

The Classification of Moraceæ

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New subgenera:—*Trophis* P. Br. subgen. *Prototrophis* Corner.

New sections:—*Broussonetia* L'Herit. sect. *Allaeanthus* (Thw.) Corner; *Maclura* Nutt. sect. *Cardiogyne* (Bur.) Corner, sect. *Cudrania* (Tréc.) Corner; *Streblus* Lour. sect. *Bleekrodea* (Bl.) Corner, sect. *Paratrophis* (Bl.) Corner, sect. *Phyllochlamys* (Bur.) Corner, sect. *Pseudostreblus* (Bur.) Corner, sect. *Pseudotrophis* (Warb.) Corner, sect. *Sloetia* (Teysm. et Binn.) Corner, sect. *Taxotrophis* (Bl.) Corner; *Trophis* P. Br. sect. *Calpidochlamys* (Diels) Corner, sect. *Maillardia* (Frapp. et Duch.) Corner.

New series:—*Maclura* Nutt. sect. *Cudrania* (Tréc.) Corner ser. *Connatae* Corner, ser. *Liberæ* Corner.

New species:—*Streblus perakensis* Corner. *S. solomonensis* Corner.

New varieties:—*Antiaris toxicaria* Lesch. var. *macrophylla* (R. Br.) Corner, v. *welwitschii* (Engl.) Corner; *Broussonetia luzonica* (Blanco) Bur. v. *glabra* (Warb.) Corner; *Maclura antboinensis* Bl. v. *paucinervia* Corner; *Streblus glaber* (Merr.) Corner v. *australianus* Corner, *S. urophyllus* Diels v. *salicifolius* Corner, *S. asper* Lour. v. *monoica* (Gagnep.) Corner.

New specific combinations:—*Broussonetia kurzii* (Hook. f.) Corner, *B. zeylanica* (Thw.) Corner; *Maclura africana* (Bur.) Corner, *M. cochinchinensis* (Lour.) Corner and var. *pubescens* (Tréc.) Corner, *M. fruticosa* (Roxb.) Corner, *M. greveana* (Baill.) Corner, *M. humbertii* (Léandri) Corner, *M. regia* (A. Chev.) Corner, *M. thorelii* Gagnep.) Corner; *Streblus anthropophagorum* (Secm.) Corner, *S. crenatus* (Gagnep.) Corner, *S. elongatus* (Miq.) Corner, *S. glaber* (Merr.) Corner, *S. ilicifolius* (Vid.) Corner, *S. indicus* (Bur.) Corner, *S. insignis* (Bl.) Corner, *S. laxiflorus* (Hutch.) Corner, *S. madagascariensis* (Bl.) Corner, *S. smithii* (Cheeseman) Corner, *S. spinosus* (Bl.) Corner, *S. tahitensis* (Nadcaud) Corner, *S. tonkinensis* (Stapf) Corner; *Trophis branderhorstii* (Diels) Corner, *T. drupacea* (Diels) Corner, *T. philippinensis* (Bur.) Corner.

Genera fully reviewed:—*Antiaris* Lesch., *Broussonetia* L'Herit., *Maclura* Nutt., *Plecosperrum* Tréc., *Streblus* Lour.

Introduction—Distinction from Urticaceæ—Subdivision of Moraceæ (filaments; extrorse, introrse anthers; plicate leaves: perianth; pistillode; ovary; fruit; seed; embryo; number of floral parts; microscopic characters; inflorescence; spines)—Proto-Moraceæ—Affinity of Urticales—Geographical table of Moraceous genera and species—Definition of Moraceæ—Key to the tribes of Moraceæ—Moreæ—Artocarpeæ—Olmedieæ—Brosimeæ—Dorsteniacæ—Ficeæ—Genera excludenda—References.

Introduction

No family has such small standardised flowers, yet such an astonishing array of infructescences. Acquaintance with *Morus* leads to the supposition that these tropical accomplishments are recent developments of little significance to scientific theory. Acquaintance with the tropical plants shows, in contrast, that *Morus* is one of the more derived and reduced genera conforming with temperate simplicity. By denying itself so much in this way that is tropical, botany loses its grip. *Ficus* and *Artocarpus* are two vivid lights, but no student of the phylogeny of flowering plants has seen them. As morphology shifts to the tropics, the family will be appreciated. It holds many fascinating problems of vestigial features, transference of function, and parallel evolution. My contribution now is merely an interim development of the static classification into which the family has subsided. Much has still to be learnt of the American genera, not only from the herbarium, but from the forests in which they survive. There is, for instance, the unique *Palmolmedia* described by Dueke in 1939.

Distinction from Urticaceae

This is a problem. In the diagnosis of *Moraceae* on p. 209 the main differences are italicised. Chief are the orthotropous ovule and the lack of latex in the Urticaceae. On the ovular test Conocephaloideae must be transferred to Urticaceae and, this done, the genera in each family hold together. Latex-tubes are said to occur in the bark, at least the primary bark, of all Conocephaloideae (*Cecropia*, *Coussapoa*, *Musanga*, *Myrianthus*, *Poikilospermum*, and *Pourouma*), but not in the leaves or inflorescences and infructescences. This tribe may seem, therefore, intermediate between the two families, but other features as the shape of the stigma, the small seed, and the small embryo ally them with Urticaceous, not Moraceous, genera. Trifling as these two distinctions may seem, they delimit two large families, and the seeming triviality arises from lack of appreciation of the two characters. *Fatoua* is not an Urticaceous herb, but a Moraceous parallel. *Cecropia* is not a Moraceous tree, but an Urticaceous parallel.

The function of latex is unknown, yet it permeates as a capillary system giant Moraceous trees from root-tip to stem-tip, and it is initiated in the embryo. The function of ovular shape is also unknown, but it relates to angiospermous ancestry. The evidence, anatomical and taxonomical, suggests not that the direct orthotropous ovule is primitive, but that it is derived from the anatropous ovule transferred to the base of the ovary and straightened in conformity with its improved position for food-supply. In anatomical evidence, Bechter (1921) described the flexure of the ovular vascular bundle in *Boehmeria* and *Laportea*, which first ascends in the ovary-wall as if to an apical position, and then descends to the basal attachment. Certain tropical genera as

Stenochasma and, indeed, *Pourouma* have sub-basal and even laterally placed ovules which turn abruptly into the long orthotropous body. In this respect they appear intermediate with Moraceae, but details of flower and fruit again refer them unquestionably among Urticaceae.

Urticaceae are derivatives of Proto-Moraceae which lost the latex and in which the ovule was transferred from the lateral (appendicular) position to the axile. Conocephaloideae are the Urticaceous group with traces of Proto-Moraceous ancestry. Actually there is no difficulty whatever in separating most Moraceae, as *Artocarpus* or *Ficus*, from Urticaceae; the trouble arises in the very derived and simplified genera as *Dorstenia*, *Morus*, and *Streblus*, convergent with Urticaceous derivatives.

Lack of latex distinguishes also the Ulmaceae, the flowers of which are generally functionally bisexual. The combination of Ulmeae with Celtideae in one family introduces several of the difficulties met in the subdivision of the Moraceae, especially the two subfamilies Moroideae and Artocarpoideae. As I will show, these two subfamilies cannot be maintained, at least in their present light, because the nature of the stamen, inflexed or straight in bud, though useful enough in the material on which taxonomists have to rely, has not the phyletic significance which practice would attribute. The same solutions will probably fit Ulmaceae and, then, the position of the Cannabiaceae will be ascertained.

Subdivision of Moraceae

To the student of *Ficus* the classification and, therefore, the comprehension of Moraceae is confused with excessive genera. The fig (syconium) is so characteristic that no one is willing to make *Ficus* a tribe or family and raise its subdivisions to generic or tribal rank. Further, there is a continuum through *Ficus* linking the first with the last. It is a genus which preserves a great deal of its evolution, and its products may still be strung together. But, suppose no other Moraceae existed and that most modern *Ficus* had disappeared, then *Ficus* would be a family with several distinct genera. In this light other Moraceae must be considered; they are fragments only from a greater past.

An exception was Miquel. Where others have seen in *Ficus* merely specific variety, and have failed, only too often, even to dissect the flowers, Miquel studied deeply and was so impressed with the great range of floral variation in the genus that he proposed many genera in place of the one. His prowess defeated him; he was overwhelmed with sterile material for identification and had to forgo his principle. Yet, if the flowers were on the outside of the head, instead of inside the fig, many would have seen without difficulty and have followed him and argued that a colossal monoecious banyan with unistaminate flowers and simple stigma could not be congeneric with a slender dioecious creeper with

bistaminate flowers and bifid stigma. The enormous bracteate fig of *Danmaropsis* differs as much from that of *F. carica* as the Olmedieae do from the Artocarpeae, yet *Danmaropsis* is also sunk in *Ficus*. The point is not that there is so much variation in this genus but that the extremes are linked by intermediates. For instance, the group of *F. hirta* (2 stamens, peculiar seed, no cystoliths, palmate-leafed trees) is very distinct from that of *F. subulata* (1 stamen, gall-ovary in the male flower, simple seed, cystoliths, simple-leafed epiphyte), but the remainder of their sections *Ficus* and *Sycidium* link these extremes together.

I take *Ficus* as demonstrative, and where monoecism or dioecism, staminal number, perianth-construction, stigmatic and seed-details, ovary-position, microscopic differences in cystoliths, gland-hairs, hypodermis, etc., and differences in habit and leaf are the chief distinctions between genera, I treat them with suspicion. Caution is needed, nevertheless, in recombining the fragments of other Moraceae. There has been much parallel evolution, even *Sparattosyce* simulating *Ficus*, so that similar effects need meticulous care in separation, and endless tables of comparison must be prepared to sort out the details. Endless because it is always found that much critical information is lacking and cannot be obtained from the bits of the plants in herbaria; too often the American and African plants are in default. Yet, the pieces of the puzzle are so strange, so splendidly different from the banalities of many other families, that the monography of the Moraceae is one of the most exciting chapters in angiosperm taxonomy. To relate a mulberry and a bread-fruit, one superficially the aggrandisement of the other, and add the little *Fatoua* calls for a working hypothesis of flowering-tree evolution. A concept of Proto-Moraceae is essential.

Filaments. The form of the filament in the flower-bud has been taken as a primary means of distinguishing subfamilies or tribes. The filament may be short and lengthen directly to project the anther or it may be inflexed under tension until the flower opens and the filament straightens and flicks the pollen from the anther. Such is the Urticaceous stamen, and the difference between subfam. Moroideae (inflexed filament) and subfam. Artocarpoideae (straight filament). Certain facts discredit this criterion.

Because of their orthotropous ovule and general affinity in other respects, the subfam. Conocephaloideae must be transferred to the Urticaceae. This at once introduces the straight stamen (*Musanga*, *Myrianthus*, *Cecropia*, *Coussapoa*, *Pourouma*) into the Urticaceae. *Poikilospermum* has always been placed in the Urticaceae because of its inflexed filament. This character holds only for one part of the genus; the other part (*Conocephalus* Bl.) has the straight stamen and has always been referred to the Moraceae. It is acknowledged now that these two subgenera are congeneric; some species, indeed, have such slightly inflexed filaments that it is not clear on this point alone to which subgenus they should be

referred. Then, *Cudrania*, placed in Artocarpoideae, has straight filaments but, as I will show, is merely a section of *Maclura* (Moroideae) with inflexed filaments; there is the reputed hybrid *Macludrania* (*M. pomifera* \times *C. tricuspidata*), but its filament has not been described. Again, for the same reason *Sorocea* and *Clarisia* are placed in Artocarpoideae where their racemose or spicate inflorescences and non-syncarpous fruits are entirely anomalous; in fact, they are nearer to *Trophis* (Moroideae) with inflexed filaments. *Craterogyne* (inflexed filaments) has been placed in Dorsteniaceae and *Trymatococcus* (straight filaments) in Brosimeae, yet other differences are so slight that I would refer them to one genus of Brosimeae. Lastly, so far as I have been able to find out, subinflexed filaments are described by Woodson (1960) in *Batocarpus* (Artocarpeae).

The inflexed filament has a small anther, often reniform or bilobed. The flower has at least two stamens (*Craterogyne*, *Dorstenia*), generally 3-5, and it has a pistillode against which the anthers are pressed immovably in the bud. The filaments are at first short and straight; in lengthening they are forced to curve outwards against the bulging concave tepals and so they become, as it were, inflexed; they never inflex. The inflexed filament, therefore, in this as in other cases, such as the Caesalpinoideae, is related with the immovability of the anther in bud. In some genera, nevertheless, the pistillode is minute or even absent, and one must suppose that the connivent anthers caused the so-called inflection.

The straight filament commonly bears a rather large anther, often mucronate, typical of the normal angiosperm stamen. Its flower is often unistaminate, but may be 2-5 merous, and there may be 7-8 stamens (*Antiaris*, *Ficus*). It rarely has a pistillode (present in *Ficus* pr. p., *Antiaropsis*, *Sparattosyce*). In development the anther fills most of the bud-cavity, and not until the flower begins to open does the filament elongate. Extended anther-growth and retarded filament-growth distinguish this flower from that with inflexed filament. Now which may be ancestral?

The straight filament is generally associated with the advanced, capitate or condensed, inflorescence, as in Artocarpeae, Brosimeae, Olmedieae, and Ficeae. The inflexed filament is associated with the less advanced spicate, racemose, cymose, and paniculate inflorescences, an exception being the Dorsteniaceae. The straight filament is more suited to the compacting of flowers because it does not need the elbow-room for the explosive stamen. For this reason the inflexed filament seems the more primitive. It is the straight filament, however, which has the less specialised anther. The minute anther of *Artocarpus* is clearly as derived as it is diminished from the large anther shown by *Parartocarpus*. The best developed anthers, strongly mucronate, occur in *Ficus* sect. *Rhizocladus* (climbers). Likewise the small anther of the inflexed filament must be derived. Possibly therefore the inflexed filament

is derived from the stamen with small anther, in turn derived from the stamen with large anther and straight filament, and one suits one kind of inflorescence, the other another. It may be recalled that in all flowering plants the anther develops before the filament which is an intercalary growth. The ability of the anther to fill the bud-cavity determines the form of the filament. So the large anther and necessarily short filament seems the primitive condition, and it brings the Moraceous stamen into line with the theory of Parkin (1951).

It follows that the inflexed filament has been evolved in parallel in different Moraceous and, even Urticaceous and Ulmaceous, groups or genera. That such parallel evolution may well have taken place is shown by the parallel occurrence of the extraordinary turbinate anther with transverse equatorial dehiscence found in *Ficus sterrocarpa* Diels, *Brosimum alicastrum* Sw., and *Craterogyne kameruniana* (Engl.) Lanjouw (Fig. 1, L, N).

I conclude that the form of the filament is not useful for primary distinctions and that it leads to artificial grading. Further, I conclude that the presence of the straight stamen in Moraceous groups with condensed inflorescences shows that they are variously derived from states with expanded inflorescences, and that any attempt to relate them directly is short-sighted, because they are the survivors of as varied Proto-Moraceae which have given rise at any stage of inflorescence-evolution to forms with inflexed filaments.

Extrorse, introrse anthers. *Ficus*, *Antiaropsis*, and *Antiaris* have introrse anthers. Other genera, so far as I can determine, have extrorse anthers. In those with inflexed filaments, the anthers are often described as introrse, but in bud they are extrorse and only after they have been pulled out and rotated on the filaments do they become introrse. The distinction is important because the introrse anther would not be so effective in the wide-spread explosive stamen-mechanism.

Plicate leaves. Engler used this character to define subfam. Moroideae in contrast to the inrolled or convolute leaf in subfam. Artocarpoideae. However, all the smaller elliptic leaves of Moroideae are convolute as in *Maclura* and *Streblus*, and all the larger palmate, pinnate, or cordate leaves of Artocarpoideae are plicate, as *F. carica*, and *Artocarpus incisa*. Large leaves, plicate in bud, seem to be the pachycaulous character, small leaves convolute in bud the leptocaulous as in other families and, indeed, genera.



Fig. 1. Stamens of Moraceae, $\times 10$. A, *Ficus sphaeroidea* Corner. B, *F. robusta* Corner. C, *F. subulata* Bl. v. *gracillima* (Diels) Corner. D, *Antiaropsis decipiens* K. Schum. E, *Artocarpus kemando* Miq. F, Diagrams of the introrse anthers of *F. robusta* and the extrorse anthers of *Parartocarpus*. G, *Parartocarpus venenosus* Zoll. et Mor. H, Diagrams of extrorse anthers as in Moreae, and introrse anthers of *Antiaropsis*. I, *Ficus obliqua* Forst. f., with oblique crescentic dehiscence. J, *Maclura (Cudrania) fruticosa* (Roxb.) Corner, with flanged and ridged filament curved at the tip. K, Stamens with incurved filament, as in Moreae. L, Diagram of the stamen of *Ficus sterrocarpa* Diels. M, Diagram of the stamen of *F. hesperidiiformis* King. N, *F. sterrocarpa*. O, *F. hesperidiiformis*.

Perianth. The more or less free tepals of many genera contrast with the gamophyllous or utriculate perianth of others, and both with the state without perianth. All states occur in *Ficus*. To attempt to use them as primary distinctions leads to confusion. Thus *Artocarpus* subgen. *Pseudojaca*, *Hullettia*, and *Trymatococcus* are not to be classed together because they have practically no perianth, any more than *Streblus* sect. *Bleekrodea*, *Malaisia*, and *Ficus* sect. *Sycocarpus* are to be classed together because of their utriculate perianth. These peculiarities have also been evolved in parallel.

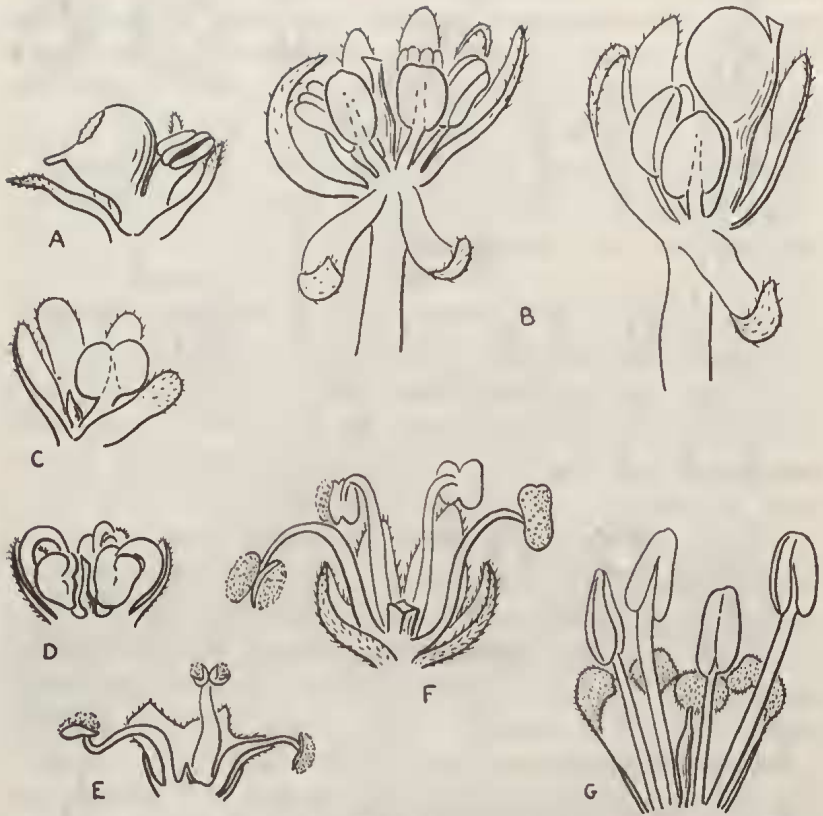


Fig. 2. Male flowers of Moraceae to show the pistillodes, $\times 10$. A, *Ficus obscura* Bl. B, *F. henryi* Diels, two flowers. C, *F. wassa* Roxb. D, *Plecospermum spinosum* Tréc. E, *Streblus elongatus* (Miq.) Corner. F, *Morus macroura* Miq. G, *Maclura thorelii* (Gagnep.) Corner.

Pistillode. This diminutive sterile structure of the male flower, apparently indicative of the bisexual origin of the Urticalean flower, poses several problems. It is best developed as a short quadrate-columnar structure in Moreae and Urticaceae: against it press the four anthers with inflexed filaments. In contrast it is a minute, but very persistent, spike in *Fatoua*, *Streblus* (sect. *Bleekrodea*, *Pseudostreblus*, *Sloetia*), *Sloetiopsis*, and *Neosloetiopsis*. It is absent from *Clarisia* and *Sorocea*. To separate these sections of *Streblus* and classify them with *Fatoua* on this ground is unreasonable in the face of their overwhelming resemblance in other respects with the rest of *Streblus*. A similar pistillode occurs in *Antiaropsis* and *Sparattosyce* in the Olmedieae and, sometimes, as the merest vestige, in *Parartocarpus* and *Treculia* in the Artocarpeae, and *Trypanatococcus* in the Brosimeae. In other Artocarpeae, as *Broussonetia*, *Maclura*, and *Plecospermum*, the pistillode is better developed as a small ligulate ovary with a minute style and, even, stigmatic arms. In *Helianthostylis*, generally placed in Artocarpeae but problematic, it is long, filiform, and exsert from the flower. Finally, in *Ficus*, it varies from a vestigial, but clearly

recognisable, ovary to a minute spike, or it is absent. In two cases, however, namely *Ficus henryi* Diels and sect. *Sycidium* subsect. *Palaeomorphe*, the pistillode functions as a gall-ovary with insect. These are the nearest approach to the functionally bisexual flower in the family. Of all the taxonomic characters in the family, the pistillode is the most demonstrative of the value of vestigial inheritance.

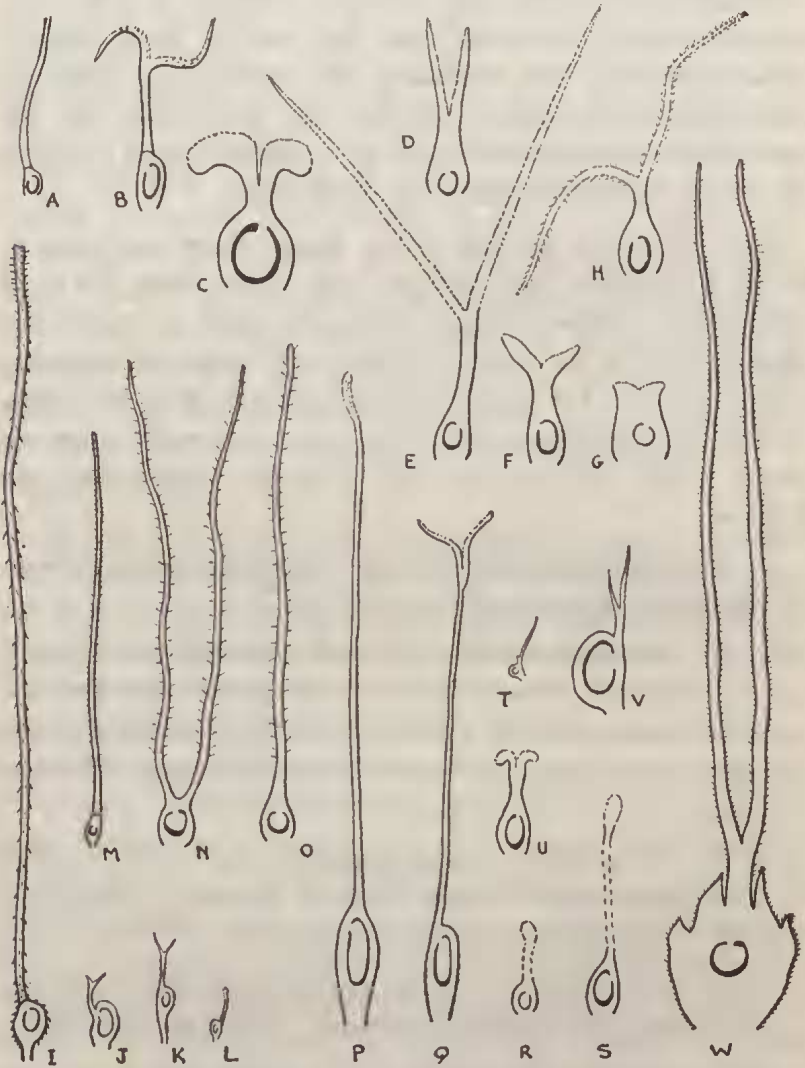


Fig. 3. Ovaries of Moraceae, $\times 7$. A, *Machura cochinchinensis* (Lour.) Corner. B, *M. thorelii* (Gagnep.) Corner. C, *M. fruticosa* (Roxb.) Corner. D, *Streblus glaber* (Merr.) Corner. E, *S. asper* Lour. F, *S. macrophyllus* Bl. G, *S. solomonensis* Corner. H, *Malaisia*. I, *Ficus macrostyla* Corner. J, *F. deltoidea* Jack. K, *F. aurantiaca* Griff. L, *F. fistulosa* Reinw. M, *Broussonetia papyrifera* (L.) Vent. N, O, *Plecosperrum andamanicum* King. P, *Artocarpus hirsutus* Lam. Q, *A. lanceifolius* Roxb. R, *A. vrieseanus* Miq. S, *Parartocarpus venenosus* Zoll. et Mor. T, *Fatoua*. U, *Prainea frutescens* Becc. V, *Antiaropsis*. W, *Antiaris toxicaria* Lesch., the I-flowered female inflorescence with inferior ovary.

