

## PALEOBIOGEOGRAPHY

Paleobiogeography is the study of the ancient geographic distribution of organisms and how they got to be where they are found today. Until recently, there was not much rigorous study or analysis of the methods of paleobiogeography. In the past, most paleobiogeography was done on a very casual, informal basis—the

distribution of the organisms was mapped, and an explanation was concocted to explain this distribution. In recent years, the theory and methodology of biogeography has developed greatly, so now there are competing schools of theoretical biogeography as there are in systematics and other fields.

Such research begins with maps of biogeographic provinces. Some provinces, such as the realms recognized for terrestrial animals, correspond roughly to the boundaries of continents. Most of North America is the Nearctic Realm; South America is part of the Neotropical Realm; Eurasia makes up most of the Palearctic Realm; Australia comprises its own realm. The exceptions are areas of marked ecological change, such as the Sahara Desert, which separates the sub-Saharan Ethiopian Realm from North Africa (which is climatically more like the rest of the Mediterranean), or the tropical rain forests of Southeast Asia or Central America, which are distinct from the temperate regions of North America or Eurasia.

In the case of plant biomes, however, there are much finer-scale subdivisions. Plants are much more sensitive to variations in temperature and precipitation, so their biomes are subdivided into latitudinally defined climatic belts. For example, there are distinct regions of tundra, evergreen coniferous forest, deciduous forest, grasslands, deserts, and rain forest that correspond to certain latitudes, regardless of which continent they are found on. Clearly, the primary controlling factor is temperature, with the highest temperatures found in the tropics and the lowest found near the poles. Another important factor is precipitation, which is also latitudinally controlled.

### Dispersalist Biogeography

Before the scientific understanding of plate tectonics, biogeographers looked at faunal and floral provinces as static entities on static continents. The chief problems were defining the province and its boundaries and determining how adjacent provinces had interacted and how organisms could disperse from one to another. This school of biogeography was later called dispersalism, since it assumes that land masses are relatively stable and that most biogeography can be explained by the dispersal abilities of organisms.

In dispersalist biogeography, the first task is to evaluate the similarity and/or differences between regions. For example, the mammals of North America are fairly similar across the continent, allowing for differences in climate and vegetation. At the ordinal level, 100 percent of the mammals in New York also occur in Oregon, and 83 percent of the mammals in Oregon also occur in New York. The similarity decreases slightly at the level of families, genera, and species (which are more restricted in geographic range), but it is clear that as a whole, temperate North America is faunally homogeneous, with few barriers to dispersal. This is called a corridor, since there are few or no barriers to dispersal, and organisms can move about freely within suitable habitats.

When one compares regions, however, the barriers to dispersal, such as oceans or mountain ranges, rapidly decrease the faunal similarity. For example, there are striking differences between the mammals of Eurasia and those of North America (separated by the Bering Sea) or between those of North and South America (connected only by the Isthmus of Panama). As we look at this pattern in the geologic past, the contrast is even more striking. For example, during the Ice Age, the Bering Strait was a major land bridge, allowing many "Old World" mammals (such as mammoths and bison) to migrate from Eurasia to North America,

and "New World" mammals (such as horses and camels) to migrate to Eurasia. However, the Bering route was not a freeway. For some reason, several Old World natives (such as woolly rhinos and pigs) never migrated to North America, even though woolly rhinos were just as cold-adapted as woolly mammoths. Likewise, some North American native animals (such as pronghorns and peccaries) never migrated to the Old World, although pronghorns live side by side with bison and other Old World immigrants. Such a selective route is called a filter bridge, since it allows some animals to pass, while others do not cross.

The most difficult route for dispersal is crossing major barriers, such as large oceans. In these cases, the probabilities of dispersal are very low, and any organism that manages to cross does so under unusual circumstances. The islands in the middle of the ocean are thousands of kilometers from land, so their only inhabitants are organisms that blew in on a major storm or rafted there on floating vegetation. Hawaii, for example, has no native mammals (except for bats) nor any reptiles, amphibians, or freshwater fishes, so all its land animals (especially birds, snails, and insects) were blown in by storms and have since evolved into a distinctive native fauna that is endemic (restricted) to Hawaii. Such a low probability transport is called a sweepstakes route, since its odds of success are about the same as winning a sweepstakes or the lottery—it is highly improbable, but over the long span of geologic time it will happen sooner or later.

