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The Complex of Ficus deltoidea; A Recent Invasion of the Sunda Shelf

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THE COMPLEX OF *FICUS DELTOIDEA*; A RECENT INVASION OF THE SUNDA SHELF

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A detailed account of the complex of *F. deltoidea* Jack and *F. oleaefolia* King is given in order that its problems may be taken up in the field. Thirteen varieties of *F. deltoidea* are distinguished, eight of *F. oleaefolia*. The link between them is *F. deltoidea* v. *motleyana* (Miq.) Corner. Clear evolutionary trends to very small figs and leaves and to dichotomous venation supply the evidence for the conclusions that the most reduced state *F. deltoidea* v. *angustifolia* (Miq.) Corner is the most widely spread; that the complex advanced into the lowland and mountain forests of the Sunda Shelf from Borneo; that the original connexion was with the ancestors of ser. Podosyceae Corner in the Philippines; that the large seed is a primitive retention; that the complex did not evolve through vicarious disruption of a widespread ancestor; and that, as a recent development of *Ficus*, possibly still in the making, it represents most clearly the manner of speciation and geographical distribution prevalent in the genus.

New taxa: *F. deltoidea* Jack var. *kinabaluensis* (Stapf) Corner, *F. oleaefolia* King var. *linearifolia* Corner and var. *valida* Corner.

Introduction

Since the publication of the check-list of *Ficus* (Corner 1965), numerous collections of *F. deltoidea* and *F. oleaefolia* have been sent to me from Borneo and I have been able to study on two Royal Society Expeditions several varieties of this complex on Mt Kinabalu. These are the two species of sect. *Ficus* ser. Erythrogyneae. I listed twelve varieties and four forms (as the taxonomic category below that of variety) for *F. deltoidea* and five varieties for *F. oleaefolia*. I now add one more for *F. deltoidea*, namely v. *kinabaluensis* (Stapf) stat.nov. which I had merged with v. *intermedia* Corner, and two more for *F. oleaefolia*, namely v. *linearifolia* v.nov. and v. *valida* v.nov. They have led me to re-examine *F. deltoidea* v. *motleyana* which can be seen to unite both

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species. I am unwilling, however, to alter nomenclature at this stage because it is clear that my results need much further evaluation from field-studies. No one has been able to do this hitherto because of the absence of a critical account and because of the pressure of general collecting. The complex of shrubs, epiphytes and small trees is easily recognized and could become an interesting subject of research by a botanist resident in Malaya, Sumatra or Borneo. There is a great deal of local variation and there is great need for field-analysis of the apparent intermediates between many of the varieties.

This is the crux of the problem. Intermediates seem to occur from the extreme of v. *motleyana* to the extremes of v. *angustifolia* or v. *kunstleri*, and *F. oleaefolia* v. *dodonaeiformis* or v. *linearifolia*. The extremes are so different that in isolation they would never be considered conspecific. But, as the endeavour is made to split the complex into structural taxa and a biogeographical pattern emerges, absolute criteria become more difficult to find; characters seem to interchange as well as intergrade. Individual plants seem to run through varietal stages in the course of their lives such that v. *deltoidea* may go through an *angustifolia*-stage and a *motleyana*-stage before stabilizing as *deltoidea*; v. *intermedia* in Malaya seems never to stabilize; yet plants of v. *angustifolia* and v. *motleyana* never become v. *deltoidea* or v. *intermedia*. *F. diversifolia* Bl., though a synonym, was a good name for *F. deltoidea*.

The complex presents not only the ultimate state of form-making in *Ficus*, when variation abounds in trivialities, but one of its most progressive states into the suffrutescent habit, so reduced that the venation becomes dichotomous and the figs so small as to contain merely one or two female flowers. Thus v. *angustifolia* may have a 1-seeded syconium, comparable with a 1-seeded capitulum. *F. deltoidea* v. *peltata* may be compared with a rather woody *Hydrocotyle* and *F. oleaefolia* with a small-leafed *Rhododendron* tree.

The complex occurs mainly in Malaya, Sumatra, Java and Borneo on the Sunda Shelf, with extensions to Celebes, Mindanao, Palawan and lower Thailand. The greatest representation is in Borneo. Here the least reduced state occurs commonly as v. *motleyana* and it has been found elsewhere only in central Sumatra (Pajakumbuh). There is an uncertain record of it from east Pahang (Gunong Tapis) and some uncertain records from Celebes. I think it is clear that v. *motleyana* did not occur in Java, and that it is absent generally from Malaya and Sumatra. In contrast, the highly reduced v. *angustifolia* is the most widespread (lower Thailand, Malaya, Sumatra, Borneo, Palawan). These facts are set out in table 1, along with the number of herbarium collections (not specimens), for they are a rough guide to the common occurrence or rareness of the varieties. The facts in table 1 point to the following conclusions: (1) the complex first evolved in Borneo (? in the Tertiary Period); (2) it spread in new forms until climate and geographical barriers prevented it; (3) the evolution continued most actively in the region of origin (14 varieties in Borneo, 7 being endemic); (4) the more widespread members of the complex are the more advanced.

These conclusions confirm the general impression about the manner of evolution and dispersal in *Ficus* which I have gathered while studying the genus. They are at variance, however, with those advanced by Croizat from his panbiogeographical studies (Croizat 1968, pp. 127–130). He considers that such a complex of forms represents the range of an ancestor which split up into modern species or varieties within this range and, in doing so, the ancestor disappeared. He seems to insist on a geographical stasis for any such complex, defined by its ancestral limitations, and to deny it further means of geographical extension. He would derive *Ficus* from the neighbourhood of Madagascar on Gondwanaland where its representation is feeble, and, in

Table 1. Distribution of the *F. deltoidea* complex

	Th	Ma	S	J	B	C	Mi		number of collections
deltoidea	.	—	—	.	—	.	.		122
angustifolia	—	—	—	.	—	.	.	Palawan, Anamba, Natuna	95
arenaria	.	.	.	.	—	?	.	Biliton	15
bilobata	.	—	.	.	.	.	.	.	17
borneensis	.	.	.	.	—	.	.	.	25
intermedia	.	—	.	.	—	.	.	.	98
kinabaluensis	.	.	.	.	—	.	.	.	22
kunstleri	—	—	.	.	.	.	.	.	22
lutescens	.	.	—	—	—	.	.	.	142
longipedunculata	.	.	—	—	.	.	.	.	27
subsessilis	.	.	—	—	.	.	.	.	33
motleyana	.	?	—	.	—	?	.	.	84
oligoneura	.	.	—	.	.	.	.	.	8
peltata	.	.	—	.	.	.	.	.	2
trengganuensis	.	—	.	.	.	.	.	.	16
oleaefolia	.	.	—	.	.	.	.	.	13
dodonaeiformis	.	.	.	.	—	.	.	.	7
epiphytica	.	.	.	.	.	—	—	.	21
linearifolia	.	.	.	.	—	.	.	.	2
memecylifolia	.	.	.	.	—	—	.	.	48
myrsinoides	.	.	.	.	—	.	.	.	31
riparia	.	.	.	.	—	.	.	.	3
valida	.	.	.	.	—	.	.	.	6
23	2	7	9	3	14	2	1	.	859
endemics	0	2	3	0	7	0	0	.	

Th, Thailand; Ma, Malaya; S, Sumatra; J, Java; B, Borneo; C, Celebes; Mi, Mindanao.

support of this hypothesis, he would interpret the syconium as a flower with inferior ovary and the cauliflorous spray of syconia as an inflorescence of such flowers. I do not intend to discuss these very questionable ideas in this place, but to show that the complex of *F. deltoidea*, recent though it be, has a link with the pre-*Ficus* parallel of *Antiaropsis* in New Guinea, that it has nothing to do with Madagascar and Gondwanaland, that it has evolved ecologically as well as morphologically and so spread into habitats beyond the range of its ancestor, and that the most flower-like syconium with one ovary is the most advanced state in the genus. I shall discuss the variation in the complex and its evolutionary trends before returning with this evidence to validate my conclusions. Then I shall give the classification and description necessary for the field-work through which the research must be advanced. It is a step in my purpose to learn about the evolution of flowering plants from a large genus. The story of *Ficus* must first be read from its existing species, but the very size of the genus prevents the telling all at once. It may or may not agree with conclusions from other sources, but without this story I do not see how it can be ascribed to Gondwanaland or elsewhere. Until I had prepared the check-list for Asia and Australasia, the science of *Ficus* was at a standstill; there was such confusion in identity and classification that none of its array of information was serviceable.

COLLECTIONS

Because the members of this complex are usually conspicuous small plants of the undergrowth or epiphytes with olive-brown backs to the leaves, they have been better collected than most species of the genus. One learns from field-work that one or two collections, say of *F. oleaefolia* from Mt Kinabalu, represent hundreds of wild plants, but there can be no such certainty about the lesser known and apparently rare varieties, and the likelihood of yet undiscovered local variation begins to weigh. There is an acute need of further exploration, mountain by mountain, ridge by ridge, among sandy heaths and in all places of poor, well-drained soil. The field-worker must give more attention to the collection of young, mature and old stages of a population and of gall-plants as well as seed-plants. A single collection of these polymorphic plants is inadequate unless it is copiously annotated.

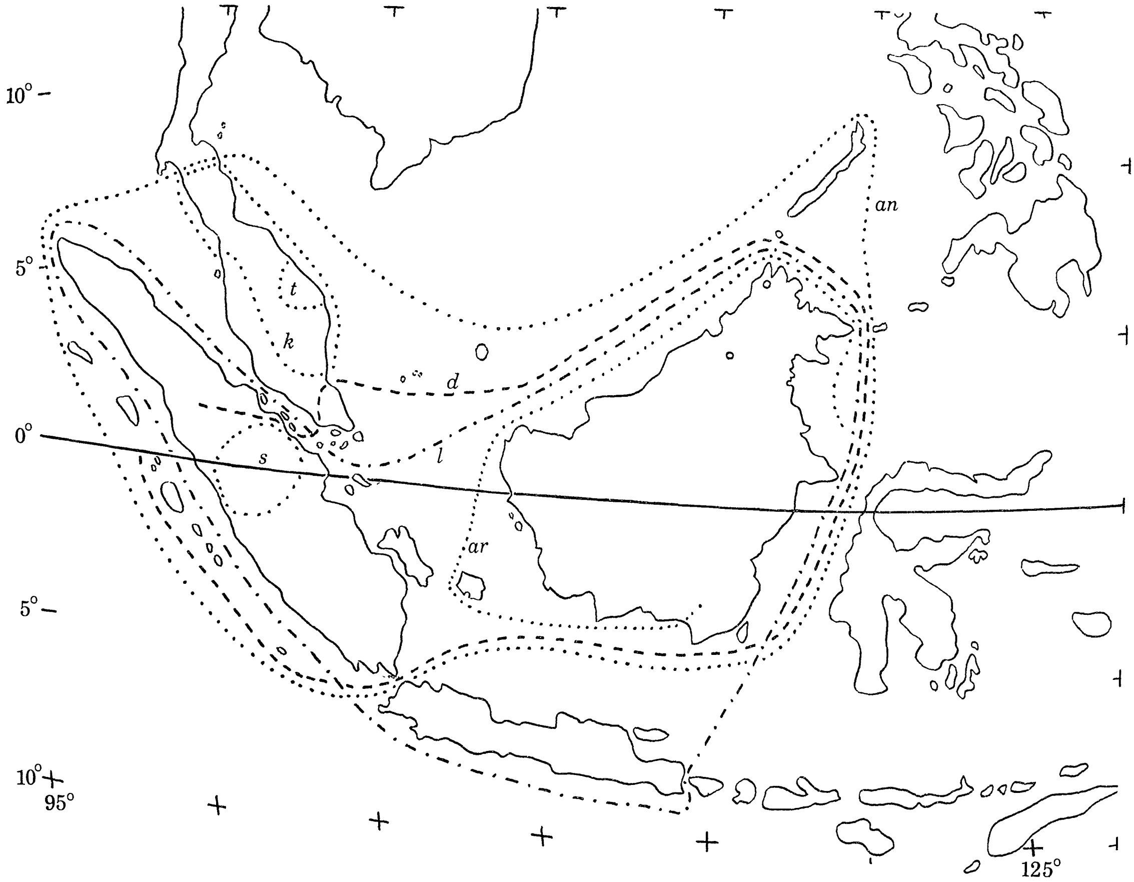

FIGURE 1. Distribution of *Ficus deltoidea*; *an*, v. *angustifolia* (outer dotted line); *ar*, v. *arenaria* (inner dotted line round Borneo, uncertain in S.E. Borneo and Celebes); *d*, v. *deltoidea* (broken line through S.E. Malaya and the Sunda Strait, uncertain in north Sumatra); *k*, v. *kunstleri*; *l*, v. *lutescens* (dot–dash line); *s*, central Sumatra with v. *motleyana*, v. *oligoneura*, v. *peltata*; *t*, v. *trengganuensis*. Add v. *borneensis* in Borneo and, for the two small circles in north Borneo, v. *kinabaluensis*.

HABIT

Usually the form is shrubby with ascending twigs and spirally arranged leaves. It is the form in exposed places from sandy beaches and sea-rocks to mountain top. Var. *motleyana* carries it into the coastal, peat-swamp, and sandy heath (*kerangas*) forest of Borneo where it may become a spindly tree up to 6 m high. The small-leafed varieties of *F. oleaefolia*, as v. *memecylifolia* and v. *myrsinoides*, become bushier small trees up to 12 m high (trunk up to 20 cm thick) in the mountain forest of Borneo. But, generally, in the lowland forest the complex is present as more or less erect, epiphytic bushes the abundance of which along the rivers may be very considerable; so little is known, however, of this riverine epiphyte ecology that the plants of *F. deltoidea* are seldom, if ever, enumerated. Over the greater part of the lowland forest, in fact, the form is that of the epiphytic bush and it carries on into the mountain forest where the distinction between the epiphyte and saxicolous or humicolous forms begins to disappear; v. *memecyloides* and v. *myrsinoides* are as often epiphytic or terrestrial as the *Rhododendron* bushes with which they grow. Lastly there are creeping forms such as *F. deltoidea* v. *kinabaluensis* and v. *peltata*. The habit is certainly facultative in v. *kinabaluensis* which creeps and struggles in the thick undergrowth of *Drimys* on the ridges and becomes a compact bush on exposed rocks. It never becomes a small tree and this habit alines it with *F. deltoidea* rather than the tree-like derivatives of *F. oleaefolia*.

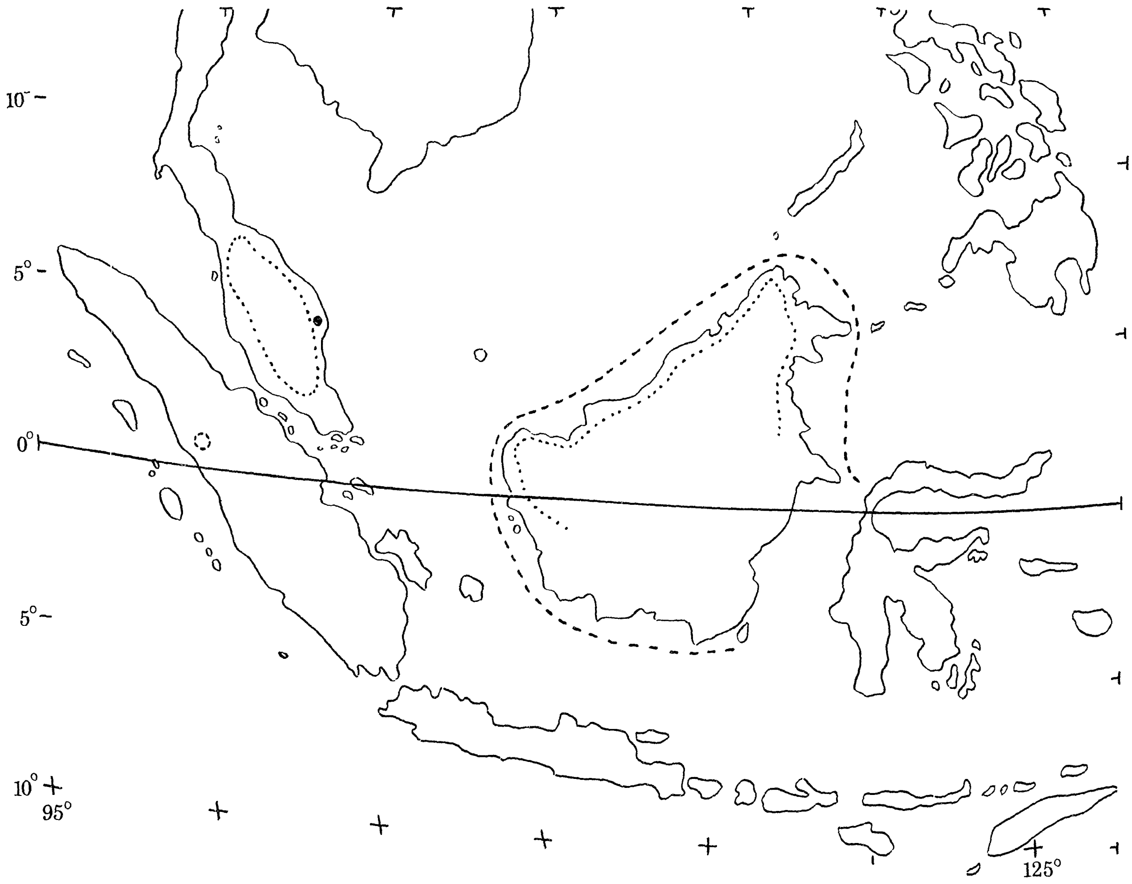

FIGURE 2. Distribution of *F. deltoidea* v. *intermedia* (dotted line in Malaya and Borneo) and v. *motleyana* (broken line in central Sumatra and in Borneo, with the black circle on the east coast of Malaya).

