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The Phytogeographical Relationships and Origin of the New Hebrides Fern Flora

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The phytogeographical relationships and origin of the New Hebrides fern flora

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[Plates 1 and 2]

The principal features and distribution of the New Hebrides fern flora are described and discussed as a source of evidence on the origin and relationships of the flora. The evidence presented supports the view that it is a young flora of mixed origin derived by transoceanic dispersal from the neighbouring archipelagos of the Solomon Islands and Fiji and to a lesser extent New Caledonia.

1. Introduction

The ferns are an important group to consider in relation to biogeographical problems of islands and archipelagos because of their high and substantially equivalent capacity for dispersal by air transport. They have, however, compared with the phanerogams, been rather neglected as a source of biogeographical data.

The present paper deals with the general features of the New Hebrides fern flora and the distribution patterns of the ferns as a source of evidence on the origin and relationships of the flora. Although the fern flora of the archipelago is now adequately known for a general evaluation of its relationships, there is considerable variation in the intensity of collecting of the different islands so that much still remains to be discovered on the detailed distribution of ferns within the archipelago. There are virtually no fern collections from the northeastern arc of islands, Epi, Ambrym, Pentecost, Maewo and the Banks Group. The present account is, therefore, confined entirely to the islands visited during the expedition, Espiritu Santo, Malekula, Efate, Erromanga, Tanna and Aneityum (see figure 1 in Lee, this report).

The data obtained during the expedition have been supplemented where possible by records from earlier publications on the New Hebrides ferns. These include works by Kuhn (1869) based on Milne's and MacGillivray's collections chiefly from Aneityum but also from Erromanga and Tanna, by Copeland (1932*a*) based on specimens collected by Kajewski, again mainly from the southern islands, principally Aneityum, and by Chambers, Jermy & Crabbe (1971) based on a recent collection made by Chambers from the south coast and Pic Santo, Espiritu Santo. In addition specimens collected by Morrison mainly from the southern islands, particularly Aneityum, and duplicates of specimens collected by Kajewski on Vanikoro, Santa Cruz group, which is here included with the New Hebrides, have been available in the Herbarium, Royal Botanic Gardens, Kew.

The results are provisional in the sense that the data, particularly at the species level, is subject to differing taxonomic opinions and no doubt future taxonomic studies of some of the more critical groups will change the status of some species or alter their distribution. Further exploration will almost certainly yield new discoveries and will modify the picture in detail.

Nevertheless the general outline of the flora shown by the present analysis is not expected to be substantially altered by future studies.

2. The genera

The distribution of the genera of ferns in the New Hebrides is shown in table 1. A total of 83 genera are represented in the flora and a full list is given in Appendix A. In compiling this list the delimitation of the genera for the most part follows Copeland (1947) except where recent studies have either shown his generic concepts to be too narrow or have provided a better understanding of some of the more taxonomically difficult groups. In these cases I have relied on the judgements of other taxonomists, e.g. Hymenophyllaceae (Morton 1968), Gleicheniaceae (Holttum 1959), Cyatheaceae (Holttum 1963), Lindsaceae (Kramer 1970, 1971), *Taenitis* (Holttum 1968) and Thelypteridaceae (Holttum 1971).

Table 1. Analysis of the distributions of New Hebrides fern genera

cosmopolitan or pantropic	47	
palaeotropic wide	15	
Indomalesian–Pacific	18	
Ceylon/India		12
Malaya/Burma		4
E. Malesian		2
New Caledonian	1	
Austral	2	
total	83	

Genera in the ferns are generally much more widely distributed than the corresponding taxa in the flowering plants (cf. Smith 1972), a feature which can in most cases be attributed to their greater dispersability rather than their longer geological history. It is, therefore, not surprising to find a high proportion of the New Hebrides fern genera with a very wide distribution; the three categories, cosmopolitan, pantropic and palaeotropic, accounting for 75.6 % of the flora.

The remaining 24.4 % of the genera are of a more restricted distribution although by flowering plant standards many of these would be considered as 'wides'. These fall into the three categories, the Indomalesian–Pacific, the New Caledonian and the Austral. There are no endemic fern genera.

The Indomalesian–Pacific element may be further divided according to their western limits. The majority of the genera extend westwards to India or Ceylon and eastwards to Fiji, e.g. *Tapeinidium*, *Taenitis*, and *Pronephrium*, or to Samoa or beyond, e.g. *Leucostegia*, *Diplaziopsis*, *Dipteris*, *Lomagramma*, *Prosaptia*, *Calymnodon*, and *Vaginularia*. There are, however, some conspicuous gaps in their distributions. *Diplaziopsis* has not yet been recorded from the Solomon Islands, *Lomagramma* and *Vaginularia* are not found in New Caledonia and *Leucostegia* has not yet been found in the Solomon Islands, Fiji or New Caledonia but is known in Samoa and Tahiti. The four Malesian genera are *Lomariopsia* and *Mesophlebion*, which are both wide ranging genera in the Pacific, and *Syngramma* and *Stenosemia*. *Syngramma* has so far only been found in the Santa Cruz islands in the New Hebrides and reaches its easternmost limit in Fiji. The tectarioid genus, *Stenosemia*, ranges from Sumatra to the New Hebrides but is not known from New Caledonia and is the only genus in the Indomalesian element reaching its easternmost limit in the group. It is a locally common terrestrial fern in the lowland forest on the coral terraces in the lower part of the Apuna Valley, Espiritu Santo. The two E. Malasian genera are *Scyphularia*, ranging from

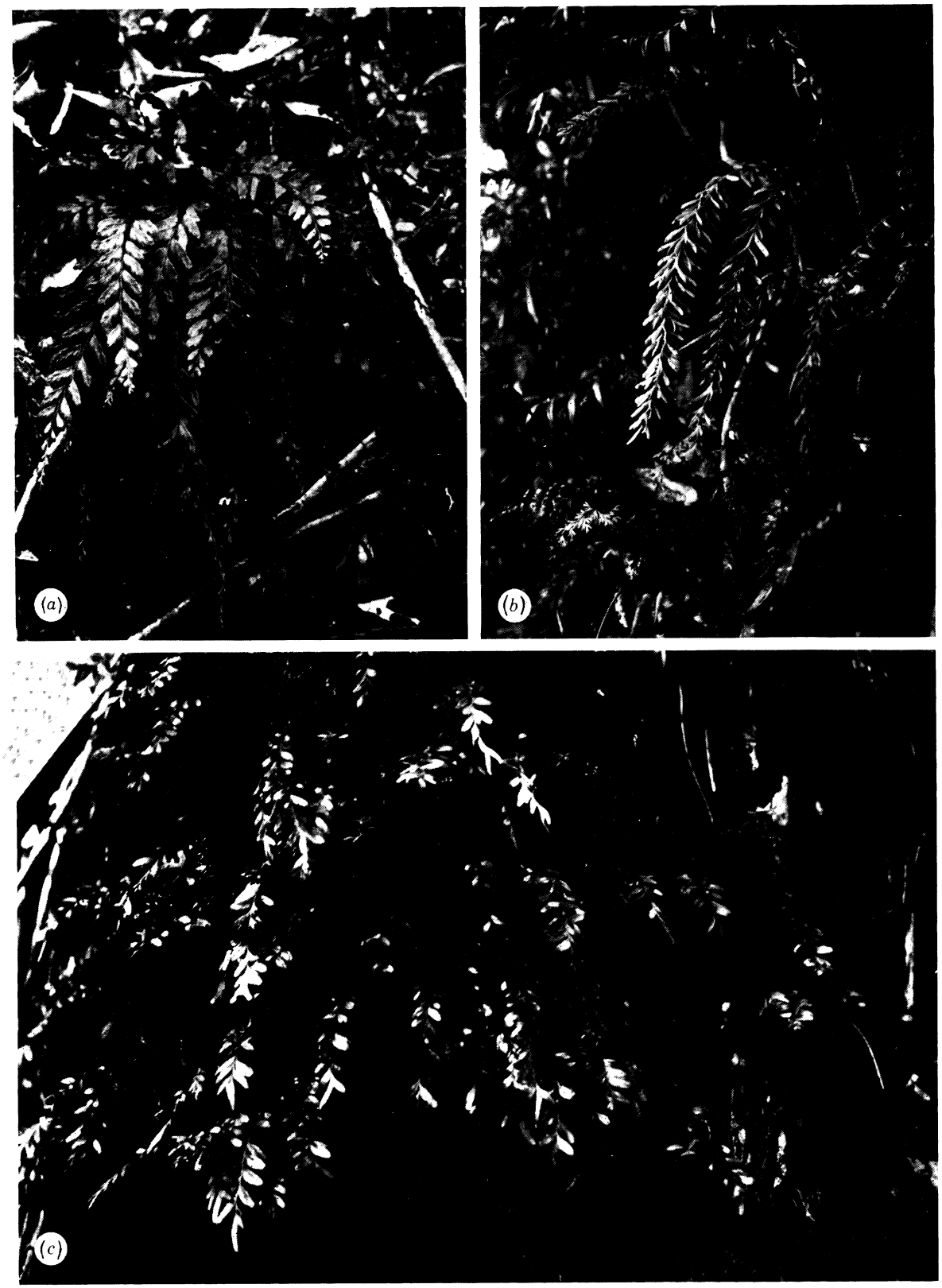

FIGURE 1. (*a*) *Aspleniopsis decipiens* (Mett.) Kuhn growing on the bank of the Nuangkau River, Erromanga. (*b*) *Tmesipteris tannensis* (Spr.) Bernh. growing near the base of a trunk of *Cyathea lunulata* (Forst.) Copel. on the west slopes of Mt. Toukosmeru, Tanna. (*c*) *Tmesipteris* sp. epiphytic on the trunk of *Metrosideros*, Ancityum.

