PLATE TECTONICS AND ANGIOSPERM DISTRIBUTION*

ROBERT F. THORNE**

ABSTRACT. Plate tectonics, which has so revolutionized geology and quite demolished the dogma of permanency of continents and ocean basins, is outlined in much abbreviated form. Continental movements, especially major fragmentations and conjunctions, are examined as possible causes of various kinds of continental disjunctions in the ranges of angiospermous taxa. Such continental displacement must be accepted as one of the principal explanations of major angiosperm disjunctions along with differential extinction within once vast ranges, passage over land- and filter-bridges, and long-distance dispersal, including island- and mountain-hopping. Continental movements as an explanation, however, must not be overworked but kept in proper perspective, especially in view of the largely mid-Cretaceous disengagement of Africa from South America, Madagascar, India, and Australia-Antarctica and the primarily Tertiary appearance in the fossil record of most angiospermous families and genera. Normal dispersal overland remains the prevailing migratory strategy for most terrestrial species, but chance long-range carriage of disseminules of some species over great distances, across oceans, continents, and tropics, and even from the Arctic to the Antarctic, still continues.

INTRODUCTION

The modern theory of plate tectonics has revolutionized the science of geomorphology and has forced the rejection of the long-accepted dogma of the permanency of continents and ocean basins. According to plate tectonics the lithosphere, the strong, cold, and rigid outermost layer of the earth, perhaps 100 km thick, is broken into about a dozen large plates and additional subplates that move over a hotter, weaker, slightly plastic asthenosphere. The plates include oceanic crust primarily of basalt (sima) and often thicker, lighter continents of granitoid rock (sial) "floating" well above the oceanic floor. As the plates move in relation to one another, perhaps driven or pulled by thermal convection currents in the underlying mantle, the firmly-anchored, buoyant continents are rafted passively by the plates much as giant boulders are carried in glacial ice.

Through the welling up of basaltic lava from the mantle, new lithosphere is created between the plates at suboceanic rifts along the oceanic ridges and rises that wind through the ocean basins of the world for some 40,000 km. Just as this sea-floor spreading generates new lithosphere at the plate margins, old lithosphere is consumed where the plates converge and one plate plunges under another and is reabsorbed into the mantle at a subduction zone, often marked by a deep oceanic trench. Thus a truly global conveyor-belt system is in operation. Since oceanic floor, rather than the bulky, buoyant continents, is thus subducted, no oceanic crust is recorded as more than 170 million years old (Pitman 1977) despite the billions of years of age ascribed to the ancient continental cratons. Where ocean floor moves under a stationary continent, a volcanic island arc is formed, as the Indonesian, Philippine, Japanese, or

---

* Based upon a paper prepared for a symposium on "Plate Tectonics, Biotic Distribution, and Diversification", presented at Miami University, Oxford, Ohio, on April 21, 1977.

** Rancho Santa Ana Botanic Garden, Claremont, California 91711, U.S.A.

Aleutian arc of islands. An oceanic plate overridden by a moving continental margin results, on the other hand, in a mountain range like the Andes of South America, the Sierra Nevada of California, or the coastal ranges of British Columbia (Burke & Wilson 1976).

Hot spots on the surface of the earth, representing volcanic plumes rising from deep within the mantle, have considerable importance in plate tectonic theory (Burke & Wilson 1976). They mark the passage of plates, as the plume-produced, successively older Hawaiian and Leeward Islands and Emperor Seamounts, a volcanic trail, from the single Hawaiian hot spot record the speed and direction of movement of the Pacific plate. Similar are the Austral and Tuamotu island chains and their respective seamount chains. Or, as in Africa they can attest to that continent being relatively stationary for the past 30 million years. Concentrations of hot spots, with their basin-and-swell and rift topography, may mark the location of future continental fractures and the opening of new oceans. Just as the Arabian plate has apparently split off relatively recently, in Miocene time, from the African plate, it appears possible that the East African Rift valley system will ultimately lead to the creation of an East African plate (Dietz & Holden 1970).

The various phenomena encompassed by plate tectonics seem to have been operating continuously on the earth for at least two billion years, for continental reassembly is evidenced by aulacogens, ancient sediment-filled rift valleys, and ophiolites, raised fragments of ocean basins, on the present continents (Dewey 1972; Valentine & Moores 1974; Burke & Wilson 1976). The fragmentation of continents, their dispersal over the earth's surface, their reassembly, the creation of vast mountain ranges, the emergence of new and disappearance of old archipelagos, and other cataclysmic changes in the earth's geography and environment thus have been relatively continuous features of the planet for much of its history. They must have played an enormous part in the evolution and distribution of the earth's biota.

The current tectonic cycle that has led to the present configuration of continents and ocean basins about the world began perhaps less than two hundred million years ago with the breakup of Pangaea, the world continent (Wilson 1963; Hurley 1968; Dietz & Holden 1970; Dewey 1972). The dating of the various continental separations and conjunctions, so important to the proper understanding of biotic distribution patterns, has been determined, probably with reasonable accuracy, through various methods of dating, like the development of a time-scale of magnetic reversals (magnetic anomalies) in the oceanic crust created by sea-floor spreading (Heirtzler 1968; Bullard 1969; Pitman 1977), radioactive-dating of rocks, and dating of offshore sediments, continental tillites, and fossiliferous strata.

The plate tectonic events most critical to the biogeographer are summarized briefly here, largely as accepted by Raven & Axelrod (1974), though some of the dates will surely be modified as dating techniques become more refined for all tectonic events. Direct migration over land was last possible between West Gondwanaland, combined Africa and South America, and East Gondwanaland, combined Australasia and Antarctica, about 110 million years ago. Similar land passage terminated about 100 million years ago between Africa and Madagascar and perhaps also India, and between Africa and South America. Direct migration was last possible between Australia and the original land masses of New Zealand and New Caledonia about 80 million years ago; between Africa and Eurasia, prior to the Miocene, about 63 million years ago; across the North Atlantic 49 million years ago; and between Australia and South America across Antarctica about 49 to 39 million years ago. Relatively recent critical dates are the conjunction of India and Asia about 45 million years ago and the re-establishment of broad connections between Africa and Eurasia 17 million years ago; the possibility of direct migration between Asia and Australia across Indonesia and New Guinea about 15 million years ago; and the possibility of migration between South and North America via an uplifted Central America 5·7 million years ago. Similarly important dates marking milestones in the evolution of the Angiospermae, also critical for the plant geographer, are the appearance of the first certain angiospermous fossils (pollen) about 125 million years ago in Barremian time (Brenner 1976; Doyle & Hickey 1976); the overtaking in abundance and diversity of fern spores and gymnosperm pollen by angiosperm pollen by Turonian and Senonian time, 95 to 70 million years ago; and the appearance in the fossil record of extant angiospermous families (13 surely determined) and genera (14) by Maastrichtian time, about 68 to 65 million years ago (Muller 1970). During the Cenozoic the variety of angiospermous taxa in the fossil record became increasingly great despite numerous extinctions of other angiospermous taxa, and by Oligocene time, about 38 million years ago, the fossil pollen floras assumed a very modern aspect (Muller 1970).

