FICUS IN THE SOLOMON ISLANDS AND ITS BEARING ON THE POST-JURASSIC HISTORY OF MELANESIA

By E. J. H. CORNER, F.R.S.

Botany School, University of Cambridge

(*Received* 20 *April* 1967)

CONTENTS

The fig-flora of the Solomon Islands (Bougainville to San Cristobal) is exceptionally rich (63 species, 23 endemic). It is related to that of New Guinea but differs in the species of four groups, namely subgen. *Pharmacosycea* (3 endemics), subgen. *Ficus* sect. *Sycidium* ser. *Scabrae* (6 endemics), sect. *Sycocarpus* subsect. *Auriculisperma* (5 endemics), and subsect. *Sycocarpus* (8 endemics); the other endemic is in sect. *Adenosperma*. The effect is a flora that defines the Solomons as a geographical unit.

These four subgeneric groups appear to have arisen in this part of Melanesia and to have spread thence with varying success through Malaysia to the Asian mainland. Eastwards ser. *Scabrae* has evolved in Polynesia and subgen. *Pharmacosycea* in New Caledonia.

Most of the 36 species common with New Guinea terminate their eastward distribution in San Cristobal; nine extend to New Hebrides and two of these to Polynesia. Four dispersal arcs are recognized: (i) the Melanesian Foreland linking northern New Guinea, New Ireland, New Britain, the Solomons, New Hebrides and, perhaps, Fiji; (ii) the Australian Foreland linking southern New Guinea, Queensland and New Caledonia; (iii) a subsidiary connexion between the Solomons, New Hebrides and New Caledonia; (iv) the tropical Pacific fig-route which, as the oldest, connected with tropical America. These conclusions put Melanesia as a centre of *Ficus*-evolution and, therefore, the distribution of the Melanesian groups of *Ficus* becomes a prime chronological factor in the post-Jurassic history of Melanesia.

Ficus is taken as an example of the durian theory in the sense of the evolution of the modern tree. The rule is formulated that, without a pachycaul predecessor, there can have been no major subgeneric evolution. Surviving pachycauls are descendents of the stocks from which the new groups have spread. Hence pachycaul geography becomes a basis for phytogeography.

New taxa are: *F. cristobalensis*, *F. dissipata*, *F. illiberalis*, *F. immanis*, *F. macrothyrsa* var. *lancifolia*, *F. novae-georgiae*, *F. oleracea* var. *villosa*, *F. pseudowassa*, *F. scaposa* and *F. tanypoda*.

Vol. 253. B.783. (Price £2. 11s.; U.S. $6.65) 4 [Published 21 December 1967

1. Introduction

The study of *Ficus* began with the Indian and West Indian species. Then came those of Brazil, the Malay Archipelago, China, Japan, Australia, and Fiji. They were followed by the species of Africa, tropical America in general, New Guinea, and New Caledonia. The one great fig-flora that has never been dealt with in its entirety is that of the Solomon Islands. Sixty-three species have now been collected on the islands from Bougainville to San Cristobal. Twenty-three are endemic and six of these, along with *F. vitiensis* from Fiji, make the unique subsect. *Auriculisperma* of sect. *Sycocarpus*. Some of these endemics are the most spectacular species of the genus. The largest of all fig-leaves, rivalling those of any dicotyledonous tree, belong to *F. salomonensis* (figures 42, 49, 50). *F. cristobalensis* (figure 16), here described, has the stoutest pachycaul construction of the Old World species of subgen. *Pharmacosycea*. *F. oleracea* (figure 28) has the largest leaves and figs in sect. *Sycidium*. *F. longibracteata* (figures 56–58) and *F. gryllus* (figure 33) display the rare multibracteate fig. Sect. *Sycocarpus* (figures 56–69) has developed a regional series of geocarpic species related with *F. longibracteata*. There is an intensity of evolution with a harbouring of relics that cannot be ignored.

Nearly all these endemics are common throughout the islands. The figs of San Cristobal are practically the same as those of Bougainville; this largest island, indeed, has no richer a fig-flora than the small island of Kolombangara. Westwards in New Britain, which is less than half as far from Bougainville as it is from San Cristobal, the fig-flora changes abruptly and takes the character of New Guinea. Such striking New Guinea species as *F. hadroneura*, *F. scratchleyana*, *F. pungens*, *F. primaria*, *F. subcuneata* and *F. itoana* are common in New Britain but do not reach the Solomons; and none of the striking endemics of New Guinea, such as *F. dammaropsis*, *F. complexa* and *F. iodotricha*, seem to occur even in New Britain. Thus, *Ficus*, which is by far the largest genus of trees in the Solomons, naturally defines these small islands as the remains of a greater phytogeographical entity. According to the recent list of Solomon Islands trees (Whitmore 1966), few genera have as many as ten to fifteen species (*Aglaia*, *Barringtonia*, *Canarium*, *Diospyros*, *Dysoxylum*, *Evodia*, *Litsea*, *Macaranga*, *Myristica*, *Piper*, *Planchonella* and *Terminalia*). Even the combination of *Eugenia* (20 spp.) and *Syzygium* (17 spp.) falls short of *Ficus*.

Now, in the lowland tropics of Asia and Australasia, the abundance of fig-species is a good measure of the richness of the environment in plant and animal life. By leaf, fruit, and easily rotted wood fig-plants supply an abundance of surplus produce. Unfortunately biologists have been shy of the genus. Too many species have been created; descriptions have frequently been inadequate and without illustration; satisfactory keys to identification have been lacking. The ecologist, in consequence, has never been able to do justice to this prime element in the lowland rain-forest, and the botanist has never been able to appreciate the amount of forest-evolution which it represents: for there is not another genus of woody plants to equal in variety the display of *Ficus*.

Since 1930, when I began to study *Ficus* in Malaya, I have examined nearly every collection, totalling 21 000, that has been made in Asia and Australasia, and I have seen over 300 species in their wild state. I have reduced about 2600 specific names to *ca.* 480, and these results have been summarized by a check-list with keys to identification

(Corner 1965, also 1960–61). I refer to this list for all specific authority, synonymy, classification and distribution. With this immense taxonomic burden relinquished, it is now possible to examine from the entirely new angle of the Solomons the significance of *Ficus* in the evolution of tropical forest and its phytogeographical wanderings. Since most of the species in the Solomons have not been illustrated and are still practically unknown, I have provided line-drawings, descriptions, and keys to identification. There is still much to be learnt about their variability and their ecology, and this must come from field-study in the islands. Comparison has first to be done in the herbarium, but the final assessment comes from the living plants.

Collections of *Ficus* from the Solomons have been made mainly by K. Rechinger on Bougainville (1905), J. H. L. Waterhouse (1929–33) on Bougainville and New Georgia, S. F. Kajewski (1929–31) on Bougainville and Guadalcanal, L. J. Brass (1932–33) on Ysabel, Florida and San Cristobal, E. S. Brown (1955–56) on Guadalcanal, C. T. White (1945) and T. C. Whitmore (1962–64) throughout the British Solomon Islands Protectorate. For my part, I visited Bougainville in 1960 in the neighbourhood of Kieta with J. Womersley. Then in 1965 I took part in the Royal Society Expedition to Guadalcanal, San Cristobal, Malaita, Ysabel and Kolombangara.

A general account of the flora of the Solomons has been provided by Whitmore (1966) and of their phytogeographical relationships by Balgooy (1960). I shall restrict my remarks mainly to the evidence supplied by *Ficus*.

2. General affinity of *Ficus* in the Solomon Islands

Table 1 gives, from the points of view of New Guinea and the Solomons, the general occurrence of *Ficus* from the Asian mainland to Samoa. The relationship with New Guinea, which has the richest fig-flora in the world, rivalled only by that of Borneo, is shown

Table 1. Comparison of fig-floras, India to Samoa

	total species (endemics in brackets)	species in common with New Guinea (% of total in brackets)	species in common with the Solomons		
			total	wides	remainder
India	59 (5)	10 (17%)	7	7	0
Malaya	102 (2)	15 (15%)	10	10	0
Borneo	137 (46)	19 (14%)	12	12	0
Philippines	96 (23)	24 (25%)	15	15	0
Celebes	85 (12)	32 (38%)	20	18	2
Moluccas	64 (5)	42 (66%)	25	17	8
N. Guinea	141 (75)	141 (100%)	36	19	17
N. Britain	43 (2)	39 (91%)	36	19	17
Solomons	63 (23)	36 (57%)			
N. Hebrides	16 (1)	9 (56%)	10	7	3
Fiji	14 (7)	2 (14%)	4	2	2
Samoa	8 (4)	2 (25%)	2	2	0
Australia	33 (12)	18 (55%)	13	10	3
N. Caledonia	25 (18)	3 (12%)	4	3	1

graphically in figure 1. The specific numbers are taken from my check-list and a few recent additions. They must be reconsidered, so far as concerns the Solomons, in the light of nineteen widely distributed species of the kind which Willis called in his biogeographical

work 'wides' (1922, p. 59). They are the species which occur in the Solomons and range extensively beyond in the same manner as the genera *Canarium*, *Dillenia*, *Fagraea*, *Gonostylus*, *Gynotroches* and *Melastoma* (van Steenis 1963, 1966). They are listed in table 2 under their probable source as estimated from their regional alliance of species or massing (Croizat 1958). The islands of Malaysia and Melanesia make convenient geographical regions, but

TABLE 2. WIDE-SPREAD SPECIES OF THE SOLOMONS ACCORDING TO THEIR GEOGRAPHICAL DERIVATION

Asian base	Philippine–New Guinea base	Melanesian base
F. virens	*F. prasinicarpa*	*F. microcarpa* (?)
F. caulocarpa	*F. virgata*	*F. obliqua*
F. drupacea		*F. polyantha*
F. crassiramea		*F. gul*
F. subcordata (?)		*F. copiosa*
F. benjamina (?)		*F. wassa*
F. tinctoria (?)		*F. melinocarpa*
F. subulata (?)		*F. variegata* (?)
		F. septica

in the case of India and Malaya, treated by political boundaries, the limits are not phytogeographical. Thus, the high endemism of the Sino–Himalayan region and of the Sunda shelf does not appear. The purpose, however, is to bring out the close affinity of the fig-flora of the Solomons with that of New Guinea, and to show that in spite of their small area the Solomons have one of the richer fig-floras of the world.

As an example of wides, *F. tinctoria* (figure 36) is represented by three subspecies from Pakistan and China to the limits of the genus in Polynesia (Corner 1963). Then, *F. drupacea*

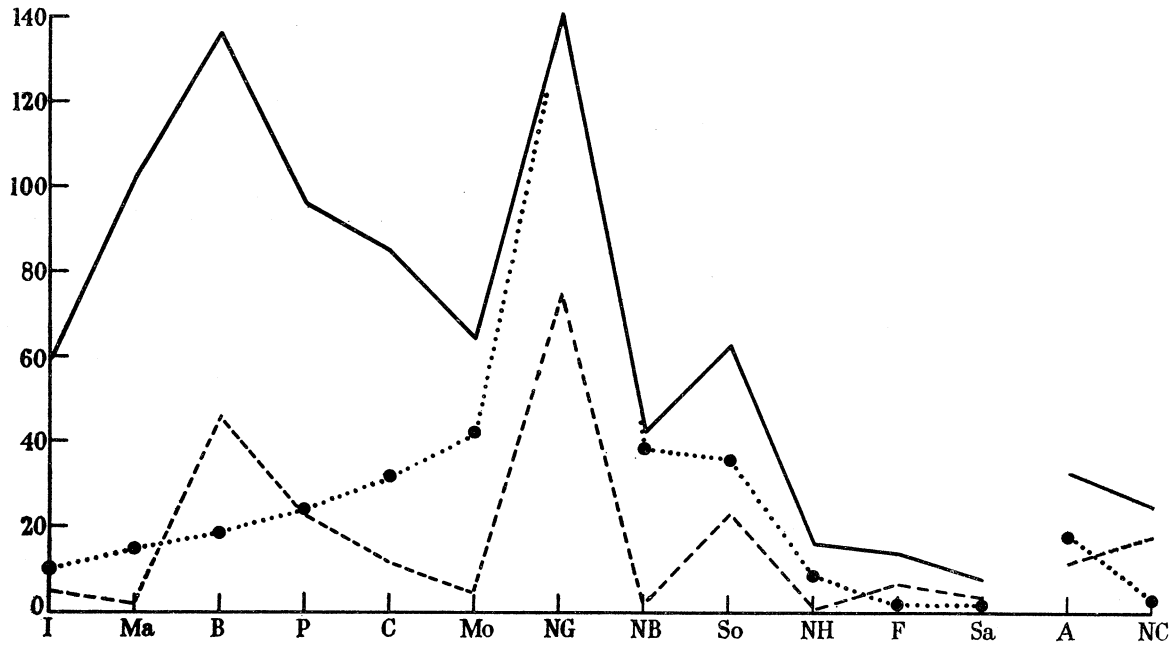

FIGURE 1. Graph to show total fig-floras (solid line), endemic floras (dashed line), and the proportions of New Guinea species (dotted line) in the fig-floras from India to Samoa. A, Australia; B, Borneo; C, Celebes; F, Fiji; I, India; Ma, Malaya; Mo, Moluccas; NB, New Britain; NC, New Caledonia; NG, New Guinea; NH, New Hebrides; P, Philippines; Sa, Samoa; So, Solomons.

(figure 7), *F. benjamina* (figure 9), and *F. subulata* (figure 37) extend from India to the Solomons. *F. obliqua* (figure 11) extends from Celebes to Fiji. The wides of Asian base have the bulk of their allies in Indo-Malaya or, in the case of *F. virens* and *F. prasinicarpa* (figure 6), they extend also to Africa. Such wides correspond clearly with the large Indo–Malaysian element in the Solomons, as instanced by *Alstonia scholaris*, *Canarium indicum*, *Dolichandrone*, *Eugenia malaccensis*, *Gynotroches axillaris*, *Horsfieldia irya*, *Kleinhovia hospita*, *Pterocarpus indicus* and *Terminalia calamansanai*, in as many different families. None of these Asian figs has evolved another centre or massing of species in eastern Malaysia, unless the alliance of *F. subcordata* is really Melanesian. The wides of New Guinea base would seem to be of New Guinea origin, but the richness of *Ficus* in the Solomons raises the question, to be taken up later under the groups *Pharmacosycea*, *Sycidium*, and *Sycocarpus*, whether their source was not further northwards and eastwards where the Melanesian Foreland gave rise to New Britain and the Solomons. This argument may apply also to the wides which extend from the Philippines to New Guinea and which may have a parallel in the archaic genus *Sararanga* (Pandanaceae), in the palm *Clinostigma*, and in *Terminalia samoensis* (van Steenis 1966). It is noteworthy that the wides of Asian base are the banyans or strangling figs of subgen. *Urostigma*, which bear the stamp of highly advanced members of a very ancient group (Corner 1961).

New Guinea

Although the fig-flora of the Solomons impinges on that of New Guinea and New Britain, there are many striking differences. New Guinea is particularly rich in banyans of subgen. *Urostigma* sect. *Malvanthera* (9 spp., 6 endemic), merely three of which reach the Solomons without further evolution unless, perhaps, the form of *F. obliqua* in the Solomons (figures 10, 11). New Guinea is very rich in root-climbers of subgen. *Ficus* sect. *Rhizocladus* (31 spp., 27 endemic), merely five of which reach the Solomons with little or no elaboration (figures 21, 22). The root-climbers of sect. *Kalosyce*, strongly developed in western Malaysia, cease at New Britain. Very few of the New Guinea species of sect. *Sycidium* (28 spp., 10 endemic) and sect. *Sycocarpus* (21 spp., 12 endemic) occur in the Solomons. Similarly, with sect. *Adenosperma* (17 spp., 9 endemic, in New Guinea), merely four reach the Solomons where the most leptocaul and derived *F. verticillaris* is endemic (figures 38–40). New Guinea has, of course, much greater size, more complicated topography, and more extensive phytogeographical relations than the Solomons, but its greater number of species must not obscure the high endemism of these islands. They correspond in area with the Moluccas which have lain athwart the migration-routes between Celebes, the Philippines and New Guinea and, yet, have no larger a fig-flora and one that is far less characteristic.

New Britain, New Ireland

The flora of New Britain and, more so, that of New Ireland are inadequately known. The fig-evidence places them clearly with New Guinea, but their endemism is extremely low and comparable with that of the Moluccas. New Britain has two common and striking endemics in sect. *Sycocarpus*, namely *F. praestans* and *F. neobritannica*, to which I refer later, and there is certainly another very peculiar pachycaul fig, one sterile specimen of which I found near Keravat. But New Britain has two species which occur in the Solomons as

members of two of their characteristic groups and not in New Guinea; they are *F. erinobotrya* (sect. *Sycidium*) and *F. subcongesta* (sect. *Sycocarpus*). So far as known, neither occurs in New Ireland where no endemic fig has been found. These deficiencies emphasize the richness of the Solomons.

New Hebrides

It cannot be said that these islands have been fully explored. What is known of their figs indicates a key-position between the Solomons, Fiji and New Caledonia. Thus, as shown in table 3, the presence of *F. adenosperma*, *F. austrina*, *F. septica*, *F. wassa*, and the banyans *F. subcordata* and *F. glandifera*, indicate the eastern limit of the New Guinea element. They hand on, as it were, *F. smithii* (figure 20) of the Solomons to Fiji and, through *F. aspera*, *F. scabra*, and *F. storckii*, they relate the Fijian endemics of sect. *Sycidium* with those so well developed in the Solomons. In contrast, they have the Australian species *F. fraseri* (sect. *Sycidium*) which is in New Caledonia but neither New Guinea nor the Solomons. Lastly, the possibly endemic *F. granatum* links the species of subgen. *Pharmacosycea* in the Solomons with the great efflorescence of the group in New Caledonia. What is remarkable is that, apart from the very reduced *F. smithii*, none of the striking endemics of the Solomons has been found in New Hebrides. New Guinea passed its more advanced and reduced species on to the Solomons, and they have passed a smaller number to New Hebrides, but none has proceeded to Fiji, unless it be *F. obliqua*, the route of which seems rather to have been via New Caledonia.

New Caledonia

The great botanical peculiarities of this island are well known (Dawson 1963; Good 1964; Guillaumin, Thorne & Virot 1965). The distinction is reflected in its figs of which there are twenty-five species. Nineteen of these belong to subgen. *Pharmacosycea* and eighteen of them are endemic. As this subgenus is also well represented in the Solomons, I searched in 1965 for the New Caledonian species in the Solomons and found none; in fact, I am convinced that none of the peculiar seed-plants of New Caledonia has been overlooked in the Solomons. Of the other six species of *Ficus*, two relate with New Hebrides, Fiji and Polynesia, namely *F. scabra* (sect. *Sycidium*) and *F. prolixa* (subgen. *Urostigma*); this is the very problematic Polynesian banyan that resembles the American species of the subgenus and does not occur west of New Hebrides (Corner 1963). Then *F. fraseri* belongs in the complex of *F. opposita* (sect. *Sycidium*), so characteristic of Australia. Hence I am led to believe that the other three banyans, *F. obliqua*, *F. microcarpa* and *F. virgata*, also reached New Caledonia from Australia. There is detailed evidence. *F. microcarpa* occurs in the Solomons as var. *naumanni*, which is also in New Guinea, but it is not the variety in New Caledonia which has var. *hillii* of Papua and Queensland. Similarly, as already mentioned, the form of *F. obliqua* in the Solomons does not seem to be the widespread state which occurs from Celebes to Fiji. When to these facts there is added the absence of the wides *F. benjamina*, *F. drupacea*, and *F. crassiramea*, even *F. glandifera* and *F. xylosycia*, from New Caledonia, there would seem to have been no banyan connexion between it and the Solomons. As these stranglers often grow without tree-support on coastal rocks and cliffs and their fruits are much eaten by birds and bats, they should on the principle of chance dispersal have been among the most likely to reach New Caledonia; 'island hopping' to

TABLE 3. *FICUS* IN EASTERN MELANESIA AND POLYNESIA
(S, also in the Solomons; e, endemic)

	New Caledonia	Loyalty Isl.	New Hebrides	Fiji	Samoa	Tonga
Urostigma	prolixa obliqua (S) microcarpa (S)	prolixa obliqua (S) (microcarpa)	prolixa obliqua (S) subcordata (S) glandifera (S)	prolixa obliqua (S)	prolixa obliqua (S)	prolixa obliqua (S)
Pharmacosycea	— habrophylla 18 endemics	(granatum) habrophylla	granatum (e) smithii (S)	pritchardii (e) smithii (S)	—	—
Sycidium	fraseri scabra	fraseri scabra	fraseri scabra storckii aspera (e) wassa (S)	— scabra storckii 5 endemics	— scabra 4 endemics	— scabra
Palaeomorphe	virgata (S)	—	virgata (S) tinctoria (S)	— tinctoria (S)	— tinctoria (S)	— tinctoria (S)
Adenosperma	—	—	adenosperma (S) austrina (S)	—	—	—
Sycocarpus	—	—	septica (S)	(theophrastoides) (S)	—	—
	—	—	—	vitiensis (e)	—	—
Total	25	7	16	14	8	4

this extent is not the way of *Ficus*, possibly because the insects on which they depend for seeding are too delicate to sustain more than a few hours of exposure.

As final proof that New Caledonia had little contact with the arc of the Melanesian Foreland but rather with the Australian, there is the absence of *F. tinctoria* (sect. *Sycidium*) from New Caledonia, and it can hardly have been overlooked. It is the most widespread fig in the Old World and, as ssp. *tinctoria*, it ranges on the coasts, islets and inland hills from Hainan and Formosa to Tahiti. In Australia it is known only from a single old collection from Rockingham Bay in north Queensland. The conclusion is that the only parts of tropical Asia and Australasia where *F. tinctoria* is not at home are Australia and New Caledonia. The conclusion is the more remarkable because there is evidence that the green wood of this species was carried about by early man as a means of maintaining fire. The botanical facts of *Ficus*, nevertheless, accord with such others as those of *Agathis*, *Fagaceae* and *Nepenthes*, which reach New Caledonia and miss the Solomons, while the equally widespread *Elatostema* flourishes in the Solomons and misses New Caledonia (van Steenis 1966).

Australia

The tropical flora of Queensland has much in common with that of New Guinea, and one might expect some connexion with the fig-flora of the Solomons. Apart, however, from the wides which have been mentioned, merely two species of sect. *Adenosperma*, so characteristic of New Guinea, and one of *Rhizocladus* unite the Solomons and Australia; they are *F. adenosperma* and *F. mollior* (figure 38), and *F. pantoniana*. None of the characteristic figs of sect. *Malvanthera* or sect. *Sycidium* ser. *Scabrae* of Australia occurs in the Solomons; and the groups that have evolved endemics in the Solomons are those which are not, or are but scarcely, represented in Australia.

The purpose of these remarks is to show that fig-floras define clearly phytogeographical regions around the Solomons, that the size of these regions is not a measure of their productivity of *Ficus*, and that none can explain the source of the peculiar fig-flora of the Solomons. The particular issues of *Ficus* in these regions are these:

New Guinea—subgen. *Urostigma* sect. *Malvanthera*, subgen. *Pharmacosycea* ser. *Nervosae*, subgen. *Ficus* sect. *Kalosyce*, sect. *Rhizocladus*, sect. *Sycidium* ser. *Pungentes*, *Phaeopilosae* and *Copiosae*, sect. *Adenosperma*, sect. *Neomorphe*, sect. *Sycocarpus*.

Solomon Islands—subgen. *Pharmacosycea* ser. *Nervosae*, subgen. *Ficus* sect. *Sycidium* ser. *Scabrae*, sect. *Sycocarpus* subsect. *Auriculisperma* and subsect. *Sycocarpus*.

Fiji—subgen. *Ficus* sect. *Sycidium* ser. *Scabrae*.

New Caledonia—subgen. *Pharmacosycea* ser. *Austrocaledonicae*.

Australia—subgen. *Urostigma* sect. *Malvanthera*, subgen. *Ficus* sect. *Sycidium* ser. *Scabrae* of the alliance of *F. opposita*.

3. Ecology of *Ficus* in the Solomon Islands

Apart from the regions of ultrabasic soil, fig-plants are so abundant in the islands up to 1400 m altitude that any walk in primary or secondary forest will introduce a dozen or more species. Probably the old secondary forest, derived from old garden country adjoining primary forest, is the richest. An exceptionally luxuriant valley of this kind occurs at

500 m altitude on the way to Kupei in Bougainville; nearly every fifth tree was a fig and most species of the Solomons were represented. The first impression, therefore, is that *Ficus* contributes mainly to undergrowth and to such open situations as would under primary forest have been the borders of rivers and streams and landslips. Nevertheless, several species are large buttressed canopy trees of primary forest and this, of course, is the situation of the stranglers. As independent top-storey trees there are the seven species, *F. variegata* and *F. nodosa* (sect. *Neomorphe*, figure 41), *F. melinocarpa* (sect. *Sycidium*, figure 26), *F. erythrosperma* (sect. *Adenosperma*, figure 40), and three species of subgen. *Pharmacosycea* *F. hombroniana*, *F. illiberalis*, and *F. polyantha* (figures 12, 17, 18). Indeed, *F. polyantha* and *F. melinocarpa* become two of the tallest and common trees in the islands.

The ultrabasic soils, so far as I saw them on Guadalcanal and Ysabel, are by contrast so poor in *Ficus* that I noted the general absence of stranglers and large trees, the occasional presence of a few small trees of sect. *Sycocarpus* and *Sycidium* by the streams, and the fair abundance of the slender *F. verticillaris* (figure 39), but this species is not restricted to such soils. The variable *F. erinobotrya* var. *solomonensis* is represented under these conditions in the *Casuarina* forest as a slender subscandent shrub.

At the upper altitudinal limit, *ca.* 1400 m, of *Ficus* on Popomanasiu, which is the highest mountain of the Solomons in Guadalcanal, eight species of undergrowth trees were still fairly abundant, at least by the steep streams. They grew as small trees, up to 10 m high, and they were *F. copiosa*, *F. wassa*, and *F. pseudowassa* in sect. *Sycidium*, *F. adenosperma*, *F. mollior*, and *F. verticillaris* in sect. *Adenosperma*, and *F. longibracteata* and *F. indigofera* in sect. *Sycocarpus*. A few trees of *F. macrothyrsa* var. *lancifolia* were found in fruit at 1700 m on the same mountain. All these species are abundant in the lowlands, even at or near the coast, and there appears to be no particular montane species; this is a difference from Borneo and New Guinea where montane species occur to altitudes above 3000 m. *F. austrina*, of sect. *Adenosperma*, is on the other hand a coastal tree. *F. adenosperma* is essentially a riverside and streamside tree, taking the place of willows in temperate countries. *F. nodosa* belongs to the alluvial plains. *F. septica* var. *cauliflora* seems to prefer mangrove swamps and raised coral beaches, and this habit is favoured by *F. erinobotrya* var. *solomonensis*. The huge-leafed *F. salomonensis* grows best in the alluvial land, but it may be found on steep hillsides to an altitude of 600 m. There is, in fact, considerable freedom in the more obvious ecological requirements of these figs, just as with many other trees of the islands, such as *Alstonia scholaris*, *Kleinhovia hospita*, *Pometia pinnata* and *Pterocarpus indicus*; under the more exacting conditions of the rich forest of western Malaysia these species have much more restricted habitats.

Several common coastal species survive as stunted trees on the remains of headlands in the spray-belt. Such are *F. benjamina*, *F. glandifera*, *F. drupacea*, *F. microcarpa*, *F. tinctoria*, *F. virgata* and *F. virens*. They are more or less widespread banyans, but *F. austrina is* such a tree, and among the commoner is the small endemic tree *F. indigofera* to disprove any facile assumption that coastal figs are necessarily widespread.

Seven species appear to be limited to single islands or groups of islands. *F. arawaensis*, *F. bougainvillei* and *F. pantoniana* have been found only on Bougainville, *F. novae-georgiae* on the central group of New Georgia, *F. gryllus* on the east end of Ysabel, and on San Cristobal *F. cristobalensis* and *F. illiberalis*.

4. Evolution in *Ficus*

Taxonomy is a subject still sequestered in temperate tradition. Its practice restrains *Ficus* as a genus of Moraceae by the rules which make *Capsella* a genus of Cruciferae. The Moraceae comprise relatively simple or ordinary members and many with extravagantly diversified inflorescence and syncarp. They serve as forerunners, counterparts, and parallels to the ultimate complexity of *Ficus* which traps flower, insect, and seed inside the invaginated inflorescence, or syconium, and presents thereby one of the most advanced methods of reproduction among flowering plants. Thus, by the word syconium, the genus *Ficus* is defined and there is concealed the fact that *Ficus* has greater diversity in vegetative mechanism than any other genus of flowering plant and, indeed, of most families. It exceeds in diversity of flower and compound fruit not only such minor families as Cruciferae, Convolvulaceae and Labiatae, but even that which is reckoned highest, namely Compositae. This is the reason why, as the most amplified pantropical genus of plants, *Ficus* defines tropical and many subtropical floras. Its definition of the Solomons fits exactly that which Balgooy gave (1960) on the basis of genera which are not pantropical; he excluded *Ficus* because of its ubiquity, though the real reason seems to have been the absence of monographic treatment. A tropical taxonomy, in contrast to the temperate, would take *Ficus* as a prime and reduce most temperate genera to much inferior status. It is often said that such and such a genus is at once distinguished by vegetative habit coupled with some reproductive character. So, if all other Moraceae were extinct and there were no allies to lead up to it, *Ficus* would spring forth as a family with most of its series treated as genera to the number of three or four dozen; and none would be pantropic. It is easier to distinguish most series of *Ficus* than the genera of Compositae. What is revealed by *Ficus*, therefore, concerning forest-evolution applies not so much to other genera of dicotyledons, but to their big families.

The taxonomic subdivision of *Ficus* follows in the first place diversification in flower and seed. Then there appear in serial rank the vegetative diversifications. The reproductive evolution preceded the vegetative. So, in most sections of the genus, there are little trees and big, large leaves and small, spiral construction and distichous, as well as climbers, shrubs and, even, epiphytes. In this way by its minor taxonomic categories *Ficus* displays most of the growth-forms and timbering of the tropical forest. It could by itself make a liane forest of major trees exceeding 45 m in height, and fill the undergrowth, though the herb-layer would consist mainly of its seedlings. It has practically achieved this in a few parts of the Solomon Islands, for instance in the valley near Kupei. Here, then, is a genus highly advanced in reproductive method, yet showing the vegetative evolution of broad-leafed tropical forest which has been the achievement of the dicotyledonous tree and which, presumably, took place among less advanced families, as the Ranalean, long before *Ficus* existed. From what growth-form did *Ficus* start?

The sequence in evolution of the modern dicotyledonous tree is not simply from small to large but, as I have shown under various aspects of the durian theory (Corner 1949, 1953–54), from the short tree of massive primary construction (the pachycaul, figure 42) to that of slender construction (the leptocaul), which builds most loftily. It follows that the main evolution of dicotyledons into families took place in the pachycaul state before their

vegetative progress into tall forest trees; that this started as often as a pachycaul family emerged with constructive genome; and that such families with advanced reproductive mechanism, having come later into competition than the more primitive as Magnoliaceae and Leguminosae, retain more traces of the pachycaul ancestry. Once started into tree-evolution, the various families have followed in parallel the same course which ends in leptocaul similarity; lofty beech, dipterocarp, poplar, and poplar-leafed fig are polyphyletic. Thus it is that in the Solomon Islands, near to a centre of *Ficus*-evolution, the lofty trees of this phyletically late genus belong to four taxonomic sections in each of which the pachycaul origin can be detected. Tree-evolution can be likened to a piece of clock-work which, once wound up, proceeds in a set manner (Corner 1961); the clock-work has been wound up at different times and in different places, and hence the complexity of forest. In the geological history of the Solomons, the clock of *Ficus* has been wound up at least four times, once very early for the evolution of subgen. *Pharmacosycea*, then for subgen. *Ficus* ser. *Scabrae*, and later still, so that the products have not escaped to New Guinea, for sect. *Sycocarpus* subsect. *Auriculisperma* and *Sycocarpus*. This last section, distinguished by the most advanced state of the perianth and by the greatest divergence between the gall- and seed-flowers, seems to have been the last effort of the genus in reproductive evolution; thus it shows better than any other, the nature of the pachycaul *Ficus* and, though it has produced leptocaul species with small leaf and fig, none of its species has achieved canopy-status in the primary forest.

The pachycaul fig, 3–10 m high, evidently had a primary twig 10–20 mm thick, spiral phyllotaxis, short internodes, and sparse branching which simply repeated the main stem with less effect. The large terminal bud was rendered more massive by the large persistent stipules (figures 16, 43, 46). The large, elliptic or obovate, and dentate leaf had many lateral veins, up to 30 pairs (if not 50), and intercostal veins, but a short petiole. The large figs were axillary and multibracteate (figures 33, 56, 57). The indumentum was composed of long stiff brown hairs. Evolution into leptocauly brought smaller buds, caducous stipules, smaller leaves with fewer veins, smaller figs with bractless body, longer internodes, shorter white indumentum or glabrousness, and loftier habit with profuse branching and buttressing. The spiral construction passed into the distichous on side-branches or it became decussate. The leaves became basipetal, ovate or cordate, with long petiole, or asymmetric and distichous with short petiole. The final result in every series of *Ficus* is the lanceolate leaf on the slender twig, and these willow-leafed figs, as end-products of *Ficus*-evolution, differ in systematic origin in every major phytogeographic region, as evidence that the clock started at different times, and, therefore, in different groups in different places. In the Solomons the willow-leafed figs are *F. adenosperma* and *F. erythrosperma* in sect. *Adenosperma*, as in New Guinea, and *F. macrothyrsa* var. *lancifolia* (sect. *Sycocarpus*, figure 69).

There is no such completely primitive fig in existence. Three subsections of *Sycocarpus* have species which are but little derived. Perhaps the most striking is *F. dammaropsis* of New Guinea, which has a simplified phyllotaxis resulting in long internodes and caducous stipules, but its axillary figs, 10–15 cm wide, are the largest and most bracteate in the genus with the clearest relics of cymose internal construction; and as evidence of its primitive nature, it is one of the few species in the section with two stamens. The second subsection

is *Auriculisperma*, which is endemic in the Solomons except for a Fijian outlier; several of its species have two, even three, stamens. The third is subsect. *Sycocarpus* in which *F. praestans* of New Britain and *F. longibracteata* of the Solomons have considerable bearing on the special development of the subsection in the Solomons. Both of these subsections are reviewed more fully in later pages.

Multibracteate figs are a sure sign of primitiveness. The smooth fig with a minimum of two to three basal bracts is the common product of parallel evolution in all the main groups. The multibracteate is so rare that, outside sect. *Sycocarpus*, which has about twelve species with this character well developed (four in Melanesia, seven in Borneo, one in Lower Burma), it occurs merely in three species of sect. *Sycidium* (*F. complexa* and *F. conocephalifolia* of New Guinea, *F. gryllus* of the Solomons) and three New Guinea species of sect. *Adenosperma* (*F. megalophylla*, *F. ochrochlora*, *F. saccata*). The intermediate state with one or two small bracts on the fig-body is not uncommon in subgen. *Ficus*. Neither state occurs typically in the monoecious and, presumably, older subgenera *Urostigma*, *Pharmacosycea*, and *Sycomorus*, the figs of which have become wholly advanced. The persistence of these multibracteate and pachycaul species in New Guinea, New Britain and the Solomons provides the evidence that fig-species of primitive construction can persist long after their allies have progressed in forest ways. *F. gul* (figure 24) is the widespread derivative of the stock of *F. complexa*, *F. adenosperma* of sect. *Adenosperma*, and, as I will show, several species of subsect. *Sycocarpus* in the Solomons must have come from the stock of *F. praestans* in New Britain. All the pachycaul species have, in fact, very restricted occurrence. In terms of gene-pools, they are the rare, heavily stocked genomes which should be saved.

5. Venation of fig-leaves

This morphological section must be introduced into the account of the biogeography of *Ficus* because the venation reveals in large measure the evolutionary advancement of the leaf and, thus, the advanced nature of the wides. The leaf is as important as the syconium or the flower in assessing the evolutionary status of a species, whether primitive or advanced, and in this case, whether advanced by complication or by neotenic simplification. For example, most of the widespread stranglers which occur in the Solomons have advanced and complicated venation confirming the evidence of the syconium that they are species with a long biogeographical history, though possessed of a primitive flower-arrangement. In contrast the species with primitive multibracteate syconia have in Melanesia a venation that is primitive for the simple leaf. This venation holds in subsect. *Auriculisperma* which is geologically a recent peculiarity of the Solomons, stemming from a primitive ancestor that must have remained dormant, as it were, since the origin of *Sycocarpus*; yet, the venation is becoming simplified neotenically in the leptocaul *F. indigofera*. In local floras it is usually possible to identify species of *Ficus* from their leaves, as is necessary in most ecological work, but this is done by matching specimens in the herbarium rather than by reading the venation which has never been sufficiently explained.

The venation must be studied down to the third order of veins. The first is the midrib. The second comprises the lateral veins, or costas, arising from it. The third consists of the veinlets, or intercostals, which strut the intervals between the lateral veins. Higher orders

cover the finer reticulations which perfuse the mesophyll in the same manner as that in which the intercostals arise. These intercostals must be studied exactly because they give to the entire lamina its character. The point is shown in figure 2 where five fig-leaves, identical in size and shape, have five different kinds of venation, indicating as many ways of lamina-development (Corner 1958*a*).

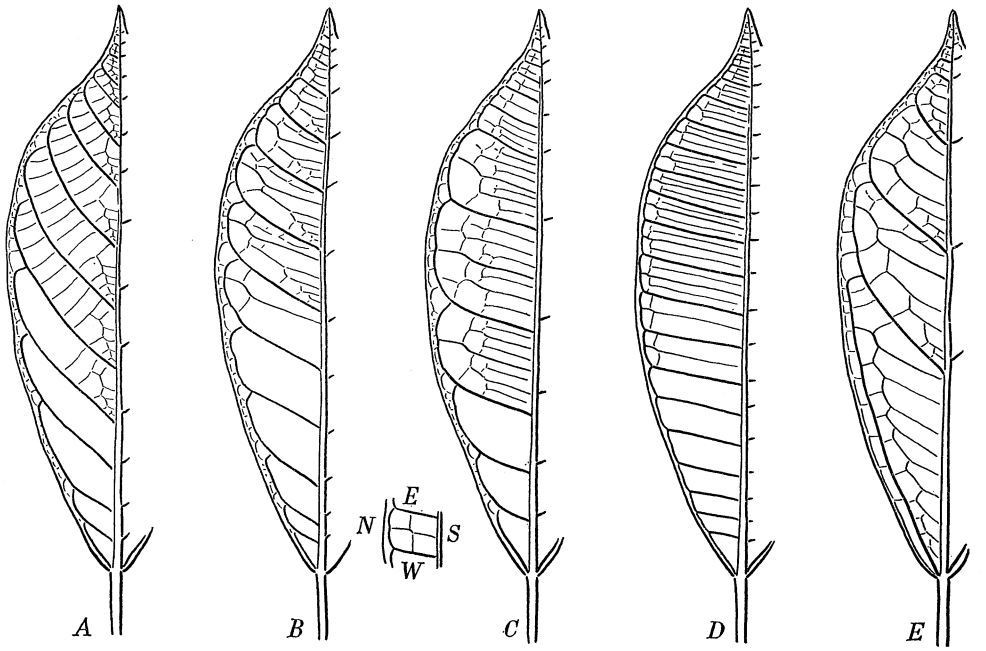

FIGURE 2. *Ficus*-leaves of the same shape and size but different venation, showing midrib, costas (main lateral veins), and intercostals. *Inset*, the primary subdivision of the intercostal area by two veins *NS* and *EW*, as visible near the tips of the leaves. *A*, *F. annulata* with transverse intercostals from the *NE* and *NW* quadrants; *B*, *F. globosa*, with a cascade vein from the *SW* quadrant; *C*, *F. vasculosa*, with the *SE* and *SW* quadrants equally developed; *D*, *F. elastica*, with *SE* and *SW* quadrants predominant; *E*, *F. sundaica*, as *B*, but triplinerved.

In figure 2*A* the intercostals lie transversely between the lateral veins; in figure 2*D* they are parallel to them; in the other leaves they are variously oblique. The differences become understandable when the development of the intercostal areas is followed, which can be done very simply by examining the areas from the leaf-apex down to the base; that is in the reverse order from that in which they arose.

Lateral veins form acropetally in the young leaf, more or less alternately right and left, behind the apex. The first lateral veins, therefore, are those at the base of the lamina. They can be numbered from below upwards, but in *Ficus* it is customary to refer to the first pair as the basal veins because they are often more distinct and they relate to the palmate leaf with multiple development of basal veins. The number of lateral veins depends on the amount of apical growth of the leaf. In figure 2*A*, with 11–12 pairs of lateral veins, apical growth has been more prolonged than in figure 2*E* with 4–5 pairs, or 2*C* with 8–9 pairs. The lamina is brought to the same size and shape in each case by the various development of the intercostal areas. Fortunately, as a general rule, the order in which the veins have developed is shown by their thickness in the adult leaf; the earlier a vein forms, the thicker

it becomes in that part of the leaf because, as more veins are added in the growing mesophyll, so extra phloem and xylem are added to the pre-existing. Thus, the order of development can be detected more readily in dried herbarium-material than in living plants or in the developing leaves, which are usually covered densely with hairs. But the principle can be applied only to comparable parts of the leaf; in figure 2*A* the basal veins are little developed; neither they nor their intercostals become as thick as the later formed laterals or their intercostals.

The intercostal areas, roughly square to begin with, are divided first by a vein parallel to the lateral veins and at right angles to the midrib. Then, as each rectangle enlarges, and becomes square, it is divided by a vein at right angles to the first and, meeting in the centre of the original square, they form a cross with the arms slipped at the 120° angle; this is shown in the inset *NSEW* in figure 2. The cross becomes the stoutest vein in the intercostal area as it expands and deforms. By following it to the base of the leaf, the deformation which gives the character to the intercostal areas can be understood. In figure 2*D*, the cross stays near the leaf-margin and the mesophyll of the intercostal area develops in the direction of the *NS* vein by extending the *SE* and *SW* quadrants. They are subdivided longitudinally by their order of *NS* veins, there being little transverse development of the area in the *EW* direction. There results a leaf with fine venation in which the first intercostals (*NS*) are developed almost as strongly as the lateral veins. This is the characteristic of *F. elastica*, all the stranglers of sect. *Malvanthera* and those of sect. *Conosycea* ser. *Benjamineae* (figures 9–11). It resembles the monocotyledonous, particularly the Scitamineous, because it is basipetal growth of the lamina along the flanks of the midrib, and in like manner these fig-leaves are rolled up longitudinally in the bud. It is an advanced pattern typical of these advanced stranglers.

In figure 2*C* the pattern is similar, but there is some enlargement of the *NE* and *NW* quadrants as well as expansion in the *EW* direction; more second-order *NS* veins are added in the *SE* and *SW* quadrants. Figure 2*B* has the same general effect, but it is disturbed by the greater enlargement of the *SW* quadrant than the *SE*. The part of the midrib subtending this quadrant lengthens more than that subtending the *SE*, and the lateral veins in consequence are pitched forwards (figure 17). As successive orders of *NS* and *W* veins develop in the *SW* quadrant the effect is to produce a cascading vein proceeding in steps from the centre of the cross to the *SW* corner. The cascade-veins are shown more clearly in figure 2*E*. This leaf has little apical growth but great intercalary growth of the midrib where it subtends the *SW* quadrants, particularly in the first intercostal area; it results in greatly elongate basal veins which make the triplinerved leaf-base of descriptions (figures 7, 32, 60).

Figure 2*A* appears very different, but the position of the cross can be gauged from the small cascade-vein developed in every *SW* quadrant. The intercostal areas in this leaf have extended by enlarging mainly the *NE* and *NW* quadrants. The median *NS* vein, however, has hardly been developed and there is a succession of *EW* veins, as transepts or cross-bars, developed in order towards the leaf-margin. The main growth of this intercostal area is intramarginal or acropetal in respect of the growth of the lateral veins towards the margin; it is, in fact, a much less derived state than that of figure 2*D*. It is the usual venation in subgen. *Ficus* when the leaves are plicate in bud, folded along the line of the *NS* veins

(figures 16, 41), but it is the least easy to understand because of the defection of the *NS* veins. Nevertheless, it is the common form of venation in such plicate leaves as those of *Fagus*, *Dipterocarpus*, or *Artocarpus*, and it is the primitive venation of the simple leaf derived by webbing from the pinnate or pinnately lobed. When this manner of intercostal growth occurs in subgen. *Urostigma* and *Pharmacosycea*, then the bits of the *NS* vein extensions between successive *EW* veins are more or less retained (figures 13, 18). So, figure 2*A* represents intramarginal acropetal growth, figure 2*D* intercalary basipetal growth, and figure 2*C* is the neotenic effect with simple enlargement of the original pattern; it is the venation of the willow-leafed figs which reduce the lamina by omitting intercostal complications (figure 36).

There are other significant modifications. If apical growth much exceeds intercostal expansion the leaf-tip narrows abruptly and becomes acuminate or caudate to form the well-known drip-tip in which many more pairs of lateral veins can be detected (figures 31–33). The total of all lateral veins that can thus develop in fig-leaves may be as many as seventy. If all developed normal intercostal areas, the result would be a leaf twice the length of that of *F. salomonensis* and, of course, a twig commensurably pachycaul. The chief ways, therefore, in which leaf-size and complexity are reduced to fit leptocauly are first by limiting apical growth, then by restricting intercostal expansion to the earlier or proximal intercostal areas, and lastly by limiting this expansion to mere expression of the original cross-pattern. The reason why drip-tips are rare in temperate and subtropical forest is simply because the leaves of these forest trees are nearly all much reduced and only in the tropical rain-forest are there the really large leaves which can supply in their leptocaul progress the necessary vestigial construction.

Ovate and cordate leaves are another modification. The base of the lamina is broadened in them by the addition of more basal veins below the first pair; hence, when there is more than one pair of basal veins, their order of development is basipetal and the reverse of that of the lateral veins (figures 16, 28, 46). In well-developed examples the first, second, and even third pair develop their own sets of lateral veins in acropetal, but unilateral, order on the basiscopic side. Ovate-cordate leaves are usually long-petiolate to project the wide leaf-base from the stem, unlike the short-petiolate obovate leaf; and this extension of the petiole is intercalary. A modification is the distichous short-petiolate leaf which becomes asymmetric through unilateral cordate growth (figures 33–35). Mostly, in these cases, the basiscopic side of the lamina (away from the stem-apex) is thus auricled, but it is occasionally the acroscopic side, as in the common *F. imbricata* of the Solomons.

Finally leaf-toothing must be considered. When the lamina is entire, the lateral veins inarch near the margin. When strongly toothed, these veins end in the tooth. When the toothing is slight, a rudimentary veinlet extends from the intra-marginal arch of the lateral vein into the tooth; it is the tip of the lateral vein that entered the tooth in the very young leaf and, failing to develop further, became displaced by intercalary growth. As a number of fig-trees have strongly toothed sapling leaves and entire adult leaves, this effect of the loss of toothing can be followed (figure 41). In other species the tooth is strongly developed into a lobe of the lamina which then appears pinnately lobed; the lateral veins in this case act as the midribs for the lobes and develop their own acropetal succession of lateral veins (figures 24, 25). Thus it becomes clear that teeth are reduced and vestigial pinnate

lobes, themselves reduced pinnae, and that the fig-leaf is derived from a pinnate structure in which apical growth of the pinnae is restricted and gradually taken over by intramarginal intercostal growth, the lateral veins inarching as the teeth are lost. The final result is either the pattern of figure 2*C* or the basipetal pattern of figure 2*D*. If the lobing affects only the basal veins, the result is the palmately lobed leaf which, in course of modification, turns into the cordate and then the ovate before, finally, becoming lanceolate as another source of the willow-leaf; it is the way of sect. *Ficus* in Asia, but the group does not occur in the Solomons.

6. Subgenus *Urostigma*

Because of their unusual habit, the banyans or strangling figs which compose this subgenus are often regarded as specialized late-comers in the tropical forest. The evidence from their wide distribution and advanced structure points, however, to their being the oldest. *Urostigma* is the only pantropical subgenus. In leaf and fig, the species are far advanced; leaf-toothing and lateral bracts have completely disappeared. Most species are fully leptocaul with small leaves and small sessile figs. Specific differences involve trivialities. Most species range widely; endemism in Malaysia and Melanesia is extremely low (Corner 1958*b*). This advancement implies much time and it must have been achieved before the subgenus became pantropical, though where it began is uncertain. The subgenus is stamped with three primitive marks; they are monoecism, interfloral bracts, and lack of sharp distinction between gall- and seed-flowers. Thus it fits well to the early stock of *Ficus* which specialized in the strangling habit suited to the primitive pachycaulous forest. The great banyan, *F. benghalensis*, in the Calcutta Botanic Gardens, started as an epiphyte in a palm-crown some 200 years ago, much as its ancestors may have started in palm-ancestors pre-Cretaceous. Now the subgenus is played out into long established micro-species. It has evolved merely two pronounced modifications which repeat in parallel the peculiarity of the inflexed, instead of interlocking, apical bracts; they form the bibracteate section *Galoglychia* of Africa and sect. *Malvanthera* of New Guinea and Australia, and it is only this fairly recent section which displays much endemism. Thus *Urostigma* contrasts with subgen. *Ficus*, restricted to Asia and Australasia except for a few species in Africa, and its climbers are mostly root-climbers among which the same character of inflexed apical bracts has also appeared, namely in sect. *Rhizocladus*. There is no evidence that *Urostigma* has arisen in Melanesia and, as one would expect, it has not produced any new species in the Solomons which are almost at the eastern extremity of its range.

Eight of the eleven species in the Solomons reach their easterly limit in Malaita and San Cristobal. Two reach New Hebrides, namely *F. glandifera* and *F. subcordata*, and *F. obliqua* reaches Fiji. Seven of these eight are wides, as shown in table 2, and five of them are coastal species, but this habit does not seem to have availed them, as already mentioned, of wide distribution in Melanesia. One species, *F. crassiramea*, shows how the direction of evolution coincides with that of distribution. Its easternmost state, var. *patellifera* (figure 7) of New Guinea and the Solomons, has the smallest fig. That with the largest fig occurs in the Philippines where it impinges on the more massively constructed *F. stupenda* of the Sunda shelf. Then the fig-size diminishes again northwards to Indo-China in the allied, if not conspecific, *F. phanrangensis*.

The most widely distributed species in sect. *Malvanthera* is *F. obliqua* and it is the most reduced species of the least advanced series *Platypodeae*, which has its fullest representation in Australia. It shows a common feature in the distribution of *Ficus*, which is that the more advanced species are the wider spread. As already mentioned, it seems to have a special form in the Solomons, but collections are yet too few to be certain.

7. Subgen. *Pharmacosycea* and the tropical Pacific fig-route

Phylogeny

The problem set by this subgenus in Melanesia is the counterpart of that of *Urostigma*. *Pharmacosycea* has the same three primitive marks but adds four more in possessing two or three stamens in the male flower of many species, the common presence of a pistillode (representing the gall-ovary) in the male flower, the bifid stigma of the usual Moraceous kind, and the very occasional presence of lateral bracts on the fig-body, as in *F. edelfeltii* var. *bougainvillei* (figure 14). Thus it seems to connect with an even earlier stock of *Ficus*, but its distribution is not pantropic. Then it is not a group of stranglers dependent on trees for their elevation into the canopy, but a series of normal shrubs, small trees, and great trees which rival in Melanesia the tallest in the forest. It has not developed any peculiarities in venation but has evolved in the usual manner its own series of tree-forms with simple, coriaceous, entire lamina in parallel with many other successful trees of the tropics, as Sapotaceae or Guttiferae (where *Clusia* takes the part of *Urostigma*). And instead of diminishing in specific variety and size of leaf and fig from Asia eastwards, it diminishes from Melanesia westwards.

Distribution

Pharmacosycea occurs in tropical America, Asia and Australasia, but not in Africa except for *F. assimilis* in Madagascar. With three new species here described, the total in the Old World is 48. Of these, 36 occur in Melanesia distributed in this way; New Guinea 11, New Britain at least 6; Solomon Islands 8, New Hebrides 2, Fiji 2, and New Caledonia 19 (of which 18 are endemic). The exact number in America is not known but it may not be much over a dozen, and there is less diversity in habit and structure. The subgenus has clearly a trans-Pacific tropical history and it is not that of small islands but of high inland forest, for the species are usually large trees of the lowland interior; thus they are absent from Micronesia and the greater part of Polynesia. Australia can be ruled out as a source because its only species, *F. albipila*, almost identical with the Madagascan *F. assimilis*, is a wide from Thailand to New Britain and its five allies occur in western Malaysia. Botanists, it must be admitted, usually fail to notice these large and, often, sterile trees, but they are cared for by the foresters in their methodical enumerations, and one can write with fair competence on their general distribution. I have seen more than a thousand herbarium collections from Asia and Australasia, and have studied many trees of eighteen species in the forests.

New Caledonia

The chief problem is how this subgenus came to predominate in New Caledonia where it comprises 80% of the fig-flora compared with 13% in the Solomons, 8% in New Guinea, 4% in Borneo, and 3% on the Asian mainland. The proportions are quite out of

relation with land-mass and indicate a focus about New Caledonia, whence the subgenus has spread to Asia, though not by the route along which *F. microcarpa* and *F. obliqua* entered New Caledonia; for in that case *Pharmacosycea* would have flourished in Queensland. The conclusion is borne out by the great morphological diversity of the species in Melanesia, particularly New Caledonia which has large-leafed pachycaul treelets along with big trees and the unique willow-leafed *F. cataractorum*, as a shrub of waterfalls; it has, in fact, the first and the last of fig-habits. Evidently the escape route was via the Solomons. I undertook, therefore, during the Royal Society Expedition, the first deliberate search that has been made for *Pharmacosycea*. Though rewarded by three new species, I failed, as I have mentioned, to find any of the New Caledonian ones.

The new look brought into the subgenus by the flora of New Caledonia is the brown hairiness, sometimes almost furriness, of twig, leaf, and fig, coupled with the rosettes of large leaves, the many-veined obovate lamina with cordate base and short petiole, and the large fig. All these are more or less primitive and pachycaul signs in *Ficus*, just as in *Artocarpus* where stiff brown hairs also give way to white and to glabrousness. The look begins to enter with *F. edelfeltii* in New Guinea. It gathers in the Solomons where this species is variable and simulates some of those in New Caledonia. *F. novae-georgiae*, here described. is an advance and greatly resembles the New Caledonian *F. dzumacensis* and *F. habrophylla*. But the new species *F. cristobalensis*, from the south-east extremity of the Solomons, excels as the most pachycaulous, large-leafed, and large-figged species of *Pharmacosycea* in the Old World. If it had two stamens in the male flower and internal bristles on the fig-wall, it would have all the characters needed to produce by simplification the rest of the subgenus. Though I classify it for convenience in ser. *Nervosae* with *F. edelfeltii*, it might as well go with *Austrocaledonicae*.

Ser. *Nervosae* terminates in Ceylon and peninsular India, too late to connect with Madagascar, with one of the more reduced forms, namely *F. nervosa* var. *minor* with small lanceolate leaf and small fig. This reduction has happened, too, in New Guinea with *F. ihuensis*, in the Solomons with *F. smithii*, and in New Caledonia, for ser. *Austrocaledonicae*, with *F. vieillardiana*; they are all astonishingly similar. Thus, the route to Asia spells out the evolution of *Pharmacosycea* as it is condensed in the islands round its source.

The tropical Pacific fig-route

If the series *Vasculosae*, to which *F. albipila* and the Madagascan *F. assimilis* belong, is disregarded as a speciality of south-east Asia, I conclude that the remainder of *Pharmacosycea* (41 spp.) in the Old World originated in the region that connected the Solomons, New Hebrides, and New Caledonia. It expanded in New Caledonia where it was beyond competition with the later evolved species of sect. *Sycocarpus*, *Adenosperma*, and most of *Sycidium*, which make the substorey of *Ficus* in the rest of Melanesia. It travelled via New Guinea to Asia as large buttressed trees that could excel the substorey with the addition from sect. *Ficus* in western Malaysia. It sent a few small leptocaul trees from the declining centre via New Hebrides to Fiji. But, very early, a detachment went to tropical America. This geographical history is unique in *Ficus* and could not have been ascertained without detailed knowledge of the fig-flora of the Solomons. It is, nevertheless, repeated in a more circumscribed way by the later groups of sect. *Sycidium* ser. *Scabrae* and sect. *Sycocarpus*

subsect. *Auriculisperma*, as I will show subsequently, but they were too late to make the passage to America.

These three groups, *Pharmacosycea*, *Scabrae* and *Auriculisperma*, reveal the Solomons as a relic of the Melanesian Foreland or Land Mass (Croizat 1958, pp. 577, 605) or the Melanesian Plateau of Hedley, to whose prophetic reconstruction in 1893 attention has been drawn by Good (1964, p. 265). The foreland or plateau bordered the north side of the Jurassic New Guinea syncline and was a source of the sediments deposited in it (van Bemmelen 1949; Arkell 1956). It is followed now by the great seismic zone which passes from the Philippines along the north of New Guinea to Fiji. It is represented, perhaps, in bathymetric charts by the 4000 m line to the north of New Guinea. But *Pharmacosycea* shows that there must have been a connexion with tropical America, such as the great extension of the 4000 m line to the west of Peru suggests. This land connexion is demanded by other Moraceous genera as *Antiaris*, *Antiaropsis*, *Sparratosyce* and *Trophis* (Corner 1962), as well as by the monocotyledons *Dianella*, *Heliconia* and *Spathiphyllum* in very diverse families. It is demanded by the Euphorbiaceous alliance *Aleurites–Hevea*. It is demanded by other such diverse dicotyledons as *Batis*, *Kopsia-Vallesia*, *Microtropis*, *Perrottetia*, *Nicotiana*, *Picrasma*, and *Xylosma* (van Steenis & Balgooy 1966), as well as by many of the 38 genera with trans-Pacific character listed by Good (1964, p. 442).

Some would have this connexion across the south Pacific via New Zealand, Antarctica, and Chile because of the range of such south temperate genera as *Nothofagus*, *Drimys*, *Fuchsia*, *Coriaria* and *Fitzroya*. In that case the connexion must have been tropical in lowland climate and have sustained mountains, at least 2000 m high, to carry these cold-climate genera which do not occur in the environment of *Pharmacosycea* or, indeed, in the Solomons. I am forced to conclude that there were two separate crossings, namely the tropical and earlier which for emphasis I call the fig-route, and the temperate or south Pacific *Nothofagus*-route. If, as Darlington concludes (1965, p. 121), there is no evidence of tropical conditions having occurred in Antarctica, the *Nothofagus*-route could not have been followed by *Ficus*. If, again, as Darlington concludes (1965, pp. 86–87), South America has been one piece since the late Palaeozoic and isolated in this one mass from the late Jurassic until the Pliocene, when it connected with North America, then there was no other ingress for *Pharmacosycea* to tropical South America except from the west during the Jurassic period. This is not too early because angiosperms appear in full force in the Cretaceous and this indicates a very much earlier time of origin. It agrees, also, with the Jurassic age of the Melanesian Foreland and, perhaps, with that of the 4000 m bathymetric contour. And North America could not have been the source of supply of *Pharmacosycea* to South America.

It is worth noting that the fig-route is the exact line indicated by the durian fruited palms *Manicaria* and *Phytelephas* (trop. America), *Pelagodoxa* (Polynesia), *Sommiera* (New Guinea), and *Teysmannia* (western Malaysia) to which I have drawn attention, if not also the route of the coryphoid genera related to *Pritchardia* of Fiji and Hawaii, the explanation of the Asian–American distribution of arecoid palms, and the source of *Cocos nucifera* (Corner 1966).

The tropical Pacific fig-route is contrary to the theory of continental drift. The alternative is to suppose that, before the continents had begun to separate, that is to say in the

Permo-Triassic, the palaeo-equator passed to the east of what is now Japan and Borneo, through the South Pole to Ecuador and the North Pole. The absence of evidence for tropical conditions having occurred in Antarctica and the well established evidence of the Permo-Carboniferous glaciation of the southern hemisphere forbid such an assumption.

If so much of *Ficus*, palms, and other angiosperms originated on and dispersed from the Melanesian Foreland, it can be seen why the greater part of the world has provided no fossil evidence of the origin of angiosperms; it should be looked for in the shallow water Jurassic deposits of Malaysia and Melanesia. The great botanical value of Jurassic geology

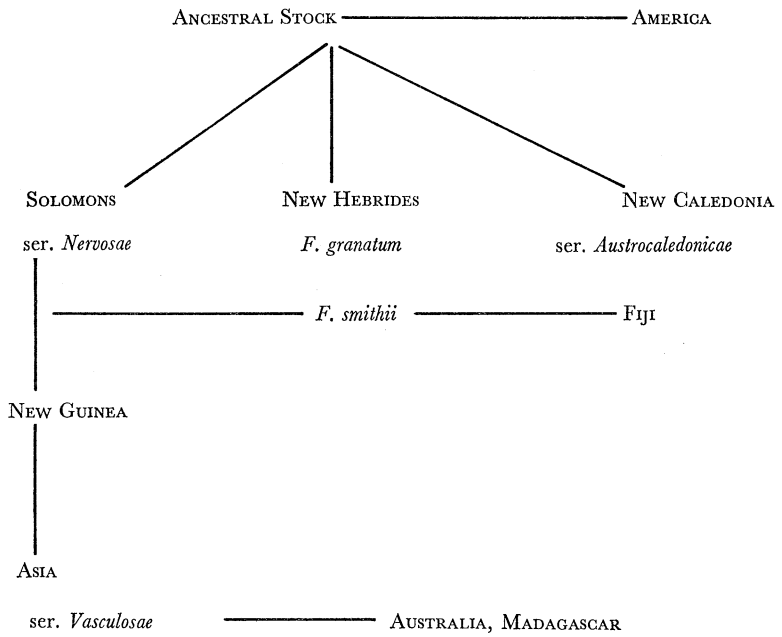

FIGURE 3. The biogeographical evolution of subgen. *Pharmacosycea*.

is the indication of vast land-masses that have disappeared and, in doing so, filled the Jurassic synclines.

For convenience and emphasis, the evidence of *Pharmacosycea* is shown diagrammatically in figure 3. Again, the more advanced species are those which have travelled farthest from the origin. Thus, the glabrous and subdistichous *F. polyantha*, which is the tallest buttressed tree in the genus, ranges from the Solomons to the Moluccas and Philippines, and it carries on westwards in the glabrous, subdistichous *F. magnoliifolia* of western Malaysia to the most reduced *F. nervosa* of the Asian mainland. The most pachycaul and primitive species remain in the nexus of San Cristobal, New Hebrides, and New Caledonia.

8. SUBGEN. *FICUS* SECT. *SYCIDIUM*

Over 100 species make this the largest section of subgen. *Ficus*. It has the widest distribution from West Africa to the limits of the genus in Polynesia. It presents problems of origin in continental Asia, central Malaysia, New Guinea, the Solomons and Polynesia. It is by no means certain that it is a natural group for it is defined by the absence of the peculiarities of the other sections. The sixteen species in the Solomons are classified in this way:

subsect. *Sycidium*.

ser. *Phaeopilosae* 2 spp., *Copiosae* 2 spp., *Scabrae* 9 spp. (6 endemic).

subsect. *Palaeomorphe* 3 spp.

