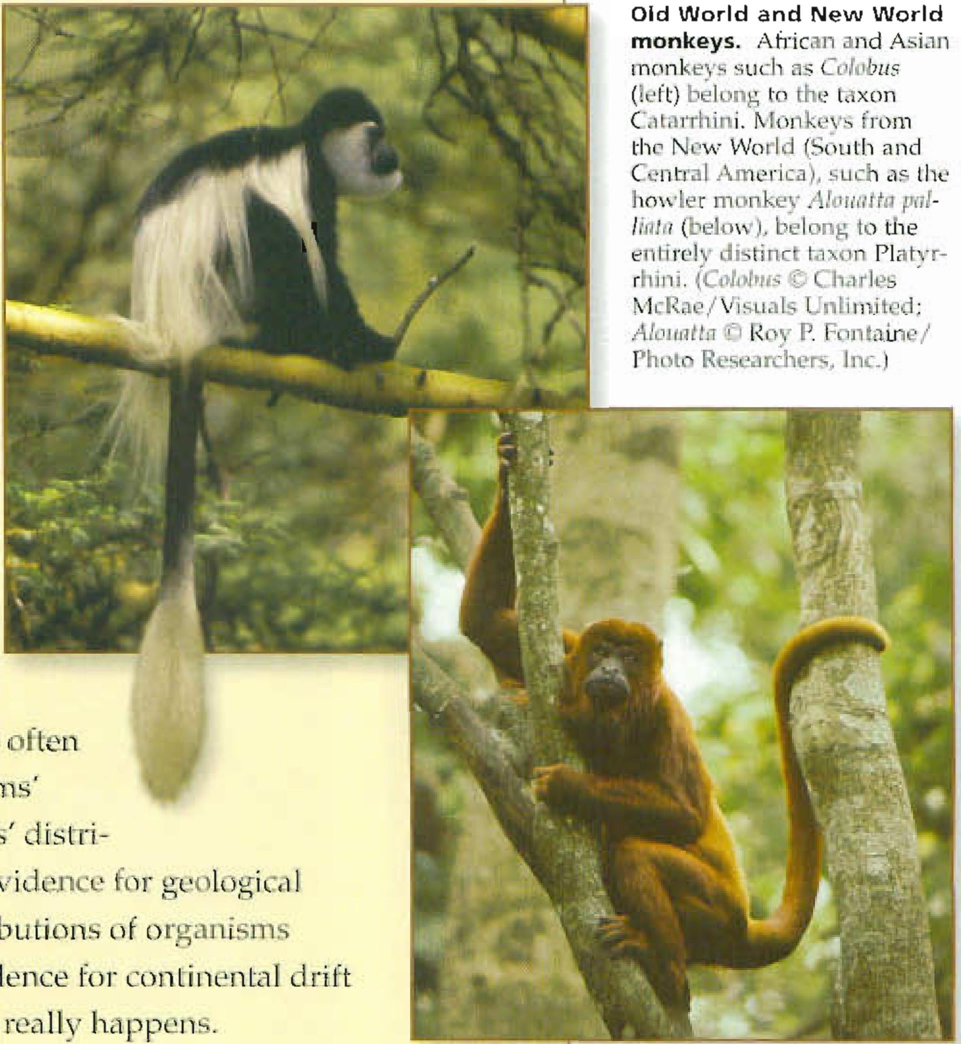
6

The Geography of Evolution

Where did humans originate, and by what paths did they spread throughout the world? Why are kangaroos found only in Australia, whereas rats are found worldwide? Why are there so many more species of trees, insects, and birds in tropical than in temperate zone forests?

These questions illustrate the problems that **biogeography**, the study of the geographic distributions of organisms, attempts to solve. ZOOGEOGRAPHY and PHYTOGEOGRAPHY are subdivisions of biogeography, concerning the distributions of animals and plants, respectively. The evolutionary study of organisms' distributions is intimately related to geology, paleontology, systematics, and ecology. For example, geological study of the history of the distributions of land masses and climates often sheds light on the causes of organisms' distributions. Conversely, organisms' distributions have sometimes provided evidence for geological events. In fact, the geographic distributions of organisms were used by some scientists as evidence for continental drift long before geologists agreed that it really happens.



Old World and New World monkeys. African and Asian monkeys such as *Colobus* (left) belong to the taxon Catarrhini. Monkeys from the New World (South and Central America), such as the howler monkey *Alouatta palliata* (below), belong to the entirely distinct taxon Platyrrhini. (*Colobus* © Charles McRae/Visuals Unlimited; *Alouatta* © Roy P. Fontaine/Photo Researchers, Inc.)

In some instances, the geographic distribution of a taxon may best be explained by historical circumstances; in other instances, ecological factors operating at the present time may provide the best explanation. Hence the field of biogeography may be roughly subdivided into **historical biogeography** and **ecological biogeography**. Historical and ecological explanations of geographic distributions are complementary, and both are important (Brown and Lomolino 1998; Myers and Giller 1988; Ricklefs and Schluter 1993).

Biogeographic Evidence for Evolution

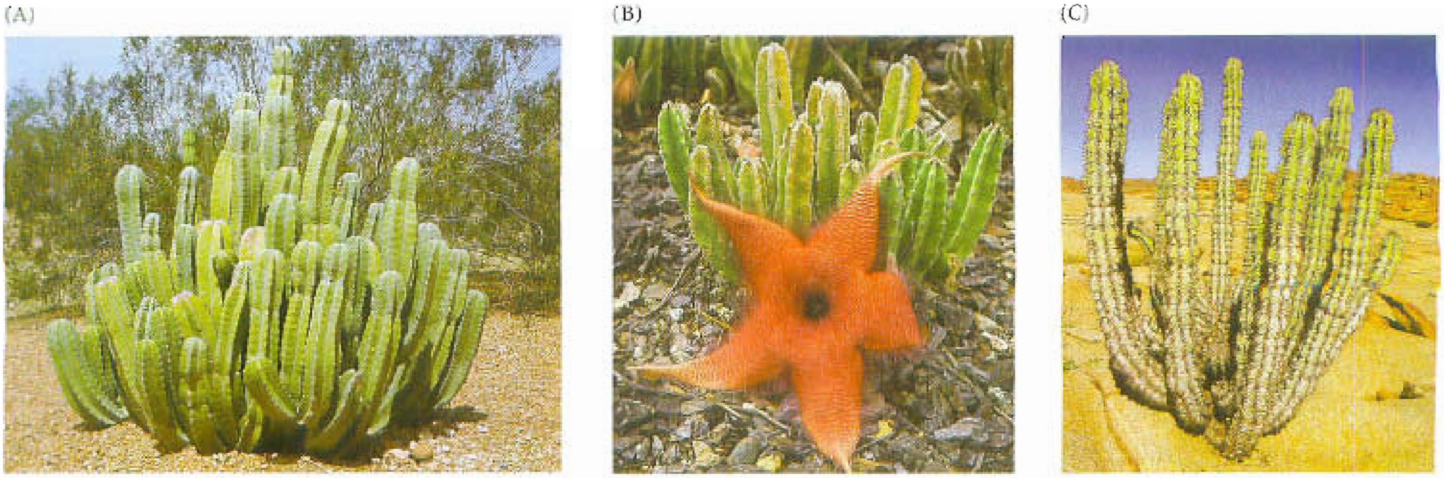
Darwin and Wallace were both very interested in biogeography. Wallace devoted much of his later career to the subject and described major patterns of zoogeography that are still valid today. The distributions of organisms provided Darwin with inspiration and with evidence that evolution had occurred. To us, today, the reasons for certain facts of biogeography seem so obvious that they hardly bear mentioning. If someone asks us why there are no elephants in the Hawaiian Islands, we will naturally answer that elephants couldn't get there. This answer assumes that elephants originated somewhere else: namely, on a continent. But in a pre-evolutionary world view, the view of special divine creation that Darwin and Wallace were combating, such an answer would not hold: the Creator could have placed each species anywhere, or in many places at the same time. In fact, it would have been reasonable to expect the Creator to place a species wherever its habitat, such as rain forest, occurred.

Darwin devoted two chapters of *The Origin of Species* to showing that many biogeographic facts that make little sense under the hypothesis of special creation make a great deal of sense if a species (1) has a definite site or region of origin, (2) achieves a broader distribution by dispersal, and (3) becomes modified and gives rise to descendant species in the various regions to which it migrates. (In Darwin's day, there was little inkling that continents might have moved. Today, the movement of land masses also explains certain patterns of distribution.) Darwin emphasized the following points:

First, said Darwin, *"neither the similarity nor the dissimilarity of the inhabitants of various regions can be wholly accounted for by climatal and other physical conditions."* Similar climates and habitats, such as deserts and rain forests, occur in both the Old and the New World, yet the organisms inhabiting them are unrelated. For example, the cacti (family Cactaceae) are restricted to the New World, but the cactuslike plants in Old World deserts are members of other families (Figure 6.1). All the monkeys in the New World belong to one great group (Platyrrhini), and all Old World monkeys to another (Catarrhini)—even if, like the howler and colobus monkeys shown at the opening of this chapter, they have similar habitats and diets.

Darwin's second point is that *"barriers of any kind, or obstacles to free migration, are related in a close and important manner to the differences between the productions [organisms] of various*

Figure 6.1 Convergent growth form in desert plants. These plants, all leafless succulents with photosynthetic stems, belong to three distantly related families. (A) A North American cactus (family Cactaceae). This species, *Lophocereus schottii*, is native to Baja California. (B) A carrion flower of the genus *Stapelia* (Apocynaceae). These fly-pollinated succulents can be found from southern Africa to east India. (C) A species of *Euphorbia* (Euphorbiaceae) in the Namib Desert of Africa. (A–C © Photo Researchers, Inc. A by Richard Parker; B, by Geoff Bryant; C by Fletcher and Baylis.)



regions." Darwin noted, for instance, that marine species on the eastern and western coasts of South America are very different.

Darwin's "third great fact" is that *inhabitants of the same continent or the same sea are related, although the species themselves differ from place to place*. He cited as an example the aquatic rodents of South America (the coypu and capybara), which are structurally similar to, and related to, South American rodents of the mountains and grasslands, not to the aquatic rodents (beaver, muskrat) of the Northern Hemisphere.

"We see in these facts," said Darwin, "some deep organic bond, throughout space and time, over the same areas of land and water, independently of physical conditions. ... The bond is simply inheritance [i.e., common ancestry], that cause which alone, as far as we positively know, produces organisms quite like each other."

For Darwin, it was important to show that a species had not been created in different places, but had a *single region of origin*. He drew particularly compelling evidence from the inhabitants of islands. First, distant *oceanic islands generally have precisely those kinds of organisms that have a capacity for long-distance dispersal* and lack those that do not. For example, the only native mammals on many islands are bats. Second, *many continental species of plants and animals have flourished on oceanic islands to which humans have transported them*. Thus, said Darwin, "he who admits the doctrine of the creation of each separate species, will have to admit that a sufficient number of the best adapted plants and animals were not created for oceanic islands." Third, most of the species on islands are clearly *related to species on the nearest mainland*, implying that that was their source. This is the case, as Darwin said, for almost all the birds and plants of the Galápagos Islands. Fourth, the *proportion of endemic species on an island is particularly high when the opportunity for dispersal to the island is low*. Fifth, *island species often bear marks of their continental ancestry*. For example, Darwin noted, hooks on seeds are an adaptation for dispersal by mammals, yet on oceanic islands that lack mammals, many endemic plants nevertheless have hooked seeds.

It is a testimony to Darwin's knowledge and insight that all these points hold true today, after nearly a century and a half of research. Our greater knowledge of the fossil record and of geological events such as continental movement and sea level changes has added to our understanding, but has not negated any of Darwin's major points.

Major Patterns of Distribution

The geographic distribution of almost every species is limited to some extent, and many higher taxa are likewise restricted (**endemic**) to a particular geographic region. For example, the salamander genus *Plethodon* is limited to North America, and *Plethodon caddoensis* occupies only the Caddo Mountains of western Arkansas. Some higher taxa, such as the pigeon family (Columbidae), are almost cosmopolitan (found worldwide), whereas others are narrowly endemic (e.g., the kiwi family, Apterygidae, which is restricted to New Zealand; see Figure 6.13).

Wallace and other early biogeographers recognized that many higher taxa have roughly similar distributions, and that the taxonomic composition of the biota is more uniform within certain regions than between them. Based on these observations, Wallace designated several **biogeographic realms** for terrestrial and freshwater organisms that are still widely recognized today (Figure 6.2). These are the *Palearctic* (temperate and tropical Eurasia and northern Africa), the *Nearctic* (North America), the *Neotropical* (South and Central America), the *Ethiopian* (sub-Saharan Africa), the *Oriental* (India and Southeast Asia), and the *Australian* (Australia, New Guinea, New Zealand, and nearby islands). These realms are more the result of Earth's history than of current climate or land mass distribution. For example, WALLACE'S LINE separates islands that, despite their close proximity and similar climate, differ greatly in their fauna. These islands are on two lithospheric plates that approached each other only recently, and they are assigned to two different biogeographic realms: the Oriental and the Australian.