(*Facing p.* 294)

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FIGURE 8. *Marattia smithii* (Forst.) Hoffm. in ridge side forest, S.W. Malekula.

FIGURE 9. *Blechnum gibbum* (Labill.) Mett., a New Caledonian species, growing on a stone bed in the Nuangkau River, Erromanga.

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New Guinea to Fiji but absent from New Caledonia, and *Selliguea* distributed from Java to the Marquesas.

The New Caledonian element is represented by the monotypic genus, *Aspleniopsis* (figure 1*a*, plate 1). The affinities of this genus have not been definitely established but are generally presumed to be with the *Taenitis–Syngramma* group of genera and more particularly with *Rheopteris* from New Guinea (R. E. Holttum, personal communication). It is a fairly common terrestrial fern in the deep shade of forest at mid-altitudes on Aneityum above Anelcauhat Bay, and has been found once in southern Erromanga but is otherwise unknown in the group. There is a questionable record of this genus from New Ireland in the Bismarck Archipelago which remains to be confirmed.

The small Austral element in the flora is made up of *Tmesipteris*, one of the fern allies, and the osmundaceous genus, *Leptopteris*. *Tmesipteris* (figure 1*c*, plate 1) is of particular interest in the New Hebrides since the genus was originally described from a Forster specimen collected from Tanna. This specimen has been lost, probably destroyed in Berlin during the last war, so that the expedition collections may assist in clarifying some of the taxonomic confusion surrounding the type species *Tmesipteris tannensis* (Spr.) Bernh. In addition to *T. tannensis* there are two or possibly three further species in the New Hebrides. One of these species (figure 1*b* plate 1) which has only been found on Aneityum is unusual in being terrestrial or epiphytic but never on tree ferns. It is closely allied to *T. oblanceolata* Copel of the Solomon Islands and also to some undescribed terrestrial material from New Caledonia.

At the generic level the analysis clearly shows a flora lacking any peculiarity which is dominated by wide ranging and Indomalesian genera with a very small Austral element and an even smaller, but nevertheless significant, New Caledonian element.

In the broader context of the southwest Pacific region the New Hebrides fern flora falls into a broad pattern of fern floras with a decreasing number of genera as the distance increases southwards and eastwards from New Guinea and with little or no generic endemism (table 2).

TABLE 2. GENERIC ENDEMISM IN SOME OF THE MAJOR TROPICAL ISLANDS AND ARCHIPELAGOS OF THE SOUTHWEST PACIFIC

	no. of genera	endemic genera	endemism (%)
New Guinea	156	6	4†
Solomon Islands	98	0	0
New Hebrides	83	0	0
New Caledonia	83	3	3.6
Fiji	88	0	0
Samoa	83	0	0
Society Islands	71	0	0

† Figures from Smith 1972; all other figures the result of the authors own compilations.

Although much smaller, the individual floras share in the majority of cases virtually all their genera with New Guinea which suggests their probable derivation from the E. Malesian region. The general pattern is documented in greater detail in table 3 where it is shown that the decrease in genera is mainly confined to the Indomalesian element while the wide ranging genera of the cosmopolitan, pantropic and palaeotropic elements remain reasonably constant. Thus the widely distributed genera increasingly dominate the fern floras of the eastern Pacific. Tryon (1970) demonstrated a similar correlation for the fern floras of oceanic islands at the species level.

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TABLE 3. ANALYSIS OF DISTRIBUTION OF GENERA IN THE ISLAND FLORAS OF THE SOUTHWEST PACIFIC

	Solomon Islands	New Hebrides	New Caledonia	Fiji	Samoa	Society Islands
cosmopolitan and pantropic	46	47	45	48	47	44
palaeotropic wide	16 (3)	15	16	16	17 (2)	14
Indomalesian–Pacific						
Ceylon/India	16 (2)	12	9	13 (4)	11 (3)	7
Malaya/Burma	11 (3)	4 (1)	4 (1)	5 (2)	5 (2)	4
E. Malesian	7 (5)	2	1	2 (1)	1	1
New Caledonian	—	1	—	—	—	—
Austral	2	2	3	4	2	1
endemic	—	—	3	—	—	—
others	—	—	2	—	—	—

Numbers in brackets show the numbers of genera in any category with their easternmost limit in the particular island group.

The attenuation of the Indomalesian element is particularly marked in the New Hebrides. The flora lacks several characteristic Malesian genera such as *Christensenia*, *Cystodium*, *Diplora*, *Stenolepia*, *Dryopolystichum*, *Merinthosorus* and *Aglaomorpha* which are found in the Solomon Islands, *Acrophorous* and *Arcypteris* which reach Fiji and *Pleocnemia*, *Lemmaphyllum* and *Acrosorus* which range as far as Samoa. The absence of endemic fern genera is characteristic of the fern floras of the majority of the oceanic islands and archipelagos in the tropical southwest Pacific. Apart from the endemic genera of New Guinea, the only other endemic genera are *Stromatopteris*, *Rosenstockia* and *Cionidium* of New Caledonia which reflect the well known floral peculiarities and high endemism of the flora.

A simple and convenient method of expressing numerically the floral relationships between pairs of islands or island groups, irrespective of their different areas or ecological differences is Colgan's index of floral diversity (Praeger 1911). The index for any pair of islands A and B is given by:

$$\frac{a+b}{a+b+x},$$

where a = number of genera found in A only, b = number of genera found in B only, x = number of genera shared by A and B.

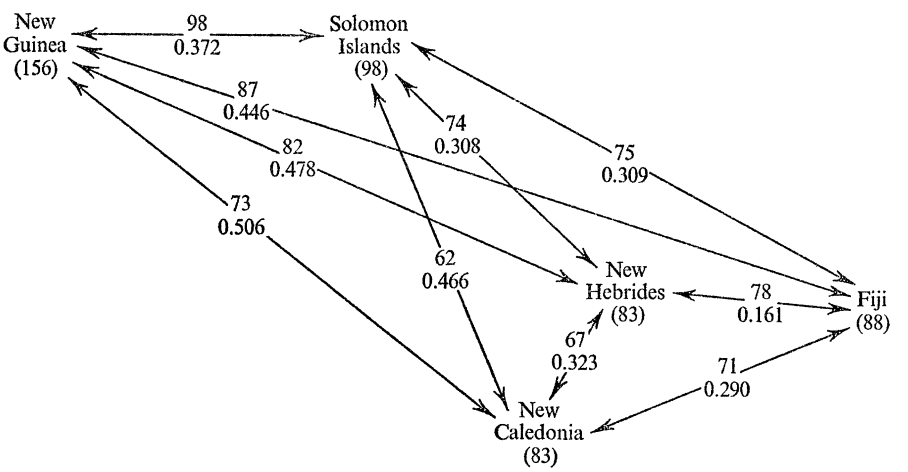

FIGURE 2. Numbers of fern genera common to the different islands and archipelagos in Melanesia and to New Guinea and indices of floral diversity (see text). The numbers in brackets indicate the total number of genera in each flora.

The indices calculated on the information available for the fern genera of New Guinea and of the major islands and archipelagos of Melanesia and the numbers of shared genera are given in figure 2. The figures show that the New Hebrides are somewhat more closely related to Fiji than to the Solomon Islands or New Caledonia. It should, however, be emphasized that the figures are provisional since further collecting particularly in the Solomon Islands and to a lesser extent in Fiji may yield new generic records.

