The Climbing Species of Ficus: Derivation and Evolution

E. J. H. Corner

Phil. Trans. R. Soc. Lond. B 1976 **273**, 359-386
doi: 10.1098/rstb.1976.0021

THE CLIMBING SPECIES OF *FICUS*: DERIVATION AND EVOLUTION

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

(*Received* 19 *June* 1975)

CONTENTS

Climbers have arisen independently in three groups of *Ficus*. They have specialized leptocaul progress in two ways. The strangling habit has been modified into epiphytic climbing in subgen. *Urostigma* (5 spp. of climber) and subgen. *Ficus* sect. *Sycidium* subsect. *Palaeomorphe* (4 spp. of climber). The systematic origin of these nine species is fairly clear. *F. subulata* is a stoloniferous climber building epiphytic thickets. In contrast, ground-based root-climbing with the evolution of bathyphylls distinguishes the whole of subgen. *Ficus* sect. *Rhizocladus* (57 spp.) and sect. *Kalosyce* (20 spp.). Their origin is not clear. The more pachycaul Bornean *F. spiralis* suggests derivation from the ancestry of sect. *Ficus* ser. *Cariceae* and ser. *Podosyceae* by modification of the pachycaul tree. Stranglers apart, fig-climbers appear to be an Indo-Malesian distinction. *F. rhopalosycia* Diels is redescribed.

INTRODUCTION

The purpose of this account is to provide new evidence for the general theory of angiosperm evolution from pachycaul to leptocaul vegetation. It is a story of the forests of tropical Asia and Australasia where, among nearly 500 species of *Ficus*, there are about 86 species of climbers derived in part from the stranglers of subgen. *Urostigma* and subsect. *Palaeomorphe* of sect. *Sycidium*, and in the main from trees or shrubs of sect. *Ficus*. Most are leptocaul species, few retaining traces of pachycaul ancestry, and many have developed in the long run such small leaves and figs that outwardly they appear alike, and details of flowers and seeds are necessary for their correct classification. I have introduced, therefore, much detail both as proof and as a guide to others who may pursue this study where there is still so much to be discovered. I have omitted the strangling habit except where in juvenile form it has led to the epiphytic climbers.

[Published 5 February 1976

The origin of the banyan or strangler is a problem of early pachycaul forest; that of the root-climbers, which excel in abundance and variety, is a problem of the lofty forest up the trunks of which they ascend. Structure and distribution confirm this distinction. There are no such climbers, apparently, among the fig-species of Africa and America. Only *F. subulata* retains the primitive mark of lateral bracts on the fig; small and inconspicuous though they are, the one or two vestigial scales are a great help in identification.

It is often assumed, though seldom proven, that climbers are derived from trees and shrubs. The abundance of *Ficus* supplies the pachycaul answer. The theory of pachycauly receives little recognition, largely through unfamiliarity with these tropical plants. I refer, therefore, with pleasure to four recent accounts of the tree-senecios and the tree-lobelias where the primitiveness of pachycauly has been established (Mabberley 1973, 1974, 1975). I expect that the climbers of *Senecio* and *Lobelia*, and those of *Solanum*, *Bauhinia*, and *Schefflera*, will supply the evidence of the leptocaul trend as in *Ficus*.

CLIMBERS OF SUBGEN. *UROSTIGMA*

This subgenus consists in Asia and Australasia of 96 species of strangling figs and 5 species of rather slender climbers limited to the lowland forests of southeast Asia. The climbers belong in three alliances, namely ser. *Validae* with *F. depressa* and *F. globosa*, ser. *Perforatae* with *F. acamptophylla* and *F. microsyce*. and ser. *Drupaceae* subser. *Crassirameae* with *F. paracamptophylla*. By comparison with the stranglers to which they are allied, the climbers have thinner primary twigs, smaller leaves, and simpler venation. Similar leptocaul derivatives occur among the stranglers in most of the 22 series or subseries into which they can be classified. As examples, I cite the following seven pairs of relatively pachycaul and truly leptocaul species, the primary thickness of the twig being indicated in brackets

ser. *Superbae: F. superba* (7–12 mm), *F. concinna* (1–2 mm).
ser. *Drupaceae*
subser. *Crassirameae: F. stupenda* (10–12 mm), *F. subgelderi* (3–5 mm).
subser. *Indicae: F. altissima* (5–7 mm), *F. kerkhovenii* (3–4 mm).
ser. *Subvalidae: F. sundaica* (3–5 mm), *F. delosyce* (1.5–3 mm).
ser. *Benjamineae: F. subcordata* (3–4 mm), *F. benjamina* (1–2 mm).
ser. *Calophylleae: F. calophylla* (4–6 mm), *F. microcarpa* (2–3 mm).
ser. *Malvanthereae: F. hesperidiiformis* (7–10 mm), *F. xylosycia* (3–6 mm).

The leptocaul construction does not diminish the size of the whole strangler for *F. kerkhovenii*, *F. delosyce*, *F. benjamina*, and *F. microcarpa* become immense. Thus it is remarkable (1) that the lepotcaul habit should have led in so few cases to climbers, and (2) that these climbers should themselves be plants of relatively small bulk.

So far as I have observed without intent study, these climbers begin as epiphytes in the manner of stranglers, but not so high on the host-trees. They prefer the lower parts of the forest, short secondary forest, or the verge of riverside or coastal forest; some, nevertheless, may establish themselves on wet rocks. The seedling stem lengthens and branches, and sooner or later slender adventitious roots descend from the nodes and reach the ground. The branches flop on to the surrounding vegetation and attach themselves by adventitious roots. Only a few long slender roots 1–3 mm thick develop from a node; they do not thicken and anastomose as the cables or root-trunk of the strangler, and no strangling part develops from the main root. Nevertheless, tangles of these slender roots develop in rotting logs and branches which may thus be suspended

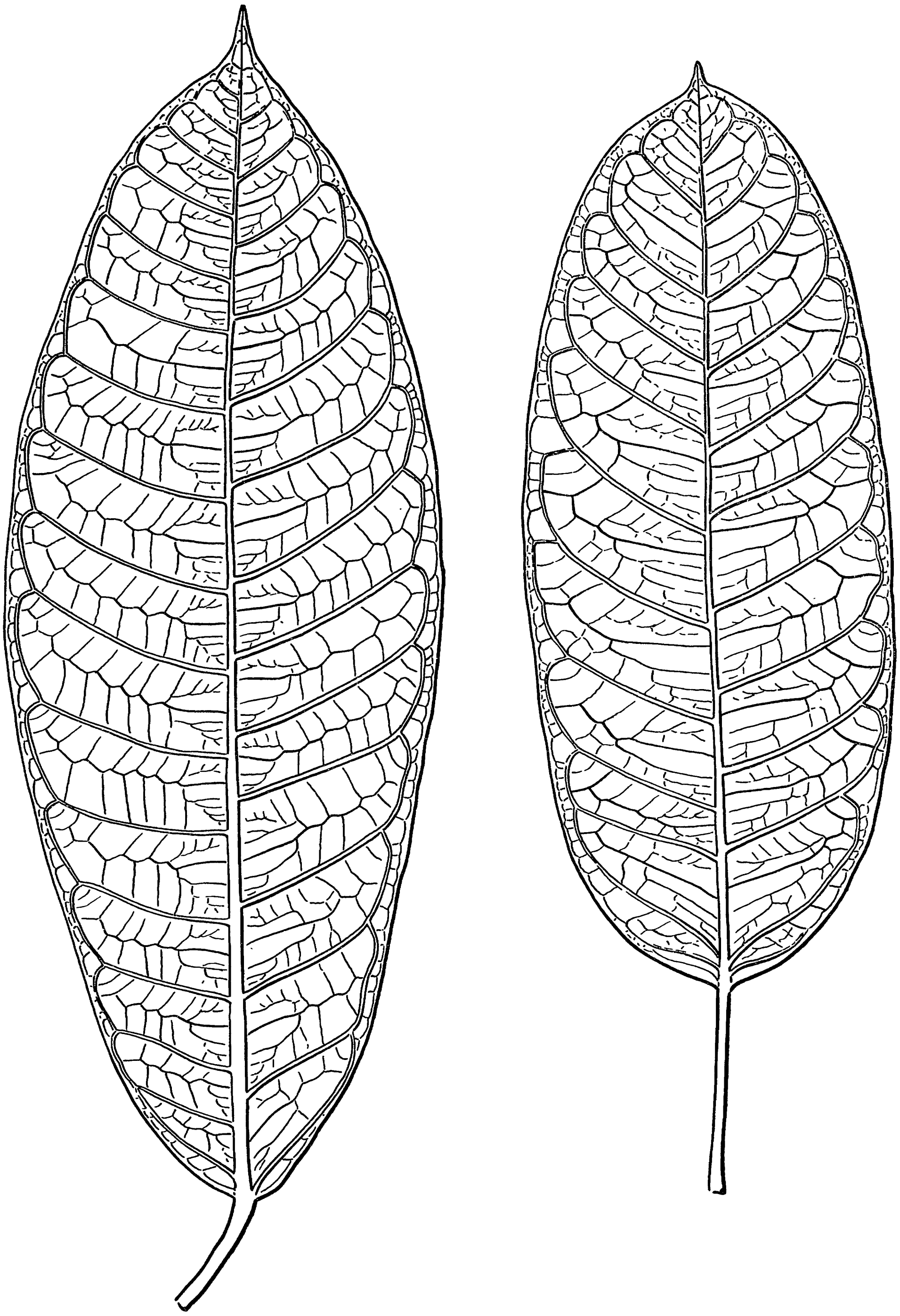

FIGURE 1. *Ficus annulata* (left) with *ca.* 15 pairs of lateral veins, the lamina developed mostly by transverse intercostals intercalated submarginally, the cascade-veins restricted to a narrow strip along the midrib. *F. globosa* (right) with *ca.* 10 pairs of lateral veins, the intercostal areas developed mainly basipetally with extended cascade-veins. (Half natural size.)

in the air. Exact details are not known and we need a thorough study of these climbers which seem to have been overlooked by systematist and ecologist. *F. depressa* may reach 30 m long, probably more, and *F. acamptophylla* may festoon tall trees along the smaller rocky rivers of Sarawak and Brunei. *F. globosa* is found in more exposed thickets, but *F. microsyce* is a small epiphyte of forest undergrowth. *F. paracamptophylla* is the more pachycaul; it seems to branch little and to reach no great length.

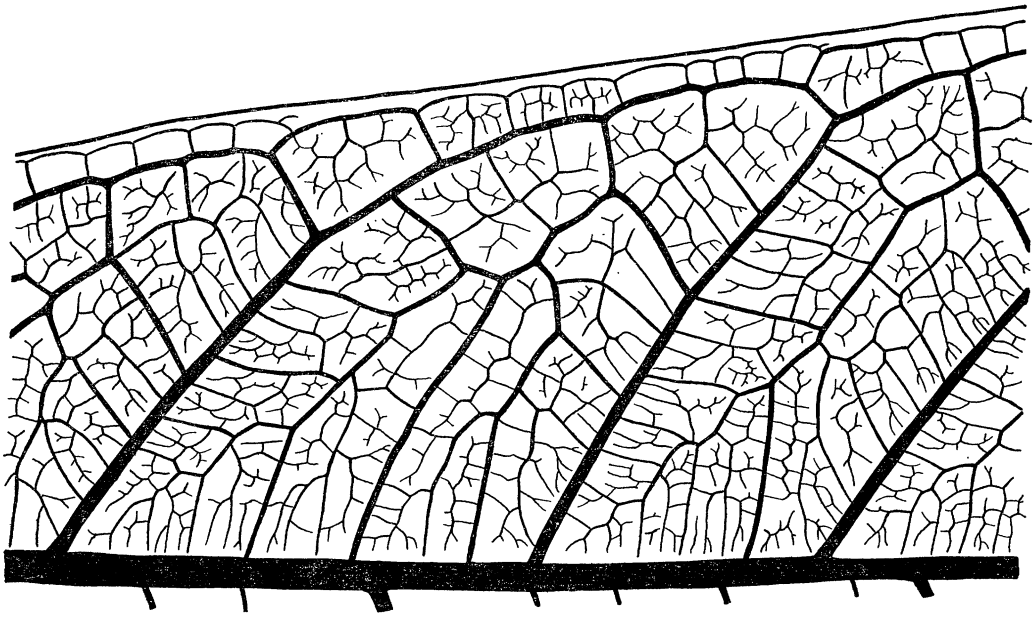

FIGURE 2. *Ficus globosa*, an intercostal area developed mainly by basipetal extension with an elongate cascade-vein. (Magn. × 3.)

The contrast with stranglers is considerable. Adventitious roots do not develop from the branches of most stranglers though these plants can readily be propagated from cuttings or loppings which then root adventitiously. A few stranglers normally develop such roots from the branches and they can become the pillar-roots or prop-roots that anastomose as secondary root-trunks; such are the great banyan *F. benghalensis*, *F. microcarpa*, *F. kurzii*, and some individuals of *F. benjamina* and *F. elastica*. *F. altissima* and *F. subcordata* may have this tendency at the base of some main branches. However no strangler has the almost hair-like festoons of slender roots from all the branches in the manner of the climbers, and none of these prop-rooting banyans belong to the alliances of the climbers. There must be a profound difference between the two habits which will explain the comparative rareness of climbing species in *Urostigma*. The internal structure of the aerial roots needs investigation for comparison with those of *F. benghalensis* (Kapil & Rustagi 1966), and *F. benjamina* (Zimmermann, Wardrop & Tomlinson 1968). The article on root-grafts in *F. globosa* (Rao 1966) seems not to refer to that species.