Ser. Scabrae

Interest centres on the endemism of this series. It has a remarkable insular distribution, if Australia is regarded as an island, for it is spread from Madagascar, Mauritius and Seychelles to Sumatra and Ryu Kyu, through Malaysia to Tonga and Samoa, but it nowhere sets foot on the Asian mainland. This insularity and the increasing representation of the series in the fig-floras from Madagascar to Samoa are shown in table 4. Other diverse genera, as *Alphitonia*, *Geniostoma*, *Tristiropsis* and *Vavaea* offer parallels (van Steenis & Balgooy 1966).

TABLE 4. GEOGRAPHICAL OCCURRENCE OF SECT. *SYCIDIUM* SER. *SCABRAE*

	species of ser. *Scabrae*	total species of *Ficus*	*Scabrae* % of total
Asian mainland	0	*c.* 170	0
Madagascar	2	17	12
Ryu Kyu	2	11	18
Formosa	3	23	13
Sumatra	2	91	2
Borneo	2	137	1·5
Philippines	11	96	11
Celebes	11	85	13
Moluccas	5	64	8
N. Guinea	9	141	6
N. Britain	5	43	12
Solomons	9	62	15
Fiji	7	14	50
Samoa	5	8	62
Tonga	1	4	25
Australia	6	33	18
N. Caledonia	2	25	8

The species of ser. *Scabrae* fall naturally into two groups, which should perhaps be given distinctive names. One has opposite or spirally arranged leaves and, as the alliance of *F. cumingii* and *F. opposita*, comes near to ser. *Copiosae*. The species of Madagascar, Mauritius, Seychelles and Australia (except *F. coronata*) belong to this alliance, and one member *F. fraseri* (*F. proteus*) extends to New Caledonia. *F. opposita* has a relict station on Pulau Sangiang (Dwars-in-den-Weg) off Java and it extends into New Guinea whence *F. cumingii* spreads through the Philippines to Formosa and North Borneo. The southerly limit of this alliance follows the great southerly arc of *Nepenthes* which, in the east, ends in New Caledonia and omits the Solomons; the distribution of *Hibbertia* and the proteaceous genera *Gevuina* and *Kermadecia* have much in common (van Steenis & Balgooy 1966). The alliance picks out more clearly the phytogeographic difference between the Solomons and New Caledonia, which was noted under *Urostigma*.

The second alliance, that of *F. ampelas* and *F. melinocarpa*, has distichous, short-petiolate, and more or less asymmetric leaves. It extends from Sumatra and Ryu Kyu to Tonga and Samoa, with *F. coronata* in Australia and *F. scabra* in New Caledonia as well as farther east. It is the alliance which predominates in Malaysia, New Guinea, the Solomons, Fiji, and Samoa. It consists of advanced leptocaul trees. Traces of ancestry, therefore, are to be deduced from leaf size, number of lateral veins, fig-size, and the presence of lateral bracts.

Two species at once stand out in the Solomons. *F. oleracea* has the largest leaves with most lateral veins and the largest figs. *F. gryllus* has well-developed lateral bracts, as well as moderately large leaves. Compared with these two, the species of other countries are variously reduced in leaf and fig, though not necessarily in tree-size. *F. gryllus* and its ally *F. erinobotrya* (New Britain, Solomons) are shrubs or treelets. *F. oleracea* is a small tree. In contrast, *F. melinocarpa* grows into a massive buttressed tree over 30 m high, as the largest in the whole subsect. *Sycidium*; in fact it is exceeded in size only by the banyans *F. tinctoria* and *F. virgata* in sect. *Sycidium*, and possibly by *F. variegata* (sect. *Neomorphe*) in the rest of subgen. *Ficus*.

Now, *F. melinocarpa* and its ally *F. ampelas*, which is a smaller tree with reduced leaves and figs, are common and widespread species that have been known from the flora of Java for over 150 years, but there has been no explanation how they got there or why they surround the periphery of the Sunda shelf without reaching its centre in Malaya. Both stretch through the Malay Archipelago to New Britain, and *F. melinocarpa* reaches the Solomons with its eastern limit in San Cristobal. *F. ampelas* extends northwards to Ryu Kyu. They have no close allies in central Malaysia, except for the equally reduced *F. irisana* and *F. guyeri* of the Philippines, but in New Guinea, New Britain, and the Solomons there is *F. trachypison*. It is so like *F. melinocarpa* that it does not seem possible always to distinguish them, at least in the herbarium, and *F. trachypison* var. *pallida* leads to *F. ampelas* var. *soronensis*, which is the less reduced state of *F. ampelas* in the Moluccas, New Guinea, and New Britain. Then, *F. trachypison* is not so very different from *F. imbricata* and *F. pseudowassa* both of which are endemic in the Solomons and lead through *F. arawaensis* to *F. oleracea*, as the massively constructed representative of this line of fig-evolution. If *F. oleracea* developed thinner twigs, smaller leaves with asymmetric base fitting the distichous habit, fewer lateral veins, and smaller figs, in the usual manner of leptocaul evolution, it could not be distinguished from *F. melinocarpa* which, in the same way, has hairy and glabrous forms, while *F. trachypison* represents the very scabrid state of *F. oleracea* var. *pugnans*. The common endemics of the Philippines, *F. fiskei* and *F. ulmifolia*, likewise relate with *F. oleracea*. The endemics of New Guinea, such as *F. quercetorum* and *F. macrorrhyncha*, as well as the more widespread *F. tonsa*, its Queensland ally *F. leptoclada*, and the reduced *F. todayensis*, *F. irisana*, and *F. tenuicuspidata* of Celebes and the Philippines, relate with *F. trachypison* and, so, with *F. oleracea*. This species, restricted to the Solomons and unknown until a few years ago, stands out as the archetype of this alliance of ser. *Scabrae*.

Eastwards of the Solomons a new complex develops about *F. aspera* and *F. scabra*. It introduces deeply pinnatisect sapling leaves, which have not been found in other species of ser. *Scabrae*, and it includes most of the species of Fiji, Samoa, and Tonga. Yet, as *F. melinocarpa* may be derived from *F. oleracea*, so may *F. aspera* and *F. scabra*. This last species is the only one of the *F. oleracea*-alliance that has reached New Caledonia, evidently by way of New Hebrides and Loyalty Islands. Thus, the western and eastern parts of this alliance of *Scabrae* are connected in the Solomons very much as the species of subgen. *Pharmacosycea*; but *Pharmacosycea* reached India and China, developed copiously in New Caledonia, and sent merely two species to Fiji. It is difficult to see why the advanced *F. nervosa* (*Pharmacosycea*) reached the Asian mainland and neither of the equally advanced *F. ampelas* and *F. melinocarpa* did, except as a matter of geological time and land-bridge.

The last step from Sumatra, Java, or Borneo to Malaya would seem to have been the latest and the easiest, yet these two species missed it, and so did *F. septica* (sect. *Sycocarpus*); this is the problem of the Riouw pocket which foiled many species, both from Asia and from Malaysia, but it lies outside the present scope (Corner 1958*b*). One must conclude that the more primitive *Pharmacosycea* travelled westwards much earlier than the advanced *Scabrae*. This group was also too late to reach New Caledonia, but it is not clear on this reasoning why *Pharmacosycea* should seem to have missed the late opportunity to invade Fiji in force.

In respect of its fig with well-developed lateral bracts, *F. gryllus* is one of the more primitive species of sect. *Sycidium*; it is exceeded in this respect only by the pachycaul *F. complexa* (ser. *Phaeopilosae*) of New Guinea. *F. erinobotrya* represents the reduction of *F. gryllus* until *F. erinobotrya* var. *solomonensis* comes to resemble *F. melinocarpa* so closely in twig, leaf and fig that it may be very difficult to distinguish these fragments in the herbarium; in the forest they cannot be mistaken for var. *solomonensis* is a shrub or treelet in which the sapling leaves have the asymmetry more accentuated, whereas those of *F. melinocarpa* are symmetrical. Then, *F. fulvopilosa* of Fiji seems closely related with *F. erinobotrya*, rather than with *F. scabra* and the other Fijian species of the alliance. If *F. fulvopilosa* occurred in the Solomons it might hardly be distinguishable from *F. erinobotrya*, unless as a larger tree with deeply pinnatisect sapling leaves. This feature seems, as already mentioned, to distinguish most of the Fijian species of the series, but it needs corroboration. It relates to the primitive pinnatisect moraceous leaf which ancestral *Ficus* turned into the simple leaf. Possibly, therefore, the Fijian species were derived from the Melanesian stock of ser. *Scabrae*, older than *F. oleracea*.

I conclude that ser. *Scabrae* shows the two routes that linked Asia with Melanesia. There was the route of the Melanesian Foreland, which leads now through New Guinea and the Philippines and was followed by *Pharmacosycea* and, later, by *F. ampelas* and *F. melinocarpa* (Corner 1963). And there was the route of the Australian Foreland from New Caledonia to Queensland, southern New Guinea, the Timor–Java arc and Madagascar; it was followed by the alliance of *F. opposita*. The Australian Foreland was the southern boundary of the Jurassic New Guinea syncline which gave place to the Cretaceous–Tertiary orogene from New Zealand to New Guinea (Arkell 1956, p. 445; Dawson 1963). The map given by Croizat (1958, p. 853, f. 238) for the distribution of parrots in and around the Orient and Australia shows the same features; but, then, parrots are fond of figs, eating not only the fruits but the glands on the back of the leaves.

Ser. Phaeopilosae and Copiosae

Both series are less advanced than *Scabrae* because they have spirally arranged, or decussate, long-petiolate and symmetrical leaves. *Phaeopilosae* have the more primitive purple or brown hairs. In both the sapling leaves are often pinnately lobed. The two species of *Copiosae* in the Solomons, *F. copiosa* and *F. wassa*, are closely allied small trees, much confused in the herbarium but distinct enough in the field; *F. copiosa* is the more pachycaul and *F. wassa* the more leptocaul, there being, apparently, no qualitative difference. They are spread from Celebes to San Cristobal and are related to the more pachycaul *F. heteropoda* of the Philippines, Moluccas and Celebes. The large tree, *F. primaria*, of New Guinea

and New Britain may also be related. Possibly all come from the stock of *Sycidium* on the Melanesian Foreland which produced the Fijian species with pinnately lobed sapling leaves. It is noteworthy that *F. copiosa* is the only fig, other than five widespread stranglers, to occur in the Carolines and Marianas (Corner 1963). Moreover, the westward extension of *Copiosae* to Asia has resulted mainly in small reduced species as *F. montana*.

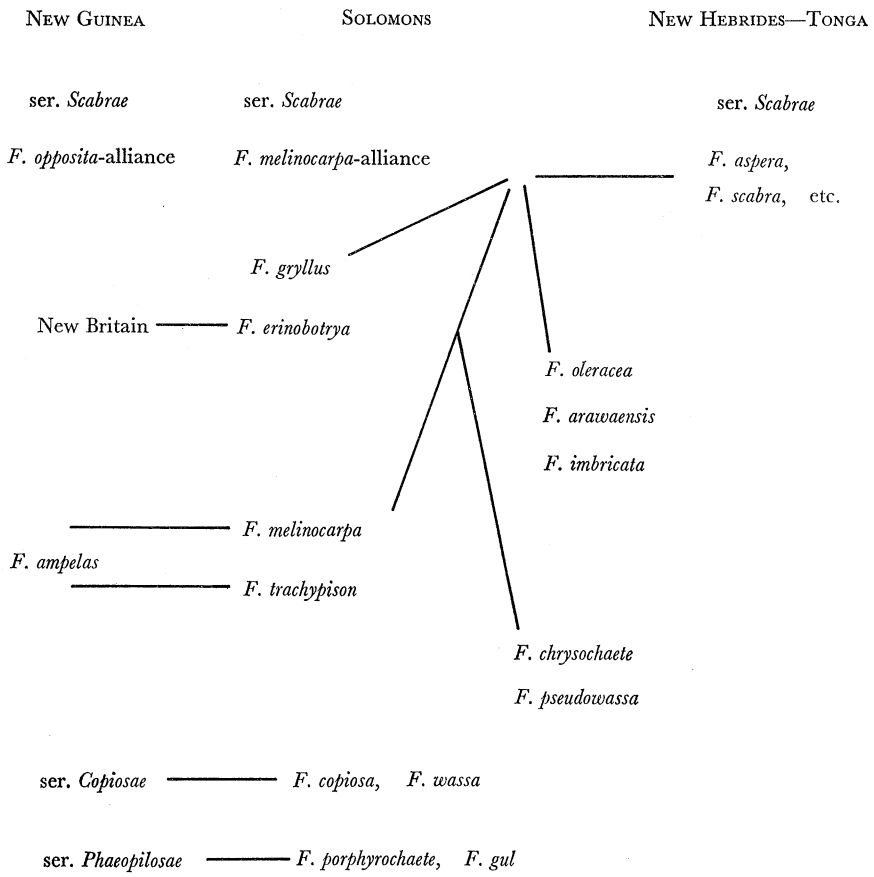

FIGURE 4. The biogeographical evolution of sect. *Sycidium* subsect. *Sycidium* in the Solomons.

Ser. *Phaeopilosae* are more closely knit with New Guinea where their pachycaul allies *F. complexa* and *F. conocephalifolia* have multibracteate figs. *F. porphyrochaete* appears to be a close derivative of these which has reached the Solomons. *F. gul* is an advanced and reduced member of the series and ranges most widely from North Borneo and the Philippines to the Solomons. It has a variety, var. *eubracteata*, in New Guinea with strong lateral bracts approaching those of *F. complexa*, and var. *solomonensis* has smaller lateral bracts, but the most widely distributed form over the whole specific range is var. *gul.* with the smallest figs and vestigial lateral bracts. The series has developed no new species outside New Guinea.

Figure 4 is a diagram of the alliances of subsect. *Sycidium*, centred on New Guinea and the Solomons.

Subsect. Palaeomorphe

The three species which reach the Solomons, *F. subulata*, *F. tinctoria* and *F. virgata*, are wides. Whence they have come is unknown, but they are advanced and simplified species.

Like the stranglers of *Urostigma*, along whose route they may have travelled eastwards; they have undergone no further development in the Solomons. The distinction of the subsection is the functional gall-ovary in the male flower. It seems a primitive mark, like the bifid stigma of *Pharmacosycea*, because abortive gall-ovaries are frequent in the male flowers of many species of *Sycidium*, as they are in *Pharmacosycea*. The specific massing of the subsection is in western Malaysia. There are no pachycaul species to guide and no instance of the multibracteate fig. This indicates a long phase of evolution, which is corroborated by the reduced venation and the very small figs in most species. Then, *F. tinctoria* and *F. virgata* are immense stranglers; in fact, they are the only figs with this habit outside *Urostigma* and it must indicate as great an age for them. Many species of smaller growth are epiphytes with long descending roots, but they are not powerful enough to become stranglers; such is *F. subulata*, commonly mistaken for a young strangler. Other species have become twiners or loopers, as may happen in *Urostigma*, but again there are no root-climbers. There stands, however, in the forests of Celebes the one tall, independent tree, *F. celebensis*, of the subsection and it is willow-leafed. This variety and distribution imply great age for the subsection, and the three of its older species which reach the Solomons have no more contribution to make there.

The absence of *F. tinctoria* from New Caledonia has been noted. *F. subulata* is also absent. This is to be expected because it does not occur in Australia. *F. virgata* is common in the forests of Queensland and seems to be abundant in New Caledonia.

9. Subgen. *Ficus* sect. *Sycocarpus*

This Asian and Australasian section bears out the hypothesis of the Melanesian centre of evolution for a great part of *Ficus*. It corroborates the evidence of *Pharmacosycea* and *Scabrae* (in the alliance of *F. melinocarpa*) and amplifies it because, as the most advanced floral product of *Ficus*, it is recent enough to have retained early stages of evolution which are lacking in the other two. Thus, the perianth has become an entire sack or cup round the ovary; it reduces further to a minute collar in many species and is absent from some Bornean geocarpic species which have, in consequence, naked and ebracteate flowers. There is more dimorphism between the gall- and female flowers than occurs in any other group of *Ficus*. The section has more pachycaul, megaphyllous, and multibracteate species than any other, and these species centre in Melanesia where several of them retain the primitive mark of two or three stamens in the male flower. The persistence of such primitives in a group of advanced character implies recent evolution from pachycaul ancestors that survived in this state long after the progress of other sections. Accordingly, the section has very few wides, and two-thirds of its species, totalling *ca.* 75, are regionally endemic. The main features of its distribution are given in the following enumeration, the number of endemics being placed in parentheses after the number of species: India 5 (1), Malaya 11 (0), Borneo 23 (13), Philippines 14 (6), Celebes 12 (4), New Guinea 21 (11), New Britain 9 (2), Solomons 16 (13 or 14), New Hebrides 1 (0), Fiji 1 or 2 (1), New Caledonia 0, Queensland 3 (0).

In the Solomons the section has developed out of all proportion to the area. There is only one wide, *F. septica*, and *F. subcongesta* occurs also in New Britain. The other species are endemic and widespread from Bougainville to San Cristobal except that *F. bougainvillei*

seems limited to that island and *F. theophrastoides* may occur naturally in Fiji. The break between New Britain and the Solomons is astonishing because many of the species in the Solomons are exceedingly conspicuous with their large leaves and cauliflorous figs; landing in Bougainville is for the sycologist like entering a new world.

Subsect. Auriculisperma

The smooth, compressed, and often auriculiform seed without prominent hilum distinguishes this small subsection from that of *Sycocarpus* (figures 42–55). There are seven species, for I add here the new *F. immanis*. Five are known only from the Solomons and it would seem that *F. theophrastoides* may really be another of their endemics. This species was described in 1868 from the small island of Ovalau in Fiji and it has since been found only once near Suva in Viti Levu (J. D. Tothill 426, March 1928, in the Kew herbarium). In the Solomons it is very abundant, especially in old garden country. It has not been collected in New Hebrides, and there is evidence that Solomon islanders migrated to Ovalau more than a century ago, in which case they might have taken the seeds with them. Proof of the natural or imported status of the species in Fiji will come from the discovery whether the plants of Fiji have the insects of the species in the Solomons. The truly Fijian species, *F. vitiensis*, is closely related to *F. indigofera* of the Solomons; both are relatively advanced leptocaul species. The pachycaul are *F. salomonensis*, *F. cynaroides* and *F. immanis*. The intermediate are *F. lancibracteata* and *F. theophrastoides*. The leptocaul make the taller trees, but neither very large trees nor those with distichous leaves have been evolved. If *Ficus* were treated as a family, *Auriculisperma* would be one of the peculiar genera of the Solomons. It impinges, nevertheless, on subsect. *Dammaropsis* and *Papuasyce* in New Guinea; in all three, two or three stamens occur in the male flower in contrast with the single stamen in the rest of the section. Then in shape of ovary and seed, *Auriculisperma* relates with sect. *Adenosperma* centred in New Guinea and, otherwise, of obscure affinity.

I conclude that there lurked in the forest of the Melanesian Foreland an alliance of pachycaul figs that, relatively recently, gave rise to *Adenosperma*, *Dammaropsis*, and *Papuasyce* in New Guinea, and that from the same stock as *Adenosperma* there arose more recently in the Solomons *Auriculisperma*, whence *F. vitiensis* reached Fiji. Compared with other groups of *Ficus*, there is no reason to suppose that the evolution of *Auriculisperma* is completed.

Subsect. Sycocarpus

This is the largest and most advanced group of the section. It has about sixty species which have differentiated their alliances in different parts of Malaysia and Melanesia. It is distinguished by the prominent hilum of the plump seed, the sides of which are usually rough; it has consistently the single stamen, and the perianth is often much reduced. Structurally, it is advanced beyond *Auriculisperma*, but it must be much older because it has produced in nearly every biogeographical subregion of its range willow-leafed species of local affinity. The ten species in the Solomons include the wide, *F. septica*, and *F. subcongesta* of New Britain. Seven of the eight endemics form with *F. subcongesta* such a close alliance as to suggest an almost continuous series in the usual manner of *Ficus*-evolution. The pachycaul *F. longibracteata* is one of the commoner and more distinct, but the others, namely *F. tanypoda*, *F. profusa*, *F. baccaureoides*, *F. scaposa*, *F. dissipata*, *F. subcongesta* and

F. macrothyrsa gradually transform the pachycaul into the extreme willow-leafed leptocaul *F. macrothyrsa* var. *lancifolia* (figure 69). While there seems no doubt about the distinction of the species in the forest, considerable overlap appears with the fragments in the herbarium. They need much further study in the field from sapling stages to the uppermost ramification with smallest leaf.

TABLE 5. SUBSECT. *SYCOCARPUS* IN MELANESIA

	New Guinea	New Britain	Solomons
pachycaul, lateral bracts	*F. pachyrachis* var. *porrecta*	*F. praestans*	*F. longibracteata* (s) *F. tanypoda* (s)
subpachycaul, large basal bracts	*F. pachyrachis*	*F. neobritannica*	*F. profusa* (s)
leptocaul, small basal bracts	*F. d'albertisii*		*F. baccaureoides*
	F. calopilina	*F. calopilina*	*F. scaposa* (s)
	F. papuana		*F. dissipata* (s)
	F. bernaysii	*F. bernaysii*	*F. macrothyrsa* (s)
	F. adelpha		
	F. hahliana		
	F. vrieseana (s)		
	F. iodotricha (s)		
	F. sublimbata		
	F. congesta		
	F. hispida	*F. subcongesta*	*F. subcongesta* var. *symmetrica* (s)
	F. arfakensis (s)		
	F. hispidioides	*F. hispidioides*	
	F. saurauioides		
	F. septica	*F. septica*	*F. septica*
	F. ternatana (s)		*F. bougainvillei*

(s) Species with geocarpic stolons

This endemic series, possibly too recent for specific segmentation, has a close parallel in New Guinea, as shown in table 5. I have carefully compared the species in the herbarium and I know many of them in the field, but I conclude that there is no specific identity between those of New Guinea and those of the Solomons. Those of New Guinea are essentially ser. *Calopilinae*; probably a special name should be given to those of the Solomons, but it is hard to find a diagnostic character. Nevertheless, there is a much greater tendency to the geocarpic habit in the species of the Solomons. *F. arfakensis*, related with *F. congesta*, is the willow-leafed end-product in New Guinea. In my check-list (Corner 1965), I confused it with *F. macrothyrsa* var. *lancifolia*, the relation of which is clearly with *F. profusa*.

New Britain has not produced a similar series, yet in its situation between the two it has the endemic pachycaulous and multibracteate *F. praestans* and its ally *F. neobritannica*. They supply the requirements for the ancestry of the two series, and *F. praestans* has the fig which relates with that of *F. dammaropsis*. In other words, the two common endemics of New Britain relate the series of New Guinea and the Solomons. Thus, three more lines of *Sycocarpus* emerge from the Melanesian Foreland in addition to that of *Auriculisperma*.

F. septica is a wide, like *F. ampelas*, that ranges from Ryu Kyu and Sumatra to New Hebrides without landing on the Asian mainland, and it was described at the same time from Java; its origin has also remained obscure. Its one close ally is *F. bougainvillei*, which is stouter, more hairy, and scabrid and supplies details antecedent to the smooth and almost

glabrous *F. septica*. In my check-list I placed *F. septica* next to *F. fistulosa* of western Malaysia but this now seems an error arising from the convergent similarity of the two. *F. septica* fits as well with the alliance of *Sycocarpus* in the Solomons. It is my experience that before there is sufficient understanding of the whole problem, the tendency is to classify into grades of superficial similarity. The fig-flora of the Solomons has rectified this error.

The wide distribution of *F. septica* is to be expected for it is an advanced leptocaul with axillary figs, but there is the problem how it could have escaped so early along the route of ser. *Scabrae* to western Malaysia, when the rest of the alliance of *F. longibracteata* arose so much later as to be confined practically to the Solomons. The alliance consists mostly of pachycaul or cauliflorous species, neither of which characters seem to go generally with wide distribution, though there are exceptions, e.g. *F. copiosa*, *F. wassa*, *F. variegata*, and the two Asian species *F. hispida* and *F. racemosa*. It is noteworthy, as part of the problem, that the cauliflorous state of *F. septica*, namely var. *cauliflora*, is limited almost to Melanesia. An alternative explanation would relate *F. septica* with *F. pleyteana* and *F. ternatana*, which are geocarpic species of the Moluccas, but they seem to fit better with the New Guinea alliance of *F. congesta*. Comparison of the fig-insects and artificial hybridization may help to solve the problem.

10. Subgen. *Ficus* sect. *Adenosperma*

This small section of eighteen species, the alliance of which seems to be with *Auriculisperma*, has the same distribution as subgen. *Urostigma* sect. *Malvanthera*, though they differ so much in habit, leaf and fig. The range is from Celebes to New Hebrides and Queensland, omitting New Caledonia, and the centre for *Adenosperma* is New Guinea where it has three more or less pachycaul species (*F. megalophylla*, *F. ochrochlora* and *F. saccata*). They belong to the series *Amphigenae* with cystoliths on both sides of the leaf, in contrast with *Hypogenae*, which seem to be more derived. The advanced leptocaul trees of each series, *F. adenosperma* and *F. erythrosperma*, cover the whole range of the section, except that *F. erythrosperma* is not known from Queensland. The Solomons have four widely distributed species and the endemic *F. verticillaris*, which closely resembles *F. smithii* of subgen. *Pharmacosycea*. But, whereas *F. smithii* seems to have come from New Hebrides, the allies of *F. verticillaris* are *F. arbuscula* and *F. umbonata* of New Guinea and the Moluccas; all three may occur in New Britain. However, this island marks also with its species of *Adenosperma* the break between the floras of New Guinea and the Solomons. The large trees *F. funiculosa* and *F. subcuneata* stop in New Britain, and *F. verticillaris* is as common in Bougainville as in San Cristobal.

It is worth noting that the distribution of *Adenosperma* and *Malvanthera* is closely followed by that of the marsupial *Phalanger* which lives in their trees and feeds on their fruits and leaves (Croizat 1958, p. 758, f. 228).

11. Subgen. *Ficus* sect. *Neomorphe*

This very small section of six or seven species of buttressed forest trees ends its eastward distribution in San Cristobal. It has a centre in New Guinea, which suggests the origin of *F. variegata*. As a leptocaul species it is widely spread to the Himalayas, exactly as *F. subulata*

and the species of subgen. *Pharmacosycea*. The more pachycaul *F. nodosa* reaches the Moluccas. Neither has developed any peculiarities in the Solomons or, indeed, over the whole of this wide range, though *F. variegata* has some minor varieties in western Malaysia. The section has much in common with subgen. *Sycomorus*. This is an African group that differs mainly in being monoecious, but one species, *F. racemosa*, extends into India, western Malaysia, along the Java–Timor arc to Queensland and the Merauke district of south New Guinea; it follows, that is, the northern front of Gondwanaland and the Australian Foreland, but it does not reach New Caledonia. *Sycomorus* and *Neomorphe* have little in common geographically, but where they meet in south-east Asia with the overlap of their most derived species, there is the Sino–Malayan complex of *F. auriculata* and *F. oligodon*, which has to be assigned to *Neomorphe*. It would seem that this has nothing to do with problems of the Solomons, but the very intractability of sect. *Neomorphe* raises an alternative possibility.

Neomorphe may have come from the stock of *Adenosperma* on the Melanesian Foreland, and this stock may have been connected with that of *Sycomorus*, so that *Neomorphe* is an eastern parallel to it. There is entomological evidence. *Sycomorus*, *Sycocarpus*, *Adenosperma*, *Neomorphe*, and two series of *Sycidium* (*Prostratae*, *Pungentes*), which do not occur in the Solomons, are distinguished by having *Ceratosolen* as the pollinating insect, so far as they have been sampled (Wiebes 1963, 1965, 1966). Despite their differences, it may be necessary to combine them in subgen. *Sycomorus* in contrast with the remainder of subgen. *Ficus*, pollinated by *Blastophaga*. The difficulty is to find a diagnostic character for such a complex. Then ser. *Copiosae* and *Phaeopilosae* of sect. *Sycidium* have pollinators somewhat intermediate between *Ceratosolen* and *Blastophaga* (Wiebes 1963). They are the series in New Guinea, Celebes, and the Philippines which come nearest to the *Ceratosolen*-pollinated *Pungentes* of similar distribution. All impinge on the Melanesian Foreland, if not immediately with the flora of the Solomons. Here is a case where, at last, the entomology of *Ficus*, for which we have been waiting, is beginning to throw light.

12. Subgen. *Ficus* sect. *Rhizocladus*

This and sect. *Kalosyce*, which is not in the Solomons, consist entirely of advanced root-climbers. The habit is fitted to the ascent of tall trees from the debris on the floor of the forest from which the seedlings start. Even those of the very small-leafed *F. agapetoides* accomplish this in the Solomons and spread through the crowns of big trees. In sect. *Rhizocladus* this advanced habit is associated with the rather primitive mark of two, often large and mucronate, stamens in the male flower. It suggests a specialized and early offshoot of subgen. *Ficus*, similar to *Urostigma* among the monoecious figs, but adapted to the high forest. The section has three massings, two being in Asia and western Malaysia, and the third in New Guinea comprises ser. *Ramentaceae*, *Trichocarpeae*, and *Distichoideae*. They total 31 species in New Guinea, and merely five reach the Solomons without further evolution, unless *F. agatepoides* var. *solomonensis* should prove to be a distinct species from the little known var. *agapetoides* in New Guinea. If figs could have been dispersed by chance across the seas, it is remarkable that so few of this large number have reached the Solomons. Those which have bear the stamp of advancement; four are practically glabrous and the

hairy *F. baeuerleni* is reduced ally of *F. odoardi*. They prove that where a region has not participated in the prime evolution of a group, its fraction consists of the more advanced with little or no capacity for further evolution.

13. Phytogeographical summary

The occurrence, affinity, and state of evolution of the species of *Ficus* in the Solomons lead to two main conclusions. The geological history of the Melanesian Foreland has been closely linked with the evolution of *Ficus*, and *Ficus* sustains in its explicit detail a record

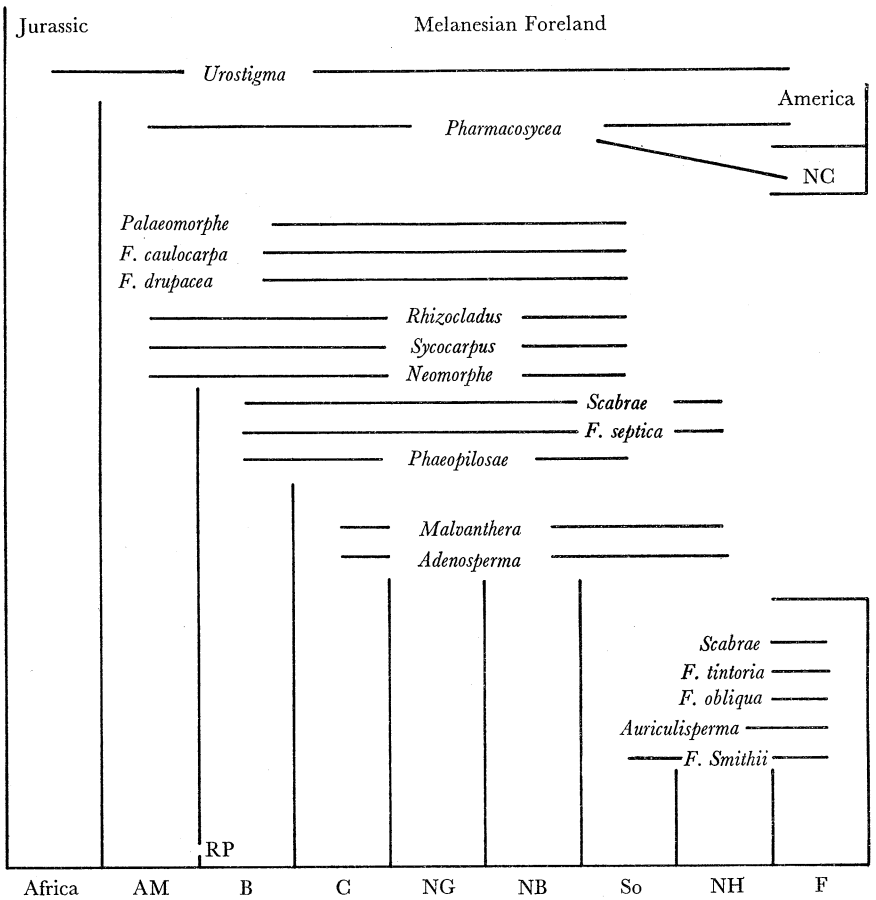

Figure 5. The biogeographical evolution of *Ficus* in Melanesia; the isolation of geographical regions shown by vertical lines. AM, Asian mainland; B, Borneo; C, Celebes; F, Fiji; NB, New Britain; NC, New Caledonia; NG, New Guinea; NH, New Hebrides; RP, Riouw pocket; So, Solomons.

of this history. This record is shown diagrammatically in figure 5; the method has limitations and there are uncertainties, but it is a plan to test. There has been a succession of lands where *Ficus* has undergone form-building and the species have been dispersed according to the opportunities arising from connexions between these lands. The phyletic classification of *Ficus* is too closely knit with geography to admit the prevalence of random dispersal. Ocean currents, wind, birds, and bats may have carried the seeds across the sea, but propagation requires the insect. So *Ficus* is hemmed in by ocean barriers and narrow seas, such as those which separate Sumatra and Malaya or New Britain and the Solomons.

The continuity of the fig-flora of their islands implies previous land-connexions between them.

In figure 5 the main features of *Ficus*-evolution, as they have affected the Solomons, are inserted as group-names or species between the base-line of modern geography and the upper, possibly Jurassic, period when *Urostigma* became pantropic. The names are placed where taxonomic evidence indicates their origin, and the spread of the group or species is shown by horizontal lines. The succession in time is based on the principle of exclusive passage. Thus, if group A enters region Y from region X and no other groups now in Y occur in X, the exclusive passage of A must have been before the appearance of the other groups in Y; if not, these other groups could have entered X. If the passage of *Pharmacosycea* to New Caledonia is synchronized with the movement of *F. smithii* between the Solomons and Fiji, then many other species would have been admitted to New Caledonia which are not there. Exclusive passage, however, may be modified into exclusive entry. If a chain of land-connexions disappeared successively as A progressed, the last connexion, say from N to Y, would have enabled A to enter Y and the other groups in Y to have reached N without further progress to X. The succession in time sets up barriers, therefore, to migration and these, as the thick lines in the diagram, define the modern phytogeographic regions. So New Caledonia is shut off early.

The principle may seem to break down in the passage of *Urostigma* and *Pharmacosycea* to America, for none of their Old World groups occurs in America. In such cases it may well have been the prototypes which travelled and subsequently evolved on arrival; or the present groups may have evolved too far away, as sect. *Urostigma* in Afro-Asia, to have caught the passage. *F. prolixa* of Polynesia seems to be the relic of the prototype of *Urostigma* on its way to America (Corner 1963).

The connexion between the Solomons, New Hebrides, and Fiji is difficult to insert. It must have allowed to Fiji a species of *Auriculisperma*, which became *F. vitiensis*, and *F. scabra* and *F. storckii* of *Scabrae* along with the three other species given in figure 5. Yet, somehow, *F. glandifera*, *F. subcordata*, *F. adenosperma*, *F. septica* and *F. wassa* were prevented, though they are the west Melanesian wides. Probably there is not enough known about the flora of New Hebrides. If *Auriculisperma* is really absent from them, *F. vitiensis* must have reached Fiji by some other route of the Melanesian Foreland. Alternatively, the principle of exclusive entry prevailed which these absentees were unable to catch.

14. Pachycauly and evolution

The four groups of *Ficus* in the Solomons, which have developed series of endemics, have in every case a more or less pachycaul species associated with the more numerous leptocaul. Such a stand-by is in accordance with the durian theory, for the pachycaul is considered to be the primitive growth-form of the flowering plant. It is likely, therefore, to have disappeared from widespread groups of long geological age. Nevertheless, pachycauly can be detected in some measure in most Asian and Australasian subdivisions of *Ficus*. These are listed in table 6; the groups omitted are the purely leptocaul alliances where specific differences are minor ones of shape and venation, for example subsect. *Palaeomorphe*.

A rule can be formulated, at least for *Ficus*, that there has been no major evolution into

a new series, section, or subgenus anywhere without the presence of a pachycaul starter. Where leptocaul species cover a wide area and, in so doing, have encountered many different situations, they cannot produce more than subspecies or varieties; for instance, *F. benjamina*, *F. microcarpa*, *F. nervosa*, *F. gul*, *F. ampelas*, *F. tinctoria*, *F. adenosperma*, *F. variegata* and *F. septica*. They do not indicate centres of origin. The pachycaul, in contrast, are

TABLE 6. PACHYCAUL GEOGRAPHY OF *FICUS*

	subgen. *Urostigma*	
sect. *Urostigma*	Sino-Himalaya	*F. hookeriana, orthoneura*
	West Malaysia	*F. superba*
sect. *Conosycea*	South India	*F. beddomei, drupacea*
	West Malaysia	*F. annulata, stupenda*
sect. *Malvanthera*	New Guinea	*F. hesperidiiformis*
	subgen. *Pharmacosycea*	
ser. *Nervosae*	Solomons	*F. cristobalensis*
ser. *Austrocaledonicae*	New Caledonia	*F. crescentioides*
ser. *Vasculosae*	West Malaysia	*F. callosa*
	subgen. *Ficus*	
sect. *Ficus*		
ser. *Eriosyceae*		
subser. *Eriosyceae*	Indo-China	*F. esquiroliana*
subser. *Trichosyceae*	Malaysia	*F. halmaherae, mollissima*
subser. *Dehiscentes*	Philippines	*F. ruficaulis*
ser. *Auratae*	Borneo	*F. bruneiensis*
sect. *Rhizocladus*		
ser. *Ramentaceae*	New Guinea	*F. odoardi, sphaerocarpa*
ser. *Trichocarpeae*	New Guinea	*F. fuscata, hypophaea*
sect. *Kalosyce*	Borneo	*F. apiocarpa*
sect. *Sycidium*		
ser. *Pungentes*	East Malaysia	*F. pungens*
ser. *Phaeopilosae*	New Guinea	*F. complexa*
ser. *Copiosae*	East Malaysia	*F. copiosa, heteropoda*
ser. *Scabrae*	Solomons	*F. oleracea*
sect. *Adenosperma*	New Guinea	*F. megalophylla, saccata*
sect. *Neomorphe*	New Guinea	*F. nodosa, robusta*
	Sino-Himalaya	*F. auriculata*
sect. *Sycocarpus*		
subsect. *Auriculisperma*	Solomons	*F. cynaroides, salomonensis*
subsect. *Sycocarpus*		
ser. *Longetuberculatae*	Philippines	*F. cassidyana*
ser. *Tuberculifasciculatae*		
subser. *Praestantes*	New Britain	*F. praestans*
subser. *Calopilinae*	New Guinea	*F. pachyrachis*
subser. *Fulvidulae*	Borneo	*F. cereicarpa*
subser. *Geocarpicae*	Borneo	*F. megaleia*

characteristically localized in the midst of their leptocaul swarms. Thus, as already emphasized, the more derived and leptocaul species generally spread furthest, the pachycaul least. This makes an important proviso to Willis's theory of Age and Area, which holds that all species of a group spread at the same rate and that the most widespread are the oldest and the primitive which have given rise to the new species enclosed within their ambit, as wheels within wheels (Willis 1922). For instance, the distribution of *F. dammaropsis* in New Guinea is contained within that of *F. congesta*, which is contained within that of *F. septica*, contained within that of *F. variegata*, contained within that of *F. tinctoria*, and this represents surely the thesis of Age and Area, but *F. dammaropsis* is a primitive pachycaul that for some reason has failed to spread; even if a recent species, its ancestor failed to spread.

This rule appears to have very wide application in the study of flowering plants, but it is so contradictory to many assumptions that one is forced to consider the durian theory in reverse as an alternative and regard, for the sake of argument, the leptocaul plant as the apparently primitive. Then the following difficulties arise:

(i) The most primitive species are the commonest and most widespread. This practically does away with the need for palaeobotany because it means that thousands of primitive members of flowering plant genera are thriving. It is in defiance of biogeography which shows the primitive as relics.

(ii) The pachycaul species are the most advanced but, with their least branching, they make the least contribution to that forest construction which the flowering plants have been evolving. The conclusion takes no account of the evolution of tree-form, except to imply that many genera of trees have been devolving into rare pachycaul oddities. It means, also, that a very successful group as *Urostigma*, without pachycaul effect, has never been able to achieve this supposed climax of tree-form.

(iii) The most leptocaul examples in *Ficus* have the simplest construction of the syconium which supplies no evidence of its evolution. It is the pachycaul which has the large multibracteate fig with subcymose clustering of the flowers on internal processes to show the relationship with the Moraceous cymose panicle.

(iv) The leptocaul have generally in *Ficus* the simplest flowers, unistaminate in the male. In the case of sect. *Sycocarpus* ser. *Geocarpicae* of Borneo, *F. beccarii* and *F. uncinata* would have to be taken as the primitive species but their gall- and female ovaries are without perianth. The evolution of this structure would then have to be read from a minute rim or collar to the saccate, which covers the ovary, and then this would have to be divided into segments, supplied with more stamens in the male flower and a pistillode, until it became like the generalized moraceous flower. This assumption is in accordance with the theory that regards the naked flower as primitive but, unfortunately, these two species belong to the group of *Ficus* which has the greatest dimorphism between the gall- and female flowers, and this peculiarity has no part in the general evolution of flowers. The assumption means that the moraceous flower has been evolved from the simplest beginnings inside the syconium in dark through the agency of extremely specialized insects, and this is its surest refutation.

Further absurdities could be adduced. I revert to the durian theory which explains the pachycaul as the primitive growth-form, the relic of limited distribution in which the retention of ancestral points, such as the two or three stamens in the male flower in *Ficus* and the multibracteate syconium, are understandable, and that which has now disappeared from the long established groups of *Ficus*. A morphological series can be read in either direction; the ecological factor supplies time's arrow. In this case it is the build-up of tropical forest into gigantic leptocaul trees. The durian theory shows the pachycaul as the heavily endowed plant which, by limitation of this endowment through the process of neoteny, leads to the small twigs, leaves, flowers, fruits, and seeds required by advanced vegetation. It explains without violence to the rest of botany the reduction of the fig-flower inside the syconium to the limit compatible with the inherited method of pollination.

The theory not only explains many common problems of plants but directs attention. *F. pseudopalma* (sect. *Ficus*) in the Philippines and *F. dammaropsis* (sect. *Sycocarpus*) in New

Guinea are two pachycauls that seem not to have given rise to leptocaul derivatives. If *F. pseudopalma* had an entire perianth, which seems a detail, it would be close to *F. dammaropsis*, and both have *Ceratosolen* as the pollinator (Wiebes 1966). The divided perianth distinguishes *Adenosperma* from *Auriculisperma*, and the other groups of *Ficus* pollinated by *Ceratosolen* from *Sycocarpus* in general. It is the main feature which separates *F. auriculata* from *F. oligodon* in their *Ceratosolen*-complex of *Neomorphe* in Sino-Malaya. One is lead to ponder deeply whether *F. pseudopalma* and *F. dammaropsis* are not bistaminate remnants, as yet inactivated, of the pachycaul ancestry of *Ficus* drawn out along the pachycaul front of *Sararanga* from the time when the primitive pachycaul forest of flowering plants in ancient Melanesia was becoming leptocaul. Then the pachycaul ancestry for these dioecious figs must have linked up with the older monoecious ancestry of the African *Sycomorus* in continental Asia, where the *Ceratosolen* group of sect. *Sycidium* ser. *Prostratae*, as well as *F. auriculata*, call for their origin. One is lead to ponder, that is, a pachycaul front from Africa to the Melanesian Foreland where the most intensive evolution of *Ficus* has since taken place.

Ficus may seem an exceptionally suitable example of the durian theory in its sense of the evolution of the modern tree. This is because *Ficus* has not been dissolved in the way of temperate taxonomy into microgenera. If the alliances of microgenera in other great tropical families, such as Euphorbiaceae or Apocynaceae, were combined to the morphological level of *Ficus*, their supergenera would be as apt. The study of flowering plants needs pachycaul infusion. It needs the geography, morphology, ecology, physiology, and genetics of pachycaul plants to supply the evolutionary directive to the confused knowledge of space, form and function. There is evidence now of the post-Jurassic progress of angiosperms. It was the discovery of *F. cristobalensis*, tucked away in the south-east corner of the Solomon Islands, that revealed the wide significance of their fig-flora.

15. Classified list of species in the Solomons

(Numbered according to the check-list, Corner 1965)

subgen. *Urostigma* (Gasp.) Miq.

sect. *Urostigma*

6. *F. prasinicarpa* Elm.
10. *F. virens* Ait.
12. *F. caulocarpa* Miq.

sect. *Conosycea* (Miq.) Corner

27. (*F. drupacea* Thunb.) var. *glabrata* Corner
39. (*F. crassiramea* Miq.) var. *patellifera* (Warb.) Corner
66. *F. subcordata* Bl.
68. *F. benjamina* L.
72. (*F. microcarpa* Linn. f.) var. *naumanni* (Engl.) Corner

sect. *Malvanthera* Corner

83. *F. glandifera* Summerh. var. *brachysyce* Corner
91. *F. obliqua* Forst. f.
98. (*F. xylosycia* Diels) var. *cylindrocarpa* (Diels) Corner

subgen. *Pharmacosycea* Miq.

ser. *Nervosae* Corner

110. *F. hombroniana* Corner
111. *F. edelfeltii* King var. *bougainvillei* Corner
111A. *F. novae-georgiae* Corner
111B. *F. cristobalensis* Corner
112A. *F. illiberalis* Corner
113. *F. polyantha* Warb.
120. *F. pachystemon* Warb.
140. *F. smithii* Horne

subgen. *Ficus*

sect. *Rhizocladus* Endl.

211. *F. pantoniana* King

subgen. *Ficus* (*cont.*)

226. *F. baeuerleni* King
243. *F. phatnophylla* Diels
245. (*F. agapetoides* Diels) var. *solomonensis* Corner
255. *F. nasuta* Summerh.

sect. *Sycidium* Miq.
subsect. *Sycidium*
ser. *Phaeopilosae* Corner
292. *F. porphyrochaete* Corner
293. *F. gul* Laut. et K. Schum. var. *solomonensis* Corner
ser. *Copiosae* Corner
301. *F. copiosa* Steud.
302. *F. wassa* Roxb.
ser. *Scabrae* Miq.
316. *F. melinocarpa* Bl.
317. *F. trachypison* K. Schum.
327. *F. oleracea* Corner var. *pugnans* Corner var. *villosa* Corner
328. *F. imbricata* Corner var. *subcordata* Corner
329. *F. chrysochaete* Corner
330. *F. arawaensis* Corner
330A. *F. pseudowassa* Corner
331. *F. gryllus* Corner
332. *F. erinobotrya* Corner var. *solomonensis* Corner f. *glabrior* Corner

subsect. *Paleomorphe* (King) Corner
357. *F. tinctoria* Forst. f.
358. *F. virgata* Reinw. var. *sessilis* (Bur.) Corner
360. *F. subulata* Bl.

sect. *Adenosperma* Corner
382. *F. mollior* Benth.
385. *F. verticillaris* Corner var. *robusta* Corner
386. *F. adenosperma* Miq. var. *chaetophora* (Warb. var. *glabra* Corner
387. *F. austrina* Corner
394. *F. erythrosperma* Miq.

sect. *Neomorphe* King
397. *F. variegata* Bl.
399. *F. nodosa* Teysm. et Binn.

sect. *Sycocarpus* Miq.
subsect. *Auriculisperma* Corner
402. *F. cynaroides* Corner
402A. *F. immanis* Corner
403. *F. lancibracteata* Corner
404. *F. salomonensis* Rech.
405. *F. theophrastoides* Seem.
406. *F. indigofera* Rech.

subsect. *Sycocarpus*
419. *F. longibracteata* Corner
423. *F. profusa* Corner
423A. *F. tanypoda* Corner
423B. *F. scaposa* Corner
423C. *F. dissipata* Corner
424. *F. baccaureoides* Corner
437. (*F. subcongesta* Corner) var. *symmetrica* Corner
463. *F. bougainvillei* Rech.
464. *F. septica* Burm. f. var. *cauliflora* Corner
474. *F. macrothyrsa* Corner var. *lancifolia* Corner

16. Field key to the species of *Ficus* in the Solomon Islands

Root-climbers. ..... Group A
Strangling figs; leaves entire, coriaceous, not scabrid. ..... Group B
Large, usually buttressed, trees; trunk 30 cm or more in diameter. ..... Group C
Small trees or shrubs; trunk usually less than 20 cm in diameter; leaves often scabrid or asymmetric at the base. ..... Group D

Group A (root-climbers)

1. Leaves small. Figs 4–8 mm wide.
   2. Leaf acute. ..... *F. phatnophylla*
   2. Leaf obtuse. ..... *F. agapetoides*

1. Lamina 8 cm or more long. Fig larger.
   3. Fig ripening greenish yellow (? to purple); basal bracts persistent; orifice not sunken; internal bristles often conspicuous; flowers sessile. Lamina ovate to cordate, acuminate; basal veins elongate. More or less glabrous. *F. nasuta*
   3. Fig ripening red; basal bracts early caducous; orifice sunken; internal bristles minute or none; flowers sessile and pedicellate.
      4. Rather strongly hairy. Lamina elliptic, acuminate, strongly veined; basal veins short. ... *F. baeuerleni*
      4. Glabrous or sparsely hairy. Lamina ovate to subcordate, subacute to acuminate, not strongly veined; basal veins elongate or not. ..... *F. pantoniana*

Group B (strangling figs)

1. Petiole disarticulating from dried or fallen leaves. Deciduous. Figs 6–12 mm wide, ripening pink to purple.
   2. Fig without internal bristles, shortly pedunculate; basal bracts caducous. Lamina ovate to subcordate. ..... *F. prasinicarpa*
   2. Fig with abundant chaffy internal bristles; basal bracts persistent.
      3. Lamina oblong; lateral veins 9–16 pairs. Fig 5–8mm wide, shortly pedunculate. Twigs often stout, up to 8 mm wide. ..... *F. caulocarpa*
      3. Lamina ovate or elliptic; lateral veins 6–11 pairs. Fig 8–12 mm wide, often sessile. ... *F. virens*

1. Petiole not disarticulating. Fig often ripening orange to red, often large.
   4. Lateral veins well-spaced with a distinct pattern of intercostals.
      5. Figs 12–20 mm wide or more, sessile. Twigs 4–8 mm thick. Leaves more or less spirally arranged. Monoecious.
         6. Fig oblong; basal bracts concealed. Young shoots brown hairy. Lamina often subcordate; basal veins 2–5 pairs, short. ..... *F. drupacea*
         6. Fig round; basal bracts conspicuous. Lamina elliptic or narrowly obovate; basal veins 1 pair, elongate. ..... *F. crassiramea*
      5. Figs smaller, usually stalked, often without a collar of 3 basal bracts. Twigs 1·5–4 mm thick. Leaves distichous. Dioecious; gall-figs yellow, seed-figs red.
         7. Lamina submembranous, acute or acuminate. Fig stalked, with 1–2 small lateral bracts on the body. Epiphyte, never strangling. ..... *F. subulata*
         7. Lamina coriaceous. Large stranglers. Fig-body without lateral bracts.
            8. Lamina obtuse or subacute. Fig stalked. ..... *F. tinctoria*
            8. Lamina very acute. Fig often sessile, often with a collar of 3–6 basal bracts. ... *F. virgata*
   4. Lateral veins fine, parallel, close, numerous, without conspicuous intercostal pattern.
      9. Stipules of the terminal bud 3–17 cm long.
         10. Fig cylindric, stalked. Lamina often narrowly elliptic. ..... *F. xylosycia*
         10. Fig seated on a thick, cupule-like stalk ..... *F. glandifera*
      9. Stipules shorter.
         11. Fig with stalk 1–5 mm long; basal bracts caducous; body 7–12 mm wide. ..... *F. microcarpa*
         11. Fig seated on a thick, cupule-like stalk 4–7 mm wide. ..... *F. obliqua*
         11. Fig sessile; basal bracts concealed.
            12. Fig 20–40 mm long. Lamina 10–25 cm long. Copious stout aerial roots. ..... *F. subcordata*
            12. Fig and leaf smaller. ..... *F. benjamina*

Group C (large trees)

1. Cauliflorous. Figs 30–50 mm wide, long-stalked. Deciduous. Lamina ovate or cordate.
   2. Twigs 4–8 mm thick. Lamina 15–40 × 10–30 cm. Fig coarsely tuberculate–lenticellate. Tepals fimbriate. ..... *F. nodosa*
   2. Twigs thinner. Lamina smaller. Tepals entire. ..... *F. variegata*

1. Not cauliflorous or, if so, with smaller, shortly stalked figs.
   3. Lamina scabrid, more or less asymmetric. ..... *F. melinocarpa*
   3. Lamina smooth, symmetric.
      4. Monoecious. Leaves coriaceous, entire. ..... subgen. *Pharmacosycea*
      4. Dioecious. Leaves often submembranous. ..... sect. *Adenosperma*

Group D (small trees and shrubs)

1. Geocarpic with stolons. ..... subsect. *Sycocarpus*

1. Not geocarpic.
   2. Lamina 30 cm or more long, short-petiolate.
      3. Leaves distichous, drooping, usually scabrid. ..... *F. oleracea*
      3. Leaves spirally arranged.
         4. Leaves 1–2 m long. Figs cauliflorous, tuberculate towards the apex. ..... *F. salomonensis*
         4. Leaves shorter. Figs not tuberculate.
            5. Figs axillary, 4–6 cm wide. Much branched tree to 12 m high. ..... *F. cristobalensis*
            5. Figs axillary and in bunches at the base of the stem. Leaves narrowly elongate–obovate. Unbranched or sparingly branched tree, 2–7 m high. ..... *F. theophrastoides*
   2. Lamina shorter or long-petiolate.
      6. Lamina 20–40 cm long, long-petiolate.
         7. Twig 8–12 mm thick. Stipules 3–13 cm long. Fig axillary, sessile.
            8. Fig 30–40 mm wide. Lamina with cordate base and prominent venation; basal veins elongate. ..... *F. immanis*
            8. Fig smaller. Lamina not cordate; venation scarcely prominent; basal veins usually short ..... *F. cynaroides*
         7. Twigs thinner. Stipules shorter. Figs cauliflorous, stalked.
            9. Glabrous or with whitish hairs or with stiff short spines. Leaves often opposite. Figs 25–40 mm wide, depressed-globose, long-stalked, usually without a collar of basal bracts ..... *F. copiosa*
            9. Hairs brown, purple, or black.
               10. Fig without a collar of basal bracts. Hairs stiff, irritant, purple brown..... *F. porphyrochaete*
               10. Fig with a collar of three basal bracts. Hairs not irritant.
                  11. Fig-peduncles 3–10 cm long; fig 3–5 cm wide ..... *F. scaposa*
                  11. Peduncles 1–2·5 cm long; fig smaller.
                     12. Hairs dark brown to black, stiff ..... *F. dissipata*
                     12. Hairs pale brown, soft ..... *F. baccaureoides*
      6. Lamina shorter, or short-petiolate.
         13. Leaves distichous, short-petiolate.
            14. Epiphyte, simulating a young strangler. Leaves smooth. Figs small, with 1–2 lateral bracts on the body, stalked. ..... *F. subulata*
            14. Not epiphytic.

15. Leaf more or less scabrid and asymmetric. Figs mostly without a collar of basal bracts. .....sect. *Sycidium* ser. *Scabrae*
15. Leaf smooth, symmetric, narrow, acuminate. Tall tree. Figs axillary, small, with a collar of basal bracts. .....*F. erythrosperma*

13. Leaves spirally arranged.
16. Fig without a collar of three basal bracts.
17. Brown hairy. .....*F. gul*
17. Not brown hairy.
18. Leaf 10–18 cm wide. Fig 25–40 mm wide. .....*F. copiosa*
18. Leaf and fig smaller. .....*F. wassa*
16. Fig with a collar of basal bracts.
19. Purple brown hairy. Fig sessile, axillary, with conspicuous apical bracts. ..... *F. lancibracteata*
19. Not so. Fig stalked.
20. Twigs slender, 1–3 mm thick, curved-ascending with verticils of small leaves.
21. Leaf very coriaceous; venation indistinct. Glabrous or white puberulous. Dioecious. .....*F. verticillaris*
21. Leaf with distinct venation. Young parts finely brown hairy. Monoecious. *F. smithii*
20. Twigs stouter, or leaf larger, not verticillate.
22. Fig not ribbed towards the apex, often with 1–2 lateral bracts, ripening green, brown, or yellow. Flowers always sessile; perianth of separate tepals.
23. Brown hairy. .....*F. mollior*
23. Glabrous or whitish hairy.
24. Lamina 8–15 cm wide. Stipule 2–5 cm long. Fig 2 cm wide. Seashore. *F. austrina*
24. Smaller in all parts. River- and stream-side. .....*F. adenosperma*
22. Fig ribbed towards the apex, without lateral bracts. Flowers sessile and pedicellate; perianth usually entire.
25. Leaves with pale whitish veins. Stipule 2–6 cm long. Fig ripening white or yellow.
26. Leaf scabrid. Fig axillary. .....*F. bougainvillei*
26. Leaf smooth. Figs axillary or cauliflorous. .....*F. septica*
25. Leaves without such pale veins. Stipule shorter. Figs ripening red, pink, or brown.
27. Figs finely appressedly silky, axillary or cauliflorous. Leaves often congested and auricled at the base. .....*F. indigofera*
27. Figs more or less glabrous, cauliflorous. Twigs, petioles, and stipules more or less brown hairy.
28. Figs in long hanging racemes 1–3 m long; basal bracts caducous; Leaf usually asymmetric; lateral veins inarching. .....*F. macrothyrsa*
28. Figs on shorter leafless twigs; basal bracts persistent. Leaf symmetric; lateral veins oblique, with close intercostals. .....*F. subcongesta*

17. Key to the taxonomic groups of *Ficus* in the Solomon Islands

1. Monoecious with male, gall-, and seed-flowers in the same fig. Leaf entire, usually coriaceous. Interfloral bracts mostly present.
2. Trees, not stranglers. Leaf with glands in the axils of the basal veins on the underside.

Stamens 1–3. Style usually bifid. Fig-wall entirely sclerotic or pulpy. ..... subgen. *Pharmacosycea* (p. 72)

2. Stranglers. Leaf-gland at the back of the petiole-apex, or absent. Stamen 1. Style usually simple. Fig-wall with outer and inner sclerotic layers. .....subgen. *Urostigma* (p. 62)

3. Apical bracts of the fig inflexed. Anther with two pollen-sacs, dehiscing crescentically. Lamina with the secondary lateral veins almost as well-developed as the primary. ..... sect. *Malvanthera*

3. Apical bracts interlocking. Anther with four pollen-sacs, dehiscing by two longitudinal slits.

4. Male flowers ostiolar. Ovary wholly red-brown or in the upper half. Petiole articulate to the lamina. Cystoliths hypogenous. .....sect. *Urostigma*

4. Male flowers disperse. Ovary white with a red mark at the base on the stylar side. Cystoliths amphigenous. .....sect. *Conosycea*

1. Dioecious (plants bearing figs with either male and gall-flowers or seed-flowers). Leaf entire or dentate, often plicate in bud. Male flowers ostiolar. .....subgen. *Ficus*

5. Root-climbers. Leaves distichous, entire, coriaceous. Stamens 2. Seed oblong, compressed, keeled. ..... sect. *Rhizocladus* (p. 85)

5. Trees or shrubs, varying epiphytic or strangling. Seed of different form.

6. Perianth entire, saccate or annular. Stamens 2 or 1. Lamina with or without glands in the axils of the basal veins; usually with a subnodal gland on the twig. ..... sect. *Sycocarpus*

7. Seed 1·4–2 mm long, more or less auriculiform, subcompressed, smooth, without prominent hilum. Stamens 2 or 1. .....subsect. *Auriculisperma* (p. 122)

7. Seed 0·5–1·5 mm long, plump, rounded, with prominent hilum and, usually, rough or tuberculate sides. Stamen 1. .....subsect. *Sycocarpus*

6. Perianth of separate tepals or, if joined, then deeply lobate. Lamina usually with a pair of glands in the axils of the basal veins on the underside.

8. Stamens 2; male flowers, sessile, compressed. Large buttressed, cauliflorous trees. ... sect. *Neomorphe* (p. 120)

8. Stamen 1, rarely 2.

9. Flowers usually sessile. Seed strongly compressed, generally with a double keel at the base, smooth. Ovary dark red or red-spotted; style nearly basal or markedly lateral. Leaves entire, usually symmetric, spirally arranged. .....sect. *Adenosperma* (p. 114)

9. Flowers usually stalked. Seed lenticular to shortly oblong. Ovary white; style subterminal. Lamina often toothed or asymmetric. .....sect. *Sycidium*

10. Seed shortly oblong, smooth, generally keeled or knobbed at the apex. Male flower with a normal gall-ovary. Fig without a collar of lateral bracts. Leaves entire, distichous. Epiphytic, often strangling. .....subsect. *Palaeomorphe* (p. 110)

10. Seed lenticular, smooth, rough, or subtuberculate. Male flowers without a functional gall-ovary. Figs with or without a collar of basal bracts. Leaves usually dentate. Not epiphytic. .....subsect. *Sycidium* (p. 89)

11. Leaves distichous, usually scabrid and asymmetric, short-petiolate. Hairs white or yellowish. .....ser. *Scabrae*

11. Leaves spirally arranged or opposite, symmetric, often long-petiolate.

12. Hairs brown or purple, stiff, often wiry. .....ser.. *Phaeopilosae*

12. Hairs white, short, or none .....ser. *Copiosae*

18. Specific descriptions

Subgen. *Urostigma* (Gasp.) Miq.

The key to the species is given under Group B, p. 58.

6. *F. prasinicarpa* Elm. (figure 6)

Fairly large strangler without copious aerial roots, sometimes independent. Leaves spirally arranged. Glabrous or with thinly villous stipules and basal bracts. Twigs 2–3 mm thick, light brown. Stipules up to 10 mm long. Lamina 6–18 × 3·5–9 cm, ovate-elliptic, acuminate with the tip 7–17 mm long, base subcordate to truncate, rounded or widely cuneate, thinly coriaceous, smooth, drying green to pale brown; lateral veins (5–) 7–11 pairs, 0–3 intercostals, slightly raised on both sides as the reticulations; basal veins 1–2 pairs, not elongate; petiole 12–50 mm long, articulate, slender. Figs axillary, paired, and on the twigs below the leaves, shortly stalked, ripening purple; peduncle 1–2·5 mm long; basal bracts 3, 1–1·5 mm long, ovate, eventually caducous; body 9–13 mm wide (5–8 mm, dried), subglobose, the small plane orifice closed by 2–3 apical bracts; internal bristles and scales none; fig-wall thin. Male flowers ostiolar in one ring, sessile; perianth almost wholly gamophyllous. Gall-flowers sessile or shortly pedicellate; perianth almost wholly gamophyllous or 2–3-partite, red; ovary dark red, sessile or stalked. Female flowers sessile; tepals 3, free or shortly gamophyllous, ovate lanceolate; ovary dark red. Lamina with cystoliths only on the lower side.

Distr. Philippines, Celebes, Moluccas, Waigeo, Key Isl., Aru Isl., New Guinea, New Ireland, Solomons.

Ecology. Chiefly coastal, widespread in the Solomons.

Kwara-ae. hai serian.

Collections. BSIP 1939, NGF 13406, RSS 2760, T. Wolff 3092.