Habitat

Poor, acid, well-drained soils seem to be the preference. With this go such xeromorphic features as the coriaceous leaf, particularly in its deltoid form, and the well-developed hypodermis on its upper side, but the stomata are superficial. Rocks and upper dunes on the sea-shore, quartzite ridges, leached tops of limestone hills, and mountain and mossy forest are the common habitats as well as the epiphytic. *F. deltoidea* v. *deltoidea* and v. *kunstleri* are predominantly epiphytes; v. *borneensis* and v. *trengganuensis* are predominantly terrestrial, and this seems to be the case with v. *motleyana* and v. *kinabaluensis*. Most varieties occur below 1200 m alt., but others are characteristic of the higher mountain regions above the dipterocarp forest, for instance *F. deltoidea* v. *intermedia*, *F. oleaefolia* and most of its varieties. The one variety which seems to range from sea-shore to mountain-top is *F. deltoidea* v. *lutescens* in Java and Sumatra. Nevertheless, *F. oleaefolia* v. *memecylifolia* has been found at 200 m on a limestone hill near Kuching. The highest record seems to be that of v. *kinabaluensis* at 3180 m on the east ridge of Mt Kinabalu; it seems, indeed, the altitudinal record for the genus. The very narrow-leaved varieties, *F. deltoidea* v. *angustifolia* and *F. oleaefolia* v. *dodonaeiformis*, v. *linearifolia* and v. *riparia*, would seem

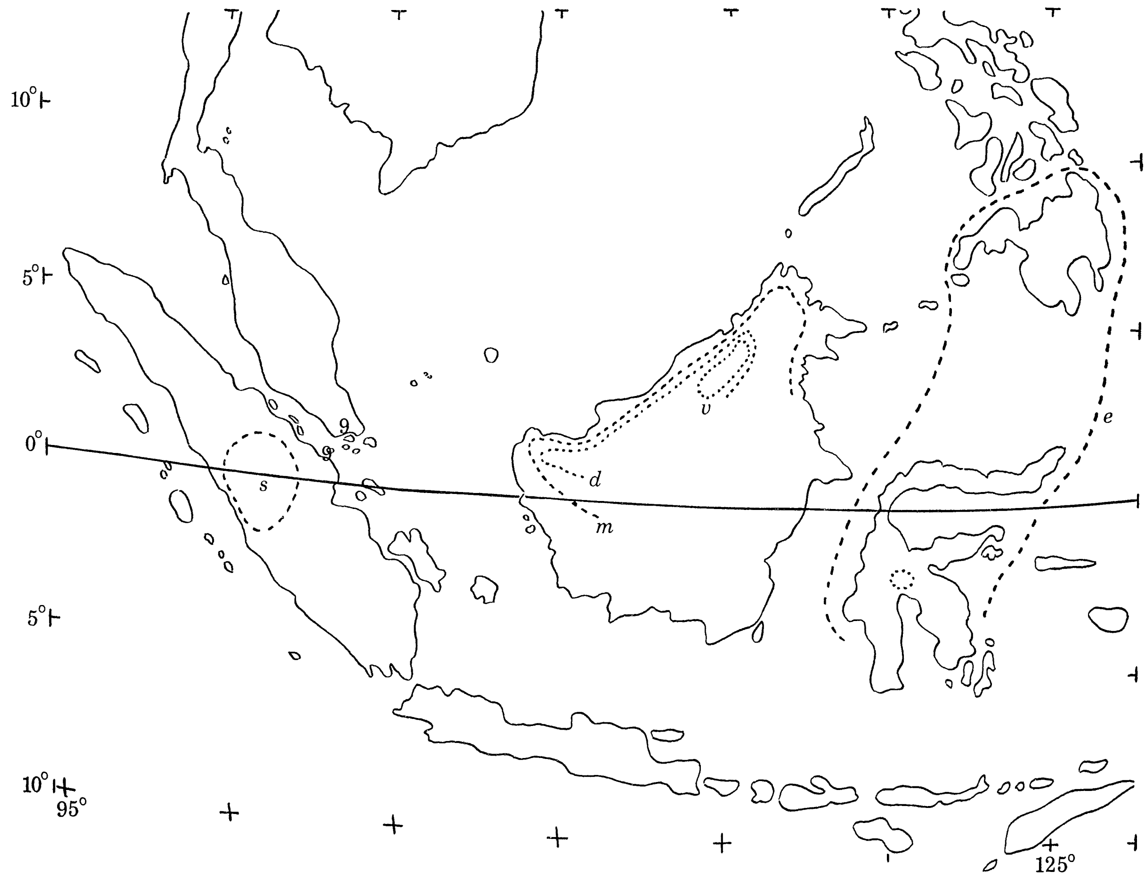

Figure 3. Distribution of *F. oleaefolia*; *d*, v. *dodonaeiformis* (dotted line); *e*, v. *epiphytica* (broken line, Celebes, Mindanao); *m*, v. *memecylifolia* (also Celebes) and v. *myrsinoides*; *s*, v. *oleaefolia* (broken line, Sumatra); *v*, v. *valida*, v. *riparia*, and v. *linearifolia* (dotted line).

to be riverside or streamside but the evidence points to their being merely undergrowth shrubs which may happen to grow in places by the streams.

Clearly the complex has exploited many habitats with varying habit and few of the varieties seem widely tolerant. To what extent the ecological specialization demands physiological reaction is not known. The fourteen varieties, sympatric in Borneo, may represent as many different habitats. The geographical distribution is, thus, only a rough measure of their occurrence which needs in explanation some continuity or proximity of special habitat. This would have been easier for lowland than mountain varieties and may explain the widespread occurrence of the predominantly lowland v. *deltoidea* and v. *angustifolia* and the facultatively lowland v. *lutescens*. They are the more advanced xeromorphic forms able to grow, evidently, under a greater variety of circumstances than the lowland v. *motleyana*. I believe that this adaptability is one of the reasons, if not the main reason, for the wide distribution of advanced species of *Ficus* compared with the restricted occurrence of the more primitive forest species, especially the pachycaulous. In other words, the structural evolution implies a physiological leading to greater distribution by opening up new habitats. It is extremely unlikely that this complex was derived from a widespread forest treelet of almost ubiquitous adaptability.

The ecological evolution of *Ficus* is known merely in outline. This complex offers the opportunity for detailed research in a close alliance within easy access from a single laboratory, for instance at Kuching, Kuala Lumpur or Singapore. By comparison with the other epiphytes in the genus, which are the strangling figs of subgen. *Urostigma* and subgen. *Ficus* subsect. *Palaeomorphe*, the epiphytes of the *F. deltoidea*-complex are distinguished by their short roots which, in general, never reach the ground. The character would seem to be inherited from v. *motleyana*, though the root-system of this plant is not known, and may have been the prime factor which led the ancestors of the complex into the 'motleyana-habitat' in the forest. It seems unreal to discard the ecological implications, as Croizat would do, in the phyletic or progressive aspect of biogeography.

LEAF

The acute penninerved leaf (figures 8, 15) with pinnate venation and the obtuse deltoid leaf with dichotomous venation (figure 10) offer the most striking difference in the complex. I have never shown an example of each to a botanist but he has been astonished to think that two such leaf-forms could belong to the same species. It is well known, however, to field botanists that such forms may occur on the same plant and intermixed on the same twig; hence Blume's *F. diversifolia*. This is the case with v. *deltoidea*, v. *intermedia* and v. *lutescens*; their seedlings or saplings tend to have acute leaves while the adult foliage has the obtuse. Intermediates are many. They show how, by loss of apical dominance of midrib growth, the venation becomes progressively more dichotomous. Acute leaves with full, even mucronate, apical dominance have no dichotomy. Obtuse leaves may be penninerved almost to the apex (figure 11). Deltoid leaves lose the apical dominance early in their development and the midrib comes to be dichotomous below the middle of the lamina, at its first branching (figure 13). The peltate leaf is, then, produced by basipetal growth (figure 14). The transition may be so gradual that one is impelled to the other extreme and tempted to consider the dimorphousness as a universal character of the complex. Careful study of living plants and herbarium collections shows that this is not true. Some plants never develop deltoid leaves, such as v. *motleyana* or v. *oleaefolia*; others develop only a subapical dichotomy, as v. *intermedia*; while the commoner, more widespread varieties, as v. *deltoidea* or v. *angustifolia*, pass quickly to the state with profound dichotomy. Then, through herbarium study, it is found that these ranging states of evolution in venation are connected with other characters and that these varieties, so recognized, have their ecological and geographical distinctions. Thus the leaf-form and venation become leading characters in the complex.

The question is which came first, the penninerved or the dichotomous. The general theory of leaf-form puts the dichotomous first, from which by overtopping the monopodial with pennineration was derived. But this is a very ancient phase of leaf-evolution, referable to the marine ancestry on early land-migration of green plants. The dichotomous venation in *Ficus*, which is a highly evolved genus of Moraceae, and solely in one of its more reduced and advanced series cannot be a primitive retention. Moreover, it is not leaf-dichotomy in *Ficus*, though it may be indicated in *F. deltoidea* v. *bilobata* (figure 8), but merely dichotomy of the main veins within the angiosperm lamina of usual intercalary growth. Analysis of the growth-factors in this lamina supplies an alternative explanation.

The acute leaf-tip with its two rows of small costas, topping the main lamina, is the index of apical growth in the leaf-primordium by which the costas are developed in acropetal succession. As apical growth and dominance become less pronounced, the midrib develops a slightly zigzag course between the costas. It begins to relapse, that is, into dichotomy which, in angiosperm leaves, is normally overcome by the factors of apical monopodial growth. The incipient steps may be seen in most obtuse leaves, whether fern or angiosperm. In extreme cases, such as v. *borneensis* and v. *kunstleri* (figures 10, 13), this apical direction clearly disappears so early in leaf-development that only the basal costas are formed; the next branching of the midrib is dichotomous and it is followed by 2, 3 or 4 other dichotomies of lessening extent. The obtuse lamina is dilated progressively into the obovate, deltoid, suborbicular or, even, bilobate form by intercalary growth as shown by the cascade-effect of the intercostal veins (Corner 1967). This modification occurs also in the development of the inarching and marginal loops of the costas as the pinnae, which their apical growth would construct, reduce to teeth and finally disappear to give the entire leaf-margin separated from the midrib by intercalary growth of the intercostal area.

This alternative explanation is simple. Apical dominance converts dichotomy into monopodial direction. Loss of apical dominance restores dichotomy. The process is gradual and, thus, a series of stages can be found leading through v. *intermedia* or v. *arenaria* to v. *deltoidea* and, finally, with reduction in intercalary growth to v. *angustifolia* f. *angustissima*. In parallel, the penninerved leaf shortens by earlier cessation of apical growth and narrows by early cessation of intercalary growth into the small-leafed varieties of *F. oleaefolia*; and incipient subapical dichotomy may occur in these reduced leaves, as in v. *myrsinoides* (figure 19). The size, shape and venation of the leaf indicate the direction of evolution required to interpret the geographical expansion of the complex. *F. deltoidea* v. *peltata* is not therefore the primitive peltate leaf but, as with that of *Nymphaea*, an advanced form derived neotenically through early cessation of normal growth and its basipetal displacement, or transfer (Corner 1958*a*).

Syconium

The fig, or syconium, may be oblong, ellipsoid or subglobose. The peduncle may be very short, of medium length 4–12 mm, or longer. The fig-body may be 4–6, 6–10, or 10–15 mm wide. Large figs may have eight to ten seeds, small figs one to three. On ripening, the fig may colour orange to red, or as in *F. deltoidea* v. *kunstleri* and v. *trengganuensis*, pink to rose-red before becoming purple-black, which may be the final state in all varieties.

As v. *motleyana* has a relatively large, oblong fig with rather short peduncle 1–6 mm, ripening orange to red, I assume that these are the primitive characters associated with its relatively large and primitive leaf. Reduction in size of the twig accompanies reduction in leaf-size and is reflected in the smaller fig-body with its fewer flowers. Thus the small, few-seeded figs of v. *angustifolia* and v. *memecylifolia* are advancements. Big figs do not occur with small leaves or small figs with big leaves in this complex of axillary, not cauliflorous, position of the fig.

The colour change of the fig cannot be learnt from dried collections without field-notes, which are rarely made. Often the shape cannot be determined, also, from dried collections because immature figs shrink on the sides, though the apex remains strutted by the ostiolar bracts, and they become ellipsoid, even oblong. These are details for field-study.

Shortening or lengthening of the peduncle, which is the single internode below the basal bracts, seems to be a fortuitous variation in most taxa. The short peduncle seems, nevertheless, to distinguish v. *kinabaluensis*. This variation should be studied in the field because it may be connected with the habitat.

Flowers

Male flowers, female flowers and seeds show little variation. They are generally slightly smaller in small figs. Thus the seeds in v. *motleyana* are 4–6 mm long, in v. *dodonaeiformis* merely 2.5–3 mm long.

The gall-flowers introduce two variations. The red tepals may be rather thin, ligulate, and as long as the ovary or longer, or they may be thick, spathulate, and much shorter than the ovary. Then, the ovary may be smooth or its wall may be thickened, crustaceous, and angular-rugose. The differences are constant enough to be a criterion in identifying gall-plants, but exceptions seem to occur. The two kinds of ovary suggest different fig-insects as do, indeed, the different sizes of fig but only one species *Blastophaga quadrupes* Mayr has yet been reported, probably from v. *lutescens* because the collections were made in Java and Sumatra (Wiebes 1966). The entomology of the complex needs field-study as much as the botany. If no variety covers the whole range of the complex from Thailand to Java and Mindanao, and from sea-level to 3000 m altitude, it will be surprising to find an insect so gifted. Thus, as I have maintained, the entomology will be a check on the botany, but the facts of both must be assembled independently.

The angular-rugose gall-ovary with ligulate tepals occurs in v. *motleyana* and in the acute-leafed *F. oleaefolia*. The smooth gall-ovary occurs in the more or less advanced varieties of *F. deltoidea* (v. *intermedia*, v. *kinabaluensis*, v. *lutescens*, v. *peltata*). I assume that the state in v. *motleyana* is primitive for the complex though the smooth gall-ovary is normal for the whole genus. There are other exceptions with angular-crustaceous ovary as, for instance, *F. obscura* and *F. subulata*.

TAXONOMY

Historically the three specific names *F. deltoidea* Jack (1822), *F. motleyana* Miq. (1867) and *F. oleaefolia* King (1888) are critical. I reduced *F. motleyana* in my check-list to a variety of *F. deltoidea* because v. *arenaria* affects the transition. I maintained *F. oleaefolia* because the small globose fig and constantly lanceolate leaf seemed distinctive, and the similarity between v. *memecylifolia* and v. *myrsinoides* was so great that the blunt leaf of v. *myrsinoides* seemed a parallel evolution in *F. oleaefolia* to that in *F. deltoidea*. The more recent collections from Borneo begin to throw doubt on this disposition. Thus *F. oleaefolia* v. *valida*, here described, seems to differ from v. *motleyana* only in the smaller subglobose fig and to lead thereby to the Bornean state of *F. deltoidea* v. *intermedia* and v. *kinabaluensis*.

Four possibilities emerge. The classification in the check-list may be satisfactory. In contrast, the three species *F. deltoidea*, *F. motleyana* and *F. oleaefolia* may be required. Thirdly, *F. oleaefolia* may be reduced to *F. motleyana* as distinct from *F. deltoidea*. Lastly, all may be reduced to *F. deltoidea*.

In the taxonomic work I have used the terms variety and form in their nomenclatural significance as subordinate ranks in the specific hierarchy. I have avoided the rank subspecies because this is now taken to imply geographical separation. In this intricate complex, geographical limits are not exactly known and to stretch the meaning to include ecological separation would also imply more knowledge than there is. The varieties are distinguished morphologically. Some have different geographical ranges, as v. *deltoidea* and v. *kunstleri*; others seem to have identical ranges, as v. *memecylifolia* and v. *myrsinoides*; yet others partly overlap, as v. *deltoidea* and v. *angustifolia* or v. *motleyana* and v. *oleaefolia*. The geographical overlap is shown in figures 1 to 3. The maps for ecological separation must be worked out through detailed exploration.

EVOLUTION OF THE VARIETIES

The relationships indicated in the key to identification (p. 298) are set out in figure 4. The main seat of evolution seems clearly to have been in Borneo and this is what I have meant by saying that the complex is centred in Borneo, even though it has spread excentrically westwards. Croizat calls this the massing of forms or species and implies that it does not necessarily indicate the centre of origin. However, since regions are ruled out as centres of origin because the complex does not occur there, e.g. Jamaica, Fiji, Ceylon and Formosa, so one rules out the peripheral representation in Thailand, Java, Palawan and Mindanao as the centre and comes logically to that of massing as the centre of origin. The validity of the argument is well shown in this complex and, as I have found from my studies in oriental *Ficus*, it seems to apply very generally to other varietal complexes as *F. hirta*, *F. sarmentosa*, or *F. obscura*, and for the specific complexes of series and subsections. Hence I will repeat the reasons for the case in the complex of *F. deltoidea*.

First, there is no evidence that the ancestor extended over the whole geographical range of the complex. If it had, then there would be traces in this alliance which its diversity, abundance, and geographical restriction show to have been fairly recent. Secondly, these traces are shown by v. *motleyana* which, structurally, is the most primitive state, and while it occurs commonly in Borneo and possibly in Celebes, it has an outlying, possibly relict, station in central Sumatra (Pajakumbuh) and perhaps, in Malaya (Gunong Tapis near Kuantan on the east coast of

Pahang). Thirdly, the most widespread variety, v. *angustifolia* (Thailand, Malaya, Sumatra, Java, Borneo, Palawan, Anamba and Natuna Islands), is one of the most reduced in leaf, fig and seed. Fourthly, the next most widely spread varieties are v. *deltoidea*, which may well have been the ancestor of v. *angustifolia*, and v. *lutescens*, both being advanced states with deeply dichotomous venation. Fifthly, the complex of *F. oleaefolia* resembles that of v. *motleyana*: it is mainly Bornean but it has outlying stations also in Sumatra. Sixthly, the connexion between v. *deltoidea* and v. *motleyana* seems to be through v. *arenaria* (Borneo, Biliton, and possibly Celebes). Lastly, the amount of endemism of the varieties follows the excentric dispersal of the complex (table 1) in agreement with the thesis that the massing of forms indicates centres of origin.

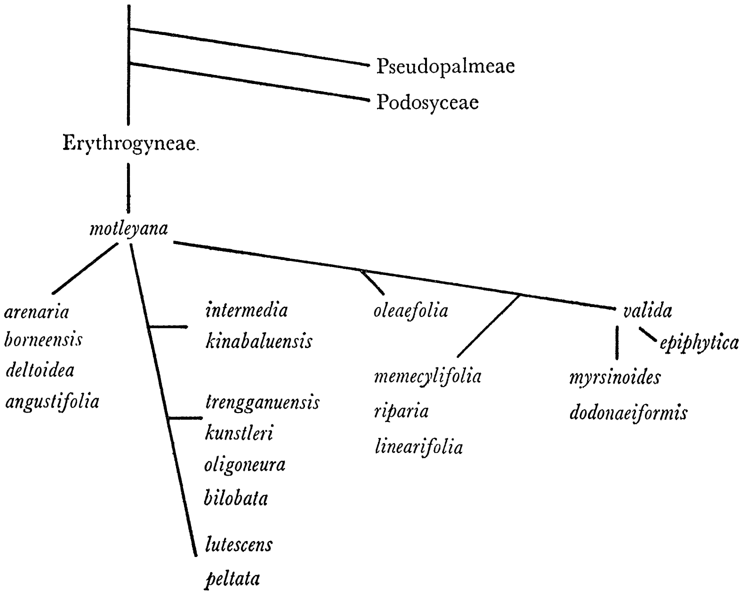

FIGURE 4. The relationship of the *F. deltoidea* complex.

