Ficus dammaropsis and the Multibracteate Species of Ficus Sect. Sycocarpus

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FICUS DAMMAROPSIS AND THE MULTIBRACTEATE SPECIES OF *FICUS* SECT. *SYCOCARPUS*

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CONTENTS

The syconium of *F. dammaropsis* (New Guinea) is presented as the the primitive state of this structure in the advanced sect. *Sycocarpus*. The rare *F. griffithii* (Burma, Thailand) may be related to *F. dammaropsis* or to *F. auriculata* (sect. *Neomorphe*). Subser. *Praestantes*, *Fulvidulae*, *Geocarpicae*, and *Axillares* are considered in their alliance with *F. dammaropsis*. Entomological evidence largely supports the botanical. Geocarpy is shown to be a consequence of leptocaul cauliflory. Subsect. *Macrostyla* provides a theory of the protoblastophagous syconium with emergent female styles.

Introduction

The part of *Ficus* which has been most helpful to me in tracing the course of generic evolution is the well marked section *Sycocarpus*. The name displaces that of *Covellia* (Corner 1960*b*) under which the Indo-Malayan and Chinese species were illustrated by King (1888) and the Malayan species by myself (Corner 1933). The section now contains about 80 species distributed from the Himalayas to Australia and Fiji, with the notable exception of New Caledonia. It is distinguished in the dioecious subgen. *Ficus* by the advanced character of the perianth, which is not partite but saccate and entire, cupular, annular, or even lacking, and by the advanced dimorphism of the gall- and female styles (Corner 1965). Yet, it has a number of species which retain primitive generic features. Thus, alone in subgen. *Ficus* (*ca.* 350 species) two species of sect. *Sycocarpus* are monoecious, namely *F. microdictya* (New Guinea) and *F. pritchardii* (Fiji), which I have discussed in my account of subgen. *Pharmacosycea* (Corner 1970*b*). Then, multibracteate figs, or syconia, occur in 12 species in contrast with 9 species in the rest of subgen. *Ficus* (*Sinosycidium* 1, *Sycidium* 5 or 6, *Adenosperma* 3). I discussed the primitive nature of this syconium in my account of sect. *Adenosperma* (Corner 1969*b*). There are several more or less strongly pachycaul species of which the most remarkable is *F. salomonensis* with the largest leaf of the genus, if not the largest single blade among dicotyledons. The species are mostly trees of small or moderate stature, even shrubs, and they have not advanced into forest-building with canopy trees, epiphytes, stranglers, or climbers. They have exploited, nevertheless, more fully than other groups of *Ficus* the understories of the forest in such ways as cauliflory and geocarpy. The section, therefore, is a contrast in advanced blastophagy and in both primitive and advanced structural features. I have explained this situation by the thesis that reproductive evolution in flowering plants occurred mainly in the primitive pachycaul phase of tree-evolution (Corner 1949, 1961*a*). Thus, it appears that the ancestors of sect. *Sycocarpus* remained in the pachycaul phase longer than those of other sections of the genus and *Sycocarpus* has retained, in consequence, a large number of primitive marks. Proof is found in the most astonishing species of the genus, namely *F. dammaropsis*.

In this paper I shall firstly give an account of this species. Then I shall consider its position in sect. *Sycocarpus* and the alliances of the other species with multibracteate figs. Lastly, I present a picture of the primitive syconium, as indicated by *Sycocarpus*. The nomenclature that I use is that of my check-list (Corner 1965).

Ficus dammaropsis Diels

This rather common species of New Guinea was first described as *Dammaropsis kingiana* by Warburg (1891) from a collection by C. L. Ledermann (n. 11890, Sattelberg, Finschhaven). He compared the multibracteate syconium with the cones of *Dammara*, which is now called *Agathis*. Diels (1933) showed that this syconium was not peculiar enough for generic distinction but occurred in less elaborate form in other species of *Ficus*, such as his *F. megalophylla* which I have placed in sect. *Adenosperma* (Corner 1969*b*). In reducing *Dammaropsis* to *Ficus*, Diels was obliged to change the specific epithet because of the existence of the previous *F. kingiana* Hemsley, published in 1897, though this is merely a synonym of the common *F. ampelas*. In floral detail *F. dammaropsis* has the entire and saccate perianth more or less covering the ovary, which is distinctive of sect. *Sycocarpus*; I placed it there in its own subsection *Dammaropsis* (Corner 1960*b*). My reasons were the bistaminate male flower (mostly unistaminate in *Sycocarpus*), the red perianth and white ovary, and the unspecialized seed, all of which when taken together with the remarkable syconium singled this one species out from the rest of the section. The coloration of the perianth and ovary contrasts with the condition in the large subsect. *Sycocarpus* (68 species) where the perianth is colourless and the ovary reddish brown. Whether this is a functional detail of blastophagy in the dark interior of the fig calls for investigation. The red perianth and white ovary, as in *F. dammaropsis*, occurs also in subsect. *Papuasyce*, *Lepidotus*, and *Auriculisperma* ser. *Theophrastoides*; it is the condition which relates them and is usual in subgen. *Ficus*. Furthermore, these groups of *Sycocarpus* have the same kind of unspecialized seed as in *F. dammaropsis*, and it is the form that is common in subgen. *Ficus*; it contrasts with the seed with prominent hilum that distinguishes subsect. *Sycocarpus*. Thus, in reproductive

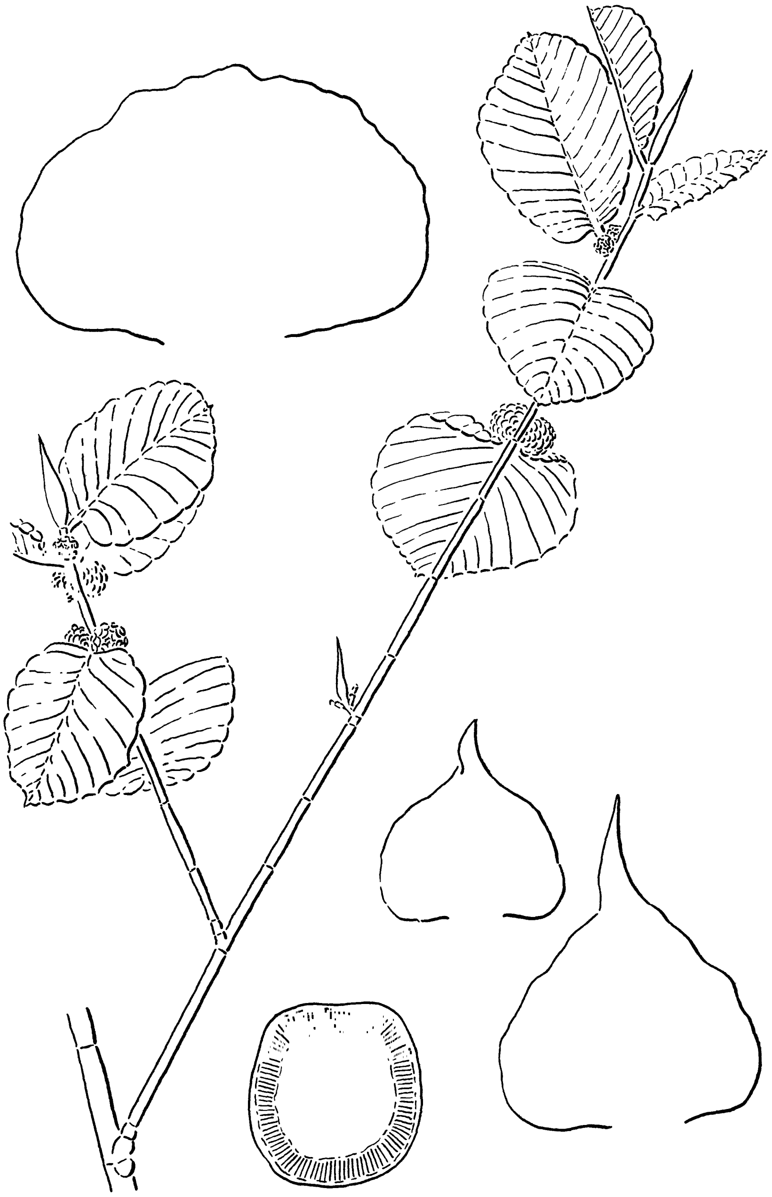

FIGURE 1. *Ficus dammaropsis* var. *obtusa*; twig of a plant 4m tall, magn. × 1/10; obtuse bract of var. *obtusa* and two acuminate bracts of var. *dammaropsis*, magn. × 1; twig of var. *obtusa* in t.s. (wood striated), magn. × 1.

details of stamens, perianth, ovary, and seed, *F. dammaropsis* is in primitive agreement with sect. *Ficus*.

The habit of *F. dammaropsis* is that of a pachycaul shrub or small tree up to 10 m high. The straggling branches, projected by conspicuous internodes, end in loose clusters of large, spirally arranged leaves and a giant conical stipule over the terminal bud (figures 1 to 4). The stiff leaves, though not as large as in *F. salomonensis*, are the next biggest in the genus; in robust saplings, the strongly ribbed and shiny lamina, often with red veins, can reach 90 × 60 cm. The primary twig is 10–15 mm thick, but is certainly thicker in saplings. The conical stipule, up to 26 cm long, is equalled in *Ficus* only by that of some species of subgen. *Urostigma* sect.

Malvanthera, as well as by saplings of *F. elastica*. Branches arise at a considerable distance from the apex of the parent stem and, with progressive ramification, so the thickness of the primary twig and the size of the lamina diminish. The lamina has an entire, if sinuous, margin with practically no submarginal venation; in this it resembles the proximal half of the leaf of *F. auriculata*, to which I shall refer. The habit recalls saplings of *Artocarpus* but the prominent basal veins of the lamina direct one to *Ficus*.

The figs are axillary, sessile, singly or in pairs, subglobose, and covered entirely by the massive lateral bracts. Befitting their position on the pachycaul twigs, they are extremely massive and the largest of all syconia. At maturity they reach an overall width of 8–15 cm and, in the larger, the fig-body inside the bracts may reach 13 cm. They ripen rose-red to reddish brown, but there are evidently variations. A note on one collection (L. R. Brownhill n. 1, Territory of New Guinea) says that the raw figs are eaten by villagers, but there is no information concerning wild animals such as marsupial, bat, or bird. On sectioning the fig, it can be seen that the flowers are borne on lobing processes from the inner surface, which is unlike the even interior of the

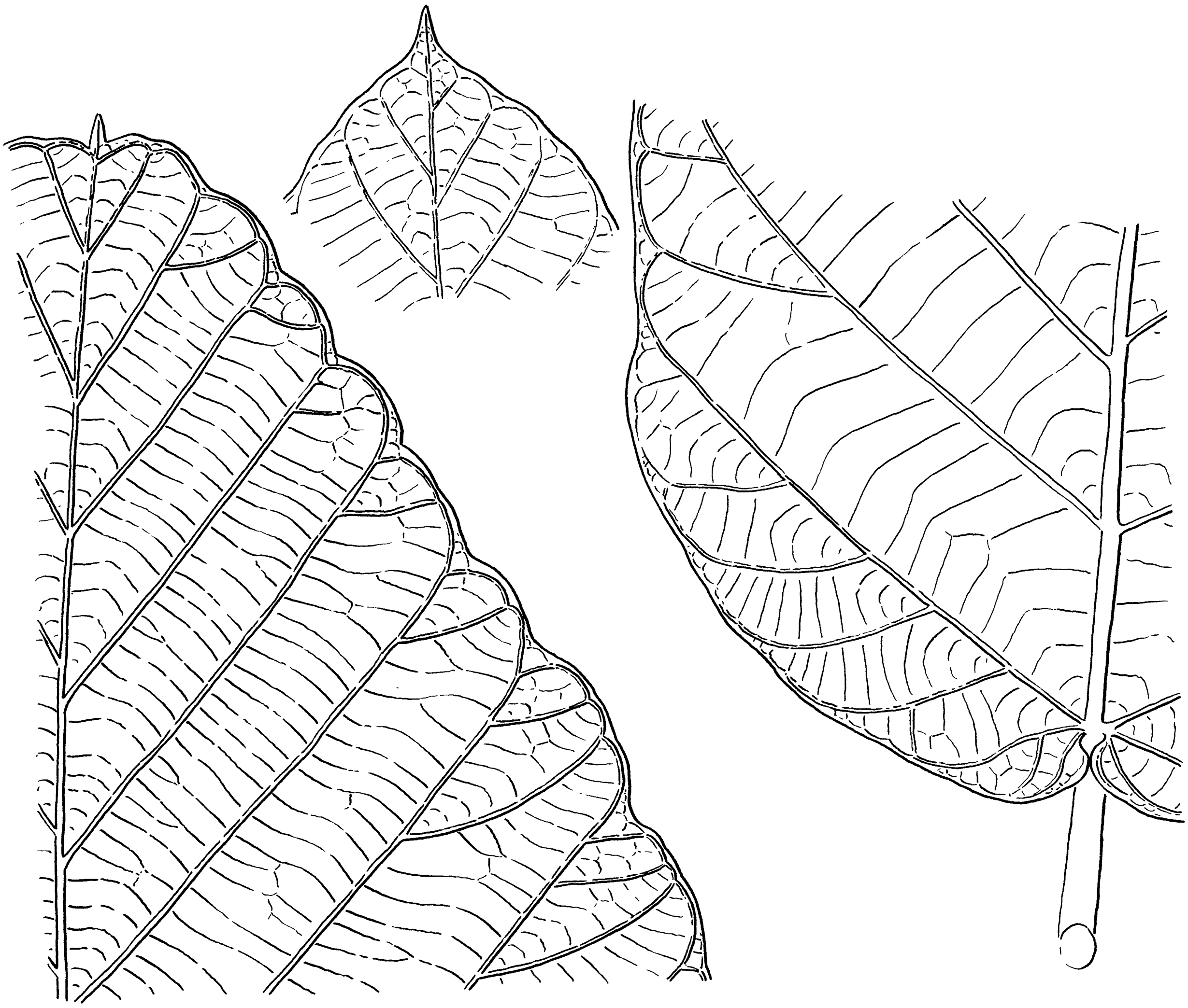

FIGURE 2. *Ficus dammaropsis*; var. *obtusa* (left) with leaf-apex from the underside; var. *dammaropsis* with leaf-apex and base from the upperside; magn. × ½.

majority of figs. Such processes, which occur in lesser degree in the large figs of some other groups of *Ficus*, appear to be the vestiges of the originally branched and cymose Moraceous inflorescence; they add, thus, another primitive mark to this species. The fig-wall is devoid of sclerotic cells and there are no internal bristles or bracteoles except between the male flowers at the orifice.

Geographically *F. dammaropsis* is also remarkable. It is wild throughout New Guinea except for the dry region of *Banksia* and *Eucalyptus* around Port Moresby. It grows well in the uplands at 1000–2300 m, but it has been found almost at sea-level in west New Guinea. It is not an inhabitant of dense primary forest but of temporary openings by streams and rivers and of secondary forest on landslips. However, it has been spread widely by villagers who use the bark for fibre, the young leaves (especially the midrib) as a vegetable, the mature leaves for wrapping food during cooking, and who eat the ripe fruit, presumably only the seed-figs. The trees, therefore, are more often to be found in and around villages or in areas of deserted cultivation. While, however, of such general occurrence in New Guinea, it has not been found in the Admiralty Islands, New Ireland, or New Britain, with floras closely akin to that of New Guinea. It is certainly absent from the Solomon Islands, New Hebrides, Fiji, New Caledonia, and Australia, as it is absent from the Moluccas, the Key and the Aru Islands. It exemplifies the restricted distribution of pachycaul plants.

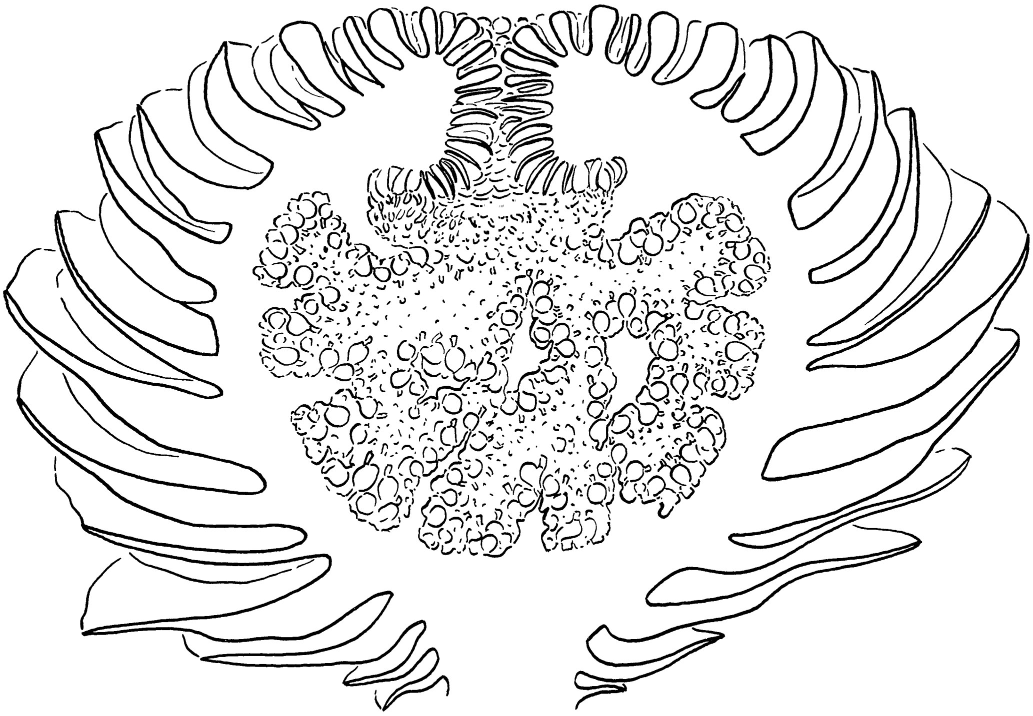

FIGURE 3. *Ficus dammaropsis* var. *obtusa*; gall-fig in l.s., with ostiolar male flowers, magn. × 1.

