

PLANT-GEOGRAPHY OF THE PACIFIC

AS BASED ON A CENSUS OF PHANEROGAM GENERA

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SUMMARY

In 1960 I made a preliminary analysis of the floristic distribution of the native Phanerogam genera of the Pacific islands, which amounted to 1511 genera in all.

The aims of the present work have been to record these more accurately and more critically in detail, especially with regard to native versus introduced, to complete the survey with new records from new explorations made during the interval, and to evaluate new taxonomic literature on Pacific genera. The present list amounts to a total of 1666 genera, as far as known in July 1969, listed in an Appendix.

The floristic relationships of the Pacific islands and the surrounding continental areas are established and a hierarchical subdivision of the flora of the Pacific islands based on demarcations in it is made. Furthermore a nomenclatural stabilization of the names and ranks of the subdivisions is attempted. Chapter IV, 3.

An attempt was also made to find factual data on the correlation between distribution and means of dispersal. Chapter IV, 4.

Secondary aims were to review earlier attempts towards a subdivision of the Pacific flora (Chapter II), two other secondary purposes to see whether traces of the historic plant-geography of the Pacific flora

are still reflected in the present flora (Chapter V), and finally to compare geographic subdivisions and other data from non-Phanerogam taxa, mostly animals, with floristics. Chapter VI.

Chapter III is devoted to an explanation and a discussion of the methods employed.

Arguments are given why only Phanerogams have been considered and why only native genera have been used for computing results. Chapter III, 1—2.

Arguments are given for employing the genus as a working unit. It is shown that the genus is much less susceptible to variability in taxonomic concepts than either the species or the family. Besides it is comparatively easy to establish the distribution of a genus fairly reasonably from literature. Chapter III, 3.

Chapter III, 4 is devoted to a discussion on the sources of information on which this work is based, comprising i.a. literature, herbarium collections and personal information. Many errors are contained in the first two of these and it cannot be avoided that some mistakes have not been detected. Also, the island groups have been investigated with a varying degree of intensity.

The island groups in the Pacific are taken as geographic units of which there are 36. The surrounding land masses are divided into 12 main areas. Chapter III, 5. Of each genus occurring in any of the 36 Pacific unit areas the full distribution is traced. See Appendix.

From a comparative study of generic ranges, it has appeared that they exhibit a restricted number of recognizable patterns, 17 of which have been distinguished. These I have called *distribution types* in this work. Chapter III, 6. The choice of geographic unit areas introduces a certain element of arbitrariness.

Each island group can then be characterized by its set of distribution types: the *distribution types spectra*. It is also possible to calculate floristic relationships or resemblance between the island groups, for which a number of methods are discussed and evaluated. It appears that basically all methods lead to more or less similar conclusions. Chapter III, 9.

As a test for the validity of the conclusions based on the distribution of all genera, similar calculations were performed on 345 revised or otherwise well-known taxa. Although the percentages of the distribution types are slightly different the general conclusions are corroborated. Chapter III, 7.

In addition, an attempt has been made to find whether there is a correlation between the distribution and the means of dispersal of these revised or otherwise well-known taxa. Chapter III, 8.

One of the most important results of this work is the census of Pacific genera. See Appendix.

By using the method of distribution types spectra, demarcation knots and other methods it has been possible to find demarcations and to define phytochores. The main demarcation is that between the New and Old World floras. A hierarchy is set up of subdivisions which is illustrated in fig. 35 and tabulated in table 6.

It appears that a strong demarcation exists between the islands on the American side of the Pacific (Galapagos, Juan Fernandez, etc.) and the western islands. Hawaii and SE. Polynesia form the easternmost frontier of the Old World flora. This conclusion was reached almost unanimously by all phytogeographers, one of the earliest being Engler after whom I have proposed to name this demarcation: *Engler's line*.

In the W. Pacific Bonin in the north and New Zealand and adjacent islands in the south show a sharp demarcation from the rest, Bonin forming part of the E. Asiatic region, and New Zealand forming a distinct subregion of the Australian. New Caledonia cannot be satisfactorily placed. It shows relations with New Guinea, Queensland and the Pacific in about equal measure. Besides it abounds in endemics, some of which are highly peculiar in various aspects. The remaining part of the Pacific shows an essentially Malesian character, decreasing in strength from west to east. The New Hebrides with Fiji, Samoa and Tonga form a subprovince as does SE. Polynesia, Hawaii is considered a separate province of the Malesian subregion.

Unlike the islands west of Engler's line the American Pacific islands show very little mutual floristic alliance, but they all have a characteristic American flora.

Comparisons with subdivisions and demarcations of other groups of organisms show that often, but not always, the same barriers are respected by unrelated groups.

My data give certain indications about the past but no attempt has been made to correlate the conclusions with contemporary geological theories.

The regularity of distribution patterns, the close floristic alliance among the islands west of Engler's line independent of their distance from each other, combined with the fact that dispersal spectra show no clear correlation between distribution and 'dispersibility', suggests an old relictual character of the flora rather than a young one built up by random long-distance dispersal. This applies especially to the W. Carolines, the Melanesian islands, Lord Howe I. and New Zealand, i.e. islands more or less within the Andesite line, which are much richer and contain many poor dispersers. For Hawaii also a better accessibility in the past seems indicated.

The regular decrease in the number of taxa in proportion to their distance from source areas is discussed. An attempt is made to explain the phenomenon. A tentative conclusion is reached that impoverishment and other phenomena attributed to oceanic islands are not restricted to these. A large scale comparative study of continental and island floras is needed.

I. INTRODUCTION

This paper is both a continuation and an extension of a preliminary report that I published ten years ago (van Balgooy, 1960). In this I tried to frame a hierarchical subdivision of the Pacific based on the distribution of 1511 Phanerogam genera. Method and procedure were only summarily discussed, no actual distribution data were presented and hardly any literature was cited. This was done deliberately as I intended to elaborate on these at a later date.

Many new facts concerning the Pacific flora have come to light in the years that have elapsed between the issue of my preliminary paper and the present one. In these years I have tried to check old data and incorporate the new records.

In this interval several genera were recorded for the Pacific for the first time. In this connection the large collections made by Dr T. C. Whitmore c.s. in the Solomons deserve mention.*) Of other genera already known from the Pacific the range was extended; some genera were reduced, others split up. Genera that had been accepted as native in my former paper had on second consideration to be regarded as introduced and had hence to be deleted, or the other way round. On the whole the increase, which in part is also caused by the inclusion of the Revilla Gigedo and Cocos Islands exceeds the decrease.

The conclusions reached in the preliminary analysis had also to be re-evaluated in the light of the new facts.

Despite much checking and rechecking of the data I realize that the list of genera presented here is still incomplete and will contain errors in detail and omissions. This cannot be avoided as botanical exploration and taxonomical research are steadily progressing. No new data that came to my notice after July 1969 have been incorporated. So the subdivision of the *Podocarpaceae* follows the treatment of Buchholz and Gray (1948 onwards) and not the more recent one by De Laubenfels (1969). (Additional records and corrections can be found after the Appendix).

There are good reasons to assume, however, that the main conclusions reached here will stand the test of a new analysis in future, at least when the same working principles are applied. I base this on examples in the past. The main features of the Australian flora described by J. D. Hooker more than a century ago (Hooker, 1860) have never been seriously challenged despite the enormous increase of knowledge of the Australian flora since. The floristic analysis of the Lesser Sunda Islands by Kalkman (1955) has confirmed the earlier conclusions of Van Steenis (1936) based on only a fraction of the flora, viz. only the microtherm genera. When I had finished the manuscript of my preliminary analysis the Flora of Tonga by Yuncker (1959) appeared. Although this Flora contained many records new for the islands it hardly affected my conclusions on their floristic status. Likewise the greatly increased knowledge of the Solomons flora has been of little consequence to its floristic status as established on the much more incomplete data of 1960: 431 genera were then known against 654 in this paper, an increase of c. 50 %. In my opinion there is therefore no serious obstacle to publishing the present data, however incomplete for several sadly underexplored island groups and although many taxa are insufficiently understood. Moreover, to wait for representative collections from all over the Pacific and for critical revisions of all taxa involved, would probably mean to wait for ever.

*) The results of the Royal Society Expedition to these islands in 1965 were not yet available at the time this paper was finished.

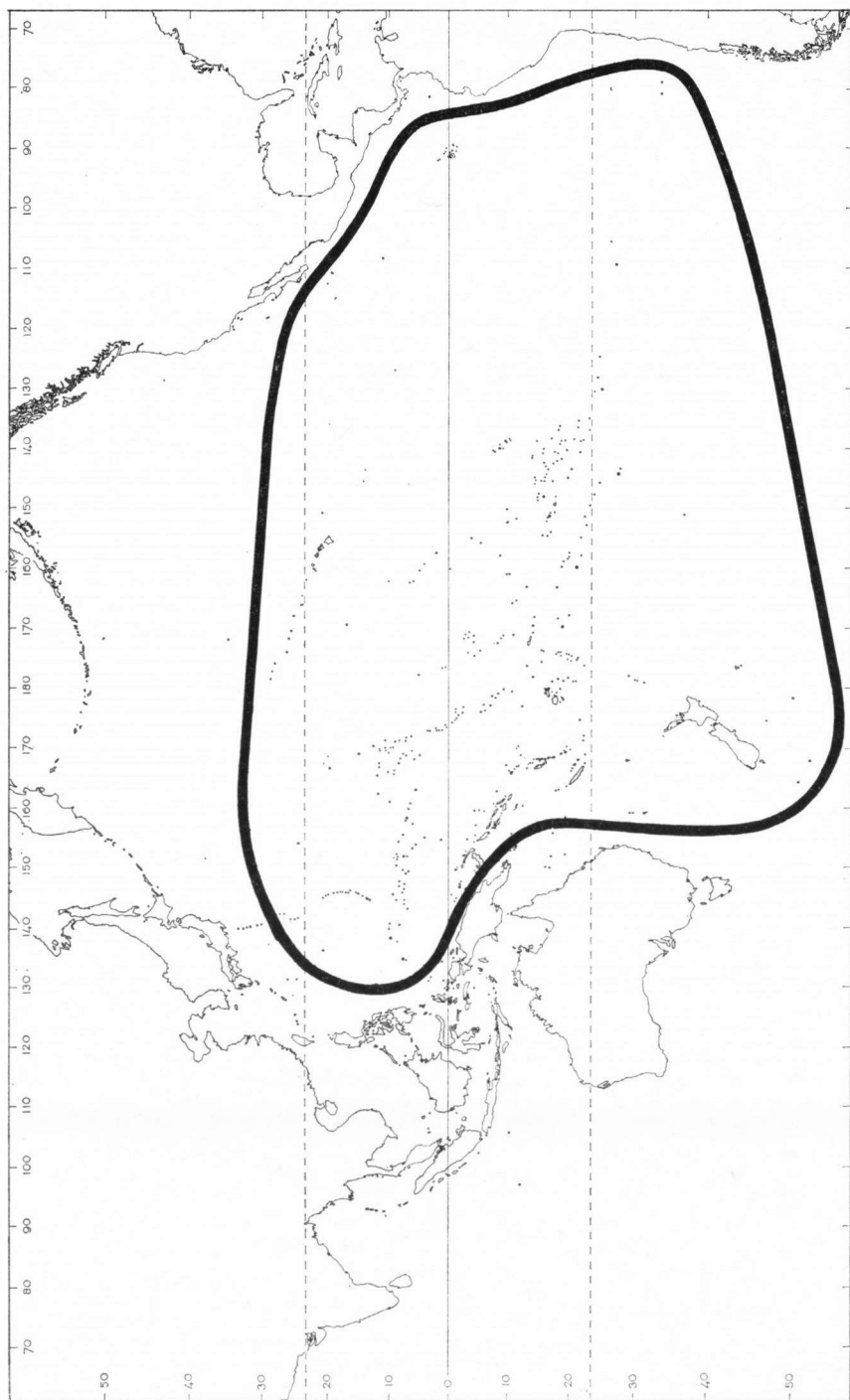


Fig. 1. Limits of the Pacific as understood in the present paper.

I have tried to follow the advice of Darlington (1957), which was actually meant for zoogeographers but which is equally applicable to phytogeographers. He said among other things: 'Define and limit both the work to be done and the factual material to be worked with. Present the selected material fully and fairly. Formulate working principles.'

The part of the world considered as 'Pacific' for the present purpose is indicated in fig. 1 (see also fig. 16). It stretches from 30° N to 60° S and from 120° E to 80° W. It is bounded in the west by Japan, Ryu Kyu, Formosa, Philippines, New Guinea, and Australia; in the north by Kamchatka and the Aleutians; in the east by the Americas; and in the south by Antarctica. Off-shore islands very close to any of the land areas just mentioned, such as Botel Tobago southeast of Formosa, the Louisiades east of New Guinea, Cedros and Guadelupe off Mexico are excluded, as is Macquarie I. south of New Zealand.

The immediate purpose of this plant-geographic account was to find out the floristic relationships between these islands and the surrounding continental areas, discontinuities in the relations, and to see whether they could be grouped in a hierarchical system.

Additional aims were to check whether relationships could be traced between distribution and means of dispersal and to try and find out whether the distribution and distribution patterns of the present Pacific flora still reflect its genesis.

Finally I was curious to see in how far the regularities found in floristics could be found reflected in geographical studies of non-Phanerogams.

To attain these aims a method and terminology had to be worked out for the arrangement of the data and their statistical elaboration. The method followed is here briefly explained.

In the first place the essential study is based only on Phanerogam genera indigenous to the Pacific islands.

They can be assigned to a number of recognizable distribution patterns, here called *distribution types*.

Each island can be characterized by the set of distribution types peculiar to it; this has been named its *distribution types spectrum*.

Many genera do not occur beyond a certain line in the Pacific. The number of genera that terminate their distribution on either side of that line is a measure of the strength of the demarcation and has been termed *demarcation knot*.

The number of genera that any two regions have in common gives a measure of the strength of their relation, here called *floristic affinity*.

Doubts have been expressed about the sense of this kind of primarily floristic work. One author (Willis, 1922) put it thus: 'It is difficult to understand why so much labour has been applied to the problem of differentiating floral regions, for one fails to perceive any object which is gained by defining them.' But then what is the intrinsic value of classification anyway? And we may as well question the sense and use of taxonomy.

I think that the propensity for classification and order is an innate part of human nature, besides I am convinced that classifications as proposed here help to place the Pacific in a certain geographical perspective. The plant-geographical delimitation of the area to be covered by the 'Flora Malesiana project' was established only after a careful analysis of the distribution of the genera in much the same way as carried out here. As a matter of fact it served as a model for this study. See Van Steenis (1950).

The knowledge of floristic Pacific relationships has some distinct practical advantage, especially for local and monographic taxonomic studies, and as appeared earlier from similar work on Malesia, for obtaining indications regarding floristically vital relationships with surrounding areas. The greater part of the Pacific links up with Malesia. So, if e.g.

a Flora of Fiji or even SE. Polynesia is planned, a thorough knowledge of the Malesian flora and especially that of New Guinea is needed. A constant comparison of the specimens with Malesian material and species based thereon should be made in order to avoid unnecessary description of new species. When studying the flora of Rapa one should in addition be alert for both Neo-Zealandic and Hawaiian relations.

Furthermore, distribution data, especially when studied in conjunction with similar studies on other groups of organisms may throw light on possible migration routes and the genesis of the Pacific biota. However, I am inclined to be rather cautious with giving a historical interpretation of the facts. In the first place this study is based on present day distribution, and secondly, Phanerogams form only a fraction, though a bulky one, of the total biota. Moreover, so much more has to be learned in the fields of ecology, dispersal, geology, etc. that it would be rather premature to draw any far-reaching conclusions on the genesis of the extremely diverse flora of the Pacific. Yet the present day distributions are real. The past developments have resulted in the present configuration of plant distribution. During the past, at least onwards of the Upper Cretaceous, a large number of events have taken place, all affecting plant distribution. And it is tempting to the biogeographer to try and fit the facts of present distribution with current hypothesis about the past history of that part of the globe. No hypothesis ignoring the facts can be accepted.

This study will, I hope, also contribute to a stabilization of phytogeographic nomenclature in this part of the world. All too often we come across terms as Indo-Malesia, Indo-Malaya, Australasia, Melanesia, Hinterindien, Araucariengebiet, Monsungebiet, and Polynesia as often as not followed by such suffixes as Region, District or Area, which appear to have different meanings. In some cases we do not have an accurate idea of how the region is defined, what its limits are and on what grounds it is based. Also there is no agreement among various authors as regards the rank of their phytogeographic unit even if indicated with the same suffix.

This study has already given rise to some 'by-products', as my paper on the diversity of island floras (van Balgooy, 1969) and a study on the relations between *Aceratium*, *Aristotelia* and *Sericolea-Elaeoc.* (van Balgooy, 1963) were directly stimulated by it. This in turn got a strong impulse from my share in the project 'Pacific Plant Areas' of which two volumes have now appeared (van Steenis, 1963a; van Steenis & van Balgooy, 1966).

There is no doubt that students of the Pacific, whether they are plant taxonomists, ecologists, entomologists, foresters, ethnologists, or agriculturists may occasionally make use of the list of genera here prepared. I hope that it may also stimulate collectors to fill the many 'distribution gaps' and taxonomists to solve many problems presented by ill-understood taxa.

Readers may notice discrepancies between the numbers of genera given for some island groups in my paper on island diversity (van Balgooy, 1969) and the present one. This is in part due to new records but is also a result of the fact that in the present paper a number of genera have been split up in smaller entities. For *Ficus-Morac.* alone 12 sections have been entered in the census.

For the convenience of the readers I have added the family name in abbreviated form behind each genus name. This helps orientation in case of less known genera.

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Last but not least it is my pleasure to express my gratitude to Prof. Dr C. G. G. J. van Steenis, for attracting my interest to plant-geography; at his suggestion I undertook the preliminary analysis and later he entrusted me with the compilation of Pacific Plant Areas. He urged me to write this thesis, and I have had the advantage of his helpful advice and constructive criticism.

II. HISTORICAL SURVEY OF DEMARCATION LINES AND SUBDIVISIONS PROPOSED FOR THE PACIFIC

Before proceeding to a discussion of the material and methods of this paper the subdivisions that have been proposed so far for the Pacific should be considered.

I shall confine myself to the more important papers dealing with the Phanerogam-flora. Papers dealing with only a single family give only an incomplete picture and are left out of consideration. The same holds for several older studies which are only of historical interest. A marked exception is Hooker's essay on the phytogeographic position of New Zealand which is still of basic importance. Another exception is Schlechter's paper on Micronesian Orchids as this author was the first to indicate a demarcation line that in later literature has become known as one of two 'lines of Kanehira'. At a later stage I also will survey the most important literature on non-Phanerogams.

The only comprehensive survey of biogeographic lines, though only those of the west part, including Micronesia and Melanesia, was presented by Fosberg (1952). A full survey of the biogeography of the Pacific up to 1963 was ably presented by Thorne (1963).

J. D. Hooker (1853) made an analysis of the species of Phanerogams of New Zealand. After their distribution he classified them into six groups as follows:

| | |
|---|-----|
| <i>Endemic</i> (confined to New Zealand) | 507 |
| <i>Australian</i> (otherwise known only from Australia). | 193 |
| <i>S. American</i> (confined to New Zealand and S. America). | 89 |
| <i>S. American + Australian</i> | 77 |
| <i>European</i> (species spread northwards beyond the equator, not necessarily to Europe) | 60 |
| <i>Antarctic</i> (widespread in the southern hemisphere). | 50 |
| Total | 976 |

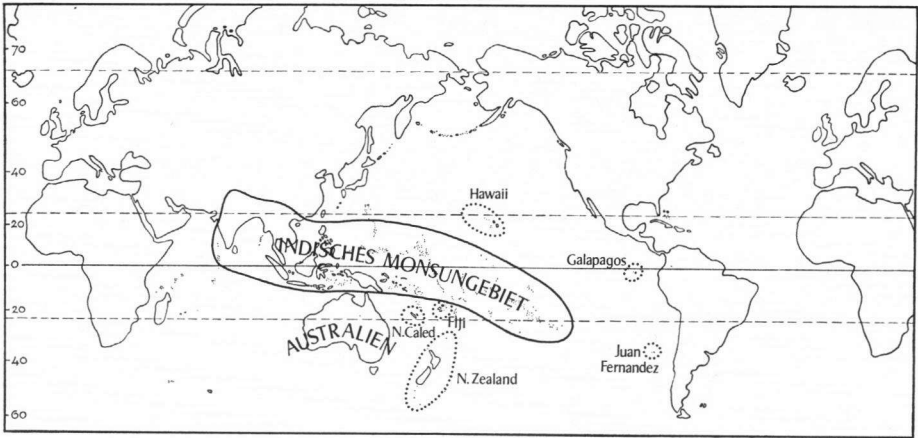


Fig. 2. Subdivision of the Pacific after Grisebach (1872).

Although these figures no longer hold, the phytogeographic position of New Zealand was herewith well settled. Hooker concluded that the affinity was clearly strongest with Australia. Among the endemics also there were many which he considered closely allied to Australian species. Yet he found the absence of so many characteristic Australian forms just as striking. There were also strong ties with S. America. The most peculiar aspect according to Hooker was the relatively strong representation of 'European' species, certainly an unexpected feature for a so isolated predominantly south temperate country. The Antarctic species mainly inhabit South Island and the mountains. Botanical affinity with S. America and Tasmania is also indicated by the alliance of the endemic genera.

In the earliest phytogeographic papers the central part of the Pacific was treated as a whole. One of the earliest attempts at a subdivision of the Pacific was A. Grisebach's (1872). See fig. 2. His book, though primarily dealing with the vegetation of the world in relation to climate, also takes into consideration the floristic composition of the various countries and islands. His 'Indisches Monsun-Gebiet' stretches from India through Malesia eastwards to the Marquesas and Tuamotus. The Sunda Is. are regarded as the 'vegetation centre' of this 'Gebiet', which is distinct from Fiji by the large number of endemics assigned to it. Otherwise Fiji is said to be closely allied to the 'Monsun-Gebiet'.

Even sharper is the demarcation with Hawaii, which island group is said 'not to belong to any continent' on account of its peculiar and high degree of endemism.

New Caledonia is also sharply distinct from the 'Monsun-Gebiet'. Its vegetation resembles that of Australia more closely but cannot be included in it on account of the high degree of endemism in New Caledonia. New Zealand is said to be closer to Antarctic S. America in vegetation character than to Australia.

The Galapagos of which 50 % of the species are endemic is said to be otherwise wholly American in character. Juan Fernandez despite its proximity to Chile has a high degree of endemism, the affinity of some of the taxa not being with American forms. In its vegetation the islands are said to resemble New Zealand most closely.

This shows that Grisebach despite very inadequate and incomplete data already understood some of the salient features of the Pacific flora: the strong and wide Indo-Malesian influence, the meagre Australian, and the limited American one.

The exclusion of Fiji from the 'Monsun-Gebiet' is based on the supposed high incidence of endemism, now known to be much exaggerated. The same applies to Hawaii but with more justification. The resemblance he saw between Australia and New Caledonia and New Zealand and Antarctic S. America is partly a matter of convergence due to comparable climate.

A. Engler (1882) divided the world into four 'Florenreiche' on the basis of the genus distribution of a number of well known families. See fig. 3.

He included the whole Pacific except Juan Fernandez and Galapagos in his 'Paläotropisches Florenreich'. He was the first to regard Hawaii as part of the Old World flora.

The high degree of endemism of Hawaii induced him to give it the same rank as his 'Malayisches Gebiet'. The latter is more extensive than what is now regarded as Malesia (van Steenis, 1950) in a phytogeographic sense, as it includes N. tropical Australia and Melanesia as far east as Fiji but exclusive of New Caledonia. Fiji is incorporated in the 'Austro-malayische Provinz', which is more justified than his inclusion of N. Australia therein.

The Polynesian Region ('Polynesisches Gebiet') includes all of Micronesia, Bonin, Central and SE. Polynesia. He probably put these together as they all lack 'character'. No subdivision was attempted. His 'Araucarien Gebiet' includes E. Queensland, New Caledonia, Norfolk I., the Chathams and North I. of New Zealand. The name was evidently chosen for want of a better one, as he surely knew that *Araucaria* occurred in S. America but not in New Zealand (except as fossil). New Guinea where the presence of *Araucaria* must have been known to him is excluded, though he said that perhaps part of it should be included, but he preferred to leave it out on account of the high degree of endemism in the New Guinean flora. But then one wonders why the same argumentation

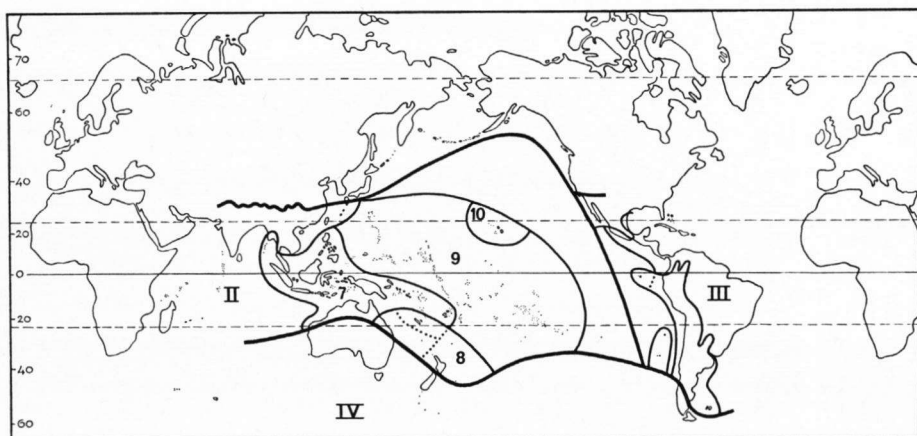


Fig. 3. Subdivision after Engler (1882). (II) Paläotropisches Florenreich, (III) Südamerikanisches Florenreich, (IV) Altozeanisches Florenreich, (7) Malayisches Gebiet, (8) Araucarien Gebiet, (9) Polynesisches Gebiet, (10) Gebiet der Sandwich Inseln.

is not applied to New Caledonia. We shall see later that also Guillaumin attached great value to the common occurrence of some genera in New Caledonia and Queensland.

To place the boundary between two floral kingdoms (the Old World and Antarctic) between North and South Island of New Zealand is a 'tour de force' not further explained.

O. Drude (1890) distinguished four 'Florenreiche'. Of these three were topographical: his 'Boreales, Tropisches und Australes Florenreich'. The fourth, his 'Ozeanisches Florenreich' concerns the marine flora generally.

The Pacific is discussed briefly. According to Drude the major element in the Pacific is the tropical 'Indo-Malayan' one, the Australian one is limited to the mountains. 'Individuality' of the Pacific flora, as expressed in the percentage of endemics, is reasonably high but only in Hawaii does it reach a degree comparable to that of St. Helena, in the Atlantic Ocean. New Zealand also has a high degree of species endemism. Its relations are strongest with Australia but are limited to the alpine portion of its flora.

E. Drake del Castillo (1893) in his Flora of French Polynesia also discussed the relations of the flora. Unfortunately he did not discriminate between indigenous and naturalised species.

According to him the families best represented by endemics the *Campanulaceae* and *Compositae* are apparently of American derivation. The affinities of the *Araliaceae*, *Orchidaceae*, *Rubiaceae*, and *Rutaceae* are with the Old World.

The 588 species of Phanerogams and Pteridophytes of French Polynesia were divided after their total distribution as follows:

| Confined to French Polynesia | Oceanic but not in Indo-Malesia | Indo-Malesian | Others | Total |
|------------------------------|---------------------------------|---------------|-----------|-------|
| 161 (27.4 %) | 123 (20.9 %) | 297 (50.6 %) | 7 (1.2 %) | 588 |

More than half of the species are accordingly also found in Indo-Malesia from whence the flora is mainly derived.

R. Tate (1893) studied the distribution of the Vascular flora of Lord Howe and Norfolk to see whether they should be subordinated under Australia or New Zealand. The terrestrial fauna was known to be more closely allied to that of New Zealand and Polynesia.

He arranged the genera in five and the species in four main distribution types as tabulated on page 11.

Tate's data were of course rather incomplete, especially as regards Norfolk. Besides there are a number of obvious mistakes; he for example mentions '*Drimys*' (= *Bubbia*) from Norfolk. Several of the distribution records especially of the species are erroneous. Moreover, his criteria for classification are questionable. Among his Australasian genera there are several that could as well be classed as Oriental, e.g. *Pittosporum*-Pitt., *Geniostoma*-Log. and *Ochrosia*-Apoc. Among his Oriental genera for example *Sicyos*-Cuc. centres in America and extends into the Pacific as far as the New Zealand region, while *Achyranthes*-Amarant., *Canavalia*-Leg., and *Ipomoea*-Conv. all are widespread genera.

Despite these errors Tate's conclusions on the floristic status of the islands, especially as based on the genus distribution, are essentially correct. Norfolk, although equidistant to New Caledonia, Australia and New Zealand, has strongest relations with the last. It also

| | Lord Howe | Norfolk | Common to both |
|--|-----------|---------|----------------|
| <i>Genera</i> | | | |
| I Extra-Australian | | | |
| Endemic | 4 | 2 | — |
| Extra-limital (also found elsewhere in the Pacific) | 3 | 5 | — |
| II Australasian (occurring in Australia and Pacific) | 29 | 17 | 14 |
| III Australian | 4 | 4 | 1 |
| IV Cosmopolitan | 69 | 31 | 25 |
| V Oriental (Indo-Malesian and paleotropical) | 45 | 17 | 16 |
| Total | 154 | 76 | 56 |
| <i>Species</i> | | | |
| I Extra-Australian | | | |
| Endemic | 56 | 42 | 5 |
| Extra-limital | 9 | 11 | 4 |
| II Australasian | 49 | 23 | 15 |
| III Oriental + Cosmopolitan | 59 | 8 | 7 |
| IV Australian | | | |
| Extra-Australian (centering in Australia but also found outside the continent) | 26 | 5 | 2 |
| Australian (strictly continental) | 8 | 1 | 1 |
| Total | 207 | 90 | 34 |

has a distinct affinity with Lord Howe I. This island although much closer to Australia has still strong relations with New Zealand. It has more taxa in common with Australia than with New Zealand but in view of the strong endemic element and its relations with Norfolk he suggests that it is better to keep Lord Howe I. as a 'companion outlier to Norfolk of the New Zealand region.'

F. Reinecke (1903, 1906) wrote two papers which dealt mainly with the vegetation and floristic status of Samoa but also treated the general aspects of the Pacific flora.

His conclusions regarding the Pacific can be summarized as follows:

- (1) American types fail except in Hawaii.
- (2) The Australian flora is hardly represented in Polynesia and not even in Melanesia.
- (3) There is no relation between Samoa and Hawaii.
- (4) There is no relation between New Caledonia and Polynesia.
- (5) Neither between New Guinea and Polynesia.
- (6) There are distinct relationships between Fiji and Polynesia; few Samoan genera fail on Fiji.
- (7) The number of species decreases from West to East.
- (8) There are few endemics in Polynesia.
- (9) The flora of Samoa (and Polynesia) is young, it is completely Malesian in aspect.
- (10) Most numerous in the Polynesian flora are families with wind and current dispersed diaspores.
- (11) Next come families dispersed by birds.
- (12) The vegetation is dominated by few polymorphic genera.
- (13) Most of the Phanerogams are anemophilous.

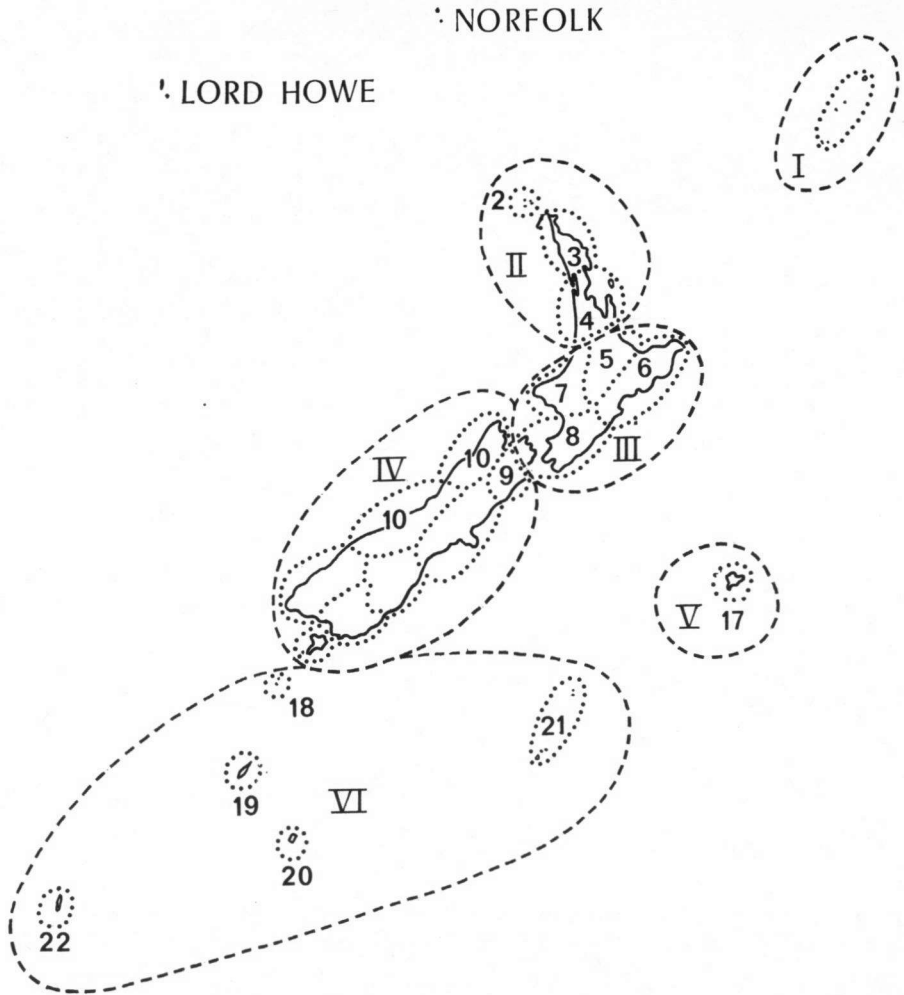


Fig. 4. Floristic provinces and districts of the New Zealand area after Cockayne (1921, map 2, modified). For explanation see text.

The latter two points fall beyond the scope of our present discussion. One can partly agree with Reinecke's conclusions but his statement that there is no floristic relation between New Caledonia and New Guinea and Polynesia is obscure. It may be partly due to lack of knowledge of the New Caledonian and New Guinean floras at that time. But it also contradicts his conclusion on the Malesian character of Samoa. His conclusions regarding dispersal are not corroborated by mine.

He distinguished five floral regions in the Pacific: 1. Hawaii, 2. New Zealand, 3. New Caledonia, 4. New Hebrides, Solomons, Bismarck and New Guinea, and 5. the Pacific-Malaysian (or Eupacific) region, subdivided into: a. Micronesia (Bonins, Marianas, Carolines, Marshalls, Gilbert, Ellice, Phoenix), b. Central Polynesia (Fiji, Samoa, Tonga,

Tokelau), and c. Eastern Polynesia (Cook, Austral, Society, Marquesas and Tuamotu Is.).

W. R. B. Oliver (1909) analysed the flora of Lord Howe, Norfolk, and Kermadec Is. His analysis of species distributions of all vascular plants led to the following results:

Of the 114 Kermadec species 95 occur also in New Zealand, 78 also in Australia, 68 occur on Lord Howe or Norfolk or both, 62 are found also in Polynesia (incl. New Caledonia).

Of the 208 Norfolk species 117 also occur in New Zealand, 176 in Australia, 126 in Polynesia and 121 also occur on Lord Howe or Kermadec or both.

The 212 Lord Howe species are distributed as follows: 105 also occur in New Zealand, 181 also in Australia, 110 in Polynesia and 101 occur also on Norfolk or Kermadec or both.

These figures show that the percentage of species in common with New Zealand decreases from East to West, which is correlated with an increase of species in common with Australia.

On all three there is a much stronger representation of Polynesian elements than in New Zealand according to Oliver.

Despite its proximity to Australia even Lord Howe lacks representatives of the most typical genera of that continent. Oliver decided that floristically these islands could not be incorporated with Australia nor with New Zealand. He proposed a 'Subtropical islands province' for the three island groups.

Although agreeing with Oliver that these islands are relatively independent from both Australia and New Zealand, in my opinion the best procedure would be to include all three in the Australian region, together with New Zealand. His figures suggest that the affinity of Lord Howe and Norfolk is closest with Australia, that of Kermadec with New Zealand.

L. Cockayne (1921) made a detailed analysis of the New Zealand flora and adjacent islands.

There are 1771 species (and 'taxa of equal rank') of which 162 are Pteridophytes, 397 Monocotyledons and 1212 Dicotyledons. After their distribution the area is divided into a number of provinces and these again in districts.

The boundaries of the provinces are said to be determined by abrupt changes in floristic composition, but the boundaries of the districts are very much 'subject to changes', with which is probably meant that they are not very sharp. For his classification the reader is referred to fig. 4.

- I Kermadec Province
 - 1 Kermadec District
- II Northern mainland Province
 - 2 Three Kings District
 - 3 N. Auckland
 - 4 S. Auckland
- III Central Province
 - 5 Volcanic Plateau District
 - 6 East Cape District
 - 7 Egmont-Wanganui District
 - 8 Ruahine-Cook District

- IV Southern Province
 - 9 NE. South Island District
 - 10 NW. South Island District
 - 11 Eastern South Island District
 - 12 Western South Island District
 - 13 North Otago District
 - 14 South Otago District
 - 15 Fiord District
 - 16 Stewart District
- V Chatham Province
 - 17 Chatham District
- VI Subantarctic Province
 - 18 Snares District
 - 19 Auckland District
 - 20 Campbell District
 - 21 Antipodes District
 - 22 Macquarie District

The fact that the boundary between the Central and Southern Province is drawn across the NE. corner of South I. and not through Cook Strait is striking but he corrected this later (Cockayne & Allan, 1926).

Although in my opinion the ranks assigned to the units are too high, this classification agrees rather well with my own, which is based on Phanerogam genera only and is insufficiently detailed especially as regards the main islands.

Schlechter (1921) in a survey of the Micronesian orchids made some remarks on the floristic status of these islands.

He enumerated 38 genera, with 69 species of which 59 are considered endemic. All genera are also known from New Guinea. The non-endemic species are widespread in E. Malesia (Philippines and New Guinea). Nearly all the endemics have close allies in New Guinea, so that on orchid evidence there is no demarcation between New Guinea and Micronesia, but there is one between the latter and the Philippines. This view was later confirmed by Kanehira (1940) who considered the whole flora. In the present work I have proposed calling this 'Schlechter's line.'

A. Hayek's (1926) subdivision of the world flora was based on the distribution of characteristic taxa of various rank; both their presence and their absence was taken into account.

It agrees with Engler's in drawing the boundary between Old and New World 'Florenreiche' in the E. Pacific.

The most important deviation is that New Zealand is considered a separate region of the Old World Kingdom, whereas Engler placed North I. in his 'Araucariengebiet' and South I. in the Antarctic Kingdom.

The following ranks are distinguished:

| | | |
|-------------|---|----------|
| Florenreich | = | Kingdom |
| Gebiet | = | Region |
| Provinz | = | Province |

(Unterprovinz)
 Bezirke = District
 (Unterbezirke)

In his 'Palaeotropisches Florenreich' (see also fig. 5) Hawaii and New Zealand are regarded as 'Gebiete'. So is the rest of the Pacific including Malesia and SE. Asia.

Obviously he was more impressed by the absence of so many Australian taxa in New Zealand than by the presence of others. Anyhow, I cannot agree to giving New Zealand and Hawaii the same status as the whole area between India and Marquesas.

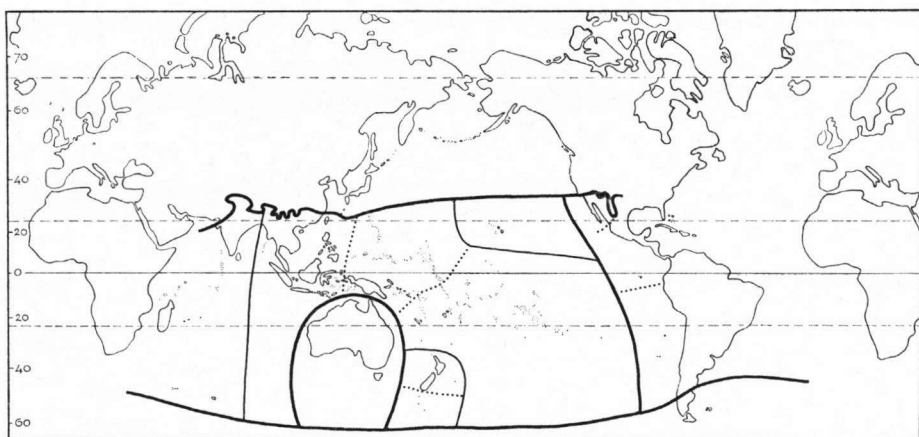


Fig. 5. Subdivision after Hayek (1926). The whole Pacific forms part of the 'Paläotropisches Florenreich' in which Hawaii and New Zealand form separate 'Gebiete' (Regions) equivalent to the whole of SE. Asia, Malesia and the rest of the Pacific together.

Hayek included Micronesia in the Melanesian Province and following authors before him, also included Bonin in it. He evidently attached great value to the strait between the Solomons and New Hebrides as a demarcation line. It is remarkable and not quite clear to me, in view of the high rank assigned to Hawaii and New Zealand, why New Caledonia is not even treated as a province in its own right.

Setchell (1928) made an interesting analysis of the Tahitian flora. He accepted 368 Phanerogams and 158 Pteridophyte species as native, and according to their total distribution grouped them into the following elements ('geographical elements' in the sense of Wulff, 1943):

| element | Phanerogams | Pteridophytes |
|-----------------------|-------------|---------------|
| Pantropic | 65 | 20 |
| Paleotropic | 66 | 79 |
| Neotropic | 3 | 1 |
| Australia/New Zealand | 7 | 14 |
| Polynesian | 71 | 26 |
| Endemic | 147 | 25 |

The totals do not agree; there are 9 Phanerogams and 5 Pteridophytes short. Probably these could not be fitted in any of his categories.

Grouped according to their affinity the following figures are obtained (these are 'genetic elements' in the sense of Wulff, 1943):

| element | Phanerogams | Pteridophytes |
|--------------|-------------|---------------|
| Indo-Malayan | 310 | 136 |
| Antarctic | 42 | 27 |
| Boreal | 4 | 2 |
| Neotropic | 5 | 2 |

Again the totals do not agree. But this can hardly have influenced his only possible conclusion on the Tahitian flora: It is for an overwhelming part derived from the West and partly also from the South.

F. B. H. Brown (1931, 1935) in an analysis of the SE. Polynesian flora distinguished six 'floral regions'. See fig. 6.

It is not clear, however, whether this subdivision was arrived at empirically or was constructed beforehand. Moreover, although his papers bear the title 'Flora of SE. Polynesia', he dealt only with his own collections made mainly in the Marquesas and supplemented with significant records from other parts of SE. Polynesia (Brown, 1931, p. 7).

It is obvious that this author cannot have been very familiar with the flora he treated. He gave a list of 'introduced species' belonging to *Bacopa*, *Caesalpinia*, *Hibiscus*, *Vigna*, and *Wedelia* that are certainly native.

In the six regions (or rather districts) the degree of endemism is highest in Rapa and the Marquesas, lowest in the Austral islands. Endemism is, however, claimed too readily.

Nevertheless his conclusion on the relatively high degree of species endemism in Rapa and the Marquesas is probably correct. He also pointed out floristic affinities between Rapa and New Zealand.

Brown is one of the few authors who regard SE. Polynesia (and Hawaii) as part of the American flora. His remarkable reasoning can best be illustrated by a few examples. *Pelea*, *Rut.* of Hawaii and the Marquesas is a genus generally considered closely allied to the Old World genera *Evodia* and *Melicope*. The group to which these genera belong is according to Brown better represented in the Neotropics than in the Paleotropics. So *Pelea* is considered an American element in the Marquesas flora. The SE. Polynesian *Araliaceae* are all either endemic or extend to the Old World but according to Brown they are all allied to *Schefflera* (which I doubt), which again is allied to the American *Oreopanax*. *Schefflera* is, moreover, said by him to be best developed in America. Hence the Polynesian *Araliaceae* are of American derivation. By this reasoning he came to the conclusion that 82 % of the SE. Polynesian flora is of American derivation!

Two papers by A. Guillaumin (1928, 1934b) have to be discussed simultaneously as they are essentially of the same content. Two things have to be kept in mind when discussing these papers: 1. The Pacific is regarded to comprise Australia, E. Malesia and New Guinea besides the Pacific proper. 2. In the English summary of his first paper his 'Kingdom' apparently corresponds to 'Region' in the more customary sense. Fig. 7 illustrates Guillaumin's views on the floristic subdivision of the Pacific.

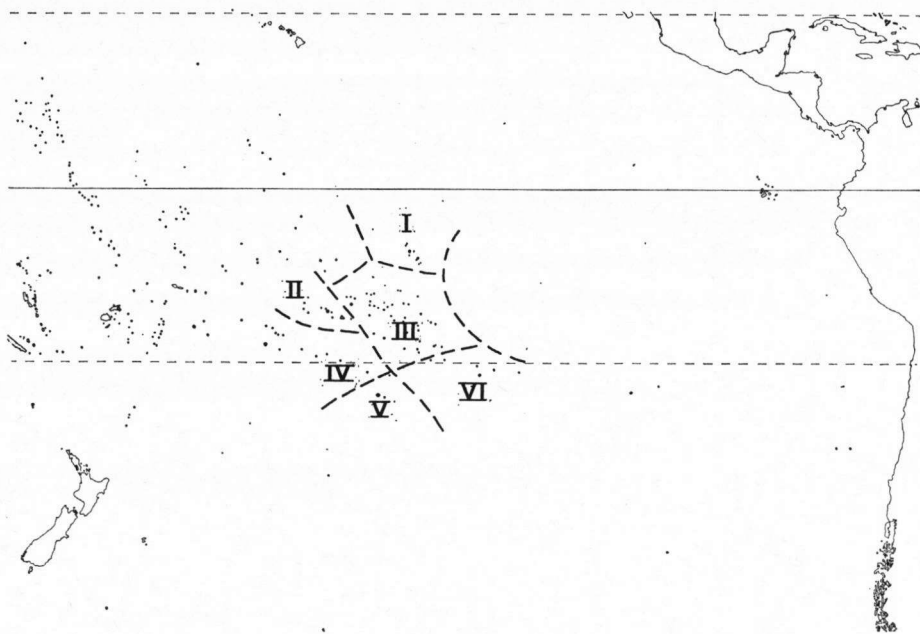


Fig. 6. Floral districts of SE. Polynesia according to Brown (1935). (I) Marquesas, (II) Societies, (III) Tuamotus, (IV) Austral Islands, (V) Rapa, (VI) Mangareva-Henderson.

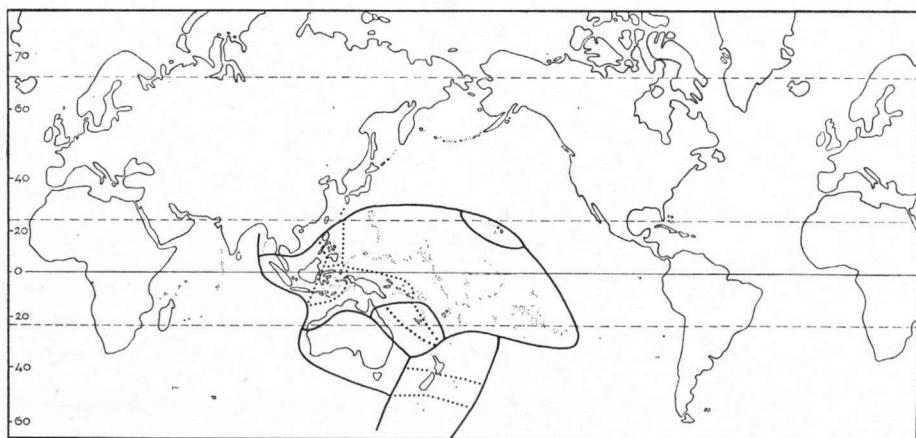


Fig. 7. Guillaumin's (1934b) subdivision of the Pacific. Extratropical Australia forms one 'Royaume' (Kingdom), New Zealand another and Malesia including the greater part of the Pacific and tropical Australia a third. Hawaii, which from the figure appears to form part of the latter Kingdom, is said in the text to belong to the Mexican 'Royaume'. A special region is formed by E. Queensland, New Caledonia and the New Hebrides, the 'Région Canaque'.

Australia minus the N. and E. parts forms one 'Kingdom', New Zealand with the Kermadecs, Chathams and Subantarctic islands another. Though most of the New Zealand non-endemic genera also occur in Australia, many of the most abundant Australian genera are absent. This is of course true but still I think that to assign such a high status to New Zealand overemphasizes its discordance with Australia.

E. Australia, New Caledonia, the New Hebrides, Lord Howe, and Norfolk Is. form his 'Region Canaque'. It corresponds to Engler's 'Araucarien Provinz' already discussed, but it is not clear to which 'Royaume' it belongs.

His ideas about the rest of the 'Pacific' are rather confusing. The Sunda Is. and the Philippines are said to form part of the 'Asian Kingdom' but this does not appear from his map, where the 'Kingdom' boundary is drawn between Formosa and the Philippines and through N. Malaya. He also wrote of the 'Malesian Kingdom' comprising all Polynesia (minus Hawaii), N. Australia and apparently E. Malesia.

Another incongruity between text and map is the status of Hawaii which on the map is indicated as a separate unit within the Malesian region but in the text is said to form part of the Mexican Kingdom. Guillaumin is the only author besides Brown who regards Hawaii as part of the New World flora.

In another paper Guillaumin (1934a) discusses the floristic status of the New Hebrides.

The number of Phanerogam species accepted as indigenous is 569 and of these 207 are regarded as endemic.

By tracing the total distribution of the remaining 362 non-endemics the 'phytogeographic affinity' of the islands was established.

A few figures are reproduced here:

New Hebrides species also occurring in :

| | |
|------------------------|-----|
| New Caledonia | 239 |
| Queensland | 133 |
| New Zealand | 13 |
| Fiji | 178 |
| Society Is. | 121 |
| New Guinea | 160 |
| Hawaii | 54 |
| Malesia (-New Guinea?) | 183 |

A great number of New Hebrides species occur all the way from India far into Polynesia. When these are deleted the remaining species are found to be mostly confined to New Hebrides and the 'Region Canaque' (Queensland and New Caledonia), to New Hebrides and the Papuan region (New Guinea, Bismarck, Solomons) or to the New Hebrides and 'Polynesia' (Fiji, Samoa, Tonga, Society, etc.). No figures were given, however, and therefore it is not quite clear how Guillaumin came to include the New Hebrides in the Kanaka Region.

Although numerically they have the most species in common with New Caledonia, one wonders whether this is not partly due to the author's acquaintance with the New Caledonian flora. Moreover the sizes of the floras with which the New Hebridean one is compared are very different.

T. Hosokawa (1934) was the first to elaborate the sharp floristic break between the Bonins and Marianas.

The author gives lists of the following groups:

- (1) Families and genera common to the Bonins and Marianas.
- (2) Families common, genera different in the two groups.
- (3) Species in common.
- (4) Genera in common, species different.
- (5) Endemic species in each.
- (6) Species found in Marianas not in the Bonins.
- (7) Species found in Bonins not in the Marianas.
- (8) Complete list of species of the Marianas.

Unfortunately his lists contain several clearly introduced species, although the title of his paper suggests that the 'vernacular' (= indigenous) species are under discussion.

The conclusions, which I endorse, are as follows:

- A. The Bonin plants are divided into two groups:
 - (1) derived from temperate E. Asia.
 - (2) derived from the 'Monsoon region' (= Indo-Malesia).
- B. The flora of the Marianas is not appreciably affected by that of temperate Asia.
- C. The 'monsoon element' appears to have reached the Bonins by two routes: one via the south (New Guinea, Melanesia), another via Formosa and Ryu Kyu.
- D. The northern element in Bonin is to be regarded as the southernmost outpost of the temperate Asian flora.
- E. The Marianas are likewise considered to be the northernmost outpost of the 'Monsoon flora'.
- F. The floristic discontinuity between the Bonins and Marianas is of the same order as that between Formosa and the Philippines. For the former demarcation Kanehira (1935) later proposed the name Hosokawa's line.

R. Kanehira (1935, 1940) dealt with the flora of Micronesia which is by him understood to comprise the Marianas, Carolines and Marshalls. The second paper is an elaboration of the former.

Although this large archipelago contains c. 1400 islands the bulk of the land area (2150 km²) is made up by only a few large and elevated islands, the only ones supporting a rather rich flora. A list of these high islands (curiously omitting Guam) is given. All genera occurring in Micronesia are tabulated and their complete distribution indicated. Also this author forgot to distinguish between indigenous and introduced: several of the tabulated genera are represented in Micronesia only by introduced species. Of the seven genera regarded as endemic only one now remains: *Guamia-Annon.* of the Marianas.

Micronesia shares more species and genera with New Guinea than with the Philippines. A demarcation line is hence indicated between the Philippines and Palau as already pointed out by Schlechter (1921).

Another floristic discontinuity exists between the West and East Carolines. In the text it is said that Truk belongs to the West Carolines but on his map (Kanehira, 1935, p. 244 pl. 2) 'Kanehira's line' is drawn between Yap and Truk. See fig. 8. The line between the Philippines and Carolines is also called 'Kanehira's line', but to avoid confusion I propose to indicate this as 'Schlechter's line'.

A paper not directly bearing on Pacific demarcations but interesting as it led to my own study of Pacific phytogeography is Van Steenis's work (1950) on the delimitation of Malesia.

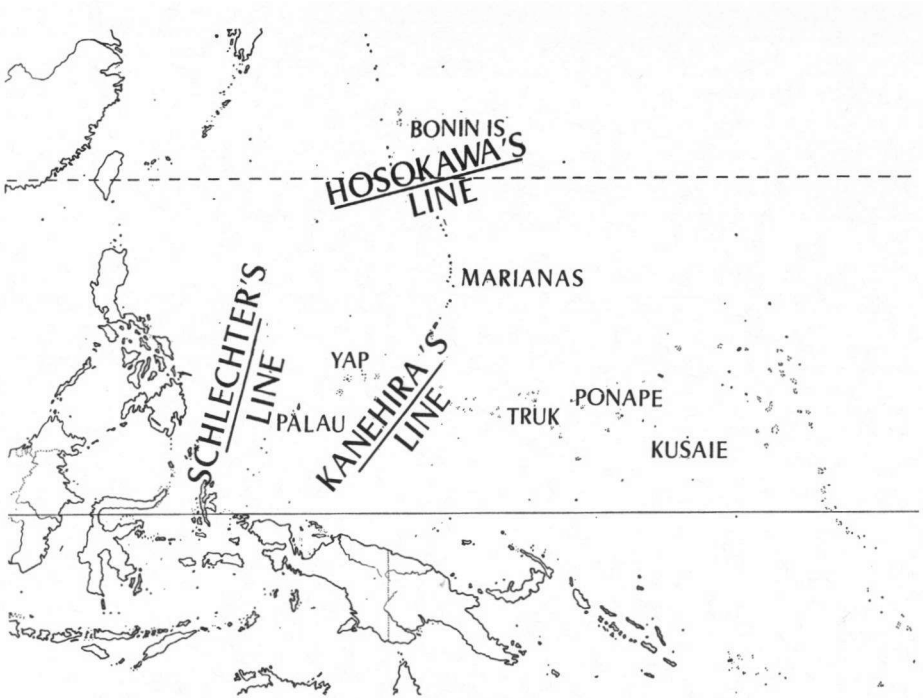


Fig. 8. Demarcation lines in Micronesia. 'Schlechter's line' between Carolines and Philippines is given here as an alternative name to one of the two lines referred to as 'Kanehira's line'. See Fosberg (1952).

The 2178 Phanerogam genera indigenous in the archipelago were found to form six distribution types:

- Type 1 : Occurring through Asia, Malesia and Australia, no distinct centre in the Paleotropics.
- Type 2 : Centering in Asia extending to Malesia, not (or hardly) in Australia.
- Type 3 : Centering in Malesia, not or hardly occurring in Asia or Australia.
- Type 3a: Endemic to one island (or island group).
- Type 4 : Centering in Australia, extending to Malesia and not or hardly to Asia.
- Type 5 : Centering in the Pacific and/or the Subantarctic area.

The complete result of this concise survey need not be discussed in any detail here. It suffices to mention that the Malesian flora shows predominantly an Asiatic affinity. Floristic distinction from Australia is strongest, that from SE. Asia and Formosa/China is of approximately the same order. Against Micro- and Melanesia no demarcation knot of comparable size could be obtained, partly due to lack of knowledge about the flora but mainly to its poverty not compensated by a distinct 'character' comparable with the floras of Asia and Australia. 'The demarcation of Flora Malesiana against these islands is artificial and we know it.' No comment is necessary.

R. Good (1953) devoted a chapter to an attempt at dividing the world into floristic regions.

He distinguished six kingdoms, divided into 37 regions. His classification will be discussed only as far as the Pacific is concerned. See fig. 9.

The bulk of the Pacific falls within his Paleotropical Kingdom (II) which is divided into an African, Indo-Malesian and Polynesian subkingdom. The Bismarcks are included in the Malesian region (19) of the Indo-Malesian subkingdom. For 'practical reasons' the line is drawn between New Guinea and Bismarcks. The Polynesian subkingdom comprises: 20. the Hawaiian region, 21. the New Caledonian region (New Caledonia, the Loyalties, Lord Howe, and Norfolk Is.), 22. the region of Melanesia and Micronesia (the Solomons, New Hebrides, Carolines, Marshalls, Gilberts, Ellice, Marianas, and Bonin Is.), and 23. the Polynesian region (Fiji, Samoa, Tonga, the Cook, Society, Tubuai, Tuamotu, Marquesas, Phoenix, Tokelau, Line, and Easter Is.).

New Zealand including the Kermadec, Chatham and Subantarctic islands form the New Zealand region (35) of his Antarctic Kingdom (VI).

The remaining islands are included in the Neotropical Kingdom (III). The Caribbean region (24) comprises among others Revilla Gigedos and Cocos I. The Galapagos Is. are included in the Andine region (28) and the Juan Fernandez Is. are placed in a region of their own (30).

Good's classification was largely modelled on Engler's scheme. No figures are given to support his classification. He stated that his classification is into regions each of which may be regarded as supporting a characteristic flora of its own, that has developed within the region. But a characteristic flora may not have originated on the spot.

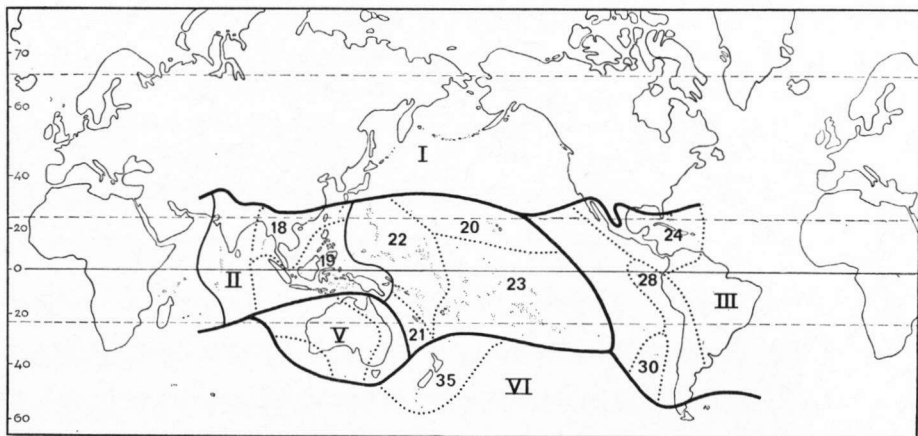


Fig. 9. Floristic subdivision after Good (1953, pl. 4, modified). For explanation of symbols see text.

