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## The Origin and Distribution of the Flora of Aldabra

S. A. Renvoize

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## The origin and distribution of the flora of Aldabra

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This paper is concerned with an analysis of the flora of Aldabra and the neighbouring islands of Cosmoledo, Astove and Assumption, which together form the Aldabra group. The flora includes 206 species of which 166 are indigenous and 40 are introduced. Only the indigenous flora is considered in detail.

On the basis of geographic distribution these 166 species can be amalgamated into the following eight groups: Pantropical, Indo-Pacific, widespread-African, East African, Madagascan, Mascarene, Seychelles and Endemic, which indicate that the flora has been derived from a complete range of sources from widespread to very local. As assessment of the contributions made by each geographical group to the indigenous flora shows that about 55 % of the species are of widespread distribution and 45 % are found only in the region of East Africa and Madagascar. Furthermore, the majority of species of widespread distribution are associated with coastal habitats, whereas the majority of species of local distribution are associated with inland habitats.

One hundred and sixty-six species is an exceptionally large number for a coral island since few others support more than a handful of indigenous species and these are invariably associated with coastal habitats usually being species of widespread distribution. Plenty of coral islands have produced endemics but none on the same scale as Aldabra which had 31 endemic species.

A brief survey of possible means of plant introduction is given and these can be roughly grouped into sea, wind and animals, the first being associated mainly with the coastal and widespread species and the last two being associated mainly with the inland and more regional species.

From this analysis of the flora of Aldabra several important facts emerge. Aldabra can support a large number of species and this is due mainly to the large terrestrial area which provides a variety of habitats. The flora includes a high percentage of local species and although still dominated by the widespread species the difference in numbers between widespread and local species is considerably less than on most other coral islands. Aldabra has a large number of species found only in inland habitats due again to the large terrestrial area and finally Aldabra has a very high percentage of endemism, almost 20 % of the indigenous flora.

## 1. INTRODUCTION

The flora of Aldabra is exceptional for an isolated coral island in having a large number of species and a high percentage of endemism. Whereas the flora of most coral islands consists basically of species with a widespread distribution, normally associated with strand-line or coastal habitats, on Aldabra just over one-third of the indigenous flora fits into this category and the remainder is mostly of a more local distribution, usually found in inland habitats.

The land surface of Aldabra has been elevated by about 5 m and so provides habitats relatively free from the direct influence of the sea. In addition, this process of elevation has exposed an exceptionally large land area available for plant colonization. Aldabra can probably be counted among the largest atolls in terms of terrestrial land area, and it is this combination

of a large area raised up beyond the influence of the sea that has provided habitats for many species additional to the characteristic strand line and coastal type flora of most coral islands.

The flora of Aldabra and its neighbouring islands consists of 206 species.