This widespread species, often growing on coral sand, can be mistaken for *F. virens* which has thicker twigs, larger and less rounded leaves, larger figs with persistent basal bracts and copious chaffy internal bristles. It grows far into the mountains in New Guinea, but it has not been found in such places in the Solomons.

10. *F. virens* Ait.

Large deciduous strangler, with or without tufts of aerial roots from the branches. Leaves spirally arranged. Glabrous or the stipules finely puberulous. Twigs 3–5 mm thick, brown. Stipules up to 5 mm long, but much longer and leafy on opening shoots. Lamina 8–20 × 4–10 cm, ovate-elliptic to elliptic, shortly and often obtusely acuminate with the tip up to 12 mm long, base subcordate, rounded, subtruncate or cuneate, thinly coriaceous, smooth, drying brownish; lateral veins 7–12 pairs, 1–4 intercostals, slightly raised below as the reticulations; basal veins 1–2 pairs, not elongate; petiole 25–65 mm long, articulate. Figs axillary, paired, or on the twigs below the leaves (?also on short burrs on older twigs) ripening whitish to pink, purple, and black; peduncle 1–6 mm long; basal bracts 1·5–3 × 2–4 mm, ovate, subacute or obtuse, glabrous or puberulous, persistent; body 12–20 mm wide (7–12 mm, dried), globose, the small orifice closed by 3 flat apical bracts in a disk 1 mm wide; internal bristles abundant, white, chaffy, vesicular. Male flowers ostiolar sessile, in 2–3 rings; tepals 2–3, ovate, acute, free or shortly gamophyllous. Gall-

flowers sessile or shortly pedicellate; tepals 3–4, reddish, spathulate to linear–lanceolate, free, rarely two joined; ovary sessile or stalked, red-brown. Female flowers sessile; tepals 3–4, free; ovary red-brown, sessile or stalked. Lamina with cystoliths only on the underside.

Distr. Ceylon, India, South China to the Solomons and north Australia.

Ecology. Common on headlands in the Solomons.

Var. *sublanceolata* (Miq.) Corner

Differs in the sessile fig.

Distr. As var. *virens*.

Collections. Brass 3224, Waterhouse 315 ('hisigusigu', Siwai, Bougainville), Waterhouse 362 ('kalala lakori', New Georgia).

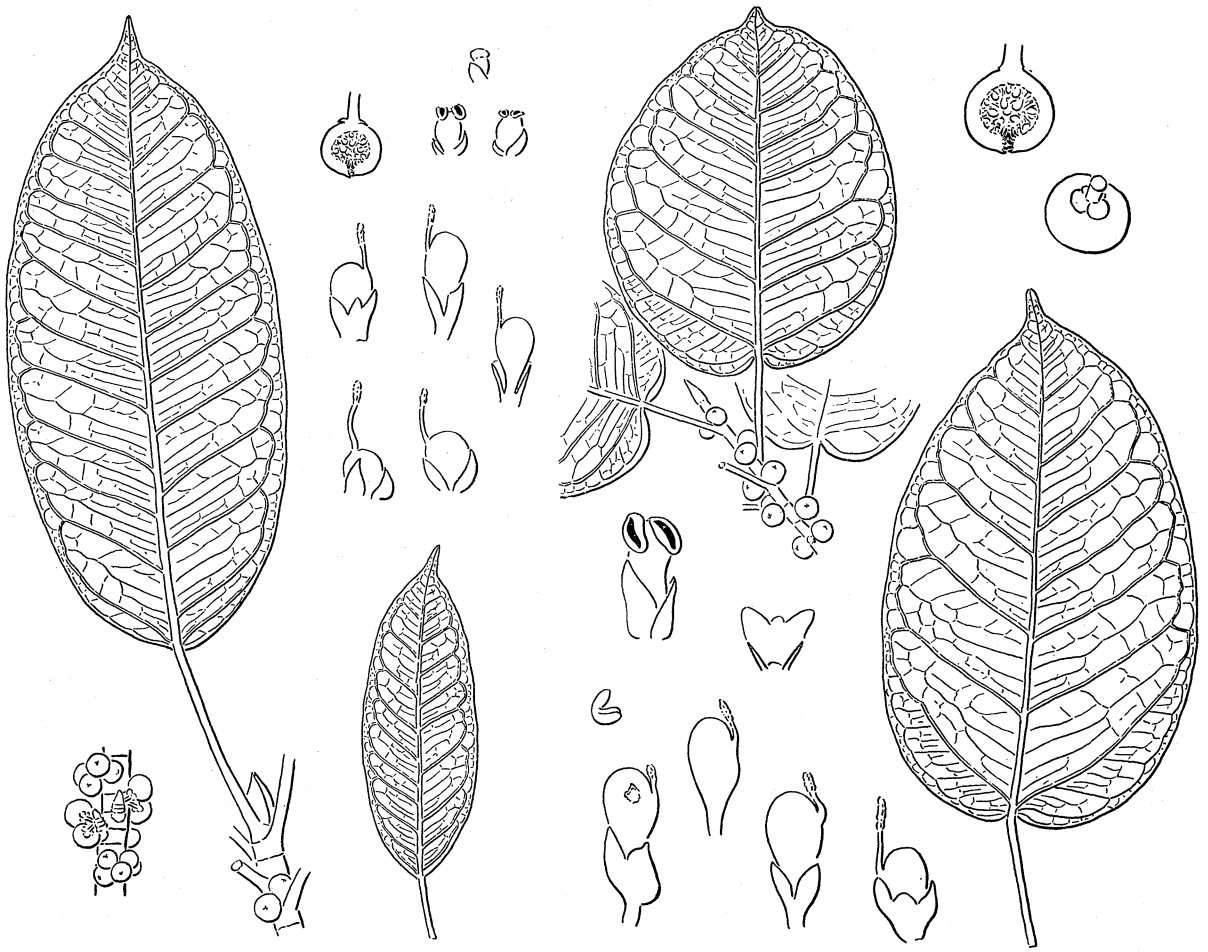

FIGURE 6. Subgen. *Urostigma*. Right, *F. prasinicarpa*, RSS 2760. Left, *F. caulocarpa*, Carr 12814 (Papua). Leaf and twig $\times \frac{1}{2}$, fig $\times 1$, flowers $\times 10$.

12. *F. caulocarpa* Miq. (figure 6)

Large deciduous strangler, developing a reticulate root-trunk, often with bunches of aerial roots on the trunk and main branches. Leaves spirally arranged. Glabrous except the silky stipules; twigs and peduncles sometimes puberulous. Twigs 3–8 mm thick, dark brown. Stipules up to 15 mm long, foliaceous up to $10 \times 1{\cdot}2$ cm on the opening shoots. Lamina $6–22 \times 3–8{\cdot}5$ cm, elliptic to oblong or slightly obovate, more or less acuminate

with a tip up to 15 mm long, base rounded to cuneate, thinly coriaceous, smooth, drying dull dark brown; lateral veins 9–16 pairs, slightly raised below, 0–3 intercostals, reticulations scarcely visible; basal veins 1–2 pairs, short; petiole 15–80 mm long, articulate. Figs in groups of 2–8 in the axils of the old leaves and on the bare twigs, ripening white to pink, purple, and black; peduncles 1–4 mm long, glabrous, puberulous, or thinly villous; basal bracts 3, free or usually joined in a glabrous or puberulous disk, 3–4 mm across, splitting into 4–6 lobes; body 8–12 mm wide (5–8 mm, dried), subglobose, the small orifice closed by 3 flat or slightly prominent apical bracts; internal bristles abundant, chaffy, vesicular. Male flowers ostiolar in 2–3 rings, sessile; tepals 1–2, saccate–lanceolate, free or joined. Gall-flowers sessile or shortly stalked, female flowers sessile; tepals 3–4, reddish brown, lanceolate or spathulate, free to almost wholly gamophyllous; ovary dark red, sessile or shortly stalked. Lamina with cystoliths only on the lower side.

Distr. Ceylon, Burma, Thailand to the Solomons.

Ecology. Coastal and lowland forest.

No fertile specimens have been collected in the Solomons, but several sterile specimens were found in the lowland forest of Guadalcanal during the Royal Society Expedition. It is easily recognized from the fallen leaves by their oblong shape with numerous lateral veins and by the disarticulating petiole.

27. *F. drupacea* Thunb. (figure 7)

Large, apparently evergreen, strangler with abundant descending aerial roots round the host-trunk, without tufts of aerial roots from the branches. Leaves spirally arranged to subdistichous on the ultimate twigs. Young parts thickly covered with bright brown hairs 2–4 mm long, soon glabrescent or remaining hairy at the distal node. Twigs 3–6 mm thick. Stipules up to 20 mm long, enclosing a young brown hairy leaf. Lamina 8–26 × 3–13 cm (up to 35 × 16 cm in saplings), elliptic, oblong–elliptic, or obovate, shortly acuminate, base narrowly to widely cordate, rounded, or cuneate, smooth, thinly coriaceous, drying light brownish; lateral veins 7–12 pairs, 3–7 more or less regular intercostals, distinctly raised on both sides; basal veins 3–5 pairs, or 1–2 in small leaves, short; petiole 10–45 mm long. Figs axillary, sessile, paired, at first covered with a stout conical tomentose stipule, ripening yellow-ochre to orange and red; basal bracts 1–3 mm long and wide, hidden beneath the fig-body, often small and crescentic, brown hairy; body 15–35 × 12–20 mm, oblong, the orifice closed by 3–4 small umbonate apical bracts, not as a flat disk; internal bristles few or none, short. Tepals free. Male flowers scattered, few, with pedicels up to 4 mm long; tepals 2–3; filament bristly at the base; anther wide. Gall-flowers pedicellate; tepals (2–) 3. Female flowers sessile; tepals 3–4. Lamina with cystoliths on both sides, often sparse below; stomata superficial or shallowly sunken.

Distr. India to the Solomons, Queensland.

Var. *glabrata* Corner

Often glabrous or whitish hairy, varying brown hairy. Basal bracts 0·5–1 mm long, crescentic, not brown hairy.

Distr. Java, Sumbawa, Sumba, Flores, Alor, Timor Laut, Solomons.

Ecology. Common in the lowland forest throughout the Solomons.

Collections. Guppy 116, Kajewski 2073, NGF 13408, RSS 2869, T. Wolff 3089.
Only the more glabrous var. *glabrata* has been found in the Solomons.

39. *F. crassiramea* Miq. (figure 7)

Large strangler, without aerial roots from the branches, the basketing root-trunk becoming strongly buttressed; bark pinkish brown. Leaves spirally arranged. Glabrous or the stipules silky or villous. Twigs 5–9 mm thick, brownish ochraceous to dark brown. Stipules 15–30 mm long, coriaceous, hard to waxy-brittle, foliaceous up to 15 cm long and striped yellow and pink on the opening shoots. Lamina 9–23 × 2·5–11 cm, up to 30 × 11 cm on saplings, elliptic to elliptic–obovate, shortly and bluntly acuminate, rarely acute, base cuneate, thinly to firmly coriaceous, smooth, drying brownish areolate beneath;

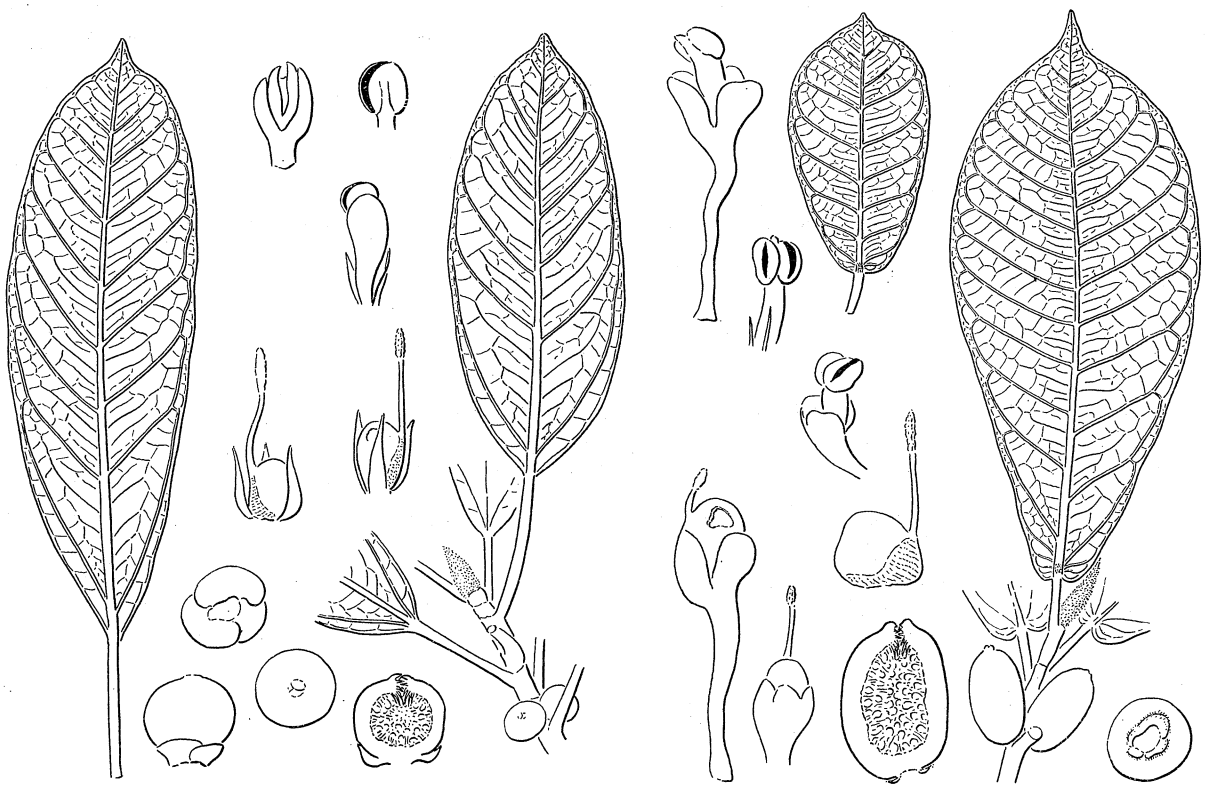

FIGURE 7. Subgen. *Urostigma*. Right, *F. drupacea*, NGF 13408. Left, *F. crassiramea* var. *patellifera*. Leaf and twig × ½, fig × 1, flowers × 10.

lateral veins 6–9 pairs, curved ascending, rather flat, little raised beneath, with 2–6 zig-zag intercostals, the areolae slightly sunken beneath; basal veins 1 (–2) pairs, elongate one quarter to one half the lamina; petiole 20–70 mm long. Figs axillary, sessile, paired, ripening yellow to dark red and blackish; basal bracts 8–12 × 14–18 mm, obtuse, semi-circular, half-enclosing the fig-body, thick, waxy-resinous, yellow-green; body 15–20 mm wide, subglobose, the orifice closed by 2 flat, hard, shining, waxy–resinous apical bracts in a slightly raised disk 4–6 mm wide; internal bristles none. Tepals free. Male flowers scattered, abundant, pedicellate 1–2 mm; tepals (2–) 3; anther broad, dehiscing longitudinally and over the apex. Gall-flowers sessile or pedicellate; tepals 2–3. Female flowers sessile; tepals 3–4. Lamina with cystoliths on both sides; stomata deeply sunken.

Distr. Lower Burma, Thailand Malaya, Sumatra, Java, Bangka, Borneo, Philippines, Talaud Isl.

Var. *patellifera* (Warb.) Corner

Basal bracts 5–8 × 10–15 mm, covering one third of the fig-body 12–15 mm wide, the apical disk 3 mm wide.

Distr. New Guinea, New Britain, Solomons.

Ecology. Common in lowland forest throughout the Solomons.

Kwara-ae. baolafau.

Collections. BSIP 906, 1441, 2005, 2739, 2896, 2970, 3541, 3646, 3825, 5341, 5893; RSS 2850.

This is a common species throughout Malaysia and western Melanesia. The variety, var. *celebensis*, with the biggest figs occurs in Celebes. The basal bracts of the small-fruited var. *patellifera* curve out on drying to form a saucer round the fig-body.

66. *F. subcordata* Bl. (figure 8)

Very large strangler developing a single stout root-trunk, then 2–4 other root-trunks, with many stilt-roots up to 10 m high, without forming a basket-trunk; secondary stilt-roots mostly directed inwards; aerial roots from the branches few or none. Leaves spirally

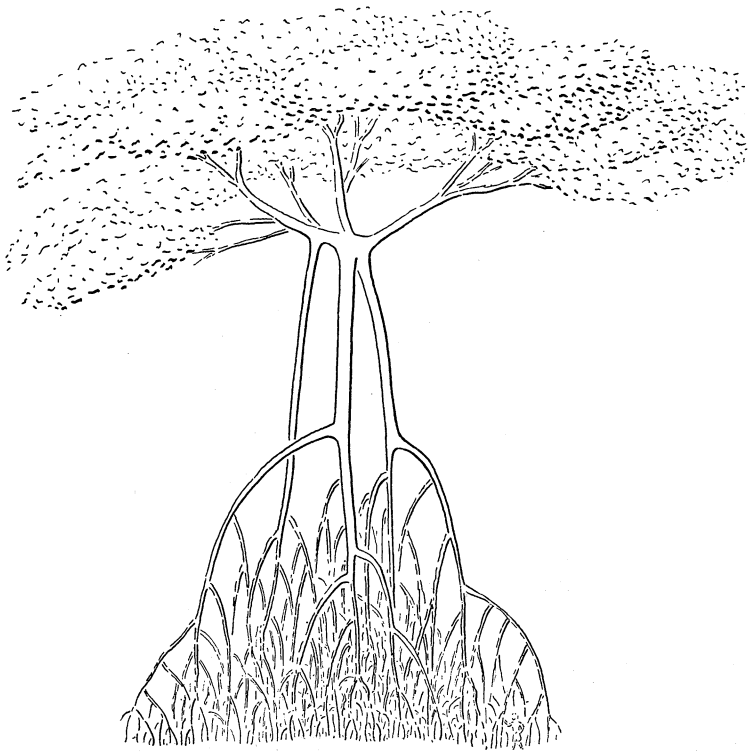

FIGURE 8. Subgen. *Urostigma.* The root-trunk of *F. subcordata*, × $\frac{1}{100}$.

arranged to subdistichous. Glabrous or the twigs, stipules, young leaves, and basal bracts more or less white hairy. Twigs 2–4 mm thick, light ochraceous to pallid brown. Stipules 13–22 mm long, paired. Lamina 8–20 × 3–9 cm, elliptic varying ovate or oblong, shortly

acuminate with the tip up to 15 mm long, base cuneate, but rounded-subcordate in saplings, smooth, thinly coriaceous, drying greenish to light brown; lateral veins 8–16 pairs at a wide angle, distinctly raised on both sides of the dried lamina, the secondary lateral veins almost as prominent, venation as in *F. elastica*; basal veins 1–2 (–3) pairs, short; petiole 13–50 mm long. Figs axillary, sessile, paired, ripening yellow to red and black; basal bracts 2–3, 1·5–5 × 2–6 mm, ovate, obtuse or crescentic, concealed beneath the fig-body, often one missing or the larger two connate; body 17–35 × 14–25 mm, ellipsoid to oblong, the orifice closed by three small flat apical bracts in a disk 2 mm wide; internal bristles none. Tepals 3–4, free. Male flowers scattered, abundant, pedicellate; anther shortly mucronate. Gall-flowers pedicellate, female sessile. Lamina with cystoliths on both sides, or few to none below; stomata slightly sunken.

Distr. Tonkin and Java to New Hebrides.

Ecology. Common in lowland forest throughout the Solomons.

Kwara-ae. baula garanggara.

Collections. BSIP 955, 3109; Kajewski 2607.

This vast strangler is rare in western Malaysia but becomes abundant in New Guinea and eastwards. It is easily recognized in the forest from the enormous trunk of rarely anastomosing roots, like a gigantic pandan, and this feature, coupled with the wide-spreading limbs, makes it a dangerous object to fell. In the herbarium it seems to grade into the large-fruited state of *F. benjamina* var. *nuda*, but this has not the same habit, the leaves are smaller, and the fig is generally pear-shaped. In fact, there is no easier banyan to recognize in the forest than *F. subcordata*.

68. *F. benjamina* L. (figure 9).

Large strangler with few or no aerial roots from the branches, the trunk more or less basketing. Leaves subdistichous. Glabrous or thinly white puberulous. Twigs 1–2 mm thick. Stipules up to 12 mm long, paired. Lamina 3–12 × 1·5–6 cm, elliptic varying lanceolate or ovate, acute or acuminate, base widely to narrowly cuneate, rarely rounded or subcordate, smooth, shining, thinly coriaceous, drying greenish to brownish; lateral veins 6–11 (–14) pairs, with prominent secondary laterals as in *F. subcordata*, raised on both sides of the dried lamina; basal veins 1 (–2) pairs, short; petiole 4–16 mm long. Figs axillary, sessile, paired, ripening yellow to red, rarely pink to purple; basal bracts 2–3, 0·5–1·5 mm long and wide, often crescentic, minute, concealed; body 8–12 × 7–10 mm, ellipsoid, ovoid, obovoid, or subglobose, sometimes with a slight thick pedicel, the orifice closed by three small apical bracts in a disk 1·5–2 mm wide; internal bristles none. Tepals 3 (male) or 3–4, free. Male flowers scattered, abundant, pedicellate; anthers small. Gall-flowers pedicellate, female sessile. Lamina with cystoliths on both sides; stomata superficial.

Distr. India and south China throughout Malaysia to the Solomons, north Australia.

Ecology. Lowland forest and often planted in villages, towns, and roadsides.

Kwara-ae. baula garanggara, haisi hena, sirifena.

Collections. BSIP 1090, 1279, 2895; E. S. Brown 2824, 5080, 8760 ('susumindi', Guadalcanal, San Cristobal); Kajewski 1568, 1858 ('too-varrie', Buin, Bougainville), 2454 ('orme', Berande, Guadalcanal), 2584.

Var. *nuda* (Miq.) Barrett

Fig-body 20–28 × 15–25 mm, subglobose or pyriform with a short thick pedicel; basal bracts minute or one enlarged 2–2·5 × 6–8 mm.

Distr. As var. *benjamina.*

Collections. BSIP 33, RSS 6324.

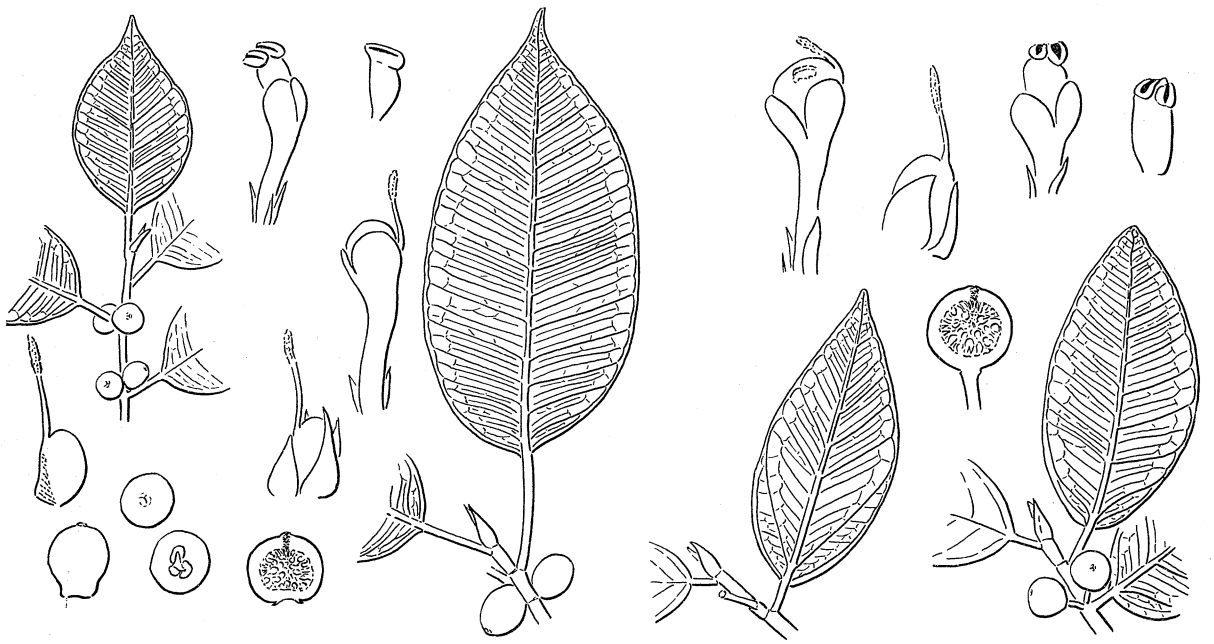

FIGURE 9. Subgen. *Urostigma.* Right, *F. microcarpa* var. *naumanni*, RSS 2658. Left, *F. benjamina*, NGF 13566. Leaf and twig × ½, fig × 1, flowers × 10.

72. *F. microcarpa* Linn. f.

Large, spreading strangler with copious aerial roots from the branches developing into pillar-roots, evergreen; bark grey. Leaves spirally arranged to subdistichous. Glabrous or the twigs, petioles and basal bracts puberulous. Twigs 2–3 mm thick, brown. Stipules up to 15 mm long. Lamina 3–11 × 1·5–6 cm, up to 18 × 8 cm in saplings, elliptic–obovate varying almost lanceolate, often slightly inequilateral, shortly acuminate, acute or obtuse, base widely to narrowly cuneate, smooth, thinly coriaceous; lateral veins 5–9 pairs, at an acute angle, slightly raised below; basal veins 1(–2) pairs, short or reaching one quarter to one half of the lamina; petiole 3–20 mm long. Figs axillary, sessile, paired, ripening pink to purple and black; basal bracts 1·5–3·5 × 1·5–2·5 mm, ovate–lanceolate, obtuse to subacute, often split and gibbous at the base; body 8–13 mm wide, subglobose to pyriform, the plane orifice closed by 2–3 flat apical bracts in a disk 2–2·5 mm wide, finally slightly gaping; internal bristles up to 0·5 mm long, abundant or sparse. Tepals 3(–4), spathulate obovate, free. Male flowers scattered, few, sessile or pedicellate. Gall-flowers pedicellate, female sessile. Lamina with cystoliths on both sides; stomata superficial to shallowly sunken.

Distr. India and south China to New Britain, Queensland, New South Wales.

Ecology. Sea-coasts, tidal river-banks, limestone hills, rarely in lowland inland forest.

Var. *naumanni* (Engl.) Corner (figure 9).

Lamina 3–12 × 1·7–7·5 cm, narrowly to broadly elliptic, base rounded subcordate to cuneate. Fig with a more or less distinct peduncle 1–5 mm long, rarely sessile; basal bracts 2–3 mm long, caducous early; body ripening orange to red; internal bristles few or none.

Distr. Eastern New Guinea, New Britain, New Ireland, Solomons.

Ecology. Sea-shores and inland forest up to 800 m alt., frequent and widespread throughout the Solomons.

Kwara-ae. sususu

Collections. RSS 68, 2658; T. Wolff 3006.

Only var. *naumanni* has been found in the Solomons. It seems not to develop the copious aerial roots which are generally characteristic of var. *microcarpa*, but the species is variable in all respects.

83. *F. glandifera* Summerh. (figure 10)

Large strangler with several stout descending roots developing a basket-trunk, becoming strongly buttressed; bark grey. Leaves spirally arranged. Glabrous or the young leaves and peduncle puberulous. Twigs 3–6 mm thick, brown. Stipules 3–17 cm long, usually very prominent. Lamina 7–26 × 4–13 cm, ovate-elliptic, subacute to shortly acuminate, base rounded to cuneate, coriaceous, smooth, drying brown; lateral veins 17–26(–30)

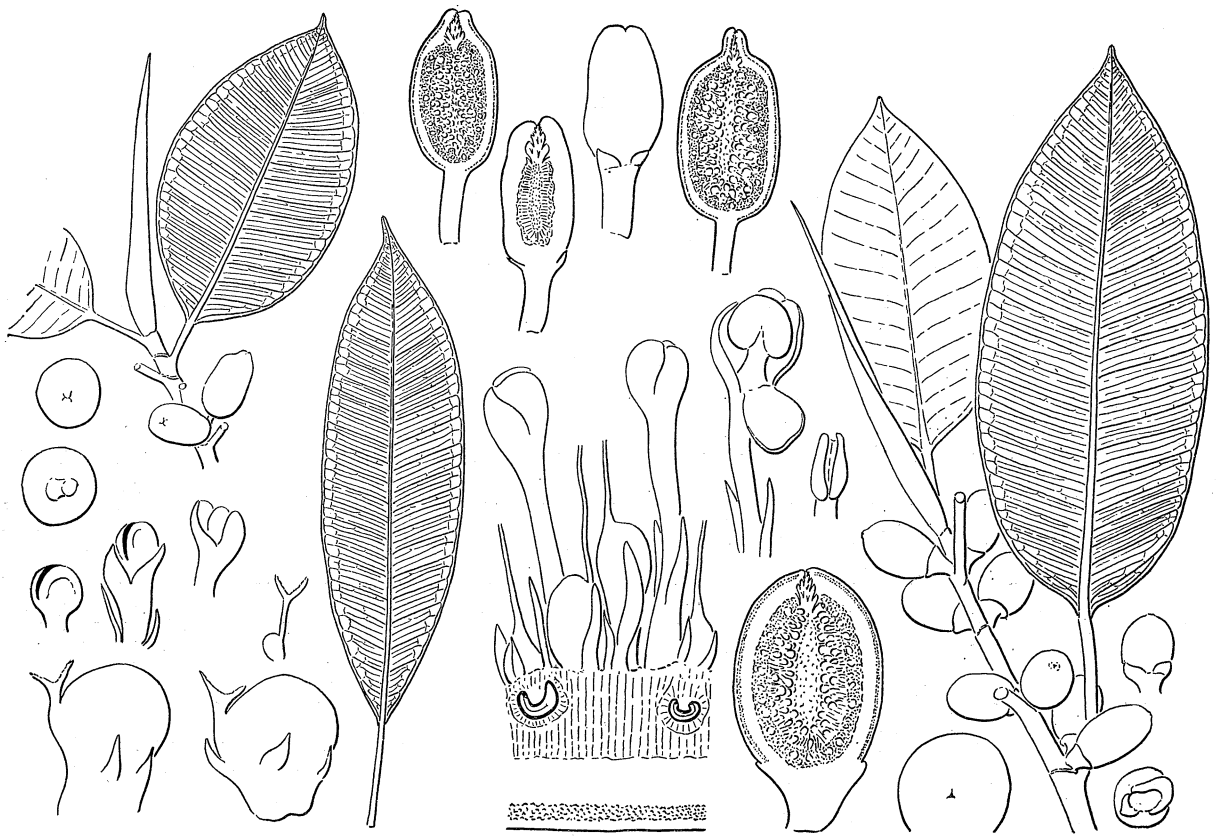

FIGURE 10. Subgen. *Urostigma*. Right and lower centre, *F. glandifera*, RSS 2811. Left, *F. xylosycia* var. *cylindrocarpa*, NGF 13742. Leaf and twig × ½, fig × 1, young figs of var. *cylindrocarpa* (top centre) × 2, flowers × 10.

pairs, distinct on both sides of the dried leaf, venation as in *F. elastica*; basal veins short; petiole 25–70 mm long. Figs axillary, solitary or paired, thickly pedunculate, ripening yellow to red; peduncle 5–10 × 9–16 mm, wider than long, appearing as a thick green cupule with a slight free rim; basal bracts 2, 1·5–3·5 mm long, much broader, early caducous; body 20–35 × 14–18 mm, oblong–ellipsoid, the apex slightly to distinctly mammillate with a minute slit-like orifice, the apical and internal bracts inflexed; internal bristles none; inner fig-wall with or without slight processes to the interior. Male flowers scattered, abundant, pedicellate; tepals 3–4, spathulate, free; stamen 1; anther reniform with crescentic dehiscence, filament short. Gall-flowers sessile to subpedicellate, not immersed in the fig-wall; tepals 3–4, lanceolate, free, red; ovary sessile. Female flowers sessile, with the lower part of the ovary immersed in the fig-wall. Lamina with cystoliths on both sides; stomata deeply sunken.

Distr. Papua, New Britain, Solomons, Santa Cruz Isl., New Hebrides.

Ecology. Sea-coasts and lowland forest, common in the Solomons.

Kwara-ae. baolafau.

Collections. Brass 3274, 3494; BSIP 1051, 1725, 3738, 3957, 4098, 4387, 4402, 5448; E. S. Brown s.n.; Guppy s.n.; Kajewski 1581, 2443, 2777, 3274; RSS 23, 24, 2811; Stoddard 32.

Var. *brachysyce* Corner

Lamina 4–14 × 2–6 cm, elliptic; lateral veins 11–15 pairs. Fig-body 10–15 mm long and wide, subglobose or ovoid; peduncle 2·5–6 mm long, 10–13 mm wide; basal bracts 2, 4–5·5 mm long, densely puberulous, early caducous. Gall- and female flowers with 1–3 tepals; stigma simple.

Distr. South-east Celebes, Territory of New Guinea, Solomons.

Ecology. As var. *glandifera.*

Collections. H. Dissing 2746 (Rennell Isl.).

This is one of the common large banyans of the Solomons, the large orange-red figs superficially like those of *F. drupacea.*

91. *F. obliqua* Forst. f. (figure 11)

Large strangler with few or no aerial roots from the branches. Glabrous or the twigs, stipules and figs puberulous. Leaves spirally arranged. Twigs 2–3·5 mm thick, brown, somewhat flattened. Stipules up to 20 mm long, foliaceous up to 50 mm long on opening shoots. Lamina 4–14 × 1·5–5 cm, elliptic to subobovate or sublanceolate, subacute to subacuminate, base cuneate, thinly to stiffly coriaceous, smooth; lateral veins (6–)8–13(–17) pairs, oblique, faint or slightly raised below in dried leaves, venation as in *F. elastica*; basal veins short; petiole 4–30 mm long. Figs axillary, paired, with a short thick peduncle, ripening orange to red; peduncle up to 4 × 2–3 mm, often slightly expanded up to 4 mm wide at the apex, cupule-like or as a cushion 1 × 2·5 mm, green; basal bracts 2, 3 × 5 mm, covering the young fig, early caducous; body 6–10 mm wide, subglobose, the plane or slightly raised orifice minutely triradiate, the small apical bracts and few internal bracts inflexed; internal bristles none. Male flowers scattered, abundant, or few or none in figs with abundant female flowers; pedicel 0·5–2 mm long; tepals 4–6, free, spathulate;

anther reniform, with oblique or median crescentic dehiscence, filament short; Gall-flowers more or less sessile; tepals 4–5, lanceolate, free, reddish; ovary sessile to substipitate, reddish except at the base and the stylar side; stigma subbifid to entire. Female flowers sessile, as the gall-flowers, the ovary not immersed in the fig-wall. Lamina with cystoliths on both sides or few to none below; stomata deeply sunken.

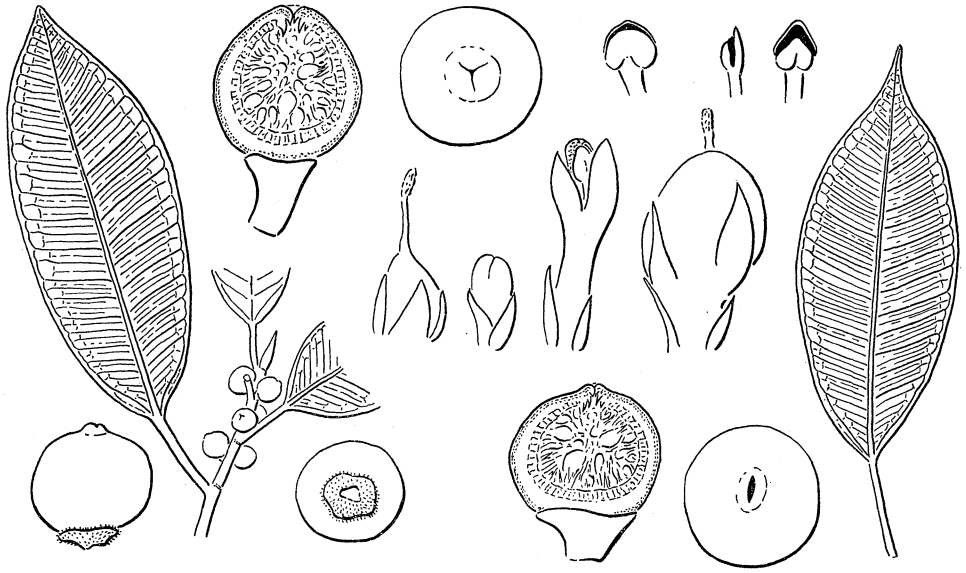

FIGURE 11. Subgen. *Urostigma*. *F. obliqua*; right, RSS 6170, the form in the Solomons with bilabiate fig-orifice; left, Carr 14292 and 15764 from Papua. Leaf and twig $\times \frac{1}{2}$, fig $\times 2$, flowers $\times 10$.

Distr. Celebes, Ternate, New Guinea, Australia, New Caledonia, Loyalty Isl., New Hebrides, Solomons, Fiji, Tonga, Samoa, Niue.

Ecology. Coastal and inland forest.

This species has its greatest abundance in Australia. The specimens from the Solomons differ in several respects, particularly the bilabiate or slit-like orifice of the fig. They appear in fact like diminutive representatives of *F. glandifera*, but they do not have the ovaries of the female flowers sunk in the fig-wall. Typical *F. obliqua* has not been found in the Solomons. As these collections need further inquiry, I give their peculiarities:

Lamina up to 10×4 cm, small, acute to subacuminate. Fig-body 8–9 mm wide (dried), subglobose, the orifice bilabiate; peduncle $2–4 \times 4–7$ mm, broader than long, as a puberulous green cup; basal bracts 2; flowers as in *F. obliqua*.

Distr. Shortlands, New Georgia, San Cristobal.

Ecology. On sea-coasts.

Collections. BSIP 2879, 5827; RSS 6170.

98. *F. xylosycia* Diels (figure 10)

Large strangler, developing a basket-trunk. Leaves spirally arranged to subdistichous. Glabrous or the young parts puberulous. Twigs 3–6 mm thick. Stipules 6–14 cm long, prominent on the opening shoots, 1 cm or less on the dormant buds. Lamina $10–18 \times 2–8$ cm, lanceolate–elliptic to elliptic, more or less acuminate with the tip 8–15 mm long, base cuneate, smooth, thinly coriaceous; lateral veins 15–25(–30) pairs, venation as in

F. elastica; basal veins short; petiole 13–50 mm long. Figs axillary, solitary or paired, ripening yellow to red; peduncle 2–15 × 2–4 mm; basal bracts 3, 0·5–1·5 mm long, obtuse, subpersistent or caducous; pedicel none; body 40–50 × 20–35 mm (30–40 × 17–23 mm, dried), broadly ellipsoid to subcylindric, glabrous or closely puberulous, the orifice closed by 2–3 small inflexed apical scales with umbonate base; internal bristles none; fig-wall with processes into the interior. Male flowers scattered abundant, sessile or pedicellate; tepals 3–4, imbricate, hooded, free, reddish; anther sessile, reniform with crescentic dehiscence. Gall- and female flowers sessile; tepals 3–4, lanceolate to linear or spathulate, thin, free, reddish; ovary sessile, dark red, the female ovary immersed in the fig-wall; style with two long arms. Lamina with cystoliths only on the upperside, or sparse below; stomata superficial or shallowly sunken.

Distr. Eastern New Guinea.

Ecology. Mountain forest, 1000–2000 m.

Var. *cylindricarpa* (Diels) Corner

Fig narrowly cylindrical, smaller, with slender peduncle, ripening yellowish to pink, purple and black, not red; peduncle 3–15 × 1·5–2·5 mm; basal bracts 1–3 × 2–3 mm, ovate, acute, caducous; pedicel 0–4 mm long; body 15–42 × 7–20 mm, the apex umbonate to shortly rostrate 2–5 mm long.

Distr. Eastern New Guinea, Solomons.

Ecology. Lowland and submontane forest up to 1300 m alt., throughout the Solomons.

Kwara-ae. baolafau.

Collections. Brass 3245; BSIP 2274, 2470, 4134; Kajewski 2528 ('garutoo', Uolo, pr. Tatuve, Guadalcanal); NGF 13742; RSS 80.

Only var. *cylindrocarpa* occurs in the Solomons. It can generally be distinguished by the narrower leaf from *F. glandifera*.

Subgen. *Pharmacosycea* Miq.

Key to the species of the Solomons

1. Twigs 10–20 mm thick, stipules persistent. Lamina 30–45 × 13–24 cm. Fig 4–6 cm wide. ..... *F. cristobalensis*
1. All parts smaller. Stipules caducous. Fig ripening red (except *F. polyantha*).
   2. Fig sessile with conspicuous basal bracts 3–7 mm long. Lamina oblong lanceolate, subacute ..... *F. pachystemon*
   2. Fig stalked.
      3. Lamina spathulate with rounded obtuse apex, 8–15 × 3–5 cm. Figs 10–12 mm wide. Glabrous ..... *F. illiberalis*
      3. Lamina elliptic or obovate, subacute to acuminate.
         4. Lamina subacute; lateral veins close. Stipules 2–7 cm long, prominent. Fig pedicellate. *F. hombroniana*
         4. Lamina acuminate; lateral veins spaced. Fig generally pedunculate.
            5. Leaves more or less distichous, often long. Twigs with well developed internodes, ending in a prominent stipule 2–5 cm long. Fig 25–40 mm wide. Glabrous. ..... *F. polyantha*

5. Leaves spirally arranged in compact rosettes.
   6. Twig, underside of lamina, and fig brown villous. Leaf-base subcordate ..... *F. novae-georgiae*
   6. Appressedly hairy to glabrous. Leaf-base rarely subcordate.
      7. Twig 2–4 mm thick, slender. Lamina 8–15 × 2·5–5 cm, base tapered. Fig 6–8 mm wide. ..... *F. smithii*
      7. Twig 4–6 mm thick. Lamina and fig larger; leaf-base rounded or widely cuneate. ..... *F. edelfeltii*

110. *F. hombroniana* Corner (figure 12)

Tree up to 33 m high, buttressed up to 1·3 m, with *Terminalia*-branching, latex rather watery. Leaves spirally arranged. Glabrous or the twigs, petioles, stipules, and underside of the veins pale brown appressedly hairy. Twigs 2–4 mm thick, dark brown. Stipules 20–75 mm long, subulate, curved, caducous. Lamina 7–21 × 3·5–11·5 cm, elliptic, mostly obovate, obtuse or subacute, base cuneate, entire, smooth, subnitid, coriaceous, drying brown; lateral veins 9–13 pairs, close, at a wide angle, 0–4 indistinct intercostals, scarcely raised below in dried leaves; basal veins 1(–2) pairs, short, with 2 basal glands; petiole 5–22 mm long. Figs axillary, paired, glabrous, ripening red to purple; peduncle 0–2 mm long; basal bracts 2–3, 1–1·5 mm long, ovate–acute, appressedly puberulous; pedicel 2–12 mm long; body 10–12 mm wide (dried), subglobose, the plane orifice 1–1·5 mm wide, closed by 2–3 small apical bracts; internal bristles none; sclerotic cells very abundant

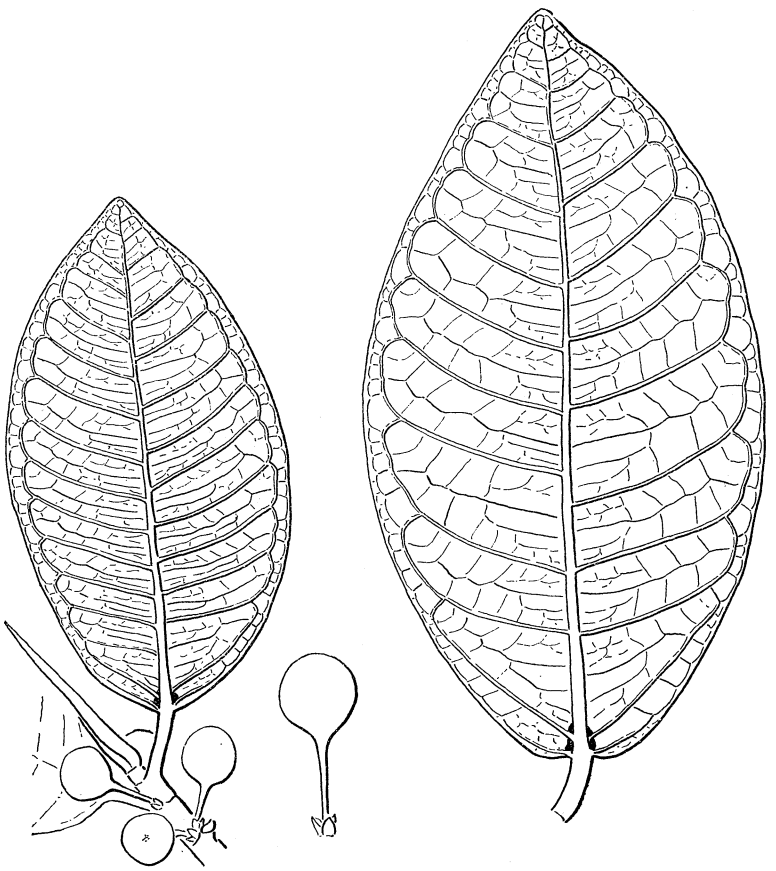

FIGURE 12. Subgen. *Pharmacosycea*. *F. hombroniana*; right RSS 6155A, leaf; left, Brass 28598 (New Guinea). Leaf and twig × ½, fig × 1.

through the thick fig-wall. Perianth red, more or less gamophyllous with 2–3 short lobes, glabrous. Male flowers ostiolar and sessile in 1–2 rows, and scattered pedicellate, equalling or exceeding the gall-flowers; stamen 1. Gall- and female flowers sessile or pedicellate; ovary white; stigma bifid; the fruiting ovaries becoming embedded in sockets in the wall. Leaf with cystoliths only on the lower side.

Distr. Moluccas, New Guinea, Solomons.

Ecology. Canopy tree in lowland forest, rather scattered.

Kwara-ae. lasi, la'ua.

Collections. BSIP 3483, 4481; RSS 6155; Waterhouse B286*a* ('tarimu', 'tuparemu' Siwai, Bougainville).

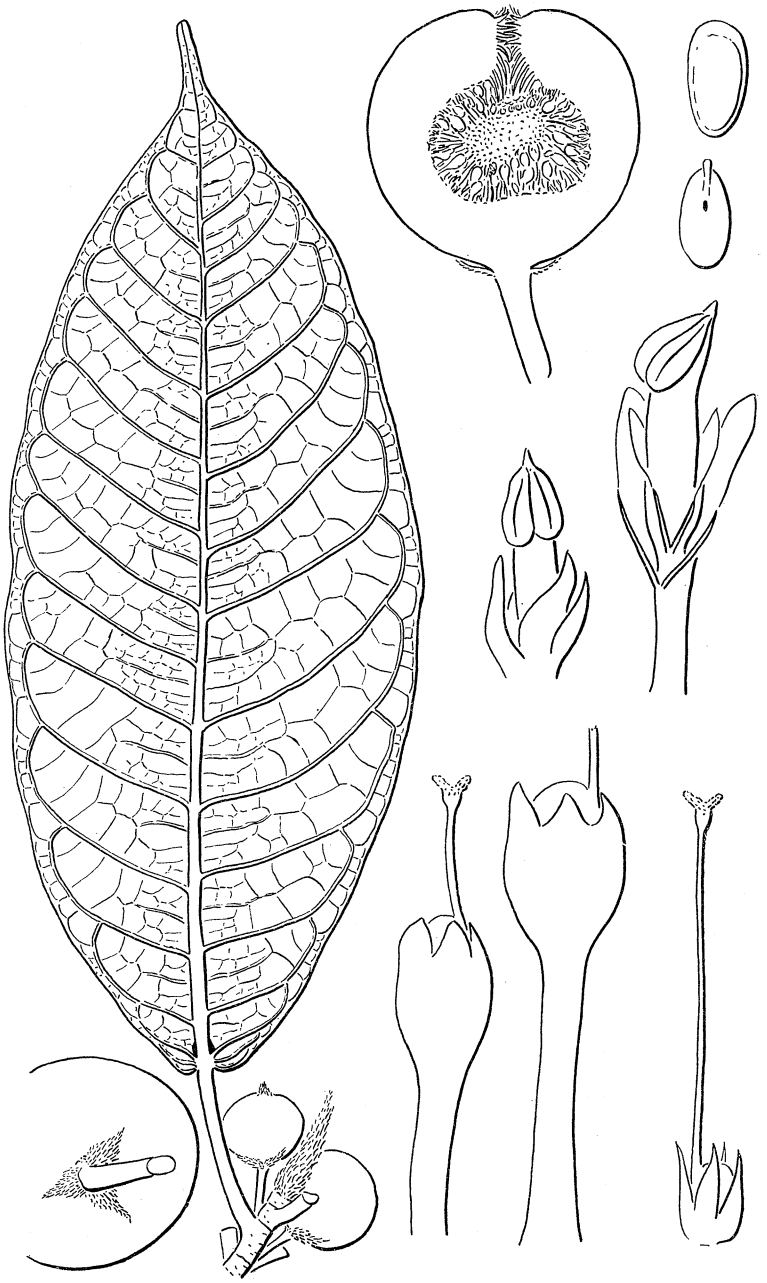

FIGURE 13. Subgen. *Pharmacosycea. F. edelfeltii*, RSS 2. Twig $\times \frac{1}{2}$, fig $\times 1$, flowers $\times 10$.

111. *F. edelfeltii* King (figures 13, 14)

Tree up to 24 m high, shortly buttressed, with *Terminalia* branching; latex white, copious. Leaves spirally arranged. Twig, stipule, petiole, underside of midrib, and fig thinly appressedly brown hairy, varying almost glabrous. Twig 3–6 mm thick, brown.

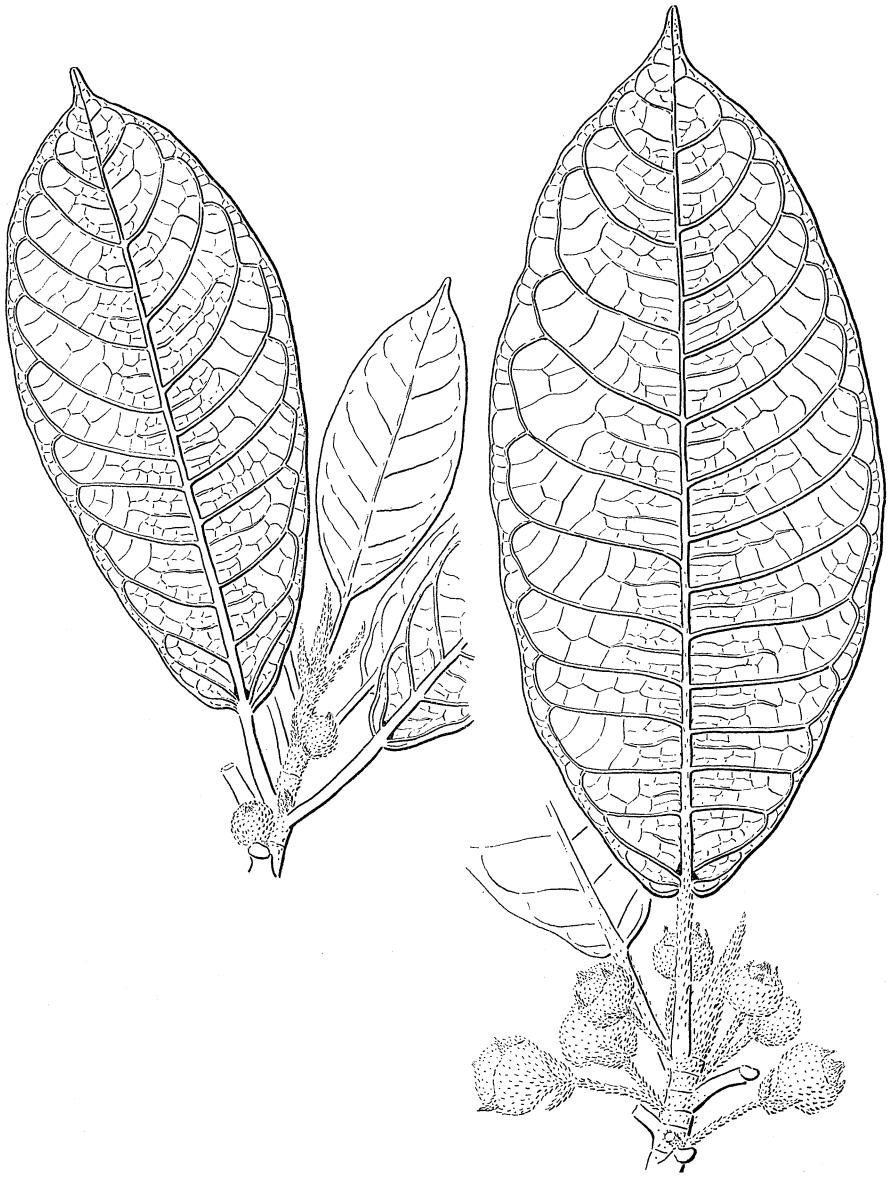

FIGURE 14. Subgen. *Pharmacosycea*. *F. edelfeltii*; right, var. *bougainvillei*, NGF 13570; left, var. *edelfeltii* RSS 167; $\times \frac{1}{2}$.

Stipule 12–30 mm long, caducous. Lamina 13–36 × 5·5–14 cm, elliptic, acuminate with the tip up to 18 mm long, base cuneate (rounded subcordate in saplings), rather stiffly subcoriaceous, smooth, drying brown; lateral veins 9–15 pairs, strongly raised beneath, 2–9 intercostals raised beneath; basal veins 1(–2) pairs, short, with 2 basal glands; petiole 7–50 mm long. Figs axillary, paired, ripening deep red, shining; peduncle 1–15 × 3–6 mm, stout, reddish; basal bracts 3, 1–3 mm long, ovate acute, appressedly hairy; pedicel none; body 30–40 mm wide (15–25 mm, dried), subglobose, the apical bracts projecting in a

slight cone; internal bristles none; fig-wall thick, white, with copious sclerotic cells. Perianth of (2–) 3–4 tepals, often extensively gamophyllous. Male flowers scattered, pedicellate, a few sessile, occasionally with abortive pistillode. Stigma shortly bifid. Lamina with cystoliths only on the underside.

Distr. New Guinea, Solomons.

Ecology. Widespread in lowland forest up to 800 m alt., throughout the Solomons.

Kwara-ae. malifo.

Collections. BSIP 699, 5656; RSS 2, 167, 1238, 2656, 6180.

Var. *bougainvillei* Corner (figure 14)

Figs pedicellate with longer peduncles and basal bracts, and usually with 3(–4) lateral bracts; peduncle 5–28 mm long; basal bracts 5–9 mm long, ovate–lanceolate, acute; pedicels up to 5 mm long; lateral bracts 3–6 mm long, more or less in a whorl about the middle or in the distal half of the body. Twigs up to 7 mm thick. Often more densely hairy.

Distr. Bougainville Isl.

Ecology. Lowland and mountain forest up to 1200 m alt.

Vern. mono, kekera (Siwai).

Collections. NGF 13559, 13568, 13570; Waterhouse B313.

In leaf and fig this species resembles *F. polyantha*, but the manner in which the leaves are carried gives to their trees a very different appearance. The fig-stalk of *F. edelfeltii* varies considerably and seems to be shorter in New Guinea material. Whether var. *bougainvillei* is a distinct species remains for enquiry. Some small-leafed collections tend towards *F. smithii*.

111A. ***F. novae-georgiae*** sp.nov. (figure 15)

Arbor usque 18 m alta, habitu *F. edelfeltii*, trunco basim versus usque 1 m alato. Ramuli, stipulae, petioli, syconia, et costa media (subtus) pilis fulvis v. subferrugineis 0·5–1 mm longis laxe patentibus hispido-villosi. Ramuli 4–5 mm crassi. Stipulae usque 25 mm longae, caducae. Lamina 15–40 × 6·5–15 cm, obovata acuminata basi rotundata v. anguste cordata; costis lateralibus utrinsecus 9–12, basalibus 3–4 brevibus; petiolo 20–40 mm longo. Syconia axillaria, *ca.* 20 mm lata; pedunculo 2–12 mm longo; bracteis basalibus 2·5–4 mm longis; setis internis nullis; cellulis scleroticis copiosis. Tepala 4–5. Flores masculi dispersi; stamen 1. Insulis Solomonensibus. BSIP 1275, typus, L.

Tree up to 18 m high, buttressed to 1 m, with *Terminalia*-branching; latex white. Leaves spirally arranged. Twigs, stipules, petioles, underside of main veins, and figs hispid–villous with fulvous to subferruginous spreading hairs 0·5–1 mm long; underside of the other veins villous with shorter and paler hairs. Twigs 4–5 mm thick. Stipules up to 25 mm long, caducous. Lamina 15–40 × 6·5–15 cm, obovate with a subacute acumen 9–18 mm long, base rounded and narrowly cordate; lateral veins 9–12 pairs, strongly raised beneath; intercostals 3–7, slightly raised beneath; basal veins 3–4 pairs, short, with 2 basal glands; petiole 20–40 mm long. Figs axillary, closely fulvous–villous; peduncle 2–12 mm long; basal bracts 2·5–4 mm long, appressedly hairy; body 20 mm wide (dried), without lateral bracts, the orifice concealed by the hairs; internal bristles none; sclerotic cells abundant in the endocarp. Tepals 4–5, longer than the ovaries, shortly gamophyllous in the female flowers. Male flowers disperse, more or less pedicellate; tepals free, spathulate, imbricate;

stamen 1. Female flowers sessile to pedicellate, the tepals lanceolate in the sessile flowers, spathulate in the pedicellate; style bifid. Seed *ca.* 1·5 mm long. Leaf with cystoliths only on the underside.

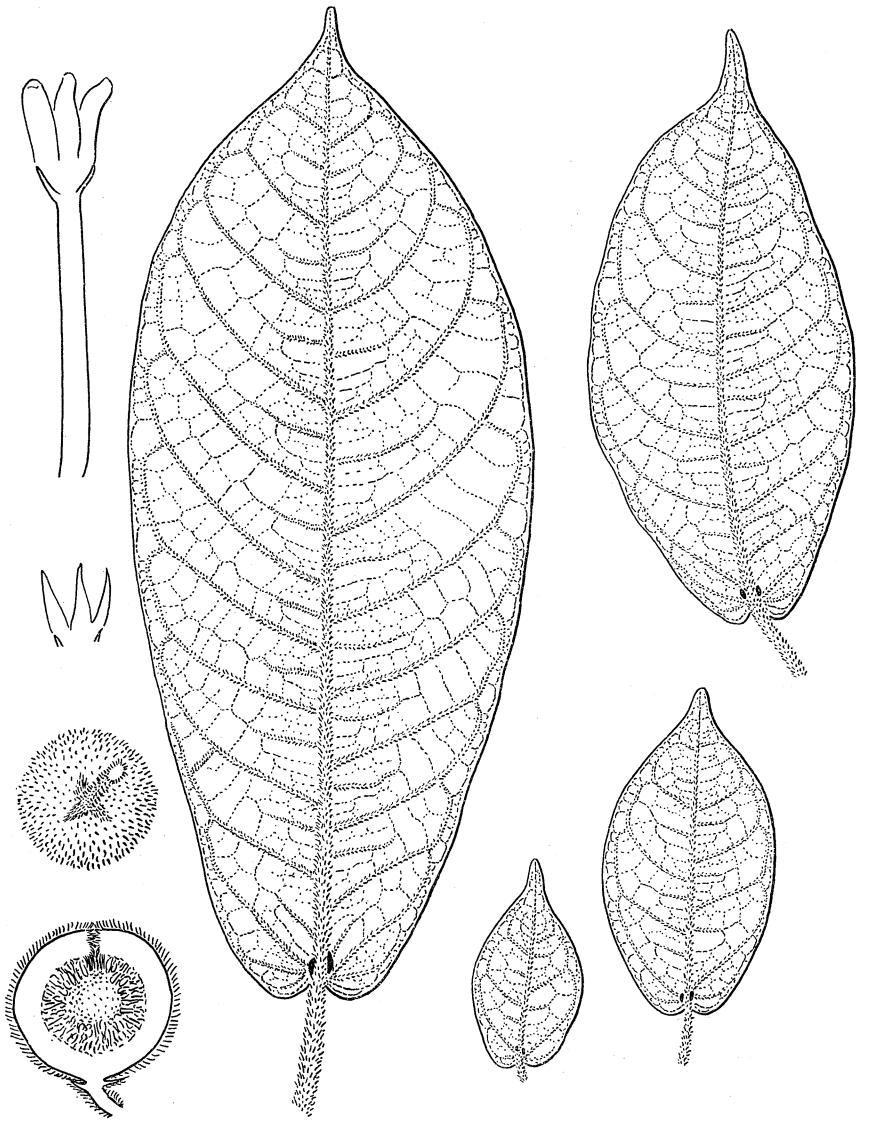

FIGURE 15. Subgen. *Pharmacosycea. F. novae-georgiae*; leaves, RSS 1172, $\times\frac{1}{2}$; BSIP 1275, fig $\times$ 1, perianth of sessile and pedicellate flowers $\times$ 10.

Distr. New Georgia, Kolombangara, north-east Guadalcanal, Vangunu.

Ecology. In lowland and hill forest.

Kwara-ae. malifo.

Collections. BSIP 1275, Vangunu, in steep hill forest, leg. T. C. Whitmore 17 Dec. 1962, type, Leiden; BSIP 2785, Rere river, north-east Guadalcanal; RSS 1172, Kolombangara river, in *Terminalia brassii* forest.

This may briefly be described as a very brown hairy *F. edelfeltii* with more cordate leaf-base, but in size of leaf it is approaching *F. cristobalensis*. Young shoots show a transition from small to large leaves below the compact rosette and these reduced leaves have the form of those of the New Caledonian *F. mutabilis*.

111B. ***F. cristobalensis*** sp.nov. (figure 16)

Arbor usque 12 m alta, trunco basim versus haud alato, ramis laxis paucis, foliis spiraliter dispositis. Ramuli stipulae petioli et syconia pilis fulvidulis usque 1 mm longis dense appresse hirsuti, glabrescentes. Ramuli crassissimi 10–20 mm. Stipulae 25–50 mm longae persistentes. Lamina 30–45 × 13–24 cm, obovata, breviter acuminata, basim versus angustata cordata, integra levis glabra; costis lateralibus utrinsecus 15–18, basalibus 4–5 brevibus; petiolo 25–40 mm longo, crasso. Syconia axillaria 4–6 cm lata (2·5–4 cm st. sicc.), maturitate flavescentia; pedunculo 0–5 mm longo; bracteis basalibus 3(–4), 7–11 mm longis lanceolatis; pariete 5–8 mm crasso, cellulis sclerotics paucis; setis internis nullis. Tepala 5(–6), libera. Flores masculi dispersi pauci; stamen 1. Stigma breviter bifidum. Insulis Solomonensibus. RSS 6119, San Cristobal, typus, K.

