Plate tectonics in biogeography

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Plate tectonics deals with the motions of the Earth's rocky shell, or lithosphere, which cause the gradual shift of continents and are also responsible for mountain building, volcanic islands, and thermal vents. These geological processes have influenced the distribution of biodiversity. Prior to the identification of a geophysical mechanism that could drive movement at the Earth's surface, its effects had been predicted. The concept of "continental drift" is usually attributed to Alfred Wegener, who presented his ideas on the origin of continents and oceans in 1915. However, in the 1500s the Belgian mapmaker Abraham Ortelius had noted that the coincidence of the coastal outlines of the Americas, Africa, and Europe implied former juxtaposition. In the 1800s, the "father of biogeography," Alfred Russell Wallace, developed his ideas with the benefit of geographer Charles Lyell's *Principles of Geography*. Lyell had noted that "Continents … shift their positions entirely in the course of ages." Nevertheless, in the 1900s continental drift was strongly opposed by many, and the rejection of this hypothesis, which was built on extensive evidence, represents a notable failure of twentieth-century scientific method. The claim that consideration of the theory required demonstration of a geophysical mechanism was unjustified, but was nevertheless assuaged in the 1950s and 1960s when a tectonic model was presented. Today, paleomagnetism, radiometric dating, stratigraphy, and spatial information allow detailed interpretation and paleogeographic reconstruction.

One type of evidence presented in support of continental drift by Wegener and others was (paleo)biogeographic: the widespread distribution of certain fossil animals and plants across landscapes that are now disconnected (Figure 1). However, although widely reiterated even today, the occurrence of fossils did not in truth inform on the process of continental isolation. An alternative idea (land bridging) resolves the spatial discontinuity of biota problem equally well and makes the same biological assumptions. As with continental drift, land bridging assumes that the organisms of interest were unlikely to disperse between patches of suitable habitat. Thus both hypotheses require habitat continuity if species (or their lineages) are to be shared among areas. In biogeography, distribution patterns are often taken as evidence of past processes but they provide only the basis for formulating alternative hypotheses about the processes that might explain them. This is a subtle but vital distinction that underpins scientific method; a proposition cannot be simultaneously proposed and tested using the same observations.

In later editions of his book, Wegener recognized that his continental drift hypothesis was not to be tested with fossils, or for that matter a coincidence of continental crust outline. Rather, the best approach to testing the hypothesis was geodetics (Earth measurement), because the hypothesis that continents had moved in the past generated the prediction that continents would still be moving. Wegener died in his tent during a trip to Greenland to confirm longitudinal drift,

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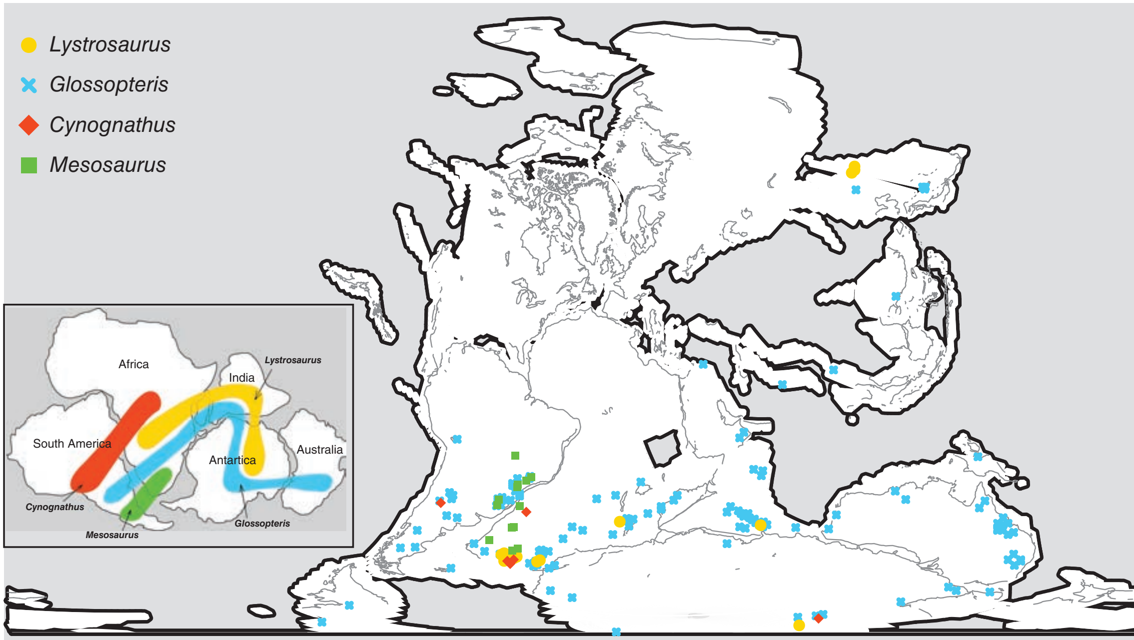