Plate tectonic theory as thus outlined in much abbreviated form is now too well established and widely accepted by knowledgeable geologists and geophysicists for biologists to question its general validity. There is still considerable quibbling among the geologists about details, particularly as to the relative positions of the various continents at different times, but these minor arguments will in due course be resolved. Accepting the broad outlines of plate tectonics, biogeographers now must put continental displacement as a possible explanation of major biotic disjunctions into perspective with other widely accepted explanations for such disjunctions. Migration over land- and filter-bridges, differential extinction within once continuous ranges, and long-distance dispersal, including island- or mountain-hopping, must not be abandoned just because we have an exciting, newly validated explanation for range lacunae. It is never wise to discard entire tool chests because one shiny new tool has been obtained. Several biologists already, like the continental-drifters of yore, have become so enamoured of tectonic-plate movement as an explanation of continental disjunctions that they have rather lost touch with the realities of timing and direction of continental displacements, timing of origins of taxa and their dispersal, and the often rapid and distant dissemination of organisms about the world. The currently widely dispersed continents in general attained their present distribution over the planet some fifteen or more million years ago, a very long time indeed for the accomplishment of dispersal among vagile taxa. Edmunds (1975) also has expressed concern about the development of a new dogma of continental drift.

I should like here, therefore, to consider to what extent continental movements may be acceptable as one explanation for some of the major patterns of seed-plant disjunction, as classified and discussed by me earlier and illustrated by generalized distribution maps (Thorne 1973a, 1973b).

When I prepared those discussions, I was still viewing with scepticism the rafting of continents on tectonic plates. I gave inadequate attention, therefore, to the possible extent to which continental displacement might have participated in the production of major disjunctions. In understanding any major break in ranges, it is vitally important to consider the probable age and origin of the taxon, the vagility of its disseminules, the time of disjunction of the continents or continental fragments involved, and the lack of disjunction, including endemism, of comparable taxa of the same areas. Different taxa surely have achieved similar disjunction patterns by different vectors using different routes from different centres of dispersal at different times. Each taxon should, therefore, be studied on its own merits (Thorne 1973a), yet certain explanations are strongly favoured by given distribution patterns.

Raven & Axelrod (1974) have already reviewed for various groups of angiosperms the extent to which continental movements may have affected their present distribution patterns. I disagree with them in many details, especially as to the ancientness of origin of various families and genera and the degree to which continental displacement has been involved in their dispersal. Also I believe their conclusions are in some cases unjustified by the information currently available to us, especially in regard to centres of origin of the angiosperms (Thorne 1977). Dependence on negative evidence, as in the suggested extinction in Africa of groups that may never have been there, is particularly distressing and detracts from the considerable value of their survey. Nonetheless, they have performed an important service, and their review obviates any necessity here to examine the impact of past continental movements on each angiospermous order and family.

EURASIAN-NORTH AMERICAN DISJUNCTIONS

Because so few extant angiospermous genera and families have been recognized in the fossil record (Muller 1970) before Tertiary time, we must concern ourselves largely with geologic events in the Late Cretaceous and Cenozoic. Angiosperm paleobotanists recognize in the Late Cretaceous two large pollen provinces in the northern hemisphere, the Normapolles flora dominant in the present eastern United States and Europe and the Aquilapollenites flora dominant in western North America and eastern Asia (Muller 1970; Wolfe 1975). Both Eurasia and North America were effectively divided in two parts by epicontinental seaways, the Turgai Straits in Asia and Mid-Continent Seaway in North America, thus explaining the isolation of the two pollen floras. Within the Normapolles floral region Wolfe found significant differences between eastern North America and Europe, indicating little floristic interchange at middle and lower latitudes, perhaps because the terrestrial links between the two northern continents (Laurasia) were then only at higher latitudes in a cool climate. The European Plate had begun to separate from the North American Plate in the Late Cretaceous about 81 million years ago (Raven & Axelrod 1974), but the terrestrial links at high latitudes were not severed for mammalian migration until about 49 million years ago (McKenna 1975). The Bering Strait linkage was at a still higher paleolatitude, about 75° N according to Raven & Axelrod (1974).

With the disappearance of the Mid-Continental Seaway about 60 million years ago and the Turgai Straits perhaps 40 million years ago, the distinctions between the Normapolles and Aquilapollenites provinces became blurred in the Paleogene. Wolfe (1975) reported high similarity between the European and western North American boreo-tropical flora with numerous common genera, genera that are clearly Indo-malayan in present distribution. Wolfe found that the Beringian area, though a major floristic link between North America and Eurasia during the Paleogene, was not a major pathway between Asia and North America during the Neogene. Hence, the floristic relationships, at least of the deciduous-leaved ligneous plants of the middle latitudes in later Cenozoic time basically reflect Paleogene patterns (Wolfe 1975).

The well-known seed-plant genera that largely populate the temperate areas of North America and Eurasia thus presumably achieved their wide ranges across the northern hemisphere by normal dispersal mechanisms in the Paleogene over land connections in the Beringian and North Atlantic areas. Some long-distance dispersal may also have taken place into the earlier Neogene, involving island-hopping via the Faeroes-Iceland-Greenland route or perhaps in rare instances by a more southern route involving the Azores and other Atlantic islands. Many (118) of these Circum-North Temperate genera retain their vast Tertiary ranges, 56 of them also being represented in South Temperate areas. Many more, 204 Fragmentary North Temperate genera and 21 families or subfamilies, have been eliminated from most of their former ranges, retaining a severely restricted representation in some (rarely all) of the scattered North Temperate summer-green forests of northeastern Asia, lower Himalayan slopes, Near Eastern-Caspian-Caucasus-Black Sea area, Europe, eastern and western North America, and the Mexican and Central American highlands (Thorne 1973a).

The two or three Amphi-Atlantic Temperate genera of the warmer parts of Europe and North America have probably achieved their disjunct ranges by long-distance dispersal. Six species displaying this distribution pattern are insular, maritime, aquatic, or ruderal in their habitats. The 35 genera, four families or subfamilies, and 18 groups of vicarious species or species-pairs (Stebbins & Day 1967) of the Mediterranean-American disjunction type have received much attention lately (Raven 1971, 1973 and Axelrod 1975 among others). Probably most of the genera, certainly the ligneous ones, are remnants of the old mesic widespread Holarctic Tertiary forests like *Arbutus*, *Cupressus*, *Ephedra*, *Lavatera*, and *Pistachia* that have become adapted to dry climates, as suggested by Wolfe (1975). I agree with him that there is no necessity to postulate a former continuity of arid habitats and Tertiary island-hopping across a narrower Atlantic, as apparently favoured by Axelrod (1975). Some of the herbaceous genera, species, or species-groups or pairs, especially the annuals like the readily dispersible *Oligomeris linifolia* (Vahl) Macbr., *Evax*, *Filago*, *Micropus*, and *Stylocline* may owe their widely disjunct ranges to long-distance dispersal, including island-hopping over the Atlantic, possibly on occasion assisted unwittingly by man. The shrubby Mediterranean-Californian *Styrax officinalis* L. needs more study and explanation. If its now greatly disjunct range is a relic of Paleogene distribution, rather than faulty taxonomy, its mutation rate must be extraordinarily slow, for it appears to have diverged only subspecifically in California and the Mediterranean region.