In ser. *Validae*, *F. depressa* and *F. globosa* are leptocaul versions of their stout ally *F. annulata*. Thus, *F. annulata* is a medium-sized strangler (apparently not destructive of its host) with twigs 6–10 mm thick and lamina with 12–17 pairs of lateral veins strutted with 4–9 intercostals (figure 1). *F. depressa* has twigs 2–5 mm thick and 7–11 pairs of lateral veins with 1–4 intercostals. *F. globosa* has twigs 4–7 mm thick and 6–12 pairs of lateral veins between which the

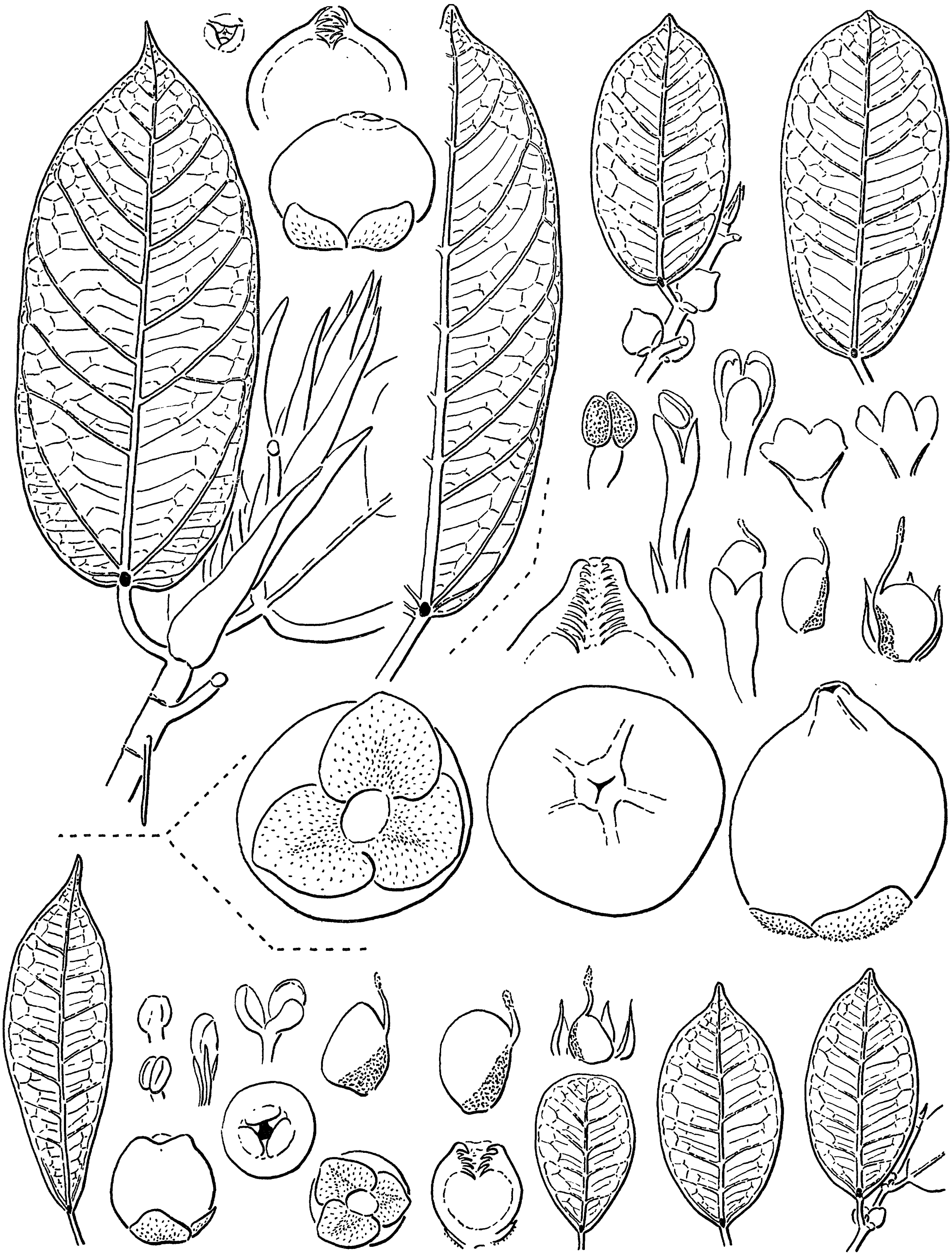

FIGURE 3. *Ficus paracamptophylla* (upper left); figs, magn. × 2. *F. acamptophylla* (upper right), figs, magn × 3. *F. microsyce* (lower line) with an acuminate bathyphyll leaf on the left; figs × 3. Leaves and twigs half natural size; flowers magn. × 10, with the red patch on the ovary stippled.

intercostals are scarcely developed but the cascade vein is prolonged by basipetal growth (figures 1 and 2). The figs of all three are distinctive, and *F. globosa* has a brown scurfiness on the young parts which the others lack. *F. depressa* resembles *F. annulata* so closely in leaf and twig that the two have often been mistaken in the herbarium, though their habits in the forest are so different, and microscopic study is nearly always required for verification of sterile specimens. The cuticle on the lower side of the leaf of *F. annulata* has countless short gyrose plications which may even conceal the stomata; they are absent from *F. depressa*. In *F. globosa* they occur only in a narrow zone round every stoma. Now *F. annulata*, in my recollection, may develop adventitious roots on the lower parts of its main branches near the trunk of the host-tree and, thus, may be physiologically at the outset of becoming a climber.

The three other climbers of *Urostigma* (figure 3) belong in a different alliance which is shown also by the presence of a lower hypodermis (one cell thick) in the leaf and the sunken stomata; ser. *Validae* has no such hypodermis and the stomata are superficial. The leaves are stiffly coriaceous and in *F. acamptophylla* and *F. microsyce* the venation is obscure. I have placed these two in ser. *Perforatea* because of the perforate orifice of the fig. *F. microsyce* is near to other members of the series, namely *F. pellucidopunctata*, *F. pisocarpa*, and the leptocaul *F. binnendijkii*, but *F. acamptophylla* with more oblique lateral veins and often acute apex to the dried fig bears such a resemblance to *F. paracamtophylla* (sect. *Conosycea* subser. *Crassirameae*) that, until I had studied both as they grow in Sarawak, I thought that *F. paracamptophylla* might be the sapling of *F. acamptophylla*. That is wrong. *F. paracamptophylla* has stout twigs 5–9 mm thick, large persistent stipules up to 80 mm × 20 mm and often tenanted by ants, a large lamina with 6–9 pairs of lateral veins and 1–4 intercostals, and an imperforate fig. *F. acamptophylla* has twigs 2.5–4 mm thick, short caducous stipules up to 20 mm long, smaller lamina with the same number of lateral veins but without intercostals, and smaller perforate figs. I saw no instance among the living plants either that the upper branches of *F. paracamptophylla* attenuated into those of *F. acamptophylla*, or that young plants of *F. acamptophylla* had the character of *F. paracamptophylla*. Now this species fits closely in subser. *Crassirameae* with eight others of which *F. stupenda* (listed above) is the most pachycaul example. I have no doubt that *F. paracamptophylla* and *F. acamptophylla* are climbers derived from the stock of *F. stupenda* whereas *F. microsyce* comes from the stock of subsect. *Dictyoneuron* and, in particular, ser. *Subvalidae*. *F. microsyce* retains the xerophytic leaf of the stranglers even in the undergrowth of the rain-forest.

I conclude that the five species of climber in *Urostigma* have evolved in parallel from three sources in the subgenus. They represent an ultimate leptocaul specialization which may have arisen neotenically through persistence of the slender seedling-sapling construction of the ancestral strangler. Support for this conclusion comes from geographical distribution. That of the climbers falls within the ambit of their more pachycaul and allied stranglers; there is no evidence for vicariism because strangler and climber are different modes of life in the same forest. There are 34 species in all for consideration, 9 in ser. *Validae*, 9 in subser. *Crassirameae*, 10 in ser. *Subvalidae*, and 6 in ser. *Perforatae*. With three exceptions all lie in Indo-Malaysia, that is western Malesia with India, Yunnan, the Philippines, and Celebes as the limits. The exceptions are *F. chrysolepis* (Philippines, Celebes, Moluccas), *F. novoguineensis* (New Guinea, New Britain, New Ireland), and *F. crassiramea* (Lower Burma to the Solomons). If, for simplicity, *F. chrysolepis* and *F. novoguineensis* are regarded as varieties of *F. annulata*, as *F. crassiramea* has var. *celebica*, var. *clementis*, and var. *patellifera* in this eastward range, then merely two species (*F. annulata*, *F. crassiramea*) are extended into eastern Malesia where there are no climbing species of *Urostigma*. *F. acamptophylla* and *F. microsyce* occupy the Riouw-pocket (Corner 1958), which is covered by the ambit of *F. stupenda*. This is the case with *F. annulata* and *F. globosa* in ser. *Validae* but *F. depressa* is one of the species absent from the southern part of the Malay Peninsula and the Riouw Archipelago; it appears to be absent from the east side of Sumatra and south west Borneo; and the records from Indochina are all *F. annulata*. Another wide-spread strangler related with ser. *Validae*, namely *F. glaberrima*, is also strikingly absent from the Riouw-pocket; in fact it has not been found in the whole Malay Peninsula or the Riouw Archipelago, and I have seen merely four collections from Sumatra (northern half) and two from Borneo (var. *bracteata*, Sarawak, East Koetei).

Climbers of subgen. *Ficus* sect. *Sycidium*

This section is mainly Indo-Pacific. There are 107 species of which four or five are exclusively on the African mainland and four are Mascarene. Two of the three subsections, namely *Sycidium* (76 spp.) and *Varinga* (11 species), consist of trees of short to large size (up to 30 m or more) or shrubs which are erect or decumbent with rooting nodes. In subsect. *Palaeomorphe* (20 spp.), however, there is an unusual diversity; it suggests that the group consists of leptocaul relics of a varied and, possibly, strangling past. Twelve species are epiphytic bushes or small trees of the lower layers of the forest, rooting to the ground as if incipient stranglers, for which they are commonly mistaken, but never developing a root-trunk and not destroying the host with which they have come to terms. One species is a moderate-sized tree of willow-habit (*F. celebensis*); perhaps this is the case also with the uncertain *F. stipata*. Two species are large stranglers with root-trunks destructive of the host (*F. tinctoria*, *F. virgata*). Three species are climbers with coiling and twining stems, often epiphytic at first (*F. heteropleura*, *F. parietalis*, and ?*F. lasiocarpa*). And one species, the common *F. subulata*, is an epiphytic stoloniferous climber. Two African species in subsect. *Varinga* have been described as climbers, namely *F. asperifolia* and *F. pendula*, but this is erroneous according to the revision by DeWolf (1964). Here, then, as in *Urostigma*, climbing is associated with the incipient phase of strangling, and this is shown in an unusual way by *F. subulata* which, in other respects, is so similar to *F. virgata* that they are often confused.

F. subulata, which I have illustrated for the fig-flora of the Solomon Islands (Corner 1967), is an epiphytic shrub or small tree without main trunk at heights of 2–10 m above ground, rarely more. The seedling sends roots round the host-trunk which clasp it in position and, then, along the trunk to the ground, but they do not form a root-trunk. When established on one tree, it produces lax branches with long internodes and much reduced leaves. The branches can reach up to 6 m long, perhaps more, and, on sagging, they contact the branches and trunks of nearby trees to which they attach themselves with encircling roots in the manner of the seedling; a new crown is then developed with its set of descending roots. The process is repeated until aerial thickets are constructed and the stand of host-trunks looks as if it had received a heavy infection of seeds, though all may have started from one. *F. subulata* is, in fact, a juvenile strangler propagating this state by aerial stolons. If it grew on the ground it would be a stoloniferous shrub.

The leaves of *F. subulata* vary much in size. The differences are positional, not environmental. Strong stems, 3 mm thick, have leaves with the lamina 20–35 cm × 7–12 cm with 9–14 pairs of lateral veins and 5–8 intercostals. On branching, the lamina on the side-branches, 1–2 mm thick, abruptly diminishes with fewer lateral veins and intercostals but, usually, with a longer drip-tip (see Corner 1967, figure 37). Yet there are plants, especially in New Guinea, which have generally large leaves and others, known as var. *gracillima*, which have very small leaves, the lamina being 3–13 cm × 1–3 cm without intercostals, on twigs 1 mm thick. There is, also, a form, perhaps that of var. *gracillima* developed on the ground, which has large leaves on the few main stems and, suddenly, the small leaves of var. *gracillima* on the side-shoots, but instead of axillary figs three are clusters of small figs on short cauliflorous and leafless twigs, up to 15 mm × 2–3 mm, developed on the old main stems. This state, if such it is, has been named *F. otariophylla*. It is known merely from five collections from east New Guinea and has never been carefully studied in the forest. The long drip-tip, up to 40 mm long even on large leaves with 12 pairs of lateral veins, shows that the leaf of *F. subulata* is itself reduced from a large ancestral and obovate form with many more functional lateral veins. Thus, *F. subulata* is a leptocaul diminishing in New Guinea into var. *gracillima*. It has an ally in *F. armiti* of New Guinea but I have never detected the aerial stolons in it and it seems to be simply an epiphytic shrub similar in habit to the first growth of *F. subulata*.

The stranglers allied with *F. subulata*, namely *F. tinctoria* and *F. virgata* (Corner 1967), can become immense trees over 40 m high, supported by a dense column of descending aerial roots, individually up to 30 cm thick. Seedlings begin epiphytically, in the manner of *F. subulata*, but commonly at greater heights in the forest, and they never develop the proliferating stolons. The descending roots thicken and branch but scarcely anastomose, and a basketing trunk, such as most stranglers develop, is not formed; in fact these columns of aerial roots are the best way of identifying these two stranglers on first encounter in the forest; a similar column of roots is formed by *F. elastica* which, as a wild tree, is now rarely to be found. The two stranglers are leptocaul with twigs 1.5–3 mm thick and shortly petiolate distichous leaves, as in *F. subulata*, with similar venation but few or no intercostals, and the leaf-tip is not caudate but acuminate to acute or, even, obtuse in *F. tinctoria*. They show also the abrupt diminution in size of the lamina consequent on branching. *F. tinctoria* ssp. *gibbosa* may have acuminate leaves almost as small as those of *F. subulata* var. *gracillima*. *F. tinctoria* ssp. *parasitica* var. *anastomosans* is a small shrub creeping on the ground with small dentate leaves. Thus these species show the diminution in size of the parts which accompanies leptocaul progress, and the persistently juvenile habit in var. *anastomosans*, perhaps also in the creeping shrub *F. tinctoria* ssp. *swinhoei*.

F. tinctoria and *F. virgata* make the only instance of the strangling habit outside subgen. *Urostigma*. This may be taken to imply that the habit is a recent evolution in the two groups. That this cannot hold, however, for the pantropical *Urostigma* I have shown elsewhere (Corner 1961). There is still much evidence in *Urostigma* to show the evolution of the leptocaul stranglers from the massively constructed pachycaul with spirally arranged leaves, but all this has disappeared from the ancestry of *Palaeomorphe*. The origin of strangling *Urostigma* dates, rather, from the early pachycaul stage of dicotyledonous forest with short trees. The same argument applies to *F. tinctoria* which has the greatest distribution of all species of *Ficus*, from north west India to the Tuamotu islands.

Now subsect. *Palaeomorphe* is part of subgen *Ficus* with the dioecious character advanced upon the monoecious subgenera *Urostigma*, *Pharmacosycea*, and *Sycomorus*; these last two consist of trees and shrubs without stranglers, epiphytes or climbers. Apart from a few species in Africa, subgen. *Ficus* is Indo-Pacific, and *F. tinctoria* covers most of this range. Almost as wide-spread are seven advanced stranglers of *Urostigma*, namely *F. virens*, *F. caulocarpa*, *F. drupacea*, *F. crassiramea*, *F. subcordata*, *F. benjamina*, and *F. microcarpa*, to which may be added *F. glaberrima* and the alliance of *F. annulata*; none of these reach Fiji or eastwards. The strangling habit might be held responsible for the wide distribution but the cauliflorous tree *F. variegata* is as widely distributed as *F. benjamina*, and so is the advanced and scrambling epiphyte *F. subulata* of forest undergrowth. Presumably, therefore, the distribution represents the land-connections and archipelagic possibilities for these successful and advanced species since the Cretaceous period. Viewed in this perspective, subsect. *Palaeomorphe*, which is morphologically primitive in the presence of a functional gall-ovary in the male flower, is seen as an ancient line of stranglers, parallel with *Urostigma*, but specialising into small, non-strangling, epiphytes.