3. The species

On the information available at present about 250 species of ferns and fern allies are known from the New Hebrides. There are, however, doubts about the taxonomic status of a few species, notably some of the endemic species and species with closely related Malesian counterparts. A number of endemics described from the islands have not been recognized and one or two Pacific species have been considered conspecific with their Malesian counterpart. These are only two instances reflecting the general need for critical revisions of many Indomalesian–Pacific and Pacific species or groups of species.

3.1. *General characteristics of the flora*

Some of the general features of the fern flora are summarized in table 4 with the corresponding data for the fern floras of other islands and archipelagos in the southwest Pacific.

Table 4. Some general features of the fern floras of islands and archipelagos in the Pacific

	area / km²	altitude / m	no. species	species per km²	species per genus	Raunkiaer's† pteridophyte quotient
Solomon Islands	42000	2439	*ca.* 310	0.007	3.16	4.4
New Hebrides	12000	1879	249	0.021	3.01	7.2
New Caledonia	19000	1650	245	0.013	2.95	2.1
Fiji	18000	1324	*ca.* 290	0.016	3.29	4.0
Samoa	3000	1858	218	0.066	2.63	—
Society Islands	—	2232	146	—	2.06	—

† $\frac{\text{no. species of pteriodophytes} \times 25}{\text{no. species of phanerogams}}$ (see text).

In terms of the number of species the flora is smaller than those of the Solomon Islands and Fiji, being about the same size as that of New Caledonia. Although similar in size to the New Caledonian flora in purely numerical terms, it does not show the same high degree of species endemism or other peculiarities of that flora.

The richness of the flora in terms of species per unit area is greater than those of the Solomon Islands, Fiji or New Caledonia, although it should be recognized that density is a very crude measure since it takes no account of climatic, topographical or ecological factors. Nevertheless it is interesting to see that it is the richest of the Melanesian fern floras on the basis of area and is noticeably richer than New Caledonia. This relative richness may well be related to the latitudinal range of the archipelago and also to the number of sources which have been available for colonization of the islands.

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The average number of species per genus, though higher than the corresponding value (Chew 1975) for the phanerogams, falls within the small range of values calculated for the major islands and archipelagos of the south Pacific in table 4. Some 31 genera are represented in the flora by a single species. The most diverse genera tend also to be the larger fern genera and include *Lycopodium* (*ca.* 15 species), *Trichomanes* (21 species), *Cyathea* (*ca.* 8 species), *Humata* (5 species), *Lindsaea* (9 species), *Blechnum* (9 species), *Adiantum* (5 species), *Pteris* (*ca.* 9 species), *Tectaria* (5 species), *Pneumatopteris* (5 species), *Diplazium* (7 species), *Asplenium* (*ca.* 18 species) and *Grammitis* (7 species). Compared with New Guinea where it is estimated that there are probably about 6 species per genus, the flora, in common with those of the other Pacific archipelagos, displays a lack of diversity or impoverishment.

Disharmony, as shown by the higher proportion of pteridophytes to phanerogams compared with the world as a whole, is a well established feature of the floras of oceanic islands (Raunkiaer 1934, 1937). Raunkiaer's pteridophyte quotient is calculated on a supposedly normal proportion of twenty-five phanerogams to every one pteridophyte for the world as a whole. The figures calculated for the Melanesian floras in table 4 show that the pteridophyte quotient for the New Hebrides is higher than those for the Solomon Islands, Fiji or New Caledonia. If disharmony is related to the age of a flora then these figures would suggest that the New Hebrides flora is the youngest in Melanesia.

3.2. *Geographical relationships of the fern flora*

A provisional analysis of the overall distribution of the fern species is shown in table 5. The three most important elements which indicate relationships of the flora with the Solomon Islands, Fiji and New Caledonia will be considered in greater detail in the sections which follow. On the basis of the number of species shared with the neighbouring archipelagos (figure 3) the closest relationships are with the Solomon Islands and Fiji, with Fiji marginally the closer, and, despite the close proximity of New Caledonia and a very distinctive group of New Caledonian species in the flora, there is a sharp demarcation between the floras of the two archipelagos.

Table 5. Analysis of the geographical distribution of the New Hebrides species

cosmopolitan/pantropic	12		
palaeotropic wide	29		
Indomalesian–Pacific	112		(eastern limit)
Ceylon/India		26	(2)
Malaya/Burma		36	(11)
Borneo/Philippines		23	(5)
New Guinea		27	(10)
Pacific	74		(western limit)
Melanesian		23	(9)
Polynesian		51	(19)
New Caledonian	7		
Austral	4		
Endemic	11		
total	249		

3.21. *Indomalesian – Pacific species*

The Indomalesian element in the flora accounts for 112 of the 249 species (or 45 %) and these have been subdivided in table 5 according to their western limits.

(i) Widely distributed species in Malesia and the Pacific and adjoining mainland and extending west to Ceylon or India, e.g. *Lycopodium serratum* Thunb., *Trichomanes proliferum* Bl., *Microlegia strigosa* (Thunb.) Presl, *Adiantum diaphanum* Bl., *Pteris ensiformis* Burm. *Diplaziopsis javanica* (Bl.) C. Chr., *Blechnum patersoni* (R.Br.) Mett., *Calymnodon cucullatus* (Nees & Bl.) Presl, *Prosaptia contigua* (Forst.) Presl and *Antrophyum plantagineum* Kaulf. The majority range to Samoa or beyond but two species, *Lygodium circinnatum* (Burm.) Sw. and *Elaphoglossum angulatum* (Bl.) Moore, reach their southeasternmost limit in the Pacific in the New Hebrides. Three species are not yet recorded from the Solomon Islands, *Diplaziopsis javanica*, *Elaphoglossum angulatum* and *Adiantum diaphanum*, while others such as *Blechnum patersoni* and *Trichomanes proliferum* are not found in New Caledonia. One species, *Dryopteris hirtipes* (Bl.) O. Ktze found in the mossy forest on the summit of Mt Tabwemasana, Espiritu Santo, is not recorded from New Guinea and is only known from Samoa in the Pacific.

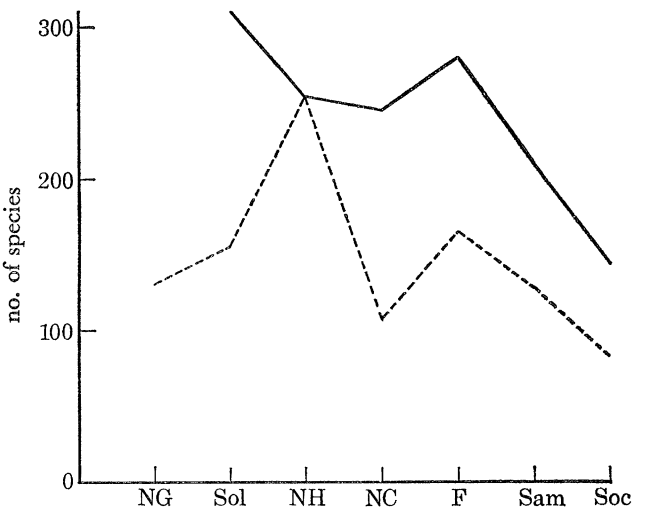

FIGURE 3. Graph to show the proportion of New Hebrides species (broken line) in the fern floras from New Guinea to the Society Islands. F, Fiji; NC, New Caledonia; NG, New Guinea; NH, New Hebrides; Sam, Samoa; Soc, Society Islands; Sol, Solomon Islands.

(ii) Widely distributed Malesian species extending west to Malaya or Burma and eastwards to the New Hebrides, Fiji, Samoa or beyond.

Eleven species in this group reach their easternmost limit in the New Hebrides, e.g. *Gleichenia hirta* Bl. (Vanikoro only), *Hymenophyllum treubii* Racib., *Trichomanes atrovirens* Presl., *Stenosemia aurita* (Sw.) Presl, *Lindsaea pulchella* (J.Sm.) Mett ex Kuhn, *Adiantum malesianum* Ghatak and *Grammitis hirtella* (Bl.) Tuyama. *Grammitis hirtella* has not been recorded from the Solomon Islands and *Adiantum malesianum* has not so far been found in New Guinea or the Solomon Islands but is virtually the only one of these eleven species which is also found in New Caledonia.

