CHAPTER 16

George Gaylord Simpson & the Question of Continental Drift

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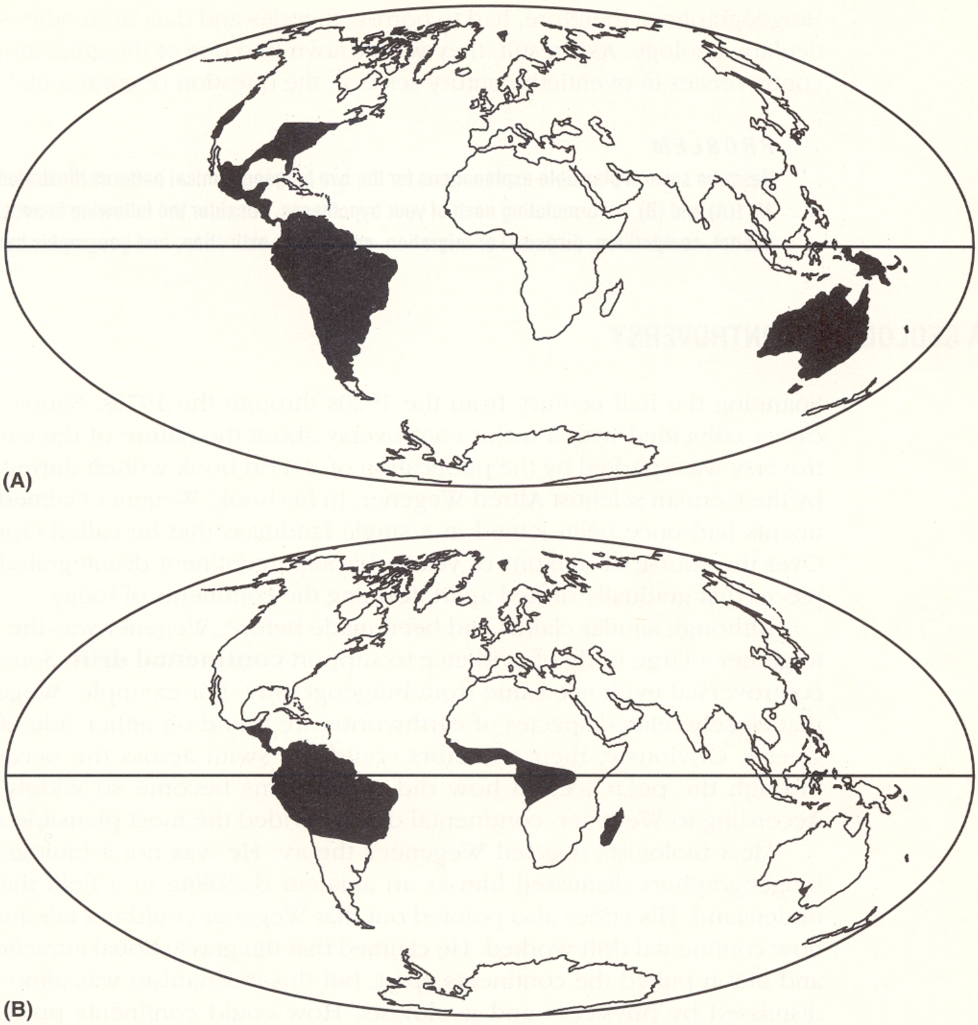
INTRODUCTION

When Europeans began worldwide exploration in the 1500s, they were confronted with a wealth of biological information. The discovery of exotic species from new lands raised troubling questions. Why are there so many species? Why do countries with similar climates often have different species of plants and animals? Did all species originate in one spot? If so, how could they migrate to distant parts of the world?

It is easy to chuckle at early attempts to answer these questions. Faced with the problem of accommodating hundreds of new species, some scientists painstakingly recreated the floor plan of Noah's ark. Others debated the problems faced by penguins and reindeer migrating back to their polar homes after the Flood. However unscientific these efforts may strike us, they were the first attempts to explain the geography of plants and animals. This early biogeographical tradition provided a background for the evolutionary theories proposed by later naturalists such as Charles Darwin and Alfred Russel Wallace.

