J. mar. biol. Ass. India, 1973, **15** (1): 236-241

CONTINENTAL DRIFT AND THE DISTRIBUTION OF THE ISLAND FLORAS OF THE INDIAN OCEAN*

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ABSTRACT

The floras of the low lying archipelagos of the Indian Ocean are of a uniform type and can be accounted for by trans-ocean colonisation, but those of the high islands are diversified, with high degrees of endemism, signifying long periods of isolation. An explanation of this situation can be found in continental drift. As the land masses surrounding the Indian Ocean were formerly parts of the Gondwana continent of late paleozoic and mesozoic times, an understanding of the former arrangement of the fragments and the manner in which they broke apart from one another is necessary to account for modern biological distributions. Many attempts at reconstruction of the Gondwana continent have been made by geologists and geophysicists, but generally without taking the palaeontological evidence into account. A new reconstruction of Gondwanaland is proposed and the sequene of its disruption in the Indian region discussed. This suggests that Madagascar was separated from both Africa and India in the first phase of the drift process but remained close to India until India broke away from the remaining parts of Gondwanaland. The Mascarenes were probably formed along the mid oceanic ridge at an early stage in the drift of India when it was close to Madagascar. The distributions resulting from these earth movements include those of the **Canellaceae** linking Madagascar with Africa and the West Indies on the one side and **Adansonia** on the other linking Africa through Madagascar to Australia. The close relationship between the Mascarene floras may be due to temporary land connection along the mid ocean rise at an early stage in the drift, later broken by subsidence. Some examples are discussed.

The high rate of endemism in the flora of Madagascar is a reflection of its long isolation , which has also allowed the survival of some primitive features. Such are the glossopteroid leaves of **Foetidia**, replaced by a more advanced type in the Mauritian species, and they give an indication of the interest and scientific importance of the islands of the Western Indian Ocean for phytogeographical and evolutionary studies.

INTRODUCTION

THE region of the Indian Ocean is one of great biological interest. The floras of the larger elevated islands have many unique features and pose some difficult problems for the phytogeographer. On the other hand, the low-lying island groups, such as the Maldive, Laccadive and Chagos archipelagos are of comparatively recent origin and bear very similar floras of widespread tropical species that have arrived in their present stations by transport across the ocean, either by ocean currents or by birds. They are of relatively little interest and will not be alluded to further. At the other extreme, Madagascar has a large and very diversified flora of about 6000 species with the highest rate of generic endemism in the world. Ceylon is also very rich in endemics and the Mascarenes and Seychelles rather less so, as might be anticipated from their smaller size. The distinctiveness of these island floras is no doubt due to long isolation, but for an explanation of their interrelationships and their relation to the floras of the adjacent continents we must look to the sequence of earth movements during past geological epochs caused by continental drift.

*Presented at the 'Symposium on Indian Ocean and Adjacent Seas—Their Origin, Science and Resources' held by the Marine Biological Association of India at Cochin from January, 12 to 18, 1971.

The land masses surrounding the Indian Ocean, Africa, Arabia, India, Australia and Antarctica, all have fossil floras of Permian age characterised by a group of early seed plants, the *Glossopteridae*. There is now general agreement that all of these territories were united in one continent, called Gondwanaland, in Permian times, but there are many conflicting opinions on the arrangement of the fragments in the former continent. Much geophysical and physiographical evidence bearing on this problem in the Indian Ocean has accumulated in recent years, but the picture is still incomplete. The final solution will come from the integration of data from many disciplines. Some of the basic evidence is supplied by palaeomagnetism (Creer, 1964) which assigns approximate positions for the principal land masses. Computer matchings have been made of the coasts of southern Africa (Dietz and Sproll, 1970) and of southern Australia with parts of the coastline of Antarctica (Sproll and Dietz, 1969). The fact that Kerguelen is a continental fragment with coal and other terrestrial fossils and that the submerged bank on which it stands must come between South Africa and Antartica invalidates the fit against South Africa. Schopf (1970) has taken account of Kerguelen and of palaeobotanical evidence, but has accepted a position for Madagascar opposite Kenya which does not appear to be justified.

