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Autor: Wild, H.
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Phytogeography and the Gondwanaland position of Madagascar

H. WILD

SUMMARY

The distributions of about 80 species common to Madagascar and the mainland of Africa are considered in relation to three alternative suppositions regarding the Gondwanaland position of Madagascar prior to fragmentation.

The proportion of southeast African — Madagascar — distributions is about four times that for the northern area, i.e. the Somali — Kenya — Tanzania coast, but the pattern as a whole is considered to favour the northern position of Madagascar, followed by a movement south to its present position opposite Mozambique.

RÉSUMÉ

Les aires de répartition d'environ 80 espèces qui sont communes à Madagascar et au continent africain, sont prises en considération selon trois possibilités de position de Madagascar par rapport au Gondwana avant la fragmentation de ce dernier.

La proportion des aires de répartition communes au sud-est africain et à Madagascar est à peu près quatre fois celle de la région du nord, c'est-à-dire la côte de la Somalie, du Kenya et de la Tanzanie.

Le modèle de l'ensemble, cependant, est favorable à une position initiale septentrionale de Madagascar suivie d'un déplacement vers le sud jusqu'à sa position actuelle en face du Mozambique.

Introduction

Recent estimates of the fit of the various land masses concerned prior to the fragmentation of Gondwanaland, such as those of King (1962) and Smith & Hallam (1970) have been most encouraging to phytogeographers concerned with the flora of the Gondwanaland area. Not only do they permit a logical interpretation of the patterns of distribution throughout the supercontinent as discussed briefly by Wild (1968) but the Gondwanaland position of Madagascar in relation to Africa should help explain the affinity between the flora of Madagascar and of the African mainland, particularly of East Africa and South Central Africa.

Unfortunately, it appears that there is disagreement among geophysicists writing in the geomagnetic field, and geomorphologists, as to the movement and position of Madagascar (Anon., 1970). The older view, as expressed recently by Wright & McCurry (1970) is that "Madagascar followed India and the Seychelles northeast-

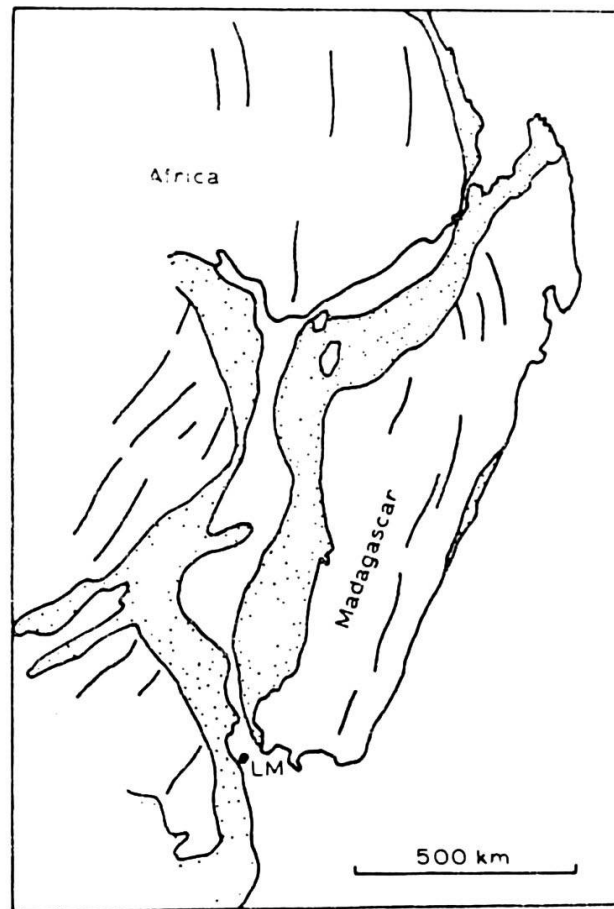


Fig. 1. — Gondwanaland position of Madagascar (Wright & McCurry, 1970).

wards, having originally occupied the Inhambane delta region northeastwards of Lourenço Marques". If this suggestion proves to be true then close affinities between the floras of Madagascar and the adjacent mainland are very likely (Fig. 1).

Flower & Strong (1969), on the other hand, consider that Madagascar has been in its present position relative to Africa since at least the late Carboniferous and probably since the Precambrian. Although there is still no direct fossil evidence for the time of origin of the flowering plants, the range of estimates as given by Takhtajan (1970) is between the Triassic and the Jurassic. As, in any case, a considerable time must be allowed for the attainment of the taxonomic and morphological diversity which is evident in the highly evolved angiosperm floras common to both Madagascar and Africa, a separation between the two land masses as early and continuous as suggested by Flower & Strong (1969) would therefore not produce affinities unless substantial migration across the Mozambique Channel were possible. It is difficult to say how likely such migration might be but the relationship between the islands of the Gulf of Guinea and the mainland may be of interest in this connexion (Exell, 1944). These islands are of recent, probably Tertiary, volcanic origin and so the similarities of their flora and that of the mainland dealt with in detail by Exell must be by means of migration across the sea. However, Fernando Po is only 32 km from the mainland,

Principe about 220 km from the mainland and S. Tomé a little more (135 km SSW of Principe). The ocean barrier of the Mozambique Channel is 250-500 km approximately at present, so migration across it is less likely, but it is difficult to say to what extent it would be diminished or whether it would be insignificant.

