30 June 1972, Volume 176, Number 4042 **SCIENCE**

Plate Tectonics and Australasian Paleobiogeography

The complex biogeographic relations of the region reflect its geologic history.

Peter H. Raven and Daniel I. Axelrod

The biogeographic relationships shown by the plants and animals of Australasia have long fascinated biologists. Because many widely different taxa (such as marsupials and *Nothofagus*) are common to temperate South America and to temperate Australia–Tasmania or New Zealand, some biologists, especially those in the Southern Hemisphere (*1, 2*), have espoused Wegener's (*3*) idea of continental drift to explain the relationships. In contrast, biologists in the Northern Hemisphere have remained largely skeptical (*4*) or have placed changes in the relative positions of land masses so far in the past that they would have had little or no effect on modern distributions (*5*).

During the past 5 years, however, the emergence of the theory of plate tectonics has provided a better understanding of the history of the earth's crust (*6*) and, hence, a more reasonable basis for explaining many problems of biogeography. As lavas form new ocean floor and grow laterally from ridges, the lighter, buoyant continents are rafted to new positions at rates of several centimeters per year through periods (and eras) of geologic time. Fully half the ocean floor is therefore of Cenozoic age, whereas the continents include the oldest rocks. Plate tectonics has subsumed earlier ideas of continental drift and is now generally accepted by geologists.

A reevaluation of the distribution of organisms in the light of plate tectonics is now called for, with a focus on the past positions of the continents and other lands. In this article we review the complex distributional problems in Australasia and the southwestern Pacific (Fig. 1) (*5, 7–9*). Our thesis is that the history of the biota in these widely scattered lands has been determined by (i) the Late Cretaceous position of the Australian plate, (ii) its northward movement during the Tertiary, (iii) the disruption of its eastern flank to form a series of microcontinents and archipelagos (Fig. 2), and (iv) its later Tertiary fusion with the Asian plate, which built island steppingstones to Asia.

Geologic History of Australasia

In the middle Cretaceous, about 100 million years ago, Australia, New Zealand, and Antarctica were united with South America and with India–Madagascar–Africa, all forming a part of Gondwanaland (*10–19*). Australia was then in direct contact with lands now well removed from it—not only Antarctica, India, New Zealand, New Caledonia, Lord Howe Island, and Norfolk Island, but also rises now submerged (Lord Howe Rise, Norfolk Ridge, Queensland Plateau), composed of continental rocks (*17, 20–24*). The New Guinea part of the Australian plate was largely submerged (*15, 25, 26*). The present regional geography of Australasia (Fig. 1) resulted from the breakup and spreading out of a geosynclinal belt of Mesozoic to Paleozoic age on the eastern (Pacific) margin of Gondwanaland. The fragments moved north and east into the Pacific by sea-floor spreading and transcurrent faulting (*17, 20–24*) as the north-moving Australian plate and the west-moving Pacific plate interacted.

The results are arcs spreading east from Australia, separated by basins that are now mostly inactive (*21, 27*). The scattered lands adjacent to the outer arc include New Zealand and Fiji along the "andesite line," marked by the Kermadec–Tonga Trench, which evidently has been a frontal arc since the early Tertiary (*21, 27*). By contrast, the basins of the inner arcs consist of linear ridges and troughs that are probably no older than Pliocene. That they were formed by extensional rifting within an older frontal arc seems probable, for the small, deep basins include younger volcanic archipelagos as well as young sea floor (*21, 27*).

Disruption of the Australian plate probably commenced from a Late Cretaceous (80 million years ago) arrangement like that assembled by Griffiths and a colleague (*17, 28*) (Fig. 2). Sea-floor magnetic records indicate that the Campbell Plateau (including New Zealand) separated from West Antarctica and began moving northwest as the Pacific-Antarctic rise was formed 80 million years ago (*11, 18, 29*). Somewhat later, northward movement of Australia resulted from activation of the Indian-Antarctic rise in the middle Eocene (45 million to 49 million years ago), the last time Australia was linked with South America via Antarctica (*12, 13, 30*). As Australia moved north it entered lower, warmer latitudes. Australia moved about 15° north from the Indian-Antarctic rise, Antarctica about 15° south (*11–13, 15–17, 31, 32*). Reconstructions that

---

Dr. Raven is director of the Missouri Botanical Garden, 2315 Tower Grove Avenue, St. Louis 63110, and professor of biology at Washington University, St. Louis. Dr. Axelrod is professor of geology and of botany at the University of California, Davis 95616.

place Australia 30° south of its present position are in conflict with biological evidence bearing on the position of Antarctica before the commencement of the movement (*33*). Current reconstructions of the positions of continents differ because plate movements are relative, and to indicate them, one area (such as Africa or Antarctica) has to be considered fixed.

By Miocene time, Australia had been rafted to about 10° south of its present position (*14, 15, 32*). The northward movement of New Zealand has been much less, and its isolation has been increased by the foundering of the Campbell Plateau.

These tectonic reconstructions are consistent with geologic evidence. New Zealand (*34*) and New Caledonia (*35*) consist of similar rocks of lower Mesozoic, Paleozoic, and probably greater age (*36*). Fiji is composed of ophiolites (slices of ocean floor, upper mantle rocks, and associated sedimentary rocks) that can be associated with the growth of island arcs. It was uplifted in the Eocene, probably as a result of the collision of the Pacific and Australian plates. However, the Solomon Islands and New Hebrides consist of rocks formed in inner arcs, and are Miocene archipelagos constructed behind the frontal arc system (*12, 27, 37*). The opening up of the Tasman basin, which contains continental rocks in Lord Howe Rise and Norfolk Ridge (*23, 36, 38*), has been related to the separation of Australia and Antarctica in the middle Eocene (45 million to 49 million years ago). A similar age has been postulated for the formation of the New Caledonia, South Fiji, and Coral Sea basins (*24, 27*). Topologically, reversing the movements would close the Tasman Sea and pull back the Campbell Plateau, New Caledonia, Fiji, Lord Howe Rise, and Norfolk Ridge close to the Australian mainland in the Paleocene (*15, 17, 22, 28*) (Fig. 2).

New Guinea, which defines the leading edge of the Australian plate, was largely submerged during its early northward movement (*15, 25, 26*). A period of moderate uplift that began in the late Oligocene and continued through the Miocene resulted from interaction between the Australian and Asian plates (*26, 39, 40*).

At the start of its northward movement 45 million to 49 million years ago, northern Australia, consisting of present northern Queensland and the now submerged Queensland Plateau (*41*), was all well south of the Tropic of Capricorn and mostly south of latitude 28°S, at approximately the present latitude of Brisbane. The emergence of large lowland areas of New Guinea above the sea during the Miocene advanced the land edge of the Australian plate about 10° of latitude, for the first time providing extensive land areas within the tropics (*15*).

Many of the events in the area, including uplift of the mountains of New Guinea (*26, 39, 40*) and Malaysia (*42*) as well as Australia (*43*) and New Zealand (*44*), and the associated submergence of the Queensland Plateau (*41*), occurred in the past few million years. Much of this resulted from collision of the Australian with the Asian plate (*24, 26, 39, 40*).

Manifestly, (i) the northward rafting of the Australian plate and its fragments to new climates, (ii) the isolation of plate fragments by local sea-floor spreading, (iii) the appearance of new volcanic archipelagos and large islands, and (iv) the subsidence or foundering of old plate fragments had profound consequences for the history of life in this region.