There are about 30 herbarium collections, but the small number in this case is no measure of abundance for the species is easily recognized and it is laborious to collect. I have distinguished two varieties according to the size of the fig and the shape of the lateral bracts (Corner 1960*b*); they need investigation in the field. Var. *dammaropsis* of Indonesian New Guinea and the Territory of New Guinea has the smaller figs with the fig-body up to 8 cm wide, and comparatively small, acuminate, lateral bracts 4–6 × 3 cm (figure 1); var. *obtusa* of Papua and the Territory of New Guinea has the fig-body up to 13 cm wide and much larger, obtuse, and almost semicircular, lateral bracts up to 3.5 × 7 cm. Possibly there is a third variety, which I have in ms. as var. *parvibracteata*, with ovate-acute bracts merely 11–22 mm long and wide, imperfectly covering the fig-body; these are, conceivably, depauperate figs from old trees of var. *dammaropsis*. There are two collections of this possible variety, namely L. R. Brownhill n. 1 from the Sepik district, which gives the tree an exceptional height of 13 m, and Kostermans and Soegang n. 13 from Hollandia; they give the tree as up to 7 m high and very common in 'gardens'. Then there are differences in hairiness, for some collections are glabrous and others softly white hairy, and in the colour of the ripe figs. The field-note of NGF 3396 (Aijura, var. *obtusa*) states that some trees have figs ripening red and others in which they remain green; this may be merely a difference between seed-figs (red) and gall-figs (green or ? yellowish). Kalkman n. 4086 (Orio Mts, West Irian, var. *dammaropsis*) gives the bracts as yellow. Brass n. 8892 (Hollandia, var. *dammaropsis*) and Brass n. 23340 (Milne Bay, var. *obtusa*) were said to have purple or brown figs, which may be their colour before ripening red. The species clearly calls for the further investigation of living plants to ascertain both the variation and the wild occurrence.

The fig-wasps, collected from both varieties, have been named *Ceratosolen abnormis* (Wiebes 1965*a*, 1966*a*, 1966*b*). This genus, so far as known, pollinates subgen. *Sycomorus* and certain groups of subgen. *Ficus*, namely sect. *Sycocarpus*, sect. *Adenosperma*, sect. *Neomorphe*, sect. *Sycidium* (ser. *Prostratae* and ser. *Pungentes*), and sect. *Ficus* (ser. *Pseudopalmeae*). It has also been reported from a few species of subgen. *Urostigma* (sect. *Conosycea*, sect. *Malvanthera*, and sect. *Galoglychia*) but some of these records are doubtful; and it must be remembered that for the majority of species of *Ficus* the pollinating insects are unknown. This botanical assemblage of possible phylogenetic significance was first pointed out by Wiebes (1963, 1966*a*). I looked into the problem and pointed out that it was impossible to find any botanical means of segregating these groups of *Ficus* into a definable unit (Corner 1967, 1970*b*). Recently, without referring to this earlier work, Ramirez (1974) has transferred all these sections and series of subgen. *Ficus*, supposedly pollinated only by *Ceratosolen*, to subgen. *Sycomorus*, but without the least botanical explanation. I find such a disposition of no more use to the botanist than to reduce subgen. *Urostigma* to subgen. *Ficus* because they appear to be pollinated only, or mainly, by *Blastophaga*. Certainly, as Wiebes and I have emphasized, the entomology and botany of *Ficus* needs to be combined, but far more entomological investigation is needed.

With regard to *Ceratosolen abnormis*, Wiebes relates it with *C. armipes* of *F. itoana* (subsect. *Papuasyce*; Corner 1970*b*), with *C. boschmai* of *F. salomonensis* (subsect. *Auriculisperma* ser. *Theophrastoides*; Corner 1967), and with *C. sordidus* of *F. cynaroides* (subsect. *Auriculisperma* ser. *Cynaroides*; Corner 1967). This seems clearly to be independent evidence of the affinity of these groups of sect. *Sycocarpus*.

In summary, *F. dammaropsis* presents the outstanding combination of the following primitive characters in sect. *Sycocarpus*: pachycaul habit with massive leaf, massive multibracteate axillary syconia with internal floral processes, bistaminate male flowers, red perianth with white ovary, and sublenticular seeds. In contrast, *F. dammaropsis* is advanced in the following points: dioecious habit, saccate perianth, lack of internal bristles, caducous stipules, entire leaf,

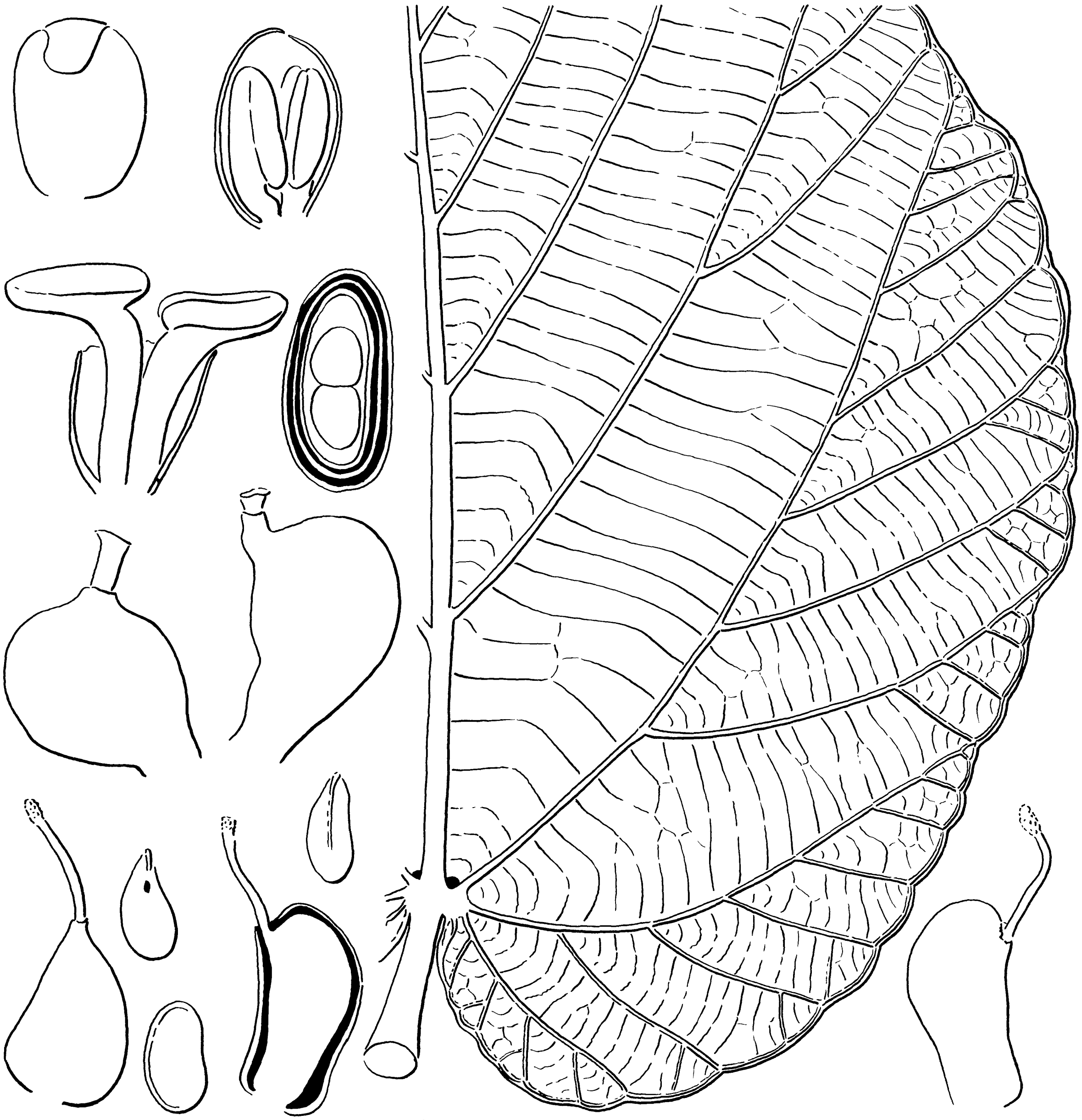

FIGURE 4. *Ficus dammaropsis* var. *obtusa*; leaf-base, magn. × ½; male, gall- and female flowers, seeds, and male flowers in t.s. to show the two bracteoles, magn. × 10.

prominent basal veins, long internodes, and hypogenous cystoliths. It has no close allies and it seems not to have had leptocaul derivatives.

SECT. *SYCOCARPUS* SUBSECT. *PAPUASYCE*

The form of the seed and the colouring of perianth and ovary, though seemingly trivial, are the features which fundamentally separate *F. dammaropsis* from the main subsect. *Sycocarpus* and to ally it with the few species entered as subsections *Papuasyce*, *Auriculisperma* (ser.

Theophrastoides), and *Lepidotus*. In contrast, also, with subsect. *Sycocarpus*, these subsections have no internal bristles (the importance of which I have shown in connection with subgen. *Pharmacosycea*; Corner 1970*b*), no sclerotic cells in the fig-wall (or a few scattered cells in *F. itoana* and *F. microdictya*), and no subnodal glands on the twigs distinctive of subsect. *Sycocarpus*. Instead, they have a pair of basal glands on the underside of the lamina, one in the axil of each main basal vein, but there is an exception in ser. *Theophrastoides*; the pair of basal glands occur in *F. theophrastoides* whereas in *F. salomonensis* there is the conspicuous subnodal gland of subsect. *Sycocarpus* and, most unusually, there are two basal glands on the upperside of the lamina. Except for this last point, the other distinctions from subsect. *Sycocarpus* are shared also with sect *Ficus*, which has the free tepals and is pollinated, so far as known, by *Blastophaga*. Nevertheless, two more exceptions must be mentioned to show the difficulty in relying on any single character in the classification of *Ficus*. In subsect. *Sycocarpus*, the Bornean *F. francisci* has two basal glands, no subnodal gland, and a seed which lacks the prominent hilum of the subsection; by these points it should be referred to subsect. *Papuasyce*, but it has the red ovary of subsect. *Sycocarpus* where it fits closely with the Bornean *F. cereicarpa* in subser. *Fulvidulae* (Corner 1965, p. 160). Then, the little known Sumatran *F. gilapong* of the same subseries appears to have the white ovary of subsect. *Papuasyce*, though the colour of the saccate perianth of the gall-ovary is not known.

It has been impossible to fit the allies of *F. dammaropsis* into a simple phyletic sequence. They have various relict features and they are variously advanced in their parallel evolution into leptocauly, but they point to a pachycaul ancestor with multibracteate syconium on the Melanesian Foreland (Corner 1967, 1969*b*, 1970*b*, 1975*b*, 1976). I note that this devious manner of descent in subgeneric taxa has wide, if not universal, occurrence in flowering plants and has given rise to speculation on reticulate evolution, as if through hybridization between different sections, of which there is no evidence. What is ignored seems to be the enormous amount of species-making during the pachycaul phase; modern pachycauls are specialized relics of what may have been that stupendous promiscuity. With this precaution it is necessary to re-examine continually the tenets of classification, especially when dealing with tropical plants for which, too often, only herbarium fragments have been available.

The uncertain position of the cauliflorous *F. pritchardii* of Fiji led me to transfer it from subgen. *Pharmacosycea* to sect. *Sycocarpus* subsect. *Papuasyce* (Corner 1970*b*). This subsection consists of the dioecious *F. itoana* of New Guinea, New Britain, and New Ireland, the monoecious *F. microdictya* of New Guinea, and the monoecious *F. pritchardii*, all of which I have illustrated (Corner 1970*b*). There are no other examples of monoecism in subgen. *Ficus*. When there was but the one instance of *F. microdictya*, I treated it as an odd reversion in an otherwise advanced and leptocaul species derived from the ancestry of *F. itoana*. The addition of *F. pritchardii*, however, dissolves this notion because it is highly improbable that a similar reversion would have occurred a second time in a species so widely separate geographically, though both are comprehended in Melanesia. It is more probable that the monoecism was inherited from the primitively monoecious state of subgen. *Ficus*, connected perhaps with that of subgen. *Pharmacosycea*. For *F. itoana*, therefore, one must look for a different origin, and this seems to connect with subsect. *Dammaropsis* where *F. itoana* becomes the leptocaul derivative and cauliflorous; it has the perianth, ovary, bistaminate male flower, and hypogenous cystoliths of *F. dammaropsis*, though greatly simplified in leaf and fig. In contrast, *F. pritchardii* has amphigenous cystoliths and unistaminate male flowers, but *F. microdictya* has the mixture of

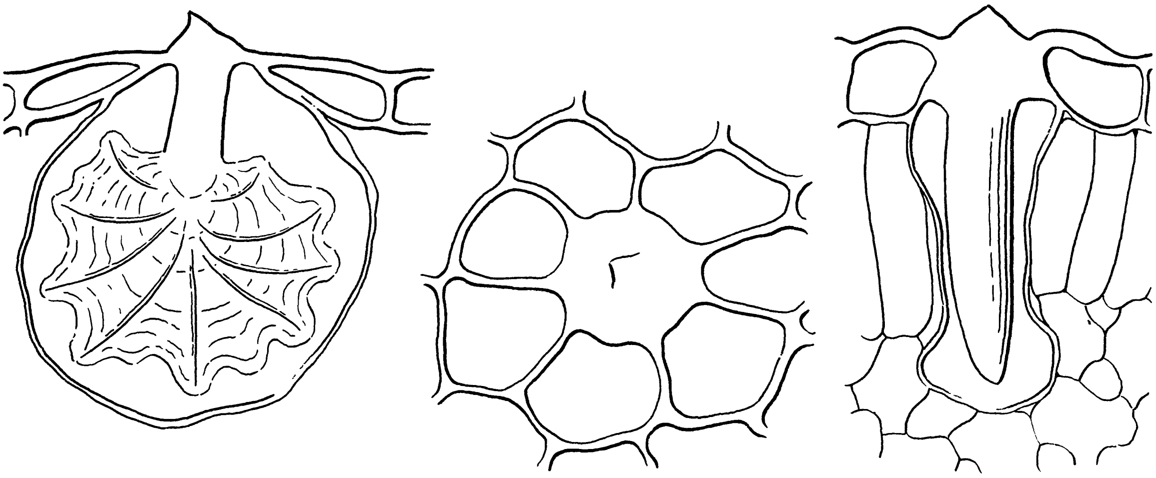

FIGURE 5. *Ficus theophrastoides*; cystoliths from the lower side of the lamina (left) and the upperside (right), with a cystolith facet from the upperside of the lamina; magn. × 310. (E. S. Brown 2568, Solomon Islands.)

hypogenous cystoliths and 1–2 stamens in the male flower. Both species, nevertheless possess a peculiar cystolith, which resembles a microscopic nail driven into the epidermal cell (figure 5). This cystolith has a very stout columella and little or no secretion into the cell-cavity. It does not occur in *F. dammaropsis* or in *F. itoana* but it is present in the pachycaul (and dioecious *F. theophrastoides* of the Solomons, though not in its apparent ally *F. salomonensis*. Both these species of ser. *Theophrastoides* have amphigenous cystoliths but they differ, as already mentioned, in the position of the leaf-glands. I am led to suppose that I have over-simplified the concept of both subsect. *Papuasyce* and ser. *Theophrastoides*; it is an easy mistake when, in dealing with a large number of species, the first concern is the disposition of the majority. It may be necessary to split subsect. *Papuasyce* into *F. itoana*, as the type-species, in alliance with subsect. *Dammaropsis*, and a new subsection for the monoecious *F. microdictya* and *F. pritchardii* from the stock of which the dioecious *F. theophrastoides* and, possibly, the progenitors of subsect. *Sycocarpus* arose.