Biogeography provided such crucial evidence for evolution that Darwin devoted two chapters to the topic in his book *On the Origin of Species.* When he had visited the Galapagos Islands as a young man, Darwin was amazed to find that although the birds, tortoises, and lizards were similar to those found in South America, the species were not the same. In fact, some islands had unique species found nowhere else in the world. Darwin reasoned that all of these species had evolved from a few South American ancestors accidently carried to the islands by storms or ocean currents. Because the islands are somewhat isolated from one another and their environmental conditions are not the same, a new species might evolve on one island, but not on others.

This type of evolutionary explanation revolutionized biogeography, but it did not provide ready-made answers to such questions as why kangaroos and their diverse relatives (marsupials) are common in Australia and the New World continents but absent from Europe, Africa, and Asia (see Figure 16.1(A)). One of the twentieth-



(A)

(B)

FIGURE 16.1 (A) The discontinuous distribution of the order Marsupialia, which includes kangaroos, koalas, opossums, wallabies, and many other pouched mammals. (B) The discontinuous distribution of species in the genus *Symphonia*. This genus of small shrubs includes 2 species found only in South America, 1 species found both in South America and Africa, and 18 species restricted to the island of Madagascar.

century biogeographers who tried to answer this question was George Gaylord Simpson, a paleontologist and leading authority on the evolution of mammals.

To explain such unusual patterns of distribution, Simpson and other biogeographers had to consider a wide variety of factors including climate, habitat, competition, dispersal, speciation, extinction, and geographic barriers. Although these factors are partly biological, they are also heavily influenced by the physical environment.

Biogeographers, therefore, had to borrow theories and data from other sciences, particularly geology. As a result, they were drawn into one of the great interdisciplinary controversies in twentieth-century science: the question of continental drift.

PROBLEM

Describe several plausible explanations for the two biogeographical patterns illustrated in Figure 16.1(A) and (B). In formulating each of your hypotheses, consider the following factors: climate, habitat, competition, dispersal or migration, speciation, extinction, and geographic barriers.

A GEOLOGICAL CONTROVERSY

Spanning the half century from the 1920s through the 1970s, Simpson's scientific career coincided with a major controversy about the nature of the earth. The controversy was sparked by the publication of a short book written during World War I by the German scientist Alfred Wegener. In his book, Wegener claimed that all continents had once been joined in a single landmass that he called Gondwanaland. Over the course of millions of years, this supercontinent disintegrated into several pieces that gradually drifted apart, forming the continents of today.

Although similar claims had been made before, Wegener was the first scientist to gather a large body of evidence to support **continental drift**. Some of his most controversial evidence came from biogeography. For example, Wegener claimed that closely related species of earthworms are found on either side of the Atlantic Ocean. Obviously, their ancestors could not swim across the ocean or burrow through the polar ice, so how did earthworms become so widely distributed? According to Wegener, continental drift provided the most plausible explanation.

Most biologists rejected Wegener's theory. He was not a biologist, and many biogeographers dismissed him as an amateur dabbling in a field that he did not understand. His critics also pointed out that Wegener could not adequately explain how continental drift worked. He claimed that the gravitational attraction of the sun and moon pulled the continents apart, but this mechanism was almost universally dismissed by physicists and geologists. How could continents push through the solid, rocky crust of the earth? What force was sufficiently powerful to drive this movement? It seemed about as likely as pushing this book through a concrete wall. Without a convincing mechanism for continental drift, most biogeographers rejected the theory as a wild flight of fancy.

PROBLEM

Reconsider your explanations for the patterns of distribution illustrated in Figure 16.1. Would Wegener's theory help you to explain these biogeographical patterns? If so, how would you use it in each example? Before you could explain these biogeographical patterns, why would you also need to know *when* Gondwanaland broke up and *how long* it took for the new continents to drift apart?

If continents did not move, perhaps they had once been connected by **land bridges**. For example, if Brazil and Africa had been connected by such a passageway, plants and animals could have freely migrated between the continents (Figure