The majority of the remaining species range to Samoa or beyond, e.g. *Hymenophyllum imbricatum* Bl., *Trichomanes humile* Forst., *T. maxima* Bl., *Davallia solida* (Forst.) Sw., *Leucostegia pallida* (Mett.) Copel., *Oleandra neriiformis* sl., *Blechnum vulcanicum* (Bl.) Kuhn, *Dipteris conjugata* Reinw., *Drynaria rigidula* (Sw.) Bedd., and *Lycopodium carinatum* Desv., while a few reach their easternmost limit in Fiji, e.g. *Lindsaea rigida* J. Sm. and *Asplenium excisum* Presl. *Asplenium excisum* has not yet been recorded from the Solomon Islands or New Caledonia and a few others such as

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Oleandra neriiformis s.l. and *Blechnum vulcanicum* are not found in New Caledonia. One species, *Leucostegia pallida*, has not yet been found in the Solomon Islands, Fiji or New Caledonia.

(iii) Species ranging west to the Philippines, Borneo or Java and east to the New Hebrides, Fiji or beyond.

Those ranging east to Fiji or beyond include *Trichomanes tahitense* Nad., *Culcita straminea* (Labill.) Maxon, *Dennstaedtia flaccida* (Forst.) Bernh., *Humata sessilifolia* (Bl.) Mett., *Oleandra sibbaldii* Grev., *Bolbitis quoyana* (Gaud.) Ching, *Pneumatopteris costata* (Brack.) Holtt., *Asplenium amboinense* Willd. and *Asplenium oceanicum* C. Chr. Examples of those with their eastern limit in the New Hebrides are *Gleichenia milnei* Bak. and *Humata pusilla* (Mett.) Carr.

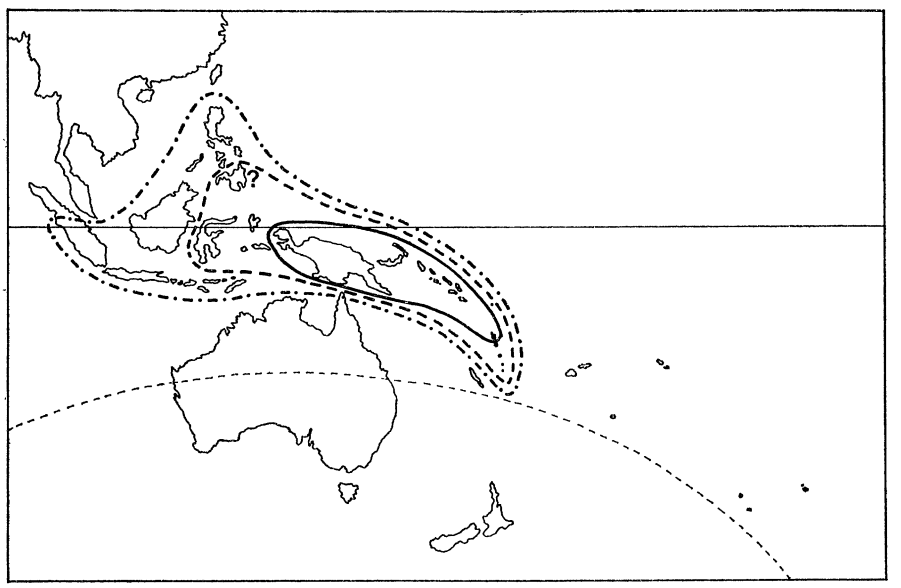

FIGURE 4. Distribution of *Stenosemia aurita* (Sw.) (Presl –·–·–·–), *Gleichenia milnei* Bak. (– – – –) and *Cyathea archboldii* C. Chr. (———). Examples of Malesian species reaching their easternmost limit in the New Hebrides.

One species, *Tectaria menyanthidis* (Presl) Copel., ranging from Borneo to Fiji is found only in the Banks Group in the New Hebrides. Of this group *Dennstaedtia flaccida* has not been collected in the Solomon Islands and only about a third are found in New Caledonia.

(iv) Species of more restricted distribution from the Moluccas or New Guinea to the Pacific.

This Papuan group includes species such as *Lygodium trifurcatum* Bak., *Cyathea archboldii* C. Chr., *Pneumatopteris sogerensis* (Gepp.) Holtt., *Syngramma quinata* (Hook.) Catt. (Vanikoro only), *Adiantum aneitensis* Carr. and *Xiphopteris glanduloso–pilosum* Brause found in Moluccas/New Guinea, Solomon Islands and New Hebrides only.

Other species extend east to Fiji, e.g. *Hymenophyllum pseudotunbridgense* Watts, *Dryopteris aneitensis* (Hook.), C. Chr., *Taenitis pinnata* (J. Sm.) Holtt., *Pronephrium beccarianum* (Cesati) Holtt., and *Selaginella sepikensis* Hier. (Vanikoro only), or Samoa, e.g. *Leptopteris wilkesiana* (Brack.) Christ, *Nephrolepsis saligna* Carr., *Dennstaedtia samoensis* (Brack.) Moore, and *Phymatodes powellii* Bak. while others are widely distributed Pacific species ranging to the Society Islands, e.g. *Humata brackenridgei* Brownl., *Sphaerostephanos invisus* (Forst.) Holtt. *Antrophyum alatum* Brack and *Lycopodium phlegmarioides* Gaud. Virtually all these species have been recorded from the Solomon Islands although *Taenitis pinnata* and *Dryopteris aneitensis* have yet to be found there, and a fair proportion of the more widely distributed species are also found in New Caledonia.

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A summary of the distribution of the Indomalesian–Pacific species in the major islands and archipelagos around the New Hebrides is given in table 6.

TABLE 6. SUMMARY OF THE DISTRIBUTION OF THE INDOMALESIAN–PACIFIC SPECIES IN THE NEIGHBOURING ISLANDS AND ARCHIPELAGOS

	NG	Sol	NH	F	Sam	NC
Indomalesian	24	17	26	14	13	16
Malesian	32	27	36	18	19	15
E. Malesian	18	14	19	12	8	7
New Guinea	30	27	30	18	12	9
total	104	85	111	62	52	47

While it seems clear from the data that much of this Indomalesian element has been derived from the Papuan region, possibly directly through the Solomon Islands, there are a considerable number of species which have not been found in the Solomon Islands but are known from either Fiji or Samoa or New Caledonia. Further collecting may fill in many of these gaps but the possibility cannot be excluded on present evidence that some of this element, particularly some of the more wide ranging species, has reached the New Hebrides from Fiji or Samoa to the east or even New Caledonia to the south.

The attenuation of the Indomalesian flora, particularly the Papuan species, is very marked between the Solomon Islands and the New Hebrides. The New Hebrides flora lacks approximately 85 Indomalesian fern species which reach their easternmost limit in the Solomon Islands, over half of these being confined to New Guinea and the Solomon Islands. Thus there is a strong demarcation in the ferns between the Solomon Islands and the New Hebrides, as is the case with the flowering plants (van Balgooy 1960), which marks a useful boundary between western and eastern Melanesia.

3.22. *Pacific species*

The Pacific element of 74 species has been subdivided into the Melanesian (excluding those found only in the New Hebrides and New Caledonia (§3.23)) and the Polynesian or more widely distributed species extending to Samoa or further east.

(i) Melanesian. The Lindsaceae are strongly represented in this group with *Tapeinidium denhamii* (Hook.) C. Chr. found in the Admiralty Islands, Bismarck Archipelago, Solomon Islands, New Hebrides and Fiji, *T. melanesicum* Kramer in the Solomon Islands, Vanikoro, and Fiji and *Lindsaea lapeyrousii* (Hook.) C. Chr. in the Bismarck Archipelago, Vanikoro and Fiji but not the Solomon Islands. This last pattern is repeated by *Pronephrium rubrinerve* (Mett.) Holtt. This is a large thelypteroid fern likely to attract the attention of collectors so that it is difficult to believe it has been overlooked in the Solomon Islands. Other species in this group such as *Histiopteris sinuata* (Brack.) J. Sm. and *Lomariopsis oleandrifolia* (Brack.) Mett. are confined to the Solomon Islands, New Hebrides and Fiji, while others are found only in New Caledonia, New Hebrides and Fiji, e.g. *Gonocormus assimile* Mett. and *Selaginella firmuloides*. Warb.

Five species are found only in the Solomon Islands and the New Hebrides, e.g. *Cyathea solomonensis* Holtt. and *Taenitis diversifolia* Holtt. and a further nine are confined to the New Hebrides and Fiji, e.g. *Hymenophyllum* sp. nov. (aff. *multifidum* Forst.), *Bolbitis rivularis* (Brack.) Ching, *Pneumatopteris rotumaensis* (St. John) Holtt., *Ctenopteris hornei* Bak. and *Lycopodium parksii* Copel.