Ovary. There are three states. Firstly, the ovary is superficial. Secondly, it is sunk in loculi or sockets of the receptacle with the perianth free from the walls of the loculus (*Artocarpus* subgen. *Artocarpus*, *Craterogyne*, *Plecosperrimum*), or there is no perianth (*Artocarpus* subgen. *Pseudojaca*, *Hullettia*, *Parartocarpus*). Thirdly, the ovary is truly inferior and only the ovule is free in the loculus of the receptacle (*Antiaris*, *Castilloa*, *Trophis*, and many *Brosimeae*); in several cases the ovary is partly inferior, (*Sorocea*, *Maclura* sect. *Cudrania*). The semi-inferior ovary occurs also in *Ficus* subgen. *Urostigma* sect. *Malvanthera* and this shows that ovary-displacement has also suffered parallel evolution and is not a primary criterion for classification.

Fruit. The ovary develops into a drupe. There are traces in *Morus* of two loculi, each with an ovule, in the drupe, but in all other genera, whether there are one or two styles, or one or two stigmatic arms to the single style, ovary and drupe are unilocular and uni-ovulate. The largest drupes with best developed pulpy exocarp and woody endocarp occur, so far as known, in the advanced genera *Parartocarpus* and *Treculia*. Modifications are these:—

1. The drupe diminishes to a drupelet (*Fatoua*, *Ficus*, *Dorstenia*, *Broussonetia*).
2. The drupe develops a strongly thickened parenchymatous base and dehisces over the thin apex to eject the seed (in endocarp) forcibly (*Streblus* sect. *Phyllochlamys*, *Sloetia*, *Taxotrophis*, and possibly *Bleekrodea*; *Ficus* spp., *Dorstenia* spp.).
3. The perianth (always persistent) becomes fleshy, often at the expense of the exocarp (*Morus*, *Ampalis*, *Pachytrophe*, *Maclura*, *Artocarpus* subgen. *Artocarpus*).
4. The receptacle becomes pulpy to form the fleshy syncarp (most *Artocarpeae*, *Brosimeae*, *Olmedieae*, and *Ficus*).

These modifications have occurred in parallel evolution. The second is highly peculiar because it re-instates dehiscence by a transverse, not longitudinal, rupture in the indehiscent drupe. It is a problem whether this is the original fruit-form in *Streblus* or a subgeneric product. In some species of *Ficus*, without systematic significance, and in *Dorstenia* the crustaceous endocarp is squeezed out of the pulpy drupelet.

Seed. By seed I imply not only the correct botanical usage but the practical. I intend the endocarp and its enclosed true seed: strictly it is a pyrene, not an achene, but everyone calls these bodies the seeds. There are small seeds 0.5–3 mm. long, and large seeds 4–20 mm. long. The one genus with both kinds is *Ficus*; its seeds are mostly 1–2 mm. long, but seeds 3–5 mm. long occur in *F. deltoidea* and its immediate allies. According to my durian-theory (Corner, 1954) the large seed is primitive. This conclusion agrees in general with the primitive state of the straight filament, for most genera with this character are tropical forest-plants with large seeds. Small seeds preponderate in genera, including Urticaceae, with inflexed filaments, both tropical and extra-tropical (*Broussonetia*, *Morus*), and also herbaceous (*Dorstenia*, *Fatoua*). The exception is *Ficus* which is the small-seeded derivative with straight stamens, adaptable in consequence to secondary vegetation and the epiphytic habit. The conclusion emphasizes again the retention of primitive features in Artocarpeae, Brosimeae, and Olmedieae with advanced inflorescence.

Embryo. There is such diversity in embryo-characters that it would seem that they should be of prime importance in classification. From this standpoint I have retired after much trial. There can be no doubt from the impossibility of fitting embryo-characters into a satisfactory scheme of classification that they represent also parallel evolution. Small seeds have small simple embryos with relatively long radicle and flat, thin cotyledons (*Broussonetia*, *Dorstenia*, *Fatoua*, *Ficus*, *Morus*); they are not primitive but neotenic, derived from the complicated embryos of the large seeds. The variety is shown in Fig. 4, 5. There is every gradation from curved embryos with plicate-conduplicate cotyledons to straight embryos with two thick, flat cotyledons and those with such very unequal cotyledons as to be functionally monocotyledonous. *Streblus* and *Maclura*, even *Ampalis* and *Pachytrophe*, reveal what has happened, for they show the range from rather thin, plicate-conduplicate cotyledons, which most resemble the foliage leaf with plicate vernation (otherwise lost in these genera), to the simple state with incumbent radicle (*Streblus*) or accumbent (*Ampalis*, *Maclura*). The trend is roughly parallel with the diminution of seed-size. Then comes thickening of the cotyledons, leading to the hypogeal, non-photosynthetic state, accompanied by loss of folding and by unequal development of the two. There are considerable differences depending on the exact shape of the

ovule, whether anatropous or campylotropous, the unequal development of the ovary or ovule after fertilisation, and the orientation of the embryo about the sagittal plane of the ovule. These are intricate points which require copious material for elucidation, together with seedling-studies. They have been worked out in some species of *Artocarpus*, *Parartocarpus*, and *Prainea* by Jarrett (1959, 1960). The conclusion must be that the small and simple embryos of *Broussonetia*, *Ficus*, and *Morus* are parallel with those of *Urticaceae*; that the fleshy cotyledons specialise as hypogeal food-stores for the plumule; and that the primitive state with the cotyledons resembling the foliage leaf is as rare as in most other families. Similar argument will apply to the *Ulmaceae*.

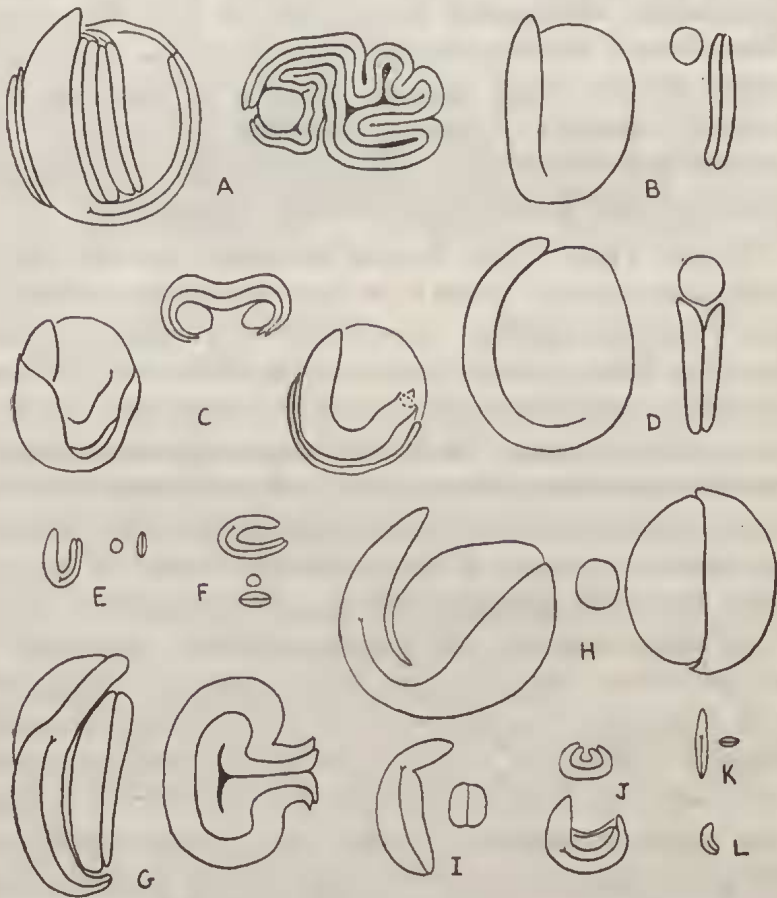


Fig. 4. Moraceae embryos, $\times 5$. A, *Maclura africana* (Bur.) Corner. B, *M. pomifera* (Raf.) Schneid. C, *M. cochinchinensis* (Lour.) Corner. D, *M. thorelii* (Gagnep.) Corncr. E, *Broussonetia papyrifera* (L.) Vent. F, *Morus macrourea* Miq. G, *Antiaropsis decipiens* K. Schum. H, *Trophis branderhorstii* (Diels) Corner. I, *Ficus deltoidea* Jack. J, *F. hesperidiiformis* King. K, *F. rhizophoriphylla* King. L, *F. grossularioides* Burm. f.

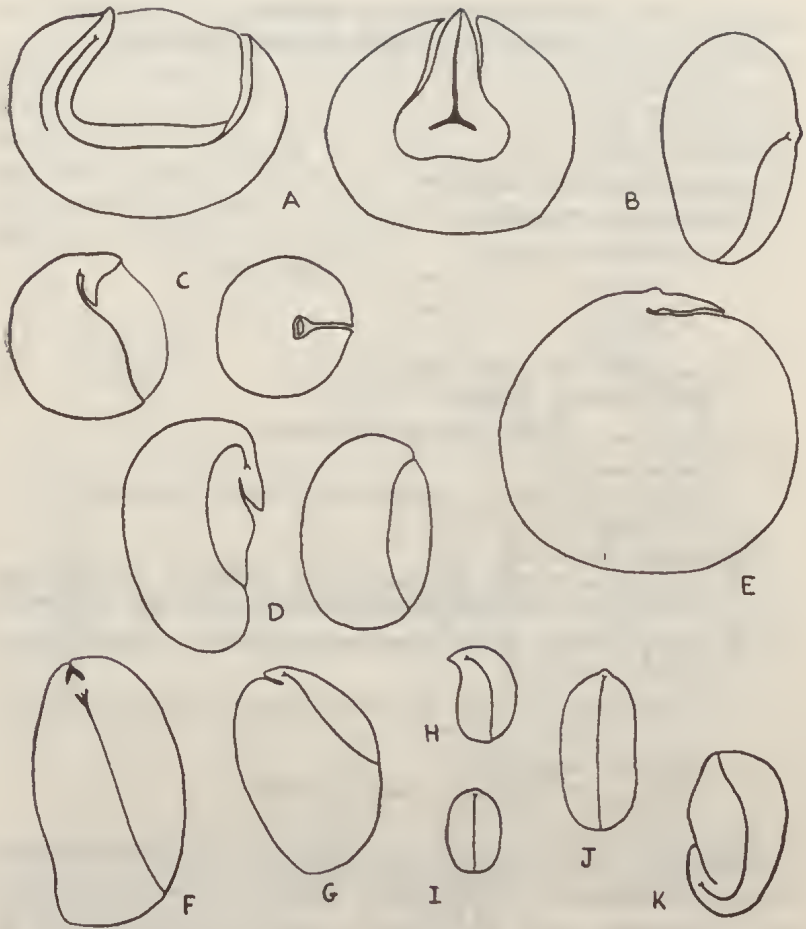


Fig. 5. Moraceous embryos, $\times 5$: those of *Artocarpus* and *Parartocarpus*, $\times 1$. A, *Plecosperrum spinosum* Tréc. B, *Streblus insignis* (Bl.) Corner. C, *S. asper* Lour. D, *S. indicus* (Bur.) Corner. E, *S. elongatus* (Miq.) Corner. F, *Artocarpus integer* Linn. f. G, *A. heterophyllus* Lam. H, *A. elasticus* Reinw. I, *A. glaucus* Bl. J, *A. auisophyllus* Miq. K, *Parartocarpus venenosus* Zoll. et Mor.

The embryos may be classified as follows:—

A. Cotyledons rather thin.

1. Cotyledons conduplicate, plicate; radicle long.

Broussonetia kurzii; *Maclura* sect. *Cardiogyne*, sect. *Cudrania* pr.p.;
Pachytrophe, *Sparattosyce*, *Streblus* sect. *Paratrophis* pr.p.

2. Cotyledons conduplicate, not plicate.

Ficus pr.p.

3. Cotyledons flat or curved, not folded.

a. Radicle incumbent.

i. Embryo longitudinal in fruit.

Broussonetia, *Streblus* sect. *Paratrophis* pr.p.

ii. Embryo transverse in fruit.

Dorstenia, *Fatoua*, *Ficus* pr.p., *Morus*.

- b. Radicle obliquely incumbent to accumbent.
Ampalis, Maclura sect. *Maclura* and sect. *Cudrania* pr.p.
 - c. Embryo straight.
Ficus pr.p.
- B. Cotyledons thick, fleshy.
- 1. Radicle long, often incumbent.
 - a. Cotyledons conduplicate.
 - i. Cotyledons subequal.
Antiaropsis, Streblus sect. *Paratrophis* pr.p.
 - ii. Cotyledons very unequal.
Treculia.
 - b. Cotyledons not folded, equal.
Parartocarpus, Trophis.
 - 2. Radicle short, curved: cotyledons not folded.
 - a. Cotyledons equal.
Artocarpus subgen. *Artocarpus* pr.p. (radicle incumbent or accumbent.).
 - b. Cotyledons unequal.
Artocarpus subgen. *Artocarpus* pr.p., *Malaisia, Plecospermum, Sorocea; Streblus* sect. *Pseudostreblus, Streblus* and *Taxotrophis*.
 - 3. Radicle very short, almost none; embryo straight or slightly curved.
 - a. Cotyledons equal.
Anonocarpus, Antiaris, Artocarpus subgen. *Pseudojaca, Castilloa, Hulletia, Noyera, Prainea*.
 - b. Cotyledons unequal.
Streblus sect. *Bleekrodea* and sect. *Sloetia*.

Number of Floral Parts. In *Ficus* there are many differences in number of stamens (1–8) and tepals (0–8); the style may have one or two stigmatic arms, and the gall-stigma may differ. These numerical points have been exaggerated into generic characters in other tribes, chiefly because their species are more relictual and the trivialities appear profound. In the light of *Ficus*, the pentamery of *Pseudostreblus* and the trimery of *Sloetia* are not generic differences from the tetramerous *Streblus*.

Microscopic characters. The striking taxonomic differences in the occurrence of cystoliths, hypodermis, crystals, resin-cells, gland-hairs, papillate hairs, and so on, in the leaf were first explained by Renner (1907). Their value is shown also by *Ficus*, where they have variously subgeneric, sectional, and specific rank. The temptation is to believe that they may be generic characters in the fragmentary tribes. A detail worth pursuing is the nature of the resin-cells which occur in the mesophyll of *Artocarpus, Maclura* sens. lat., *Malaisia*, and *Prainea*. These cells are known to be absent from *Broussonetia, Plecospermum*, and *Parartocarpus*, all of which I classify in the Artocarpeae, but there are still many genera in which they have not yet been studied. In *Prainea* and *Artocarpus* subgen. *Artocarpus*, yellow resin-cells are scattered in the mesophyll. In *Artocarpus altilis* (Miq.) J.J.Sm. they

are aggregated into compact glands (masses of yellow resin-cells) in the leaf-teeth. In *Maclura* they are aggregated into 2-7 yellow glands immersed in the mesophyll of the bracts and/or the tepals. In *Malaisia* they form a glandular cylinder, or ring in transverse section, in the mesophyll of the pericarp. In *Prainea*, further, they form small masses in the mesophyll of the perianth. Yet, from *Artocarpus* subgen. *Pseudojaca*, with the exception of *A. altilis*, the resin-cells are absent.

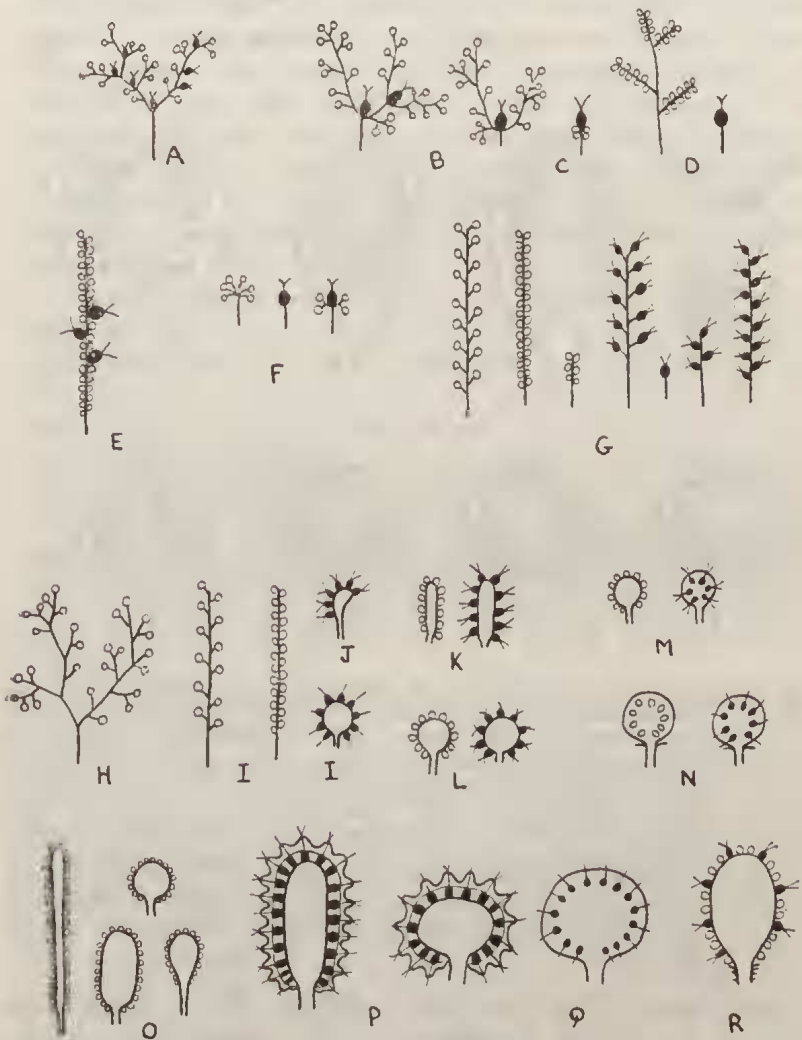


Fig. 6. Diagrams of the inflorescences of Moreaceae (A-G) and Artocarpeae (H-R). A, *Fatoua*. B, *Streblus (Bleekrodea) insignis* (Bl.) Corner. C, *S. madagascariensis* (Bl.) Corner. D, *S. (Pseudostreblus) indicus* (Bur.) Corner. E, *S. (Sloetia) elongatus* (Miq.) Corner. F, *S. (Streblus) asper* Lour. G, *Streblus* sect. *Pseudotrophis* and sect. *Paratrophis* (pedicellate flowers) and sect. *Paratrophis* (sessile flowers). H, *Maclura* sect. *Maclura*. I, *Broussonetia*. J, *Malaisia*. K, *Maclura* sect. *Chloroxylon*. L, *Maclura* sect. *Cudrania*. M, *Plecosperrnum*. N, *Parartocarpus*. O, *Artocarpus*, male. P, subgen. *Artocarpus*. Q, *Artocarpus* subgen. *Pseudojaca*. R, *Treculia*.

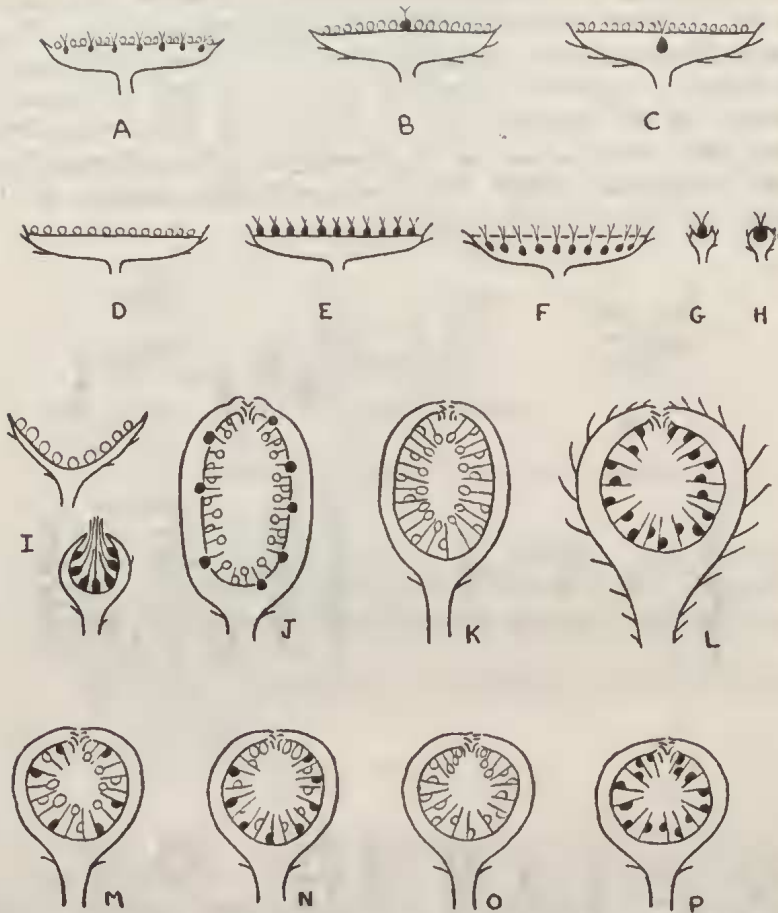


Fig. 7. Diagrams of inflorescences of Dorstenieae (A), Brosimeae (B, C), Olmedieae (D-I), and Ficus (J-P). G, H, I-flowered female inflorescences of *Olmedia* and *Antiaris* respectively. I, Male and female inflorescences of *Sparattosyce*. J, *Ficus* subgen. *Urostigma* sect. *Malvanthera*, the ovaries immersed in the fig-wall. K, gall-fig of *Ficus* subgen. *Kalosyce* sect. *Kalosyce*, with disperse pedicellate male flowers. L, multibracteate seed-fig of *Ficus* subgen. *Ficus* sect. *Sycocarpus*. M, *Ficus* subgen. *Urostigma*, male, gall-, and seed-flowers disperse in the same fig. N, *Ficus* subgen. *Sycomorpus*, with male flowers ostiolar and sessile. O, P, *Ficus* subgen. *Ficus*, gall-fig with ostiolar male flowers and seed-fig, dioecious.

Inflorescence. The shape and structure of the inflorescence seems to be the only satisfactory basis for primary classification. *Ficus* is one example, Brosimeae another, because they are conspicuous. Far less obvious is the unity of the relatively unspecialised panicles, racemes, spikes, and heads of Moreace. Because the advanced inflorescences resulting in syncarps must have been derived from less advanced inflorescences, as shown by the Moreace, the tendency is to regard this tribe as primitive. Its genera, however, are all advanced in many respects, and much more can be learnt about Proto-Moraceae from the other tribes.

When defined broadly, these tribes stand by themselves and point as variously back to Proto-Moraceae. The splitting of genera and tribes in a confusion of floral detail has obstructed a clear view of the family. Indeed, so far as clarification is now needed, the question must be considered whether there is not just one genus for each tribe, comparable with *Ficus*. The point, as already explained, is that *Ficus*, as the most recent ebullition of the family, still shows a fairly continuous spectrum of evolution. The other tribes have merely fragments of their spectra. It is the lack of detailed knowledge to bridge these gaps which makes the putting together of these genera at present highly dubious. I have joined several genera into *Streblus* and have felt inclined to join all into one genus *Morus* for the Moreae. I have joined three or four genera in *Maclura*, and united *Allaeanthus* with *Broussonetia*. Compare, then, the small genera *Malaisia*, *Prainea*, and *Plecosperrnum*, and it will be seen how difficult it is to place them with satisfaction. *Artocarpus*, *Parartocarpus*, and *Treculia* introduce another set of differential details.