This evidence, morphological and geographical, points to the evolution of the complex about the course of the rivers which drained the Sunda Shelf from the direction of Sumatra north-eastwards and of Borneo north-westwards into the China Sea in the Tertiary Period (Hill 1968; van Bemmelen 1949). Thence various elements of the complex evolved structurally and ecologically, and spread outwards as the topography and climate allowed. Some advanced varieties spread farthest, presumably because they arose earliest before the disruption and drowning of the Tertiary Sunda Shelf. Other varieties, presumably later in their evolution, were caught in various parts of the Shelf as it broke up, and appear now as the endemics. But the earliest state of the complex persisted as v. *motleyana* in the remains of the original habitat.

This explanation differs greatly from that which Croizat infers not only in general but for this particular complex (Croizat 1968, pp. 140–143). Our standpoints differ. He views *Ficus* and this particular complex as another set of organisms which must obey certain standard tracks, revealed by the distribution of all sorts of land animal and plant. These tracks are not paths of migration but the now broken remains of Jurassic or early Cretaceous land occupied by the progenitors of these organisms (p. 142, footnote). This clear statement is very important because it gives the basis from which the biologist must follow the evolution and distribution of land organisms to the present time. But out of this he extracts almost mystical dicta. Thus (p. 108) he writes 'descendants are not found in a range which the progenitor has never entered'. He denies to all land-organisms any power of enlarging their domain since those ancient times. He has to deny spatial advance through ecological evolution because this would clearly involve overstepping the Mesozoic tracks. A montane progenitor might, for instance, evolve a lowland form which would have a greater area to occupy. If the progenitor of the *F. deltoidea*-complex were the mountain *F. oleaefolia*, which occupies one of the tracks (Philippines–Borneo–Sumatra), then v. *angustifolia* as a lowland derivative would have had during the Tertiary Period all the lowlands of the Sunda Shelf to exploit, northwards to modern Thailand where it may still be advancing. But this obviously reasonable assumption has to be denied as contrary to the theory of tracks. Therefore, Croizat postulates (p. 143) that the complex has been derived from the most widespread v. *angustifolia* fulfilling five or six tracks which intersect variously on the Sunda Shelf (fig. 17, p. 141, and fig. 19, p. 162). He does not realize that v. *angustifolia* is, structurally, the most reduced and, therefore, the most advanced state in the whole genus. Then he stops v. *lutescens* at the east end of Java, not because it could not cross to Bali, but because the progenitor never fulfilled the Lesser Sunda Island track (Sumatra to Timor) during the Mesozoic. He allows the complex in Celebes because a track links the south of Borneo with the south of Celebes (though we do not know the state of the complex in either territory) and connects thence through Mindanao with the rest of the Philippines. A ritual enters into this theory when he has to state that distribution 'is not due to chance or climate' (p. 141); I should be very surprised to learn that v. *kinabaluensis* had established itself at sea-level. In postulating the origin of *Ficus* in Gondwanaland, about the position of Madagascar, where by no means incidentally its modern representation is very poor and the *F. deltoidea* complex is absent, he admits dispersal. Then, in denying any subsequent dispersal, v. *angustifolia* is supposed somehow to have produced itself at every locus of occurrence of the complex on the Sunda Shelf to stay put where by this unintelligible means it is supposed to have arisen as many times as there are loci. I find the inferences of his theory untenable. Thus it is, to counteract my argument, that Croizat disrupts a perichalazal ovule (fig. 11, p. 88), declares the syconium to be an inferior ovary, and tempts one to suppose that v. *angustifolia* is the most primitive fig with one flower and one seed in this inferior structure.

I can see no reason whatever to deny post-Jurassic expansion of distribution by species of *Ficus*. In my account of the Solomon Island figs (Corner 1967), I show that it is the morphologically primitive species which have the very limited occurrence and the advanced which become the wides. The problem in *Ficus*, as I believe in other flowering plants, has been how to escape from the pachycaul state with its ecological restrictions and to evolve plastic, neotenic forms of greater adaptability. The complex of *F. deltoidea* has escaped and shows how, in terminating its line of leptocauly it has continued to evolve structurally and ecologically and so to spread beyond the territory of its progenitor; it goes, I repeat, as a bush on to the branches of the modern forest where there are no Mesozoic rules to confine it. Thus I seek through the particular knowledge of *Ficus* to test the validity of current thought on the evolution of flowering plants.

The common denominator in our arguments is the past distribution of land and sea. Accordingly, the distribution of *Ficus* must coincide more or less with that of many other plants and animals. This does not mean, however, that *Ficus* has evolved species in the same manner as birds (c.f. Croizat on vicariism, p. 130 footnote). The idea that a widespread progenitor fulfilled all the possibilities of life for the *F. deltoidea*-complex on the Mesozoic tracks and then split up into Tertiary statics on the Sunda Shelf is not only highly improbable, for it means that the ancestor was lowland, montane, coastal, inland, terrestrial and epiphytic, with an equally pliable insect-pollinator, in Mesozoic forest which was certainly not identical ecologically with Tertiary forest, but it is without support from the facts that are available. I endeavour to argue from the facts, but Croizat argues and with epicycles endeavours to incorporate them under his laws.

THE ORIGIN OF THE COMPLEX

The complex is connected with ser. Podosyceae. This consists of the *F. neriifolia–F. erecta* complex of Sino-Himalaya, the *F. pedunculosa*-complex which is particularly Philippine, and the complex of subser. Basitepalae which is both Sino-Himalayan and Philippine. None of these links directly with the *F. deltoidea*-complex through Thailand except that the riverine *F. ischnopoda* extends from Assam to central Malaya and shows that there should have been a panbiogeographic track which stopped north of Johore. But *F. ischnopoda* is a reduced willow-leafed species, an end-product of the *F. neriifolia*-complex, that is unlikely to have come out of the stony river-bed as the fount of the prolific evolution of *F. deltoidea*: indeed, it merely becomes smaller in Malaya (v. *angustifolia* Ridley), where the Johore rivers are too hot and muddy for it.

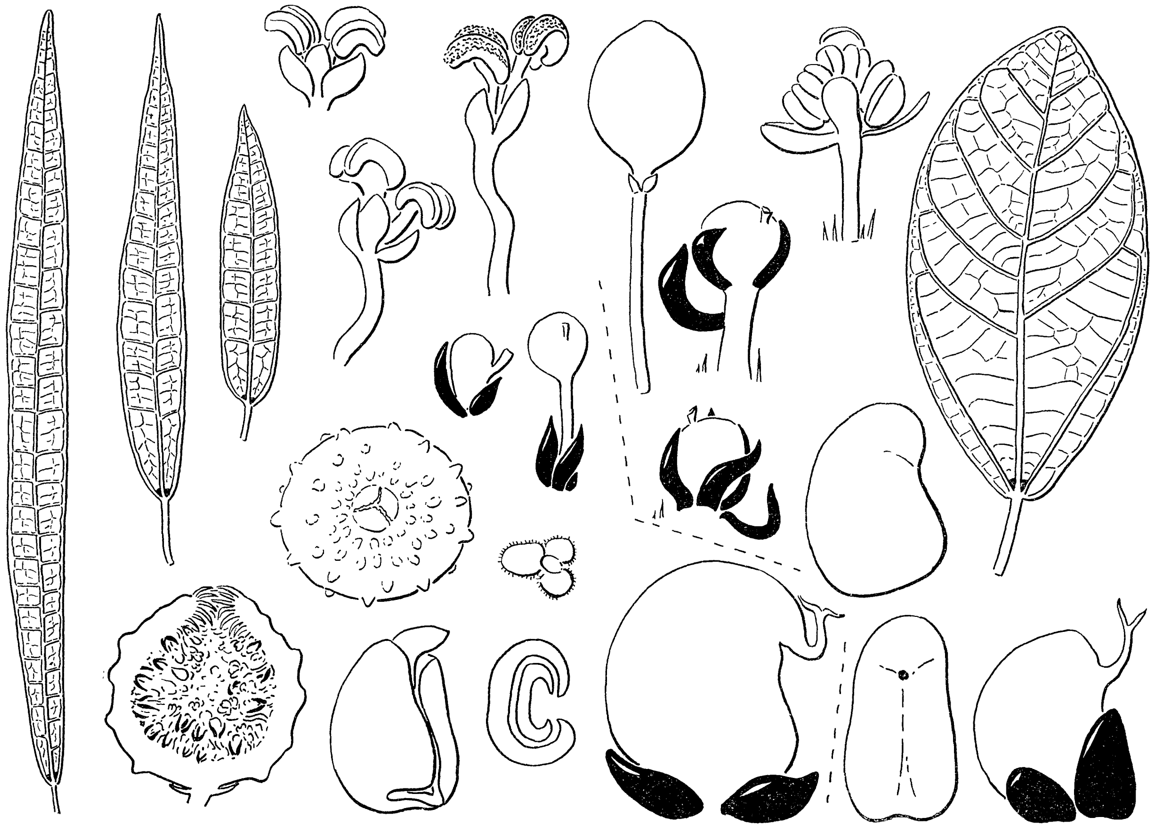

FIGURE 5. *Ficus* ser. *Podosyceae*. Left, *F. pustulata* v. *lanceifolia*; figs × 3, male and gall-flowers × 10, Elmer 12875; female flower and embryo × 10, Elmer 12876; leaves × $\frac{1}{2}$. Right, *F. pedunculosa*; leaf × $\frac{1}{2}$, fig × 3, male (3 stamens) and gall-flowers × 10, Cuming 1941; female flower and seeds × 10, PNH 17146.

Ser. Podosyceae differs from the *F. deltoidea*-complex (ser. Erythrogyneae) in the scattered male flowers. This is the antecedent condition to ostiolar male flowers, which distinguish Erythrogyneae. The scattered arrangement occurs very generally in the monoecious and, in other ways, more primitive subgenera *Urostigma* and *Pharmacosycea*. The ostiolar arrangement characterizes most of the advanced groups of the dioecious subgenus *Ficus* where it appears as the better arrangement, permitting the late development of the male flowers by late initiation at the periphery of the young syconium. Yet, the disperse arrangement persists as a primitive feature around the China Sea (ser. Podosyceae, ser. Sinosyceae, sect. *Kalosyce*, and the ser. Distichae and Trichocarpeae in sect. *Rhizocladus*). This region would appear, then, to be the source of origin of ser. Erythrogyneae.

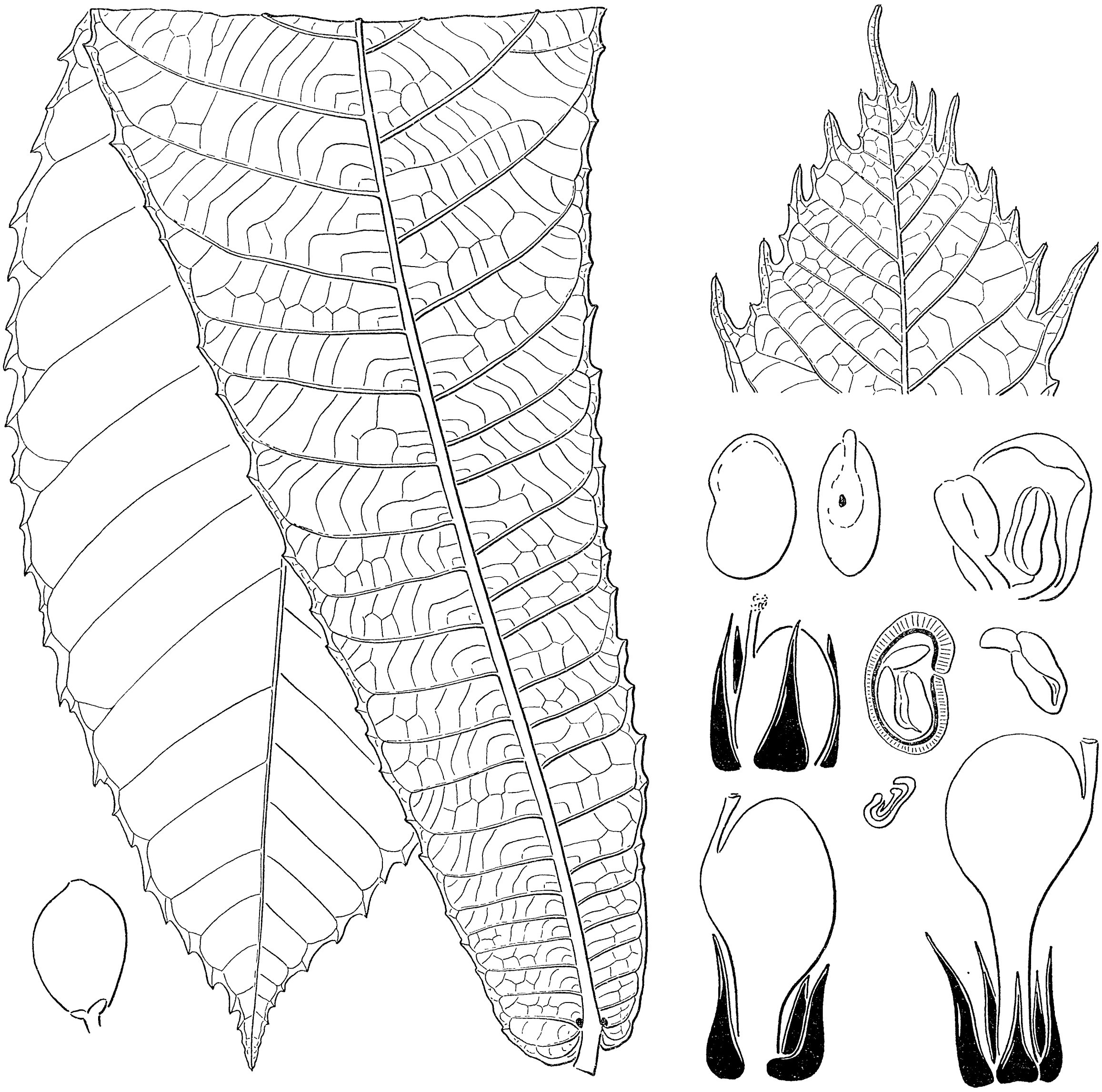

FIGURE 6. *Ficus pseudopalma*; adult leaf (Bur. Sc. 983) and the apex of a sapling leaf (PNH 18506), × ½; female flower with sessile ovary, seeds and embryo × 10, PNH 11723; male and gall-flowers with stalked ovary × 10, PNH 16343; fig × ½.

The other feature which distinguishes ser. Erythrogyneae is the relatively large seed. Small seeds, 1–2 × 1–1.5 mm, are typical of most species of *Ficus*. Larger seeds, resembling those of *F. deltoidea*, occur in ser. Podosyceae (figure 5), thus in *F. pedunculosa* (2–3 × 2 mm), *F. glareosa* (2.5 × 2 mm), and *F. pustulata* (3 × 2.5 mm). They are Philippine species and the last two were thought to be endemic to Palawan, but I have received a collection of each purporting to come from a well-known part of Luzon. All these large seeds have a shape and a locus, as the endocarp of a superior ovary with bifid stigma, and a curved embryo with incurved cotyledons exactly as the larger seeds (7 × 4.5 mm) of *Antiaropsis* in New Guinea (figure 7). Thus they relate with the generally large seed of other Moraceae, typical of successful families of forest trees. The inflorescence of *Antiaropsis*, by no means incidentally, represents a state antecedent to that of the multibracteate syconium; it is multibracteate, congested (without internodes between the bracts as homologues of leaf-primordia), and with discoid centre, but there is no cymose intercalation of later flowers such as occurs in the big syconia of *Ficus*. Therefore I see no objection to the conclusion that ser. Erythrogyneae has retained almost uniquely in *Ficus* the large seed and embryo of pre-*Ficus*. This conclusion explains why v. *angustifolia* and v. *memecylifolia*, as

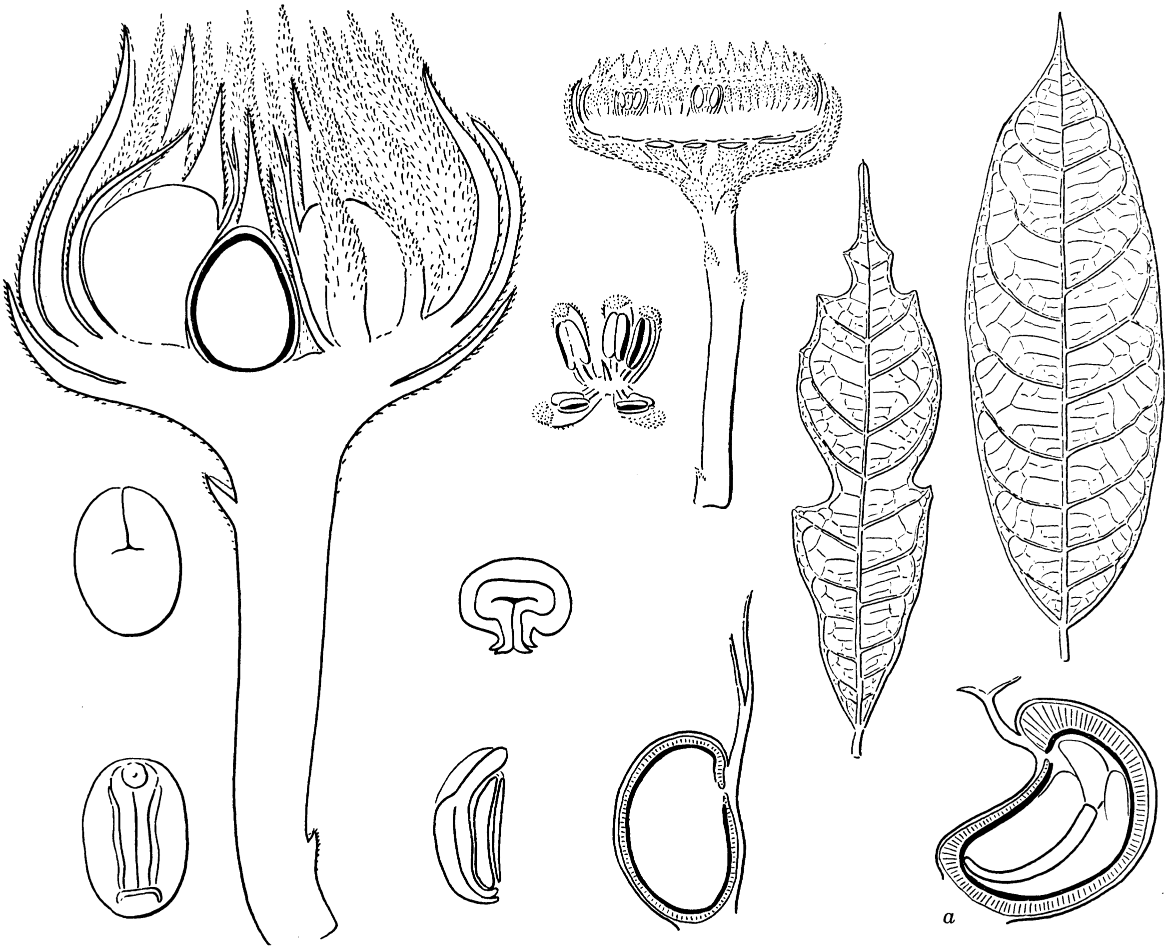

Figure 7. *Antiaropsis decipiens*; infructescence × 3, female flower in fruit and embryos × 4, and lobed sapling leaf × ½, Janowsky 194; male inflorescence × 3, and flower × 8, Schlechter 16045; adult leaf × ½, v. Royen 3608. *a*, *F. pustulata* v. *lanceifolia*, fruit in section × 10.

extremely reduced forms of the genus, have one-seeded syconia; their very small syconia can accommodate only one fruit. Other species of the genus with quite as small syconia accommodate numerous small seeds in them, e.g. *F. microsphaera*, and *F. rubrocuspidata*.