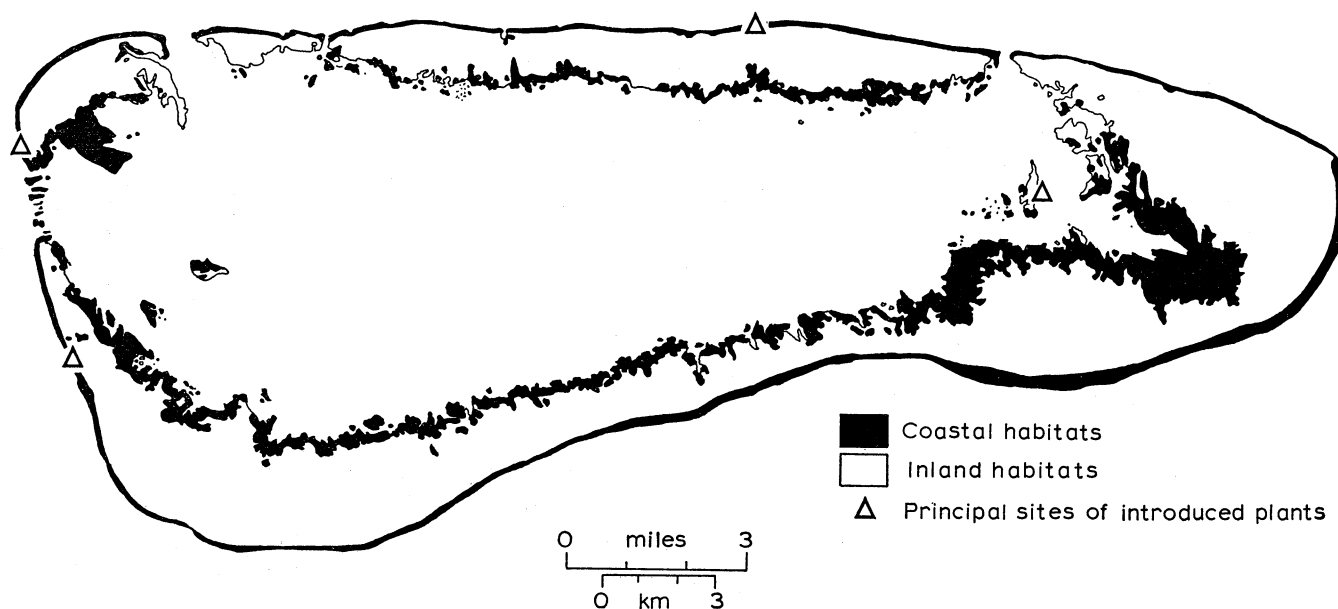


FIGURE 1. Map of Aldabra, showing the distribution of coastal and inland habitats, and the principal sites of introduced plants.

## 2. INTRODUCED SPECIES

Forty species are easily identified as deliberate or accidental introductions associated with man's activities on these islands and with few exceptions are only found around areas of settlement and fishing camps. On Aldabra a comparatively small area has been affected in this way, as can be seen from figure 1. Unfortunately the same cannot be said of Menai Island, Cosmoledo Atoll, and of Astove, where coconut plantations are more extensive than on Aldabra, and of Assumption where a large area has suffered the ravages of guano mining. Associated with the plantations there is the inevitable ground flora of pantropical weeds.

I do not wish to consider these introduced species any further in this paper except to list in tables 1 to 3 the more important cultivated species and common weed species.

TABLE 1. IMPORTANT CULTIVATED SPECIES ON ALDABRA AND NEIGHBOURING ISLANDS

<i>Cocos nucifera</i>	coconut	<i>Agave sisalana</i>	sisal
<i>Ricinus communis</i>	castor oil	<i>Zea mays</i>	maize
<i>Carica papaya</i>	paw paw	<i>Gossypium hirtum</i>	cotton
<i>Citrus limon</i>	lemon	<i>Moringa oleifera</i>	horse-radish tree

TABLE 2. INCIDENTAL AND DECORATIVE SPECIES ON ALDABRA AND NEIGHBOURING ISLANDS

<i>Tabebuia pentophylla</i>	<i>Tamarindus indica</i>
<i>Delonix regia</i>	<i>Erythrina variegata</i>

TABLE 3. IMPORTANT WEED SPECIES ON ALDABRA AND NEIGHBOURING ISLANDS

<i>Datura metel</i>	<i>Stachytarpheta jamaicensis</i>
<i>Catharanthus roseus</i>	<i>Digitaria horizontalis</i>
<i>Lantana camara</i>	<i>Tribulus cystoides</i>
<i>Sida acuta</i>	<i>Passiflora suberosa</i>
<i>Turnera ulmifolia</i>	

### 3. INDIGENOUS SPECIES

The 166 species remaining I consider to constitute the true indigenous flora which has arrived on Aldabra and the neighbouring islands by natural means independent of man. The first part of this paper is concerned with an analysis of the world distribution of these 166 species from which it is possible to get some idea of where the present flora of the Aldabra group has come from. The exact mechanisms which have been responsible for the transportation of these species will be dealt with in a later part of this paper.

