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E. J. H. Corner

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Ficus in the New Hebrides

By E. J. H. Corner, F.R.S.
91 *Hinton Way, Great Shelford, Cambridgeshire CB*2 5*AH*

The fig-flora of the New Hebrides (17 species including two endemics *F. aspera* and *F. granatum*) is disappointing in comparison with neighbouring island-groups. It consists mainly of immigrant species, 8 of affinity with New Guinea, 6 with Polynesia, and one uncertain connexion with New Caledonia (*F. fraseri*). *F. subulata* and *F. storckii* var. *storckii* are recorded for the first time. The unity of the fig-flora sets the limit for overseas dispersal of *Ficus* at *ca.* 100 km. It is concluded that the New Guinea element reached the islands by a relatively late connexion with the Melanesian Foreland, not by way of the Solomons, and that the Polynesian connexion was southerly as along the Hunter Ridge. The paucity of endemism is attributed to the lack of pachycaul immigrants. A field-key is given for identification. Collections are listed for all species.

Introduction

The rich fig-flora of the Solomon Islands, the peculiarity of that of New Caledonia, and the high endemism in that of Fiji lead me to suppose that the New Hebrides, in a central position, might also be a source of surprise. Their figs had been collected sporadically since the time of Cook's arrival, when the two endemics, *F. granatum* and *F. aspera*, became known. In 1929 Kajewski made what is now clearly the most thorough exploration, and on his evidence I listed 16 species of *Ficus* for the New Hebrides (Corner 1967). The Royal Society and Percy Sladen Expedition, 1971, contributed 80 collections of *Ficus* and at the time when I was studying them, I was lent from Kew 18 duplicates of collections made a few years previously by L. Bernardi. This century of specimens has added but one species, the well-known and wide-spread *F. subulata*, from Espiritu Santo, which brings the total to 17 species, and one of Bernardi's collections from Aneityum adds *F. storckii* var. *storckii* to the previous record of var. *kajewskii*. The fig-flora must be now almost completely known. It is meagre but, phytogeographically, instructive. The islands have received from north and east and evolved little. The problem is why in the midst of such diversity there should be so little.

Biogeographical unity of the New Hebrides

In the course of my study of *Ficus* in Asia and Australasia I have come to realize that fig-floras, recognizable both from endemic species and from their ensemble, distinguish geographical regions whether continental or insular. In the whole region there are about 500 species and they are so abundant that they make up 1–2 % of general collections of flowering plants from the lowlands (Corner 1970*b*, 1972). If to this preponderance there is added an understanding of evolution in the genus as I have explained in my treatment of the figs of the Solomon Islands and New Caledonia (Corner 1967, 1970*a*), then it will be seen that the occurrence of fig species indicates a direction of migration and fig-floras become a decisive factor in biogeography. In eastern Malesia, Melanesia, and Polynesia the biogeographical units do not agree well with those which have been proposed without reference to *Ficus* (Good 1964; Thorne 1963). The omission of one of the main genera leads to misapprehension which is repeated in the belief that the New Hebrides have been colonized by plants and animals in random dispersal from any direction.

The seventeen New Hebridean species are set out in a classified list on p. 352. There are eight species of eastern Malesia, which might be supposed to have come from the Solomons, but I prefer to call them the Melanesian element, and there are six species of Polynesian or Fijian direction. One species (*F. fraseri*), the natural occurrence of which in the New Hebrides has yet to be proved, may indicate a connexion with New Caledonia. This is a unique assemblage nowhere else repeated in the world. It appears that this assemblage occurs in the main throughout the islands, certainly from Espiritu Santo to Aneityum. There are, however, four exceptions which may be real or merely casualties of collecting. Thus,

(1) *F. austrina*, which is a wide-spread sea-shore tree (Key Isl., New Guinea, Bismarck Archipelago, Solomons, Santa Cruz Isl.), was found in the north island of Vanua Lava (Banks Group) by Kajewski who reported it as common. It is unlikely that this tree of striking stature would have passed unnoticed if it occurred in the more southerly and better known islands, from which I conclude that it is absent.

(2) The large, inland, and endemic tree, *F. granatum*, has been collected on Ambrim, Erromanga, Tanna, and Aneityum, not further north. *F. granatum* var. *minor* is known from Erromanga and Aneityum. No extensive collection of plants from the time of Forster has failed to include *F. granatum*. Thus its southerly limitation appears real.

(3) The small inland tree, *F. smithii* var *robusta*, known also from Fiji and in typical form from the Solomons, has been collected only on Aneityum. In Fiji and the Solomons, it is common, often in fruit, and therefore unlikely to have been overlooked.

(4) The large and widely dispersed banyan, *F. glandifera*, originally described from Aneityum and Tanna where Kajewski reported it as common, was not collected by members of the Royal Society and Percy Sladen Expedition, and it has not been reported from other islands. Yet, as it is distributed from Celebes to the Santa Cruz Islands and is very abundant in parts of the Solomons, I must conclude that it has been overlooked. Kajewski collected it in February and March; hence it may have been out of season for fruit during the Expedition's visit in July. I note, also, an aversion from the abundant *Ficus* by ecologists who seldom, if ever, report its occurrence.

The first three exceptions indicate a northerly and southerly element in the fig-flora, but the uniquity of the majority seems to prove, at last, in this young island-chain the extent to which species of *Ficus* may be distributed overseas. According to Dr Mallick in his account of the geological development of the islands, they appeared as uplifted coral islets about one and a half million years ago and have been elevated subsequently to their present size at various intervals. They never formed a closer chain. The maximum distance between two islands is *ca.* 100 km (Efate-Erromanga). Therefore it must be concluded that species of *Ficus* can be distributed overseas to this distance. It is the limit of such short distance dispersal which was set by van Steenis (1962). It cannot be assumed that, given indefinite time, either wind or ocean current or migratory bird or mammal would have distributed a species of *Ficus* to any greater distance. For its species to survive, a specific insect as well as the seed must arrive and, in the case of dioecious species, at least two seeds of opposite 'sex' (seed-bearing and insect-bearing) must arrive, which multiplies the unlikelihood of the establishment of these frail and minute insects at great distances. Thus, as I will explain, New Caledonian figs have not arrived (250 km to the Loyalty Islands, 350 km to New Caledonia), nor those of the Solomons (450 km to San Cristobal), nor those of the Santa Cruz Islands (170 km) unless that was the direction of *F. austrina*. But the same distance of 170 km between Buka and New Ireland marks the sharp and great differences between the fig-floras of the Solomons and the Bismarck Archipelago. Even 50 km separates figs typical of Malaya from those of Sumatra, both of which were evidently united in the glacial period. Hurricanes may have assisted in the greater dispersal of figs in the New Hebrides, but they seem also to set the limit of *ca.* 100 km, which accounts for the non-random dispersal of *Ficus*. Direct entry of their fig insects from the Solomon Islands, Fiji, New Caledonia and further away must be ruled out from the biogeography of *Ficus* in the New Hebrides. This done, the fig routes must apply to other plants and animals.

SOLOMON ISLANDS

The flora of the Solomon Islands, as listed by Whitmore (1966), though incomplete, is much richer than that of the New Hebrides. The point is proven not only by *Ficus* but by other genera of trees with considerably more species in the Solomons, e.g. *Barringtonia*, *Calophyllum*, *Dysoxylum*, *Elaeocarpus*, *Eugenia* (including *Syzygium*), *Garcinia*, *Glochidion*, *Macaranga*, and *Terminalia*. Then, of twelve timer-trees listed as important for the Solomons, namely *Calphyllum kajewskii*, *Campnosperma brevipetiolatum*, *Dillenia salomonensis*, *Elaeocarpus sphaericus*, *Endospermum medullosum*, *Gmelina moluccana*, *Maranthes corymbosa*, *Parinari salomonensis*, *Pometia pinnata*, *Schizomeria serrata*, *Terminalia brassii* and *T. calamansanai*, only *Pometia pinnata* occurs in the New Hebrides where six of these genera appear to be absent. *Artocarpus*, *Parartocarpus*, *Gironniera*, *Octomeles*, and *Belliolum*, common in the Solomons, do not occur in the New Hebrides. There are many more examples among herbaceous plants and monocotyledons.

The Solomon Islands have 64 species of *Ficus* of which 24 are endemic. Though many are common, not one endemic reaches the New Hebrides, where they have no close allies. Then, also, there are 21 wide-spread species common in the Solomons where they find their eastern limit. The list is so impressive to anyone familiar with *Ficus* that I give it in some detail, thus-

subgen. *Urostigma: F. virens*, *F. caulocarpa*, *F. drupacea*, *F. crassiramea*, *F. benjamina*, *F. microcarpa*, *F. xylosycia*.
subgen. *Pharmacosycea: F. hombroniana*, *F. edelfeltii*, *F. polyantha*.
subgen. *Ficus*
  sect. *Rhizocladus: F. pantoniana*, *F. baeuerleni*, *F. agapetoides*, *F. nasuta;* (note, no climbing figs in the New Hebrides except *F. subulata* of sect. *Sycidium*).
  sect. *Sycidium: F. gul*, *F. copiosa*, *F. melinocarpa*.
  sect. *Adenosperma: F. mollior*, *F. erythrosperma*.
  sect. *Neomorphe: F. nodosa*, *F. variegata*.

Of these 21 species, 7 range from continental Asia, 1 from the Sunda Islands, 2 from Celebes and the Philippines, and 11 from New Guinea. Notworthy is the absence of root-climbers of sect. *Rhizocladus* from the New Hebrides. Yet, more remarkable is the absence of the sea-shore, river-side, and lowland banyan *F. microcarpa*; it ranges from Ceylon, India, China and Ryu Kyu to the Solomons and New Caledonia; it seems impossible that, if it occurred in the New Hebrides, it could have been overlooked by that ardent collector Kajewski. *Ficus* is the largest genus of woody plants in the Solomons and the New Hebrides, perhaps also in New

Guinea and the Bismarck Archipelago, and here is a break between the fig-floras of the Solomons and the New Hebrides even greater than that between the Solomons and the Bismarck Archipelago. It is impossible to ascend a river in the Solomons without meeting *F. gul*, *F. mollior*, *F. erythrosperma* and *F. macrothyrsa*; it is impossible to walk behind the coastal fringe of forest without meeting *F. erinobotrya*, *F. indigofera*, and the big-leafed *F. theophrastoides* and *F. salomonensis*, to go through the secondary forest without meeting the red twigs of *F. longibracteata*, or to scramble up the gullies without meeting the fan-twigs of *F. chrysochaete*, the cherry-like fruiting sprays of *F. imbricata*, the harsh leaves of *F. oleracea*, or the buttressed and cauliflorus trunks of *F. variegata*. It is impossible to believe that these have all been overlooked in the New Hebrides. The break in the fig-floras proves that the sea-gap has been too wide to be crossed. The nearest island of the Solomons, that is San Cristobal, has 46 species of *Ficus*.

I conclude that the fig-flora of the New Hebrides did not come by way of the Solomons.

SANTA CRUZ ISLANDS

Possibly these islands supplied the Melanesian element to the New Hebridean figs. They have not been satisfactorily explored, but the following 13 species, all of which occur in the Solomons, have been found, and 8 (marked NH) occur in the New Hebrides:

F. glandifera (NH), *F. hombroniana*, *F. illiberalis*, *F. smithii* var. *smithii* (NH, but as var. *robusta*), *F. nasuta*, *F. wassa* (NH), *F. melinocarpa*, *F. erinobotrya* var. *solomonensis*, *F. tinctoria* (NH), *F. virgata* (NH), *F. adenosperma* (NH), *F. austrina* (NH, Banks Group), and *F. septica* var. *cauliflora* (NH).

None of the Polynesian species of *Ficus*, abundant in the New Hebrides, has been found in the Santa Cruz Islands, the fig-flora of which seems to be an attenuate version of that of the Solomons. Yet, San Cristobal is *ca.* 380 km from the Santa Cruz Islands and the distance seems too great for overseas dispersal. Unfortunately it is not known whether the critical *F. virens* (Malesia) or *F. prolixa* (Polynesia) occurs, or if the other banyans of the Solomons are really absent; the answers would clinch the affinity of the fig-flora.

