J. C. Briggs

biogeography and plate tectonics

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J. C. Briggs

Department of Marine Science, University of South Florida, St. Petersburg, Florida, U.S.A.

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PREFACE

> But if rivers come into being and perish and if the same parts of the earth are not always moist, the sea also must necessarily change correspondingly. And if in places the sea recedes while in others it encroaches, then evidently the same parts of the earth as a whole are not always sea, nor always mainland, but in process of time all change.
>
> Aristotle, *Meteorologica,* ca. 335 B.C.

Our modern living world, the biosphere, may be subdivided into a number of biogeographic regions and provinces, each with its own distinctive complex of species. An important goal of research is to become better acquainted with the history of these various biogeographic units, for the composition of the ecosystem in each is a reflection of its past. We find, that as time has gone on, the relationship of the biota of the various units to one another has changed and that such changes may often be correlated with the gradual geographical alteration of the earth's surface. The historical approach to biogeography not only helps us to understand the biological effects of the geological changes but often sheds additional light on the geological events themselves. Perhaps most important, the more we learn about the interrelationship between historical biology and geology, the better we understand the evolutionary process.

Not long ago, Jardin and McKenzie (1972), in a brief overview of the biological effects of continental drift (plate tectonics), observed that the facts of continental drift had become so firmly established that it was no longer profitable for biologists to speculate about the past arrangements of land masses. In a similar vein, van Andel (1979) stated that the reconstruction of paleogeography can be carried on based only on physical data without recourse to paleobiogeographical evidence; he noted further that the physical world of the past, thus resurrected, can be used to interpret the biological one without the danger of circular reasoning. If these enthusiastic remarks were indeed true, the task of biogeographical research would be greatly simplified!

This attempt to provide information about continental relationships based on biological evidence to compare with geophysical data, is made with the realization that our lack of knowledge about the history of the various groups of animals and plants is difficult to overcome. At the family level, certainly fewer than one percent of the groups can be said to be reasonably well known in a systematic sense. In the final analysis, our knowledge about the evolution and geographical distribution of families and higher categories depends on competent systematic work. However, relatively little of this kind of research is being done. It is paradoxical, that, on one hand, we are so dependent on the systematist (including those who work with fossil as well as recent materials) for the facts about evolutionary relationship yet, on the other hand, systematics is considered by many to be old fashioned and unworthy of support. If we are to continue to improve our knowledge about the biological history of the earth, it is vital that systematic research be continued.

In analyzing distributional patterns and relating them to continental drift, it is important to attempt to separate effects of drift from various kinds of migration. As is noted in this book, most predrift relationships are very old in a biological sense. For example, Madagascar-India probably separated from Africa, and Euramerica was apparently cut off from Asia, in the mid-Jurassic. By late Jurassic/early Cretaceous times, South America departed from Africa and Africa from Euramerica. In evaluating the evolutionary effects of such events, it is necessary to consider phylogenetic relationships at the level of order, suborder, or family.

Although it is clear that the rate of speciation is quite variable, it is probably safe to say that most living species are not over five million years old and that the great majority of modern genera are Tertiary in origin, making them less than 65 million years old. Most of the families in such relatively well known groups as the birds, mammals, and flowering plants are not older than Cretaceous (65 – 130 million years) in age. This means that for widespread species and genera and for some families we should look for relatively recent (Tertiary) means of dispersal rather than attempting to invoke continental movement that took place in the Mesozoic. Claims that continental drift was responsible for the separation of extant species (Ferris et al., 1976; Platnick, 1976; Tuxen, 1978) are particularly suspect.

Since we know so little about the phylogeny of the various widespread groups of plants and animals, it is important to take advantage of all the information that does exist. The most complete analysis of terrestrial biogeography currently available was based on vertebrate animals only and was published 29 years ago (Darlington, 1957). When one adds the more recent information about the land and freshwater vertebrates, plus the results of systematic work on terrestrial and freshwater invertebrates and plants, and finally data on the distribution of some marine plants and animals, it is possible to obtain a better, if still woefully incomplete, idea of the history of oceanic and continental relationships.

