Bothalia 14, 3 & 4: 325–328 (1983)

The migration and evolution of floras in the southern hemisphere

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ABSTRACT

As modern groups of angiosperms have appeared over a period of more than 80 million years, the relative position of the southern continents has changed. For the first 20 m.y. of this period, opportunities for migration were good between Africa and Europe, and this constituted the main pathway for migration between the northern and southern hemispheres. South America progressively moved away from Africa and towards North America over the past 90 m.y. Southern South America and Australasia shared a rich, warm temperate rainforest flora until about 40 m.y. ago. The development of modern climates during the past 10 m.y. has set up modern patterns of vegetation.

RÉSUMÉ

LA MIGRATION ET L'ÉVOLUTION DES FLORES DE L'HÉMISPHERE AUSTRAL

Alors que les groupes modernes d'angiospermes sont apparus au cours d'une période de plus de 80 millions d'années, la position relative des continents du Sud a changé. Durant les premiers 20 millions d'années de cette période, les occasions de migration entre l'Afrique et l'Europe furent favorables et ceci constitua la voie principale de la migration entre les hémisphères sud et nord. L'Amérique du Sud s'écarta progressivement de l'Afrique en direction de l'Amérique du Nord au cours des 90 derniers millions d'années. L'Amérique du Sud et l'Australasie partagèrènt une flore forestière riche et tempérée chaude jusqu'à il y a 40 millions d'années. Le développement des climats modernes pendant les derniers 10 millions d'années a mis en place des types de végétation modernes.

The patterns of migration and evolution of floras in the southern hemisphere have occupied the attention of botanists and geographers for well over a century, ever since the principal patterns became evident following the intensive exploration of the far-flung southern lands during the mid-19th century and subsequently. It will be the purpose of this brief review to set the stage for the papers that follow by providing an overview of (1) the past positions and movements of the relevant continents and islands; (2) the history of the angiosperms; and (3) the evolution of vegetation types in the southern lands. We shall concern ourselves with the last 135 m.y. of earth history, the period during which the angiosperms appeared in the fossil record and later assumed worldwide dominance. The first six papers listed in the references are basic to this entire paper and will not be repeated.

West Gondwanaland, consisting of Africa and South America, began to split apart in the South Atlantic about 125–130 m.y. BP with the last direct land connection being severed about 90 m.y. BP. Even subsequently, 88–86 m.y. BP, the Rio Grande-Walvis ridges would have formed an almost continuous overland series of stepping stones across the South Atlantic at about 30°S lat, with the Brazil-Angola Basin isolated to the north and the Cape-Argentine Basin to the south (Kennedy & Cooper, 1975, Van der Linden, 1980 and Reyment, 1980). Bonati & Chermak (1981), basing their conclusions on recent deep sea drilling results, discuss the probable role of shallow or emergent crust in the South Atlantic even into the early Cenozoic (less than 65 m.y. ago), which they believe may have formed chains of islands or intermittent land bridges over which migration of plants and animals could have taken place. Thus dispersal was more direct between Africa and South America than between North and South America until about 45 m.y. BP. South America gradually converged on North America during the past 90 m.y., with the ultimate elevation of the Isthmus of Panama 3,1–3,6 m.y. BP connecting them by land for the first time (Marshall *et al.*, 1979).

At the start of the Cretaceous, 135 m.y. BP, East Gondwanaland consisted of India, Australia and its bordering lands, and Antarctica, with direct overland migration possible to West Gondwanaland *via* both Antarctica and India-Madagascar. From about 135 to about 80 m.y. BP, India separated slowly from this landmass, providing a fairly direct but interrupted dispersal route across the Indian Ocean between Africa and Australia throughout this period. Starting about 80 m.y. BP, India commenced rapid northward movement until its collision with Asia about 53 m.y. BP; its subsequent movement northward has thrust up the Himalayas and the Tibetan Plateau.

Antarctica has been in its present polar position for at least 90–100 m.y., possibly with some rotational movement. The Tasman Sea between New Caledonia-New Zealand and Australia-Antarctica formed in the period 82–60 m.y. BP, with a considerable amount of land elevated between New Caledonia and Queensland, as well as between New Caledonia and New Zealand, until the end of this period. Australia began to separate from Antarctica and move northward about 53 m.y. BP, with more or less direct migration through the Tasmanian area *via* the South Tasman Rise between Australia and Antarctica possible until about 38 m.y. BP. There is no evidence that any part of Southeast Asia or Indonesia was a part of Gondwanaland and moved northward at any time since the start of the Cretaceous (Hamilton, 1979). As Australia commenced its northward movement, all of New Guinea and much of northern Australia

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were subsea, so that the northernmost land on the Australian plate was at about 38°S lat, approximately the present latitude of Melbourne.

