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Ficus glaberrima Bl. and the Pedunculate Species of Ficus Subgen. Urostigma in Asia and Australasia

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FICUS GLABERRIMA BL. AND THE PEDUNCULATE SPECIES OF *FICUS* SUBGEN. *UROSTIGMA* IN ASIA AND AUSTRALASIA

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CONTENTS

The resemblance between the Malesian *F. glaberrima* Bl. and the Indian *F. arnottiana* Miq. is considered to be the result of convergent simplification. The origin of *F. glaberrima* is referred to the stock of the Malesian *F. depressa* Bl., that of *F. arnottiana* to the stock of the Indochinese *F. orthoneura* Lévl. et Vant. Both ancestral stocks are considered to have arisen on the Indochina–Philippines–New Guinea track leading to the Melanesian Foreland. In support of these conclusions evidence is drawn from ser. *Callophylleae*, *F. talboti* King, *F. maclellandi* King, *F. calcicola* Corner, *F. elastica* Roxb., and sect. *Malvanthera*. Leaf-structure in the xerophytic strangling figs is discussed. *F. glaberrima* var. *siamensis* Corner is reduced to *F. arnottiana* var. *subcostata* Corner.

Introduction

The strangling fig *F. glaberrima* is puzzling both in systematic position and geographical distribution. Its small pedunculate syconium resembles that of *F. arnottiana*, placed by me in subsect. *Conosycea* ser. *Validae* along with *F. annulata* and its Malesian allies (Corner 1960, 1965). Its leaf, however, has the simplified venation of subsect. *Dictyoneuron* where I placed *F. glaberrima*, in its own ser. *Glaberrimae*, along with many Malesian species with sessile syconia (figure 1). *F. arnottiana* and *F. glaberrima* overlap geographically in northern India (figure 3). For each I made a variety from a few collections, namely *F. arnottiana* var. *subcostata* from northwest India and Nepal and *F. glaberrima* var. *siamensis* from Thailand. I drew attention to their resemblance and now, a collection from southwest Thailand (K. and S. S. Larsen 33627, to be mentioned later) proves that they are the same taxon; accordingly I reduce var. *siamensis* to var. *subcostata*. In so doing I have been led to review the position of *F. glaberrima* and that of the other pedunculate species of subgen. *Urostigma* in Asia and Australasia. By pedunculate is meant a syconium with a peduncle below the collar of basal bracts, not pedicellate with a stalk above the basal bracts, because this pedicel is often more or less of an artefact of drying the syconium.

Pedunculate species of subgen. *Urostigma* (Asia, Australasia)

The following is the systematic list of the species with the pedunculate syconium.

sect. *Urostigma*
- ser. *Caulobotryeae*: all species except *F. cupulata*, but all varying to sessile syconia except *F. caulocarpa*.
- ser. *Orthoneurae*: *F. orthoneura*.
- ser. *Superbae*: all species, but varying sessile in *F. concinna*.

sect. *Conosycea*
- subsect. *Conosycea*
  - ser. *Validae*: *F. arnottiana*, *F. beddomei*, *F. costata*, *F. dalhousiae*; *F. annulata*, *F. chrysolepis* *F. depressa*, *F. globosa*, *F. novoguineensis*.
- subsect. *Dictyoneuron*.
  - ser. *Glaberrimae*: *F. glaberrima*.
  - ser. *Subvalidae*: *F. talboti*, but usually with sessile syconium.
- subsect. *Benjamina*
  - ser. *Callophyllae*: *F. balete*, *F. microcarpa* var. *naumanni*.

sect. *Stilpnophyllum*: *F. elastica*.

sect. *Malvanthera*: numerous species.

I have used the nomenclature in my check-list of *Ficus* (Corner 1965).

The pedunculate syconium and leaf-venation

In the course of my work on *Ficus* I have been obliged to learn how to identify sterile specimens. They are often collected, especially from the strangling figs with seasonal fruiting, and ecologists wish to identify such plants so prominent in the tropical rain-forest. Moreover, the type-specimens of several old and critical species are sterile. Then, many species are cultivated

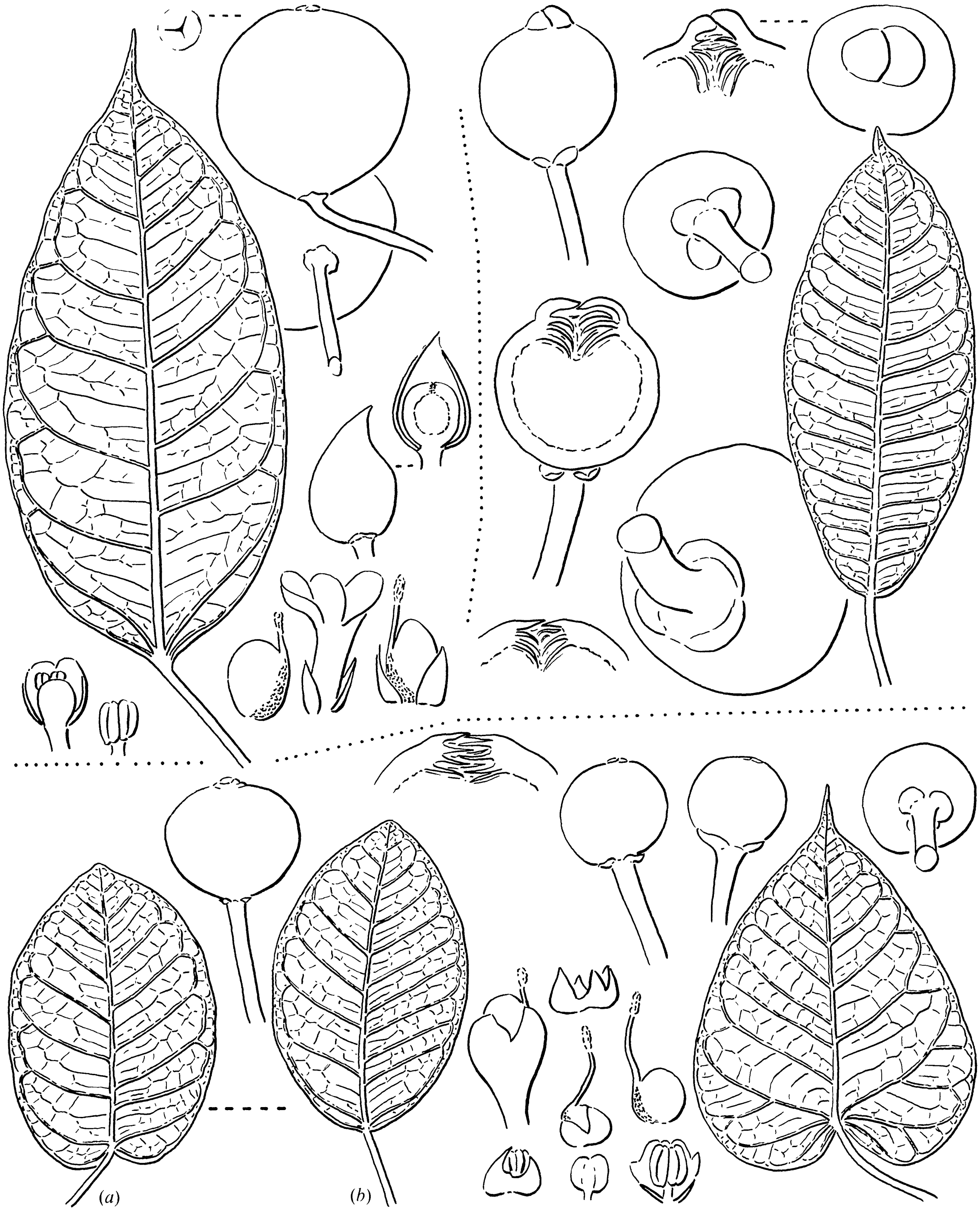

FIGURE 1. *Ficus arnottiana* (lower row) with var. *arnottiana* (right) and var. *subcostata* (left); (*a*) Larsen 33627; (*b*) Nielsen 651. *F. glaberrima* (upper row) with var. *glaberrima* (left) and var. *bracteata* (right). Leaves, magn. $\times \frac{1}{2}$; figs, magn. $\times 3$; orifice of fig, magn. $\times 6$; flowers, magn. $\times 10$; young fig of var. *glaberrima* with subtending conical bract, magn. $\times 5$.

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in greenhouses or as pot-plants, and the larger trees and stranglers never reach maturity under such conditions; yet, horticulturalists must know their names. The best instance of these is *F. elastica* which has regained popularity as a household plant; it is readily raised from cuttings and, with the large sapling leaves, it remains sterile. Hence I have turned to venation and the microscopic structure of the lamina, discernible in dried as well as living material, and I have found so many characters that it is possible to identify most, though not all, the species of Asia and Australasia merely from the leaf.

In subgen. *Urostigma* the leaves are entire, more or less coriaceous, and often very similar in size and shape. The important differences in venation are shown by *F. dalhousiae* (figure 2), *F. glaberrima* (figure 1), *F. talboti* (figure 14), *F. callophylla* (figure 10), and *F. elastica* (figure 15). The almost parallel lateral venation of *F. callophylla* and *F. elastica* was recognized by King (1887). It is the result of loss of intercostal growth by means of submarginal transverse intercostals and its substitution by basipetal growth along the midrib which lengthens the secondary and tertiary veins (Corner 1967). The basipetal growth is revealed by the convolute vernation in subgen. *Urostigma* as opposed to the plicate vernation common in subgen. *Ficus*. Actually some degree of basipetal growth occurs even in the leaf of *F. dalhousiae* or that of *F. religiosa*, possibly by basipetal extension of the transverse intercostal veining. I used these differences to distinguish subsect. *Conosycea* with transverse intercostal venation from subsect. *Dictyoneuron* without such intercostals, and subsect. *Benjamina* with that pronounced basipetal growth along

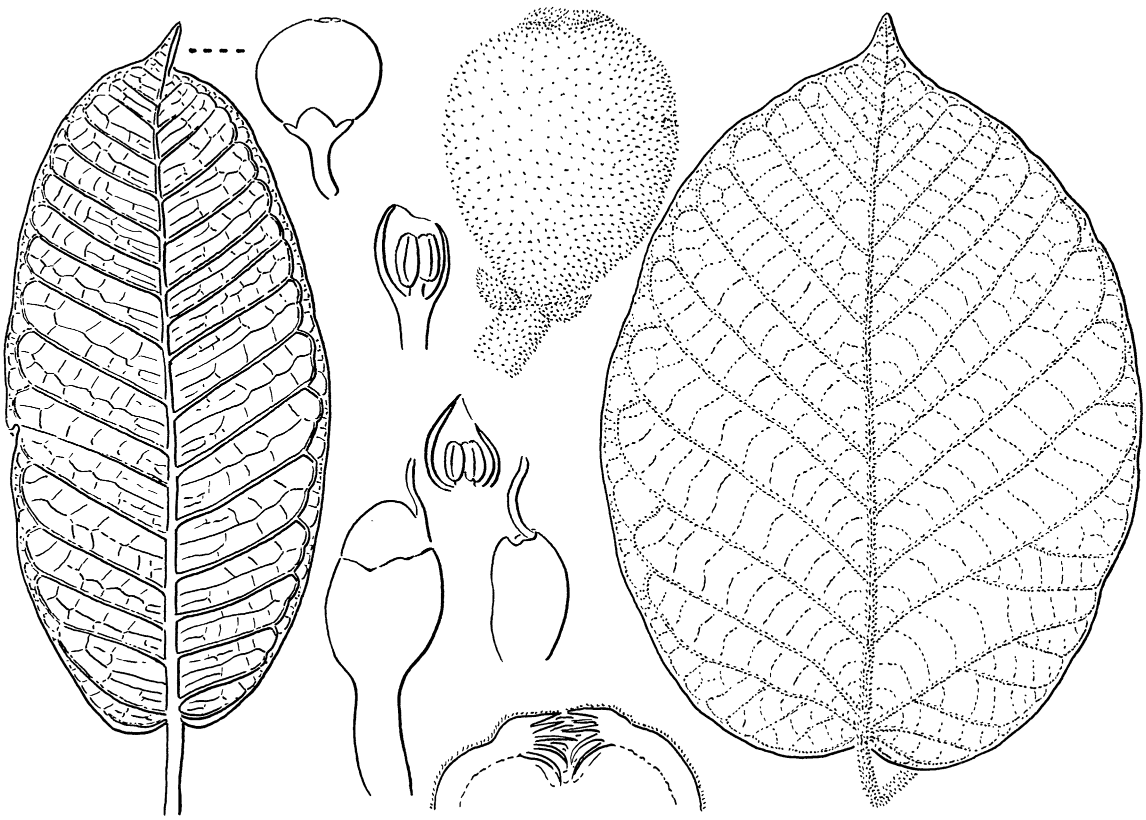

FIGURE 2. *Ficus costata* (left) with leaf and glabrous fig (magn. × 1). *F. dalhousiae* (right) with hairy leaf and fig (magn. × 3), and flowers (magn. × 10). Leaves, magn. × ½; fig-orifice, magn. × 6.