Each biogeographic realm is inhabited by many higher taxa that are much more diverse in that realm than elsewhere, or are even restricted to that realm. For example, the endemic taxa of the Neotropical realm (South America) include the Xenarthra (anteaters

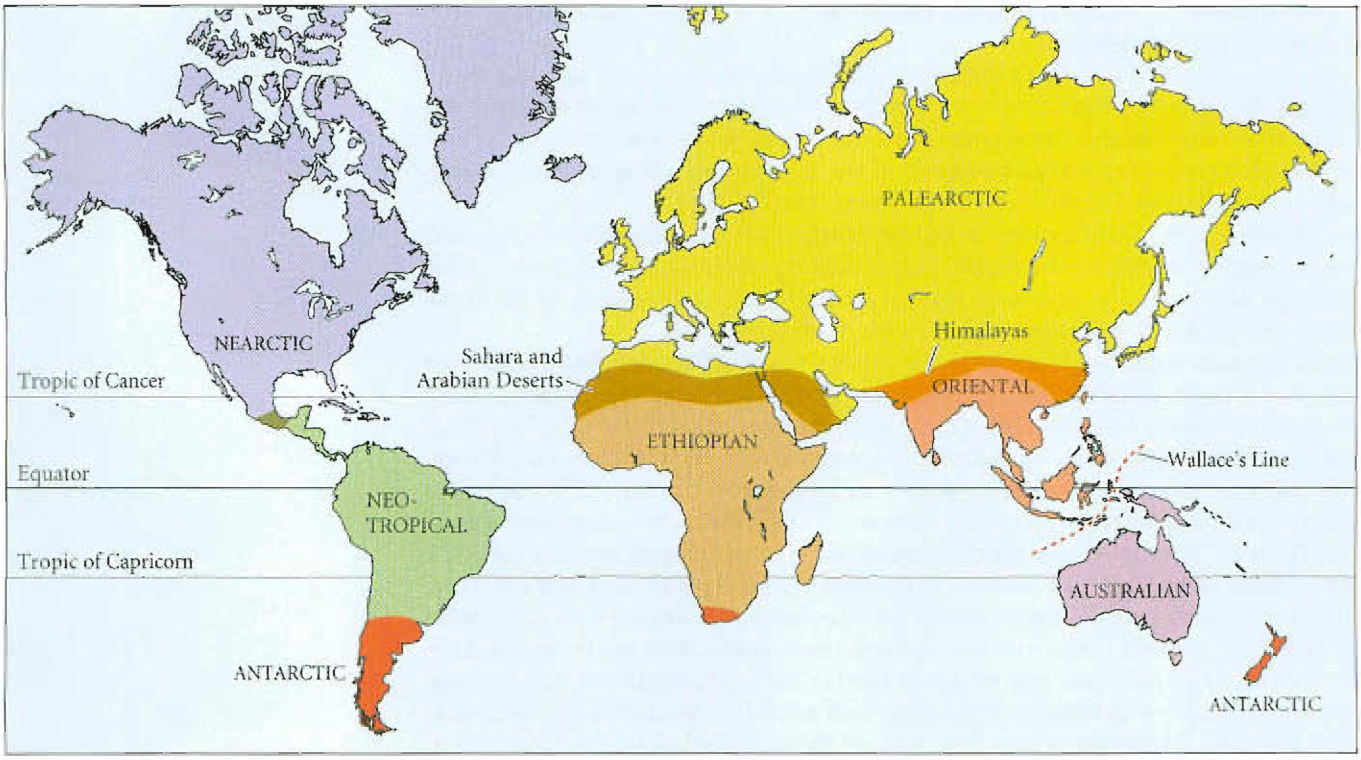


Figure 6.2 Biogeographic realms. The biogeographic realms recognized by A. R. Wallace are the Palearctic, Ethiopian, Oriental, Australian, Nearctic, and Neotropical. Some authors consider parts of southern South America, Africa, and New Zealand to be another realm, the Antarctic.

and allies), platyrrhine primates (such as spider monkeys and marmosets), hummingbirds, a large assemblage of suboscine birds such as flycatchers and antbirds, many families of catfishes, and plant families such as the pineapple family (Bromeliaceae) (Figure 6.3; see also the chapter-opening figure). Within each realm, individual species may have more restricted distributions; regions that differ markedly in habitat, or which are separated by mountain ranges or other barriers, will have rather different sets of species. Thus a biogeographic realm can often be divided into faunal and floral PROVINCES, or regions of endemism (Figure 6.4).

The borders between biogeographic realms (or provinces) cannot be sharply drawn because some taxa infiltrate neighboring realms to varying degrees. In the Nearctic realm

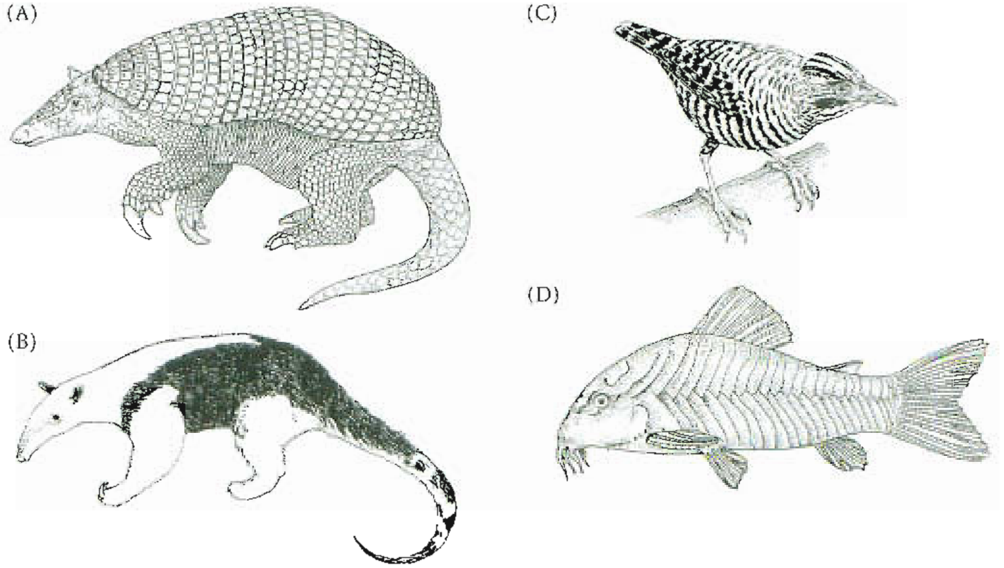
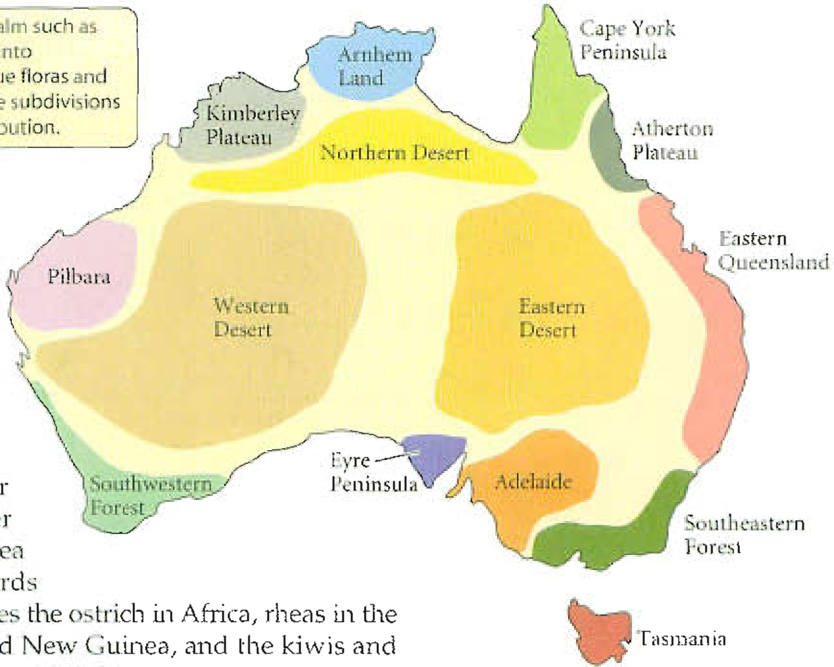


Figure 6.3 Examples of taxa endemic to the Neotropical biogeographic realm. (A) An armadillo (order Xenarthra). (B) An anteater (order Xenarthra). (C) An antshrike (Formicariidae), representing a huge evolutionary radiation of suboscine birds in the Neotropics. (D) An armored catfish (Callichthyidae), one of many families of freshwater catfishes restricted to South America. (A, B after Emmons 1990; C after Haverschmidt 1968; D after Moyle and Cech 1983.)

Figure 6.4 Provinces, or regions of endemism, in Australia, based on the pattern of distribution of birds. Distributions of other vertebrates form similar patterns. (After Cracraft 1991.)



A biogeographic realm such as Australia is divided into "provinces" of unique floras and faunas such as these subdivisions based on bird distribution.

(North America), for instance, some species, such as bison, trout, and birches, are related to Palearctic (Eurasian) taxa. But other Nearctic species are related to, and have been derived from, Neotropical stocks: examples include the armadillo, the opossum, and the Spanish moss (*Tillandsia usneoides*), a bromeliad that festoons southern trees.

Some taxa have **disjunct distributions**; that is, their distributions have gaps. Disjunctly distributed higher taxa typically have different representatives in each area they occupy. For example, the mostly flightless birds known as ratites are a monophyletic group that includes the ostrich in Africa, rheas in the Neotropics, the emu and cassowaries of Australia and New Guinea, and the kiwis and the recently extinct moas of New Zealand (see Figure 6.13). Many other taxa are also shared between two or more southern continents, such as lungfishes, marsupials, cichlid fishes (see Figure 6.12), and southern beeches (*Nothofagus*) (Goldblatt 1993). Another common disjunct pattern is illustrated by alligators (*Alligator*), skunk cabbages (*Symplocarpus*), and tulip trees (*Liriodendron*), which are among the many genera that are found both in eastern North America and in temperate eastern Asia, but not in between (Wen 1999). We will investigate the reasons for some of these patterns later in this chapter.

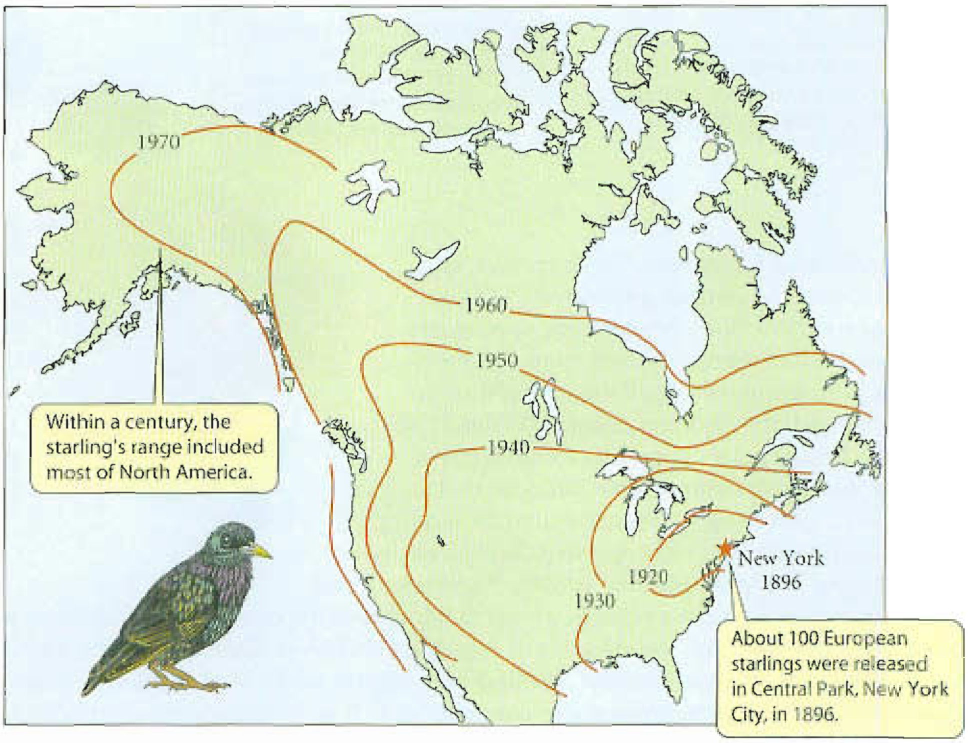
Historical Factors Affecting Geographic Distributions

The geographic distribution of a taxon is affected by both contemporary and historical factors. The limits to the distribution of a species may be set by geological barriers that have not been crossed, or by ecological conditions to which the species is not adapted. In this section, we will focus on the historical processes that have led to the current distribution of a taxon: extinction, dispersal, and vicariance.

The distribution of a species may have been reduced by the extinction of some populations, and that of a higher taxon by the extinction of some constituent species. For example, the horse family, Equidae, originated and became diverse in North America, but it later became extinct there; only the African zebras and the Asian wild asses and horses have survived. (Horses were reintroduced into North America by European colonists.) Likewise, extinction is the cause of the disjunction between related taxa in eastern Asia and eastern North America. During the early Tertiary, many plants and animals spread throughout the northern regions of North America and Eurasia. Their spread was facilitated by a warm, moist climate and by land connections from North America to both Europe and Siberia. Many of these taxa became extinct in western North America in the late Tertiary due to mountain uplift and a cooler, drier climate, and were extinguished in Europe by Pleistocene glaciations (Wen 1999; Sanmartín et al. 2001).

Species expand their ranges by **dispersal** (i.e., movement of individuals). Some authors distinguish two kinds of dispersal: RANGE EXPANSION, or movement across expanses of more or less continuous favorable habitat, and JUMP DISPERSAL, or movement across a barrier (Myers and Giller 1988). Some species of plants and animals can expand their range very rapidly. Within the last 200 years, many species of plants accidentally brought from Europe by humans have expanded across most of North America from New York and New England, and some birds, such as the starling (*Sturnus vulgaris*) and the house sparrow (*Passer domesticus*), have done the same within a century (Figure 6.5). Other species

Figure 6.5 The history of range expansion of the European starling (*Sturnus vulgaris*) following its introduction into New York City in 1896. (After Brown and Gibson 1983.)