The 166 species in the Aldabra flora are divided into eight geographical groups according to their world distribution, which are: Pantropical, Indo-Pacific, widespread-African, East African, Madagascan, Seychelles, Mascarene islands, Endemic.

In addition to a division of the flora on a geographical basis a further division is made on a broad ecological basis into coastal and inland species. The terms *coastal* and *inland* as used in this paper are not comparable with their use in the context of continental land masses. Thus *coastal* in the context of Aldabra and neighbouring islands includes the strand line and areas effected by the sea in the form of salt spray or tidal inundation. The term *inland* includes areas not effected directly by the sea, although the whole land area of Aldabra will obviously be effected indirectly through the influence of the sea on the climate. However, on the criteria given above a division of the flora into coastal and inland species is useful and will help further to illustrate important features of the flora in the discussion which follows.

I will now examine each geographical group in turn with discussions and examples of the relevant species.

The *pantropical* group includes 36 species which are distributed throughout the tropics and many are a common component of any tropical island or continental strand-line flora. These species include trees, shrubs and herbs which are found throughout the islands in the group and on Aldabra account for almost a quarter of the flora. In this group 25 species are of coastal and strand-line habitats and 11 species are of inland habitats. Of the coastal species the most prominent are as follows:

*Dactyloctenium aegyptium*, a low-spreading grass growing in loose sand.

*Sesuvium portulacastrum*, *Portulaca oleracea*, *Evolvulus alsinoides*, *Ipomoea pes-caprae*, *I. tuba*, *Solanum nigrum* and *Asystasia gangetica*, all of which are herbs growing in pockets in the rough coastal champignon.

*Sporobolus virginicus*, a rhizomatous, short, spreading grass fixing vast areas of sand along the southern coast of Aldabra.

*Sophora tomentosa*, a tall shrub growing on rough coastal champignon along the northeastern coast of Aldabra.

*Suriana maritima*, a low shrub growing on rough coastal champignon or on the landward edge of the lagoon mangroves.

*Casuarina equisetifolia*, a tall tree with needle like leaves, usually growing along the strand

line but occurring inland in large groves, probably due to transplantation by the natives as well as natural means.

Of the inland occurring species the following are most prominent:

*Acrosticum aureum*, the mangrove fern which is frequent throughout Aldabra.

*Cyperus ligularis*, *Fimbristylis ferruginea* and *F. spathacea*, sedges occurring frequently in areas of platin rock.

*Cassytha filiformis*, a leafless, wiry, parasitic vine.

*Abrus precatorius*, a climbing, entwining plant.

*Colubrina asiatica*, a large spreading shrub.

The *Indo-Pacific* group includes 39 species which are commonly found throughout the Indian and Pacific ocean areas and these account for almost a quarter of the Aldabra flora. In this group 26 species are of coastal or strand-line habitats and 13 species are of inland habitats. Of the coastal species the most important are as follows:

*Ceriops tagal*, *Bruguiera gymnorhiza*, *Rhizophora mucronata* and *Avicennia marina*, all commonly occurring mangrove trees.

*Xylocarpus moluccensis*, *X. granatum* and *Sonneratia alba*, rarely occurring mangrove trees.

*Lumnitzera racemosa*, shrubs or trees occurring in both coastal situations and around inland pools.

*Cymodocea rotundata*, *C. ciliata*, *Thalassia hemprichii*, *Halodule uninervis* and *Syringodium isoetifolium*, all small, herbaceous marine angiosperms.

*Boerhavia repens*, *Sida parvifolia*, *Launaea sarmentosa* and *Melanthera biflora*, all herbs growing in sand or pockets in rough coastal champignon.

*Tournefortia argentea*, *Pisonia grandis*, *Guettarda speciosa*, *Pemphis acidula*, *Cordia subcordata* and *Scaevola taccada*, all trees or shrubs.

*Lepturus repens*, a prostrate grass growing mainly in sandy pockets in coastal champignon.