Figure 1 Distribution of four Permian and Triassic fossil groups used as biogeographic evidence for continental drift, and land bridging. *Mesosaurus* included a small number of meter-long marine reptile species recorded in early Permian time (299–280 Ma). It is said that *Mesosaurus* could not have crossed the Atlantic but this is speculative, and at least one popular web resource incorrectly states that these were freshwater reptiles. *Lystrosaurus* included a debated number of species of pig-like land reptiles less than 1 m long. The genus is unusual in being present on either side of the Permian-Triassic extinction boundary (255–241 Ma). *Cynognathus* (*C. crateronotus*) was a meter-long predatory mammal-like reptile usually treated as one species that existed in early to mid-Triassic time (247–237 Ma). *Glossopteris* was a group of woody gymnosperm plants with wide but mostly southern (i.e., Gondwanan) distribution in the Permian (290–252 Ma). The identification of *Glossopteris* from northern areas has been questioned, and estimates of diversity vary.

Fossil sites were mapped using the database and tools of the Fossilworks Paleobiology Database, Macquarie University (John Alroy). Paleogeographic reconstruction is for Permian-Triassic time (250 mya). The inset on left is a version of a popular iconographic but misleading depiction of the fossil distributions (The Snider-Pellegrini Wegener fossil map; WikiCommons). Permian Map by C.R. Scotese, PALEOMAP Project. Reproduced by permission of C.R. Scotese.

but geodetic data have since demonstrated the fact that continents move. Plate tectonics explains how. Geological (rather than biogeographic) data informs paleogeographic reconstruction, and in doing so provides the context for biogeography. Plate tectonics is not, however, only about drifting continents; it generates short- and long-term environmental changes that influence the distribution and evolution of biological diversity, in many different ways.

Continental drift vicariance

Recognition of the potential for continental-scale effects of plate tectonics on biology developed side by side with plate tectonic theory. The founding concept of continental drift was that most of the Earth's land had formerly been connected in a single supercontinent (Pangea). Fossils of Permian age indicate that Pangea existed more than 250 mya, and modern evidence supports this (see Figure 1). In fact the key fossils occur primarily across the southern part of this continent, a region usually referred to as Gondwana (or Gondwanaland), and it is noteworthy that this term was also used by land-bridgers who also envisaged a former extensive continent, parts of which subsequently disappeared. Although the geophysical evidence for a supercontinent is very clear, we now know that it did not include all continental areas at any one time. The idea that past breakup of a supercontinent (up to 200 million years later) could result in the establishment of biotas that are visible today makes many assumptions, among them that a supercontinent would have a homogeneous environment with continuous distributions of plants and animals, that other global events did not cause local changes in biotic assemblages, and that dispersal between continents had little influence on biological assemblages. In fact, paleoecological evidence indicates diverse and sometimes extreme environmental conditions existed across Pangea. Continental drift itself resulted in changes in climatic conditions so that natural selection on the biota would change, an extreme case being the wholesale extinction of Antarctic biota due to the drift of the continent over the South Pole. Mass extinctions across the globe radically altered biotas and dispersal between continents influenced regional biotic composition through time.