Austral Distribution Patterns

Many disjunct distribution patterns in the Southern Hemisphere reflect the geography of the region in the middle Cretaceous, when Africa, South America, and Australia were connected with Antarctica. The temperate parts of this austral landmass supported a mixed forest of austral gymnosperms and evergreen angiosperms, including members of the Podocarpaceae, Araucariaceae, Araliaceae, Myrsinaceae, Proteaceae, Winteraceae, Atherospermataceae (*45*), Lauraceae, Malvaceae, Loranthaceae (*46*), Sapindaceae, Casuarinaceae, and Myrtaceae, as well as *Nothofagus* and *Gunnera* (*47–51*). Associated with the forest were herbaceous and shrubby plants, such as Cruciferae (*49*), Pedaliaceae (*50*), Liliaceae (*49*), Epacridaceae, and possibly Umbelliferae subfamily Hydrocotyloideae; many groups of insects, among them Peloridiidae, Idiostolidae (*52*), Belidae, Plecoptera (*53*) and Carabidae-Migadopinae; other invertebrates, such as Onychophora (*2, 5, 7, 54–56*); and some bryophytes (*57*). The descendants of a number of these groups have become disjunct between South America and Australasia (*58, 59*). Direct overland migration between South America and Australia probably was feasible until approximately 45 million to 49 million years ago (*50, 55, 60*). Consequently, these two regions share more similar plants and animals

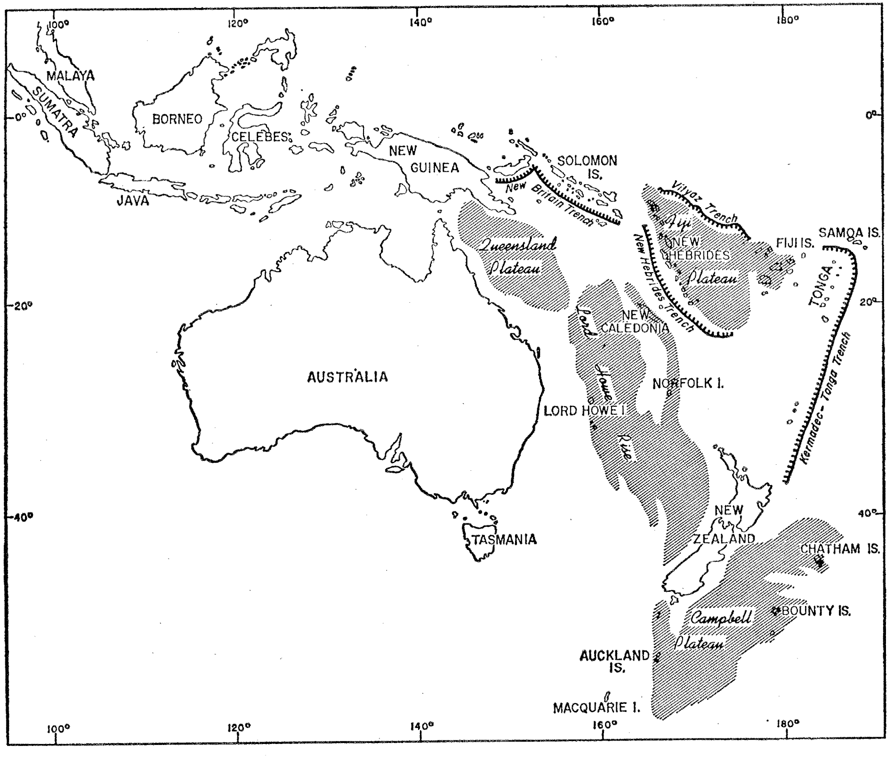

Fig. 1. Present regional geography of Australasia and southern Malaysia.

than do other southern lands, as stressed by Brundin (*61*).

Among the vertebrates, marsupials must have been present in association with this forest (*62*). They first appear in the fossil record in the Albian of North America (more than 100 million years ago) and may have originated there or in South America, where they are first known from the Upper Cretaceous (perhaps 80 million years ago). There was interchange between the landmasses of the Northern and Southern hemispheres during the Cretaceous, and marsupials certainly reached Australia via Antarctica (*63, 64*). Six endemic families had developed in Australia by the late Oligocene (*65*), when the group first appears in the fossil record. Marsupials are, and seem always to have been, absent from New Zealand (*51*), which implies that they reached Antarctica after New Zealand separated from it, about 80 million years ago (*11, 18, 29*).

Hylid frogs evidently originated in South America and had a history similar to that of the marsupials, as suggested by their absence from the Old World tropics and Africa; Ockham's razor rules out Darlington's elaborate alternative hypothesis based on radiation from the Old World tropics (*4*). Leptodactylid frogs (*66, 67*) and chelyid and meiolaniid turtles (*5*) evidently were present on this continuous southern land, but like marsupials, they seem to have reached Australia after New Zealand separated from Antarctica.

Ratite birds appear to have crossed Antarctica to reach their scattered stations in the Southern Hemisphere (*2, 7, 68, 69*). Their presence in Africa and New Zealand suggests that this occurred by the middle Cretaceous, more than 90 million years ago. Ceratodont lungfishes must also have reached Australia from the south during the Mesozoic, contrary to the arguments of Darlington (*5*). Most modern birds (*70*), lizards, and snakes (*4*), on the other hand, attained their present distributions after the lands of the southwestern Pacific reached approximately their present positions, in the late Tertiary and subsequently.

In general, it is the more generalized or primitive representatives of a particular group that display austral distribution patterns, as emphasized by Mackerras (*56*). This implies that in many groups the more advanced forms have evolved or radiated in post-Eocene time.

Austral Biota in Africa

The separation of Africa from South America took place in the early Albian (about 110 million years ago) (*12, 13, 16, 71*), while the separation of Africa from Antarctica seems to have taken place as much as 20 million years later. Even long after these lands had separated, access across narrow seas and via volcanic islands on the midocean ridges continued to be possible. Although Africa is now all north of latitude 35°S, and thus affords much less scope for cool-temperate plants and animals than South America, Australia, or New Zealand, it does have some taxa of austral affinity. These reflect the time when it was joined with Antarctica and was some 15° south of its present position, approximately 90 million years ago.

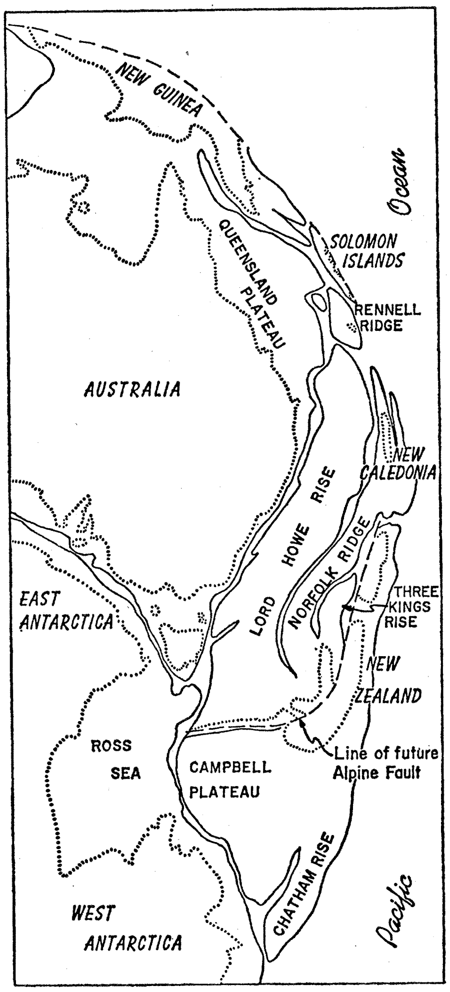

Fig. 2. Reconstruction of Australasia by Griffith and colleague (*17, 28*). A Senonian date (80 million years ago) appears reasonable. Proteaceae and *Nothofagus* were present in Australia, New Zealand, and doubtless New Caledonia at this time (*49, 50, 77*), but mammals do not seem to have arrived until later, since they are absent (except for bats) on the islands east of Australia. Monotremes are apparently of Triassic origin, but it is not known when or how they reached Australia.