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the midrib which leads to the extreme, almost banana-like, venation in *F. elastica* and most species of sect. *Malvanthera*. The classification brought together closely related species and the evolution of the venation appeared to have been monphyletic in the Asian and Australasian species. Yet. *F. glaberrima* seems to be an exception, similar in most ways to *F. arnottiana* but without the intercostal venation. Certainly the loss of transverse intercostal venation has occurred independently in subgen. *Ficus* and subgen. *Pharmacosycea*, even within specific limits e.g. *F. sinuata* (Corner 1976). In such cases the lamina becomes narrower and does not retain its usual width through the basipetal intercalary growth which, in *Urostigma*, restores both size and shape.

The alternative is to classify the species of *Urostigma* into those with pedunculate and those with sessile syconia. The pedunculate is the first stable form to emerge in evolution from the primitive multibracteate syconium, and it leads by loss of the peduncle to the sessile or the most advanced state. The development of the peduncle varies, however, more than the manner of venation, and both pedunculate and sessile forms occur in numerous species both in *Urostigma* and in subgenera of *Ficus*, e.g. *F. aurata*, *F. chartacea*, *F. lepicarpa* and *F. mollior* in subgen. *Ficus*. The feature is less helpful in classification but it implies that all groups of *Ficus* with syconia without lateral bracts have come from a pedunculate ancestor. Flowers and seeds offer no means of subdividing the species of sect. *Conosycea* which number over sixty.

Microscopic leaf-structure

The strangling figs begin life as epiphytic bushes subject to varying degrees of water-deficiency. Their leaves are not thin and denticulate, as in so many shrubs and trees of *Ficus*, but entire and more or less coriaceous with xerophytic construction; thus, *F. xylophylla* is well named because its obtuse leaf is the thickest and toughest in the genus. A thick cuticle, a multiple hypodermis on both sides of the lamina for water-storage, and, in consequence, sunken stomata become prevalent. Hairs seem to play little part for the adult leaves are generally glabrous, though young leaves on opening buds of some species are thickly hairy, e.g. *F. consociata* and *F. drupacea*. The simplest and, most probably, the primitive state in this sequence is shown by sect. *Urostigma* which lacks a general hypodermis and has rather thin leaves, superficial stomata, hypogenous cystoliths and, as a peculiarity, crystal-cells along the hypodermal tissue on the underside of the veins; the habit in this section seems generally to be deciduous. Ser. *Orthoneura*, however, has an upper hypodermis (one cell thick), and this construction, though with amphigenous cystoliths, prevails in the alliance of *F. arnottiana* in ser. *Validae* of sect. *Conosycea*. In the alliance of *F. annulata* in this ser. *Validae* the hypodermis is commonly two cells thick. In the rest of sect. *Conosycea*, especially in subsect. *Dictyoneuron* and ser. *Callophylleae*, the upper hypodermis is 2–3 cells thick and there is a lower hypodermis 1–2 cells thick in which the stomata are sunken. In sect. *Stilpnophyllum* (*F. elastica*) and sect. *Malvanthera* the hypodermis on both sides of the leaf is 2–3 cells thick and the deeply sunken stomata often have a frustrum-like extension of the cuticle over the exterior of the stomatal recess. The leaf of *F. glaberrima* is intermediate with a hypodermis 1–2 cells thick on both sides, slightly sunken stomata, and amphigenous cystoliths; it fits subsect. *Dictyoneuron* in microscopic structure and venation rather than ser. *Validae* with *F. arnottiana*.

In the course of this investigation one meets an unusual and specific character that is critical in the identification of sterile specimens. It is the gyrose-plicate cuticle with close, short, and sinuous folds on the underside of the lamina; the folds often project over and partly obscure the stomata. This cuticle distinguishes four species of ser. *Validae*, namely *F. costata*, *F. annulata*, *F. chrysolepis*, and *F. novoguineensis*, and both species of ser. *Orthoneurae*, namely *F. hookeriana* and *F. orthoneura*. In contrast the cuticle is smooth in other Asian and Australasian species of *Urostigma* except for an intermediate state in which it is somewhat plicate-striate immediately around the stomata and, frequently, the cystoliths. This intermediate state occurs in *F. arnottiana*, its var. *subcostata*, and in *F. globosa*; indeed, in one collection of *F. globosa* (Kerr 19796 from Thailand) the cuticle is almost gyrose-plicate as in its ally *F. annulata*. Elsewhere I have found this gyrose-plicate cuticle in the African *F. laurifolia* Lamk, which may belong to the alliance of *F. costata*, in the Madagascan *F. grevei* Baill. (sect. *Galoglychia*, or subgen. *Bibracteatae*), in the American *F. maxima* P. Miller (subgen. *Pharmacosycea*, DeWolf 1967), and in the Bornean *F. macilenta* (subgen. *Ficus*, Corner 1970*a*). I assume that this cuticle is an innovation from the primitively smooth cuticle, just as in the west Malesian *F. lowii* (sect. *Conosycea*) the lower epidermal cells have an external papilla on which the cuticle is very shortly plicate, as an innovation from the smooth cuticle of the allied *F. sundaica*.

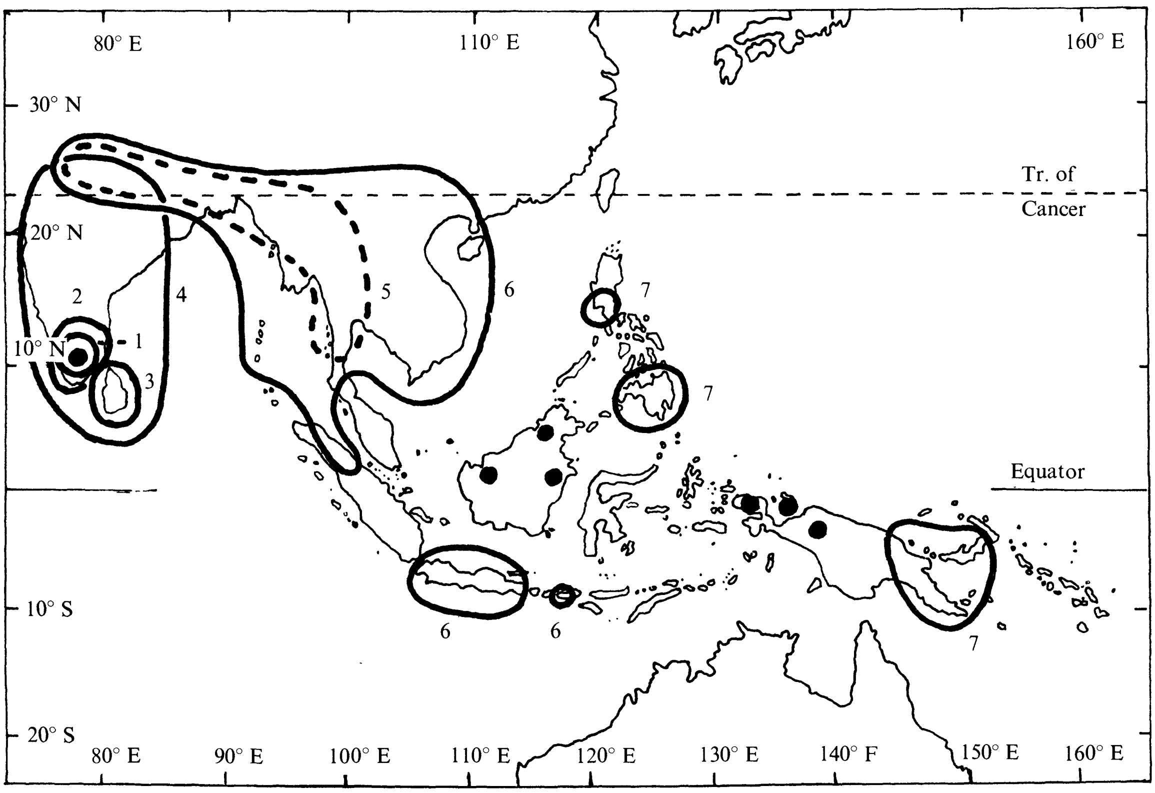

FIGURE 3. Distributions of: (1) *Ficus beddomei*; (2) *F. dalhousiae*; (3) *F. costata*; (4) *F. arnottiana* var. *arnottiana*; (5) var. *subcostata*, broken line; (6) *F. glaberrima* var. *glaberrima*, north and south distribution; (7) var. *bracteata*, isolated collections shown by black circles, one coinciding with the distribution of *F. beddomei*.

SER. *VALIDAE*

This group with pedunculate figs bears most strongly on the problem of *F. glaberrima*. The nine species can be divided into the Indian alliance of *F. arnottiana* and the Malesian alliance of *F. annulata*. In the Indian the leaf-base is rounded to cordate, the hypodermis is one cell thick, and the figs, so far as known, ripen yellow to red and, finally dark purple; *F. arnottiana* is deciduous but the habit of the other species is unrecorded. In the Malesian alliance the leaf-base is cuneate, the hypodermis is mostly two cells thick, and the figs ripen merely pinkish orange (*F. annulata*), dull yellowish (*F. depressa*), brownish yellowish (*F. novoguineensis*) or green to blackish without yellow or red (*F. globosa*); all the species are evergreen. Into both alliances, however, there enters the distinction in cuticle. In the Indian alliance *F. costata* has the gyrose-plicate cuticle, by which means I identified the sterile type at the British Museum (Natural History); it represents a sapling pot-plant that had been grown at Kew and had been reported in the Index Kewensis as originating from the Nicobar Islands, but this may have been an error; it has not been collected there again and it is identical with *F. caudiculata*, *F. mooniana*, and *Urostigma wightianum* var. *majus*, all of which came from Ceylon (Corner 1960). The intermediate state of the cuticle occurs in *F. arnottiana*, but *F. beddomei* and *F. dalhousiae* have the smooth cuticle. In the Malesian alliance the cuticle is gyrose-plicate in *F. annulata* and its close allies *F. chrysolepis* and *F. novoguineensis*, and to some extent in *F. globosa*, but it is smooth in *F. depressa* where it is often the surest means of distinguishing poor or sterile herbarium-specimens from *F. annulata* (Corner 1976).

In the Indian alliance *F. beddomei*, *F. dalhousiae*, and *F. costata* are relatively pachycaul with twigs 6–10 mm thick, large lamina with numerous lateral veins (10–16 pairs), and figs 12–20 mm wide (figure 2). Their distribution in south India and Ceylon is extremely limited (figure 3); collections are few and there are no recent records of living trees; I would place all on the list of extremely rare, if not extinct, plants. *F. arnottiana* is leptocaul with twigs 3–5 mm

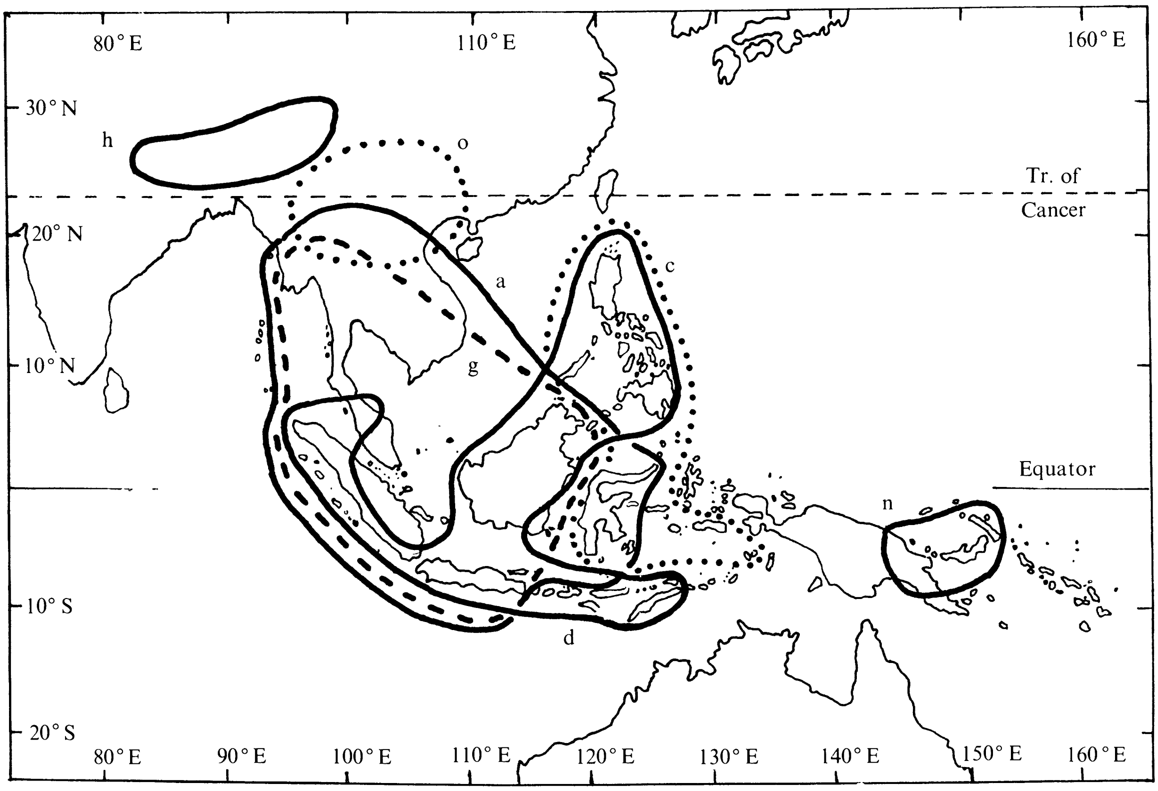

FIGURE 4. Distributions of *F. annulata* and its allies and of ser. *Orthoneurae*. (*a*) *F. annulata*; (*c*) dotted line, *F. chrysolepis*; (*d*) *F. depressa*; (*g*) *F. globosa*, broken line; (*n*) *F. novoguineensis*; (*h*) *F. hookeriana*; (*o*) dotted line, *F. orthoneura*.

thick, smaller lamina with 5–7 pairs of lateral veins, and smaller figs 6–11 mm wide (figure 1). It is fairly common, and var. *subcostata* extends its range into Thailand. There is a collection of *F. costata* from Indochina (Ch. d'Alleizette s.n., 2 June 1909, pr. Tourane); it is fertile and the flowers with simple stigma agree with *F. costata*, not with *F. orthoneura*. Tourane has been a well collected locality and, as no other collections of this species have been found there, I suspect that it was an introduced tree. I did not find insects or seeds in the dried figs, and *F. costata* has been in sporadic cultivation for nearly 200 years.

