer and Maxson, 1982); also, many of the species in the widespread lowland genus *Leptodactylus* date from the Eocene. The differentiation among some genera of hylids seems to have occurred as long ago as the Late Cretaceous or early Cenozoic. For example, *Cryptobatrachus* in the northern Andes and *Stefania* in the Guiana Shield were estimated to have diverged in the Late Cretaceous (Duellman and Hoogmoed, 1984), and some lowland species of *Gastrotheca* differentiated in the Paleocene or Eocene (Scanlan et al., 1980), as did some groups of *Bufo* (Maxson, 1984). On the other hand, speciation in some old genera is relatively recent. For example, Andean species of *Telmatobius* differentiated in the Miocene to the Pleistocene (Maxson and Heyer, 1982). Similar recent dates of speciation were determined for Andean species of *Gastrotheca* (Scanlan et al., 1980). Although representing relatively few taxa, the immunological data strongly suggest that many of the genera and some of the species of South American anurans evolved early in the Cenozoic.

Inter-American Interchange.—The complex history of the Central American isthmus and the West Indies has received considerable attention from biogeographers. J. Savage (1982) provided a detailed analysis of the Central American herpetofauna. He proposed that a brief Late Cretaceous and/or early Paleocene connection between the Central American appendage of North America and South America allowed for the dispersal of taxa from one continent to another. There is no evidence for any North American amphibians having dispersed to South America

in the Paleocene, but several groups dispersed northward (Fig. 18-6). These include caecilians, phyllomedusine hylids (ancestral stock of *Agalychnis* and *Pachymedusa*), microhylines (ancestral stock of *Gastrophryne* and *Hypopachus*), two stocks of *Bufo*, at least one stock of hylids (including *Hyla*), and at least one stock of leptodactylids (including *Eleutherodactylus*).

These Paleocene entrants into Central America were the stocks that evolved into several Mesoamerican groups of *Hyla*, *Bufo*, and *Eleutherodactylus*, plus many endemic genera (e.g., *Crepidophryne*, *Plectrohyla*, *Triprion*, and the eleutherodactyline derivatives—*Hylactophryne*, *Synrhophus*, and *Tomodactylus*). Moreover, some of these stocks presumably were associated with the formation of the Greater Antilles, where hylids are represented by three lineages of *Hyla*, plus *Osteopilus* and *Calypthahyla*.

Some West Indian *Eleutherodactylus* (including the Cuban *Sminthillus*) seem to have been derived from Central American groups, whereas others apparently represent the evolutionary results of the dispersal of *Eleutherodactylus* from South America via the Lesser Antilles to the Greater Antilles. The Bufonidae is represented in the Greater Antilles by the endemic *Peltophryne* (8 species), which may have been derived from a Central American bufonid stock.

The Paleocene separation of North American and South American stocks of some hylids is supported by immunological data, which used as an evolutionary clock, indicate times of divergence of *Agalychnis* from *Phyllomedusa* to have been no later than the Late Cretaceous (Maxson, 1976) and groups of North and South American *Hyla* to have been in the Paleocene (Maxson and A. Wilson, 1975). Moreover, distances between the West Indian hylid *Osteopilus septentrionalis* and various North American hylids indicate a divergence in the Paleocene (Maxson and A. Wilson, 1975).

With the closure of the Panamanian Portal in the Pliocene, a great interchange of South American and Central American taxa took place. Principal groups of anurans that dispersed northward include some *Eleutherodactylus*, *Leptodactylus*, *Physalaemus*, *Atelopus*, some *Bufo*, dendrobatids, centrolenids, some *Hyla*, *Phrynohyas*, and *Phyllomedusa*. Some South American taxa have dispersed no farther than Panama; this may be the result of either temporal or ecological limitations. Included in this group are *Pipa*, *Pleurodema*, *Rhombophryne*, *Gastrotheca*, *Hemiphractus*, *Chiasmocleis*, and *Relictivomer*. At the same time, some Central American groups dispersed into South America. Some genera (e.g., the hylids *Agalychnis* and *Smilisca*) dispersed only into the northwestern part of the continent. *Rana* seems to be a recent invader from North America; it is represented in South America by a species that also occurs in Central America.