Tree up to 12 m high, not buttressed; branches rather few, lax, spreading, terminating in large rosettes of spirally arranged leaves; latex white, copious. Twigs, petioles, stipules, and young figs densely appressedly fulvous hairy, the hairs up to 1 mm long, glabrescent. Twigs 10–20 mm thick, with indistinct internodes, the wide pith often hollowed by ants. Stipules 25–50 mm long, broadly lanceolate–subconic, persistent. Lamina 30–45 × 13–24 cm, obovate, shortly acuminate, narrowed to the cordate base, entire, subcoriaceous, smooth, glabrous; lateral veins 15–18 pairs, strongly inarching, strongly raised below; intercostals 6–11, slightly raised below; basal veins 4–5 pairs, short, with 2 basal glands; petiole 25–40 mm long, stout, short. Figs axillary, paired or solitary, glabrescent, ripening greenish yellow, concealed by the leaf-bases and stipules; peduncle 0–5 mm long, inconspicuous, stout; basal bracts 3(–4), 7–11 mm long, lanceolate–triangular, appressedly hairy, persistent; body 4–6 cm wide (2·5–4 cm, dried), sessile, depressed subglobose, without lateral bracts, the small orifice at first concealed by a small cone of hairs, gaping up to 6 mm wide at maturity and pervious to the fig-centre; wall 5–8 mm thick, with few sclerotic cells; internal bristles none. Flowers with glabrous white pedicels; tepals 5(–6), red, free, as long as or longer than the ovaries and stamen. Male flowers scattered, rather sparse, pedicellate; tepals oblong, acute; stamen 1, without pistillode. Female flowers sessile with narrow lanceolate tepals and developing seeds, or pedicellate with oblong tepals and developing seeds or insects; ovary and style white, glabrous; stigma very shortly bilobed. Seed oblong–lenticular, narrowly keeled, smooth.

Distr. San Cristobal.

Ecology. Common undergrowth tree in steep hill forest at the Warahito-Pegato confluence, lowland.

Kwara-ae. malifo.

Collection. RSS 6119, Aug. 1965, type, at Kew.

This is the most pachycaulous species of the subgenus in the Old World. The very large leaves in compact rosettes and the persistent stipules collect the falling debris of the forest. Ants often make their abodes among the leaf bases and bore galleries into the soft pith, but the plants are not myrmecophilous in the sense of providing ready made galleries. The figs are concealed, large as they are, and trees appear sterile. As those of *F. polyantha*, they do not turn red. The insects escape before the fig ripens and softens. Then flying foxes eat the ripe figs and carry them off to their roosting places. The general aspect of the trees is that of *F. edelfeltii*, but with more massive and fewer parts so that the crown is rather open and the stature less. The species has not been found anywhere else in the Solomons and,

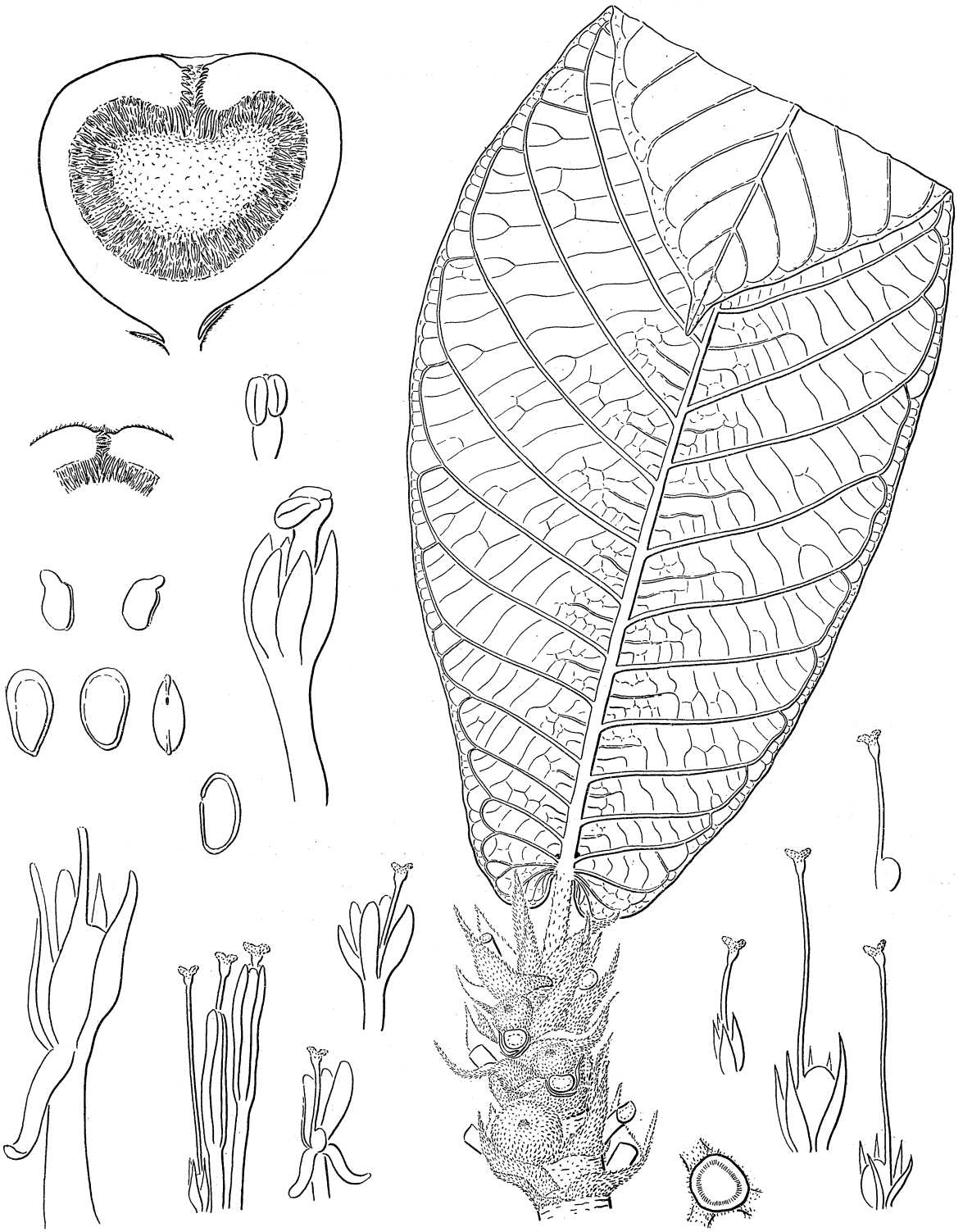

FIGURE 16. Subgen. *Pharmacosycea*. *F. cristobalensis*, RSS 6119. Twig $\times \frac{1}{2}$, fig $\times 1$, flowers (young and full-grown) $\times 10$.

as it was found early in the course of the Royal Society Expedition, I looked for it in all other islands that were visited.

The alliance of *F. cristobalensis* is clearly with *F. edelfeltii*, but six species of New Caledonia have to be taken into account. Among these *F. crescentioides* and its close ally *F. heteroselis* have almost as massive twigs and leaves, which are longer in *F. crescentioides*, the cordate leaf-base, and the persistent stipules. Their figs are smaller with shorter basal bracts and they have abundant internal bristles and sclerotic cells; moreover, their male flowers are ostiolar with two stamens. The little known *F. auriculigera* is smaller in all its parts and approaches *F. asperula*; it has merely three to four tepals and ostiolar male flowers, but the fig-wall has few or no sclerotic cells and the internal bristles, though abundant, are minute. These seemingly trivial matters of the fig-wall are resolved by *F. habrophylla*, *F. dzumacensis*, and *F. leiocarpa*, for they have few or no internal bristles or sclerotic cells; however, they are much less pachycaulous with caducous stipules, longer petioles, bistaminate male flowers, and extensively gamophyllous perianth. *F. cristobalensis*, in fact, connects ser. *Nervosae* and ser. *Austrocaledonicae* structurally and geographically.

112A. ***F. illiberalis*** sp.nov. (figure 17)

Arbor usque 30 m alta, trunco basim versus usque 1 m alato, glabra, foliis spiraliter dispositis. Ramuli usque 3 mm crassi. Stipulae usque 13 mm longae, caducae. Lamina 8–15 × 2·7–5 cm, anguste obovata v. spathulata obtusa, basim versus angustata, integra, levis; costis lateralibus utrinsecus 7–10, intercostis 0–2, basalibus 1 brevibus; petiolo 8–20 mm longo. Syconia axillaria, 10–12 mm lata, subellipsoidea, maturitate rubra; pedunculo 3–6 mm longo; bracteis basalibus 3, 1–1·5 mm longis; pedicello 0·5–2 mm longo, distincto; setis internis nullis; cellulis scleroticis copiosis, vix evolutis. Tepala 4 libera. Flores masculi dispersi et ostiolares, pauci; stamen 1 (–2). Stigma bifidum. Insulis Solomonensibus. RSS 20, typus, K.

Tree up to 30 m high, buttressed to 1 m; latex white, rather thin. Leaves spirally arranged. Glabrous or the basal bracts and peduncles puberulous. Twigs 3 mm thick. Stipules up to 13 mm long, caducous. Lamina 8–15 × 2·7–5 cm, lanceolate–obovate to spathulate, obtuse (the midrib very shortly dichotomous at the apex), tapered to the narrowly cuneate base, entire, coriaceous, smooth, drying greyish green; lateral veins 7–10 pairs, raised below in the dried leaf; intercostal 0–2, feebly developed; basal veins 1 pair, short, with 2 basal glands generally confluent with a gland-patch at the top of the petiole on its abaxial side; petiole 8–20 mm long, rather stout, becoming brown flaky. Figs paired, axillary, crimson; peduncle 3–6 mm long; basal bracts 3, 1–1·5 mm long, ovate acute, persistent; pedicel 0·5–2 mm long; body 10–14 × 10–12 mm, smaller on drying, subglobose to ellipsoid, smooth, the slightly sunken orifice with 3 minute apical bracts; internal bristles none; sclerotic cells frequent in the endocarp but little differentiated. Tepals 4, white then pink, subspathulate, as long as the ovary. Male flowers ostiolar and disperse, few, more or less pedicellate; stamen 1, rarely 2. Female flowers sessile or pedicellate; ovary white; stigma bifid. Lamina with cystoliths only on the underside.

Distr. San Cristobal, ?Santa Cruz Isl. (Vanikoro).

Ecology. In hill forest *ca.* 500 m alt. between the Warahito and Pegato rivers, rather common.

Collections. RSS 20, type at Kew; ? BSIP 1627, Vanikoro, (lamina 12–20 × 7–10 cm narrowed to a subcordate base, ? sapling).

In its reduction, this comes near to *F. ihuensis* of New Guinea, *F. kjellbergii* of Celebes, and *F. vieillardiana* of New Caledonia, but all these have pedicellate figs, as in *F. hombroniana*, not pedunculate. Then *F. vieillardiana*, which is very similar, has ostiolar male flowers with, usually, two stamens and the gall-flowers have a gamophyllous perianth, *F. kjellbergii* (one stamen, gamophyllous perianth) and *F. ihuensis* (two stamens) have more or less acute leaves. The collection from Vanikoro is fertile with figs and flowers as in *F. illiberalis*, but the leaf is much larger.

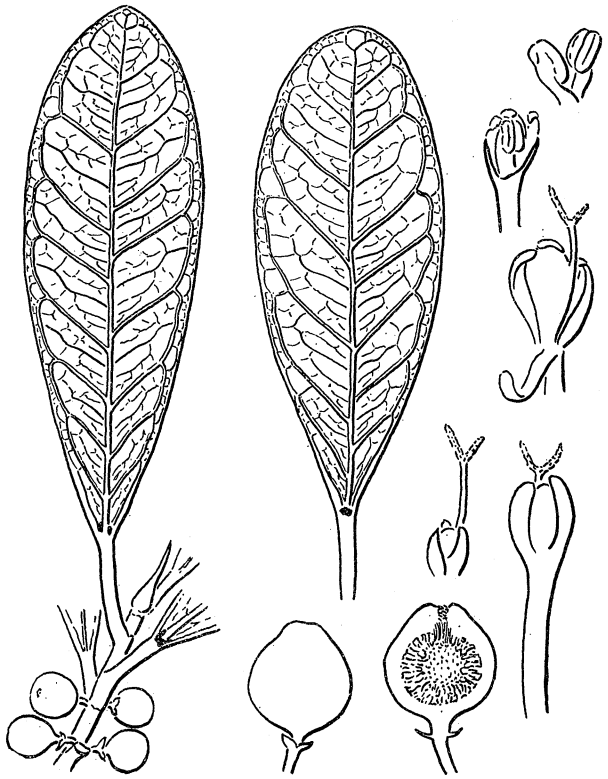

FIGURE 17. Subgen. *Pharmacosycea. F. illiberalis*, RSS 20. Leaf and twig × ½, fig × 1, flowers × 10.

113. *F. polyantha* Warb. (figure 18)

Tree up to 45 m high, bole up to 28 m long, buttressed to 5 m high, glabrous; latex white, copious. Leaves laxly spirally arranged to sub-distichous. Twigs 2–4 mm thick, brown. Stipules 20–50 mm long, prominent, curved, caducous. Lamina 7–32 × 5–13 cm, elliptic or slightly ovate, varying oblong, subacute to subacuminate, base rounded or widely cuneate to subcordate, thinly coriaceous, smooth, drying brown; lateral veins 9–15 pairs, slightly raised beneath in dried leaves, 3–7 intercostals; basal veins 2(–3) pairs, short, with 2 basal glands; petiole 7–30 mm long. Figs axillary, solitary, glabrous, ripening green to yellowish; peduncle 1–15 mm long; basal bracts 3, often scattered, 1 mm long, ovate, acute; pedicel 0–7 mm long; body 25–40 mm wide (18–30 mm, dried), subglobose, the plane orifice with several small apical bracts; internal bristles none; sclerotic cells few to abundant, mostly thin-walled, the fig-wall 2–5 mm thick. Tepals 2–3 in male and gall-flowers, 3–4 in female, more or less extensively gamophyllous, red, glabrous; pedicels dark

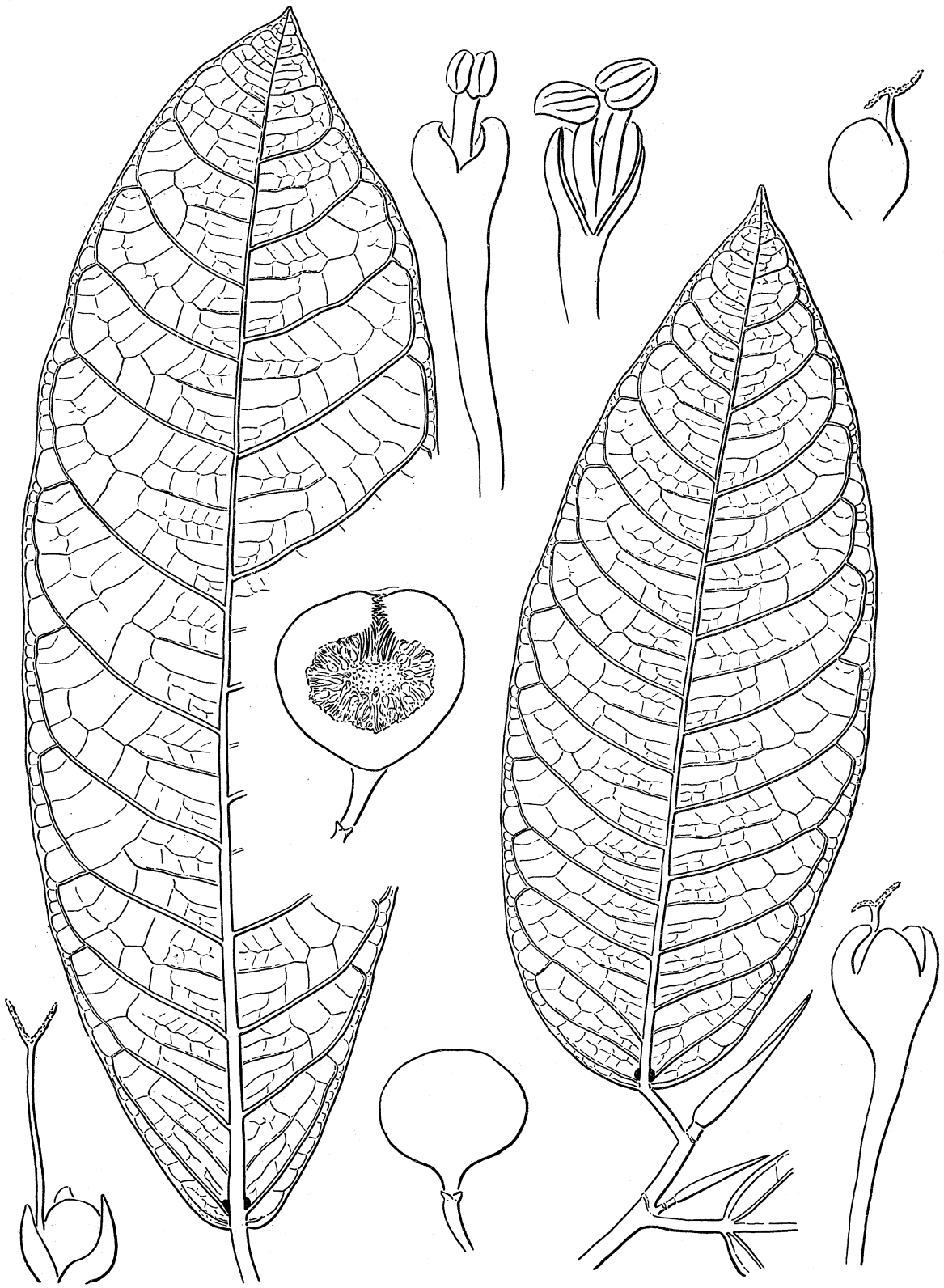

FIGURE 18. Subgen. *Pharmacosycea*. *F. polyantha* (Corner s.n., Lae, New Guinea).
Leaves (left, from lower branch; right, from upper branch) and twig $\times \frac{1}{2}$, fig $\times 1$, flowers $\times 10$.

red. Male flowers scattered, pedicels up to 4·5 mm long, mostly exceeding the gall-flowers; stamens 1–2. Gall-flowers pedicellate. Female flowers sessile; stigma bifid. Lamina with cystoliths only on the lower side.

Distr. Philippines, Moluccas, New Guinea, New Ireland, New Britain, Solomons.

Ecology. Canopy tree of the lowland forest throughout the Solomons, frequent.

Kwara-ae. lasi.

Collections. BSIP 2721, 3848, 4405; RSS 1174.

Because of its size and the abundance of climbers and epiphytes which grow on it, it is difficult to collect more than fallen leaves and figs from this species. The largest tree seen in the Solomons during the Royal Society Expedition was *ca.* 40 m high and buttressed to 5 m high. It is, in fact, the largest tree, other than the stranglers, in the genus and it is one of the great contributions of Melanesia to forest botany.

120. *F. pachystemon* Warb. (figure 19).

Tree up to 20 m high, sometimes flowering as a riverside shrub 2–3 m high; latex white. Leaves laxly spiral or subdistichous. Glabrous or the stipules and the underside of the midrib of young leaves appressedly brownish hairy. Twigs 2–4 mm thick, brown. Stipules

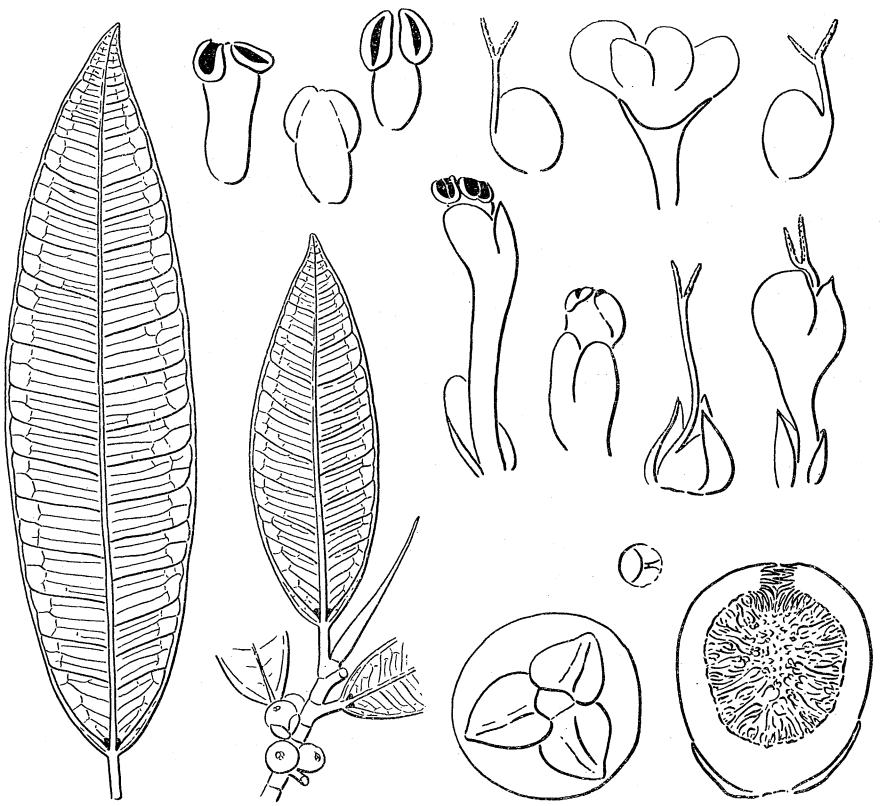

FIGURE 19. Subgen. *Pharmacosycea. F. pachystemon*; Brass 23925, New Guinea, twig and sapling leaf $\times \frac{1}{2}$; Carr 12416, New Guinea, fig $\times 1$, flowers $\times 10$.

20–55 mm long, subacute, caducous. Lamina 5–21 × 1·5–6 cm, oblong–lanceolate, shorter and subovate–lanceolate in old trees, lanceolate–elliptic on saplings, subacute to subacuminate, base cuneate, coriaceous, smooth, entire, drying rich brown; lateral veins

11–19 pairs, at a wide angle, 9–11 pairs in the smaller upper leaves, not raised in the dried leaf, without intercostals, the secondary veins almost as well developed as the primaries; basal veins 1 pair, short, with 2 basal glands; petiole 4–13 mm long, short, thick, blackish in dried leaves. Figs axillary, paired, sessile, ripening yellow to red; basal bracts 3, 3·5–7 mm long, very variable, occasionally one to 11 mm; body 14–18 × 12–16 mm (10–14 mm wide, dried), subglobose or ellipsoid, the plane orifice closed by 3 small apical bracts in a disk 2·5 mm wide; internal bristles none; sclerotic cells abundant in the fig-wall. Tepals 3–4, red, free or more or less gamophyllous. Male flowers scattered, abundant, pedicellate; stamen 1. Gall-flowers pedicellate, rather scarce. Female flowers sessile; stigma bifid. Lamina with cystoliths only on the underside.

Distr. New Guinea, New Ireland, New Britain, Solomons.

Ecology. Lowland forest, commonly on riversides and stony riverbeds, apparently not common in the Solomons.

Kwara-ae. bubulia.

Collection. BSIP 4353, San Cristobal, Wairaha river.

140. *F. smithii* Horne (figure 20)

Small or slender tree up to 15 m high. Leaves spirally arranged in upturned rosettes, each rosette projected by the elongation of 2–3 internodes with abortive leaves. Glabrous or the twigs, stipules, and petioles rather closely appressedly hairy with fawn brown hairs 1–1·5 mm long, glabrescent. Twigs 2·5–4 mm thick, light brown. Stipules 7–12 mm long, caducous or subpersistent on young shoots. Lamina 8–17 × 2·5–5 cm, narrowly elliptic, elliptic–obovate, or lanceolate, obtusely acuminate with the tip up to 15 mm long, base attenuato-cuneate, entire, thinly coriaceous, smooth, drying light brown; lateral veins 7–9 (–12) pairs, slightly raised below in dried leaves, 0–1 intercostals; basal veins 1 pair, short, with 2 basal glands; petiole 4–14 mm long. Figs axillary, solitary or paired, glabrous, ripening orange to red; peduncle 6–15 mm long, very slender; basal bracts 3, 0·5–1 mm long, ovate-acute, caducous; pedicel 0–3 mm long; body 7 × 6 mm (5–6 mm wide, dried), subglobose, the plane orifice closed by 3 small apical bracts; internal bristles none; sclerotic cells abundant in the middle and inner part of the fig-wall. Tepals 3, more or less joined, especially in the male and gall-flowers, red, glabrous. Male flowers ostiolar, sessile, few disperse and pedicellate; stamen 1. Gall-flowers pedicellate, female sessile; ovary yellowish white; stigma shortly bifid. Lamina with cystoliths only on the underside.

Distr. Fiji, Solomons.

Ecology. Frequent small tree in the forest up to 1200 m alt., throughout the Solomons.

Kwara-ae. aitia, maragona, bubulia.

Collections. BSIP 1452, 1547, 1887, 2908, 3463, 3577, 4412; Kajewski 2660; NGF 13573; RSS 1239.

This is a slender tree with subverticillate leaves resembling *F. verticillaris* (sect. *Adenosperma*) and can be distinguished by the much less coriaceous leaves with distinct venation, as well as by the colour of the figs. The species has a more robust form with thicker twigs and larger leaves and figs in New Hebrides and Fiji. It is this form, var. *robusta*, which links with *F. granatum* of New Hebrides.

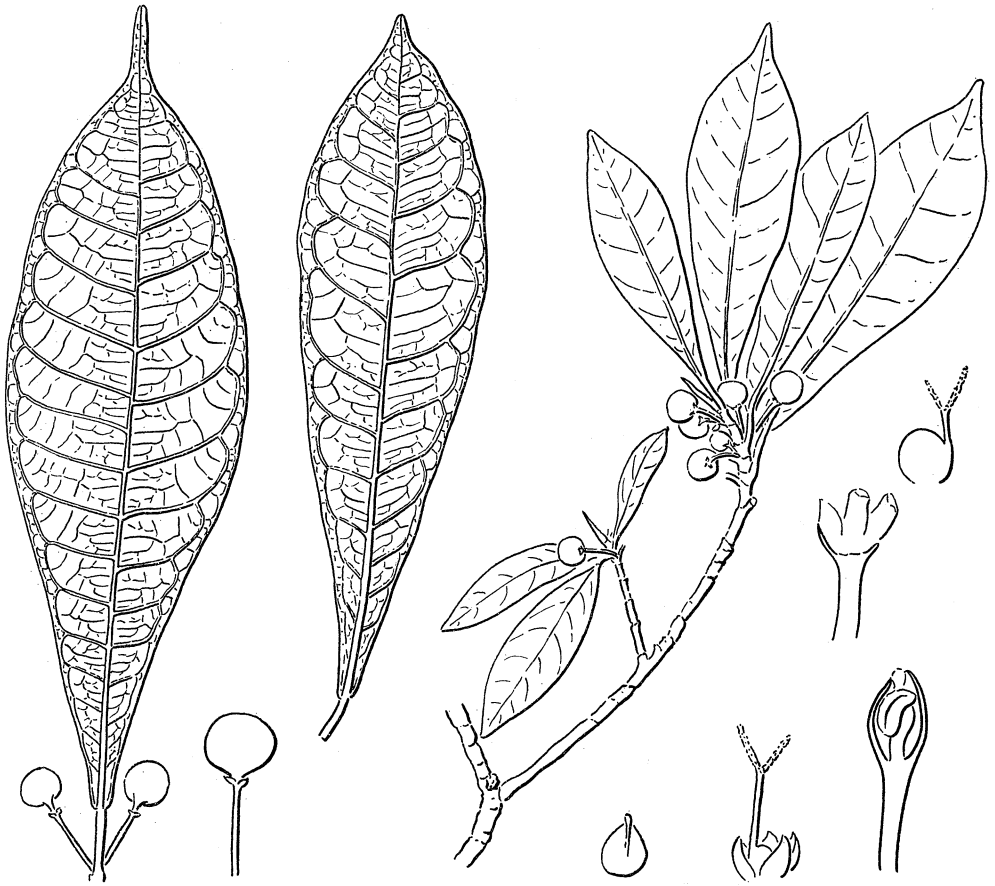

FIGURE 20. Subgen. *Pharmacosycea*. *F. smithii*; right, NGF 13573; left, RSS 1239. Leaf and twig $\times \frac{1}{2}$, fig $\times 1$, flowers $\times 10$.

Subgen. *Ficus* sect. *Rhizocladus* Endl.

For the key to the species, see Group A, p. 57.

211. *F. pantoniana* King

Large climber with distichous leaves. Glabrous or thinly appressedly brown hairy at first, or with a few spreading hairs 1–2 mm long at the nodes. Twigs 1·5–2·5 mm thick. Stipules up to 12 mm long, conical, appressedly hairy or glabrous. Lamina 6–16 × 2–6·5 cm, ovate-elliptic, subacute to acuminate, base subcordate to widely cuneate, entire, smooth, thinly subcoriaceous, drying brown; lateral veins 4–7 pairs, 2–8 intercostals, slightly raised below; basal veins 1(–2) pairs, not elongate or reaching one third to one half of the lamina, with two basal glands; petiole 7–22 mm long. Figs axillary and on short leafless twigs or burrs on the branches and main stem, minutely brown scurfy, glabrescent, ripening rose-red to scarlet, then purple-black; peduncle 0–10 mm long; basal bracts 3, 1·5–2 mm long, ovate, subacute, early caducous; pedicel 2–10 mm long; body 12–17 mm wide (dried), subglobose, subpyriform, or broadly ellipsoid, sometimes with a slight equatorial thickening and subtruncate apex, the orifice small and slightly to deeply sunken, sometimes with a raised border; internal bristles few, minute, or none; sclerotic cells abundant in the fig-wall. Flowers sessile and pedicellate; tepals 3(–4), free or slightly joined, lanceolate–oblong, glabrous, red. Male flowers in several rings round the orifice;

stamens 2, with mucronate anthers and shortly connate filaments. Gall- and female flowers with red pedicels; ovary white to pale reddish, sessile; style glabrous, simple. Seed 1·5–2 mm long, narrowly keeled all round. Lamina with cystoliths on both sides.

Distr. Moluccas, New Guinea, New Britain, Solomons.

Ecology. In lowland forest.

Collections. NGF 16416, Bougainville Isl., Taki village, 6° 10′ S, 155° 20′ E.

This is a fairly common species in New Guinea, but only this one collection is known from the Solomons. It may be limited to Bougainville, for it was not seen during the Royal Society Expedition to the other islands. It can usually be distinguished from the other, more or less glabrous, climber with medium-sized leaves, namely *F. nasuta*, by the narrower and less acuminate, even almost obtuse, leaf.

226. *F. baeuerleni* King (figure 21)

Large root-climber. Twigs, petioles, underside of main veins, and figs lanuginous or villous with appressed or spreading, more or less flexuous, pale fulvous hairs 1–3 mm long, shorter on the smaller veins. Twigs 2·5–4 mm thick. Stipules up to 12 mm long, appressedly hairy. Lamina 10–25 × 4–11 cm, elliptic with acuminate tip 10–20 mm long, base subcordate to rounded or broadly cuneate, subcoriaceous, drying rather pale brown, the veins not or scarcely impressed above, the areolae brown beneath; lateral veins 5–9 pairs, often with glands in the axils, to 9 intercostals, slightly raised below; basal veins 2–3 (–4) pairs, reaching one third to one half the lamina, with 2 small basal glands; petiole 2–18 mm long. Figs axillary, solitary or paired, ripening rose-red; peduncle 2–8 mm long; basal bracts early caducous; pedicel 4–7 mm long; body 23–30 mm wide (17–20 mm, dried), subglobose, often subumbonate round the depressed orifice with hairy canal; internal bristles few, minute, or none; fig-wall without sclerotic cells. Male flowers ostiolar in several rows, pedicellate, tepals red; stamens 2 with large mucronate anthers. Gall- and female-flowers sessile or pedicellate, with red tepals. Seed 1·5–1·7 mm long, oblong, compressed, narrowly keeled all round. Lamina with cystoliths on both sides.

Distr. New Guinea, Solomons.

Ecology. Frequent in lowland forest throughout the Solomons.

Collections. NGF 13750, 13771, 13772.

Var. *vulcaniformis* Corner

Fig-body with a prominent conical apex leading by a glabrous tube to the deeply sunken apical bracts. Often less hairy, or with shorter hairs.

Distr. New Guinea, New Britain, Solomons.

Collections. Brass 3458, Kajewski 2618 ('alafasu', Guadalcanal), RSS 209.

This is the only large-leafed and closely hairy climbing fig in the Solomons. It appears to be evergreen.

243. *F. phatnophylla* Diels

Slender root-climber. Twigs and petioles thinly hairy with short, straight, erect or oblique, brown hairs up to 0·5 mm long, glabrescent. Twigs 1·5–2·5 mm thick. Stipules up to 6 mm long, often thinly appressedly hairy. Lamina 8–12 × 2·5–4·5 cm, ovate to elliptic with an acuminate tip up to 12 mm long, base rounded subcordate to widely

cuneate, stiffly coriaceous, subscabrid beneath; lateral veins 5–7 pairs, 0–1 intercostals, not raised beneath in the dried leaf; basal veins 1 pair, short, with 2 small basal glands; petiole 4–10 mm long. Figs axillary, paired, red; peduncle 1·5–2 mm long, thinly puberulous; basal bracts 1 mm long, ovate, subacute, thinly appressedly hairy, persistent; body

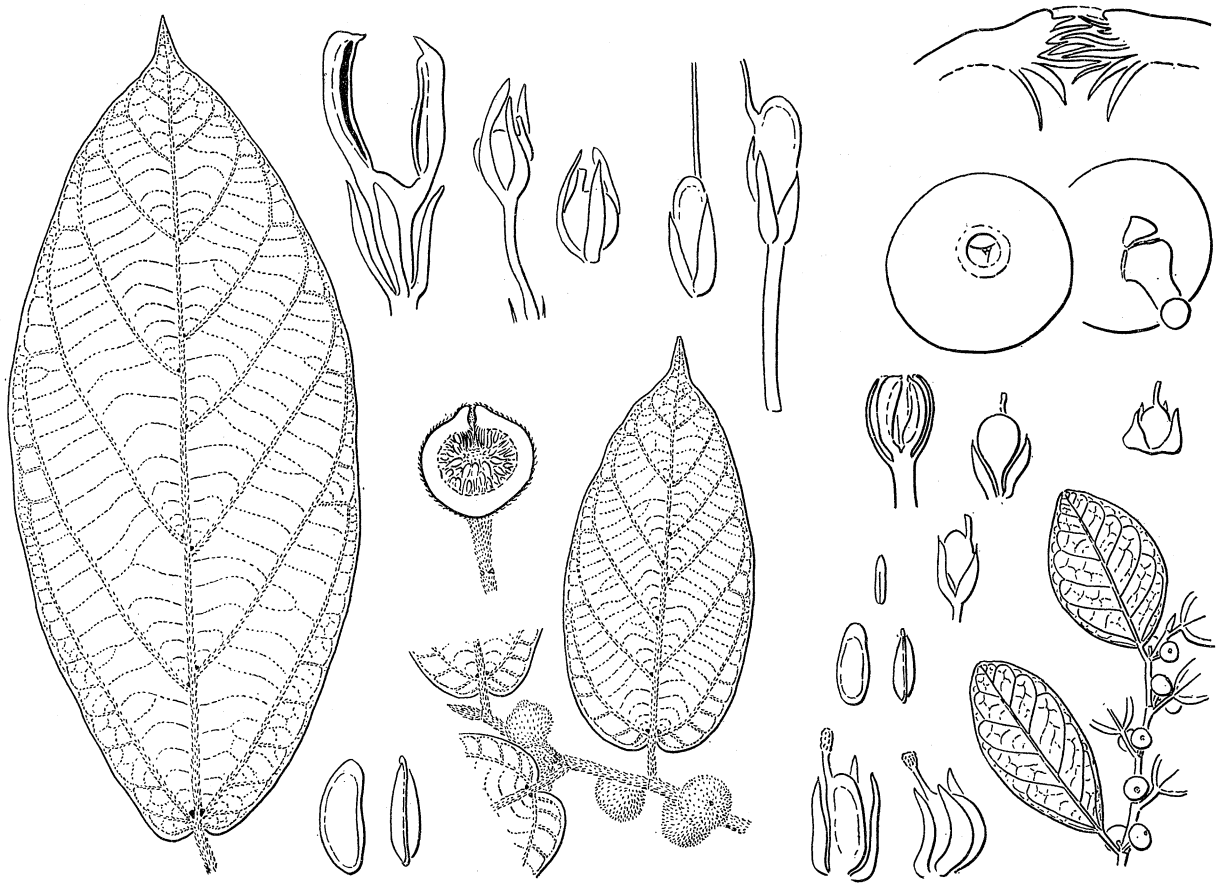

FIGURE 21. Sect. *Rhizocladus*. Right, *F. agapetoides* var. *solomonensis*, RSS 74, fig ×2. Left, *F. baeuerleni*, RSS 209, fig ×1. Leaf and twig ×½, flowers ×10.

4–5 mm wide (dried) subglobose, glabrous the orifice slightly sunken; internal bristles none; sclerotic cells frequent in the endocarp of seed-figs. Male flowers ostiolar in 1–2 rows sessile or shortly pedicellate; tepals 3, free or shortly joined, red; stamens 2, anthers not mucronate, filaments free. Gall- and female flowers sessile with 3 free, red tepals. Seed 1 mm long, oblong, compressed, slightly keeled all round. Lamina with cystoliths on both sides.

Distr. New Guinea, Solomons.

Ecology. Lowland and montane forest.

Collection. BSIP 3531, Kiu, south-west Malaita.

This is an inconspicuous species that seems to be rare wherever it occurs.

245. *F. agapetoides* Diels var. *solomonensis* Corner (figure 21)

Tall, slender root-climber, the main stems up to 5 cm thick, evergreen. Glabrous or the stipules and basal bracts with puberulous edges. Twigs 1–2 mm thick. Stipules up to 7 mm

long, caducous. Lamina 3–7 × 1·5–4 cm, elliptic or obovate, obtuse, base cuneate, rather stiffly coriaceous; lateral veins 4–6 pairs, 0–2 intercostals; basal veins 1 pair, short; petiole 3–12 mm long; bathyphylls on lower creeping stems 5–12 × 3–6 mm, elliptic or lanceolate, obtuse, membranous, symmetrical, with 2–3 pairs of lateral veins, the petiole 1–3 mm long. Figs axillary, paired red, 5–7 mm wide, the orifice not or slightly sunken; peduncle 1–3 mm long; basal bracts 1 mm long, ovate, caducous at maturity; internal bristles none; sclerotic cells in a thin layer in the fig-wall. Flowers as in *F. phatnophylla*; tepals 3–4. Lamina with cystoliths on both side; stomata deeply sunken.

Distr. New Guinea, Solomons.

Ecology. Common throughout the Solomons in lowland forest to 800 m alt.

Kwara-ae. aidiu, diu.

Collections. E. S. Brown 1168, BSIP 3992; Kajewski 1946, 2654; NGF 13574, 13575, 13576; RSS 74, 175, 1173, 6175, 6306; Waterhouse 95 (Yale Museum Forestry 22699), B 201, 749 ('kung', 'lusko', Siwai, Bougainville).

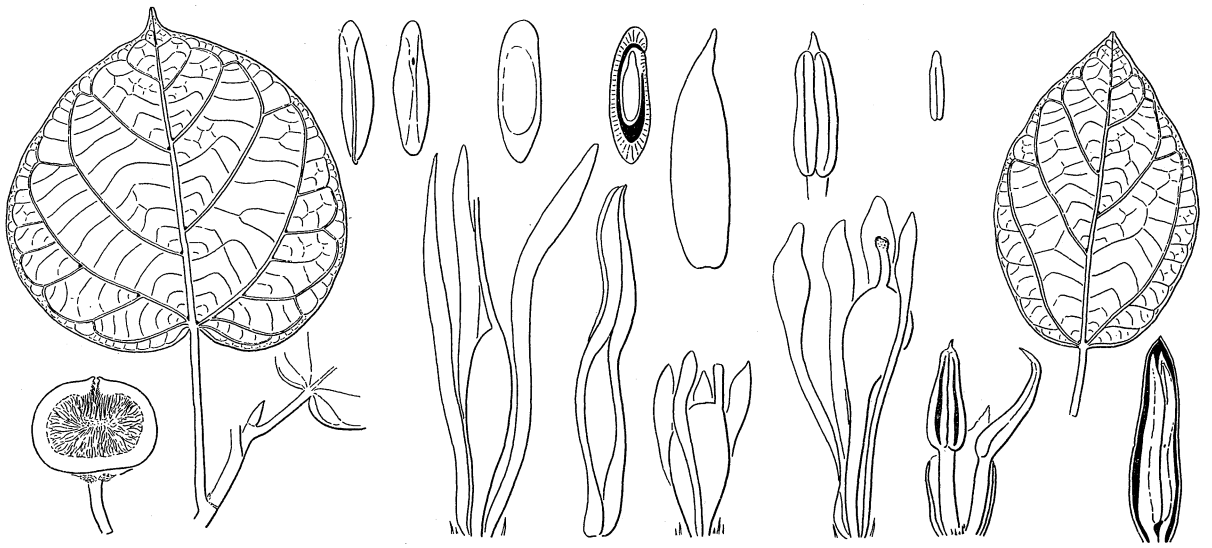

FIGURE 22. Sect. *Rhizocladus*. *F. nasuta*, Clemens 1170 (New Guinea).
Leaf and twig × ½, fig × 1, flowers × 10.

This variety differs from the little known var. *agapetoides* of New Guinea in having larger leaves with sunken stomata, smaller figs, and caducous basal bracts. It is the commonest climbing fig in the Solomons, easily recognized from the small obtuse leaves.

255. *F. nasuta* Summerh. (figure 22)

Tall deciduous root-climber. Leaves laxly spirally arranged. Glabrous except for the brown sericeous stipules and basal bracts, or the twigs, petioles, and figs brown velutinate, sometimes the underside of the main veins thinly appressedly hairy, glabrescent. Twigs 3 mm thick. Stipules up to 12 mm long. Lamina 8–15 × 6–13·5 cm, ovate or suborbicular, shortly acuminate, the base deeply cordate to rounded or widely cuneate, entire, thinly coriaceous, smooth; lateral veins 4–5 (–6) pairs, often with an axillary gland, to 8 intercostals, distinctly raised beneath in dried leaves; basal veins 2(–3) pairs, reaching one

half to two thirds of the lamina, with 2 basal glands; petiole 13–50 mm long. Figs axillary, paired, ripening greenish yellow (? to purple) on the bare twigs; peduncles 10–25 mm long; basal bracts 2–4 mm long, ovate, obtuse to subacute, persistent; body 25–35 mm wide (17–25 × 20–30 mm, dried), subglobose or subpyriform, the small orifice slightly umbonate (dried); internal bristles abundant to sparse or none, brown to white, 0·5–1 mm long; sclerotic cells abundant in the wall of gall-figs, absent from seed-figs. Male flowers scattered, abundant, sessile; perianth almost wholly gamophyllous, conical; stamens 2, mucronate. Gall- and female flowers sessile; tepals 4, free, linear-spathulate, reddish, much longer than the ovary; ovary dark red-brown and rather long-stalked in the gall-flowers, sessile or shortly stalked and white in the female; styles glabrous. Seed 2·5–3 × 0·8–0·9 mm, oblong, slightly keeled all round. Leaf with cystoliths only on the lower side.

Distr. Solomons, Santa Cruz Isl.

Ecology. In lowland forest, up to 300 m alt., frequent.

Kwara-ae. diu, kualo-ufi.

Collections. E. S. Brown 1149; BSIP 158, 1301, 2946, 3835, 5755, 5791, 5926; Kajewski 2094; RSS 1169; Waterhouse B133 ('tukopuri', Siwai, Bougainville).

This species has a glabrous variety, var. *glabrata*, in New Guinea. The nose-like umbo at the end of the fig is absent from the fresh fig, but develops more or less on drying.

Subgen. *Ficus* Sect. *Sycidium* Miq. subsect. *Sycidium*

Key to the species of the Solomons

1. Leaves spirally arranged or decussate, long-petiolate, symmetric. Figs usually pedicellate without a collar of basal bracts, generally becoming cauliflorous.
   2. Brown or purple-brown hairy.
      3. Hairs bristly, irritant, purple-brown. Lamina 20–40 × 6–20 cm. Fig 12–20 mm wide.... *F. porphyrochaete*
      3. Not irritantly hairy. Lamina and fig smaller. ..... *F. gul*
   2. Hairs white or yellowish, or merely scabridulous.
      4. Twigs 3–8 mm thick. Lamina 6–20 cm wide, usually cordate. Figs 25–40 mm wide, stalks 2–5 cm long. ..... *F. copiosa*
      4. Smaller in all parts. Lamina usually cuneate. ..... *F. wassa*
1. Leaves distichous, short-petiolate, usually asymmetric.
   5. Tepals white. Figs axillary, with copious internal bristles to 1·5 mm long. Small trees or bushes.
      6. Densely hispid-scabrid. Lamina ovate, large, very unequal at the base, with a broad cordate auricle concealing the petiole. Fig 20–25 mm wide, with prominent hispid apical bracts. Ysabel Isl. ..... *F. gryllus*
      6. Softly hairy. Lamina not or slightly asymmetric. Figs smaller, long-stalked, pendent on the underside of the twigs, usually solitary. ..... *F. chrysochaete*
   5. Tepals red or pink, often fading white. Figs often cauliflorous; internal bristles usually shorter.
      7. Lamina 15–40 × 5–14 cm, oblong, deeply cordate equally or unequally. Fig 25–50 mm wide. ..... *F. oleracea*
      7. Lamina and figs smaller.

8. Large buttressed tree; latex watery. Figs axillary and on the twigs behind the leaves. ... *F. melinocarpa*

8. Smaller trees with white or yellowish latex.

9. Figs solitary, pendent on stalks 10–30 mm long from the underside of the twigs, also cauliflorous. Lamina usually with a small auricle on the acroscopic side towards the twig-apex. ..... *F. imbricata*

9. Without such character.

10. Glabrous, smooth. Leaf lanceolate-elliptic with 11–16 pairs of lateral veins; basal veins short. ..... *F. arawaensis*

10. Hairy or scabrid. Lateral veins fewer.

11. Lamina ovate, strongly asymmetric or unilaterally cordate. Figs hispidulous when young. ..... *F. erinobotrya*

11. Lamina not so asymmetric. Figs scabridulous.

12. Very harshly scabrid. Figs axillary and on the twigs behind the leaves. Lamina elliptic, shortly acuminate. ..... *F. trachypison*

12. Less scabrid. Figs axillary to cauliflorous from the base of the trunk. Lamina narrowly elliptic, long acuminate. ..... *F. pseudowassa*

292. *F. porphyrochaete* Corner (figure 23)

Tree up to 13 m high; latex slightly milky; leaves spirally arranged. Twigs, petioles, and figs hispid with stiff, irritant, spreading, purple-brown hairs 1–4 mm long (1–3 mm on the veins and figs), paler and often appressed on the underside of the main veins, shorter and spreading on the reticulations. Twigs 5–7 mm thick. Stipules 15–35 × 6–12 mm, persistent or caducous in old trees, appressedly hairy. Lamina 20–40 × 6–20 cm, elliptic to obovate, the acuminate tip up to 35 mm long, base rounded to subcordate, denticulate, membranous, scabrid on both sides, harshly above, drying greyish green to brownish; lateral veins 6–8 pairs, curved ascending, raised below, with large axillary glands; 6–12 intercostals raised below; basal veins 3 pairs, reaching one quarter to half the lamina, with 2 basal glands; petiole 25–80 mm long. Figs axillary and in large clusters (up to 60 figs) on the trunk and main branches on leafless branched twigs up to 7 cm × 5–10 mm, without internodal elongation, ripening brown to red, purple setose; pedicels 3–20 mm long, short in the axillary figs, with 1–3 scattered lateral bracts 1–2 mm long; body 18–30 mm wide (8–12 mm, dried), with a few scattered lateral bracts 1–3 × 3–5 mm, apical bracts 1–1·5 mm, erect, crowded, the outer with recurved tips; internal bristles short, sparse to abundant, rarely none, brown; no sclerotic cells in the fig-wall. Tepals 4–6, dark red with white border, free, oblong, glabrous to hispidulous. Male flowers ostiolar in 1–2 rings, sessile or stalked; stamen 1, not mucronate, with or without a pistillode. Gall- and female flowers sessile or with white, glabrous or hairy, pedicels up to 2·5 mm long; ovary sessile, whitish; style glabrous. Seed 0·8–1 mm long, subcarinate, smooth, the hilum slightly prominent. Lamina with cystoliths on both sides or mostly below.

Distr. Papua, Solomons.

Ecology. In lowland forest to 1200 m alt., chiefly by streams.

Kwara-ae. amote, mamote.

Collections. RSS 2378, 2453; Waterhouse 146 ('mumukumita', Siwai, Bougainville), 236 ('lupo', New Georgia).

This is like a large, very bristly state of *F. gul*, but it is by no means so common.

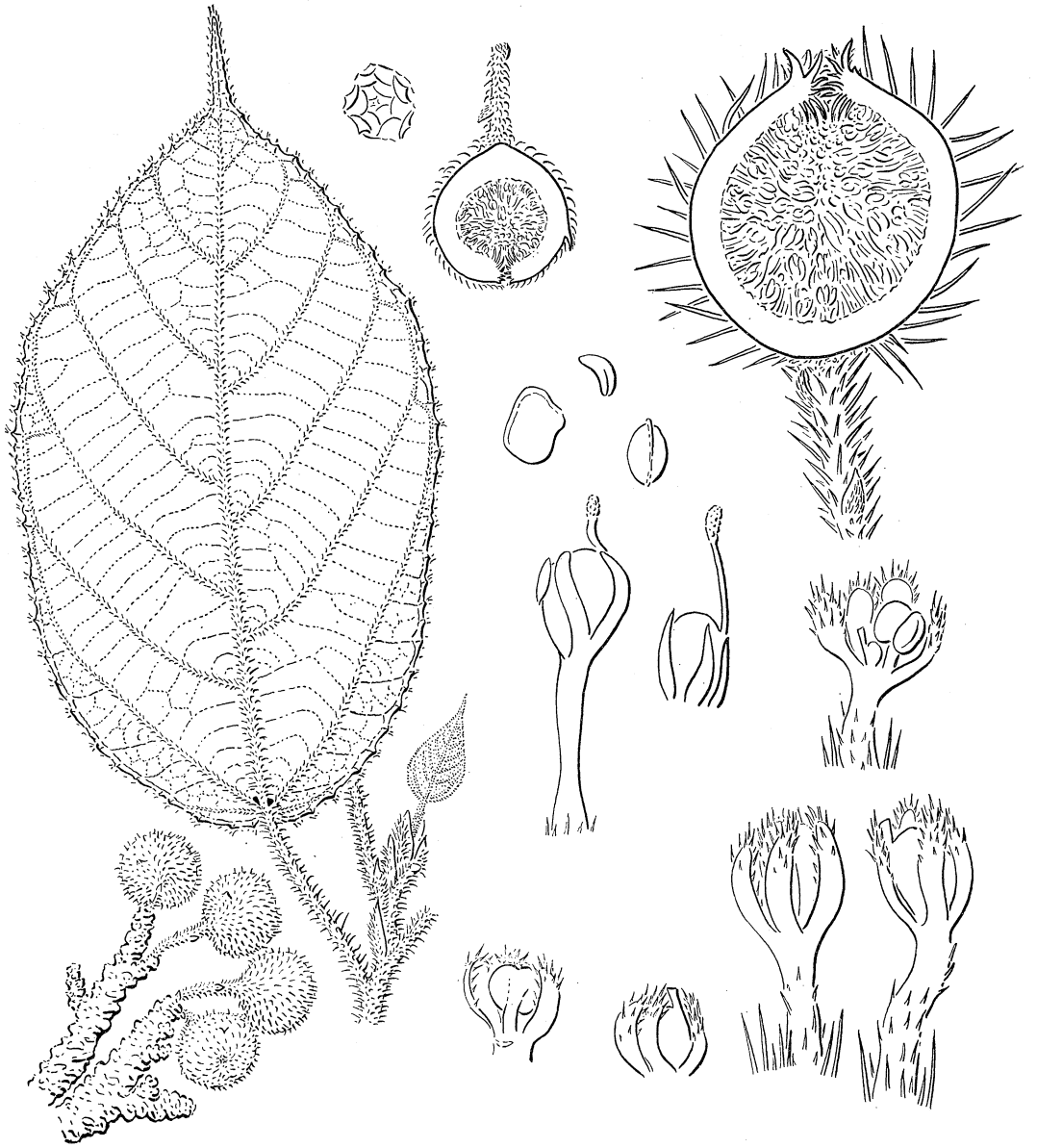

FIGURE 23. Sect. *Sycidium* ser. *Phaeopilosae*. *F. porphyrochaete*; RSS 2378, leaf, twig, and cauliflorous fruiting twigs × ½, fig-section × 1, orifice × 3, male and gall-flowers × 10; Brass 24162, fig-section × 3; Carr 16381 (Papua), female flower with glabrous tepals and seeds × 10.

293. *F. gul* Laut. et K. Schum. (figure 24)

Tree up to 20 m high, not buttressed, possibly deciduous; latex rather scant; leaves spirally arranged. Young shoots and figs shortly brown hairy to brown villous with hairs 1–3 mm long, glabrescent, at least the upperside of the leaf; all parts scabridulous. Twigs 2–4 mm thick. Stipules up to 9 mm long, caducous. Lamina 7–18 × 3·5–9·5 cm (up to 26 × 12 cm in saplings), elliptic or obovate, the acuminate tip 6–28 mm long, base rounded subcordate to cuneate, denticulate to subentire, membranous, scabrid on both sides, drying greenish grey to brownish; lateral veins 4–9 pairs, raised below; 3–8 intercostals, rather lax, slightly raised below; basal veins 1–2 (–3) pairs, not elongate or reaching one quarter to half the lamina, with 2 basal glands; petiole 7–80 mm long (up to 120 mm in

saplings); sapling leaf with 2–4 pinnate lobes on each side. Figs axillary and in clusters of 3–8 on the twigs below the leaves, glabrescent, scabridulous, ripening dull purple red; pedicel 3–12 (–18) mm long, with 1–3 small, scattered, lateral bracts, rarely in a collar; body 10–12 mm wide (6–8 mm, dried), subglobose, with 1–4 small, scattered, appressed,

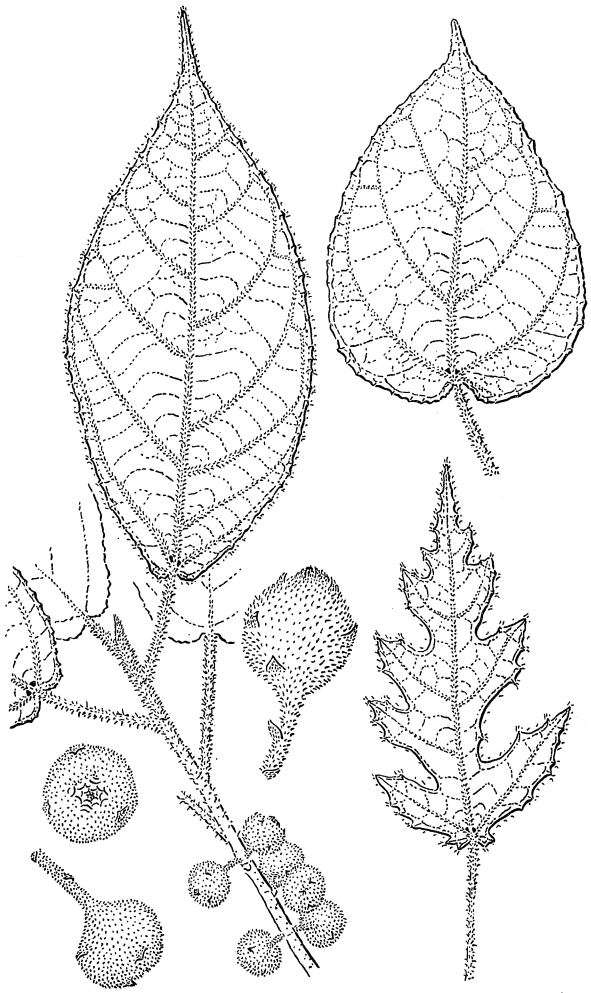

FIGURE 24. Sect. *Sycidium* ser. *Phaeopilosae*. *F. gul*, RSS 246, two figs (lower left) × 1, sapling leaf × ½. Var. *solomonensis*, RSS 2654 (centre) × ½, fig × 1; RSS 77, cordate leaf (upper right).

lateral bracts, the orifice plane or slightly sunken, with small apical bracts; internal bristles abundant, minute, white, 0·3 mm long; sclerotic cells none. Tepals (3–)4–5, dark red, free, glabrous, spathulate or oblong. Male flowers in 1–2 rings round the orifice, subsessile; stamen 1(–2), not mucronate, without pistillode or merely a minute spike. Gall- and female flowers sessile or with a short, white pedicel up to 0·7 mm long; ovary sessile, whitish; style glabrous. Seed 0·8 mm long, slightly keeled, distinctly compressed, smooth. Leaf with cystoliths on both sides.

Distr. Borneo (north, east), Philippines, Celebes, Moluccas, Tenimber Isl., Key Isl., Flores, New Guinea, New Ireland, New Britain, Admiralty Isl., Solomons.

Ecology. Lowland forest, chiefly by streams, to 1200 m alt., common throughout the Solomons.

Kwara-ae. aimomote, aimote mote.
Collections. BSIP 5688, RSS 246.

Var. *solomonensis* Corner

Fig often slightly larger, persistently brownish hispid with hairs 0·5 mm long; lateral bracts on the body 1·5–3 mm long, more conspicuous, the apical bracts projecting up to 1·5 mm. Tepals hairy at the tips; flower-pedicals often hairy. Often becoming cauliflorous with leafless twigs up to 5 cm long, without internodes.

Distr. Solomons, frequent throughout.

Collections. Brass 2578; Kajewski 1651, 1712, 2118, 2796; NGF 13582; RSS 77, 262, 2654, 6052.

This species is very variable in the development of the lateral bracts on the fig, in the position of the figs which varies from ramiflorous to mainly cauliflorous in different trees, and in the size of the leaf.

301. *F. copiosa* Steud. (figure 25)

Tree up to 20 m high, usually much smaller, not or slightly buttressed, crown heavy, branches spreading. Leaves spirally arranged or, typically, decussate in unequal pairs. Twigs, petioles, underside of midrib, and fig-pedicels thinly to rather closely muriculate with short, white, spicate, often curved hairs up to 1 mm long, varying glabrous. Twigs 3–7 mm thick, hollow. Stipules 7–25 × 3–5 mm, caducous, or persistent in saplings, linear–lanceolate, paired. Lamina 6–35 × 3·5–18 cm (up to 50 × 27 cm in saplings), elliptic, ovate to obovate, the acuminate tip up to 15 mm long, base widely subcordate to widely cuneate, dentate to entire, pinnately lobed in saplings, subcoriaceous, rather stiff, scabrid to nearly smooth, drying grey-green; lateral veins (4–) 6–10 pairs, 5–10 intercostals, slightly to distinctly raised below; basal veins 2–3 pairs, reaching one quarter to one third of the lamina, with 2 basal glands; petiole 10–95 mm long. Figs axillary to cauliflorous on the branches and trunk on short leafless tubercles or twigs up to 6 cm long, often in very large clusters, ripening yellow; pedicel 9–60 mm long, short in the leaf-axils, with 1–3 small, scattered, lateral bracts; body 23–60 mm wide (15–25 mm, dried), depressed globose, with 1–2 small lateral bracts, the orifice 2·5–3·5 mm wide, closed by a rosette of small apical bracts; internal bristles minute, abundant, few, or none; sclerotic cells none or a few in the wall of gall-figs. Tepals 4–7, pink, fading white, broadly lanceolate or oblong, longer than the ovary, free, denticulate and puberulous upwards, varying glabrous and entire. Male flowers in 2 rings round the orifice, sessile to pedicellate; stamen 1–2, usually with a pistillode, rarely with normal gall-ovary, often puberulous at the base of the filament. Gall- and female flowers sessile or with pedicels up to 3 mm long; ovary sessile or shortly stalked; style glabrous or, in female flowers, varying puberulous. Seed 1·3 mm long, slightly compressed and keeled, smooth. Leaf with cystoliths on both sides.

Distr. Celebes, Moluccas, Tenimber and Aru Isl., New Guinea, New Ireland, New Britain, Solomons, Queensland, Palau, Yap.

Ecology. Lowland primary and secondary forest up to 1300 m alt., often grown in villages.

Kwara-ae. amau, sakwari.

Collections. E. S. Brown 764; BSIP 751, 764, 2610, 3412, 4359, 5840; RSS 2837.

Var. *pubescens* Corner

Twigs, petioles, underside of the leaf, and young figs shortly velvety or hispidulous with white hairs up to 1 mm long, more or less muriculate.

Distr. Moluccas, New Guinea, New Ireland, New Britain, Solomons, Queensland.

Collections. Brass 2580, 3193, 3196; Kajewski 1836 ('tunanni', Bougainville, Buin); Rechinger 4713; Waterhouse 156 (Yale Mus. For. 22867), 226, B324, 801 ('hogopopu', 'kaqua', 'poi', 'surasai', 'uanos', Bougainville, Siwai).

This village tree with edible young leaves has many vernacular names. It is variable in all respects, but it can always be distinguished in the field from its close ally *F. wassa*, which is smaller in all parts. They make a good example of a pair of *Ficus* species, apparently overlapping in the herbarium, though not in nature.

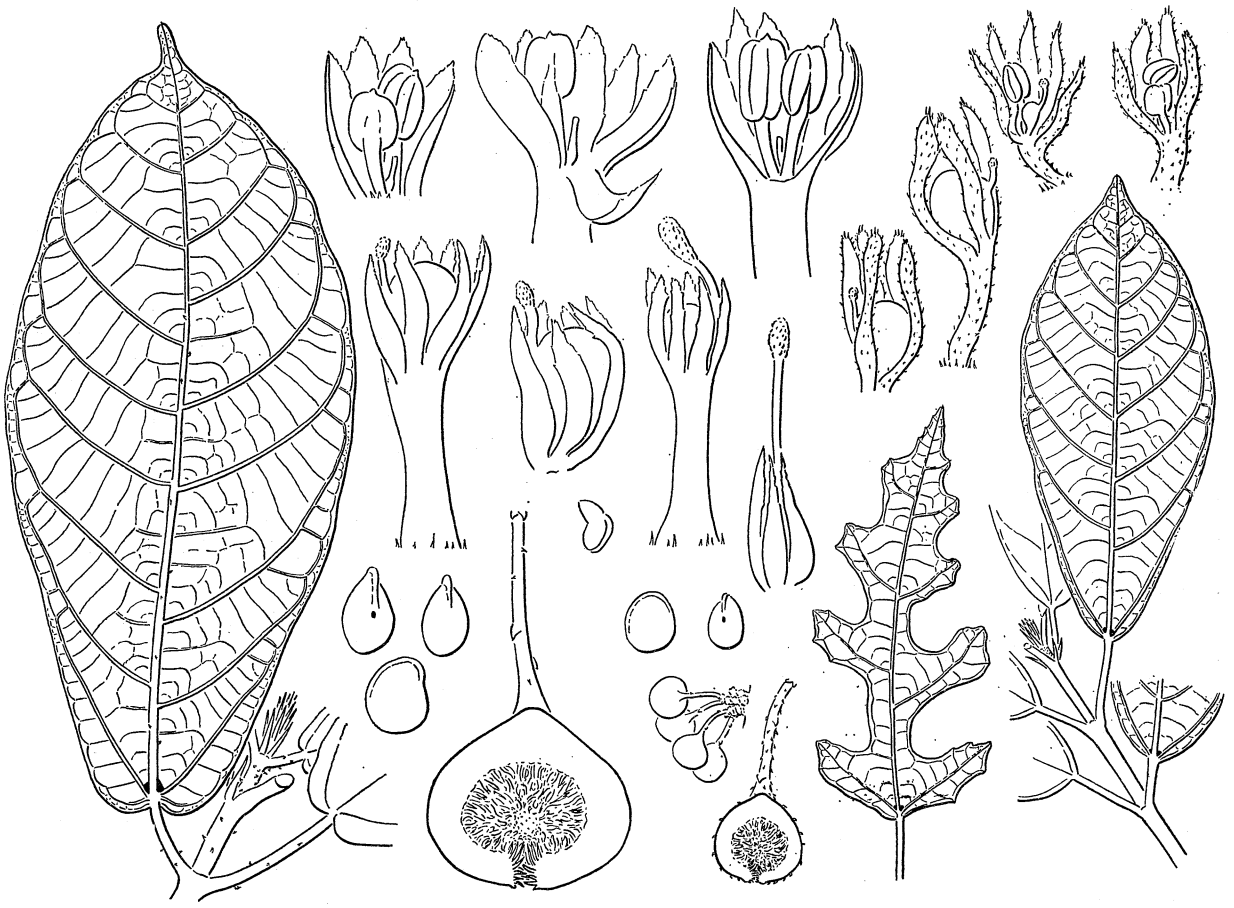

FIGURE 25. Sect. *Sycidium* ser. *Copiosae*. Right, *F. wassa*. Left, *F. copiosa*, larger in all parts. Leaf and twig $\times \frac{1}{2}$, fig $\times 1$, flowers $\times 10$.