In the Malesian alliance, which extends from Burma to New Guinea, the more pachycaul *F. annulata* (twigs 6–10 mm thick, lateral veins 12–17 pairs) has the widest distribution. It is abundant and variable; a form with more or less sessile syconia is frequent in Java, Borneo, and Celebes. *F. chrysolepis* and *F. novoguineensis* are close and could be regarded as further variations, or subspecies, of *F. annulata*. *F. novoguineensis*, however, is a destructive strangler of much greater size than *F. annulata* which seldom kills its host; the habit of *F. chrysolepis* has been described as that of an independent tree, such as *F. annulata* may form, and that of a large strangler. The two more leptocaul species, *F. depressa* and *F. globosa*, are straggling climbers with many slender descending roots that fasten on to surrounding vegetation, but never thicken into root-trunks or pillar-roots (Corner 1976). The small fig of *F. globosa* resembles that of *F. costata* except in its colour when ripening, and the large fig of *F. depressa* resembles that of *F. annulata*. The distribution of neither, however, fits with such possibilities (figure 4).

The distribution of the *F. arnottiana* alliance suggests derivation in south India from Gondwanaland, but there are no allies in Madagascar, other islands of the west Indian Ocean, Australia, or South Africa. The distribution of the *F. annulata* alliance suggests a pachycaul ancestry along the Indochina-Philippines-New Guinea track which has evolved into the western *F. annulata*, the central *F. chrysolepis*, and the eastern *F. novoguineensis*; the first two overlap in Celebes and can scarcely be considered vicarious. *F. globosa* appears, then, as the west Malesian climber derived from this ancestry, possibly before the strongly gyrose-plicate cuticle was evolved. *F. depressa*, with smooth cuticle, indicates a more remote derivation, in spite of its resemblance in leaf and fig with *F. annulata*. Its central distribution, avoiding the Riouw pocket, which lies in the triangle between Singapore, Palembang, and Pontianak, curiously resembles that of *F. glaberrima*, though *F. depressa* is absent from continental Asia except in the north of Malaya and the extreme south of Thailand (figures 3 and 4).

SER. *ORTHONEURAE*

Two Sino-Himalayan species, *F. hookeriana* and *F. orthoneura*, compose this series which links sect. *Urostigma* with sect. *Conosycea*. They have the red-brown ovaries, hypogenous cystoliths, and crystal-cells along the veins as in sect. *Urostigma*, but the non-articulate petiole, the disperse male flowers, and the one-celled upper hypodermis of the lamina as in sect. *Conosycea*. Then both have the gyrose-plicate cuticle which occurs in sect. *Conosycea* but not in sect. *Urostigma*. The pedunculate fig of *F. orthoneura* relates with that of ser. *Validae*. In fact, *F. orthoneura* resembles *F. costata* so closely that external distinctions are hard to find in herbarium-material; the lamina is less acuminate, even obtuse, in *F. orthoneura*, the lateral veins are more widely spaced almost perpendicular to the midrib, the figs may be ellipsoid rather than subglobose (ripening yellow to red in both species), and there is a slight annulus below the basal bracts in *F. orthoneura*, the better developed state of which marks *F. annulata*. Inside the syconia,

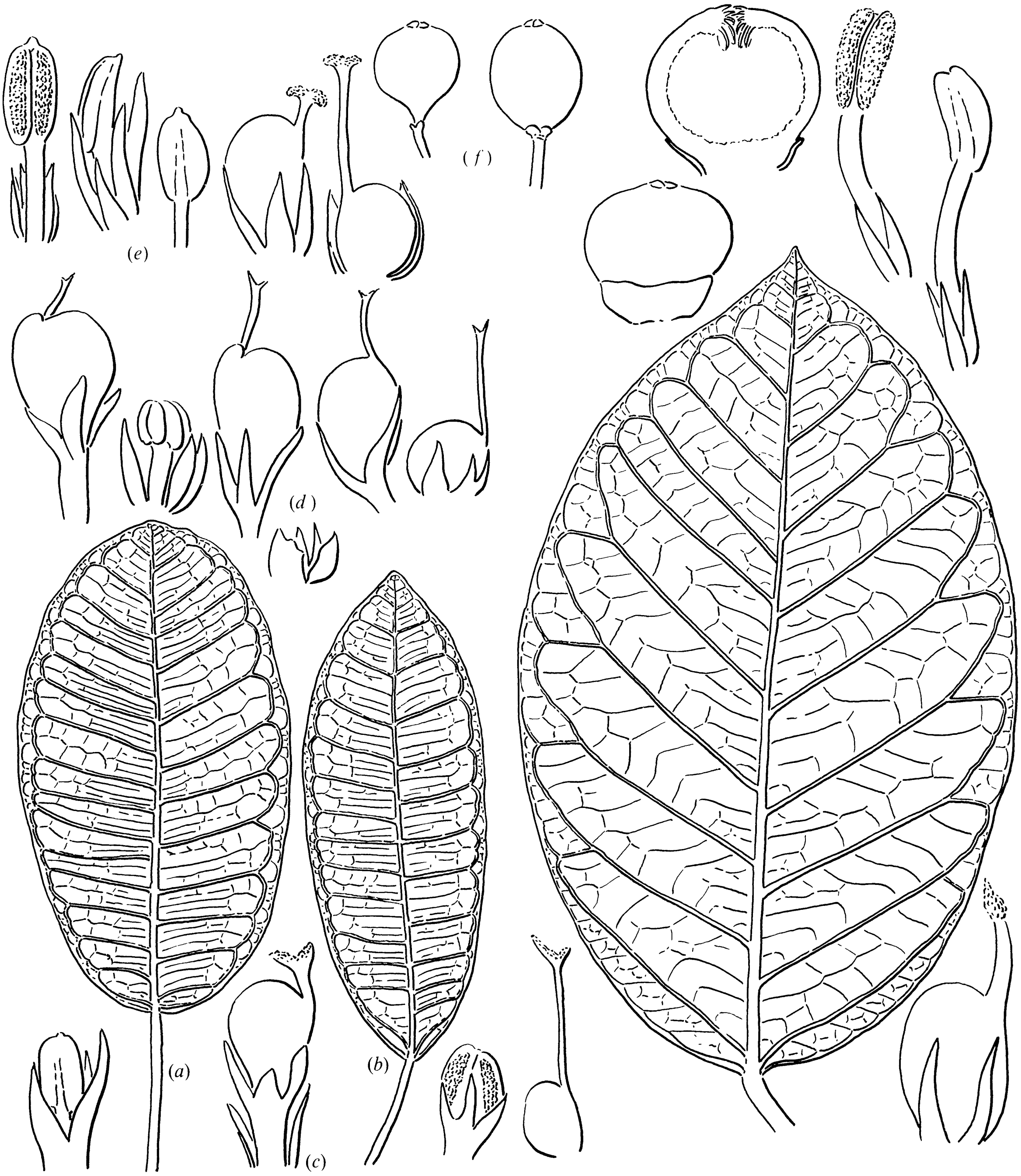

FIGURE 5. *Ficus orthoneura* (left); (*a*) Chevalier 37625; (*b*) Cavalerie 2050; (*c*) Cavalerie 2050; (*d*) Esquirol 7584; (*e*) Tsiang 21864; (*f*) Chevalier 37625. *F. hookeriana* (right), Hooker 120. Leaves, magn. × $\frac{1}{2}$, figs, magn. × 1; flowers, magn. × 10.

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however, there is the distinction in colour of the ovaries and, very remarkably, the bifid stigma of both gall- and female flowers of *F. orthoneura*. The bifid stigma occurs in several species of sect. *Malvanthera* as a primitive mark of the Moraceous stigma, but not elsewhere in subgen. *Urostigma*. It distinguishes subgen. *Pharmacosycea* and I thought, at first, that *F. orthoneura* might belong there. It has been described as a shrub or small tree up to 7 m high, never as a strangler, but the colour of the ovaries, the double sclerotic layer in the fig-wall, and the leaf-structure are features of subgen. *Urostigma*. This is confirmed by its undoubted alliance with *F. hookeriana* which is described as an epiphyte with aerial roots (a habit unknown in *Pharmacosycea*), and which has the simple stigma of subgen. *Urostigma*. *F. hookeriana* differs also from *F. orthoneura* in the larger leaf, the size of which is caused by the greater amount of growth in the reticulum that separates the main veins in the intercostal areas (figure 5), and in the sessile fig half-covered by a large cupule of connate basal bracts. *F. hookeriana* has been described as deciduous in the field-notes of Kingdon-Ward 17110 from Burma, and from the leaves of some collections of *F. orthoneura* it seems that this may be its habit, as in sect *Urostigma*. Both species appear to be locally common. I have seen 8 collections of wild trees of *F. hookeriana* and 11 of *F. orthoneura*, but no living plants of either.

The key-position of *F. orthoneura* has not been understood. *F. caesia* Hand. Maz., which is a synonym, was referred to sect. *Covellia*, intending thereby sect. *Sycocarpus*, which is very wide of the mark. If, as seems probable, ser. *Orthoneurae* is related to *F. costata*, there is interposed the geographical gap in their distributions. It may be filled in part by *F. arnottiana* as the descendent of the pachycaul line which led to the species with gyrose-plicate cuticle, and in part by *F. beddomei* and *F. dalhousiae* as descendents of the more remote state with smooth cuticle. *F. hookeriana* is the advance in leaf, sessile cupulate fig, and simple stigma. A considerable sequence of intermediates must have disappeared and, in spite of their apparently discrete though practically contiguous distributions, the two survivors of ser. *Orthoneurae* cannot be regarded simply as vicarious products of one ancestral species.

Ficus glaberrima

There are two varieties of this species, differing in details of the fig, and they confer on *F. glaberrima* the widest distribution of any pedunculate species of sect. *Conosycea* (figure 3). The varieties could be regarded as geographical subspecies because, so far as known, their distributions do not overlap; yet, it is possible that var. *glaberrima* may occur in Borneo with var. *bracteata*. Their distinction lies mainly in the basal bracts which are well formed, if small, in var. *bracteata*, but absent from var. *glaberrima* (figure 1.) At the top of the peduncle in var. *glaberrima* there is a narrow annular scar which I long considered to be the scar where three caducous basal bracts had fallen off while the fig was still very small. Some recent collections with very young figs have shown, however, that there are no basal bracts and that the scar comes from a short, conical, and stipular bud-scale that covers the young syconium (figure 1). Usually this bud-scale is at the base of the peduncle as in var. *bracteata* and in *F. elastica* which has, as well, three small and caducous basal bracts (figure 15). In var. *glaberrima* the bud-scale has evidently been transferred to the top of the peduncle to take the place of the basal bracts; it is a unique construction. The fig of var. *bracteata* has also more prominent apical bracts and the leaf may have rather more numerous lateral veins; there is no other distinction except the geographical. The figs ripen yellow to red and those of var. *bracteata* are extremely like those of *F. arnottiana*, though the basal bracts of *F. arnottiana* are evidently caducous, and the two taxa are widely separate geographically. The leaf of *F. glaberrima* has the venation and microscopic structure of subsect. *Dictyoneuron*; it has an upper and lower hypodermis 1–2 cells thick, amphigenous cystoliths, slightly sunken stomata, and a smooth cuticle.