Laurasian Dispersal of Gondwanan Groups. With the exception of South American taxa that occur in Cen-

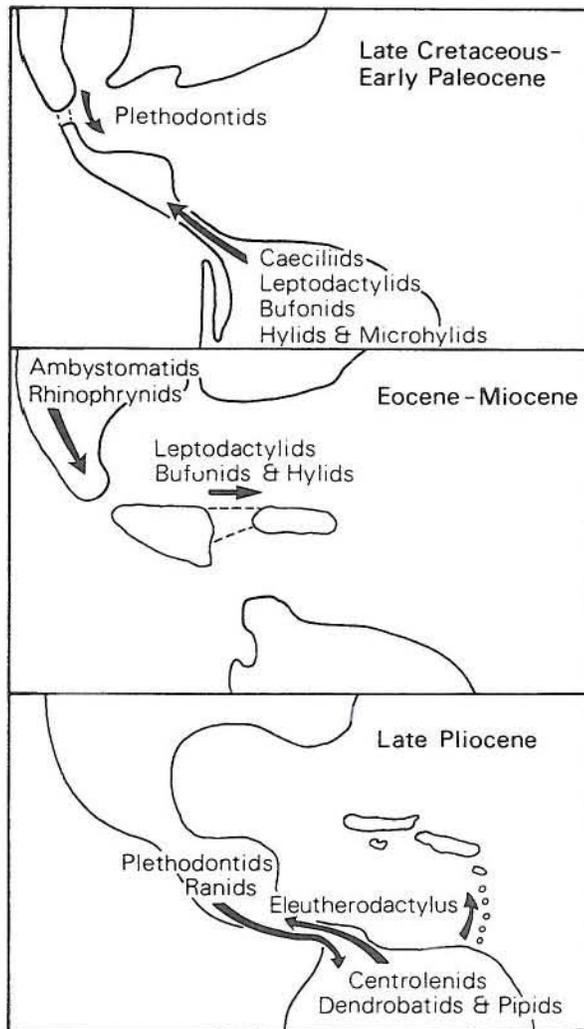


Figure 18-6. Dispersal of families of amphibians between North America, Central America, South America, and the West Indies from the Late Cretaceous through the Pliocene.

tral America, southern Mexico, and the West Indies, and the Gondwanan groups that occur in the Oriental tropics, there are only three genera of anurans that are Gondwanan in origin and widely distributed in the northern continents. Three other genera of hylids are endemic to North America.

Bufo presumably was extant before South America separated from Africa, and there is evidence that there was dispersal of South American *Bufo* back to Africa toward the end of the connection (Maxson, 1984). Subsequently, at least two stocks of *Bufo* entered North America from South America in the Paleocene. These dispersed into Eurasia via Beringia. The first of these was a tropical group that probably entered Eurasia in the Eocene and had a secondary radiation in southern Asia. The second was a temperate-adapted group that crossed Beringia in the Oligocene and became holarctic in distribution.

Tree frogs of the genus *Hyla* also dispersed from South America to North America in the Paleocene; they appear in the North American fossil record in the Oligocene. In North America, the hylid stock differentiated into a number of species, some of which are recognized as different genera—*Acris*, *Limnaeodius*, and *Pseudacris*. A temperate-adapted *Hyla* crossed Beringia probably in the Oligocene; the earliest Eurasian fossil *Hyla* are from the Miocene of Europe. From this species, the *Hyla arborea* group of species evolved in temperate habitats in Asia and Europe. Dating of times of divergence from immunological data shows the differentiation of hylids in North America to be a Cenozoic phenomenon and the divergence of the Eurasian *Hyla arborea* from North American hylids to be no less than 28 my in the Oligocene (Maxson and A. Wilson, 1975).

J. Savage (1973) suggested that *Rana* invaded Europe from Africa in the early Tertiary. However, after the formation of the Tethys Sea in the Jurassic, Africa was not connected with Eurasia until the end of the Miocene. *Rana* is known in the fossil record from the Oligocene through the Pleistocene of Europe. Therefore, it seems more likely that the ranine stock that reached Asia via drifting India was the source for the non-African members of the genus *Rana*. Beginning in the Oligocene, *Rana* dispersed and differentiated. Probably at least two stocks of *Rana* dispersed from Asia to North America via Ber-

ingia. At least one invasion occurred prior to the late Miocene, when *Rana* first appears in the fossil record of North America. Southward dispersal of *Rana* is limited. Only one species reaches South America, and only one reaches Australia. During the late Miocene and early Pliocene when a land connection existed between northwestern Africa and the Iberian Peninsula of Europe, *Rana* was able to disperse southward into mesic habitats in North Africa.

Timing of divergence of some lineages of holarctic *Rana* has been determined from immunological data. Uzzell (1982) noted that several European species of *Rana* differentiated in the Oligocene and Miocene (15–35 my). Divergence of the North American *R. catesbeiana* group from the Eurasian *R. temporaria* complex was in the Oligocene, and times of separation of the western North American *R. boylei* complex from the Eurasian *R. temporaria* complex vary from 33 to 17 million years (Oligocene and Miocene) (Post and Uzzell, 1981). Immunological distances between the European *R. perezi* and the North African *R. saharica* indicate a divergence time of about 7 million years, which is in accord with the time of the land connection between those continents (Uzzell, 1982). These data are not overly informative, but they do not refute the hypothesis of an Asian origin of holarctic *Rana*.