Within a century, the starling's range included most of North America.

About 100 European starlings were released in Central Park, New York City, in 1896.

have crossed major barriers on their own. The cattle egret (*Bubulcus ibis*) was found only in tropical and subtropical parts of the Old World until about 75 years ago, when it arrived in South America, apparently unassisted by humans (Figure 6.6). It has since spread throughout the warmer parts of the New World.

If a major barrier to dispersal breaks down, many species may expand their ranges more or less together, resulting in correlated patterns of dispersal (Lieberman 2003). For example, many plants and animals moved between South and North America when the Isthmus of Panama was formed in the Pliocene (see Chapter 5), and between Europe and North America over a trans-Atlantic land bridge in the early Tertiary (Sanmartín et al. 2001).

Vicariance refers to the separation of populations of a widespread species by barriers arising from changes in geology, climate, or habitat. The separated populations diverge, and they often become different subspecies, species, or higher taxa. For example, in many fish, shrimp, and other marine animal groups, the closest relative of a species on the Pacific side of the Isthmus of Panama is a species on the Caribbean side of the isthmus. This pattern is attributed to the divergence of populations of a broadly distributed ancestral species that was sundered by the rise of the isthmus in the Pliocene (Lessios 1998). Vicariance sometimes accounts for the presence of related taxa in disjunct areas.

Dispersal and vicariance are both important processes, and neither can be assumed, a priori, to be the sole explanation of a taxon's distribution. In many cases, dispersal, vicariance, and extinction all have played a role. We have seen, for example, that during the Pleistocene glaciations, species shifted their ranges by dispersal into new regions

Figure 6.6 A cattle egret (*Bubulcus ibis*) accompanying a cow in Alabama. This heron feeds on insects stirred up by grazing ungulates in both the Old World and the New World. (Photo © A. Morris/Visuals Unlimited.)

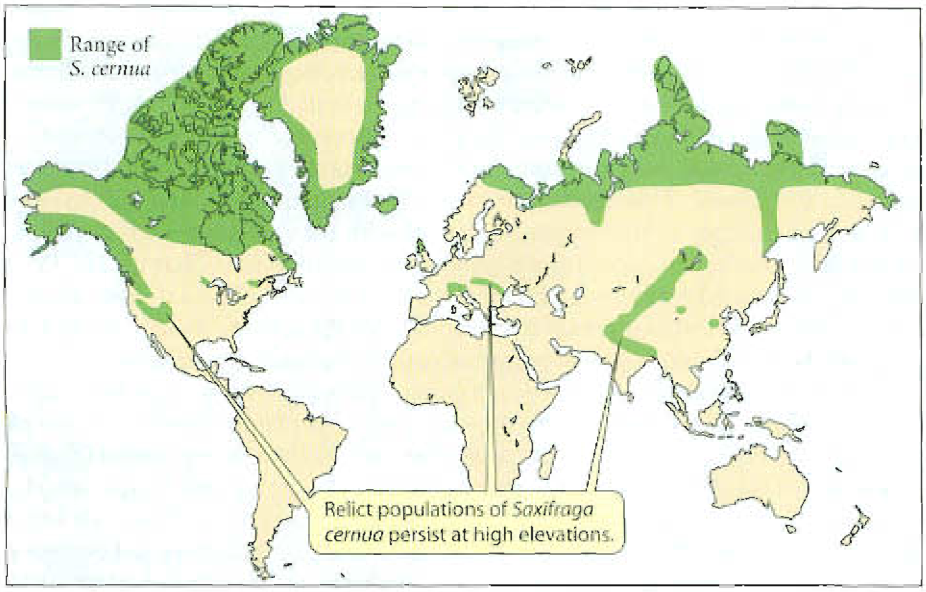


Figure 6.7 The disjunct distribution of a saxifrage (*Saxifraga cernua*) in northern and mountainous regions of the Northern Hemisphere. Relict populations persist at high elevations, following the species' retreat from the southern region that it occupied during glacial periods. (After Brown and Gibson 1983; photo courtesy of Egil Michaelsen and the Norwegian Botanical Association.)

(see Figure 5.29). Some northern, cold-adapted species became distributed far to the south. When the climate became warmer, southern populations became extinct, except for populations of some such species that survived on cold mountain tops (Figure 6.7). In this case, the vicariant disjunction of populations, due to the formation of inhospitable intervening habitat, went hand in hand with extinction.

Testing Hypotheses in Historical Biogeography

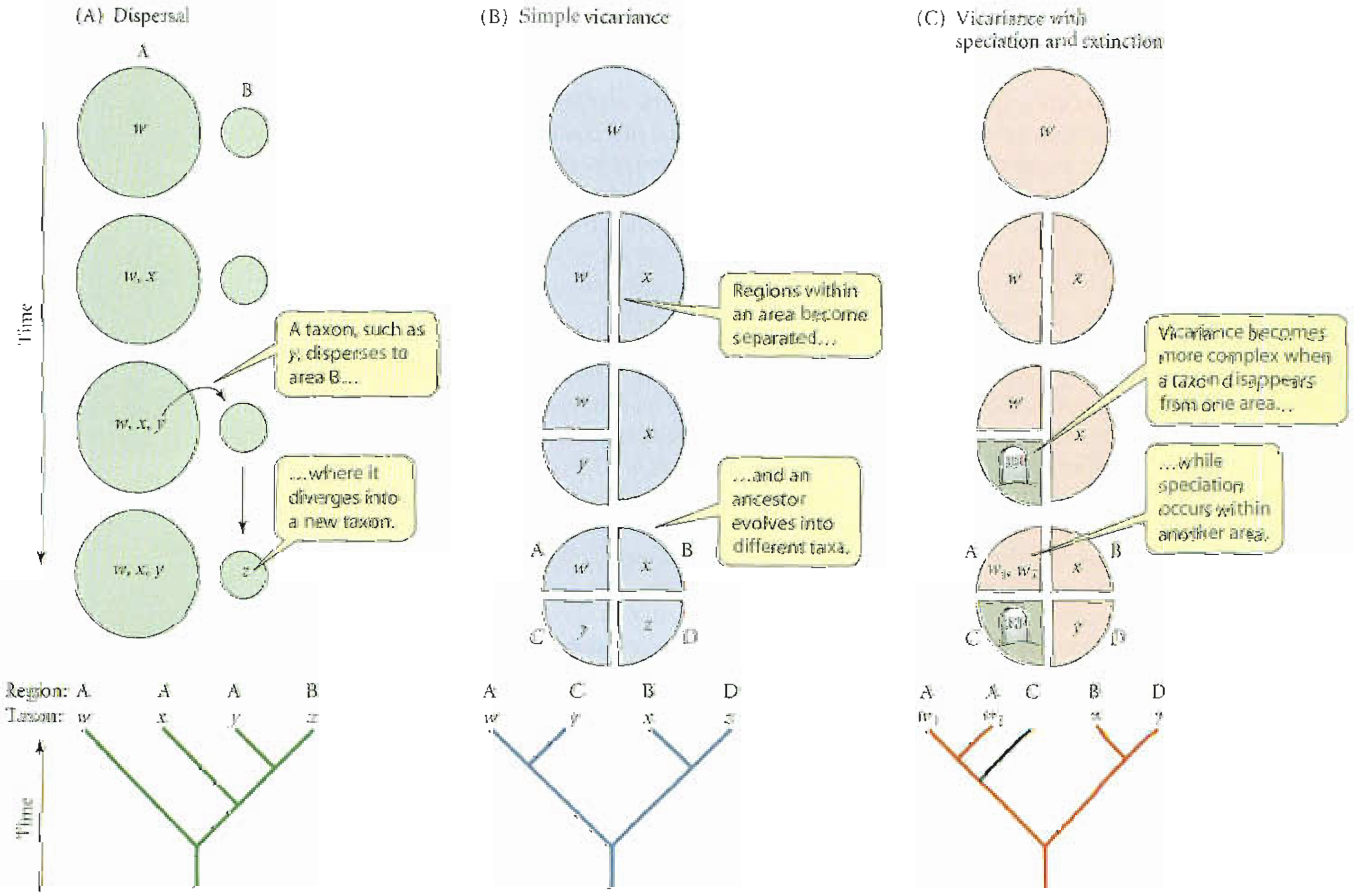
Biogeographers have used a variety of guidelines for inferring the histories of distributions. Some of these guidelines are well founded. For example, the distribution of a taxon cannot be explained by an event that occurred before the taxon originated: a genus that originated in the Miocene cannot have achieved its distribution by continental movements that occurred in the Cretaceous. Some other guidelines are more debatable. Some authors in the past assumed that a taxon originated in the region where it is presently most diverse. But this need not be so, as the horse family shows: although now native only to Africa and Asia, horses are descended from North American ancestors.

The major hypotheses accounting for a taxon's distribution are dispersal and vicariance. For example, one might ask whether the ratite birds dispersed from one continent to another, or whether they descended from ancestors on a single land mass that split into the several southern continents. Phylogenetic analysis plays a leading role in evaluating these hypotheses, but other sources of evidence can be useful as well. For example, an area is often suspected of having been colonized by dispersal if it has a highly "unbalanced" biota—that is, if it lacks a great many taxa that it would be expected to have if it had been joined to other areas. This assumption has been applied especially to oceanic islands that lack forms such as amphibians and nonflying mammals. The fossil record can also provide important evidence (Lieberman 2003)—for instance, it may show that a taxon proliferated in one area before appearing in another—and geological data may describe the appearance or disappearance of barriers. For example, fossil armadillos (see Figure 6.3A) are limited to South America throughout the Tertiary and are found in North American deposits only from the Pliocene and Pleistocene, after the Isthmus of Panama was formed. This pattern implies that they dispersed into North America from South America. Paleontological data must be interpreted cautiously, however, because a taxon may be much older, and have inhabited a region longer, than a sparse fossil record shows.

Phylogenetic methods are the foundation of most modern studies of historical biogeography. Several such methods have been developed, especially by Daniel Brooks (1990), Roderick Page (1994), and Fredrik Ronquist (1997), to analyze geographic patterns. There are important differences among these methods, but they all use a parsimony approach to reconstruct the geographic distributions of ancestors from data on the distributions of living taxa. (Inferring ancestral distributions from a phylogeny resembles, to some extent, inferring ancestral character states; see Figure 3.3.) Ronquist's method, DISPERSAL-VICARIANCE ANALYSIS (DIVA), most fully accounts for the importance of dispersal and is therefore most biologically realistic. This method assumes that vicariance is the "null hypothesis" accounting for changes in distribution, in accord with the well-supported principle that new species are generally formed during geographic isolation (see Chapter 16). Whenever either dispersal or extinction must be invoked in order to explain a distribution, a "cost" is exacted. The historical hypothesis that accounts for the species' distributions with the lowest "cost" is considered the most parsimonious, or optimal, hypothesis.

Under the vicariance hypothesis, we expect monophyletic groups to occupy different areas, and we expect the sequence of geographic disjunctions implied by the phylogeny to match the sequence in which the areas themselves became separated (Figure 6.8). For example, in a clade distributed throughout Africa, Australia, and South America, species in Australia and South America should be more closely related to each other than to African species, because Africa was the first of these land masses to become separated from the rest of Gondwanaland. In contrast, if species in area B are nested within a clade that otherwise is distributed in area A, dispersal from A to B may be likely (Figure 6.8A). Some biogeographers hold that vicariance should separate populations of many taxa simultaneously, so that the taxa should manifest common phylogenetic patterns of distribution. Dispersal can also engender common patterns among different taxa, especially when barriers to dispersal break down (Lieberman 2003).

Figure 6.8 Phylogenetic relationships as indicators of biogeographic history. (A) Dispersal from area A to area B, followed by divergence, is likely to yield a paraphyletic pattern of distribution of related species. (B) A vicariant history of successive separation of faunas is likely to yield a phylogeny of taxa that parallels the separation of the areas. (C) Complications in an otherwise vicariant history can arise for several reasons, including extinction (here, in area C) and speciation within an area (in area A).



