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AN INTRODUCTION TO THE DISTRIBUTION OF FICUS

by

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CONTENTS

SUMMARY

Ficus displays many problems fundamental to the distribution of tropical plants. As a natural genus, one of the most derived of its family, it shows that these problems refer not to the origin of the genus or of its major groups, but to the subsequent course of sectional evolution. Detailed morphological revision must, therefore, precede phytogeography. The facts, here epitomised, are based on monographic revision of the species of Asia and Australasia, and have not been called from other writings.

Seed-dispersal in Ficus must be accompanied by dispersal of the pollinating wasp. It seems true, as Beccari pointed out, that the large banyans have an advantage in this respect over small trees impeded by the dense forest.

Two subgenera, *Pharmacosycea* and *Urostigma,* suggest a southern migration, but the third subgenus *Ficus* suggests a northern origin and dispersal. Pharmacosycea, hitherto regarded as American, has 46 species in Asia and Australasia, and it comprises most of the fig-flora of New Caledonia (26 species in all, 20 endemic species of Pharmacosycea). *Ficus prolixa* (Polynesia) seems related to sect. Americana of Urostigma. The *F. elastica* group (Queensland, Papua, Solomon Islands) seems related to the African sect. Bibracteata of Urostigma. The *F. benghalensis* group parallels the distribution of the Dipterocarpaceae, but does not occur in Africa.

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Regarding subgen. Ficus, all the sections show the main problems of Indomalaysian phytogeography, which are even borne out by the subspecies of the wide-spread *F. tinctoria*. The Chinese flora is distinguished by the abundance of the *F. erecta* group of section Ficus. The polynesian flora is distinguished by the *F. scabra* section of *Sycidium*. *Sycocarpus* (Covellia) and *Synoecia* are typically Malaysian sections. Synoecia, centred in North Borneo, points to the ancestral connection between the four groups of climbing figs of sect. Ficus and of the *F. erecta* group, and it indicates the Philippine-Asiatic connection as an important historical locus. This is supported by the disjunct distribution of the *F. cunia*- *F. pungens* alliance (Sycidium) and the *F. pomifera*- *F. itoana* alliance (Sycocarpus).

The new section *Adenosperma* of eastern Malaysia shows the repetitive, or orthogenetic, and dyschronous evolution which the sections of Ficus have undergone.

Formosa has roughly equal numbers of species from the Philippine flora and that of the Asiatic mainland. Ryu Kyu is similar but about half as rich. Japan has merely four species of the mainland, which also occur in Formosa. These facts support the Philippine-Asiatic mainland connection. The Philippine flora has almost equal numbers of Sundaland and Papualand species; it is esentially the same as the Celebes fig-flora, except for the endemic development of the *F. erecta* group in the Philippines and the presence of the Adenosperma section in Celebes; any direct connection of the Philippines with New Guinea is but feebly indicated. Wallace's Line between Borneo and Celebes indicates a much greater barrier to westward migration of Papualand species than the eastward migration of Sundaland. Eastern New Guinea is nearly twice as rich in species as western, presumably because of its topography and because of its connections with the Solomon Islands and Queensland. There is considerable evidence for the use of the Timor-Sumatra track in both directions, but none of the particular Australian species has been found in Timor.

The fig-floras of New Hebrides, Fiji, Samoa, Tonga, and Tahiti are related to that of the Solomon Islands. The New Caledonian flora must be ancient, for in addition to the 20 endemic species of Pharmacosycea it contains only six widely distributed species, and none of the groups characteristic of Malaysia.

The peculiarities of the Riouw Archipelago and the adjacent parts of the Malay peninsula and Borneo are indicated as the Riouw pocket.

Five tables of distribution are provided.

The new section *Adenosperma* (subgen. Ficus) is described, with its two new series *Amphigenae* and *Hypogenae*.

PREFACE

The need for critical studies of large genera has lead me to investigate *Ficus*. For several years I have been busy with the morphological classification; there now emerges a pattern of geographical distribution which is fascinating and encouraging. If anyone mistrust the efficacy of morphological enquiry, I advice apprenticeship to a similar problem, sorting hundreds of species into closer and clcser groups until, of their own accord, other aspects begin to obtrude; a picture forms in such harmonious revelation that proves the power of the analysis.

That *Ficus* is a natural genus is shown by the inflorescence and peculiar pollination; the gall-flowers are adapted to the hatching of the pollinators. The inflorescence may be foreshadowed in other Moraceae, but not, apparently, the method of pollination; neither *Dorstenia* nor *Sparattosyce*, often cited as progenitors, have gall-flowers. It is, therefore, an isolated genus. The sections are generally satisfactory but, in all cases, there are a few species which overstep the boundaries in some way. The genus is coherent and cannot be broken into separate units of different ancestry. We may be confident, then, that in *Ficus* we have the enormous expansion of a natural unit which, if it were not for the existence of the other Moraceae, would be treated as a family.

There are about nine hundred species. I estimate 500 for Asia and Australasia. Many are very common; most are conspicuous; and nearly all can easily be recognised as such and are accordingly collected by botanists, even though the plants are sterile. The genus is well-represented in herbaria, and the charge cannot be made that the material is inadequate. Attention to microscopic details of the leaf will usually secure the identification of the sterile material, though this may not be possible with juvenile dissected leaves until transitional series become available.

The magnitude of such research delays completion. I have studied about 95% of the species of Asia and Australasia, and have made a hasty examination of African and American. Completion would take several more years, and may not be accomplished. This preliminary account will, I hope, encourage the collector to fill gaps, and the botanist to realise that *Ficus* is not an ivory-tower of the species-monger, but a scientific problem. We have in the world to-day the evidence of the evolution of trees, climbers, and epiphytes, and of the wanderings which they have undergone in a fullness scarcely possible in another genus.

INSECT AND SEED DISPERSAL

Dispersal in *Ficus* is a double problem: the pollinating insect must accompany the plant. There is much evidence that the insects are specific to their hosts, as one would imagine from the intimate development of the larva in the gall-ovary, as well as from the way, presumably olfactory, in which the insect discovers the immature fig. It is well-known that introduced fig-plants do not seed unless their particular insect has also been introduced: such plants generally do not mature the figs or, if matured, the fruits (drupelets) are empty. The point was proven on the introduction of *F. carica* to California, though the necessity for caprification had long been realised, and by Pemberton (1921) in the case of *F. macrophylla* on introduction to Hawaii from Australia. It is also commonly to be observed in such as *F. benghalensis*, *F. lyrata* (Africa) and *F. aspera* (New Hebrides) in many parts of the tropics; *F. punctata* (Asia) ripens its seed-figs in the Royal Botanic Gardens in Edinburgh, but they contain no seeds. About 1930 several common Malayan species, as *F. fistulosa* and *F. grossularioides* (= *F. alba*), were introduced to Hawaii to help recover the deforested hills; they grew well, but set no seed until the insects were introduced. Dr. Fosberg informs me that the insects were liberated on one island and, in a few years, spread to others where the figs were growing. It appears from this important experiment, which seems not to have been published, that the insects may be spread far and wide by wind and be no handicap, therefore, to the dispersal of the plants. Certainly, the insects are produced in immense numbers, which lead to the congregation of swifts and fly-catchers above the crowns of big trees; several authors speak of the clouds of insects emitted from the ripe fruits (Ridley, 1930). For the fig-trees of sea-coasts there may be no problem of insect-dispersal, and many of them, as *F. tinctoria*, *F. retusa*, and *F. superba*, are very wide-spread, but it is not clear that this will apply to plants in the interior of the forest. The life of the adult insect appears to be short; Pemberton gives two to three days, and Williams (1928) rather longer. The difficulty for the pioneer-plant may lie in the simultaneous proximaty of insect and fig at the correct stage of development. In Singapore, and , I believe, in Malaya generally *F. elastica* does not seed, though commonly planted; yet it seems to be wild on the limestone hills in the north of the country. Wide dispersal of insects over and through tropical forest may be ruled out.