A peculiar point about the spicate inflorescences of Moreae and some Artocarpeae is the presence of a sterile longitudinal strip on one side, to which Baillon first drew attention. It needs investigation. It does not occur in the racemose or paniculate inflorescences with pedicellate flowers, and it is absent from the capitate inflorescences, though vestigial in the subcapitate female inflorescence of *Malaisia*.

I have united Broussonetieae with Artocarpeae because I can find no sharp separation. Perhaps this sterile groove is significant. It occurs in the spicate male inflorescences of *Broussonetia*, *Maclura*, and *Malaisia*, but not in the spicate inflorescences of *Artocarpus*.

Spines. Short shoots ending in a spine (stem-tip) distinguish *Streblus* sect. *Phyllochlamys*, sect. *Pseudotrophis* (excluding *S. inacrophyllus* Bl.), and sect. *Taxotrophis*, and also *Maclura* (except for the African trees of sect. *Chlorophora*). In *M. africana* (*Cardiogyne*) the spines end short leafy shoots: in the others the spines are leafless, or nearly so. It seems that the feature has developed in parallel in these two genera, just as the spinous leaf-edge of *Streblus ilicifolius* parallels that of *Sorocea*. It is remarkable that the habit has not developed in any other genus, though in *Ficus* there is the solitary example of a spinous leaf-edge in *F. macilenta* King var. *ilicifolia* Corner.

Proto-Moraceae

To present an archetype is often considered mere speculation. Then, what is it that systematists imply when they put into genera and tribes the remnants of ancient groups? Must they be blind to the pictures this sort of pattern will show? Every taxon implies, unless one disbelieves evolutionary theory, an antecedent.

The more numerous the taxa, the clearer should become the antecedent. Taxonomy which denies itself this duty to speculate grows more and more minute and is well-labelled microtaxonomy. Without a hypothesis of origins, the taxonomist cannot appreciate what he is doing. I often think that taxonomy is a larder of notions awaiting thought.

The following is my view on the ancestors of Moraceae, supported by reasons.

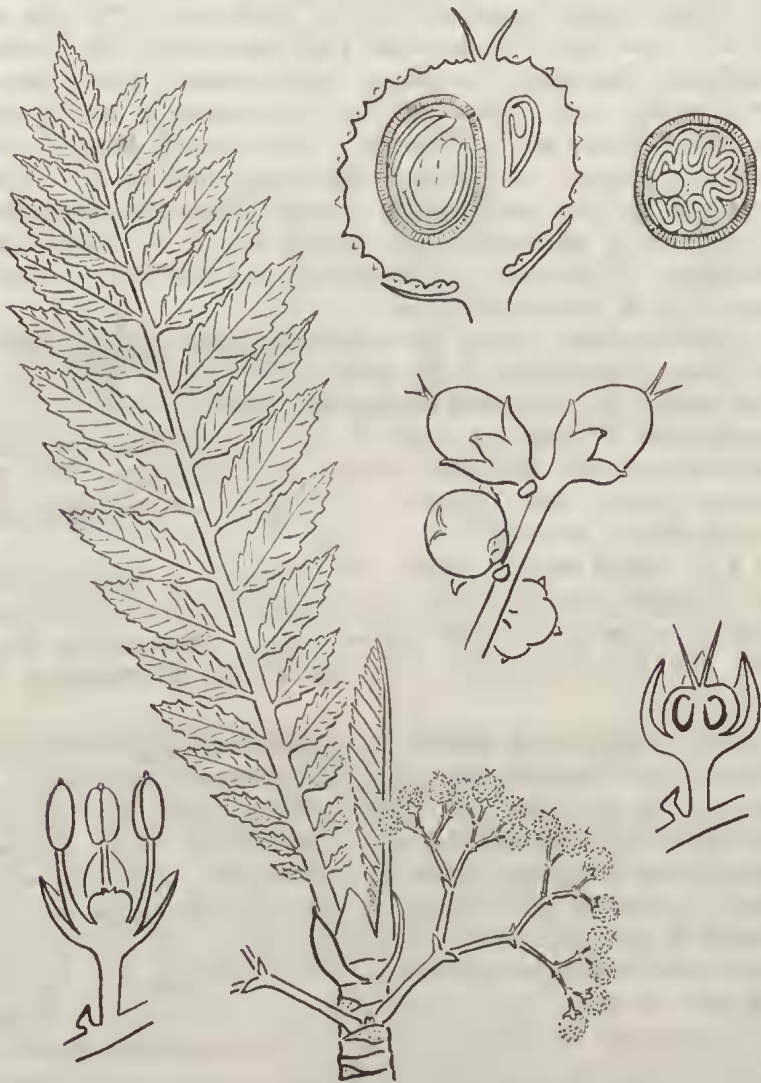


Fig. 8. Proto-Moraceae in reconstruction. Pinnate-leaved pachycaul stem, $\times 1/6$. Male and female flowers, $\times 3$. Fruits, one with echinulate drupe, the other with smooth drupe and spinous perianth-segments, $\times 1$. Seed (endocarp) in section, $\times 1$.

Characters of Proto-Moraceae.—Monoecious, pachycaul, pinnate-leaved; stipules foliaceous, amplexicaul; latex present. Inflorescences cymose-paniculate; flowers unisexual, pedicellate, apetalous, male and female in the same inflorescence; perianth with

5-8 imbricate tepals. Male flowers with the stamens opposite the tepals; anthers large, mucronate; filaments straight in bud; pistillode as a sterile ovary. Female flowers (?with abortive stamens); ovary superior, with 2 loculi or one; styles 2, long, or one with two long stigmatic arms; ovule one in each loculus, subapical, anatropous. Drupe large, with woody endocarp, surrounded at the base by the persistent spicate tepals. Seed with membranous testa, enclosed in the endocarp, with little endosperm. Embryo curved; radicle long, incumbent; cotyledons foliaceous, plicate-conduplicate; germination epigeal. Leaf with cystoliths on both sides; hypodermis ? none; stomata superficial on the lower side; microscopic gland-hairs multicellular, ? subglobose or peltate; hairs papillate.

Monoecious. This state is indicated as the primitive in *Ficus* subgen. *Urostigma*, *Pharmacosycea*, and *Sycomorus*, and there is clear evidence of the derivation of the male and female inflorescences, leading ultimately to dioecism, in *Streblus* sect. *Bleekrodea* and sect. *Streblus*, in *Treculia* and in *Parartocarpus*.

Pachycaul, megaphyllous, with foliose stipules. This ancestral state is shown by *Ficus* sect. *Sycidium*, *Sycocarpus*, and *Adenosperma*, perhaps also by sect. *Galoglychia* (subgen. *Urostigma*). It is shown for Olmedieae in *Palmolmedia*. Except for the foliaceous stipules it is the state of *Artocarpus anisophyllus* and *A. incisus*. It is indicated in *Bagassa*, allied with *Maclura*, in *Broussonetia*, and in *Dorstenia*. Specialisation in all these genera displaying pachycaul origin leads to the leptocaul and the willow-leaved habit in their more derived species. The point is important because it means that the family Moraceae and its tribes arose as short pachycaul trees and that such genera as *Ficus*, *Artocarpus*, *Maclura*, *Broussonetia*, and *Antiaris* have been independantly evolved into large trees, as some of them have been evolved into climbers. Comparative anatomy must learn from the anatomy of pachycaul plants, knowledge and, indeed, appreciation of which is still so deficient. The communities of banyans, which assemble on the ruins of civilisations, are not primitive fig-forests, the nature of which is to be seen rather in the secondary vegetation of pachycaul figs in Borneo, New Britain, and Bougainville Island.

Inflorescence. When traced from their inception, the flowers even of *Ficus* and *Dorstenia* are found to arise in a cymose pattern (Bernbeck, 1932). Intercalation of internodes into capitate inflorescences leads back to the racemose-cymose state, and this leads, by branching, to the paniculate. The cymose monoecious remnants as *Streblus* sctt. *Bleekrodea*, Brosimeae, and Dorstenieae indicate that there was a central female flower, terminal and surrounded by male flowers as in Euphorbiaceous inflorescences. Conversely, condensation of such an inflorescence with or without dioecism leads to the variety of the Moraceae. The strong protogyny in bisexual Moraceous inflorescences also indicates the cymose construction with terminal female flower.

Flower-structure. The conclusions, argued on preceding pages, agree with those of Bechtel, based on vascular anatomy. Problematic is the antitepalous position of the stamens. It suggests missing petals of which there is no external sign in the Urticales. In *Ulmus americana*, Bechtel found abortive vascular bundles between and alternating with those of the tepals and stamens, as internal vestiges of petals; also, in this flower of floral formula $P(8)/A8$, there were six abortive vascular bundles internal to and alternating with the staminal; the ovary has four vascular bundles. Thus, the Ulmaceous flower gives evidence of $\frac{3}{8}$ phyllotaxis in perianth and androecium, descending to $\frac{1}{2}$ in the gynoceium. In most Moraceae this has become $\frac{1}{2}$ phyllotaxis throughout the flower, as $P\ 2+2\ A2+2\ G1$, with two styles or stigmatic branches. Such falling phyllotaxis is proof that the Proto-Moraceous flower is descended from one of massive construction with many parts.

Fruit. Of an antecedent drupe there can be no doubt, but the Proto-Moraceae must be considered along with other flowering plants. The syncarps of *Artocarpus* subgen. *Artocarpus*, of *Parartocarpus*, and of *Treculia* strongly resemble the fruit of the durian (*Durio zibethinus*). The spines of the durian are outgrowths of the ovary located beneath peltate scales; the pulp of the durian-seed is a true aril, its testa the outer integument. The spines of the Moraceous syncarps are thickened perianths, tepals or bracts; the peltate scales are bracts with peltate tops; the seed is a pyrene, the endocarp of which forms a false testa; the pulp is the outer part of the ovary-wall or the perianth. Transfer, then, the testa-lignification of *Durio* from the outer integument to the endocarp, the aril-pulpiness to the exocarp, the spinous character to the tepals and bracts, and there is the transformation into *Parartocarpus* or *Treculia*. In *Artocarpus* subgen. *Artocarpus* the perianth is divided into two parts, a proximal and a distal, both free from their neighbours but fused together with them laterally by a middle layer; the proximal part becomes the pulpy false aril and the distal part becomes the spine. A simple transfer of function, or gene-action, by one or two tissue-layers away from the ovule occurs and the durian-fruit is converted into the Moraceous syncarp. This false fruit is a syncarp not of carpels but of syncarpous ovaries; it is a second-order fruit, and thus every durian-feature is displaced outwards from its primary position to a secondary. That is, the stem-apex forms not floral primordia to become large flowers, but floral primordia so reduced and neotenic that they become, as it were, single uni-ovulate carpels which function as arillate seeds, and the reduced tepals are converted into spines. It requires the crowding of primordia on an embryonic condensed inflorescence for such displacement of differentiation. Thus it is the elaborate syncarp of Artocarpeae, not the simple drupe of Moreae, which has the primitive characters.

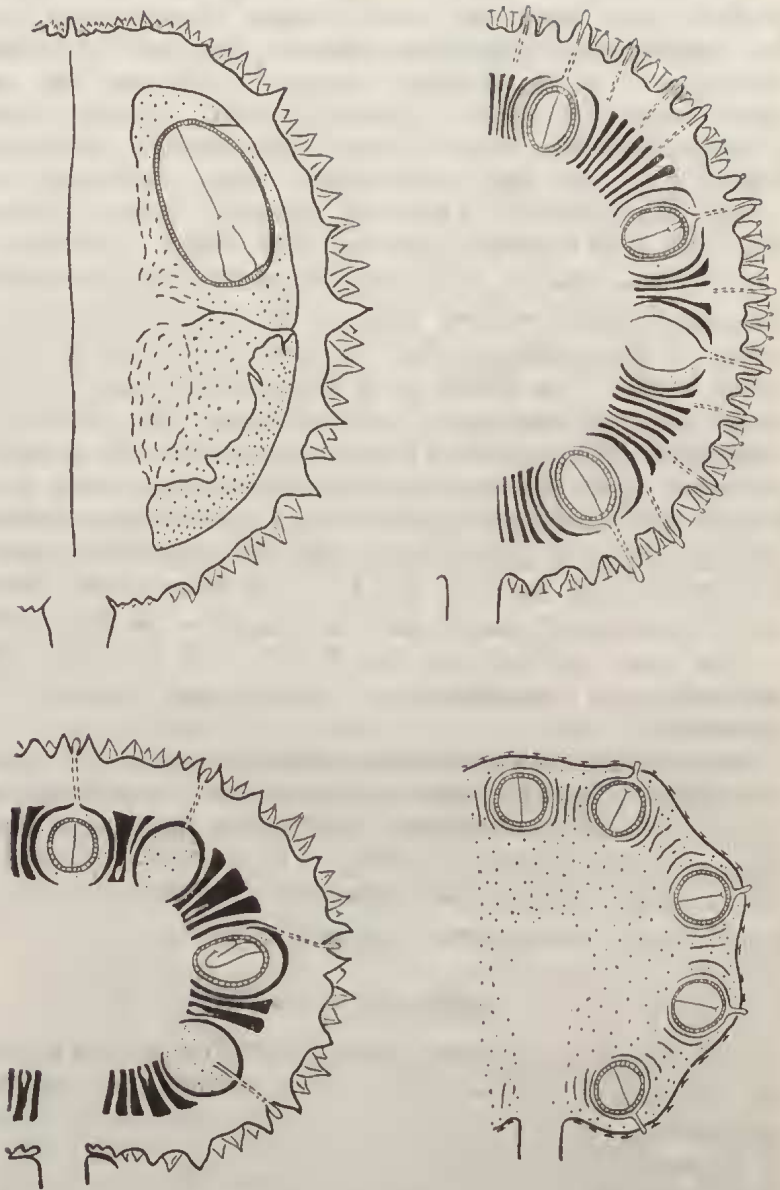


Fig. 9. Fruit of *Durio* (upper left) and syncarps of *Artocarpus* subgen. *Artocarpus* (upper right), subgen. *Pseudojaca* (lower right), and *Parartocarpus* (lower left), diagrammatic, $\times \frac{1}{2}$. The pulpy part of each fruit is dotted, namely aril (*Durio*), pericarp (*Parartocarpus*), perianth (subgen. *Artocarpus*), and the whole syncarp-tissue (subgen. *Pseudojaca*). Note, in subgen. *Artocarpus*, the utricular perianths (perforated by the style) are fused in their middle part, the strands between the fertile flowers being sterile perianths; in *Parartocarpus* and subgen. *Pseudojaca*, the ovaries are inferior in sockets of the receptacle and the strands between the fruiting ovaries are receptacular tissue. In *Artocarpus* the petalate interfloral bracts are shown.

It is necessary to argue this way because the durian-theory (Corner, 1954) shows that, for the modern flowering plant (not for a hypothetical pteridosperm ancestor), the arillate seed and spinous pericarp are primitive features. To suppose that the simple drupe of Moraceae is primitive and the syncarp a novel durian-anologue is to beg the question; this reasoning implies that Moreae never had the durian-features while *Artocarpus* discovered them anew only to lose them again in its subgen. *Pseudojaca* which in all respects is advanced upon subgen. *Artocarpus*.

Sapindaceae show the derivation of spineless drupes from spiny pericarps (*Nephelium*), and what are the sublamellate excrescences on the indehiscent fruit of *Planera* (Ulmaceae) if not durian-vestiges? That spines are a morphological entity, as vasculated epidermal outgrowths, the durian shows. That spines have biochemical precursors in the genotype is shown by the action of gall-insects which provoke durian-like galls in plants which seem to have lost the ability to produce spines, e.g. *Artocarpus canarana* Miq. which is galled *Hopea wightiana* (Dipterocarpaceae). Recently in North Borneo I found a small shrub (sterile) which bore a terminal pedunculate gall resembling a small durian-fruit 4–5 cm. long, but filled with flies. The day will come when the biochemistry of durianology is revealed and genetics will apprehend.

The lost history of Moraceae now begins to appear. It is not in the advanced leptocaul states of Moreae but in the pachycaul states of Artocarpeae, Olmedieae, Dorstenieae, and Ficeae. These tribes are not derived from Moreae, but all from Proto-Moraceae. *Morus* can be likened to sect. *Ficus*; behind *Morus* lies as much lost history as there is present evidence in *Ficus*.

Affinity of Urticales

Several botanists as Weddell, Hallier (1905), Bessey, and Bechtel have favoured affinity with Malvales. The Proto-Moraceous reconstruction, Fig. 8, is a remarkable parallel with Euphorbiaceae of the same alliance. Critical would be the microscopic structure of the seed-coat, but all Moraceous and Urticaceous seeds seem to be enclosed in endocarp (? transferred testa), and do not develop typical testa-structure. Then Hallier (1912), Tippe (1939), and Hutchinson (1959) refer Urticales to the affinity of Hamamelidales, which may lead back to a similar pachycaulous ancestor. It is necessary to consider pachycaulous ancestry because, as Moraceae show, family-characters, even tribal and generic, of flower and fruit must have been evolved in this state of flowering plant evolution. The pachycaulous is, in fact, the chief phase of flowering plant evolution which, as would be expected from its primitiveness, is widely missing.

GEOGRAPHICAL TABLE OF MORACEOUS GENERA AND SPECIES

Gen./Spp.	America	Africa	Asia and Australasia	Tribes
10/68	4/19	6/13	4/36	Moreae
15/95	8/20	2/7	7/68	Artocarpeae
18/69	13/58	2/5	4/6	Olmedieae
8/44	1/6	7/38	..	Brosimeae
1/120	1/80?	1/40?	1/1	Dorstenieae
1/1000?	1/150?	1/250?	1/600?	Ficeae
53/1397	27/333	18/353	17/711	Total Moraceae

Australasia has been included with Asia in this Table because it has only one peculiar genus, namely *Sparattosyce* with two species in New Caledonia; it has also six species of *Streblus* along with a few wide-spread species of *Artocarpus*, *Antiaris*, *Fatoua*, and *Malaisia*.

Excluding *Ficus* and *Dorstenia*, as satisfactory genera, the ratio of genera to species in America is 1/4, in Africa 1/3.7, and in Asia 1/7.3. The number of genera in America and Africa may well be halved, but these low ratios indicate that, excepting *Dorstenia* and *Ficus*, the genera are relics.

Moraceae Lindl.

Veg. Kingd. (1847) 266; Bureau, DC. Prodr. 17 (1873) 211; Engl. Nat. Pflanzenf. 3, 1 (1894) 66; Veg. Erde IX, vol. 3, 1 (1915) 17; Dalle Torre et Harms Gen. Siph. (1900) 120; Lemée, Dict. Phan. 7 (1939) 184; 8b (1943) 8, 14, 17.—*Artocarpaceae* Bur. DC. Prodr. 17 (1873) 280.—subfam. *Artocarpoideae* A.Br. ex Aschers. Fl. Prov. Brandenb. 1 (1864) 57; Engl., l.c. 80; D. Torre et Harms, l.c. 121.—subfam. *Moroideae* Engl. l.c. 70; D. Torre et Harms, l.c. 120.

Trees, shrubs, climbers, or herbaceous (*Dorstenia*, *Fatoua*). *Latex present*, generally milky. Leaves pinnate, palmate, incised, or simple, stipulate. Inflorescences axillary, typically paired, unisexual or bisexual, monoecious or dioecious, paniculate, racemose, spicate, capitate, or urceolate. Flowers small, unisexual, apetalous; tepals 8-0, generally 4, free or gamophyllous, imbricate or valvate, persistent; stamens isomerous and antitepalous, or reduced to 3, 2, or 1; filaments straight, free or connate, or inflexed; anthers large, mucronate, to small, bilobate and non-mucronate, varying crescentic to turbinate (with transverse equatorial dehiscence); pistillode present in male flower or not; ovary 1-, rarely 2-, locular, superior to inferior, or immersed in sockets in the

inflorescence-axis; styles 2 or 1 with two stigmatic arms, or one stigmatic arm; *stigma not capitate or peltate; ovule 1, anatropous or campylotropous*, apical or subapical. *Fruits drupaceous, discrete or more or less connate in large fleshy syncarps. Seeds large or small*, invested in endocarp; testa membranous or disintegrated. *Embryos various*, curved or straight; radicle long or short, incumbent or accumbent; cotyledons plicate, conduplicate, or plane, foliaceous or thickened, equal to very unequal. Lamina with or without cystoliths. Chromosome haploid numbers 12, 13, 14, with intrageneric polyploidy. Gen. 53, pantropic, few temperate; species c. 1400 (Ficus c. 1000 spp.).

Key to the Tribes of Moraceae

1. Flowers inside urceolate receptacles (syconia), numerous; styles not extruded from the receptacles. Blastophagous with sterile insect-inhabited female flowers. Stamens, when 2 or more, with introrse anthers; filaments straight in bud. Female flowers stalked or sessile
Ficeae.
1. Flowers not so enclosed or, if so, the styles exerted from the receptacle, not blastophagous. Stamens mostly extrorse. Female flowers mostly sessile.
 2. Inflorescences bisexual, discoid or compressed-elongate, globose or urceolate. Not spinous.
 3. Female flowers numerous in each receptacle, each surrounded by many sessile male flowers; stamens 1-3, mostly 2, the filaments inflexed in bud; ovaries immersed in sockets. Receptacles flattened, discoid to variously elongate, bracteate round the margin, forming syncarps. Seeds small. Herbs or suffrutescent
Dorstenieae.
 3. Female flower solitary in the centre of each receptacle, surrounded by many sessile male flowers; stamens 1-4, the filaments straight in the bud or, rarely, inflexed; ovaries free or immersed. Receptacles discoid, globose, or urceolate, not elongate, forming syncarps. Seeds rather large. Trees, shrubs *Brosimeae.*
 2. Inflorescences unisexual or, if bisexual, not discoid. Trees, shrubs, climbers, rarely herbs.
 4. Female inflorescence racemose or spicate with slender axis or 1-flowered, or the inflorescence bisexual (cymose or spicate), neither capitate nor discoid; ovaries mostly free, if inferior then not in sockets. Male inflorescence paniculate, racemose, spicate or capitate, often with a sterile groove; stamens 5-1, filaments mostly inflexed in bud, in some cases straight; pistillode generally present. Spinous or not *Moreae.*
 4. Female inflorescence capitate or thickly spicate, mostly syncarpous; ovaries often immersed in sockets of the receptacle or connate with it. Male flowers mostly without pistillode.
 5. Male and female inflorescences discoid, obconic, or urceolate, with an involucre of 1-several bracts; female inflorescences varying 1-flowered. Syncarpous or not. Stamens 8-1, the filaments straight in bud. Not spinous *Olmedieae.*
 5. Male and female inflorescences of different shape, involucre or not. Female inflorescence thickly spicate to capitate-globose, never 1-flowered, syncarpous. Male inflorescence paniculate, racemose, spicate, or capitate; stamens 4-1, the filaments straight or inflexed in bud. Spinous or not *Artocarpeae.*

Tribe Moreae Gaud.

Voy. Freyc. (1826); Endl. Prodr. Fl. Norf. (1833) 40; Gen. Pl. (1841) 277; Suppl. 1, 1375; Suppl. 4 (1842) 33; Miq. Mart. Fl. Bras. 4, 1 (1852) 154; Bur. DC Prodr. 17 (1873) 234; Baill. Hist. Pl. 6 (1875) 167; Benth et Hook. Gen. Pl. 3 (1880) 343 (sub Urticaceae); Engl. Nat. Pflanzenf. 3, 1 (1894) 72; Veg. Erde IX, 3, pt. 1 (1915); Dalle Torre et Harms, Gen. Siph. (1900) 120.—*Soroceae* Miq. Mart. Fl. Bras. 4, 1 (1852) 111 (subtrib.); Bur. DC Prodr. 17 (1873) 288.—*Strebleae* Bur. id. 215; Benth. et Hook. l.c. 344 (ut subtribus); Dalle Torre et Harms l.c. 120.—*Fatoucae* Benth. et Hook. l.c. 344 (ut subtribus); Engl. Nat. Pflanzenf. 3, 1 (1894) 71; Dalle Torre et Harms, l.c. 120.—*Eumoreae* Benth. et Hook. l.c. 345.

Inflorescence paniculate, cymose, racemose, spicate, or (male) capitate, (the axis not expanded into a discoid, urceolate, globose, or stoutly spicate receptacle), bisexual or mostly unisexual. Female inflorescence cymose, racemose, spicate, or 1-flowered, never capitate. Filaments incurved or (*Sorocea*, *Clarisia*) straight in bud; anthers extrorse; pistillode commonly present. Ovary generally superior, inferior in a few genera. Fruit drupaceous, never in syncarps. Trees, shrubs, or (*Fatoua*) herbs, spinous or not, monoecious or dioecious. Gen. c. 10, species c. 68, pantropical or (*Morus*) temperate.