New Guinea began to appear above the sea for the first time about 40 m.y. BP, and at that time was at about 15°S lat, near the present latitude of Cairns. It moved steadily northward with the Australian plate, coming into contact with the proto-Indonesian island arc and coalescing into an extensive land area about 15–20 m.y. BP (Axelrod & Raven, 1982). Therefore, at the start of the northward movement of the Australian plate, its northernmost land was separated from the island arc at the south edge of tropical Asia by about 3 000 km of largely open water. For comparison, the present gap between Africa and South America is about 2 500 km. By 15 m.y. BP, New Guinea constituted an extensive land area immediately adjacent to lands occupied by the rich and diverse biota of Southeast Asia, a relationship that readily accounts for the predominantly Asian nature of its plants and animals.

For the past 40 m.y. or so, South America has been converging on North America, with ever-increasing opportunities for dispersal between them. Connections between Antarctica and southern South America *via* West Antarctica, an archipelago of closely spaced islands, seem to have been quite direct until about 28 m.y. BP (Tarling, 1980), but the last opportunity for more or less direct migration overland between South America and Australia *via* Antarctica was lost at least 10 m.y. earlier, as reviewed above.

From the start of the period being considered here, 135 m.y. BP, until about 50 m.y. BP, a gap of about 3 000 km, as mentioned above, separated the nearest land areas in Australasia from those in Asia. During the same period of time, a gap that was initially as large between South America and North America closed to about half that distance. Meanwhile, Africa, during the interval 148–80 m.y. BP, converged some 2 800 km toward Europe, with continuing compression until about 63 m.y. BP, resulting in the formation of the Alpine system. For about the next 10 m.y., Africa moved away from Europe. These relationships indicate unequivocally that during the first half of angiosperm history, the only relatively direct connections between the northern and southern hemispheres were those involving Europe and Africa. From about 53 m.y. BP until about 18 m.y. BP, when connections were re-established, Africa again converged on Europe, with increasingly great opportunities for dispersal of plants and animals between them.

Before discussing the relevance of these continental movements for the distribution of angiosperms, it is first necessary to review the history of the group in broad outline. The following comments will depend heavily upon the outstandingly useful review by Muller (1981) of fossil pollen records of extant angiosperms, as well as on the references mentioned above. Angiosperms first appear in the fossil record of southern Eurasia and North America and that of northern Africa and South America about 120 m.y. BP, with the sort of tricolpate pollen that is characteristic of most dicotyledonous plants appearing throughout the same area about 10–15 m.y. later. By about 80 m.y. BP, a number of extant groups had appeared, including Chloranthaceae, Ulmaceae, Fagaceae (*Nothofagus*), Betulaceae, Myricaceae, Lecythidaceae, Haloragaceae, Sapindaceae-Cupanieae, and Aquifoliaceae. Additional groups appear progressively, with a majority of modern families seemingly present by about 45 m.y. BP and nearly all presumably so by the start of the Miocene (22,5 m.y. BP). Looking at these relationships another way, angiosperms became dominant in fossil floras over ferns and gymnosperms about 90 m.y. BP in the areas where they first appeared, although the great majority of the angiosperms in existence in those ancient times had pollen that cannot be related directly to that of existing taxa.

Both northward and southward from southern Eurasia and North America, northern South America and Africa, the angiosperms as a whole, as well as particular groups of angiosperms, appear more recently. This relationship strongly supports a hypothesis of origin in the area outlined, followed by progressive poleward migration. In Australasia, for example, the earliest recognizable angiosperm pollen appears about 107 m.y. BP (Raven, 1982), followed by the appearance of extant taxa about 80 m.y. BP and by the ascendancy to dominance in fossil floras of the group at about 70 m.y. BP, at least 20 m.y. after this had occurred in more tropical regions. Similar age relationships appear to have been true for southern South America also, which seems to have had fossil floras more similar to those of Australia, Antarctica, and India than to those of northern South America until about 50 m.y. BP.

In the light of these relationships, we divide the history of extant groups of angiosperms roughly into three phases: (1) 80–60 m.y. BP, first modern families present; (2) 60–20 m.y. BP, most modern families present; (3) 20 m.y. to present, essentially modern floras. Each period will now be discussed in terms of its geographical relationships and the most feasible pathways for migration and dispersal at that time.

During the first period, migration between the northern and southern hemispheres would have been almost exclusively between Europe and Africa. All of the southern lands were in relatively direct contact when the first existing families of angiosperms began to appear in the fossil record, with Africa and South America relatively close and water gaps across the Indian Ocean made much narrower than at the present position of India.

