

## CHRYSOBALANACEAE (G.T. Prance, Kew)<sup>1</sup>

Trees or shrubs (or rarely suffrutices outside Malesia). *Leaves* simple, alternate, often coriaceous, glabrous or with an indumentum on undersurface, margin entire; petioles often with 2 lateral glands. *Stipules* 2, minute and caducous to large and persistent, usually linear-lanceolate. *Inflorescence* racemose, paniculate or cymose; flowers bracteate and usually bibracteolate; bracts and bracteoles small and caducous or larger and enclosing flower or groups of flowers and persistent. *Flowers* actinomorphic to zygomorphic, hermaphrodite or rarely polygamous, markedly perigynous. *Receptacle* campanulate to cylindrical or rarely flattened cupuliform, often gibbous at base; calyx lobes 5, imbricate, often unequal, erect or reflexed. *Petals* 5 (absent in some Neotropical species), inserted on margin of disk, commonly unequal, imbricate, deciduous, rarely clawed. *Stamens* indefinite, 2–60 (to 300 in Neotropics), inserted on margin of the disk, in a complete circle or unilateral, all fertile or some without anthers and often reduced to small tooth-like staminodes; filaments filiform, free or ligulately connate, short and included to long and far exserted; anthers small, 2-locular, longitudinally dehiscent, glabrous or rarely pubescent. *Ovary* basically of three carpels but usually with only one developed, the other two aborted or vestigial, variously attached to (the base, middle or mouth of) receptacle, usually sessile or with short gynophore, pubescent or villous; ovary unilocular with two ovules or bilocular with one ovule in each locule. *Ovules* erect, with micropyle at base (epitropous). *Style* filiform, basally attached; stigma 3-lobed or truncate. *Fruit* a fleshy or dry drupe of varied size, interior often densely hairy; endocarp much varied, thick or thin, fibrous or bony, often with a special mechanism for seedling escape. *Seed* erect, exalbuminous, the testa membranous; cotyledons amygdaloid, plano-convex, fleshy, sometimes ruminant. *Germination* hypogeal with the first leaves opposite or alternate or epigeal with opposite first leaves.

An extensive review of the generic limits of the family has been published: G.T. PRANCE & F. WHITE, *The genera of Chrysobalanaceae: a study in practical and theoretical taxonomy and its relevance to evolutionary biology*, Phil. Trans. Roy. Soc. London 320 (1988) 1–184. This contains full details of taxonomic history, morphology, anatomy, pollen, ecology and distribution of the family. A condensed version of these subjects is given here. Details of the Neotropical members of the family are given in: G.T. PRANCE, *Chrysobalanaceae*, *Flora Neotropica* 9 (1972) 1–410. The African members of the family were treated in: F. WHITE, *The taxonomy, ecology and chorology of African Chrysobalanaceae (excluding Acioa)*, Bull. Jard. Bot. Nat. Belg. 46 (1976) 265–350.

**Distribution.** Pantropical with 456 species in 17 genera; 365 species in the Neotropics, 57 in Africa, and 34 in Asia, Malesia and the Pacific.

Seven genera are native to the Flora Malesiana region and one species of an eighth genus, *Chrysobalanus*, from Africa and South America, has naturalized in Malesia and Fiji and is therefore included in this treatment. All four tribes of *Chrysobalanaceae* are represented in the region. The genera treated here fall into the following tribes of PRANCE & WHITE:

Tribe *Chrysobalaneae*: *Chrysobalanus*, *Licania*, *Parastemon*.

(1) Drawings made by Bobbi Angell, David Woolcott, Kirsten Tind, and Julia Loken; David Johnson assisted with the distribution maps.

Tribe *Parinariaceae*: *Hunga*, *Parinari*.

Tribe *Couepieae*: *Maranthes*.

Tribe *Hirtelleae*: *Atuna*, *Kostermanthus*.

The genera *Atuna*, *Hunga*, *Kostermanthus*, and *Parastemon* are confined to the Malesian and Pacific region. *Licania* is predominantly a Neotropical genus (186 species there) with a single species in West Africa and three in Malesia. *Parinari* is a pantropical genus with almost equal representation in all three major regions of the tropics, and *Maranthes* is predominantly an African genus with one abundant and widespread species in Malesia and the Pacific and a single closely related species in Central America.

**Morphology.** All species of *Chrysobalanaceae* are woody and most are trees or treelets. All are leptocaul. Several, including species of *Atuna*, *Kostermanthus*, *Licania* (Neotropical), *Magnistipula* (African), *Maranthes* and *Parinari*, exceed a height of 30 m and are important constituents of the upper forest canopy or are emergents. Six African and Neotropical species belonging to *Licania*, *Magnistipula* and *Parinari* are geoxylic suffrutices with massive woody underground parts, but rather exiguous aerial shoots which are capable of only limited upward growth and a similar form occurs in *Parinari nonda* in Australia.

In their architecture and growth-dynamics those *Chrysobalanaceae* that have been studied exhibit the model of TROLL. This has been demonstrated only in African and Neotropical species.

Herbarium specimens of *Atuna* show a distinct pattern of branching which is difficult to describe except in terms of development based on the living plant.

Buttresses are normally absent but frequently well-developed in some species of *Parinari* and *Atuna*, for example, *P. canarioides*, *P. costata*, *P. oblongifolia*, *A. cordata* and *A. excelsa*, and the trunk of some species of *Parinari*, e.g. *P. parva* and *P. gigantea* is often fluted at the base.

The leaves, which are simple and spirally inserted, are frequently arranged distichously. Most species have stiff, coriaceous, evergreen leaves which contain abundant silica inclusions.

Stipules are nearly always present but are sometimes small and caducous. In some Neotropical species of *Parinari* the stipules reach a length of 7 cm, they are up to 4 cm in *Parinari parva*. In *Atuna* they are prominently keeled, a unique feature in the family.

The lamina is entire, in all Malesian species. In nearly all species of *Parinari*, and a few Neotropical species of *Licania*, the veins on the lower surface are extremely prominent and form a dense network occupying more than half of the leaf surface so that the stomata are confined to relatively small sunken crypts which are densely filled with short curly hairs.

Foliar glands occur in most, possibly all, species. They secrete nectar which is eaten by ants, and function chiefly on young leaves. On mature leaves of herbarium specimens they are not always clearly visible. The structure and distribution on the leaf of the glands varies greatly from genus to genus and provides characters of considerable taxonomic importance. Small discoid glands occur in various places on the lower surface or margins of the lamina in *Parastemon*. There are larger, sometimes ill-defined, glandular areas towards the base of the lamina in *Maranthes*. In *Parinari* conspicuous glands occur on the petiole.

The inflorescence is very variable. In *Chrysobalanus* the few-flowered inflorescence is a short raceme of cymules or is cymose throughout, or is a false raceme or a sessile fascicle. In *Parastemon* the inflorescence is a simple or branched raceme. *Hunga* and Malesian species of *Licania* have simple or branched racemes of usually congested cymules. More complex mixed inflorescences with cymose ultimate units are found in *Kostermanthus* and *Parinari*, and the inflorescence of *Maranthes* is corymbose.

Since the inflorescence is usually cymose, at least in part, a distinction between bract and bracteole cannot always be drawn. Bracts and bracteoles are usually small but in nearly all species of *Parinari* they are relatively large and enclose small groups of developing flowers.

In most species the flowers appear to be bisexual, but future field work may show that this is not always so. *Parastemon urophyllus* is said to be polygamodioecious.

Floral symmetry varies from almost completely actinomorphic, apart from the lateral style, in

*Chrysobalanus*, *Parastemon*, and most species of *Licania* to strongly zygomorphic in *Kostermanthus*. Actinomorphic flowers are patelliform or shallowly cupuliform, and zygomorphic flowers usually have a long receptacle-tube, but in *Kostermanthus* the strongly zygomorphic flowers have a very short receptacle. In the *Chrysobalanaceae* the receptacle-surface is always lined with nectar-secreting tissue, which sometimes, as in *Maranthes corymbosa*, almost completely fills the tube. In most genera the entrance to the receptacle tube is blocked by long straight retrorse hairs, but these are lacking in *Kostermanthus*. In *Parastemon* the nectariferous lining of the receptacle is freely exposed.

There are always five, completely free, slightly to strongly imbricate sepals which vary from subequal in *Chrysobalanus* to markedly unequal in *Kostermanthus*. In most genera they are acute or subacute but in *Kostermanthus* and *Maranthes* they are suborbicular and deeply concave.

Petals are present in all Malesian species but absent in many Neotropical species of *Licania*. There are always five. They are mostly caducous. In shape they vary from linear-spathulate (*Chrysobalanus*) to orbicular. They are usually subequal, but in *Kostermanthus* they are very unequal in shape and size and are strongly unguiculate.

Stamens vary in number from two in *Parastemon urophyllus* to 40 in *Maranthes*. In *Chrysobalanus*, most species of *Licania*, *Parastemon versteeghii*, and *Maranthes* they form a complete or almost complete circle round the entrance to the flower and all or most are fertile. Otherwise the fertile stamens are inserted unilaterally opposite the carpel. Staminodes are frequently present opposite the style. In several genera the filaments appear to be united at the base, but it is sometimes difficult to decide whether this represents true union or whether the filaments are free but inserted on a development of a receptacular rim. In *Maranthes* the stamens are inserted in two or more rows on the outer surface of what appears to be a receptacular annulus. In length the filaments vary from much shorter than the calyx, as in *Hunga*, *Parastemon* and some species of *Licania*, to very much longer in *Maranthes*. In *Kostermanthus* the filaments are united for at least half of their length to form a conspicuous ligule.

The gynoecium fundamentally is composed of three carpels which are free except for the gynobasic style. In most species there is only one functional carpel, though one or two small rudimentary carpels can sometimes be seen. Due to the development of a false dissepiment the ovary is bilocular in *Hunga*, *Parinari*, and *Atuna*.

The fruit is basically a drupe but there is considerable variation in detail, apparently associated with dispersal and germination. In *Chrysobalanus*, *Parastemon* and *Hunga* the endocarp has a smooth surface and is sharply differentiated from the mesocarp. In the other genera the differentiation is less well-defined. In *Chrysobalanus* and *Hunga*, seedling escape is effected by means of longitudinal lines of weakness. In *Parastemon* and *Maranthes* two large lateral plates fall away permitting the seedling to emerge. In *Parinari* there are two small basal 'plugs' or obturators. All other genera seem to lack specialized means of seedlings escape.

In *Chrysobalanus*, *Licania*, *Parastemon*, *Parinari*, and *Atuna*, germination is cryptocotylar, whereas in *Maranthes* it is phanerocotylar.

**Vegetative Anatomy.** — *Leaf anatomy.* Indumentum, if present, consisting of long unicellular hairs. Various glands (extrafloral nectaries) with slender upright epidermal secretory cells commonly present. Wax present as platelets (FEHRENBACH & BARTHOLOTT, 1988). Stomata mostly paracytic, confined to the lower leaf surface. Upper epidermis often composed of tall cells; with mucilaginous inner walls in some species. Hypodermis often present. Mesophyll entirely composed of palisade-like cells, more rarely dorsiventral and differentiated into palisade and spongy tissue. Asterosclereids occasionally present in mesophyll. Veins mostly with sclerenchyma sheaths including sclereids with U-shaped wall thickenings, sometimes vertically transcurrent. Midrib and distal end of petiole with a closed vascular cylinder, with or without additional adaxial or medullary collateral bundles. Silica bodies and silicified cell walls common, especially in epidermis.

*Young stem.* Cork arising superficially. Pericyclic sclerenchyma ring composed of fibres and

sclereids with U-shaped wall thickenings. Secondary phloem occasionally with secretory (tannin?) cells. Sieve tube plastids of the S-type (BEHNKE, 1984). Silica bodies often present in pericycle, phloem and xylem rays, and in pith.

*Wood anatomy.* Growth rings absent or, if present, defined by differences in the spacing of tangential parenchyma bands. Vessels diffuse, often in a weakly oblique pattern, (almost) exclusively solitary, tending to be of two distinct sizes, the larger ones very wide (200–300 µm). Vessel perforations simple. Tyloses often present in heartwood, sclerotic in some species. Vessel–ray pitting including elongate horizontal or oblique to almost vertical pits with strongly reduced borders, often unilaterally compound. Fibres often thick-walled, with distinctly bordered pits throughout the tangential walls, and in the radial walls often confined to fibre–ray contacts (fibre–tracheids); in contact with vessels often less thick-walled and with biseriate bordered pits (= vasicentric tracheids). Parenchyma in fine uniseriate or locally bi(–tri)-seriate, regular or irregular wavy tangential bands. Parenchyma strands typically long, of up to 16 cells. Some axial parenchyma cells with spiral thickenings in *Atuna p.p.*, *Licania*, *Maranthes p.p.*, and *Kostermanthus* (TER WELLE, 1975). Rays predominantly uniseriate, but in some taxa also biseriate, typically weakly heterogeneous with (often weakly) procumbent central cells and one row of square to upright marginal cells (Kribs type III), sometimes homogeneous and composed of procumbent cells only. Silica bodies universally present in ray cells, more rarely in axial parenchyma cells. Rhomboidal crystals in chambered axial parenchyma cells noted in *Parastemon*.

*Taxonomic notes based on vegetative anatomy.* The above general anatomical description is based on the literature (for leaf and young stem anatomy mainly KÜSTER, 1897, as abstracted by SOLEREDER, 1899; and PRANCE, 1972, and PRANCE & WHITE, 1988, for wood anatomy from many sources), amplified with original observations on slides present in the Rijksherbarium at Leiden. A number of anatomical characters may prove to be of considerable taxonomic significance at the genus or species level (mucilaginous leaf epidermis, distribution of silica grains in leaves, young stem, and wood, vascular pattern and sclerenchyma support of leaf veins and petiole, fibre and sclereid distribution pattern of the mature bark (ROTH, 1981), spiral thickenings in axial parenchyma cells of the wood, ray width and histology, etc.). However, for the Malesian *Chrysobalanaceae* their diagnostic value remains largely untested. On the whole the *Chrysobalanaceae* are anatomically rather homogeneous, and as repeatedly emphasized, quite distinct from the *Rosaceae*. Anatomically *Chrysobalanaceae* are also distinct from the numerous families to which they have been compared in the search for closest relatives.