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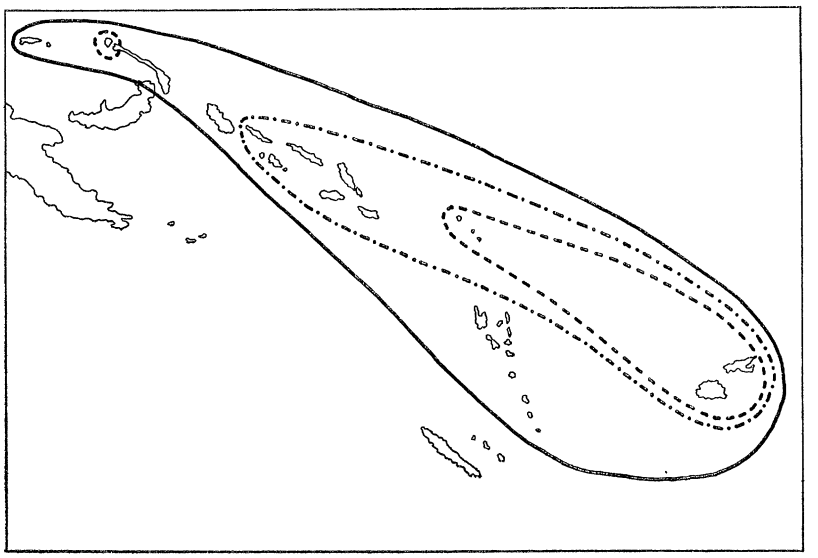

FIGURE 5. Distribution of some Melanesian Lindsaceae. *Tapeinidium denhamii* (Hook.) C, Chr, (———), *T. melanesicum* Kramer (–·–·–·–) and *Lindsaea lapeyrousii* (Hook.) C. Chr. (– – – – –).

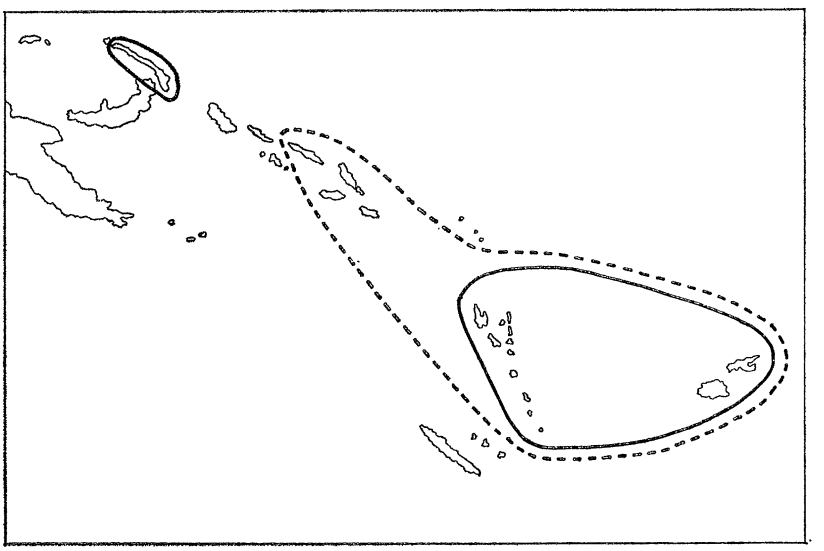

FIGURE 6. Distribution of two Melanesian species, *Pronephrium rubrinerve* (Mett.) Holtt. (——) and *Histiopteris sinuata* (Brack.) J. Sm. (– – – –).

(ii) Polynesian. The much larger Polynesian group contains many characteristic and widely distributed Pacific species extending to the Society Islands or beyond. Some of these widely distributed species range west to the Bismark Archipelago, e.g. *Cyathea lunulata* (Forst.) Copel, *Davallia epiphylla* (Forst.) Spr., *Lindsaea harveyi* Carr. ex Seem., *Mesophlebion brackenridgei* Mett. while others reach their western limit in the Solomon Islands, e.g. *Cyathea decurrens* (Hook.) Copel., *Lindsaea pacifica* Kramer, *Asplenium horridum* Kaulf. *Asplenium insiticium* Brack., *Selliguea plantaginea* Brack. A considerable number reach their western limit in the New Hebrides, e.g., *Lastreopsis davallioides* (Brack.) Tind., *Trichomanes boryanum* Kunze, *Cyathea medullaris* (Forst.) Sw., *Lomariopsis brackenridgei* Carr., *Antrophyum subfalcatum* Brack., *Vaginularia angustissima*

(Brack.) Mett. and a smaller group reach New Caledonia, e.g. *Humata banksii* Alston, *Trichomanes dentatum* v.d.B., *Bolbitus palustris* (Brack.) Hennipm., *Lycopodium nutans* Brack. or Australia, e.g. *Lygodium reticulatum* Schk and *Hypolepis tenuifolia* (Forst.) Bernh., but have not been reported from the Solomon Islands.

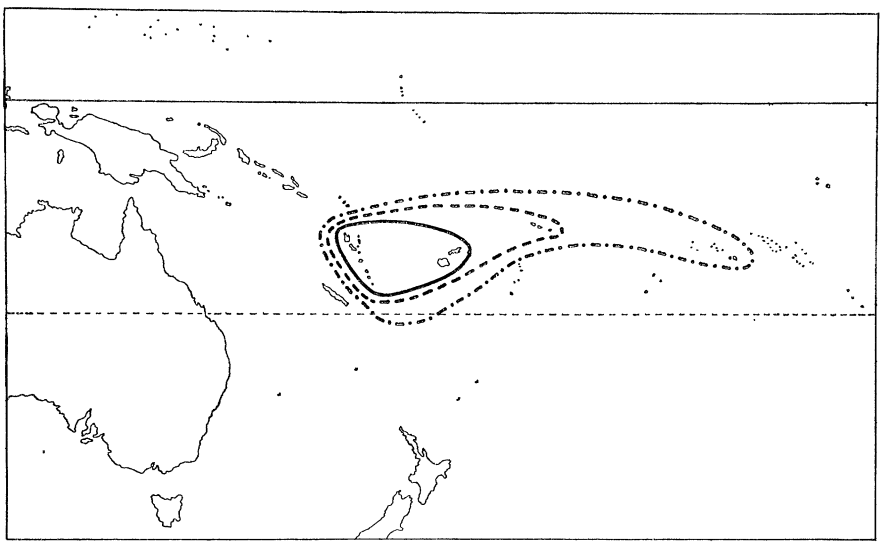

FIGURE 7. Distribution of *Lastreopsis davallioides* (Brack.) Tind. (–·–·–·–), *Marattia smithii* (Forst.) Hoffm. (– – – –) and *Ctenopteris hornei* Bak. (———). Examples of Pacific species reaching their western limits in the New Hebrides.

Just over a third of the Polynesian group have a more restricted distribution extending only to Samoa. These include *Lindsaea pulchra* (Brack.) Carr. ex Seem ranging west to the Bismarck Archipelago, *Gleichenia oceanica* Kuhn, *Dicksonia brackenridgei* Mett., *Cyathea truncata* (Brack.) Copel., *Pneumatopteris glandulifera* (Brack.) reaching the Solomon Islands and *Marattia smithii* (Forst.) Hoffm. (figure 8, plate 2), *Elaphoglossum feejeense* Brack., *Lomagramma cordipinna* Holtt., *Dryopteris arbreoscens* (Bak.) O. Ktze, *Diplazium bulbiferum* Brack., *Loxogramma parksii* Copel. and *Grammitis conformis* (Bak.) J. Sm. reach their western limit in the New Hebrides. A few species such as *Microlepia nudisora* C. Chr. and *Grammitis vaupelii* (Brause) are found in the New Hebrides and Samoa but have not yet been reported from Fiji.

The overall distribution of the Pacific element in the neighbouring archipelagos is summarized in table 7.

TABLE 7. SUMMARY OF THE DISTRIBUTION OF THE PACIFIC SPECIES IN THE NEIGHBOURING ARCHIPELAGOS

	Sol	NH	F	Sam	NC
Melanesian	10	24	19	—	—
Polynesian	19	50	41	41	16
total	29	74	60	41	16

The variety of distribution patterns in the Melanesian and Polynesian species is perhaps partly the consequence of the casual nature of dispersal and migration and undercollecting but it is also no doubt a reflection of the complexity of the origin of the New Hebrides fern flora.

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Nevertheless the data indicates a strong connection with Fiji and suggests that much of this element (except for those species confined to the Solomon Islands and the New Hebrides) can only have reached the New Hebrides from the east and more particularly from the Fiji–Samoa region.