On turning to the entomological evidence, I find that Wiebes assigns the insects of *F. dammaropsis*, *F. itoana*, *F. microdictya*, and *F. salomonensis* to the group of *Ceratosolen armipes*, but that of *F. pritchardii* to the group of *C. pygmaeus*. This, as Wiebes (1963) pointed out, introduces some botanical perplexity because the *C. armipes* group pollinates also, so far as known, sect. *Adenosperma*, while the *C. pygmaeus* group pollinates sect. *Sycidium* ser. *Pungentes*. If the entomology is preferred, then sect. *Sycocarpus* appears to consist botanically of two lines of descent, one in connection with *Adenosperma* and the other with *Pungentes*, but I find as yet no botanical substantiation. Subsequently Wiebes (1965*b*) drew attention to the presence of the plantar protuberance on the male tarsus of some species of *Ceratosolen* which, if phyletic, would exclude the insects of *F. dammaropsis* and *F. salomonensis* from this circle, but admit that of *F. pritchardii*. While I claim no finality for my classification of *Ficus*, the disentanglement of which has cost me many years, it is clear that, before it can be tested satisfactorily on entomological grounds, we need to know about the insects of the many species of *Adenosperma* and *Sycocarpus* which have yet to be collected. In the old days, a botanist might collect insects; now it seems that students are too specialized.

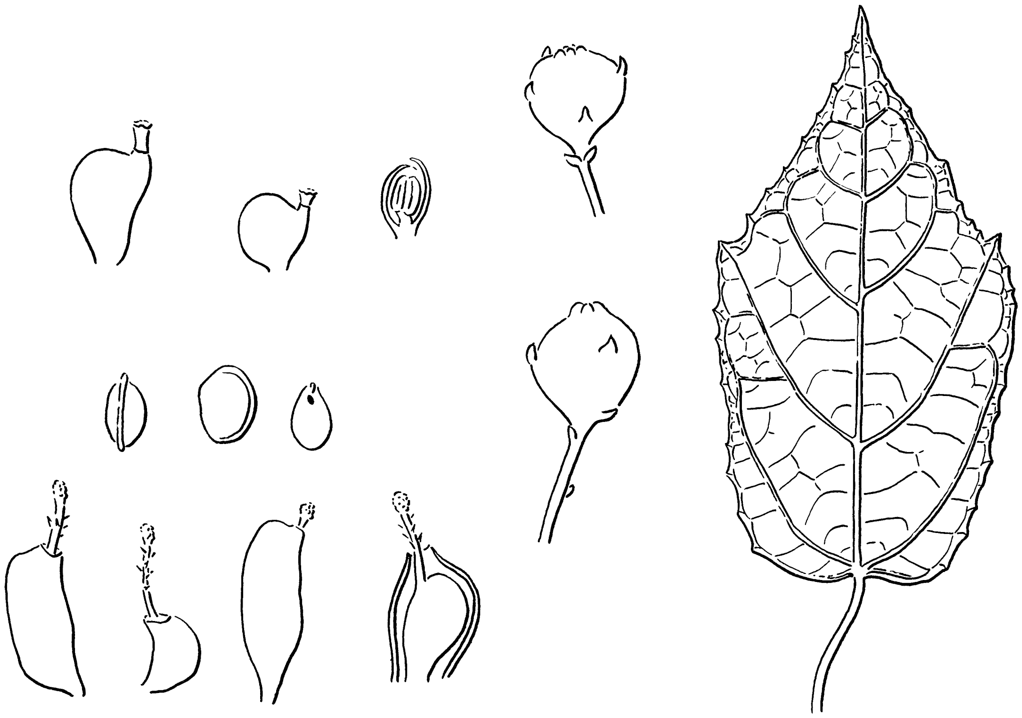

FIGURE 6. *Ficus griffithii*; leaf, magn. × ½; figs, magn. × 1; female flowers and seeds, magn. × 10; from Griffith 1143. Male and gall-flowers, magn. × 10; Kerr 1125.

SECT. *SYCOCARPUS* SUBSECT. *LEPIDOTUS*

In this subsection there is the single, rare, and little known *F. griffithii* of lower Burma and Thailand (figure 6). It is a shrub, perhaps a small tree, of which merely three collections appear to have been made, namely Griffith 1143 (Mergui), and two by A. F. G. Kerr from Saraburi, n. 1125 from Ban Nawng Bua and 7049 from Menam Sak. It has no close ally in Asia but, if it occurred in New Guinea, it might qualify as a leptocaul derivative of *F. dammaropsis*, in some ways leading to *F. itoana*, but distinguished by the habit, the unistaminate male flower, the small and scattered lateral bracts on the pedunculate figs, the persistent but short stipules, and the membranous dentate lamina with few lateral veins. It is to be hoped that it will be rediscovered and that its insects will be collected. The structural similarity with *F. dammaropsis* leads me now to reconsider two other subsections of subgen. *Ficus*, one of which (sect. *Neomorphe*) introduces the well known ellipse of Malesian biogeography with foci in southeast Asia and Melanesia.

SECT. *FICUS*, SECT. *NEOMORPHE*, AND SECT. *SINOSYCIDIUM*

In discussing the complex of *F. deltoidea*, I introduced the Philippine *F. pseudopalma* as a pachycaul species that seemed nearest to the ancestry of the complex (Corner 1969*a*). It bears, also, on the origin of ser. *Theophrastoides*. The habit of *F. pseudopalma* has been illustrated by Condit (1969, fig. 16). Its strong resemblance to *F. theophrastoides* is heightened by a similar shortly pedunculate fig without lateral bracts, internal bristles, or sclerotic cells, by the two basal glands of the lamina, and by the amphigenous cystoliths which have in *F. pseudopalma* a similar, if not so stout, columella (Corner 1967, figs 42, 51, 52; 1969*a*, fig. 6). The fig-wasp of *F. pseudopalma* is *Ceratosolen bakeri*, referred by Wiebes (1963) to the *C. armipes* group which, as just mentioned, is that concerned with *F. dammaropsis*, subsect. *Papuasyce*, and ser. *Theophrastoides*. In contrast, the complex of *F. deltoidea* is pollinated by *Blastophaga*, though one would like confirmation from the Bornean varieties *arenaria* and *motleyana*. The main distinction between *F. pseudopalma* and *F. theophrastoides* lies in the perianth the free tepals of which in the first puts it in sect. *Ficus* and the cupular form puts the second in sect. *Sycocarpus*. Yet, this very distinction, here of sectional significance, is exactly that which separates two closely allied species in sect. *Neomorphe*, namely *F. auriculata* and *F. oligodon* of continental south east Asia; their domain encompasses that of *F. griffithii*.

The problem of these two species is conveyed in figure 7, where I have copied my earlier drawings of the flowers of *F. oligodon* made from living material but published under the synonym of *F. pomifera* Wall. (Corner 1933). I must note that this synonym is not *F. pomifera* Kurz, which is a synonym of the climber *F. aurantiacea* of sect. *Kalosyce* (Corner 1976); the two have been confused by Croizat (1968, pp. 133–135). *F. auriculata* and *F. oligodon* are Sino-Himalayan trees, the first to the north of latitude 17° N, the second also extending south into the Malaya Peninsula as far as Selangor and Pahang. Their large cauliflorous figs, 4–8 cm wide (living), without lateral bracts, ripen red or reddish brown to purple, and the seed-figs are edible, if insipid. *F. auriculata* is well known in cultivation (Condit 1969, fig. 10). It is the smaller tree, up to 12 m high, with brownish bark and large cordate leaves (lamina up to 40 × 32 cm) which are dentate in the distal half but entire in the proximal half developed from the elongate basal veins. *F. oligodon* grows to 15 m high, probably more, and has greyish white bark and smaller, rarely cordate, leaves which are rather coarsely and distantly toothed. Both have bistaminate ostiolar male flowers in which the filaments of the stamens are joined at the base in the manner of sect. *Neomorphe*. The perianth of the gall- and female flowers consists in *F. auriculata* of three red tepals shortly joined at the base; in *F. oligodon* this red perianth is saccate and normally covers the white ovary. The female style of *F. auriculata* is hairy, that of *F. oligodon* glabrous. Thus, typically, these species are readily distinguished; *F. auriculata* fits sect. *Neomorphe* but *F. oligodon* must be keyed out also in sect. *Sycocarpus*. Where, however, both species grow together about 17° N, there appear to be hybrids. Some herbarium specimens from Assam, Burma, north Thailand, and Indo-China have the leaves of *F. oligodon* and the flowers of *F. auriculata*, or vice versa while some specimens have intermediate forms of perianth (figure 7*a*, *c*) associated with either form of leaf. On first meeting one or two such specimens, I took them to be mixtures such as may happen in the collection of cauliflorous trees when after drying, detached figs are bundled up with the wrong leaves, but such collections became too numerous for this assumption. There is, perhaps, another explanation of the leaf-variation. To save time and labour in the collection of the large leaves of *F. auriculata*, the collector may take the leafy ends of the cauliflorous twigs where the leaves are small, reduced, and often similar to those of *F. oligodon*; but this does not explain the differences in perianth and the intermediate forms.

The botanical alliance between *F. auriculata* and *F. oligodon* has been proved entomologically (Wiebes 1963, 1966*a*); they have the same fig-wasp *Ceratosolen emarginatus*, from which one may conclude that they can hybridize. It was, indeed, this fact of the insect which induced me to transfer *F. oligodon* from the neighbourhood of *F. itoana* to sect. *Neomorphe* (Corner 1962*b*, p. 395). The fig-wasp is related by Wiebes to the *C. appendiculatus* group which pollinates both sect. *Neomorphe* and the monoecious subgenus *Sycomorus*.

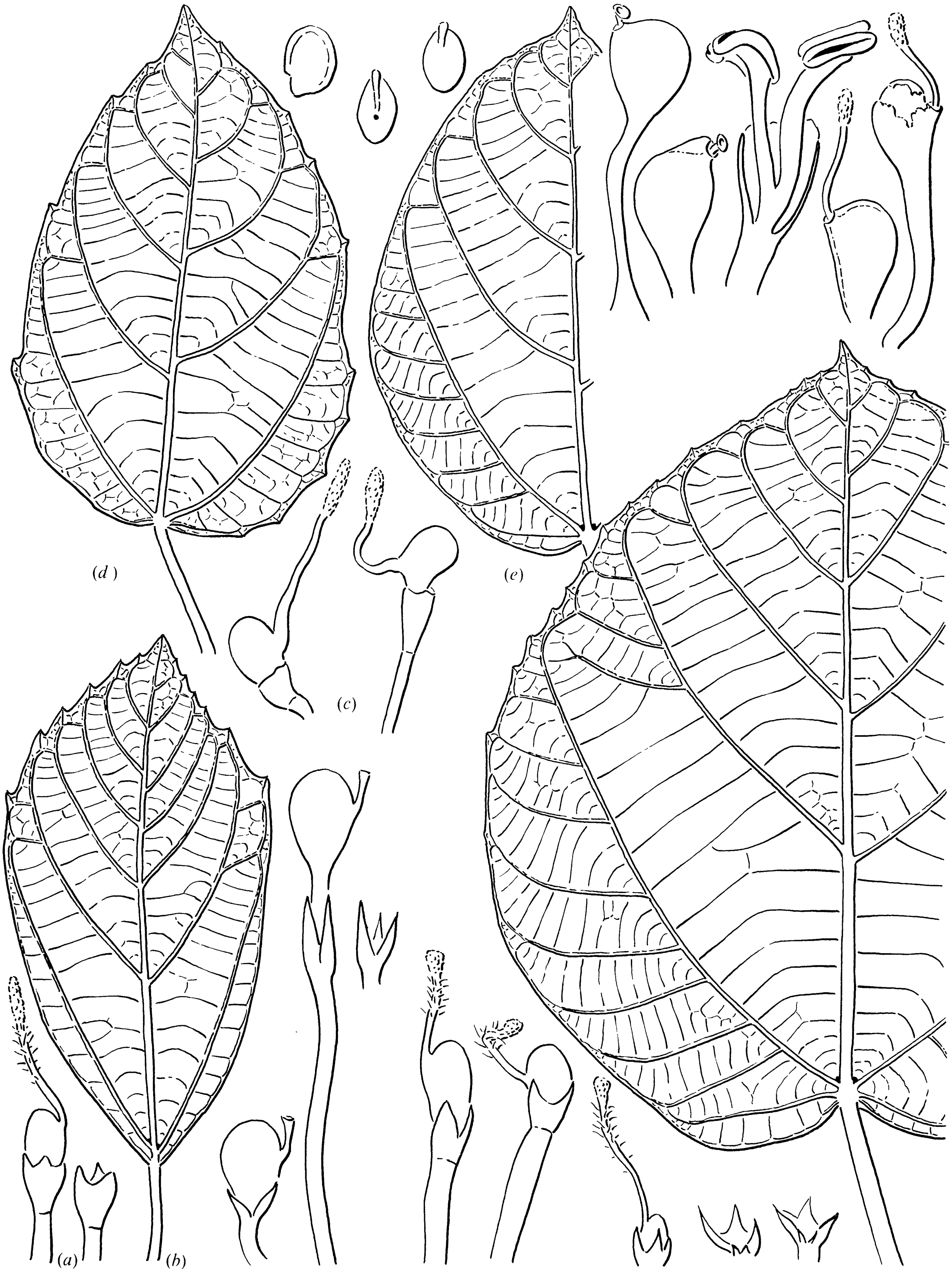

FIGURE 7. *Ficus auriculata* (lower row), with tripartite perianth, cordate leaf, and two female perianths cut open; (*a*) female flowers of W. T. Tsang 29392 (Tonkin), with perianth of intermediate form; (*b*) narrow leaf of C. d'Alleizette (Tonkin). *F. oligodon* (upper row), with saccate perianth; (*c*) female flowers with short perianth from Hook.f. et Thom. Covellia 8; (*d*) typical leaf from Kerr 3410; (*e*) leaf as in *F. auriculata* from Kerr 4946.

Other instances can be given in which the normally partite perianth becomes more or less gamophyllous. It happens among various species of subgen. *Urostigma* and *Pharmacosycea*, and it is merely varietal in such as *F. hirta* var. *malayana* (sect. *Ficus*), *F. calodictya* var. *gamophylla* (sect. *Rhizocladus*), *F. casearioides* var. *gamosepala* (sect. *Adenosperma*), and, indeed, *F. variegata* var. *chlorocarpa* (sect. *Neomorphe*; Hill 1967). The situation in *F. auriculata* and *F. oligodon* is, however, more indicative because on structural grounds I have separated them as ser. *Auriculatae* from the main body of sect. *Neomorphe* in ser. *Variegatae*. They lack the subsessile flowers, the compressed male flowers, and the red ovary, all of which features relate ser. *Variegatae* with subgen. *Sycomorus*; instead, they have the pedicellate flowers of sect. *Sycocarpus*, its strongly dimorphic styles which, in the gall-flowers, are short and dilated into the infundibuliform stigma, and the white ovaries distinctive of the more primitive subsections of *Sycocarpus*. The male flowers of ser. *Variegatae* have more or less gamophyllous tepals; in *F. auriculata* the tepals are free but in *F. oligodon* they are united into the saccate perianth. Moreover, the very numerous, suberect, apical bracts of *F. auriculata* recall those of *F. dammaropsis* rather than those of

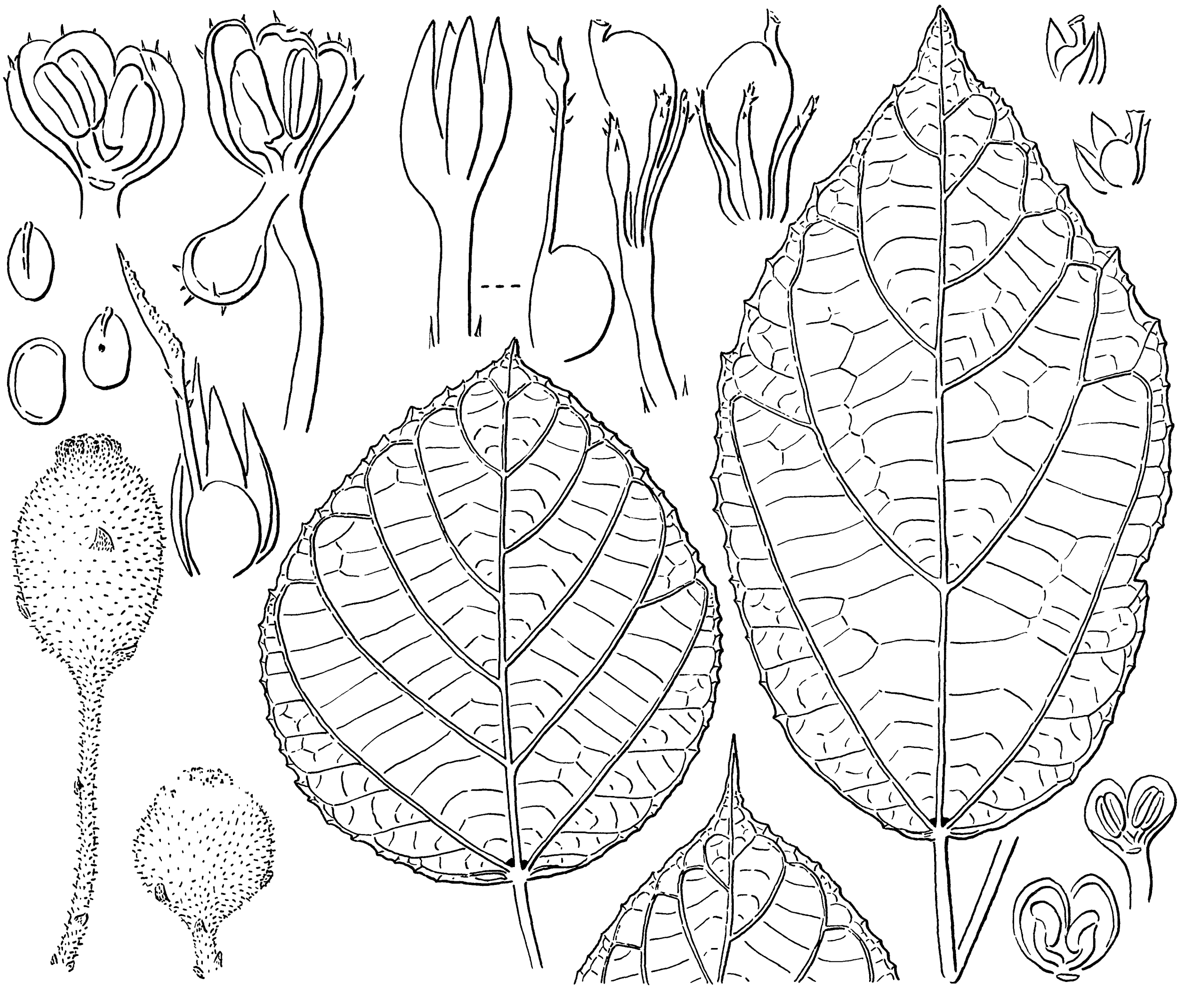

FIGURE 8. *Ficus tsiangii*; ovate leaf, shortly stalked fig, gall- and male flowers with hispidulous tepals, from Henry 9407; large leaf, from W. P. Fung 2566; long-stalked fig and young gall- and male flowers with glabrous tepals, from H. C. Chow 540; female flowers and seeds, from Tsiang 4315. Leaves, magn. × ½; figs, magn. × 1; flowers and seeds, magn. × 10.

