

## MADAGASCAR AND NEW CALEDONIA

### A problem in plant geography

by

RONALD GOOD, M. A., Sc. D.

(Dept. of Botany, University College of Hull).

A perusal of the most recent full-length presentation of the Angiosperms, the great and valuable compilation of Lemée (1), recalls vividly to mind a point of plant geography which, though familiar enough, has scarcely received the critical consideration it deserves, namely the not infrequent association, in matters phytogeographical, of Madagascar (and the other islands of the western Indian Ocean) and New Caledonia, two regions which from their relative positions would hardly be expected to show any considerable relationship.

This is because Lemée pays particular attention to both these areas, doubtless because they are both French possessions, but they are also areas of exceptional phytogeographical interest and although political circumstances may perhaps have increased the similarities of their adventive floras, they can scarcely be held responsible for any resemblances which may exist between their native floras.

But the political relation is not the only one between the two and there are other parallels which may have greater botanical significance. The relative situations and shapes of the two main areas are alike: both lie at the same south latitude at very roughly the same sort of distance east of a continental land-mass, and have no appreciable land eastwards of themselves for thousands of miles: both are rather alike in shape though not in orientation or size, Madagascar being thirty times as extensive as New Caledonia. Their physiographic structure is also curiously similar, the eastern two-thirds or so of each being of igneous rocks rising to a considerable elevation, and the western parts being covered with Permian or younger sedimentary rocks. Largely because of these various similarities the climatic values also correspond notably.

How far these resemblances may be genetical in any real sense is a matter for geologists but they certainly reinforce the impression left by Lemée's work that an attempt to discover how far a floristic relation exists between the two is well worth making. To do this exhaustively would necessitate a careful and complete systematic study of both floras but a preliminary answer to the question can be given by something a good deal less ambitious and laborious, namely a brief geographical analysis of the flora of the smaller, New Caledonia, in certain particular

ways and with special reference to the larger, and such an analysis is the subject here.

Although it has been convenient so far to speak rather of Madagascar only, all the islands of the East African Island Region, namely the Comoros, the Seychelles and the Mascarenes in addition, are concerned in the problem, and hereafter the term Madagascar, unless qualified, is used in this wider sense to include them all. The phytogeographical data quoted may be assumed, in absence of any definite reference, to be derived from such general sources as the first edition of the "Pflanzenfamilien", "Index Kewensis" and Lemée's "Dictionnaire".

### The Flora of New Caledonia.

The flora of New Caledonia has long aroused interest as one of the richest and most peculiar in the world, but the chief more modern sources of information about it are the accounts of the explorations there of Sarasin and Roux (2) and of Compton (3, 4) and the many systematic studies of Guillaumin (5). The first of these in particular contains, from the pen of the last-named, a detailed analysis of the flora, especially from the floristic point of view, in which its general features are well displayed and the conclusion reached that it is mainly Australian in relationship; that it contains also approximately equal Malaysian, Papuan and Polynesian elements; and that there are also distinct but more distant relationships with South Africa and South America. Unfortunately in these comparisons Madagascar receives no particular mention except for the statement that it is the only place with a higher degree of endemism than New Caledonia, a point perhaps not altogether unrelated to our present problem.

From the various sources that have been mentioned it is possible to build up a reasonably complete annotated list of the genera of New Caledonia and this list is considered below in two ways calculated to reveal something at least of any relationship with Madagascar which there may be and to warrant some conclusion on the question at issue.

The list contains over 800 genera, including adventives, and this is of course only one expression of various taxonomic conceptions but since it is not necessary to make the analyses here strictly quantitative this imponderable factor need not cause undue concern.

The genera in the list can first be divided into three:

1. Genera of wide distribution represented in New Caledonia by wide (not endemic) species only. These include some special types such as strand plants, and many others are doubtless adventives.
2. Genera not endemic to New Caledonia but represented there by endemic species.
3. Genera endemic to New Caledonia.

It is scarcely likely that any prolonged consideration of the first of these will be profitable if only because of the uncertainty of the status of many of its members in the island. It is, moreover, the 'expected' element of the flora, that may be anticipated simply having regard to the position of the island in the south-eastern part of the Old World

tropics. For both these reasons no more need be said about it here, though this is not to suggest that it is quite without interest. The second and third, on the other hand, are clearly of considerable possible significance because they constitute the characteristic part of the flora, and to these careful attention must be given.