T. Tuyama (1953) discussing the phytogeographic status of the Bonin (and Volcano) Is. stated that there are 220 species of indigenous flowering plants. The degree of endemism is said to be high, the relationships of the flora strongest with E. Asia, however no figures are given.

There are some distinct Pacific elements in the flora that have their northern- and westernmost station in the Bonins, e.g. *Metrosideros-Myrt.* and *Santalum-Sant.*

These are thought to form the oldest relic component of the flora. The islands have to be reckoned to the E. Asiatic flora but as a distinct district.

A. C. Smith (1955) investigated Fiji's importance as a terminus for plant groups. An analysis at species level would not have been very revealing, as according to the author 70 % of the species are endemic and of the remaining 30 % many are widely distributed. He therefore preferred to consider the genera (of Phanerogams only). He is of the opinion that perhaps Tonga could best be included as it has a flora very similar to but poorer than Fiji. No up-to-date flora of Tonga was, however, available at that time.

He found that of the 445 genera accepted as native, 101 do not occur to the east of the Fiji islands. Of these 13 are endemic, but all with affinities to the west, 11 occur also in Australia/New Caledonia, 43 in Indo-Malesia, and 34 are widespread west of Fiji. The latter category, though comprising some genera also occurring in the Neotropics, are regarded as terminating in Fiji. As the majority of the constituent species seem to have been derived from Indo-Malesia, no transpacific migration is thought to be involved. The only exceptions are *Lindenia-Rub.* and *Stillingia-Euph.* Thus 23 % of the genera reach their eastern limit in Fiji, indicating that a sharp phytogeographic break occurs in or immediately east of the Fiji Is.

Though some of these 101 genera later appeared to occur east of Fiji, additional ones were found that reached their eastern limit in it. So Smith's conclusion is still valid.

Skottsberg (1956) discussed the phytogeographic status of the Juan Fernandez and Easter Is.

According to him the Juan Fernandez flora when grouped according to present day distribution of the species shows the following floristic elements:

| Elements | Angiosperms | Pteridophytes |
|--------------------------|-------------|---------------|
| Andine-Chilean | 69 (46.9 %) | 34 (64.1 %) |
| Subantarctic-Magellanian | 15 (10.2 %) | 4 (7.5 %) |
| Neotropical | 19 (12.9 %) | 9 (17 %) |
| Pacific | 26 (17.7 %) | 5 (9.4 %) |
| Atlantic-S. African | 6 (4.1 %) | — — |
| Eu-Fernandezian | 12 (8.2 %) | 1 (1.9 %) |

These elements can be tabulated according to their taxonomic relationships as follows:

| Elements | Angiosperms | Pteridophytes |
|--------------------|-------------|---------------|
| Antarcto-Tertiary | 62 (42.2 %) | 32 (60.4 %) |
| Neotropical-Andean | 54 (36.7 %) | 20 (37.7 %) |
| Arcto-Tertiary | 23 (15.6 %) | 1 (1.9 %) |
| Paleotropic | 2 (1.4 %) | — — |
| Austral-Seaside | 6 (4.1 %) | — — |

The Easter I. flora consists of 31 Angiosperms and 15 Pteridophyte species, distributed as follows:

| Elements | Angiosperms | Pteridophytes |
|---------------------|-------------|---------------|
| Paleotropical | 22 (70 %) | 11 (73.3 %) |
| Austral-circumpolar | 4 (12.9 %) | 3 (20 %) |
| Neotropical | 5 (16.1 %) | 1 (6.7 %) |

The Juan Fernandez flora though no doubt forming part of the New World flora and being especially related to that of S. Chile and the Andes, shows a remarkably high percentage of western elements.

The Easter I. flora obviously belongs to that of the Old World.

M. G. Baumann-Bodenheim (1956) studied the relations of the New Caledonian Phanerogam flora. Two main groups are distinguished according to their thermo-ecological requirements. Each of these main groups is then classified according to geographical distribution. In each group he has given several examples of which I have selected one in every case.

A. Southern hemisphere and subtropical genera

- | | |
|---|-----|
| 1. Endemic (<i>Amborella-Monim.</i>) | 120 |
| 2. New Caledonia, Queensland, Fiji (<i>Balanops-Balan.</i>) | 27 |
| 3. as above, but also incl. New Guinea and New Zealand (<i>Corynocarpus-Coryn.</i>) | 24 |
| 4. Austromelanesian (<i>Dracophyllum-Epacr.</i>) | 29 |
| 5. as above, but also in E. Indo-Malesia (<i>Quintinia-Sax.</i>) | 70 |
| 6. as 5, but also incl. Madagascar (<i>Myoporum-Myop.</i>) | 24 |
| 7. as 6, but also incl. Africa (<i>Pittosporum-Pitt.</i>) | 33 |
| 8. as 7, but also incl. extratropical S. America (<i>Cleidion-Euph.</i>) | 46 |

B. Eutropical genera

- | | |
|--|----|
| 1. Endemic (<i>Maxwellia-Bomb.</i>) | 15 |
| 2. (E.) Indo-Malesian (<i>Dysoxylum-Meliac.</i>) | 27 |
| 3. Paleotropical (<i>Gardenia-Rub.</i>) | 33 |
| 4. Pantropical (<i>Psychotria-Rub.</i>) | 91 |

Unclassified

c. 40

Some of the categories have been further divided. So e.g. in B. 4 (pantropical genera) distinction is made between those centering in the Neotropics, the Paleotropics and those without a centre of species development. This attempt to separate genera with different thermo-ecological requirements is certainly an interesting approach as each genus may tell its own 'different tale'.

His criteria of distinction are, however, not explained. Among the above mentioned examples one wonders why *Cleidion* is placed in the subtropical group. Also the difference between category A. 3 and A. 5 is not clear to me. The two cited examples (*Corynocarpus* and *Quintinia*) have practically identical distributions.

Although some genera are certainly erroneously classed (*Ascarina-Chlor.* is said to be limited to Fiji and New Caledonia, *Xylosma-Flac.* is said to be pantropical), I think the author has correctly indicated the floristic character of New Caledonia: high degree of endemism (135 out of c. 580 is, however, too high), preponderance of Old World

genera, special relations with Queensland, E. Malesia and Pacific (Fiji, New Zealand).

I cannot subscribe to his conclusion that the flora of New Caledonia has a subtropical character. Baumann has confused range of genera and preponderance of species with the thermo-ecology of the genera. One cannot simply stamp a genus as tropical or subtropical according to its range, as many of his so-called subtropical genera (e.g. *Cleidion*, *Pittosporum*, *Corynocarpus*, *Myoporum*) although ranging widely in the subtropics occur in the tropical lowlands as well, obviously having a wide ecological amplitude. Conversely, he classified *Psychotria* as tropical, although it extends to a high altitude in the tropics and also occurs far outside the tropics.

S. F. Glassman (1957) analysed the phytogeographic affinity of the vascular flora of Ponape (E. Carolines). All species are grouped into distribution classes (elements).

Only indigenous species are considered; these comprise 104 species of Vascular Cryptogams and 249 Angiosperms.

Judged by the figures of the distribution classes the affinities are greatest with the Indo-Pacific and Paleotropics generally. There is no special close relation with New Guinea as stated by Kanehira (1940). The Ponape flora is according to Glassman a Malesian derivative, only distinct on account of its high degree of endemism at species level. I believe, however, that he is too optimistic about its incidence.

In the enumeration below some of Glassman's elements have been omitted.

| Element | Vascular Cryptogams | Angiosperms |
|------------------------------|---------------------|-------------|
| Micronesian (Ponape only) | 15 (8) | 114 (70) |
| Polynesian | 2 | 3 |
| Melanesian | 1 | 2 |
| New Guinean | 3 | 1 |
| Philippine | 3 | 2 |
| Indo-Pacific | 39 | 57 |
| Austral | 5 | 1 |
| Paleotropical | 13 | 12 |

W. R. B. Oliver (1957) undertook a new analysis of the New Zealand flora. By tracing the distribution of the 1094 Dicotyledon species of the mainland he attempted to find evolutionary patterns reflecting the history of the group.

The boundaries chosen for delimiting the seven districts are in agreement with Cockayne (1921) as corrected by Cockayne & Allan (1926) and are indicated on fig. 10.

The distribution of species over the seven districts is tabulated on page 25.

According to Oliver the figures show that South I. with its more varied physiographic features has produced more species than North I. The boundary between districts 3 and 4 (Cook Strait) is the most important barrier, next come those between 1 and 2 and between 4 and 5. Thus four provinces can be distinguished. The highest concentrations of endemics are in district 4, 6 and 1, in that order.

The low degree of endemism of Stewart I. (district 7) is ascribed to its proximity to South I. Foveaux Strait presents a formidable barrier as it stops 456 species.

Oliver states that the Cook and Foveaux Straits are primarily water barriers (i.e. barriers to dispersal), the other barriers being primarily climatical (in other words ecological barriers).

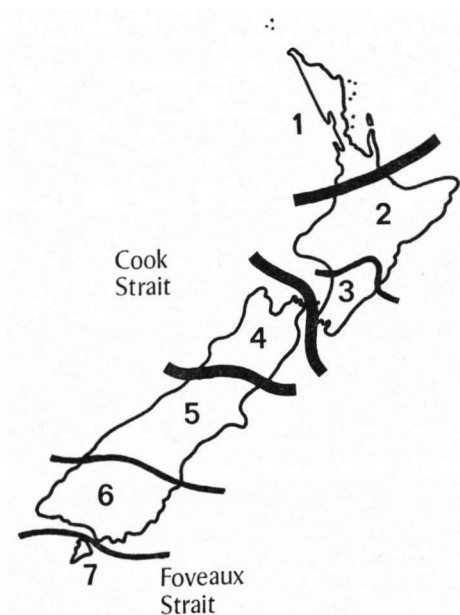
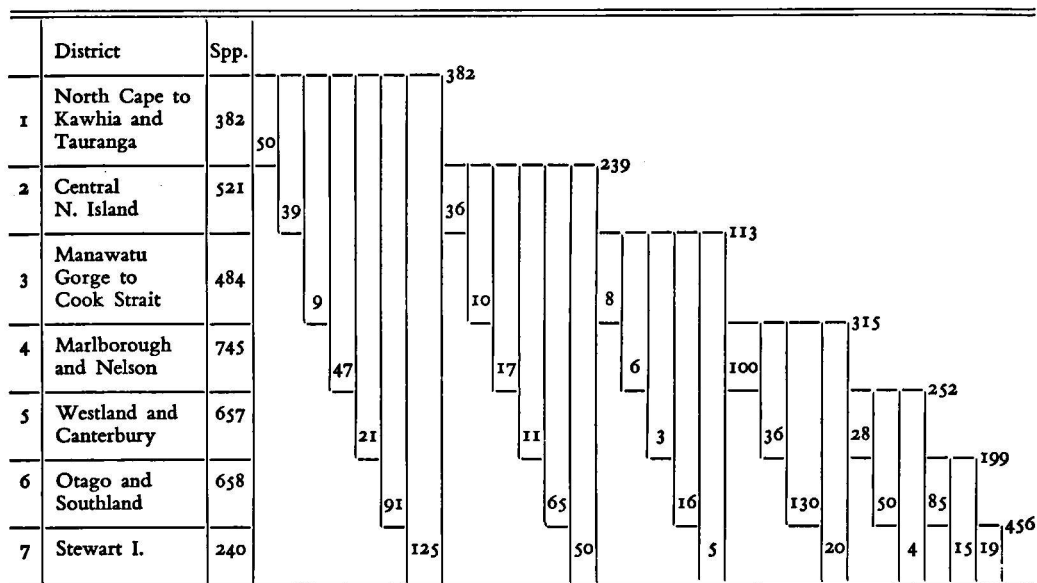


Fig. 10. Boundaries of provinces (thick) and districts (thin) in New Zealand after Oliver (1957).

I doubt whether this is entirely correct. If his figures are presented in a slightly different way it will be readily seen that Cook Strait is a most formidable barrier to southern (288 spp.) and Foveaux Strait to northern species (437).

| District | 1 | 2 | 3 | 4 | 5 | 6 | 7 |
|--------------------------------|-----|-----|-----|-----|-----|-----|-----|
| Total species | 382 | 521 | 484 | 745 | 657 | 658 | 240 |
| Species stopped at S. boundary | 50 | 75 | 27 | 170 | 99 | 437 | — |
| Species stopped at N. boundary | — | 189 | 38 | 288 | 82 | 100 | 19 |

In the case of Cook Strait, as South I. is much higher and more diversified, the climate may also form a barrier. In the second case the low altitude and small size of Stewart I. may be determining factors.

L. Diels (last ed. 1958) wrote a very good, concise booklet on Plantgeography in the 'Göschén' Series, the latest edition of which was revised by Mattick.

Diels accepted six 'Florenreiche', the Holarctic, the Paleotropic, the Neotropic, the Cape, the Australian and the Antarctic. The Paleotropic Kingdom is divided into two 'Gebiete' or Regions: his 'Afrikanisches Gebiet' comprises tropical Africa, Madagascar and India. The 'Malesisches Gebiet' extends west to Ceylon, includes the whole of Malesia and the Pacific east to Hawaii and SE. Polynesia. The inclusion of New Zealand in it is especially remarkable, the more so as Hawaii is called an 'appendix' to the Malesian region, whereas the floristic alliance with Malesia of this island group is certainly stronger than that with New Zealand. The Subantarctic islands are included in the Antarctic Kingdom, Galapagos and Juan Fernandez in the Neotropical.

W. B. Turrill (1959) in a very readable account of the history, aim and methods of phytogeography also gave his opinion on the classification of the world into phytochoria (phytogeographical units). His 'Realm' corresponds to 'Kingdom' of which four are distinguished. As no map is provided I have prepared one. See fig. 11.

Nearly all of the Pacific is included in his Paleotropical Realm as a region. Galapagos and Juan Fernandez are included in his Neotropical Realm. New Zealand is ranked as a region alongside Australia, the Cape and southern S. America in the Southern Realm.

Some years ago (van Balgooy, 1960) I attempted a subdivision of the Pacific based on the present-day ranges of Phanerogam genera in the Pacific. All genera of the Pacific were tabulated and their complete range determined. Fifteen distribution classes were distinguished. Each island group could then be characterized by its 'floristic generic spectrum'.

The strength of the floristic boundary between any two island groups, the 'demarcation knot' (van Steenis, 1950) was calculated as the percentage of the total number of genera restricted to either of the two island groups compared, by means of the following formula:

$$\frac{\text{number of genera confined to one group}}{\text{total number of genera on both groups}} \times 100$$

In this way a hierarchical subdivision of the Pacific was attempted as illustrated by fig. 12 and the following scheme:

Hierarchical subdivision of the Pacific (van Balgooy, 1960)

| Region | Province | Subprovince | District | Subdistrict |
|----------------|-------------|-------------|----------|-------------|
| Indo-Malesian | E. Asiatic | | | |
| | SE. Asiatic | | | |
| | Malesian | W. Malesian | | |
| | | S. Malesian | | |
| | | E. Malesian | | |
| New Caledonian | Hawaiian | SW. Pacific | | |
| | | | | |
| | | | | |
| | | | | |
| | | | | |
| Australian | | | | |
| | | | | |
| | | | | |
| | | | | |
| | | | | |

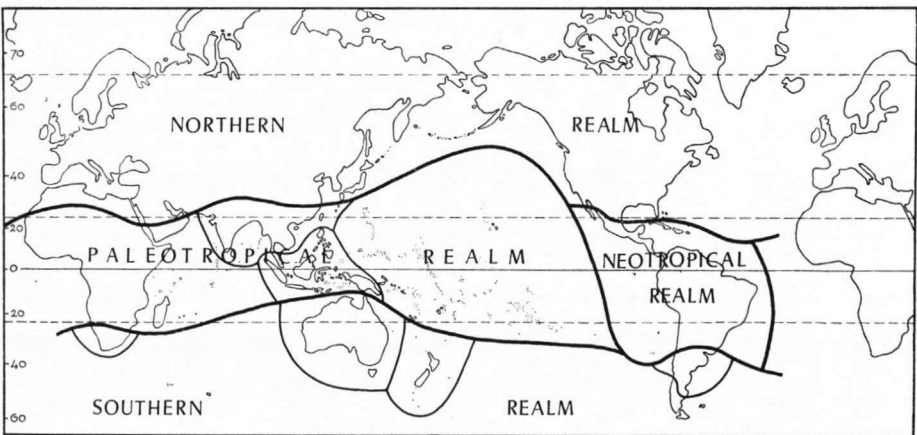
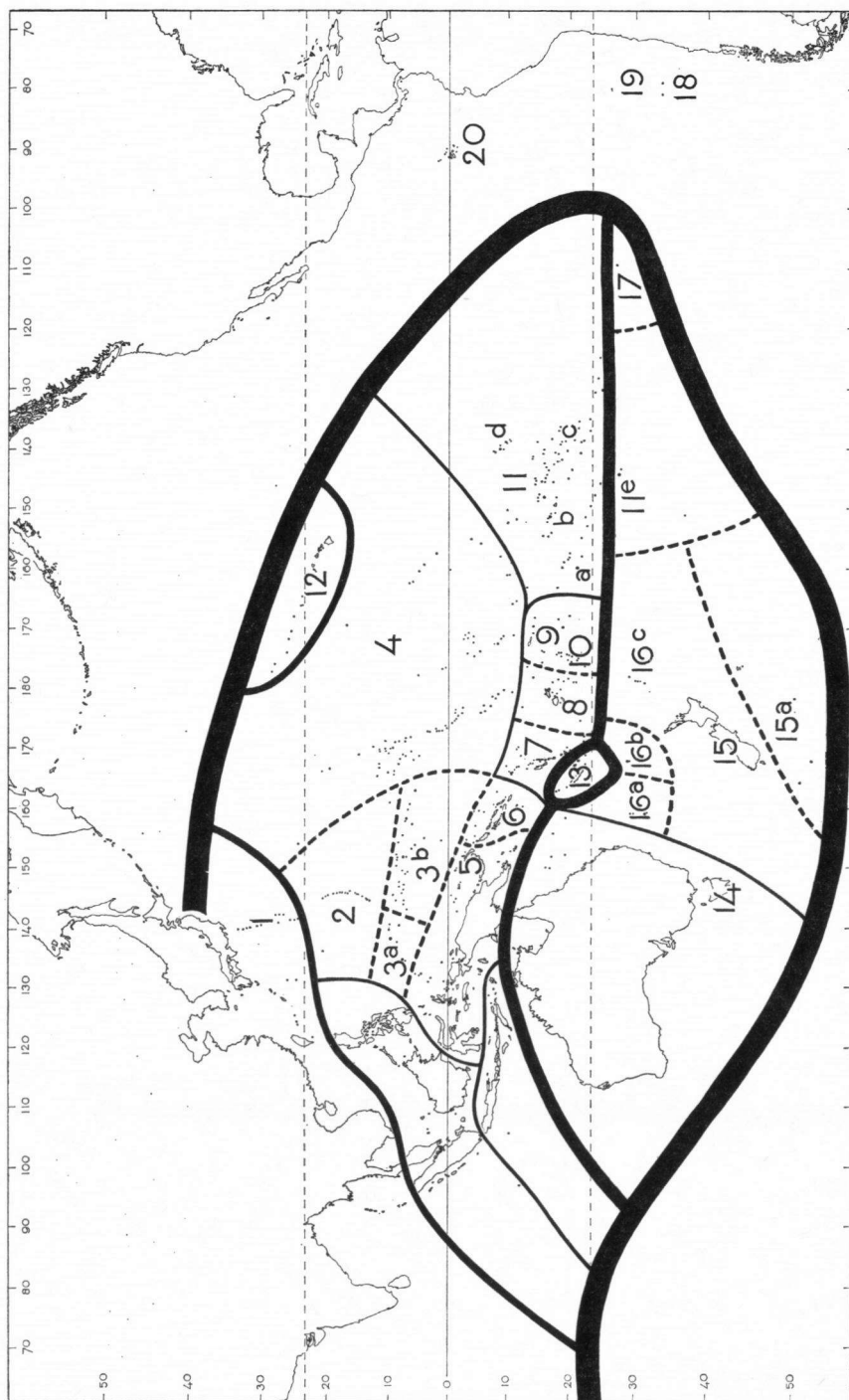


Fig. 11. In Turrill's (1959) classification the Pacific is divided over three of his four Realms (Kingdoms), Galapagos and Juan Fernandez form part of the Neotropical, New Zealand is regarded as a separate region of the Southern and the rest of the Pacific as a separate region of the Paleotropical Realm.



The main conclusions from this analysis were:

- a) That there is a sharp break between Old and New World floras in the eastern Pacific between Hawaii and SE. Polynesia on the one hand and Galapagos and Juan Fernandez on the other.
- b) That the Malesian character is widespread in the Pacific flora.
- c) That representation of the Australian element in the Pacific is limited.
- d) That a high rank had to be assigned to New Caledonia as it could not be included in the Australian, Pacific, and Indo-Malesian Regions, to which its affinity was equally strong, and in addition its high degree of endemism.

Skottsberg (1960) attempted to subdivide the southern hemisphere focussing attention on taxa with 'Antarctic distribution'. According to the author two main patterns can be distinguished: a strict Subantarctic and an Austral one, the latter being more subtropical in character and hence extending more northward. It is obvious that Skottsberg is referring to 'ecological elements' in the sense of Wulff (1943), the term 'pattern' is rather inappropriate here, as the thermo-ecological requirements and not the distribution form the primary criterion.

The following subdivision is proposed:

- I Antarctic zone: S. of 60° SL but incl. South Georgia and Bouvet I.
- II Subantarctic zone: between 48—60° SL
 - (a) Magellanian Province
 1. W. Patagonian—Fuegian District
 2. Andine Patagonian—Fuegian District
 3. Falkland and South Georgia District
 - (b) Kerguelen Province
 - (c) Subantarctic islands of New Zealand Province
- III Austral zone (not specified)
 - (a) Valdivian Province
 - (b) South I. of New Zealand, Chatham, Tasmanian table land
- IV W. Pacific Borderland
 - (a) Australia, Lord Howe, Norfolk, New Caledonia, New Guinea
 - (b) Fiji, Samoa, Malesia, E. Asia
- V Polynesia: SE. Polynesia and Hawaii
- VI E. Pacific Borderland: Andes up to Central and N. America
- VII S. Atlantic outposts of Magellanian Province in Tristan da Cunha
- VIII Afro-Indian outposts: Africa, Madagascar, Mascarenes, St. Paul, Amsterdam

The point of this very detailed division in headings without figures or percentages is not clear.

Fig. 12. Hierarchical floristic subdivision of the Pacific after Van Balgooy (1960). (1) Bonins, (2) Marianas, (3a) W. Carolines, (3b) E. Carolines, (4) Central Polynesia, (5) Bismarcks, (6) Solomons, (7) New Hebrides + St. Cruz, (8) Fiji, (9) Samoa, (10) Tonga, (11a) Cook Is., (11b) Societies, (11c) Tuamotus, (11d) Marquesas, (11e) Rapa I., (12) Hawaii + Leeward Is., (13) New Caledonia + Loyalties, (14) Tasmania, (15) New Zealand, (15a) Subantarctic Is. of New Zealand + Chathams, (16a) Lord Howe I., (16b) Norfolk I., (16c) Kermadecs, (17) Easter I., (18) Juan Fernandez Is., (19) Desventuradas Is., (20) Galapagos. See text for explanation.

M. Hotta (1962) discussed the phytogeography of Tonga as based on the distribution of indigenous Phanerogam and Pteridophyte species. The following conclusions were reached:

- a) The island groups of Fiji, Samoa and Tonga constitute a region of which the parts are closely related phytogeographically.
- b) About one third of the Tonga species are not found beyond the region cited above.
- c) Sixty percent of the Pteridophyte and 25 % of the Phanerogam species of Tonga also occur in continental Asia.
- d) A smaller number of Tonga species also occurs in New Zealand or Australia.
- e) Most of the Tonga species are allied to or identical with Malesian-Asiatic species.
- f) Slightly more than 10 % of the species are endemic to Tonga.
- g) The greatest differentiation seems to have taken place on the geologically oldest island: Eua.

'Region' is here obviously used as a neutral term, and not to indicate the major phytogeographic unit as is usual. 'Province' would have been more appropriate.

R. F. Thorne (1963) in discussing biotic distribution patterns in the Pacific stated that biogeographic inferences should be based on the geographic distribution of all organisms, and not only on one special group and that conclusions based on only a small section of the total biota may be conflicting with those arrived at by a study of another. Darwin (1859) had already pointed out the importance of this principle. It was more recently stressed among others by Merrill (1936) and Skottsberg (1956).

Thus, after reviewing all the biogeographic literature concerning the Pacific, Thorne attempted to make a subdivision of the Pacific that 'could in general be meaningful to most biologists.'

Although in a later paper he was rather sceptical about this subdivision (Thorne, 1965), I think it is the nearest approach to a generally acceptable hierarchical classification of the Pacific, although of course one may differ about the rank assigned to some of the biogeographical subdivisions or the strength and position of certain demarcations.

No map was given, so I have attempted to prepare one that reflects his opinion. In this map (fig. 13) only the names of Regions and Subregions have been indicated; for the names of the further subdivisions see the accompanying scheme on page 32. From this all names not concerning the Pacific proper and also the names of the islands belonging to the various districts which were given in the original paper have been omitted.

F. Mattick (1964) in edition 12 of Engler's *Syllabus* presented a subdivision of the world very similar to the ones proposed by Good (1953) and Diels (1958). See fig. 14. He distinguished six 'Florenreiche' (I. Holarctic, II. Paleotropic, III. Neotropic, IV. Cape, V. Australian, VI. Antarctic).

Most of the Pacific is included in the 'Paläotropisches Florenreich' which is divided into three 'Unterreiche': the African, Indo-Malesian and Polynesian.

The Polynesian 'Unterreich' comprises five 'Florengebiete': 24. Hawaii, 25. Polynesia

Fig. 13. Biogeographical subdivision of the Pacific after Thorne (1963). This classification is an attempt to combine all hitherto suggested phyto- and zoogeographical subdivisions. Broken lines represent boundaries between districts, the solid lines according to increasing thickness boundaries of provinces, subregions and regions. See text for further explanation.

Subdivision of the Pacific after Thorne (1963)

| Region | Subregion | Province | District |
|-------------|----------------|---------------|---|
| Oriental | Indochinese | | |
| | Indomalayan | | |
| | Papuan | Moluccan | |
| | | Papuan | |
| | | Torresian | |
| | | Bismarckian | { Bismarckian Solomonian |
| | | Fijian | { New Hebridian Fijian |
| | Polynesian | Polynesian | { Micronesian Polynesian |
| | | Hawaiian | |
| | Neo Caledonian | | |
| Australian | Australian | | |
| | Neo-Zeylandic | Kermadecian | { Lord Howeian Norfolkian Kermadecian |
| | | Neo-Zeylandic | { Chathamian Antipodian Neo-Zeylandic |
| Antarctic | Subantarctic | Kerguelian | Macquarian |
| | Antarctic | Magellanian | |
| Neotropical | Chilean | Fernandezian | |
| | Peruvian | Galapagean | |
| Holarctic | Nearctic | Caribbean | Mexico (incl. Revilla Gigedo & Clipperton) |
| | Palearctic | | |

(Fiji, Samoa, Tonga, Tokelau, Phoenix, Cook, Society, Tubuai, Tuamotu, Marquesas, and Easter Is.), 26. Melanesia and Micronesia (Bonin, Marianas, Carolines, Marshall, Gilbert, Ellice, Bismarck, Solomons, New Hebrides), 27. New Caledonia (New Caledonia, Loyalty, Lord Howe and Norfolk Is.), 28. New Zealand (incl. Kermadec and Chatham Is. but excl. the southern part of South I. and the Subantarctic islands).

The boundary between the Paletropic and Antarctic Kingdoms runs through South I. This part of New Zealand together with the Subantarctic islands form a 'Florengebiet' (40) within the Antarctic Kingdom.

The Neotropical Kingdom a.o. comprises: 29. the Caribbean 'Florengebiet' incl. Revilla Gigedo Is., 33. the Andine 'Florengebiet' incl. Galapagos Is., and 34. the Juan Fernandez 'Florengebiet'.

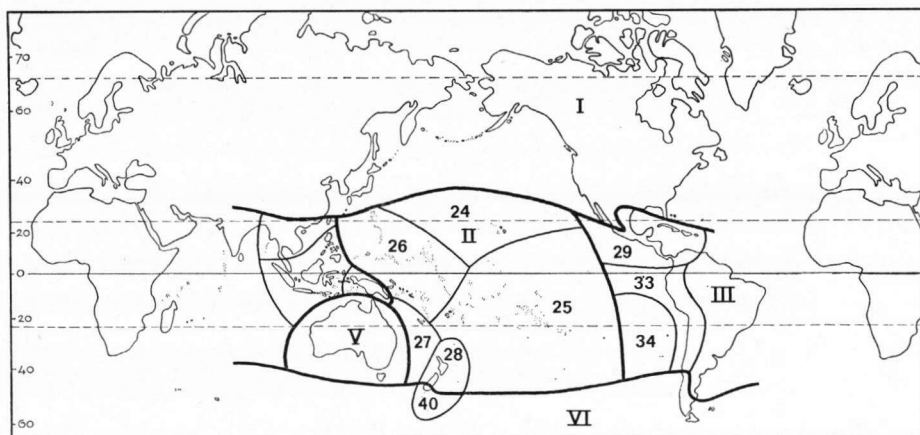


Fig. 14. Subdivision of the world flora after Mattick in Engler (1964). (I) Holarctisches Florenreich, (II) Palaetropisches Florenreich, (III) Neotropisches Florenreich, (IV) Australisches Florenreich, (V) Antarktisches Florenreich, (VI) Antarktisches Florenreich, (24) Hawaii, (25) Polynesien, (26) Mela-, Micronesien, (27) Neu Caledonien, (28) Neu Seeland.

R. F. Thorne (1965) discussed the floristic relationship of New Caledonia with the surrounding areas at genus and family level.

He stressed the difficulties of subdividing this part of the Pacific biogeographically. His criticism on the arbitrariness of geographic classification in general will be discussed in full later (Chapter III, 3).

The floristic relationships of New Caledonia were established by calculating what percentage of its 660 genera (97 endemic) also occur in each of the surrounding areas (the Solomons excepted) and the percentage confined to New Caledonia and each of these areas.

| Area | genera | endemic | shared with N. C. | shared % of total genera from area and N.C. | % of genera from area shared with N.C. | limited to area and N.C. |
|--------------|--------|------------|-------------------|---|--|--------------------------|
| Loyalty Is. | 259 | 0 | 257 | 38.8 | 99.2 | 4 |
| New Hebrides | 371 | 2 (0.54) | 283 | 37.8 | 76.3 | 5 |
| Fiji | 449 | 12 (2.67) | 303 | 37.6 | 67.5 | 4 |
| Queensland | 1268 | 45 (2.78) | 474 | 32.8 | 37.4 | 17 |
| New Guinea | 1350 | 141 (10.4) | 482 | 31.5 | 35.7 | 1 |
| New Zealand | 336 | 31 (9.23) | 118 | 13.4 | 35.1 | 3 |

His conclusions can be summarized as follows:

- 1) The flora of the Loyalties and New Caledonia is best treated as one unit.
- 2) The high percentage of New Hebrides and Fiji genera also represented in New Caledonia suggests that they have one common source area.

- 3) The much higher degree of endemism on New Caledonia is to be attributed to its longer and more profound isolation.
- 4) The relative paucity of the New Hebrides flora is not only due to insufficient collecting but also to the greater age of New Caledonia and Fiji.
- 5) The shared percentage of the total number of genera found in New Caledonia and New Hebrides, Fiji, Queensland and New Guinea respectively is remarkably similar: 37.8, 37.6, 32.8, and 31.5, indicating equally strong relationships of New Caledonia with all these surrounding areas.
- 6) Of the 660 New Caledonian genera 474 are shared with Queensland and 482 with New Guinea. Apart from the endemics, some of which probably merit family rank, two families are not represented in Queensland and three not in New Guinea. Conversely, 50 Queensland and 55 New Guinea families are unknown from New Caledonia. Of the restricted genera 17 are known from Queensland and New Caledonia and only one (*Pelma*, now reduced to *Bulbophyllum*, *Orch.*) is limited to New Caledonia and New Guinea, but in view of the available land and distance it is a fairer comparison to cite the 17 genera that New Caledonia shares with Melanesia (New Guinea-Samoa). This confirms my statement (van Balgooy, 1960, p. 419) that New Caledonia is equally related to Malesia and Australia.
- 7) Relations between New Caledonia and New Zealand are rather weak: only 13.4 % of their total genera occur in both. It is not surprising in view of the higher latitude of New Zealand. The same percentage is found when New Caledonia is compared with Tasmania.

I want to comment on his ascribing (in point 3) the high degree of endemism on New Caledonia to 'a longer and more profound isolation', than presumably Fiji and the New Hebrides. How can that apply to New Guinea, with 141 endemic genera, it is an island but is surrounded by land on all sides, by islands and a continent, and must have been so for a considerable time?

Hosokawa (1967) decided that on the basis of vegetation character and floristic composition Micronesia forms a well defined province. He once more stressed the sharp floristic discontinuity (Hosokawa's line) with the Bonins which form part of the temperate E. Asiatic region. The Micronesian Province is closely related to New Guinea, and forms part of the Papuan Region the extent of which, however, is not indicated. Another demarcation line is drawn between Micronesia and the Marshall Is. which are included in his Polynesian Province. This province is characterized by a flora and vegetation that are poor compared with Micronesia. He does not state to which region the Polynesian province belongs.

For the subdivision of Micronesia one is referred to the table below. A new rank (Sector) is introduced to indicate phytochoria between subprovince and district.

(A) Province of Micronesia

- (1) Subprovince Marianas
 - (a) Sector N. Marianas
 - (b) Sector S. Marianas
- (2) Subprovince Palau and Carolines
 - (a) Sector Palau
 - (i) District Palau
 - (ii) District Yap

- (b) Sector Carolines
 - (i) District Ponape and Kusaie
 - (ii) District Truk

(B) Province of Polynesia, comprising the Marshall, Gilbert, Ellice, Phoenix and Line Is.

It will later be seen that Hosokawa's conclusions agree well with mine, except that my phytochoria have lower ranks.

A noteworthy recent contribution towards a phytogeographic subdivision of the world is that made by A. Takhtajan (1969). He distinguished six Kingdoms and 37 regions each characterized according to the degree of endemism and the rank of the endemic taxa. It is reminiscent of Engler's and Good's subdivisions, but it reveals much independent thought and attention to detail although one may differ in opinion about some of his ideas.

New Zealand and the adjacent islands, for instance, form a region of his Antarctic Kingdom, together with Patagonia and the Subantarctic islands. Although there is something to say for this conception it conceals the relations between New Zealand and Australia.

The peculiar nature of New Caledonia is recognized by giving it the rank of Subkingdom (Dominion) of the Paleotropical Kingdom alongside an African, a Madagascar, an Indo-Malesian and a Polynesian Subkingdom. The Indo-Malesian Subkingdom is divided into four regions, one of which is the Papuan (F. Malesia including the Bismarcks and Solomons). The Polynesian Subkingdom consists of three regions, the Hawaiian, the Polynesian and the Fijian (St. Cruz, New Hebrides, Fiji, Samoa, and Tonga). One may object to the last group of islands being given the same high rank of region as E. Malesia as the latter is certainly more distinctive.

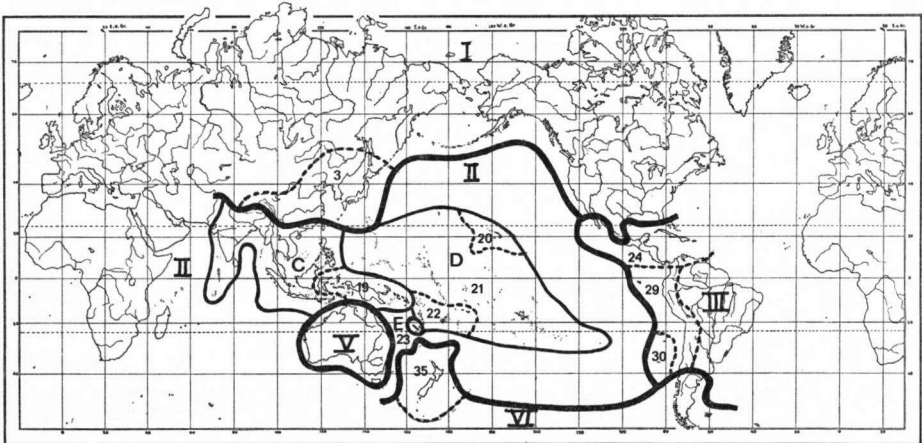


Fig. 15. Takhtajan's (1969) subdivision. (I) Holarctic Kingdom, (II) Paleotropical Kingdom, (III) Neotropical Kingdom, (IV) Australian Kingdom, (V) Antarctic Kingdom, (C) Indo-Malesian Subkingdom, (D) Polynesian Subkingdom, (E) Neo-Caledonian Subkingdom, (19) Papuan Region, (20) Hawaiian Region, (21) Polynesian Region, (22) Fijian Region, (24) Caribbean Region, (29) Andean Region, (30) Fernandezian Region, (35) New Zealand Region.

The Revilla Gigedo Is. are placed in the Caribbean, the Galapagos and Cocos Is. in the Andean region. Juan Fernandez and Desventuradas form the Fernandezian region. All these make part of the Neotropical Kingdom.

Takhtajan's views on the subdivision of the world are illustrated in fig. 15, as far as the Pacific is concerned.

III. MATERIAL AND METHODS

1. Only Phanerogams

This study only concerns the Phanerogams. Among the many groups of organisms inhabiting the Pacific the Phanerogams are perhaps not the largest but they are certainly the most important in bulk, and among the most important as regards number of taxa.

Moreover many organisms, such as insects and birds, are dependent in one way or another on them. To know the distribution of such an ecologically dominant group as the Phanerogams may be of advantage to students in other fields of biogeography.

Phanerogams have the advantage of being one of the best collected and studied groups in the world, in general they are less easily overlooked than e.g. non-vascular Cryptogams. It is, moreover, a group with which I am personally best acquainted. Had I extended this study to include the whole plant kingdom I would no longer have the advantage of 'inside knowledge'. The material basis would of course have been much broader but at the same time it would have been more unwieldy and heterogeneous. It is also uncertain from what I know of Pteridophyte and Bryophyte distributions, whether the same picture would have emerged as presented by an analysis of Phanerogam distribution. There are certainly non-Phanerogam genera of which the distribution almost exactly matches that of some Phanerogams. I expect that most Pteridophyte genera could be placed in the distribution classes that have been distinguished here, but the quantitative representation in the various classes would probably be different. The distribution of some *Cyatheaceae* genera offer good examples. *Dicksonia* matches that of *Nertera-Rub.* (compare maps 166 and 54 in van Steenis & van Balgooy, 1966). *Cibotium* has a distribution like that of *Distylium-Ham.* or *Perrottetia-Celast.* (ibid. maps 167, 73, and 52).

On the other hand the strong demarcation that exists between the Phanerogam floras of Formosa and the Philippines was not confirmed by Imahori (1957) for the species of the Chlorophycean family *Characeae*. In this family the affinity of the Formosan species was found to be with those of the Philippines and not with those of continental Asia.

Still I am looking forward to an analysis along the same lines as proposed here of non-Phanerogam groups by persons better qualified than I am.

2. Only native taxa

In the census (Appendix) the taxa found in the Pacific islands have been listed.

However, not all have been used for the plant-geographical analysis which is based solely on those taxa which owe their presence to natural causes and not to human activity.

This distinction between indigenous and non-indigenous plants is in some cases notoriously difficult and subject to dispute.

Of course the majority of the genera presents no difficulties: all the genera represented in the Pacific exclusively by weed species, such as *Ageratum*, *Siegesbeckia-Comp.* and *Stachytarpheta-Verb.*, have been omitted from the census.

Also all the genera that in the Pacific are always associated with agriculture or horticulture have been left out. Such genera are e.g. *Ananas-Brom.*, *Angelonia-Scroph.*, *Broussonetia-Urt.*, *Colocasia-Arac.*, and *Rosa-Ros.*

The difficulty arises with those genera which have some species certainly or probably native in a part of the Pacific but which also have other species associated in one way or another with man. The exact natural range of the genus in most such cases cannot be defined with certainty. To mention a few examples: *Aleurites-Euph.*, *Cananga-Annon.*, *Cocos-Palm.*, and *Spondias-Anac.* These genera, though taken up in the census, have not been used for the analysis.

Generic records that in my opinion were insufficiently documented, or genera of doubtful taxonomic status have been listed but were not used for the analysis. For example the records of *Beilschmiedia-Laur.* for the New Hebrides and of *Arundina-Orch.* for Tahiti were not accepted, nor of the questionable genus *Serresia* for New Caledonia.

Furthermore, those genera occurring on both sides of the Pacific ('amphipacific' sensu van Steenis, 1962) but not actually entering it were not entered in the census. Examples: *Mitrastemon-Raffl.* (E. Asia, Malesia, Central America) and *Orites-Prot.* (Australia, South America).

Some genera are represented by indigenous species in parts of the Pacific and by introduced ones in others, or are represented on the same island group by both introduced and native species. Such genera are e.g. *Aristida-Gram.*, *Bidens-Comp.*, *Euphorbia-Euph.*, *Ludwigia-Onagr.*, and *Psidium-Myrt.* In such cases unless there was reasonable certainty about the natural range of the genus I have preferred to leave it out of the analysis.

If a monograph or a local revision of the genus exists I have followed the author's opinion. For the genera for which these do not exist, I had to rely on personal judgment, which I realize may not always meet general approval. I have e.g. considered *Lemna-Lemn.* as introduced and accepted *Lindernia-Scroph.* as indigenous in the Pacific. The habitat of a species and the native use made of it may give a clue to whether it is indigenous or not. Species invariably found near houses or along roads are almost always introduced weeds. But locally an indigenous species may also behave like a weed, and not all species utilized by man have necessarily been introduced by him. Many local and indigenous plants were used by the early Polynesians for making instruments, for the 'tapa culture', or for dyeing purposes (see e.g. Buck, 1957, Zepernick 1967a & b, and Kooyman, in press).

The fact that a species is described as 'endemic' for an island is no guarantee for its being native there. It is far easier to describe a specimen as new than to make critical comparisons with species from elsewhere. Many of these endemics may prove to be aberrant forms resulting from long isolation after having been introduced by man.

In some such cases I have consulted the herbarium material (if available) but in general I have not tried to investigate all 'doubtfuls' myself. The amount of work involved in clarifying a few cases of uncertainty is hardly rewarding and does not substantially contribute to the accuracy of the whole. A quotation from Hooker's famous introductory essay in the 'Flora Tasmaniae' (Hooker, 1860, p. iii) is exactly applicable to my work and at the same time supports my arguments for using the genus as working unit, as will be discussed in the next paragraph: 'To many who occupy themselves with smaller and better worked botanical districts, such results as . . . I have compiled . . . may seem too crude, . . . But it is not from a consideration of specific details that such problems as . . . origins and distributions . . . will ever be solved, though we must eventually look to these details for proofs of the solutions we propose. The limits of the majority of species are so indefinable that few naturalists are agreed on them . . .

On the other hand, when dealing with genera or other combinations of species, all that is required is that these be classified in natural groups. It is to an investigation of the extent, relations, and proportions of these natural combinations of species, then, that we must look for the means of obtaining and expressing the features of a flora. Further . . . , if the species are limited and estimated by one mind and eye, the errors made under each genus will so far counteract one another, that the mean results for the genera and orders will scarcely be affected. As it is, the method adopted has absorbed many weeks of labour during the last five years, and a much greater degree of accuracy could only have been obtained by a disproportionately greater outlay of time, whilst it would not have materially affected the general results.'

Owing to the fact that for this work I have been more critical in accepting genera as native, it will be noticed that for some island groups a smaller number of genera is given than in my preliminary analysis. For New Caledonia I accepted 660 genera against 655 here, despite a few new generic records since 1960. For Hawaii the figures are 238 and 226 respectively.

3. The genus as working unit

'... il est difficile de ne pas sentir dans la distribution des genres quelques chose de plus élevé, quelque chose d'antérieur à l'état actuel du monde.'

(A. de Candolle, 1855, p. 1293)

As was said in the introduction the genus is the basic working unit of this paper, as it was in my preliminary analysis. In the latter I have summarized my reasons for preferring the genus instead of the species as is more common usage. In most phytogeographic papers taxa of various rank are often used side by side. To my knowledge it was Van Steenis (1950) who was the first to use the genus solely and consistently as working unit. It must be added, however, that many others, such as De Candolle (1855), Hooker (1860), and Good (1947), have favoured the genus in phytogeographic considerations. A more extensive argumentation of the advantages and a plea for its future use in this kind of analysis is appropriate here.

It has been argued that the species distribution gives a clearer and more detailed 'phytogeographic picture'. There are moreover many more species than genera, which gives us a much broader base for theoretical speculations. Although this cannot be disputed, the systematic delimitation of a species is much more subject to the personal taste of the student than is the genus. Much more collecting and much more study is required to establish the taxonomic limits and the geographic extent of a species than of a genus.

An analysis of the Pacific flora at species level would at this stage be highly premature and unbalanced. It can easily be demonstrated that the number and names of species for any given region is much more liable to fluctuations than that of the genera. This is particularly clear when the number of species recorded for a given region before and after a revision are considered. The use of families has the disadvantage of not only strongly reducing the statistical material, but moreover they are in general much wider distributed than genera and show less clear patterns. In addition it cannot be said that families are more stable taxonomically than genera. Genera quite firmly established and accepted are often tossed from one family to the other.

The above arguments can be most fruitfully discussed by means of some typical examples.

Boerlage (1899b) in his 'Handleiding' recognized 21 genera of *Convolvulaceae* for Malesia*). Van Ooststroom & Hoogland (1953) in their *Flora Malesiana* revision of this family reduced three of these, one genus was newly recorded for the region, whereas two were later newly described bringing the total back to 21.

In the *Flacourtiaceae* Boerlage (1890a) accepted 13 genera for Malesia (under *Samydaceae* and *Bixaceae*). Of these two were later accommodated in other families, of the remaining 11 one was reduced and another lowered to sectional rank by Sleumer (1954). A number of genera were described or recorded between the issue of Boerlage's and Sleumer's papers. All but one of these were retained by Sleumer, the total of Flacourtiaceous genera now accepted for Malesia being 19. The increase is rather considerable, but it is striking how few were reduced.

In the *Thymelaeaceae* (incl. *Gonystylaceae*) Boerlage (1900) distinguished nine genera for Malesia. Domke (1934) retained eight, reinstated three that had been reduced by Boerlage and described one genus as new, thus raising the total to 12. All but one of these were accepted by Airy Shaw (1953) and Ding Hou (1960). One genus was newly described.

Of the 12 genera of *Loganiaceae* recognized by Boerlage (1899a) Leenhouts (1962) reduced only one, another was excluded from the family, whereas one genus was newly recorded for Malesia.

The last two examples again show that despite the very incomplete material available to Boerlage, in a lapse of about 60 years comparatively little has changed as far as the number of genera for Malesia is concerned.

How the number of species and particularly the incidence of endemism for a limited area may change after an overall revision of the genus can be illustrated by examples from the Philippines and Indo-China.

The figures given by Merrill (1923—1926) in his 'Enumeration of Philippine Plants' are compared with figures taken from recent revisions.

| | species | endemic |
|-----------------------|---------|---------|
| <i>Canarium-Burs.</i> | | |
| Merrill | 45 | 45 |
| Leenhouts (1959) | 9 | 4 |
| <i>Capparis-Capp.</i> | | |
| Merrill | 17 | 13 |
| Jacobs (1965) | 9 | 1 |
| <i>Dillenia-Dill.</i> | | |
| Merrill | 15 | 13 |
| Hoogland (1952) | 12 | 10 |
| <i>Ficus-Morac.</i> | | |
| Merrill | 144 | 116 |
| Corner (1965) | 87 | 20 |

*) Actually Boerlage only treated part of Malesia, viz. the former Dutch East Indies, but this hardly affects the figures presented here.

The following figures from Indo-China have been taken from Vidal (1964):

| | taxa | endemic |
|--------------------|------|---------|
| <i>Capparis</i> | | |
| Gagnepain (1939) | 24 | 17 |
| Jacobs (1960) | 33 | 8 |
| <i>Connaraceae</i> | | |
| Lecomte (1908) | 21 | 15 |
| Gagnepain (1951) | 30 | 23 |
| Vidal (1962) | 18 | 2 |
| <i>Dillenia</i> | | |
| Gagnepain (1938) | 13 | 7 |
| Hoogland (1952) | 8 | 1 |

Jacobs (1965) revised the genus *Capparis* for the area between the Indus and the Pacific. There were no less than 234 published specific names for the genus in this area. Only 74 or 32 % of these were retained, whereas 8 were described as new. The first records of the genus for various parts of the area date from 1753 for India and Ceylon, from 1790 for the Marianas, from 1824 for Java, the Moluccas, Timor and Australia, from 1835 for the Philippines, from 1854 for Burma, from 1861 for Sumatra, and from 1870 for Celebes and New Guinea. This shows that the genus distribution for the area was already established as regards its main features as early as 1870.

Capparis is a genus of shrubs showing preference for periodically dry conditions, but *Canarium*, a genus of primary forest trees, shows almost identical figures and the same reduction percentage. In Leenhouts' monograph (1959) the number of species recognized is 75; 14 of these had been proposed as new by the same author earlier in the course of his work. The total number of specific names proposed in *Canarium* before was 213 (pre-Linnean ones and nomina nuda excluded); the 61 species retained by Leenhouts represent nearly 29 % of this number. The genera *Canariellum*, *Canariopsis*, and *Pimela*, for which a number of species had also been described, were already reduced to *Canarium* by Boerlage (1890b). It must, however, be remarked that due to the work by Lam and others the generic pattern of the family is quite different from that adopted by Boerlage.

As *Canarium* and *Capparis* are both lowland genera, it is interesting to consider a montane genus as well. A good example is provided by *Rhododendron-Eric.* revised for Malesia by Sleumer (1966). *Rhododendron*, a genus of alpine, subalpine, and montane shrubs and treelets, shows different figures as regards the reduction percentage but is equally instructive. Due to its habitat it was formerly perhaps not so well collected as either *Capparis* or *Canarium*. Its showy flowers and horticultural possibilities combined with the fact that the montane habitats are nowadays more easily accessible especially in New Guinea has of late resulted in considerable collections. From Sleumer's revision the following figures can be gleaned. Species were first described from the major Malesian islands as follows: Malaya, 1822; Java, 1823; Celebes, 1839; Borneo, 1848; Sumatra, 1850; New Guinea, 1878; Philippines, 1885.*)

*) All these first descriptions were incidentally also new records of the genus for the islands in question.

In 1885 a total of 41 species had been described for Malesia. Many more species from various parts of the archipelago have since been described (mostly uncritically), especially between 1900 and 1920. Very few new species were described after 1940 until Sleumer started his revision. A great amount of new material had accumulated in the meantime, besides numerous 'paper species'. Many of these had to be reduced, but about the same number was described as new, the total ultimately accepted being 282 species.

The example of *Rhododendron* shows two things:

- a) The number of species for Malesia has in the course of the years shown considerable changes, the intensive collecting of late years has yielded many new species but has resulted in the reduction of many others.
- b) As early as 1885, when only 41 Malesian species were known to science, and of which incidentally 10 were reduced in later years, the genus was known from all major islands. So the generic area as far as Malesia is concerned was established 75 years before the genus was subjected to a regional revision.

As a final illustration we may compare the number of families, genera and species of Dicotyledons accepted as native to New Zealand in the course of c. 100 years.

| Author | Families | Genera | Species |
|------------------|----------|--------|---------|
| Hooker (1864) | 74 | 220 | 702 |
| Cheeseman (1906) | 77 | 225 | 1029 |
| Allan (1961) | 87 | 236 | 1253 |

The increase of the various taxa in Cheeseman's flora compared with Hooker's is:

| | | | | |
|----------|-----|----|------|---|
| families | 3 | or | 4 | % |
| genera | 5 | or | 2.3 | % |
| species | 327 | or | 46.6 | % |

Compared with Cheeseman's flora the increase in Allan's is:

| | | | | |
|----------|-----|----|------|---|
| families | 10 | or | 13 | % |
| genera | 11 | or | 5 | % |
| species | 224 | or | 21.8 | % |

Finally comparing the increase of taxa in Allan's flora in relation to Hooker's we find the following figures:

| | | | | |
|----------|-----|----|------|---|
| families | 13 | or | 17.5 | % |
| genera | 16 | or | 7.3 | % |
| species | 551 | or | 78.5 | % |

These figures show that, contrary to the strong increase of species recognized, the number of genera has remained quite stable, even more so than the number of families. It may be objected that the number of taxa recognized is also a matter of the author's taxonomical conceptions. The above examples demonstrate clearly that even if this is true it apparently does not apply to the genera.

The choice of the genus as the unit for plant-geographical purpose appears to be well supported by the examples given above.

In some cases, however, I have deviated from this general principle. The main purpose of this paper is to find floristic affinities and to establish phytogeographic boundaries. In cases where a section or other infrageneric part of the genus is more informative, this has been used instead of the genus. This procedure was only followed if the infrageneric taxon was well defined and described.

The treatment of genera and families has been rather conservative. So *Monimiaceae* here include *Amborellaceae*, *Atherospermataceae*, *Sphenostemonaceae*, *Trimeniaceae*, recognized as distinct families by various authors.

Beuzenberg (1961) advanced cytogenetic arguments, supported by morphological ones, in favour of uniting *Hymenanthera* with *Melicytus-Viol.*

Similarly Carlquist (1967b) on anatomical evidence found that the Juan Fernandez genera *Hesperoseris*, *Phoenicoseris* and *Rea-Comp.* are ranked too high and should be regarded as subgenera of *Dendroseris*, another endemic of the islands.

Morton (1962) in a cytotaxonomic study of W. African *Labiatae* showed that *Coleus* cannot be upheld as distinct genus against *Plectranthus*, an opinion also supported by Launert (1968).

In all these cases there is, however, no formal taxonomic revision and I have preferred to keep the above mentioned genera separate provisionally.

The genus *Exocarpos-Sant.* excellently monographed by Stauffer (1959) offers a good example of a genus of which the infrageneric taxa are more useful for my purpose than the genus as a whole, which extends from SE. Asia through Malesia and Australia into the Pacific (see map 76 in van Steenis & van Balgooy, 1966). Subg. *Exocarpos* centers in Australia, one species extends to Malesia, endemic species occur in New Caledonia, Lord Howe, New Zealand, Fiji, Rapa, and Hawaii. Subg. *Phyllodanthos* is confined to New Caledonia and Norfolk. Subg. *Xylophylos* has endemic species in New Caledonia and New Guinea and one is distributed from New Guinea to Vietnam. Australia has nine species all belonging to one subgenus, but the six New Caledonian species are members of three subgenera.

Styphelia-Epacr. in the sense of Sleumer (1964) consists of five subgenera. These are considered by some to merit genus rank and by others are not recognized as entities at all. In this case I have followed Sleumer's treatment, as he is the only person who has studied material from the entire range of *Styphelia* and is thus considered to be in the best position to judge. Whatever the rank one wishes to assign to the entities is irrelevant for my purpose, what matters is the fact that *Styphelia* as a whole is less informative than its five components of which three are represented in the Pacific (see map 170—171 in van Steenis & van Balgooy, 1966): subg. *Cyathodes* occurs in SE. Australia and Tasmania, E. New Guinea and is scattered over the Pacific, subg. *Cyathopsis* is confined to New Caledonia, and subg. *Leucopogon* of which the bulk of the species occurs in Australia and some extend to Malesia, SE. Asia and the Pacific.

Goodspeed's study of *Nicotiana-Sol.* (1954) shows that the species of Juan Fernandez and Revilla Gigedo belong to sections that are otherwise exclusively American, whereas the remaining Pacific species all belong to the Australian section *Suaveolentes*.

The genus *Erythroxylum-Erythr.* of pantropical distribution is represented in the Pacific by the exclusively Old World section *Coelocarpus* (map 136 in van Steenis & van Balgooy, 1966). For my purpose it therefore makes more sense to include the section than the genus.

The genus *Sanicula-Umb.* presents an opposite case. The Hawaiian species form a well

defined section *Sandwicensens* (Shan & Constance, 1951). It is more meaningful, however, to take the genus as a whole, which is distributed over the northern hemisphere with some extensions to the southern, than to take the endemic section (see fig. 20); this would give no clue as to its floristic affinity.

One of the most striking examples is of course *Ficus-Morac*. The genus as a whole is of worldwide, principally pantropical distribution, but the detailed studies by Corner (1958, 1960, 1963, 1965) have revealed many interesting distribution patterns of the infrageneric taxa.

If a genus can be split into a number of infrageneric taxa each with the same distribution as the genus these have not been entered separately. Of *Diospyros-Eben*. two subgenera occur in the Pacific (Bakhuizen van den Brink, 1936—1955), *Diospyros* and *Maba* both being pantropical.

The genus *Parsonsia-Apoc*. according to Pichon (1950) consists of many sections; he did not, however, carry out a complete revision, so that it is doubtful if they will be maintained eventually. *Parsonsia* is here taken in its widest sense.

On the other hand in *Ochrosia* it is possible to distinguish two groups rather easily. It is irrelevant whether one follows Merrill & Perry (1943), as I have done, in raising the groups to the rank of genera (*Ochrosia* and *Bleekeria*) or to treat them as sections of one genus as done by Pichon (1947).

Clarke (1883) wrote a monograph of the genus *Cyrtandra-Gesn*. His treatment no doubt was a very good one for its time, but as his material was only a fraction of what is now available it is uncertain whether his subdivision of the genus still holds.

A great number of other complex genera, such as *Carex-Cyper.*, *Euphorbia*, *Phyllanthus-Euph.*, *Psychotria-Rub.* could be divided into many infrageneric categories if properly studied.

A somewhat different problem is presented by those genera of which the area is determined by a single species with aberrant distribution. If there is a strong discrepancy between the distribution of such a species and the remainder of the genus the distribution of this species is given separately but it is not used in the analysis as a separate entity.

A good example is offered by the genus *Scaevola-Good*. A number of sections can be distinguished, some also represented in the Pacific. One of these, section *Scaevola*, has local inland species in Malesia, New Hebrides, New Caledonia, Fiji, Marquesas, and Hawaii. As a whole, however, this section is pantropic, but this is due to two littoral species: *S. taccada* (Gaertn.) Roxb. is distributed from Madagascar eastwards as far as Hawaii and Marquesas, and *S. plumieri* (L.) Vahl occurs from the Galapagos Is. through tropical America and Africa to Ceylon.

Casuarina-Casuar. the natural range of which is from E. Africa to SE. Polynesia owes this wide range to a single species, *C. equisetifolia* L., which for some reason has obtained a much wider distribution than the remaining species of the genus which occur in Malesia, New Caledonia and especially in Australia.

