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PLATE TECTONICS AND CONTINENTAL DRIFT

The idea that the continents are not fixed in place, but capable of shifting around the Earth's surface, is an old one. As soon as decent maps of the world became available, several scholars noticed that the Atlantic coasts of Africa and South America were a good match, suggesting that these two continents once fit together. But it was not until the twentieth century that the idea of continental drift went from a wild notion to the prevailing orthodoxy among geologists.

In 1915 the German meteorologist Alfred Wegener published the first detailed work to argue that continents had moved over time. His ideas were ridiculed by geologists; no one could imagine the continents plowing through the oceanic crust without leaving huge crumpled mountains built from the ocean floor in front of them. However, some Southern Hemisphere geologists (especially in South Africa) were advocates of continental drift. They pointed to the peculiar distribution of distinctive Permo-Triassic plants (such as the seed fern *Glossopteris*) and animals (the aquatic reptile *Mesosaurus*, the synapsids *Lystrosaurus* and *Cynognathus*) as evidence for the former existence of a southern continent called Gondwanaland, consisting of Africa, South America, India, Australia, Antarctica, and Madagascar. They also pointed to three distinct Late Paleozoic floral provinces: a southern flora, dominated by *Glossopteris*, found on most of the Gondwana continents, which were at temperate and polar latitudes; a northern flora found in the great coal swamps of the late Carboniferous, which was dominated by lycopsids (scale trees and club mosses) and located in the ancient tropics; and a third, distinctive Asiatic floral province. These provinces are oddly scattered on a modern map of the world, but if they were placed in their late Paleozoic continental positions, all the Gondwana fragments (Africa, South America, India, Australia, and Antarctica) would come together, as would the northern continents, to form a supercontinent known as Laurasia (North America plus western Eurasia). In the Pennsylvanian, the fragments of Asia had not yet collided with Siberia, but in the Permian this collision formed a single global continent called Pangaea.

The continental drift hypothesis was scorned by Northern Hemisphere geologists until the late 1950s and 1960s, when new evidence emerged from the seafloor and from geophysics. Ancient magnetic directions recorded in rocks around the world showed their continents had moved long distances with respect to the Earth's magnetic poles. Oceanographic surveys showed that there was an immense range of mountains (the longest and highest in the world) that ran down the middle of the Atlantic, and that there were also ranges in the middle of the Pacific and Indian oceans. These midocean ridges turned out to the be sites where the Earth's crust pulls apart in a process called seafloor spreading. In addition, at the edges of some continents, there were long chains of volcanoes and regions of high seismic activity, such as the "ring of fire" around the Pacific. Geophysical data showed that in these regions one continent is plunging underneath another in a process called subduction. The friction between the overriding and downgoing slabs produces earthquakes, and the melting of the downgoing slab as it plunges into the hot mantle produces the chain of volcanoes above each subduction zone.

By the mid-1960s geology had undergone a scientific revolution in its understanding of the Earth, known as plate tectonics. The Earth's crust is broken up into more than 20 distinct tectonic plates that move around and slide over the mantle and pull away or collide with one another as they do so. Where they separate, new oceanic crust is formed by seafloor spreading; where they collide, crust is consumed in subduction zones. In a few places, the plates are neither spreading nor colliding, but sliding past one another in what are known as transform faults. These great fault zones, such as the San Andreas Fault of California, generate enormous friction and huge earthquakes as two plates grind past one another.

In the 30 years since the plate tectonic revolution, many scientists have reconstructed detailed maps showing the ancient distribution of continents (e.g., Bambach et al. 1980; Scotese and Golonka 1992). For the last 200 million years, the present continents have been moving apart as they split away from the global supercontinent of Pangea. In the late Triassic and Jurassic, North America separated from Pangea, causing the opening of the North Atlantic. In the Cretaceous, South America and Africa split open along the South Atlantic, and both separated from Antarctica-Australia. Also in the Cretaceous, India broke away from the southern continents and raced across the Indian Ocean, plowing into southern Asia in the Early Eocene to form the Himalayas. Australia did not separate from Antarctica until the Late Eocene, and it is now beginning to collide with Asia. Since the Cretaceous, a great tropical Tethyan seaway ran from the Mediterranean to Indonesia. It was fragmented when India collided with Asia, and Africa began its collision with Eurasia to form the Alps and the collision zone between the Arabian Peninsula and Iran.