302. *F. wassa* Roxb. (figure 25)

Tree up to 20 m high, generally 5–8 m, fruiting as a shrub 0·3–1 m high. Leaves spirally arranged or decussate in more or less unequal pairs. Glabrous, scabridulous, or thinly puberulous with white hairs up to 1 mm long on the twigs, petioles, and underside of the midrib, varying sparsely muriculate with stouter, conical hairs up to 0·5 mm long. Twigs

2–4 mm thick. Stipules 6–13 mm long, linear–lanceolate, paired, clustered over the terminal bud. Lamina 9–20 × 3–8 cm (up to 26 × 10 cm in saplings), elliptic to obovate, the acuminate tip up to 12 mm long, base cuneate, rarely narrowly subcordate, denticulate to entire, more or less pinnately lobed in saplings, membranous to stiffly coriaceous, scabrid, drying grey-green to brownish; lateral veins 4–7(–8) pairs, up to 11 in saplings, 3–7 (–11) intercostals, slightly raised below; basal veins 1(–2) pairs, short or reaching one third of the lamina, with 2 basal glands; petiole 10–55 mm long, up to 110 mm in saplings. Figs axillary, ramiflorous, and cauliflorous from the base of the trunk, on short leafless knobs or twigs up to 2 cm long, scabridulous, ripening white to yellow, pink, red, and purple; pedicel 5–35 mm, with 1–2 minute basal bracts and 1–2 small, scattered, lateral bracts; body 12–18 mm wide (9–13 mm, dried), subglobose, often with 1–2 small lateral bracts, the orifice 1–1·5 mm wide, closed with several small apical bracts; internal bristles none or minute; sclerotic cells none, or few in the gall-figs. Flowers as in *F. copiosa*. Seeds 1–1·5 mm long. Leaf with cystoliths on both sides.

Distr. Moluccas, Alor, Aru and Key Isl., New Guinea, New Ireland, New Britain, Solomons, Santa Cruz Isl., New Hebrides.

Ecology. Lowland forest to 1400 m alt., common throughout the Solomons.

Kwara-ae. ngo-ngo, sakwari.

Collections. Brass 2627, 2671, 3194, 3508; Brown 1179, 3909, 5765; BSIP 644, 1164, 2858, 4084, 4111, 4165, 4411, 4744; Kajewski 2112 ('tunigi', Bougainville, Buin), 2425, 2637 ('kemanduma', Guadalcanal, Vulolo); Rechinger 3537, 4094, 4447, 4886; RSS 2585, 6176; Waterhouse 10 (Yale Mus. For. 21141; 'bavau', 'hikavarai', 'utosih', Bougainville, Buin), 38, 135 ('paduri', New Georgia), B 237, 705.

This is a common small tree, easily recognized from the clusters of yellow to pink and red figs on the trunk. In the Solomons, however, it can be mistaken for the very similar *F. pseudowassa* with distichous leaves.

316. *F. melinocarpa* Bl. (figure 26)

Large buttressed tree up to 35 m high; buttresses up to 4 m high; latex watery, colourless. Leaves distichous. Twigs, petioles, and underside of the main veins stiffly villous or hispid with straight, erect, white or yellowish hairs up to 1·5 mm long, or the petioles and veins nearly glabrous. Twigs 2–3 mm thick. Stipules up to 12 mm long, caducous. Lamina 7–22 × 2·5–13 cm, 4–8 × 2·5–4 cm on the upper twigs of old trees, elliptic, varying ovate to obovate, subacute or shortly acuminate, the tip up to 9 mm long, base more or less unequal, shallowly cordate to cuneate, denticulate to entire, stiffly membranous to coriaceous, scabrid on both sides, varying nearly smooth; lateral veins 4–9 (–11) pairs, 6–11 intercostals, slightly raised below; basal veins 1–2 (–3) pairs, short or reaching one third of the lamina, 1–2 basal glands; petiole 6–30 mm long. Figs axillary and on the twigs behind the leaves, never truly ramiflorous or cauliflorous, shortly hairy, glabrescent, scabridulous, ripening yellow to red and purple-black; peduncle 2–10 (–15) mm; basal bracts 3, small, in a collar, or occasionally displaced; pedical 0–10 mm long; body 12–20 mm wide (10–14 mm, dried), subglobose, without lateral bracts, the apical bracts slightly projecting; internal bristles short or minute, abundant; sclerotic cells few to abundant in the rather thick fig-wall. Tepals 4–6, reddish pink, fading white from the

base, free, oblong, blunt, glabrous or sparsely hairy at the tips, entire. Male flowers in 1–2 rings round the orifice, sessile or shortly stalked; stamen 1(–2), not mucronate, rarely with a minute pistillode. Gall- and female flowers sessile or with white pedicels up to 2·5 mm long; ovary sessile to shortly stalked, white; style glabrous. Seed 1 mm long,

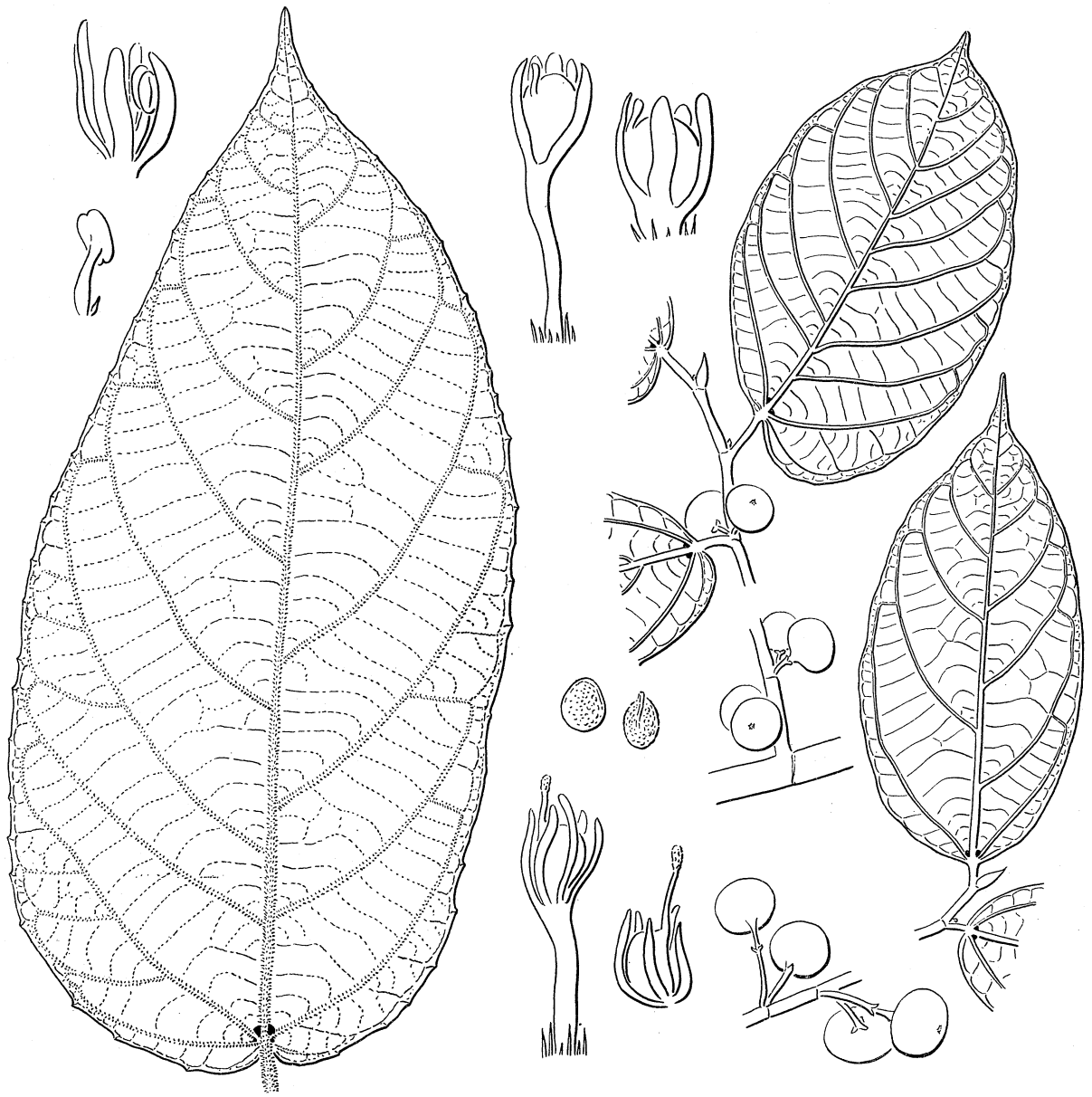

FIGURE 26. Sect. *Sycidium* ser. *Scabrae*. *F. melinocarpa*; NGF 13746, sapling leaf; NGF 13569 (lower right), RSS 59 (upper right) with flowers and seeds × 10. Leaf and twig × ½.

lenticular, scarcely keeled, minutely subreticulate to nearly smooth. Leaf with cystoliths on both sides.

Distr. Sumatra (south), Java, Borneo (north, east), Celebes, Philippines, Moluccas, Aru Isl., New Guinea, New Britain, Solomons.

Ecology. Lowland forest, locally common, as a canopy tree throughout the Solomons.

Kwara-ae. siinangaina, siinaonina.

Collections. BSIP 2894, 3946; Kajewski 2435 ('wandiloma', Guadalcanal, Berande), 2611; NGF 13569; RSS 59, 2888.

This fine tree, generally recognizable from the small orange-pink figs fallen round the buttressed trunk, may have glabrous leaves. This form is var. *hololampra* (Diels) Corner, but from the evidence of several saplings I suspect that all trees become more or less glabrous after the sapling stage up to 5–10 m high. Fragments in the herbarium may be almost indistinguishable from *F. erinobotrya* var. *solomonensis* f. *glabrior* which is a cauliflorous shrub or small tree with the leaves on the main stem more asymmetric than on the side-branches; in *F. melinocarpa* these leaves are borne spirally and are symmetric. The latex has been reported as irritant.

317. *F. trachypison* K. Schum. (figure 27)

Tree up to 30 m high, slightly buttressed; latex watery, whitish, turning yellow on exposure; ? deciduous. Leaves distichous. Twigs, petioles, underside of the veins, and figs densely scabrid with short, pustular hairs and, usually, hispidulous on the twigs and petioles with erect, white to brownish, hairs up to 1 mm long. Twigs 2–4 mm thick.

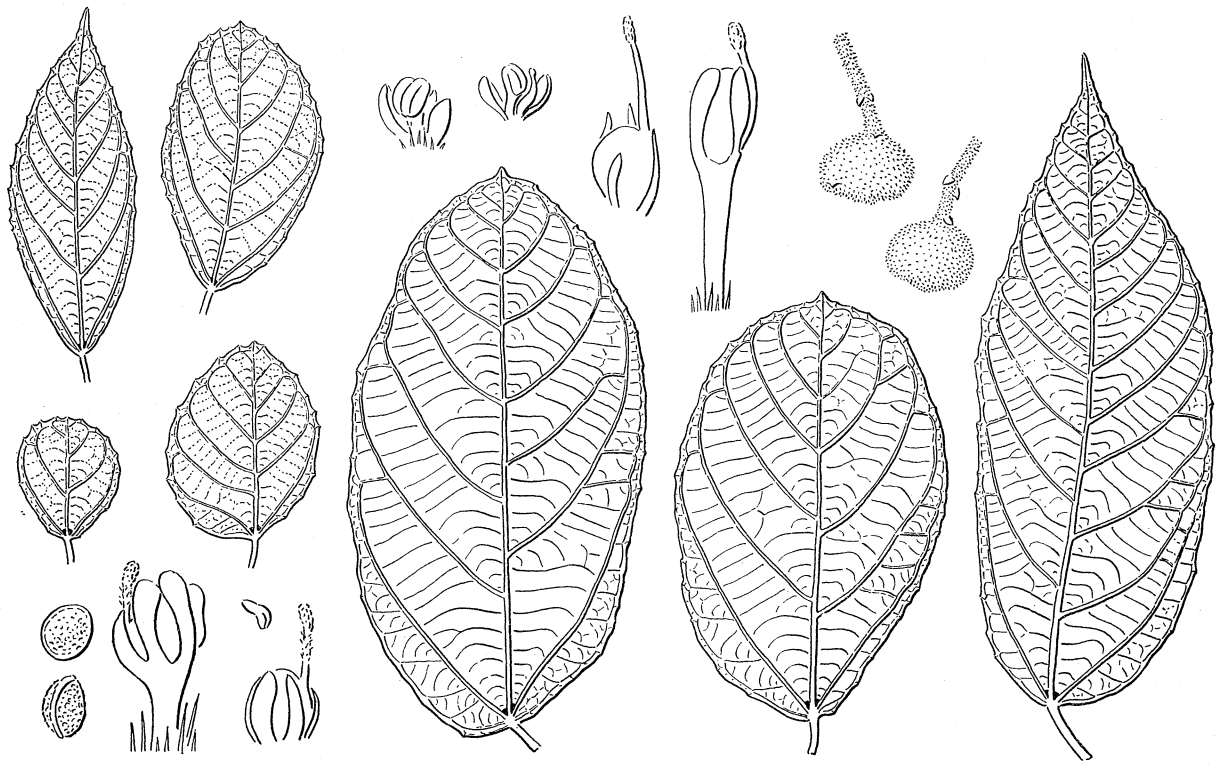

FIGURE 27. Sect. *Sycidium* ser. *Scabrae*. *F. trachypison*, material from New Guinea; Carr 14844 (left) with small leaves; Carr 12779, 14736, 16075, the other leaves from left to right; Carr 14736, figs × 1, flowers with glabrous style (top centre) × 10; Carr 15788, flowers with hairy style (bottom left) × 10.

Stipules up to 10 mm long, caducous, appressedly brownish hairy. Lamina 8–23 × 5–12·5 cm elliptic, varying ovate to subobovate, the short acuminate tip up to 12 mm long, base usually strongly asymmetric, shallowly cordate to widely cuneate, stiffly coriaceous, very harshly scabrid on both sides, denticulate to entire, drying brown; lateral veins 5–10 pairs,

2–6 in small leaves, 3–11 regular intercostals, strongly raised below; basal veins 1–2 (–3) pairs, short or reaching to one half of the lamina, with 2 basal glands; petiole 4–20 mm long. Figs axillary and on short woody knobs on the branches, ripening yellow to red and purple, scabrid; peduncle 2–10 mm long; basal bracts 3, small, in a collar or more or less scattered; pedicel 0–4 mm long; body 10–13 mm wide (6–9 mm, dried), rather depressed globose, often with 1–2 small lateral bracts, the plane orifice closed by several small apical bracts; internal bristles abundant, white, up to 1 mm long; sclerotic cells absent from the fig-wall. Tepals 4–6, dark to pale red, fading white from the base, glabrous or hispidulous at the apex, free, spathulate–oblong. Flowers and seed as in *F. melinocarpa*; style of female flowers often puberulous. Leaf with cystoliths on both sides.

Distr. Amboina, Aru and Key Isl., New Guinea, New Ireland, New Britain, Solomons.

Ecology. Lowland forest throughout the Solomons.

Kwara-ae. samota.

Collections. NGF 13782.

Var. *pallida* Corner

Shrub or small tree up to 15 m high, scabrid but not hispidulous. Leaves rather thin, the intercostals scarcely raised below, drying grey-green. Tepals white, hispidulous at the apex.

Distr. New Guinea, Solomons.

Collections. BSIP 5856; Waterhouse 32 (Yale Mus. For. 21163; 'kautoro' Siwai, 'ivoi' Tiop, Bougainville).

This species differs from *F. melinocarpa* in the stiffer, much more scabrid and strongly veined leaves, the smaller ramiflorous figs with small lateral bracts on the body, and the darker red tepals; it seems also to be a smaller tree with yellowing latex. It needs, however, careful comparison in the field, particularly in regard to var. *pallida*. The twigs develop seasonally and the short twigs bear the leaves differing in shape and size from base to apex so that brief description is almost impossible.

327. *F. oleracea* Corner (figure 28)

Tree up to 20 m high, not buttressed; branches few, long; crown open. Leaves distichous drooping; young leaves in pink flushes. Glabrous or the twigs and petioles laxly pubescent with soft, pale, spreading hairs up to 3 mm long. Twigs 3–6 mm thick. Stipules up to 15 mm long, lanceolate, paired, glabrous, subpersistent on sapling shoots. Lamina 16–35 × 5–12 cm (up to 47 × 15 cm on saplings), oblong or ovate–oblong, the short acuminate tip 10–20 mm long, base more or less strongly cordate, symmetric or asymmetric with one or both lobes obscuring the petiole, entire, coriaceous, smooth or subscabrid below, drying grey-green to brown; lateral veins (7–) 9–20 pairs at a wide angle; 5–10 intercostals, slightly raised below; basal veins 3–4 pairs, short, with 2 basal glands; petiole 5–12 mm long, short and stout. Figs axillary, ramiflorous, and cauliflorous from the base of the trunk, developing in large masses, ripening cream to pink and dark red, or the gall-figs yellow to pink; peduncle 3–20 mm long; basal bracts 3, in a collar, 1–1·5 mm long; pedicel 0–12 mm long; body 25–50 mm wide (15–32 mm, dried), subglobose, without lateral bracts, at first laxly hairy, the orifice closed by 3–4 apical bracts in a small rosette

2–4 mm wide; internal bristles up to 0·6 mm long, white, few to abundant; fig-wall 2–3 mm thick, without sclerotic cells. Tepals 4–6, reddish then pallid, lanceolate or linear, free, entire, longer than the ovary, glabrous or puberulous. Male flowers in 1–2 rings round the orifice, pedicellate; stamen 1, hairy at the base, often with a pistillode. Gall- and female flowers sessile or with glabrous white pedicels up to 4·5 mm long; ovary white, sessile; style in female flowers strongly lateral, glabrous or puberulous. Seed 1·2 mm long, lenticular, scarcely keeled, minutely reticulate. Leaf with cystoliths on both sides.

Distr. Solomons.

Ecology. Lowland forest up to 800 m alt., frequent throughout the islands.

Kwara-ae. roroketa.

Collections. BSIP 2603, 5229; Comins 174; Kajewski 1721, 1912 ('or-worku', Buin, Bougainville); NGF 13560, 13579; RSS 2831, 2851; Waterhouse 124 (Yale Mus. For. 22835; 'puijo', Siwai, Bougainville), 133, B 203, 779, 847 ('koropuru', Maisua, Bougainville).

Var. *pugnans* Corner

Lamina very harshly scabrid above, villosulous beneath. Twigs, petioles, underside on midrib, and figs villosulous with minute white to brownish hairs up to 0·5 mm long, shorter on the smaller veins. Figs axillary and on the twigs immediately behind the leaves, smaller, up to 15 mm wide; peduncle 2–3 mm long; pedicel 2–3 mm.

Ecology. Common throughout the islands.

Collections. Kajewski 1941 ('in fighting days, leaves used to sandpaper spears', Buin, Bougainville); RSS 207, 2870.

Var. ***villosa*** var. nov.

Ut var. *pugnans* sed ramuli petioli costae (subtus) pilis albidis v. brunneolis mollibus 1–2 mm longis dense villosi; nervae minores pilis flexuosis usque 0·5 mm longis villosae. Lamina subtus villosa, supra scabra. Syconia pilis 0·5 mm longis dense villosa.

Collections. RSS 2119, Gallego, Hidden Valley, July 1965; RSS 2121, Guadalcanal, Monitor Creek, July 1965, typus K; Waterhouse B301, Bougainville, Siwai, Sept. 1930, 'ukumura'.

This is one of the striking species of the Solomons, but it is surprisingly variable. Var. *villosa* has the leaves as scabrid as in var. *pugnans* but much hairier than it and than var. *oleracea*. In both var. *pugnans* and var. *villosa* the figs are smaller with much shorter stalks and they are not cauliflorous, but further collections of older trees may revise this possible difference.

328. *F. imbricata* Corner (figure 29)

Tree up to 20 m high, not or scarcely buttressed, usually rather small. Leaves distichous; young leaves pale green. Twigs, petioles, and underside of the main veins closely to laxly pilose with spreading white to pale yellow hairs 1–2 mm long, sparse and short on the smaller veins. Twigs 1–2 mm thick. Stipules up to 13 mm long, lanceolate, paired, caducous. Lamina 10–18 × 3·5–7·5 cm, elliptic, inequilateral, the acuminate tip up to 17 mm long, base rounded to widely cuneate and asymmetric, often with a small rounded lobe

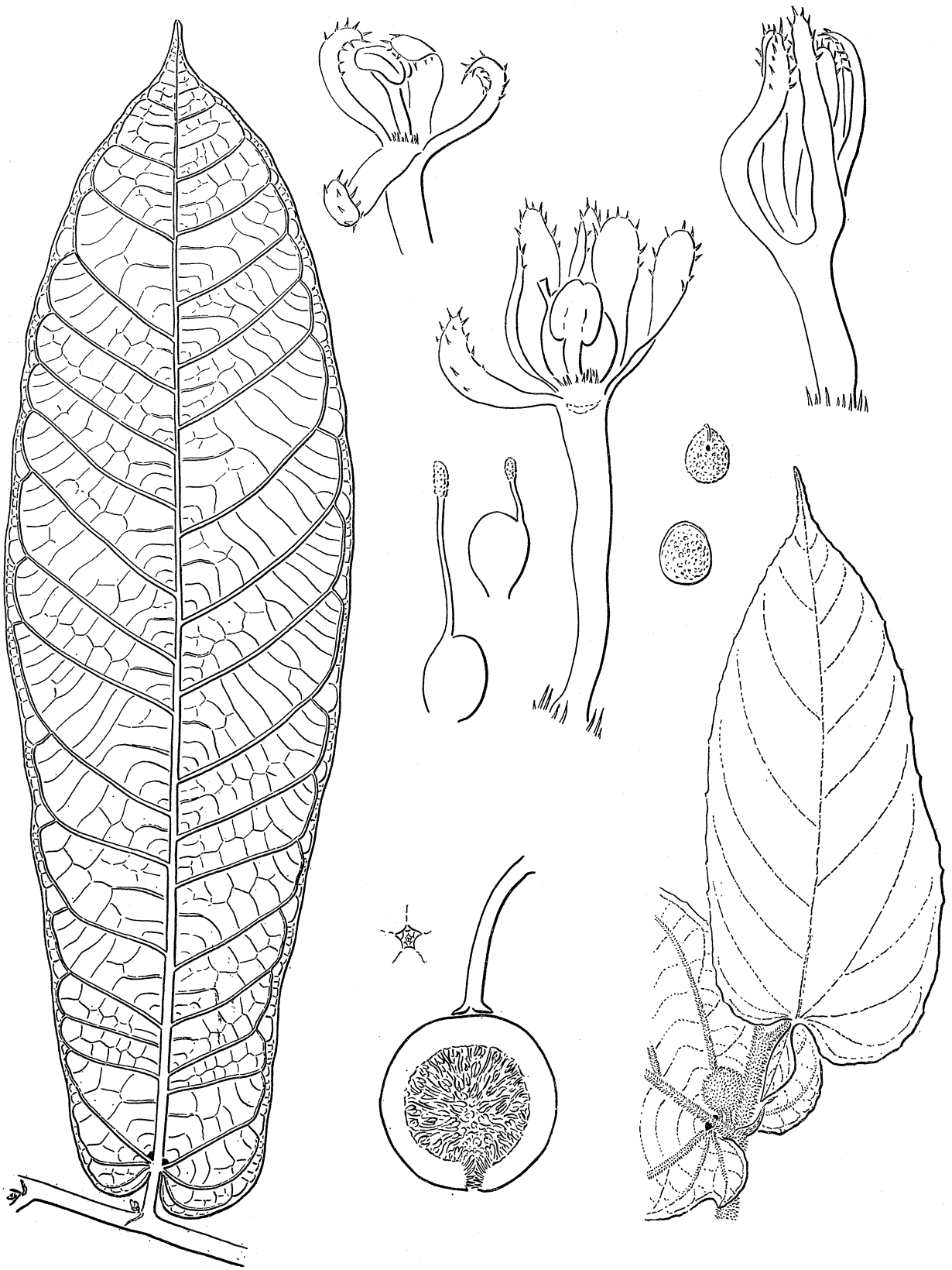

FIGURE 28. Sect. *Sycidium* ser. *Scabrae*. Left, *F. oleracea* var. *oleracea*, RSS 2851 with fig and gall-flowers, NGF 13560 female flowers. Right, var. *villosa*, RSS 2121. Twig $\times \frac{1}{2}$, fig $\times 1$, flowers $\times 10$.

on the acroscopic side, denticulate to entire, scabrid above, scabrid-hairy beneath, stiffly membranous, drying grey-green; lateral veins 4–7 (–9) pairs, oblique or curved ascending, up to 10 intercostals, raised below; basal veins 2–3 (–4) pairs, the larger reaching one third to one half of the lamina, with 2 basal glands; petiole 3–10 mm long. Figs axillary, solitary, pendent on the underside of the twigs, eventually in some trees becoming cauliflorous on short leafless twigs up to 5 cm long without internodes, thinly hispidulous with stiff, pale

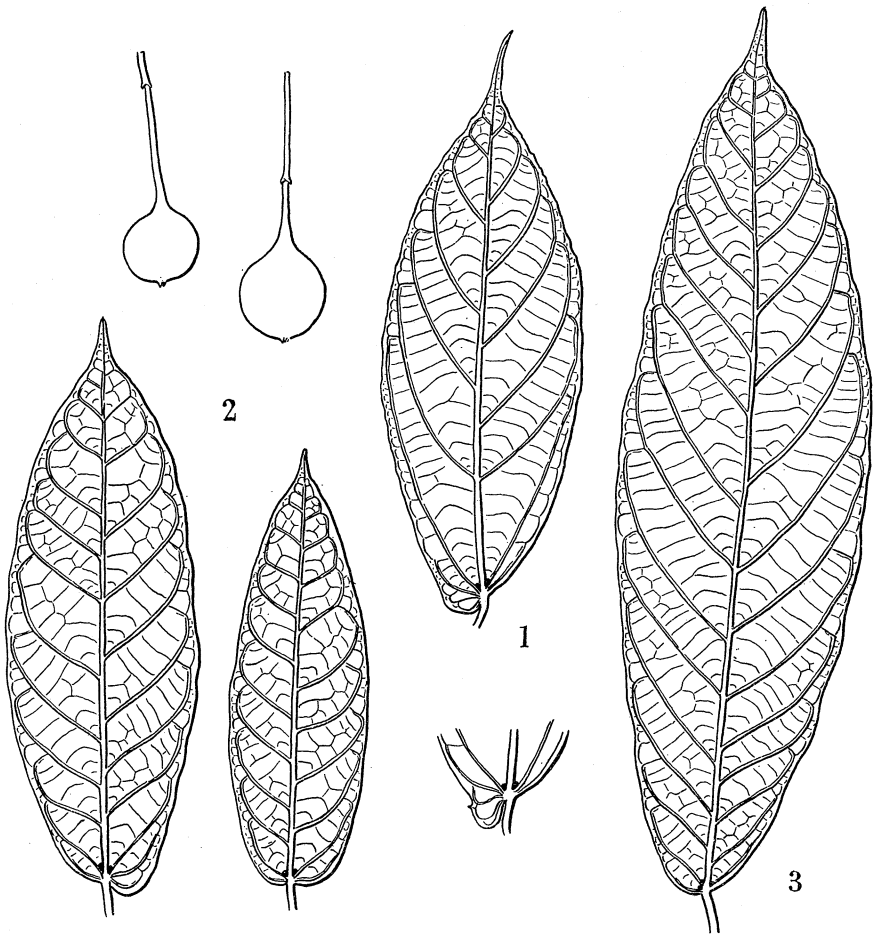

FIGURE 29. Sect. *Sycidium* ser. *Scabrae*. *F. imbricata*, Waterhouse 818, with figs; 2, var. *subcordata*; 3, *F. awaraensis*, NGF 13557. Leaves $\times \frac{1}{2}$, figs $\times 1$.

brown, spreading hairs, subglabrescent, ripening red; peduncle 5–18 mm long; basal bracts 3, in a collar, 1·5–2 mm long, lanceolate; pedicel 4–18 mm long, slender; body 20–25 mm wide (10–14 mm, dried), subglobose, often with flattened end, without lateral bracts; internal bristles 0·5 mm long, white, rather few; fig-wall without sclerotic cells. Flowers and seeds as in *F. oleracea*; tepals dark red, fading white, thinly hispidulous at the apex; seed 0·7–0·8 mm long, subreticulate on the sides. Lamina with cystoliths on both sides.

Distr. Solomons, in lowland forest up to 700 m alt., throughout the islands.

Kwara-ae. samota.

Collections. Kajewski 1724; NGF 13564; RSS 2117, 2428, 6139, 6245; Waterhouse B37 ('uasas', Buka, Bougainville), 176, 818 ('gula', 'katut', 'sisi', Siwai, Bougainville).

Var. *subcordata* Corner

Glabrous with smooth leaf. Lamina 5–17 × 1·5–5·5 cm, narrowly elliptic to oblong, the rounded or subcordate base almost or quite symmetric; lateral veins 7–11 pairs; intercostals 2–5; basal veins short.

Distr. Bougainville Isl., in forest up to 1500 m alt. near Kupei.

Collections. Kajewski 1657, NGF 13768.

This species and *F. chrysochaete* are recognizable in the forest from the solitary figs pendent from the underside of the twigs. *F. chrysochaete* is usually hairier, and has shorter fig-stalks, white and very hairy tepals, and copious internal bristles.

329. *F. chrysochaete* Corner (figure 30)

Tree up to 13 m high, fruiting as a shrub. Leaves distichous, often set fan-wise at the ends of the twigs; young leaves pale green. Twigs and petioles pubescent or villous with soft, spreading, white, pale golden, or brownish hairs 1–3 mm long; underside of main veins with sparser, shorter hairs. Twigs 1–2 mm thick. Stipules up to 12 mm long, thinly

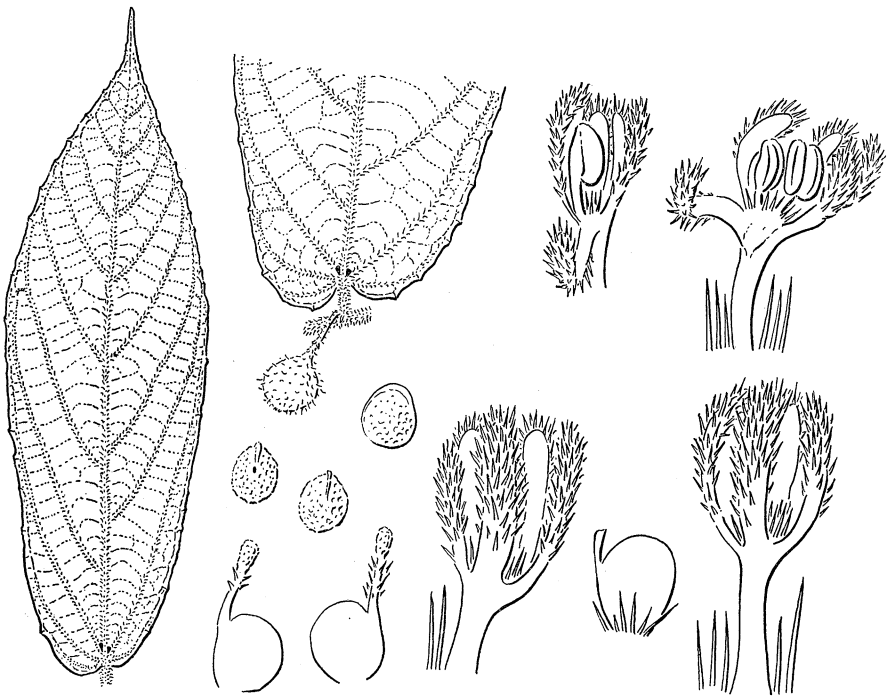

FIGURE 30. Sect. *Sycidium* ser. *Scabrae*. *F. chrysochaete*; Waterhouse 201, leaf (left); Kajewski 2148, leaf-base and fig; Brass 3199, female flower and seed; Kajewski 2317, male and gall-flowers. Leaf × ½, flowers × 10.

white hairy, subpersistent on young shoots. Lamina 11–25 × 3–8 cm, narrowly oblong–elliptic or subovate, the acuminate tip 7–35 mm long, base shallowly cordate, symmetric or with a slight acroscopic lobe, denticulate to entire, membranous to subcoriaceous, harshly scabrid above, hispidulous beneath, drying grey-green; lateral veins 6–9 (–10) pairs, reaching one quarter to one half of the lamina, with two basal glands; petiole 5–10 mm long. Figs axillary, solitary, pendent from the underside of the twigs, becoming

cauliflorous on short woody knobs in some trees, hispidulous with white erect hairs up to 0·5 mm long, glabrescent, scabridulous, ripening red; peduncle 5–10 mm long; basal bracts 3, in a collar, 1–1·5 mm long, ovate–acute or lanceolate; pedicel 0–7 mm long; body 12–20 mm wide (8–14 mm, dried), subglobose without lateral bracts; internal bristles up to 1 mm long, abundant, white to pale golden; fig-wall without sclerotic cells. Flowers as in *F. oleracea*; tepals 5–6, white, densely appressedly bristly; stamen and ovary very bristly at the base; female style shortly hairy: Seed 0·8 mm long, finely reticulate on the sides. Lamina with cystoliths on both sides.

Distr. Solomons, in lowland forest up to 900 m alt., common throughout.

Kwara-ae. samota.

Collections. Brass 2960, 3199; BSIP 2409, 3542, 3702, 3969, 5313, 5428, 5732; Kajewski 1983 ('labutsio', Kugumaru, Bougainville), 2148 ('karsikerie', Koniguru, Bougainville), 2317; NGF 13584, 13773; RSS 155, 213a, 239, 2830, 2920; Waterhouse 201 ('lavusu', Malaita), 232 ('minisu', Siwai, Bougainville).

This is one of the characteristic undergrowth forest trees of the Solomons. Compare *F. imbricata.*

330. *F. arawaensis* Corner (figure 29)

Tree up to 12 m high, cauliflorous, glabrous. Leaves distichous. Twigs 2–3 mm thick. Stipules 7–12 mm long. Lamina 10–27 × 2·5–8 cm, lanceolate–elliptic, the acuminate tip up to 20 mm long, base cuneate and symmetric or broader on the acroscopic side, not auricled, dentate-sinuate to entire, membranous to subcoriaceous, smooth, drying greenish brownish; lateral veins 11–16 pairs, mostly 13–14, oblique, scarcely inarching, with 5–11 intercostals, raised below; basal nerves 1 pair, short, without or with obscure basal glands; petiole 7–14 mm long. Figs clustered on short, knobbly, sparingly branched twigs up to 2 cm × 4–5 cm, without internodes, on the trunk and main branches from ground-level; peduncle 4–12 mm long; basal bracts 3, in a collar, very small, 0·5 mm long; pedicel 4–16 mm long, slender; body 9–10 mm wide (dried); internal bristles 0·3 mm long, abundant, white; fig-wall without sclerotic cells. Flowers as in *F. imbricata.* Lamina with cystoliths on both sides.

Distr. Bougainville Isl., in lowland forest near Arawa; NGF 13557.

Further collections will probably show that this is only a glabrous variety of *F. imbricata* with numerous lateral veins. The cauliflorous habit may or may not be characteristic. The impression is that this feature is important, but familiarity with wild trees often reveals great variety in this respect. Thus *F. gul*, *F. imbricata*, and *F. chrysochaete* have well-grown trees which may have only axillary figs and others with cauliflorous figs without the axillary. *F. arawaensis*, however, leads from *F. oleracea* to the more advanced *F. imbricata.*

330A. ***F. pseudowassa*** sp.nov. (figures 31, 32)

Arbor usque 8 m alta (? usque 25 m), cauliflora, foliis distichis, glabra sed ramulis foliis syconiisque minute scabridulis. Ramuli 1·5–3 mm crassi. Stipulae usque 7 mm longae, caducae. Lamina variabilissima, plus minus oblongo-elliptica, valde acuminata, asymmetrica, basi cuneata, scabrida; costis lateralibus utrinsecus 6–8, 4–6 in laminis brevibus; basalibus 1(–2) ad $\frac{1}{4}$–$\frac{1}{3}$ laminae elongatis; petiolo 4–20 mm. Syconia raro axillaria, 13–15 mm lata (7–11 mm st. sicco), scabridula, maturitate rubra (feminea) v. luteo-carnea (cecidiophora); stipite 5–18 mm longo, bracteis lateralibus 2–3,

1 mm longis, dispersis v. ad medium stipitem verticillatis; setis internis minutis copiosis; cellulis scleroticis nullis. Tepala 4–6, rubro-carnea, pallescentia, libera, spathulata. Stamen 1. Stylus glaber. Semina 0·7–0·8 mm longa, lenticuliformia, tenue reticulata. Cystolitha amphigena. Ins. Solomonenses. RSS 2613 Ysabel, typus K.

Tree up to 8 m high (? up to 25 m), becoming cauliflorous. Leaves distichous. Glabrous, but all parts minutely scabridulous. Twigs 1·5–3 mm thick. Stipules up to 7 mm long, paired, caducous. Lamina very variable, oblong–elliptic 18–33 × 7–13 cm, to rather

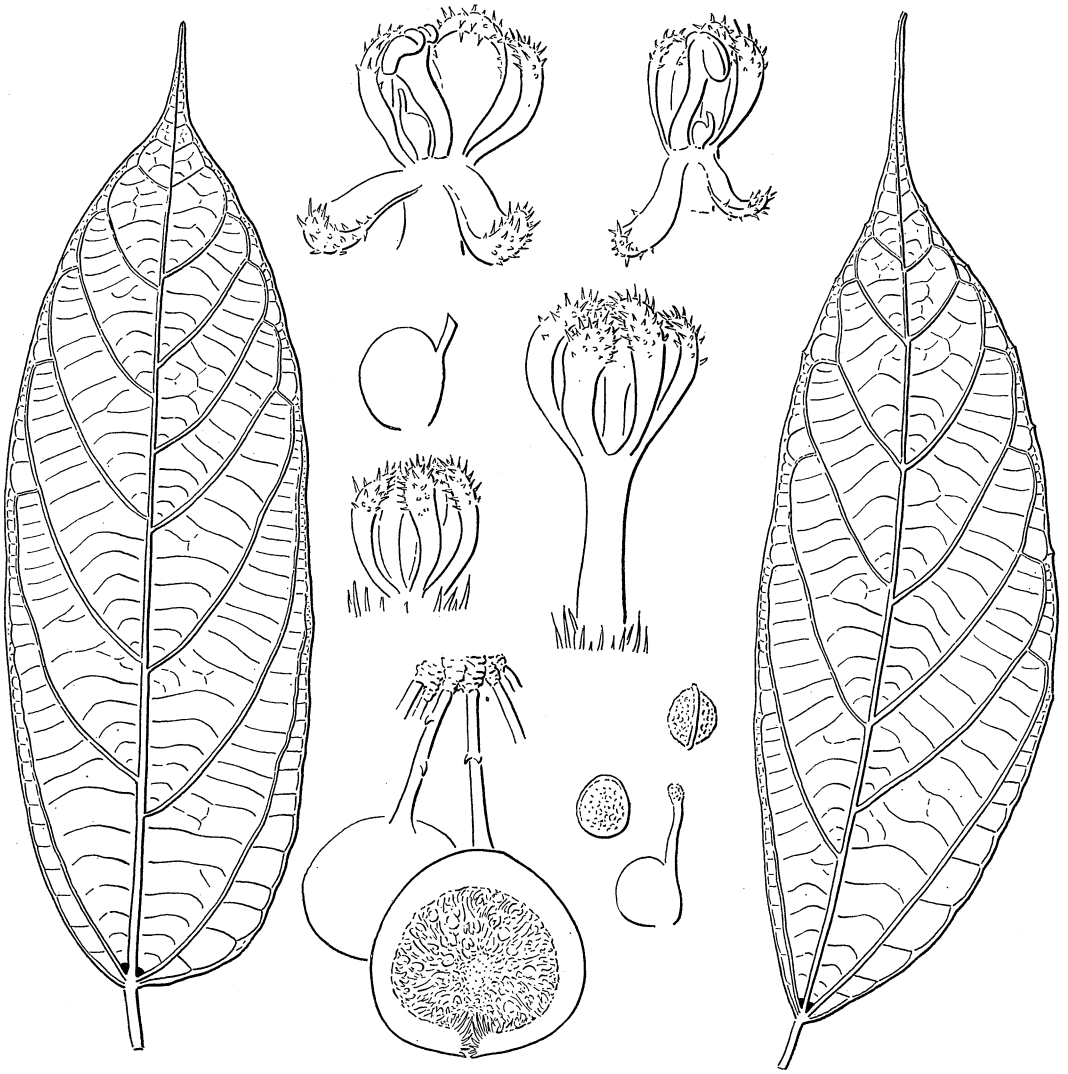

FIGURE 31. Sect. *Sycidium* ser. *Scabrae*. *F. pseudowassa*; RSS 1170, leaf (left), figs, male and gall-flowers; RSS 2726, female flower and seed; NGF 13762, sapling leaf (right). Leaf × ½, fig × 1½, flowers × 10.

broadly elliptic 10–22 × 3–11 cm, or lanceolate–elliptic, the acuminate tip 11–20 mm long (up to 50 mm in saplings), base asymmetric, cuneate on one side, widely cuneate to rounded or subtruncate on the broader side, rarely subsymmetric and cuneate, entire or denticulate, scabrid on both sides, thinly subcoriaceous, drying grey-green or brownish underneath; lateral veins 6–8 pairs, 4–6 in shorter leaves, slightly raised on both sides;

intercostals up to 9, regular, fairly close, slightly raised below, 2–5 in shorter leaves; basal veins 1(–2) pairs, reaching one quarter to one third of the lamina, with 2 basal glands; petiole 10–20 mm long, 4–12 mm in small leaves. Figs mostly on the twigs behind the leaves, becoming ramiflorous and cauliflorous to the base of the trunk on small woody knobs, rarely axillary, ripening red (seed-figs) or pinkish yellow (gall-figs); stalk 5–18 mm

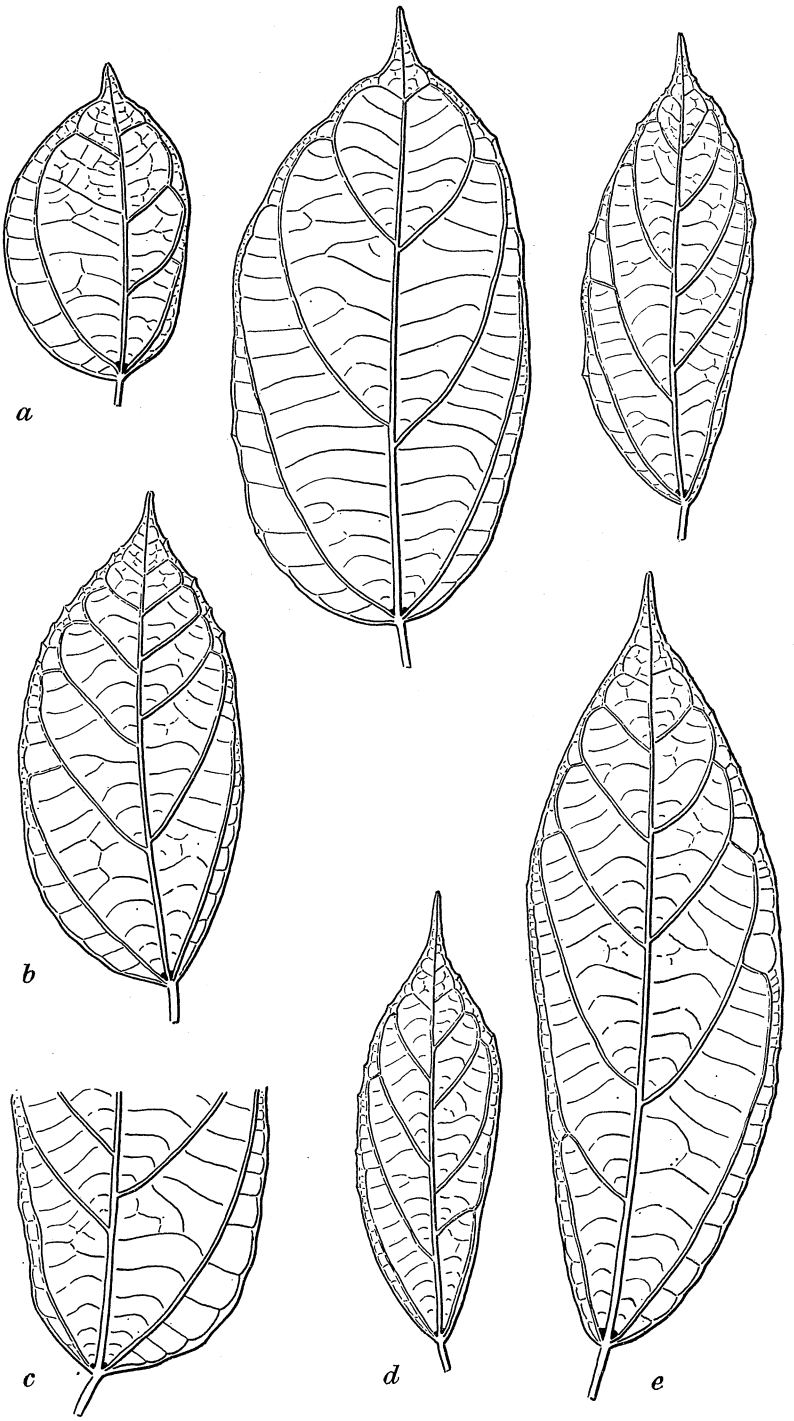

FIGURE 32. Sect. *Sycidium* ser. *Scabrae*. *F. pseudowassa*; *a* Kajewski 2050, three leaves from the same twig, the lowest leaf on the left, the uppermost on the right; *b* to *e* RSS 2852, leaves from the same twig in succession from below (*b*) upwards.

long, with 2–3 small scattered lateral bracts 1 mm long, or 3 in a collar about the middle of the stalk; body 13–15 mm wide (seed-figs) or 15–20 mm wide (gall-figs), 7–11 mm when dried, subglobose, without lateral bracts, the orifice small and plane; internal bristles minute, abundant, white; fig-wall without sclerotic cells. Tepals 4–6, mostly 5, reddish pink, fading white, free, spathulate, rather closely hispidulous and denticulate distally. Male flowers in 2–3 rings round the orifice, sessile to shortly stalked; stamen 1, often with a pistillode. Gall- and female flowers sessile or with glabrous pedicels; style glabrous. Seed 0·7–0·8 mm long, lenticular, slightly keeled, finely reticulate. Cystoliths on both sides of the lamina.

Distr. Solomons, widespread in lowland forest up to 1400 m alt.

Collections. Kajewski 1783 (Buin, Kugumaru, 'koturra'; tree 15 m high, common); Kajewski 2050 (Buin, Koniguru, 900 m alt.; tree up to 25 m high, common, young leaves appearing after the shedding of the old leaves); NGF 13762 (Bougainville, Kupei, 1400 m alt.; slender sterile shrub among the roots of stilted *Pandanus*); RSS 1170, Kolombangara; RSS 2609, 2613 (type, Kew), 2726, 2852 Ysabel; BSIP 1265, New Georgia, West Vangunu.

This can be described as *F. wassa* with distichous, asymmetric, and short-petiolate leaves. The trunks of both, when covered with the small reddish pink figs, seem identical, but the crown of *F. wassa* with ascending twigs is bushy, that of *F. pseudowassa* with applanate, spreading twigs is more open. Many small trees of this habit were seen during the Royal Society Expedition and, from them, I was able to identify the sterile collection of saplings found at a fairly high altitude in Bougainville (NGF 13762). The two collections of Kajewski indicate, however, that it may grow to a much greater size and be deciduous. Certainly, the new shoots develop in flushes and they have the change in leaf-shape from base to apex of the twig which distinguishes many species with this habit. Saplings, then, have the long leaf, which shortens until the fully deciduous habit is reached in the large cauliflorous trees with short, few-veined leaves. It is a species that requires more careful study in the forest.

Outside the Solomons, *F. pseudowassa* has several parallels. *F. schumanniana* (New Guinea, New Britain) is hairy and has a symmetric lamina with a single gland on the back at the top of the petiole; its figs are shortly pedunculate and the tepals are glabrous. *F. tonsa* var. *leptodictya* (New Guinea) and *F. leptoclada* (Queensland) have symmetrical leaves, laxer venation, and dark red tepals. *F. storckii* (New Hebrides, Fiji) has a wider leaf, but is very similar in most other respects. The widespread *F. ampelas* differs in the smaller leaf, the presence of sclerotic cells in the fig-wall, and the more or less glabrous tepals. Considering the great abundance and variety of ser. *Scabrae* in the region from New Guinea to Fiji, I consider *F. pseudowassa* to be a leptocaul derivative of the stock of *F. oleracea*, that has become a large tree, parallel with *F. melinocarpa*, but restricted to the Solomons by late evolution.

331. *F. gryllus* Corner (figure 33)

A low shrub or sprawling tree up to 5 m high. Leaves distichous. Twigs, petioles, stipules, figs, and underside of the main veins densely hispid-scabrid and irritant with white to pale brown, stiff, spreading hairs 1–2 mm long; underside of the smaller veins with shorter hairs; upperside of the lamina hispid-scabrid with stiff white hairs up to 1 mm

long with pustulate bases. Twigs 4–6 mm thick, often hollow. Stipules 20–30 mm long, large, caducous. Lamina 14–37 × 7–16 cm, ovate, asymmetric, the acuminate tip 30–40 mm long, base very strongly asymmetric, broadly and deeply cordate on the basiscopic side, cuneate–subcordate on the other, dentate, membranous, scabrid on both sides, drying

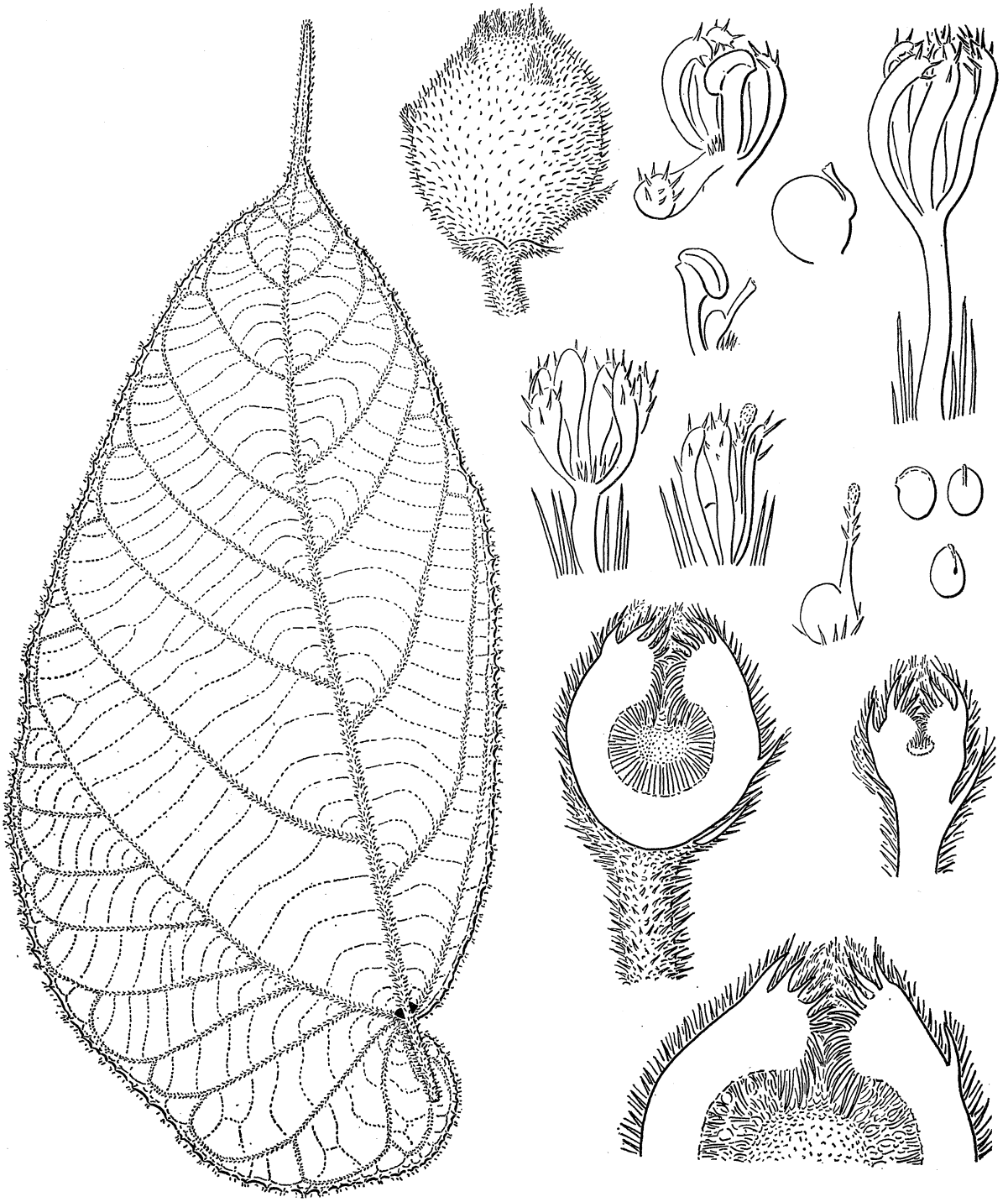

FIGURE 33. Sect. *Sycidium* ser. *Scabrae*. *F. gryllus*; Brass 3407, leaf, fig, female flowers, and seed; RSS 2871, developing figs in section, male and gall-flowers. Leaf × ½, fig × 1, fig-sections × 4, flowers × 10.

grey-green; lateral veins 6–8 pairs, up to 12 intercostals, raised below; basal veins 2 on the narrow side, 4–5 on the wide side, reaching one half of the lamina, with 2 basal glands; petiole 10–40 mm long, concealed by the broad auricle. Figs solitary and paired, axillary, densely hispid, ripening yellow to orange (gall-figs) or red (seed-figs); peduncle 3–10 mm long; basal bracts 3, 3–5 mm long, ovate–lanceolate, acute, hispid, in a collar; body 20–28 × 20–25 mm (15 × 12 mm, dried), ellipsoid with a few scattered lateral bracts 2–4 mm long, crowded round the orifice with many erect hispid apical bracts 2–3 mm long; internal bristles abundant, white, up to 1·5 mm long; fig-wall without sclerotic cells. Tepals 5–6, white with orange-brown tips, spathulate, bristly towards the tips, free. Male flowers in 2–3 rows round the orifice, sessile or pedicellate; stamen 1, hairy at the base on one side, often with a pistillode. Gall- and female flowers sessile or with glabrous pedicels up to 2 mm long, or the pedicels hairy near the base; ovary white, sessile, hairy round the base; female style sparsely hairy. Seed 0·8–0·9 mm long, lenticular or slightly oblong, slightly keeled, smooth. Lamina with cystoliths only on the lower side.

Distr. Ysabel Isl., by streams in the forest up to 600 m alt. (Tiratona and Tetamba).

Collections. Brass 3407; RSS 2868, 2871.

As one of the peculiar species of the Solomons, known previously only from Brass's collection, I searched for this in 1960 and 1965 in Bougainville and the islands visited by the Royal Society Expedition, but I found it only along a stream a few miles west of Tetamba, where it was fairly common. It is a relic of the multibracteate ancestors of sect. *Sycidium* and, as such, it seems to be a relic confined to Ysabel. The following species appears to be a more successful descendant.

332. *F. erinobotrya* Corner var. *solomonensis* Corner (figure 34)

Shrub or small tree up to 11 m high, cauliflorous. Leaves distichous, asymmetric. Twigs, petioles, figs, and sometimes the underside of the main veins more or less hispid with white hairs up to 1 mm long. Twigs 1–3 mm thick. Stipules up to 12 mm long, caducous. Lamina 6–30 × 3–16 cm, smaller on the side-branches, ovate–elliptic, the acuminate tip up to 17 mm long, the base strongly asymmetric, the broad side cordate and not or scarcely overlapping the petiole, the narrow side subcuneate, denticulate to entire, membranous, scabrid on both sides, drying grey-green to brownish; lateral veins 5–8 pairs, often with a gland in the axil of the lower ones, up to 11 intercostals, raised below; basal veins 2–3 on the narrow side, 4–5 on the broad side, reaching one third to one half of the lamina, with 2 basal glands; petiole 5–27 mm long. Figs axillary but mostly ramiflorous and cauliflorous on leafless twigs up to 20 cm long without internodes, ripening orange to red and purple; peduncles 2–9 mm long, with a collar of small basal bracts and a pedicel 0–9 mm long, or the basal bracts scattered; body 15–18 mm wide (7–11 mm, dried), subglobose without lateral bracts; internal bristles up to 0·5 mm long, abundant, white; fig-wall without sclerotic cells. Tepals 4–5, reddish, fading white, lanceolate to spathulate, free, hispidulous upwards or glabrous. Male flowers in 2 rows round the orifice, sessile or pedicellate; stamen 1. Gall- and female flowers sessile and pedicellate, the pedicels often hairy; ovary white, sessile; female style slightly hairy or glabrous. Seed 0·7–0·8 mm long, lenticular, slightly keeled, smooth. Leaf with cystoliths on both sides.

Distr. Solomons, common throughout in lowland primary and secondary forest up to

1400 m alt., often on raised coral beaches near the sea and, occasionally, on ultrabasic soil in *Casuarina* forest as a slender scrambling bush.

Kwara-ae. raranga.

Collections. Brass 3294, 3483; BSIP 4342, 4410; Kajewski 2364; NGF 13776, 16406; RSS 57, 163, 166, 214, 2384, 2451, 2889; Waterhouse B99, 148, 794 ('hituru', 'kiruka', 'lavusu', 'takumpapar', Siwai, Bougainville), 165 ('elokale', New Georgia).

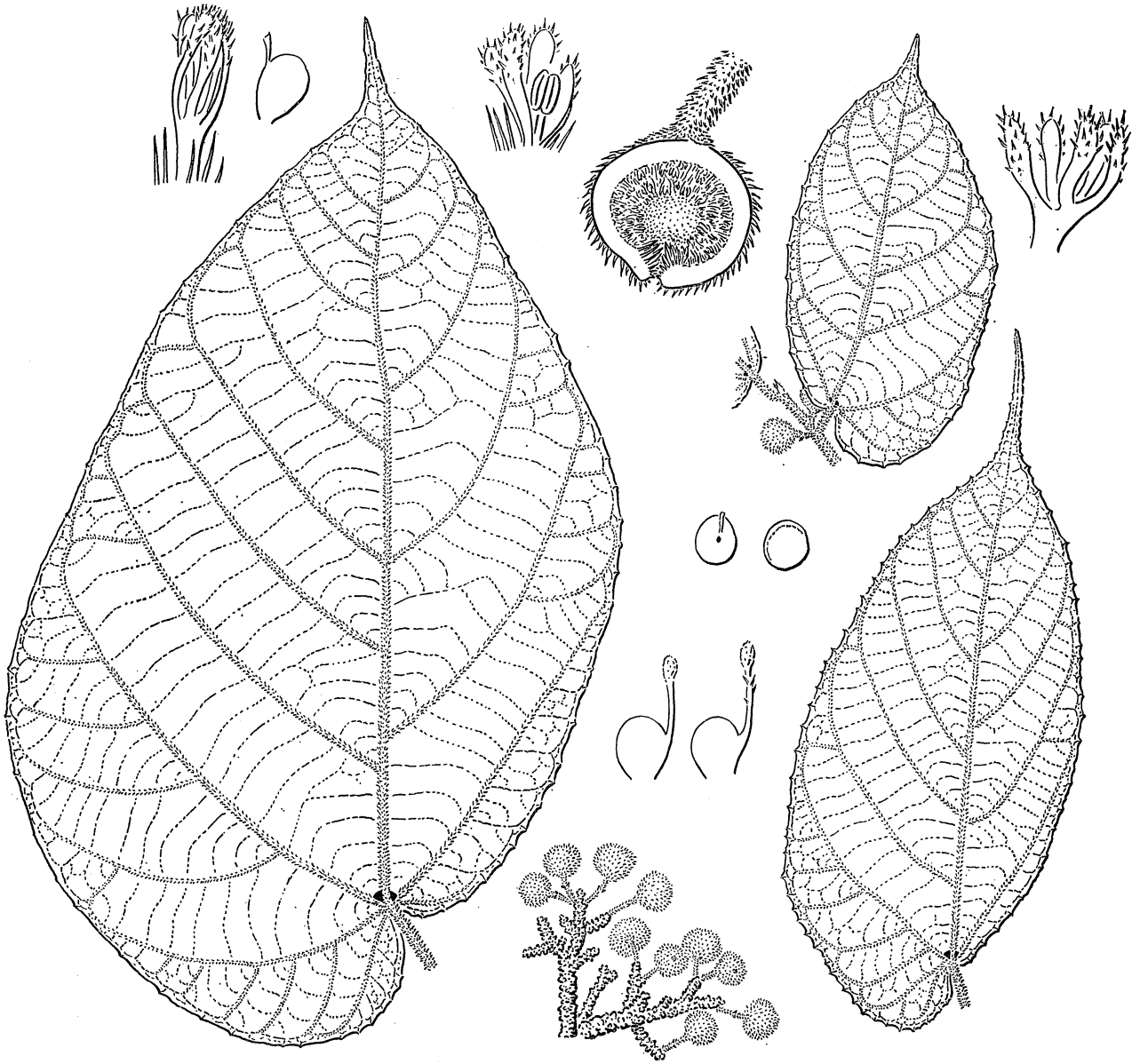

FIGURE 34. Sect. *Sycidium* ser. *Scabrae. F. erinobotrya* var. *solomonensis*; RSS 2451, leaf from the main stem, cauliflorous fig-cluster, female ovaries and seed; RSS 166, leaf (lower right); Kajewski 2364, leaf and twig (upper right), fig-section, male and gall-flowers. Leaf and fig-cluster, $\times \frac{1}{2}$, fig-section $\times 3$, flowers $\times 10$.

f. *glabrior* Corner (figure 35)

Sparsely brownish hispidulous to glabrous. Lamina often less asymmetric, especially on the ultimate twigs.