Of the inland species the following are most prominent:

*Premna obtusifolia*, *Azima tetracantha*, *Apodytes dimidiata*, *Flacourtia indica*, and *Scutia myrtina*, *Pandanus tectorius* and *Deeringia polysperma*, all trees and shrubs.

*Cyperus dubius*, a sedge and *Phyllanthus maderaspatensis*, a small herb.

To distinguish between pantropical and Indo-Pacific distributions in the context of the Aldabra flora may seem rather superfluous, although on a larger scale the distinction would be important. If we amalgamate these first two groups therefore we find that 75 species, which is just under half the total indigenous flora of Aldabra, are widespread in the tropics and, furthermore, two-thirds of these widespread species are restricted to coastal and strand-line habitats. The exact significance of this will be discussed later.

The next group of species are those which are widely distributed throughout tropical and subtropical Africa extending northwards into the Mediterranean region and middle Asia but not extending farther east than the western coast of India. In this widespread-African group there are 14 species, five of which are coastal and nine inland.

The coastal species are:

*Arthrocneum glaucum*, *Canavalia rosea*, *Launaea intybacea*, *Cyperus conglomeratus* and *Capparis cartilaginea*, which are herbs or low shrubs.

The inland species are:

*Mystroxydon aethiopicum*, *Clerodendrum glabrum* and *Maytenus senegalensis*, all trees or shrubs.

*Abutilon angulatum*, *Kyllinga polyphylla*, *Cyperus obtusiflorus*, *Boerhavia elegans*, *Hedyotis caespitosa* and *Sarcostemma viminale*, all herbs.

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The next group is of 15 species restricted to *East Africa* from Kenya to Mozambique and the Madagascar region. Only two of these species are coastal, *Cleome stricta* and *Crotalaria laburnoides*. The remaining 13 species, which are all inland, are as follows:

*Tarenna nigrescens*, *Canthium bibracteatum*, *Macphersonia hildebrandtii*, *Polysphaeria multiflora*, *Gouania scandens*, *Maerua pubescens*, *Allophyllus alnifolius*, *Terminalia boivinii* and *Tricalysia sonderana*, all of which are trees or shrubs.

*Enteropogon sechellensis*, *Pleurostelma cernuum*, *Tephrosia pumila* var. *aldabrensis* and *Viscum triflorum*, all of which are herbs.

The next group is of 24 species which are restricted to Madagascar, the Seychelles and Mascarene islands, five of these are coastal and 19 inland. The most important coastal species are two grasses, *Daknopholis boivinii* and *Sclerodactylon macrostachyum* and a leafless tufted wiry plant, *Plumbago aphylla*.

The most important inland species are:

*Ficus avi-avi*, *Ficus reflexa*, *Dracaena reflexa*, *Ochna ciliata*, *Poupartia gummifera* and *Ehretia corymbosa*, which are all trees and shrubs.

*Lomatophyllum borbonicum*, an aloe type plant.

The Mascarene group consists of two species:

*Asparagus umbellulatus* and *Pandanus vandermeeschii*, both occurring in inland habitats.

The Seychelles group includes five species which are all found in inland habitats, the most important species are:

*Wielandia elegans*, *Ficus nautarum* and *Psychotria pervillei*, which are all trees.

The final group is of the 31 species which occur only on Aldabra and neighbouring islands all but one of which occur inland. The coastal species is *Peponium* sp.\* The inland species are as follows:

*Cassipourea thomassetii*, *Vernonia aldabrensis*, *Solanum aldabrense*, *Pithecellobium ambiguum*, *Phyllanthus cheloniphorbe*, *Grewia salicifolia*, *G. aldabrensis*, *Euphorbia abbottii*, *Erythroxyton acranthum*, *Acalypha claoxyloides*, *Triainolepis fryeri* var. *fryeri*, *Sideroxylon inerme* subsp. *cryptophlebium*, *Tarenna trichantha*, all of which are trees or shrubs.