Prior to the Permian supercontinent, a number of different plate configurations were found in the Paleozoic. The Gondwanaland supercontinent has existed for at least 800 million years. However, the northern continents jostled around in a variety of configurations during the Paleozoic. For example, North America was located in the tropics and rotated by 90 degrees during the Cambrian. By the Devonian, North America had collided with Europe to form the Caledonian-Acadian mountains. In the Pennsylvanian, southern North America began to collide with the African and South America portions of Gondwanaland, causing the Appalachian mountain belt. In the Permian, Siberia collided with Europe, crumpling up the Ural Mountains between them.

Prior to the Paleozoic, the positions of the continents are more controversial, since the evidence is difficult to interpret. Most geologists agree that about 700 million years ago there was another supercontinent, known as Rodinia, which placed western North America adjacent to Antarctica and placed fragments of Africa and South America adjacent to eastern North America and Europe; Siberia abutted Greenland. However, there are many other interpretations of how these Late Proterozoic continents were assembled, and so far no reconstruction is supported by all the evidence. Plate reconstructions prior to 700 million years ago are much more speculative, since the evidence is so poor.

The motions of continents are important not only in explaining past geographic puzzles, but they also had climatic and oceanographic effects that were equally important. For example, the circum-Antarctic current currently circulates around Antarctica in a clockwise fashion, locking the cold air and water in around the South Pole. Consequently, there is little mixing of tropical and temperate water with the cold Antarctic waters, enhancing not only the refrigeration of the South Pole but also the extremes between poles and equator. But in the Eocene, Antarctica was still connected to both South America and Australia, and there was no connection of the South Atlantic, South Pacific, and Indian Oceans. Instead, each of these oceans was much warmer and milder because tropical and temperate waters mixed with those of the polar regions. When Australia broke away in the Late Eocene and South America in the Late Oligocene, the circum-Antarctic current formed, and the Antarctic has been refrigerated ever since. This current is ultimately responsible for the global cooling that has occurred in the last 50 million years.

Plate Tectonics and Paleobiogeography

Once the mobility of continents was appreciated, many biogeographic puzzles finally were solved. Paleontologists long had been mystified by the fact that Cambrian trilobite provinces did not follow the present-day distribution of continents. The European faunal province, characterized by the trilobite *Paradoxides*, was found not only in Europe but also in the southeastern United

States, Boston, Rhode Island, Nova Scotia, and eastern Newfoundland. Most of North America was one distinct American province, the *Ogygopsis* fauna, but so was Scotland and western Newfoundland. Paleontologists tried to explain this odd pattern by suggesting differences in water depths or land barriers, but nothing made sense. Only after plate tectonics came along did an explanation present itself. Apparently the southeastern United States, eastern New England, Nova Scotia, and eastern Newfoundland were on the European side of the Proto-Atlantic Ocean during the Cambrian, while Scotland was on the North American side. The Proto-Atlantic then closed in the Late Paleozoic, forming the supercontinent of Laurasia. When the present-day Atlantic was formed by splitting up this supercontinent in the Triassic and Jurassic, it did not follow the line of closure of the old ocean, but split open along a new line, and it left parts of ancient Africa (the southeastern United States) and ancient Europe (New England, Nova Scotia, and eastern Newfoundland) attached to present-day North America and parts of ancient North America (Scotland) attached to Europe.

Paleobiogeographic evidence not only suggested that continents had drifted apart, but even opened the door to our understanding of how continents are put together. Decades ago, paleontologists found Permian fusulinid foraminifera (single-celled organisms) in the central British Columbia Rockies that had affinities with the Tethyan seaway that once stretched from the Straits of Gibraltar to Indonesia. How did these peculiar Permian foraminifera get there? Was there an arm of the warm tropical Tethys that reached up to British Columbia? Or were they part of a moving continental fragment that used to be in the Tethys but crossed the Pacific and became sutured to British Columbia? Although the latter idea seems outrageous at first, as more and more evidence accumulated, it became the best explanation. It turns out that the western Cordillera of North America is made up of numerous exotic terranes that have rafted from across the Pacific and collided with North America at various times during the Mesozoic and Cenozoic. Several of these terranes not only have peculiar Tethyan faunas, but the temperature preferences of their fossils suggest that in the Permian the Cache Creek terrane was part of the tropical Tethys, the Alexander terrane was at subtropical to warm-temperate latitudes, and Wrangellia came from the cool southern latitudes. Today, Wrangellia is the bedrock for southeastern Alaska and Vancouver Island, and the Cache Creek and Alexander terranes are located deep in the British Columbia Rockies—quite a distance for that much land to travel in about 250 million years. In addition to fusulinids, the Triassic ammonoids show the previous position of these terranes, and the Jurassic ammonites have been used as evidence of dramatic northward movement of many of these terranes (for a review of these data, see Hallam 1986).