#### The genera with endemic species in New Caledonia.

The number of genera not themselves endemic to New Caledonia but which have endemic species there appears to be about 250 and these can be sorted into the following four categories:

1. Wide, often pantropical genera, with endemic species well scattered over their ranges, amount to about 24 %.
2. Asiatic-Australian-Polynesian genera of Asiatic preponderance amount to about 20 %.
3. Asiatic-Australian-Polynesian genera of Australasian preponderance amount to about 28 %.
4. Others, amounting to about 28 %.

Of these four the first may reveal facts of interest if and when the detailed affinities of individual species are worked out but otherwise is not likely to help our enquiry much. Similarly the second and third can be passed over here without attention because they do not occur in Madagascar. The fourth category, on the other hand, is the crucial one.

When the 75 or so genera of this fourth category are examined it is found that all save one or two of them either belong to one or other of four types of distribution, or are so similar in some significant way that they can be treated as anomalous examples of them.

A. The first of these is the African-Asiatic-Australian, or 'Old World', type as it may be called because its genera are found in Africa as well as further east and thus, in their fullest expression, cover all the tropics of the eastern hemisphere. It might be expected, considering the considerable total number of genera of this sort, that this would be the largest group, as indeed it is, but even so it amounts to only twenty genera of which three are doubtful, and this is tantamount to saying that of the many Old World tropical genera only a very few have endemic species in New Caledonia. The explanation of this seems to lie in the fact that, with two dissimilar exceptions, the seventeen satisfactory genera are moderately large genera with most of their species either in both Africa and Indo-Malaya or in the latter only, suggesting that they are genera of the northern tropics which have spread southward. The genera of these two kinds are, respectively, *Albizzia*; *Garcinia* (7); *Grewia*, strongly represented in Madagascar; *Macaranga* (7), well represented in Madagascar and in Australasia and slightly anomalous because most of the Asiatic species are in the southern part of the Malay Archipelago; *Maesa*; *Plectronia*; *Scolopia* (7); and *Secamone*, well represented in Madagascar, on the one hand, and *Cleistanthus* (7), in which the species of Africa and of Madagascar form a single section of the genus; *Harpullia* and *Hetaeria*, which are but slightly represented in Africa; *Loranthus* (7); *Pandanus*; *Phajus*; *Syzygium*; and *Tylophora*.

The two exceptions are *Flagellaria* and *Helichrysum*. The former has one species in Fiji and Samoa, one in New Caledonia, and one throughout the Old World tropics (7), but Thonner (6) says it has economic uses in Africa, which might mean that it is not native there. Neither source mentions it for Madagascar.

*Helichrysum* is of special interest. The geography of Composite genera is notoriously difficult but *Helichrysum* is clearly marked as a southern genus, as are all its immediate relations in the *Gnaphalieae*. At least half its species are South African; tropical Africa has a considerable number; there are more than this in Madagascar; and more still in Australia. It is interesting too to note that the New Caledonian species belongs to the Australian section *Ozothamnus* and was the first endemic Composite to be described from the island (11).

The three other genera are *Gymnosporia*, which if rightly considered as having endemic species in New Caledonia merely adds another to the genera that are predominantly Indo-Malayan; *Oberonia*, which is variously interpreted but included here on the authority of Thonner (6), is another predominantly Indo-Malayan genus; and *Schefflera* which may be noted, but about which little useful can be said.

B. The second is the Asiatic-Australasian-American type, in which the genera, though comparatively widely distributed, do not occur in Africa and/or Madagascar. There are about a dozen such, and although they are of somewhat less interest here because of their absence from Madagascar, they call for short notice. The best and most familiar instance is *Symplocos*, the only genus of its family, though *Erythrodès* has a very similar range. *Lucuma* and *Roupala* are chiefly American and in the Old World restricted to Australia and New Caledonia: *Licania* and *Calycorectes* are similar but absent from Australia. The New Caledonian species of the latter are sometimes reckoned as an endemic genus *Spermolepis*. *Litsea* is rather the converse, having but few American species.

Other less typical genera associated with this group are, *Cleidion* (7), which is said to have a single species in Africa; *Myrtus*, a puzzling genus which occurs in the Mediterranean region and has perhaps a South African representative; *Santalum*, the New Caledonian species of which has now been recorded also from the New Hebrides, and which is represented in the New World only on Juan Fernandez; and *Osmanthus*, in which an endemic species from New Caledonia has been named.

Lastly *Oxalis* may be mentioned. This is another predominantly southern genus with its highest species concentrations in South America and South Africa, but the New Caledonian members constitute a special section among American sections (7).