Another curious case is that of *Messerschmidia-Borag.* which according to Johnston (1935a) comprises three species, one in temperate Eurasia from Japan to Rumania, another in tropical Atlantic America, and the third, the well-known coastal *M. argentea* (L. f.) Johnston., throughout the Indian and Pacific Oceans.

Dodonaea-Sapind. has a centre of specific development in Australia, a few other species occur in the tropics of Africa and America. The genus is hence of pantropic distribution. One species, *D. viscosa* Jacq., is represented almost throughout the tropical and subtropical parts of the world, but as the genus is pantropic anyway this species has not been listed separately. The same holds for *Evolvulus-Conv.* centering in America but with two

pantropical species (van Ooststroom, 1934), and for *Hibiscus-Malv.* represented with several species in all tropical regions and one species, *H. tiliaceus* L., practically covering the range of the genus. To list such species separately would make little sense as it gives no important additional information.

For the same reason such species as *Fagraea berteriana* A. Gray-Log., *Barringtonia asiatica* (L.) Spreng.-Lecyth., and *Stackhousia intermedia* F. M. Bailey-Stackh. have not been entered as separate entities. They have a wider but not essentially different distribution than the remaining part of the genus to which they belong.

A plea for the use of the genus as the working unit would not be complete without considering the objections that can be raised against this type of work.

A serious disadvantage, but one holding for floristics generally, is that it treats all taxa on the same level. This objection can be lodged against any numerical classification assigning equal weight to all characters of the units.

The units of my analysis, the genera, differ in various ways. One can safely say that not a single genus is like another. The size of the genus, in other words the number of species, is not considered. A monotypic genus carries the same weight as one comprising a hundred species. A genus represented with 20 species in island A and with only one in island B is indicated in the same way. If, however, the genus has an unbalanced representation outside the Pacific, this is of importance in determining its distribution type (see paragraph 6 of this chapter).

The distribution and affinity of the individual species represented on any one island group is also not taken into account. The genus *Cordia-Borag.* is of pantropical distribution. It is represented in the Galapagos with several species allied to or identical with American ones. In the rest of the Pacific it is represented by species widespread throughout the Paleotropics. In genetic phytogeography *Cordia* would be classed as a Neotropical element in Galapagos and as a Paleotropical one in the rest of the Pacific. Here it is classed as a 'wide', see III, 6. A parallel case is *Scaevola-Good.*, already discussed. The Paleotropic *Brackenridgea-Ochn.* has a single Pacific species: *B. nitida* A. Gray ssp. *nitida* in Fiji. It is represented by ssp. *australiana* (F. v. M.) Kanis in Queensland (Kanis, 1968). The New Caledonian species of *Nothofagus-Fag.* are most closely allied to the New Guinean ones, with which they form a separate subsection (van Steenis, 1953), but the genus occurs also in Australia, New Zealand and South America. The *Fuchsia-Onagr.* of Tahiti is allied to the New Zealand species and not to the American ones which form the bulk of the genus (Munz, 1943).

The genus *Canarium-Burs.* (Leenhouts 1955, 1959) is widespread from tropical Africa to Samoa and Tonga in the Pacific. The New Caledonian species belong to section *Canariellum*, otherwise only found in E. Australia. The two other sections, *Canarium* and *Pimela*, to which the remaining Pacific species belong, extend to tropical Africa and India respectively.

The genera *Exocarpos-Sant.* and *Ficus-Morac.* are other examples and have already been discussed.

The lack of this type of detailed information is inherent to genera that have not been revised.

Another point in which the units differ and which is not revealed by a floristic analysis is their ecology. One aspect is the thermo-ecological class to which the genus belongs. Schröter (1905), Skottsberg (1930), Van Steenis (1933), and Troll (1960) amongst many others have stressed that the lowland and montane floras may 'tell quite different stories'. On account of its greater diversity the lowland flora will dominate the outcome of the

results. This objection combined with the inadequate knowledge of taxonomy and distribution of the Indo-Australian flora (which is certainly true at species level) prompted Airy Shaw (1943) to state that it is senseless to attempt a phytogeographic study based on the distribution of taxa. He states that divisions should be based primarily on considerations of geology, climate and ecology. Apart from the question whether our state of knowledge is so much better in these fields, I think this idea is basically wrong and that any plant-geographical division should be based on the plants themselves and on nothing else. If Shaw means that our present knowledge is inadequate for far-reaching historical-geographical speculations he is nearer the truth.

The distinction into lowland and montane plants is of course only one of the many that can be made. The lowland plants e.g. could be further divided into mangrove, rain-forest, monsoon-forest, savannah plants, etc.

Various life form classes could be distinguished following Raunkiaer (1934) or Lems (1960).

According to their mode of dispersal it is further possible to distinguish between various dispersal classes, e.g. according to Dansereau & Lems (1957) or Van der Pijl (1969).

A last point in which the units differ is the *phytosociological importance* of the taxa. In a paper by Van den Hoek & Donze (1967) e.g. distinction is made between dominant, abundant, and rare species.

All the above mentioned methods of classification might be welcome additions for synthesis, but our knowledge of the data needed for their compilation is usually too inadequate. Besides, in floristics it is primarily more important to know whether a species is present or not than whether it is present in small or large numbers, what its life-form is, etc.

For the historical geographer it is very important to know how and when a certain taxon arrived and established itself in a certain area, whether it existed in other areas, where it is now absent and if so, why. Hence, means of dispersal are an important item.

In floristics only the present day state counts. For indicating land connections e.g. the presence of an ancient genus with heavy, inedible fruits that are highly sensitive to seawater means much more than the presence of a hundred others that have the capacity and can be assumed to be easily spread over large distances. Now a widespread but rare rain-forest tree with heavy fruits, an abundant epiphyte with dust seed, a rare alpine herb with fleshy fruits, and a littoral widespread and common shrub with buoyant fruits are all treated alike in the analysis.

My reluctance to introduce such detailed distinctions in the analysis is rooted in the following two considerations:

- a) The genus as unit is too crude. The species composing it often belong to more than one life-form class, dispersal class, etc. It may contain species limited to the lowland as well as those confined to montane habitats.
- b) Our knowledge of ecology, dispersal methods etc. is inadequate. The fact that a fruit is fleshy does not automatically imply that it is bird dispersed, a winged seed need not be carried by the wind, a diaspore without any apparent functional structure cannot simply be classed as 'without means of dispersal'.

The species would be a much more suitable unit as in general it is much more uniform in all respects. To make detailed distinctions at genus level at the present stage would only increase the margin of error.

Genera that have been recently revised or are for other reasons well known as regards

taxonomy, distribution and their ecology, broadly speaking, are a much safer object, as will be discussed more fully in paragraph 7: 'Revised taxa'.

Thorne (1965) in discussing the floristic relationships of New Caledonia commented on the difficulties of biogeographic subdivisions in general. The kind of embarrassment he felt is probably familiar to all attempting this kind of work and deserves to be cited in full (l.c., p. 11—12):

'The difficulty and artificiality of attempting to set up a biogeographical subdivision of the Pacific islands and border lands is particularly evident in the Papuan-Australian-New Caledonian-New Zealand sections. Perhaps little value can accrue from attempting to subdivide these islands biogeographically, though I have attempted it elsewhere. Plant and animal groups mostly have quite different dispersal capacities and biogeographical histories. Hence, whether or not a particular subdivision is acceptable to a biologist will depend to a large extent upon the group in which he specializes.'

'The tropical and sub-tropical rain forest areas of coastal, eastern Queensland and the adjacent northeastern corner of New South Wales have been classified with the Torres Strait islands as the Torresian Province of the Papuan Subregion of the Oriental Region though the province is best considered a zone of heavy overlap with the Australian Region. As indicated above, the biota of New Caledonia has its closest affinities with the rain forest biotas of New Guinea, coastal Queensland and the Melanesian islands to the north and east. Like them, it surely belongs to the Oriental Region, but it deserves recognition as a separate Neocaledonian Subregion on the basis of its highly relict, distinctive, endemic and disharmonic biota.'

'The placement of temperate New Zealand in the Australian Region is indicated by the large percentage of genera of plants and animals shared with Australia and Tasmania. However, since New Zealand lacks some of the largest and most characteristic groups of Australian vascular plants and vertebrate animals and shares many genera with South America and with New Caledonia, it certainly merits treatment, along with its adjacent islands and Lord Howe and Norfolk Islands, in its own distinct Neozeylandic Subregion. This classification unfortunately tends to obscure the close ties between the New Zealand and montane New Caledonian biotas. Elevation of the Neozeylandic Subregion to regional status equivalent to the Australian Region would probably emphasize too strongly the Subantarctic-Neotropical and Neocaledonian-Papuan elements in its biota. These difficulties of classification point out all too clearly the arbitrariness and doubtful worth of biogeographical subdivisions.'

Though I can accept several generalities put forward by Thorne, it is not clear to me why he calls a biogeographical subdivision 'artificial', pointing out the 'arbitrariness and doubtful worth of biogeographical subdivisions', simultaneously complaining of the overlapping and vagueness of the boundaries. It is a truism recognized long ago. In nature boundaries are nowhere sharp, except when working with a very limited group (Merrill, 1936; van Steenis, 1950). Perhaps we should speak of transition belts rather than of boundaries (Turrill, 1959). To indicate these and give a measure for the degree of their distinctness is one of the tasks of floristic geography. But any such subdivision is based on factual distribution. In my opinion Thorne confuses two things, floristic and genetic plant-geography. His negative view on floristic divisions is derived from the idea that a floristic subdivision should to a high degree reflect the genesis of the plant world. This is an impossible point of view, for the reasons he provided himself. In addition there is the certainty that the living taxa must be of quite different age. However, it should

be admitted, that floristic plant-geography may yield valuable data for genetic plant-geography.

In spite of this criticism of his reasoning I must say that Thorne's subdivision of the Pacific is one of the most acceptable biogeographically (see fig. 13).

The result of our classification, be it the species of the taxonomist or the phytochoria of the phytogeographer, will never be quite equivalent. They will always carry the stamp of subjectivity, however faint.

The fact that various groups have different 'demarcation lines' can be no objection against subdivisions. It is only to be expected in view of the different properties, such as age, dispersal capacity, ecological tolerance and other properties of the group, combined with changes of geological, climatical or other nature, which have taken place in the region.

As I alluded to before, the units of floristic plant-geography are historically certainly not equivalent. One might contemplate making a bridge between floristic and genetic plant-geography, to make the first more meaningful for those who wish to fathom the genesis of the plant world. This could be achieved, possibly, by assigning different values in proportion to their 'importance'. But importance in what respect? If *Nothofagus* is given an evaluation of say 100 on account of its restricted ecological requirements, its seeds not possessing any obvious dispersal adaptations and its importance in sociological respects, what value should be given to *Astelia*, to *Scaevola*, to *Bulbophyllum*? Are they 'worth' 50, 40, or 10?

Every genus has its own characteristics, distributional, ecological and other characteristics. Therefore, giving the genera different numerical evaluations will increase the arbitrariness and subjectivity, which is precisely what should be avoided as much as possible. The safest base for phytogeographic speculation is to make a meticulous study of each of the Pacific genera and also those occurring in the periphery. Not only the presence but also the absence of a genus can be meaningful. With the present data it is only possible to give a broad outline of distribution patterns and floristic affinity, which together provide a certain measure for hierarchical subdivision. As far as revised genera are concerned an attempt should be made to see whether there is any correlation between distribution and dispersal mechanisms.

There can only be certainty regarding observations on the recent, contemporary flora and it is uncertain whether these can be applied to processes which have taken place in the past. The present day ecological amplitude of a genus may have been different in the past, and have changed, widened or narrowed, during its evolution effecting its distribution as we see it today.

To mention a single example: the woody habit of so many *Compositae* on islands. Is this woodiness a 'primitive' character, retained only in isolation? And did most of the continental members of the family evolve herbaceous forms later? Or did many of the island *Compositae* develop a woody habit after they had established themselves on islands? Carlquist (1967b) after an anatomical investigation of the *Dendroseris*-complex in Juan Fernandez suggests that the woodiness of this complex is of secondary nature, that it is derived from an herbaceous ancestor. I am not qualified to judge his arguments but it would be very rash to conclude that all species and their ancestors have always had the same habit.

As regards ecology and habitat there is the same kind of uncertainty as to their constancy in Time. It can be observed that a certain species is mostly found in the same kind of habitat. This does not mean that in this habitat it finds ideal conditions or has originated on a site of optimum conditions, and that all through its history it has always been bound

to this particular environment. A species growing in the mangrove will be classed as a mangrove element but it does not mean that it needs a tidal environment, e.g. *Sonneratia-Sonn.* has been found outside the mangrove in nature.

There is an astounding variability in ecological amplitude, especially as regards thermoeology, both in genera and species. There are taxa in which this response is very restricted, but in others it may vary considerably, and moreover may vary from place to place. *Nothofagus-Fag.* is generally bound to cool to temperate climatic conditions. It occurs in New Guinea from 750—3000 m, but in New Caledonia the altitude for the five species is from 150—1350 m.

Regarding the classification of dispersal methods great caution is needed. All too often the dispersal mechanism is deduced from the morphology of the diaspore. There is probably no other field of botanical science where so much is taken for granted. For a recent critical review of the matter I refer to Van der Pijl (1969).

A winged fruit should not be claimed automatically as being 'wind dispersed'. The wings of many *Dipterocarpaceae* probably have nothing to do with wind dispersal. A fleshy fruit need not be eaten by birds or bats. And if it is, it is necessary to know whether the fruits or seeds are actually dispersed in a viable state or not, and to know the distance over which dispersal takes place. Fruits found in the flotsam of the sea need not be dispersed by sea currents, they may neither be able to stand immersion in salt water, nor be capable of growing on the beach. On the other hand if the diaspore does not exhibit any obvious means of dispersal it should not be concluded that it is not dispersed. The seeds of many marsh plants have been found caked to the feet of wading birds (Ridley, 1930; van der Pijl, 1969). With Darwin (1859, p. 314) it should be acknowledged 'how ignorant we are with respect to the many curious means of occasional transport . . .'

There are plants with two or more means of dispersal (diplochores and polychores). The fruits of *Sonneratia* are eaten by bats and monkeys but the seeds are also buoyant. The fruits of some *Terminalia-Combr.* species are eaten by bats and also are very buoyant. So they may be transported from shore to shore by sea currents and from the shore inland by bats (van der Pijl, 1957). This subject will be treated in paragraph 8: 'Dispersal classes'.

Another difficulty is that the age of the genera is not known. Does the history of the Pacific flora, at least in some parts, go back to the origin of Angiosperms or is it geologically recent, and if so, how recent? Ideally a statistical correlation between dispersal mechanisms and actual distribution should be based on taxa of the same age and of the same ecological requirements. Only then is it possible to find an answer to the question whether and to what extent dispersal mechanisms have been effective.

Conclusions on the synchronous genesis of sympatric ranges should not be rashly made and should be sustained by ample, well-considered circumstantial evidence from all sources. It cannot be concluded, for example, that in comparing the rather equiformal ranges of *Nertera-Rub.* and *Coprosma-Rub.*, which both have berries and share a similar ecology, *Nertera* is older because its range is greater than that of *Coprosma*, or alternatively that its means of dispersal are superior. Equiformal or subequiformal ranges need not always be 'progressive' in Hultén's sense (Hultén, 1937), especially not in the tropics and in the Pacific which have been subject to an extremely long period of environmental changes of all sorts. Post-Glacial equiformal ranges in the Arctic may be well synchronous and progressive, but it cannot be concluded without further evidence that plants with the greatest ranges have a more efficient means of dispersal than those with smaller ranges; the different ranges may also be due to different ecological adaptation.

The indication concerning dispersal only refers to the condition in the Pacific represen-

tatives. All but one species of *Dolichandrone*-Bign. have pods containing winged seeds, but the only species occurring in the Pacific, *D. spathacea* (L. f.) K.Sch., has corky buoyant seeds (van Steenis, 1963a).

It is clear that a meaningful statistical analysis of dispersal (mechanisms) needs more than a simple indication whether a plant has buoyant or fleshy diaspores. What we can do is to indicate roughly the most likely agent(s) of dispersal and see if there is any difference in the dispersal spectrum of compared floras.

Besides, it must also be kept in mind that in handling the concept 'means of dispersal', this relates only to our idea about the possible 'mechanism' in a morphological sense, which is of course not at all synonymous with 'effective dispersal', by which we know or suppose that the dispersal has led to permanent establishment.

Carlquist (1967a) has made a similar study on the flora of SE. Polynesia and Hawaii. It should be borne in mind that the value of such a dispersal spectrum is limited, although it may give a clue to the genesis of the Pacific flora.

4. Sources and their reliability

No attempt will be made to enumerate all the numerous sources from which I gleaned my information. The sources were of three kinds: literature, herbarium material, and personal information.

The literature on Pacific Phanerogams is scattered over a great number of periodicals and books. I consulted some 3500 references, but it would serve no good purpose to enumerate them all. The bulk of them contain only detail data on floristics, nomenclature, and records. I have therefore restricted the bibliography to the major works and especially to those which are mentioned in the text.

Merrill and Walker's 'Bibliography' (1947) was indispensable for tracing pre-1948 literature on the Pacific. The selected Flora Malesiana bibliography (van Steenis, 1955) and the bibliography published in the annually issued Flora Malesiana Bulletin (1947, onwards) were also used to great advantage. Other bibliographic information was obtained from Blake and Atwood's 'Guide' (1942, 1967) and Merrill & Walker's (1938) and Walker's (1960) Bibliography of E. Asiatic Botany.

There are two approaches for finding out which genera occur and how they are distributed. One method is to collect data on the various islands by consulting local floras, enumerations and the like, the other is to take the taxa as starting point, in other words to make use of revisions and monographs.

In employing the first method papers varying from uncritical species lists to comprehensive local floras such as Allan's 'Flora of New Zealand' (1961) are met with. A great number of botanists with varying abilities have occupied themselves with the taxonomy of Pacific plants. As variable as their capacities were their taxonomic concepts. Data from simple species lists had of course to be handled with much more caution than those from a critical flora.

The same species may have been enumerated under different names. Checking of the synonymy was therefore one of my main concerns. In general, however, the genus identity proved to be correct.

For many island groups no flora or enumeration exists. And of those that do exist, the data are not necessarily complete or correct. I have already mentioned Allan's Flora as exemplary, but most of the local 'Floras', such as Brown's Flora of SE. Polynesia (1931, 1935) deal only with the results of a single expedition, in Brown's case the Bayard

Dominick Expedition, the title of the flora being further misleading as it principally covers the Marquesas. Christophersen's 'Flora of Samoa' (1935, 1938) similarly is an enumeration and description of the author's own collections. Many of the early Floras as Guillemain's (1836—37), Montrouzier's (1860) and Nadeaud's (1873) contain many obscure names and have consequently to be handled critically. This does not hold for Hillebrand's 'Flora of the Hawaiian Islands' (1888) which, though somewhat outdated, is still one of the best and most complete sources of information ever written on any part of the Pacific.

The data thus obtained were supplemented by data from revisions and monographs. A complete monograph is of course the most ideal source of phytogeographic information, but the number of genera so treated is deplorably low.

In the Flora Malesiana series the species of families treated are mostly provided with accurate and detailed geographic data, also where the Pacific is concerned, and so they form a reliable source for a limited set of genera. A number of Pacific genera have been mapped in the unfinished series 'Pflanzenareale' (Hannig & Winkler, 1926—1940). The maps published herein are very reliable, at least for their time.

The project 'Pacific Plant Areas', of which two volumes have so far appeared (van Steenis, 1963a; van Steenis & van Balgooy, 1966) aims at giving accurate maps of Pacific plant taxa. Some 100 odd Pacific Phanerogam genera have been mapped so far. Furthermore, it contains a complete bibliography on all maps of Pacific taxa compiled by Mrs M. J. van Steenis-Kruseman.

Many, but not all families are treated in Engler's 'Pflanzenfamilien' and 'Pflanzenreich'. Though these works are of immense help, the treatments are compilations rather than monographs. Moreover, the geographic data are often insufficient. The same objections hold for such invaluable sources of general information as Lemée's 'Dictionaire' (1929—1943) and Willis's 'Dictionary' (ed. 6, 1948) and its 7th edition revised by Airy Shaw (1966). Data such as 'Hinterindien bis Polynesien, auch vereinzelt in den Tropen der Neuen Welt' or 'India to Japan and Fiji' do give a general idea but not the detailed kind of information I needed. Much use was also made of Engler's 'Syllabus' (1964) and Hutchinson's 'Families of Flowering Plants' (1959) and 'Genera of Flowering Plants' (1964, 1967).

For more detailed local information various enumerations and Floras of countries surrounding the Pacific were consulted, e.g. Burbidge (1966) for Australia and Tasmania, Hooker (1872—1897) for India, Lecomte & Gagnepain (1907—1951) for Indo-China, Li (1963) for Formosa, Merrill (1923—1926) for the Philippines, Ohwi (1965) for Japan, and Van Royen (1959) for New Guinea. Prof. van Steenis allowed me to use his unpublished data on the distribution of genera in Malesia and extracts of plant-geographical literature intended for Flora Malesiana vol. 3.

The Index Kewensis was another source of information. It has, however, to be used with caution. It only takes up species described for the first time, it cannot be used to find new records of a species already described. Moreover, the later fate of a species is almost impossible to trace, as it may have been transferred to another genus, etc. One may find for instance *Ternstroemia vitiensis* Seem. described from Fiji, but not Evans' reduction of the species under *Balanops* (Evans, 1966). *Pseudomacodes* was described as a monotypic genus from the Solomons (Rolfé, 1892) but it is very hard to find out from the Index Kewensis that the same author reduced the genus to *Macodes* in 1911. Willis and to a lesser extent De Dalla Torre & Harms (1900—1907) and Lemée have proved very helpful in this respect.

Every genus recorded from any part of the Pacific was entered in a table where the

columns represent the unit areas and the rows the genera and other taxa. These were arranged alphabetically under the families, which themselves were listed alphabetically. Different symbols were used to indicate the nature of the record (see Appendix). A card index was kept of all literature consulted. After completing the literature survey a number of doubtful cases still remained. Wherever necessary herbarium material (Rijksherbarium, Leyden) was consulted to supplement the range and to verify records open to suspicion. No attempt was made, however, to check every individual genus. Many of the records accepted here are not to be found in the literature. They are based on collections deposited in the Rijksherbarium identified by various persons of this institute and by others. This pertains mainly to material recently collected in the Solomons and Bismarcks.

Several botanists have helped in various ways to 'polish' the records and nomenclature, as acknowledged in the introduction.

Information of non-botanical nature, such as data on the size of the area, elevation, etc. was obtained from atlases and maps, such as Andree's 'Handatlas' (ed. 8, 1924), the Times Atlas (1955—1959) and various maps notably those published by the National Geographic Magazine and Robson's 'Pacific Islands Yearbook' (ed. 6, 1950, ed. 7, 1959). Some of these data were incorporated in my paper on diversity of island floras (van Balgooy, 1969). Finally, most of the local Floras contain concise notes on geology, climate, area, elevation, vegetation, influence of man, amount of exploration, and other data useful for their better understanding.

It has been shown that the published information contains a number of mistakes and shortcomings and these will now be reviewed in order to get a good idea of the reliability of our data.

Incomplete collecting is one source of error. The state of exploration and publication of the floras of the various island groups differ widely. It may be safely stated that very little, if any, new genus records can be expected from Hawaii, Juan Fernandez or New Zealand, but that many more await discovery in the New Hebrides, St. Cruz and the Bismarcks.

But it is impossible to say what percentage of the flora of each of the island groups is recorded.

The situation would be very much worse if our working unit had been the species.

Apart from incomplete collecting it is quite possible that on certain islands part of the flora and with it some species were destroyed by the inhabitants before any collections were made. A clue in this direction is the fact that so many plants have only been collected once by an early expedition and have never been found again since: *Aerva sericea* Moq.-Amarant. in Hawaii, *Pimia rhamnoides* Seem.-Stereac. and *Stillingia lineata* (Lamk) M. A.-Euph. in Fiji, *Santalum-Sant.* has become extinct in Juan Fernandez in the last century, and *Streblorrhiza-Leg.* on Norfolk. One wonders how many had become extinct before the arrival of botanical collectors.

Introduced and native plants are often hard to tell apart. This study is based on the native flora, but in many cases it is impossible to tell whether a species in a given locality has got there by the help of man or by natural agencies. There can be little doubt that species like *Ageratum conyzoides-Comp.*, *Lantana camara-Verb.*, *Psidium guajava-Myrt.*, *Stachytarpheta jamaicensis-Verb.* and many others are relatively recent introductions.

Now these examples are all aliens, but a native species may behave as an alien or weed under certain circumstances, e.g. ground that has been cleared is soon covered by light demanding species.

In many cases there is little unanimity of opinion as to whether a certain species is indigenous or not. *Sonchus oleraceus* L.-*Comp.* is found on many Pacific islands. Is it an alien? It certainly behaves like one. But there is an apparently quite distinct *Sonchus* species in New Zealand!

The fact that a species is widely used by man cannot be used as a criterion. Man may make use of local plants as well as of those that have come with him. Kooyman (in press) and Zepernick (1967) e.g. discuss the use of many local plants in the 'tapa' culture and for dyeing respectively. Certain species of *Ficus-Morac.* and of *Pandanus-Pand.*, *Casuarina equisetifolia-Cas.*, *Inocarpus edulis-Leg.*, *Cocos nucifera-Palm.*, *Aleurites moluccana-Euph.* and a host of others are used for various purposes. It is impossible to tell exactly where a species is distinctly native, where it has been carried by man, and where it arrived by natural means but is maintained by man. Collectors have not always been consistent in indicating whether a species is introduced or native. Admittedly it is not always easy and often impossible to do so, especially for species that have been used since ancient times.

Anyhow, in a case of doubt, the genus was deleted from the analysis.

Mistakes in the published record are the most serious source of error.

Specimens misidentified, described in the wrong genus, wrongly labelled or otherwise erroneously entered in the record are none too rare.

A wrong record tends to be perpetuated in literature, unless the material is critically re-examined. But even then one may not come across the correction even if it is published.

Moreover, many authors are at variance as regards taxonomic concepts but, as has been stated before, the disagreement is mainly one at specific level; most authors agree about generic delimitation.

Sometimes, however, there is no unanimity of opinion concerning the place of a genus in the family or other suprageneric category. This is important for endemic genera. As far as possible, I have indicated the affinity of these if no serious controversy existed.

Although errors in detail of distribution and systematics are inevitable, most of the data in the Appendix are I think correct.

A special word has to be said about maps of Pacific plants hitherto published and listed in the bibliography of 'Pacific Plant Areas', where they are cited without comment on their accuracy. It was rather disappointing to discover that many of these maps are in some way or other incomplete or deficient, and not seldom contain serious errors. *Agathis-Conif.* is as often as not indicated for Indo-China and the Solomons, where it definitely does not occur except in cultivation. Admittedly many maps were only meant as outlines and have been compiled from literature. But even revisions are sometimes accompanied by a map that is not in keeping with the written text.

Cufodontis (1960), who produced an otherwise excellent map of *Pittosporum-Pitt.*, indicated this genus for Christmas I. in the Central Pacific in error for Christmas I. in the Indian Ocean.

Kostermans (1959) in his revision of *Heritiera-Sterc.* indicates this genus not further east than the Solomons. In fact one of the species (*H. littoralis*) extends to Tonga. In the text he states that this species occurs in the Pacific, but this is not apparent from the map.

Florin (1963) in his great work on Conifers erroneously indicated *Agathis* for the Solomons.

5. The geographic units

For tabulating the genera the first requisite is a division of the Pacific into smaller geographic units. The divisions accepted here are given in fig. 16. In the Pacific each of

the island groups or isolated island was taken as a unit. The surrounding land areas were more or less arbitrarily divided, although the boundaries do incidentally coincide with accepted biogeographic ones in some cases.

Thus certain phytogeographic units are accepted a priori; in an island area such as the Pacific or Malesia this is facilitated by the presence of natural boundaries. In doing so an element of arbitrariness is introduced: the position of our phytogeographic boundaries is clearly influenced by the choice of phytogeographic units.

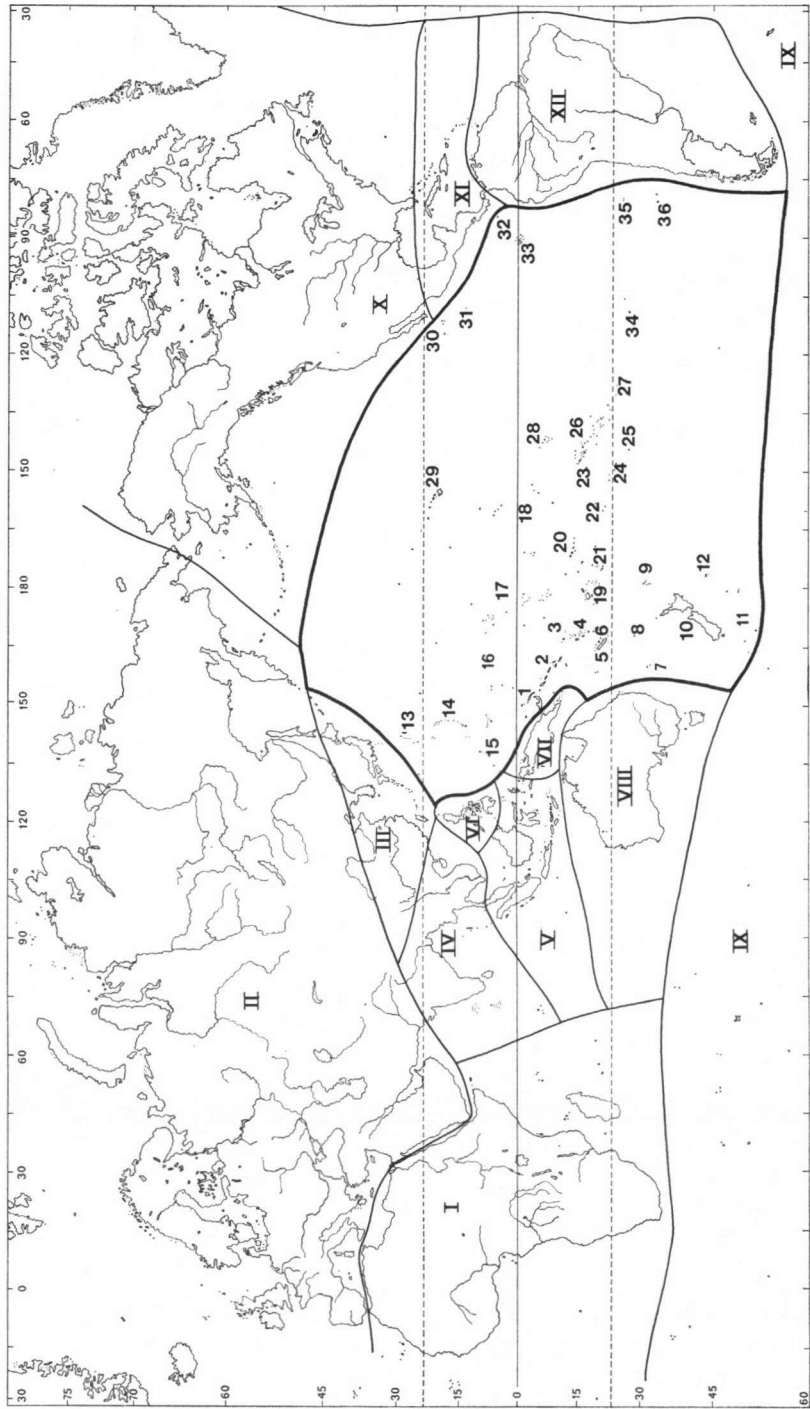
In some cases I have been able to profit from foregoing studies. Kanehira (1935) has for instance shown that the West and East Carolines are floristically distinct. In my preliminary analysis I have shown that Rapa I. cannot be simply included with the Austral islands to which it belongs geographically. In the present paper I have also distinguished between the S. and N. Tuamotus, following Brown (1931). Chatham is listed separately and is no longer included under 'Subantarctic islands of New Zealand'. In my preliminary analysis I also tentatively incorporated the St. Cruz Is. in the New Hebrides. Now that more material is available it is shown that the former can better be merged with the Solomons. The Loyalty Is. which I had merged with New Caledonia, are again listed separately to show which genera occur on them and to illustrate my reasons for uniting them with New Caledonia. If the flora of the Bismarck Archipelago were better known it might very well turn out that a demarcation exists between New Britain and New Ireland and that the latter may prove to be floristically closer allied to Bougainville, one of the Solomon Islands. But finer subdivisions need more exact data, not yet available, and, moreover, should perhaps be based on the distribution of species rather than on that of genera. My main purpose is now to establish the framework of Pacific Phanerogam phytogeography.

Practical considerations may also play a role in the choice of our phytogeographic boundaries. The Torres Strait between New Guinea and Australia is generally held to be one of the outstanding phytogeographic demarcations (see van Steenis, 1950). In fact the whole flora of Cape York Peninsula and the southern peninsula of New Guinea forms a large area of overlap as already pointed out by F. von Mueller (1890) and others. For example if the number of genera occurring either north or south of the Torres Strait, i.e. in New Guinea as a whole or Queensland as a whole are added up, a strong demarcation can be found (this is what Van Steenis calls 'demarcation knot'). Similarly if the flora of Cape York Peninsula and S. New Guinea are opposed to the genera occurring in the remainder of New Guinea a demarcation of equal magnitude may be expected. But the great difficulty then would be where exactly in New Guinea this demarcation would have to be drawn. So for practical reasons it is better to maintain the Torres Strait as the demarcation between New Guinea and Australia.

The Pacific is made up of a great number of natural units, the islands. The exact procedure would be to take every individual island as unit. Our knowledge of the Pacific flora is however, much too incomplete for this.

For continental areas or large islands where no such natural units exist but of which the flora is known in detail at species level a grid system could be applied. The meshes of the grid could be chosen to suit the degree of accuracy one wished to pursue. Recently Jalas and Suominen (1967) proposed a grid system in a mapping project of the European flora. But whether this is to serve for a system of plant-geographical provinces and districts is unknown to me.

In fig. 16 the 'Pacific' has been delineated by a full line. Within this line the various island groups have been indicated by numbers. The rest of the world's land surface has been divided into a number of unit areas ('regions'). These regions are by no means of



equal rank neither as to surface nor as to number of genera. Some of them proved to have parts of special importance which are separately indicated. For instance within region VIII (Australia) Queensland has many genera not found elsewhere in that region. In region I there are many taxa that do not occur in Africa proper but are confined to Madagascar.

The following unit areas are distinguished:

I. Africa

The African continent, together with the Macaronesian islands (Canaries, Madeira, Cap Verdes) and Malagassy (Madagascar, Mascarenes and Seychelles). Some genera occurring in the Pacific extend westwards only as far as Malagassy and not to Africa proper. This has been specially indicated; also if the genus in this region is confined to the South or North.

II. Eurasia

The whole of Europe and Asia with the exception of the eastern and southeastern parts of Asia.

III. E. Asia

This unit area includes Japan, Korea, Ryu Kyu, Formosa, Botel Tobago, and most of China.

IV. SE. Asia

Ceylon, most of India, Burma, Indo-China, and Hainan; also the Nicobar and Andaman Is.

V. Malesia

'Malesia', as used here, excludes the Philippines and New Guinea, so it is limited to the Greater and Lesser Sunda Is., Malaya, and Moluccas.

VI. Philippines

The Philippine islands, including also Batan Is. and Palawan.

VII. New Guinea

Apart from the main island some of the offshore islands are also included, such as Waigeo, Schouten, Louisiades and d'Entrecasteaux Is., but not the Bismarcks.

Fig. 16. Within the Pacific as understood here the following unit areas are distinguished: (1) Bismarcks, (2) Solomons, (3) St. Cruz Is., (4) New Hebrides, (5) New Caledonia, (6) Loyalties, (7) Lord Howe I., (8) Norfolk I., (9) Kermadecs, (10) New Zealand, (11) Subantarctic islands of New Zealand, (12) Chathams, (13) Bonins, (14) Marianas, (15) W. Carolines, (16) E. Carolines, (17) W. Central Polynesia, (18) E. Central Polynesia, (19) Fiji Is., (20) Samoa Is., (21) Tonga Is., (22) Cook Is., (23) Society Is., (24) Tubuai Is., (25) Rapa I., (26) N. Tuamotus, (27) S. Tuamotus, (28) Marquesas, (29) Hawaiian Is., (30) Revilla Gigedo Is., (31) Clipperton I., (32) Cocos I., (33) Galapagos, (34) Easter I., (35) Desventuradas Is., (36) Juan Fernandez Is. The surrounding land areas outside the heavy line consist of the following units: (I) Africa, (II) Eurasia, (III) E. Asia, (IV) SE. Asia, (V) Malesia, (VI) Philippines, (VII) New Guinea, (VIII) Australia, (IX) Subantarctic islands, (X) North America, (XI) Central America, (XII) South America.

VIII. Australia

Australia proper and Tasmania. If a genus occurs only in a small part of the region (Queensland, the Southeast, or Tasmania) this has been indicated.

IX. Antarctica

Apart from the Antarctic continent where hardly any Phanerogams exist, this region includes the 'Subantarctic islands': South Georgia, South Orkney, Tristan da Cunha, Gough, Prince Edward, Kerguelen, Amsterdam/St. Paul, and Macquarie. The Subantarctic islands of New Zealand with the exception of Macquarie are not included, the Falklands are placed under South America.

X. North America

Canada, the U.S.A. (incl. Alaska), and North Mexico.

XI. Central America

Besides the Central American countries and South Mexico also included are the West Indies (Cuba, Jamaica, Haiti, Bahamas, Trinidad, etc.)

XII. South America

The South American continent from Venezuela to Fuegia and Falkland Is. Some genera are limited to the Andes, the extreme South and Falklands. These have been indicated.

XIII. Pacific

The assembly of islands delineated by the heavy line in fig. 1 and 16. The island groups have for convenience sake been arranged in 3 rows from Northwest to Southeast.

(1) The *Bismarcks*, consisting of the main islands New Britain and New Ireland and a number of smaller ones. The Admiralty Is. have been included here but their flora is hardly known. (2) The *Solomons*; Bougainville is included though politically it does not belong to the rest of the group. (3) *St. Cruz Is.*, though still a badly underexplored group, its flora now permits of a tentative analysis. In my former paper I combined the St. Cruz Is. with the New Hebrides. (4) *New Hebrides*, from the Banks Group in the north to Aneityum in the south. My impression is that this island group is an area of overlap and that if a more detailed analysis could be made a demarcation might prove to exist between the northern and southern parts of the group. This is one of the least explored parts of the whole Pacific. (5) *New Caledonia*, comprising the main island, Ile de Pins and Belep Is. (Ile d'Art). (6) *Loyalties*, a group of 3 islands between New Caledonia and Aneityum. (7) *Lord Howe I.*, including the Admiralty islets and Ball's Pyramid. (8) *Norfolk I.*, including also Philip I. (9) *Kermadec Is.* (10) *New Zealand*, consisting of the large North and South Is., furthermore of Three King's Is., Great Barrier I. and Stewart I. among others, but not the more distant islands such as (11) *Subantarctic islands* of New Zealand, comprising the Antipodes, Auckland, Bounty, Campbell, and Snares groups, but not the Chathams and Macquarie I. (12) *Chatham Is.*; these were in my former paper treated together with the Subantarctic islands of New Zealand, but are here listed separately.

(13) *Bonin Is.*, also including the Volcano Is. (14) *Marianas*, with Guam as the most important island. (15) *West Carolines*, with Palau and Yap as main constituents. (16) *East Carolines*, of which the main islands are: Truk, Ponape and Kusaie. Perhaps Nauru and Ocean I. should be included but next to nothing is known of their flora. (17) *West Central Polynesia*, comprising the Marshall, Gilbert and Ellice Is., consisting exclusively of low, flat coral islands. (18) *East Central Polynesia*; as the foregoing made up entirely of coral islands and comprising the following groups: Phoenix, Tokelau, and Line Is. (19) *Fiji Is.*; chief islands are Viti Levu and Vanua Levu. There is a large number of islands of decreasing size. Also included are Wallis and Rotuma although little is known of their Phanerogam flora. (20) *Samoa Is.*, also including the Manua Is. (21) *Tonga Is.*, also including Niue I. (22) *Cook Is.*; the main island Rarotonga is the only one well explored. (23) *Society Is.*; chief island is Tahiti; Moorea and Raiatea come next in importance. (24) *Austral or Tubuai Is.*, exclusive of the easternmost Rapa. (25) *Rapa I.*, also including Morotiri or Bass Rocks. (26) *N. Tuamotus* from Matahiva and Makatéa in the west to Marutéa and Morané in the east, consisting of coral islands, some raised. (27) *S. Tuamotus*; Mangareva, Pitcairn and Henderson belong here. (28) *Marquesas Is.*

(29) *Hawaiian Is.*, comprising besides the large eastern islands such as Kauai, Oahu and Hawaii also the chain of small islets to the west: the Leeward Is., terminating with Kure. (30) *Revilla Gigedo Is.*, with Socorro as most important island. (31) *Clipperton I.* (32) *Cocos I.* (33) *Galapagos Is.* (34) *Easter I.* (35) *Desventuradas Is.* (36) *Juan Fernandez Is.*

6. The distribution types

It may be safely stated that every genus has a unique distribution, no genus has exactly the same range as an other. Yet the genera are generally not haphazardly distributed but are arranged in certain patterns.

Before discussing the classification adopted the difficulties connected with it should be considered. Part of the subject has been touched upon in the discussion of advantage and disadvantage of the genus as working unit (Chapter III, 3).

It must be conceded that although the geographic unit areas have been chosen without any preconceived ideas and the distribution types were established empirically, it is impossible to avoid some arbitrariness and subjectivity.

The various island groups have been accepted as unit areas, as explained in the preceding section. This is at first sight a rather obvious thing to do but it obscures any floristic boundaries that may exist inside an island group. This is not so serious for the Pacific as most of the groups consist of small islands with by and large the same floristic composition.

The establishment of *distribution types*, although obtained empirically, also carries some subjectivity with it. Even if, as Holloway and Jardine (1968) have done, these distribution types are defined mechanically by means of a computer, arranging the various ranges in a dendrogram, it is the human mind, which has to decide and select what it is going to regard as a distinct pattern. I have therefore refrained from following their example and have rather relied on my experience and common sense.

The general principle of classification is easy: all that has to be done is to see in which unit areas the genus occurs in and outside the Pacific. Yet two genera with approximately the same range may have to be assigned to different categories. Suppose that a genus with numerous species occurs throughout Malesia and Indo-China and one of the species extends further to Queensland and Fiji and that another genus with its species centre in

Queensland is represented with one species extending throughout Malesia to Indo-China and also in Fiji. When on a map the two genus ranges are outlined approximately the same picture is obtained for each, but the first centres in SE. Asia and the second in Australia; thus the first genus is an Indo-Malesian and the second an Australian genus. For the first one speaks of an Indo-Malesian element and for the second of an Australian element in the Fiji flora.

This leads to a discussion of the concept 'element', a term frequently met in the foregoing pages. It was first introduced in phytogeography by Areschoug (1866) although Christ (1867), who applied the term independently a year later, is usually given the credit.

It is useful to discuss briefly the various interpretations the term has been given and the meaning it will have in this work.

How Areschoug and Christ intended to use their 'pflanzengeographisches Element' is not quite clear. It was probably used chiefly in a floristic (geographic) sense but as Christ considered 'mass centre' identical with centre of origin, it also had a historic-plantgeographical meaning. Later authors applied it in a historical sense, still others used it in such a way that it could refer either to present day distribution or to origin of the taxon or both.

M. Jerosch (1903) was the first to distinguish between 'geographic element' referring to the present day distribution of the taxon, 'genetic element' referring to its origin and 'historical element' referring to the migration pattern.

Reichert (1921) gave an excellent review of the use of the term up to that time. In view of the confusion around 'element' since its introduction this author suggested the use of 'component' instead of floristic element, but as far as I can see this has not been followed by later authors. Reichert further distinguished between: 'locative elements' for taxa originated in the same place, 'historical elements' for taxa having the same age, 'locative migrants' for taxa following the same migration route, and 'historical migrants' for taxa following the same route at the same time.

Wangerin (1932) stated that owing to the various undefined interpretations of the term there is no unanimity in the terminology of 'floral elements' in Europe. He favours the use of 'Arealtyp' when the concept is used in a floristic way.

Wulff (1943) gave the most complete account of the term. He devoted a chapter to it in his textbook, of which the following is a summary:

The idea of dividing the flora of a given region into elements is not new. Willdenow and Hooker had already done this although they did not use the term element.

When analyzing the flora of any region it should be divided in the following five ways:

- (1) Geographical elements: species grouped according to their present day range. This is insufficient to trace the origin of the flora.
- (2) Genetic elements: species grouped according to their place of origin. This is only possible, if at all, with a thorough monographic study.
- (3) Migration elements: species grouped according to the routes by which they entered the region under study. This also is not always easy, besides, more than one migration route may be involved.
- (4) Historical elements: species grouped according to the time in which they entered the region studied.
- (5) Ecological elements: species grouped according to their habitat preference.

Walter (1954) in his textbook on phytogeography distinguished the following sets of elements:

- (1) Geoelement: species with the same distribution.
- (2) Genoelement: species with a common origin.
- (3) Chronoelement: species of the same age.
- (4) Migroelement: species that entered a certain area by the same route or from the same direction.
- (5) Coenoelement: species having distinct phytosociological bonds.
- (6) Oekoelement: species with the same life-form or having the same ecological requirements.

Other authors have used the term element in the following sense:

To Braun Blanquet (1923) 'phytogeographic element' is the floristic and phytosociologic expression of a territory of limited extent; it includes the taxonomic units and the phytogeographic groups characteristic of a given region. This is the widest definition of the term in its original static sense.

Cain (1944) preferred to use the term in its widest sense and to indicate the meaning by using different adjectives. He introduced the term 'intraneous' and 'extraneous' according to whether a taxon is found in an area where it is characteristic or outside it.

Fleming (1963) used the term for the 'sum total of organisms that came to an area along a given dispersal avenue, but ecological bonds between the different organisms that used the same avenue are neither implied nor denied.' This corresponds to Wulff's 'Migration element'.

Polunin (1960) defined (floristic) element as the floristic expression of a territory of limited extent, in that it involves the taxa and phytogeographic groupings characteristic of a given phytogeographic area. He follows Wulff's distinction of 5 types of elements.

Although I agree with Wulff that a flora should ideally be analysed according to the above mentioned principles, and although I could even think of some more classes, e.g. those of life-form as treated by Raunkiaer (1934) or Dansereau & Lems (1957) and of dispersal and pollination classes, this is impracticable for the Pacific flora. My units are genera and therefore much less homogeneous in nearly all respects than species. In one genus the various species may have originated in various places and it would be impossible to assign the genus as a whole to any genetic element.

As Wulff rightly remarked only a monographic study may enable one to assign species to genetic elements. And how many Pacific genera have been revised? The same applies to 'migration elements'.

I will illustrate this with a few examples:

Von Wettstein (1896) and later also Du Rietz (1940) considered *Euphrasia-Scroph.* as an originally northern hemisphere genus as there most of its species are found. It is believed to have spread to Malesia and thence migrated southward to New Zealand and from there to South America. Van Steenis (1962, p. 259), however, seeks the origin of the genus in the SW. Pacific, where the greatest morphological diversity is found although there are less species described from this area than the northern hemisphere. He considers that from the SW. Pacific the genus spread to South America on the one hand and to E. Asia on the other, from where it spread out over the northern hemisphere. The present species centre cannot always be used as a clue to the origin of a genus as is frequently done; and unfortunately reliable palaeontological records to establish the former range of a genus are scarce. It is always more or less tacitly assumed that every taxon has origi-

nated somewhere else, but already Drude (1890) and later Skottsberg (1928, 1956) among others have rightly questioned the validity of this assumption.

The present range of *Acropyle-Tax.* is confined to New Caledonia and Fiji, but the fossil record has proven it to be widespread in the southern hemisphere (Florin, 1963). Now *Acropyle* happens to be a genus of which there is a fossil record, but of so many others there is none or only a very incomplete one. Moreover, to put it in Croizat's words 'the age of fossilization is not the age of being' (Croizat, 1958). But it is the best that can be obtained and certainly provides an idea about the minimum age.

With regard to the ecological elements of Wulff the genera could certainly be accommodated roughly into ecological groups such as 'mangrove', 'rain-forest', 'lowland peat-forest', 'beach plants', 'monsoon-forest', etc. Of course it has to be kept in mind that every taxon has its own ecological amplitude, even closely allied species may have different autecological requirements. *Lumnitzera littorea* (Jack) Voigt-Combr. and *L. racemosa* Willd. (van Steenis & van Balgooy, 1966, maps 87 & 88) are both mangrove plants. Although their areas overlap a great deal they are rarely found together.

I have refrained from attempting an ecological classification as I consider the knowledge concerning the ecology of the Pacific taxa insufficient and again the genus too crude a unit.

The easiest classification is into geographical elements as it is the least subject to interpretation and deduction. Yet here also there are numerous pitfalls. Again most ideally a monograph or complete revision should be the basis. But there are few monographs and these are of various quality; some have proved more reliable and complete than others. The state of knowledge of the Pacific genera has not got beyond the stage of an incomplete inventarization and even this could only be compiled after a time-consuming consultation of literature and herbarium material as has been discussed in paragraph 4 of Chapter III.

The present data do not yet lend themselves to making classifications in the sense of Wulff. I shall limit myself therefore to a classification into distribution types corresponding to Wulff's 'geographical elements'. Unless otherwise stated 'element' in my paper will have a floristic meaning and this study is hence essentially a floristic one.

From the above it is clear that my distribution types are floristically defined. Earlier in this paragraph I stated that two genera with approximately the same distribution will sometimes have to be classified differently. Conversely two genera that are reckoned to the same distribution type need not have exactly the same range.

This can best be illustrated by a few examples. My type 4 comprises those genera widespread in the tropics of the Old World: Africa, Asia, Malesia, Australia, e.g. *Intsia-Leg.* (van Steenis & van Balgooy, 1966, map 86). *Melastoma-Melast.* (ibid., map 122) also occurs in all four sectors, but in the African sector it is represented marginally (1 sp. in the Seychelles) whereas there are numerous species in the rest of its range. Therefore I have referred it to type 4 a (Indo-Australian genera).

Stackhousia-Stackh. (ibid., map 143) and *Flindersia-Rut.* both extend from Malesia over Australia to the Pacific (New Zealand and New Caledonia respectively) but *Stackhousia* has 15 species in Australia, of which one also occurs in Malesia, and *Flindersia* has c. 15 in Australia and 4 in New Guinea. I have placed the former in type 6 (Australian genera), the latter in type 6 a (Australian-Papuan genera).

If the map of *Nothofagus-Fag.* (ibid., map 163) is compared with that of *Nertera-Rub.* (ibid., map 54) it is seen that they agree in having a southern Pacific distribution, the latter, however, extends much farther north to China, Hawaii and Central America. Hence they disagree in detail but as far as the Pacific basin is concerned the distri-

bution is essentially similar and they have been placed in the same distribution type.

In the main I have followed the example set by Van Steenis (1950) and Kalkman (1955) who analysed respectively the Malesian and Lesser Sunda Islands floras. Malesia has four 'points of contact': Philippines/Formosa, Malaya/Indo-China, New Guinea/Australia and New Guinea/Pacific. The Lesser Sunda Is. have virtually only two points of contact: to the east and to the west. Van Steenis distinguished 6 and Kalkman 4 distribution types. The Pacific, however, being so much larger and covering so many more degrees of latitude and with so many points of contact naturally displays many more distribution types. As said before, I have maintained my former classification whenever possible to allow comparison with my preliminary analysis.

Van den Hoek & Donze (1967) in a paper on algal phytogeography in Europe showed that the many algal provinces proposed for Europe do not appear to exist. They state that evidently these provinces were taken for granted but were never demonstrated. The mistake according to these authors lies in the fact that distribution types were defined *a priori* and not in accordance with actual observation, and then floral regions were defined according to the distribution type best represented. The distribution types are determined by the subjective appraisal of the various authors, which leads to contradictory results. At the same time, however, the authors have shown how such a subdivision should be done properly. After a careful analysis of 237 species in 11 unit areas, they found two discontinuities enclosing a region showing a reasonable homogeneous floristic composition, corresponding to a floristic algal province.

In the present work, the great majority of the genera could easily be fitted into the adopted classification. A few, however, were found hard to 'squeeze' into any of the categories. This must sound familiar to persons involved in taxonomic or other classificatory work. It is a difficulty inherent in any biological classification. The human mind expects clear-cut boundaries and distinct classes, but what is found are more or less distinct transitions, and there are always individuals or groups that 'do not fit' or are 'hard to place'.

Some changes in the scheme of my preliminary analysis were inevitable. Some of my former categories proved unsatisfactory, and some genera had to be transferred because of changed taxonomic concepts and new records.

The following changes were considered necessary: type 2 in my former paper comprised all those genera occurring in the extratropical parts of the northern hemisphere, irrespective of whether they occurred in America or not. Only strictly E. Asiatic genera were excluded. Here type 2 is restricted to those genera with a holarctic or boreal distribution: extratropical Eurasia and America. Type 3 here comprises those genera confined to the part of the Old World in the northern hemisphere, including those confined to E. Asia. Type 4 formerly comprised all Old World genera not limited to the extratropical regions, in the present work distinction is made between genera spread throughout the Paleotropics and those not represented in Africa or Madagascar.

A new distinction has been made between general Malesian genera, type 5 a, and those confined to the eastern part of Malesia, type 5 b. These were formerly united under type 5 a.

New is also type 6 a; this type was made to accommodate those genera which are restricted to or centre in E. Malesia and Australia. In the preliminary analysis most of these were placed in type 5 b which, as stated before, now comprises the E. Malesian genera.

The following is a description of the distribution types, illustrated with examples and maps.

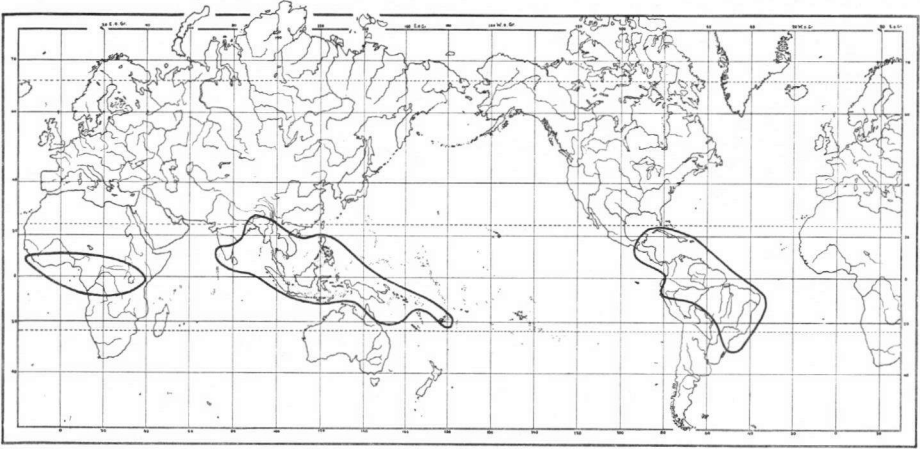


Fig. 17. Pantropical distribution of *Connarus-Conn.* modified after Schellenberg (1928, Pflanzenarcale 2, Heft 1, map 6a). Example of distribution type 1.

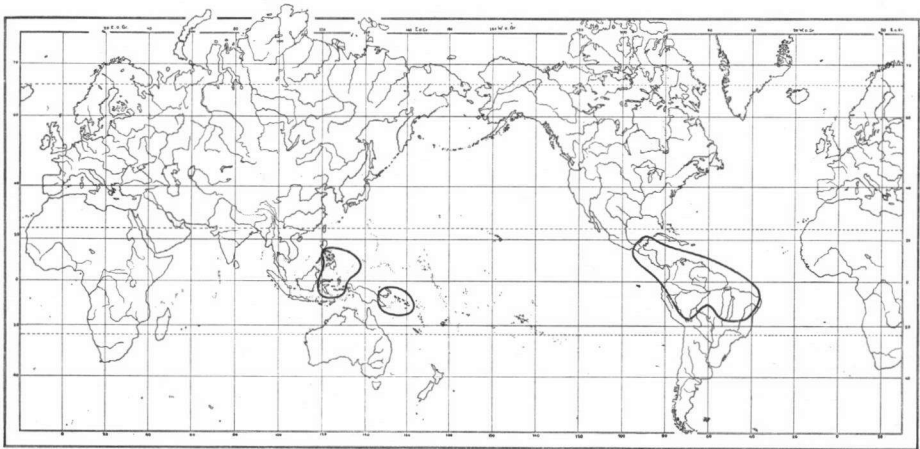


Fig. 18. Amphipacific distribution of *Spathiphyllum-Arac.* (see also Pac. Pl. Areas 2, map 36). Another example of type 1.

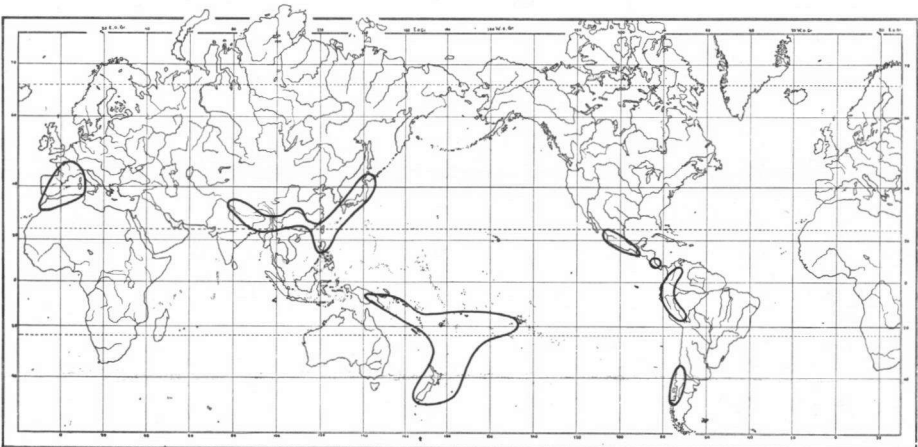


Fig. 19. Distribution of *Coriaria-Cor.*, occurring in extratropical parts of both hemispheres and montane stations in the tropics (see also Pac. Pl. Areas 2, map 67). Example of distribution type 1 a.

Type 1. — World-wide and transpacific (van Steenis, 1962) genera. Fig. 17, 18.

This type comprises all genera that, irrespective of their further distribution, are represented in both the Indo-Australian and American tropics, i.e. east and west of the Pacific. This could, if desired, be further subdivided. Some are widely distributed, such as *Carex-Cyp.* and *Solanum-Sol.* Such genera are often said to be 'cosmopolitan' or 'ubiquist' or 'universal'. Of course no taxon is so distributed. It simply means that the taxon is found on all continents, both in and outside the tropics. Another subtype is that formed by the 'panropical' genera, of which *Connarus-Conn.* (fig. 17) and *Xylopia-Ann.* are good examples. The species representation in both subtypes is about equal in the Old and the New World. In other genera of this type the 'gravity centre' may be either in the Old World as in *Impatiens-Bals.* and *Litsea-Laur.* or in the New World as in *Evolvulus-Conv.* and *Stillingia-Euph.*

In this distribution type I have also placed those genera that are confined to both the east and west sides of the Pacific (amphi-Pacific genera sensu Van Steenis, 1962). Species representation may be of about equal strength on either side: *Batis-Bat.* (van Steenis & van Balgooy, Pac. Pl. Areas 2, 1966, map 129)*), *Saurauia-Saurau.* and *Xylosma-Flac.* (P.P.A.-2, map 106). In other cases the 'gravity centre' may be distinctly on the east or on the west side of the Pacific. *Spathiphyllum-Arac.* (fig. 18) is a good example of the former, *Schismatoglottis-Arac.* of the latter.