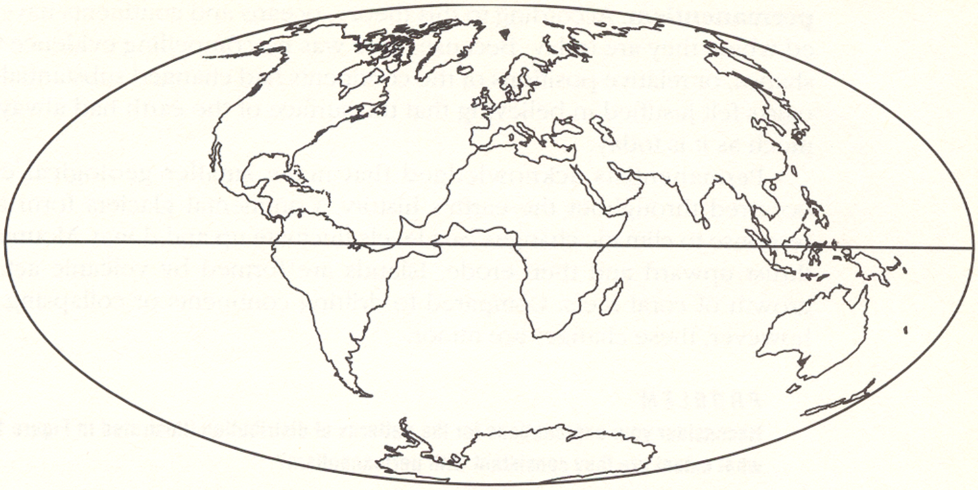


FIGURE 16.2 Hypothetical land bridge connecting South America and Africa. As late as World War II, some biogeographers used land bridges to explain the global distributions of plants and animals.

16.2). Later, if the bridge had collapsed, isolated populations on either side of the Atlantic Ocean could have evolved independently. This was a convenient theory for biogeographers, and during the late nineteenth century they postulated numerous land bridges joining the continents.

What might have caused these massive bridges to disappear? Most geologists in the 1800s believed that the earth originated in a molten state. As it cooled and shrank, tremendous stresses built up in the thin, rocky crust surrounding the still-molten core. Periodically, these stresses were released by the catastrophic collapse of parts of the crust. During these cataclysms, some geologists believed, old land bridges sunk into the ocean floors and new ones were sometimes formed.

Land bridges had been popular among biogeographers, but by the time Wegener wrote his book, the theory was losing support. The discovery of radioactivity around 1900 challenged the assumption of a cooling earth. Perhaps radioactivity deep in the earth's core generated a uniform output of heat. Rather than cooling, the earth's temperature might actually have remained fairly constant. If so, there would be no contraction to cause the earth's crust to buckle and collapse. And was there any evidence for land bridges? If they once existed, the remnants should still be found on ocean floors. Despite efforts to find them, however, the hypothetical land bridges seemed to have disappeared without a trace.

PROBLEM

Reconsider your explanations for the patterns of distribution illustrated in Figure 16.1. How would land bridges help you to explain these biogeographical patterns? Explain whether a biogeographer would be justified in accepting hypothetical land bridges without evidence for their prior existence.

Continental drift and land bridges attracted a few supporters after World War I, but most biogeographers, including Simpson, accepted a third geological theory:

permanentism. According to this theory, oceans and continents have always existed where they are today. Because there was no compelling evidence that the sizes, shapes, or relative positions of the continents had changed substantially, most geologists felt justified in believing that the surface of the earth had always been pretty much as it is today.

Permanentists acknowledged that many smaller geological changes have occurred throughout the earth's history. Continental glaciers form and retreat in response to climatic changes. Sea levels fluctuate up and down. Mountain ranges are thrust upward and then erode. Islands are formed by volcanic action or by the growth of coral reefs. Compared to drifting continents or collapsing land bridges, however, these changes are minor.

PROBLEM

Reconsider your explanations for the patterns of distribution illustrated in Figure 16.1. To what extent are they consistent with permanentism?

The situation faced by biogeographers from about 1920 to 1970 is not unusual in science. Scientists are usually trained as specialists—experts in rather narrow areas of research. Yet solving scientific problems often requires theories, data, or instruments borrowed from other fields. In this case, biogeographers needed a geological theory, but most of them were not experts in geology. The geologists who they turned to for guidance strongly disagreed over the three alternative theories. On what rational basis could a biogeographer, such as Simpson, choose among the competing geological theories?

To some extent, Simpson's choice might be influenced by teachers or other scientists. Some of Simpson's teachers were prominent opponents of continental drift. American scientists were almost unanimous in supporting permanentism, and very few American biogeographers argued for land bridges or continental drift. In Europe, the situation was slightly different. There, continental drift and land bridges were also controversial, but they did have some prominent supporters.