The ancestral locus is indicated as the region connecting Borneo and the Philippines (Corner 1958*b*, p. 35), but there is a disjunction. Though v. *angustifolia* occurs in Palawan, it does not seem common and no other variety of the complex has been reported there. Another reduced variety, v. *epiphytica*, occurs frequently in Mindanao. These are clearly outlying regions which the small, reduced varieties have been able to reach. Ser. Podosyceae, however, is present in both Palawan and Mindanao, but does not reach the Sunda Shelf; *F. pedunculosa*, nevertheless, is present with *F. oleaefolia* v. *epiphytica* in Celebes, whence by one of Croizat's tracks it should be in Borneo, where it has not been discovered.

There occurs also in the Philippines the unique *F. pseudopalma* (figure 6) which, as a pachycaul with large leaf, seems vegetatively near to the ancestor of subgen. *Ficus*. It has advanced to a smooth (not multibracteate) syconium with ostiolar male flowers and small seeds (2 mm long). It indicates, therefore, yet another primitive feature of subgen. *Ficus* in the Philippines. Hence I am led to infer that the pachycaul ancestor of the *F. deltoidea*-complex with disperse male flowers and large seed was part of the ancestry of subgen. *Ficus*; that it lived in the Philippine–Borneo part of West Malaysia, south of the Formosa–Philippines arc; that it has completely disappeared, but that its characters persist in ser. Pseudopalmeae, Podosyceae and Erythrogyneae. The last invaded Sundaland where this ancestor never existed, in so far as there is no evidence that it did, and therefore the theory of vicariism fails. It may seem curious that the successful advance of ser. Erythrogyneae was not retarded by the retention of the primitive big seed, but this seed has been no hindrance to the evolution of the epiphytic habit. Elsewhere in Moraceae, as I have mentioned, this habitat has been developed only by the small-seeded strangling figs of subgen. *Urostigma* and subgen. *Ficus* subsect. *Palaeomorphe*. They have strong root-systems and by sending roots to the ground the epiphytic sapling develops into small, large and enormous trees. The *F. deltoidea*-complex seems to have become epiphytic in a new and advanced way with a reduced root-system, inherited from the evidently reduced system of v. *motleyana*. Here is another cogent reason for field-study of the complex. Extremely little is known about the root-systems of tropical plants. In *Ficus* the roots may be 100 m long, but in the epiphytic *F. deltoidea* it is doubtful if they reach 1 m. Such a difference must affect the size of the plant, its habit, its habitat, its distribution and its geographical pattern.

The illustrations of *F. pseudopalma*, *F. pedunculosa*, *F. pustulata* and *Antiaropsis* supply, however, the evidence not only for the source of the *F. deltoidea*-complex but for the evolution of the syconium on Moraceous lines. For this Croizat has sought afar until in that uncertain offshoot of the Moraceous ancestry leading to Urticaceae, namely Conocephaloideae, he decides schematically to flatten a branch of the inflorescence of *Pourouma* into a few-flowered, or one-flowered, cup, deck it with bracts, and convert it into a figlet. Then, stringing these figlets together, for they are merely branches of an inflorescence, he holds this assembly equivalent to a cauliflorous twig of syconia, as in *Ficus* sect. *Sycocarpus*. Then he reduces this twig to one or two branches in order to derive the single or paired axillary figs of the genus, and finally re-multiplies the flowers inside the structure to produce the many-flowered, monoecious syconium (Croizat 1968, f. 8, p. 62). One could schematize, of course, on paper from several other Urticaceous genera, but the test is whether any such scheme fits the facts of *Ficus*. The immediate objections to Croizat's scheme are that no ally of *Pourouma* has done this and that

Pourouma in tropical America is right away from the centre of *Ficus*-evolution in Malaysia, particularly from the cauliflorous *Sycocarpus*.

By contrast, the infructescence of *Antiaropsis* with red bracts and tepals and blue-green drupes shows in a lively way the Moraceous image of the pro-syconium; the infructescence is derived from an entire axillary inflorescence, not from a branch of it. Beginning, therefore, with this real structure, then by urceolation in the classical manner of hyponasty and basipetal growth the whole inflorescence of *Antiaropsis* closes into an axillary, multibracteate and red syconium fitted for blastophagy as required phyletically. Such a structure would be very similar to the multibracteate syconia of *Ficus* sect. *Sycidium* and *Sycocarpus*. Then, by loss of most lateral bracts through basipetal restriction of urceolation to a few proximal internodes, the syconia of *Sparattosyce* could be formed; these have the styles extruded for external pollination through the orifice of the syconium and, as it is not blastophagous, *Sparattosyce* is a close parallel with the more advanced *Ficus*. Thus the facts are that two Moraceous genera, bordering on the main scene of *Ficus*, *Antiaropsis* in New Guinea and *Sparattosyce* in New Caledonia, parallel *Ficus* in the pro-blastophagous phase, as classical theory would expect. These two genera consist of one or two species each. What do these represent?

The leaf in both genera is reduced to that comparatively small state when copious transverse intercostal veining is becoming limited neotenically to the intercalary expansion of the initial cruciate venation, as in *F. deltoidea* v. *motleyana*. How this state is related to the large and relatively primitive leaf of *F. pseudopalma* is shown by *F. pedunculosa* in the usual manner of *Ficus* where, in all its sections, the simple venation of the more or less lanceolate leaf can be seen to be derived from the more complex with transverse intercostals. Thus the species of *Antiaropsis* and *Sparattosyce* appear as highly advanced, leptocaul relics of their lines of pre-*Ficus* evolution the pachycaul derivation of which is lost. *Ficus* must have begun with the evolution of blastophagy in the primitive pachycaul phase, but through the persistent success of the genus it has retained the intermediates which show how such relics can be understood. If only *F. deltoidea* persisted, the case of blastophagous *Ficus* would be as enigmatic. Thus, too, the species of *Streblus* show up as leptocaul relics of the tribe Moreae. Because the urceolate syconium with internal pollination by blastophagy is so obviously one of the most spectacular modifications of the inflorescence in Moraceae, indeed among all angiosperms, without parallel in Urticaceae, I regard it as recent in Moraceous evolution and its genus *Ficus* to be the most recent ebullition of this successful family. It happened independently of Urticaceae and Conocephaloideae.

I conclude from the evidence available in *Ficus* that the *F. deltoidea*-complex evolved directly from the ancestral stock of subgen. *Ficus* in the Borneo–Philippine region, if not in Borneo; that this stock is now represented in v. *motleyana* from which neotenic and pliable derivatives have invaded the dipterocarp and montane forests of the Sunda Shelf as forest treelets, shrubs and epiphytes. And as a mark of this progress the most progressive and reduced varieties have become most successful and widespread. Parallels are *F. chartacea*, *F. subulata*, *F. benjamina*, *F. septica*, and *F. adenosperma*, all of which will require for explanation a discussion of their series.

Key to the species and varieties of the *F. deltoidea* complex

1. Leaves penninerved, acute or obtuse with the midrib dichotomous at the apex. Gall-tepals usually equal to or exceeding the angular-rugose ovary, or absent (v. *epiphytica*), but shorter in v. *memecylifolia*. Figs subglobose, 3–10 mm wide (dried)............*F. oleaefolia*

  2. Leaves narrow, elongate, 3–10 mm wide. Figs 3–5 mm wide. Borneo.

    3. Lamina obtuse, narrowly spathulate. Peduncles (3–)9–12 mm. .... v. *dodonaeiformis*

    3. Lamina acute or attenuato-subacute. Peduncles 1–7 mm. .... v. *linearifolia*

  2. Leaves wider.

    4. Leaves mostly obtuse, rather small. Figs 4–7 mm wide; peduncles 1.5–8 mm.

      5. Veins more or less invisible. Gall-tepals absent or scattered between the ovaries. Celebes, Mindanao v. *epiphytica*

      5. Veins distinct. Gall-tepals normal. Borneo. ....v. *myrsinoides*

    4. Leaves acute, sometimes a few obtuse.

      6. Figs 6–10 mm wide. Lamina often rather large.

        7. Gall-ovary angular-rugose.

          8. Fig ellipsoid or fusiform, 10–20 × 6–10 mm; peduncle 1–6 mm. ....*F. deltoidea* v. *motleyana*

          8. Fig globose or shortly ellipsoid; peduncle 5–8 (–15) mm. ....*F. oleaefolia* v. *valida*

        7. Gall-ovary smooth or scarcely angular.

          9. Peduncles 4–12 (–15) mm. ....*F. deltoidea* v. *intermedia*

          9. Peduncles 1–3 mm. Lamina stiffly coriaceous ....*F. deltoidea* v. *kinabaluensis*

      6. Figs 4–6 mm. wide. Lamina often small.

        10. Peduncles 0.5–2 mm. Gall-tepals equal to or exceeding the ovary. ....v. *oleaefolia*

        10. Peduncles 3–14 mm slender. Gall-tepals shorter than or equal to the ovary. ....v. *memecylifolia*

1. Leaves generally obtuse, with a gland at the dichotomy of the midrib, in some cases mixed with acute penninerved leaves. ....*F. deltoidea*

  11. Gall-ovary smooth or faintly angled; tepals equal to or exceeding the ovary. Figs 4–10 mm wide, usually subglobose.

    12. Lamina suborbicular, narrowly peltate. Creeping shrub with lax internodes. Sumatra. ......v. *peltata*

    12. Lamina not peltate. Usually erect shrubs or small trees with short internodes.

      13. Obtuse leaves often nearly as wide as long, the midrib dichotomous at or below the middle of the lamina. Peduncle of various lengths. ....v. *lutescens*

      13. Obtuse leaves generally much longer than wide, the midrib dichotomous in the distal third and usually without an axillary gland.

        14. Peduncles 1–3 mm long. Leaves stiffly coriaceous, mostly acute. ....v. *kinabaluensis*

        14. Peduncles longer. ....v. *intermedia*

  11. Gall-ovary distinctly angular-rugose.

    15. Gall-tepals thick, spathulate, much shorter than the ovary.

      16. Adult plants with acute penninerved leaves and obtuse leaves with the midrib dichotomous at or above the middle of the lamina. Fig 7–10 mm wide; peduncle 1–9 mm. ....v. *arenaria*

      16. Adult plants with only obtuse leaves.

        17. Lamina spathulate to narrowly obovate, much longer than wide, the midrib dichotomous at or above the middle of the lamina. Fig 4–6 mm wide; peduncles (1.5–) 5–15 mm. .... v. *angustifolia*

        17. Lamina broadly obovate, the midrib dichotomous at or below the middle.

          18. Figs 8–11 mm wide (11–15 mm, living); peduncle 0–6 mm. Twigs 2–5 mm thick. Lamina 3–9 cm wide. Varying finely hairy. ....v. *borneensis*

          18. Figs smaller; peduncle 3–15 mm. Twigs 1–2 mm. Lamina usually smaller. ....v. *deltoidea*

    15. Gall-tepals lanceolate or ligulate, as long as the sessile ovary and often as long as the stalked ovary.

      19. Fig less than 10 mm wide (7–12 mm, living). Leaf more or less bilobed. v. *bilobata*

19. Figs wider (12–20 mm, living). Gall-flowers often pedicellate.
  20. Peduncle 1–4 mm long. Leaves dimorphous; obtuse leaves with the midrib dichotomous in the upper third of the lamina, without an axillary gland. Gall-ovary subsessile. Sumatra. .... v. *oligoneura*
  20. Adult plants with obtuse leaves only, the midrib with a gland at the dichotomy. Gall-ovary often long-stalked as well as pedicellate. Malaya, Thailand.
    21. Stout plant. Lamina as wide as long, 5–14 cm; midrib dichotomous in the lower third of lamina; glands 5–9. .... v. *kunstleri*
    21. Lamina 2–5 cm wide, longer than wide; midrib dichotomous at or above the middle; glands 3–4 (–5). .... v. *trengganuensis*

Sect. *Ficus* subsect. *Ficus* ser. *Erythrogyneae* Corner

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Shrubs or small trees, often epiphytic. Leaves lanceolate-acute, penninerved, or obovate-obtuse with dichotomous midrib, often dimorphous on the same plant, without transverse intercostals, entire, not palmately or pinnately lobed: cystoliths hypogenous. Figs paired, mostly pedunculate, generally without pedicels. Tepals dark red, often thick, always much shorter than the seed-ovary, free. Male flowers ostiolar: stamens 2, not mucronate. Ovaries white or yellowish, the gall-ovary generally crustaceous and angular-rugose. Female style unequally

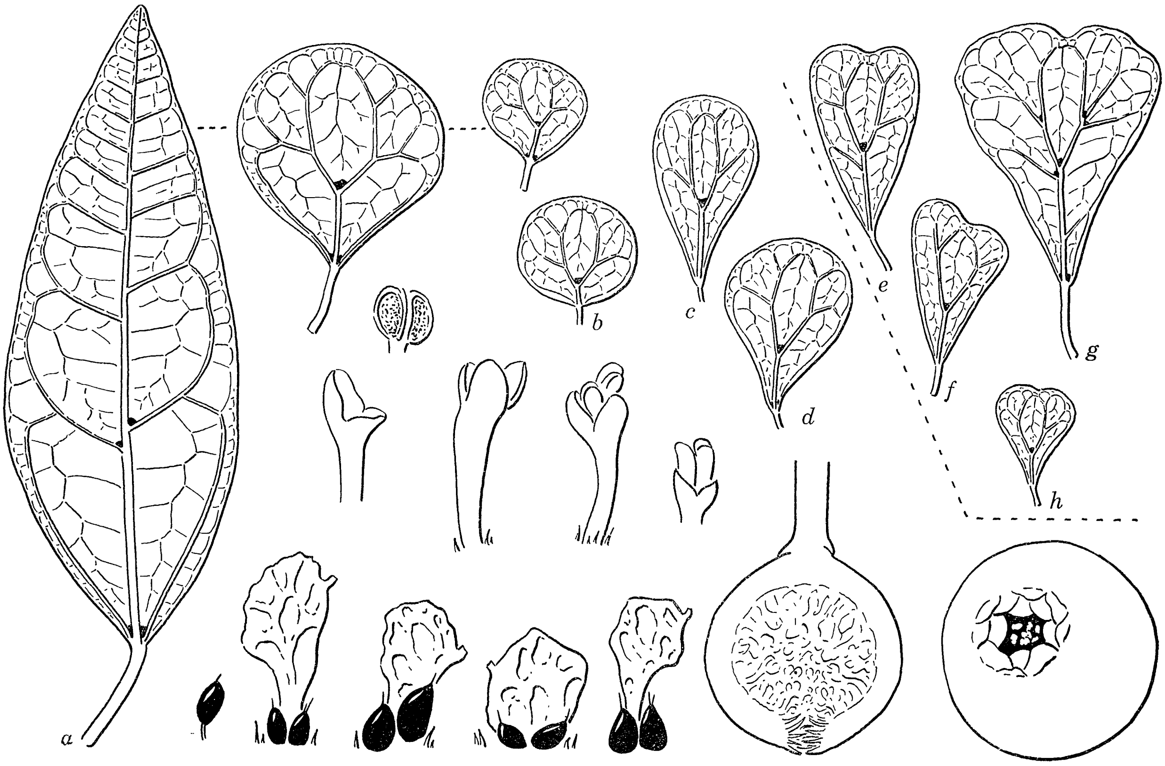

FIGURE 8. *F. deltoidea* v. *deltoidea*, *a–d*; *a*, sapling and adult leaves, Nieuwenhuis s.n., Borneo; *b*, Amdjah 243, Borneo; *c*, Mondi 76, Borneo; *d*, Achmad 1210, Sumatra; male and gall-flowers and gall-figs (one with gaping orifice), SFN 32240. Var. *bilobata e–h*; *e–f*, Corner s.n., Pahang; *g*, SFN 21235, Kedah (approaching v. *kunstleri*); *h*, SFN 2368. Leaves × ½, figs × 3, flowers × 10.

bifid. Seeds 2.5–6 mm long, subreniform, smooth, scarcely keeled, few in each fig: embryo large with conduplicate cotyledons. Species 2, Western Malaysia.

F. deltoidea Jack, *Mal. Misc.* **2** (1822), 71

Shrub, epiphytic or terrestrial, up to 2 m high. Glabrous, or ciliate on the edges of the stipules and basal bracts. Twigs 1–2 mm thick. Lamina 2–8 × 1.5–7.5 cm, broadly spathulate to rounded obovate, varying subrotund, obdeltoid or slightly bilobed with cuneate base, stiffly coriaceous, thick, ferruginous to olive brown or ochre beneath when living; midrib dichotomous at or below the middle of the lamina, generally in the lower third: glands 3, two basal, one at the dichotomy of the midrib: leaves in young plants and those at the base of lower branches lanceolate-acute, penninerved: petiole 2–15 (–20) × 1–2 mm. Figs axillary, paired, ripening orange: peduncle 3–15 × 1–2 mm: basal bract *ca.* 1 mm: body 5–7 mm wide (7–10 mm, living), subglobose in the gall-figs and often gaping when ripe, ellipsoid in the seed-figs, orifice closed by three flat apical bracts, then gaping slightly to show the male flowers at maturity: internal bristles few, short: no sclerotic cells. Male flowers in several rings in the distal half of the fig, sessile to pedicellate, rarely disperse: tepals 2–3, red, free, glabrous: stamens 2. Gall-flowers sessile: tepals 3–4, much shorter than the ovary, thick, fleshy, hard, red, mostly with a hair at the tip and a short slender stalk; ovary sessile or with a stalk up to 1 mm long, yellow, strongly rugose-angular, hard, crustaceous: style very short. Female flowers sessile, few: tepals as in the gall-flowers, often scattered among the ovaries rather than forming a distinct perianth: ovary white, smooth, sessile or stalked: stigma bifid. Seed 3.5–4.5 × 2 mm, smooth, subreniform, scarcely compressed, not or slighty keeled: embryo curved, cotyledons conduplicate. Leaf with cystoliths only on the lower side.

Var. **deltoidea** (figure 8)

As above

Distr. Malaya (Singapore, East Johore, S.E. Pahang), Riouw and Lingga Archipelagos, Bangka, Sumatra, Borneo.