Collections. Brass 2557; Brown 5054, 5762, 5763, W/265; BSIP 859, 1265, 2425, 4069, 5233, 5559, 5682; RSS 36, 6159, 6202, 6230, 6231, 6347; Waterhouse B260, B315 ('hisigu-sigu', 'koutoro', Siwai, Bougainville).

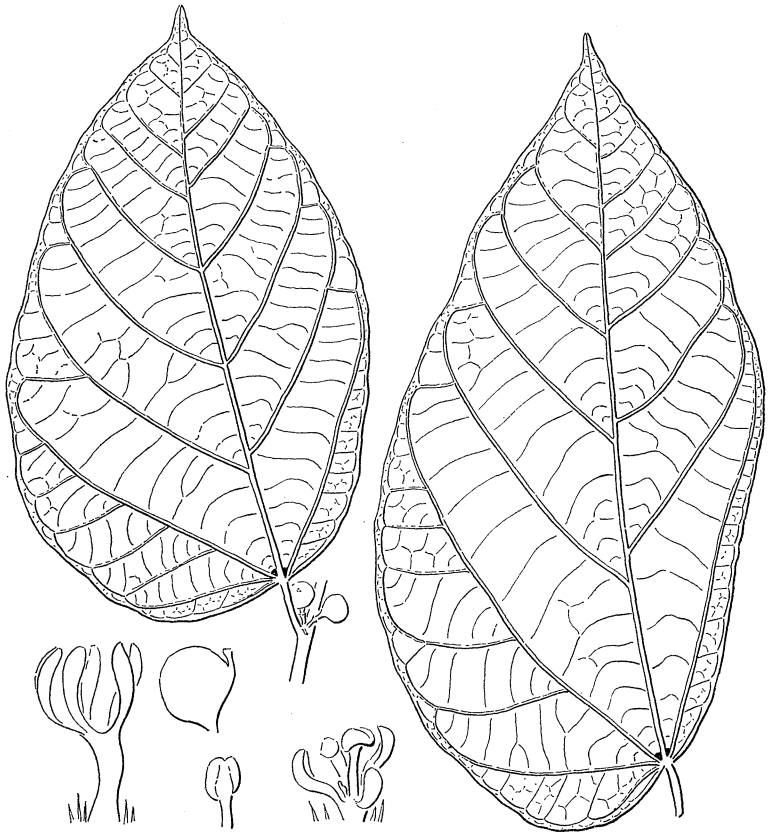

FIGURE 35. Sect. *Sycidium* ser. *Scabrae. F. erinobotrya* var. *solomonensis* f. *glabrior*, Brass 2557, leaf (right), male and gall-flowers; RSS 36, leaf and twig (left). Leaf and twig $\times \frac{1}{2}$, flowers $\times 10$.

These forms of *F. erinobotrya* in the Solomons are progressively more glabrous with smaller and less asymmetric leaves than the typical state in New Britain. The result is a ramiflorous twig that greatly resembles the normal twig of *F. melinocarpa*, but there is no evidence that *F. erinobotrya* develops into a large tree. Nevertheless it resembles, also, the medium-sized tree *F. fulvopilosa* of Fiji. In the Solomons this species seems to be more adaptable in habitat than other species of *Ficus*.

Subgen. *Ficus* sect. *Sycidium* subsect. *Palaeomorphe*

Key to the species in the Solomons

1. Fig with 1–3 small lateral bracts on the body, without sclerotic cells in the wall, drying shrunken. Leaf firmly membranous, without a hypodermis; intercostals 3–8. Terminal stipule often curved. Epiphyte, not strangling. ..... *F. subulata*
1. Fig without lateral bracts on the body, with sclerotic cells (at least the gall-figs), drying smooth. Lamina coriaceous with a hypodermis 1–2 cells thick; intercostals in 1–2. Terminal stipule straight. Strangling figs.

2. Lamina strongly acuminate, more or less symmetric, base cuneate, drying grey-green; lateral veins 7–13 pairs. Fig 7–10 mm wide (dried), often sessile. Tepals thinly hairy. Stomata superficial. ..... *F. virgata*
2. Lamina obtuse to subacute or shortly acuminate, more or less asymmetric, the base rounded to subcordate on the broad side, drying brown areolate beneath; lateral veins 5–9 pairs. Fig larger, always stalked. Stomata sunken. ..... *F. tinctoria*

357. *F. tinctoria* Forst. f. ssp. *tinctoria* (figure 36)

Large strangling fig, sometimes an independent tree up to 15 m high, or dwarfed to a shrub, developing copious aerial roots as a strangler. Leaves distichous. Glabrous except the minutely scabrid–puberulous figs. Twigs 1·5–3 mm thick. Stipules up to 18 mm long, conical, straight. Lamina 6–30 × 3·5–13 cm, oblong–elliptic to ovate–elliptic, acute to

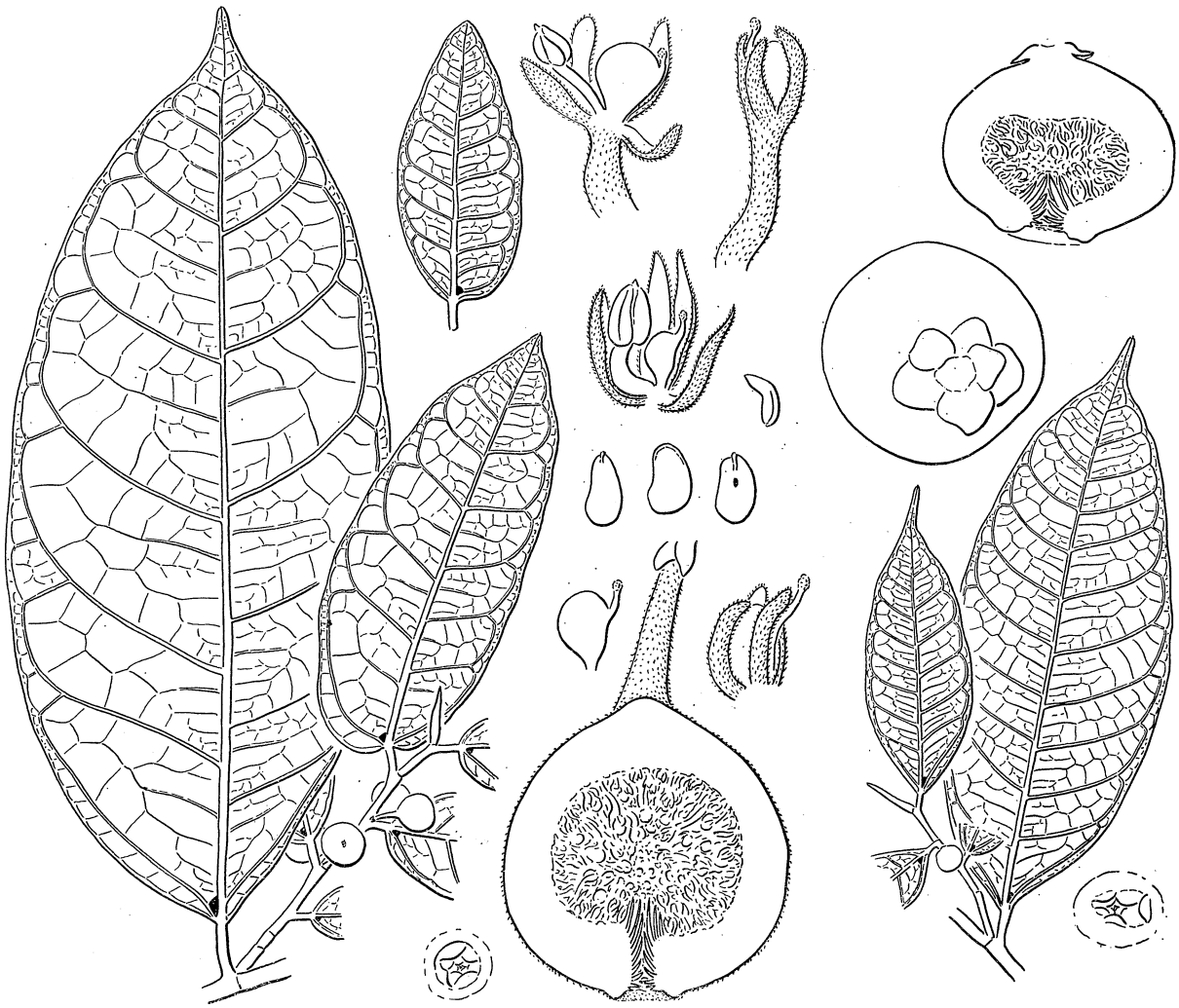

FIGURE 36. Sect. *Sycidium* subsect. *Palaeomorphe*. Right, *F. virgata* var. *sessilis*. Left, *F. tinctoria*. Collections from the Solomons, Corner s.n. Leaf and twig × ½, fig × 3, flowers × 10.

subacuminate or blunt, the base more or less asymmetric, shallowly cordate to rounded on the broad side, rounded to cuneate on the narrow side, entire, coriaceous, subscabrid or smooth, usually drying brown areolate beneath; lateral veins 5–9 (–10) pairs, 1–2 inter-

costals, scarcely raised below; basal veins 1 (–2) short, with a gland on the broader side; petiole 4–20 mm long. Figs axillary, ripening golden-yellow (gall-figs) or red (seed-figs), scabridulous; peduncle none; pedicel 1·5–10 mm long, with 3 small bracts 1–2 mm long at the base; body 10–17 mm wide (dried), pyriform subglobose, without lateral bracts, the plane orifice closed by several small apical bracts; internal bristles minute, abundant; sclerotic cells abundant in the inner wall of gall-figs, few or none in seed-figs. Tepals 3–4 (–5), white, closely puberulous, oblong or lanceolate, free; flower-pedicels puberulous. Male flowers ostiolar in 1–2 rows, sessile or pedicellate; stamen 1, mucronate, with a normal gall-ovary. Gall- and female flowers sessile or pedicellate; ovary white, sessile. Seed 1–1·3 mm long, oblong, subcompressed, not or slightly keeled. Leaf with an upper hypodermis 1–2 cells thick; stomata deeply sunken; cystoliths on both sides.

Distr. Hainan, Formosa, Philippines, Celebes, Sumbawa, Moluccas, Alor, New Guinea, New Britain, New Ireland, north Australia, Micronesia, Polynesia, Solomons.

Ecology. Lowland forest, coastal, mangrove, hill-sides, and ridges to 400 m alt., often as an independent tree or shrub on sea-cliffs and shores.

Kwara-ae. sirifena, sususu.

Collections. Brass 2936; BSIP 873, 1079, 1091, 2541, 2848, 3995, 4711; Brown 118, 708, 3728, W/156; Kajewski 2112; RSS 6184; Waterhouse B 173, 501, 745 ('tari', 'tupare', Siwai, Bougainville; 'wood smoulders and is often used by natives to carry fire about'; 'dried timber burns very slowly and surely').

This is the most widespread species of *Ficus*. It extends as ssp. *parasitica* from West Pakistan and China, through ssp. *gibbosa* in western Malaysia, to Tahiti, but its final spread through Polynesia may have been extended by the use of its timber for carrying fire, as Waterhouse observed in his field-notes. As a strangler, it is distinguished by developing very copious, rather slender, aerial roots in the manner of *F. elastica*, and in the same way these roots do not combine to form a massive, buttressed, basket-trunk. The leaves on the main branches are large but, as in *F. virgata*, they become suddenly much smaller on the side-shoots.

358. *F. virgata* Reinw.

Large strangling fig as *F. tinctoria*, differing in the following points. Lamina with acuminate tip 7–25 mm long, the base cuneate and more or less symmetric, drying grey-green to brownish, not brown areolate beneath; lateral veins 9–13 pairs, but 4–7 in small leaves. Fig-body 7–10 mm wide (dried); basal bracts 0·5–1 mm long. Tepals sparsely puberulous. Gall-flowers often with indurated tepals and ovary. Seed slightly to distinctly knobbed at the apex. Stomata superficial.

Distr. Ryu Kyu, Formosa, Philippines, Celebes, Moluccas, Flores, Alor, Wetar, Timor, Aru and Key Isl., New Guinea, New Britain, New Ireland, Solomons, New Hebrides, New Caledonia, Queensland, Ponape.

Ecology. As *F. tinctoria* but mainly inland, common throughout the Solomons.

Kwara-ae. sirifena, sususu.

Collections. Brass 3162; BSIP 673, 730, 1830, 2551, 2716, 3097, 3328, 3540, 3826; Kajewski 2390.

var. *sessilis* (Bur.) Corner (figure 36)

Fig more or less sessile, without distinct pedicel, often solitary; basal bracts 3–6, 1–3 mm long, ovate–obtuse.

Distr. Luzon, Soela Isl., New Guinea, New Britain, Solomons, New Hebrides, Loyalty Isl., New Caledonia.

Ecology. Common along with var. *virgata.*

Collection. Brass 2556.

The sessile fig with relatively large basal bracts makes a good distinction from *F. tinctoria* whereby to learn the vegetative differences between it and *F. virgata.*

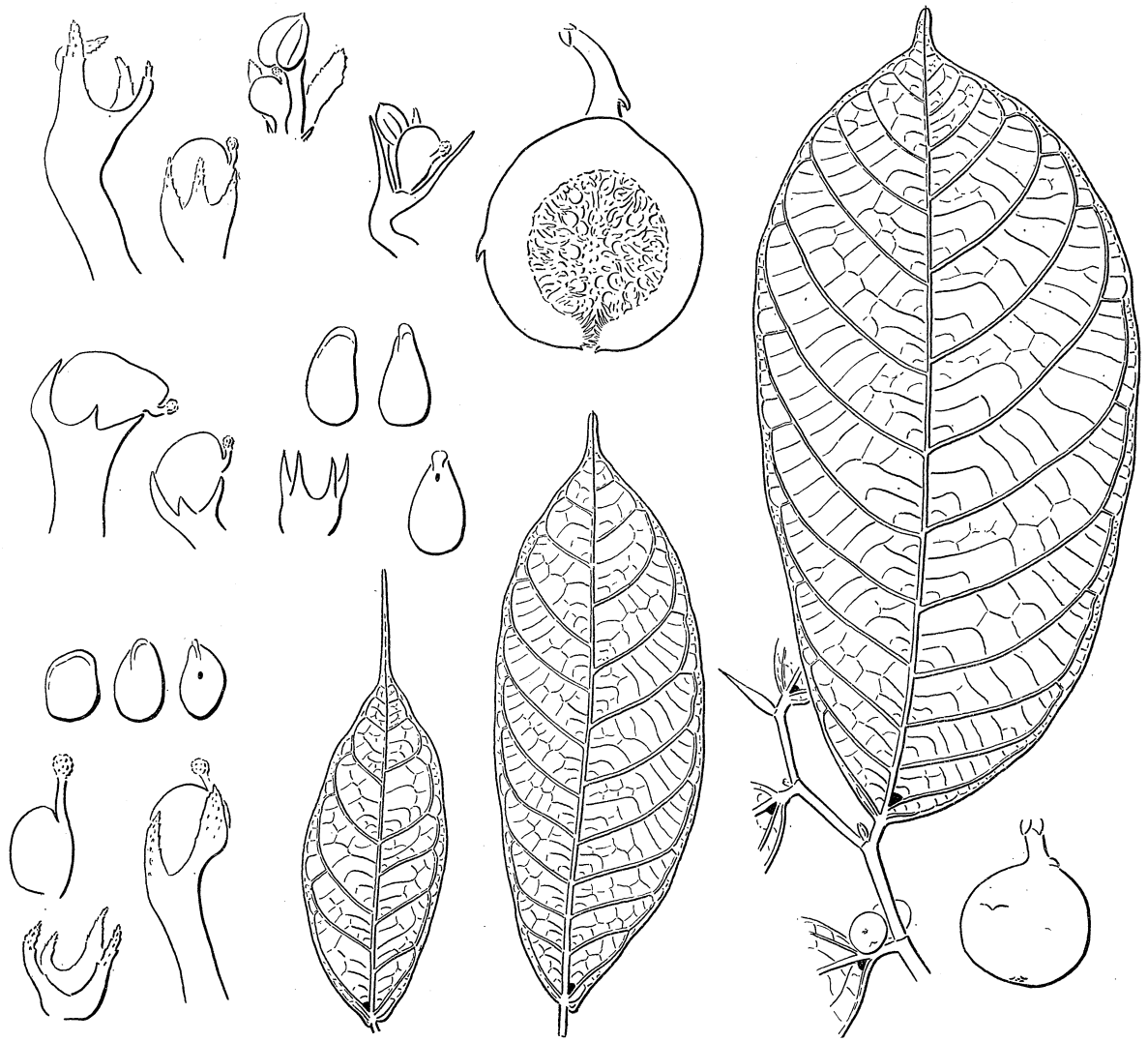

FIGURE 37. Sect. *Sycidium* subsect. *Palaeomorphe. F. subulata,* Corner s.n., Solomons. Leaf and twig $\times \frac{1}{2}$, fig $\times 1$, fig-section $\times 2$, flowers $\times 10$.

360. *F. subulata* Bl. (figure 37)

Shrub or slender tree up to 15 m high, usually epiphytic with a few descending roots, not strangling but often emitting long scrambling and rooting branches. Glabrous or the young parts appressedly puberulous. Twigs 1·5–3 mm thick. Stipule 9–27 mm long,

crescentic–subulate. Lamina 8–28 × 2·5–9 cm (up to 35 × 12 cm in saplings), oblong elliptic, mostly obovate, often somewhat asymmetric, the acuminate or caudate tip 10–30 mm long, base widely to narrowly cuneate, mostly slightly asymmetric, even slightly auricled on one side or unequally decurrent, entire, firmly membranous, smooth, drying grey-green to brownish; lateral veins 8–14 pairs, 3–8 intercostals, slightly raised beneath; basal veins 1 pair, short, with 1 basal gland (sometimes in the axil of the first or second lateral vein); petiole 3–14 mm long (up to 24 mm in saplings). Figs axillary, paired, and in small clusters on the bare twigs, ripening orange (gall-figs) or red (seed-figs); pedicel 1–5 mm long, with 1–3 minute bracts at the base and 1–3 scattered lateral bracts; body 10–16 × 11–20 mm (6–11 mm wide, dried), subglobose, with 1–3 small lateral bracts; internal bristles none; sclerotic cells absent from the rather fleshy fig-wall. Male flowers in 1–2 rings round the orifice, sessile or shortly stalked; tepals 3–4, white, glabrous or puberulous distally, lanceolate-subulate to subspathulate; stamen 1, with a normal gall–ovary. Gall-flowers sessile or with a hard, sclerotic, yellowish pedicel up to 1·5 mm long; tepals as in the male, slightly joined; ovary white, sessile; style glabrous. Female flowers as the gall-flowers but the pedicel not indurate and the style longer. Seed 1–1·3 × 0·6–0·8 mm, oblong, slightly compressed, slightly keeled or not. Lamina with cystoliths only on the lower side; stomata superficial; hypodermis none.

Distr. Sikkim and south China throughout Malaysia to the Solomons.

Ecology. Lowland inland forest in the undergrowth, often swarming on tree-trunks and spreading by the subsarmentose branches to others, but without killing them.

Collections. Brass 2704; Brown 989; BSIP 3335; Kajewski 1584, 1745, 2059, 2263, 2266 ('labit-si-oro', Buin, Bougainville); NGF 13770; RSS 2312.

This rather slender plant is often confused with *F. virgata* and *F. tinctoria*, but it differs in so many points that it readily is distinguishable in the field and the herbarium. A useful mark of identity is the presence of the single gland on the underside of the leaf in the axil of the first or second lateral vein on the broader side of the lamina.

Subgen. *FICUS* sect. *ADENOSPERMA* Corner

Key to the species in the Solomons

1. Leaves with cystoliths on both sides (dried leaves minutely pimply on both surfaces). ser. *Amphigenae.*
   2. Brown hairy. Intercostals numerous, regular. ..... *F. mollior*
   2. Not brown hairy. Intercostals few, lax, or obscure.
      3. Glabrous. Leaves small, in verticils on slender twigs, coriaceous with obscure veining. Fig-stalks 10 mm or more long, slender. ..... *F. verticillaris*
      3. Often whitish hairy. Leaves not so coriaceous, venation distinct, not set in verticils. Fig-stalks mostly shorter. River- and stream side, common. ..... *F. adenosperma*
1. Leaves with cystoliths only on the lower side (dried leaves with smooth upper surface). ser. *Hypogenae.*
   4. Glabrous or puberulous. Lamina 8–15 cm wide, obovate. Stipule 2–5 cm long. Fig 2 cm wide, without lateral bracts and internal bristles. Seashores. ..... *F. austrina*
   4. Young shoots silky hairy. Lamina narrower, often lanceolate, with close intercostals. Stipule shorter. Fig smaller, with 1–2 small lateral bracts and copious internal bristles. Inland forest. ..... *F. erythrosperma*

382. *F. mollior* Benth. (figure 38)

Tree up to 25 m high, not or scarcely buttressed. Leaves spirally arranged. Twigs, petioles, underside of main veins, and figs closely pubescent with appressed or spreading, pale fulvous to brown hairs 1–2·5 mm long, thinly villous with shorter hairs on the smaller veins beneath. Twigs 2–3 mm thick. Stipule up to 15 mm long, caducous, appressedly

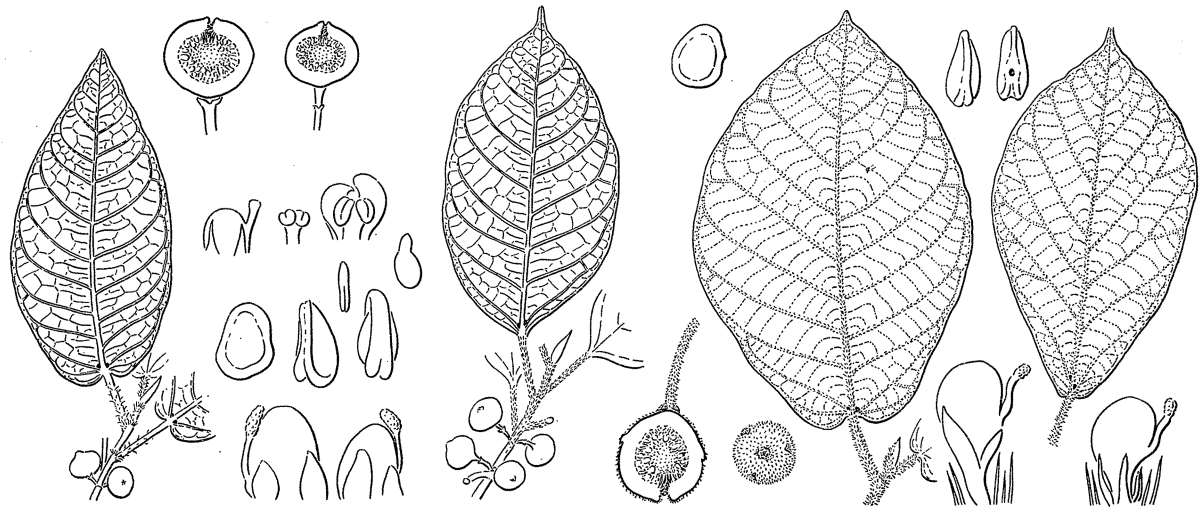

FIGURE 38. Sect. *Adenosperma*. Right, *F. mollior*, RSS 2833. Centre, *F. adenosperma* and left var. *chaetophora*, RSS 6140. Leaf and twig $\times\frac{1}{2}$, fig $\times 1$, flowers $\times 10$.

hairy on the keel. Lamina 7–19 × 4–12 cm., reducing to 3–6 × 2–3·5 cm on tall trees, broadly elliptic to obovate, subacute to bluntly acuminate with a tip up to 10 mm long, rarely subcaudate, base widely cuneate to rounded or subcordate, entire or crenato-sinuate on young plants, subcoriaceous, smooth, drying fulvous brown; lateral veins 6–9 (–10) pairs, 3–9 regular intercostals raised below; basal veins 2–4 pairs, short, with 2 basal glands; petiole 10–60 mm long. Figs axillary, paired, to ramiflorous and cauliflorous in clusters from the base of the trunk, on short leafless twigs up to 30 × 6 mm, without internodes, ripening yellowish; peduncle 2·5–10 mm long, or 10–20 mm in cauliflorous figs, basal bracts in a collar, 1–2·5 mm long, persistent; body 12–18 mm wide, subglobose, with a few small lateral bracts, sometimes without, the orifice surrounded by 5–9 umbonate peripheral bracts with many smaller inner ones; internal bristles abundant, white, 0·5–1 mm long; sclerotic cells as a continuous layer in the endocarp of gall-figs, few or none in seed-figs. Tepals 3 (–4), free or 2–3 shortly joined, reddish, spathulate or broadly lanceolate in the female flower, glabrous. Male flowers sessile in 1–2 rings round the orifice; stamen 1, without pistillode. Gall- and female flowers sessile or shortly stalked; ovary sessile or stalked, reddish or red-spotted with pale sides; style strongly lateral, especially in the female flower, glabrous. Seed 1·3–1·4 × 1·0 × 0·6–0·7 mm, rather strongly keeled. Leaves with cystoliths on both sides.

Distr. Amboina, New Guinea, New Britain, New Ireland, Solomons, Queensland.

Ecology. Lowland forest up to 1400 m alt., particularly by streams, common throughout the Solomons.

Kwara-ae. aitia, alanggia.

Collections. BSIP 1098, 2851, 3449, 5839; Kajewski 1684; NGF 13553, 13558, 13565; RSS 84, 144, 206, 1525, 2833, 6054.

This is distinguished from *F. adenosperma* by the brown hairiness and the numerous regular intercostals. It is variable for some trees have only axillary figs, others only cauliflorous, and yet others have both kinds. Then, some trees lack the lateral bracts on the fig. They may be mistaken for *F. indigofera* which has very short appressed pubescence.

385. *F. verticillaris* Corner (figure 39)

Shrub or small tree up to 16 m high. Leaves spirally arranged in close rosettes, generally appearing verticillate, stiff, rigid, glossy, drying brittle. Glabrous. Twigs 1·5–2·5 mm thick. Stipule small, caducous. Lamina up to 11 × 5 cm, narrowly elliptic or obovate, obtusely

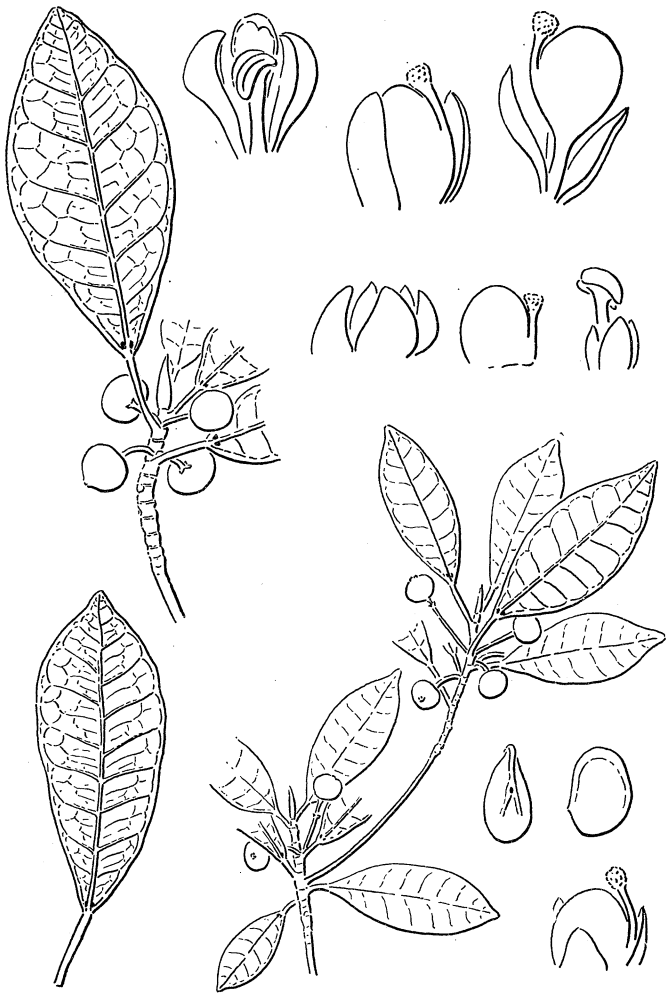

FIGURE 39. Sect. *Adenosperma. F. verticillaris* and var. *robusta* (upper left). Leaf and twig × ½, flowers × 10.

subacute to subacuminate, base cuneate, entire, subscabrid, drying grey-green; lateral veins 8–13 pairs, 0–1 intercostals, only the main veins visible beneath; basal veins 1 pair, short; petiole 10–18 mm long. Figs axillary, solitary or paired, ripening red to purple-black; peduncle 4–18 mm long, slender; basal bracts 3, minute, in a collar, up to 0·5 mm

long, caducous; pedicel 2–6 mm long; body up to 12 mm wide (7–8 mm, dried), subglobose, without lateral bracts; internal bristles few, brownish, or none; sclerotic cells abundant in the endocarp of the fig-wall. Tepals 4–5, red, ovate, free, glabrous, equal to or shorter than the ovary. Male flowers in one ring round the orifice, sessile; stamen 1. Gall-flowers sessile; ovary sessile, pale ochraceous then reddish. Female flowers sessile; tepals 3–4, subtriangular, shorter than the white ovary; style strongly lateral or nearly basal. Seed with slight median and very slight lateral keels, the base not keeled. Lamina with cystoliths on both sides; stomata superficial.

Distr. Solomon Islands, frequent throughout in lowland forest up to 1400 m alt.

Kwara-ae. fa-adila, fadiyala, fihadila, ha-adila.

Collections. Brass 2838, 3488, 3523; BSIP 202, 608, 1247, 1379, 2231, 2966, 3139, 3539, 3718, 3965, 4114, 4142, 4176, 4278, 5261, 5517, 5647, 5831; Kajewski 2155 ('kera-rom', Buin, Bougainville), 2366, 2584; NGF 13763; RSS 2608.

Var. *robusta* Corner

Twigs, petioles, figs, and underside of lamina puberulous. Twigs 3–4 mm wide. Stipule up to 18 mm long. Lamina up to 12 × 4·5 cm, scabrid below; lateral veins 8–9 pairs; petiole up to 18 mm long. Fig 12–15 mm wide; peduncle up to 10 mm long; basal bracts 1·5 mm long. Stomata deeply sunken.

Distr. Solomon Islands, widely distributed as var. *verticillaris*.

Collections. Brass 2883; Brown W/347; BSIP 1017, 3092, 4333, 4403, 4407.

This small tree has the most small-leafed crown of any species of *Ficus* in the Solomons, but the leaves are unusually coriaceous, and this feature is the best distinction from the similar *F. smithii* of subgen. *Pharmacosycea*. It is an endemic and its alliance appears to be with the little known riverside shrub *F. arbuscula* (Moluccas to New Guinea). Var. *robusta* is stouter in all parts and has sunken stomata; this point turns up now and again in several species of *Ficus*, as in *F. agapetoides* var. *solomonensis* and *F. tinctoria*, and it is caused by the deepening of the lower epidermal cells so as to raise the epidermis beyond the level of the stomata. In subgen. *Urostigma*, by contrast, where sunken stomata are common, a lower hypodermis is developed to project the lower epidermis. Possibly the key-species that joins *F. verticillaris*, *F. arbuscula*, and *F. adenosperma*, as well as *F. umbonata* (Moluccas to New Guinea) with sunken stomata, is the New Guinea endemic *F. comitis*.

386. *F. adenosperma* Miq. (figure 38)

Tree up to 20 m high, not or slightly buttressed, fruiting at 5 m; branches widespreading. Leaves spirally arranged. Twigs, petioles, and underside of the main veins closely and more or less appressedly hairy with pale fulvous hairs 1–2 mm long, slowly glabrescent. Twigs 1·5–2·5 mm thick. Stipules 7–25 mm long, glabrous or hairy on the keel, caducous. Lamina 5–18 × 3–7·5 cm, elliptic, ovate, or lanceolate, subacute to subacuminate, base subcordate to cuneate, rarely cordate, entire, subcoriaceous, smooth, drying grey-green; lateral veins 8–13 pairs, 1–4 lax and often ill-defined intercostals; basal veins 1–2 (–3) pairs short, with 2 basal glands; petiole 6–40 mm long. Figs axillary, paired, then in many trees ramiflorous to cauliflorous on short leafless twigs, thinly appressedly hairy, glabrescent, ripening greenish yellow; peduncle 1–11 mm long; basal bracts 3, 1–1·5 mm long, in a

collar or scattered; pedicel 0–3 mm long; body 9–18 mm wide (7–11 mm, dried), subglobose to pyriform, mostly with 1–3 small lateral bracts, the plane orifice closed by 3–5 small apical scales; internal bristles 0·5–1 mm long, few, white to brownish; sclerotic cells abundant in the fig-wall, or few in seed-figs. Tepals 3–4, reddish, glabrous, free, lanceolate to subspathulate, shorter than the ovary. Male flowers in one ring round the orifice, sessile; stamen 1, no pistillode. Gall- and female flowers sessile; ovary red or red-spotted; style nearly basal, glabrous. Seed 1·5–1·8 × 1·1–2 × 0·5 mm, much compressed, bluntly keeled all round, smooth. Leaves with cystoliths on both sides.

Distr. Celebes, Moluccas, Tenimber and Aru Isl., New Guinea, Admiralty Isl., New Ireland, New Britain, Solomons, New Hebrides.

Ecology. Very common by rivers and streams in lowland forest up to 1400 m alt., especially along de-forested banks, often forming thickets on sand-banks and among boulders.

Kwara-ae. alanggia.

Collections. BSIP 977, 1061, 1537, 1783, 1859, 3282, 3364, 4737; RSS 6053, 6140.

Var. *chaetophora* (Warb.) Corner (figure 38)

Twigs and petioles with spreading white to brown hairs 1–3 mm long, especially at the nodes. Lamina narrowly cordate, rounded, or widely cuneate, with 2–4 (–5) pairs of basal veins. Figs laxly brown pilose when young.

Distr. New Guinea, New Britain, New Ireland, Solomons, New Hebrides.

Ecology. As var. *adenosperma.*

Collections. BSIP 3675, 4281.

Var. *glabra* Corner

Almost or completely glabrous. Lamina often rather narrow, cuneate at the base; lateral veins (5–) 8–12. Fig without lateral bracts on the body; peduncle often short or absent and, then, with bracts at the base of the pedicel.

Distr. Key Isl., New Guinea, New Britain, Solomons, Queensland.

Ecology. As var. *adenosperma.*

Collections. Brass 3378; Brown 1423; BSIP 930, 2042; Kajewski 1546, 2121 ('too-ror-lee', Buin, Bougainville), 2338, 2448, 2480, 2787; NGF 13555; RSS 2459.

This is the commonest fig of the Solomons, where it may extend for long distances on the banks of lowland rivers. It is, in fact, the riverside willow-fig from Celebes to New Hebrides and, thus, the most widespread and one of the most advanced species of sect. *Adenosperma.* Its varieties seem in no way limited geographically or ecologically. Var. *chaetophora* approaches in hairiness *F. mollior*, but there are practically all transitions to var. *glabra.* The greenish yellow figs are produced in vast numbers, often littering the pebbly riversides, and are eaten mainly by flying foxes.

387. *F. austrina* Corner (figure 401)

Tree up to 20 m high, with *Terminalia*-habit. Leaves spirally arranged. Twigs and petioles appressedly hairy with pale fulvous straight hairs up to 1 mm long, varying almost glabrous. Twigs 3–5 mm thick. Stipules 20–50 mm long, lanceolate, glabrous, projecting, caducous. Lamina 11–23 × 6–15 cm, obovate, obtuse or subacute, base rather narrowly subcordate

to rounded-cuneate, entire, smooth, membranous to subcoriaceous, drying light grey-brown; lateral veins 5–11 pairs, rather widespaced, slightly raised below; intercostals 5–12, lax, not raised below; basal veins 3 (–4) pairs, short or reaching one third of the lamina; petiole 10–40 mm long. Figs axillary, stalked or sessile, glabrous, ripening greenish yellow or yellow; peduncle 0–13 mm long, rather short and thick; basal bracts 3, in a collar, 1–2 × 2–2·5 mm, subcrescentic, obtuse; body 25–30 mm wide (15 mm, dried), depressed globose, without lateral bracts, the five peripheral apical bracts slightly projecting, forming a small umbo in the dried fig; internal bristles none; sclerotic cells abundant in the fig-wall. Flowers sessile. Tepals 3–5, pinkish, spathulate or, in female flowers, lanceolate, free, as long as or longer than the ovary. Male flowers in one ring round the orifice; stamen 1, no pistillode. Ovary sessile or shortly stalked, red-brown; style glabrous, strongly lateral. Seed without the double basal keel. Lamina with cystoliths only on the lower side.

Distr. Key Isl., (? Amboina), west New Guinea (Ransiki), New Ireland, Solomons, New Hebrides (Banks Group, Vanua Levu).

Ecology. On sandy coasts and coral limestone near the sea, locally abundant throughout the Solomons.

Kwara-ae. aitia, bubulia.

Collections. Brass 2574; BSIP 2166, 2240; RSS 26, 54, 2780; Waterhouse 176.

This characteristic seashore tree appears to be near to the inland forest tree *F. casearioides* of New Guinea. In habit it bears much resemblance to *Terminalia catappa* and seems also to be deciduous, but the old leaves wither yellow. Brass and Waterhouse remark in their field notes on its handsome bearing.

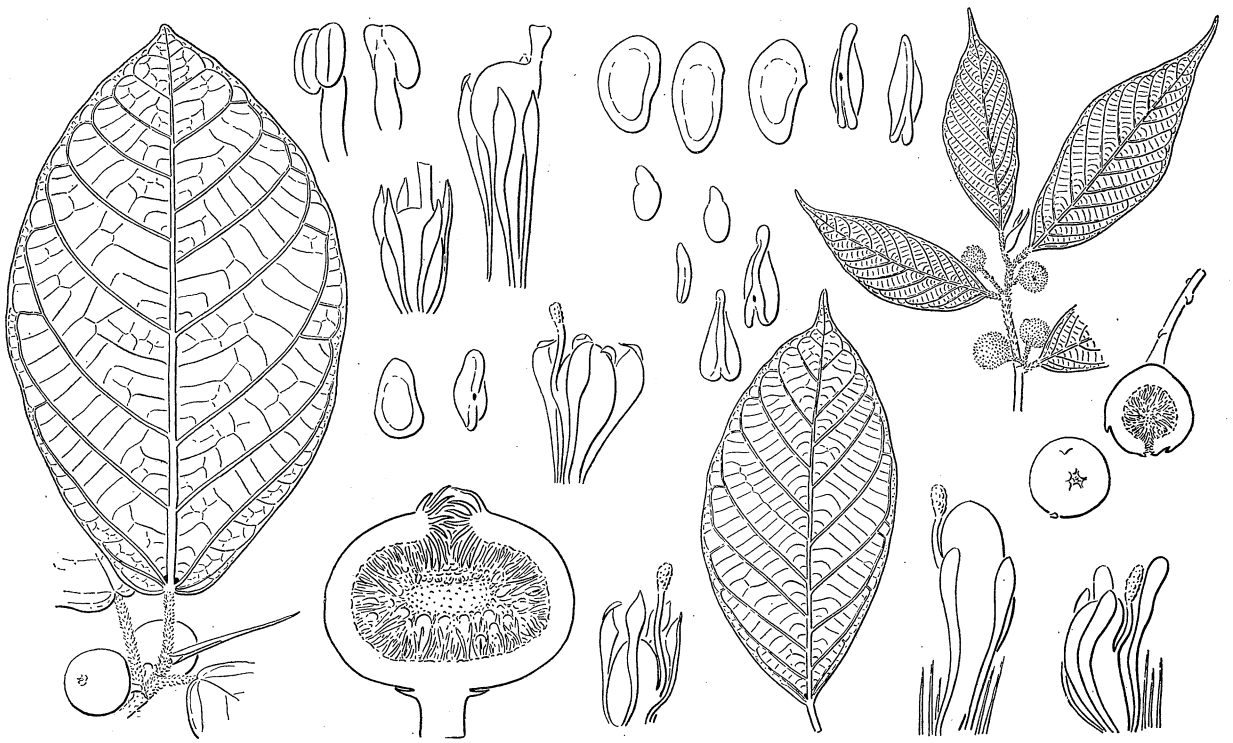

FIGURE 40. Sect. *Adenosperma*. Right, *F. erythrosperma* and left, *F. austrina*. Leaf and twig × ½, fig-section × 1½, flowers × 10.

394. *F. erythrosperma* Miq. (figure 40)

Tree up to 28 m high, becoming buttressed up to 3 m high, fruiting as a slender sapling 2 m high; bark pinkish or orange-brown, rather scaly. Leaves spirally arranged, often laxly, to subdistichous, young leaves reddish, mature leaves often red-veined beneath. Twigs, stipules, petioles, underside of main veins, and figs thinly appressedly pubescent with straight, pale fulvous hairs 1–2 mm long, glabrescent, or the twigs subvillous for some time with short flexuous hairs; young leaves densely hairy on emergence. Twigs 2–3 mm thick. Stipules 10–27 mm long, caducous. Lamina 5·5–18 × 1·5–8 cm, elliptic varying subobovate to lanceolate, with a shortly acuminate or subcaudate tip 7–12 mm long, base cuneate, often slightly asymmetric, entire or subcrenate distally, membranous to subcoriaceous, smooth, drying brown; lateral veins 7–12 pairs, oblique, with 5–11 regular and close intercostals, slightly raised beneath; basal veins 1 (–2) pairs, short, with 1–2 basal glands; petiole 5–20 mm long. Figs axillary or, in some trees, eventually cauliflorous on short woody tubercles, soon glabrous, ripening greenish yellow; peduncle 1–10 mm long; basal bracts 3, 1–2 mm long, in a collar; pedicel 0–15 mm long, generally longer than the peduncle; body 15–20 mm wide (10–15 mm, dried), subglobose to pyriform, 0–2 small lateral bracts, the orifice surrounded by 5–7 small, umbonate, apical bracts; internal bristles copious, white to fulvous, 0·5–1 mm long; fig-wall without sclerotic cells. Flowers sessile. Tepals 4–5, red, free, glabrous, linear–spathulate, equal to or longer than the sessile ovaries. Male flowers in 1–2 rings round the orifice; stamen 1, no pistillode. Ovaries sessile or thickly stalked, dark red; style strongly lateral, glabrous. Seed 1·8–2 mm long, compressed, rather strongly and narrowly keeled. Leaves with cystoliths only on the lower side.

Distr. North Celebes, Ceram, Ternate, Amboina, Key Isl., New Guinea, New Ireland, New Britain, Solomons.

Ecology. Common in lowland forest up to 1200 m alt., sometimes reaching the canopy, generally as a smaller riverside or streamside tree, throughout the Solomons.

Kwara-ae. aitia, aitia-misu.

Collections. Brass 2691; BSIP 700, 758, 932, 1095, 1451, 3269, 3354, 3639, 4049, 5333, 5497; Kajewski 1689, 2260, 2550; NGF 13725, 13767; RSS 31, 1245, 2295, 2531, 6179, 6201; Waterhouse B 212 ('koesakura', Siwai, Bougainville).

This species in ser. *Hypogenae* is comparable in distribution and advancement with *F. adenosperma* in ser. *Amphigenae*. It frequently develops lanceolate leaves in streamside situations, but it is not adapted to the open habitats of *F. adenosperma*. It can generally be detected in the forest, especially when trunks are wet, from the very unusual orange bark. There seems to be much variation in the degree of hairiness, but I have been unable to draw any varietal limits.

Subgen. *FICUS* sect. *NEOMORPHE* King

For the key to the two species, see Group C, §2, p. 59.

397. *F. variegata* Bl. (figure 41)

Deciduous tree up to 40 m high, strongly buttressed; bark pinkish brown. Glabrous or the young parts finely white pubescent, or the leaves finely subvillous beneath at first. Twigs 2–4 mm thick. Stipules 6–18 mm long, caducous. Lamina 8–33 × 3–15 cm, ovate,

acute or acuminate with the tip up to 15 mm long, base cordate, rarely rounded, membranous to coriaceous, smooth, entire, but coarsely dentate in the sapling, drying brown; lateral veins 4–8 pairs, 5–10 regular intercostals, raised below; basal veins 2 pairs, reaching one third to one half of the lamina, generally with two small glands in axillary slits by the main basal veins; petiole 2–14 cm. long, becoming brown scurfy. Figs ramiflorous and cauliflorous on leafless, clustered, sparingly branched twigs up to 12 cm long, sometimes so numerous as to conceal the trunk and branches, ripening rose-red, often faintly striped; peduncle 15–60 mm long; basal bracts 3, in a collar, 1–1·5 mm long; pedicel 0–5 mm long; body 25–35 mm wide (15–25 mm, dried), subglobose or shortly pyriform, without lateral bracts, the orifice plane or slightly sunken, closed by numerous small apical bracts; internal bristles none; sclerotic cells few or none. Tepals 3–4, lanceolate or spathulate, free or shortly joined, glabrous, entire, red to brown. Male flowers in 2 rings round the orifice, sessile, compressed; perianth extensively gamophyllous; stamens 2 (1–3), occasionally with a pistillode, the filaments shortly joined. Gall- and female flowers sessile or shortly stalked; ovary red or red-brown, sessile or shortly stalked; style short, glabrous; stigma stout, conical, simple. Seed 1–1·5 mm long, lenticular, slightly keeled, smooth. Lamina with cystoliths only on the lower side.

Distr. India, throughout Malaysia to the Solomons and Queensland.

Ecology. Lowland forest and secondary forest up to 1200 m alt., common throughout the Solomons.

Kwara-ae. sala; meto (Ari-ari, Malaita).

Collections. BSIP 3121, 5625; Comins 128 ('aramanu', San Cristobal); RSS 2915, 6141, 6232; Waterhouse B 28 ('beo', Buka), 358 ('duri', New Georgia); D. de Coppet s.n. 1964, 'bark beaten, used for babies wear, as calico in olden times for women and men at Guadalcanal; waistcoat against arrows'.

This large tree is readily recognized in the forest from its pinkish brown bark, strong sharp buttresses, and white latex.

399. *F. nodosa* Teysm. et Binn. (figure 41)

Tree up to 30 m high, resembling *F. variegata* but larger in all parts and with different tepals. Twigs 4–8 mm thick. Lamina 10–40 × 8–30 cm, ovate acute, more or less deeply cordate; lateral veins 4–7 pairs, up to 10 regular intercostals; basal veins 3–4 pairs, reaching one half to two thirds of the lamina; petiole 2–15 cm long. Figs on cauliflorous and ramiflorous twigs up to 60 cm long, ripening yellow to purple-brown, strongly pustulate with lenticels; peduncle 5–13 × 3–5 mm; basal bracts 3–4 mm long; body 30–50 mm wide (25–35 mm, dried); fig-wall with internal projections bearing the flowers. Tepals laciniate–dentate, more or less joined.

Distr. Moluccas, New Guinea, New Ireland, New Britain, Solomons.

Ecology. Lowland swampy forest, particularly by riversides, throughout the Solomons.

Kwara-ae. sala.

Collections. Brass 2659; Brown 5484, W/82; BSIP 1083, 4282; Waterhouse B 303 ('nung', Siwai, Bougainville).

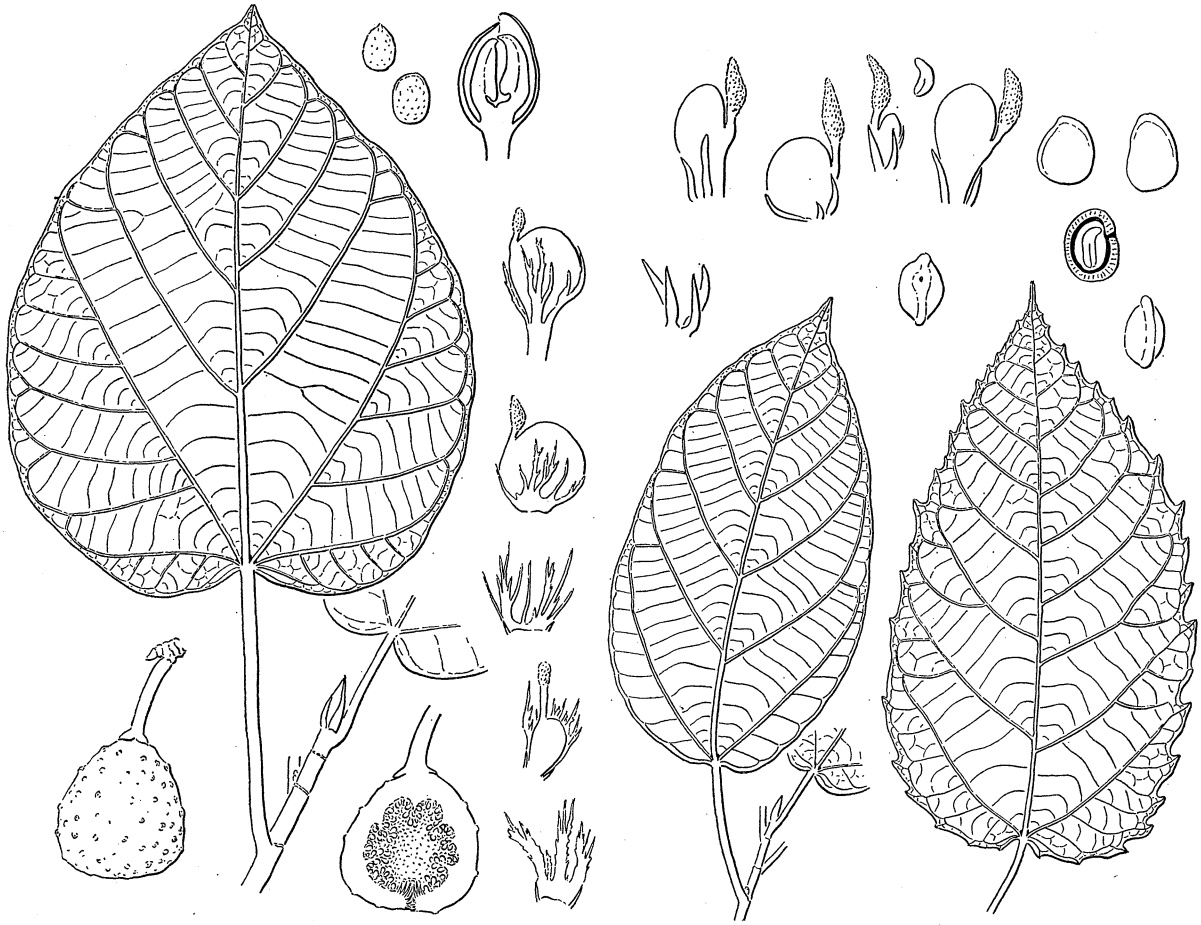

FIGURE 41. Sect. *Neomorphe*. Right, *F. variegata* with dentate sapling leaf, and left, *F. nodosa*. Leaf and twig $\times \frac{1}{2}$, fig $\times \frac{1}{2}$, flowers $\times 10$.

Subgen. *FICUS* sect. *SYCOCARPUS* Miq. subsect. *AURICULISPERMA*

Key to the species in the Solomons

1. Stiffly brown hairy, the hairs 3–7 mm long. Long-petiolate. Figs sessile, axillary, often concealed by the large persistent stipules; basal bracts 7–25 mm long; apical bracts projecting. Stamens 2–3; anthers mucronate; ovary red-brown. ..... ser. *Cynaroides*
   2. Basal veins reaching one third of the lamina or less; lateral veins 9–16 pairs, with close intercostals little prominent. Lamina entire, widely cuneate. Figs without lateral bracts, concealed by the glabrous or silky stipules 9–13 cm long. Twigs 10–12 mm thick, ... *F. cynaroides*
   2. Basal veins reaching one half of the lamina; lateral veins 7–11 pairs, very prominent. Lamina often denticulate. Figs with lateral bracts. Stipules glabrous or brown hairy.
      3. Leaf-base cordate. Stipules up to 10 cm long, persistent. Twigs 8–12 mm thick. Figs 30–40 mm wide. ..... *F. immanis*
      3. Leaf-base cuneate to rounded. Stipules up to 4 cm long, often caducous. Twigs 4–6 mm thick. Fig 20–25 mm wide. ..... *F. lancibracteata*
1. Glabrous or whitish hairy. Figs stalked, cauliflorous and axillary. Stamen 1; anther not mucronate.

4. Freely branched small leptocaul tree. Twigs 2–3 mm thick. Lamina up to 23 × 14 cm, with slender petiole. Figs 18–25 mm wide; basal bracts 1–3 mm long. Ovary red-brown. Ser. *Vitienses*. ..... *F. indigofera*

4. Unbranched or sparingly branched pachycaul trees or shrubs. Twigs 5–20 mm thick. Lamina over 30 cm long; petiole short, thick. Ovary yellowish white. Ser. *Theophrastoides*.

5. Tree. Twigs 12–20 mm thick. Lamina 80–200 cm long, scabrid. Figs verrucose, cauliflorous in large masses; lateral bracts 9–16 mm long; peduncle 30–80 mm long. ..... *F. salomonensis*

5. Shrub. Twigs 5–10 mm thick. Lamina 30–90 cm long, smooth. Figs smooth, without lateral bracts, axillary and in bunches at the base of the stem; basal bracts 1·5–9 mm long; peduncles 3–10 mm long. ..... *F. theophrastoides*

FIGURE 42. Sect. *Sycocarpus* subsect. *Auriculisperma*. Left, *F. salomonensis* and sapling. Centre, *F. theophrastoides*. Right, *F. cynaroides* and sapling, $\times\frac{1}{100}$.

402. *F. cynaroides* Corner (figures 42 to 45)

Tree up to 13 m high with rather few, stout, widespread branches ending in compact rosettes of large, spirally arranged leaves; bark grey, smooth; latex white, copious, very rubbery. Twigs, petioles, and upperside of midrib strigose with spreading dark brown to purple-brown wiry hairs 2–7 mm long; underside of veins minutely and closely puberulous to nearly glabrous; figs densely hispid with stiff purple-brown hairs 1–2 mm long. Twigs 10–12 mm thick. Stipules 7–13 × 2–3 cm, lanceolate, very long, scarious, persistent, concealing the figs, closely pallid silky-hairy to nearly glabrous. Lamina 20–40 × 10–25 cm, elliptic, ovate or subobovate, shortly acuminate, base widely cuneate, entire, thinly coriaceous, smooth or subscabrid below, drying brown; lateral veins 9–13 (–16) pairs,

oblique, raised below, with 10–22 regular intercostals slightly raised below; basal veins 3 pairs, short or reaching to one third of the lamina, with 2 basal glands; petiole 2–12 cm × 4–6 mm (up to 45 cm × 8 mm, sapling), without a subnodal gland. Figs axillary, paired, compressed, sessile, ripening greenish brown; basal bracts 3–4, 7–15 × 2–4 mm, lanceolate, appressedly brown hairy; body 24–28 mm wide (16–20 mm, dried), depressed globose, without lateral bracts, the apical bracts 6–8, 4–6 mm long, ovate–lanceolate, erect, incurved, in a loose rosette; internal bristles none; sclerotic cells none. Male flowers in 2 rings round the orifice, stalked, with 2 bracteoles; perianth saccate; stamens 2, anthers mucronate, filaments free, no pistillode. Gall-flowers sessile to stalked; perianth cupular, entire, covering one quarter to two thirds of the dark red ovary, often oblique. Female flowers as the gall; perianth reaching the base or lower third of the red-brown ovary; style glabrous. Seed 1·4–1·6 × 1·0 × 0·8 mm, auriculiform, smooth, the hilum not projecting. Leaf with cystoliths only on the lower side.

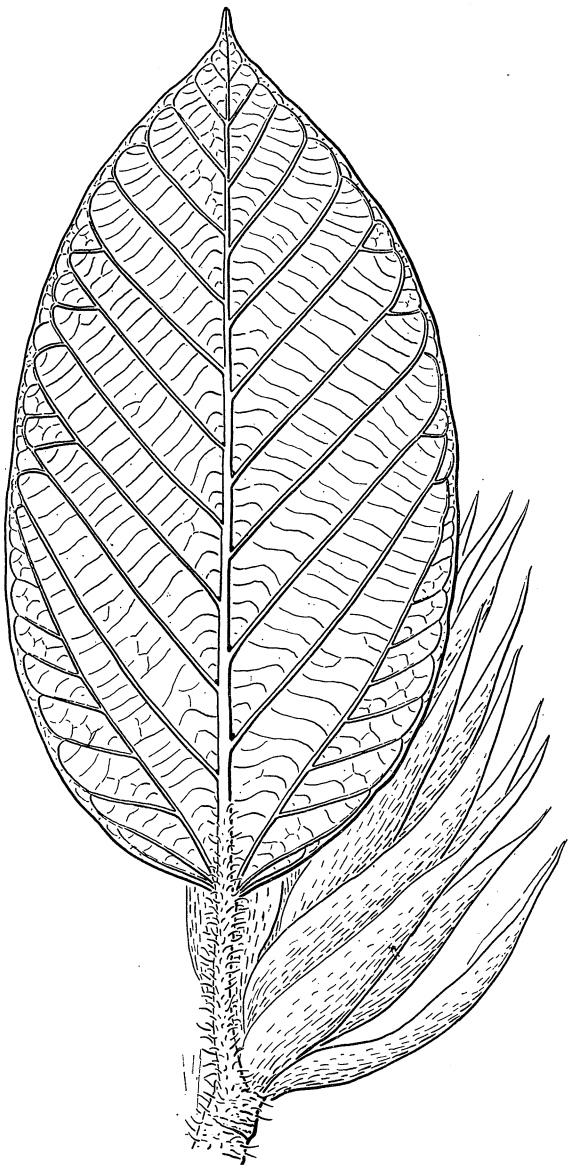

FIGURE 43. Sect. *Sycocarpus* subsect. *Auriculisperma*. *F. cynaroides*, Kajewski 1856, × ½.

Distr. Solomons, frequent throughout in lowland forest, on hill-sides and by streams up to 800 m alt.

Kwara-ae. aidadela, aita-hisi-oro (rainbow tree), dedelanone.

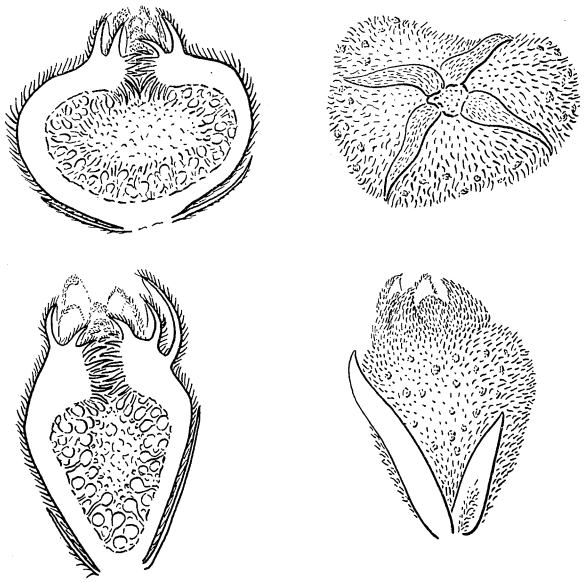

FIGURE 44. Sect. *Sycocarpus* subsect. *Auriculisperma. F. cynaroides*, Kajewski 1856 (above) × 1½; Corner s.n. Ysabel, (below) × 1.

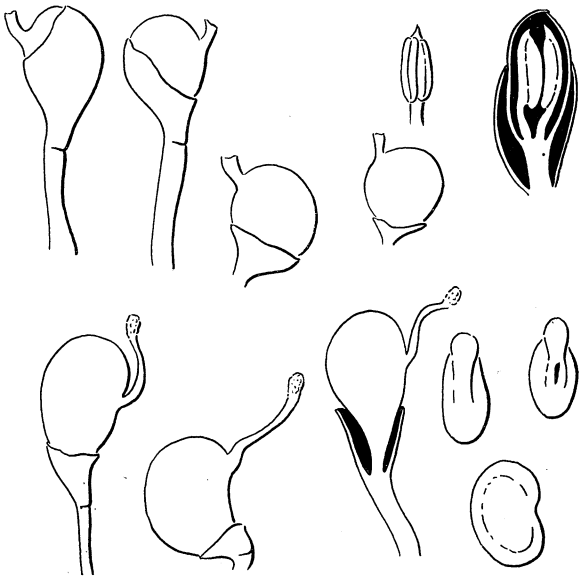

FIGURE 45. Sect. *Sycocarpus* subsect. *Auriculisperma. F. cynaroides*, Waterhouse 845 (above) male and gall-flowers; Kajewski 1856 (below) female flowers and seed; × 10.

Collections. BSIP 904, 1173, 1986, 2657, 2745, 3255, 5339; Kajewski 1856 ('oogonu', Buin, Bougainville); NGF 13744 ('marero', Kupei, Bougainville); RSS 1246; Waterhouse 202, 265, 578, 845 ('hongokokihoi', 'mukamuka', Siwai, Bougainville).

The twigs of this striking tree appear to end in globe-artichokes, made of the clusters of

long stipules. The figs are hidden within these so that trees generally appear sterile. The name 'rainbow fig' refers to the purplish brown or ruddy cast of the leaves as seen from below, especially in saplings.

402A. ***F. immanis*** sp.nov. (figures 46, 47)

Arbor usque 10 m alta, habitu *F. cynaroides*, foliis longipetiolatis, spiraliter dispositis. Ramuli petioli costaeque (subtus) pilis rigidis purpureo-brunneis usque 6 mm longis setosi. Ramuli 8–12 mm crassi. Stipulae 2–10 cm longae, glabrae v. basim versus brunneo-setosae, persistentes. Lamina

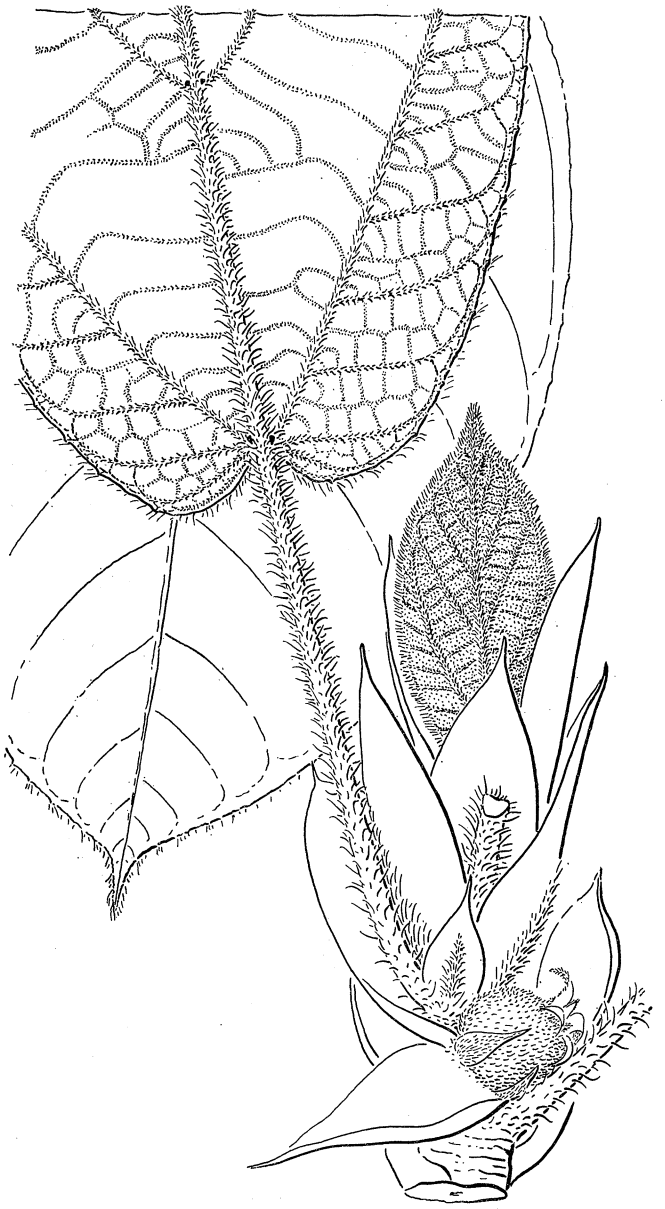

FIGURE 46. Sect. *Sycocarpus* subsect. *Auriculisperma*. *F. immanis*, RSS 1522, ×½.