Intriguingly, although vicariance biogeography associated with continental drift is a highly attractive and popular idea, contrary evidence of the power of biota to disperse and colonize across habitat discontinuities is abundant and well understood (e.g., colonization and speciation on oceanic islands such as the Galapagos). In studies of living biota, evidence for plate tectonic vicariance can come from dated phylogenetic analysis (see Phylogeography and landscape genetics). Appropriate sampling and fossil calibration (see Figure 2) allow the timing of evolutionary events and continental drift to be compared. A match between the estimated time of origins of regional biota and the time of continental separation is consistent with, but not proof of, vicariance.

Land bridges and sea barriers

Plate tectonics can result in the connection of formerly disjunct land areas and simultaneously the sundering of marine environments, through volcanics, accretion, orogenics, and deformation. Although land bridging has been largely rejected from consideration of ancient biological history of Earth, younger examples show its influence. The Central American (or Panama) isthmus between North America and South America is a narrow strip of land (60–177 m wide) that finally shut off the equatorial link between Atlantic and Pacific oceans (the Central American seaway) in the late Pliocene (about 3 million years ago). Several tectonic plates intersect in the region (Figure 3) and their interaction appears to have led to the formation of numerous volcanic islands starting at about 5.5 mya. Sediment accumulation between these islands is one mechanism proposed for the land bridge.

Closure forced the Gulf Stream to carry warm equatorial water into the northern Atlantic Ocean, where it influences the composition and ecology of regional marine biota. Separation was accompanied by other environmental change; upwelling on the Pacific side see ms to have increased while salinity has increased in the Caribbean. Around Central America,