Geographically, var. *glaberrima* is the only pedunculate species to have reached Hainan and the Andaman Islands. It has, also, a disjunct distribution in Java and Sumatra. It avoids the Riouw pocket and, in this way, recalls *F. depressa*. I conclude that *F. glaberrima* has evolved from the ancestral stock of *F. depressa* in central Malesia and has spread eastwards in the more primitive state as var. *bracteata* and westwards as var. *glaberrima*, with a preference, as it seems, for the monsoon climate. The central Malesian focus is emphasized by the pedunculate *F. balete*, as will be discussed later, and the latitudinal spread by other species of ser. *Callophylleae* with sessile figs.

As already mentioned, I must now reduce *F. glaberrima* var. *siamensis* Corner (1960) to *F. arnottiana* var. *subcostata* Corner (1960). Var. *siamensis* was described from four collections from the limestone hills of Thailand; in venation they tended to *F. glaberrima* but they had a widely cuneate to subcordate leaf-base which did not fit, and the figs had caducous basal bracts such as I had wrongly assumed to be the case in var. *glaberrima* and which, then, I did not know were typical of *F. arnottiana*. Var. *subcostata* was described from three Himalayan collections (northwest India, Nepal), distinguished by the less cordate lamina with subacute to obtuse apex. In both varieties the cuticle was plicate-striate round the superficial stomata and the leaf-hypodermis was one cell thick as in *F. arnottiana*. A new collection from southwest Thailand has a distinctly cordate leaf, as in *F. arnottiana*, from which it differs only in the subacute apex

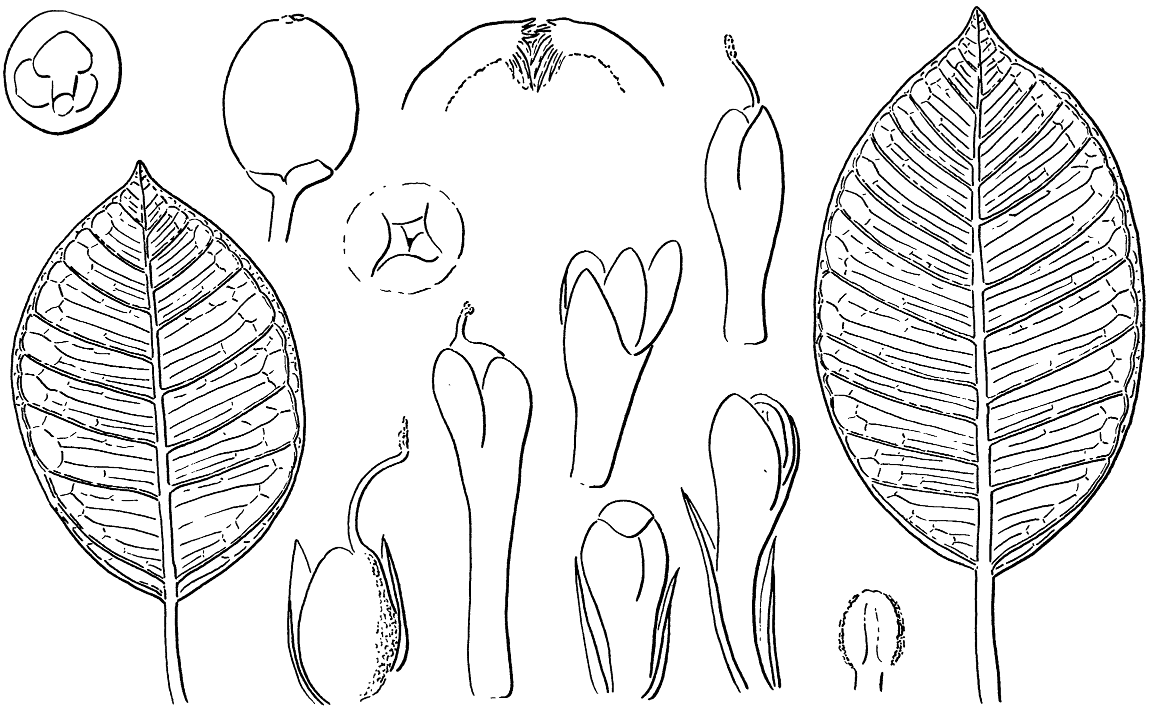

FIGURE 6. *Ficus balete*; leaves, magn. × ½; figs, magn. × 1; fig-orifice, magn. × 3; flowers, magn. × 10; from Bur. Sci. P.I. 22246, 31516, and Elmer 18266.

of the lamina (figure 1). This collection is K. and S. S. Larsen 33627 from a limestone range near the sea at Sam Roy Yot, Prachap Kiri Khan, 12° 15′ N 99° 55′ E; it was described as a tree 6–7 m high on the top of a limestone mountain *ca.* 300 m high. The dried specimen still showed the pink veins of the young leaf which are typical of *F. arnottiana* (Worthington 1959). When I reflect on the way in which *F. arnottiana* grows among huge boulders in arid places in Ceylon, an extension to limestone hills seems natural. This extension of the distribution of *F. arnottiana* fills also the central part of the extension of *F. glaberrima* var. *glaberrima* into northern India, and it leads me to suppose that var. *subcostata* may be found on the limestone hills of *Malaya*, to suppose, indeed, that it is a relic of a much more prosperous state before this ancient limestone plateau was depleted into ranges and hillocks. Thus, the extreme similarity between var. *subcostata* and var. *glaberrima* must be the result of convergent simplification. I note that typical *F. arnottiana* is pollinated by *Blastophaga arnottiana*, but the insects of *F. glaberrima* are not known (Wiebes 1966).

SUBSECT. *BENJAMINA* SER. *CALLOPHYLLEAE*

As mentioned, this group of sect. *Conosycea* introduces the lamina with pronounced basipetal growth along the midrib and with secondary lateral veins almost as strongly developed as the primary. There are no transverse intercostals apart from the initial which becomes displaced towards the margin through this basipetal growth. This venation is an advance on that of subsect. *Dictyoneuron*, but not so advanced as in *F. elastica* and sect. *Malvanthera*. There are two series, *Benjamineae* (3 species) with sessile figs and *Callophylleae* (11 species) with the pedunculate fig in *F. balete* and *F. microcarpa* var. *naumanni*. Thus ser. *Callophylleae* takes the progress of sect. *Conosycea* a step further, and it reveals the restricted range of the more primitive pedunculate species in contrast to the extended range of the advanced with sessile figs into a distribution that corresponds closely with that of *F. glaberrima* (figure 7). I will consider first the pedunculate species.

F. balete (figure 6) has a fairly robust fig with peduncle up to 12 mm long, large basal bracts 5–8 mm wide, and body up to 23 × 18 mm in dried specimens; it ripens yellow to red. The leaf-structure with deeply sunken stomata and smooth cuticle agrees with subsect. *Dictyoneuron*. The species occurs only in the northern half of the Philippines where, as a large strangler, it seems to be infrequent; I have seen 18 collections in herbaria. It fits with the geographical position of the ancestors of *F. depressa* and *F. glaberrima*. Its insects are not known.

F. microcarpa var. *naumanni* has a much smaller pedunculate fig, also ripening yellow to red, with small caducous basal bracts (Corner 1967). Other varieties of *F. microcarpa* have sessile figs with persistent basal bracts. That of var. *naumanni* resembles closely that of *F. glaberrima* var. *bracteata* and the distribution of both species is similar (figures 3 and 7). Indeed, without *F. balete* and *F. glaberrima* var. *glaberrima*, both var. *naumanni* and var. *bracteata* could be regarded as descendents from a common ancestor in New Guinea. *F. microcarpa* in its wide distribution has, however, other ancestral marks (figure 8). Var. *rigo*, of the neighbourhood of Port Moresby, has a larger fig, 10–15 mm wide; var. *latifolia* has a bigger leaf much as in *F. balete* (figure 10); var. *eubracteata* in Thailand has larger basal bracts 4–5 mm long and wide; var. *microcarpa* f. *pubescens* in Thailand and the Philippines (Surigao) has shortly, but closely, hairy twigs, stipules and figs; and var. *hillii* of Australasia has short basal veins. The precursor of *F. microcarpa* has left traces of a more robust and hairy ancestor with the venation of subsect. *Dictyoneuron*

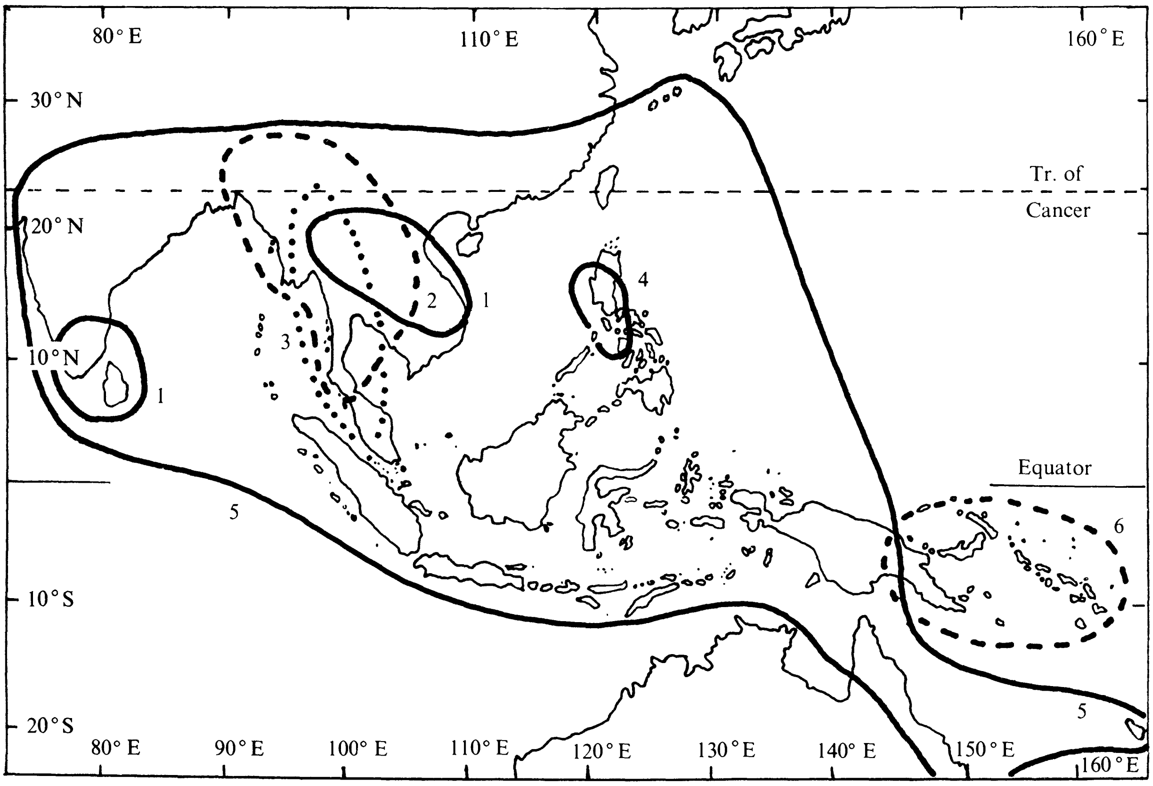

FIGURE 7. Distributions of: (1) *Ficus talboti*, south India and Indochina; (2) *F. malcellandi*, broken line; (3) *F. calcicola*, dotted line; (4) *F. balete*; (5) *F. microcarpa* var. *microcarpa*; and (6) var. *naumanni*, broken line.

from Thailand to the Solomons and New Caledonia over the whole broken range of *F. glaberrima*; in fact, the leptocaul *F. microcarpa* is spread over the whole range of sect. *Conosycea* and almost that of sect. *Urostigma* from north west India eastwards. The insects of var. *naumanni* are not known, but they should prove the botanical position of the variety; it was described originally as a distinct species.