Genera of type 1, though they cannot be used generally to establish East—West demarcations, often do show large distributional gaps in the Pacific. From the maps of *Connarus* and *Spathiphyllum* (fig. 17 and 18) wide gaps are seen between Fiji and the Solomons eastwards as far as the Neotropics.

Type 1 a. — Wide temperate or bipolar (Du Rietz, 1940) genera. Fig. 19.

This distribution type is in fact only a variant of the former one. It includes genera widely distributed over the extratropical parts of both hemispheres. If represented in the tropics they are as a rule confined to the mountains. Examples are *Euphrasia-Scroph.* (P.P.A.-2, map 53) and *Coriaria-Cor.* (fig. 19). Not included in this type are those genera that distinctly centre in one hemisphere and are only weakly represented in the other, as e.g. *Wahlenbergia-Camp.* with a majority of species in the southern hemisphere and only a few in the northern, or *Sanicula-Umb.* of which the bulk of the species is confined to the northern hemisphere and of which some species cross the equator in Africa, Malasia and South America. As said before genera with many extratropical species but also occurring in the tropical lowland are classed with type 1. Example: *Carex-Cyp.*

Type 2. — Northern, temperate to subtropical (holarctic and boreal) genera. Fig. 20.

To this type belong all genera ranging and centering in the extratropical parts of the northern hemisphere, and if represented in the tropics confined to the mountains. A few may have stray representatives in the southern hemisphere as *Sanicula-Umb.* (fig. 20) mentioned earlier. Another example is *Rhododendron-Eric.* *Perrottetia-Celast.* (P.P.A.-2, map 52) although almost wholly tropical in distribution but largely montane has also been classed here.

*) As many examples of distribution types will be quoted from the hitherto published two volumes of Pacific Plant Areas, they will be referred to as P.P.A.-1 and P.P.A.-2 for the sake of brevity.

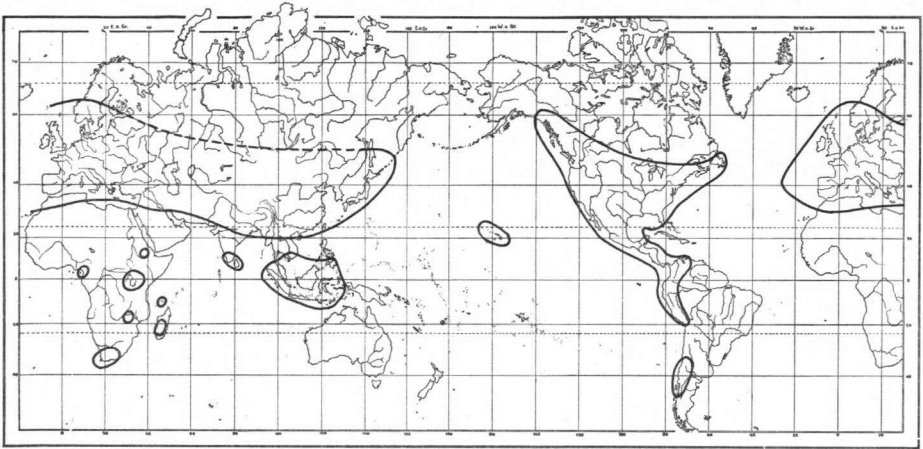


Fig. 20. Distribution of *Sanicula-Umb.*, after data from Shan & Constance (1951). Bulk of the species in the northern hemisphere, fewer in montane localities in the tropics. Example of type 2.

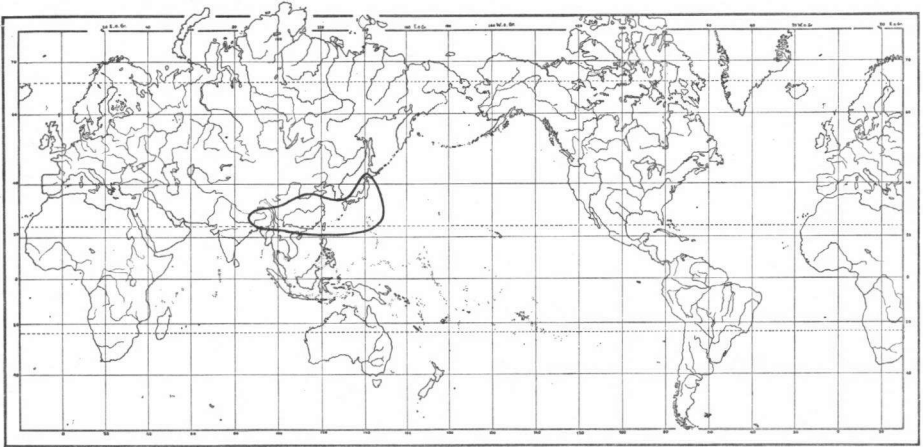


Fig. 21. Eastern Asiatic range of *Stachyurus-Stach.* after data from Li (1943). Example of type 3.

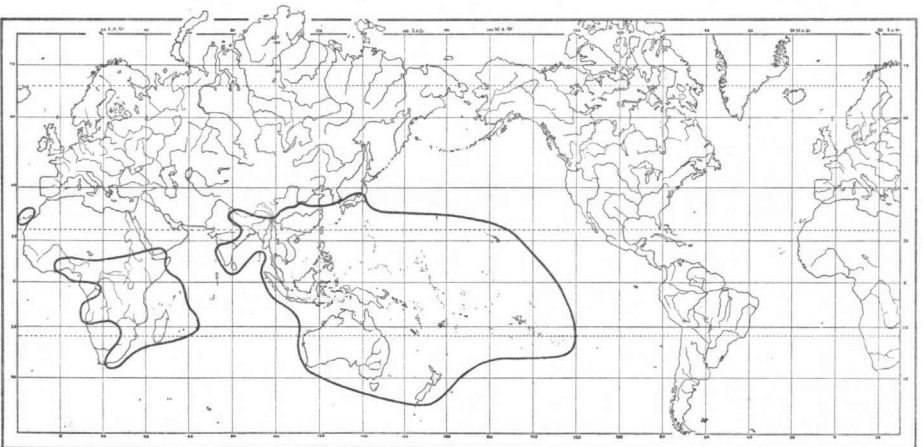


Fig. 22. Old World range of *Pittosporum-Pitt.* (see also Cufodontis (1960) and Pac. Pl. Areas 2, map 101). Example of type 4.

Type 3. — Eurasian temperate and subtropical genera. Fig. 21.

Essentially the same type of distribution as the former, but not represented in America. Most of the genera reckoned to this class are confined to or centre in E. Asia, as e.g. *Stachyurus-Stach.* (fig. 21). Others are widely distributed over Eurasia, as e.g. *Aeginetia-Orob.* *Dichroa-Sax.* centering in continental Asia and represented by a single montane species in Malesia, has also been included here.

Type 4. — Old World genera. Fig. 22.

Genera of this type extend in most cases from Africa through Indo-Malesia, Australia and into the Pacific, but do not reach America.

In my preliminary analysis I called this distribution type 'Paleotropical'. This is not quite appropriate as besides truly tropical genera it also includes those that extend into the subtropical or temperate regions such as *Pittosporum-Pitt.* (fig. 22). The species centre may lie in the African sector (*Tristellateia-Malp.*), Asia (*Balanophora-Balanoph.*), Malesia (*Canarium* subg. *Canarium-Burs.*) or Australia (*Cassytha-Laur.*). *Nepenthes-Nepenth.* (P.P.A.-2, map 82) has also been classed here. The present day centre is Borneo, but according to the monographer of the genus, Danser (1928), the oldest species group ('*Vulgatae*') covers the range of the genus with the most primitive species inhabiting the Malagassian area. The great species development in Malesia is assumed to be secondary. *Gastonia-Aral.* with a similar distribution but failing in both Asia and Australia has, however, been classified as type 5 a (Malesian genera).

Type 4 a. — Indo-Australian genera. Fig. 23.

In the preliminary analysis this type was merged with type 4 which it resembles except that it is absent from the African sector. In most cases the species are about equally well represented in Asia, Malesia and Australia, e.g. *Aegiceras-Myrs.* (fig. 23) and *Freycinetia-Pand.*, but there may be concentrations in Asia (*Melastoma-Melast.*), in Malesia (*Dysoxylum-Meliac.*) or Australia (*Alphitonia-Rhamn.*). Genera clearly centering in Indo-Australia and with only a stray representative in the African sector have also been placed here. Example: *Melastoma* (P.P.A.-2, map 122), which has a single species in the Seychelles.

Type 5. — Indo-Malesian genera. Fig. 24.

This type comprises genera centering in or confined to Asia and Malesia, not or hardly represented in Australia. Examples: *Globba-Zing.* and *Kopsia-Apoc.* (fig. 24). Also placed under this type are genera extending to the African sector such as *Mussaenda-Rub.* and *Pericopsis-Leg.* (P.P.A.-2, map 111). *Erycibe-Conv.* has the bulk of its species in Malesia and SE. Asia and a single one in Australia (Van Ooststroom & Hoogland, 1953). Some genera have a preponderance of species in Asia, e.g. *Daphniphyllum-Daph.* (Huang, 1965, 1966) or in Malesia, e.g. *Poikilospermum-Urt.* (Chew Wee Lek, 1963).

Type 5 a. — Malesian genera. Fig. 25.

Included here are all genera centering in Malesia and not or sparingly represented in either Asia or Australia. A typical example is *Cyrtandra-Gesn.* (fig. 25) having a great number of species in Malesia and the Pacific and one species only in both SE. Asia and Queensland. *Dendromyza-Sant.* (P.P.A.-2, map 151) is also characteristic for this type. *Leucosyke-Urt.* with a single Formosan, and *Hornstedtia-Zing.* with a single Queensland species are included here as well.

Some genera here classed as 'Malesian' have generally been considered as 'Pacific'.

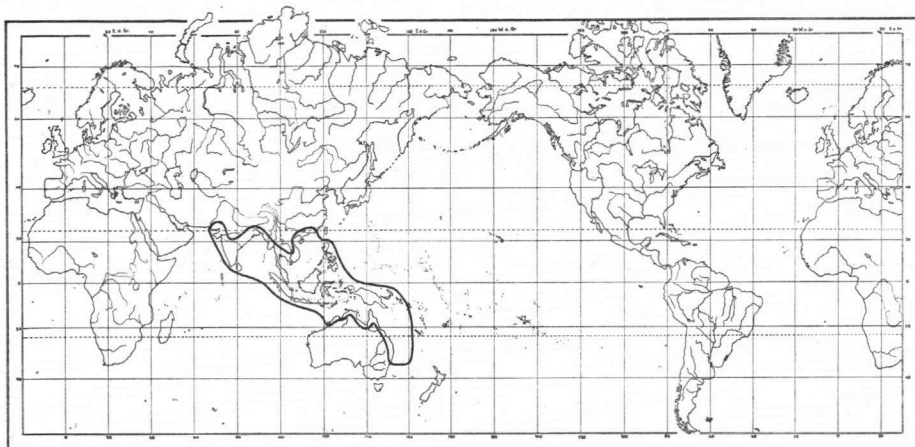


Fig. 23. Distribution of *Aegiceras-Myrs.* (see also Pac. Pl. Areas 2, map 92), extending from Asia to Australia. Example of type 4 a.

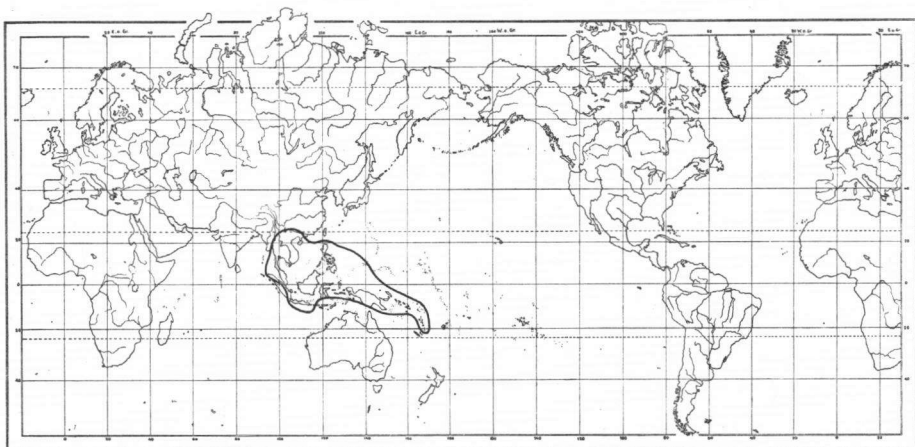


Fig. 24. Area of *Kopsia-Apoc.*, extending from Asia to Malesia, not in Australia (see also Pac. Pl. Areas 2, map 124). Example of type 5.

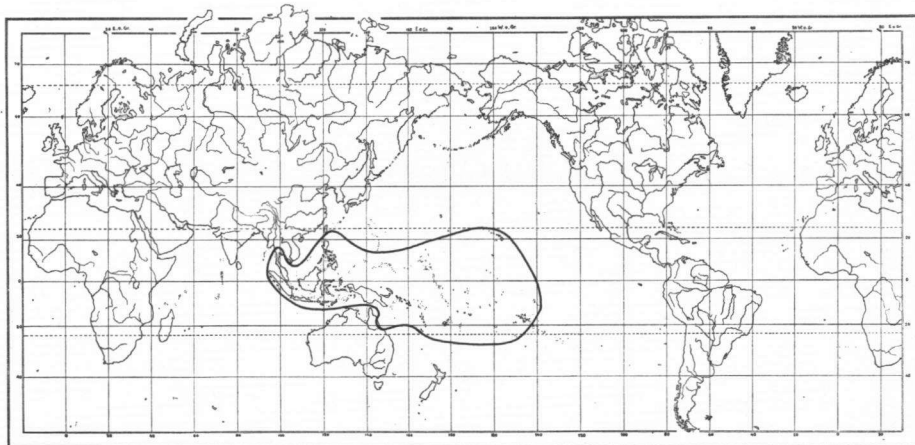


Fig. 25. Distribution of *Cyrtandra-Gesn.* Bulk of the species in Malesia and the Pacific, single species in Asia and Australia (see also Pac. Pl. Areas 2, map 71). Example of type 5 a.

Such genera as for example *Inocarpus* and *Serianthes-Leg.* and *Joinvillea-Flag.* could be considered as extraneous elements in the Malesian flora. But in all these cases there is no clear preponderance of species in the Pacific part of the range. If the centre of species development is clearly situated in the Pacific as e.g. in *Ascarina-Chlor.* (Swamy, 1953; P.P.A.-2, map 64) or *Veitchia-Palm.* they have been placed in type 8.

Type 5 b. — E. Malesian or Melanesian genera. Fig. 26.

No distinction was made in my former paper between genera occurring throughout Malesia and those centering in or confined to the eastern part. Most of these have their focus in New Guinea. They may extend to W. Malesia (*Amaracarpus-Rub.*) or Australia (*Calyptrocalyx-Palm.*) or both (*Hydnophytum-Rub.*). Typical examples are: *Trimenia-Monim.* (fig. 26), *Sararanga-Pand.* (P.P.A.-2, maps 28 & 29). But *Aceratium-Elaeoc.* with most species in New Guinea (c. 10) and 5 species in Queensland has been classified as type 6 a.

Type 6. — Australian genera. Fig. 27.

To this type belong all genera centering in or confined to Australia including Tasmania and not or hardly represented in Asia or Malesia. Here again a number of subtypes can be distinguished. Some are widespread outside the continent but clearly centre there, e.g. *Hibbertia-Dill.* (P.P.A.-2, map 133) and *Myoporum-Myop.* (fig. 27). Some occur throughout Australia (*Logania-Log.*), others are confined to one sector only: *Emmenosperma-Rham.* to the northern, *Argophyllum-Sax.* (P.P.A.-2, map 45) to the eastern, *Westringia-Lab.* to the southern sector, and *Campynema-Amaryl.* to Tasmania. Genera that clearly centre in the Pacific and extend to Australia have been classified as type 8, e.g. *Dracophyllum-Epacr.* (P.P.A.-2, map 43).

Type 6 a. — Australian-Papuanian genera.*) Fig. 28.

This is another type not distinguished in my former paper. It is a distribution type intermediate between types 5 b and 6, restricted outside the Pacific to Australia and E. Malesia or nearly so. Examples: *Agathis-Conif.* (P.P.A.-2, map 89) and *Quintinia-Sax.* (fig. 28). If the 'gravity centre' lies clearly in either New Guinea or Australia the genus is assigned to other types: *Calyptrocalyx-Palm.* with many species in E. Malesia and but a single one in E. Australia and *Grevillea-Prot.* with c. 170 species in Australia and only 4 in E. Malesia are placed in types 5 b and 6 respectively. But *Olearia-Comp.* of which most of the species are Australian (c. 70) but represented by c. 20 species in New Guinea (Koster, 1966) cannot be said to centre distinctly in Australia and is hence classed as type 6 a. Also *Aceratium-Elaeoc.* with c. 10 species in New Guinea and 5 in Queensland is placed here.

Type 7. — Pacific Subantarctic genera. Fig. 29.

Genera occurring disjunctively in extratropical and Andine South America and the extratropical and montane tropical parts of Indo-Australia and/or New Zealand. The

*) This distribution is often called 'Australasian', a term probably going back to Sclater (1858) and to be discussed later. 'Australasia' according to this author comprised Australia and the Pacific. Later the extent of the area denoted by this term was reduced to Australia (incl. Tasmania) and New Zealand, sometimes including New Caledonia and New Guinea. It is regrettable that this name came into being, as it has nothing to do with Asia as the name suggests, in analogy with 'Eurasia'. There is at present no proper name to denote Asia, Malesia and Australia as a whole. Indo-Australia refers often to the tropical parts only.

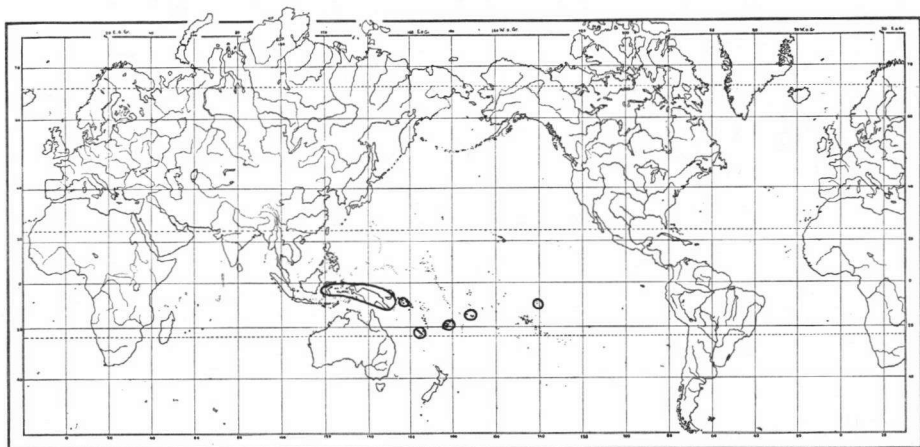


Fig. 26. Distribution of *Trimenia-Monim*. Like the former confined to Malesia and the Pacific, but in Malesia restricted to the eastern part. Example of type 5 b.

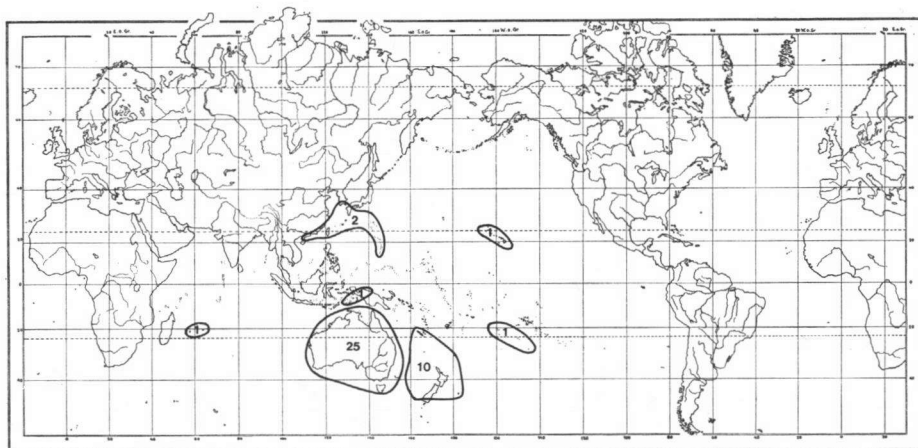


Fig. 27. Australia centred distribution of *Myoporum-Myop.* (see also Pac. Pl. Areas 2, map 59, figures indicate number of species). Example of type 6.

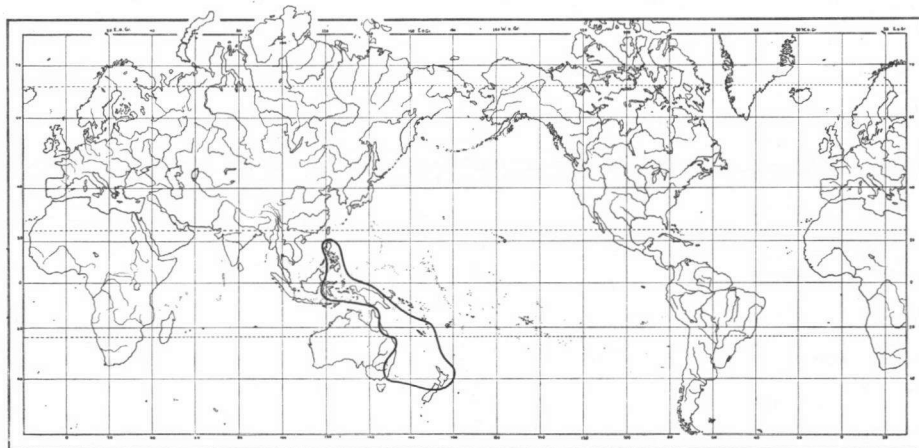


Fig. 28. Distribution of *Quintinia-Sax.*, ranging from E. Malesia and Australia to the Pacific. Example of type 6 a.

representation may be equal in east and west, as e.g. in *Oreobolus-Cyp.* (fig. 29) or be unbalanced: *Hebe-Scroph.* (P.P.A.-2, map 55) centering in New Zealand and *Fuchsia-Onag.* (P.P.A.-2, map 81) centering in South America. Not included are Andine genera that only extend to Juan Fernandez, e.g. *Escallonia-Sax.* (Sleumer, 1968), which is placed in type 9.

Type 7 a. — Indian Subantarctic genera. Fig. 30.

This type comprises the genera confined to S. Africa/Malagassy and the Pacific, absent from SE. Asia and Malesia but very often found in S. Australia, in other words occurring across the Indian Ocean. Example: *Pelargonium-Geran.* (fig. 30) with its focus in S. Africa and extending with rapidly decreasing numbers of species to SW. Asia, S. Australia and New Zealand. *Bulbinella-Lil.* is confined to S. Africa and New Zealand. Also included here are such curiously distributed genera like *Cossignia-Sapind.* (Mascarenes, New Caledonia, Fiji) and *Nesogenes-Verb.* (Africa, Malagassy, Tuamotus).

Type 7 b. — Pan-Subantarctic*) genera. Fig. 31.

This type is an extended version of type 7 being further represented in the African sector: S. Africa, or at least to the Subantarctic islands of both the Atlantic and Indian Ocean (Kerguelen, Tristan da Cunha). Further distinction could be made following Skottsberg (1960) according to extent of penetration in the tropical mountains. *Colobanthus-Car.* is confined to the Subantarctic islands and the extreme south of Patagonia, *Weinmannia-Cun.* and *Gunnera-Halor.* (fig. 31) have a much wider distribution to the north.

Type 8. — Pacific genera. Fig. 32.

Genera occurring in more than one island group within the boundaries of the Pacific as defined here, either confined to or very distinctly centering in the Pacific. *Nesoluma-Sapot.* (P.P.A.-2, map 94) and *Crossostylis-Rhiz.* (fig. 32) are examples of genera not found outside the Pacific. *Hedycarya-Monim.* which in New Caledonia alone has c. 15 species and only one each in New Guinea and Australia, is also classed as type 8. More difficult to place was *Soulamea-Sim.* with seven species endemic in the Pacific, another one extending to Malesia and a ninth endemic in the Seychelles. Another difficult case was *Ascarina-Chlor.* (P.P.A.-2, map 64). According to Swamy (1953) only one species occurs in E. Malesia. Two sections comprising six species occur in the Pacific. This induced me to place the genus in type 8.

Joinvillea-Flag. after the latest conspectus (Newell, 1969) comprises two species, both occurring in the Pacific and one also in Malesia. There is hence no clear species centre and I have classed the genus as Malesian (type 5 a).

Geniostoma-Log. (P.P.A.-2, map 39) is best represented in the Pacific, particularly in New Caledonia, but there are so many species in Australia, Malesia and even the Mascarenes, that it cannot be regarded as a Pacific genus. I have placed it in type 4.

Type 8 a. — Pacific endemic genera. Fig. 33.

This type comprises the genera that are confined to a single island or island group in

*) Skottsberg (1936a, 1940) has coined the term 'tricentric' for this distribution type. Genera occurring in two extratropical regions of the southern hemisphere are called 'bicentric'. I prefer the terms chosen here as, first, no centre is necessarily involved and, secondly, Skottsberg's designation does not indicate where the taxon occurs.

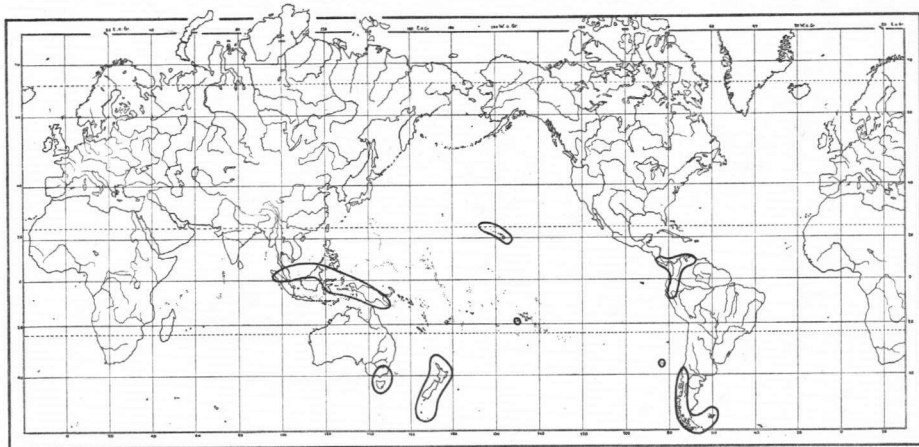


Fig. 29. *Oreobolus-Cyp.* has many species in New Zealand, extratropical Australia and South America, other species occur in montane localities of tropical America, the Pacific, and Malesia (see also Pac. Pl. Areas 2, map 74). Example of type 7.

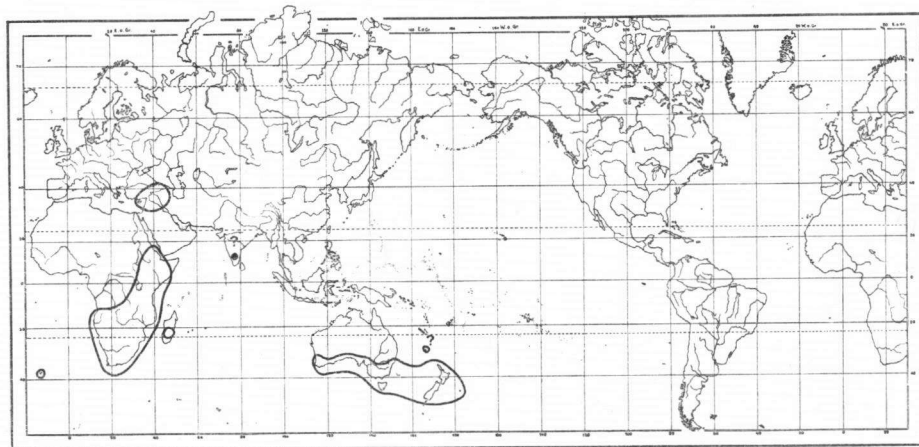


Fig. 30. *Pelargonium-Geran.* is distributed disjunctly, from Africa across the Indian Ocean to South Australia and New Zealand (see also Pac. Pl. Areas 2, map 159). Example of type 7 a.

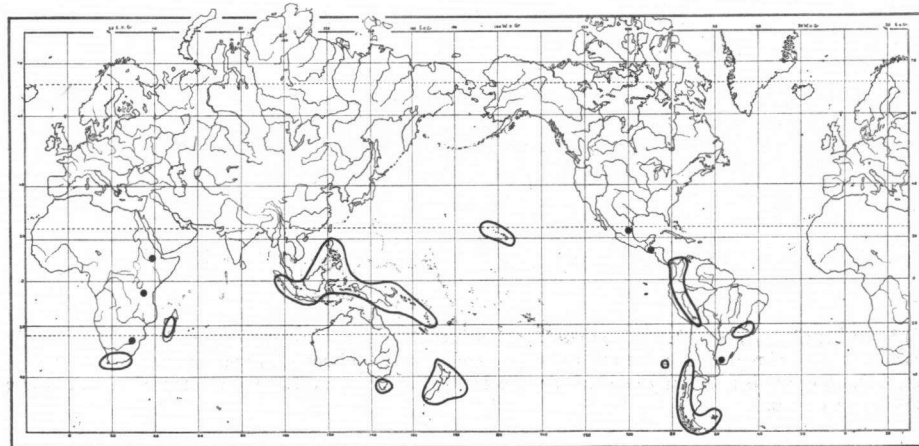


Fig. 31. *Gunnera-Halor.* ranges widely throughout the southern hemisphere, a good example of type 7 b.

the Pacific. I have not attempted to indicate the degree of distinctiveness of the genera. As is known endemic genera can be either young offshoots, 'neo-endemics' or taxonomically isolated relics, 'paleo-endemics' (see e.g. Wulff, 1943, for a discussion). What I have tried to do is to find out the nearest ally of the genus in question and this had been indicated in the Appendix. A few examples: *Dissochondrus*-Gram. is closely related to the widespread *Setaria*, *Labordia*-Log. is near the Old World *Geniostoma*, *Entelea*-Til. is of African, *Bobea*-Rub. of Indo-Malesian, *Boronella*-Rut. of Australian and *Juania*-Palm. of American alliance. Some genera have their closest ally in the Pacific itself. Thus *Negria* of Lord Howe, *Coronanthera* and *Depanthus* of New Caledonia and *Rhabdothermus* of New Zealand form the tribe *Coronantherinae* of the *Gesneriaceae*. The relationships of many genera are obscure. Most striking are of course those genera forming monotypic families, such as *Degeneria*-Deg., *Lactoris*-Lact. and *Strasburgeria*-Strasb. (see fig. 33), while *Amborella*-Monim., *Canaomyrica*-Myric. and *Oceanopapaver*-Capp. are taxonomically isolated genera within their respective families. There is a striking abundance of such genera in New Caledonia.

Type 9. — American genera. Fig. 34.

All genera confined to America and the Pacific, e.g. *Vallesia*-Apoc. (P.P.A.-2, map 125), others may extend to Africa as e.g. *Laguncularia*-Combr. (fig. 34) or as far east as India (but not to Malesia or Australia), e.g. *Calliandra*-Leg. A further distinction can be made between essentially tropical and lowland genera such as *Tillandsia*-Brom. and *Vallesia*-Apoc. (P.P.A.-2, map 125) and genera confined to the extratropical parts of South America and the Andes, e.g. *Escallonia*-Sax. and *Rhaphithamnus*-Verb. Tropical genera centering in America but extending across the Pacific have been assigned to type 1 (*Evolvulus*, *Heliconia*). Andine and temperate South American genera crossing the Pacific at least as far as New Zealand have been placed in type 7 (e.g. *Fuchsia*).

Anomalous distributions

In general it can be said that most genera follow a certain recurrent pattern. It can often even be successfully predicted that a genus will turn up in a given locality from where it is yet unknown. Van Steenis (1950, p. xviii) discussed how plant-geography can be applied to check wrongly localized specimens. Similarly most of the unusual distributions may be regarded with some suspicion. Most of the 'problematic' genera have been discussed in the descriptions of distribution types above. There are, however, a number of truly anomalous cases. Many more were formerly on record, but in the course of time quite a few have proved to be based on wrong identifications, insufficient collecting, mislabelling or a combination of these. *Calyptosepalum*, for example, was originally described as a monotypic genus of *Santalaceae* from Sumatra. A second species was described by Bailey and Smith (1953) from Fiji. Later the genus proved to be a synonym of the widespread *Drypetes*-Euph. (van Steenis, 1960; Smith & Ayensu, 1964).

Centrostachys-Amarant. was as recently as 1949 mentioned for Norfolk I. by Backer, its further distribution being from Africa to W. Malesia. This mistake apparently goes back to Moquin (1849, p. 321), later repeated by Schinz (1934) in 'Pflanzenfamilien'.*)

Chroniochilus-Orch. was originally described as a monotypic genus from Java, a second species was later described from Fiji. This remained a curious case of disjunct distribution for a long time, but it now appears that other species occur in Malaya, Indo-China,

*) Robert Brown (Prodr. Fl. Nov. Holl., 1810, 417) described *Achyranthes arborescens* and *A. aquatica* (*Centrostachys aquatica*) but attributed only the former to Norfolk I., the second to 'India orientalis'.

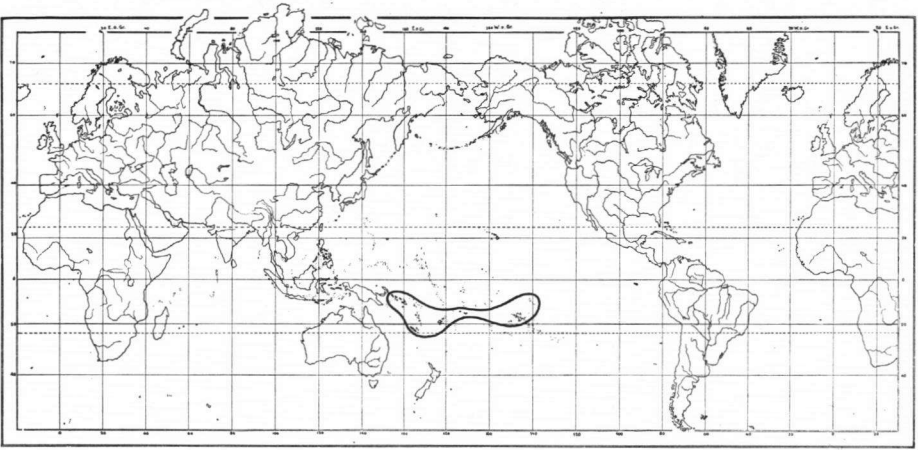


Fig. 32. Range of *Crossostylis-Rhiz.* (see also Pac. Pl. Areas 1, map 23). Other genera of distribution type 8 may have stray representatives in one or more of the surrounding continental areas but the 'gravity centre' is always clearly in the Pacific.

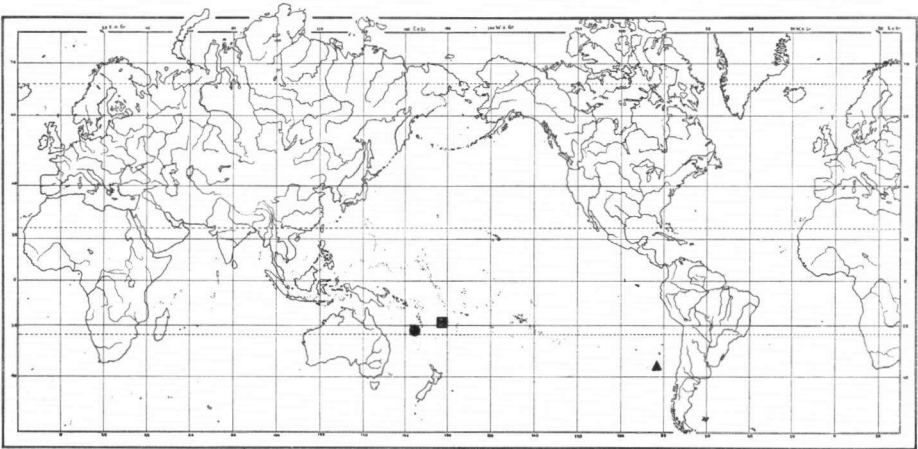


Fig. 33. Three examples of distribution type 8 a: ● *Strasburgeria-Strasb.*, confined to New Caledonia, ■ *Degeneria-Deg.* known from two islands of the Fiji group, and ▲ *Lactoris-Lact.*, limited to Mas a Tiera, Juan Fernandez Is.

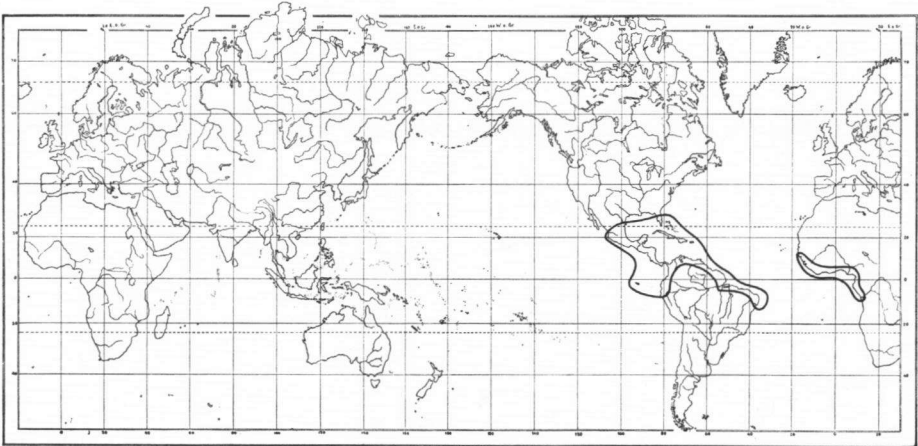


Fig. 34. Distribution of *Laguncularia-Combr.* To distribution type 9 are reckoned all genera confined to America and, as in this case, genera extending to the Old World across the Atlantic.

Admiralty Is. and Tonga (Hunt & Summerhayes, 1966, and Hunt in litt.). It may yet turn up in some more intermediate localities.

Lipochaeta-Comp. was at one time credited to Hawaii, Galapagos, New Caledonia, New Hebrides and Loyalties. The Melanesian *L. lifuana* Hochr. proved to be a *Wedelia* (S. le M. Moore, in Rendle c.s., 1922) and the Galapagos species was referred to *Macraea* (Harling, 1962).

Of the Australian *Lysiana-Lor.* one species was described from the New Hebrides. It was recently transferred to *Amylothea* (Barlow, 1963).

Of course it is a matter of opinion whether a distributional range is termed normal or anomalous. In fact any taxon showing great gaps in its range could be called 'anomalous'. It is curious to find *Lactoris*, the only member of a separate family on such a small and isolated island as Mas a Tiera, and *Canacomyrca-Myric.* isolated on New Caledonia whereas the other two genera of its family are largely confined to the northern hemisphere, although one (*Myrica*) occurs as far south as New Guinea.

Calophanes-Acant. which occurs in America, Africa, SE. Asia, W. Malesia and Fiji, *Byttneria-Sterc.* centering in South America and further represented in Africa, Asia, Malesia and SE. Polynesia (to give but a few examples) have in fact a very curious distribution, but despite the wide gaps they can be 'recognized' as wides and were hence classed as type 1.

Lepinia-Apoc. only known from Tahiti, Ponape and the Solomons has disjunctions 2000—6000 km wide, but its distributional area can be considered a relic version of that of *Crossostylis-Rhiz.* (fig. 32) which ranges from the Solomons to the Marquesas.

As 'anomalous' I consider those genera with distributions that are both disjunct and cannot be readily referred to any of the categories distinguished. Most of these 'difficult cases' have already been mentioned in the discussion of the description of distribution types. A few are left and are listed below together with the type to which they are assigned. Their taxonomy still needs to be carefully scrutinized.

| Genus-Fam.: | Distribution: | Assigned to: |
|----------------------------|---|--------------|
| <i>Acridocarpus-Malp.</i> | Africa-New Caledonia | type 7 a |
| <i>Artia-Apoc.</i> | 1 sp. in SE. Asia, W. Malesia, several in New Caledonia & Loyalties | type 8 |
| <i>Cossignia-Sapin.</i> | Mascarenes-New Caledonia, Fiji | type 7 a |
| <i>Dietes-Irid.</i> | S. Africa-Lord Howe I. | type 7 a |
| <i>Epistephium-Orch.</i> | America-New Caledonia | type 9 |
| <i>Hiptage-Malp.</i> | Asia, W. Malesia-Fiji | type 5 |
| <i>Koelreuteria-Sapin.</i> | China, Formosa-Fiji | type 3 |
| <i>Lindenia-Rub.</i> | Neotropics-Fiji, New Caledonia | type 9 |
| <i>Nastus-Bamb.</i> | Africa, Malagassy-New Guinea, Solomons | type 5 b |
| <i>Nesogenes-Verb.*)</i> | Africa, Malagassy-Tuamotus | type 7 a |
| <i>Stillingia-Euph.</i> | Neotropics-Mascarenes-S. Malesia-Fiji | type 1 |
| <i>Yoania-Orch.</i> | N. Africa-E. Asia-New Zealand | type 3 |

*) Miss Burbidge (1966) erroneously recorded this genus for Australia, viz. Whitsunday I. off Queensland. This is a mistake for Whitsunday I. in the Tuamotu archipelago, one of the islets from where *N. euphrasoides* DC. was originally described. See also Hemsley (1913) and Brown (1935, p. 246).

7. Revised taxa

Revised taxa can be regarded as a random sample to test the results based on the whole flora. It is to be expected that the data on the taxonomic status, the distribution and other relevant aspects of a recently revised taxon will be more reliable than of one of which the data have been casually compiled from literature or other sources.

It is perhaps not quite correct to speak of a 'random sample', however, as the choice of a taxon for a revision may be determined by various reasons. It is conceivable that geographic, taxonomic, or economic importance, size, difficulties in species delimitation and other factors play a role in the choice the student makes. It will later be seen that actually more genera of 'Subantarctic' and Malesian distribution than of world-wide distribution have been revised. This may slightly distort the picture, but revised genera still form the most reliable basis for classification and geographic speculations. Weimarck (1941) gave an excellent analysis of the Cape flora based on a limited number of revised taxa. Kalkman (1955) tested the results of his phytogeographical analysis of the Lesser Sunda Islands which was based on all genera with a small set of species of which the taxonomy and distribution were well established. He found the latter corroborated the conclusions based on the whole flora. In the analysis the primary consideration is the evidence for the whole flora. This is dealt with first and is later compared with the evidence from the revised taxa.

As 'revised' I have considered all those genera of which a reliable monograph or revision not earlier than 1925 exists. Revisions based on incomplete material, e.g. material from a single herbarium (most 'Pflanzenreich' and 'Pflanzenfamilien' revisions), or those containing such gross errors as the citation of the same collection number under more than one species, and omission of many published names, did not qualify for inclusion. On the other hand genera have been included of which only a local revision exists if this, apart from being sound taxonomically, embodies the bulk of the species and extant material. Various genera treated in the 'Flora Malesiana' series can therefore be regarded as being virtually revised. Some widespread genera of which local revisions exist in different parts of the world have also been included. There are revisions of the African (Cufodontis, 1960), the Asian (Gowda, 1951; Li, 1953), the Malesian (Bakker, 1957), the 'Australasian' (Cooper, 1956) and the Hawaiian (Sherff, 1942) species of *Pittosporum*-*Pitt*. Of course the quality of these revisions may be different as are the species concepts of the various authors, but the area of the genus is well established and a fairly good impression of the diversity of the genus in the various parts of its area can be obtained through a comparison of the descriptions. Most of the Pacific genera included in the series 'Pflanzenareale' and all those in 'Pacific Plant Areas' have been taken up. Many of these were not formally revised but their delimitation and area of distribution have been well established.

Finally I have included all genera that although not meeting any of the above mentioned qualifications, are unlikely to be confused with anything else and for which no essential range extensions are to be expected. Examples: *Aristotelia*-*Elaeoc.*, *Degeneria*-*Deg.*, *Gunnera*-*Halor.*, *Rhododendron*-*Eric.*, *Scaevola*-*Good*. These 'revised genera' have been marked in the Appendix with an exclamation note (!).

Data on the dispersal of these genera, or at least on the nature of their diaspores, were collected. Floristic spectra of the island groups could then be correlated with dispersal spectra.

For a better evaluation of the results dispersal spectra of the surrounding continental areas as well would have been desirable but this would have taken too much time.

8. Dispersal classes

For the revised genera I have tried to find out the normal method of dispersal so that the 'dispersal spectra' of the various island groups can be compared in the same way as with the distribution types.

In assigning the genera to dispersal classes I have based the classification on actual observations and the agent of transport rather than on the morphology of the diaspore, as was done amongst others by Dansereau and Lems (1957). Also I have not made any distinction according to the character of the diaspore. This may be the seed, the fruit, vegetative parts of the plant or a combination of these. There is no need for a detailed classification as can be found in Van der Pijl (1969) as many of his dispersal classes will be of little importance to us. Saurochory (dispersal by reptiles) or myrmecochory (dispersal by ants) will only be of local importance. Anyhow the genus is too crude a unit for detailed work. Thus if a plant is known to be eaten by both birds and ants it will be classified as bird-dispersed. Neither have I followed the example set by Carlquist (1967a) who assigned a (long-distance) dispersal vector to every taxon in his analysis of the Hawaiian flora. If the mode of dispersal of a genus is unknown I have preferred to classify it as such rather than to credit it with dispersal potentials it may or may not have. Thus I have not classified every winged diaspore as wind-dispersed or every fleshy fruit as bird-dispersed. I may have been too pessimistic regarding dispersal capacities in some cases but also too optimistic in others. The well-known and widespread *Nertera granadensis-Rub.* has small, red, fleshy drupes borne in profusion and seemingly ideally suited for bird dispersal. Apart from observations on Tristan da Cunha (Ridley, 1930) I have never come across any record of bird dispersal of this species. Docters van Leeuwen (1933), who paid special attention to its dispersal, never found any indication of this species being eaten by birds. *Allophylus-Sapind.*, which according to Leenhouts (1967) consists of a single very variable and widespread species has conspicuous red arillate seeds. Yet he found only a single record of starlings feeding on them.

Nevertheless I have classified these two genera as bird-dispersed, but they illustrate the slenderness of the evidence upon which the 'dispersal classification' is really based.

A good example of the caution needed in this respect is offered by the well-known occurrence of *Sisyrinchium-Irid.* in Greenland and Ireland, always accepted as an indubitable example of long-distance dispersal by geese. Chromosome counts and taxonomic re-investigation proved the existence of geographically separate species, so that, to put it in Löve's (1963) words: 'A most striking example of long distance dispersal becomes an example of a major taxonomical error, emphasizing the great need for taxonomic exactness in all kinds of phytogeographic studies'.

Another example of the same kind is offered by *Eriocaulon-Erioc.*, the single European (Ireland) population of which proved to have a different chromosome number than its N. American congeners (Löve, A. & D., 1956), but this was known to be a distinct species.

Cyrtandra-Gesn. is a genus widespread throughout the Pacific and Malesia (fig. 25 and Van Steenis & Van Balgooy, 1966, map 156). Although it generally has fleshy berries containing numerous small seeds, these do not seem to be touched by birds or any other animals. I think the most correct procedure is to classify the genus as of unknown dispersal instead of 'bird-dispersed'. Likewise the genus *Lepinia-Apoc.* with its spectacular distribution and equally curious fruit (see Van Steenis, 1962, p. 303, fig. 2) has seeds enclosed in fibrous mesocarp. It may well be that in dry state the fruit structure is buoyant but, as

there are no observations whatever to sustain this supposition, I prefer to classify the genus as being of 'unknown dispersal'.

Some will perhaps find that this procedure results in too many 'unknowns'. It should be remembered that I have used only revised genera for this investigation and if these give reason for caution it strongly emphasizes the need for careful and unbiased recording of dispersal phenomena.

I should add that if I have classed a genus as 'unknown' it does not mean that I deny it any possibility for (long-distance) dispersal. It is always possible that some of the 'unknowns' may prove to have dispersal capacities. Small seeded marsh plants, for instance, may be accidentally transported in mud caked to the feet or plumage of waders and other birds or may prove to be suited for wind or water dispersal but as long as there is no reliable evidence, I prefer to admit ignorance.

On the other hand the observation that the fruits of a certain species are eaten by birds does not automatically imply that it is bird-dispersed. Seeds found in flotsam have not necessarily been dispersed by ocean drift in a viable state. As a rule no more is known of a diaspore than that it has the mechanical facility to be dispersed in this or that way. Successful transport is of course still a quite different matter than effective dispersal, that is final permanent establishment.

It is clear that my classification could only be rough. Yet if there is a correlation between dispersal and distribution it should be revealed despite the imperfection of the method.

In most revisions notes can be found on dispersal. In addition I consulted Guppy (1906) and Ridley (1930). The following classes were distinguished:

(1) Dispersal by wind (Anemochores)

Many genera with dust seed, winged, plumed or filiform seeds belong here, e.g. in the families *Orchidaceae*, *Asclepiadaceae* and *Compositae*, furthermore in *Astronia-Melast.* and *Nepenthes-Nepenth.*

(2) Dispersal by water (Hydrochores)

The majority of shore and mangrove genera belong here or have species in the Pacific with buoyant diaspores, such as *Barringtonia-Lecyth.*, *Aegiceras-Myrs.*, *Hernandia-Hern.*, *Lumnitzera-Combr.* and *Suriana-Sim.*

(3) Dispersal by animals (Zoochores)

This of course is a rather heterogeneous class. Only two groups of animals were considered to be of importance for dispersal over any distance: birds and bats. The former are apparently the most important. Moreover many fruits eaten by bats are also sought by birds. Therefore I have only distinguished between (a) endozoic dispersal (seeds or fruits eaten and transported internally) and (b) epizoic dispersal (diaspore carried externally on plumage or other body parts).

Examples of bird-dispersed genera are *Astelia-Lil.*, *Coprosma-Rub.* and *Myristica-Myrist.*, of bat-dispersed genera *Pometia-Sapind.*, and of genera dispersed by both bats and birds *Ficus-Morac.* and *Freycinetia-Pand.*

In the case of bats the fruit is often not swallowed but carried in the beak.

Examples of genera exhibiting epizoic dispersal are *Pisonia-Nyct.* with viscid fruits, *Acaena-Ros.* with hooked barbs. The seeds of several *Loranthaceae* are enveloped in a sticky mass. They are eaten but very often adhere firmly to external parts of the bird and are only removed with great difficulty (see Docters van Leeuwen, 1927). These *Loranthaceae*

ceous genera as well as the 'bat fruit' genera have been placed in the endozoic dispersal class.

(4) Dispersal in more than one way (Diplochores)

Many plants are dispersed by more than one agent. It is possible that the majority of plants are accidentally dispersed in various ways and should then properly be called polychores. In this class I have only placed those genera for which at least two (sometimes more) agents are normally operative. In *Sonneratia-Sonn.* the fruits are eaten by monkeys and bats and the seeds are buoyant. Another example is *Scaevola-Good.* The fruits of the two widespread littoral species *S. taccada* and *S. plumieri* are suited for dispersal by ocean currents, but some of the inland species have fruits eaten by birds. It may well be that for *Scaevola* water dispersal is the more important for the wide distribution of the genus. But I think it is justified to have a separate class for such genera with a double dispersal mechanism which presumably gives them an extra advantage over those genera with a single dispersal agent.

(5) Dispersal method unknown

As stated earlier there are many genera of which the dispersal agent, if any, is unknown. Included here are a number of 'autochores', genera with a mechanism for self-dispersal. Carlquist (1962) described a beautiful case in *Trematolobelia-Camp.* the seeds of which are shaken out of the fruit through pores. Also placed in this class are genera with heavy fruits which may be eaten by hogs and squirrels which can hardly lead to dispersal over large distances. The only distinction made is between 'small' and 'large' diaspores. As a rather arbitrary measure I have considered diaspores 1—3 mm across as small and 4 mm or larger as large. This was done as small seeds may be accidentally dispersed by wind or birds. Ridley mentions many cases of small diaspores especially of marsh plants (e.g. *Carex*, *Polygonum*, etc.) which have been found in mud adhering to the feet of various bird species.

The 'large diaspore' class comprises the genera with the poorest dispersal capacities and which are therefore the most significant in speculations on land connections. Examples are *Araucaria-Conif.*, *Nothofagus-Fag.*, *Pangium-Flac.*, and *Parinari-Ros.* Some heavy fruited genera such as *Canarium-Burs.* and *Myristica-Myrist.* have, however, frequently been found to be eaten by fruit pigeons and are hence classed as 'bird-dispersed'.

In the Appendix the following abbreviations will be used: A = air flotation or wind dispersal, W = water dispersal (ocean drift), I = internal or endozoic dispersal by birds and/or by bats, E = epizoic dispersal, D = diplochores, diaspores spread by more than one agent, e.g. by birds and water, S = small diaspores (1—3 mm \varnothing) of unknown dispersal, L = large diaspores (> 4 mm \varnothing), dispersal method unknown.

9. Floristic affinity and demarcations

In the foregoing paragraphs I have shown that the basic unit, the genus, though being more constant than the species, is not a unit which can be used for mathematical statistical purpose. It is therefore clear that the figures cannot lead to exact calculations. They should only be used to make relations 'tangible' in Hooker's sense, and an absolute value should not be attached to them.

Figures, however, are meaningless if not placed in a certain perspective, if they cannot be compared and evaluated. What is the use of telling the reader that area A and B have

100 genera in common if one does not add how many taxa there are on A and B, how many are in common with other areas and what taxa are involved?

One of my problems therefore was to find a satisfactory way to express floristic affinity or similarity and its counterpart dissimilarity in figures.

In my paper on the diversity of island floras (van Balgooy, 1969) I discussed a number of factors affecting the size of floras, such as available area, altitude, age, proximity of source areas, state of exploration, etc. In the Pacific the islands in general decrease in size as the distance from the continents increases, they vary in altitude and have been explored to a varying degree of intensity. The ideal situation in which all island groups compared have approximately the same number of genera does not exist.

In delimiting the Malesian floral region from Asia and Australia Van Steenis (1950) found the 'demarcation knot' method very satisfactory. This method expresses the strength of a floristic demarcation by the number of genera that do not occur beyond a certain imaginary line. Thus he found 575 genera 'respected' the Isthmus of Kra, 686 genera occurred either in Formosa or in the Philippines, and 984 were found in New Guinea but not in Queensland or the other way round. As the floras compared are all of approximately the same order of magnitude the Torres Strait is clearly the most important demarcation of the three.

If the floras are of different size there are various ways to express similarity or dissimilarity. My starting point in finding such a formula was that it should be easy to handle and that its value should vary between zero for complete dissimilarity and one or 100 for complete similarity.

It appeared that various authors, many of them independently, had invented such formulas with a varying degree of mathematical sophistication. They can be found especially in sociological and zoogeographical papers. A few will be discussed here.

Floristic alliance, or rather resemblance, is expressed in the proportion of taxa that two areas have in common to the number of taxa confined to either or the total number of taxa in both. These values are denoted in literature on the subject by a number of symbols. In the rest of this chapter I will use the following symbols:

- A = the number of genera occurring in the first area
- B = the number of genera in the second area, which is smaller than A
- C = the number of genera common to both areas

Then $A - C$ is the number of genera limited to the first area, $B - C$ is the number confined to the second, and the total number of genera in both areas will be $A + B - C$.

One of the most frequently used formulas is $\frac{C}{A + B - C}$. To express this value in percentages it has to be multiplied by 100. It was first introduced into botanical literature by Jaccard (1908). Recently it was applied by Van den Hoek & Donze (1967) in their analysis of the NW. European algal flora. It will be readily seen that if the two areas have nothing in common the value of this parameter will be zero and if resemblance is complete, in other words if every taxon occurs in both areas, it will attain a value of 100%.

Another expression meeting the condition of attaining zero value with total dissimilarity and 100 % with total similarity is $\frac{2C}{A + B}$. The first botanist to employ it was

Soerensen (1948) but he was preceded (apparently independently) by the zoologist Dice (1945). Again it has to be multiplied by 100 to obtain the percentage.

In both cases the value obtained is strongly affected by the size difference between A and B. This effect can be minimized by using a formula proposed by Kroeber (1916) in

his analysis of the Galapagos flora, viz. $\frac{\frac{C}{A} + \frac{C}{B}}{2}$. This formula gives the average resemblance of the two areas. The same formula was applied by Imahori (1957) in his paper on the *Characeae* of Formosa and the Philippines, and who was unaware of Kroeber's paper. It can also be written in simplified form thus: $\frac{C(A+B)}{2AB}$, as was done by Long (1963). Again it has to be multiplied by 100 to express it as a percentage. It will be seen that the value of this parameter ranges from zero in case of total dissimilarity to 100 % in case of complete similarity.

An even simpler formula was used to give what is currently known in zoological literature as 'Simpson's figure' (Simpson, 1943): $\frac{C}{B}$. In other words only the poorer of the two regions is taken into consideration. To be expressed as a percentage this value has to be multiplied by 100. The underlying assumption is that there is no reason to suppose that either peculiar or common taxa are on the average more collected, in other words that collecting has been random. If the first area has twice the number of taxa as the second, the number of taxa common to both can be presumed to be doubled when the second area has the same number of taxa as the first. The first botanists to apply this reasoning were Exell and Wild (1961) again apparently totally unaware of 'Simpson's figure'. They recommend the use of 'Exell's quotient' which is obtained in exactly the same way.

The formulas discussed so far have in common that they are based on similarity between the two areas under consideration. The degree of dissimilarity can also be considered.

In my preliminary analysis (van Balgooy, 1960) as a measure of dissimilarity I used the proportion of genera confined to either of the two areas to the total number in both, in

formula: $\frac{A+B-2C}{A+B-C} \times 100$. This I termed the 'demarcation knot'. As mentioned before, in the original sense of Van Steenis 'demarcation knot' only denoted the total number of genera not crossing a certain boundary, without reference to the number that do. A few years before me Oliver (1957) applied a similar formula in his analysis of the New Zealand flora, where it is called 'quotient of dissimilarity'. This will further be denoted as 'demarcation knot percentage' to avoid confusion.

It is clear that the value of this formula will be zero in case of maximum similarity, in other words if the two areas have all genera in common and will be 100 % if the two areas do not have a single genus in common.

The values of the different coefficients vary with varying relations between A, B and C. This is tabulated in table 1 and is shown graphically in fig. 35.

In practice it has been found that the size relations between the floras compared are from 1 : 1 (1.0) to 1 : 3 (0.33), e.g. Bismarck-Solomons: 632 : 654 (0.97), Bonin-Marianas: 164 : 215 (0.76), Solomons-New Hebrides: 652 : 396 (0.61), Fiji-Tonga: 476 : 263 (0.55), Galapagos-Cocos: 190 : 61 (0.32).