NEW CALEDONIA AND THE LOYALTY ISLANDS

The rich flora of New Caledonia with its very high rate of endemism is in strong contrast with the neighbouring condominium. The New Caledonian belongs to a different and much older mountain range which has produced the extent of ultra-basic soil where many of the endemics are restricted. Nevertheless, there are raised coral reefs producing soils similar to those of the New Hebrides, especially on the Loyalty Islands which have the character of the New Caledonian flora in simpler form. Yet this flora has contributed little, if anything, to the New Hebrides. The sea-gap has been too great for *Ficus* and, as it seems for most other plants. The remarkable evolution of *Ficus* subgen. *Pharmacosycea*, which has taken place on the ultra-basic soils of New Caledonia, has not dispersed its species overseas except for *F. lifouensis* in the Loyalty Islands (Corner 1970*a*).

There are five species of *Ficus* common to these three island groups, and they are not species of ultra-basic soil. Three are Polynesian, in the sense that they characterize the Fijian flora, namely the banyans *F. prolixa* and *F. obliqua*, and the shrub or small tree *F. scabra*. The others are the east Malesian *F. virgata* and the Australian shrub or small tree *F. fraseri*, the wild occurrence of which in the New Hebrides is uncertain. That there was no direct interchange between the New Hebrides and the New Caledonian group is proved by (1) the absence of *F. wassa*, *F. septica*, *F. tinctoria*, and *F. subulata* from the New Caledonian group, and (2) the absence of *F. microcarpa* from the New Hebrides. All of these are common and widely distributed species, often growing near or beside the sea (except the inland *F. subulata*). In fact, here is a curious situation in the wide extent of these species interposed, as it were, by the Coral Sea.

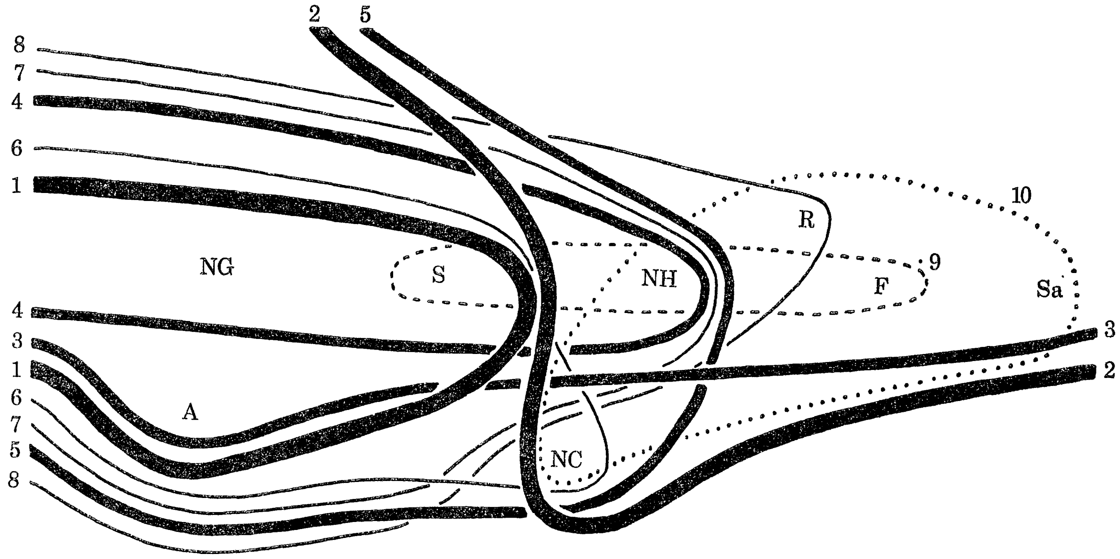

Figure 1. The distribution of ten wide-spread species of *Ficus* around the New Hebrides. 1, *F. virens*. 2, *F. prolixa* 3, *F. tinctoria* ssp. *tinctoria*. 4, *F. subulata*. 5, *F. virgata*. 6, *F. microcarpa*. 7, *F. septica*. 8, *F. adenosperma*. 9, *F. smithii*. 10, *F. scabra*. A, Australia. F, Fiji. NC, New Caledonia. NG, New Guinea. NH, New Hebrides. R, Rotuma. S, Solomon Islands. Sa, Samoa.

F. subulata, *F. virgata*, and *F. tinctoria* are closely allied; they are commonly mistaken, especially in the herbarium, but the first is an epiphytic climber, rather like the ivy in habit though never so massive, while the other two pass through this phase and become strangling figs with copious aerial roots; and there are, of course, critical differences in leaf, fig, flower, and seed but, unfortunately, the insects have not yet received a critical study. *F. tinctoria*, with three subspecies, extends from the Himalayas and China to the Marquesas Islands, except for New Caledonia and the Loyalty Islands (Corner 1963, figure 3). *F. subulata* accompanies it to the New Hebrides but omits Australia. *F. virgata* accompanies them from Celebes and the Philippines to the New Hebrides, New Caledonia and north Queensland. They part company round the Coral Sea. *F. microcarpa* extends with *F. tinctoria* to the Solomons, New Caledonia, and north Queensland but omits the New Hebrides. *F. septica* extends from Sumatra and Ryu Kyu (not the Asian mainland) to the New Hebrides and north Queensland but omits New Caledonia. *F. wassa* extends from Flores and the Moluccas to the New Hebrides, but omits Australia and New Caledonia. When one considers the changes in climate, soil, vegetation, and sea-gaps over this vast area, random dispersal cannot account for this ultimate diversion around the Coral Sea (figure 1). I conclude, as I will take up in more detail, that there were islands of sufficient proximity to allow the dispersal of *Ficus* from Australia to New Caledonia across the Bellona Plateau and from Fiji to New Caledonia along the Hunter Ridge, but none from the Loyalty Islands or New Caledonia to the New Hebrides where there is the New Hebridean Trench.

POLYNESIA

East of New Caledonia and the New Hebrides the fig-flora of Polynesia consists in the main of the three banyans *F. obliqua*, *F. prolixa*, and *F. tinctoria* and a total of twelve species of sect. *Sycidium* ser. *Scabrae*. Fiji adds from subgen. *Pharmacosycea* the small tree *F. smithii* and from subgen. *Ficus* sect. *Sycocarpus* the two endemic trees *F. pritchardii* and *F. vitiensis* (Corner 1967, 1970*a*). The Fijian islands, which are said to date from the Eocene (Menard & Hamilton 1963) is the most easterly site of fig-evolution. Beyond Samoa and Niue the fig-flora reduces to *F. prolixa* and *F. tinctoria*. Merely two species, *F. obliqua* and *F. tinctoria*, enter from New Guinea, and they may have been distributed by early man.

Interest centres on ser. *Scabrae* because three species of Fijian ancestry have reached the New Hebrides, namely *F. aspera*, *F. scabra*, and *F. storckii*. The sea-gap of 800 km is excessive for the transit of their insects, 'gall-seeds', and 'female seeds'. The whole series contains about fifty species. They are insular in the sense that none occurs on the mainland of Africa or Asia, though there are six in Australia. Endemic species occur in Madagascar, the Philippines, Celebes, New Guinea, the Solomons, the New Hebrides, Fiji, Samoa, and Australia. There are no endemic species at the periphery of the range in Asia; that is in Ryu Kyu, Formosa, and the Sunda islands. The twelve Polynesian species are apportioned in this way: Fiji (7 species of which 5 are endemic), Samoa (5 species, 2 endemic), Niue (3 species, 2 restricted to Samoa and Niue). Tonga appears to have only the most wide-spread Polynesian *F. scabra*. In my check-list of *Ficus* (Corner 1965), the Polynesian species were keyed out with the Asian and Australasian mainly on gross characters of leaf and fig. The intention was to afford ready identification and to ensure distinction on grounds other than geographical isolation. It is clear, however, that the Polynesian species are a natural unit with leptocaul trends paralleled in other geographical units; indeed, some of the species seem to intergrade in Fiji. Pachycaul ancestry with thicker twig and larger leaf is shown by *F. fulvopilosa*, *F. greenwoodii*, and *F. masoni*, all endemic in Fiji as the nucleus of the Polynesian unit. The species of ser. *Scabrae* in the Solomons have their unit of affinity distinct from that of Polynesia; they tend to an ancestry about *F. oleracea*, endemic in the Solomons.

The problem of the derivation of the New Hebridean species is enlightened by the fig-flora of Rotuma Islands, which lie about 500 km north of Fiji and over 1000 km east of the Santa Cruz Islands. Through the courtesy of Professor H. St John, I was able to study in 1969 the seventeen collections of *Ficus* which he had made on those islands; they are the only gatherings from this source that I have seen. There are five species. As one would expect, there are the three banyans *F. obliqua*, *F. prolixa*, and *F. tinctoria* but, unexpectedly, there are the east Malesian *F. adenosperma* and the Polynesian *F. scabra*. The collections had fertile seeds and insects to show that the fig-species were naturally established. The nearest known occurrence of *F. adenosperma* is in the Santa Cruz Islands, but it may occur on Tikopia 200 km east of these islands. The nearest occurrence of *F. scabra* is in Fiji. *F. adenosperma* must have reached Rotuma from the west and *F. scabra* from the south, but the distances are too great for trans-oceanic dispersal. I conclude that *F. adenosperma* reached Rotuma along the Melanesian Foreland, of which these little islands seem to be the eastern end, and that for *F. scabra* there must have been a southerly island-arc leading to Fiji, or relics of the ancestral route of the Fijian flora, unless these islands were very much closer than now. I emphasize again that *F. adenosperma*, which is the very common river-side fig of east Malesia, has not crossed the shorter distances between Celebes and Borneo, Mindanao, Flores or Timor, or from New Guinea to Australia, or from the New Hebrides to the Loyalty Islands. The fig-flora of Rotuma is, in fact, a depleted state of that characteristic of the New Hebrides. Aneityum and Rotuma are the eastern limits of *F. adenosperma* as Rotuma and the New Hebrides are the northern and western limits of *F. scabra*

A contrast is supplied by the New Hebridean endemic *F. aspera*, which is better known in its variegated form as *F. parcelli* of horticulture, even as *Artocarpus canoni*. It is closely allied with the Samoan endemic *F. uniauriculata*; if the two grew together, they might be regarded as varieties of one species. Their unification comes in the hairy ancestor which must be postulated for the Fijian endemic *F. greenwoodii*. The absence of all three from Rotuma implies a southerly dispersal from the Fijian centre, which may be identified with the Hunter Ridge to the New Hebrides. This route will explain not only the presence of *F. aspera*, *F. scabra*, and *F. storckii* in the New Hebrides but, also, that of the Fijian *F. smithii* var. *robusta* in Aneityum and that of *F. scabra* in New Caledonia. That this route did not permit the passage of *F. fraseri*, *F. microcarpa*, and *F. virgata* from New Caledonia to Fiji is probably to be explained by its closure before that across the Bellona Plateau allowed these species to reach New Caledonia from Australia. Clearly the origin of the Fijian flora is critical for the biogeography of Melanesia and Polynesia; that it was early is shown by the endemic *Degeneria*, allied with Magnoliaceae, the nearest representative of which is *Elmerillia* in New Guinea. It seems that a southerly hook of the Melanesian Foreland led to the Fiji Plateau and that, at a later date, there was this westerly connexion with the recent New Hebrides. The two endemic species of sect. *Sycocarpus* in Fiji require this extension of the Melanesian Foreland because, without intervening allies, *F. vitiensis* (figure 4) relates with subsect. *Auriculisperma* (Solomon Islands) and *F. pritchardii* relates with *F. microdictya* of New Guinea (Corner 1970*a*). This second pair are significant because both species are monoecious in the primitive manner of *Ficus*, unlike the remainder of sect. *Sycocarpus;* they appear as advanced leptocaul remnants of the primitive stock of *Sycocarpus* on the Melanesian Foreland.

