

MORACEAE GENERALA OTHER THAN FICUS

(C.C. Berg, E.J.H. Corner† & F.M. Jarrett)¹

FOREWORD

The following treatments of *Artocarpus*, *Hullettia*, *Parartocarpus*, and *Prinea* are based on the monograph by Jarrett (1959–1960) and on the treatments she made for this Flora in cooperation with Dr. M. Jacobs in the 1970s. These included some new *Artocarpus* species described in 1975 and the re-instatement of *A. peltata*. *Artocarpus lanceifolius* subsp. *clementis* was reduced to the species, in *A. nitidus* the subspecies *borneensis* and *griffithii* were reduced to varieties and the subspecies *humilis* and *lingnanensis* included in var. *nitidus*. The varieties of *A. vrieseanus* were no longer recognised. More new Malesian species of *Parartocarpus* were described by Corner (1976), Go (1998), and in *Artocarpus* by Kochummen (1998). A manuscript with the treatment of the other genera was submitted by Corner in 1972. Numerous changes to the taxonomy, descriptions, and keys have been made to the original manuscripts, for which the present first author is fully responsible.

References: Corner, E.J.H., A new species of *Parartocarpus* Baillon (Moraceae). *Gard. Bull. Singapore* 28 (1976) 183–190. — Go, R., A new species of *Parartocarpus* (Moraceae) from Sabah. *Sandakania* 12 (1998) 1–5. — Jarrett, F.M., Studies in *Artocarpus* and allied genera I–V. *J. Arnold Arbor.* 50 (1959) 1–37, 113–155, 298–368; 51 (1960) 73–140, 320–340. — Jarrett, F.M., Four new *Artocarpus* species from Indo-Malesia (Moraceae). *Blumea* 22 (1975) 409–410. — Kochummen, K.M., New species and varieties of Moraceae from Malaysia. *Gard. Bull. Singapore* 50 (1998) 197–219.

MORACEAE

Moraceae Link, *Handbuch* 2 (1831) 444 (Moriformes), nom. cons.; Baill., *Hist. Pl.* 6 (1875) 137–216 (Ulmacées); Benth. & Hook.f., *Gen. Pl.* 3, 1 (1880) 341–395 (Urticaceae); Engl. in Engl. & Prantl, *Nat. Pflanzenfam.* 3, 1 (1888) 66–98; Corner, *Gard. Bull. Singapore* 19 (1962) 187–252; C.C. Berg, *Taxon* 27 (1978) 39–44; Proc. Kon. Ned. Akad. Wetensch. C, 91 (1988) 345–362; Cronquist, An integrated system of classification of flowering plants (1981) 195–199.

Trees, shrubs, woody climbers, or herbs (*Dorstenia*, *Fatoua*), terrestrial, hemi-epiphytic (or holo-epiphytic), dioecious or monoecious, with milky sap. Leaves spirally arranged or distichous, (sub)opposite or subverticillate; stipules fully amplexicaul or semi-amplexicaul and lateral or intrapetiolar, free or connate; lamina basally attached (or peltate), with the margin entire or incised (to seemingly compound), venation pinnate or subpalmate, brochidodromous. Inflorescences typically in pairs, unisexual or bisexual, racemose, spicate, globose-capitate, capitate with a discoid to cup-shaped

1) With contributions by P. Baas (wood anatomy), R.P.W. Kromhout & R.W.J.M. van der Ham (pollen morphology), R. Hegnauer (phytochemistry and chemotaxonomy). Most of the original drawings are by R. van Crevel and some by E.J.H. Corner.

receptacle (and then with or without involucre), or with an urceolate receptacle, multi- to uniflorous, bracteate. *Flowers* unisexual, free or connate (or also adnate to the receptacle). *Staminate flowers*: tepals 2–4(–7) and free or connate, or perianth lacking; stamens 1–4(–6), straight or inflexed before anthesis; pistillode present or absent. *Pistillate flowers*: tepals (3–)4(–8), free or connate; pistil 1, ovary unilocular, free or adnate to the perianth; stigmas 1 or 2, various in shape; ovule 1, (sub)apically attached, anatropous to campylotropous. *Fruit* an achene or drupaceous (dehiscent or indehiscent), free or adnate to the perianth, often forming a drupaceous whole with the fruiting perianth or also with the (fleshy) receptacle. *Seed* large without endosperm or small with endosperm; embryo various.

DISTRIBUTION

The family comprises 37 genera and c. 1050 species represented by 14 native genera with in total 422 indigenous species; 8 species are introduced in Malesia of which 3 belong to *Ficus*.

The family is essentially tropical. Two genera, *Broussonetia* and *Morus*, are associated with and morphologically adapted to northern warm-temperate conditions. The genera *Ficus* and *Maclura* extend with a few members into warm-temperate conditions in the northern hemisphere and with two species of *Streblus* into those of the southern hemisphere.

Most species of Moraceae (c. 600 spp.) occur in the forest complex of tropical Asia and Australasia, where the large number of *Ficus* and, to a lesser extent, of *Artocarpus* swell the total. Africa with c. 185 species and America with c. 270 species are specifically poorer, but are richer in endemic genera: 7 out of 17 and 14 out of 19, respectively.

The third largest genus of the Moraceae, *Artocarpus*, is largely Malesian. About half of the species of the largest genus of the family, *Ficus*, occurs in the Malesian region.

The Asian element links closely to the Australasian, which can be regarded as an extension of the Asian. It is distinguished by the monotypic genus *Sparattosyce*, endemic to New Caledonia, and by some endemic or subendemic subdivisions of *Ficus* and *Streblus*.

Only six of the native genera, apart from *Sparattosyce*, are confined to the Asian–Australasian region. The other genera also occur in Madagascar, the African continent, and/or the Neotropics.

There are several links between the Asian moraceous flora and the African one. One pattern is formed by a number of subdivisions of *Ficus* (subsect. *Pedunculatae* of subg. *Pharmacosycea*, subsect. *Urostigma* of subg. *Urostigma*, sect. *Sycidium* of subg. *Sycidium*, and subsect. *Ficus* of subg. *Ficus*) which are centred in western Asian dry or seasonal forest but with linking elements in African savannah woodland. Another pattern is that between the Madagascan region, the eastern Asian mainland, and Malesia exhibited by the genera *Bleekrodea*, *Broussonetia*, *Fatoua*, *Streblus*, *Trophis*, and *Ficus* subg. *Sycomorus* sect. *Sycomorus*. Other links are formed by the close relationship between the African genus *Treculia* and the Asian genus *Artocarpus* and the African genus *Milicia* and Asian *Moreae*, and by *Antiaris toxicaria* ranging from West Africa

to the Tonga Islands. Two other species occur in Asia and Africa: *Ficus exasperata* and *F. palmata*.

The links with America are much weaker and are realized by *Ficus* (subg. *Pharmacosycea*) and *Trophis*, which connect the north western part of the Neotropics to the eastern part of the Asian–Australasian region. The Neotropics and Africa are linked by the tribes *Dorsteniae* and *Castilleae*.

Ficus, *Maclura*, and *Trophis* are pantropical genera. The essentially northern warm-temperate genus *Morus* extends into the montane tropics of Asia and America and lowland Africa. *Dorstenia*, speciose in America and Africa, is represented in Asia by only one Indian species.

Within Malesia the greatest numbers of Moraceae coincide with those of the Dipterocarpaceae, except for the development of *Ficus* in New Guinea. Most genera (and subgenera of *Ficus*) have one or more widespread species. A Sino-Himalayan element infiltrates the Malay Peninsula and some of the species reach Sumatra, Java, and Borneo. An Australian element is evident in *Ficus* subsect. *Malvanthera*. It penetrates only the adjacent part of the Malesian region and the Pacific. The Australasian *Streblus* sect. *Parastreblus* extends to New Zealand and New Caledonia. The genera endemic to Malesia are *Antiaropsis*, restricted to New Guinea, and the more widespread *Prainea*. *Parartocarpus* slightly exceeds Malesia.

Two neotropical genera, *Castilla* and *Dorstenia*, have been introduced, each with one species. A few other species introduced in the Malesian region belong to *Broussonetia*, *Ficus*, and *Morus* and are of Asian origin.

FIELD CHARACTERS

The presence of milky sap (latex) and stipules which often leave circular scars distinguish Moraceae. The former feature is shared with Euphorbiaceae, for which diagnostic features are the geniculate petiole and the presence of glands at the apex of the petiole, or on the lower margin of the lamina. In the majority of the *Ficus* species, waxy glands occur on the lower surface of the lamina, often in the axils of the basal lateral veins, or on the base of the midrib. Such glands are absent in other Moraceae. If not by the waxy glands, the majority of the *Ficus* species can be distinguished by aerial secondary roots that make them hemi-epiphytes ('stranglers'), or root climbers, whereas many others are cauli- or flagelliflorous. Smooth grey bark, marked with leaf scars and exuding latex on cutting, will also distinguish moraceous trees. A bright orange-brown or grey-brown roughish bark, with thick copious latex, will often distinguish *Artocarpus*. Dark red lateral roots with latex will distinguish some species of *Artocarpus*, as yellow roots with latex will distinguish *Parartocarpus*. The presence of thorns distinguishes the climbers of *Maclura* and the small trees of several *Streblus* species. *Antiaris* shows the architectural 'model of Cook' (Hallé & Oldeman 1970; Berg 1977; Hallé et al. 1978), characterised by spirally arranged leaves on the trunk and main branches, and distichous on the horizontal lateral branches which also may bear the inflorescences. Each axillary bud produces a lateral branch which ultimately is detached (by abscission) leaving a concave scar.

References: Berg, C.C., The Castilleae, a tribe of the Moraceae, renamed and redefined due to the exclusion of the type genus Olmedia from the 'Olmedieae'. *Acta Bot. Neerl.* 26 (1977) 73–82. — Hallé, F. & R.A.A. Oldeman, *Essai sur l'architecture et la dynamique de croissance des arbres tropicaux*. Masson, Paris (1970). — Hallé, F., R.A.A. Oldeman & P.B. Tomlinson, *Tropical trees and forests – an architectural analysis*. Springer-Verlag Berlin, Heidelberg, New York (1978).

MORPHOLOGY

Habit — The family consists chiefly of lowland trees. In Malesia, tall canopy trees or emergents are found in *Antiaris*, *Artocarpus*, *Ficus*, *Parartocarpus*, *Prainea*, and *Streblus*. They often have buttresses. Smaller, undergrowth trees of varying stature belong to *Antiaropsis*, *Broussonetia*, *Ficus*, *Hullettia*, *Streblus*, and *Trophis*. Shrubs and treelets are found in *Bleekrodea*, *Ficus*, *Maclura*, and *Streblus*. Species which can become tall trees, such as *Streblus elongatus*, may flower as shrubs or treelets.

Most tree species are evergreen, but some are deciduous both in seasonal and ever-wet forest. The trees have intermittent growth, with sometimes conspicuous buds that are temporarily dormant.

Monocaulous or sparingly branched trees, with relatively thick branches and terminal tufts of large leaves (pachycladous, or in Corner's terminology pachycaul, trees), occur in several species of *Ficus* (e.g., *F. pseudopalma*), one species of *Dorstenia* (Africa), and one species of *Naucleopsis* (America). A wide range of tree forms occur between the pachycladous tree and the more common leptoclados one, with slender branches and small leaves mostly evenly distributed on the leafy twigs.

There are c. 100 species of climbers in Malesia, many of them belonging to *Ficus* and *Maclura*. Moreover, this habit is found in single species in *Broussonetia* and *Trophis*, and sometimes in *Prainea scandens*. The climbing habit is rare in Africa and America, in each restricted to a single species of *Maclura* and to one or two (sub)liancescent *Ficus* species. The climbers may be twining or straggling (*Trophis scandens* and species of *Ficus* subg. *Sycidium* sect. *Palaeomorphe*), scramblers with thorns (*Maclura*), or root climbers (*Ficus* subg. *Synoecia*).

Most species are unarmed, although thorns are found in *Maclura* and *Streblus*, in the former often to assist climbing. Spiny leaf margins and/or apices occur in some species of *Streblus* and also in the neotropical genera *Clarisia* and *Sorocea*.

Fatoua is predominantly herbaceous as are the majority of *Dorstenia*. In the latter genus there are a wide range of herbaceous life forms: stem succulents, tuber succulents, geophytes, epiphytes, and annuals (Berg & Hijman 1999). In both of these genera, plants can be suffrutescent. Suffrutescence is also known in the essentially woody *Ficus* (e.g., *F. griffithii* Miq. (Asia) and *F. suffruticosa* Corner (New Guinea)) and the neotropical *Perebea* (*P. humilis* C.C. Berg).

Hemi-epiphytism is a prominent life form in *Ficus*, which also has two species that can be holo-epiphytes. The very wide range of life and growth forms in *Ficus* are described under the genus.

The twig apices are shed in *Morus* and *Broussonetia*, and elongation of twigs is performed by the meristem in the upper most lateral bud; the resting buds are scaled. This trait is also found in other elements of northern temperate forest, such as *Tilia* and

Ulmus. Shoot apices are even abscised in tropical lowland species of the two moraceous genera.

Trichomes — The unicellular hairs vary in length, diameter, shape, septation, and colour; they show particularly great variation in *Ficus*, including interwoven and irritating hairs. Uncinate hairs are quite common as in most other Urticales. They occur frequently in the Dorstenieae, often in Artocarpeae and Moreae, but are absent in Castilleae, and in *Ficus* only known from three species. Cystolith hairs form scabrous surfaces as in many *Ficus* species and *Antiaris* (Renner 1907). Pluricellular trichomes are very common and varied in shape and colour. The pluricellular, globose or ellipsoid, capitate trichomes that occur in (nearly?) all species of Moraceae have often been described as glandular.

They are mostly whitish and can be found on the young plant parts. The heads vary in shape (Bhat & Kachroo 1979) and may have diagnostic value. Pluricellular trichomes may also be elongate and can be found in many species of *Ficus* (in particular of the monoecious subgenera), and are then mostly brown.

Exudates — The family is characterized by the presence of latex, usually milky, sometimes ± watery (as in some *Ficus* species) or entirely watery as in *Fatoua*. The latex can be poisonous as in *Antiaris toxicaria*, *Ficus magnolifolia*, and *Parartocarpus venenosus*, or coagulate into rubber (as in *Ficus elastica*). That of *Ficus tinctoria* is used to prepare a red dye (Florence 1997).

Glands — Nearly all species of *Ficus* have glandular spots with a waxy surface. They occur on the leaves or on the nodes of leafy twigs (see FM 17-2: 84). Glands in similar positions to many *Ficus* species are found in most species of *Artocarpus* subg. *Pseudojaca* (see p. 108); it is not clear whether they exude wax as in *Ficus*. *Artocarpus altissima* has glands on the margin of the lamina, which is unique in Moraceae.

Leaves — The leaves are mostly alternate and spirally arranged or distichous. Opposite leaves are found in some groups of *Ficus* (subg. *Sycidium* and subg. *Sycomorus*), often in combination with alternate arrangement. Opposite leaves may also occur in *Broussonetia papyrifera* and are characteristic for the neotropical genus *Bagassa*. Subverticillate leaves occur in some species of *Ficus* subg. *Sycidium*. Such arrangement of the leaves occurs occasionally in *Artocarpus* (subg. *Pseudojaca*).

The lamina varies from large, up to 2 m long in *Ficus solomonensis* or up to 1 m wide in *F. dammaropsis*, to very small, not more than 3 cm long in *F. vaccinoides* King from Taiwan, and from 2 cm in *F. humbertii* C.C. Berg from Madagascar, or some neotropical *Dorstenia* species. The lamina is usually basally attached (peltate in some species of *Dorstenia*). It is mostly entire, less commonly pinnately or palmately incised. Pinnately incised laminas occur in some species of *Artocarpus*, *Dorstenia*, and *Ficus*, palmately incised ones in *Broussonetia*, *Dorstenia*, *Ficus*, and *Morus*. The venation is mostly brochidodromous. The tertiary venation is basically scalariform, with numerous parallel transverse veins in the intercostal area. This type of venation evolved into a reticulate pattern, and, in some groups of *Ficus*, subsequently into tertiary venation largely parallel to the secondary venation.

The texture of the lamina varies from thickly coriaceous to chartaceous, or even membranaceous in herbaceous genera. The margin is usually entire in coriaceous laminas (of evergreen forest species) and often dentate in thinner ones. The petiole varies from long to short. Long petioles are generally associated with cordiform laminas.

The stipules are often fully amplexicaul, leaving annular scars, by which so many Moraceae can be recognized, but they may also be semi-amplexicaul or lateral. The stipules vary from large (more than 10 cm long) to small (down to 1 mm long). They are mostly caducous but may be persistent or subsessile.

Inflorescences — The inflorescences are mostly paired as in other families of the Urticales. The types of inflorescences range from cymes, to racemes, to spikes (slender or thick and almost spadix-like), to heads, either globose- to ellipsoid-capitate, or discoid (bisexual or unisexual, involucrate or not), or to urceolate structures (opening or remaining closed).

They have a simple structure: racemose, spicate, cymose, or capitate, and mostly unisexual in the tribe Moreae and in the neotropical genera of the tribe Artocarpeae. The staminate ones often resemble catkins of Amentiferae, but the pistillate ones in fruit look different owing to the fleshy pericarp, perianths and/or interfloral bracts. In the majority of the Moraceae the inflorescences are complicated by condensation of axes, by fusion of homologous or adjacent structures, more prominent bracts, and bisexuality of inflorescences. These complex structures are mostly the functional entities with regard to pollination, and in fruiting state, to dispersal, as is very clearly the case in the syconium or fig of *Ficus*. The complex inflorescences can be pseudoflorous, but are more often pseudocarpous and they usually bear numerous flowers. Reduction to the uniflorous state sometimes occurs (e.g., in *Ficus oleifolia*, and in the neotropical *Perebea humilis*).

The abaxial sterile strip or groove, which is particularly clear in elongate inflorescences, indicates adaxial orientation of the flowers in essentially racemously constructed inflorescences. Pistillate flowers tend to occur in the centre of bisexual (essentially cymosely constructed) inflorescences and staminate flowers in the periphery (Berg 1977).

Some flowers and inflorescences show clear adaptation to the mode of pollination. In other cases the primary modifications seem to be for the protection of developing stamens and ovaries against predation by insect larvae (cf. Berg 1990). This protection can often be related to insects breeding in staminate inflorescences before later pollination.

The inflorescences are mostly axillary. They may occur below the leaves on previous season's growth, often so in deciduous species. Ramiflorous inflorescences are born on short-shoots which are often already present in the leaf axils and often continue to bear inflorescences below the leaves, even down to the smaller branches. Cauliflorous inflorescences on short spur-like branchlets or on branches with long internodes are found in *Artocarpus* and in *Ficus*. In the latter genus such branches produced at the base of the trunk may become stolon-like (flagelliflory or geocarpy). Cauliflory is also found in the African genus *Treculia* and the neotropical genus *Clarisia*.

Flowers — Moraceous flowers are small, monochlamydeous, and usually unisexual. Flowers with stamens and non-functional pistils are found in *Ficus* subg. *Sycidium*. The flower is often 4-merous, but the number of tepals may be more or less than 4, or the perianth may be absent (e.g. in *Brosimum* (male, America), in *Hullettia* (male and female?), *Treculia* (female, Africa), and *Trilepisium* (male, Africa), or strongly reduced as in several species of *Ficus* subg. *Sycomorus* sect. *Sycocarpus* (female, Asia).

The number of stamens is rarely more than 4 (e.g. in subg. *Ficus*), but often less; *Artocarpus* and many species of *Ficus* have only one. The tepals are either imbricate or valvate (as in *Trophis*), or narrow and not touching or overlapping each other (e.g. in *Ficus* subg. *Synoecia*). They may be free, or connate, forming tubular perianths, which can be fused with the ovary (e.g. in *Trophis*). Perianths of pistillate flowers either are or become ± fleshy; *Fatoua* and *Ficus* are notable exceptions.

The ovaries contain a single apically or subapically attached, anatropous to campylotropous ovule. There are two stigmata, or one by reduction. The stigmata vary in shape from filiform, to tongue-shaped, to truncate. Heterostyly is found in *Ficus*.

The stamens are straight in the bud in most genera, but in the majority of the species of the tribe Moreae inflexed and at anthesis bend outwards elastically. The anthers have two thecae but, due to fusion, seemingly only one in *Ficus* subsect. *Malvanthera*.

Pistillodes are found in flowers with the urticaceous type of stamens where they may play a role in keeping the anther in position. They are, moreover, characteristic for *Ficus* subg. *Sycidium*, in which they may be as large as pistils. Pistillodes are often found in flowers of *Ficus*, e.g. in subg. *Pharmacosycea* and only occasionally in other groups of Moraceae.

Sexuality — The flowers are unisexual, or in some species of *Ficus* subg. *Sycidium* sect. *Palaeomorphe*, functionally so. The inflorescences are bisexual or unisexual and the plants monoecious or dioecious.

Bisexual inflorescences occur in *Bleekrodea*, *Fatoua*, *Ficus* (subg. *Pharmacosycea*, subg. *Urostigma*, and some species of subg. *Sycomorus*), in some *Streblus* species, as in *S. elongatus*, *S. tonkinensis* (Eberh. & Dubard) Corner, and *S. asper* (sometimes), and in most of the Dorstenieae. Bisexuality of inflorescences is usually found in those that are basically cymose and circular in outline.

Monoeicism, combined with unisexual inflorescences, is found in *Artocarpus*, *Hullettia*, and *Streblus* p.p. A single pistillate inflorescence with several staminate inflorescences on the same node (or short-shoot) are often found in species of the Castilleae, as in *Antiaris* and *Castilla*.

Dioecism is found in *Antiaropsis*, *Broussonetia*, *Maclura*, *Morus*, *Parartocarpus*, *Prainea*, *Streblus* p.p., and *Trophis*. In *Ficus*, the subgenera *Ficus*, *Sycidium*, *Synoecia*, and *Sycomorus* p.p. are morphologically gynodioecious, but functionally dioecious. In functionally female inflorescences of *Ficus*, neuter flowers may substitute the staminate flowers.

Androdioecism, in combination with bisexual and unisexual inflorescences, is known from the American *Helianthostylis* Baill. It may occur in the African *Bosqueiopsis* De Wild. & T. Durand, and in combination with unisexual inflorescences in *Castilla*.

Fruits — The distribution of the family suggests that the dehiscent drupe might be the basic fruit type of Moraceae (Berg 1977). The exocarp is whitish, stipitate at the base, and laterally thickened. The turgid halves clasp the endocarp body, kept in its position by the vascular bundle running on top of it. When this bundle breaks the endocarp body is ejected from the fruit if it is small, or is squeezed out if it is large. It can also be ejected as in *Streblus elongates* and *S. macrophylla*, in the latter up to 10 m from the tree (pers. comm. Dr. D.J. Middleton). Small endocarp bodies, as can be found in *Fatoua* (and *Dorstenia*), are white and tuberculate; large ones are black and smooth (*Antiaropsis*, *Streblus*). Dehiscent drupes are found in *Antiaropsis*, *Bleekrodea*, *Broussonetia*, *Dorstenia* (except for the only epiphytic species, see Berg & Hijman 1999), some species of *Ficus*, *Fatoua*, *Scyphosyce* Baill. (Africa), *Sparattosyce* Bureau (New Caledonia), and *Utsetela* Pellegr. (Africa). Some of the features of the pericarp of the dehiscent drupe, such as the basally narrowed and/or laterally thicker pericarp, can also be found in indehiscent types.

The ovary is often fused with the perianth and the features described above are obliterated. Fruits with dry pericarps are found in the majority of the *Ficus* species. The stipitate base often found in the achene of *Ficus* might be homologous to the stipitate base of the dehiscent fruit.

The seed coat, protected by the more or less hard endocarp, is thin, but often conspicuously vascularised. Small seeds contain endosperm, as in *Ficus*, but in large seeds it is (almost) lacking. The embryos of small seeds are simple, those of large seeds more elaborate with thick, folded and/or unequally large cotyledons and short or long radicles.

References: Berg, C.C., Urticales, their differentiation and systematic position, in: K. Kubitzki (ed.), Flowering plants – Evolution and classification of higher categories. Pl. Syst. Evol., Suppl. 1 (1977) 349–374. — Berg, C.C., Differentiation of flowers and inflorescences of Urticales in relation to their protection against breeding insects and to pollination. Sommerfeltia 11 (1990) 13–34. — Berg, C.C. & M.E.E. Hijman, The genus Dorstenia (Moraceae). Ilicifolia 2 (1999) 1–211. — Bhat, M.M. & P. Kachroo, The trichome in phylogeny of Urticales, in: C.P. Malik (ed.), Annual Rev. Pl. Sci. 1 (1979) 375–407. — Florence, J., Flore de la Polynésie Française 1. Paris (1997). — Renner, O., Beiträge zur Anatomie und Systematik der Artocarpeen und Conocephaleen insbesondere der Gattung *Ficus*. Bot. Jahrb. Syst. 39 (1907) 319–448.

WOOD ANATOMY

(P. Baas - Leiden & E.A. Wheeler - Raleigh, North Carolina)

Wood anatomy — For a very full bibliography of the wood anatomy of the Moraceae see Gregory 1994. The microscopic wood structure of numerous Malesian taxa is also documented with coded wood descriptions (following the standard codes of the IAWA Committee 1989) on the InsideWood web page (<http://insidewood.lib.ncsu.edu>). The general description of the Malesian genera treated in this volume (i.e., Moraceae excluding *Ficus*) is based on these coded descriptions, which in turn are based on literature cited at the end of this section. Of the genera *Bleekrodea*, *Fatoua*, *Hullettia* no wood anatomical data were available to us.

Heartwood is either distinct and dark, or not clearly demarcated from the sapwood. The texture of the wood is usually medium to coarse. Interlocked grain fairly often occurs in the family.

Growth ring boundaries are absent or faint except in some species of *Antiaris*, *Artocarpus*, *Broussonetia*, *Maclura*, *Morus*, and *Prainea* where they can be distinct. Wood typically diffuse-porous, but semi-ring-porous to ring-porous in *Broussonetia* p.p., *Maclura*, and *Morus* p.p., rarely with a tendency towards tangential (*Morus*) or diagonal to dendritic (*Antiaris* p.p.) vessel pattern.

Vessels both solitary and in short radial multiples; in *Artocarpus* p.p., *Maclura*, and *Morus* also partly in clusters. Vessel diameter usually ranging from 100–200 µm but smaller in some species, wider in others; vessels tending to be of two size classes (with the smaller vessels in clusters or multiples) in *Antiaris*, *Broussonetia*, and *Morus*. Vessel frequency usually low (< 5/mm²) to intermediate (5–20 mm²); more rarely higher, especially in *Streblus* p.p. Perforations simple. Intervessel pits non-vestured, alternate, round to polygonal, medium-sized to large (>> 7 µm diam.), but small (4–7 µm) in *Broussonetia* p.p., *Dorstenia*, *Prainea* p.p., and *Streblus* p.p. Vessel-ray pits typically with reduced borders to simple, elongate or round; non-reduced pit borders occur in *Artocarpus* p.p., *Morus* p.p., *Prainea* p.p., and *Trophis*. Tyloses commonly present in heartwood. Gummy and other deposits only recorded in *Artocarpus* p.p. Helical vessel wall thickenings present in *Maclura* (variable) and *Morus*.

Fibres libriform (that is, with simple to minutely bordered pits largely confined to the radial walls); mostly non-septate, but septate in *Antiaris*, *Antiaropsis*, *Castilla*, and *Prainea*; ranging from thin-walled to very thick-walled in close correlation with the density and hardness of the timber.

Parenchyma predominantly paratracheal, usually in a combination of scanty paratracheal to vasicentric and aliform to confluent. Regular tangential parenchyma bands occur in *Artocarpus* p.p., *Dorstenia* p.p., *Maclura*, *Prainea* p.p., *Streblus*, and *Trophis*. Marginal parenchyma bands may occur in species with growth ring boundaries. Parenchyma strands 2–4(–8) cells long.

Rays varying in width and mostly including broad rays over 4 cells wide, but multi-seriate rays 2- or 3-seriate in *Antiaropsis*, *Broussonetia* p.p., *Dorstenia*, *Parartocarpus* p.p., *Streblus* p.p., and *Trophis*; typically heterocellular with 1–4 (or even more) marginal rows of square to upright cells; homocellular and composed of procumbent cells only in *Parartocarpus* and *Maclura* p.p. Sheath cells of varying distinctness present in some of the taxa.

Laticifers usually present in the rays, absent from *Artocarpus* p.p., *Morus*, *Prainea*, and *Streblus*. Prismatic crystals recorded in rays and axial parenchyma cells of *Antiaris*, *Broussonetia*, *Maclura*, *Morus*, *Parartocarpus* p.p., and *Streblus* p.p. Druses recorded in *Broussonetia kurzii*. Silica bodies absent, but vitreous silica sometimes present in some of the genera.

The wood anatomical diversity in the Moraceae is of great systematic significance and also allows microscopic wood identification down to the genus or to groups of related genera. A detailed comparison of the wood diversity pattern in the Moraceae from all over the world, as comprehensively documented in a series of papers by Koek-Noorman, Ter Welle, and Topper with a modern DNA-based phylogenetic classification of the Moraceae is long overdue.

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POLLEN MORPHOLOGY

(R.P.W. Kromhout & R.W.J.M. van der Ham)

Pollen descriptions and illustrations of 25 out of the 37 genera of Moraceae are available (literature cited by Thanikaimoni & Van der Ham 1999). Of the current seven tribes, Antiaropsidæ, Artocarpeæ, Castilleæ, Dorstenieæ, Ficeæ, Moreæ, and Soroceæ (Datwyler & Weiblen 2004, Berg 2005), the tribes Antiaropsidæ, Artocarpeæ, Castilleæ, Moreæ, and Soroceæ show a similar pollen type. The pollen grains belonging to this type are very small to medium-sized (9–33 µm) and 2–6-porate. The shape of 2-porate grains is ellipsoid to spheroidal, if ellipsoid, then often slightly asymmetrical. The shape of 3-porate grains is spheroidal to almost triangular in polar view and oblate to spheroidal in equatorial view. Pollen grains with more than three pores are pantoporate (never stephanoporate) and suboblate to spheroidal. The number of pores per pollen grain may vary within a species and even within individuals. The pores are circular and usually 1–2.5 µm in diameter, but a few species of *Morus* show pores up to 5.5 µm. The exine is thin, up to 1.5 µm thick and tectate. The ornamentation is clearly scabrate using scanning electron microscopy, but indistinctly scabrate or psilate using light microscopy. Commonly, the sexine and nexine are more or less equally thick, while the infratextum is indistinctly columellate. Sometimes, exine stratification is indistinct, using light microscopy. The pollen of tribe Ficeæ (*Ficus*) is similar, but smaller (7–22 µm) and 2- or sometimes 3-porate (Langeveld & Van der Ham 2005). Tribe Dorstenieæ has different pollen, although the size range is more or less the same (10–33 µm) and grains with more than three pores are also pantoporate. The sexine is always thicker than the nexine, and nearly always only faintly stratified. The pollen of *Brosimum*,

Helianthostylis, and *Trymatococcus* is much like the 2-porate pollen of the previous type, but *Brosimum* has a thicker, undifferentiated exine, and the pores may have an annulus and an operculum. *Helianthostylis* and *Trymatococcus* have an annulus and no operculum. The pollen grains of the monotypic genus *Bosqueiopsis* are 3- or 4-angular or asymmetrical and 22–27 µm in diameter. They are 3–6-porate, with slightly annulate pores up to 6 µm. The exine is thin, flexible and scabrate. The genus *Trilepisium* has pollen like that of *Bosqueiopsis*, but the grains are smaller (19–23 µm), have more (8–12) and slightly smaller pores without annuli or aspides. The scabrate ornamentation is slightly more coarse. *Utsetela*, another monotypic genus, has according to Hoen & Punt (1989) the most primitive pollen in the tribe. It is pantoporate, with 15–20 sunken pores, and a thick, slightly scabrate exine with distinct columellae. It lacks annuli, aspides and operculi. *Dorstenia* is the largest genus in the tribe (c. 170 species). Hoen & Punt (1989) found nine different pollen types in a study of approximately one third of the total number of species. *Dorstenia* pollen is ellipsoid to spheroidal. The grains are 6–80-pantoporate, and may have annuli, aspides, and operculi.

The pores are usually distinctly sunken. The exine is mostly thin, but varies in thickness due to the presence of annuli, aspides, and the often verrucate ornamentation. Usually, scabrae are present as well. Columellae are faint, but visible, using light microscopy.

An important factor in pollen morphological diversity in plant groups is the presence of different pollination syndromes. Unfortunately, pollination data of Moraceae (except *Ficus*) are scarce. Very little is known of pollination in the pollen morphologically most diverse tribe Dorstenieae. Beetles have been found on flowers of *Dorstenia* species, but their role in pollination has not yet been satisfactorily demonstrated (Hoen & Punt 1989, Berg & Hijman 1999). Other *Dorstenia* species have flower types that are usually associated with wind pollination, or have flowers that seem to suggest pollination by flies (Berg & Hijman 1999). Further pollination studies may elucidate the origin of the remarkably diverse pollen morphology in the Dorstenieae.

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PHYTOCHEMISTRY AND CHEMOTAXONOMY

(R. Hegnauer)

Relatively few members of the family have been examined thoroughly by phytochemists. So the chemical characterisation must be regarded as a very incomplete and provisional one. The following features seem to be typical to some extent of Moraceae:

- 1) Most members of the family deposit large amounts of silicic acid and calcium carbonate in the walls of leaf cells, especially hairs and unspecialised epidermal cells. Cystoliths and crystals of calcium oxalate are ubiquitous.
- 2) Mucilage cells and ducts occur frequently. Thorough chemical characterisation of different kind of mucilage of Moraceae are still lacking.

- 3) Latex-cells and non-articulated latex tubes are widespread. Some species produce rubber-rich latex. In other species, ‘resins’ (triterpenic alcohols and their acetates and cinnamates) or ‘waxes’ (ethers of cerotinic acid, esters of triterpenic alcohols with several fatty acids) predominate. Still other species produce protein-rich latex; ficin is a papain-like enzyme from the latex of several species of *Ficus*, ficin containing latex is used locally as anthelmintic (in the Neotropics).

A few genera are known to contain cardio-toxic compounds; these have been isolated from, or demonstrated to be present in, latex of *Antiaris*, *Castilla*, *Naucleopsis* (= *Ogcodeia*), barks of *Streblus*, and seeds of *Antiaris*, *Antiaropsis*, *Castilla*, and *Naucleopsis*. The latex of *Antiaris toxicaria* is used as arrow poison in eastern Asia, and that of some species of *Naucleopsis* for the same purpose in the Neotropics (Bisset & Hylands 1977). Still other species seem to produce latexes which are very rich in phenolic compounds; Vreede (1949) observed flavonoids (not definitely defined) in yellow latexes of several species of *Ficus*. Chlorogenic acid was isolated from the latex of *Castilla elastica*.

- 4) Polyphenolic compounds are common in Moraceae. Derivates of p-coumaric acid, caffeic acid, kaempferol, and quercetin occur frequently in leaves. Myricetin is less common. Leucoanthocyanins are absent of the leaves of many species, but often present in species of *Ficus*. The so-called tannin-idioblasts of the anatomical literature are present in the mesophyll of many species. They probably contain catechins and leucoanthocyanins, but no true tannins, which have yet to be demonstrated in Moraceae for certain.
- 5) The compounds of most interest from the systematic point of view are the highly characteristic phenolic compounds which seem to be rather common in the roots, stems, fruits, and sometimes the leaves. These phenolics may roughly be classified in four groups: C₆-C₃-compounds (coumarins), represented by furanocoumarins and dimethylpyranocoumarins); C₆-C₁-C₆-compounds (benzophenones like maclurin and xanthones); C₆-C₂-C₆-compounds (stilbenes like chlorophorin and hydroxyresveratrol); C₆-C₃-C₆-compounds (highly characteristic flavonoids like cyanomaclurin, morin, artocarpetin, cycloartocarpin, and pomiferin). The resistance of the woods of some members of the family to the attack by fungi, insects, and termites, and the tinctorial properties of the woods of others, are largely due to such polyphenolic compounds.
- 6) Saponins and alkaloids seem to be rather rare in Moraceae. Alkaloids are known from some species of *Ficus*. No taxonomic implications are apparent at present from these occurrences.

To sum up, the accumulation of minerals in leaves (SiO₂, CaCO₃), and the production of a whole array of unusual phenolic compounds represent the most striking, currently known, phytochemical features of Moraceae.

With regard to the different mineralizations (including the presence of cystoliths) the family resembles Cannabidaceae and Urticaceae.

Some outstanding features of phenolic compounds of Moraceae indicate similarities in secondary metabolism with members of the rosaceous alliance, especially with Leguminosae.

These features are: production of furanocoumarins, isoflavones (osajin, pomiferin), stilbenes, flavonoids with a resorcin-type hydroxylation pattern of the B-ring (cyanomacclurin, artocarpetin, morin, etc.), and the frequent attachment of isoprenoid substituents to aromatic rings (coumarins, stilbenes, and flavonoids).

Isoprenylation also marks moraceous xanthones (alvaxanthone, macluraxanthone), in which respect the family resembles Guttiferae. Knowledge of the distribution of all these types of phenolics is still rather scanty. It would be cautious therefore not to put too much weight on the metabolic similarities mentioned. A more comprehensive review of chemical characters may be found in Hegnauer (1969).

Volatile compounds produced by inflorescences of *Ficus* play an important role in attraction of pollinators. Compounds extracted from receptive syconia of *F. carica* include benzyl alcohol, linanol, linanol oxides (furanoid), several aromatic compounds (cinnamic aldehyde, cinnamic alcohol) and indole¹ (Gibernau et al. 1997).

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CYTOTAXONOMY

There are two series, one with the haploid number of 13 and the other with 14 (Fedorov 1969; Oniguma & Tobe 1995). *Brosimum*, *Broussonetia*, *Streblus* p.p., and *Ficus* belong to the first series. *Ficus* are mostly diploids, but some (mainly African species) are or can be tetraploid, and *F. elastica* triploid (Ohri & Khoshoo 1987). The genera belonging to the second series are *Antiaris*, *Artocarpus*, *Castilla*, *Clarisia*, *Maclura*, *Morus*, *Pseudolmedia*, *Scyphosyce* (cf. Berg 1977), *Streblus* p.p., and *Trophis*. Some *Artocarpus* species are tetraploid (or hexaploid in cultivars of *A. altilis*) and some *Morus* species polyploid, up to $2n = 308$. *Dorstenia* shows much variation in its chromosome numbers: $2n = 24, 26, 28, 30, 32, 36, 38, 40, 42, 48, 52$, and c. 64 (Berg & Hijman 1999). Deviating numbers are reported for *Maclura tricuspidata*, $2n = 50$ (Morawetz & Samuel 1989) and *Naucleopsis guianensis*, $2n = 20$ (Dmitrieva & Parfenov 1985). The haploid chromosome number of both *Cecropiaceae* and *Ulmaceae* is 14, that of *Urticaceae* varies from 7 to 14. The chromosome numbers of the *Cannabidaceae* deviates from the general pattern in the order.

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ECOLOGY

The majority of the species are elements of lowland, mostly evergreen forest or less frequently, seasonal forest. Trees of coastal, riparian, and secondary growth occur mainly in *Ficus*, but *Streblus asper* is characteristic of the more seasonal forest of western Malesia.

Some species of *Ficus* (*F. deltoidea* and *F. oleifolia*) often occur on poor sandy soil in kerangas forest. Other species of *Ficus* are associated with calcareous substrates (*F. anastomosans*, *F. calcarata*, *F. calcicola*, *F. subcaudata* (?), and the form *F. tinctoria* described as *F. swinhoei*). A form (ecotype) of *F. ulmifolia* is associated with extreme ultra basic soil (Philippines).

Hemi-epiphytic species can be hemi-epilithic on exposed rocky surfaces.

Some species of *Ficus* are more or less clearly rheophytic (see FM17-2: 27), e.g., *F. ischnopoda*, *F. macrostyla*, and *F. squamosa*, the latter two with fruitlets with long persistent styles and retrorse stiff hairs on the style and the margin of the fruit body morphologically adapted to the unusual substrate.

In general, the upper altitudinal limit of lowland species is 1500 m. Montane species, above 2000 m, are found in *Ficus* and *Streblus*. *Morus macroura* can also be regarded as montane. The hardier Moraceae of Sino-Himalaya do not reach Malesia.

REPRODUCTIVE BIOLOGY

Pollination — Wind-pollination occurs in Moraceae with urticaceous type stamens and may occur in some other species, such as those with long pendulous staminate inflorescences. Anemophily is also reported for patent (scentless) staminate inflorescences of some species of *Artocarpus* (e.g., *A. elasticus* and *A. rigidus* (Corner 1940, 1988; Jarrett 1959) that give off clouds of pollen. The ballistic release of pollen from urticaceous type stamens allows plants to inhabit the forest undergrowth where they can make use of weak air currents, as above streaming water, for the transport of pollen. This type of pollination is described and discussed for *Streblus pendulinus* and *Trophis scandens* by Williams & Adam (1993).

Geitonogamy might occur in species with bisexual inflorescences, such as *Dorstenia*.

Insect-pollination is probably the predominant mode of pollination in the family. The unique mode in *Ficus* is well-documented (see FM 17-2: 51–54). Another is described for *Artocarpus* (Van der Pijl 1953), in which species with staminate inflorescences (e.g., *A. dadah* and *A. integer*; Corner 1940) emit a sweet scent of honey and burnt sugar, to attract small flies and beetles which subsequently breed in the inflorescence. Pollination based on insects breeding in staminate inflorescences is common in many tropical plant groups with reduced and unisexual flowers (such as palms), and is probably widespread in those Moraceae with dense unisexual inflorescences as well. In *Castilla*

elastica and *Antiaropsis decipiens* this role is played by thrips (Sakai 2001; Zerega et al. 2004), which could be the case in other genera where the staminate inflorescences are (\pm) closed before anthesis. In some species of *Artocarpus* with scentless staminate inflorescences, clouds of pollen are given off, e.g. in *A. elasticus* and *A. rigidus* (Corner 1938, 1940; Jarrett 1959).

An unusual mode of pollination is described for *A. integer* in Sarawak (Sakai et al. 2000): staminate inflorescences infected and covered by fungus are visited by a species of gall midge that feeds on the mycelium and oviposits on the inflorescence. The midges transport pollen to pistillate inflorescences. It is not clear whether this is a local phenomenon or widespread in the species.

Dispersal — The seeds are usually animal dispersed, although this may not be the case if the fruits are dehiscent drupes. Here, small endocarp bodies (kernels) are ejected (*Dorstenia* and *Fatoua*) or, if large, are squeezed out (*Antiaropsis* and *Streblus* p.p.), and drop on the forest floor or into water (by which they are carried on) or are ejected (see p. 8). The endocarp bodies, which are animal dispersed, remain inside the infructescence (*Broussonetia* and *Ficus*). Alternatively they may be large, black, and embedded in structures with contrasting colours (e.g. white of the exocarp and red of tepals as in *Antiaropsis*), in which case they may be dispersed by birds. In the majority of the Moraceae the fruits (and seeds) are enclosed in fleshy structures consisting of connate perianths and interfloral bracts (*Artocarpus* and related genera), or also adnate to the receptacle (*Hullettia*), or enclosed in fleshy receptacles (*Ficus*). The infructescence may more simply be just aggregations of flowers in fruit of which the fleshy perianths are the attractive parts (*Morus*). More or less solitary fleshy (dehiscent or indehiscent) fruits occur in *Streblus*. The colour of individual fruits or of infructescences varies from red to orange. Large infructescences are often greenish to yellowish. The infructescences of *Ficus* can be blackish, or sometimes brown or purplish and then taken by fruit bats.

Moraceous fruits and infructescences are taken by birds, monkeys, squirrels, and other arboreal animals by day. By night the same fruits, or those of allied species, are taken by nocturnal animals, such as fruit bats and civet cats. Cauliflorous species of *Artocarpus* and *Ficus* may also be dispersed by bats as well as by ground mammals, ranging from elephants and rhinoceros to pigs and mouse deer.

Water may play a role in distribution of diaspores ejected or fallen into streams. The fruitlets of some rheophytic *Ficus* species are adapted to attachment to the substrate.

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DELIMITATION AND SUBDIVISION OF THE FAMILY

In the classification by Engler (1888) the family Moraceae included the subfamily Conocephaloideae, with six genera, including the Asian genus *Conocephalus* Blume. In a revisional study by Chew (1963) the genus was united with the urticaceous genus *Poikilospermum* Zipp. ex Miq. This led to proposals to transfer some or all the genera of the Conocephaloideae (Chew 1963 and Corner 1962, respectively) to the Urticaceae. For these six genera the family Cecropiaceae Berg (1978) was established.

The order Urticales constitute a clear-cut and coherent group. Moraceae differs from the Urticaceae in the presence of milky sap (or latex), the apical attachment of the ovule, the common presence of two stigmas, the absence of elongate cystoliths, and the predominantly woody habit in Urticaceae. The stamens are always inflexed in the bud and bend outwards suddenly, throwing the pollen into the air. Urticaceous stamens also occur in most species of the tribe Moreae. Inflexed stamens resembling those of Urticaceae occur in some genera of the Ulmaceae. The family Cecropiaceae is entirely woody and differs from the Moraceae in some features shared with Urticaceae, such as the basally attached ovule and single stigma, by strict dioecism, the absence of milky sap, the presence of adventitious roots (in the woody genera of Moraceae only present in *Ficus*), and the always spirally arranged leaves. Ulmaceae share with Moraceae the apically attached ovule, but lack milky sap. In contrast to the other families, the flowers are morphologically and often also functionally bisexual. Judd et al. (1994) suggested including Cannabidaceae, Cecropiaceae, Moraceae, in the Urticaceae, leaving the Celi-daceae and Ulmaceae as two much smaller urticalean families.

The Urticales show rather clear morphological affinities to the Malvales and somewhat remotely to the Euphorbiales, but they do not show links to the other families traditionally ranked among the Hamamelidae. Molecular studies place Urticales among the Rosales (Sytsma et al. 2002), but this contradicts patterns of morphological differentiation, ecology, and phytogeography, which suggest a different evolutionary history of the group (but see chapter ‘Phytochemistry and Chemotaxonomy’, p. 11).

For the reduced family Moraceae Corner (1962) proposed seven tribes, which with some adjustments was reduced to five tribes (Berg 1988, 2001): Moreae (8 genera, 70–75 spp., centred in Asia and characterized by the urticaceous type of stamen, see p. 7); Castilleae (8 genera, 50–60 spp., centred in the Neotropics and characterized by trees with the architectural model of Cook (see p. 138); Dorstenieae (8 genera, 125–130 spp., amphi-atlantic and characterized by circular bisexual inflorescences); and Ficeae (1 genus, 720–750 spp., characterized by essentially bisexual, urceolate inflorescences). More recently the tribe Artocarpeae was redefined and two additional tribes established (Berg 2005): Artocarpeae (4 genera, c. 55 spp, centred in Asia and characterized by many-seeded infructescences, mostly formed by connate flowers, but with free fruits); Antiaropsideae (2 genera, 3 or 4 spp.), in New Caledonia and New Guinea and characterized by involucrate inflorescences and dehiscent drupes); and Soroceae (5 genera, 23

spp., neotropical and characterized by simply constructed, Moreae-like inflorescences but with stamens straight in the bud).

In the classification of Moraceae proposed by Corner (1962) the number of genera previously recognised for the Asian–Australasian region was reduced considerably. This study and others by Berg (e.g., 1986, 1988), in which some of the Asian–Australasian representatives of the family were involved, resulted in the recognition of 37 genera worldwide. These appear to be largely natural ones and show interesting patterns in geographical distribution and taxonomic relationships.

A molecular phylogenetic study by Datwyler & Weiblen (2004) largely supports distinctness and homogeneity of Castilleae, Dorstenieae, and Ficeae, but not so of Artocarpeae (*sensu stricto*), Moreae, and Soroceae, not even at the generic level. Moreover, the study indicates affinities of Antiaropsideae to Castilleae and Ficeae. Support for this phylogeny from morphology and phytogeography is still wanting. The phylogeny of the more recent molecular study by Zerega et al. (2005) is rather similar and pays attention to biogeography and divergence times, but hardly to patterns in morphological differentiation.

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USES

Streblus elongatus and several species of *Artocarpus* are, or have been, outstanding producers of timber. Lesser known are the timber trees found in the genera *Antiaris*, *Parartocarpus*, and *Prainea* (Boer & Sosef 1998). *Ficus elastica* and the American *Castilla elastica* have been used for rubber and remains of their plantations may be found throughout Malesia, but they have given place to *Hevea* because of their resinous milksap. Poisonous milksap occurs in the famous upas tree *Antiaris* (see Boer et al. 1999) and in the much less common *Parartocarpus*; that of both is used as (one of the components of) dart and arrow poison in South-east Asia. The sap of many species of *Artocarpus*, by contrast, being very sticky and innocuous, is used for birdlime and

general adhesive; whereas that of *A. lowii*, is oily and greasy and is used as an ointment and for cooking. Fibrous and easily-stripped bark of several species of *Artocarpus*, such as *A. elasticus*, is made into coarse bark cloth and binding material, but this is disappearing even from the life of jungle folk; many anthropological exhibits in museums are held together by this material. The fibrous bark of *Ficus* is used for string, even for bow strings, but being readily cropped these plants have not been commercialised. Paper is manufactured from the inner bark of the paper mulberry *Broussonetia papyrifera*, as well as fibre clothing and string among primitive people (Berg 2003). Edible fruits are the mulberries (*Morus*), various kinds of figs (*Ficus*), several kinds of *Artocarpus*, and indeed *Antiaris*, the fruits of which seem always devoid of poison. Introduced mulberries have found little favour in Malesia. The cultivated fig (*Ficus carica*) is rarely seen because it succumbs readily to insect attacks. Sometimes the Indochinese *Ficus auriculata* is cultivated, but its fruit is inferior. Certain wild figs are, however, not despised. The best known fruit trees of the family in Malesia are the jackfruit (*Artocarpus heterophyllus*) and the chempedak or chemedak (*A. integer*). They are grown both for the edible pulp around the seeds and for the seeds themselves which are roasted. Some varieties of the jack produce infructescences, which may hold the world record for fruit size. Few fruits can equal in stench some varieties of the chempedak. The breadfruit tree (*Artocarpus altilis*), commonly seen in villages, is extremely abundant both wild and cultivated in New Guinea, where it is grown for the unripe fruit which is baked, roasted, or boiled more like a tuber than a fruit; the seedless form is most usually cultivated. *Artocarpus odoratissimus* is cultivated in Borneo and the Philippines for the sweet pulp round the seed. *Artocarpus nitidus*, with the uniformly succulent kind of infructescence, is sometimes found in gardens in West Malesia, where it is used also for jam and conserves. Other species of *Artocarpus* are mostly wild trees which have been spared from felling for sake of their fruit. Leaves and young figs of several *Ficus* species are eaten either cooked or raw as vegetables.

Yellow dye is extracted from wood of *Maclura cochinchinensis* (Heyne 1927).

References: Berg, C.C., *Broussonetia papyrifera* (L.) L'Hér. ex Vent., in: M. Brink & R.P. Escobin (eds), *Plant Resources of South-East Asia 17, Fibre plants* (2003) 91–95. — Boer, E., M. Brink & M.S.M. Sosef, *Antiaris toxicaria* Lesch., in: L.S. de Padua, N. Bunyaphraphatsara & R.H.M.J. Lemmens (eds), *Medicinal and poisonous plants 1. Plant Resources of South-East Asia 12 (1)* (1999) 126–129. Backhuys Publishers, Leiden. — Boer, E. & M.S.M. Sosef, *Antiaris, Parartocarpus, and Prainea*, in: M.S.M. Sosef, L.T. Hong & S. Prawirohatmodjo (eds), *Timber trees: Lesser known timbers. Plant Resources of South-East Asia 5 (3)* (1998) 73–75, 425–427, 469–470. Backhuys Publishers, Leiden. — Heyne, K., *De nuttige planten van Nederlandsch-Indië* ed. 2, 1 (1927). Ruygrok & Co., Batavia.

KEY TO THE TRIBES

- 1a. Inflorescences urceolate, the opening entirely closed by (ostiolar) bracts; waxy glandular spots on the lamina lower surface (on the base of the midrib, in the axils of lateral veins and/or furcations of lateral veins), or on leafy twigs just below the nodes **Ficeae**
- b. Inflorescences mostly spicate, capitate, or discoid, or if urceolate, then the opening not entirely closed; waxy glandular spots mostly absent (present in *Artocarpus* subg. *Pseudojaca*) 2

- 2a. Stamens bent inwards in bud, at anthesis bending outwards suddenly and elastically, or if straight in the bud, then the plant armed with thorns on the branches **Moreae**
- b. Stamens straight or bent outwards in bud or, if bent inwards, then straightening gradually; plants without thorns 3
- 3a. Inflorescences discoid-, turbinate- or globose-capitate, bisexual, or if (secondarily) unisexual, then fruits adnate to the perianth (and receptacle), or the plant herbaceous **Dorstenieae**
- b. Inflorescences spicate, clavate- to globose- (to discoid-)capitate, or discoid-capitate to urceolate and involucrate, (primarily) unisexual; plant woody 4
- 4a. Trees with self-pruning branches; inflorescences discoid and involucrate with imbricate bracts; fruit adnate to the perianth, if not so, then the exocarp indehiscent **Castilleae**
- b. Trees without self-pruning branches; inflorescences not involucrate (or subinvolucrate), or if involucrate, with imbricate bracts and the fruits with a dehiscent exocarp 5
- 5a. Inflorescences discoid to urceolate, involucrate with basally attached imbricate bracts enclosing the flowers, at least before anthesis; fruits dehiscent drupes **Antiaropsideae**
- b. Inflorescences spicate to clavate-, ellipsoid-, to globose-, or discoid-capitate, if the heads subtended by bracts, then these short and not enclosing flowers before anthesis; fruits indehiscent **Artocarpeae**

KEY TO THE GENERA

- 1a. Plants herbaceous or suffrutescent 2
- b. Plants woody 3
- 2a. Plants branched; sap watery **Fatoua**
- b. Plants monocaul and subacaule; sap milky **Dorstenia**
- 3a. Plants armed with thorns 4
- b. Plants unarmed 5
- 4a. Staminate and pistillate inflorescences globose-capitate; stamens straight in the bud **Maclura**
- b. Staminate inflorescences spicate, racemose or capitate and stamens inflexed in the bud; pistillate inflorescences with 1–3 flowers **Streblus** p.p.
- 5a. Inflorescences urceolate and stigmas and anthers not exposed at anthesis; waxy glandular spots on the lamina lower surface (at the base of the midrib, in the axils of lateral veins and/or furcations of lateral veins), or on the nodes of leafy twigs **Ficus**
- b. Inflorescences not urceolate and stigmas and anthers exposed at anthesis; waxy glandular spots mostly lacking, but present on the lamina beneath in the axils of lateral veins only in *Artocarpus* subg. *Pseudojaca* 6
- 6a. Stipules fully amplexicaul 7
- b. Stipules not fully amplexicaul to lateral 8

- 7a. Stipules connate **Castilla**
 b. Stipules free **Artocarpus** p.p.
- 8a. Leaves of lateral (flower-bearing) branches spirally arranged (or subopposite)
 9
 b. Leaves of lateral (flower-bearing) branches distichous 13
- 9a. Stipules connate **Parartocarpus**
 b. Stipules free 10
- 10a. Pistillate flowers connate; staminate flowers with 1 stamen **Artocarpus** p.p.
 b. Pistillate flowers free; staminate flowers with 2–4 stamens 11
- 11a. Inflorescences discoid- to turbinete-capitate with marginal bracts **Hullettia**
 b. Inflorescences spicate or globose-capitate 12
- 12a. Lamina with 3 or 4 pairs of lateral veins (*S. ascendens*) **Streblus**
 b. Lamina with 5–9 pairs of lateral veins (*B. papyrifera*) **Broussonetia**
- 13a. Inflorescences bisexual 14
 b. Inflorescences unisexual 15
- 14a. Inflorescences cymose; perianth of the pistillate flower tubular **Bleekrodea**
 b. Inflorescences spicate; perianth of the pistillate flower with free imbricate
 tepals (*S. elongatus*) **Streblus**
- 15a. Inflorescences discoid-capitate or uniflorous, involucrate with basally attached
 imbricate bracts, or bracts concentrated in the upper part of the receptacle of the
 pistillate inflorescence with a single flower adnate to the receptacle 16
 b. Inflorescences globose-capitate, spicate, racemose, cymose, or if uniflorous, then
 not involucrate 17
- 16a. Receptacle of the pistillate inflorescence infundibuliform, enclosing and fused
 with a single flower; involucral bracts small and partly scattered on the receptacle;
 staminate inflorescences usually several together **Antiaris**
 b. Receptacle of the pistillate inflorescence discoid, the flower(s) free and the invo-
 lucral bracts large, in 4 or 5 rows imbricate; staminate inflorescences solitary ..
 **Antiaropsis**
- 17a. Scaled axillary resting buds present; apices of branches abscised, elongation of
 the branch by the terminal apical lateral bud 18
 b. Scaled resting buds absent (or weakly developed) and apical bud persistent . 19
- 18a. Pistillate inflorescences globose-capitate; stigma 1; tepals of the staminate flower
 valvate **Broussonetia**
 b. Pistillate inflorescences spicate to subcapitate; stigmas 2; tepals of the staminate
 flower imbricate **Morus**
- 19a. Staminate material 20
 b. Pistillate material 28
- 20a. Stamen 1, straight in the bud 21
 b. Stamens 3, 4, or 5, inflexed in the bud 22
- 21a. Stipules lateral; heads globose to obovoid; perianth 2-lobed to subentire ..
 **Prainea**
 b. Stipules fully amplexicaul or, if lateral, then heads usually distinctly longer than
 wide and perianth 2–4-lobed to parted **Artocarpus**

22a.	Inflorescences spicate, all flowers sessile	23
b.	Inflorescences racemose or cymose or subcapitate, all or some of the flowers pedicellate	27
23a.	Tepals valvate	24
b.	Tepals imbricate	25
24a.	Midrib of the lamina impressed above; stamens 4	Broussonetia p.p.
b.	Midrib of the lamina prominent above; stamens 3 (or 4) (<i>T. scandens</i>)	Trophis
25a.	Bracts basally attached	Streblus p.p.
b.	Bracts (partly) peltate	26
26a.	Midrib prominent above (<i>T. philippinensis</i>)	Trophis
b.	Midrib impressed above	Streblus p.p.
27a.	Inflorescences cymosely branched	Bleekrodea
b.	Inflorescences unbranched	Streblus p.p.
28a.	Flowers connate	Artocarpus
b.	Flowers free	29
29a.	Tepals free	Streblus
b.	Tepals connate	30
30a.	Stigma 1	Broussonetia
b.	Stigmas 2	31
31a.	Perianth fleshy in fruit; ovary adnate to the perianth, or if not, then the plant scandent	Trophis
b.	Perianth membranaceous in fruit; fruit free and the plant a shrub	Bleekrodea

Tribe MOREAE

Moreae Gaudich. in Freyc., Voy. Uranie, Bot. (1830) 509; Corner, Gard. Bull. Singapore 19 (1962) 211; C.C. Berg, Proc. Kon. Ned. Akad. Wetensch. C, 91 (1988) 345.

Broussonetiaeae Gaudich. in Freyc., Voy. Uranie, Bot. (1830) 508.

Strebleae Bureau in DC., Prodr. 17 (1873) 215.

Fatoueae Engl., Nat. Pflanzenfam. 3, 1 (1888) 71.

Trees, shrubs, or in *Fatoua*, herbs or subshrubs, dioecious or sometimes monoecious, with or without uncinate hairs. Leaves alternate and distichous, or less commonly spirally arranged, sometimes (sub)opposite; stipules small to large, lateral to semi-amplexicaul. Inflorescences unisexual or less commonly bisexual, racemose, spicate, cymose, capitate, or uniflorous pedunculate, bracteate; staminate flowers with 3, 4, or 5 tepals; stamens 3, 4, or 5, inflexed in the bud and bending outwards suddenly and elastically at anthesis, or sometimes straight in the bud; pistillode usually present; pistillate flowers with 4, free or connate, tepals; ovary mostly free, stigmas 2 and then equally or unequally long, or 1. Fruit drupaceous, dehiscent and releasing or ejecting the endocarp body, or indehiscent, achene-like, or forming a drupaceous whole with the fleshy perianth. Seed small and with endosperm, or large and endosperm (almost) lacking; testa mostly with a thickened vascularised part below the hilum; embryo various.

Distribution — This tribe comprises eight genera, seven of them represented in Malesia. The eighth genus is *Milicia* Sim, with two species, is confined to the African

continent. The number of species is c. 70, c. 47 of them occur in the Asian–Australasian region. Nine species occur in the Neotropics and two are confined to the North American continent. Twelve species occur in the African region, seven of them are endemic to Madagascar and adjacent islands. These numbers show that the Asian–Australasian region is the centre of this tribe. The largest genus in this region is *Streblus*.

The genera *Morus* and *Broussonetia* can be regarded as elements of the northern warm temperate region (see below). Some species of *Maclura* and *Streblus*, most of them thorn-bearing shrubs, small trees or climbers, are elements of relatively dry climatic conditions.

Staminate flowers and pollination — This tribe is characterised by stamens similar to those characteristic of Urticaceae, but are absent in *Maclura* sect. *Cudrania*. The stamens are inflexed in the flower bud, and bend outwards suddenly and elastically, throwing pollen in the air. This mechanism of ballistic release of pollen requires a well-developed perianth and sufficient space in the inflorescence for the opening of the perianth. In contrast to other tribes, pistillodes are commonly present. They are often quadrangular and apparently play a role in keeping the stamens under tension until anthesis. In the Moreae the inflorescences are relatively simply constructed, and the staminate flowers at least not densely packed – a connection with the ballistic release of pollen. The perianth and the number of stamens is not reduced as often happens in other tribes and the relatively simple construction of the pistillate inflorescences could be related to the requirement of simple staminate inflorescences. Pistillate flowers are mostly free, but (partly) connate in some subdivisions of *Maclura*: sect. *Plecospermum* and sect. *Cudrania* ser. *Connatae*.

Habit — The habit varies from tall primary forest trees to small trees and shrubs, sub-shrubs, to herbs (in *Fatoua*), and climbers (in species of *Maclura* and *Trophis scandens*). Thorns are found in the species of *Maclura* and in some species of *Streblus*, in the former genus they facilitate climbing. Milky sap is absent in *Fatoua*.

Inflorescences — The inflorescences of the Moreae are mostly unisexual. Bisexual inflorescences are typical for *Bleekrodea*, *Fatoua*, and *Streblus elongatus*, although in these taxa the inflorescences can be unisexual, pistillate and/or staminate. In the other taxa the inflorescences are normally unisexual and the plants mostly dioecious. The inflorescences are short-branched cymes, racemes, spikes, heads, or uniflorous (as the pistillate ones in several species of *Streblus*).

Fruits — Dehiscent drupes occur in *Bleekrodea*, *Broussonetia*, *Fatoua*, and some of the *Streblus* species. In other *Streblus* species the fruits are red or black coloured berries. In the other genera the fruits are largely or entirely enveloped by fleshy, mostly coloured perianth.

Delimitation — The tribe as currently defined includes most of the genera referred to this tribe by Corner (1962), but it also includes the other genera with urticaceous stamens such as *Broussonetia*, *Maclura*, and *Malaisia*, as well as the neotropical genus *Olmedia*. The latter two have been reduced to sections of *Trophis* (Berg 1988).

However, the neotropical genera *Clarisia* and *Sorocea* are currently included in the tribe Soroceae (see Berg 2005).

References: Berg, C.C., The genera *Trophis* and *Streblus* (Moraceae) remodelled. Proc. Kon. Ned. Akad. Wetensch. C, 91 (1988) 345–362. — Berg, C.C., Flora Malesiana precursor for the treatment of Moraceae 8: other genera than *Ficus*. Blumea 50 (2005) 535–550. — Corner, E.J.H., The classification of Moraceae. Gard. Bull. Singapore 19 (1962) 187–252.

KEY TO THE GENERA OF THE MOREAE

- 1a. Plants herbaceous (or suffrutescent) **Fatoua**
- b. Plants woody 2
- 2a. Shoot apices deciduous 3
- b. Shoot apices persistent 4
- 3a. Tepals of the pistillate flowers free; stigmas 2, equal **Morus**
- b. Tepals of the pistillate flowers connate; stigma 1, or if 2, then unequal **Broussonetia**
- 4a. Plants armed with curved or straight spines; pistillate inflorescences globose-capitate; tepals and bracts mostly with yellow dye accumulated in immersed glands **Maclura**
- b. Plants unarmed, or if armed, then with straight spines; the pistillate inflorescences not globose-capitate and tepals and bracts without yellow dye containing glands 5
- 5a. Plants mostly with thorns or lamina scabrous above; inflorescences spicate or unisexual; tepals of the pistillate flowers (almost) free **Streblus**
- b. Plants without thorns, lamina smooth above; inflorescences cymose if bisexual; tepals of the pistillate flowers connate 6
- 6a. Inflorescences bisexual, cymose; tepals of the staminate flowers 4 or 5 **Bleekrodea**
- b. Inflorescences unisexual, spicate; tepals of the staminate flowers 4 or 3 **Trophis**

MORUS

Morus L., Sp. Pl. (1753) 986; Endl., Gen. Pl. (1837) 278; Gen. Pl., Suppl. 4 (1848) 33; Bureau in DC., Prodr. 17 (1873) 237; Baill., Hist. Pl. 6 (1875) 190; Benth. & Hook.f., Gen. Pl. 3 (1880) 364; Engl. in Engl. & Prantl, Nat. Pflanzenfam. 3, 1 (1888) 72; Nakai, J. Arnold Arbor. 8 (1927) 234; Gagnep., Fl. Indo-Chine 5 (1928) 706; C.C. Berg, Fl. Neotrop. Monogr. 83 (2001) 25.

Morophorum Neck., Elem. Bot. 3 (1790) 255.