25–40 × 13–20 cm, elliptica, breviter acuminata, basi plus minus cordata, integra v. subdenticulata, supra levis, subtus subscabra; costis lateralibus utrinsecus 8–11, prominentibus, intercostis 7–13; basalibus 3–4, ad mediam laminam elongatis; petiolo 4–23 cm longo. Syconia axillaria sessilia, primo tenue brunneo-pilosa, glabrescentia, maturitate flavescentia, 30–40 mm lato (25–30 mm, st.

sicc.), subglobosa; bracteis basalibus 3–5, 15–25 × 5–10 mm, lanceolatis; bracteis lateralibus 0–2, ut basalibus; bracteis apicalibus erectis numerosis 9–20 × 5–10 mm, saepe recurvatis; pariete 4 mm crasso; setis internis cellulisque scleroticis nullis. Stamina 2–3, breviter mucronata. Perianthium femineum et cecidiophorum breviter cupulatum; ovarium rubro-brunneum; stylus glaber. Semina 1·4–1·6 × 0·8–1 × 0·5–0·6 mm. Cystolitha hypogena. Ins. Solomonensibus. RSS 1522, typus, K.

Tree up to 10 m high, with spreading branches of *Terminalia* habit, ending in rosettes of spirally arranged, long-petiolate leaves. Twigs, petioles, underside of the main veins, edge of lamina, and the keel of the stipules setose with dark purple-brown wiry hairs up to 6 mm long, appressed or spreading; shorter, 0·5–1·5 mm long, on the small veins beneath;

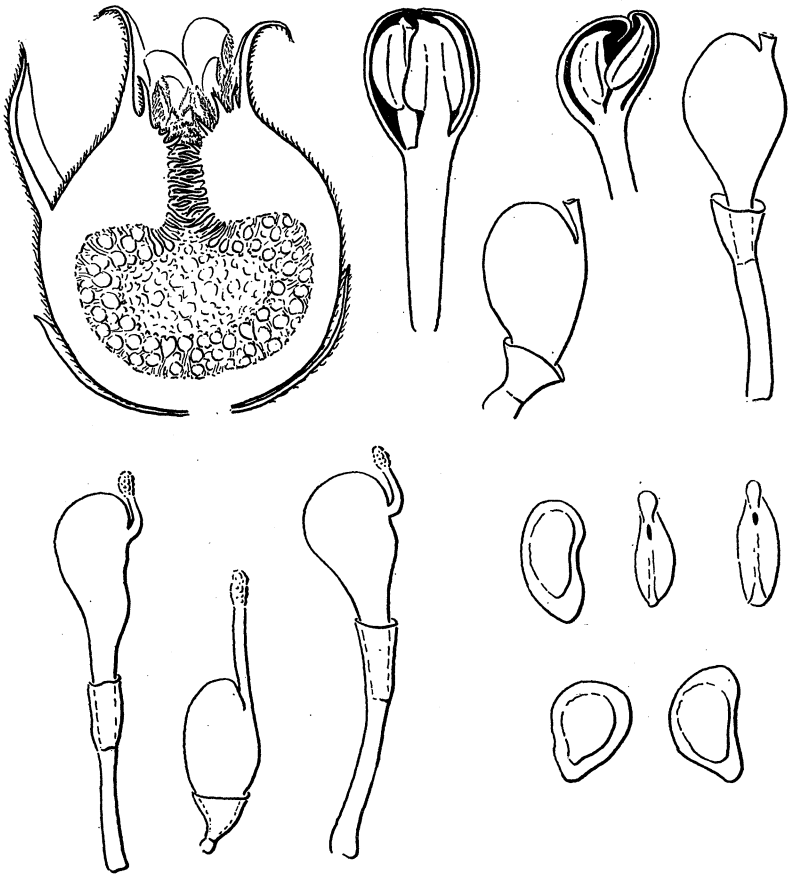

FIGURE 47. Sect. *Sycocarpus* subsect. *Auriculisperma*. *F. immanis*, RSS 1522 (above) fig, male and gall-flowers; RSS 196 (below) female flowers and seed. Fig × 1, flowers × 10.

upperside of lamina soon glabrous. Twigs 8–12 mm thick. Stipules 2–10 cm. long, 15–40 mm wide, broadly lanceolate or oblong with short acuminate tip, long persistent, for the most part glabrous. Lamina 25–40 × 13–20 cm, elliptic, the short acuminate tip 10–15 mm long, base shallowly cordate, edge entire or subdenticulate, subcoriaceous, soon smooth above, subscabrid below, drying brown; lateral veins 8–11 pairs, oblique, strongly raised below, mostly with a small axillary gland; intercostals 7–13, strongly raised below; basal veins 3–4 pairs, reaching one half of the lamina, with 2 basal glands; petiole 4–23 cm long. Figs axillary, sessile, concealed until maturity by the stipules, at first closely and finely brown hairy, glabrescent, ripening yellow; basal bracts 3–5, 15–25 × 5–10 mm, lanceolate–acuminate, appressedly hairy; body 30–40 mm wide (25–30 mm,

dried), subglobose or shortly oblong, with 0–2 lateral bracts as the basal bracts, with a large rosette 10–17 mm wide of erect apical bracts, the larger 9–20 × 5–10 mm, often recurved, finely brown hairy; fig-wall 4 mm thick (living), without sclerotic cells; internal bristles none. Male flowers in 2–3 rings round the orifice, pedicellate; perianth saccate, covering the stamens, surrounded by a cupular bracteole; stamens 2–3, free, anthers shortly mucronate. Gall-flowers sessile to shortly stalked; perianth cupular, short, at the base of the ovary or its stalk; ovary red-brown, sessile or stalked; style short. Female flowers as the gall, ovary stalk often longer; style long, glabrous. Seed 1·4–1·6 × 0·8–1·0 × 0·5–0·6 mm, auriculiform, bluntly keeled except at the slightly sunken hilum, smooth. Leaves with cystoliths only on the underside.

Distr. Solomons, Guadalcanal; frequent by streams in the forest at Nuhu and Tambalusu in the Balasuna Valley, up to 600 m alt.

Collections. RSS 196, 1522, 2118.

In my original work on subsect. *Auriculisperma*, about ten years ago, I noted that *F. cynaroides* was related to *F. lancibracteata*, but that there were such considerable differences that more species were probably to be discovered. *F. immanis*, found on the Royal Society Expedition, comes exactly between the two and could be alined with either. It has the massiveness of *F. cynaroides* but the prominent venation and large fig with its long channel of overlapping apical bracts as in *F. lancibracteata*; it has the long stipules of *F. cynaroides* and the short perianth of gall- and female flowers of *F. lancibracteata*. What is still missing is the more leptocaul state, allied with *F. lancibracteata*, which will link up with *F. indigofera* and *F. vitiensis*.

403. *F. lancibracteata* Corner (figure 48)

Tree up to 13 m high, much branched. Leaves spirally arranged. Twigs, petioles, edge of lamina, and underside of the veins bristly with dark brown or purple, wiry, spreading, hairs, 3–7 mm long on the twig and petiole, shorter on the veins, sparse on the smaller veins; upperside of lamina with similar appressed hairs. Twigs 4–6 mm thick, with short internodes. Stipules 20–45 mm long, caducous or subpersistent, glabrous or setose in the lower part. Lamina 10–18 × 6–11 cm, up to 25 × 17 cm in saplings, elliptic, ovate or obovate, the acuminate tip up to 12 mm long, base cuneate or rounded, subcordate in saplings, often attenuate to each end, denticulate or subentire, membranous, not scabrid or slightly below, drying dark brown; lateral veins 7–10 pairs, up to 13 regular intercostals, strongly raised below; basal veins 2 (–3) pairs reaching one third to one half of the lamina, without basal glands but usually with a small gland in the axils of the lateral veins; petioles 1·8–15 cm long, without subnodal glands. Figs axillary, not cauliflorous, sessile, villous or setose with pale brown hairs 1–2 mm long, ripening brown; basal bracts 3–7, more or less in a collar, varying 7–12 mm long or 15–20 × 9–12 mm, ovate, lanceolate, with caudate tip, flat, glabrous or puberulous; body 20–22 mm wide (15–17 mm, dried), ovoid, with numerous lanceolate or subulate, setose, lateral bracts with broad base, 10–17 mm long, often incurved or curved to one side, crowded and erect round the orifice with the longer apical bracts up to 10 × 6 mm, completely covering the young fig, often absent from the sides of the mature fig; internal bristles none; sclerotic cells absent from the fig-wall. Male flowers in 1 (–2) rings round the orifice, with white pedicels; perianth

saccate, enveloped in a subcupular bract; stamens 2 (–3), anthers shortly mucronate. Gall-flowers subsessile or with white pedicels; perianth short, cupular, entire; ovary dark red-brown, more or less stalked. Female flowers sessile or shortly pedicellate; perianth as a

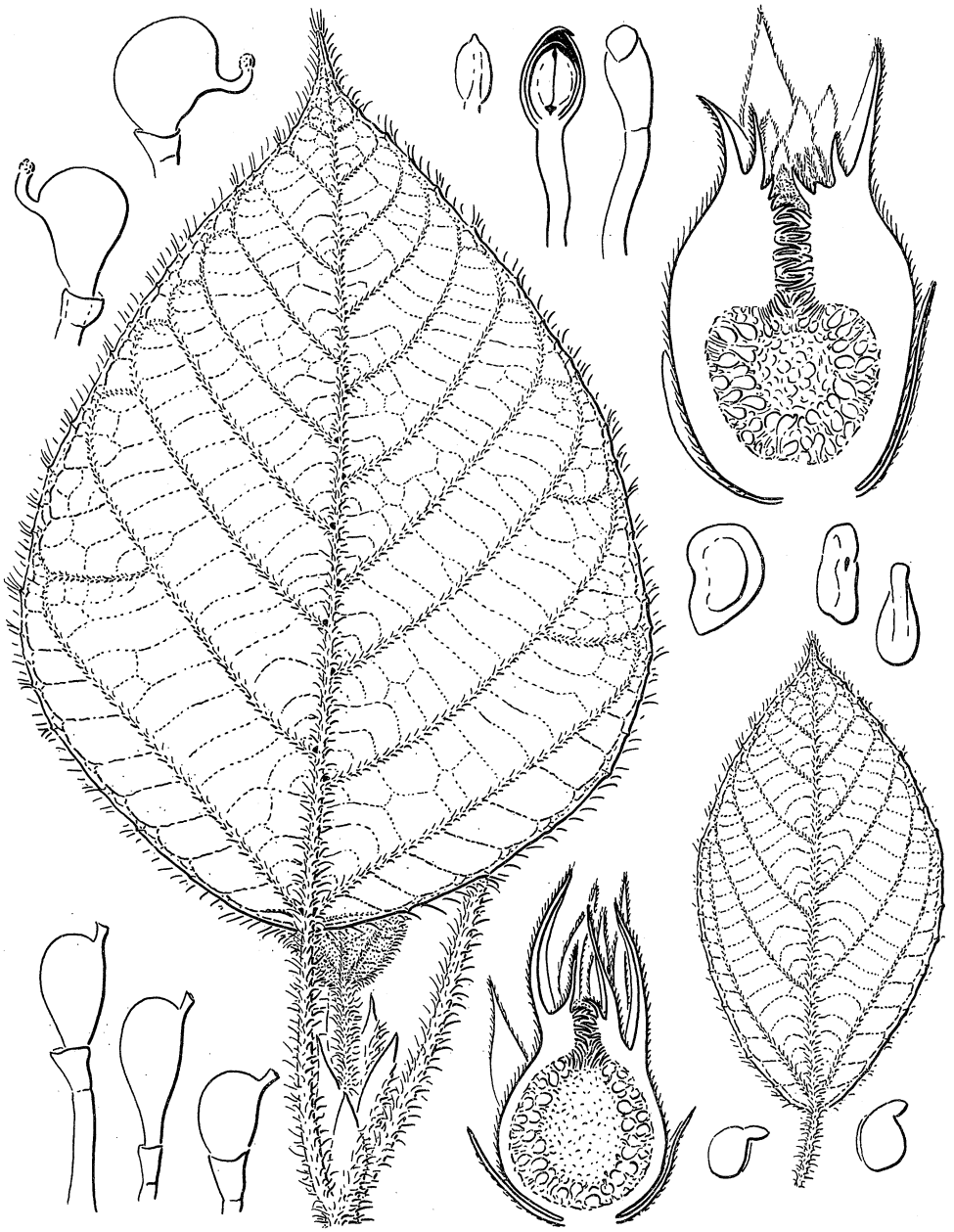

FIGURE 48. Sect. *Sycocarpus* subsect. *Auriculisperma*. *F. lancibracteata*, RSS 1230, twig, gall-fig, male and gall-flowers (lower left); Kajewski 2032, small leaf, seed-fig, female flowers (upper left), seed, and embryo. Leaf and twig $\times \frac{1}{2}$, figs $\times 2$, flowers $\times 10$.

short cupule round the stalk of the dark red-brown ovary; style lateral, glabrous. Seed 1·4–1·5 × 0·6 mm, strongly compressed, auriculiform, bluntly keeled, smooth, the hilum sunken. Lamina with cystoliths only on the underside.

Distr. Solomons; Bougainville, Kolombangara, Ysabel.

Ecology. Lowland forest up to 800 m alt., often frequent in gullies.

Kwara-ae. dedela.

Collections. BSIP 2204; Kajewski 2032 ('sitsileu', Buin.); NGF 13771A ('sisipu', Kupei, Bougainville); RSS 1230.

This is easily recognized from the wildly bracteate, axillary figs, not concealed by the stipules as they are in the allied *F. immanis*.

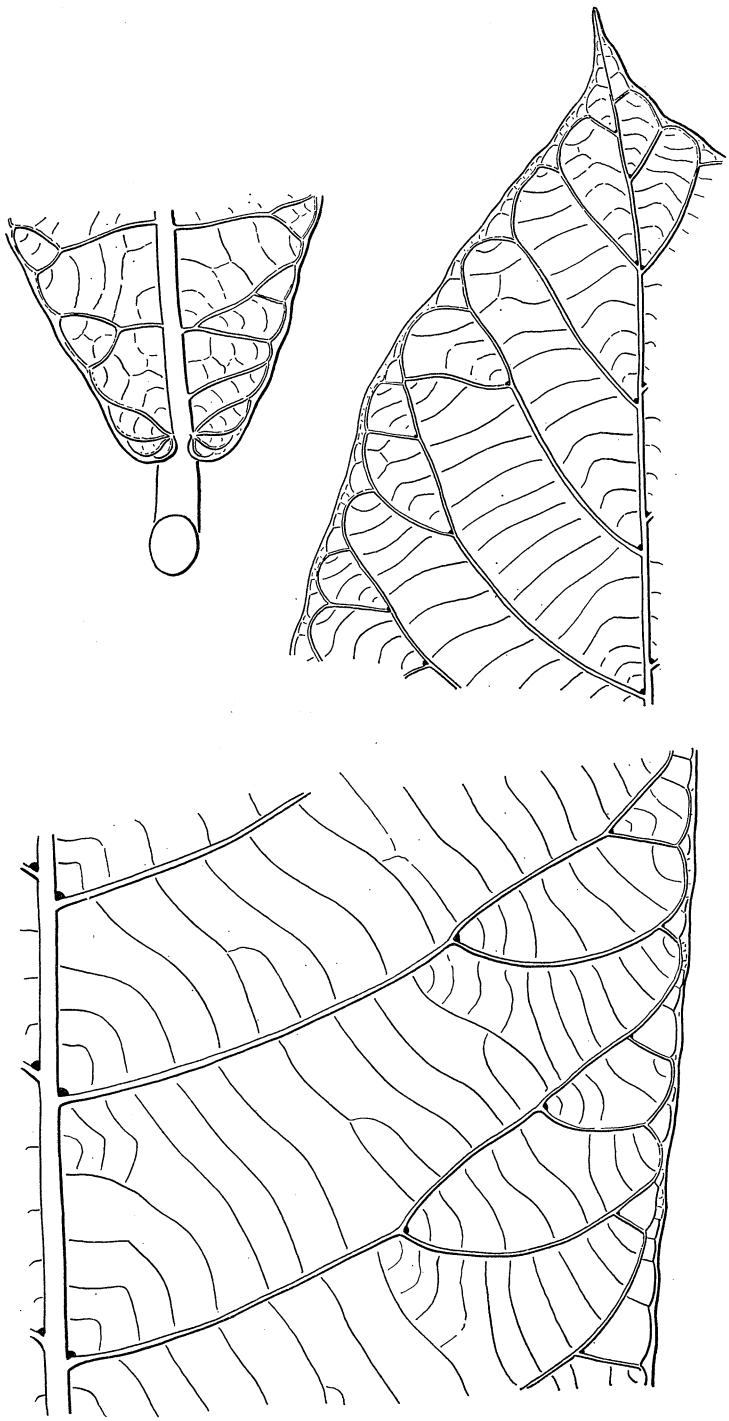

FIGURE 49. Sect. *Sycocarpus* subsect. *Auriculisperma*. *F. salomonensis*, Brass 3365, parts of the lamina $\times \frac{1}{2}$.

404. *F. salomonensis* Reching. (figures 42, 49, 50)

Tree up to 15 m high, sparingly branched, the stout twigs ending in large rosettes of broad leaves, spirally arranged; young leaves green or reddish. Twigs, petioles, stipules, both sides of the veins, and the figs downy-subvillous with white erect straight hairs 0·5 (–1) mm long, rather stiff on the petioles. Twigs 12–20 mm thick, solid. Stipules 4–12 × 2–3·5 cm, broadly lanceolate, caducous. Lamina 80–200 × 30–60 cm, oblong–obovate, acute or very shortly acuminate, narrowed to the cordate base, entire or denticulate, membranous, scabrid hispidulous on both sides or subvillous beneath, drying brown;

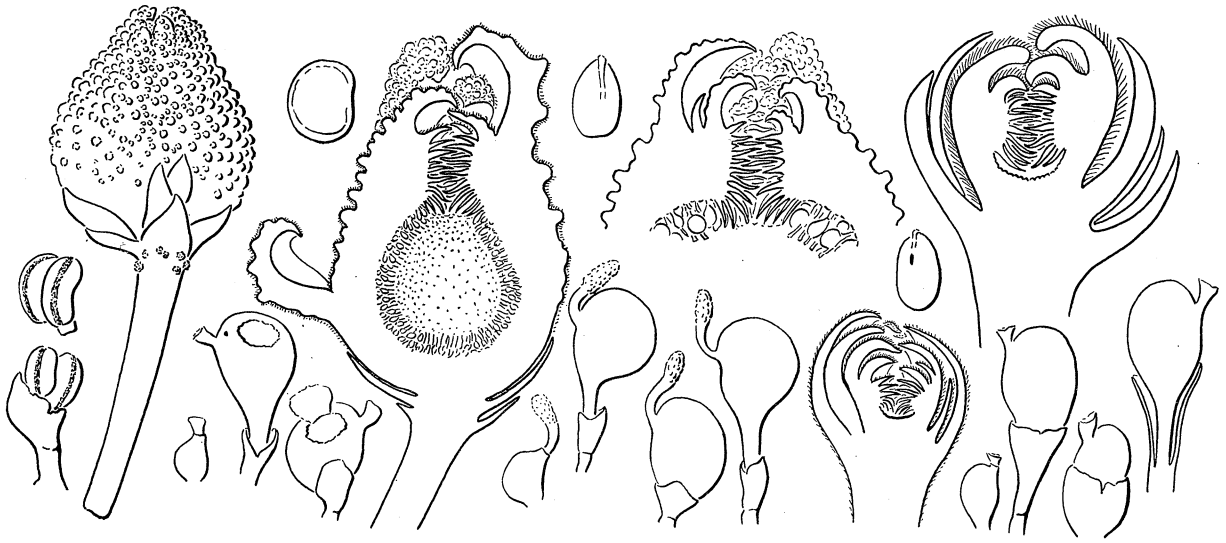

FIGURE 50. Sect. *Sycocarpus* subsect. *Auriculisperma*. *F. salomonensis*, Corner s.n. Bougainville. Mature fig × 1, young fig-sections (right) × 2, flowers × 10.

lateral veins 23–26 pairs, at a wide angle, often with an axillary gland, forking once or twice towards the margin, with a small gland in the fork, strongly raised below; intercostals 9–15; basal veins 4–5 pairs, short; petiole 15–30 × 10–15 mm, very stout, with a conspicuous subnodal gland and two yellowish glands on the upperside of the petiole at the junction with the lamina. Figs crowded on short woody twigs without internodes, set densely in masses up to 30 cm wide on the trunk to a height of 3 m, ripening dull brown, paler and slightly pinkish at the base of the body, often encrusted with earth from ants' nests and the old figs rotting *in situ* with the peduncles persistent; peduncles 35–80 mm long; basal bracts 3, 9–12 mm long, stoutly lanceolate, spreading; lateral bracts 5–9, set often in 3 distinct parastichies immediately above the basal bracts, 9–16 mm long, lanceolate, often with 1–2 similar bracts scattered on the body; fig-body 30–38 × 25–32 mm (20–25 mm wide, dried), ellipsoid, densely warted in the upper half with processes 1–1·5 mm long, finely villous, glabrescent, with 6–8 stoutly lanceolate apical bracts 5–9 mm long, set in a projecting rosette; internal bristles and sclerotic cells none. Male flowers in 1–2 (–3) rings round the orifice, sessile or shortly stalked; perianth saccate, entire; stamen 1, the large anther subsessile, not mucronate. Gall-flowers sessile to shortly pedicellate; perianth saccate, covering the young ovary to the base of the style, not enlarging but splitting into 2 small lobes at the base of the mature, pale yellowish ovary. Female

flowers as the gall; style glabrous. Seed 1·6–1·7 × 1·4–1·5 mm, lenticular, smooth, very slightly keeled, hilum not prominent. Lamina with cystoliths on both sides.

Distr. Solomons, in lowland forest by rivers, streams, and hill-sides up to 600 m alt., frequent throughout the islands.

Kwara-ae. roroketa.

Collections. Brass 3365; BSIP 824, 3019; NGF 13556; RSS 2438; Rechinger 4100.

This is the most notable species of the genus and deserves detailed study in cultivation. It seems that the largest leaves are borne when the tree is about 7 m high. The figs are peculiarly unattractive. All that remains of the type seems to be the two figs preserved at Kew. J. Womersley and I rediscovered it in the type locality (Kieta, Bougainville).

I draw attention, again, to the most remarkable relict front of pachycauly along the Melanesian Foreland drawn by *F. pseudopalma* (Philippines), *F. dammaropsis* (New Guinea), and the two species of the Solomons, *F. salomonensis* and *F. theophrastoides*. Possibly they should be combined into one section.

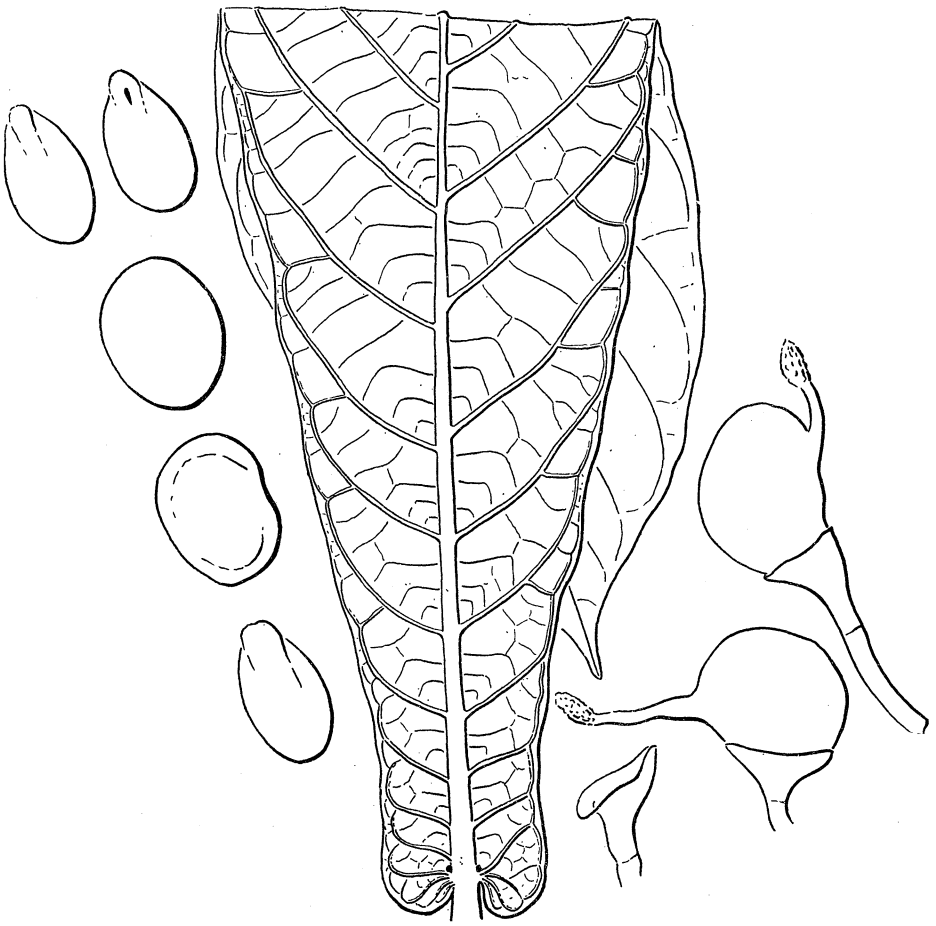

FIGURE 51. Sect. *Sycocarpus* subsect. *Auriculisperma*. *F. theophrastoides*, E. S. Brown 2568. Leaf × ½, female flowers and seed × 10.

405. *F. theophrastoides* Seem. (figures 42, 51, 52)

Shrub or treelet up to 5 m high, fruiting at 1 m, unbranched or sparingly branched. Leaves spirally arranged. Glabrous or the young parts puberulous with minutely hooked

hairs, often persistent on the underside of the lamina. Twigs 5–10 mm thick, solid, with close internodes. Stipules 1·5–2·5 cm long, scarious, brown, subpersistent, glabrous. Lamina 30–90 × 10–25 cm, oblong–obovate, the acuminate tip up to 15 mm long, narrowed gradually to the cordate-auricled base, entire, firmly membranous, smooth or slightly scabrid below, drying greenish to brownish; lateral veins (15–) 20–27 pairs, at a wide angle; intercostals 4–9, lax, slightly raised below; basal veins 4–5 pairs, short; petiole

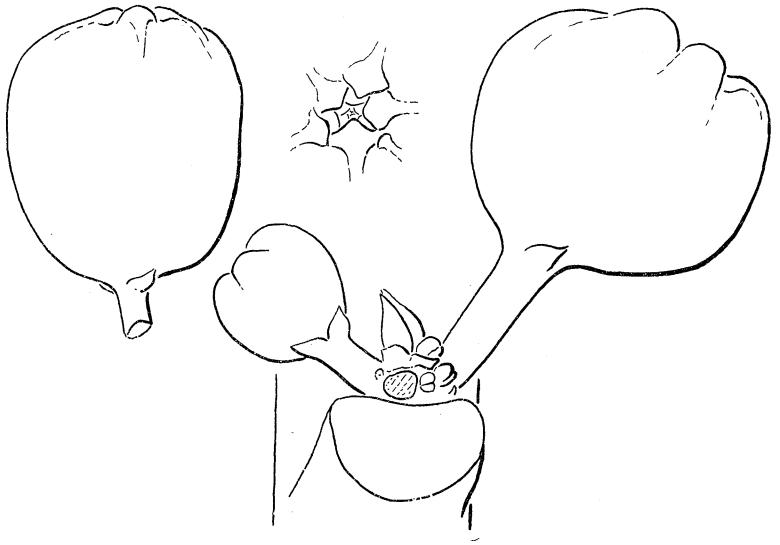

FIGURE 52. Sect. *Sycocarpus* subsect. *Auriculisperma*. *F. theophrastoides*, NGF 13385, fig and axillary fig-cluster, × 2.

5–18 × 3–8 mm, with 2 yellow glands on the upperside at the junction with the midrib, and 2 small basal glands on the underside, without subnodal glands. Figs axillary paired, concealed by the leaf-bases, then developing groups of 3–6 figs by persistent growth of the axillary bud, finally cauliflorous and often only at the base of the stem with the fig-clusters more or less immersed in the ground, not stoloniferous, ripening yellowish to pinkish; peduncle 3–10 × 2–3 mm; basal bracts 2, rarely 3, 1·5–3 mm long, or 3–9 × 3–7 mm in other plants (Fiji-specimens), ovate–acute persistent; body 25–35 mm wide (15–20 × 14–17 mm, dried), ellipsoid or pyriform, compressed, without lateral bracts, ridged distally towards the 5–6 subumbonate apical bracts; internal bristles and sclerotic cells none. Flowers sessile or shortly pedicellate. Male flowers in 2 rings round the orifice; perianth saccate; stamen 1, anther not mucronate, filament short. Gall-flowers with the perianth covering two thirds or the whole of the young ovary, not enlarging but sheathing the base of the mature yellowish white ovary, or variously split. Female flowers with pink or white perianth, as in the gall; ovary white; style glabrous. Seed 2–2·2 × 1·5–1·7 × 1·2–1·3 mm, lenticular, smooth, not or obscurely keeled, hilum not prominent. Lamina with cystoliths on both sides or only on the underside.

Distr. Solomons, lowland forest up to 800 m alt., by rivers, streams and on ridges, often in old garden-country, common throughout the islands; ? Fiji.

Kwara-ae. roroketa, raurauketa.

Collections. Brown 2568, 2696; BSIP 1050, 2343, 2746, 2902, 3687, 5526; Guppy 353;

Kajewski 1971; NGF 13385; RSS 21, 6330; Waterhouse 132 ('hinukutu', New Georgia), 297 ('huhura', Siwai, Bougainville).

Though related to *F. salomonensis*, this is the species that comes nearest to *F. pseudopalma* of the Philippines. It is to be hoped that the links between them are still to be discovered in New Guinea or New Ireland. Whether the species is natural or introduced to Fiji has still to be determined; it enters undoubtedly into village life, for Waterhouse noted that the juice of the bark (latex?) was used for eye-injuries on New Georgia, and thus it may have been taken to Fiji by Solomon colonists (p. 48). In habit, the plants resemble saplings of *Campnosperma*.

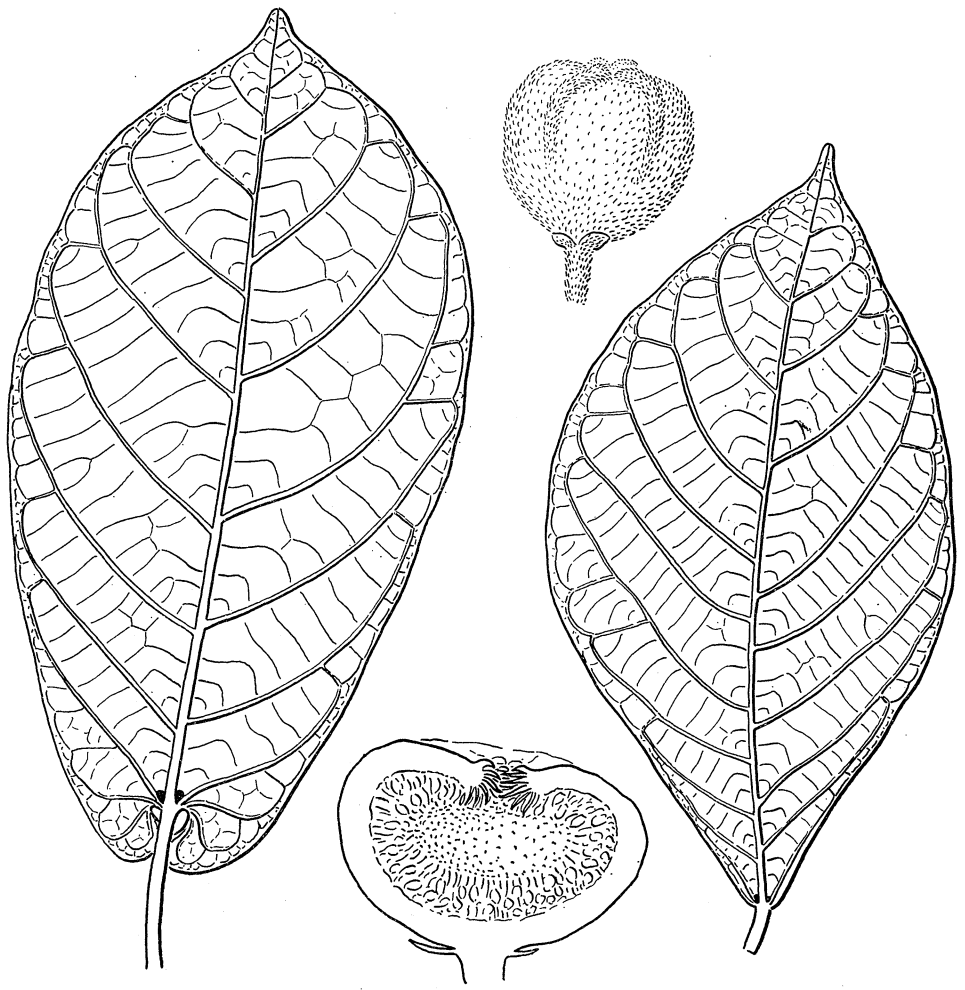

FIGURE 53. Sect. *Sycocarpus* subsect. *Auriculisperma*. *F. indigofera*, Kajewski 1655, leaf (left) and ripe fig-section (below); Brass 3085, leaf (right); Kajewski 1818, young fig (above). Leaf $\times \frac{1}{2}$, fig $\times 2$.

406. *F. indigofera* Reching. (figures 53 to 55)

Small tree up to 15 m high, with *Terminalia*-branching, the leaves generally in small compact rosettes; young leaves pale green or, in other trees, deep purple; bark grey to pale brown; latex white. Glabrous or the young parts finely appressedly puberulous with white to yellowish hairs. Twigs 2–3 mm wide. Stipules up to 17 mm long, caducous. Lamina 8–23 × 3–14 cm, obovate, bluntly subacuminate with a tip up to 10 mm long, base narrowly cuneate or, in other trees, subcordate to shortly bilobed or auricled, entire,

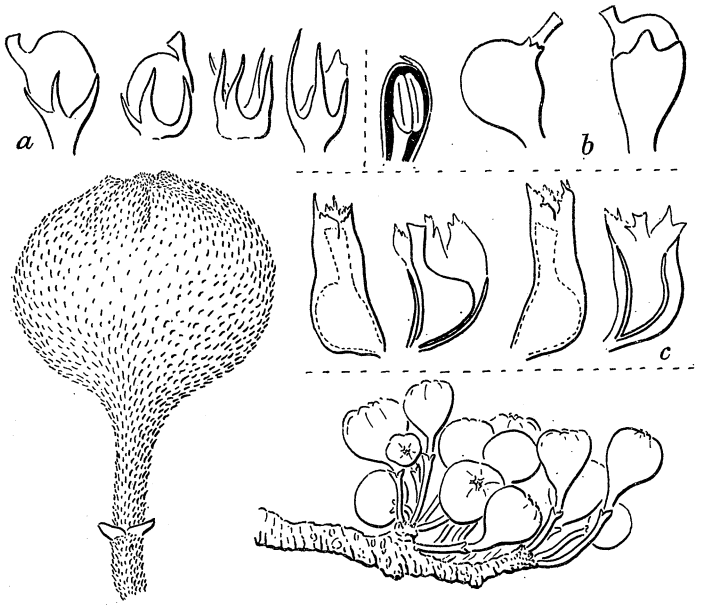

FIGURE 54. Sect. *Sycocarpus* subsect. *Auriculisperma*. *F. indigofera*, *NGF* 13580, fig ×2; RSS 6193, fig-cluster ×½; male and gall-flowers, *a*, NGF 13563; *b*, Kajewski 1818; *c*, RSS 6193, ×10.

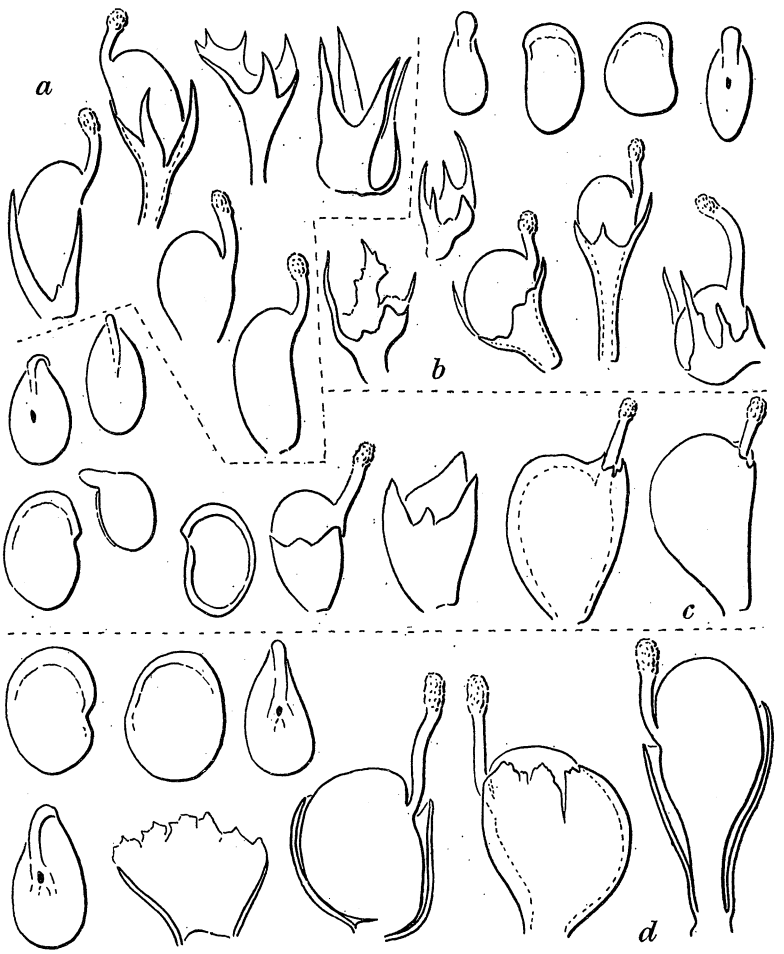

FIGURE 55. Sect. *Sycocarpus* subsect. *Auriculisperma*. *F. indigofera*, female flowers and seeds ×10; *a*, NGF 13580; *b*, Brass 3085; *c*, Kajewski 1904; *d*, RSS 2729.

subcoriaceous, smooth, drying bluish green to brown; lateral veins 7–12 pairs, 3–10 intercostals, not or slightly raised below; basal veins 1–3 pairs, short, with 2 basal glands; petioles 5–35 (–80) mm long. Figs axillary, paired, and on the twigs immediately below the leaves, varying cauliflorous in other trees with rather short, stout, compactly branched, leafless twigs up to 20 cm long or, in other trees, more elongate branching twigs up to 35 cm long, not ramiflorous, ripening pink or red to purple; peduncles 1–8 mm long, up to 15 mm in cauliflorous figs; basal bracts 3, in a collar, 1–3 mm long, glabrous, subacute; pedicel 0–8 mm long; body 16–20 × 18–24 mm (10–12 × 11–18 mm, dried), subglobose to depressed globose, without lateral bracts, at first with 5–6 ridges towards the slightly sunken orifice, with 5 peripheral apical bracts; internal bristles and sclerotic cells none. Perianth wholly gamophyllous and covering the stamen or ovary, or commonly with 2–5 irregular, acute or obtuse, lanceolate lobes (not splittings), very thin, white. Male flowers subsessile in one ring round the orifice; stamen 1, anther not mucronate. Gall- and female flowers sessile or with a short pedicel; ovary sessile or stalked, dark red to reddish pink; style glabrous, the gall-style narrowly infundibuliform. Seed 1·4–1·6 × 1 × 0·7–0·8 mm, subcompressed, slightly keeled, smooth, hilum not prominent. Leaf with cystoliths on both sides.

Distr. Solomons, lowland forest up to 800 m alt., often on raised coral beaches near the sea, common throughout the islands.

Kwara-ae. aitia.

Collections. Brass 2717, 2746, 3085, 3293; BSIP 692, 3150; Kajewski 1561, 1655, 1818, 1904 ('ai-ki-orlu', Buin), 2321 ('it-ombora', Malaita), 2427; NGF 13563, 13580; Rechinger, 4363, 4618, 4688, 4701; RSS 28, 32, 145, 200, 210, 252, 703, 1199, 1231, 1242, 1258, 1523, 2217, 2729, 2767, 2890, 6193, 6205; Waterhouse B 26, 127, 261, 293, 730.

This is a variable species that may be mistaken for the hairier *F. mollior*, which usually has lateral bracts on the fig-body. The relation between trees with cuneate leaf-base and those with the cordate and bi-auricled needs investigation because they may be distinct varieties, if not species. Thus, on Ysabel, and subsequently on Malaita, I found numerous small trees up to 9 m high of the bi-auriculate kind which had always deep purple young leaves set in the midst of compact rosettes of entirely glabrous leaves in the rather open and sparingly branched crown (RSS 2729, 2890). The figs on these trees were either axillary, sparse, solitary, and hidden in the leaf-bases, or in compact clusters from the very base of the trunk, often more or less immersed in the ground, in the manner of *F. theophrastoides*. This form contrasted strongly with the more branched crown of trees with light green young leaves, developing the cuneate leaf-base and the more extended cauliflorous twigs. However, they did not differ in flower or fig, and there are collections, without the critical field-notes, that seem intermediate. Possibly the bi-auriculate form has larger seeds, 1·7–2 × 1·2–1·4 × 0·8–1 mm.

Subgen. *FICUS* sect. *SYCOCARPUS* Miq. subsect. *SYCOCARPUS*

Key to the species in the Solomons

1. Figs with basal bracts or lateral bracts more than 5 mm long. Leaves spirally arranged, long-petiolate, often large. Stoloniferous, geocarpic, often with axillary figs. Seed-flowers with hairy style.

2. Basal and lateral bracts 7–30 mm long, lanceolate, often concealing the fig-body. Leaves large, entire, smooth. Young twigs, petioles, and veins red. ..... *F. longibracteata*
2. Basal bracts 3, shorter, caducous; lateral bracts not concealing the fig-body (except when very young). Leaves scabrid, denticulate. Brown hairy.
3. Fig 25–30 mm wide (up to 40 mm, living), with 1–3 stout lateral bracts 4–10 mm long. Lamina with short basal veins. Hairs pale brown. ..... *F. tanypoda*
3. Fig smaller, without lateral bracts. Lamina often widely cordate to rounded cordate, basal veins reaching one third to one half of the lamina. Hairs dark brown. ..... *F. profusa*

1. Basal bracts 1–4 mm long; lateral bracts absent. Fig mostly 10–17 mm wide (dried). Leaves with short basal veins.
4. Leaves with pale whitish veins (living) and lax intercostals, short-petiolate. Stipule 2–6 cm long. Fig ridged towards the apex. Not brown hairy.
5. Leaves scabrid. Figs axillary. ..... *F. bougainvillei*
5. Leaves smooth. ..... *F. septica*
Figs axillary. ..... var. *septica*
Figs cauliflorous. ..... var. *cauliflora*
4. Veins not whitish. Brown hairy. Cauliflorous, often with geocarpic stolons.
6. Fig-peduncles 25–100 mm long. Hairs dark brown. ..... *F. scaposa*
6. Peduncles shorter.
7. Hairs on twigs and petioles 3–5 mm long, wiry, dark brown, purple, or black. ..... *F. dissipata*
7. Hairs shorter or paler and softer. Style of seed-flowers sparsely hairy to glabrous.
8. Hairs 2–4 mm long, white to pale brown, spreading. Leaves spirally arranged, long-petiolate. Lamina 14–30 × 11–17 cm, with cordate or rounded base. Figs on spreading leafless twigs up to 1 m long; basal bracts caducous. Twigs 4–6 mm thick. ..... *F. baccaureoides*
8. Hairs up to 1·5 mm long, brown, more or less appressed. Leaves becoming subdistichous or opposite; petioles 5–30 mm long. Lamina up to 25 × 10 cm generally entire. Twigs 1·5–4 mm thick.
9. Figs on leafless twigs less than 1 m long, not stoloniferous; basal bracts persistent. Lamina symmetric often shallowly cordate; lateral veins oblique with close intercostals. ..... *F. subcongesta* var. *symmetrica*
9. Figs in hanging racemes 1–3 m long, often becoming geocarpic stolons; basal bracts caducous. Lamina with asymmetric base, not cordate; lateral veins inarching. ..... *F. macrothyrsa*
10. Lamina elliptic. ..... var. *macrothyrsa*
10. Lamina lanceolate. ..... var. *lancifolia*

419. *F. longibracteata* Corner (figures 56 to 58)

Shrub or tree up to 15 m high, laxly branched, geocarpic; young twigs, petioles, and veins red. Leaves spirally arranged. Glabrous or the young twigs, petioles, stipules, and underside of the main veins with short appressed white to brown hairs up to 1 (–1·5) mm long, sparser, paler and shorter on the smaller veins; upperside of the lamina often sparsely white hairy. Twigs 5–8 mm thick. Stipules 2–10 × 1·2–2·5 cm, large, broadly lanceolate, persistent, obscuring the bud. Lamina 17–37 × 11–26 cm, elliptic, shortly and obtusely acuminate, base shallowly cordate to rounded cuneate, entire, membranous to subcoriaceous, smooth, drying dark brown; lateral veins 6–10 pairs, often with an axillary

gland, up to 12 regular intercostals, raised below; basal veins 3–4 pairs, reaching one quarter to one half of the lamina, without basal glands; petiole 4–11 cm long, with a subnodal gland. Figs axillary, solitary or paired, and on long stipulate, leafless, geocarpic

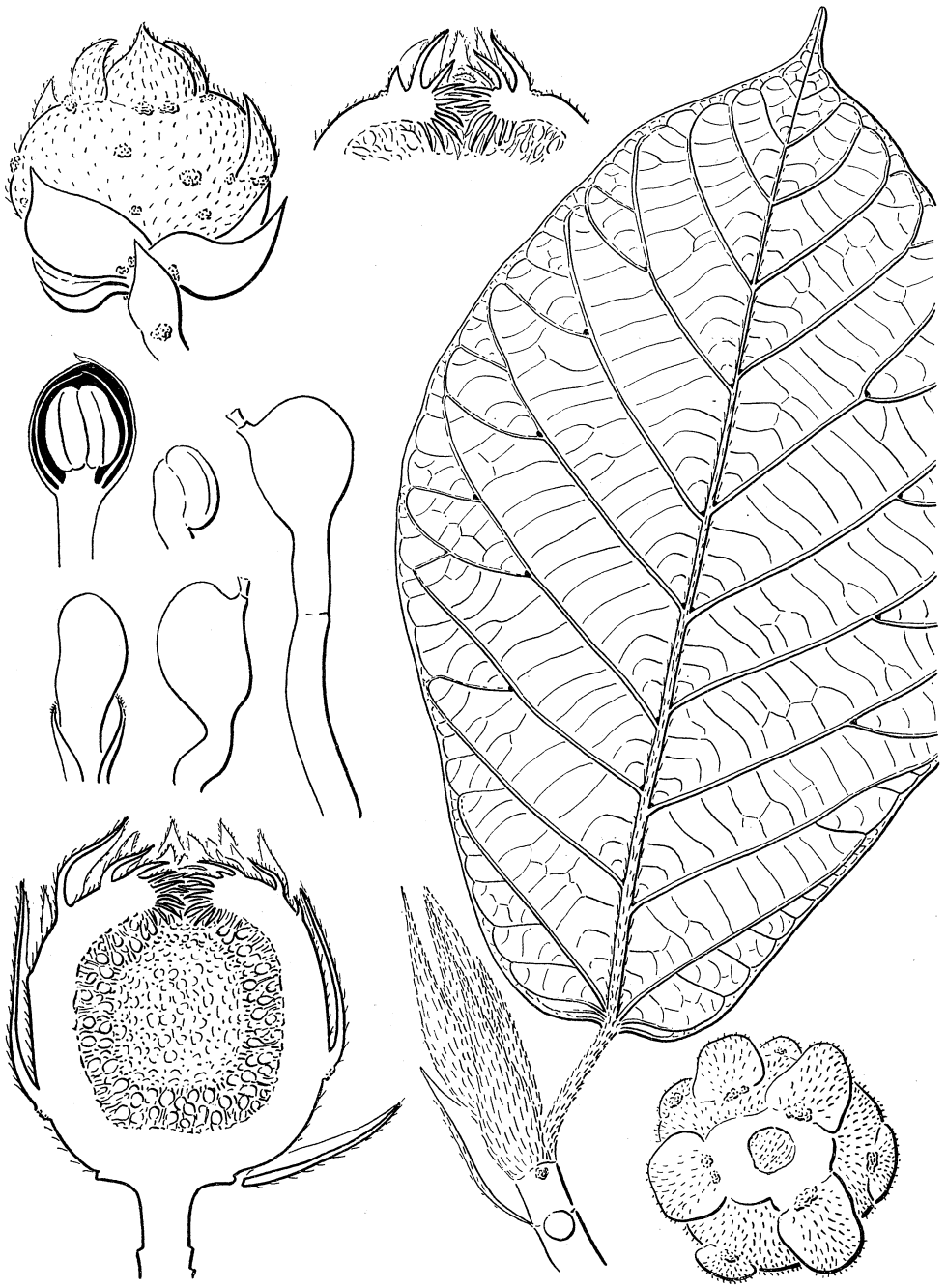

FIGURE 56. Subsect. *Sycocarpus*. *F. longibracteata*, E. S. Brown W/199, twig $\times \frac{1}{2}$; Brown 2705, gall-fig $\times 1$, male and gall-flowers $\times 10$. Var. *lebetoides* (top left), Kajewski 2642, fig and orifice-section $\times 2$.

stolons up to 6 m long, 5–7 mm thick, with reddish young internodes 2–5 cm long, ripening reddish pink; peduncle 3–13 mm long, more or less concealed, sometimes dilated into a disk at the apex; basal bracts 3 or more, not in a distinct collar, 20–30 × 11–15 mm,

broadly lanceolate, persistent, appressedly brown hairy; body 30–45 mm wide (15–22 mm, dried), subglobose, more or less concealed by the many, large, lanceolate, appressedly brown hairy, lateral bracts decreasing in size towards the orifice, the larger bracts usually with a large lenticel at the base, the body thinly hispid with brown hairs up to 0·5 mm

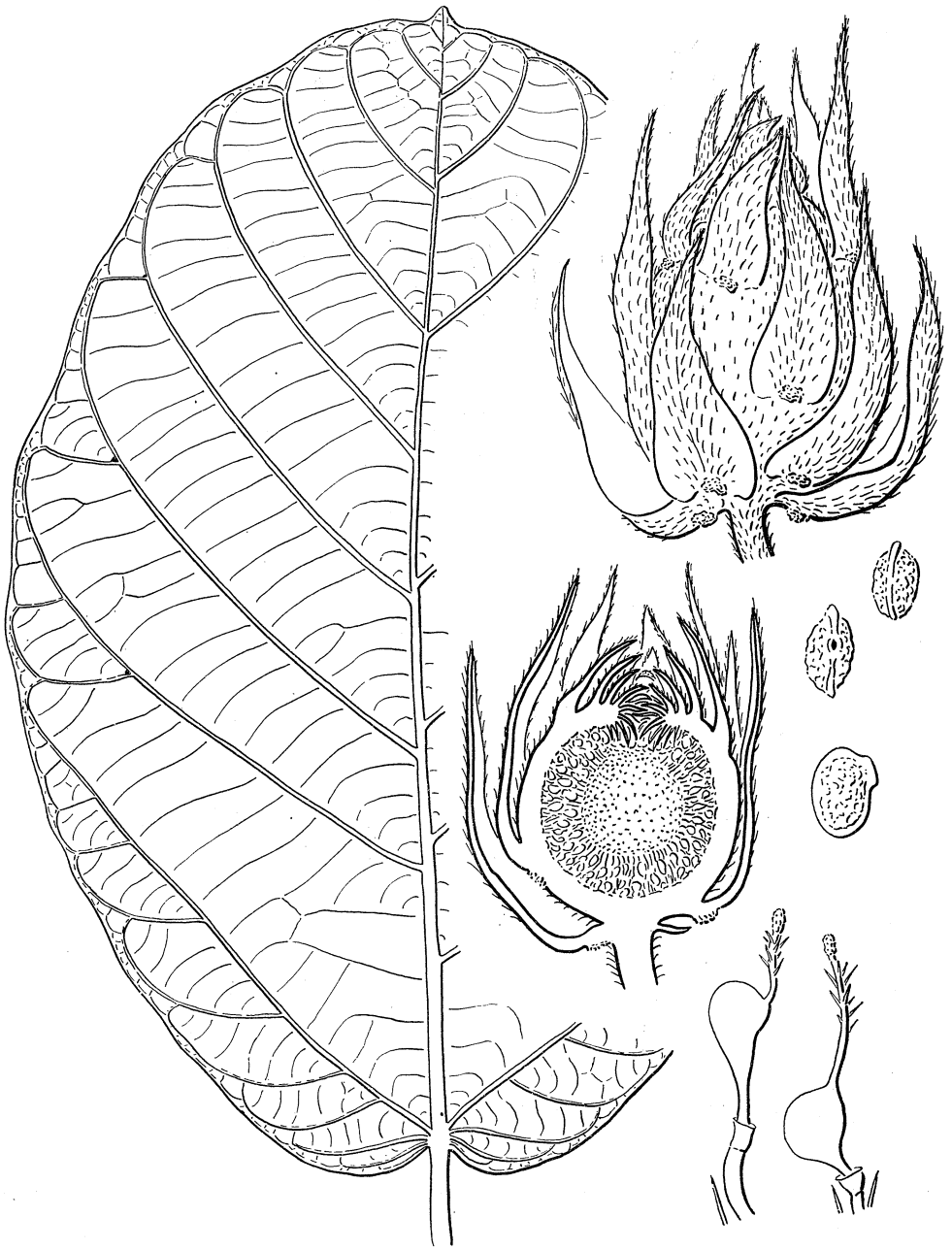

FIGURE 57. Subsect. *Sycocarpus*. *F. longibracteata*, Brass 3492, leaf × ½, seed-fig × 2, seed-flowers × 10; Brown W/199, seed × 10.

long; internal bristles short, rather sparse, white; fig-wall without sclerotic cells or few in the seed-figs. Male flowers in 3–4 rings round the orifice, with a bilobed bract and, at the top of the pedicel, a tubular bracteole with bilobed apex; perianth tubular-saccate; stamen 1, anther not mucronate. Gall-flowers mostly long-pedicellate; perianth covering

the ovary to the base of the style. Female flowers more or less pedicellate; perianth as a short collar at the base of the ovary-stalk; ovary red-brown; style hairy. Seed 1–1·3 × 0·8 × 0·7 mm, sublenticular, slightly keeled, subtuberculate rough, the hilum prominent. Lamina with cystoliths only on the lower side.

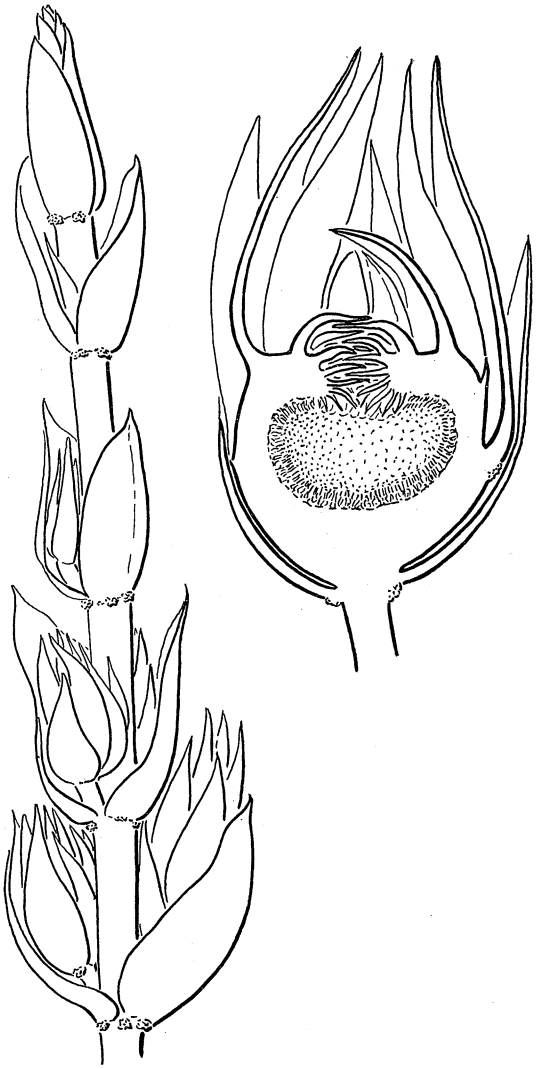

FIGURE 58. Subsect. *Sycocarpus*. *F. longibracteata*, Corner s.n. apex of fertile stolon with young figs covered by bracts in the axils of paired stipules, × ½; young fig in section × 2.

Distr. Solomons, lowland forest up to 1400 m alt., in old garden-country and coconut plantations, common throughout the islands.

Kwara-ae. ai-dedela, dedela.

Collections. Brass 3492; Brown W/199, 2705 ('tetele', 'kokora', Rua Vatu, Guadalcanal); BSIP 809, 916, 1048, 1824, 1860, 3533, 4758, 5235, 5424, 5485; Kajewski 1864 ('cong-co-mela', Buin); NGF 13577, 13741; RSS 1202, 2120, 2383.

This is one of the striking, common, and characteristic figs of the Solomons. It is related with *F. praestans* of New Britain, which has very obtuse lateral bracts and is not stoloniferous.

Var. *lebetoides* Corner (figure 56)

Fig-body not concealed by the sparse lateral bracts 5–8 mm long, the apical bracts 3–6 mm long projecting in a rosette 7–8 mm wide; basal bracts 7–10 × 3–6 mm. Lamina with 4–7 pairs of lateral veins.

Distr. Solomons, Guadalcanal, in forest up to 1200 m alt., common.

Collection. Kajewski 2642, Dulolo, Mt. Tatuve.