The austral gymnosperms *Araucaria* (now extinct in Africa) and *Podocarpus* (*48, 72*), some chironomid midges (*61*), and perhaps ratite birds (*2, 73*) seem to have reached Africa overland from the south. Very few angiosperm distribution patterns are comparable, however, which accords with a Tertiary origin for most genera. Pollen that can definitely be referred to living angiosperm genera is first known from the Senonian (*67, 74, 75*), that is, about 75 million years ago. It is problematic whether any living genera of angiosperms existed when Africa was directly connected by land with South America (110 million years ago) or Antarctica (about 90 million years ago), but some evidently evolved when there was fairly direct communication between these lands. There are numerous transtropical links involving Africa and South America (*71, 76*). Despite intensive searching, *Nothofagus*, which first appears in the fossil record of Australia, New Zealand, and Chile about 75 million years ago (*49, 50, 77*), has not yet been found in Africa (*78, 79*).

On the other hand, a few austral groups of angiosperms do seem to reflect former connections. The pattern of relationship in Proteaceae, best developed in Australia but with three groups in Africa [*Brabeium, Dilobeia,* and 13 of 19 genera of the tribe Proteeae (*80*)], is difficult to explain in any other way. The much closer relationships between the South American–Australian and Asian-Australian proteads than between the African-Australian ones is in accordance with the suggested relationships. Proteaceae first appear in the fossil record with *Nothofagus* in the Senonian, that is, 75 million years ago (*67, 74, 75*), when Africa and Antarctica were still relatively close. Possibly Restionaceae, with a very diverse assemblage of genera in Australia and one very distinct group of genera centering around *Restio* s. str. that radiated extensively in southern Africa (*81*), provide another example. In addition, the families Chloranthaceae and Winteraceae and the genera *Hibbertia* (Dilleniaceae), *Keraudrenia* and *Rulingia* (Sterculiaceae) are disjunct between the Australasian region and Madagascar (*19*), but do not occur on the mainland of Africa, where they may have become extinct. Analogous distributions, differing in detail, are found in *Adansonia*, *Cossignia*, *Cunonia*, Monimiaceae, and Brexiaceae (*82*). Most herbaceous plants disjunct between the two areas [for example, Compositae; but compare (*75, 83*)] probably attained their present distributions as a result of long-distance dispersal during the late Tertiary (*84*).

Relationships with the Northern Hemisphere

The ancestors of some southern plants and animals, like *Nothofagus* (*79, 85*), the marsupials, and hylid frogs, probably passed between the Northern and Southern hemispheres by way of Africa and Europe, since land connections were absent in Middle America (*64, 86*). The relatives of *Nothofagus* are all northern, and the evidence for its presence in the fossil record in Africa is weak (*78, 79*). Such a path is also implied by the existence of pollen of Proteaceae in the Late Cretaceous of North America, South America, and Nigeria; its simultaneous predominance (with *Nothofagus*) in Australia and Antarctica; and its absence in Borneo, where extensive samples have been studied (*67, 74, 75*). The occurrence of such present-day austral plants as *Hibbertia* (Dilleniaceae), *Leucopogon* (Epacridaceae), and Restionaceae in the Paleocene London Clay of southern England (*87*), *Araucaria* in the Mesozoic (*48*) and lower Tertiary (*87*) of Europe, and *Podocarpus* in the Tertiary of Europe (*88*) and North America (*89*) is evidence of Cretaceous links between the two hemispheres. This is not surprising for many plant families that are best developed today in the tropics and subtropics also reach into both the northern and southern mild-temperate regions (for example, Lauraceae, Palmae). The extinction of austral taxa in the north in response to more extreme climates has resulted in their present restriction to the Southern Hemisphere.

Other groups migrated into the Southern Hemisphere by long-distance dispersal across mountains uplifted in Malaysia and New Guinea in the late Pliocene and Pleistocene (*90, 91*); these presumably include *Veronica* (*59, 92*), *Euphrasia* (*75, 93*), *Poa*, *Carex*, the apioid Umbelliferae, and others that account for many bipolar distributions (*94–96*). The rich secondary radiation of species of some of these taxa in the newly formed subalpine and alpine habitats of New Zealand (*95*) has at times led to the unwarranted assumption that they must possess great antiquity in Australasia, although it agrees in rate with other examples of adaptive radiation on islands (*97*). We suggest that all these groups reached New Zealand from Australia by means of the prevailing westerlies in the Pliocene or more recently (*98*).

The post-Eocene northward movement of Australia has been responsible for strengthening the prevailing westerlies (roaring forties, screaming fifties) into a dominant feature of world meteorology (*98*). This change in pattern may be related to the cooling trend in Antarctica that was evident by the late Miocene (*99*). With an ever-increasing thermal gradient between higher and lower latitudes, the winds would increase in velocity, and the opportunities for dispersal of seeds, spores, and small animals between the scattered southern lands would be enhanced (*58, 59*).

Australia

Many groups of archaic angiosperms occur today in the region from Australasia to Assam (*85, 100*). They became associated in this part of the world only in the Miocene, when the north-moving Australian plate collided with the Asian plate. Thus, the region as a whole could not have been an important early seat of evolution. Wallace's line (*4, 101*), which defines the region of mixing of Oriental and Australian plants and animals, came into existence when the plates collided. Many angiosperms crossed this line after the late Miocene [for example, *Drimys, Eucalyptus, Helicia,* Cunoniaceae, Philydraceae, Casuarinaceae (*67, 102*), Magnoliaceae, Dipterocarpaceae, Annonaceae], as have a great number of other plants and animals (*4, 101, 103*).

The northward movement of Australia across at least 15° of latitude in the past 45 million to 49 million years took place during a worldwide trend to decreased temperatures (*49, 104*). This movement into more moderate climates favored the survival of many archaic angiosperms, especially on islands. Although Australasia as a whole has become more accessible to immigration from Malaysia, islands such as New Caledonia and Fiji have become more isolated, and relict biota have survived in their highly equable climates.

The Australian desert and semidesert developed in post-Eocene time as the continent moved into the horse latitudes, the worldwide belt of reduced precipitation at the edge of the tropics. As stressed by Herbert (*105*), the taxa that made up the xeric vegetation of Australia can readily be linked with ancestral forms that occur in more mesic sites marginal to present desert and semidesert areas (*80, 106*). Communities of plants adapted to semiarid conditions may have existed locally along the northern margins of Australia even during Late Cretaceous time, as suggested by the presence of *Adansonia* and the great diversity of the bee family Colletidae (*107*). Pockets of sclerophyll vegetation almost certainly existed on infertile soils at this time and may have formed important source areas during the Tertiary. Descendants of the plants and animals found in these habitats became widespread as aridity achieved a continental scope in the Tertiary. Thus, evolution in response to expanding dry climate accounts for the rich flora and fauna of semiarid and arid Australia (*107*), a phenomenon typical of other dry regions as well.

As Australia continues to move north (*108*), the cool-temperate rain forest in its southeastern corner and in Tasmania will be replaced by subtropical and then by tropical rain forest, aside from the effects of human disturbance. The areas of mediterranean climate in its southwestern and southern parts will become desert, and the thousands of species of plants and animals that typify its mediterranean ecosystem will become extinct. At the same time, the central area of *Acacia* shrublands and low woodlands will change to savanna and then to rain forest, and the present desert area will become more moist and suitable for open, xeric woodlands and savanna.