One needs to look at only a small portion of the enormous literature on plate tectonics that has been published in the last 15 years to realize that there are many differences among the various reconstructions that have been presented. It becomes obvious that, although there is a general agreement about the presence of an assembly of continents (a Pangaea) in the early Mesozoic, there is considerable disagreement among earth scientists as to the configurement of the assembly and the manner and timing of the subsequent dispersal. While the revolution in geophysics was taking place, systematic work in paleontology and neontology was going on. There now is a need to incorporate this biological evidence into the theory of plate tectonics.

In order to understand the biological effects of the continental disbursement that took place beginning in the early Mesozoic, it is important to set the stage by first reviewing the consequences of continental assembly. Although the Permian/Triassic boundary has been recognized for many years as a time of severe extinction in the fossil record, the magnitude of this event was not fully appreciated until an analysis was made by Raup (1979). Using data on well-skeletonized marine vertebrate and invertebrate animals, he determined the percent extinction for the higher taxonomic groups. Then, using a rarefaction curve technique, he calculated the percent of species extinction that must have been responsible for the disappearance of the higher groups. His results indicated that as many as 96% of all marine species may have become extinct.

Although the fossil data pertaining to terrestrial forms are not plentiful enough to permit a direct comparison, there is little doubt that extensive extinctions took place there also. Padian and Clemens (1985) noted a sharp drop in the generic diversity of terrestrial vertebrates at the end of the Permian. The coming together of continental faunas that have developed in isolation for a long time may be expected to result in an extensive loss of species. The best documented example took place when North and South America were joined in the late Pliocene by the rise of the Isthmus of Panama (Simpson, 1980; Marshall, 1981; Webb, 1985b). The great losses caused by this event, especially in South America, prompted Gould (1980) to remark that it must rank as the most devastating biological tragedy of recent times.

Why did so many animals (and presumably plants) die out all of a sudden at the end of the Permian? In the marine environment, as the various continents closed with one another, the total amount of shore line and the associated continental shelf habitat (where the marine species diversity is the greatest) became greatly reduced. This restriction was undoubtedly accompanied by a loss of marine provinces (Schopf, 1980). A concurrent event was a significant drop in the salinity of the world ocean. Many salt deposits accumulated in isolated ocean basins that were being closed during the Permian (Flessa, 1980). Most marine species are quite stenohaline and would not be able to survive a significant drop in salinity. Stevens (1977) estimated that the accumulation of salt deposits during the Permian was equal to at least 10% of the volume of salt now in the oceans. But Benson (1984) maintained that this salinity reduction was not enough to cause a general reduction of the normal marine faunas.

In the terrestrial environment, in addition to the major loss almost certainly due to continental linkage, the advent of a severe continental climate associated with the assembled continents would cause further losses (Valentine and Moores, 1972). One may conclude that the coalition of continents, which resulted in the formation of the Triassic supercontinent of Pangaea, was a disastrous event for the world's biota. It was, in fact, the greatest catastrophe ever recorded. It took the world millions of years to recover the diversity that had existed in the early Permian. Additional, but less drastic, extinctions have taken place since the Permian/Triassic event. There is some evidence that these may have occurred at approximate 26 Ma intervals (Raup and Sepkoski, 1984) but there are no indications that these are attributable to plate tectonics.

In 1977, Smith and Briden devoted an entire volume to a series of Mesozoic and Cenozoic paleocontinental maps so that students, teachers, and research workers could use them to plot their own paleogeographic, paleontologic, or paleoclimatic data. The maps were computer drawn based on the input of geophysical data by the authors. These maps, while providing the outlines of the major continental blocks, gave no indication of the position of ancient shore lines and thus no separation between the terrestrial and marine environments.

An attempt to remedy the situation was made by Barron et al. (1981) by the production of a series of "paleogeographic" maps covering the same time period. They drew a distinction between paleocontinental maps, defined as those based on geophysical data, and paleogeographic maps which also utilized fossil and other sedimentary data. In their maps, ancient shore lines are depicted allowing the maps to be more useful for paleoclimatic and paleobiogeographic purposes. However, even though they represent a significant advance, the maps by Barron et al. (1981) need to be improved in order to accurately reflect the continental and oceanic relationships that are indicated by fossil and contemporary biological data.