There are two conflicting explanations of the range and diversity of *F. microcarpa*. One assumes that the pedunculate ancestor occupied the whole range and diversified vicariously into the modern variations. The other supposes an eastern origin about New Guinea and a westward dispersal. In favour of the first there is the instance of *F. annulata* with *F. chrysolepis* and *F. novoguineensis*, and to a lesser extent there is the case of *F. glaberrima* which may be in the process of disappearing from the central part of Malesia. In favour of the second there are several points. Most of the varieties occur in east Malesia. For the occurrence of var. *naumanni* in the Solomons I have indicated a southerly dispersal from the Melanesian Foreland along with other widespread species (Corner 1967), and the westward connection of this Foreland through the Philippines to Indochina carries many pedunculate species the issue of which may also have migrated southwards, as I shall show with *F. callophylla* and its allies. I note that *F. microcarpa* var. *saffordii* appears to have migrated northwards from this track. Then it is difficult to understand how the pedunculate ancestor with the range of modern *F. microcarpa* could have been converted over such a vast area into var. *microcarpa* without leaving traces other than var. *naumanni*. Var. *microcarpa* is, however, the most leptocaul state with small leaves and figs, the

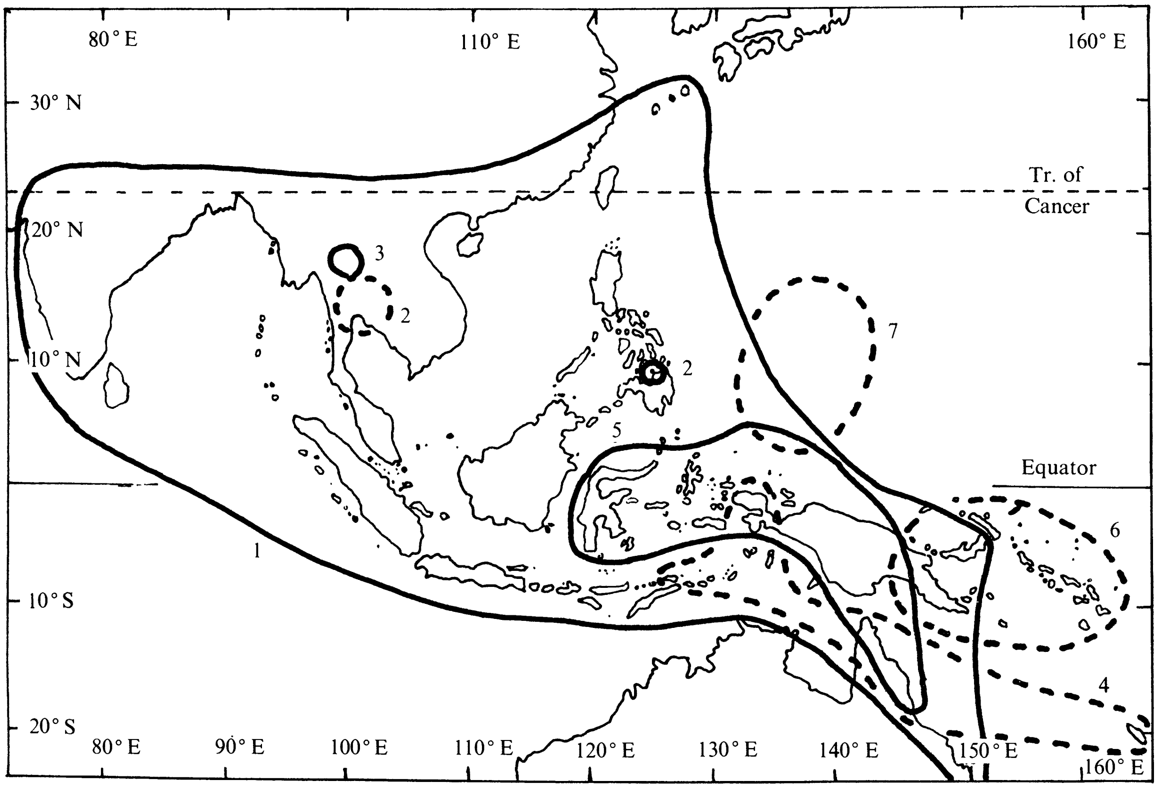

FIGURE 8. Distributions of the varieties of *Ficus microcarpa*; (1) var. *microcarpa*; (2) f. *pubescens*, Thailand and the Philippines; (3) var. *eubracteata*; (4) var. *hillii*, broken line; (5) var. *latifolia*; (6) var. *naumanni*, broken line; and (7) var. *saffordii*, broken line.

seeds of which would be most readily dispersed because small figs can be swallowed whole by the large number of small birds. The varieties seem to have no ecological preferences and the greater facility for dispersal seems the only explanation of the wide range of var. *microcarpa*. Then, sect. *Malvanthera* with many pedunculate species is centred on New Guinea and Australia to prove that there was an ancestral focus of evolution in this region. Hence I incline to an intermediate standpoint and see the ancestry of *F. microcarpa* in the eastern part of the Indochina–Philippines–Melanesian Foreland track, its diversification there into modern varieties, and their subsequent dispersal.

The nine other species of ser. *Callophylleae* map the Indomalesian region with customary precision (figure 9). They are a closely knit alliance with similar foliage in which the species differ mainly in details of fig and flower, to some extent in habitat. All but *F. curtipes* and *F. tristaniifolia* are large stranglers. The most widespread *F. callophylla* of west and central Malesia (figure 10) grows in the tidal freshwater reaches of rivers. It varies considerably in the size of the fig but it is not yet possible to assign geographical limits to these varieties. Var. *malayana* with the largest fig (15–20 mm wide) and the more massive construction appears to be restricted to the Asian mainland and Sumatra. Var. *minor* with the smallest fig (7–10 mm wide) and the more slender construction is known from Celebes and Sumbawa. Var. *callophylla* of intermediate size ranges widely from Hong Kong along the eastern border of the Asian mainland to Trengganu; then it appears in south Sumatra, Java, Borneo, the Philippines, and

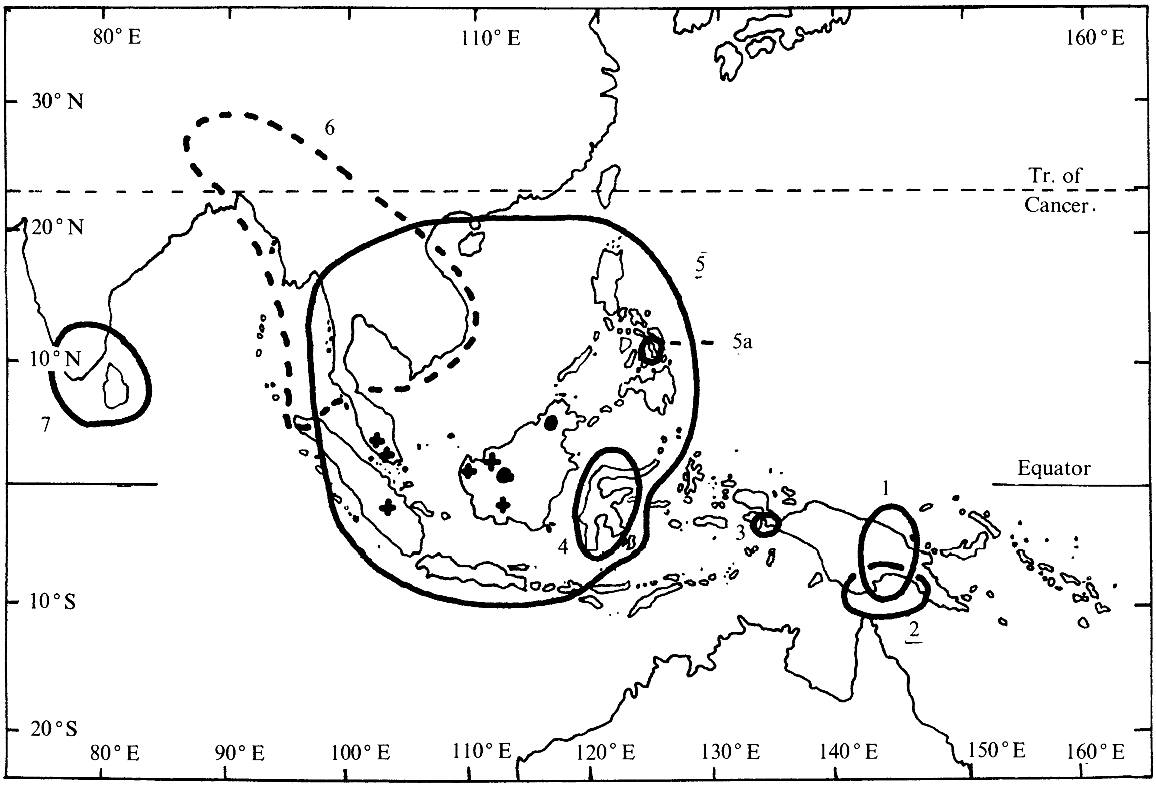

FIGURE 9. Distributions of ser. *Callophylleae* other than *F. balete* (figure 7) and *F. microcarpa* (figure 8). *F. archboldiana* (1); *F. benjaminoides* (2); *F. patellata* (3); *F. polygramma* (4); *F. callophylla* (5); *C. callophylla* var. *leytensis* (5*a*); *F. curtipes* (6); *F. trimenii* (7); *F. palaquiifolia* (black circles), and *F. tristaniifolia* (+).

Celebes. This association of space and form suggests the derivation of *F. callophylla* from an Indochinese source connected with that of *F. balete*. The figs of var. *callophylla* and var. *malayana* ripen bright pink to deep purple, without yellow or red; this difference seems to occur also in *F. microcarpa* for the figs of var. *microcarpa* ripen pink to purple and those of other varieties yellow to red, but there a few records of this striking field-character.

Close to *F. callophylla* comes the Indochinese *F. curtipes* with more narrowly obovate and obtuse lamina, short petiole, and depressed globose fig with thick woody wall, ripening yellow to red (figure 10). It overlaps the distribution of *F. callophylla* in Indochina and Thailand and has a station in the northern tip of Sumatra (Koorders 10584, Atjeh, Pulau Bras, on coral sand). As a species of monsoon forest, not riversides as *F. calophylla*, it is common along the foothills of the eastern Himalayas and on the limestone hills of Indochina, Thailand, and the Langkawi Islands which mark its sole occurrence in Malaya. Though commonly epiphytic, it seems not to become a large strangler or to kill its host. Its foliage is distinctly spiral-ascending without the applanate tendency of *F. callophylla*. It points also to an Indochinese ancestry but with so many differences from *F. callophylla* it is not a simple vicariant. To explain the distribution of *F. curipes*, Croizat (1968, p. 6) seems to imply a derivation from Madagascar or Gondwanaland without realizing that its ancestry is connected with that of *F. balete*. However, as I mention later under *F. talboti*, the Madagascan *F. menabeensis* may connect with this Indian species as a diversion, not a source, of the Indo-Malesian flora.

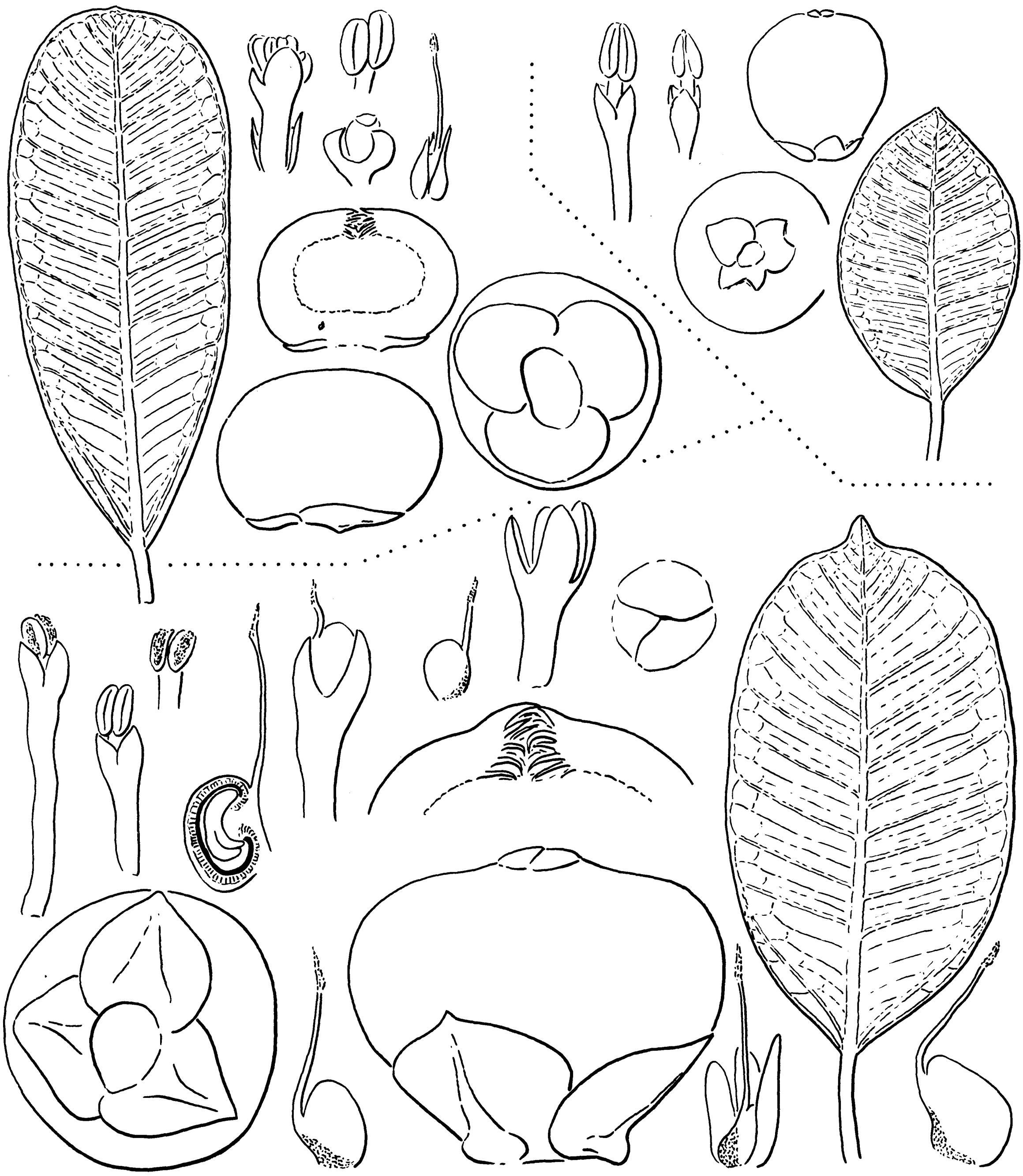

FIGURE 10. *Ficus callophylla* var. *malayana* (lower figure), *F. curtipes* (upper left), and *F. trimeni* (upper right). Leaves, magn. × ½; figs, magn. × 3; flowers, magn. × 10.