More recently there has appeared among geomorphologists a fairly widespread acceptance of a suggestion first made by Du Toit (1937) and supported by several workers, including a recent computer fit of the southern continents (Smith & Hallam, 1970), which places Madagascar in a reconstruction of Gondwanaland in a more northerly position along the present southern-Somali/Kenya/Tanzania coastline (Fig. 2). Nevertheless, as Hallam has said as recently as 1973 (p. 81), "The position of Madagascar is clearly the most enigmatic piece in the whole puzzle".

The botanist cannot expect to tell the geomorphologist or geophysicist what his results should indicate but it may be useful to express what is the more likely alternative from a phytogeographical point of view. As a botanist who was working in the relevant area, the present author had collected data some years ago which he thought pointed to the likelihood of a southern or Mozambique position of Madagascar (Wild, 1951: 5). These data have expanded since then but proved to be somewhat variable and did not always favour the southern position of Madagascar. Hilliard & Burtt (1971: 379-381, Fig. 50) have also produced evidence supporting the northern position. They postulate a northern (in our sense) centre of origin of the genus *Streptocarpus* which fits best their conclusions on the evolution of the sections of the genus at present distributed in Madagascar and the African mainland.

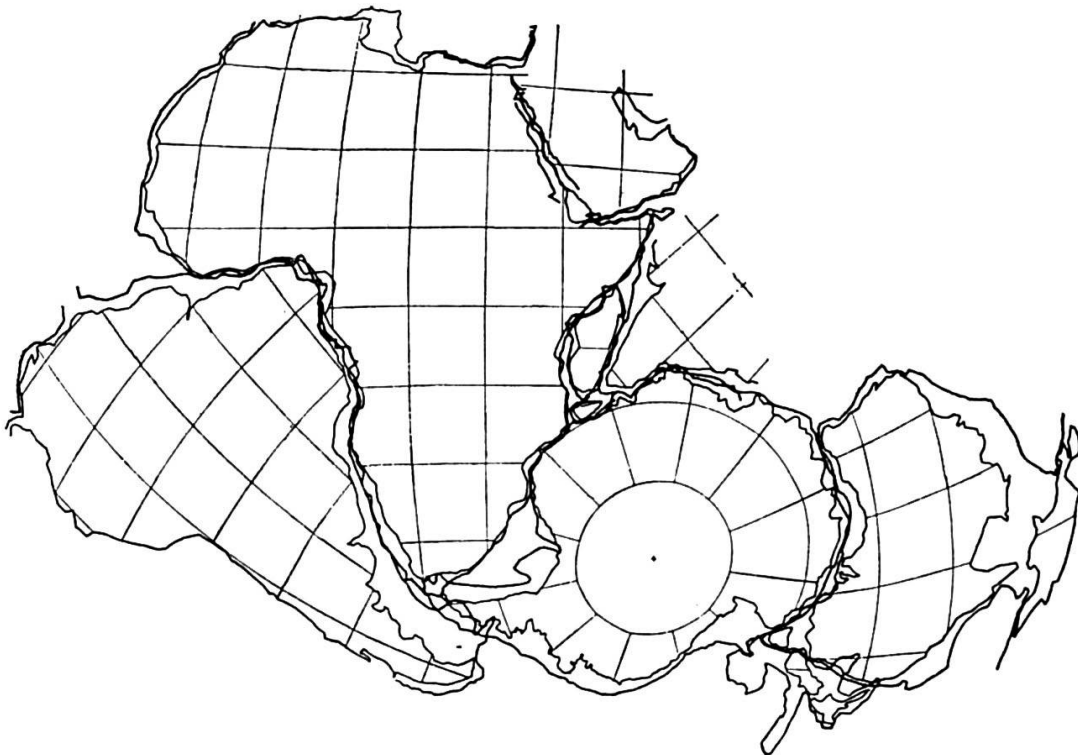


Fig. 2. — The fit of the southern continents (Smith & Hallam, 1970).

This is an intriguing piece of evidence but rests, however, on what can only be a hypothesis as far as past evolution of *Streptocarpus* is concerned and on evidence from one genus.