New Zealand

Much of the present lowland flora of New Zealand (*109, 110*) is similar to that of temperate Gondwanaland 80 million years ago. Relationships with other lands (*110, 111*) reflect the common origin of these lands and New Zealand in the breakup of the Australasian region. New Zealand has been forested throughout most of its history and has been an archipelago since the Late Cretaceous (*51, 112*), at times much smaller than at present. It has always had a highly equable oceanic climate that was maintained at a relatively stable temperature range as the archipelago moved north. In the Cretaceous, New Zealand was joined to West Antarctica (Marie Byrd Land) and fronted the broad Pacific, whereas Australia was joined to East Antarctica (Wilkes Land) and was situated in the lee of Africa-Madagascar-India. Consequently, New Zealand would have had a colder, cloudier, and rainier climate than Australia, even at that time. Hence, the absence of such characteristically Australian plants as *Acacia*, *Eucalyptus*, and *Xanthorrhoea* may be explained partly on ecological grounds (*105*). Moreover, New Zealand has been isolated from Australia-Antarctica for some 80 million years, which helps to explain the distinctiveness of its plants and animals (*61*).

The frog *Leiopelma*, the tuatara (*Sphenodon*), and ratite birds almost certainly reached New Zealand overland when it was joined to West Antarctica (80 million years ago), as did many gymnosperms and ferns and some angiosperms. Biogeographic evidence suggests that mammals had not reached Antarctica by this time, since they are absent from New Zealand (except for bats). Snakes are absent from New Zealand because they evolved in the Late Cretaceous; the geckos and skinks of New Zealand presumably reached it across the sea in Neogene times (*4*). The absence of large Mesozoic terrestrial reptiles in New Zealand (*4*) is presumably related to the scanty record of nonmarine rocks (*51*), since such fossils occur in both Australia and Antarctica (*62*).

As the Campbell Plateau foundered and as New Zealand moved farther away from possible source areas, some taxa became extinct. The Proteaceae, now represented in New Zealand by one species of *Knightia* and *Persoonia*, had a dozen or more taxa in the Paleogene (*113*). *Casuarina* (*51, 114*), *Araucaria* (*48*), *Athrotaxis* (*48*), and many others (*49*) also became extinct in New Zealand during the Tertiary, as did the birds *Malacorhynchus* and *Harpagornia* in the Pleistocene (*115*). The *brassii* group of *Nothofagus*, now confined to New Guinea, New Caledonia, and southern Argentina, disappeared from Australia and Tasmania in the Pliocene and from New Zealand in the Pleistocene (*79, 85*), presumably as a result of the lowered temperatures (*112*).

Such plants as *Rhopalostylis* (a palm), *Phormium* (Liliaceae), and *Coprosma* (Rubiaceae), which first appear in the Paleogene of New Zealand and occur today on Norfolk Island as well, support an Eocene connection between a much enlarged Norfolk Island and New Zealand.

An endemic species of *Araucaria* persists on Norfolk Island, and there is an endemic genus of the archaic, austral hemipteran family Peloridiidae (*Howeria*) on Lord Howe Island, which in general has the more archaic flora and fauna. Numerous taxa must have become extinct as Lord Howe Rise, Norfolk Ridge, and Campbell Plateau foundered in Paleogene and later times. The possibility of migration between New Zealand and New Caledonia was probably reduced by the same processes.

New Zealand has become increasingly isolated during the past 80 million years, but has received immigrants from many sources (*112*), no doubt at a declining rate (*116*). Subtropical climates appeared in northern North Island in the Miocene (*51*), probably as a consequence of its northward component of movement. The newly emerged volcanic archipelagos to the north served as source areas for invading subtropical taxa. The uplift of the mountains and spread of novel subalpine, alpine, and semiarid habitats in the late Pliocene and Pleistocene accommodated new immigrants such as *Dodonaea* (*49*) and *Veronica* (*59, 92*), some of which have radiated extensively (*95*).

New Guinea

The distinctive plants and animals of Australia are mostly derived from temperate ancestors that evolved in response to increasing aridity as Australia moved north. When New Guinea, the leading edge of the Australian plate (*117*), was first elevated to form an extensive land area in the late Oligocene (*15, 25, 26*), it was colonized largely from the adjacent rich tropical lowlands of Malaysia (*7, 118–120*). Biogeographic affinities with Australia are poorly developed, but there has been a spectacular late Tertiary radiation of many groups. Among them are orchids (*121*), ferns, Sapotaceae (*122*), *Ficus* (*123*), *Elaeocarpus* and *Psychotria*, the beetle families Cerambycidae and Chrysomelidae (*124*), and the birds, for which New Guinea has become an important secondary source area (*125*).

As the high mountains of New Guinea were uplifted in the late Pliocene and Pleistocene (*26, 39, 40*), extensive temperate montane areas appeared for the first time. *Nothofagus*, now richly represented there (*111, 126*), first appears in New Guinea in the upper Miocene (*79, 85, 127*), which suggests that the island may have been connected by land with the old, eroded mountains of the Cape York Peninsula and the now-submerged Queensland Plateau when it was first raised above the sea. Land connections between Australia and New Guinea are also suggested by the mid-Pliocene appearance of the marsupials (*65*). Other Australian groups, such as Winteraceae, Proteaceae, *Araucaria*, and the monotremes, colonized New Guinea at various times (*103*). In the lee of the young mountains of New Guinea, an extensive rain shadow developed along the southern coast of Papua in the late Pliocene. Many Australian plants and animals, adapted to semiarid conditions, occur only in this part of New Guinea, which they could not have invaded before this time.

Northern plants and animals likewise reached the young mountains of New Guinea, where *Nothofagus* is associated with *Castanopsis* and *Rhododendron*. The island as a whole is a region of faunal and floral mixing, survival, and evolution in the middle to late Tertiary.

The Solomon Islands and New Hebrides have floras (*8, 9*) and faunas [especially land snails (*119*)] heavily dominated by Indo-Malaysian taxa carried across water barriers, mainly by way of New Guinea (*9, 119, 128*). This is not surprising, for these islands are archipelagos of Miocene age (*37*) and would therefore not be expected to have numerous temperate austral links.

New Caledonia

The flora of New Caledonia is very rich in seed plants that represent archaic taxa. This small island (about 17,000 square kilometers in area) is only one-seventh as large as North Island, New Zealand, yet it has about 40 endemic gymnosperms, several vesselless angiosperms (Winteraceae, *Am-*

borella), and numerous other taxa (including Monimiaceae, Escalloniaceae, Cunoniaceae, Sapindaceae, *Nothofagus*, Araliaceae, Rutaceae, palms) that are relicts (*9*, *129*). In strong contrast, it has a very poor representation of more advanced groups of Tertiary origin (*67*, *74*, *75*), such as Sympetalae in general, which probably reflects its isolation since the Late Cretaceous (perhaps 80 million years ago).

The New Caledonian flora appears to be a surviving, modified sample of the Late Cretaceous flora of eastern Australia. New Caledonia was then near latitude 35°S. The flora was preserved in isolation on serpentine (altered old sea floor) as the island moved north and east to its present position. Its survival was no doubt aided by late Cenozoic uplift (*35*), which provided mild temperatures in upland sites for taxa of basically temperate requirements as the island moved into warmer latitudes.

The archaic, austral land snails (*119*), some of the insects (*120*, *130*), and possibly even galaxiid freshwater fish (*131*) and the endemic bird family Rhynochetidae presumably were derived from ancestors associated with the flora when the island was joined with Australia. The presence of terrestrial giant horned turtles of the family Meiolaniidae in southern South America in the early Tertiary, and in eastern Australia, Lord Howe Island, and on Walpole Island southeast of New Caledonia in the Pleistocene, provides further evidence of former land connections, as noted by Evans (*2*) and contrary to Darlington (*69*). Plants such as *Libocedrus* s. str., *Knightia*, and *Xeronema*, now restricted to New Zealand and New Caledonia, and other indications of biotic communality between these two lands (*9*, *129*) can be related to the geography in Cretaceous and Paleogene time (Fig. 2).