Another atlas of continental movement maps, covering the past 200 million years, was published by Owen (1983). This work provided two series of maps, one assuming an earth of constant modern dimensions with the second assuming an earth expanding from a diameter of 80% of its modern mean value 180 – 200 million years ago to its modern size. While the expanding earth concept appears to solve some difficulties in the fit of the continental blocks, the technique is basically that of taking the continents in their modern dimensions and moving them about on the globe. There is no consideration of changes brought about by continental accretion or eustatic variation in sea level. Consequently, the use of these maps for biogeographical purposes is very limited.

The idea that we live on a world in which the geographical relationships of the continents are constantly changing has had a far reaching effect. It has not only caused a revolution in the earth sciences but it has stimulated the biological sciences and the public imagination. Hundreds of articles have appeared in the popular literature and even school children are sometimes introduced to continental drift as a part of their beginning geography. In both the scientific and popular press, the concept of Pangaea and the drift sequences tend to be depicted in a positive manner which does not indicate that our knowledge about such things is still very fragmentary.

It is particularly important to attempt to obtain dependable information about certain critical times in the history of continental relationships. We need to know when the terrestrial parts of the earth were broken apart and when they were joined together. The present investigation makes it clear that we cannot depend entirely on evidence from plate tectonics nor will purely biological evidence suffice. The world of the geophysicist is different from that of the biologist and unfortunately there is very little contact between the two camps.

This work represents an attempt to correlate biological events with the general history of continental movement. The biological data include information on many widespread groups of plants and animals. The intercontinental relationships of each group is of value to the overall scheme but the various groups are seldom easily comparable. Each group has its own age, evolutionary rate, area of origin, and dispersal ability. In some, such as certain mammalian orders and families, there is sufficient fossil evidence to help provide a fairly complete look into the past, but for the great majority, fossils are scarce or absent. For all the biotic groups, systematic works which attempted to reconstruct the evolutionary history were of great value. The result has been the accumulation of a large mass of data which by themselves are not very meaningful but when put together provide important insights into the course of continental relationships.

Since the general acceptance of the theory of plate tectonics, there have been published a number of papers on individual groups of organisms in which the authors have interpreted modern patterns in terms of the past relationships of the continents. However, there has been no comprehensive effort to relate to continental movement evidence about the biogeography of many, widespread groups of organisms. As such, this work represents a new departure in the study of biogeography. Also, almost all previous books on the subject have attempted to depict ancient distributional events on modern world maps. That practice needs to be abandoned. In this work, if there are indications that the major part of a distributional pattern was established at a given time in the past, it is depicted on a map appropriate to that time.

A continuing difficulty in the pictorial presentation of continental drift is that most published illustrations have been made using some kind of lateral projection that give an equatorial view of the earth. The distortions inherent in such projections become greatly magnified when one is attempting to illustrate events that took place in the high latitudes of the globe. It is more useful and realistic to use projections that utilize the equal area concept and also show both poles. The accompanying series of maps (see Appendix) use the Lambert equal-area type of projection and attempt to provide outlines of land and sea that appear to be indicated by our present knowledge of biology and geophysics.

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CONTENTS

INTRODUCTION: THE DEVELOPMENT OF THE SCIENCE

> The first appearance of animals now existing can in many cases be traced, their numbers gradually increasing in the more recent formations, while other species continually die out and disappear, so that the present condition of the organic world is clearly derived by a natural process of gradual extinction and creation of species from that of the latest geological periods.
>
> Alfred R. Wallace, *On the Law Which has Regulated the Introduction of New Species,* 1855

For the past 20 years, the time during which the geophysical concept of continental drift has become fully accepted, there has developed a need for biogeographers to take a fresh look at their discipline in the light of past changes in the relationships of the land masses and oceanic basins of the world. As the new plate tectonic framework becomes adopted, biogeography will undergo a change from an emphasis on modern distributional patterns to a greater appreciation for the historical development of such patterns.