Ecol. Generally epiphytic in lowland and mountain forest, up to 1200 m alt. (Kinabalu), also terrestrial on rocks and sea-shores.

This is a small shrub, never as large as the much commoner v. *intermedia* and v. *lutescens*, with smaller figs ripening orange to red (not pink, red, black). Though young plants have a few lanceolate, penniveined leaves, these are not found on the adult plant. Further, the strongly rugose-angular ovary is a distinction from these varieties. Thus defined, v. *deltoidea* has a restricted distribution, particularly in Malaya, and it has not been collected in Java. There may be intermediates to v. *angustifolia* and v. *arenaria*. I have seen no specimen from Palawan.

Var. **angustifolia** (Miq.) Corner, *Gdns' Bull., Singapore* **17** (1960), 421 (figure 9)

Shrub up to 4 m high. Lamina 2–7 × 0.8–3 cm, spathulate or lanceolate obovate, rarely obscurely lobed at the apex: midrib dichotomous at or above the middle of the lamina: gland 1, at the fork of the midrib, rarely a slight basal gland or at subsequent dichotomies of the midrib: petiole 2–10 mm: young plants with lanceolate-acute, penninerved leaves. Fig ripening yellow to orange (? red): peduncle 5–15 × 1 mm, slender: body 6–8 × 4–6 mm. Gall-flowers with the tepals shorter than the rugose-angular ovary, with 1–2 hairs at the tip. Seeds 4 × 2 mm, 1–3 per fig.

Distr. Lower Thailand, Malaya, Riouw Archipelago, Sumatra, Borneo, Anamba and Natuna Isl., Palawan.

Ecol. Epiphytic in lowland and mountain forest up to 1500 m alt.; common on seashores.

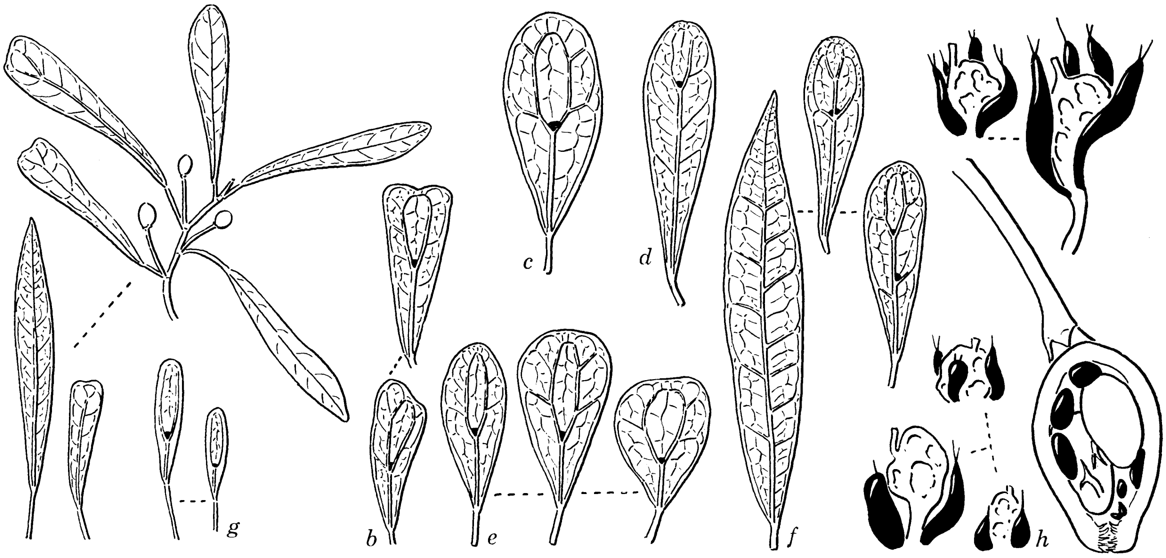

FIGURE 9. *F. deltoidea* v. *angustifolia a–f* and *h*, and f. *angustissima*, *g*; *a*, PNH 4, Palawan; *b*, Franck s.n., Malaya; *c*, King's collector 4997; *d*, For. Dept. Malaya 23374; *e*, SFN 27340, 26623, and 26414 (left to right), Borneo; *f*, SFN 34120, sapling and adult leaves, Malaya; *g*, SFN 14753, Sipora Isl.; *h*, gall-flowers of SFN 27340 (above, Borneo), Wallich 4526 (below, Penang), and SFN 24130 (fig with 2 seeds). Leaves × ½, fig × 3, flowers × 10.

Generally this is easily distinguished from v. *deltoidea* by the narrow, spathulate leaf but a few collections seen intermediate. A shortly peduncled form occurs on the mountains of Sarawak and Sabah which may need distinction, but field-study is required to learn whether it may not be a parallel derivative from v. *intermedia* in Borneo. Its features are as follows: lamina 1.6–3.2 cm wide; peduncle 1.5–6 mm long; fig-body 6–8 × 5–6 mm; gall-tepals short and thick, but a few ligulate and as long as the ovary; gall-ovary angular, crustaceous varying (in Kinabalu collections) to almost smooth. Kinabalu, 1500 m, SFN 26414, 26623, 27340; Hose Mts, Sarawak, S 19070, 900 m; Ulu Tiau, Balleh, Sarawak, S. 21188, 400 m (figure 9*e*, *h*).

From Palawan I have seen one collection, PNH 4 (Mt Mantalingahan, Brooke's Point, 1400 m, 3 m shrub, along streams in the forest on the south slope). Most of the leaves are acute and penninerved (figure 9*a*), but I can see no reason to distinguish it from v. *angustifolia*.

Forma **angustissima** Corner, *Gdns' Bull., Singapore* **17** (1960), 421 (figure 9*g*)

Twigs 1–1.5 mm thick. Lamina 2–3.3 × 0.5–1 cm, narrowly spathulate, blunt, attenuate to the base; midrib dichotomous below the middle of the lamina; gland 1, at the dichotomy of the midrib; petiole 5–11 mm. Fig-body 5 × 3–4 mm; peduncle 2–5 mm. Seeds 1–2 per fig.

Distr. Mentawei Islands (Batoe, Siberut, Sipora).

This is the most slender form of *F. deltoidea*. Normal v. *angustifolia* has been collected on Siberut Island.

Var. **arenaria** Corner, *Gdns' Bull., Singapore* **17** (1960), 421 (figure 15*e*)

Shrub up to 2 m high. Lamina 2.5–11 × 1.8–4 cm, mostly elliptic to narrowly obovate, acute to subacuminate, penninerved, 3–5 pairs of lateral nerves; a few upper leaves obovate, obtuse, with the midrib dichotomous at or above the middle, often near the apex, longer than wide, small. Fig-peduncle 1–9 mm long; body 10–12 × 7–9 mm, ellipsoid, or 7–9 mm wide and subglobose, ripening red. Gall-tepals much shorter than the somewhat angular, thinly crustaceous ovary. Seeds 1–5 per fig.

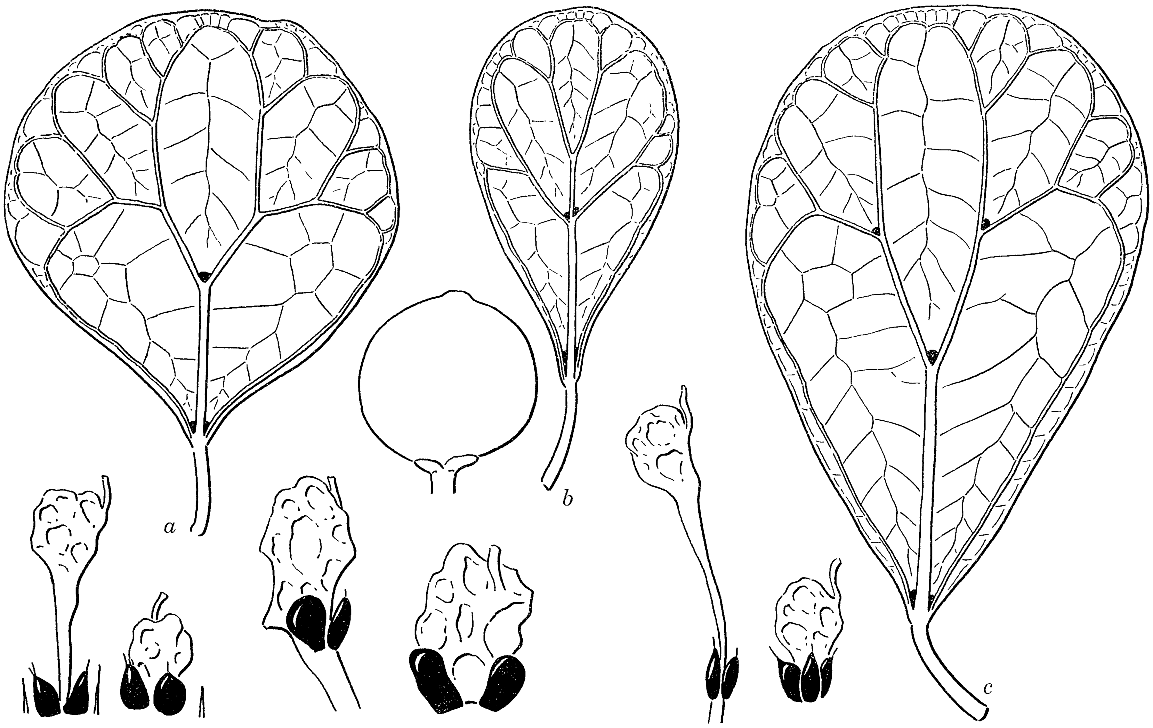

FIGURE 10. *F. deltoidea* v. *borneensis*; *a*, S 12930; *b*, SFN 27370; *c*, Corner s.n. 1959; gall-flowers (left) Clemens 21907, (centre) Endert 3920, (right) Sar. Mus. 4807; fig, Endert 3920. Leaves × ½, fig × 2, flowers × 10.

Distr. Borneo, Biliton (Celebes?).

Ecol. On sandy soil, coastal and inland, generally in secondary vegetation.

This is the Bornean plant which seems to come between v. *motleyana* and v. *intermedia*. From both it differs in the short gall-tepals, thus suggesting that it should be v. *deltoidea*, but it has mostly acute leaves and red oblong figs, which are not the character of v. *deltoidea*. I have seen many living plants of all these varieties and conclude that it is necessary to separate this. It may be a characteristic plant of the *kerangas*-vegetation, where it has hitherto been collected. Seed-plants may not be distinguishable in the herbarium. One collection from Celebes (Riedel 7134, Menado) may belong here.

Collections. Brunei 5352, Kuala Belait, in *Dryobalanops rapa* forest, (type). Brunei 5367, Badas, in *Shorea albida* forest. Bur. Sci. (P.I.) 290, Sandakan. Dunselman 103, Singkawang, on sandy padang. Hose 211, Marudi, Baram district. Purseglove 5024, Sarawak, Bako National Park, kerangas. Richards P.W., 2644, 2645, Marudi, on burnt white sand. Alston 13092, Sampit. Kornasi s.n., Biliton, Tg. Pandan.

Var. **bilobata** Corner, *Gdns' Bull., Singapore* **17** (1960), 422 (figure 8*e–h*)

Shrub or small tree up to 5 m high. Lamina 2–7 × 1–3.5 cm, spathulate, obovate or obdeltoid, shortly bilobed at the apex, particularly in narrow leaves transitional from the penninerved, varying entire: midrib dichotomous at or below the middle of the lamina: gland 1 at the dichotomy at the midrib, sometimes also 1–2 basal glands, or 3–7, basal and at the main dichotomies of the veins: petiole 3–25 mm long. Figs 5–8 mm wide: peduncle 2–10 mm long. Gall-flower with ligulate tepals as long as the rugose-angular ovary.

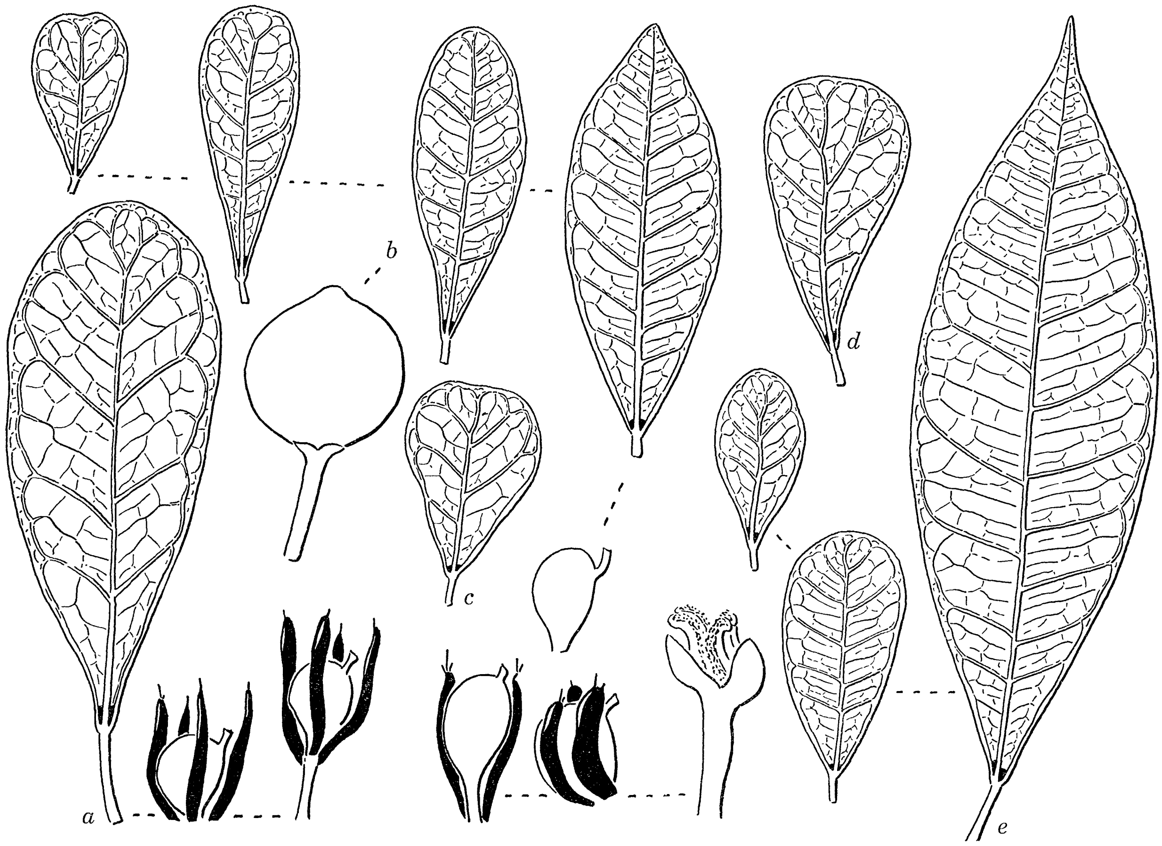

Figure 11. *F. deltoidea* v. *intermedia* from Malaya; *a*, Stone 6559, leaf and gall-flower; *b*, Corner s.n. (Pahang), leaves, fig and gall-flowers; *c*, Kloss 12256; *d*, Wray 2830; *e*, SFN 17761. Leaves ×½, fig ×2, flowers ×10.

Distr. Malaya (Selangor and Pahang to Kedah).

Ecol. In ridge or summit forest, 1000–2000 m high, and on the leached tops of limestone hills.

I cannot place this satisfactorily with any other variety in Malaya. It approaches v. *lutescens*, v. *trengganuensis*, v. *intermedia*, v. *angustifolia*, and even mountain forms of v. *kunstleri*. It must be singled out, therefore, for field-study. It may be that all these varieties converge to this form with small bilobate leaf. Thus the specimens from the limestone hills have 3–7 glands on the underside of the obdeltoid lamina, whereas those from the granite mountains of the main range, which are typical v. *bilobata*, have 1 (–3) glands on the more spathulate lamina, as in v. *angustifolia* and v. *intermedia*.

Var. **borneensis** Corner, *Gdns' Bull., Singapore* **17** (1960), 422 (figure 10)

Twigs 2–5 mm thick. Lamina 4.5–13 × 3–9 mm, obovate, blunt, or subrotund: midrib dichotomous at or just below the middle of the lamina, rarely above the middle: glands 2, basal, occasionally another at the midrib-dichotomy: petiole 4–25 × 3–4 mm, stout. Fig-body 8–12 mm wide (11–16 mm wide, living), colour?: peduncle 0.5–6 mm: basal bracts 2–2.5 × 3–4 mm. Gall-flowers sessile or shortly stalked: tepals much shorter than the sessile or long-stalked, strongly rugose-angular ovary.

Distr. Borneo (generally).

Ecol. Lowland and mountain, up to 1500 m alt.

This approaches v. *kunstleri* in the large leaf and fig, but it differs in the short peduncle, short gall-tepals, and fewer leaf-glands: possibly the petiole is shorter, but it may vary much on different parts of the plant. I have not seen v. *kunstleri* from Borneo. Var. *borneensis* suggests the less reduced state of v. *deltoidea*. Only a few leaves at the base of the stem are acute and penninerved.

Forma **subhirsuta** Corner, *Gdns' Bull., Singapore* **17** (1960), 422

Peduncle, basal bracts, and fig-body thinly appressedly hairy, sometimes also the twigs.

Distr. Sarawak, South Borneo.

Hairiness is unusual in this series of *Ficus*.

Var. **intermedia** Corner, *Gdns' Bull., Singapore* **17** (1960), 423 (figures 11, 12*c*, *d*)

Shrub up to 4 m high. Leaves generally dimorphous: penninerved lamina as in v. *motleyana*: obtuse, spathulate lamina 3–16 × 1.5–6 cm, longer than wide, the midrib dichotomous in the distal third of the lamina, often near the apex: glands 2, basal: petiole 2–15 mm long, short. Figs ripening red to purple-black: peduncle 1–11 (–15) mm long: basal bracts 1–3 mm long: body 6–10 mm wide, subglobose or shortly ellipsoid. Gall-flowers with ligulate or lanceolate tepals exceeding the smooth or slightly angular ovary.

Distr. Malaya, Borneo, (? Celebes).

Ecol. Mountain forest, 800–2600 m alt., terrestrial or epiphytic, often in mossy forests.

Bornean collections. Kinabalu, Clemens 28787, 29916, 30294, 30296, 30766, 30988, 31503, 33193, 33625, 40696, 40696A; SFN 26400, 27714, 28007c.—Sarawak, C.W.L. 386, Hotta 14754, on Gunong Mulu; Burtt and Martin B 5492, on Gunong Murud; S 20103 in Ulu Baram, Bario; Clemens 20161, Mt Poi; SK 29, 136, Merurong Plateau, Bintulu (SK 29 with obtuse leaves).—Indonesian Borneo, Endert 3912, 3917, Mt Kemoel, west Koetai.