*Stenotaphrum clavigerum*, *Stenotaphrum* sp., *Sporobolus* sp. A., *Sporobolus* sp. B., *Panicum assumptionis*, *Panicum* sp., *Eragrostis* sp. A., *Secamone fryier*, *Nesogenes dupontii*, *Lagrezia madagascariensis*, *Lagrezia* sp., *Hypoestes aldabrensis*, *Cassia aldabrensis*, *Barleria* sp., *Achyranthes* sp., *Portulaca* sp., *Bacopa* sp., which are all herbs.

From this analysis it can be seen that the flora of Aldabra is made up of species ranging in distribution from world wide to Aldabra only. The proportion of the total indigenous flora contributed by each geographical group varies and is tabulated in table 4.

TABLE 4. CONTRIBUTIONS TO THE FLORA OF ALDABRA MADE BY EACH GEOGRAPHICAL GROUP

	species	%
pan-tropical	36	21.7
Indo-Pacific	39	23.5
widespread-African	14	8.8
East African	15	9.0
Madagascar	24	14.2
Mascarene	2	1.2
Seychelles	5	0.3
Aldabra	31	18.6

\* Many endemic species are new to science and as yet undescribed.

## 4. COASTAL AND INLAND HABITATS

Of the total flora of 166 species 64 are coastal or strand line and 102 are inland. The contribution made by each geographical group to each of these ecological divisions varies such that the widespread pantropical and Indo-Pacific groups contribute more species to the coastal habitats than they contribute to the inland habitats and with the local species the opposite is the case, more species being contributed to the inland habitats than to the coastal habitats. These varying contributions to the two major ecological regions are tabulated in table 5.

TABLE 5. CONTRIBUTIONS MADE BY EACH GEOGRAPHICAL GROUP TO THE COASTAL AND INLAND HABITATS OF ALDABRA

	species	coastal	inland
pantropical	36	25	11
Indo-Pacific	39	26	13
widespread-African	14	5	9
East African	15	2	13
Madagascan	24	5	19
Mascarene	2	0	2
Seychelles	5	0	5
Aldabra	31	1	30

The extent of these two regions is shown in figure 1.

If the lagoon fringing habitats, which are dominated by the mangrove species are excluded the coastal area is very small indeed and yet it carries 50 of the 166 species which amounts to about 30% of the flora. Thus about one-tenth of the land area provides habitats for just under one-third of the flora and nine-tenths of the land area carries just over two-thirds of the flora. Remembering that the coastal habitats are dominated by species of widespread distribution it leaves the local species dominating the much larger inland area. The term dominance is used here in a floristic sense in as much as, of the number of species represented in the inland vegetation most are of local distribution and vice versa for the coastal vegetation. The local species are not dominant in a vegetative sense since the most frequently occurring species in the inland mixed scrub are often of widespread distribution. This serves to emphasize what may be considered the most important feature of the Aldabra flora, that a large number of species with local distributions are gathered together in the most extensive habitats on Aldabra, i.e. inland champignon and platin.

## 5. DISTRIBUTION PATTERNS OF LOCAL SPECIES

The geographical regions forming possible sources of the Aldabra flora have already been discussed but closer study of the distributions of the more regional plants reveals more precise evidence of colonizing sources.

Of the 15 species occurring in East Africa, seven also occur in Madagascar and the other eight have colonized Aldabra but somehow missed colonizing Madagascar.

Of the 24 species occurring in Madagascar only two have spread to the Seychelles and these are both figs. The other 22 species have colonized Aldabra without colonizing the Seychelles.

The five Seychelles species and two Mascarene species are not found elsewhere except on Aldabra. In the latter case this is particularly interesting since the position of the Mascarene islands in relation to Aldabra is not in a direct line and the forces responsible for the transportation of these two species have avoided depositing their load on Madagascar, Farquhar and the Seychelles.