C. The third type is really an extension of the last because it includes the genera that are found in Asia-Australasia-America and also in Madagascar, though not in Africa, and is of outstanding interest here. Strictly speaking there seem to be only two genera of this kind, both familiar to plant geographers, namely *Weinmannia* (7, 8, 9), which is found on Madagascar itself, and *Astelia*, which, according to Skottsberg (8, 10), is found on Réunion, but there are other related con-

ditions. Species of *Ilex* have been described from Madagascar and from New Caledonia and the distribution of the genus will be referred to again later. *Polyscias*, one of the difficult Araliaceous genera, should perhaps be defined in a sense which would include it here. *Hernandia* is, according to Hutchinson (9) typical except that it occurs on Fernando Po and St. Thomé. *Calophyllum* (7) is a wide tropical genus, but the New Caledonian endemic belongs to a section which occurs in the New World and in Madagascar but which is absent from Africa.

D. The fourth and most important type is that in which the genera are found in Asia-Australasia and Madagascar only. In other words they are the Old World genera of New Caledonia which find their western limits somewhere in the islands of the western part of the Indian Ocean. First and foremost here there are the two genera said to occur only in New Caledonia and these islands, namely *Cohnia* (7, 8) and *Cossinia* (8). Both have their western stations in the Mascarenes and not in Madagascar proper. Whether or no these are in all respects good genera the fact remains that they show an extraordinarily close relation between the two regions and they are justifiably maintained here because it is thus that they most plainly show this relation. It may be added that the Cyperaceous genus *Lophoschoenus* has been credited with a similar range and may indeed properly belong here though the generic distinctions in this family are difficult.

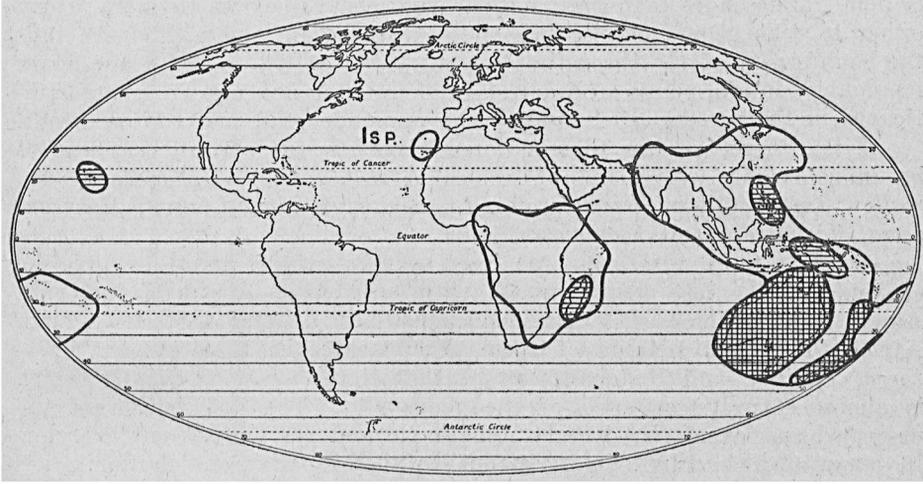
Other genera affording good examples of this type, though their wider occurrences in Australasia make them less conspicuous, are *Alyxia*, well developed in New Caledonia; *Soulamea* (7), with most species in New Caledonia; *Evodia* (7); *Myoporum*, predominantly Australian; *Geniostoma*, well developed in New Caledonia; *Ochrosia*; and *Timonius*. *Dianella* is often considered as another, and includes one species which ranges from Madagascar through India to Australia; Guillaumin (5) mentions 8 species from New Caledonia. *Tieghemopanax* and *Galeola* should perhaps be added but are confused. In *Calpidia* (7) one of the two sections (*Timeroya*) ranges from the Mascarenes to Polynesia.

Three other genera worth notice here are *Canarium* (7), *Homalium* (7) and *Acalypha* (7) because, although they occur in Africa, the species of New Caledonia and of Madagascar are in sections without African representatives, so that they illustrate this fourth type on a subgeneric scale.

Other related genera of significance here, though not strictly belonging to the type are *Cunonia* (7), which is exclusively Australasian except for one species in South Africa (compare *Myrtus*); *Acridocarpus*, said to have numerous species in South Africa but elsewhere only one in New Caledonia, and if this is so a striking converse to *Cunonia*; *Metrosideros*, which in one definition at least includes a species in Madagascar and one in South Africa; *Ventilago*, which occurs in Angola as well as in Madagascar; and *Barringtonia*, which reaches both Madagascar and the East African coast. *Goodyera* may in part also exemplify this type of distribution.