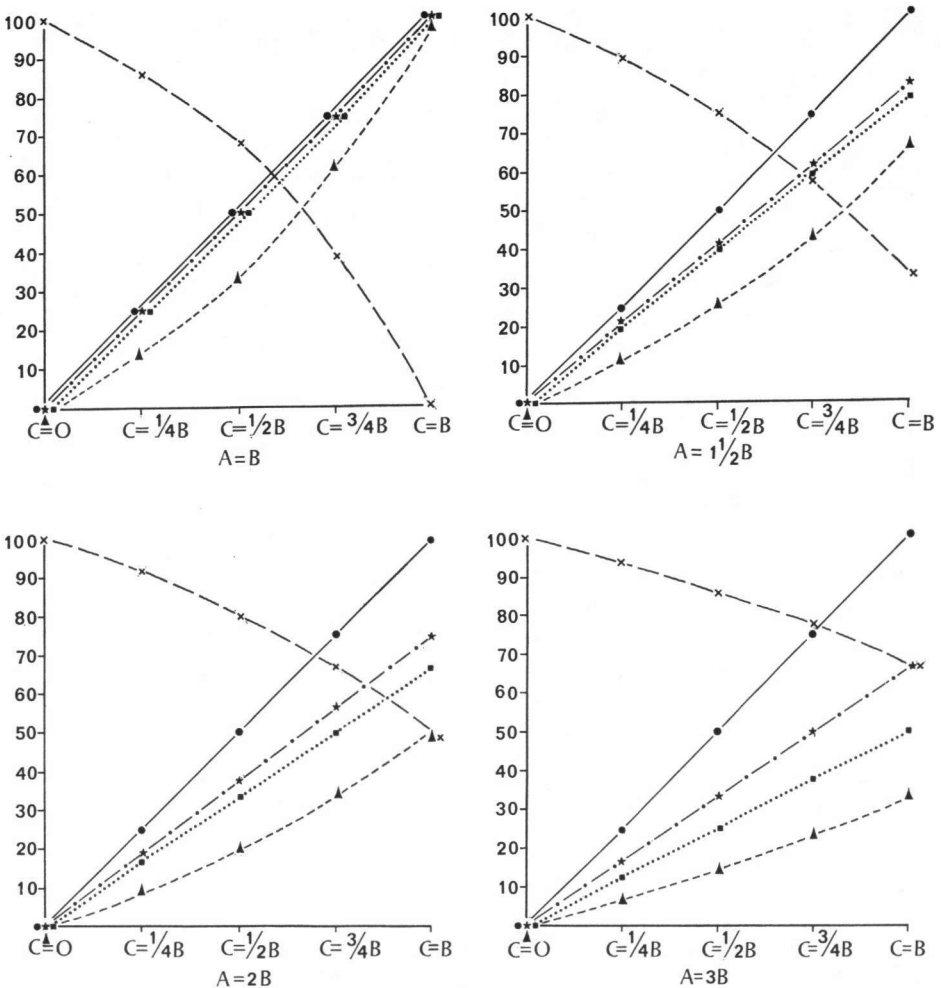


Fig. 35. Graphical depiction of coefficient values, with A constant and B and C varying: ———●, Exell's, —.—.—*, Kroeber's,■, Soerensen's and ———▲, Jaccard's coefficient, ————x, demarcation knot percentage.

The figures in fig. 35 show parabolic curves for Jaccard's and demarcation knot formulas, straight lines for the other three. If j = Jaccard's quotient and s = Soerensen's quotient and d = demarcation knot percentage/100, it can be shown that the following

relation exists: $j = \frac{1}{\frac{2}{s} - 1} = 1 - d$. This means that j , s and d have the same intrinsic significance, only differing in the representation of the data.

Exell's coefficient is independent of the size relation between A and B. In all similarity coefficients the lowest value, in case of complete dissimilarity, is always zero. The maximum value is lower the larger A is in relation to B. For example if $A = B$ the coefficients

Table 1. — Values of the various coefficients of similarity and dissimilarity with A constant and B and C varying. See also fig. 35.

| Relation between A and B Relation between B and C | A = B | A = 1.5 B | A = 2 B | A = 3 B |
|---|-------|-----------|---------|---------|
| C = B | | | | |
| Jaccard $\left(\frac{100 C}{A + B - C} \right)$ | 100 | 66.7 | 50 | 33.3 |
| Soerensen $\left(\frac{200 C}{A + B} \right)$ | 100 | 80 | 66.7 | 50 |
| Exell $\left(\frac{100 C}{B} \right)$ | 100 | 100 | 100 | 100 |
| Kroeber $\left(\frac{50 C (A + B)}{AB} \right)$ | 100 | 83.3 | 75 | 66.7 |
| Dem. knot % $\left(\frac{100 (A + B - 2C)}{A + B - C} \right)$ | 0 | 33.3 | 50 | 66.7 |
| C = 0.75 B | | | | |
| Jaccard | 62.5 | 42.9 | 33.3 | 23.1 |
| Soerensen | 75 | 60 | 50 | 37.5 |
| Exell | 75 | 75 | 75 | 75 |
| Kroeber | 75 | 62.5 | 56.3 | 50 |
| Dem. knot % | 37.5 | 57.1 | 66.7 | 76.9 |
| C = 0.5 B | | | | |
| Jaccard | 33.3 | 25 | 20 | 14.3 |
| Soerensen | 50 | 40 | 33.3 | 25 |
| Exell | 50 | 50 | 50 | 50 |
| Kroeber | 50 | 41.7 | 37.5 | 33.3 |
| Dem. knot % | 66.7 | 75 | 80 | 85.7 |
| C = 0.25 B | | | | |
| Jaccard | 14.3 | 11.1 | 9.1 | 6.7 |
| Soerensen | 25 | 20 | 16.7 | 12.5 |
| Exell | 25 | 25 | 25 | 25 |
| Kroeber | 25 | 20.8 | 18.8 | 16.7 |
| Dem. knot % | 85.7 | 88.9 | 90.9 | 93.3 |
| C = 0 | | | | |
| Jaccard | 0 | 0 | 0 | 0 |
| Soerensen | 0 | 0 | 0 | 0 |
| Exell | 0 | 0 | 0 | 0 |
| Kroeber | 0 | 0 | 0 | 0 |
| Dem. knot % | 100 | 100 | 100 | 100 |

range from 0—100, but if $A = 2B$ Soerensen's coefficient ranges from 0—66.7 and Kroeber's from 0—75. It will be clear e.g. that a Kroeber coefficient of 50 % where $A = B$ has a different meaning than where $A = 2B$. It is only comparable if the size relations are of the same order. Examples of such sets of comparable island groups in the Pacific are: Solomons-New Hebrides (654 : 396) with Fiji-Samoa (476 : 302) or Solomons-Fiji (654 : 476) with Marianas-Bonin (215 : 164) but not Bismarcks-Solomons (632 : 654) with Solomons-St. Cruz (654 : 126).

The expressions for 'floristic affinity' or, rather similarity, and dissimilarity so far discussed have no theoretical basis. Attempts have been made to find values founded on mathematical reasoning.

C. B. Williams (1947) worked out a method based on earlier work by Fischer. It was found that in mixed populations of both plants and animals the number of species represented by one, two, three or more individuals fall into a logarithmic order. If two areas are regarded as random samples of the same population the number of species expected to be common between these two areas can be calculated. If the actual number of species in common between the two areas is known the ratio $\frac{\text{expected common species (taxa)}}{\text{actually common species (taxa)}}$ gives a measure of how closely the two areas are allied. If completely identical the ratio tends to 1 (or 100 if expressed as a percentage).

The reader interested in the details of this method is referred to the original paper of Williams and Exell's discussion following it and to Exell (1956).

A few assumptions have to be made. The average density of individuals should be the same for the two areas and they should have unequal surfaces; the largest of the two areas should be richest in taxa. Another point is that I do not know whether the logarithmic order found for species in a population has the same form in the genera found in a given area. Moreover it cannot readily be calculated.

Another noteworthy method was developed by Preston (1962). This is based on the fact that the number of taxa increases lognormally with area (this of course only holds for an ecologically homogeneous area). Preston arrives at the following formula $x^{1/z} + y^{1/z} = 1$, which he calls the 'resemblance equation', x being the fraction in the first area (number of taxa in the first area/total number of taxa in both areas) and y the fraction in the second. The theoretical value of z lies between 0 and 1.

If the two floras are very much alike the z value tends to zero and if they have very little in common the z value approaches 1. It was found that z had as a rule values between 0.2 and 0.35. This parameter may be denoted as 'dissimilarity quotient' and its reciprocal $1 - z$ as the 'similarity quotient'.

The derivation of the 'resemblance equation' will not be discussed here. Those interested should consult Preston's lengthy paper.

This is certainly a very useful formula as it has the advantage over Williams's formula that the areas need not be known, only the number of taxa and the number common to both. It will presently be shown that it closely follows values obtained by applying one of the more traditional methods. Preston's formula has recently been applied by Holloway and Jardine (1968) and Holloway (1969).

In order to test the conclusions on floristic affinity arrived at by using the various

methods discussed so far a practical example will now be worked out for which I have chosen the islands in the Gulf of Guinea as based on work by Exell (1944).

The number of species of each island and the number shared is presented in the following matrix:

| Island | Number of species | Sao Tomé | Species in common Principe | Annobon |
|---------------|-------------------|----------|-------------------------------|---------|
| 1 Fernando Po | 826 | 187 | 128 | 47 |
| 2 Sao Tomé | 556 | | 183 | 80 |
| 3 Principe | 276 | | | 52 |
| 4 Annobon | 115 | | | |

In the following table the values for Williams's quotient have been taken from Williams (l.c.). Preston's dissimilarity quotients were calculated with the help of his table (Preston, l.c., p. 419). The figures could be multiplied by 100 to make comparisons with the other quotients easier. The highest similarity and the lowest dissimilarity quotient values are printed in bold type. The lowest similarity and the highest dissimilarity quotient values are printed in italics.

| | | 1/2 | 1/3 | 1/4 | 2/3 | 2/4 | 3/4 |
|-------------|---------------|------|------|------|-------------|-------------|------|
| Jaccard | SIMILARITY | 15.7 | 13.1 | 5.3 | 28.0 | 13.5 | 15.3 |
| Soerensen | | 27.1 | 23.2 | 10.0 | 44.0 | 23.8 | 26.6 |
| Exell | | 33.6 | 46.4 | 40.9 | 66.3 | 70.0 | 45.2 |
| Kroeber | | 28.1 | 31.0 | 23.3 | 49.6 | 42.5 | 32.0 |
| Williams | | 49 | 44 | 41 | 69 | 71 | 49 |
| Preston | DISSIMILARITY | 0.79 | 0.77 | 0.86 | 0.60 | 0.68 | 0.76 |
| Dem. knot % | | 84.3 | 86.9 | 94.7 | 72.0 | 86.5 | 84.7 |

From the above figures it may be concluded that according to the Jaccard, Soerensen, Kroeber, Preston and demarcation knot formulas the closest affinity is between Sao Tomé and Principe. According to the Exell and Williams formulas the affinity between Sao Tomé and Annobon is slightly greater than for Sao Tomé and Principe. In our example Annobon has an impoverished Sao Tomé flora which is best expressed by Exell and Williams. All formulas agree that the weakest alliance is between Fernando Po and Annobon except Exell's which gives the lowest similarity value for Fernando Po and Sao Tomé.

This example shows that there is fair but not complete agreement between the conclusions to which the various approaches lead. Anybody asked to judge the data in the matrix without using formulas would in my opinion decide that Sao Tomé and Principe show the closest affinity and Fernando Po and Annobon the weakest, and would probably find it hard to evaluate the affinities between the other islands as these would be found to be of approximately the same order. This is exactly what must be concluded from

Jaccard's, Soerensen's, Kroeber's, Preston's, and demarcation knot figures, which hence agree best with intuition.

Besides numerical data it is also necessary to know what taxa are involved. In the above example for instance it could be that Annobon has a flora of mainly widespread shore plants and that Fernando Po and Sao Tomé are the only islands with a considerable number of montane species which they have in common. They may agree in the absence of certain families etc. Such qualitative data must be incorporated in the floristic evaluation of the areas compared.

Then, if no absolute value can be given to the similarity and dissimilarity coefficients, I prefer to use one of the non-analytical formulas that can easily be calculated.

In discussing the distribution spectra of the various islands I make use of the 'demarcation knot %' formula, to allow comparisons with my preliminary analysis. In addition I give a survey of the floristic affinities between all islands using Kroeber's formula, which I think should be preferred as it takes into consideration both the poorer and the richer of the two areas compared.

10. Mechanical elaboration of data

The tabular form in which the distribution data are given (see Appendix) enables one to make corrections and to consult it easily at any time. To work out the results and to put them in a surveyable form was an immense task. The following computations had to be made:

- a) The total number of genera revised and unrevised.
- b) The sum of the various distribution and dispersal types and their percentage.
- c) The sum and percentage of distribution and dispersal type for each island group (distribution and dispersal spectra).
- d) Detailed additional information for each distribution type, such as: the number of genera of type 1 that are amphi-Pacific; the number of type 4 that centre in Malesia; the number of New Caledonian endemics that have affinities with Australian taxa etc.
- e) The number of genera that each island group has in common with any other (revised and unrevised genera).
- f) The strength of the demarcation knot and floristic affinity between each of the island groups employing different formulas.
- g) Other complex calculations, such as: The number of Solomons genera that do not occur elsewhere in the Pacific; the number of genera in the whole of SE. Polynesia and how many of these occur in Hawaii.

It is clear that the sorting out of so many data and the performance of the numerous calculations involved calls for some mechanical device. All data that can be found in the Appendix were transferred to I.B.M. punch cards, one card being used for every genus. A code system was devised for the available data. To give a few examples: if the genus was revised a 1 was punched in column 5, if not revised a 0 was punched. Columns 10—11 were used for the distribution types. A much finer distinction was made than in the text. In type 1 nine subtypes were distinguished, for instance 01 denoting truly ubiquitous genera such as *Cyperus*, 02 strictly pantropical ones (*Conarus*) and 06 genera restricted to both sides of the Pacific (amphi-Pacific) not centering in either New or Old World (*Citronella*). Among the endemic genera distinction was made between genera allied to widely distributed taxa, e.g. *Dissochondrus* allied to *Setaria* which was coded as

Table 2. — Survey and definition of distribution types.

-
1. World-wide and transpacific genera, occurring at least in the Indo-Australian and American tropics. Fig. 17 and 18.
 - 1 a. Wide temperate or bipolar genera. A variant of type 1, in the tropics as a rule montane. Fig. 19.
 2. Northern temperate to subtropical (Holarctic and Boreal) genera. Fig. 20.
 3. Eurasiatic temperate to subtropical genera. A variant of the former, not represented in America. Fig. 21.
 4. Old World genera, represented in all Old World continents. Fig. 22.
 - 4 a. Indo-Australian genera, differs from foregoing in being absent from Africa. Fig. 23.
 5. Indo-Malesian genera, occurring in Asia and Malesia, not in Australia, but some found in Africa. Fig. 24.
 - 5 a. Malesian genera, not or hardly represented in Asia or Australia. Fig. 25.
 - 5 b. E. Malesian genera, like former, but in Malesia restricted to the eastern part (New Guinea, Moluccas, etc.). Fig. 26.
 6. Australian genera, not or hardly in Asia or Malesia. Fig. 27.
 - 6 a. Australian-Papuan genera, represented in both Australia and (E.) Malesia, not distinctly centering in either. Fig. 28.
 7. Pacific Subantarctic genera, extratropical and montane tropical parts of South America and Indo-Australia. Fig. 29.
 - 7 a. Indian Subantarctic genera, occurring from Africa to the Pacific, not in America or Indo-Malesia. Fig. 30.
 - 7 b. Pan-Subantarctic genera, counterpart of type 2: southern temperate and subtropical, tropical-montane. Fig. 31.
 8. Pacific widespread genera, at least in two Pacific island groups. Fig. 32.
 - 8 a. Pacific endemic genera, confined to one island or island group in the Pacific. Fig. 33.
 9. American genera, some extending to the Old World across the Atlantic Ocean but not reaching Indo-Australia. Fig. 34.
-

56; genera with Malesian affinity (*Gouldia*) by 59, and those without clear relationships as 63 (*Lactoris*). Columns 14—25 were used for the 12 geographical units outside, and columns 26—61 for the units inside the Pacific. A 0 was punched to denote absence and a 1 for presence. Where necessary other punchings were used. In column 14 e.g. a 1 meant Africa generally, a 6 Madagascar only and a 9 Seychelles only.

All above mentioned calculations were performed at the University Computing Centre ('Centraal Reken Instituut') at Leyden. The time saved by using a computer for this type of work is considerable, an additional advantage being the greater accuracy attained. The time taken to prepare the punched cards, to write and test the program and print the final output was three months. To sort out all the data and make the numerous calculations would have cost me at least a year and a headache!

IV. RESULTS

1. Distribution types spectra

In the following survey the 'distribution types spectrum' of each island group and its affinity will be discussed. These are based on all genera. For facilitating the visualisation of the figures in the distribution types spectra I have added table 2 (here opposite), in which the distribution types have been concisely defined. At the end of this paragraph the figures based on the 'revised taxa' only as condensed in table 5 will be presented for comparison.

The 1666 genera and other taxa are segregated according to their distribution types as follows (the figures for revised taxa are added in brackets):

| Type | Number of genera | Percentage |
|--------|------------------|--------------|
| 1 | 299 (39) | 17.9 (11.3) |
| 1 a | 64 (6) | 3.8 (1.7) |
| 2 | 37 (5) | 2.2 (1.4) |
| 3 | 17 (2) | 1.0 (0.6) |
| 4 | 145 (38) | 8.7 (11.0) |
| 4 a | 121 (22) | 7.3 (6.4) |
| 5 | 144 (30) | 8.6 (8.7) |
| 5 a | 50 (15) | 3.0 (4.3) |
| 5 b | 88 (20) | 5.3 (5.8) |
| 6 | 100 (24) | 6.0 (7.0) |
| 6 a | 70 (25) | 4.2 (7.2) |
| 7 | 47 (21) | 2.8 (6.1) |
| 7 a | 15 (2) | 0.9 (0.6) |
| 7 b | 18 (8) | 1.1 (2.3) |
| 8 | 69 (32) | 4.1 (9.3) |
| 8 a | 243 (44) | 14.6 (12.8) |
| 9 | 139 (12) | 8.3 (3.5) |
| Totals | 1666 (345) | 99.8 (100.0) |

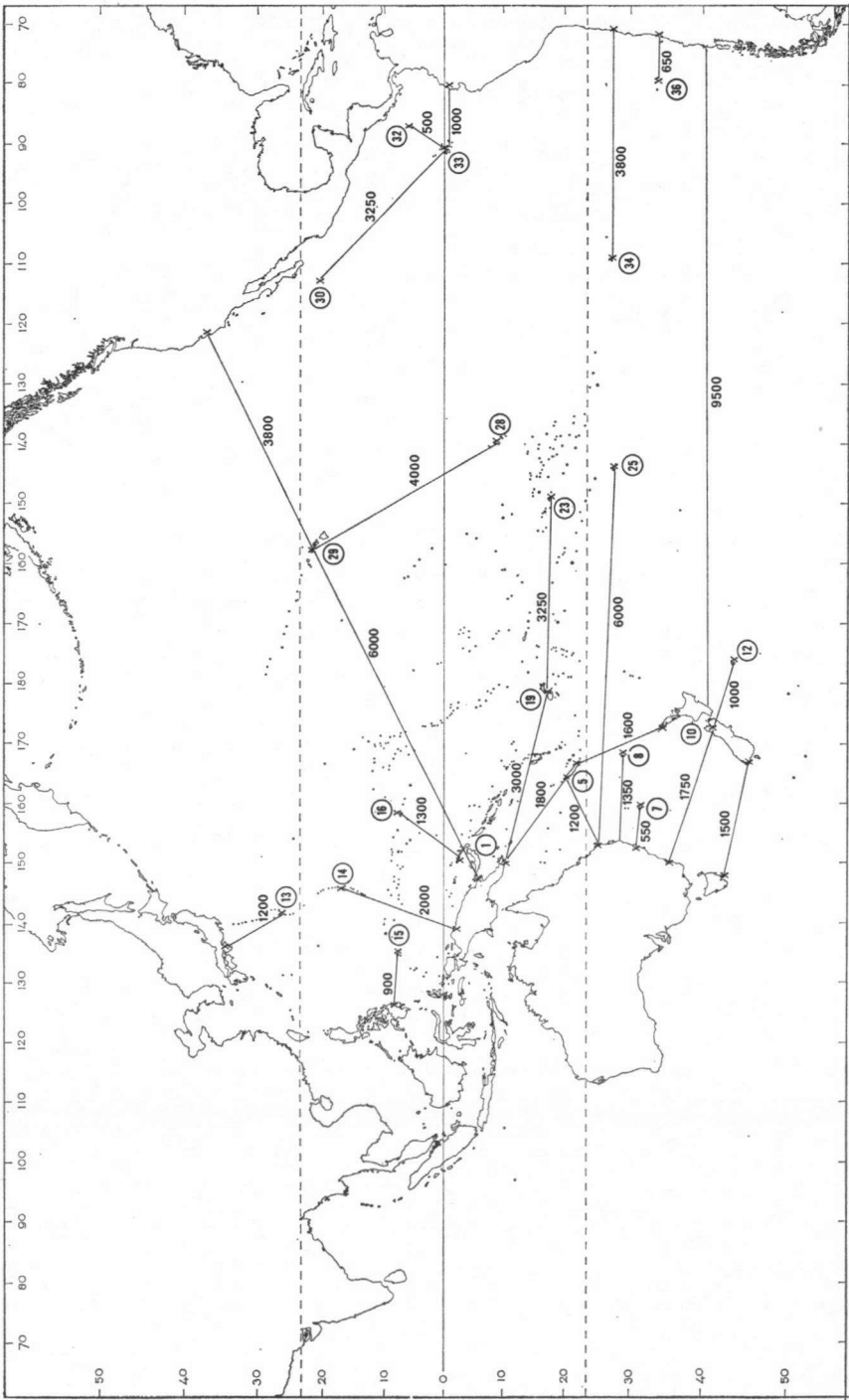


Fig. 36. Some distances between Pacific island groups and surrounding continental areas in kilometres. For names of island groups (encircled figures) see fig. 16.

When discussing the various distribution spectra the number of genera in each of the distribution types should always be considered.

An interesting thing revealed by this survey is the fact that the Old World (type 4), Malesian (types 5 a and 5 b), Subantarctic (types 7 and 7 b) and Pacific (type 8) taxa have been best revised. Widespread (types 1, 1 a and 2) and American (type 9) taxa are least revised.

For each of the islands or island groups I have given approximate data on position, size and altitude. These have been derived from the Times Atlas, 'Pacific Islands Year-book' (Robson, 1950, 1959) and Van Balgooy (1960, 1969). To facilitate orientation the distances between some Pacific island groups and some distances to continental areas is given in fig. 36. At the end of the discussion on each island group the most important literature about the group in question is given.

1. Bismarcks, 1—6° S, 146—154° E, 45,000 sq.km, 2400 m

Collections made by the Forestry Department at Lae and by the Noona Dan expedition in 1963, as far as results have become available, have raised the total number of genera from 514 in 1960 to 632 at present. Several of these are 'herbarium records' not to be found in literature.

| Type | Number | % |
|-------|--------|-------|
| 1 | 196 | 31.0 |
| 1 a | 2 | 0.3 |
| 2 | 3 | 0.5 |
| 3 | 1 | 0.2 |
| 4 | 107 | 16.9 |
| 4 a | 83 | 13.0 |
| 5 | 103 | 16.3 |
| 5 a | 34 | 5.4 |
| 5 b | 52 | 8.2 |
| 6 | 4 | 0.6 |
| 6 a | 35 | 5.6 |
| 7 | 4 | 0.6 |
| 7 a | 0 | — |
| 7 b | 4 | 0.6 |
| 8 | 3 | 0.5 |
| 8 a | 1 | 0.2 |
| 9 | 0 | — |
| Total | 632 | 100.1 |

What I wrote of the phytogeographic status of the Bismarcks in 1960 can almost be repeated here. The Bismarcks very clearly belong to the Paleotropics and more specifically to the Malesian Region. The number of genera limited to the Old World (types 3, 4, 4 a, 5, 5 a, 5 b, 6, 6 a & 7 a) is 419 or 66.3 % of the total. Of these again 189 or 30 % are Malesian (types 5, 5 a & 5 b). Of the genera in types 4 & 4 a there are 31 centering in Malesia (5 %). Floristic affinities are particularly strong with New Guinea with which this group has all but five genera in common. It is further emphasized by the strong representation of E. Malesian genera (type 5 b). Of the c. 1400 New Guinean genera (van Balgooy, 1969) c. 800 are unknown from the Bismarcks. Although this figure will no doubt decrease after further exploration of the Bismarcks, which are among the least explored islands of the Pacific, there will always be this strong, one-sided, discrepancy between the two floras. Exactly the same situation is encountered in the Loyalties and

New Caledonia. The Bismarcks have a flora that is an impoverished version of the New Guinean one as is to be expected from its much smaller size and lower altitude. The Australian element is weak, as is the Pacific one. All Pacific genera (type 8) are also represented in Malesia and the single endemic genus *Clymenia-Rut.* is closely allied to the Indo-Malesian *Citrus*. All four Australian genera (type 6) occur also in New Guinea.

There are no American taxa (type 9) but among the 'wides' (type 1) there are 15 (2.4 %) that centre in America (e.g. *Heliconia-Mus.*).

Relations with Pacific island groups are strongest with the Solomons, with which they have 501 genera in common. Hence 130 of the Bismarck genera are unknown from the Solomons; conversely 152 Solomons genera are unknown from the Bismarcks, or 282 out of a total of 783, giving a demarcation knot percentage of 36.2 %. No other nearby island group, however, has a comparably rich flora. With Micronesia as a whole (Marianas and Carolines) totaling 414 genera the Bismarcks have 309 genera in common. This is approximately the same relation as exists with the New Hebrides of which 298 out of 396 genera also occur in the Bismarcks. Demarcation knots with regard to Micronesia and New Hebrides amount to 58.0 and 59.2 % respectively.

In conclusion it may be stated that the subordination of the Bismarcks in the E. Malesian Province as suggested in 1960 is entirely confirmed by the present figures.

Literature: Diels et al. (1930), Hemsley (1885), Lauterbach (1911), Peckel (1945), M. Record (1945), Schumann (1898), Schumann & Lauterbach (1901, 1905).

2. Solomons, 5—11° S, 154—162° E, 40,000 sq.km, 2850 m

Despite the great increase in the number of genera now known from the islands (431 in 1960 against 654 now) I see no reason to alter my conclusions on their floristic status. The resemblance of the Bismarck and Solomons spectra is striking. There are 431 genera confined to the Old World, i.e. 66 % of the total. Relations with Malesia are equally strong, viz. 200 genera of type 5, 5 a & 5 b (30.6 %), and of the Paletropical genera (type 4 & 4 a) there are 30 (4.6 %) that centre in Malesia. Again there is a strong link with New Guinea expressed in a high percentage of type 5 b, 10.1 %, which is higher than found for the Bismarcks, but there are 17 Solomons genera that are not represented in New Guinea. Hence the 'individuality' of the Solomons is stronger than

| Type | Number | % |
|-------|--------|-------|
| 1 | 189 | 28.9 |
| 1 a | 3 | 0.5 |
| 2 | 3 | 0.5 |
| 3 | 0 | — |
| 4 | 108 | 16.5 |
| 4 a | 80 | 12.2 |
| 5 | 95 | 14.5 |
| 5 a | 39 | 6.0 |
| 5 b | 66 | 10.1 |
| 6 | 6 | 0.9 |
| 6 a | 37 | 5.7 |
| 7 | 3 | 0.5 |
| 7 a | 0 | — |
| 7 b | 5 | 0.8 |
| 8 | 17 | 2.6 |
| 8 a | 3 | 0.5 |
| 9 | 0 | — |
| Total | 654 | 100.0 |

that of the Bismarcks. This is also emphasized by the presence of three endemic genera: *Allowoodsonia-Apoc.*, *Kajewskiella-Rub.*, *Whitmorea-Icac.* and the presence of 17 Pacific genera of which nine are unknown from Malesia. Several other genera have been described as endemic but in the meantime have been reduced or have been found elsewhere.

Relations with Australia are as weak as in the Bismarcks: there are six genera belonging to type 6.

Here also there are no genera of type 9, but 13 genera of type 1 have their centre in America and the endemic *Allowoodsonia* is according to its author, Markgraf (1967), allied to *Malouettia*, a Neotropical-W. African genus, making a total of 14 genera or 1.8%.

The Solomons have retained their position as an important eastward and northward terminus: 162 Solomons genera (24.9 %) are unknown from the islands to its East, against 97 out of 431 (22.5 %) in 1960.

With the surrounding island groups the following relations exist: with the Bismarcks (632 genera) they have 501 genera in common, with the E. Carolines 197 out of 228, with the St. Cruz Is. 121 out of 126, with the New Hebrides 328 out of 396, with Fiji 358 out of 476, and finally with New Caledonia 332 out of 655 genera. The E. Carolines and St. Cruz floras are so small that the demarcation knot value will be affected too much by the size discrepancy. Leaving these island groups out of consideration, it is found that relations are strongest with the Bismarcks: the demarcation knot is as has already been seen 36.2 %. New Caledonia has 323 genera not in the Solomons and the Solomons 322 genera not in New Caledonia, i.e. 645 genera confined to either group out of a total of 977, making a demarcation knot of 66.2 %. The demarcation knots with the New Hebrides and Fiji can be calculated as 54.6 and 53.6 %. The floristic relations with the latter islands are thus of about equal strength. Bearing in mind that the demarcation knot value is exaggerated by the discrepancy in size of the floras it may be said that as regards floristic alliance with the New Hebrides and Fiji the Solomons are intermediate between New Caledonia and the Bismarcks.

In conclusion I maintain my former opinion that the Solomons form a separate district of the E. Malesian floristic Province.

3. St. Cruz Is., 10–12° S, 166° E, c. 800 sq.km, 1000 m

| Type | Number | % |
|-------|--------|-------|
| 1 | 41 | 32.5 |
| 1 a | 0 | — |
| 2 | 0 | — |
| 3 | 0 | — |
| 4 | 24 | 19.0 |
| 4 a | 16 | 12.7 |
| 5 | 15 | 11.9 |
| 5 a | 6 | 4.8 |
| 5 b | 10 | 7.9 |
| 6 | 2 | 1.6 |
| 6 a | 7 | 5.6 |
| 7 | 2 | 1.6 |
| 7 a | 0 | — |
| 7 b | 0 | — |
| 8 | 3 | 2.4 |
| 8 a | 0 | — |
| 9 | 0 | — |
| Total | 126 | 100.0 |

The St. Cruz Is. flora is very much underexplored. I expect that the actual number of genera on the islands will be more than doubled if the group is explored on the same scale as the Solomons. The genera now known from the islands are mainly based on collections made by the Forestry Department at Honiara, which understandably concentrated on woody specimens. This explains why so few genera of herbaceous families such as the *Gramineae*, *Cyperaceae* and *Orchidaceae* are known from St. Cruz.

In 1960 the situation was so much worse, with only c. 20 genera on record, that for purely geographic reasons I reckoned the islands among the New Hebrides. I hinted, however, at the possibility that the islands might have stronger links with the Solomons.

The distribution spectrum based on the still incomplete records shows great correspondence with that of the Bismarcks, the Solomons and, as will be seen later, the E. Carolines. The total number of Gerontogean genera is 80 (63.6 %) of which 31 (24.6 %) are Malesian. Only three genera, *Geissois-Cun.* (type 6), *Chelonospermum-Sapot.* and *Crossostylis-Rhiz.* (both type 8) are absent from New Guinea. The Neotropical element is also missing and only two genera of type 1 centre in America.

The number of genera is now sufficient to allow the testing of floristic affinities with the New Hebrides and the Solomons. Of the 126 St. Cruz genera the majority (90) are known from both. Of the remaining 36 genera 31 are known from the Solomons but not from the New Hebrides. As 23 of these are known from other parts of the Pacific (New Caledonia, Fiji, Samoa, etc.) at least some of these may eventually turn up in the New Hebrides. Examples: *Connarus-Conn.*, *Loeseneriella-Celastr.*, *Maranthes-Ros.* and *Tristellateia-Malp.* Conversely there are only four genera known from the St. Cruz and the New Hebrides that are absent from the Solomons. These include *Geissois-Cun.*, *Agathis-Conif.* and *Manilkara-Sapot.*, all tree-genera not likely to have been overlooked. The fourth genus is *Amyema-Loranth.* This genus turns up repeatedly in preliminary identification lists from the Solomons, but so far all material that have come to my notice was found to belong to *Amylotheca*. I would be surprised, however, if genuine *Amyema* remains among the Solomons absentees as it has been found in the Bismarcks too. Only one genus, or rather a section, is unreported from both New Hebrides and Solomons: *Podocarpus* § *Polypodiopsis-Conif.*

Despite the striking absence of four St. Cruz genera from the Solomons I think their number is so small that the islands can best be treated as a subdistrict of the Solomons. The absence of 31 genera from the New Hebrides that are closer geographically is even more striking.

The combined Solomons/St. Cruz flora of 659 genera would be an east- and northward terminus for 175 genera or 26.5 % of the total.

Literature (Solomons & St. Cruz): Fosberg (1940), Guillaumin (1948b), Guppy (1887), Hemsley (1895), Rechinger (1908—1913), Walker (1948), Whitmore (1966), numerous papers by Merrill and Perry.

4. New Hebrides, 13—20° S, 166—170° E, 15,000 sq.km, 1800 m

The state of exploration of the New Hebrides has hardly improved since my preliminary report was written. The latest census was by Guillaumin (1948) and few new finds have been recorded since. Besides, I am none too confident about the proper identification of some taxa. A large-scale exploration of the islands as recently carried out on the Solomons is badly needed. The more so as the islands occupy a crucial position in the West Pacific, being the pivot between such important island groups as the Solomons, Fiji and New Caledonia.

A comparison of the floristic spectrum with the three island groups discussed so far is

| Type | Number | % |
|-------|--------|-------|
| 1 | 134 | 33.8 |
| 1 a | 4 | 1.0 |
| 2 | 1 | 0.3 |
| 3 | 0 | — |
| 4 | 77 | 19.4 |
| 4 a | 48 | 12.2 |
| 5 | 35 | 8.8 |
| 5 a | 15 | 3.8 |
| 5 b | 19 | 4.8 |
| 6 | 15 | 3.8 |
| 6 a | 24 | 6.1 |
| 7 | 0 | — |
| 7 a | 0 | — |
| 7 b | 3 | 0.8 |
| 8 | 21 | 5.3 |
| 8 a | 0 | — |
| 9 | 0 | — |
| Total | 396 | 100.1 |

highly interesting. The total number of Gerontogean genera is 233 or 59 %, which is lower than hitherto found. It appears that the percentage of the widespread Old World genera (types 4 & 4 a) has remained unchanged, but there is an appreciable decrease in all Malesian type genera (types 5, 5 a & 5 b), totaling 69 or 17.4 %, which is compensated by a proportional increase in Australian (type 6), Australian-Papuan (type 6 a) and Pacific genera (type 8). All genera once described as endemic for the New Hebrides have in the past years been relegated to the synonymy of others of wider distribution.

The special floristic relation expressed in the percentage of genera in type 5 b and 6 a is still comparatively strong but is much less than for Bismarcks and Solomons.

There are 25 genera unknown from New Guinea, of which 12 belong to the Pacific element (type 8).

Again type 9 is not represented, but there are 10 genera (2.5 %) of type 1 that centre in America.

With the other surrounding archipelagoes the following relations can be found. With the Solomons they have 328, with New Caledonia 315, with the Loyalties 193, and with Fiji 307 genera in common. The Solomons (654 genera) and New Caledonia (655 genera) have comparably rich floras. The demarcation knots of 54.6 and 58.6 % give a reliable indication of the closer alliance of the New Hebrides flora to that of the Solomons. The floras of Fiji (476 genera) and the Loyalties (262 genera) are much poorer. Demarcation knots are here 45.6 and 58.5 %. If the combined flora of Fiji, Samoa and Tonga is taken as a whole there are 509 genera of which 317 also occur in the New Hebrides, giving a demarcation knot of 46 %. This figure can be compared with the demarcation knot with the Loyalties as the flora size relations Loyalties—New Hebrides and New Hebrides—Fiji/Samoa/Tonga are approximately of the same order. Thus floristic alliance appears to be stronger with the latter, despite the greater distance. Although the Solomons flora is richer than the combined Fiji/Samoa/Tonga flora the demarcation knot with the Solomons is so much larger it may be safely considered that the New Hebrides are more closely allied to the islands to the East than to the Solomons despite the presence of an intermediate island group (St. Cruz) and their greater proximity to the Solomons than to Fiji. This also appears from the distribution spectra, which apart from a higher percentage in type 6 is almost identical to that of e.g. Samoa. The strait between the Solomons and

the New Hebrides can be regarded as the eastern boundary of the E. Malesian Province.

Literature: Guillaumin (1931, 1932, 1933, 1935, 1937, 1948a).

5. **New Caledonia**, 19—23° S, 163—168° E, 22,000 sq.km, 1650 m

6. **Loyalties**, 20—23° S, 169—170° E, 2000 sq.km, 75 m

| New Caledonia | | | Loyalties | | Combined | |
|---------------|--------|-------|-----------|-------|----------|-------|
| Type | Number | % | Number | % | Number | % |
| 1 | 186 | 28.4 | 112 | 42.7 | 186 | 28.4 |
| 1 a | 17 | 2.6 | 8 | 3.1 | 17 | 2.6 |
| 2 | 2 | 0.3 | 0 | — | 2 | 0.3 |
| 3 | 0 | — | 0 | — | 0 | — |
| 4 | 99 | 15.1 | 53 | 20.2 | 99 | 15.1 |
| 4 a | 61 | 9.3 | 34 | 13.0 | 61 | 9.3 |
| 5 | 23 | 3.6 | 6 | 2.3 | 23 | 3.6 |
| 5 a | 8 | 1.2 | 3 | 1.1 | 9 | 1.4 |
| 5 b | 14 | 2.1 | 2 | 0.8 | 14 | 2.1 |
| 6 | 51 | 7.8 | 12 | 4.6 | 51 | 7.8 |
| 6 a | 36 | 5.5 | 15 | 5.7 | 36 | 5.5 |
| 7 | 9 | 1.4 | 2 | 0.8 | 9 | 1.4 |
| 7 a | 4 | 0.6 | 1 | 0.4 | 4 | 0.6 |
| 7 b | 8 | 1.2 | 4 | 1.5 | 8 | 1.2 |
| 8 | 31 | 4.7 | 4 | 1.5 | 31 | 4.7 |
| 8 a | 104 | 15.9 | 6 | 2.3 | 104 | 15.8 |
| 9 | 2 | 0.3 | 0 | — | 2 | 0.3 |
| Total | 655 | 100.0 | 262 | 100.0 | 656 | 100.1 |

In my preliminary report I showed that the Loyalties flora is an impoverished New Caledonian one. According to the latest data there is only one genus, *Cyrtandra-Gesn.* (type 5 a) occurring in the Loyalties and not in New Caledonia. The demarcation knot is 60.3 %. Although many of the typical genera of New Caledonia are absent from the Loyalties the floristic break between the two is one-sided so that there is no reason to treat them separately. The six genera in type 8 a are not real endemics, they include amongst others *Oxera-Verb.* and *Phelline-Aquif.* that are best developed on the main island. Even considering the much smaller size and lower elevation of the Loyalties it is surprising that so many genera with scores of species on New Caledonia are not even represented by a single species on the Loyalties.

Comparison of the distribution spectrum of New Caledonia with those of the island groups so far discussed yields the following differences. There is an increase in the wide temperate genera (type 1 a) which is to be expected from its more southerly position. Also the number of Subantarctic taxa (type 7 & 7 b) has increased.

The number of Old World genera is 296 (45.3 %) which means a distinct reduction compared with the Bismarcks, Solomons, etc. Of these genera the Malesian taxa (type 5, 5 a & 5 b) number 45 (6.9 %), a strong decrease. But also the percentage of widespread Palearctic genera (type 4 & 4 a) is less. On the other hand there is a significant increase in Australian genera (type 6): 51 genera (7.8 %).

Again there is a high percentage of Pacific genera, but even more striking is the enormous number of 104 (c. 16 %) endemic genera (type 8 a). What adds greatly to the

exceptional character and appearance of great antiquity of the flora is the fact that most of these endemics belong to what are generally believed to be primitive families such as *Coniferae*, *Myricaceae*, *Monimiaceae*, *Palmae*, *Proteaceae*, *Winteraceae*, etc. and few of the putatively modern families like *Acanthaceae*, *Campanulaceae*, *Compositae*, *Labiatae*, etc. (see e.g. Takhtajan, 1969, and Muller, 1970). Many are taxonomically so isolated that some have been proposed as monotypic families and others could be if anything scientific or practical were to be gained by it. As it is such genera as *Amborella*, *Canacomyrica*, *Maxwellia*, *Oceanopapaver*, *Oncotheca* and *Paracryphia* are taxonomically isolated from the other genera of the families to which they have been assigned.

There are two genera belonging to type 9: *Epistephium*-*Orch.* and *Lindenia*-*Rub.* (the latter also on Fiji), which form the puzzling American element.

In view of the difficulties of a satisfactory floristic classification of New Caledonia some of the distribution types will now be considered in greater detail.

Of the 186 genera assigned to type 1 53 are ubiquitous and 122 are pantropical. Of these 12 have a distinct centre in the Old and 14 in the New World. Of 11 amphi-Pacific genera (occurring on either side of the Pacific only) there are two centering in the Old and three in the New World.

Of the 99 genera in type 4 17 centre in Asia or Malesia and two in Australia; of type 4 a out of 61 genera there are 16 centering in Asia/Malesia and five in Australia. Of the Indo-Malesian (type 5) and Malesian (type 5 a & 5 b) genera numbering 46 in total there are seven genera that also reach Australia, conversely of the 51 Australian genera (type 6) there are 21 that penetrate into Malesia. Of the 36 Australian-Papuan genera (type 6 a) most are evenly represented in E. Malesia and Australia, three genera have their greatest development in the latter and three in the former. Of the 31 Pacific genera (type 8) 15 do not occur in either Australia or Malesia (one of these reaches South America), five are represented on both, six only in Malesia, and five only in Australia.

The 104 endemic genera show the following features: 8 are allied to widespread genera, 22 have their closest affinity with widespread Old World genera, two have their nearest relative in Indo-Malesia, nine in Australia, and 15 are allied with Pacific or Subantarctic genera. Three endemics have Neotropical affinities and no less than 46 are of obscure alliance.

From the above figures it is clear that New Caledonia has American affinities, mostly 'hidden' among both widespread and endemic genera, distribution types 1 and 8 a respectively. Yet it very distinctly belongs to the Old World flora.

It is rather difficult to decide whether it should be subordinated with the Australian or the Indo-Malesian Region as the affinities to both are approximately equal. On the whole there are slightly more Malesian or Malesia-centred Paleotropical genera than Australian or Australia-centred Paleotropical genera.

The number of genera found on New Caledonia and New Guinea unknown from Australia is 59, whereas, conversely, there are 50 genera known from New Caledonia and Australia unreported from New Guinea. On the other hand there are 13 taxa known exclusively from Australia and New Caledonia and only one (*Sloanea* § *Antholoma-Elaeoc.*) from New Caledonia and New Guinea. Both figures could be increased by the addition of some more genera that are not strictly exclusive as e.g. *Castanospermum*-*Leg.* (Australia, New Caledonia, New Hebrides) or *Dubouzetia*-*Elaeoc.* (New Caledonia, New Guinea and Moluccas), or by taking up more sections of genera. Of *Nothofagus*-*Fag.* the subsection *Bipartitae* is confined to New Caledonia and New Guinea. This would, however, not change the picture, viz. that there are more taxa exclusive to New Caledonia and Australia than to it and New Guinea.

New Caledonia has 331 genera in common with the Solomons (654 genera), 308 with the New Hebrides (396), 326 with Fiji (476), and 121 with New Zealand (344). This gives us demarcation knots of 66.2, 58.6, 59.5 and 86.2 % respectively. It is clear from these figures that affinity is weakest with New Zealand, although the demarcation knot is slightly exaggerated on account of the smaller size of the New Zealand flora. The New Caledonia/Solomons demarcation is strong; weaker but still sharp is the demarcation with Fiji and the New Hebrides.

All the above considerations lead us to the conclusion that New Caledonia cannot be subordinated with either the Malesian or the Australian Regions. None of the other Pacific island groups, the Loyalties excepted, can be regarded a subdivision of the New Caledonian flora. I see no other solution than to give New Caledonia the rank of Region. The only argument against this is the relatively small size of the flora, but this is to be expected from its small land surface in relation to the other regions. At the same time it makes the presence of so many endemics of great taxonomic interest even more striking.

Literature (New Caledonia & Loyalties): Däniker (1929—1933), Guillaumin (1911, 1948b, and numerous papers between 1909 and 1969).

7. Lord Howe I., 31° 30' S, 159° E, 13 sq.km, 850 m

The Lord Howe I. flora can certainly be regarded as well-known at genus level.

The tendency towards a decreasing percentage of Old World genera found in New Caledonia is continued in the Lord Howe I. flora. There are 53 Gerontogean genera

| Type | Number | % |
|-------|--------|-------|
| 1 | 51 | 37.0 |
| 1 a | 15 | 10.9 |
| 2 | 1 | 0.7 |
| 3 | 0 | — |
| 4 | 15 | 10.9 |
| 4 a | 12 | 8.7 |
| 5 | 0 | — |
| 5 a | 0 | — |
| 5 b | 0 | — |
| 6 | 16 | 11.6 |
| 6 a | 7 | 5.1 |
| 7 | 2 | 1.5 |
| 7 a | 3 | 2.2 |
| 7 b | 6 | 4.3 |
| 8 | 6 | 4.3 |
| 8 a | 4 | 2.9 |
| 9 | 0 | — |
| Total | 138 | 100.1 |

(38.5 %). This decrease is caused by the complete absence of any (Indo-)Malesian genera (types 5, 5 a & 5 b), the percentage of Australian genera, however, is considerably larger in proportion to that of New Caledonia. The only links with (E.) Malesia are through genera of type 6 a, such as *Bubbia-Wint.* and *Pandorea-Bign.* The most remarkable Old World genus is *Dietes-Irid.* (originally described as *Moraea*) which otherwise only occurs in S. Africa and which despite doubts, see e.g. Paramonof (1963), I consider to be indigenous. Paramonof suggested that the Lord Howe I. species was introduced by the early whalers in the eighteenth century, but I do not see why whalers would introduce a plant of ornamental value and not really useful plants. I also fail to see how an entirely new

species could develop in so short a time, as *Dietes robinsoniana* appears to be amply distinct from its African congeners.

Another peculiar feature is the presence of four endemic genera on this tiny piece of land so close to a continent (550 km from Australia). They are *Negria*-*Gesn.* allied to the New Caledonian *Depanthus* and the New Zealandic *Rhabdothermus*, and the palm genera *Hedyscepe*, *Howeia* and *Lepidorrhachis*. *Howeia* is allied to the Indo-Malesian *Pinanga*, *Hedyscepe* belongs to the tribe *Ptychospermae* ranging from the Mascarenes to Melanesia, and *Lepidorrhachis* belongs to the *Clinostigmeae* which centre in Melanesia.

Floristically Lord Howe I. clearly belongs to the Australian Region. It has, however, no particularly strong affinities with any of the surrounding floras. It has 129 taxa in common with Australia, 102 with New Caledonia, 75 with New Zealand, and 66 with Norfolk I. This decrease in common genera is correlated with the sizes of the various floras. The Three King Is. off the N. cape of New Zealand, which have not been listed separately, have 53 out of 113 genera in common with Lord Howe I. Hardly any of the typical Australian genera, e.g. in the *Leguminosae*, *Proteaceae* or *Myrtaceae*, are represented in Lord Howe I., despite the greater proximity and richness of the Australian flora. Only one genus, *Westringia*-*Lab.*, is confined to both Australia and Lord Howe I. There is one genus, *Carmichaelia*-*Leg.*, confined to Lord Howe I. and New Zealand, none to Lord Howe I. and Norfolk I. or New Caledonia.

The presence of four endemic genera gives the island a marked 'individuality', especially considering the small land surface. I think the best solution is to maintain Lord Howe I. as a district within the New Zealand Subregion, as I suggested in 1960.

Literature: Green (1970), Maiden (1898), Oliver (1917).

8. Norfolk I., 29° S, 168° E, 40 sq.km, 310 m

Though poorer and less peculiar than the Lord Howe I. flora much of what was written about that island is also true for Norfolk I. There are no Indo-Malesian genera among the Old World taxa which number 36 (34.6 %).

Here also the number of Australian genera is relatively high: nine (8.7 %). There are more Pacific genera, but there is only one endemic genus, *Streblorrhiza*-*Leg.*, closely allied to *Clianthus*, with which it has been united by some. Hutchinson (1964) places it in the

| Type | Number | % |
|-------|--------|-------|
| 1 | 39 | 37.5 |
| 1 a | 12 | 11.5 |
| 2 | 1 | 1.0 |
| 3 | 0 | — |
| 4 | 14 | 13.5 |
| 4 a | 9 | 8.7 |
| 5 | 0 | — |
| 5 a | 0 | — |
| 5 b | 0 | — |
| 6 | 9 | 8.7 |
| 6 a | 3 | 2.9 |
| 7 | 3 | 2.9 |
| 7 a | 1 | 1.0 |
| 7 b | 4 | 3.8 |
| 8 | 8 | 7.7 |
| 8 a | 1 | 1.0 |
| 9 | 0 | — |
| Total | 104 | 100.2 |

Carmichaelieae, which centre in New Zealand. Norfolk I. is also clearly part of the Australian Region. Of the 104 taxa 98 also occur in Australia, it has in common 66 with Lord Howe I., 82 with New Caledonia, 39 with the Kermadecs, and 62 with New Zealand. No genus is limited to Australia and Norfolk I., but *Lagunaria-Malv.* is known from E. Australia, Lord Howe and Norfolk Is. A section of *Exocarpos-Sant.* is confined to Norfolk I. and New Caledonia. *Ileostylus-Lorant.*, *Phormium-Lil.*, and *Rhopalostylis-Palm.* are known from Norfolk I. and New Zealand, the last two also extend to the Chathams and Kermadecs + Chathams respectively. On the whole the floristic links of Norfolk I. are stronger with New Zealand than with Australia.

Norfolk I. can best be regarded as a district within the New Zealand Subregion of the Australian Region, similar to Lord Howe I.

Literature: Laing (1915), Maiden (1903), Turner, Smithers & Hoogland (1968).

9. Kermadecs, 29—32° S, 178° 30' W, 32 sq.km, 520 m

The distribution spectrum can best be described as being intermediate between those of Lord Howe and Norfolk Is. on the one hand and that of New Zealand on the other. There are more 'temperate' (types 1 a, 7 & 7 b) and less Old World genera than in the former. Of the 13 genera (21.3 %) seven belong to type 6. Again (Indo-)Malesian taxa are absent. The difference with New Zealand is that there are no endemic genera.

| Type | Number | % |
|-------|--------|-------|
| 1 | 23 | 37.7 |
| 1 a | 12 | 19.7 |
| 2 | 1 | 1.6 |
| 3 | 0 | — |
| 4 | 1 | 1.6 |
| 4 a | 2 | 3.3 |
| 5 | 0 | — |
| 5 a | 0 | — |
| 5 b | 0 | — |
| 6 | 7 | 11.5 |
| 6 a | 2 | 3.3 |
| 7 | 4 | 6.6 |
| 7 a | 1 | 1.6 |
| 7 b | 4 | 6.6 |
| 8 | 4 | 6.6 |
| 8 a | 0 | — |
| 9 | 0 | — |
| Total | 61 | 100.1 |

The Kermadecs clearly belong to the New Zealand Subregion. They have 54 genera in common with New Zealand and only 21 with Tonga which is as far away but poorer (263 against 344 in New Zealand).

I did not list the Three Kings Islands separately but it is interesting to give the floristic relations of these with Lord Howe I., Norfolk I. and Kermadecs and of these three groups with each other. This can be seen on the following matrix in which the figure in brackets represents the number of genera in each island group, the figures above the line the genera in common between two island groups and the figures below the line the demarcation knot percentage.

| | Lord Howe | Norfolk | Kermadecs | Three Kings |
|-------------------|-----------|---------|-----------|-------------|
| Lord Howe (138) | | 66 | 38 | 53 |
| Norfolk (104) | 62.5 | | 39 | 41 |
| Kermadecs (61) | 76.4 | 69.2 | | 48 |
| Three Kings (113) | 73.2 | 76.7 | 61.9 | |

These figures show that Lord Howe I. is floristically nearest Norfolk I., and that Kermadec is most strongly related with the Three Kings Is.

The Kermadecs, despite the absence of endemic genera, should have the status of separate district within the New Zealand Subregion as there are still seven genera unknown from New Zealand proper, amongst others *Boehmeria-Urt.*, *Homalanthus-Euph.* and *Imperata-Gram.*

Literature: Allan (1961), Cheeseman (1888), Oliver (1909).

10. New Zealand, 34—47° S, 166—178° E, 265,000 sq.km, 3750 m

The percentage of temperate genera as can be expected from its position and elevation is higher than in any of the locations hitherto discussed. The number of temperate 'wides'

| Type | Number | % |
|-------|--------|-------|
| 1 | 47 | 13.7 |
| 1 a | 55 | 16.0 |
| 2 | 4 | 1.2 |
| 3 | 2 | 0.6 |
| 4 | 9 | 2.6 |
| 4 a | 12 | 3.5 |
| 5 | 1 | 0.3 |
| 5 a | 0 | — |
| 5 b | 1 | 0.3 |
| 6 | 62 | 18.0 |
| 6 a | 16 | 4.6 |
| 7 | 44 | 12.8 |
| 7 a | 11 | 3.2 |
| 7 b | 18 | 5.2 |
| 8 | 23 | 6.7 |
| 8 a | 39 | 11.3 |
| 9 | 0 | — |
| Total | 344 | 100.0 |

(type 1 a) exceeds that of the general 'wides' (type 1). Some northern hemisphere genera penetrate into New Zealand, e.g. *Sparganium-Sparg.* Both these and the temperate wides are very often also represented in the mountains of Malesia (*Euphrasia-Scroph.*, *Coriaria-Coriar.*)

A curious case is that of the very small genus *Yoania-Orch.*, recently added to the New Zealand record (Hatch, 1963). The genus is otherwise only known from E. Asia, the Himalayas and N. Africa, and is hence placed in type 3. *Yoania* belongs to the saprophytes and these are as a rule short-lived and flower rarely, so that they may easily be overlooked. They may also be unintentionally introduced, but this is unlikely in the case of *Yoania* as

the New Zealand representative is a distinct species. In the saprophytic family *Burmanniaceae* there are also many cases of disjunct distribution (See Jonker, 1938).

Another remarkable phenomenon is the presence of 11 genera in type 7 a which extend to Africa but do not occur in Indo-Malesia. They are mostly also found in Australia, e.g. *Cassinia-Comp.* or *Pelargonium-Geran.*, but two are not: *Bulbinella-Lil.* and *Lobelia § Mezliera-Camp.*

Of the 115 Gerontogean genera (33.3 %) 62 belong to type 6. The majority of these are confined to the temperate parts of Australia, including Tasmania, five are confined to that island and New Zealand. Of the 62 Australian genera 21 also extend to Malesia. There are 21 Paleotropical genera (types 4 & 4 a) but the Indo-Malesian element only (types 5, 5 a & 5 b) comprises two genera (0.6 %).

The 44 Pacific Subantarctic genera (type 7) are mostly about equally well represented in the Old and New World, e.g. *Nothofagus-Fag.* and *Oreobolus-Cyp.*; seven genera clearly centre in the west (*Hebe-Scroph.*) and eight in the east part of their range (*Microseris-Comp.*), eight do not extend west of New Zealand, in other words are unknown from New Guinea or Australia, e.g. *Griselinia-Corn.* Of the 23 Pacific genera (type 8) 13 do not occur in either Australia or Malesia, five are found in both, one only in Malesia (*Ascarina-Chlor.*) and three only in Australia; one reaches South America (*Astelia § Asteliopsis-Lil.*).

The 39 endemic taxa (type 8 a) show the following affinities: eight are allied to widespread genera, four are of general Paleotropical affinity, three have their affinity in the African sector (including *Hectorella-Hect.* allied to *Lyallia* from Kerguelen and nearby islands), two in Australia and 10 have their nearest ally among Pacific or Subantarctic genera. These include among others *Hachettea-Balanoph.* allied to the New Caledonian *Dactylanthus*. The affinity of 12 genera is obscure.

Its relations to surrounding continental floras can be expressed in figures as follows: with Australia (+ Tasmania) it has 270 taxa in common, with New Guinea 175, and with South America 161.

As has been seen there are eight genera confined to South America and New Zealand, one is known only from the latter and New Guinea, and 34 are known exclusively from Australia (+ Tasmania) and New Zealand (+ Subantarctic islands).

Despite the existence of a strong demarcation (the two have 121 genera in common, which yields a demarcation knot of 86.2 %) New Zealand has special relations with New Caledonia through the presence of *Libocedrus s.s.-Conif.*, *Knightia-Prot.* and *Xeronema-Lil.* confined to both.

The relations with New Guinea, considering the difference in latitude, and that with South America, considering the distance, are certainly remarkable. On the whole, however, both the figures presented above and the distribution types spectrum suggests that New Zealand should be considered as floristically forming part of the Australian Region. Yet the absence of so many typical Australian taxa, e.g. among the *Leguminosae*, *Myrtaceae*, *Proteaceae*, etc., and the strong endemic element indicate relative independence from this continent. I suggest therefore that New Zealand s.l. should be ranked as a subregion within the Australian Region. This subregion should also include Lord Howe I., Norfolk I., Kermadecs, Chathams, and the Subantarctic islands of New Zealand, as will be presently shown.

Literature: Allan (1961), Cheeseman (1906, 1925), Hooker (1864—1867).

11. Subantarctic islands of New Zealand

| | |
|---|-----------------------------|
| Antipodes 50° S, 179° E, 60 sq.km, 150 m | } total land area 775 sq.km |
| Aucklands 51° S, 166° E, 600 sq.km, 660 m | |
| Campbell 52° S, 169° E, 112 sq.km, 500 m | |
| Snares 48° S, 166° 30' E, 3 sq.km, 150 m | |

| Type | Number | % |
|-------|--------|-------|
| 1 | 6 | 7.7 |
| 1 a | 23 | 29.5 |
| 2 | 0 | — |
| 3 | 0 | — |
| 4 | 0 | — |
| 4 a | 0 | — |
| 5 | 0 | — |
| 5 a | 0 | — |
| 5 b | 0 | — |
| 6 | 10 | 12.8 |
| 6 a | 5 | 6.4 |
| 7 | 14 | 18.0 |
| 7 a | 3 | 3.8 |
| 7 b | 9 | 11.5 |
| 8 | 6 | 7.7 |
| 8 a | 2 | 2.6 |
| 9 | 0 | — |
| Total | 78 | 100.0 |

The Subantarctic islands of New Zealand can best be discussed together with the Chathams, as they have many features in common.

In my preliminary paper I did not list them separately, moreover, I also included Macquarie I. On reconsideration of the data I have excluded the latter on account of its poor flora consisting of widespread Subantarctic genera. The Chathams are sufficiently distinct floristically to enter them separately.

Literature: Allan (1961), Chilton (1909).