An attempt has been made therefore to analyse the general distribution data obtainable from most if not all the reliable taxonomic works which cover the area concerned. These are the "Flore de Madagascar et des Comores" (Humbert, 1936-), the "Flora Zambesiaca" (Exell & al., 1960-), the "Flora of Tropical East Africa" (Turrill & Milne-Redhead, 1960-) and a number of monographic or revisional works mentioned in their appropriate places later. A more general but very comprehensive global review of Madagascar phytogeographic relationships can be found in DeJardin & al. (1973).

Firstly, there is a group of species with widespread distribution in Africa and Madagascar, and even in some cases in various parts of Asia also. These have no significance from our point of view and so only a selection has been listed below. Another category occurs in Madagascar and in eastern Africa from either Ethiopia, Somaliland, or Kenya southwards more or less continuously to southern Mozambique or S. Africa which favour neither a northerly (Somaliland/Kenya/Tanzania) or a southerly (Mozambique) position for Madagascar. These have, however, been fairly comprehensively listed. The remainder have been divided into "northern position" distributions and "southern position" distributions. The taxa chosen are *species* mostly, with common Africa-Madagascar distributions, which must illustrate very close phytogeographical linkages. This is interesting since Hawkes & Smith (1965) thought it sufficiently remarkable to stress that some modern *genera* such as *Gossypium* and *Solanum* were older than Continental Drift and it seems possible that a good many *species* may have been also. The value of the evidence given below in this connexion will depend on the relative importance we place on the independent stabilities of the floras of Madagascar and the mainland and the extent of migration across the Mozambique Channel at its present day width, or at narrower intervals if Smith & Hallam's (1970) view is correct and Madagascar must be assumed to have parted company with the Somali/Kenya/Tanzania region about the Upper Cretaceous (about 100×10^6 years ago) (Smith & Hallam, loc. cit.: 143) and then moved southwards to its present position at distances from the mainland about which we have no knowledge.

MADAGASCAR—AFRICA DISTRIBUTIONS

(F. M. = Flore de Madagascar et des Comores; F. T. E. A. = Flora of Tropical East Africa; F. Z. = Flora Zambesiaca)

I. Selection of species widespread in Africa and Madagascar, etc.

1. *Hibiscus panduriformis* Burm. f.
Madagascar, Trop. Afr., Asia & Australia.—Hochr. in F. M. *Malvac.*: 56 (1955).
2. *Hibiscus physaloides* Guill. & Perr.
Madagascar & Seychelles, Trop. Afr. & S. Afr.—Hochr. tom. cit.: 81 (1955).
3. *Ilex mitis* (L.) Radlk.
Madagascar, the mountains of Trop. & S. Afr.—Perrier in F. M. *Aquifoliac.*: 2 (1946); Mendes in F. Z. 2,1: 353 (1966).

4. *Harungana madagascariensis* Lam. ex Poir.
Madagascar & Mascarenes, Trop. Afr., Fernando Po, S. Tomé, Zanzibar & Pemba.—Perrier in F. M. *Hypericac.*: 12 (1950); Robson in F. Z. 1, 2: 393 (1961).
5. *Melanthera scandens* subsp. *madagascariensis* (Bak.) Wild
Madagascar, widespread in Trop. Afr. from Zaire to SW. Afr. and Ethiopia to Mozambique.—Wild in *Kirkia* 5, 1: 7 (1965).