RECONSTRUCTION OF GONDWANALAND

The reconstruction of Gondwanaland favoured by the writer (Fig. 1) places Madagascar at the mouth of the Zambesi, where it makes the best physical fit (Wellington, 1955) and has mineralogical similarities, rather than the northern position advocated by Smith and Hallam (1970). Ceylon should then be placed against the east coast of Madagascar where graphite, gem stones and geological features indicate its affinity. India should then be placed in line with Ceylon to the

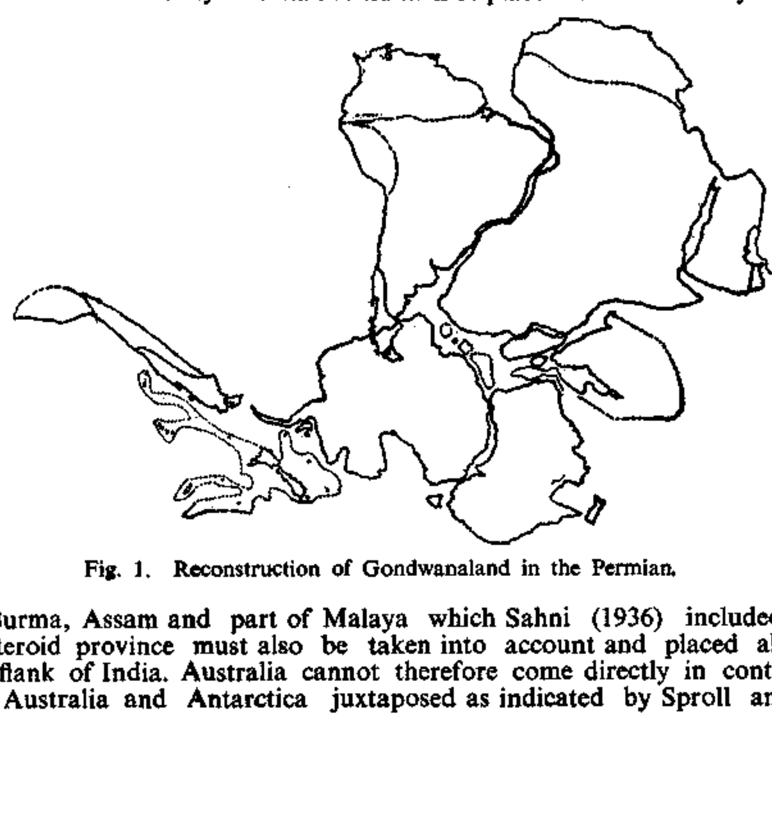

Fig. 1. Reconstruction of Gondwanaland in the Permian.

north. Burma, Assam and part of Malaya which Sahni (1936) included in his glossopteroid province must also be taken into account and placed along the eastern flank of India. Australia cannot therefore come directly in contact with India. Australia and Antarctica juxtaposed as indicated by Sproll and Dietz

(1969), can then be moved against the other fragments to produce a close-packed result. In this reconstruction the southern part of Patagonia overlaps onto Antarctia. This is justified, as already pointed out (Melville, 1966) because Chile plus Patagonia did not suffer the Permo-carboniferous glaciation and geological and palaeoclimatic evidence indicate that this sector was not attached to South America in the Permian.

The proposed reconstruction of Gondwanaland is tentative but it is consistent with many biological facts without, so far as I can judge from available data, violating geological and geophysical evidence. It brings Western Australia closer to South Africa than other reconstructions and considerably shortens the gap between the two major distribution areas of the *Proteaceae* and *Restionaceae*. Madagascar, also, is relatively close to Australia with which it shares a some modern genera.