*References:* BEHNKE, Ann. Missouri Bot. Gard. 71 (1984) 824–831; DESCH, Manual of Malayan Timbers 2 (1954) 474–485; BURGESS, Timbers of Sabah (1966) 434–436; FEHRENBACH & BARTHLOTT, Bot. Jahrb. 109 (1988) 407–428; FURUNO, Anatomy of Papua New Guinea Wood (Continued), Res. Report of Foreign Wood 8, Shimane Univ. (1979); HAYASHI c.s., Micrographic Atlas of Southeast Asian Timber, Kyoto Univ. (1973); LECOMTE, Les bois de l'Indochine (1926) 59–61; METCALFE & CHALK, Anatomy of the Dicotyledons 1 (1950) 550–553; MOLL & JANSSONIUS, Mikrographie des Holzes der auf Java vorkommenden Baumarten 3 (1914) 222–230; PRANCE, Flora Neotropica 9 (1972) 1–19; PRANCE & WHITE, Phil. Trans. Roy. Soc. Lond. B 320 (1988) 1–184; ROTH, Encycl. Plant Anatomy 9, 3 (1981) 286–295, 402–403; SOLEREDER, Systematische Anatomie der Dicotyledonen (1899) 341–351; TER WELLE, Acta Bot. Neerl. 24 (1975) 397–405; IAWA Bulletin 1976/2 (1976) 19–29; TER WELLE & DÉTIENNE, Flora of the Guianas A 85 (1986) 109–126. – P. BAAS.

*Palynology.* The pollen of *Chrysobalanaceae* is very uniform, but is different from that of *Rosaceae*. It is of little value for distinguishing between the genera of *Chrysobalanaceae* or for arranging them in groups.

Most species have grains with three furrows, but some species have three or four; there are no special features except occasional equatorial constrictions. With light microscopy the pores are indistinct, and in some species are difficult to observe. The grains are usually distinctly triangular in shape in polar view, except when four-furrowed; they are elliptical to circular in equatorial view

and are oblate-spheroidal, prolate-spheroidal or subprolate in shape as indicated by the ratio: polar length  $\times$  100, divided by the equatorial length = 85–150. The size is very variable from one genus to another; the polar area is usually small, sometimes medium, but never large. The exine is medium to rather thick with very little patterning; it is usually scabrous to verrucose, but never striate.

The pollen of *Chrysobalanaceae* and *Rosaceae* is similar but readily distinguishable. The former is markedly triangular in polar view in the expanded grain, whereas in *Rosaceae* it is never more than weakly triangular. Most *Rosaceae* have more distinctive pores, and many have more patterning on the wall. A feature that occurs frequently in the *Rosaceae* is a distinct wedge-shaped protrusion from the middle of the furrow, obvious in polar view, which does not occur in *Chrysobalanaceae*.

ERDTMAN (1952) states 'pollen morphological objections cannot be raised against regarding the *Chrysobalanaceae* as a separate family.' Our own study of *Rosaceae* pollen (*sensu lato*) confirmed that three main types of pollen occur: the *Rosaceae sensu stricto*, the *Chrysobalanaceae*, and the *Neuradoideae* types (PRANCE, 1963). The differences between pollen of *Chrysobalanaceae* and *Rosaceae* are, however, comparatively small. By contrast, the pollen of the *Tropaeolaceae*, *Geraniaceae*, *Limnanthaceae*, *Linaceae*, *Polygalaceae*, and *Sapindaceae*, families which various phylogenists (HALLIER, 1923; BONNE, 1926; HAUMAN, 1951; GUTZWILLER, 1961) have suggested are closely related to *Chrysobalanaceae*, is very different. Pollen morphology thus provides reasons for keeping the *Chrysobalanaceae* near to the *Rosaceae* in the *Rosales*, and not for removing it to the *Geraniales* or *Sapindales*.

The pollen of *Chrysobalanaceae* is so uniform that it does not provide good generic characters. *Kostermanthus heteropetala* is distinct from all other *Chrysobalanaceae* examined, including *Dactyladenia* (Africa) and *Acioa* (America) with which it shares a staminal ligule, in having three swellings on each of the triangular sides of the grain in polar view. Apart from *Kostermanthus* no other genus is clearly definable on pollen characters.

*References:* BONNE, C. R. Hebd. Séanc. Acad. Sci. Paris 182 (1926) 1404–1406; ERDTMAN, Pollen morphology and plant taxonomy, Angiosperms (1952) 380–383; GUTZWILLER, Bot. Jahrb. 81 (1961) 1–49; HALLIER, Beih. Bot. Centralbl. 39 (1923) 1–178; HAUMAN, Bull. Jard. Bot. État Brux. 21 (1951) 167–198; PRANCE, A taxonomic study of the *Chrysobalanaceae*. Thesis, Oxford (1963).

*Phytochemistry.* Chemical knowledge about the family *Chrysobalanaceae* is still scanty. HEGNAUER (1973) treated it as *Chrysobalanoideae sub Rosaceae*. *Chrysobalanaceae* are noteworthy for their tendency to accumulate silica (SiO<sub>2</sub>) in leaves and in the wood where usually every ray cell contains one globular silica inclusion. Leaf flavonoid patterns are dominated by the flavonols quercetin and kaempferol; some taxa also have myricetin. Proanthocyanidins (formerly called leucoanthocyanidins), *i.e.* condensed tannins, were demonstrated to be present in leaves of few species of *Chrysobalanus*, *Licania*, and *Parinari*, but galli- and ellagitannins have not yet been traced in the family. The recent flavonoid investigation of 21 species of *Parinari* (CORADIN, GIANNASI & PRANCE, 1985) resulted in the identification of a number of 3-glycosides of kaempferol, quercetin and myricetin, and showed restriction of myricetin glycosides to four African species; dihydroquercetin('taxifolin')-3-glycosides were noticeable only in Asian *Parinari insularum* from the Pacific islands and vicenin-like C-glycoflavones only in a few African populations of *P. excelsa*. Myricetin was also observed in leaves of *Licania macrophylla* which besides has much condensed tannins in all parts, saponins in leaf, pericarp, seed, and stem and root bark; alkaloids in stem and root bark (GRENAND, MORETTI & JACQUEMIN, 1987). Cyanogenic glycosides which are characteristic of a number of Rosaceous taxa have not been traced in *Chrysobalanaceae* hitherto. The most noteworthy chemical character known from the family at present is the fatty acid pattern of their seed triglycerides; conjugated trienoic and tetraenoic C<sub>18</sub>-acids such as alpha-elaostearic and parinaric acids are present as major fatty acids in seed oils of species of *Chrysobalanus*, *Licania*, and *Parinari s.l.* (*i.e.* including *Atuna*, *Maranthes* and the African *Neocarya*).

This character, however, which links *Chrysobalanaceae* biochemically with *Prunoideae* (same type of seed oils in some *Prunus s.l.* species) seems not to be universal in the family. According to JONES & EARLE (1966) seed kernels of a species of *Couepia* (Central & South America) contained an oil without conjugated unsaturation. Still too little is known from the chemistry of this taxon to allow a sound chemotaxonomic discussion.

*References:* CORADIN, GIANNASI & PRANCE, *Brittonia* 37 (1985) 169–178; GRENAND, MORETTI & JACQUEMIN, *Pharmacopées traditionnelles en Guyane*, ed. ORSTOM, Paris (1987); HEGNAUER, *Chemotaxonomie der Pflanzen* 6 (1973) 84–130; JONES & EARLE, *Econ. Bot.* 20 (1966) 137; PRANCE & WHITE, *Phil. Trans. Roy. Soc. London B* 320 (1988) 28–29. — R. HEGNAUER.

*Dispersal.* The fruits of *Chrysobalanaceae* are very uniform in basic structure but remarkably diverse in functional detail. Despite their uniformity they have become adapted to a wide range of dispersal agents, sometimes within a single genus or species; however, few species have been studied in the field.

*Chrysobalanus icaco ssp. icaco* is dispersed by ocean currents, and also by bats, rodents and monkeys, and possibly by birds; *C. cuspidatus* is said to be dispersed by birds.

Some Neotropical species of *Licania* are bat-dispersed, whereas the fruits of several South American riverine species float and are also eaten by fish; those of the African species *L. elaeosperma* are also transported by water. The Malesian species *L. splendens* is dispersed by the fruit pigeon *Ducula aenea*.

Various species of *Parinari* are known to be dispersed by bats, elephants, baboons and other primates, a scatter-hoarding squirrel, fruit pigeons, rheas, emus, agoutis and fish. Species of *Couepia*, *Licania* and *Parinari* are frequently eaten by bats in the Neotropics.

*Maranthes corymbosa* is dispersed by birds, most notable hornbills and fruit pigeons, and, at least for short distances, by a scatter-hoarding squirrel. The fruits of some African species are eaten by monkeys which are possibly mainly destructive.

*Atuna* is dispersed by ocean currents and a scatter-hoarding squirrel and possibly by wild pigs.

*Uses.* Members of the *Chrysobalanaceae* are used by the local people everywhere, for building, fuel, charcoal and in folk medicine. The fruits and seeds of some species are highly esteemed, and others are eaten in times of scarcity; some are used in the preparation of alcoholic beverages. At present, *Chrysobalanaceae* are only of local importance commercially, but, with improved communications and technology, their potential as a source of construction timber, fruits, and edible and industrial oils appears to be promising.

The Malesian standard timber name for various genera of *Chrysobalanaceae* is *merbatu*.

*Edible fruits and seeds.* *Chrysobalanus icaco* is tinned and bottled in syrup and sold in Colombia and Venezuela under the name *Icacos*. The fruit of several Neotropical species of *Couepia* and *Parinari* are eaten. In Amboina a dish called *Koku koku* is prepared from the mashed seeds of *Atuna excelsa* mixed with raw or fried small fish, ginger, onions, chillies and lime juice.

*Wood.* Despite the large supplies of *Chrysobalanaceae* wood potentially available, commercial sawn timber is produced only in relatively small amounts. This is because its high silica content blunts even tungsten-tipped saws. Because the wood of many species is resistant to marine borers, it is used throughout the tropics for piers and other marine constructions.

*Caulking and waterproofing agent.* In the Solomon Islands the principal use of *Atuna excelsa sensu lato* is for caulking the seams of plank-built canoes. The seeds, which are known as 'putty nut' are pounded to a putty-like consistency. After application the putty hardens and darkens, but if exposed too long to the sun it cracks, so canoes drawn up on the beach are often kept in the shade of sheds. In the central and south-eastern Solomons it is used for setting shell inlay in wood bowls, figures and other articles. The north-western Solomon Islanders also use it for waterproofing bottles made from gourds. In the Admiralty Islands (Manus) coiled baskets are coated with it to make them waterproof (B.A.L. CRANSTONE, in litt., 14 June 1983).

*History of Parinari.* The taxonomic history of *Parinari* is complex. At least some species of all Malesian genera except *Chrysobalanus*, and *Parastemon* have at one time or another been placed in *Parinari*.

All species of *Atuna* and *Maranthes* have been included in *Parinari*. Despite their considerable differences from *Parinari sensu stricto* in virtually all other respects, these genera have one feature in common – a bilocular ovary. It was the adoption of this character as a generic criterion, especially by BENTHAM (1849), that led to the increasingly artificial nature of *Parinari*. As *Parinari* became more and more heterogeneous even some species with unilocular ovaries were included, for example, the species now placed in *Kostermanthus*.

In the original description of *Parinari*, which was based on *P. campestris* and *P. montana* from French Guiana, AUBLET (1775) mentioned the bilocular ovary, but he does not appear to have attached much importance to it.

DE JUSSIEU (1789), who brought all previously described genera of *Chrysobalanaceae* together for the first time, knew some of them only from the original descriptions and illustrations. His implication that *Parinari* differs from the other genera principally in its bilocular ovary seems to have laid the foundations for the subsequent confused history of the group.

DE JUSSIEU was the first to extend the concept of *Parinari* to another continent by citing in synonymy two manuscript names of ADANSON from Senegal, *Mampata* and *Neou*. The former was subsequently described as *P. excelsa* and the latter as *P. macrophylla* by SABINE.

The following year, in his Prodomus, DE CANDOLLE (1825), who only knew the four species mentioned above, divided *Parinari* into two sections. Section *Petrocarya* (correctly section *Parinari*) was based on a superfluous generic name which SCHREBER (1789) substituted for the earlier *Parinari*. It included AUBLET's original species. Section *Neocarya* was based on *P. senegalensis* DC. [now *Neocarya macrophylla* (SABINE) PRANCE], but *P. excelsa* was associated with it, probably because its type-description is inadequate to characterize it properly. *Parinari macrophylla* is not mentioned by DE CANDOLLE. He was also apparently unaware of the first true *Parinari* to be described from Asia, *P. sumatrana* BENTH., which had been described by JACK in the illegitimate genus *Petrocarya* in 1822. DE CANDOLLE indirectly emphasized the importance of the bilocular ovary of *Parinari* by describing the ovary of all other genera as unilocular.

During the first half of the nineteenth century, in addition to *Neocarya macrophylla*, a few other species, which belong to other genera, were described in *Parinari* or its illegitimate synonym *Petrocarya*, because of their bilocular ovary. Thus JACK (1822) described *Petrocarya excelsa* (now *Atuna excelsa*), and BENTHAM (1840) published *Parinari coriacea* (now *Exellodendron coriacea*), but it was BENTHAM's treatment of *Parinari* in HOOKER's Niger Flora (1849) that firmly established *Parinari* as an artificial genus.

Whereas earlier workers had implied that the bilocular ovary is a diagnostic character of *Parinari*, BENTHAM referred to the spurious dissepiment which separates the ovules as 'the essential character.' BENTHAM divided *Parinari* into three sections as follows:

**Section 1:** *Petrocarya* (correctly *Parinari*) included the African species *P. excelsa* and *P. curatellifolia*, all the known American species including *P. coriacea* (now *Exellodendron coriaceum*), and, with some doubt, three species BENTHAM had not seen himself, namely *P. sumatrana* BENTH. (a true *Parinari*), *P. glaberrima* HASSK. (now *Atuna excelsa*) and *P. scabra* HASSK. (now *Atuna scabra*).

**Section 2:** *Sarcostegia* BENTH. included two new species, *P. polyandra* (now *Maranthes polyandra*) and *P. griffithiana* (now *Maranthes corymbosa*), and, with some doubt, also *P. jackiana* BENTH. (based on *Petrocarya excelsa*, now *Atuna excelsa*) which BENTHAM had not examined.