Trees, dioecious, unarmed, shoot apices shed, with axillary scaled resting buds. Leaves distichous; lamina pinnately veined or trinerved to triplinerved, with cystoliths usually only above; stipules free, almost lateral. Inflorescences unisexual, usually solitary on the lower leafless nodes of new (short-)shoots arising from well-developed scaly resting buds on wood of the previous season, ebracteate or bracteate. Staminate inflorescences spicate (or racemose); perianth 4-parted, segments imbricate; stamens 4, inflexed in the bud. Pistillate inflorescences capitate to spicate; perianth 4-parted; ovary free, style subterminal, stigmas 2. Fruiting perianth enlarged, more or less suc-

culent; fruit with a broad base, exocarp thin-fleshy, thicker on the seed-bearing side, indehiscent, endocarp crustaceous with a woody plug towards the hilum; seed with endosperm, embryo curved, cotyledons equal and flat, not enclosing the long radicle.

Distribution — The genus comprises ten to fifteen species, most of them in temperate to subtropical regions of the northern hemisphere, some in montane habitats in the tropics (*M. insignis* Bureau in the Neotropics and *M. macroura* in SE Asia and Malesia), one in the tropical lowlands of Africa (*M. mezozygia* A. Chev., as evergreen tree in rain-forest or as deciduous tree in drier conditions), and one in dry regions of SE United States and Mexico (*M. celtidifolia* Kunth). The North American *M. rubra* L. is closely related to the group of species associated with northern temperate to subtropical conditions and centred in the Himalayan and East Asian region and constituting a complex of very closely related taxa for which a recent taxonomic evaluation is still wanting; this complex comprises, e.g., *M. alba* L. and *M. nigra* L.

Morphology — The association with northern temperate conditions is morphologically expressed in the abscission of shoot apices, the presence of ± well-developed scaled resting buds, and deciduousness, features which are at least partly still pertained by the tropical lowland species.

Chromosomes — Polyploids (4x, 6x, 8x, or even 22x) are found in the Himalayan-East Asian complex of taxa.

Subdivision — Leroy (Bull. Mus. Hist. Nat. (Paris), Sér. 2, 21: 725) recognised three subgenera: *Afromorus* (with *M. mezozygia*), *Gomphomorous* (with *M. insignis*), and *Eumoros* with the rest of the species.

Uses — The genus has a very long historical association with mankind for edible fruits of many species and for the cultivation of the slik-moth.

KEY TO THE SPECIES

- 1a. Lower surface of the lamina barbate, with tufts of hairs in the axils of lateral veins and major furcations of lateral veins; stipules 0.4–1.2 cm long; pistillate spikes to 3.5 cm long, in fruit black or blackish red. — Widespread, in cultivation
..... **1. *M. alba***
- b. Lower surface of the lamina not barbate, hairs ± evenly distributed on the veins; stipules 1–2.5 cm long; pistillate spike (1–)4–8 cm long, in fruit greenish or yellowish. — Sumatra, Java
..... **2. *M. macroura***

1. *Morus alba* L.

Morus alba L., Sp. Pl. (1753) 986; Ser., Descr. Cult. Muriers (1855) 19, t. 1–18; Bureau in DC., Prodri. 17 (1873) 238.

Tree up to 10(–15) m tall. Leafy twigs 1–4 mm thick, (minutely and/or sparsely) puberulous; resting buds 0.3–0.8 cm long. Leaves distichous; lamina ovate or subovate (in outline), 10–20 by 6–15 cm, entire or 3–5(–9)-lobed to -fid, apex acuminate, base rounded to cordate, margin crenate- to serrate-dentate; upper surface minutely white puberulous to hispidulous, scabridulous to smooth, lower surface puberulous to hispidulous on the (main) veins, with concentrations of hairs in the axils of lateral veins and

furcations of lateral veins, scabridulous to smooth; lateral vein (3–)4–6(–7) pairs, the basal pair up to 1/2(–2/3) the length of the lamina, branched, the other lateral veins also branched or furcate far from the margin, tertiary venation loosely scalariform; petiole 1–6 cm long, 2–2.5 mm thick, minutely puberulous; stipules 0.5–1.2 cm long, puberulous, caducous (or subpersistent). *Staminate inflorescences* axillary (often in the axils of scale leaves at the base of new shoots), solitary or in pairs, spicate to racemose, ebracteate; peduncle 0.5–1.5 cm long, minutely white puberulous to tomentellous; spike 0.5–2 cm long; flowers 5–20, sessile or up to 1.5 mm long pedicellate; perianth 1–2 mm long, minutely white puberulous, stamens 2–3.5 mm long, anthers c. 0.5 mm long. *Pistillate inflorescences* axillary (often in the axils of scale leaves at the base of new shoots), solitary (or in pairs), spicate to subcapitate, ebracteate; peduncle 0.5–1.5 cm long, white puberulous to tomentellous; spike 0.5–2 cm long; flowers 15–50; tepals 1–1.5 mm long, sparsely white puberulous or only ciliolate; ovary c. 1 mm long, style 0–1.5 mm long, stigmas 1.5–3.5 mm long. *Infructescences* 0.8–3.5 cm long, 0.5–1.5 cm thick, reddish to black.

Distribution — From Afghanistan through the Himalaya region to China and Japan, wild or cultivated; in *Malesia*: introduced and cultivated in Sumatra (also Simalur), Malay Peninsula, Java, Borneo, Philippines, Celebes, Lesser Sunda Islands (Lombok, Timor), Moluccas (Ambon, Tanimbar Islands), New Guinea; naturalised in parts of Java and N Luzon.

Habitat — Grown at altitudes up to 2000 m.

Uses — This species is in cultivation for its fruits.

Notes — Numerous names at the rank of species and below that rank have been attached to material of the genus *Morus* with minor morphological differences. This was a reason for Bureau (1873) to include them in *M. alba*. This broadly construed species also comprised material (with long pistillate inflorescences) under the name var. *laevigata* that is now included in *F. macroura*. For the remainder (with short pistillate inflorescences) two groups of varieties and subvarieties were recognized: those with short (0–c. 0.5 mm long) and those with long (c. 0.5–1.5 cm) styles. In material introduced outside the natural range to various parts of the tropics, these two categories can also be recognized, the former in general in plantations for silk production and temperate climatic conditions, the latter especially in trees used as fruit trees and in tropical lowland. A good number of specimens with pistillate inflorescences cannot be included in one of the two forms because of ± intermediate style lengths. Due to the lack of correlated characters in staminate inflorescences and in vegetative parts the best provisional solution could be to treat the form with short styles as var. *alba* and the other as var. *indica* (L.) Bureau (in DC., Prodr. 17 (1873) 243, based on *Morus indica* L. (1753) 986). However, a thorough study on the *Morus alba* complex with traditional and modern methodology is needed to arrive at its taxonomic understanding. For this reason no synonyms are listed.

The long-styled material is often identified as *Morus australis* Poir., according to Bureau (1873) based on material of *Broussonetia papyrifera* (L.) Vent. The name has been reintroduced for *Morus* material by Rehder (J. Arnold Arbor. 10 (1929) 123) and since often applied for long-styled material in cultivation mainly in lowland tropics.

2. *Morus macroura* Miq.

Morus macroura Miq., Pl. Jungh. (1851) 42; Fl. Ned. Ind. 1, 2 (1859) 280; Bureau in A.DC., Prod. 17 (1873) 247; Boerl., Bijdr. Fl. Sum. (1884) 32; Koord., Exkurs.-Fl. Java 2 (1912) 84, f. 4F; Atlas Baumart. Java (1924) t. 745; Corner, Gard. Bull. Singapore 19 (1962) 215; Backer & Bakh.f., Fl. Java 2 (1965) 15. — *Morus alba* L. var. *laevigata* Wall. ex Bureau in A.DC., Prod. 17 (1873) 245. — *Morus laevigata* (Wall. ex Bureau) Hook.f., Fl. Brit. India 5 (1888) 492; Gagnep., Fl. Indo-Chine 5 (1928) 708; Bor, Man. Ind. For. Bot. (1953) 137.

Tree up to 32 m tall, deciduous. Leafy twigs 1.5–3 mm thick, puberulous to hirtellous to subtomentose; resting buds 0.3–1 cm long. Leaves distichous; lamina ovate to subovate to elliptic, 6–16(–23) by 4–11(–14) cm, entire (or when juvenile 3-lobate), chartaceous to subcoriaceous, apex acuminate to acute, base subcordate to rounded (to subcuneate), margin serrate-denticulate (to subentire); upper surface hispidulous to puberulous, mainly on the main veins, ± scabrous to smooth; lower surface puberulous to subtomentellous on the veins; lateral veins 3–6 pairs, tertiary venation scalariform; petiole 1.5–6 cm long, puberulous to hirtellous; stipules 1–1.5 cm long, sparsely to

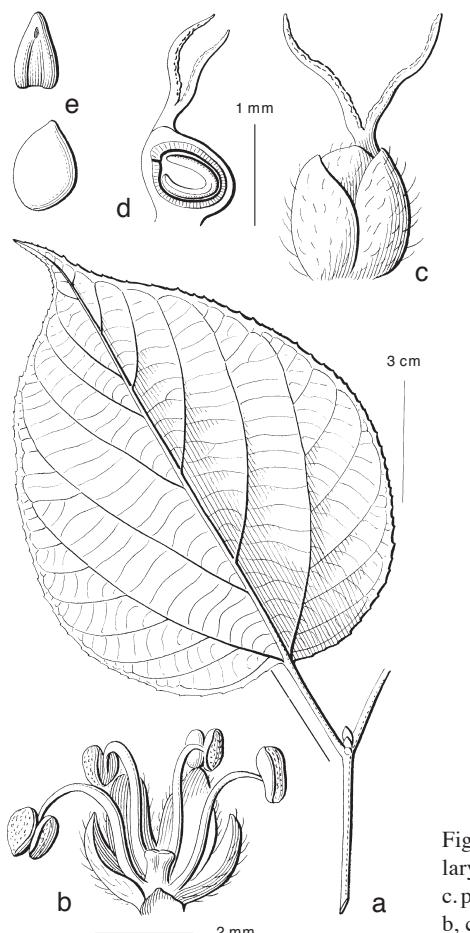
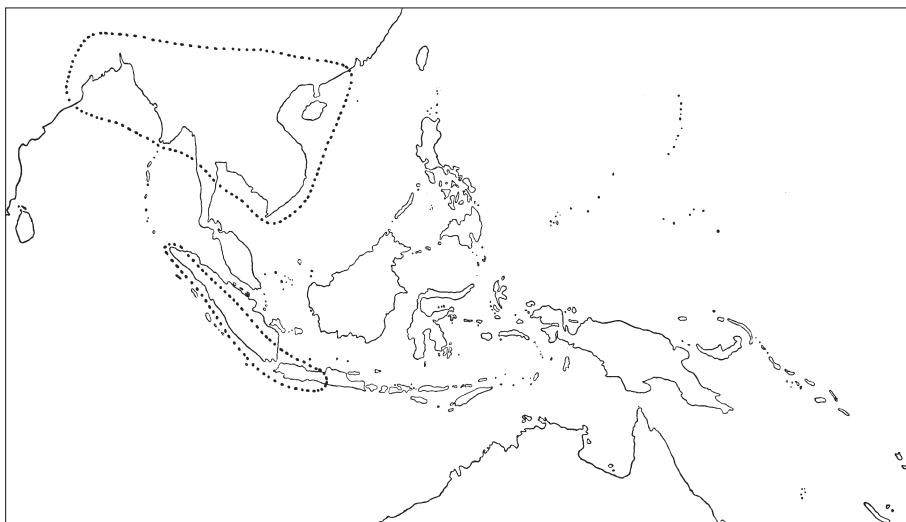


Fig. 1. *Morus macroura* Miq. a. Leafy twig with axillary resting bud; b. staminate flower with pistillode; c. pistillate flower; d. fruit; e. endocarp bodies (a: Raub 1; b, c, e: Bosschaert 2; d: Plasschaert s.n., Sumatra).



Map 1. Distribution of *Morus macroura* Miq.

densely puberulous to hirtellous, caducous (or subpersistent). *Staminate inflorescences* axillary (often in the axils of scale leaves at the base of new shoots), solitary or in pairs, spicate (or racemose); peduncle 0.4–1.5 cm long, puberulous; spike (1–)4–8 cm long; flowers numerous; pedicel 0–1.5 mm long; perianth c. 1.5 mm long, puberulous to tomentellous; stamens c. 2.5 mm long, anthers c. 0.8 mm long. *Pistillate inflorescences* axillary, (often in the axils of scale leaves at the base of new shoots), solitary (or in pairs), spicate, ebracteate; peduncle 0.5–1.5 cm long, puberulous; spike 6–12 cm long; flowers numerous; tepals c. 1.5 mm long, sparsely puberulous; ovary c. 1 mm long, style c. 0.5 mm long, stigmas 1.5–2 mm long. *Infructescences* green to pale yellow. *Endocarp body* ellipsoid to ovoid, c. 0.7 mm long. — **Fig. 1; Map 1.**

Distribution — India (Assam), Sikkim, Bhutan, South China (incl. Hainan), Myanmar, Cambodia, Thailand; in Malesia: Sumatra, Java.

Habitat — Montane and submontane forest, often on volcanic soil, at altitudes between 400 and 2500 m.

Uses — Its timber is useful for house construction.

Note — The features, including the long pistillate inflorescences, show similarities to *M. insignis* Bureau, a species of humid montane forests in the Neotropics.

BLEEKRODEA

Bleekrodea Blume, Ann. Mus. Bot. Lugduno-Batavi 2 (1856) 87; Benth. & Hook.f., Gen. Pl. 3 (1880) 358, ‘*Bleekrodia*’; Leandri, Fl. Madagasc. fam. 55 (1952) 5; C.C. Berg, Proc. Kon. Ned. Akad. Wetensch. C, 91 (1988) 359. — *Streblus* Lour. sect. *Bleekrodea* (Blume) Corner, Gard. Bull. Singapore 19 (1962) 216; Phytomorphology 25 (1975) 6, t. 5, 6.

Shrubs or treelets, monoecious, unarmed. *Leaves* distichous; lamina pinnately veined; stipules free, lateral. *Inflorescences* bisexual (or unisexual), short-branched cymose to

subcapitate, sometimes subinvolucrate. *Staminate flowers* several to one (or lacking), pedicellate; tepals 4 or 5, valvate in the bud; stamens 4 (or 5), inflexed in the bud. *Pistillate flowers* 1 or 2 in the centre of the inflorescence (or lacking), (sub)sessile; tepals 4, connate, forming a tubular, dentate perianth; ovary free, stigmas 2, equal. *Fruiting perianth* enlarged, slightly fleshy, pink; fruit free, a dehiscent drupe, whitish, endocarp thinly crustaceous; seed without endosperm, cotyledons thick, flat, unequal to subequal, radicle short.

Distribution — The genus comprises two species, one in Malesia and the other one in Madagascar.

Morphology — These two species are rather similar in their features.

The inflorescences are bisexual with 1 or 2 pistillate flowers or unisexual. The staminate inflorescences contain several to many flowers and are in structure similar to the pistillate ones. The pistillate inflorescences are uniflorous and bear a few bracts.

The structure of the inflorescences of *Streblus asper* and *S. tonkinensis* (see p. 42) resemble that of *Bleekrodea*, but this genus is distinct by the tubular perianth of the pistillate flower and the presence of uncinate hairs.

1. *Bleekrodea insignis* Blume

Bleekrodea insignis Blume, Ann. Mus. Bot. Lugduno-Batavi 2 (1856) 88, f. 28. — *Streblus insignis* (Blume) Corner, Gard. Bull. Singapore 19 (1962) 219; Phytomorphology 25 (1975) t. 5.

Streblus malayanus Corner, Phytomorphology 25 (1975) 11, t. 6. — *Bleekrodea malayana* (Corner) C.C. Berg, Proc. Kon. Ned. Akad. Wetensch. C, 91 (1988) 359.

Treelet. *Leafy twigs* 1–2 mm thick, minutely puberulous, partly with uncinate hairs. *Leaves* distichous; lamina elliptic to subobovate, 5–14(–21) by 2–5(–7.5) cm, subcoriaceous, apex acuminate to subcaudate, base cuneate, margin crenate-dentate; upper and lower surface sparsely puberulous on the main veins, smooth; lateral veins 6–10, tertiary venation reticulate (to subscalariform); petiole 0.3–1 cm long, minutely puberulous, partly with uncinate hairs; stipules 0.3–0.6 cm long, puberulous, subpersistent. *Inflorescences* axillary, solitary, bisexual or staminate and 0.7–2 cm wide or pistillate and uniflorous; peduncle 0.5–1.2 cm long, minutely puberulous; staminate flowers: pedicel 0.5–1.5 mm long, perianth 1.5 mm long, puberulous, stamens 2–2.5 mm long, anthers c. 1 mm long; pistillate flower(s): perianth 3–4 mm, in fruit up to c. 6 mm long, densely puberulous, style 3–6 mm long, stigmas 3–8 mm long; bracts ovate to narrowly ovate, 2–3 mm long, puberulous, bracteoles narrowly ovate to subulate, 3–5 mm long, puberulous. *Endocarp body* c. 1 cm long. — **Fig. 2.**

Distribution — Malay Peninsula (Kelantan: Gua Musang), Borneo.

Habitat — Lowland forest, in the Malay Peninsula on limestone.

Notes — 1. The collection from Peninsular Malaysia described as *Streblus malayanus* and an additional collection from the same locality largely match material known from Borneo.

2. The variation in the composition of the inflorescences resembles that of the Madagascan species, *Bleekrodea madagascariensis* Blume (see Berg, Bull. Jard. Bot. Belg. 47 (1977) 367).

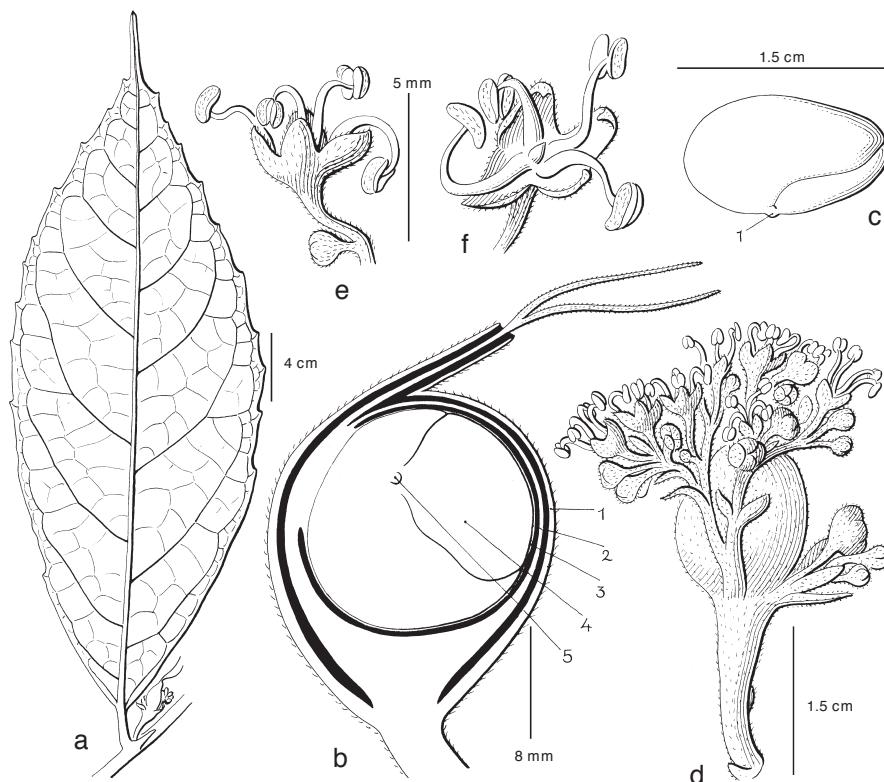


Fig. 2. *Bleekrodea insignis* Blume. a. Leaf; b. ripe fruit in section: 1 = utricular perianth, 2 = exocarp, 3 = membranous testa, 4 = cotyledon, 5 = radicle; c. embryo in section: 1 = radicle; d. inflorescence at anthesis of the staminate flowers, one pistillate flower in fruit; e, f. staminate flowers (a–f: *Jaheri* 1541).

BROUSSONETIA

Broussonetia L'Hér. ex Vent., Tabl. Règn. Vég. 3 (1799) 547, nom. cons., non Gomez Ortega, Nov. Rar. Pl. Hort. Matr. Descr. (1798) 61 (Legum.); Blume, Ann. Mus. Bot. Lugduno-Batavi 2 (1856) 85; Bureau in A.DC., Prodr. 17 (1873) 223; Baill., Hist. Pl. 6 (1875) 192; Benth. & Hook.f., Gen. Pl. 3 (1880) 361; Engl. in Engl. & Prantl, Nat. Pflanzenfam. 3, 1 (1888) 76; Boerl., Handl. Fl. Ned. Ind. 3 (1900) 316; Corner, Gard. Bull. Singapore 19 (1962) 233; H.L. Li, Woody Fl. Taiwan (1963) 112; Ohwi, Fl. Japan, new ed. (1965) 383; C.C. Berg, Bull. Jard. Bot. Belg. 47 (1977) 355.

Papyrius Lam., Tabl. Encycl. (1798) t. 762.

Allaeanthus Thwaites, Hooker's J. Bot. Kew Gard. Misc. 6 (1854) 302; Bureau in A.DC., Prodr. 17 (1873) 222; Benth. & Hook.f., Gen. Pl. 3 (1880) 361; Engl. in Engl. & Prantl, Nat. Pflanzenfam. 3, 1 (1888) 74 ('Allacanthus'); Boerl., Handl. Fl. Ned. Ind. 3 (1900) 317. — *Broussonetia* L'Hér. ex Vent. sect. *Allaeanthus* (Thwaites) Corner, Gard. Bull. Singapore 19 (1962) 234.

Smithiodendron Hu, Sunyatsenia 3 (1936) 106.

Trees (or climbers), dioecious, unarmed, deciduous, shoot apices shed, with (small) axillary scaled resting buds. Leaves distichous, spirally arranged or (sub)opposite;

lamina pinnately veined; stipules free, semi-amplexicaul. *Inflorescences* unisexual, usually solitary in the leaf axils or on leafless nodes at the base of fertile twigs, bracteate. *Staminate inflorescences* spicate, sometimes subcapitate, with a rather distinct abaxial sterile strip; perianth 4-parted, segments valvate in the bud; stamens 4, inflexed in the bud. *Pistillate inflorescences* globose-capitate, sometimes elongated; perianth unequally 2–4-lobed to 2–4-dentate; ovary free, stigmas 2, one of them strongly reduced; interfloral bracts longer than the perianth, their upper parts cohering by entangling hairs. *Fruiting perianth* enlarged, membranous; fruit usually short-stipitate and slightly compressed, exocarp fleshy, for the greater part rather thinly so, thicker at the base and on the seed-bearing side; endocarp crustaceous, with a thickened crest-like part at the apex and a small woody plug towards the hilum; seed with endosperm, embryo curved, cotyledons unequal or almost equal, subconduplicate to almost flat, straight or the apex reflexed, not enclosing the long radicle, or if the cotyledons unequal, then the larger cotyledon more or less clasping the smaller one; bracts more or less fused at the base and hardened at the apex in fruit.

Distribution — A genus of eight species, seven in tropical to subtropical Asia, and one in Madagascar.

Subdivision — Two sections (*Broussonetia* and *Allaeanthus*) have been recognised by Corner (Gard. Bull. Singapore 19 (1962) 234). As he indicated, the differences between these sections are very small, and are not maintained in the present treatment.

KEY TO THE SPECIES

- 1a. Leaves spirally arranged or subopposite; lamina scabrous above. — Widespread, in cultivation **3. *B. papyrifera***
- b. Leaves distichous; lamina smooth above 2
- 2a. Tree; margin of the lamina entire. — Philippines, Celebes **2. *B. luzonica***
- b. Climber; margin of the lamina dentate. — Sumatra. **1. *B. kurzii***

1. *Broussonetia kurzii* (Hook.f.) Corner

Broussonetia kurzii (Hook.f.) Corner, Gard. Bull. Singapore 19 (1962) 234. — *Allaeanthus kurzii* Hook.f., Fl. Brit. India 5 (1888) 490; Gagnep., Fl. Indo-Chine 5 (1928) 721; Kanjilal & A.C. Das, Fl. Assam 4 (1940) 275.

Malaisia tortuosa (non Blume) Kurz, Forest Fl. Burma 2 (1877) 466.

Climber, deciduous. *Leafy twigs* 1–3 mm thick, appressedly puberulous. *Leaves* distichous; lamina narrowly elliptic to elliptic or subovate to ovate, 4–12 by 2.5–6 cm, ± asymmetric, chartaceous, apex acuminate to subacute, base rounded to subcordate, margin crenate- to serrate-dentate; upper surface sparsely appressedly puberulous on the main veins, smooth; lower surface sparsely appressedly puberulous on the veins; midrib impressed above, lateral veins 5–8 pairs, tertiary venation scalariform; petiole 0.6–1.5 cm long, sparsely appressedly puberulous; stipules 0.3–0.9 cm long, ovate, sparsely minutely puberulous, caducous or subpersistent. *Staminate inflorescences* clustered on short-shoots or on the base of leafy twigs, spicate; peduncle 0.3–2 cm long, minutely puberulous; spike (0.5–)1–5 cm long; perianth 1.5–2 mm long, minutely puberulous;

stamens 2.5–3 mm long, anthers 0.6–0.8 mm long; bracts ovate to linear, puberulous. *Pistillate inflorescences* solitary on up to 4 cm long leafless branchlets, or at the base of leafy twigs, capitate; peduncle 0.3–1 cm long, minutely puberulous to tomentellous; head globose, 0.2–0.4 cm diam.; perianth c. 0.5 mm long, 4-dentate; ovary c. 0.3 mm long, stigma 7–10 mm long; interfloral bracts clavate to subpeltate, c. 0.7 mm long, densely puberulous to tomentellous, bracts subtending the head ovate, 0.5–1 mm long, sparsely minutely puberulous. *Infructescences* globose, 0.5–0.8 cm diameter.

Distribution — India (Assam), Myanmar, Thailand; in *Malesia*: N Sumatra (Atjeh, known by a single collection).

Habitat — Lowland rain forest (edges).

Note — The infructescences are eaten by gibbons.

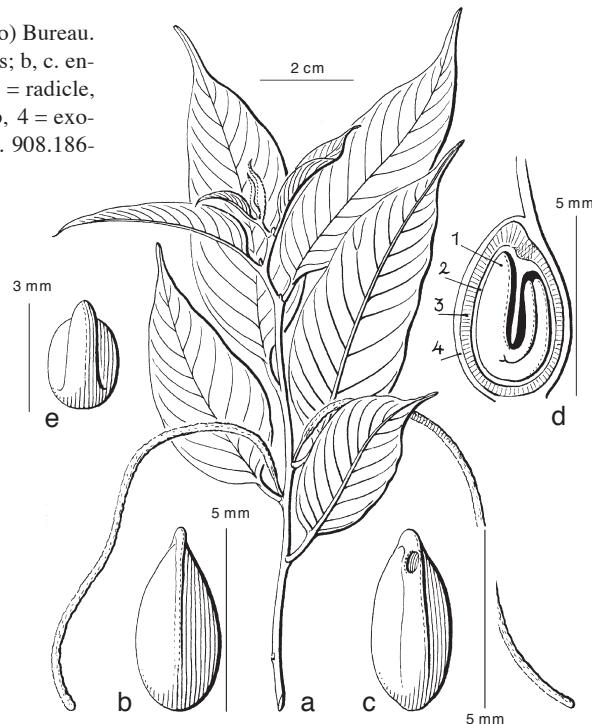
2. *Broussonetia luzonica* (Blanco) Bureau

Broussonetia luzonica (Blanco) Bureau in A. DC., Prodr. 17 (1873) 224; Corner, Gard. Bull. Singapore 19 (1962) 235. — *Morus luzonica* Blanco, Fl. Filip. (1837) 703. — *Allaeanthus luzonicus* (Blanco) Fern.-Vill., Nov. App. (1880) 198; S. Vidal, Sin. Gen. Pl. Leños Filip. (1883) 39, t. 86 f. A; Phan. Cuming. Philipp. (1885) 145; Revis. Pl. Vasc. Filip. (1886) 250; Merr., Sp. Blancoan. (1918) 122; Enum. Philipp. Flow. Pl. 2 (1923) 37.

Broussonetia luzoniensis Blanco, Fl. Filip. ed. 2 (1845) 488; ed. 3, 3 (1879) 107, t. 278.

Allaeanthus glaber Warb. in Perkins, Fragm. Fl. Philipp. 3 (1905) 166. — *Allaeanthus luzonicus* (Blanco) Fern.-Vill. var. *glaber* (Warb.) Merr., Enum. Philipp. Flow. Pl. 2 (1923) 37. — *Broussonetia luzonica* (Blanco) Bureau var. *glabra* (Warb.) Corner, Gard. Bull. Singapore 19 (1962) 235.

Fig. 3. *Broussonetia luzonica* (Blanco) Bureau.
a. Twig with staminate inflorescences; b, c. endocarp bodies; d. fruit in section: 1 = radicle, 2 = membranous testa, 3 = endocarp, 4 = exocarp; e. embryo (a: Herb. Lugd. Bat. 908.186-118; b–e: Bur. Sci. 42294).



Tree up to 10 m tall (or more?), deciduous. *Leafy twigs* 1.5–2.5 mm thick, sparsely to densely puberulous to (sub)tomentellous. *Leaves* distichous; lamina subovate to ovate, 6–17 by 2.5–6 cm, ± asymmetric, chartaceous, apex acuminate to subacute, base rounded to obtuse or to subcordate, margin entire; upper surface sparsely puberulous, smooth; lower surface sparsely to densely puberulous, to tomentose on the veins; midrib impressed above, lateral veins 7–12 pairs, tertiary venation scalariform; petiole 0.6–1.5 cm long, sparsely to densely puberulous to tomentose; stipules narrowly ovate, 0.3–0.9 cm long, puberulous, ribbed, caducous. *Staminate inflorescences* axillary, solitary, spicate; peduncle 1–1.5 cm long, puberulous to tomentellous; spike 5–26 cm long; perianth 1–1.5 mm long, densely minutely puberulous; stamens c. 2 mm long, anthers c. 0.7 mm long; bracts ovate to narrowly elliptic, 0.5–1 mm long, minutely puberulous. *Pistillate inflorescences* axillary, solitary, capitate; peduncle 0.6–1 cm long, puberulous to tomentellous; head globose, 0.4–0.7 cm diam.; perianth c. 1 mm long, 4-dentate; ovary c. 0.5 mm long, stigma 5–15 mm long; interfloral bracts clavate to subpeltate, 1–1.3 mm long, densely puberulous to tomentellous. *Infructescences* globose, 1.5–2 cm diameter.—**Fig. 3.**

Distribution — Philippines, Celebes.

Habitat — Lowland forest

3. *Broussonetia papyrifera* (L.) Vent.

Broussonetia papyrifera (L.) Vent., Tabl. Règn. Vég. 3 (1799) 547; Blume, Mus. Bot. 2 (1856) 85; Miq., Ann. Mus. Bot. Lugduno-Batavi 2 (1866) 198; Bureau in A.DC., Prodr. 17 (1873) 224; Hook. f., Fl. Brit. India 5 (1888) 490; Koord. & Valeton, Bijdr. Boomsoort. Java 11 (1906) 3; Koord., Exkurs.-Fl. Java 2 (1912) 87; Atlas Baumart. Java (1924) t. 746; Gagnep., Fl. Indo-Chine 5 (1928) 717, f. 88; F. Brown, Bull. Bish. Mus. 130 (1935) 33; T.S. Liu, Ill. Lign. Pl. Taiwan 2 (1962) 708; H.L. Li, Woody Fl. Taiwan (1963) 113; Ohwi, Fl. Japan, new ed. (1965) 384; Backer & Bakh.f., Fl. Java 2 (1965) 16; Barker, Curtis's Bot. Mag. 19 (2002) 8, cum t.; C.C. Berg, Proseia 17 (2003) 91, cum t. — *Morus papyrifera* L., Sp. Pl. (1753) 986.

Broussonetia papyrifera (L.) Vent. forma *sumatrana* Miq., Fl. Ned. Ind., Eerst Bijv. (1861) 416. —

Broussonetia papyrifera (L.) Vent. var. *sumatrana* (Miq.) Bureau in DC., Prodr. 17 (1873) 224.

Smithiodendron artocarpoideum Hu, Sunyatsenia 3 (1936) 106.

Tree up to 35 m tall, deciduous. *Leafy twigs* 1.5–3 mm thick, subtomentose to hirtellous to puberulous. *Leaves* spirally arranged or (sub)opposite; lamina ovate to cordiform or to elliptic, 5–20 by 4–12 cm, entire or lobate, ± asymmetric, chartaceous, apex acuminate to subacute, base cordate to rounded to subcuneate, margin crenate- to serrate-dentate; upper surface hispidulous, scabrous; lower surface ± densely puberulous, to subtomentose on the veins; midrib impressed above, lateral veins 5–9 pairs, tertiary venation scalariform; petiole (1–)2–9(–15) cm long, subtomentose; stipules 0.5–1.5 cm long, ovate, puberulous, ± ribbed, caducous. *Staminate inflorescences* axillary or below the leaves, solitary or clustered on short-shoots, spicate; peduncle 1–2.5 cm long, puberulous to tomentellous; spike 3–10 cm long; perianth 1.5–2 mm long, puberulous; stamens 3–3.5 mm long, anthers c. 0.8 mm long; bracts subulate, 1.5–2.5 mm long, puberulous. *Pistillate inflorescences* axillary or below the leaves, solitary, capitate; peduncle 0.3–1.5 cm long, puberulous to tomentellous; head globose, 1–1.2 cm diam.; perianth c. 1 mm long, 4-dentate; ovary 0.5 mm long, stigma 7–10 mm long; interflo-

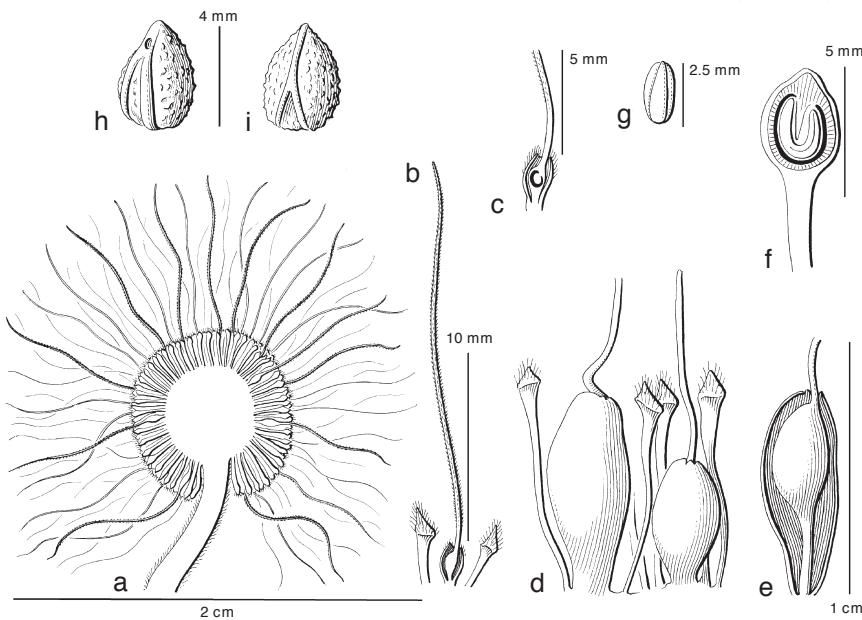


Fig. 4. *Broussonetia papyrifera* (L.) Vent. a. Pistillate inflorescence in section at anthesis; b. pistillate flower at anthesis, with bracts, the perianth cut open; c. base of pistillate flower; d. fruit-containing perianths with elongate bracts; e. fruit with the enlarged utricular perianth cut open; f. stalked drupe in section; g. embryo; h, i. endocarp bodies (material from Cambridge Botanic Garden).

ral bracts clavate to subpeltate, 1–1.5 mm long, densely puberulous to tomentellous. *Inflorescences* (sub)globose, 2–2.5 cm diam.; endocarp body ovoid, 2–2.5 mm long.

— Fig. 4.

Distribution — India (Assam), China (incl. Taiwan), Indochina, Japan (introduced in the Ryukyu Islands), Myanmar, Thailand, Polynesia; in *Malesia*: introduced in Sumatra, Java, Philippines, Celebes, Lesser Sunda Islands (Flores, Timor, Alor, Wetar), Moluccas, New Guinea.

Habitat — Lowland and highlands, in particular in parts with seasonal climate.

Uses — The bark is used to make cloth and paper (see Barker 2002 and Berg 2003).

FATOUA

Fatoua Gaudich. in Freyc., Voy. Uranie, Bot. (1830) 509; Bureau in A.DC., Prodr. 17 (1873) 255; Baill., Hist. Pl. 6 (1875) 197; Benth. & Hook.f., Gen. Pl. 3 (1880) 358; Engl. in Engl. & Prantl, Nat. Pflanzenfam. 3, 1 (1888) 71; C.C. Berg, Bull. Jard. Bot. Belg. 47 (1977) 370.

Subshrubs or herbs, monoecious, latex absent. *Leaves* distichous; lamina pinnately veined, with cystolith hairs beneath; stipules free, lateral. *Inflorescences* bisexual (or unisexual), in pairs or solitary in the axils of the leaves, short-branched cymose or spike-like, abaxially without flowers. *Staminate flowers* sessile or short-pedicellate; perianth

4-parted, segments valvate; stamens 4, inflexed in the bud, *Pistillate flowers* sessile; perianth 4-parted, segments valvate; ovary free, style lateral, one of the stigmas strongly reduced. *Fruiting perianth* enlarged, not fleshy; exocarp thick, white fleshy and dehiscent (probably) ejecting the endocarp body; seed with endosperm, embryo curved, cotyledons equal and flat, radicle long.

Distribution — The genus comprises two species, one extending from Japan to New Caledonia and the other only known from Madagascar.

Morphology — The genus shows similarities to *Bleekrodea* in the bisexual inflorescences and the dehiscent drupes. Moreover, in *F. villosa* the inflorescence is short-branched cymose like in *Bleekrodea*. However, in the Madagascan species, *F. madagascariensis* Leandri (1948), the inflorescence is racemose to spicate.

An anatomical study by Leandri, Mem. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 1 B (1948) 4 revealed the absence of lactiferous elements in the Madagascan species.

1. *Fatoua villosa* (Murray) Nakai

Fatoua villosa (Murray) Nakai, Bot. Mag. (Tokyo) 41 (1927) 516. — *Urtica villosa* Murray, Syst. Veg. ed. 14 (July 1784) 851; Thunb., Fl. Jap. (Aug. 1784) 70.

Urtica japonica Thunb., Fl. Jap. (Oct. 1784) 70, non L.f. 1781.

Fatoua pilosa Gaudich. in Freyc., Voy. Uranie, Bot. (1830) 509; Gaudich., Voy. Bonite, Bot. (1844) t. 84 f. 1; Bureau in A.DC., Prodr. 17 (1873) 256; Benth., Fl. Australia 6 (1873) 182; Engl. in Engl. & Prantl, Nat. Pflanzenfam. 3, 1 (1888) 71, f. 50A, B; Warb., Bot. Jahrb. Syst. 13 (1891) 294; F.B. Forbes & Hemsl., J. Linn. Soc., Bot. 26 (1894) 454; Koord., Atlas Baumart. Java (1924) t. 743; Gagnep., Fl. Indo-Chine 5 (1928) 715; Backer & Bakh.f., Fl. Java 2 (1965) 14.

Fatoua aspera Gaudich. in Freyc., Voy. Uranie, Bot. (1830) 510; Miq., Fl. Ned. Ind. 1, 2 (1859) 282; Ann. Mus. Bot. Lugduno-Batavi 3 (1867) 192.

Fatoua cordata Gaudich. in Freyc., Voy. Uranie, Bot. (1830) 510.

Fatoua lanceolata Decne., Nouv. Ann. Mus. Hist. Nat. 3 (1834) 492; Gaudich., Voy. Bonite, Bot. (1844) t. 84 f. 3; Miq., Fl. Ned. Ind. 1, 2 (1859) 282.

Urtica manillensis Walp., Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. 19, Suppl. 1 (1843) 423.

Fatoua subcordata Gaudich., Voy. Bonite, Bot. (1844) t. 84 f. 2.

Fleurya glechomaefolia Miq. in Zoll., Syst. Verz. 2 (1854) 106. — *Fatoua pilosa* Gaudich. (var. *cordata*) subvar. *glechomaefolia* (Miq.) Bureau in A.DC., Prodr. 17 (1873) 257.

Fleurya globulifera Miq. in Zoll., Syst. Verz. 2 (1854) 106. — *Fatoua pilosa* Gaudich. (var. *cordata*) subvar. *globulifera* (Miq.) Bureau in A.DC., Prodr. 17 (1873) 257.

Fatoua japonica Blume, Ann. Mus. Bot. Lugduno-Batavi 2 (1856) t. 38.

Fatoua pilosa Gaudich. var. *lanceolata* Bureau in A.DC., Prodr. 17 (1873) 257.

Herb or subshrub up to 1 m tall, usually branched, erect; roots yellow. *Leafy twigs* 0.5–2 mm thick, minutely puberulous and with longer mostly curved to uncinate hairs. *Leaves* distichous; lamina cordiform to ovate (to narrowly ovate), 1–6(–9) by 0.5–4(–5) cm, membranaceous, apex acuminate to (sub)acute, base cordate to truncate to rounded (to subcuneate), margin dentate to serrate or to crenate; upper surface hispidulous to puberulous to hirtellous, scabrous to smooth; lower surface minutely puberulous, on the veins the short indumentum intermixed with longer hairs; lateral veins 3–7(–10), running into the margin or faintly loop-connected, tertiary venation subscalariform to reticulate; petiole 0.5–4 cm long, minutely puberulous and with longer curved to uncinate hairs; stipules 0.3–0.5 cm long, puberulous to hirtellous,

subpersistent. *Inflorescences* subcapitate, 0.3–1 cm diam.; peduncle 0.5–2.5 cm long, minutely puberulous; staminate flowers: tepals c. 1 mm long, puberulous, stamens c. 1.5 mm long, anthers c. 0.5 mm long; pistillate flowers: tepals c. 1 mm long, style 2–3 mm long. *Endocarp body* c. 0.8 by 0.6 mm.

Distribution — China (incl. Taiwan), Japan, Thailand, Indochina, Australia, Solomon Islands, New Caledonia; in *Malesia*: Java (also Madura and Bawean), Philippines, Celebes (also Buton), Lesser Sunda Islands, Moluccas (Halmahera, Banda, Ceram, Tanimbar Islands, Kai Islands), New Guinea (also Bismarck Archipelago).

Habitat — Forest edges, seacoasts, light secondary forest, waste places, on calcareous soil; at altitudes up to c. 1200 m.

Notes — 1. There are no clear indications that the species is in *Malesia* represented by perennials (*Fatoua pilosa*?) and annuals (*F. villosa*?) see Zhou Zhekun & H.G. Gilbert, Fl. China 5 (2003) 22.

2. The species is very variable as with regard to habit, indumentum, and leaf characters, but varieties cannot be distinguished.

3. The venation of the lamina is craspedodromous rather than brochidodromous as characteristic for the family.

MACLURA

Maclura Nutt., Gen. N. Amer. Pl. 2 (1818) 233, nom. cons.; Blume, Ann. Mus. Bot. Lugduno-Batavi 2 (1856) 81; Bureau in A.DC., Prodr. 17 (1873) 226; Baill., Hist. Pl. 6 (1875) 193; Benth. & Hook. f., Gen. Pl. 3 (1880) 363; Engl. in Engl. & Prantl, Nat. Pflanzenfam. 3, 1 (1888) 74; Lemée, Dict. Gen. Pl. Phan. 4 (1932) 230; Corner, Gard. Bull. Singapore 19 (1962) 235; C.C. Berg, Proc. Kon. Ned. Akad. Wetensch. C, 91 (1986) 243; Fl. Neotrop. Monogr. 83 (2001) 53.

Vanieria Lour., Fl. Cochinch. 1 (1790) 564.

Ioxylon Raf., Amer. Monthly Mag. & Crit. Rev. 2 (1817) 118; 4 (1818) 188 ('*Toxylon*'),

Chlorophora Gaudich. in Freyc., Voy. Uranie, Bot. (1830) 509. — *Maclura* Nutt. sect. *Chlorophora* (Gaudich.) Corner, Gard. Bull. Singapore 19 (1962) 236.

Fusticus Raf., New Fl. Am. 3 (1836) 43.

Sukaminea Raf., New Fl. Am. 3 (1836) 44.

Cudrania Rumph. ex Trécul, Ann. Sci. Nat., Bot. sér. 3, 8 (1847) 122, nom. cons.; Bureau, Ann. Sci. Nat., Bot. sér. 5, 11 (1869) 377; Bureau in A.DC., Prodr. 17 (1873) 285; Baill., Hist. Pl. 6 (1875) 202; Benth. & Hook.f., Gen. Pl. 3 (1880) 374; Hook.f., Fl. Brit. India 5 (1888) 538; Engl. in Engl. & Prantl, Nat. Pflanzenfam. 3, 1 (1888) 82; Boerl., Handl. Fl. Ned. Ind. 3 (1900) 329 ('*Cudravia*'); Renner, Bot. Jahrb. Syst. 39 (1907) 361. — *Cudranus* Rumph. [Herb. Amboin. 5 (1747) 22] ex Miq., Fl. Ned. Ind. 1, 2 (1859) 290. — *Maclura* Nutt. sect. *Cudrania* (Trécul) Corner, Gard. Bull. Singapore 19 (1962) 237.

Plecospermum Trécul, Ann. Sci. Nat., Bot. sér. 3, 8 (1847) 124; Corner, Gard. Bull. Singapore 19 (1962) 241. — *Maclura* Nutt. sect. *Plecospermum* (Trécul) C.C. Berg, Proc. Kon. Ned. Akad. Wetensch. C, 91 (1986) 245.

Cardiogyne Bureau in A.DC., Prodr. 17 (1873) 232; C.C. Berg, Bull. Jard. Bot. Belg. 47 (1977) 359. — *Maclura* Nutt. sect. *Cardiogyne* (Bureau) Corner, Gard. Bull. Singapore 19 (1962) 237.

x *Maclucudrania* André, Rev. Hort. 77 (1905) 363.

Climbers, trees or shrubs, dioecious, armed with straight to curved, reduced branchlets ending in a spinose tip (sometimes only in juvenile specimens). *Leaves* distichous or spirally arranged; lamina pinnately veined; stipules free or fused, lateral to semi-amplexicaul, often very small. *Inflorescences* usually solitary, in the leaf axils or on

short-shoots, often yellow (dye-containing) glands embedded in the bracts and/or the (fruiting) perianths. *Staminate inflorescences* globose-(sub)capitate, spicate, or (sub)racemose; perianth with 4, free or basally connate, tepals, decussate, imbricate in the bud; stamens straight or inflexed in the bud. *Pistillate inflorescences* globose-capitate; flowers free or connate; tepals free or connate, decussate, imbricate in the bud; ovary free or the lower part adnate to the perianth, stigmas 2, mostly strongly unequal in length, or 1. *Fruiting perianth* enlarged, more or less fleshy; fruit free or adnate to the perianth, when free slightly drupaceous, endocarp crustaceous; seed small to rather large, endosperm present (but scarce) or absent, embryo various, mostly with (rather) thin, folded or flat, cotyledons and a long radicle.

Distribution — The genus comprises eleven species of which ten occur in the tropics (seven in Asia, one in Africa, and two in the Neotropics) and one in North America.

Subdivision — The genus can be subdivided into five sections (Berg 1986): *Cardiogyne* (one species in Africa and another in the Neotropics), *Chlorophora* (one species in the Neotropics), *Cudrania* (four species in Asia), *Maclura* (a single species in North America), and *Plecospermum* (two species in Asia). The species of sect. *Cudrania* do not have the urticaceous type of stamen and are exceptional in the tribe Moreae.

The species occurring in the Malesian region represent sect. *Cudrania* ser. *Connatae* Corner (Gard. Bull. Singapore 19 (1962) 238). It differs from the three other species of this section in the basally connate pistillate flowers with one stigma or two unequally long ones.

Dispersal — The orange-coloured pulpy infructescences are dispersed by birds (Ridley, Dispersal of plants throughout the world, 1930).

Section CUDRANIA

Maclura Nutt. sect. *Cudrania* (Trécul) Corner, Gard. Bull. Singapore 19 (1962) 237.

Climbers or shrubs. *Staminate inflorescences* globose-capitate; stamens straight in the bud. *Pistillate flowers* free or connate; tepals and bracts accumulating yellow dye.

1. *Maclura cochinchinensis* (Lour.) Corner

Maclura cochinchinensis (Lour.) Corner, Gard. Bull. Singapore 19 (1962) 239; Backer & Bakh.f., Fl. Java 2 (1965) 17; Steenis, Mt Fl. Java (1972) pl. 30–7. — *Vanieria cochinchinensis* Lour., Fl. Cochinch. (1790) 564; Merr., Enum. Philipp. Flow. Pl. 2 (1923) 39; Nakai, Bot. Mag. (Tokyo) 41 (1927) 515. — *Procris cochinchinensis* (Lour.) Spreng., Syst. Veg. 3 (1826) 846. — *Cudrania cochinchinensis* (Lour.) Kudô & Masam., Ann. Rep. Taihoku Bot. Gard. 2 (1932) 27; Merr., Comm. Fl. Cochinch. (1935) 134; Kudô & Masam., Trans. Nat. Hist. Soc. Taiwan (1938) 292; Backer, Blumea 6 (1948) 302; T.S. Liu, Ill. Lign. Pl. Taiwan 2 (1962) 709; H.L. Li, Woody Fl. Taiwan (1963) 113, f. 36; Ohwi, Fl. Japan, new ed. (1965) 384.

Vanieria alternifolia Stokes, Bot. Mat. Med. 4 (1812) 381.

Trophicis spinosa Blume, Bijdr. (1825) 489, non Willd. 1806, nec Roxb. 1832. — *Cudrania spinosa* (Blume) Hochr., Bull. New York Bot. Gard. 6 (1910) 271; Koord., Exkurs.-Fl. Java 2 (1912) 90.

Morus tinctoria (non L.) Blanco, Fl. Filip. (1837) 704. — *Broussonetia tinctoria* Blanco, Fl. Filip. ed. 2 (1845) 488; ed. 3, 3 (1879) 108, t. 418, non (L.) Kunth 1817. — *Maclura gerontogea* Siebold & Zucc., Abh. Akad. München 4, 3 (1846) 220; Blume, Ann. Mus. Bot. Lugduno-Batavi 2 (1856) 84. — *Vanieria cochinchinensis* Lour. var. *gerontogea* (Siebold & Zucc.) Nakai, Bot. Mag. (Tokyo)

- 41 (1927) 516. — *Cudrania cochinchinensis* (Lour.) Kudô & Masam. var. *gerontogea* (Siebold & Zucc.) Kudô & Masam., Ann. Rep. Taihoku Bot. Gard. 2 (1932) 27.
- Cudrania pubescens* Trécul, Ann. Sci. Nat., Bot. sér. 3, 8 (1847) 125; Miq., Fl. Ned. Ind. 1, 2 (1859) 290, ‘*Cudranus pubescens*’; Kurz, Forest Fl. Burma 2 (1877) 435; Koord., Exkurs.-Fl. Java 2 (1912) 91; Gagnep., Fl. Indo-Chine 5 (1928) 727. — *Vanieria pubescens* (Trécul) Chun, J. Arnold Arbor. 8 (1927) 21. — *Maclura cochinchinensis* (Lour.) Corner var. *pubescens* (Trécul) Corner, Gard. Bull. Singapore 19 (1962) 239. — *Maclura pubescens* (Trécul) Z.K. Zhou & M.G. Gilbert, Fl. China 5 (2003) 36.
- Plecospermum spinosum* Trécul var. *javanensis* Trécul, Ann. Sci. Nat., Bot. sér. 3, 8 (1847) 125.
- Cudrania javanensis* Trécul var. *indica* Trécul, Ann. Sci. Nat., Bot. sér. 3, 8 (1847) 123.
- Cudrania obovata* Trécul, Ann. Sci. Nat., Bot. sér. 3, 8 (1847) 126; Miq., Fl. Ned. Ind. 1, 2 (1859) 290, ‘*Cudranus obovatus*’; Gagnep., Fl. Indo-Chine 5 (1928) 730.
- Cudrania sumatrana* Miq., Pl. Jungh. (1851) 44; Fl. Ned. Ind. 1, 2 (1859) 291, ‘*Cudranus sumatrana*’.
- Cudrania acuminata* Miq. in Zoll., Syst. Verz. 2 (1854) 90 nomen, 96 descr.; Miq., Fl. Ned. Ind. 1, 2 (1859) 291, ‘*Cudranus acuminatus*’.
- Plecospermum cuneifolium* Thwaites, Hooker’s J. Bot. Kew Gard. Misc. 6 (1854) 303.
- Maclura timorensis* Blume, Ann. Mus. Bot. Lugduno-Batavi 2 (1856) 54.
- Maclura javanica* Blume, Ann. Mus. Bot. Lugduno-Batavi 2 (1856) 83; Miq., Fl. Ned. Ind. 1, 2 (1859) 280. — *Cudrania javanensis* Rumph. ex Trécul, Ann. Sci. Nat., Bot. sér. 3, 8 (1847) 123, t. 3, f. 76–85; Wight, Icon. Pl. Ind. Orient. 6 (1853) t. 1960; Miq., Fl. Ned. Ind. 1, 2 (1859) 290; Bureau, Ann. Sci. Nat., Bot. sér. 5, 11 (1869) 378; Benth., Fl. Australia 6 (1873) 179; Hook.f., Fl. Brit. India 5 (1888) 538; in Trimen, Fl. Ceylon 4 (1898) 98; K. Schum. & Lauterb., Fl. Schutzgeb. Südsee (1901) 266; Merr., Interpr. Herb. Amboin. (1917) 189; Sp. Blancoan. (1918) 123, ‘*javensis*’; Koord., Exkurs.-Fl. Java Atlas (1924) t. 750; Ridl., Fl. Malay Penins. 3 (1924) 356; Gagnep., Fl. Indo-Chine 5 (1928) 726; Diels, Bot. Jahrb. Syst. 67 (1935) 174. — *Cudranus rumphii* Thwaites, Enum. Pl. Zeyl. (1861) 262. — *Cudranus spinosus* Kuntze, Revis. Gen. Pl. 2 (1891) 625. — [*Cudranus bimanus* sive *javanus* Rumph. Herb. Amboin. 5 (1747) 22, t. 15, f. 2.]
- Maclura amboinensis* Blume, Ann. Mus. Bot. Lugduno-Batavi 2 (1856) 84; Corner, Gard. Bull. Singapore 19 (1962) 239; Backer & Bakh.f., Fl. Java 2 (1965) 17. — *Cudranus amboinensis* (Blume) Miq., Fl. Ned. Ind. 1, 2 (1859) 290; Kurz, Fl. Burma 2 (1877) 434, ‘*Cudrania*’; Warb., Bot. Jahrb. Syst. 13 (1891) 294. — [*Cudranus amboinicus* Rumph., Herb. Amboin. 5 (1747) 22, t. 15 f. 1, t. 16.]
- Cudrania rectispina* Hance, J. Bot. 14 (1876) 365; F.B. Forbes & Hemsl., J. Linn. Soc., Bot. 26 (1899) 470.
- Cudrania grandifolia* Merr., Philipp. J. Sci. 18 (1921) 52. — *Vanieria grandifolia* (Merr.) Merr., Enum. Philipp. Flow. Pl. 2 (1923) 39.
- Cudrania cambodiana* Gagnep., Bull. Soc. Bot. France 72 (1925) 808; Fl. Indo-Chine 5 (1928) 729, t. 89; 9–14, 90; 1–3.
- Maclura amboinensis* Blume var. *paucinervia* Corner, Gard. Bull. Singapore 19 (1962) 239.

Shrub, often much-branched with long scrambling sprays, or climber, with up to 4 cm long straight or curved thorns. Leafy twigs 1.5–4 mm thick, brownish to whitish puberulous to subglabrous, often drying brown with numerous whitish lenticels. Leaves spirally arranged to distichous; lamina elliptic to (sub)ovate to narrowly elliptic, (0.5–)4–8(–12) by (0.3–)2–5 cm, subcoriaceous to chartaceous, apex (short-)acute to subacute (to apiculate or to rounded), base obtuse to rounded or to cuneate, margin entire; upper surface glabrous; lower surface (very) sparsely minutely puberulous on the (main) veins to glabrous; midrib impressed above, lateral veins 6–9(–14) pairs, tertiary venation reticulate or subscalariform; petiole 0.3–1.5(–2) cm long, (sub)glabrous; stipules 0.2–0.3 cm long, puberulous, caducous or subpersistent. Staminate inflorescences axillary, in pairs or solitary, capitate; peduncle 0.3–1 cm long,

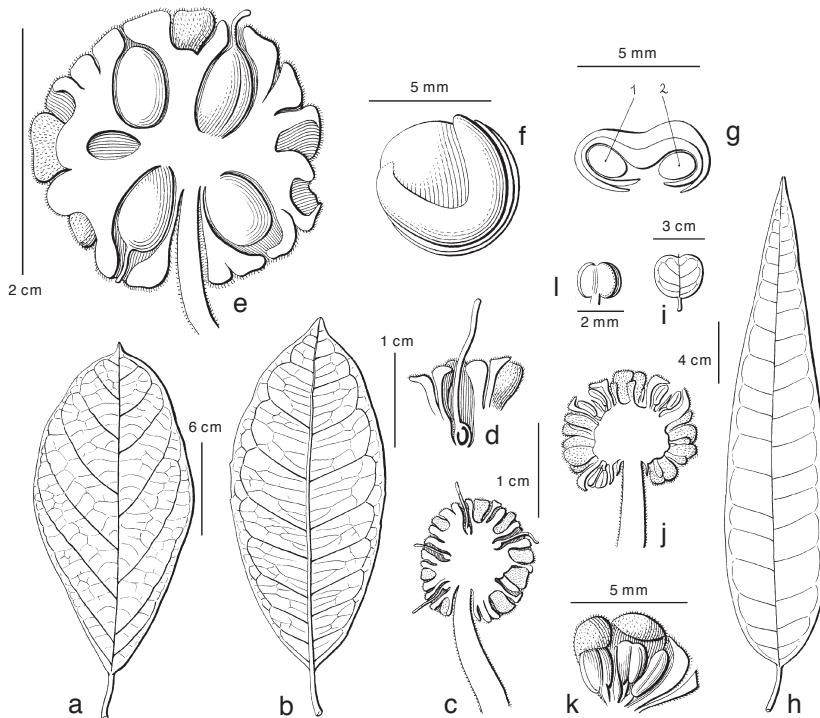


Fig. 5. *Maclura cochinchinensis* (Lour.) Corner. a. Leaf showing the transverse intercostal veins; b. leaf showing the absence of transverse intercostals; c. pistillate inflorescence at anthesis in section; d. pistillate flower at anthesis, showing basally connate flowers; e. infructescence in section; f. embryo with the cotyledon-folds cut away to show the long radicle; g. embryo in transverse section: 1, 2 = radicle; h. sapling leaf; i. leaf of a very young plant; j. staminate inflorescence at anthesis, in section, the anthers not exserted; k. open staminate flower in section; l. mature stamen (a: Herb. Lugd. Bat. 908.157-618; b: Reinwardt s.n.; c-f: Bunnemeijer 8110; h, i: Bakhuizen van den Brink 2949; j-l: Walsh 300).

puberulous to tomentellous; head globose, 0.4–1 cm diam.; tepals c. 1.5 mm long, minutely puberulous; stamens c. 1 mm long, anthers c. 0.5 mm long; bracts basally attached, 0.5–1 mm long, minutely puberulous. *Pistillate inflorescences* axillary, in pairs or solitary, capitate; peduncle 0.4–1.2 cm long, puberulous to tomentellous; head globose, 0.4–0.6 cm diam.; flowers basally connate; perianth c. 1 mm long, densely white puberulous to tomentellous; ovary c. 1 mm long, style 0.5 mm long, stigmas 2–3 mm long, twisted; bracts basally attached, 0.5–1 cm long, in fruit up to 3 mm long, sparsely to densely puberulous. *Infructescences* globose, 1.5–2 cm diam., yellow to orange to red. — **Fig. 5.**

Distribution — Sri Lanka, India, Bhutan, Sikkim, Japan, Australia, New Caledonia; in *Malesia*: throughout.

Habitat — Lowland forest, chiefly forest edges, by mangrove forest, riverbanks, and in secondary forest, rarely in high forest, at altitudes up to 1800 m.

Uses — The infructescences are edible and the wood is used for dyeing silk yellow or green.

STREBLUS

- Streblus* Lour., Fl. Cochinch. (1790) 615; Bureau in A.DC., Prodr. 17 (1873) 218; Baill., Hist. Pl. 6 (1875) 195; Benth. & Hook.f., Gen. Pl. 3 (1880) 359; Engl. in Engl. & Prantl, Nat. Pflanzenfam. 3, 1 (1888) 78; Boerl., Handl. Fl. Ned. Ind. 3 (1900) 314; Merr., Comm. Fl. Cochinch. (1935) 134; Corner, Gard. Bull. Singapore 19 (1962) 215; Blumea 18 (1970) 393; Phytomorphology 25 (1975) 1; C.C. Berg, Proc. Kon. Ned. Akad. Wetensch. C, 91 (1988) 356; Kochummen, Tree Fl. Malaya 3 (1978) 167; Go, Tree Fl. Sabah & Sarawak 3 (2000) 329; C.C. Berg, Blumea 50 (2005) 547.
- Achimus* Juss., Dict. Sci. Nat. 1, Suppl. (1816) 31; Poir., Dict. Sci. Nat. 51 (1827) 91, ‘*Achimus*’.
- Epicarpurus* Blume, Bijdr. (1825) 488.
- Albrandia* Gaudich. in Freyc., Voy. Uranie, Bot. (1830) 509; D. Dietr., Syn. Pl. 5 (1852) 280, ‘*Albrandia*’.
- Calius* Blanco, Fl. Filip. (1837) 698.
- Ampalis* Bojer, Hort. Maurit. (1837) 291; Corner, Gard. Bull. Singapore 19 (1962) 214; C.C. Berg, Bull. Jard. Bot. Belg. 47 (1977) 343. — *Streblus* Lour. sect. *Ampalis* (Bojer) C.C. Berg, Proc. Kon. Ned. Akad. Wetensch. C, 91 (1988) 356.
- Taxotrophis* Blume, Ann. Mus. Bot. Lugduno-Batavi 2 (1856) 77; Hutch., Bull. Misc. Inform. Kew (1918) 147. — *Streblus* Lour. sect. *Taxotrophis* (Blume) Corner, Gard. Bull. Singapore 19 (1962) 218.
- Paratrophis* Blume, Ann. Mus. Bot. Lugduno-Batavi 2 (1856) 81; Cheeseman, Man. New Zealand Fl. (1906) 631. — *Streblus* Lour. sect. *Paratrophis* (Blume) Corner, Gard. Bull. Singapore 19 (1962) 216.
- Sloetia* Teijsm. & Binn. ex Kurz, J. Linn. Soc., Bot. 8 (1864) 168. — *Streblus* Lour. sect. *Sloetia* (Teijsm. & Binn. ex Kurz) Corner, Gard. Bull. Singapore 19 (1962) 218.
- Pseudomorus* Bureau, Ann. Sci. Nat., Bot. sér. 5, 11 (1869) 372; Skottsb., Acta Horti Gothob. 15 (1944) 347; Stearn, J. Arnold Arbor. 28 (1947) 426.
- Diplocos* Bureau in A.DC., Prodr. 17 (1873) 215.
- Phyllochlamys* Bureau in A.DC., Prodr. 17 (1873) 217. — *Streblus* Lour. sect. *Phyllochlamys* (Bureau) Corner, Gard. Bull. Singapore 19 (1962) 217.
- Pseudostreblus* Bureau in A.DC., Prodr. 17 (1873) 219; Hook.f., Fl. Brit. India 5 (1888) 487. — *Streblus* Lour. sect. *Pseudostreblus* (Bureau) Corner, Gard. Bull. Singapore 19 (1962) 217; Phytomorphology 25 (1975) 6, t. 3C.
- Pachytrophe* Bureau in A.DC., Prodr. 17 (1873) 234; Corner, Gard. Bull. Singapore 19 (1962) 214; C.C. Berg, Bull. Jard. Bot. Belg. 47 (1977) 339.
- Uromorus* Bureau in A.DC., Prodr. 17 (1873) 236.
- Pseudotrophis* Warb., Bot. Jahrb. Syst. 13 (1890) 291. — *Streblus* Lour. sect. *Pseudotrophis* (Warb.) Corner, Gard. Bull. Singapore 19 (1962) 217.
- Sloetiopsis* Engl., Bot. Jahrb. Syst. 39 (1907) 573.
- Teonongia* Stapf in Hook., Icon. Pl. 30 (1913) t. 2947; Gagnep., Fl. Indo-Chine 5 (1928) 710.
- Neosloetiopsis* Engl., Bot. Jahrb. Syst. 51 (1914) 426.
- Dimerocarpus* Gagnep., Bull. Mus. Hist. Nat. (Paris) 27 (1921) 441.
- Chevalierodendron* Leroy, Compt. Rend. Hebd. Séances Acad. Sci. 227 (1948) 146.