DISMEMBERMENT OF GONDWANALAND

The dismemberment of the Gondwana continent must now be considered as this is crucial to an understanding of modern distributions. The first episode of the drift process was the separation of Africa plus South America from the rest of Gondwanaland. This took place, according to palaeomagnetic evidence (Creer, 1964) early in the Triassic. By a forking of the rifts Madagascar was probably separated at this period from both Africa and India and Ceylon, but as Africa drifted away Madagascar remained close to India in much the same way as Greenland has remained close to North America. Some modern distributions are probably the result of this episode. For example, Madagascar has 120 species of palm, all but two of which are endemic and 13 out of 18 of the genera are endemic (Jumelle, 1945). Madagascar is several times richer in palms than the whole of Africa and moreover the subfamily *Areceae* to which the Madagascan species belong is not represented in Africa (Good, 1953). The number of Angiosperm genera common to both Africa and Madagascar is much less than would be expected from their present proximity and they form only a small proportion of the total number of African genera. The number of genera endemic to Madagascar, also, is greater than the number held in common. In this connection, the baobabs (*Adansonia*) are of interest as they link Africa, Madagascar and Australia. The African species is less closely related to those of Madagascar (6) than are the two Australian.

In the second episode of the drift the mid-Indian Ocean rise and the Indian-Antarctic rise became active and India and Australia were pushed northward in unison until the S.W. corner of Australia had reached about 30° south latitude. In the interval a rift had formed separating the gondwanic parts of Burma and Thailand from India and the gap between India and Madagascar had opened. During this period volcanic activity along the mid-Indian rise produced Reunion, Mauritius and Rodriguez and the Seychelles. It is likely that these volcanic mountains were for a time in land connection along the ridge and perhaps for a brief period in the early stages of this movement with Madagascar and Ceylon. In this way various elements in their floras would have been acquired before wide separation made dispersal impossible.

By the time S.W. Australia had reached 30° south latitude activity along the mid-Indian rise had intensified and introduced an east-west component into the drift movement. This pushed Madagascar to the west and Australia to the east along the line of the Broken Ridge. Seychelles, Mauritius and Reunion with the

Seychelles-Mauritius ridge were then pushed westwards while Rodriguez, remained centrally on the mid-Indian rise. To the east, the gondwanic sectors of Burma and Thailand were pushed eastwards as the Bay of Bengal opened and Ceylon was moved eastwards out of line with India as the main northward drift of India continued.

Whether or not this tentative interpretation proves to be correct, it does account for the main features of the Indian Ocean and can explain many biological distributions. With regard to timing, Madagascar is assumed to have been an island since sometime in the Triassic. The beginning of the movement of India and Australia was probably about mid-Cretaceous and the movement of India was virtually finished by the Miocene as at this time the Himalaya were being upraised, presumably as a result of isostatic readjustment following the under-thrusting of part of the Indian tectonic plate under Tibet. The creation of the Mascarenes may have been in mid-Cretaceous and they were probably moving to their present positions at the end of the Cretaceous. As an example of African relationships, the genus *Psiadea* (*Compositae*) may be mentioned. There are about 30 species in Africa, Madagascar has about 20 endemics and there are about 15 more in the Mascarenes. A similar pattern is shown by *Dombeya* in the *Sterculiaceae* which has a number of species in Africa, 187 in Madagascar of which only one is shared with Africa and a further 28 species confined to the Mascarenes of which 5 are shared with Madagascar. These two genera, in common with a number of others which show considerable diversification in Madagascar and the Mascarenes reflect the long isolation of these islands.

Looking to the east, there are many strong floral links between these Islands and India, Ceylon and Malaysia. The family *Dipterocarpaceae* has preponderantly an Indo-Malaysian distribution and is represented in Africa by two genera only: *Marquesia* with 4 species and *Monotes* with 48 species and one Madagascar endemic. On the Indian side *Vateria* has one species in India, 15 endemic in Ceylon and one in the Seychelles.