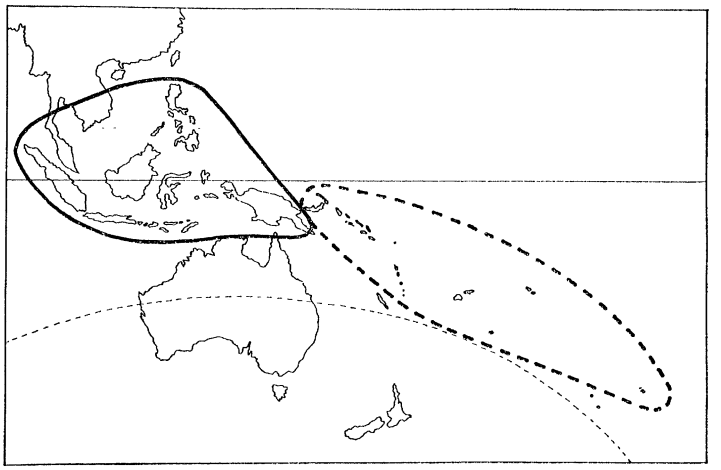

FIGURE 10. Distribution of the Malesian species. *Davallia denticulata* (Burm.) Mett. (——) and its Pacific counterpart *D. epiphylla* (Forst.) Spr. (– – – –).

The Pacific element in the flora is part of a rather uniform and closely related assemblage of ferns which are found in Fiji and Samoa and to a lesser extent on other islands and archipelagos of the southwest Pacific. Many species in this Pacific assemblage have a closely related Indomalesian or Malesian counterpart. A few examples are given below:

Malesian	Pacific
Trichomanes javanicum Bl.	*T. boryanum* Kunze
Trichomanes obscurum Bl.	*T. dentatum* v.d.B.
Hypolepis punctata (Thunb.) Mett.	*H. tenuifolia* (Forst.) Bernh.
Davallia denticulata (Burm.) Mett.	*D. epiphylla* (Forst.) Spr.
Humata pectinata (Sm.) Desv.	*H. banksii* Alston
Humata vestita (Bl.) Moore.	*H. brackenridgei* Brownl.
Tapeinidium longipinnulum (Cesati) C. Chr.	*T. melanesicum* Kramer
Lindsaea obtusa J. Sm.	*L. harveyi* Carr. ex Seem.
Lomagramma sinuata C. Chr.	*L. cordipinna* Holtt.
Dryopteris subarborea (Bak.) C. Chr.	*D. arborescens* (Bak.) O. Ktze
Dryopteris hasseltii (Bl.) C. Chr.	*D. aneitensis* Hook.
Diplazium silvaticum (Bory) Sw.	*D. bulbiferum* Brack.
Antrophyum semicostatum Bl.	*A. subfalcatum* Brack.

In some cases the differences between the two members of these Malesian–Pacific pairs are very small and future critical comparisons of the Malesian and Pacific material may show some of these species pairs to be conspecific. In the majority of cases (figure 10) the morphological differences are constant and uniform over the whole of the Pacific region and are accompanied in some instances by cytological differences (figure 11). Since polyploidy is generally accepted as an irreversible process, species such as *T. boryanum* provide positive evidence for the

Indomalesian derivation of the Pacific fern flora and confirm the underlying Indomalesian nature of the floras of the Pacific region.

It is clear that after the initial migration of Indomalesian ferns into the Pacific region, before the New Hebrides and perhaps even the Solomon Islands existed, there must have been an important secondary centre of speciation, possibly in the Fiji area (Christensen 1940; Copeland 1948), which gave rise to this assemblage of Pacific species. The species then subsequently radiated and dispersed westwards, southwards and eastwards onto the archipelagos as they appeared and exist today.

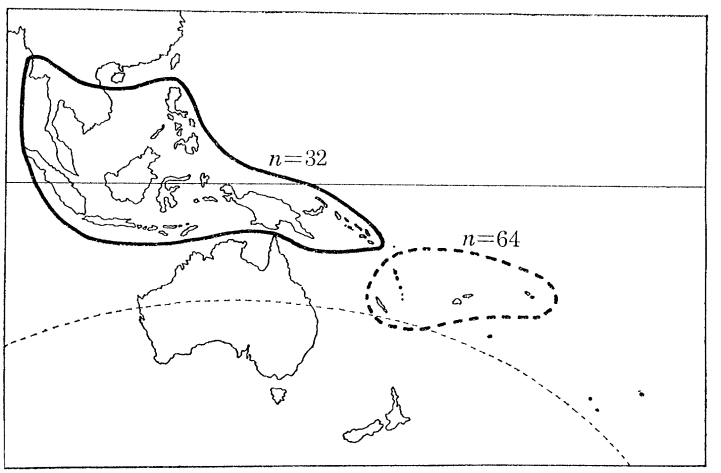

FIGURE 11. Distribution of the Malesian species *Trichomanes javanicum* Bl. (——) and its Pacific counterpart *T. boryanum* Kunze (– – – –). *T. javanicum* has been reported from the Solomon Islands with 32 chromosomes at meiosis (Braithwaite 1969) and twice this number has recently been found in specimens of *T. boryanum* from the New Hebrides and Fiji (Braithwaite, unpubl.).

3.23. *New Caledonian species*

The New Caledonian element is small, consisting of seven species, which is less than 3% of the total fern flora. Nevertheless it includes some very distinctive species such as *Aspleniopsis decipiens* (Mett.) Kuhn, *Blechnum gibbum* (Labill.) Mett., a handsome trunk forming species usually found growing on stone beds in rivers and streams (figure 9, plate 2), *Blechnum opacum* Mett., *Sphaerostephanos arbusculoides* Holtt ined. and *Asplenium subflexuosum* Ros. The three remaining species in this element are closely allied to more widely distributed species. *Trichomanes flavo-fusca* v.d.B. is related to *Trichomanes caudata* Brack., ranging from Queensland across the Pacific to Tahiti; *Trichomanes cuneatum* Christ. is related to *Trichomanes lyallii* Hook. of Australia and New Zealand, whilst *Grammitis neocaledonica* Copel. belongs to the *G. reinwardtia-hookeri* group distributed in Malesia and across the Pacific to Hawaii. One possible member of this element, *Blechnum obtusatum* (Labill) Mett., a species recorded by Kuhn (1869), is doubtfully present in the New Hebrides.

This element is clear enough but as far as the ferns are concerned is not sufficiently extensive to merit any serious consideration of a previous land connection between the New Hebrides and New Caledonia, as suggested by Cheeseman (1957). It seems more reasonable to interpret the small New Caledonian element in the New Hebrides fern flora as the result of casual dispersal across the intervening ocean. Solem (1958) reached a similar conclusion after studying the distribution of snails. This view is perhaps supported by the fact that five of the seven species in this

New Caledonian element have only been found so far on Aneityum, Tanna or Erromanga, the southern islands in closest proximity to New Caledonia.

Although the New Hebrides share approximately 108 species with New Caledonia (figure 3), it is clear that its flora possesses few of the distinctive neocaledonian species, despite its close proximity. Out of a total of 245 species in New Caledonia some 137 species are unknown from the New Hebrides and in the other direction approximately 142 of the 249 species recorded from the New Hebrides are not found in New Caledonia. Thus out of a total of 387 species known from both archipelagos only 108 or 28 % are common to both. It is remarkable that two archipelagos separated by less than 320 km should have such relatively distinct fern floras.

The distinctive portion of the New Caledonian flora can at least be partly accounted for by its greater age and past isolation and much of the present disparity between the two floras can probably be explained largely in terms of geological, climatic, topographical factors and the consequent vegetational differences between the two archipelagos, as well as by the absence of any past land connection. For example some of the New Caledonian peculiarities, such as *Stromatopteris monoliformis* Mett. and many of the endemics, are found on the extensive serpentine areas in the south of the main island, a formation virtually absent from the New Hebrides apart from a small area on Pentecost. However, further careful ecological studies are needed before a detailed explanation can be attempted.

3.3. *Endemism*

One of the most striking features of the fern flora of the New Hebrides is the very low level, even by fern standards, of species endemism.