The seeds, which are really the pyrenes of drupelets, vary 0.5—5 mm long, and are more or less compressed. They are dispersed by animals swallowing the seeds or biting at the fig and dropping it, or by the figs falling into streams and floating with the current (Ridley, 1930). This method certainly explains the abundance of many species along river-banks where deforested, and floods deposit seeds in the interior of the forest. However, when the distribution of *Ficus* is viewed systematically, it is seen, as Beccari noticed (1940), that the large trees, climbers, and particularly the banyans (strangling figs) are in general more wide-spread than the smaller trees and climbers of the interior or periphery of the forest. The larger plants, reaching the top of the forest, are visited by the stronger-flying birds and bats, and must therefore be more wide-spread. The subgenus Urostigma, comprising nearly all the banyans, is the only one to occur throughout the tropics, and the 'false banyan' *F. tinctoria* (sect. Sycidium) is the most widely distributed species in the East, ranging from Ceylon, India and Ryu Kyu to Polynesia. In the high forest banyans need to germinate on branches well above the ground, their seedlings or saplings very rarely occurring in the lower layers, and suitable habitats cannot be nearly so abundant as the extent of the forest would suggest; but some species can establish themselves on the ground, or rocks, of sea-coasts and on cliffs whence they may pass again to the upper layer of the forest, and this is true of some small epiphytes as *F. deltoidea*. On the other hand, the large buttressed trees as *F. variegata* and *F. albipila* (*F. microtricherinos* of Java, and *F. colossea of* Queensland), which are distributed from the Asiatic mainland to New Guinea and Queensland, require low-level dispersal and ground-germination. *Ficus variegata*, like the majority of fig-trees, occurs mainly in secondary forest and along streams and river-banks, as a pioneer of open places, and the spread of such plants before human interference must have been as precarious as for the banyans. Nowadays the abundance of such plants, as *F. fistulosa*, *F. hispida*, *F. grossularioides*, *F. copiosa*, *F. cumingii* and *F. ampelas*, is as artificial as the open places where their seeds are dropped. Under such conditions of broken-up forest, the specific evolution of many other plants has broken down through hybridisation, as in *Crataegus*, *Rosa*, *Rubus*, and *Salix*, but I have seen no evidence of this whatever in *Ficus*, which goes to prove the specificity of the pollinators. A similar and, in a sense, artificial abundance of banyans may be seen too in villages near the forest, where forest-trees and large fruit-trees occur in the open: they become infested with banyans, as with Loranthaceae, because they become the roosting places of birds. In the forest, the banyans are as scattered as any large tree-species.

In contrast with *F. variegata*, *F. albipila* is a true inhabitant of the high forest, and it poses the problem how small seeds, c. 1 mm long, become established. They survive, it seems either in places temporarily denuded of humus, as by rainwash or the overturning of trees, or, indeed, on the fallen trunks themselves. It cannot be assumed, therefore, however obvious the general method, that all fig-plants have equal means of dispersal and establishment: much more specific investigation is required.

WORLD DISTRIBUTION

Ficus occurs in all parts of the world where desert and frost do not prevail. From Asia Minor, South China and Japan it extends through Africa, Asia, Australia and Polynesia to the Tuamotu Archipelago, and from the southern United States through Central America and the Caribbean to north Argentina: that is, roughly, between the latitudes of 35° north and south. It is absent from Hawaii, though *F. prolixa* Forst. f. occurs in Fanning Island about 900 miles to the south (Guppy, 1906), and, more remarkably, from New Zealand, though *F. macrophylla* Desf. occurs in Lord Howe Island, and introduced species now flourish in both Hawaii and New Zealand. A few species ascend tropical mountains to an altitude of 2000 m, but the great majority belongs to the lowlands.

It is not possible to compare the numbers of species in the different continents because of the inordinate synonymy and the differences in specific concept in the various floras, but there can be no doubt that the rain-forest region from Assam to the Solomon Islands is by far the richest in species, sections and growth-forms. America has the trees of the subgenus Pharmacosycea and the banyans of subgen. Urostigma sect. Americana. Africa has the trees and shrubs of the sections Sycomorus and Sycidium of subgen. Ficus and the banyans of subgen. Urostigma sect. Urostigma and Bibracteata. Asia has, in addition to Pharmacosycea, Sycomorus, Sycidium and sect. Urostigma, the sections Ficus, Sycocarpus (Covellia), Adonosperma, and Synoecia of subgen. Ficus, with many climbers and epiphytes; and these groups extend with varying attenuation into Australia and Polynesia.

CLASSIFICATION

The first division of Ficus is into the monoecious and dioecious species, but it is more convenient to recognise three subgenera, namely the monoecious banyans (Urostigma), the monoecious trees (Pharmacosycea), and the dioecious Ficus. I give a synopsis for reference:

subgen. Pharmacosycea Miq.
subgen. Urostigma (Gasp.) Miq.
    sect. Americana Miq., Bibracteata Mildbr. & Burr., and Urostigma.

subgen. Ficus

sect. Ficus (Eusyce)

Sycomorus (Gasp.) Miq., including Neomorphe King, Sycocarpus Miq. (Covellia auct.), Adenosperma sect. nov. (see Appendix, p. 43), Sycidium Miq., including Palaeomorphe King, Synoecia (Miq.) Benth. et Hook.

This poses a phytogeographical problem. On the grounds of 'Age and Area' (Willis, 1949), the pantropic subgen. Urostigma is the oldest. On grounds of multiplicity of species and life-forms, indicating the centre of origin, subgen. Ficus is the oldest. On morphological grounds I can make no clear distinction: male flowers with 2—3 stamens (—5, in sect. Ficus) and a sterile ovary occur in Pharmacosycea and Ficus: large-leafed, more or less pachycaul tree-forms, which I would regard as primitive (Corner, 1954), occur in all three subgenera and most sections: large, multibracteate figs occur chiefly in sect. Sycocarpus, which in floral construction is the most advanced. The presence of neuter flowers in place of male in the seed-figs of several sections of subgen. Ficus suggest that the monoecious state is the primitive. If, then, Urostigma is more primitive, the derivation of Ficus becomes a problem of the southern hemisphere; if subgen. Ficus, then it is a problem of the Indomalaysian forests and the ancestral forests of the Tethys sea in the northern hemisphere. In neither case do I suppose that the present distribution indicates the origin of the genus, which must have been a Cretaceous problem or earlier, followed by a north-south dichotomy. But the sections of the genus have since undergone regional diversification, which may disclose their migrations.

DISTRIBUTION IN ASIA AND AUSTRALASIA

General. Table 1 is a synopsis, so far as I have checked, of the distribution in political territories, except that New Guinea and Polynesia are treated as units. Minor alterations must be expected, but the main picture can hardly change. It is not a fair assessment, however, of the Asiatic mainland, where plant-distribution does not follow governmental boundaries and African, Sinohimalayan, Sundaland, and Mascarene elements must be distinguished. To balance, therefore, the large numbers of New Guinea, I have given a column (AM) for the Asiatic mainland: it is, of course, omitted from the systematic totals, for the species are also itemized under the countries.

Table 1. Distribution of *Ficus* in Asia and Australasia;

Sections	AM	Ni	An	Cy	I	B	Jp	RK	F	C	IC	Th
Pharmacosycea	6 (2)	—	3	2	2	3	—	—	2	2	4	4
Urostigma	74 (29)	2	9	12 (2)	25 (5)	23	1	2	3	17 (1)	38 (2)	26
Sycomorus	4 (1)	—	1	1	1	2	—	1	1	3	3	4
Sycocarpus	14 (5)	1	1	1	5 (1)	9	—	2	3	4	3	9
Adenosperma	—	—	—	—	—	—	—	—	—	—	—	—
Sycidium	18 (6)	1	2 (1)	4	6	7	—	4	6	7	10 (2)	11
Ficus	51 (24)	1	4	2 (1)	18 (1)	20	5 (2)*	3	8 (3)	30 (3)	30	18
Synoecia	3	1	—	—	—	1	—	—	1	—	1	2
Totals	170 (67)	6	20 (1)	22 (3)	57 (7)	65	6 (2)*	12	24 (3)	63 (4)	89 (4)	74

* Bonin Isl. + Fiji

AM, Asiatic mainland; Ni, Nicobar Islands; An, Andaman Islands; Cy, Ceylon; IC, Indo-China; Th, Thailand; M, Malaya; S, Sumatra; B, Borneo; J, Java; LS, Lesser luccas; NG, New Guinea; Sl, Solomon Islands; NC, New Caledonia; A, Australia;

sections and numbers of species, endemics in brackets.