II. Species of the northern position (Somaliland-Kenya-Tanzania) and Madagascar

1. *Commelina madagascariensis* C. B. Cl.
Madagascar, Ruwenzori area.—Perrier in F. M. *Commelinac.*: 19 (1938).
2. *Commelina ramulosa* Perr.
Madagascar, Seychelles, Zanzibar.—Perrier in F. M. *Commelinac.*: 21 (1938).
3. *Commelina scandens* Welw.
Madagascar, Tanzania & Angola.—Perrier in F. M. *Commelinac.*: 14 (1938).
4. *Rhopalophila umbellata* (Baill.) Engl.
Madagascar, Kenya—Mozambique.—Cacavo & Keraudren in F. M. *Opiliac.*: 4 (1955).
5. *Obetia pinnatifida* Bak.
Madagascar, northern Tanzania.—Brenan, Check-Lists For. Trees, Shrubs. Brit. Emp. 5, Tanganyika Terr. 2: 627(1949).
[= *O. radula* (Bak.) Hook. & Jacks. fide Léandri in F. M. *Urticac.*: 4 (1965).]
6. *Psilotrichum boivinianum* (Baill.) Cavaco
Madagascar, Kenya (Mombasa), Tanzania.—Cavaco in F. M. *Amaranthac.*: 46 (1954).
[= *P. axillare* C. B. Cl. in Fl. Trop. Afr. 6, 1: 60 (1909).]
7. *Cucumis saculeuxii* Paill. & Bois
Madagascar, Uganda, Kenya, Tanzania, Zanzibar, Zaire, Zambia.—Keraudren in F. M. *Cucurbitac.*: 147 (1966); Jeffrey in F. T. E. A. *Cucurbitac.*: 97 (1967).
8. *Zehneria emirnensis* (Bak.) Keraudren
Madagascar, Tanzania.—Keraudren in F. M. *Cucurbitac.*: 47 (1966); Jeffrey in F. T. E. A. *Cucurbitac.*: 124 (1967).
9. *Zehneria peneyana* (Naud.) Aschers. & Schweinf.
Madagascar, Sudan, Kenya, Tanzania.—Keraudren in F. M. *Cucurbitac.*: 43 (1966); Jeffrey in F. T. E. A. *Cucurbitac.*: 127 (1967).
10. *Senecio petitiianus* A. Rich.
Madagascar, Comores, Ethiopia.—Humbert in F. M. *Compos.* 3: 767 (1963).
11. *Sonchus afromontanus* R. E. Fr.
Madagascar, Mts. of Kenya, Tanzania & Zaire.—Humbert in F. M. *Compos.* 3: 888 (1963); Jeffrey in *Kew Bull.* 18: 480 (1966).
12. *Hermannia exappendiculata* (Mast.) K. Schum.
Madagascar, Somali Republic, Kenya, Zanzibar.—Arènes in F. M. *Sterculiac.*: 138 (1959).

III. Species occupying areas on the mainland more or less continuous through the northern and southern positions

1. *Cyanotis nodiflora* Kunth
Madagascar, Eritrea to S. Africa.—Perrier in F. M. *Commelinac.*: 34 (1938).
2. *Uvaria acuminata* Oliv.
Madagascar, Kenya, Mozambique (Zambezia).—Cavaco & Keraudren in F. M. *Annonac.*: 15 (1958); Robson in F. Z. 1, 1: 112 (1960).
3. *Byrsocarpus orientalis* (Baill.) Bak.
Madagascar, Kenya, Tanzania, Mozambique (also in Rhodesia, Botswana & SE. Zaire).—Keraudren in F. M. *Cornac.*: 4 (1958).
4. *Phyllanthus nummularifolius* Poir.
Madagascar, Ethiopia to Mozambique and Rhodesia.—Léandri in F. M. *Euphorbiac.* 1: 40 (1958).
5. *Salacia madagascariensis* (Lam.) DC.
Madagascar, Southern Somalia to Mozambique (Sul do Save).—Perrier in F. M. *Hippocrateac.* 3 (1946); Robson in F. Z. 2, 2: 400 (1966).
6. *Stadmania oppositifolia* Poir.
Madagascar, Réunion, Kenya, Tanzania (as subsp. *oppositifolia*); Rhodesia, Mozambique and Transvaal (as subsp. *rhodesica* Exell).—Exell in F. Z. 2, 2: 533 (1966).

7. *Deinbollia borbonica* Scheff.
Madagascar, Somali Republic to northern Mozambique (i.e. predominantly northern position).—Exell in F. Z. 2, 2: 522 (1966).
8. *Bivinia jalbertii* Tul.
Madagascar, Kenya, Mozambique (Tanzania border), Rhodesia.—Perrier in F. M. *Flacourtiac.*: 67 (1946); Wild in F. Z. 1, 1: 296 (1960).
9. *Terminalia boivinii* Tul.
Madagascar, Kenya to Mozambique (Zambezia).—Capuron in F. M. *Combretac.*: 59 (1954); Exell in *Kirkia* 7, 2: 230 (1970).
10. *Strychnos decussata* (Pappe) Gilg
Madagascar, Kenya to the Transvaal.—Leeuwenberg in *Meded. Landbouwhogeschool* 69, 1: 1-316 (1969).
11. *Strychnos henningsii* Gilg
Madagascar, Sudan to Eastern Cape, S. Africa.—Leeuwenberg loc. cit.
12. *Strychnos spinosa* Lam.
Madagascar, Ethiopia to Cape Province, S. Africa.—Leeuwenberg loc. cit.
13. *Strychnos pangaensis* Gilg
Madagascar, Kenya to Lourenço Marques.—Leeuwenberg loc. cit.
14. *Strychnos magadascariensis* Poir.
Madagascar, Somalia to Natal.—Leeuwenberg loc. cit.
15. *Priva meyeri* Jaub. & Spach
Madagascar, Uganda and Tanzania to Cape Province.—Moldenke in F. M. *Verbenac.*: 29 (1956).
16. *Utricularia appendiculata* E. A. Bruce
Madagascar, widespread in E. & Central Africa.—P. Taylor in *Kew Bull.* 18: 20 (1964).
17. *Utricularia cymbantha* Oliv.
Madagascar, widespread in E. & Central Africa.—P. Taylor loc. cit.
18. *Utricularia welwitschii* Oliv.
Madagascar, widespread in E. & Central Africa.—P. Taylor loc. cit.
19. *Blepharispermum zanguebaricum* Oliv. & Hiern
Madagascar, Kenya, Zanzibar & Mozambique (Niassa Distr.).—Humbert in F. M. *Compos.* 2: 378 (1962).
20. *Momordica trifoliolata* Hook. f.
Madagascar, Kenya, Uganda, Tanzania, Mozambique.—Keraudren in F. M. *Cucurbitac.*: (1966); Jeffrey in F. T. E. A. *Cucurbitac.*: 37 (1967).
21. *Lobelia anceps* L. f.
Madagascar, Somali Republic to Mozambique and S. Africa.—Wimmer in F. M. *Lobeliac.*: 8 (1953).
22. *Monopsis stellarioides* (Presl) Urban
Madagascar, Ethiopia to Cape Province.—Wimmer in F. M. *Lobeliac.*: 29 (1953).
23. *Erythroxylum platycladum* Boj.
Madagascar, northern Kenya to northern Mozambique.—Perrier in F. M. *Erythroxylac.*: 33 (1952); Robson in F. Z. 2, 1: 106 (1963).