In order to realize the importance of the new plate tectonic approach, one should take the time to place it in the context of significant changes that have occurred in the past. As is true of many disciplines, unless one is familiar with its historical progression, one cannot appreciate its present position in the stream of events, nor predict its future course.

IN THE BEGINNING

In the 17th century, the task of biogeographers was a relatively simple one. The book of Genesis told how all men were descended from Noah and that they had made their way from Armenia to their present countries. Since there had been a single geographical and temporal origin for man, the consensus was that this was also true for all animals and that they had a common origin from which they too had dispersed (Browne, 1983). So scholars like Athanasius Kircher (1602 – 1680) and his contemporaries set themselves the task of working out the details of the structure of the Ark so that it could accommodate a pair of each species of animal. It is interesting to see that this exercise of deducing the structure, and eventual grounding place, of the Ark has been repeated dozens of times in the past 300 years. In the year of 1985, there were news reports of five different expeditions busily combing the slopes of Mt. Ararat for the remains of the Ark.

Since well before Kircher's time, travelers and explorers had been bringing back to Europe thousands of specimens representing unknown species of animals. As these were described, secular scholars were obliged to find room for them aboard the Ark. No one seemed to have worried about the thousands of species of plants that could not have survived the Deluge. By the time the 18th century arrived, the idea of the Ark had to be abandoned by people who were informed on the subject of natural history. However, the concept of the Deluge was still strongly entrenched so that a reasonable substitute for the Ark had to be found.

The person who came to the rescue was a young man in Sweden named Carl Linnaeus (1707 – 1778). He was a deeply religious person who felt that God spoke most clearly to man through the natural world. In fact, it has been said that Linnaeus considered the universe a gigantic museum collection given to him by God to describe and catalogue into a methodical framework (Browne, 1983). Linnaeus proceeded to solve the Ark problem by telescoping the story of the Creation into that of the Deluge. He proposed that all living things had their origin on a high mountain at about the time the primeval waters were beginning to recede. Furthermore, he proposed that this Paradisical mountain contained a variety of ecological conditions arranged in climatic zones so that each pair of animals was created in a particular habitat along with other species suited for that place.

As the flood waters receded, Linnaeus envisioned the various animals and plants migrating to their eventual homes where they remained for the rest of time. For him, species were fixed entities that stayed just as they were created. In other works, Linnaeus emphasized that each species had been given the structure that was the most appropriate for the habitat in which it lived. This insistence on a close connection between each species and its habitat, exposed Linnaeus to criticism by other scholars. How could the reindeer, which was designed for the cold, have made its way across inhospitable deserts to get from Mt. Ararat to Lapland?

The Comte de Buffon (1707 – 1788), who published his great encyclopedia, *Histoire Naturelle* in 1749 – 1804, was influential in persuading educated people to give up the Garden of Eden concept and also the idea that species did not change through time. He apparently believed that life originated generally in the far north during a warmer period and had gradually moved south as the climate got colder. Because the New and Old Worlds were almost joined in the north, the species in each area were the same. But, as the southward progression took place, the original populations were separated. In the New World, some kind of a structural degeneration took place which caused those species to depart from the primary type. In regard to mammals, Buffon observed that those of the New and Old World tropics were exclusively confined to their own areas. This has been subsequently referred to as ''Buffons Law'' and interpreted to mean that such animals had evolved in situ and had not migrated from Armenia (Nelson, 1978).

As the result of the influence of Buffon and others, the idea of a single biblical center for all species was replaced by the idea of many centers of creation, each species in the area where it now lived (Browne, 1983). This, and the Linnaean concept of the importance of species as identifiable populations that existed in concert with other species, encouraged naturalists to think in terms of groups of species characteristic of a given geographic area. Linnaeus and his students and others began to emphasize the contrasts among different parts of the world by publishing various ''floras'' and ''faunas''. Johannes F. Gronovius published his *Flora Virginica* in 1743; Carl Linnaeus his *Flora Suecica* in 1745, *Fauna Suecica* in 1746, and *Flora Zeylandica* in 1747; Johann G. Gmelin his *Flora Sibirica* in 1747 – 1769; and Otto Fabricius his *Fauna Groenlandica* in 1780.

