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PALEOBIOGEOGRAPHY OF VERTEBRATES

Biogeography has always been one of the cornerstones of evolutionary biology. Charles Darwin devoted two chapters in *The Origin of Species* to the subject of distribution, and his approach strongly influenced biogeographic analysis for the next hundred years. Although Darwin was expressing many ideas that were in the writings of numerous contemporaneous biologists, coming from Darwin they have had added impact: "The view of each species having been produced in one area alone, and having subsequently migrated from that area as far as its powers of migration and subsistence under past and present conditions permitted, is the most probable." This concept of distributional history was clearly linked with his strong opinion that it was highly improbable that "our continents which now stand quite separate have been continuously, or almost continuously united with each other, and with the many existing oceanic islands."

These two ideas—that continents have not moved relative to one another and that organisms, therefore, must originate in one area and disperse to another—have dominated the thinking of most workers since the time of Darwin, and later they were adopted and promoted by three of the most influential biogeographers of the 20th century, Matthew (1915), Simpson (1947, 1965), and Darlington (1957, 1965). The biogeographic hypotheses postulated by these workers to explain vertebrate distribution patterns ruled out interchange of faunas among the southern continents, except perhaps by chance dispersal, and instead called for the origin and differentiation of major groups in the large land masses of North America and Eurasia followed by dispersal to South America, Africa, and Australasia. The influence of continental drift and prior continental ligations, with the notable exception of narrow land bridges, was either denied or assumed to have occurred so long ago that they could be discounted.

The publication of Wegener's *The Origin of the Continents and Oceans* (1915) and DuToit's *Our Wandering Continents* (1915) presented an alternative viewpoint: the earth's crust is not stable but dynamic, and through time the continents have shifted their positions and interconnections. Both Wegener and DuToit

had short discussions on biotic distribution in which they suggested that continental drift offered an explanation for the disjunct distributions of many plants and animals.

From 1920 until the 1960s, biologists debated whether or not it was necessary to invoke continental drift to explain biogeographic patterns. A critical history of this debate has not yet been written, but it is fair to say that the viewpoints of the stabilists prevailed, at least in the scientific circles of North America. Nevertheless, some biologists continued to insist that the distributions of plants and animals were consistent with continental drift and that additional, unnecessary ad hoc hypotheses had to be proposed if biogeographic explanations were to rely solely on dispersal from one region to another, all upon a stable geography (notes on the history of biogeographic thinking can be found in Nelson, 1973, and Croizat et al., 1974).

An advance in biogeographic theory accompanied a new conceptual and methodological approach to the analysis of phylogenetic relationships introduced by Willi Hennig in the 1950s and 1960s. This method of analysis—termed phylogenetic systematics (see *Systematic Philosophies*)—emphasizes a precise definition of phylogenetic relationship and a rigorous approach to the construction of hypotheses about the phyletic branching sequences of the organisms being studied (Hennig, 1966a,b, Brundin, 1966). From these branching sequences, then, it is possible to reconstruct the distributions of the unknown common ancestors of each lineage and thus postulate a biogeographic history for the group (Nelson, 1969).

In recent years, another theoretical approach has been used in biogeographic analysis that does not place emphasis on reconstructing centers of origin and pathways of dispersal. This approach, termed the *panbiogeographic* or *vicariance model* of biogeography, was first formulated most comprehensively by the botanist Croizat (see particularly 1958, 1962). The principles are very simply stated (Nelson, 1974; Croizat et al., 1974; Cracraft, 1975):

1. The components of a biota evolve together and significant changes in geography or climate must effect parallel influences on the components of that biota.
2. Biogeographic analysis consists of attempting to reconstruct the history of biotas through time; thus, we seek generalizations about the similarities in distributional history of floras and faunas rather than the particulars of individual taxonomic components.
3. Biotic distribution is to be looked upon as the result of subdivision or vicariance of ancestral biotas

- rather than as origin in one region and dispersal to another.
4. Evidence for dispersal is seen in the sympatry of individual or group distributions, and thus the problem of dispersal can be considered only after the generalized vicariance patterns have been established.

See Ball (1976) for a further treatment of biogeographic theory).

If an attempt is made to examine the interrelationships of the higher taxa of vertebrates in terms of their phyletic (cladistic) affinities, repeated patterns are discovered when the distributions of close relatives are plotted on a world map. In many cases, these joint patterns seem to reflect ancestral vertebrate faunas that were fragmented during the breakup and drift of the continents during the Mesozoic and Cenozoic.