Subgenus *Pharmacosycea*

Two species of this subgenus, *F. smithii* and the endemic *F. granatum*, occur in the southern half of the New Hebrides. They are not closely related. As I have explained in dealing with the species of New Caledonia (Corner 1970*a*), *F. granatum* belongs with the primitive group of *Pharmacosycea* around the Coral Sea. How it reached only the New Hebrides is a mystery. In structure it is nearest to a group of New Caledonian species and it seems to be a relic of the ancestry of the subgenus as it arrived in New Caledonia. I note here that I had supposed *F. granatum* var. *minor* to be merely the twigs from an old tree, for Kajewski's original field-note gave it as a tree up to 25 m high. Three recent collections of the Expedition correct this notion; the field-notes give it as a small tree 5–8 m high. I conclude that it is a leptocaul derivative of var. *granatum* and, possibly, a separate species.

F. smithii occurs in the Solomons in its leptocaul form as var. *smithii*. In Fiji, where it is common, and in Aneityum it is in the stouter form of var. *robusta*. Neither has been collected in the Santa Cruz Islands where a close ally *F. illiberalis* (described from the Solomons) occurs. I had first supposed that the species belonged to ser. *Austrocaledonicae* but I have corrected this impression and transferred it to ser. *Nervosae* (Corner 1970*a*). Kajewski's collections of var. *robusta* were referred by Summerhayes to *F. austrocaledonica* but better acquaintance with this fairly common, New Caledonian, species shows me that it differs in most points such as the elliptic lamina, the pedicellate rather than pedunculate figs, the larger basal bracts, and the ostiolar male flowers with two stamens. The geographical and morphological evidence point to the entry of *F. smithii* var. *robusta* into the New Hebrides by the southerly route of ser. *Scabrae* from Fiji. It is perplexing, however, that the species should be absent from Rotuma where it must have linked with var. *smithii* on the Melanesian Foreland. As with *F. granatum*, the two varieties may be separated as two species divergent from a pachycaul ancestor of the Melanesian Foreland.

Ficus obliqua, *F. prolixa*, and *F. tinctoria*

These banyans form a triumvirate of remarkable regularity on most islands of Polynesia (Corner 1963). Eastwards of the New Hebrides and New Caledonia they are the only banyans, but they are not closely related. *F. obliqua* and *F. prolixa* belong in two widely different sections of the monoecious subgenus *Urostigma*. *F. tinctoria* belongs in the dioecious subgen. *Ficus* sect. *Sycidium*. They have been brought together through their ability to grow on the coasts of coral islands and, as seems very likely, through the agency of man. Sea-rovers carried many plants with them, among which there may have been living branches of these banyans to stake on the islands where they landed. The fruits of these banyans are edible; though small and scarcely palatable, they are produced in great quantity and they are known variously in Melanesia and Polynesia as the 'poor man's food' or 'starvation food'. Their young leaves are edible. The green wood of *F. tinctoria* smoulders and was used by the Solomon islanders to carry fire about; (I have noted the same procedure in Malaya where the faster smouldering stems of the Urticaceous climber *Poikilospermum* are used). Then as banyans striking roots from branches, they feature as religious trees and in burial grounds. I think that it may be impossible to discover their original distribution. The most interesting in this respect is the oceanic *F. prolixa* which tends towards the American allies in subgen. *Urostigma* in its disperse male flowers, though in other respects it is close to the Asian *F. virens* and the African *F. ingenus*. There is no corresponding link between the African species of sect. *Urostigma* and these American banyans of sect. *Americana*. Now the break between the distribution of *F. virens* and that of *F. prolixa* is (1) in the break between the Solomons with *F. virens* only and the New Hebrides with *F. prolixa* only, and (2) in the similar break between Australia and New Caledonia (figure 1). I know of no land with both species. Since it extends to Micronesia, the Marshall Islands, and Fanning Island, *F. prolixa* appears to be a species of the Melanesian Foreland, while *F. virens* is a species of Afro-Asia. Thus, *F. prolixa* places the New Hebrides botanically in Polynesia.

Conclusion

The idea of the Melanesian Foreland seems necessary to explain the fundamental similarity between the different fig-floras of New Guinea (with the Bismarck Archipelago), the Solomons, (with the Santa Cruz Islands), the New Hebrides, Rotuma, and Fiji. There has been speciation in all except Rotuma and the ancestors must have come from somewhere which was not to the south because New Caledonia offers no source of any group of *Ficus* other than subgen. *Pharmacosycea*.

The only evidence of latitudinal dispersal between the island groups is the occurrence of the three Polynesian, or Fijian, species of ser. *Scabrae* in the New Hebrides. Therefore these fig-floras must have had a northerly derivation (figure 2). The Melanesian Foreland appears as the tract where Laurasian, Pacific, and Australian tectonic plates were converging; islands may have been thrown up, as in the Tertiary period, of proximity sufficient for the dispersal of *Ficus*. These islands must have led southwards along four independent routes to the present sites of the four fig-floras. The Melanesian Foreland to the north and these southerly routes would have been available, of course, for other plants and animals, for which it seems unnecessary to invoke rare freaks of adventure in explanation of their arrival across wide oceanic gaps (Zimmerman 1963). *Ficus* has diversified greatly during this period and in this region of the world; thus it enables one to analyse the complex.

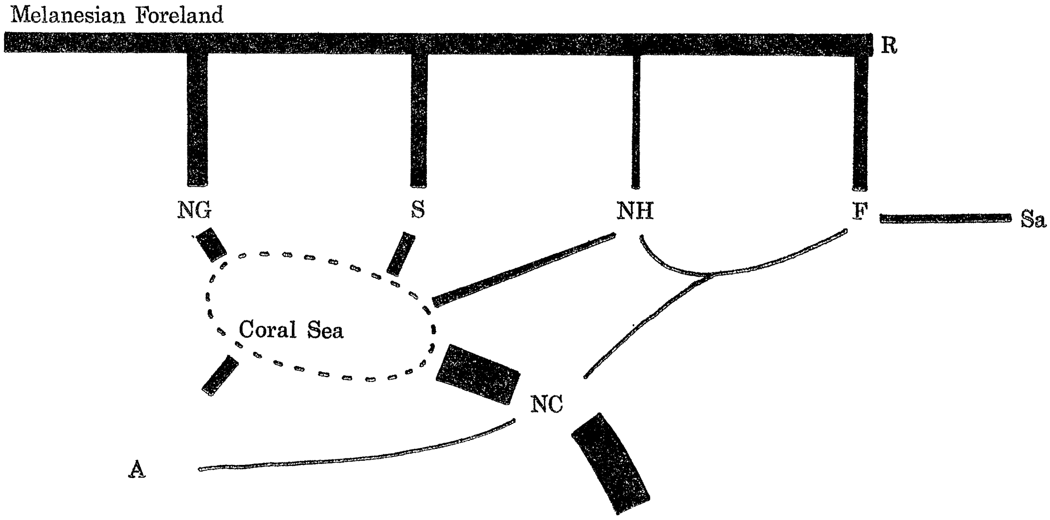

FIGURE 2. Diagram to illustrate the hypothesis of the derivation of the fig-floras of New Guinea (NG), the Solomon Islands (S), the New Hebrides (NH), Rotuma (R), Fiji (F), Samoa (Sa) and New Caledonia (NC) from the Melanesian Foreland in relation to Australia (A) and the Coral Sea. The thickness of the lines indicates the relative age of the flora from the older (thick lines) to the younger (thin lines).

For unknown reasons not all species of *Ficus* disperse with equal facility. The primitive pachycaul species, perhaps more intimately dependent on the nature of the soil, disperse least, if at all; the advanced leptocaul species disperse most widely (Corner 1967). Thus *F. adenosperma* and *F. scabra* occur in Rotuma as the eastern outpost of the Melanesian Foreland, and the most recent southerly extension of the Foreland to the New Hebrides has brought only widely dispersed and leptocaul species, hardly capable of further and endemic evolution. The pachycaul phase of evolution was over for *Ficus* before the appearance of the New Hebrides which lack the outstanding endemics of the other three fig-floras. Yet these islands picked up *F. granatum*. The thrust which produced New Caledonia is lost at the western end in the Coral Sea. About this end the relatively primitive subgenus *Pharmacosycea* appears to have evolved (Corner 1970*a*); it is the only subgenus of significance in New Caledonia. As the Melanesian Foreland led southwards, so the New Caledonian range may have led northward and carried *Pharmacosycea*, as ser. *Nervosae*, to New Guinea, the Solomons and, even, Fiji, from which complex the structurally older *F. granatum* has survived in the southern New Hebrides and *F. smithii* travelled afield.

The botany of Melanesia and Polynesia, which is learnt from surface features, implies more land in the past than geology is able to provide from sub-surface investigation, but the botanical facts cannot be explained away by the facile supposition that all flowering plants have dispersed widely overseas in any direction. This is no more the case with such different plants as *Degeneria*, *Nothofagus*, *Casuarina*, *Sararanga*, and indeed *Agathis*, than it is with *Ficus* or *Artocarpus*.

Classified list of *Ficus* in the New Hebrides

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

subgen. *Urostigma*

  sect. *Urostigma* ser. *Caulobotryae*
    13. *F. prolixa* Forst. f.

  sect. *Conosycea* ser. *Benjamineae*
    66. *F. subcordata* Bl.

  sect. *Malvanthera*
    83. *F. glandifera* Summerhayes
    91. *F. obliqua* Forst. f.

subgen. *Pharmacosycea*

  ser. *Austrocaledonicae*
    133. *F. granatum* Forst. f.

  ser. *Nervosae*
    140. *F. smithii* Horne var. *robusta* Corner

subgen. *Ficus*

  sect. *Sycidium* subsect. *Sycidium*

    ser. *Copiosae*
      302. *F. wassa* Roxb.

    ser. *Scabrae*
      336. *F. fraseri* Miq.
      339. *F. aspera* Forst. f.
      341. *F. scabra* Forst. f.
      342. *F. storckii* Seem.

  sect. *Sycidium* subsect. *Palaeomorphe*
    357. *F. tinctoria* Forst. f. ssp. *tinctoria*
    358. *F. virgata* Reinw.
    360. *F. subulata* Bl.

  sect. *Adenosperma*
    386. *F. adenosperma* Miq.
    387. *F. austrina* Corner

  sect. *Sycocarpus*
    464. *F. septica* Burm. f.