Most of the concepts of biogeography were developed under the assumption that the continents were fixed. When plate tectonics came along, it was possible for organisms (or their fossils) to get from point A to point B without doing the walking themselves. M.C. McKenna (1973, 1983) suggested several other possible mechanisms where the plates do most of the traveling. If a landmass were to rift away from one area, travel across the ocean, and then collide into another, it could transport its inhabitants to a new land. McKenna (1973) called this a Noah's Ark since it bears similarities to the transport of animals by the biblical boat. Although it is hard to document examples of Noah's Ark transport in the fossil record, several authors have suggested that the transport of India from Gondwanaland to the southern part of Asia may be such a case. India drifted away from Gondwanaland in the Cretaceous and may have had its own endemic archaic mammals. India began its collision with Asia, forming the Himalayas, in the Early Eocene. This is when several advanced groups of mammals (both even-toed artiodactyls and odd-toed perissodactyls, as well as advanced primates) suddenly appeared in Asia and around the world. If those groups had evolved in isolation in India and then spread during the Early Eocene after India docked, it would explain why we do not see them, or their ancestors, anywhere in the world during the Early Paleocene. Unfortunately, we do not yet have much of a fossil record for the Cretaceous or Paleocene in India to test this hypothesis.

But the organisms do not even have to be alive for the plates to move them around. They can just as easily be incorporated as fossils in the rocks, and then be found in another area when continents collide. McKenna (1973) called these beached Viking funeral ships, in reference to the way the Vikings used to send their dead warriors to Valhalla on their longboats, filled with their weapons and wealth and then set ablaze. The Cambrian European trilobites in North America and American trilobites in Scotland mentioned previously are examples of this phenomenon, as are the Tethyan fusulinids now found in British Columbia.

It is even possible that the geographic range of the organisms is older than the land they are living on. McKenna (1983) suggested two mechanisms that could produce this interesting paradox. Midocean ridge islands, such as Iceland, are continually changing as their spreading ridge drifts apart and sinks down into the ocean. The oldest rocks in Iceland are only 13 million years old, yet it is likely that there has been an island in Iceland's position since the North Atlantic first opened in the Jurassic. If so, then an organism could stay on the island for millions of years while the island slowly spread apart and sank away underneath it, analogous to staying in one place by walking up the down escalator (or escalator counterflow in McKenna's terminology).

A similar mechanism might be called escalator hopscotch. The Hawaiian Islands, for example, are part of a long chain of seamounts that extend to the submerged Emperor Seamount chain in the western Pacific. Each Hawaiian island erupted and formed as it sat over the mid-Pacific mantle hotspot, then sank away as its plate moved away from the hotspot. The hotspot is currently under the big island of Hawaii (producing the active Kilauea Volcano), and the rest of the extinct volcanoes of the other Hawaiian Islands are progressively older as you move northwest along the chain. Thus, an organism could hopscotch from a dead, sinking island that is about to become a submerged seamount to an active volcanic island, and the faunas of such an island chain could be older than the islands themselves. So far, no clear-cut cases of either of these mechanisms have been documented, but they are clearly plausible.

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See also Faunal and Floral Provinces; Paleobiogeography; Paleoecology; Seas, Ancient; Seismic and Surface Activity

Works Cited

Bambach, R.K., C.R. Scotese, and A.M. Ziegler. 1980. Before Pangea: Geographies of the Paleozoic world. *American Scientist* 68:26–38.

Hallam, A. 1986. Evidence of displaced terranes from Permian to Jurassic faunas around the Pacific margins. *Journal of the Geological Society of London* 143:209–16.

McKenna, M.C. 1973. Sweepstakes, filters, corridors, Noah's arks, and beached Viking funeral ships in paleogeography. *In* D.H. Tarling and S.K. Runcorn (eds.), *Implications of Continental Drift to the Earth Sciences.* London and New York: Academic Press.

———. 1983. Holarctic land mass rearrangement, cosmic events, and Cenozoic terrestrial organisms. *Annals of the Missouri Botanical Garden* 70:459–89.

Scotese, C., and J. Golonka. 1992. *Paleogeographic Atlas.* Arlington: Department of Geology, University of Texas.

Further Reading

Bambach, R.K., C.R. Scotese, and A.M. Ziegler. 1980. Before Pangea: Geographies of the Paleozoic world. *American Scientist* 68:26–38.

Condie, K.C. 1976. *Plate Tectonics and Crustal Evolution.* New York: Pergamon; 4th ed., Oxford and Boston: Butterworth Heineman.