Key to the Genera of Moreae

1. Seeds small, 1–2 mm. wide, somewhat compressed; endocarp crustaceous. Embryo with long, incumbent, transverse radicle; cotyledons flat. Male flowers with pistillode; filaments 4, inflexed in bud.
 2. Herb. Inflorescence cymose, bisexual or unisexual. Madagascar, Asia, Australasia *Fatoua*.
 2. Trees. Inflorescence racemose or spicate, unbranched, unisexual. Dioecious or monoecious. Asia, North America *Morus*.
1. Seeds 4–12 mm. wide, rounded. Radical not transversely elongate; cotyledons often folded or much thickened, often unequal. Leaves distichous. Spinous or not.
 3. Male flower without pistillode. Filaments straight in bud. Female perianth utricular, 4-dentate. Ovary (drupe) inferior. Unarmed or with spinous-dentate leaf. America.
 4. Stamens 4, Male inflorescence racemose, spicate or (*Paraclarisia*) capitate *Sorocea*.
 4. Stamen 1. Male inflorescence spicate *Clarisia*.
 3. Male flower with pistillode. Filaments (3–5, mostly 4) inflexed in bud.
 5. Fruiting perianth fleshy as in *Morus*. Madagascar
Ampalis, *Pachytrophe*.
 5. Fruiting perianth not fleshy, but the drupe thinly fleshy or with thickly fleshy base.
 6. Ovary (drupe) inferior. Unarmed. America, Malaysia, Madagascar *Trophis*.
 6. Ovary (drupe) superior. Spinous or not. Asia, Australasia, (Africa ?) *Streblus*.
(Africa, *Neosloetiopsis*, *Sloetiopsis*).

Too many genera on insufficient and invalid grounds trouble this small tribe. I have reduced eleven to sections, or synonyms, of *Streblus*, and I have considered reducing *Streblus* to *Trophis*, and all genera to *Morus*. The variety in the tribe is certainly much less than that of *Ficus*, but insufficient knowledge and the difficulty in assessing relic plants such as *Fatoua*, *Morus*, *Ampalis*, and *Pachytrophe* render wholesale reduction at this stage unwise.

The tribe represents the relics of that part of the family in which the female inflorescence, though sometimes reduced to the one-flowered state, is not specialised in form through thickening of the axis.

Sexuality. The bisexual inflorescence of *Fatoua* and *Streblus* sect. *Bleekrodea* has been used to separate these two genera into a tribe Fatoueae. The Madagascan species of *Fatoua*, however, has unisexual inflorescences and sect. *Bleekrodea* merges through *Streblus tonkinensis* (*Teonongia* Stapf) with *S. asper*. The inflorescences of *S. tonkinensis* vary from the condition of sect. *Bleekrodea* with the female flower surrounded by males to the condition in *S. asper*, though monoecious, but Gagnepain has described var. *monoica* of *S. asper* as having a female flower in the male cluster. Then, because of its bisexual spike, *Sloetia* has been placed in Dorstenieae, where it is entirely out of place. In flower, fruit, seed, and leaf-structure *Sloetia* and *Bleekrodea* are closely allied and both, by analogy with *Ficus*, are merely sections of *Streblus*.

Sterile groove in male spike. As already noted, this feature occurs in all spicate inflorescences of Moreae and in *Broussonetia*, *Maclura*, and *Malaisia* of Artocarpeae. It has yet to be explained morphologically. It would seem to be a sign of affinity, yet the racemose and paniculate inflorescence of *Streblus* sens. lat., *Trophis*, and *Maclura* lack the sterile groove. In spite of its peculiarity it is difficult to give it a primary value in classification.

Capitate male inflorescence. The inflorescence of shortly pedicellate male flowers in *S. asper* seems a good generic character until it is realised that the insertion of a female flower into the centre of it, as may happen in *S. asper* var. *monoica*, turns it into the bisexual cyme of *Streblus* sect. *Bleekrodea*, with *S. tonkinensis* as the bridge. *Streblus* sect. *Phyllochlamys* has also a capitate male inflorescence, but the fruit-characters ally the single species with sect. *Taxotrophis* and indicate that the capitate male inflorescence is here a condensed raceme. *S. crenatus* (sect. *Pseudotrophis*) and *S. perakensis* (sect. *Paratrophis*) have almost capitate male inflorescences, but they have the sterile groove which indicates that they are derived from condensed spikes. It must be concluded that the condensation of the male inflorescence has occurred independently in several lines of the genus.

Female inflorescence. Unlike the male, the female inflorescence never condenses into a head; that is the character of Artocarpeae. Instead, reduction leads to fewer flowers and ends with the solitary pedunculate female flower, arrived in parallel in *Streblus* sect. *Streblus*, *Phyllochlamys*, *Pseudostreblus*, *Taxotrophis*, *Pseudotrophis*, and *Paratrophis*, in *Trophis* sect. *Maillardia*, and, perhaps, in the African *Neosloetiopsis*.

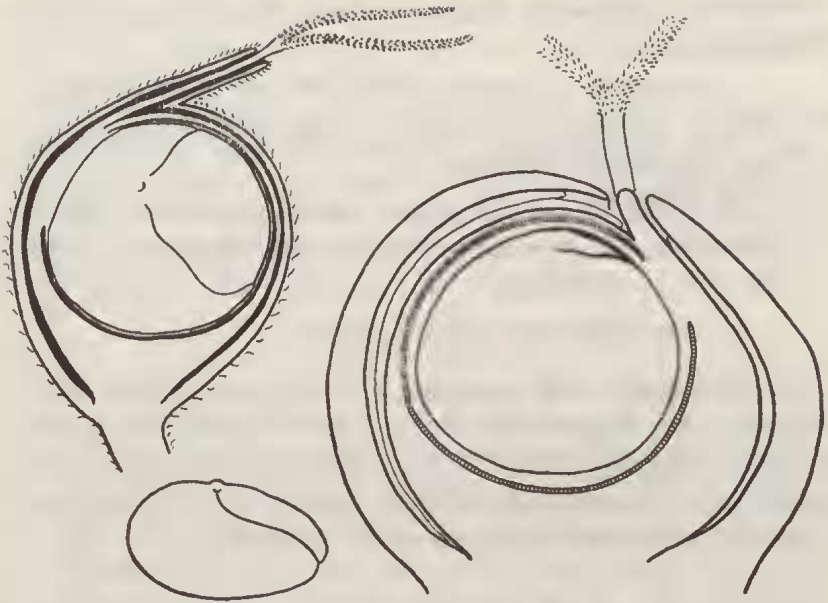


Fig. 10. Fruits in section, $\times 5$. *Streblus* (*Bleekrodea*) *insignis* (Bl.) Corner, left, with embryo. *Streblus* (*Sloetia*) *elongatus* (Miq.) Corner, right, with thickened fruit-base; the lignified endocarp hatched.

Pulpy fruit-base. The drupes of *Streblus* sect. *Phyllochlamys*, *Sloetia*, and *Taxotrophis* have a strongly swollen base and they actually dehisce crescentically over the apex in a plane at right angles to that of the style. When this happens in *S. elongatus*, and presumably in the other species, the seed is forcibly ejected by the snapping together of the two sides of the swollen, white, edible and sweet-tasting base. It seems a good character for a genus, but there are transitions with slightly fleshy base as in sect. *Bleekrodea* (drupe dehiscent at the apex), and in sect. *Pseudotrophis* and *Paratrophis* in which the drupe is mostly, if not always, indehiscent. The drupelets of *Ficus* are often fleshy at the base and, in a few species, dehisce at the apex to liberate the seed into the fig-cavity, but the character has no classificatory value. Nevertheless, it may be a primary distinction between *Streblus* and *Morus*, though most species of *Streblus* seem to have lost it.

Pulpy tepals. Together with the small seed, the pulpy fruiting tepals are the chief distinction of *Morus*. The Madagascan *Ampalis* and *Pachytrophe* have also pulpy tepals, but this character occurs in *Maclura* with which they seem more nearly allied. Pulpy tepals occur, too, in many groups of *Ficus*, particularly sect. *Ficus*. The character seems to contrast with that of *Streblus*, and this is the main reason why I refrain from uniting *Streblus* with *Morus*.

Pistillode. This feature offers three states which may be a basis of classification:—

1. Pistillode quadrate-columnar; *Morus*, *Ampalis*, *Pachytrophe*; *Streblus* sect. *Streblus*, *Taxotrophis*, *Pseudotrophis*, and *Paratrophis*; *Trophis*.

2. Pistillode minute, spicate, subulate, or conic; *Fatoua*, *Neosloetiopsis*, *Sloetiopsis*; *Streblus* sect. *Bleekrodea*, *Pseudostreblus*, and *Sloetia*.

3. Pistillode none; *Clarisia*, *Sorocea*.

In Artocarpeae with pistillode it is the second kind, which appears as the degeneration of the sterile ovary towards the final state of complete absence. The quadrate-columnar state is that typical of Urticaceae with inflexed stamens. *Streblus*, therefore, seems to show stages in the loss of the pistillode.

Ampalis Bojer and **Pachytrophe** Bur.

Bojer, Hort. Maurit. (1837) 291; Bur. DC Prodr. 17 (1873) 234; Leandri, Fl. Madag. fam. 55 (1952) 6, 9.—*Streblus* Lour. subgen. *Parastreblus* Bl. Mus. Bot. Lugd. Bat. 2 (1856) 80 (= *Ampalis*).

These two small genera of Madagascar resemble *Streblus* in many ways but the fruiting tepals become fleshy as in *Morus* and, indeed, as in *Maclura*. *Ampalis* has the embryo of *Maclura*, consisting of two small flat cotyledons and a rather long accumbent radicle. *Pachytrophe* has an embryo like that of several species of *Streblus* sect. *Paratrophis*, with foliaceous conduplicate cotyledons and incumbent radicle, but this embryo also occurs in *Maclura* sect. *Cardiogyne*. The ovule of *Pachytrophe* is attached to a much thickened placenta which becomes a woody plug at the side of the seed, and this feature occurs in various Moraceae, without mark of affinity, such as *Broussonetia kurzii*, *Parartocarpus*, *Streblus solomonensis*, *Treculia*, and *Trophis branderhorstii*. It seems as if both genera are related with *Maclura*, as relies of its less specialised ancestry, and, if so, this will necessitate a re-definition of Artocarpeae, or the fusion of it with Moreae. Compare, however, *Neosloetiopsis*.

Morus L.

The ovate-cordate lamina of *Morus*, with plicate venation, corresponds with the state of tree-evolution seen in *Ficus* subgen. *Sycomorus* and in various groups of subgen. *Ficus*. From it the simpler, inrolled, leaf of *Streblus* has been derived.

M. macroura Miq. Pl. Jungh. 1 (1851) 42.—*M. laevigata* Wall. ex Hook. Fl. Br. Ind. 5 (1888) 492.—*M. alba* L. var. *laevigata* Bur. DC Prodr. 17 (1873) 245.

I can see no distinction whatever between these two species and, therefore, reduce *M. laevigata*. The species becomes, then, a wide-spread tree from Sikkim to Hainan with a relict status in Sumatra, as a mountain tree, and, perhaps, in Java though it may have been introduced to this country from Sumatra. Comparable is the group of *Ficus hirta* in *Ficus* sect. *Ficus*.

Streblus Lour.

Fl. Cochinch. (1790) 615; Blume. Mus. Bot. Lugd. Bat. 2, (1856) 79, f. 30; Miq. Fl. In. Bat. 1, 2 (1859) 277; Bur. DC Prodr. 17 (1873) 218; Baill. Hist. Pl. 6 (1875) 146, 195; Benth. et Hook. Gen. Pl. 3 (1880) 359; Engl. Nat. Pflanzenf. 3, 1 (1894) 78, f. 57 A-C.—*Achymus* Vahl ex Juss. Diet. Sc. Nat. 1, suppl. (1816) 31.—*Achinus* Poir. id. 5 (1827) 51.—*Epicarpurus* Bl. Bijdr. (1824) 488.—*Albrandia* Gaud. Voy. Freye. Bot. (1826) 509.—*Albradia* D. Dietr. Syn. Pl. 5 (1852) 280.—*Calius* Blanco, Fl. Filip. (1837) 698; Bur. DC Prodr. 17 (1873) 278.—*Bleekrodea* Bl. Mus. Bot. Lugd. Bat. 2 (1856) 87; Bur. DC Prodr. 17 (1873) 254; Baill. Hist. Pl. 6 (1875) 147, 198; Benth. et Hook. Gen. Pl. 3 (1880) 358; Engl. Nat. Pflanzenf. 3, 1 (1894) 71, f. 50 C,D; Leandri, Fl. Madagasc. fam. 55 (1952) 5.—*Paratrophis* Bl. Mus. Bot. Lugd. Bat. 2 (1856) 81; Bur. DC Prodr. 17 (1873) 235; Baill. Hist. Pl. 6 (1875) 143, 191; Benth. et Hook. Gen. Pl. 3 (1880) 364; Engl. Nat. Pflanzenf. 3, 1 (1894) 72; Cheeseman, Man. N. Zeal. Fl. (1906) 631.—*Taxotrophis* Bl. Mus. Bot. Lugd. Bat. 2 (1856) 77; Miq. Fl. Ind. Bat. 1, 2 (1859) 278; Bur. DC Prodr. 17 (1873) 216; Baill. Hist. Pl. 6 (1875) 146, 195; Benth. et Hook. Gen. Pl. 3 (1880) 358; Engl. Nat. Pflanzenf. 3, 1 (1894) 77; Hutchinson. Kew Bull. (1918) 147.—*Sloetia* Teysm. et Binn. ex Kurz, J. Linn. Soc. Bot. 8 (1864) 168; Bur. DC Prodr. 17 (1873) 257; Baill. Hist. Pl. 6 (1875) 147, 198; Benth. et Hook. Gen. Pl. 3 (1880) 365; Engl. Nat. Pflanzenf. 3, 1 (1894) 79.—*Diplocos* Bur. DC Prodr. 17 (1873) 215; Baill. Hist. Pl. 6 (1875) 148, 199. *Phyllochlamys* Bur. DC Prodr. 17 (1873) 217; Baill. Hist. Pl. 6 (1875) 146, 196; Benth. et Hook. Gen. Pl. 3 (1880) 359; Engl. Nat. Pflanzenf. 3, 1 (1894) 77.—*Pseudomorus* (Endl.) Bur. Ann. Sc. Nat. ser. 5, 11 (1869) 372; DC Prodr. 17 (1873) 249; Baill. Hist. Pl. 6 (1875) 143, 191; Benth. et Hook. Gen. Pl. 3 (1880) 364; Engl. Nat. Pflanzenf. 3, 1 (1894) 72; Skottsberg, Act. Hort. Gotob. 15 (1944) 347; Stearn, J. Arn. Arb. 28 (1947) 426.—*Pseudostreblus* Bur. DC Prodr. 17 (1873) 219; Baill. Hist. Pl. 6 (1875) 146, 195; Benth. et Hook. Gen. Pl. 3 (1880) 357; Hook. Fl. Br. Ind. 5 (1888) 487; Engl. Nat. Pflanzenf. 3, 1 (1894) 71.—*Uromorus* Bur. DC Prodr. 17 (1873) 236.—*Pseudotrophis* Warb. Bot. Jahrb. 13 (1891) 294; Engl. Nat. Pflanzenf. Nachtr. 1 (1897) 119.—*Teonongia* Stapf. Hook. le. Pl. 30 (1911) t. 2947; Gagnep. Fl. Gen. I.-C. 5 (1928) 710, f. 86.—*Dimerocarpus* Gagnep. Bull. Mus. Hist. Nat. Paris 27 (1921) 441; Bull. Soc. Bot. Fr. 70 (1923) 204; Fl. Gen. I.-C. 5 (1928) 704.—*Diplothorax* Gagnep. Bull. Soc. Bot. Fr. 75 (1928) 98; Fl. Gen. I.-C. 5 (1928) 705.—*Chevalierodendron* Leroy, Compt. Rend. Ae. Sei. Paris 227 (1948) 146.—[*Balanostreblus* Kurz = *Sorocea*, vid. Jarrett, J. Arn. Arb. 39 (1958) 107.].

Trees, unarmed or spinous, monoecious or dioecious. Leaves distichous, mostly oblong-elliptic to lanceolate, denticulate or entire, mostly short-petiolate, without glands. Inflorescences axillary, bisexual or unisexual, pedunculate, varying cymose, racemose, spicate, and capitate, or the female flower solitary. Male flower with a pistillode, 3–5 merous, mostly 4–merous; tepals more or less valvate, free or shortly joined; filaments inflexed in bud; anthers small, reniform, extrorse. Female flowers 4–merous; tepals decussate, imbricate, free or more or less joined; ovary superior. Drupe rather large, 5–14 mm. wide, thinly fleshy, often with a thickened fleshy base, dehiscent or not, the thin tepals investing the drupe or not. Seed large, round, invested by the thin membranous endocarp; embryo various. Cystoliths amphigenous, hypergenous, or none, not papillate except sect. *Streblus*; microscopic gland-hairs various; hairs simple, aseptate, smooth except sect. *Streblus*; stomata superficial. Species 22, Asia, Australasia, (Africa ?); 13 in Malaysia.

As reconstituted, this genus represents the existing remains of the Proto-Moraceae with most generalised inflorescence. Vegetatively it has advanced to the applanate foliage with distichous leaves. The inflorescences show every reduction to the spicate condition, and the female to the one-flowered state. The fruit seems to retain traces of dehiscence. Sterile the genus may be confused with some groups of *Ficus*, but the leaves invariably lack glands. *Trophis*, in the Old World, differs not only in flower but in the hypogenous cystoliths. See, also, sect. *Sloetia*.

sect. **Bleekrodea** (Bl.) Corner stat. nov.—*Bleekrodea* Bl.

Unarmed, monoecious. Inflorescence bisexual, composed of 1–2 female flowers surrounded by more or less pedicellate male flowers, solitary. Male flower with 4–5 tepals, gamophyllous in the lower half; pistillode minute, conic. Female perianth utricular, minutely 4-dentate, investing the ovary; style and stigmatic arms long. Drupe with a thinly fleshy base, dehiscent, enclosed in the enlarged utricular perianth; endocarp not or scarcely differentiated. Cotyledons thick, fleshy, unequal, not folded; radicle short. Cystoliths amphigenous, not papillate; microscopic gland-hairs 1–4-celled, cruciate; hairs smooth, often hooked at the tip; epidermal cells undulate-stellate. Species 2, Borneo, Madagascar. Type, *S. insignis* (Bl.) Corner.—The inflorescence recalls *Fatoua*, but in all other respects the section is near sect. *Streblus*.

sect. **Paratrophis** (Bl.) Corner stat. nov.—*Paratrophis* Bl.; *Pseudomorus* (Endl.) Bur.; *Uromorus* Bur.; *Chevalierodendron* Leroy.

Unarmed, dioecious. Male spike unbranched, with a sterile groove; flowers sessile, 4-merous, 4-partite, valvate; pistillode quadrate-columnar. Female spike many to 1-flowered; flowers in 2 rows, sessile. Bracts ovate-lanceolate or peltate-reniform. Drupe without fleshy base, the tepals little enlarged (except *S. perakensis*), indehiscent. Embryo curved; cotyledons equal, foliaceous and conduplicate to small and flat, not much thickened; radicle rather long, incumbent. Cystoliths hypergenous or none, not papillate; microscopic gland-hairs various; hairs smooth; epidermal cells generally polygonal (subundulate in *S. solomonensis*); hypodermis none or 1-celled (*S. glaber*, *S. perakensis*, *S. urophyllus*). Species 9, Asia, Australasia. Type, *S. heterophyllus* (Bl.) Corner.

sect. **Phyllochlamys** (Bur.) Corner stat. nov.—*Phyllochlamys* Bur.

Twigs spinous. Dioecious. Male inflorescence capitate or very shortly racemose, without interfloral bracts; flowers pedicellate, 4-merous, tepals gamophyllous in the lower half; pistillode quadrate-columnar. Female flower solitary. Drupe with thick fleshy base, ? dehiscent, much exceeded by the enlarged foliaceous tepals. Cotyledons thick, fleshy, subequal; radicle short. Cystoliths hypergenous, not papillate, or also scattered on the lower side of the lamina along the veins; gland-hairs ?; prismatic crystals abundant in the sheath of the veins; epidermal cells mainly polygonal; hypodermis 1-celled. Species 1, Asia, *S. taxoides* (Heyne) Kurz.—This section is very close to sect. *Pseudotrophis* and *Taxotrophis*.

sect. **Pseudostreblus** (Bur.) Corner stat. nov.—*Pseudostreblus* Bur.

Unarmed. Monoecious. Male inflorescence subspicate, branched, with a sterile groove; flowers sessile to shortly pedicellate, 5-merous; tepals free, imbricate; pistillode minute, conic. Female flower solitary, pedunculate; tepals 4. Drupe not thickened at the base, ? indehiscent, invested by the much enlarged tepals. Embryo curved; cotyledons fleshy, unequal; radicle short. Cystoliths none; microscopic gland-hairs clavate, multicellular; hairs smooth, microscopic; epidermal cells undulate; hypodermis none. Species 1, Asiatic mainland, Hainan; *S. indicus* (Bur.) Corner.

sect. **Pseudotrophis** (Warb.) Corner stat. nov.—*Pseudotrophis* Warb.; *Dimerocarpus* Gagnep.

Unarmed or with spinous twigs. Dioecious. Male inflorescence spicate, unbranched, with a sterile groove; bracts ovate-lanceolate to peltate-reniform; flowers sessile, 4-merous; pistillode quadrate-columnar. Female inflorescences racemose, 8-1-flowered; flowers more or less pedicellate. Drupe with thick fleshy base, dehiscent, more or less covered by the enlarged tepals. Embryo curved;

cotyledons thick, fleshy, unequal, the smaller spatulate or cylindrical and surrounded by the large; radicle short. Cystoliths amphigenous, not papillate; microscopic gland-hairs 1-many celled, capitate; hairs smooth; epidermal cells polygonal to undulate; hypodermis 1-celled. Species 3, Asia. Type, *Pseudotrophis laxiflora* Warb. = *S. ilicifolius* (Vidal) Corner.

sect. **Sloetia** (Teysm. et Binn.) Corner stat. nov.—*Sloetia* Teysm. et Binn.

Unarmed. Monoecious. Inflorescences spicate, bisexual or male, with a sterile groove. Male flowers sessile, many, trimerous; pistillode minute, spicate. Female flowers 0–4 per spike, 4-merous. Drupe with thick fleshy base, dehiscent, more or less covered by the enlarged tepals. Cotyledons fleshy, generally very unequal, but varying equal; radicle very short. Cystoliths amphigenous, small, not papillate; microscopic gland-hairs 4–8-celled, cruciate to capitate-peltate; hairs smooth; upper epidermal cells polygonal; hypodermis none. Species 1, Malaya, Sumatra; *S. elongatus* (Miq.) Corner.

sect. **Streblus**.—*Achymus* Vahl (*Achimus* Poir.); *Albrandia* Gaud. (*Albradia* D. Dietr.); *Calius* Blanco; *Epicarpurus* Bl.; *Teonongia* Stapf; *Diplothorax* Gagnep.

Unarmed. Monoecious or dioecious. Inflorescence bisexual and capitate with a central sessile female flower surrounded by males, or unisexual with the male capitate and the female as a solitary pedunculate flower. Male inflorescence with few small bracts surrounding the capitulum, not between the flowers; tepals 4–5, free or shortly joined; stamens 4 (–2); pistillode small, subconic, columnar to quadrate, with 2 minute stigmata. Female flower with 1–2 minute bracts at the base of the peduncle, sometimes one on the peduncle, and 2 larger bracteoles at the base of the perianth; tepals 4, free; style short, with 2 long stigmatic arms. Drupe dehiscent or not, enclosed at first in the enlarged tepals, without fleshy base. Embryo curved; cotyledons thick, fleshy, equal to very unequal; radicle short, incumbent. Cystoliths amphigenous, papillate as the hairs; microscopic gland-hairs 1–4-celled, capitate; no crystal-cells in the epidermis; epidermal cells undulate-stellate. Species 2, South-east Asia; type, *S. asper* Lour.

sect. **Taxotrophis** (Bl.) Corner stat. nov.—*Taxotrophis* Bl.; *Diplocos* Bur.; *Pseudotrophis* Warb.