The following 40 m.y. commenced with relatively poor contacts between the northern and southern hemispheres. The floras of Africa, South America, and Australasia evolved mostly in isolation during this period. By the end of the period, overland connections between Africa and Europe had been established, North and South America were close enough that there seems to have been an active exchange of plants and invertebrates, and plants and animals of Asian origin were entering New Guinea in large numbers from the north and west. New Caledonia became separated from Australia as a 'living museum' of the plants and animals that populated that continent at the start of this period. A common, rich, warm temperate flora and fauna found in southern South America and Australia at the start of the period was fragmented as the world climate began to deteriorate.

During the past 20 m.y., the cooling trend in the southern hemisphere that apparently began with the formation of a water passage around Antarctica 10–15 m.y. earlier was accelerated (Raven, 1982). The East Antarctic ice sheet began to spread rapidly about 16 m.y. BP and reached its greatest extent about 13 m.y. BP as the southern hemisphere ice age began. The maximum extension of ice in the south caused a worldwide lowering of sea level that precipitated the Messinian Crisis in the Mediterranean as it was cut off from the Atlantic (Schnitker, 1980). The West Antarctic ice sheet formed over an archipelago starting about 9 m.y. BP, pushing the world climate into its contemporary dimensions with extremely dry conditions during the past 5–6 m.y. The earliest glacial deposits in South America are 7,2–5,4 m.y. old. Widespread ice sheet formation in the northern hemisphere, almost certainly triggered by events in the south, began 3–2,5 m.y. ago.

The implications of the continental movements and climatic changes just reviewed for the migration of organisms are evident. During the past 20 m.y., when the continents may be thought of as occupying their present positions, climatic change and the evolution of extreme, drought-adapted vegetation types has gradually led to increased diversification at the generic and specific levels, with progressively decreased opportunities for migration by taxa occupying humid forest and corresponding increased opportunities for migration by those of arid-land and mountain communities. For example, the migration of the plants and animals of aseasonal forest around the Indian Ocean between Africa and tropical Asia was essentially uninterrupted 20 m.y. ago, but now involves huge gaps. By the same token, Africa, South America, and Australia were largely clothed with evergreen rainforest of tropical to warm temperate character 20 m.y. ago, and the development of the characteristic vegetation types seen today has occurred subsequently.

In both South America and Africa, thousands of metres of uplift during this period has expanded habitats for the plants and animals characteristic of cooler areas to the north and to the south, and greatly enhanced the opportunities for north-south migration. The spreading aridity associated with the cool currents resulting from massive glaciation, particularly during the past several million years, has decimated the flora of Africa and allowed savannas to spread on a continental scale at the expense of the rainforest. In South America, the aridity associated with cool water offshore has largely been confined to the areas west of the Andes, with extensive areas of humid forest persisting to the east, except at times of maximum glaciation. The uplift of the Andes, with their fantastic array of habitats lying across the full tropics, as well as the persistence of rainforest across much of the Amazon basin, seem to be the leading factors involved in the great difference between the numbers of angiosperm species of tropical South America (more than 80 000) as compared with tropical Africa (roughly 30 000 *fide* Brenan, 1978), despite the much greater size of the latter. The flora of Madagascar, proportionately much richer than that of continental Africa (Leroy, 1978), deserves continued special attention, especially in view of its threatened status (Rauh, 1979).

In Australia, a rich subtropical to warm temperate rainforest that occupied most of the continent until perhaps 12 m.y. ago is now restricted to a series of rainforest patches scattered from Queensland to Tasmania originally amounting to no more than 20 000 km^2, and now slashed back to only half that extent. Australia is now three-quarters desert, with the remainder largely savanna and sclerophyll communities rich in endemics. In these tiny patches of rainforest that survive in Australia, together with the additional 300 km^2 of rainforest in New Caledonia (1350 of 1499 species, 82 of 365 genera, and 5 of 108 families endemic *fide* Morat, Veillon & Mackee, 1981), and the more extensive areas in New Guinea and New Zealand occurs the most remarkable array of archaic angiosperms found anywhere in the world, these probably having survived in the outlying extremities of angiosperm migration, where they have not been replaced by migration from the central areas of radiation in northern Africa, northern South America, and adjacent lands of the northern hemisphere. Although southern South America demonstrably shared this flora in the early Tertiary, it has largely become extinct there, presumably as a result of mountain-building and glaciation.

Axelrod (1979) has provided a very full account of the spread of deserts to a continental scale during the past few million years; they are more extensive at present than has ever been the case in the past. The kinds of sclerophyllous plant communities that occur chiefly in areas of the world with a mediterranean (summer-dry) climate, and in which families such as Proteaceae and Myrtaceae have proliferated to such a remarkable degree, seem to owe their origins to the preadaptation of such plants to these recently derived climates. Especially in Australia and southern Africa, such plants probably originated starting approximately 60 million years ago on areas of highly infertile soil (Johnson & Briggs, 1981). Why the fynbos in southern Africa has spread so extensively under the influence of man, while comparable plant communities in Australia appear to have contracted, is unknown.

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