The information available at present indicates that there are no more than 11 endemic species which represents 4.4 % of the total flora. A list of the endemic species with a summary of their distribution and relationships, where these are known, is given below:

Cyathea aneitensis Hook.	Aneityum, Erromanga. Doubtfully distinct from *C. vieillardii* Mett. of New Caledonia.
Cyathea leucolepis Mett.	Aneityum, Tanna. Closely related to *C. obovata* A. Braith ined. from the Solomon Islands and *C. moseleyi* Bak. of the Admiralty Islands.
Cyathea sp.nov.	Efate, Malekula, Espiritu Santo.
Davallia leptocarpa Mett.	Known only from the type collection from Aneityum.
Humata multifida (Bak.) Carr. ex Brownl.	Aneityum, Tanna. Closely related to *H. brackenridgei* Brownl., a widely distributed Pacific species found also in the northern New Hebrides.
Diplazium oblongifolium (Hook.) Jermy	Aneityum, Erromanga, Espiritu Santo.
Asplenium brachycarpum (Mett.) Kuhn	Aneityum, Malekula, Espiritu Santo. Doubtfully distinct from *A. gibberosum* (Forst.) of Fiji.
Asplenium diplotion Bak.	Known only from type collection from Malekula.
Grammitis sp. nov.	Tanna. Related to *G. monticola* Sledge of Samoa.
Grammitis sp. nov.	Espiritu Santo.
Vaginularia subfalcata (Hook.) C. Chr.	Malekula, Espiritu Santo.

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Although the present list is subject to revision by further fieldwork and future taxonomic studies, it is already evident that there is very little endemism, even at the species level, in the flora. Furthermore some of the endemics are only weakly differentiated from their nearest relatives in the Solomon Islands, Fiji or New Caledonia, and critical taxonomic studies may reduce their number even further. The present estimate of 4.4% could therefore perhaps be regarded as marginally too high.

The corresponding figures for the fern floras of other Pacific islands and archipelagos are:

Solomon Islands	10% (Braithwaite unpubl.)
New Caledonia	46% (Brownlie 1969)
Fiji	21.7% (Copeland 1929)
Samoa	17.5% (Christensen 1943)
Society Islands	30% (Copeland 1932*b*)
New Zealand	37% (Brownlie 1962)

The figures for Fiji and the Society Islands are probably rather too high because of Copeland's narrow interpretation of species, and Christensen considered his figure for Samoa as rather too high. Even so future revisions of these floras are unlikely to reduce the percentages to the level of that found in the New Hebrides. The flora therefore is conspicuous in the Pacific region in possessing the lowest level of species endemism of any of the larger islands or archipelagos.

The low level of species endemism and the presence of weakly differentiated species in the New Hebrides fern flora leaves the impression of a young flora which has not been isolated long enough to allow any extensive species differentiation.

3.4. *Floras of the different islands*

One of the interesting features of the present information available on the fern floras of the different islands is the richness of the southernmost island of Aneityum in relation to its area when compared with the other islands. The relevant figures are given below:

	no. of species	endemic species	area / km²
Espiritu Santo	167	5	4225
Malekula	65	4	2005
Efate	64	1	910
Erromanga	60	2	850
Tanna	51	3	550
Aneityum	135	6	165

There are 135 species recorded from Aneityum, which is approximately 165 km², while Espiritu Santo, which is at least 20 times larger, has only 167 species. The richness of Aneityum is further enhanced by the fact that six of the endemic species are found on the island. The remaining islands have between 51 and 65 species, Malekula being noticeably poor in relation to its area.

Some of the apparent differences in the richness of the fern floras can be attributed to unevenness of collecting and also to topographical, climatic and ecological differences between the various islands.

Aneityum has traditionally attracted the attention of plant collectors because of its close

proximity to New Caledonia and can certainly be considered as the most thoroughly explored of the various islands in the New Hebrides.

Espiritu Santo has received much less attention from collectors generally and can be regarded as underexplored, so that the present figure may well be increased with further exploration. In this connection it is, however, worth noting that Chambers (see Chambers *et al.* 1971), collecting in the southern part of the island and Pic Santo (1697 m), recorded only two species which were not collected during our expedition in the Apuna Valley and Mt Tabwemasana areas, in the north of the island. It is, therefore, not anticipated that the numbers of species recorded for Espiritu Santo will be increased dramatically. Much of the eastern part of the island is made up of extensive low altitude limestone terraces which, in the lower part of the Apuna Valley, were noticeably poor in ferns.

The remaining islands, apart from Erromanga, are less well explored and the figures are therefore less reliable. The low figure for Malekula can also be partly explained by topographical, climatic and ecological factors. It lacks any high mountains with mist forest and much of the forest seen on the extensive raised limestone terraces on the west coast was dry and poor in ferns. The figure for Tanna is partly a reflection of the difficulties in collecting experienced by the expedition there, but no doubt also reflects a depauperate flora possibly caused by severe volcanic disturbance known to have occurred there in relatively recent times.

While much of the apparent difference in the richness of the floras of the different islands can be explained by climatic, altitudinal and ecological differences it is doubtful whether these factors can explain fully the relative richness of Aneityum.

It is too early for a detailed comparison of the floras of the different islands because of the incomplete floral lists available at present for the reasons just stated. Nevertheless some general observations may be made at this stage on the distribution of ferns within the archipelago.

A crude measure of floral uniformity within the group may be made by comparing the fern floras of Aneityum and Espiritu Santo. The two islands share approximately 86 species, which represents 64 % of the flora of Aneityum and 51 % of the flora of Espiritu Santo. Although these two islands at opposite ends of the archipelago share a large number of species there are still appreciable differences in their respective floras. The corresponding figures for the northern group of islands, Efate, Malekula and Espiritu Santo, and the southern group of Aneityum, Tanna and Erromanga, provide a similar picture. There are approximately 115 species found in both the northern and southern group which represents 73 % of the total number of species in the southern islands and 57 % of the known flora of the northern islands.

There are about 40 species at present known only from the southern islands and approximately 79 which have been found only in the northern group of islands, many of them only from Espiritu Santo. These figures will doubtless be reduced as the islands are further explored, so that some of the present apparent regional differences may be attributed to undercollecting. Other differences can be accounted for by ecological factors. The New Hebrides spans 8° of latitude and there are striking climatic changes from north to south. Several species in the large group found in the northern islands are high altitude ferns and have so far been found on Mt Tabwemasana (1879 m) and Pic Santo (1697 m), Espiritu Santo. These mountains are considerably higher than those on the remaining islands and some at least of these high altitude species could therefore not be expected to occur elsewhere in the group. Examples in this category include *Lycopodium serratum* Thunb., *Lycopodium parksii* Copel., *Lycopodium volubile* Forst., *Hymenophyllum bamlerianum* Ros., *H. treubii* Racib., *Cyathea medullaris* (Forst.) Sw.

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C. truncata (Brack.) Copel., *Oleandra sibbaldii* Grev., *Elapholgossum angulatum* (Bl.) Moore, *Elaphoglossum yunnanense* (Bak.) C. Chr., *Dryopteris hirtipes* (Bl.) O. Ktze, *Pronephrium beccarianum* (Cesati) Holtt. *Asplenium insiticium* Brack., *Diplaziopsis javanica* (Bl.) C. Chr. and *Xiphopteris glandulosopilosum* Bause.

The distribution outside the New Hebrides of the northern and southern groups of species are analysed in table 8. In the southern group the New Caledonian and endemic element are both

TABLE 8. ANALYSIS OF DISTRIBUTION OF SPECIES FOUND IN THE NORTHERN ISLANDS, EFATE, MALEKULA AND ESPIRITU SANTO, AND IN THE SOUTHERN ISLANDS, ANEITYUM, TANNA AND ERROMANGA

	northern group	southern group
pantropic	—	1
palaeotropic	3	3
Indomalesian–Pacific	12 (2 reaching eastern limit in New Hebrides)	44 (18 reaching eastern limit in New Hebrides)
Pacific	13 (2 reaching western limit in New Hebrides)	25 (12 reaching western limit in New Hebrides)
New Caledonian	5	2
endemic	6	3
Austral	2	1
	total 41	79

strongly represented compared with the flora as a whole. It would therefore appear that part of the flora peculiar to the southern islands can be accounted for by increased endemism and by enrichment from New Caledonia. Other more widely distributed species in this southern group may also be derived from New Caledonia. Two dry country ferns, *Cheilanthes tenuifolia* (Burm.) Sw. and *C. hirsuta* (Poir.) Mett., found so far only on Aneityum may fall into this category. Both species are found in New Caledonia but have not yet been recorded in the Solomon Islands, Fiji or Samoa, and could well be relatively recent immigrants which have colonized the dry coastal scrubland on the lower parts of Aneityum left after the clearance of the forest. Such enrichment from New Caledonia could be a factor contributing to the relative richness of the flora of Aneityum mentioned earlier in this section.

In the larger northern group, the Indomalesian–Pacific element is strongly represented and nearly half of this element reach their easternmost limit in the New Hebrides, most of them in Espiritu Santo, but a few only reach the Santa Cruz Islands.

While these regional differences may be explicable in terms of the similarities of the climate of the southern New Hebrides and New Caledonia on the one hand, and the northern New Hebrides and the Malesian region on the other; it is possible in some instances the differences may be the consequence of relatively recent migration from New Caledonia and the Solomon Islands or Fiji respectively, and that the species have not yet had time or the opportunity to radiate throughout the archipelago.