A biogeographer might also choose a theory based on the type of organism studied. For example, after 1920 a few European botanists cautiously accepted continental drift. They needed to explain how closely related species of plants were sometimes separated by vast expanses of ocean (see Figure 16.1(B)). In many cases it was hard to imagine how plants could disperse over such large geographic areas. Seeds are quickly killed by seawater, so it seemed unlikely that they floated from one continent to another. Migratory birds might carry a few seeds, but only along well-established flyways. On the other hand, if the continents had moved, then many troubling patterns of distribution could be explained. Despite its unpopularity, these botanists were willing to accept the intellectual risk of using continental drift as a tentative "working hypothesis." Although they admitted that it was speculative, they hoped that one day geologists would successfully explain how the process worked.

Like Simpson, most zoologists did not believe in drifting continents or massive land bridges. They knew that, over the course of millions of years, even slow-moving animals can disperse very widely. Tiny insects and other small animals can sometimes be carried for hundreds of miles by wind. Darwin and other early biogeographers had also pointed out that animals floating on driftwood rafts occasionally are carried very long distances by ocean currents. Such movements could explain many unusual patterns of animal distribution. Not surprisingly, almost all zoologists were strong supporters of permanentism. It required fewer assumptions than the competing theories, and it appealed to common sense. The alternative theories required a belief in unproved—perhaps unprovable—geological forces of enormous magnitudes. If geologists were skeptical of these speculative theories, why should zoologists seriously consider land bridges or continental drift?

A PERMANENTIST GEOGRAPHY OF ANIMALS

Like many paleontologists, Simpson (Figure 16.3) was trained as a geologist. As a student at Yale University, however, he also took many biology courses. He developed a keen interest in heredity and was strongly influenced by theories of Darwinian natural selection and Mendelian genetics (Chapter 15). As a scientist at the American Museum of Natural History in New York, Simpson became an authority on the evolution of mammals. He wrote over 700 books and articles, including several on evolutionary theory aimed at general audiences. His views on the geography of animals, including his criticisms of continental drift and land bridges, were widely read and highly influential.

FIGURE 16.3 George Gaylord Simpson, paleontologist, biogeographer, and leading critic of continental drift. *Source:* Simpson, G. G. 1965. *Concession to the Improbable: An Unconventional Autobiography*. New Haven, CT: Yale University Press.

Although he usually discussed mammals, Simpson believed that the same basic principles could explain the geographical distribution of all animals and even plants. When climatic conditions are favorable, species migrate quite freely across large expanses of land called **corridors**. The broad connection between Europe and Asia is a good example of a corridor uninterrupted by an ocean or other major geological barriers.

Filter bridges are temporary connections between continents. Such bridges include the Isthmus of Panama between North and South America and the chain of Aleutian Islands in the Bering Sea between Asia and North America. At some times during the earth's history, these bridges have been completely above water, and at other times they have been submerged. As the term implies, filter bridges allow some species to migrate but restrict the movements of others. For example, many mammals from temperate regions crossed the filter bridge between Asia and North America, but the Bering region was too cold for tropical mammals to successfully make the journey. By restricting dispersal, filter bridges periodically allow populations to evolve in isolation from one another.

Sweepstakes routes are ocean currents that carry animals on logs or other floating debris from island to island ("island hopping") or from one continent to another. As the name implies, sweepstakes routes involve a large element of chance. Although rarely traveled, these routes can have major evolutionary consequences when rafters "hit the jackpot." A single pregnant female landing on an isolated island might serve as the starting point for the evolution of a unique and diverse fauna.

Perhaps the best example of this type of random, sweepstakes dispersal is found on the Hawaiian Islands. Because the islands are only a few million years old and are isolated in all directions by hundreds of miles of ocean, it is unlikely that they were ever connected to any of the continents. Therefore, the ancestors of all island species must have floated across the ocean. Hawaii has no native mammals which apparently never crossed the sweepstakes route. But over 3,700 unique species of insects live on the islands. Claiming that these insects evolved from about 250 ancestral species, Simpson estimated that, on average, an insect successfully crossed a sweepstakes route to Hawaii about once every 20,000 years.

PROBLEM

Why might insects be much more successful than mammals at crossing sweepstakes routes like the ones leading to the Hawaiian islands?

To understand how Simpson used these ideas to explain evolution and geographical distribution, consider the marsupials (see Figure 16.1(A)), which diverged from placental mammals perhaps 100 million years ago. For about 30 million years, marsupials competed on even terms with primitive placentals.

Modern placentals evolved about 65 million years ago and drove most of the earlier groups of mammals to extinction. Marsupials flourished in only two remote geographical refuges: Australia and South America.