423. *F. profusa* Corner (Figures 59 to 61)

Tree up to 15 m high. Leaves spirally arranged, long-petiolate. Twigs, stipules, petioles, veins on both sides, and young figs closely appressedly brown hairy, the hairs 1–1·5 mm long, shorter, fewer and more spreading on the upperside of the smaller veins, the figs

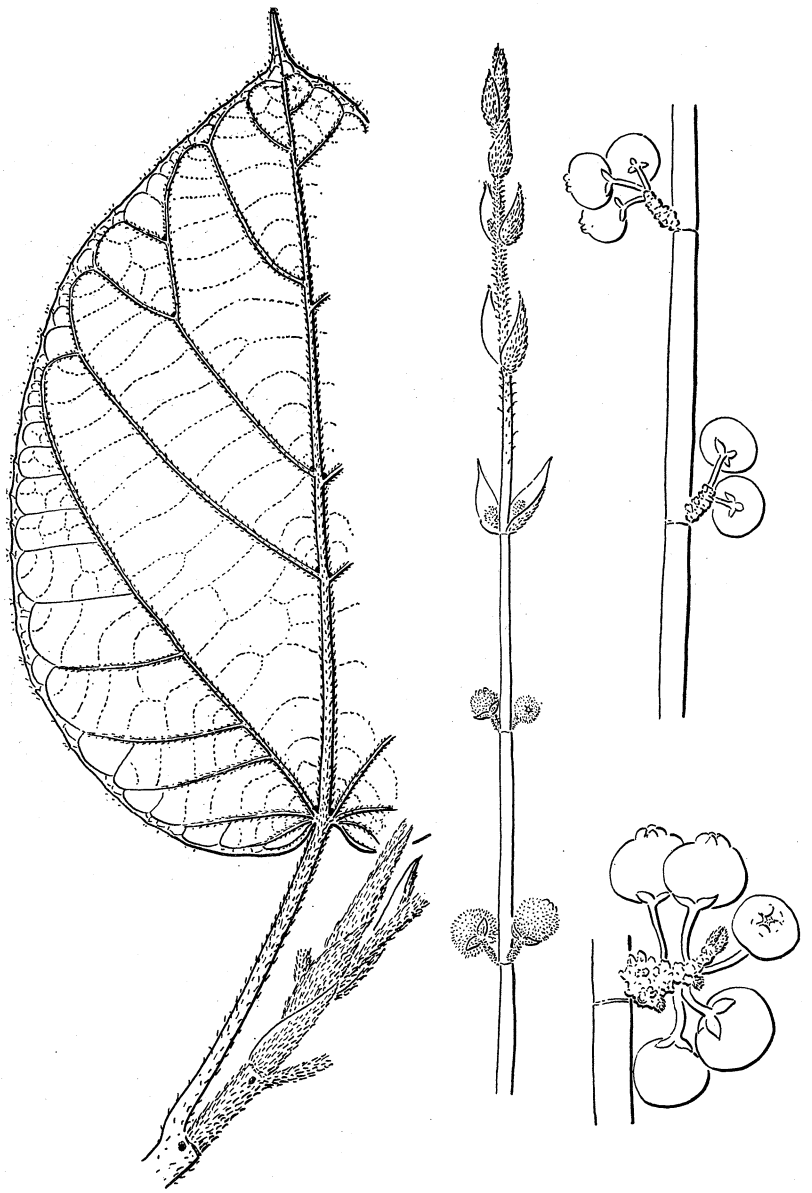

FIGURE 59. Subsect. *Sycocarpus*. *F. profusa*, RSS 2386, twig, tip of young stolon (centre), older part of the same stolon (upper right); NGF 13775, node of an old stolon (lower right); × ½.

glabrescent; upperside of the lamina scabrid with rather numerous, appressed, stiff, whitish hairs. Twigs 3–4 mm thick, up to 8 mm in saplings. Stipules up to 35 mm long, caducous or subpersistent, up to 5 cm long and persistent in saplings. Lamina 11–25 × 7·5–17 cm, up to 40 × 20 cm in saplings, ovate or elliptic, shortly subacuminate, base cordate or

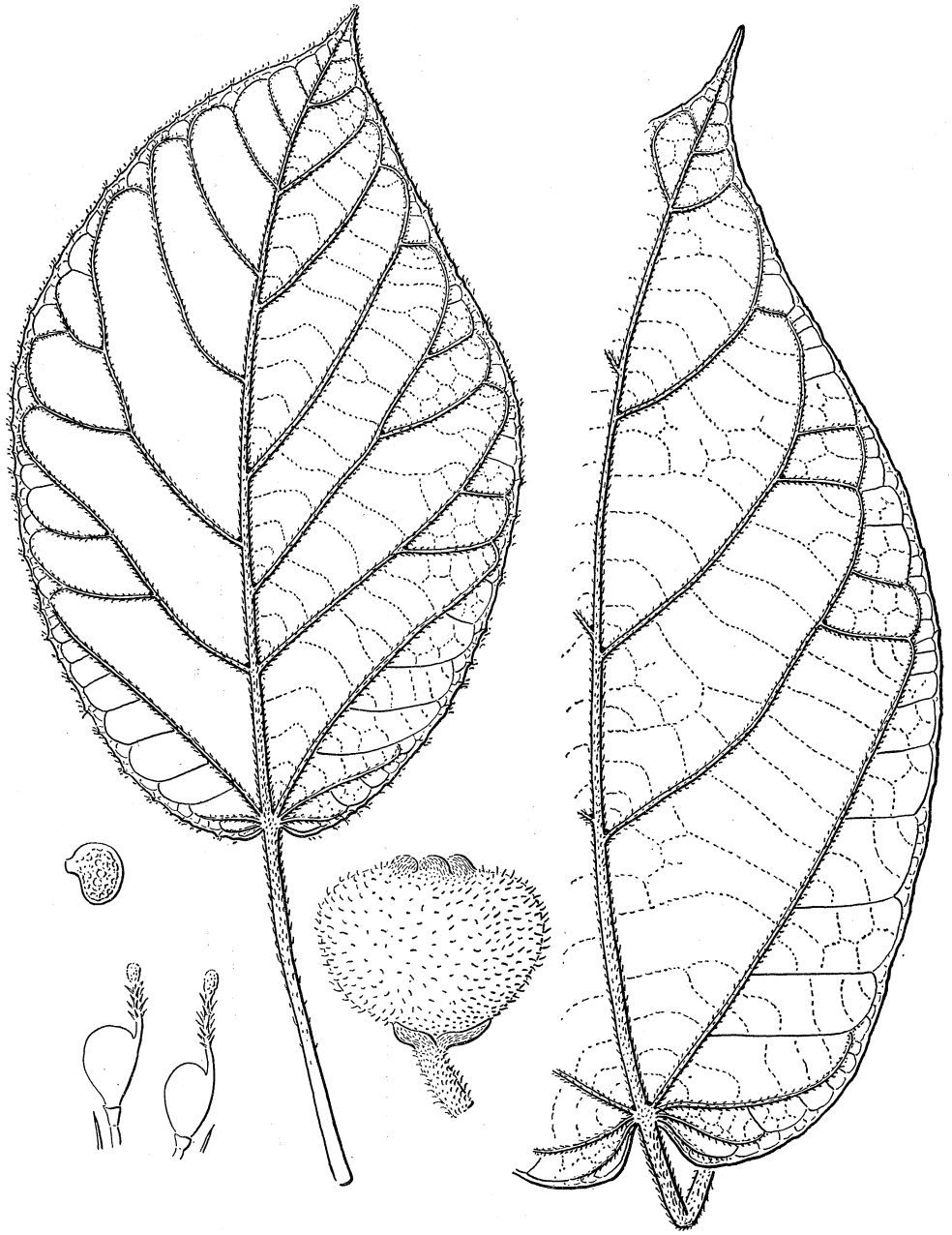

FIGURE 60. Subsect. *Sycocarpus*. *F. profusa*, Kajewski 1743, leaf (left), fig, female flower, seed; RSS 2386, leaf (right). Leaf × ½, fig × 2, flowers × 10.

rounded, ciliate–denticulate to subentire, membranous, scabrid on both sides, drying greenish fuscous; lateral veins 4–6 or 6–8 pairs, 7–10 pairs in saplings, mostly with axillary glands and a gland at the forkings towards the margin; intercostals 5–9 (–13), rather lax, slightly raised below; basal veins 3–4 pairs, reaching one third or, occasionally, one half of the lamina, rarely short, with 2 basal glands; petiole 2–12 cm long, up to 18 cm in saplings,

with a subnodal gland. Figs cauliflorous and ramiflorous on leafless twigs up to 1 m long, developing into geocarpic stolons up to 5 m long with internodes 2–7 × 1 cm, the figs mostly

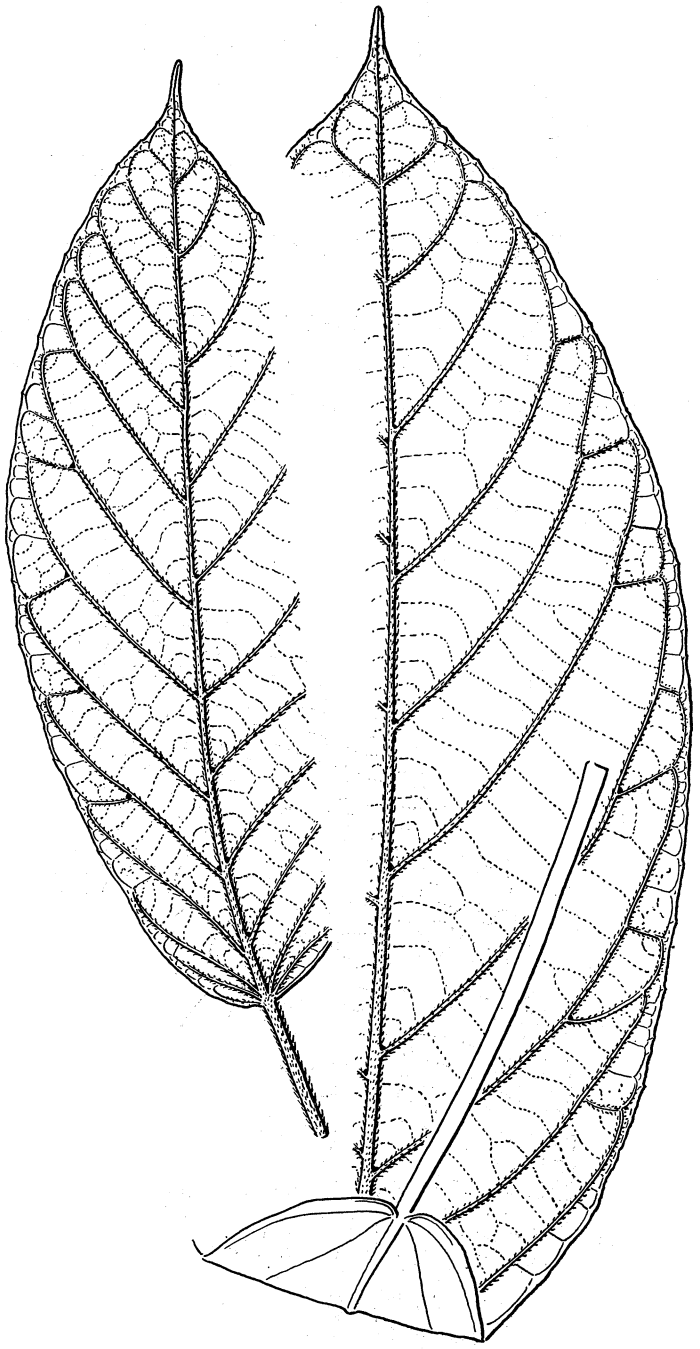

FIGURE 61. Subsect. *Sycocarpus*. *F. profusa*, RSS 6120, leaf with short basal veins, × ½.

congested on short lateral, simple or sparingly branched spikes 1–3 cm long without internodal elongation, ripening yellowish to dark bronze; peduncle 4–18 mm long; basal bracts 3, 5–8 × 3–5 mm, lanceolate–elliptic, appressedly hairy, eventually caducous, rather thick and incurved; body 25 × 30 mm (15–17 mm wide, dried), depressed globose, without lateral bracts, slightly ridged towards the apical rosette 6 mm wide, with 5 umbonate

peripheral bracts 3–5 mm long round the orifice; internal bristles brown, not copious; sclerotic cells in the endocarp of gall-figs, absent from the seed-fig. Male flowers in 1–2 rings round the orifice, pedicellate; perianth saccate; stamen 1. Gall-flowers sessile or shortly pedicellate; perianth covering the ovary but often splitting. Female flowers as the gall; perianth very short, as a collar at the base of the dark red-brown ovary; style thickly hairy. Seed 0·8–1 mm long, slightly keeled, subtuberculate, hilum prominent. Leaf with cystoliths only on the lower side.

Distr. Solomons, lowland forest up to 1000 m alt., widespread throughout the islands.

Kwara-ae. aimomote, aimotemote.

Collections. Brass 2823; BSIP 827, 3266, 4399; Kajewski 1743; NGF 13775; RSS 6, 8, 2386, 6118, 6120, 6166.

This is a variable species in hairiness and leaf-shape. It needs careful study from sapling to old tree to discover the modifications undergone in the life-time of the plant. The fig and flowers seems fairly constant, but some collections have rather small figs. Compare *F. tanypoda*.

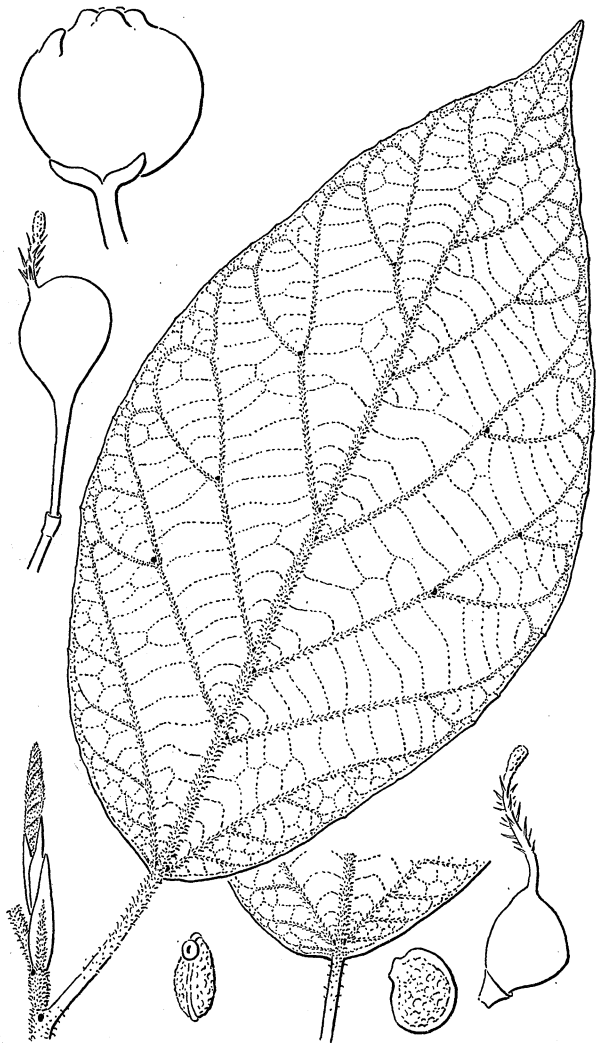

FIGURE 62. Subsect. *Sycocarpus*. *F. tanypoda*, RSS 170. Leaf and twig $\times \frac{1}{2}$, fig $\times 1$, flower and seed $\times 10$.

423A. **F. tanypoda** sp.nov. (figures 62 to 64)

Arbor usque 13 m alta, foliis spiraliter dispositis. Ramuli pilis brunneis v. fulvis setosis patentibus dense strigosi; petioli costaeque (subtus) pilis fulvidulis v. subalbidis 0·5–1·5 mm longis villosi, glabrescentes. Ramuli 4–6 mm crassi, ultimi 3–4 mm. Stipulae 12–35 mm longae, sericeae, basim versus brunneo-strigosae, caducae vel arboribus juvenilibus subpersistentes. Lamina 22–34 × 12–20 cm. in arboribus altis 8–20 × 4–9·5 cm, ovatocordata symmetrica acuminata, basi cordata, denti-

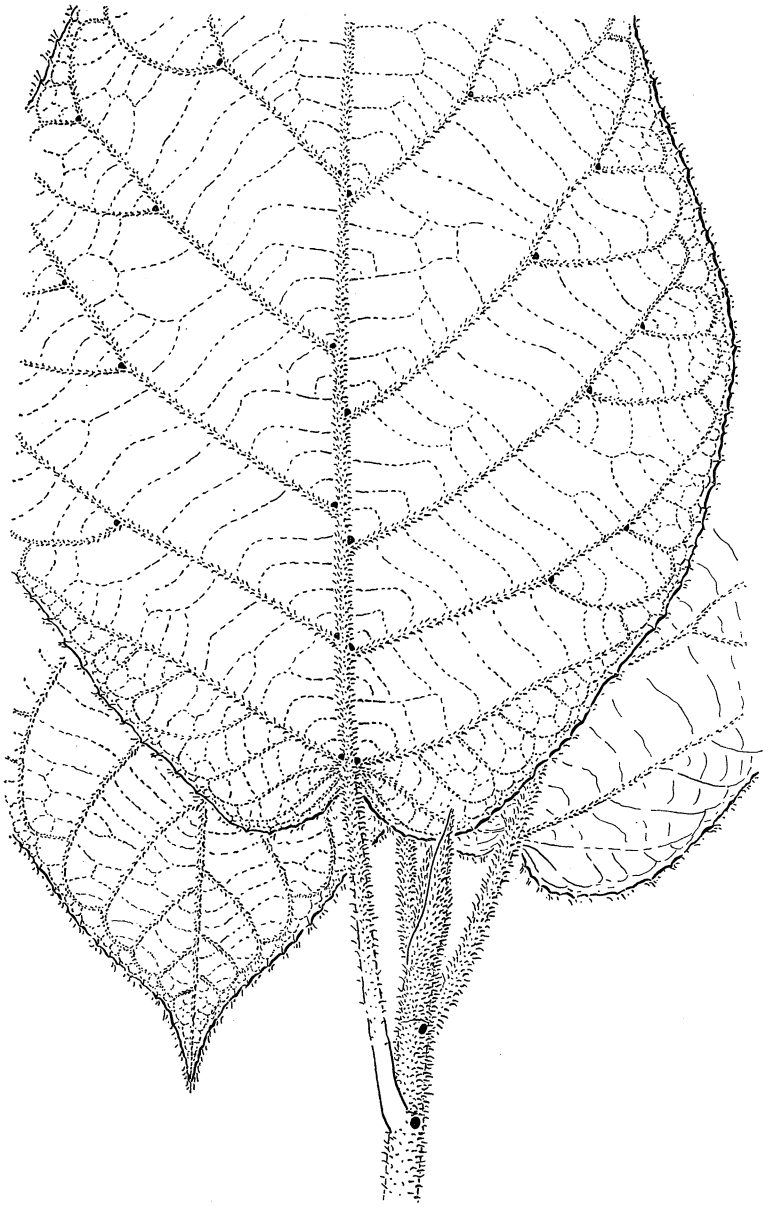

FIGURE 63. Subsect. *Sycocarpus*. *F. tanypoda*, RSS 1229, × ½.

culata, etiam in altis elliptica, basi subcuneata, submembranacea, scabrida; costis lateralibus utrinsecus 8–10, 6–8 in altis, intercostis usque 10; basalibus 3–4, brevibus; petiolo 2–14 cm longo, Syconia cauliflora ad ramulos efoliatos usque 15 cm longos, etiam ad stolones elongatos subterraneos, internodiis 2–9 cm longis, raro axillaria, primo tenue brunneo-pilosa, glabrescentia, 30–50 mm lata (25–30 mm, st. sicc); pedunculo 5–20 mm; bracteis basalibus 3, 4–8 mm longis, caducis; bracteis

lateralibus 1–3, 4–10 × 3–7 mm; pariete 4–5 mm crasso, cellulis scleroticis copiosis; setis internis sparsis brevibus brunneolis. Stamen 1. Perianthium cecidiophorum saccatum ovarium obtegens, femineum breve ovarii stipitem amplectans. Stylus femineus sparsim setosus. Semina 1 mm longa, subtuberculata, hilo prominenti. Ins. Solomonensibus. RSS 2382, typus K.

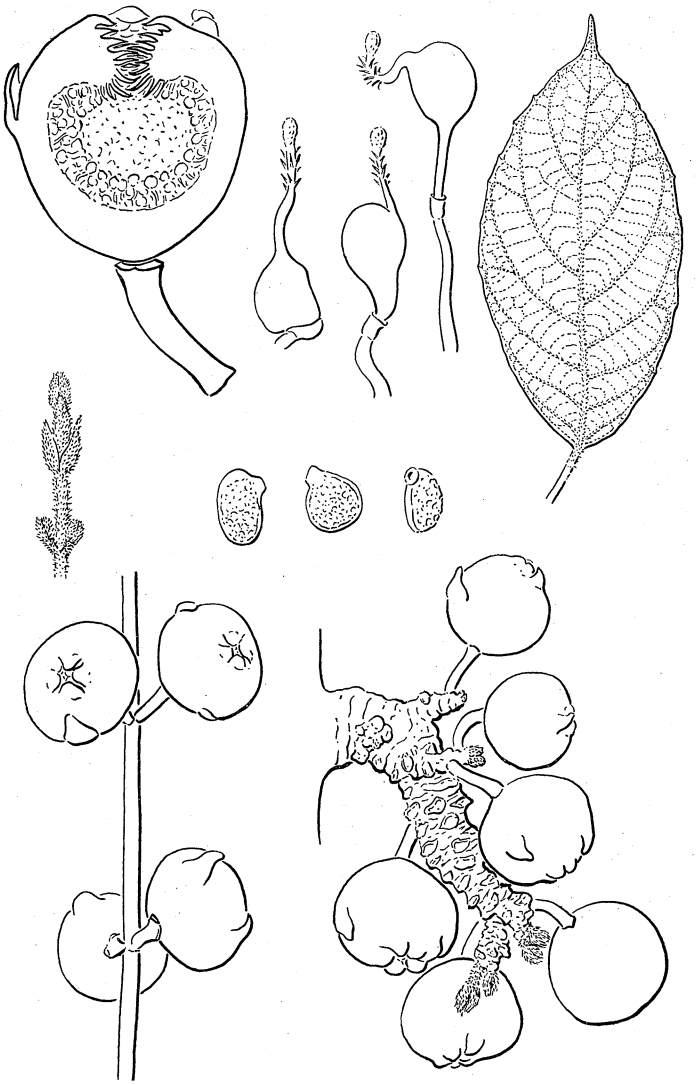

FIGURE 64. Subsect. *Sycocarpus*. *F. tanypoda*, RSS 2382, cauliflorous fruiting twig and stolon, × ½; fig-section × 1; female flowers and seeds, × 10; RSS 2452, leaf × ½.

Tree up to 13 m high. Leaves spirally arranged. Twigs thickly strigoso-pubescent with stiff, spreading, brown or fulvous hairs 1–2 mm long, glabrescent; petiole and underside of main veins with spreading white or brownish hairs 0·5–1·5 mm long, at first densely villous, glabrescent; underside of smaller veins villous or sparsely set with short white hairs; upperside of lamina thinly white hairy. Twigs 4–6 mm thick, 3–4 mm in ultimate branchings. Stipules 12–35 mm long, appressedly silky, brown strigose on the keel towards the base, caducous or subpersistent on saplings. Lamina 22–34 × 0·2–20·5 cm, reducing to 8–20 × 4–9·5 cm in old and high trees, ovate–cordate, acuminate with the tip up to 20 mm long, base cordate, symmetrical, denticulate, becoming elliptic with subcuneate base on

old and high trees, somewhat scabrid above, scabrid–villous beneath, drying greenish to brownish; lateral veins 8–10 pairs, 6–8 in smaller leaves, slightly raised below, mostly with an axillary gland and with a gland at the marginal forkings; intercostals up to 10, scarcely raised below; basal veins 3–4 pairs, not elongate or to one third of the lamina, the largest with axillary glands; petiole 2–14 cm long, with a subnodal gland. Figs cauliflorous, rarely a few axillary, on stout woody leafless twigs up to 15 cm long without internodes, up to 4 m high on the trunk, and on long geocarpic stolons 5–6 mm wide, with internodes 2–9 cm long, ripening greenish ochre, sometimes dull orange-pink, reddish, or wholly red; peduncle 5–20 mm long, shorter on the stolons; basal bracts 3, 4–10 mm long, early caducous; pedicel none; body 30–50 mm wide (25–30 mm, dried), subglobose or subturbinate, usually with 1–3 stout, obtusely lanceolate, lateral bracts 4–10 × 3–7 mm, the orifice closed by a rosette 8–12 mm wide, with 5–6 gibbous peripheral bracts; fig-wall 4–5 mm thick (living), with abundant sclerotic cells in the endocarp of gall-figs, few or none in seed-figs; internal bristles sparse, short, brownish. Male flowers in 1–2 rings round the orifice, pedicellate; stamen 1. Gall- and female flowers sessile to pedicellate; perianth covering the ovary and base of the style in gall-flowers, as a short tube in female flowers; ovary subsessile to long-stalked, red-brown; female style rather sparsely hairy. Seed 0·9–1·0 mm long, slightly keeled, subreticulate-rough, the hilum prominent. Leaf with cystoliths only on the lower side.

Distr. Solomons (Kolombangara, New Georgia, Guadalcanal).

Ecology. Lowland forest up to 800 m alt., and in old garden-country frequent.

Kwara-ae. aimomote; monomano (New Georgia).

Collections. BSIP 2911, 4733; RSS 170, 1229, 1248, 1448, 2382, 2437, 2452.

This species comes between *F. neobritannica* of New Britain and *F. profusa*. It has the large figs of the first and the stoloniferous habit of the second. The leaves on the stouter branches are large and shaped as in *F. neobritannica*, but ovate rather than obovate. The smaller leaves on the smaller twigs of older, more branched trees become elliptic with narrowed subcuneate base as in *F. profusa*. *F. baccaureoides* is similar but has paler hairs and smaller figs on cauliflorous twigs, and it is not stoloniferous. I have seen many trees of the four species and consider them worthy of specific rank, though apparent intermediaries occur in the herbarium fragments. They require study in all stages from sapling to the oldest tree.

423B. **F. scaposa** sp.nov. (figure 65)

Arbor usque 13 m alta, foliis spiraliter dispositis. Ramuli petioli costaque media (subtus) pilis fuscobrunneis 1–3 mm longis patentibus dense setosii; costae laterales pilis similibus usque 1·5 mm longis. Ramuli 2–4 mm crassi. Stipulae usque 25 mm longae, ex integra v. basim versus brunneo-pilosae. Lamina 12–27 × 5–16 cm, elliptica acuminata, basi subcordata, denticulata scabrida; costis lateralibus utrinsecus 6–9, intercostis usque 7; basalibus 3, brevibus v. paullo elongatis; petiolo 1·5–10 cm longo. Syconia cauliflora ad ramulos efoliatos usque 1 m longos, etiam ad stolones subterraneous plus minus elongatos, primo breviter brunneo-pilosa, glabrescentia, 3–5 cm lata (viva), maturitate rubro v. purpureo-brunnea; pedunculo 2·5–10 cm longo; bracteis basalibus 3, 2–4 mm longis; bracteis lateralibus nullis, raro singulis; setis internis 0·5–1 mm longis brunneolis, copiosis; cellulis scleroticis copiosis. Perianthium femineum breve, ovarii stipitem amplectans; stylo dense setoso. Semina subtuberculate, hilo prominenti. Ins. Solomonensibus, RSS 168, typus, K.

Tree up to 13 m high. Leaves spirally arranged. Twigs, petioles, stipules, and underside of the midrib densely setose with fuscous brown, spreading hairs 1–3 mm long; lateral veins with shorter hairs up to 1·5 mm long beneath. Twigs 2–4 mm thick. Stipules up to

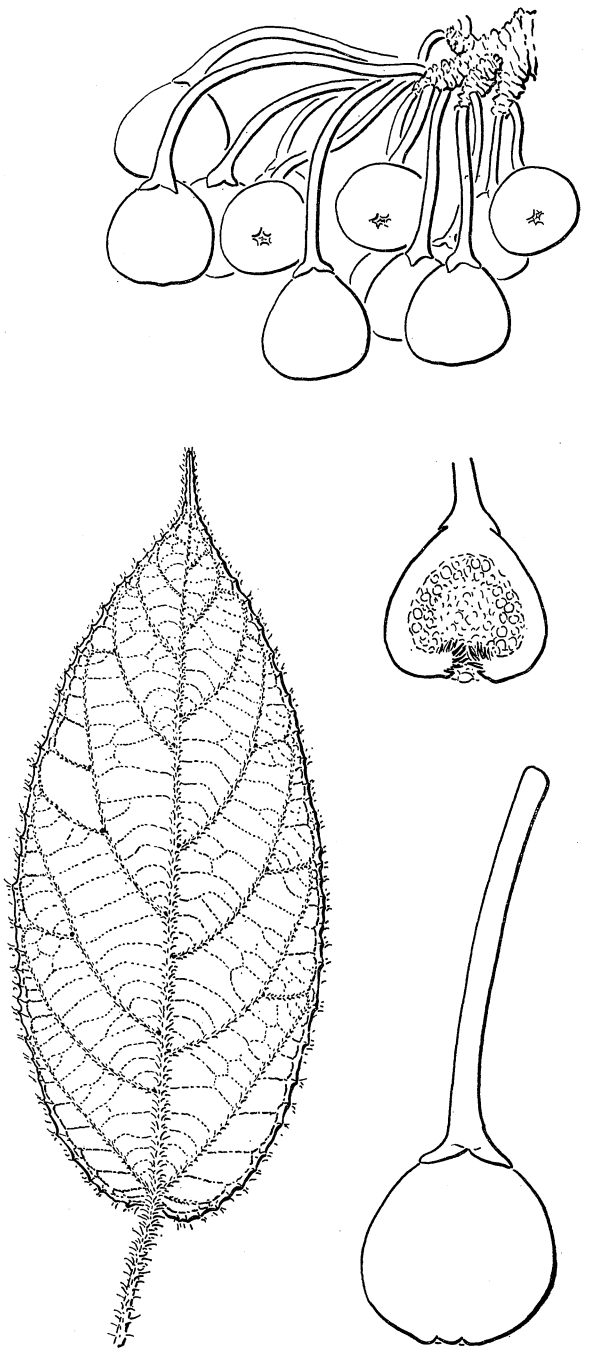

FIGURE 65. Subsect. *Sycocarpus*. *F. scaposa*, RSS 168, leaf and fig (below); RSS 2437A, cauliflorous twig and fig-section. Leaf and twig $\times \frac{1}{2}$, figs $\times 1$.

25 mm long, entirely brown-setose or at the base only, caducous. Lamina 12–27 × 5–16 cm, elliptic, acuminate with the tip up to 20 mm long, base subcordate, denticulate, ciliate on the edge, scabrid, submembranous; lateral veins 6–9 pairs, the larger with axillary glands

and, often, with a gland at the forkings towards the margin; intercostals up to 7, scarcely raised below; basal veins 3 pairs, short or reaching one quarter of the lamina; petiole 1·5–10 cm long, with a subnodal gland. Figs in compact clusters up to 25 cm wide on stout cauliflorous twigs up to 1 m long, from ground-level to a height of 4 m on the trunk, or (RSS 169) on geocarpic stolons, shortly brown hairy, then glabrous, ripening red or purple-brown; peduncle 2·5–10 cm long; basal bracts 3, 2–4 mm long; body 3–5 cm wide (20–30 mm, dried), rarely with a lateral bract, the umbonate apical bracts in a slightly sunken rosette 5–6 mm wide; internal bristles 0·5–1 mm long, pale brown, fairly abundant; sclerotic cells in the endocarp of gall-figs. Male flowers with 1 stamen. Gall-flowers with the perianth covering the ovary. Female flowers shortly pedicellate or subsessile; perianth as a short tube round the ovary-stalk; style densely setose. Seed 1 mm long, subtuberculate, with prominent hilum. Leaf with cystoliths only on the lower side.

Distr. Solomons (Kolombangara, Rendova, Guadalcanal).

Ecology. Lowland forest and in old garden-country, locally common, up to 1300 m alt. (Popomanasiu).

Kwara-ae. aimomote, ramomote.

Collections. BSIP 827, 1916; RSS 168, 169, 2437A.

In leaf this is practically indistinguishable from *F. tanypoda*, but the long peduncles and short basal bracts seem characteristic. It is, also, massively cauliflorous, rather than geocarpic. Many trees found near the mouth of the Kolombangara river were cauliflorous without a trace of stolons.

423C. **F. dissipata** sp.nov. (figure 66)

Arbor usque 12 m alta. foliis spiraliter dispositis. Ramuli petioli costaque media (subtus) pilis rigidis 2–5 mm longi brunneis v. purpureo-brunneis v. nigris patentibus setosi. Ramuli 3–4 mm crassi. Stipulae 20–40 mm longae, plerumque glabrae, basim versus brunneo-setosae, caducae v. subpersistentes. Lamina 14–25 × 6–15 cm elliptico-obovata acuminata symmetrica, basim versus angustata cuneato-subcordata, denticulata scabrida; costis lateralibus utrinsecus 8–10, intercostis usque 10; basalibus 2–3, brevibus; petiolo 1·5–6 cm longo. Syconia cauliflora ad ramulos efoliatos, etiam ad stolones elongatos subterraneos, internodis usque 7 cm longis, raro axillaria, glabra, 20–25 mm lata (12–15 mm, st. sicc.); pedunculo 9–20 mm longo; bracteis basalibus 3, 2–3 mm longis; bracteis lateralibus nullis; setis internis 0·5–1 mm longis, brunneolis, sparsis v. copiosis; cellulis scleroticis copiosis. Stamen 1. Perianthum cecidiophorum ovarium obtegens; femineum breve, ovarii stipitem amplectans; stylus femineus dense setosus. Semina subtuberculata, hilo prominenti. Ins. Solomonensibus. RSS 226, typus K.

Tree up to 12 m high. Leaves spirally arranged. Twigs, petioles, and underside of midrib setose with stiff, spreading, dark brown, purple, or black hairs 2–5 mm long. Twigs 3–4 mm thick. Stipules 20–40 mm long, glabrous or brown setose towards the base, caducous or subpersistent. Lamina 14–25 × 6–15 cm, elliptic–obovate, the acuminate tip up to 15 mm long, symmetric, narrowed to the cuneato-subcordate base, denticulate, scabrid; lateral veins 8–10 pairs, 2–10 intercostals, slightly raised below; basal veins 2–3 pairs, short; petiole 1·5–6 cm long. Figs cauliflorous in large masses on leafless twigs and, also, on geocarpic stolons with internodes up to 7 cm long, rarely axillary, glabrous, ripening reddish purple; peduncle 9–20 mm long; basal bracts 3, 1–3 mm long; pedicel 0–1 mm long; body 20–25 mm wide (12–15 mm, dried), subglobose, without lateral bracts,

with 5 small umbonate apical bracts in a rosette 4–5 mm wide; internal bristles 0·5–1 mm long, brownish, sparse to abundant; sclerotic cells abundant in the fig-wall. Male flowers in 1–2 rings round the orifice, pedicellate; perianth saccate; stamen 1. Gall-flowers sessile or pedicellate; perianth covering the ovary. Female flowers as the gall; perianth as a short tube or collar round the ovary stalk; style densely setose. Seed 1 mm long, subtuberculate, with prominent hilum. Lamina with cystoliths only on the lower side.

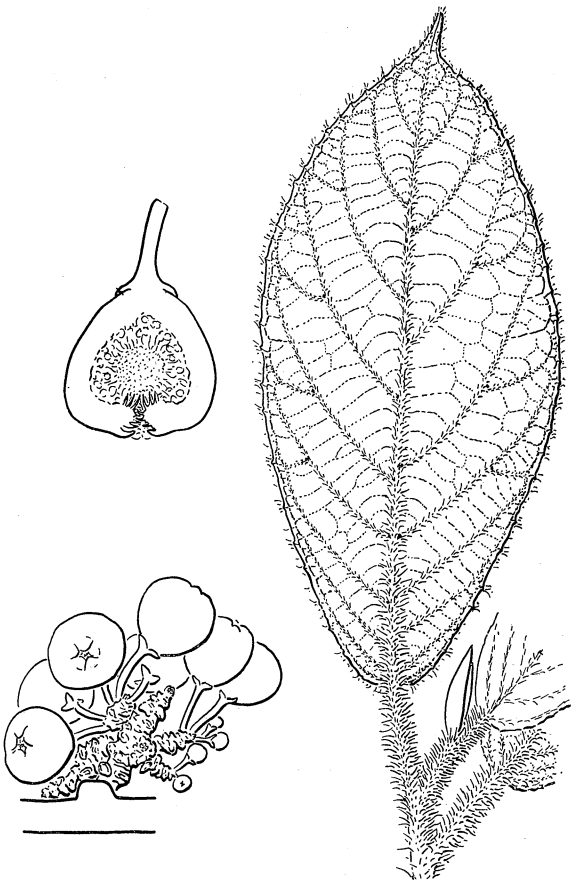

FIGURE 66. Subsect. *Sycocarpus*. *F. dissipata*, RSS 226, twig and part of stolon $\times \frac{1}{2}$, fig $\times 1$.

Distr. Solomons (Gizo, Kolombangara, New Georgia, Rendova, Vangunu, Guadalcanal).
Ecology. Lowland forest and old garden-country, frequent.
Kwara-ae. aimomote, mango-mango; mongmanu (New Georgia).
Collections. BSIP 703, 917, 1356, 1448, 1916, 2020, 2972, 4326; RSS 226, 228.

This differs from *F. scaposa* and *F. tanypoda* in the very dark hairs and the small fig. It needs, however, further enquiry.

424. *F. baccaureoides* Corner (figure 67)

Tree up to 13 m high. Leaves spirally arranged. Twigs, petioles, and underside of the main veins hispid with spreading or decurved, white to dark brown hairs 2–4 mm long, rather flexuous on the twigs and petioles, the smaller veins shortly hispidulous; upperside of the lamina scabrid–hispid with rather sparse, stiff hairs. Twigs 4–6 mm thick, solid. Stipules 15–30 mm long, glabrous, caducous. Lamina 14–30 × 11–17 cm, obovate, the acuminate tip up to 12 mm long, base narrowed cordate to rounded cuneate, symmetric,

denticulate to subentire, membranous, scabrid–hispid on both sides, drying dark brown; lateral veins 7–10 pairs, strongly raised below, forking about half-way to the margin with a gland in the fork, up to 12 intercostals, raised below; basal veins 4–5 pairs, short, without

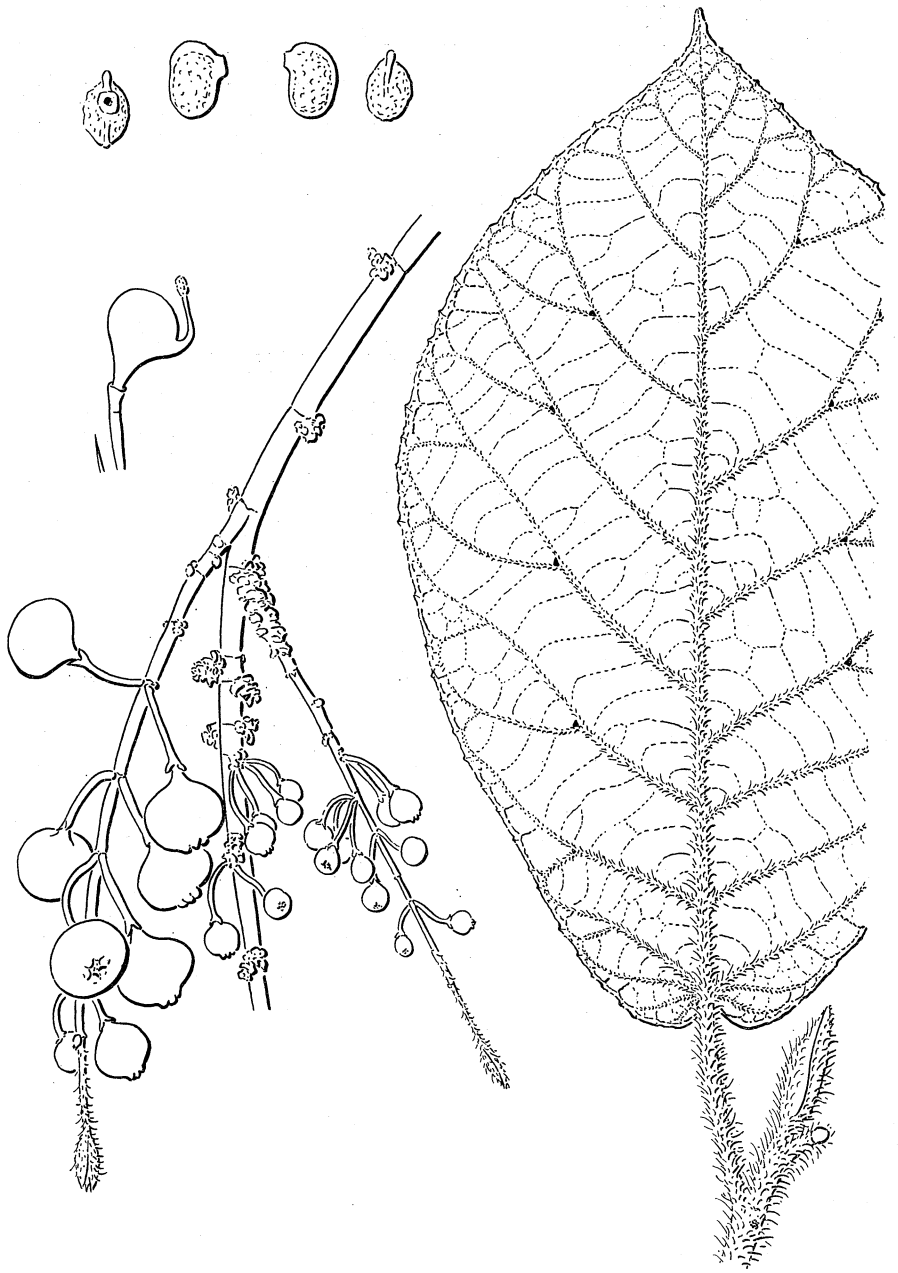

FIGURE 67. Subsect. *Sycocarpus*. *F. baccaureoides*, Kajewski 1927, twig $\times\frac{1}{2}$, female flowers and seed $\times 10$; RSS 2653, cauliflorous twig $\times\frac{1}{2}$.

basal glands; petiole 15–65 mm long, with a slight subnodal gland. Figs cauliflorous on leafless twigs up to 1·5 m long, 3–6 mm thick, but thickened at the base up to 5 cm, the internodes 1–5 cm long, unbranched or sparingly branched, arising from the trunk up to a height of 6 m, the lower twigs lying on the ground, not stoloniferous; peduncle 11–25 mm long; basal bracts 3, 2–4 mm long, ovate–lanceolate, subacute, caducous; body 21–25 mm

wide (13–16 mm, dried), depressed globose, sometimes with a short pedicel, without lateral bracts, the orifice closed by 5–6 umbonate, projecting, apical bracts 3–4 mm long, not ridged; internal bristles 0·5–1 mm long, brown, rather sparse; sclerotic cells abundant in the inner wall of the gall-figs, few to abundant in seed-figs. Male flowers in 1–2 rings round the orifice, pedicellate; perianth saccate; stamen 1. Gall- and female flowers sessile or pedicellate; perianth covering the red-brown gall-ovary, as a short tube round the stalk or base of the red-female ovary; female style glabrous or sparsely puberulous. Seed $1 \times 0{\cdot}6$ mm, distinctly keeled, nearly smooth, hilum prominent. Lamina with cystoliths only on the underside.

Distr. Solomons, in lowland forest by rivers and on hill-sides, locally frequent, throughout the islands, up to 1300 m alt.

Kwara-ae. aimomote, raumomote, samota.

Collections. BSIP 5809, 5911; Kajewski 1927 ('tau-tore', Buin); NGF 13562, 13712; RSS 2653, 2873; Waterhouse 7, 208 ('havona', Tiop; 'iri', Siwai; Bougainville).

This species is remarkable among those of subsect. *Sycocarpus* in the Solomons in not being geocarpic with stolons. The cauliflorous twigs stand out obliquely from the trunk until they sag under the weight of fruit. It appears that in some collections the figs become abnormally galled and develop short peduncles with long-pedicellate, narrowly pyriform bodies without proper flowers. The leaves resemble in shape those of *F. neobritannica*.

437. *F. subcongesta* Corner var. *symmetrica* Corner

Tree up to 8 m high. Leaves spirally arranged to opposite. Twigs, petioles, stipules, and underside of the main veins rather densely appressedly hairy with dark brown hairs 1–1·5 mm long, the underside of the smaller veins thinly villous with paler, spreading hairs up to 0·5 mm long. Twigs 2–3 mm thick. Stipules up to 15 mm long, caducous. Lamina $12–20 \times 5–7$ cm, elliptic to elliptic-obovate, the acuminate tip up to 17 mm long, base narrowed cordate and symmetric, minutely denticulate, membranous, slightly scabrid on both sides, drying grey-brown; sapling lamina up to 26×11 cm, with broadly cordate, symmetric base; lateral veins 6–8 pairs, intercostals 3–6, rather lax, raised below; basal veins 3 pairs, short; petiole 15–25 mm long, with a subnodal gland. Figs on superficial or geocarpic stolons up to 3 m long from the base of the trunk, with internodes 3–7 cm $\times$ 3–4 mm, ripening yellow to pink; peduncle 5–15 mm long; basal bracts 2–3 mm long, persistent; pedicel 0–7 mm long; body 20–25 mm wide (12–15 mm, dried), subglobose, shortly brown hairy, glabrescent, with 5–6 humps round the slightly sunken apical rosette 4–5 mm wide; internal bristles few or none, brownish; sclerotic cells few, in clusters round the vascular bundles. Male flowers in 1–2 rings round the orifice; stamen 1. Gall- and female flowers sessile or pedicellate; perianth covering the red-brown ovary in each; female style, hairy. Seed 0·8–0·9 mm long, asperate, slightly keeled, hilum prominent. Lamina with cystoliths only on the lower side.

Distr. Solomons (Bougainville, Guadalcanal).

Ecology. Lowland forest up to 1200 m alt., apparently infrequent.

Collections. NGF 13735, 13737, 13739; RSS 81.

This variety comes in some ways between *F. subcongesta* of New Britain and *F. macrothyrsa* of the Solomons; it differs from both in the symmetric leaf with more or less cordate base.

It has the indumentum, venation, and persistent basal bracts of *F. subcongesta*, but the pedicellate fig and stoloniferous tendency of *F. macrothyrsa*.

463. *F. bougainvillei* Reching.

Tree up to 12 m high; latex buff. Leaves spirally arranged, varying opposite, the veins pallid white. Twigs, petioles, underside of main veins, and figs hispid–villous with white or yellowish to pale brown hairs 1–1·5 mm long, the smaller veins thinly puberulous beneath; upperside of the lamina shortly and thinly appressedly hairy. Twigs 3–4 mm thick. Stipules 20–30 mm long, glabrous, caducous. Lamina 11–35 × 8–19 cm, elliptic to obovate, narrowed to the subacute to shortly acuminate apex, base rather widely cuneate, nearly or quite symmetric, entire, membranous, hispidulous–scabrid on both surfaces, drying light brownish; lateral veins 7–8 pairs, with axillary glands, distant, curved ascending, raised below; intercostals 4–7, fairly regular and close, thinly hispidulous beneath; basal veins 1 (–2) pairs, short, without basal glands; petiole 18–25 mm long, with a subnodal gland. Figs axillary, solitary or paired, thinly hispidulous, ripening yellowish white; peduncle 2–6 mm long; basal bracts 3, 1–2 mm long, glabrous; body 11–13 × 16–20 mm, depressed globose, slightly ridged towards the slightly sunken apex, the apical rosette 3–4 mm wide composed of many small appressed apical bracts; internal bristles up to 1 mm long, white, numerous; fig-wall 2–3 mm thick, with densely sclerotic inner layer. Male flowers in 2 rings round the orifice; stamen 1. Gall-flowers sessile or pedicellate; perianth covering all or most of the red-brown ovary, entire or slightly lobed. Female flowers sessile or pedicellate; perianth as a thin funnel or collar round the base of the stalk of the white ovary, even almost absent; style very hairy. Seed 1 mm long, lenticular, rough, slightly keeled, the hilum more or less prominent. Leaf with cystoliths on both sides or only on the underside.

Distr. Bougainville Isl.

Ecology. Lowland forest up to 800 m alt., frequent in secondary forest.

Collections. Kajewski 1537; NGF 13554, 13743, 13745 ('momo', Arawa); Rechinger, 3903, 4761, 4837; Waterhouse 52 ('bao', 'vabihubihu', Teop), 109 ('kaikai', Siwai), 152 ('erevat', 'huhu', 'makemake', 'wahirihiri', Siwai), B264, 798 ('makemake', Siwai; children make native tops 'make' from the fruits).

This is the only species that is close to *F. septica*. It may be regarded as a scabrid-hairy form with the figs less ridged, yet it seems not to occur on other islands.

464. *F. septica* Burm. f. (figure 68)

Tree up to 25 m high, commonly small, fruiting almost as a shrub; latex serous, yellowish. Leaves spirally arranged or decussate. Glabrous or the young internodes and petioles somewhat hispid with white to yellowish hairs up to 1 mm long. Twigs 2–4 mm thick, up to 10 mm in saplings, hollow. Stipules 7–50 mm long, lanceolate, caducous. Lamina 7–28 × 3–13·5 cm, up to 35 × 24 cm in saplings, ovate–cordate to ovate and, eventually, narrowly elliptic, subacute or, in old trees, subacuminate, base cordate to cuneate, often slightly asymmetric, entire, smooth, membranous to subcoriaceous, drying green to pale brown; lateral veins 6–12 (–14) pairs, at a wide angle, sometimes with an axillary gland; intercostals 3–6, lax, scarcely raised below; basal veins 1–2 (–3) pairs,

short, no basal glands; petiole 8–50 mm long, up to 9 cm in saplings, with a subnodal gland. Figs axillary, paired, or on the twigs behind the leaves, glabrous, ripening white to yellow; peduncle 2–12 mm long, rarely none; basal bracts 3, 1–2 mm long, subacute, persistent; pedicel usually none, rarely up to 7 mm long; body 20–35 mm wide (18–25 mm dried), depressed globose, rarely ellipsoid, without lateral bracts, with 7–12 rather prominent ridges converging towards the slightly sunken orifice with 4–6 peripheral bracts and

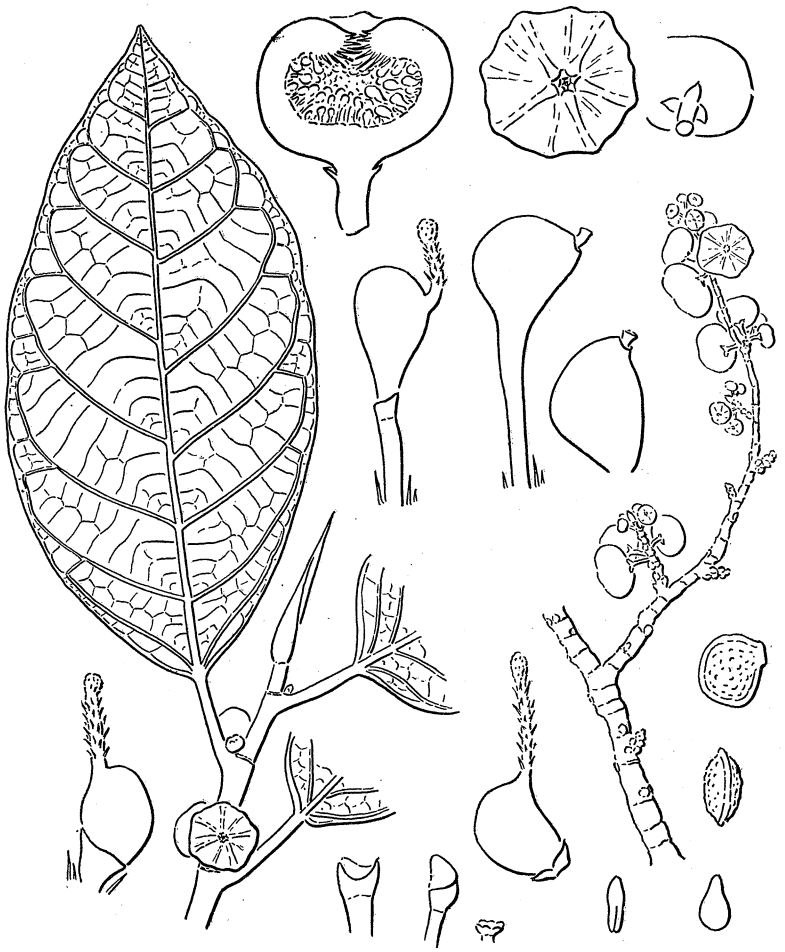

FIGURE 68. Subsect. *Sycocarpus*. *F. septica*, RSS 2431, twig $\times \frac{1}{2}$, figs $\times 1$, flower and seed $\times 10$. Var. *cauliflora*, RSS 6207, cauliflorous twig (right) $\times \frac{1}{2}$.

several small apical bracts; internal bristles short, few, white; sclerotic cells in a dense layer in the inner part of the fig-wall. Male flowers in 1–2 rings round the orifice, pedicellate; perianth saccate; stamen 1. Gall-flowers sessile or pedicellate; perianth covering the ovary, entire or obscurely lobed. Female flowers sessile or pedicellate; perianth very short, cupular or shortly lobed or prolonged on one side, at the top of the pedicel or at the base of the sessile red-brown ovary; style hairy. Seed 1 mm long, slightly keeled, subtuberculate, the hilum prominent. Leaf with cystoliths only on the lower side.

Distr. Sumatra, Java, Borneo, Formosa, Ryu Kyu, through Malaysia to New Hebrides and Queensland.

Ecology. Lowland forest, chiefly riverside, up to 1400 m alt., common in old garden-country, throughout the Solomons.

Kwara-ae. angalu, ngalu.

Collections. Brown 210, 780A, 2702 ('adenou', Guadalcanal); BSIP 740, 978, 1093, 1174, 1513, 1743, 2230, 2853, 2974, 3288, 3455, 3671, 4180, 4718, 5527, 5713, 5821; A. W. Herre 110; Kajewski 2412, 2597 ('irure', 'nure', Guadalcanal); RSS 2431, 2807, 6154.

Var. *cauliflora* Corner (figure 68)

Figs cauliflorous in dense bunches on long racemosely branched leafless twigs up to 50 cm long, 3–5 mm thick, 10 mm at the base, internodes 1–4 cm long, the short side-branches up to 4 cm long and generally without internodes; peduncle 8–12 mm long; basal bracts 1–2·5 mm long; body often only slightly ridged.

Distr. Timor Laut, Admiralty Isl., New Ireland, Solomons, Santa Cruz Isl., New Hebrides, Queensland.

Ecology. Lowland forest, often near the shore on coral rock and in mangrove, infrequent.

Collections. Brown 5482; RSS 70, 2584, 6207; T. Wolff 3039.

This is the most widely distributed species of sect. *Sycocarpus*. It has no close allies except *F. bougainvillei* and its cauliflorous variety is essentially Melanesian. Hence I regard it as a product of the Melanesian series of the section, similar to *F. ampelas* and *F. melinocarpa* in sect. *Sycidium*, and neither of these has reached the Asian mainland.

474. *F. macrothyrsa* Corner (figure 69)

Tree up to 15 m high; latex white. Leaves subdistichous or, chiefly at points of branching, opposite in unequal pairs. Twigs, petioles, and young figs sparsely appressedly hairy with white to pale brown hairs up to 1 mm long, the underside of the veins very sparsely and shortly appressedly hairy. Twigs 3–4 mm thick. Stipules up to 25 mm long, sparsely appressedly hairy in the lower part, caducous. Lamina 12–25 × 5–12 cm, elliptic, somewhat asymmetric (even on erect shoots) with the acuminate tip up to 20 mm long, base more or less asymmetric, rounded on one side, cuneate on the other, the smaller lamina of a pair symmetric and subcordate, entire, thinly coriaceous, smooth, drying greenish to light brown; lateral veins 6–8 pairs, slightly raised below, distinctly inarching at the margin; intercostals 2–6, lax; basal veins 1–2 pairs, short; petiole 10–30 mm long, sometimes with a small subnodal gland. Figs borne on elongating leafless twigs up to 3 m long, 10–15 mm thick at the base, with internodes 1–4 cm long, hanging from the trunk up to a height of 5 m, the lower ones trailing on the ground, and some becoming geocarpic stolons with sparse long branches, but nearly every node with one or a pair of short, fertile branches up to 4 cm long without internodal extension bearing the figs in clusters, the figs soon glabrous and ripening yellow to pinkish brown and rose-red; peduncle 5–20 (–34) mm long; basal bracts 3, 1·5–3 mm long, lanceolate, early caducous; pedicels 1–5 mm long, developing only in dried figs; body 20–25 mm wide (14–17 mm, dried), depressed globose and subtruncate, slightly ridged from the base to the 5–6 subumbonate apical bracts set in a rosette 4–5 mm wide, not sunken; internal bristles short, white, sparse; sclerotic cells abundant in the inner part of the fig-wall, often few or none in seed-figs. Male flowers in one ring round the orifice, pedicellate; perianth saccate; stamen 1. Gall-flowers sessile or pedicellate; perianth covering the red-brown ovary. Female flowers more or less pedicellate; perianth as a short tube or collar round the stalk

of the red-brown ovary; style sparsely hairy to glabrous. Seed 1 mm long, subtuberculate, the hilum prominent. Leaves with cystoliths only on the lower side.

Distr. Solomons, lowland and hill-forest up to 1700 m alt., frequently by rivers and streams, common in old garden-country, throughout the islands.

Kwara-ae. mango-mango.

Collections. BSIP 633, 2302, 2404, 2488, 4409, 5384, 5474, 5482; NGF 13571; RSS 1, 5, 10, 184, 185, 245, 2294, 2914, 6121, 6182.

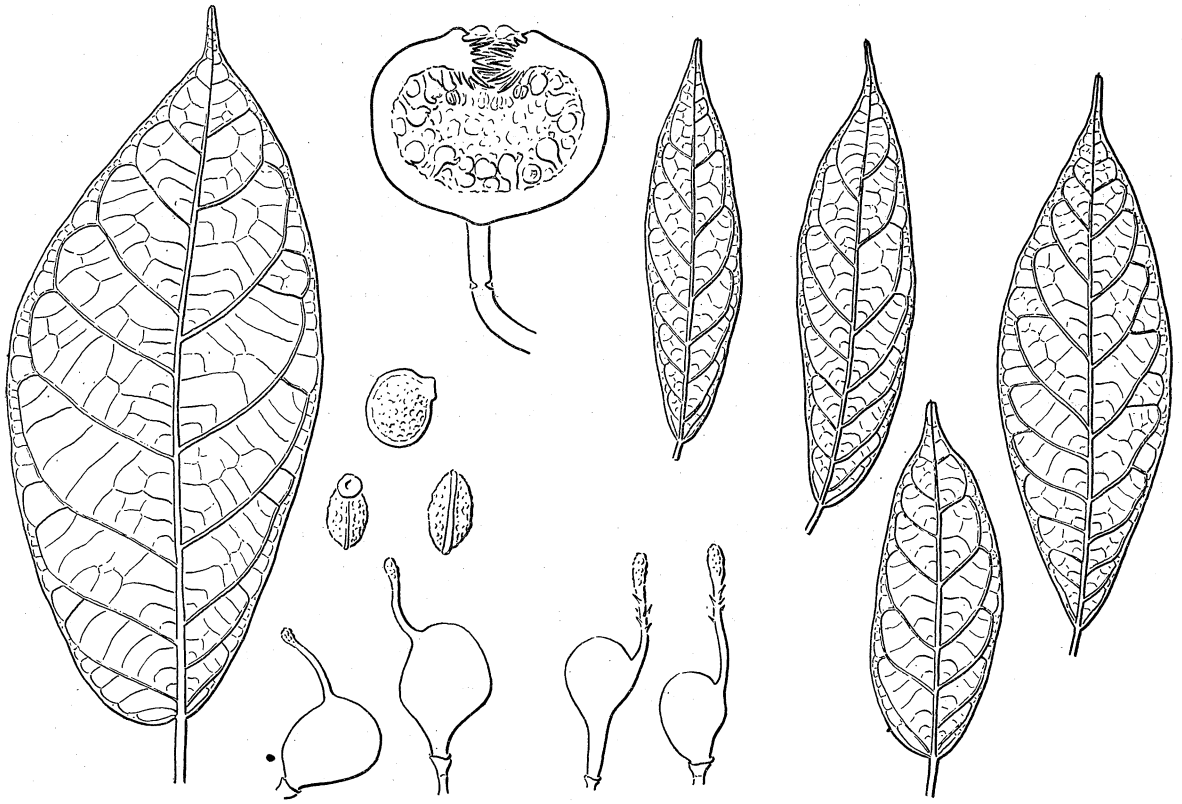

FIGURE 69. Subsect. *Sycocarpus*. *F. macrothyrsa*, NGF 13571, leaf $\times \frac{1}{2}$, fig $\times 2$. Var. *lancifolia* (right), leaves in order from left to right RSS 154, 2829, 105, Brown 2488 (below), $\times \frac{1}{2}$; female flowers with glabrous styles (Brown 2488) and hairy styles (RSS 154), $\times 10$.

Var. **lancifolia** var. nov. (figure 69)

Ramuli 1·5–2 mm crassi, graciliores. Lamina 7–16 × 2·3–4·2 cm, lanceolata v. anguste elliptica, apice attenuato v. subacuminato, basi attenuato-cuneato; costis lateralibus utrinsecus 7–10, intercostis 1–4; petiolo 4–15 mm longo. Receptacula minora; pedunculo 4–15 mm longo; bracteis basalibus 1–2 mm longis; pedicello 2–7 mm longo; corpore syconii 15–20 mm lato (8–10 mm, st. sicc.); setis internis nullis. Ins. Solomonensibus. RSS 6055, typus K.

a. Ramuli, petioli, costae (subtus) pilis albidis appressis usque 1 mm longis sparsim vestiti; stipulae caducae: Bougainville, NGF 13765 (det. *F. arfakensis*); Guadalcanal RSS 105, 154, 198, 199, 6055, BSIP 633, Brown 2488.

b. Ramuli etc. pilis brunneis appressis v. subpatentibus 0·5–1·5 mm longis plus minus dense vestiti; stipulae saepe persistentes: Ysabel, RSS 2829, 2846, 2855.

Twigs 1·5–2 mm thick, more slender. Lamina 7–16 × 2·3–4·2 cm, lanceolate or narrowly elliptic, apex attenuate or subacuminate, base attenuate–cuneate; lateral veins 7–10 pairs, 1–4 intercostals; petiole 6–12 mm long. Figs smaller; peduncle 4–15 mm long; basal bracts

1–2 mm long; pedicel 2–7 mm; body 15–20 mm wide (8–10 mm, dried); internal bristles none. Twigs, petioles, and underside of the main veins sparsely set with white appressed hairs up to 1 mm long and the stipules caducous; or these parts rather densely clothed with appressed or somewhat spreading brown hairs 0·5–1·5 mm long, and the stipules subpersistent.

This species is very variable in the way in which the cauliflorous twigs develop. Generally they hang down in long loose strands, but in many trees they certainly become geocarpic stolons when they reach the ground. Possibly gall-trees and seed-trees behave differently in this manner, but the wild trees are usually in different stages of their growth, when available for comparison, and it is difficult to resolve this point without growing them.

Var. *lancifolia* differs only in the smaller, narrower leaves and smaller figs. It seems to be a riverside variety, equally inclined to be stoloniferous. It is this variety which I referred to *F. arfakensis* in my check-list. The two are very similar, but there are differences in leaf-shape and venation. *F. arfakensis* has a longer, more acutely acuminate lamina and its lateral veins are more elongate, upcurving without inarching, and supplied with more numerous and regular intercostals. Var. *lancifolia* is clearly a willow-leafed derivative of *F. macrothyrsa* which has not been found in New Guinea. *F. arfakensis* is a parallel derived, perhaps, from *F. congesta.*

F. macrothyrsa is placed at the end of my check-list, but this is an error; it should come next to *F. subcongesta.* The Melanesian explanation of sect. *Sycocarpus*, discovered from the Solomons' flora, has improved understanding of these reduced species.

19. References

Arkell, W. J. 1956 *Jurassic geology of the world.* Edinburgh: Oliver and Boyd Ltd.

Balgooy, M. M. J. van 1960 Preliminary plant-geographical analysis of the Pacific. *Blumea* **10**, 385–430.

Bemmelen, R. W. van 1949 *The geology of Indonesia*, vol 1A. The Hague: Government Printing Office.

Corner, E. J. H. 1949 The durian theory or the origin of the modern tree. *Ann. Bot.* (N.S.) **13**, 367–414.

Corner, E. J. H. 1953–54 The durian theory extended. Parts I, II, III. *Phytomorphology* **3**, 465–476; **4**, 152–165, 263–274.

Corner, E. J. H. 1958*a* Transference of function. *J. Linn. Soc. Bot.* **56**, 33–40.

Corner, E. J. H. 1958*b* An introduction to the distribution of *Ficus*. *Reinwardtia* **4**, 15–45.

Corner, E. J. H. 1960–61 Taxonomic notes on *Ficus* Linn., Asia and Australasia. Sections 1–6, Addenda 1–2. *Gard. Bull. Singap.* **17**, 368–485; **18**, 1–69, 83–97; **19**, 385–401.

Corner, E. J. H. 1961 Evolution; in A. M. Macleod and L. S. Cobley, *Contemporary botanical thought*, pp. 95–114. Edinburgh; Oliver and Boyd.

Corner, E. J. H. 1962 The classification of Moraceae. *Gard. Bull. Singap.* **19**, 187–252.

Corner, E. J. H. 1963 *Ficus in the Pacific region. Pacific Basin Biogeography; a Symposium* (ed. J. Linsley Gressitt). Honolulu: Bishop Museum Press.

Corner, E. J. H. 1965 Check-list of *Ficus* in Asia and Australasia with keys to identification. *Gard.Bull. Singap.* **21**, 1–186.

Corner, E. J. H. 1966 *The natural history of palms.* London: Weidenfeld and Nicolson.

Croizat, L. 1958 *Panbiogeography*, Vol. II*a*, *b*, 452–985. Caracas: L. Croizat.

Darlington Jr., P. J. 1965 *Biogeography of the southern end of the world.* Cambridge, Mass.: Harvard University Press.

Dawson, J. W. 1963 New Caledonia and New Zealand—a botanical comparison. *Tuatara* **11**, 178–193.

Good, R. 1964 *The geography of flowering plants*, 3rd edition. London: Longmans Green and Co. Ltd.

Guillaumin, A., Thorne, R. F. & Virot, R. 1965 Floristic relationships of New Caledonia. *Stud. nat. Hist. Iowa Univ.* **20**, 1–65.

Steenis, C. G. G. J. van 1963 Pacific plant areas. Vol. I. National Institute of Science and Technology, *Republic of the Philippines. Monograph* no. 8.

Steenis, C. G. G. J. van 1964 On the origin of island floras. *Advanc. Sci.* pp. 79–92.

Steenis, C. G. G. J. van & Balgooy, M. M. J. 1966 Pacific plant areas, Vol. 2. *Blumea* (Suppl.), v.

Thorne, R. F. 1963 *Biotic distribution patterns in the tropical Pacific. Pacific Basin Biogeography. A Symposium* (ed. J. Linsley Gressitt). Honolulu: Bishop Museum Press.

Whitmore, T. C. 1966 *Guide to the forests of the British Solomon Islands.* Oxford University Press.

Wiebes, J. T. 1963 Taxonomy and host-preferences of Indo-Australian fig wasps of the genus *Ceratosolen* (Agaonidae). *Tijdschr. Ent.* **106**, 1–112.

Wiebes, J. T. 1965 Indo-malayan and Papuan fig wasps 4. Agaonidae from *Ficus* sect. *Adenosperma*. *Zool. Meded. Leiden* **40**, 225–233.

Wiebes, J. T. 1966 Provisional host catalogue of fig wasps (Hymenoptera, Chalcidoidea). *Zool. Verh. Leiden* **83**, 1–44.

Willis, J. C. 1922 *Age and area.* Cambridge University Press.

20. Index to *Ficus*