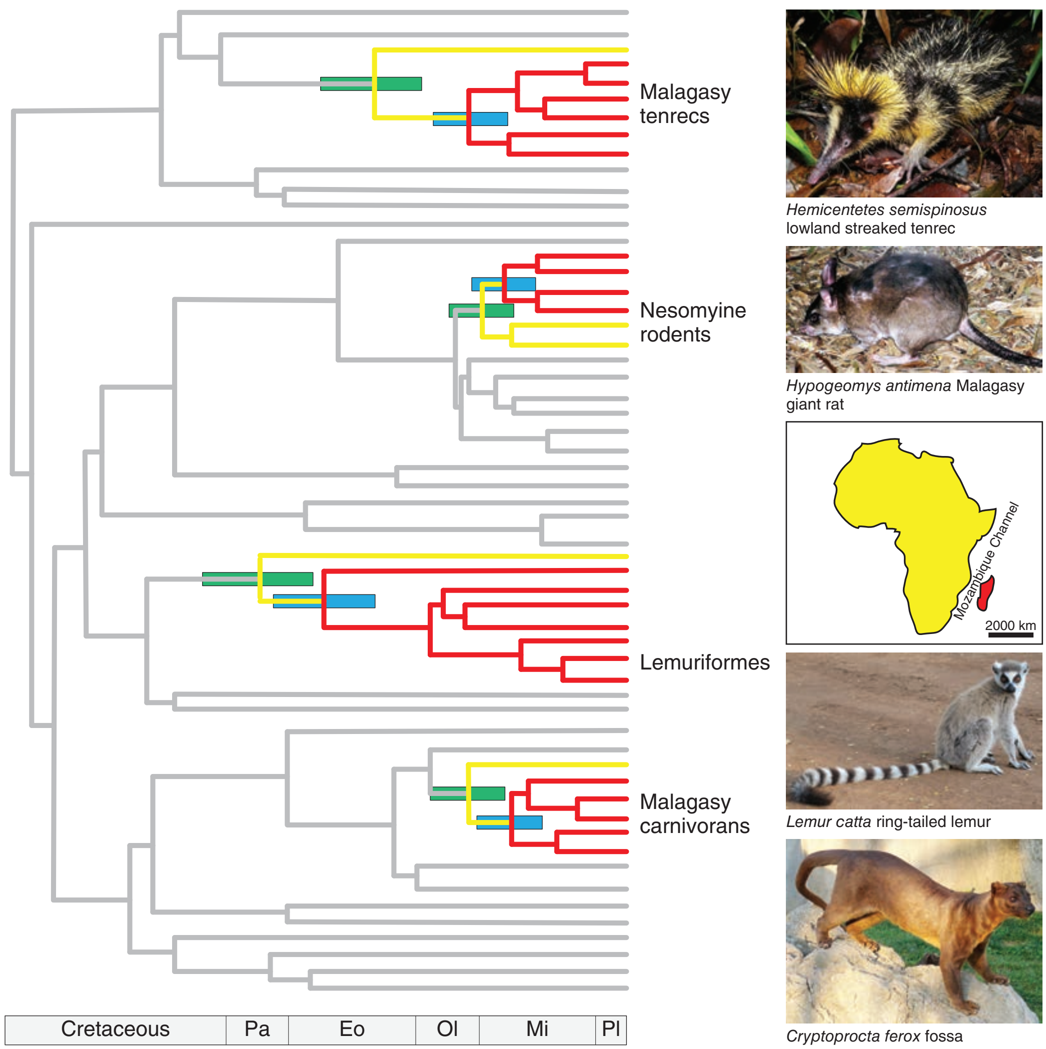


Figure 2 Dated phylogenetic analysis of four Madagascan mammal lineages using multiple nuclear DNA gene sequences and fossil calibrations. Origins and diversification of the Madagascan mammal fauna substantially postdate the pre-Cretaceous plate tectonic separation of Madagascar (red) from Africa (yellow) (≈83 mya). Very different dates for each of the mammal groups suggest no single mechanism for their arrival in Madagascar is supported. Tectonic crustal movements may have resulted in some parts of the Mozambique Channel being raised above sea level in the upper Eocene. Although there is no evidence for a continuous land bridge, islands might have facilitated mammals colonizing Madagascar. However, this speculation is not supported by the current phylogenetic analysis. Red branches lead to Madagascan species, yellow branches to nearest African relatives, grey branches represent outgroup taxa. Green and blue bars at nodes indicate 95% credibility intervals (bounds of uncertainty) for Madagascan stem and crown group, respectively. Tertiary time periods are Paleocene (Pa), Eocene (Eo), Oligocene (Ol), Miocene (Mi), and Pliocene (Pl). Adapted from Poux *et al.* 2005, by permission of Oxford University Press. Animal photographs from WikiCommons.