I now exclude *F. kinabaluensis* from the synonymy of this variety, but the whole problem of v. *intermedia* needs careful study in the field. The Malayan plants of v. *intermedia* have acute and obtuse leaves intermingled on the same twig. They have been considered identical with v. *lutescens* but the midrib dichotomises in the distal half or third of the lamina in v. *intermedia*. The Bornean plants seem nearly always to have only the acute leaves; in some collections there are a few obtuse leaves as in the Malayan plants and it is impossible to know, as yet, if the apparent difference is real or merely a hazard of collecting. The Bornean plants may have larger leaves with the lamina 5–18 × 1.5–6 cm and may become bigger plants up to 6 m high. The Malayan plants thus seem to be slightly more advanced in leaf-reduction. Var. *kinabaluensis* connects with the Bornean state of v. *intermedia*.

The Bornean state appears superficially very like the Bornean *F. oleaefolia* v. *valida* which has the angular-rugose gall-ovary with thick red tepals characteristic of *F. oleaefolia*. Seed-plants would seem indistinguishable in the herbarium. They need recognition and comparison in the field. The round, not oblong, figs distinguish them from v. *motleyana* which seems also to occur, mainly if not entirely, in the lowland forest.

Var. **kinabaluensis** (Stapf) stat.nov. (figure 12*a*, *b*, *e*)—*F. kinabaluensis* Stapf. *Trans. Linn. Soc. Lond.* (Bot. ser.), **2**, 4 (1894), 226—*F. deltoidea* v. *intermedia* Corner (pr. p.), *Gdns' Bull., Singapore* **17** (1960), 423

Twigs 2–3 mm thick, dark brown. Stipules up to 20 mm. Lamina 2–12 × 1.4–5 cm, elliptic-acuminate, occasionally spathulate and obtuse, penninerved, strongly coriaceous, the edge slightly thickened and often incurved, drying dark brown; midrib dichotomous at the apex of obtuse leaves; costas 7–12 or 4–6 in small leaves; petiole 1–3 mm long, thick. Peduncles 1–3 × 0.7–1 mm. Fig-body 9–11 × 7–8 mm, subglobose to shortly ellipsoid, the seed-fig with 2–3 seeds. Gall-tepals as long as or longer than the more or less smooth ovary (subangular in Clemens 10996 and 29257).

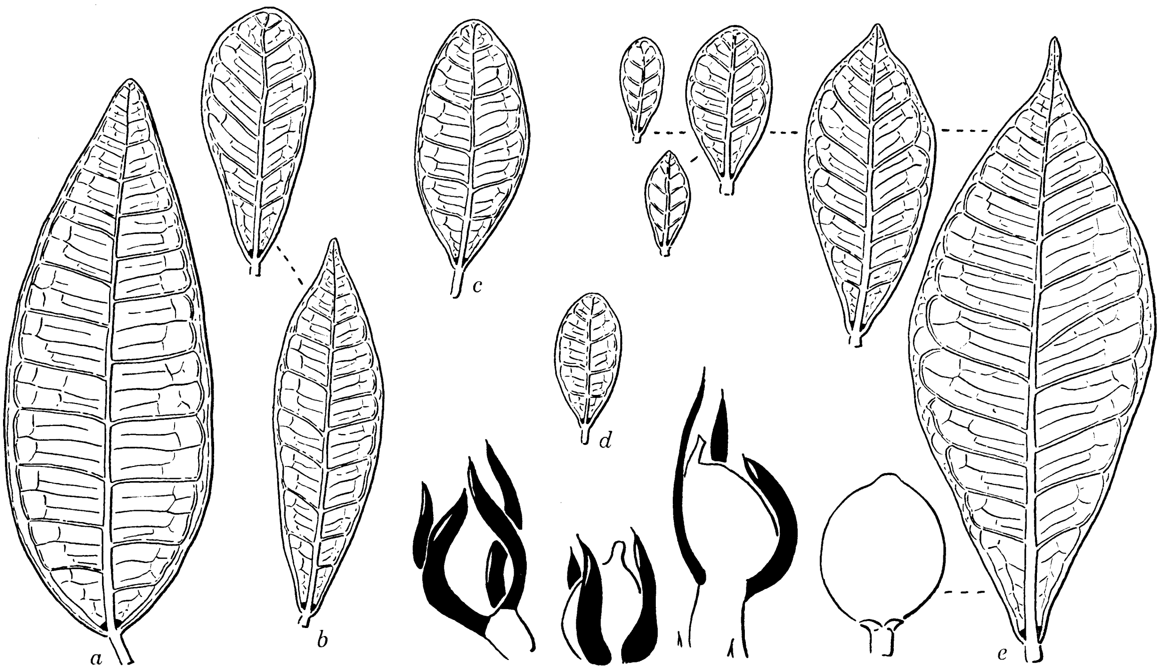

FIGURE 12. *F. deltoidea* v. *kinabaluensis* (*a*, *b*, *e*) and v. *intermedia* from Borneo (*c*, *d*); *a*, Clemens 10996; *b*, SFN 27695; *c*, Clemens s.n. 1933; *d*, Burtt & Martin B5492; *e*, RSNB 715 and 871, sapling and adult leaves, fig and gall-flowers. Leaves × $\frac{1}{2}$, fig × 2, flowers × 10.

Distr. Borneo (Sarawak, Sabah).

Ecol. High mountain forest 1800–3000 m, creeping in thickets or becoming a small shrub in open places.

Collections. Kinabalu, Haviland 1216 (type), 1215; Clemens 28932, 29257, 30292, 31665, 32936, 32937, 32940, 33830, 50635, 51082; PNH 24330 (= Clemens, 10700) 26075 (= Clemens 10996); RSNB 715, 871A, 871B; SFN 27524, 27695.—Sarawak, Burtt and Martin B5489, B5536, Gunong Murud.

This probably grades into v. *intermedia* of Borneo with larger peduncle and larger, less coriaceous leaf, and perhaps, also, into v. *valida*. It appears to be the variety that grows in the highest altitudes, almost to the tree-limit. Thus it would be interesting to know how it might grow at sea-level and whether it has any epiphytic ability. At the highest altitude on the east ridge of Mt Kinabalu the specimens were without gall-insects and without seeds. The gall-ovary is slightly angled in Clemens 10996 and 29257.

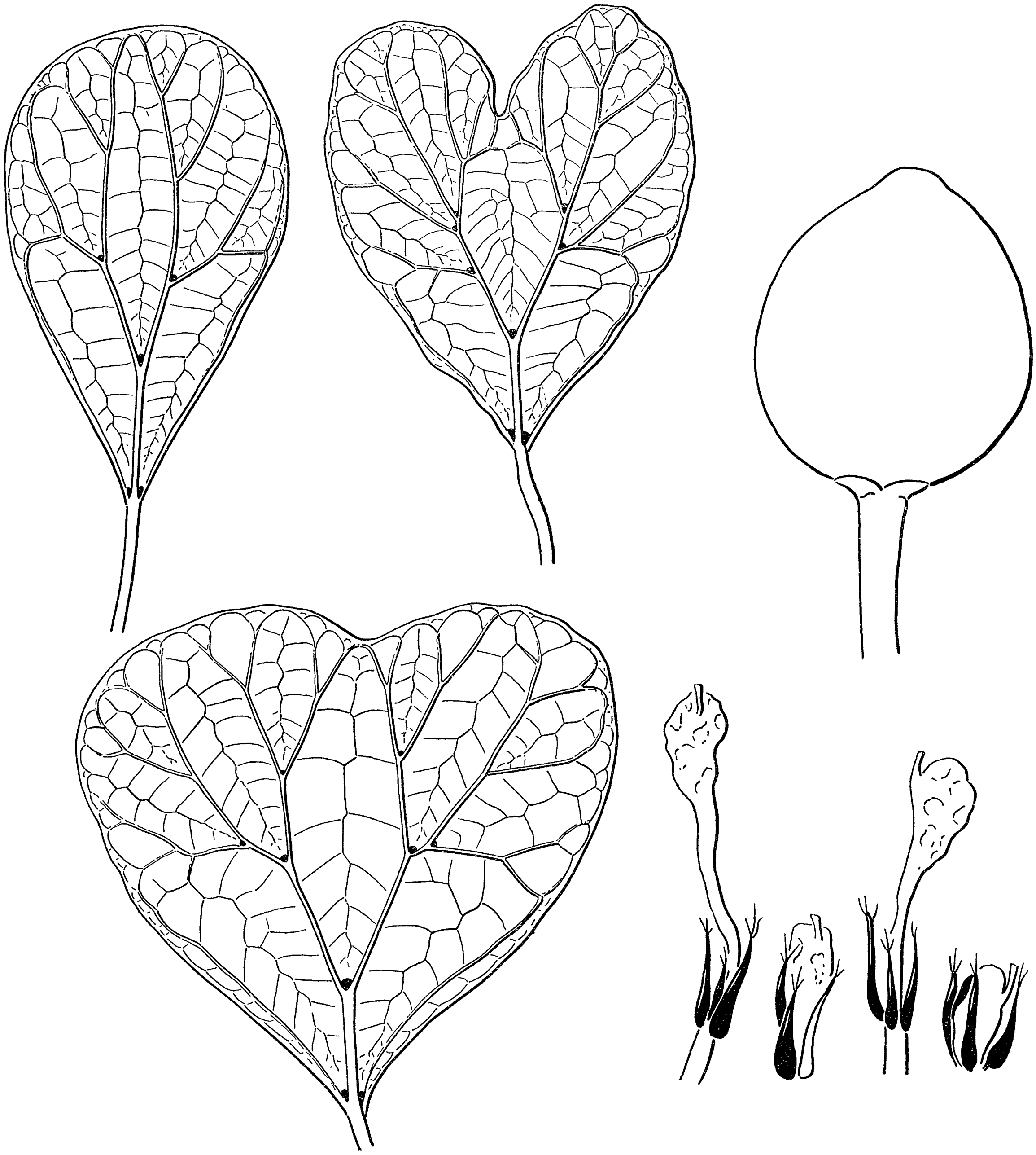

FIGURE 13. *F. deltoidea* v. *kunstleri*; leaves (upper left) Scortechini 483, (upper right) Ridley 2314, (below) SFN 21925; gall-fig and flowers SFN 21925. Leaves ×½, fig ×2, flowers ×10.

Var. **kunstleri** (King) Corner, *Gdns' Bull., Singapore* **17** (1960), 423 (figure 13)

Massive in all parts. Twigs 3–5 mm thick. Lamina (3–) 6–14 × (3–) 5–14 cm, rounded-obovate to subdichotomous, generally as broad as long: midrib dichotomous in the lower third of the lamina, its branches 4 times dichotomous: glands 5–9, two basal, the others at the

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dichotomies of the larger nerves: petiole 13–90 × 2–4 mm, flattened. Fig 12–20 mm wide (15–25 × 12–22 mm, living), subglobose to ellipsoid, rose-red to dark purple: peduncle 6–15 × 2–4 mm, often closely puberulous: basal bract 1.5–2.5 mm long. Gall-flowers sessile or shortly stalked: tepals 4, lanceolate with 2–4 hairs at the tip, as long as the ovary, varying much shorter than the long-stalked ovaries: ovary angular-rugose, crustaceous. Seed 3.5–4.5 × 2 mm.

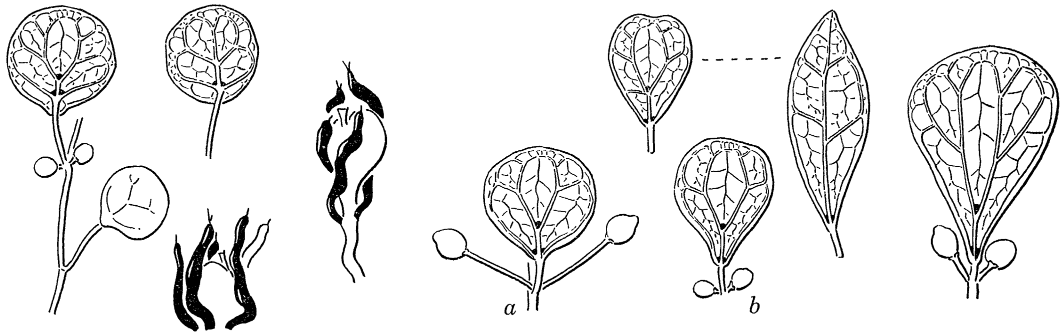

FIGURE 14. *F. deltoidea* v. *lutescens* (right, Forbes s.n., Java; sapling and adult leaves SFN 7267) with f. *longipedunculata* (*a*, Meier 5008) and f. *subsessilis* (*b*, Forbes 843B). Left, v. *peltata* with gall-flowers (Meier 3980). Leaves × ½, flowers × 10.

Distr. Lower Thailand, Malaya (Mt Ophir northwards).

Ecol. Epiphytic in lowland forest, particularly riverine, and on mountains up to 1500 m. alt.

This robust variety is common on the *neram* rivers of Malaya and Lower Thailand (*neram* = *Dipterocarpus oblongifolus*). It spreads also to the west and to the south in Malaya, but it has not been recorded from Johore. Mountain forms have smaller leaves and slightly smaller figs and the question arises whether it varies into v. *bilobata* or v. *trengganuensis*. The long gall-tepals, as well as the long peduncle and more numerous leaf-glands, distinguish it from v. *borneensis*, and I have detected no specimens from Borneo.

Var. **lutescens** (Desf.) Corner, *Gdns' Bull., Singapore* **17** (1960), 423 (figure 14)

Shrubs or small tree up to 7 m high. Twigs 2–3 mm thick. Stipules up to 12 mm. Leaves dimorphous: penninerved lamina 4–14 × 1.7–5.5 cm (up to 18 × 6 cm), lanceolate, varying somewhat elliptic or obovate, subacuminate, base cuneate, 5–8 (–14) pairs of lateral nerves, 2 basal glands (occasionally in the axils of the lower lateral nerves), petiole 5–45 mm: dichotomously veined lamina 3–10.5 × 2.5–6 cm, broadly spathulate to obdeltoid, round at the apex or shortly bilobed, blunt, midrib dichotomous in the lower half of the lamina: glands 2, basal, sometimes also at the dichotomy of the midrib, petiole 3–25 mm. Figs ripening pink to red, then black: peduncle 4–14 × 1–1.5 mm: basal bracts 1–2 mm long: pedicel 0–2.5 mm: body 6–9 mm wide (8–11 × 7–9 mm, or 6–9 × 6–8 mm in gall-figs, living). Gall-tepals longer than the smooth or slightly angular ovary, ligulate or spathulate. Seeds 3.5–4.5 × 2–2.5 mm, 5–9 per fig.

Distr. Sumatra, Java, Sarawak, North Borneo.

Ecol. Epiphytic in mountain forest 700–2500 m alt., and on rocks or on the ground in mossy forest.

I restrict v. *lutescens* to plants with the gall-flowers as in v. *intermedia* but with broad blunt leaves, the midrib dichotomous at or below the middle. A continuous series of herbarium specimens could be arranged from v. *lutescens* through v. *intermedia* to v. *motleyana*, but it has yet to be shown that such a series exists on the same plant, in the same locality, or even in the same country. Certainly v. *intermedia* of Malaya and Borneo never attains such pronounced dimorphism of the leaf as v. *lutescens*.

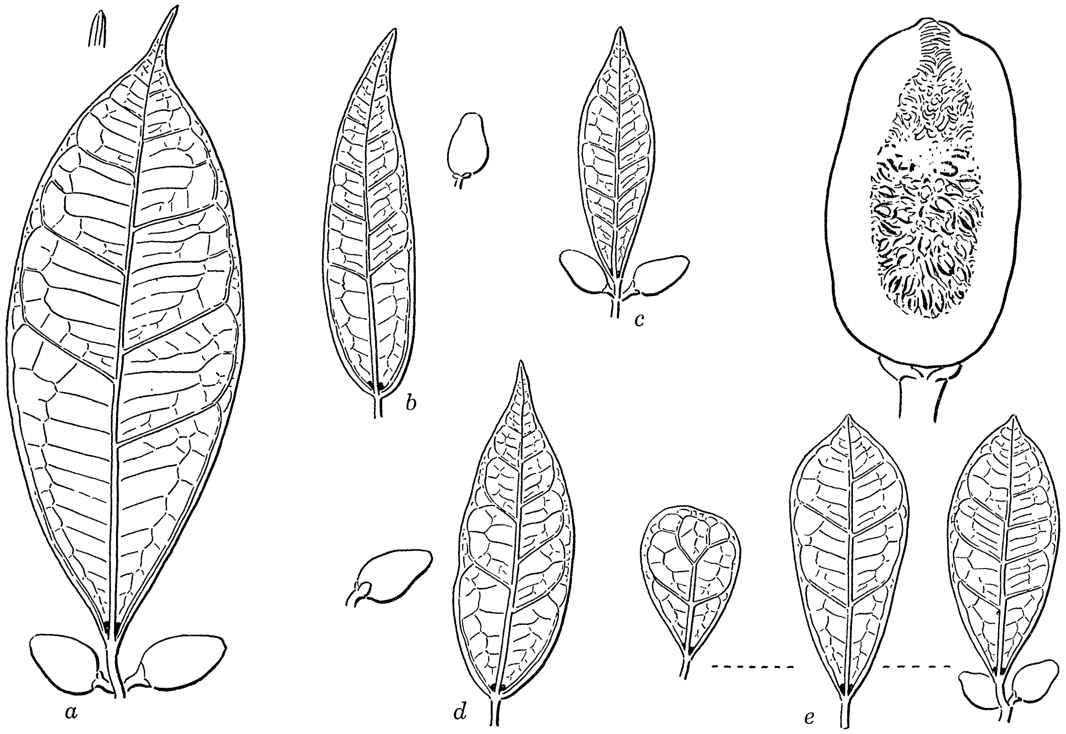

FIGURE 15. *F. deltoidea* v. *motleyana* (*a–d*) and v. *arenaria* (*e*); *a*, SFN 35609; *b*, Haviland 125; *c*, Hotta 14359; *d*, SFN 28905 (type of *F. landoni*, Gunong Tapis); *e*, Hose 211. Leaves × ½, fig of v. *motleyana* in section × 1½.

Compared with the many collections from Sumatra and Java, those from Borneo are few. Among these, S 4290, San 17580 and San 27911 have more or less strongly angular-rugose gall-ovaries as in v. *motleyana*.

Bornean collections. RSNB 589, 2775, Kinabalu; S 4290, Baram River; San 17580, Lungmanis, Sandakan; San 27911, Sepilok Forest, Sandakan.

Forma **longipedunculata** Corner, *Gdns' Bull., Singapore* **17** (1960), 424 (figure 14*a*)

Peduncles 14–30 mm long.

Distr. Java, Sumatra.

Forma **subsessilis** (Miq.) Corner, *Gdns' Bull., Singapore* **17** (1960), 424 (figure 14*b*)

Peduncle of fig 0–4 mm long.

Distr. Java, Sumatra, Borneo.

The Bornean collection is San 4592 (Kimanis Forest Reserve, Papar district, Sabah).