M	S	B	J	LS	Fl	T	PI	Cl	Ml	NG	Sl	NC	A	P	Totals
4	5	5	5	2	1	3	5 (2)	7 (3)	4	12 (8)	3	20 (20)	1	3 (1)	46 (34)
46 (1)	29	38 (1)	30	11	2	9	28 (2)	21 (1)	13	24 (9)	6	3	15 (7)	7	107 (31)
3	2	2	2	1	—	2	3	3	2	4 (2)	1	—	2	—	9 (2)
11	10 (2)	19 (8)	6	3	1	2	15 (7)	11 (4)	10 (3)	18 (11)	10 (6)	—	3	3 (1) +	65 (43)
—	—	—	—	—	—	—	—	3	7	16 (9)	4 (1)	—	2	1†	18 (10)
11	15 (2)	22 (7)	14	2	4	4	24 (5)	23 (4)	16	29 (13)	15 (4)	3	9 (5)	15 (12)	90 (55)
26 (1)	27 (2)	33 (12)	16	2	—	2	20 (8)	14	11 (2)	31 (23)	4	—	1	2	119 (58)
3	3	10 (6)	3 (1)	1	—	1	5 (3)	3	1	4 (4)	—	—	—	—	19 (14)
103 (2)	91 (6)	129 (34)	76 (1)	22	8	23	100 (27)	85 (12)	64 (5)	138 (79)	43 (11)	26 (20)	33 (12)	31 (14)	473 (247) ×

† New Hebrides × Excluding the Asiatic Mainland

I, India; B, Burma; Jp, Japan; RK, Ryu Kyu Islands; F, Formosa; C, China;
Sunda Islands; Fl, Flores; T, Timor; PI, Philippine Islands; Cl, Celebes; Ml, Mo-
P, Polynesia.

Table 2. Distribution of *Ficus* in Asia and Australasia;

Groups	AM	Ni	An	Cy	I	B	Jp	RK	F	C	IC	Th
Urostigma												
F. religiosa gr.	15 (9)	1	4	6	10 (1)	7	1	1	2	6	10	4
F. benghalensis gr.	58 (20)	1	5	6 (2)	15 (4)	16	—	1	1	11 (1)	28 (2)	22
F. elastica gr.	1	—	—	—	—	?	—	—	—	—	—	?
Sycidium												
F. scabra gr.	6 (4)	—	1 (1)	—	2	4	—	2	3	2	3 (1)	3
F. tinctoria gr.	8 (1)	1	1	1	1	1	—	2	3	3	4	7
F. heterophylla gr.	4 (3)	—	—	3	3	2	—	—	—	2	3 (1)	1
Ficus												
Miscellaneous	4 (3)	—	—	—	2	1	1* (1)	—	—	3 (1)	2	1
F. hirta gr.	10 (4)	1	2	—	2	4	—	—	—	5	6	6
F. aurata gr.	1	—	—	—	1	1	—	—	—	—	1	1
F. erecta gr.	19 (16)	—	—	—	6	6	2 (1)*	1	6 (3)	17 (2)	13	2
F. foveolata gr.	5 (2)	—	—	1	4 (1)	3	2	2	2	4	4	2
F. ramentacea gr.	11 (2)	—	2	1 (1)	3	5	—	—	—	1	3	5
F. obtusa gr.	1	—	—	—	—	—	—	—	—	—	1	1

* Bonin Isl.

AM, Asiatic mainland; Ni, Nicobar Islands; An, Andaman Islands; Cy, Ceylon; IC, Indo-China; Th, Thailand; M, Malaya; S, Sumatra; B, Borneo; J, Java; LS, Lesser luccas; NG, New Guinea; Sl, Solomon Islands; NC, New Caledonia; A, Australia;

divisions of sections *Urostigma*, *Sycidium*, and *Ficus*.

	S	B	J	LS	Fl	T	PI	Cl	M	NG	Sl	NC	A	P	Totals
5	2	2	4	3	1	5	5	6	6	4	1	1	2	2	17 (1)
9 (1)	26	36 (1)	25	7	1	4	23 (2)	14 (1)	6	11 (4)	3	1	2	2	71 (18)
1	1	—	1	1	—	—	—	1	1	9+ (5)	2	1	11 (7)	3	19 (12)
3	4	7 (1)	6	1	3	2	15 (4)	15 (3)	10	22 (10)	12 (4)	2	8 (5)	14 (12)	65 (41)
7	9 (2)	13 (5)	6	1	1	2	9 (1)	8 (1)	6	7 (3)	3	1	1	1	19 (12)
1	2	2 (1)	2	—	—	—	—	—	—	—	—	—	—	—	6 (2)
—	—	—	—	—	—	—	1 (1)	—	—	—	—	—	—	—	6 (3)
9 (1)	11 (2)	6 (1)	6	1	—	1	2	5	3 (1)	1	—	—	—	—	18 (5)
1	1	8 (7)	—	—	—	—	1†	—	—	—	—	—	—	—	8 (7)
3	3	3	1	—	—	—	7 (5)	4	1	1	—	—	—	—	30 (11)
2	1	?	1	—	—	—	—	—	—	—	—	—	—	—	5 (1)
.0	10	15 (4)	7	1	—	1	6	4	7 (1)	19 (14)	3	—	1	1	39 (20)
1	1	1	1	—	—	—	3 (2)	1	—	10 (9)	1	—	—	1	13 (11)

† One from West New Guinea × Palawan

I, India; B, Burma; Jp, Japan; RK, Ryu Kyu Islands; F, Formosa; C, China;
Sunda Islands; Fl, Flores; T, Timor; PI, Philippine Islands; Cl, Celebes; Ml, Mo-
P, Polynesia.

As centres of endemism stand out the Sinohimalayan region, Sundaland with Borneo as the peak, the Philippines, New Guinea, Australia, and Polynesia, but especially, New Caledonia, where endemism is no measure of area or altitude and there is the most peculiar fig-flora in the world. Such conclusions have long been known from other plants, but it is remarkable to me that the highly specialised Ficus should conform: it shows that the distribution of flowering plants in this part of the world has been conducted by events long subsequent to their origins.

The second pivot is the Philippine flora, to understand which the sections must be analysed.

Pharmacosycea. Custom places the monoecious species of the Old World in sect. Urostigma. Miquel (1847) made a section Oreosycea for *F. nervosa* Heyne (Asiatic mainland), and again (1848) a section Leiosycea for *F. vasculosa* Wall. (Indomalayan). King (1887) distinguished *F. vasculosa* and *F. callosa* Willd. from the rest of Urostigma without a special name. I find that these three, along with many others, totalling 46, belong to a distinct group of trees (not banyans) with characteristic fig- and flower-structure. It is this group exclusively which makes the astonishing endemism of New Caledonia (20 out of 26 species): it also contributes to the Fiji flora with two species. As other examples, there are *F. pubinervis* Bl., *F. gigantifolia* Merr., *F. granatum* Forst. f., and *F. polyantha* Warb. (*F. frondosa* S. Moore) which, in reaching a height of 150 feet, with bole 92 ft. long and 4 ft. in diameter at breast-height (NGF 1409), is the largest independent tree yet recorded for the genus. In contrast with these endemics, New Caledonia has merely three true banyans (sect. Urostigma), namely the wide-spread *F. retusa* auct. (non Linn.) and the wide-spread Polynesian species *F. prolixa* and *F. obliqua* Forst. f.: all three are mainly coastal or estuarine of the strand-flora. I was about to resurrect Miquel's Oreosycea, when I realised that it was no other than Pharmacosycea. There is, in fact, an astounding resemblance between many American species and those of the Old World, though none appears conspecific. Admittedly in Asia some species have but one stamen in the flower (2—3 in the American), but others have 1—2, 2, and 2—3, with such gradation that the character is of little importance. If the species of New Caledonia were planted in Ecuador, they would be classified unhesitatingly in Pharmacosycea. The species vary in New Caledonia from somewhat megaphyllous and pachycaul shrubs, as *F. asperula* Bur., to cauliflorus and geograpic trees with distichous leaves, as *F. racemigera* Bur., with which the Fijian *F. pritchardii* Seem. is allied: several occur on the serpentine soils. Here must be a relic-nest of ancient evolution, which has spread westward with decreasing numbers of species and increasing uniformity without, evidently, reaching Africa. The largest and most wide-spread species is the buttressed tree *F. albipila* (Miq.) King, which was first described from Sumatra in the sterile state as a species of *Morus*: it is known from Thailand, Malaya, Java, Borneo, New Guinea, and Queensland, and it suggests migration westwards along the Timor-Sumatra track (van Steenis 1934, 1936). There is no New Zealand or Tasmanian connection and, certainly, no northerly route by the Bering Strait. Whence lay the connection with America? Good (1950) mentions a few more instances of the American affinities of New Caledonia, such as *Licania* and *Calycorectes*, but I can find no affinity between it and Madagascar in Ficus.