F. racemosa (subgen. *Sycomorus*) to the fig-wasp of which (*C. fusciceps*) that of *F. auriculata* and *F. oligodon* is said to be close (Wiebes 1963). Hence, in spite of the astonishing resemblance in general between ser. *Auriculatae* and ser. *Variegatae*, the former may belong with *F. griffithii* to the ancestral stock of sect. *Sycocarpus* in continental Asia, while ser. *Variegatae* represent a dioecious derivative from the stock of subgen. *Sycomorus*, now principally African. Between them and the Melanesian stock of *Sycocarpus* there is the relict *F. pseudopalma* of the Philippines. It adds the large seed which the complex of *F. deltoidea* signifies for the ancestral stock of *Ficus* itself. As a test of this hypothesis, we await the discovery of the fig-wasp of the Philippine *F. rivularis* (Corner 1969*b*).

In describing sect. *Sinosycidium* of subgen. *Ficus* for the small Chinese tree *F. tsiangii* (Corner 1960*a*, p. 24), I emphasized its relation with sect. *Ficus* (disperse and ostiolar, bistaminate, male flowers) and with sect. *Sycidium* (vegetative features, cauliflory, pedicellate fig with scattered lateral bracts, and free pinkish setulose tepals). The introduction of *F. pseudopalma*, *F. auriculata*, and *F. griffithii* into the problematic ancestry of *F. dammaropsis* and sect. *Sycocarpus* implies consideration also of *F. tsiangii* (figure 8). The disperse male flowers, which it possesses, are a primitive mark. They preponderate in the monoecious subgen. *Urostigma* and subgen. *Pharmacosycea* where the exclusively ostiolar male flowers appear to be a restriction. In subgen. *Ficus*, disperse male flowers are found merely in two series (Tricocarpeae, Distichae) of the climbing sect. *Rhizocladus* of uncertain ancestry (Corner 1976), besides the case of *F. tsiangii*. I conclude that the disperse male state was part of the equipment of the primitively multibracteate syconium of which *F. tsiangii* is the modern relic. It emphasizes the western focus of the elliptical distribution of subgen. *Ficus* and, possibly, the link through the Philippines with the eastern focus, for this is the range of *F. pedunculosa* (Corner 1976), as I have discussed in connection with the figs of the New Hebrides (Corner 1975*b*) and those of the Solomons (Corner 1967). It appears that there is considerable variation in detail in *F. tsiangii*, the fig-wasp of which is not known. It is to be hoped that Chinese botanists will resolve these matters.

Figure 9 is an attempt to collate all these conclusions about the ancestry of sect. *Sycocarpus* which can be derived from living species. It differs from the scheme drawn up for sect. *Adenosperma* (Corner 1969*b*, fig. 5) because it is centred on *F. dammaropsis*. Most series or species in this diagram appear as relics and indicate the large number which has become extinct. In contrast, sect. *Adenosperma*, ser. *Cynaroides*, and especially subsect. *Sycocarpus* retain a remarkably full record of diversity which I attribute to their relatively late evolution without, as yet, the extinction of the more primitive or the intermediate. Thus, in ser. *Cynaroides*, *F. immanis* comes exactly between *F. cynaroides* and *F. lancibracteata* (Corner 1967, p. 128). There are very close fits between *F. mollior* and *F. adenosperma* and between *F. funiculosa* and *F. erythrosperma* in the two main series of sect. *Adenosperma*. In subsect. *Sycocarpus* there are numerous examples of this specific intricacy. I postulate the ancestral form of this great alliance as pachycaul, brown hairy, with multibracteate syconia, monoecious, polytepalous, with disperse male flowers 2–3 (–5) staminate, with red tepals, ? red ovary, internal bristles, large seed, and amphigenous cystoliths. Whether this ancestor occupied the whole range from Laurasia through the Philippines and north Borneo to the Melanesian Foreland in their Eocene or Cretaceous state, as Croizat supposes in his theory of tracks, or migrated with evolutionary progress from a Laurasian base, which subgen. *Sycomorus* and sect. *Ficus* imply, there is no decisive evidence. I favour the second possibility because it seems improbable *Ficus* or subgen. *Ficus* or sect. *Sycocarpus* came into uniform existence over the whole of this range.

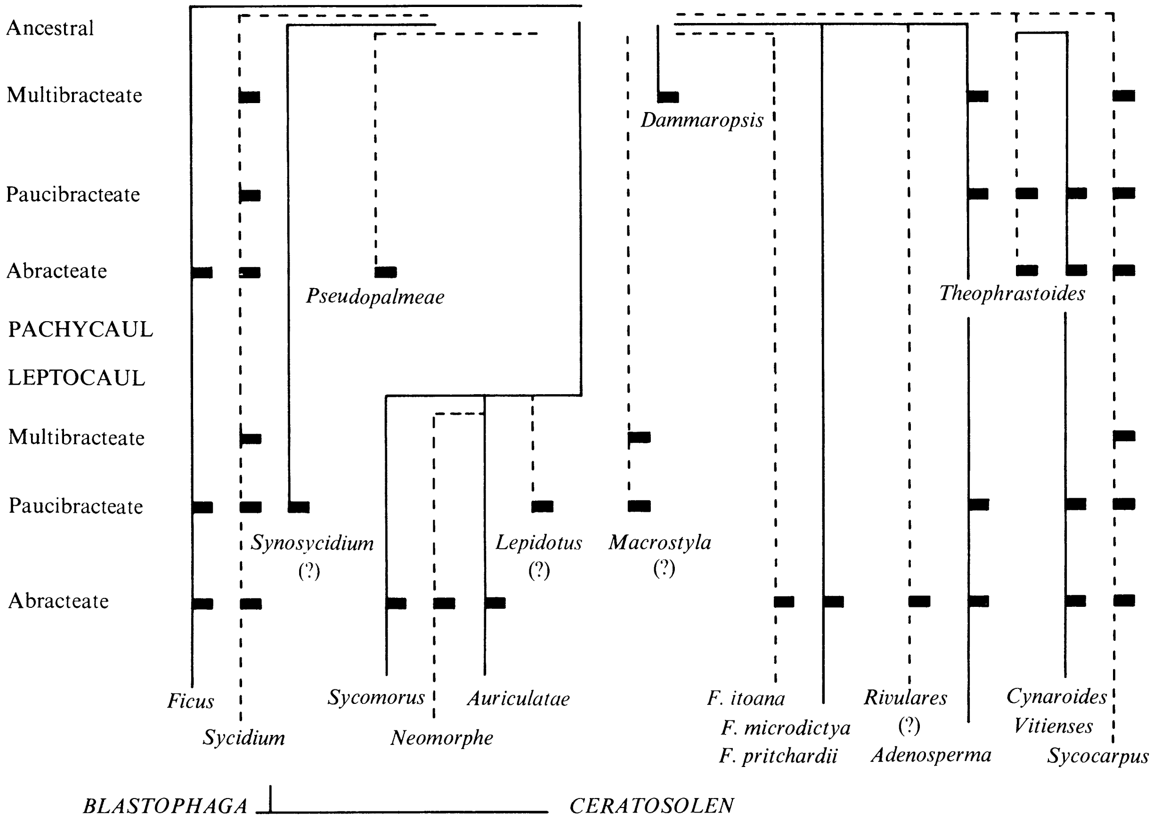

Figure 9. Diagram to show the relations of the series and sections of subgen. *Ficus* and subgen. *Sycomorus* to sect. *Sycocarpus* centred on *F. dammaropsis*, according to blastophagy. The presence of vegetative and fig forms in the groups is shown by thick dashes relating to the lists on the sides of the diagram. For clarity, lines of descent are shown alternately by continuous and broken lines. (?) signifies an unknown pollinating insect.

Multibracteate species in subsect. *Sycocarpus*, and the origin of geocarpy

It is this group of *Ficus* which supplies most evidence for the following conclusions:

1. From pachycaul treelets with multibracteate syconia the leptocaul trees and shrubs with simpler construction have been derived.
2. This evolution has taken place repeatedly in *Ficus* and in parallel in all its successful lines of descent.
3. The pachycaul is geographically limited while the leptocaul may spread widely.

Apart from one or two exceptions, as already mentioned, subsect. *Sycocarpus* is defined by the prominent seed-hilum, the red-brown ovary, the colourless perianth which is often much reduced in the gall- and seed-flowers, and the subnodal glands on the twigs. Multibracteate syconia occur in 8 species and about a dozen have small and scattered lateral bracts. The eight species occur in the following three subseries of ser. *Tuberculifasciculatae* and, as usual, they are either west Malesian or Melanesian:

subser. *Praestantes*; *F. praestans* (New Britain), *F. longibracteata* (Solomons).

subser. *Fulvidulae*; *F. cereicarpa* (Borneo).

subser. *Geocarpicae*; *F. megaleia* (Borneo), *F. uncinata* (Borneo, Malaya), *F. beccarii* (Borneo, Malaya), *F. geocharis* (Borneo), *F. subterranea* (Borneo).

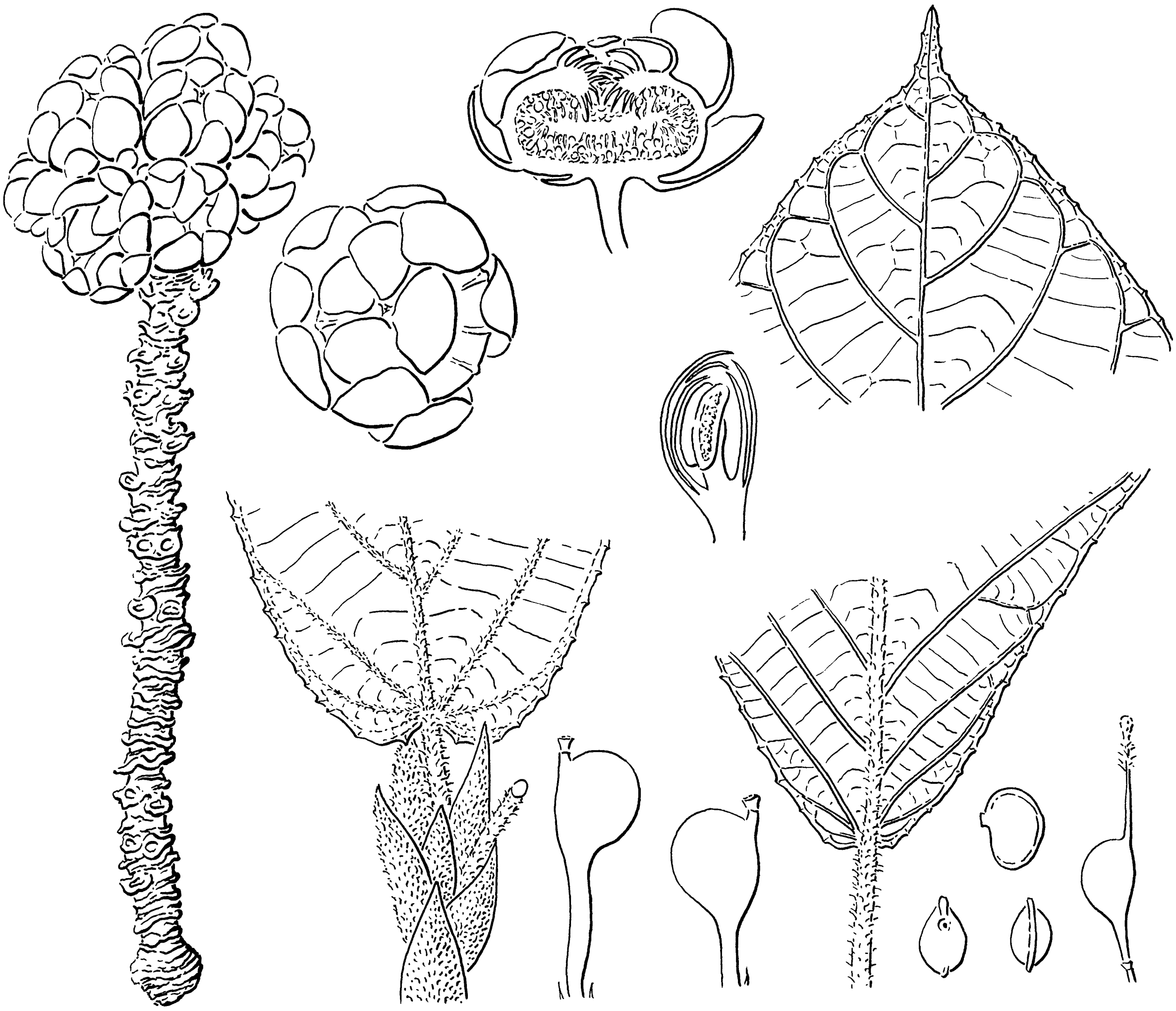

Figure 10. *Ficus praestans*; fruiting twig, stipulate twig, figs, male and gall-flowers, from NGF 13546; leaf apex and base, female flowers and seeds, from NGF 13777. Twigs and leaves, magn. × ½; figs in apical view and section, magn. × 1; flowers and seeds, magn. × 10.

In both species of subser. *Praestantes* the male flowers have one stamen, the gall-perianth covers the ovary, and the female perianth is reduced to a collar round the ovary-stalk. The fig of *F. praestans* resembles a small fig of *F. dammaropsis* var. *obtusa* (figure 10); that of *F. longibracteata* is more like that of var. *dammaropsis* (Corner 1967, figs 56–58). *F. praestans* grows into a rather bushy small tree of forest-valleys. Its twigs, 8–12 mm thick, are not as pachycaul as in *F. dammaropsis* from which it differs also in the brown and microscopically papillate hairs typical of subsect. *Sycocarpus*, in the membranous and denticulate leaf without prominent basal veins, and in the moderately large, persistent, stipules (20–65 × 12–25 mm). The cystoliths are hypogenous as in all species of ser. *Tuberculifasciculatae*. The figs are cauliflorous on stout, unbranched or very sparingly branched, leafless twigs without internodes but with large subpersistent stipules at the ends; this cauliflory comes, evidently, from the massive nature of the figs unsuited to the leaf-axils. Except for the reduced female perianth, *F. praestans* is the most primitive member of subsect. *Sycocarpus*. *F. longibracteata* differs in most details, especially in becoming geocarpic with long stipulate stolons. Connecting species have not been found, and by no simple vicariance can one jump from the one to the other.