The source of *F. tinctoria* appears to have been on the Asian mainland where ssp. *parasitica* alone has the superficial stomata – a matter that I have checked in every one of the several hundred collections that have been made. *F. virgata* belongs in east Malesia. The diversification of *F. subulata* is in New Guinea and may be connected with the ancestry of *F. virgata*. Of other groups of *Palaeomorphe*, ser. *Cuspidatae* and ser. *Fibrosifoliae* are west Malesian; ser. *Auritae* is central Malesian; and here enters the enigmatic leptocaul tree *F. celebensis* of Minahassa. There is no really pachycaul relic, but the most fully developed leaf is found in *F. rubromidotis* (ser. *Fibrosifoliae*) of Borneo, with lamina up to 45 cm × 14 cm, caudate tip to 50 mm long, 12–20 pairs of lateral veins, and 6–10 intercostals (figure 12). It has the kind of leaf from which that of *F. subulata* has evolved.

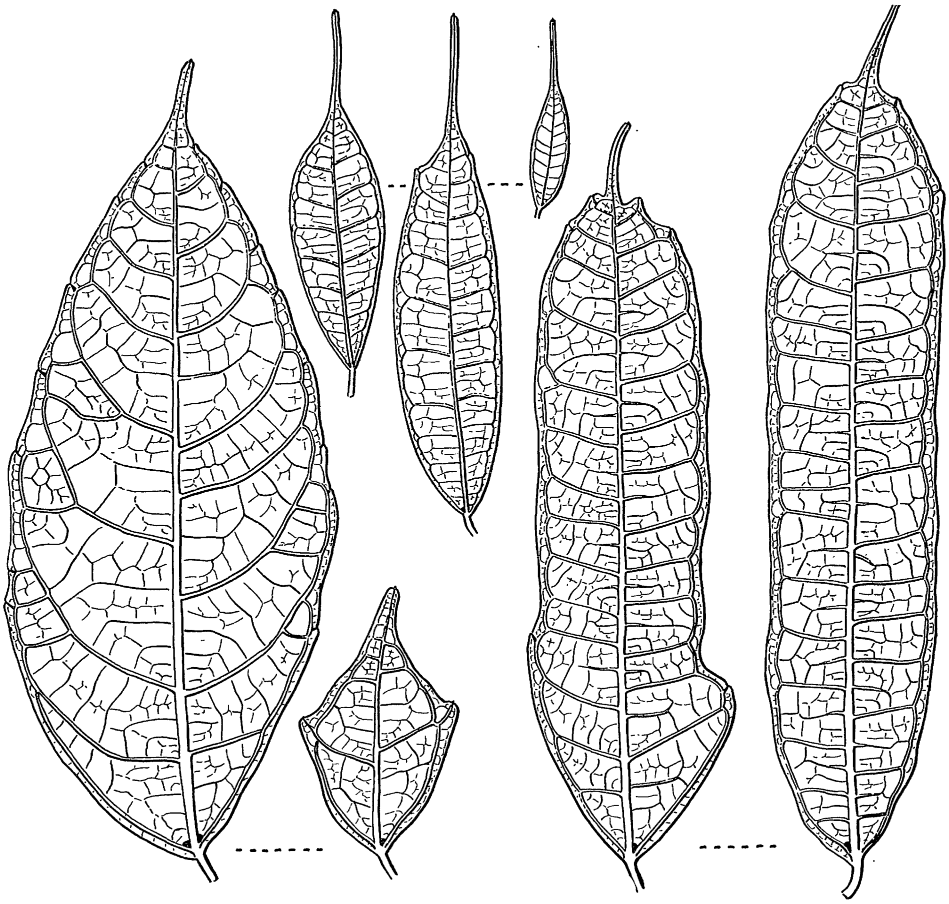

FIGURE 4. *Ficus sinuata* var. *sinuata* (left) with transverse intercostal venation. Ssp. *cuspidata* (upper centre), three leaves with caudate tip and reduced lamina without intercostal venation. Var. *oblonga* (right) two leaves with more numerous pairs of lateral veins and slight development of transverse intercostals. (Half natural size.)

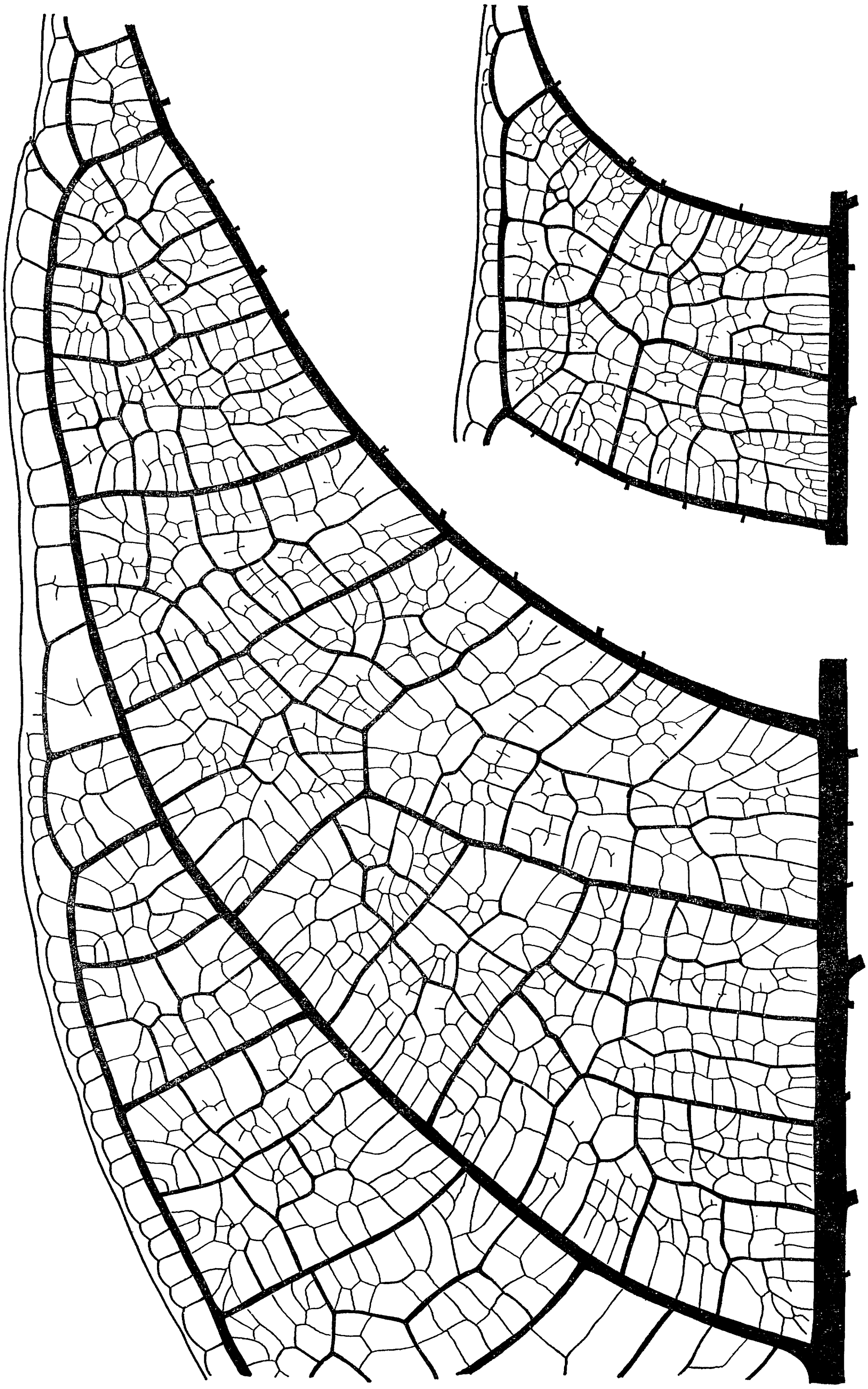

FIGURE 5. *Ficus sinuata* var. *sinuata*, an intercostal area with 4 transverse intercostals developed submarginally. Var. *oblonga* (upper right), an intercostal area without transverse intercostals. (Magn. × 3.)

It should be noted that *F. tinctoria* and *F. subulata* are absent from the Riouw-pocket, as if this were a vagary of southerly and westerly dispersal.

Ser. *Cuspidatae* (subsect. *Palaeomorphe*) comprises four species distributed from Assam to the Moluccas and Flores, but chiefly on the Sunda-shelf. They are leptocaul shrubs, small trees, or tortuous climbers, commonly epiphytic as *F. subulata* but not stoloniferous. The shortly petiolate and more or less distichous leaves are borne on twigs 1–3 mm thick, but it is not clear if leaf-size diminishes abruptly on branching. *F. sinuata* (figure 4) is a lax shrub or treelet but ssp. *cuspidata* may have such straggling decumbent branches as to appear an unspecialized scrambler. In *F. heteropleura*, *F. parietalis*, and probably *F. lasiocarpa*, long stems twine irregularly, looping and curling around neighbouring branches and around themselves. Thus they hold themselves up and are, uniquely in *Ficus*, coiling climbers. *F. heteropleura*, epiphytic at heights up to 12 m, develops these coiling branches up to 20 m long (when pulled straight, though often impossible to unravel); the main descending root may thicken up to 13 cm in diameter, and it is attached to the host-trunk by slender lateral roots of considerable length; older branches thicken up to 10 cm in diameter. *F. parietalis*, which is a handsome climber with dark glossy leaves and russet-orange figs, is more robust with longer branches, but I have no measurements. The habit of the Sumatran *F. lasiocarpa*, which I know only from herbarium-material, is unrecorded but, because it is so close in other respects to these coiling climbers, I think it is also such a climber. Nevertheless, *F. lasiocarpa* approaches the epiphytic shrub *F. obscura* (ser. *Fibrosifoliae*) in the shape of the fig-orifice, the glands in the axils of several pairs of lateral veins, and in the primitive brown hairiness (figure 9).

Both *F. sinuata* and *F. heteropleura* attenuate into forms with small leaves and reduced venation (figures 5, 7). *F. sinuata* ssp. *cuspidata* recalls *F. subulata* var. *gracillima*; with twigs 1–1.5 mm thick, the lanceolate caudate lamina has 3–7 pairs of lateral veins and 0–1 intercostals. *F. sinuata* ssp. *sinuata* divides into two varieties; var. *sinuata* has an elliptic caudate lamina with 5–10 pairs of lateral veins and 2–5 intercostals; var. *oblonga* has a narrowly oblong caudate lamina with 8–12(–17) pairs of lateral veins and 1–3 intercostals. Whereas ssp. *cuspidata* is montane, generally above 1000 m in altitude, ssp. *sinuata* is lowland and its two varieties may grow together without vicarious or ecological distinction. *F. heteropleura* var. *mindanaensis*, with twigs 2–3 mm thick, has a large lamina up to 42 cm × 18 cm with 6–9 pairs of lateral veins and 3–8 intercostals; var. *heteropleura* has a smaller, more caudate lamina with 2–6 pairs of lateral veins, 1–3 intercostals, and elongate basal veins reaching up to a half of the length of the lamina. The extremes suggest different species, as they have been recognized, but many collections are intermediate, especially in the Philippines where all states of the species occur and the intermediates are known as *F. caudatifolia*. It might be thought that var. *mindanaensis* represented the main branches with larger leaves and figs and that, on ramification, it would turn through *F. caudatifolia* into var. *heteropleura*, but the big leaves of var. *mindanaensis* have not been found outside the Philippines, and I have never seen them in the many plants of var. *heteropleura* that I have examined; its larger leaves are the intermediates of *F. caudatifolia*: in other words, var. *mindanaensis* has the large to medium-sized leaf and var. *heteropleura* has the medium-sized to small leaf with basipetal elongation. This elongation occurs also in *F. parietalis* and *F. lasiocarpa* (figures 8, 9); it is noticeably absent from the leaves of *F. tinctoria*, *F. virgata*, and *F. subulata*. Var. *mindanaensis* is the hairy state of the species; var. *heteropleura* is the advanced and glabrescent state of wide distribution; var. *hirta*, restricted apparently to north Borneo, is brown hairy var. *heteropleura*.

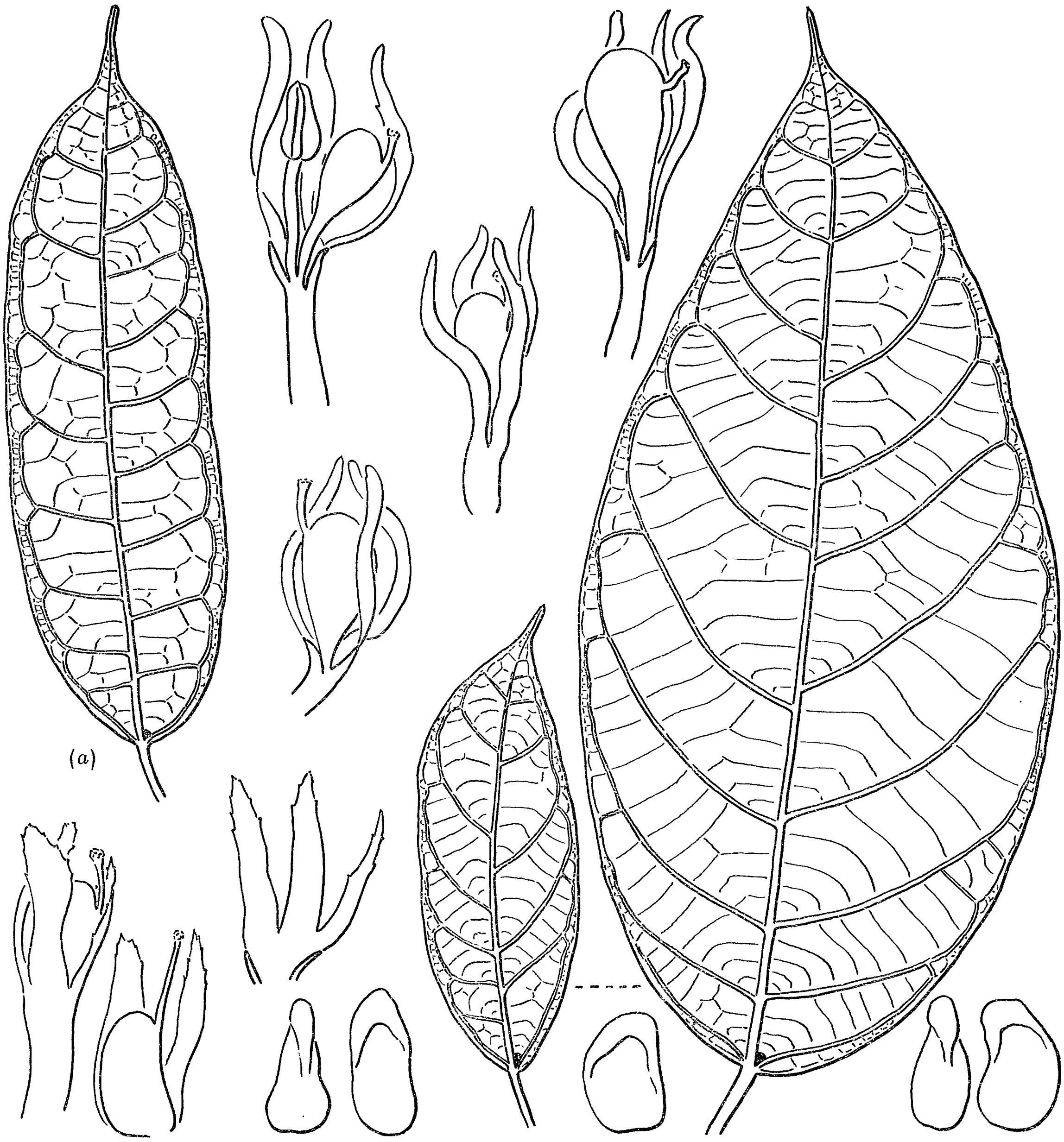

FIGURE 6. *Ficus heteropleura* var. *mindanaensis*, two leaves from the same twig. (*a*) The Philippine form of *F. heteropleura* known as *F. caudatifolia*, with numerous lateral veins but 0–1 intercostals. Leaves: half natural size; flowers and seeds: magn. × 10.