Biogeographers have documented many remarkable ways in which organisms can disperse across large barriers. Large rafts of floating vegetation with small mammals clinging to them have been found at sea, apparently launched when a major river flooded. These are capable of transporting small mammals across oceans, although the odds of success are decidedly low. Small land invertebrates, such as snails, have been known to be carried long distances in the mud on birds' feet. Land plants have remarkable ways of getting across oceans. Many different seeds float long distances or fly in the wind for thousands of kilometers. The coconut's hard seed is adapted for floating long distances to a new island, where the pounding of the surf finally cracks the shell and allows it to germinate near the beach. In addition to birds and bats, many other land animals also can cross enormous distances in the wind. Young spiders disperse from their mother's web by releasing strands of silk as a parachute or balloon and letting the wind carry them wherever it will.

In the marine realm, the problem of dispersal is the mirror image of that on land. What are considered bridges to land animals are barriers to the dispersal of marine life. For example, when the Panamanian land bridge closed in the Pliocene, it allowed mammals to migrate between the Americas, but it shut off the connection between Caribbean and Pacific marine faunas, which have since diverged. In addition, the ocean is not homogeneous but divided into provinces and water masses defined by temperature, salinity, and other properties. Nevertheless, most marine organisms have mechanisms for spreading over much of the ocean. Most have planktonic larvae that are released by the millions, allowing them to float wherever the currents take them and settle in any unoccupied spot. Others, such as jellyfishes, sea turtles, and bony fishes, can migrate or float huge distances across the ocean.

under the right circumstances. The principles of dispersal in the marine realm are similar to those on land, although there are also important differences.

South America provides an excellent example of many of these concepts. During most of the Cenozoic, this continent was isolated from the rest of the world. It had no direct land connection to North America until the Pliocene, and it had lost its supercontinent connection to Antarctica sometime in the Oligocene. Consequently, it has a highly endemic fauna of land mammals and large predatory birds, most of which are only distantly related to animals on other continents. Sometime in the Cretaceous it began to lose its faunal connection to the landmasses that had made up the supercontinent Gondwanaland, so it ended up with only a few native groups: the edentates (sloths, armadillos, anteaters, and their kin), marsupials (which evolved into the main carnivorous groups in the absence of placental carnivores, including remarkable hyenalike, wolflike, and saber-toothed marsupials), and archaic hoofed mammals (which evolved in parallel to resemble horses, hippos, camels, giraffes, antelopes, mastodons, and many other ecological niches found on other continents). A few South American natives (such as the arctostyloids, an ungulate family) managed to get to North America and China, and a few North American taxa (groups; singular, taxon) (such as the pantodonts, an order of large, tusked herbivores) seemed to get from Asia and North America to South America in the Paleocene, so there was the possibility of some sweepstakes dispersal, or island hopping, during the Paleocene, but the continent was isolated through most of the early Cenozoic.

In the Oligocene two more mammalian groups appeared in South America: the New World monkeys and the caviomorph rodents (today represented by chinchillas, guinea pigs, capybaras, agoutis, caviets, and their kin). Both groups have their nearest relatives in Africa, so they must have rafted across the South Atlantic by some kind of sweepstakes route. South America's isolation continued until the Late Miocene, when mastodons, raccoons, and some other North American groups apparently island-hopped across the Central American archipelago. Finally, the isolation ended in the mid-Pliocene with the completion of the Panamanian Isthmus, which became a filter bridge. Many North American natives (mastodons, horses, camels, deer, and placental carnivores, such as bears, lions, and saber-toothed cats) moved south, but others (such as pronghorns) did not. Only a few of the South American natives (armadillos, ground sloths, and capybaras) managed to invade North America, while the majority stayed at home and may have died out in the face of competition from North American invaders.

### Vicariance Biogeography

When the theory of plate tectonics became accepted in the 1960s and 1970s, some predicted that it would revolutionize biogeography. After all, what could be more fundamental than the overturning of the assumption that geographic regions were fixed? Paleontologists eagerly replotted their fossils on the new plate tectonic maps, and novel transport mechanisms were proposed.

One group of scientists, however, looked at biogeography in a wholly new light and found that plate tectonics fit their predic-

tions nicely. This school of thought is now known as vicariance biogeography, and in the 1970s it was embraced by the same scientists who had fought the wars over cladistics (a theory of systematics based on the possession of common traits and ancestry) a few years earlier. They argued that vicariance methods changed biogeography from the ad hoc, storytelling, untestable approach of dispersalist theory to something rigorous and testable. The battle between the vicariance and traditional biogeographers raged for years along many of the same battle lines that had been drawn between cladistic and traditional systematists: cladograms (branching diagrams of relationships, in this case of landmasses as well as organisms); formulation of testable hypotheses; and rejection of scenarios, storytelling, or anything considered untestable. Unlike the cladistic revolution in systematics, however, vicariance biogeography never quite caught on, and in recent years interest has declined to occasional papers in a few journals. Nevertheless, it has forced all scientists to be more careful about how they propose and test their biogeographic ideas.