Trees or shrubs, dioecious or monoecious, unarmed or armed with thorns, uncinate hairs often present. Leaves distichous or sometimes spirally arranged; lamina pinnately veined, with cystoliths above and beneath, only beneath, or absent; stipules free or sometimes fused, lateral or sometimes almost fully amplexicaul. Inflorescences unisexual or sometimes bisexual, racemose, spicate or subcapitate, bracteate; stamineate inflorescences multi- to pluriflorous; pistillate inflorescences multi- to uniflorous. Staminate flowers with 3, 4, or 5 tepals, imbricate or valvate in the bud; stamens 3, 4, or 5, inflexed in the bud. Pistillate flowers 4-merous; tepals (almost) free, more or less unequal in size; ovary free, stigmas 2, equal. Fruiting perianth enlarged or not,

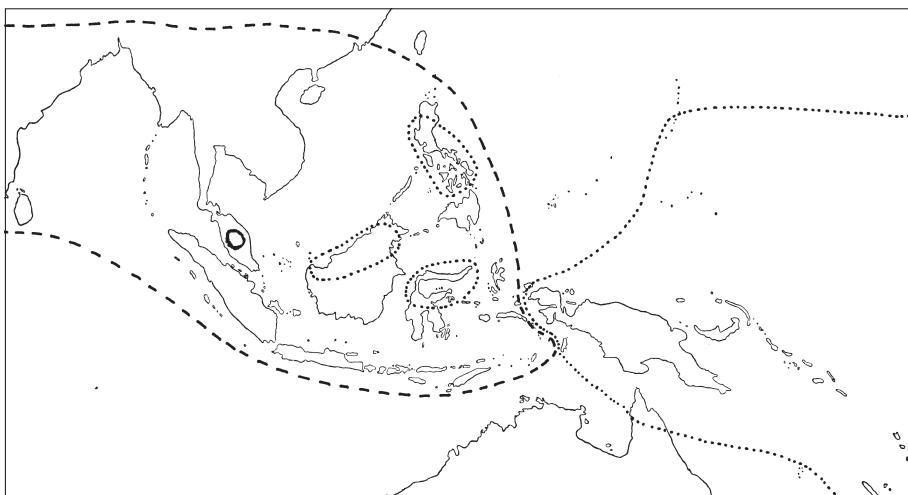
somewhat fleshy or not, mostly greenish; fruit free, drupaceous, dehiscent and whitish or indehiscent and yellow, orange, red, or blackish, endocarp (thinly) crustaceous; seed without endosperm, cotyledons folded or not, equal or unequal, radicle short or long.

Distribution — The genus comprises 23 species in the tropics of the Old World.

Subdivision — By reduction of many former genera to sections, Corner (1962) has widened the circumscription of the genus considerably. Corner (1962, 1970) recognised eight sections in the genus. A more simplified subdivision has been proposed by Berg (1988), who excluded sect. *Bleekrodea*, because of the structure of the inflorescences and the utriculate perianth of the pistillate flower, and included three African–Madagascan species. The sections recognised are: section *Ampalis* (comprising two Madagascan species), section *Paratrophis* (comprising eight Australasian–Asian species), the monotypic sections *Protostreblus* and *Sloetia*, and the Asian–African section *Streblus* (comprising eight Asian and one African species). Section *Streblus*, in this narrow sense, differs from the other sections in the enlarged fruiting perianths, and includes four non-aculeate species with mostly subcoriaceous laminas and dentate margins. Section *Taxotrophis* comprises six aculeate species and section *Pseudostreblus* (Bureau) Corner the non-aculeate species with coriaceous laminas and entire margins (the latter contains only *S. indicus* (Bureau) Corner (1962), ranging from Myanmar to northern Thailand, South China (incl. Hainan) and Cambodia (see Berg 2005)). — **Map 2.**

Morphology — In several features including inflorescences, leaves, ecological differentiation, and number of species *Streblus* shows clear similarities to the neotropical genus *Sorocea* A. St.-Hil. In several species of sect. *Streblus* thorns are formed. In some species the drupes are dehiscent.

Ecology — Several species of sect. *Streblus* are associated with relatively dry and/or seasonal conditions, whereas some species of sect. *Paratrophis* are associated with southern warm-temperate conditions, or (*S. glaber*) partly with montane conditions.



Map 2. Distribution of *Streblus* Lour. sect. *Paratrophis* (Blume) Corner in dotted line (the westward extension of sect. *Paratrophis* is the submontane distribution of *S. glaber* in central and western Malaysia), and the other sections in broken line. Distribution of *S. perakensis* in closed line.

Relationships — The genus shows parallel morphological differentiation to the genus *Trophis* and the similarities suggest that the two genera are closely related. The free tepals of \pm unequal size of the pistillate flower, not becoming fleshy in *Streblus*, versus the fused ones of equal size, usually becoming fleshy in *Trophis*, is the major differentiating character. In all *Trophis* species, except for the peculiar Central American *T. involucrata* W.C. Burger, the perianth becomes enlarged to fully enclosing the fruit, and turns red, purplish, or orange at maturity.

References: Berg, C.C., The genera *Trophis* and *Streblus* (Moraceae) remodelled. Proc. Kon. Ned. Akad. Wetensch. C, 91 (1988) 345–362. — Berg, C.C., Fl. Neotrop. Monogr. 83 (2001) 32. — Corner, E.J.H., The classification of Moraceae. Gard. Bull. Singapore 19 (1962) 187–252. — Corner, E.J.H., New species of *Streblus* and *Ficus* (Moraceae). Blumea 18 (1970) 393–411.

KEY TO THE SECTIONS

- 1a. Leaves spirally arranged; petiole 1.5–6 cm long; upper surface of the lamina \pm scabrous and base of the lamina cordate to rounded Sect. **Protostreblus**
- b. Leaves distichous, petiole up to 1.5 cm long, or if longer (up to 3.5 cm), then upper surface of the lamina smooth and base of the lamina cuneate to rounded 2
- 2a. Inflorescences, bisexual or staminate, spicate; staminate flowers 3-merous
..... Sect. **Sloetia**
- b. Inflorescences unisexual, spicate, racemose, (sub)capitate, or (pistillate ones) uniflorous, if bisexual, then the inflorescence (sub)capitate with a single pistillate flower; staminate flowers 4-merous 3
- 3a. Pistillate inflorescences spicate to subcapitate, usually with 2 or more flowers and the perianth not enlarged in fruit; staminate inflorescences spicate and the peduncle usually at least 0.4 cm long; bracts peltate or basally attached
..... Sect. **Paratrophis**
- b. Pistillate inflorescences racemose with 2–15 flowers, or uniflorous, the perianth in fruit enlarged; staminate inflorescences spicate and the peduncle short (0–0.4 cm long) or capitate; bracts basally attached 4
- 4a. Plants without thorns, often monoecious; lamina mostly subcoriaceous and the margin dentate; staminate inflorescences capitate; pistillate inflorescences uniflorous; tepals of staminate flowers imbricate; tepals of pistillate flowers in fruit reflexed Sect. **Streblus**
- b. Plants (always or sometimes) with thorns, dioecious; lamina mostly coriaceous and the margin and/or acumen spinulose; pistillate inflorescences (sub)racemose or uniflorous; staminate inflorescences spicate (to subcapitate); tepals of staminate flowers valvate; tepals of pistillate flowers not reflexed in fruit
..... Sect. **Taxotrophis**

Section STREBLUS

Streblus Lour. sect. *Streblus*; Corner, Gard. Bull. Singapore 19 (1962) 218; C.C. Berg, Proc. Kon. Ned. Akad. Wetensch. C, 91 (1988) 357.

Achymus Juss., Dict. Sci. Nat. 1, Suppl. (1816) 31.

Epicarpurus Blume, Bijdr. (1825) 488.

Albrandia Gaudich. in Freyc., Voy. Uranie, Bot. (1830) 509.

Calius Blanco, Fl. Filip. (1837) 698.

Sloetiopsis Engl., Bot. Jahrb. Syst. 39 (1907) 573; C.C. Berg, Bull. Jard. Bot. Belg. 47 (1977) 363.

Teonongia Stapf, Hooker's Icon. Pl. 30 (1911) t. 2947.

Neosloetiopsis Engl., Bot. Jahrb. Syst. 51 (1914); C.C. Berg, Bull. Jard. Bot. Belg. 47 (1977) 363.

Diplothorax Gagnep., Bull. Soc. Bot. France 75 (1928) 98.

Trees or shrubs, monoecious or dioecious, without spines. *Leaves* distichous; lamina elliptic, subcoriaceous to chartaceous or to coriaceous, margin dentate; petiole short; stipules free, lateral. *Inflorescences* bisexual or unisexual, capitate or cymose, pistillate ones usually uniflorous, bracts basally attached; staminate flowers 4-merous, tepals imbricate; fruiting perianth more or less enlarged, reflexed (or not). *Drupe* dehiscent or not.

Distribution — This section comprises four species, two of them in the Asian mainland and western Malesia, one in Celebes and the fourth in Africa.

Morphology — Monoecy occurs in *Streblus asper* and, more pronouncedly so in *S. tonkinensis* (Eberh. & Dubard) Corner (incl. *S. monoicus* Gagnep. = *S. asper* var. *monoicus* (Gagnep.) Corner), a species from Laos and Vietnam. The African species, *S. usambarensis* (Engl.) C.C. Berg (Bull. Jard. Bot. Belg. 47 (1977) 364; Proc. Kon. Ned. Akad. Wetensch. C, 91 (1988) 357) is distinct in the spicate staminate inflorescences and the fruiting perianth remaining patent; the latter feature may prove to occur in *S. celebensis* as well.

KEY TO THE SPECIES

- 1a. Indumentum whitish; lamina ± scabrous above; lateral veins 4–7(–8) pairs. — Widespread **1. *S. asper***
- b. Indumentum predominantly dark brown; lamina glabrous above; lateral veins (7–) 8–10 pairs. — Celebes **2. *S. celebensis***

1. *Streblus asper* Lour.

Streblus asper Lour., Fl. Cochinch. 1 (1790) 615; Blume, Ann. Mus. Bot. Lugduno-Batavi 2 (1856) 79, f. 33; Hook.f., Fl. Brit. India 5 (1888) 489; Koord. & Valeton, Bijdr. Boomsoort. Java 11 (1906) 7; Koord., Exkurs.-Fl. Java 2 (1912) 88; Merr., Sp. Blancoan. (1918) 123; Enum. Philipp. Flow. Pl. 2 (1923) 38; Koord., Exkurs.-Fl. Java, Atlas (1924) f. 747; Gagnep., Fl. Indo-Chine 5 (1928) 712, f. 86: 10–16, 87: 1–2; Diels, Bot. Jahrb. Syst. 67 (1935) 172; Merr., Comm. Fl. Cochinch. (1935) 134; Alston, Kandy Fl. (1938) 35, F. 184; Corner, Wayside Trees Malaya ed.1 (1940) 692, t. 255; Worth., Ceylon Trees (1959) pl. 424; Corner, Gard. Bull. Singapore 19 (1962) 228; Backer & Bakh. f., Fl. Java 2 (1965) 16; Corner, Phytomorphology 25 (1975) 3, t. 1B, 3D; Fl. Ceylon 1.2 (1977) 156, t. 28; Wayside Trees Malaya ed. 3 (1988) 555, t. 168.

Trophis aspera Retz., Observ. Bot. 5 (1788) 30; Roxb., Fl. Ind., ed. Carey 3 (1832) 761; Wight, J. Bot. 1 (1834) 62, t. 121.

Trophis cochinchinensis Poir., Encycl. 8 (1808) 123.

Trophis aculeata Roth, Nov. Pl. Sp. (1821) 868.

Epicarpurus orientalis Blume, Bijdr. (1825) 488; Hassk., Pl. Jav. Rar. (1848) 197; Miq., Pl. Jungh. (1851) 42; Wight, Icon. Pl. Ind. Orient. 6 (1853) t. 1961; Zoll., Syst. Verz. (1854) 89.

Calius lactescens Blanco, Fl. Filip. (1837) 698; ed. 3, 3 (1879) 1103, t. 171. — *Streblus lactescens* (Blanco) Blume, Ann. Mus. Bot. Lugduno-Batavi 2 (1856) 80.

Achymus pallens Sol. ex Blume, Ann. Mus. Bot. Lugduno-Batavi 2 (1856) 79.

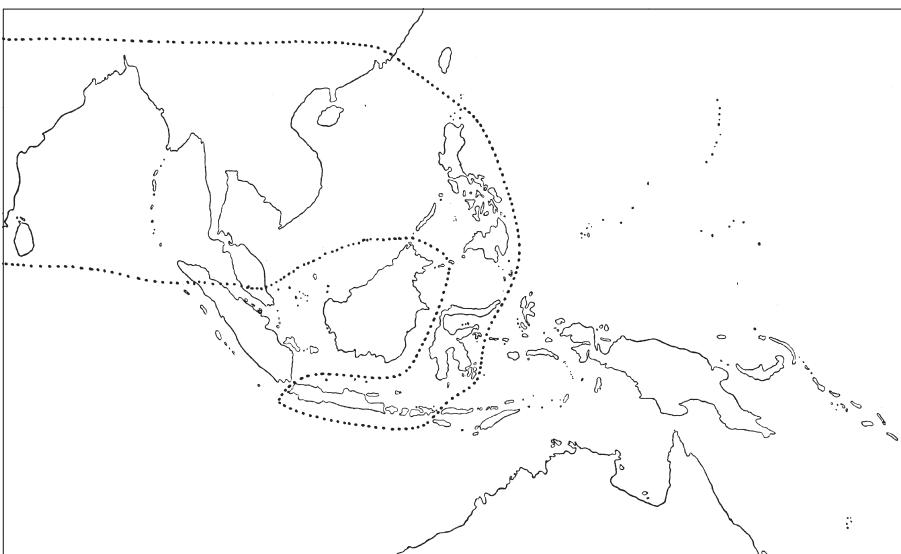
Cudrania crenata C.H. Wright, J. Linn. Soc., Bot. 26 (1899) 469; Merr., Lingnan Sci. J. 16 (1937) 187.

— *Vanieria crenata* (C.H. Wright) Chun, J. Arnold Arbor. 8 (1927) 21.

Diplothorax tonkinensis Gagnep., Bull. Soc. Bot. France 75 (1928) 98.

Shrub or tree up to 10(–15) m tall, much-branched, branches often drooping; lower ones (often?) prostrate, monoecious or dioecious. *Leafy twigs* 1–2 mm thick, whitish puberulous. *Leaves* distichous; lamina elliptic to obovate or subobovate, 1–8(–13) by 0.5–3.5(–6.5) cm, coriaceous to subcoriaceous, apex (sub)acuminate to acute, base rounded to subcordate to obtuse, margin crenate to dentate; upper surface sparsely whitish hispidulous to puberulous, ± scabrous (or almost smooth); lower surface whitish hispidulous to puberulous, ± scabrous; midrib ± prominent in the lower part of the lamina, ± impressed in the upper part, lateral veins 4–7(–8) pairs, tertiary venation reticulate (to subscalariform); petiole 0.1–0.3(–0.5) cm long, whitish puberulous; stipules 0.3–0.5 cm long, puberulous, caducous (or subspersistent). *Staminate inflorescences* axillary, in pairs or solitary, capitate; peduncle 0.2–1.5 cm long, sparsely minutely whitish puberulous; head 0.4–1 cm diam.; flowers 4–15; perianth 1.5–2 mm long, whitish minutely puberulous; stamens 2–2.5 mm long, anthers c. 1 mm long; bracts few, basally attached, 0.5–2 mm long, sparsely minutely puberulous. *Pistillate inflorescences* axillary, in pairs or solitary, uniflorous (or biflorous); peduncle 0.4–1.5 cm long, minutely whitish puberulous; tepals 2–2.5 mm long, minutely puberulous, in fruit 5–8 mm long, reflexed; ovary c. 1 mm long, style c. 1 mm long, elongating up to 3 mm, stigmas 2–4 mm long, elongating up to 12 mm; bracts few, basally attached, 0.5–2 mm long, sparsely minutely puberulous. *Drupe* (sub)globose, 0.6–0.8 cm long, indehiscent, yellow to orange at maturity. — **Fig. 6; Map 3.**

Distribution — Sri Lanka, India, Bhutan, Bangladesh, Myanmar, Andaman Islands, Nicobar Islands, Thailand, South China (incl. Hainan), Indochina; in Malesia: Sumatra



Map 3. Distribution of *Streblus asper* Lour.

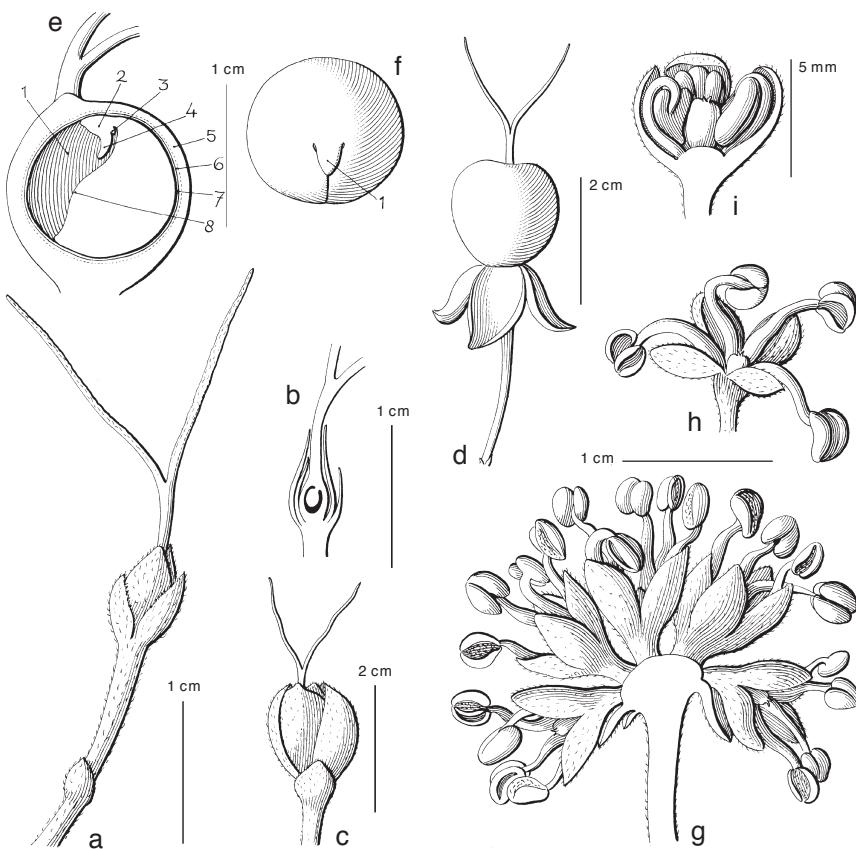


Fig. 6. *Streblus asper* Lour. a. Pistillate inflorescence, one-flowered, at anthesis; b. the same in section; c. with nearly ripe fruit; d. ripe fruit; e. ripe fruit in section: 1 = side of the large cotyledon, 2 = radicle, 3 = plumule, 4 = small cotyledon, 5 = exocarp, 6 = endocarp, 7 = membranous testa, 8 = inner face of the large cotyledon; f. embryo in end-view, showing the radicle (1) and large cotyledon; g. staminate inflorescence in section; h. staminate flower; i. staminate flower-bud in section (material from Penang).

(Atjeh, Medan), Malay Peninsula (Penang, Kedah, Perlis, Kelantan), Java (also Madura and Kangean Island), Philippines, Celebes, Lesser Sunda Islands (Bali, Lombok, Sumbawa, Flores, Sumba), Moluccas (Ambon).

Habitat — Strongly seasonal monsoon climate, chiefly in secondary forest, by rice-fields and in open places; at low altitudes.

Uses — The fruits are edible, sweet and the leaves can be used as cattle fodder.

2. *Streblus celebensis* C.C. Berg

Streblus celebensis C.C. Berg, Blumea 50 (2005) 547.

Shrub, 1 m tall, without spines, dioecious. Leafy twigs 1–2 mm thick, puberulous, mainly with dark brown appressed hairs. Leaves distichous; lamina subcoriaceous,

(sub)ovate, 6–15 by 2–7 cm, apex acuminate to subcaudate, base obtuse, margin coarsely crenate-dentate towards the apex; upper surface (subglabrous) smooth; lower surface sparsely appressed puberulous with dark brown appressed hairs, scabridulous; midrib prominent or prominent in a groove above, lateral veins (7–)8–10 pairs, tertiary venation subscalariform to reticulate, slightly prominent; petiole 0.3–0.7 cm long, c. 1 mm thick, puberulous with dark brown appressed hairs; stipules 0.1–0.2 cm long, sub-persistent (or caducous). *Staminate inflorescences* axillary, solitary, subsessile, subcapitate with 3–5 flowers; tepals 4, valvate in the bud, c. 1.5 mm long, outside appressed puberulous with dark brown hairs, the margin white tomentellous; stamens 4, inflexed in the bud, anthers c. 1 mm long, pistillode obconical, c. 0.5 mm long; bracts basally attached ovate 1–2 mm long, appressed puberulous. *Pistillate inflorescences* axillary, solitary, uniflorous; peduncle c. 0.2 cm long; tepals 4, decussate imbricate, c. 1.5 mm long, outside appressed puberulous with dark brown hairs, margin white ciliolate; ovary c. 1 mm long, style c. 3 mm long, stigmas 2, filiform, 6–8 mm long; bracts few, basally attached, ovate, c. 0.2 mm long, appressedly puberulous; tepals enlarging and probably enveloping the fruit at full maturity.

Distribution — Celebes (only known from Batudaka Island).

Habitat — Humid forest at low altitudes.

Section PARATROPHIS

Streblus Lour. sect. *Paratrophis* (Blume) Corner, Gard. Bull. Singapore 19 (1962) 216; Phytomorphology 25 (1975) 1; C.C. Berg, Proc. Kon. Ned. Akad. Wetensch. C, 91 (1988) 357. — *Paratrophis* Blume, Ann. Mus. Bot. Lugduno-Batavi 2 (1856) 81.

Uromorus Bureau in A.DC., Prodr. 17 (1873) 236.

Chevalierodendron Leroy, Compt. Rend. Hebd. Séances Acad. Sci. 227 (1948) 146.

Trees, unarmed, dioecious. *Leaves* distichous; lamina elliptic to narrowly elliptic; petiole short; stipules free, lateral. *Inflorescences* unisexual, spicate, bracts peltate or basally attached; staminate flowers 4-merous, tepals valvate in the bud; pistillate flowers usually 2 or more; fruiting perianth not or hardly enlarged. *Drupe* indehiscent, red or blackish at maturity.

Distribution & Delimitation — This section comprises eight species and it is distinguishable from sect. *Protostreblus* by the distichous arrangement of the leaves, and from the other Asian-Australasian sections by the tepals of the pistillate flower, which are not or only slightly enlarged in fruit. This section is distinctly concentrated in the eastern part of the range of the genus. One of the species, *Streblus pendulinus*, extends just into the Malesian region. Only *S. glaber* is widespread in this region and occurs also in Australia (Queensland). The other five are elements of the Pacific region: *Streblus anthropophagorum* (Seem.) Corner, incl. *S. solomonensis* Corner (from the Solomon Islands to Marquesas Islands), *S. banksii* (Cheeseman) C.J. Webb (New Zealand J. Bot. 25 (1987) 136) in New Zealand, *S. heterophyllus* (Blume) Corner (1962) in New Zealand, *S. sclerophyllus* Corner (Blumea 18 (1970) 399, t. 4) in New Caledonia, *S. smithii* (Cheeseman) Corner (1962) in New Zealand, and *S. tahitensis* (Nadeaud) Corner (1962) in Tahiti.

KEY TO THE SPECIES

- 1a. Midrib of the lamina ± prominent above, margin mostly subentire, lamina (sub)coriaceous. — Widespread..... **3. *S. glaber***
 b. Midrib of the lamina impressed above, margin serrate to subspinulose dentate, lamina chartaceous to subcoriaceous. — New Guinea **4. *S. pendulinus***

3. *Streblus glaber* (Merr.) Corner

Streblus glaber (Merr.) Corner, Gard. Bull. Singapore 19 (1962) 221; Phytomorphology 25 (1975) 2, t. 3B; Go, Tree Fl. Sabah & Sarawak 3 (2000) 331, t. 16. — *Gironniera glabra* Merr., Philipp. J. Sci., 1, Suppl. (1906) 42; Enum. Philipp. Flow. Pl. 2 (1923) 35. — *Paratrophis glabra* (Merr.) Steenis, J. Bot. 72 (1934) 8. — *Chevalierodendron glabrum* (Merr.) Leroy, Compt. Rend. Hebd. Séances Acad. Sci. 227 (1948) 146.

Tree up to 40 m tall or shrub, dioecious. *Leafy twigs* 0.5–2 mm thick, (sub)glabrous or whitish minutely puberulous. *Leaves* distichous; lamina narrowly elliptic to elliptic to subovate to narrowly ovate (or to subrhombic or linear), 1.5–16 by 0.5–4.5 cm, (sub)coriaceous, apex acuminate to subcaudate, base cuneate to almost rounded (or to subattenuate), margin subentire (or dentate); upper surface glabrous; lower surface puberulous on the main veins or glabrous, often with minute red or red-brown pluricellular trichomes; midrib ± prominent above, lateral veins 5–18 pairs (or if the lamina is linear, then up to 30 pairs), tertiary venation reticulate; petiole 0.3–1.7 cm long, sparsely whitish appressedly puberulous; stipules 0.2–0.5 cm long, minutely whitish appressedly puberulous, caducous. *Staminate inflorescences* axillary, up to 5 together, spicate (or uniflorous); peduncle 0.3–1.5 cm long, sparsely minutely puberulous; spike 0.8–2 cm or up to 3 cm long; flowers (1–)3–15 or up to 30; perianth 1–2 mm long, minutely puberulous or only ciliolate, stamens 2.5–3 mm long, anthers 1–1.2 mm long; bracts basally attached, 0.3–1 mm long, sparsely minutely puberulous. *Pistillate inflorescences* axillary, up to 5 together, short-spicate to subcapitate or uniflorous; peduncle 0.5–2 cm long, minutely puberulous; flowers 1–3(–9); tepals 1–1.5 mm long, ciliolate or subglabrous, in fruit hardly enlarged; ovary 1.5–2 mm long, stigmas c. 2 mm long; bracts basally attached, 0.3–1 mm long, ciliolate or subglabrous. *Fruit* ellipsoid to ovoid, 0.8–1.2 cm, dark red to purple at maturity.

Notes — 1. Two subspecies can be recognised in the Malesian region: the typical subspecies widespread in lowland to submontane and a montane one confined to eastern New Guinea. The main differentiating morphological character is the presence or absence of teeth in the margin of the lamina. However, in Sabah subsp. *glaber*, which has normally an entire lamina margin, can have a dentate one. There is an overlap of the altitudinal ranges of the two subspecies and transitional forms are encountered.

2. The number of inflorescences in the leaf axils is more than the common pair, as short-shoots are formed in the leaf axils with solitary or paired inflorescences on the nodes. This axillary leafless shoot sometimes becomes longer and may bear up to 12 inflorescences.

3. The Australian material of *S. glaber* (Merr.) Corner, Gard. Bull. Singapore 19 (1962) 221 (— *Paratrophis australiana* C.T. White, Contr. Arnold Arbor. 4 (1933) 15) occurring at altitudes up to 1000 m, differs from both subspecies in the usually crenate-

dentate margin of the lamina. It was referred to *S. glaber* var. *australianus* (C.T. White) Corner (Gard. Bull. Singapore 19 (1962) 221) and is currently recognised as subsp. *australianus* (C.T. White) C.C. Berg (Blumea 50 (2005) 548).

KEY TO THE MALESIAN SUBSPECIES

- 1a. Lamina dentate, at least 2 teeth in the upper part of the lamina. — E New Guinea
..... b. subsp. ***urophyllus***
b. Lamina entire (sometimes dentate in Borneo). — Widespread . . . a. subsp. ***glaber***

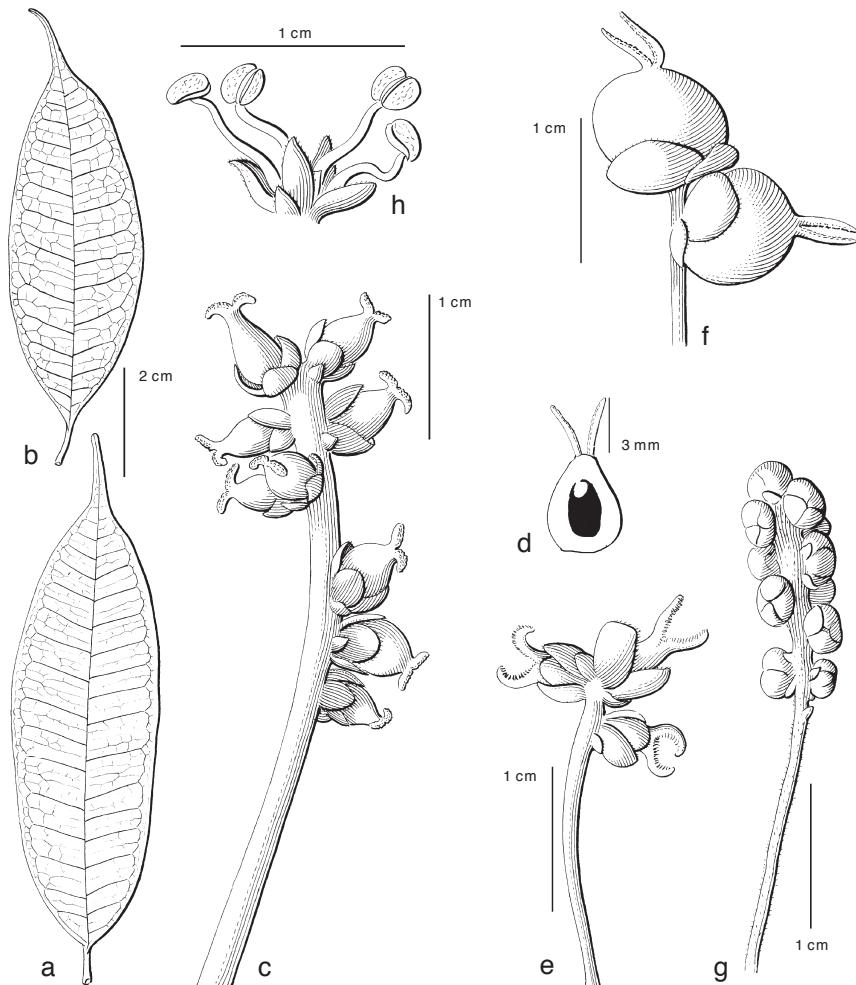


Fig. 7. *Streblus glaber* (Merr.) Corner subsp. *glaber*. a, b. Leaves showing the absence of transverse intercostal veins; c. many-flowered pistillate inflorescence; d. ovary in section; e. few-flowered pistillate inflorescence; f. fruits; g. staminate inflorescence; h. staminate flower (a: Clemens 32132; b: NGF 6924; c, d: Elmer 22014; e: Eyma 4863; f: SFN 26946; g, h: Clemens 29321).

a. subsp. glaber

Aphananthe negrosensis Elmer, Leafl. Philipp. Bot. 2 (1909) 575.

Pseudostreblus caudatus Ridl., J. Fed. Malay States Mus. 6 (1915) 54; Fl. Malay Penins. 3 (1924) 324.
Streblus laevifolius Diels, Bot. Jahrb. Syst. 67 (1935) 171.

Tree up to 25(–40) m tall. *Lamina* elliptic or to narrowly ovate, (1.5)–3–16 by (0.5)–1–4.5 cm, margin of the lamina usually entire, but sometimes dentate in the upper part of the lamina (in Borneo: Sabah); lateral veins 7–18 pairs. — **Fig. 7.**

Distribution — Solomon Islands; in *Malesia*: Sumatra, Malay Peninsula, Borneo (mainly Sabah), Philippines (Luzon, Mindoro, Negros, Cebu), Celebes, Moluccas (Aru Islands), New Guinea.

Habitat — Montane forest, sometimes on limestone or in relatively dry areas; mostly at altitudes between 700 and 2500 m, rarely down to sea level.

Note — In the Philippines, the inflorescences are usually longer (up to 3 cm long) and both staminate and pistillate inflorescences tend to have more flowers, often more than 15 or 3, respectively.

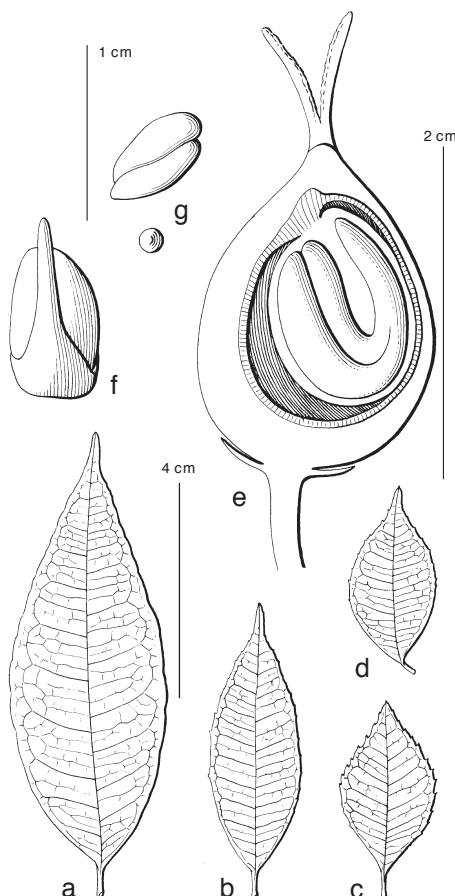


Fig. 8. *Streblus glaber* (Merr.) Corner subsp. *urophyllus* (Diels) C.C. Berg. a–d. Leaf-variation; e. fruit in section; f, g. embryos to show the obliquity (a: J.C. Sanders 879; b: Robbins 199; c, d: Pullen 310; e–g: Hoogland & Pullen 5529).

b. subsp. *urophyllus* (Diels) C.C. Berg

Streblus glaber (Merr.) Corner subsp. *urophyllus* (Diels) C.C. Berg, Blumea 50 (2005) 548; Corner, Gard. Bull. Singapore 19 (1962) 225. — *Streblus urophyllus* Diels, Bot. Jahrb. Syst. 67 (1935) 172.

Streblus urophyllus Diels var. *salicifolius* Corner, Gard. Bull. Singapore. 19 (1962) 225.

Shrub or tree up to 15 m tall. *Lamina* narrowly elliptic to elliptic to subovate to narrowly ovate (or to subrhombic) or linear, 2–8(–15) by 0.5–3(–4.5) cm, margin of the lamina dentate to denticulate, at least two teeth in the upper part of the lamina; lateral veins 5–10 pairs, but if the lamina linear (willow-leaf shaped) then up to 30 pairs.

— **Fig. 8.**

Distribution — New Guinea (eastern).

Habitat — Primary (or secondary) forest at altitudes between (1600–)2400 and 3000 m, occasionally on limestone.

Note — For this subspecies a form with linear laminas and (therefore) numerous lateral veins has been described as var. *salicifolius*.

4. *Streblus pendulinus* (Endl.) F. Muell.

Streblus pendulinus (Endl.) F. Muell., Fragm. Phyt. Australiae 6 (1868) 192; Corner, Gard. Bull. Singapore 19 (1962) 222; Blumea 18 (1970) 397, t. 2. — *Morus pendulina* Endl., Prod. Fl. Norfolk. (1833) 40. — *Pseudomorus pendulina* (Endl.) Stearn, J. Arnold Arbor. 28 (1947) 427.— *Pseudomorus brunonianiana* (Endl.) Bureau var. *pendulina* (Endl.) Bureau, Ann. Sci. Nat., Bot. sér. 4, 11 (1869) 373.

Morus brunonianiana Endl., Atakta Bot. 4 (1835) t. 32. — *Streblus brunoniananus* (Endl.) F. Muell., Fragm. Phyt. Australiae 6 (1868) 192. — *Pseudomorus brunonianiana* (Endl.) Bureau, Ann. Sci. Nat., Bot. sér. 4, 11 (1869) 373; Rock, Indig. Trees Haw. Isl. (1913) 114. — *Pseudomorus brunonianiana* (Endl.) Bureau var. *australiana* Bureau, Ann. Sci. Nat., Bot. sér. 4, 11 (1869) 373.

Pseudomorus brunonianiana (Endl.) Bureau var. *obtusata* Bureau, Ann. Sci. Nat., Bot. sér. 4, 11 (1869) 373.

Pseudomorus sandwicensis O. Deg., Fl. Hawaïensis (1938) fam. 96. — *Pseudomorus brunonianiana* (Endl.) Bureau var. *sandwicensis* (O. Deg.) Skottsb., Acta Horti Gothob. 15 (1944) 347.

Shrub or tree up to 13 m tall, dioecious (or monoecious). Leafy twigs 1–2 mm thick, (minutely) whitish puberulous. Leaves distichous; lamina elliptic to (sub)ovate, (1.5–)4–10(–14) by (0.5–)1.5–4.5(–6.5) cm, chartaceous to subcoriaceous, apex acuminate to (sub)acute to subobtuse, base subcordate to cuneate, margin serrate to subspinulose-dentate, sometimes lobate; upper surface glabrous and smooth (or scabrous); lower surface whitish puberulous on the main veins, scabridulous; midrib impressed above, lateral veins (4–)7–10(–14) pairs, tertiary venation reticulate; petiole 0.2–1.1 cm long, (minutely) whitish puberulous; stipules 0.2–0.4 cm long, whitish puberulous, caducous. Staminate inflorescences axillary, solitary or in pairs, spicate; peduncle (0.2–)0.4–0.7 (–2.5) cm long, (minutely) puberulous; spike 2–18 cm long; flowers numerous; perianth 1–1.5 mm long, sparsely minutely puberulous, stamens c. 2.5 mm long, anthers c. 0.8 mm long; bracts peltate, c. 0.5 mm diam., ciliolate. Pistillate inflorescences axillary, solitary or in pairs, short-spicate to subcapitate; peduncle 0.2–0.8 cm long; flowers 2–9; tepals 1–1.5 mm long, ciliolate, in fruit hardly enlarged; ovary 1.5–2 mm long, stigmas 2–3 mm long; bracts (sub)peltate, 0.5–1 mm diam., ciliolate. Fruit ellipsoid

to ovoid to subglobose, 0.6–1 cm long, yellow to reddish to brownish or to purple at maturity.

Distribution — Australia (Queensland, New South Wales), and in the Pacific: New Hebrides, New Caledonia, Norfolk Island, Fiji, Rapa, Hawaii, Guam, Saipan, Rota; in *Malesia*: New Guinea (eastern).

Habitat — Lowland forest (as on limestone hills), on seashore, and in swamps, often under seasonal conditions.

Note — Collection *W. Moi 149* from Papua New Guinea, Morobe Province, deviates from the other collections from New Guinea in being monoecious and having laminas scabrous above.

Section PROTOSTREBLUS

Streblus Lour. sect. *Protostreblus* Corner, Blumea (1970) 393; C.C. Berg, Proc. Kon. Ned. Akad. Wetensch. C, 91 (1988) 358.

Trees, unarmed, dioecious. Leaves spirally arranged; lamina ovate to subcordiform; petiole long; stipules free, lateral. Inflorescences unisexual, bracts basally attached. Staminate inflorescences unknown. Pistillate inflorescences spicate, multiflorous; fruiting perianth hardly enlarged. Drupe indehiscent, yellow to orange (or red?) at maturity.

Delimitation — This section comprises a single species and is distinguished by the spirally arranged leaves with long petioles.

5. *Streblus ascendens* Corner

Streblus ascendens Corner, Blumea 18 (1970) 395, t. 1; Phytomorphology 25 (1975) 2.

Tree up to 23 m tall, with buttresses up to 1.5 m high, dioecious. Leafy twigs 2–4 mm thick, whitish to brownish puberulous. Leaves spirally arranged; lamina ovate to subcordiform, 9–14(–24) by 5–8(–15) cm, subcoriaceous, apex acuminate, base (sub)cordate to rounded, margin subentire to irregularly crenate-dentate; upper surface sparsely whitish puberulous, ± scabrous; lower surface whitish puberulous to subtomentose; midrib slightly impressed above, lateral veins 3 or 4 pairs, tertiary venation scalariform; petiole 1.5–6 cm long, whitish appressedly puberulous; stipules 0.4–0.6 cm long, ± densely whitish to yellowish appressedly puberulous, caducous. Staminate inflorescences unknown. Pistillate inflorescences axillary, solitary, spicate; peduncle 0.7–1.2 cm long, minutely puberulous; flowers numerous; tepals c. 2 mm long, minutely puberulous, in fruit up to 4 mm long; ovary c. 1.5 mm long, stigmas 1.5–2 mm long; bracts basally attached, 0.3–1 mm long, minutely puberulous. Drupe obovoid, c. 0.7 cm long when dry, yellow to orange (to red?) at maturity. — Fig. 9.

Distribution — Solomon Islands (Kolombangara); in *Malesia*: New Guinea (Manokwari).

Habitat — Lowland forest.

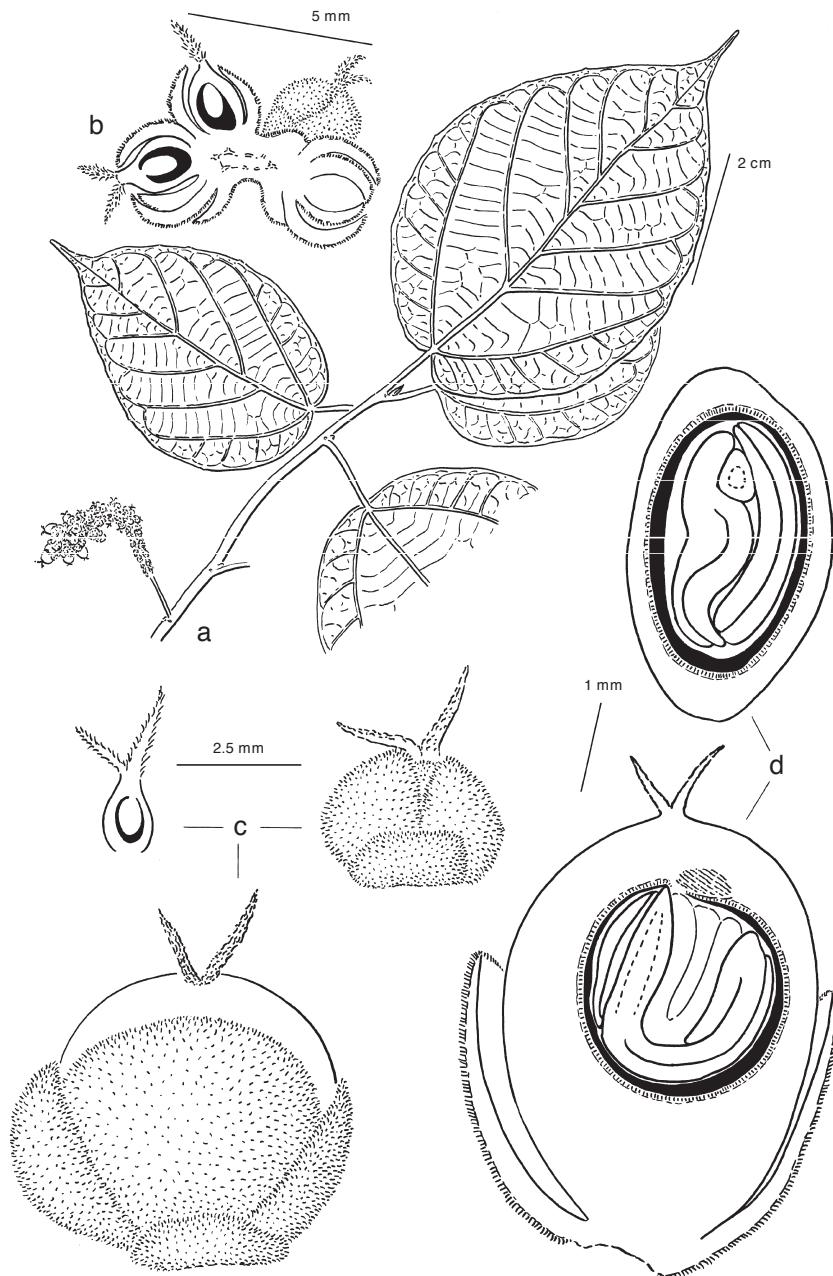


Fig. 9. *Streblus ascendens* Corner. a. Leafy twig with pistillate inflorescence; b. pistillate spike in section; c. pistillate flowers; d. ripe fruit (endocarp and hilar plug hatched) (all: BSIP 8624).

Section SLOETIA

Streblus Lour. sect. *Sloetia* (Teijsm. & Binn. ex Kurz) Corner, Gard. Bull. Singapore 19 (1962) 218; Phytomorphology 25 (1975) 4; C.C. Berg, Proc. Kon. Ned. Akad. Wetensch. C, 91 (1988) 358. — *Sloetia* Teijsm. & Binn. ex Kurz, J. Linn. Soc., Bot. 8 (1864) 168.

Trees, unarmed, monoecious. *Leaves* distichous; lamina elliptic; petiole short; stipules free, nearly fully amplexicaul. *Inflorescences* bisexual or staminate, spicate, bracts peltate; staminate flowers numerous, 3-merous, tepals imbricate in the bud; pistillate flowers 0–4; fruiting perianth enlarged. *Drupe* dehiscent.

Delimitation — This section comprises a single species and is distinguished by the spicate, mostly bisexual inflorescences and 3-merous staminate flowers.

6. *Streblus elongatus* (Miq.) Corner

Streblus elongatus (Miq.) Corner, Gard. Bull. Singapore 19 (1962) 227; Phytomorphology 25 (1975) 4, t. 1D, 3E; Kochummen, Tree Fl. Malaya 3 (1978) 168, t. 11; Go, Tree Fl. Sabah & Sarawak 3 (2000) 330. — *Artocarpus elongatus* Miq., Fl. Ned. Ind., Eerste Bijv. (1861) 419. — *Sloetia elongata* (Miq.) Koord., Exkurs.-Fl. Java 2 (1912) 90, Koord., Atlas Baumart. Java (1924) t. 749; Burkill, Dict. Econ. Prod. Malay Penins. (1935) 2035; Corner, Wayside Trees Malaya ed.1 (1940) 691, t. 254.

Sloetia sideroxylon Teijsm. & Binn. ex Kurz, J. Linn. Soc., Bot. 8 (1864) 168, t. 13; Bureau in A.DC., Prodr. 17 (1873) 257; Hook.f., Fl. Brit. India 5 (1888) 493; Foxw., Malayan Forest Rec. 3 (1927) 129.

Sloetia sideroxylon Teijsm. & Binn. ex Kurz var. *brevipes* Bureau in A.DC., Prodr. 17 (1873) 258.

Sloetia penangiana Oliv., Hooker's Icon. Pl. (1886) t. 1531; Hook.f., Fl. Brit. India 5 (1888) 493.

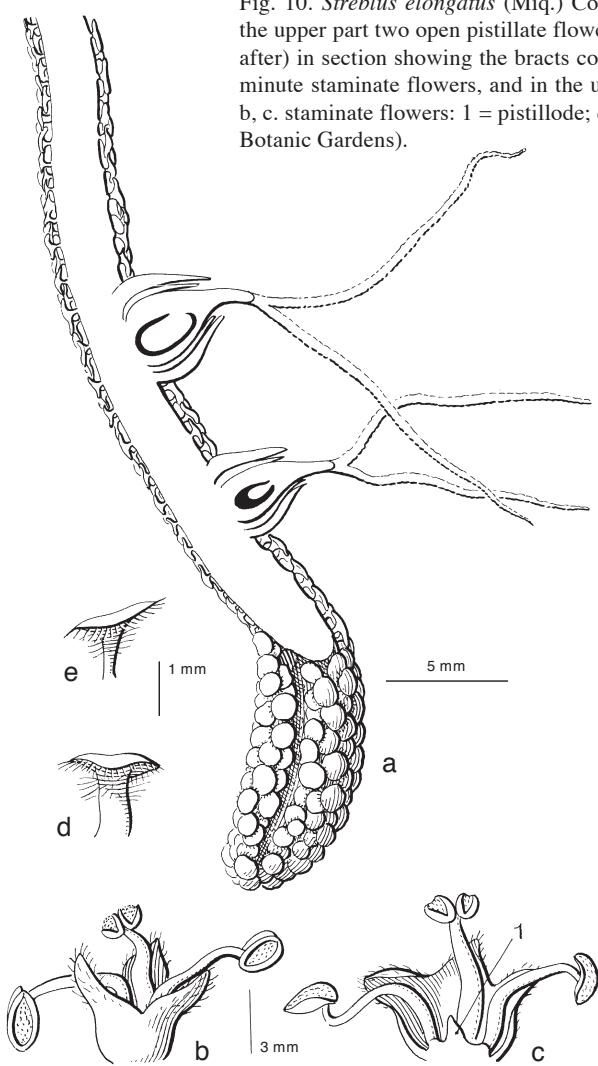
Sloetia wallichii King ex Hook.f., Fl. Brit. India 5 (1888) 493.

Tree up to 35 m tall, often flowering as shrub, monoecious. *Leafy twigs* 1.5–2.5 mm thick, sparsely whitish puberulous with uncinate hairs. *Leaves* distichous; lamina narrowly elliptic to subobovate to narrowly ovate (or to elliptic), 6–25(–38) by 1.5–8(–16) cm, usually ± asymmetric, coriaceous to subcoriaceous, apex acuminate, base cuneate to obtuse, margin entire (or towards the apex sparsely denticulate); upper surface glabrous; lower surface sparsely whitish puberulous on the main veins, smooth (or scabridulous); midrib prominent above, lateral veins 10–20 pairs, tertiary venation (sub)scalariform; petiole 0.2–1.8 cm long, sparsely whitish puberulous to subglabrous; stipules 0.5–1(–1.5) cm long, sparsely minutely whitish puberulous to subglabrous, caducous (or subpersistent). *Inflorescences* axillary, solitary or in pairs, spicate, staminate or bisexual and protogynous; peduncle 0.2–1 cm long, sparsely puberulous to subglabrous; spike 3–20 cm long; staminate flowers numerous; perianth 3- (or 4-) merous, 1–1.2 mm long, minutely puberulous; stamens 3 (or 4), 2–2.5 mm long, anthers 0.6–0.8 mm long; pistillate flowers 0–4; tepals 4, c. 1.5 mm long, ciliolate, in fruit 8–12 mm long; ovary 1–1.5 mm long, style 2–5 mm long, stigmas 8–20 mm long; bracts peltate, 0.5–1 mm diam., ciliolate. *Fruit* ellipsoid, 1–1.3 cm long, dehiscent, whitish; endocarp body 0.6–0.8 cm long, smooth. — **Fig. 10.**

Distribution — Sumatra (also Riouw Archipelago), Malay Peninsula (Penang, Perak, Trengganu to Singapore), Borneo, Celebes.

Habitat — Lowland forest, common in secondary forest.

Fig. 10. *Streblus elongatus* (Miq.) Corner. a. Part of inflorescence and in the upper part two open pistillate flowers (one at anthesis, the other shortly after) in section showing the bracts concealing the very young and, as yet, minute staminate flowers, and in the upper part the abaxial sterile groove; b, c. staminate flowers: 1 = pistillode; d, e. bracts (material from Singapore Botanic Gardens).



Uses — The species yields very hard, durable, strong, and heavy timber.

Notes — 1. Inflorescences are often deformed by glomerules of globose 'bracteate' structures (galls?).

2. The endocarp body is ejected for several meters. The exocarp is eaten by monkeys, squirrels, and birds.

Section TAXOTROPHIS

Streblus Lour. sect. *Taxotrophis* (Blume) Corner, Gard. Bull. Singapore 19 (1962) 218; Phytomorphology 25 (1975) 5. — *Taxotrophis* Blume, Ann. Mus. Bot. Lugduno-Batavi 2 (1856) 77. *Diplocos* Bureau in A.DC., Prodr. 17 (1873) 215.

Phyllochlamys Bureau in A.DC., Prodr. 17 (1873) 217. — *Streblus* Lour. sect. *Phyllochlamys* (Bureau) Corner, Gard. Bull. Singapore 19 (1962) 217; Phytomorphology 25 (1975) 6.

Pseudotrophis Warb., Bot. Jahrb. Syst. 13 (1890) 291. — *Streblus* Lour. sect. *Pseudotrophis* (Warb.) Corner, Gard. Bull. Singapore 19 (1962) 217; Phytomorphology 25 (1975) 5.

Dimerocarpus Gagnep., Bull. Mus. Hist. Nat. (Paris) 27 (1921) 441.

Trees or shrubs, mostly (or sometimes) with lateral or terminal thorns, dioecious. Leaves distichous; lamina elliptic to narrowly elliptic, coriaceous, the margin often spinulose-dentate and/or the acumen spinulose; petiole short; stipules free, lateral. Inflorescences unisexual, the bracts basally attached; staminate inflorescences spicate to subcapitate; pistillate inflorescences racemose to spicate to uniflorous; staminate flowers 4-merous, tepals valvate; fruiting perianth more or less enlarged, not reflexed in fruit. Drupe dehiscent or not.

Distribution — This section comprises six species and ranges from Sri Lanka to New Guinea.

Morphology — All species bear thorns and/or have spinose-dentate leaf margins. The thorns are formed terminally on leafy twigs or are lateral. In some species thorns appear to be present on all specimens, in others they may be absent on individuals, or regionally, or very rare (*S. macrophyllus* and *S. perakensis*). It is difficult to tell from herbarium material whether or not the drupes are dehiscent.

This section is also distinct by the indumentum, occurring on the twigs unilaterally only or unilateral more densely and on the petioles mostly adaxially only or adaxially more densely.

KEY TO THE SPECIES

- 1a. Midrib of the lamina prominent above and acumen of the lamina spinulose-dentate, with 1 or 3 teeth; lamina smooth and the margin often spinulose-dentate. — Widespread **7. *S. ilicifolius***
- b. Midrib of the lamina impressed above or ± prominent only in the upper part of the lamina and then the lamina usually scabrous; acumen of the lamina not spinulose-dentate or, if apiculate, then in between 2 non-spinulose lobes 2
- 2a. Plants usually with thorns 3
 - b. Plants occasionally with thorns 5
- 3a. Thorns lateral; acumen of the lamina apiculate and often 2-lobed. — Sumatra, Java, Lesser Sunda Islands **10. *S. spinosus***
 - b. Thorns terminating leafy twigs; acumen of the lamina not apiculate and/or lobed. 4
- 4a. Plants usually with short-shoots bearing tufts of leaves and/or inflorescences; petiole 0.1–0.4(–0.6) cm long, usually hairy adaxially; acumen of the lamina mostly acute; leafy twigs usually distinctly hairy; tepals of the pistillate flower narrowly ovate, acute. — Malay Peninsula, Java, Philippines, Celebes, Lesser Sunda Islands **11. *S. taxoides***
 - b. Plants rarely with short-shoots; petiole (0.2–)0.4–0.7 cm long, often glabrous; acumen of the lamina mostly obtuse; leafy twigs often subglabrous; tepals of the pistillate flower broadly ovate to suborbicular, obtuse to rounded. — Malay Peninsula **9. *S. perakensis***

- 5a. Staminate inflorescences spicate and 1.5–14 cm long; pistillate inflorescences with (1–)2–10 flowers. — Malay Peninsula, Borneo, Philippines, Celebes
..... **8. *S. macrophyllus***
- b. Staminate inflorescences capitate or spicate and up to 0.8 cm long; pistillate inflorescences with 1 (or 2) flowers. — Malay Peninsula **9. *S. perakensis***

7. *Streblus ilicifolius* (S. Vidal) Corner

Streblus ilicifolius (S. Vidal) Corner, Gard. Bull. Singapore 19 (1962) 227; Phytomorphology 25 (1975) 5, t. 2, 3F; Keng, Malaysian Seed Pl. (1969) f. 83. — *Taxotrophis ilicifolia* S. Vidal, Revis. Pl. Vasc. Filip. (1886) 249; Merr., Interpr. Herb. Amboin. (1917) 188; Ridl., Fl. Malay Penins. 3 (1924) 322; Corner, Gard. Bull. Singapore 10 (1939) 288; Wayside Trees Malaya ed.1 (1940) 693; Go, Tree Fl. Sabah & Sarawak 3 (2000) 333.

Pseudotrophis laxiflora Warb., Bot. Jahrb. Syst. 13 (1891) 294.

Taxotrophis obtusa Elmer, Leafl. Philipp. Bot. 5 (1913) 1813.

Taxotrophis laxiflora Hutch., Bull. Misc. Inform. Kew (1918) 151. — *Streblus laxiflorus* (Hutch.) Corner, Gard. Bull. Singapore 19 (1962) 229.

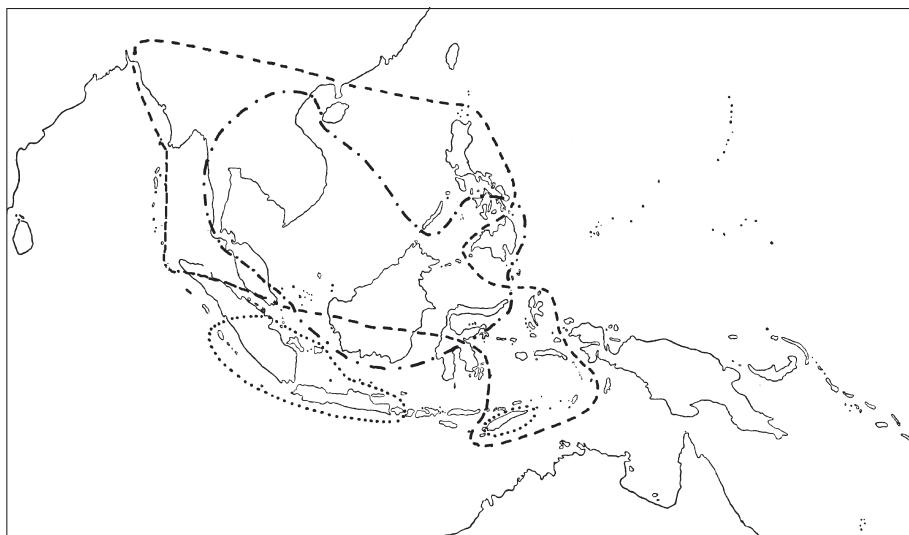
Taxotrophis triapiculata Gamble, Bull. Misc. Inform. Kew (1913) 188.

Taxotrophis eberhardtii Gagnep., Fl. Indo-Chine 5 (1928) 700; Corner, Gard. Bull. Singapore 19 (1962) 229.

Taxotrophis macrophylla auct. non Boerl.: Burkill, Dict. Econ. Prod. Malay Penins. (1935) 2126.

Shrub or tree up to 10(–20) m tall, much-branched, often with up to 4.5 cm long lateral (or terminal) thorns, dioecious. Leafy twigs 1–3 mm thick, brownish to whitish puberulous, usually unilaterally only or more densely (or glabrous). Leaves distichous; lamina elliptic to suborbicular to ovate or to obovate, 4–25 by 2–10.5 cm, coriaceous, apex acuminate to acute, acumen spinulose, usually with 3 teeth, base rounded to cuneate, margin spinulose-dentate or entire; upper and lower surface glabrous; midrib prominent above, lateral veins 8–12 pairs, tertiary venation largely parallel to the lateral veins; petiole 0.2–1 cm long, whitish puberulous adaxially (hairy round about or glabrous); stipules 0.3–0.8 cm long, free or basally connate, (sub)glabrous, caducous; terminal bud aculeate in dry material. Staminate inflorescences axillary, solitary (or in pairs), spicate; peduncle c. 0.1 cm long, sparsely minutely puberulous; spike 1–5 cm long; flowers numerous; perianth 1–1.2 mm long, minutely puberulous; stamens 2–2.5 mm long, anthers 0.6–0.8 mm long; bracts basally attached, 0.3–1.3 mm long, sparsely minutely puberulous. Pistillate inflorescences axillary, solitary, (sub)racemose or uniflorous; peduncle 0.3–1.5 cm long, minutely puberulous; flowers 1–3(–15); pedicel 2–8 mm long, minutely puberulous; tepals 1–2 mm long, ciliolate, in fruit the outer ones up to 3 mm long, the inner ones up to 10 mm long; ovary 1–1.5 mm long, style 0.5–1 mm long, stigmas 2–3.5 mm long; bracts basally attached, 0.3–0.5 mm long, ciliolate. Drupe 1–1.3 cm long, dehiscent, whitish; endocarp body subglobose to ellipsoid, 0.6–0.8 cm long. — **Map 4.**

Distribution — Bangladesh, Myanmar, South China (incl. Hainan), Indochina, Thailand; in Malesia: Sumatra (northern), Malay Peninsula, Borneo, Philippines (Palawan, Luzon, Mindoro, Basilan, Panay, Sulu Islands), Celebes (also Buton Island), Lesser Sunda Islands (? Timor), Moluccas (Halmahera, Ambon, Ceram, Sula Islands, Key Islands), New Guinea (Batanta Island).



Map 4. Distribution of *Streblus ilicifolius* (S. Vidal) Corner (broken line), *S. macrophyllus* Blume (dot-dash line), and *S. spinosus* (Blume) Corner (dotted line).

Habitat — Dry rocky forest, especially in limestone hills and rocky coasts; at altitudes up to c. 1100 m.

Uses — The timber is valuable.

Notes — 1. On the continent, in the Malay Peninsula, Sumatra and Borneo, the plants often bear thorns, the margin of the lamina is usually spinulose dentate, and the pistillate inflorescences contain usually 1–3 flowers, whereas in the Philippines, Celebes, the Moluccas, and New Guinea, the lamina is often entire and only the acumen spinulose. Moreover, the plants are usually without thorns and the pistillate inflorescences often bear more flowers, often up to c. 6, less commonly up to c. 15.

2. Terminal thorns are rare in Malesia; they are mainly found in Thailand.

3. The presence of this species in Timor could not be verified at L.

8. *Streblus macrophyllus* Blume

Streblus macrophyllus Blume, Ann. Mus. Bot. Lugduno-Batavi 2 (1856) 80; Corner, Gard. Bull. Singapore 19 (1962) 227; Phytomorphology 25 (1975) 5, t. 2, 3G; Go, Tree Fl. Sabah & Sarawak 3 (2000) 333. — *Diplocos ? macrophyllus* (Blume) Bureau in A.DC., Prodr. 17 (1873) 216. — *Taxotrophis macrophylla* (Blume) Boerl., Handl. Fl. Ned. Ind. 3 (1900) 359; Merr., Enum. Philipp. Flow. Pl. 2 (1923) 38, excl. *Taxotrophis ilicifolia*; Burkitt, Dict. Econ. Prod. Malay Penins. (1935) 2126.

Pseudotrophis mindanaensis Warb. in Perkins, Fragm. Fl. Philipp. 1 (1905) 165; Elmer, Leafl. Philipp. Bot. 5 (1913) 1815, ‘*Taxotrophis mindanaensis*’ in nota.

Paratrophis caudata Merr., Philipp. J. Sci., 1, Suppl. (1906) 183.

Taxotrophis balansae Hutch., Bull. Misc. Inform. Kew (1918) 151.

Dimerocarpus brenieri Gagnep., Bull. Mus. Hist. Nat. (Paris) 27 (1921) 441; Fl. Indo-Chine 5 (1928) 704, f. 84.

Tree up to 12 m tall, rarely with up to 0.5 cm long axillary thorns, dioecious or sometimes monoecious. Leafy twigs 1–2.5 mm thick, minutely brownish puberulous, mostly

only unilaterally, or glabrous, young parts often \pm compressed (often drying yellowish). *Leaves* distichous; lamina elliptic to subovate to subobovate or to narrowly ovate, 6–22 by 2–7.5 cm, often \pm asymmetric, subcoriaceous, apex acuminate to subcaudate, acumen acute, base rounded to obtuse to cuneate, margin subentire to crenate-dentate to denticulate; upper surface glabrous; lower surface glabrous or whitish (minutely) appressedly puberulous on the midrib; midrib \pm impressed above, lateral veins 6–10 pairs, tertiary venation subscalariform to reticulate; petiole 0.2–0.8 cm long, glabrous or whitish minutely puberulous, often adaxially more densely; stipules 0.2–1 cm long, subglabrous or appressedly puberulous, subpersistent or caducous, terminal bud slender, \pm aculeate when dry. *Staminate inflorescences* axillary, solitary, spicate; peduncle 0.2–0.4 cm long, minutely puberulous; spike 1.5–14 cm long; flowers numerous; perianth 1–1.2 mm long, minutely puberulous; stamens c. 2 mm long, anthers 0.6–0.8 mm long; bracts basally attached, 0.3–0.8 mm long, sparsely minutely puberulous. *Pistillate inflorescences* axillary, solitary, racemose (or uniflorous); peduncle 0.2–1 cm long, minutely puberulous; flowers (1–)2–10; pedicel 0.5–10 mm long, minutely puberulous; tepals 1–2 mm long, minutely puberulous, in fruit the outer ones 2–4 mm long, the inner ones 7–10 mm long; ovary c. 1 mm long, style c. 1 mm long, stigmas

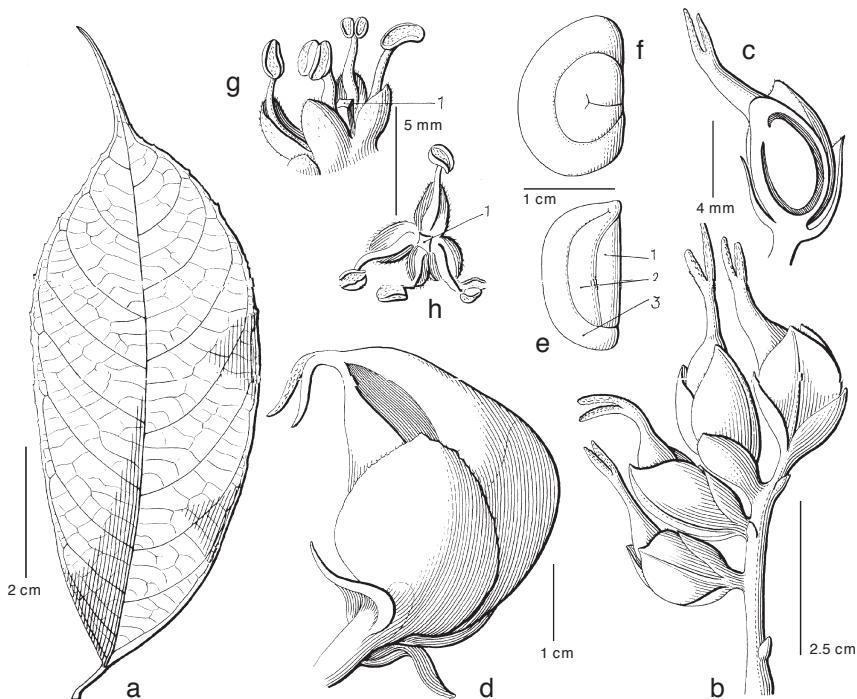


Fig. 11. *Streblus macrophyllus* Blume. a. Leaf to show the intercostal veins in Bornean material; b. fruiting spike; c. pistillate flower in section; d. dehiscing fruit; e, f. embryos in transverse and longitudinal section: 1 = recurved lobe of outer cotyledon, 2 = inner cotyledon, 3 = outer cotyledon; g, h. staminate flowers: 1 = pistillode (a–c: *Jaheri 1234*; d: *Endert 3068*; e: *Santos 4215*; g, h: *Bur. Sci. 15485*).