**Section 3:** *Neocarya* DC. contained *P. macrophylla* (now *Neocarya macrophylla*) and its synonym *P. senegalensis*.

BENTHAM's circumscription of *Parinari* was probably much wider than he imagined, largely because of the inclusion of the Asian species he only knew from the literature. He appears to have adopted it with some reservation. *Parinari polyandra* has c. 40 fertile stamens and BENTHAM mentions that this, in conjunction with the glandular leaves and fleshy 'calyx', might 'suggest the establishment of a distinct genus.' He clearly believed that the stamen number of *Parinari* varies more or less continuously, but the evidence he cites is partly on the species he had not studied.

BENTHAM's circumscription of *Parinari* included five genera which are now regarded as distinct, namely, in addition to *Parinari* itself, *Atuna* RAFIN., *Exellodendron* PRANCE, *Maranthes* BLUME and *Neocarya* PRANCE. Two of these from Malesia had enjoyed a brief period of generic recognition. Thus, *Maranthes* was described by BLUME in 1825, but three years later he transferred the type species to his illegitimate *Exitelea*. *Atuna* was described by RAFINESQUE in 1838, but remained disregarded for more than 100 years, though one of its species was independently described by HASSKARL in 1842 as the type of his new genus *Cyclandrophora*. It appears that HASSKARL had little faith in his new genus for he united it with *Parinari* within a year of its publication, although it has little in common with the latter, other than the bilocular ovary.

Since BENTHAM (1849) nearly all species of *Chrysobalanaceae* with false dissepiment (and even some without) were automatically placed in *Parinari* regardless of any other consideration.

As new species now placed in *Exellodendron*, *Maranthes* and *Atuna* were described they were all placed in *Parinari*. Likewise, equally disparate elements which are now placed in *Bafodeya* PRANCE, *Hunga* PANCHER ex PRANCE and *Kostermanthus* PRANCE joined the assemblage.

KEY TO THE GENERA  
based on flowering material

1. Stamens free, not united into a ligule; petals not clawed, ovary uni- or bilocular.
  2. Ovary unilocular, inserted at or near base of receptacle.
    3. Inflorescence a panicle of cymules; fertile stamens 7–26.
      4. 'Stamens 15–26, the filaments hairy, exerted ..... 1. *Chrysobalanus*
      4. Stamens 7–10, the filaments glabrous, included ..... 2. *Licania*
    3. Inflorescence racemose; fertile stamens 2 or 5 ..... 3. *Parastemon*
  2. Ovary bilocular, inserted at mouth or midway up receptacle.
    5. Fertile stamens 6–8(–9), markedly unilateral, the filaments equal or not exceeding the calyx lobes.
      6. Lower leaf surface glabrous or lanate, with stomatal cavities; bracteoles not enclosing small groups of flowers; inflorescence a panicle of cymules; ovary inserted midway up receptacle ..... 4. *Hunga*
      6. Lower leaf surface usually areolate with stomatal cavities; bracteoles enclosing small groups of flowers; inflorescence a much-branched panicle; ovary inserted at mouth of receptacle ..... 5. *Parinari*
    5. Fertile stamens 10–50, usually inserted around complete circle; the filaments far exerted beyond calyx lobes.
      7. Stamens 10–25; inflorescence little branched panicles, or racemes ..... 6. *Atuna*
      7. Stamens c. 45; inflorescence much-branched corymbose panicles ..... 7. *Maranthes*
1. Stamens united into a strap-shaped ligule; the 2 anterior petals unguiculate and enveloping the ligule in buds; ovary unilocular ..... 8. *Kostermanthus*

KEY TO THE GENERA  
based on fruiting material

1. Epicarp crustaceous-verrucose; mesocarp thick, hard, fibrous; endocarp breaking up irregularly on germination; cotyledons at least slightly runcate.
  2. Stamens free to base (can often be seen persistent around base of young fruit). Cotyledons runcate ..... 6. *Atuna*
  2. Stamens united into a unilateral ligule. Cotyledons only slightly runcate ..... 8. *Kostermanthus*
1. Epicarp smooth and glabrous or distinctly lenticellate but not crustaceous; if lenticellate then endocarp opening by a pair of basal stoppers to allow seedling escape. Cotyledons not runcate.
  3. Epicarp lenticellate; opening by a pair of basal stoppers to allow seedling escape, always thick and woody; fruit bilocular, but often only one loculus developing seed. .... 5. *Parinari*
  3. Epicarp glabrous and smooth without lenticels; opening by lateral plates, longitudinal lines or no special mechanism of seedling escape; fruit uni- or bilocular.
    4. Endocarp opening by a pair of lateral plates to allow seedling to escape; endocarp thick and woody or thin and bony.
      5. Fruit unilocular; endocarp very thin, bony ..... 3. *Parastemon*
      5. Fruit bilocular; endocarp thick, woody ..... 7. *Maranthes*

4. Endocarp not opening by lateral plates, usually opening longitudinally; endocarp thin and bony.  
 6. Fruit usually bilocular, 1.5–5 cm long, sometimes sagittate with a distinct stipe, not ridged
4. Hunga
6. Fruit unilocular, either 1–1.3 cm long, ellipsoid or 2–5 cm long and ridged.  
 7. Fruit ridged. *Leaves* orbicular..... 1. *Chrysobalanus*  
 7. Fruit smooth, not ridged. *Leaves* oblong to elliptic..... 2. *Licania*

### 1. CHRYSOBALANUS

LINN. Sp. Pl. 1 (1753) 513; DC. Prod. 2 (1825) 525; HOOK. *f.* in Benth. & Hook. *f.*, Gen. Pl. 1 (1865) 606; HOOK. *f.* in Mart., Fl. Bras. 14 (2) (1867) 7; PRANCE, Fl. Neotrop. 9 (1972) 14. — Fig. 1.

Shrubs or small trees. *Stipules* small, connate-axillary, caducous. *Leaves* glabrous on both surfaces, without stomatal crypts. Petioles eglandular. *Inflorescence* terminal or axillary cymules or a panicle of cymules. Bracts and bracteoles to 2 mm long, eglandular, not enclosing groups of flower buds. *Flowers* hermaphrodite. *Receptacle* campanulate, symmetric, tomentose on exterior and interior; calyx lobes 5, acute, equal. *Petals* 5, longer than calyx lobes, not clawed. *Stamens* 15–26, all fertile, inserted on margin of disk; filaments hairy, united in groups for half length, exserted. *Ovary* inserted at base of receptacle, densely pilose; carpel unilocular, with 2 ovules. *Style* pubescent. *Fruit* a small fleshy drupe, epicarp smooth and ridged, endocarp hard, thin, glabrous on interior, with 4–8 prominent longitudinal ridges which correspond to lines of fracture for seedling escape.

**Distr.** Three species, one in West Africa and the Neotropics, two confined to the Neotropics. One species naturalized in *Malesia* and Fiji.

**Uses.** Edible fruit. The shrub is used for the stabilization of dunes.

**1. *Chrysobalanus icaco*** LINN. Sp. Pl. 1 (1753) 513; BROWNE, Nat. Hist. Jamaica (1756) 250; JACQ. Sel. Stirp. Am. Hist. (1763) 155; DC. Prod. 2 (1825) 525; HOOK. *f.* in Mart., Fl. Bras. 14 (2) (1867) 7; PRANCE, Fl. Neotrop. 9 (1972) 15; SMITH, Fl. Vit. Nov. 3 (1985) 50. — Fig. 1.

Shrub or small tree to 5 m tall, the branches glabrous and lenticellate. *Stipules* 1–3 mm long, caducous. *Leaves* orbicular to ovate-elliptic, 2–8 by 2–6 cm, retuse, rounded or with short blunt acumen at apex, subcuneate at base, glabrous on both surfaces; petioles 2–4 mm. *Inflorescences* small terminal and axillary cymules or panicles of cymules, the rachis and branches grey-puberulous. *Flowers* 4–6 mm long. *Receptacle* campanulate-cupuliform, symmet-

rical, tomentose on exterior and interior. Calyx lobes rounded to acute, tomentellous on both surfaces. *Petals* white, glabrous, exserted. *Stamens* 15–26, the filaments joined for up to half of length in small groups, densely hairy, exserted. *Ovary* at base of receptacle, pilose. *Fruit* ovate to obovate, 2–5 cm long; epicarp smooth with longitudinal ridges; mesocarp thin and fleshy; endocarp thin, hard, ridged on exterior.

**Distr.** Neotropics, mainly in coastal areas; West & Central Africa, naturalized in Fiji, cultivated in Vietnam; in *Malesia* cultivated in Singapore where it has escaped and naturalized. Fig. 1D.

**Ecol.** Dunes, beaches and coastal scrub.

**Uses.** Edible fruit.

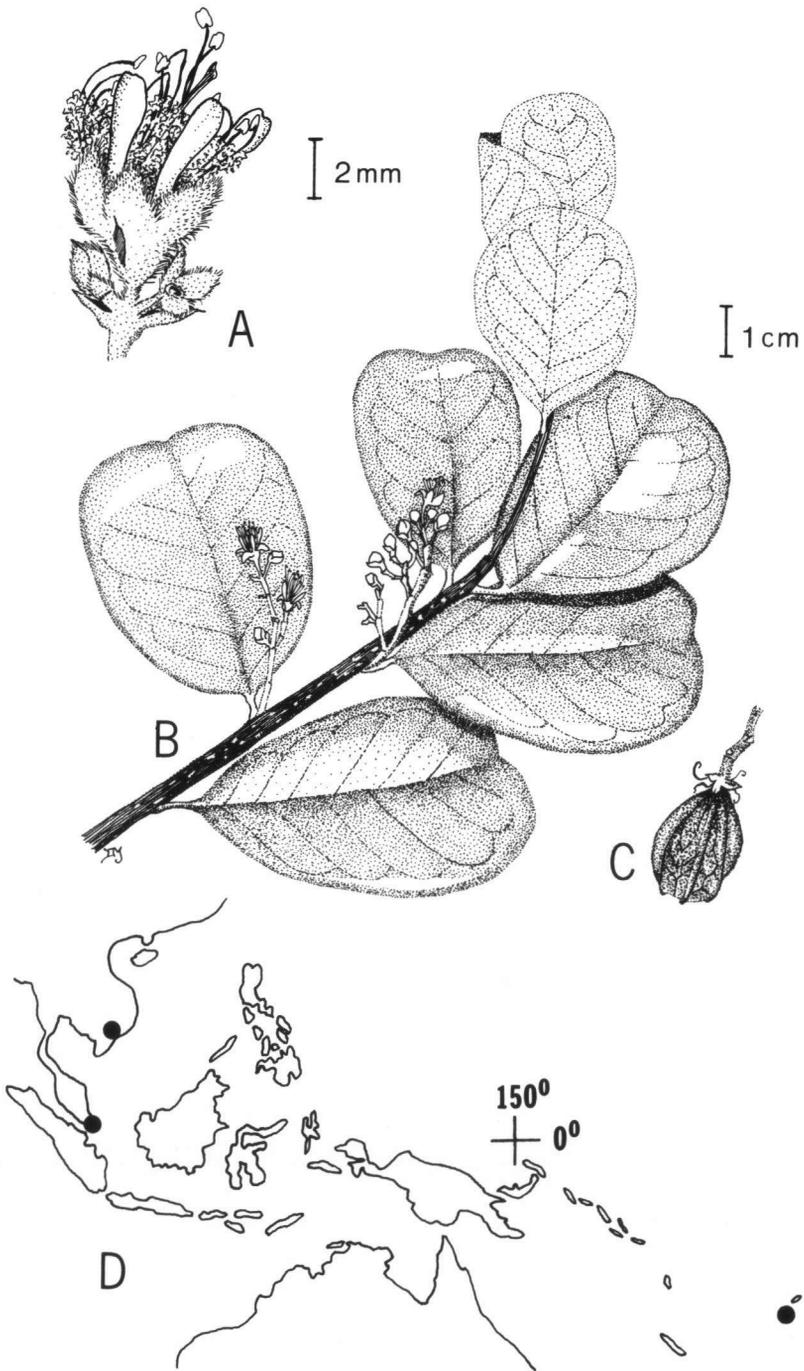


Fig. 1. *Chrysobalanus icaco* LINN. A. Detail of flower; B. habit; C. fruit; D. distribution in Malesia.

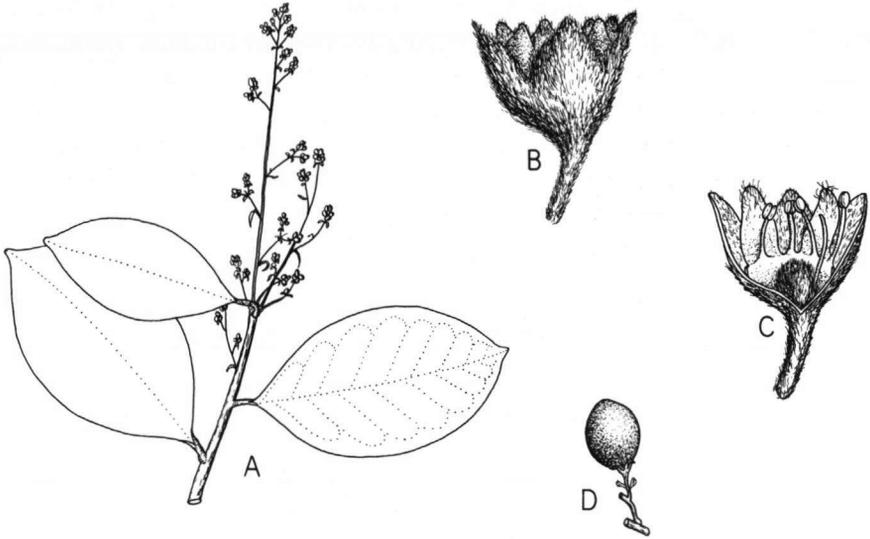


Fig. 2. *Licania splendens* (KORTH.) PRANCE. A. Habit,  $\times 0.5$ ; B. flower,  $\times 9$ ; C. flower section,  $\times 9$ ; D. fruit,  $\times 1$  (A-C ELMER 20916, D RAMOS & CONVOCAR 83437).