FIELD-KEY TO *FICUS* IN THE NEW HEBRIDES

1. Strangling or climbing epiphytes with aerial or basketing roots. Leaves entire.
    2. Creeping epiphyte, not strangling, rather small. Leaves submembranous, more or less acuminate, often slightly asymmetric, with a gland near the base on the underside of the broader half. Figs stalked, orange or red, 1–2 small lateral bracts. Dioecious. *F. subulata*
    2. Strangling figs, becoming large trees. Figs without lateral bracts.
        3. Lateral veins fine, close, numerous, without distinct intercostal veins. Monoecious.
            4. Stipule of terminal bud 3–17 cm long. Fig seated on a thick cupule-like stalk. *F. glandifera*
            4. Stipule shorter.
                5. Figs 14–25 mm wide, sessile; basal bracts concealed. *F. subcordata*
                5. Figs 6–10 mm wide, seated on a short thick cupule-like stalk; basal bracts very soon caducous. *F. obliqua*
        3. Lateral veins spaced, with distinct intercostal veins.
            6. Petiole disarticulating from the dried fallen leaves. Deciduous. Figs ripening white to pink and purple-black. Monoecious. *F. prolixa*
            6. Petiole not disarticulating. Lamina usually with one gland at the base on the underneath of the broader side, often slightly asymmetric. Figs ripening yellow to orange or red. Dioecious.
                7. Lamina obtuse or subacute. Fig stalked. *F. tinctoria*
                7. Lamina very acute. Fig often sessile with a collar of 3–6 basal bracts. *F. virgata*
1. Trees or shrubs, without aerial roots, rarely epiphytic.
    8. Leaves distichous along the branches, submembranous, more or less scabrid, often denticulate, generally asymmetric; basal veins elongate; petiole relatively short. Trees or shrubs becoming cauliflorous. Dioecious.
        9. Lamina 4–10 × 2–5 cm; lateral veins 2–5 pairs. *F. storckii* v. *kajewskii*
        9. Lamina larger; lateral veins generally more numerous.
            10. Leaf-base strongly asymmetric, the cordate side generally obscuring the petiole. Twigs, petioles, and figs shortly villous. Tepals reddish or pink. *F. aspera*
            10. Leaf-base not so asymmetric; petiole not obscured. Thinly hairy, puberulous, or glabrous.
                11. Cystoliths only on the lower side of the lamina. Tepals hairy, reddish or pinkish. *F. scabra*
                11. Cystoliths on both sides of the lamina. Tepals more or less glabrous, white. *F. storckii*
    8. Leaves spirally arranged or opposite, not or slightly asymmetric.
        12. Leaves generally opposite, scabrid, often denticulate. Dioecious.
            13. Petiole 10–20 mm long. Lamina elliptic, not acuminate, harshly scabrid; lateral veins 3–4 pairs; basal veins elongate. Fig with a collar of basal bracts and projecting apical bracts. Tepals white, hispidulous. *F. fraseri*
            13. Petiole 10–55 mm long (–100 mm in saplings). Lamina often obovate, acuminate; lateral veins 4–8 pairs; basal veins short. Fig without a collar of basal racts; apical bracts not projecting. Tepals pink fading white, puberulous to glabrous. Cauliflorous. *F. wassa*
        12. Leaves spirally arranged (also opposite in *F. septica*), smooth, entire.
            14. Lamina without basal glands on the underside. Twig with a gland at the base of the petiole on one side. Figs ripenings white to yellow, often ridged, axillary and cauliflorous. Latex yellowish, watery. Dioecious. *F. septica*
            14. Lamina with a gland in the axil of each main basal vein on the underside. Twig without glands. Latex white, milky.
                15. Leaves coriaceous, drying brown, subacute to obtuse. Fig ripening red. Flowers stalked. Monoecious.
                    16. Leaf elliptic. Fig with copious internal bristles; flower-pedicels hairy. Stamens 2–3. *F. granatum*
                    16. Leaf commonly obovate. Fig without internal bristles; flower-pedicels glabrous. Stamen 1. *F. smithii*
                15. Leaves membranous to subcoriaceous, not drying brown, acute or shortly acuminate. Fig ripening green or yellowish. Flowers sessile. Dioecious.
                    17. Leaf 6–15 cm wide; cystoliths only on the lower side. Stipule 20–50 mm long. Figs 25–30 mm wide (living). *F. austrina*
                    17. Leaf smaller; cystoliths on both sides. Stipule shorter. Figs smaller. *F. adenosperma*

SPECIFIC NOTES ON *FICUS* IN THE NEW HEBRIDES

In these notes I have not described species with which I have already dealt in the account of *Ficus* in the Solomon Islands (Corner 1967). I have referred to collections made by the members of the Royal Society and Percy Sladen Expedition as RSNH numbers in the same way as the Bornean numbers (RSNB) and those of the Solomons (RSS). RSNH numbers are listed under the collector's name and under the various islands in the brochure on Collecting Data for the Expedition, published in 1974 by the Royal Society.

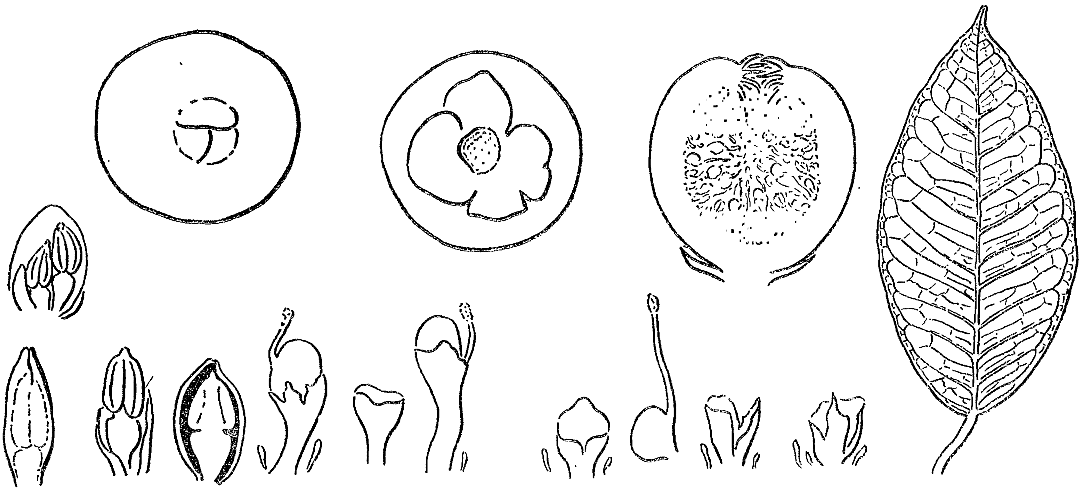

FIGURE 3. *Ficus prolixa*. Leaf, × $\frac{1}{2}$; figs, × 3; male, gall-, and female flowers, × 10. (H. S. McKee 3082, New Caledonia.)

13. ***F. prolixa*** Forst. f. (figure 3).

Sykes (1970) figure 33.

Large deciduous strangler developing many descending, more or less anastomosing, roots, in some cases with aerial roots along the branches; latex copious; leaves spirally arranged. Glabrous or the young parts minutely puberulous. Twigs 2–4 mm thick. Stipules on the dormant buds small, on opening shoots –9 × 1 cm, leafy, caducous. Lamina 5–16 × 2–6.5 cm, elliptic to lanceolate elliptic, subacuminate to shortly acuminate, base rounded-cuneate to narrowly cuneate, entire, thinly subcoriaceous, smooth, drying grey-green to brownish; lateral veins 6–12 pairs, slightly raised below on drying; intercostals few, zig-zag, vague or none; basal veins 1 (–2) pairs, short or reaching $\frac{1}{4}$–$\frac{1}{3}$ of the lamina; petiole 8–30 mm long, articulate to the lamina and separating in fallen leaves. Figs axillary, paired, sometimes on the twigs below the leaves, sessile to subpedunculate, glabrous, ripening whitish to pink and purple-black; peduncle 0–3 × 1.5 mm; basal bracts 3, 1.5–4 mm long and wide, ovate, subacute to obtuse, persistent; body 6–10 mm wide (dried), subglobose, the orifice closed by 3 almost plane apical bracts; internal bristles rather abundant, subvesicular, white. Perianth reddish then hyaline, gamophyllous, entire or variously 2–3 lobed. Male flowers ostiolar and disperse, numerous or in some cases sparse; stamen 1(–2), submucronate, anther exsert. Gall-flowers shortly pedicellate; ovary red-brown, substipitate. Female flowers sessile; ovary red-brown. Seed smooth. Lamina with cystoliths only on the lower side.

Distr. Micronesia, Polynesia (New Hebrides and New Caledonia eastwards).

Ecol. Sea-coasts, mangrove, rain-forest and mossy forest –1000 m alt., open country; often merely a bush in exposed places.

Vern. nekang (Erromanga).

Collections. Aneityum, Kajewski 29, 900; Efate, RSNH 16036; Erromanga, Kajewski 273, RSNH 169 and 1323; Malekula, RSNH 338; Tanna, Barclay 3484, Bernardi 12859 and 13074, Kajewski 113, RSNH 1221 and 1241.

It would be interesting to know the seasons of this deciduous tree. An ally, *F. caulocarpa*, is known to shed its leaves three times a year in Singapore at intervals of 5, 4 and 3 months, when the crown is bare for 24–48 h. Sykes mentions that in Niue the trees of *F. prolixa* are not all deciduous at the same time.

F. virens differs in the absence of disperse male flowers, in the longer petiole and in the larger basal bracts. Though slight, these differences seem never to fail and the geographical ranges of the two species are distinct. *F. virens* is deciduous but its seasons are not known.

66. ***F. subcordata*** Bl.

Corner (1967) 66, figure 8.

Vern. nepluth (Aneityum).

Collections. Aneityum, J. P. Wilson 999; Efate, A. Morrison s.n., 28 Aug. 1896; Malekula RSNH 340.

83. ***F. glandifera*** Summerhayes.

Corner (1967) 69, figure 10.

Collections. Aneityum, Kajewski 802; Tanna, Kajewski 80.

91. ***F. obliqua*** Forst. f.

Corner (1967) 70, figure 11.

Collections. Ambrim, Aubert de la Rue s.n., Aug. 1934; Aneityum, Kajewski 67, 781; Efate, RSNH 4; Erromanga, Bernardi 13271, Kajewski 253, RSNH 168; Tanna, Bernardi 12846 and 13076, RSNH 1204 and 16180.

These collections have the typical triradiate orifice to the fig, not the bilabiate as in collections from the Solomons.

133. ***F. granatum*** Forst. f.

Corner (1970*a*) 413, figure 18.

Vern. naren (Tanna).

Collections. Ambrim, Aubert de la Rue s.n., Jan. 1936; Aneityum, Kajewski 722; Erromanga, RSNH 3006; Tanna, Aubert de la Rue s.n. March 1936, Bernardi 12864, Forster s.n., Kajewski 124, RSNH 110.

var. ***minor*** Corner.

Collections. Aneityum, Kajewski 732, 956; Erromanga, Kajewski 324, RSNH 112, 136, 1286.

140. ***F. smithii*** Horne.

Corner (1967) 84, figure 20.

var. ***robusta*** Corner (figure 4).

Glabrous except the thinly appressedly brownish hairy stipules and young twigs. Twigs 2–5 mm thick. Stipules 10–22 mm long. Lamina 7–22 × 3.5–9.5 cm, elliptic to elliptic obovate, obtuse or subacute; lateral veins 8–13 pairs; intercostals 0–4, zig-zag; basal veins 1–2 pairs; petiole 15–35 × 1.5–3 mm. Fig-peduncle 7–15 × 1–1.5 mm; basal bracts 1–1.5 m long, persistent or caducous; pedicel 0–5 mm; body 10–13 mm (–18 mm, living); fig-wall soft, without sclerotic cells except in a loose layer in the inner part of the wall and in the indurate stalks of male and gall-flowers. Tepals free or shortly gamophyllous. Male flowers ostiolar and disperse, abundant; pedicels 0.5–2.5 mm long, indurate; stamen 1. Seed narrowly keeled.

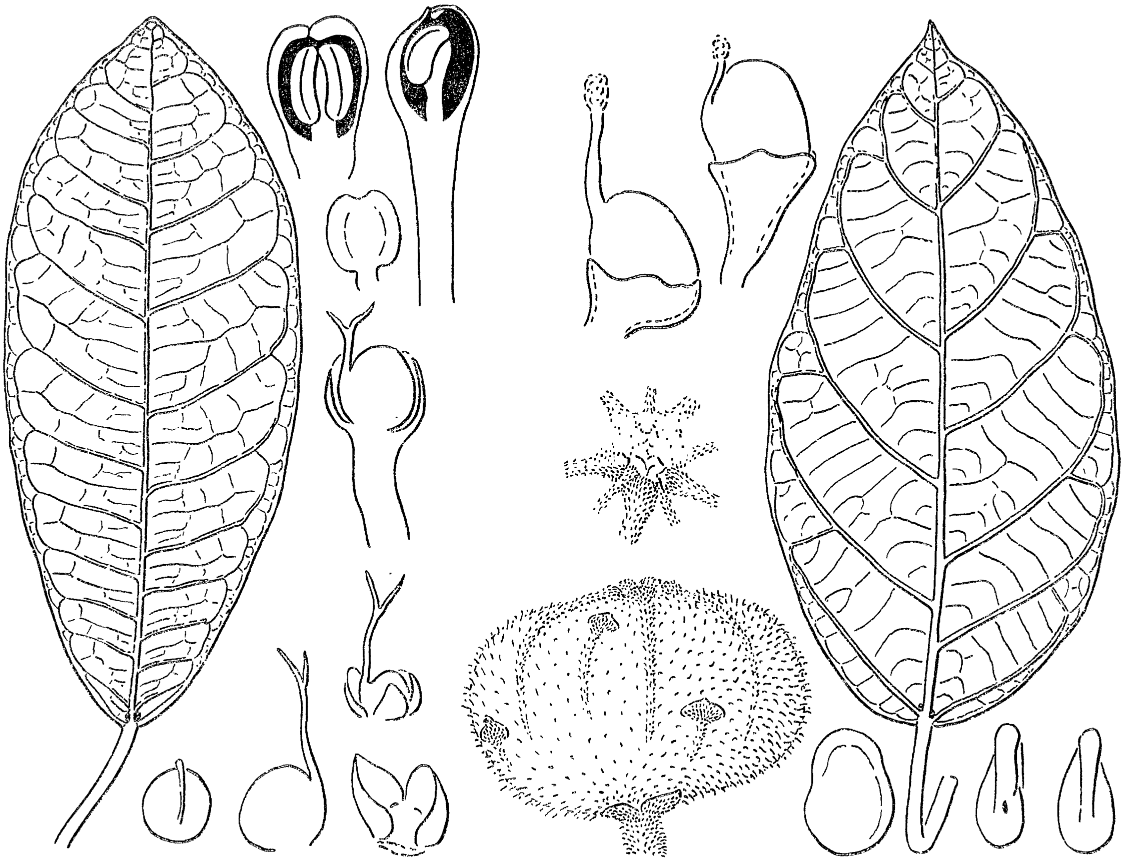

FIGURE 4. Left, *Ficus smithii* var. *robusta* (A. C. Smith 8339, Fiji). Right, *F. vitiensis* with fig, fig-orifice, seed-flowers, and seeds (A. C. Smith 9349; fig and flowers, A. C. Smith 9076; Fiji). Leaf, × ½; figs, × 2; flowers and seeds, × 10.