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F. tristaniifolia appears as a derivative of *F. callophylla* with very tough, spathulate leaves and small figs (figure 12). It is a rare epiphyte that does not attain any great size. It is known from six collections, all from the lowland peat-swamp forest, not the freshwater swamp-forest, around the Riouw pocket (figure 9). It may be regarded as an ecological vicariant of *F. callophylla* but there are numerous small differences. I have found it in the peat-swamp forests of south west Johore and Ridley found it in Malacca, but I never found it in the Sedili basin of east Johore where *F. callophylla* was common, and it has not been found in Singapore. Croizat (1968) uses *F. tristaniifolia* also to explain his idea of the emanation of the Indo-Malesian *Ficus* from Madagascar, but I cannot find any evidence; its arc of distribution, as given by Croizat in his fig. 1, has its focus in the China Sea or the Indochina-Philippines connection as one would expect from its alliance with *F. balete* and *F. callophylla*; it points, that is, to this particular region of Laurasia and not to Gondwanaland.

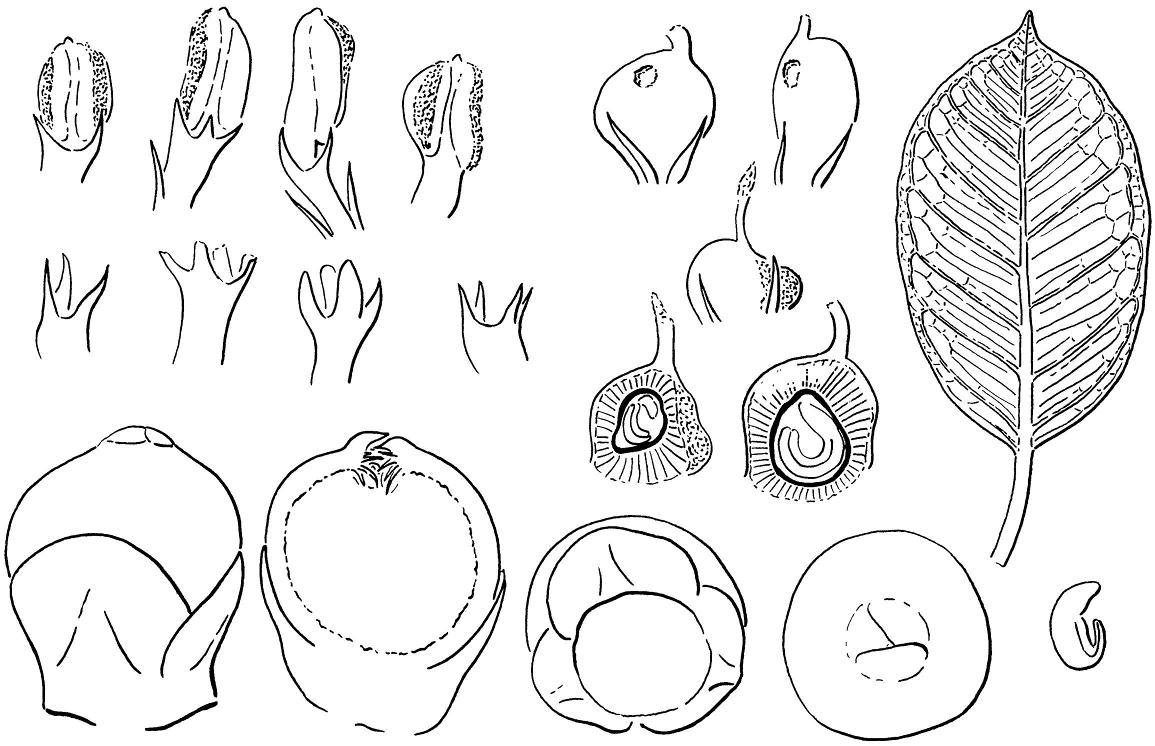

FIGURE 11. *Ficus palaquiifolia* (Singapore Field n. 26703). Leaf, magn. × ½; figs, magn. × 3; flowers and embryo, magn. × 10; two seed-flowers in section to show the thick sclerotic endocarp, one with the red pulpy tissue of the mesocarp.

F. callophylla, *F. curtipes*, and *F. tristaniifolia* agree in the strongly coriaceous, more or less obtuse, lamina often with elongate basal veins, and in the depressed globose fig. The other six species of the series have a thinner, acute to shortly acuminate, lamina without elongate basal veins. The fig is more or less pyriform in *F. trimeni* (Ceylon, south India) *F. palaquiifolia* (Borneo) and *F. polygramma* (Celebes) but in the three species from New Guinea it is shortly oblong in *F. archboldiana* and subglobose in *F. benjaminoides* and *F. patellata*. These are the almost trivial external distinctions revealed by herbarium-specimens, though there are specific details in the basal bracts, the flowers and the seeds.

Concerning *F. trimeni* (figure 10) little can be said. It is a rare species that I feared to be extinct save for the large old tree in the Royal Botanic Gardens at Peradeniya, but in 1974 a collection was made from a wild tree in the Monaragala district of Ceylon where it grew as a large strangler in remnant gallery-forest. Otherwise it has been recorded by one collection from south India (Canara) and by the original of Thwaites, namely n. 2220 collected at Kaduganawa and Ekiriankumburu, where it is now extinct. It seems to be a derivative of *F. callophylla* and to be comparable with its var. *minor* in Celebes.

F. palaquiifolia is another rare or very local species, known from two mountain ranges in Borneo. It may not be uncommon on Mt Kinabalu where I saw a few sterile trees, as large stranglers, on the east shoulder. It is a montane species at *ca.* 1200 m in high rain-forest and is, thus, far removed from the habitat of *F. callophylla*, *F. curtipes*, and *F. tristaniifolia*; these species show well the unpredictable diversity of *Ficus* and, in the rarity of several, there is the sign that many more may have existed. In detail, *F. palaquiifolia* has large basal bracts, a thin fig-wall, very narrow tepals, large anther, and thick-walled seeds which press into the thin wall of the dried figs, giving a rugulose appearance to them (figure 11). It may represent a particular line of descent from the ancestry of *F. balete*.

F. polygramma is known from three collections from Celebes where, as a montane species at *ca.* 1200 m, it seems to have been not uncommon as a counterpart to *F. palaquiifolia*. Both may be inhabitants of the *Trigonobalanus*-forest that occurs at this altitude in these two countries,

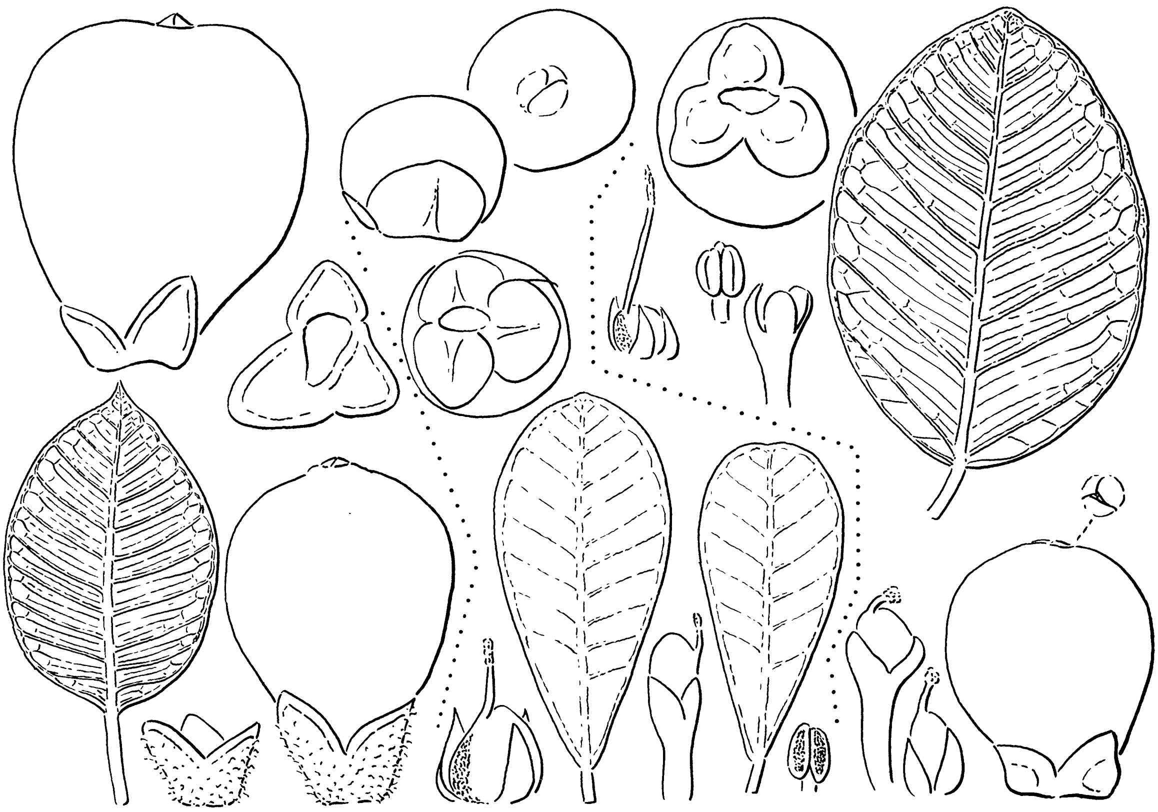

FIGURE 12. *Ficus polygramma* (left), *F. tristaniifolia* (centre, with thickly coriaceous obovate leaf), and *F. microcarpa* var. *latifolia* (right). Leaves, magn. × ½; figs, magn. × 3; flowers, magn. × 10.

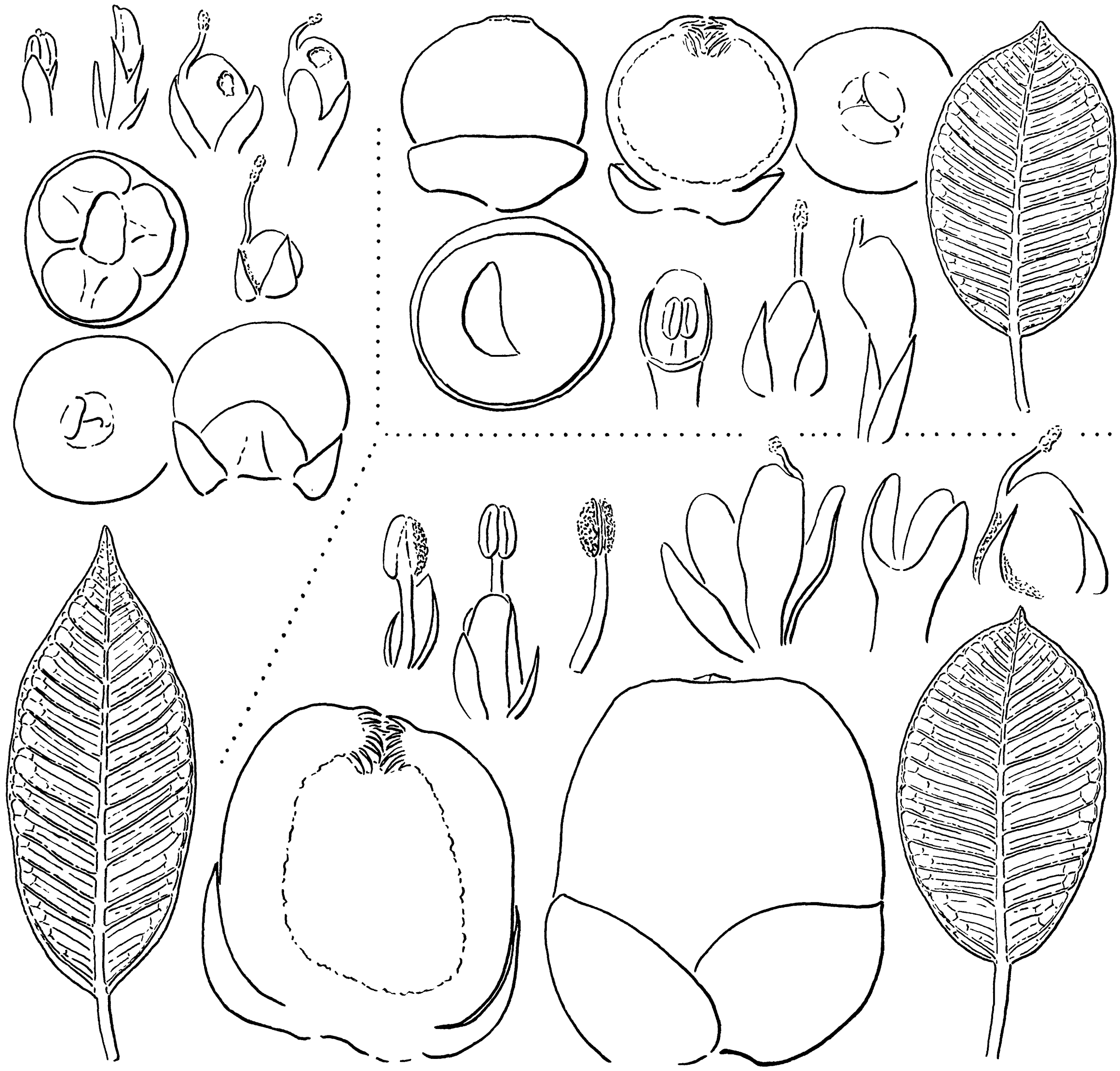

FIGURE 13. *Ficus benjaminoides* (left, Carr 12092), *F. patellata* (upper right, Aet 141), and *F. archboldiana* (lower right; Ledermann 8033a, leaf; Carr 12778, fig). Leaves, magn. × ½; figs, magn. × 3; flowers, magn. × 10.