The Arctic and Boreal Eurasian-North American disjuncts include many species and species-pairs (probably at least 1,000) but relatively few genera (perhaps 67, including *Adoxa* of the monotypic Adoxaceae). These wide-ranging plants of the higher latitudes may have originally attained wide ranges in Tertiary times by normal dispersal over land and survived maximum Pleistocene glaciation in refugia north of or immediately south of the ice sheets. With the retreat of the ice sheets, they obviously have spread rapidly into their present far northern ranges (Thorne 1973a). Many of the Amphi-Atlantic-Arctic and -Boreal disjuncts may have had much more nearly Circum-Arctic or Circum-Boreal ranges before elimination from much of their ranges by glaciation. Some, however, may have migrated from centres on either side of the Atlantic via sea currents, floating ice, birds, or by wind blowing the disseminules over the frozen Polar Sea (Hultén 1963). Late Tertiary or Quaternary terrestrial links over the North Atlantic seem unnecessary to account for these disjuncts and are not indicated by geological evidence. Beringian-Arctic and Beringian-Boreal disjuncts are the reverse of the Amphi-Atlantic disjuncts and probably survived in nunatak areas in eastern Siberia, Alaska-Yukon, or the northern part of the present Bering Sea (Hultén 1937). With greatly lowered sea level during glacial times, they would have had no problem dispersing over the Beringian land-ridge.

AMPHI-PACIFIC TROPICAL DISJUNCTIONS

The 89 genera and 19 families, subfamilies, tribes, or subtribes that are represented only on the Pacific borders of tropical America and tropical Asia, particularly Indo-malesia, can hardly be explained by continental displacement, since the American continents have long been moving westward presumably narrowing the Pacific Ocean. In as much as 25 of the 89 genera have reached the Hawaiian Islands, surely by long-distance dispersal involving much island-hopping, some of these genera may have reached the opposing Pacific shores by similar long-distance, chance dispersal, especially *Batis*, *Calophyllum*, *Perrottetia*, and *Suriana*. However, many of these genera, now basically Indo-malesian in distribution, have been recognized in Tertiary deposits from Alaska. Among them are *Cinnamomum*, *Clethra*, *Illicium*, *Magnolia*, *Meliosma*, *Nelumbo*, *Nyssa*, *Persea*, and *Saurauia* (mostly listed in Wolfe & Leopold, 1967; and Wolfe 1969, 1972, 1975). Along with these were numerous genera now restricted essentially to Indo-malesia, warm-temperate eastern Asia, or both areas, among the more interesting being *Anamirta*, *Barringtonia*, *Cananga*, *Cercidiphyllum*, *Corylopsis*, *Cunninghamia*, *Engelhardtia*, *Eucommia*, *Euodia*, *Euptelea*, *Exbucklandia*, *Fokienia*, *Fortunearia*, *Ginkgo*, *Gironniera*, *Glyptostrobus*, *Kalopanax*, *Kandelia*, *Knema*, *Koelreuteria*, *Limacia*, *Mastixia*, *Melanorrhoea*, *Metasequoia*, *Myristica*, *Ostryopsis*, *Parashorea*, *Phytocrene*, *Platycarya*, *Pterocarya*, *Pycnarrhena*, *Sinowilsonia*, *Stemonurus*, *Tetracentron*, and *Trochodendron* (Wolfe 1972). The genera in these lists, especially the stenothermally tropical genera of Annonaceae, Icacinaceae, Lecythidaceae, Menispermaceae, and Myristicaceae, attest strongly to the tropical or subtropical nature of the Beringian region in Paleogene time and the efficacy of the Beringian land-bridge for the migration of presently Amphi-Pacific tropical disjuncts. Most of these disjuncts represented today in South America presumably reached that continent from

North America since the development of the Central American land-bridge in the Pliocene, though some may have reached the austral continent much earlier by island-hopping through a Central American archipelago. A few like *Fuchsia*, *Nicotiana*, and *Passiflora* may have originated in South America and reached the tropics of the southwestern Pacific by long-distance dispersal; a few like *Bredemeyera* and *Muehlenbeckia* may be of Australasian origin and reached the New World tropics by similar dispersal. It seems unlikely that any tropical genera successfully migrated through cool temperate Antarctica during the Tertiary.

PANTROPICAL DISJUNCTIONS

About 231 genera of seed plants are represented by indigenous species in each major tropical area of the world and another 103 are missing only from the Australasian tropics. Thus a total of 334 genera and 59 angiosperm families are essentially pantropical, though many of these have also some temperate species. Some of these genera undoubtedly passed through the Beringian land-bridge as did many of the Amphi-Pacific Tropical disjuncts just listed. Wolfe (1969, 1972) listed from Alaskan Tertiary deposits such presently circumtropical genera as *Allophyllus*, *Celastrus*, *Clerodendron Cocculus*, *Ilex*, *Sageretia*, *Vitis*, and *Zizyphus*, and such presently widespread tropical Old World genera as *Alangium*, *Firmiana*, and *Macaranga*. More than half, 194, of the pantropical genera have reached oceanic islands in the Pacific Ocean, 56 even to the Hawaiian Islands in the centre of the Pacific Basin, convincing proof that these genera at least achieved part of their vast ranges by long-distance dispersal. Some of these same genera and many of the others with pantropical representation probably owe some of their dispersal to the tectonic convergence of North and South America, Africa and Eurasia, and Australasia and Asia. Some may have crossed an Atlantic Ocean much narrower in the Tertiary than it is today.

AFRICAN-EURASIAN-PACIFIC DISJUNCTIONS

At least 555 genera and 15 families of seed plants have an enormous range including Africa and Eurasia and mostly beyond into Malesia, Australasia, or even into the Pacific Basin. Forty-seven additional genera with similar wide ranges are absent from the African mainland but represented on Madagascar or other Indian Ocean islands. These latter may have once occurred in Africa and become extinct there, may have reached the continent but have been unable to establish themselves there, or perhaps never reached Africa at all. Without an adequate fossil record in mainland Africa, it would be hard to determine which of these possibilities is the more nearly correct explanation. Considering the vagility of plants that reach oceanic islands, like those in the Indian Ocean, I favour the first possibility.

Because more than 600 genera and 15 families of seed plants share this vast distribution pattern from Africa, Madagascar, or the other Indian Ocean islands to Eurasia and mostly beyond into Malesia, Australasia, and the

Pacific Basin, we must seek a more likely explanation than accidental long-distance dispersal. Such dispersal surely accounts for some of the maritime, aquatic, tiny-seeded, or fleshy-fruited taxa on islands via sea and air currents and birds, but the majority of the taxa must have accomplished most of their dispersal by normal short-distance movement overland or by short hops over narrow water barriers such as occur today in Malesia.