U r o s t i g m a. Thus shorn of Pharmacosycea, subgen. Urostigma in Asia and Australasia, as well, probably, as in Africa, consists entirely of banyans, or strangling figs. A few, as *F. bracteata* Wall., are epiphytes rather then stranglers, and *F. globosa* Bl. is more of a lax root-climber. Many can grow on their own, rather short, trunks, especially when planted, but in the forest they are essentially epiphytes developing extensive roots to the ground and, mostly, supplanting the host-tree. Their distribution is very different from that of Pharmacosycea. Three main groups of section Urostigma must be distinguished (Table 2).

1. The F. r e l i g i o s a g r o u p has 17 species, for the most part widely distributed. *Ficus infectoria* sensu Roxb. (*Ficus lacor* auct.; I have not yet discovered the correct name for it) is spread from Ceylon to Australia and from China to the Caroline Islands, and it is exceedingly close to the African *F. ingens*. *Ficus superba* Miq. spreads along the coasts from Japan to Queensland as *F. rumphii* Bl. does from India to the Moluccas. Yet, in contrast, wild specimens of *F. religiosa* have been collected merely from south China and north Indochina. Fifteen species occur on the Asiatic mainland, to which nine are restricted, and about a dozen species occur in Africa from the Cape northwards. The group appears to be Afro-Indian, but there is a difficulty. To the east, where *F. infectoria* stops, there begins the Polynesian *F. prolixa* and it is exceptional in the group in having the male flowers scattered in the fig as in the sect. Americana. It is, indeed, very like some West Indian species, but it has three basal bracts as in sect. Urostigma, not two as in sect. Americana. Nevertheless, it may be the link with the American banyans.

2. The F. benghalensis group, including such as *F. retusa* auct. and *F. annulata* Bl., is much the largest and is centred in Sundaland, with Malaya as the peak. It also contains many wide-spread species, as *F. retusa, F. pilosa* Reinw. and *F. benjamina* Linn., which stretch from India to the Solomon Islands, and there are few endemics. The group diminishes markedly in India and does not enter Africa, though there are a few Arabian species. It is, in fact, a group of the Indomalaysian rain-forests with a distribution similar to that of the Dipterocarpaceae (Merrill, 1926; Symington, 1944). In a sense, these banyans are the great parasites of the dipterocarp forests, which they exceed only at their extremities, but why they should be so restricted, or so evolved, in parallel with the Dipterocarpaceae when they differ so much in habit, flower, and seed, is a problem deserving more enquiry. On the principle of 'Age and Area', it is an old group, but, contrary to a corollary of the principle, the endemic rate is low. Even if one takes the whole of the Malay peninsula and Sundaland as a unit, the endemic rate is but 12 in 43 species. This contrasts greatly with the rate in the sections of Ficus and in Pharmacosycea, and suggests that this old group, in conformity with the standardised leaf and fig is played out.

3. The F. elastica group, including *F. obliqua* Forst. f., *F. platypoda* A. Cunn., *F. marcophylla* Desf. and *F. watkinsiana* F. M. Bailey, is by contrast restricted mainly in eastern New Guinea and Queensland with high endemism. *Ficus elastica* is an outlying species of Java, Sumatra, Malaya, and, perhaps, Burma, and it lacks the crescentic or transverse dehiscence of the anther, typical of the rest of the group: it suggests the Timor-Sumatra track. *Ficus obliqua* is widespread from eastern New Guinea and Queensland into Polynesia. The other species are endemics, several with large and peculiar figs and, yet, leaves very like those of *F. elastica.* Some of these have the paired and caducous basal bracts and the slit-orifice with inflexed, not interleafing, apical bracts which are the features of the African section Bibracteata, though I am not aware that the Bibracteata have the peculiar dehiscence of the anther. This resemblance in fig-structure is either a parallel evolution or it is a phyletic connection between Papualand and Africa; we must await comparison with the African species.

Because of the occurrence of the American Pharmacosycea in Asia and Australasia, the affinity of the Polynesian *F. prolixa* with the American sect. Americana of subgen. Urostigma, and the apparent connection of the *F. elastica* group with the African Bibracteata, I conclude that the migration, if not the derivation, of the subgenera Pharmacosycea and

Urostigma must be a problem of the southern hemisphere. It concerns the distribution of lowland, tropical, rainforest trees and of banyans of this high forest, and it cannot be contemplated in terms of proto-angiospermous vegetation or of mountain or temperate floras. It indicates a late phase of angiosperm evolution.

Sycomorus. This small section consists of the monoecious subsection Sycomorus, which is African (c. 12 spp.) except for the Asiatic *F. racemosa* Linn. (*F. glomerata* Roxb.), and the dioecious Indomalaysian subsection Neomorphe. Systematically it relates to Pharmacosycea, but there are important differences and the connections with Neomorphe, which leads to Sycocarpus, are much closer. *Ficus racemosa*, as the outlier of Sycomorus, is a species of the Asiatic mainland which extends along the Sumatra-Timor track to S. E. Celebes and Queensland in several varieties (var. *elongata* King, *F. henrici* King, *F. acidula* King): it is absent from New Guinea, the Moluccas, the Philippines, and Formosa. Neomorphe extends from Burma, China, and Ryu Kyu throughout Indomalaysia to Queensland and the Solomon Islands; *F. variegata* Bl. covers very nearly the whole range. *F. nodosa* Teijsm. & Binn. is an eastern species from the Moluccas to the Solomon Islands, and it has two allies in New Guinea. The Philippines and Celebes have in common *F. sycomoroides* Miq., which is only a variety of *F. variegata*, and *F. ilangoides* Elm.

Sycocarpus (Covellia). This complicated section is typically Indomalaysian. It extends from Ceylon, India and China to Fiji, but is absent from New Caledonia. Borneo, the Philippines, Celebes, the Moluccas, New Guinea, and the Solomon Islands are all regions of endemism. The section consists of small to medium-sized trees, often cauliflorous, which are so intricate in their relationships that for most of the species I have not succeeded in delimitating satisfactory groups. It is characterised, on the one hand, by the advanced feature of a wholly gamophyllous perianth, which is gradually reduced until it is completely absent in a few species. On the other hand it shows features such as the multibracteate fig and the megaphyllous pachycaul habit, which appear primitive; and it is more varied than any other section of the genus. It serves to correct any facile notions of the origin and evolution of Ficus.

A group of six species can be defined by the seed-shape. It is the least specialised group and it relates with the next section Adenosperma. It contains the remarkable *F. dammaropsis* Diels (New Guinea) with the largest and most primitive fig in the genus, two stamens in the male flower, large leaves, and stout twigs, as the antecedent of the section would require. Related with it are two new species from the Solomon Islands, retaining the two stamens but simplified in other respects. A third species of the Solomon Islands is *F. indigofera* Rech. which is a normal small fig-tree and is related closely with the Fijian endemic *F. vitiensis* Seem. The fourth species in the Solomon Islands and the other in Fiji is the remarkable pachycaul treelet, *F. theophrastoides* Seem., which has the biggest leaves of the genus (up to 1½ m long). It is all the stranger that such plants are not represented in New Caledonia; its Pharmacosycea is well represented in New Guinea and to a proportional extent in both the Solomon Islands and Fiji.

The other species which enters Polynesia is the wide-spread *F. septica* Burm. f.; it belongs to the main group of the section and is often mistaken for the western *F. fistulosa* Reinw., though its affinity seems more with another species of the Solomon Islands. It has an insular distribution, paralleled by *F. ampelas* Burm. f. (sect. Sycidium). It has been found, often abundantly, in all the islands from Ryu Kyu, Borneo, and Sumatra to the New Hebrides, the Solomon Islands, and Queensland, but it is absent from Hainan, the Anambas and Natuna Islands, Flores, New Caledonia, and the whole of the Asiatic mainland from Singapore north. Certainly it is well-known as a cure for skin-diseases and wounds, and may well have been carried by man, but then one would have expected it in the remaining islands of Polynesia if human agency had been predominant. Nevertheless, in Timor Laut, the Admiralty Islands, the Solomon Islands, and the Santa Cruz Islands, as Summerhayes noted (1941), *F. septica* is a large cauliflorous tree; elsewhere, it bears the figs in the axils of the current leaves or on the twigs just behind them; and this difference suggests that the widely distributed plants may belong to a different variety from the forest trees or the eastern islands.