Distr. New Hebrides (Aneityum), Fiji.

Ecol. Lowland forest –700 m alt.

Vern. natvizia (Aneityum).

Collections. Aneityum, Kajewski 862 and 975, RSNH 1132.

I am not certain about the classification of this variety. The collections from Aneityum agree with those from Fiji and have the stouter twigs, larger leaves, and larger figs than those from the Solomon Islands. The type of *F. smithii* (J. Horne 516, Fiji) is the same as the plants from the Solomons, yet twelve other collections that I have seen from Fiji are var. *robusta*; in Fiji it is a frequent tree that can reach 30 m in height. The slender trees of the Solomons may reach 15 m;

they are fairly common throughout the islands where I saw no instance of var. *robusta*. The field-notes on var. *robusta* in Aneityum give it as a small tree up to 7 m high, and Kajewski recorded it as common. The distinction between the robust and slender forms in *Ficus* may be impossible to assess in the herbarium without copious specimens and adequate field-notes, because the difference may be one of age between sapling and adult, e.g. *F. copiosa* and *F. wassa* (Corner 1967).

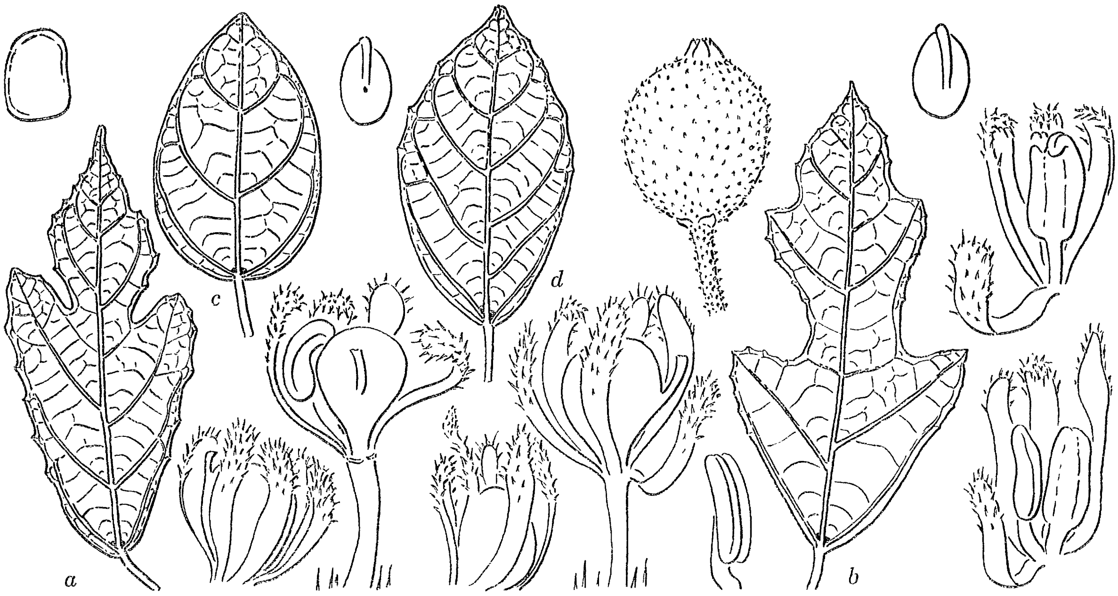

FIGURE 5. *Ficus fraseri*, collections from New Caledonia. Sapling leaves; *a*, C. Moore 27; *b*, C. T. White 7743. Mature leaves: *c*, Vieillard 1247; *d*, Compton 521. Flowers; male and gall-flowers, Compton 1963; female flowers and seeds, Schlechter 14734. Leaves, × $\frac{1}{2}$; fig, × 2; flower and seeds, × 10.

302. ***F. wassa*** Roxb.

Corner (1967) 94, figure 25.

Collections. Aneityum, A. Morrison s.n.; Efate, RSNH 1040, 1090, 16031; Erromanga, A. Morrison s.n.; Espiritu Santo, Baker 67, RSNH 254, 16286, 16290, 16414, 24139; Malekula, RSNH 317, 331, 1522, 6311; Tanna, Bernardi 12881, 12893 and 13068, L. E. Cheesman s.n., Kajewski 24; Vanua Lava, Kajewski 469.

This little tree, so characteristic of eastern Malesia, seems to be common throughout the New Hebrides. I have seen no evidence that it is seasonal. Some of the earlier collections were identified in error as *F. copiosa*. This species, often grown in villages for its edible leaves, has not been collected in the New Hebrides and its absence seems to refute any general introduction of fig-species by primitive man.

336. ***F. fraseri*** Miq. (figure 5).

Shrub or small tree –12 m high, rarely –25 m, deciduous. Leaves spirally arranged to opposite. All parts minutely and harshly scabridulous with hairs less than 0.5 mm long, often also puberulous when young, not muriculate. Twigs 2–3 mm thick, dark brown. Stipules –7 mm long, caducous. Lamina 5–15 × 2.8–8 cm, elliptic, acute or subacute, symmetrical, base rounded to cuneate, obscurely denticulate to dentate, brittle-chartaceous, strongly scabrid on both sides, drying grey-green to light brownish; lateral veins 3–4 pairs; intercostals 2–5, slightly

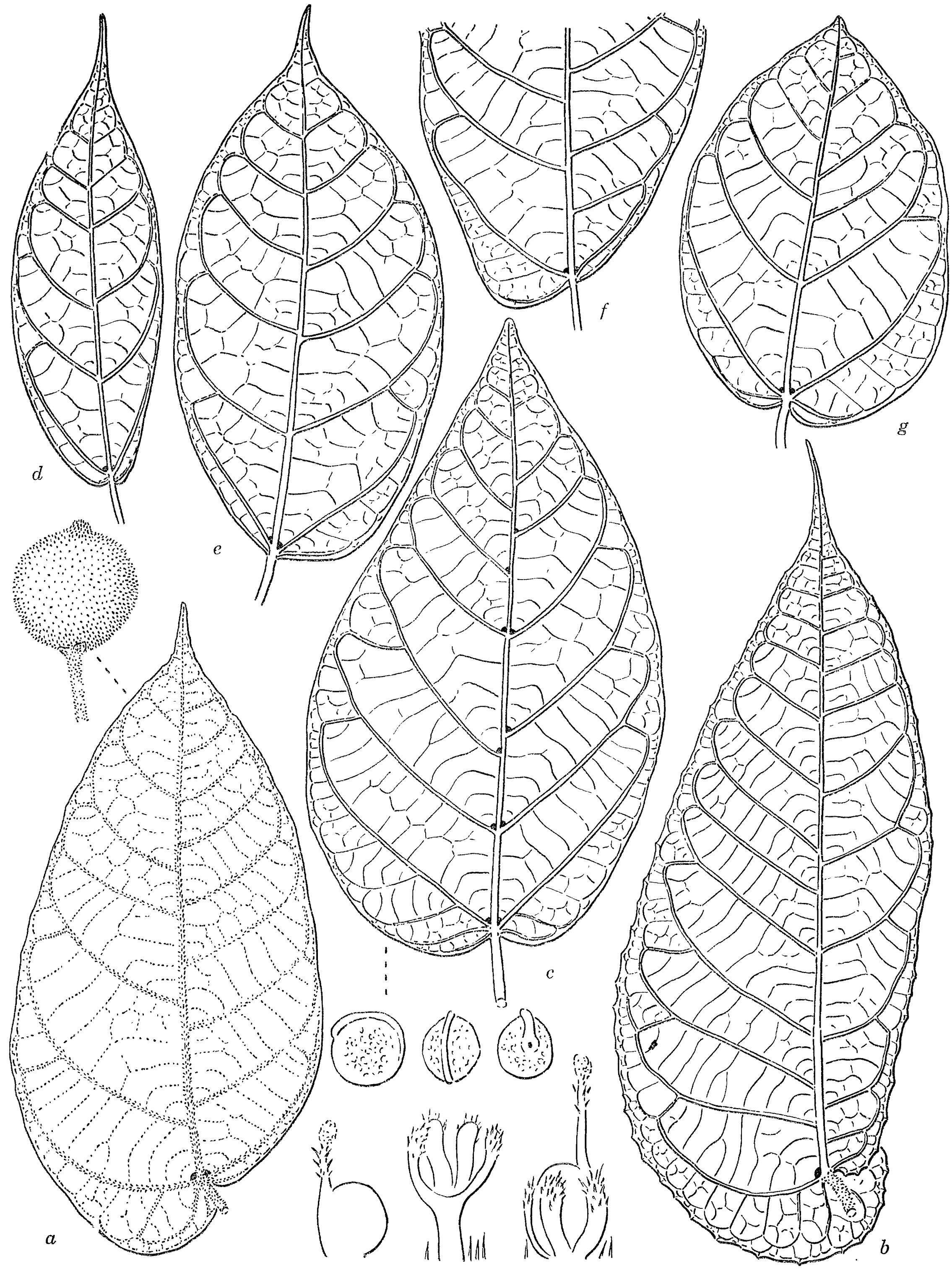

Figure 6. *a*, *Ficus aspera*, leaf and fig (cultivated in Singapore as var. *parcelli*); *b*, *F. uniauriculata* (Whitmee s.n., 1876–77). *c–g*, *F. scabra*; *c*, Eames 159, Samoa, with flowers and seeds; *d*, RSNH 1311; *e*, RSNH 16215; *f*, RSNH 16253; *g*, Bonati 1057, New Caledonia. Leaves, × ½; fig, × 1; flowers and seeds, × 10.

raised beneath on drying; basal veins 1–2 pairs, reaching $\frac{1}{3}$–$\frac{1}{2}$ of the lamina, with 2 slight basal glands or none; petiole 10–20 mm long; sapling leaves pinnately lobed or dentato-lobate with 4–7 pairs of lateral veins. Figs axillary and on the twigs below the leaves, solitary or paired, ripening dark purple; peduncle 5–7 × 1 mm; basal bracts 3, 1–1.5 mm long, ovate, acute, in a collar; body 9–11 × 8–10 mm (dried), ellipsoid, rarely with 1–2 lateral bracts, the ovate apical bracts projecting –1 mm in a small rosette; internal bristles short to minute, abundant to sparse, white; sclerotic cells absent from the fig-wall. Tepals 4–6, white, hispidulous, free. Male flowers ostiolar in several rows, sessile to shortly pedicellate; stamen 1 (–2), rarely with a normal or vestigial gall-ovary. Gall-flowers sessile or with a pedicel –1.7 mm long; ovary sessile, white. Female flowers as the gall; style puberulous. Seed 1.2–1.3 mm, lenticular, keeled, smooth. Lamina with cystoliths on both sides.