Twigs spinous. Dioecious. Male inflorescence racemose, unbranched, without a sterile groove; bracts ovate-lanceolate; flowers 4-merous, pedicellate, often unevenly spaced; pistillode quadrate-columnar. Female inflorescence shortly racemose, few-flowered to 1-flowered. Drupe without a fleshy base. Cotyledons subequal, folded, radicle long; or cotyledons fleshy, unequal, radicle short. Cystoliths ? Species 3, Asia. Type, *S. spinosus* (Bl.) Corner = *Taxotrophis javanica* Bl.

Key to the sections of *Streblus*

- 1. Inflorescence cymose, often condensed, bisexual, with 1-2 protogynous female flowers in the centre; or the male inflorescence capitate (without a sterile groove) and the female flower solitary. Cotyledons very unequal, one strongly thickened or both fleshy and equal; radicle short.
- 2. Spinous tree. Fruiting tepals much exceeding the drupe with fleshy base. Male inflorescence capitate; pistillode quadrate-cylindric. Female flower solitary. Dioecious. Ceylon to Timor
Phyllochlamys.
- 2. Unarmed. Fruiting tepals equal to or shorter than the drupe.
 - 3. Female perianth with free tepals. Inflorescence bisexual or the male capitate and the female flower solitary; pistillode conic to columnar. Monoecious or dioecious. Ceylon to Celebes *Streblus*.
 - 3. Female perianth utricular, covering the drupe but free. Inflorescence bisexual. Pistillode minute conic. Madagascar, Borneo
Bleekrodea.
- 1. Male inflorescence elongate-racemose, simple or branched, or spicate. Female flowers spicate or solitary.
 - 4. Male inflorescence branched racemose-spicate, with a sterile groove; flowers 5-merous; pistillode minute conic. Female flower solitary, 4-merous; tepals covering the large drupe. Cotyledons unequal, fleshy. Monoecious, unarmed. India, China, Thailand
Pseudostreblus.
 - 4. Male inflorescence unbranched; flowers 4-merous or 3-merous.
 - 5. Spike bisexual with a sterile groove; male flower 3-merous; pistillode minute conic; female flower 4-merous. Drupc dehiscent with fleshy base, covered by the tepals. Cotyledons equal, fleshy, or one much reduced. Unarmed. Malaya, Riouw, Sumatra
Sloetia.
(Male flower 4-merous. East Africa *Sloetiopsis*).
 - 5. Spikes unisexual, dioecious. Flowers 4-merous. Pistillode quadrate-columnar.
 - 6. Male and female flowers pedicellate, the racemes without a sterile groove. Spinous. Ceylon to Flores *Taxotrophis*.
 - 6. Male flowers sessile, the male spike with a sterile groove.
 - 7. Female flowers more or less pedicellate. Drupc fleshy at the base, dehiscent, more or less covered by the enlarged tepals. Cotyledons thick, unequal, one large and fleshy. Spinous or not. India to Molucca Isl. *Pseudotrophis*.
 - 7. Female flowers sessile, more or less distichous, or solitary and pedunculate. Drupc not fleshy at the base, ? indehiscent, mostly not covered by the tepals. Cotyledons various. Unarmed. Malaysia, Australasia *Paratrophis*.
(West Africa; pistillode minute, spicate .. *Neosloetiopsis*).

Streblus sect. *Bleekrodea*

Key to the Species

- Male flowers pedicellate, rather laxly clustered, equal to or exceeding the female flower and fruit. Radicle very short. Stipules indurate, persistent. Lamina 8-21 × 3-8 cm. Borneo *S. insignis*.
- Male flowers subsessile, in clusters shorter than the female flower and fruit. Radicle shortly elongate, incumbent on the smaller cotyledon. Lamina generally small. Varying deciduous. Madagascar
S. madagascariensis.

S. insignis (Bl.) Corner comb. nov.—*Bleekrodea insignis* Bl. Mus. Bot. Lugd. Bat. 2 (1856) 88, t.28. Type, Korthals, G. Sakoembang, Borneo, at Leiden.

- S. madagascariensis** (Bl.) Corner comb. nov.—*Bleekrodea madagascariensis* Bl. id. 88; Leandri, Fl. Madagasc. fam 55 (1952) 5.

Streblus sect. Paratrophis

Key to the Species

1. Bracts reniform or peltate. Male inflorescences often long, female often many-flowered, never 1-flowered. Lamina more or less membranous, usually without hypodermis. Micronesia, Melanesia, Polynesia.
 2. Cotyledons flat, rather small; radicle incumbent. Lamina often scabrid, the basal nerves often as long as the lateral; cystoliths none. Male spike 2–18 cm. long; female 5–22 mm. long, 2–9-flowered. Monoecious or dioecious *S. pendulinus*.
 2. Cotyledons foliaceous, conduplicate, the radicle incumbent in the sinus of the cotyledons. Lamina smooth, basal nerves shorter than the lateral.
 3. Male spikes 1–5 cm. long; female 6–25 mm. long, 3–8-flowered. Drupe 4 mm. wide, red. Leaves often small; cystoliths abundant on the upper side. New Zealand *S. heterophyllus*.
 3. Male and female spikes longer, many-flowered. Lamina often with 1–3 intercostals; cystoliths none.
 4. Male and female spikes 10–20 cm. long. Lamina 9–30 × 3–15 cm.; lateral nerves 7–14 pairs; petiole 15–65 mm. *S. anthropophagorum*.
 4. Spikes –10 cm. long. Lamina 8–20 × 3–10 cm.; petiole 10–20 mm.
 5. Stigmatic arms very short. Lateral nerves 8–11 pairs *S. solomonensis*.
 5. Stigmatic arms –1.5 mm. long, distinct.
 6. Lateral nerves 10–15 pairs. Drupe black *S. tahitensis*.
 6. Lateral nerves 6–8 pairs. Drupe red *S. smithii*.
 1. Bracts ovate-lanceolate, sessile. Male and female spikes 10–25 mm. long, often few-flowered, or the female flower solitary. Lamina narrowly elliptic to lanceolate, mostly thinly coriaceous and with a hypodermis (1-cell thick); petiole 2–12 mm.; intercostals none.
 7. Fruiting tepals much enlarged, covering the drupe; stigmata very short. Male spike –10 mm. long. Female flower solitary. Cotyledons somewhat thickened, conduplicate; radicle rather short. Cystoliths hypergenous, sparse, or none. Prismatic crystals in the lower spider-mis along the veins. Malaya *S. perakensis*.
 7. Fruiting tepals scarcely enlarged, not concealing the drupe. Male spike 10–25 mm. long. Female spike 1–9-flowered. Cotyledons flat, not conduplicate; radicle rather long, incumbent. Cystoliths none. Small sphaerocrystals in the lower epidermal cells.
 8. Lamina dentate, shortly acuminate, often stiffly coriaceous; lateral nerves 6–13 pairs. Male flowers 3–7 per spike, 2.5–3.5 mm. wide in bud, subglomerate. New Guinea *S. urophyllus*.
 8. Lamina entire or crenulate, rather long attenuate or acuminate or caudate; lateral nerves 9–18 pairs. Male flowers often numerous, smaller, not glomerate. Malaya to New Guinea and Queensland *S. glaber*.
- S. anthropophagorum** (Seem.) Corner comb. nov.—*Trophis anthropophagorum* Seem. Fl. Vit. (1868) 258, t. 68.—*Uromorus anthropophagorum* (Seem.) Bur. DC Prodr. 17 (1873)

236.—*Paratrophis anthropophagorum* (Seem.) Benth. et Hook. ex Drake 111. Ins. Mar. Pacif. f. 7 (1892) 296.—*P. ostermeyri* Rechinger, *P. viridissima* Rechinger, *P. zahlbruckneri* Rechinger, Fedd. Rep. 5 (1908) 130.

Distr. Fiji, Samoa, Cook Isl., Niuc.

The very long, many-flowered, male and female inflorescences and the large leaves, often with rather long petioles, distinguish this species. In Fiji and Samoa it varies into forms with shorter inflorescences, which seem exactly intermediate with *S. tahitensis*; such are the three species of Rechinger, described from Upolu (Samoa), and not specifically distinct. To this complex belong *S. smithii* and, possibly, *S. solomonensis*. They need field-study. For instance, it is not clear if the long inflorescences and large leaves are borne on saplings, and that they become smaller as the tree grows larger. Does *S. anthropophagorum* become as large a tree, —20 m. high, as *S. solomonensis*?

This group of species suggests a Pacific centre for the genus *Streblus*, whence the species have migrated and, in the Moraceous manner, become smaller in leaf and inflorescence, as they have diverged. The genus has reached Hawaii but not, apparently, the American tropics.

S. glaber (Merr.) Corner comb. nov.—*Gironniera glabra* Merr. Philip. J. Sci. 1 (1906) suppl. 42.—*Paratrophis glabra* (Merr.) v. Steen. J. Bot. 72 (1934) 8.—*Chevalierodendron glabrum* (Merr.) Leroy, Compt. Rend. Ac. Sci. Paris 227 (1948) 146.—*Aphananthes negrosensis* Elmer, Leaflet. Philip. Bot. 2 (1909) 575.—*Pseudostreblus caudatus* Ridley, J. Fed. Mal. St. Mus. 6 (1915) 54.—*Streblus laevifolius* Diels, Bot. Jahrb. 67 (1935) 171.—(*Excoecaria baccifera* Elm. ined., Elmer 22014).

var. **glaber**

Distr. Malaya, Borneo, Philippine Isl., Celebes, New Guinea; mountain forest, 700–2,500 m. alt.

var. **australianus** Corner var. nov.—*Paratrophis australiana* C. T. White, Contr. Arn. Arb. 4 (1933) 15.

Alabastra mascula minora —1 mm. lata, plura. Lamina crenulata.

Distr. Queensland; Kajewski 1378, 1383, Herberton Range.

In leaf, inflorescence, and fruit, *S. glaber* is the most attenuate species of the section and it has the widest range.

S. heterophyllus (Bl.) Corner comb. nov.—*Epicarpurus microphyllus* Raoul, Ann. Sci. Nat. ser. 3, 2 (1844) 117.—*Taxotrophis microphylla* (Raoul) F.v.M. Fragm. Phyt. Austral. 6 (1868) 193.—*Paratrophis microphylla* (Raoul) Cockayne, Bot. Notes Kennedy's Bush and Sci. Res. (1915) 3.—*Paratrophis heterophylla* Bl. Mus. Bot. Lugd. Bat. 2 (1856) 81.

var. **heterophylla**

Male spikes -25 mm. long; female spikes 6-12 mm. long, 3-8-flowered. Drupes 1 (-3) per spike, 4 mm. wide. Lamina small, -35 mm. long, the juvenile lamina pinnatifid to serrate.

Distr. New Zealand.

var. **elliptica** Kirk.—*Paratrophis heterophylla* Bl. var. *elliptica* Kirk, Tr. N.Z. Inst. 29 (1897) 500, t. 46.—*Trophis opaca* Banks et Sol. ex Hook. f. Fl. Nov. Zel. 1 (1853) 224.—*P. banksii* Cheeseman, Man. N. Zeal. Fl. (1906) 633.—*P. opaca* Druce, Rep. Bot. Exch. Cl. Br. Isles (1916-17) 639.

Male spikes -5 cm. long; female spikes -25 mm. long, 8-25-flowered. Drupes several per spike, -6 mm. wide. Lamina -8.5 cm. long, crenate-dentate.

Distr. New Zealand.

That this is only a variety of *S. heterophyllus* is shown by the hybrids recorded by Allen as \times *Paratrophis micropaca* (Genetica 9, 1927, 145; id. 7, 1925, 290, f.3).

The combination *S. microphyllus* is antedated by Kurz's synonym of *S. taxoides*.

S. pendulinus (Endl.) F.v.M. Fragm. Phyt. Austral. 6 (1868) 192.—*Morus pendulina* Endl. Prodr. Fl. Norf. (1833) 40.—*M. brunoniana* Endl. Atakta Bot. (1835) t. 32.—*Streblus brunonianus* (Endl.) F. v. M. l.c. (1868) 192.—*Pseudomorus brunoniana* (Endl.) Bur. Ann. Sci. Nat. ser. 5, 11 (1869) 373.—*Pseudomorus sandwicensis* Degener, Fl. Hawaii. (1938) 21/22.—*Ps. brunoniana* (Endl.) Bur. var. *australiana* Bur., v. *obtusata* Bur., v. *pendulina* (Endl.) Bur., v. *scabra* Bur. l.c. (1869) 373.—*Ps. brunoniana* v. *sandwicensis* (Degener) Skottsberg, Act. Hort. Gotob. 15 (1944) 347.—*Ps. pendulina* (Endl.) Stearn, J. Arn. Arb. 28 (1947) 427.

This is a variable plant. When young, it has large leaves with 10-16 pairs of lateral nerves. Larger trees have smaller leaves with 7-12 pairs of lateral nerves. The larger leaves are ovate-elliptic to ovate-oblong; the smaller are elliptic to elliptic-lanceolate and less toothed. I doubt if the three or four varieties which have been made are more than such differences in growth, though some collections have scabrid leaves. Almost identical differences occur in *Malaisia scandens* and are not to be distinguished in the field. Of *S. pendulinus* I have seen 33 collections from the whole range of the species and have been unable to draw any sharp line. Leaves typical of *P. sandwicensis* occur on collections from Micronesia and the side-twigs of these have the leaves of var. *australiana*; collections from Queensland may have the subacute leaves of v. *obtusata* (New Caledonia). There is no sectional distinction between *Pseudomorus* and *Paratrophis*.

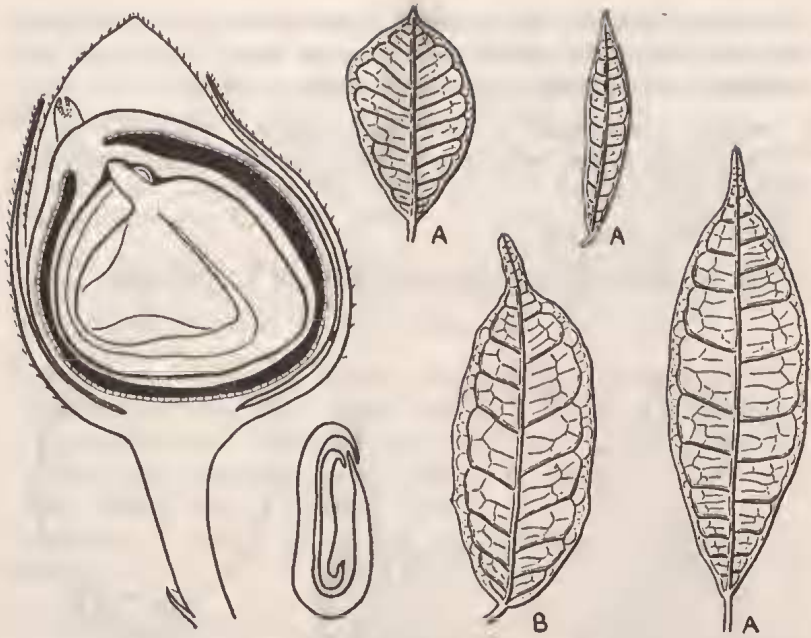


Fig. 11. *Streblus perakensis* Corner. Leaves, $\times \frac{1}{2}$; A, coll. Forest Ranger s.n., Chikus, 1933; B, Ridley 16171. Fruit and embryo in section, $\times 6$; coll. For. Dept. 27338.

S. perakensis Corner sp. nov. Fig. 11.

Arbor parva glabra inermis, foliis distichis. Ramuli 1–1.5 mm. crassi, fusco-brunnei. Stipulac 1.3–3.5 mm. longae, caducae. Lamina 2.5–12 \times 0.7–4 cm., anguste elliptica v. lanceolata v. suboblongata, ad apicem mucronatum attenuata v. acuminata, ad basim anguste cuneata v. anguste rotundata, integra v. subdenticulata, coriacea, laevis, sicco brunnea; costis lateralibus utrinsecus 8–15, patentibus, subtus elevatis, inarcuratis, intercostis nullis; costis basalibus brevibus; petiolo 2–7 mm. longo. Inflorescentia mascula axillaris 1–3, immatura –5 mm. longa, breviter pedunculata, uno latere sterilis, flores c. 6 sessiles secundos gerens; bracteis 1 mm. longis, ovatis, obtusis; tepalis 4, extus puberulis; staminibus 4; pistillodio minuto, 4-angulato. Flos femineus solitarius, breviter pedunculatus. Drupa c. 7 mm. lata, tepalis decussatis ovato-subacutis puberulis duobus externis brevioribus obiecta; pedunculo 4–9 mm. longo, bracteis 1–2 parvis basim versus praedito; tepalis externis 5–7.5 mm. longis, internis 8–10 mm.; stylo nullo v. brevissimo; stigmatibus 2 subulatis 0.7 mm. longis; endocarpio tenuissimo subsclerotico. Embryon curvatum; radícula brevi recta; cotyledonibus inaequalibus, minori a majori implicato. Cystolitha nulla v. pauca hypergena.

Distr. Malaya (Perak, Pahang); For. Dept. 27338 (Chikus Forest Res., leg C. L. Carrier, fructu; typus, herb. Singapore); Forest Ranger s.n., Chikus Forest Res. March 1933, *lelimau*, floribus masculis; Ridley 16171, Kuala Tcku.

S. crenato armato comparanda, differt costis lateralibus pluribus, stylo subnullo, drupa basim versus haud incrassata, cotyledonibus subaequalibus, cystolithis nullis v. sparsis.

S. smithii (Cheeseman) Corner comb. nov.—*Paratrophis smithii* Cheeseman Trans. N.Z. Inst. 20 (1888) 148; Man. New Zeal. Fl. (1906) 631.

Distr. New Zealand.

This is near to *S. anthropophagorum* and *S. tahitensis*.

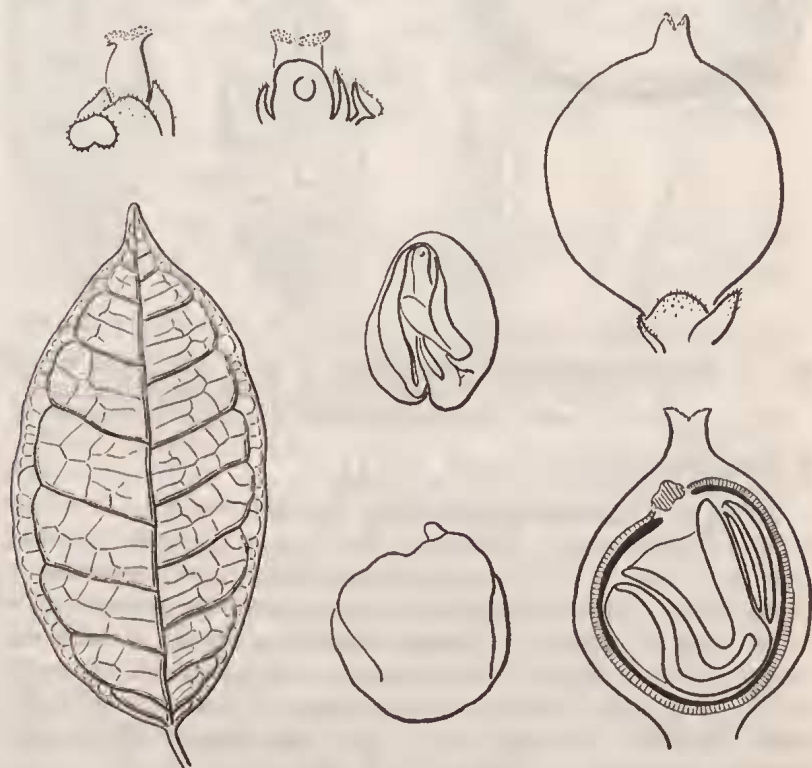


Fig. 12. *Streblus solomonensis* Corner. Leaf, $\times 1$. Flower, $\times 6$. Fruit and embryo, $\times 4$. Coll. Kajewski 2396.

S. solomonensis Corner sp. nov. Fig. 44.

Arbor 20 m. alta, glabra, foliis distichis. Ramuli 1.5–2 mm. crassi, fusco-olivacei dein pallide ochracei. Stipulae –6 mm. longae, caducae. Lamina 8–12 \times 3–9 cm., elliptica, saepe subsymmetrica, apice –14 mm. longo acuminata, basi cuneata, integra, membranacea, laevis, sicco griseo-viridis; costis lateralibus utrinsecus 8–11, subtus vix elevatis; intercostis 1–3 laxis; costis basilibus brevibus; petiolo 10–20 mm. longo. Inflorescentia mascula? Inflorescentia feminea –15 mm. longa, in fructu –5 cm. longa, axillaris 1–2, floribus sessilibus distichis; pedunculo 2–6 mm. longo; bracteis 0.5–0.7 mm. longis, reniformibus subpeltatis, minute fimbriatis, inferioribus multis sterilibus; tepalis 4 decussatis, 1 mm. longis, ovatis subacutis v. obtusis; stylo brevissimo;

stigmatibus 2, 0.5 mm. longis. Drupae 3–5 per infructescentiam, 7–8 mm. latae, tepalis vix amplificatis 1.5 mm. longis; endocarpio ligneo tenui. Embryon curvatum; radícula recta longa; cotyledonibus subaequalibus, plicatis. Cystolitha nulla.

Distr. Bougainville Isl., Guadalcanal Isl.; Kajewski 2006, Bougainville Isl., Koniguru, Buin, 800 m. alt., *keru*; Kajewski 2396, Guadalcanal Isl., Berande River, *torgapbagi* (typus, herb. Kew).

This is said to be a common tree in rain-forest, the young leaves being cooked and eaten, the timber used for houses. The extremely short style and stigmatic arms distinguish it.

S. tahitensis (Nadeaud) Corner comb. nov.—*Uromorus tahitensis* (Nadeaud) Bur. DC Prodr. 17 (1873) 237.—*Pseudomorus brunoniana* var. *tahitensis* Nadeaud, En. Pl. Tahiti, p. 43.—*Paratrophis tahitensis* (Bur.) Benth. et Hook. ex Drake, II1. Ins. Mar. Pacif. f. 7 (1892) 296.

Possibly a variety of *S. anthropophagorum*. I have seen no material.

S. urophyllus Diels, Bot. Jahrb. 67 (1935) 172.

var. **urophyllus**

Distr. New Guinea, 2,400–3,000 m. alt.

Closely allied with *S. glaber* and perhaps a high mountain state of it.

var. **salicifolius** Corner v. nov.

Frutex 3 m. altus. Lamina 5–14 × 0.6–1.5 cm., oblongo-lanceolata, acuta v. subacuminata, basi cuneata, denticulata v. integra, coriacea; costis lateralibus utrinsecus 18–25 rectangulatis; petiolo 3–7 mm. longo.

Distr. New Guinea; L. J. Brass 30220, Terr. New Guinea, Eastern Highlands, Mt. Wilhelm, east slopes, 3,000 m. alt., typus herb. Leiden.

Streblus sect. Phyllochlamys

S. taxoides (Heyne) Kurz, For. Fl. Burm 2 (1877) 465.—*Trophis taxoides* Heyne ap. Roth, Nov. Pl. Ind. Or. (1821) 368.—*T. taxiformis* Spreng. Syst. Veg. 3 (1826) 902.—*T. spinosa* Roxb. Fl. Ind. 3 (1832) 762.—*Epicarpurus timorensis* Decne. Nouw. Ann. Mus. Hist. Nat. 3 (1834) 499, t. 21.—*E. spinosus* (Roxb.) Wight, Ic. Ind. 6 (1835) 7, t. 1962 (partim).—*Taxotrophis roxburghii* Bl. Mus. Bot. Lugd. Bat. 2 (1856) 78.—*Phyllochlamys spinosa* (Roxb.) Bur. DC Prodr. 17 (1873) 218.—*Streblus microphyllus* Kurz, Prel. Rep. For. Pegu (1875) App. A, p. cxviii; App. B, p. 84 (in clavi); For. Fl. Burm 2 (1877) 464 (in clavi).—*S. taxoides* (Heyne) Kurz var. *microphylla* Kurz, For. Fl. Burm. 2 (1877) 465.—*Phyllochlamys wallichii* King, Hook. Fl. Br. Ind. 5 (1888) 489.—*P. taxoides* (Heyne) Kds.

Exkursiofl. Java 2 (1912) 89.—*P. taxoides* var. *parvifolia* Merr. Philip. J. Sci. 17 (1920) 247.—*P. tridentata* Gagnep. Fl. Gen. I.-C. 5 (1928) 714.—*Taxotrophis poilanei* Gagnep. id. 701.