In contrast, *F. hispida* Linn. f., so common in open country on the Asiatic mainland, extends along the Timor-track to south Celebes, south Papua and Queensland, without reaching the remainder of New Guinea, the Moluccas, the Philippines or Formosa. *F. squamosa* Roxb. (*F. saemocarpa* Miq.) is remarkable in the whole genus for the very long style (6—10 mm) such as occurs in the New Caledonian Sparratosyce, in which, however, the styles project from the mouth of the receptacle; it is a Sinohimalayan species, but its only ally is an undescribed species from Sarawak with the figs densely covered with lateral bracts and style 12—15 mm. long. Any account of Ficus must fail which does not accomodate these two species. The long style suggests another, and unexpected, primitive feature in Sycocarpus, and detracts attention from the Solomon Islands.

Lastly, in this connection, I will mention the discontinuity and classificatory problem of *F. pomifera* Wall. and *F. itoana* Diels. The first is usually, but erroneously, classed in Neomorphe. It occurs in India and south China to the middle of Malaya, about Kuala Lumpur. This is the distribution of *F. auriculata* Lour. (*F. roxburghii* Miq.) which seems truly to belong to Neomorphe. Yet, the two species are so similar that I cannot distinguish them without examining the perianth; a few collections from Indochina seem, indeed, intermediate. The next ally is *F. itoana* of New Guinea, without there being a trace of either, or of an ally, in the interval. But *F. itoana* is close to *F. microdictya* Diels of New Guinea. This species has the perianth of Sycocarpus but it is monoecious as Sycomorus (which does not occur in New Guinea). Sycocarpus suggests the efflorescence of some lost stock of Ficus, and, as further proof, I will mention a case which really belongs with Sycidium, but which it has been customary to refer to Sycocarpus. The *F. cunia* group of three species is distributed exactly as *F. pomifera*, and its nearest allies are the species of the *F. pungens*-*F. minahassae* group of the Philippines and Celebes eastward to New Guinea. This group points to an ancestor which would combine not merely Sycidium with Sycocarpus and Sycomorus, but also with sect. Ficus. Such a problem obviously requires detailed exposition. I have mentioned it to show firstly that it is the systematic complexity of Sycocarpus which prevents clear phytogeographical analysis; secondly that plants exists with which to probe the derivation of the sections of Ficus; thirdly that without such enquiry much of the significance of phytogeography may be lost or misapprehended; and fourthly that it is such plants of scientific interest which botanic gardens should endeavour to maintain in cultivation, as well as the pantropic round of fine blossom.

Adenosperma (see Appendix, p. 43). The species of this section, such as *F. adenosperma* Miq. and *F. erythrosperma* Miq., have been scattered through most sections of the genus. When detected on agreement in flower and seed, they form an exceedingly distinct group of trees and shrubs, often riparian, which characterise the lowland rainforests from Celebes to the Solomon Islands and Queensland. New Guinea is their centre, and the species fall off rapidly to the east and west. In habit, leaf, and fig they show the same specific diversity as other sections. Now it is impossible to believe that *F. adenosperma*, *F. erythrosperma*, and *F. subcuneata*, which reach Celebes and which, as large subcanopy trees and river-bank pioneers, compete there and in New Guinea with such as *F. melinocarpa* Bl. (Sycidium), *F. variegata* (Sycomorus) and *F. congesta* (Sycocarpus), could not have survived with them also in Borneo an the

Philippines, if they had caught the land-connections: and, similarly, eastwards to Fiji. I conclude that (a) the section is the most recent of evolution and, accordingly has missed the migration routes to western Malaysia and Polynesia; (b) evolution in Ficus is orthogenetic and limited to the development of similar habit, leaf, and fig in all sections: and (c) this evolution has not been contemporaneous. The affinity of Adenosperma is which the small group of Sycocarpus which includes *F. dammaropsis* and *F. theophrastoides.*

Sycidium. This is another complicated section that proves the necessity for morphological analysis before the phytogeographical. It would be easy to suppose that the species of Polynesia were all different from those of continental Asia, or the species of Celebes from those of Sumatra, but such generalisations would be false. The section is poorly represented in the Sinohimalayan flora. It comprises most of the fig-flora of Polynesia. By far the greater number of species and variety of construction occur in New Guinea. Three groups can be distinguished according to the shape of the seed.

1. The F. scabra group, with 65 species, is complicated, but it is centred in Papualand, whence it has spread effectively into Polynesia with twelve endemics and little competition from other sections of the genus. *Ficus ampelas, F. melinocarpa, F. rudis* Miq. and *F. scabra* Forst. f. are examples of the main complex. Merely two, *F. montana* Burm.f. and its ally *F. madurensis* Miq., reach the Asiatic mainland; they belong to the *F. copiosa* alliance and seem to have followed the Timor-Sumatra track. Similarly, *F. opposita* Miq., of Australian affinity, must have followed this track to Java. On the other hand, the *F. rudis* alliance reaches Borneo and through the Philippines to Formosa and Ryu Kyu. In other words, this group shows all the established migration routes and must have existed previously.

2. The F. tinctoria group, corresponds mainly with sect. Palaeomorphe King. It shows, on the one hand, the greatest range of all species of the genus, and, on the other, a concentration in Sundaland. It resembles, thus, sect. Urostigma. As the group in which the male flower has normally a well-developed gall-ovary, suggesting the primitive hermaphrodite flower, it may be held to retain a primitive character and, perhaps, to retain in some measure a primitive distribution. It contains the few banyans, other than those of Urostigma, namely *F. tinctoria* and *F. virgata* Reinw. (*F. philippinensis* Miq.), but many of the small trees and shrubs are facultative epiphytes developing small baskets of clinging roots, e.g. *F. subulata* Bl. and *F. obscura* Bl. As already mentioned, *F. tinc-*

toria covers the whole range of Ficus in Asia and Australasia except for Japan, Lord Howe and Fanning Islands, and except for New Caledonia and Australia in of which the closely related *F. virgata* occurs. In detail, *F. tinctoria* resolves into three subspecies, intergrading in Celebes and the Sinohimalayan region. The eastern subspecies *tinctoria* occurs in Polynesia, Solomon Isl., New Guinea, the Moluccas, Celebes, the Philippines, Formosa, and Ryu Kyu; it has a rather broad leaf with sunken stomata: in Polynesia it seems to be generally a tree on its own trunk, but there are records from most of its range that it may be banyan. The central subspecies *gibbosa* (*F. gibbosa* Bl.) is a large banyan with narrow leaf and sunken stomata; it occurs in Sundaland and reaches Celebes where it seems to intergrade with subsp. *tinctoria*. The third subspecies *parasitica* (*F. parasitica* Willd.) has a subrhombic leaf with superficial stomata and it is one of the great banyans of India and Ceylon; in Burma, Indochina and south China it intergrades with subsp. *gibbosa* in leaf-shape and in the stomata, which vary from sunken to superficial on the same leaf. Subsp. *tinctoria* occurs, also, in Timor, and subsp. *gibbosa* in Palawan, Hainan and the Andaman Islands. Thus, within this species, there arises the whole set of problems of the distribution of Ficus in the Old World. As an infra-specific distribution, it cannot be argued away by migration routes of birds carrying seeds, or by wind-routes deflecting insects; it must imply the geological history of the region. But, last year, I came upon the field-notes of J. H. L. Waterhouse on his collection of this species in the Solomon Islands. He wrote "the dried timber burns very slowly and surely", and "the wood smoulders and is often used by natives to carry fire about". A fire-tree may well have been carried by early man through Malaysia to Polynesia!

Close to *F. tinctoria* is the small, often epiphytic, tree *F. subulata*, which extends from north-east India to the Solomon Islands, but is absent from Ceylon, South India, Formosa, New Caledonia and Polynesia. As an undergrowth, shade-loving tree of the rain-forests, it is not subject to the same distributing agents as *F. tinctoria;* thus, its wide distribution confirms the belief in the early origin of the group. Nevertheless, it shows a detail which may be significant. It does not occur in Singapore nor, apparently, in Johore, and there is no collection from the Riouw archipelago, though it is common in Sumatra, Java, Borneo and the northern half of Malaya. Here is an empty pocket, presumably the effect of recent geological activity, and it is amplified by the two wide-spread banyans *F. glaberrima* Bl. and *F. altissima* Bl. (sect. Urostigma) which have not been found in Malaya, which has the highest specific content of this

F. benghalensis group, and for which there is only one record (*F. glaberrima*) from Borneo. I suspect that similar pockets may be found in other parts of Malaysia; in time they would be invaded, if human intervention permitted. In New Guinea *F. subulata* varies into a small creeper (*F. gracillima* Diels) and it has a close ally in *F. armiti* King, but I doubt if this implies a Papualand derivation.