IV. Species with predominantly southern position but overlapping into Tanzania

1. *Macphersonia hildebrandtii* O. Hoffm.
Madagascar, Tanzania, Zanzibar, Mozambique (as far south as Sul do Save).—Exell in F. Z. 2, 2: 534 (1966).
2. *Sorindeia madagascariensis* Thou.
Madagascar, Tanzania, Zanzibar, Malawi and Mozambique (as far south as Zambezia).—Perrier in F. M. *Anacardiace.*: 26 (1946); A. & R. Fernandes in F. Z. 2, 2: 568 (1966).
3. *Olax dissitiflora* Oliv. (= *O. andronensis* Bak.)
Madagascar, Tanzania (Dar-es-Salaam), south to the Transvaal.—Cavaco in F. M. *Olacac.*: 59 (1955).
4. *Boehmeria platyphylla* D. Don
Madagascar, Tanzania to Mozambique and Rhodesia.—Léandri in F. M. *Urticac.*: 72 (1965).

5. *Canarium madagascariensis* Engl.
Madagascar, Tanzania south to Mozambique (Zambezia).—Perrier in F. M. *Burserac.*: 43 (1946); Wild in F. Z. 2, 1: 283 (1963).
6. *Clerodendrum incisum* Klotzsch
Madagascar, Tanzania, Mozambique and Rhodesia.—Moldenke in F. M. *Verbenac.*: 163 (1956).
7. *Aphloia theiformis* (Vahl) Benn.
Madagascar, Tanzania, Malawi, Mozambique, Rhodesia and the Transvaal.—Perrier in F. M. *Flacourtiac.*: 13 (1946); Wild in F. Z. 1, 1: 279 (1960).
8. *Brexia madagascariensis* Thou. ex Ker-Gawl.
Madagascar, Tanzania (Bagomoyo southwards) and Mozambique.—Mendonça & Wild in F. Z. 1, 1: 14 (1960).
9. *Mascarenhasia variegata* Britt. & Rendle
Madagascar, Tanzania (Morogoro and Mafia I.), Rhodesia, Mozambique.
10. *Strychnos potatorum* L. f.
Madagascar, Tanzania, Mozambique to the Transvaal.
Leeuwenberg in *Meded. Landbouwhogeschool* 69, 1: 218 (1969).