1.5–3 mm long; bracts basally attached, 0.3–1 mm long, minutely puberulous. *Drupe* 1–1.4 cm long, dehiscent, whitish; endocarp body 0.8–1 cm long. — **Fig. 11; Map 4.**

Distribution — Thailand, Indochina; in *Malesia*: Malay Peninsula, Borneo, Philippines (Mindanao, Leyte, Basilan, Cebu, Surigao, Bohol), Celebes.

Habitat — Lowland forest.

9. *Streblus perakensis* Corner

Streblus perakensis Corner, Gard. Bull. Singapore 19 (1962) 223, t. 11; Phytomorphology 25 (1975) 3.

Shrub or tree up to 10 m tall, without or with lateral or terminal up to 1 cm long, often ± curved thorns, dioecious; often concentrations of persistent stipules (or scale-leaves) and lenticels at branching points. *Leafy twigs* 1.5–3 mm thick, glabrous or minutely whitish puberulous, unilaterally only or more densely. *Leaves* distichous; lamina narrowly elliptic to subobovate, (2.5–)5–12(–16) by (1–)2–5(–7) cm, often ± asymmetric, subcoriaceous to coriaceous, apex acuminate, acumen obtuse to subacute, base rounded to cordulate, margin irregularly dentate to denticulate or subentire; upper surface glabrous; lower surface glabrous or sparsely puberulous on the midrib; midrib ± impressed above, lateral veins 6–8 pairs, tertiary venation reticulate; petiole (0.2–)0.4–0.7 cm long, glabrous or minutely whitish puberulous adaxially; stipules 0.1–0.3 cm long, appressedly puberulous, (sub)persistent. *Staminate inflorescences* axillary, solitary or in pairs, spicate (or racemose), subsessile; spike (or raceme) 0.3–0.8 cm long; flowers 5–20, sessile (or up to 1 mm long pedicellate); perianth c. 1.5 mm long, minutely puberulous; stamens c. 3 mm long, anthers c. 0.8 mm long; bracts basally attached, few, 0.2–0.5 mm long, sparsely puberulous. *Pistillate inflorescences* axillary, solitary or in pairs, uniflorous, sessile or pedunculate; peduncle up to 0.4 cm long, subglabrous; tepals 2–3 mm long, minutely puberulous, in fruit the outer ones 3–4 mm long, the inner ones 10–12 mm long, suborbicular; ovary c. 1.5 mm long, style c. 1 mm long, stigmas 3–5 mm long; bracts 2, basally attached, 0.3–1 mm long, minutely puberulous or subglabrous. *Drupe* subglobose, 1–1.2 cm long, dehiscent, whitish; endocarp body subglobose, c. 0.7 cm long.

Distribution — Peninsular Thailand; in *Malesia*: Malay Peninsula.

Habitat — Primary (and secondary) forest, sometimes on limestone hills; at altitudes up to c. 500.

Notes — 1. In the very short and almost sessile staminate inflorescences this species matches *S. taxoides*, from which it can be distinguished by somewhat longer petioles and the absence of short-shoots bearing tufts of leaves and/or inflorescences. Also, the shape of the tepals of the pistillate flower is distinctly different. The pistillate inflorescences are often sessile at anthesis. Spines are formed, but apparently not as frequently and consistently as in *S. taxoides*. Concentrations of persistent scales and lenticels can often be found on branching points.

2. Corner (1962) included *S. perakensis* in sect. *Paratrophis*. Corner (1975) maintained the species in this section with some doubt. However, the enlarged tepals in fruit and the presence of thorns clearly indicate its correct position.

3. The distribution range of this species is quite small compared to the other species of the section.

10. *Streblus spinosus* (Blume) Corner

Streblus spinosus (Blume) Corner, Gard. Bull. Singapore 19 (1962) 229; Backer & Bakh.f., Fl. Java 2 (1965) 16.

Urtica spinosa Blume, Bijdr. (1825) 507. — *Taxotrophis spinosa* (Blume) Steenis in Backer & Bakh.f., Fl. Java 2 (1965) 16.

Taxotrophis javanica Blume, Ann. Mus. Bot. Lugduno-Batavi 2 (1856) 77, t. 26; Bureau in A.DC., Prodr. 17 (1873) 217; Koord. & Valeton, Bijdr. Boomsoort. Java 11 (1906) 4, 6; Koord., Exkurs.-Fl. Java 2 (1912) 88, f. 26; Hutch., Bull. Misc. Inform. Kew (1918) 149; Rendle, J. Bot. 63, Suppl. (1925) 105.

Shrub or treelet up to 4 m tall, much-branched, with up to 1.5 cm long lateral thorns, dioecious; short-shoots often present, bearing (clusters of) leaves and/or inflorescences. Leafy twigs 1–2.5 mm thick, whitish to brownish puberulous unilaterally or all over (or glabrous). Leaves distichous; lamina elliptic to (sub)ovate or to narrowly ovate, 3–12(–18) by 2–6(–7.5) cm, coriaceous, apex acuminate to subacute, acumen apiculate and usually 2-lobed, base rounded to obtuse, margin subspinulose-denticulate in the upper part of the lamina or subentire; both surfaces glabrous; midrib ± impressed above, lateral veins 6–10 pairs, tertiary venation reticulate; petiole 0.2–0.5 cm long, whitish puberulous unilaterally only or all over (or glabrous); stipules 0.2–0.3 cm long, (sub)glabrous, caducous (or subsessile); terminal bud spinose in dry material. Staminate inflorescences axillary, solitary or in pairs, racemose; peduncle 0.1–0.3 cm long, sparsely minutely puberulous; raceme 0.5–2.5 cm long; flowers numerous; pedicel c. 0.1 mm long, minutely puberulous; perianth c. 1 mm long, minutely puberulous; stamens 2–2.5 mm long, anthers c. 0.8 mm long; bracts basally attached, few, 0.5–1.5 mm long, sparsely minutely puberulous. Pistillate inflorescences axillary, solitary, uniflorous; peduncle 0.2–2 cm long, minutely puberulous; tepals 1–1.5 mm long, minutely puberulous, in fruit hardly enlarged, up to 3 mm long; ovary c. 1 mm long, style 0–4 mm long, stigmas 1–2 mm long; bracts basally attached, few, 0.3–1 mm long, minutely puberulous. Drupe subglobose to ellipsoid, 0.6–1 cm long, dehiscent (?), whitish. — Map 4.

Distribution — Sumatra (also Enggano), Java, Lesser Sunda Islands (Bali, Flores, Timor).

Habitat — Lowland and submontane forest at altitudes up to 1200 m; chiefly in open country or rocky forest, on coral.

11. *Streblus taxoides* (B. Heyne ex Roth) Kurz

Streblus taxoides (B. Heyne ex Roth) Kurz, Forest Fl. Burma 2 (1877) 465; Corner, Gard. Bull. Singapore 19 (1962) 225; Backer & Bakh.f., Fl. Java 2 (1965) 16; Corner, Phytomorphology 25 (1975) 3, t. 1C, 2, 3A; Fl. Ceylon 1.2 (1977) 158, t. 29. — *Trophis taxoides* B. Heyne ex Roth, Nov. Pl. Sp. (1821) 368. — *Trophis taxiformis* Spreng., Syst. Veg. 3 (1826) 902, nom. nov. illeg. — *Phyllochlamys taxoides* (B. Heyne ex Roth) Koord., Exkurs.-Fl. Java 2 (1912) 89; Merr., Philipp. J. Sci. 14 (1920) 247; Enum. Philipp. Flow. Pl. 2 (1923) 38; Koord., Atlas Baumart. Java (1924) t. 748; Burkill, Dict. Econ. Prod. Malay Penins. (1935) 1720; Corner, Wayside Trees Malaya ed.1 (1940) 690.

Trophis spinosa Roxb., Fl. Ind., ed. Carey 3 (1832) 762, non Willd. 1806, nec Blume 1826. — *Epicarpus spinosus* (Roxb.) Wight, Icon. Pl. Ind. Orient. 6 (1853) 7, t. 1962, p.p. — *Phyllochlamys*

- spinosa* (Roxb.) Bureau in A.DC., Prodr. 17 (1873) 218; Hook.f., Fl. Brit. India 5 (1888) 488; Koord. & Valeton, Bijdr. Boomsoort. Java 11 (1906) 10; Ridl., Fl. Malay Penins. 3 (1924) 323.
- Epicarpurus timorensis* Decne., Nouv. Ann. Mus. Hist. Nat. 3 (1834) 499, t. 21; Span., Linnaea 15 (1841) 344.
- Epicarpurus zeylanicus* Thwaites, Hooker's J. Bot. Kew Gard. Misc. 3 (1851) t. 11; 4 (1852) 1. — *Streblus zeylanicus* (Thwaites) Kurz, Forest Fl. Burma 2 (1877) 464; Corner, Gard. Bull. Singapore 19 (1962) 229; Phytomorphology 25 (1975) 5, t. 1A; Fl. Ceylon 1.2 (1977) 160, t. 30. — *Diplocos zeylanica* (Thwaites) Bureau in A.DC., Prodr. 17 (1873) 215.
- Taxotrophis roxburghii* Blume, Ann. Mus. Bot. Lugduno-Batavi 2 (1856) 78; Miq., Fl. Ned. Ind. 1, 2 (1859) 279.
- Taxotrophis zeylanica* Thwaites, Enum. Pl. Zeyl. (1864) 264.
- Streblus microphyllus* Kurz, Prelim. Rep. Forest Pegu (1875) App. A, cxviii; App. B, 84; Forest Fl. Burma 2 (1877) 464, in clavi. — *Streblus taxoides* (B. Heyne ex Roth) Kurz var. *microphylla* (Kurz) Kurz, Forest Fl. Burma 2 (1877) 465.
- Phyllochlamys wallichii* King ex Hook.f., Fl. Brit. India 5 (1888) 489; Ridl., Fl. Malay Penins. 3 (1924) 322; Corner, Wayside Trees Malaya ed.1 (1940) 690.
- Taxotrophis caudata* Hutch., Bull. Misc. Inform. Kew (1918) 149.
- Phyllochlamys taxoides* (B. Heyne ex Roth) Koord. var. *parvifolia* Merr., Enum. Philipp. Flow. Pl. 2 (1923) 38.
- Taxotrophis poilanei* Gagnep., Fl. Indo-Chine 5 (1928) 701.
- Taxotrophis crenata* Gagnep., Fl. Indo-chine 5 (1928) 702, t. 82. — *Streblus crenatus* (Gagnep.) Corner, Gard. Bull. Singapore 19 (1962) 226.
- Phyllochlamys tridentata* Gagnep., Fl. Indo-Chine 5 (1928) 714.

Shrub or treelet up to 5 m tall, much-branched, with thorns up to 1.5 cm long, mostly terminating (short) leafy twigs, dioecious; short-shoots often present, bearing (clusters of) leaves and/or inflorescences. Leafy twigs 1–2.5 mm thick, brown to whitish puberulous unilaterally only or all over (or glabrous). Leaves distichous; lamina elliptic to narrowly ovate or (sub)obovate, (1–)2–10(–18) by (0.5–)1–4.5(–6.5) cm, subcoriaceous to coriaceous, apex acuminate to acute (to rounded), acumen acute to obtuse, base obtuse to rounded to cordulate, margin dentate to denticulate (to crenate), mainly in the upper part of the lamina; both surfaces glabrous and smooth; midrib impressed above, lateral veins 6–12 pairs, tertiary venation reticulate; petiole 0.1–0.4(–0.6) cm long, brown to whitish puberulous, adaxially only (or more all over); stipules 0.2–0.5 cm long, ciliolate, subpersistent. Stamine inflorescences axillary, 1–4 on short-shoots, short-spicate to (sub)capitate (or to racemose), (sub)sessile; spike (or raceme) 0.4–0.8 cm long; flowers 8–14, (sub)sessile (or up to 1 mm long pedicellate); perianth c. 1.5 mm long, subglabrous or minutely puberulous; stamens 2–2.5 mm long, anthers 0.6–0.8 mm long; bracts basally attached, 0.2–0.6 mm long, minutely puberulous. Pistillate inflorescences axillary, solitary (sometimes clustered on short-shoots), uniflorous; peduncle 0.3–0.6 cm long, subglabrous; tepals ovate, 2–5 mm long, glabrous, in fruit up to 2 cm long; ovary c. 1.5 mm long, style c. 1 mm long, stigmas 0.5–3 mm long; bracts usually 2, ovate to narrowly ovate, c. 1.5 mm long, subglabrous. Drupe ellipsoid, 0.5–1 cm long, dehiscent (?), whitish. — **Fig. 12.**

Distribution — Sri Lanka, India, Bhutan, Myanmar, South China (Hainan), Thailand, Indochina; in *Malesia*: Malay Peninsula, Java, Philippines (Mindoro, Palawan), Celebes (south-eastern), Lesser Sunda Islands (Flores, Timor).

Habitat — Lowland forest in rocky or dry places.

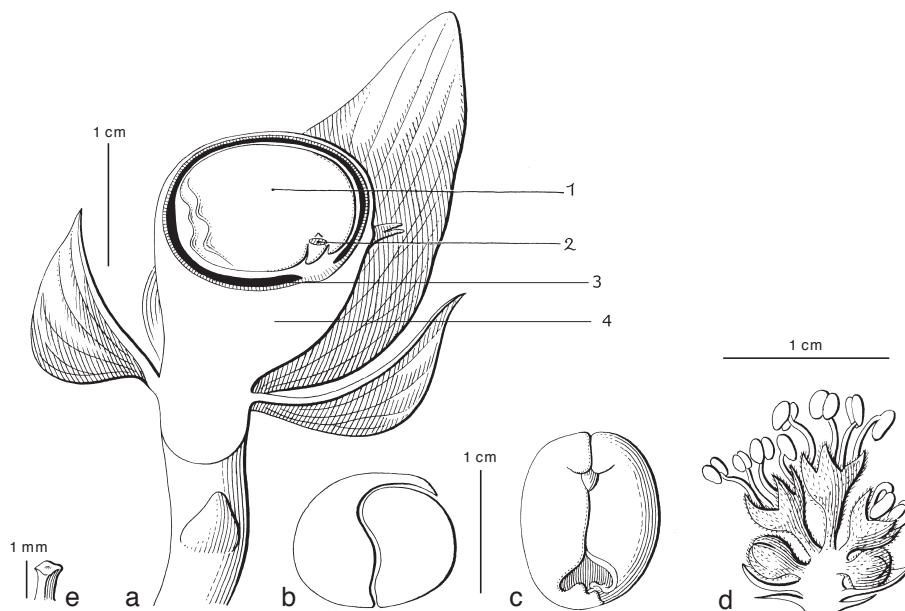


Fig. 12. *Streblus taxoides* (B. Heyne ex Roth) Kurz. a. Ripe fruit in section: 1 = cotyledon, 2 = scar of the cotyledon cut off, 3 = endocarp, 4 = exocarp; b. embryo in section; c. embryo from the lower side; d. staminate inflorescence in section; e. pistillode (a–c: material from Singapore Botanic Gardens; d, e: Rabil 380, Thailand).

Notes — 1. This species can be easily confused with *S. spinosus*. In *S. taxoides*, the thorns are normally borne at the end of leafy twigs, the acumen of the lamina has an acute apex, the stipules do not form an aculeate terminal bud and are subpersistent. In the other species the thorns are borne laterally on twigs, the acumen of the lamina is normally 2-lobed with a small tooth in between these lobes, the stipules form an aculeate terminal bud and are caducous.

2. Staminate inflorescences are or can be subinvolucrate, due to enlargement of the bracts, at least in Sri Lanka, India, and Thailand. In the Malesian region the bracts are (always?) small.

3. In Thailand the tepals of the pistillate flowers are sometimes narrowly ovate.

4. *Streblus zeylanicus* is included as differentiating characters are absent.

TROPHIS

Trophis P. Browne, Civ. Nat. Hist. Jamaica (1756) 357, nom. cons.; Trécul, Ann. Sci. Nat., Bot. sér. 3, 8 (1847) 146; Bureau in A.DC., Prodr. 17 (1873) 251; Baill., Hist. Pl. 6 (1875) 192; Benth. & Hook.f., Gen. Pl. 3 (1880) 365; Engl. in Engl. & Prantl, Nat. Pflanzenfam. 3, 1 (1888) 73; Bot. Jahrb. Syst. 40 (1908) 543; W.C. Burger, Ann. Missouri Bot. Gard. 49 (1962) 6; Corner, Gard. Bull. Singapore 19 (1962) 230; C.C. Berg, Proc. Kon. Ned. Akad. Wetensch. C, 91 (1988) 352; Fl. Neotrop. Monogr. 83 (2001) 33.

Bucephalon L., Sp. Pl. (1753) 1190.

Olmedia Ruiz & Pav., Syst. Veg. Fl. Peruv. Chil. 1 (1798) 257; C.C. Berg, Fl. Neotrop. Monogr. 7 (1972) 14. — *Trophis* P. Browne sect. *Olmedia* (Ruiz & Pav.) C.C. Berg, Proc. Kon. Ned. Akad. Wetensch. C, 91 (1988) 354.

Malaisia Blanco, Fl. Filip. (1837) 789; ed. 2 (1845) 543; ed. 3, 3 (1879) 196; Planch., Ann. Sci. Nat., Bot. sér. 4, 3 (1855) 293; Blume, Ann. Mus. Bot. Lugduno-Batavi 2 (1856) 75; Miq., Fl. Ned. Ind. 1, 2 (1859) 281; Bureau in A.D.C., Prodr. 17 (1873) 221; Benth. & Hook.f., Gen. Pl. 3 (1880) 360; Engl. in Engl. & Prantl, Nat. Pflanzenfam. 3, 1 (1888) 76; Boerl., Handl. Fl. Ned. Ind. 3 (1900) 315; Corner, Gard. Bull. Singapore 19 (1962) 240. — *Trophis* P. Browne sect. *Malaisia* (Blanco) C.C. Berg, Proc. Kon. Ned. Akad. Wetensch. C, 91 (1988) 354.

Dumartroya Gaudich., Voy. Bonite, Bot. (1844) 165, t. 97.

Cephalotrophis Blume, Ann. Mus. Bot. Lugduno-Batavi 2 (1856) 75.

Maillardia Frapp. ex Duch., Notes sur l'île de la Réunion, Annexe Phanerogamique (1862) 148; Bureau in A.D.C., Prodr. 17 (1873) 220; Leandri, Fl. Madagasc. fam. 55 (1952) 15. — *Trophis* P. Browne sect. *Maillardia* (Frapp. ex Duch.) Corner, Gard. Bull. Singapore 19 (1962) 230.

Calpidochlamys Diels, Bot. Jahrb. Syst. 67 (1935) 172. — *Trophis* P. Browne sect. *Calpidochlamys* (Diels) Corner, Gard. Bull. Singapore 19 (1962) 230.

Skutchia Pax & K. Hoffm. ex C.V. Morton, J. Wash. Acad. Sci. 27 (1937) 306.

Caturus Lour. auct. non L. (1767): Fl. Cochinch. (1790) 612; Baill., Hist. Pl. 6 (1875) 193.

Trees or shrubs (scandent in *T. scandens*), dioecious, unarmed, uncinate hairs lacking or present. Leaves distichous; lamina pinnately veined; stipules free, lateral. Inflorescences unisexual, racemose, spicate, subcapitate, or discoid-capitate and involucrate, bracteate. Staminate inflorescences multi- to pluriflorous, flowers with 3 or 4 tepals, valvate or imbricate in bud; stamens 3 or 4, inflexed in bud. Pistillate inflorescences multi- to uniflorous; flowers with 4 connate tepals, equal in size and forming a tubular or a collar-shaped perianth; ovary free or adnate to the perianth; stigmas 2, equal. Fruiting perianth enlarged, fleshy, orange or red, enclosing the free and indehiscent or adnate fruit, endocarp crustaceous to woody; seed without endosperm, embryo with thick, flat, equal or (very) unequal cotyledons, radicle short or rather long.

Distribution — The genus comprises nine species in the Old World (not on the African continent) and New World.

Subdivision — The genus can be subdivided into six sections (Berg 1988): *Calpidochlamys* (one species in Malesia), *Echinocarpa* (one species, *T. involucrata* W.C. Burger, in Central America), *Maillardia* (two species in Madagascar and Réunion), *Malaisia* (one species in SE Asia), *Olmedia* (one species, *T. caucana* (Pittier) C.C. Berg, in the Neotropics, and *Trophis* (3 species in the Neotropics, see Berg 2001). This subdivision replaces that of Corner (1962).

Morphology — This genus shows pronounced morphological similarities to *Streblus* but differs in the connate tepals of the pistillate flower.

References: Berg, C.C., The genera *Trophis* and *Streblus* (Moraceae) remodelled. Proc. Kon. Ned. Akad. Wetensch. C, 91 (1988) 345–362. — Berg, C.C., Fl. Neotrop. Monogr. 83 (2001) 32. — Corner, E.J.H., The classification of Moraceae. Gard. Bull. Singapore 19 (1962) 187–252.

KEY TO THE SPECIES

- 1a. Tree; staminate inflorescences spicate, 6–26 cm long; pistillate inflorescences 1.5–4 cm long. — Eastern Malesia **1. *T. philippinensis***

- b. Climber; staminate inflorescences spicate to subcapitate, 0.5–3.5(–5) cm long; pistillate inflorescences capitate to short-spicate, 0.3–1.5 cm long. — Widespread
..... **2. *T. scandens***

Section CALPIDOCHLAMYS

Trophis P. Browne sect. *Calpidochlamys* (Diels) Corner, Gard. Bull. Singapore 19 (1962) 230; C.C. Berg, Proc. Kon. Ned. Akad. Wetensch. C, 91 (1988) 356. — *Calpidochlamys* Diels, Bot. Jahrb. Syst. 67 (1935) 172.

Trees. *Staminate inflorescences* spicate; tepals 4, imbricate in the bud. *Pistillate inflorescences* spicate; fruiting perianth enlarged, fleshy, dark purple to black. *Fruit* adnate to the perianth; cotyledons subequal.

Distribution — This section comprises only *T. philippinensis*.

1. *Trophis philippinensis* (Bureau) Corner

Trophis philippinensis (Bureau) Corner, Gard. Bull. Singapore 19 (1962) 231. — *Uromorus philippinensis* Bureau in A.DC., Prodr. 17 (1873) 237; S. Vidal, Cat. Met. Pl. Leños. (1880) 43. — *Paratrophis philippinensis* (Bureau) Fern.-Vill., Nov. App. (1880) 98; S. Vidal, Phan. Cuming. Philipp. (1885) 145; Revis. Pl. Vasc. Filip. (1886) 250; Merr., Enum. Philipp. Flow. Pl. 2 (1923) 36.

Sloetia minahassae Koord., Versl. Minahasa (1898) 645; Suppl. Fl. Celebes 2 (1922) pl. 5; 3 (1922) 3. *Paratrophis grandifolia* Elmer, Leafl. Philipp. Bot. 5 (1913) 1814; Merr., Enum. Philipp. Flow. Pl. 2 (1923) 36.

Calpidochlamys branderhorstii Diels, Bot. Jahrb. Syst. 67 (1935) 173. — *Trophis branderhorstii* (Diels) Corner, Gard. Bull. Singapore 19 (1962) 231.

Calpidochlamys drupacea Diels, Bot. Jahrb. Syst. 67 (1935) 173. — *Trophis drupacea* (Diels) Corner, Gard. Bull. Singapore 19 (1962) 231.

Tree up to 30 m tall. *Leafy twigs* 1.5–2.5 m thick, brownish to whitish puberulous, mostly drying dark brown with conspicuous lenticels. *Leaves* distichous; lamina narrowly elliptic to elliptic to subobovate, (4–)10–20(–28) by (2–)4–9(–14), usually ± asymmetric, coriaceous to subcoriaceous, apex acuminate, base cuneate to obtuse (to almost rounded), margin entire, often ± revolute, at least towards the base; upper surface glabrous; lower surface brownish to whitish puberulous to strigillose on the veins or (sub)glabrous; midrib prominent above, lateral veins 9–16(–20) pairs, tertiary venation scalariform; petiole 0.8–2.5 cm long, brownish to whitish puberulous to subglabrous; stipules 0.5–1 cm long, sparsely appressedly brownish to whitish puberulous, caducous. *Staminate inflorescences* axillary, solitary or in pairs, spicate; peduncle 0.3–2 cm long, (sub)glabrous; spike 6–26 cm long; staminate flowers numerous; perianth 1–1.2 mm long, sparsely hairy to glabrous; stamens c. 2 mm long, anthers c. 0.5 mm long; bracts peltate, 0.5–1 mm diam., (sub)glabrous or sparsely ciliolate. *Pistillate inflorescences* axillary, solitary or in pairs, spicate; peduncle 0.2–0.6 cm long, subglabrous; spike 1.5–4 cm long; flowers 2–10; perianth c. 2 mm long, sparsely minutely puberulous, 4-dentate; ovary c. 1 mm long, style 1–2 mm long, stigmas 2–3.5 mm long; bracts peltate, 0.5–1 mm diam., sparsely ciliolate. *Fruiting perianth* ellipsoid to subglobose, when fresh up to 3 cm long, when dry 1.5–2 cm long, dark purple to black at maturity.

— Fig. 13.

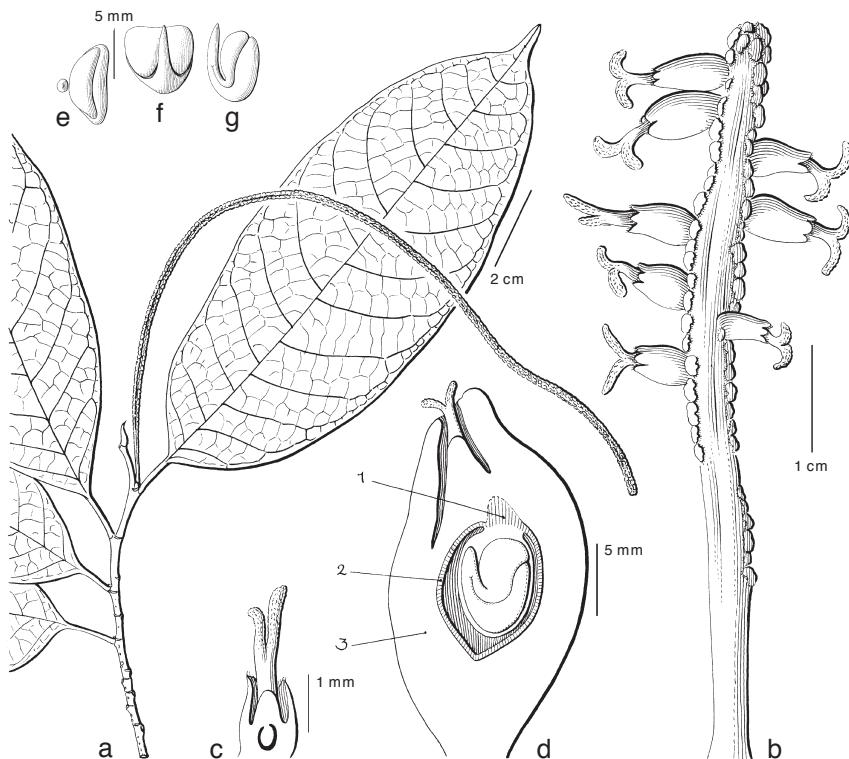


Fig. 13. *Trophis philippinensis* (Bureau) Corner. a. Leafy twig with staminate inflorescence; b. pistillate inflorescence at anthesis; c. pistillate flower in section; d. fruit in section: 1 = thickened hilar plug of endocarp, 2 = endocarp, 3 = fruiting perianth; e–g. embryo (a: Ramos 1638; b, c: BW 363; d: Cel./V-193; e–g: Branderhorst 273).

Distribution — Borneo (Sarawak), Philippines (Luzon, Samar, Mindanao, Palawan), Celebes, Lesser Sunda Islands (Sumba, Flores), Moluccas (Halmahera), New Guinea (also Yapen and New Britain).

Habitat — Primary (and secondary) forest at altitudes up to 1500 m.

Uses — Young leaves are cooked and eaten; wood is used for house building.

Section MALAISIA

Trophis P. Browne sect. *Malaisia* (Blanco) C.C. Berg, Proc. Kon. Ned. Akad. Wetensch. C, 91 (1988) 354. — *Malaisia* Blanco, Fl. Filip. (1837) 789

Climbers. *Staminate inflorescences* spicate to subcapitate; tepals 3 (or 4), valvate in the bud. *Pistillate inflorescences* (sub)capitate; perianth enlarged in fruit, fleshy, red. *Fruit* free, somewhat drupaceous; cotyledons unequal.

Distribution — This section comprises only *T. scandens*.

2. *Trophis scandens* (Lour.) Hook. & Arn.

Trophis scandens (Lour.) Hook. & Arn., Bot. Beechey Voy. (1837) 214; C.C. Berg, Proc. Kon. Ned. Akad. Wetensch. C, 91 (1988) 354. — *Caturus scandens* Lour., Fl. Cochinch. (1790) 612. — *Malaisia scandens* (Lour.) Planch., Ann. Sci. Nat., Bot. sér. 4, 3 (1855) 293; Blume, Ann. Mus. Bot. Lugduno-Batavi 2 (1856) 76; Merr., Philipp. J. Sci., 1, Suppl. (1906) 43; Koord., Exkurs.-Fl. Java 2 (1912) 86; Merr., Sp. Blancoan. (1918) 122; Enum. Philipp. Flow. Pl. 2 (1923) 37; Comm. Fl. Cochinch. (1935) 132; Specht, Rec. Amer.-Austral. Sci. Exped. Arnhem Land, 3, Bot. Pl. Ecol. (1958) 218, 330; T.S. Liu, Ill. Lign. Pl. Taiwan 2 (1962) 747; H.L. Li, Woody Fl. Taiwan (1963) 127, f. 38; Backer & Bakh.f., Fl. Java 2 (1965) 15. — *Alchornea scandens* (Lour.) Müll.Arg., Linnaea 34 (1865) 170; Müll.Arg. in A.DC., Prodr. 15, 2 (1866) 906. — *Malaisia tortuosa* Blanco var. *scandens* (Lour.) Bureau in A.DC., Prodr. 17 (1873) 222.

Morus javanica Blume, Bijdr. (1825) 488. — *Cephalotrophis javanica* (Blume) Blume, Ann. Mus. Bot. Lugduno-Batavi 2 (1856) 76, t. 27; Miq., Fl. Ned. Ind. 1, 2 (1859) 281.

Malaisia tortuosa Blanco, Fl. Filip. (1837) 789; Blume, Ann. Mus. Bot. Lugduno-Batavi 2 (1856) 75; Miq., Fl. Ned. Ind. 1, 2 (1859) 282; Benth., Fl. Australia 6 (1873) 180; Bureau in A.DC., Prodr. 17 (1873) 221; Fern.-Vill., Nov. App. (1880) 198; S. Vidal, Sin. Gen. Pl. Leños Filip. (1883) 39, t. 86 f. B; Phan. Cuming. Philipp. (1885) 145; Revis. Pl. Vasc. Filip. (1886) 250; Merr., Publ. Gov. Lab. Philipp. 27 (1905) 78; Ridl., Fl. Malay Penins. 3 (1924) 325; Gagnep., Fl. Indo-Chine 5 (1928) 696 (sub var. *scandens*), t. 83: 1–4.

Dumartroya fagifolia Gaudich., Voy. Bonite, Bot. (1844) 165, t. 97.

Malaisia viridescens Planch., Ann. Sci. Nat., Bot. sér. 4, 3 (1855) 293. — *Malaisia tortuosa* Blanco var. *viridescens* (Planch.) Bureau in A.DC., Prodr. 17 (1873) 222.

Malaisia acuminata Planch., Ann. Sci. Nat., Bot. sér. 4, 3 (1855) 294. — *Malaisia tortuosa* Blanco var. *acuminata* (Planch.) Bureau in A.DC., Prodr. 17 (1873) 222.

Malaisia cunninghamii Planch., Ann. Sci. Nat., Bot. sér. 4, 3 (1855) 294.

Cephalotrophis ? puberula Miq., Fl. Ned. Ind., Eerste Bijv. (1861) 416. — *Malaisia puberula* (Miq.) Bureau in A.DC., Prodr. 17 (1873) 222.

Caturus torulosus Seem., Fl. Vit. (1868) 254.

Malaisia tortuosa Blanco var. *racemosa* Bureau in A.DC., Prodr. 17 (1873) 222.

Malaisia scandens (Lour.) Planch. var. *rolfei* K. Schum., Bot. Jahrb. Syst. 9 (1888) 199.

Malaisia blancoi Elmer, Leafl. Philipp. Bot. 5 (1913) 1812.

Climber, or shrub with climbing branches, these with long internodes and rudimentary leaves. Leafy twigs 1.5–2.5 mm thick, brownish to whitish puberulous, partly with uncinate hairs, mostly drying dark brown with conspicuous lenticels. Leaves distichous; lamina narrowly elliptic to narrowly ovate, 4–16(–20) by 1.5–6.5(–8), usually ± asymmetric, subcoriaceous, apex acuminate, base rounded to subcordate (or to subcuneate), margin entire or denticulate to dentate towards the apex, often ± revolute, at least towards the base; upper surface minutely whitish puberulous on (the lower part of) the midrib; lower surface sparsely whitish puberulous on the (main) veins; midrib prominent above, lateral veins 7–12 pairs, tertiary venation (sub)scalariform; petiole 0.3–1(–1.5) cm long, (sparsely) puberulous; stipules 0.1–0.5 cm long, sparsely whitish appressedly puberulous, caducous or subpersistent. Staminate inflorescences axillary, solitary, in pairs or up to 6 together on short-shoots, spicate; peduncle 0.5–1.5 cm long, puberulous to tomentellous; spike 0.5–3.5(–5) cm long, often interrupted; perianth c. 1.5 mm long, minutely puberulous; stamens c. 2.5 mm long, anthers c. 0.8 mm long; bracts basally attached, ovate to narrowly ovate, 0.5–1 mm long, minutely puberulous. Pistillate inflorescences axillary, solitary, in pairs or up to 6 together on short-shoots, capitate to short-spicate (or uniflorous); peduncle 0.4–2 cm long, puberulous to tomen-

telous; head 0.3–0.5 cm diam., spike up to 1.5 cm long; flowers 1–8; perianth 1–1.5 mm long, glabrous except for the densely white puberulous apex, faintly 4-dentate to subentire; ovary c. 1 mm long, style 1–2 mm long, stigmas 5–15 mm long; bracts basally attached, ovate to subulate, 0.5–1 mm long, densely white puberulous to sub-tomentellous. *Fruiting perianth* ellipsoid, when dry 0.6–0.8 cm long, dark pink to red at maturity. — **Fig. 14.**

Distribution — South China (incl. Hainan and Taiwan), Indochina, Thailand, Australia (Darwin, Arnhem Land, Queensland, New South Wales) and Pacific: New Cale-

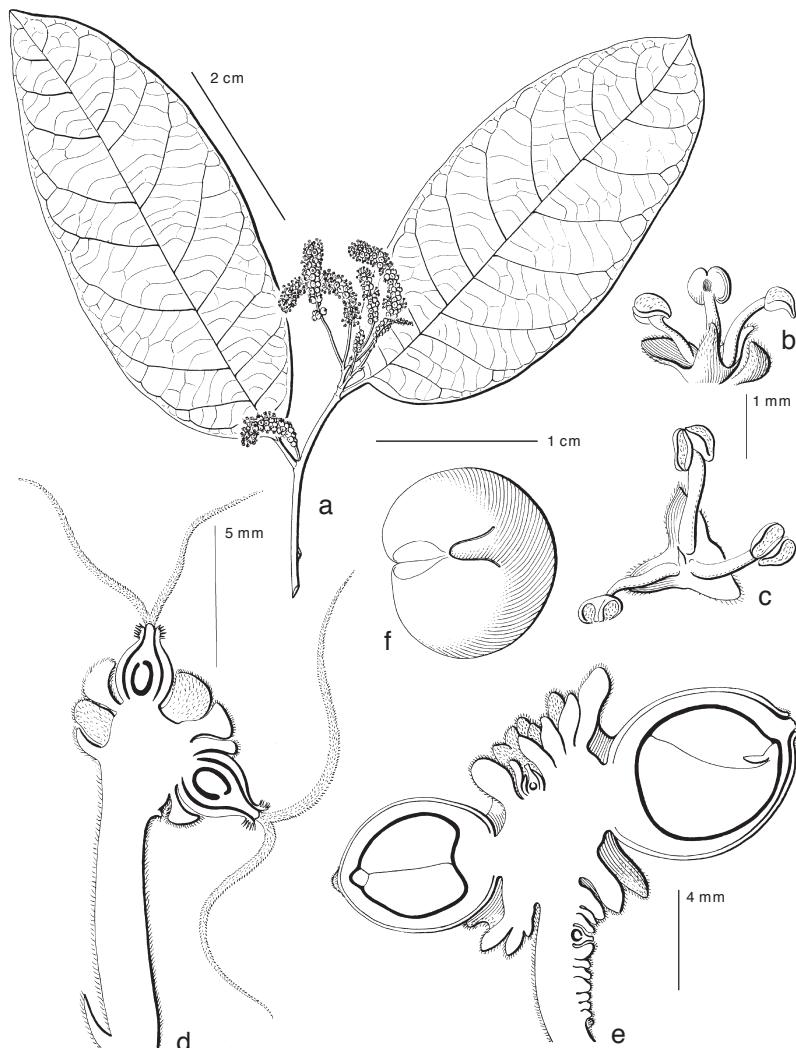


Fig. 14. *Trophis scandens* (Lour.) Hook. & Arn. a. Leafy twig with staminate inflorescences; b, c. staminate flowers; d, pistillate inflorescence in section, just after anthesis; e, pistillate inflorescence in fruit; f. embryo (a: Pullen 1167; b, c: PNH 15730; d–f: Corner s.n., New Guinea).

donia, Lord How Island, Vanuatu, Fiji; in *Malesia*: Sumatra, Malay Peninsula, Borneo, Java, Philippines, Celebes, Lesser Sunda Islands (Bali, Sumbawa, Flores, Timor, Wetar), Moluccas (Sula Islands, Banda, Ambon, Tanimbar Islands), New Guinea.

Habitat — Forest, mainly forest edges, floodplain forest, in humid to dry habitats, sometimes on limestone at altitudes up to 1300 m.

Tribe ANTIAROPSIDEAE

Trees, dioecious, without uncinate hairs. *Leaves* distichous or to laxly spirally arranged; lamina entire; venation subscalariform to reticulate; stipules free, lateral to almost fully amplexicaul. *Inflorescences* axillary, unisexual; receptacle discoid to urceolate, involucrate with imbricate or few ± scattered basally attached bracts, possibly interfloral bracts in *Antiaropsis*. *Flowers* free, tepals 4 or 5, free; stamens (2–)4–6, straight in the bud; pistillode present; ovary free, stigmas filiform, 2 and equally or unequally long, or 1. *Fruit* a dehiscent drupe.

Distribution — The tribe comprises two genera, *Antiaropsis* confined to New Guinea, with 2 species and *Sparattosyce*, confined to New Caledonia, with one (or two?) species.

Morphology — The tribe shows similarities to the Castilleae in the structure of the inflorescences but it clearly differs in the absence of connate tepals, the non-fleshy tepals of pistillate flowers in fruit, the free dehiscent drupes, and the absence of self-pruning branches (as part of the architectural model of Cook (Hallé & Oldeman, *Essai sur l'architecture et la dynamique de croissance des arbres tropicaux* (1970); Berg, *Acta Bot. Neerl.* 26 (1977)).

ANTIAROPSIS

Antiaropsis K. Schum., Fl. Kais. Wilh. Land (1889) 40; Boerl., Handl. Fl. Ned. Ind. 3 (1900) 327; K. Schum. & Lauterb., Fl. Schutzgeb. Südsee (1900) 267; Engl. in Engl. & Prantl, Nat. Pflanzenfam. Nachtr. 2 (1908) 96; Diels, Bot. Jahrb. Syst. 67 (1935) 174; Corner, Gard. Bull. Singapore 19 (1962) 249, ‘*Antiaropsi*’.

Trees or shrubs, dioecious. *Leaves* distichous; lamina pinnately veined; stipules free, lateral. *Inflorescences* discoid and involucrate, with interfloral bracts (?), pedunculate. *Staminate flowers* with 4 or 5 (or 6), (almost) free, imbricate tepals; stamens (2–)3–5(–6). *Pistillate flowers* numerous, tepals 4, free; stigmas 2, filiform. *Fruit* a dehiscent drupe; seed without endosperm, cotyledons equal, rather thick, involute, radicle apical, short.

Distribution — The genus comprises two closely related species and is only known from New Guinea.

Morphology — The pistils are surrounded by 4, ± conduplicate tepals. In the pistillate inflorescences of *A. decipiens*, in addition to the tepals, similar, somewhat larger and flat, structures occur on the receptacle, which could be regarded as interfloral bracts, but might be ‘displaced’ tepals. Such ‘interfloral bracts’ have not yet been detected in the material available of staminate inflorescences.

Chemistry — α -antiarin and antioside, cardenolides known from *Antiaris* have also been found in seeds of *Antiaropsis* (Bisset, Ann. Bogor. 2 (1957) 219).

KEY TO THE SPECIES

- 1a. Lamina (usually) longer than 10 cm, often \pm scabrous beneath; pistillate inflorescences with numerous flowers; involucral bracts (rather) sparsely hairy; up to 1250 m altitude **1. A. decipiens**
- b. Lamina up to 10 cm long, smooth beneath; pistillate inflorescences with one flower; involucral bracts densely hairy; 1400–3200 m altitude **2. A. uniflora**

1. Antiaropsis decipiens K. Schum.

Antiaropsis decipiens K. Schum., Fl. Kais. Wilh. Land (1889) 40; K. Schum. & Lauterb., Fl. Schutzgeb. Südsee (1900) 267; Diels, Bot. Jahrb. Syst. 67 (1935) 174; Corner, Gard. Bull. Singapore. 19 (1962) 249.

Shrub or tree up to 12 m tall. *Leafy twigs* 1–2.5 mm thick, appressedly puberulous. *Leaves* distichous; lamina elliptic to subobovate or subovate or to narrowly ovate, (2.5–)6–14(–23) by (1.5–)2.5–6(–10.5) cm, coriaceous to subcoriaceous, apex acuminate to subcaudate, base cuneate to obtuse (to truncate), margin entire (or coarsely dentate towards the apex to lobate); upper surface (sub)glabrous; lower surface sparsely appressedly puberulous on the main veins, \pm scabrous or smooth; midrib prominent above, lateral veins (5–)7–14(–17) pairs, tertiary venation (sub)scalariform; petiole 0.5–1.3 cm long, sparsely puberulous; stipules 0.2–0.6 cm long, puberulous, caducous. *Staminate inflorescences* axillary, solitary; peduncle 8–15 mm long, puberulous, mostly with some small scattered bracts; head discoid, 5–15 mm diam., involucral bracts in 3 or 4 rows, ovate, 1–4 mm long, appressedly puberulous, orange to red; tepals 4 or 5 (or 6), 1.5–2 mm long, spatulate-cucullate, puberulous; stamens (2–)3–5(–6), 2–3 mm long, filaments free, 0.5–0.8 mm long, anthers 1–1.5 mm long, apiculate or not. *Pistillate inflorescences* axillary, solitary, at maturity of the fruits pendulous; peduncle 1.2–3.5 cm long, puberulous, mostly with some small scattered bracts; head discoid, 1–1.5 cm, in fruit up to 3 cm diam.; involucral bracts in 5 or 6 rows, ovate to narrowly ovate, 3–10 mm long, appressedly puberulous, in fruit red; flowers numerous; tepals narrowly elliptic to narrowly ovate, c. 5 mm, in fruit up to 10 mm long, \pm conduplicate, appressedly puberulous, in fruit orange to red; style 2–3 mm long, stigmas filiform, 1.5–3 mm long, equal or unequal in length; ‘interfloral bracts’ subovate to narrowly elliptic 5–7 mm long, in fruit up to 10 mm long, flat, appressedly puberulous. *Endocarp* body ellipsoid, 6–7 mm long, blackish, the exocarp white. — **Fig. 15a–j.**

Distribution — New Guinea.

Habitat — Evergreen forest at altitudes up to 1250 m.

Notes — 1. Shrubs as little as 0.5 m high may already flower.

2. Var. *parvifolia* Diels (1935), with lamina 4.5–6.5 by 2.5 cm and 4 or 5 pairs of lateral veins, prominent beneath, is not included as the type could not be examined and its identity is uncertain because of lack of details of the venation. For the same reasons the type could not be included in the other species.

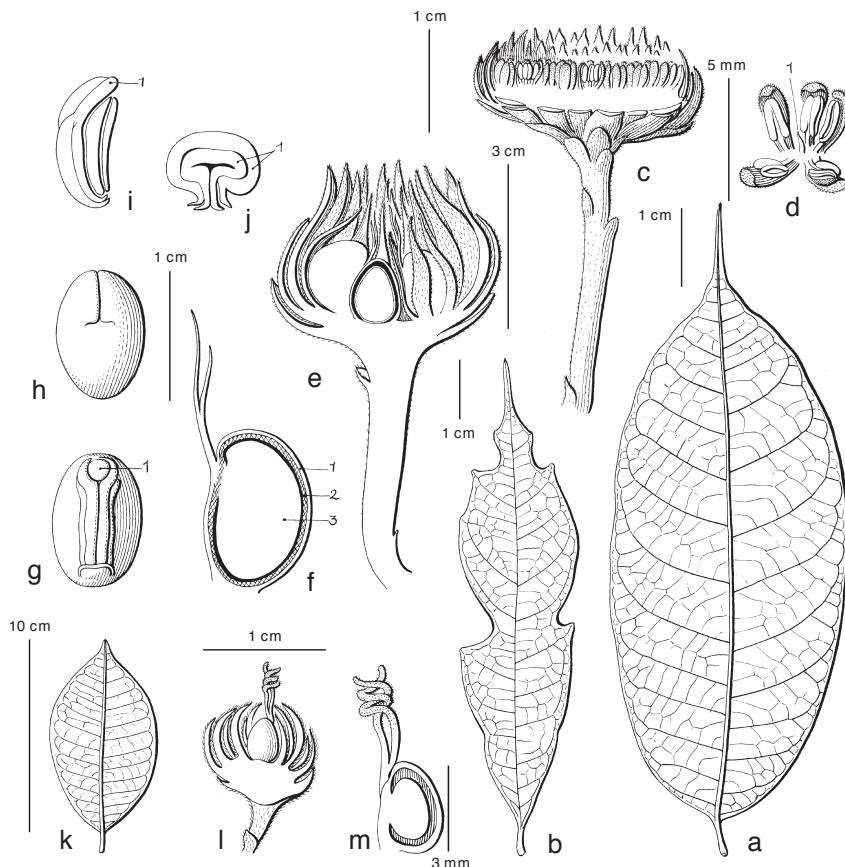


Fig. 15. a–j: *Antiaropsis decipiens* K. Schum. a. Leaf; b. sapling leaf; c. staminate inflorescence in section; d. staminate flower: 1 = pistillode; e. infructescence in section; f. drupe in section: 1 = exocarp, 2 = endocarp, 3 = seed; g–j. embryo: 1 in g and i = radicle, 1 in j = cotyledons. — k–m: *Antiaropsis parvifolia* C.C. Berg. k. Leaf; l. pistillate inflorescence in section; m. pistil in section (a: Nooroh 18l; b, e–j: Janowsky 194; c, d: Schlechter 16045; k–m: McAdam s.n., Wau).

3. The blackish endocarp body, the white exocarps, and the red to orange coloured tepals establish a set of contrasting colours, common in angiosperms to attract birds for dispersal.

4. This species is pollinated by thrips, as has been described in detail by Zerega et al., Int. J. Pl. Sci. 165 (2004) 1017–1026.

2. *Antiaropsis uniflora* C.C. Berg

Antiaropsis uniflora C.C. Berg, Blumea 50 (2005) 539.

?*Antiaropsis decipiens* K. Schum. var. *parvifolia* Diels, Bot. Jahrb. Syst. 67 (1935) 174; Corner, Gard. Bull. Singapore 19 (1962) 250.

Tree up to 23 m tall. *Leafy twigs* 1–2 mm thick, appressed puberulous. *Leaves* distichous; lamina elliptic, 3–10 by 1.5–3.5 cm, coriaceous to subcoriaceous, apex acuminate to subcaudate, base (sub)cuneate, margin entire; upper surface glabrous; lower surface sparsely appressed puberulous on the main veins, smooth; midrib prominent above, lateral veins 8–12 pairs, tertiary venation reticulate; petiole 0.4–0.8 cm long, sparsely puberulous; stipules 0.2–0.4 cm long, puberulous, caducous. *Staminate inflorescences* unknown. *Pistillate inflorescences* axillary, solitary; peduncle 1–2.5 cm long, puberulous, without bracts; head discoid, c. 5 mm diam., in fruit up to c. 10 mm diam.; involucral bracts in 4 or 5 rows, semicircular to narrowly elliptic, 2–8 mm long, densely white appressedly puberulous, the inner ones obtuse; flower one; tepals 4, narrowly elliptic to elliptic, c. 5 mm, in fruit up to 10 mm long, ± conduplicate, appressedly puberulous, in fruit orange to red; style 1.5–2 mm long, stigmas filiform, 1.5–2 mm long. *Endocarp body* ellipsoid, 7–8 mm long. — **Fig. 15k–m.**

Distribution — New Guinea.

Habitat — Evergreen forest at altitudes between c. 1400 and 3200 m.

Notes — 1. Even though the material presently available is sparse, this taxon, regarded as a variety by Diels (1935) and by Corner (1962), is distinct enough to be recognised as a species, as considered by Corner in the Flora Malesiana manuscript. It is distinct from the lowland *A. decipiens* in the habit, becoming a tree of more than 20 m tall, the small leaves, up to 10 cm long, the lack of bracts on the peduncle of the pistillate inflorescences, the broader and more densely hairy involucral bracts, and the presence of a single flower in the pistillate inflorescence.

2. The same contrasting colours as found in the inflorescences of *A. decipiens* probably also occur in this species in fruit.

3. As the type of *A. decipiens* var. *parvifolia* is not extant, it is not certain whether it belongs to this species or whether it is just a small-leaved form of *A. decipiens*.

Tribe ARTOCARPEAE

Artocarpeae R. Br. in Tuckey, Narr. Exped. Zaire, App. 5 (1818) 454; Gaudich. in Freyc., Voy. Uranie, Bot. (1830) 511; Corner, Gard. Bull. Singapore 19 (1962) 231; C. C. Berg, Proc. Kon. Ned. Akad. Wetensch. C, 91 (1988) 357; Blumea 50 (2005) 535. — *Euartocarpeae* Trécul, Ann. Sci. Nat., Bot. sér. 3, 8 (1847) 108.

Trees or shrubs (or climbers?), monoecious or dioecious, with or without uncinate hairs. *Leaves* spirally arranged or distichous; stipules fully amplexicaul to lateral or intrapetiolar, free or connate. *Inflorescences* usually unisexual, axillary or cauliflorous, spicate to capitate and then clavate, globose, or discoid, pedunculate, bracteate; interfloral bracts often peltate or subpeltate varying to spatulate, clavate, rod-shaped to spine-shaped. *Staminate flowers* numerous, with 2–4 connate tepals, stamens 1–4, straight in the bud, pistillode rarely present. *Pistillate flowers* free or connate, tepals 2–4(–5) and connate or absent (in *Treculia*), ovary free or adnate to the perianth, stigmas 1 or 2. *Fruit* large, free, with a dry pericarp or ± drupaceous, indehiscent embedded in the pulpy part of the (many-seeded) infructescence; seed without or with scanty endosperm, embryo curved or straight, with thick, equal or unequal cotyledons.

Distribution — This tribe comprises five genera of which four, *Artocarpus* (c. 45 spp.), *Hullettia* (2 spp.), *Parartocarpus* (2 spp.), and *Prainea* (2 spp.) occur in Asia and are speciose in Malesia, two of them, *Artocarpus* and *Parartocarpus* extending to Australia and/or the Pacific. The fifth genus, *Treculia* (with 3 spp.) occurs in continental Africa and Madagascar (see Berg, Bull. Jard. Bot. Belg. 47 (1977) 378).

Morphology — The very large infructescences formed by some species are remarkable and in *Artocarpus* resemble Durian fruits. Also notable are the wide range of shapes derived from the basically peltate bracts and the presence of glands or glandular spots in species of *Artocarpus* subg. *Pseudojaca*.

KEY TO THE GENERA

- 1a. Inflorescences involucrate with relatively large basally attached bracts at the base of the globose receptacle, or bracts at the margin of the turbinete to discoid receptacle; staminate flowers usually with 2 stamens 2
- b. Inflorescences without subtending bracts; staminate flowers with one stamen .. 3
- 2a. Stipules free, linear, subpersistent **Hullettia**
- b. Stipules fused, broader, caducous **Parartocarpus**
- 3a. Trees dioecious; pistillate flowers free **Prainea**
- b. Trees monoecious; pistillate flowers connate **Artocarpus**

ALTERNATIVE KEY TO THE GENERA

- 1a. Leaves spirally arranged 2
- b. Leaves distichous 4
- 2a. Stipules fully amplexicaul (leaving an annular scar) **Artocarpus** subg. **Artocarpus**
- b. Stipules not fully amplexicaul 3
- 3a. Stipules lateral, subulate, subpersistent **Hullettia**
- b. Stipules intrapetiolar, broader, caducous **Parartocarpus**
- 4a. Trees dioecious; pistillate flowers free **Prainea**
- b. Trees monoecious; pistillate flowers connate ... **Artocarpus** subg. **Pseudojaca**

ARTOCARPUS

Artocarpus J. & G. Forst., Char. Gen. Pl., ed. 2 (1776) 101, t. 51, 51a, nom. cons.; L.f., Suppl. (1781) 61, 411; Lam., Encycl. 3 (1789) 207; Willd., Sp. Pl. 4 (1805) 188; Pers., Syn. Pl. 2 (1807) 531; Blume, Bijdr. (1825) 479; Roxb., Fl. Ind., ed. Carey 3 (1832) 521; Blanco, Fl. Filip. (1837) 666; Trécul, Ann. Sci. Nat., Bot. sér. 3, 8 (1847) 109; Miq., Fl. Ned. Ind. 1, 2 (1859) 284; Fl. Ned. Ind., Eerste Bijv. (1861) 417; Ann. Mus. Bot. Lugduno-Batavi 3 (1867) 211; Blanco, Fl. Filip. ed. 3, 3 (1879) 73; Benth. & Hook.f., Gen. Pl. 3 (1880) 376; Engl. in Engl. & Prantl, Nat. Pflanzenfam. 3, 1 (1888) 82; King in Hook.f., Fl. Brit. India 5 (1888) 539; King, Ann. Roy. Bot. Gard. (Calcutta) 2 (1889) 1; Engl. in Engl. & Prantl, Nat. Pflanzenfam. Nachtr. 2 (1900) 17; Boerl., Handl. Fl. Ned. Ind. 3 (1900) 330, 370; Becc., For. Borneo (1902) 625; Koord. & Valeton, Bijdr. Boomsoort. Java 11 (1906) 11; Renner, Bot. Jahrb. Syst. 39 (1907) 363; Elmer, Leafl. Philipp. Bot. 2 (1909) 609; Koord., Exkurs.-Fl. Java 2 (1912) 91; Merr., Enum. Philipp. Flow. Pl. 2 (1923) 40; Ridl., Fl. Malay Penins. 3 (1924) 351; Gagnep., Bull. Soc. Bot. France 73 (1926) 86; Fl. Indo-Chine 5 (1928) 731;

- Burkill, Dict. Econ. Prod. Malay Penins. (1935) 247; Corner, Wayside Trees Malaya ed.1 (1940) 649; F.G. Browne, For. Trees Sar. & Brunei (1955) 349; F.M. Jarrett, J. Arnold Arbor. 40 (1959) 113; Backer & Bakh.f., Fl. Java 2 (1965) 18; F.M. Jarrett, Blumea 22 (1975) 409; Kochummen, Tree Fl. Malaya 3 (1978) 120; Corner, Wayside Trees Malaya ed. 3, 2 (1988) 511; Kochummen, Tree Fl. Sabah & Sarawak 3 (2000) 187.
- Sitodium* Banks & Sol. ex Parkinson, J. Voy. South Seas (1773) 45; Thunb., Philos. Trans. 69 (1779) 465; Gaertn., Fruct. Sem. Pl. 1 (1788) 344, t. 71, 72; Fosberg, Amer. J. Bot. 26 (1939) 230; Taxon 3 (1954) 114.
- Radermachia* Thunb., Kongl. Svenska Vetensk. Acad. Handl. 37 (1776) 251 ('*Rademachia*'); Houtt., Nat. Hist. II, Pl. 11 (1779) 446.
- Polyphema* Lour., Fl. Cochinch. (1790) 546.

Trees, monoecious. Leaves spirally arranged (subg. *Artocarpus*) or distichous (subg. *Pseudojaca*); lamina pinnately veined or sometimes subtriplinerved, entire or pinnately divided, sometimes down to the midrib; stipules free, amplexicaul (subg. *Artocarpus*) or lateral (subg. *Pseudojaca*). Inflorescences unisexual, solitary or in pairs in the leaf axils or on short-shoots on the older wood, pedunculate (or subsessile), bracteate or ebracteate. Staminate inflorescences spicate, ellipsoid to cylindrical to clavate to sub-globose-capitate; flowers numerous, free; perianth tubular, subentire or 2–4-lobed to -parted; stamen 1. Pistillate inflorescences (sub)globose to ellipsoid-capitate, flowers numerous, with the upper parts of the perianth (or entirely) fused with adjacent perianths and/or interfloral bracts; perianth tubular with a narrow aperture; ovary free, stigma 1 or 2 of equal or unequal length. Infructescences consisting of a solid outer layer with a smooth areolate surface or with various protuberances, a soft, more or less fleshy middle layer containing the fruits, and a solid central part; fruit free, with a chartaceous to coriaceous to crustaceous pericarp or endocarp; seed without endosperm, embryo straight, longitudinally to obliquely aligned, cotyledons equal or unequal, radicle minute. — **Fig. 16.**

DISTRIBUTION

The genus comprises c. 45 species and ranges from Sri Lanka to South China and through Malesia to the Solomon Islands and Australia; 32 of these species occur as wild trees in Malesia, *A. heterophyllus* only as cultivated species. These species are elements of forest in ever wet climates or where there is a short dry season, mostly below 1000 m. Some species can be found at altitudes up to 1500 or to 1800 m, and in New Guinea up to 2000 m.

The number of species of the genus represented in the Sino-Himalayan region is uncertain (see p. 94 and p. 107). At most three species, including *A. heterophyllus*, are endemic to the western part of the Indian Peninsula and Sri Lanka. Three species (if not also the wild form of *A. altilis*) extend through New Guinea to the Solomon Islands. The only species found in Australia is the widespread *A. glaucus*.

MORPHOLOGY

Habit — The trees of several species can become very tall and the trunks then often have buttresses. The leafy twigs are slender (leptocladous) to thick (pachycladous),

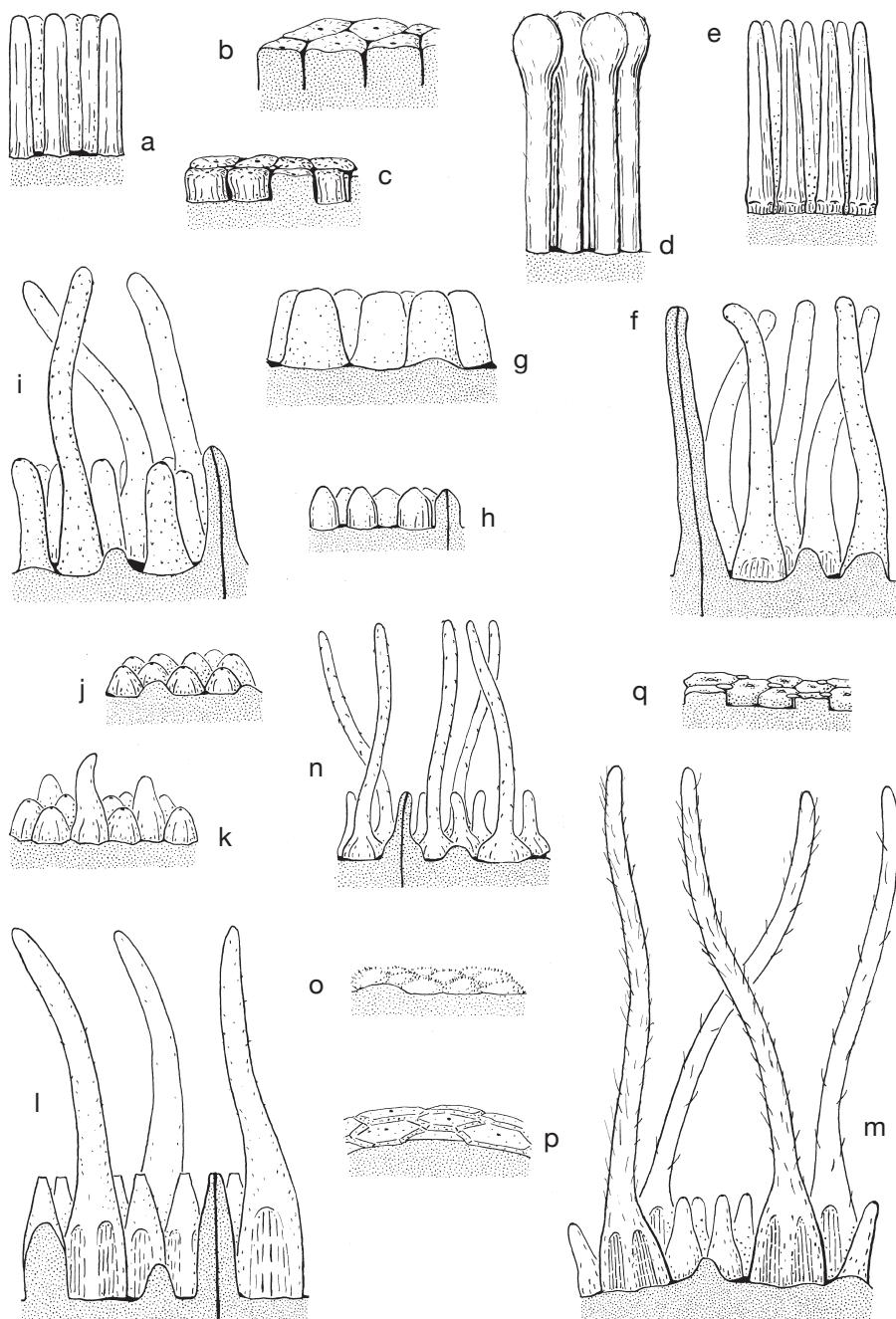


Fig. 16. Species of *Artocarpus* J. & G. Forst., the surface of infructescences. a. *A. anisophyllus*; b. *A. lanceifolius*; c. *A. brevipedunculatus*; d. *A. odoratissima*; e. *A. rigidus*; f, h, i. *A. debilis*; g. *A. treculianus*; j. *A. lowii*; k. *A. teijemannii*; l. *A. elasticus*; m. *A. sericicarpus*; n. *A. tamaran*; o, p. *A. kemando*; q. *A. sepicanus* (after F.M. Jarrett, J. Arnold Arbor. 40 (1959) 367; all approx. $\times 2.3$).

the latter type in combination with large leaves and infructescences that can become large as in *A. altilis*. Two species with more or less large infructescences, *A. heterophyllus* and *A. integer*, are leptoclados but cauliflorous, with the inflorescences in short branchlets on the trunk or main branches. Most species are evergreen and show continuous growth. In subg. *Pseudojaca* some species have intermittent growth, as described below (p. 108).

Leaves — They are spirally arranged in subg. *Artocarpus* and distichous in subsp. *Pseudojaca*. At germination the first leaves may be opposite or they may be reduced to scale-leaves. In the juvenile state the lamina is pinnately lobed to more deeply incised. In some species (of subg. *Artocarpus*) the lamina is (also) incised in the adult state, in *A. anisophyllus* usually down to the midrib and the segments petiolulate, thus the lamina being seemingly compound.

The two subgenera do not only differ in the arrangement of the leaves but also in the presence of glandular spots or glands on the lamina as described below for subg. *Pseudojaca* (see p. 108), and in features of the stipules.

Stipules — The stipules are free and in subg. *Artocarpus* fully amplexicaul and relatively large, longer than 1 cm, up to 25(–35) cm in *A. altilis*. In subg. *Pseudojaca*, the stipules are lateral and short, mostly 0.2–0.5 cm long, or if subpersistent on opening shoots, then sometimes up to 1 cm long; in species with intermittent growth they may be subpersistent, forming terminal buds.

Inflorescences — Usually solitary and axillary, but in particular staminate inflorescences occur on short-shoots on the older wood (ramiflorous) in some species of subg. *Pseudojaca*. Cauliflory is found in subg. *Artocarpus*.

The flower-bearing parts vary from spikes to clavate spadices or narrowly ellipsoid to ellipsoid or globose heads; considerable variation can be found in the same species. The flowers are densely set and free in the staminate inflorescences and (partly) fused in the pistillate ones. The flowers are intermixed with bracts.

Bracts — Interfloral bracts are basically peltate, but often modified, as described under the subgenera. The transformation of bracts from the basically peltate state into various other states is also found in the African genus *Treculia* (see Berg, Bull. Jard. Bot. Belg. 47 (1977) 380). Interfloral bracts, in particular peltate ones, can be caducous, in certain species consistently so, or not. Presence or absence of interfloral bracts is rather erratically distributed within the genus, its subdivisions, and even in species.

In several species, the flower-bearing part can be subtended by small basally attached scale-like bracts, not essentially different from the inflorescences of *Parartocarpus*.

Pistillate flowers — The lower parts of the perianths of the pistillate flowers surrounding the ovaries are free. More apically the perianths are connate, forming the solid ‘skin’ of the infructescence (see Jarrett 1976). The uppermost parts of the perianths are free, become more or less hardened and (partly) form the varied ‘ornamentation’ of the surface of the infructescence, in particular of those of subg. *Artocarpus* (see Fig. 16). The free apices of the perianths remain mostly flat in subg. *Pseudojaca*, but in some species they may become low-pyramidal and hardened.

The style runs through a very narrow channel (see Fig. 16d–f). In subg. *Artocarpus* the stigmas are usually either bifid (with equally or unequally long arms), or simple, but both states can be found in the same species. In subg. *Pseudojaca* the stigmas are simple with exception of those of *A. altissimus*.