Distr. Ceylon, India, Indochina, Thailand, Hainan, Malaya, Java, Lesser Sunda Isl. to Timor, Celebes (S.E.), Mindoro, Palawan.

I am indebted to Dr. Chew Wee Lek for the synonymy of this species.

Streblus sect. Pseudostreblus

S. indicus (Bur.) Corner comb. nov.—*Pseudostreblus indicus* Bur. DC Prodr. 17 (1873) 219.

Distr. Khasia Mts., North Thailand, Yunnan, Kwangsi-Kwangtung border, Hainan.

This seems a local or rare plant. I have seen merely six collections:—Hook. f. et Thompson (*Epicarpurus* 8), Kerr 6453, Sino-Soviet Exp. (1957) 8137 (Yunnan), F. C. How 43790 and 73223 (Hainan), and W. T. Tsang 22641 (Kwangsi). The last collection gives "fairly common in dry soil; fruit yellow".

Streblus sect. Pseudotrophis

Key to the Species

1. Unarmed. Lamina membranous-chartaceous, acuminate, with 1–6 intercostals. Male spike 40–140 mm. long. Cotyledons somewhat unequal. Twigs and lamina often drying yellowish. Cystoliths amphigenous; no crystal cells in epidermis *S. macrophyllus*.
1. Spinous. Lamina coriaceous, acute or attenuate. Male spike shorter. Cotyledons very unequal, the inner not folded.
 2. Male spike 10–50 mm. long; female 2–6-flowered; bracts reniform. Lamina 6–20 × 3.5–10 cm., often spinous-dentate. Cystoliths hypergenous; single prismatic crystals abundant in the upper epidermal cells and along the veins beneath *S. ilicifolius*.
 2. Male spike 5–10 mm. long; female flower solitary; bracts ovate. Lamina 3–9 × 1–4 cm., acute, crenate-denticulate, base rounded to cordate. Cystoliths amphigenous; crystal cells none in epidermis *S. crenatus*.

(Unarmed. Leaf-base cuncate. Drupe-base not thickened. Cystoliths none or few and hypergenous; crystal-cells along the veins on the underside of the leaf *S. perakensis*).

S. crenatus (Gagnep.) Corner comb. nov.—*Taxotrophis crenata* Gagnep. Fl. Gen. I.-C. 5 (1928) 702, f. 82.

Distr. Indochina (Cambodia, Laos, Cochinchina).

This comes very near to *S. taxoides*, but the male spike, though very short, has a sterile groove and the fruiting tepals are not larger than the drupc. Nevertheless it seems impossible to distinguish sterile plants and those with young female flowers.

S. ilicifolius (Vidal) Corner comb. nov.—*Taxotrophis ilicifolius* Vidal, Rev. Pl. Vasc. Filip. (1886) 249.—*Pseudotrophis laxiflora* Warb. Bot. Jahrb. 13 (1891) 294.—*Taxotrophis obtusa* Elmer, Leafl. Philip. Bot. 5 (1913) 1813.—*T. triapiculata* Gamble, Kew Bull. (1913) 188.

Distr. Chittagong, Burma, Indochina, Thailand, Hainan, Malaya, Philippine Isl., Celebes, Molucca Isl., Key Isl., Timor.

I am indebted to Dr. Chew Wee Lek for this synonymy. I have also seen the type of *P. laxiflora* Warb., loaned from Berlin; it is the more easterly state of *S. ilicifolius* with few or no spinous leaf-teeth.

S. macrophyllus Bl. Mus. Bot. Lugd. Bat. 2 (1856) 80.—*Diplocos* ? *macrophyllus* (Bl.) Bur. DC Prodr. 17 (1873) 216.—*Paratrophis mindanaensis* Warb. Perk. Fr. Fl. Philip. 1 (1904) 165.—*P. caudata* Merr. Philip. J. Sci. 1 (1906) Suppl. 183.—*Taxotrophis mindanaensis* Elm. Leafl. Philip. Bot. 5 (1913) 1815.—*T. balansae* Hutch. Kew Bull. (1918) 151.—*Dimerocarpus brenieri* Gagnep. Bull. Mus. Hist. Nat. Paris 27 (1921) 441.

Distr. Indochina, Malaya, Borneo, Celebes, Philippine Isl.

The types have been studied by Dr. Chew Wee Lek and myself. The species has been reduced erroneously to *S. ilicifolius*.

Streblus sect. Sloetia

S. elongatus (Miq.) Corner comb. nov. *Artocarpus elongatus* Miq. Fl. Ind. Bat. Suppl. (1861) 172, 419.—*Sloetia sideroxylon* Teysm. et Binn. ex Kurz, J. Linn. Soc. Bot. 8 (1864) 168, t. 13.—*Sl. pinangeana* D. Oliver, Hook. Ic. Pl. (1886) t. 1531.—*Sl. wallichii* King, Hook. Fl. Br. Ind. 5 (1888) 493.

Distr. Malaya (Penang to Singapore), Riouw Archipelago, Sumatra.

This well-known timber-tree of Malaya is strangely limited in distribution and seems not to occur in Borneo. Its affinities are also strange. The bisexual spicate inflorescence with few female flowers is repeated only in the insufficiently known *Sloetiopsis* of East Africa (4-merous male flowers; fruit unknown). If the male and female flowers were on different inflorescences *S. elongatus* would agree with sect. *Pseudotrophis*, as *S. macrophyllus*, except for the minute conic pistillode and the 3-merous male flowers. *Neosloetiopsis* (West Africa), also insufficiently known, may represent this dioecious state, but it may be allied rather with *Ampalis*. On the other hand, if the bisexual spike were contracted into a head, the affinity would be with sect. *Bleekrodea*, except for the perianth. Then, again, if the bisexual spike were extended into a branched raceme, sect. *Sloetia* would be the antecedent condition to sect. *Pseudostreblus*. Thus, this timber-tree is not a unique monotypic genus but a central species in the complex of *Streblus*.

Streblus sect. Streblus

Key to the Species

1. Lamina smooth, membranous, lanceolate-acuminate, base attenuate. Monoecious, the male inflorescence with or without a female flower. Male flowers with 4–5 tepals and stamens; pistillode quadrate. Female tepals 3–4 mm. long (anthesis), ? the fruiting tepals not reflexed; stigmatic arms 3–4 mm. long. Drupe dehiscent
S. tonkinensis.
1. Lamina typically rough, chartaceous-coriaceous, attenuate at the apex, often narrowly rounded-cuneate at the base. Tepals 4. Pistillode columnar, not quadrate, with 2 minute stigmata. Female tepals 2 mm. long (anthesis), reflexed in fruit; stigmatic arms lengthening 6–12 mm. in fruit. Drupe indehiscent Cotyledons very unequal . . . *S. asper*.
2. Dioecious, rarely monoecious. Male head without a female flower; stamens 4 v. *asper*.
2. Monoecious. Male head often with a female flower in the centre. Stamens 2 v. *monoica*.

S. asper Lour. var. *asper*.—*Diplothorax tonkinensis* Gagnep. Bull. Soc. Bot. Fr. 75 (1928) 98.

Distr. Ceylon, India, South China, Hainan, Indochina, Thailand, Malaya (north), Sumatra (north), Java, Bali, Lombok, Sumbawa, Celebes, Philippine Isl.

This species is absent from the Riouw-pocket of south Malaya, south Sumatra, and, apparently, all of Borneo. I do not give the full synonymy which is well-known. The type of *D. tonkinensis* consists of a twig with male inflorescences and another with female. The female perianth consists of four tepals, and is not utriculate as Gagnepain described.

var. *monoica* (Gagnep.) Corner stat. nov.—*Streblus monoicus* Gagnep. Lec. Not. Syst. 14 (1950) 36.

This is intermediate with *S. tonkinensis* and comes from the same region (Laos, Xieng-Kouang; Spire 176 and 200).

S. tonkinensis (Dub. et Eberh.) Corner comb. nov.—*Bleekrodea tonkinensis* Dub. et Eberh. Compt. Rend. Ac. Sci. Paris 114 (1907) 631; Bull. Econ. Indoch. 10, 868–870 (ut *Streblus* sp.); id, 13, 175 (ut *Bleekrodea*).—*Teonongia tonkinensis* (Dub. et Eberh.) Stapf Hook. Ic. Pl. 30 (1911) t. 2947; Gagnep. Fl. Gen. I.-C. 5 (1928) 710, f. 86.

Distr. Tonkin, along the Chinese frontier and in Ninh-Binh and Hoa-Binh south of the Red River.

This is very like *S. asper*, with which Gagnepain partly confused it. Indeed, in view of *S. asper* v. *monoica*, it is not clear how distinct *S. tonkinensis* may be. The joining of the inner tepals of the female flower is more marked than in *S. asper*, but not a specific difference.

Streblus sect. **Taxotrophis**

Key to the Species

1. Female spike 2-6-flowered; style 0.5-1 mm. long, the stigmatic arms 2 mm. long. Bracts ovate. Fruiting tepals generally enlarged. Embryo with long radicle and subequal, folded cotyledons. Lateral nerves 6-9 pairs *S. zeylanicus*.
1. Female flower solitary. Radicle short, the cotyledons very unequal.
 2. Bracts ovate. Style 3-4 mm. long, the stigmatic arms 1-2 mm. Fruiting tepals not or little enlarged. Lamina drying yellow-brown; lateral nerves 6-10 (-12) pairs *S. spinosus*.
 2. Bracts peltate. Style very short, the stigmatic arms 1 mm. long. Fruiting tepals enlarged. Lamina often with spinous teeth; lateral nerves 10-14 pairs *S. laxiflorus*.

S. laxiflorus (Hutch.) Corner comb. nov.—*Taxotrophis laxiflora* Hutch. Kew Bull (1918) 151.—*T. eberhardtii* Gagnep. Fl. Gen. I.-C. 5 (1928) 700.

Distr. Indochina, Malaya (Perlis, Kedah, Penang, Perak).

Examination of the type of *T. eberhardtii* by Dr. Chew Wee Lek showed that it differed in no way from *T. laxiflora*. Whether the pistillode is 3-lobed, 4-lobed, or practically entire, though emphasized by Gagnepain, is immaterial.

S. spinosus (Bl.) Corner comb. nov.—*Urtica spinosa* Bl. Bijdr. (1825) 507.—*Taxotrophis javanica* Bl. Mus. Bot. Lugd. Bat. 2 (1856) 77, t. 26.—*T. spinosa* (Bl.) v. Steen. Backer Bekn. Fl. Java 6 (1948) 9.

Distr. Sumatra, Java, Lesser Sunda Isl. to Timor.

S. zeylanicus (Thw.) Kurz, For. Fl. Burm. 2 (1877) 464.—*Epicarpurus zeylanicus* Thw. Kew J. 4 (1852) 1; id. 3 (1851) t. 11. *Taxotrophis zeylanica* Thw. En. Pl. Ceyl. (1864) 264.—*Diplocos zeylanica* (Thw.) Bur. DC Prodr. 17 (1873) 215.—*Taxotrophis caudata* Hutch. Kew Bull. (1918) 149.

Distr. Ceylon, India, Burma, China, Indochina.

I am indebted to Dr. Chew Wee Lek for the synonymy of this species, which he has checked from the types.

Species Incertae Sedis

S. mitis Kurz, For. Fl. Burm. 2 (1877) 464; Hook. Fl. Br. Ind. 5 (1888) 489.

Unknown to Hooker, who wrote "probably not a *Streblus*". I have seen no specimen.

Trophis P. Br.

Nat. Hist. Jamaica (1756) 357; Linn. Syst. Nat. ed. 10 (1759) 1289; Sp. Pl. ed. 3, 2 (1764) 1451; Trécul, Ann. Sci. Nat. ser. 3, 8 (1847) 146; Bur. DC Prodr. 17 (1873) 251; Baill. Hist. Pl. 6 (1875) 143, 192; Benth. et Hook. Gen. Pl. 3 (1880) 365; Engl. Nat. Pflanzenf. 3, 1 (1894) 73; Engler, Bot. Jahrb. 40 (1908) 543, f.1; Woodson and Schery, Ann. Mo. Bot. Gdn. 47 (1960) 119, f. 37; (*nomen conservandum*).—*Bucephalon* L. Sp. Pl. (1753) 1190; ed. 3, 2 (1764) 1661; (*nomen rejiciendum*).—*Maillardia* Frapp. et Duch. in Maillard, Notes sur l'île Réunion (1863) annexe P, 3; Bur. DC Prodr. 17 (1873) 220; Leandri, Fl. Madagasc. fam. 55 (1952) 15.—*Calpidochlamys* Diels, Bot. Jahrb. 67 (1935) 173.—? *Skutchia* Pax et Hoffm. ex Morton, J. Wash. Ac. Sci. 27 (1937) 306.

Trees or shrubs, unarmed, dioecious. Leaves distichous. Stipules paired, small, caducous. Inflorescences axillary, solitary or paired, pedunculate, paniculate, racemose, or spicate and then with a sterile groove; bracts very small. Flowers 4-merous. Male tepals valvate, joined below; filaments inflexed in bud; pistillode quadrate-columnar. Female tepals small, free; ovary inferior, the ovule immersed in the receptacle; style short, with 2 long stigmatic arms. Drupe inferior, the persistent tepals little enlarged, fleshy with chartaceous to ligneous endocarp, indehiscent. Seed rounded to oblong, 5–12 mm. wide, or the endocarp angled. Embryo straight or curved; cotyledons fleshy, not folded, equal or subequal; radicle very short to rather long, incumbent. Species 11, Trop. America (3), Madagascar (5), Malaysia (3). Type; *T. americana* Linn.

subgen. **Prototrophis** Corner subgen. nov.

Inflorescentiae paniculatae v. racemosae, floribus pedicellatis, bracteis minutis. Embryo ?. Typus, *T. mexicana* Bur.

subgen. **Trophis**

Inflorescentiae spicatae, floribus sessilibus, masculae sulco sterili praeditae, bracteis peltatis.

sect. **Trophis**.—Endocarpium chartaceum. Embryon rectum; cotyledonibus crassis, subglobosis, aequalibus; radicula brevissima. Spica feminea floribunda. Stigmata longiuscula, ex integro puberula. Cystolitha amphigena. Typus, *T. americana* L.

sect. **Calpidochlamys** (Diels) Corner stat. nov.;—Endocarpium ligneum, 0.2–0.3 mm. crassum, toro ligneo in loco hili obturatum. Embryon curvatum; cotyledonibus crassiusculis, curvatis, haud plicatis, subaequalibus; radicula longiusecula, incumbenti. Spica feminea pauciflora. Stigmata brevia, unilateraliter papillosa. Cystolitha hypogena. Typus, *T. drupacea* (Diels) Corner. Asia, spp. 3.

sect. **Maillardia** (Frapp. et Duch.) Corner stat. nov.;—Endocarpium ? tenue. Embryon ? curvatum.; cotyledonibus valde inaequalibus, majore plicato, alterum amplectenti; radicula brevissima. Flores feminei solitarii v. binati. Cystolitha hypergena. Madagascar, spp. 4; Reunion, sp. 1.

Key to the species of sect. *Calpidochlamys*

1. Female inflorescence 15–40 mm. long, many-flowered. Endocarp not angled. Lamina acuminate, base cuneate; lateral nerves 9–16 (20) pairs *T. philippinensis*.
1. Female inflorescence 30–70 mm. long, with few fertile flowers. Endocarp 3-angled, pyramidal.
 2. Lamina acuminate, base rounded; lateral nerves 15 pairs
T. drupacea.
 2. Lamina attenuate or subacuminate, base cuneate; lateral nerves 8–10 pairs *T. branderhorstii*.

T. branderhorstii (Diels) Corner comb. nov.—*Calpidochlamys branderhorstii* Diels, Bot. Jahrb. 67 (1935) 173.

Distr. Neth. New Guinea.

Possibly not separable from *T. drupacea*. I have examined the type, Branderhorst 273.

T. drupacea (Diels) Corner comb. nov.—*Calpidochlamys drupacea* Diels, Bot. Jahrb. 67 (1935) 173.

Distr. North-east New Guinea (Sepik-district).

I have found no specimen of this.

T. philippinensis (Bur.) Corner comb. nov.—*Uromorus philippinensis* Bur. DC Prodr. 17 (1873) 237; Vidal Cat. Pl. Prov. Manila (1880) 43.—*Paratrophis philippinensis* (Bur.) F. Vill. Noviss. App. Blanco Fl. Filip. ed. 3 (1880) 198; Vidal, Phan. Cuming. Philip. (1885) 145; Rev. Pl. Vasc. Filip. (1886) 250; Merr. En. Philip. 2 (1923) 36.—*Sloetia minahassae* Kds. N.O. Cel. Versl. (1898) 612, 645; Suppl. 2, t. 5; Suppl. 3, p. 3.—*Paratrophis grandifolia* Elm. Leaflet. Philip. Bot. 5 (1913) 1814; Merr. En. Philip. 2 (1923) 36.

Distr. Philippine Isl. (widespread), Celebes, Flores, Soemba, Halmahera, New Guinea, New Britain.

Artocarpeae R. Br.

Bot. Congo (1818) 454; Gaud. Voy. Freyc. Bot. (1826) 511; Bartl. Ord. Nat. (1830) 104; Endl. Gen. Pl. (1841) 278; Suppl. 1, 1375; Suppl. 4 (1842) 36; Miq. Mart. Fl. Bras. 4, 1 (1852) 79, 81; Bur. DC Prodr. 17 (1873) 281, 284; Baill. Hist. Pl. 6 (1875) 167; Benth. et Hook. 3 (1880) 343, 346.—*Broussonetiaeae* Gaud. Voy. Freyc. Bot. (1826) 508; Bur. DC Prodr. 17 (1873) 221; Benth. et Hook. Gen. Pl. 3 (1880) 345 (subtribus); Engl. Nat. Pflanzenf. 3, 1 (1894) 73; Dalla Torre et Harms, Gen. Siph. (1900) 120.—*Euartocarpeae* Tréc. Ann. Sci. Nat. ser. 3, 8 (1847) 77, 108; Benth. et Hook. Gen. Pl. 3 (1880) 347; Engl. Nat. Pflanzenf. 3, 1 (1894) 80; Dalla Torre et Harms, Gen. Siph. (1900) 121.

Inflorescences unisexual (in a few cases bisexual), monoecious or dioecious. Female inflorescence globose-capitate or thickly spicate, many-flowered, syncarpous or not; involucre of one row of bracts or none; ovaries free or immersed in sockets, or connate with the receptacle. Male inflorescences paniculate, racemose, spicate, or capitate, with or without a sterile groove; stamens 4-1; filaments straight or inflexed in bud; anthers extrorse; pistillode present or not. Seed small or large. Embryos various. Trees, shrubs, climbers, spinous or not. Gen. 15 (Asia 7, Africa 2, America 8); spp. 95 (Asia 68, Africa 7, America 20).

Key to the Asiatic Genera of Artocarpeae

1. Female tepals 4, free (at least in the distal half), well-developed, de-
cussate, imbricating, fleshy in fruit. Bracts and/or tepals with 2-7
immersed yellow glands. Seed compressed, with ligneous endocarp.
Dioecious, often spiny *Maclura*.
1. Female perianth differently constructed, without immersed yellow
glands.
 2. Male inflorescence racemose-spicate, unbranched, with a sterile
groove; filaments inflexed in bud; pistillode present. Female peri-
anth utricular; ovaries not in receptacular loculi; styles long. Em-
bryo curved. Dioecious, unarmed.
 3. Syncarp globose, thickly set with slender stalked bracts of various
shapes more or less covering the drupes. Seeds 2-3 mm. long;
endocarp crustaceous to ligneous. Cotyledons equal, condupli-
cate to plane; radicle long, accumbent. Stipules membranous
Broussonetia.
 3. Syncarp with few strongly projecting drupes each invested by the
utricular perianth, the bracts short. Seed 6-7 mm. long; endo-
carp membranous. Cotyledons very unequal, the large thickly
fleshy and folded. Climber *Malaisia*.
 2. Male inflorescence clavate or capitate; if spicate, then without a
sterile groove and with the filaments straight in bud.
 4. Male flowers 4-merous; filaments inflexed in bud; pistillode pre-
sent. Female perianth reduced to 4 minute teeth; ovaries em-
bedded in sockets of the receptacle; styles long. Embryo curved,
transversely elongate; cotyledons unequal, conduplicate, fleshy;
radicle short. Dioecious spiny climbers *Plecosperrnum*.
 4. Male flowers with 4-1 stamens, the filaments straight in bud; pis-
tillode none. Styles often short. Embryo elongate longitudinally.
Unarmed trees (? *Prainea scandens*).
 5. Dioecious. Male and female heads similar, globose. Perianths
utricular; ovaries superficial. Stamen 1. Drupes projecting
strongly from the syncarp. Embryo straight; cotyledons thick
equal, plane; radicle very short *Prainea*.
 5. Monoecious. Drupes embedded in the more or less fleshy syn-
carp.
 6. Male heads usually of different shape from the female, vary-
ing spicate to clavate or capitate; flowers superficial; stam-
en 1. Female perianth utricular, much reduced, or none;
ovaries sunk in receptacular sockets or concealed beneath
the layer of connate utricular perianths. Embryo straight
or slightly curved; cotyledons thick, equal or unequal; ra-
dicle short *Artocarpus*.
 6. Male and female heads similar, globose, distinctly involucrate
with bracts. Stamens 2-3, sunk like the ovaries in recepta-
cular sockets, the filaments and style projecting between
the free conic or truncate tepals. Embryo curved; radicle
rather long, ascending *Parartocarpus*.

Artocarpus J. R. and G. Forster

Char. Gen (1776) 101, t. 51; Jarrett, J. Arn. Arb. 40 (1959) 113-368; id. 41 (1960) 73-140.

This genus presents the extreme reduction of the male inflorescence as a spike or head of minute unistaminate flowers with tubular perianth and minute anther. The female inflorescence retains a well-developed, if unusual, utricular perianth in subgen. *Artocarpus*, but the perianth disappears more or less entirely in subgen. *Pseudojaca*. The ovaries are superior in subgen. *Artocarpus*, though hidden from the outside by the connate middle parts of the perianths, but they become inferior in sockets of the receptacle in subgen. *Pseudojaca*. The fruiting perianths of subgen. *Artocarpus* become fleshy, at least in their proximal parts surrounding the ovaries, thus making the false aril around the false seed. In subgen. *Pseudojaca* the pulpy character of the fruit is transferred to the receptacular tissue which forms, thus, the whole pulpy body of the false fruit. Ripe syncarps of subgen. *Artocarpus* must be torn open to cut the false aril; those of subgen. *Pseudojaca* can be bitten directly, as an apple. This kind of syncarp resembles that of *Plecosperrnum*, but there are so many differences between it and *Pseudojaca* in other respects that the two must be regarded as parallel conclusions in Moraceous fruits. The state of *Pseudojaca* is presumably derived by simplification from that of *Artocarpus* by loss of the free internal parts of the perianths followed by loss of the free external parts. Detailed developmental studies of these female inflorescences are needed in a variety of species to clarify the exact construction of the syncarps.

Broussonetia L'Herit. ex Vent.

Tabl. Regn. Veg. 3 (1799) 547 (gen. conserv.); Bl. Mus. Bot. Lugd. Bat. 2 (1856) 85; Miq. Fl. Ind. Bat. Suppl. (1861) 415; Bur. DC Prodr. 17 (1873) 223; Baill. Hist. Pl. 6 (1875) 143, 192, f. 102-107; Benth. et Hook. Gen. Pl. 3 (1880) 361; Engl. Nat. Pflanzenf. 3, 1 (1894) 76, f. 54, 55.—*Broussonetia* Ortega, Nov. Pl. Descr. (1798) 61, t. 7.—*Papyrius* Lam. Ill. Gen. Pl. (1798) t. 762.—*Allacanthus* Thw. Hook. J. Bot. Kew Gard. Misc. 6 (1854) 302, t. 9b; Bur. DC Prodr. 17 (1873) 222; Benth. et Hook. Gen. Pl. 3 (1880) 361; Hook. Fl. Br. Ind. 5 (1888) 490; Engl. Nat. Pflanzenf. 3, 1 (1894) 74 (ut *Allacanthus*).—*Smithiodendron* Hu, Sunyatsenia 3 (1936) 106.