12. Chatham Is., 44° S, 177° W, 950 sq.km, 300 m

In both the Chathams and the Subantarctic islands of New Zealand many distribution types are not or poorly represented. In the latter the Old World element is made up only of types 6, 6 a and 7 a, totaling 18 genera (24 %). The percentages of wide temperate genera (type 1 a) and the southern temperate taxa are even higher than found in New Zealand; this is in accordance with the more southerly position of the islands.

The two endemic genera are *Stilbocarpa-Aral.*, of obscure alliance, and *Pleurophyllum-Comp.* which is near *Celmisia* and *Olearia*, both well represented in New Zealand. Apart from these two only *Plantago* § *Palaeopsyllium-Plant.* is not known from New Zealand proper. On the other hand nine taxa are unknown from Australia, which shows that within the Australian Region the Subantarctic islands should be subordinated to the New Zealand Subregion.

The Chathams have a richer and somewhat more varied distribution spectrum. As in the Subantarctic islands the majority of the 30 Old World taxa (28.4 %) belong to type 6, but they also include two tropical taxa: *Gastrodia* (type 4) and *Sarcochilus* (type 4 a), both Orchids. The only endemic genus, *Myosotidium-Borag.* is closely allied to the wide tem-

| Type | Number | % |
|-------|--------|------|
| 1 | 15 | 14.2 |
| 1 a | 30 | 28.3 |
| 2 | 1 | 0.9 |
| 3 | 1 | 0.9 |
| 4 | 1 | 0.9 |
| 4 a | 1 | 0.9 |
| 5 | 0 | — |
| 5 a | 0 | — |
| 5 b | 0 | — |
| 6 | 18 | 17.0 |
| 6 a | 4 | 3.8 |
| 7 | 10 | 9.4 |
| 7 a | 4 | 3.8 |
| 7 b | 10 | 9.4 |
| 8 | 10 | 9.4 |
| 8 a | 1 | 0.9 |
| 9 | 0 | — |
| Total | 106 | 99.8 |

perate *Myosotis*. It is the only genus not represented in New Zealand. *Coxella-Umb.* described as a Chatham endemic was very recently placed in the synonymy of *Aciphylla* by Dawson (1968).

Despite the strong agreement of their distribution types spectra there is no special floristic alliance with the Subantarctic islands; they have 46 genera in common, giving a demarcation knot of 67.3 %.

Both island groups belong to the New Zealand subregion, but as separate districts.

Literature: Allan (1961), Cheeseman (1925).

13. Bonin Is., 24—28° N, 141—142° E, 105 sq.km, 900 m

The distribution spectrum of the Bonins is quite different from any of the other Pacific island groups. This is caused by the high percentages of genera in type 2 and 3, northern

| Type | Number | % |
|-------|--------|------|
| 1 | 78 | 47.6 |
| 1 a | 5 | 3.0 |
| 2 | 19 | 11.6 |
| 3 | 13 | 7.9 |
| 4 | 21 | 12.8 |
| 4 a | 13 | 7.9 |
| 5 | 5 | 3.0 |
| 5 a | 0 | — |
| 5 b | 0 | — |
| 6 | 1 | 0.6 |
| 6 a | 3 | 1.8 |
| 7 | 1 | 0.6 |
| 7 a | 0 | — |
| 7 b | 2 | 1.2 |
| 8 | 1 | 0.6 |
| 8 a | 2 | 1.2 |
| 9 | 0 | — |
| Total | 164 | 99.8 |

temperate and Asiatic genera, most of which do not occur elsewhere in the Pacific.

The total number of Gerontogean genera is 56 (34 %).

Relations with Malesia are weak. Typical Malesian genera (types 5 a & 5 b) are absent and there are only five Indo-Malesian genera (3 %).

In view of the strong demarcation from the other Pacific islands it is rather surprising to find an Australian genus (*Myoporum-Myop.*), three Australian-Papuan genera (*Bleekeria-Apoc.*, *Metrosideros-Myrt.* and *Santalum* § *Santalum-Sant.*) and a Pacific genus (*Clinostigma-Palm.*) on these islands. *Metrosideros* and *Santalum* are curiously absent from Micronesia. The presence of southern temperate taxa (*Schoenus-Cyp.*, type 7, *Dianella-Lil.* and *Machaerina-Cyp.*, type 7 b) is also remarkable for an island group so far North.

There are two endemic genera, *Dendrocacalia-Comp.*, which is near the widespread *Senecio*, and *Boninia-Rut.* allied to the Paleotropical *Evodia*.

The Bonins are floristically very distinct from the adjacent Marianas with which they have 84 genera in common; 93 being limited to the former and 129 to the latter, the demarcation knot can be calculated as 71.5 %. They obviously form part of the East Asiatic Region, but as six genera, including the two endemics, are unknown from Japan, China, etc., it should certainly rank as a separate district.

Literature: Hara & Kanai (1959), Masamune (1931), Tuyama (1953, and numerous other papers).

14. Marianas, 13—20° N, 144—146° E, 650 sq.km, 950 m

Comparing the distribution spectra of the Marianas with that of the Bonins a number of striking differences become apparent. The genera belonging to types 2 and 3 so prominent in the Bonins are here altogether absent.

| Type | Number | % |
|-------|--------|-------|
| 1 | 118 | 54.9 |
| 1 a | 1 | 0.5 |
| 2 | 0 | — |
| 3 | 0 | — |
| 4 | 48 | 22.3 |
| 4 a | 23 | 10.7 |
| 5 | 8 | 3.7 |
| 5 a | 3 | 1.4 |
| 5 b | 3 | 1.4 |
| 6 | 2 | 0.9 |
| 6 a | 2 | 0.9 |
| 7 | 1 | 0.5 |
| 7 a | 0 | — |
| 7 b | 2 | 0.9 |
| 8 | 3 | 1.4 |
| 8 a | 1 | 0.5 |
| 9 | 0 | — |
| Total | 215 | 100.0 |

The Old World genera number 89 (41.4 %), of these the Paleotropical 'wides' (types 4 & 4 a) are most numerous and form 33 % of the total. There is a stronger Indo-Malesian element (types 5—5 b) than in the Bonins, viz. 14 genera (6.5 %) which is still rather weak in comparison with the Carolines as will be shown in the next paragraph.

The only endemic genus, *Guamia-Annon.*, is allied to *Oncodostigma*, known from E. Malesia and the New Hebrides. It is the only genus absent from Malesia.

There are three taxa known from the Marianas and the Philippines not recorded for New Guinea and conversely seven from the Marianas and New Guinea unknown from the Philippines. This points to a slightly stronger alliance with New Guinea.

As has been seen there is a strong demarcation with the Bonins, which has become known as the 'Hosokawa line'. Demarcations with the Carolines are strikingly weaker. Of the 215 Marianas genera 46 do not occur in the W. Carolines, of the 336 W. Carolines genera 167 are not recorded from the Marianas. This gives a demarcation knot of 55.8 %. With the E. Carolines (228 genera) the figures are respectively 82 and 95, yielding a demarcation knot of 57.1 %. Both percentages are much lower than the 71.5 % found for the Bonin/Marianas demarcation.

The above leads us to regard the Marianas as a district of the E. Malesian Province.

Literature: Hosokawa (1934), Kanehira (1933, 1935), Merrill (1914), Safford (1905). Numerous papers by Hosokawa and Kanehira.

15. West Carolines, 7—10° N, 134—142° E, 700 sq.km, 240 m

16. East Carolines, 1—9° N, 143—163° E, 700 sq.km, 750 m

| West Carolines | | | East Carolines | |
|----------------|--------|-------|----------------|-------|
| Type | Number | % | Number | % |
| 1 | 131 | 39.0 | 96 | 42.1 |
| 1 a | 0 | — | 0 | — |
| 2 | 0 | — | 0 | — |
| 3 | 0 | — | 0 | — |
| 4 | 72 | 21.4 | 51 | 22.4 |
| 4 a | 42 | 12.5 | 24 | 10.5 |
| 5 | 46 | 13.7 | 23 | 10.0 |
| 5 a | 14 | 4.2 | 12 | 5.5 |
| 5 b | 14 | 4.2 | 11 | 4.8 |
| 6 | 4 | 1.2 | 1 | 0.4 |
| 6 a | 7 | 2.1 | 5 | 2.2 |
| 7 | 1 | 0.3 | 1 | 0.4 |
| 7 a | 0 | — | 0 | — |
| 7 b | 2 | 0.6 | 1 | 0.4 |
| 8 | 3 | 0.9 | 3 | 1.3 |
| 8 a | 0 | — | 0 | — |
| 9 | 0 | — | 0 | — |
| Total | 336 | 100.0 | 228 | 100.0 |

In view of the many common features exhibited by their distribution spectra the two island groups can best be treated together. The W. Carolines are by far the richest of the Micronesian island groups: their number of genera exceeds both that of the Marianas and the E. Carolines by over 100 genera.

As in the Marianas there are no genera of types 2 and 3. There is, however, a strong increase in the Old World genera: 199 (59.2 %) for the W. Carolines and 127 (55.8 %) for the E. Carolines. Again the percentage of Paletropical genera (types 4 & 4 a) is high: 33.9 and 32.9 %, but at the same time there is a strong increase in Malesian taxa (types 5—5 b): 22.1 and 20.3 %.

All three Pacific genera of the W. Carolines are also found in Malesia (*Badusa-Rub.*,

Meryta-Aral. and *Soulamea-Sim.*), but two of the three of the E. Carolines are unknown from Malesia (*Clinostigma-Palm.* and *Lepinia-Apoc.*). Several endemic genera have at various times been described for the Carolines, but all have disappeared in the synonymy of wider distributed genera.

The W. Carolines have 17 genera also known from New Guinea but not from the Philippines and four genera also known from the Philippines but not from New Guinea. For the E. Carolines these figures are eight and two. Both are hence more closely allied to New Guinea.

Of the 336 genera in the W. Carolines 145 do not occur in the E. Carolines, conversely 37 of the 228 E. Carolines genera are unknown from the W. Carolines. This gives a demarcation knot of 48.8 %, a lower figure than found for the Marianas/W. Carolines (55.8 %) and the Marianas/E. Carolines (57.1 %).

Both island groups show approximately the same floristic relation with New Guinea as the Bismarcks.

Literature: Glassman (1952), Kanehira (1933, 1935), Volkens (1901). Numerous papers by Hosokawa and Kanehira.

17. West Central Polynesia, 10° S—15° N, 160—180° E, 450 sq.km, 25 m

18. East Central Polynesia, 12° S—6° N, 150—178° W, 600 sq.km, 12 m

| West Central Polynesia | | | East Central Polynesia | |
|------------------------|--------|------|------------------------|-------|
| Type | Number | % | Number | % |
| 1 | 46 | 69.7 | 29 | 72.5 |
| 1 a | 0 | — | 0 | — |
| 2 | 0 | — | 0 | — |
| 3 | 0 | — | 0 | — |
| 4 | 16 | 24.2 | 8 | 20.0 |
| 4 a | 2 | 3.0 | 1 | 2.5 |
| 5 | 2 | 3.0 | 2 | 5.0 |
| 5 a | 0 | — | 0 | — |
| 5 b | 0 | — | 0 | — |
| 6 | 0 | — | 0 | — |
| 6 a | 0 | — | 0 | — |
| 7 | 0 | — | 0 | — |
| 7 a | 0 | — | 0 | — |
| 7 b | 0 | — | 0 | — |
| 8 | 0 | — | 0 | — |
| 8 a | 0 | — | 0 | — |
| 9 | 0 | — | 0 | — |
| Total | 66 | 99.9 | 40 | 100.0 |

For the same reasons as for the W. and E. Carolines, the western and eastern island groups of Central Polynesia are discussed together, both are coral island groups and have a poor flora, but the western group is richer on account of the fact that a number of genera extend to the Marshalls by way of the Carolines.

Both have a very restricted distribution types spectrum, characterized by the absence of many types. The genera present are nearly all of very wide distribution (types 1 and 4). Most are pantropical or Paleotropical. Only four genera in each are of somewhat restricted

distribution. These are *Hemigraphis-Acanth.* (type 5), *Ochrosia-Apoc.* (type 4 a), *Procris-Urt.* (type 5) occurring in both, and *Rhaphidophora-Arac.* (type 4 a) only in W. Central Polynesia.

The islands thus show very little 'individuality', though still clearly belonging to the Old World flora. They could perhaps best be appended to the Malesian Region as sub-districts.

Literature: Chock & Hamilton (1962), Christophersen (1927), Degener & Gillaspay (1955), Sachet (1957), Taylor (1950).

19. Fiji Is., 15—20° S, 177° E—178° W, 18,500 sq.km, 1300 m

The flora of the Fiji Is. is one of the better known floras of the Pacific, mainly through the numerous publications of Dr A. C. Smith (1936—onwards).

| Type | Number | % |
|-------|--------|-------|
| 1 | 167 | 35.1 |
| 1 a | 5 | 1.1 |
| 2 | 0 | — |
| 3 | 1 | 0.2 |
| 4 | 80 | 16.8 |
| 4 a | 57 | 12.0 |
| 5 | 46 | 9.7 |
| 5 a | 22 | 4.6 |
| 5 b | 27 | 5.7 |
| 6 | 7 | 1.5 |
| 6 a | 20 | 4.2 |
| 7 | 2 | 0.4 |
| 7 a | 1 | 0.2 |
| 7 b | 4 | 0.8 |
| 8 | 26 | 5.5 |
| 8 a | 10 | 2.1 |
| 9 | 1 | 0.2 |
| Total | 476 | 100.1 |

There is great similarity between the distribution spectra of Fiji and, as we will see later, those of Samoa and Tonga and that of the New Hebrides.

The number of Old World genera is 261 (54.8 %), among which 95 (20 %) Malesian taxa (types 5—5 b). This percentage of Malesian genera is higher than that found in the New Hebrides (17.4 %). On the other hand both Australian (type 6) and Australian-Papuanian genera (type 6 a) are more weakly represented: 1.5 and 4.2 against 3.8 and 6.1 %.

Pacific and endemic genera (types 8 & 8 a) are well represented. Of the former 15 out of 26 do not reach either Australia or New Guinea, 10 extend to New Guinea, five to Australia.

There is a fairly high number of endemic genera. About a century ago the number of Fijian 'endemics' was believed to be 50—60, but most have in the meantime been reduced to the synonymy of widespread genera or have proved to occur elsewhere. Only 10 are now left, five of these belonging to the *Rubiaceae*: *Hedstromia* and *Readea* are near the pantropical *Psychotria*, *Sukunia* is closely allied to the Paleotropical *Gardenia*, *Gillespiea* to the Pacific *Calycosia*, and *Squamellaria* to the E. Malesian *Hydnophytum*. Of the three *Palmae* *Neoveitchia* is rather isolated, *Goniocladus* and *Taveunia* belong to the mainly Melanesian tribe *Clinostigmeae*. *Pimia* is a very rare and probably extinct *Ster-*

culiacea of uncertain affinities. *Degeneria*, though clearly a member of the *Magnoliales* and placed in the *Winteraceae* by Hutchinson (1964), is by many authors considered to form a separate family, the *Degeneriaceae*.

Some genera call for special attention. *Koelreuteria-Sapin.* (type 3) is otherwise only known from China and Formosa, 7500 km away. *Cossignia* (type 7 a) of the same family is known from Fiji, New Caledonia and with a disjunction of c. 14,000 km in the Mascarenes. As puzzling is the distribution of *Lindenia-Rub.* (type 9), found in the Neotropics but represented with one species in New Caledonia and Fiji, another great disjunction of c. 11,000 km.

Both the distribution spectrum and the fact that Fiji has 430 taxa in common with New Guinea and 348 with Australia indicate that the islands belong to the Indo-Malesian Region.

Relations with the surrounding island groups are as follows: the New Hebrides have 308 of its 396 genera, Samoa 281 out of 302, Tonga 246 out of 263 and New Caledonia has 326 out of 655 in common with Fiji. The demarcation knots can be calculated as 45.3, 43.3, 50.1 and 59.5 % respectively. These figures are not quite comparable. Fiji has a number of genera approximately intermediate between that of New Caledonia on the one hand and the New Hebrides and Samoa on the other. Demarcation is strongest with New Caledonia, despite the fact that 13 genera known from both are unknown elsewhere in the Pacific. Of these *Acmopyle-Conif.*, *Piliocalyx-Myrt.* and *Storckiella-Leg.* are confined to both. Fiji could best be united in one Province with New Hebrides, Samoa and Tonga, as will be further argued in the paragraph on Tonga.

The importance of Fiji as eastern terminus for many Phanerogam genera has been observed by A. C. Smith (1955). He stated that 101 out of 445 Fijian genera reach their eastern limit in the islands (22.7 %). According to my data the figures are 124 out of 476 genera (26.1 %) which, however, includes a number of subgeneric taxa.

Literature: Gillespie (1930, 1931, 1932), Parham (1964), Seemann (1865—1873), A. C. Smith (1936, 1942, and numerous other papers).

20. Samoa, 13—15° S, 168—173° W, 3100 sq.km, 1850 m

| Type | Number | % |
|-------|--------|-------|
| 1 | 118 | 39.1 |
| 1 a | 1 | 0.3 |
| 2 | 1 | 0.3 |
| 3 | 0 | — |
| 4 | 56 | 18.5 |
| 4 a | 42 | 13.9 |
| 5 | 25 | 8.3 |
| 5 a | 14 | 4.7 |
| 5 b | 15 | 5.0 |
| 6 | 2 | 0.7 |
| 6 a | 9 | 3.0 |
| 7 | 1 | 0.3 |
| 7 a | 0 | — |
| 7 b | 3 | 1.0 |
| 8 | 14 | 4.7 |
| 8 a | 1 | 0.3 |
| 9 | 0 | — |
| Total | 302 | 100.1 |

The Samoa islands will probably still yield a number of new genus records, although they cannot be expected to be as rich as Fiji on account of their smaller size.

As stated in the paragraph on Fiji the distribution spectra of the New Hebrides, Fiji, Samoa and Tonga are very similar. The number of Old World genera is 163 (54 %) which is of about the same order as found in Fiji. Of these the Malesian taxa (types 5—5 b) number 54 (17.9 %), slightly less than in Fiji, but equal to the New Hebrides.

There is also a decrease in the percentage of Australian and Australian-Papuan taxa.

Of the 14 Pacific genera (type 8) 10 are absent from New Guinea and Australia.

The only genus still regarded as endemic is *Sarcopygme-Rub.* which according to Dr Bakhuizen van den Brink (personal communication) is near the pantropical *Morinda* and not a member of the *Naucleae*, as originally believed.

There are no genera of peculiar distribution as in Fiji. The demarcation with Fiji has been discussed. Relations with Tonga and the role of Samoa as eastward terminus in the Pacific will be discussed in the next paragraph on Tonga.

Literature: Christophersen (1935, 1938), Lauterbach (1908), Reinecke (1896, 1898), Setchell (1924), Yuncker (1945).

21. Tonga & Niue, 18—22° S, 170—175° W, 900 sq.km, 1000 m

The Tonga flora is fairly well collected and described. Yet a few novelties at genus level can perhaps be expected.

| Type | Number | % |
|-------|--------|-------|
| 1 | 118 | 44.9 |
| 1 a | 1 | 0.4 |
| 2 | 0 | — |
| 3 | 1 | 0.4 |
| 4 | 55 | 20.9 |
| 4 a | 36 | 13.7 |
| 5 | 13 | 4.9 |
| 5 a | 9 | 3.5 |
| 5 b | 2 | 0.8 |
| 6 | 3 | 1.1 |
| 6 a | 12 | 4.6 |
| 7 | 0 | — |
| 7 a | 0 | — |
| 7 b | 4 | 1.5 |
| 8 | 9 | 3.4 |
| 8 a | 0 | — |
| 9 | 0 | — |
| Total | 263 | 100.1 |

The distribution spectrum is almost similar to that of Samoa but there are more 'wides' (type 1). The number of Gerontogean genera is 131 out of 263 (49.8 %) which gives a lower percentage than found for Samoa; the Malesian taxa (types 5—5 b) show a sharp drop from 20 % in Fiji and 17.9 % in Samoa to 9.2 % in Tonga. Tonga is also poorer in Pacific genera and there are no endemics.

In the paragraphs on the Kermadecs and New Zealand it has already been seen that a strong floristic break exists between these islands and Tonga, with demarcation knots of 93.1 and 92.2 %.

The relations between Fiji, Samoa and Tonga will now be discussed. Fiji (476 genera) and Samoa (302) have 282 genera, Fiji and Tonga (263) have 245 and Samoa and Tonga

have 209 genera in common. The demarcation knots between the island groups can be calculated as 43.3, 50.1 and 41.6 % respectively. The combined Samoa/Tonga flora consists of 356 genera of which 323 are also known from Fiji. As has been seen Fiji has 308 genera in common with the New Hebrides (396 genera). The demarcation knot against Samoa/Tonga is 36.5 and 45.3 % against the New Hebrides, which indicate a stronger affinity of Fiji with the former.

The importance of Fiji as eastern terminus in the Pacific has been shown. Many more genera extend to just beyond Fiji and reach either Samoa or Tonga or both. Out of the 356 Samoa/Tonga genera 144 (40.4 %) reach their easternmost limit in these islands. There is hence a strong floristic break to the East of Samoa/Tonga, approximately corresponding to the andesite line. A similar strong break was found to the East of the Solomons. These two breaks mark the western and eastern boundaries of what I propose as the E. Melanesian Province, which comprises the New Hebrides, Fiji, Samoa and Tonga.

Literature: Hemsley (1894), Hotta (1963, 1965), Hürlimann (1967), Yuncker (1943, 1959).

22. Cook Is., 19–22° S, 157–160° W, 250 sq.km, 660 m

Of this island group only one, Rarotonga, the highest and largest island, has been well explored.

| Type | Number | % |
|-------|--------|-------|
| 1 | 66 | 52.4 |
| 1 a | 0 | — |
| 2 | 1 | 0.8 |
| 3 | 1 | 0.8 |
| 4 | 28 | 22.2 |
| 4 a | 11 | 8.7 |
| 5 | 2 | 1.6 |
| 5 a | 3 | 2.4 |
| 5 b | 1 | 0.8 |
| 6 | 2 | 1.6 |
| 6 a | 4 | 3.2 |
| 7 | 0 | — |
| 7 a | 0 | — |
| 7 b | 2 | 1.6 |
| 8 | 5 | 4.0 |
| 8 a | 0 | — |
| 9 | 0 | — |
| Total | 126 | 100.1 |

Comparing the distribution spectrum with that of the islands to the West, a number of differences become apparent.

There is an increase in the percentage of 'wides' (type 1) and a decrease in Old World genera which for the Cook Is. number 52 (41.2 %). Only the percentage of type 4 has remained constant. The Indo-Malesian genera (types 5—5 b), already fewer in Tonga, undergo another drop: six genera (4.8 %).

There is not much difference in the representation of Australian, Australian-Papuan or Pacific taxa. Endemics are absent.

In the paragraph on Tonga it has already been seen that this island group (and Samoa) is an important eastward terminus. Of the 263 Tongan genera 105 are also known from the Cooks, of the 201 genera in the Societies 110 have also been recorded from the

Cooks. Expressed in demarcation knots the figures are 63.0 and 49.3 % respectively. It is clear that the Cook Is. are floristically much more allied to the Society Is. than to Tonga.

The Cook Is. have an impoverished Indo-Malesian flora lacking most of the typical elements still well represented in the islands to its West.

Literature: Cheesemann (1903), Wilder (1931).

23. Society Is., 16—18° S, 148—155° W, 1700 sq.km, 2250 m

The mountainous interiors of the islands, especially of Tahiti, probably still harbour a number of genera awaiting discovery. Such genera as *Fuchsia-Onagr.* and the recently

| Type | Number | % |
|-------|--------|-------|
| 1 | 86 | 42.8 |
| 1 a | 3 | 1.5 |
| 2 | 1 | 0.5 |
| 3 | 0 | — |
| 4 | 39 | 19.4 |
| 4 a | 19 | 9.5 |
| 5 | 9 | 4.5 |
| 5 a | 6 | 3.0 |
| 5 b | 3 | 1.5 |
| 6 | 2 | 1.0 |
| 6 a | 6 | 3.0 |
| 7 | 3 | 1.5 |
| 7 a | 0 | — |
| 7 b | 4 | 2.0 |
| 8 | 18 | 9.0 |
| 8 a | 2 | 1.0 |
| 9 | 0 | — |
| Total | 201 | 100.2 |

discovered *Oreobolus-Cyp.* have come from the almost inaccessible mountains. The distribution spectrum, though more diversified than that of the Cook Is., shows the same features. The number of Old World genera is 84 i.e. 41.8 %, the same percentage as found for the Cook Is. The Indo-Malesian genera (types 5—5 b) number 18 (9 %). This is approximately the Tonga figure but is much less than that of e.g. Fiji. Australian and Australian-Papuan elements are both weakly represented. The striking feature in the spectrum is the high representation of Pacific taxa (type 8), viz. 18 (9 %). Of these, 13 do not extend to Australia and Malesia, four reach both, and one (*Ascarina-Chlor.*) occurs also in Malesia. The two endemics, *Bonnierella-Aral.* and *Tahitia-Til.*, are allied to respectively the Paleotropical *Polyscias* and the Indo-Malesian *Berrya*.

There are no American taxa (type 9), but some genera assigned to other distribution types have their centre of species development in the New World. *Byttneria-Sterc.* (type 1) centres in the Neotropics. *Fuchsia-Onagr.* (type 7) has its focus in Andine South America, but is represented with four species in New Zealand and one in Tahiti; this species is most closely allied to the New Zealand ones.

The floristic relations of SE. Polynesia, including that of the Society Is., will be treated more fully at the end of the paragraph on Hawaii. It is now sufficient to say that the Society Is. still clearly form part of the Paleotropical flora, the closest affinity is with the Indo-Malesian Region.

Literature: Drake del Castillo (1893), Moore (1933, 1934, 1963), Nadeaud (1873), Papy (1951—1955).

24. Tubuai Is. (Austral), 22—24° S, 145—155° W, 125 sq.km, 430 m

These islands also are floristically insufficiently known.

The distribution spectrum is almost a replica of that of the Cook Is. What has been said of these is therefore also applicable to Tubuai.

| Type | Number | % |
|-------|--------|-------|
| 1 | 44 | 50.0 |
| 1 a | 0 | — |
| 2 | 1 | 1.1 |
| 3 | 0 | — |
| 4 | 21 | 23.9 |
| 4 a | 4 | 4.5 |
| 5 | 1 | 1.1 |
| 5 a | 3 | 3.4 |
| 5 b | 0 | — |
| 6 | 2 | 2.3 |
| 6 a | 2 | 2.3 |
| 7 | 0 | — |
| 7 a | 0 | — |
| 7 b | 3 | 3.4 |
| 8 | 7 | 8.0 |
| 8 a | 0 | — |
| 9 | 0 | — |
| Total | 88 | 100.0 |

The number of Old World genera is 33 i.e. 37.5 %, a slightly lower percentage than in the Cook Is. Among these are four (4.5 %) Indo-Malesian genera (types 5—5 b). A notable difference is the higher percentage of Pacific genera.

As will be elaborated in the next paragraph, Rapa I., geologically the end of a chain from the Cooks over Tubuai, is floristically very distinct from the other islands of this chain.

Of the 88 genera on record for Tubuai 68 are also known from the Cooks (with 126 genera), 79 are among the 201 known genera from the Society Is., and 44 also occur on Rapa (with 93 genera). The resulting demarcation knots are 53.4, 62.4 and 67.9 % respectively. The high value of the second figure is of course also due to the fact that the Society Is. flora is much richer.

Literature: Brown (1931, 1935).

25. Rapa I., 27° 30' S, 144° W, 40 sq.km, 600 m

In my preliminary analysis I already pointed to the rather unexpected composition of the Rapa spectrum. It shows an interesting deviation from the other islands of SE. Polynesia and resembles those of Lord Howe and Norfolk.

There are more genera of type 1 a than in the other SE. Polynesian islands. Of the 26 Old World genera (28 %) 19 are generally Paleotropical (types 4 & 4 a), four of these having their centre clearly in Asia or Malesia: *Balanophora*-*Balanoph.*, *Fagraea*-*Log.*, *Freycinetia*-*Pand.*, and *Premna*-*Verb.*, two are (Indo-)Malesian: *Eurya*-*Theac.* and *Serianthes*-*Leg.* The three Australian genera are: *Exocarpos* § *Exocarpos*-*Sant.*, *Haloragis*-*Halor.* and *Myoporum*-*Myop.*; the two Australian-Papuan ones: *Olearia*-*Comp.* and *Metrosideros*-*Myrt.*, the former with greatest specific development in Australia. The only genus in type 7 is *Hebe*-*Scroph.* with its focus in New Zealand. The representation of Pacific taxa is very strong; of the 12 (12.9 %) eight do not reach Australia and Malesia. They include such interesting genera as *Fitchia*-*Comp.* belonging to American-centred *Heliantheae*

(Carlquist, 1957), *Nesoluma-Sapot.* linking it to Hawaii, *Astelia* § *Asteliopsis-Lil.* centering in Hawaii but extending to New Caledonia and Patagonia. Three extend to New Zealand, Australia and Malesia, e.g. *Coprosma-Rub.*, one only to New Zealand and Australia: *Corokia-Sax.* The one endemic genus, *Metatrophis*, is of uncertain affinities. It was originally described in *Moraceae* (Brown, 1935) but was transferred to *Urticaceae* later (Corner, 1962).

| Type | Number | % |
|-------|--------|-------|
| 1 | 42 | 45.2 |
| 1 a | 7 | 7.5 |
| 2 | 1 | 1.1 |
| 3 | 0 | — |
| 4 | 15 | 16.1 |
| 4 a | 4 | 4.3 |
| 5 | 1 | 1.1 |
| 5 a | 1 | 1.1 |
| 5 b | 0 | — |
| 6 | 3 | 3.2 |
| 6 a | 2 | 2.2 |
| 7 | 1 | 1.1 |
| 7 a | 0 | — |
| 7 b | 3 | 3.2 |
| 8 | 12 | 12.9 |
| 8 a | 1 | 1.1 |
| 9 | 0 | — |
| Total | 93 | 100.1 |

What adds to the peculiarity of the Rapa I. flora is that many of the genera represented are widely isolated geographically. A few examples with the distribution type and nearest locality in brackets may illustrate this: *Corokia* (type 8, New Zealand), *Eurya* (type 5, Samoa), *Haloragis* (type 6, New Zealand), *Lysimachia-Prim.* (type 1 a, New Hebrides) and *Olearia* (type 6 a, New Zealand). Of the 93 taxa 17 are unknown from any of the SE. Polynesian island groups. Conversely 166 taxa from SE. Polynesia are unrecorded for Rapa. This and the relatively strong representation of Australian and Subantarctic elements made me decide to include Rapa in the New Zealand Province in my preliminary analysis. This, however, obscures the obvious relations with SE. Polynesia, notably with the Marquesas and Society Is. and even Hawaii. A few figures may illustrate that despite some striking links with the New Zealand sector the Rapa I. flora is on the whole more closely allied to that of SE. Polynesia. Rapa has in common with Lord Howe (out of 138 genera) 41, with Norfolk (104) 34, with New Zealand (344) 38, with Chatham (106) 18, with Cook (126) 56, with Society (201) 67, with Marquesas (113) 53, and with Hawaii (226) 52 taxa.

The island is as difficult as New Caledonia to fit into either the Australian or the Malesian Region: 16 of its genera do not occur in Australia and exactly as many are unknown from New Guinea.

I think the best solution is to place Rapa in the SE. Polynesian Province, to be discussed in the paragraph on Hawaii, as an anomalous district.

Literature: Brown (1931, 1935), Riley (1926).

26. North Tuamotus, 14—21° S, 137—149° W, 800 sq.km, 100 m

27. South Tuamotus, 21—25° S, 124—137° W, 50 sq.km, 450 m

| North Tuamotus | | | South Tuamotus | |
|----------------|--------|-------|----------------|------|
| Type | Number | % | Number | % |
| 1 | 44 | 62.9 | 47 | 58.0 |
| 1 a | 0 | — | 2 | 2.5 |
| 2 | 0 | — | 0 | — |
| 3 | 0 | — | 1 | 1.2 |
| 4 | 18 | 25.7 | 17 | 21.0 |
| 4 a | 2 | 2.9 | 2 | 2.5 |
| 5 | 1 | 1.4 | 1 | 1.2 |
| 5 a | 0 | — | 0 | — |
| 5 b | 0 | — | 0 | — |
| 6 | 1 | 1.4 | 1 | 1.2 |
| 6 a | 1 | 1.4 | 2 | 2.5 |
| 7 | 0 | — | 0 | — |
| 7 a | 1 | 1.4 | 0 | — |
| 7 b | 0 | — | 1 | 1.2 |
| 8 | 2 | 2.9 | 7 | 8.6 |
| 8 a | 0 | — | 0 | — |
| 9 | 0 | — | 0 | — |
| Total | 70 | 100.0 | 81 | 99.9 |

The northern group consisting of coral islands and atolls and the southern consisting of 'high islands' show great similarity in their distribution spectrum. Probably both will still yield a number of new genera in future.

In both there is a high percentage of 'wides'. The number of Old World genera is 24 (34.3 %) in the N. Tuamotus and also 24 (29.7 %) in the southern group. The majority belong to type 4, of these in the N. Tuamotus three centre in Asia or Malesia against one in Australia. In the S. Tuamotus the relation is two to one. Although there is no preponderance of Indo-Malesian over Australian elements as in Tubuai and Society Is. the affinity on the whole is with Malesia rather than with Australia.

The most puzzling genus in the N. Tuamotus is *Nesogenes-Verb.*, otherwise only known from Africa and Malagassy. The two Pacific taxa (type 8), *Hedyotis* § *Oceanica-Rub.* and *Pritchardia-Palm.*, do not reach either Australia or Malesia. In the S. Tuamotus seven taxa are of this type, two of these reach Australia and E. Malesia: *Coprosma-Rub.* and *Meryta-Aral.* There are no strict endemics and there are no American genera to counterbalance the decrease in Old World genera.

Literature: Brown (1931, 1935), Drake del Castillo (1893), St. John & Philipson (1962), Wilder (1934).

28. Marquesas, 8—11° S, 138—141° W, 1300 sq.km, 1200 m

This island group also doubtless harbours some unrecorded genera. A new genus was described only very recently.

Again the distribution spectrum shows a high percentage of 'wides'. The Old World genera number 32 (28.3 %), 19 of which belong to types 4 & 4 a and of these four centre in Asia or Malesia against one (*Alphitonia-Rhamn.*) in Australia. The five (Indo-)Malesian taxa are: *Dichrocephala-Comp.*, *Procris-Urt.* (type 5), *Cyrtandra-Gesn.*, *Inocarpus*, *Serianthes-*

| Type | Number | % |
|-------|--------|------|
| 1 | 62 | 54.9 |
| 1 a | 0 | — |
| 2 | 1 | 0.9 |
| 3 | 0 | — |
| 4 | 14 | 12.4 |
| 4 a | 5 | 4.4 |
| 5 | 2 | 1.8 |
| 5 a | 3 | 2.6 |
| 5 b | 1 | 0.9 |
| 6 | 4 | 3.5 |
| 6 a | 3 | 2.6 |
| 7 | 0 | — |
| 7 a | 0 | — |
| 7 b | 3 | 2.6 |
| 8 | 13 | 11.5 |
| 8 a | 2 | 1.8 |
| 9 | 0 | — |
| Total | 113 | 99.9 |

Leg. (type 5 a) and *Trimenia-Monim.* (type 5 b). Type 6 is represented by *Casuarina-Cas.*, *Commersonia-Sterc.*, *Nicotiana* § *Suaveolentes-Sol.* and *Gahnia* § *Gahnia-Cyp.* The first two taxa are represented by species widespread in the Old World. *Nicotiana* has its greatest species development in America but the species found in the Marquesas is a widespread one in the Pacific belonging to an exclusively Australian section. *Gahnia* is widespread from continental Asia and Australia and the Pacific. The Australian-Papuan genera are *Bleekeria-Apoc.*, *Decasynina-Lorant.*, and *Metrosideros-Myrt.*

As in the Society and Rapa Is. there is a strong Pacific element (type 8) consisting of 13 genera (11.5 %) of which 10 are unknown from either Malesia or Australia.

Of the two endemic genera *Cyrtandroidea* was originally described in the *Campanulaceae*, but Burt (1968) has recently shown that its correct place is in *Gesneriaceae* near *Cyrtandra*, widespread in Malesia and the Pacific, the other, the recently described *Lebronnecia-Malv.* (Fosberg & Sachet, 1966), is near the Hawaiian *Kokia*.

It is remarkable that also in this island group, nearer to America than any island group so far discussed, there is no representation of American genera (type 9). But among type 1 there are five genera centering in the New World against six in the Old World. As said above, the Marquesas *Nicotiana* is a widespread Pacific species belonging to an exclusively Australian section. Finally *Astelia* § *Asteliopsis-Lil.*, centering in Hawaii, extending west to New Caledonia and east to Patagonia, forms another 'indirect' link with the American flora. On the whole, however, there is no doubt that the islands form part of the Old World flora, as do all other islands of SE. Polynesia. This is in contrast to Brown's (1935) conclusion about the floristic status of the islands. He considered the Marquesas flora as almost entirely of American derivation. His highly prejudiced and peculiar reasoning was severely criticized by Merrill (1936) and Skottsberg (1956). See also p. 16.

Within SE. Polynesia the affinities of the Marquesas are strongest with the Societies, of which among 201 genera 96 are also known from the Marquesas.

Literature: Brown (1931, 1935), Drake del Castillo (1893).

29. Hawaiian Is., 18—28°30' N, 155—178° W, 16,000 sq.km, 4200 m

The flora of the Hawaiian Islands is one of the best known in the Pacific, at least at genus level. It will be noticed that in this paper less genera are accepted as indigenous to Hawaii than in my preliminary analysis.

| Type | Number | % |
|-------|--------|------|
| 1 | 82 | 36.3 |
| 1 a | 19 | 8.4 |
| 2 | 9 | 4.0 |
| 3 | 1 | 0.4 |
| 4 | 19 | 8.4 |
| 4 a | 6 | 2.7 |
| 5 | 4 | 1.8 |
| 5 a | 2 | 0.9 |
| 5 b | 3 | 1.3 |
| 6 | 3 | 1.3 |
| 6 a | 4 | 1.8 |
| 7 | 3 | 1.3 |
| 7 a | 0 | — |
| 7 b | 8 | 3.5 |
| 8 | 12 | 5.3 |
| 8 a | 43 | 19.0 |
| 9 | 8 | 3.5 |
| Total | 226 | 99.9 |

The distribution spectrum is remarkable as all types except 7 a are present. The strong representation of types 1 a and 2 (together 28 genera) is no doubt due to the high elevations of the islands allowing for many microtherm taxa. Equally remarkable and to be ascribed to the same cause is the relatively large number of 'Subantarctic' taxa so far north. However, no other island group in the Pacific except New Zealand, reaches altitudes over 3000 metres.

Of the 82 'wides' (type 1) nine centre in the New and seven in the Old World.

Hawaii is the first island group so far discussed to show any appreciable representation of the New World element (type 9). Though the Old World genera are more weakly represented than in any of the foregoing islands they still number 42 (18.6 %), that is, about five times the number of American genera of which there are eight (3.5 %). This is remarkable if one takes into consideration the greater proximity of Hawaii to America than to any part of the Old World continents. These eight genera are: *Argemone*-Pap., *Hesperocnide*-Urt., *Lepechinia*-Lab., *Nama*-Hydrophyl., *Sisyrinchium*-Irid., *Spermolepis*-Umb., *Urera*-Urt., and *Verbena*-Verb.

Among the 25 genera of types 4 & 4 a there are four centering in (Indo-)Malesia and two in Australia. The Indo-Malesian element proper (types 5—5 b) comprises nine genera. Of the three Pacific Subantarctic genera (type 7) *Sicyos*-Cuc. has its focus in America. There are 12 Pacific taxa (type 8), of these eight are strictly Pacific, two extend to Malesia and Australia (*Coprosma*-Rub. and *Styphelia* § *Cyathodes*-Epac.) and also two to America (*Astelia* § *Asteliopsis*-Lil. and *Pritchardia*-Palm). Nearly all genera of this type also occur in SE. Polynesia.

The endemic element in the Hawaiian flora is considerable. Stone (1967) in a review of all endemic Hawaiian taxa accepted 32 Phanerogam genera as endemic. There are 43 according to my information but this includes a number of subgeneric taxa, such as *Geranium* § *Neurophyllodes*-Ger., *Santalum* § *Hawaiiensia* and *Solenanthes*-Sant.

The majority of the endemics are not very isolated taxonomically, 11 are allied to widespread genera, e.g. *Dissochondrus*-Gram. to *Setaria*, 18 are allied to Old World or Pacific genera, e.g. *Labordia*-Log., which is near *Geniostoma*, *Bobea*-Rub. close to *Timonius*. Also included here are a number of endemic sections of widespread genera (*Lobelia*-Camp., *Santalum*-Sant., *Geranium*-Geran.).

Only four taxa are of manifestly American derivation. *Dubautia* (including *Raillardia*), *Hesperomannia*, *Wilkesia*, and Hawaii's most famous genus, *Argyroxiphium*-Comp. according to Carlquist (1959) belong to the American-centred *Madiinae*. This is in agreement with Hillebrand (1888) and St. John (1950) but not with Keck's (1936) claims for alliance with Asiatic genera. Nevertheless within the tribe these genera, especially *Argyroxiphium*, have a very isolated position. I consider nine genera as having no clear affinities, amongst others *Hillebrandia*-Beg. and *Brighamia*-Camp. However, no separate family has ever been proposed for any of them as has so frequently happened with New Caledonian endemics. Moreover, many of the latter belong to families or orders generally assumed to be of great antiquity such as *Coniferae*, *Magnoliales*, etc. which are altogether absent from Hawaii. Of the 43 endemic taxa seven are *Compositae* and eight *Campanulaceae*. The degree of endemism in the islands, though of the same order as in New Caledonia, is less pronounced.

The above considerations lead to the conclusion that Hawaii, as generally agreed, belongs to the Old World flora. Of the 226 taxa accepted here 123 occur in both the Old and New World, 51 do not occur in either, 44 are known from the Old but not from the New World and eight only from America and not from the Old World. Within the Old World relations are strongest, or rather least feeble, with Malesia.

Further analysis shows that floristic alliance is most pronounced with SE. Polynesia. This appears from the common and exclusive occurrence of eight taxa: *Bidens* § *Campylothecca*-Comp. (also Tonga), *Charpentiera*-Amaran., *Cheirodendron*-Aral., *Hedyotis* § *Polyne-siotes*-Rub., *Nesoluma*-Sapot., *Pelea*-Rut., *Phyllostegia*-Lab., and *Reynoldsia*-Aral. (also Samoa). In addition some 20 genera suggest links between Hawaii and SE. Polynesia by the occurrence of closely allied or identical species, e.g. *Lycium*-Sol., *Osteomeles*-Ros., *Sophora* § *Tetraptera*-Leg., *Styphelia*-Epac. It can be further demonstrated by the following figures. SE. Polynesia as a whole has 259 genera, of which 117 also occur in Hawaii. Other Pacific islands with approximately the same number of genera have much less in common: Bonin (with 164 genera) has 67, the Marianas (215 genera) 70, Samoa (302) 80, Tonga (263) 75, and Galapagos (190) 57 genera in common with Hawaii.

I propose the inclusion of Hawaii and SE. Polynesia, each with the rank of Province within the Malesian Region s.l.

Literature: Christophersen & Caum (1931), Fosberg (1948), Hillebrand (1888), Skottsberg (1925—1926, 1936b, 1944), Stone (1967).

30. Revilla Gigedo Is., 19° N, 111—115° W, 220 sq.km, 1150 m

Genera new to the islands are likely to be found in the future, especially on the highest and largest of the group: Socorro I.

The distribution spectrum is strikingly one-sided: nearly all genera belong either to type 1 or to type 9. Only six belong to other types, viz. 1 a and 2 and are also widespread. They are *Cressa*-Conv., *Erigeron*-Comp. and *Hypericum*-Gutt. (type 1 a) and *Eupatorium*-Comp., *Meliosma*-Sab. and *Prunus* subg. *Padus*-Ros. (type 2).

The 31 American taxa are mostly widespread in the Neotropics, five extend to Africa, e.g. *Laguncularia*-Combr.

There are no endemic genera, although Johnston (1931) considered over 30 % of the

| Type | Number | % |
|-------|--------|-------|
| 1 | 49 | 57.0 |
| 1 a | 3 | 3.5 |
| 2 | 3 | 3.5 |
| 3 | 0 | — |
| 4 | 0 | — |
| 4 a | 0 | — |
| 5 | 0 | — |
| 5 a | 0 | — |
| 5 b | 0 | — |
| 6 | 0 | — |
| 6 a | 0 | — |
| 7 | 0 | — |
| 7 a | 0 | — |
| 7 b | 0 | — |
| 8 | 0 | — |
| 8 a | 0 | — |
| 9 | 31 | 36.0 |
| Total | 86 | 100.0 |

species as being endemic and most of them even as very distinct so as to obscure relationships with continental species.

Relations with the Indo-Pacific islands are very weak: with Hawaii (226 genera) they have only 30 genera in common and they have very little floristic alliance with the American Pacific islands; of the 86 genera only 13 also occur in Cocos I. (with 60 genera) and 49 are also found in the Galapagos (with 190 genera).

Literature: Johnston (1931).

31. Clipperton I., 10° N, 109° W, 2 sq.km, 30 m

This isolated coral island was only taken up in the survey for the sake of completeness. The native flora consists of 18 genera, all of them ubiquitous or pantropical (type 1). Sachet (1962) mentions *Zostera-Potam.* for the island. This would be the only genus in type 1 a, but as the identification was made from a photograph not giving much detail and, moreover, Dr Den Hartog thinks its presence doubtful for ecological reasons, I have not accepted the record.

As we have seen the coral islands in the Central Pacific and the N. Tuamotus have a flora mainly consisting of 'wides' but have a number of other distribution types as well.

Literature: Sachet (1962).

32. Cocos I., 5° 30' N, 87° W, 25 sq.km, 825 m

The island doubtless harbours some unrecorded genera.

Here, as in the Revilla Gigedo Is., the most striking feature is the absence of so many distribution types.

But for *Rooseveltia-Palm.*, which is very near, if not identical, with one of the Central American genera, all genera are either world-wide or American in distribution. Among the 'wides', six distinctly centre in the New, none in the Old World. Of the 32 genera of type 9 four extend to Africa, e.g. *Ocotea-Laur.*

A striking feature of the American Pacific islands is that in contrast to the Indo-Pacific islands they have so little in common. Cocos I. lying in between Galapagos and Central America could be expected to have acted as a 'stepping stone' and hence to have most

| Type | Number | % |
|-------|--------|-------|
| 1 | 27 | 45.0 |
| 1 a | 0 | — |
| 2 | 0 | — |
| 3 | 0 | — |
| 4 | 0 | — |
| 4 a | 0 | — |
| 5 | 0 | — |
| 5 a | 0 | — |
| 5 b | 0 | — |
| 6 | 0 | — |
| 6 a | 0 | — |
| 7 | 0 | — |
| 7 a | 0 | — |
| 7 b | 0 | — |
| 8 | 0 | — |
| 8 a | 1 | 1.7 |
| 9 | 32 | 53.3 |
| Total | 60 | 100.0 |

of its genera in common with Galapagos. Actually only 23 of its 60 genera are also found there.

The Revilla Gigedos and Cocos I. only have 13 genera in common, despite the great resemblance in the distribution spectra.

Literature: Fosberg & Klawe (1966), Stewart (1912), Svenson (1935).

33. Galapagos Is., 1° N—2° S, 89—93° W, 7700 sq.km, 1500 m

The intensified interest in the islands of late has resulted in the discovery of some genera new to its flora. I think that at genus level few novelties can be expected.

In another paper (van Balgooy, 1969) I have already pointed out that considering the size of the islands the flora is poor.

The distribution spectrum is more remarkable for what is absent rather than for what is present. Old World distribution types are absent. The majority of the genera

| Type | Number | % |
|-------|--------|-------|
| 1 | 101 | 53.2 |
| 1 a | 11 | 5.8 |
| 2 | 2 | 1.1 |
| 3 | 0 | — |
| 4 | 0 | — |
| 4 a | 0 | — |
| 5 | 0 | — |
| 5 a | 0 | — |
| 5 b | 0 | — |
| 6 | 0 | — |
| 6 a | 0 | — |
| 7 | 2 | 1.1 |
| 7 a | 0 | — |
| 7 b | 0 | — |
| 8 | 0 | — |
| 8 a | 4 | 2.1 |
| 9 | 70 | 36.8 |
| Total | 190 | 100.1 |

are either widespread or are otherwise only found in America. Yet there are some features that make the Galapagos flora more special than that of Revilla Gigedo or Cocos. For a relatively low island group lying on the equator, it is peculiar to find non-tropical centred genera so well represented. This no doubt is due to the influence of the cold Humboldt Current which ameliorates the temperature in comparison with other tropical island groups. See e.g. Alpert (1963). There are 11 genera of type 1 a (wide temperate), two of mainly northern hemisphere distribution (*Aster-Comp.* and *Salvia-Lab.*) and two Pacific-Subantarctic genera (*Pernettya-Eric.* and *Sicyos-Cuc.*) both best developed in the New World.

There are four endemics, all belong to the *Compositae* and are shrubby or arborescent as most members of this family endemic on islands. Harling (1962) discussed the systematics of the Galapagos endemics. *Darwiniothamnus* is allied to the widespread *Conyza* and *Erigeron*, *Macraea* is a monotypic genus originally described in *Lipochaeta*, which is now considered a Hawaiian endemic, both are near the pantropical *Wedelia*. The relations of the other two, *Lecocarpus* and *Scalesia* are not clear, like *Macraea* they belong to the *Heliantheae*.

Of the 70 genera of type 9, 59 are either widespread in America or are confined to the Neotropics, 11 extend beyond the Atlantic Ocean to Africa.

Early authors writing on the Galapagos plants, probably impressed by the curious and spectacular development of the Tortoises, Iguanid Lizards and 'Darwin's Finches', described many new endemics from the islands. Svenson (1946) has, in my opinion rightly, stripped the islands of their 'endemic lustre'. Many of the Galapagos 'endemics' proved to be present in the coastal area of Ecuador. The Galapagos flora certainly does not rival those of Hawaii or Juan Fernandez for peculiarity.

The islands form no more than a district within the Neotropics.

Literature: Robinson (1902), Stewart (1911), Svenson (1935, 1946).

34. Easter I., 27° S, 109° 30' W, 120 sq.km, 530 m

The Easter I. flora is remarkable for its poverty. In my preliminary analysis I ascribed this to human influence, but in my paper on island floras I came to the conclusion that the main cause of this poverty is the island's great isolation as suggested earlier by Skottsberg (1956). Nearly all genera and most species are herbs of very wide distribution. The

| Type | Number | % |
|-------|--------|-------|
| 1 | 13 | 59.1 |
| 1 a | 6 | 27.3 |
| 2 | 0 | — |
| 3 | 0 | — |
| 4 | 0 | — |
| 4 a | 0 | — |
| 5 | 0 | — |
| 5 a | 0 | — |
| 5 b | 0 | — |
| 6 | 1 | 4.5 |
| 6 a | 0 | — |
| 7 | 0 | — |
| 7 a | 0 | — |
| 7 b | 2 | 9.1 |
| 8 | 0 | — |
| 8 a | 0 | — |
| 9 | 0 | — |
| Total | 22 | 100.0 |

few endemic species described are only feebly distinguishable from widespread congeners. Even if the island once had a rich and diversified flora it is unlikely that only the ubiquists would have been preserved. Other islands have been badly disturbed by man (some of the Hawaiian islands, Pitcairn, Juan Fernandez, St. Helena), but still have peculiar indigenous species or genera. The Desventuradas, discussed below, even poorer in genera, have a number of curious rare taxa. The only genera not belonging to types 1 & 1 a on Easter I. are the Australian genus *Dichelachne*-Gram. (type 6), *Tetragonia*-Aiz. and *Sophora* § *Tetraptera*-Leg. (type 7 b), the latter being the only woody indigenous plant of the island. On account of the one genus of type 6 the island should be placed in the Australian Region.

Literature: Guillaumin, Camus & Tardieu Blot (1936), Skottsberg (1922, 1927).

35. Desventuradas Is., 26° S, 80° W, 7 sq.km, 450 m

In a poor way the Desventuradas have quite an interesting flora, contrary to that of Easter I.

Of the 17 genera eight are of wide distribution. There are no Old World genera. The Subantarctic genera are *Sicyos*-Cuc. (type 7) and *Tetragonia*-Aiz. (type 7 b).

| Type | Number | % |
|-------|--------|------|
| 1 | 5 | 29.4 |
| 1 a | 3 | 17.6 |
| 2 | 0 | — |
| 3 | 0 | — |
| 4 | 0 | — |
| 4 a | 0 | — |
| 5 | 0 | — |
| 5 a | 0 | — |
| 5 b | 0 | — |
| 6 | 0 | — |
| 6 a | 0 | — |
| 7 | 1 | 5.9 |
| 7 a | 0 | — |
| 7 b | 1 | 5.9 |
| 8 | 0 | — |
| 8 a | 4 | 23.5 |
| 9 | 3 | 17.6 |
| Total | 17 | 99.9 |

For a flora that is so poor it is certainly remarkable that it includes four endemic genera: *Nesocaryum*-Bor. has no particularly close relationship with other genera, *Sanctambrosia*-Caryoph. is allied to the mainly northern hemisphere *Paronychia*, of the two endemic *Compositae*, *Lycapsus* and *Thamnosseris*, the former is rather isolated and the latter has its closest links with the Juan Fernandez *Dendroseris*.

Of the three American genera two are of general and one of Andine distribution (*Cristaria*-Malv.).

Apart from *Thamnosseris* there is no indication of any special floristic alliance with nearby Juan Fernandez. Only five of the 17 genera are also found on these islands.

Literature: Johnston (1935 b), Skottsberg (1937, 1963).

36. Juan Fernandez Is., 33° 30' S, 80° W, 150 sq.km, 1500 m

Despite their relative floristic poverty the Juan Fernandez Is. are highly peculiar.

| Type | Number | % |
|-------|--------|-------|
| 1 | 13 | 14.6 |
| 1 a | 22 | 24.7 |
| 2 | 3 | 3.4 |
| 3 | 0 | — |
| 4 | 0 | — |
| 4 a | 0 | — |
| 5 | 0 | — |
| 5 a | 0 | — |
| 5 b | 0 | — |
| 6 | 1 | 1.1 |
| 6 a | 0 | — |
| 7 | 7 | 7.9 |
| 7 a | 0 | — |
| 7 b | 8 | 9.0 |
| 8 | 2 | 2.2 |
| 8 a | 17 | 19.1 |
| 9 | 16 | 18.0 |
| Total | 89 | 100.0 |

As in New Zealand there is a preponderance of wide temperate genera (type 1 a) over general 'wides' (type 1). There are three northern hemisphere genera that cross the equator in the American sector: *Berberis-Berb.*, *Paronychia-Caryoph.*, and *Empetrum-Emp.*

As can be expected from the strong representation of the types 1 a and 2 there is also a strong representation of southern temperate genera (types 7 & 7 b).

The most curious feature of the Juan Fernandez flora is the presence of three genera unknown from the New World: *Haloragis-Halor.* (type 6), *Coprosma-Rub.*, and *Santalum-Sant.* (type 8). In all the other American Pacific islands all genera apart from the endemics are also known from the American continent.

The great distinctiveness of the Juan Fernandez flora is enhanced by the presence of 17 endemic genera, of which nine are arborescent *Compositae*. Carlquist (1967 b) has shown that of these the genera *Dendroseris*, *Hesperoseris*, *Phoenicoseris* and *Rea* form a closely knit complex, each of the components not deserving more than subgeneric rank, but even so these taxa are confined to Juan Fernandez. Also *Rhetinodendron* and *Robinsonia* are closely allied. According to Mattfeld (1928) they are nearest to *Brachionostylum* of New Guinea. The remaining Composite genera, *Centaurodendron*, *Symphiochaeta* and *Yunquea*, occupy isolated taxonomic positions. *Podophorus-Gram.* is an ally of the widespread *Bromus*, *Nothomyrcia* belongs to a complex formerly lumped together under *Myrtus* and best represented in South America and the SW. Pacific (Australia, Melanesia and New Zealand). See Burret (1941). *Cuminia-Lab.*, *Juania-Palm.* and *Ochagavia-Brom.* have Andine relationships. *Selkirkia-Borag.* and *Megalachne-Gram.* are difficult to place taxonomically. Most interesting is the famous *Lactoris*, taxonomically so isolated that it is regarded as a family in its own right. Even as a family its relationships are not clear. It has tentatively been associated with the *Piperales* and *Magnoliales*.

The American element (type 9) is represented by 16 genera, of which 11 centre in the Andes.

The Juan Fernandez Is. thus clearly form part of the New World flora, but their above discussed peculiar floristic composition and weak but distinct Old World links induce me

to give it a high rank within the Andine Region, despite its relative poverty. For the sake of convenience but not on account of close alliance the Juan Fernandez Province should include the Desventuradas Is. as a separate district.

Literature: Skottsberg (1922, 1956).

Summary of distribution types spectra

The distribution types as a whole will now be reviewed by means of table 3.

Widespread genera (types 1 & 1 a) are best represented in island groups that are either small, remote or low. Examples are the Marianas, Central Polynesia, Cook, Tuamotus, Marquesas, Clipperton, Galapagos and Easter Is. There is, as can be expected, a greater percentage of wide temperates (type 1 a) on the non-tropical islands, such as New Zealand and adjacent islands and Juan Fernandez.

Northern temperate genera (type 2) as well as E. Asiatic genera (type 3) are only well represented in the Bonin Is. This distinguishes this group from all other islands in the Pacific.

Of the Old World genera those with the widest distribution (type 4) are proportionally evenly distributed over the tropical Pacific as far east as Hawaii and the Marquesas, and to a slightly lower degree also in New Zealand and adjacent island groups. In other words, those genera with the widest distribution towards the west (Africa) are in general also found widely in the E. Pacific.

Old World genera with distribution terminating westward in continental Asia (India, Indo-China) are well represented in the Carolines, Marianas, Bismarcks, Solomons, New Hebrides, Fiji, Samoa, and Tonga, but their percentages drop rather rapidly beyond these island groups.

The Malesian genera as a whole (types 5, 5 a & 5 b) show high percentages in Bismarcks, Solomons, New Hebrides, Fiji, Samoa, and the Carolines; beyond these islands the percentages drop sharply. They are not or hardly represented in the New Zealand sector. Type 5 b (E. Malesian genera) is particularly well represented in the Bismarcks and Solomons.

Australian genera (type 6) are mainly found in those W. Pacific islands which are poor in Malesian taxa: New Zealand, Lord Howe and other islands in the New Zealand sector. Thus, Malesian genera show a preponderance in the tropical, and Australian genera in the subtropical and temperate parts of the Pacific. Towards the east, however, the dominance of Malesian over Australian taxa fades. This point will be discussed in greater detail later.

Australian-Papuan genera (type 6 a) are well represented in the triangle the Bismarcks, Fiji, New Zealand. In other words both in the 'Malesian' and in the 'Australian' Pacific islands.

The Indian-Subantarctic genera (type 7 a) are almost confined to those islands with a strong Australian element: New Zealand and adjacent islands.

The Subantarctic genera of type 7 and 7 b, as can be expected, are most abundant on the islands south of the Tropic of Capricorn but have some striking representations on some of the tropical 'high islands', notably Hawaii, and on the much lower islands of SE. Polynesia (See also Skottsberg, 1936 a).