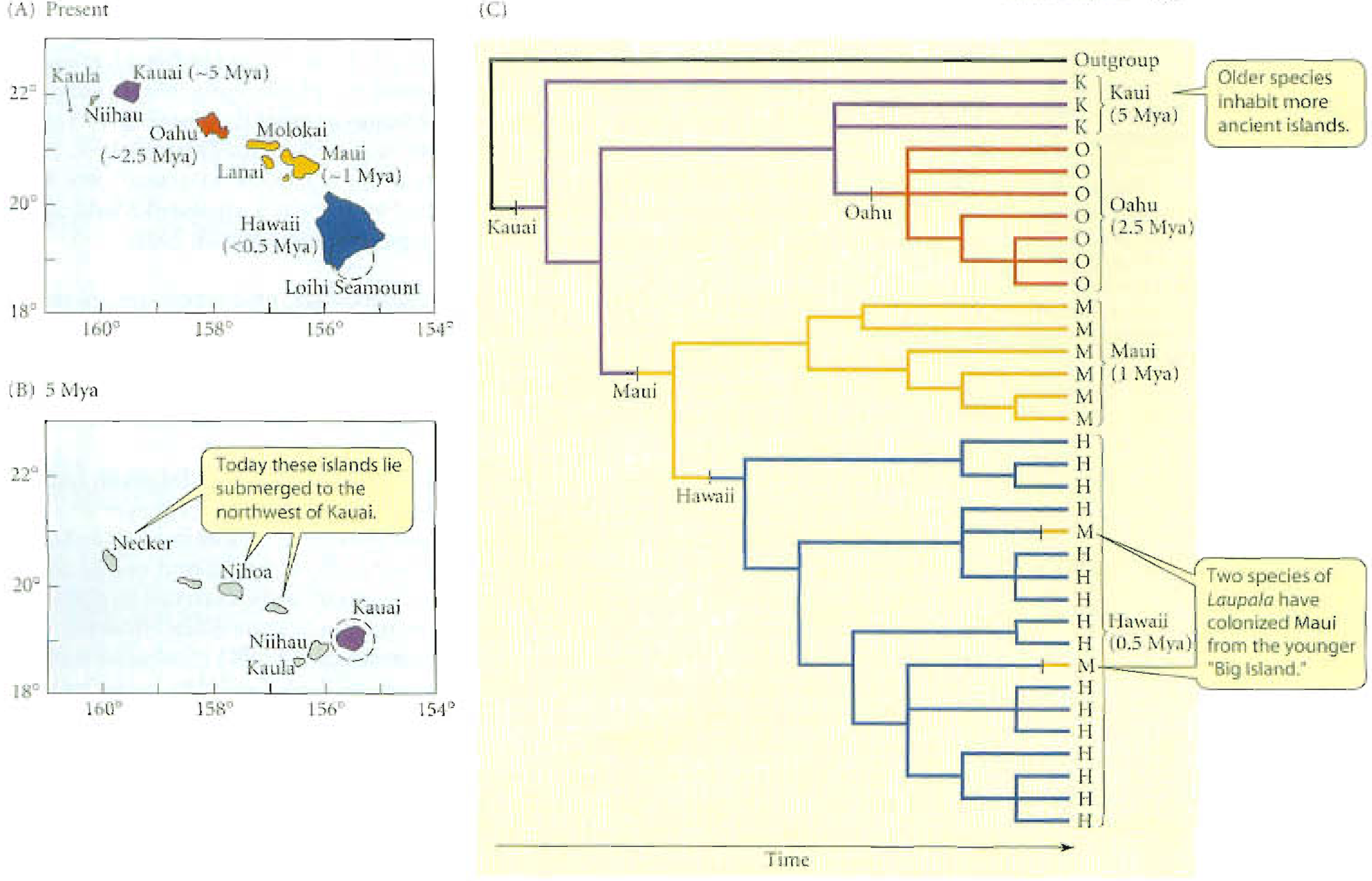
Examples of historical biogeographic analyses

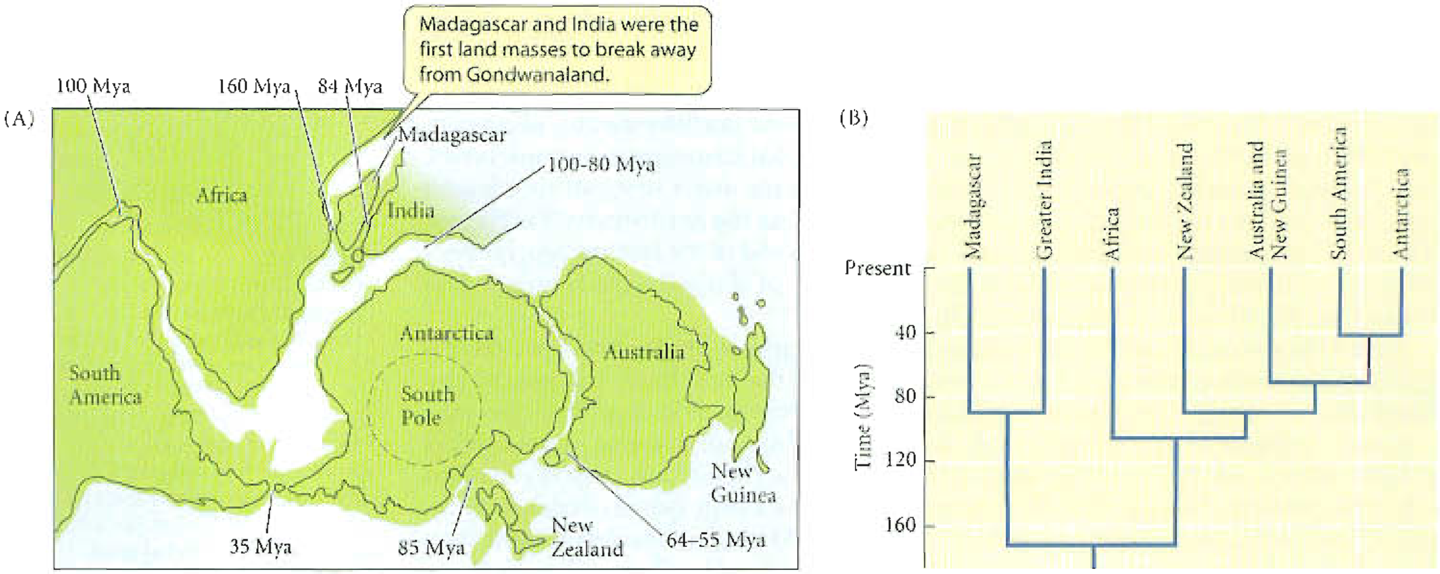
ORGANISMS IN THE HAWAIIAN ISLANDS. The Hawaiian Islands, in the middle of the Pacific Ocean, have been formed as a lithospheric plate has moved northwestward, like a conveyor belt, over a "hot spot," which has caused the sequential formation of volcanic cones. This process has been going on for tens of millions of years, and a string of submerged volcanoes that once projected above the ocean surface lies to the northwest of the present islands. Of the current islands, Kauai, at the northwestern end of the archipelago, is about 5.1 Myr old; the southeasternmost island, the "Big Island" of Hawaii, is the youngest, and is less than 500,000 years old (Figure 6.9A,B).

Given the geological history of the archipelago, the simplest phylogeny expected of a group of Hawaiian species would be a "comb," in which the most basal lineages occupy Kauai and the youngest lineages occupy Hawaii. This pattern would occur if species successively dispersed to new islands as they were formed, did not disperse from younger to older islands, and did not suffer extinction. Kerry Shaw (1995) found just this pattern when she performed a molecular phylogenetic analysis of a large genus of crickets (*Laupala*) (Figure 6.9C). Except for two species that colonized Maui from Hawaii, colonization has proceeded from older to younger islands, and each island has been colonized only once. Within each island, the rate of speciation has been quite high.

ANIMALS IN MADAGASCAR. East of Africa lies the large island of Madagascar, whose highly endemic (and endangered) biota includes many groups, such as lemurs (see Figure 6.10B), that occur nowhere else. Together with India, Madagascar was the first land mass to split from Gondwanaland, having broken away from eastern Africa about 160–120 Mya (Fig-

Figure 6.9 The Hawaiian Islands and the phylogeny of some Hawaiian crickets. (A) The Hawaiian archipelago at present. The Big Island, Hawaii, lies just to the northwest of the "hot spot," shown by the broken circle, where islands have been successively formed. (B) The archipelago 5 million years ago, when Kauai was emerging over the hot spot. (C) A phylogeny of cricket species (*Laupala*) in the Hawaiian Islands, in which each species' name is replaced by an abbreviation of the name of the island on which it occurs. Successively younger groups are found on younger islands, although two species have colonized Maui from the younger island of Hawaii. (A, B after H. L. Carson and D. A. Clague 1995; C after Shaw 1995.)





Madagascar and India were the first land masses to break away from Gondwanaland.

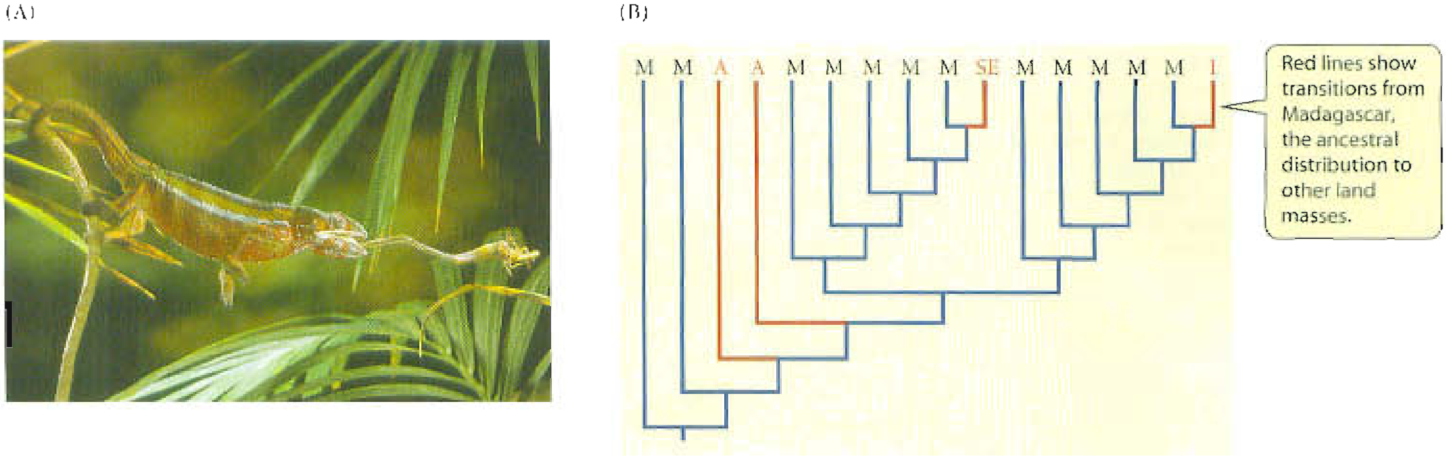
Figure 6.10 (A) A view of Gondwanaland in the early Cretaceous (120 Mya), centered on the present South Pole, indicating the approximate times at which connections among the southern land masses were severed. The current configurations of the continents are shown by the black lines; green areas beyond these lines were also exposed land during the early Cretaceous. (B) A branching diagram, sometimes called an "area cladogram," that attempts to depict the history of the breakup of Gondwanaland. "Greater India" was a large land mass that includes the present subcontinent of India and Sri Lanka. This branching tree does not show how different contiguous areas of some land masses (e.g., South America) separated at different times, as the map does. (A after Cracraft 2001.)

ure 6.10). India became separated from Madagascar 88–63 Mya, and collided with southern Asia about 50 Mya. For many years, biogeographers postulated that many of the endemic Madagascan taxa originated by vicariant separation from their relatives on other southern land masses. However, recent molecular phylogenetic studies indicate that dispersal has played the major role.

Raxworthy et al. (2002) analyzed the phylogeny of chameleons—slow-moving lizards that catch insects with their extraordinary projectile tongues (Figure 6.11A). Chameleons are distributed mostly in Africa, Madagascar, India, and islands in the Indian Ocean. Whereas the vicariance hypothesis would imply that Madagascan and Indian chameleons together should form the sister group of African forms, the phylogeny strongly supports the hypothesis that chameleons originated in Madagascar after the breakup of Gondwanaland and dispersed over water to Africa, India, and the islands (Figure 6.11B). Similar analyses of the lemurs (Primates) and the Madagascan mongoose-like carnivores indicated dispersal in the other direction: the ancestors of both groups colonized Madagascar from Africa, long after these land masses became separated (Yoder et al. 2003).

GONDWANAN DISTRIBUTIONS. Many other intriguing biogeographic problems are posed by taxa that have members on different land masses in the Southern Hemisphere. The simplest hypothesis is, of course, pure vicariance: the breakup of Gondwanaland isolated descendants of a common ancestor. However, phylogenetic analyses show that the story is not that simple, and the histories of some groups are still very controversial. Three examples will make the point.

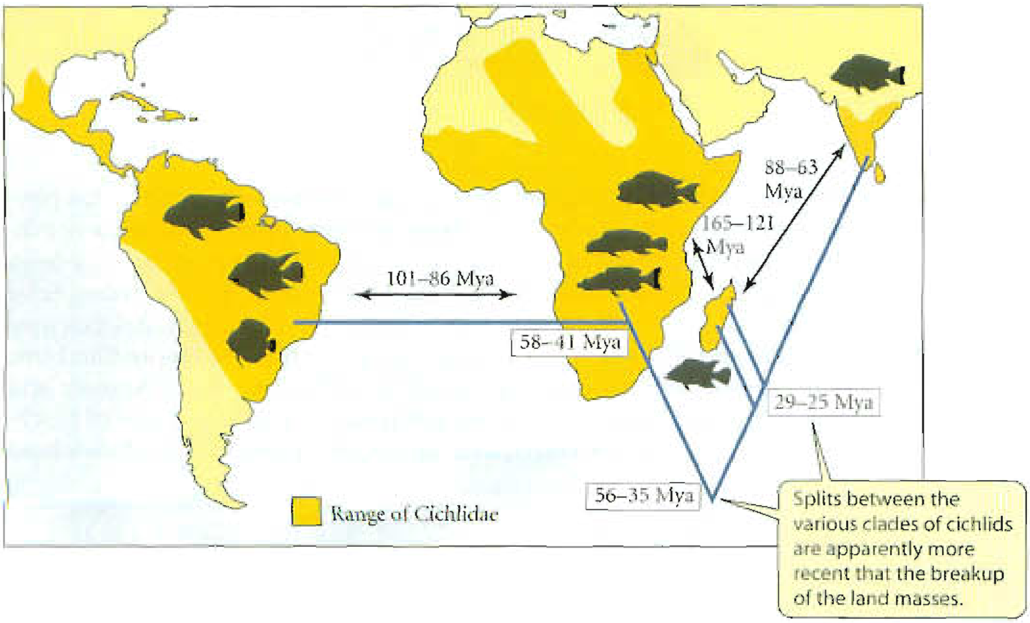
Cichlids are freshwater fishes found in tropical America, Africa, Madagascar, and India. In molecular phylogenetic analyses by several investigators (e.g., Vences et al. 2001; Sparks 2004), two sister clades have been found, one consisting of Indian and Madagascan species and the other of two monophyletic groups, one in Africa and one in South America. This is exactly the branching pattern predicted by the vicariance hypothesis, since it exactly parallels the separation of these four regions (Figure 6.12). However, in a careful study of rates of DNA sequence evolution, Vences et al. (2001) concluded that the splits between clades of cichlids are much more recent than the splits between land masses; for example, the divergence between the Indian/Madagascan and African/Neotropical clades is no more than 56 million years old, whereas Madagascar and India separated from Africa at least 120 million years ago. Moreover, cichlids are a highly derived group within a huge clade of spiny-finned fishes that are not known before the late Cretaceous, long after the Gondwanan breakup. It seems likely that the cichlids achieved their distribution by dispersal, rather than by being rafted on fragments of Gondwanaland.