Diocious unarmed trees, shrubs, or climbers, often (? always) deciduous. Leaves spirally arranged, opposite, or distichous, palmately lobed to undivided, generally cordate to rounded or widely cuneate at the base, dentate to entire, membranous; intercostals numerous; stipules membranous. Bracts and perianth without immersed yellow glands. Male inflorescence racemose to spicate, with a sterile groove; bracts ovate to clavate, truncate, or umbonate, the interfloral bracts generally stalked, those bordering the sterile groove sessile; flowers shortly pedicellate to sessile;

tepals 4, joined in the lower half, valvate; filaments 4, inflexed in bud; pistillode spicate, minute. Female inflorescence capitate, globose, without a sterile groove; bracts as in the male, becoming stipitate in fruit; perianth utricular with 2-4 small lobes or teeth; ovary sessile or becoming stipitate in fruit (sect. *Broussonetia*); style 1 (-2), long. Syncarp globose, 10-25 mm. wide, the flowers not connate, ripening orange-red, more or less pulpy. Drupes thinly pulpy, invested by the thinly pulpy, yellow to red, perianth. Seeds 1.7-2.5 mm. long, ovoid-compressed, faintly keeled; endocarp crustaceous to ligneous, smooth or asperate. Embryo curved; cotyledons equal, thinly fleshy, conduplicate to flat; radicle long, incumbent. Cystoliths hypergenous, hypogenous, or none, often as cystolith-hairs; microscopic gland-hairs 1-3-celled, rather large, capitate; hairs smooth or papillate, often hooked (especially microscopic hairs); sphaero-crystal-cells in the lower epidermis along the veins, or none. Species ? 7.

sect *Broussonetia*

Drupe stipitate within the sessile perianth. Seed slightly compressed, papillate-asperate, crustaceous, the keel double at the base. Cotyledons flat. Cystoliths hypergenous or none. Leaves spirally arranged to distichous. Spp. 4; type, *B. papyrifera* (L.) Vent.

sect. *Allaeanthus* (Thw.) Corner stat. nov.—*Allaeanthus* Thw.

Drupe sessile. Seed compressed, smooth, ligneous, the keel not double. Cotyledons conduplicate or flat. Cystoliths hypogenous. Leaves distichous. Male bracts often ovate, sessile. Spp. 3; type, *B. zeylanica* (Thw.) Corner.

There are no major differences between these sections, which are not generically distinct. There appears to be an undescribed species from West Borneo, represented by the sterile collections NIFS bb 8015 and 8016; possibly it belongs to sect. *Allaeanthus*, but its leaves have no cystoliths.

Key to the Species of sect. *Allaeanthus*

1. Climber. Syncarp -10 mm. wide. Seeds with the endocarp much thickened into a lip at the hilar end. Cotyledons conduplicate corrugated. Lamina crenate-dentate; lateral nerves 3-6 (-8) pairs; stipules entire. Male spike -5 cm. long *B. kurzii*.
1. Trees. Syncarps -20 mm. wide. Seeds without the thickened lip to the endocarp. Lateral nerves 7-15 pairs.
 2. Lamina serrate; stipules denticulate. Male spike -6 cm. long. Cotyledons ? corrugate *B. zeylanica*.
 2. Lamina and stipules entire. Male spike 10-26 cm. long. Cotyledons flat *B. luzonica*.

B. kurzii (Hook. f.) Corner comb. nov.—*Allaeanthus kurzii* Hook. f. Fl. Br. Ind. 5 (1888) 490; Kurz, For. Fl. Burm. 2 (1877) 466 (ut *Malaisia tortuosa*); Gagnep. Fl. Gen. I.-C. 5 (1928) 721.

Distr. Assam, Upper Burma, Yunnan, Laos, Cochinchina, Thailand.

This large deciduous climber is at once distinguishable from *Malaisia* by the numerous close intercostals.

B. luzonica (Blanco) Bur. DC Prodr. 17 (1873) 224.—*Morus luzonica* Blanco, Fl. Filip. (1837) 703.—*Broussonetia luzonensis* Blanco, Fl. Filip. ed. 2 (1845) 488.—*Allaeanthus luzonicus* (Blanco) Vidal, Noviss. App. (1880) 198.

var. luzonica

Pubescent.—Philippine Isl. (Luzon).

var. **glabra** (Warb.) Corner comb. nov.—*A. glaber* Warb. Perk. Fragm. Fl. Philip. 1 (1904) 166.—*A. luzonicus* (Blanco) Vidal var. *glaber* (Warb.) Merr. En. Philip. 2 (1923) 37.

Puberulous, soon glabrous.

Distr. Luzon, Basilan, Mindoro, Celebes (Gorontalo, Moena).

B. zeylanica (Thw.) Corner comb. nov.—*Allaeanthus zeylanicus* Thw. Hook. J. Bot. Kew Gard. Misc. 6 (1854) 302, f. 9b; Worthington, Ceylon Trees (1959) pl. 425.

Bureau described the cotyledons of this species, which is known only from Ceylon, as strongly corrugated-foliaceous. It seems that they must resemble those of *B. kurzii*, but all the seeds of the collections which I could examine, including the type, were empty.

Maclura Nutt.

Gen. Amer. Pl. 2 (1818) 233 (gen. conserv.); Bur. DC Prodr. 17 (1873) 227; Benth. et Hook. Gen. Pl. 3 (1880) 363; Engl. Nat. Pflanzenf. 3, 1 (1894) 74; Lemée, Dict. Phan. 4 (1932) 230.—*Vaneria* Lour. Fl. Cochinchin. (1790) 564.—*Toxylon*, *Joxylon* Raf. Am. Month. Mag. (1817) 118 and (1818) 188, 195.—*Chlorophora* Gaud. Voy. Freyc. Bot. (1826) 509.—*Fusticus* Raf. New Fl. Am. 3 (1836) 43.—*Sukaninea* Raf. id. 44.—*Cudrania* Tréc. Ann. Sci. Nat. ser. 3, 8 (1847) 122 (gen. conserv.); Bur. Ann. Sci. Nat. ser. 5, 11 (1869) 377; DC Prodr. 17 (1873) 285; Baill. Hist. Pl. 6 (1875) 145, 194; Benth. et Hook. Gen. Pl. 3 (1880) 374; Hook. Fl. Br. Ind. 5 (1888) 538; Engl. Nat. Pflanzen. 3, 1 (1894) 82, f. 60B, C; Renner. Bot. Jahrb. 39 (1907) 361.—*Cudranus* Rumph. ex Miq. Fl. Ind. Bat. 1, 2 (1859) 290; Rumph. Herb. Amb. V, 22, t. 15, 16.—*Cardiogyne* Bur. DC Prodr. 17 (1873) 232.—*Milicia* Sim, For. Fl. Port. E. Africa (1909) 97, t. 72.

Diocious trees, shrubs, climbers, generally with axillary spines. Leaves spirally arranged to distichous, simple, without glands. Male inflorescences paniculate, spicate with a sterile groove, or capitate. Female inflorescences capitate or shortly spicate. Bracts and/or tepals with 2–7 immersed yellow glands. Bracts spatulate to clavate or none. Male flowers 4-merous; tepals free; anthers small, extrorse to laterally dehiscent; filaments inflexed or straight in bud; pistillode subulate or as a slender sterile ovary or none. Female flowers sessile, free or connate proximally; tepals 4, decussate, obtuse, free or gamophyllous to the middle, fleshy in fruit;

ovary free or sunk in sockets in the receptacle; stigmatic arms 1–2, short or long. Drupes very thinly pulpy, enclosed in the fleshy perianth, generally not projecting, often conerescent below into a fleshy syncarp. Seed compressed, with more or less ligneous endocarp 2.5–10 mm. long. Embryo curved; radicle long, asymmetrically incumbent to accumbent; cotyledons equal, folded or not, rather thin. Cystoliths amphigenous or none; microscopic gland-hairs 4-celled, capitate; generally with sphaerocrystal cells in the lower epidermis, at least along the veins; hypodermis none; hairs smooth. Species 12, America, Africa, Asia.

Key to the Sections of *Maclura*

1. Filaments straight in bud. Style or stigmatic arms short, 1–2.5 mm. long. Male heads capitate. Spines axillary, not on short leafy shoots. Cotyledons folded or flat. Cystoliths none. Trees, shrubs, climbers. Asia, Australasia sect. *Cudrania*.
1. Filaments inflexed in bud. Style or stigmatic arms 8–20 mm. long.
 2. Male heads capitate. Ovaries immersed in sockets of the receptacle. Style undivided. Syncarp fleshy. Cotyledons much folded. Cystoliths none. Spines ending short leafy shoots, or decurved with 1–2 scale-leaves. Climber. Africa sect. *Cardiogyne*.
 2. Male heads not capitate. Ovaries not in sockets. Cotyledons flat, small. Trees.
 3. Male inflorescence paniculate, ebracteate; flowers pedicellate. Stigmatic arms 1–2. Syncarp depressed subglobose, 8–14 cm. wide. Cystoliths none. Generally spiny. America sect. *Maclura*.
 3. Male inflorescence spicate with a sterile groove; flowers sessile. Style undivided. Syncarp globose to shortly oblong, smaller. Cystoliths amphigenous. Spinous or not. America, Africa sect. *Chlorophora*.

sect. **Maclura**.—*Maclura* subgen. *Eumaclura* Bl. Mus. Bot. Lugd. Bat. 2 (1856) 82.

Tree, generally spinous. Inflorescences apparently ebracteate. Male inflorescence paniculate; flowers pedicellate; tepals free; filaments inflexed in bud; pistillode ? none. Female tepals with 2 immersed yellow glands; ovaries not in sockets of the receptacle; stigmatic arms 1–2, 9–20 mm. long. Syncarp massive, fleshy, the drupes immersed. Seeds 9–10 mm. long. Cotyledons flat, thin; radicle obliquely incumbent. Cystoliths none. Species 1, *M. pontifera* (Raf.) Schneid. (*M. aurantiaca* Nutt.).

sect. **Chlorophora** (Gaud.) Bur. DC Prodr. 17 (1873) 228.—*Chlorophora* Gaud., *Milicia* Sim.

Trees spinous or not. Inflorescences bracteate; bracts and tepals with immersed yellow glands. Male inflorescence spicate with a sterile groove; tepals free; filaments inflexed in bud; pistillode as a small flattened ovary. Ovaries not embedded in sockets of the receptacle; style undivided, 8–10 mm. long. Syncarp —20 mm. wide. Seeds 2.5–4 mm. long. Cotyledons flat, thin; radicle accumbent. Cystoliths amphigenous, often sparse below. Species 5, America, Africa. Type, *M. tinctoria* (L.) Don.

America:—**M. tinctoria** (L.) Don.

Africa:—**M. excelsa** (Welw.) Bur.

M. regia (A. Chev.) Corner comb. nov.—*Chlorophora regia* A. Chev. Bull. Soc. Bot. Fr. 58 (1912) 209.

Madagascar:—**M. greveana** (Baill.) Corner comb. nov.—*Ampalis greveana* Baill. Grandid. Hist. Madag. Pl. (1891) t. 293A.—*Chlorophora greveana* (Baill.) Leandri, Mem. Inst. Sci. Madag. ser. B, 1 (1948) 18; Fl. Madag. fam. 55 (1952) 12, f. III 1–8.

M. humberti (Leandri) Corner comb. nov.—*Chlorophora humberti* Leandri, l.c. (1948) 20; l.c. (1952) 14, f. III 9.

This section needs further resolution. The American species is generally spiny and has globose female head and syncarp; there may be two species. The African and Madagascan species are unarmed. *M. greveana* has a globose female head and syncarp, but the other three have distinctly oblong female heads and syncarps. In *M. excelsa*, too, the lamina is less reduced than in other species of the genus and has 14–18 pairs of lateral nerves. *Chlorophora* was first sunk in *Maclura* by Endlicher (Gen. Pl. 1841, 277).

sect. **Cardiogyne** (Bur.) Corner stat. nov.—*Cardiogyne* Bur.

Climber with short leafy shoots ending in a spine, or the decurved axillary spine with 1–2 scale-leaves. Inflorescences bracteate; tepals with 2 immersed yellow glands. Male inflorescence capitate; flowers sessile; filaments inflexed in bud; pistillode ligulate. Female perianths 4-partite, gamophyllous below and connate laterally at the base; ovaries sunk in sockets of the receptacle; style undivided, –18 mm. long. Syncarp –20 mm. wide, the drupes concealed. Seed 5–6 mm. long. Cotyledons much folded; radicle obliquely incumbent. Cystoliths none. Species 1, Africa.

M. africana (Bur.) Corner comb. nov.—*Cardiogyne africana* Bur. DC Prodr. 17 (1873) 232.

sect. **Cudrania** (Tréc.) Corner comb. nov.—*Cudrania* Tréc., *Vanieria* Lour., *Cudranus* Rumph. ex Miq.—*Maclura* Nutt. subgen. *Leptosura* Bl. Mus. Bot. Lugd. Bat. 2 (1856) 83.

Trees, shrubs, climbers, with leafless axillary thorns in place of short shoots. Male and female inflorescences capitate, both bracteate; bracts subulate, lanceolate, spatulate, to subpeltate, with 2 immersed yellow glands, often 2–4 bracts per flower, often adnate to the tepals, usually several sterile bracts at the base of the capitulum. Tepals free or gamophyllous in the lower half, with 2–7 immersed yellow glands in each. Male flowers with the filaments straight in bud; pistillode subulate. Female perianths free or connate in the lower part; ovaries free or embedded in sockets of the receptacle; style short, undivided or with two short

arms. Syncarp fleshy, —40 mm. wide, the drupes generally concealed. Seeds 4–9 mm. long. Cotyledons broad with infolded margins and obliquely incumbent radicle, or small and flat with accumbent radicle. Cystoliths none. Species 5, Asia, Australasia. Type, *Maclura cochinchinensis* (Lour.) Corner.

Ser. **Liberæ** Corner ser. nov.

Flores feminei liberi, ovario superficiali, stylo saepissime bilobato. Flores masculi filamentis quam antheris exsertis bis usque quater longioribus. Semina 5–9 mm. longa. Radicula accumbens. Species 2. Typus, *M. fruticosa* (Roxb.) Corner.

Ser. **Connatae** Corner ser. nov.

Flores feminei partibus inferioribus connati, tepalis basim versus gamophyllis, ovario in cavo parvo receptaculi immerso, stylo indiviso raro ramulo dentiformi praedito. Flores masculi filamentis quam antheris brevioribus v. vix longioribus, antheris vix exsertis. Semina 3–5 mm. longa. Cotyledones marginibus inflexis, radicula eorumdem uno lateri incumbenti. Species 3. Typus, *M. cochinchinensis* (Lour.) Corner.

Key to the species of sect. *Cudrania*

1. Female flowers free; ovary superficial; style mostly with 2 stigmatic arms. Filaments 2–4 times as long as the exsert anthers
ser. *Liberæ*.
2. Tepals free; style less than 0.5 mm. long; stigmatic arms thick, blunt; filaments flattened, anther minute. Syncarp —15 mm. wide, irregularly lobate from the separately projecting fruits. Seed 5–9 mm. long; endocarp 0.3 mm. thick. Cotyledons subequal, rather thick. Twigs, petioles, puberulous to glabrous. Lamina long acuminate, base cuneate; lateral nerves 4–5 pairs, oblique, scarcely inarching; basal nerves 1/3–2/3 lamina; intercostals 3–8, regular
M. fruticosa.
2. Perianth tubular in the lower half; style 1.5 mm. long; stigmatic arms slender, as long; filaments cylindric; anthers 1.5 mm. long. Syncarp —4 cm. wide, fleshy, evenly subglobose. Seed 7–8 mm. long; endocarp 0.6–0.7 mm. thick, very hard. Cotyledons rather thin. Twigs, petioles, underside of veins fulvous brown tomentose. Lamina obtuse to acute, base rounded or subcordate; lateral nerves 4–6 pairs, inarching; basal nerves not elongate; intercostals 3–5, faint *M. thorelii*.
1. Female flowers connate at the base, the perianth tubular in the lower part; ovaries in sockets of the receptacle; style simple, rarely with a minute branch. Filaments shorter or slightly longer than the not or scarcely exsert anther. Syncarp 15–25 mm. wide, fleshy, evenly subglobose. Seed 3–5 mm. long; endocarp 0.2 mm. thick. Cotyledons thin, with infolded edges; radicle obliquely incumbent. Basal nerves of lamina short ser. *Connatae*.
3. Lateral nerves inarching strongly, 6–9 (–14) pairs; intercostals none or indistinct; petiole 3–15 mm. Tepals closely villosulous, all with 2 immersed glands. Filaments very short. Climber
M. cochinchinensis.
3. Lateral nerves ascending, slightly inarching; intercostals 2–5, distinct. Filaments 1–1½ times as long as the anthers. Petiole often longer.

4. Tree or shrub. Lamina-base rounded to widely cuneate; lateral nerves 3-5 pairs, often very oblique; petiole -35 mm. long. Male heads 7-10 mm. wide; tepals with 2 immersed glands
M. tricuspidata.
4. Climber. Lamina-base cuneate; petiole -20 mm. long. Male heads 5-7 mm. wide; tepals (male) thinly puberulous, generally without immersed glands *M. amboinensis*.
5. Lateral nerves 6-9 pairs v. *amboinensis*.
5. Lateral nerves 4-6 pairs v. *paucinervia*.

M. amboinensis Bl. Mus. Bot. Lugd. Bat. 2 (1856) 84.—*Cudrania amboinensis* (Bl.) Miq. Fl. Ind. Bat. 1, 2 (1859) 290 (ut *Cudranus*).—*C. grandifolia* Merr. Philip. J. Sci. 18 (1921) 52.

var. **amboinensis**

Lateral nerves 6-9 pairs.

Distr. Thailand, Malaya, Sumatra, Java, Borneo, Celebes, Amboina (type, leg. Zippel), New Guinea.

var. **paucinervia** Corner var. nov.—*C. grandifolia* Merr.

Costae laterales utrinsecus 4-6.

Distr. Philippine Islands, New Guinea. Typus, Elmer 15530 (Luzon, Mt. Bulusan, prov. Sorsogon, det. *Cudrania javanensis* Tréc.; herb. Kew).

M. cochinchinensis (Lour.) Corner comb. nov.—*Vanieria cochinchinensis* Lour. Fl. Cochinch. (1790) 564.—*Cudrania javanensis* Tréc. Ann. Sci. Nat. ser. 3, 8 (1847) 123, pl. 3, f. 76-85.—*C. obovata* Tréc. id. 126.—*Maclura javanica* Bl., *M. timorensis* Bl. Mus. Bot. Lugd. Bat. 2 (1856) 83.—*C. cochinchinensis* (Lour.) Kudo et Masumune, Ann. Rept. Taihoku Bot. Gard. 2 (1932) 272.—*C. cambodiana* Gagnep. Bull. Soc. Bot. Fr. 72 (1925) 808; Fl. Gcn. I.-C. 5 (1928) 729, f. 89, 90.

Distr. Ceylon, India, China, Japan to New Britain, Australia, and New Caledonia.

There are several other well-established synonyms of this common species.

var. **pubescens** (Tréc.) Corner comb. nov.—*Cudrania pubescens* Tréc. Ann. Sci. Nat. ser. 3, 8 (1847) 125.

Twigs and underside of leaves brown hairy or velvety, but with all transitions to the glabrous state of v. *cochinchinensis*.

var. **bancrofti** Bailey, Compr. Cat. Queensl. Pl. (1910) 504.

Foliage variegated.

M. fruticosa (Roxb.) Corner comb. nov.—*Batis fruticosa* Roxb. Fl. Ind. 3 (1832) 763.—*Cudrania fruticosa* Wight ex Kurz, For. Fl. Burm. 2 (1877) 434; Hook. Fl. Br. Ind. 5 (1888) 539.—*Vanieria fruticosa* (Wight) Chun, J. Arn. Arb. 8 (1927) 21.

This species is remarkable in two ways. The very tips of the flattened filaments are contracted and slightly inflexed, as a vestige of the state with normally inflexed filaments. Then, as many of the female flowers seem sterile or do not fruit, the drupes project individually from the infructescence, each in its own decussate fleshy perianth, simulating the syncarp of *Malaisia*.

M. thorelii (Gagnep.) Corner comb, nov.—*Cudrania thorelii* Gagnep. Bull. Soc. Bot. Fr. 72 (1925) 810; Fl. Gen. I.-C. 5 (1928) 725.

This species approaches ser. *Connatae* in the tubular lower half of the perianth. It is remarkable for the large, strongly exsert anthers, 1.5 mm. long, with filaments 3–4 mm. long, and for the large syncarp, 4 cm. wide. If there were 2–3 stamens, instead of 4, the species would be truly artocarpoid, but the flattened seed with thick endocarp and the embryo place it in *Maclura*.

M. tricuspидata Carr. Rev. Hort. (1864) 390, f. 37; id. (1872) 56, f. 7.—*Cudrania triloba* Hance, J. Bot. 6 (1868) 49; Hook. Ic. Pl. (1888) t. 1792.—*C. tricuspидata* (Carr.) Bur. Lavallée Arb. Segrez. (1877) 243.—*Morus integrifolia* Lévl. et Van. Bull. Ac. Intern. Geogr. Bot. 17 (1907) 210; Rehder, J. Arn. Arb. 17 (1936) 73.—*Vanieria tricuspидata* (Carr.) Hu, J. Arn. Arb. 5 (1924) 228.—*V. triloba* (Hance) Satake, J. Fac. Sci. Tokyo sect. 3, Bot. 3 (1931) 497.

The inflorescences and syncarp of this species seem identical with these of *M. cochinchinensis*. It seems that many twigs, particularly the upper ones, are unarmed. As a silk-worm tree it is said to be as good as *Morus* but too thorny for convenient picking.

Macludrania hybrida André (Rev. Hort. 1905, 362) is said to be a hybrid between *M. pomifera* and this species. The few sterile specimens that I have seen in herbaria could not be distinguished from *M. pomifera*.

Malaisia Blanco

Fl. Filip. (1837) 789.—*Dumartroya* Gaud. Voy. Bonite (1844) t. 97.—*Cephalotrophis* Bl. Mus. Bot. Lugd. Bat. 2 (1856) 75, t. 27.

The position of this monotypic genus is problematic. The male flower and embryo resemble those of *Streblus* sect. *Sloetia*. The female flower resembles that of *Streblus* sect. *Bleekrodea*. The male inflorescence fits *Streblus* but the contracted female inflorescence, which is not exactly capitate, and the fleshy syncarp, particularly, agree rather with *Prainea*. Furthermore, the yellow resin-cells of the drupe-wall in *Malaisia* agree with the yellow glands of *Maclura* and the resin-cells of *Artocarpus*. The genus seems a relic of the ancestors of *Prainea* and *Artocarpus*.

The sole species is *M. scandens* (Lour.) Planch. The second species, which is generally dragged in without enquiry, is *M. puberula* (Miq.) Bur., but after examining the type I can find no other difference than the 4-merous male flower, which seems at most varietal. Similar variation occurs in *Streblus* sect. *Sloetia*.

Parartocarpus Baill.

Adansonia 11 (1875) 294; Jarrett, J. Arn. Arb. 41 (1960) 320.

This genus is well-named because it shows the durian-factors developed in parallel with those of *Artocarpus*. In *Parartocarpus* the free bracts and tepals become the spines of the syncarp, not the tips of the utricular perianths; it is the ovary-wall or exocarp of the drupe which becomes the false aril of the false seed, not the proximal parts of the perianth. In fact, the drupe of *Parartocarpus* in size and succulence, with well-developed endocarp, is more primitive than any drupe or drupelet of Moraceae. The "straps" between the drupes of *Artocarpus* subgen. *Artocarpus* are the undeveloped perianths of unfertilised or sterile flowers; in *Parartocarpus* they are straps of receptacular tissue between the flowers as in subgen. *Pseudojaca*. The large anthers and 2-3 stamens indicate, also, a less advanced state than *Artocarpus*. Thus *Parartocarpus* has advanced to the sunken ovaries of subgen. *Pseudojaca* while remaining less advanced in other respects. It is an off-shoot of pre-*Artocarpus* which has attained the syncarp of subgen. *Pseudojaca* by parallel evolution.

Plecosperrnum Tréc.

Ann. Sci. Nat. ser. 3, 8 (1847) 124, pl. 4, f. 121-126.

Spiny dioecious climbers, some of the twigs modified into leafless spines. Leaves distichous. Inflorescences capitate, pedunculate; bracts small, lanceolate-obtuse, both bracts and tepals without immersed glands; flowers sessile, 4-merous. Male perianth shortly gamophyllous; filaments inflexed in bud; pistillode filiform or as a minute ovary. Female heads with the ovaries immersed singly in sockets of the receptacle; tepals minute, round the mouth of the socket; ovary free from the receptacular wall; styles 1-2, long, undivided. Syncarp fleshy, bulging from the included seeds, with many aborted flowers. Seeds 7-9 mm. long, plump; endocarp membranous. Embryo large, curved; radicle very short; cotyledons very unequal, both folded and fleshy, the larger surrounding the smaller, both with long stalks. Cystoliths none. Species 2 (-3). India, Ceylon, Burma, Indochina, Thailand, Andaman Isl.