The idea originated with an obscure Venezuelan botanist by the name of León Croizat, who spent decades documenting the geographic ranges of many different species of plants and animals. His approach was so unconventional, and his writing was so idiosyncratic, difficult to read, and quarrelsome that he was forced to publish his ideas privately at his own expense in three long monographs spanning more than 10,000 pages (the shortest of these is Croizat 1962). Thus, he was not widely read in the scientific community. For decades, his influence was so minor that George Gaylord Simpson never mentioned his work in print except in a footnote, a sure sign of obscurity. Then, when cladistics came along in the 1970s, Gary Nelson and Donn Rosen at the American Museum in New York saw how vicariance methods could be combined with cladistics to make biogeographic hypotheses that were more rigorous and testable. Suddenly, Croizat was rescued from obscurity and placed in the center of a noisy controversy, although he was unhappy with the way his ideas had been transformed. Before he died in 1982, he was at odds not only with his critics but even with supporters such as Nelson. He even hated the term "vicariance biogeography" for a concept that he originally had christened "panbiogeography."

What is vicariance biogeography, and why is it so controversial? Croizat rejected the central assumption of dispersalist biogeography: that organisms have a center of origin and they gradually spread from that point to their present range. Instead, Croizat argued that biogeographic ranges are initially large (in other words, he viewed dispersal as instantaneous rather than gradual), and that biogeographic patterns are determined more by the fragmentation (whether by plate movements, sea level changes, or mountain ranges) of formerly large ranges into smaller areas. In each of these areas, a vicar species represents a fragment of a formerly much larger range, hence the name "vicariance." (A "vicar" in Latin is a representative or replacement for something else, so we get vicarious thrills when we experience them for someone else; a vicar in the clergy is Christ's representative.) Croizat analyzed these fragmented ranges by drawing lines (tracks) between the remnants of a geographic distribution to show their original connections. When this was done for a variety of organisms, the tracks

began to overlap and many had the same pattern, producing generalized tracks that show the biogeographic affinities of major regions. For example, Croizat was struck by the large number of tracks that connected South America and Africa, yet geologists insisted that there was no way the continents could have been connected. His ideas were developed before plate tectonics showed that Africa and South America had once been connected, so these ideas were at least a decade ahead of the geological discoveries that made them plausible.

When Croizat's ideas were embraced by Nelson, Rosen, and others, these scientists adapted them to cladistic methods and hypothesis testing. Instead of generalized tracks, they generated a cladogram of landmasses, based on their time of divergence. They would then analyze the cladistic relationships of a variety of different organisms found on those landmasses and see what patterns emerged. If the cladograms of landmasses and taxa were congruent, it suggested that the present distribution of those taxa resulted from the fragmentation of the region on which they originated, and did not result from recent dispersal from one place to another. For example, a number of animals have cladistic relationships that suggest that their distribution resulted from fragmentation of Gondwanaland. The flightless ratite birds—the ostrich in Africa, rhea in South America, emu and cassowary in Australia, kiwi and extinct moa in New Zealand, and extinct elephant bird *Aepyornis* in Madagascar—are all found on Gondwana fragments. (However, several scientists have argued that the ratite birds once were distributed worldwide, and today they just happen to survive on Gondwana continents.) This remnant Gondwanaland distribution is true of marsupial mammals, osteoglossine fishes, galliform birds, hylid frogs, and a variety of insects. When many different cladograms are congruent, it is no accident; it is statistically significant.

The primary appeal of vicariance biogeography, however, lies in its testability. If the cladograms of areas and taxa are congruent, then they provide a positive test of the hypothesis. If they are not, then the vicariance interpretation is falsified. Such cannot be said for the old school of dispersalist biogeography, which was dominated by storytelling rather than hypothesis testing. If the oldest fossil of a given taxon was found in area A, then the dispersalist said that it migrated from area A to area B; if another, older fossil was found in area B, then the direction of dispersal was arbitrarily reversed. There was no rigorous method of deciding where a taxon originated and when and in what direction dispersal had occurred. Just about any scenario could be made to fit the distributional data, so there was no criterion for deciding whether a given hypothesis had been falsified or not.

Vicariance biogeographers do not deny that dispersal occurs, only that hypotheses based on dispersalist ideas cannot be rigorously tested. Instead, they advocate doing the necessary systematic and cladistic analyses first to see if a vicariant pattern emerges, in which case there is no need to postulate dispersal at all. In their view, biographers for too long had been content to invoke easy dispersalist explanations without looking harder at systematic relationships to see if vicariant explanations fit better. Of course, if there is no vicariant pattern, then one can fall back to dispersalism by default, but it should not be the first step in the analysis.