No collections of *F. parietalis* have been made from west Johore, Singapore, the Riouw Archipelago, or Bangka, but it is found in east Johore and west Borneo; hence it may narrowly define the Riouw-pocket.

CLIMBERS OF SUBGEN. *FICUS* SECT. *RHIZOCLADUS*

Sect. *Rhizocladus* (57 spp.) and sect. *Kalosyce* (20 spp.) consist entirely of root-climbers. Their seeds germinate on the forest-floor. The seedling creeps with adventitious roots from the nodes and ascends living and dead trunks to which its stem adheres by means of very numerous short roots. The stem is often somewhat flattened against the host-trunk, which led Blume to describe the common *F. sagittata* as *F. compressicaulis*. Adult plants are not truly epiphytic because they retain their primary connection with the ground by means of a thick stem; whether they die off in the upper part on severance of the stem or this may root again to the ground is not known, for these beautiful plants are not usually available for this drastic experiment. Then, they are not stranglers because the adventitious roots are slender and do not basket the host-trunk. The main stem may thicken up to 15 cm or more and become more elliptic in cross-section, but some species retain slender stems; the large stems simulate the grey descending roots of a strangler, but they keep the hoop-marks of the nodes. Not a few species become some of the very large climbers of the forest; they ramify along the branches of the support into the canopy, but not overgrowing it and smothering it; thus, they too have come to terms with the host. The figs are borne on short leafy sprays which dangle freely, though cauliflory on the main stem is common in sect. *Kalosyce*. This precise habit of root-climbing does not occur in other groups of *Ficus*, and there is no clear evidence how it has evolved.

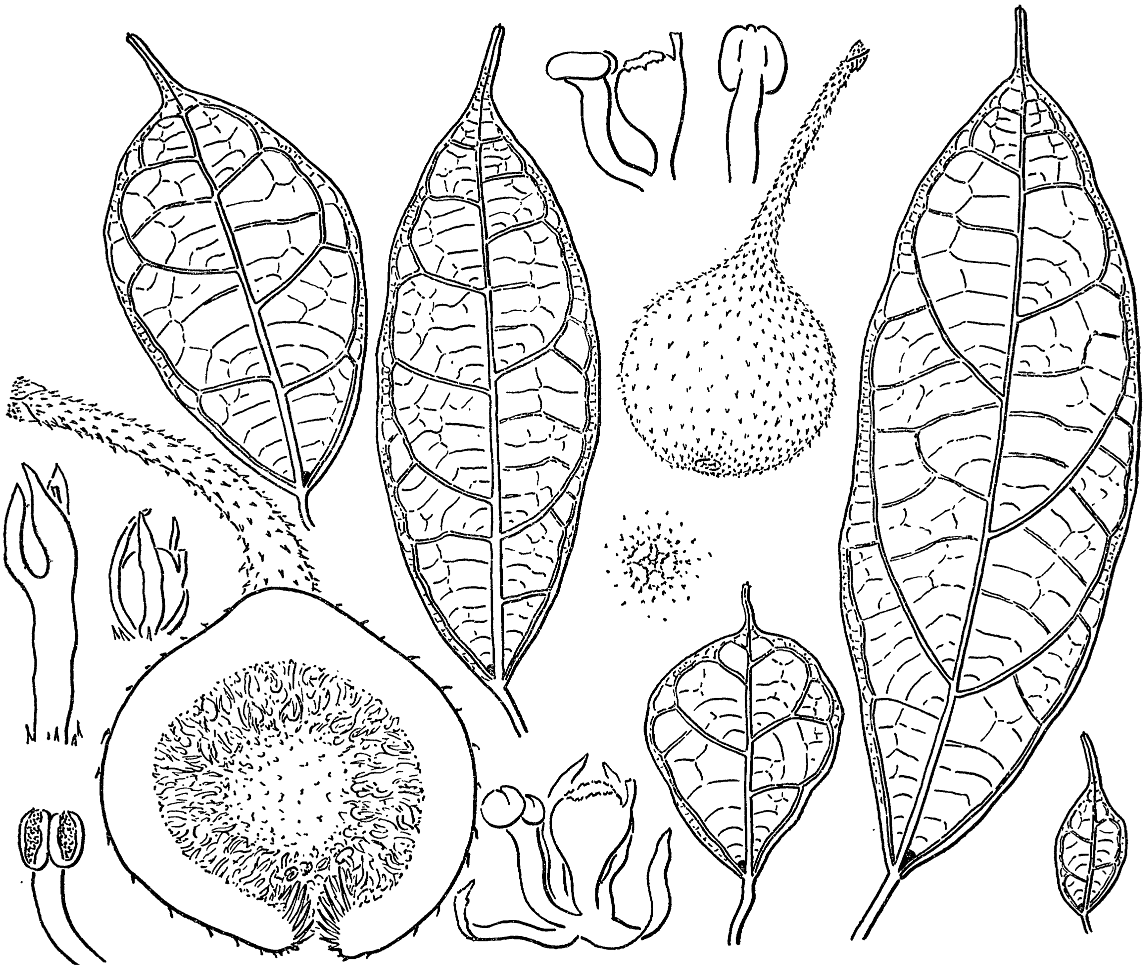

FIGURE 7. *Ficus heteropleura* var. *heteropleura*, leaves of various Malayan collections with 2–6 pairs of lateral veins. Leaves, half natural size; figs, with orifice, magn. × 3; flowers, magn. × 10.

Both sections have advanced features in addition to the habit. They are dioecious. The leaves are entire, shortly petiolate, and more or less distichous; they have, also, such xerophytic marks as sunken stomata, foveolate areolae caused by the bulging of the lower epidermis or the lower side of the veins around the areolae with crowded stomata (figure 10), and a multiple hypodermis of large water-storing cells. The venation is often much reduced and many species have distinct

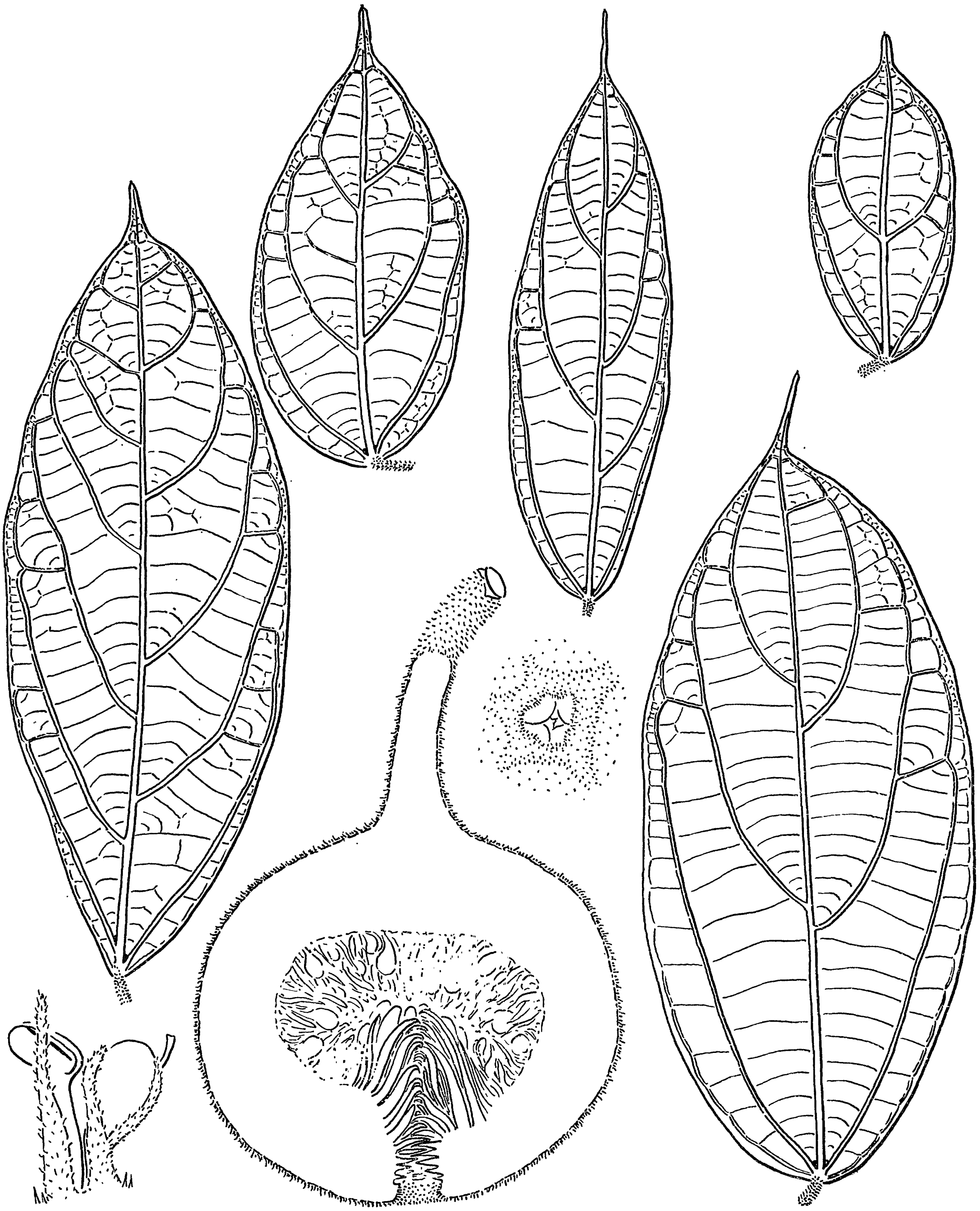

FIGURE 8. *Ficus parietalis*, leaves of various collections with 2–6 pairs of lateral veins and elongate basal veins, half natural size; fig. with orifice, magn. × 3; male flower, magn. × 10.

bathyphylls. These are the small leaves of special shape produced not only by the creeping seedlings but by any branch developed low down in the forest shade; the upper or adult leaves are called acrophylls (Holttum 1932, 1937). Then the figs have a collar of basal bracts without lateral bracts and in many species of *Rhizocladus* the apical bracts are inflexed, not interlocked. The seed in both sections has a distinctive form which is oblong, compressed, and narrowly bordered with a thin rim, but there are exceptions in *Kalosyce*. Primitive features are found merely in the two stamens in the male flower of *Rhizocladus*, the disperse male flowers of *Kalosyce* and *Rhizocladus* p.p., the bifid stigma, and in such microscopic details as the septate hairs and peltate gland-hairs.

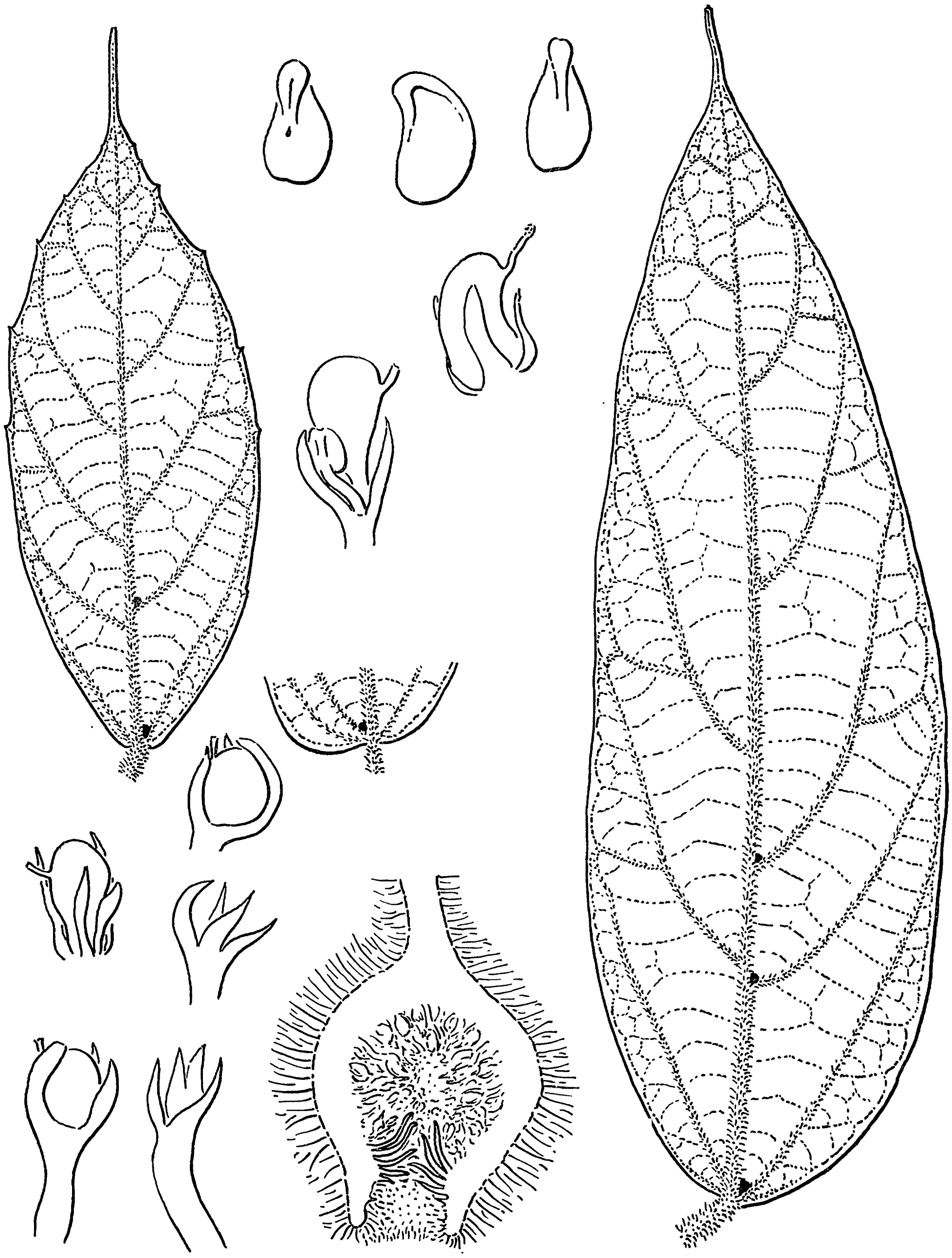

FIGURE 9. *Ficus lasiocarpa*, leaves, half natural size; fig, magn. × 3; flowers and seeds, magn. × 10.