Var. **motleyana** (Miq.) Corner, *Gdns' Bull., Singapore* **17** (1960), 424 (figure 15)

Shrub or small tree up to 6 m high. Lamina 3.5–26 × 1.2–6 cm, smaller on older plants, lanceolate or elliptic-lanceolate to narrowly obovate, acute or acuminate with a tip up to 17 mm long, base cuneate, penninerved, rarely with a blunt or subdeltoid leaf with the midrib dichotomous near the apex: lateral nerves 3–5 pairs, or 5–10 on the lower leaves: basal veins 1 pair, not or occasionally elongate, 2 basal glands: petiole 2–15 mm long, generally short. Figs ripening red; peduncle 1–6 × 1–2 mm, short, thick: basal bracts 2–3 mm long: body 10–20 × 5–10 mm, ellipsoid to fusiform (dried). Gall-flowers with lanceolate or ligulate tepals, equal to, longer than, or somewhat shorter than the angular ovary. Seed 4.5–6 × 3–4 × 2.5–3 mm, 6–8 per fig.

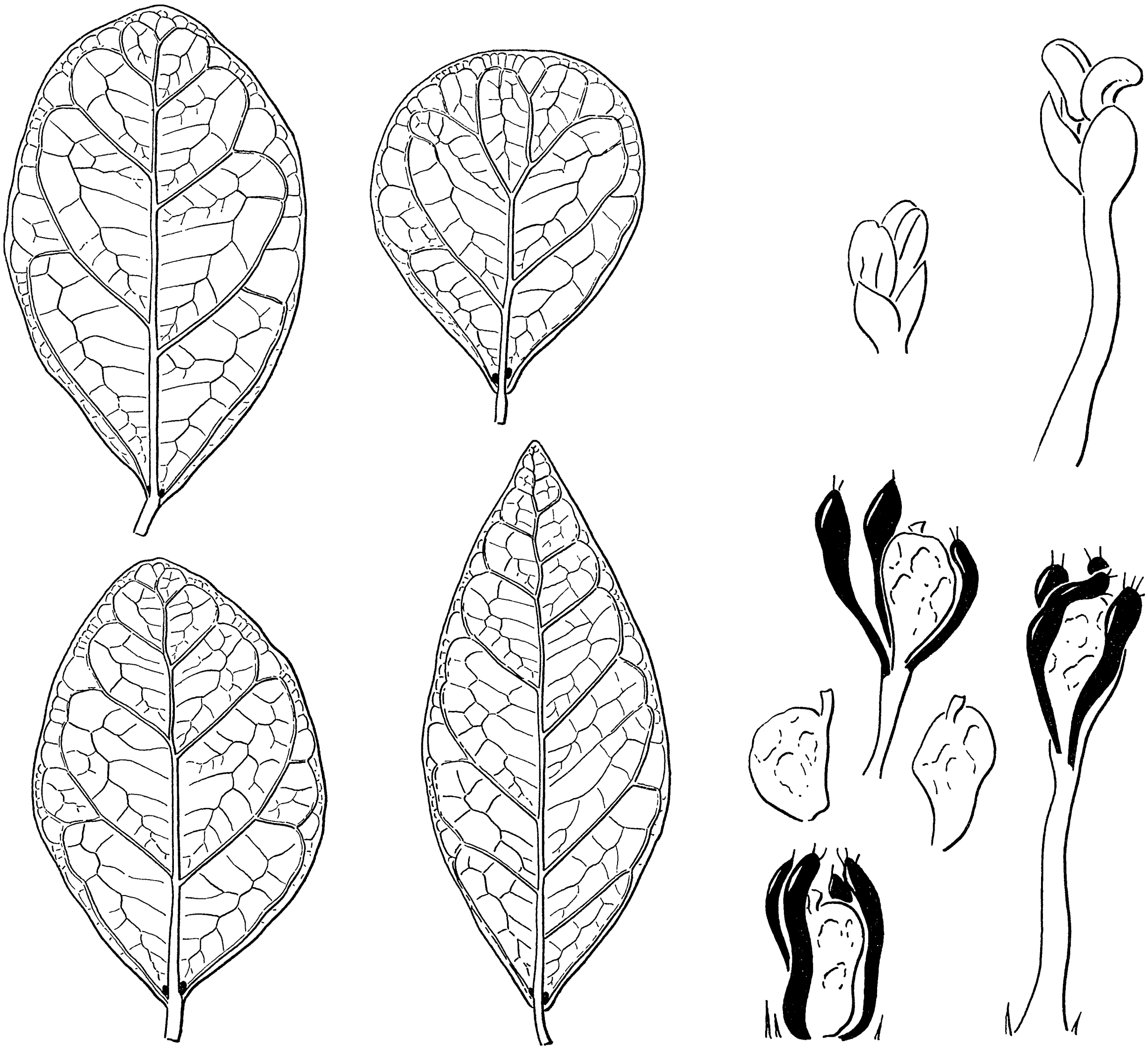

FIGURE 16. *F. deltoidea* v. *oligoneura*; leaves (upper left) Bünnemeyer 3091 (upper right, lower left) Hagerup s.n.;. 1917, (lower right) Schiffner 1873, × ½; male and gall-flowers, Bünnemeyer 301, × 10.

Distr. Borneo, Malaya (G. Tapis, Pahang), Sumatra (Pajakumbuh), ? Celebes.

Ecol. Lowland and mountain forest up to 1100 m alt., common in sandy heath-forest and in heath swamp-forest, ? not epiphytic.

The rather large acute leaf, the oblong fig, and the angular gall-ovary with ligulate tepals distinguish this variety which seems not to become epiphytic. However it almost certainly intergrades with v. *arenaria* and, if the fig becomes globose, it may lead into *F. oleaefolia* v. *valida*.

It is typically Bornean. The one Malayan record is the type of *F. landonii* SFN 28908 (G. Tapis), and it requires further investigation because of its short leaves. Certainly v. *motleyana* has not been found in lowland Malaya which has been more thoroughly explored than Borneo. The Sumatran records come from the neighbourhood of Pajakumbuh and suggest a relict station similar to that in Malaya. The Biliton record in my check-list is v. *arenaria* and this is probably the nature of the Celebes records (Riedel 7134, Teysmann 7134, Eyma 3675). The Indochinese records are *F. gasparriniana*.

Malaya: SFN 28908, Gunong Tapis, n.e. Pahang (lamina 4–10 × 1.5–4 cm, acute; peduncle 3–4 mm; fig-body 15–19 × 7 mm, dried; *F. landonii*).

Sumatra, near Pajakumbuh at 600–1000 m; Meijer 3969, 5248 (Harau Canyon), 7064 (Taram), 7549 (Halabran); Jacobs 4594 (Harau Canyon).

Var. **oligoneura** (Miq.) Corner, *Gdns' Bull., Singapore* **17** (1960), 424 (figure 16)

Twigs 2–4 mm thick. Lamina up to 17 × 8 cm, very variable, elliptic or ovate-elliptic, acute or subacute to blunt and obovate, even on the same twig: midrib dichotomous above the middle of the lamina: glands 2, basal: penninerved leaves with 4–7 lateral nerves: petiole 2–14 × 2–3.5 mm, short, stout. Fig-body 11–15 mm wide (16–20 × 14–16 mm, living), subglobose to ellipsoid: peduncle 1–4 mm, short, stout. Gall-flowers sessile or with pedicel up to 3.5 mm long: tepals 3–4, as long as or longer than the subangular, crustaceous, more or less sessile ovary. Seed 5–5.5 × 3 × 2 mm.

Distr. Central Sumatra.

Ecol. Mountain forest *ca.* 100 m alt.

This is known from the mountains in the region of Fort de Kock and Bukit Tinggi (Karbouwengat). It has larger figs than in v. *lutescens* and long pedicellate gall-flowers (not long-stalked ovaries). The leaf is also larger, but so variable that it is impossible to define.

Var. **peltata** Corner, *Gdns' Bull., Singapore* **17** (1960), 424 (figure 14)

Slender creeping shrub with rather long internodes. Lamina 1.5–2.7 cm wide, suborbicular, narrowly peltate at the base, thinly coriaceous: midrib dichotomous below the middle (rarely above): glands 3, two basal, one at the dichotomy of the midrib: petiole 10–18 × 1 mm. Fig-body 8 × 5 mm, ellipsoid: peduncle 1–1.5 mm, short: basal bracts *ca.* 1 mm long: pedicel 2–3 mm long. Gall-flowers sessile or pedicellate: tepals 4–5, ligulate, equal to or exceeding the smooth ovary.

Distr. Sumatra (Mt Sago, Harau-canyon).

Ecol. Creeping on rock-walls.

The habit seems remarkably different from the normal erect growth of *F. deltoidea*, but in spite of this and of the narrowly peltate lamina, the variety is close to v. *lutescens*.

Var. **trengganuensis** Corner, *Gdns' Bull., Singapore* **17** (1960), 425 (figure 17)

Twigs 2 mm thick. Lamina 2.3 × 1.8–5.5 cm, elliptic to rounded-obovate or somewhat bilobed: midrib dichotomous about $\frac{1}{2}$–$\frac{2}{3}$ lamina; glands 3–4 (–5), two basal, the others at the dichotomies of the main veins: petiole 10–50 × 1–2 mm. Fig-body 9–12 mm wide (14–18 × 11–14 mm, living), rose-red to purple-black: peduncle 6–20 × 1.5 mm: basal bracts 1–1.5 mm. Gall-flowers sessile or with stalks up to 1.5 mm long: tepals 3–4, ligulate or lanceolate, as long as the rugose-angular ovary, often with a hair at the tip.

Distr. Malaya (Trengganu, east coast of Pahang).

Ecol. Coastal shrub and in *Leptospermum* forest at 1300 m alt., also epiphytic in lowland forest.

This is a handsome bush of the Pahang and Trengganu coasts, but it has also been collected on G. Padang (Trengganu), and as an epiphyte on *Dipterocarpus oblongifolius* in Trengganu.

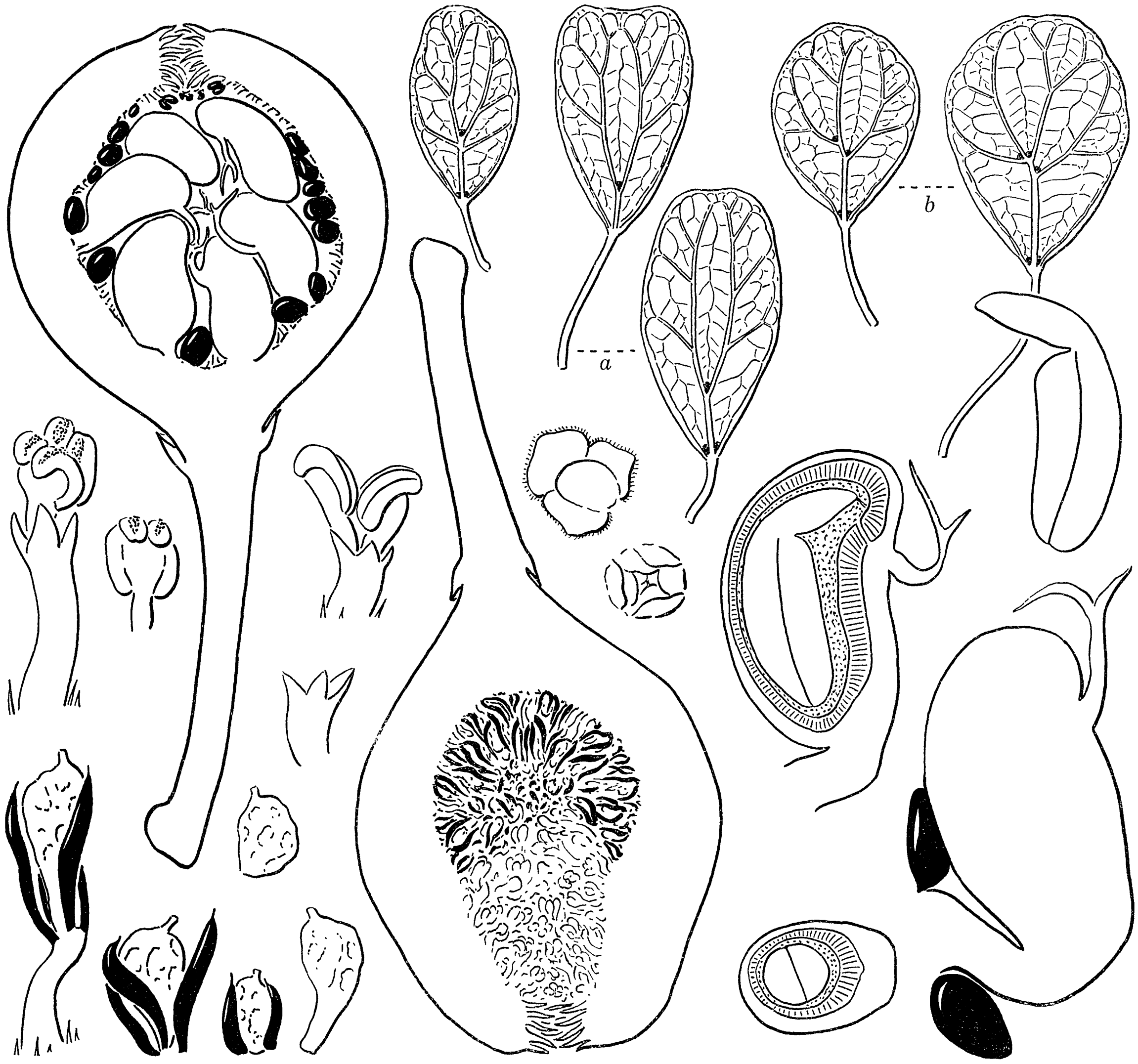

FIGURE 17. *F. deltoidea* v. *trengganuensis*; female and gall-figs ×3, flowers and seeds ×10, Corner s.n., Trengganu; *a*, SFN 15346; *b*, SFN 30079. Leaves ×½.

In size it comes between v. *kunstleri* and v. *intermedia*. Its leaves are characteristically elliptic and long-petiolate, in which it inclines to v. *kunstleri*, but the gall-flowers are nearly those of v. *intermedia*. Compare, also, the mountain v. *bilobata*.

F. oleaefolia King, *Spec. Ficus* **2** (1888), 160, pl. 204B

Shrub or small tree up to 5 m high, often epiphytic. Glabrous, or the petiole and the edges of the stipules and basal bracts puberulous. Twigs 1–2 mm thick, dark brown, subangular. Stipules up to 7 mm. Lamina 2–9 × 1–3 cm, lanceolate-elliptic, subacute or subacuminate with blunt tip, base cuneate, entire, subcoriaceous, smooth, drying fuscous-green to brown: lateral nerves 5–9 pairs, at a wide angle, no distinct intercostals: basal nerves 1 pair, short: basal glands 2: petiole 1.5–15 mm. Figs axillary, paired, ripening orange to red, then dark purple: peduncle 1.5–4 mm long: basal bracts 1 mm long, ovate, blunt: body 4–5 mm wide, subglobose, often drying subumbonate, orifice plane: internal bristles and sclerotic cells none. Tepals 3–4, red, free. Male flowers ostiolar in several rings: tepals spathulate. Gall-flowers sessile: tepals ligulate, as long as or somewhat shorter than the angular-rugose ovary, with 1–2 bristles at the tip. Female flowers and seed? Leaf with cystoliths only on the lower side.

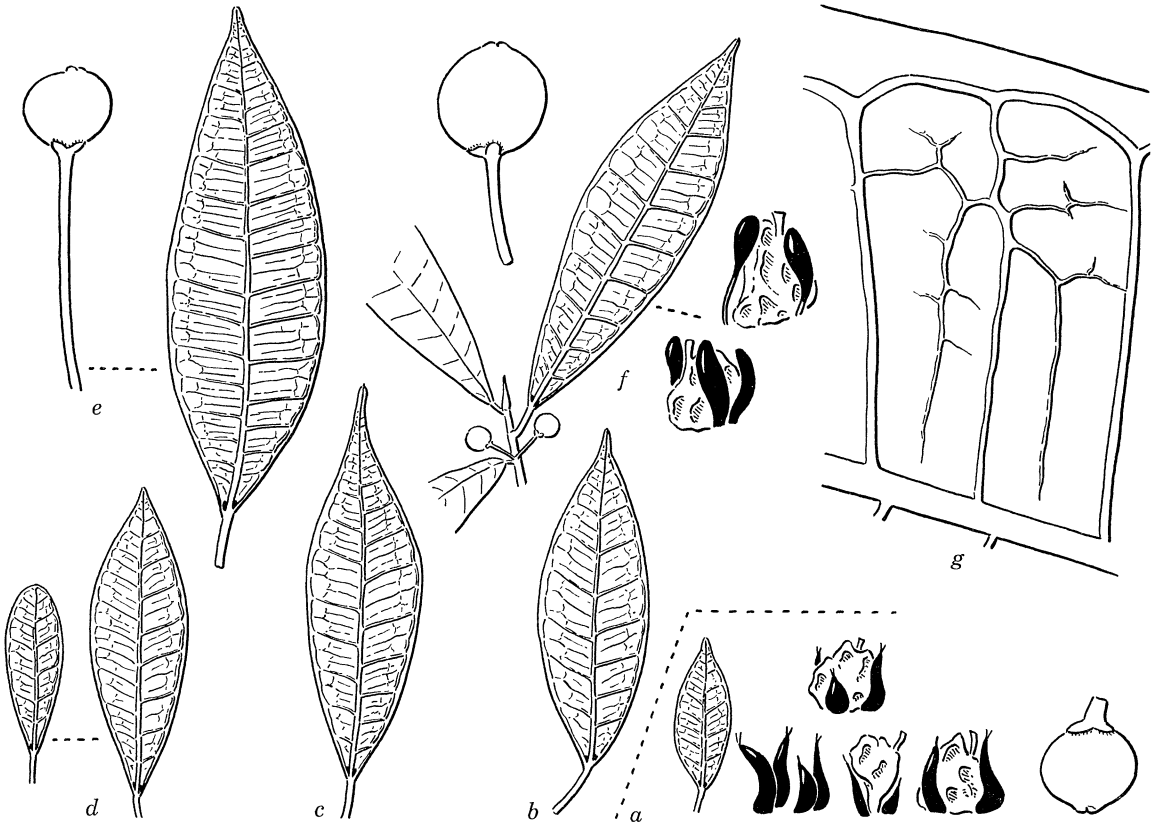

FIGURE 18. *Ficus oleaefolia* v. *oleaefolia* (*a*, *b*) and v. *valida* (*c*–*g*); *a*, Beccari 82 (type); *b*, Beccari 812 (v. *major* King); *c*, S 19068; *d*, S 4528; *e*, Burtt & Martin B 5254; *f*, S 17142; *g*, S 4528, details of intercostal veining × 5. Leaf × ½, figs × 2, flowers × 10.