Nevertheless, *F. praestans* comes near to subser. *Calopilinae*, most species of which occur in Melanesia. The nearest is *F. neobrittanica* which grows with *F. praestans* in the same valleys and is so much alike, differing mainly in the caducous stipules and the figs without lateral bracts (Corner 1961 *b*, fig. 5), that sterile trees need careful inspection to distinguish them. Both may occur in New Ireland but they have not been found in the well-collected fig-flora of New
they certainly do not occur in the Solomons or eastwards. A close ally, however, of *F. neobrit*-
Guinea; they certainly do not occur in the Solomons or eastwards. A close ally, however, of

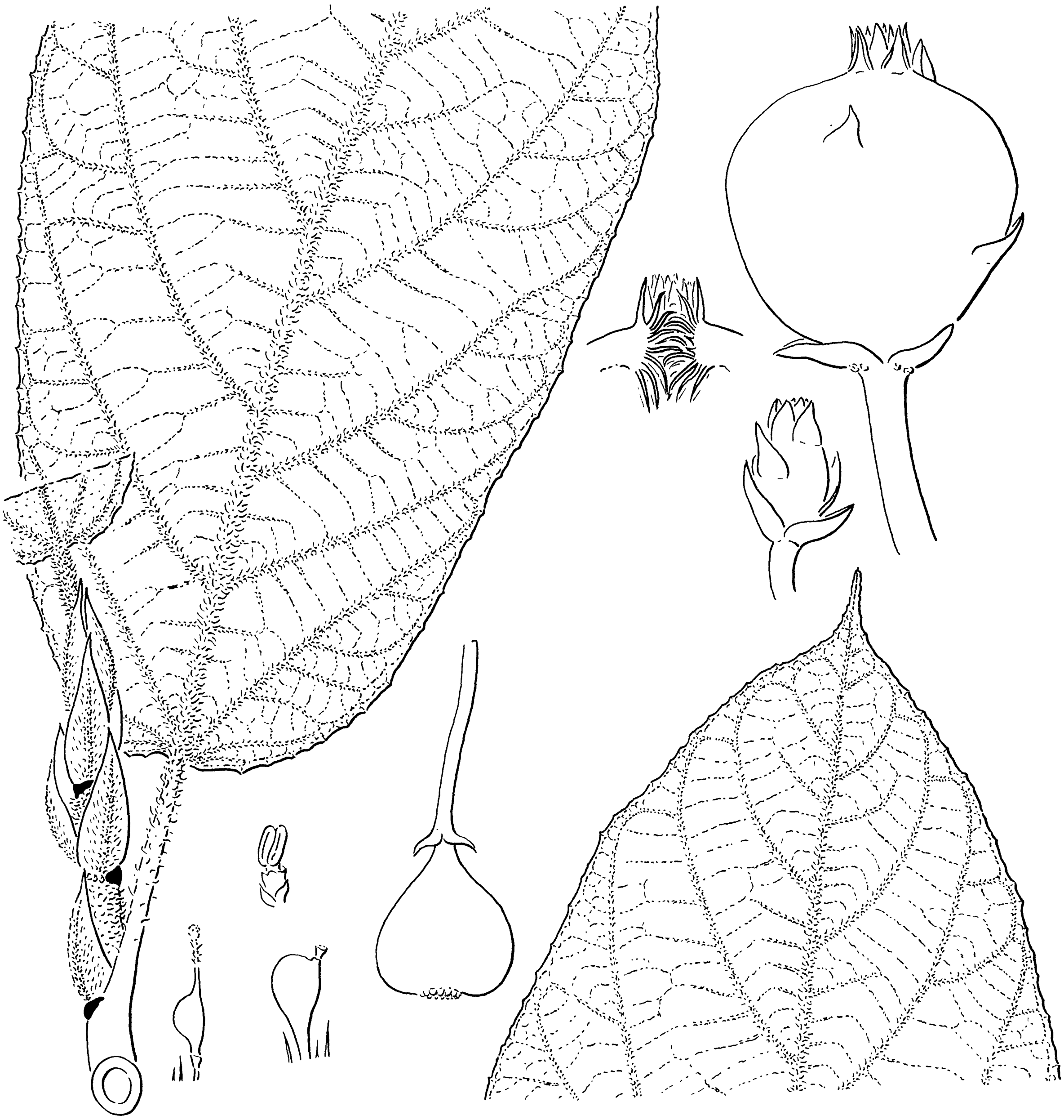

FIGURE 11. *Ficus pachyrrachis*, Hoogland 9140; leaf and fig, magn. × $\frac{1}{2}$; flowers and seed, magn. × 10. var. *porrecta*, BW 682 (upper right); mature and young figs, magn. × 2.

F. neobrittanica is *F. pachyrrachis* of New Guinea which has thicker and more scabrid leaves, prominent basal veins, persistent stipules, smaller apical bracts round the depressed fig-orifice, and larger basal bracts (figure 11); its var. *porrecta*, from west New Guinea, has a few scattered lateral bracts on the figs as a vestige of the multibracteate condition. *F. pachyrrachis* could be regarded as vicariant with *F. neobrittanica* but, whereas this species seems not to have evolved further, *F. pachyrrachis* leads on to the common *F. calopilina*, *F. hispidioides*, and the geocarpic *F. iodotricha* of New Guinea, of which the two former occur in New Britain. This alliance of *F. pachyrrachis* is so closely knit that several collections appear to bridge the specific differences.

Allies of *F. longibracteata* are the following endemic species of the Solomons, which I have illustrated (Corner 1967): *F. profusa*, *F. tanypoda*, *F. scaposa*, *F. dissipata*, and *F. baccaurioides*. This, too, is a closely knit alliance which requires further study in the field. The species often grow together and cannot be regarded as vicarious although, presumably, they have some ecological differences.

Here, then, are two lines of evolution into leptocauly with loss of the lateral bracts. The geographical restriction of *F. praestans*, *F. pachyrrachis*, and *F. longibracteata* is as noteworthy as that of *F. dammaropsis*. They do not grow together, unlike the species which appear to be descended from them; and the advanced leptocaul *F. hispidioides* becomes common and widely spread. A similar line of evolution occurs in ser. *Cynaroides* leading to the leptocaul ser. *Vitienses*.

The Bornean counterpart of *F. praestans* is *F. cereicarpa* in subser. *Fulvidulae* (figure 12); it differs in the soft pale hairs, the smaller lateral bracts, and the abundant internal bristles. It begins a Bornean line of evolution which ends with the common, leptocaul, and geocarpic *F. treubii*, generally without lateral bracts. *F. cereicarpa* is a small tree up to 9 m high, growing in rocky watercourses in the mountain forest of north and central Borneo. Its few branches end in clusters of big leaves which scarcely compact into a crown. In precipitous gorges the trunks project horizontally from crevices in the rock and the thin leaves flutter incessantly in the cool breezes which play along these passages. It is subpachycaul with twigs 5–10 mm thick, subpersistent stipules, and lamina up to 40 × 20 cm in saplings, declining to 13–26 × 6.5–12.5 cm on the branches. The trees appear sterile until one discovers at the base of the stem, more or less hidden in leaf-mould, scaly figs in masses up to 50 cm across formed by stout, leafless, cauliflorous twigs without internodes. I studied many plants on Mt Kinabalu, especially in the Mahmud valley, and saw no instance of an axillary fig. The fig-body, up to 8 cm wide when living, though drying to 3–5 cm, has many small lateral bracts the tips of which become characteristically incurved towards the orifice. The figs ripen brown to pink and are probably eaten by pig, deer, rhinoceros, and rats.

The nearest ally of *F. cereicarpa* is the more leptocaul *F. francisci* which frequents the banks of more sluggish streams in the lowlands of Borneo. About 1000 m alt., they may grow together until, at higher altitudes, *F. cereicarpa* takes over. *F. francisci* (figure 13) has twigs 2–5 mm thick, smaller leaves, figs without lateral bracts, ripening yellow and borne in similar cauliflorous masses. The botanical alliance is proved entomologically because the fig-wasp (*Ceratosolen josephi*) of *F. francisci* is close to *C. pilipes* of *F. cereicarpa* (Wiebes 1963). A third species of fig, *F. virescens* (Corner 1962*b*, fig. 8), known only from Mt Kinabalu, connects these species with spirally arranged leaves and long petioles to the distichous, shortly petiolate, and geocarpic *F. treubii* (figure 13). This has small figs with few or no lateral bracts and a characteristically caudate leaf which dries light green in the herbarium. It seems to be common in lowland and mountain forest throughout Borneo. The four allies, growing on the slopes of Mt Kinabalu, are

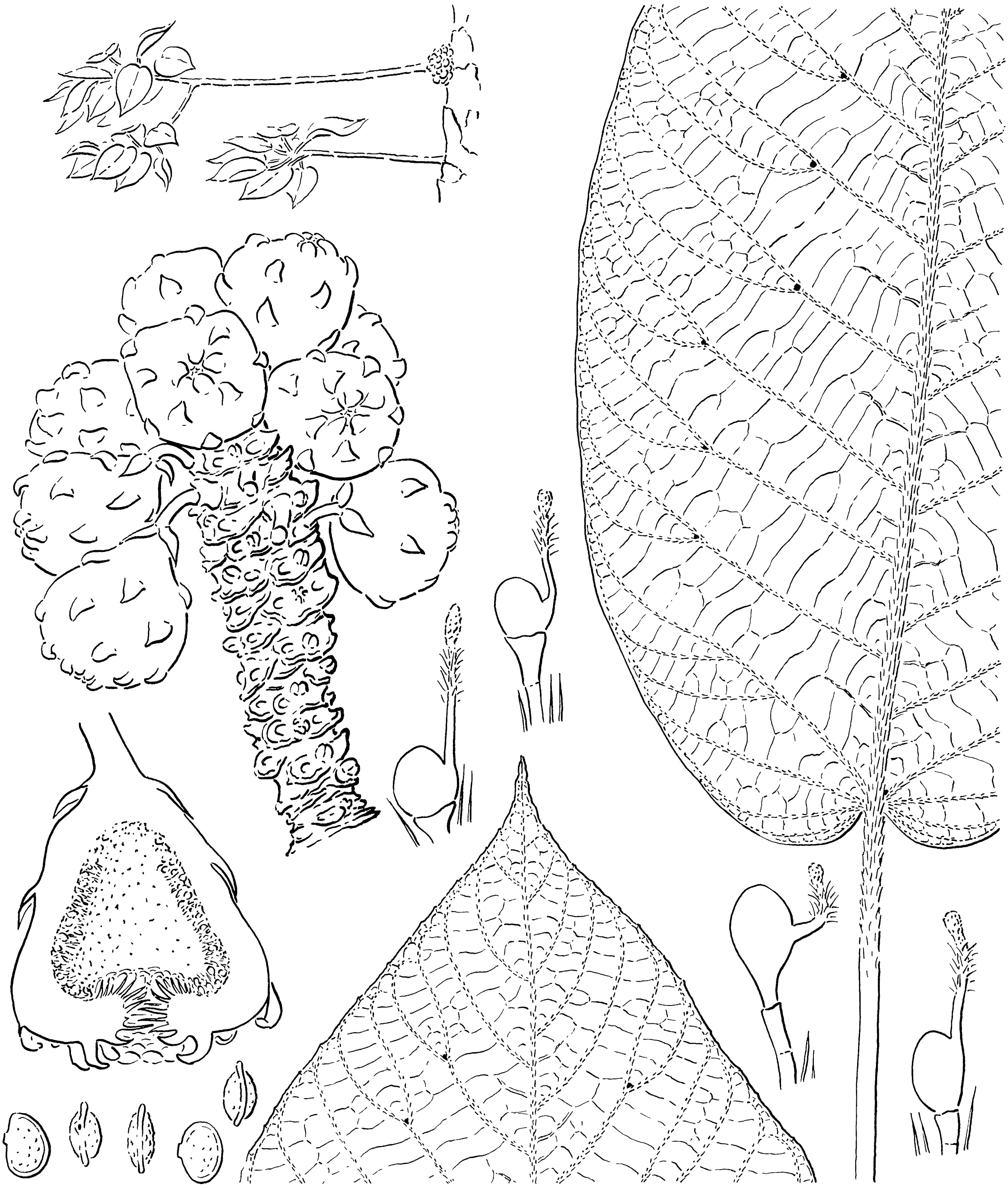

FIGURE 12. *Ficus cereicarpa*; habit of trees in the rocky gorges of Mt Kinabalu, with a cluster of figs at the base of the trunk, magn. × 1/25; leaf, magn. × ½; cauliflorous twig from the fruiting bunch, magn. × ½; fig in section, magn. × 1; female flowers with various perianths and seeds, magn. × 10.

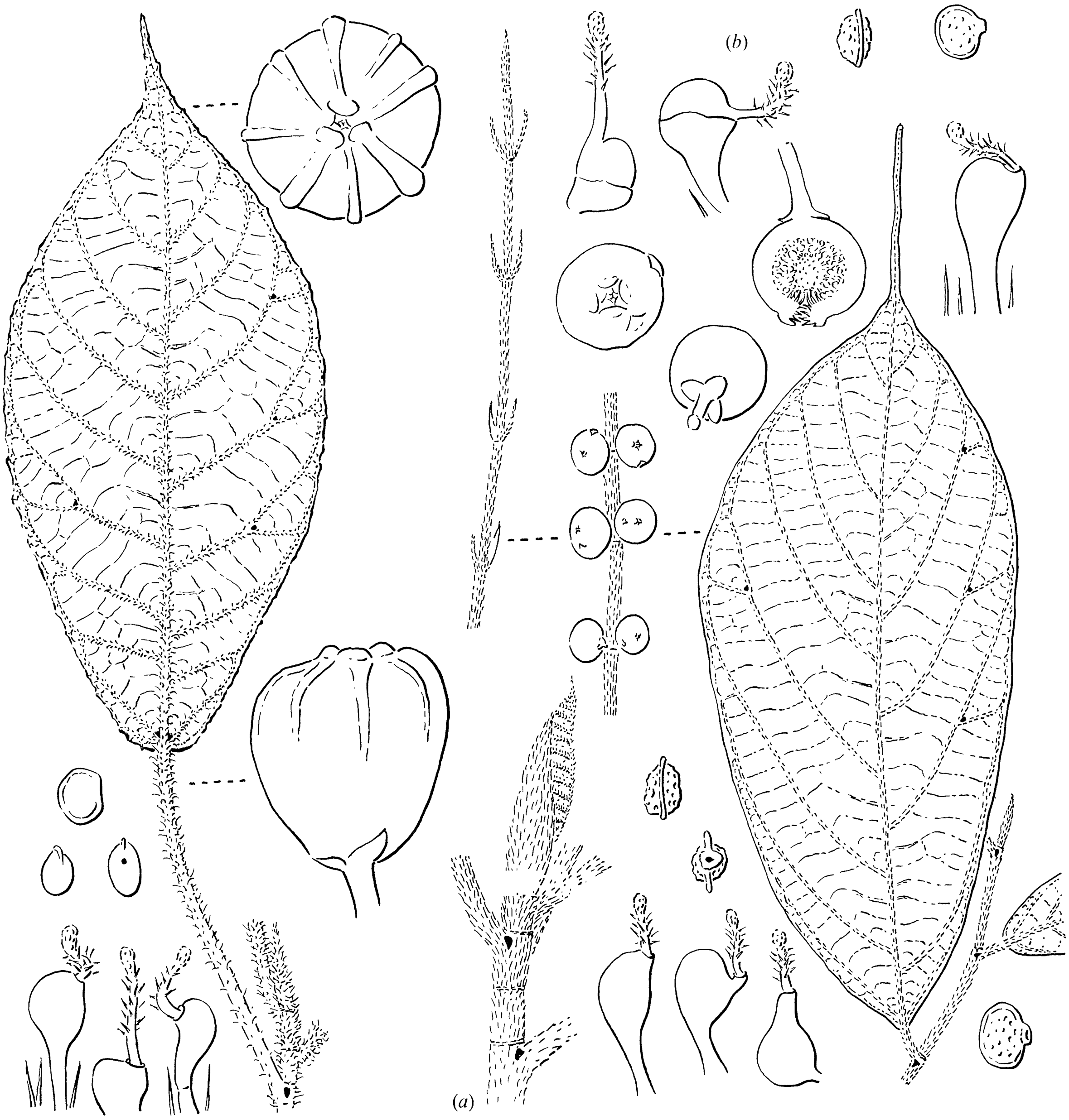

FIGURE 13. *Ficus francisci* (left) with long petiole, two figs (magn. × 2), female flowers and seeds, from Endert 4723. *F. treubii* (right) with short petiole and distichous leaves, geocarpic stolons (mag. × $\frac{1}{2}$), three figs (magn. × 1), female flowers with saccate perianth, and seeds, from Keith A8. (*a*) *F. cereicarpa*, twig with petiolar bases. (*b*) *F. treubii*, female flowers with cupular perianth and slightly pitted seeds, from SFN 26805. Twigs and leaves, magn. × $\frac{1}{2}$; flowers and seeds, magn. × 10.

not vicarious though they differ ecologically; yet, *F. treubii* infiltrates the habitats of the other three. To this alliance I would add the rare *F. gilapong* of Sumatra, known from three collections, as another geocarpic derivative retaining the spirally arranged leaves; its small figs have no lateral bracts. Geographically it presents the disjunction seen also in *F. oleaefolia* (Corner 1969*a*).