## 2. LICANIA

AUBL. Hist. Pl. Guiane Fr. 1 (1775) 119, t. 45; DC. Prod. 2 (1825) 527; HOOK. *f.* in Benth. & Hook. *f.* Gen. Pl. 1 (1865) 606; FRITSCH, Ann. Naturh. Mus. Wien 4 (1889) 33; FOCKE in E. & P. Nat. Pfl. Fam. 3, 3 (1891) 58; PRANCE, Fl. Neotrop. 9 (1972) 21; PRANCE & WHITM. Tree Fl. Malaya 2 (1973) 328; WHITE, Bull. Jard. Bot. Nat. Belg. 46 (1976) 280; PRANCE, Brittonia 31 (1979) 94. — *Moquilea* AUBL. Hist. Pl. Guiane Fr. 1 (1775) 521, t. 208; DC. Prod. 2 (1825) 526; HOOK. *f.* in Benth. & Hook. *f.*, Gen. Pl. 1 (1865) 606; FOCKE in E. & P. Nat. Pfl. Fam. 3, 3 (1891) 58. — *Dahuronia* SCOP. Introd. (1777) 217, *nom. illeg.* — *Hedycrea* SCHREB. in Linn., Gen. Pl. ed. 8, 1 (1789) 160, *nom. illeg.* — *Angelesia* KORTH. Ned. Kruidk. Arch. 3 (1854) 384; BOERL. Handl. Fl. Ned. Ind. 1 (1890) 424; BURK. Dict. (1935) 159; CORNER, Wayside Trees (1940) 526; HUTCH. Gen. Flow. Pl. 1 (1964) 191. — *Trichocarya* MIQ. Fl. Ind. Bat. 1, 1 (1855) 358; *ibid.* 6 (1858) 1084, *p.p. quoad T. splendens tantum.* — *Geobalanus* SMALL, Fl. Miami (1913) 80; HUTCH. Gen. Flow. Pl. 1 (1964) 191. — *Coccomelia* RIDLEY, J. Str. Br. Roy. As. Soc. n. 82 (1920) 183; Fl. Mal. Pen. 1 (1922) 671. — *Afrolicania* MILDBR. Notizbl. Bot. Gart. Berlin-Dahlem 8 (1921) 483. — Fig. 2.

Small to large trees. Stipules small, free, caducous. Leaves glabrous on both surfaces, without stomatal crypts. Petioles eglandular. Inflorescence a panicle of cymules. Bracts and bracteoles to 1.5 mm long, membraneous, eglandular, not enclosing groups of flower buds. Flowers hermaphrodite. Receptacle campanulate, slightly asymmetric, tomentose on exterior, tomentose within; calyx

lobes 5, acute, unequal. *Petals* 5, small, not exceeding the calyx lobes, not clawed. *Stamens* 7–10, all fertile, inserted on margin of disk; filaments glabrous, included, slightly united at base. *Ovary* inserted at or near base of receptacle, pilose on exterior; carpel unilocular, with 2 ovules. *Style* pubescent at base, the stigma capitate. *Fruit* a small, fleshy drupe, narrowed to a shortly stipitate base; epicarp smooth, not ridged, glabrous, not lenticellate; mesocarp thin, fleshy; endocarp thin, hard, bony, breaking up in longitudinal lines during germination, tomentose within.

*Distr.* About 180 species in the Neotropics, one species in West Africa; three species in Malesia from the Malay Peninsula to New Guinea and the Philippines, but not in the Lesser Sunda Islands.

*Uses.* The timber is strong and durable and resistant to marine borers. It is hard to work because of silica.

*Note.* The description above is for the Malesian element of *Licania*; the genus is much more variable in the Neotropics. The three Asian species are placed in subgenus *Angelesia* by PRANCE & WHITE, *Phil. Trans. Roy. Soc. London* 320 (1988) 94.

#### KEY TO THE SPECIES

1. Fruit 1–1.3 cm long, ellipsoid, not narrowed towards base or apex.
2. Leaves oblong, the apices distinctly acuminate; inflorescence rachis densely puberulous 1. *L. splendens*
2. Leaves elliptic to oblong-elliptic, the apices acute to rounded and emarginate; inflorescence rachis sparsely puberulous ..... 2. *L. palawanensis*
1. Fruit 2.5–5 cm long, narrowed at apex and base, fusiform ..... 3. *L. fusicarpa*

1. *Licania splendens* (KORTH.) PRANCE, *Fl. Neotrop.* 9 (1972) 172. – *Angelesia splendens* KORTH. *Ned. Kruidk. Arch.* 3 (1854) 384; BOERL. & KOORD. *ic. Bog.* 1, 4 (1901) 59, t. 96; MERR. *Philip. J. Sc.* 10 (1915) Bot. 307; *Enum. Philip. Pl.* 2 (1923) 236; CORNER, *Wayside Trees* (1940) 526; BROWNE, *For. Trees Sarawak & Brunei* (1955) 307. – *Licania angelesia* BLUME, *Mélang. Bot.* 2 (1855) 358. – *Chrysobalanus splendens* KORTH. *ex MIQ. Fl. Ind. Bat.* 1, 1 (1855) 358, in syn. – *Parinarium fragile* TEJISM. & BINN. *Cat. Hort. Bog.* (1866) 253, *nom. nud.* – *Parinarium nitidum* HOOK. *f. Fl. Brit. India* 2 (1878) 310. – *Ferolia nitida* (HOOK. *f.*) RIDLEY, *J. Str. Br. Roy. As. Soc. n.* 82 (1920) 183; *Fl. Mal. Pen.* 1 (1922) 671. – *Parinarium philippinense* ELMER, *Leafl. Philip. Bot.* 10 (1939) 3809. – **Fig. 2.**

Tree to 25 m tall, the young branches sparsely lanate, soon glabrous. *Stipules* linear-lanceolate, to 3 mm long, caducous. *Leaves* 4–11 by 1.8–4.2 cm, oblong, usually acuminate at apex, cuneate at base, glabrous beneath; petioles 2–5 mm, canaliculate, glabrous when mature. *Inflorescence* terminal and axillary panicles of cymes, 1.5–14 cm long, the rachis and branches grey-puberulous. *Flowers* c. 2 mm long. *Receptacle* campanulate, slightly swollen to one side, grey-tomentellous on exterior, tomentose within; pedicels c. 1 mm long. *Calyx lobes* acute, tomentellous on both surfaces. *Petals* pubescent on exterior. *Stamens* 7–10, slightly unilateral, the filaments glabrous. *Ovary* at or near base of receptacle,

unilocular, pilose on exterior. *Fruit* ellipsoid, 1–1.3 cm long; epicarp smooth, glabrous; mesocarp thin, fleshy; endocarp thin, hard, bony, breaking open by longitudinal lines of weakness, tomentose within.

*Distr.* Thailand; in *Malesia*: Sumatra, Malay Peninsula, W. Java, Borneo, Philippines. **Fig. 3.**

*Ecol.* Commonest in forest, including dipterocarp forest, on hill slopes and ridges, but wide-ranging in peat swamp, freshwater swamp forest, on seashores, and in rocky places; 0–400(–800) m altitude.

*Uses.* The timber is strong, durable and resistant to marine borers and is used for saltwater piles, railroad ties, etc. However, it is extremely hard to work and requires special tools because of silica. The fruit is edible but is not widely used.

*Vern.* Malay Peninsula: *champrai, medang merah, m. puteh, membatu, mepadang, merbatu kechil*; Borneo: *piasau-piasau, Kedayan, gandulong, Dusun, tampaluan*, Sabah, *sampaluan*, Brunei, *buku-buku, bunga, djentihan burung, mauhi*, Kalimantan; Philippines: *taguilom bay, amayan, balik*, D.Bis., *dagingan, dagingdingan*, S.L.Bis., *gapas, maralibus*, Tagb.

2. *Licania palawanensis* PRANCE, *Brittonia* 31 (1979) 94.

Shrub, young branches sparsely puberulous soon becoming glabrous. *Stipules* lanceolate, 1–2 mm long, glabrous, caducous. *Leaves* 3–6 by 1.4–3 cm,

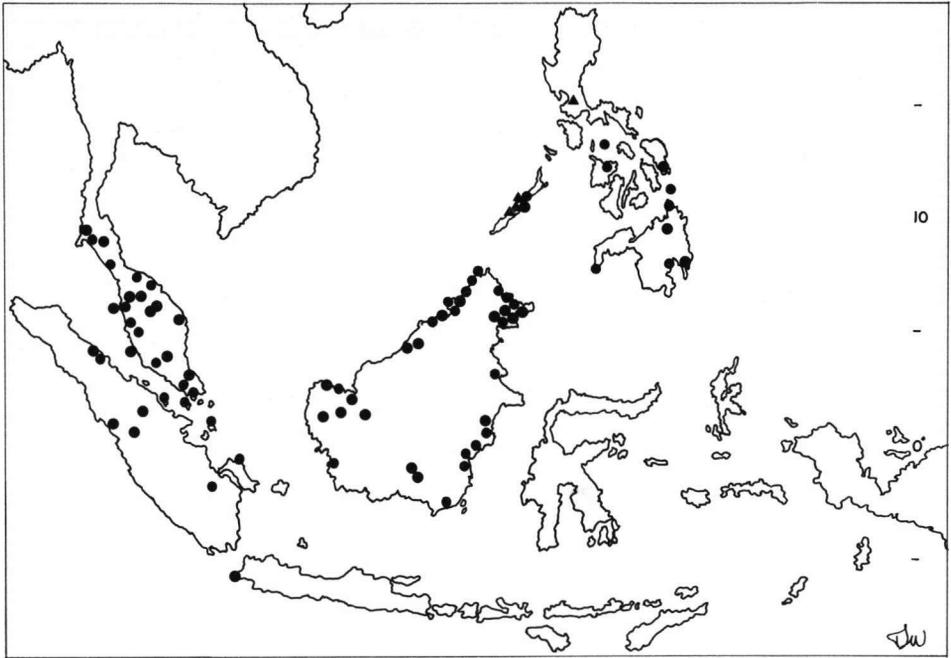


Fig. 3. Distribution of *Licania splendens* (KORTH.) PRANCE (dots) and *L. palawanensis* PRANCE (triangles).

elliptic to oblong elliptic, rounded to acute at apex, emarginate, subcuneate at base, glabrous beneath; petioles 1–3 mm long, c. 1.5 mm wide, lanate becoming glabrous with age, rugose. *Inflorescences* panicles of cymules, 3–4 cm long, the rachis and branches sparsely puberulous. *Flowers* c. 2 mm long. *Receptacle* campanulate, slightly swollen to one side, grey-tomentellous on exterior, tomentose within; pedicels c. 1 mm long. Calyx lobes acute, tomentellous on exterior, puberulous within. *Petals* puberulous on exterior. *Stamens* 7, inserted around complete circle, the filaments glabrous. *Ovary* inserted at base of receptacle, lanate-pilose, unilocular. *Fruit* (immature) ellipsoid, epicarp smooth, glabrous; mesocarp thin; endocarp thin, hard, bony, tomentose within, breaking open by longitudinal lines of weakness.

Distr. Malesia: Philippines (Palawan). Fig. 3.

Ecol. Confined to ultrabasic rock formation; 0–300 m altitude, including sea-shore forest.

3. *Licania fusicarpa* (KOSTERM.) PRANCE, *Brittonia* 39 (1987) 366. – *Hunga fusicarpa* KOSTERM. *Reinwardtia* 10 (1985) 123.

Tree to 7 m tall, young branches puberulous, glabrescent, with small prominent round lenticels. *Stipules* not seen. *Leaves* 5–10 by 1–4.5 cm, chartaceous, oblong to elliptic, acute to bluntly acuminate at apex, cuneate at base, glabrous and glossy on both surfaces, decurrent onto petiole; petioles 2–3 mm long, rugose, puberulous becoming glabrous with age. *Inflorescences* terminal and axillary panicles of cymules, few-flowered, the rachis and branches sparsely puberulous. *Flowers* c. 2 mm long. *Receptacle* campanulate, grey-tomentellous on exterior, tomentose within; pedicels 2–3 mm long. Calyx lobes acute, narrow, tomentellous on exterior, puberulous within. *Petals* not seen. *Stamens* persistent beneath young fruit, 0.5–1 mm long, connate at base. *Fruit* (2.5–)3–5 cm long, narrowly spindle-shaped, narrowed at apex to a tip 2–3 mm long, narrowed at base in stipe 5–10 mm long; epicarp smooth, glabrous; mesocarp thin; endocarp hard, bony, c. 1 mm thick, densely lanate within, without lines of dehiscence.

Distr. Malesia: E. Papua New Guinea (Milne Bay Prov., Ferguson I., Morobe Prov.). Fig. 5.

Ecol. Coastal rain-forest, 0–300 m altitude.

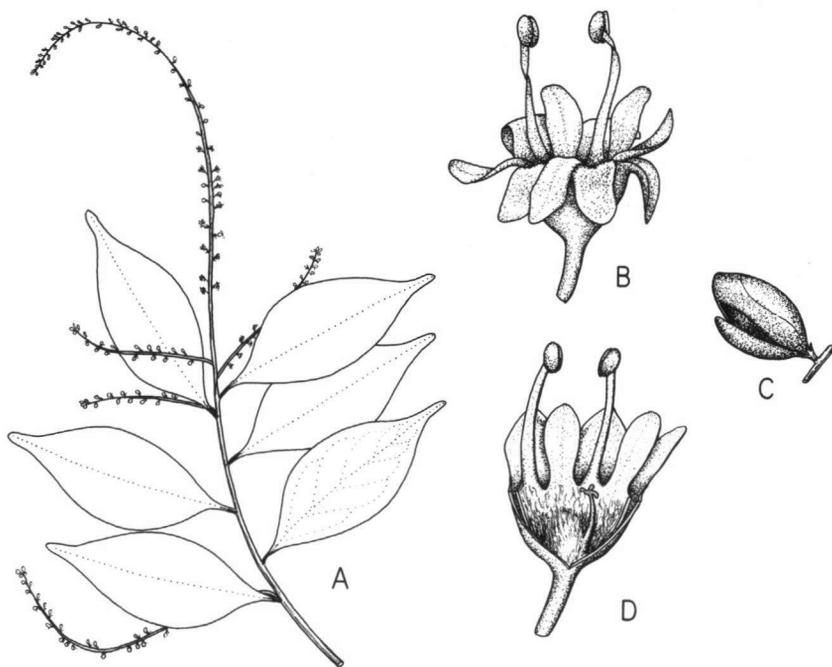


Fig. 4. *Parastemon urophyllus* (WALL. ex A.DC.) A.DC. A. Habit,  $\times 0.5$ ; B. flower,  $\times 10$ ; C. fruit,  $\times 1$ ; D. flower section,  $\times 10$  (A, B SINCLAIR 39504, C, D SINCLAIR 3319).