Red lines show transitions from Madagascar, the ancestral distribution to other land masses.

Figure 6.11 (A) A Madagascan panther chameleon, *Chamaeleo pardalis*, catches insects with its projectile tongue. (B) A phylogeny of some species of chameleons, showing their distribution in Africa (A), India (I), Madagascar (M), and the Seychelles Islands (SE) in the Indian Ocean. Because the phylogenetic distribution over these areas differs from the sequence by which the areas became separated (see Figure 6.10B), the distribution of chameleons is best explained by dispersal from Madagascar, rather than vicariance caused by the breakup of Gondwanaland. (A © Stephen Dalton/Photo Researchers, Inc.; B after Raxworthy et al. 2002.)

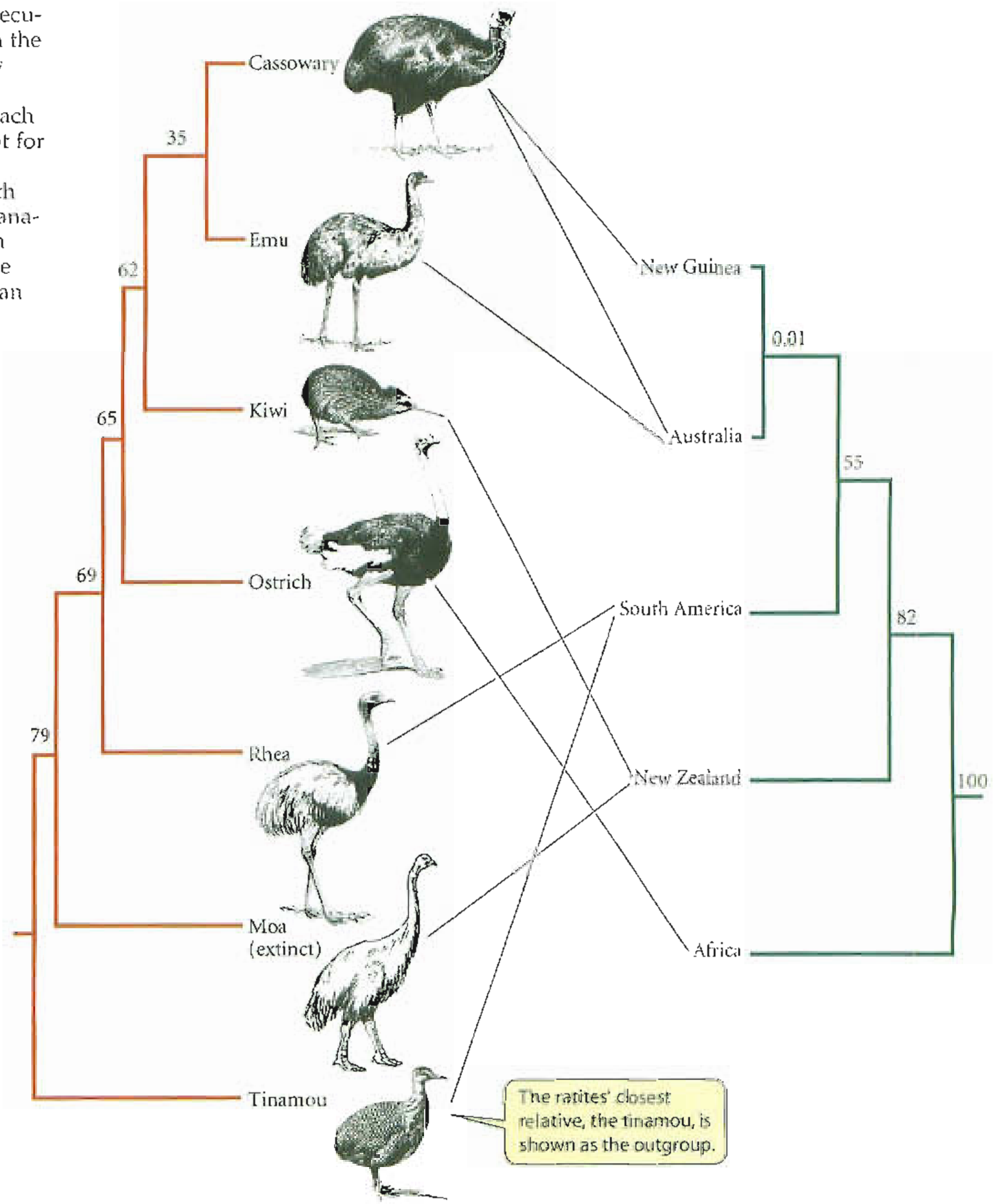
The ratite birds provide some support for Gondwanan vicariance—but only to a point (Haddrath and Baker 2001). These flightless birds, most of which are very large, stem from an ancient ancestor: along with tinamous, they are the sister group of all other living birds. They include not only the extant ostrich, rheas, cassowaries, emu, and kiwis, but also the moas of New Zealand, which were extinguished by indigenous people but have left bones from which DNA can be extracted. Because of their "Gondwanan distribution" and the great age of the clade, the ratites are a prime suspect for vicariance due to the breakup of Gondwanaland. Indeed, a phylogenetic study using complete sequences of the mitochondrial genome provided evidence that the moas diverged first, at about 79 Mya, which is consistent with the early (82 Mya) separation of New Zealand from Gondwanaland (Figure 6.13). The later divergence between the South American and Australian ratites, at about 69 Mya, is consistent with the later separation (at 55–65 Mya) of Australia from South America and Antarctica. But the divergence of the African ostrich (65 Mya) and the New Zealand kiwis (62 Mya) is much later than the separation of their homelands from the rest of Gondwanaland (Africa at 100 Mya and New Zealand at 82 Mya), and they appear to have employed some mode of dispersal.



Splits between the various clades of cichlids are apparently more recent that the breakup of the land masses.

Figure 6.12 A phylogeny (blue tree) of the family Cichlidae, mapped onto its geographic distribution. The boxes indicate the divergence times between clades, estimated from DNA sequence differences; these clade divergence dates are younger than the dates of separation of the land masses (double-headed arrows). (After Vences et al. 2001.)

Figure 6.13 A comparison of a molecular phylogeny of the ratites (left) with the history of separation of the areas they occupy (right). Lines connect birds to their homelands; estimated dates at each branch are in millions of years. Except for the kiwi and ostrich, the branching sequence and dates are consistent with separation by the breakup of Gondwanaland. The kiwi and tinamou are much smaller than the other species, and are not drawn to the same scale. (After Van Tyne and Berger 1959; Haddath and Baker 2001.)



The ratites' closest relative, the tinamou, is shown as the outgroup.

Joel Cracraft (2001) has demonstrated that some of the most basal branches in the phylogeny of birds are consistent with Gondwanan origin and vicariance. DNA sequence divergence strongly suggests that most of the orders of birds are old enough to have been affected by the breakup of Gondwanaland, even though fossils of only a few orders have been found before the late Cretaceous. The phylogeny of several orders indicates that they originated in Gondwanaland. For example, the basal lineages of both the chickenlike birds (Galliformes) and the duck order (Anseriformes) are divided between South America and Australia (Figure 6.14A), and almost all of the basal lineages of the huge order of perching birds (Passeriformes) are likewise distributed among fragments of Gondwanaland (Figure 6.14B).

The composition of regional biotas

The taxonomic composition of the biota of any region is a consequence of diverse events, some ancient and some more recent. Certain taxa are **allochthonous**, meaning that they

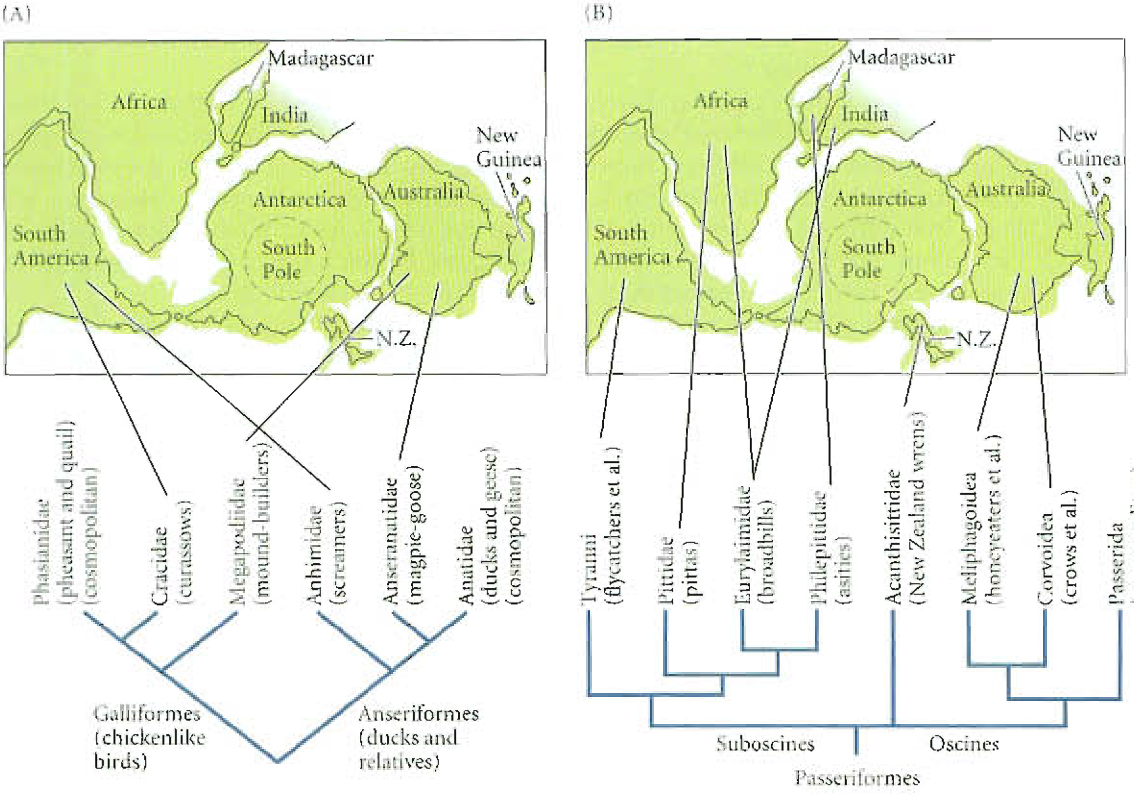


Figure 6.14 Phylogeny of major lineages in three orders of birds, showing their association with land masses, which are pictured as they were situated in the early Cretaceous, in a view centered on the present South Pole. The present continental boundaries are outlined in black; fringing areas shown in green were exposed during the Cretaceous. (A) The orders Galliformes and Anseriformes together form one of the oldest clades of birds. In each order, the basal lineages are divided between South America (curassows, screamers) and Australia (mound-builders, magpie-goose). In each order, a more derived lineage (Phasianidae; Anatidae) has a cosmopolitan (worldwide) distribution. (B) The order Passeriformes (perching or songbirds) has three major clades: suboscines, New Zealand wrens, and oscines. All three of these clades have basal lineages in the southern continents and appear to have originated in Gondwanaland. The relationships among the many families of the cosmopolitan Passerida are too poorly known to determine whether they also originated in a Gondwanan region. (After Cracraft 2001.)

originated elsewhere. Others are **autochthonous**, meaning that they evolved within the region. For example, the biota of South America has (1) some autochthonous taxa that are remnants of the Gondwanan biota and are shared with other southern continents (e.g., lungfishes, rheas); (2) groups that diversified from allochthonous progenitors during the Tertiary, after South America became isolated by continental drift (e.g., New World monkeys, guinea pigs and related rodents); (3) some allochthonous species that entered from North America during the Pleistocene (e.g., the mountain lion, *Panthera concolor*, which also occurs in North America); and (4) a few species that have colonized South America within historical time (e.g., the cattle egret, *Bubulcus ibis*, which apparently arrived from Africa in the 1930s; see Figure 6.6).