Subser. *Geocarpicae*, as the main group of geocarpic figs in west Malesia introduces a fascinating alliance of common, yet little known, species. There are seven, and six of these occur in Borneo where four are endemic (*F. megaleia*, *F. geocharis*, *F. subterranea*, and *F. stolonifera*) *F. beccarii* and *F. uncinata* var. *strigosa* extend to Malaya and Lingga (Riouw Archipelago), though neither has been found in southern Johore or Singapore. *F. geocarpa*, allied with *F. stolonifera*, is endemic to Celebes. Perhaps the Moluccan *F. pleyteana* and *F. ternatana* are more distant relatives but they seem rather to connect with subser. *Calopilinae* of New Guinea. Subser. *Geocarpicae* has progressed vegetatively to shortly petiolate distichous leaves and, often, the asymmetric leaf-base. It is advanced in the prevalent geocarpic habit and in the great reduction of the perianth in the gall- and seed-flowers; it becomes a slight rim round the ovary stalk or disappears altogether in *F. megaleia*, *F. beccarii*, *F. uncinata*, *F. geocharis*, and *F. subterranea* (figures 14–16). Yet these five species retain the primitive multibracteate syconium; in *F. geocarpa* and *F. stolonifera* it has advanced to the state with a collar of three basal bracts and merely a few lateral bracts. Such advanced syconia show how the close succession of bracts in the multibracteate is dividing into the peduncular internode and that of the fig-body, very much as the intermediate state of *F. salomonensis* (Corner 1967, fig. 50). The gall-perianth of these two species at first covers the ovary, but that of the seed-flower is a short collar (figure 17).

The shape of these geocarpic trees, which appear always to be sterile, readily identifies them in the secondary or seral forest where they abound. With oblique stems a few metres high and

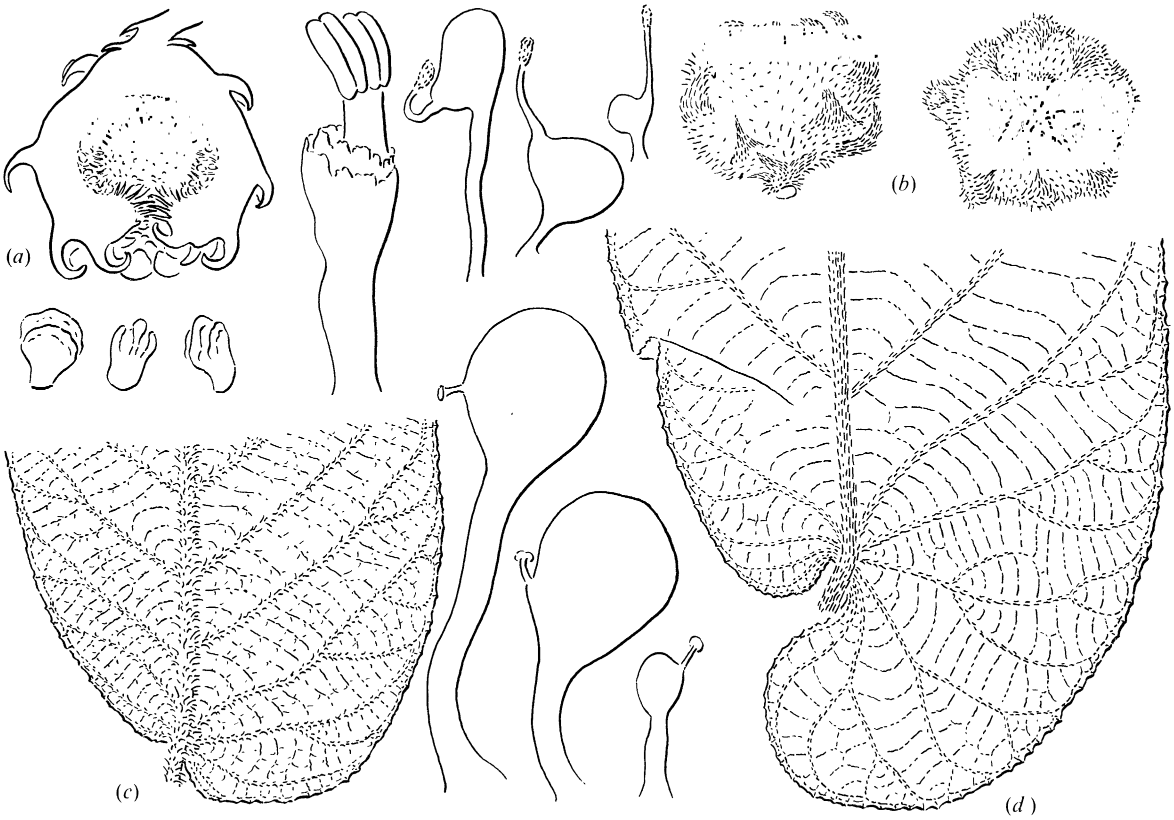

FIGURE 14. (*a*) *Ficus uncinata* var. *uncinata*, glabrous fig in section, magn. × 1. (*b*) *F. beccarii*, hispid figs, magn. × 1; (*c*) *F. uncinata* var. *strigosa*, leaf-base, magn. × ½. (*d*) *F. megaleia*, leaf-base, magn. × ½. (*e*) Gall- and female flowers, male flowers, and seeds of *F. beccarii*, magn. × 10.

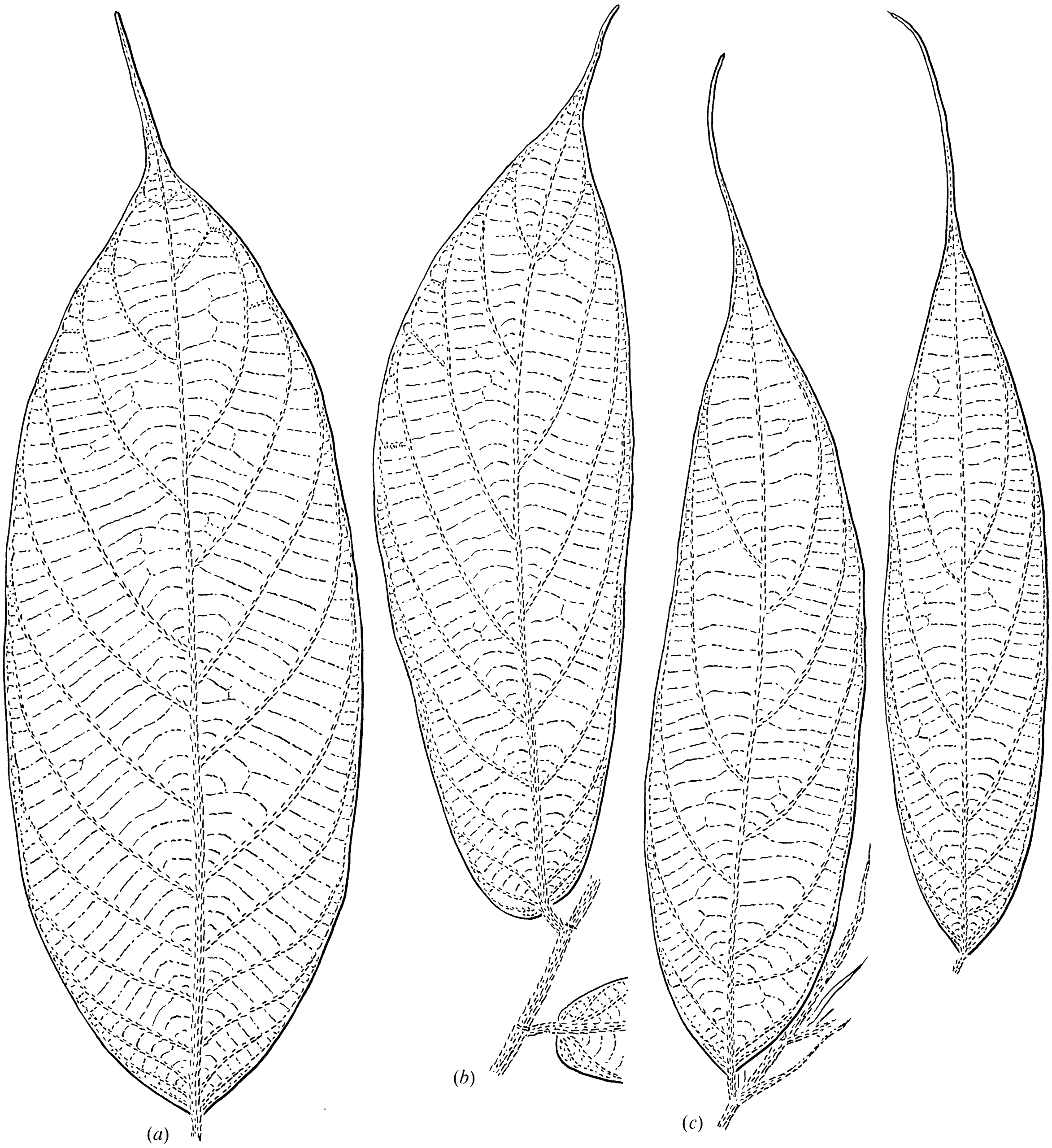

FIGURE 15. *Ficus beccarii*; leaves to show the narrowing of the lamina with decreasing number of lateral veins, the increasing obliquity of the lateral veins with loss of submarginal loops, and the lengthening of the leaf-tip, magn. × ½. (*a*) var. *latifolia*. (*b*) var. *asymmetrica*. (*c*) var. *beccarii*.

branches that often sag with drooping leaves, they construct thickets because the geocarpic stolons turn up at the end of their subterranean growth into leafy saplings; they are, in fact, terricolous counterparts of the stoloniferous epiphyte *F. subulata* (Corner 1976) An exception is *F. stolonifera*; it is an upright tree, reaching 15 m high, of primary forest and its stolons ramp up to 7 m from the trunk through the humus without proliferating. All these stems, as I continually emphasize to draw the attention of collectors, appear sterile because the figs are never

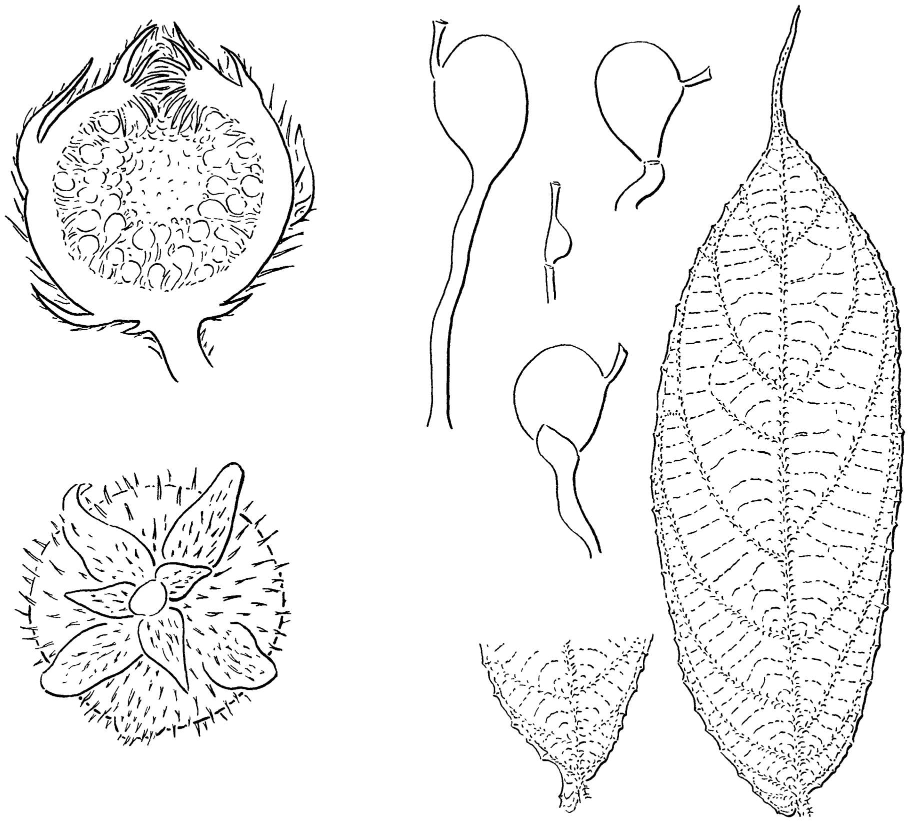

FIGURE 16, *Ficus geocharis*; leaf and leaf-base with the auricular vestige of the cordate base, magn. × ½; figs, magn. × 2; gall-flowers, magn. × 10.

axillary; they are borne underground. If a stolon is grasped near the stem from which it issues, it can be pulled up with its bunches of figs, though in heavy ground into which the leafless stolons burrow and in the tangle of roots and fallen branches by a forest clearing this may be impossible. Since two or more of these species often grow together, care must be exercised in collecting so as to associate the figs and stolons with the appropriate leafy stem. The point is important because the size and form of the seed is evidently specific though fig and flower may appear identical; I have reason to believe that not a few collections are misleading mixtures. I have studied wild plants of all the Bornean species, but I know living *F. geocarpa* only from the moribund specimen in the Kebun Raya at Bogor. In my first account of these species (Corner 1933), I followed custom and used the name *F. geocarpa* for the Malayan plants which, as I later discovered, really represent var. *strigosa* of the Bornean *F. uncinata*.

The study of leaf-development, particularly the venation, in these geocarpic species is to be recommended, because it leads to an unusual state for the genus. The largest leaves, up to 100 × 35 cm, occur in the subpachycaul *F. megaleia* with twigs 4–7 mm thick. In var. *multinervia* the lamina has 14–24 pairs of lateral veins, indicative of considerable apical growth as in *F. pseudopalma* and *F. theophrastoides*. In var. *megaleia* there are 9–12 pairs and in var. *subuncinata* 7–10 pairs, as an expression of curtailed apical growth. The most leptocaul species, with twigs 1–2 mm thick, are *F. beccarii* var. *beccarii*, *F. subterranea*, and *F. uncinata* var. *gracilis* and var. *parva*. They have smaller, caudate-acuminate, leaves with 11–15 pairs of lateral veins in *F. subterranea*, 8–11 in *F. uncinata* var. *parva*, and merely 4–6 pairs in var. *gracilis* and some states

PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

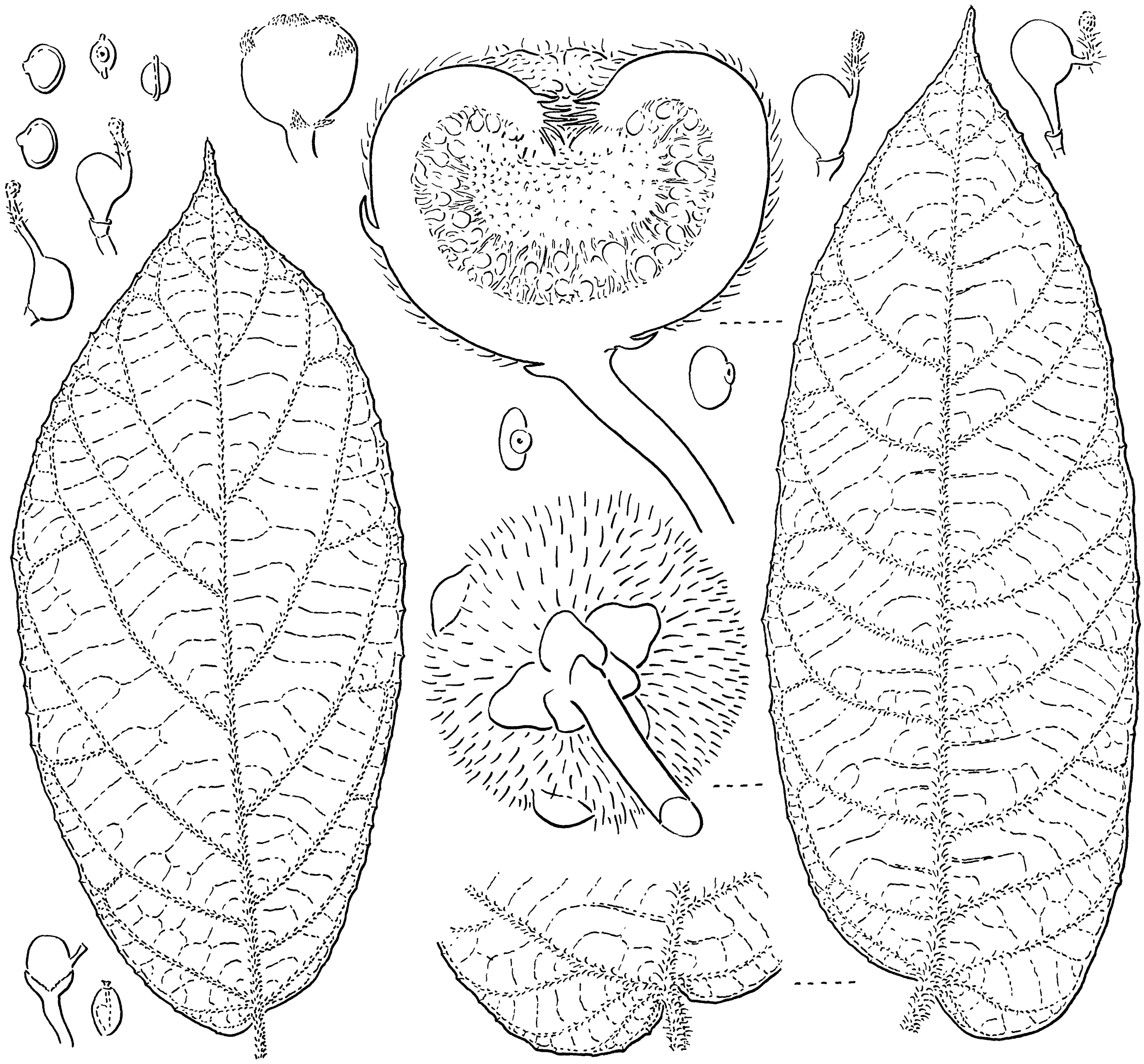

FIGURE 17. *Ficus stolonifera* (left); leaf, fig with hairy bracts (magn. × 2), gall-flowers with split perianth. *F. geocarpa* (right); fig with glabrous bracts, from Herb. Bogor. 5364. Leaves, magn. × $\frac{1}{2}$; flowers and seeds, magn. × 10.