According to Raven & Axelrod (1974) geological evidence indicates that Africa was joined to Europe until 63 million years ago in the Early Paleocene via the Iberian Peninsula and possibly was then also broadly connected with Asia through Arabia. Africa and Europe became more widely separated during the next ten million years, then converged to a direct connection again some 17 million years ago. Bornean pollen (Wolfe 1975) contains characteristic northern hemisphere Aquilapollenites and does not include the more characteristic African pollen types, like *Ctenolophon*, until the Neogene. Nor do the Dipterocarpaceae, with boreotropical records in the Paleogene, appear in the African record until the Neogene. The apparently negligible floristic interchange then between the Eurasian and African plates may be due to inhibition of interchange of terrestrial biota by the Tethyan and other epicontinental seaways (Wolfe 1975). Thus this very common type of wide African-Eurasian-Pacific disjunct pattern is probably of Miocene or more recent derivation. Most of the Pacific and Australasian portion of the range must have been attained in the past 15 million years since the Australasian plate converged with the Asiatic plate and allowed direct intermingling of the Asian and Australasian biotas (Raven & Axelrod 1974). Because India is thought to have broken away from Africa and Madagascar some 100 million years ago (Raven & Axelrod 1974) or much earlier (Schuster 1976), it is unlikely that any extant angiospermous genera or perhaps even families had at the beginning of the Late Cretaceous evolved in Gondwanaland to be "ferried" north to mainland Asia, which India is said to have reached by Middle Eocene time (Raven & Axelrod 1974). Schuster (1976) has stressed the importance of the migration northward of the Indian plate and the introduction of Gondwanalandic elements into Laurasia. Possibly this scenario could account for the presence in India of Gondwanalandic hepatics and conifers (Florin 1963), but I have seen no convincing evidence of any impact on the present flowering-plant flora of India or the rest of southeastern Asia by Indian "rafting."

These wide distributions achieved in Neogene times presumably were possible due to a formerly more completely humid North African-Arabian-Iranian-Indian-Malesian-Australasian arc of continental masses and archipelagos (Thorne 1973b). The onset of great aridity in much of the African-western Asian continental portions of this grest land-mass has created enormous gaps in the ranges of many of the African-Eurasian-Pacific taxa, as especially *Ctenolophon*, *Combretodendron*, *Airyantha*, and *Aeginetia*. The frequently cultivated *Myrsine africana* L., a dioecious shrub or small tree, has perhaps the widest range of any woody plant in the Old World, from South Africa and the Azores through Africa and Arabia to the Himalayas, central China, and Taiwan. It has succulent baccate fruits. Usually only the xerophytic taxa have more or less complete ranges across the presently arid lands of North Africa, Arabia, Iran, and Pakistan. A few good examples of these are *Anastatica hierochuntica* L., *Citrullus colocynthis* (L.) Schrad., *Cornulaca monacantha* Del., *Gymnocarpus decander* Forssk., *Lycium shawii* Roem. & Schultes, *Moltkiopsis ciliata* (Forssk.) I. M. Johnst., *Neurada procumbens* L., *Salvia aegyptiaca* L. and the genera *Fagonia* and *Farsetia* (Davis & Hedge 1971; Hedge & Wendelbo 1978).

AMPHI-INDIAN OCEAN DISJUNCTIONS

West Gondwanaland, including Africa and Madagascar, separated from Australia at least 110 million years ago and Madagascar from mainland Africa about 100 million years ago (Raven & Axelrod 1974). It is extremely unlikely, therefore, that any extant angiospermous genera or families had evolved early enough to have had their ranges divided by these events. Certainly the 18 genera restricted to Africa and Australasia and the additional ten represented only in Australasia and Madagascar or the Mascarene or Seychelle Islands are too recent to have been around 110 million years ago. Since 15 of the 28 genera have island representatives other than those on Australia, Tasmania, and Madagascar, long-distance dispersal is the obvious explanation for these disjuncts. A few families, like the Proteaceae, Restionaceae, Rutaceae, and Thymelaeaceae, are very heavily represented in South Africa and Australia, and may have evolved early enough to have crossed a narrower Indian Ocean when the two continents were closer together than they are today. None of these families is represented by common genera on the two continents (Burbidge 1960; Johnson & Briggs 1975), though relatively closely-related genera do link the two continents. A few taxa, like *Adansonia*, may have had formerly an African-Eurasian-Australasian distribution with later exstirpation of representatives in northern Africa through Indo-malesia.

ASIAN-PACIFIC DISJUNCTIONS

At least 460 genera and 4 families have a wide range between Asia and Australasia, the Pacific Islands, or both. Normal dispersal overland and over narrow water gaps can account for the Asian genera that reach Malesia, Australia, and the other close continental islands. Lowered sea levels during Pleistocene glaciations would have eliminated water barriers among most of the islands and between Asia and western Malesia and between New Guinea and Australia. New Caledonia and New Zealand have been rather isolated since their prototype land masses separated from Australia-Antarctica about 80 million years ago (Raven & Axelrod 1972, 1974). Only the conifers and the most primitive angiosperm families (Thorne 1965, 1969) might have been in Australia early enough to have participated in these partitions. All other taxa must have reached the two island groups by long-distance dispersal or evolved on them from taxa that did so.

For the Asian genera that have reached such isolated continental islands as the Solomons and beyond to Tonga, at least limited over-water dispersal was necessary (Thorne 1965, 1969). The oceanic, volcanic islands of the Pacific Basin could only have been reached by disseminules carried by birds or sea or air currents over long distances or by island-hopping when high islands were more numerous in the Pacific as stepping stones (Thorne 1963; Carlquist 1965, 1966, 1967, 1970, 1974).

Oceanic disjunctions

Not really very different from the Asian-Pacific disjuncts are those limited to the islands, including Australia, of the Pacific and Indian Oceans. Having discontinuous distributions between at least two Pacific island groups but not reaching either the Asiatic or American mainlands are 370 genera and 7 families (Thorne 1973a). The explanations offered above for wide-ranging taxa reaching oceanic islands are pertinent to these plants with more limited ranges. Most wide-ranging of these Pacific disjuncts are the 22 genera that reach the Hawaiian or other Polynesian islands from western Malesia or New Guinea, two from Australia to Polynesia, and the 14 disjunct within the Pacific Basin. Van Balgooy (1971) listed 1666 genera as being indigenous on the Pacific islands (those west of Japan, the Bonins, Philippines, New Guinea, and Australia). These include genera that are endemic on one island or one island group.

Some of the Indian Ocean-Eurasian-Pacific and Amphi-Indian Ocean disjuncts discussed above can also be treated here as Pacific-Indian Ocean disjuncts. Twelve genera range from Madagascar and the other Indian Ocean islands to Australasia or beyond: *Arthropodium*, *Astelia*, *Bleekeria*, *Cohnia*, *Cossinia*, *Geniostoma*, *Hibbertia*, *Humea*, *Keraudrenia*, *Pipturus*, *Rulinga*, and *Soulamea*.

The northern Pacific marine genus *Phyllospadix* and two more tropical Pacific-Indian Ocean sea-grasses, *Enhalus* and *Thalassodendron*, also must be considered oceanic disjuncts. Even wider ranging are the sea-grasses found in the Caribbean and Atlantic as well as in the Pacific and Indian Oceans. They are interoceanic disjuncts now separated by the continents. They include *Zostera* of cool waters and *Halodule*, *Halophila*, *Syringodium*, and *Thalassia* of more tropical seas. *Cymodocea* and *Posidonia* are unknown from American coasts but each one has species that ranges from the Atlantic coasts of Iberia or North Africa through the Mediterranean Sea and into Australian waters. Some mangrove genera and other strand plants have similar vast oceanic ranges. No non-maritime species are believed to possess this pattern of disjunction.

At least some of the sea-grasses probably achieved their present disjunct oceanic ranges via the Tethys Sea in Paleogene time before the Mediterranean was closed off from the Red Sea in the Miocene or before the Pliocene elevation of the Central American isthmus blocked the seaway connecting the Atlantic and Pacific oceans between the two American continents. The present distribution of the sea-grasses and various mangrove and strand species seem to favour Den Hartog's suggestion (1970) that the sea-grasses crossed the Atlantic rather than the eastern Pacific. Those sea-grasses found today in the Mediterranean must have arrived there in relatively recent times, for six million years ago the Mediterranean basin was an isolated desert 10,000 feet deep (Hsü 1972).