### 3. PARASTEMON

A.DC. Ann. Sci. Nat. Bot. sér. 2, 18 (1842) 208; MIQ. Fl. Ind. Bat. 1, 1 (1855) 359; HOOK. f. in Benth. & Hook. f., Gen. Pl. 1 (1865) 607; Fl. Brit. India 2 (1878) 312; BOERL. Handl. Fl. Ned. Ind. 1 (1890) 426; FOCKE in E. & P. Nat. Pfl. Fam. 3, 3 (1891) 60; MERR. Philip. J. Sc. 10 (1915) Bot. 307; RIDLEY, Fl. Mal. Pen. 1 (1922) 672; MERR. & PERRY, J. Arn. Arb. 21 (1940) 197; CORNER, Wayside Trees (1940) 526; HUTCH. Gen. Flow. Pl. 1 (1964) 193. — *Diemenia* KORTH. Ned. Kruidk. Arch. 3 (1854) 388; BOERL. Handl. Fl. Ned. Ind. 1 (1890) 425. — *Trichocarya* MIQ. Fl. Ind. Bat. 1, 1 (1855) 357, *p.p.* — Fig. 4.

Tree or shrub. *Stipules* small and triangular, caducous. *Leaves* glabrous on both surfaces, without stomatal cavities, with 2 small discoid glands at base of lamina; petioles eglandular. *Inflorescence* an axillary or rarely terminal simple or sparsely branched raceme. Bracts and bracteoles small, eglandular, not enclosing groups of flower buds. *Flowers* hermaphrodite or polygamo-dioecious. *Receptacle* patelliform or shallowly cupuliform, shortly hairy within; calyx lobes 5, acute, subequal. *Petals* 5, not exceeding calyx lobes, not clawed. *Stamens* either 5 and all fertile or 2 fertile with 3 staminodes; the filaments glabrous, shorter than the calyx lobes. *Ovary* centrally inserted at base of recep-

tacle, glabrous or densely hairy on exterior; carpel unilocular, with 2 ovules. *Style* filiform, puberulous towards the base, with 3 large undivided lobes at apex or 1 obscure lobe and 2 large, sometimes deeply divided lobes. *Fruit* a small drupe to *c.* 1.5 cm or *c.* 3 cm long; epicarp smooth, not lenticellate; endocarp thin, hard, bony, smooth on exterior, glabrous within; with 2 large lateral plates which break away on germination to allow seedling escape.

**Distr.** Three species; Nicobar Islands; in *Malesia*: Malay Peninsula, Sumatra, Borneo, Moluccas, New Guinea, Admiralty Is.

#### KEY TO THE SPECIES

1. Fruit 1–1.5 mm long. Primary veins of leaves 8–11 pairs.
  2. Receptacle shallowly cup-shaped, glabrous on exterior; fertile stamens 2; style 3-lobed at apex. Inflorescence glabrous ..... 1. *P. urophyllus*
  2. Receptacle saucer-shaped, puberulous on exterior; fertile stamens 5; style with one obscure and two large bifid apical lobes. Inflorescence villous ..... 2. *P. versteeghii*
1. Fruit 2.3–3.5 mm long. Primary veins of leaves 5–6 pairs ..... 3. *P. grandifructus*

1. *Parastemon urophyllus* (WALL. ex A.DC.) A.DC. Ann. Sci. Nat. Bot. sér. 2, 18 (1842) 208; MIQ. Fl. Ind. Bat. 1, 1 (1855) 359; BOERL. & KOORD. Ic. Bog. 1, 4 (1901) 61, t. 97; RIDLEY, Fl. Mal. Pen. 1 (1922) 672; BURK. Dict. (1935) 1693; CORNER, Wayside Trees (1940) 526; BROWNE, For. Trees Sarawak & Brunei (1955) 308; KOCHUM. & WYATT-SMITH, Mal. For. Rec. 17 (1964); PRANCE & WHITM. Tree Fl. Malaya 2 (1973) 331. — *Embelia urophylla* [WALL. Cat. (1830) n. 2309, *nom. nud.*] ex A.DC. Trans. Linn. Soc. 17 (1837) 131. — *Diemenia racemosa* (KORTH.) MIQ. Fl. Ind. Bat. 1, 1 (1855) 358. — *Licania diemenia* BLUME, Mélang. Bot. 2 (1855) 10; HASSK. Flora 41 (1858) 256, *nom. illeg.* — *Parastemon spicatus* RIDLEY, J. Str. Br. Roy. As. Soc. n. 75 (1917) 29. — Fig. 4.

Tree to 40 m tall, or shrub, the young branches glabrous, the trunk often buttressed. *Stipules* triangular, *c.* 1 mm long, caducous. *Leaves* thinly coriaceous, narrowly oblong, 2.5–8 by 1.4–2.5 cm, cuspidate acuminate at apex, the tip 5–15 mm, cuneate at base; midrib plane above, prominulous beneath; primary veins 8–11 pairs; petioles 4–5 mm long, canaliculate, glabrous. *Inflorescence* of axillary and rarely terminal racemes or occasionally slightly branched, 4–14 cm long, the rachis glabrous. *Flowers* polygamo-dioecious, *c.* 1.5 mm long. *Receptacle* broadly cupuliform to flattened saucer-shaped, glabrous on exterior, tomentose within; pedicels up to 2 mm long. Calyx lobes acute, glabrous on exterior. Petals 5. *Stamens* 2 fertile and 3 sterile staminodes opposite. *Ovary* inserted at base of receptacle, pilose on exterior, unilocular. *Style* pilose at base, glabrous above, the stigma trifid. *Fruit* ellipsoid, 1–1.5 cm long; epicarp smooth, glabrous; mesocarp

thin, hard; endocarp thin, hard, bony, glabrous within, opening by 2 lateral plates.

**Distr.** Nicobar Islands; in *Malesia*: Malay Peninsula, Sumatra, Borneo. Fig. 5.

**Ecol.** Characteristic of peat swamp forest where it is a common large tree, but wide ranging into shorter, more open scrub forest.

**Uses.** The wood is hard to use because of the silica content, but it is used locally for general construction, posts, and as firewood.

**Vern.** Malay Peninsula: *kelat, k. pasir, k. puteh, nylas*; Sumatra: *galam tabanga, kayu gelang, malas, meriawak*; Borneo: *mandailas, Brunei, Besaya, sempalawan, Brunei, tempalawan, Bajau, mengilas, ngilas padang, obah*, Sarawak.

**Notes.** The only record of this species from Java (BLUME *s.n.*, L) is very dubious since the collector's name was added later. It is probably either mislabelled or from cultivated material. The only difference given between *P. spicatus* and *P. urophyllus* is that the former is a shrub with sessile flowers. Some forms of *P. urophyllus* have extremely short pedicels and most sessile-flowered individuals are recorded as being small trees. There is thus no reason to maintain *P. spicatus* as a distinct species.

2. *Parastemon versteeghii* MERR. & PERRY, J. Arn. Arb. 21 (1940) 197.

Tree to 40 m tall, the young branches sparsely puberulous, soon glabrous. *Stipules* triangular, *c.* 1 mm long, caducous. *Leaves* thinly coriaceous, narrowly oblong, 5–9.5 by 1.8–3.7 cm, cuspidate acuminate at apex, the tip 7–15 mm long, cuneate at base; midrib plane above, prominulous beneath; primary veins 8–12 pairs, inconspicuous, slightly



Fig. 5. Distribution of *Licania fuscarpa* (KOSTERM.) PRANCE (diamond), *Parastemon urophyllus* (WALL. ex A.DC.) A.DC. (dots), *P. grandifructus* PRANCE (squares), and *P. versteeghii* MERR. & PERRY (triangles).

prominulous beneath; petioles 3–7 mm long, terete, glabrescent. *Inflorescence* of axillary and terminal racemes, 2–9 cm long, the rachis sparsely villous. *Flowers* hermaphrodite, c. 1.5 mm long; pedicels 1.5–3 mm, sparsely villous. *Receptacle* broadly cupuliform-flattened, sparsely villous on exterior, tomentose within. Calyx lobes acute, with hirsute margins. Petals 5, with hirsute margins. *Stamens* 5, all fertile, opposite the petals in a complete circle. *Ovary* inserted at base of receptacle, glabrous on exterior except at base, unilocular. *Style* pilose at base, glabrous above, the stigma with two large apical lobes, the third reduced or missing. *Fruit* ellipsoid, c. 1.6 cm long; epicarp smooth, glabrous; mesocarp thin, hard; endocarp thin, hard, bony, glabrous within, opening by two lateral plates.

*Distr. Malesia:* Moluccas (Morotai), New Guinea, and Admiralty Is. Fig. 5.

*Ecol.* Usually in well-drained hill forest up to 700 m altitude, but also reported from secondary forest, swampy (*Campnosperma*) forest and even beach forest.

*Vern.* New Guinea: *mangu*, Tobelo, *noeng*, Irian, *gorsawu*, Tor, *gwarsau*, Wainlag, *sirebo*, *sisero*, Kemtoek, *sosopi*, Japen, *telek*, Mooi, *sino-ree*, Biak.

### 3. *Parastemon grandifructus* PRANCE, Brittonia 39 (1987) 366.

Tree to 30 m tall, the young branches glabrous, the trunk lightly buttressed to 1 m. *Stipules* caducous (not seen). *Leaves* coriaceous, narrowly oblong, 5–8.5 by 1.8–3.2 cm, with long cuspidate acuminate apex, the tip 10–16 mm long, cuneate at base, glabrous on both surfaces; midrib prominent above, prominulous or plane beneath; primary veins 5–6 pairs, prominulous above, plane beneath; petioles 5–8 mm long, glabrous, slightly canaliculate, slightly swollen at base. *Inflorescence* of axillary and terminal racemes, the rachis glabrous. *Flowers* seen only in fruiting specimens. Calyx lobes 5, acute, glabrous on exterior, glabrous within except for a few hairs around base. *Receptacle* glabrous on exterior in fruiting condition. *Style* persistent below fruits, the stigma bifid or trifid. *Fruit* ellipsoid, 2.3–3.5 by 1.3–1.5 cm, epicarp smooth, glabrous; mesocarp thin, 0.25 mm; endocarp thin, hard, bony, 0.25 mm thick, glabrous within, opening by 2 lateral plates 1.9–2 cm long.

*Distr. Malesia:* Borneo (Sarawak, Sabah). Fig. 5.

*Ecol.* Upland white sand areas.

*Vern.* Borneo: *ngilas*, Iban, *praus*, Dyak.

## 4. HUNGA

PANCHER ex PRANCE, Brittonia 31 (1979) 79; Fl. Nouv. Caléd. et Dép. 12 (1983) 106. – Fig. 6, 8.

Shrubs or small trees. *Stipules* lanceolate and persistent (absent or very early

caducous in New Caledonian species). *Leaves* usually glabrous on both surfaces (lanate beneath in some New Caledonian species), with a pair of, often obscure, marginal glands towards the base, without stomatal cavities; petioles eglandular. *Inflorescence* a few-flowered terminal or axially raceme of cymules. Bracts and bracteoles small, persistent, not enclosing the flowers in small groups. *Flowers* hermaphrodite, slightly zygomorphic. *Receptacle* campanulate, slightly asymmetric, shortly puberulous on exterior, densely pubescent within. Calyx lobes 5, acute. Petals 5, small, not exceeding calyx lobes, not clawed. *Stamens* 5–9, not exceeding calyx lobes, unilateral with 3–7 staminodes opposite. *Ovary* inserted midway up receptacle, densely hairy on exterior; carpel bilocular with one ovule in each loculus. *Style* truncate but distinctly 3-lobed at apex. *Fruit* small, fleshy, bilocular or often with one loculus underdeveloped; epicarp smooth, not ridged, not lenticellate; mesocarp thin, fleshy; endocarp thin, hard, bony, with a smooth surface, interior very hairy, with 4–6 longitudinal lines of weakness which allow the seedling to escape.

**Distr.** There are 11 species, 8 of which occur in New Caledonia and the Loyalty Is., 3 in *Malesia*: Papua New Guinea.

#### KEY TO THE SPECIES

1. Inflorescence branches glabrescent; flowers glabrescent on exterior. Leaves with conspicuous anastomosing venation, oblong-elliptic to elliptic, 4–8.5 cm broad.
2. Leaves elliptic, 7.5–8.5 cm broad ..... 1. *H. novoguineensis*
2. Leaves oblong-elliptic, 4–6.5 cm broad ..... 2. *H. papuana*
1. Inflorescence branches lanate to puberulous; flowers pubescent on exterior. Leaf with venation not conspicuously anastomosing, oblong-lanceolate, 2–3.7 cm broad ..... 3. *H. longifolia*

1. *Hunga novoguineensis* PRANCE, Brittonia 31 (1979) 88. – Fig. 6 G, H.

Tree 4 m tall, the young branches puberulous, soon glabrous, lenticellate. *Stipules* lanceolate, puberulous, c. 5 mm long, persistent. *Leaves* coriaceous, elliptic, 15–19 by 7.5–8.5 cm, glabrous on both surfaces, apex acuminate, the acumens 8–10 mm long, subcuneate at base; primary veins 11–14 pairs, anastomosing 4 mm away from margins, prominent above, prominent beneath; petioles 5–6 mm long, puberulous soon becoming glabrous, slightly canaliculate, eglandular. *Inflorescence* of terminal and axillary panicles, the rachis and branches puberulous. Bracts and bracteoles 1–2 mm long, puberulous, persistent. *Flowers* not seen. *Fruit* sagittate pyriform, c. 3.5 cm long, the upper part triangular, 2–2.5 cm long, the base with a stipe 6–10 mm long; epicarp glabrous, smooth, mesocarp thin, fleshy; endocarp thin, hard, bony, lanate within.

**Distr.** *Malesia*: Papua New Guinea, two collections, from Morobe and Milne Bay Prov. Fig. 7.

**Ecol.** Oak forest on slopes, at c. 800 m altitude.

2. *Hunga papuana* (BAKER f.) PRANCE, Brittonia 31 (1979) 88. – *Angelesia papuana* BAKER f. J. Bot. 61, Suppl. (1923) 13. – Fig. 6 A–F.