The species of *Rhizocladus* fall into the five series *Plagiostigmaticae* (4 spp., Asian mainland, but *F. laevis* extending to the Sunda-shelf), *Ramentaceae* (30 spp., India to the Solomon Islands), *Distichae* (5 spp., Asian mainland to the Moluccas), *Distichoideae* (5 spp., Moluccas to the Solomons), and *Trichocarpeae* (13 spp., Asian mainland to the Solomons and Santa Cruz islands).

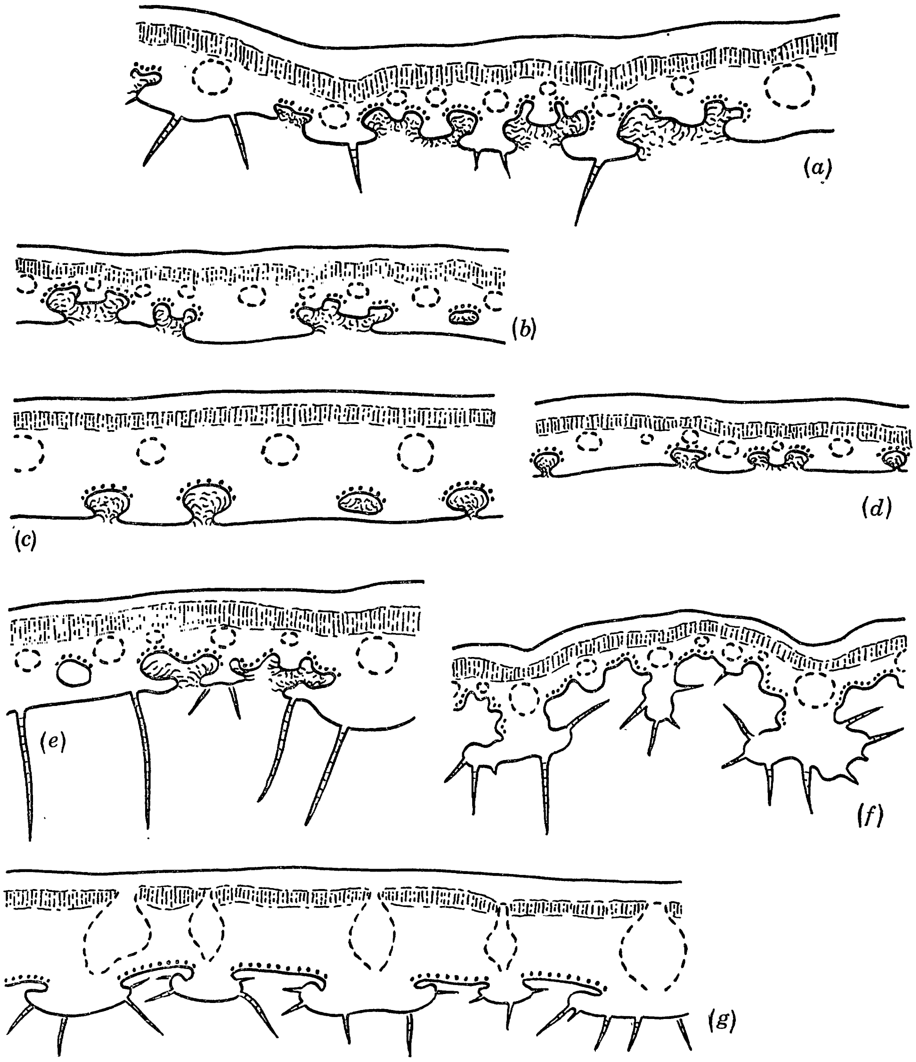

Figure 10. Leaves of *Ficus* sect. *Kalosyce* in section (magn. × 25) to show the structure of the stomatal pits; palisade-tissue striated; v.b. with broken lines; stomata as dots. (*a*) *F. carri*; (*b*) *F. ruginervia*; (*c*) *F. scratchleyana* var. *aurantiola*; (*d*) *F. aurantiacea*, *F. punctata*; (*e*) *F. tulipifera*; (*f*) *F. sarawakensis*; (*g*) *F. gymnorygma*, with trabeculate v.b. and interrupted palisade.

It is noteworthy that only *F. pantoniana* (ser. *Ramentaceae*) has been found in Australia; there are three collections from the neighbourhood of Cairns where it was said to be common in the *Licuala* swamp-forest at Innisfail. Yet *Rhizocladus* has 32 species in New Guinea, several of which are common in Papua but do not reach Australia. *Kalosyce* has 3 species in New Guinea, none in Australia. There are no such climbing figs in New Caledonia, the New Hebrides (Corner 1975), or Fiji. Ceylon, at the western limit, has two species of *Rhizocladus* and none of *Kalosyce*. These facts are a useful check to the facile supposition of unbridled dispersal in *Ficus*.

Ser. *Plagiostigmaticae* has three species in the subtropical and warm temperate parts of the Asian mainland, namely *F. pubigera* (with a relict station at Cameron Highlands in Pahang, either from the ice-age or through degradation of the mountains), the well-known *F. pumila* of horticulture, and the extremely versatile *F. sarmentosa* some varieties of which have leaves as large as those of *F. pubigera* and others have a small glabrous lamina (2–8 cm × 1–3 cm) comparable with *F. subulata* var. *gracillima*. The fourth species, *F. laevis*, is more or less tropical (Ceylon, India, south China to Sumatra, Java, and Borneo). It is one of the few species among all these root-climbers to have spirally arranged and long-petiolate leaves, in which respect it appears to be the most primitive species in the section. Oddly enough, sterile specimens of *F. laevis*, without a note on the habit of growth, can easily be mistaken for those of the common tree *F. variegata*. The series indicates a west Malaysian origin for *Rhizocladus*, perhaps in connection with sect. *Ficus* ser. *Sinosyceae*. The long male flowers are similar to those of *F. carica* between which and *F. pumila* a hybrid has indeed been raised (Condit 1969).

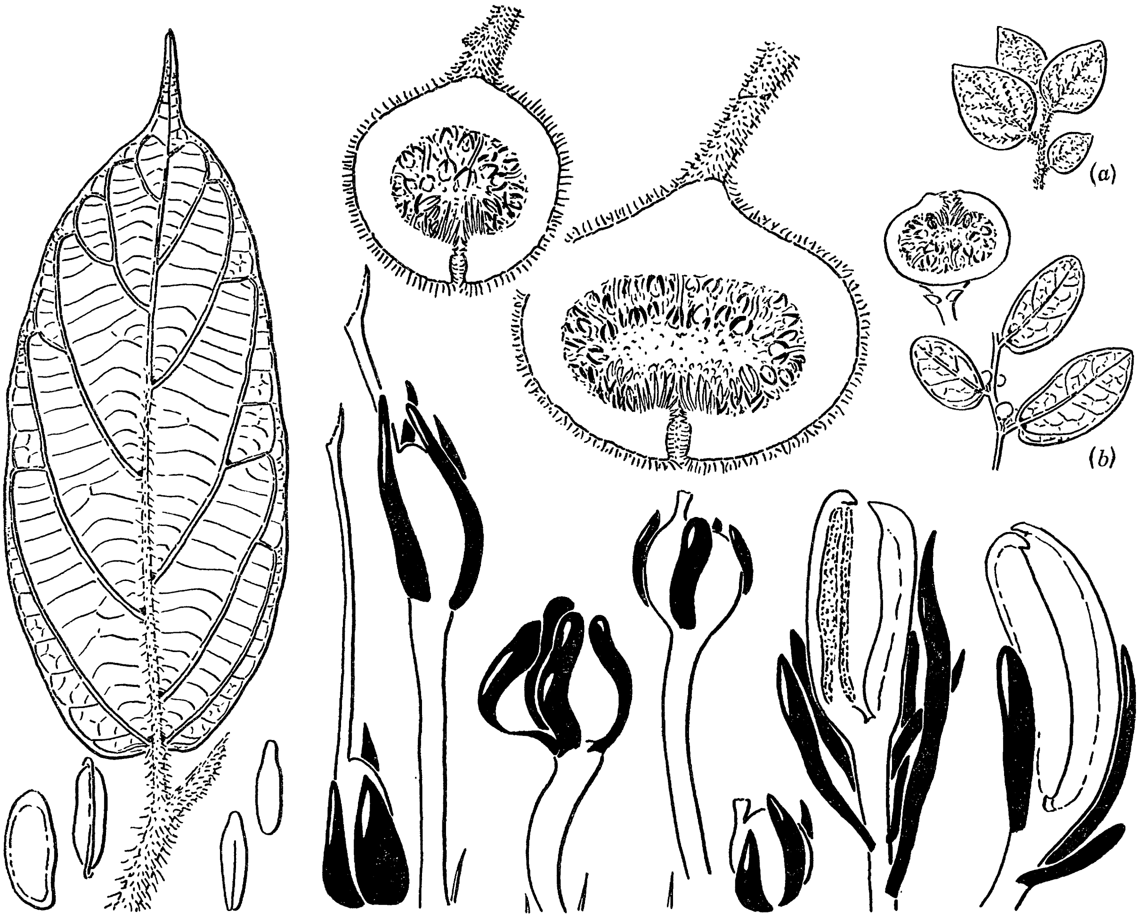

FIGURE 11. *Ficus odoardi* with immature and mature figs, magn. × 1; seeds, embryos, female, male and gall-flowers magn. × 10. (*a*) *F. ceanothifolia*; (*b*) *F. callicarpides*, with section of the fig, magn. × 3. Leaves and twigs, half natural size.

The numerous species of ser. *Ramentaceae* are closely knit and I am not satisfied with the six subseries that I have recognized (Corner 1965). I have illustrated the figs of this series (Corner 1962) and *F. baeuerleni* (Corner 1967). Three subseries, *Pantonianae*, *Balanotae*, and *Irritantes*, each with five species, occur in east Malesia, especially in New Guinea. The other three, *Ramentaceae* (10 spp.), *Excavatae* (4 spp.), and *Araneosae* (1 sp.), belong mainly in west Malesia, but two species of subser. *Ramentaceae* may be wrongly classified. Thus, *F. baeuerleni* (New Guinea to the Solomons) is close to *F. odoardi* (New Guinea, figure 11) and *F. camptandra* (Aru islands, New Guinea) may be near to *F. pantoniana* (Moluccas, New Guinea to the Solomons,

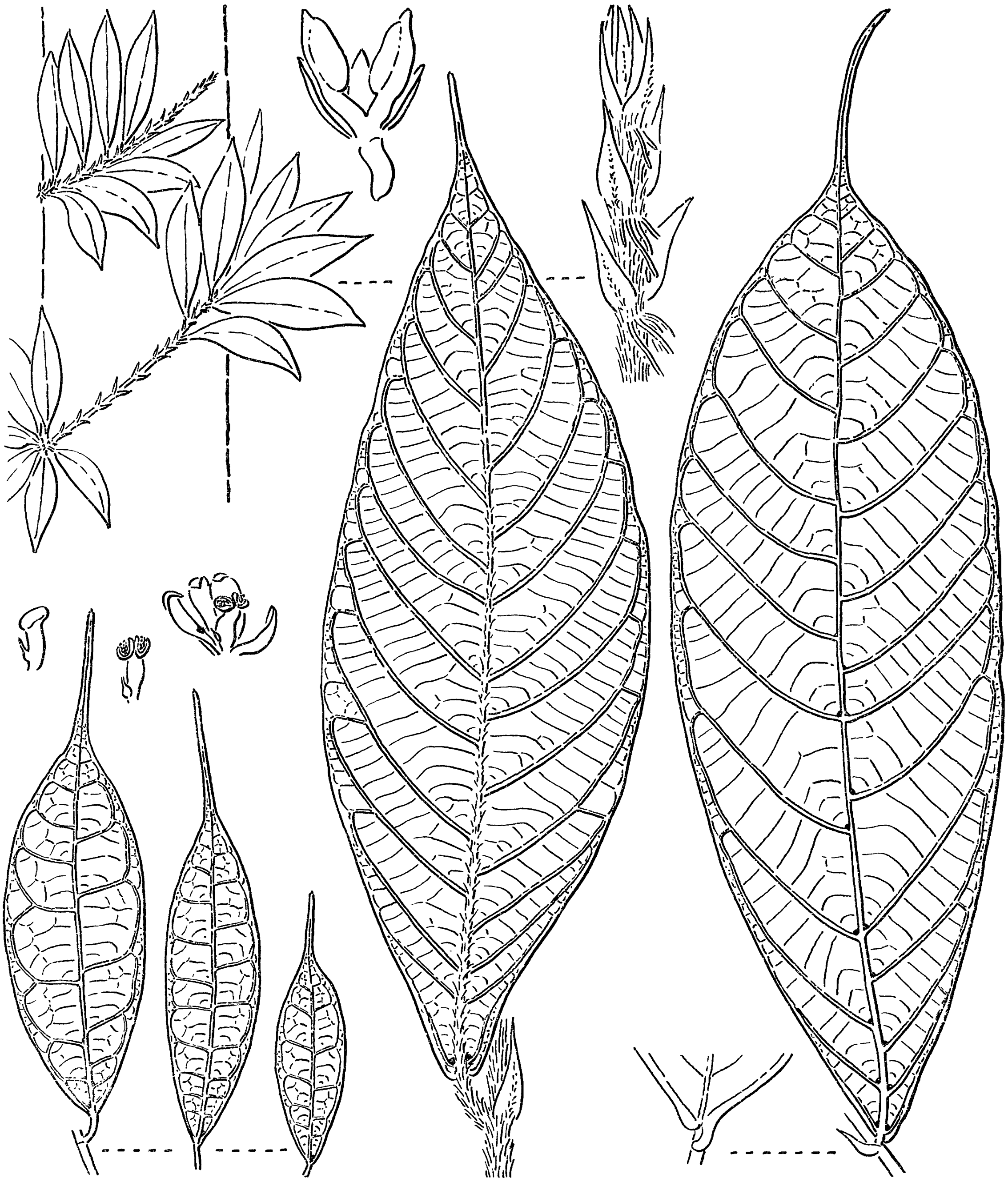

FIGURE 12. *Ficus spiralis* (sect. *Rhizocladus*, centre) with the stipulate end of the stem with adventitious roots, male flower, and sketch of habit. *F. rubromidotis* (sect. *Sycidium*, right) for comparison of the similar leaf. *F. rubrocuspidata* (sect. *Sycidium*, left) with small and simply veined leaves, and male flower with vestigial ovary. Leaves half natural size; flowers, magn. × 10.