Distr. Queensland, northern New South Wales, New Caledonia, Loyalty Islands, New Hebrides.

Ecol. Lowland forest, mangrove creeks.

Collections. Efate, D. Levat s.n., Port Vila, Oct. 1883; Pentecost, Aubert de la Rue s.n., Mt. Lerip, 30 Dec. 1935; Tanna, Forster s.n., a specimen mounted with the type of *F. scabra* at BM(NH), of doubtful origin.

Though these collections seem correctly named, better specimens are needed to be sure that the species occurs naturally in the New Hebrides.

339. ***F. aspera*** Forst. f. (figure 6).

Shrub or tree –20 m high, becoming slightly buttressed; branches spreading; latex thin; leaves distichous, sometimes variegated (var. *parcelli*). Twigs, petioles, and figs villous with short white spreading hairs –1 mm long, in some cases only 0.1–0.2 mm, slowly or rapidly glabrescent; underside of the main veins of the leaf thinly villous, veinlets puberulous to glabrous, areolae glabrous; upperside of the leaf thinly appressedly hairy or villous, soon glabrous. Twigs 1–3 mm thick, often zig-zag. Stipules 6–15 mm long, caducous, appressedly hairy. Lamina 9–32 × 4–15.5 cm, ovate or oblong ovate to elliptic, rather obtusely subacuminate but the tip 15–40 mm long in sapling leaves, base very asymmetric with a cordate auricle on one side obscuring the petiole, the other side cuneate to subcordate, varying almost symmetric and cordate in small leaves, rather coarsely dentate to crenate or entire, thinly coriaceous, slightly scabrid above, velutinous to scabridulous below, drying grey-green; lateral veins 5–9 pairs, raised below; intercostals 3–8, regular, rather close, not or scarcely raised below; basal veins 3–5 on the broad side, 2–3 on the narrow, reaching $\frac{1}{4}$–$\frac{1}{2}$ of the lamina, with 2 basal glands; petiole 5–20 × 1–2 mm, mostly obscured by the leaf-auricle; sapling leaves pinnately dentate to pinnately lobed. Figs axillary, solitary or paired, or on the twigs below the leaves, becoming cauliflorous along most of the trunk, white villous or velvety, ripening yellow to orange or red; peduncle 3–11 mm long; basal bracts 3, 1–2 mm long, in a collar; body 12–25 mm wide (dried), subglobose, with 0–2 small lateral bracts, the apical bracts slightly projecting in a small rosette; internal bristles abundant, 0.5 mm long, white; sclerotic cells absent from the fig-wall. Flower-pedicels glabrous. Tepals 3–4, reddish fading brownish to whitish, rather broadly spathulate or oblong, distally hispidulous, free. Male flowers ostiolar in one ring; stamen 1. Gall- and female flowers sessile or shortly pedicellate; female style thinly hispidulous. Seed lenticular, keeled, finely subreticulate. Lamina with cystoliths only on the lower side, the larger papillate; cuticle not striate round the stomata.

Distr. New Hebrides.

Ecol. Sea-shore, river-side, and in lowland forest –300 m alt., evidently common.

Uses. Figs boiled and eaten.

Collections. Aneityum, RSNH 55; Aoba, Aubert de la Rue s.n. July 1934; Efate, RSNH 15, 1068, 16029; Erromanga, A. Morrison s.n. 1 Aug. 1896; Espiritu Santo, RSNH 268, 24243; Malekula, RSNH 385; Tanna, Barclay 3500, L. E. Cheesman 7, Forster s.n., Kajewski 49, 103.

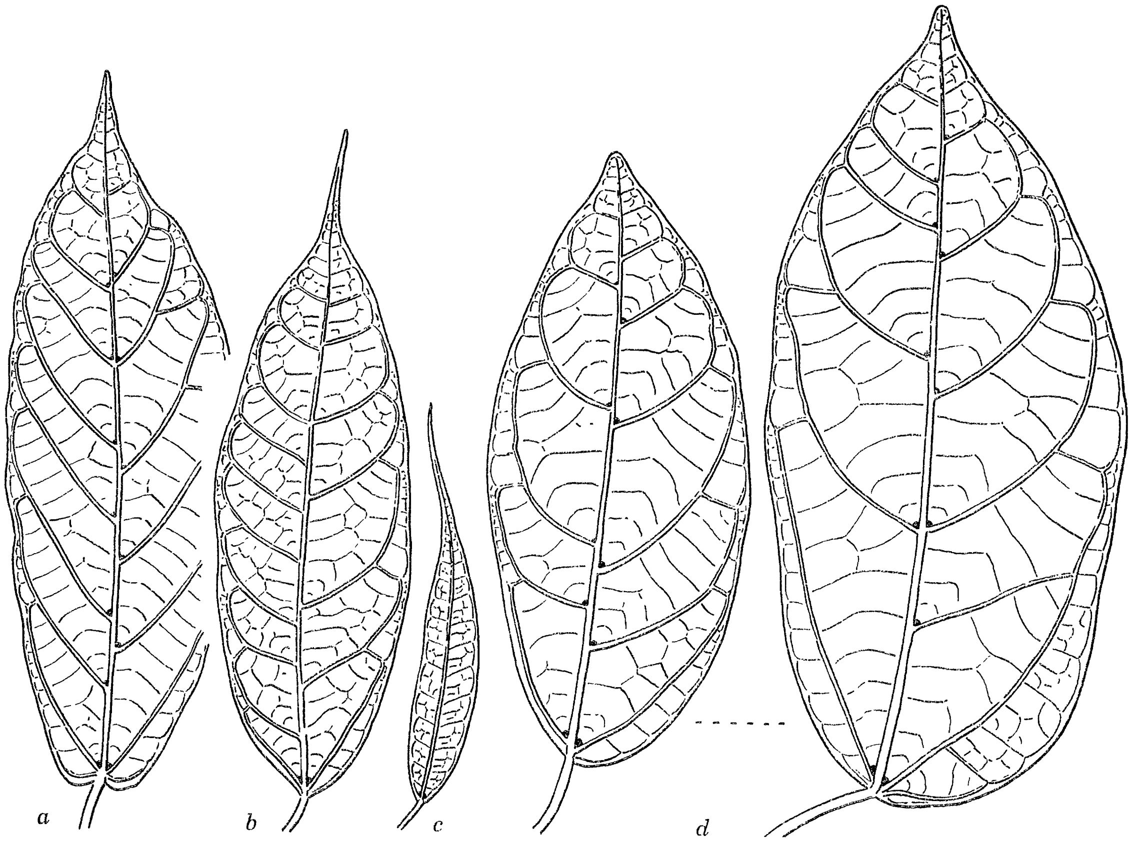

FIGURE 7. *a, Ficus scabra* (Anderson s.n. 1774, Tanna); *b, F. longecuspidata* (Reinecke 154, type, Samoa); *c, F. samoensis* (Christopherson and Hume 181); *F. godeffroyi* (Reinecke 126, left; Reinecke 73, right; syntypes, Samoa). Leaves, × ½.

I have never understood why this species was called *F. aspera* for the leaves are but slightly rough; perhaps it was to contrast with *F. granatum.* The species is distinguished by the very asymmetric leaf, the white velvety fig, and the red tepals. It seems to vary much, however, in hairiness as I have noted in the description. I am not certain of the colour of the ripening figs; field-notes of the Expedition give yellow to red but unpollinated figs of var. *parcelli*, cultivated in various parts of the world for the variegated leaves, may ripen pink to purple. The species comes nearest to *F. uniauriculata* of Samoa (figure 6). *F. scabra*, co-extensive with both, has smaller and usually glabrous figs, entire and less asymmetric leaves with short tip and few lax intercostals, and usually white tepals. *F. aspera* has frequently been mistaken for the Australian *F. coronata.*

341. ***F. scabra*** Forst. f. (figures 6 and 7)

Sykes (1970) figure 34.

Shrub (fruiting at 30 cm high) or tree –18 m high; bark grey, smooth; latex scant (? yellowish) or practically none; leaves distichous. Twigs, petioles, underside of veins, and figs villous with white spreading hairs –0.5 (–1) mm long, varying puberulous to glabrous. Twigs 2–3 mm thick, pale to dark brown. Stipules 5–12 mm long, appressedly hairy to glabrous, caducous. Lamina 8–22 × 4–9 cm (–35 × 22 cm in saplings or coppice-shoots), ovate elliptic to lanceolate elliptic, subacute or rather obtusely subacuminate (? varying acuminate), base cordate to broadly cuneate, symmetric to slightly asymmetric but not auricled, entire, membranous to subcoriaceous, slightly scabrid on both sides or smooth above, in some cases villous or puberulous below, drying grey-green to brownish olive; lateral veins 4–8(9) pairs, slightly raised below; intercostals 2–6, lax, slightly raised below; basal veins 1–2 pairs, reaching $\frac{1}{4}$–$\frac{1}{3}$(–$\frac{1}{2}$) of the lamina, with 2 basal glands and sometimes a gland in the axils of the lower lateral veins; petiole 5–28 × 1.5–3 mm. Figs axillary, often solitary, becoming ramiflorous and cauliflorous, even to the base of the trunk on short woody twigs, villous to puberulous, soon glabrous, ripening yellow to red, finally purple-black; peduncle 2–14 mm long, with 2–3 small bracts, 0.5 mm long, towards the apex or in a collar; body 7–11 mm wide (10–16 mm, living), subglobose, rarely with 1–3 small lateral bracts, the plane orifice closed by 3–4 small apical bracts; internal bristles abundant, short, white; sclerotic cells absent from the fig-wall. Tepals 4–6, or 3–4 in

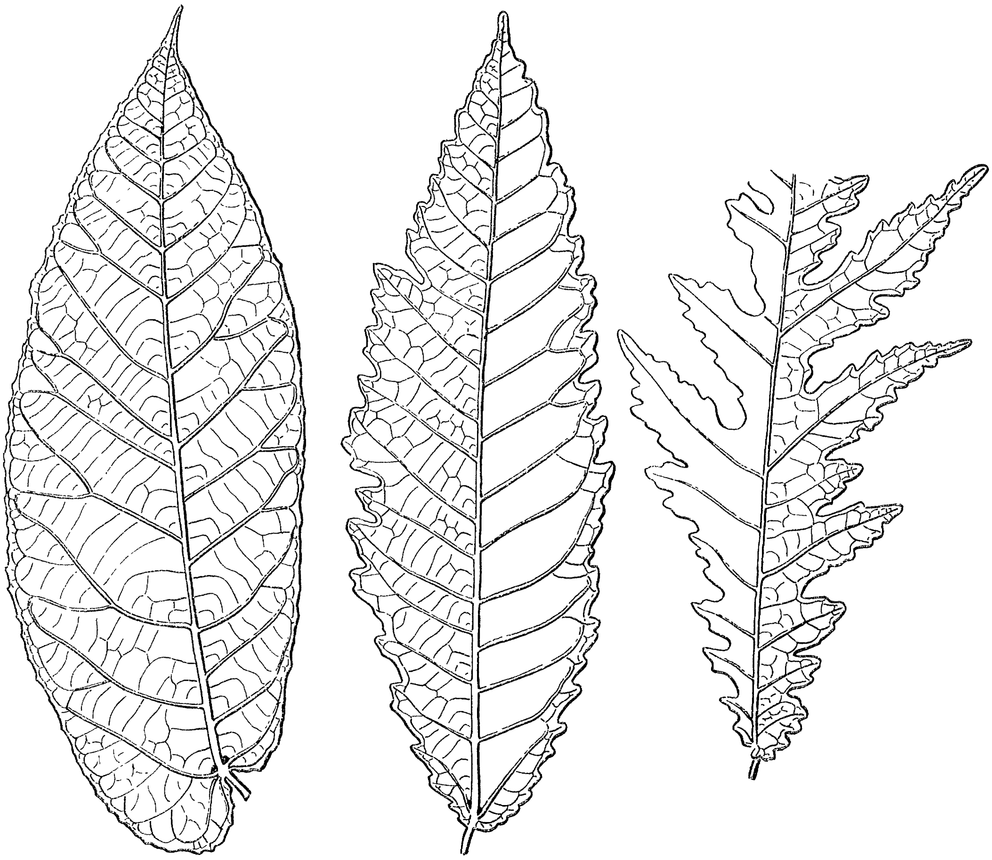

FIGURE 8. *Ficus greenwoodii*, from Fiji. Left, adult form of leaf (Williams s.n. 1860). Right, sapling leaves (Greenwood s.n.). Leaves, × ½.

the female flowers, white to pale pink, hispidulous distally, spathulate or oblong, free. Male flowers ostiolar in 1–2 rings; stamen 1. Gall- and female flowers sessile or with a short, white glabrous pedicel; ovary sessile, white; female style puberulous to glabrous. Seed *ca.* 1 mm, lenticular, slightly keeled, subreticulate. Lamina with cystoliths only on the lower side, not papillate.