This is another problematic relic, related perhaps with *Malaisia*. The two species resemble *Maclura* sect. *Cudrania* in climbing habit, leaf, and spines, but the seed and embryo are those of *Malaisia*, and the inflorescences are an advance on this genus towards *Artocarpus* subgen. *Pseudojaca*. Experimental hybridisation may elucidate the affinity.

Key to the species of *Plecosperrum*

Glabrous or finely puberulous. Lamina 5–8 cm. long. Style 1, 3–5 mm. long. Syncarp 10–15 mm. wide, finely brown velvety . . . *P. spinosum*.

Twigs, stipules, young leaves, inflorescences, and syncarp brown tomentose. Lamina 6–14 × 3–8 cm. Styles 1 or 2, 10–13 mm. long. Syncarps 15–30 mm. wide *P. andamanicum*.

P. andamanicum King, Hook Fl. Br. Ind. 5 (1888) 491—*Cudrania poilanei* Gagnep. Bull. Soc. Bot. Fr. 72 (1925) 809; Fl. Gen. I.-C. 5 (1928) 724 (excl. Poilane 10038, floribus masculinis = *Maclura cochinchinensis*).

Distr. Laos, Annam, Cochinchina, Burma, Thailand, Andaman Isl.

To judge from herbarium-material, this seems to be deciduous.

P. spinosum Tréc. l.c.; Hook. Fl. Br. Ind. 5 (1888) 491; Alston, Kandy Fl. (1938) 34, f. 183.—*Trophis spinosa* Heyne, Willd. Sp. Pl. 4 (1806) 734.—*T. aculeata* Roth, Nov. Sp. Pl. (1821) 368.—*Batis spinosa* Roxb. Fl. Ind. 3 (1832) 762.

Distr. Ceylon, India.

Evergreen ?

P. bureaui Richter, Termeszetrarzi Futezek 15 (1895) 296.

This is unknown to me.

Species Excludendae

P. cuneifolium Thw. is *Maclura cochinchinensis* (Lour.) Corner.

P. laurifolium Baill. is *Pachytrophe obovata* Bur. var. *laurifolia* Leandri, Mem. Inst. Sci. Madag. ser. B, 1 (1948) 16; Fl. Madag. fam. 55 (1952) 11, f.2.

P. obovatum Bur. ex Richter is *Pachytrophe obovatum* Bur.

Prainea King

Hook. Fl. Br. Ind. 5 (1888) 546; Jarrett, J. Arn. Arb. 40 (1959) 30.

This genus agrees with *Artocarpus* in the capitate male and female inflorescences, the tubular perianths, the single stamen with straight filament and small anther, and the short stigmatic arms. Yet it is dioecious and the syncarp, so unlike that of *Artocarpus*, resembles closely that of *Malaisia*. Further, both *Prainea* and *Malaisia* have membranous endocarp. The perianth of *Prainea* has many clusters of yellow resin-cells in its mesophyll, such as occur in the ovary (pericarp) wall of *Malaisia*, but not, so it seems, in the floral parts of *Artocarpus*. On the other hand, *Prainea* has the peltate (4–8-celled) microscopic gland-hairs and mesophyll resin-cells of subgen. *Artocarpus* and it lacks the cystoliths of *Malaisia*; this last point, however, is of very doubtful value and there are very rudimentary cystoliths along the underside of the veins in some species of *Prainea*. A microscopic character of *Prainea* is the strongly stellate form of the epidermal cells of the leaf.

A peculiarity of *Prainea*, described by Jarrett, lies in the manner in which the ovule is moved from a subapical position in the ovary at anthesis to a sub-basal position in fruit. It is possible, therefore, that the embryo is developed transversely inside the ovule though longitudinally in relation to the ovary-cavity, such as happens in *Plecospermum*. *Parartocarpus* has the same peculiarity, but it differs in so many ways from *Prainea* that the similarity seems to be parallel.

According as one or other character is emphasized, so *Prainea* inclines to *Malaisia* or to *Artocarpus*, and retains its own character.

Treculia Decne ex Trec.

Ann. Sci. Nat. ser. 3, 8 (1847) 108.

This genus, even its best known species *T. africana*, requires much more investigation. It is placed near *Artocarpus*, but it lacks the characteristic female perianths of subgen. *Artocarpus* and it does not have the sunken ovaries of subgen. *Pseudojaca*. The slender umbonate-peltate bracts of the syncarp much resemble those of *Broussonetia*. *T. africana* is said to be dioecious but solitary specimens in Malaya fruit and seed; their fruit-heads are strongly protogynous and then develop copious male flowers with dehiscent stamens and, apparently, viable pollen, while the seeds are forming; some small heads are wholly male. As a monoecious and partly monoclinal plant it has the character antecedent to Brosimeae. The male flower with 2-4 stamens and large anthers resembles that of *Parartocarpus* but retains a utricular perianth. The drupe resembles that of *Parartocarpus*, but the embryo is orientated the other way round, having the radicle away from the raphe-side of the seed. The genus may be a parallel with *Artocarpus*, but, to show how inadequate published descriptions may be, there seems from the literature little to choose between the African *Acanthotreculia*, generally sunk in *Treculia*, and subgen. *Pseudojaca*.

Olmedieae Tréc.

Ann. Sci. Nat. ser. 3, 8 (1847) 126; Miq. Mart. Fl. Bras. 4, 1 (1852) 79; Bur. DC Prodr. 17 (1873) 281; Benth. et Hook. Gen. Pl. 3 (1880) 346; Engl. Nat. Pflanzenf. 3, 1 (1894) 83; Dalla Torre et Harms. Gen. Siph. (1900) 121.

Inflorescences unisexual, discoid, obconic, or urceolate, with an involucre of 1-several rows of bracts, the male many-flowered, the female many to 1-flowered; flowers sessile. Stamens 8-1; filaments straight in bud; anthers introrse or extrorse; pistillode present or not. Ovaries superficial or immersed. Infructescence syncarpous or not. Seeds large. Embryo various. Monoecious or dioecious. Trees, shrubs, not spinous. Gen. 18 (America 13, Africa 2, Asia 4); species 69 (America 58, Africa 5, Asia 6).

Antiaris Lesch.

Ann. Mus. Hist. Nat. Paris 16 (1810) 478, t.22 (gen. conserv).

Seventeen species have been described. After studying the abundant collections in London, Paris, Leiden, Singapore, and Bogor, I have reduced the number to four, namely *A. africana*, *A. toxicaria*, and the two Madagascan species *A. humbertii* and *A. madagascariensis*. Several of the proposed species are clearly synonyms, but the variability of the wide-spread *A. toxicaria* is the real cause of the superfluity and, indeed, of the uncertainty. On broad principles only one species may be recognised because there are no essential differences, merely variations of size and shape, in leaf and fruit. Thus, the small leaf distinguishes *A. humbertii*; the ovate-elliptic, tapered leaf may distinguish *A. toxicaria* var. *macrophylla*; the prominent venation distinguishes *A. africana*; but, without fruit, *A. madagascariensis* cannot be distinguished from *A. toxicaria*. These distinctions are supported geographically and ecologically. *A. africana* belongs to the drier forests of west and central Africa, where its timber is recognised as different from that of *A. toxicaria*. The Madagascan species belong to the xerophytic scrub on calcareous and sandstone rock. In contrast, *A. toxicaria* is a primary rain-forest tree of the lowland hylea and, in this capacity, has the widest and most continuous range of any Moraceous plant, from West Africa to South China and Fiji. It is absent from Madagascar and other Mascarene islands, from the Australian mainland, and from New Caledonia. It reaches 1,500 m. alt. in North Borneo and New Guinea and its occurrence in South China suggests a certain adaptability to a seasonal climate. On the periphery of its range occur the other species.

The nearest allies of the genus seems to be the American *Olmedia* and *Pseudolmedia*, both with a single superficial ovary, more or less gamophyllous perianth, and distinctly exsert anthers. *Ogcodeia* differs more in having several flowers in the female inflorescence. The little known *Mesogyne* of Africa may be another species of *Antiaris*, but its stamens are extrorse and the ovary is partly superior. Though placed by Engler in Dorstenieae, the filaments of *Mesogyne* are straight in the bud and the inflorescences accord well with *Antiaris*.

Habit. *A. toxicaria* is a large tree. The form cultivated in the Solomon Islands, Fiji, and Tonga is a shrub or small tree. Its leaves and large fruits place it in var. *macrophylla*, collections of which from New Guinea and New Hebrides seem to show all gradations to large trees. Perhaps, nevertheless, there is a dwarf form. *A. africana* is also a large tree. The Madagascan species are small trees or shrubs. The evidence of field-notes shows that all the species have intermittent growth and that, as adult plants, they become deciduous.

Saplings. The saplings of *A. toxicaria* have brown-hispid or setose-scabrid leaves and twigs. The leaves are larger, thinner, more obovate, more attenuate to the base, and more toothed than the adult leaves which, with the twigs, seem to become more shortly hairy and, finally, practically glabrous. Nevertheless, there may be persistently hairy and persistently less hairy varieties. *A. rufipila* Miq. was based on a fertile, brown-hispid specimen. The sapling form seems identical in *A. africana*. In both the adult foliage becomes coriaceous, but the feature is much more pronounced in *A. africana*. Since specimens of saplings are commonly collected for identification, they make the wide use of *A. toxicaria* desirable.

Fruit. The size and shape of the fruit, or drupe (omitting the stalk), is important. *A. africana* and *A. toxicaria* have ellipsoid or pyriform drupes, the size of which increases from Africa to Polynesia. There is some overlap but all African collections have small drupes, $10-15 \times 7-12$ mm. when dried, compared with the Far Eastern drupes, $20-45 \times 17-26$ mm., when dried. In western Malaysia there is considerable variation but no fruits so large as the eastern. Celebes seems the boundary. Here are trees with small fruits indistinguishable from the African var. *welwitschii*, trees with large fruits and leaf-shape approaching var. *macrophylla*, and others exactly resembling the intermediate var. *toxicaria*. Celebes is also a meeting ground for east-west variation in figs, e.g. *F. tinctoria*. The Madagascan species have nearly spherical drupes almost as large as those of *A. toxicaria* var. *macrophylla*; and this shows that they are not the same species as on the African mainland. Now, in *Ficus* as a rule, the further a species is from its geographical centre of alliance the smaller are its fig-fruits. Applying this rule to *Antiaris*, *A. toxicaria* must have spread westwards from eastern Malaysia and Australasia and to this far eastern centre of alliance the Madagascan species relate. The progressive xerophily of the leaf in *A. toxicaria* conforms with this westward trend. Yet, *Antiaris* has no close ally in eastern Malaysia, and it is absent from New Caledonia, the figs of which are predominantly allied in subgen. *Pharmacosycea* with those of tropical America. Nevertheless, as *Trophis* shows the alliance between America and Polynesia or Eastern Malaysia, so may *Antiaris* at the end of its evolutionary course.

The fruit-variation is summarised in the accompanying table. Two collections from Soemba are without fruit and cannot be placed exactly. One collection from east Flores (Solor Isl.) is sterile but appears to be var. *macrophylla*. Of four collections from Timor, two belong to var. *macrophylla* (NIFS bb. 20,062, and 27,073), the others being without fruit.

TABLE OF FRUIT-SIZES IN ANTIARIS

(Measurements refer to the dried drupe, excluding the stalk)

—	Drupe (mm.)	Country	Leaf-shape
<i>A. africana</i>	10-15 × 9-10	Africa	as in var. <i>toxicaria</i>
<i>A. toxicaria</i>			
v. <i>welwitschii</i>	10-15 × 7-12	Africa	do.
v. <i>toxicaria</i>	15-25 × 11-20	Continental Asia to Celebes	obovate, acuminate
	12-20mm. long	Celebes	do.
v. <i>macrophylla</i>	20-25 × 17-20	Moluccas	Ovate- elliptic. attenuate
	25-38 × 20-26	New Guinea	do.
	30-45 × 22-25	Solomon Isl. Fiji	do.
	20-24 × 17-19	Philippines	do.
<i>A. humbertii</i>	20-30 × 20-30	Madagascar	as in var. <i>toxicaria</i>
<i>A. madagascariensis</i>	do.	do.	do.

Toxicity. There is much conflicting evidence on the toxicity of the latex and seeds of *A. toxicaria*. That many trees have poisonous latex, used for arrow-poison in West and Central Malaysia, is well known. The poison is caused by cardiac glycosides, particularly antiarin. Yet, there are reports of harmless trees (*A. innoxia* Bl.) and there seem to be no reports of such arrow-poisons from the trees of Africa, New Guinea, and Melanesia. Bisset informs me *in litt.* that in these cases the glycoside-content is probably very low. The fruits of *A. toxicaria* are eaten with impunity though those of the Madagasean species are said to be poisonous. Bisset (1957) found essentially the same cardiac glycosides in *Antiaris*, *Antiaropsis*, and the American *Ogcodeia*. This chemical evidence suggest the derivation of the American allies of *Antiaris* from the New Guinea centre of *Antiaropsis*.

Key to the species and varieties of *Antiaris*

1. Drupes subglobose 20–30 mm. wide. Madagascar.
 2. Lamina -4×3 cm., harshly scabrid; lateral nerves 5–6 pairs
A. humbertii.
 2. Lamina larger, becoming more or less smooth; lateral nerves 8–14 pairs *A. madagascariensis*.
1. Drupes ellipsoid or pyriform.
 3. Costal and intercostal venation strongly raised on the underside of the scabrid, coriaceous lamina. Drupe 10–15 mm. long
A. africana.
 3. Intercostal venation not or scarcely raised. Adult lamina subscabrid or smooth *A. toxicaria*.
 4. Lamina ovate-elliptic, attenuate. Drupe $20-45 \times 17-26$ mm. Moluccas, Philippines, eastwards v. *macrophylla*.
 4. Lamina elliptic-obovate, acuminate.
 5. Drupe 12–25 mm. long. Asia to Celebes v. *toxicaria*.
 5. Drupe 10–15 mm. long. Africa v. *welwitschii*.

A. africana Engl. Bot. Jahrb. 33 (1902) 119; Keay, Fl. W. Trop. Afr. ed. 2, 1, pt. 2 (1958) 612.

Lamina as in *A. toxicaria* v. *toxicaria* but strongly coriaceous, strongly marked beneath by the raised costas and intercostals. Male inflorescence -15 mm. wide. Drupe $10-15 \times 9-10$ mm., ellipsoid.

West and central Africa, in drier forest.

An earlier name may well be *A. challa* (Schw.) Engl., though this is generally reduced to *A. toxicaria* v. *welwitschii*. Saplings of *A. africana* seem indistinguishable from those of *A. toxicaria*.

A. humbertii Leandri, Not. Syst. 13 (1948) 175; Fl. Madag. fam. 55 (1952) 32, f. vi.

Lamina -4×3 cm., small, cordate at the base, subacuminate, harshly scabrid-hairy; lateral nerves 5–6 pairs, not prominent beneath. Drupe 20–30 mm. wide, subglobose, poisonous.

Madagascar; shrub or small tree in xerophytic bush.

A. madagascariensis H. Perrier, Arch. Bot., Bull 1–4 (1927) 70; Leandri, Fl. Madag. fam. 55 (1952) 32, f. vi.

Lamina as in *A. toxicaria* v. *toxicaria*. Drupe 20–30 mm. wide, subglobose, poisonous.

Madagascar; on sandstone and calcareous rocks, more or less xerophytic.

A. toxicaria Lesch. 1.c.

v. **toxicaria**

Lamina mostly elliptic obovate, acuminate, base cordate to cuneate and often somewhat asymmetric, thinly to rather strongly coriaceous, subscabrid to smooth when adult. Male inflorescence -20 mm. wide. Drupe 12-25 × 11-20 mm., ellipsoid to pyriform.

Distr. Ceylon, India, Burma, South China, Hainan, Indochina, Thailand, Andaman Isl., Malaya, Sumatra, Java, Borneo, Celebes; rainforest to 1,500 m. alt.

The leaves vary greatly in size and shape even on the same twig. Possibly each new shoot bears a regular succession of differing leaves.

var. **macrophylla** (R.Br.) Corner stat. nov.—*Antiaris macrophylla* R.Br. Flind. Voy. 2 (1814) 602, t. 5.—*A. bennettii* Seem. Bonplandia 9 (1861) 259; id. 10 (1862) 3, t. 7. Arbor toxicaria mas, Rumph. Herb. Amb. 2, 263, t. 87.

Lamina ovate-elliptic or elliptic, attenuate to the acute apex, base cordate to widely cuneate, scabridulous to smooth. Drupe 20-45 × 17-26 mm. Tree or shrub.

Distr. Philippinc Isl. Molucca Isl., Timor, (? Flores, Solor Isl.), (? Soemba), New Guinea, Solomon Isl., New Hebrides, Fiji, Tonga, North Australia (Company's Isl. off Arnhem Land); lowland rainforest.

The shrubby plant of Melanesia may be a cultivar spread by sea-farers.

var. **welwitschii** (Engl.) Corner stat. nov.—*Antiaris welwitschii* Engl. Bot. Jahrb. 33 (1902) 118; Keay, Fl. W. Trop. Afr. ed. 2, 1, pt. 2 (1958) 613.—*A. usambarensis* Engl. id. 119.—*A. kersitingii* Engl. Veg. Erde 9, 3 (1), (1915) 33.—? *Ficus challa* Schw. Bull. Herb. Boiss. 4, app. 2 (1896) 144.—? *A. challa* (Schw.) Engl. Veg. Erde 9, 3 (1), (1915) 33.—*A. challa* Blatt. Rec. Bot. Surv. Ind. 8 (1923) 446.

Leaf as in v. *toxicaria*. Male inflorescence -15 mm. wide. Drupe 10-15 × 7-12 mm.

Distr. Tropical Africa; lowland forest tree.

I maintain this variety in deference to the geographical homogeneity, the larger fruited specimens which occur in Asia not having been collected from Africa, but specimens from Celebes match those from Africa almost exactly in leaf and fruit; in no way can I distinguish the leaf of this variety from that of var. *toxicaria*. Possibly the male inflorescence is slightly smaller. Several herbarium sheets show that the variety is monoecious, as in the whole genus.

A. challa may be *A. africana*. I have been unable to see the type.

List of species and synonyms in *Antiaris*

A. *africana* Engl.

A. bennettii Seem. is *A. toxicaria* Lesch. var. *macrophylla* (R.Br.) Corner.

A. challa (Schw.) Engl. is *A. africana* Engl. or *A. toxicaria* Lesch. var. *welwitschii* (Engl.) Corner.

A. challa Blatt. is *A. toxicaria* Lesch. var. *welwitschii* (Engl.) Corner.

A. dubia Span. is *A. toxicaria* Lesch. var. *toxicaria*.

A. *humbertii* Leandri.

A. innoxia Bl. is *A. toxicaria* Lesch. var. *toxicaria*.

A. kerstingii Engl. is *A. toxicaria* Lesch. var. *welwitschii* (Engl.) Corner.

A. macrophylla R.Br. is *A. toxicaria* Lesch. var. *macrophylla* (R.Br.) Corner.

A. *madagascariensis* H. Perrier.

A. palembanica Miq. is *Artocarpus dadah* Miq.

A. rufa Miq. is *A. toxicaria* Lesch. var. *toxicaria*.

A. saccidora (Nimmo) Dalz. is *A. toxicaria* Lesch. var. *toxicaria*.

A. *toxicaria* Lesch.

A. turbinifera Hemsl. is not *Antiaris*. The type at Kew from the Solomon Isl. seems to be a mixture of fallen leaves, flowers, and fruits from as many different trees.

A. usambarensis Engl. is *A. toxicaria* Lesch. var. *welwitschii* (Engl.) Corner.

A. welwitschii. Engl. is *A. toxicaria* Lesch. var. *welwitschii* (Engl.) Corner.

A. zeylanica Seem. is *A. toxicaria* Lesch. var. *toxicaria*.

***Antiaropsis* K. Schum.**

Fl. Kaiser-Wilhelmsl. (1889) 40; Laut. et K. Schum. Fl. Deutsch. Schutzgeb. Suds. (1901) 267; Diels, Bot. Jahrb. 67 (1935) 174.

So far as concerns the female inflorescence this genus is central in the Olmedieae. The superior ovaries, the free tepals, and the interfloral bracts render it the least specialised of the tribe. If this inflorescence were bisexual, containing male and female pedicellate flowers, and became urceolate, it would represent a big step towards the receptacle of *Ficus*. *Sparattosyce* Bur., of New Caledonia, represents dioecious *Antiaropsis* with such an urceolate receptacle splitting open at anthesis of the male flowers and at maturity of the syncarp; at anthesis of the female receptacle the

styles project through its ostiole in a manner not known in *Ficus*, though conceivably its ancestral state. *Sparattosyce* has been placed in the Ficeae, but is not blastophagous and its anthers are extrorse; in *Antiaropsis* and *Ficus* they are introrse, which is unusual in the family.

Antiaropsis is a leptocaul tree. If converted into an ancestral pachycaul, it would have the possibilities of the non-blastophagous *Ficus*-ancestor. I have defined *Ficus* not only on its inflorescence but on its blastophagy, and have, therefore, transferred *Sparattosyce* to the Olmedieae. The work of Bisset (1957) on the cardiac glycosides of Moraceae has shown that *Antiaris*, *Antiaropsis*, *Castilloa*, *Ogcodeia*, and *Pseudolmedia* have much the same glycosidal content, particularly in possessing antiarin and antioside, but that *Sparattosyce*, as he informs me *in litt.*, does not have them.

There may be a second species of the genus, which passes as *A. decipiens* var. *parvifolia* Diels. One collection of this (T. McAdam s.n., Wau, Terr. New Guinea, 1939) has a small female inflorescence, 4–5 mm. wide, with a single female flower. Whether it is merely depauperate or a new species, the collections are insufficient to decide, but it shows how the one-flowered state of *Antiaris* may have arisen.

Brosimeae Tréc.

Ann. Sci. Nat. ser. 3, 8 (1847) 138; Miq. Mart. Fl. Bras. 4, 1 (1852) 79; Bur. DC Prodr. 17 (1873) 282; Benth et Hook. Gen. Pl. 3 (1880) 346; Engl. Nat. Pflanzenf. 3, 1 (1894) 87; Dalla Torre et Harms, Gen. Siph (1900) 122.

Inflorescences bisexual, discoid, capitate-globose or urceolate, more or less involucrate. Female flower central, solitary, surrounded by numerous sessile, superficial male flowers. Stamens 4–1; filaments inflexed or straight in bud; anthers (? extrorse), varying subglobose with transverse equatorial dehiscence; pistillode none. Ovary superficial or more or less immersed in the receptacle. Seed medium-size to large. Embryo (so far as known) straight; radicle short; cotyledons not folded, equal or unequal. Trees, unarmed. Genera 8 (Africa 7, America 1); species 44 (Africa 38, America 6).

I include in this tribe *Craterogyne* Lanjouw, which was placed in Dorstenieae.

Dorstenieae Gaud.

Voy. Freyc. (1826) 510.

I consider that this tribe contains only the genus *Dorstenia*. I refer *Craterogyne* to Brosimeae and *Mesogyne* to Olmedicac.

Ficeae Gaud.

Voy. Freyc. (1826) 510.

I consider that this tribe contains only the genus *Ficus*. I refer *Sparattosyce* to Olmedieae.

Genera Excludenda

Conocephaloideae: *Cecropia* L., *Coussapoa* Aubl., *Musanga* R.Br., *Myrianthus* Beauv., *Poikilospermum* Zipp., and *Pourouma* Aubl. to be transferred to Urticaceae.

Stenochasma Miq. belongs with Urticaceae.

Botrymorus Miq. is *Pipturus* Wedd. (see Koord. et Val., Bijdr. 12, 1910, 724).

Metatrophis F. Brown, Bull. Bish. Mus. Honolulu n. 130 (1935) 34.—This may be Urticaceae or Euphorbiaceae.

In conclusion, I express my gratitude to Dr. Chew Wee Lek, of the Singapore Botanic Gardens, for his critical and detailed help in the treatment of Conocephaloideae, *Streblus* sens. lat., and Urticaceae in general.

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