The style remains terminal as in subg. *Pseudojaca*, some species of subg. *Artocarpus*, those included in sect. *Duricarpus* by Jarrett (1959), whereas in the other species, those included in sect. *Artocarpus*, the style becomes lateral to subbasal during seed-setting.

Fruits — Ellipsoid (to globose), with a ± crustaceous to cartilaginous pericarp or endocarp varying in size, being either (0.6–)0.8–1.2(–1.5) or c. 2–3 cm long. Large seeds are associated with the cultivated form of the species.

Seeds — They are longitudinally aligned and with equal cotyledons in the groups with terminal styles and oblique and with unequal cotyledons in the groups in which the style becomes lateral to subbasal.

Seedlings — The features of seedlings of several species have been described by Burger (1972) and Troup (1921); the germination is hypogeal; the seeds are not dormant.

Leaf anatomy — Leaf anatomical features, including the variation in pluricellular (or glandular) trichomes, are described by Renner (1907) and Jarrett (1959); none of them has detected the *Ficus*-like glandular spots in subg. *Pseudojaca* (see p. 108).

References: Burger, D., Seedlings of some tropical trees and shrubs mainly of South East Asia (1972). Pudoc, Wageningen. — Jarrett, F.M., Studies in *Artocarpus* and allied genera, I. J. Arnold Arbor. 40 (1959) 1–29. — Jarrett, F.M., The syncarp of *Artocarpus* – a unique biological phenomenon. Gard. Bull. Singapore 29 (1976) 35–39. — Renner, O., Beiträge zur Anatomie und Systematik der Artocarpeen und Conopephaleen, insbesondere der Gattung *Ficus*. Bot. Jahrb. Syst. 39 (1907) 319–448. — Troup, R.S., The silviculture of Indian trees 3 (1921). Clarendon Press Oxford.

CHROMOSOME NUMBERS

A chromosome number of $2n = 56$ has been reported for the species (Fedorov 1969; Chen 1993; Oginuma & Tobe 1995), but the seedless (= sterile) variety of *A. altilis* is hexaploid and has $2n = 84$ chromosomes (see Ragone 2001).

References: Chen., R.-Y (ed.), Chromosome atlas of Chinese fruit trees and their close wild relatives. Chromosome atlas of Chinese principal economic plants (1993). International Academic publishers, Beijing. — Fedorov, A.A. (ed.), Chromosome numbers of flowering plants (1969). St. Petersburg. — Oginuma, K. & H. Tobe, Karyomorphology of some Moraceae and Cecropiaceae (Urticales). J. Pl. Res. 108 (1995) 313–326. — Ragone, D., Chromosome numbers and pollen stainability of three species of Pacific island breadfruit (*Artocarpus*, Moraceae). Amer. J. Bot. 88 (2001) 693–696.

SUBDIVISION AND DELIMITATION

The genus comprises two markedly distinct subgenera: *Artocarpus* and *Pseudojaca*. The differences are such that these two entities and *Parartocarpus* could be considered as equivalent at the subgeneric rank. The latter is distinct in the basally attached bracts,

larger than those usually found in the two subgenera, and differs from subg. *Artocarpus* in the small connate stipules, and from subg. *Pseudeojaca* in the intrapetiolar position of the connate stipules. *Prainea* is also very close to *Artocarpus*, differing in the free pistillate flowers.

Literature: Corner, E.J.H., Notes on the systematy and distribution of Malayan phanerogams, II. The jack and the chempedak. Gard. Bull. Singapore 10 (1938) 56–81. — Corner, E.J.H., Wayside Trees of Malaya ed. 1, 1 (1940). Government Printing Office, Singapore. — Corner, E.J.H., Wayside Trees of Malaya ed. 3, 1 (1988). Malayan Nature Society, Kuala Lumpur. — Jarrett, F.M., Studies in Artocarpus and allied genera, III. J. Arnold Arbor. 40 (1959) 113–155. — Van der Pijl, L., On the flower biology of some plants from Java – with general remarks on fly-traps (species of Annona, Artocarpus, Typhonium, Gnetum, Arisaema and Abrroma). Ann. Bogor. 1 (1953) 77–99.

DISPERSAL

Seeds are mainly dispersed by various arboreal animals such as monkeys, squirrels, and civet cats. Monkeys and squirrels bite the infructescence into pieces and carry off the seeds. Yellow, red, or purple infructescences are also eaten by birds. The large infructescences of the cauliflorous species, *A. integer* and *A. heterophyllus*, particularly in the latter species which can reach considerable dimensions, are probably dispersed by forest ungulates including elephants (Ridley 1930).

References: Ridley, H.N., The dispersal of plants throughout the world (1930). Reeve & Co. Ltd., Ashford.

USES

The genus includes two commonly cultivated trees as fruit trees throughout the tropics: *A. altilis* (Breadfruit) and *A. heterophyllus* (Jack or Jackfruit); *A. integer* (Chempedak) is widely grown in Malesia and *A. odoratissimus* (Marang) is in cultivation in the Philippines and Borneo (see for these species Rajendran, Soepadmo, Jansen, and Dela Cruz, respectively, PROSEA 2 (1991) 83–96). The infructescences of several other species, not in cultivation, are harvested for the juicy perianth parts and/or the seeds which are often eaten roasted (see Seibert & Jansen 1991).

The lightweight hardwood of several *Artocarpus* species is used for several purposes such as for construction, veneer, and various utensils (see Djarwaningsih et al. 1995). Several *Artocarpus* species also produce exudates such as latex (see Boer & Ella 2000) to use as birdlime or as medicine or stimulants (see Van der Vossen & Wessel 2000) and/or (bark) fibres to make cloth (see Brink & Escobin 2003).

References: Boer, E. & A.B. Ella (eds), Plant resources of South-east Asia 18. Plants producing exudates (2000) 139–140. Backhuys Publishers, Leiden. — Brink, M. & R.P. Escobin (eds), Plant resources of South-east Asia 17. Fibre plants (2003) 304–305. Pudoc, Wageningen. — Dela Cruz, F.S., Artocarpus odoratissimus, in: E.W.M. Verheij & R.E. Coronel (eds), Plant resources of South-east Asia 2, Edible fruits and nuts (1991) 94–96. — Djarwaningsih, T., D.S. Alonzo, S. Sudo & M.S.M. Sosef, Artocarpus J.R. & G. Forster, in: R.H.M.J. Lemmens, I. Soerianegara & W.C. Wong (eds), Plant resources of South-east Asia 5, 2, Timber trees: Minor commercial timbers (1995) 59–71. Pudoc, Wageningen. — Jansen, P.C.M. 1991. Artocarpus integer, in: E.W.M. Verheij & R.E. Coronel (eds), Plant resources of South-east Asia 2, Edible fruits and nuts (1991) 91–94. Pudoc, Wageningen. — Rajendran,

R., *Artocarpus altilis*, in: E.W.M. Verheij & R.E. Coronel (eds), Plant resources of South-east Asia 2, Edible fruits and nuts (1991) 83–86. Pudoc, Wageningen. — Seibert, B. & P.C.M. Jansen, *Artocarpus* J.R. & G. Forster, in: E.W.M. Verheij & R.E. Coronel (eds), Plant resources of South-east Asia 2, Edible fruits and nuts (1991) 79–83. Pudoc, Wageningen. — Soepadmo, E., *Artocarpus heterophyllus*, in: E.W.M. Verheij & R.E. Coronel (eds), Plant resources of South-east Asia 2, Edible fruits and nuts (1991) 86–91. Pudoc, Wageningen. — Van der Vossen, H.A.M. & M. Wessels (eds), Plant resources of South-east Asia 16. Stimulants (2000) 139. Pudoc, Wageningen.

TAXONOMIC HISTORY

For the complex taxonomic history of the genus, in particular with regard to species in cultivation and the confusion concerning the names of these species see Jarrett, J. Arnold Arbor. 40 (1959) 115–125, and for an account on the nomenclatural problems related to *Artocarpus integer* see Corner, Gard. Bull. Singapore 10 (1938) 56–81.

DUBIOUS NAMES

For dubious names and nomina nuda linked to the Malesian region see Jarrett, J. Arnold Arbor. 41 (1960) 139–140.

KEY TO THE SUBGENERA

- 1a. Leaves spirally arranged; stipules fully amplexicaul, 1 cm or longer
Subg. **Artocarpus**
- b. Leaves distichous; stipules lateral, shorter than 1 cm Subg. **Pseudojaca**

Subgenus ARTOCARPUS

Artocarpus J. & G. Forst. subg. *Artocarpus*: F.M. Jarrett, J. Arnold Arbor. 40 (1959) 129. — *Artocarpus* J. & G. Forst. subg. *Jaca* Trécul, Ann. Sci. Nat., Bot. sér. 3, 8 (1847) 110. — *Artocarpus* J. & G. Forst. sect. *Jaca* (Trécul) Renner, Bot. Jahrb. Syst. 39 (1907) 363.

Artocarpus J. & G. Forst. subg. *Artocarpus* sect. *Duricarpus* F.M. Jarrett, J. Arnold Arbor. 40 (1959) 137.

Artocarpus J. & G. Forst. subg. *Artocarpus* sect. *Duricarpus* F.M. Jarrett ser. *Laevifolii* F.M. Jarrett, J. Arnold Arbor. 40 (1959) 138.

Artocarpus J. & G. Forst. subg. *Artocarpus* sect. *Duricarpus* F.M. Jarrett ser. *Asperifolii* F.M. Jarrett, J. Arnold Arbor. 40 (1959) 143.

Artocarpus J. & G. Forst. subg. *Artocarpus* sect. *Artocarpus* ser. *Incisifolii* F.M. Jarrett, J. Arnold Arbor. 40 (1959) 298.

Artocarpus J. & G. Forst. subg. *Artocarpus* sect. *Artocarpus* ser. *Cauliflori* F.M. Jarrett, J. Arnold Arbor. 40 (1959) 327.

Artocarpus J. & G. Forst. subg. *Artocarpus* sect. *Artocarpus* ser. *Angusticarpi* F.M. Jarrett, J. Arnold Arbor. 40 (1959) 338.

Artocarpus J. & G. Forst. subg. *Artocarpus* sect. *Artocarpus* ser. *Rugosi* F.M. Jarrett, J. Arnold Arbor. 40 (1959) 343.

Leaves spirally arranged; lamina without glands or glandular spots; stipules fully amplexicaul, usually longer than 1 cm. *Staminate flowers* with largely connate tepals. *Pistillate flowers* with cushion shaped, pyramidate, conical, spine-like, subulate,

or filiform free apices, indurated in fruit. *Flowers* often intermixed with peltate to spathulate (in pistillate inflorescences often (partly) caducous) bracts, or in staminate inflorescences with rod-shaped interfloral processes, and in pistillate inflorescences with conical, subulate or filiform processes, or else bracts and processes absent.

DISTRIBUTION

This subgenus is concentrated in the western part of the Malesian region with 19 indigenous species, some species extending to the Asian mainland and some species to western New Guinea. *Artocarpus altilis* is clearly eastern Malesian, extending into Micronesia, Melanesia, and Polynesia, mainly with cultivars. *Artocarpus sepicanus* is endemic to New Guinea and *A. teijsmannii* extends with its subsp. *subglabrus* to the Solomon Islands.

Artocarpus nobilis Thwaites is endemic to Sri Lanka. The origin of *A. heterophyllus* lies probably in the western Indian Peninsula. Clear morphological connections of *A. hirsutus* with material from the Sino-Himalayan region (as indicated below under *A. hispidus*, see p. 93) makes it uncertain whether *A. hirsutus* is a distinct species and another endemic of the Indian Peninsula.

MORPHOLOGY

Interfloral bracts — In staminate inflorescences, the bracts are basically peltate (to spathulate), but may be modified into rod-shaped ‘processes’, which were described by Jarrett as sterile flowers.

In pistillate inflorescences lacking (sub)peltate bracts, the flowers are often intermixed with rigid ‘processes’ varying in shape and length from conical to filiform, and from straight to ± curved. These are apparently also modified bracts. These ‘processes’ often resemble the hardened free apices of the perianths which vary from cushion shaped to pyramidal to conical to spine-like to subulate to filiform (and straight to curved). The perianth apices can be distinguished from ‘processes’ by the perforate apex or also by the persisting stigmata. The variation of the apices of perianths and the interfloral ‘processes’ is illustrated in Fig. 16.

SUBDIVISION

A group of species included by Jarrett (1959) in sect. *Duricarpus* is characterised by globose (to ellipsoid) infructescences with indurated apices ranging from cushion shaped to (up to 1 cm long) cylindrical to spine-like to clavate (persistent or caducous) peltate interfloral bracts, terminal styles and longitudinally aligned embryos with equal cotyledons. This group comprises *A. anisophyllus*, *A. annulatus*, *A. asperula* Gagnep. (Indochina), *A. brevipedunculatus*, *A. calophylla* Kurz (Myanmar), *A. chama* Buch.-Ham. (Sikkim to Vietnam), *A. hirsutus* Lam. (India), *A. hispidus*, *A. lanceifolius*, *A. nobilis* Thwaites (Sri Lanka), *A. odoratissimus*, *A. rigidus*, and *A. sarawakensis* (but see p. 93). *Artocarpus hirsutus* deviates in the pendulous spicate staminate inflorescences and in the absence of peltate interfloral bracts.

A second main group (section) comprises species included in sect. *Artocarpus* which is characterised by the frequent absence of peltate interfloral bracts, being substituted by elongate processes, or totally absent. The apices of the perianths varies from cushion shaped to spine-like. The style is lateral to subbasal. The embryos are obliquely aligned with unequal to equal cotyledons. The group can be subdivided into four subgroups:

- 1) Plants with cauliflorous species: *A. heterophyllus* and *A. integer*.
- 2) Plants usually with incised laminas in the adult state: *A. altilis* and possibly also *A. treculianus* in which the lamina is sometimes pinnately incised in the adult state. The latter species also shows affinities to *A. teijemannii*.
- 3) Plants with entire laminas in the adult state, the staminate inflorescences with smooth surfaces and the vegetative parts inconspicuously whitish (to brownish) hairy or glabrous: *A. excelsus*, *A. lowii*, *A. sepicanus*, and *A. teijemannii*.
- 4) Plants with entire laminas in the adult state, the staminate inflorescences with sulcate to tuberculate surfaces and the vegetative parts more or less conspicuously brown hairy: *A. elasticus*, *A. kemando*, *A. sericicarpus*, and *A. tamaran*.

KEY TO THE SPECIES OF SUBGENUS ARTOCARPUS

- | | |
|--|-----------------------------------|
| 1a. Inflorescences borne on stems and/or branches (cauli- or ramiflorous) | 2 |
| b. Inflorescences axillary | 3 |
| 2a. Indumentum whitish; peduncle broadened into a rim. — Widespread, in cultivation | 7. <i>A. heterophyllus</i> |
| b. Indumentum brownish or absent; peduncle not broadened into a rim. — Widespread, indigenous or in cultivation | 9. <i>A. integer</i> |
| 3a. Lamina deeply pinnately incised with 12–20 segments on each side, the incisions down to near the midrib. — Philippines | 1. <i>A. altilis</i> |
| b. Lamina entire or pinnately incised, if deeply so and with up to 12 segments on each, then these mostly petiolulate | 4 |
| 4a. Staminate and pistillate inflorescences with peltate interfloral bracts | 5 |
| b. Staminate and pistillate inflorescences without interfloral bracts, or if present, then not peltate | 17 |
| 5a. Epidermis of petiole flaking off. — New Guinea | 17. <i>A. sepicanus</i> |
| b. Epidermis of petiole persistent | 6 |
| 6a. Lateral veins 4–6 pairs; uncinate hairs on leafy twigs, petioles, and margin of the lamina (or glabrous). — Borneo | 3. <i>A. annulatus</i> |
| b. Lateral veins 6–20 pairs; straight and persistent hairs on leafy twigs, petioles, and margin of the lamina | 7 |
| 7a. Lamina of adult specimens incised down to the midrib, the segments often petiolulate. — Malay Peninsula, Sumatra, Borneo (and Philippines?) 2. <i>A. anisophyllus</i> | |
| b. Lamina of adult specimens entire or, if pinnately incised, then not down to the midrib | 8 |
| 8a. Lamina of adult specimens usually pinnately incised; petiole 3–9(–13); stipules usually 10–15 cm long. — Widespread | 1. <i>A. altilis</i> |
| b. Lamina of adult specimens entire (or 3-lobed to -fid); petiole 1–3(–4) cm long; stipules 1–5(–8) cm long | 9 |

- 9a. Leafy twigs and stipules glabrous. — New Guinea
 **20b. A. teijsmannii** subsp. **subglabrus**
- b. Leafy twigs and stipules hairy 10
- 10a. Hairs on the stipules longer at the apex (subsericeous) than lower down (appressedly puberulous). — Widespread **20a. A. teijsmannii** subsp. **teijsmannii**
- b. Hairs on the stipules equally long 11
- 11a. Lamina glabrous and both surfaces smooth. — Malay Peninsula, Sumatra, Borneo **11. A. lanceifolius**
- b. Lamina hairy, at least beneath on the main veins, often scabrous or scabridulous above and/or beneath 12
- 12a. Hairs on the leafy twigs appressed 13
- b. At least some hairs on the leafy twigs ± patent 15
- 13a. Stipules 0.5–1 cm long; lateral veins usually 7–10 pairs; lamina smooth above.
 — Borneo **4. A. brevipedunculatus**
- b. Stipules 1–5(–8) cm long; lateral veins usually 10–20 pairs; lamina ± scabrous above 14
- 14a. Peduncle of the pistillate inflorescences 5–14 cm long and the free parts of the perianth clavate, 8–12 mm long; head of staminate inflorescences 4–9 cm long.
 — Borneo, Philippines **14. A. odoratissimus**
- b. Peduncle of the pistillate inflorescences 0.8–4 cm long and the free parts of the perianth cylindrical, 3–8 mm long; head of staminate inflorescences 1.5–3 cm long. — Sumatra, Malay Peninsula, Java, Borneo, Lesser Sunda Islands, Malay Peninsula **15. A. rigidus**
- 15a. Lamina smooth above. — Sumatra, Borneo **16. A. sarawakensis**
- b. Lamina ± scabrous above 16
- 16a. Stipules 0.5–1(–2) cm long and petioles 1–1.5(–2) cm long; peduncle of the staminate inflorescences 1–3 cm long; peduncle of the pistillate inflorescences 2.5–3.5 cm long. — Malay Peninsula **8. A. hispidus**
- b. Stipules 1–5(–8) cm long and petioles (1.5–)2–3 cm long; peduncle of the staminate inflorescences usually 3–13 cm long; peduncle of the pistillate inflorescences 5–14 cm long. — Borneo, Philippines **14. A. odoratissimus**
- 17a. Surface of the staminate inflorescences sulcate or tuberculate, or the flowers intermixed with subulate processes and/or the pistillate inflorescences with numerous subulate to filiform interfloral processes, these at least 2 times longer than the free parts of the perianths 18
- b. Staminate inflorescences with a smooth surface and the pistillate inflorescences without interfloral processes or if processes present, then few and less than 2 times as long as the perianths, or else c. 3 times as long as the perianths and pyramidalate 22
- 18a. Lateral veins (13–)18–24 pairs, rarely branched or forked away from the margin; stipules 3–9 cm long; petiole 3.5–4 cm long. — Borneo **19. A. tamaran**
- b. Lateral veins (6–)10–16(–18) pairs, most or some of them branched or forked away from the margin, or if rarely branching, then the stipules 0.7–2 cm long and petiole 1–3 cm long 19

- 19a. Leafy twigs 2–3 mm thick; stipules 0.7–2 cm long; lateral veins rarely branched or forked away from the margin; peduncle of staminate inflorescences 0.3–2 cm long; peduncle of pistillate inflorescences 0.3–0.8 or 1–4 cm long, brown velutinous. — Malay Peninsula, Sumatra, Borneo **10. A. kemando**
- b. Leafy twigs 2–20 mm thick; stipules mostly longer than 2 cm; lateral veins mostly branched or forked away from the margin; peduncle of staminate inflorescences usually more than 2 cm long, and of pistillate inflorescences more than 4 cm long or if less than 4 cm long, then minutely whitish puberulous 20
- 20a. Hairs on vegetative parts minute to short, appressed and white, except for the brown subsericeous apex of the stipules; staminate inflorescences with subulate interfloral processes. — Widespread **20a. A. teijsmannii** subsp. **teijsmannii**
- b. Hairs on vegetative parts predominantly brown, on the stipules not distinctly different in length and colour; staminate inflorescences without subulate interfloral processes 21
- 21a. Hairs on petioles and peduncles ± patent; indumentum on processes of the pistillate inflorescences partly hirtellous. — Borneo, Philippines, Celebes, Moluccas **18. A. sericicarpus**
- b. Hairs on petioles and peduncles appressed; indumentum on processes of the pistillate inflorescences puberulous to hispidulous. — Sumatra, Malay Peninsula, Java, Borneo, Philippines (Palawan), Lesser Sunda Islands **5. A. elasticus**
- 22a. Petiole 3–7(–10) mm thick, (2.5–)3.5–10 cm long; stipules often longer than 10 cm and brown hirsute 23
- b. Petiole 1–3 mm thick, mostly 1–3.5 cm long, or if up to 5 cm long, then the hairs on the stipules appressed; stipules up to 8 cm long 24
- 23a. Lamina of adult specimens mostly pinnately incised; areoles of lamina flat beneath. — Widespread **1. A. altilis**
- b. Lamina of adult specimens usually entire; areoles of lamina bullate beneath. — Widespread **5. A. elasticus**
- 24a. Lateral veins 7–10 pairs 25
- b. Lateral veins 10–20 pairs 27
- 25a. Hairs on the stipules becoming longer towards the apex. — Widespread
- 20a. A. teijsmannii** subsp. **teijsmannii**
- b. Hairs on the stipules about equally long 26
- 26a. Indumentum on leafy twigs predominantly brown(ish); petiole 1–2 mm thick. — Sumatra, Malay Peninsula, Borneo **10. A. kemando**
- b. Indumentum on leafy twigs predominantly whitish; petiole 2–3 mm thick. — Borneo **13. A. obtusus**
- 27a. Petioles and peduncles with (longer) uncinate hairs. — Malay Peninsula
- 12. A. lowii**
- b. Petioles and peduncles without uncinate hairs 28
- 28a. Stipules 6–18 cm long; petiole 3–8 cm long. — Philippines **21. A. treculianus**
- b. Stipules usually 0.7–5 cm long; petiole 1–3.5 cm long 29
- 29a. Stipules 0.7–2 cm long; petiole 1–2 mm thick; indumentum predominantly brown(ish). — Sumatra, Malay Peninsula, Borneo **10. A. kemando**

- b. Stipules usually 2–6 cm long; petiole usually 2–3 mm thick, or if 1–2 mm thick, then the indumentum predominantly whitish 30
 30a. Hairs of the stipules becoming longer towards the apex. — Widespread
 20a. *A. teijsmannii* subsp. *teijsmannii*
 b. Hairs of the stipules about equally long — Borneo. 6. *A. excelsus*

1. *Artocarpus altilis* (Parkinson) Fosberg

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- Artocarpus horridus* F.M. Jarrett, J. Arnold Arbor. 40 (1959) 306.
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- [*Soccus lanosus* Rumph., Herb. Amboin. 1 (1741) 110, t. 32.]
- [*Soccus granosus* Rumph., Herb. Amboin. 1 (1741) 112, t. 33.]
- [*Soccus sylvestris* Rumph., Herb. Amboin. 1 (1741) 114, t. 34.]

Tree up to 35(–40) m tall, with buttresses, evergreen or deciduous. *Leafy twigs* 5–22 mm thick, minutely whitish appressedly puberulous to subglabrous, often also brown (to yellowish) (sub)hirsute or setose (to strigose), drying brown to blackish; lenticels concentrated in the upper part of the internodes or ± scattered, few or numerous. *Leaves* spirally arranged; lamina coriaceous to chartaceous, elliptic to subrhombic to obovate in outline, 20–80(–100) by 15–50(–60) cm, mostly pinnatifid with 1–5(–9, occasionally –20) pairs of lateral lobes or segments, the incisions mostly to halfway, occasionally down to near the midrib, base cuneate to rounded (to subcordate), apex short-acuminate to acute, margin subentire to repand (to coarsely dentate), ± revolute; upper surface whitish to brownish (appressedly) puberulous to hirtellous or to subhispidulous, also brown set(ul)ose to strig(ill)ose on the main veins (or subglabrous), smooth to scabridulous; lower surface whitish to brownish appressedly puberulous (or to subhirtellous) on the veins, the hairs straight, on the smaller veins the hairs patent and all or some uncinate, all hairs on the smaller veins minute and appressed, or on the main veins also brown set(ul)ose, strig(ill)ose, or subhirsute, scabridulous to smooth; lateral veins 9–13(–18) pairs, (in entire laminas) some or most branched or forked away from the margin, tertiary venation scalariform, ± prominent; petiole 3–9(–13) cm long, 3–7(–10) mm thick, whitish to brownish appressedly puberulous, often also brown (sub)hirsute or set(ul)ose (or strigillose); stipules (3–)10–25(–35) cm long, whitish to brownish appressedly puberulous, often also brownish (sub)strigillose to (sub)hirsute or setose (to strigose), or brownish to yellowish subsericeous to subvillous or hirsute, caducous. *Staminate inflorescences* axillary, solitary; peduncle 1–6 cm long, whitish to brownish appressedly puberulous to substrigillose or to hirtellous, or also brown (sub)hirsute or setulose (to strigose), ± scabrous to smooth; head cylindrical to clavate to spicate, 5–30(–40) by (0.5–)1–3(–5.5) cm; perianth tubular, 1–2 mm long, the apex 2-lobed, subhispidulous or subglabrous; stamen 1.5–2.8 mm long, anther 0.6–0.8 mm long; interfloral bracts absent (or present and peltate). *Pistillate inflorescences* axillary, solitary; peduncle 2–14 cm long, whitish strigillose and also brown setulose or brown to yellowish hirtellous to (sub)hirsute, ± scabrous to smooth; head ovoid, ellipsoid, subglobose, or cylindrical; perianth tubular, c. 1 mm long, whitish to brownish (retroversely) hispidulous to puberulous (or subglabrous), the apex 2-lobed to convex; stigma bifid or simple; interfloral bracts usually absent, sometimes present, and then

often as rod-shaped processes. *Inflorescences* ellipsoid to subglobose to obovoid or to cylindrical, 5–10(–15) by 5–10 cm or 15–30 by 10–30 cm diam., covered by 2–3 mm long pyramidal, 2–8 mm long cylindrical, or 8–15 mm long subulate to filiform, often ± curved apices of the perianths, sometimes intermixed with 0.5–2 cm long subulate to filiform, often ± curved processes, rarely with peltate bracts; fruits ellipsoid, 1–1.2 or 2–2.5 cm long. — **Fig. 17.**

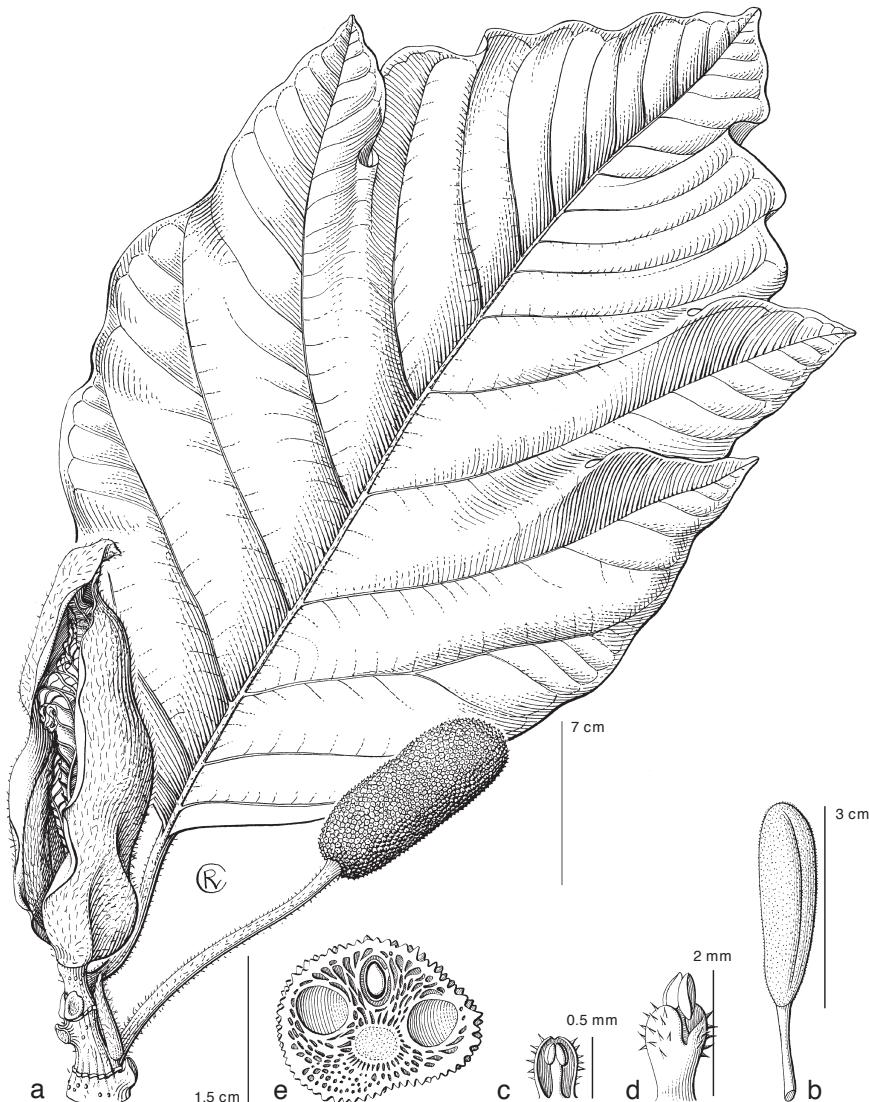


Fig. 17. *Artocarpus altilis* (Parkinson) Fosberg. a. Leafy twig with pistillate inflorescence; b. staminate inflorescence; c. length section of young staminate flower; d. mature staminate flower; e. cross section of infructescence (all: Beguin 1976).

Distribution — Melanesia, Micronesia, Polynesia; in *Malesia*: Philippines, Celebes, Lesser Sunda Islands (Flores), New Guinea; in these islands also the cultivated seeded and seedless forms of the species; these are also in cultivation elsewhere in Malesia (and throughout the tropics) (see also Barrau in Simmonds, Evolution of crop plants (1979) 202); there are some indications that the wild form extends to the Solomon Islands. Seeded cultivars may naturalize.

Habitat — Evergreen forest at low altitudes.

Notes — 1. In Malesia, three forms can be distinguished: the wild form with relatively small infructescences (up to 10 or 15 cm long) with relatively small seeds (1–1.2 cm long) and two cultivated forms with larger infructescences (up to 30 cm long or wide), the seeded form with larger fruits (2–2.5 cm long). The wild form is, with regard to the indumentum, rather variable: varying from sparse to dense on various parts (such as the stipules), from short to long, from rather weak to rigid and pungent (or setose), from straight to uncinate (when juvenile?), from whitish to yellowish to (dark) brown. Material with stiff and pungent hairs was included in *A. horridus* (by Jarrett 1959) and is the common form in the Moluccas and western New Guinea. The wild form also shows a considerable variation in shape and length of the apices of the perianths of the pistillate flowers, varying in length from 2 to 15 mm, and in shape from pyramidal to filiform. Plants with the longer perianths (10–15 mm) and filiform apices are mainly found in the Philippines (but do occur elsewhere, e.g., in Flores). These have been included in *A. blancai* (by Jarrett 1959), but perianth with short-tubular apices also occur in Luzon and Palawan. The stigmas are simple or bifid, short or rather long, and straight or twisted. Lack of adequate material makes it difficult to figure out to what extent the variation mentioned above is also found in the cultivated form(s) in Malesia and other tropical regions where the species is in cultivation.

2. The infructescences and seeds of this species, known as the ‘breadfruit’, are (and have been) important food sources. A detailed account on the economic importance and history, and morphological variation of the cultivated forms was presented by Jarrett (J. Arnold Arbor. 40 (1959) 309–323), Barrau (1979: 201–202), Zerega (2003/2004), and Zerega et al. (2004).

3. The names *Artocarpus camansi* and *A. rima* are based on vernacular names applied in the Philippines to the seeded and seedless cultivars of the species.

4. The normal chromosome number of this species is $2n = 56$, and is linked with normal seed and pollen production. The seedless cultivars have $2n = 84$ and pollen production is poor. The situation is less clear in Micronesia (see below).

5. Molecular studies by Zerega et al. (2004) confirmed the complexity of origin and distribution of cultivated forms of the species. The study recognizes three main groups (treated as species): ‘*A. camasi*’ probably representing the material indicated as the wild form above, ‘*A. mariannensis*’, a somewhat different Micronesian wild form of the species (and its derivates in cultivation), and ‘*A. altilis*’, representing the diverse cultivated material from Melanesia and Polynesia.

6. Fosberg (1960) referred the Micronesian material of this species partly to *Artocarpus mariannensis*, partly to *A. altilis*, and the rest to hybrids between the two ‘species’. A study by Ragone (2001) on chromosome numbers and fertility in *Artocarpus* material of the Pacific also revealed partial and full sterility in tetraploid material.

7. It is with some hesitation that *A. multifida* and *A. pinnatisectus* are included, not because of the numerous lobes of the lamina, or the anomalous staminate inflorescences (see Jarret, J. Arnold Arbor. 40 (1959) 324), but because of the presence of the few peltate interfloral bracts in the pistillate inflorescences. Presence or absence of interfloral bracts is not consistent in the subgenus and interfloral bracts (or processes) tend to occur in material of the species from the Philippines, but not (or rarely) elsewhere within the species range.

References: Barrau, J., Breadfruit and relatives, in: I. Simmonds (ed.), Evolution of crop plants (1979). Longman, New York. — Fosberg, F.R., Introgression in *Artocarpus* (Moraceae) in Micronesia. Brittonia 12 (1960) 101–113. — Ragone, D., Chromosome numbers and pollen stainability of three species of Pacific breadfruit (*Artocarpus*, Moraceae). Amer. J. Bot. 88 (2001) 693–696. — Zerega, N.J.C., The breadfruit trail, the wild ancestors of staple food illuminate human migrations. Natural History (2003/2004) 46–51. — Zerega, N.J.C., D. Ragone & T.J. Motley, Complex origins of breadfruit (*Artocarpus altilis*, Moraceae): implications for human migrations in Oceania. Amer. J. Bot. 91 (2004) 760–766.

2. *Artocarpus anisophyllus* Miq.

Artocarpus anisophyllus Miq., Fl. Ned. Ind., Eerste Bijv. (1861) 422; Renner, Bot. Jahrb. Syst. 39 (1907) 366; Merr., Pl. Elmer. Born. (1929) 45; Corner, Wayside Trees Malaya (1940) 652, t. 191, 192; F.G. Browne, For. Trees Sar. & Brunei (1955) 352; F.M. Jarrett, J. Arnold Arbor. 40 (1959) 138; Kochummen, Tree Fl. Malaya 3 (1978) 123, t. 2; Corner, Wayside Trees Malaya ed. 3, 2 (1988) 515, t. 155, 156; Kochummen, Tree Fl. Sabah & Sarawak 3 (2000) 191, t. 2.

Artocarpus klidang Boerl., Handl. Fl. Ned. Ind. 3 (1900) 333, 371, in clavi.

Artocarpus superba Becc., For. Borneo (1902) 625; Merr., Philipp. J. Sci. 18 (1921) 51; Enum. Philipp. Flow. Pl. 2 (1923); Ridl., Fl. Malay Penins. 3 (1924) 356.

Artocarpus anisophyllus Miq. var. *sessilifolius* Kochummen, Gard. Bull. Singapore 50 (1998) 200.

Tree up to 45 m tall, evergreen. Leafy twigs 10–20(–40) mm thick, ± densely brown (to whitish) appressedly puberulous to hispidulous, scabridulous or smooth, drying brown; lenticels scattered. Leaves spirally arranged; lamina coriaceous, 30–100(–150) cm long, pinnately incised down to the midrib, with 5–12 segments on each side, these alternate or subopposite, mostly 1–6(–8) cm long petiolulate, subovate to ovate to elliptic, (3.5–)10–20(–40) by (2–)4–8(–13) cm, apex acuminate, base subcordate to subcuneate, usually ± decurrent, margin subentire (or pinnately lobed to parted); upper surface glabrous; lower surface sparsely brownish strigillose on the midrib; lateral veins 7–20 pairs, ‘tertiary’ venation scalariform slightly prominent; ‘rachis’ sparsely brownish strigillose, terminal segment often 3-lobate; petiole 4–9(–16) cm long, (2.5–)5–12 mm thick, sparsely brownish strigose, the lower part ± thickened, the epidermis persistent; stipules fully amplexicaul, (2–)4–10(–17) cm long, brown substrigose to sub-hirsute, caducous. Staminate inflorescences axillary, usually solitary; peduncle 3–6.5 cm long, brownish (to whitish) appressedly puberulous; head ellipsoid to narrowly ellipsoid to cylindrical, 3–7.5 by 1.5–2 cm; perianth tubular c. 1.8 mm long, the apex 2-lobed, minutely puberulous to subglabrous; stamen 2–2.5 mm long, anther c. 0.2 mm long; interfloral bracts peltate, the apical part 0.6–0.8 mm diam., radially appressedly puberulous. Pistillate inflorescences axillary, usually solitary; peduncle 5–11 cm long, brownish (to whitish) appressedly puberulous; head ellipsoid to subglobose; perianth tubular, the apex convex to flat, minutely brown puberulous to muriculate, aperture

surrounded by a rim; stigma simple; interfloral bracts peltate, caducous, the apical part 0.6–0.8 mm diam., radially appressedly puberulous. *Infructescences* subglobose, 7–8(–10) cm diam., covered with 6–8 mm long, cylindrical apices of the perianths; fruits ellipsoid, 1–1.5 cm long.

Distribution — Sumatra, Malay Peninsula, Borneo, Philippines (see note 2).

Habitat — Evergreen forest, at altitudes up to c. 1300 m.

Notes — 1. The leaf is not truly compound as there is no articulation between ‘leaflet’ and ‘rachis’. When juvenile, the lamina may not (yet) have petiolulate segments, but segments broadly attached to the ‘rachis’, a feature sometimes retained in the adult state.

2. The species is also recorded for the Philippines (Basilan, Mindanao, Palawan) by Merrill (1921) under *Artocarpus superba*, but the collections were not traced by Jarrett (1959), nor for the present treatment. Possibly specimens of *A. altilis* with lamina’s with numerous incisions were misidentified as *A. anisiophyllus*.

3. *Artocarpus annulatus* F.M. Jarrett

Artocarpus annulatus F.M. Jarrett, Blumea 22 (1975) 409; Kochummen, Tree Fl. Sabah & Sarawak 3 (2000) 192.

Tree up to 25 m tall, evergreen. Leafy twigs 3–5 mm thick, sparsely brown puberulous with (retrorse) uncinate hairs, glabrescent, smooth, drying brown; lenticels scattered, few. Leaves spirally arranged; lamina subcoriaceous, entire, elliptic to obovate, 10–25 by 5–16 cm, apex short-acuminate, base cuneate to obtuse, often mostly almost equal, margin entire, ± revolute; both upper and lower surface (sub)glabrous, but initially with brown uncinate hairs on the margin, sometimes the midrib minutely brown puberulous beneath, smooth; lateral veins 4–6 pairs, some or none forked away from the margin, tertiary venation scalariform, flat; petiole 2.5–5 cm long, 2–3 mm thick, puberulous with brown (retrorse) uncinate hairs, glabrescent, the epidermis persistent; stipules fully amplexicaul, 1–2 cm long, sparsely brown hirtellous or partly puberulous with retrorse uncinate hairs, caducous. Staminate inflorescences axillary, solitary; peduncle 1.5–2.5 cm long, puberulous with brown (retrorse) uncinate hairs, glabrescent; head ellipsoid to ovoid, up to 4 by 2 cm, with annular grooves; perianth tubular, c. 0.8 mm long, the apex 2(–4)-lobed, minutely puberulous; stamen c. 1 mm long, anther c. 0.1 mm long; interfloral bracts (sub)peltate, the apices 0.2–0.4 mm diam., puberulous. Pistillate inflorescences axillary, solitary; peduncle c. 3 cm long, puberulous with brown (retrorse) uncinate hairs; head ellipsoid; perianth tubular, brown puberulous to subhispidulous, the apex convex; stigma simple; flowers intermixed with interfloral bracts, these spatulate to peltate, the apices 2–4 mm diam., brown puberulous. Infructescences ellipsoid, up to 8 by 6 cm (immature), covered with 6–8 mm long, subulate apices of the perianths; fruits not seen.

Distribution — Borneo (Sarawak).

Habitat — Evergreen forest at low altitudes, on limestone.

Notes — 1. The species is characterised by the small number of lateral veins and the presence of uncinate hairs on various parts. Straight hairs are only present on the stipules and sometimes on the midrib of the lamina beneath.

2. The infructescence is (very) fragrant.

4. *Artocarpus brevipedunculatus* (F.M. Jarrett) C.C. Berg

Artocarpus brevipedunculatus (F.M. Jarrett) C.C. Berg, Blumea 50 (2005) 541. — *Artocarpus melinoxylus* Gagnep. subsp. *brevipedunculatus* F.M. Jarrett, J. Arnold Arbor. 40 (1959) 144; Kochummen, Tree Fl. Sabah & Sarawak 3 (2000) 202.

Tree up to 25 m tall, evergreen. *Leafy twigs* 3–7 mm thick, ± densely brown strigillose to hispidulous (or also hirtellous to subhirsute), often scabridulous, drying brown; lenticels scattered. *Leaves* spirally arranged; lamina coriaceous, entire, elliptic to subobovate, (4–)10–20(–30) by (2–)5–9(–18) cm, apex short-acuminate, base cuneate to obtuse, margin entire; upper surface sparsely brownish strigillose to subhirtellous on the midrib (and lateral veins), smooth; lower surface brownish strigose to strigillose to puberulous to hispidulous, or on the veins, ± scabrous; lateral veins (6–)7–10 pairs, none branched or forked away from the margin, tertiary venation subscalariform to reticulate, slightly prominent; petiole 1–2 cm long, 2–2.5 mm thick, brown strigillose (or also hirtellous to subhirsute), the epidermis persistent; stipules 0.5–1 cm, brown strigillose or sometimes hirtellous, caducous. *Staminate inflorescences* axillary, solitary; peduncle 3–3.5 cm long, brown (to whitish) appressedly puberulous; head subglobose to ellipsoid, 1.5–2 by 1–1.5 cm; perianth tubular c. 1 mm long, the apex (deeply) 2- (or 3-)lobed, minutely puberulous; stamen c. 1.5 mm long, anther c. 0.2 mm long; interfloral bracts peltate, the apical part 0.3–0.4 mm diam., radially appressedly puberulous. *Pistillate inflorescences* axillary, solitary; peduncle 1–4 cm long, densely brown appressedly puberulous; head subglobose to ellipsoid; perianth tubular, brown puberulous, the apex ± convex, the aperture surrounded by a rim; stigma simple; interfloral bracts peltate, the apical part 0.3–0.4 mm diam., radially appressedly puberulous. *Infructescences* subglobose, 3–4 cm diam., sometimes ± lobed, covered with c. 3 mm long, cylindrical apices of the perianths; fruits ellipsoid, 1–1.5 cm long.

Distribution — Borneo.

Habitat — Evergreen forest at low altitudes.

Note — The material included in this species was initially referred to a subspecies of *A. melinoxylus* which was included in the synonymy of *A. chama* Buch.-Ham. (see Zhekun & Gilbert, Fl. China 5 (2003) 31), a species ranging from Sikkim to Vietnam or part of a more broadly construed species, see note under *A. hispidus*. *Artocarpus brevipedunculatus* differs from *A. chama* (s.str.) in the cuneate to obtuse base of the lamina, the absence of ramification of the lateral veins, the shorter stipules and peduncles.

5. *Artocarpus elasticus* Reinw. ex Blume

Artocarpus elasticus Reinw. ex [Blume, Cat. (1823) 101, nomen] Blume, Bijdr. (1825) 481; Miq., Fl. Ned. Ind. 1, 2 (1859) 285; Ann. Mus. Bot. Lugduno-Batavi 3 (1867) 211, p.p.; Koord. & Vleton, Bijdr. Boomsoort. Java 11 (1906) 13; Koord., Exkurs.-Fl. Java 2 (1912) 92; W.H. Br., Min. Prod. Philip. For. 2 (1921) 70, f. 24; Burkill, Dict. Econ. Prod. Malay Penins. (1935) 251; Corner, Wayside Trees Malaya (1940) 653, t. 193, 194; F.G. Browne, For. Trees Sar. & Brunei (1955) 352; F.M. Jarrett, J. Arnold Arbor. 40 (1959) 346; Backer & Bakh.f., Fl. Java 2 (1965) 19; Kochummen, Tree Fl. Malaya 3 (1978) 124, t. 3; Corner, Wayside Trees Malaya ed. 3, 2 (1988) 516, t. 157, 158, 159; Kochummen, Tree Fl. Sabah & Sarawak 3 (2000) 196.

Artocarpus pubescens Blume, Bijdr. (1825) 481, non Willd. 1805; Moritzi, Syst. Verz. (1846) 75.

Artocarpus blumei Trécul, Ann. Sci. Nat., Bot. sér. 3, 8 (1847) 111, t. 4, f. 116; Miq. in Zoll., Syst. Verz. 2 (1854) 89; Fl. Ned. Ind. 1, 2 (1859) 285; Ann. Mus. Bot. Lugduno-Batavi 3 (1867) 211; Kurz, Natuurk. Tijdschr. Ned.-Indië 27 (1864) 182; Becc., For. Borneo (1902) 632.

Artocarpus kunstleri King in Hook.f., Fl. Brit. India 5 (1888) 540; Ann. Roy. Bot. Gard. (Calcutta) 2 (1889) 9, t. 4; Ridl., Trans. Linn. Soc. London, Bot. 3 (1893) 355; Fl. Malay Penins. 3 (1924) 353.
— *Artocarpus blumei* Trécul var. *kunstleri* (King) Boerl., Handl. Fl. Ned. Ind. 3 (1900) 370.

Artocarpus scorTechinii King in Hook.f., Fl. Brit. India 5 (1888) 542; Ann. Roy. Bot. Gard. (Calcutta) 2 (1889) 12, t. 9; Ridl., Fl. Malay Penins. 3 (1924) 355; Corner, Wayside Trees Malaya (1940) 657; F.M. Jarrett, J. Arnold Arbor. 40 (1959) 344; Kochummen, Tree Fl. Malaya 3 (1978) 134, t. 6; Corner, Wayside Trees Malaya ed. 3, 2 (1988) 521.

Artocarpus corneri Kochummen, Gard. Bull. Singapore 50 (1998) 197; Tree Fl. Sabah & Sarawak 3 (2000) 194, t. 3.

Artocarpus jarrettiae Kochummen, Gard. Bull. Singapore 50 (1998) 198; Tree Fl. Sabah & Sarawak 3 (2000) 198.

Tree up to 45(–65) m tall, evergreen (or deciduous?), with buttresses. *Leafy twigs* (5–)7–20 mm thick, brown to whitish appressedly puberulous to subhispidulous or to hirtellous or hirsute, sometimes only on the scars of the stipules, ± scabrous or smooth, drying dark brown to blackish; lenticels in the upper part of the internode; scars of the stipules prominent. *Leaves* spirally arranged; lamina coriaceous to chartaceous, entire, elliptic 13–40(–60) by 6–20(–35) cm, or when juvenile pinnately incised with 3 or 4 (or 5) pairs of lobes, apex short-acuminate, base rounded to cuneate (to subattenuate), margin entire to repand to lobate (or denticulate towards the apex); upper surface minutely whitish puberulous to (sub)hispidulous, on the main veins to hirtellous, ± scabrous or smooth; lower surface brownish to whitish appressedly puberulous or partly strigillose to (sub)hirtellous on the veins, scabridulous or smooth; lateral veins 10–16 pairs, most of them branched or forked away from the margin, tertiary venation scalariform, prominent; areoles usually bullate; petiole 2.5–10 cm long, 2–6 mm thick, brown appressedly puberulous, the epidermis persistent; stipules fully amplexicaul, 4–20 cm long, brown (sub)hirsute to subvillous or to subsericeous, caducous. *Staminate inflorescences* axillary, solitary; peduncle 3.5–7.5 or 9.5–18 cm long, brown appressedly puberulous; head cylindrical, 6–15 by 1–2.5 cm, sulcate, the grooves often interrupted and almost straight; perianth tubular c. 0.6 mm long, the apex 2-lobed, minutely puberulous; stamen c. 0.9 mm long, anther 0.2–0.4 mm long; interfloral bracts absent. *Pistillate inflorescences* axillary, solitary; peduncle 4.5–12 cm long, brown appressedly puberulous; head ellipsoid to cylindrical; perianth tubular, brownish (to whitish) puberulous to hispidulous, the apex convex to flat; stigma bifid (with equally or unequally long arms); the flowers intermixed with subulate to filiform (± recurved) 6–12 mm long processes, these brown hispidulous or absent. *Infructescences* ellipsoid to cylindrical (or to subglobose), (6–)8–12(–17) by 5.5(–10) cm, covered with 1–4 mm long cushion shaped to pyramidal to cylindrical apices of the perianths, intermixed with elongate processes or not; fruits ellipsoid, 0.8–1 cm long.

Distribution — Myanmar, Thailand; in *Malesia*: Sumatra, Malay Peninsula, Borneo, Java, Philippines (Palawan), Lesser Sunda Islands (Bali, Lombok, Sumbawa).

Habitat — Evergreen forest at low altitudes, sometimes up to c. 1500 m.

Uses — Cloth is made from bark. The infructescence has an unpleasant smell, but the seed are eaten roasted.

Notes — 1. The pistillate inflorescences are quite different with regard to the presence of subulate to filiform processes among the flowers. The form without such processes has been recognised as *Artocarpus scortechinii* (Jarrett 1959). The upper surface of the lamina of specimens with such inflorescences is often smooth, but can be scabrous. The other form, in which the lamina is usually ± scabrous above, has elongated processes and has been recognised as *A. elasticus*. The latter is more widespread than the former, of which most collections (with a smooth upper surface of the lamina) have been made in the Malay Peninsula and Sumatra, but some, including the type of *A. corneri*, all with a scabrous upper surface of the lamina, are made in northern Borneo (Sarawak, Brunei). As there are no other differentiating characters in the vegetative parts than the inconsistent difference in the roughness of the upper surface of the lamina, and without differences in the staminate inflorescences and flowers, distinction at the species level is not justified. It might be convenient to indicate specimens (including the type of *A. jarrettiae*) with interfloral processes as the ‘*elasticus*’-form, those without processes and a smooth upper surface of the lamina as the ‘*scortechinii*’-form, and that without processes but with the lamina ± scabrous above (from Borneo) as the ‘*corneri*’-form.

Artocarpus teijmannii is another species with an even more erratic presence of interfloral processes.

2. *Artocarpus sericicarpus* is very close to *A. elasticus* and included in the synonymy of the latter by Kochummen (2000: 196). A form with interfloral processes, can be distinguished by the ± patent brown hairs on the petiole and peduncle of the pistillate inflorescence and is maintained as a distinct species, at least provisionally. Except for the indumentum on the petiole and peduncle and the longer interfloral processes with longer hairs, the two entities are similar. The similarities, the nature of the differences and the slight overlap in the ranges of distribution provide arguments to reduce *A. sericicarpus* to a subspecies. In Borneo (E Kutai) the two taxa have been collected in the same locality, which is an indication that they are good species.

3. *Artocarpus tamaran* which shares the presence of elongate interfloral processes and an uneven surface of the staminate inflorescence with *A. sericicarpus* and *A. elasticus* p.p. is distinct enough to be maintained as a distinct species.

4. The infructescences are eaten by monkeys; they are favoured by orang-utans.

6. *Artocarpus excelsus* F.M. Jarrett

Artocarpus excelsus F.M. Jarrett, Blumea 22 (1975) 409; [J. Arnold Arbor. 40 (1959) 340, as probably new species]; Kochummen, Tree Fl. Sabah & Sarawak 3 (2000) 197.

Tree up to 35 m tall, evergreen. *Leafy twigs* 3–4(–5) mm thick, minutely whitish appressedly puberulous, smooth, drying blackish; lenticels scattered, few. *Leaves* spirally arranged; lamina coriaceous, entire, elliptic, (4–)6–16 by (1.5–)2–5 cm, apex shortly (sub)acute, base cuneate to rounded, often slightly unequally, margin entire; upper surface sparsely minutely whitish appressedly puberulous to (sub)glabrous, smooth; lower surface minutely whitish appressedly puberulous on the midrib or also on the lateral veins, smooth; lateral veins 14–20 pairs, tertiary venation scalariform, almost flat; petiole (0.5–)1–2(–3) cm long, 1–2 mm thick, minutely whitish appressedly puberulous, the epidermis persistent; stipules fully amplexicaul, 2–4.5 cm long, whitish

(to brownish) appressedly puberulous, on the whole outer surface or only on the keel, caducous. *Staminate inflorescences* axillary, solitary; peduncle 1–1.5 cm long, minutely whitish appressedly puberulous; head cylindrical to spicate, 1.5–20 by 0.5 cm; perianth tubular c. 0.8 mm long, the apex 2-lobed, minutely puberulous; stamen c. 1 mm long, anther c. 0.2 mm long; interfloral bracts absent. *Pistillate inflorescences* axillary, solitary; peduncle 1.5–2.5 cm long, minutely whitish (appressedly) puberulous (or also with patent brown uncinate hairs); head ellipsoid to cylindrical; perianth tubular, sparsely minutely brownish puberulous, the apex convex; stigma simple; interfloral bracts absent. *Infructescences* ellipsoid, up to 7 by 4 cm, covered with 1–2 mm long pyramidal apices of the perianths; fruits ellipsoid, c. 1.2 cm long.

Distribution — Borneo (Sabah, most collections from Mt Kinabalu).

Habitat — Evergreen forest, at altitudes between c. 1400 and 1800 m.

Note — This species is closely related to *A. lowii*, from which it mainly differs in the smaller leaves; the status of subspecies should be considered.

7. *Artocarpus heterophyllus* Lam.

Artocarpus heterophyllus Lam., Encycl. 3 (1789) 210; Tabl. Encycl. (1797) t. 745; Trécul, Ann. Sci. Nat., Bot. sér. 3, 8 (1847) 117; Miq., Fl. Ned. Ind. 1, 2 (1859) 287; Corner, Gard. Bull. Singapore 10 (1939) 56; Wayside Trees Malaya (1940) 654; Quisumb., Med. Pl. Philipp. (1951) 228; F.M. Jarrett, J. Arnold Arbor. 40 (1959) 334; Backer & Bakh.f., Fl. Java 2 (1965) 19; Kochummen, Tree Fl. Malaya 3 (1978) 127, t. 4; Corner, Wayside Trees Malaya ed. 3, 2 (1988) 517; Soepadmo, Prosea 2 (1991) 86, cum t. — *Artocarpus integrifolia* L.f. var. *heterophylla* (Lam.) Pers., Syn. Pl. 2 (1807) 531.

Sitodium cauliflorum Gaertn., Fruct. Sem. Pl. 1 (1788) 345, t. 71, 72.

Artocarpus philippensis Lam., Encycl. 3 (1789) 210.

Polyphema jaca Lour., Fl. Cochinch. (1790) 546. — *Artocarpus integrifolia* L.f. var. *glabra* Stokes, Bot. Mat. Med. 4 (1812) 331.

Artocarpus maxima Blanco, Fl. Filip. (1837) 669.

Artocarpus integrifolia auct. non L.f.: Willd., Sp. Pl. 4 (1805) 189; Pers., Syn. Pl. 2 (1807) 531; Roxb., Pl. Coromandel (1815) t. 250; Blume, Bijdr. (1825) 482; Hook., Bot. Mag. 55 (1828) t. 2883, 2884; Roxb., Fl. Ind., ed. Carey 3 (1832) 522; Decne., Herb. Timorensis Descr. (1835) 169; Span., Linnaea 15 (1841) 343; Wight, Icon. Pl. Ind. Orient. 2 (1843) t. 678; Blanco, Fl. Filip. ed. 2 (1845) 466; Trécul, Ann. Sci. Nat., Bot. sér. 3, 8 (1847) 115; Griff., Notul. Pl. Asiat. 4 (1854) 402; Miq., Fl. Ned. Ind. 1, 2 (1859) 287; Ann. Mus. Bot. Lugduno-Batavi 3 (1867) 211; Blanco, Fl. Filip. ed. 3, 3 (1879) 75; Fern.-Vill., Nov. App. (1880) 203; King in Hook.f., Fl. Brit. India 5 (1888) 541; Ann. Roy. Bot. Gard. (Calcutta). 2 (1889) 16 et errata (record from Deccan, India); Warb., Bot. Jahrb. Syst. 13 (1891) 296; Koord. & Valeton, Bijdr. Boomsoort. Java 11 (1906) 19; Elmer, Leafl. Philipp. Bot. 2 (1909) 612; Koord., Exkurs.-Fl. Java 2 (1912) 93; Ridl., Fl. Malay Penins. 3 (1924) 351; Gagnep., Fl. Indo-Chine 5 (1928) 732; Subba Rao, J. Mysore Univ., B 1 (1940) 63.

Artocarpus integer auct. non (Thunb.) Merr.: Merr., Sp. Blancoan. (1918) 124; W.H. Br., Min. Prod. Philip. For. 2 (1922) 262, t. 15, 16; Merr., Enum. Philipp. Flow. Pl. 2 (1923) 41; Ochse & Bakh., Fruit (1931) 69, t. 28; Veg. Dutch East Indies (1931) 490; Burkill, Dict. Econ. Prod. Malay Penins. (1935) 253; Merr., Comm. Fl. Cochinch. (1935) 135; Mendiola, Philip. Agric. 28 (1940) 789.

[*Tsjaka-maram* Rheede, Hort. Mal. 3 (1682) 17, t. 26–28.]

[*Saccus arboreus* major Rumph., Herb. Amboin. 1 (1741) 104, t. 30.]

Tree up to 10(–30) m tall, sometimes with short buttresses, evergreen. *Leafy twigs* 2–6 mm thick, minutely whitish appressedly puberulous (to subpunctate), smooth, drying brown to greyish; lenticels scattered. *Leaves* spirally arranged; lamina (sub)coriaceous,

entire (or if juvenile 3-lobed), elliptic to (sub)obovate, 4–15 by 2–8(–12) cm, apex short-acuminate to obtuse, base cuneate to rounded, mostly ± decurrent, margin entire, ± revolute; upper surface often initially with sparse (retrorse) whitish uncinate hairs, soon glabrous, smooth; lower surface sparsely minutely whitish appressedly puberulous on the main veins or only on the midrib, often initially also sparse (retrorse) uncinate hairs, smooth; lateral veins 6–10 pairs, tertiary venation scalariform, slightly prominent; petiole 0.8–3 cm long, 1–2 mm thick, sparsely minutely whitish appressedly puberulous, the epidermis persistent; stipules fully amplexicaul, 1–5(–8) cm long, minutely whitish appressedly puberulous, caducous. *Staminate inflorescences* axillary or cauliflorous on slender leafy branchlets, solitary; peduncle 1–5.5 cm long, minutely whitish appressedly puberulous, at the apex broadened into a rim; head cylindrical to spicate or to subellipsoid, 2.5–7 by 0.8–2.8 cm; perianth tubular 0.7–1 mm long, the apex 2-lobed, minutely puberulous; stamen 1.5–2 mm long, anther c. 0.3 mm long; flower intermixed with numerous (to few?) cylindrical processes, these as long as the flowers, or processes absent. *Pistillate inflorescences* axillary, ramiflorous or cauliflorous on leafy branchlets, solitary; peduncle 3–10 cm long, minutely whitish (appressedly) puberulous, the apex broadened into a broad rim; head ellipsoidal to cylindrical; perianth tubular, white puberulous to subhispidulous, the apex convex; stigma simple; interfloral bracts (sometimes?) present, these peltate with the apical part 0.2–0.4 mm diameter. *Infructescences* ellipsoid to narrowly ellipsoid to pyriform, 30–100 by 25–50 cm, covered with c. 3 mm long conical to pyramidate apices of the perianths; fruits ellipsoid, c. 3 cm long.

Distribution — In Malesia cultivated and (occasionally) naturalised in areas with evergreen and semi-evergreen forest; probably (only) indigenous in western peninsular India; cultivated throughout the tropics (under the names Jack, Jak, Jaquier, Jaca, etc.).

Uses — The sweet fleshy perianths in fruit are eaten; the seeds are eaten roasted or boiled; the wood is used, e.g., for construction.

Notes — 1. There are two main forms in cultivation: one with firm fruiting perianths and the other with soft ones.

2. The presence of processes among staminate flowers or bracts among pistillate flowers is rather erratic.

8. *Artocarpus hispidus* F.M. Jarrett

Artocarpus hispidus F.M. Jarrett, J. Arnold Arbor. 40 (1959) 149; Kochummen, Tree Fl. Malaya 3 (1978) 27, t. 4.

Tree up to 20 m tall, evergreen. *Leafy twigs* 4–7 mm thick, ± densely brown hirsute, the long hairs with swollen bases and intermixed with much shorter hairs, ± scabrous, drying brown; lenticels scattered. *Leaves* spirally arranged; lamina subcoriaceous, entire, elliptic to subobovate, (6–)10–22 by (2.5–)4.5–9 cm, short-acuminate to sub-acuminate or to acute (and apiculate) or to obtuse, base cuneate to obtuse, margin dent(icul)ate towards the apex; upper surface brownish hispidulous, to hirtellous on the main veins, ± scabrous; lower surface brownish (sub)hispidulous to puberulous, to hirtellous on the main veins, scabridulous; lateral veins (8–)12–15 pairs, not branched or forked away from the margin, tertiary venation scalariform (to reticulate), prominent;

petiole 1–1.5(–2) cm long, 2–4 mm thick, brown hirtellous to subhirsute, the epidermis persistent; stipules 0.5–1(–2.5) cm, brown subhirtellous to strigose, caducous. *Staminate inflorescences* axillary, solitary; peduncle 1–3 cm long, brown hirtellous, ± scabrous; head ellipsoid to obovoid, 1.5–3 by 1–2 cm; perianth tubular c. 0.6 mm long, the apex 2-lobed, minutely puberulous; stamen c. 0.7 mm long, anther 0.1 mm long; interfloral bracts peltate, the apical part 0.2–0.3 mm diam., yellowish puberulous. *Pistillate inflorescences* axillary, solitary; peduncle 2.5–3.5 cm long, brown hirtellous, ± scabrous; head ellipsoid to subglobose; perianth tubular, hispidulous, the apex ± convex; stigma simple; interfloral bracts peltate, the apical part 0.2–0.3 mm diam., yellowish puberulous. *Infructescences* subglobose, 4–5.5 cm diam., covered with 5–6 mm long cylindrical apices of the perianths; fruits ellipsoid, 1–1.3 cm long. — **Fig. 18a.**

Distribution — Malay Peninsula.

Habitat — Evergreen forest, at altitudes up to c. 350 m.

Notes — 1. This species resembles *A. rigidus*, from which it differs in the longer peduncle of the staminate inflorescence, the denticulate margin of the lamina, and the indumentum of the leafy twigs, consisting of long ± patent hairs with swollen bases, intermixed with distinctly shorter hairs.

2. This species, *A. asperulus* Gagnep., *A. calophyllus* Kurz, *A. hirsutus*, and *A. rigidus* share the globose (to ellipsoid) infructescence densely covered with up to 3–9 mm long cylindrical indurated apices of the flowers. The material north of the Malay Peninsula differs from *A. hispidus* and *A. rigidus* in the frequently branched or forked lateral veins, the tendency of having fewer lateral veins, often up to 10 pairs, and a rounded to

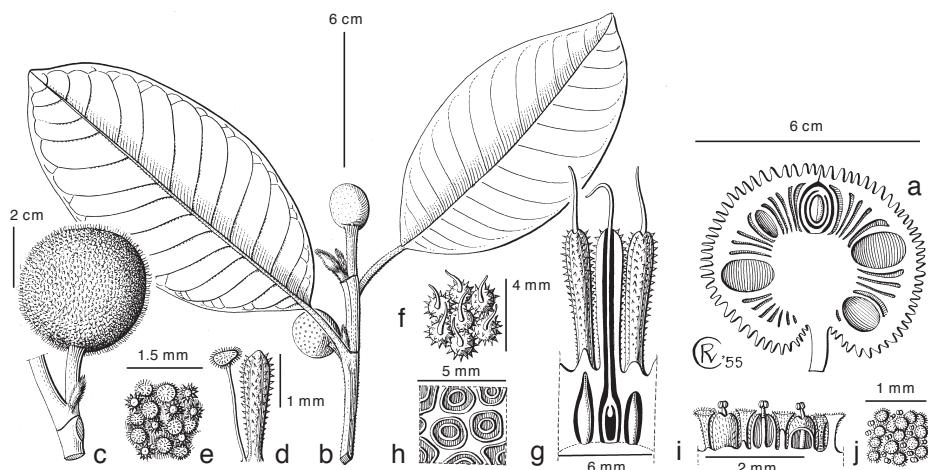


Fig. 18. a: *Artocarpus hispidus* F.M. Jarrett. Longitudinal section of infructescence. — b–i: *Artocarpus rigidus* Blume. b. Leafy twig with pistillate inflorescence; c. pistillate inflorescence; d. young pistillate flower with interfloral bract; e. surface view of young pistillate inflorescence; f. surface view of mature pistillate inflorescence; g. longitudinal section of portion of mature pistillate inflorescence; h. tangential section of portion of mature pistillate inflorescence; i. longitudinal section of staminate inflorescence; j. surface view of staminate inflorescence (a: Corner SFN 37035; b, d–h, i, j: 24 T 1P 195; c: 24 T 27).

subcordate base of the lamina. *Artocarpus hirsutus* from the Indian Peninsula is distinct in the pendulous spicate staminate inflorescences and the absence of interfloral bracts in the pistillate inflorescence; the other species have subglobose staminate inflorescences as in *A. hispidus* and *A. rigidus*. In the material occurring north of Peninsular Malaysia, the indumentum on leafy twigs and petioles can be appressed or ± patent, the stipules are of widely varying length, the margin of the lamina is entire or denticulate, the upper surface of the lamina smooth or ± scabrous, and the length of the peduncles varies considerably. Some of this variation may just enter Peninsular Malaysia, in Kedah and Langkawi Island (in the material indicated by Kochummen 1978: 132) as the ‘asperulus’-form. Pending the results of further study on the complex in continental Asia and its relation to the Malesian region, it is preferable to recognise for Malesia *A. hispidus* and *A. rigidus*, both as species and not as forms as has been proposed by Kochummen (1978), where the sparsely hairy and more densely hairy forms of *A. rigidus* are indicated as var. ‘*glabra*’ and var. ‘*tomentosa*’, respectively.