Biogeographic Patterns of Fossil Vertebrates

To a great extent the distributions of fossil and living vertebrates can be explained by or are consistent with our current knowledge of paleogeography and paleoclimatology. Exceptions to this statement are primarily the result of (1) inadequate understanding of phyletic relationships, (2) lack of distributional data on fossil groups because of the absence of particular strata at a given locality or the absence of sufficient paleontological sampling, or (3) gaps in our basic knowledge about the configurations of the continents or the chronology of their movements. Nevertheless, we recognize a number of major patterns that provide evidence for ancestral biotas that were once common to two or more previously united landmasses (reviews can be found in Keast, 1972, 1973; Hallam, 1973; Cox, 1974; Cracraft, 1973, 1974, 1975).

The relative positions of the continents prior to the late Paleozoic formation of the supercontinent Pangaea are still uncertain in a number of cases. Likewise, the vertebrate faunas are not sufficiently known to demonstrate convincingly intercontinental biogeographic patterns; and, prior to the upper Permian and Triassic, terrestrial vertebrate faunas for any reasonably restricted time interval are lacking on a world-wide scale (see Cox, 1974, for a review of those patterns that might be present). This situation improves for paleontological samples taken from Mesozoic and Cenozoic sediments, but here too the data are still incomplete. Mesozoic fossils provide several important lines of evidence that support biogeographic patterns recognized for the modern vertebrate faunas (Colbert, 1971, 1973; Cox, 1974). The Triassic tetrapod

fauna is cosmopolitan and strongly indicates that Pangaea had not yet dispersed sufficiently to subdivide and isolate this fauna. This finding is compatible with the geological data in that Pangaea apparently did not commence significant breakup until the end of the Triassic (see *Paleogeographic Maps*). Jurassic faunas are very poorly known, but the few that have been studied suggest that faunas in Laurasia and Gondwanaland, the two main components of Pangaea, were still similar. Seemingly, this further reflects the fact that interconnections among the continents were still present. While vertebrate faunas of the Cretaceous continue to show some similarities, further breakup of Laurasia and Gondwanaland and the transgressions of seas upon the continents progressively divided and isolated these faunas. By the end of the Cretaceous, South America was isolated from Africa, India from Antarctica and Africa, and New Zealand from Antarctica. Although North America and Eurasia were still united across the North Atlantic, both were divided by extensive epicontinental seas. Thus, provinciality of the continental vertebrate faunas increased through the Cretaceous.

Modern Vertebrate Distribution and Continental Drift

An analysis of the distributions of living vertebrates reveals a number of well-defined biogeographic patterns that reflect the imprint of Mesozoic and Cenozoic continental breakup. Each intercontinental pattern is composed of groups that are found on each of the continents in question and of groups that are restricted to one of the continents but whose closest relatives are located on the other continent comprising the pattern. Five major biogeographic patterns can be recognized among the continents, representing ancestral faunas that were divided by the breakup of Laurasia or Gondwanaland.

1. **Africa-South America.** The vertebrate links between these two continents are particularly strong. They share at least six families of freshwater fishes in addition to the important order Siluriformes (catfishes), and at least five families of amphibians. Moreover, four families of reptiles in South America have their closest relatives in Africa; within the ratite birds, the South American rheas are closely related to the African ostriches; and finally, monkeys and caviomorph rodents are also shared. These similarities, along with those of the plants and invertebrates, suggest an ancestral biota that was subdivided and later differentiated following continental separation. Present geological evidence indicates an early

Late Cretaceous separation of Africa and South America.

2. **South America-Australia.** Links between these two continents are not as numerous as those between Africa and South America, but they do include a representative sample of vertebrates, thus indicating substantial land connections at one time: lungfishes, osteoglossid fishes, several families of frogs, two families of turtles, ratite and galliform birds, and marsupials and monotremes. Again, additional similarities in various plant and invertebrate groups also support the vicariance (subdivision) of a biota that was once continuous from southern South America, across E Antarctica, to Australia. Separation of these continents, and thus isolation of the faunas, seems to have taken place early in the Cenozoic.

3. **South America-New Zealand.** Although the links between these two continents are not strong within vertebrates, several different taxa show relationships indicating a trans-Antarctic pattern: leiopelmatid frogs, ratite birds, penguins, and a group of gruiform birds including the Eurypygidae of South America and the Rhynchotidae of New Caledonia and Aptornithidae of New Zealand. Relationships between South America and New Zealand are strong in some invertebrate and plant groups. New Zealand drifted northward from W Antarctica beginning in the Late Cretaceous, thus the ancestral biota was vicariated, split, long ago.