Simpson combined evidence, logic, and speculation to recreate this evolutionary history of the marsupials. Comparing the characteristics of living species suggested that the ancestral marsupial was similar to an opossum. For example, opossums have relatively unspecialized, general-purpose limbs, compared to the highly specialized, jumping hind legs of kangaroos. It seemed logical that a specialized leg evolved from a more generalized leg, rather than vice versa. Other anatomical comparisons among living and fossil marsupials also supported this hypothesis. Because the oldest opossum fossils had been found in North America, Simpson concluded that this was probably the area where marsupials originated.

Abundant fossils provided strong evidence that marsupials migrated to South America soon after they originated. When the filter bridge at the Isthmus of Panama submerged, the marsupials—and also some primitive placentals—were protected from competition with the more modern placentals which began to evolve about 65 million years ago. Marsupials flourished and diversified in this isolated habitat until the filter bridge was reestablished about 2 million years ago. Although most of the pouched mammals did not survive the onslaught of better-adapted placentals which migrated from the north, several groups of well-adapted marsupials persisted in South America.

Simpson who was an expert on South American mammals, provided a convincing explanation for how marsupials became widespread in South America. But how did the early marsupials disperse to the remote island continent of Australia?

Fossil evidence could not help Simpson answer this question because very few marsupial fossils had been found in Europe, and none had ever been found in Asia. Simpson reasoned, however, that because so many other ancient mammals had successfully crossed the Bering Strait, there was no reason to think that marsupials had failed to use this filter bridge connecting North America and Asia. If this were true, then it was only a matter of time before marsupial fossils would be discovered in Asia.

Once established in Asia, Simpson believed that some ancient marsupials had island hopped across a sweepstakes route from southeast Asia to Australia. Was Simpson justified in proposing this speculative hypothesis without direct fossil evidence to support it? In response, he argued that compared to the alternative hypotheses, his was the most reasonable explanation.

Simpson denied that land bridges were involved in the diversification and spread of marsupials. Some earlier zoologists had claimed that marsupials migrated from southeast Asia to Australia across a land bridge. Yet this hypothesis could not easily explain why placental mammals failed to invade Australia. Furthermore, Simpson pointed out, there was no convincing evidence that such a land bridge had ever existed. It seemed more logical to hypothesize a sweepstakes route that just by chance allowed marsupials, but not placentals, to reach Australia.

Simpson also dismissed Wegener's claim that Australia, Antarctica, and South America had once formed a single continent. Although this might explain why marsupials are so common in both Australia and South America, continental drift was too speculative to take seriously. Echoing Simpson's view, a popular textbook author in the 1950s bluntly concluded that the present distribution of mammals was a product of moving animals, not moving continents.

PERMANENTISM ADRIFT

During the 1950s, when Simpson's biogeographical writings had their greatest influence, the theory of permanentism seemed as rock solid as the apparently unmovable continents. Twenty years later, both the theory and the continents were adrift.

Geologists and oceanographers were gathering convincing evidence that the continents were indeed moving, although not in the way that Alfred Wegener had claimed. According to the new **theory of plate tectonics**, the crust of the earth is composed of several huge plates that float on the molten mantle below. Circulating currents of hot magma in the mantle push the plates in various directions. In certain parts of the world (subduction zones), the leading edge of one plate dips beneath its neighbor. At the trailing edge of the plate, new crust is formed by upwelling magma from the earth's mantle. The continents sit atop the huge crustal plates and move along with them. Two continents on adjacent plates will drift together or apart depending on the movements of the underlying plates.

Plate tectonics revolutionized the way geologists thought about the earth, and it also had important implications for biogeography. It now seemed likely that the shapes and relative positions of continents had been in a constant state of flux. Like huge arks, the drifting continents carried populations of plants and animals—sometimes joining, sometimes isolating the floras and faunas. This could profoundly influence both evolution and dispersal.

The revolution in geology placed Simpson and most other biogeographers in a difficult position. For over 20 years he had been a leading critic of continental drift. His views, published in many books, had been widely accepted by other biologists. Although he was in his late sixties, Simpson continued to write about evolution and biogeography. He admitted that the evidence for continental drift was overwhelming and that it was an important factor in animal distribution. For example, it now appeared that Alfred Wegener had been correct in claiming that Australia, Antarctica, and South America once formed a single continent, or at least had been neighboring islands. Simpson's earlier claim that marsupials had migrated from Asia to Australia now seemed unlikely. Rather than assuming that marsupial fossils would one day be found in Asia, he now thought it more likely that marsupials had never been on the continent.