Corner (*123*) has noted the highly endemic character of the fig (*Ficus*) flora of New Caledonia, which is consistent with its continental origin and subsequent rafting into greater isolation. In contrast, the more modern fig floras of New Guinea, the Solomons, and New Hebrides include many closely related species and are clearly derived from the Malaysian region. *Nothofagus* almost certainly has been present in New Caledonia since the Late Cretaceous; there is no biologic or geologic indication that it came via New Guinea in the upper Tertiary.

Fiji

This isolated island group has sometimes been regarded as having a continental flora and fauna, and sometimes an insular one (*120*, *130*). Nearly 23 percent of the 445 indigenous plant genera, including *Dacrydium*, *Acmopyle*, *Agathis*, *Kermadecia* (Proteaceae), *Clematis*, and *Casuarina* div. *Gymnostomae*, and the families Annonaceae, Cunoniaceae, and Epacridaceae, among others, reach their eastern limits in the Pacific in Fiji (*9*, *132*). *Balanops*, the only genus of Balanopaceae and one of very few austral Amentiferae, is confined to Queensland, New Caledonia, and Fiji. Other unusual taxa there include the primitive angiosperm *Degeneria*, as well as some land snakes and frogs. Among the plants of Fiji are many forest trees with large seeds (*132*), and it is unlikely that they or the animals mentioned dispersed over broad water gaps to reach Fiji; zoological evidence has been regarded as equivocal concerning this point (*4*, *120*, *130*).

We prefer to consider that Fiji arose from the sea close to the main Australian landmass and possibly connected with it at this time (Eocene). As it incorporated slices of sea floor (ophiolites) when it moved northeast to its present position, its climate was becoming more tropical. Hence, immigrants from across the water that played a progressively more important role in the flora were of Malaysian (*9*, *132*) and Polynesian (*120*, *130*) character. At the same time, numerous taxa with more temperate or marginally tropical requirements must have become extinct as the land area was rafted into warmer regions.

Summary

Complex tectonic events determined by plate movements had a guiding role in the biotic history of the Australasian region. These movements commenced in the middle Cretaceous, when Australia–Antarctica was still in proximity to Africa, India, and New Zealand, before the disruption of Gondwanaland. Ties between the Australian, Antarctic, and American plates provided routes of migration for southern temperate forests and associated land animals into later Eocene time. As the Australian plate was rafted north, it met the west-moving Pacific plate and underwent fragmentation, resulting in the development of a complex series of basins, plateaus, island arcs, and foredeeps. The isolated lands provided areas for the survival of ancient taxa, some of which occur in distant regions (such as Madagascar and Chile). Many new taxa also evolved over the lowlands as these lands were rafted north to warmer climates. In Australia, the mixed gymnosperm-evergreen dicot forest of Cretaceous to Eocene time was replaced progressively by taxa adapted to mediterranean and desert climates, xeric shrublands and low woodlands, savanna, and tropical forest as the plate moved into lower latitudes. The collision of the Australian with the Asian plate in the Miocene established Wallace's line, and the mixing of Oriental and Australasian taxa commenced. In the late Cenozoic, the elevation of high mountains from Malaysia to New Guinea and Australia–New Zealand provided dispersal routes for numerous herbs from cool-temperate parts of the Holarctic and new sites for their rapid evolution.

References and Notes

1. For example, L. Harrison, *Rep. Meet. Aust. N. Z. Ass. Advan. Sci.* **18**, 332 (1928).
2. J. W. Evans, in *Continental Drift. A Symposium*, S. W. Carey, Ed. (Geology Department, University of Tasmania, Hobart, 1958), p. 134.
3. A. Wegener, *Die Entstehung der Kontinente und Ozeane* (Viewieg, Braunschweig, 1915).
4. P. J. Darlington, Jr., *Zoogeography: The Geographical Distribution of Animals* (Wiley, New York, 1963).
5. ———, *Biogeography of the Southern End of the World* (Harvard Univ. Press, Cambridge, Mass., 1965).
6. A. L. Hammond, *Science* **173**, 40, 133 (1971).
7. R. F. Thorne, in *Pacific Basin Biogeography*, J. L. Gressitt, Ed. (Bishop Museum Press, Honolulu, 1963), p. 311.
8. M. M. J. van Balgooy, *Blumea* **17**, 138 (1969); *ibid.* (Suppl. 6), 1 (1971).
9. ———, *ibid.* **10**, 385 (1960).
10. W. P. Sproll and R. S. Dietz, *Nature* **222**, 345 (1969); E. Irving and W. A. Robertson, *J. Geophys. Res.* **74**, 1026 (1969); D. E. Hayes and W. C. Pitmann III, *Antarct. J.* **5**, 70 (19 → A. G. Smith and A. Hallam, *Nature* **225**, 139 (1970); I. W. D. Dalziel and D. H. Elliott, *ibid.* **233**, 246 (1971); A. Keast, *Quart. Rev. Biol.* **46**, 335 (1971).
11. X. Le Pichon and J. R. Heirtzler, *J. Geophys. Res.* **73**, 2101 (1968).

→ R. S. Dietz and J. C. Holden, *ibid.* **75**, 4939 (1970).

13. D. H. Tarling, *Nature* **229**, 17 (1971).
14. M. W. McElhinny, *ibid.* **228**, 977 (1970).
15. J. G. Jones, *ibid.* **230**, 237 (1971).
16. J. J. Veevers, J. G. Jones, J. A. Talent, *ibid.* **229**, 383 (1971).
17. J. R. Griffiths, *ibid.* **234**, 203 (1971).
18. J. R. Heirtzler, in *Research in the Antarctic*, L. O. Quam, Ed. (AAAS, Washington, D.C., 1971), p. 667.
19. ——— and R. H. Burroughs, *Science* **174**, 488 (1971).
20. W. J. M. van der Linden, *Rec. Proc. 12th Pac. Sci. Congr.* **1**, 390 (1971).

→ D. E. Karig, *J. Geophys. Res.* **75**, 239 (1970).

22. D. J. Cullen, *N. Z. J. Geol. Geophys.* **13**, 7 (1970).
23. G. G. Shor, Jr., H. K. Kirk, H. W. Menard, *J. Geophys. Res.* **76**, 2562 (1971).
24. C. G. Chase, *Geol. Soc. Amer. Bull.* **82**, 3087 (1971).
25. J. E. Thompson, *Aust. Petrol. Explor. J. Assoc.* **7**, 83 (1967); H. L. Davies and I. E. Smith, *Geol. Soc. Amer. Bull.* **82**, 3299

(1971); J. G. Sclater, J. W. Hawkins, Jr., J. Mammerickx, C. G. Chase, *ibid.* **83**, 505 (1972).