V. Species of the southern position (Mozambique and southwards into S. Africa)

1. The genus *Coleotrype* C. B. Cl.
6 species in Madagascar, one species in Natal and Rhodesia.—Perrier in F. M. *Commelinac.*: 36-46 (1938); Wild in *Proc. Rhodesia Sci. Assoc.* 43: 5 (1951).
2. *Floscopa glomerata* Hassk.
Madagascar, Malawi, Rhodesia, S. Africa.—Perrier in F. M. *Commelinac.*: 30 (1938).
3. *Dianella ensifolia* (L.) Red.
Madagascar, Mascarenes, Rhodesia (also in Asia and Australia).—Perrier in F. M. *Liliac.*: 17 (1938); Wild in *Kew Bull.* 1953: 251 (1953).
4. *Faurea forficuliflora* Bak.
Madagascar, Malawi, Mozambique and Rhodesia.—Wild in *Proc. Rhodesia Sci. Assoc.* 44: 11 (1956).
5. *Korthasella opuntia* var. *gaudichaudii* (Van Tiegh.) Danser
Madagascar, Eastern and Northern Cape Province.—Balle in F. M. *Loranthac.*: 113 (1964).
6. *Erythroxylum gerrardii* Bak.
Madagascar, Mozambique (Niassa to Manica and Sofala).—Perrier in F. M. *Erythroxylac.*: 12 (1952); Robson in F. Z. 2, 1: 105 (1963).
7. *Polygala filicaulis* Baill.
Madagascar, Mozambique.—Perrier in F. M. *Polygalac.*: 3 (1955); Exell in F. Z. 1, 1: 327 (1960).
8. *Androstachys jonhsonii* Prain
Madagascar, Rhodesia, Mozambique and N.E. Transvaal.—Codd, *Trees & Shrubs Kruger Nat. Park*: 95 (1951); Wild in *Acta Phytogeogr. Suec.*: 207 (1968).
9. *Neopalissya castaneifolia* (Baill.) Pax
This species, and genus, are recorded as endemic to Madagascar [Pax in Engl., *Pflanzenr. Euphorb. Mercurial.*: 16 (1914)]. However, in 1946 specimens were collected in Chirinda Forest, Rhodesia, of a species either identical with, or closely related to, the Madagascan species [Wild in *Proc. Rhodesia Sci. Assoc.* 43: 5 (1951)].
10. *Abutilon angulatum* var. *macrophyllum* (Bak. f.) Hochr.
Madagascar, Malawi, Mozambique, Rhodesia, Transvaal and Natal.—Hochr. in F. M. *Malvac.*: 139 (1955); Meeuse in F. Z. 1, 2: 489 (1961).
11. *Hypericum wilmsii* R. Keller
Madagascar, Rhodesia, Transvaal, Lesotho and Cape Province.—Perrier in F. M. *Hypericac.*: 4 (1950), as *H. rupestre* and *H. bojeranum* sensu Perrier; Robson in F. Z. 1, 2: 383 (1961).
12. *Hyalocalyx setiferus* Rolfe
Madagascar, Mozambique (Quelimane).—Perrier in F. M. *Turnerac.*: 4 (1950).

13. The genus *Piriqueta* Aubl.
3 species in Madagascar, 1 species S. African, 1 species tropical American.—Perrier in F. M. *Turnerac.*: 7 (1950).
14. *Meiostemon tetrandrus* subsp. *australe* Exell
This subsp. shows transition to *M. humbertii* (Perrier) Exell ex Stace (= *Combretum humbertii* Perrier). Occurs in the Zambesi valley.—Capuron in F. M. *Combretac.*; Exell in *Kirkia* 7, 2: 230 (1970).
15. *Utricularia capensis* Spreng.
Madagascar, Transvaal, Lesotho and Cape Province.—Taylor in *Kew Bull.* 18: 135-144 (1964).
16. *Pseudocalyx saccatus* Radlk.
Madagascar, Rhodesia.—Benoist in F. M. *Acanthac.*: 20 (1967); S. Moore in *J. Linn. Soc., Bot.* 40: 156 (1911).
17. *Corollocarpus bainesii* (Hook. f.) Meeuse
Madagascar, Rhodesia, Mozambique, Transvaal.—Meeuse in *Bothalia* 8: 41 (1962); Keraudren in F. M. *Cucurbitac.*: 70 (1966).
18. *Cucumella cinerea* (Cogn.) Jeffrey
Madagascar, Angola Rhodesia, SW. Africa.—Keraudren in F. M. *Cucurbitac.*: 54 (1966).
19. *Cucumis africanus* L. f.
Madagascar, Angola, Rhodesia, Mozambique, Transvaal, Natal.—Keraudren in F. M. *Cucurbitac.*: 142 (1966).
20. *Cucumis hirsutus* Sond.
Madagascar, Zambia, Rhodesia, Transvaal, Natal.—Keraudren in F. M. *Cucurbitac.*: 143 (1966).
21. *Lobelia filiformis* Lam. var. *filiformis*
Madagascar, Réunion, Mauritius, Natal.—Wimmer in F. M. *Lobeliac.*: 20 (1953).
22. *Lobelia filiformis* Lam. var. *krebsiana* (Presl) Wimmer
Madagascar, Natal.—Wimmer in F. M. *Lobeliac.*: 26 (1953).
23. *Lobelia filiformis* Lam. forma *multipilis* Wimmer
Madagascar, Rhodesia, Mozambique, Angola.—Wimmer in F. M. *Lobeliac.*: 20 (1953).
24. *Ani opappus anemonifolius* (DC.) G. Tayl.
Madagascar, Angola, Zambia.—Wild in *Kirkia* 4: 58 (1964).
25. *Anisopappus dentatus* (DC.) Wild
Madagascar, Rhodesia, Zambia.—Wild in *Kirkia* 4: 63 (1964).
26. *Blumea cafra* (DC.) O. Hoffm.
Madagascar, Southern Zambia, Rhodesia, Mozambique, S. Africa.—Humbert, in F. M. *Compos.* 2: 364 (1962); Wild in *Kirkia* 7, 1: 126 (1969).
27. *Cotula villosa* DC.
Madagascar, S. Africa.—Humbert in F. M. *Compos.* 3: (1963).
28. *Gnaphalium glomerulatum* Sond.
Madagascar, S. Africa.—Harv. in Harv. & Sond. *Fl. Cap.* 3: 262 (1865).
29. *Hieracium capense* L.
Madagascar, Rhodesia, Transvaal, Natal, Cape Province.—Humbert in F. M. *Compos.* 3: 893 (1963).
30. *Senecio madagascariensis* Poir. var. *madagascariensis* (= *S. ruderalis* Harv.)
Madagascar, Natal.—Humbert in F. M. *Compos.* 3: 736 (1963).
31. *Senecio helminthoides* (Schultz Bip.) Hilliard
Madagascar, Mozambique, Rhodesia (Wedza), Natal, Cape, Transvaal, Swaziland.—Humbert in F. M. *Compos.* 3: 773 (1963); Hilliard & Burt in *Notes Roy. Bot. Gard. Edinburgh* 32: 379 (1973).
32. *Sonchus dregeanus* DC.
Madagascar, Eastern Cape.—Humbert in F. M. *Compos.* 3: 889 (1963).
33. The genus *Stoebe* L.
2 endemic species in Madagascar, one in Tanzania, one in Angola, one in Rhodesia and on the Drakensberg, the remainder, of which there are about 30, in the Cape.—Weimarck in *Acta Univ. Lund.* n. f. 2, 37, 5: 1-141 (1941).