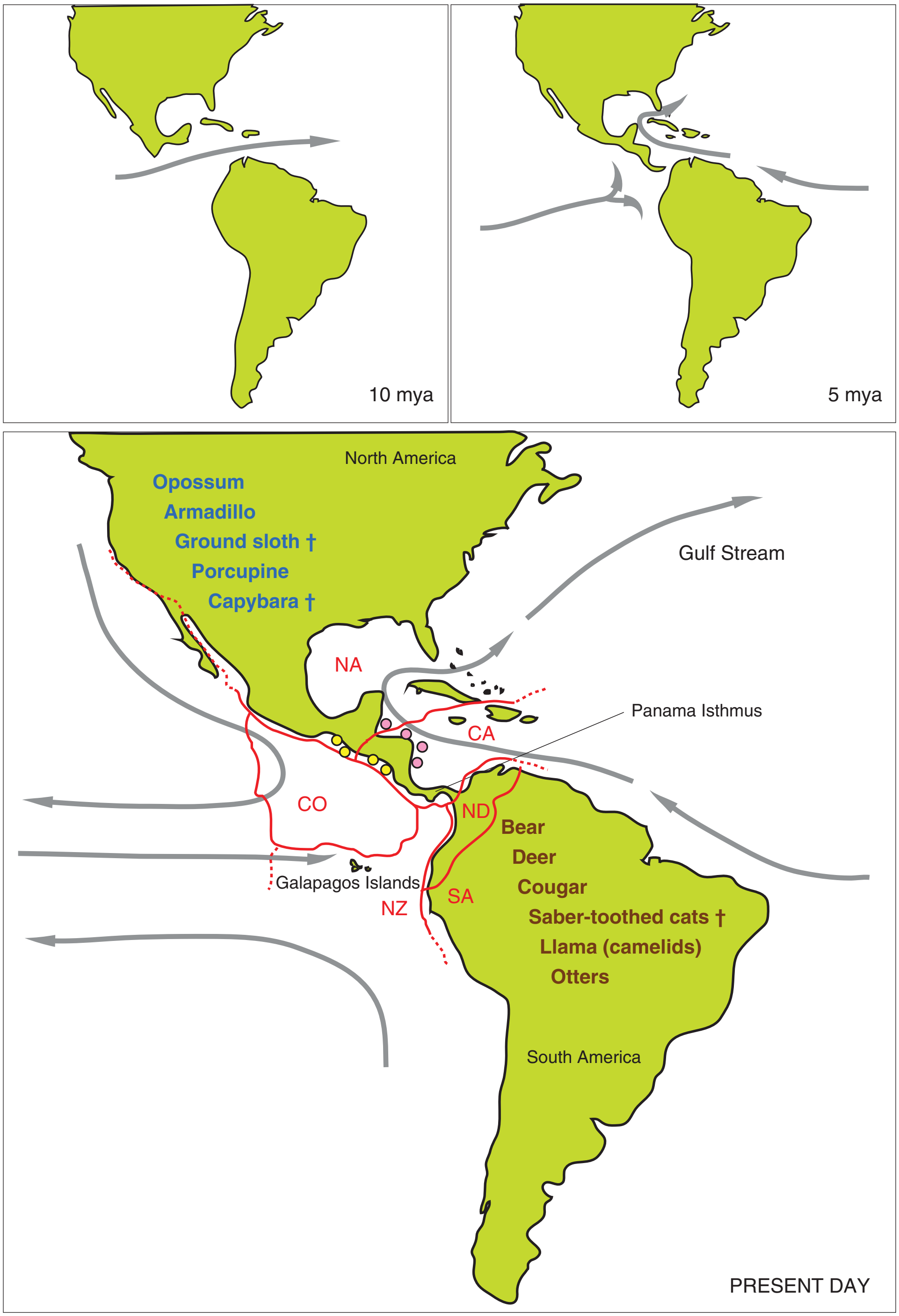
populations of marine creatures (and even seabirds that are reluctant to fly over land) were split between western Atlantic and eastern Pacific communities. On land, the isthmus led to changes in rainfall and climate patterns and facilitated the exchange of land creatures (a.k.a. the Great American Biotic Interchange). Many animals are inferred to have moved between continents and contributed to biotic mixing and thus elevated biodiversity in Central America.

The late Pliocene formation of the Panama Isthmus demonstrates a way that plate tectonics influences biogeography, which is counter to the effects of continental drift vicariance. This geologically, ecologically, and phylogenetically well-studied phenomenon is precisely the type of land bridge proposed by Charles Schuchert and others to explain exchange of biota between continents in past times. Their ideas replaced earlier, simplistic land bridge models that required special, unknown, processes to destroy large parts of continents. Systems similar to the Panama Isthmus might be geologically short-lived and thus hard to detect after the passage of time. Clearly, however, small and short-lived geophysical phenomena can have a profound influence on biogeography.