The alliances of *F. obscura* and *F. rostrata* Lam. belong in the *F. tinctoria* group. They relate particularly to Sundaland, but they extend to the Philippines, Celebes and the Moluccas, and *F. aurita* reaches New Guinea. *Ficus parietalis* reaches Palawan, but not the rest of the Philippines. The most wide-spread species is the climbing *F. heterophylla* Bl. (*F. urophylla* Wall., *F. caudatifolia* Warb.).

3. The F. heterophylla group consists of the African species of Sycidium (about 12) and a few Asiatic, which are puzzling to classify on superficial grounds. Thus the three Indian and Sinohimalayan species, *F. exasperata* Vahl, *F. heterophylla* Linn. f., and *F. cyrtophylla* Wall. can be placed with many other species of Sycidium on general resemblance. *Ficus cyrtophylla* seems, indeed, scarcely distinguishable from the Fijian *F. fulvopilosa* Summerh., until the criterion of the seed is used. Then it is found that these apparently anomalous species take a suitable position systematically and phytogeographically with the African, similar to the species of the *F. religiosa* group of Urostigma. *Ficus fulvopilosa, F. obscura,* and *F. cyrtophylla* are, in fact, convergences in the three groups of Sycidium.

Ficus (Eusyce). This essentially Asiatic section (c. 120 spp.) can be divided easily into six natural groups except for a few miscellaneous species, mostly allied with *F. carica* Linn. A few reach Queensland, the Solomon Islands and the New Hebrides, but are not endemic. The section is concentrated in Sinohimalaya, Sundaland, and Papualand with very different representation.

Among the miscellaneous species predominate *F. carica* (Asia Minor), its close ally *F. palmata* Roxb. (Asia Minor, India), *F. iidaiana* Wilson (Bonin Islands), and *F. pseudopalma* Blanco (Philippines). They skirt the rainforest. *Ficus carica,* introduced to Malaya, grows vigorously, but quickly succumbs to boring insects. Highly anomalous, but possibly of this alliance, are *F. henryi* Diels with 3—5 stamens and a gall-ovary in the male flower (as the most satisfactory moraceous flower in the genus) and *F. tsiangii* Merr., both of China and Indochina. Here, too, I place the well-known *F. clavata* Wall., hithero placed in Sycidium where it is entirely out of keeping; most collections of *F. henryi* have been misnamed *F. clavata.*

1. The F. hirta group consists of two alliances. The *F. hirta* alliance belongs to Sinohimalaya and Sundaland, but *F. grossularioides* Burm.f. (*F. alba* Reinw.) reaches Celebes, and the Moluccas have both *F. fulva* Reinw. and a remarkable endemic allied with the rare *F. mollissima* Ridley of Malaya; the alliance is absent from the Philippines and Formosa. The *F. glandulifera* alliance extends from Sinohimalaya to the Philippines and New Guinea (*F. glandulifera*). *Ficus chartacea* Wall. is one of the few species of the Asiatic mainland which reaches Sumatra but not Java. *Ficus ruficaulis* Merr. is restricted to the Philippines and Celebes. In *F. ruficaulis*, *F. glandulifera*, and *F. lamponga* Miq. (*F. lepidosa* Wall.) the ripe fig splits open irregularly, no other figs seems to dehisce in this way, but I can detect no such regularity as occurs in Sparattosyce.

2. The F. aurata group is centred in Borneo, mainly on Mt. Kinabalu, where all the species occur. It is near the preceding group, but differs consistently in flower and, in several, species the male flower has one, not two, stamens, thus simulating Sycidium.

3. The F. erecta group is divisible into three alliances, namely the *F. erecta* alliance of the Asiatic mainland, the *F. pedunculosa* alliance of the Philippines to New Guinea, and the Sundaland alliance of *F. deltoidea*. In such trichotomies one has to think of the nature and source of the progenitor. I incline to see in this respect the large seed of *F. deltoidea* Jack (*F. diversifolia* Bl.) and the scattered male flowers of *F. erecta* Thunb. combined, as they are in *F. pedunculosa* Miq., which would make its group the central: and here neatly fit the Palawan species *F. glareosa* and *F. cardinalicarpa* Elm. In other words, this large group seems to have emanated east, west, and south from the former extension of the Philippines. The *F. erecta* alliance is the main group of small fig-trees of China and north Indochina; it reaches Selangor in Malaya as *F. ischnopoda* Miq. (*F. pyriformis* auct.), but is absent from the rest of Sundaland and the Timor-track. This alliance is to China what the *F. scabra* group is to *Polynesia*. The *F. deltoidea* alliance reaches south Thailand, Mindanao, and Celebes, but is absent from Palawan. The *F. pedunculosa* alliance extends from the Philippines to Formosa and through Celebes, the Moluccas and New Guinea to New Britain and New Ireland. Noteworthy is the fact that the very variable *F. deltoidea* partitions the floristic regions of Sundaland with its varieties, and the var. *deltoidea* occupies the Riouw pocket omitted by *F. subulata* and others.

4. The remaining three groups consist of root-climbers, and in this habit they agree with sect. Synoecia in representing one of the most derived vegetative forms of the genus: perhaps, they should be another

section of the subgen. Ficus. The F. foveolata group is Sinohimalayan, but I have included with it *F. laevis* Bl., which has one or two allies in peninsular India and may belong to the Mascarene species. The southernmost limit of the true *F. foveolata* group is the record of *F. pubigera* Wall. from the Telom Valley in Pahang. The F. ramentacea group stretches through the Idomalaysian forests and has most species in New Guinea with a second development in Borneo. As lofty climbers with rather small figs, excepting the *F. odoardi* alliance in New Guinea, they may have been widely spread by birds. One new species shows the characteristic distribution of Sarawak, North Borneo, the Natuna Islands and Johore. *Ficus diversiformis* Miq. of Ceylon is aberrant and may be Mascarene. The F. obtusa group shows clearly the Papualand derivation.

The shrub- and tree-groups of sect. Ficus belong to the Asiatic mainland and western Malaysia, in contrast with sect. Sycidium. So, the fig-flora of China is intrinsically different from that of Polynesia. How the two might compete would be interesting to discover. Yet, in each case, the climbers appear to have arisen at the opposite end of Malaysia, those of sect. Ficus (excl. the *F. foveolata* group) in the east, and those of Sycidium in the west: even in Africa there is a climbing Sycidium.

Synoecia. This small section of large root-climbers combines many features of the climbers of the section Ficus, and yet clearly belongs to none of them; the single stamen excludes them from sect. Ficus. Geographically it holds a central position, ten out of the nineteen species being limited to Borneo, and the four less specialised species (without stomatal pits) occurring in Sundaland, the Philippines and Celebes. The climbing groups of sect. Ficus tend to segregate into eastern and western blocks, which is further emphasized in the discontinuous *F. cunia- F. pungens* group of Sycidium and the *F. pomifera- F. itoana* group of Sycocarpus. They suggest ancestral forms centred in Malaysia. Synoecia may be a derivative of the ancestral group of climbing figs of sect. Ficus, and such an origin would impinge on that of the *F. erecta*-group.

Summary. The main conclusions on the sectional distribution may be summarised:

Pharmacosyce is concentrated in New Caledonia, where it forms most of the fig-flora, and it diminishes westwards to Ceylon, without entering Africa. Eastwards it reaches Fiji. The alliance is American.

The *F. religiosa* group of Urostigma is African and continental Asian, but is widespread throughout Malaysia; the Polynesian *F. prolixa* seems related with the sect. Americana. The *F. benghalensis* group paralles the distribution of the Dipterocarpaceae. The *F. elastica* group is chiefly Papuan and Australian (Queensland), and it may be allied with the African sect. Bibracteata.

Sycomorus, typically African, has *F. racemosa* extending from continental Asia along the Timor-track to Queensland; the subsection Neomorphe is Malaysian.

Sycocarpus is Indomalaysian, developed especially in Borneo, the Philippines, Celebes, New Guinea and the Solomon Islands, but it contains several primitive and aberrant species, in spite of the advanced character of the perianth, and these species are widely separated geographically.