Phylogeography

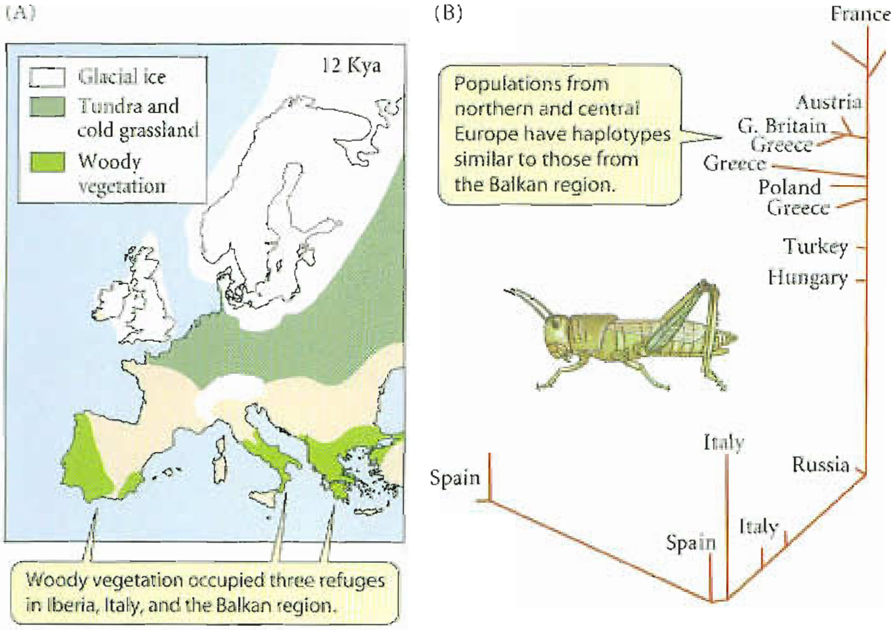
Phylogeography is the description and analysis of the processes that govern the geographic distribution of lineages of genes, especially within species and among closely related species (Avise 2000). These processes include the dispersal of the organisms that carry the genes, so phylogeography provides insight into the past movements of species and the history by which they have attained their present distributions. It relies strongly on phylogenetic analysis of variant genes within species; that is, on inferring gene genealogies (see Chapter 2).

We know, for example, that many northern species occurred far to the south of their present distributions during Pleistocene glacial periods, and that they moved northward after the glaciers receded (see Chapter 5). Fossils, especially fossil pollen, provide some evidence of where these events took place, but the record is incomplete. Moreover, we know that different species occupied different glacial refuges and had different paths of movement. Many species have left no fossil traces of their paths, but phylogeographic analysis can help to reconstruct them (Taberlet et al. 1998; Hewitt 2000).

Fossil pollen shows that refuges for deciduous vegetation in Europe during the most recent glacial period were located in Iberia (Spain and Portugal), Italy, and the Balkans (Figure 6.15A), and that the vegetation expanded most rapidly from the Balkans as the glacier retreated. The grasshopper *Chorthippus parallelus*, sampled from throughout Europe, has unique haplotypes in Iberia and in Italy, whereas the haplotypes found in central and northern Europe are related to those in the Balkans (Figure 6.15B). Thus we can conclude that this herbivorous insect expanded its range chiefly from the Balkans, but did not cross the Pyrenees from Iberia, nor the Alps from Italy (Figure 6.15C). A similar analysis of hedgehogs (*Erinaceus europaeus* and *E. concolor*) indicated, in contrast, that these insectivorous mammals colonized northern Europe from all three refugial areas.

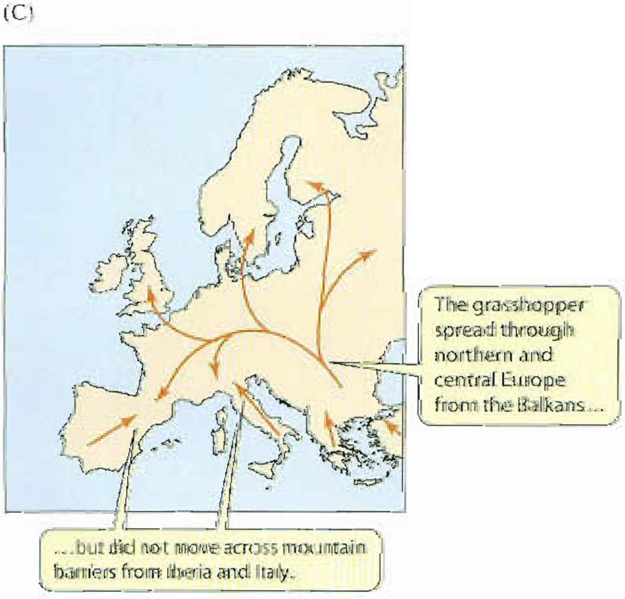
Phylogeography has also been applied to our own distribution. We saw in Chapter 4 that *Homo erectus* was broadly distributed throughout Africa and Asia by about a million years ago and had evolved into "archaic *Homo sapiens*" by about 300,000 years ago. How these ancient populations are related to the different human populations of today has been a controversial question (Relethford 2001; Klein and Takahata 2002; Templeton 2002).

Based on the morphology of fossil specimens, advocates of the MULTIREGIONAL HYPOTHESIS hold that archaic *sapiens* populations in Africa, Europe, and Asia all evolved into modern *sapiens*, with gene flow spreading modern traits among the various populations (Figure 6.16A). According to this hypothesis, there should exist genetic differences among



Woody vegetation occupied three refuges in Iberia, Italy, and the Balkan region.

Populations from northern and central Europe have haplotypes similar to those from the Balkan region.



The grasshopper spread through northern and central Europe from the Balkans...

...but did not move across mountain barriers from Iberia and Italy.

Figure 6.15 The recolonization of Europe from glacial refuges by the grasshopper *Chorthippus parallelus*, inferred from patterns of genetic variation. (A) Europe during the last glacial maximum (about 12,000 years ago). (B) Genetic relationships among contemporary grasshopper populations. The length of a line segment reflects both the number of mutational differences between haplotypes and the difference in proportions of those haplotypes among populations from the areas indicated. (C) Arrows show the inferred spread of *Chorthippus parallelus* after the glacier melted back. (A after Taberlet et al. 1998; B after Cooper et al. 1995; C after Hewitt 2000.)

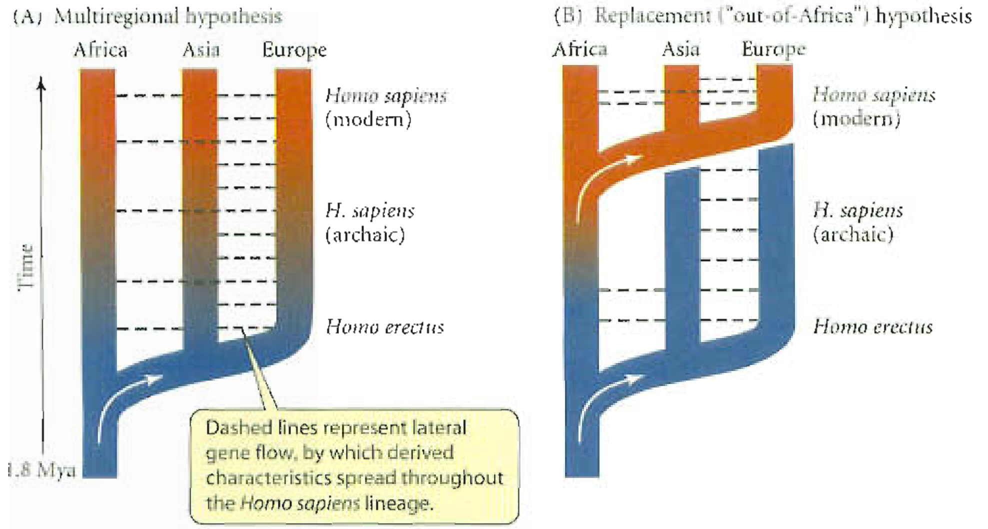
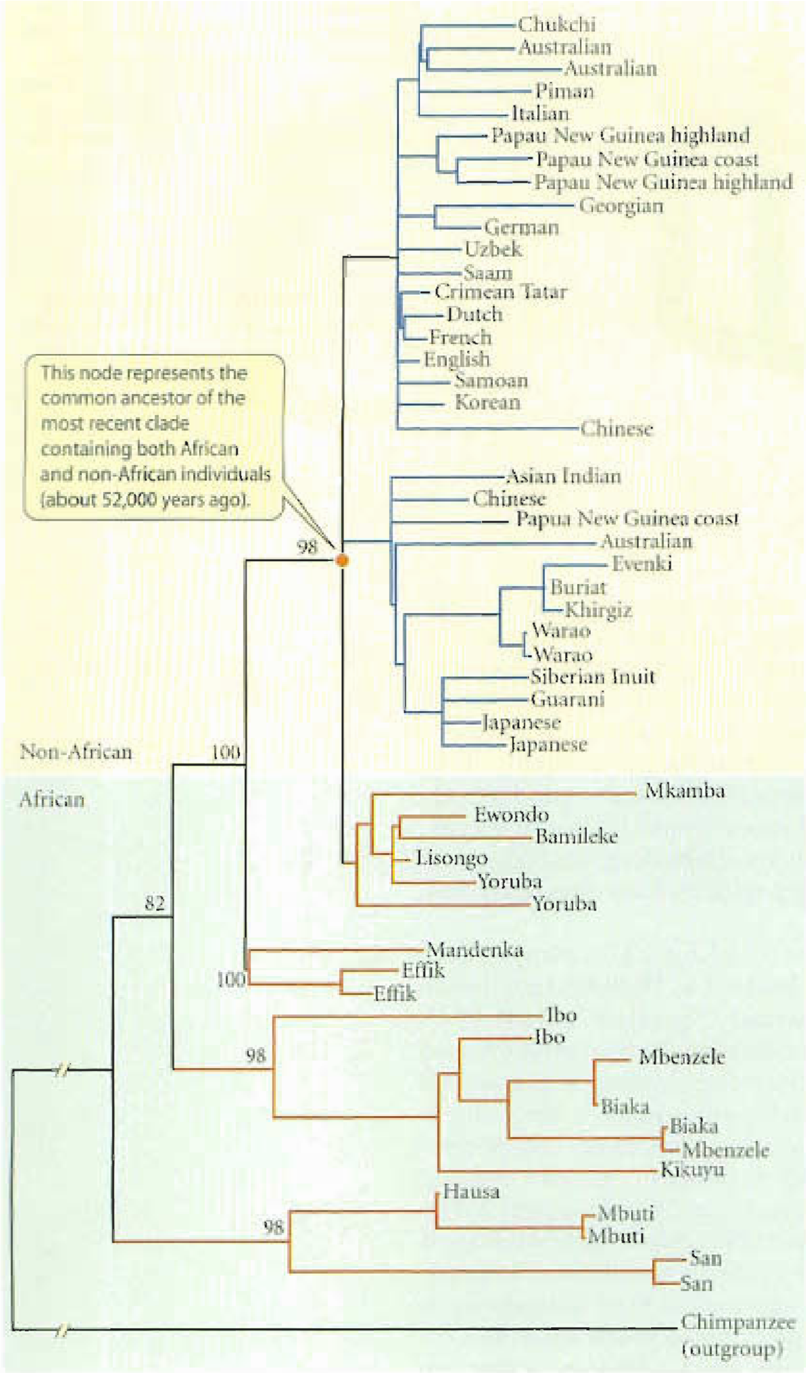


Figure 6.16 Two hypotheses on the origin of modern humans. (A) The multiregional hypothesis posits a single wave of expansion by *Homo erectus* from Africa to parts of Asia and Europe, and continuity of descent to the present day. (B) The replacement hypothesis proposes that populations of *H. erectus*, derived from African ancestors, gave rise to archaic *sapiens*, but that Asian and European populations of archaic *sapiens* became extinct when modern *sapiens* expanded out of Africa in a second wave of colonization.

modern Africans, Europeans, and Asians that trace back to the genetic differences that developed among populations of *erectus* and archaic *sapiens* nearly a million years ago. In contrast, the REPLACEMENT HYPOTHESIS, or OUT-OF-AFRICA HYPOTHESIS, holds that after archaic *sapiens* spread from Africa to Asia and Europe, modern *sapiens* evolved from archaic *sapiens* in Africa, spread throughout the world in a second expansion, and replaced the populations of archaic *sapiens* without interbreeding with them to any substantial extent (Figure 6.16B). That is, the modern *sapiens* that evolved from archaic *sapiens* in Africa was reproductively isolated from Eurasian populations of archaic *sapiens*—it was a distinct biological species. According to this hypothesis, most of the world's populations of archaic *sapiens* became extinct due to competition, and most genes in contemporary populations are descended from those carried by the population that spread from Africa.

Although this question is still subject to some debate (Templeton 2002), many genetic studies support the replacement hypothesis (Nei 1995; Jorde et al. 1998; Underhill et al. 2001). The first such studies employed sequence diversity in mitochondrial DNA (mtDNA) (Cann et al. 1987; Vigilant et al. 1991). A more extensive study of mtDNA used the complete mitochondrial sequence of 53 humans of diverse geographic origin, using a chimpanzee as an outgroup (Ingman et al. 2000). The phylogenetic analysis showed several basal clades of African haplotypes and a derived clade that includes not only several African haplotypes, but also all the non-African populations from throughout the world (Figure 6.17). Moreover, the non-African haplotypes vary less in nucleotide sequence than those found in Africa. These observations strongly support the replacement hypothesis. If, as in the multiregional hypothesis, some contemporary Asian populations were descended from indigenous populations of archaic *Homo sapiens* (and from indigenous *H. erectus*), and thus had a separate ancestry extending back a million years, we would expect some of their genes to have accumulated far more mutational differences than are observed. Indeed, mtDNA sequences from Neanderthal fossils are markedly divergent from modern human sequences (Ovchinnikov et al. 2000). It therefore appears likely that modern humans evolved from archaic *Homo sapiens* in Africa, and then colonized the rest of the world only about 200,000 to 30,000 years ago (see Chapter 10), replacing archaic *sapiens* without interbreeding (Klein 2003). This is a conclusion of the greatest importance, for it means that such genetic differences as exist among geographic populations of humans arose very recently, and that the human species is genetically much the same throughout the world.