3. The suggested study should also include *A. chama* Buch.-Ham. (= *A. chaplasha* Roxb. = *A. melinoxylus* Gagnep.) which in vegetative characters largely matches the continental material circumscribed above, differing only in the shorter apices of the pistillate flowers which are up to 4 cm long (or up to 6 mm long according to Gagnep., Fl. Indo-Chine 5 (1928) 734).

9. *Artocarpus integer* (Thunb.) Merr.

Artocarpus integer (Thunb.) Merr., Interpr. Herb. Amboin. (1917) 190; Corner, Gard. Bull. Singapore 10 (1939) 56, t. 1, 2; Wayside Trees Malaya ed.1 (1940) 655; F.M. Jarrett, J. Arnold Arbor. 40 (1959) 329; Backer & Bakh.f., Fl. Java 2 (1965) 19; Kochummen, Tree Fl. Malaya 3 (1978) 127; Corner, Wayside Trees Malaya ed. 3, 2 (1988) 518, t. 157; P.C.M. Jansen, Prosea 2 (1991) 91, cum t.; Kochummen, Tree Fl. Sabah & Sarawak 3 (2000) 199. — *Radermachia integra* Thunb., Kongl. Svenska Vetensk. Acad. Handl. 37 (1776) 254; Houtt., Nat. Hist. II, 11 (1779) 453. — *Sitodium macrocarpon* Thunb., Philos. Trans. 69 (1779) 467, substitute name. — *Artocarpus macrocarpon* (Thunb.) Dancer, Cat. Bot. Gard. Jamaica 1 (1792); Mabb., Taxon 30 (1981) 12. — *Artocarpus integrifolia* L.f., Suppl. (1781) 411, substitute name. — *Artocarpus integrifolia* L.f. var. *hirsuta* Stokes, Bot. Mat. Med. 4 (1812) 330.

Artocarpus jaca Lam. var. β, Encycl. 3 (1789) 209.

Polyphema champeden Lour., Fl. Cochinch. (1790) 546, pro max. parte. — *Artocarpus champeden* (Lour.) Stokes, Bot. Mat. Med. 4 (1812) 330; Spreng., Syst. Veg. 3 (1826) 804; Merr., Interpr. Herb. Amboin. (1917) 190; Ochse & Bakh., Fruit (1931) 67, t. 27; Veg. Dutch East Indies (1931) 486; Burkill, Dict. Econ. Prod. Malay Penins. (1935) 249; Merr., Comm. Fl. Cochinch. (1935) 135; Mendiola, Philip. Agric. 28 (1940) 789.

Artocarpus polyphema Pers., Syn. 2 (1807) 531; Blume, Bijdr. (1825) 481; Span., Linnaea 15 (1841) 343; Trécul, Ann. Sci. Nat., Bot. sér. 3, 8 (1847) 115; Miq., Fl. Ned. Ind. 1, 2 (1859) 286; Hoola van Nooten, Fl. Fr. & Feuill. Java (1863) t. 26; Miq., Ann. Mus. Bot. Lugduno-Batavi 3 (1867) 211; King in Hook.f., Fl. Brit. India 5 (1888) 542; Ann. Roy. Bot. Gard. (Calcutta) 2 (1889) 11, t. 7B; Warb., Bot. Jahrb. Syst. 13 (1891) 296; Ridl., Trans. Linn. Soc. London, Bot. 3 (1893) 355; Koord. & Valeton, Bijdr. Boomsoort. Java 11 (1906) 21; Koord., Exkurs.-Fl. Java 2 (1912) 94; Ridl., Fl. Malay Penins. 3 (1924) 354; Gagnep., Fl. Indo-Chine 5 (1928) 734.

Artocarpus hirsutissima Kurz, Natuurk. Tijdschr. Ned.-Indië 27 (1864) 182.

Artocarpus integer (Thunb.) Merr. var. *silvestris* Corner, Gard. Bull. Singapore 10 (1939) 76; F.M. Jarrett, J. Arnold Arbor. 40 (1959) 351; Kochummen, Tree Fl. Malaya 3 (1978) 128, t. 4.

[*Saccus arboreus* minor Rumph., Herb. Amboin. 1 (1741) 107, t. 31.]

Tree up to c. 30 m tall, evergreen. *Leafy twigs* 2–4 mm thick, whitish puberulous (or punctate) and also brown hirtellous to (sub)hirsute, sometimes only (and sparsely) on and near the nodes, the hairs with swollen bases and sometimes uncinate, sometimes glabrous, drying dark brown to blackish; lenticels scattered, few. *Leaves* spirally arranged; lamina subcoriaceous, entire (or when juvenile to 3-lobate), elliptic to (sub)ovate, (4–)8–20(–27) by (1.5–)4–8(–12) cm, apex acuminate, base cuneate to obtuse to rounded, often slightly unequally, margin entire, ± revolute; upper surface whitish puberulous and brownish strigillose on the whole surface or only on the main veins or midrib, or glabrous; lower surface whitish puberulous and brown hirtellous on the whole surface or only on the main veins, the hairs all or partly uncinate, or (becoming) glabrous, smooth; lateral veins 6–12 pairs, tertiary venation towards the margin (obliquely) scalariform or largely reticulate, slightly prominent to almost flat; petiole 0.8–3 cm long, 1–2 mm thick, brown (sub)hirsute or also whitish puberulous, the epidermis persistent; stipules fully amplexicaul, 1.5–5(–9) cm long, (sparsely) brown (sub)hirsute to hirtellous to strigillose, the hairs with ± swollen bases and some uncinate, or also whitish puberulous, caducous. *Staminate inflorescences* axillary or cauliflorous on slender leafy branchlets, solitary; peduncle 2.5–6 cm long, brown hirtellous, also white puberulous; head narrowly ellipsoid to cylindrical to spicate, 1.5–5.5 by 0.9–1.2 cm; perianth tubular 0.7–1 mm long, the apex 2-lobed, minutely puberulous; stamen 1–1.3 mm long, anther 0.2–0.3 mm long; interfloral bracts absent. *Pistillate inflorescences* axillary, ramiflorous or cauliflorous on slender leafy branchlets, solitary; peduncle 1.5–6.5(–10) cm long, brown hirtellous to (retrorsely) strigillose and most hairs uncinate or also whitish puberulous; head cylindrical to subobovoid; perianth tubular, brown puberulous to subhispidulous, the apex truncate to convex; stigma simple; interfloral bracts absent. *Infructescences* narrowly ellipsoid to ellipsoid to ovoid (to subglobose), 15–35 by 10–15 cm, covered with 1.5–3 mm long, cylindrical to conical to pyramidal apices of the perianths; fruits ellipsoid, c. 3 cm long.

Distribution — Thailand; in *Malesia*: Sumatra, Malay Peninsula, Borneo, Java, Celebes, Moluccas (Sula Islands, Ambon), New Guinea (western).

Notes — 1. Several collections from the Malay Peninsula and Sumatra have been included in var. *silvestris*, distinct by the odourless and almost tasteless infructescences as well as by the colour of withering leaves (see Jarrett 1959). The material tends to be glabrous or glabrescent (losing uncinate hairs on the lamina, mainly on the midrib beneath and the margin). Corner (1939: 75) regarded the variety as the wild form of the species.

2. As explained by Corner in much detail (1939: 56–81), *Radermachia integra* is based on different elements. The type sheet comprises material with hirsute leafy twigs of the present species together with material without such indumentum which belongs to *A. heterophyllus*, the Jack. This has created considerable (nomenclatural) confusion, partly because of moving in renaming (as *Sitodium macrocarpon*) and in describing the accent from the first element to the second (Thunberg, Kongl. Svenska Vetensk. Acad. Handl. 37 (1779)). The element on the type sheet that should function as the type for *A. integer* was clearly indicated by (Svedelius and) Corner (1939: plates 1 and 2).

10. *Artocarpus kemando* Miq.

Artocarpus kemando Miq., Fl. Ned. Ind., Eerste Bijv. (1861) 418; Becc., For. Borneo (1902) 628; Ridl., Fl. Malay Penins. 5 (1925) 335; Merr., Pl. Elmer. Born. (1929) 46; Burkhill, Dict. Econ. Prod. Malay Penins. (1935) 256; Corner, Gard. Bull. Singapore 10 (1939) 282; Wayside Trees Malaya (1940) 656; F.G. Browne, For. Trees Sar. & Brunei (1955) 353; F.M. Jarrett, J. Arnold Arbor. 40 (1959) 354; Kochummen, Tree Fl. Malaya 3 (1978) 129, t. 5; Corner, Wayside Trees Malaya ed. 3, 2 (1988) 519; Kochummen, Tree Fl. Sabah & Sarawak 3 (2000) 200.

Artocarpus maingayi King in Hook.f., Fl. Brit. India 5 (1888) 542; Ann. Roy. Bot. Gard. (Calcutta) 2 (1889) 11, t. 8A; Ridl., Fl. Malay Penins. 3 (1924) 354; Corner, Gard. Bull. Singapore 10 (1939) 282; Wayside Trees Malaya (1940) 657; F.M. Jarrett, J. Arnold Arbor. 40 (1959) 357; Kochummen, Tree Fl. Malaya 3 (1978) 131, t. 5; Corner, Wayside Trees Malaya ed. 3, 2 (1988) 520.

Artocarpus brunneifolia S. Moore, J. Bot. 63, Suppl. (1925) 112.

Artocarpus sumatranaus F.M. Jarrett, J. Arnold Arbor. 40 (1959) 353.

Tree up to 35 m tall, evergreen, with (short) buttresses. Leafy twigs 2–3 mm thick, brown (to whitish) appressedly puberulous to appressed-hispidulous or to hirtellous (with part of the hairs uncinate and ± retrorse), scabridulous, drying (dark) brown; lenticels scattered. Leaves spirally arranged; lamina coriaceous, entire, elliptic to subobovate, (3–)7–15(–18) by (1.5–)3–10 cm, apex short-acuminate to obtuse or to rounded, base cuneate to rounded, margin entire, ± revolute; upper surface (sparsely) minutely whitish puberulous, on the midrib the hairs often longer (and brownish), or subglabrous, smooth; lower surface (sparsely) minutely whitish puberulous, on the main veins the hairs longer and brownish, smooth; lateral veins 8–15 pairs, usually unbranched, tertiary venation scalariform, slightly prominent; petiole 1–3 cm long, 1–2 mm thick, brownish appressedly puberulous, the epidermis persistent; stipules fully amplexicaul, 0.7–2 cm long, brown appressedly puberulous to strigillose, caducous. *Staminate infl-*

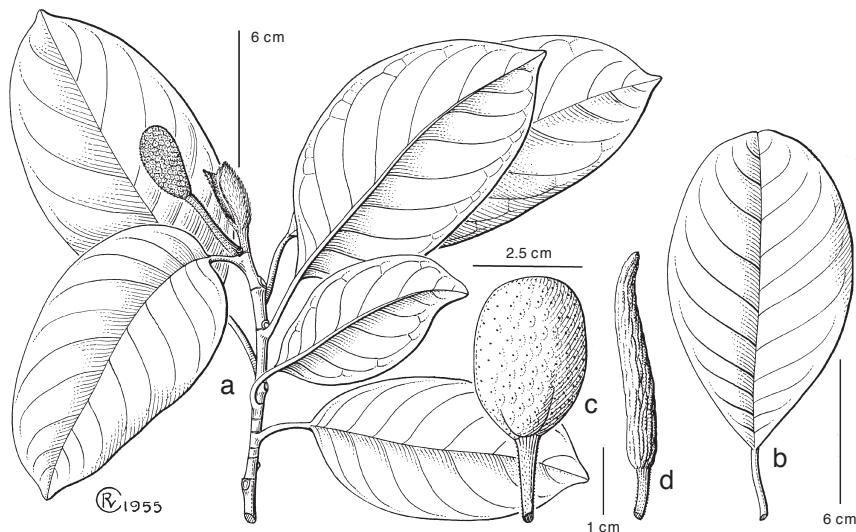


Fig. 19. *Artocarpus kemando* Miq. a. Leafy twig with pistillate inflorescence; b. leaf; c. pistillate inflorescence; d. staminate inflorescence (a–c: no. 90 E IO 755; d: FRI bb 19850).

rescences axillary, solitary (or in pairs) peduncle (0.3–)0.7–1.5(–2) cm long, brown velutinous or appressedly puberulous; head cylindrical to spicate, 2–4 by 0.3–0.5 cm, (irregularly) sulcate, occasionally subtended by some 0.5–1 mm long scale-like bracts; perianth tubular c. 0.4 mm long, the apex 2-lobed, minutely puberulous; stamen 0.4–0.5 mm long, anther c. 0.2 mm long; interfloral bracts absent. *Pistillate inflorescences* axillary, solitary (or in pairs); peduncle 1–4 or 0.3–0.8 cm long, brown velutinous; head ellipsoid to ovoid, occasionally subtended by some 0.5–1 mm long scale-like bracts; perianth tubular, densely brown puberulous, the apex flat to concave; stigma simple; interfloral bracts absent. *Infructescences* ellipsoid to subglobose, up to 4 by 2.5 cm, covered with c. 2 mm long (concave) cushion-shaped (or pyramidate to 3 mm long) apices of the perianths; fruits ellipsoid, c. 0.8 cm long. — **Fig. 19.**

Distribution — Thailand; in *Malesia*: Sumatra, Malay Peninsula, Borneo.

Habitat — Evergreen forest at low altitudes, often in swampy places.

Notes — 1. The differences between *A. kemando* and *A. maingayi* as recognised by Jarrett (1959) are so small that uniting them seems to be justified. Material ranked under the latter always has peduncles shorter than 1 cm and the lamina tends to have a rounded apex.

2. The differences between *A. kemando* and *A. sumatranaus* are not of such importance that recognition of the latter as species is justified.

11. *Artocarpus lanceifolius* Roxb.

Artocarpus lanceifolius Roxb. [Hort. Bengal. (1814) 103, nomen] Fl. Ind., ed. Carey 3 (1832) 527, as ‘*lanceofolia*’ and ‘*lanceaeifolia*’, respectively; Wight, Icon. Pl. Ind. Orient. 2 (1843) t. 679; Trécul, Ann. Sci. Nat., Bot. sér. 3, 8 (1847) 122; King in Hook.f., Fl. Brit. Ind. 5 (1888) 543; Ann. Roy. Bot. Gard. (Calcutta) 2 (1889) 13, t. 11; Renner, Bot. Jahrb. Syst. 39 (1907) 366; Ridl., Fl. Malay Penins. 3 (1924) 354; Foxworthy, Malayan Forest Rec. 3 (1927) 128, with plates; Burkhill, Dict. Econ. Prod. Malay Penins. (1935) 256; Corner, Wayside Trees Malaya (1940) 656, t. 197; F.M. Jarrett, J. Arnold Arbor. 40 (1959) 140; Kochummen, Tree Fl. Malaya 3 (1978) 129, t. 5; Corner, Wayside Trees Malaya ed. 3, 2 (1988) 519, t. 157, 160; Kochummen, Tree Fl. Sabah & Sarawak 3 (2000) 2001.

Artocarpus clementis Merr., J. Straits Branch Roy. Asiatic Soc. 85 (1922) 164. — *Artocarpus lanceifolius* Roxb. subsp. *clementis* (Merr.) F.M. Jarrett, J. Arnold Arbor. 40 (1959) 142.

Tree up to 35 m tall, evergreen. Leafy twigs 6–8 mm thick, ± densely brown (to whitish) appressedly puberulous, drying brown; lenticels scattered. Leaves spirally arranged; lamina coriaceous, entire, elliptic, sometimes 3-lobed to pinnately incised, 10–40 by 3.5–17(–30) cm, apex short-acuminate, base cuneate to obtuse, margin entire to repand (to sublobate); upper surface glabrous, smooth; lower surface glabrous or sparsely whitish appressedly puberulous on the midrib, smooth; lateral veins 9–14 pairs, mostly some of them forked away from the margin or branched venation scalariform, slightly prominent; petiole 1–3(–5.5) cm long, 2–5 mm thick, minutely whitish appressedly puberulous, the epidermis persistent; stipules fully amplexicaul, 1–4.5 cm long, brown appressedly puberulous, caducous. *Staminate inflorescences* axillary, solitary; peduncle 2–7 cm long, brown (to whitish) appressedly puberulous; head ellipsoid to subobovoid to narrowly elliptic to cylindrical, 3–6 by 1–1.5(–2) cm; perianth tubular c. 2 mm long, the apex 2-lobed, minutely puberulous to subglabrous;

stamen 3–3.5 mm long, anther c. 0.3 mm long; interfloral bracts peltate, the apical part 0.3–0.4 mm diam., radially appressedly puberulous. *Pistillate inflorescences* axillary, solitary; peduncle 2.5–7 cm long, densely brown (to whitish) appressedly puberulous; head subglobose; perianth tubular, brown puberulous, the apex ± convex; stigma bifid; interfloral bracts peltate, caducous or persistent, the apical part 0.3–0.4 mm diam., radially appressedly puberulous. *Infructescences* subglobose, 6–7 cm diam., sometimes ± lobed, covered with 3–4 mm long, cylindrical apices of the perianths; fruits ellipsoid, 1–1.5 cm long.

Distribution — Thailand; in *Malesia*: Sumatra, Malay Peninsula, Borneo (north-eastern).

Habitat — Evergreen forest at altitudes up to c. 1200 m.

Uses — The pulp around seeds is eaten by man.

Note — The material from Borneo, recognised by Jarrett (1959) as a distinct subspecies, differs slightly from that from Thailand, Sumatra, and the Malay Peninsula, in the usually more slender petioles and persistent interfloral bracts of the pistillate inflorescence.

12. *Artocarpus lowii* King

Artocarpus lowii King in Hook.f., Fl. Brit. India 5 (1888) 542; Ann. Roy. Bot. Gard. (Calcutta) 2 (1889) 10, t. 7A; Ridl., Fl. Malay Penins. 3 (1924) 353; Burkill, Dict. Econ. Prod. Malay Penins. (1935) 257; Corner, Gard. Bull. Singapore 10 (1939) 283; Wayside Trees Malaya (1940) 656; F.M. Jarrett, J. Arnold Arbor. 40 (1959) 339; Kochummen, Tree Fl. Malaya 3 (1978) 131; Corner, Wayside Trees Malaya ed. 3, 2 (1988) 519.

Tree up to 25 m tall, evergreen. *Leafy twigs* 3–6 mm thick, minutely whitish appressedly puberulous, smooth, drying blackish; lenticels scattered, few. *Leaves* spirally arranged; lamina (sub)coriaceous, entire, narrowly elliptic, 10–36(–55) by 4–13(–20) cm, apex short-acuminate to acute, base cuneate (to obtuse), often slightly unequally, margin entire to repand; upper surface (sub)glabrous, smooth; lower surface minutely whitish appressedly puberulous on the midrib, smooth; lateral veins 11–16 pairs, tertiary venation scalariform, slightly prominent; petiole 1.5–3.5 cm long, 1–2 mm thick, minutely whitish appressedly puberulous or also with sparse brown uncinate hairs, the epidermis persistent; stipules fully amplexicaul, 1–5(–8) cm long, minutely whitish appressedly puberulous, caducous. *Staminate inflorescences* axillary, solitary; peduncle c. 4 cm long, minutely whitish appressedly puberulous or also with brown (retrorse) uncinate hairs; head cylindrical to spicate or to subellipsoid, 2–2.5 by c. 0.5 cm; perianth tubular c. 0.8 mm long, the apex 2-lobed, minutely puberulous; stamen c. 1.5 mm long, anther c. 0.2 mm long; interfloral bracts absent. *Pistillate inflorescences* axillary, solitary; peduncle 3.5–5.5 cm long, minutely whitish (appressedly) puberulous or also with brown (retrorse) uncinate hairs; head ellipsoid to cylindrical; perianth tubular, minutely brownish puberulous, the apex convex; stigma simple; interfloral bracts absent. *Infructescences* cylindrical, up to 6.5 by 3.5 cm, covered with 1–2 mm long, pyramidal apices of the perianths; fruits ellipsoid, c. 0.7 (?) cm long.

Distribution — Sumatra (eastern), Malay Peninsula.

Habitat — Evergreen forest at low altitudes.

Uses — The milk sap is greasy and used as ointment.

13. *Artocarpus obtusus* F.M. Jarrett

Artocarpus obtusus F.M. Jarrett, Blumea 22 (1975) 410; Kochummen, Tree Fl. Sabah & Sarawak 3 (2000) 204.

Tree up to 35 m tall, base of trunk fluted, evergreen. *Leafy twigs* 3–6 mm thick, minutely whitish appressedly puberulous, smooth, drying blackish; lenticels scattered, few. *Leaves* spirally arranged; lamina coriaceous, entire, elliptic, 18–23 by 4–19 cm, apex rounded to obtuse, base rounded to obtuse (to subcordate), often slightly unequally, margin entire, ± revolute; both upper and lower surface (sub)glabrous and smooth; lateral veins 7–10 pairs, some of them branched or forked away from the margin, tertiary venation scalariform, flat; petiole 1–3.5 cm long, 2–3 mm thick, (sub)glabrous, the epidermis persistent; stipules fully amplexicaul, 1–4 cm long, minutely brownish to whitish appressedly puberulous, caducous. *Staminate inflorescences* axillary, solitary; peduncle 1.2–3.5 cm long, sparsely minutely whitish puberulous and also with brown uncinate hairs; head ovoid to conical, up to 2.5 by 1 cm; perianth tubular, c. 0.7 mm long, the apex 2-lobed, minutely puberulous; stamens immature; interfloral bracts absent. *Pistillate inflorescences* axillary, solitary; peduncle 3–7.5 cm long, minutely whitish puberulous and also with brown uncinate hairs; head ellipsoid; perianth tubular, brownish hispidulous, the apex convex; stigma bifid; flowers intermixed with interfloral processes. *Infructescences* ellipsoid, up to 8 by 6 cm, covered with 2–3 mm long, pyramidal apices of the perianths, intermixed with 6–10 mm long spine-like, slightly curved processes; fruits ellipsoid to subglobose, c. 1.5 cm long.

Distribution — Borneo (Sarawak).

Habitat — Evergreen forest at low altitudes.

Note — The species is characterised by (sub)glabrous lamina with rounded apex.

14. *Artocarpus odoratissimus* Blanco

Artocarpus odoratissimus Blanco, Fl. Filip. (1837) 671; Fern.-Vill., Nov. App. (1880) 203; Elmer, Leafl. Philipp. Bot. 2 (1909) 618; Wester, Philipp. Agric. Rev. 8 (1915) 108, t. 7d, 9b; Merr., J. Straits Branch Roy. Asiat. Soc. 76 (1917) 80; Sp. Blancoan. (1918) 124; Enum. Philipp. Flow. Pl. 2 (1923) 42; Wester, Philipp. Agric. Rev. 17 (1924) 24; Bull. Bur. Agric. Philipp. 39 (1924) 129, t. 15b, 32b; F.M. Jarrett, J. Arnold Arbor. 40 (1959) 147; F.S. dela Cruz, Prosea 2 (1991) 94, cum t.; Kochummen, Tree Fl. Sabah & Sarawak 3 (2000) 205.

Artocarpus tarap Becc., For. Borneo (1902) 626.

Artocarpus mutabilis Becc., For. Borneo (1902) 627.

Tree up to 25 m tall, evergreen. *Leafy twigs* 4–12 mm thick, ± densely brown strigillose to hispidulous, ± scabrous or hirsute, the long hairs with swollen bases, intermixed with much shorter hairs or not, drying brown; lenticels scattered. *Leaves* spirally arranged; lamina subcoriaceous (to chartaceous), entire, elliptic (to subrhombic) to obovate, 10–30(–55) by (6–)10–15(–30) cm, apex subacuminate to apiculate, base cuneate to subdecurrent, margin entire, repand, denticulate, or (unilaterally) lobate (when juvenile 3-lobed to pinnately incised with 1 or 2 pairs of lateral lobes); upper surface brownish hispidulous, on the main veins to strigillose, or hirtellous, ± scabrous; lower surface brownish (sub)hispidulous to puberulous, on the main veins to strigillose, or hirtellous, scabridulous; lateral veins 13–20 pairs, often branched or forked

away from the margin, tertiary venation scalariform, prominent; petiole (1.5–)2–3 cm long, 3–4 mm thick, brown strigillose (to hirtellous), or hirsute, the epidermis persistent; stipules 1–5(–8) cm, brown strigillose to subhirtellous or to strigose, or hirsute, caducous. *Staminate inflorescences* axillary, solitary; peduncle (2.5–)3–13 cm long, brown appressedly puberulous to hispidulous or hirtellous to subhirsute, ± scabrous; head ellipsoid to obovoid to clavate, 4–9 by 2.5–3.5 cm; perianth tubular c. 1.8 mm long, the apex 2-lobed, minutely puberulous; stamen c. 2 mm long, anther 0.1–0.2 mm long; interfloral bracts peltate, the apical part 0.3–0.4 mm diam., yellowish puberulous. *Pistillate inflorescences* axillary, solitary; peduncle 5–14 cm long, densely brown appressedly puberulous to hispidulous, or hirtellous to subhirsute, ± scabrous; head ellipsoid to subglobose; perianth tubular, hispidulous or hispid, the apex ± convex; stigma simple; interfloral bracts peltate, the apical part 0.3–0.4 mm diam., yellowish puberulous. *Infructescences* subglobose, 8–15 cm diam., sometimes ± lobed, fruit-containing part 5.5–12 cm diam., covered with 8–12 mm long cylindrical apices of the perianths; fruits ellipsoid, c. 1 cm long.

Distribution — Borneo, Philippines (Mindoro, Mindanao, Basilan, Sulu Archipelago; see note 2).

Notes — 1. Two forms can be recognised: one with short ± appressed hairs and the other with long ± patent hairs with swollen bases, hirsute on the leafy twigs, petioles, and stipules and hirtellous on the lamina and the hairs on the pistillate perianth longer. Only one of the collections examined, *W. Meijer 1851*, from Tarakan, is more or less intermediate. The latter form is indicated on some labels as subsp. *barbatum* by Jarrett, an unpublished name.

2. According to Jarrett (1959) the species might have been introduced to the Philippines from Borneo.

15. *Artocarpus rigidus* Blume

Artocarpus rigidus Blume, Bijdr. (1825) 482; Trécul, Ann. Sci. Nat., Bot. sér. 3, 8 (1847) 114; Miq. in Zoll., Syst. Verz. 2 (1854) 89, 95; Miq., Fl. Ned. Ind. 1, 2 (1859) 286; Fl. Ned. Ind., Eerste Bijv. (1861) 418; Ann. Mus. Bot. Lugduno-Batavi 3 (1867) 211; King in Hook.f., Fl. Brit. India 5 (1888) 540; Ann. Roy. Bot. Gard. (Calcutta) 2 (1889) 8, t. 3; Koord. & Valeton, Bijdr. Boomsoort. Java 11 (1906) 17; Koord., Exkurs.-Fl. Java 2 (1912) 93; Ridl., Fl. Malay Penins. 3 (1924) 352; K. Heyne, Nutt. Pl. Ned.-Ind. (1927) 564; Burkill, Dict. Econ. Prod. Malay Penins. (1935) 258; Corner, Wayside Trees Malaya (1940) 657, t. 198, 199; F.G. Browne, For. Trees Sar. & Brunei (1955) 353; F.M. Jarrett, J. Arnold Arbor. 40 (1959) 150; Kochummen, Tree Fl. Malaya 3 (1978) 131, t. 6; Corner, Wayside Trees Malaya ed. 3, 2 (1988) 521, t. 157, 163, 164; Kochummen, Tree Fl. Sabah & Sarawak 3 (2000) 208, t. 5; B. Seibert & P.C.M. Jansen, Prosea 2 (1991) 81, cum t.

Artocarpus echinata Roxb., [Hort. Bengal. (1814) 66, nomen] Fl. Ind., ed. Carey 3 (1832) 527; Wight, Icon Pl. Ind. Orient. 2 (1843) t. 680; Trécul, Ann. Sci. Nat., Bot. sér. 3, 8 (1847) 113.

Artocarpus cuspidatus Griff., Notul. Pl. Asiat. 4 (1854) 400.

Artocarpus kertau Zoll. ex Miq. in Zoll., Syst. Verz. 2 (1854) 89, 95; Miq., Fl. Ned. Ind. 1, 2 (1859) 287; Koord., Exkurs.-Fl. Java 2 (1912) 95.

Artocarpus dimorphophylla Miq., Fl. Ned. Ind., Eerste Bijv. (1861) 417.

Artocarpus varians Miq., Fl. Ned. Ind., Eerste Bijv. (1861) 417.

Artocarpus chaplasha auct. non Roxb.: Gagnep., Fl. Indo-Chine 5 (1928) 735.

Tree up to 35 m tall, with buttresses, evergreen. *Leafy twigs* (1–)2–8 mm thick, ± densely brown strigillose, scabridulous, drying brown; lenticels scattered. *Leaves*

spirally arranged; lamina (sub)coriaceous, entire, elliptic to (sub)obovate, (3–)10–20(–30) by (1.5–)5–10(–15) cm (or pinnately lobed to parted and up to 55 by 35 cm), rounded to short-(sub)acuminate to apiculate, base obtuse to cuneate or to rounded, margin entire to repand (or crenate towards the apex), ± revolute; upper surface brownish puberulous to densely strigillose or to only (sparsely) strigillose on the midrib, smooth or scabridulous; lower surface brownish strigillose on the main veins to puberulous or to hispidulous on the smaller veins, smooth or ± scabrous; lateral veins (6–)10–20 pairs, none (or rarely one) branched or forked away from the margin, tertiary venation scalariform, ± prominent; petiole (0.5–)1–2(–2.5) cm long, 2–3 mm thick, brown strigillose, the epidermis persistent; stipules (0.5–)1–2(–4) cm, brown strigillose to strigose, caducous. *Staminate inflorescences* axillary, solitary; peduncle 0.2–1 cm long, brownish strigillose, ± scabrous; head obovoid to subglobose, 1.2–2 cm diam.; perianth tubular, c. 1.2 mm long, the apex 2-lobed, minutely puberulous; stamen c. 1.3 mm long, anther 0.1 mm long; interfloral bracts peltate, the apical part 0.2–0.3 mm diam., yellowish puberulous. *Pistillate inflorescences* axillary, solitary; peduncle 0.8–3(–4) cm long, brown strigillose, ± scabrous; head ellipsoid to subglobose (to depressed-globose); perianth tubular, hispidulous to muriculate, the apex ± convex; stigma simple; interfloral bracts peltate, the apical part 0.2–0.3 mm diam., yellowish puberulous. *Infructescences* subglobose, 4–9 cm diam., covered with 3–8 mm long, cylindrical apices of the perianths; fruits ellipsoid, 1.2–1.5 cm long. — **Fig. 18b–i.**

Distribution — Myanmar, Thailand; in *Malesia*: Sumatra, Malay Peninsula, Borneo, Java, Lesser Sunda Islands (Bali?).

Habitat — Evergreen forest at altitudes up to 700(–1000) m.

Note — This species is closely related to *A. hispidus*, under which the differences and relations to material and names in continental Asia are discussed.

16. *Artocarpus sarawakensis* F.M. Jarrett

Artocarpus sarawakensis F.M. Jarrett, Blumea 22 (1975) 410; Kochummen, Tree Fl. Sabah & Sarawak 3 (2000) 210.

Tree up to 25 m tall, evergreen. *Leafy twigs* 4–7 mm thick, ± densely brown hirsute (to substrigose), long hairs with a swollen base intermixed with minute whitish hairs or else densely brown puberulous, drying (dark) brown; lenticels scattered. *Leaves* spirally arranged; lamina coriaceous, entire, elliptic to subobovate, 25–45 by 14–25 cm, apex short-acuminate, base cuneate (to obtuse), margin repand; upper surface sparsely brown hirtellous on the midrib, glabrescent, smooth; lower surface whitish to brownish strigillose to appressedly puberulous on the main veins or also sparsely brown subhirsute on the midrib, scabridulous; lateral veins 12–20 pairs, some forked away from the margin, tertiary venation scalariform, slightly prominent; petiole 1–2.5 cm long, 2–5 mm thick, brown hirsute, the long hairs intermixed with minute whitish hairs, the epidermis persistent; stipules fully amplexicaul, 1–4(–6) cm long, brown to yellowish hirsute or hirtellous, caducous. *Staminate inflorescences* axillary, solitary; peduncle 3.5–8 cm long, brown hirsute to strigose, the long hairs intermixed with minute whitish hairs; head obovoid to subobvoid to cylindrical, 3–6 by 1–2.5 cm; perianth tubular c. 0.8 mm long, the apex 2-lobed, minutely puberulous to subglabrous; stamen c. 1.3

mm long, anther c. 0.1 mm long; interfloral bracts peltate, the apical part c. 0.2 mm diam., puberulous. *Pistillate inflorescences*: peduncle c. 5.5 cm long, brown hirsute to strigose, the long hairs intermixed with minute whitish hairs or brown subvelutinous and with retrorse uncinate hairs; head subglobose; perianth tubular, brown puberulous, the apex ± convex; stigma bifid; interfloral bracts peltate, the apical part c. 0.2 or c. 5 mm diam., puberulous (with hairs of similar or different length). *Infructescences* subglobose or ellipsoid, 3–5 cm diam., covered with cushion-shaped 2–3 mm long apices of the perianths; fruits ellipsoid, c. 1.3 cm long.

Distribution — Sumatra (Riau Province), Borneo (Sarawak).

Habitat — Evergreen forest at low altitudes.

Notes — 1. This species shows similarities to *A. lanceifolius*, particularly the large-leaved specimens from the Malay Peninsula, but differs in the presence of hairs on the lamina below and the ± patent (longer) hairs on the stipules.

2. The species also resembles *A. odoratissimus* from which it differs in the coriaceous lamina, smooth above and with a repand margin.

3. The single collection from Sumatra differs from the (five examined) collections from Sarawak in the absence of long hairs on the leafy twig, petiole, and midrib of the lamina lower surface. The hairs on the stipules are shorter and the dense short brown indumentum of the peduncle is intermixed with longer retrorse uncinate hairs. The apical parts of the peltate interfloral bracts are larger.

17. *Artocarpus sepicanus* Diels

Artocarpus sepicanus Diels, Bot. Jahrb. Syst. 67 (1935) 176; F.M. Jarrett, J. Arnold Arbor. 40 (1959) 362.

Tree up to 40 m tall, evergreen, sometimes with buttresses; bark flaking off. Leafy twigs 3–5 mm thick, brown, glabrous, drying dark brown to blackish; lenticels scattered. Leaves spirally arranged; lamina coriaceous, entire, elliptic to subobovate, (6–)10–25(–30) by (2.5–)5–10(–12) cm, apex short-acuminate, base subcordate to rounded, unequal, margin entire to repand; both surfaces glabrous, smooth; lateral veins 9–16 pairs, tertiary venation scalariform, almost flat; petiole 1–2.5 cm long, 1–2 mm thick, glabrous, the epidermis flaking off; stipules fully amplexicaul, 1–3 cm long, glabrous, caducous. *Staminate inflorescences* axillary, solitary; peduncle 1.5–3 cm long, glabrous; head cylindrical to spicate, 2–3 by 0.5–0.7 cm; perianth tubular c. 0.8 mm long, the apex 2-fid, minutely puberulous; stamen c. 1 mm long, anther c. 0.4 mm long; interfloral bracts peltate, the apical part 0.4–0.5(–1) mm diam., ciliolate. *Pistillate inflorescences* axillary, solitary; peduncle 2.5–4.5 cm long, glabrous; head cylindrical; perianth tubular, minutely puberulous, the apex convex; stigma bifid; interfloral bracts peltate, the apical part 0.4–0.5(–1) mm diam., ciliolate. *Infructescences* ellipsoid to subglobose, up to 4.5 by 1.5 cm, covered with 1–2 mm long cushion shaped apices of the perianths; fruits ellipsoid, c. 0.5 cm long.

Distribution — New Guinea.

Habitat — Evergreen forest at low altitudes.

Note — This species is characterised by the exfoliating epidermis of the petiole and the glabrous vegetative parts.

18. *Artocarpus sericicarpus* F.M. Jarrett

Artocarpus sericicarpus F.M. Jarrett, J. Arnold Arbor. 40 (1959) 350; Kochummen Tree Fl. Sabah & Sarawak 3 (2000) 196.

Artocarpus elasticus auct. non Blume: Fern.-Vill., Nov. App. (1880) 202; Staph., Kew Bull. (1894) 108; Wester, Philipp. Agric. Rev. 8 (1915) 109, t. 8a; Merr., Enum. Philipp. Flow. Pl. 2 (1923) 41; Wester, Bull. Bur. Agric. Philipp. 39 (1924) 78, t. 196, 32 c; W.H. Br., Useful Pl. Philipp. (1941) 463, f. 188.

Artocarpus blumei auct. non Trécul: S. Vidal, Revis. Pl. Vasc. Filip. (1886) 254; Elmer, Leafl. Philipp. Bot. 2 (1909) 613.

Tree up to 40 m tall, evergreen. *Leafy twigs* 10–20 mm thick, minutely brown to whitish appressedly puberulous and also brown strig(ill)ose to subhirsute, smooth, drying dark brown to blackish; lenticels in the upper part of the internode; scars of the stipules prominent. *Leaves* spirally arranged; lamina subcoriaceous, entire, elliptic, 20–40(–70) by 10–25(–50) cm, or when juvenile ± pinnately incised with 2 or 3 pairs of lobes, apex short-acuminated, base rounded to cuneate, margin entire to repand or lobate; upper surface sparsely brown hirtellous on the midrib, smooth; lower surface brownish puberulous to strigillose on the smaller veins to subhirsute on the main veins or midrib, usually scabridulous; lateral veins 10–16 pairs, most of them branched or forked away from the margin, tertiary venation scalariform, prominent; areoles usually bullate; petiole 2–7.5 cm long, 3–6 mm thick, minutely brownish appressedly puberulous and also brown hirtellous to subhirsute or strigillose, the epidermis persistent; stipules fully amplexicaul, 6–12 cm long, brown subhirsute to subvillous, caducous. *Staminate inflorescences* axillary, solitary; peduncle 3–10 cm long, brown appressedly puberulous; head cylindrical, 3.5–10 by 1.5–2 cm, sulcate, the grooves ± (spirally) twisted; perianth tubular c. 1.5 mm long, the apex 2-lobed, minutely puberulous; stamen c. 1.8 mm long, anther c. 0.4 mm long; interfloral bracts absent. *Pistillate inflorescences* axillary, solitary; peduncle 6–18 cm long, brown appressedly puberulous and hirtellous; head ellipsoid to cylindrical; perianth tubular, brownish appressedly puberulous, the apex convex; stigma simple, twisted; the flowers intermixed with 1–3.5 cm long filiform processes, these brown puberulous to strigillose hirtellous and thickened at the apex. *Infructescences* ellipsoid to cylindrical or to subglobose, up to (6–)8–12(–17) by 5.5(–10) cm, covered with 3–4 mm long conical apices of the perianths (hidden by the processes); fruits ellipsoid, c. 1 cm long.

Distribution — Borneo, Philippines (Luzon, Samar, Biliran, Negros, Mindanao), Celebes, Moluccas (Talaud and Sula Islands, Buru).

Habitat — Evergreen forest at low altitudes, sometimes up to c. 1000 m.

Note — This species is closely related to *A. elastica*, as discussed under the latter.

19. *Artocarpus tamaran* Becc.

Artocarpus tamaran Becc., For. Borneo (1902) 626; F.M. Jarrett, J. Arnold Arbor. 40 (1959) 352; Kochummen, Tree Fl. Sabah & Sarawak 3 (2000) 210.

Tree up to 40 m tall, evergreen, with buttresses. *Leafy twigs* 5–10 mm thick, whitish puberulous and brown hirsute to subvillous, smooth, drying dark brown to blackish; lenticels scattered. *Leaves* spirally arranged; lamina coriaceous, entire, elliptic to

narrowly elliptic to subovate, 20–35 by 11–17 cm, or when juvenile, up to c. 100 cm long, pinnately incised (down to the midrib), with up to 8 pairs of segments, the ‘rachis’ often narrowly winged, apex short-acuminate to subacute, base rounded to obtuse, margin entire to repand, ± revolute; upper surface (sub)glabrous, smooth; lower surface whitish puberulous on the veins and brown strig(ill)ose to hirtellous on the main veins, smooth; lateral veins (13–)18–24 pairs, rarely branched or forked away from the margin, slightly impressed above, tertiary venation scalariform, prominent; petiole 3.5–4 cm long, 2–3 mm thick, whitish puberulous and brown subhirsute, the epidermis persistent; stipules fully amplexicaul, 3–9 cm long, (dark) brown (sub)hirsute to subvillosus, caducous (or subpersistent). *Staminate inflorescences* axillary, solitary; peduncle 3.5–5.5 cm long, brown appressedly puberulous; head cylindrical, 6–7 by 1–1.5 cm, tuberculate with 2–3 mm high cushion shaped processes covered by dark brown hairs; perianth tubular c. 0.6 mm long, the apex 2-lobed, minutely puberulous; anther c. 0.2 mm long; interfloral bracts absent. *Pistillate inflorescences* axillary, solitary; peduncle 5.5–10 cm long, whitish puberulous and brown hirsute; head ellipsoid; perianth tubular brown puberulous to hispidulous, the apex convex; stigma simple; the flowers intermixed with 6–10 mm long filiform processes, these brown retrorsely puberulous to hispidulous. *Infructescences* ellipsoid, up to 10(–14) by 5(–8) cm, covered with 3–4 mm long conical to cushion shaped apices of the perianths, intermixed with elongate processes; fruits ellipsoid, c. 0.6 cm long.

Distribution — Borneo.

Habitat — Evergreen forest at low altitudes.

Uses — Cloth is made from bark.

Note — This species differs from *A. elasticus* and *A. sericicarpus*, e.g., in the more numerous lateral veins which are usually not branched or forked and the tuberculate surface of the staminate inflorescence.

20. *Artocarpus teijsmannii* Miq.

Artocarpus teijsmannii Miq., Fl. Ned. Ind., Eerste Bijv. (1861) 418; Boerl., Handl. Fl. Ned. Ind. 3 (1900) 333, 371; K. Heyne, Nutt. Pl. Ned.-Ind. (1927) 565; F.M. Jarrett, J. Arnold Arbor. 40 (1959) 341; Kochummen, Tree Fl. Malaya 3 (1978) 134, t. 6; Tree Fl. Sabah & Sarawak 3 (2000) 211.

Artocarpus peduncularis Kurz, J. Bot. 13 (1875) 331; King in Hook.f., Fl. Brit. India 5 (1888) 541; Ann. Roy. Bot. Gard. (Calcutta) 2 (1889) 10, t. 6; Becc., For. Borneo (1902) 632; Ridl., Fl. Malay Penins. 3 (1924) 353; Burkill, Dict. Econ. Prod. Malay Penins. (1935) 258; Corner, Gard. Bull. Singapore 10 (1939) 283; F.M. Jarrett, J. Arnold Arbor. 40 (1959) 341.

Tree up to 40 m tall, sometimes with buttresses, evergreen. *Leafy twigs* 3–8 mm thick, minutely whitish to brownish appressedly puberulous or glabrous, smooth, drying blackish to brown or to greyish; lenticels (very) few, scattered; scars of the stipules prominent. *Leaves* spirally arranged; lamina (sub)coriaceous, entire, elliptic to (sub)ovate, (5–)10–25(–40) by (3–)6–13(–17) cm, apex short-acuminate to acute or to obtuse, base cuneate to rounded (to subcordate), often slightly unequal, margin entire, often ± revolute; upper surface minutely whitish puberulous, the hairs slightly longer and appressed on the main veins, or glabrous, smooth; lower surface minutely whitish puberulous, the hairs slightly longer and appressed on the main veins, or glabrous,

smooth; lateral veins 6–16(–18) pairs, often branched or forked away from the margin, tertiary venation scalariform, almost flat; petiole (1–)2–5 cm long, (1–)2–3 mm thick, minutely whitish appressedly puberulous or glabrous, the epidermis persistent; stipules fully amplexicaul, 1–5(–8) cm long, whitish to brownish appressedly puberulous, towards the apex brownish subsericeous, or glabrous, caducous. *Staminate inflorescences* axillary, solitary; peduncle 2–8 cm long, minutely whitish appressedly puberulous or subglabrous; head spicate, 3.5–7.5 by 0.5–0.7(–0.9) cm; perianth tubular c. 1.5 mm long, the apex 2-lobed, minutely puberulous; stamen 1–2 mm long, anther c. 0.5 mm long; flowers intermixed with 1–2 mm long subulate processes or with peltate bracts, the apical part 0.2–0.3(–1) mm diameter. *Pistillate inflorescences* axillary, solitary; peduncle 3–10 cm long, minutely whitish (appressedly) puberulous or subglabrous; head cylindrical; perianth tubular, minutely brownish to whitish puberulous, the apex convex; stigma simple or bifid; flowers often intermixed with 0.3–0.6 mm long subulate processes. *Infructescences* cylindrical to clavate, up to 8.5 by 4.5 cm, covered with 1–2 mm long and pyramidal, or sometimes up to 6 mm long and subulate, apices of the perianths, (in some infructescences none, in others some or numerous) up to 6 mm long subulate processes; fruits ellipsoid, c. 0.7 (?) cm long.

Note — The species can be subdivided into two disjunct subspecies.

a. subsp. *teijsmannii*

Artocarpus peduncularis Kurz, J. Bot. 13 (1875) 331; King in Hook.f., Fl. Brit. India 5 (1888) 541; Ann. Roy. Bot. Gard. (Calcutta) 2 (1889) 10, t. 6; Becc., For. Borneo (1902) 632; Ridl., Fl. Malay Penins. 3 (1924) 353; Burkill, Dict. Econ. Prod. Malay Penins. (1935) 258; Corner, Gard. Bull. Singapore 10 (1939) 283; F.M. Jarrett, J. Arnold Arbor. 40 (1959) 341.

Leafy twigs, leaves, and stipules whitish to brownish minutely appressedly puberulous; stipules brown subsericeous or with a comose apex. *Peduncles* minutely puberulous. *Perianth of the pistillate flower* puberulous.

Distribution — India (Nicobar Islands), Thailand; in *Malesia*: Sumatra, Malay Peninsula, Borneo, Celebes, Moluccas (Ceram, Sula Islands), New Guinea (western).

Habitat — Evergreen forest at low altitudes, often in swampy areas.

Notes — 1. The minute hairs on both the upper and lower surface of the lamina and the brown subsericeous or comose apex of the stipules are characteristic for this subspecies.

2. Subulate processes (1–2 mm in length) are present in staminate inflorescences of some collections, but in those made in New Guinea the flowers are intermixed with peltate bracts. The occurrence of subulate interfloral processes is rather erratic in the pistillate inflorescences: they vary from totally absent to few scattered among the flowers or concentrated at the base of the head, or else may occur abundantly. The processes may be abundant on one or two inflorescences on a branch and totally absent on the others. The situation can be confusing if the apices of the perianths also become subulate. These subulate structures can be distinguished from the processes by the perforation at the top through which the style or stigma is protruding.

3. In most pistillate inflorescences the stigmas are simple, but some may be bifid. In others, such as *Moll BW 11572*, all stigmas are bifid.

b. subsp. *subglabrus* C.C. Berg

Artocarpus teijsmannii Miq. subsp. *subglabrus* C.C. Berg, Blumea 50 (2005) 543.

Ficus ralumensis K. Schum., Notizbl. Bot. Gart. Berlin-Dahlem 2 (1898) 112; Fl. Schutzgeb. Südsee (1901) 282; Diels, Bot. Jahrb. Syst. 67 (1935) 231; Corner, Gard. Bull. Singapore 21 (1965) 99; C.C. Berg, Flora Malesiana, Ser. I, 17-2 (2005) 702.

Leafy twigs, leaves, and stipules glabrous. *Peduncles* glabrous or with few uncinate hairs. *Perianth of the pistillate flower* puberulous only at the apex.

Distribution — Solomon Islands (Guadalcanal); in *Malesia*: New Guinea (Bismarck Archipelago, Morobe Province).

Habitat — Evergreen forest at low altitudes.

Note — Because only two fertile collections are known, it is not certain whether the variation in the presence of interfloral bracts and processes as described for subsp. *teijsmannii* applies to this subspecies; the only collection with a staminate inflorescence has interfloral bracts, of which those at the base of the head are large, c. 1 mm diam. and the pistillate inflorescences does not have processes among the pyramidal perianth apices. Both simple (in the collection from the Solomon Islands) and bifid stigmas (in New Guinea) are found.

21. *Artocarpus treculianus* Elmer

Artocarpus treculianus Elmer, Leafl. Philipp. Bot. 2 (1909) 617; Merr., Enum. Philipp. Flow. Pl. 2 (1923) 43; F.M. Jarrett, J. Arnold Arbor. 40 (1959) 302.

Artocarpus nigrescens Elmer, Leafl. Philipp. Bot. 2 (1909) 614; Merr., Enum. Philipp. Flow. Pl. 2 (1923) 42.

Artocarpus ovatifolia Merr., Philipp. J. Sci., Bot. 9 (1914) 268; Enum. Philipp. Flow. Pl. 2 (1923) 42.

Artocarpus ovatifolia Merr. var. *dolichostachys* Merr., Enum. Philipp. Flow. Pl. 2 (1923) 43.

Artocarpus communis auct. non J.R. & G. Forst.: Merr., Philipp. J. Sci., Bot. 3 (1908) 401.

Tree up to 15(–40?) m tall, with small buttresses, evergreen. *Leafy twigs* 4–10 mm thick, whitish minutely appressedly puberulous to strigillose, drying dark brown to blackish; lenticels scattered. *Leaves* spirally arranged; lamina (sub)coriaceous, entire, elliptic to subrhombic, 15–28 by 9–17 cm, or pinnatifid, with 1–4 pairs of lateral lobes, 18–28 by 11–24 cm, base cuneate to rounded, apex subacute to acute, margin subentire to repand; upper surface white appressedly puberulous on the main veins or only at the base of the midrib, sometimes also sparsely hirtellous on the midrib, smooth; lower surface whitish puberulous on the main veins, scabridulous; lateral veins 10–13 pairs, at least the lower ones mostly branched or forked away from the margin, tertiary venation scalariform, almost flat; petiole (2–)3–8 cm long, 1.5–3 mm thick, whitish appressedly puberulous, the long hairs intermixed with much shorter hairs; stipules 6–18 cm long, whitish appressedly puberulous, caducous. *Staminate inflorescences* axillary, solitary; peduncle 1.2–2.5 cm long, whitish appressedly puberulous; head spicate, 1–21 cm long, 0.4–0.7 cm diam.; perianth tubular, 1–1.8 mm long, the apex 2-lobed, minutely puberulous; stamen 1.5–2.8 mm long, anther 0.3–0.5 mm long; interfloral bracts absent. *Pistillate inflorescences* axillary, solitary; peduncle 1.5–5 cm long, whitish appressedly puberulous; head ellipsoid; perianth tubular brown to yellow-

ish puberulous to muriculate, the apex convex; stigma bifid; interfloral bracts absent. *Infructescences* ellipsoid, up to 7 by 5 cm, often irregularly shaped, covered with c. 3 mm long cylindrical apices of the perianths; fruits ellipsoid, c. 1.2 cm long.

Distribution — Philippines (widespread).

Habitat — (Semi-)evergreen forest at altitudes up to c. 800 m.

Notes — 1. Jarrett (1959: 305) described several staminate collections deviating in larger anthers (0.6–0.8 mm long) and/or the presence of interfloral subulate processes (indicated as sterile flowers); these anomalies have not been found in the material examined for the present treatment. The discrepancies may be caused by mixed collections as the size of the anthers matches that of *A. altilis* which also has interfloral bracts or processes, see note under *A. altilis* (p. 86).

2. Collection *Elmer 12468* differs from the other collections by lacking the branched lateral veins.

3. The majority of the collections have entire laminas but some have pinnately incised ones which resemble those of *A. altilis* and apparently also occur in adult specimens.

4. This species shows similarities to *A. teijsmannii* and is probably more closely related to the latter than to *A. altilis*, as suggested by Jarrett (1959).

Subgenus PSEUDOJACA

Artocarpus J. & G. Forst. subg. *Pseudojaca* Trécul, Ann. Sci. Nat., Bot. sér. 3, 8 (1847) 117; F.M. Jarrett, J. Arnold Arbor. 41 (1960) 73. — *Artocarpus* J. & G. Forst. sect. *Pseudojaca* (Trécul) Renner, Bot. Jahrb. Syst. 39 (1907) 368.

Artocarpus J. & G. Forst. subg. *Pseudojaca* Trécul sect. *Pseudojaca* (Trécul) Renner ser. *Peltati* F.M. Jarrett, J. Arnold Arbor. 41 (1960) 83.

Artocarpus J. & G. Forst. subg. *Pseudojaca* Trécul sect. *Pseudojaca* (Trécul) Renner ser. *Clavati* F.M. Jarrett, J. Arnold Arbor. 41 (1960) 130.

Artocarpus J. & G. Forst. subg. *Pseudojaca* Trécul sect. *Glandulifolium* F.M. Jarrett, J. Arnold Arbor. 41 (1960) 134.

Leaves alternate and distichous, entire (when adult); lamina with glands on the margin, on the midrib above the basal lateral veins, or in their axils and the axils of other lateral veins; stipules lateral, short, 0.3–0.5(–1) cm long. *Inflorescences* axillary (or staminate ones on short-shoots on the older wood), interfloral bracts peltate (or cylindrical or spatulate). *Staminate flowers* with 2–4, partly connate (or free) tepals. *Free parts of apices of pistillate flowers* mostly not prominent, in some species (sometimes) forming low pyramidate hardened processes.

DISTRIBUTION

The subgenus is represented by up to 21 species in an area ranging from Sri Lanka to the Solomon Islands and Australia, mostly as elements of evergreen forest. The subgenus is concentrated in the western Malesian region and the adjacent part of the Asian mainland. The most widespread species is *A. lacucha*, from India and China to the Solomon Islands. Fourteen species are found in the Malesian region, the others in China and Indochina. Four of them have been treated by Jarrett (1960), four from China

(Sichuan and Yunnan) were added (see Zhekun & Gilbert, Fl. China 5 (2003) 32–33), and one is described from Thailand (see below).

MORPHOLOGY

Habit — Several species show intermittent growth with differences in the colour and indumentum of the current growth compared to that of the previous season. In some species the transition is marked by a concentration of the stipular scars which formed terminal buds. In some species, as *A. tomentosulus*, lateral buds are also formed. Intermittent growth is associated with deciduousness, at least in *A. lacucha*. The lamina of species with intermittent growth is subcoriaceous to chartaceous and the margin is sometimes (in *A. lacucha* nearly always) denticulate towards the apex or (only) at the acumen.

Indumentum — Uncinate hairs are often present, especially in the juvenile state. They can be consistently present on some parts of the plant and may then have diagnostic value.

The following groups of species can be recognised based on the presence, colour, and denseness of the indumentum of twigs and laminas.

- 1) Hairs present in the areoles, and not only on the venation: *A. fulvicortex*, *A. glaucus* (in Malesia and Australia), *A. hypargyreus* Hance (China), *A. styracifolius* Pierre (China and Indochina), and *A. thailandicus* C.C. Berg (Blumea 50 (2005) 531 from northern Thailand, and probably also two or three of the more recently described Chinese species (see above)).
- 2) Hairs predominantly brown(ish) and usually dense on various parts: *A. albobrunneus* (?), *A. fulvicortex*, *A. lacucha*, *A. longifolius*, *A. subrotundifolius*, and *A. tomentosulus*. This group has intermittent growth (and can be deciduous).
- 3) Hairs predominantly whitish and sparse on leafy twigs and leaves (except for the hairy form of *A. gomezianus* in India and Sri Lanka): *A. gomezianus*, *A. nitidus*, *A. reticulatus*, *A. rubrovenius*, and *A. vrieseanus*. This group probably consists of evergreen species without intermittent growth.

Leaves — The leaves are occasionally opposite (in *A. lacucha*).

Lamina — The base of the lamina is sometimes ‘peltate’ with a narrow strip of laminar tissue connecting both sides of the base over the apex of the petiole. This phenomenon is found in several species. The base of the lamina is often ± unequal, probably correlated with the distichous arrangement of the leaves.

Glands — The glandular-crenate margin of the lamina of *A. altissimus* is highly peculiar, as such glands are not known in other Moraceae. Almost as peculiar are the (waxy?) glandular spots on the midrib above the base and in the axils of the lateral veins of the lamina lower surface. The glands on the midrib can be short or long, extending to the next lateral vein. They are found in all species with the exception of *A. altissimus*, but are not always manifest; more in the species with hairy leaves than in those with subglabrous leaves. They are in their positions quite similar to those in numerous *Ficus* species.

Stipules — The stipules are mostly 0.3–0.5 cm long, in some species on opening shoots up to 1 cm long, and then often subpersistent. Stipules cover terminal and lateral (resting) buds.

Bracts — Interfloral bracts are mostly peltate with short stalks. They are (nearly) always caducous though sometimes persistent in pistillate inflorescences of some species; shedding is not a consistent character. In *A. styracifolius* Pierre (China and Indochina) the interfloral bracts are represented by cylindrical processes up to c. 5 mm long and ± curved in pistillate inflorescences (in fruit). The bracts of staminate inflorescences of *A. petelotii* Gagnep. (China and Indochina) are spathulate (according to Jarrett 1960: 130).

In several species, the bracts at the base of the head are basally attached instead of peltate and somewhat larger than the others.

Pistillate flowers — The apices of pistillate flowers usually form (hairy) rims which surround the emerging stigma and persist in fruit. In some species the apices become low and hardened pyramidal processes: always in *A. reticulatus* and sometimes in *A. lacucha*.

DELIMITATION AND SUBDIVISION

This subgenus clearly differs from subg. *Artocarpus* in the distichous arrangement of the leaves, the short(er than 1 cm) non-amplexicaul (lateral) stipules, the presence of glands and glandular spots, and the mostly smooth surface of the infructescence.

The three groups of species which can be recognised by their indumentum and the highly peculiar *A. altissimus* (sect. *Glandulifolium* F.M. Jarrett) could be regarded as natural subdivisions. It is doubtful whether the separation of species into a group with peltate interfloral bracts (ser. *Peltati*) and a group with non-peltate ones (ser. *Clavati*) reflects natural alliances since modified peltate bracts (cylindrical processes) also occur in subg. *Artocarpus* and in the African genus *Treculia*

KEY TO THE SPECIES OF SUBGENUS PSEUDOJACA

- 1a. Margin of lamina with glands. — Sumatra, Borneo **2. A. altissimus**
- b. Margin of lamina without glands 2
- 2a. Lower surface of lamina hairy in the areoles, ± glaucous when fresh 3
- b. Lower surface of lamina hairy only on the venation 4
- 3a. Indumentum on veins of lower surface of lamina whitish. — Sumatra, Malay Peninsula, Borneo, Java, Lesser Sunda Islands **4. A. glaucus**
- b. Indumentum on veins of lower surface of lamina brown. — Sumatra, Malay Peninsula **3. A. fulvicortex**
- 4a. Lamina ± densely hairy on midrib above and venation beneath 5
- b. Lamina sparsely hairy to subglabrous on midrib above and venation beneath 10

- 5a. Petiole 0.2–0.8 cm long and (2–)3–4 mm thick; indumentum brown. — Borneo **7. A. longifolius**
- b. Petiole at least 0.8 cm long, or if shorter, then c. 1.5 cm thick and the indumentum whitish (and occurring in New Guinea) 6
- 6a. Lateral veins 6–10 pairs 7
- b. Lateral veins 10–20 pairs 8
- 7a. Apex of the lamina rounded, leafy twigs for the greater part sparsely hairy, petiole 0.8–1.5 cm long. — Borneo **1. A. albobrunneus**
- b. Apex of the lamina acuminate, or if rounded, then the leafy twigs densely hairy and the petiole usually 3–7 cm long. — Widespread **6. A. lacucha**
- 8a. Lateral veins for the greater part furcate far from the margin or branched. — Philippines **11. A. subrotundifolius**
- b. Lateral veins not or sometimes one or few furcate far from the margin 9
- 9a. Epidermis of petiole flaking off; margin of lamina entire. — Borneo **12. A. tomentosulus**
- b. Epidermis of petiole (usually) persistent; margin of the lamina (usually) denticulate towards the apex, at least at the acumen. — Widespread **6. A. lacucha**
- 10a. Lamina ± scabrous beneath; base of lamina often minutely auriculate. — Celebes, Moluccas **9. A. reticulatus**
- b. Lamina (usually) smooth beneath; base of lamina never auriculate 11
- 11a. Lateral veins 5–10(–11) pairs 12
- b. Lateral veins (8–)10–20 pairs 14
- 12a. Head of staminate inflorescence ellipsoid to obovoid, 1–1.5(–2) cm diam. and infructescence to c. 8 cm diameter. — Philippines **10. A. rubrovenius**
- b. Head of staminate inflorescence subglobose, or if ellipsoid to obovoid, then 0.2–0.5 cm diam. and infructescence to c. 4.5 cm diameter. — Philippines 13
- 13a. Peduncle of staminate inflorescence 1.2–1.7 cm long, peduncle of pistillate inflorescence (in fruit) 2.5–5.5 cm long. — Celebes, Moluccas .. **13. A. vrieseanus**
- b. Peduncle of staminate inflorescence 0.1–0.4 cm long; peduncle of pistillate inflorescence (in fruit) 0.1–0.5(–2.5) cm long. — Sumatra, Malay Peninsula, Borneo, Philippines, New Guinea **8. A. nitidus**
- 14a. Peduncle of staminate inflorescence 0.5–1.7 cm long and peduncle of pistillate inflorescence (in fruit) 1.5–4.5 cm long. — Sumatra, Malay Peninsula, Java, Philippines **5. A. gomezianus**
- b. Peduncle of staminate inflorescence 0.1–4 cm long and peduncle of pistillate inflorescence (in fruit) usually 0.1–0.5 cm long (or in Borneo up to 2.5 cm long, but then the epidermis of the petiole flaking off instead of persistent). — Sumatra, Malay Peninsula, Borneo, Philippines, New Guinea **8. A. nitidus**

1. Artocarpus albobrunneus C.C. Berg

Artocarpus albobrunneus C.C. Berg, Blumea 50 (2005) 541.

Tree, evergreen (?). Leafy twigs 2–3 mm thick, sparsely brown minutely puberulous, more densely hairy towards the base of the petiole, smooth, drying dark brown to blackish. Leaves distichous; lamina coriaceous, elliptic to subobovate, 6–13 by

2.5–6.5 cm, apex rounded, base rounded to cordulate, slightly unequal, margin entire, ± revolute (towards the base); upper surface brownish minutely puberulous mainly on the midrib, smooth; lower surface minutely brownish puberulous on the main veins to whitish puberulous on the smaller veins, smooth; lateral veins 7–9(–10) pairs, none of them forked away from the margin, tertiary venation scalariform, (and also the smaller veins) prominent; petiole 0.8–1.5 cm long, 1–1.5 mm thick, densely minutely brown puberulous, the epidermis flaking off; stipules lateral, 0.2–0.4 cm long, brownish puberulous, caducous. *Staminate inflorescences* not seen. *Pistillate inflorescences* axillary, solitary; (in fruit) peduncle 1.5–2.5 cm long, densely brownish puberulous; head subglobose (?); stigma simple; interfloral bracts peltate, the apical part c. 0.2 mm diam., puberulous, persistent in the central part of the infructescence, largely caducous in the peripheral part. *Infructescences* discoid and strongly lobed around the fruits, the central part whitish velutinous, the peripheral part (lobes) red-brown velutinous.

Distribution — Borneo (E Kalimantan).

Habitat — Evergreen forest at low altitudes.

Note — This species is unusual among the species of *Artocarpus* subg. *Pseudojaca* in the coriaceous lamina that dries greenish. The different colour of parts of the infructescence are curious, — a way to create contrast colours to attract dispersers?

2. *Artocarpus altissimus* (Miq.) J.J. Sm.

Artocarpus altissimus (Miq.) J.J. Sm., Icon. Bogor. 3 (1907) 79, t. 233; [Teijsm. & Binn., Cat. Hort. Bot. Bogor. (1866) 85, nomen]; Douglas & Baas-Beck., Bull. Jard. Bot. Buitenzorg III, 17 (1947) 197, 291; F.M. Jarrett, J. Arnold Arbor. 41 (1960) 135. — *Morus* ? *altissima* Miq., Fl. Ned. Ind., Eerste Bijv. (1861) 415.

Grewia ? *subcordata* Miq., Fl. Ned. Ind., Eerste Bijv. (1861) 404; Burret, Notizbl. Bot. Gart. Berlin-Dahlem 9 (1926) 736.

Tree up to 30 m tall, sometimes with buttresses, deciduous. *Leafy twigs* 1.5–3 mm thick, brownish to whitish puberulous, sometimes partly with retrorse uncinate hairs, smooth, drying dark brown to blackish. *Leaves* distichous; lamina subcoriaceous to chartaceous, entire or 3–5-lobate when juvenile, ovate to subovate to elliptic to narrowly elliptic, 6–20 by 5–13 cm, apex acuminate, base cordate to subcordate to rounded, (almost) equal, margin glandular-crenate, ± revolute, at least towards the base; upper surface whitish to brownish puberulous on the main veins (to subglabrous), smooth (to scabridulous); lower surface sparsely to densely whitish to brownish puberulous to subtomentose on the (main) veins, smooth (to scabridulous); lateral veins 5–9 pairs, the basal pair branched, tertiary venation scalariform, ± prominent; petiole 1–3.5 cm long, 1.5–2.5 mm thick, ± densely brownish to whitish puberulous, the epidermis flaking off; stipules lateral, 0.3–0.5 cm long, brownish to whitish appressedly puberulous, caducous. *Staminate inflorescences* axillary or on short-shoots on the older wood; peduncle 5–7 mm long, brownish velutinous; head ellipsoid to cylindrical, 5–8 mm long, 2–3 mm diam.; perianth with 4 free tepals, c. 0.7 mm long; stamen not exserted, anther c. 0.4 mm long; interfloral bracts peltate, the apical part c. 0.6 mm diam., puberulous. *Pistillate inflorescences* axillary or on short-shoots on the older wood; peduncle up to 12 mm long, brownish velutinous; head globose, at anthesis c. 5 mm diam.; stigma bifid; interfloral bracts peltate. *Infructescences* not seen.