Of the 31 endemic species, 12 appear to be most nearly related to East African species, 15 to Madagascan species, three to Mascarene species and one to a Ceylon species. Figure 2 shows the islands and archipelagoes of the southwest Indian Ocean which constitute the local or regional areas referred to in this paper.

Broadly speaking 55 % of the indigenous flora has come from sources of widespread species in Africa and the Indian and Pacific Ocean areas, and 45 % from local sources in East Africa, Madagascar, the Mascarenes and Seychelles. Furthermore, within the localized region a distinct majority of species, i.e. 37 out of 77 local species, are derived from Madagascar alone.

Such a situation is no more than would be expected considering the position of the Aldabra group in relation to Madagascar, although it is certainly peculiar that certain species colonizing Aldabra from Africa, Madagascar, the Seychelles and the Mascarenes have not become more widely distributed throughout the western Indian Ocean.

The only explanation I can offer for this is that Aldabra became available as a habitat for terrestrial plants comparatively recently, long after the vegetation of Africa, Madagascar and the Seychelles had become established. Previous to the appearance of terrestrial environments on Aldabra, any plants becoming dispersed between land masses around the western Indian Ocean in recent times would probably have met with considerable competition from the already well established species. We have some examples of species breaking through this competition barrier in the 13 African species which are established on Madagascar, but this is assuming that these species evolved in Africa and that that is their centre of distribution. When Aldabra appeared, however, these species being dispersed across this corner of the Indian Ocean may have found themselves in a habitat which offered no resistance to colonization, at least in the form of competition from other plants; as long as they could survive the rigours of establishing themselves on bare limestone rock with only a minimal amount of soil, they would survive. In this way Aldabra and its neighbouring islands received plants, which had been unable to colonize other islands, from several different areas.

It might be argued that the East African coast, together with Madagascar and the surrounding islands, should be regarded as one phytogeographical area. However, from the study of the plant distributions in the Aldabra flora just outlined it appears that some species occur in some areas but not in others. The division of this region into further phytogeographical areas indicates that Madagascar, the Seychelles and the Mascarene islands represent three independent sources of species which have become distributed as far as Aldabra. Evidence from the Aldabra flora for the distinction of these regions may seem a little thin but it is a well-known fact that the flora of each of these areas includes a large number of endemic species which is further proof of their individuality. Another possible reason for the discontinuous distributions shown by some of the Aldabra species may of course be due to their extinction elsewhere. A more comprehensive study of all the plants in this region than an analysis of the Aldabra flora can offer, is required before a precise assessment of the phytogeographic regions of the western Indian Ocean can be made.