African-american disjunctions

The most dramatic of all the major disjunctions in the ranges of plant and animal taxa is that between Africa and South America. This disjunction prompted in 1915 the original concept of continental drift (Wegener 1966 edition) and caused numerous controversies about the probable explanation for Amphi-South Atlantic distributions. The African-American disjunction is a very evident and strong one that I have detailed elsewhere (Thorne 1973b). Eighteen families or subfamilies, 10 tribes or subtribes, and 110 genera are limited essentially to Africa and America, the majority of them more heavily represented on the American continents. Careful taxonomic study will show that the representatives of many additional wide-ranging genera and higher categories on these two austral continents will have their closest relatives on either side of the Atlantic.

Since there is no argument about the reality and importance of this disjunction, the real problem is how the disjunction was brought about in taxa of different ranks. The explanations have ranged from a sundered West Gondwanaland to vast land-bridges, sunken continents (as Atlantis), and long-distance dispersal, most biogeographers advocating one explanation to the practical exclusion of all others. Land-bridges, at least in the sense of massive trans-Atlantic isthmuses are as unrealistic as sunken continents and have no basis in geological fact. However, in the sense that taxa might have reached South America or Africa from the northern continents by passage over a Central American, West Indian, Ibero-Moroccan, or Arabian-Somalian isthmus or filter-route, land bridges surely have played a part, presumably with subsequent dispersal from one southern continent to the other. Or possibly a taxon reached South America from North America and Africa from Eurasia with subsequent extinction of the taxon from the two northern continents.

The presently accepted scenario for the sundering of West Gondwanaland and the migration apart of the African and South American plates has been outlined by Raven & Axelrod (1974), and is briefly summarized here. Separation of the two plates apparently commenced about 127 million years ago with the final marine connection between the North and South Atlantic occurring about 100 million years ago. For another ten million years the two continents remained in near contact with only a narrow strait separating the present Gabon from northeastern Brazil. By the end of the Cretaceous, about 65 million years ago, perhaps 800 km separated the two continents at their closest points though they are said to have been linked by numerous volcanic islands. As South America moved away from Africa and converged with North America, it became "equidistant" between the two in early Eocene time about 50 million years ago. Since then, South America has become more isolated from Africa and closer to North America until the establishment of the direct land connection between the two American continents via the elevation of the Central American Isthmus in the Pliocene 5·7 million years ago. The present distance between Africa and South America at the closest points is about 2,500 km.

Accepting this scenario as reasonably accurate (though I have some grave reservations about the distances separating the American continents), we must determine to what degree the sundering and movement apart of Africa and South America can be used to explain the present degree of relationship between the seed-plant floras of the two continents. When in Late Cretaceous or Tertiary time most extant angiospermous taxa evolved becomes critical, as do also the possibilities of their successful migration by long-distance dispersal. Raven & Axelrod (1974) have emphasized the break-up of West

Gondwanaland as the principal explanation for the African-American disjunction because they assume rather early Cretaceous origins for many extant families, and even genera, of angiosperms.

In my discussion earlier of the problem (Thorne 1973a, 1973b), I perhaps overreacted to the excesses of the continental-drifters, who attributed nearly all relationships between Africa and South America to Wegenerian continental drift. I underestimated the rather long period of Late Cretaceous and Paleogene time in which South America is presumed to have remained closer to Africa than to North America. None the less, I still believe that few, if any extant families, and surely no extant genera had evolved in West Gondwanaland before the final sundering of South America from Africa 100 million years ago (see Muller 1970). Possibly certain superorders or orders, like the Annoniflorae, Arecales, Chenopodiales, Cistiflorae, Cornales, Euphorbiales, Geraniales, Liliales, Malvales, Rosales, Santalales, Theales, and Zingiberales or their prototypes, were recognizably differentiated on Gondwanaland early enough to have participated in its break-up. Thus, a few angiospermous relationships at the ordinal level between the two continents may antedate the final split. In general, however, direct migration overland by normal dispersal methods cannot be the explanation for most of the family, tribal, generic and specific trans-Atlantic relationships. Long-distance dispersal began early in the movement apart of the two continents and certainly continues today. I think many of the familial, tribal and generic relationships date from Paleogene time.

The degree of distinctness between African and South American taxa may give a very rough approximation of the time in which successful dispersal was accomplished across the Atlantic Ocean. Thus, the break-up of Gondwanaland may have allowed the proto-Chenopodiales to evolve in isolation into the Aizoaceae and Didiereaceae in Africa and Madagascar and the Basellaceae, Cactaceae, Halophytaceae, Nyctaginaceae, Phytolaccaceae, and Portulacaceae in South America with subsequent dispersal of members of most of these families to other parts of the world, including some later dispersal across the South Atlantic. Families like the Annonaceae, Arecaceae, Araceae, Balanophoraceae, Buxaceae, Canellaceae, Caricaceae, Chrysobalanaceae, Hydnoraceae, Iridaceae, Loasaceae, Loganiaceae, Olacaceae, Strelitziaceae, Turneraceae, and Zingiberaceae; sub-families like the Caesalpinoideae, Herrerioideae, Ixonanthoideae, Microteoideae, Mimosoideae, Napoleonoideae, and Vellozioideae; and tribes like the Coussareae, Cynometreae, Cytineae, Erismeae, Lagenocarpeae, Ocimoideae, Swartzieae, and Tecomeae in very Late Cretaceous, Paleocene, or Eocene time probably were carried over an Atlantic much narrower than the present ocean.

Genera well represented on both sides of the Atlantic may, with some island-hopping, have migrated across the Atlantic in later Paleogene or Neogene time. Among them may have been *Acioa*, *Annona*, *Carapa*, *Carpodiptera*, *Copaifera*, *Guarea*, *Heisteria*, *Hirtella*, *Lippia*, *Mendoncia*, *Ocotea*, *Renealmia*, *Sabicea*, *Savia*, *Swartzia*, *Tapura*, *Tetrorchidium*, *Thamnosma*, *Trymatococcus*, and *Vismia*. The majority of the genera common to Africa and America have greatly unbalanced representation on the two continents with often only one or two species on one side of the Atlantic. These, many species-pairs, and the 108 species (Thorne 1973b) believed to be restricted essentially to Africa and America probably crossed the presently wide

Atlantic in Neogene or Recent times. Because of quite unequal evolutionary rates, the actual history of the African-American disjuncts can never be fully known. Nevertheless, it is more realistic to explain this type of disjunction by a combination of explanations including migration of some taxa into both continents from the north, some retention of higher categories (super-orders or orders) from a Gondwanaland break-up, and much long-distance dispersal across an Atlantic Ocean of increasing width from Late Cretaceous to Recent time.

North American–South American disjunctions

The number of tropical disjuncts between the two American continents is expectedly very large, though as yet uncounted, due to the efficacy of the massive Central American land-bridge connecting North and South America since the Pliocene and the much older Antillean chains of islands connecting Florida with Trinidad and South America, broken today only by relatively narrow water gaps (Thorne 1973a).