26. J. J. Hermes, *Geol. Mijnbouw* **47**, 81 (1968).
27. D. E. Karig, *J. Geophys. Res.* **76**, 2542 (1971).
28. J. R. Griffiths and R. Varne, *Nature Phys. Sci.* **235**, 83 (1972).
29. W. C. Pitman III, E. M. Herron, J. R. Heirtzler, *J. Geophys. Res.* **73**, 2069 (1968).
30. Date of marine transgression: W. A. Berggren, *Nature* **224**, 1072 (1969); B. McGowran, "Paleontology Report 10/71" (Department of Mines, South Australia, unpublished, 1971); see also (*11, 18, 29*).
31. E. Irving, *Paleomagnetism* (Wiley, New York, 1964).
32. This would be in agreement with the calculation of an early Eocene (51.6 million years ago) latitude of 52°S for Canberra [P. Wellman, M. W. McElhinny, I. McDougall, *Geophys. J. Roy. Astron. Soc.* **18**, 371 (1969)].
33. D. I. Axelrod and P. H. Raven, in *Future Directions in the Life Sciences*, J. A. Behnke, Ed. (American Institute of Biological Sciences, Washington, D.C., in press).
34. C. A. Fleming, *Quart. J. Geol. Soc. London* **125**, 125 (1970).
35. A. R. Lillie and R. N. Brothers, *N. Z. J. Geol. Geophys.* **13**, 145 (1970).
36. J. L. Aronson and G. R. Tilton, *Geol. Soc. Amer. Bull.* **82**, 3449 (1971).
37. P. Quantin, *Rec. Proc. 12th Pac. Sci. Congr.* **1**, 5 (1971); B. D. Hackman, *ibid.*, p. 366; D. I. J. Mallick, *ibid.*, p. 368.
38. D. J. Woodward and T. M. Hunt, *N. Z. J. Geol. Geophys.* **14**, 39 (1971).
39. D. B. Dow, *Geol. Mijnbouw* **47**, 37 (1968).
40. T. W. E. David and W. R. Browne, *The Geology of the Commonwealth of Australia* (Arnold, London, 1950), vol. 1, p. 682.
41. M. Ewing, L. V. Hawkins, W. J. Ludwig, *J. Geophys. Res.* **75**, 1953 (1970).
42. For Mt. Kinabal→ B. Collenette, *Proc. Roy. Soc. London Ser. B* **161**, 56 (1964).
43. T. W. E. David and W. R. Browne, *The Geology of the Commonwealth of Australia* (Arnold, London, 1950).
44. R. P. Suggate, *N. Z. Geol. Surv. Bull. 56* (1957); M. Gage, *Trans. Roy. Soc. N. Z.* **88**, 631 (1961); C. Cotton, *Tuatara* **10**, 5 (1962); D. A. Brown, K. S. W. Campbell, K. A. W. Crook, *Geological Evolution of Australia and New Zealand* (Pergamon, New York, 1968), p. 351.
45. R. Schodde, *Taxon* **19**, 324 (1970).

→ B. A. Barlow and D. Wiens, *ibid.* **20**, 291 (1971).

47. L. M. Cranwell, *Nature* **184**, 1782 (1959); D. J. McIntyre and G. J. Wilson, *N. Z. J. Bot.* **4**, 315 (1966).
48. R. Florin, *Acta Horti Bergiani* **20**, 121 (1963).
49. R. A. Couper, *N. Z. Geol. Surv. Paleontol. Bull. 32* (1960).
50. L. M. Cranwell, in *Paleoecology of Africa*, E. M. van Zinderen Bakker, Ed. (Balkema, Cape Town, 1969), p. 1.
51. C. A. Fleming, *Tuatara* **10**, 53 (1962).
52. C. W. Schaefer and D. Wilcox, *Ann. Entomol. Soc. Amer.* **62**, 485 (1969).
53. J. Illies, *Verh. Deut. Zool. Ges. Bonn-Rhein 1960*, 384 (1960).
54. J. L. Gressitt, *Pac. Insects Monogr.* **23**, 295 (1970); E. E. Riek, in *The Insects of Australia* (Melbourne Univ. Press, Melbourne, 1970), p. 168.
55. W. Hennig, *Pac. Insects Monogr.* **9**, 1 (1966).
56. I. M. Mackerras, in *The Insects of Australia* (Melbourne Univ. Press, Melbourne, 1970), p. 187.
57. G. O. K. Sainsbury, *Roy. Soc. N. Z. Bull. 5* (1955); R. M. Schuster, *Taxon* **18**, 46 (1969).
58. Many disjunct distributions between the southern lands were attained more recently. These involve plants with dustlike seeds, floating seeds, or fruits; fleshy fruits eaten by migratory birds; or adherent seeds or fruits. Examples are *Juncus*, *Colobanthus*, orchids, ferns, *Carpobrotus*, *Sophora*, *Tetragonia*; *Astelia*, *Pernettya*, *Fuchsia*, and *Acaena* and *Uncinia*. In the absence of a fossil record, all distributions must be interpreted with caution. W. R. B. Oliver, *Proc. 7th Pac. Sci. Congr.* **5**, 131 (1949); H. N. Barber, H. E. Dadswell, H. D. Ingle, *Nature* **184**, 204 (1959); E. J. Godley, *ibid.* **214**, 74 (1967); W. R. Sykes and E. J. Godley, *ibid.* **218**, 495 (1968).
59. C. A. Fleming, in *Pacific Basin Biogeography*, J. L. Gressitt, Ed. (Bishop Museum Press, Honolulu, 1963), p. 369.
60. Forest vegetation persisted in Antarctica until at least the Oligocene [D. J. MacIntyre and G. J. Wilson, *N. Z. J. Bot.* **4**, 315 (1966); (*50*)]. On other grounds W. Hennig (*55*) has calculated that Australian–South American disjunct groups are at least Oligo-Miocene (26 million years) in age.
61. L. Brundin, *Evolution* **19**, 496 (1965); *Kgl. Sven. Vetensk. Handl.* **11**, 1 (1966); *Annu. Rev. Entomol.* **12**, 149 (1967); in *Antarctic Ecology*, M. W. Holgate, Ed. (Academic Press, New York, 1970), p. 41.
62. Unfortunately, no fossil vertebrates younger than the Triassic amphibians and reptiles discussed by E. H. Colbert [*Quart. Rev. Biol.* **46**, 250 (1971)] have yet been discovered in Antarctica [J. W. Kitching, J. W. Collinson, D. H. Elliot, E. H. Colbert, *Science* **175**, 524 (1972)].
63. R. Hoffstetter, *C. R. H. Acad. Sci. Ser. D* **271**, 388 (1970); C. B. Cox, *Nature* **226**, 767 (1970); W. A. Clemens, *Annu. Rev. Ecol. Syst.* **1**, 357 (1970); R. H. Tedford, *Geol. Soc. Amer. Abstr. Programs* **3**, part 7, 730 (1971); B. H. Slaughter, *J. Linn. Soc. London Zool.* **50**, 131 (1971); N. Jardine and D. McKenzie, *Nature* **235**, 20 (1972).
64. J. Fooden, *Science* **175**, 894 (1972).
65. E. D. Gill, *Trans. N.Y. Acad. Sci.* **28**, 5 (1965); R. A. Stirton, R. H. Tedford, M. O. Woodburne, *Univ. Calif. Publ. Geol. Sci.* **77**, 1 (1968).
66. J. D. Lynch, *Misc. Publ. Univ. Kans. Mus. Nat. Hist.* **53**, 1 (1971). The presence of a leptodactylid frog in the Eocene of India (*4*) is of special interest, because in the Cretaceous, India was part of Gondwanaland. The extinction of these frogs in India presumably occurred as it crossed the hotter equatorial zone. Proteaceae and *Casuarina* have also been reported from the Eocene of India, and other austral plants and animals should be sought (*67*).
67. Y. K. Mathur, *Quart. J. Geol. Mining Met. Soc. India* **38**, 33 (1966).
68. J. Gentili, *Emu* **49**, 85 (1949).
69. P. J. Darlington, Jr., *Quart. Rev. Biol.* **23**, 1 (1948).
70. E. Mayr, *Proc. 6th Pac. Sci. Congr.* **4**, 197 (1939).

→ D. I. Axelrod, *Bot. Rev.* **36**, 277 (1970).

72. J. B. Hair, in *Pacific Basin Biogeography*, J. L. Gressitt, Ed. (Bishop Museum Press, Honolulu, 1963), p. 401.
73. In evaluating the relationship between the ostriches of Africa and the rheas of South America, the close similarity of their external and internal parasites is significant [J. W. Evans (*2*)].