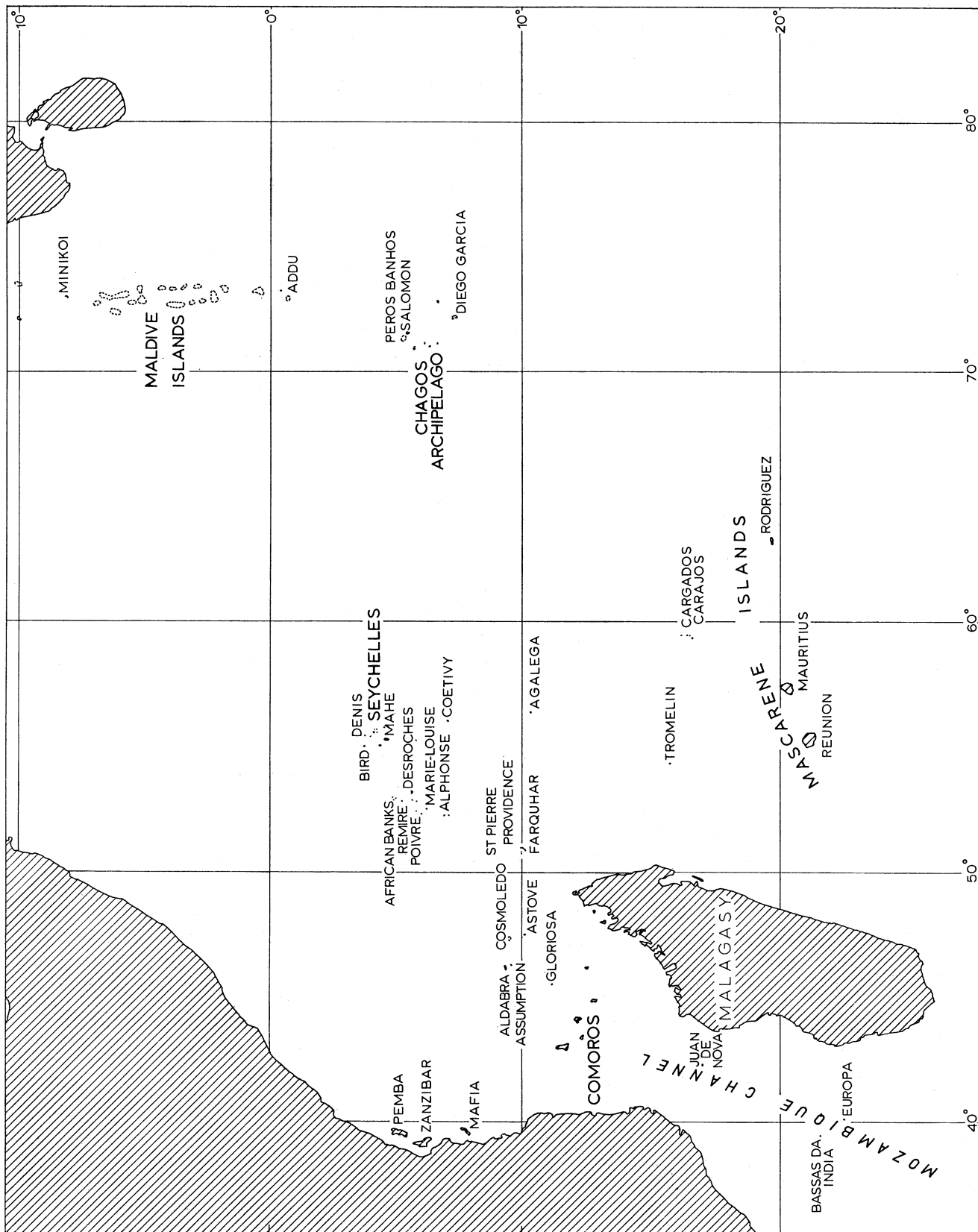


Figure 2. Map of the western Indian Ocean

## 6. DISPERSAL AND COLONIZATION MECHANISMS

To try to suggest mechanisms by which each of the species recorded from Aldabra have arrived on the island would be a rather arduous task, but some examples of dispersal mechanisms which could account for most of the flora reaching Aldabra may be briefly discussed.

The most obvious dispersal mechanism for the coastal species is by ocean currents and there are on Aldabra numerous well-known examples of species dispersed in this way: *Sophora tomentosa*, *Caesalpinia bonduc* (both of which have hard shelled, small, round seeds), *Terminalia catappa* and *Ipomoea pes-caprae*. In conjunction with ocean currents there is the possibility of seeds becoming lodged in pieces of drift wood and Guppy (1890) suggests that *Tournefortia*, *Suriana*, *Pemphis* and *Portulaca oleracea* are transported in this way. There is of course the possibility that several other species may be transported on drift wood. Around the shores of Aldabra there was certainly no shortage of timber washed up by storms.

As far as marine angiosperms such as *Thalassia* and *Cymodocea* are concerned, they appear to flower so infrequently that the most likely method of dispersal is by bits of rhizome being broken off and transported by ocean currents.

These methods however only account for the coastal species which occur over a comparatively small area of Aldabra. How then have the inland species, which are the most important element of the vegetation, arrived?