According to Raven & Axelrod (1974) during most of the Cretaceous about 3,000 km separated Oaxaca on the southern margin of the North American continent from the Guyana Shield on the northern margin of South America, although in the Late Cretaceous there were large continental islands in the region of present Central America and present Colombia and a chain of volcanic islands linking the two areas. Other volcanic chains may have also linked with island stepping stones the Greater Antilles and the Guyana Shield. If South America was equidistant from Africa and North America in the Early Eocene, 1250 km then must have separated the two American mainlands, which were finally linked 5·7 million years ago. These reputed distances between the Americas seem much exaggerated and unrealistic. Other authors, as Ladd (1976) indicate closer links.

The obviously heavy interchange of biota that has taken place between the two American continents via Central America and the Antilles needs no discussion. However, there are Tertiary relationships between the continents far earlier than the Pliocene link-up that must be explained. The endemic American Sarraceniaceae, for example, are represented in the Guyana Highlands by *Heliamphora*, in California and Oregon by the monotypic *Darlingtonia*, and in the south-eastern, eastern, and boreal parts of North America by *Sarracenia*. This is certainly an old, relict distribution of a rather primitive group of the Theales (Sarraceniineae of DeBuhr 1975). Much data points to the Guyana Shield as being the point of origin of the group. To have reached North America and evolved about nine species in two distinctive genera, the disseminules of the proto-Sarraceniaceae must have been carried over a very long distance, probably in Paleogene time. The Asiatic-American disjunct family Styracaceae must have reached South America early in Tertiary time to have evolved the quite distinct Brazilian *Pamphilia*. Likewise the Laurasian Meliosmaceae must have reached South America early to have produced the endemic *Meliosma* sect. *Lorenzanea* and *Ophiocaryon*. The diverse representation in South America of such Laurasian genera as *Aristolochia*, *Clethra*, *Helianthemum*, *Hedyosmum*, *Magnolia*, *Saurauia*, *Symplocos*, and *Taulauma* seems to require pre-Pliocene dispersal from the north for each genus. In the other direction, South American taxa like the

Caricaceae, Loasaceae, *Philodendron* sect. *Meconostigma*, Phytolaccaceae, Sapotaceae, and Tecophilaeoideae must have reached North America in pre-Pliocene time to have evolved their distinctive North American representatives.

The temperate North American-South American disjunction has received so much attention from various botanists (Bray 1898; Johnston 1940; Raven & Lewis 1959; Constance et al. 1963; Thorne & Lathrop 1970; Moore & Raven 1970; Raven 1971, 1973; Wood 1972; Hunziker et al. 1973; Axelrod 1974; Solbrig 1973; Thorne 1973a; Raven & Axelrod 1974; Porter 1974) that it needs only the briefest mention here. Among the amphitropical American disjuncts are 65 primarily North American genera and 90 more widely ranging North Temperate genera that have jumped over or passed through the tropics. Raven (1963) listed 128 species, species-pairs, or species-groups that have amphitropical American disjunct ranges. Most of these appear to have reached temperate South America by Pleistocene or more recent long-distance dispersal, presumably carried by birds. Another group of largely woody species is disjunct in desert areas of the two continents, and seems to have reached North America from South America also presumably via birds in rather recent times. Most of the amphitropical disjuncts are plants of open communities, grasslands, vernal pools and marshes, or desert scrub. Some genera like *Alnus*, *Berberis*, *Caltha*, *Carex*, *Epilobium*, *Gentianella*, *Hydrangea*, *Juglans*, *Montia*, *Ribes*, *Thalictrum*, *Valeriana*, and *Viburnum* have more nearly continuous montane distribution across the American tropics, and probably have achieved their ranges by short hops along the mountains of the nearly continuous western American cordilleras.

Raven (1963) listed 26 species or species-pairs of seed plants that have a Bipolar distribution, 24 of them Circum-boreal or Circum-Arctic as well. Among the better known genera are *Armeria*, *Empetrum*, *Euphrasia*, *Hippuris*, *Honkenya*, *Koenigia*, *Littorella*, *Phippsia*, and *Primula*. Relatively recent long-distance dispersal from the far north by migratory water- or shore-birds again is indicated for these taxa, since many are not specifically distinct or are barely so from their northern relatives. At least one of the genera, *Euphrasia*, however, has reached Fuegia by a different route. According to Du Rietz (1960) the South American species are much more closely related to the Australasian than they are to the North American species.

TEMPERATE SOUTH AMERICAN–AUSTRALASIAN DISJUNCTIONS

Seven families and 48 genera of seed plants are largely restricted to temperate South America and Australasia, with some straying north along the Andes at one end of the range or through the tropical Old World highlands at the other end to southeastern Asia or even to Hawaii, Madagascar, or mainland Africa. Another 28 more widely distributed genera and 2 families are likewise linked by common or closely related species in the two temperate regions. Among the better known of the first group are the families Araucariaceae, Centrolepidaceae, Coriariaceae, Epacridaceae, Eucryphiaceae, Stylidiaceae, and Winteraceae and the genera *Araucaria*, *Aristotelia*, *Astelia*, *Azorella*, *Celmisia*, *Colobanthus*, *Coriaria*, *Donatia*, *Eucryphia*, *Fuchsia*, *Gaimardia*, *Griselinia*, *Hebe*, *Laurelia*, *Muehlenbeckia*, *Nothofagus*, *Nertera*, *Oreomyrrhis*, *Oreobolus*, *Pernettya*, *Phyllachne*, *Rostkovia*, *Selliera*, *Tetrachondra*, *Uncinia*, *Vittadinia*, and *Weinmannia* (Thorne 1973a).

Although New Zealand and New Caledonia separated from Australia and Antarctica about 80 million years ago (Raven & Axelrod 1972, 1974), Australia did not separate from Antarctica until 49 million years ago with close links through the South Tasman Rise possible for another 10 million years, thus allowing nearly direct migration between Australia and South America via Antarctica until well into the Oligocene. Such migration would probably have been necessary for the larger-seeded plants like *Araucaria*, *Eucryphia*, *Laurelia*, *Nothofagus*, *Gevuina*, *Lomatia*, *Oreocallis*, and *Orites*. Species of many of the other genera have fleshy, bird-dispersed fruit and wide distribution on oceanic islands in the Pacific and Indian Oceans. These genera probably have achieved their disjunctions rather recently and by long-distance dispersal. Among them are *Astelia*, *Coriaria*, *Dacrydium*, *Dianella*, *Fuchsia*, *Gaimardia*, *Griselinia*, *Leptocarpus*, *Nertera*, *Oreobolus*, *Oreomyrrhis*, *Ourisia*, *Pernettya*, *Pseudopanax*, *Rostkovia*, *Selliera*, *Tetrachondra*, *Uncinia*, and *Weinmannia*.

TEMPERATE SOUTH AMERICAN–ASIAN DISJUNCTIONS

Closely related taxa with disjunctions across the entire width of the Pacific Ocean between temperate South America and Asia are as difficult to interpret as they are rare. A few genera of the asteraceous Mutiseae and a pair of bignoniaceous genera were discussed by Stebbins (1940) as displaying this disjunction pattern, also the cichorioid *Hypochoeris* and the family Lardizabalaceae (Thorne 1973a). Although no indigenous species of *Hypochoeris* nor of the Lardizabalaceae are known in North America, I expect that fossils of both taxa will one day be found from North American Tertiary deposits. This rare type of disjunction is probably a relict one closely related to that of the Circum-North Temperate genera also represented in South Temperate areas.