of *F. beccarii*. As the number of lateral veins decreases, the leaf-tip becomes more caudate from the great number of undeveloped laterals (as in the drip-tip of *F. religiosa*), but the lateral veins which develop become more oblique and their submarginal loops disappear (figure 15). This oblique venation occurs in the narrow leaves of many dicotyledons, and it is not clear how it is achieved. Instead of the basal veins elongating from basipetal growth, as usual in *Ficus*, they remain short in these geocarpic figs while intercalary growth increases acropetally with successive lateral veins until the last pair to develop become the most elongate and oblique. The leaf-base is usually asymmetric and most basal veins are developed in *F. megaleia* (figure 14). In contrast, *F. beccarii* var. *beccarii* has a narrowly cuneate leaf-base that is almost symmetrical. All gradations between these extremes are supplied by *F. uncinata* and other varieties of *F. beccarii*. *F. geocharis* retains a vestigial auricle (figure 16). I conclude that the least modified leaf of the subseries is that of *F. megaleia* var. *multinervia* with large acuminate lamina and cordate auricle, and that it was derived from a symmetrically cordate and long-petiolate lamina, the leaves being set spirally on the twig as in *F. cereicarpa*. The ancestral pachycaul may have had leaves massive enough to develop 40–50 pairs of lateral veins; and I hope that, as experimental morphology enlarges its scope, such spectacular plants will be reconstituted.

Since Borneo has clearly been the scene of origin of subser. *Geocarpicae*, so the Bornean subser. *Fulvidulae* with similar pale hairs, but with spirally arranged leaves, point to the ancestral stock which with pronounced cauliflory led to geocarpy. The glabrous fig of *F. uncinata* (figure 14) resembles closely that of *F. cereicarpa*. From the stock of subser. *Fulvidulae* there seems to have been two lines, at least, of leptocaul and geocarpic progress. One has led to *F. treubii* and *F. gilapong*, the other to *F. megaleia* and its allies. Perhaps a third led to *F. geocarpa* and *F. stolonifera* unless they were an early offshoot from the stock of *F. megaleia* which became paucibracteate while retaining the perianth of the gall- and female flowers and the less specialised form of seed. Independent evolution of geocarpy is found in the African species of subgen. *Sycomorus*, in three series of the Indo-Malesian sect. *Sycidium* (ser. *Prostratae*, *Phaeopilosae*, and *Pungentes*), as well as in five other groups of sect. *Sycocarpus*, namely ser. *Longituberculatae* and ser. *Tuberculiasciculatae* subser. *Praestantes*, *Calopilinae*, *Hispidae*, and *Tuberculifasciculatae*. It is a manner of parallel evolution that calls for morphological explanation.

Since the syconium is an inflorescence functioning as a fruit, cauliflory in *Ficus* fits the general explanation of this state provided by the durian theory (Corner 1949). The leptocaul shoot becomes physiologically incapable of bearing the primitively massive fruit. Either the fruit becomes smaller and simpler to fit the thinner twig as a neotenic complex, or dormant buds on the old and physiologically mature parts of the tree develop into stout, leafless or merely stipulate, reproductive shoots to bear the massive fruits. Hence ramiflory and cauliflory enter. The primitively massive and multibracteate syconium of *F. dammaropsis* fits the pachycaul shoot. The less massive but multibracteate syconia of *F. praestans* and *F. cereicarpa* no longer fit the attenuating shoot and are transferred to leafless pachycaul shoots from the trunk. These shoots, in turn, undergo leptocauly. Thus the commonest state of cauliflory in *Sycocarpus* has medium-sized to small syconia (without lateral bracts) on rather slender and branching cauliflorous twigs in which some internodal elongation occurs, e.g. *F. schwarzii* of west Malesia, *F. nota* of the Philippines, and *F. bernaysii* of New Guinea. Leptocauly of the cauliflorous twigs introduces in subtle and scarcely perceivable degrees lengthening of internodes below successive pairs of stipules, and these twigs often develop small leaves as their tips project further from the trunk. With long internodes of insufficient strength, the cauliflorous twigs will sag; the lower ones will reach the ground, root adventitiously, and proceed into the humus or loose soil to bear subterranean figs; and these will conform with the leptocaul twigs which produce them because there is no escape to another source of cauliflory. Geocarpic syconia tend, therefore, to be small and simplified, as in the examples of sect. *Sycidium*. The pecularity of the group of *F. megaleia* is the persistance of the multibracteate syconium while its size diminishes. As regards pollination, the insects must become adapted to the subterranean life, which they may have done merely by acute olfactory sense and enhancement of the burrowing instinct that drives them normally through the tight orifice of the young syconium. In both *F. ribes* and *F. hispida* there are gradations, possibly as distinct varieties, among the individual trees from those which are merely ramiflorous, to those which are cauliflorous, and those which are geocarpic; presumably, all these states are pollinated by the same specific insect. In subser. *Fulvidulae* and *Geocarpicae* such transitions are not known, and their geocarpy seems to have had a more ancient origin and to have suffered the elimination of the preceding stages. In escaping from their subterranean nests, the female insects may follow chinks in the soil but it seems more likely that the rooting of pigs and other animals in search of the edible seed-figs churns up the ground and exposes the gall-figs.

Concerning the systematic entomology, there is both confirmation of these botanical conclusions and some discrepancy. Fig-wasps are known from *F. beccarii* var. *latifolia* (*Ceratosolen humatus*), *F. subterranea* (also *C. humatus*), and *F. uncinata* var. *strigosa* (*C. albulus*). They were referred by Wiebes (1963) to the *C. pilipes* group which pollinates *F. cereicarpa* and *F. francisci*. This confirmation is the more satisfactory because at the time of Wiebes' publication I had not given the evidence for the close alliance of these subseries of *Ficus*. The discrepancies arise with *F. stolonifera* and *F. treubii*. What little is known of the fig-wasps of the first (*Ceratosolen sp.*) seems to disagree with the *C. pilipes* alliance. The fig-wasps of *F. treubii* (*C. brongersmai*) were referred by Wiebes to the *C. solmsii* group which pollinates *F. hispida* (*C. solmsii*), but he noted affinity with the fig-wasps of subser. *Geocarpicae* (Wiebes 1963 p. 87; 1965*b*, p. 233). I doubt if *F. treubii* is so close to *F. hispida* which is a common and widespread species, yet strangely rare in Borneo. There are but two records of *F. hispida* from Borneo; one is from west Koetai and the other lacks precise locality. I have never seen *F. hispida* in Sarawak, Brunei, or Sabah, where *F. treubii* is common; it grows, as said, in primary forest whereas *F. hispida* belongs to open secondary forest. However, on Mt Kinabalu, I found in secondary forest *F. moderata* which appears to connect *F. hispida* with *F. congesta* (subser. *Congestae*) and it has not been found in Borneo (Corner 1962*b*). The fig-wasp of *F. moderata* (*C. moderatus*) is placed by Wiebes in the *C. crassitarsus* group which pollinates a variety of species in ser. *Longituberculatae* and ser. *Tuberculifasciculatae* subser. *Praestantes*, *Calopilinae*, *Congestae*, and *Axillares*; he considers that the *C. solmsii* group connects that of *C. crassitarsus* with that of *C. pilipes* (Wiebes 1963, pp. 86, 87). Here is a complexity that calls for the collection of the fig-wasps from many more species of subsect. *Sycocarpus*.

I conclude, nevertheless, that subser. *Geocarpicae* came from the stock of subser. *Fulvidulae* which, in turn, came from the stock of subser. *Praestantes*. There is no obviously multibracteate species in the intervening areas of the Philippines, Moluccas, and New Guinea, except for a few of unsatisfactory classification which I will now consider.

I brought together as subser. *Axillares* five species, for the slender reason that they had axillary figs, not cauliflorous, of similar shape with rather large basal bracts, and none seemed to fit with other subseries (Corner 1960*b*). Two of these, *F. decipiens* of Celebes and *F. saurauioides* of New Guinea (figure 18), are small subpachycaul shrubs with remarkable pinnatifid-palmatifid leaves, unique in sect. *Sycocarpus*. Later I was able to add a third species to this alliance, namely *F. nana* of New Britain (Corner 1975*a*), where I took the opportunity to discuss the subseries. *F. nana*, with scattered lateral bracts, comes near to *F. praestans*, also of New Britain, and shows that this small alliance, stretched to Celebes where *F. geocarpa* is endemic, may be the remnant of the pachycaul ancestry of subser. *Fulvidulae* and *Geocarpicae*. I draw attention now to the three other species of subser. *Axillares*, namely the Moluccan *F. calcarata*, the Celebes *F. latimarginata*, and the west and central Malesian *F. lepicarpa*.

F. calcarata (figure 19) is a subpachycaul tree up to 10 m high, known from 8 collections made in Halmahera, Morotai, and Ternate. It has brown-hispid twigs 5–7 mm thick, persistent stipules (like spurs), and fairly large leaves (lamina up to 30 × 18 cm) which resemble those of *F. cereicarpa* and *F. praestans*. The sessile, axillary, and brown-hispid figs (15–22 m wide when dried) have a few small lateral bracts and large basal bracts 4–11 × 3–6 mm as in *F. cereicarpa*.

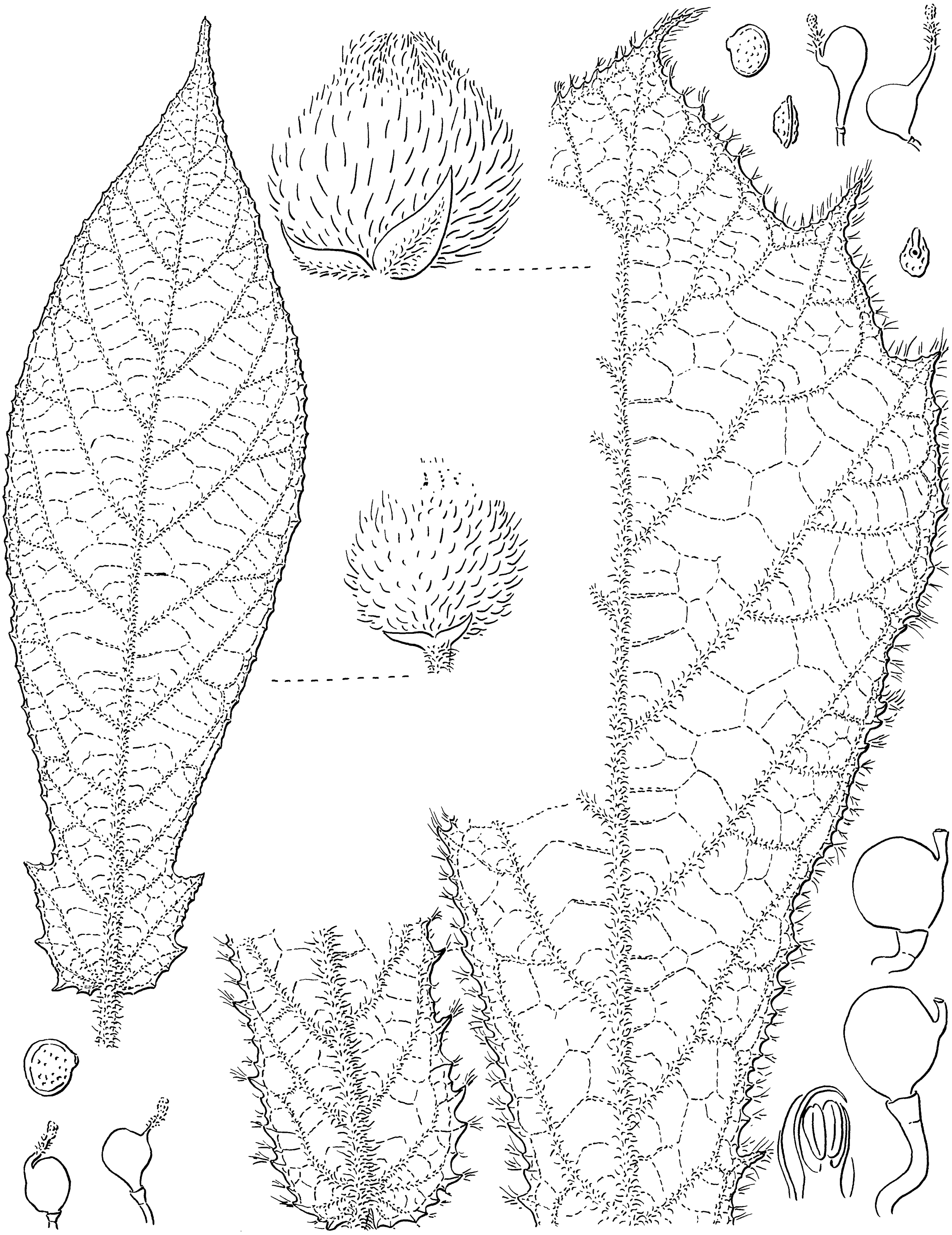

Figure 18. *Ficus decipiens* (right, Koorders 19172) and *F. saurauioides* (left; Ledermann 7224; leaf, Docters van Leeuwen 9095). Leaf, magn. × ½; figs, magn. × 2; flowers and seeds, magn. × 10.

If the ancestor of *F. calcarata* had been more pachycaul and the figs multibracteate, it would have come between *F. cereicarpa* and *F. praestans*. If its leaf had been partly dissected, it would have served for the ancestor of the alliance of *F. decipiens*; perhaps this is the case with the saplings of the little known *F. latimarginata* which fits in many ways between *F. calcarata* and *F. decipiens*. Hence I regard *F. calcarata* as the modernized relic of the ancestral stock that connected subser. *Fulvidulae* with subser. *Praestantes*, and *F. decipiens*, *F. saurauioides*, and *F. nana* as dwarf derivatives of this stock. From this stock, too, the sixth species, *F. lepicarpa*, may have been derived. As a more or less glabrous and leptocaul tree, it is the most advanced of the subseries and it is the most widely distributed for it evidently inhabits the rocky banks of all forest streams up to 1600 m alt. between Burma and the Moluccas. The fig-wasp of *F. lepicarpa* (*C. vechtii*) is placed by Wiebes in the *C. crassitarsus* group which pollinates, among others, the alliance of *F. praestans* and is related to the *C. pilipes* group of subser. *Fulvidulae* and *Geocarpicae*. Unfortunately the insects of the other five species are not known; their discovery will be critical.

Geocarpy, as already mentioned, has developed also in ser. *Longituberculatae* which is distinguished in subsect. *Sycocarpus* by the amphigenous cystoliths. It is fully developed in some states of *F. ribes*, which can be so spectacular in the forests of Java and Sumatra with its besom-like masses of slender cauliflorous twigs, but it is imperfect in the eastern *F. botryocarpa* the stolons of which trail up to 4 m over the ground without burrowing. *F. ribes* is the most simplified member of this series of four species, and it is the most widely distributed from Thailand to Java and, in varietal form, in the Philippines, but it has never been found in Borneo where the series is absent. The most primitive member is the Philippine *F. cassidyana* with large spirally arranged leaves and large figs on short cauliflorous twigs. None is multibracteate but small and scattered lateral bracts occur in the fourth species, *F. parvibracteata* of Celebes (figure 19); it, too, has the spirally arranged leaves but their derived state is shown by their narrow and glabrous form with entire edge. Nevertheless, this series points also to derivation from a multibracteate pachycaul in eastern Malesia such as might link up with subsect. *Auriculisperma* ser. *Vitienses* with amphigenous cystoliths. The importance of this detail has been discussed in connection with sect. *Adenosperma* (Corner 1969*b*); it crops up continually in the study of *Ficus* and is best developed in the primitive subgen. *Urostigma*. In the case of ser. *Longituberculatae* the reliability of the character is supported entomologically. Wiebes (1963) has described *Ceratosolen crassitarsus* from *F. ribes*, *C. gracilis* from *F. ribes* var. *cuneata* (Philippines), and *C. corneri* for *F. botryocarpa* var. *subalbidoramea*; he placed them in the *C. crassitarsus* group which pollinates *F. praestans* etc.