Intriguingly, while many mammals appear to have walked between continents once the Panama Isthmus formed, molecular and fossil data indicate that habitat connectivity is not essential for exchange. For example, the best explanation for the initial presence in South America of several mammal lineages involves oversea dispersal from Africa. This includes some that were subsequent North American colonists (e.g., porcupine). The marsupials, for instance, are represented by just one species in North America, about 100 in South America, and about 230 in Australia. However, the oldest fossils (65 mya) are from North America. Expansion southwards through South America and Antarctica probably took marsupials to Australia and eventually Borneo and Sulawesi, while the group disappeared from North America. Genetic analysis suggests that all living marsupials have their ancestors in South America. This makes sense because the only living marsupial in North America (opossum) arrived over the Panama Isthmus. Little is known about how these types of animal interacted when they met, and consequently ad hoc interpretations are common. For example, the extinction of placental mammals in Australia is often attributed to the arrival of marsupials, yet the reverse (replacement of marsupials by placentals) is suggested for North America. Very little is known about the marsupial fauna that must have existed in Antarctica, and none of course are there today. Modern species distributions are therefore revealed to be poor indicators, in many cases, of biogeographic history.

Other land bridges have resulted not from tectonic activity but from sea level change. Most recently, during the Pleistocene (<2.6 mya),

Figure 3 The Panama Isthmus formed about 3 million years ago. Ocean currents (grey arrows) were altered. Range extension of various mammals is attributed to land bridging, from south to north (examples in blue) and north to south (examples in brown). Several of these have subsequently become extinct (†). Caribbean (pink spots) and Pacific populations (yellow spots) of marine organisms were separated from one another. Red lines and letters refer to tectonic plates that intersect around the Panama Isthmus (NA, North American; CO, Cocoas; CA, Caribbean; NZ, Nazca; ND, North Andes; SA, South America). To the southwest is the Galapagos archipelago, with its famous biodiversity that stimulated Charles Darwin's ideas about evolution. These volcanic islands grew from beneath the ocean as a result of plate tectonic activity, and the founding biota must have arrived by dispersal over the sea.



10 mya
5 mya
North America
Opossum
Armadillo
Ground sloth †
Porcupine
Capybara †
Gulf Stream
NA
Panama Isthmus
CA
CO
ND
Bear
Deer
Cougar
Saber-toothed cats †
Llama (camelids)
Otters
Galapagos Islands
NZ
SA
South America
PRESENT DAY

Figure 3

lowered sea level resulting from water being locked into polar ice caps created land connection in many parts of the world. Habitable continents were linked as recently as 13 000 years ago through features such as the Bering land bridge between Siberia and Alaska that enabled the migration of many plants and animals, including humans.

Mountains

Linear mountain ranges form when continental plates collide, and it is routinely suggested that the formation of mountain ranges is a likely driver of allopatric speciation in terrestrial ecosystems. Populations sundered by geophysical barriers such as mountain ranges could evolve independently of one another if gene flow between them was sufficiently impeded. Mountain formation provides an appealing scenario for terrestrial vicariance because it generates abrupt environmental discontinuity (similar to land bridges dividing marine environments). Abrupt changes in environmental conditions are expected to influence population density, range sizes, and natural selection, but proven examples of the emergence of mountains causing speciation through vicariance are few. Cases where related species occupy habitat either side of mountains provide the expected distribution patterns but might also have resulted from occupation of habitat patches after mountains formed. They might also be the remnants of species distributions that predate mountain formation.

Mountain building contributes to biogeography in another way. The steep environmental gradients and habitat mosaics that mountain ranges produce appear to have stimulated adaptive radiations in many taxa. Examples include alpine buttercups in New Zealand, paper daisies in South Africa, and Andean hummingbirds in South America. Species that evolve to use alpine conditions in one location may also be successful on other ranges where similar ecological opportunities exist even though these are island-like, and this can result in disjunct distributions that are suggestive of vicariance.