→ J. H. Germeraad, C. A. Hopping, J. Muller, *Rev. Palaeobot. Palynol.* **6**, 189 (1968). *Casuarina* is also known from the Eocene of India, which was then in south temperate latitudes [Y. K. Mathur (*67*)].

→ J. Muller, *Biol. Rev.* **45**, 417 (1970).

76. G. S. Myers, *Copeia* **1966**, 766 (1966); *Stud. Trop. Oceanogr. Inst. Mar. Sci. Univ. Miami* **5**, 614 (1967).
77. E. Dettmann and G. Playford, in *Stratigraphical and Palaeontological Essays in Honour of Dorothy Hill*, K. F. W. Campbell, Ed. (Australian National Univ. Press, Canberra, 1969), p. 174.
78. The report of *Nothofagus* pollen from Nigeria mentioned by S. K. Srivastava [*Bot. Rev.* **33**, 260 (1967)] may be valid; but see (*79*).
79. L. M. Cranwell, in *Pacific Basin Biogeography*, J. L. Gressitt, Ed. (Bishop Museum Press, Honolulu, 1963), p. 387. It cannot have reached the Southern Hemisphere via Malaysia as proposed by C. G. G. J. van Steenis (*85*).
80. L. A. S. Johnson and B. G. Briggs, *Aust. J. Bot.* **11**, 21 (1963).
81. D. F. Cutler, in *Taxonomy, Phytogeography and Evolution*, D. H. Valentine, Ed. (Academic Press, London, in press).
82. J. H. Willis, *Muelleria* **1**, 61 (1956); B. P. G. Hochreutiner, *Ann. Conserv. Jard. Bot. Genève* **11–12**, 136 (1908). One other genus of Cunoniaceae, the monotypic *Platylophus*, is found in South Africa.
83. Compositae are unknown in the fossil record prior to the lower Miocene, despite the fact that they produce abundant, easily recognized pollen [J. Muller (*75*)]. As might have been expected, trans-Antarctic distributions are almost completely absent in this family, which probably arose in the Oligocene [G. L. Stebbins, Jr., *Proc. 6th Pac. Sci. Congr.* **3**, 649 (1940)].
84. Relationships between the biota of Madagascar and New Caledonia [R. Good, *Blumea* **6**, 470 (1950)], like those between the biota of Madagascar and the West Indies [W. T. Stearn, *Bull. Brit. Mus. Nat. Hist. Bot.* **4**, 261 (1971); (4)] came about because of extinction on the adjacent continents. Iguanid lizards, a dominant group in the New World, are represented in the Old World only in Madagascar and Fiji (*4*).
85. C. G. G. J. van Steenis, *Blumea* **19**, 65 (1971).
86. G. L. Freeland and R. S. Dietz, *Nature* **262**, 20 (1971).
87. M. E. J. Chandler, "The Lower Tertiary Floras of Southern England," *Monogr. Brit. Mus. Nat. Hist. Geol.* (Suppl.), part 1 (1961); G. Erdtman, *Bot. Notis.* **113**, 46 (1960).
88. D. K. Ferguson, *Palaeogeogr. Palaeoclimatol. Palaeoecol.* **3**, 73 (1967).
89. D. L. Dilcher, *Science* **164**, 299 (1969).
90. The ancient continuous pathways envisioned by C. G. G. J. van Steenis [*Bull. Bot. Gard. Buitenzorg III* **13**, 139, 389 (1934); *ibid.* **14**, 56 (1936)] and G. E. DuRietz (*91*) are geologically impossible. All of the high mountain flora of Malaysia evolved locally or migrated into the area by long-distance dispersal during the late Pliocene and more recently, after the uplift of the mountains.
91. G. E. DuRietz, *Svensk. Bot. Tidskr.* **25**, 500 (1931); *ibid.* **42**, 99, 348 (1948).
92. Pollen of the entire *Veronica* complex, including *Hebe*, first appears in New Zealand in the Pleistocene, as stressed by C. A. Fleming (*59*) and W. F. Harris [in *The Natural History of Canterbury*, G. A. Knox, Ed. (Reed, Wellington, 1969), p. 334].
93. The austral distribution of this advanced sympetalous hemiparasite cannot be accounted for by postulating that it evolved into its modern form in the Cretaceous, as proposed by G. E. DuRietz (*91*). A Pliocene dispersal from Asia into Australasia, with subsequent dispersal to South America, is more consistent with the available facts. Differentiation of the order Scrophulariales into families seems to have been a Paleogene event [J. Muller (*75*)].
94. G. E. DuRietz, *Acta Phytogeogr. Suecica* **13**, 215 (1940). Many genera have reached the Southern Hemisphere independently in the Old World and the New World (*95*).
95. P. H. Raven, in *Taxonomy, Phytogeography and Evolution*, D. H. Valentine, Ed. (Academic Press, London, in press).
96. Other plant genera that may also have reached the Southern Hemisphere by way of South America in the Upper Cretaceous are *Geum* subg. *Oncostylus*, *Caltha*, and *Acaena*, although in the absence of a fossil record it cannot be determined that any one has been in the Southern Hemisphere so long [D. M. Moore, in *Taxonomy, Phytogeography and Evolution*, D. H. Valentine, Ed. (Academic Press, London, in press)].
97. W. J. Bock, *Evolution* **24**, 704 (1970).
98. The persistence of these winds is demonstrated by the flight of a balloon released from Christchurch, New Zealand, held at about 12 kilometers elevation, and tracked by satellite. It circled the world eight times in 102 days, reaching South America in just over 5 days [J. Mason, *Nature* **233**, 382 (1970); H. H. Lamb, *Quart. J. Roy. Meteorol. Soc.* **85** (No. 363), 1 (1959); R. Tyron, *Biotropica* **2**, 76 (1970)].
99. J. T. Tollin, in *Palaeoecology of Africa*, E. M. van Zinderen Bakker, Ed. (Balkema, Cape Town, 1969), p. 109.
100. A. Takhtajan, *Flowering Plants: Origin and Distribution* (Oliver & Boyd, Edinburg, 1969); A. C. Smith, *Univ. Hawaii Lyon Arbor. Lect. 1* (1970).
101. A. R. Wallace, *J. Linn. Soc. London* **4**, 172 (1860); E. Mayr, *Quart. Rev. Biol.* **19**, 1 (1944); R. Melville, *Nature* **207**, 48 (1965); *ibid.* **211**, 116 (1966); J. W. Dawson, *Tuatara* **18**, 94 (1970).
102. Of the two divisions of *Casuarina*, the more primitive *Gymnostomae* include 19 species ranging from the Philippines and Sumatra to Fiji, New Caledonia, and northern

Queensland; they are also known from the Miocene of Argentina [J. Frenguelli, *Notas La Plata Univ. Nac. Mus. Paleontol.* **8**, 349 (1943)]. The *Cryptostomae*, with 45 species, are primarily Australian but a few species have also crossed Wallace's line. Pollen of *Casuarina* is known from the Eocene of India, which was then in south temperate latitudes [Y. K. Mathur (*67*); L. A. S. Johnson, personal communication].