CIRCUM–SOUTH TEMPERATE AND CIRCUM–ANTARCTIC DISJUNCTIONS

Seven families or subfamilies and nine genera are widely represented and largely restricted to the three austral continents, although all the families and some of the genera have tropical representatives and even reach north of the equator. They are the Cunoniaceae, Escallonioideae, Gunneraceae, Luzuriagoideae, Podocarpaceae, Proteaceae, and Restionaceae, *Acaena*, *Carpobrotus*, *Carpha*, *Cotula*, *Gunnera*, *Podocarpus*, *Pratia*, *Wahlenbergia*, and *Tetragonia* (Thorne 1973a). Most of these are dispersed by birds or sea-currents, but at least some members of the Cunoniaceae, Escallonioideae, and Proteaceae are less well-adapted for long-distance dispersal and probably require more nearly complete land connections for normal overland migration, as through a warmer Antarctica when it still linked Australia and South America.

The limited land areas of the sub-Antarctic include the southern tip of South America (Fuegia), the Grahamland peninsula of Antarctica, and such high latitude islands around the Antarctic as are within or near the northern limit of drift ice. Because of their remoteness, constant strong, cold winds, and much permanent ice, these subantarctic lands have but a meagre flora of perhaps 100 species, with about 30 of these with widely disjunct distributions. Among them are *Acaena adscendens* Vahl, *Azorella selago* Hook. f., *Callitriche antarctica* Engelm. ex Hegel, *Myriophyllum elatinoides* Gaud., and *Ranunculus biternatus* Sm. in Rees. Since Pleistocene ice covered most of these subantarctic lands, it is obvious that these species have been widely distributed very recently, presumably by oceanic birds (Falla 1960; Holdgate 1960) mostly from southern South America and New Zealand.

Subcosmopolitan disjunctions

Plant taxa represented on all the continents in tropical to cold climates are here described as subcosmopolitan, no taxon being entirely cosmopolitan on all parts of the earth's surface. Ninety families, best represented by the Poaceae, and at least 125 genera of seed plants are subcosmopolitan in their distributions and disjunctions. Seventy-two of the genera are aquatic or grow in moist places or in maritime or riparian habitats. Another 26 genera include weedy species. The remainder have small seeds or fleshy, bird-dispersed fruits. Among the subcosmopolitan genera are *Callitriche*, *Carex*, *Crassula*, *Cuscuta*, *Drosera*, *Elatine*, *Euphorbia*, *Juncus*, *Lemna*, *Montia*, *Myriophyllum*, *Najas*, *Nymphaea*, *Oxalis*, *Ruppia*, *Senecio*, *Triglochin*, *Typha*, *Utricularia*, *Urtica*, *Vallisneria*, and *Wolffia*. A few aquatic species, like *Ceratophyllum demersum* L., *Brasenia schreberi* J. F. Gmel., *Lemna minor* L., *Najas marina* L., *Phragmites australis* (Cav.) Trin., *Potamogeton pectinatus* L., and *Zannichellia palustris* L. are subcosmopolitan and certainly owe their vast ranges to dispersal by water- and shore-birds (Thorne 1973a).

Anomalous disjunctions

A few taxa have patterns of disjunction, probably mostly relict, that do not exactly fit into any of the major disjunctions discussed above. The taxa most difficult to interpret are the mycophytes or parasites like *Pilostyles* (Thorne 1973a), whose dispersal mechanisms are still largely unknown. I can offer no logical explanation for the widely disjunct distribution of *Pilostyles*, an internal parasite of woody legumes, on all the continents.

Acknowledgments

I am grateful to the many curators who have given me permission to study their specimens in their herbaria for distributional information and to those botanists over the years who have supplied me with examples of disjunct taxa that I might have otherwise overlooked. I also wish to thank my geologist cousin, David Folger, for relevant suggestions.

References

Axelrod, D. I. (1975). Evolution and biogeography of Madrean-Tethyan sclerophyll vegetation. *Ann. Miss. Bot. Gard.* 62:280–334.

Balgooy, M. M. J. van (1971). Plant-geography of the Pacific as based on a census of phanerogam genera. *Blumea* 6, Suppl.: 1–222.

Bray, W. L. (1898). On the relation of the flora of the Lower Sonoran Zone in North America to the flora of the arid zones of Chile and Argentina. *Bot. Gaz.* 26:121–147.

Brenner, G. J. (1976). Middle Cretaceous floral provinces and early migrations of angiosperms. In Beck, C. B. (ed.), *Origin and Early Evolution of Angiosperms* 23–47. Columbia Univ. Press, New York & London.

Bullard, E. (1969). The origin of the oceans. *Sci. Amer.* 221:66–75.

Burbidge, N. T. (1960). The phytogeography of the Australian region. *Austral. J. Bot.* 8:75–212.

Burke, K. C. & Wilson, J. T. (1976). Hot spots on the earth's surface. *Sci. Amer.* 235:46–57.

Carlquist, S. (1965). *Island Life, a Natural History of the Islands of the World.* Natural Hist. Press, Garden City, New York.

——(1966). The biota of long-distance dispersal, I: Principles of dispersal and evolution. *Quart. Rev. Biol.* 41:247–270.

——(1967). The biota of long-distance dispersal, V: Plant dispersal to Pacific islands. *Bull. Torrey Bot. Club* 94:129–162.

——(1970). *Hawaii, A Natural History.* Natural Hist. Press, Garden City, New York.

——(1974). *Island Biology.* Columbia Univ. Press, New York & London.

Constance, L., Heckard, L. R., Chambers, K. L., Ornduff, R., & Raven, P. H. (1963). Amphi-tropical relationships in the herbaceous flora of the Pacific Coast of North and South America: a symposium. *Quart. Rev. Biol.* 38:109–177.

Davis, P. H. & Hedge, I. C. (1971). Floristic links between NW Africa and SW Asia. *Ann. Naturhistor. Mus. Wien* 75:43–57.

DeBuhr, L. E. (1975). Phylogenetic relationships of the Sarraceniaceae. *Taxon* 24:297–306.

Dewey, J. F. (1972). Plate tectonics. *Sci. Amer.* 226:56–68.

Dietz, R. S. & Holden, J. C. (1970). The break-up of Pangaea. *Sci Amer.* 223:30–41.

Doyle, J. A. & Hickey, L. J. (1976). Pollen and leaves from the Mid-Cretaceous Potomac Group and their bearing on early angiosperm evolution. In Beck, C. B. (ed.), *Origin and Early Evolution of Angiosperms* 139–206. Columbia Univ. Press, New York & London.

Du Rietz, G. E. (1960). Remarks on the botany of the southern cold temperate zone. In Pantin, C. F. A. (ed.), A discussion on the biology of the southern cold temperate zone 500–507. *Proc. Roy. Soc.* (*London*) *Ser. B, Biol. Sci.* 152:429–682.

Edmunds, G. E., Jr. (1975). Phylogenetic biogeography of mayflies. *Ann. Miss. Bot. Gard.* 62:251–263.

Falla, R. A. (1960). Oceanic birds as dispersal agents. In Pantin, C. F. A. (ed.), A discussion on the biology of the southern cold temperate zone, 655–659. *Proc. Roy. Soc.* (*London*) *Ser. B, Biol. Sci.* 152:429–682.