In retrospect, it would be easy to conclude that Simpson and most other biogeographers had chosen the wrong geological theory. But was he "wrong" during the 1940s and 1950s when he rejected continental drift? Simpson later defended his choice by pointing out important differences between Wegener's early theory of continental drift and the newer theory of plate tectonics. Prior to the rise of plate tectonics, there was no convincing mechanism for continental movement. Geologists and physicists could not agree whether such movement was even theoretically possible. The geographical distribution of animals, and particularly mammals, could be adequately explained without continental drift. Permanentism seemed to be the simplest, least speculative, and most logical of the three alternative geological theories. In the end, however, it also turned out to be untenable.

Continental drift, once so unpopular, came to play a critical role in explaining biogeography. As Simpson later pointed out, however, it didn't automatically solve biogeographical problems. For example, knowing that South America, Antarctica, and Australia had once been neighboring islands did not fully explain marsupial migration patterns. Where had the marsupials originated? In what direction or directions had they moved? When did the movements occur? These questions could not be adequately answered without continental drift, but answering them also required some of Simpson's data and ideas. Corridors, filter bridges, and sweepstakes routes remained important parts of any biogeographical theory. The rise of plate tectonics was a great scientific revolution. Like all revolutions, however, it did not completely overthrow the past.

☐ EPILOGUE

Almost all living species of marsupials are found in Australia (120 species) and South America (80 species). Several species occur in Central America, but only 2 species (both opossums) are found in the United States. No marsupial species live in Europe, Asia, or Africa. This discontinuity continues to intrigue biologists.

In contrast to earlier theories, most zoologists now believe that marsupials were never distributed worldwide. According to the modern theory, marsupials arose in North America. Fossils suggest that a few early marsupials migrated to Europe, which was still connected to North America. But all marsupials in the Northern Hemisphere became extinct between 15 and 20 million years ago.

Long before the northern extinction occurred, a few marsupials rafted to South America, which was an island widely separated from North America and Africa. The tip of South America was close to another large island continent made up of what is now Antarctica and Australia. Although this continent was situated near the South Pole, it had a temperate climate. Recently discovered fossils prove that at different times during the Cretaceous Period (from about 145 to 65 million years ago), dinosaurs and mammals thrived on this ancient continent.

At the end of the Cretaceous Period, Australia separated from Antarctica and began drifting to its present location. Without competition from placental mammals, marsupials continued to diversify on this isolated island. The American continents drifted together about 2 million years ago, allowing modern placental mammals to migrate south across the Isthmus of Panama. This led to the extinction of many marsupial species that had previously flourished on the island of South America. Others, like the modern opossums, moved northward.

Although marsupials are less diverse today than in the past, it would be a mistake to dismiss them as poorly adapted, "second-class mammals." Consider the opossum, which is probably similar to some of the earliest marsupials. Since the colonial period, opossums have expanded their range about 500 miles northward through the eastern United States and into Canada. After being artificially introduced into California by settlers, these familiar marsupials rapidly spread throughout all of the Pacific states. The success of these highly adaptable marsupials should remind us that evolution is an ongoing process, and that many factors continually shape the geographical distribution of animals.

QUESTIONS AND ACTIVITIES

1. What does this case show about the following aspects of doing biology?
   — relationship between data and theories
   — expertise and interdisciplinary problems
   — revision of scientific theories
   — resolving scientific controversies

2. Simpson drew a sharp distinction between his filter bridges and the land bridges that earlier biogeographers had hypothesized (see Figure 16.2). Discuss the similarities and differences between the two ideas.
3. Many scientists believe that choices among competing theories should be made on the basis of *parsimony*. According to this principle, a scientist should always choose the simplest explanation or the one involving the fewest assumptions. Did Simpson follow this principle before 1970? Did he follow it after 1970? What about the botanists who used continental drift in the 1920s to explain the geographical distribution of plants?
4. Although Simpson was an expert on mammalian evolution, he believed that his biogeographical ideas (corridors, filter bridges, and sweepstakes routes) could be used to explain the distribution of all organisms (plants and animals). Are mammals typical of other organisms? What mammalian characteristics might make their migration patterns unusual?

SUGGESTED READING

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