Adenosperma, centred in New Guinea, is the most recent section of Ficus and has limited distribution: it is related to Sycocarpus.

The *F. scabra* group of Sycidium is centred in New Guinea and spread westward to Sundaland, but is little represented on the Asiatic mainland: eastwards it spreads into Polynesia and makes up most of its indigenous fig-flora. The *F. tinctoria* group is extremely wide-spread, but the *F. obscura* and *F. rostrata* alliances are developed mainly in Sundaland. The *F. heterophylla* group consists of the African species of Sycidium, five species of the Asiatic mainland and one of Borneo.

Ficus (Eusyce) has the shrub- and tree-groups of *F. carica*, *F. erecta*, *F. hirta*, and *F. aurita* on the Asiatic mainland, Sundaland and the Philippines. Of the climbers, the small *F. foveolata* group belong to the Asiatic mainland, except that *F. laevis* (if rightly placed here) may be Mascarene. The *F. ramentacea* group is widespread in Indomalaysia, but principally in New Guinea, and this is shown more clearly in the *F. obtusa* group; *F. diversiformis* (Ceylon) may be Mascarene.

Synoecia is Indomalaysian, chiefly Bornean, but with a minor development in New Guinea.

WALLACE'S LINE

Table 3 shows how the species of the Asiatic mainland and Sundaland decrease eastwards and the Papualand species westwards. Wallace's line between Borneo and Celebes seems to have been a more effective barrier to westward than to eastward migration. The fig-flora implies that Borneo was first severed from Papualand, then the Philippines, than Celebes, and then the Moluccas. This is borne out particularly by the Adenosperma section.

	Species of Sundaland and the Asiatic Mainland	Species of Celebes, Moluccas, New Guinea
Malaya	94	0
Borneo	109	9
Philippines	52	43
Celebes	32	35
Moluccas	16	37
New Guinea	5	122

Table 3. Species of *Ficus* in Malaysian Islands (excluding widely distributed species).

The Bornean fig-flora is essentially that of Sundaland. Merely two Sinohimalayan species occur (*F. chartacea* Wall., *F. heterophylla* Linn. f.), but it has two endemic species of similar connection, the one allied with *F. squamosa* (Sycocarpus) and the other with the *F. heterophylla* group (Sycidium). The Philippine element is even less, being represented by *F. nota* Merr. in North Borneo and a variety of *F. uniglandulosa* (*F. copelandii* C. B. Robinson) ; the Philippine species of the *F. erecta* group are noticeably absent from Borneo. There are no species restricted to Borneo and Celebes, which shows that their endemics have not crossed Wallace's line, but the easterly *F. rudis*, *F. minahassae* and *F. irisana* Elm. occur in East Borneo, as if migrant from Celebes. Synoecia, as a critical section for the climbing figs of sect. Ficus, has its main development in Borneo.

In the Philippine flora, the Asiatic mainland is represented by the two banyans *F. concinna* Miq. and *F. infectoria* sensu Roxb., and by six endemic species of the *F. erecta* group (*F. cardinalicarpa*, *F. confertifolia*, *F. edanoi*, *F. glareosa*, *F. mearnsii*, and *F. rivularis*) ; here, too, must come the peculiar endemic *F. pseudopalma*, apparently allied with *F. carica*. Sundaland and Papualand species are about equally represented. Eight species are restricted to the Philippines and Celebes (*F. cordatula* Merr., *F. ruficaulis*, *F. ilangoides*, *F. sycomoroides*, *F. semicordata*, *F. todayensis*, *F. peninsula*, and one undescribed), or nine if the Moluccas are included (*F. heteropoda*), *Ficus ulmifolia* of the Philippines is closely related to *F. riedelii* of Celebes, and *F. odorata* to *F. semicordata*. In fact, except for the Asiatic mainland element, the Philippine flora is closely related to that of Celebes. In contrast, only one species seems to be limited to the Philippines and New Guinea, namely *F. cumingii*, though a variety occurs in Formosa; strangely, this species, so common in the Philippines, has never been collected in Celebes. The Philippine *F. gigantifolia* (Pharmacosyce), *F. fiskei* (Sycidium) and *F. bakeri* (sect. Ficus) are closely related to New Guinea species. The only group which seems to have originated in or about the Philippines is the *F. erecta* group. The Philippines have, also, served as a route to Formosa and Ryu Kyu.

I have not analysed the Celebes flora in detail. In contrast with the Philippine it has a number of species which have entered the south, evidently from the Sumatra-Timor track, such as *F. superba, F. rumphii, F. fulva, F. tricolor, F. hispida,* and *F. racemosa.* In Celebes end abruptly the limits of the Adenosperma section, of several New Guinea species of Sycocarpus, and of *F. copiosa* (Sycidium). Concerning the banyans and climbers it is, perhaps, too soon to decide, for these are the species most difficult to collect and most readily overlooked.

Timor has six species of the Asiatic mainland, four of Sundaland, and five of Papualand, with eight widely distributed. Among those which belong to the Sumatra-Timor track (Kalkman, 1955) may be reckoned *F. hispida, F. racemosa, F. fulva, F. superba,* and *F. rumphii,* though neither of the last two has been reported from Sumatra. It seems, also, that the following may have passed westwards along the track: *F. septica, F. ampelas, F. madurensis, F. opposita,* and, perhaps both *F. elastica* and *F. albipila.* All these are widely ranging species, so that it is clear that Timor has been no gathering ground for Ficus. Indeed, neither *F. opposita* nor any characteristic Australian species has been collected on Timor.

New Guinea. The number of species in western New Guinea is much less than in eastern New Guinea, presumably because of the more mountainous terrain of the east and because of its connections with the Solomon Islands and with Australia. This is shown in Table 4.

Table 4. Species of *Ficus* in New Guinea

	Western New Guinea	Eastern New Guinea	Common to both
Pharmacosycea	6	12	6
Urostigma	9	22	8
Sycomorus	3	3	2
Sycocarpus	13	16	12
Adenosperma	10	15	9
Sycidium	17	26	15
Ficus	13	27	9
Synoecia	3	3	2
total	74	124	63

The Australian fig-flora is undoubtedly derived from that of New Guinea, with a few immigrants via Timor. The Australian endemics are related to the species of New Guinea, and none seems to have escaped along the Timor-track. Hence I agree with Good's recent conclusions (1957).

EXTRA-MALAYSIAN ISLANDS

Formosa, Ryu Kyu, and Japan. Of the 24 species in Formosa (Sata, 1944), eight appear to have been derived from the Asiatic mainland and twelve from the Philippines, being identical with the Philippine species; *F. retusa* auct. is too widely distributed to be indicative; and the three endemics belong to the *F. erecta* group of the Asiatic mainland. The species of Ryu Kyu are the same as the Formosan, but merely ten, four belonging to the Asiatic mainland and six being Philippine. Japan has four species, all of which occur in China and Formosa. The Bonin Islands have two endemics, namely *F. iidaiana* Wilson, which looks like a poor *F. carica*, and *F. boninsimae* Koidzumi which resembles the Formosan endemic *F. garanbiensis* Hayata, both near to the Philippine *F. edanoi* Merr. Thus, this are of islands seems to have derived many of its figs from the Philippines. In contrast, the only species of the Asiatic mainland in Formosa which occurs in the Philippines is *F. fistulosa*, and this, as a common species of Sundaland, may well have reached the Philippines through Borneo. None of the Philippine species of Formosa occurs on the Asiatic mainland. If, now, the Philippine species entered Formosa after its severance from the mainland, it cannot be understood why the mainland species did not enter the Philippines. Conversely, if the mainland species entered Formosa after its Philippine species, these should have reached the mainland. One requires a promontory from Formosa to the south which received both elements and, then, disappeared, while these elements were transmitted to Ryu Kyu.

Caroline and Marianas Islands. The following eight species occur:

Urostigma, 3 spp.: *F. infectoria* sensu Roxb., *F. prolixa*, *F. retusa* auct.

Ficus: *F. ramentacea* Roxb. (Palau).

Sycidium, 4 spp.: *F. ampelas*, *F. copiosa* Steud., *F. virgata* Reinw., *F. tinctoria* subsp. *tinctoria*.