3.5. *Dispersal and migration*

The high proportion of pteridophytes to angiosperms in insular floras has been noted by many plant geographers and has often been cited as evidence of the importance of long distance dispersal of spores by winds in colonizing oceanic islands. The high proportion of pteridophytes has already been discussed (§3.1) and similar arguments may be applied to the New Hebrides.

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Tryon (1970) has recently reviewed some aspects of the dispersal of fern spores, emphasizing their high and substantially equivalent capacity for dispersal by air, and has also discussed the importance of a fit between the genotype of the dispersed spore and the new (island) environment necessary for successful migration, and the differences between species in their ability to migrate. It is not intended to review the evidence here in detail.

The efficacy of long distance dispersal of spores by wind is perhaps best seen in some of the more remote oceanic islands such as Tristan da Cunha. Wace & Dickson (1965), from their detailed studies of the Tristan–Gough group, concluded that much of the flora had been derived across 4000 km of ocean from South America and found it 'difficult to see how the relative abundance of cryptogamic species in the native flora of the Tristan–Gough group can be accounted for other than by admitting the efficiency of long range windborne dispersal of their spores'. The evidence for the air transport of fern spores over distances much greater than those separating the New Hebrides from neighbouring archipelagos seems so compelling that it scarcely seems necessary to examine other views in detail.

Doubts have, however, been expressed about the capacity of fern spores to disperse widely by Christ (1910) in his *Geographie der Farne* and by Copeland (1940) who wrote 'Ten miles of water is no barrier to their spread, once they are picked up by the wind. A thousand miles, though, seems to be, in general, an impossible barrier'. Lovis (1959) agreed with this view when he explained the relationship between the fern floras of Australia and New Zealand by Continental Drift. More recently, however, Brownlie (1962) has explained the same relationship by chance dispersal from Australia to New Zealand.

The importance of the adaptability of the genotype-phenotype of the dispersed spore and ecological factors in relation to successful establishment, and the associated differences of species in their ability to migrate are perhaps shown by the demarcation already discussed in §3.23 between the fern floras of the New Hebrides and New Caledonia.

3.6. *Age and origin of the flora*

The general geological history of the New Hebrides summarized by Mallick (1975) suggests the western islands began developing during the Tertiary by accumulation of calc-alkaline volcanics on the submarine slopes below small reef fringed volcanic islands, during the Oligocene and Middle Miocene. A second volcanic phase from Late Miocene to Early Pliocene gave rise to wholly submarine volcanoes in the eastern and southern parts of the archipelago, while calcareous sediments were forming in the western islands. During a third volcanic phase, from Pliocene to Recent times, general uplift has led to most of the volcanoes becoming subaerial, and extensive limestone terraces appeared round some of the older islands. Thus the land area of the New Hebrides has increased rapidly during Quaternary times. Mallick (1975) estimates that up to the Quaternary the total land surface was less than a tenth of the present day area.

The New Hebrides have, therefore, probably been available as a suitable habitat for terrestrial plants at least since the Oligocene but, perhaps of greater significance to biogeographers, any appreciable area of land surface only became available during the Quaternary.

There is at present no geological evidence to indicate any land connections with the neighbouring archipelagos, a situation which seems on the whole to demand that the flora should be treated as one which has arisen by transoceanic dispersal.

All the evidence from the ferns presented in this paper supports the view that it is a young flora derived by transoceanic dispersal from the neighbouring archipelagos of the Solomon

Islands, Fiji, and to a lesser extent New Caledonia. The evidence may be summarized as follows:

(*a*) low species endemism and weak differentiation of some of the endemic species (§3.3);
(*b*) disharmony in the flora (§3.1) and the possibility that the flora has not reached internal harmony by local radiation of immigrant ferns (§3.4);
(*c*) the affinity of the flora with the Solomon Islands (§§3.21, 3.22 and 3.3);
(*d*) the affinity of the flora with Fiji (§§3.22 and 3.3);
(*e*) a small but distinctive New Caledonian element in the flora (§§3.23, 3.3);
(*f*) the high dispersability of fern spores (§3.5).

It is difficult in the case of ferns to estimate the relative contribution to the flora of each of the neighbouring archipelagos because of the nature of their distribution. A considerable proportion of the fern flora is found in either two or all three of the surrounding archipelagos. Nevertheless it is evident that its closest relationships are with the Solomon Islands to the north and Fiji to the east, with Fiji perhaps marginally the closer. This is consistent with the directions of the major dispersal agencies for spores, the Southeast Trades and tropical hurricanes which impinge on the islands from the east and north respectively. Thus the relationships of the flora to the north and east are largely what might be expected from the present position of the New Hebrides in relation to the Solomon Islands and Fiji.

There still remains the apparent paradox of the weak relationship of the fern flora with its nearest neighbour, New Caledonia. Although it has been suggested (§3.23) that much of the demarcation between the floras of the two archipelagos can be explained by geological, climatic, topographical and the consequent vegetational differences, other factors may also be involved. The two archipelagos may be more isolated than their present geographic positions indicate, because the New Hebrides, particularly the southern islands, present a very small target for the reception of spores, or they may have been further part in the past, as is suggested by Mallick (1975) in his discussion of ocean floor spreading and its effect on the relative positions of New Caledonia and the New Hebrides. Whatever the final explanation the problem presented by these two floras is a challenging one which demands further critical study.

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Appendix A

New Hebrides fern genera (arranged after Holttum 1959)

PSILOTOPSIDA
PSILOTALES
Psilotaceae
Psilotum
Tmesipteridaceae
Tmesipteris

LYCOPSIDA
LYCOPODIALES
Lycopodiaceae
Lycopodium
Selaginellaceae
Selaginella

SPHENOPSIDA
EQUISETALES
Equisetaceae
Equisetum

PTEROPSIDA
OPHIOGLOSSALES
Ophioglossaceae
Helminthostachys
Ophioglossum
MARATTIALES
Marattiaceae
Angiopteris
Marattia
FILICALES
Osmundaceae
Leptopteris
Schizaeaceae
Lygodium
Schizaea
Gleicheniaceae
Dicranopteris
Gleichenia
Hymenophyllaceae
Hymenophyllum
Trichomanes
Cyatheaceae
Culcita
Cyathea
Dicksonia
Polypodiaceae *s.s.*
Belvisia
Dipteris
Drynaria
Goniophlebium
Loxogramme
Microsorium
Phymatodes
Pyrrosia
Selliguea
Grammitidaceae
Calymnodon
Ctenopteris
Grammitis
Prosaptia
Xiphopteris

Remaining genera of ferns (in Groups, alphabetically)

Adiantum group
Adiantum
Aspleniopsis
Cheilanthes
Doryopteris
Pityrogramma
Syngramma
Taenitis

Asplenium group
Asplenium

Athyrium group
Diplaziopsis
Diplazium
Lunathyrium

Blechnum group
Blechnum

Davallia group
Davallia
Humata
Leucostegia
Scyphularia

Dennstaedtia group
Dennstaedtia
Histiopteris
Hypolepis
Microlepia
Orthiopteris
Pteridium

Dryopteris group
Arachnoides
Dryopteris
Polystichum

Lindsaea group
Lindsaea
Sphenomeris
Tapeinidium

Lomariopsis group
Bolbitis
Elaphoglossum
Lomagramma
Lomariopsis

Nephrolepis group
Nephrolepis
Oleandra

Pteris group
Acrostichum
Pteris
Stenochlaena

Tectaria group
Lastreopsis
Stenosemia
Tectaria

Thelypteris group
Christella
Cyclosorus
Macrothelypteris
Mesophlebion
Pneumatopteris
Pronephrium
Sphaerostephanos

Vittaria group
Antrophyum
Vaginularia
Vittaria

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FIGURE 1. (*a*) *Aspleniopsis decipiens* (Mett.) Kuhn growing on the bank of the Nuangkau River, Erromanga. (*b*) *Tmesipteris tannensis* (Spr.) Bernh. growing near the base of a trunk of *Cyathea lunulata* (Forst.) Copel. on the west slopes of Mt. Toukosmeru, Tanna. (*c*) *Tmesipteris* sp. epiphytic on the trunk of *Metrosideros*, Aneityum.

FIGURE 8. *Marattia smithii* (Forst.) Hoffm. in ridge side forest, S.W. Malekula.

FIGURE 9. *Blechnum gibbum* (Labill.) Mett., a New Caledonian species, growing on a stone bed in the Nuangkau River, Erromanga.