Numerous studies in Europe and elsewhere show that plants and animals responded to Pleistocene climate cycling by range shifting, and this is contrary to the idea that mountains (and other geophysical features) routinely make biological barriers. The distribution across Europe of genetic variation within species and species groups shows that only in some cases do some mountain ranges correspond with species limits. In these cases, of course, the mountains are already present but the climate zones and species move. Distinguishing between mountains (and similar features) as drivers of lineage splitting and their longer-term influence on environmental gradients and ecosystem processes is challenging and exposes a general problem for biogeography. Mountains may come to be correlated with the limits of species and assemblage ranges or they might provide convenient landscape markers for biogeographers, even if they were not the mechanism of population sundering in the first place. Instead of looking for absolute interactions between geology and biology that focus on allopatric processes of lineage splitting, modern biogeography now recognizes the ways gene flow, environmental gradients, environmental fluctuations (e.g., climate change), extinction, sympatry, and uneven selection pressures across species ranges influence biotic composition.

Deep sea hydrothermal vents

Mineral-rich hot water emerges at temperatures of 400 °C or more in submarine conditions where tectonic plates meet. The heat and chemical resources fuel specialized faunas that constitute the only major biological systems that do not draw their energy from the sun. Secondary production from Archaea and chemosynthetic bacteria supports faunas that include giant worms, shrimps, clams, and limpets, at depths of 1–4 km below the sea's surface. The habitat of hydrothermal vent faunas is dictated almost entirely by tectonic processes that result in a patchy distribution around the globe. These islands have histories tens of millions of years long but their biological isolation appears to be influenced by their chemistry and the ecology of their fauna. Gene flow between invertebrate populations living around widely spaced geothermal vents is mediated by planktonic larvae. Plate tectonic activity may be implicated in the origins of life in the ancient seas of Earth as it has been proposed that the thermal, chemical (e.g., acidity), and physical (e.g., high pressure) conditions around hydrothermal vents could have supplied the environment suitable for initial emergence of replicating organic molecules and protocells. There is evidence for hydrothermal vents in the Earth's oceans in the appropriate time frame more than 3 billion years ago.

Volcanoes

Oceanic volcanoes create virgin land that is physically separate from existing, inhabited land areas. Although separated from other pieces of land, islands are not isolated. Island biogeographers recognize that the fauna and flora of islands develops through the interaction of colonization, speciation, and extinction and these components are in some cases quantifiable. There is some evidence that the rate of colonization is influenced by the size and distance of islands from potential biological sources, but increasingly it is apparent that establishment of migrant species is strongly influenced by the composition of the biota that has already arrived.

Classically, Charles Darwin's observations of life on the Galapagos archipelago were instrumental in the founding of evolutionary theory (Figure 3). Volcanic island systems of this sort provide natural laboratories where the effects of colonization, natural selection, and population isolation can be observed. Because volcanic rocks are readily aged using radiometric analysis, maximum ages for the local biota can be determined.

Volcanoes both destroy life and create opportunities, as has been demonstrated on a local, recent scale in systems such as Krakatau in Indonesia. On a much more profound scale, volcanic activity is implicated in one or more ancient global mass extinctions. Extreme volcanic activity associated with the Central Atlantic Magmatic Province is strongly indicated as driving end-Triassic (201 mya) extinctions. Flood basalt eruptions at the end of the Permian (252 mya) are likely to have contributed to extinction via increased atmospheric carbon dioxide, climate warming, and associated ice melt methane production. The end of the Permian was marked by the extinction of about 70% of land animal species and 90% of marine animals. Among the casualties were the formerly widespread Glossopertid plants, the fossils of which were so influential in paleogeography. The Triassic saw the emergence of new ecological strategies in mammal and dinosaur diversification. Ammonites emerged in the oceans, and crocodiles, pterosaurs, frogs, and sphenodonts diversified on land.

Conclusion

On large and small scales, short and long time frames, plate tectonics influences the formation and distribution of biological diversity; however, many of the details of how this happens remain to be thoroughly tested. A traditional focus on spatial effects (vicariance) is gradually being replaced by more in-depth analysis of the way geophysical attributes of the planet influence evolutionary ecology.

SEE ALSO: Biodiversity; Biogeography: history; Mountain biogeography; Ocean biogeography; Zoogeography

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