Small tree, the young branches lanate, soon glabrous. *Stipules* lanceolate, 3–6 mm long, puberulous, persistent. *Leaves* coriaceous, oblong-elliptic, 10–19 by 4–6.5 cm, finely acuminate at apex, the tip 8–16 mm, rounded to subcuneate at base, glabrous on both surfaces; primary veins 9–13 pairs, prominent above, prominent beneath, conspicuously anastomosing 5 mm from margin; petioles 2–4 mm long, shallowly canaliculate, sparsely puberulous when young, soon glabrescent, rugose. *Inflorescences* of terminal and axillary panicles, 3–10 cm long, the rachis and branches sparsely lanate-puberulous when young. Bracts and bracteoles 0.5–2 mm long, sparsely puberulous-glabrescent on both surfaces. *Flowers* 1.5–2 mm long. *Receptacle* campanulate, glabrous externally, tomentose within. Calyx lobes glabrous on both faces except for ciliate margins. *Petals* glabrous. *Stamens* c. 7, unilateral with toothed staminodes opposite. *Ovary*

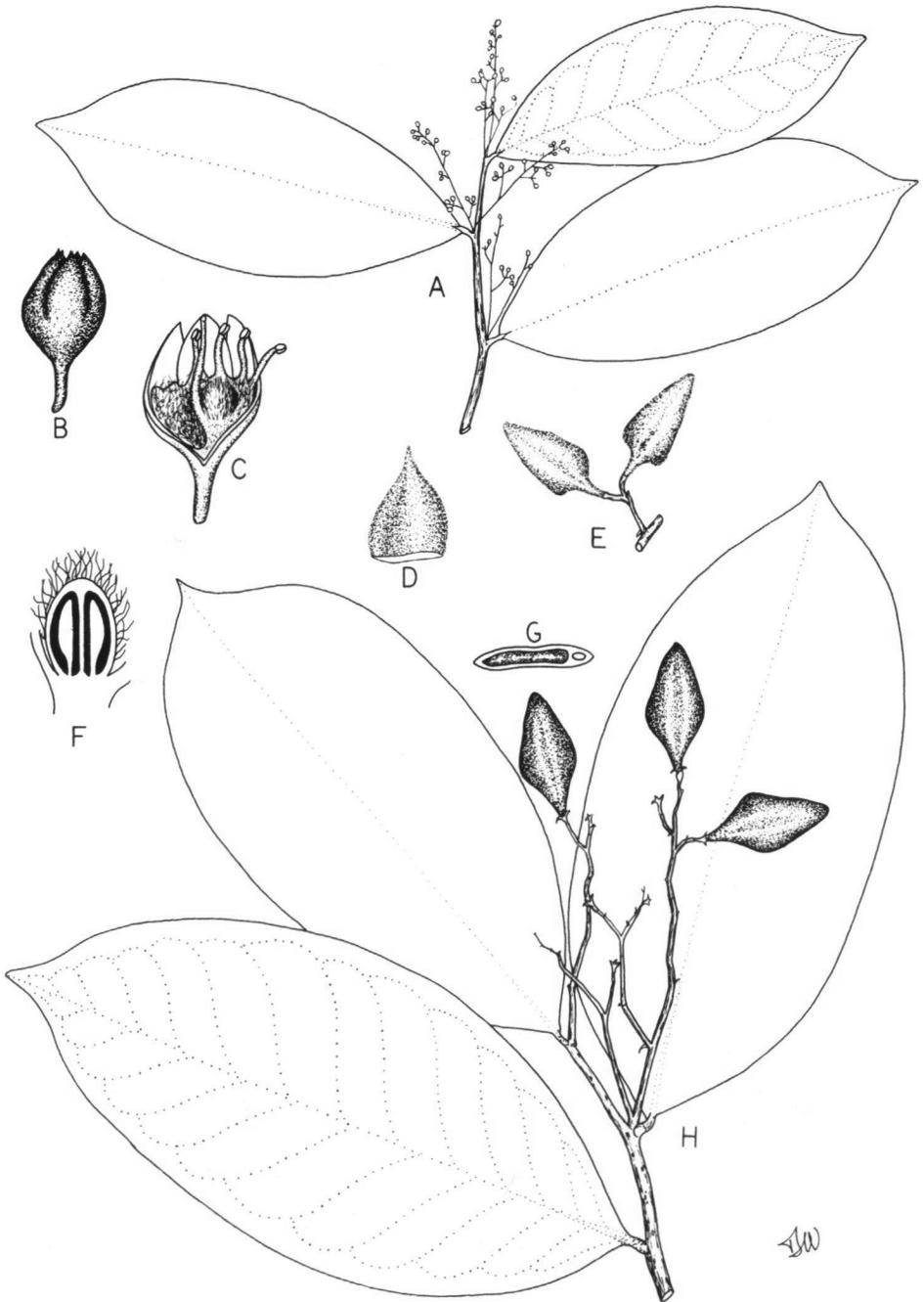


Fig. 6. *Hunga papuana* (BAKER f.) PRANCE. A. Habit,  $\times 0.5$ ; B. flower,  $\times 7$ ; C. flower section,  $\times 9$ ; D. petal,  $\times 15$ ; E. fruit,  $\times 0.5$ ; F. ovary section,  $\times 15$ . — *H. novoguineensis* PRANCE. G. Young fruit section,  $\times 1$ ; H. habit,  $\times 0.5$  (A–C FORBES 504, D–F WOMERSLEY NGF 19307, G, H HARTLEY 12645).



Fig. 7. Distribution of *Hunga longifolia* PRANCE (star), *H. novoguineensis* PRANCE (dots), and *H. papuana* (BAKER f.) PRANCE (triangles).

bilocular, lanate-pilose externally. *Style* pilose at base, glabrous above, stigma truncate. *Fruit* sagittate-pyriform, unilocular, to 5 cm long, the upper portion triangular, 2–3.5 cm long, the base narrowly and abruptly tapered to a stipe 0.6–1 cm long; epicarp smooth, glabrous; mesocarp thin, fleshy; endocarp thin, hard, bony, lanate-tomentose within.  
 Distr. *Malesia*: Papua New Guinea. Fig. 7.  
 Ecol. Oak forest; 500–1000 m altitude.

3. *Hunga longifolia* PRANCE, *Brittonia* 31 (1979) 84. – Fig. 8.

Tree 15 m tall, the young branches puberulous, soon glabrous. *Stipules* linear-lanceolate, 5–6.5 mm long, puberulous, subsistent. *Leaves* coriaceous, oblong-lanceolate, 7–13 by 2–3.7 cm, acute to bluntly acuminate at apex, cuneate at base, glabrous on both surfaces; petioles 3–5 mm long, shallowly canaliculate, lanate when young, glabrescent with

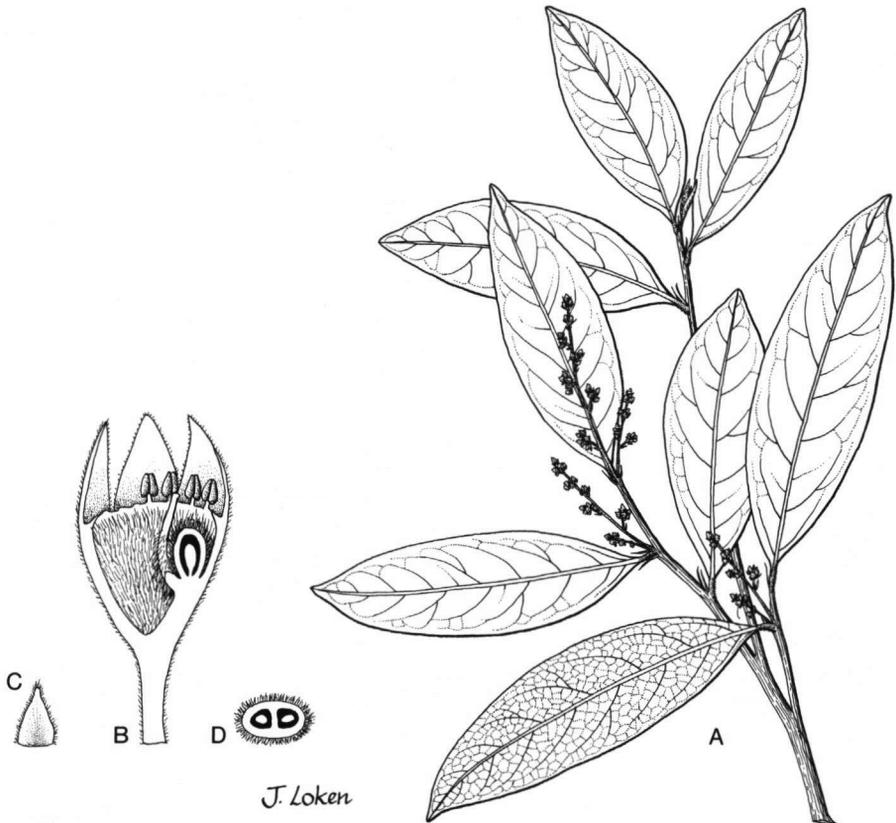


Fig. 8. *Hunga longifolia* PRANCE. A. Habit,  $\times 0.5$ ; B. flower; C. petal; D. ovary section, all  $\times 20$ .

age, slightly rugose. *Inflorescences* axillary and terminal panicles of cymules 1.5–6 cm long, the rachis and branches appressed lanate when young, becoming puberulous. Bracts and bracteoles 1–3.5 mm long, sparsely puberulous-glabrescent on both surfaces. *Flowers* 2–2.5 mm long. *Receptacle* campanulate, swollen slightly to one side, lanate-tomentose on exterior, tomentose within. Calyx lobes pubescent on both surfaces. *Petals* glabrous except

for ciliate margins. *Stamens* 6–8, unilateral with 3–5 short staminodes opposite them. *Ovary* bilocular, inserted midway up receptacle tube, pilose on exterior. *Style* pilose at base. *Fruit* not seen.

Distr. *Malesia*: Papua New Guinea (Misima I.), known from a single collection. Fig. 7.

Ecol. Rain-forest on N. slope, at 300 m altitude. *Fl.* July.

## 5. PARINARI

AUBL. Hist. Pl. Guiane Fr. 1 (1775) 204; HAUMAN, Bull. Jard. Bot. Brux. 21 (1951) 184, *quoad subg. Euparinari tantum*; BACKER & BAKH.f. Fl. Java 1 (1964) 521, *p.p.*; HUTCH. Gen. Flow. Pl. 1 (1964) 192, *p.p. excl. syn. Maranthes etc.*; KOSTERM. Reinwardtia 7 (1965) 7, *excl. syn. Thelira, Ferolia, Mampata et Neou*; PRANCE, Fl. Neotrop. 9 (1972) 178; PRANCE & WHITM. Tree Fl. Malaya 2 (1973) 332; WHITE, Bull. Jard. Bot. Nat. Belg. 46 (1976) 310; Distr. Pl. Afr. 10 (1976) 327; Fl. Zamb. 4 (1978) 36; PRANCE, Fl. Venez. 4 (1982) 325; SMITH, Fl. Vit. Nov. 3 (1985) 44. — *Dugortia* SCOP. Introd. (1777) 217, *nom. illeg.* — *Parinarium* JUSS. Gen. Pl. (1789) 342; LAMK, Encycl. Méth. Bot. 5 (1804) 17; ST.HIL. Expos. Fam. 2 (1804) 194, *p.p.*; R.BR. in Tuckey, Nar. Exped. Riv. Zaire Cong. (1818) 433; STEUD. Nom. (1821) 591; DC. Prod. 2 (1825) 526; POIR. Dict. Sci. 37 (1825) 544; BARTL. Ord. Nat. (1830) 406; G.DON, Gen. Syst. 2 (1832) 478; MEISSN. Gen. (1836/42) 102; BENTH. Hook. J. Bot. 2 (1840) 211, 218; ENDL. Gen. (1840) 1252, *n.* 6411; BENTH. in HOOK., Niger Fl. (1849) 333; MIQ. Stirp. Surin. Select. 2 (1850) 7; BLUME, Mus. Bot. Lugd.-Bat. 2 (1852) 94; Mélang. Bot. 2 (1855) 10; MIQ. Fl. Ind. Bat. 1, 1 (1855) 352; *ibid.* (1858) 1084; C.MUELL. in Walp., Ann. 4 (1857) 644; MIQ. Suppl. Sumatra (1860) 306; BENTH. Fl. Austr. 2 (1864) 426; HOOK. *f.* in Benth. & Hook.*f.*, Gen. Pl. 1 (1865) 607; MIQ. Ann. Mus. Bot. Lugd.-Bat. 3 (1867) 237; HOOK. *f.* in Mart., Fl. Bras. 14 (2) (1867) 49; BAILL. Hist. Pl. 2 (1869) 435, 482; KURZ, For. Fl. Burma 1 (1877) 432; HOOK.*f.* Fl. Brit. India 2 (1878) 308; FRITSCH, Ann. Naturh. Mus. Wien 4 (1889) 33; BOERL. Handl. Fl. Ned. Ind. 1 (1890) 421, 424; FOCKE in E. & P. Nat. Pfl. Fam. 3, 3 (1891) 60; KING, J. As. Soc. Beng. 66 (1897) 276; K. & V. Bijdr. 5 (1900) 332; BAILEY, Queensl. Fl. 2 (1900) 524; BRANDIS, Indian Trees (1906) 278; BACKER, Schoolfl. Java 1 (1911) 445; RIDLEY, Fl. Mal. Pen. 1 (1922) 666; MERR. Enum. Philip. Flow. Pl. 2 (1923) 235; BURK. Dict. (1935) 1693; CORNER, Wayside Trees (1940) 527. — *Petrocarya* SCHREB. in Linn. Gen. Pl. ed. 8, 1 (1789) 245, *nom. superfl.* — *Parinarium sect. Petrocarya* DC. Prod. 2 (1825) 526; BENTH. in Hook., Niger Fl. (1849) 335, *p.p. excl. P. glaberrima et P. scabra.* — *Parinarium sect. Neocarya* DC. Prod. 2 (1825) 526, *p.p. quoad P. excelsum.* — *Balantium* DESV. ex BUCH.-HAM. Prod. Pl. Ind. Occ. (1825) 34. — *Parinarium subg. Petrocarya* (DC.) MIQ. Fl. Ind. Bat. 1, 1 (1855) 352. —

*Lepidocarpa* KORTH. Ned. Kruidk. Arch. 3 (1854) 385. — *Ferolia* O.KUNTZE, Rev. Gen. Pl. 1 (1891) 216, *p.p.* (*non Ferolia* AUBL.). — Fig. 15.