Genetic similarities and differences among human populations have also been used to trace later movements. For example, sequence variation in a cluster of genes on the Y chromosome, which is carried only by men, has been studied on a worldwide basis (Underhill et al. 2001). Populations differ in both their proportions of different haplotypes and in



This node represents the common ancestor of the most recent clade containing both African and non-African individuals (about 52,000 years ago).

Figure 6.17 A gene tree based on complete sequences of mitochondrial genomes from human populations throughout the world. Haplotypes from individuals in Africa (green background) are phylogenetically basal, as expected given the African origin of the human species, and show high sequence diversity (represented by the lengths of the branches). Haplotypes taken from individuals in the rest of the world (yellow background) form a single clade of very similar haplotypes (denoted by short branches), as expected if these populations had been recently derived from a small ancestral population. Some populations (e.g., Australian) are represented by more than one individual. Numerals represent bootstrap values (see Box B in Chapter 2.) (After Ingman et al. 2000.)

how greatly those haplotypes differ in sequence from one another. The interpretation of such data can be difficult, partly because movements of people among populations over the course of time can obscure the genetic patterns that may have developed from the original course of colonization. Nonetheless, two groups of Y chromosome haplotypes that are basally located in the gene genealogy (groups I and II in Figure 6.18A) are restricted to Africa, supporting the replacement hypothesis. Non-African populations are characterized by haplotypes in the rest of the gene tree, consisting of several groups that are each more prevalent in some regions than in others. For example, group V is found in aboriginal Australians, whose ancestors arrived in Australia about 50,000 years ago, at about the same time that other humans were spreading throughout Eurasia (Figure 6.18B). Other groups of haplotypes differentiated in various parts of Europe and Asia, including Siberia, and were spread from one region to another by subsequent population movements. Group X haplotypes, descended from haplotypes found in Siberian populations, have a high frequency in Native American populations in both South and North America. Starting perhaps 15,000 to 12,000 years ago, several populations in northeastern Asia may have dispersed into North America at different times (Santos et al. 1999). The history suggested by Y chromosomes (which is considerably more complex than this brief description) supports inferences that had been previously drawn from other kinds of genetic data. The genetic relationships among populations parallel their linguistic relationships to some extent, suggesting that both genes and languages have a common history of divergence in isolation (Cavalli-Sforza et al. 1994).

Ecological Approaches to Biogeography

Whereas systematists often look first to evolutionary history in order to understand the reasons for a taxon's distribution, ecologists tend to look to factors operating now or in the very recent past. Whether a historical or an ecological perspective is most suitable may

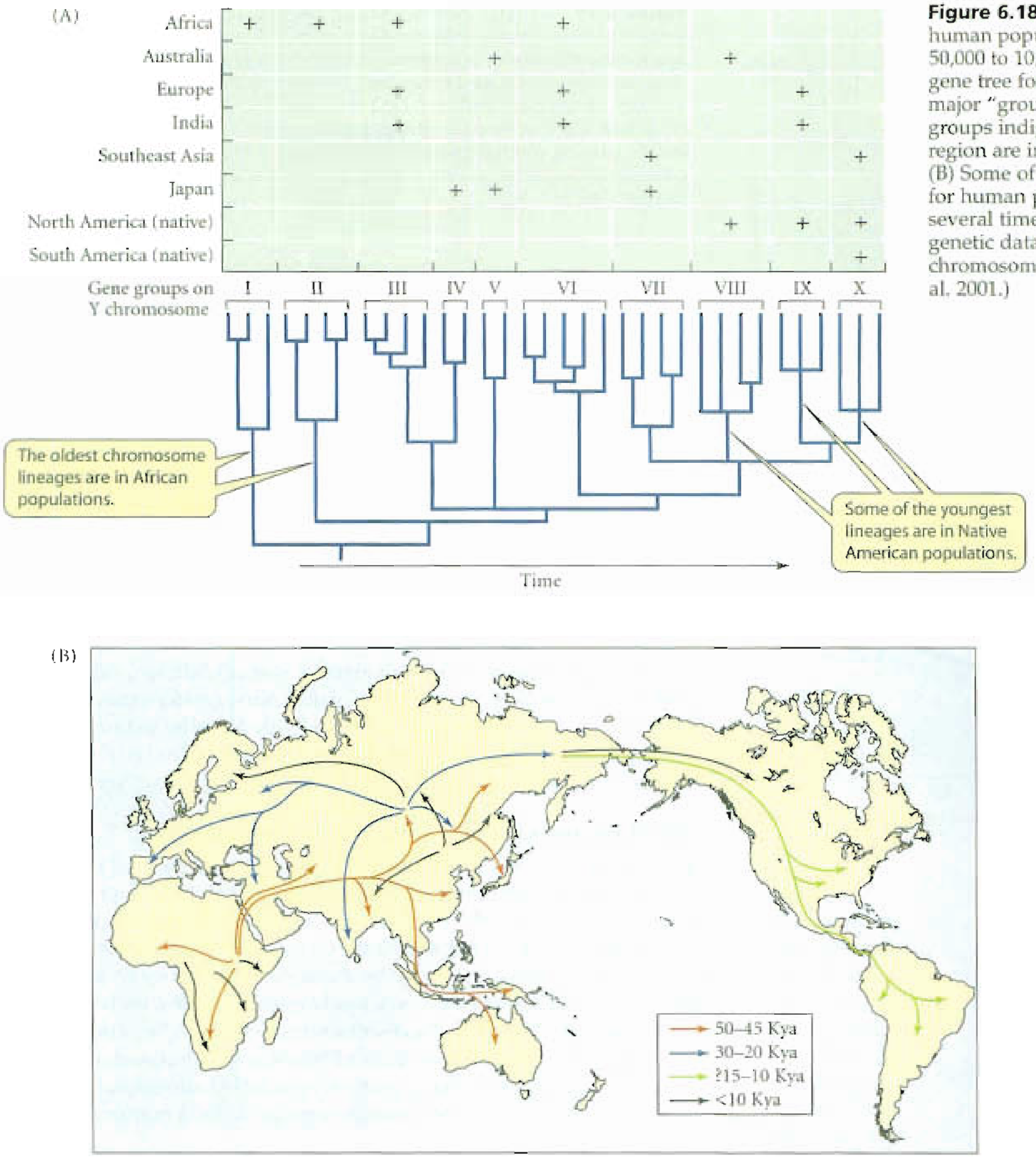


Figure 6.18 The movement of human populations from about 50,000 to 10,000 years ago. (A) A gene tree for Y chromosomes has 10 major "groups." The principal groups indigenous to each world region are indicated by plus signs. (B) Some of the routes postulated for human population dispersal at several times in the past, based on genetic data such as that from Y chromosomes. (After Underhill et al. 2001.)

depend on the particular questions posed and the spatial scale of the distributions under study. For example, phylogenetic history is likely to explain why cacti are native only to the Americas, but to explain why the saguaro cactus (*Carnegiea gigantea*) is restricted to certain parts of the Sonoran Desert, we would have to look toward ecological factors, such as the species' tolerance for rainfall and temperature, or perhaps the effects of competitors, herbivores, or pathogens. We might then assume that the species' range is at equilibrium (i.e., that it is not changing). Alternatively, we might entertain a NONEQUILIBRIUM HYPOTHESIS, such as the proposition that the species is still expanding from a glacial refuge. Although a species' range limit may have reached a short-term equilibrium determined by its present physiological tolerance, it might not have achieved an evolutionary equilibrium if its tolerance is still evolving.

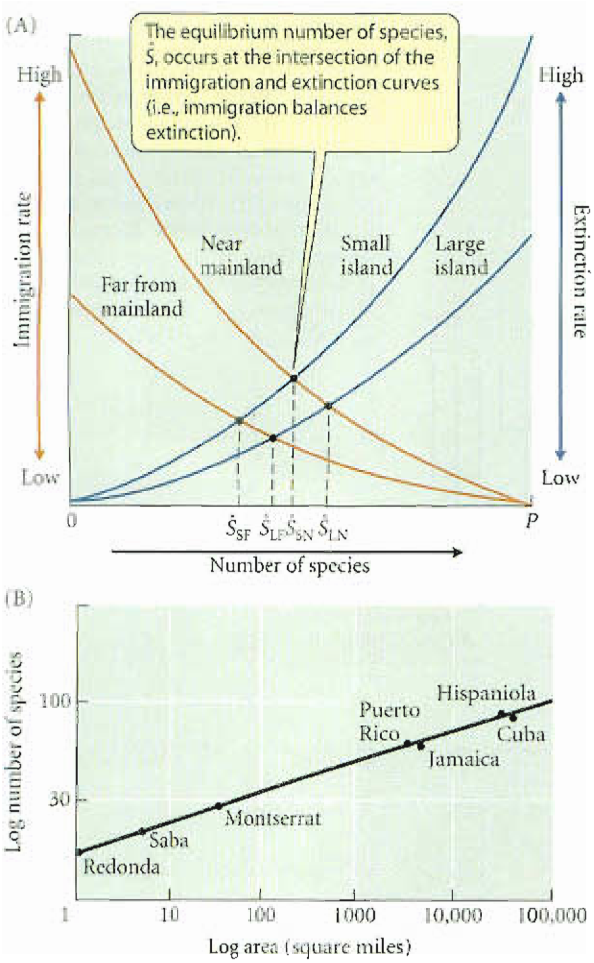


Figure 6.19 (A) The theory of island biogeography. The rates of immigration of new species and of extinction of resident species are plotted against the number of species on an island at a given time. Differences in rates of immigration and extinction, which may depend on distance from a source of colonists and on island size, respectively, result in different equilibria. (B) The number of species of amphibians and reptiles on West Indian islands, plotted against island area on a log-log plot. Larger islands consistently support greater numbers of species. (After MacArthur and Wilson 1967.)

The theory of island biogeography

One of the major topics in ecological biogeography is variation in the diversity of species among regions or habitats. For example, what determines the number of species on an island? Islands typically have fewer species than patches of the same size on continents. The traditional nonequilibrium hypothesis was that most of the continental species have not reached the islands yet (but presumably will, in the fullness of time).

Robert MacArthur and Edward O. Wilson (1967) proposed an equilibrium hypothesis instead (Figure 6.19A). The number of species on an island is increased by new colonizations, but decreased by extinctions. As long as the rate of new colonizations exceeds the rate of extinction, the number of species grows, but when the rates become equal, the number no longer changes; it is at equilibrium. MacArthur and Wilson suggested that smaller islands have greater extinction rates because smaller populations are more likely to suffer extinction. This theory of island biogeography appears to explain the correlation between island area and the number of indigenous species (Figure 6.19B).

Structure and diversity in ecological communities

Ecologists have debated whether or not the numbers of species in many communities are at an equilibrium. The chief factor presumed to produce consistent community structure is interactions—especially competition—among species. Competition should tend to prevent the coexistence of species that are too similar in their use of resources. The result may be a consistent number of sympatric species that partition resources in consistent ways. Closely related species, with very similar requirements, may have mutually exclusive distributions. For example, three species of nectar-feeding honeyeaters occur in the mountains of New Guinea, but each mountain range has only two species, and those two have mutually exclusive altitudinal distributions. Which species is missing from a mountain range appears to be a matter of chance (Figure 6.20).

Community convergence

Many examples of convergent evolution of individual taxa are known. For example, desert plants have independently evolved similar morphological features in many parts of the world (see Figure 6.1), and several groups of birds have independently evolved features suitable for feeding on nectar, such as a long, slender bill (see Figure 3.8). The question arises, are these individual instances part of a larger pattern of convergence of whole communities? If two regions present a similar array of habitats and resources, will species evolve to utilize and partition them in the same way? If so, it would suggest that communities have achieved an evolutionary equilibrium.

A striking example of community-level convergence has been described in the anoles (*Anolis*) of the West Indies (Williams 1972; Losos 1990, 1992; Losos et al. 1998). Anoles are a species-rich group of insectivorous, mostly arboreal Neotropical lizards (Figure 6.21). Different species are known to compete for food, and this competition has influenced the

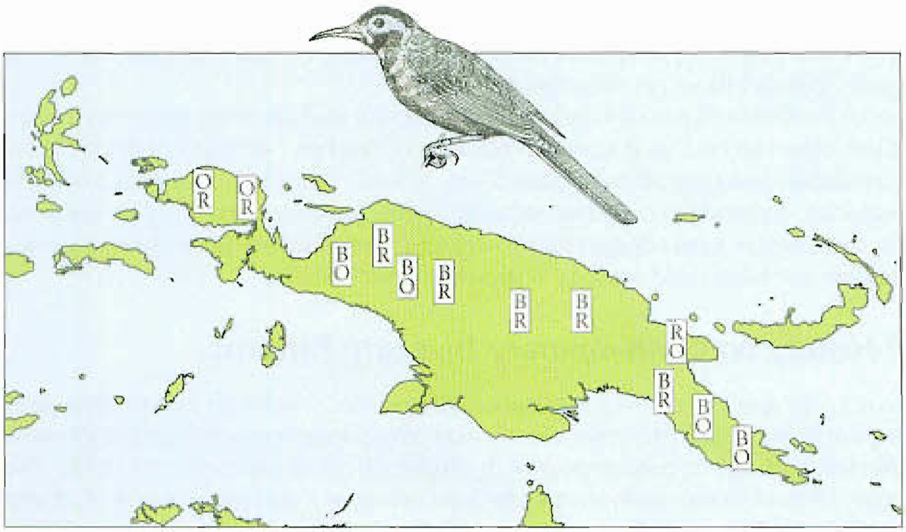


Figure 6.20 A "checkerboard" distribution in which species replace each other haphazardly. Among the various mountain ranges in New Guinea, three species of honeyeaters (*Melidectes*), denoted by letters O, R, and B, are distributed in pairs. Each pair has mutually exclusive altitudinal ranges, as shown by the stacked letters. The three species do not all coexist in any mountain range. (After Diamond 1975.)

structure of anole communities. Each of the small islands in the Lesser Antilles has either a single (solitary) species or two species. Solitary species are generally moderate in size, whereas larger islands have a small and a large species that can coexist because they take insect prey of different sizes and also differ in their microhabitats. The small species of the various islands are a monophyletic group, and so are the large species. Thus it appears that each island has a pair of species assembled from the small-sized and the large-sized clades.