Distribution — Thailand; in *Malesia*: Sumatra, Borneo (western).

Habitat — Evergreen forest at low altitudes.

Notes — 1. This rare species is distinguishable by the glandular margin of the lamina.

2. Fertile herbarium material is scarce and, therefore, the species description is incomplete.

3. *Artocarpus fulvicortex* F.M. Jarrett

Artocarpus fulvicortex F.M. Jarrett, J. Arnold Arbor. 41 (1960) 116; Corner, Wayside Trees Malaya (1940) 658, t. 197, 'Artocarpus sp.'; Kochummen, Tree Fl. Malaya 3 (1978) 126, t. 4; Corner, Wayside Trees Malaya ed. 3, 2 (1988) 517, t. 157, 160.

Tree up to 35 m tall, with intermittent growth and terminal and axillary buds, deciduous. Leafy twigs 2.5–6 mm thick, densely brown puberulous, smooth, drying brown to blackish. Leaves distichous; lamina (sub)coriaceous, entire, elliptic to subrotundate, 9–21 by 5.5–16 cm, apex short-acuminate to rounded, base rounded to cuneate (to subattenuate), ± unequal, margin entire, revolute to flat; upper surface brownish puberulous mostly on the main veins, smooth; lower surface brownish strigillose to appressedly puberulous on the midrib, patently puberulous on the smaller veins, minutely whitish appressedly puberulous in the areoles, smooth, nearly glabrous when fresh; lateral veins 6–10 pairs, often one or more forked away from the margin, tertiary venation scalariform, prominent, also the smaller veins; petiole (1.5–)3–7 cm long, (1.5–)2.5–3 mm thick, densely brown puberulous, the epidermis persistent; stipules lateral, 0.3–0.5 cm long, brownish to yellowish puberulous, caducous. *Staminate inflorescences* axillary, solitary (or in pairs); peduncle 1–2 mm long, brown short-velutinous; head subglobose, 4–6 mm diam.; perianth with 2 partly connate tepals, c. 0.7 mm long; stamen c. 0.8 mm long, anther c. 0.2 mm long; interfloral bracts peltate, the apical part 0.3–0.5 mm diam., puberulous. *Pistillate inflorescences* axillary, solitary (or in pairs); peduncle 2–4 mm long, brown short-velutinous; head subglobose; stigma simple; interfloral bracts peltate, persistent, the apical part 0.3–0.5 mm diam., puberulous, persistent. *Infructescences* subglobose, up to 4 cm diam., subvelutinous, smooth to scabridulous; fruits ellipsoid, c. 1 cm long.

Distribution — Sumatra, Malay Peninsula.

Habitat — Evergreen forest at low altitudes.

4. *Artocarpus glaucus* Blume

Artocarpus glaucus Blume, Bijdr. (1825) 483; Trécul, Ann. Sci. Nat., Bot. sér. 3, 8 (1847) 121; Miq. in Zoll., Syst. Verz. 2 (1854) 90, 96; Miq., Pl. Jungh. (1854) 293; Fl. Ned. Ind. 1, 2 (1859) 288; Ann. Mus. Bot. Lugduno-Batavi 3 (1867) 212; Koord. & Valeton, Bijdr. Boomsoort. Java 11 (1906) 26; Koord., Exkurs.-Fl. Java 2 (1912) 95; 4 (1924) 479; F.G. Browne, For. Trees Sar. & Brunei (1955) 353; F.M. Jarrett, J. Arnold Arbor. 41 (1960) 118; Backer & Bakh.f., Fl. Java 2 (1965) 19; Kochummen, Tree Fl. Malaya 3 (1978) 126; Chew, Fl. Australia 3 (1989) 23; Kochummen, Tree Fl. Sabah & Sarawak 3 (2000) 198.

Artocarpus glaucescens Trécul, Ann. Sci. Nat., Bot. sér. 3, 8 (1847) 120; Miq. in Zoll., Syst. Verz. 2 (1854) 90; Fl. Ned. Ind. 1, 2 (1859) 288; Ann. Mus. Bot. Lugduno-Batavi 3 (1867) 212.

Artocarpus zollingeriana Miq. in Zoll., Syst. Verz. 2 (1854) 90, 95; Fl. Ned. Ind. 1, 2 (1859) 289.

Artocarpus biformis Miq., Fl. Ned. Ind., Eerste Bijv. (1861) 419.

Artocarpus tephrophylla Miq., Fl. Ned. Ind., Eerste Bijv. (1861) 422. — *Artocarpus glaucescens* Trécul var. *tephrophylla* (Miq.) Miq., Ann. Mus. Bot. Lugduno-Batavi 3 (1867) 212.

Artocarpus denisoniana King in Hook.f., Fl. Brit. India 5 (1888) 544; Ann. Roy. Bot. Gard. (Calcutta) 2 (1889) 14, t. 8B; Ridl., Fl. Malay Penins. 3 (1924) 355; Burkill, Dict. Econ. Prod. Malay Penins. (1935) 251.

Tree up to 40 m tall, sometimes with buttresses, evergreen. *Leafy twigs* 1.5–4 mm thick, (sparsely) whitish to brownish appressedly puberulous, smooth, drying pale to dark brown. *Leaves* distichous; lamina (sub)coriaceous, entire or pinnatifid to 3–5-lobate when juvenile, elliptic to (sub)ovate, (2–)10–20(–33) by (1–)4–12(–16) cm, apex acuminate, base cuneate to rounded (occasionally peltate with a narrow strip of laminar tissue connecting both sides), margin entire, ± revolute; upper surface (sub)-glabrous, smooth; lower surface densely minutely whitish puberulous to tomentose in the areoles or also on the reticulum, to sparsely whitish appressedly puberulous to subtomentose on the main veins, smooth, glaucous when fresh; lateral veins (6–)8–15 pairs, rarely forked away from the margin, tertiary venation scalariform, ± prominent; petiole (0.5–)1–2.5(–4.5) cm long, 1–2.5 mm thick, sparsely to densely whitish appressedly puberulous, the epidermis persistent; stipules lateral, 0.3–0.5 cm long, brownish appressedly puberulous, caducous. *Staminate inflorescences* axillary, solitary or in pairs; peduncle 1–3 mm long, minutely brownish puberulous; head cylindrical to clavate to ellipsoid, (5–)10–15(–25) mm long, 2–4 mm diam.; perianth 2- or 3-parted, c. 0.5 mm long; stamen c. 0.8 mm long, anther c. 0.2 mm long; interfloral bracts (sub)peltate, the apical part c. 0.4 mm diam., puberulous. *Pistillate inflorescences* axillary, solitary; peduncle 2–5 mm long, densely brown puberulous; head subglobose; stigma simple; interfloral bracts peltate, the apical part 0.2–0.3 mm diam., puberulous. *Inflorescences* subglobose, up to 7 cm diam., densely whitish to brownish puberulous (to velutinous); fruits ellipsoid, c. 1 cm long.

Distribution — Australia (Northern Territory); in *Malesia*: Sumatra, Malay Peninsula, Borneo, Java, Lesser Sunda Islands (Flores, Sumba, Roma), Moluccas (Tanimbar Islands).

Habitat — Evergreen forest at low altitudes.

Notes — 1. This species is characterised by the minute indumentum in the areoles.

2. The base of the lamina is occasionally ‘peltate’ (see p. 108): *Ambri* & *Arifin* W882 (L) from East Kalimantan.

5. *Artocarpus gomezianus* Wall. ex Trécul

Artocarpus gomezianus Wall. ex Trécul, Ann. Sci. Nat., Bot. sér. 3, 8 (1847) 118; King in Hook.f., Fl. Brit. India 5 (1888) 544; Ann. Roy. Bot. Gard. (Calcutta) 2 (1889) 15, t. 14A; Burkill, Dict. Econ. Prod. Malay Penins. (1935) 253; Kanjilal et al., Fl. Assam 4 (1940) 269; F.M. Jarrett, J. Arnold Arbor. 41 (1960) 88; Backer & Bakh.f., Fl. Java 2 (1965) 19; Mabb., Taxon 26 (1977) 535; Kochummen, Tree Fl. Malaya 3 (1978) 126, t. 4; Corner, Wayside Trees Malaya ed.3, 2 (1988) 517.

Artocarpus petiolaris Miq., Fl. Ned. Ind., Eerste Bijv. (1861) 422.

Artocarpus pomiformis Teijsm. & Binn., Natuurk. Tijdschr. Ned.-Indië 25 (1863) 400; Koord. & Valeton, Bijdr. Boomsoort. Java 11 (1906) 23; J.J. Sm., Icon. Bogor. 3 (1907) 87, t. 235; Koord., Exkurs.-Fl. Java 2 (1912) 94.

Tree up to 40 m tall, evergreen. *Leafy twigs* 2–4 mm thick, sparsely whitish appressedly puberulous, smooth, drying pale to dark brown. *Leaves* distichous; lamina coriaceous, entire, elliptic, 10–25 by 6–16 cm, apex acuminate (mostly shortly and abruptly so) to rounded, base cuneate (to subattenuate) to rounded to subcordate, slightly unequal to equal, margin entire, ± revolute; upper surface sparsely minutely whitish appressedly puberulous on the midrib or subglabrous, smooth; lower surface sparsely minutely whitish appressedly puberulous on the midrib or main veins, smooth (to scabridulous); lateral veins 7–10(–15) or 10–15(–20) pairs, mostly some of them (in the upper part of the lamina) forked away from the margin, tertiary venation scalariform, slightly prominent; petiole (1–)1.5–3 cm long, 1.5–2.5 mm thick, sparsely minutely whitish appressedly puberulous, the epidermis persistent; stipules lateral, 0.3–0.5 cm long, white appressedly puberulous, caducous. *Staminate inflorescences* axillary, solitary; peduncle 5–15 mm long, minutely white puberulous; head obovoid to subglobose, 10–15 mm diam.; perianth 2- or 3-parted, c. 0.5 mm long; stamen c. 0.6 mm long, anther c. 0.2 mm long; interfloral bracts (sub)peltate, the apical part c. 0.3 mm diam., puberulous. *Pistillate inflorescences* axillary, solitary; peduncle 15–45 mm long, densely minutely whitish to brownish puberulous; head obovoid to subglobose; stigma simple; interfloral bracts peltate, caducous, the apical part c. 0.3 mm diam., puberulous. *Infructescences* subglobose, up to 8 cm diam., densely whitish to brownish puberulous (to velutinous); fruits ellipsoid, c. 1.2 cm long.

Distribution — India (Andaman Islands), Myanmar, Thailand, Indochina; in *Malesia*: Sumatra, Malay Peninsula, Java, Philippines (Luzon, Cagayan Sulu).

Habitat — Evergreen and semi-evergreen forest at low altitudes.

Notes — 1. In Sri Lanka and India the species is also represented by a form with dense whitish indumentum on the lamina, petiole and leafy twig (subsp. *zeylanicus* F.M. Jarrett, J. Arnold Arbor. 41 (1960) 90).

2. As the species is not known from Borneo, Jarrett (1941) suggested that it was introduced in Cagayan Sulu, but a recent collection (*Ridsdale et al.* 1394) from Luzon may indicate that the species is indigenous. The fact that the leaves of material from the Philippines normally have fewer lateral veins (7–10 pairs, whereas elsewhere normally 10–15 pairs) would support the latter view.

6. *Artocarpus lacucha* Buch.-Ham.

Artocarpus lacucha Buch.-Ham., Mem. Wern. Nat. Hist. Soc. 5 (1826) 333; Mabb., Taxon 26 (1977) 529; A.J.C. Grierson & D.G. Long, Fl. Bhutan 1, 1 (1983) 100. — *Artocarpus lakoocha* Roxb., Fl. Ind. 3 (1832) 524; [Hort. Bengal. (1814) 66 nomen, ‘*lacucha*’]; Graham, Cat. Pl. Bombay (1839) 193; Wight, Icon. Pl. Ind. Orient. 2 (1843) t. 681; Trécul, Ann. Sci. Nat., Bot. sér. 3, 8 (1847) 117; Kurz, Forest Fl. Burma 2 (1877) 433; King in Hook.f., Fl. Brit. Ind. 5 (1888) 543; Ann. Roy. Bot. Gard. (Calcutta) 2 (1889) 14, t. 13; Renner, Bot. Jahrb. Syst. 39 (1907) 370; Burkhill, Dict. Econ. Prod. Malay Penins. (1935) 257.

Artocarpus ovatus Blanco, Fl. Filip. (1837) 666; ed. 3, 3 (1879) 73, plate; S. Vidal, Revis. Pl. Vasc. Filip. (1886) 254; Ahern, Timber Tree Sp. Philip. (1901) 21, plate; F.M. Jarrett, J. Arnold Arbor. 41 (1960) 84.

Artocarpus cumingiana Trécul, Ann. Sci. Nat., Bot. sér. 3, 8 (1847) 119, t. 117, 118; Fern.-Vill., Nov. App. (1880) 203; Elmer, Leafl. Philipp. Bot. 2 (1909) 620; Whitford, Bull. Bur. Forest. Philipp. Islands 10, 2 (1911) 28, t. 6; Merr., Sp. Blancoan. (1918) 125; W.H. Br., Min. Prod. Philip. For. 2 (1921) 70, f. 23; Merr., Enum. Philipp. Flow. Pl. 2 (1923) 40.

- Artocarpus dadah* Miq., Fl. Ned. Ind., Eerste Bijv. (1861) 420; Ann. Mus. Bot. Lugduno-Batavi 3 (1867) 213; S. Moore, J. Bot. 63, Suppl. (1925) 112; Corner, Gard. Bull. Singapore 10 (1939) 282; Wayside Trees Malaya (1940) 653; F.G. Browne, For. Trees Sar. & Brunei (1955) 352; F.M. Jarrett, J. Arnold Arbor. 41 (1960) 91; Kochummen, Tree Fl. Malaya 3 (1978) 126, t. 4; Corner, Wayside Trees Malaya ed. 3, 2 (1988) 516; Kochummen, Tree Fl. Sabah & Sarawak 3 (2000) 194.
- Artocarpus mollis* Miq., Fl. Ned. Ind., Eerste Bijv. (1861) 420.
- Artocarpus rufescens* Miq., Fl. Ned. Ind., Eerste Bijv. (1861) 420.
- Artocarpus tampang* Miq., Fl. Ned. Ind., Eerste Bijv. (1861) 421.
- Ficus tampang* Miq., Fl. Ned. Ind., Eerste Bijv. (1861) 425.
- Ficus inconstantissima* Miq., Fl. Ned. Ind., Eerste Bijv. (1861) 431. — *Artocarpus inconstantissima* (Miq.) Miq., Ann. Mus. Bot. Lugduno-Batavi 3 (1867) 211.
- Artocarpus fretessii* Teijsm. & Binn. in Hassk., Abh. Naturf. Ges. Halle 9 (1866) 189, ‘fretissii’; Merr., Interpr. Herb. Amboin. (1917) 191; F.M. Jarrett, J. Arnold Arbor. 41 (1960) 103. — *Antiaris fretessii* Teijsm. & Binn., Cat. Hort. Bot. Bogor. (1866) 84, nomen.
- Artocarpus dadah* Miq. var. *pubescens* Miq., Ann. Mus. Bot. Lugduno-Batavi 3 (1867) 213.
- Artocarpus lakoocha* Roxb. var. *malayana* King in Hook.f., Fl. Brit. India 5 (1888) 543; Ann. Roy. Bot. Gard. (Calcutta) 2 (1889) 15; Ridl., Fl. Malay Penins. 3 (1924) 355; F.M. Jarrett, J. Arnold Arbor. 41 (1960) 113.
- Artocarpus refracta* Becc., For. Borneo (1902) 630. — *Artocarpus vrieseanus* Miq. var. *refractus* (Becc.) F.M. Jarrett, J. Arnold Arbor. 41 (1960) 98.
- Artocarpus reniformis* Becc., For. Borneo (1902) 631.
- Prainea rumphiana* Becc., For. Borneo (1902) 636. — [*Metrosideros spuria* Rumph., Herb. Amboin. 3 (1743) 26, t. 13.]
- Artocarpus dasypylla* Miq. var. *flava* J.J. Sm., Icon. Bogor. 3 (1907) 85, t. 234.
- Artocarpus leytenensis* Elmer, Leafl. Philipp. Bot. 1 (1908) 279; 2 (1909) 622; Merr., Enum. Philipp. Flow. Pl. 2 (1923) 42.
- Artocarpus paloensis* Elmer, Leafl. Philipp. Bot. 1 (1908) 280; 2 (1909) 621.
- Artocarpus acuminatissima* Merr., Philipp. J. Sci. 18 (1921) 49; Enum. Philipp. Flow. Pl. 2 (1923) 40.
- Artocarpus peltatus* Merr., J. Straits Branch Roy. Asia. Soc. 85 (1922) 166; F.M. Jarrett, J. Arnold Arbor. 41 (1960) 92; Kochummen, Tree Fl. Sabah & Sarawak 3 (2000) 205, t. 4.
- Artocarpus cumingiana* Trécul var. *stenophylla* Diels, Bot. Jahrb. Syst. 67 (1935) 177.
- Artocarpus yunnanensis* Hu, Bull. Fan Mem. Inst. Biol. Bot. 8 (1937) 32.
- Artocarpus ficiifolia* W.T. Wang, Acta Phytotax. Sin. 6 (1957) 274, t. 15, f. 23.
- Artocarpus vrieseanus* Miq. var. *papillosum* F.M. Jarrett, J. Arnold Arbor. 41 (1960) 99.
- Artocarpus dasypylla* auct. non Miq.: Merr., Pl. Elmer. Born. (1929) 46.

Tree up to 40 m tall, deciduous. Leafy twigs 1.5–5(–8) mm thick, densely brown to yellowish (patent to appressedly) puberulous often intermixed with longer brown uncinate hairs, smooth, drying brown (to blackish); with or without up to 5 mm long short-shoots on the older wood. Leaves distichous; lamina subcoriaceous to chartaceous, entire or pinnatifid to 3-lobate when juvenile, basally attached (or occasionally peltate), elliptic (to subrotundate), (3–)10–30(–33) by (2–)6–17 cm, apex acuminate, base cordate to subcordate to rounded (to obtuse to subcuneate), often slightly unequal, margin denticulate towards the apex, particularly the acumen, sometimes entire, ± revolute (at least towards the base); upper surface brownish to whitish puberulous to subtomentose (mainly) on the main veins, smooth (occasionally ± scabrous or ± minutely bullate); lower surface brownish to whitish patent to appressedly puberulous to subtomentose or to hirtellous on the veins, smooth (to scabridulous); lateral veins (6–)10–20 pairs, in the lower part of the lamina usually faintly loop-connected, the lower ones spaced or ± crowded (2 or 3 pairs departing close together), none (or sometimes one or a few)

branched or forked away from the margin, tertiary venation scalariform, ± prominent; petiole (0.5–)0.8–2(–3) cm long, 1.5–3(–4) mm thick, brown puberulous and often intermixed with longer uncinate hairs, the epidermis persistent (or flaking off); stipules lateral, 0.3–0.5(–1) cm long, brownish to whitish puberulous, caducous (or subpersistent), or persistent, at the shoot-apices forming the terminal buds (or also in the leaf axils and forming the lateral buds). *Staminate inflorescences* axillary (or just below the leaves), solitary, or 1–5 on short-shoots on the older wood, patent or deflexed; peduncle 3–35 mm long, densely brown puberulous; head subglobose to ellipsoid, to clavate (or to pulvinate), to 3 cm long, 3–15 mm diam.; perianth with 2 or 3 free tepals; stamen 0.5–0.8 mm long, anther 0.1–0.2 mm long; interfloral bracts peltate, the apical part c. 0.3 mm diam., puberulous, caducous or persistent. *Pistillate inflorescences* axillary or below the leaves (down to previous season's growth), solitary; peduncle (5–)10–80 mm long, minutely brown velutinous; head subglobose to ovoid; perianth minutely puberulous; stigma simple; interfloral bracts peltate, caducous (or persistent), the apical part c. 0.3 mm diameter. *Infructescences* to c. 7 cm diam., often ± lobed, green to orange with pink to red flesh, surface minutely velutinous; fruits ellipsoid, 1–1.2 cm long. — **Fig. 20a–e.**

Distribution — Bhutan, India, Bangladesh, China (Yunnan), Myanmar, Thailand, Indochina, Solomon Islands; in *Malesia*: Sumatra, Malay Peninsula, Borneo, Philippines, Celebes, Moluccas (incl. Aru Islands), New Guinea.

Habitat — Mostly in evergreen forest at low altitudes. In New Guinea up to 2000 m.

Notes — 1. The species as currently defined includes material that Jarrett (J. Arnold Arbor. 41 (1960) 73–136) placed in *A. dadah*, *A. fretessii*, *A. ovatus*, *A. vrieseanus* var. *papillosum* and var. *refractus*, as well as *A. peltatus*, which was separated from *A. dadah* in the Flora Malesiana manuscript. The species can be recognised by features indicating intermittent growth (in combination with deciduousness) such as the presence of terminal buds formed by some persistent stipules, the scars of which in addition to colour differences mark previous seasons' growth of branches from the current growth. The stipules are often subpersistent on opening-shoots and relatively long, to 1 cm. The lamina is chartaceous to subcoriaceous and the margin is denticulate at the apex, sometimes only at the acumen. The base of the lamina is more or less unequal, and varies from cordate through subcordate, rounded, and obtuse to cuneate. The latter state occurs most frequently in the northern part of the species range. The lamina varies in the lateral veins: the lower veins either distant or 2 or 3 pairs departing the midrib close together as often seen in the eastern part of the species range. Patterns of variation in length, direction, and colour of the indumentum are less clear, but the hairs are often more or less appressed, shorter and paler in the eastern part of the species range. The areoles of the lower surface are sometimes minutely bullate in the Malay Peninsula, more frequently further northwards. In Borneo the base of the lamina is sometimes peltate (with a narrow strip of lamina tissue connecting the two sides of the base of the lamina). This was the distinguishing character of *A. peltatus*.

2. The pistillate inflorescences vary in length of the peduncle, the shedding of the interfloral bracts, and the surface of the head in fruiting state which ranges from smooth to finely ribbed or sometimes with the free parts of the apices of the pistillate flowers short-pyramidal and hardened. Long peduncles, up to 8 cm long are found in northern

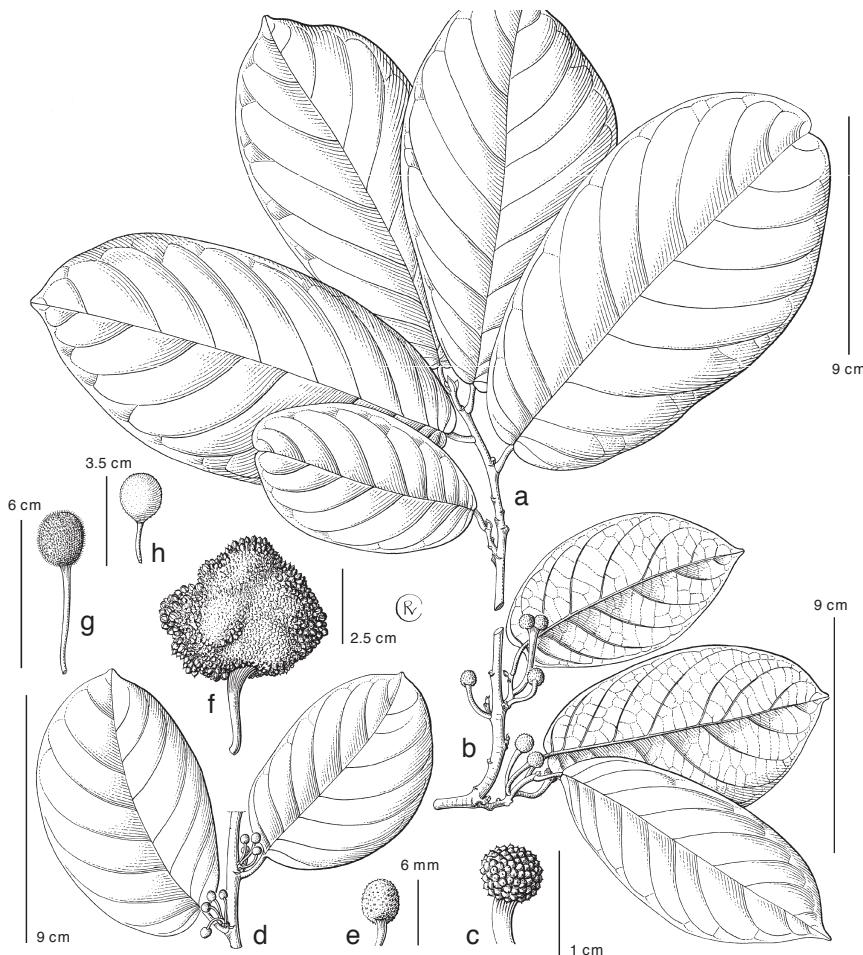


Fig. 20. a–e: *Artocarpus lacucha* Buch.-Ham. ('fretissii'-form). a. Leafy twig; b. leafy twig with pistillate inflorescences; c. pistillate inflorescences; d. leafy twig with staminate inflorescences; e. staminate inflorescence. — f–h: *Artocarpus reticulatus* Miq. f. Pistillate inflorescence; g. pistillate inflorescence; h. staminate inflorescence (a: Kostermans s.n. Hort. Bog.; b, c: Cel. I-19; d, e: Cel. III-55; f: De Vries s.n., Celebes; g, h: Cel. V-228).

Borneo (in material that was identified as *A. peltatus*) and in the Philippines (in material identified as *A. ovatus*). The peduncle becomes mostly up to 4 or 4.5 cm long. It is often shorter in the Asian mainland (in material that was identified as *A. lacucha* by Jarrett 1960). The interfloral bracts are often absent in the fruiting state and may be already shed at anthesis. However, infructescences with persistent apices can be found throughout the range of the species.

3. The staminate inflorescences vary more in their position, direction, length of the peduncle, and shape and size of the head. Long peduncles, up to 4.5 cm long, are correlated with long peduncles of pistillate inflorescences. They are often deflexed in the

Philippines. The inflorescences are normally axillary or just below the leaves, mostly solitary, sometimes in pairs, but often (also) borne on short-shoots on the older wood in Celebes and the Moluccas, less often in the Philippines and (western) New Guinea. The head varies considerably in shape, from subglobose to ellipsoid to clavate, or sometimes to pulvinate or spicate, and ranges in size from c. 0.3 cm in length or diameter, to 4 cm long in clavate to spicate ones or to 1.5 cm in diameter in subglobose ones.

4. The following informal entities can be distinguished:

‘lacucha’-form with the apex of the lamina often abruptly short-acuminate, the base of the lamina often subcuneate and clearly unequal. Staminate inflorescences axillary, solitary; peduncle 2–5 mm long; head ellipsoid to obovoid (to clavate) 1–2.5 cm long, 0.5–1.5 cm diameter. Pistillate inflorescences: peduncle to 1.5(–2.5) cm long; interfloral bracts caducous or persistent, the free apices of the pistillate flowers sometimes short-pyramidal and hardened. — India, (north-eastern & Andaman Islands), Bangladesh, Myanmar, Thailand, China (Yunnan), Indochina. — In evergreen, semi-evergreen or moist deciduous forest mostly at low altitudes.

‘dadah’-form with the base of the lamina mostly obtuse to subcordate, slightly unequal. Staminate inflorescences axillary (or just below the leaves) solitary, patent; peduncle 0.4–1.5 cm long; head subglobose (to pulvinate), 0.4–1.5 cm diameter. Pistillate inflorescences: peduncle to 3.5 cm long; interfloral bracts usually (early) caducous; free parts of apices of pistillate flowers occasionally short-pyramidal and hardened; surface of syncarp usually finely ribbed. — Myanmar (?), Thailand, Sumatra, Malay Peninsula, Borneo. — In forest at low altitudes.

‘peltatus’-form with the base of the lamina rounded to subcordate, slightly unequal, sometimes peltate. Staminate inflorescences axillary or just below the leaves, solitary, patent; peduncle 2.5–3.5 cm long; head ellipsoid to subglobose, 0.7–2 cm diameter. Pistillate inflorescences: peduncle up to 8 cm long; heads of interfloral bracts caducous; surface of ‘syncarp’ usually finely ribbed. — Borneo (northern). — In evergreen forest at altitudes up to 1000 m.

‘ovatus’-form with the base of the lamina usually cordate to subcordate, slightly unequal. Staminate inflorescences axillary, below the leaves, solitary, paired, or sometimes up to 5 together on short-shoots on the older wood, often deflexed; peduncle (0.5–)1–4.5 cm long; head obovoid to clavate, 1–3 cm long, 0.3–1.3 cm diam.; interfloral bracts persistent. Pistillate inflorescences: peduncle up to 8 cm long, deflexed at anthesis (?); interfloral bracts persistent. — Philippines. — In forest at low altitudes.

The ‘peltatus’-form and ‘ovatus’-form are largely similar and distinguished by the patent versus deflexed staminate inflorescences.

‘fretesii’-form with the base of the lamina usually rounded to cordate, slightly unequal. Staminate inflorescences predominantly on short-shoots on the older wood, 1–5 together, patent (or deflexed?); peduncle 0.3–0.7 cm long; head ellipsoid to subglobose, 0.3–0.7 mm diameter. Pistillate inflorescences: peduncle to 4.5 cm long; head subglobose to obovoid; interfloral bracts early caducous to persistent. — Celebes, Moluccas. — At low altitudes.

‘refractus’-form with the base of the lamina usually rounded to cordate, slightly unequal. Staminate inflorescences usually axillary or just below the leaves, solitary, or sometimes 1–4 on short-shoots on the older wood, patent; peduncle 0.3–1.2 cm long; head subglobose 0.3–0.6 cm diam.; interfloral bracts persistent. Pistillate inflorescences: peduncle to 5 cm long; interfloral bracts usually caducous; surface of ‘syncarp’ smooth (= not finely ribbed). — New Guinea, Solomon Islands. — Forest at altitudes up to 2000 m.

The reticulum of the lamina lower surface is prominent in the few collections between c. 1000 and 2000 m in New Guinea. This form also includes the type of *A. vrieseanus* Miq. var. *papillosum* F.M. Jarrett. The epidermis of the petiole in this form sometimes flakes off, whereas rarely in the forms treated above.

The ‘fretessii’-form and ‘refractus’-form are similar in the small subglobose, shortly pedunculate staminate inflorescences. They differ in the frequency of staminate inflorescences on short-shoots on the older wood. The ‘refractus’-form grades into a ‘stenophyllus’-form, comprising several collections which Jarret in her Flora Malesiana manuscript called the eastern variants ‘stenophyllus α and β’ of *A. vrieseanus* and related to the ‘refractus’ variant’. In this form, the indumentum is relatively sparse and on leafy twigs and lamina predominantly whitish and mostly intermixed with (\pm retrorse) uncinate hairs. The petiole is usually 0.5–0.8 cm long and its epidermis exfoliates. The leafy twigs are rather slender, mostly 2–3 mm thick, the trees are often less than 10 m tall without buttresses, and no clear indication of intermittent growth. The peduncle of the pistillate inflorescence is up to 5 cm long. — New Guinea, most frequently in the eastern part, but also found in Biak, Yapen, and in the Solomon Islands. The sympatric occurrence of the ‘refractus’-form and the ‘stenophyllus’-form together with the nature of the differentiating characters cast doubt on the distinctiveness of the latter. Future studies with more material are needed to clarify their taxonomic status. The ‘stenophyllus’-form resembles *A. nitidus* from New Guinea and the Solomon Islands, but differs in the patent hairs on the lamina lower surface and the usually denticulate margin towards the apex.

7. *Artocarpus longifolius* Becc.

Artocarpus longifolius Becc., For. Borneo (1902) 629; F.M. Jarrett, J. Arnold Arbor. 41 (1960) 83; Kochummen, Tree Fl. Sabah & Sarawak 3 (2000) 201.

Tree up to 20 m tall, of intermittent growth, with terminal (and lateral?) buds, deciduous (?). Leafy twigs (2–)4–6 mm thick, densely brownish minutely puberulous and longer uncinate hairs, smooth, drying dark brown. Leaves distichous; lamina (sub)-coriaceous, entire, elliptic, 9–33 by 5–14.5 cm, apex (sub)acute, base obtuse to rounded, margin entire, \pm revolute; upper surface brownish puberulous on the main veins or only on the midrib, smooth; lower surface \pm densely to sparsely brownish to whitish puberulous to hirtellous on the veins or to minutely puberulous on the smaller veins, smooth (to scabridulous); midrib, lateral and tertiary veins mostly \pm impressed, lateral veins (5–)8–15 pairs, not forked away from the margin, tertiary venation scalariform, prominent, the smaller veins also prominent; petiole 0.3–0.8 mm long, 3–4 mm

thick, brownish puberulous, the epidermis flaking off; stipules lateral, 0.3–0.5(–1) cm long, brownish puberulous, caducous (or subpersistent). *Staminate inflorescences* axillary, solitary; peduncle 1–3 cm long, minutely brown puberulous and with numerous longer brownish uncinate hairs; head subglobose, c. 6 mm diam.; perianth with 3 free tepals, c. 0.4 mm long; stamen c. 0.8 mm long, anther 0.1–0.2 mm long; interfloral bracts peltate, the apical part c. 0.3 mm diam., puberulous. *Pistillate inflorescences* axillary, solitary; peduncle 2–6 cm long, minutely brown puberulous and with numerous longer brownish uncinate hairs; head subglobose to ellipsoid; perianth puberulous; stigma simple; interfloral bracts peltate, persistent, the apical part 0.2–0.3 mm diameter. *Infructescences* (immature) c. 2 cm diam., densely brown puberulous (velutinous); fruit not seen.

Notes — 1. The species can be recognised by the short and thick petiole with exfoliating epidermis.

2. Jarrett (1960) assumed that subglabrous specimens represented (sub)juvenile material. However, two such specimens are fertile and a specimen bearing a pistillate inflorescence has a much shorter peduncle (c. 0.3 cm long as opposed to 2–6 cm long in ± densely hairy specimens). The differences in indumentum possibly correlate with the length of the peduncles of the pistillate inflorescences and suggest distinction of subspecies, or closely related species. More material is needed to sort out the status of these two morphological entities which are sympatric and apparently have a similar ecology.

a. subsp. **longifolius**

Lower surface of the lamina ± densely brownish puberulous to hirtellous, partly with uncinate hairs; midrib, lateral and tertiary veins mostly ± impressed above.

Distribution — Borneo.

Habitat — Evergreen forest at low altitudes

b. subsp. **adpressus** C.C. Berg

Artocarpus longifolius Becc. subsp. *adpressus* C.C. Berg, Blumea 50 (2005) 543.

Lower surface of the lamina sparsely brownish to whitish appressed puberulous on the main veins, this indumentum intermixed with patent to retrorse uncinate hairs, minutely puberulous on the smaller veins; the main veins not (never?) impressed above.

Distribution — Borneo (Brunei, Central Kalimantan).

Habitat — Evergreen forest at low altitudes.

Note — In the collection from Brunei (Tutong, Telisai, Bukit Basong, *N. Nangkat* et al. BRUN 15511), the leaves are small (9–13 by 3.5–6 cm) and have few lateral veins (5–7 pairs), whereas in the collection from Central Kalimantan (Taman Wisata, Bukit Tengkiling area, Palangka Raya, Abriansyah & Z. Arifin AA 954) the size of the lamina varies from small (as in the Brunei collection) to the normal size for subsp. *longifolius*.

8. *Artocarpus nitidus* Trécul

- Artocarpus nitidus* Trécul, Ann. Sci. Nat., Bot. sér. 3, 8 (1847) 119; Miq., Fl. Ned. Ind. 1, 2 (1859) 288; Fern.-Vill., Nov. App. (1880) 203; S. Vidal, Revis. Pl. Vasc. Filip. (1886) 254; Elmer, Leafl. Philipp. Bot. 2 (1909) 624; F.M. Jarrett, J. Arnold Arbor. 41 (1960) 121; Corner, Wayside Trees Malaya ed.3, 2 (1988) 520, t. 157, 162; Kochummen, Tree Fl. Sabah & Sarawak 3 (2000) 203.
- Artocarpus lanceolata* Trécul, Ann. Sci. Nat., Bot. sér. 3, 8 (1847) 121.
- Artocarpus gomezianus* Wall. ex Trécul var. *griffithii* King in Hook.f., Fl. Brit. India 5 (1888) 544; Ann. Roy. Bot. Gard. (Calcutta) 2 (1889) 15, t. 14B. — *Artocarpus griffithii* (King) Merr., Pap. Michigan Acad. Sci. I, 24 (1939) 64. — *Artocarpus nitidus* Trécul subsp. *griffithii* (King) F.M. Jarrett, J. Arnold Arbor. 41 (1960) 128; Kochummen, Tree Fl. Malaya 3 (1978) 131, t. 6.
- Artocarpus humilis* Becc., For. Borneo (1902) 629. — *Artocarpus nitidus* Trécul subsp. *humilis* (Becc.) F.M. Jarrett, J. Arnold Arbor. 41 (1960) 126.
- Artocarpus antiarifolia* Becc., For. Borneo (1902) 630.
- Artocarpus xanthocarpus* Merr., Philipp. J. Sci. 17 (1904) 10; Philipp. J. Sci., 1, Suppl. (1906) 43; Elmer, Leafl. Philipp. Bot. 2 (1909) 626; F.M. Jarrett, J. Arnold Arbor. 41 (1960) 102.
- Artocarpus borneensis* Merr., J. Straits Branch Roy. Asiat. Soc. 85 (1922) 165. — *Artocarpus nitidus* Trécul subsp. *borneensis* (Merr.) F.M. Jarrett, J. Arnold Arbor. 41 (1960) 127.
- Artocarpus eberhardtii* Gagnep., Bull. Soc. Bot. France 73 (1926) 87; Fl. Indo-Chine 5 (1928) 737.
- Artocarpus parva* Gagnep., Bull. Soc. Bot. France 73 (1926) 89; Fl. Indo-Chine 5 (1928) 735, t. 90.
- Artocarpus sampor* Gagnep., Bull. Soc. Bot. France 73 (1926) 90; Fl. Indo-Chine 5 (1928) 738.
- Artocarpus eberhardtii* Gagnep. var. *poilanei* Gagnep., Fl. Indo-Chine 5 (1928) 737.
- Artocarpus lingnanensis* Merr., Lingnan. Sci. J. 7 (1931) 302; 13 (1934) 56. — *Artocarpus nitidus* Trécul subsp. *lingnanensis* (Merr.) F.M. Jarrett, J. Arnold Arbor. 41 (1960) 124.
- Artocarpus vrieseanus* Miq. var. *subsessilis* F.M. Jarrett, J. Arnold Arbor. 41 (1960) 101.
- Artocarpus lamellosa* auct. non Blanco: Merr., Philipp. J. Sci. 27 (1905) 80; Sp. Blancoan. (1918) 124; Enum. Philipp. Flow. Pl. 2 (1923) 41.
- Artocarpus rubrovenius* auct. non Warb.: Merr., Philipp. J. Sci., Bot. 3 (1908) 401.
- Artocarpus lanceolata* auct. non Trécul: Merr., Enum. Philipp. Flow. Pl. 2 (1923) 42; Gagnep. Fl. Indo-Chine 5 (1928) 738.
- Artocarpus gomezianus* auct. non Wall. ex Trécul: Ridl., Fl. Malay Penins. 3 (1924) 355; Corner, Wayside Trees Malaya (1940) 654, t. 195.

Tree up to 35 m tall, sometimes with buttresses, evergreen. *Leafy twigs* (1)–2–3(–4) mm thick, (sparsely) whitish to brownish appressedly puberulous (sometimes also retrorse uncinate hairs), smooth, drying brown (to blackish). *Leaves* distichous; lamina (sub)coriaceous, entire, elliptic, (3)–6–18(–33) by (1.5)–3.5–9 cm, apex acuminate with the acumen long or short, caudate, acute, obtuse (or to rounded), base cuneate to subattenuate to rounded or to subcordate, equal to ± unequal, margin entire (or crenate towards the apex, or when juvenile pinnately lobate), ± revolute (to flat); upper surface glabrous or whitish (largely) appressedly puberulous on the main veins or only on the midrib, often partly with retrorse uncinate hairs, smooth; lower surface sparsely whitish to brownish puberulous on the (main) veins (the hairs mostly appressed or some patent or retrorse and then often uncinate) to glabrous, smooth (or scabridulous); lateral veins (5)–7–10(–15) pairs, none of them forked away from the margin, tertiary venation (sub)scalariform, almost flat to slightly prominent; petiole (0.5)–8–1.5(–2.5) cm long, 1–2 mm thick, sparsely whitish to brownish appressedly puberulous (sometimes also retrorse uncinate hairs), the epidermis persistent; stipules lateral, 0.2–0.4 cm long, brownish to whitish appressedly puberulous, caducous. *Staminate inflorescences* axillary, solitary; peduncle 1–4 mm long, densely brown to whitish puberulous; head

subglobose to ovoid to narrowly ellipsoid to clavate, 2–12 by 2–5 mm; perianth 2- or 3-lobed to -parted, c. 0.6 mm long; stamen c. 0.8 mm long, anther c. 0.2 mm long; interfloral bracts (sub)peltate, the apical part c. 0.4 mm diam., puberulous. *Pistillate inflorescences* axillary, solitary; peduncle 1–5(–25) mm long, densely brown puberulous; head subglobose to ellipsoid; stigma simple; interfloral bracts peltate, persistent or caducous, the apical part c. 0.3 mm diam., puberulous. *Infructescences* subglobose, up to c. 3(–4?) cm diam., subglabrous, sparsely hairy or densely hairy (velutinous); fruits ellipsoid, c. 1 cm long.

Distribution — India (north-eastern), Myanmar, Thailand, China (southern, according to Zhekun & Gilbert, Fl. China 5 (2003) 34 also in Lan Yu (Taiwan)), Indochina, Solomon Islands; in *Malesia*: Sumatra, Malay Peninsula, Borneo, Philippines, Moluccas (Aru Islands), New Guinea.

Habitat — Evergreen forest at altitudes up to c. 1600 m, in New Guinea up to 1750 m.

Notes — 1. The subspecies is rather variable and allows recognition of three informal entities:

‘*nitidus*’-form — Base of the lamina tending towards subcordate, lateral veins mostly 5 or 6 pairs, epidermis of the petiole persistent; heads of the staminate inflorescences mostly elongate, surface of the infructescences densely hairy (velutinous), interfloral bracts of the pistillate inflorescences sometimes early caducous. — Philippines.

‘*griffithii*’-form with the base of the lamina tending towards attenuate, lateral veins mostly 7–10, sometimes up to 15 pairs, epidermis of the petiole persistent; heads of the staminate inflorescences mostly globose, surface of the infructescences subglabrous or (in Borneo) sometimes (rather) sparsely puberulous, interfloral bracts of the pistillate inflorescences persistent. — Sumatra, Malay Peninsula, Borneo, Philippines. One of the collections from Peninsular Malaysia (*FRI 6941*) is distinct in its up to 1 cm long peduncle.

‘*borneensis*’-form with the base of the lamina and lateral veins and staminate inflorescences as in the ‘*griffithii*’-form — but the indumentum on the leafy twigs and petioles often denser and the epidermis of the petiole often flaking off; surface of the infructescence densely brown to purplish puberulous (velutinous), interfloral bracts of the pistillate inflorescence persistent. — Borneo (Brunei, Kalimantan (eastern), Sabah, Sarawak). Two collections from eastern Kalimantan are distinct in their peduncles which are up to 2.5 cm long.

‘*subsessilis*’-form with the base of the lamina cuneate to subcordate, in contrast to the western forms the midrib of the lamina is ± densely hairy above and the venation of the lamina often more prominent beneath; the peduncles are on average slightly longer; those of the pistillate inflorescences can be up to 2 cm long and of the staminate inflorescences up to 1.5 cm long. — Occurring disjunct from the main range in New Guinea and the Solomon Islands. This form includes the types of *A. vrieseanus* var. *subsessilis* and probably also of *A. antiarifolia*.

2. Some collections from the Philippines (Batan Island, Luzon) have caudate apices of the lamina.

3. The staminate inflorescences are occasionally borne on short-shoots on the older wood: see *Van Royen 3591* (Vogelkop).

4. The material from the Solomon Islands differs somewhat from New Guinean material in the hairs on the midrib above which are all straight and point towards the apex of the lamina rather than partly uncinate and retrorse.

5. As the type of *A. antiarifolia* could not be (re)examined, it is not quite certain that the name is correctly included in the synonymy.

6. The collection *FRI 19234* indicated as *Artocarpus* 'sp. B' by Kochummen (Tree Fl. Malaya 3 (1978) 135) is referred to this species with some doubt. It has all characters of *A. nitidus* (including the subglabrous head of the pistillate inflorescence of the 'griffithii'-form) except for the dense brown indumentum on the leafy twig, petiole, and the midrib of the lamina, in which it resembles *A. lacucha*. Collections with similar indumentum have been made in northern and eastern Borneo (e.g., *Endert 3191* and *Paie & Yeo S 38380*) and can be referred to the 'borneensis'-form.

9. *Artocarpus reticulatus* Miq.

Artocarpus reticulatus Miq., Ann. Mus. Bot. Lugduno-Batavi 3 (1867) 213, 'reticulata'; Renner, Bot. Jahrb. Syst. 39 (1907) 369; Koord., Suppl. Fl. Celebes 2 (1922) t. 3; 3 (1922) 1; F.M. Jarrett, J. Arnold Arbor. 41 (1960) 107.

Artocarpus dadah Miq. var. *celebica* Miq., Ann. Mus. Bot. Lugduno-Batavi 3 (1867) 213.

Tree up to 30 m tall with short buttresses, evergreen. *Leafy twigs* 3–6 mm thick, sparsely or towards the nodes more densely brownish minutely appressedly puberulous, smooth, drying brown to greyish. *Leaves* distichous; lamina subcoriaceous, entire, elliptic to subobovate, 15–35 by 8–16 cm, apex acuminate, base rounded to obtuse, broad bases usually minutely auriculate, equal, margin entire, slightly revolute to flat; upper surface sparsely brownish appressedly puberulous on the midrib, smooth, occasionally ± bullate; lower surface sparsely brownish appressedly puberulous on the midrib to whitish hispidulous on the smaller veins, ± scabrous; lateral veins 10–17 pairs, none (or one) forked away from the margin, tertiary venation scalariform, ± prominent; petiole 1–2.5 cm long, 2–3 mm thick, sparsely whitish puberulous, the epidermis persistent; stipules lateral, 0.3–0.5 cm long, brownish appressedly puberulous, caducous. *Staminate inflorescences* axillary (or on axillary short-shoots), solitary or in pairs, patent; peduncle 8–13 mm long, densely brown appressedly puberulous; head obovoid to sub-globose, c. 1.5 cm diam.; perianth with 3 or 4 free tepals, c. 0.2 mm long; stamen c. 0.5 mm long, anther c. 0.2 mm; interfloral bracts peltate, persistent, the apical part 0.4–0.6 mm diam., ciliolate. *Pistillate inflorescences* axillary, solitary; peduncle 2.5–4.5 cm long, broadened at the apex, densely minutely brown puberulous; head subglobose to ellipsoid; perianth brown puberulous; stigma simple, c. 1.5 mm long; interfloral bracts, few, peltate, the apical part c. 0.3 mm diam., persistent. *Infructescences* to c. 6 cm diam., lobed, with pyramidate hardened apices of the perianths; fruit ellipsoid, c. 1.2 cm long.

— Fig. 20f–h.

Distribution — Celebes, Moluccas (Ternate, Ambon).

Habitat — Evergreen forest at low altitudes.

Notes — 1. This species can be recognised by the sparsely hairy laminas with \pm scabrous lower surface and often minutely auriculate base.

2. The species resembles some specimens of *A. lacucha* and many species of subg. *Artocarpus* in the hardened pyramidate free apices of the perianth.

10. *Artocarpus rubrovenius* Warb.

Artocarpus rubrovenius Warb. in Perkins, Fragm. Fl. Philipp. 3 (1905) 166; Merr., Philipp. J. Sci., 1, Suppl. (1906) 43; Elmer, Leafl. Philipp. Bot. 2 (1909) 622; Merr., Enum. Philipp. Flow. Pl. 2 (1923) 43; W.H. Br., Useful Pl. Philipp. (1941) 470; F.M. Jarrett, J. Arnold Arbor. 41 (1960) 114.

Tree up to 15 m tall, evergreen (?). Leafy twigs 2–4 mm thick, sparsely brownish to whitish appressedly puberulous, smooth, drying dark brown to blackish. Leaves distichous; lamina (sub)coriaceous, entire, elliptic, 10–26 by 5–14 cm, apex acuminate, base cuneate to rounded, usually unequal, margin entire (or crenate to subdenticulate), usually flat; upper surface sparsely brownish to whitish appressedly puberulous on the main veins, smooth; lower surface sparsely brownish to whitish appressedly puberulous on the main veins, smooth; lateral veins (6–)7–10(–11) pairs, none or sometimes one forked away from the margin, tertiary venation (loosely) scalariform, slightly prominent; petiole (1–)1.5–2.5(–3) cm long, 1–2 mm thick, sparsely brownish to whitish appressedly puberulous, the epidermis persistent; stipules lateral, 0.3–0.5 cm long, brownish to yellowish appressedly puberulous, caducous. Staminate inflorescences axillary, solitary (or in pairs); peduncle 2–5 mm long, brown short-velutinous; head obovoid to ellipsoid, 1.5–3(–4.5) cm long, 1–1.5(–2) cm diam.; perianth with 2–4 free or basally connate tepals, c. 0.5 mm long; stamen c. 0.7 mm long, anther c. 0.2 mm long; interfloral bracts peltate, the apical part c. 0.3 mm diam., puberulous. Pistillate inflorescences axillary, solitary; peduncle 0.4–1 cm long, brown short-velutinous; head ellipsoid to subglobose; stigma simple; interfloral bracts peltate, persistent, the apical part c. 0.3 mm diam., puberulous. Infructescences subglobose, up to 8 cm diam., puberulous; fruit not seen.

Distribution — Philippines.

Habitat — Evergreen forest at low altitudes.

Notes — 1. This species can be distinguished from the sympatric *A. nitidus* by the larger lamina and flower heads.

2. The trees may show intermittent growth.

11. *Artocarpus subrotundifolius* Elmer

Artocarpus subrotundifolius Elmer, Leafl. Philipp. Bot. 2 (1909) 619; Merr., Enum. Philipp. Flow. Pl. 2 (1923) 43; F.M. Jarrett, J. Arnold Arbor. 41 (1960) 108.

Tree up to 25 m tall of intermittent growth with terminal and axillary buds, deciduous (?). Leafy twigs 4–6 mm thick, densely brown puberulous to velutinous, smooth, drying brown to blackish. Leaves distichous; lamina (sub)coriaceous, entire, elliptic to narrowly elliptic or to subrotundate, 18–36 by 11–27 cm, apex short-acuminate (to rounded), base cordate to rounded, usually \pm unequal to equal, margin entire to denticulate towards the apex, \pm revolute to flat; upper surface brownish to whitish puberulous

mainly on the main veins, smooth; lower surface brownish to whitish puberulous to sub-hispidulous on the veins, scabridulous; lateral veins 10–14 pairs, most of them forked or branched away from the margin, tertiary venation scalariform, prominent, also the smaller veins prominent; petiole (1.5–)3–7 cm long, 2.5–3 mm thick, densely brown puberulous to velutinous, the epidermis persistent; stipules lateral, 0.3–0.5 cm long, brownish puberulous, caducous. *Staminate inflorescences* axillary, solitary (or in pairs); peduncle (0.5–)1.5–2.2 cm long, brown short-velutinous; head obovoid to ellipsoid to subglobose, (2–)2.5–5 cm long, 2–3.5 cm diam.; perianth with 3 or 4 free tepals, c. 0.6 mm long; stamen 1 mm long, anther c. 0.2 mm long; interfloral bracts peltate, the apical part 0.3–0.5 mm diam., puberulous. *Pistillate inflorescences* axillary, solitary; peduncle 2–7 (?) cm long, brown short-velutinous; head subglobose; stigma simple; interfloral bracts peltate, the apical part 0.3–0.5 mm diam., puberulous, caducous. *Infructescences* subglobose, up to 6 cm diam., puberulous; fruits subglobose, c. 1.5 diameter.

Distribution — Philippines.

Habitat — Evergreen forest at low altitudes.

Notes — 1. The species can be recognised by the large lamina with the lateral veins frequently forked or branched away from the margin.

2. The species is probably closely related to *A. tomentosulus*.

12. *Artocarpus tomentosulus* F.M. Jarrett

Artocarpus tomentosulus F.M. Jarrett, J. Arnold Arbor. 41 (1960) 117; Kochummen, Tree Fl. Sabah & Sarawak 3 (2000) 212.

Artocarpus primackii Kochummen, Gard. Bull. Singapore 50 (1998) 199; Tree Fl. Sabah & Sarawak 3 (2000) 207.

Tree up to 30 m tall of intermittent growth with terminal and axillary buds, deciduous (?). Leafy twigs 2.5–4.5 mm thick, densely brownish to whitish minutely puberulous, smooth, drying brown. Leaves distichous; lamina (sub)coriaceous, entire, elliptic, 10–30 by 5–20 cm, apex acuminate, base obtuse to rounded to subcord(ul)ate or to cuneate, margin entire, ± revolute; upper surface whitish to brownish minutely puberulous on the main veins, smooth; lower surface ± densely whitish to brownish minutely puberulous to hispidulous on the veins, smooth to scabridulous; lateral veins (10–)12–16 pairs, none forked away from the margin, tertiary venation scalariform, prominent; petiole 1–4.5 cm long, 2–3 mm thick, densely whitish to brownish minutely puberulous, the epidermis flaking off; stipules lateral, 0.3–0.5 cm long, brownish appressedly puberulous, caducous. *Staminate inflorescences* axillary, solitary; peduncle c. 2 mm long, brown velutinous; head subglobose, c. 6 mm diam.; perianth tubular, 2-lobed; stamen not exserted, anther 0.1–0.2 mm long; interfloral bracts peltate, the apical part c. 0.3 mm diam., puberulous. *Pistillate inflorescences* axillary, solitary on short-shoots with buds lateral over the base of the peduncle; peduncle up to 4 cm long, brown velutinous; head subglobose; perianth puberulous; stigma simple; interfloral bracts peltate, persistent, the apical part 0.2–0.3 mm diam., persistent. *Infructescences* up to 6 cm diam., pinkish red at maturity.

Distribution — Borneo.

Habitat — Evergreen forest at low altitudes.

Note — The species is characterised by the dense minute indumentum on the leafy twig, petiole, lower surface of the lamina, and peduncle. The inflorescences, at least the pistillate ones, are borne on short-shoots with distinct buds, consisting of several persistent stipules.

13. *Artocarpus vrieseanus* Miq.

Artocarpus vrieseanus Miq., Ann. Mus. Bot. Lugduno-Batavi 3 (1867) 212; F.M. Jarrett, J. Arnold Arbor. 41 (1960) 95.

Tree up to 6 (or more?) m tall, evergreen. *Leafy twigs* 1.5–3 mm thick, sparsely whitish appressedly puberulous to subglabrous, smooth, drying brown to blackish. *Leaves* distichous; lamina subcoriaceous, entire, subobovate to elliptic, 7–23 by 3.5–11 cm, apex acuminate, base rounded to obtuse (to cuneate), often ± unequal, margin entire, slightly revolute to flat; upper surface (very) sparsely whitish appressedly puberulous on the main veins, smooth; lower surface very sparsely whitish appressedly puberulous to subglabrous on the main veins, smooth; lateral veins 9 or 10 pairs, none forked away from the margin, tertiary venation scalariform, slightly prominent; petiole 1–2.2 cm long, 1–2 mm thick, sparsely whitish appressedly puberulous, the epidermis persistent; stipules lateral, 0.3–0.6 cm long, whitish to brownish appressedly puberulous, caducous. *Staminate inflorescences* axillary, just below the leaves (or on short-shoots on the older wood), solitary (or in pairs), deflexed (?); peduncle 1.2–1.7 cm long, densely minutely whitish to brownish puberulous; head obovoid to subglobose, 3–5 mm diam.; perianth 2- or 3-lobed, c. 0.5 mm long; stamen c. 0.8 mm long, anther 0.1–0.2 mm long; interfloral bracts peltate, the apical part 0.2–0.3 mm diam., sparsely puberulous. *Pistillate inflorescences* axillary, solitary; peduncle 2.5–5.5 or 0.3–2 cm long, densely minutely brownish or whitish puberulous; head globose; perianth puberulous; stigma simple; interfloral bracts peltate, caducous or persistent, the apical part 0.2–0.3 mm diam., puberulous. *Infuctescences* to c. 4.5 cm diam., orange, subglabrous or sparsely to densely minutely brownish to whitish puberulous (to subpapillate); fruit subglobose, c. 1 cm diam.

Distribution — Celebes (Manado), Moluccas (Batjan).

Habitat — Evergreen forest, at altitudes up to 1000 m.

Note — *Artocarpus vrieseanus* as defined by Jarrett (1960) is too heterogeneous. The material of var. *papillosum* and var. *refractus* is included in *A. lacucha* (see p. 115, 119) and that included in var. *subsessilis* is transferred to *A. nitidus* (see p. 121, 122).

HULLETTIA

Hullettia King ex Hook.f., Fl. Brit. India 5 (1888) 547; King, Ann. Roy. Bot. Gard. (Calcutta) 5, 2 (1896) 163, t. 197; Engl. in Engl. & Prantl, Nat. Pflanzenfam. Nachtr. 1 (1897) 122; Boerl., Handl. Fl. Ned. Ind. 3 (1900) 338; Ridl., Fl. Malay Penins. 3 (1924) 358; F.M. Jarrett, J. Arnold Arbor. 41 (1960) 334.

Shrubs to small trees, monoecious. *Leaves* spirally arranged; lamina pinnately veined, entire; stipules free, lateral, subulate, subsistent. *Inflorescences* unisexual, solitary or in pairs in the leaf axils, discoid- to turbinate-capitate, pedunculate, with

a row of bracts at the margin of the receptacle (interfloral bracts present in staminate inflorescences, absent or rudimentary in pistillate ones?). *Staminate flowers* up to c. 30, completely fused and perianths indistinct; stamens 2, filaments partly connate. *Pistillate flowers* 2–6, completely fused and the perianths indistinct; ovaries free, stigma 1, capitate. *Infructescences* subglobose, fleshy, orange to yellow; pericarp crustaceous; seed without endosperm, embryo straight, longitudinally aligned, cotyledons equal, radicle basal, short.

Distribution — The genus comprises two closely related species and ranges from Myanmar to Sumatra.

Morphology — The discoid and involucrate inflorescences are reminiscent of the type found in some members of the Castilleae and species of *Dorstenia*, in which genus one of the species has been described. Small ovate to linear structures found among staminate flowers of *H. dumosa* probably represent interfloral bracts. Minute elevations with slightly different indumentum among the flowers of pistillate inflorescences may also represent such bracts, but quite rudimentary.

1. *Hullettia dumosa* King ex Hook.f.

Hullettia dumosa King ex Hook.f., Fl. Brit. India 5 (1888) 547; King, Ann. Roy. Bot. Gard. (Calcutta) 5, 2 (1896) 163, t. 197; Ridl., Fl. Malay Penins. 3 (1924) 358; Burkill, Dict. Econ. Prod. Malay Penins. (1935) 1202; F.M. Jarrett, J. Arnold Arbor. 40 (1959) 9, f. 2g–k; 41 (1960) 337; Kochummen, Tree Fl. Malaya 3 (1978) 162, t. 8.

Shrub or tree up to 10 m tall. *Leafy twigs* (2–)3–6 mm thick, densely puberulous. *Leaves* spirally arranged; lamina (narrowly) obovate to elliptic (to narrowly elliptic),

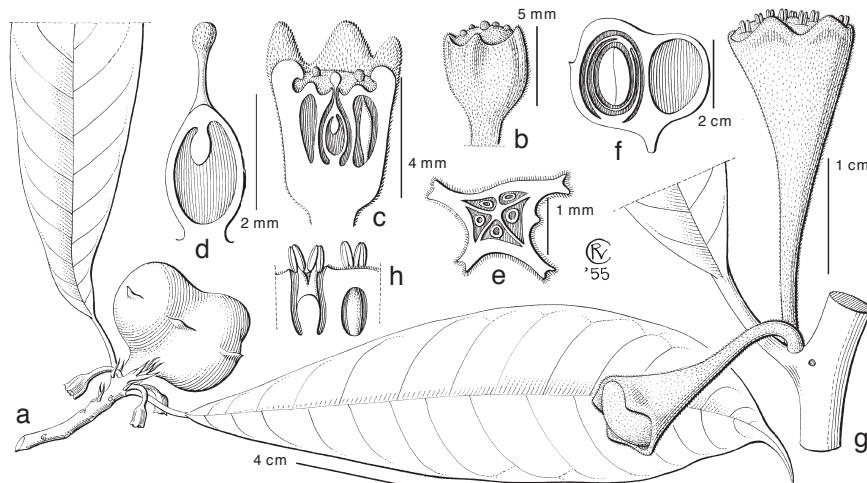


Fig. 21. *Hullettia dumosa* King ex Hook.f. a. Leafy twig with pistillate inflorescences and infructescence; b. pistillate inflorescence; c. pistillate inflorescence in length section; d. ovary in length section; e. pistillate inflorescence in tangential section; f. infructescences in length section; g. staminate inflorescences; h. part of staminate inflorescence in length section (a: Alvins 3290; b, d: Cameron s.n. 4-XI-1942; c, e: Ridley s.n. II-1921; f: Curtis 2404; g, h: Robinson s.n. 20-III-1913).

8–30(–40) by 3–9(–12) cm, coriaceous, apex acuminate, base rounded to cuneate, margin (sub)entire; upper surface glabrous; lower surface glabrous or very sparsely minutely puberulous on the midrib, ± scabrous or smooth; midrib ± prominent above, lateral veins 8–12(–15) pairs, tertiary venation reticulate (to subscalariform); petiole 1–3.5(–5) cm long, sparsely puberulous; stipules 0.3–1(–1.5) cm long, subulate, sparsely puberulous, subpersistent. *Staminate inflorescences* axillary, solitary or paired; peduncle 1–2 cm long, puberulous; receptacle discoid, c. 1 cm diam., puberulous outside, involucral bracts marginal, ovate, 3–4 mm long, puberulous; perianth c. 1.5 mm long, puberulous; stamens c. 3 mm long, filaments connate, anthers c. 1 mm long; interfloral bracts ovate to linear, puberulous. *Pistillate inflorescences* axillary, solitary or paired; peduncle 1.5–4.5(–5.5) cm long, puberulous; receptacle discoid, c. 1 cm diam., puberulous outside; involucral bracts ovate, 2–3 mm long, puberulous; flowers c. 8; perianth 1–1.5 mm long, apex densely minutely puberulous; stigmas clavate, 0.5–1 mm long. *Infructescences* subglobose to discoid, up to 5.5 cm diam., with 1–3 fruits, densely puberulous to hispidulous, often ± scabrous, orange at maturity. — **Fig. 21.**

Distribution — Thailand; in *Malesia*: Sumatra, Malay Peninsula.

Habitat — Evergreen forest at altitudes up to c. 1000 m.

Note — *Hullettia griffithii* (Kurz) King, the other species, known from peninsular Myanmar and Thailand, has not yet been recorded from *Malesia*. It is in many features similar to *H. dumosa*, but it can easily be recognised by the midrib of the lamina being slightly impressed above.

PARARTOCARPUS

Parartocarpus Baill., Adansonia 11 (1875) 294; Benth. & Hook.f., Gen. Pl. 3 (1880) 375; Engl. in Engl. & Prantl, Nat. Pflanzenfam. 3, 1 (1888) 82; Boerl., Handl. Fl. Ned. Ind. 3 (1900) 335; Becc., For. Borneo (1902) 632; Renner, Bot. Jahrb. Syst. 39 (1907) 361; Becc., Webbia 5 (1923) 559; F.M. Jarrett, J. Arnold Arbor. 41 (1960) 320; Corner, Gard. Bull. Singapore 19 (1962) 241; Backer & Bakh.f., Fl. Java 2 (1965) 17; Corner, Gard. Bull. Singapore 28 (1976) 183, t. 1–3.; Kochummen, Tree Fl. Malaya 3 (1978) 162; Go, Tree Fl. Sabah & Sarawak 3 (2000) 318.

Gymnartocarpus Boerl., Icon. Bogor. 1 (1897) 73, t. 24, 25; Handl. Fl. Ned. Ind. 3 (1900) 335; Engl. in Engl. & Prantl, Nat. Pflanzenfam. 2 (1900) 17; Koord. & Valeton, Bijdr. Boomsoort. Java 11 (1906) 28; Koord., Exkurs.-Fl. Java 2 (1912) 96; J.J. Sm., Bull. Jard. Bot. Buitenzorg III, 4 (1922) 233, t. 6–8.

Trees, dioecious. *Leaves* spirally arranged; lamina pinnately veined, entire; stipules fused, semi-amplexicaul. *Inflorescences* unisexual (or rarely bisexual), solitary in the leaf axils, pedunculate, with 3–8 large basally attached bracts at the base of the head, interfloral bracts with free apices similar to the free parts of the tepals, discoid to cushion shaped to aculeate. *Staminate inflorescences* (sub)globose or obovoid; flowers numerous, connate; perianth tubular, free parts thickened, cushion shaped to aculeate; stamens 1–3, mostly 2, filaments free or partly connate. *Pistillate inflorescences* (sub)globose; flowers numerous, connate except for the apices, apices discoid to cushion shaped to aculeate; ovary free, stigma 1. *Infructescences* with the indurated surface areolate or with cushion shaped to pyramidal to spinose processes; fruit with a firm exocarp finally decaying and leaving the stony endocarp; seed with remains of endosperm present, embryo curved, cotyledons incumbent and unequal, radicle long.