This is a wide-ranging, high mountain species with considerable variation, descending to the lowland rivers as v. *riparia* in Sarawak. Most variation occurs in Borneo. Celebes and Mindanao are the limits, and there is no record from Malaya or Java.

Var. **oleaefolia** (figure 18*a*, *b*)

As above.

Distr. Central Sumatra (Singgalang, Sago and Tudjok mountains).

Ecol. Mossy forest, 1000–2200 m alt.

In the short peduncle, this seems the most reduced variety, but it has leaves almost as large as the Bornean v. *valida*.

Var. **dodonaeiformis** (Gagnep.) Corner, *Gdns' Bull., Singapore* **17** (1960), 425 (figure 20*c–e*)

Shrub up to 4 m tall. Lamina 3.2–6.5 × 0.5–1 cm, narrowly spathulate, obtuse, tapered to the narrow base, penninerved; costas (4–) 6–8 (–12) pairs; petiole 1–3 mm. Seed-figs 3–4 mm wide; peduncle 9–12 × 0.5 mm: seeds 2.5–3 mm long, 1–2 per fig. Gall-fig peduncles 3–4 mm long.

Distr. Sarawak, Brunei.

Ecol. Epiphytic and terrestrial, possibly streamside, lowland to 1800 m alt.

Collections. Beccari P.B. 2501, Mt Matang (type); Brun. 1842, G. Pagon Priok, Brunei, 1800 m in mossy forest; Hotta 15724, S. Kakas, Bintulu, 30–80 m alt.; S 967 S. Besai, Bintulu, epiphyte in kerangas forest at low altitude; S 4697, Merurong Plateau, Bintulu, 800 m alt., epiphyte; S 18424, Ulu Tubau, Bintulu, 150 m alt., 4 m tree, much branched, elegant, with smooth red-brown bark.

This variety resembles v. *myrsinoides* with very narrowly spathulate-elongate lamina and rather long peduncles. However, the collection Brun. 1842 with short peduncles, 3–4 mm long, introduces the same variation found in other varieties of the whole complex. There appears to be no evidence that this is a riparian plant. It would seem worthy of cultivation.

Var. **epiphytica** (Elmer) Corner, *Gdns' Bull., Singapore* **17** (1960), 425 (figure 19*k–m*)

Shrub or tree up to 6 m high, stem up to 10 cm thick. Lamina 3–9 × 1.5–3 cm, lanceolate-subacute, the upper leaves shorter and obovate-obtuse, coriaceous, opaque with the veins more or less invisible below. lateral nerves 4–7 pairs: petiole 2–5 mm. Fig-body 5–7 mm wide, ellipsoid or subglobose: peduncle 2–8 × 0.5–1 mm: internal bristles few, minute in seed-figs, none in gall-figs. Gall-flowers without tepals or these few and scattered irregularly among the strongly angular-rugose ovaries. Female flowers with 3 short fleshy tepals. Seed 5 × 3 mm.

Distr. Philippine Isl. (Mindanao, Basilan), Celebes (north).

Ecol. Often epiphytic, in mountain forest 800–1700 m alt.

Collections. Mindanao, Bur. Sci. 16134 (Basilan), 26064, 38723, 38972; Clemens 1175; Copeland 1618 A; Elmer 13829; For. Bur. 4676; PNH 10689; Williams 2355 (type).—Celebes, Koorders 19225, 19309; Kjellberg 1668, 2310, 2728; Sarasin 564; Mamahit 14; Alston 16532.

This approaches *F. deltoidea* v. *intermedia*, yet it may grade into *F. oleaefolia* v. *myrsinoides*. It certainly needs further investigation.

Var. **linearifolia** var.nov. (figure 20*a*, *b*, *h*)

Ramuli 1–1.5 mm crassi, fusco-brunnei. Lamina 2.5–11 × 0.4–0.7 cm, lineari-lanceolata acuta v. ad apicem subacutum attenuata; costis lateralibus utrinsecus 7–10 v. 17–25 (Burtt et Martin B 5497); petiolo 2–9 mm longo. Receptacula 4–5 mm lata (cecidiophora, S 21115) v. 7–8 mm (feminea, Burtt et Martin B 5497); pedunculo 1–1.5 mm (cecidiophoro) v. 5–7 mm (femineo); bracteis basalibus 0.5–1 mm. Ovarium cecidiophorum subangulatum. Tepala cecidiophora ovario equalia; feminea 3, tenuia. Semina 4–5 × 3–3.5 mm 1–3 per receptaculum.

Sarawak: B. L. Burtt et A. Martin B 5497, Gunong Murud, 1300 m, 14 Oct. 1967 (typus, Edinburgh), frutex repens – 0.5 m alta; S 21115, Hose Mountains, Bukit Lumut, Carapa, 100 m leg. P. S. Ashton 14 Apr. 1964, frutex epiphytica – 3 m alta, frequens.

Whether these two collections belong to one genetic variety is uncertain. They differ slightly in leaf-shape and peduncle-length. S 21115 approaches v. *memecylifolia* as v. *dodonaeiformis* approaches v. *myrsinoides*.

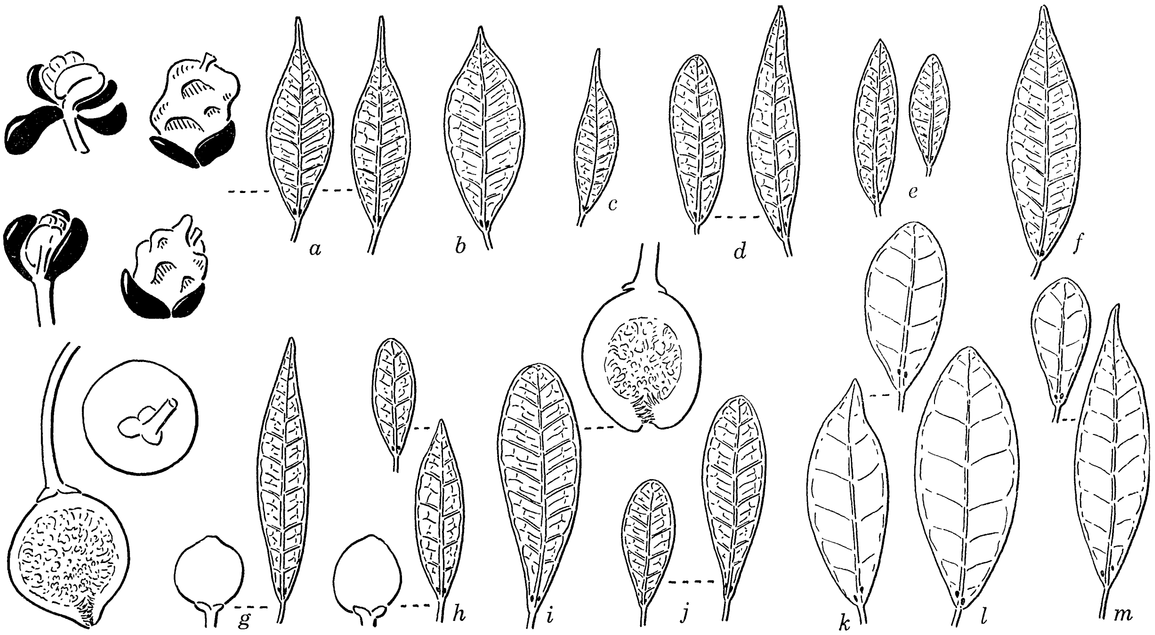

FIGURE 19. *F. oleaefolia* v. *memecylifolia* (*a–h*), v. *myrsinoides* (*i–j*), and v. *epiphytica* (*k–m*); *a*, Clemens 27939 A; *b*, Haviland 87; *c*, NIFS 227; *d*, Endert 4398; *e*, Endert 4268; *f*, Endert 3837; *g*, CWL 384; *h*, S 4536; *i*, SFN 27550; *j*, Clemens 31410; *k*, PNH 10689; *l*, Koorders 19225; *m*, Bur. Sc. 38972. Leaves × ½, figs × 3 and × 2 (*g*, *h*), flowers × 10.

Var. **memecylifolia** Corner, *Gdns' Bull., Singapore* **17** (1960), 425 (figure 19*a–h*)

Shrub or small tree up to 6 m high. Lamina 2–7 × 0.7–2.7 cm (–10 × 3) lanceolate-elliptic, acuminate but often rather bluntly: petiole 1–7 mm. Fig-body 4–5 mm wide, subglobose (gall) or 4–7 × 3–6 mm, ellipsoid (seed): peduncle 3–14 × 0.5 mm. Gall-tepals generally shorter than the strongly angled ovary. Seed 4 mm long, 1–4 per fig.

Distr. Borneo, Celebes (central, south).

Ecol. Mossy forest 900–2000 m alt. often epiphytic: also in primary forest on limestone hills at low altitude (200 m) in Sarawak.

This is a common state of *F. oleaefolia* in Borneo, distinguished by the small acute leaves, the small figs with rather long slender peduncles, and the gall-tepals usually shorter than the strongly rugose ovary. A few collections have short peduncles, thus:

Peduncles 1–2 mm long.—S 4536, CWL 384, Hotta 14730, all from G. Mulu, 1700–2200 m alt.
Peduncles 2–3 mm long: Clemens 20696 (Bidi Cave), RSNB 1462 (Kinabalu).
Peduncles 3–5 mm long: S 12235 (Bau, pr. Kuching), Hallier 2673 (Lianggagang).
Peduncles 4–6 mm long: S 8755 (Merurong Plateau, Bintulu).
Peduncles 5–10 mm long: the common state.
Peduncles 11–14 mm long: NIFS bb 227 (Masamba Lemboeng, Celebes 1700 m).

The leaves in a few collections become as large as those of var. *oleaefolia* and I have called these v. *valida* because they have the large leaf and fig of v. *oleaefolia* but the longer peduncle of v. *memecylifolia* with which they occur in Borneo. I doubt if they represent the young or sapling state of v. *memecylifolia*.

Then some collections have a few of the leaves, apparently on any part of the twig, obtuse as in v. *myrsinoides*; for instance Endert 4268 and 4398. When this feature is combined with the short peduncle, as in S 4536 (G. Mulu) the transition to v. *myrsinoides* seems complete, The colour of the ripening fig needs inspection. It seems generally to become purple black but in some plants on Mt Kinabalu it turns orange to red and in these plants the tepals are practically white and the leaves are thinner with more numerous costas.

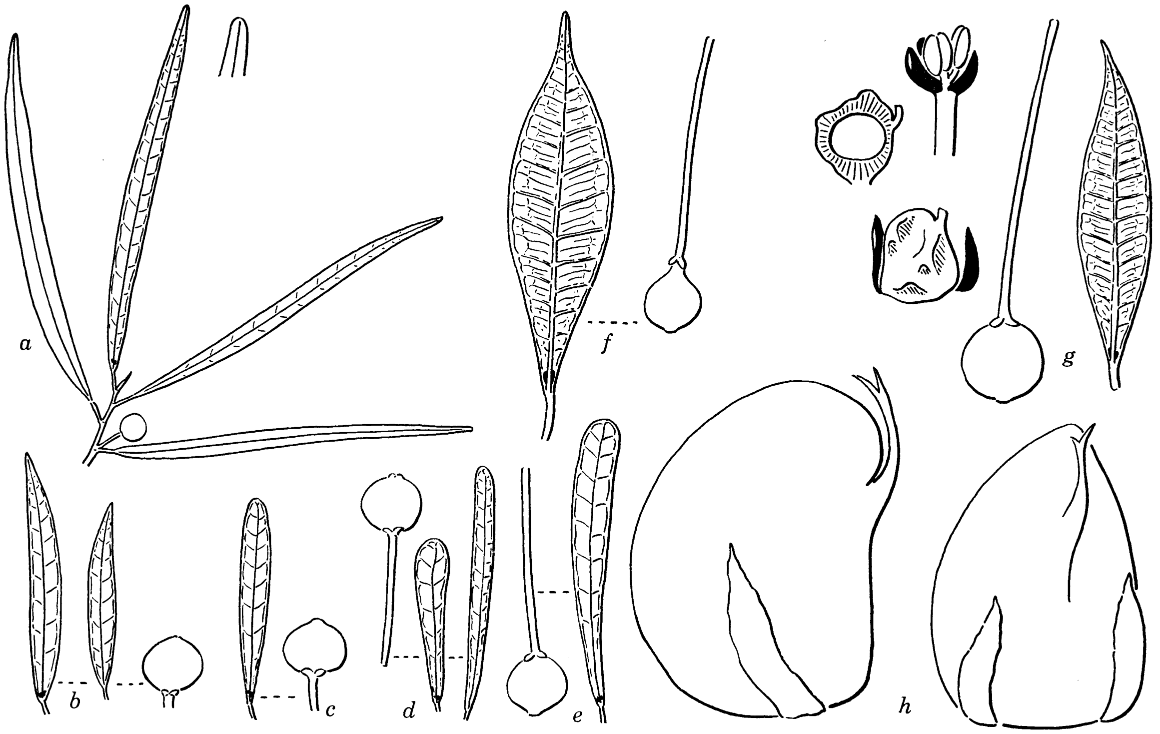

FIGURE 20. *F. oleaefolia* v. *linearifolia* (*a*, *b*, *h*), v. *dodonaeiformis* (*c*–*e*) and v. *riparia* (*f*, *g*); *a*, Burtt and Martin B 5497; *b*, S 2115; *c*, Brun 1842; *d*, Beccari 2501; *e*, S 18424; *f*, Brun 2370; *g*, SFN 6871, with male and gall-flowers; *h*, Burtt and Martin B 5497, female flowers. Leaves × ½, figs × 2, flowers × 10.

The variety occurs as a small tree or epiphyte generally at 1200–2200 m alt. The lowest records seem to be about 200 m on a limestone hill near Bau and at 800 m on a ridge in dipterocarp forest at Bt. Mersing (pr. Anap, Bintulu).

Var. **myrsinoides** Corner, *Gdns' Bull., Singapore* **17** (1960), 425 (figure 19*i*, *j*)

Shrub or small tree up to 12 m high, trunk up to 20 cm thick. Lamina 2.5–9 × 0.8–3 cm, spathulate or narrowly obovate, obtuse: petiole 1–10 mm. Seed-figs 7 × 4–5 mm, ellipsoid, gall-figs 5–6 mm wide, subglobose, ripening dark purple: peduncle 1.5–8 × 0.7 mm. Gall-tepals equal to or longer than the smooth or angular ovary. Seeds 3–4 mm long, 1–3 per fig.

Distr. Borneo.

Ecol. Mossy forest 500–2100 m alt., often epiphytic.

This variety, distinguished by the small obtuse leaf and the small, shortly pedunculate fig, seems to be almost as common as v. *memecylifolia* and is now known to extend as widely in Sarawak, North Borneo and the adjacent part of Indonesian Borneo, but there is no record from south Borneo. Intermediates with v. *memecylifolia* are occasional as mentioned under that variety. I have seen no evidence that it may merge with v. *oleaefolia* and, as far as known, it does not occur in Sumatra. But, as a much reduced state of the species with the midrib ultimately dichotomous at the tip it comes to resemble some reduced states of *F. deltoidea* v. *angustifolia*. The collection S 21123 (Sarawak, Bt. Lumut, Carapa Amau, Ulu Mujong, Balleh) I identified first as v. *myrsinoides* but it is peculiar in the long peduncle 7–9 mm; on second inspection I decide that it is more probably *F. deltoidea* v. *angustifolia*. This v. *angustifolia* certainly occurs in Borneo and adds to the difficulty of identifying Bornean derivatives of the whole alliance from small herbarium specimens.

Var. *myrsinoides*, though typically montane as v. *memecylifolia*, has been found also at 200 m on a limestone hill near Bau (S 15466) and there is a record from near Jesselton at sea-level (Kepong Field n. 71631, Kumu-Rengis) but this certainly needs verification by re-discovery in the locality.

The collection Kostermans 14027 (East Borneo, Mt. Ilas Mapula, Berouw, on limestone summit, 800 m alt. common small tree up to 5 m) has both obtuse leaves as v. *myrsinoides* and acute leaves as v. *memecylifolia*, but short peduncles (2–4 mm), and it differs from both in being minutely puberulous on the twigs, petioles, peduncles and, particularly, the fig-body with white hairs 0.1–0.2 mm long. I have referred it for convenience to v. *myrsinoides*, though it may need taxonomic recognition.

Var. **riparia** Corner, *Gdns' Bull., Singapore* **17** (1960), 426 (figure 20*f*, *g*)

Shrub or small tree. Lamina 6–11 × 0.5–2.5 cm, lanceolate, acute or shortly acuminate; costas (9–) 13–16 pairs; petiole 2–10 (–20) mm. Gall-figs 5–6 mm wide, subglobose; peduncles 15–20 × 0.7 mm, slender; pedicel 0–2.5 mm. Gall-tepals as long as or shorter than the angular ovary. Seeds?

Distr. Sarawak, Brunei.

Ecol. Lowland and mountain forest 200–1800 m.

Collections. SFN 6871, Upper Baram, Gunong Jemabok (? Tunabok), 200 m, (? = *F. riparia* Becc. nom. nud.); Ashton 2370, G. Pagon Priok, Brunei 1800 m alt.; S 8737, Marigan Range, Lawas, Sarawak, 1200 m, treelet in hill conifer forest, fig orange, peduncles 14–20 mm, costas 9–13 pairs.

This variety stands to v. *memecylifolia* as v. *dodonaeiformis* to v. *myrsinoides*, but the leaf is not so narrow as in v. *linearifolia*. Though I took up Beccari's idea of 'riparia', there seems now no evidence that this or any other of the lanceolate-leafed forms of the complex are riparian.

Var. **valida** var.nov. (figure 18*c*–*g*)

Frutex ad 4 m altus. Lamina 7–13 × 2–4 cm, late lanceolata acuta v. subacuminata, subcoriacea; costis lateralibus utrinsecus 9–12 (–14); glandulis basalibus 2; petiolo 4–11 mm. Receptacula 7–8 mm lata, subglobosa; pedunculo 5–8 (–15) mm, gracili; bracteis basalibus 1–1.3 mm. Ovarium cecidiophorum plus minus angulatum, tepalis ovario equalibus. Typus S 19068 (L).

Distr. Sarawak.

Ecol. In silvis montanis 800–2200 m alt.

Collections. B. L. Burtt and A. M. Martin B 5254, G. Murud *c.* 2000 m; G. H. Pickles 3701 (Usun Apau Plateau, 100 m), 3772 (Mt Kalutong, 1400 m); S 4528, G. Mulu 2200 m; S 17142, 19068, Hose Mountains 800–900 m.

I make this variety with much hesitation, mainly to stimulate research in the field. The plants have the characters of v. *oleaefolia* except for the long peduncle and, yet, they are extremely like the Bornean specimens of *F. deltoidea* v. *intermedia* with smooth gall-ovary; if the parts were smaller, they would be v. *memecylifolia*. It seems that in Sarawak all these varieties are thus brought together.

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