but their differences are, again, too numerous to be taken as simple instances of vicariance (figure 12). I described, however, *F. callophylla* var. *leytensis* (Corner 1960) from the single specimen Wenzel 209 (Leyte), which had been named *F. pachyphylla* Merr, but this is a homonym of *F. pachyphylla* King (1887). It has the thick leaf of *F. callophylla* but a pyriform fig with the acute basal bracts of *F. polygramma*. Thus, *F. polygramma* may be a derivative of the ancestry of *F. callophylla* independent of that of *F. palaquiifolia*.

The three species of New Guinea appear to have no geographical connection with *F. balete* and *F. callophylla* but to relate, rather, to *F. microcarpa*, especially its var. *latifolia* the distribution of which embraces that of the New Guinea species (figure 12). *F. archboldiana* has a large fig with larger basal bracts than in *F. microcarpa*, such as would be expected in the ancestry of this species (figure 13). It is known from ten collections, but living trees still need comparison with

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var. *latifolia*. *F. patellata*, known from a single collection from McCluer Bay, Jakati (Aet 141), is remarkably distinct in the small fig with saucer-like collar made, apparently, from conjoint basal bracts (figure 13); thus it parallels *F. hookeriana* and could, superficially, be keyed out with it. *F. benjaminoides*, as the name implies, resembles *F. benjamina* (figure 13, to be compared with Corner 1967, figure 9), but the dark colour of the dried leaf and the conspicuous basal bracts ally it with *F. archboldiana* as a leptocaul derivative. It is known from four collections, one of which (Brass 5433, Papua, Central Division, Mafulu) gives it as a large spreading tree planted in villages at *ca.* 1200 m altitude.

It seems, therefore, that ser. *Callophylleae* has had three main lines of evolution, derived from the ancestry of *F. balete*. That in west Malesia and on the Asian mainland has led to *F. callophylla*, *F. curtipes*, *F. tristaniifolia*, and *F. trimeni*; that in central Malesia has led to *F. palquiifolia* and *F. polygramma*; and that in east Malesia has led to *F. archboldiana*, *F. microcarpa*, *F. benjaminoides*, and *F. patellata*. Their base-line, or original track, is the westward extension of the Melanesian Foreland to Laurasia, just as with ser. *Validae* and ser. *Glaberrimae*.

Ficus talboti, *F. maclellandi*, and *F. calcicola*

The absence from continental Asia of a pedunculate species closely allied with *F. microcarpa* has led me to investigate these three species. I placed them in subsect. *Dictyoneuron* ser. *Subvalidae* (Corner 1965). Their general similarity in leptocaul construction with small leaves and figs would pass for alliance with *F. microcarpa*, but they differ from it in details upon which one must rely where parallel simplification may have occurred.

F. talboti is a large strangler with the interrupted distribution between south India with Ceylon and Indochina (figure 7). It has the minute, if often sparse, internal bristles which distinguish *F. microcarpa* and a similar leaf-structure, but the stomata vary from almost superficial to more or less deeply sunken, and the lamina is more elongate with less basipetal growth along the midrib (figure 14). The figs seem generally to be sessile but in some collections they have a very short peduncle up to 1.5 mm long. It suggests a pedunculate ally of *F. microcarpa* in its western range, comparable with the eastern var. *naumanni*. However, the gall- and female flowers lack the red mark on the ovary which distinguishes sect. *Conosycea*, and the cystoliths are absent from the lower side of the lamina or very sparse. White ovaries and hypergenous cystoliths distinguish sect. *Leucogyne* which consists of *F. amplissima* (better known as *F. tsiela*) and *F. rumphii*, but they lack internal bristles. The Indian distribution of *F. talboti* fits that of *F. amplissima* which is in Ceylon, central and south India, and the Maldive Islands, but also in the Lushai Hills of Assam; the Indochinese distribution of *F. talboti* fits that of *F. rumphii*.

Cognate with this problem there is that of *F. menabeensis*, which has the distinction of being the only species of sect. *Conosycea* in Madagascar (Léandri 1952). It is said to be a rare evergreen tree up to 15 m high; there is no mention of the strangling habit but there is a suggestion of it on one specimen in the Paris herbarium, for it has slender aerial roots from the twigs. The small fig is sessile with small basal bracts and without internal bristles, but the ovaries lack the red mark, the cystoliths are amphigenous, and the stomata are deeply sunken (superficial in sect. *Leucogyne*). Although *F. menabeensis* has no close allies in Madagascar or other islands of the west Indian Ocean there are instances of other kinds of *Ficus* in these islands which are clearly allied with species of the Asian mainland and Malesia. First, *F. densifolia* Miq., in sect. *Urostigma*, occurs in Réunion and Mauritius and is allied with *F. saxophila* (Indochina to New Guinea)

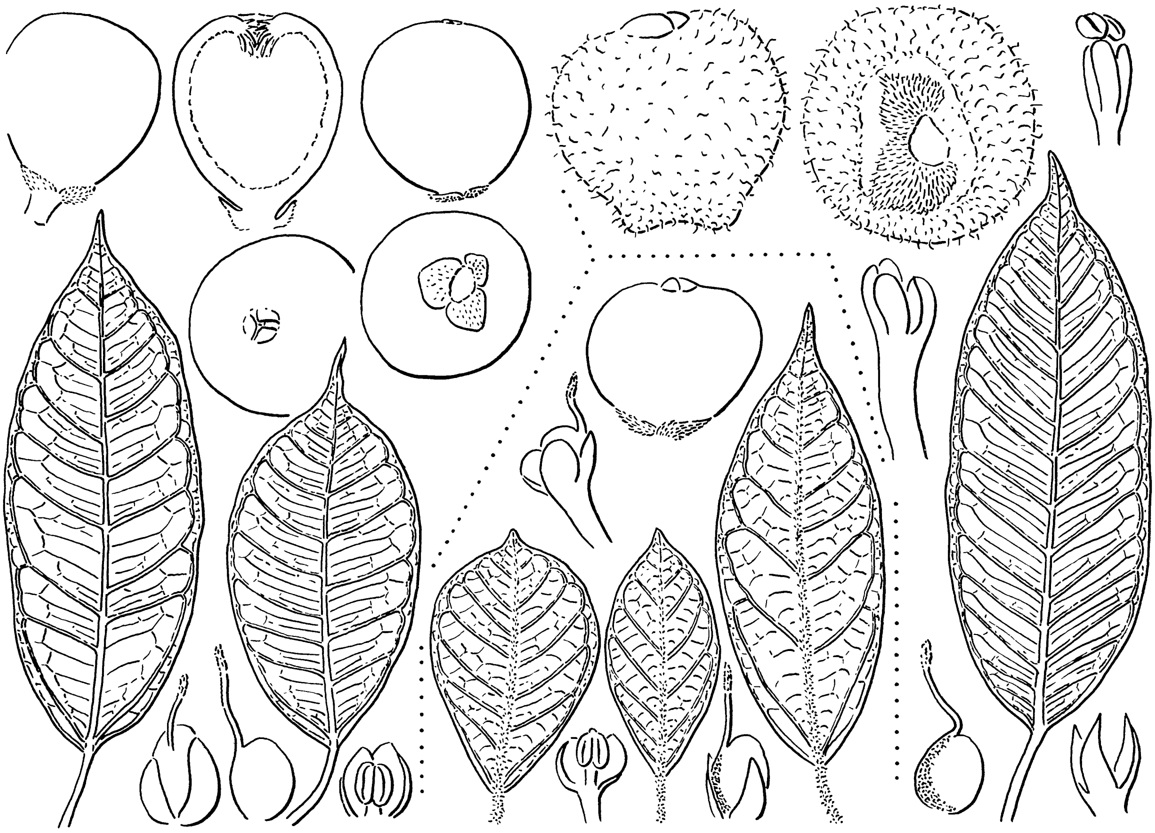

FIGURE 14. *Ficus talboti* (left), *F. calcicola* (centre), and *F. maclellandi* (right). Leaves, magn. × ½; figs, magn. × 3; flowers, magn. × 10.

which is close to *F. religiosa*. Secondly, in subgen. *Pharmacosycea*, *F. assimilis* Bak. of Madagascar is very close to the widespread *F. albipila* (Thailand to New Guinea), and the African *F. dicranostyla* Mildbr. relates with *F. capillipes* (Indochina, Thailand, Andaman Islands), as I have pointed out in a previous article (Corner 1970*b*). Thirdly, in sect. *Sycidium* of subgen. *Ficus*, the four species which occur in Madagascar, Seychelles, and Réunion relate with the insular Malesian and Australasian ser. *Scabrae* in the neighbourhood of *F. opposita*, which is by no means a primitive species of *Sycidium*. If, therefore, *F. menabeensis* is allied with *F. talboti*, it shows along with these other examples that the islands of the west Indian Ocean, perhaps during the northward surge of the bits of Gondwanaland, have received species of *Ficus* from Asia and Malesia, but have not provided them as the theory of the Gondwanaland origin of *Ficus* would suppose. I note that the very widespread coastal stranglers of Asia, such as *F. superba*, *F. virens*, *F. microcarpa*, and *F. tinctoria*, do not extend to this western part of the Indian Ocean.

The distribution of *F. maclellandi* fits that of *F. talboti* in Burma, Indochina, and Thailand, though it extends further south to Kedah Peak in north Malaya. It is also a large strangler so similar in general appearance to *F. talboti* that close affinity would be expected if it were not for details (figure 14). The ovaries of gall- and female flowers have the red mark of sect. *Conosycea*; the cystoliths are amphigenous; the stomata are sunken. It has no features to separate it from ser. *Subvalidae* unless the loose tomentum of the young shoots, but this might be a relic of the ancestry of the series, as of any glabrescent series in *Urostigma*. If the details of the ovary