The large islands of the Greater Antilles (Cuba, Hispaniola, Jamaica, Puerto Rico) harbor greater numbers of species. These anoles occupy certain microhabitats, such as tree crown, twig, and trunk, that are filled by different species on each island. The occupants of different microhabitats, called ECOMORPHS, have consistent, adaptive morphologies (see Figure 6.21). These ecomorphs have evolved repeatedly, for the species on each of the

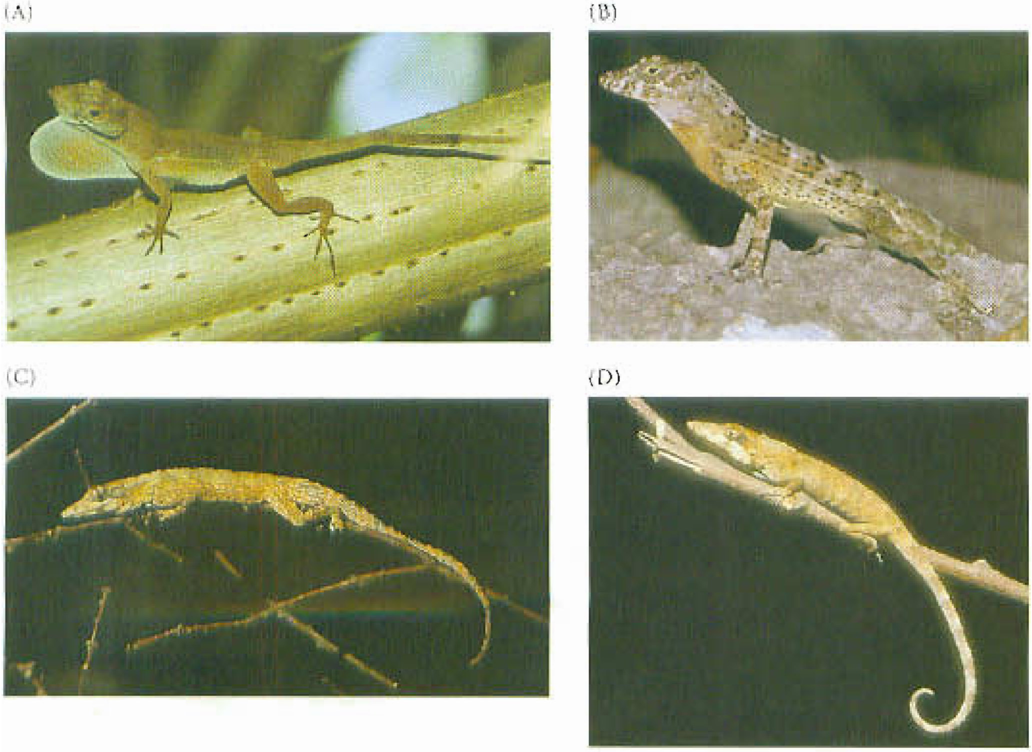


Figure 6.21 Convergent morphologies, or "ecomorphs," of *Anolis* lizards in the West Indies. (A) *Anolis lineatopus* from Jamaica. (B) *A. strahmi* from Hispaniola. Both species have independently evolved the stout head and body, long hind legs, and short tail associated with living on lower tree trunks and on the ground. (C) *Anolis valencienni* from Jamaica. (D) *A. insolitus* from Hispaniola. Both are twig-living anoles that have convergently evolved a more slender head and body, shorter legs, and long tail. (Photographs by K. DeQueiroz and R. Glor, courtesy of J. Losos.)

islands form a monophyletic group that has radiated into species that ecologically and morphologically parallel those on the other islands.

Such extreme evolution of parallel community structure and diversity suggests that an equilibrium has been reached, as if a certain number of "niches," or ways of dividing resources, are available, and they all have been filled. Not all communities appear to be saturated with species, and such a consistent structure as the anoles present may be unusual. Nevertheless, cases of this kind suggest that basic principles of interactions among species may provide both evolution and ecology with some predictability.

Effects of History on Contemporary Diversity Patterns

What explains geographic variation in numbers of species? Although competition and other contemporary ecological processes clearly play a role, long-term evolutionary events have also affected patterns of contemporary diversity (Ricklefs and Schluter 1993). The species diversity of trees in the north temperate zone provides a striking example (Latham and Ricklefs 1993). Moist temperate forests are found primarily in Europe, eastern North America, and eastern Asia. The ratio of the number of tree species in these areas is 1:2:6; Asia has by far the greatest number of species. These differences in species diversity are paralleled by the diversity at higher taxonomic levels. In Asia, a greater proportion of taxa belong to primarily tropical groups than in Europe or America. These differences are not correlated with contemporary patterns of climate.

For about the first 40 million years of the Cenozoic, the Earth was warmer than it is today. Forests were spread across northern America and Eurasia, and many genera were distributed more broadly than they are today. The temperate flora of North America was separated from the tropical American flora by a broad seaway, and the temperate flora of Europe was disjunct from the African flora, but the northern Asian flora graded into the tropical flora, as it does today, from Siberia to the Malay Peninsula (Figure 6.22). Thus, in

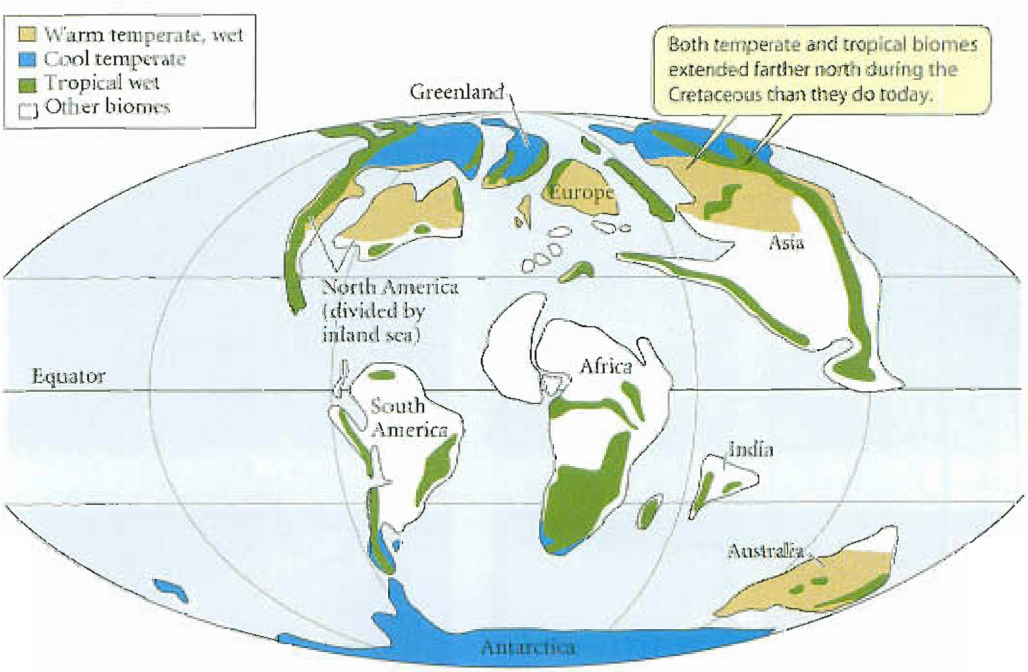


Figure 6.22 The distribution of warm temperate, cool temperate, and wet tropical biomes (vegetations types) at the end of the Cretaceous. A corridor of wet tropical vegetation extended farther south in eastern Asia than in Europe or eastern North America, which were separated from the major tropical areas. (After Latham and Ricklefs 1993.)

Asia, there was greater opportunity for tropical lineages to spread into and adapt to more temperate climates. Probably for this reason, eastern Asia in the Tertiary had more genera of trees than either Europe or eastern North America.

In the late Tertiary and the Quaternary, global cooling culminated in the Pleistocene glaciations, which extended farther south in Europe and eastern North America than in Asia. These glaciations devastated the flora of North America and especially of Europe, where its southward movement was blocked by the Alps, the Mediterranean Sea, and deserts. The continuous corridor to the Asian tropics, however, provided refuge for the Asian flora. A far greater proportion of genera became extinct in Europe and North America than in Asia. Thus contemporary differences in diversity among these regions appear to have been caused by two factors: a long Cenozoic history of differences in opportunities for dispersal, adaptation, and diversification and a recent history of differential extinction.

Summary

1. The geographic distributions of organisms provided Darwin and Wallace with some of their strongest evidence for the reality of evolution.
2. Biogeography, the study of organisms' geographic distributions, has both historical and ecological components. Certain distributions are the consequence of long-term evolutionary history; others are the result of contemporary ecological factors.
3. The historical processes that affect the distribution of a higher taxon include extinction, dispersal, and vicariance (fragmentation of a continuous distribution by the emergence of a barrier). These processes may be affected or accompanied by environmental change, adaptation, and speciation.
4. Histories of dispersal or vicariance can often be inferred from phylogenetic data. When a pattern of phylogenetic relationships among species in different areas is repeated for many taxa, a common history of vicariance is likely.
5. Disjunct distributions are attributable in some instances to vicariance and in others to dispersal.
6. Genetic patterns within species, especially phylogenetic relationships among genes that characterize different geographic populations, can provide information on historical changes in a species' distribution.
7. The local distribution of species is affected by ecological factors, including both abiotic aspects of the environment and biotic features such as competitors and predators.
8. The diversity of species in a local region may or may not be at an equilibrium. Interspecific interactions, especially competition, may limit species diversity and may result in different communities with a similar structure. In some cases, sets of species have independently evolved to partition resources in similar ways.
9. The species diversity of a higher taxon in a particular region is often a result both of current ecological factors and of long-term evolutionary factors.

Terms and Concepts

allochthonous
autochthonous
biogeographic realm
biogeography (phytogeography, zoogeography)
disjunct distribution
dispersal
ecological biogeography
endemic
historical biogeography
phylogeography
vicariance

Suggestions for Further Reading

J. H. Brown and M. V. Lomolino, *Biogeography* (Second Ed., Sinauer Associates, Sunderland, MA., 1998) is a comprehensive textbook of biogeography. A shorter textbook is C. B. Cox and P. D. Moore's *Biogeography: An ecological and evolutionary approach* (Blackwell Scientific Publications, Oxford, 1993).

R. E. Ricklefs and D. Schluter are the editors of *Species diversity in ecological communities: Historical and geographical perspectives* (University of Chicago Press, Chicago, 1993), a multi-authored collection of papers that includes both ecological and historical approaches to understanding species diversity.

Phylogeography is treated in depth by J. C. Avise in *Phylogeography* (Harvard University Press, Cambridge, Mass., 2000), and human phylogeography is included in J. Klein and N. Takahata, *Where do we come from? The molecular evidence for human descent* (Springer-Verlag, New York, 2002).

Problems and Discussion Topics

1. Until recently, the plant family Dipterocarpaceae was thought to be restricted to tropical Asia, where many species are ecologically dominant trees. Recently, a new species of tree in this family was discovered in the rain forest of Colombia, in northern South America. What hypotheses can account for its presence in South America, and how could you test those hypotheses?
2. As described in the text, the deepest split in cichlid phylogeny appears to be less than 60 million years old (see Figure 6.12). The most basal lineage of cichlids is restricted to Madagascar and India, where there are few other cichlids. If this "primitive" group's distribution is not due to ancient separation by the breakup of Gondwanaland, why should it be restricted to those areas? Why is this lineage not also found in Africa or South America? What evidence might bear on your hypotheses?
3. In their analysis of ratite biogeography, Haddrath and Baker argued that the distribution of the ostrich and kiwis is not attributable to rafting on fragments of Gondwanaland. Formulate a set of alternative hypotheses that could account for the distributions of these birds, specify what kind of evidence might support or refute each hypothesis, and then compare your analysis with these authors'.
4. Some biogeographers, subscribing to the "cladistic vicariance" school of thought (Humphries and Parenti 1986), hold that vicariance should always be the preferred hypothesis, and dispersal should be invoked only when necessary, because the vicariance hypothesis can be falsified (if it is false), whereas dispersal can account for any pattern and therefore is not falsifiable. What are the pros and cons of this position? (See Endler 1983.)
5. In some cases, it can be shown that species are physiologically incapable of surviving temperatures that prevail beyond the borders of their range. Do such observations prove that cold regions have low species diversity because of their harsh physical conditions?
6. The species diversity of plants, birds, mammals, and many other taxa declines from tropical regions toward the poles. What hypotheses account for this latitudinal gradient? What evidence is there for and against these hypotheses? (See Willig et al. 2003.)