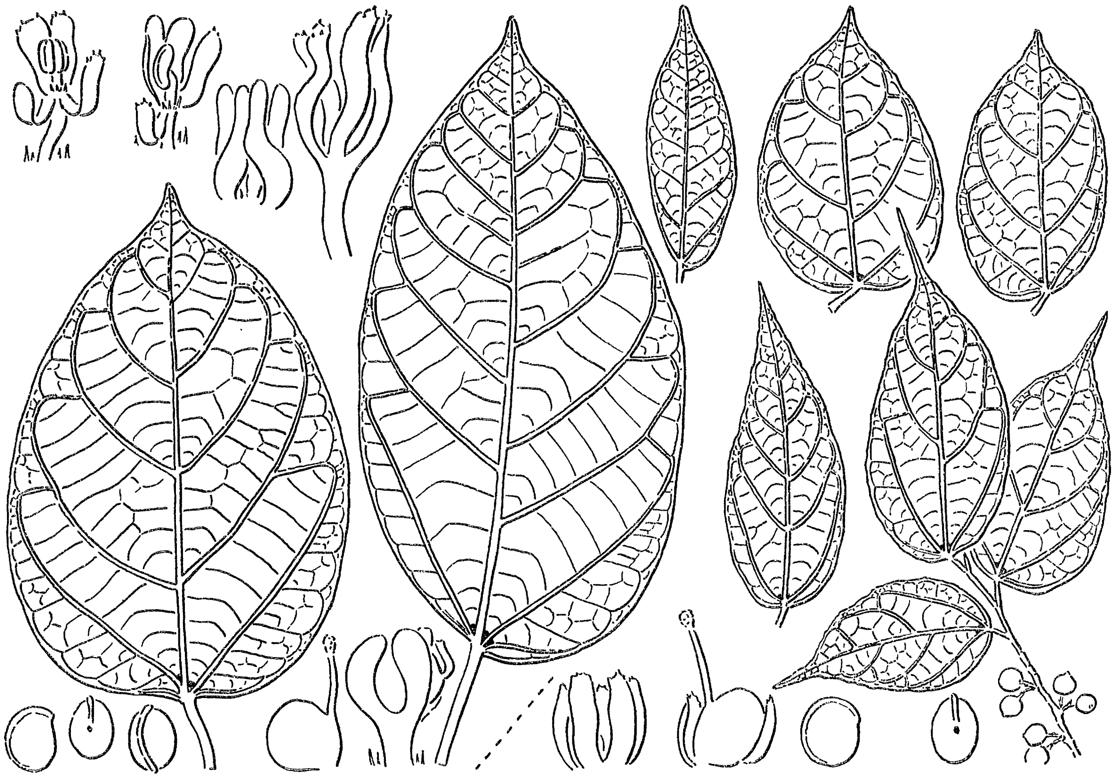

FIGURE 9. *Ficus storckii* var. *storckii* (left) and var. *kajewskii* (right, with small leaves). Leaves, from various collections, × $\frac{1}{2}$. Flowers, × 10; male and gall-flowers (var. *storckii*, A. C. Smith 7984); female flowers and seeds (var. *storckii*, Meebold 21386; var. *kajewskii*, A. C. Smith 8403).

Distr. New Caledonia, Loyalty Islands, New Hebrides, Rotuma, Fiji, Samoa, Niue, Tonga.

Ecol. Coastal and lowland forest.

Vern. nowirop (Aneityum).

Collections. Aneityum, L. E. Cheesman A2, Kajewski 731 and 788, A. Morrison s.n. 21 June 1896; Erromanga, Bernardi 13329, A. Morrison s.n. 20 July 1896, RSNH 1311, 16215, 16253, 16369; Espiritu Santo, Baker 83, RSNH 196; Tanna, Anderson s.n. 1774, Forster 247.

This seems to be a very variable species, at times so like *F. aspera* that one suspects that they may hybridise. Glabrescent specimens, which predominate in Samoa and Tonga, have been called *F. ciliata*, but there are many intermediates. The leaf-shape evidently varies from young shrubs or saplings to old trees, but it does not seem to be pinnately lobed in the sapling or coppice-shoot as it is in *F. aspera* and the Fijian *F. greenwoodii* (figure 8). Some collections from the New Hebrides (RSNH 16215, 16254) have acuminate leaves with the tip 10–22 mm long, as in *F. longecuspidata* of Samoa (figure 7). To understand *F. scabra* it will be necessary to grow the seedlings of the different leaf-forms. Wiebes (1966) records as the fig-insect *Blastophaga* ?

browni (Ashmead), which is the insect of the distantly related Philippine *F. ulmifolia*. It is to be hoped that the insects of this and other Polynesian species of ser. *Scabrae* will be collected.

F. storckii is extremely like *F. scabra*, but has cystoliths on both sides of the lamina. This is as important a distinction as in sect. *Adenosperma*. It divides the Polynesian species of ser. *Scabrae* into these two groups:

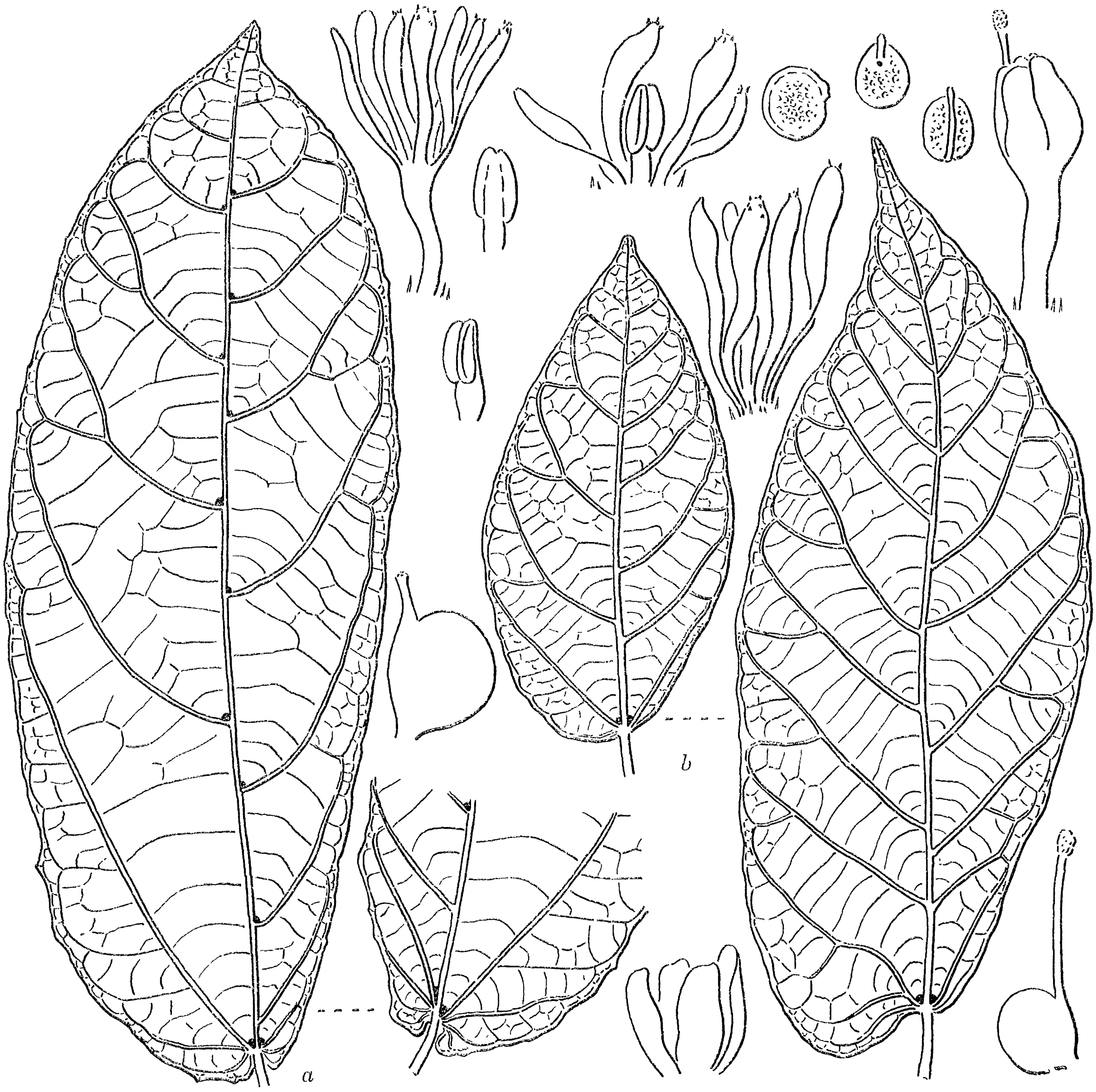

FIGURE 10. *Ficus masoni*, from Fiji. Leaves, × ½; *a*, A. C. Smith 8903; *b*, A. C. Smith 1413 (type of *F. begoniifolia*, but ? *F. greenwoodii*). Flowers, × 10; male and gall-flowers, Gillespie 2558; female flower and seeds, A.C. Smith 1413 (*F. begoniifolia*).

cystoliths amphigenous: *F. fulvopilosa* (Fiji, figure 11), *F. masoni* (Fiji, figure 10), *F. storckii* (figure 9), *F. barclayana* (figure 12), and *F. bambusaefolia* (Fiji, figure 12).

cystoliths hypogenous: *F. greenwoodii* (Fiji, figure 8), *F. aspera*, *F. scabra*, *F. uniauriculata* (Samoa, figure 6), *F. longecuspidata* (Samoa, Niue, figure 7), *F. godeffroyi* (Samoa, Niue, figure 7), and *F. samoensis* (Samoa, figure 7).

The alteration in leaf-shape runs parallel courses in both groups to the lanceolate willow-leaf. I have illustrated these species because the apparent abundance of *F. aspera* and *F. scabra*, if not of *F. storckii*, in the New Hebrides calls for critical exploration to see if any other Fijian or Samoan species may occur.