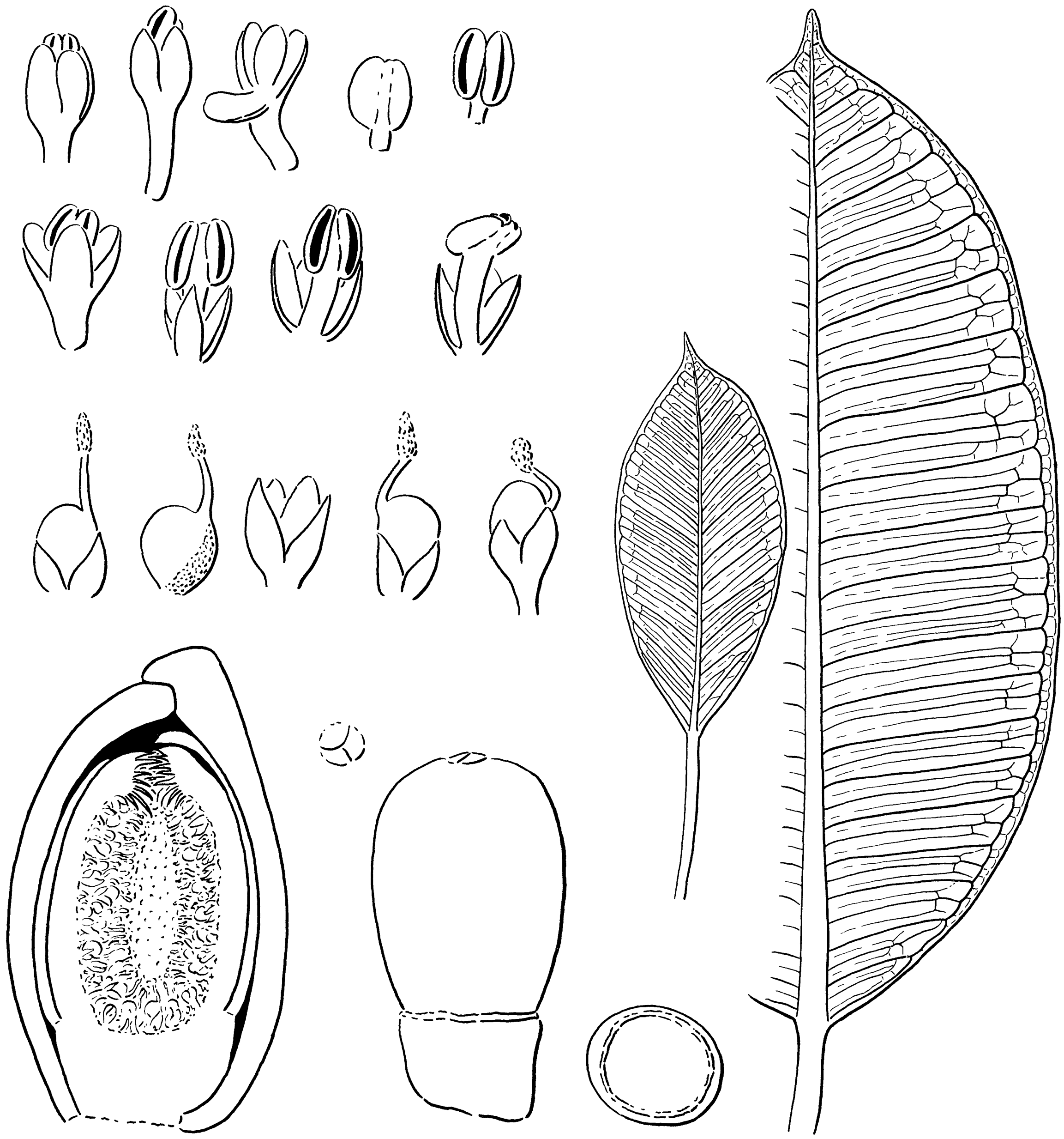

FIGURE 15. *Ficus elastica*. Sapling and adult leaves, magn. × ½; mature fig, with the orifice and the apex of the peduncle in end-view, magn. × 3; young fig in section, enclosed by the stipular bract and basal bracts, magn. × 10; male flowers (upper row, SFN 21187; lower row, Brass 641), and seed-flowers, magn. × 10.

and the structure of the lamina are reliable, then similarity with *F. talboti* must be a matter of convergence.

F. calcicola occurs on the limestone hills of Burma, Thailand, and Malaya. It is a small strangler but it can also be an independent bush or small tree. It has been confused with *F. microcarpa*, which may also be dwarfed where it occurs on the limestone, but the venation of the leaf in *F. calcicola* has distinct remnants of transverse intercostals (figure 14); it is also brownish hairy on the twigs, stipules, petioles, underside of the midrib, and the basal bracts. Unlike the aseptate hairs of *F. maclellandi*, however, those of *F. calcicola* are closely septate. This is such an exceptional feature for *Urostigma* in Asia, as it is for *Ficus* in general, though septate hairs are characteristic of the climbers of sect. *Kalosyce* and sect. *Rhizocladus*, that it renders the alliance of *F. calcicola* perplexing. Peculiar hairs occur in the stranglers *F. bracteata* and *F. consociata*, where they are twinned throughout their considerable length without being septate; in *F. retusa* they are irregularly stellate or lobulate; at present, one can merely record these strange deviations. I conclude that *F. calcicola*, of unknown ancestry, is another example of convergent leptocaul simplification: it could be placed in subser. *Crassirameae* of ser. *Drupaceae*. When the insects of all these problematical species of *Ficus* are known, the entomology may straighten the botanical tangle.

Ficus elastica

Though so well known in cultivation, the botany of this species is as puzzling as that of *F. glaberrima*. It is the only member of sect. *Stilpnophyllum* and it is the western part of the same broken distribution which, in this case, has sect. *Malvanthera* at the eastern end. King (1887) summarized the distribution of *F. elastica* as a strangling fig in damp forest at the base of the eastern Himalayas, the Khasi Hills, Assam, Burma, and the Malayan region. It is not continuous, however, and no one knows how much of it remains. Originally, Roxburgh wrote that *F. elastica* was common in the mountains of Assam, in chasms and on fallen rocks; it has not been reported in recent years. Then Kurz wrote that whole forests of *F. elastica* were said to exist in the Hookhown valley in east central Burma. Kingdon-Ward (1944) mentions it as a strangling fig in the evergreen forest near Myitkyina, but there is no mention of it in any recent accounts of the forests of Burma. For Java, Blume gave the habitat as limestone hills, and this is confirmed by later collections. Then there are two records of apparently wild trees, epiphytic in the forest, from south Sumatra (Gusdorf 299, Lampong, and Grashoff 488, Palembang). There are two records from limestone hills in Malaya (Curtis 3305, Ipoh, Perak, and Corner s.n. 1941, Gunong Baling, south Kedah). Certainly *F. elastica* does not occur in the general lowland forest of Malaya and Sumatra, and there are no records of wild trees from Thailand and Indochina. Yet this large and vigorous tree thrives in cultivation under very varied conditions. It was introduced into many tropical countries as a source of rubber and it is one of the commoner species of *Ficus* to be grown as a pot-plant (Condit 1969). All these introductions, however, are sterile for want of the pollinating insect (Hill 1967). Geographically and systematically *F. elastica* is a relic.

In the long stipule, the pronounced basipetal intercostal veining, the xerophytic construction of the lamina with thick hypodermis (2–3 cells) and deeply sunken stomata, and the thick if short, fig-peduncle with early caducous basal bracts (shed within the conical bud-scale), *F. elastica* agrees with typical species of sect. *Malvanthera*; it differs in two important details. The stamen dehisces normally, not in the hoop-like manner of sect. *Malvanthera* (figure 15; Corner 1967, figure 10). The pollinating insect, described from Java, is *Blastophaga clavigera* Mayr and not the peculiar genus *Pleistodontes* which pollinates species of *Malvanthera* (Wiebes 1966). Then, geographically, there is the wide gap in central Malesia which separates the two. Sect. *Malvanthera* extends from south east Celebes and Soemba to Tonga and Samoa with its main development in New Guinea (9 species) and Australia (12 species). Between them lies the pedunculate *F. balete* with stamens and stigma of sect. *Conosycea*, as in *F. elastica*, but not so advanced in leaf-construction.

To explain this taxonomic affinity it is necessary to make the following postulates: (1) there was an ancestral pedunculate stock with bifid stigma, normal anther, and *Blastophaga*; (2) that it occupied the Indochina-Philippines-New Guinea track; (3) that it gave rise to ser. *Callophylleae* before it advanced in leaf-structure to sect. *Stilpnophyllum* and, finally, sect. *Malvanthera* with *Pleistodontes*; (4) that it has left as relics *F. orthoneura* (bifid stigma) and *F. elastica* in the west and *F. balete* in the centre; and (5) that it is best represented in the east where sect. *Malvanthera* has been isolated. In confirmation of this vigorous eastern centre of evolution it should be noted that sect. *Malvanthera* has no endemic species outside of New Guinea and Australia and that only its more leptocaul species have spread, namely *F. glandifera* (southeast Celebes to New Hebrides), *F. obliqua* (south east Celebes and Timor to the Pacific Islands), *F. platypoda* (Soemba, Flores, Key Islands, Australia), and *F. xylosycia* var. *cylindocarpa* (New Guinea, Solomons). This eastern centre supports the conclusion that *F. glaberrima* and *F. microcarpa* evolved there also; inasmuch as they are less advanced than sect. *Malvanthera*, it seems that they had an earlier origin and were able to spread west of Celebes, possibly in the way that the even less advanced *F. annulata* spread eastwards to New Guinea.

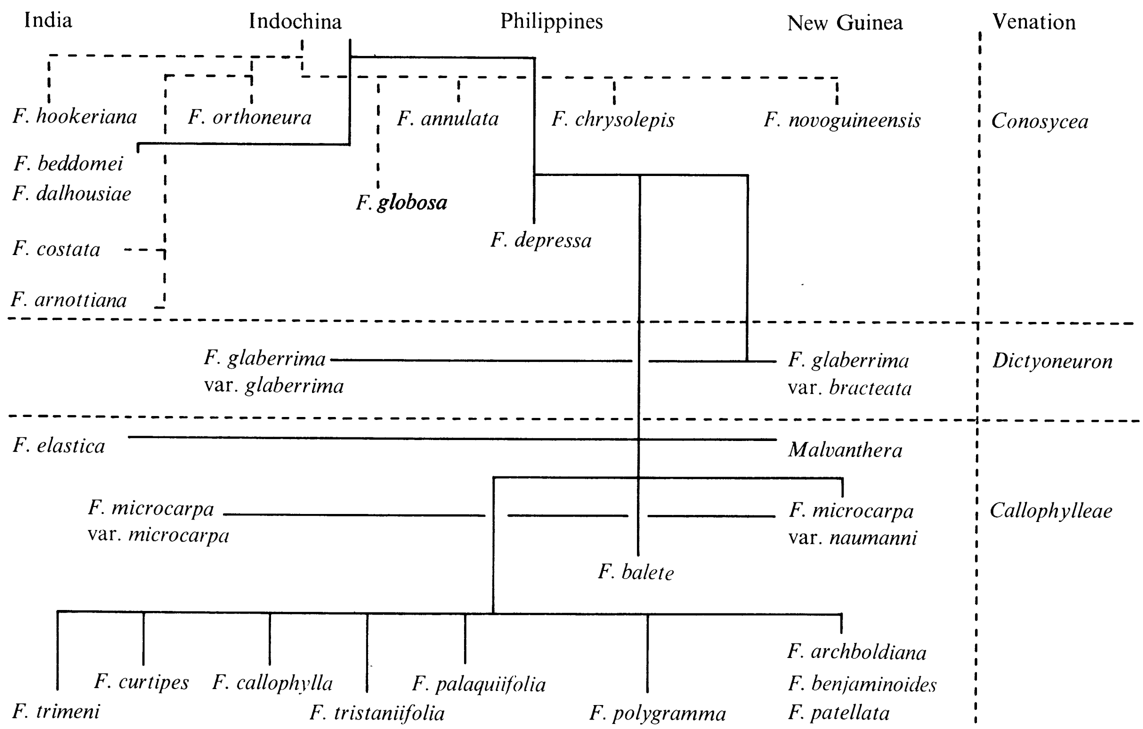

FIGURE 16. Scheme to show on geographical and morphological grounds the apparent evolutionary connections of the pedunculate species of *Ficus* subgen. *Urostigma* (excluding sect. *Urostigma*), the species of ser. *Callophylleae*, *F. elastica*, and sect. *Malvanthera*. Species with the gyrose-plicate cuticle shown by broken lines. Venation indicated by the subsectional and serial names on the right.

CONCLUSION

The outcome of this enquiry is displayed in figure 16, where geographical occurrence is plotted against venation as the chief mark of evolution. Thus *Conosycea* refers to venation with intercostals, *Dictyoneuron* to venation without intercostals, and *Callophylleae* to venation with strong basipetal growth along the midrib. The scheme is far from perfect because many other factors have been omitted. It is based on the ancestral track from Indochina through the Philippines to New Guinea followed by specific evolution into the southern territories and latitudinal dispersal. The test will come when the insects of these strangling figs have been collected and the entomology can be compared.

This track has also been inferred for subgen. *Pharmacosycea* (Corner 1970*b*) and, in the case of subgen. *Ficus*, for ser. *Scabrae* of sect. *Sycidium* (Corner 1967), for sect. *Kalosyce* and sect. *Rhizocladus* (Corner 1976), and for *F. pedunculosa* in sect. *Ficus* (Corner 1958). When given evolutionary sequence according to morphological criteria, *Urostigma* and *Pharmacosycea* are among the older groups of *Ficus*, the others among the later. It seems, therefore, that *Ficus* must have differentiated into its main groups before this track became available, Then, since *Ficus* is one of the most advanced products of Moraceae, this track was available to the primitive *Streblus*, the remnants of which are strung along it (Corner 1975), and to such widespread genera as *Artocarpus*, *Maclura*, and *Antiaris* (Corner 1962). *Pharmacosycea*, *Scabrae*, and *Antiaris* have followed the track westwards, as *F. glaberrima* and *F. microcarpa* seem to have done, but *Urostigma* in the main and *F. pedunculosa* have travelled eastwards, as *F. annulata* seems to have done, while *Kalosyce* and *Rhizocladus* have differentiated all along it, as ser. *Callophylleae* has done. There is, yet, no explanation of this track in the geological reconstruction of Malesia, and I put forward the evidence for it from the large and diversified *Ficus* because biogeography needs to be studied by means of the evolution of explicit genera.

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