Most of these are so wide-spread as strand-plants that they indicate no particular direction of immigration. *Ficus ramentacea,* however, is not known to the east of the Moluccas, and suggests a Philippine origin. *Ficus copiosa* (*F. senfftiana* Warb.) belongs to eastern Malaysia and does not occur in the Philippines. *Ficus prolixa* is the Polynesian banyan, not found in any part of Malaysia, or the Solomon Islands or Australia. The Caroline Islands are the only region where *F. prolixa* seems actually to meet its nearest ally *F. infectoria* sensu Roxb. *Ficus infectoria* (*F. carolinensis* Warb.) occurs on Yap and the Ulithi Atoll. *Ficus prolixa* has not been recorded from Yap, but the recent collections of Dr. Fosberg, which I have been privileged to examine, show that in the Caroline and Marianas, it is impossible to draw a sharp line between the two. The male flowers, normally abundant all through the fig of *F. prolixa,* may be so sparse as to be almost entirely ostiolar, as in *F. infectoria.* Notable is the absence of the insular *F. septica.*

Table 5. Polynesian Fig-floras

	New Hebrides	Fiji	Samoa	Tonga	Tahiti
Pharmacosycea	2 (1)	2 (1)	—	—	—
Urostigma	4	2	2	2	2 (1)
Sycocarpus	1	2 (1)	—	—	—
Adenosperma	2	—	—	—	—
Ficus	1	—	—	—	—
Sycidium	7 (1)	8 (5)	6 (4)	2	1
Total	17 (2)	14 (6)	8 (4)	4	2

N e w H e b r i d e s. The fig-flora (Table 5) can be analysed further:

Solomon Islands affinity: 10 species (*F. glandifera* Summerh., *F. acrorrhyncha* Summerh., *F. nasuta* Summerh., *F. septica, F. wassa* Roxb., *F. tinctoria, F. virgata,* the two spp. of Adenosperma, and one of Pharmacosycea).

New Caledonia affinity: one species of Pharmacosycea.

Queensland, New Caledonia affinity: *F. obliqua* Forst.f., *F. fraseri* Miq. (*F. proteus* Burr.)

Polynesian affinity: *F. prolixa, F. aspera* Forst.f., *F. scabra* Forst.f., *F. storckii* Seem.

Actually, the last three species, *F. aspera*, *F. scabra*, and *F. storckii*, are close to species of the Solomon Islands, though *F. scabra* also occurs in New Caledonia.

Hence I conclude with Solem (1958) that there can have been no direct connection between New Caledonia and the New Hebrides in the Tertiary period. The connection must have been between the New Hebrides and the Solomon Islands.

F i j i. The predominant Solomon Islands element, also, in this fig-flora is shown by nine species. *Ficus smithii* Horne (Pharmacosycea) also occurs in the Solomon Islands, and may be the same as one of the species of the New Hebrides. Of the two species of Sycocarpus, the strange *F. theophrastoides* occurs in both regions and *F. vitiensis* is very near *F. indigofera* of the Solomons. At least seven of the species of Sycidium are closely related to species of the Solomon Islands. But *F. pritchardii* (Pharmacosycea) seems nearest to *F. racemigera* (New Caledonia), and *F. bambusifolia* (Sycidium) seems nearest to some of the Australian species. *Ficus prolixa* is the Polynesian banyan and *F. obliqua* the Australian banyan (so near to *F. platypoda*), which extends into Polynesia.

S a m o a, T o n g a, T a h i t i. These regions have progressively attenuated Fijian fig-floras. Three of the Samoan endemics represent modifications of *F. scabra*, and the fourth (*F. uniauriculata* Warb.) is near to the New Hebridean *F. aspera*, also an ally of *F. scabra*. Tonga has *F. prolixa*, *F. obliqua*, *F. scabra*, and *F. tinctoria*. Tahiti has the first and the last of these four. As I have mentioned, the wide distribution of *F. tinctoria* is now suspect of human transport as a fire-tree.

It is interesting to compare these figures with those of S i n g a p o r e I s l a n d, of so much smaller size and lower elevation, but in one of the hubs of fig-evolution:

Pharmacosycea 2; Urostigma 18; Sycomorus 1; Sycocarpus 3; Sycidium 6; Ficus 13; Synoecia 2; total 45.

THE RIOUW POCKET

I would emphasize this small region of recent geological transformation. I mean the Riouw Archipelago, Bangka, Singapore, south east Johore, and south west Borneo, though whether part of Sumatra enters I do not know. From this area I continually meet the absence of species abundant in the surrounding countries, and, less often, particular representation. Thus, as absentees, there are such common figs as *F. tinctoria* subsp. *gibbosa*, *F. subulata*, *F. parietalis*, *F. uniglandulosa*, and *F. hispida*, while *F. ampelas, F. melinocarpa,* and *F. septica* halt in Borneo, Java, and Sumatra without entering the pocket. *Ficus deltoidea* var. *deltoidea* is limited to it except for an extension into Sumatra. *Ficus acamptophylla* Miq. is known merely from the southern half of Borneo and from Bangka, but closely allied with it is *F. microsyce* Ridley of the southern half and east coast of Malaya. I think that it is not realised how complex in detail is the flora of the southern part of Malaya. The eastern side of Johore has much in common with Sarawak, the western with Sumatra; the Burmese influence reaches just to the north; and the south has the peculiarities of the Riouw pocket.

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APPENDIX

Adenosperma, a new section of *Ficus* subgen. Ficus.

Adenosperma Corner, *sect. nov.* (subgen. Ficus)

Arbores dioicae, raro frutices. Folia spiraliter instructa, raro disticha, integra, symmetrica, raro scabrida, glandulis in axillis costarum basalium. Receptacula axillaria vel cauliflora, plerumque pedunculata, bracteis basalibus 3, saepe bracteis lateralibus praedita. *Flores sessiles vel subssesiles.* Perianthii segmenta 3—6 libera vel plus minus gamophylla, rubra, glabra. Masculini circa ostiolum ordine 1 (-2) instructi; stamen 1, pistillodium nullum. Neutri pro masculinis in receptaclis femineis. Cecidiophori et feminei *ovario rubro-brunneo vel rubro-maculato* sessili vel longe stipitato, *stylo valde laterali vel gynobasali simplici glabro. Semina (pyrenia) valde compressa, carinata, carina plerumque ad basim seminis duplici,* oblongo-ovata vel auriculiformia, laevia; embryo rectus.

Trees, rarely shrubs, dioecious, mostly with the *Terminalia*-habit of branching. Leaves spirally arranged, in a few species distichous. Lamina simple, entire, symmetric, rarely scabrid, with two basal glands in the axils of the main basal costas. Figs small to medium-sized, mostly pedunculate with a collar of three basal bracts, the body often with lateral bracts, axillary to cauliflorous, possibly even on geocarpic stolons: sclerotic cells often in the fig-wall. *Flowers sessile or subsessile.* Tepals 3—6, free or more or less gamophyllous, red or reddish, glabrous. Male flowers ostiolar in 1 (-2) rings; *stamen 1,* pistillode none. Neuter flowers generally in one ring in place of the male in female receptacles. Gall- and female flowers *with dark red or red-spotted, sessile or stalked, ovaries; style strongly lateral to gynobasic, simple, glabrous. Seed strongly compressed, keeled, the keel usually double at the base of the seed, ovate-oblong to auriculiform, smooth;* embryo straight.

Type of the section. — *F. adenosperma* Miq.

Distribution. — Celebes, Moluccas, New Guinea, New Britain, New Ireland, Solomon Islands, New Hebrides, Queensland.

Series **Amphigenae** Corner, *ser. nov.*: cystolitha amphigena (with the cystoliths on both sides of the lamina) : *F. adenosperma* Miq., *F. arbuscula* Laut. et K. Schum., *F. comitis* King, *F. endochaete* Summerhayes, *F. megalophylla* Diels, *F. mollior* Benth. (= *F. gazellae* Engl.), *F. ochrochlora* Ridley, *F. umbonata* Reinw. ex Miq.

Type of ser. Amphigenae. — *F. adenosperma* Miq.

Series **Hypogenae** Corner, *ser. nov.*: cystolitha hypogena (with the cystoliths only on the underside of the lamina) : *F. casearioides* King (= *F. hylobia* Diels), *F. erythrosperma* Miq. (= *F. pycnoneura* Laut. et K. Schum., *F. lachnocarpa* Warb., *F. xanthoxyla* Summerhayes), *F. pleioclada* Diels, *F. subcuneata* Miq. (= *F. stoechotricha* Diels, *F. trichoneura* Diels, *F. formosa* Summerhayes), *F. trichocerasa* Diels.

Type of ser. Hypogenae. — *F. subcuneata* Miq.

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