Distribution — The genus comprises two closely related species and ranges from Thailand to the Solomon Islands.

Delimitation — This genus differs from *Artocarpus* in the interpetiolar connate stipules, the well-developed basally attached bracts at the base of the head of the inflorescence, epigeal germination, and from most species of *Artocarpus* in the full connation of perianths of the pistillate flowers.

Morphology — It is not clear whether all structures indicated as processes represent the upper parts of tepals, or can be upper parts of interfloral bracts as well (see Jarrett, J. Arnold Arbor. 40 (1959) 7). Those surrounding the style and the androecium, two to four in number, are the free parts of perianths. Those not associated with style or stamens may represent interfloral bracts. However, in the neotropical genus *Naucleopsis* Miq., in which free parts of the tepals of pistillate flowers are aculeate to cushion shaped and indurated, the processes that are not clearly associated with styles can be regarded as derived from the perianth (see Berg, Fl. Neotrop. Monogr. 7 (1972) 107). In contrast to *Parartocarpus*, there is a clear tendency of increase of tepals in both staminate and pistillate flowers. Aculeate interfloral bracts are found in two species of the African genus *Treculia*; the third species of this genus has peltate interfloral bracts (see Berg, Bull. Jard. Bot. Belg. 47 (1977) 380). Variation of the shape of the processes rather similar to that as occurs in *P. venenosus* can be found in some *Naucleopsis* species.

The staminate and pistillate inflorescences are indistinguishable before anthesis.

KEY TO THE SPECIES

- 1a. Hairs on the lamina lower surface patent, usually dense; leafy twigs brown tomentose; stipules 0.5–1 cm long. — Sumatra, Malay Peninsula, Borneo **1. *P. bracteatus***
- b. Hairs on the lamina lower surface (\pm) appressed, usually sparse or absent; leafy twigs whitish to brownish, mostly appressed puberulous; stipules 0.2–0.4 cm long. — Widespread **2. *P. venenosus***

1. *Parartocarpus bracteatus* (King) Becc.

Parartocarpus bracteatus (King) Becc., For. Borneo (1902) 632; F.M. Jarrett, J. Arnold Arbor. 41 (1960) 324, t. 21a, d; Corner, Gard. Bull. Singapore 28 (1976) 186, t. 2a; Kochummen, Tree Fl. Malaya 3 (1978) 164, t. 9; Go, Tree Fl. Sabah & Sarawak 3 (2000) 319. — *Artocarpus bracteata* King in Hook.f., Fl. Brit. India 5 (1888) 540; King, Ann. Roy. Bot. Gard. (Calcutta) 2 (1889) 7 p.p. incl. t. 1B, *syncarpium solum*; Ridl., Fl. Malay Penins. 3 (1924) 352.

Artocarpus rufescens Kurz, Forest Fl. Burma 2 (1877) 431 (non Miq. 1861).

Tree up to 45 m tall, sometimes with buttresses. *Leafy twigs* 3–8 mm thick, densely brown (sub)tomentose. *Leaves* spirally arranged; lamina elliptic to obovate to sub-ovate, 8–20(–28) by 4–11(–14), coriaceous, apex short-acuminate to acute (to rounded), base rounded to cordate, margin entire, revolute; upper surface brownish puberulous, mainly on the main veins; lower surface \pm densely brownish puberulous on the veins; midrib slightly impressed above, lateral veins 8–18 pairs, tertiary veins scalariform; petiole 2–3.5 cm long, brownish puberulous to subtomentose; stipules

0.5–1 cm long, brownish puberulous, caducous. *Staminate inflorescences* axillary, solitary, capitate; peduncle 2–3.5 cm long, brown tomentose to puberulous; head globose, 2.5–3.5 cm diam.; involucral bracts 3, ovate, 0.5–1 cm long, brown tomentellous to puberulous; processes aculeate (or cushion shaped), c. 3 mm long and often slightly curved (or cushion shaped), (sub)glabrous; stamens 2, up to 8 mm long, filaments free or connate at the base, anthers 2.5–3 mm long, apiculate. *Pistillate inflorescences* axillary, solitary, capitate; peduncle 3–5.5 cm long, brown tomentose to puberulous; head globose, 2–3.5 cm diam.; involucral bracts 2–4, ovate, 0.5–1 cm long, brown tomentellous to puberulous; flowers numerous; processes aculeate, 2–4 mm long, often ± curved, basally connate in groups of 2–4 or free, subglabrous; stigmas subulate, 1–1.5 mm long. *Infructescences* subglobose, 5–9 cm diam., ± lobed, with numerous fruits; processes conical, up to 8 mm long. — **Fig. 22a–c.**

Distribution — Peninsular Thailand; in *Malesia*: Sumatra (also Simalur Island and Banka), Malay Peninsula, Borneo.

Habitat — Evergreen forest at altitudes up to 700 m.

Note — Two collections from Simalur Island (off Sumatra) match *P. bracteatus* in the features of the indumentum and the leaves, but the processes of the inflorescences are cushion shaped and resemble those of a form of *P. venenosus*.

2. *Parartocarpus venenosus* (Zoll. & Moritz) Becc.

Parartocarpus venenosus (Zoll. & Moritz) Becc., For. Borneo (1902) 632; F.M. Jarrett, J. Arnold Arbor. 41 (1960) 326, t. 21b, c, e–h; Backer & Bakh.f., Fl. Java 2 (1965) 18; Kochummen, Tree Fl. Malaya 3 (1978) 165, t. 9; Go, Tree Fl. Sabah & Sarawak 3 (2000) 323, t. 14.

Artocarpus venenosa Zoll. & Moritz, Natur-Geneesk. Arch. Ned.-Indie 2 (1845) 213; Flora 30 (1847) 471; Miq. in Zoll., Syst. Verz. 2 (1854) 89, 95; K. Schum., Notizbl. Königl. Bot. Gart. Berlin 1 (1895) 48. — *Gymnartocarpus venenosa* (Zoll. & Moritz) Boerl., Icon. Bogor. 1 (1897) 73, t. 24, 25; Handl. Fl. Ned. Ind. 3 (1900) 371; Koord. & Valetone, Bijdr. Boomsoort. Java 11 (1906) 28. — *Artocarpus venenosa* Zoll. & Moritz var. *tylophylla* Miq. in Zoll., Syst. Verz. 2 (1854) 89, 95. — *Artocarpus tylophylla* (Miq.) Miq., Fl. Ned. Ind. 1, 2 (1859) 289.

Artocarpus cerifera Miq., Ann. Mus. Bot. Lugduno-Batavi 3 (1867) 212.

Artocarpus riedelii Miq., Ann. Mus. Bot. Lugduno-Batavi 3 (1867) 213.

Parartocarpus beccarianus Baill., Adansonia 11 (1875) 294; Becc., For. Borneo (1902) 632.

Artocarpus forbesii King in Hook.f., Fl. Brit. India 5 (1888) 539; Ann. Roy. Bot. Gard. (Calcutta) 2 (1889) 7, t. 1A; Ridl., Fl. Malay Penins. 3 (1924) 352; S. Moore, J. Bot. 63, Suppl. (1925) 112. — *Parartocarpus venenosus* (Zoll. & Moritz) Becc. subsp. *forbesii* (King) F.M. Jarrett, J. Arnold Arbor. 40 (1959) 9–12, t. 2a–f, t. 3g–i, t. 4d; 41 (1960) 137, 333; Corner, Gard. Bull. Singapore 28 (1976) 187, t. 2c, 3, 4c; Go, Tree Fl. Sabah & Sarawak 3 (2000) 323.

Artocarpus involucrata K. Schum. in K. Schum. & Hollrung, Fl. Kais. Wilh. Land (1889) 39. — *Parartocarpus involucrata* (K. Schum.) K. Schum. & Lauterb., Fl. Schutzgeb. Südsee (1900) 267; Becc., For. Borneo (1902) 632; Lauterb., Bot. Jahrb. Syst. 62 (1928) 303; Diels, Bot. Jahrb. Syst. 67 (1935) 174; C.T. White, J. Arnold Arbor. 31 (1950) 82.

Parartocarpus papuana Becc., For. Borneo (1902) 633, non S. Moore 1923. — *Parartocarpus venenosus* (Zoll. & Moritz) Becc. subsp. *papuanus* (Becc.) F.M. Jarrett, J. Arnold Arbor. 41 (1960) 330; Corner, Gard. Bull. Singapore 28 (1976) 187, t. 2d, 4a.

Parartocarpus borneensis Becc., For. Borneo (1902) 634. — *Parartocarpus venenosus* (Zoll. & Moritz) Becc. subsp. *borneensis* (Becc.) F.M. Jarrett, J. Arnold Arbor. 41 (1960) 332; Corner, Gard. Bull. Singapore 28 (1976) 186, t. 2c; Go, Tree Fl. Sabah & Sarawak 3 (2000) 323.

Parartocarpus excelsa Becc., For. Borneo (1902) 634.

Artocarpus woodii Merr., Philipp. J. Sci., Bot. 3 (1908) 221; Elmer, Leafl. Philipp. Bot. 2 (1909) 623.

— *Parartocarpus woodii* (Merr.) Merr., Enum. Philipp. Flow. Pl. 2 (1923) 39. — *Gymnartocarpus woodii* (Merr.) Merr., Philipp. J. Sci. 18 (1921) 52; W.H. Br., Bull. Bur. Forest. Philipp. Islands 22, 2 (1921) 270, f. 19.

Gymnartocarpus triandra J.J. Sm., Bull. Jard. Bot. Buitenzorg III, 4 (1922) 233, t. 6–8. — *Parartocarpus triandra* (J.J. Sm.) J.J. Sm., Bull. Jard. Bot. Buitenzorg III, 6 (1924) 80; F.G. Browne, For. Trees Sar. & Brunei (1955) 357.

Parartocarpus microcarpus Corner, Gard. Bull. Singapore 28 (1976) 184, t. 1; Go, Tree Fl. Sabah & Sarawak 3 (2000) 320.

Parartocarpus spinulosus Go, Sandakania 12 (1998) 2, t. 1; Tree Fl. Sabah & Sarawak 3 (2000) 321, t. 13.

Tree up to 35 m tall, sometimes with low buttresses. *Leafy twigs* 3–7 mm thick, sparsely to rather densely whitish to brown appressedly puberulous. *Leaves* spirally arranged; lamina elliptic to obovate to subobovate to narrowly obovate, 4–20(–30) by 2.5–8(–10), coriaceous, apex rounded to short-acuminate, base rounded to cuneate or to subcordate, margin entire, flat or slightly (sometimes distinctly) revolute; upper surface (sparsely) whitish puberulous, mainly on the main veins to subglabrous, smooth (or scabrous); lower surface sparsely to rather densely whitish ± appressedly puberulous on the veins to subglabrous, smooth (or scabrous); midrib slightly impressed to flat above, lateral veins 6–16 pairs, tertiary venation scalariform to reticulate; petiole 1.5–5.5 cm long, sparsely to rather densely whitish puberulous; stipules 0.2–0.4 cm long, whitish puberulous, caducous. *Staminate inflorescences* axillary, solitary, capitate; peduncle 2–5.5 cm long, sparsely whitish puberulous; head globose to ovoid, 1.5–3 cm diam.; involucral bracts 3–4(–8), ovate, 0.2–0.6 cm long, puberulous or subglabrous; processes apiculate to conical, umbonate, or ± cushion shaped and depressed in the centre, 0.5–1.5 mm long, glabrous; stamens (1 or) 2 (or 3), 6–8 mm long, filaments partly connate or free, anthers 1.5–2.5 mm long, apiculate or not. *Pistillate inflorescences* axillary, solitary, capitate; peduncle 3–10 cm long, brown tomentose to puberulous; head globose, 2–3.5 cm diam.; involucral bracts 3–4(–8), ovate, 0.2–0.6 cm long, puberulous or subglabrous; flowers numerous; processes apiculate to conical, umbonate, 0.5–3 mm high, connate in groups of 2–4 or free, glabrous or minutely puberulous to muriculate; stigmas tongue-shaped, 1–1.5 mm long, acute. *Infructescences* subglobose, 5–18 cm diam., ± lobed, with numerous fruits; processes conical to aculeate or cushion shaped and apiculate or depressed in the centre to discoid, up to 10 mm long. — **Fig. 22d–j.**

Distribution — Peninsular Thailand, Solomon Islands; in *Malesia*: Sumatra (also Enggano, Riouw-Lingga Islands), Malay Peninsula, Borneo, Java, Philippines (Luzon, Mindoro, Samar, Leyte, Mindanao), Celebes, the Moluccas (Aru Islands) New Guinea (incl. New Britain, Manus Island, Schouten Island, Yapen, Salawati).

Habitat — Forest at altitudes up to 1000 m, in Borneo up to 1800 m; tolerating a short dry season.

Uses — The latex is used as arrow poison. The ripe infructescence is (said to be) edible; unripe seeds are poisonous.

Notes — 1. *Parartocarpus microcarpus* Corner (1976) is included as the morphological differences between the material referred to this taxon and material referred to *P. venenosus* are too small to justify recognition as distinct taxa. In the material

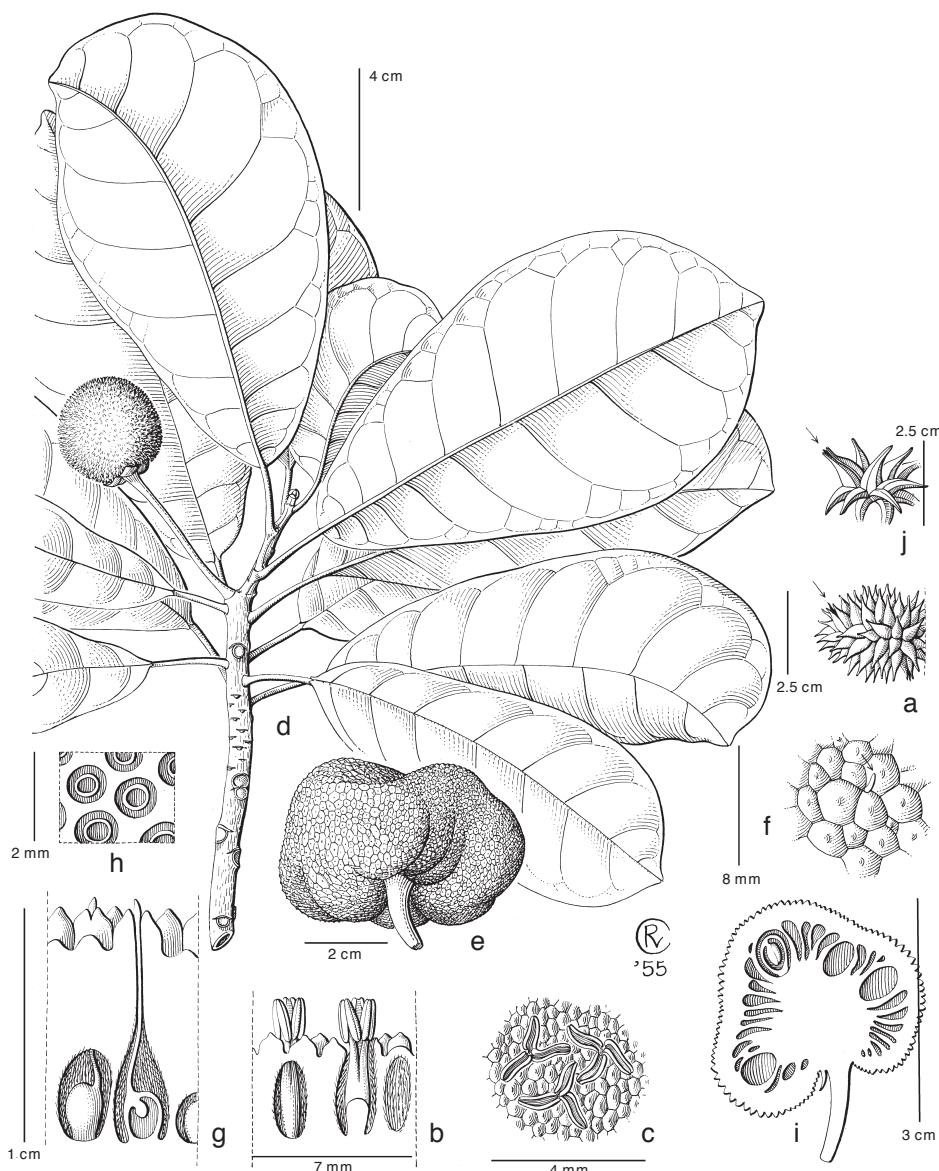


Fig. 22. a–c: *Parartocarpus bracteatus* (King) Becc. a. Surface view of pistillate inflorescence (arrow indicating stigmas); b. part of young staminate inflorescence at anthesis in section; c. surface view of older staminate inflorescence (with stamens exserted between processes). — d–j: *Parartocarpus venenosus* (Zoll. & Moritzi) Becc. d. Leafy twig and pistillate inflorescence; e. pistillate inflorescence; f. surface of pistillate inflorescence; g. in section; h. tangential section of part of pistillate inflorescence at anthesis; i. infructescence in section; j. surface view of infructescence (arrow indicating stigmas) (a: Sinclair 39426; b: Corner SFN 28145; c: Beguin 583; d–f: Brass 7476; g–i: Corner SFN 28145; j: Krukoff 4124).

referred to *P. microcarpus* the processes of the inflorescences are cushion shaped and mostly depressed in the centre, a feature which is also found in several collections from the Philippines and Celebes and from lowland localities. The collections referred to *P. microcarpus* are from altitudes between 1000 and 1800 m and may represent a small-leaved montane form of the species.

2. The species is variable, in particular in the shape of the processes of the inflorescences, and, most pronouncedly so, of the infructescences in which they vary from discoid to cushion shaped (either with an apiculate or depressed centre) to conical to aculeate (and then up to 10 mm long). Those with conical or aculeate processes are similar to those of *P. bracteatus*.

3. Collections *Leopold & Taha SAN 83547* and *Soepadmo et al. FRI 41312* (the type collection of *P. spinulosus*), both from Sabah, Sandakan district, are aberrant by the scabrous lamina with a distinctly revolute margin. The processes of the fruiting pistillate inflorescence are cushion shaped and radially ribbed. Collection *De Vogel 6216* from Celebes has similar processes and the margin of the lamina is also distinctly revolute, but the surfaces are smooth. Examination of more fertile material is needed before deciding on the identity and status of these forms.

PRAINEA

Prainea King ex Hook.f., Fl. Brit. India 5 (1888) 546; King, Ann. Roy. Bot. Gard. (Calcutta) 5, 2 (1896) 162, t. 196; Engl. in Engl. & Prantl, Nat. Pflanzenfam. Nachtr. 1 (1897) 122; Boerl., Handl. Fl. Ned. Ind. 3 (1900) 337; Becc., For. Borneo (1902) 635; Webbia 5 (1923) 563; Ridl., Fl. Malay Penins. 3 (1924) 358; Steenis, Bull. Jard. Bot. Buitenzorg III, 12 (1932) 259; F.M. Jarrett, J. Arnold Arbor. 40 (1959) 30; Corner, Gard. Bull. Singapore 19 (1962) 243; Kochummen, Tree Fl. Malaya 3 (1978) 165; Go, Tree Fl. Sabah & Sarawak 3 (2000) 326; C.C. Berg, Blumea 50 (2005) 545. — *Artocarpus* J. & G. Forst. sect. *Prainea* (King) Renner, Bot. Jahrb. Syst. 39 (1907) 366.

Trees or climbers, dioecious. *Leaves* distichous; lamina pinnately veined, entire; stipules free, lateral. *Inflorescences* unisexual, solitary or in pairs in the leaf axils, globose- to obovoid-capitate, pedunculate, with peltate, subpeltate, clavate or spatulate interfloral bracts. *Staminate flowers* numerous; perianth tubular, 2-lobed to entire; stamen 1. *Pistillate flowers* numerous, free; perianth tubular; ovary free, stigmas 2. *Infructescences* with enlarged perianths of some (1–20) of the flowers, the bracts not enlarged; pericarp membranaceous; seed with the testa absorbed except the thickened saucer-shaped basal portion, endosperm absent, embryo straight, longitudinally aligned, cotyledons equal, appressed faces oblique to median plane of ovary, radicle apical, minute; interfloral bracts persistent.

Distribution — This Malesian genus comprises two closely related species and ranges from the Malay Peninsula to New Guinea.

Morphology — The flowers and bracts of the pistillate inflorescence are free in contrast to those in the related genera *Artocarpus*, *Hullettia*, and *Parartocarpus*.

In both species, only a small number of the pistillate flowers set fruit. Uncinate hairs are present in *P. scandens*.

KEY TO THE SPECIES

- 1a. Tertiary venation distinctly scalariform; lamina often sparsely hairy above and/or beneath **1. *P. limpato***
 b. Tertiary venation reticulate or subscalariform with 1 or 2 ± straight intercostals; lamina glabrous **2. *P. scandens***

1. *Prainea limpato* (Miq.) Beumée ex K. Heyne

Prainea limpato (Miq.) Beumée ex K. Heyne, Nutt. Pl. Ned.-Ind., ed. 2 (1927) 579; F.M. Jarrett, J. Arnold Arbor. 40 (1959) 34; Kochummen, Tree Fl. Malaya 3 (1978) 167; Go, Tree Fl. Sabah & Sarawak 3 (2000) 327, t. 15. — *Artocarpus limpato* Miq., T.S. Liu, Eerste Bijv. (1861) 421; Renner, Bot. Jahrb. Syst. 39 (1907) 367.

Tree up to 30 m tall, sometimes with buttresses. *Leafy twigs* 2–5 mm thick, sparsely and minutely puberulous. *Leaves* distichous; lamina subobovate to elliptic, (4–)10–30(–40) by (2.5–)4–13 cm, often ± asymmetric, at least at the base, coriaceous, apex acuminate, base cuneate to rounded to subcordate (at one side) or to subauriculate, margin entire, often ± revolute (towards the base); upper surface glabrous, or puberulous on the veins; lower surface sparsely appressedly puberulous on the main veins to glabrous, scabridulous or smooth; midrib slightly prominent above, lateral veins (8–)12–20(–25) pairs, tertiary venation scalariform; petiole (0.3–)0.8–2(–3.5) cm long, sparsely puberulous to subglabrous, the epidermis often flaking off; stipules c. 0.2 cm long, puberulous or glabrous, caducous. *Staminate inflorescences* axillary, solitary, capitate; peduncle 1.5–4(–6) cm long, minutely puberulous (or glabrous); head globose, (0.3–)0.5–1.5(–1.8) cm diam.; perianth c. 1.5 mm long, densely minutely puberulous at the apex; stamen c. 1.8 mm long, anther c. 0.4 mm long; bracts peltate, 1.5–2 mm long, the apical part 0.2–0.3 mm diam., whitish to brownish minutely puberulous. *Pistillate inflorescences* axillary, solitary, capitate; peduncle 1–20(–25) cm long, minutely puberulous; head globose, 0.8–2.5 cm diam.; flowers numerous; perianth 3–4 mm long, densely to sparsely minutely puberulous at the apex; stigmas tongue-shaped, bifid or simple, 0.3–1 mm long; bracts (sub)peltate, 2.5–3 mm long, the upper part 0.3–0.4 mm diam., whitish to brownish minutely puberulous. *Infructescences* sub-globose, 1.5–5 cm diam., with numerous protruding fruiting perianths, these ellipsoid to ovoid, (0.8–)1.2–2.5 cm long, (sub)glabrous, yellowish to reddish at maturity.

Distribution — Sumatra, Malay Peninsula, Borneo, Moluccas, New Guinea.

Habitat — Primary and secondary evergreen forest at altitudes up to 600 m, in New Guinea up to 1200 m.

Note — The differences between the collections referred to *P. limpato* and *P. papuana* are rather small and quantitative. Treating the western and eastern Malesian entities as subspecies appears to be preferable.

a. subsp. *limpato*

Urostigma diepenhorstii Miq., Fl. Ned. Ind., Eerste Bijv. (1861) 439. — *Ficus diepenhorstii* (Miq.)

King, Ann. Roy. Bot. Gard. (Calcutta) 1 (1888) 181.

Prainea cuspidata Becc., For. Borneo (1902) 636.

Prainea multinervia Merr., Philipp. J. Sci. 29 (1926) 364; Pl. Elmer. Born. (1929) 46.

Prainea limpato (Miq.) Beumée ex K. Heyne var. *longipedunculata* Kochummen, Malaysian Forester 41 (1978) 29; Tree Fl. Malaya 3 (1978) 167, t. 10.

Lamina often scabridulous beneath; lateral veins (9–)13–20(–25) pairs. *Staminate inflorescences*: peduncle 2–4(–6) cm long; head 0.8–1.3(–1.5) cm diameter. *Pistillate inflorescences*: peduncle 7–20(–25) cm long; head 1–2(–2.5) cm diameter. *Fruiting perianth* ellipsoid to ovoid, (1.2–)1.5–2(–2.5) cm long.

Distribution — Sumatra (also Enggano), Malay Peninsula (Kedah), Borneo (also Bangey Island).

Uses — Ripe infructescences are eaten.

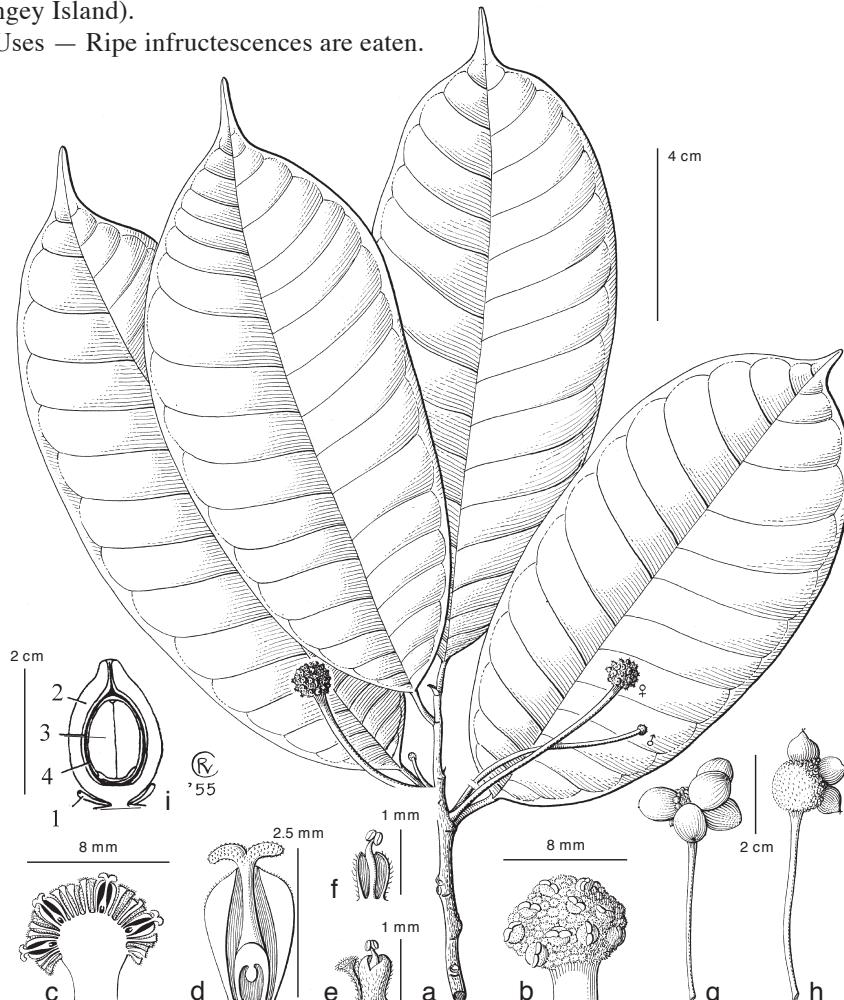


Fig. 23. *Prainea limpato* (Miq.) Beumée ex K. Heyne subsp. *papuana* (Becc.) C.C. Berg. a. Leafy twig with pistillate inflorescences; b. pistillate inflorescence; c. pistillate inflorescence in length section; d. pistillate flower; e. staminate flower with interfloral bract; f. staminate flower with interfloral bract in length section; g, h. infructescences; i. fruit in length section: 1 = unexpanded pistillate flower, 2 = fruiting perianth, 3 = embryo, 4 = testa (a, e, f: Beguin 1980; b, c, d, g, i: Beguin 1926; h: Forbes s.n.).

b. subsp. *papuana* (Becc.) C.C. Berg

Prainea limpato (Miq.) Beumée ex K. Heyne subsp. *papuana* (Becc.) C.C. Berg, Blumea 50 (2005) 545. — *Prainea papuana* Becc., For. Borneo (1902) 635; F.M. Jarrett, J. Arnold Arbor. 40 (1959) 35, f. 1a–e, 3a–c. — *Artocarpus papuanus* (Becc.) Renner, Bot. Jahrb. Syst. 39 (1907) 367, non Diels 1936. — *Parartocarpus papuana* S. Moore, J. Bot 61, Suppl. (1923) 52, non Becc. 1902. *Prainea microcephala* J.J. Sm., Bull. Jard. Bot. Buitenzorg III, 6 (1922) 80.

Lamina smooth beneath; lateral veins (8–)12–16(–20) pairs. *Staminate inflorescences*: peduncle 1.5–4 cm long; head 0.3–0.8 cm diameter. *Pistillate inflorescences*: peduncle 2–12 cm long; head (0.5–)0.8–1.5(–1.8) cm diameter. *Fruiting perianth* subglobose to ovoid, 0.8–1.3(–1.5) cm long. — **Fig. 23.**

Distribution — Moluccas (Morotai, Halmahera, Ceram, Ternate, Batjan, Obi), New Guinea (also Yapen, D'Entrecasteaux and Louisiade Islands, but not in the Bismarck Archipelago).

Habitat — Rain forest, also in secondary forest at altitudes up to 1200 m.

2. *Prainea scandens* King ex Hook.f.

Prainea scandens King ex Hook.f., Fl. Brit. India 5 (1888) 547; King, Ann. Roy. Bot. Gard. (Calcutta) 5, 2 (1896) 162, t. 196; Ridl., Fl. Malay Penins. 3 (1924) 358; F.M. Jarrett, J. Arnold Arbor. 40 (1959) 32. — *Artocarpus scandens* (Hook.f.) Renner, Bot. Jahrb. Syst. 39 (1907) 367.

Prainea frutescens Becc., For. Borneo (1902) 635; F.M. Jarrett, J. Arnold Arbor. 40 (1959) 33; Go, Tree Fl. Sabah & Sarawak 3 (2000) 327. — *Artocarpus frutescens* (Becc.) Renner, Bot. Jahrb. Syst. 39 (1907) 367.

Tree up to 30 m tall or climber. *Leafy twigs* 1.5–2.5 mm thick, sparsely and minutely puberulous, partly with uncinate hairs, or glabrous. *Leaves* distichous; lamina subobovate to elliptic, 5–16 by 3–7 cm, coriaceous, apex acuminate, base cuneate to rounded, margin entire; upper and lower surface glabrous; midrib slightly prominent above, lateral veins 6–13 pairs, tertiary venation reticulate (to subscalariform with 1 or 2 ± straight intercostals); petiole 0.7–1.8 cm long, sparsely and minutely puberulous to glabrous, the epidermis often flaking off; stipules c. 0.2 cm long, glabrous, caducous. *Staminate inflorescences* axillary, solitary, capitate; peduncle 0.5–1.5 cm long, minutely puberulous; head globose to obovoid, 0.4–0.6 cm diam.; perianth c. 0.8 mm long, densely minutely puberulous at the apex; stamen c. 1.2 mm long, anther 0.2–0.3 mm long; bracts subpeltate, 0.8–1 mm long, the apical part 0.2–0.5 mm diam., whitish minutely puberulous. *Pistillate inflorescences* axillary, solitary, capitate; peduncle 1–2.5 cm long, puberulous; head globose, c. 1 cm diam.; flowers c. 20–30; perianth 2.5–3 mm long, densely minutely puberulous; stigmas tongue-shaped, 0.5–2 mm long; bracts spatulate to truncate-clavate to subulate or to peltate, 2.5–3 mm long, the apical part 0.2–0.5 mm diam., densely whitish minutely puberulous. *Infructescences* subglobose, 1.5–2.5 cm diam., with 1–7 protruding fruiting perianths, these ellipsoid to ovoid, 1.5–2.5 cm long, puberulous at the apex, red at maturity. — **Fig. 24.**

Distribution — Peninsular Thailand; in *Malesia*: Malay Peninsula (Perak, Selangor), Borneo.

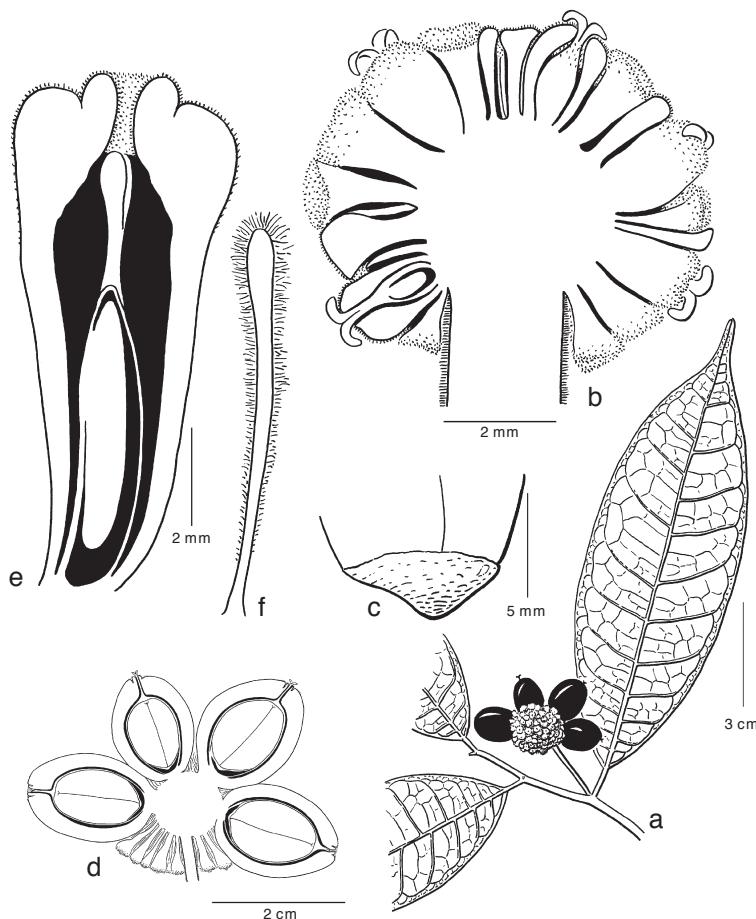


Fig. 24. *Prainea frutescens* King ex Hook.f. a. Leafy twig with infructescence; b. pistillate inflorescence in length section; c. base of seed with cotyledons and remains of testa; d. infructescence in length section; e. pistillate flower in length section; f. bract in inflorescence (a, c, d, f: SAN 43596; b, e: Haviland 3102).

Habitat — Forest, sometimes edges of peat swamps; at altitudes up to 800 m.

Notes — 1. The differences between material from the Malay Peninsula and Borneo are so small that they do not provide a basis to maintain two regional species, *P. scandens* and *P. frutescens*, respectively.

2. It is not clear how frequently and under which conditions the lianescent habit is developed.

3. Collection FRI 17082 indicated as ‘*Artocarpus* sp. A’ by Kochummen (Tree Fl. Malaya 3 (1978) 134) belongs to this species.

Tribe CASTILLEAE

Castilleae C.C. Berg, Acta Bot. Neerl. 26 (1977) 78. — ‘*Olmediae*’ Trécul, Ann. Sci. Nat., Bot. sér. 3, 8 (1847) 126, excl. *Olmedia*, being included in *Trophis*; Corner, Gard. Bull. Singapore 19 (1962) 243.

Trees or shrubs with the architectural model of Cook, dioecious or monoecious, without uncinate hairs. Leaves alternate, spirally arranged (on the main branches) and distichous (on the lateral branches); stipules fully to semi-amplexicaul. Inflorescences on the lateral branches, unisexual, capitate, discoid to cup-shaped with an involucre of basally attached bracts, pedunculate or sessile, interfloral bracts lacking (?) or structures derived from the perianth). Staminate flowers complete or with reduction in the perianth and androecium, pistillode mostly absent. Pistillate flowers with the tepals ± connate, ovary usually ± adnate to the perianth, stigmas 2 and equal. Fruit(s) forming a drupaceous whole with the perianth, with other flowers, or also with the receptacle; seed large, without endosperm, testa with or without a thickened vascularised part, embryo longitudinally aligned, with thick, equal or subequal, sometimes unequal cotyledons, radicle short and apical.

Distribution — The tribe comprises six neotropical genera (see Berg, Fl. Neotrop. Monogr. 7 (1972) 1; 83 (2001) 244) for which at present 54 species are recognised. The tribe is centred in South America. Two monotypic genera are palaeotropical: *Antiaris* ranging from the African continent to Madagascar and Yemen and from Sri Lanka to the Pacific, and *Mesogyne* confined to tropical Africa (see Berg, Bull. Jard. Bot. Belg. 47 (1977) 323).

Morphology — The tribe is characterised by the tree architecture described as the model of Cook (Hallé & Oldeman, Essai sur l’architecture et la dynamique de croissance des arbres tropicaux (1970) 110). The leaves on the stem and orthotropic branches are spirally arranged, and in the axils of each of these leaves plagiotropic branches are formed sylleptically. Inflorescences are borne on these branches, often on axillary short-shoots. The plagiotropic branches are abscised; the bases of the shed branches are conical leaving a depression in the stem. This model requires accessory buds which in the neotropical taxa are lateral but axillary in the palaeotropical genera (see Berg, Acta Bot. Neerl. 26 (1977) 73).

In the neotropical genera the involucre of imbricate bracts of the pistillate inflorescences covers the outer surface of the receptacle. In the palaeotropical genera the involucral bracts are more or less scattered on the lower part of the receptacle and concentrated in the uppermost part.

Chemistry — Cardiotoxic compounds have been found in several representatives of the tribe (see p. 12 and 17).

KEY TO THE GENERA

- 1a. Stipules not fully amplexicaul, free; pistillate inflorescences uniflorous; receptacle of the staminate inflorescence discoid. — Widespread **Antiaris**
- b. Stipules fully amplexicaul, fused; pistillate inflorescences with numerous flowers; receptacle of the staminate inflorescence flabellate and bivalvate (or infundibuliform to cyathiform). — Introduced **Castilla**

CASTILLA

Castilla Sessé in Cerv., Gaz. Lit. Mexico, Suppl. (2.vii.1794) 7; Endl., Gen. Pl. (1837) 282, ‘*Castilloa*’; Trécul, Ann. Sci. Nat., Bot. sér. 3, 8 (1847) 136; Baill., Hist. Pl. 6 (1875) 204; Benth. & Hook.f., Gen. Pl. 3 (1880) 372; Engl. in Engl. & Prantl, Nat. Pflanzenfam. 3, 1 (1888) 84; Boerl., Handl. Fl. Ned. Ind. 3 (1900) 328; O.F. Cook, Science n.s. 18 (1903) 436; Pittier, Contr. U.S. Natl. Herb. 13 (1910) 247; Woodson, Ann. Missouri Bot. Gard. 47 (1960) 139; C.C. Berg, Fl. Neotrop. Monogr. 7 (1972) 92; 83 (2001) 269.

Trees, monoecious or (andro)dioecious. *Lamina* chartaceous, more or less scabrous above, ± hairy; stipules fully amplexicaul, connate, with distinct parallel veins. *Stamine inflorescences* pedunculate, flabellate and bivalvate (these occurring together with pistillate ones), infundibuliform to cyathiform, entire to 2-lobed; stamens solitary or paired along radiating and branching ridges of the receptacle which bears membranaceous, free or connate interstaminal ‘bracts’ (probably representing reduced perianths). *Pistillate inflorescences* solitary, sessile, discoid to cupuliform or subglobose, many- to several-flowered; ovary free, partly adnate to the perianth, or immersed in the receptacle; stigmas strap-shaped, short.

Distribution — The genus is neotropical and comprises three species. Two species have been economically important for the rubber they yield: the Central American – Pacific Coastal *C. elastica* Sessé and the Amazonian *C. ulei* Warb.

1. *Castilla elastica* Sessé

Castilla elastica Sessé in Cerv., Gaz. Lit. Mexico, Suppl. (2.vii.1794) 7, Trécul, Ann. Sci. Nat., Bot. sér. 3, 8 (1847) 137, f. 139–148, ‘*Castilloa*’; Hook.f., Trans. Linn. Soc. London 2 (1886) 206; Koord. & Valeton, Bijdr. Boomsoort. Java 11 (1906) 3; Merr., Fl. Manila (1912) 177; Exkurs.-Fl. Java 2 (1912) 97; Merr., Enum. Philipp. Flow. Pl. 2 (1923) 44; Koord., Atlas Baumart. Java (1924) t. 761; Worth., Ceylon Trees (1959) 418; Woodson, Ann. Missouri Bot. Gard. 47 (1960) 140, f. 50; Little & Wadsw., Trees Puerto Rico & Virgin Is. 1 (1964) 64, fig.; Backer & Bakh.f., Fl. Java 2 (1965) 19; C.C. Berg, Fl. Neotrop. Monogr. 7 (1972) 94.

Tree up to 30(–40) m tall, monoecious or (andro)dioecious. *Leafy twigs* 2–12 mm thick, hirsute to hirtellous to velutinous. *Leaves* distichous on lateral branches; lamina elliptic to subobovate or to subovate, (10–)15–40(–55) by (5–)7–20(–30) cm, (almost) symmetric, chartaceous, apex acuminate, base (sub)cordate, margin dent(icul)ate; upper surface hispidulous, ± scabrous; lower surface hirtellous to subhirsute or strigose to subsericeous, midrib slightly prominent, lateral veins (10–)18–21(–25) pairs, tertiary venation scalariform; petiole 0.5–2(–10) cm long, hirtellous; stipules 1–11.5 cm long, sericeous to hirtellous to hirsute, on the margins tomentellous. *Stamine inflorescences*, if not accompanying pistillate ones, then peduncle 3–15 mm long; receptacle flabellate and 2- (or 3-)valved, 1–2.5 by 0.7–2(–2.5) cm; involucral bracts in 10–12 rows; if accompanying pistillate inflorescences, then peduncle 0–10 mm long; receptacle infundibuliform to cyathiform, 5–20 mm diam.; involucral bracts in 7–12 rows. *Pistillate inflorescences* discoid-capitate, 10–20 mm diam., (sub)sessile; involucral bracts in 5–10 rows, flowers numerous; stigmas strap-shaped. *Fruiting perianth* red to orange; fruit 8–10 by 5–7 mm.

Subdivision — Three subspecies are recognised, only the typical subspecies introduced in Malesia.

a. subsp. *elastica*

Ficus gummifera Bertol., Mem. Reale Accad. Sci. Ist. Bologna, ser. 1, 10 (1858) 40, t. 9. — *Castill(o)a gummifera* (Bertol.) Standl., Contr. U.S. Natl. Herb. 20 (1917) 34.

Castill(o)a lactiflua O.F. Cook, Science n.s. 18 (1903) 269.

Castill(o)a nicoyensis O.F. Cook, Science n.s. 18 (1903) 438.

Castill(o)a guatemalensis Pittier, Contr. U.S. Natl. Herb. 13 (1910) 34.

Lower surface of the lamina with patent hairs on the lateral veins or also on the midrib; fruiting perianths only basally connate.

Distribution — Central America, from Mexico to Costa Rica; introduced in Malesia, mainly in botanical gardens.

Uses — In Java, Sumatra, and the Philippines (still?) used as shade tree in cacao and coffee plantations.

Note — From this particular subspecies (known as Caicho, Central American Rubber or Panama Rubber) rubber has been extracted commercially and introduced to many tropical countries, but was soon eclipsed by the commercial success of *Hevea brasiliensis*.

ANTIARIS

Antiaris Lesch., Ann. Mus. Hist. Nat. Paris 16 (1810) 478, nom. cons.; R.Br. in Flinders, Voy. Terra Austral. (1814) 602; Blume, Rumphia 1 (1836) 56; Endl., Gen. Pl. (1837) 280; Trécul, Ann. Sci. Nat., Bot. sér. 3, 8 (1847) 142, f. 158–162; Baill., Hist. Pl. 6 (1875) 203; Benth. & Hook.f., Gen. Pl. 3 (1880) 371; Engl. in Engl. & Prantl, Nat. Pflanzenfam. 3, 1 (1888) 85; Bot. Jahrb. Syst. 33 (1902) 119; Welt Afr. 3, 1 (1915) 33, f. 20; Hutch., Fl. Trop. Afr. 6, 2 (1917) 223; Leandri, Fl. Madagascar. fam. 55 (1952) 30, f. vi; Corner, Gard. Bull. Singapore 19 (1962) 244; C.C. Berg, Bull. Jard. Bot. Belg. 47 (1977) 308; 48 (1978) 466.

Ipo Pers., Syn. 2 (1807) 566, nom. rejic.

Antscha Horsf., Verh. Batav. Gen. 7 (1814) 8.

Toxicaria Aepnel. in Steud., Nomencl. ed. 2 (1841) 694, non Schreb. 1783.

Lepurandra Graham, Cat. Pl. Bombay (1839) 193.

Trees, monoecious or dioecious. *Leaves* chartaceous to subcoriaceous, more or less hairy, margin subentire to denticulate; stipules semi-amplexicaul, free. *Inflorescences* on short-shoots in the axils of the leaves or below the leaves, with 1 or 2 pistillate inflorescences (on the lower nodes of the short-shoot) and/or up to c. 8 staminate ones. *Staminate inflorescences* discoid, pedunculate, bracts many, basally attached, those on the margin of the receptacle in 1–3 rows, imbricate, forming an involucre; flowers many, with 2–7 free tepals; stamens 2–4, straight before anthesis, anthers latrorse to extrorse; pistillode absent. *Pistillate inflorescences* sessile or pedunculate, with an involucre of several basally attached imbricate bracts; flowers 1, occasionally 2; perianth 4-lobed, the lower part adnate to the receptacle; ovary adnate to the embedded part of the perianth; stigmas 2. *Infructescences* with an orange to scarlet, fleshy receptacle, forming a whole with the fruit, the involucral bracts scattered on its outer surface; endocarp crustaceous.

Distribution — The genus comprises a single very variable species, occurring in continental tropical Africa, Yemen, Madagascar, and from Sri Lanka to Tonga.

1. *Antiaris toxicaria* Lesch.

Antiaris toxicaria Lesch., Ann. Mus. Hist. Nat. Paris 16 (1810) 478, t. 22; Blume, Rumphia 1 (1836) 56, t. 22, 23; Hook., Companion Bot. Mag. 1 (1836) 310, t. 17, cum syn. *Antiaris dubia* Span., nomen; Benn. in Benn. & R.Br., Pl. Jav. Rar. (1838) 52, t. 13; Trécul, Ann. Sci. Nat., Bot. sér. 3, 8 (1847) 143; Miq., Fl. Ned. Ind. 1, 2 (1859) 291; Fl. Ned. Ind., Eerste Bijv. (1861) 423; Ann. Mus. Bot. Lugduno-Batavi 3 (1867) 214; Baill., Hist. Pl. 6 (1875) 203, f. 119–121; Kurz, Forest Fl. Burma 2 (1877) 462; Fern.-Vill., Nov. App. (1880) 102; S. Vidal, Sin. Gen. Pl. Leños Filip. (1883) 40, t. 88 f. A; Hook.f., Fl. Brit. India 5 (1888) 537; Engl. in Engl. & Prantl, Nat. Pflanzenfam. 3, 1 (1888) 85, f. 64; Hook.f. in Trimen, Handb. Fl. Ceylon 4 (1898) 97; Becc., For. Borneo (1902) 594; Koord. & Valeton, Bijdr. Boomsoort. Java 11 (1906) 274; Renner, Bot. Jahrb. Syst. 39 (1907) 374; Merr., Philipp. J. Sci., Bot. 2 (1907) 111; Koord., Exkurs.-Fl. Java 2 (1912) 97; Merr., Interpr. Herb. Amboin. (1917) 192; Enum. Born. Pl. (1921) 220; Enum. Philipp. Flow. Pl. 2 (1923) 44; Ridl., Fl. Malay Penins. 3 (1924) 351; Koord., Atlas Baumart. Java (1924) t. 762; Gagnep., Fl. Indo-Chine 5 (1928) 721, f. 98: 1–8; Corner, Wayside Trees Malaya (1940) 648; Steenis, Blumea 6 (1948) 258; Worth., Ceylon Trees (1959) pl. 419; Corner, Gard. Bull. Singapore 19 (1962) 248; C.C. Berg, Bull. Jard. Bot. Belg. 47 (1977) 310; 48 (1978) 466; Kochummen, Tree Fl. Malaya 3 (1978) 120; Boer, Brink & Sosef, Prosea 12, 1 (1999) 126, cum t.; Go, Tree Fl. Sabah & Sarawak 3 (2000) 185, t. 1. — [*Arbor toxicaria mas* Rumph., Herb. Amboin. 2 (1741) 263, t. 87.]

Trees up to 50 m tall, (always?) deciduous. Leafy twigs 2–5 mm thick, brownish hirtellous to puberulous. Leaves distichous on the lateral branches; lamina elliptic to (sub)ovate or to (sub)ovate, 5–20(–30) by 2.5–10(–12) cm, ± asymmetric, chartaceous to subcoriaceous, apex short-acuminate to subacute or obtuse (to rounded), base cordate to rounded, margin entire or denticulate (towards the apex); upper surface puberulous to hispidulous, scabrous or (sub)glabrous and smooth; lower surface densely to (very) sparsely puberulous to hirtellous or to subtomentose on the veins, smooth; midrib slightly prominent to flat above, lateral veins 7–12 pairs, tertiary venation scalariform; petiole 0.3–1.2 cm long, puberulous to hirtellous; stipules 0.4–1 cm long, puberulous, caducous. Staminate inflorescences up to 4 together, in leaf axils, on short-shoots or at the base of lateral branches; peduncle 5–15 mm long, puberulous; head discoid, 5–12(–20) mm diam.; involucral bracts in c. 4 rows, ovate, 1–2 mm long, minutely puberulous; tepals (2–)3–5(–7), spatulate-cucullate, 1–2 mm; stamens 3 or 4, 1–2 mm long, anthers 0.8–1.8 mm long. Pistillate inflorescences solitary or in pairs on short-shoots; peduncle 3–5 mm, in fruit up to 1 cm long, puberulous; receptacle with 6–12 bracts, most of them crowded at the apex, 0.5–1 mm long, minutely puberulous; stigmas 5–15 mm long. Inflorescences ellipsoid, 1.2–4.5 cm long, red to crimson at maturity; seed ellipsoid, 0.5–2 cm long. — **Fig. 25.**

Distribution — Tropical Africa, Madagascar, Yemen, from Sri Lanka and South India to South China, Indochina, Thailand, and the Pacific (Tonga); in Malesia: throughout.

Uses — The milk sap is used to prepare arrow poison, the active substances in which cardiac glycosides (cardenolides), including forms of antiarin, which arrest the heart (see Bennett in Bennett & R. Brown, Pl. Jav. Rar (1838) 52; Bissett, Ann. Bogor. 2 (1957) 219, Planta Med. 10 (1962) 143; Lloydia 29 (1966) 1, 172; Burkhill, Dict. (1935) 174; K. Heyne, Nutt. Pl. (1950) 566; Teijsm., Natuurk. Tijdschr. Ned.-Indië 11 (1856) 175; Wehrli, Schindler & Reichstein, Helvet. Chim. Acta 45 (1962) 1083; Wehrli, Helv. Chim. Acta 45 (1962) 1206; Boer, Brink & Sosef, Prosea 12, 1 (1999) 126). The concentration of cardiac glycosides varies and may be too low for the preparation of

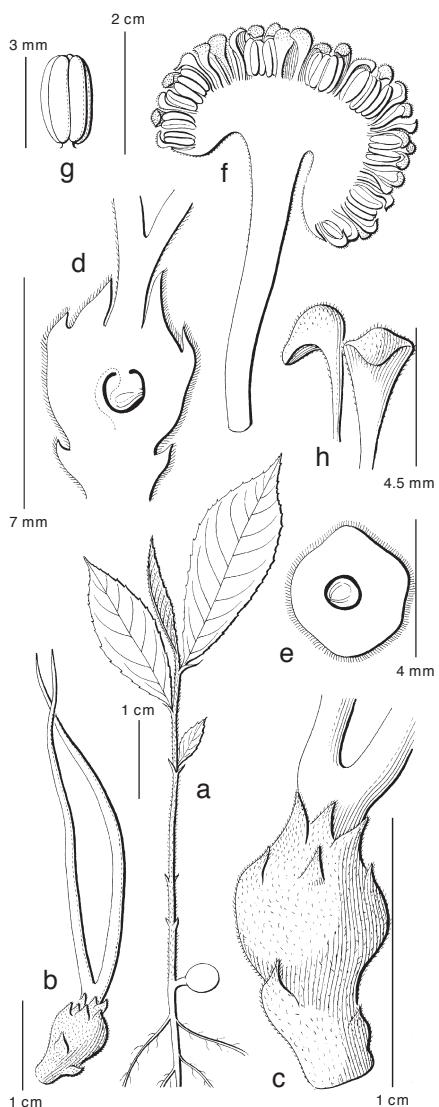


Fig. 25. *Antiaris toxicaria* Lesch. a. Seedling; b. pistillate inflorescence, one-flowered, at anthesis; c. base of the pistillate inflorescence at anthesis; d, e. pistillate inflorescence at anthesis: d. in length section, e. in cross section; f. staminate inflorescence at anthesis in length section; g. mature stamen; h. tepals of staminate flower (a: FRI bb 1379, b–h: material from Singapore Botanic Gardens).

arrow poison. Outside western and central Malesia there seems to be no native knowledge that the latex is poisonous. Latex of some species of *Naucleopsis* (a neotropical genus of the tribe Castilleae) is used to prepare arrow poison in parts of South America (see Bisset & Hylands, Econ. Bot. 20 (1977) 237).

Notes — 1. The species is very variable. Several subspecies and varieties have been recognised: for the African continent three subspecies, for Madagascar two, and for the Asian–Australasian region two (see Berg, Bull. Jard. Bot. Belg. 47 (1977) 309). Juvenile material of all these subspecies is (rather) similar, but adult (and fertile) material

can be distinguished reasonably well. The boundary between the two Asian subspecies is not clear in eastern Malesia (Moluccas and Lesser Sunda Islands).

2. Ranging from West Africa to Polynesia, this species is the most widespread of the Moraceae.

a. subsp. **toxicaria**

Ipo toxicaria Pers., Syn. Pl. 2 (1807) 566.

Antiaris innoxia Blume, Rumphia 1 (1837) 172, t. 54; Miq., Fl. Ned. Ind. 1, 2 (1859) 292.

Lepurandra saccidora Nimmo in Graham, Cat. Pl. Bombay (1839) 193. — *Antiaris saccidora* (Nimmo) Dalzell, Hooker's J. Bot. Kew Gard. Misc. 3 (1851) 232; Wight, Icon. Pl. Ind. Orient. (1853) t. 1958.

Antiaris rufa Miq., Fl. Ned. Ind., Eerste Bijv. (1861) 423; Koord., Versl. Minahasa (1898) 592.

Antiaris ? palembanica Miq., Fl. Ned. Ind., Eerste Bijv. (1861) 424.

Antiaris zeylanica Seem., Bonplandia 10 (1862) 4.

Leafy twigs appressedly to patently puberulous to hirtellous; periderm usually persistent. *Lamina* elliptic to (sub)obovate, apex acuminate to rounded; upper surface hirtellous to hispidulous to puberulous, scabrous or (in adult material) to smooth; lower surface appressedly to patently puberulous to hirtellous. *Infructescences* 1.2–2.5 cm long.

Distribution — India (southern & Andaman Islands) Sri Lanka, South China (incl. Hainan), Indochina, Myanmar, Thailand; in *Malesia*: Sumatra, Malay Peninsula, Borneo, Java, Philippines (Palawan, Luzon, Mindoro, Guimares), Celebes, Lesser Sunda Islands (Sumba, Flores, Alor), Moluccas (?).

Habitat — Forest at altitudes up to 1500 m.

b. subsp. **macrophylla** (R.Br.) C.C. Berg

Antiaris toxicaria Lesch. subsp. *macrophylla* (R.Br.) C.C. Berg, Bull. Jard. Bot. Belg. 47 (1977) 309. — *Antiaris macrophylla* R.Br. in Flinders, Voy. Terra Austral. (1814) 602, t. 5; Benth., Fl. Australia 6 (1873) 179. — *Antiaris toxicaria* Lesch. var. *macrophylla* (R.Br.) Corner, Gard. Bull. Singapore 19 (1962) 248; Backer & Bakh.f., Fl. Java 2 (1965) 20. — *Antiaris bennettii* Seem., Bonplandia 9 (1861) 259; 10 (1862) 3, t. 7; Fl. Vit. (1868) 253, t. 72.

Leafy twigs sparsely appressedly (to patently) puberulous; periderm usually flaking off. *Lamina* elliptic to subovate, apex acuminate to subacute to obtuse, upper surface (sparsely) puberulous (mainly in the midrib), smooth (in juvenile material smooth or scabridulous); lower surface sparsely appressedly puberulous to subtomentose on the veins. *Infructescences* 2–4.5 cm long.

Distribution — Pacific (Solomon Islands, New Hebrides, Vanuatu, Fiji, Tonga), Australia (Arnhemland, Company's Island); in *Malesia*: Moluccas (Batjan?, Halmahera, Aru Islands), Lesser Sunda Islands (only Timor, Wetar, and Tanimbar Islands?), New Guinea (incl. Bismarck Archipelago).

Habitat — Forest at altitudes up to 800 m.

Uses — The infructescences are edible and the (sub)species has been carried to Fiji, Tonga, and Company's Island by sea farers (see A.C. Smith, Fl. Vitensis Nova 2 (1981) 200). The small size of the plants found in Fiji (either shrubs or small trees) is linked

to this introduction. It should be noted that specimens of *A. toxicaria* subsp. *humbertii* (Leandri) C.C. Berg of Madagascar are shrubs or small trees and the same habit occurs in the other Madagascan subspecies (see Berg, Bull. Jard. Bot. Belg. 47 (1977) 318–321).

Tribe DORSTENIEAE

Dorstenieae Gaudich. in Freyc., Voy. Uranie, Bot. (1830) 510; Bureau in A.DC., Prodr. 17 (1873) 254; Benth. & Hook.f., Gen. Pl. 3 (1880) 346; Engl. in Engl. & Prantl, Nat. Pflanzenfam. 3, 1 (1888) 79; Corner, Gard. Bull. Singapore 19 (1962) 250; C.C. Berg, Proc. Kon. Ned. Akad. Wetensch. C, 91 (1998) 359.

Brosimeae Trécul, Ann. Sci. Nat., Bot. sér. 3, 8 (1847) 146; Corner, Gard. Bull. Singapore 19 (1962) 250; C.C. Berg, Fl. Neotrop. Monogr. 7 (1972) 161.

Trees, shrubs (of various growth habit) or in *Dorstenia* herbs, mostly monoecious, less commonly androdioecious or dioecious, usually with uncinate hairs. Leaves distichously or spirally arranged; lamina pinnately, subtriplinerved, (sub)palmately, or radially veined; stipules large to small, fully amplexicaul to lateral. Inflorescences bisexual (or secondarily unisexual), discoid to turbinate or to cup-shaped, circular or shaped otherwise, never distinctly involucrate, interfloral bracts mostly present and peltate. Staminate flowers often with reductions in the perianth (down to absent) and the stamens (down to one), pistillode mostly absent. Pistillate flowers mostly connate with other flowers and/or largely embedded in the receptacle; stigmas 2 and equal, but in *Dorstenia* often unequally long or only 1. Fruit a dehiscent drupe(let) or forming a drupaceous whole with other flowers and/or the receptacle; seed large and without endosperm (in *Dorstenia* small and with endosperm), testa sometimes with a thickened vascularised part; embryo with thick and often unequal cotyledons, or if seeds small, then with flat and equal cotyledons.

Distribution — This tribe comprises eight genera with in total 87 species. It has a distinct West Gondwanan distribution. Three genera of woody plants with in total 18 species are confined to the Neotropics and concentrated in the South American continent. Four genera of woody plants with in total 5 species are endemic to the African region. The eighth genus, *Dorstenia*, is largely herbaceous and is represented in both major flora regions. Only one of the 105 species, *Dorstenia indica* Wight, is Asian (Sri Lanka and W India).

Morphology — The tribe is characterised by bisexual inflorescences with one or more pistillate flowers in the centre and the staminate flowers mostly peripheral. Peltate bracts and uncinate hairs are common.

DORSTENIA

Dorstenia L., Sp. Pl. (1753) 121; L., Gen. Pl. ed. 5 (1754) 56; Endl., Gen. Pl. (1837) 278; Bureau in A.DC., Prodr. 17 (1873) 258; Baill., Hist. Pl. 6 (1875) 196; Benth. & Hook.f., Gen. Pl. 3 (1880) 366; Hook.f., Fl. Brit. India 5 (1888) 494; Engl. in Engl. & Prantl, Nat. Pflanzenfam. 3, 1 (1888) 79; Rendle, Fl. Trop. Afr. 6, 2 (1916) 25; Leandri, Mem. Inst. Sci. Madagascar, Sér. B, Biol. Vég. 1 (1948) 29; Corner, Gard. Bull. Singapore 19 (1962) 250 (passim); C.C. Berg & Hijman, Ilicifolia 2 (1999) 1; C.C. Berg, Fl. Neotrop. Monogr. 83 (2001) 144.

Kosaria Forssk., Fl. Aegypt.-Arab. (1775) 164.
Sychinium Desv., Mém. Soc. Linn. Paris 4 (1826) 216, ‘*Sichinum*’.
Ctenocladus Engl., Bot. Jahrb. Syst. 57 (1921) 246.
Craterogyne Lanj., Recueil Trav. Bot. Neerl. 32 (1935) 272.

Herbs, often partly ± succulent, rhizomatous or tuberous, or shrubs. *Leaves* spirally arranged or distichous; lamina pinnately, less often palmately or radially veined; stipules lateral, free. *Inflorescences* bisexual, in the leaf-axils, discoid to turbinate, in outline circular, elliptic, ± stellate or navicular, receptacle outside bracteate or mostly with marginal and/or submarginal appendages; flowers connate. *Staminate flowers* numerous; tepals (1 or) 2 or 3 (or 4), free or basally connate; stamens 2 or 3; pistillode usually absent. *Pistillate flowers* in the central part of the inflorescence, 1–numerous; perianth tubular, with only the apex free from the surrounding flowers; ovary free; stigmas 1 or 2, filiform to band-shaped, equal or unequal. *Fruit* a dehiscent drupe, the white fleshy part pushing out the endocarp body (pyrene) if large or ejecting the endocarp body if small; endocarp body (especially if large) subglobose and smooth or tetrahedral and tuberculate; seed large and without endosperm or small and with endosperm, cotyledons thick and unequal or flat and equal.

Distribution — The genus comprises 105 species, 46 in the Neotropics, 1 in Asia (Sri Lanka, W India), 58 in continental Africa extending to Madagascar, the Arabian Peninsula, and Socotra. *Dorstenia contrajervia* is introduced in several tropical countries.

Morphology — The majority of the species are herbaceous, eleven African species are woody (shrubs or even treelets) and some in Africa and Brazil are suffrutescent.

1. *Dorstenia contrajervia* L.

Dorstenia contrajervia L., Sp. Pl. (1753) 121; F. Overbeck, Jahrb. Wiss. Bot. 66 (1924) 467; Woodson, Ann. Missouri Bot. Gard. 47 (1960) 177, f. 62; Backer & Bakh.f., Fl. Java 2 (1965) 17; C.C. Berg, Fl. Neotrop. Monogr. 83 (2001) 198. — *Dorstenia quadrangularis* Stokes, Bot. Mat. Med. 4 (1812) 338.

Dorstenia contrajervia L. var. *houstonii* L., Sp. Pl. (1753) 121. — *Dorstenia houstonii* (L.) L., Sp. Pl. ed. 2. (1762–1763) 176. — *Dorstenia quadrangularis* Stokes var. *integrifolia* Stokes, Bot. Mat. Med. 4 (1812) 339.

Dorstenia alexiteria L., Syst. Nat. ed. 10. (1759) 889.

Dorstenia quadrangularis Stokes var. *pinnatifida* Stokes, Bot. Mat. Med. 4 (1812) 341.

Dorstenia quadrangularis Stokes var. *sinuata* Stokes, Bot. Mat. Med. 4 (1812) 339.

Dorstenia palmata Willd. ex Schult., Mant. 3 (1827) 317, non Engler (1894).

Dorstenia maculata Lem., Ill. Hort. 10 (1863) t. 362. — *Dorstenia contrajervia* L. var. *maculata* (Lem.) Bureau in DC., Prodr. 17 (1873) 260.

Dorstenia contrajervia L. subsp. *tenuiloba* Blake, Contr. U.S. Natl. Herb. 24 (1922) 2, t. 1. — *Dorstenia contrajervia* L. var. *tenuiloba* (Blake) Standl. & Steyermark, Publ. Field Mus. Nat. Hist., Bot. Ser. 23 (1944) 44.

Herb, usually rosulate; internodes usually short. *Leaves* spirally arranged; lamina broadly ovate to cordiform to sub hastate, pinnately to sub palmately to sub pedately lobed to parted or (almost) entire, 4–25 by 3.5–30 cm, membranaceous, apex acute to sub acuminate, base cordate to acute, margin crenate-dentate (to entire); upper surface hirtellous to subhirsute to strig(ill)ose, usually ± scabrous; lower surface puberulous to hispidulous, often ± scabrous; lateral veins 3–7 pairs; petiole 3–20 cm long; stipules

0.2–0.6 cm long, puberulous. *Inflorescences* green or the margin of the receptacle purplish; peduncle 5–30 cm; receptacle (0.5–)1.5–3 cm wide, ± quadrangular and/or ± irregularly lobed, excentrally attached.

Distribution — Mexico to Panama, West Indies, Colombia, northern Venezuela, western Ecuador, northern Amazonian Peru; in *Malesia*: introduced (as ornamental): Java.

Tribe FICEAE

See Moraceae: *Ficus*, Flora Malesiana, Series I, Volume 17, Part 2 (2005).