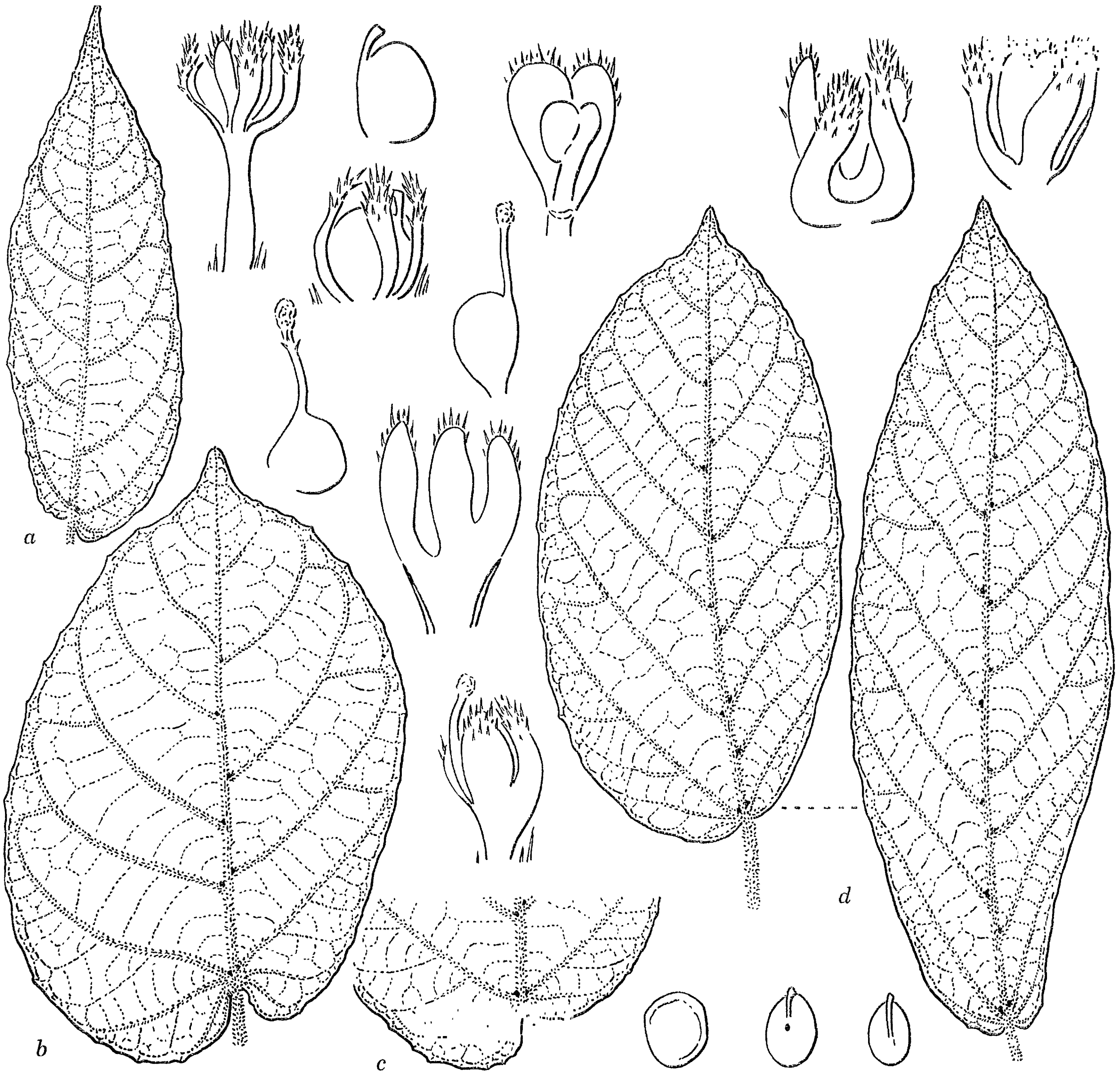

FIGURE 11. *Ficus fulvopilosa*, from Fiji. Leaves, collections of A. C. Smith, × $\frac{1}{2}$; *a*, n. 397; *b*, n. 291; *c*, n. 1326; *d*, n. 512 (type, 2 leaves). Flowers, × 10; male and gall-flowers, McKee 2813; female flowers and seeds, Greenwood 1240.

342. *F.* ***storckii*** Seem. (figure 9)

Shrub or slender tree –15 m high; leaves laxly spiral to distichous; scabridulous, not truly hairy. Twigs 1.5–2.5 mm thick, brown to greyish. Stipules –6 mm long, caducous. Lamina 6–18 × 3.7–13 cm, ovate, elliptic, or oblong elliptic, subacute to shortly acuminate, base cordate, rounded or widely cuneate, symmetrical or asymmetric, not auricled, entire, membranous to thinly subcoriaceous, scabrid on both sides, varying almost smooth, drying grey-green; lateral veins (4–)5–7(–8) pairs; intercostals 3–9, rather lax, slightly raised below; basal veins 1–2 pairs, reaching $\frac{1}{3}$–$\frac{1}{2}$ of the lamina, with 2 basal glands; petiole 7–40 × 1.5–2.5 mm. Figs axillary, paired, becoming ramiflorous and cauliflorous on short woody twigs or burrs, scabridulous, ripening yellow to orange, red, and finally purple-black; peduncle 3–5 mm long, with a collar of 3 basal bracts 0.5–1 mm long, or as a pedicel 8–14 mm long with scattered bracts; body 7–10 mm wide (–15 mm, living), subglobose, with 0–3 small appressed lateral bracts, the plane orifice closed by 3–4 small apical bracts in a disk 1–1.5 mm wide, not projecting; internal bristles –0.5 mm long, abundant, white; sclerotic cells absent from the fig-wall. Tepals 4–5, white, glabrous or puberulous at the apex, spathulate, free. Male flowers ostiolar in 1–3 rings, sessile to pedicellate; stamen 1, often with a few hairs at the base, ovary none or as a minute rudiment. Gall- and female flowers sessile or with glabrous pedicels –1.5 mm long; tepals longer than the ovary; styles glabrous. Seed 1 mm, lenticular, slightly keeled, smooth or subreticulate. Lamina with abundant cystoliths on both sides, the larger papillate.

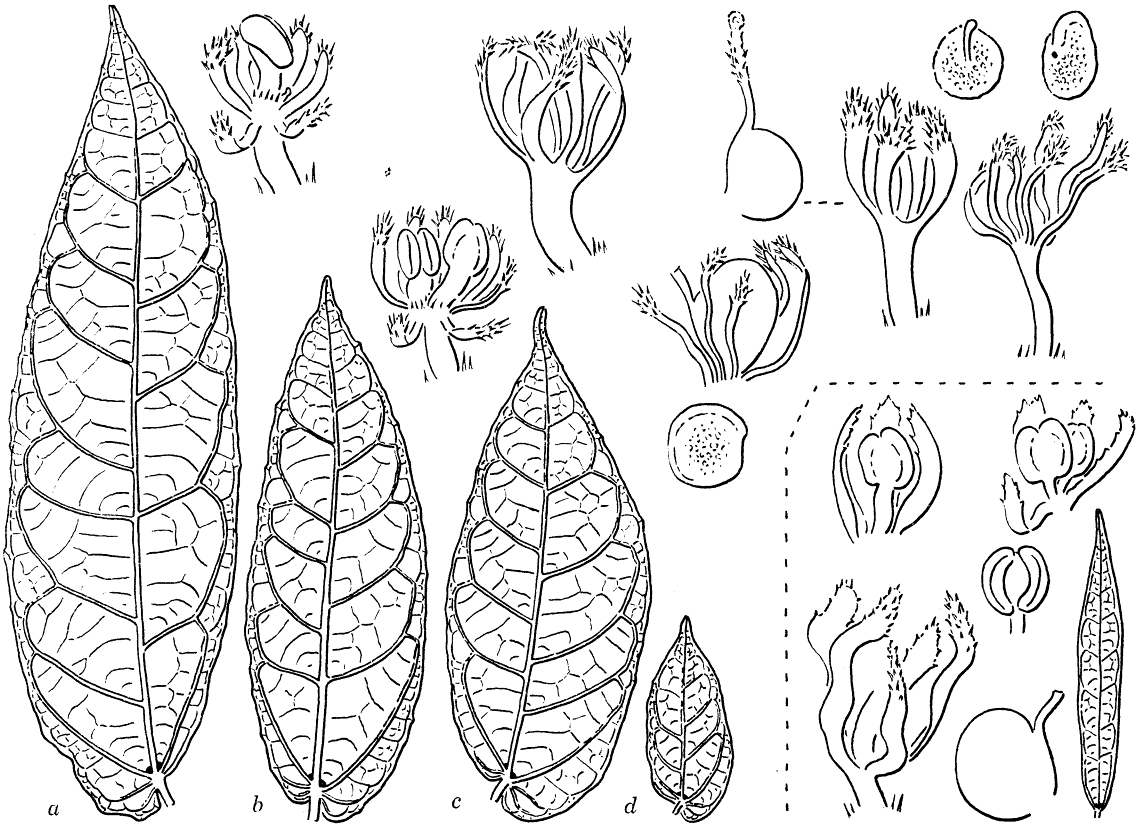

FIGURE 12. *Ficus barclayana* and *F. bambusaefolia* (inset), from Fiji. Leaves, × ½; *a*, A. C. Smith 9428; *b*, A. C. Smith 9641; *c*, A. C. Smith 381; *d*, Gillespie 4247. Flowers, × 10; male and gall-flowers, A. C. Smith 7675; female flowers and seeds, A. C. Smith 9345, 9428. *F. bambusaefolia*, A. C. Smith 8327.

Distr. New Hebrides, Fiji.

Ecol. Lowland forest.

Collection. Aneityum, Bernardi 13046.

var. ***kajewskii*** (Summerhayes) Corner (figure 9)

Lamina 4–10(–15) × 1.8–5 cm; lateral veins 2–5 pairs; petiole 3–15 mm long. Fig-body 5–7 mm wide; peduncle 1.5–5 × 0.3–0.7 mm, mostly with a collar of 3 basal bracts; apical bracts often slightly projecting. Tepals glabrous.

Distr. New Hebrides, Fiji.

Ecol. Lowland and montane forest –1400 m alt., epiphytic in *Weinmannia-Metrosideros* forest.

Vern. nemesue (Erromanga).

Collections. Ambrim, Aubert de la Rue s.n. Aug. 1937; Aneityum, Kajewski 737, RSNH 90, 1146; Efate, Kajewski 216, 233; Erromanga, Kajewski 343; Espiritu Santo, E. S. Brown s.n., RSNH 232, 16367; Tanna, Bernardi 13131, RSNH 16195.

It is necessary to examine the cystoliths on the leaf in order to ascertain the identity of *F. storckii* which, otherwise, is very like *F. scabra*. Var. *kajewskii* resembles the Malesian *F. ampelas* which has sclerotic cells in the fig-wall, narrower and more scabrid leaf, and hairy tepals. Geographical distribution helps to distinguish the end-products of evolution.

357. ***F. tinctoria*** Forst. f.

Corner (1967) 111, figure 36.

Collections. Aneityum, Kajewski 995; Efate, RSNH 1118; Espiritu Santo, RSNH 24154, 24271; Tanna, Kajewski 79, RSNH 1205, 1209.

358. ***F. virgata*** Reinw.

Corner (1967) 112, figure 36.

Vern. nevelisi (Erromanga).

Collections. Erromanga, Kajewski 265 and 395, RSNH 167; Tanna, RSNH 105.

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

Collection. Vanua Lava, Kajewski 493.

360. ***F. subulata*** Bl.

Corner (1967) 113, figure 37.

Collections. Espiritu Santo, RSNH 16291, 24136.

386. ***F. adenosperma*** Miq.

Corner (1967) 117, figure 38.

Vern. bongnute (Erromanga), nelim (Espiritu Santo).

Collections. Ambrim, Aubert de la Rue s.n.; Aneityum, Bernardi 12963, L. E. Cheesman 5 and 9, Kajewski 711, RSNH 1141; Efate, A. Morrison s.n. 22 Aug. 1896, RSNH 31, 1067; Erromanga, Bernardi 13277, Kajewski 264, A. Morrison s.n. 1896, RSNH 16252; Espiritu Santo, Baker 263, RSNH 16288, 24183, 24242; Malekula, RSNH 364, 1521; Tanna, Bernardi 12855 and 13079, L. E. Cheesman 8 and 40A, Kajewski 23 and 89, RSNH 1201; Vanua Lava, Kajewsi 417, 426.

387. ***F. austrina*** Corner

Corner (1967) 118, figure 40.

Collection. Vanua Lava, Kajewski 433.

464. ***F. septica*** Burm. f.

Corner (1967) 153, figure 68.

Vern. ubariherhon (Erromanga), wora-wora (Espiritu Santo).

Collections. Ambrim, Aubert de la Rue s.n. Aug. 1934; Aneityum, Kajewski 793; Efate, RSNH 40; Erromanga, Kajewski 271, RSNH 159; Espiritu Santo, Baker 26, RSNH 267, 16372; Tanna, Bernardi 12858 and 12886, L. E. Cheesman 40, Forster s.n.

var. ***cauliflora*** Corner

Collections. Efate, RSNH 1013, 3000, 6282; Erromanga, A. Morrison s.n. 24 July 1896; Espiritu Santo, RSNH 16284, 24129; Malekula, RSNH 348.

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