Queensland). The series divides, therefore, into groups of western and eastern Malesia, as if referring to origins from the Asian mainland and the Melanesian Foreland. There are three somewhat pachyaul species, namely *F. odoardi* and *F. sphaerocarpa* of New Guinea, and *F. spiralis* of Sarawak. Indeed, *F. spiralis* is peculiar (figure 12); I do not know of any other fig with its intermittent manner of growth and its oblique direction. It is not uncommon in wet lowland forest around Kuching where I have studied it. Instead of ascending a trunk vertically, as usual in these root-climbers, it spiralizes obliquely round the trunk with a succession of leafy and leafless portions of stem. It has fairly large green and persistent stipules up to 30 mm long.

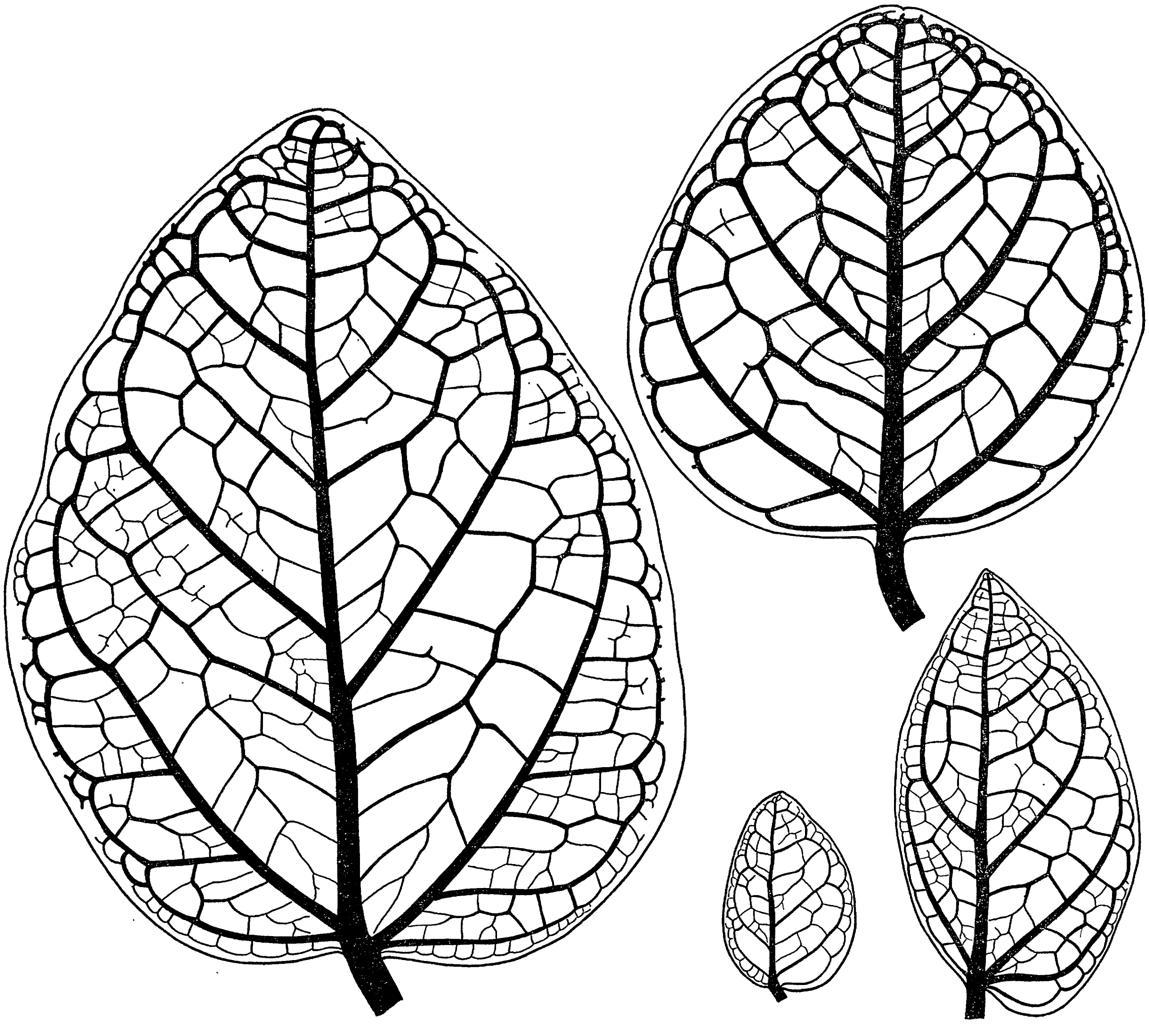

FIGURE 13. *Ficus excavata*; two mature leaves with obtuse apex, elongate basal veins, and the intercostal areas developed mainly by basipetal extension with a cascade-vein, but the first pair of intercostal areas with 2–3 transverse intercostal veins, magn. × 3; two asymmetric bathyphylls with acute apex, magn. × $1\frac{1}{2}$.

The stem produces 5–20 nodes, generally 9, with leafy stipules but no stalk or lamina; then it produces 4–7 nodes with similar stipules and large lamina, to be followed by another ‘leafless’ stage, and so on. This alternation starts early in the seedling and no bathyphylls are formed. The stem thickens little, up to 8 mm in diameter when the primary twigs are 5 mm. Short, freely hanging sprays develop from the creeping stem and, with the same interrupted leaf-arrangement, bear the small axillary figs 5–6 mm wide (dried). The lamina is the most fully developed in sect. *Rhizocladus*; it measures 28–42 cm × 8–16 cm with 12–14 pairs of lateral veins, 7–13 intercostals, and no elongation of the basal veins. If the intermittent growth is peculiar, the rather stout twig, the many-veined lamina, the persistent stipules, and the lack of bathyphylls are primitive; perhaps, too, the oblique ascent. In contrast I note the very small leaves of the extreme leptocaul species *F. ceanothifolia* (New Guinea), *F. callicarpides* (Sarawak), and *F. excavata* (Sumatra, Malaya, Borneo), as shown in figures 11 and 13. Their leaves resemble the bathyphylls of other species of *Rhizocladus*, but their advanced nature is shown by the stiffly coriaceous lamina of *F. ceanothifolia*, the foveolate lamina of *F. excavata* (though a species of swamp-forest), and the reduced venation with elongate basal veins and obtuse leaf-apex. Knowledge of several species is, unfortunately, slight because climbers are easily overlooked and difficult to collect.

I note here the strong resemblance in leaf between *F. spiralis* and *F. rubromidotis* in the very different section of *Sycidium* (figure 12). Both species grow together in the forest round Kuching, the one as a root-climber ascending from the ground, the other as an epiphytic shrub rooting to the ground. A close ally of *F. rubromidotis*, namely *F. rubrocuspidata* (figure 12), may grow with them but it is more often a riparian epiphyte. The small leaf of *F. rubrocuspidata* with simple venation is the leptocaul derivative from the more massive *F. rubromidotis*, in the same way as *F. sinuata* ssp. *cuspidata* stands to ssp. *sinuata*. *F. spiralis* has no such close ally but the small leaves of many species of its ser. *Ramentaceae* supply the leptocaul derivation via the intermediacy of such as *F. odoardi*. Reduction of lamina-factors, especially intercalary growth, concurrently with reduction in size of the apical meristem of the twig, leads to the drip-tip with many undeveloped lateral veins and to the slight intercostal veining. If the opposite view is taken that the small leaves are prototypes of the larger, then it must be assumed that, not only in these alliances, but in many other series, the more complicated lamina has been evolved independently as many times. All these shapes, sizes, and venation of the leaf occur in many other families, particularly the common form of *F. odoardi*. It is improbable in the face of all the advantages of leptocauly in exploiting ecological niches that the larger leaves are subsequent products of the evolution of the dicotyledonous lamina; the opposite hypothesis implies evolution from the specialized to the generalized, from distichous to spiral phyllotaxy. Hence I conclude that *F. spiralis* is a unique instance in sect. *Rhizocladus* arrested in the transition from pachycauly to leptocauly. In the allied sect. *Ficus* subsect. *Eriosycea*, *F. aurata*, *F. macilenta*, and *F. setiflora* show the derivation of the small leaf from the massive and pinnately lobed leaf of pachycaul trees (Corner 1970). The issue is important because it is the direction which plant-form has taken in dicotyledonous evolution. That so useful a sign has escaped notice stems from the conservatism of taxonomists who, foremost among botanists, deal with these tropical plants and, yet, attend rarely to the evolutionary consequences of their work. The bathyphyllous *F. callicarpides* fruits on the buttresses of *Shorea albida; F. spiralis* wends its way upwards; *F. odoardi*, or in west Malaysia *F. villosa*, shoots into the canopy. They represent the diversification of climbers in the forest without geographical or vicarious separation.

If, as seems likely, the distribution of male or neuter flowers in the gall- or seed-figs is an important character, then there is a remarkable convergence in the reduced species of ser. *Distichae* (west Malesia) with disperse male and neuter flowers and those of ser. *Distichoideae* (east Malesia) with the advanced limitation to ostiolar male and neuter flowers. The common *F. disticha* with small obtuse leaves comes to resemble its common counterpart in east Malesia, *F. agapetoides*. *F. disticha* relates through *F. detonsa* with *F. hederacea*, which has larger and laxly spiral leaves, just as *F. agapetoides* relates through *F. calodictya* with *F. phatnophylla* and *F. distichoidea*. Here one must note, again, the paucity of collections of ser. *Distichoideae* and the difficulty of classification; much field-work is needed. Ser. *Distichae*, like ser. *Plagiostigmaticae*, may be related with the ancestry of sect. *Ficus* ser. *Sinosyceae*. For ser. *Distichoideae* the only source seems to be the remote ancestry of ser. *Ramentaceae*. I note that, as exceptions, *F. allutacea*, *F. detonsa*, *F. disticha*, and *F. hederacea* have aseptate hairs.

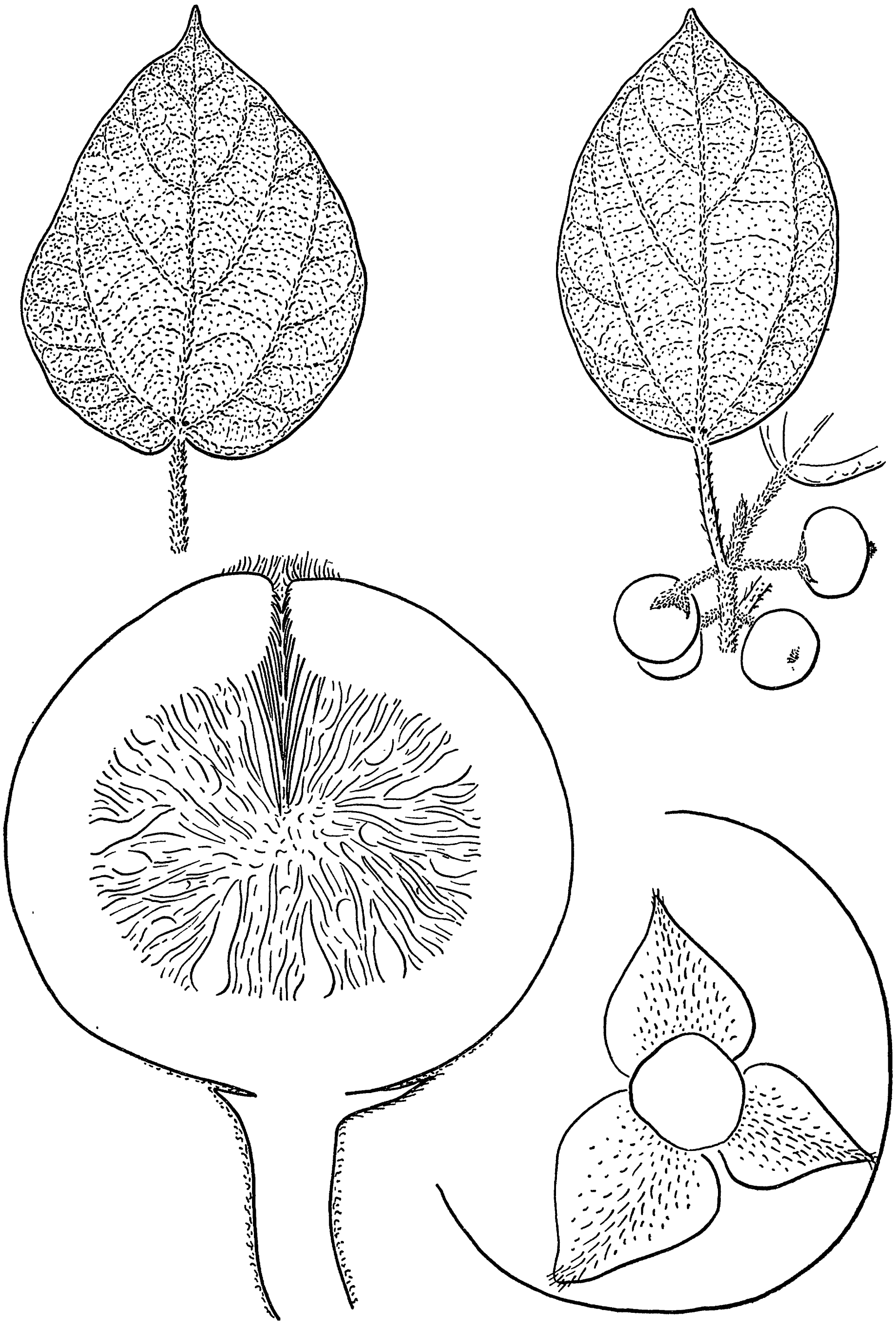

FIGURE 14. *Ficus hypophaea*; leaf and twig, half natural size; fig, magn. × 3. (Carr 15869.)

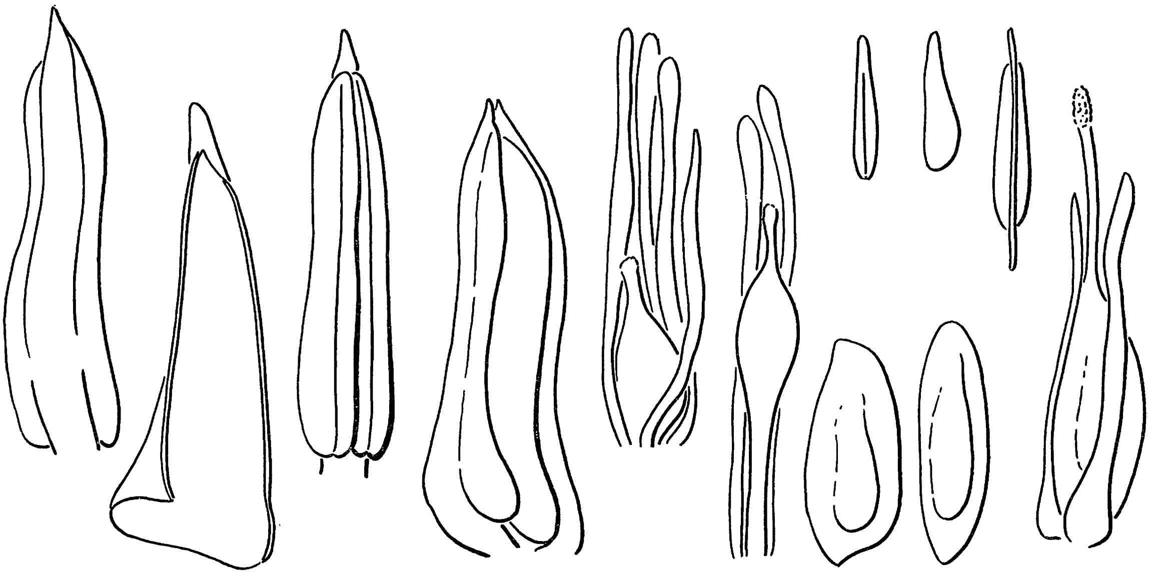

FIGURE 15. *Ficus hypophaea*; left, stamens and male perianth (cut open;) centre, two gall-flowers; right, female flower, seeds, and embryo; magn. × 10.