SECT. *SYCOCARPUS* SUBSECT. *MACROSTYLA*

Two species make this strangely unexpected subsection. It is distinguished among all kinds of *Ficus* by the extraordinarily long female styles which, with deflexed hairs, are coiled up to fill the interior of the fig. Geographically the species are knit across the China Sea from Sino-Himalaya to Sarawak. Ecologically both are rheophytes, growing as low spreading leptocaul bushes with lanceolate leaves and rooting among the boulders of fast streams subject to flash floods. Many species of sect. *Sycocarpus* are riparian on firm banks, but no others are rheophytes of shifting substratum unless, possibly, the recently discovered *F. theophrastoides* var. *angustifolia* of Choiseul in the Solomons (Corner 1972). Such rheophytes occur, however, in sect. *Ficus*,

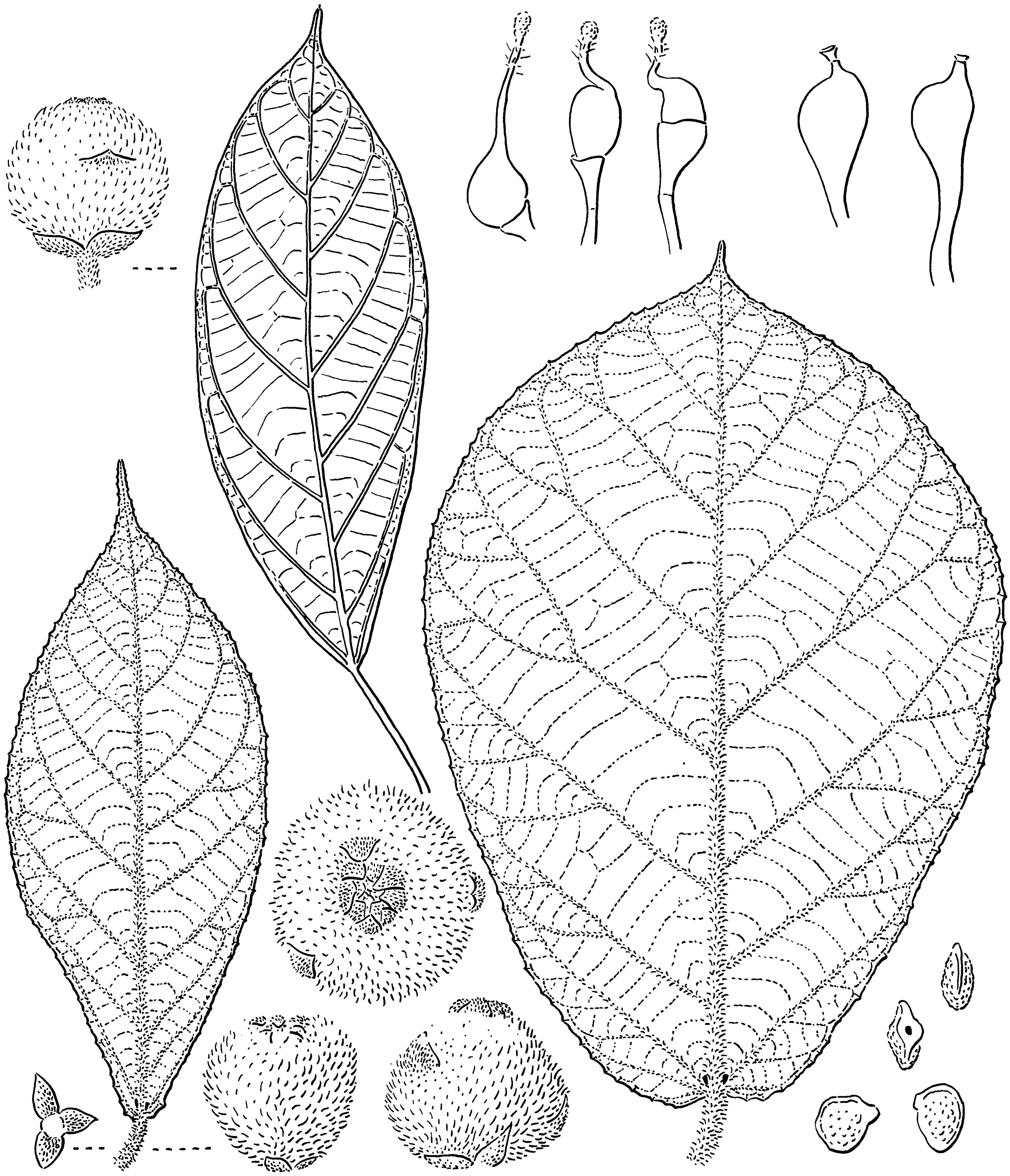

FIGURE 19. *Ficus calcarata*; broad leaf, two figs, and gall-flowers, from Kostermans 1677; narrow leaf (lower left) with an obconic fig and the collar of basal bracts, from Pleyte 286; female flowers and seeds from Kostermans 1401. *F. parvibracteata* (upper left); leaf and fig from Kjellberg 2640. Leaves, magn. × ½; figs, magn. × 1; flowers and seeds, magn. × 10.

sect. *Sycidium*, and sect. *Adenosperma*, as well as in subgen. *Pharmacosycea*, and geographical regions are mapped by the systematic occurrence of these species.

F. macrostyla has been found only in Sarawak in the small region between the Rejang river and Bintulu; that is 2–3° N and 113–114° E. I have searched for it round Kuching, in Brunei, and in Sabah without success. The other species, *F. squamosa* (formerly known as *F. saemoccarpa*), is widely distributed from the central Himalayan foot-hills to north Thailand and Yunnan. The considerable number of differences between them indicates that they are relics with the more primitive *F. macrostyla* as that with the limited distribution. *F. macrostyla* (figure 20) has multibracteate figs covered with lanceolate bracts up to 17 × 6 mm (as in *F. longibracteata* of the Solomons), brown internal bristles, a minute hairy cupular female perianth, and a seed without

FIGURE 20. *Ficus macrostyla* (right, S 18400); fertile twig, fig in l.s. (magn. × 1), female flowers, seeds, and female perianth (magn. × 30). *F. squamosa* (left); leaf, immature fig (magn. × 1), female flowers at anthesis and in fruit, gall-flowers (one with unusually large perianth, Sino-Soviet Expedition n. 7869), and seeds. Twig and leaf, magn. × $\frac{1}{2}$; flowers and seeds, magn. × 10.

a prominent hilum. *F. squamosa* has small scattered lateral bracts up to 4 mm long, no internal bristles, no perianth to the female flower, and a prominent hilum to the seed. They agree in the subpersistent stipules, the lack of basal glands on the lamina and of subnodal glands on the twigs (? the effect of the rheophytic habit), the axillary and cauliflorous figs on short leafless twigs, the reddish brown ovaries, the hypogenous cystoliths, and the microscopically papillate brown hairs. The gall-flowers of *F. squamosa* may have no perianth or it is a slight rim on the ovary-stalk or, rarely, it is a short glabrous collar; gall-plants of *F. macrostyla* have not been collected.

The affinity of the subsection is intricate. The red-brown ovaries agree with subsect. *Sycocarpus* where, too, the seed of *F. squamosa* fits with prominent hilum, but that of *F. macrostyla* agrees with subsect. *Papuasyce* and ser. *Theophrastoides* in subsect. *Auriculisperma*, where the red-brown ovary occurs in ser. *Cynaroides* and ser. *Vitienses*. This mixture, coupled with the multibracteate fig of *F. macrostyla*, indicates a pachycaul ancestry of profound antiquity for the section. Then, the long female style calls for an account. In *F. macrostyla* it measures, when uncoiled, 12–18 mm, in *F. squamosa* 6–10 mm; in other groups of *Ficus* it is 0.5–2.5 mm long but may reach 2–5 mm in species of subgen. *Pharmacosycea*. The feature can be dismissed as an oddity but the study of insect behaviour inside the syconium shows that its internal details are functional; the long style in one species might be a peculiarity without phyletic significance, but in two it calls for explanation.

There is the New Caledonian genus *Sparattosyce* as a non-blastophagous parallel to *Ficus* It is dioecious. The fig-like receptacles contain either male or female flowers, for there are no gall-flowers. At maturity the receptacles split open from apex to base to expose the open male flowers or the orange seeds displayed on the yellow inner surface. Until then in *S. dioica*, for the rare *S. balansae* is scarcely known, the female receptacles are closed except for the small apical orifice through which the long glabrous styles project up to 9 mm (Bureau 1869, pl. 6). Pollination is evidently external outside of the receptacle or pseudosyconium, though the method is unknown. Now, long styles occur in various Moraceae (Corner 1962*a*). It is not improbable, therefore, that pre-*Ficus* with incipient blastophagy may have resembled *Sparattosyce*; the long projecting styles may have been pollinated externally before the primitive fig-wasps entered the primitively monoecious syconium to oviposit in the short-styled gall-flowers. The dioecism of subgen. *Ficus* may have maintained the illusion of the female syconium; hence I explain the long styles of subsect. *Macrostyla* as relics of pre-*Ficus* now coiled up in the interior of the syconium. The stylar dimorphism in *Ficus* calls, indeed, for some such explanation.

These advanced rheophytes appear, therefore, as modernized survivors of a stage in fig-evolution when it was imperfectly blastophagous. Though sect. *Sycocarpus* is most advanced in the nature of the perianth of gall- and female flowers and in the dimorphism of their styles, it retains among its abundant and intricately related species many primitive features which, when re-assembled, imply an ancestor more primitive than that which any other group of *Ficus* can provide. Among these features, the retention of the long style, as a part of what may be called proto-blastophagy, by these subordinate rheophytes does not seem improbable.

THE EVOLUTION OF THE SYCONIUM

The general construction of the Moraceous inflorescence supplied the thesis that the discoid head with many external bracts closed up, or failed to expand, and hid the flowers thereby in the interior of the primitive syconium (Corner 1969*a*, with reference to *Antiaropsis*, fig. 7). The failure was rescued by blastophagy and became the success of *Ficus*. If the proto-blastophagous syconium had long projecting styles, this would have been the first step from open to concealed pollination. The condition would have suited the female flowers but not the gall-flowers which require a short style for oviposition. A short style in this connection suggests neoteny. In the proto-blastophagous syconium the immature lateral female flowers may have functioned in their small neotenic state as the gall-flowers, and their precocity over the male flowers, as the ultimate laterals, would have supplied that feature of the syconium which is essential for blastophagy; that is, no free pollen until the insects have hatched.

Sparattosyce and *Antiaropsis* are dioecious. Their species are advanced leptocaul trees of short stature in forest undergrowth. They give evidence of a long course of evolution from pachycaul ancestors which were probably monoecious, but there appear to be no living records of this ancestry. If the proto-blastophagous syconium had also been monoecious, it would have supplied the ancestry of the monoecious subgenera of *Ficus*. Their ancestors have also disappeared but the dimorphism of the style remains, and the ancient group of *Urostigma* is conspicuously imperfect in this respect. The dioecious subgen. *Ficus* implies ancestral monoecism, e.g. subsect. *Papuasyce*, yet dioecism may have entered into proto-blastophagy, as in *Sparattosyce* and *Antiaropsis*, and from this state subsect. *Macrostyla* may have survived. The deflexed bristles along the female style and on the ovary and perianth may have served in the first place to prevent egress of the insects from a monoecious and proto-blastophagous syconium. The general idea is conveyed in figure 21.

If modern species of *Ficus* lead back to the multibracteate pachycaul with perfected blastophagy, then for the ancestry of this state, one must consider the proto-blastophagous with projecting female styles. That it was unsatisfactory is shown by its rarity in *Sparattosyce*, but in the case of pre-*Ficus* it housed and hid the pollinating insects, and in their nurseries they seem to have rendered the young figs inedible. Birds and bats, catching the emerging females on the wing, and marauding ants carrying off the effete males testify to the palatableness of the fig-insects. Gall-figs, however, are not eaten, even when ripe. In the case of monoecious figs, I have found when collecting the insects that the females emerge a week or two before the figs ripen and become edible; birds commonly leave the orange and scarlet figs until they have darkened to purple or black. Thus pre-*Ficus* came to secure its insects, to multiply with seeds of diminishing size, and to spread the new and successful *Ficus* through the tropical forests of the Old World. For subgen. *Ficus* this was the Indo-Pacific region, and the traces of pre-*Ficus* seem to survive in the Sino-Himalayan connection with north Borneo. For many other instances of this geographical connection I refer to the discussion on the flora of Mt Kinabalu by van Steenis (1969). It is the western end of the route or island-arc from the Asian mainland to the Melanesian Foreland. At the eastern end the relict genera *Antiaropsis* (one or two species in New Guinea) and *Sparattosyce* (two species in New Caledonia) are two aspects of pre-*Ficus*. If their special Moraceous features were combined with proto-blastophagy, their pachycaul ancestor would have had the multibracteate, tardily dehiscent, large-seeded, syconium of ancestral *Ficus*. In the middle of this geographical range, where *Ficus* has evolved so intensely, there are surely other

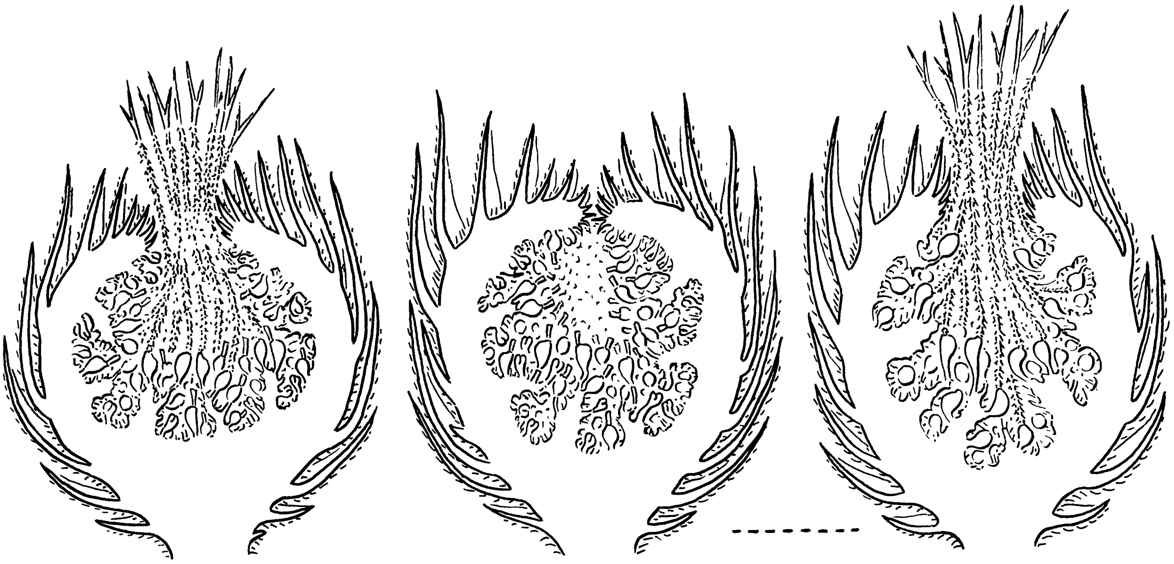

Figure 21. Diagrammatic sections of protoblastophagous syconia at the time of pollination with exsert female styles; the monoecious syconium on the left, the dioecious on the right; male flowers disperse, immature.

relics of this ancestry. Thus I view the tardy dehiscence of the figs of subgen. *Ficus* subsect. *Dehiscentes* (Corner 1970*a*), the large seed of *F. deltoidea*, and the pinnatifid-palmatifid leaf of *F. decipiens* recalling that of sapling *F. padana* (Corner 1970*a*).

Instead, therefore, of trying to relate the subgenera of *Ficus* directly, one should regard them in the brighter light of parallel evolution from proto-blastophagous pre-*Ficus* of the massive build preserved for us in *F. dammaropsis*.

The syconium is a fruit of second order, for the inflorescence has become the fruit. It follows from what has been written that the evolution of the cymose Moraceous inflorescence and its transformation into the syconium took place in the early, but lengthy, pachycaul state of nascent Moraceae contemporary, perhaps, with nascent Urticaceae. *Ficus*, though one of the very advanced angiosperm genera, stems from the ebullient pachycaul phase of angiosperm beginnings. Most dicotyledonous genera, if accorded the status of *Ficus* by subordination of the over-numerous microgenera, would prove this advent. *Artocarpus* has an externalized fruit of second order in which the perianths provide the durian spines. In *Ficus* the bracts have this function and to go beyond this degree of externalization seems impossible.

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