Cox, A., and R.B. Hart. 1986. *Plate Tectonics: How It Works.* Palo Alto, California: Blackwell.

Gray, J., and A.J. Boucot. 1979. *Historical Biogeography: Plate Tectonics and the Changing Environment.* Corvallis: Oregon State University Press.

Hallam, A. 1973a. *Atlas of Paleobiogeography.* Amsterdam and New York: Elsevier.

———. 1973b. *A Revolution in the Earth Sciences: From Continental Drift to Plate Tectonics.* Oxford: Clarendon Press.

———. 1986. Evidence of displaced terranes from Permian to Jurassic faunas around the Pacific margins. *Journal of the Geological Society of London* 143:209–16.

Hughes, N.F. (ed.). 1973. *Organisms and Continents through Time.* Palaeontological Association Special Papers in Paleontology, 12. London: Palaeontological Association.

McKenna, M.C. 1973. Sweepstakes, filters, corridors, Noah's arks, and beached Viking funeral ships in paleogeography. *In* D.H. Tarling and S.K. Runcorn (eds.), *Implications of Continental Drift to the Earth Sciences.* London and New York: Academic Press.

———. 1983. Holarctic land mass rearrangement, cosmic events, and Cenozoic terrestrial organisms. *Annals of the Missouri Botanical Garden* 70:459–89.

Scotese, C., and J. Golonka. 1992. *Paleogeographic Atlas.* Arlington: Department of Geology, University of Texas.

Wegener, A. 1924. *The Origin of Continents and Oceans.* London: Methuen; New York: Dover, 1966; as *Die Entstehung der Kontinente und Ozeane,* Braunschweig: Vieweg, 1915.

Wyllie, P. 1976. *The Way the Earth Works.* New York: Wiley.

PNEUMATIC SPACES

The presence of "pneumatic bones" (bones that include hollow air spaces) in dinosaurs was first noted by Richard Owen (1842) in the theropod *Altispinax (Megalosaurus).* He noted that the large cavities ("fossae") in the vertebrae of the back were similar to those occupied by extensions of the lungs in extant (present-day) birds. The pneumatic nature of the vertebrae of theropod and sauropod dinosaurs was accepted generally until the early 1900s, when it fell out of favor, apparently due to the influence of Henry Fairfield Osborn. During the next nine decades of the twentieth century, only Janensch (1947) conducted a study of pneumatic spaces in dinosaur bones. The pneumatic nature of bones in pterosaurs (flying reptiles), however, has been accepted almost since the group was recognized, and the interpretation has not been challenged. Recent research (Britt 1993) revived the pneumatic interpretation of the fossae and foramina, often termed "pleurocoels" in saurischian dinosaur vertebrae.

Within the Dinosauria, postcranial pneumatic bones are present only in the Saurischia (theropods, prosauropods, and sauropods), they are absent in Ornithischia. In the Sauropodomorpha (prosauropods and sauropods), in non-avian theropods, and even in the oldest bird, *Archaeopteryx,* postcranial pneumaticity is limited to the vertebrae, usually the cervical (neck) and dorsal (back) vertebrae and some ribs. This contrasts sharply with the condition in the flying archosauromorphs, pterosaurs, and extant birds. Here, an array of nonaxial postcranial bones (limb bones), are often pneumatized. Evidence that the vertebrae of pterosaurs and saurischian dinosaurs were pneumatic is based on large fossae, foramina (smaller openings), and remodelling textures preserved on and in the vertebrae—structures that closely match pneumatic features on living bird vertebrae. Typical external pneumatic features of coelurosaurian theropod vertebrae are shown in Figure 1 and internal structures in Figure 2.

To understand the pneumatic bones of extinct archosauromorphs it is important to have a basic understanding of pneumatic bones in extant birds—the only living animal with pneumatic postcranial bones. In birds, postcranial bones are filled with air (pneumatized) by air sacs (balloonlike structures) of the lungs. Simply put, bird lungs are composed of distinct components that provide for gas exchange and for pumping air. The core of the lung (paleopulmo or *pulmo arcuiformis*) is small and compact, compared to nonavian lungs, and is composed of numerous, subparallel tubes (parabronchi). Gas exchange—the uptake of oxygen and throwing off carbon dioxide—takes place in the lung core. The major air sacs, located mainly before and behind the exchange portion of the lung, act as passive bellows that control air flow. Gas exchange does not occur within the air sacs. Air sac volume is controlled by rib and sternum movement. Essentially, the air only flows forward through the core of the lung. In fact, air flows forward during both inhala-