Widespread Pacific genera (type 8) are not found in the American island groups except Juan Fernandez. In the western part of the Pacific they are absent from or nearly so on the low islands. In the high islands percentages of this type increase from west to east, the highest figures being obtained for some of the islands in SE. Polynesia.

Pacific endemics (type 8 a) show four centres: New Caledonia, New Zealand, Hawaii,

and Juan Fernandez (and Desventuradas). The flora of New Caledonia is outstanding as it includes so many endemic genera with obscure affinities.

Type 9 is almost completely confined to the American Pacific islands: Revilla Gigedo, Cocos, Galapagos, Juan Fernandez and Desventuradas. In the rest of the Pacific this type is only represented in Hawaii, Fiji, and New Caledonia.

The 17 distribution types that have been distinguished can be condensed into four main categories:

- a) Genera of wide distribution occurring in Old and New World (types 1, 1 a, 2, 7, and 7 b).
- b) Genera not occurring in America; Old World or Gerontogean genera (types 3, 4, 4 a, 5, 5 a, 5 b, 6, 6 a, 7 a).
- c) Genera confined to or centering in the Pacific (types 8 and 8 a).
- d) American or Neogean genera (type 9).

The total number of genera belonging to each of these categories are given in table 3, bottom.

The 'wides' form 30—40 % of the flora in the island groups round Malesia: W. Carolines, Bismarcks, Solomons, St. Cruz, New Hebrides, Fiji, and New Caledonia. In all other island groups the percentage of this category is higher, especially in the low, remote and small island groups with extreme values in Clipperton (100 %), Easter I. (95.5 %), E. Central Polynesia (72.5 %) and W. Central Polynesia (69.7 %).

The Gerontogean genera show a proportional decrease moving away from Indo-Australia. The decrease is most gradual in the central tropical Pacific along the line Solomons, Samoa and Marquesas. This is depicted in fig. 38, where islands having approximately the same percentage of Old World genera have been delineated. As shown above this decline is due to a decrease in the genera of restricted distribution, while that of type 4 remains virtually unchanged (see also fig. 39 and 40).

The decrease in Old World genera away from the Indo-Australian centre is only partly counterbalanced by a proportional increment of Pacific genera (types 8 & 8 a). In the series the Solomons, New Hebrides, Fiji, Society, and Marquesas, the percentages are respectively 3.1, 5.3, 7.6, 10.0, and 13.2. But the four major concentrations of Pacific genera are independent of the distance from any of the surrounding continental floras: New Caledonia, New Zealand, Hawaii and Juan Fernandez.

The Neogean genera (type 9) show a very rapid decline from 53.3 % on Cocos I. which is nearest the American mainland, to 36.8 and 36.0 % in the Galapagos and Revilla Gigedo Is., 18 % in Juan Fernandez and only 3.5 % in Hawaii.

In table 3 the figures in the distribution spectra that are characteristic will now be summarized.

The distribution spectra of the Bismarcks, Solomons, St. Cruz, W. and E. Carolines show great similarity. They are all characterized by a strong representation of Malesian taxa (types 5, 5 a & 5 b).

These are also prominent in the New Hebrides but in addition there is an increase in Australian (type 6) and Pacific taxa (type 8). In this respect and in the high percentage of Malesian genera the New Hebrides agree with Fiji, Samoa and Tonga.

New Caledonia differs from the other Melanesian islands by its much lower percentage of Malesian genera compensated by an increase in Australian genera, but above all by its very high percentage of Pacific and endemic genera.

Lord Howe, Norfolk, Kermadec, New Zealand, Subantarctic islands, and Chatham all have an increased percentage of wide temperates, a very poor representation of Malesian genera and a strong Pacific element. Subantarctic genera are also prominent

especially in the four last mentioned island groups. Lord Howe and Norfolk differ further in their high percentage of Paleotropical genera (types 4 & 4 a). Their distribution types spectra are more or less intermediate between those of New Caledonia and New Zealand. In all these six island groups Pacific genera (type 8) are well represented with a high percentage of endemics in New Zealand.

Bonin differs from all other island groups in its high percentage of types 2 and 3. Compared with other nearby island groups (Marianas, Carolines) there are few Malesian genera.

Central Polynesia is characterized by its lack of distribution types. Nearly all genera are either pantropical (type 1) or widespread in the Old World (type 4).

The islands of SE. Polynesia show a general impoverishment of Old World genera except of type 4. There is no preponderance of Malesian over Australian genera as in the tropical islands of the W. Pacific or the other way round as in the islands of the New Zealand sector. Pacific genera are well represented in most and Rapa is in addition characterized by a strong representation of temperate genera.

Hawaii has a distribution types spectrum strongly resembling that of the SE. Polynesian islands especially that of Rapa. It differs in its strong endemic element. It is furthermore the only island in the western part of the Pacific with an appreciable percentage of American genera (type 9).

Clipperton I. and Easter I. are very difficult to 'place' floristically. The former only has type 1, the latter also wide temperates. Easter Island has been reckoned to the Old World on account of a single genus in type 6.

Revilla Gigedo, Cocos I. and Galapagos have essentially the same distribution types spectra. Nearly all genera are either widespread or belong to type 9. Galapagos is the only group with endemic genera.

Desventuradas and Juan Fernandez also show great similarity in their distribution spectra, which are characterized by a high percentage of wide temperates, high degree of endemism and a relatively high percentage of American genera.

Results with revised taxa

The results will now be compared with those obtained from the revised taxa only.

The distribution types spectra based on all genera for all island groups are given in table 3 (top). From this it can be seen how the distribution types are represented over the 36 locations that have been distinguished. It should be compared with table 4 (top) presenting the distribution types spectra as based on the 345 revised taxa. Some island groups have only a very limited number of genera. Any conclusions on these have to be regarded with caution, and can better be left out of consideration.

As compared with the distribution types spectra based on all genera, it can be seen that there is a better proportional representation of some types, notably of Malesian and Subantarctic ones at the expense mainly of type 1 and 9. Yet the overall picture is not essentially affected.

Juan Fernandez and Galapagos differ in their high percentages of type 9 and in the absence of Old World distribution types. In the rest of the Pacific Bonin differs from all other groups owing to the high percentage of types 2 and 3, New Zealand and adjacent islands owing to a high percentage of types 6, 7 and 7 b. Hawaii would have to be ranked as a special case on account of its exceptionally high degree of endemism, as many of the Hawaiian endemic genera happen to have been better studied than those of wider distribution. Also New Caledonia would stand apart on account of its high degree of endem-

ism and about equally strong representations of Malesian (types 5—5 b) and Australian genera (type 6). All other island groups show more or less similar distribution spectra, with decreasing percentages of Old World genera in west-east direction, this is especially apparent in the Malesian types. This is a point that will receive more attention later (see fig. 38—43).

So far the islands have been discussed according to their floristic distribution spectra. The interrelations between the various island groups can also be studied by way of their floristic correlations.

2. Floristic correlations

Table 5 shows the number of taxa each of the Pacific island groups has in common with any other. In the same table the degree of similarity as expressed according to Kroeber's formula is given. As discussed in chapter III, 9 this coefficient can be defined

as the average similarity between two areas:
$$S = \frac{\frac{C}{A} + \frac{C}{B}}{2} \times 100 = \frac{C(A+B)}{50 AB}$$
, in which A is the number of taxa in the first B the number of taxa in the second area and C the number of taxa common to the two areas.

This parameter will now be used to find out with which island group each of the groups is most closely related.

The Bismarcks are most closely related to the Solomons followed by the New Hebrides, Fiji and W. Carolines in that order. The Solomons conversely are floristically very close to the Bismarcks, followed by the New Hebrides, Fiji and W. Carolines.

St. Cruz is closest to the Solomons and next, not to the geographically nearer New Hebrides but to the Bismarcks and Fiji.

The island groups most closely allied to the New Hebrides are Fiji and Samoa, next come the Solomons, Tonga, New Caledonia and the Bismarcks.

New Caledonia has its closest alliance with the Loyalties and next to the island groups further to its east, thus to the New Hebrides and Fiji and not to the Solomons and still less to New Zealand.

The Loyalties are nearest floristically to New Caledonia, next come the New Hebrides and Tonga.

Lord Howe I. is not closely related to any other group but Norfolk I. The affinities with the Kermadecs and New Caledonia are weaker.

Norfolk I. also has no strong floristic relations. Lord Howe I. is closest, next are the Kermadecs.

The Kermadecs in turn are closest to New Zealand and next to Norfolk I.

The strongest floristic relations of New Zealand are with the Chathams and the Subantarctic islands. These in turn have their closest alliance with New Zealand and with each other.

The Bonins stand distinctly apart. Even with their nearest neighbours (Marianas) they have no close alliance.

The Marianas are clearly allied to the other Micronesian island groups, especially the W. Carolines, with more remote island groups such as Fiji and Tonga they have stronger relations than with the nearby Bonins.

The W. Carolines are closely allied to the E. Carolines. Relations are also strong with the Marianas. Next come the Bismarcks and Solomons. Of approximately the same order are the affinities with Fiji, Samoa, Tonga, and the New Hebrides.

| Table 2. — Matrix giving the number of genera common to any two island groups and the similarity coefficient of Broder | Number of genera shared | | | | | | | | | | | | | | | | | | | | | | | |
|--|-------------------------|---------|--------------|---------------|------------|-----------|---------|----------|-------------|-------------------|---------|-------|--------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|
| | Blumensis | Solomon | New Hebrides | New Caledonia | Loyalities | Lord Howe | Kororok | Kermadec | New Zealand | Polynesia, I.S.T. | Chatham | Kauai | Hawaii | V. Carolines | S. Carolines | P. Carolines | P. Carolines | P. Carolines | P. Carolines | P. Carolines | P. Carolines | P. Carolines | P. Carolines | P. Carolines |
| Blumensis (532) | 502 | 11 | 290 | 312 | 186 | 73 | 57 | 22 | 57 | 4 | 16 | 96 | 173 | 263 | 189 | 59 | 36 | 336 | 236 | 211 | 104 | 142 | 59 | 59 |
| Solomon (654) | 76.0 | 121 | 398 | 332 | 187 | 70 | 56 | 25 | 62 | 7 | 19 | 100 | 176 | 276 | 197 | 56 | 33 | 358 | 264 | 220 | 193 | 70 | 59 | 56 |
| New Hebrides (126) | 52.9 | 97.2 | 93 | 83 | 56 | 16 | 8 | 2 | 13 | 2 | 24 | 50 | 75 | 65 | 17 | 1 | 101 | 80 | 69 | 30 | 46 | 27 | 16 | 20 |
| New Caledonia (396) | 61.3 | 66.5 | 103.7 | 308 | 193 | 69 | 58 | 29 | 62 | 8 | 20 | 90 | 153 | 206 | 167 | 54 | 34 | 308 | 237 | 207 | 190 | 131 | 63 | 57 |
| Loyalities (655) | 48.4 | 50.5 | 39.3 | 62.4 | 261 | 102 | 82 | 43 | 121 | 25 | 43 | 108 | 177 | 214 | 171 | 64 | 39 | 326 | 222 | 115 | 103 | 60 | 70 | 62 |
| Lord Howe (138) | 50.8 | 49.8 | 32.9 | 61.2 | 69.9 | 72 | 61 | 24 | 49 | 9 | 20 | 74 | 127 | 136 | 113 | 55 | 35 | 183 | 147 | 151 | 105 | 63 | 50 | 57 |
| Kororok (104) | 31.9 | 31.0 | 7.0 | 35.2 | 45.7 | 61.0 | 55.6 | 39 | 62 | 10 | 29 | 35 | 41 | 42 | 36 | 16 | 9 | 61 | 52 | 52 | 41 | 44 | 26 | 24 |
| Kermadec (61) | 19.8 | 22.6 | 2.4 | 27.4 | 38.5 | 44.9 | 50.7 | 54 | 21 | 35 | 19 | 16 | 17 | 17 | 12 | 8 | 20 | 26 | 26 | 21 | 22 | 29 | 15 | 16 |
| New Zealand (344) | 12.8 | 13.8 | 7.0 | 16.8 | 26.8 | 36.5 | 38.0 | 92.1 | 75 | 105 | 41 | 38 | 40 | 35 | 15 | 9 | 61 | 50 | 44 | 37 | 49 | 27 | 38 | 16 |
| Polynesia, I.S.T. (79) | 2.9 | 5.0 | 2.1 | 6.1 | 17.9 | 7.5 | 11.2 | 30.7 | 58.9 | 46 | 6 | 4 | 5 | 4 | 3 | 2 | 6 | 8 | 1 | 5 | 14 | 5 | 14 | 2 |
| Chatham (106) | 8.8 | 10.4 | 0.9 | 12.0 | 23.6 | 13.3 | 30.5 | 27.6 | 45.2 | 51.2 | 15 | 13 | 9 | 5 | 2 | 17 | 14 | 10 | 19 | 9 | 18 | 5 | 10 | 29 |
| Kauai (164) | 36.9 | 38.1 | 16.8 | 38.0 | 40.4 | 36.7 | 30.0 | 27.5 | 21.4 | 18.4 | 5 | 11.6 | 84 | 82 | 71 | 31 | 20 | 104 | 84 | 81 | 98 | 70 | 41 | 45 |
| Hawaii (215) | 54.0 | 54.4 | 31.5 | 44.9 | 54.7 | 53.9 | 27.4 | 20.2 | 16.8 | 14.3 | 3.5 | 9.2 | 15.1 | 169 | 133 | 55 | 35 | 174 | 146 | 147 | 90 | 115 | 68 | 53 |
| V. Carolines (336) | 60.0 | 62.2 | 40.9 | 56.7 | 48.2 | 46.3 | 34.0 | 26.4 | 16.5 | 11.7 | 3.9 | 8.1 | 37.2 | 64.5 | 191 | 57 | 31 | 228 | 168 | 168 | 91 | 116 | 66 | 50 |
| S. Carolines (228) | 56.4 | 59.3 | 40.0 | 57.8 | 50.6 | 46.4 | 22.7 | 25.2 | 17.7 | 12.7 | 3.4 | 6.2 | 37.2 | 60.1 | 70.3 | 54 | 31 | 184 | 159 | 136 | 80 | 103 | 53 | 44 |
| P. Carolines (66) | 49.4 | 46.7 | 19.6 | 47.7 | 53.4 | 22.2 | 19.0 | 19.8 | 18.9 | 13.5 | 4.2 | 6.1 | 32.9 | 54.5 | 51.7 | 52.8 | 38 | 56 | 37 | 37 | 46 | 49 | 33 | 21 |
| S. Carolines (40) | 47.5 | 43.8 | 18.1 | 46.8 | 51.7 | 50.5 | 17.7 | 15.6 | 16.6 | 12.6 | 3.8 | 3.4 | 31.1 | 53.4 | 49.0 | 45.5 | 76.3 | 32 | 33 | 34 | 31 | 34 | 26 | 13 |
| P. Carolines (495) | 58.0 | 65.0 | 50.7 | 71.3 | 59.2 | 54.3 | 36.0 | 35.7 | 25.9 | 16.2 | 6.5 | 9.8 | 42.6 | 95.7 | 97.9 | 59.7 | 48.3 | 43.4 | 282 | 246 | 115 | 167 | 74 | 61 |
| S. Carolines (263) | 56.9 | 58.7 | 40.5 | 56.2 | 53.1 | 52.4 | 30.1 | 33.6 | 25.6 | 15.6 | 4.8 | 8.9 | 39.5 | 58.1 | 57.9 | 61.2 | 52.6 | 46.7 | 76.3 | 209 | 110 | 194 | 72 | 60 |
| P. Carolines (128) | 49.5 | 50.7 | 23.8 | 57.1 | 54.4 | 47.7 | 29.6 | 36.0 | 26.8 | 20.0 | 5.2 | 9.6 | 40.7 | 56.8 | 49.7 | 49.3 | 53.1 | 51.1 | 57.1 | 61.9 | 61.6 | 110 | 68 | 56 |
| Society (201) | 46.1 | 45.1 | 26.1 | 50.7 | 51.6 | 47.9 | 30.7 | 27.3 | 23.6 | 19.3 | 6.0 | 9.4 | 35.8 | 54.5 | 47.3 | 41.7 | 43.8 | 47.3 | 49.8 | 52.8 | 54.6 | 65.6 | 64.5 | 44 |
| Palau (93) | 31.9 | 36.2 | 15.0 | 41.8 | 43.0 | 36.5 | 36.9 | 34.6 | 32.6 | 28.9 | 16.5 | 18.2 | 37.9 | 40.8 | 34.3 | 34.1 | 27.2 | 23.2 | 39.2 | 42.2 | 38.6 | 52.3 | 52.7 | 48.7 |
| S. Carolines (70) | 46.8 | 45.9 | 22.2 | 47.9 | 50.6 | 49.8 | 22.6 | 25.1 | 16.9 | 13.7 | 4.5 | 9.6 | 22.7 | 38.3 | 34.3 | 31.0 | 30.9 | 37.1 | 40.9 | 34.7 | 39.5 | 34.6 | 40.2 | 42.5 |
| S. Carolines (113) | 41.1 | 43.0 | 21.3 | 46.1 | 47.9 | 46.1 | 27.4 | 28.5 | 21.6 | 17.5 | 6.3 | 7.6 | 35.0 | 53.0 | 45.7 | 38.3 | 51.5 | 56.9 | 51.6 | 57.0 | 60.0 | 67.1 | 61.6 | 31.3 |
| Marquesas (228) | 40.7 | 44.1 | 22.5 | 47.7 | 37.1 | 30.8 | 26.0 | 23.1 | 16.5 | 8.7 | 9.5 | 37.4 | 47.3 | 40.0 | 35.7 | 38.4 | 40.6 | 49.8 | 52.3 | 47.5 | 58.8 | 66.7 | 59.6 | |
| Hawaii (86) | 29.3 | 26.7 | 13.0 | 31.4 | 34.8 | 29.3 | 30.3 | 26.8 | 26.1 | 23.8 | 21.6 | 20.1 | 35.2 | 31.8 | 22.9 | 24.7 | 31.3 | 33.8 | 32.3 | 31.0 | 30.9 | 37.1 | 40.9 | |
| Bavilla Oligo (86) | 20.5 | 18.4 | 3.9 | 18.4 | 25.0 | 20.1 | 14.2 | 15.9 | 19.0 | 10.2 | 3.7 | 6.3 | 19.5 | 22.0 | 16.8 | 16.8 | 26.8 | 27.5 | 22.7 | 16.4 | 20.1 | 20.5 | 21.6 | |
| Clipperton (18) | 37.1 | 31.4 | 3.2 | 26.1 | 42.8 | 29.7 | 18.8 | 19.6 | 18.0 | 17.5 | 3.4 | 9.7 | 24.7 | 39.1 | 29.3 | 21.0 | 28.3 | 20.1 | 34.6 | 32.4 | 32.6 | 25.4 | 30.3 | |
| Coconut (60) | 21.0 | 20.9 | 7.4 | 17.3 | 18.2 | 17.4 | 12.0 | 14.5 | 11.6 | 7.8 | 1.5 | 1.3 | 17.1 | 20.3 | 19.6 | 21.1 | 20.7 | 16.7 | 18.8 | 19.0 | 18.4 | 19.7 | 17.3 | |
| Bavilla Oligo (86) | 20.5 | 18.4 | 3.9 | 18.4 | 25.0 | 20.1 | 14.2 | 15.9 | 19.0 | 10.2 | 3.7 | 6.3 | 19.5 | 22.0 | 16.8 | 16.8 | 26.8 | 27.5 | 22.7 | 16.4 | 20.1 | 20.5 | 21.6 | |
| Clipperton (16) | 37.1 | 31.4 | 3.2 | 26.1 | 42.8 | 29.7 | 18.8 | 19.6 | 18.0 | 17.5 | 3.4 | 9.7 | 24.7 | 39.1 | 29.3 | 21.0 | 28.3 | 20.1 | 34.6 | 32.4 | 32.6 | 25.4 | 30.3 | |
| Coconut (60) | 21.0 | 20.9 | 7.4 | 17.3 | 18.2 | 17.4 | 12.0 | 14.5 | 11.6 | 7.8 | 1.5 | 1.3 | 17.1 | 20.3 | 19.6 | 21.1 | 20.7 | 16.7 | 18.8 | 19.0 | 18.4 | 19.7 | 17.3 | |
| Bavilla Oligo (86) | 20.5 | 18.4 | 3.9 | 18.4 | 25.0 | 20.1 | 14.2 | 15.9 | 19.0 | 10.2 | 3.7 | 6.3 | 19.5 | 22.0 | 16.8 | 16.8 | 26.8 | 27.5 | 22.7 | 16.4 | 20.1 | 20.5 | 21.6 | |
| Clipperton (16) | 37.1 | 31.4 | 3.2 | 26.1 | 42.8 | 29.7 | 18.8 | 19.6 | 18.0 | 17.5 | 3.4 | 9.7 | 24.7 | 39.1 | 29.3 | 21.0 | 28.3 | 20.1 | 34.6 | 32.4 | 32.6 | 25.4 | 30.3 | |
| Coconut (60) | 21.0 | 20.9 | 7.4 | 17.3 | 18.2 | 17.4 | 12.0 | 14.5 | 11.6 | 7.8 | 1.5 | 1.3 | 17.1 | 20.3 | 19.6 | 21.1 | 20.7 | 16.7 | 18.8 | 19.0 | 18.4 | 19.7 | 17.3 | |
| Bavilla Oligo (86) | 20.5 | 18.4 | 3.9 | 18.4 | 25.0 | 20.1 | 14.2 | 15.9 | 19.0 | 10.2 | 3.7 | 6.3 | 19.5 | 22.0 | 16.8 | 16.8 | 26.8 | 27.5 | 22.7 | 16.4 | 20.1 | 20.5 | 21.6 | |
| Clipperton (16) | 37.1 | 31.4 | 3.2 | 26.1 | 42.8 | 29.7 | 18.8 | 19.6 | 18.0 | 17.5 | 3.4 | 9.7 | 24.7 | 39.1 | 29.3 | 21.0 | 28.3 | 20.1 | 34.6 | 32.4 | 32.6 | 25.4 | 30.3 | |
| Coconut (60) | 21.0 | 20.9 | 7.4 | 17.3 | 18.2 | 17.4 | 12.0 | 14.5 | 11.6 | 7.8 | 1.5 | 1.3 | 17.1 | 20.3 | 19.6 | 21.1 | 20.7 | 16.7 | 18.8 | 19.0 | 18.4 | 19.7 | 17.3 | |
| Bavilla Oligo (86) | 20.5 | 18.4 | 3.9 | 18.4 | 25.0 | 20.1 | 14.2 | 15.9 | 19.0 | 10.2 | 3.7 | 6.3 | 19.5 | 22.0 | 16.8 | 16.8 | 26.8 | 27.5 | 22.7 | 16.4 | 20.1 | 20.5 | 21.6 | |
| Clipperton (16) | 37.1 | 31.4 | 3.2 | 26.1 | 42.8 | 29.7 | 18.8 | 19.6 | 18.0 | 17.5 | 3.4 | 9.7 | 24.7 | 39.1 | 29.3 | 21.0 | 28.3 | 20.1 | 34.6 | 32.4 | 32.6 | 25.4 | 30.3 | |
| Coconut (60) | 21.0 | 20.9 | 7.4 | 17.3 | 18.2 | 17.4 | 12.0 | 14.5 | 11.6 | 7.8 | 1.5 | 1.3 | 17.1 | 20.3 | 19.6 | 21.1 | 20.7 | 16.7 | 18.8 | 19.0 | 18.4 | 19.7 | 17.3 | |
| Bavilla Oligo (86) | 20.5 | 18.4 | 3.9 | 18.4 | 25.0 | 20.1 | 14.2 | 15.9 | 19.0 | 10.2 | 3.7 | 6.3 | 19.5 | 22.0 | 16.8 | 16.8 | 26.8 | 27.5 | 22.7 | 16.4 | 20.1 | 20.5 | 21.6 | |
| Clipperton (16) | 37.1 | 31.4 | 3.2 | 26.1 | 42.8 | 29.7 | 18.8 | 19.6 | 18.0 | 17.5 | 3.4 | 9.7 | 24.7 | 39.1 | 29.3 | 21.0 | 28.3 | 20.1 | 34.6 | 32.4 | 32.6 | 25.4 | 30.3 | |
| Coconut (60) | 21.0 | 20.9 | 7.4 | 17.3 | 18.2 | 17.4 | 12.0 | 14.5 | 11.6 | 7.8 | 1.5 | 1.3 | 17.1 | 20.3 | 19.6 | 21.1 | 20.7 | 16.7 | 18.8 | 19.0 | 18.4 | 19.7 | 17.3 | |
| Bavilla Oligo (86) | 20.5 | 18.4 | 3.9 | 18.4 | 25.0 | 20.1 | 14.2 | 15.9 | 19.0 | 10.2 | 3.7 | 6.3 | 19.5 | 22.0 | 16.8 | 16.8 | 26.8 | 27.5 | 22.7 | 16.4 | 20.1 | 20.5 | 21.6 | |
| Clipperton (16) | 37.1 | 31.4 | 3.2 | 26.1 | 42.8 | 29.7 | 18.8 | 19.6 | 18.0 | 17.5 | 3.4 | 9.7 | 24.7 | 39.1 | 29.3 | 21.0 | 28.3 | 20.1 | 34.6 | 32.4 | 32.6 | 25.4 | 30.3 | |
| Coconut (60) | 21.0 | 20.9 | 7.4 | 17.3 | 18.2 | 17.4 | 12.0 | 14.5 | 11.6 | 7.8 | 1.5 | 1.3 | 17.1 | 20.3 | 19.6 | 21.1 | 20.7 | 16.7 | 18.8 | 19.0 | 18.4 | 19.7 | 17.3 | |
| Bavilla Oligo (86) | 20.5 | 18.4 | 3.9 | 18.4 | 25.0 | 20.1 | 14.2 | 15.9 | 19.0 | 10.2 | 3.7 | 6.3 | 19.5 | 22.0 | 16.8 | 16.8 | 26.8 | 27.5 | 22.7 | 16.4 | 20.1 | 20.5 | 21.6 | |
| Clipperton (16) | 37.1 | 31.4 | 3.2 | 26.1 | 42.8 | 29.7 | 18.8 | 19.6 | 18.0 | 17.5 | 3.4 | 9.7 | 24.7 | 39.1 | 29.3 | 21.0 | 28.3 | 20.1 | 34.6 | 32.4 | 32.6 | 25.4 | 30.3 | |
| Coconut (60) | 21.0 | 20.9 | 7.4 | 17.3 | 18.2 | 17.4 | 12.0 | 14.5 | 11.6 | 7.8 | 1.5 | 1.3 | 17.1 | 20.3 | 19.6 | 21.1 | 20.7 | 16.7 | 18.8 | 19.0 | 18.4 | 19.7 | 17.3 | |
| Bavilla Oligo (86) | 20.5 | 18.4 | 3.9 | 18.4 | 25.0 | 20.1 | 14.2 | 15.9 | 19.0 | 10.2 | 3.7 | 6.3 | 19.5 | 22.0 | 16.8 | 16.8 | 26.8 | 27.5 | 2 | | | | | |

West and East Central Polynesia have by far the strongest relations with each other.

The affinity of Fiji is with Samoa, Tonga and the New Hebrides in this order. Next come the Solomons, Bismarcks, E. Carolines, New Caledonia and the Society Is.

Samoa has approximately equally strong relations with Fiji and Tonga, next with the New Hebrides followed by the Solomons and Societies.

The relations of Tonga are strongest with Samoa and Fiji. Next in order of importance come the New Hebrides, Marianas and Cook Is.

The Cook Is. which geographically are situated between Samoa and the Societies, clearly show closer floristic relations to the east, first of all the Societies, next Tubuai, after that the S. Tuamotus and Samoa.

The Society Is. have close floristic relations with island groups of SE. Polynesia: Cook, Marquesas, S. Tuamotus and Tubuai in that order.

Tubuai has approximately equally strong ties with the Cook Is., S. Tuamotus and Societies, but not with Rapa which geographically belongs to this group.

Rapa is rather isolated floristically. Affinities are with Cook Is., Societies and S. Tuamotus but are not pronounced.

The N. and S. Tuamotus have by far the strongest relations with each other. Next come the Societies, Tubuai, and Cook Is.

The Marquesas Is. show greatest affinity with the Societies. Next are Tubuai, the Cook Is. and S. Tuamotus in that sequence.

Hawaii is another island group without any strong relations with other groups. The relatively high Kroeber coefficient with Clipperton I. is easily explained by the fact that nearly all the widespread Clipperton genera are also found on Hawaii. The same is true for Easter I. Leaving these out of consideration, Hawaii shows distinct but weak relations with some SE. Polynesian island groups: Marquesas, Society Is., S. Tuamotus and Rapa but not with the approximately equidistant E. Carolines and Marianas or Revilla Gigedo and Galapagos Is.

The Revilla Gigedo Is. are floristically isolated from the other Pacific islands, even those with which it shares a strong American element. Affinities are least weak with the Galapagos Is.

Clipperton is also floristically closest to Galapagos due to the fact that it has all but one of its widespread genera in common with the latter islands. Low Kroeber coefficient values are to be expected on account of its poverty.

Cocos I. too is quite isolated floristically from other Pacific islands. Relations are as weak with any of the W. Pacific islands as they are with Revilla Gigedo or the nearby Galapagos.

The Galapagos Is. are also floristically isolated within the Pacific.

Easter I. and Desventuradas for the same reason as Clipperton (extreme poverty) show low coefficient values. Those for Easter I. are higher on account of the fact that most Easter I. genera are widespread.

Juan Fernandez, although likewise standing apart floristically, is interesting for the fact that it shows weaker relations with the American island groups closer to it than with some far more distant but climatically more similar islands in the west: New Zealand, Chathams, Kermadecs, etc., situated at approximately the same latitude.

3. Hierarchical subdivision of the Pacific flora

Taking the foregoing two paragraphs into account a hierarchical subdivision of the Pacific flora will now be attempted. A few words should first be said about the terminology adopted.

Burkill (1943) objected to the use of such terms as 'Province' and 'District', as they are also employed in human administrative geography. Although it is true that political and ethnological boundaries often do not correspond to biogeographic ones, I do not think that confusion is possible. The alternatives suggested by Burkill, such as 'Region' and 'Area', have also been used other than in a biogeographic sense.

I propose to adopt the following hierarchical sequence of phytochoria. Names of authors and of approximately equivalent terms found in papers discussed in this study are added.

| Proposed term | Author(s) | Alternative term(s) | Author(s) |
|---------------|--------------------------------|--------------------------|---|
| Kingdom | Good, 1953; Takhtajan, 1969 | Realm Florenreich | Burkill, 1943; Turrill, 1959 Engler, 1882; Hayek, 1926; Mattick, 1964 |
| Subkingdom | Good, Takhtajan | Unterreich (Dominion) | Mattick (Takhtajan) |
| Region | Burkill, Thorne, 1963; | Gebiet | Engler, Hayek, Mattick |
| Subregion | Turrill | Region | Good, Takhtajan |
| Province | Thorne | Domain | Turrill |
| | Thorne | Gebiet | Mattick |
| | | Provinz | Engler, Hayek |
| Subprovince | Thorne | Unterprovinz | Hayek |
| District | Thorne | Bezirke | Hayek |
| Subdistrict | | Unterbezirke | Hayek |

The alternatives given are only more or less equivalent, e.g. Good's Region and Engler's Gebiet are actually something between my region and subregion.

Criteria for the diagnosis of these phytochoria have, as far as I know, never been exactly given. The degree of genus endemism for the higher ranks are perhaps the best criterion. For a region 20—30 % endemism should be required, increasingly lower percentages for the lower ranks. It would probably be best to found districts and sub-districts at species level. This is all very general. The number of taxa should also play a role, as there would be little sense in assigning *Desventuradas* Is. the rank of subregion because four of its 17 genera are endemic.

The proposed hierarchical subdivision of the Pacific can best be understood by studying table 6 in conjunction with fig. 37. In the latter the thickness of the lines reflects the strength of floristic boundaries.

In the Pacific the boundary between the Old and New World floras is situated in the E. Pacific. This is a boundary between Kingdoms or Realms and will be indicated further as Engler's line.

The Bonins form a district of the E. Asiatic region, separated from the rest of the Pacific by Hosokawa's line. No subdivision of the E. Asiatic region is attempted here.

New Zealand s.l. (including Lord Howe, Chathams, etc.) belongs to the Australian region as a distinct subregion, most closely related to the SE. part of Australia. Of Australia also no further subdivision is made. Neither has a subdivision been attempted in any detail of New Zealand s.s.

Lord Howe and Norfolk stand somewhat apart within the subregion, with affinities to New Caledonia.

New Caledonia is somewhat problematical. To give it a rank equivalent to Australia or Indo-Malesia on account of its high degree of endemism would obscure its relationships with both New Guinea and Queensland. To include it with any of these would be equally unsatisfactory. I have therefore assigned it the rank of region, provisionally within the Australian Kingdom.

All the rest of the Pacific west of Engler's line as far west as SE. Asia forms one huge region, Malesia. Malesia here thus forms a region together with the part of the Pacific alluded to above. In the sense of the 'Flora Malesiana Project' as delimited by Van Steenis (1950) 'Malesia' comprised the Malay Peninsula, the Greater and Lesser Sunda Islands, the Philippines, the Moluccas and New Guinea, with sharp floristic boundaries with SE. Asia, Formosa and Australia. The one with Micronesia and Melanesia he found artificial, that is to say, there is an abrupt but one-sided termination of many genera toward these archipelagos. I maintain the boundary with Micronesia for practical purposes. One of the subdivisions of 'Malesia' sensu Van Steenis is the E. Malesian Province of which the Solomons form a distinct district. Micronesia including Central Polynesia is separated from this province by what I propose as Fosberg's line (see chapter II). The W. Carolines are by far the richest of the island groups and form one of the districts of the Micronesian Province separated by Kanehira's line.

Another province that can be distinguished is formed by the New Hebrides, Fiji, Samoa and Tonga. The demarcation between this and the E. Malesian Province is much more pronounced and moreover not so 'one-sided' as Fosberg's line. There is a clear floristic demarcation with SE. Polynesia. Within this SW. Pacific or E. Melanesian Province the New Hebrides stand somewhat apart on account of distinct Australian and New Caledonian features.

SE. Polynesia forms another province consisting of the Cook Is., Societies, Tubuai, Tuamotus, Marquesas and Rapa I. This province is floristically related to E. Melanesia despite a rather sharp demarcation that I propose to indicate as Smith's line; the alliance with Hawaii is weaker. Within SE. Polynesia Rapa has a special position having a better representation of Subantarctic and New Zealandic elements than in any of the other islands of SE. Polynesia.

Another island group presenting difficulties is Hawaii. It certainly belongs to the Old World flora and has distinct Indo-Malesian features. Its strongest relations are with SE. Polynesia, but the degree of endemism is high and there is a small but more distinct American element than in any of the islands groups discussed so far. I think the floristic character of Hawaii can best be evaluated by ranking it as province within the Malesian Region.

The islands east of Engler's line form part of the New World flora, for which no further subdivisions can be given. Judging by the very weak floristic relations between the island groups, I would expect that they will have to be accommodated in different provinces or even regions. Juan Fernandez on account of its high degree of endemism and weak but distinct Old World elements should certainly rank as a province of its own.

This in broad lines is the framework of a geographical subdivision of the Pacific based on Phanerogam genera. A finer and more exact subdivision into districts and subdistricts could perhaps be based on species distributions.

An analysis of all Phanerogam genera known at present should be the basis for a rational subdivision of the whole world.

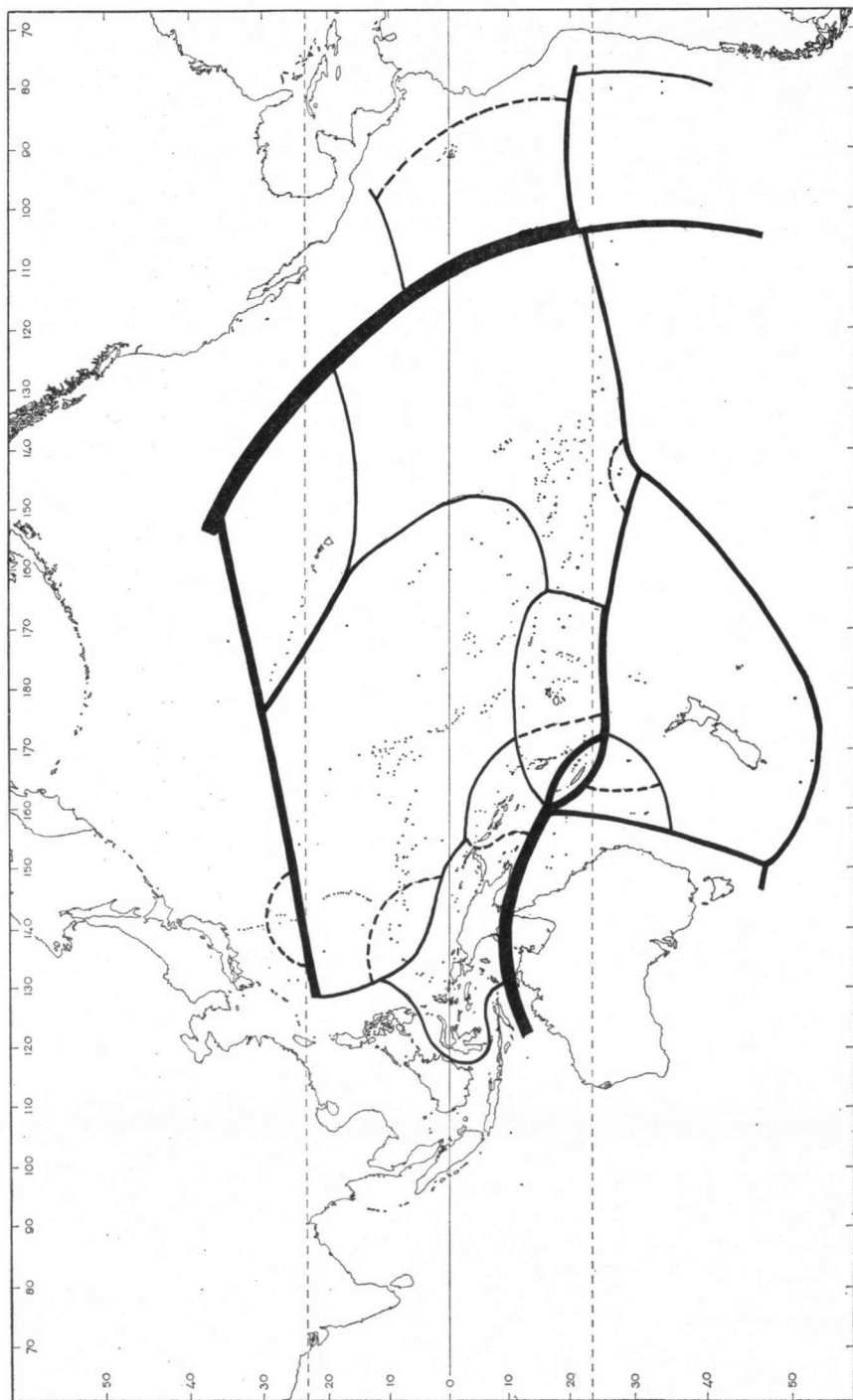


Fig. 37. Hierarchical subdivision of the Pacific. The thickness of the lines indicates the strength of floristic demarcations. See table 6 for full explanation.

Table 6. — Hierarchical subdivision of the Pacific. The subdivision below the rank of Province has not been carried out in detail. Only some of the more distinct have been enumerated, some of these could perhaps best be regarded as subprovinces.

| Kingdom | Region | Subregion | Province | Subprovince | District |
|--------------|------------------|------------------|----------------------|---------------------|---------------------|
| Holarctic | E. Asia | | | | Bonins |
| Paleo-tropic | Malesia | SE. Asia | | | |
| | | E. Malesia | W. Malesia | | |
| | | | E. Malesia s.s. | | Solomons |
| | | | Micronesia s.l. | | W. Carolines |
| | | | E. Melanesia | | New Hebrides |
| | | | SE. Polynesia..... | | Rapa |
| | | | | | Hawaii |
| Australia | New Zealand s.l. | New Zealand s.l. | New Caledonia..... | | Loyalties |
| | | | | Lord Howe + Norfolk | |
| | | | | | Subant. Is. of N.Z. |
| | | | | | Chathams |
| New World | | | | | Revilla Gigedos |
| | | | | | Galapagos |
| | | | | | Juan Fernandez |

4. Dispersal spectra (See Table 4)

As mentioned before only those genera which have been revised have been considered, i.e. 345 out of a total of 1666 (See Chapter III, 8).

These genera have been assigned to seven dispersal classes: anemochores, hydrochores, endozoochore, epizoochore, diplochore, unknowns with small diaspores up to 3 mm diameter, and unknowns with larger diaspores over 3 mm diameter.

The first four classes only contain genera for which actual observations on their dispersal exist. They are not grouped according to the morphology of their diaspores.

Under 'dispersal' is here solely understood the possibility of long distance transport. I do not wish to indulge on the effectiveness of the means of dispersal.

Table 4 (bottom) is a survey of the dispersal spectra of all Pacific island groups and is based on the revised taxa only.

Rather than discuss the dispersal spectrum of each individual island group, I will survey the characteristic feature of each dispersal class by means of table 4.

Wind-dispersed genera

It is rather surprising that relatively so few genera are wind-dispersed. It is still more surprising to find that most wind-dispersed genera are almost confined to the island groups near source areas: Bismarcks, Solomons, W. Carolines. On New Caledonia also they are well represented. Remote islands where wind-dispersed plants could be expected to be well represented, at least proportionally, are poor in such genera: Hawaii and SE. Polynesia. Also Carlquist (1967a) concluded that 'air flotation' is of little importance.

Water-dispersed genera

About 10 % of the genera considered have diaspores fit for (sea)water dispersal. These too are in general numerically best represented on the least isolated islands. Proportionally, however, they form an important portion of the genera on the most remote and often the lowest island groups in the Pacific. In Central Polynesia they form 50 % of the genera, in N. Tuamotus 37.5 % and in the Marianas 32.6 %. Also obvious is the fact that the percentages of this category are high in all but the non-tropical island groups.

Endozoochores

More than a third of the genera have diaspores that lend themselves to internal transportation by animals, in this case by birds and bats. No distinction has been made in bird- or bat-dispersed genera. Most of the 'bat-fruits' are also eaten by birds. Specific 'bat-fruits' are few in the Pacific, at least in the genera here considered.

Although the genera of this category also are most numerous on the larger and least isolated islands, proportionally they are almost evenly distributed over the Pacific.

Epizoochores

Only a small number of genera could be assigned to this category.

This is a group of genera which could be expected to be most successful in colonizing the most distant islands.

These genera are numerically best represented in New Zealand, Hawaii and Galapagos and proportionally best represented in Kermadecs, E. Central Polynesia, S. Tuamotus, and Galapagos. Thus this category comes up to expectations. In view of the small numbers, however, conclusions are rather hazardous.

Diplochores

There are also relatively few diplochores. It is possible that some genera that I have classed as either water- or bird-dispersed are actually diplochores. On the other hand, if a so-called diplochorous plant has fruits eaten by e.g. bats and at the same time is dispersed by ocean currents, it may well be that the latter agent is more important for its range.

As with the foregoing category an increase of these genera is to be expected, at least in proportion with the increasing distance from source areas.

Numerically diplochores are most abundant in the Melanesian island groups, the W. Carolines and also Hawaii. Proportionally the highest figures are found for Lord Howe I., the E. Carolines, W. and E. Central Polynesia, Fiji, Tubuai, the N. Tuamotus, Hawaii, and Galapagos. So, generally speaking the more isolated island groups have the highest figures, but again the small number of genera involved make conclusions unconvincing.

Genera with small diaspores

A rather large number of genera do not exhibit any 'adaptation' towards the dispersal agents mentioned. As 'small' I have here considered those diaspores of less than 3 mm

in diameter without any devices for dispersal. Genera of this type form c. 20 % of the total. They can be expected on the least isolated islands.

Numerically they are found to be most frequent in New Zealand, Hawaii, New Caledonia, the Bismarcks, Fiji and Juan Fernandez. Proportionally the highest figures are found for Juan Fernandez, New Zealand and adjacent islands and Hawaii, somewhat lower figures for the Societies and Marquesas. In other words, genera with small diaspores are best represented in the non-tropical islands and the highest islands in the tropics. Especially the high figures for New Zealand, Hawaii and Juan Fernandez are striking. To some extent this is reminiscent of Stapf's analysis of the Kinabalu flora (Stapf, 1894) which showed that the highest vegetation zone (the alpine zone) showed the greatest percentage of non-adapted small diaspores.

Genera with large diaspores

This category comprises the genera with 'non-adapted' diaspores larger than 4 mm in diameter. This class again forms a remarkably large percentage (nearly 20 %) of the total. These genera, even more than the foregoing, can be expected to be of very limited distribution.

Indeed they are most numerous on the Bismarcks and Solomons, which are generally believed to be (sub)continental. Also the New Hebrides, New Caledonia, the W. Carolines and Fiji have a high representation of 'barochores'. In addition to the islands just mentioned, fairly high percentages are found for the E. Carolines, Samoa, and some island groups in SE. Polynesia.

Of course this is only a very crude approach. This class contains a number of genera that appear to have poor dispersal capacity throughout their history, such as *Araucaria*, *Agathis-Conif.* and *Nothofagus-Fag.*, besides some like *Fitchia* and *Oparanthus-Comp.* that have been claimed by Carlquist (1967a) to be basically epizoid and wind-dispersed. *Nesoluma-Sapot.* that I have also placed here is considered to have drifting capacity by the same author. None of the first three genera occur beyond the Andesite line whereas the other three genera are from SE. Polynesia and Hawaii.

Summarizing the conclusions regarding the dispersal spectra and assuming that the 345 genera considered form a representative, random sample of the whole, it can be stated that:

(1) Wind is not an important agent of dispersal in the Pacific. Wind-dispersed genera are almost confined to the islands near putative 'source areas'.

(2) Genera with diaspores fit for water dispersal are proportionally best represented on isolated low islands, but at the same time their percentage is fairly large throughout the Pacific.

(3) On most islands genera with diaspores fit for endozoid dispersal are generally most numerous.

(4) Epizoid dispersal plays a minor role. There is an indication that genera of this category are better represented on the isolated high islands.

(5) Diplochores are also few in number. They are almost evenly distributed over the Pacific, but increase somewhat proportionally with increasing isolation.

(6) Genera with non-specialized small diaspores are rather numerous. Proportionally they increase slightly with increasing isolation and height of the islands.

(7) Genera with large, heavy diaspores are also rather well represented. In absolute number they are best represented mainly on the tropical islands within the Andesite line: W. Carolines, Bismarcks, Solomons, New Hebrides, New Caledonia, Fiji but proportionally they decrease only gradually from west to east.

(8) In the non-tropical islands water-dispersed genera, diplochore and 'barochore' are poorly represented.

(9) The great majority of the non-tropical islands have genera that are either fit for endozoic dispersal or have small non-specialized diaspores.

V. DISCUSSION OF HISTORICAL GEOGRAPHIC IMPLICATIONS

Can the main conclusions to which this floristic analysis has led be used for historical plant-geographical speculations?

Though the data will prove to contain some inadequacies in detail, they can be used for correlating floristics with historic plant-geography.

However, the difficulty or even hazards of such a correlation are due to the lack of basic facts regarding the speed of evolution and extinction, effectiveness of dispersal, palaeoclimatology and its bearing on the ecological response of plants, and the historic geological events involving the distribution of land and sea in the Pacific in the past.

This combined with the restricted method used in this floristic approach induces caution in the historical interpretation of the results.

Moreover, any ideas I have in this direction have already been expressed by somebody else.

It is therefore with great reluctance that I touch upon this subject at all. No doubt the outcome of this analysis can and will be found by someone to fit some theory exactly!

As is well known the peopling of the Pacific is explained by hypotheses that in their extreme forms are diametrically opposed. In brief they can be formulated as follows:

(a) The present day configuration of land and sea has approximately always been as it is. The islands are geologically young, hence the flora is recent and must have come by random oversea dispersal.

(b) The present day islands are the remnants of old foundered continents, hence the present day flora is a relictual one that has originated by slow overland dispersal.

Arguments pro and contra these hypotheses need not again be repeated. It was a subject of discussion during the Tenth Pacific Science Congress (Gressitt, 1963) and more recently during a symposium on Solomon Islands biogeography (Corner, 1969a).

Variations of the first viewpoint have been put forward by Darwin (1859), Guppy (1906), Gulick (1932), Fosberg (1948, 1963), Carlquist (1965, 1967a), and Thorne (1969); of the second by Hooker (1859), Engler (1905), Skottsberg (1928, 1940), Van Steenis (1934—1936, 1962), Florin (1940, 1963), Croizat (1952, 1958), Corner (1963, 1967), and Whitmore (1969).

The main object of this chapter is to see how the bulk of the facts can best be explained. I shall try to do this as unbiassed as possible. It is not my purpose to try and explain any hypothesis. I think a phytogeographer should not in the first place worry about the explanation of geophysical hypotheses. He can do no more than provide circumstantial evidence in favour of a theory and should not too readily dispose of a theory if he is unable to explain it.

According to the above mentioned opposed theories of a generally recent nature of the flora of the Pacific islands against a mainly relict one, the flora would be said to have an 'oceanic character' in the first case and a 'continental character' in the second.

Several authors have given the supposed characteristics of oceanic and continental islands, one of the earliest being Wallace (1880), one of the most recent ones Van Steenis (1964).

Some typical oceanic features are given: *paucity* (less taxa than in continental areas of comparable size); *disharmony* i.e. many groups are lacking (especially those with a poor capacity for crossing sea barriers), those represented showing excessive *endemic development*; *woodiness* of otherwise notably herbaceous taxa.

Though the last point falls beyond the scope of this work, it has frequently been used as a strong indication of the 'oceanic' character of islands. Although as early as 1885 Hemsley and of late Van Steenis (1964) denied that this is a characteristic feature of the flora of permanently isolated islands, the matter has of late received a new impetus through Carlquist (1965, 1970). He explains this woodiness as a response of originally short-lived herbs to the moderate climate of oceanic islands, which permits continued growth. Carlquist suggests that the wood structure of some Polynesian families, among which the *Compositae* and *Campanulaceae* and other taxa, show that they were originally herbaceous. Not being an anatomist I cannot judge the merits of this opinion. But I have two remarks to make:

(a) As has already been pointed out by the above mentioned authors there are numerous examples in continental areas of woody species of otherwise herbaceous genera, such as the woody *Lobelias* and *Senecios* of Africa, *Espeletia-Comp.* and *Puya-Brom.* in the Andes, *Olearia-Comp.* in the SE. Pacific including Australia and New Guinea, *Vernonia-Comp.* in Indo-Malesia, and various continental species of *Euphorbia*, *Phyllanthus*, *Oxalis*, *Solanum*. I think nobody would consider this woodiness is the result of 'moderate climatic conditions', which Carlquist assumes to be the cause.

(b) Even granting that the congenial climate of islands does indeed promote continued growth and thereby the formation of woody elements, it still does not answer the one basic question: How did the plants get there? If it is only a response to climatic change it becomes irrelevant.

For woodiness to be regarded as an indication for an oceanic origin of islands it should be shown that the woody island representatives have dispersal mechanisms superior to related representatives found on continents. As far as I can see this evidence is slender.

I intend to discuss the following topics in connection with the above:

- a) Impoverishment from west to east.
- b) Correlation between distance and floristic affinity.
- c) The dispersal spectra.

As these points are interrelated it will not be possible to discuss them exactly in this sequence.

In the discussion of the distribution types it has already been seen that these can be arranged in groups that differ in detail. This fact in itself is not in agreement with a completely random process.

The distribution types spectra of the tropical Pacific islands has been seen to show a decrease in Old World genera from west to east. A difficulty presenting itself is the fact that the islands are not equally well-known, but this objection is obviated by not considering the actual numbers of genera but their percentage of the total. I have already shown that for type 4 (Old World genera) the percentage remains practically the same from west to east while the other types gradually decrease. This can best be shown graphically. Fig. 38 shows the decreasing percentages of all Old World genera, fig. 39 the decrease in the Malesian types (5, 5 a & 5 b) taken as a whole and fig. 40 the decrease in Australian genera (type 6). In fig. 41—43 percentages based on the revised taxa only are given and these also show the close agreement with those based on all genera.

The figures show a decreasing percentage of Old World genera *sensu lato* (types 3—6 a & 7 a) spreading out from New Guinea, which is apparently the source area, the decrease

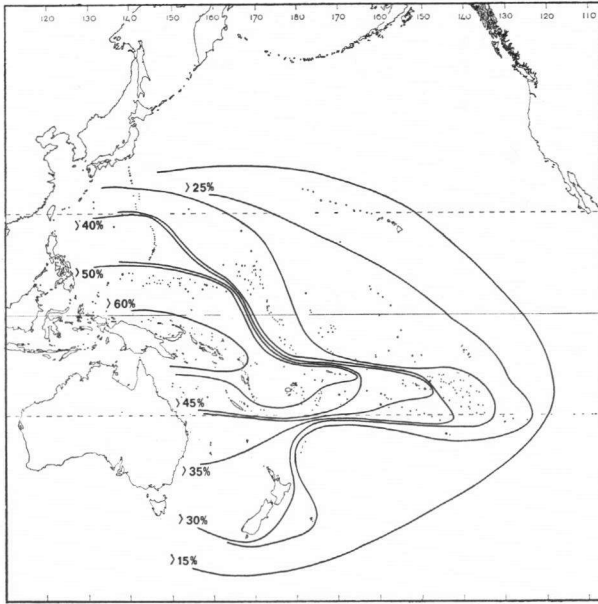


Fig. 38. Decreasing percentage of Old World genera (distribution types 3, 4, 4 a, 5, 5 a, 6, 6 a, 7 a) from west to east.

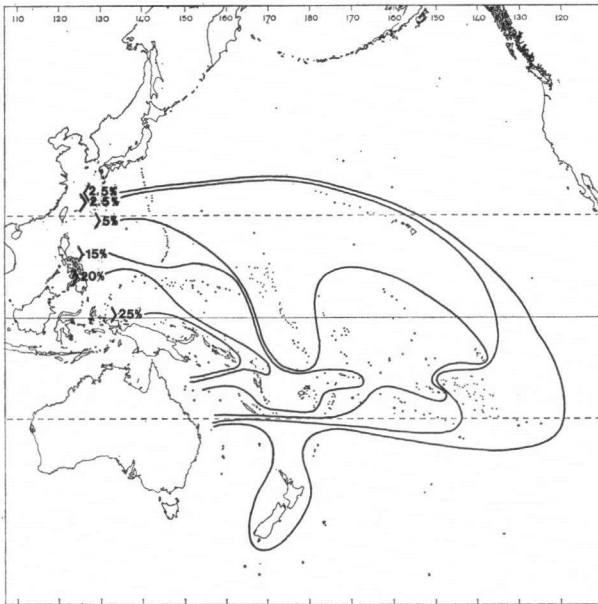


Fig. 39. Decreasing percentage of Malesian genera (distribution types 5, 5 a and 5 b) from west to east. Note the high percentage in Carolines, Bismarcks, Solomons, the New Hebrides, Fiji, and Samoa.

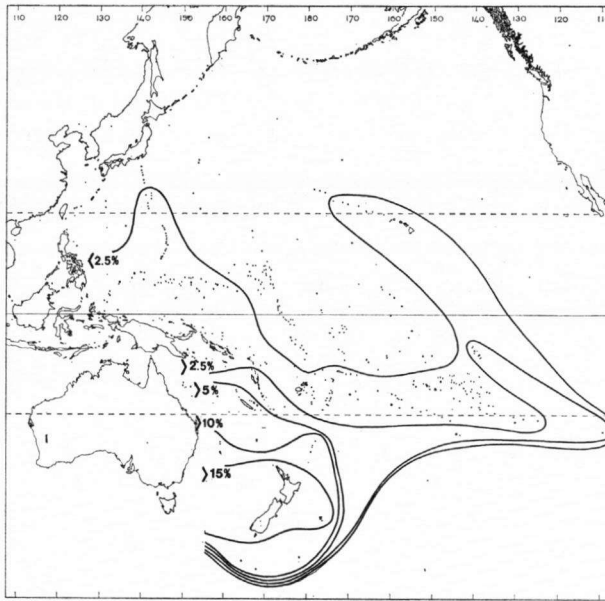


Fig. 40. Decreasing percentage of Australian genera (distribution type 6). Note the high percentage in New Zealand and adjacent islands and the uniformly low percentage in most of the rest of the Pacific.

is most gradual in a broad zone including the Solomons, Fiji, Samoa, and the Society Is. The same can be observed with the Malesian genera (types 5—5 b), most striking here is the abrupt decrease of these beyond the Carolines, Bismarcks, Solomons, New Hebrides, Fiji and Samoa. The percentage of Australian genera (type 6) is only high in New Zealand and adjacent islands.

What does this suggest? At first sight it is tempting to regard these as reflecting progressive equiformal areas as discussed by Hultén (1937) for the Arctic and Boreal flora. Australia would have to be regarded as the source area for New Zealand s.l. and New Guinea as that of the tropical islands. This idea is strengthened by the fact that there is only a weak counterbalancing increase in Pacific taxa.

However, it must be kept in mind that the percentage of distribution types will always decrease away from a centre. If the percentage of, say Malesian genera to the west were calculated, e.g. in the series: India, Kashmir and Afghanistan, the same phenomenon would be found. But in that case the percentage of other distribution types would increase. This point will be dealt with again later.

First the decrease of genera from west to east has to be considered. This phenomenon has in zoogeographical papers given rise to the idea of a 'filter effect' and is discussed among others by Zimmermann (1948), Darlington (1957) and MacArthur & Wilson (1967). Organisms spreading to islands at various distances from source areas will obviously have the greatest chance of success on the islands nearest to the source areas.

These islands may then act as a subsidiary source area or 'stepping stone'. The islands farthest from the source areas will be reached by fewest organisms and thus have the poorest biotas.

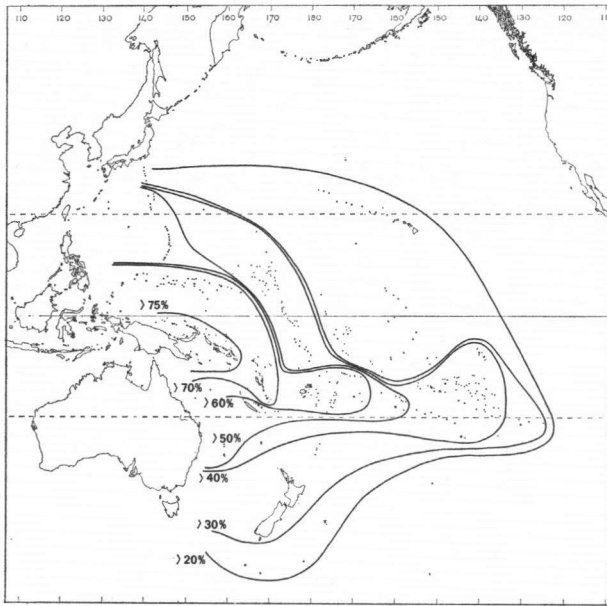


Fig. 41. As fig. 38 but based on revised genera only.