From the viewpoint of the mid-18th century, it may be seen that biogeography underwent a fundamental change during the preceding 100 years. Naturalists were at first occupied with the problems of accommodation aboard the Ark and the means by which animals were able to disperse the various parts of the world following the Deluge. The Ark concept gave way to the Paradisical mountain which in turn yielded to the idea of creation in many different places. At the same time, the Linnaean axiom of the fixity of species through time was replaced by one of change under environmental influence. Finally, naturalists began to study the associations of plants and animals in various parts of the world and, in so doing, began to appreciate the contrasts among different countries.

Johann Reinhold Forster (1729 – 1798) was a German naturalist who emigrated to England in 1766. From 1770 to 1772 he published several small works including a volume entitled *A Catalogue of the Animals of North America.* In 1772, he together with his son Georg, was given the opportunity to accompany Captain Cook on his second expedition to the South Seas. This was a three-year circum-navigation of the globe. Upon his return, Forster published his *Observations made during a Voyage round the World* in 1778. In this work, he presented a worldwide view of the various natural regions and their biota. He described how the different floras replaced one another as the physical characteristics of the environment changed. He also called attention to the way in which the type of vegetation determined the kinds of animals found in each region.

Forster compared islands to the mainland and noted that the number of species in a given area was proportionate to the available physical resources. He remarked on the uniform decrease in floral diversity from the equator to the poles and attributed this phenomenon to the latitudinal change in the surface heat of the earth. He found the tropics to be beautiful, rich, and enchanting – the area in which nature reached its highest and most diversified expression (Browne, 1983). Forster, more than any of his predecessors, understood that biotas were living communities characteristic of certain geographical areas. Thus the concept of natural biotic regions was born.

As knowledge of the organic world increased and greater numbers of species became known, naturalists tended to specialize in the study of either plants or animals. For some reason, it was the early botanists who took the greatest interest in biogeography. Karl Willdenow (1765 – 1812) was a plant systematist and head of the Berlin Botanical Garden. In his 1792 book *Grundriss der Krauterkunde*, he outlined the elements of plant geography. He recognized five principal floras in Europe and, like Forster, was interested in the effect of temperature on floral diversity. To account for the presence of the various botanical provinces, Willdenow envisioned an early stage of many mountains surrounded by a global sea. Different plants were created on the various peaks and then spread downward, as the water receded, to form our present botanical provinces.

Willdenow's most famous student was Alexander von Humboldt (1769 – 1859). Von Humboldt has often been called the father of phytogeography (Brown and Gibson, 1983). In his youth he was impressed and influenced by his friendship with Georg Forster. Von Humboldt felt that the study of geographical distribution was scientific inquiry of the highest order and that it could lead to the disclosure of fundamental natural laws (Browne, 1983). He became one of the famous explorer-naturalists and devoted much of his attention to the tropics of the New World. As a part of his great 24 volume work *Voyage aux Régions Equinoxiales du Nouveau*

Continent (1805 – 1837, with A.J.A. Bonpland), von Humboldt included his *Essai sur la Géographie des Plantes* (1805). The latter work, his best contribution to biogeography, was inspired as the result of his climbing Mt. Chimborazo, an 18,000-foot peak in the Andes. There he observed a series of altitudinal floral belts equivalent to the tropical, temperate, boreal, and arctic regions of the world.

The next significant step in the progress of biogeography was made by a Swiss botanist named Augustin de Candolle (1778 – 1841). In 1820, he published his important *Essai élémentaire de Géographie botanique.* In that work he made a distinction between "stations" (habitats) and "habitations" (the major botanical provinces). De Candolle was also the first to write about the notion of competition or a struggle for existence, noting that individuals competed for space, light, and other resources. De Candolle's work had a significant influence on such important figures as Charles Darwin, Joseph Hooker, and his own son Alphonse. The elder de Candolle was a close friend of von Humboldt and was surely influenced by him.