India is not included in a number of these eastern distributions, the relationship then being between the islands associated with the mid-Indian Ocean rise—the Mascarenes and Seychelles—and Burma and Malaysia. *Timonius* (*Rubiaceae*) is an example, with one species in the Seychelles, one in Celyon and the Nicobars (*T. jambosella*), another (*T. rumphii*) in the Andamans and Burma and extending through Malaysia. The bulk of the genus, about 150 species, is distributed through Malaysia and into the Pacific as far as Fiji. Among other genera with this kind of distribution are *Amaracarpus* (*Rubiaceae*), *Agrostophyllum* (*Orchidaeceae*), *Melastoma* (*Melastomaceae*) and the pitcher plants (*Nepenthes*). Such distributions are difficult to account for except by continental drift. With an origin in the Burma-Thailand fragment of Gondwanaland, originally close to Ceylon and India, migration onto the western islands would be possible and later, after the drift, dispersal through the rest of Indonesia would be practicable. Some far flung distributions which hitherto have been very puzzling seem to be accounted for by this migration path. *Nepenthes* with one species in the Seychelles and one in Ceylon extends as far as New Caledonia and has one species in northern Queensland which probably arrived there from New Guinea during the Tertiary.

Other links between Madagascar and Australia, such as the baobabs already mentioned, had probably reached those territories before the drift of India and Australia. They are limited in number to include *Keraudrenia* (*Sterculiaceae*) with one species in Madagascar and 6 in Australia and *Hibbertia* (*Dilleniaceae*) of which the sole Madagascan species belongs to the section *Hemistemma*, which otherwise is confined to Australia.

In addition to the part it has played in the dispersal of the Angiosperms, continental drift has been responsible for the isolation of the islands of the Indian Ocean. The absence of grazing mammals on the islands, until they were introduced by man, allowed evolution to run its course without interference. To this circumstance we can ascribe the great diversification of the genus *Dombeya* in Madagascar and of orchids in Reunion as well as the survival of endemic families and genera and of species with primitive characteristics. There are 6 endemic families on Madagascar and the monotypic *Dirachma* on Socotra and *Medusagyne* in the Seychelles each represents a relict family. Among relict genera on Madagascar is *Foetidia* (*Lecythidaceae*) with four species having leaf venation patterns little changed from the Permian *Glossopteris* (Melville, 1969). The only other species, *F. mauritiana*, on the three Mascarene islands must have migrated from Madagascar and shows the evolutionary advancement which so often accompanies migration.

ISLAND FLORAS OF INDIAN OCEAN AND NEED FOR CONSERVATION

The unique history of the Indian Ocean explains how the principal islands became centres of evolutionary diversification. For millions of years they have been natural laboratories of the utmost importance for science, especially in the fields of taxonomy, phylogeny and biogeography. Unfortunately, during the last century and a half there has been great destruction of their floras and faunas brought about by the introduction of goats and cattle, the clearing of forests for plantations and in the present century the ever-increasing pressure of exploding human populations. The need to preserve representative samples of the floras of these islands is urgent before further irreparable losses occur. Much biological capital has already been destroyed before its potential value for mankind has been investigated. On Rodriguqez no natural ecosystems still survive and the flora has been decimated. On Mauritius wise counsel prevailed and 10 nature reserves were created in 1944 but not before much damage had already been done. On Reunion the coastal forests have been destroyed to make way for commercial plantations and with them have gone a large proportion of the endemic orchids. According to Rivals (1952) the vegetation at higher altitudes is little altered, so now, surely, is the time to establish reserves. A list of the endemic plants of the Seychelles and their conservation status was published recently (Melville, 1970). *Medusagyne*, which was thought to be extinct, was found again during 1970, and nature reserves on the Seychelles are under consideration. There are no reserves on Socotra where they are urgently needed to preserve *Dirachma* and other rare endemics. Only remnants of the natural vegetation of Madagascar remain and as recently as last October the Malagasy Government held a conference with the collaboration of the International Union for the Conservation of Nature to consider the best means of conserving what remains of the flora and fauna. It is much to be hoped that effective measures will be taken and that, if necessary, international financial support will be forthcoming to attain this objective.

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NOTE ADDED IN PROOF:

Since this paper was written, investigations of the basement sediments of the ocean floor to the south and the west of Australia have established that Australia began to drift north from Antarctica 50 million years ago and that its eastwards drift began 140 million years ago. The continent was therefore pushed to the east first and then northwards and not the reverse as suggested in this paper (McElhinny, 1973; Earth sciences and the Australian continent. *Nature,* **246** : 264-268).