One would think that vicariance explanations would be unnecessary in groups with good dispersal ability. Yet even in these cases, there are surprises. For example, young spiders can disperse hundreds of miles by ballooning with threads from their spinnerets. Yet N.D. Platnick (1976) analyzed the laroniine spiders and found their distribution could be explained entirely by vicariance. The first branch point on the cladogram separated Gondwana and Laurasian taxa, and then among the Laurasian taxa there was a clear split between Asian and North American clades, corresponding to the breakup of the supercontinent Laurasia.

So how does vicariance biogeography stand today? Clearly, for groups that have long histories (at least back to the Mesozoic, when the supercontinent Pangaea broke up), it is appropriate to look for vicariant distributions to see if dispersalism is unnecessary to explain them. However, it is just as clear that the distribution of organisms with very recent histories (especially of the late Cenozoic) cannot be explained by the slow pace of continental fragmentation and collision; such distribution requires dispersalist explanations (however untestable they are). No one argues that the Great American Interchange in the Pliocene or the migrations of Ice Age mammals are anything but dispersal. Similarly, most of the migrations of mammals during the Cenozoic are simply too rapid to be the result of anything but dispersal.

Still, the vicariance advocates refuse to give up easily, and they continue to find surprising new evidence in their favor. For example, biogeographers had long argued that the circum-Pacific distribution of many plants and animals required dispersal around the Pacific Rim. Unlike the Atlantic, the Pacific was not formed by continental fragmentation. However, A. Nur and Z. Ben-Avraham (1981) have postulated the existence of a "lost Pacifica continent" that once lay in the southwest Pacific. In their view, its fragments have since migrated across the Pacific and attached to various continents as exotic terranes. If this is true, then many circum-Pacific organisms may have gotten to their present location by floating on "Noah's Arks" (i.e., landmasses that rift away from one area and transport inhabitants to another) rather than by dispersal. However, this suggestion is still very controversial. It is not clear which if any of the exotic terranes on the Pacific Rim were once part of a "lost Pacifica continent." More importantly, if these fragments had drifted away from a former supercontinent, they would have sunk down the subsidence curve of the spreading seafloor and eventually become submerged, making it very hard for land animals to survive above water until they docked on some other continent.

It is hard to tell how important vicariance biogeography will be in the future. However, it generated a storm of controversy that had a positive effect in challenging many of the stale assumptions of traditional biogeography and forcing scientists to be more rigorous. No matter what the future of biogeography, that legacy was extremely important in the history of this science.

DONALD R. PROTHERO

*See also* Faunal and Floral Provinces; Global Environment; Ocean Environment; Paleoclimatology; Plate Tectonics and Continental Drift; Seas, Ancient; Terrestrial Environment

**Works Cited**

- Croizat, L. 1962. *Space, Time, and Form, the Biological Synthesis*. Caracas: Croizat.
- Nur, A., and Z. Ben-Avraham. 1981. Lost Pacifica continent: A mobilistic speculation. In G. Nelson and D.E. Rosen (eds.), *Vicariance Biogeography: A Critique*. New York: Columbia University Press.
- Platnick, N.D. 1976. Drifting spiders or continents? Vicariance biogeography of the spider family Laroniinae (Araneae: Gnaphosidae). *Systematic Zoology* 24:101-9.

**Further Reading**

- Croizat, L. 1962. *Space, Time, and Form, the Biological Synthesis*. Caracas: Croizat.
- Darlington, P.J. 1957. *Zoogeography*. New York: Wiley.
- Hallam, A. 1973. *Atlas of Palaeobiogeography*. Amsterdam and New York: Elsevier.

- Humphries, C.J., and L.R. Parenti. 1986. *Cladistic Biogeography*. Oxford: Clarendon; New York: Oxford University Press.
- Myers, A.A., and P.S. Giller (eds.). 1988. *Analytical Biogeography*. London and New York: Chapman and Hall.
- Nelson, G., and N. Platnick. 1981. *Systematics and Biogeography, Cladistics and Vicariance*. New York: Columbia University Press.
- Nelson, G., and D.E. Rosen (eds.). 1981. *Vicariance Biogeography: A Critique*. New York: Columbia University Press.
- Nur, A., and Z. Ben-Avraham. 1981. Lost Pacifica continent: A mobilistic speculation. In G. Nelson and D.E. Rosen (eds.), *Vicariance Biogeography: A Critique*. New York: Columbia University Press.
- Pielou, E.C. 1979. *Biogeography*. New York: Wiley-Interscience.
- Platnick, N.D. 1976. Drifting spiders or continents? Vicariance biogeography of the spider family Laroniinae (Araneae: Gnaphosidae). *Systematic Zoology* 24:101-9.