Small or large trees or rarely shrubs. *Stipules* small to large, persistent or caducous. *Leaves* usually with stomatal crypts filled with pubescence on lower surface or rarely glabrous, or lanate pubescent without crypts. Petioles usually with 2 circular glands above. *Inflorescence* a many-flowered complex cyme or cymose panicle. Bracts and bracteoles eglandular, usually concealing flower buds individually and in small groups. *Flowers* hermaphrodite. *Receptacle* subcampanulate to cupuliform, slightly swollen to one side, tomentose on both surfaces; calyx lobes 5, deltate, acute, densely hairy on both surfaces. *Petals* 5, as long as or shorter than sepals, caducous. *Stamens* 6–10, unilateral, the filaments glabrous, included, with *c.* 6 minute staminodes opposite. *Ovary* inserted on upper half of receptacle tube below mouth, pilose on exterior; carpel bilocular with 1 ovule in each loculus; style arcuate, included. *Fruit* a fleshy drupe; epicarp verrucose; endocarp thick, with a rough fibrous surface, with 2 basal obturators for seedling escape.

Distr. Pantropical with 18 species in the Neotropics, 6 in Africa and 15 in tropical Asia (*P. anamensis*), Malesia, the Pacific region (*P. insularum*) and northern Queensland, Australia; in Malesia 13 species.

Uses. The fruit of several species are edible, but little-used.

Note. Since inflorescences and flowers are uniform in the Malesian region, the species are difficult to separate; a key containing all 15 Australasian species, based on leaf characters only, is given here.

#### KEY TO THE SPECIES

1. Stomatal crypts absent from leaf underside; leaf underside glabrous or with a persistent lanate pubescence and then with large persistent stipules 7–40 mm.
2. Leaf undersurface glabrous. Stipules small and caducous.
  3. Leaves elliptic to oblong or obovate-elliptic, 9.5–20.5 by 4.5–8.5 cm; primary veins 11–16 pairs. Panicles large and silvery pubescent ..... 1. *P. argenteo-sericea*
  3. Leaves ovate, 5–9 by 2–4.5 cm; primary veins 7–11 pairs. Panicles small and subsericeous brown pubescent ..... 2. *P. canarioides*
2. Leaf undersurface densely lanate pubescent, but when removed no stomatal crypts present; stipules large and persistent, 7–40 mm long, 3–5 cm broad at base.
  4. Leaves oblong-lanceolate, 5–18 cm long on flowering branches, thickly coriaceous, base cuneate ..... 3. *P. elmeri*
  4. Leaves elliptic to oblong, 11–28 cm long, chartaceous, base rounded ..... 4. *P. parva*
1. Stomatal crypts present on leaf underside; leaf undersurface lanate or at least pubescent in crypts; stipules usually small, or if larger then early caducous.
  5. Leaf lower surface with a series of small glands along lower part of margin. Calyx broadly cupuliform.
    6. Leaf apex acute or rounded but not acuminate; primary veins 10–17 pairs. Young branches with small, almost plane lenticels. Low tree of savanna, savanna forest and forest margins ..... 5. *P. nonda*
    6. Leaf apex acuminate, acumen 3–10 mm long; primary veins 16–22 pairs; young branches with extremely prominent large lenticels; large tree of rain-forest and hills ..... 6. *P. papuana*
  5. Leaf lower surface without marginal glands on lower part. Calyx usually campanulate.
    7. Primary leaf veins 20–33 pairs (16–26 pairs in *P. costata* ssp. *polyneura*).
    8. Petioles 9–17 mm long ..... 7. *P. oblongifolia*
    8. Petioles 3–6 mm long.
      9. Leaves chartaceous, primary veins prominulous above, 16–26 pairs ..... 13c. *P. costata* ssp. *polyneura*
      9. Leaves coriaceous, primary veins impressed for upper portion, 20–28 pairs ..... 8. *P. gigantea*

## 7. Primary leaf veins 20 pairs or fewer.

10. Petioles 10–20 mm long; leaves with or without a metallic sheen above.

11. Leaves with metallic sheen above; petioles 14–20 mm long; leaves 4–9 cm broad. Borneo

9. *P. metallica*

11. Leaves without metallic sheen; petioles 10–12 mm long; leaves 6.5–12 cm broad. New Guinea

10. *P. prancei*

10. Petioles 3–10 mm long; leaves without metallic sheen.

12. Leaves rigidly coriaceous, often broadest well below mid point; midrib and often primary veins lightly impressed on upper surface . . . . . 11. *P. rigida*12. Leaves thinly coriaceous or chartaceous, usually broadest at or above middle (except in *P. insularum*); midrib and primary veins usually plane or prominulous.13. Leaves ovate, with long thin acumens, tapering from well below mid point; midrib impressed above. Plants of Pacific Islands (Fiji, Tonga, Samoa, Wallis Is.) . . . . . *P. insularum*

13. Leaves elliptic to oblong-lanceolate, tapering from middle or above; midrib usually plane or prominulous. Plants of Sunda shelf.

14. Inflorescence predominantly axillary. Leaves broadly elliptic . . . . . 12. *P. sumatrana*

14. Inflorescence terminal and subterminal. Leaves elliptic to narrowly oblong.

15. Leaf apex rounded to acute. Thailand and Indochina . . . . . *P. anamensis*15. Leaf apex acuminate. Burma, Malay Peninsula, Indonesia and the Philippines 13. *P. costata*1. *Parinari argenteo-sericea* KOSTERM. *Reinwardtia* 7 (1965) 47, f. 1; 158.

Trees to 35 m tall; the young branches glabrous, prominently lenticellate. *Stipules* lanceolate, to 8 mm long, tomentose on exterior, early caducous. *Leaves* chartaceous, oblong, elliptic to subovate-elliptic, 9.5–20.5 by 4.5–8.5 cm, glabrous on both surfaces, without stomatal cavities beneath, usually 2 glands beneath at base near junction with midrib, acute to shortly acuminate at apex, the tip 7–10 mm long, rounded at base; midrib lightly impressed above except near base, prominent beneath; primary veins 11–16 pairs, plane above, prominent beneath, erect-patent; petioles 5–9 mm long, eglandular, glabrous, rugulose. *Inflorescence* a lax, much branched, terminal panicle 9–15 cm long, the rachis and branches densely grey sericeous-tomentose; bracts and bracteoles ovate, acute, densely tomentellous on exterior, glabrous within except near apex, caducous. *Receptacle* campanulate, markedly gibbous, densely grey tomentellous on exterior, 2–3 mm long; pedicels 1–3 mm long. Calyx lobes 2–3 mm long, narrowly ovate, densely grey tomentose on exterior, tomentellous within. Petals spatulate, 2 mm long, caducous. Fertile *stamens* 7–8, base forming a conspicuous fused ring with opposite tooth-like staminodes. *Ovary* densely pilose. *Style* pilose, stigma truncate. *Fruit* ovoid, 7–8 by 4.5–5.5 cm, exocarp densely lenticellate; mesocarp thin, fleshy; endocarp extremely hard and thick (1–8 cm thick), woody, granular, and very irregularly ridged, with 2 small loculi in centre, densely lanate within.

Distr. *Malesia*: North Borneo (Sabah). Fig. 9.

Ecol. Hillside forest, to 100 m altitude; forest along rivers.

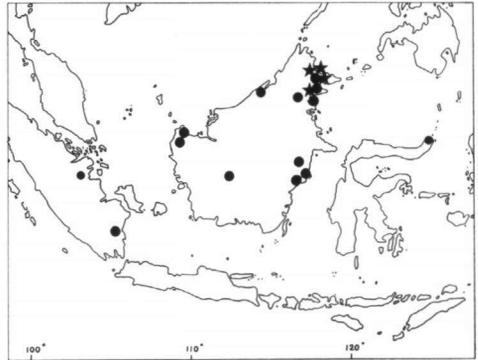
VERN. *Berangan*, Malay.

Fig. 9. Distribution of *Parinari argenteo-sericea* KOSTERM. (stars) and *P. canarioides* KOSTERM. (dots).

2. *Parinari canarioides* KOSTERM. *New & Crit. Mal. Pl.* 3 (1955) 25, t. 12 (For. Dept. Bur. of Planning, Bogor, Indonesia); *Reinwardtia* 7 (1965) 159, f. 2.

Trees to 60 m tall; trunk buttressed to 2.5 m high; young branches sparsely puberulous, glabrescent, lenticellate. *Stipules* linear, acute to 5 mm, hirsute, early caducous, present on very young leaves only. *Leaves* chartaceous, ovate, 5–9 by 2–4.3 cm, glabrous on both surfaces when mature, without stomatal crypts beneath, acuminate at apex, the tip 5–12 mm long, rounded to subcordate at base; midrib lightly impressed above, prominent beneath, sparsely pubescent when young; primary veins 7–11 pairs, plane to prominulous above, prominent beneath, arcuate; petioles 3–7 mm, glabrous when mature, eglandular or with small rather inconspicuous

ous central glands. *Inflorescences* dense-flowered axillary panicles to 4.5 cm long, the rachis and branches tomentose; bracts and bracteoles persistent, ovate, puberulous on exterior, caducous. *Receptacle* campanulate, 3 mm long, tomentose on exterior; pedicels 1–2 mm long; calyx lobes elliptic, concave, c. 2 mm, acute, sparsely puberulous on exterior, densely tomentellous on interior. Petals elliptic, obtuse, 2 mm, tapered to base. Fertile *stamens* 7–8. *Fruit* ellipsoid, 3.5–5 by 1.5–2.5 cm; epicarp densely to sparsely lenticellate; mesocarp fleshy, 1 mm thick; endocarp 5 mm thick, hard, marbled, densely lanate within.

*Distr. Malesia:* Sumatra, Borneo, Sulawesi, Philippines (Palawan). Fig. 9.

*Ecol.* Forest extending up to 800 m altitude.

*Uses.* The timber is much used, but of poor quality. Fruit edible, also eaten by pigs.

**3. *Parinari elmeri* MERR.** Univ. Calif. Publ. Bot. 15 (1929) 92; KOSTERM. *Reinwardtia* 7 (1965) 161, f. 4; PRANCE & WHITM. *Tree Fl. Malaya* 2 (1973) 335.

Trees to 32 m, without buttresses; the young branches densely tomentellous, glabrescent, obscurely lenticellate. *Stipules* lanceolate, acute, to 18 mm long by 3 mm broad at base, lateral, tomentellous, persistent. *Leaves* oblong to oblong-lanceolate, 5–18 by 1.5–7 cm, chartaceous to thinly coriaceous, glabrous above, densely lanate pubescent beneath, without stomatal cavities; acuminate at apex, the tip 5–13 mm long, subcuneate at base; midrib plane or slightly impressed and pubescent above when young, prominent beneath; primary veins 14–21 pairs, prominent beneath, curved at margin; secondary nerves more or less parallel forming ladder-like reticulation; petioles 1.5–6 mm long, tomentellous,

glandular, but glands often obscured. *Inflorescences* of raceme-like reduced terminal and axillary panicles or cymules, 1.7–3 cm long, the rachis and branches densely brown tomentose; bracts and bracteoles large, 2 mm long, ovate, persistent. *Receptacle* conical, gibbous, to 3 mm long, brown-lanate on exterior, pedicels 0.5–2 mm long. Calyx-lobes ovate, acute, 2–3 mm long, lanate on exterior. Petals white, oblong-ovate, 2–3 mm long, narrowed to base. Fertile *stamens* 7–9 with tooth-like staminodes opposite. *Fruit* oblong-ellipsoid, 6.7 by 3.7 cm; epicarp sparingly lenticellate.

*Distr. Malesia:* Malay Peninsula, Borneo (Sarawak, Brunei, Sabah, NE. Kalimantan), Philippines (Mindanao). Fig. 10.

*Ecol.* Lowland and hill forest to 900 m, including areas on ultrabasic rock.

*Uses.* The wood is used for supports of Iban long houses.

*Vern.* Borneo: *resak*, Iban.

**4. *Parinari parva* KOSTERM.** *Reinwardtia* 7 (1965) 52, f. 5; 162; PRANCE & WHITM. *Tree Fl. Malaya* 2 (1973) 335.

Tree to 15 m tall, bole often fluted at base, without buttresses; the young branches densely tomentellous, glabrescent, conspicuously lenticellate. *Stipules* lanceolate, lateral, 13–37 mm long, up to 5 mm broad at base, persistent, conspicuously reticulate and densely tomentose on exterior. *Leaves* chartaceous, oblong to elliptic, 11–28 by 5.5–11 cm, glabrous above, densely lanate-arachnoid pubescent beneath, the pubescence completely obscuring reticulate venation, but without stomatal crypts; finely acuminate at apex, the tip 3–13 mm long, rounded to subcordate at base; midrib plane and pubescent above, prominent beneath; primary veins 15–23 pairs, arcuate and anastomosing at margin, plane above, prominent beneath, pilose; petioles 5–8 mm, densely pale brown pilose, with 2–3 extremely prominent glands. *Inflorescence* of short little-branched terminal and axillary panicles to 5 cm long, sometimes borne on young woody branches, the rachis and branches densely pale-brown tomentellous; bracts and bracteoles ovate, acute, to 5 mm long, persistent. *Receptacle* campanulate, 3 mm long, pale brown tomentose on exterior; calyx lobes acute, ovate-lanceolate, 1–1.5 mm long, densely tomentose. Petals white. *Fruit* ellipsoid to narrowly ellipsoid, to 10 cm long by 3 cm broad; epicarp densely lenticellate, ridged when dry; mesocarp thin and fleshy; endocarp thick, hard.

*Distr. Malesia:* Malay Peninsula (Kelantan, Trengganu, Pahang, Johore), Sumatra, Borneo. Fig. 10.

*Ecol.* Mostly on ridge tops and hillsides to 750 m altitude.

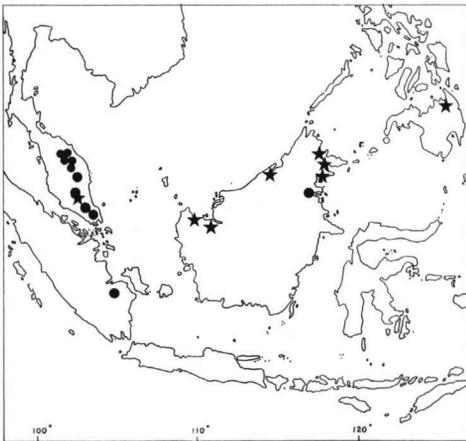


Fig. 10. Distribution of *Parinari elmeri* MERR. (stars) and *P. parva* KOSTERM. (dots).