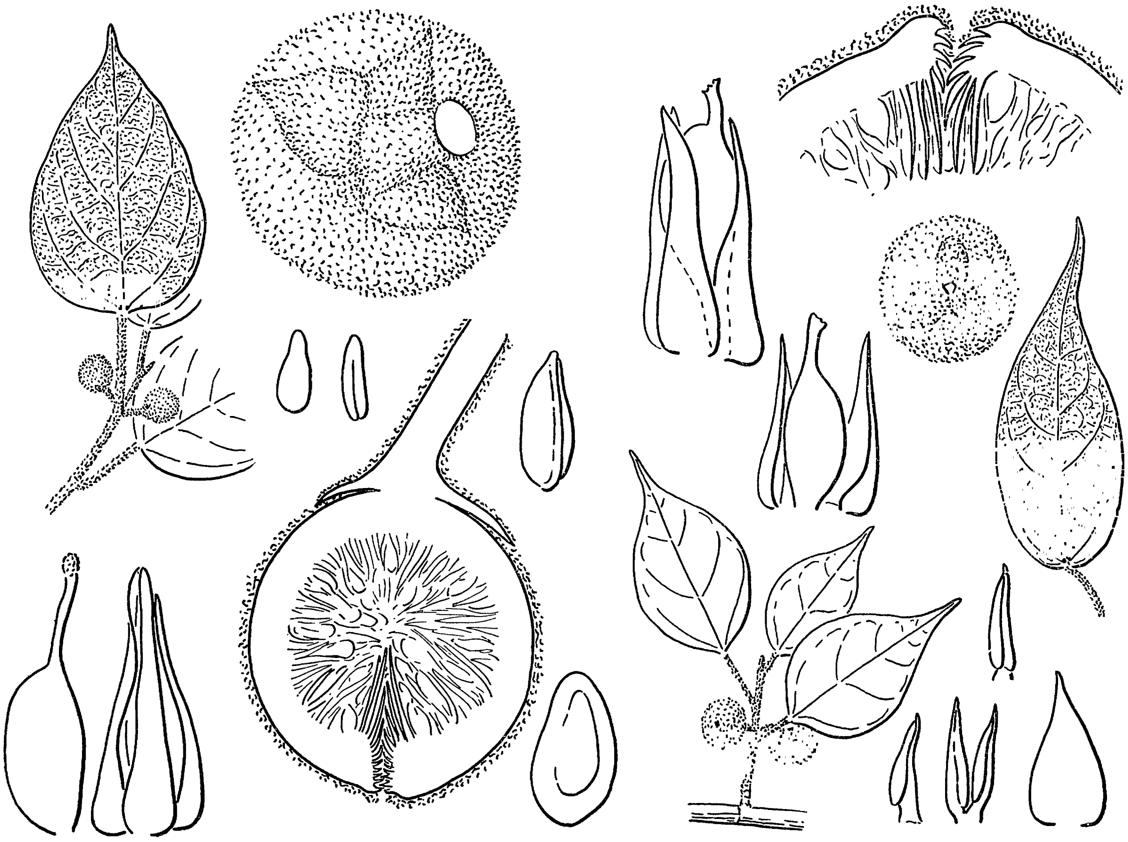

FIGURE 16. *Ficus cinnamomea* (left), with seeds and embryos. *F. hypophaeola* (right), with stamens and gall-flowers. Leaves and twigs, half natural size; figs, magn. × 3; fig-orifice (*F. hypophaeola*), magn. × 5; flowers, seeds, and embryos, magn. × 10.

Ser. *Trichocarpeae* (not to be confused with sect. *Ficus* subser. *Trichosyceae*) is thoroughly distinct and remarkably uniform. The species differ mainly in the thickness of the twig, the size of leaf and fig, and in hairiness. These are the ultimate differences that come into play in species-making in *Ficus* after details of reproduction and habit have become standardized. The series is distinguished by the usually sessile flowers, the disperse male and neuter flowers both with conical and gamophyllous perianth, the long mucronate anthers on free filaments, and the ovate-cordate lamina with constant venation of 3–5(–7) pairs of lateral veins and elongate basal veins (figures 14–16; also Corner 1967, figure 22). The series divides into three species of west and central Malesia, namely *F. trichocarpa* (Thailand, Indochina to Celebes and Flores), and *F. perfulva* and *F. bakeri* of the Philippines, and into 10 species of east Malesia where all are endemic in New Guinea except for *F. nasuta* which extends to the Santa Cruz islands. The stouter, yet scarcely pachycaul, species with twigs 3–5 mm thick are *F. hypophaea*, *F. nasuta*, and *F. supfiana* of New Guinea, and *F. trichocarpa* var. *obtusa*. Their respective diminutive allies with small leaves are *F. hypophaeola*, *F. pleiadenia*, *F. semilanata*, and *F. bakeri*. *F. perfulva* seems to connect *F. trichocarpa* with the robust species of New Guinea, and *F. bakeri* with indurate gall-flowers is close to *F. pleiadenia* and so with *F. nasuta*. Yet it must be noted that *F. trichocarpa* and *F. perfulva* are the two species in the series to have pedicellate gall- and female flowers. The source of the series appears to have been in central or east Malesia, perhaps with that of ser. *Distichoideae*.

Now, in searching the wealth of subgen. *Ficus* for a living plant that might indicate the ancestry of sect. *Rhizocladus*, I come upon *F. pedunculosa* of sect. *Ficus* ser. *Podosyceae*. It is a small tree up to 8 m high, with Terminalia-branching, deciduous at least in parts of its range which is the interrupted track from Burma and north Thailand, Formosa, the Philippines, Celebes, Moluccas, and Key Islands to the length of the north coast of New Guinea (Croizat 1968, figure 17). It is the most generalized member of a large series with 22 species all of which belong to the Asian mainland, Formosa, Ryu Kyu islands, Japan, and the Bonin islands, except for two endemic species in the Philippines. Formosa has two endemic species which creep over the ground with slender stems, rooting at the nodes, and small leaves, namely *F. tannoensis* and *F. vaccinioides*; it seems that they do not climb. Another such species is *F. tikoua* of the Asian mainland (Condit 1969). If ancestral and hairy *F. pedunculosa* with its ostiolar and disperse male flowers were pachycaul with large leaves, figs, and flowers, and inclined to this creeping habit, it would serve as the generalized ancestor of sect. *Rhizocladus* along its geographical extent which, according to Croizat, is a main track of oriental dispersal into the west Pacific, though its geological basis seems to be unknown; it is the northerly link from Asia to the Melanesian Foreland. The oblique ascension of *F. spiralis* may be a step in the transition from horizontal creeping along the ground to the vertical ascent of trunks. Yet there are microscopic discrepancies. *F. pedunculosa* has aseptate hairs, hypogenous cystoliths, and simpler, capitate or clavate, not peltate, gland-hairs.

Climbers of subgen. *Ficus* sect. *Kalosyce*

For many years I have been fascinated by this section. I can refer for most descriptions and illustrations to my revision, under the sectional synonym *Synoecia* (Corner 1939, 1960). Many species are very large climbers 50 m or more long, with the full equipment of bathyphylls, acrophylls, and dioecious figs, both axillary and cauliflorous. They challenge the collector whose basic function in botany – to discover what plants exist – is in these laboratory days too easily assumed. No novice can make a satisfactory collection of such huge and varied plants. Bathyphylls must be traced to main stems on the forest-floor; acrophylls in the canopy must be traced down to these same stems; and the stems must be searched for cauliflorous figs. All these must be disentangled from climbers and epiphytes of other families with which they grow; there is not the simplicity of studying, say, ivy, rose, or clematis in temperate forest. The section has the largest and most beautiful of figs. They ripen orange and scarlet with pale marbling and finally purple-black with delicious smell and luscious texture; yet, so extravagant, they seem rarely to be eaten. The gall-figs of *F. aurantiacea* var. *angustifolia* have an ellipsoid body as large as a mango, up to 14 cm × 10 cm with the wall nearly 2 cm thick. With luck, collections can be recovered where forest is being felled but these are too often sterile and it is extremely difficult to follow the long stems in the tangle of smashed branches on to which masses of epiphytes have been thrown down. I made little progress until I had trained monkeys as my collectors, and many hours were needed to teach them to pull off the cauliflorous figs, which were to them inedible and pointless, as well as the leafy sprays (Corner 1955). Few satisfactory collections have been made in the last thirty years and ecologists still ignore these effective plants, as if one could ignore rattans and any other big climbers in the tropical forests.

Since my original account, there have been the following changes

(1) *F. callicarpa* becomes *F. aurantiacea*; var. *crassinervia* becomes *F. ruginervia*; var. *multinervia* becomes *F. singalana*.

(2) *F. peninsula* (Philippines) is separated from *F. scratchleyana* (New Guinea); var. *aurantiola* is added to *F. scratchleyana*.

(3) *F. gymnorygma* is added from New Guinea, *F. warburgii* from the Philippines, *F. diandra* (Corner 1962) and *F. sarawakensis* (Corner 1972) from Sarawak.

(4) *F. rhopalosycia* of New Guinea is re-instated in this account.

(5) *F. bordenii* and *F. tawaoensis* are dismissed as mixtures of totally different species, clearly of collection (Corner 1965, pp. 97–99).

I now distinguish two series, *Apiocarpeae* (4 spp.) and *Punctatae* (16 spp.) (Corner 1960, 1965). The first is the less advanced because the leaves are not foveolate with stomatal pits, distinct bathyphylls are not formed (though the state in *F. peninsula* and *F. warburgii* is not known), and the figs are in most cases axillary. The discovery of *F. diandra* adds the remarkable feature of 2(–3) stamens in the male flowers, thereby defying the earlier distinction of unistaminate *Kalosyce* from bistaminate *Rhizocladus*, though I had noted the very occasional occurrence of two stamens in *F. warburgii*, which is close to *F. diandra*. To distinguish *Kalosyce* there remains, nevertheless, the presence of very abundant, pedicellate, and disperse male flowers in the gall-fig and neuter flowers in the seed-fig. Strangely, however, neuter flowers are absent from the relatively primitive *F. apiocarpa*. Ser. *Apiocarpeae* is west and central Malesian. *F. diandra* (Sarawak) and *F. warburgii* (Philippines), though with unusually small leaves and figs, suggest derivation of *Kalosyce* in central Malesia.

In ser. *Punctatae*, the distinction between subser. *Punctatae* and subser. *Ruginerviae* is useful for identification but, perhaps, insufficiently phyletic because more attention should be given to the seed which remains unknown in several species. Normally it has the flattened keeled form as in sect. *Rhizocladus* (Corner 1939, 1972), but the seeds of *F. trachycoma* (subser. Punctatae) are plump and obtusely keeled, while those of *F. rhopalosycia* (subser. *Punctatae*), *F. carri* and *F. gymnorygma* (both in subser. *Ruginerviae*) are plump, oblong, without keel, and thick-walled, as if they were the primitive form (figure 17). In this respect and in the vegetative character of both *F. dens-echini* (north Borneo) and *F. scratchleyana* (New Guinea), which have long-petiolate and laxly spiral leaves with little distinction of bathyphylls, both central and east Malesia appear as the source of ser. *Punctatae*. The most widely distributed species are the advanced *F. aurantiaceae* and *F. punctata* with obtuse, few-veined leaves, short petioles, and distinct bathyphylls. How this bathyphyll state may be carried up into the acrophylls, as if persistently juvenile, is shown by both species (Corner 1939, figures 32, 33). The neotenic persistence may explain the small, but acute, and almost symmetrical acrophylls of *F. diandra* and *F. warburgii*. For comparison the acuminate and almost caudate bathyphyll of *F. carri* is shown in figure 18.

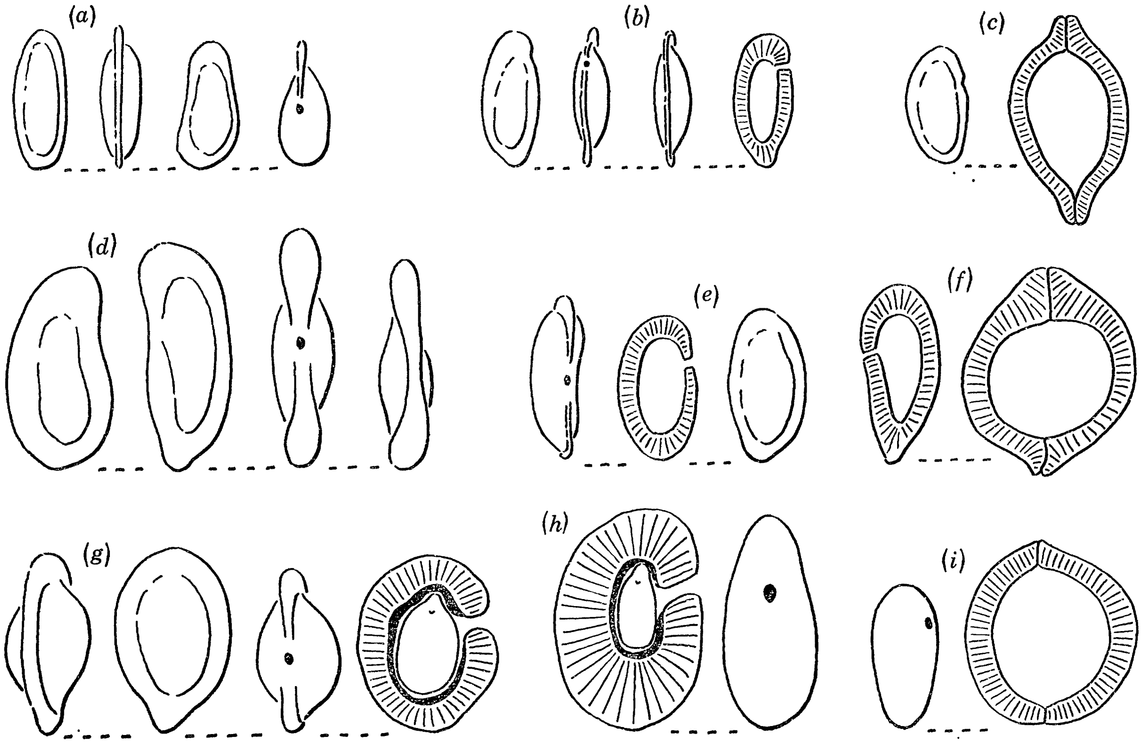

FIGURE 17. Seeds (pyrenes) of *Ficus* sect. *Kalosyce*, magn. × 10; transverse sections (right) with the woody endocarp striated, magn. × 25. (*a*) *F. peninsula* (Koorders 19109). (*b*) *F. grandiflora* (Clemens 26332). (*c*) *F. dens-echini* (Sing. F. n. 26807). (*d*) *F. gymnorygma* (Eyma 4329). (*e*) *F. gymnorygma* (Ledermann 9104). (*f*) *F. gymnorygma* (NGF 42055). (*g*) *F. trachycoma* (Teysmann s.n. 1860). (*h*) *F. rhopalosycia* (Brass 11348). (*i*) *F. carri* (RSNB 2737).