Discussion

The above survey of Africa-Madagascar flowering plant distributions reveals that if we exclude species covering the whole of Africa and Madagascar as indicating very little:

- 12 species occupy a northern position (Somali Republic—Kenya—Tanzania) approximately;
- 33 species occupy a southern position (Mozambique and adjacent countries to the west and south);
- 10 species occupy mainly a southern position but with some overlap into Tanzania;
- 23 species have a distribution starting somewhere in the northern area from Ethiopia or the Somali Republic southwards and ending in Mozambique or to the south of this territory.

These results may be tentatively interpreted as follows:

1. The opinion of Flower & Strong (1969) that Madagascar was in its present position relative to Africa (Fig. 3, Madagascar position 1) since late Carboniferous or even Precambrian time (almost certainly before the origin of the angiosperms) is not supported since although the southern connexions could be understood the northern ones would seem anomalous.
2. A "southern" Gondwanaland position (Fig., 3 Madagascar position 3), suggested as worthy of re-examination recently by Wright & McCurry (1970), is perhaps supported to the extent that, if we include those species that only occur in Tanzania a short distance from Mozambique and then are distributed to the south, the ratio of southern to northern position species is about 4:1. This is however to look at these southern distributions in isolation and the progressive overlap of distributions from north to south blurs the force of this argument.
3. If, however, we consider the suggestion presented recently by Smith & Hallam (1970) and supported by several other groups of workers, where it is suggested that before the fragmentation of Gondwanaland, Madagascar occupied a position along the present coasts of the Somali Republic, Kenya and Tanzania (Fig. 3, Madagascar position 2) and then after the break about Upper Cretaceous time moved southward to its present position, we see the sequence of species distributions that could be expected to follow. Species of the northern position would date from the pre-fragmentation period which nevertheless was significantly later than the origin of the angiosperms. Subsequently, Madagascar moved southwards, perhaps along the coast to begin with and later moving further out to sea, or moving gradually further from the coast from the beginning. An analogous case is that of Baja California which it is suggested (Dietz & Holden, 1970: 111) has begun a movement towards the northwest towards the Aleutian trench and away from California east of the San Andreas fault. This would fit sensibly into the phytogeographical position where we have distributions in a northern position, some from north to south of the whole or major part of East Africa, some intermediate between the northern and southern positions and some in the southern position. The greater number of southern distributions could be explained