Apart from those just described there is really only one other genus having endemic species in New Caledonia to be discussed and this has been left till now because of its special interest. It is the genus *Pittosporum* and its distribution is shown in the map, which is based on

information in Pritzels revision of the *Pittosporaceae* (7). It will be seen that although the genus occurs widely over tropical Africa and actually has one species in Macaronesia, so that it is really an additional Old World



Distribution of the *Pittosporaceae*, showing, by crossed lines, the areas of highest species concentrations, and by horizontal lines, secondary areas of high species concentration. Australia has 9 genera and 50 species, New Zealand—New Caledonia has 35 *Pittosporum* species, the Philippines, New Guinea, Madagascar and Hawaii have each 12—16 *Pittosporum* species.

tropical genus; it is so obviously and characteristically a Madagascar-Australasian group that it deserves separate recognition. The family is an outstanding instance of one whose fundamental relationships are all below the equator and of the nine genera of which it consists, only *Pittosporum* occurs outside Australia.

### Summary.

The first result of this survey of the wide genera which have endemic species in New Caledonia is certainly to confirm the impression that there is indeed a noteworthy geographical association between Madagascar and that island, even if it is only a particular aspect of a more general relationship between Madagascar and Australasia as a whole.

But the survey gives prominence also to another point, namely the unexpectedly small part that tropical Africa plays in the distribution of the genera reviewed. It almost seems as if there is some factor of exclusion affecting that great region, and there is no indication of any corresponding degree of relation between tropical Africa and New Caledonia such as has been detected between the latter and Madagascar.

### The endemic genera of New Caledonia.

New Caledonia appears to have about 110 endemic genera and these can be roughly classified according to their affinities, that is to say according to their relationships with other genera of their families. When this is done rather more than half of them are seen to be related most nearly either to wide genera or else to Asiatic-Australasian genera, and are thus the counterpart of the three first categories on p. 472 above. These again no doubt contain points of interest in detail but are not of great significance in the present brief study. The remainder fall under three heads.

First, there are less than a dozen genera whose affinities appear to be unmistakably with plants of tropical Africa, namely *Alphandia*, *Anisomallon*, *Cyclophyllum*, *Gonatostyles*, *Lasiochlamys*, *Menepetalum*, *Montrouzeria*, *Normandia* and *Rhopalostachyum*.

Second, there are about a dozen genera whose affinities are the converse of the last, being chiefly with both Asia, Australia and with America, and which show a conspicuous lack of any association with Africa. The most striking of these perhaps are the three genera *Oncotheca*, *Phelline* and *Sphenostemon* of the *Aquifoliaceae*, a family which is almost entirely composed of the genus *Ilex*. The distribution of the described species of *Ilex* is very remarkable and may be set out as below in a way which roughly corresponds to their spatial distribution.

N. America 26	Europe, W. Asia, 5 N. Africa etc.	China, Japan, 117 Formosa Indo-Malaya 123
C. America 69 & W. Indies		
	? S. Africa 1	
Tropical S. 150 America	Madagascar 1	Australia 1 New Caledonia 1
Temp. S. America 3		Pacific Isl. 2

The other genera here are *Adenodaphne*, *Bonatia*, *Canacomyrica*, *Dutailla*, *Exospermum*, *Morierina*, *Piliocalyx*, *Sarcomelicope* and *Zygogynum*.

The rest of the endemic genera bear more directly on the problem of Madagascar and can best be treated *seriatim*. The most striking are the dozen or so endemic genera of *Palmaceae* because all these belong to the comparatively small part of the family, the *Areceae*, which is found all over the family range except in Africa, and which is therefore a counterpart on a larger scale of the genera in the third type on p. 472 above. There are also four endemic genera of *Araliaceae*, *Dizygotheca*, *Eremopanax*, *Octotheca* and *Schizomeryta* which perhaps form a rather similar group.

*Arthroclianthus* finds a place among genera notably lacking in Africa, though one of them occurs in Madagascar; *Beauprea* and *Garnieria* are usually placed near genera from Madagascar and Tasmania; *Bocquillonia* belongs to a wide tropical group but is near an endemic genus of Madagascar; *Canaca* is in a group which is found in all the tropics (including

Madagascar, except Africa; *Greslania* finds a place among Asiatic genera of which one is also in Madagascar; *Loxodiscus* belongs to a group which is Madagascar-Asiatic except for one pantropical member; *Microsemma* is in a group with considerable representation in Madagascar but with one small genus in West Africa; *Podochrosia* and *Pterochrosia* are generally placed between genera from Malaysia and from Madagascar.