The most likely method of dispersal is probably by birds of which there were several on Aldabra which could accomplish this, such as Pigeons, Bulbuls and White-eyes, which are fruit eaters and fairly common on the island. Correlated with this we find that many of the tree species of the island mixed scrub bear fruits which are suitable for eating, *Apodytes*, *Flacourtia*, *Ficus* (3 species), *Polysphaeria*, *Sideroxylon*, *Ochna*, *Macphersonia*, *Allophyllus*, *Poupartia* and *Clerodendrum*.

Aquatic and small succulent herbs such as *Bacopa* and *Ruppia* growing in and around fresh water pools could easily have been transported on the feet of Ibises and Flamingoes.

The only other animals which could be responsible for long-distance dispersal to Aldabra are the fruit bats. They have quite a reputation for seed dispersal in Malaysia but on Aldabra it is difficult to know what plants to attribute to them, other than the figs.

One drawback in this theory however is that as far as I know these bats and birds are not known to migrate regularly to and from Aldabra so the inland plants must have come gradually with the occasional arrival of stray bats and birds blown to Aldabra by cyclones.

Other species may have arrived on Aldabra attached to birds' plumage in the form of sticky fruits. The tufted, wiry plant *Plumbago aphylla* is certainly a candidate for this mode of travel and the parasite *Viscum triflorum*, which on Aldabra is specific to *Pemphis* is likely to have arrived on the feet or beak of a bird. *Pisonia grandis* is another species occurring on Aldabra which is particularly well documented as being transported throughout the Indo-Pacific by booby birds.

The introduction of the two *Pandanus* species to Aldabra was probably by sea currents. The fruits when dry are quite fibrous and buoyant, although the particularly extensive distribution of *Pandanus tectorius* throughout the atoll is probably due to tortoises which eat the fruits and pass out the seeds with their faeces. As far as the smaller herbaceous plants are concerned it seems likely that they were borne by the wind. Cyclones are infrequent, but occasionally occur, as for example in 1966, causing considerable damage to the vegetation. If this has been happening

for the past few thousand years there must be a good chance of the smaller-seeded species being carried to the island. These could include the small herbs *Ruellia*, *Lagrezia*, *Nesogenes* and *Hypoestes*. Most of the grasses on Aldabra have very small seeds which could easily be wind carried, as could the seeds of the sedges which occur on the island.

In comparing the colonization mechanisms of the coastal and inland floras it is obvious that the coastal habitats will receive a steadier flow of colonizers than the inland habitats. This continual addition of genetic material from populations outside Aldabra must act as a substantial stabilizer to the coastal species in as much as it prevents any wandering and segregation of characters which might result in the production of new species and although increasing the range of variation of these coastal species it keeps them in a continuum of their characters.

On the other hand, the flow of new plants into the inland habitats is far less frequent and certainly erratic. The gene pools of these inland species have probably not expanded much since their first arrival on Aldabra, thus any change or reshuffling of the characters of these plants would immediately be subject to the selective forces of the Aldabra environment, the bare limestone rock, erratic climate and thin soil. It is this combination of a restricted genetic population and the influence of the environment which has resulted in the evolution of the species peculiar to Aldabra and these endemics amount to almost 20% of the indigenous flora.

#### 7. CONCLUSION

From the evidence of geographical distribution and habitats previously analysed and described several important facts emerge:

1. The indigenous flora of Aldabra comprises an exceptionally large number of species (166) for a coral island.
2. This flora has been derived from widespread and extremely local sources.
3. The proportions of the flora derived from these different sources vary considerably (see table 1 on page 228).
4. In numbers of species, those of widespread distribution have contributed mainly to the coastal flora, and those of local distribution mainly to the inland flora.
5. The high level of endemism (20%) can be attributed to the sporadic colonization of the particularly large inland area by new plants and the influence of the poor soil and exacting climate exerting selective pressures on variations of the species present.

The large and varied number of species in the flora is probably the most significant feature which makes Aldabra botanically unique amongst coral islands.

I wish to express my thanks to colleagues at Kew and to Dr F. R. Fosberg for their valuable help and advice during the preparation of this paper.

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