FLORIN, R. (1963). The distribution of conifer and taxad genera in time and space. *Acta Hort. Berg.* 20:121–312.

HARTOG, C. DEN. (1970). The sea-grasses of the world. *Verh. Koninklijke Nederl. Akad. Wetenschappen, Afd. Natuurkunde* 59, I:1–275.

HEDGE, I. C. & WENDELBO, P. (1978). Patterns of distribution and endemism in Iran. *Notes R.B.G. Edinb.* 36:441–464.

HEIRTZLER, J. R. (1968). Sea-floor spreading. *Sci. Amer.* 219:60–70.

HOLDGATE, M. W. (1960). Final discussion. In Pantin, C. F. A. (ed.), A discussion on the biology of the southern cold temperate zone 674–675. *Proc. Roy. Soc. (London) Ser. B, Biol. Sci.* 152:429–682.

HSÜ, K. J. (1972). When the Mediterranean dried up. *Sci. Amer.* 227:26–36.

HULTÉN, E. (1937). *Outline of the History of Arctic and Boreal Biota during the Quaternary Period.* Bokforlags Akteibolaget Thyle, Stockholm.

——(1963). Phytogeographical connections of the North Atlantic. In Löve, A. & Löve, D. (eds.), *North Atlantic Biota and Their History* 45–72. Pergamon Press, Oxford.

HUNZIKER, J. H., PALACIOS, R. A., VALESI, A. G. DE, & POGGIO, L. (1973). Species disjunctions in Larrea: evidence from morphology, cytogenetics, phenolic compounds, and seed albumins. *Ann. Miss. Bot. Gard.* 59: 224–233.

HURLEY, P. M. (1968). The confirmation of continental drift. *Sci. Amer.* 218: 52–64.

JOHNSON, L. A. S. & BRIGGS, B. G. (1975). On the Proteaceae—the evolution and classification of a southern family. *Bot. J. Linnean Soc.* 70:83–182.

JOHNSTON, I. M. (1940). The floristic significance of shrubs common to North and South America. *J. Arn. Arbor.* 21:356–363.

LADD, J. W. (1976). Relative motion of South America with respect to North America and caribbean tectonics. *Geol. Soc. Amer. Bull.* 87:969–976.

MCKENNA, M. C. (1975). Fossil mammals and early Eocene North Atlantic land continuity. *Ann. Miss. Bot. Gard.* 62:335–353.

MOORE, D. M. & RAVEN, P. H. (1970). Cytogenetics, distribution, and amphitropical affinities of South American Camissonia (Onagraceae). *Evolution* 24:816–823.

MULLER, J. (1970). Palynological evidence of early differentiation of angiosperms. *Biol. Rev.* 45:417–450.

PITMAN, W. C. (1977). *Paleogeographic relationships of continents during the Paleozoic and Mesozoic.* Oral symposium presentation, Miami Univ., Oxford, Ohio.

PORTER, D. M. (1974). Disjunct distributions in the New World Zygophyllaceae. *Taxon* 23:339–346.

RAVEN, P. H. (1963). Amphitropical relationships in the floras of North and South America. *Quart. Rev. Biol.* 38:151–177.

——(1971). The relationship between 'mediterranean' floras. In Davis, P. H. Harper, P. C. & Hedge, I. C. (eds), *Plant Life of South-west Asia*, 119–134. Bot. Soc., Edinburgh.

——(1973). Plant species disjunctions: a summary. *Ann. Miss. Bot. Gard.* 59:234–246.

RAVEN, P. H. & AXELROD, D. I. (1972). Plate tectonics and Australasian paleobiogeography. *Science* 176:1379–1386.

——& AXELROD, D. I. (1974). Angiosperm biogeography and past continental movements. *Ann. Miss. Bot. Gard.* 61:539–673.

RAVEN, P. H. & LEWIS, H. (1959). The relationship of clarkias from two continents. *Brittonia* 11:193–205.

SCHUSTER, R. M. (1976). Plate tectonics and its bearing on the geographical origin and dispersal of angiosperms. In Beck, C. B. (ed.), *Origin and Early Evolution of Angiosperms*, 48–138. Columbia Univ. Press, New York & London.

SOLBRIG, O. T. (1973). The floristic disjunctions between the "Monte" in Argentina and the "Sonoran Desert" in Mexico and the United States. *Ann. Miss. Bot. Gard.* 59:218–223.

STEBBINS, G. L., JR. (1940). Additional evidence for a holarctic dispersal of flowering plants in the Mesozoic era. *Proc. Sixth Pacific Sci. Congr.* 4:649–660.

STEBBINS, G. L. & DAY, A. (1967). Cytogenetic evidence for long continued stability in the genus Plantago. *Evolution* 21:409:428.

THORNE, R. F. (1963). Biotic distribution patterns in the tropical Pacific. In Gressitt, J. L. (ed.), *Pacific Basin Biogeography* 311–354. Bishop Museum, Honolulu.

——(1965). Floristic relationships of New Caledonia. *Univ. Iowa Studies Natur. Hist.* 20, 7:1–14.

——(1969). Floristic relationships between New Caledonia and the Solomon Islands. *Phil. Trans. Roy. Soc.* (*London*) *B* 255:595–602.

——(1973a). Major disjunctions in the geographic ranges of seed plants. *Quart. Rev. Biol.* 47:365–411 (for Dec. 1972).

——(1973b). Floristic relationships between tropical Africa and tropical America. In Meggers, B. J., Ayensu, E. S., & Duckworth, W. D. (eds.), *Tropical Forest Ecosystems in Africa and South America: a Comparative Review* 27–47. Smithsonian Inst. Press, Washington, D.C.

——(1977). Where and when might the tropical angiospermous flora have originated? *Gard. Bull. Singapore* 29:183–189.

THORNE, R. F. & LATHROP, E. W. (1970). Pilularia americana on the Santa Rosa Plateau, Riverside County, California. *Aliso* 7, 2:149–155.

VALENTINE, J. W. & MOORES, E. M. (1974). Plate tectonics and the history of life in the oceans. *Sci. Amer.* 230:80–89.

WEGENER, A. (1966). *The Origin of Continents and Oceans.* Transl. from 4th revised German Ed. by J. Biram. Dover Publ., New York.

WILSON, J. T. (1963). Continental drift. *Sci. Amer.* April 1963, W. H. Freeman, San Francisco, reprint, pp. 1–16.

WOLFE, J. A. (1969). Neogene floristic and vegetational history of the Pacific Northwest. *Madrono* 20:83–110.

——(1972). An interpretation of Alaskan Tertiary floras. In Graham, A. (ed.), *Floristics and Paleofloristics of Asia and Eastern North America*, 201–233. Elsevier Publ., Amsterdam.

——(1975). Some aspects of plant geography of the Northern Hemisphere during the Late Cretaceous and Tertiary. *Ann. Miss. Bot. Gard.* 62: 264–279.

WOLFE, J. A. & LEOPOLD, E. B. (1967). Neogene and Early Quaternary vegetation of northwestern North America and northeastern Asia. In Hopkins, D. M. (ed.), *The Bering Land Bridge* 193–206. Stanford Univ. Press, Stanford, California.

WOOD, C. E., JR. (1972). Morphology and phytogeography: the classical approach to the study of disjunctions. *Ann. Miss. Bot. Gard.* 59:107–124.