THE GEOLOGICAL CONNECTION

The study of extinct floras got underway with the work of Adolphe Brongniart who published his *Histoire des Végétaux fossiles* in 1828. He was followed by Alphonse de Candolle. Both men believed that life first appeared as a single primitive population evenly distributed over the entire surface of the globe. This uniform population was supposed to have gradually fragmented into many diverse groups of species (Browne, 1983). In the meantime, Georges Cuvier had begun his work on fossil vertebrates and many others soon followed. From a distributional standpoint, the first effective connection between fossil and contemporary patterns was made by Charles Lyell (1797 – 1875). In his *Principles of Geology* (1830 – 1832 and subsequent editions), Lyell undertook extensive discussions on botanical geography, including the provinces of marine algae, and on the geographical distribution of animals. In addition, he analyzed the effects of climatic and geological changes on the distribution of species and the evidence for the extinction and creation of species.

As Browne (1983) has pointed out, Lyell's suggestion that the elevation and submersion of large land masses resulted in the conversion of equable climats into extreme ones, and vice versa, according to the quantity of land left above sea level, was most important. This view meant that floras and faunas had to be dynamic entities capable of expanding or contracting their boundaries as geological agents altered topography and climates. So Lyell, the champion of gradual change to the earth's surface, brought to biogeography a sense of history and the realization that floral and faunal provinces had almost certainly been altered through time.

Edward Forbes (1815 – 1854), despite his short life, made important contributions to both terrestrial and marine biogeography. He accounted for the evident relationship between the floras of the European mountain tops and Scandanavia by supposing very cold conditions and land subsidence in the recent past. His map of the distribution of marine life together with a descriptive text that appeared in Alexander K. Johnston's *The Physical Atlas of Natural Phenomena* (1856) was the first comprehensive work on marine biogeography. In it, the world was divided into 25 provinces located within a series of 9 horizontal "homoizoic belts". A series of five depth zones was also recognized. In the same year, Samuel P. Woodward, the famous malacologist, published part three of his *Manual of the Mollusca* which dealt with the worldwide distribution of that group.

In 1859, Forbes posthumous work *The Natural History of European Seas* was published by Robert Godwin-Austen. In this work Forbes observed that (1) each zoogeographic province is an area where there was a special manifestation of creative power and that the animals originally formed there were apt to become mixed with emigrants from other provinces, (2) each species was created only once and that individuals tended to migrate outward from their center of origin, and (3) provinces to be understood must be traced back like species to their origin in past time. Another important contribution was made by James D. Dana who participated in the United States Exploring Expedition, 1838 – 1842. Through observations made on the distribution of corals and crustaceans, he was able to divide the surface waters of the world into several different zones based on temperature and used isocrymes (lines of mean minimum temperature) to separate them. His plan was published as a brief paper in the *American Journal of Science* in 1853.

The first attempt to include all animal life, marine and terrestrial, in a single zoogeographic scheme was by Ludwig K. Schmarda in his volume entitled *Die Geographische Verbreitung der Tiere* (1853). He divided the world into 21 land and 10 marine realms. However, it was P.L. Sclater who divided the terrestrial world into the biogeographic regions that, essentially, are still in use today. This was done in 1858 in a small paper entitled *On the General Geographical Distribution of the Members of the Class Aves*. Despite the fact that his scheme was based only on the distributional patterns of birds, Sclater's work proved to be useful for almost all groups of terrestrial animals. This has served to emphasize that biogeographic boundaries, found to be important for one group, are also apt to be significant for many others.

EVOLUTIONARY BIOGEOGRAPHY

When the young Charles Darwin visited the Galapagos Islands in 1835, he was struck by the distinctiveness, yet basic similarity, of the fauna to that of mainland South America. When Alfred Russel Wallace traveled through the Indo-Australian Archipelago, some 20 years later, he was puzzled by the contrasting character of the island faunas, some with Australian relationships and others with southeast Asian affinities. After considerable thought about such matters (many years on Darwin's part), each man arrived at a theoretical mechanism (natural selection) to account for evolutionary change. The key for both Darwin and Wallace was the realization that distributional patterns had evolutionary significance.

The announcement of their joint theory by Darwin and Wallace in 1858 in the *Journal of the Linnean Society of London* and, especially, the publication of Darwin's *Origin of Species* in 1859, changed the thinking of the civilized world. Darwin included two important chapters on geographical distribution in his book. In