The hairs in *Kalosyce* are septate as in *Rhizocladus* but those of the thickly villous twigs and figs of *F. apiocarpa* var. *villosa* are aseptate though the short hairs on the underside of its leaf are septate. The brown septate hairs of *F. gymnorygma* are slightly papillate in the manner that seems primitive in several groups of subgen. *Ficus*. Peltate gland-hairs are usual but in *F. diandra* there are also 8-celled capitate gland-hairs, as if incipient peltate scales.

The long pedicelate male flowers, if normally bistaminate, would bring *Kalosyce* close to ser. *Podosyceae*. The distribution of *Kalosyce* from central or east Malesia agrees with that part of the track of *F. pedunculosa*. No species of *Kalosyce* is comparable, however, with *F. spiralis* in *Rhizocladus*.

In fact, sect. *Kalosyce* is so advanced that primitive points are retained but here and there among the species as the merest traces of its ancestry.

Ser. *Podosyceae* introduces a detail of progress. The series is divided, naturally it seems, according to the pedicellate or sessile character of the gall- and seed-flowers, whether or not their ovaries above the level of the perianth are stalked or not. The flowers are pedicellate in subser.

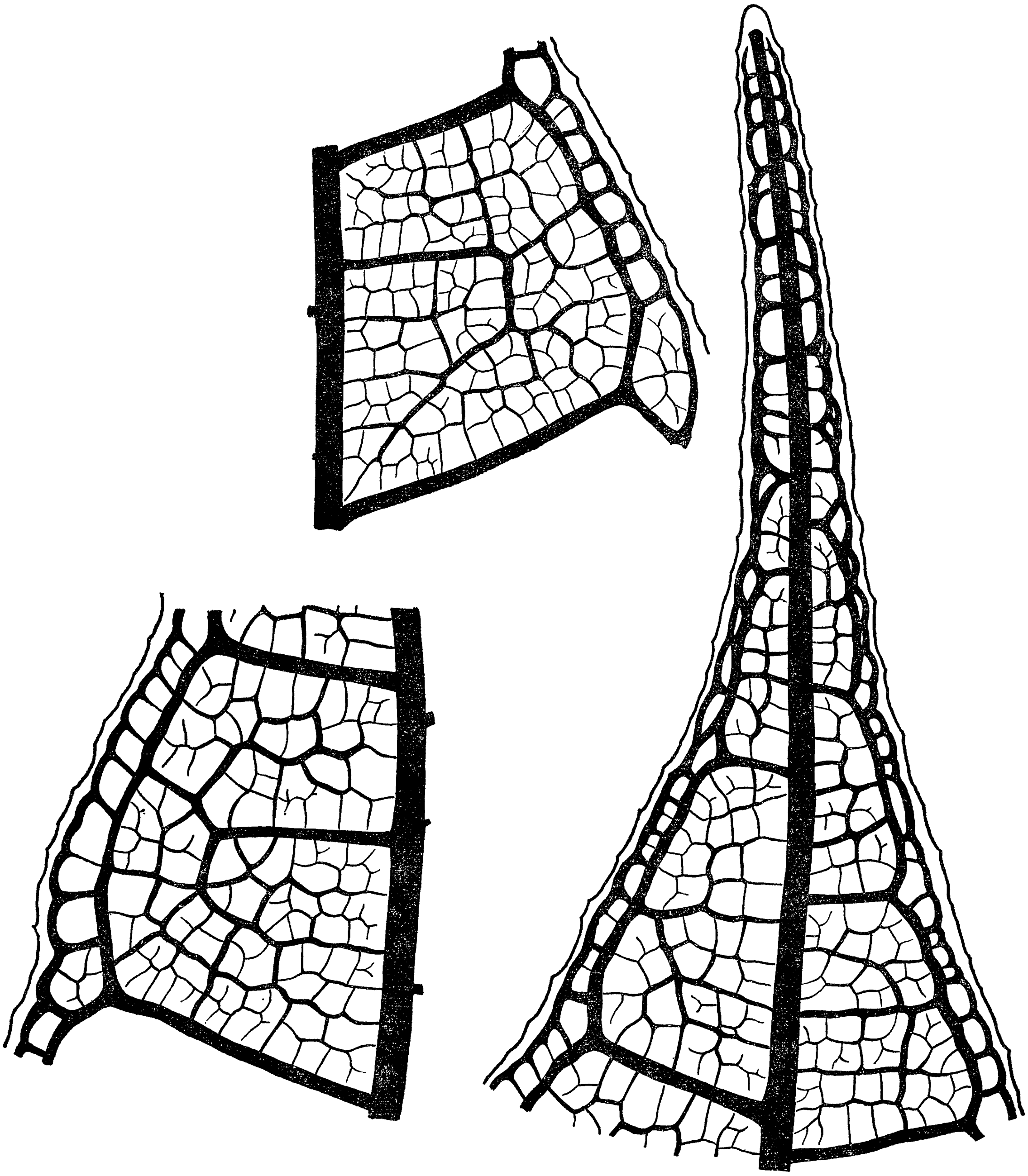

FIGURE 18. *Ficus carri*; the venation of a bathyphyll with acuminate apex (containing 12–14 pairs of undeveloped lateral veins); upper left figure fitting on to the lower right side of the leaf-apex; lower left figure fitting on to the left side of the leaf-apex; intercostal veining limited to the original N–S and E–W veins; magn. × 3.

Podosyceae and sessile in subser. *Basitepalae*. The detail is important in subgen. *Ficus*. sect. *Adenosperma*, the flowers of which are sessile (Corner 1969); it seems to be an expression of the degeneration of the inflorescence factors of Moraceae inside the syconium. The position in *Rhizocladus* and *Kalosyce*, however, is not clear. In *Rhizocladus* the primitive pedicellate flowers distinguish ser. *Plagiostigmaticae*, *Ramentaceae*, *Distichae*, and *Distichoideae*, but in the last three of these series the small figs of some species have correspondingly small flowers in which the pedicel is so short as practically to be absent; e.g. *F. callicarpides*, *F. excavata*, *F. pendens*, and *F. urnigera* in ser. *Ramentaceae*, *F. disticha* in ser. *Distichae*, *F. phatnophylla* and *F. agapetoides* in ser. *Distichoideae*. The exception is *F. diversiformis* of Ceylon (ser. *Distichae*) with pedicellate male flowers and sessile gall- and seed-flowers in contrast with the opposite states in other species of the series. The sessile, or basitepalous, form of all the flowers predominates in ser. *Trichocarpeae*, whatever the size of the fig, but pedicellate gall- and seed-flowers distinguish the west and central Malesian *F. trichocarpa* and its close ally *F. perfulva*. The situation in *Kalosyce* is more involved and, if the species need some regrouping, this detail must be borne in mind as well as the form of the seed, but here the size of the fig seems also to be irrelevant. Thus

ser. *Apiocarpeae* with gall- and seed-flowers sessile except *F. peninsula* (some pedicellate gall-flowers);

subser. *Punctatae* with gall- and seed-flowers sessile in the New Guinea species *F. rhopalosycia* and *F. scratchleyana*, but pedicellate in the other species of west and central Malesia;

subser. *Ruginerviae* with gall- and seed-flowers pedicellate in the west Malesian *F. ruginervia* and *F. singalana* and the New Guinea *F. gymnorygma*, but sessile in the closely allied Bornean group of *F. barba-jovis*, *F. carri*, *F. cataupi*, *F. sarawakensis*, and *F. tulipifera*.

DESCRIPTION OF *F. RHOPALOSYCIA*

274A ***F. rhopalosycia*** Diels, *Bot. Jb.* **67** (1935), 232. – *F. scratchleyana* King var. *rhopalosycia* (Diels) Corner, *Gdns' Bull. Singapore* **18** (1960), 24; **21** (1965), 61.

Glabrous except for the stomatal pits and young figs. Twigs 2.5–3.5 mm thick, dark brown. Stipules 1–15 mm long, caducous. Lamina 8–16 cm × 2.5–7 cm, oblong to lanceolate-elliptic, acute or shortly acuminate with the tip up to 7 mm long, base cuneate, symmetric, becoming stiffly coriaceous with incurved edge, drying brown or with the upperside greenish; lateral veins 6–10 pairs, almost perpendicular to the midrib, stout, not impressed above, distinctly raised beneath, the areolae with hairy stomatal pits 0.2–0.4 mm wide; basal veins 1 pair, short; petiole 12–30 mm long. Figs axillary, solitary, yellow-green then striped red; peduncle up to 11 mm long; basal bracts 3–4 mm long, sometimes displaced; pedicel up to 15 mm long or ill-defined; body up to 80 mm × 28 mm, pyriform (dried seed-figs) or 110 mm × 90 mm (living seed-figs, Brass 11297), puberulous at first, the orifice in dried figs as a cone up to 5 mm × 7–8 mm with minutely verrucose base and projecting apical bracts up to 2.5 mm long; fig-wall 5–6 mm thick (dried), the cavity filled with the flowers; internal bristles and sclerotic cells none. Male and gall-flowers? Female flowers 7–11 mm long, more or less sessile; tepals 3–4, up to 5 mm long, lanceolate, free, white; ovary sessile or stalked, white; stigma bifid. Neuter flowers 7–11 mm high. Seed 3–3.5 mm × 1.5–2.1 mm × 1–1.3 mm, lenticular with very obtuse edges, not keeled or winged, the sclerotic wall 0.5–0.6 mm thick but 0.7–1 mm thick at the base.

Distribution. West New Guinea (Hellwig mountains, Lake Habbena, Idenburg River); mountain forest 1700–2350 m altitude.

Collections. Pulle 643 (type, Berlin; duplicate, Utrecht), Hellwig mountains, 1750 m; Brass 12092, Idenburg River, 1800 m; Brass 11297, Lake Habbena, 2350 m; Brass 11348, Bele River 18 km NE of Lake Habbena, 2300 m; Kostermans and Soegeng 718, Baliem Valley above Wellesey.

I had reduced this to *F. scratchleyana* on the evidence of the type which has a very immature fig. The late L. J. Brass then lent to me his three unnamed collections with mature seed-figs, and these together with the collection of Kostermans and Soegeng give a much better picture of the species. It differs from *F. scratchleyana* in the large fig which, at least when dried, has a very characteristic elongate and pyriform body, in the large seeds without keel, and in the narrow leaves. Brass's field-notes suggest that the living fig is ellipsoid. Gall-figs have not been collected.

REFERENCES

Condit, I. J. 1969 Ficus: *the exotic species*. University of California, Division of Agricultural Sciences.

Corner, E. J. H. 1939 A revision of *Ficus* subgen. *Synoecia*. *Gdns. Bull. Singapore* **10**, 82–161.

Corner, E. J. H. 1955 Botanical collecting with monkeys. *Proc. R. Instn* **36**, n. 162, 1–16.

Corner, E. J. H. 1960 Taxonomic notes on *Ficus* Linn., Asia and Australasia. V. *Gdns' Bull. Singapore* **1**, 1–69.

Corner, E. J. H. 1961 *Evolution. Contemporary botanical thought* (ed. Anna M. MacLeod & L. S. Cobley), pp. 95–114. Edinburgh: Oliver & Boyd.

Corner, E. J. H. 1962 Taxonomic notes on *Ficus* Linn., Asia and Australasia. Addendum II. *Gdns' Bull. Singapore* **19**, 385–401.

Corner, E. J. H. 1965 Check-list of *Ficus* in Asia and Australasia. *Gdns' Bull. Singapore* **21**, 1–186.

Corner, E. J. H. 1967 *Ficus* in the Solomon Islands and its bearing on the post-Jurassic history of Melanesia. *Phil. Trans. R. Soc. Lond.* B **253**, 23–159.

Corner, E. J. H. 1969 *Ficus* sect. *Adenosperma*. *Phil. Trans. R. Soc. Lond.* B **256**, 318–355.

Corner, E. J. H. 1970 *Ficus* subgen. *Ficus*. Two rare and primitive pachycaul species. *Phil. Trans. R. Soc. Lond.* B **259**, 353–381.

Corner, E. J. H. 1972 New taxa of *Ficus* (Moraceae). *Blumea* **20**, 428–432.

Corner, E. J. H. 1975 *Ficus* in the New Hebrides. *Phil. Trans. R. Soc. Lond.* B **272**, 343–367.

Croizat, L. 1968 The biogeography of the tropical lands and islands east of Suez-Madagascar: with particular reference to the dispersal and form-making of *Ficus* L. and different other vegetal and animal groups. *Att. Ist. bot. Lab. critt. Univ. Pavia* (ser. 6) **4**, 3–400.

DeWolf, G. P. 1964 Provisional notes on Moraceae, I. *Elliottia* **1**, 1–18.

Holttum, R. E. 1932 On *Stenochlaena*, *Lomariopsis*, and *Teratophyllum* in the Malayan region. *Gdns' Bull. Straits Settl.* **5**, 246.

Holttum, R. E. 1937 Further notes on *Stenochlaena*. *Gdns' Bull. Straits Settl.* **9**, 139.

Kapil, R. N. & Rustagi, P. N. 1966 Anatomy of the aerial and terrestrial roots of *Ficus benghalensis* L. *Phytomorphology* **16**, 382–386.

Mabberley, D. J. 1973 Evolution in the Giant Groundsels. *Kew Bull.* **28**, 61–96.

Mabberley, D. J. 1974*a* Pachycauly, vessel-elements, islands and the evolution of arborescence in herbaceous families. *New Phytol.* **73**, 977–984.

Mabberley, D. J. 1974*b* Branching in pachycaul Senecios; the Durian Theory and the evolution of angiospermous trees and herbs. *New Phytol.* **73**, 967–975.

Mabberley, D. J. 1975 The giant Lobelias; pachycauly, biogeography, ornithophily and continental drift. *New Phytol.* **74**, 365–374.

Rao, A. N. 1966 Developmental anatomy of natural root-grafts in *Ficus globosa*. *Aust. J. Bot.* **14**, 269–276.

Zimmermann, M. H., Wardrop, A. B. & Tomlinson, P. B. 1968 Tension wood in aerial roots of *Ficus benjamina* L. *Wood Sci. Technol.* **2**, 95–104.