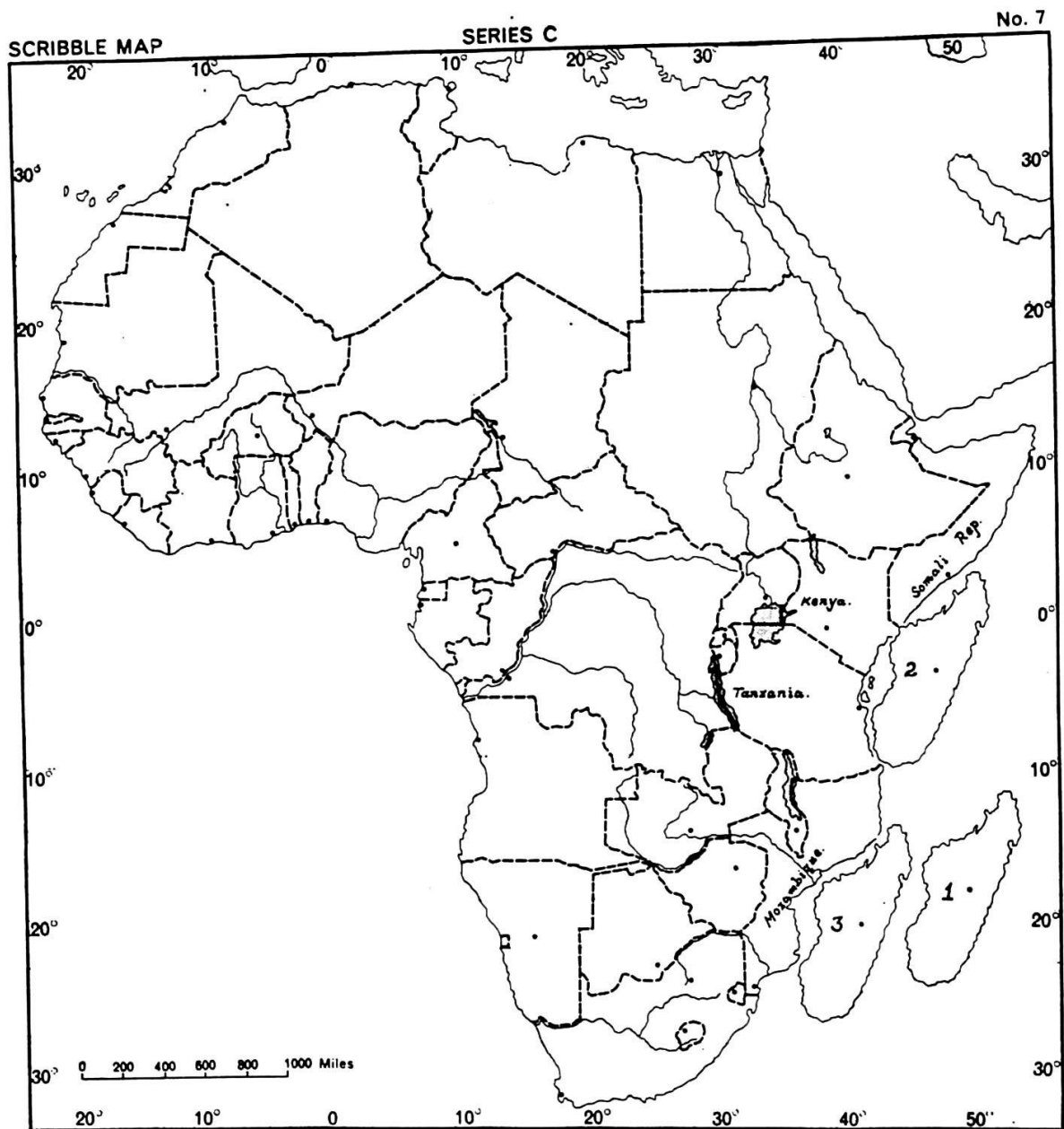


Fig. 3. — Africa and Madagascar with: 1, Madagascar in its present position; 2, Madagascar in the "northern" Gondwanaland position; 3, Madagascar in the "southern" Gondwanaland position.

if migration across the Mozambique channel were significant. As between the islands of the Gulf of Guinea and West Africa where migration has occurred on a large scale, and the Mozambique Channel, we would expect to find a reduction in migratory movements, due to the greater separation of the latter, but if Madagascar had kept a coastal or near coastal position in its movement southwards and time were in its favour the southern position could be expected to have retained more connexions. There is, however, no geomorphological evidence, as far as I know, for the type of behaviour exhibited by Madagascar and its suggested southwards movement.

On the other hand, there is no good evidence as to what a 250-500 km barrier in the Mozambique Channel means in relation to migration over this gap. If migration could take place then perhaps only a matter of the relatively longer time Madagascar spent in the southern position could explain the preponderance of southern distributions.

To conclude, the phytogeographical evidence cannot exclude any of the possibilities suggested for the position of Madagascar in a Gondwanaland context, but on the whole, it supports the view that Madagascar, until the break up in the Upper Cretaceous or thereabouts, occupied a position alongside the Somali Republic, Kenya and Tanzania and then moved southwards to its present position either near the African coast or at some unknown distance from it and ending up 250-500 km from the Mozambique coast.

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