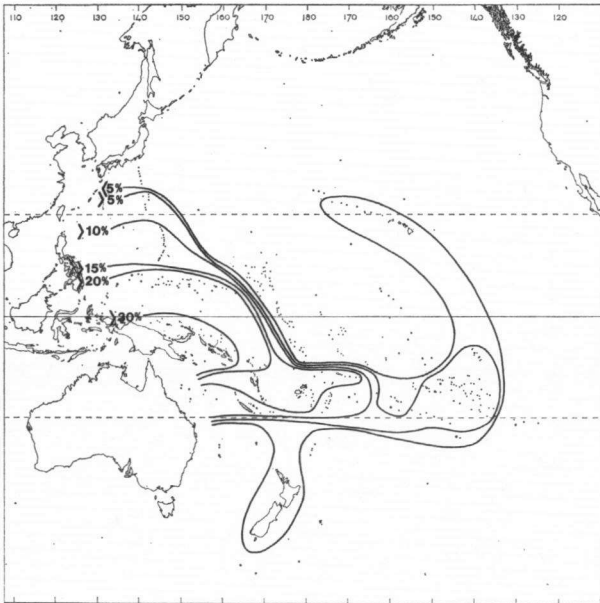


Fig. 42. As fig. 39 but based on revised genera only.

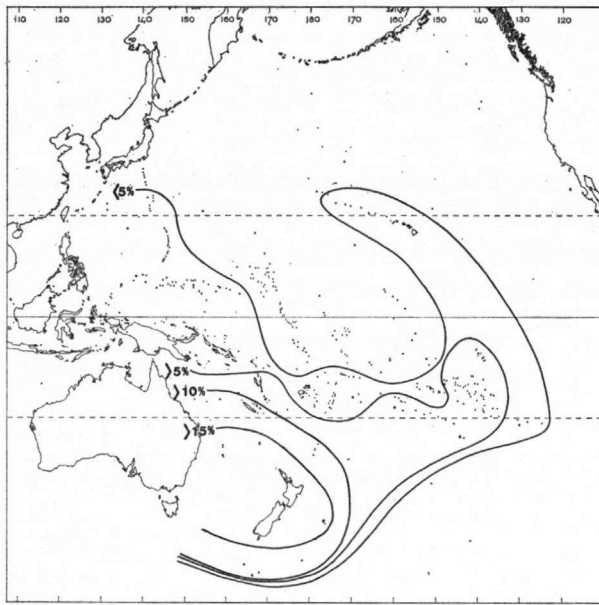


Fig. 43. As fig. 40 but based on revised genera only.

This phenomenon is unfortunately often illustrated by taking a series starting with New Guinea (c. 800.000 sq.km) and ending with the raised atoll Henderson I. (c. 25 sq.km) in the southern Tuamotus, with island groups of decreasing size (and altitude) in between.

It hardly need to be said that such a presentation of data is false, as a progressive decrease in taxa will always be found in progressively smaller areas, even on continents.

There is, however, no doubt that the west—east decrease is real, though less spectacular, when comparing islands of the same size class. The W. Carolines (336 genera) are considerably richer than the more remote E. Carolines (228 genera) and Marianas (215); the New Hebrides and Fiji (396 and 476 genera) are about twice as rich as Hawaii (226); Tonga (263) and the Loyalties (262) have more than double the number of genera known from the Marquesas (113).

In an earlier paper on the diversity of island floras (van Balgooy, 1969) I investigated this phenomenon on a world basis. It could be shown that in general there is a decrease of taxa with increasing isolation. I also argued that to regard this fact as an indubitable proof of the island's permanent isolation was insufficient. Quite independent of the question whether the plants reached the island by short-distance dispersal over land or by long-distance dispersal over sea, it must be expected that isolation leads to impoverishment. The more isolated an island is the less chance there is that any losses will be replenished. The smaller its area and elevation, the smaller and less diversified genetically its populations, the more vulnerable its flora as a whole. The flora of continental areas contains transient species that are only maintained through continuous replenishment from surrounding areas. This is comparable to the 'elevation effect', discussed by Van Steenis (1961) and Backhuys (1968), found in mountain plants. Mountain plants only occur on mountains of a certain minimum height. On these they are often found consider-

ably lower than this limit. But then they are not seldom sterile, hence they are only maintained at these low altitudes through continuous downward transport of diaspores.

The idea that the poverty of islands is probably in the first place to be ascribed to lack of ecological possibilities (niches) and not to accessibility finds further support in two papers by Runemark (1969, 1970) on the flora of the Cyclades in the Aegean Sea. This island area was continuous land about one million years ago and is 'continental' by all standards. Yet the flora is poor in comparison with the surrounding areas from which the islands are isolated by sea barriers not exceeding 20 km. Runemark ascribes this poverty to what he calls 'reproductive drift': species in a population represented by few individuals are the first to be eliminated, irrespective of their competitive ability.

Although I doubt whether this is the sole explanation, the fact remains that the flora of the Cyclades islands are 'too poor' with regard to their origin.

If paucity of the flora is a general character of islands independent of their geological history, one of the strongest indications of their oceanic origin loses its meaning, unless the increased poverty of the islands is correlated with an increasing 'dispersibility' of the flora. The result of an analysis, admittedly based only on a part of the flora, as discussed earlier was rather disappointing in this respect.

Wind dispersal appears to play only a minor role, dispersal by the sea although more important also does not come up to expectations, except for the smaller and most isolated islands. Furthermore genera with diaspores fit for epizooic dispersal and having more than one main dispersal agent, although relatively small in number show a slight increase with increasing isolation.

The most unexpected result is the large number of genera with bat and bird dispersed diaspores throughout the Pacific. Perhaps the most promising line of investigation in this field is a study of bird migrations in connection with their feeding behaviour. Recent experiments e.g. by De Vlaming & Proctor (1968) and Olson & Blum (1968) have revealed that the retention and viability of seeds in birds is much longer than generally believed. But many more experiments are needed before any generalisations can be made. The fact that bird-dispersed taxa figure so strongly in the dispersal spectra does not of course imply that the distribution of the taxa was brought about by this means. It may be only of local importance.

Genera with the poorest 'dispersibility' were found most numerous on the W. Carolines, Bismarcks, Solomons, New Hebrides, New Caledonia, and Fiji, although their presence on many much more isolated islands is puzzling. A significant fact not revealed by the figures is that several genera with the poorest dispersal capacities such as *Nothofagus-Fag.* and some Conifers (Preest, 1963) do not occur beyond the triangle Bismarcks, Tonga and New Zealand.

The representation of genera with 'small diaspores' in the dispersal spectra is curious. They could be expected to have a distribution similar to the group of 'large diaspores', that is, to be limited to the islands just mentioned. Actually, apart from being well represented in these islands, a large number are also found in Juan Fernandez and in Hawaii. Especially the strong representation in Hawaii is hard to understand in view of the present isolation of this island group.

Guppy (1906), who did more for the knowledge of plant-dispersal than anybody else, and Ridley (1930) with his unrivalled knowledge of dispersal on a world basis, both considered that the dispersal capacities of plants were insufficient to account for all distribution phenomena. To explain these Guppy resorted to unknown dispersal agents which do not longer exist. Carlquist (1965, 1967a) advanced a hypothesis that is more ingenious, the loss of 'dispersibility'. This idea may seem fantastic to some, but I think it

deserves careful consideration, although I doubt whether it can account for all distribution phenomena.

In the present state of our knowledge I cannot find a clear correlation between distribution and dispersal. The impression is that the island plants 'got there' despite lack of efficient dispersal ability rather than on account of superior dispersal capacity.

The decrease of Old World genera from west to east is, as has been seen, only partially counterbalanced by Pacific genera. This decrease is partly due to island floras being more vulnerable than continental ones. If taxa on an island become extinct they will not readily be replenished except by easily dispersed widespread genera. It will be seen from table 3 that the percentage of 'wides' increases with increasing isolation and poverty of the islands. Even if this is true one would not expect all taxa of other distribution types to disappear. Indeed the low-lying, isolated Tuamotus are still inhabited by such 'non-wides' as *Nesogenes-Verb.*, *Pritchardia-Palm.*, and the curious *Hedyotis romanzoffensis-Rub.* The islands of Central Polynesia at present consist nearly exclusively of widespread genera only (types 1 and 4) but Miss Leopold (1969) has shown that the fossil Miocene flora suggests a floristic composition not unlike that of the present day Carolines.

This all points to an impoverishment of the Pacific islands. This will have been most serious in the extra-tropical islands. The effects of Pleistocene climates in New Zealand are discussed in the papers of Burrows (1965) and Wardle (1963).

The decreasing poverty from west to east can thus be explained in other ways than purely as a result of decreasing accessibility.

Still I consider it a significant thing that many genera with the poorest dispersal capacity are limited to what roughly corresponds to the Andesite line. This combined with the fact that several primitive taxa terminate their extension into the Pacific here (*Winteraceae*, *Fagaceae*, *Balanopaceae*, *Coniferae*) must mean something. It will later be seen that some animal groups also do not occur beyond this line. As has been seen the island groups of the W. Carolines, Bismarcks, Solomons, New Hebrides, Fiji, Samoa, Tonga, and New Caledonia are also considerably richer, even allowing for size discrepancies. Thus the impression is gained that the islands to the east of the above mentioned islands obtained their flora with more difficulty. Yet the close floristic alliance between these islands and the fact that there is no clear correlation with 'dispersibility' anyhow suggests closer proximity e.g. in the form of island chains. In my opinion the best example of a truly isolated island without any terrestrial or insular connections in the Pacific is Easter I. and in the Atlantic Ascension (see also Van Balgooy, 1969).

Van Steenis (1962) argued for trans-Pacific tropical connections, anyway land surfaces in some form. If such connections existed they are hardly reflected in the present day flora of the E. Pacific. The 80 cases of amphi-transpacific tropical affinities mentioned by Van Steenis contain 12 of suprageneric rank, which suggest an older phase of the Earth's history. Moreover, some are not strictly tropical such as the eurytherm genera *Eurya-Theac.*, *Heliconia-Mus.*, *Perrottetia-Celast.* and *Weinmannia-Cun.* The 85 southern (sub-tropical to temperate) cases reflect a much closer affinity in view of the smaller number of taxa and greater distances concerned. It has been seen that American genera (type 9) are almost restricted to the islands near the American continent.

These southern affinities between South America and the SW. Pacific area include various putatively old groups such as *Winteraceae*, *Coniferae* and *Fagaceae*, and are not only of family and genus level but very often include species or species pairs, not only suggesting that migration was facilitated in the past but that it lasted longer than the tropical connections. This agrees with the claim for 'more land in the south' expressed by various authors.

I feel incompetent, however, to make any guesses regarding the possible age or duration, let alone the form, of such connections. In other words, it is irrelevant to me whether these connections involved 'bridges' or 'drift'.

Earlier in this study I have already touched upon the weak floristic affinities between the American Pacific islands as compared with those in the West Pacific. This can be illustrated by some figures presented in table 7. To make the figures comparable one pair of American Pacific islands has been contrasted with pairs of West Pacific islands with approximately the same generic ratio. For each pair the distance in kilometres between the two groups and the similarity coefficient of Kroeber is given. It is quite obvious that although in each case the distance between the American island groups is shorter floristically they are farther apart than the other island groups.

Table 7.

| Island group | Number of genera | Common | Distance (km) | Kroeber coeff. |
|----------------|------------------|--------|---------------|----------------|
| Revilla Gigedo | 86 | 13 | 3250 | 18.4 |
| Cocos | 60 | | | |
| E. Carolines | 228 | 103 | 6500 | 48.2 |
| Society Is. | 201 | | | |
| Lord Howe | 138 | 41 | 5500 | 36.9 |
| Rapa | 93 | | | |
| Galapagos | 190 | 23 | 500 | 25.2 |
| Cocos | 60 | | | |
| W. Carolines | 336 | 67 | 9000 | 40.0 |
| Marquesas | 113 | | | |
| Solomons | 654 | 153 | 5500 | 49.8 |
| Society Is. | 201 | | | |
| New Caledonia | 655 | 116 | 6000 | 34.5 |
| Hawaii | 226 | | | |
| Galapagos | 190 | 49 | 3250 | 41.4 |
| Revilla Gigedo | 86 | | | |
| Fiji | 476 | 167 | 3250 | 59.1 |
| Society Is. | 201 | | | |
| Marianas | 215 | 68 | 8000 | 54.5 |
| Tubuai | 88 | | | |

In each of the above three series it can be seen that there is conspicuously less floristic resemblance between the American Pacific islands than between those west of Engler's line, even though in most cases the distance between the latter is greater.

This suggests that the American islands are independent of each other contrary to those west of Engler's line which show more floristic coherence than expected considering the distances.

Recapitulating I think it may safely be stated that it would be impossible from the present configuration of land and sea to predict the outcome of this analysis. Thorne in his contribution to the biogeography of the Solomons (in Corner, 1969) stated that the flora of New Caledonia is exactly what one should expect; to me this is an incomprehensible statement. I myself at least would have expected an impoverished Malesian flora with some Australian and New Zealandic elements and few if any endemics. Further, I could not possibly have foreseen the other results when I started on this subject ten years ago, completely uninitiated.

Neither is the outcome in agreement with the idea of a strictly continental relic flora over the whole range. The near absence of American taxa west of Engler's line and the predominantly southern floristic connections indicated, together with the abrupt decrease of many taxa beyond the line Carolines, Bismarcks, Solomons, New Hebrides, Fiji, Samoa, Tonga and New Zealand and the fact that within this boundary many genera are found with poor dispersal capacities and primitive families, suggest that somehow migration within this area and over the south to South America was in the past much easier. I favour the theory of former continuous land connections here. The facts further suggest that accessibility beyond this boundary has been less easy. The distribution can hardly be explained under the present land configuration either. Long-distance dispersal can explain a number of facts but I favour Ladd's idea (1960) of a 'giant archipelago' which he formed from fossil mollusc evidence.

The outcome revealed by the present work can tentatively be interpreted historically as follows:

- (1) From the floristic affinity of the recent tropical Pacific flora west of Engler's line it appears that there are no indications of a recent land connection with the Neotropics.
- (2) The floras of the American Pacific islands have evolved independently of each other, each having a different set of American-allied taxa. No land connections, insular or otherwise, appear to be necessary to explain their flora. Juan Fernandez, however, is an exception in this matter, its connection must be assumed to have been indirect, via the south with Fuegia.
- (3) Westward connections from South America to the Old World must have existed. They must have been of subtropical to temperate character and must have included New Zealand.
- (4) New Zealand most likely had connections to the west with Tasmania and SE. Australia and to the north with New Caledonia or beyond. No other island group in the Pacific except the Chathams and Subantarctic islands is likely to have suffered more from climatic changes in the past. The relative poverty of these three groups should be seen in this light.
- (5) Terrestrial continuous connections are furthermore indicated for the following island groups in the W. Pacific: W. Carolines, Bismarcks, Solomons, New Hebrides, New Caledonia, Lord Howe, Fiji, and possibly also Samoa and Tonga.
- (6) The connections between New Zealand and New Caledonia must have been severed very long ago.

- (7) For the remaining part of the Pacific I do not think continuous or almost continuous terrestrial connections are needed to assume to explain the present flora. On the contrary they would explain too much. The floristic character of this part pleads for rather difficult accessibility. Yet under the present day configuration of land and sea the facts found are also difficult to explain. They can best be explained by archipelagic conditions.
- (8) The (archipelagic) connections of Hawaii towards Malesia appear not to have been direct through Micronesia, but by way of SE. Polynesia.

I do realize that this picture is very crude and tentative and leaves details unexplained. I have refrained from giving more than a broad outline of historical geography or an assessment of time. The important thing to stress is that the picture neither agrees with the idea of a young flora that colonized originally barren islands by means of random long-distance dispersal, nor with that of a flora that remained after the breaking up of a solid land mass. Of course, one can hardly speak of 'a Flora of the Pacific', because the surface involved is immense and the different parts are extremely diverse in richness and composition of the flora.

It supports the claims on various grounds for 'more land' by authors as Skottsborg (1940), Florin (1963), Corner (1963, 1967) and Van Steenis (1953, 1962). As far as my data on the present flora are concerned the assumption of tropical connections to the Neotropics is not warranted. Van Steenis (1962) rather inaptly called his theory 'land-bridge theory'. In a later paper (van Steenis, 1969a) he stressed that the crux of the theory is 'land' and not 'bridge', that the land may have existed intermittently and not have been continuous. This point cannot sufficiently be emphasized. To me it is entirely irrelevant what the exact nature of the connections were, what matters is that I cannot explain the facts of present Phanerogam distribution in the Pacific under the present configuration of land and sea.

This paper deals only with insular areas of the Pacific Basin. I have already pointed to the desirability to compare the results and conclusions of this study with one on continental floras. Such phenomena as impoverishment due to distance from source areas, and with decreasing size, endemism, woodiness of otherwise herbaceous taxa, dispersibility etc. should not only be studied for islands as is always done. It can only be properly evaluated if compared with what is found on continents. Are these basically different? And if so, why? Continental mountain floras are an especially promising field of comparable study. The authors who have made a study of these (Stapf, 1894; van Steenis, 1934—1936) have shown that the 'picture' presented is basically the same as that on true island floras.

VI. SUBDIVISIONS AND DEMARCATIIONS BASED ON NON-PHANEROGAMS

It is interesting to see what subdivisions and demarcation lines have been proposed for the Pacific by students of other groups than Phanerogams. It is not my purpose to give a full survey. Thorne (1963) has already done so rather recently. Only those papers which had aims and methods comparable to my own will be discussed, and then only if a sizeable group and a large part of the Pacific is considered.

The distribution of each group of organisms reflects its own history and potential. It is therefore not likely that in all cases the same picture will emerge. Whether it does or not both agreement and difference are worth examining. Wallace's line so important in bird

and mammal geography is of relatively little importance to Phanerogams, whereas the Torres Strait so prominent for the phytogeographer is hardly significant in mammal and bird geography.

Only three authors have in later years attempted a hierarchical subdivision of the Pacific based on large groups. These subdivisions will be discussed at the end of this chapter. Various authors have established biogeographic boundaries, most of which correspond with those also found for Phanerogams.

Historically the most important is the subdivision by P. L. Sclater (1858). He divided the world into six regions based on the distribution of birds. His Indo-Malayan region encompassed India, Indo-China, and the part of Malesia west of what later became known as Wallace's line. His Australasian region comprised Australia, New Zealand, Malesia east of Wallace's line (Celebes, Moluccas, Lesser Sunda Islands except Bali, and New Guinea) and the whole Pacific east to Hawaii and SE. Polynesia.

Wallace (1876) adopted Sclater's subdivision into regions and further divided each region into four subregions, based mainly on bird and mammal distribution, but other groups (Reptiles, Insects and Mollusca) were also taken into consideration. Sclater's Indo-Malayan region was called the Oriental region and was subdivided into an Indian, Ceylonese, Indo-Chinese and Indo-Malayan subregion. Sclater's Australasian region became more appropriately Australian region and consisted of the following subregions: Austro-Malayan (Malesia east of Wallace's line, including the Bismarcks and Solomons), Australian, New Zealand (including Lord Howe, Norfolk and Subantarctic islands) and the Polynesian subregion (rest of the Pacific inclusive of New Caledonia and Hawaii).

Nearly all subsequent authors recognized the E. Pacific as forming the boundary between Old and New World faunas and floras. The Malesian character of most of the biota of the Pacific except New Zealand was established by most subsequent authors.

H. Christ (1910) stated that the fern flora of the Pacific except Juan Fernandez, which belongs to South America, and New Zealand, which belongs to temperate Australia, but including Bonin, Hawaii, Lord Howe and New Caledonia, belongs to the Malesian region which furthermore comprises India, SE. Asia, Formosa and tropical Australia.

Herzog (1926) also accepted Hawaii and the Marquesas as the easternmost frontier of the Paleotropical bryophyte flora. Nearly the whole tropical Pacific is included as a separate region in his 'Palaeotropisches Florenreich'. The general aspect is that of an impoverished Malesian flora, with a high degree of endemism only found in Hawaii. New Caledonia, New Hebrides and Lord Howe are accommodated in his 'Australisches Florenreich'. Finally New Zealand is regarded part of the 'Austral-Antarktisches Florenreich', which furthermore comprises temperate Australia, Tasmania, the Subantarctic islands and temperate South America.

Berland (1928) stated that the Pacific spider fauna does not form a unity. New Caledonia and New Zealand despite some affinities with Malesia have even stronger relations with Australia. The Hawaiian spider fauna lacks many groups and shows highest specialization. Relations on the whole are most pronounced with America.

S. Ekman (1934) in a study on the tropical littoral fauna stressed the importance of 'the East Pacific Barrier' (Engler's line), a demarcation not only respected by species

but also by families. In a later work (1953) he again pointed to the importance of this demarcation for the Indo-Malesian warm water shelf fauna. Hawaii, despite the high degree of endemism, belongs to the Indo-Malesian region, New Zealand and its Subantarctic islands also have a distinct fauna. There are weak relations with temperate Australia and weaker still with temperate South America.

J. Forest and D. Guinot (1962) in a distribution analysis of the crab family *Brachyura* (Decapod-Crustacea) of the Tuamotu and Society Islands found these islands to be wholly Paleotropical in character with strongest affinities toward Malesia.

The abrupt decrease of many taxa to the east of Fiji was first noticed by Hedley (1899) who based his conclusions mainly on the marine molluscs, but included the whole animal life of the Pacific in his consideration.

Pilsbry (1900) dealing with the land snail fauna mentioned the great faunistic homogeneity of the Pacific in contrast to that of the islands in the Atlantic, where groups however close together are said to have less in common than Pacific island groups however far apart, such as the Carolines and Society Is. Another contrast is the absence in the Pacific of what are considered modern groups. He also stated that the Pacific land snail fauna does not show any links with America.

It has been seen that in Phanerogam geography the New Hebrides hold a rather controversial position having a more distinct Australian element than the Solomons and Fiji. The same phenomenon is recorded by Solem (1958, 1959) for the land and freshwater molluscs of these islands. This author found that in the SW. Pacific there are essentially three distribution types:

- (1) Paleo-oriental (Malesian) which according to him comprises Malesia, Solomons and NE. Australia.
- (2) Southern relict (Australasian), i.e. covering S. Australia, Tasmania, New Caledonia and New Zealand.
- (3) Pacific Ocean (Polynesian), covering the high islands of tropical Pacific.

Of the island groups surrounding the New Hebrides it was found that in Fiji group 3 dominates, in the Solomons group 1, whereas in New Caledonia group 2 is best represented. In the New Hebrides the three distribution types show a balanced representation.

Darlington (1957) surveyed the distribution of the vertebrate groups: Fishes, Amphibians, Reptiles, Birds and Mammals. Of the Fishes the most interesting group is that of the 'primary division' freshwater species in view of their intolerance of seawater. The extreme eastern limit is given in fig. 44, but the great majority actually terminate their eastward range in the Greater Sunda Islands (Sumatra, Borneo, Java). Another group highly sensitive to seawater, the Amphibia, have a wider extension into the Pacific (see fig. 44) with a very primitive representative (*Leiopelma*) in New Zealand. Reptiles are also widely distributed but show some remarkable features. The most striking is the famous Tuatara (*Sphenodon*), member of an ancient order extinct elsewhere but occurring in New Zealand. There is a lizard in Fiji and Tonga belonging to the otherwise entirely American family *Iguanidae* and endemic genera of Geckonids in New Caledonia and New Zealand (see also McCann, 1953). Of the Mammals rats are widely distributed but as they are often carried about by man they can better be disregarded. Marsupials occur native only as far east as the Solomons. As can be expected bats are of wider distribution.

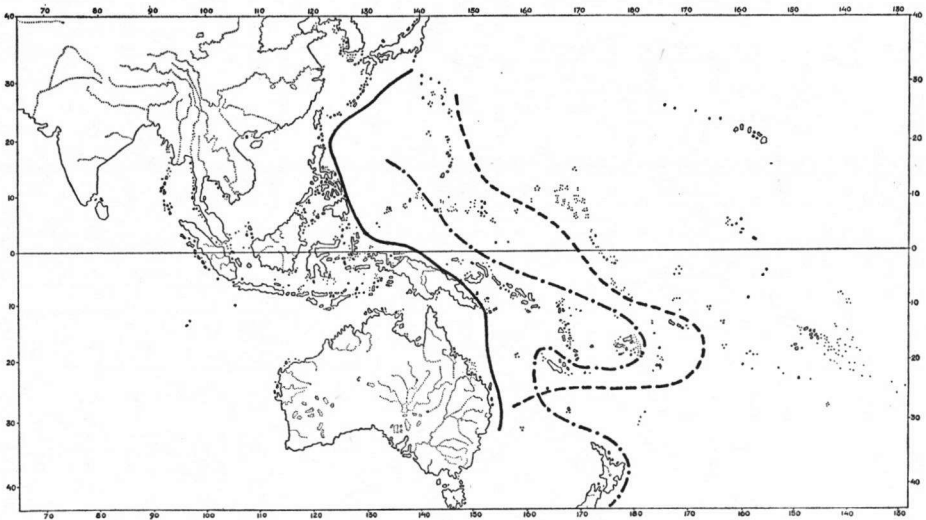


Fig. 44. Eastward boundaries in the Pacific of some important vertebrate groups: ——— primary division freshwater fishes, — . — . — *Amphibia*, — — — — — *Megachiroptera*.

A group of special interest is the *Megachiroptera* (the fruit-eating bats). They extend eastward to the Carolines, Tonga and Samoa. See also Van der Pijl (1957) and Eisentraut (1945) from whose works the eastern limit on fig. 44 has been derived. For the birds one is referred to Mayr's papers which will be discussed later:

Darlington largely accepts the old classification of Sclater as modified by Wallace. His table 10 (p. 425) is presented here in abbreviated form:

Realm Megagea

- 1 Ethiopian Region (Africa + S. Arabia)
- 2 Oriental Region (Tropical Asia + W. Malesia)
- 3 Palearctic Region (Extratropical Eurasia)
- 4 Nearctic Region (N. America + extratropical Mexico)

Realm Neogea

- 5 Neotropical Region (S. + Central America + tropical Mexico)

Realm Notogea

- 6 Australian Region (Australia, New Guinea + Pacific)

The three recent zoogeographic subdivisions of the Pacific are by Mayr, Zimmerman and Gressitt and will be discussed rather more elaborately as they can best be compared with the one I propose here.

E. Mayr (1940a) made a subdivision of the Pacific based on the distribution of land birds, and in a separate paper discussed the origin of the Pacific bird fauna (Mayr, 1940b).

Land birds are said to be ideally suited for geographic speculation as they are among the best known animal groups. Despite their potential capability of crossing sea barriers by flight, most land birds are sedentary.

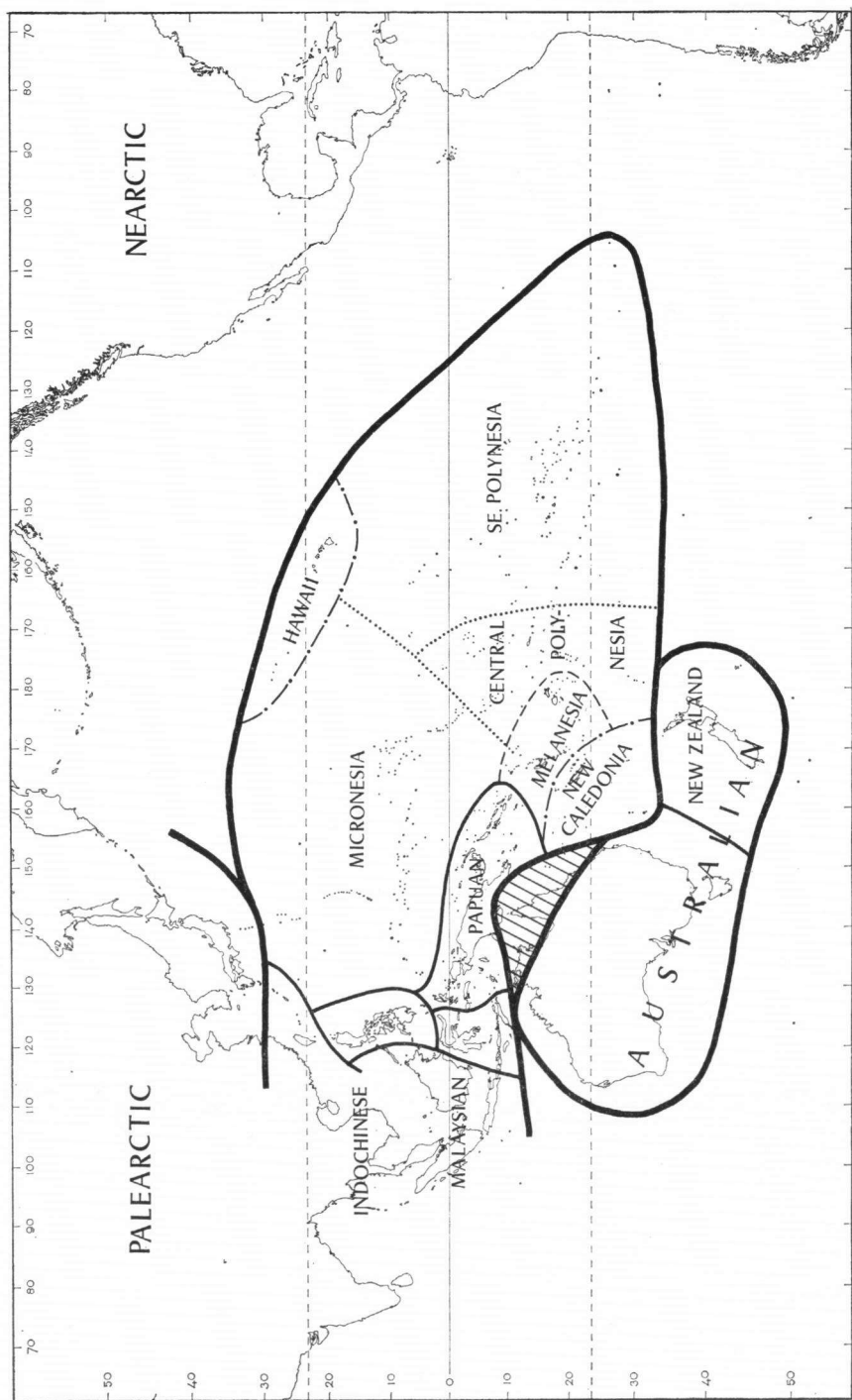


Fig. 45. Zoogeographical subdivision of the Pacific after Gressitt (1961) based mainly on insect distribution: — boundaries of regions, — boundaries of subregions, broken lines: boundaries of divisions (provinces) and subdivisions. Shaded: regions of overlap.

Mayr's 'Polynesian subregion' comprises the following four districts:

- (1) Micronesia (Palau, Carolines, Marianas, Marshalls, Gilberts). The bird fauna is relatively poor (41 genera, 8 endemic). Palau is richest and has a strong Malesian character.
- (2) Central Polynesia (Fiji, Samoa, Tonga, Union, Tokelau). There are 47 genera of which 12 endemic. Fiji is richest.
- (3) Eastern Polynesia (Cook, Society, Tubuai, Marquesas, Tuamotu and Easter I.). Poorest of the districts with 18 genera, 4 endemic.
- (4) Southern Melanesia (New Caledonia, Loyalties, New Hebrides, St. Cruz). This is the richest district, which is mainly due to New Caledonia. There are 57 genera of which 15 endemic. Relations with Australia are stronger than in the other districts.

Mayr is against placing New Caledonia in a separate subregion as often done with areas not fitting any of the major subregions. He nevertheless considers Hawaii as a subregion in its own right. There are distinct Holarctic and American elements besides an endemic family (*Drepanidae*). On the other hand there are distinct relations with the Marianas. These two subregions are linked with New Guinea. He has not decided yet whether New Guinea (including Bismarcks and Solomons) should form a subregion of Australia or a region of its own.

The Bonins form part of the Palaearctic region, Galapagos of the Neotropical region. New Zealand and adjacent islands show a predominantly Australian character.

E. C. Zimmerman (1948) in his introduction to the *Insects of Hawaii*, spent a chapter on a subdivision of the Pacific. As his ideas are largely incorporated in Gressitt's subdivision to be discussed later on, I will treat them rather briefly.

His Australian province includes Tasmania, Lord Howe, all of Australia except the Cape York Peninsula, which is part of his Papuan province, furthermore comprising New Guinea, Moluccas, Bismarcks and Solomons. New Zealand, Kermadecs, Chathams and Subantarctic islands form another province. The remainder of the Pacific except the American Pacific islands and Bonin forms another province consisting of the following subdivisions: 1) Micronesia (Marianas, Carolines, Marshalls, Gilberts), 2) E. Melanesia (St. Cruz, New Hebrides, New Caledonia, Loyalties and Norfolk), 3) Central Polynesia (Fiji, Samoa, Tonga, Ellice, Phoenix, Tokelau), 4) SE. Polynesia (Cook, Society, Tubuai, Tuamotus, Marquesas, and Line Islands) and finally the most distinct one of all 5) Hawaii.

L. J. Gressitt (1956, 1961) made a subdivision of the Pacific based mainly on two large and well collected families of beetles, the *Cerambycidae* and *Chrysomelidae*. At the same time he presented a characterization of the insect faunas of all the Pacific island groups. His survey shows some striking conformity to the situation found in the Phanerogams.

His latest version of the zoogeographical subdivision of the Pacific is reproduced here as fig. 45. All of the Pacific except New Zealand and the American Pacific islands are included in the Oriental Region. New Zealand forms a separate subregion within the Australian Region. The Bismarcks and Solomons are subordinated in the Papuan subregion of the Oriental Region, all the rest of the Pacific forms the Polynesian subregion of this and is 'a tapering fringe of the Papuan subregion with overlapping influence from the Philippine subregion and other areas'. Within the Polynesian subregion Hawaii and New Caledonia and to a lesser extent E. Melanesia (Fiji, St. Cruz, New Hebrides) hold positions of their own.

The broad outline of this subdivision agrees very well with the subdivision based on Phanerogam genera distribution.

As with the Phanerogams the limit of the Oriental Region lies east of Hawaii and SE. Polynesia.

New Zealand though having a very distinctive fauna, shows relations with South America, New Caledonia and, in particular, with SE. Australia. Yet, as with the Phanerogams many of the typical Australian taxa are lacking.

Lord Howe I. despite the striking presence of the southern family *Peloriidiidae* has an essentially tropical insect fauna many insects having their southernmost record there.

New Caledonia is assigned a high rank within the Oriental Region. Yet there is apparently nothing comparable to the highly peculiar endemic development in the Phanerogams, and no relationships with Australia. The Loyalties though faunistically belonging to New Caledonia are said to have many peculiar forms not found on either New Caledonia or the New Hebrides, which again is a feature at variance with the situation in the Phanerogams.

As in the Phanerogams there is a sharp geographic break to the east of the Solomons and Fiji. Both have very rich faunas but in Fiji several Solomon Islands genera are lacking. The New Hebrides are much poorer than either, which is also true for Phanerogams but this is in part to be ascribed to under-exploration.

In Micronesia there is an increasing poverty from west to east and from south to north; Palau is the richest as with the Phanerogams. The Bonins are said to be the northernmost station for many insects and thus belong to the Oriental Region rather than to the Palaearctic. As has been seen from the Phanerogams a sharp floristic break is indicated between the Bonins and Marianas.

For Hawaii the situation in the Phanerogams and Insects is comparable. The fauna is highly peculiar but distinctly of Old World distribution on the whole. Many families still represented in SE. Polynesia are lacking. Among the Phanerogams also a number of SE. Polynesian taxa are absent in Hawaii but conversely there are about the same number of Hawaiian taxa failing in SE. Polynesia.

SE. Polynesia is thus richer in Insects than Hawaii, but still poor compared with the islands to the west. Rapa on a small scale rivals Hawaii in the production of peculiar forms.

Comparable to the Phanerogams there is apparently little faunistic dissimilarity going from Micronesia to SE. Polynesia.

The Galapagos Is. have a highly distinctive fauna; there is hardly any relation with Polynesia. In the latter point the situation is in agreement with the Phanerogams, but as has been seen the flora can hardly be called very distinctive.

The Juan Fernandez fauna shows agreement in having relations with Polynesia and by the presence of certain forms not found on the South American continent.

Despite some differences in detail there is thus great agreement in the subdivision of the Pacific as based on Insect and on Phanerogam distribution.

Although the picture presented by the non-Phanerogams, especially the one given by Gressitt for the insects, shows some striking parallels with the Phanerogam picture, there are some points of difference just as interesting. There is agreement in the far reaching Old World character of the Pacific and the special relations with Malesia, the latter not being found in the American Pacific islands and New Zealand. There is also agreement in general that many Old World groups terminate in the western part of the Pacific.

But what strikes me even more is the apparently much stronger impoverishment of animal groups (especially vertebrates) from west to east and the much more pronounced endemic development going with it. This has led to many endemic genera and even families in such islands as Hawaii and Galapagos. Some high SE. Polynesian islands also

among the non-Phanerogams exhibit peculiar forms. The Galapagos flora does not show any unexpected spectacular development, whereas New Caledonia 'a veritable botanical museum' does not seem to have produced a parallel development in animal forms. Of course it can be said that this is due to the fact that the criteria for botanical and zoological classification need not be the same, but I doubt whether it is as simple as that.

Could it be that plant taxa are generally more conservative and that in many animal groups isolation leads to the 'speeding up' of evolution? Skottsberg (1960) found that the flora of South Georgia shows every sign of being recent. The group was apparently completely ice-covered during the Pleistocene. The present day poor flora is believed by Skottsberg (an acknowledged sceptic regarding long-distance dispersal) to have come mainly by oversea transport by westward wind from Fuegia, for which the South Georgian plants are all well suited. The plants do not show any sign of change. Yet there are two endemic species of land birds (a teal and a titlark) that similarly cannot have survived maximum glaciation.

This idea is not new. Hooker (1860) in his famous essay on the flora of Australia had remarked on the probable antiquity and greater permanence of plant forms. Further arguments in favour of this viewpoint have been worked out by Van Steenis (1969b) in a paper on species development in the Malesian tropics, and it is strengthened by the present outcome.

APPENDIX: CENSUS OF PACIFIC GENERA

The Appendix gives a survey of all Phanerogam genera recorded in literature or otherwise known to occur in the Pacific. The columns represent the unit regions, in the final two the distribution type and dispersal class are indicated. In the horizontal rows the genera and other taxa are arranged alphabetically according to families which themselves are also arranged in alphabetical sequence. The families are taken in an inclusive sense. So, *Coniferae* comprise *Araucariaceae*, *Cupressaceae*, *Pinaceae*, *Podocarpaceae*, and *Taxaceae*; *Monimiaceae* comprise *Amborellaceae*, *Atherospermataceae*, *Monimiaceae* s.s., *Sphenostemonaceae*, and *Trimeniaceae*. The most current synonyms of both families and genera (as found in Pacific literature) are added in brackets, e.g. *Myrsine* (*Rapanea*, *Suttonia*), *Ipomoea* (*Calonyction*, *Quamoclit*). Where possible the affinity of the endemic taxa has been traced. This has been indicated in two ways. After the endemic genus the genus to which it is allied is given in brackets if it also figures in the list, e.g. *Labordia* (aff. *Geniostoma*), if it is not in the list it is indicated in the column where it occurs; example: *Hesperomannia* of Hawaii has its closest allies in America, thus in the column for Hawaii 'Am' is filled in (see further below).

The following signs and symbols are used in the table.

The sign § is used for any infrageneric category above the rank of species. Examples: *Styphelia* § *Leucopogon* means subgenus *Leucopogon* of the genus *Styphelia*; *Podocarpus* § *Polypodiopsis* means section *Polypodiopsis* of the genus *Podocarpus*; *Geranium* § *Chilensia* and *Australiensia* indicates a group of allied *Geranium* species of as yet unsettled rank. Species with distributions deviating from that of the genus as a whole have been listed separately.

★ centre of species development, most likely at the same time the place of origin of the genus.

⊙ secondary centre or genus well represented, but it is uncertain whether this is also the centre of origin.

○ genus reliably recorded.

Examples: The genus *Lycium-Solan.* is represented by c. 40 species in South America, from the wealth of forms and the occurrence of allied genera it can be concluded that this is probably the centre of origin of the genus, hence in the column South America a ★ is filled in. In Africa there are about 20 species, but they are morphologically less diversified, this is indicated by the symbol ⊙, everywhere else the genus is represented by only one or a few species for which the symbol ○ is used. In a few cases instead of ○ a figure is filled in to indicate the number of species. This is done for instance to show a marked discrepancy in the representation of species, e.g. *Archidendron-Leg.* with 21 species in New Guinea and 3 in Queensland.

+ genus is endemic to the island group.

? genus is doubtfully recorded.

× genus is erroneously recorded.

↗ genus is represented by introduced species.

?↗ genus is doubtfully indigenous.

Af the endemic is closely allied to African taxa.
 Am the endemic is closely allied to American taxa.
 Aus the endemic is closely allied to Australian taxa.
 Mal the endemic is closely allied to Malesian taxa.
 Pal the endemic is closely allied to Paleotropical taxa.

! after a genus name means that the taxonomic status and geographic distribution are reasonably well known; there is either a recent revision or the genus is for other reasons well defined and studied. *Exocarpos-Sant.* and *Canarium-Burs.* are examples of genera recently revised, *Cyrtandra-Gesn.* and *Rhododendron-Eric.* are examples of genera not subjected to a recent complete revision but are nevertheless well defined and of well established distribution. A special paragraph (III, 7) has been devoted to these revised genera.

C after a genus name means that at least in the Pacific the genus is represented by cultivated species only. Although perhaps native in some parts of the area the exact limits of natural distribution cannot be established. Examples: *Abrus-Leg.*, *Aleurites-Euph.* and *Spondias-Anac.*

W after a genus name indicates that in the Pacific the genus is only represented by weeds or aliens. Only those genera have been listed that are suspected to be native in some part of the Pacific. Examples: *Aleurites-Euph.*, *Mikania-Comp.* and *Waltheria-Sterc.* Very obvious introductions such as *Ageratum-Comp.* and *Stachytarpheta-Verb.* have not been entered. Just as the foregoing category these genera have been left out of the statistical analysis.

When a genus in any of the unit areas is confined to only a limited part this has been indicated in the following ways:

| | | |
|----------------|-----|----------------------------------|
| Africa | N | = the North part |
| | E | = the East part |
| | S | = South Africa |
| | W | = the West part |
| | Md | = Madagascar |
| | Ms | = Mascarenes |
| Eurasia | Sc | = Seychelles |
| | S | = Mediterranean, Near East, etc. |
| East Asia | BT | = Botel Tobago |
| | Cn | = China |
| | F | = Formosa |
| | J | = Japan |
| | RK | = Ryu Kyu Is. |
| | S | = South China etc. |
| Southeast Asia | And | = Andamans |
| | Nic | = Nicobars |
| | In | = India (+ Ceylon) |
| | Cl | = Ceylon |

| | | |
|-------------------------------------|-----|---|
| Malesia | E | = the East part of the archipelago: Celebes, Moluccas |
| | S | = the South part: Java, Lesser Sunda Is. |
| | W | = the West part: Sumatra, Malaya |
| | Bor | = Borneo |
| | Mal | = Malaya |
| | Sum | = Sumatra |
| | Tim | = Timor |
| The Philippines | Luz | = Luzon |
| | Pal | = Palawan |
| Australia | E | = the East part of the continent: Queensland, New South Wales |
| | N | = tropical Australia: Northern Territory and North Queensland |
| | S | = Extratropical Australia (+ Tasmania) |
| | W | = West Australia |
| | SE | = Victoria and New South Wales (+ Tasm.) |
| | Q | = Queensland |
| | Tas | = Tasmania |
| Antarctica | AP | = Amsterdam/St. Paul (Indian Ocean) |
| | Cr | = Crozets (Indian Ocean) |
| | G | = Gough I. (Atlantic Ocean) |
| | K | = Kerguelen (Indian Ocean) |
| | M | = Macquarie (Pacific Ocean) |
| | SG | = South Georgia (Atlantic Ocean) |
| | T | = Tristan da Cunha (Atlantic Ocean) |
| New Zealand | 3k | = Three Kings Is. |
| | N | = North Island |
| | S | = South Island |
| Subantarctic islands of New Zealand | A | = Auckland I. |
| | Ap | = Antipodes |
| | C | = Campbell Is. |
| North America | S | = the Southern U.S. + North Mexico |
| | W | = California (and adjacent states) |
| South America | N | = tropical South America |
| | S | = temperate South America + Andes |
| | F | = Falkland Is. |

The two columns on the extreme right indicate the distribution type and (of the revised taxa) the dispersal type, for the meaning of the abbreviations the reader is referred to chapter III paragraphs 6 and 8.

For some families I have indicated in notes at the end of the Appendix which authors were consulted in addition to general sources of information such as Pflanzenfamilien, Pflanzenreich, Flora Malesiana or Pacific Plant Areas, which are not cited. Taxonomic notes on certain genera are given where deemed necessary.

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| Taxa | Geographic unit areas | | Africa | | Burma | | E. Asia | | SE Asia | | Malaya | | Philippines | | New Guinea | | Australia | | ALASKA | | Alaska | | St. Croix | | St. John | | St. Kitts | | St. Lucia | | St. Vincent | | St. John | | St. Kitts | | St. Lucia | | St. Vincent | | St. John | | St. Kitts | | St. Lucia | | St. Vincent | | St. John | | St. Kitts | | St. Lucia | | St. Vincent | | St. John | | St. Kitts | | St. Lucia | | St. Vincent | | St. John | | St. Kitts | | St. Lucia | | St. Vincent | | St. John | | St. Kitts | | St. Lucia | | St. Vincent | | St. John | | St. Kitts | | St. Lucia | | St. Vincent | | St. John | | St. Kitts | | St. Lucia | | St. Vincent | | St. John | | St. Kitts | | St. Lucia | | St. Vincent | | St. John | | St. Kitts | | St. Lucia | | St. Vincent | | St. John | | St. Kitts | | St. Lucia | | St. Vincent | | St. John | | St. Kitts | | St. Lucia | | St. Vincent | | St. John | | St. Kitts | | St. Lucia | | St. Vincent | | St. John | | St. Kitts | | St. Lucia | | St. Vincent | | St. John | | St. Kitts | | St. Lucia | | St. Vincent | | St. John | | St. Kitts | | St. Lucia | | St. Vincent | | St. John | | St. Kitts | | St. Lucia | | St. Vincent | | St. John | | St. Kitts | | St. Lucia | | St. Vincent | | St. John | | St. Kitts | | St. Lucia | | St. Vincent | | St. John | | St. Kitts | | St. Lucia | | St. Vincent | | St. John | | St. Kitts | | St. Lucia | | St. Vincent | | St. John | | St. Kitts | | St. Lucia | | St. Vincent | | St. John | | St. Kitts | | St. Lucia | | St. Vincent | | St. John | | St. Kitts | | St. Lucia | | St. Vincent | | St. John | | St. Kitts | | St. Lucia | | St. Vincent | | St. John | | St. Kitts | | St. Lucia | | St. Vincent | | St. John | | St. Kitts | | St. Lucia | | St. Vincent | | St. John | | St. Kitts | |
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NOTES TO THE APPENDIX

- 1) Bremekamp (1944, 1955, 1965), Bremekamp & Nannenga-Bremekamp (1948)
- 2) *Plectomirtha* was reduced to *Pennantia-Icac.* by Sleumer (1970).
- 3) Sinclair (1955)
- 4) Pichon (1947) reduced the Neotropical *Tonduzia* to *Alstonia*, but I have followed Markgraf in keeping it apart.
- 5) Hu (1967)
- 6) Harms (1921), Smith & Stone (1968). The systematics of the *Araliaceae* badly needs revision.
- 7) Good (1952)
- 8) *Dactylanthus* and *Hachettea* form a separate subfamily *Dactylanthoideae*.
- 9) Holttum (1967)
- 10) Johnston (1951)
- 11) *Alseuosmia*, *Memecylanthus* and *Periomphale* are also considered to form a separate family: *Alseuosmiaceae*.
- 12) Brenan (1966)
- 13) According to Davis (1948, 1949) the species from Africa, Asia and America described in *Brachycome* belong to other genera.
- 14) Solbrig (1960) refers one of the sections of *Erigeron* to *Celmisia*.
- 15) According to Carlquist (1967b) *Hesperoseris*, *Phoenicoseris* and *Rea* are closely allied and should be regarded as subgenera of *Dendroseris*.
- 16) Belcher (1956) is followed in placing the indigenous Indo-Australian species of *Erechtites* in *Senecio*.
- 17) Despite the fact that endemic species of *Taraxacum* have been described from various Pacific islands I doubt if they are truly indigenous.
- 18) Jeffrey (1962)
- 19) Dr Hoogland kindly communicated his view on the classification of Pacific *Cunoniaceae* which is followed here. *Acsmithia* is an unpublished manuscript name.
- 20) To sect. *Enantiophyllum* belongs *Dioscorea nummularia* Lamk which is probably native in the W. Pacific. To sect. *Opsophyton* belongs *D. bulbifera* L. which is sometimes cultivated but is found in the wild state throughout the Pacific.
- 21) Airy Shaw (1963, 1966, 1968, 1969)
Neowawraa was reduced to *Drypetes* by Sherff (1939), but according to Dr G. L. Webster (personal communication) it is a distinct genus; Airy Shaw (in Willis, 1966) states that it is near the pantropical *Margaritaria*.
- 22) Burt (1962)
Coronanthera, *Depanthus* and *Rhabdothamnus* constitute the tribe *Coronanthérinae*. *Cyrtandroidea* was originally described as a *Campanulaceae*.
- 23) The widespread littoral species *Scaevola plumieri* and *S. taccada* belong to sect. *Scaevola*.
- 24) Zotov (1963) has split up New Zealand *Danthonia* into a number of segregates of which I have provisionally accepted *Erythranthera* and *Pyrhanthera* but have kept *Chionochloa* and *Nothodanthonia* under *Danthonia* in view of the fact that their distribution outside New Zealand has not yet been established.
- 25) Philipson & Skipworth (1961) placed *Hectorella* in a separate family, *Hectorellaceae*, together with *Lyallia* endemic in the Kerguelen and other islands in the Indian Ocean.
- 26) Kubitzki (1969)
- 27) Den Hartog (1970)

- 28) Sleumer (1969)
- 29) *Carmichaelia*, *Chordospartium*, *Corallospartium* and *Notospartium* are allied genera. According to Hutchinson (1964) *Streblorrhiza* also belongs to this alliance.
- 30) Formerly in *Flagellariaceae*.
- 31) Danser (1929, 1933, 1936), Barlow (1966)
- 32) According to Melville (1966) the *Plagianthus* complex consists of four Australian and two New Zealand genera: *Hoheria* and *Plagianthus*.
- 33) Corner (1958, 1960, 1962, 1965, 1969b)
- 34) *Austromyrtus*, *Myrtastrum*, *Myrteola*, *Neomyrtus*, *Nothomyrcia* and *Uromyrtus* are segregates of *Myrtus*. See Burret (1941).
- 35) Hunt (1970), Hunt & Summerhayes (1966)
- 36) Beccari (1931), Beccari & Pichi-Sermolli (1955), Burret (1953), Burret & Potztal (1956), Corner (1966), Moore (1969).
Colpothrinax of Central America was reduced to *Pritchardia* by Beccari & Rock (1921), but this is not accepted by others, e.g. Read (1969). The tribe *Ptychospermeae*, distributed from the Mascarenes to the Pacific includes *Actinokentia*, *Campecarpus*, *Chambeyronia*, *Cyphophoenix*, *Hedyscepe*, *Kentiopsis*, *Strongylocaryum* and *Taveunia*. The tribe *Clinostigmeae*, confined to the SW. Pacific except for one Indian genus, includes: *Basselina*, *Brongniartikentia*, *Burretiokentia*, *Clinosperma*, *Cyphokentia*, *Cyphosperma*, *Dolichokentia*, *Goniocladus* and *Lepidorrhachis*.
- 37) Den Hartog (1970)
- 38) Virot (1968)
- 39) A. C. Smith (1936) reduced the monotypic *Dallachya* (ranging from Timor to Tonga) to the continental Asiatic *Rhamnella*.
- 40) *Osteomeles* is considered here in a strict sense, that is not including the American taxa which by several authors are considered as a separate genus *Hesperomeles*.
- 41) *Bikkia* and *Morierina* belong to a tribe centering in the Neotropics.
- 42) Swingle (1944)
- 43) The classification of the *Sapotaceae* is subject to much dispute. I have followed the classification proposed by Lam (1940, 1942). Classifications according to Baehni and Aubréville can be found at the end of this census.
- 44) *Brexia* is an endemic genus of the Mascarenes.
- 45) Burret (1926, 1936)
- 46) Dawson (1967)
- 47) Chew (1969)
- 48) Lam & Bakhuizen van den Brink (1921), Moldenke (1949)
- 49) *Hymenanthera*, *Isodendron* and *Melicytus* are allied. *Serresia* is a questionable genus and according to Dr M. Jacobs (personal communication) certainly does not belong to the *Violaceae*.
- 50) Pending a revision by Dr W. Vink I have refrained from following Smith (1943) in reducing *Belliolum* to *Bubbia*. Neither have I accepted Hutchinson's (1964) transfer of *Degeneria* to the *Winteraceae*.
- 51) Holttum (1950)
- 52) According to Porter (1969) the species of *Kallstroemia* described from Australia all belong to *Tribulus*.

ADDITIONS AND CORRECTIONS

The following data came to my notice after the completion of my manuscript and could not be incorporated in the analysis. Unless otherwise stated the data are based on herbarium records provided by Messrs H. K. Airy Shaw and P. S. Green (Kew), M. E. J. Coode (Lae), and C. E. Ridsdale (Bristol). Only new records and deletions but no name changes have been taken up. These additions make the distribution records up to date up to and including March 1971 by which time the manuscript was sent to the press. An asterisk means that the genus is new for the Pacific.

| Family | Genus | Notes |
|------------------------|----------------------------|--|
| <i>Aquifoliaceae</i> | <i>Ilex</i> | Also Bismarcks |
| <i>Araliaceae</i> | <i>Peckeliopanax</i> | Reduced to <i>Gastonia</i> (Philipson, 1970) |
| | <i>Tetraplasandra</i> | Malesian species referred to <i>Gastonia</i> , <i>Tetraplasandra</i> now confined to Hawaii (Philipson, l.c.) |
| | <i>Osmoxylon</i> * | Bismarcks and Solomons, further distribution: E. Malesia, Philippines and New Guinea |
| <i>Burseraceae</i> | <i>Garuga</i> | Also Bismarcks |
| <i>Capparidaceae</i> | <i>Capparis</i> | Also Societies |
| <i>Celastraceae</i> | <i>Lophopetalum</i> * | Bismarcks, further distribution: SE. Asia, Malesia, Philippines and New Guinea |
| <i>Combretaceae</i> | <i>Combretum</i> | Also Bismarcks |
| <i>Compositae</i> | <i>Ageratina</i> | <i>Eupatorium</i> from Revilla Gigedo belongs to <i>Ageratina</i> according to King & Robinson (1970), further distribution: America |
| | <i>Pseudelephantopus</i> * | Galapagos Is., further distribution Neotropics (Cronquist, 1970) |
| <i>Convolvulaceae</i> | <i>Cuscuta</i> | Also Bismarcks |
| <i>Coriariaceae</i> | <i>Coriaria</i> | Also Solomons |
| <i>Cucurbitaceae</i> | <i>Sicyocaulis</i> * | New endemic genus from Galapagos (Wiggins, 1970), allied to <i>Sicyos</i> |
| <i>Cyperaceae</i> | <i>Dichromena</i> | To be deleted from Galapagos |
| | <i>Rhynchospora</i> | Also Galapagos (Koyama, 1970) |
| | <i>Scirpodendron</i> | Also Bismarcks |
| <i>Elaeagnaceae</i> | <i>Elaeagnus</i> | Also Bismarcks |
| <i>Erythroxylaceae</i> | <i>Erythroxylum</i> | Also Bismarcks |
| <i>Euphorbiaceae</i> | <i>Bischofia</i> | Wilder (1931) asserted that Cheeseman (1903) had recorded the genus from the Cook Is. in error for <i>Allophylus-Sap.</i> but genuine <i>Bischofia</i> from the islands is preserved at Kew. This makes it likely that the genus also occurs (or occurred in the Societies as stated by early authors (e.g. Drake, 1893) |
| <i>Goodeniaceae</i> | <i>Scaevola</i> | A new montane species belonging to section <i>Scaevola</i> was described from Tahiti (Societies) by Carlquist (1969) |

| | | |
|-------------------------|------------------------|---|
| <i>Gramineae</i> | <i>Ancistrachne</i> * | Also New Caledonia, further distribution: E. Malesia, Australia (Blake, 1970) |
| <i>Haloragaceae</i> | <i>Gunnera</i> | Also New Hebrides |
| <i>Hamamelidaceae</i> | <i>Distylium</i> | The American species were made into a new genus <i>Molinadendron</i> by Endress (1969) |
| | <i>Sycopsis</i> * | Also Bismarcks, further distribution: SE Asia, Malesia, Philippines and New Guinea |
| <i>Hydrophyllaceae</i> | <i>Nama</i> | Also Galapagos (Eliasson, 1970) |
| <i>Leguminosae</i> | <i>Kingiodendron</i> | Also Bismarcks |
| <i>Moraceae</i> | <i>Ficus</i> | A species of section <i>Adenosperma</i> also on Rotuma I. near Fiji (Corner, 1970) |
| <i>Myrsinaceae</i> | <i>Tapeinosperma</i> | Also Bismarcks |
| <i>Oleaceae</i> | <i>Olea</i> | Also New Hebrides |
| <i>Orchidaceae</i> | <i>Acanthephippium</i> | Also Bismarcks |
| | <i>Anoectochilus</i> | |
| | <i>Ascoglossum</i> | |
| | <i>Coelogyne</i> | |
| | <i>Mediocalcar</i> | |
| | <i>Phaius</i> | |
| | <i>Schoenorchis</i> | |
| | <i>Drymoanthus</i> * | Also New Zealand, further distribution: Australia (Dockrill, 1967) |
| | <i>Sarcanthus</i> | Not Lord Howe I. |
| | <i>Plectorrhiza</i> * | Also Lord Howe I., further distribution: Australia (Dockrill, l.c.) |
| <i>Rubiaceae</i> | <i>Galium</i> | Also Galapagos (Wiggins, 1970) |
| <i>Rutaceae</i> | <i>Bauerella</i> | Not on New Caledonia and New Hebrides (= <i>Acronychia</i> according to Green, 1970) |
| | <i>Evodiella</i> * | Also Bismarcks, further distribution: New Guinea, E. Australia |
| | <i>Lunasia</i> * | Also Bismarcks, further distribution: Malesia, Philippines and New Guinea |
| <i>Scrophulariaceae</i> | <i>Hebe</i> | The SE. Australian species have been referred to <i>Parahebe</i> by Briggs & Ehrendorfer (1968) and the New Guinean species by Van Royen & Ehrendorfer (1970) |
| <i>Simaroubaceae</i> | <i>Picrasma</i> | Also Bismarcks |
| <i>Solanaceae</i> | <i>Lycianthes</i> | Also Bonins and Bismarcks |
| <i>Tiliaceae</i> | <i>Berrya</i> | Kostermans (1969) reduced this Old World genus to the Afro-American <i>Carpodiptera</i> which thus becomes pantropic in distribution. The Society Is. endemic <i>Tahitia</i> may eventually prove identical as well |
| <i>Umbelliferae</i> | <i>Bowlesia</i> * | Also Galapagos (Eliasson, 1970), further distribution: America |

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