103. Such gymnosperms as *Agathis, Phyllocladus*, and *Dacrydium* presumably entered New Guinea in the upper Oligocene or Miocene and subsequently crossed Wallace's line.
104. C. A. Fleming (*51*); W. K. Harris, *Palaeontogr. Abt. B* **115**, 75 (1965); F. H. Dorman, *J. Geol.* **74**, 49 (1966); M. Schwarzbach, *Tuatara* **16**, 38 (1968); D. R. McQueen, D. C. Mildenhall, C. J. E. Bell, *ibid.*, p. 49; and V. Scheibnerová, *Rec. Geol. Surv. N. S. W.* **13**, 1 (1971) have shown that during the Cretaceous and Tertiary the temperature curves in Australia and New Zealand first rose and then fell much more gradually than those in North America and Europe. This reflects first the northward movement of the Australian plate to lower, warmer latitudes, and second the decline in temperature following the middle Miocene.
105. D. A. Herbert, *Victorian Natur.* **66**, 227 (1950).
106. E. C. Andrews, *Proc. Linn. Soc. N. S. W.* **38**, 529 (1913); E. C. Andrews, *J. Roy. Soc. N. S. W.* **48**, 333 (1914).
107. C. A. Gardner, *J. Roy. Soc. West. Aust.* **28**, x (1944); S. Smith-White, *Cold Spring Harbor Symp. Quant. Biol.* **24**, 278 (1959); N. T. Burbidge, *Aust. J. Bot.* **8**, 75 (1960); C. D. Michener, *Bull. Amer. Mus. Nat. Hist.* **130**, 1 (1965); B. A. Barlow, *Aust. J. Bot.* **19**, 295 (1971).
108. R. S. Dietz and J. C. Holden, *Sci. Amer.* **223**, 30 (Oct. 1970).
109. J. W. Dawson and B. V. Sneddon, *Pac. Sci.* **23**, 131 (1969).
110. J. W. Dawson, *Tuatara* **11**, 178 (1963).
111. R. G. Robbins [*ibid.* **8**, 121 (1961)] stresses the relationship between the lowland rain forest of New Zealand and the montane (not lowland) rain forest of New Guinea. J. W. Dawson (*110*) discusses relationships with New Caledonia.
112. P. Wardle, *N. Z. J. Bot.* **1**, 3 (1963).
113. L. Cranwell, cited by C. G. G. J. van Steenis [*Blumea* **11**, 294 (1962)].
114. If we accept the identification of *Triorites harrisii* Coup. as *Casuarina* [C. A. Fleming (*51*)], this genus appeared in New Zealand in the uppermost Cretaceous and became extinct with the onset of Pleistocene glaciation. Pollen of *Casuarina* is still blown from Australia to New Zealand, however, and there must be some uncertainty about the ancient records [N. T. Moar, *N. Z. J. Bot.* **7**, 424 (1969)].
115. R. A. Falla, *Emu* **53**, 36 (1953).
116. R. M. McDowall, *Tuatara* **17**, 1 (1969); R. H. MacArthur and E. O. Wilson, *Monogr. Pop. Biol. 1* (1967); E. O. Wilson and D. S. Simberloff, *Ecology* **50**, 267 (196 D. S. Simberloff and E. O. Wilson, *ibid.*, p. 278; D. S. Simberloff, *ibid.*, p. 296.
117. This is contrary to the arguments of R. Good [*Aust. J. Sci.* **20**, 41 (1957); in *Pacific Basin Biogeography*, J. L. Gressitt, Ed. (Bishop Museum Press, Honolulu, 1963), p. 301].
118. H. J. Lam, *Blumea* **1**, 113 (1934).
119. A. Solem, *Nature* **181**, 1253 (1958).

1 J. L. Gressitt, *Syst. Zool.* **5**, 11 (1956).

121. R. Good, *Bull. Brit. Mus. Nat. Hist. Bot.* **2**, 205 (1960); *The Geography of Flowering Plants* (Longmans, Green, London, ed. 3, 1964).
122. H. J. Lam, *Proc. 6th Pac. Sci. Congr.* **4**, 673 (1939).
123. E. J. H. Corner, in *Pacific Basin Biogeography*, J. L. Gressitt, Ed. (Bishop Museum Press, Honolulu, 1963), p. 2 *Phil. Trans. Roy. Soc. London Ser. B* **255**, 567 (1969).
124. J. L. Gressitt, *Proc. 10th Int. Congr. Entomol.* **1**, 767 (1958); *Pac. Insects Monogr.* **2**, 1 (1961).
125. E. Mayr, *Proc. 7th Pac. Sci. Congr.* **4**, 11 (1953).
126. C. G. G. J. van Steenis, *J. Arnold Arboretum Harvard Univ.* **34**, 301 (1953).
127. Upper Pliocene records: I. C. Cookson and K. M. Pike, *Aust. J. Bot.* **3**, 197 (19 R. A. Couper, *Proc. Roy. Soc. London Ser. B* **152**, 491 (1960); L. M. Cranwell (*79*). The late Miocene record was reported by C. G. G. J. van Steenis (*85*).

1 R. F. Thorne, *Phil. Trans. Roy. Soc. Ser. B* **255**, 595 (1969).

129. R. F. Thorne, *Univ. Iowa Stud. Nat. Hist.* **20**, 1 (1965).
130. J. L. Gressitt, *Pac. Insects Monogr.* **2**, 1 (1961).
131. G. S. Myers, *Proc. 7th Pac. Sci. Congr.* **4**, 38 (1953).
132. A. C. Smith, *J. Arnold Arboretum Harvard Univ.* **36**, 273 (1955).

133. We are most grateful to B. G. Briggs, L. Brundin, J. C. Crowell, J. W. Dawson, R. S. Dietz, C. A. Fleming, J. L. Gressitt, J. C. Holden, L. A. S. Johnson, D. E. Karig, J. A. Lillegraven, A. R. H. Martin, H. A. Martin, B. McGowran, C. D. Michener, N. Moar, J. Muller, A. Ritchie, J. Sauer, V. Scheibnerová, A. G. Smith, W. R. Sykes, D. Taylor, R. H. Tedford, J. W. Walker, J. W. Warren, and G. Watson for useful discussions of some of the points considered in this article. This work has been supported by National Science Foundation grants to both authors. See also *Geotimes*, May 1972, p. 14, which appeared while this article was in press.

The Tornado Threat: Coping Styles of the North and South

Tornado death rates in Illinois and Alabama may be related to the psychology of their residents.

John H. Sims and Duane D. Baumann

Fortunately for the majority of Americans, their most vivid image of a tornado derives from their memory of the dark twister weaving across the plains of Kansas in the film *The Wizard of Oz*. But unfortunately for those living in certain areas of the North and South, the awesome force of the tornado is a very real presence (*1*). In these locations, the announcement of the tornado watch or the tornado warning are familiar spring messages (*2*). The kind of response made to these messages may determine the extent of physical injury an individual suffers or, indeed, whether he lives or dies. This article is concerned with the differences in human response to the threat of tornadoes and with the psychology affecting the nature of those differences, in order to attempt an explanation of a puzzling phenomenon—the disproportionately higher frequency of tornado-caused deaths in the South.

We begin with this fact: the number of tornado-caused deaths in the South is strikingly higher than it is in the remainder of the nation. This is best documented by Linehan (*3, 4*): "Compared with all others, Region I [the South] is characterized in superlatives. In every tornado-death attribute selected, Region I outranks each of the other three, usually by a very wide margin. . . . Region I has nearly 12 deaths per 1000 square miles, more than three times the comparable figure for the next ranking region; its 23 deaths per 100,000 inhabitants is over five times greater." What makes this phenomenon perplexing is the difficulty encountered in explaining it. The most ready explanation for this concentration of deaths is that the South experiences more tornadoes or has a higher population density, or both. In effect, it is suggested that the highest potential for casualties is in the South.

Yet when Sadowski's geographic distribution of casualty potentials is compared to the geographic distribution of actual tornado deaths, the two patterns fail to coincide (*5*). On the contrary, whereas the highest incidence of tornado-death days (*6*) is in the South (Fig. 1), the casualty potential from tornadoes is found to be highest in a zone running from Dallas, through

Dr. Sims is assistant professor of psychiatry and research associate, Committee on Human Development, University of Chicago, Chicago, Illinois 60637. Dr. Baumann is associate professor of geography, Southern Illinois University, Carbondale 62901.