4. **North America-Eurasia.** Many groups of vertebrates are shared and constitute what might be termed a Laurasian faunal element. Final separation of North America and Europe took place in the early Eocene; NW North America and Siberia have been joined repeatedly as sea levels fluctuated during the Cenozoic. Many of the vertebrates probably were once widespread across Laurasia and were isolated after final separation; others appear to have dispersed across the Bering Land Bridge during the Cenozoic.

5. **Tropical Old World.** Many similarities are shown in the tropical vertebrates of Africa and southern Asia (Cracraft, 1973). These faunas were fragmented by the early Cenozoic collision of India with Asia but particularly by the Cenozoic climatic changes that took place in Africa and southwestern Asia. Components of this vicariated fauna include numerous freshwater fishes (e.g., catfishes, perciforms), frogs (bufonids, ranids, microhylids), reptiles (agamids, elapids, viperids), many families of birds and mammals, to name just a few.

Following the breakup of Gondwanaland, continental movements brought faunas of some southern continents in contact with those to the north in Laurasia. Two examples of faunal

merging are particularly important. First, South American and North America were connected via southern Central America in the Pliocene after a long period of being broadly separated by ocean (geology and biogeography reviewed in Rosen, 1976; see also Webb, 1976). Northern faunal elements that penetrated into South America included salamanders, possibly scincid and colubrid reptiles, passerine birds, and placental mammals. Southern faunal elements extending northward were fishes of the families Cichlidae and Characidae, catfishes, numerous frogs, iguanid and teiid lizards, suboscine birds, and marsupials. The second example of faunal merging is that provided by the Cenozoic collision of Australia with the southeastern portion of Asia. Numerous Asian groups appear to have invaded Australia: ranid frogs; agamid, scincid, and varanid lizards; pythons, colubrid and elapid snakes; probably all oscine birds (songbirds) and many nonpasseriform families, and murid rodents. Australian faunal elements seem not to have penetrated very far north into Asia.

While our understanding of vertebrate biogeography is steadily increasing, some cases remain enigmatic: a prime example is the fauna of Madagascar. Recent investigators have concluded that Madagascar has remained in the same position relative to Africa since the beginning of the Mesozoic. This finding is in contrast to previous opinions of many geologists and biologists who have argued that Madagascar drifted to its present position. Indeed, the biological evidence would seem to suggest a Cretaceous or early Cenozoic connection to Africa. Large dinosaurs are known from the Late Cretaceous; aptornithid (elephant-bird) ratites were once present on both Africa and Madagascar; there are some similarities in the frog faunas; and the unique mammal fauna is said to show links to Africa (also possibly India). On the other hand, Madagascar lacks many of the groups that are characteristic of the African fauna, particularly in freshwater fishes, amphibians, and reptiles. If Madagascar had been united to Africa at one time, we might expect greater faunal similarities; and yet, if Madagascar has always remained isolated, it is difficult to believe that each of the faunal elements arrived by rafting or some other mode of chance dispersal. Hopefully, new geological data will be found to help solve this problem.

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Cross-references: *Paleogeographic Maps; Systematic Philosophies.*

PALEOBOTANY

Paleobotany is the study of plant remains preserved in the geologic record. Traditionally the study involves plant megafossils (leaves, cuticles, fruits, seeds, stems, roots) in contrast to pollen and spores (see *Palynology*). These megafossils are usually encountered as four types of preservation (see Schopf, 1975). The *impression* is an imprint of the organism or its parts showing size, shape, and general features of external morphology. The *compression* consists of organic remains flattened between strata. By suitable techniques it is possible to remove and clear compressed material such as leaves and fronds, revealing cellular details of the epidermis, stomatal apparatus, venation, trichomes, glands, indusia, sporangia, and other features. The *mold and cast* is formed when plant parts—petioles, stems, roots, cones, and seeds—are covered by sediments, and subsequently removed by microbial action creating a cavity or mold. The mold becomes filled with sediment and, if indurated, a cast is formed showing three-dimensional size and shape and reverse images of surface detail. The *petrification* forms when plant structures such as stems, roots, cones, seeds, petioles, and foliage become impregnated with carbonate or silicate minerals. If crystal size remains small and infiltration is slow and complete, considerable cellular detail can be preserved (Taylor and Millay, 1977). Petrified material may be mounted and ground into thin sections or prepared by the peel technique. The latter consists of immersing a section of petrified plant remains in acid capable of dissolving the matrix (HF for silicates, HCl for carbonates). The cellulose is unaffected and will emerge in microrelief. The surface is covered with acetone and a layer of acetate sheet. The acetone softens the acetate and slowly plant material is embedded in the partially dissolved sheet. After drying, the acetate may be peeled away providing a section revealing histological detail.

In recent years, the traditional study of plant megafossils has been supplemented by new