This brief survey of the endemic genera of New Caledonia was made in the hope that it would help to confirm or contradict the impression gained in earlier pages. It may fairly be said that it does so and supports the view that there is a greater degree of floristic affinity between Madagascar and New Caledonia than might be expected at first sight.

### Complementary notes on the flora of Madagascar.

Although, as explained earlier, this study is formally one of certain aspects of the New Caledonian flora, the conclusions so far reached make it desirable to consider, very shortly, whether there are any broad facts about the flora of Madagascar which give support to them, and the following facts are perhaps particularly relevant.

1. The proportion of endemic genera in Madagascar is very high, probably higher than anywhere else, even New Caledonia, and perhaps amounting to from 20 to 25 % of all native genera. It is difficult to arrive at a number but the data of Lemée indicate that the conservative estimate given by the present writer elsewhere (8) may be a good deal too low.

2. These endemic genera represent about 80 families and the order of these, when they are arranged according to the number of genera in each, is somewhat reminiscent of the order of families among the endemic genera of New Caledonia (2), e.g. *Palmaceae* and *Sapindaceae* are high in the list while *Compositae*, *Leguminosae* and *Gramineae* are unusually low.

3. The number of genera which are found in both Madagascar and Africa only is considerably less than the number of endemic genera in the former, and is but a small proportion of all the African genera. Moreover, the order of the families in these genera is notably different from that among the endemics, e.g. the *Compositae* are higher and the *Palmaceae* and *Bignoniaceae* much lower.

4. In addition to the endemic genera there is a notable total of other genera which are absent from Africa or north of it. Except for some half dozen found elsewhere only in America, and three in America and Australasia only, all these are found, outside Madagascar, only in Asia and/or Australia. These latter clearly comprise two types, in one of which the genera are predominantly Asiatic, and in the other of which they are predominantly Australasian, the former greatly outnumbering the latter.

### Conclusion.

It is important to realize that the various relationships which have been described in the foregoing pages are, often enough, the expression only of certain opinions regarding the classification of the plants concerned. Thus for instance when species from New Caledonia and from

Madagascar are united into a single genus the apparent affinity between the two regions is greater than it may appear to be if the respective species are placed in different genera. But this is a familiar difficulty in plant geography, and although on particular occasions it may be a very real one, in general it may be accepted that classification is more right than wrong and does express relationship and geographical affinity, if not in detail, then at least in broad terms. This being so the foregoing analyses may be treated as reasonably sound and objective and as expressing facts, even if the quantitative values attributed to them are open to modification.

If this opinion is accepted then two conclusions seem inescapable. The first is that there does indeed exist a floristic relationship between Madagascar and New Caledonia greater than can be accounted for merely by chance or coincidence, and, further, that this relationship is a particular aspect of a larger relation between the islands of the western Indian Ocean and Australasia in the wider sense. The second is that in some ways the peculiarities of the Madagascar flora are greater, and its affinities other than might be expected from its situation in respect of tropical Africa. Especially it seems to have more relationship with America and Asia-Australasia and less with Africa than might be anticipated. It is noteworthy that there is in the Madagascar flora the distinct impression of the presence of two floristic elements describable respectively as 'African' and 'non-African', and that a considerable part of the latter finds its affinities so distinctly below the equator as to merit the term 'southern'.

To postulate and maintain any particular explanation of these facts would need not only a much more detailed study than has been made here but would necessitate also, if the danger of arguing from the particular to the general is to be avoided, taking into due account many other facts of plant geography. Nevertheless it is perhaps permissible in conclusion to suggest one circumstance in which the facts described above would be considerably less formidable than they appear to be. This is the suggestion that Madagascar, instead of being primarily a recent dismemberment of middle Africa is rather primarily one of a series of land surfaces, including South America, Antarctica and Australia, which once, less separated than they are now, were the 'original home of a flora rather distinctive of the southern hemisphere. If this indeed should be the case, then the presence in the flora of Madagascar of an older 'southern' element, overlaid now by a younger but stronger 'African' element, is only what might reasonably be expected, and may throw light on some of the many problems of the antarctic regions which still await solution.

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