5. *Parinari nonda* F.v.M. ex BENTH. Fl. Austr. 2 (1864) 426; BANKS & SOL. Bot. Cook's Voy. 1 (1900) t. 92; BAILEY, Queensl. Fl. 2 (1900) 524; Compreh. Cat. Queensl. Pl. (1913) 167; PULLE, Nova Guinea, Bot. 8, 2 (1910) 367; KOSTERM. Reinwardtia 7 (1965) 170, f. 11a, excl. syn. *P. papuanum* et *P. salomonense*. — *Ferolia nonda* (F.v.M. ex BENTH.) O. KTZE, Rev. Gen. Pl. 1 (1891) 216.

Trees to 15 m tall, without buttresses, the young branches sparsely puberulous, soon glabrous, with small prominulous lenticels. *Stipules* lanceolate, membranous, tomentellous, to 5 mm long, very early caducous. *Leaves* chartaceous to thinly coriaceous, oblong, 4–11 by 1.8–4.2 cm, glabrous above, with stomatal crypts filled with lanate pubescence beneath, rounded to acute (or rarely bluntly acuminate) at apex, subcuneate at base; midrib plane or prominulous, sparsely tomentellous when young above, prominent beneath; primary veins 10–17 pairs, curved at margins; secondary nerves reticulate slightly flattened, with a series of marginal glands at veins on lower portion; petioles 5–10 mm long, tomentellous, terete, with 2–4 prominent, conspicuous glands near mid point. *Inflorescence* of spreading terminal and subterminal panicles, 5–11 cm long, the rachis and branches rather sparsely grey-brown tomentellous; bracts and bracteoles large, ovate, 2.5–3 mm long, tomentose, caducous. *Receptacle* campanulate, 2–3 mm long, tomentose on exterior; pedicels 0.5–1 mm long. Calyx lobes triangular, acute, c. 1 mm long, tomentose on exterior, tomentellous within. Petals 5, white, acute. Fertile *stamens* 7–9, with tooth-like staminodes opposite, lanate around base. *Ovary* villous. *Style* villous lanate on lower portion, glabrous above; stigma capitate. *Fruit* ovoid, epicarp sparingly lenticellate.

Distr. Australia (Queensland and Northern Territory) and in *Malesia*: southern extreme of Papua New Guinea and Irian Jaya. Fig. 11.

Ecol. Savanna, open forest, forest on rocky areas in lowlands.

Vern. Papua New Guinea: *warrem*.

6. *Parinari papuana* C.T. WHITE, J. Arn. Arb. 31 (1950) 86. — *Parinari nonda auct. non BENTH.*: KOSTERM. Reinwardtia 7 (1965) 170, *p.p.*

Large trees to 40 m tall, buttressed or unbuttressed, the young branches puberulous, soon glabrous, with clusters of large prominent lenticels with central slit. *Stipules* lanceolate, very early caducous. *Leaves* thickly coriaceous to chartaceous, oblong, 4–18 by 1.5–6.5 cm, glabrous above, with stomatal crypts filled with lanate pubescence beneath, acuminate at apex, the tip 3–10 mm long, rounded to subcuneate at base; midrib plane or slightly impressed and sparsely tomentellous when young above, prominent beneath; primary veins 16–22 pairs,

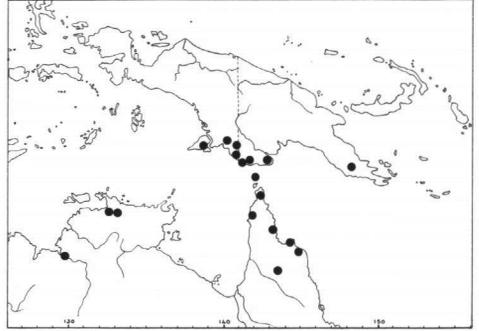


Fig. 11. Distribution of *Parinari nonda* F.v.M. ex BENTH.

curved and anastomosing at margins; secondary nerves reticulate, slightly flattened, with a series of marginal glands at vein endings on lower portion; petioles 2–8 mm long, tomentellous when young, terete or slightly canaliculate, with 2 conspicuous or sometimes obscure glands. *Inflorescence* of terminal and subterminal panicles, 2–6 cm long, the rachis and branches densely tomentose or tomentellous; bracts and bracteoles large, ovate, 2–2.5 mm long, tomentose on exterior; pedicels 0.2–1.5 mm long. Calyx lobes triangular, acute, c. 1 mm long, tomentose on exterior, tomentellous within. Petals 5, white, acute. Fertile *stamens* 7–8, with tooth-like staminodes opposite, lanate around base. *Ovary* villous, style villous on lower portion, glabrous above; stigma capitate. *Fruit* ovoid, 4–6 cm long; epicarp sparingly to densely lenticellate; mesocarp thin, fleshy; endocarp hard, thick, marbled, lanate within.

#### KEY TO THE SUBSPECIES

1. Leaves coriaceous, 4–11 by 1.9–5 cm. Mature fruit c. 6 cm long when dry. Montane

a. *ssp. papuana*

1. Leaves chartaceous, 7–18 by 2.5–7 cm. Lowland.

2. Fruit sparsely lenticellate, small, c. 4 cm long. Leaf base subcuneate . . . . . b. *ssp. salomonense*

2. Fruit densely lenticellate, large, c. 6.5 cm long. Leaf base usually rounded . . . . . c. *ssp. whitei*

#### a. *ssp. papuana*

Unbuttressed tree. Leaves thickly coriaceous, 4–11 by 1.9–5 cm, subcuneate at base. Mature fruit c. 6 cm long when dry; densely lenticellate on exterior.

Distr. *Malesia*: Northern, Central and Eastern Papua New Guinea. Fig. 12.

Ecol. Mountains, 500–2000 m altitude. Fig. 12.

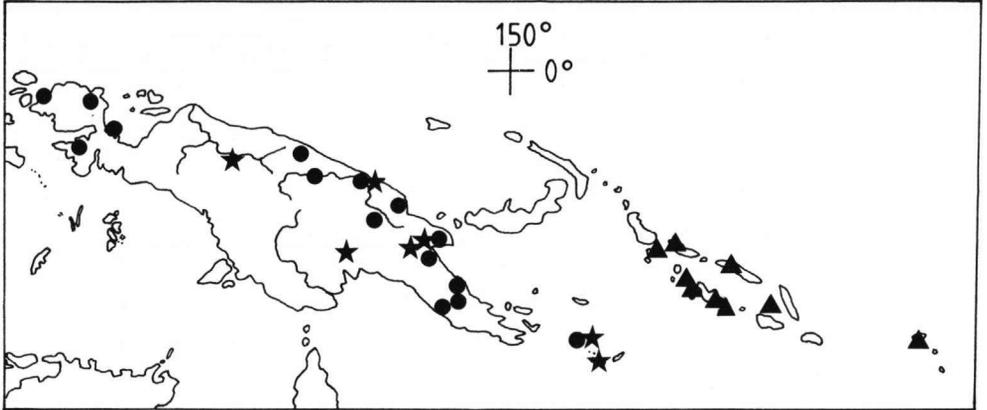


Fig. 12. Distribution of *Parinari papuana* C.T. WHITE *ssp. papuana* (dots), *ssp. salomonensis* (C.T. WHITE) PRANCE (triangles), and *ssp. whitei* PRANCE (stars).

Vern. *Korafe, morni, Aiyura, puwirini, Was-kuk, Tor, Anona*.

b. *ssp. salomonense* (C.T. WHITE) PRANCE, *Brittonia* 39 (1987) 369. — *Parinari salomonense* C.T. WHITE, *J. Arn. Arb.* 31 (1950) 87.

Buttressed tree. Leaves chartaceous, 7–12 by 3–7 cm, subcuneate at base. Mature fruit c. 4 cm long, sparsely lenticellate on exterior.

Distr. Solomon Islands. Fig. 12.

Ecol. Lowland forest, hillsides and ridges to 300 m altitude.

Vern. *Malmone, Kwara'ae, nakisi, one one, sautalu, susui*.

c. *ssp. whitei* PRANCE, *Brittonia* 39 (1987) 369.

Unbuttressed tree. Leaves chartaceous, 7–18 by 2.5–6.5 cm, rounded at base. Mature fruit c. 6.5 cm long, densely lenticellate on exterior.

Distr. *Malesia*: West Irian and Papua New Guinea along northern coast from extreme west to east. Fig. 12.

Vern. *Lowka, Manikiong, ogelet, Mooi*.

7. *Parinari oblongifolia* Hook. *f. Fl. Brit. India* 2 (1878) 309; KING, *J. As. Soc. Beng.* 66 (1897) 279; RIDLEY, *Agr. Bull. Str. & Fed. Mal. St. 1* (1902) 144; *Fl. Mal. Pen. 1* (1922) 668; FOXW. *Mal. For. Rec.* 3 (1927) 175; CORNER, *Wayside Trees* (1940) 527; KOSTERM. *Reinwardtia* 7 (1965) 165, *f. 8*; PRANCE & WHITM. *Tree Fl. Malaya* 2 (1973) 335. — *Ferolia oblongifolia* (Hook. *f.*) O. Ktze, *Rev. Gen. Pl.* 1 (1891) 216. — *Parinari borneense* MERR. *Univ. Calif. Publ. Bot.* 15 (1929) 93.

Trees to 40 m tall, trunk low thick buttressed to 2 m, the young branches minutely tomentellous, gla-

brrescent, conspicuously prominently lenticellate. *Stipules* ovate to lanceolate, acute, 3–5 mm, pilose on exterior, early caducous. *Leaves* coriaceous, elliptic to oblong, 14–23 by 4–9 cm, glabrous above, with stomatal cavities filled with grey lanate pubescence beneath, shortly acuminate at apex, the tip 3–13 mm long, rounded to subcordate at base; midrib plane above, glabrous when mature except at base, prominent, glabrescent beneath; primary veins 23–35 pairs, erect, plane above, flattened and prominent beneath; secondary veins prominulous and parallel  $\pm$  ladder-like beneath; petioles 9–17 mm long, thick, tomentellous, when young, glabrescent, eglandular or glandular. *Inflorescences* of large, spreading terminal panicles, 10–21 cm long by 7–12 cm broad, the rachis and branches yellow-grey tomentellous; bracts and bracteoles ovate, 3 mm long, early caducous. *Receptacle* campanulate, slightly gibbous, 3 mm long, densely grey tomentose on exterior; pedicels 1–3 mm long; calyx lobes ovate, acute, 1.5–2 mm long, unequal, grey tomentose. *Petals* white to bluish, lanceolate to spatulate, narrowed towards base, c. 2 mm long, glabrous. *Stamens* 8–10, with tooth-like staminodes opposite. *Ovary* pilose; style glabrous; stigma truncate. *Fruit* ellipsoid, 5–9 by 3–4 cm, epicarp densely lenticellate; mesocarp 1.5–2 mm thick; endocarp hard, thick, marbled, 7–13 mm thick, fibrous, densely lanate within.

Distr. *Malesia*: Malay Peninsula (S. Kelantan to Johore), Sumatra, Borneo (Sabah, Kalimantan). Fig. 13.

Ecol. Lowland rain-forest and beside rivers or in valleys extending to 450 m altitude.

Vern. Malay Peninsula: *bedara hutan, kemalau, mentelor, merbatu; dungun bukit*, Malay; Borneo: *mankudar, mengkudu*, Kalimantan.

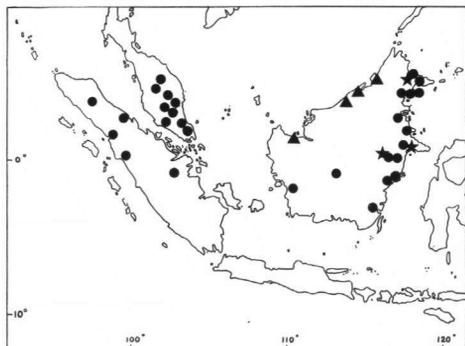


Fig. 13. Distribution of *Parinari oblongifolia* Hook.f. (dots), *P. gigantea* KOSTERM. (stars), and *P. metallica* KOSTERM. (triangles).

**8. *Parinari gigantea* KOSTERM.** Reinwardtia 7 (1965) 182, f. 19.

Large trees to 40 m tall, trunk fluted at base, the young branches densely lanate pubescent, glabrescent, with conspicuous small lenticels. *Stipules* lanceolate, acute, to 25 mm long, caducous, membranous, densely appressed tomentellous on exterior, glabrous within. *Leaves* coriaceous, elliptic, 9–17 by 5–8 cm, glabrous above, with dense conspicuous stomatal crypts beneath, bluntly acuminate at apex, the tip 3–6 mm long, rounded at base; midrib plane above, prominent and pilose, glabrescent beneath; primary veins 20–28 pairs, slightly impressed on upper portion, prominulous on lower portion of upper surface, straight, erect, parallel; secondary veins  $\pm$  parallel; petiole thick, 4–7 mm long, tomentellous when young, with 2 small round glands on mid point above. *Flowers* not seen. *Infructescence* axillary, 3–5 mm long. *Fruit* irregularly ellipsoid, 6.5 cm long, 4 cm broad; epicarp densely lenticellate; mesocarp fleshy; endocarp hard, bony, irregularly ribbed, lanate within.

Distr. *Malesia*: Borneo (W. Kalimantan, Sabah). Fig. 13.

Ecol. Lowland forest.

Vern. *Lempong*, Kalimantan.

**9. *Parinari metallica* KOSTERM.** Reinwardtia 7 (1965) 49, f. 3; 160, f. 3.

Trees to 16 m tall, unbuttressed, the young branches appressed strigose, glabrescent, conspicuously lenticellate. *Stipules* ovate-lanceolate, acute, 8–15 mm long, densely brown tomentose, membranous, early caducous. *Leaves* thickly coriaceous, elliptic, 8–17 by 4–9 cm, glabrous and shiny with metallic sheen above when dry, with dense stomatal crypts filled with hairs, apex rounded to shortly blunt acuminate, the tip 0–3 mm long, rounded or subcuneate

at base; midrib plane above, prominent beneath; primary veins 10–15 pairs, prominulous to plane above, prominent beneath, erect, curved only at margin; petioles 14–20 mm long, glabrescent, with inconspicuous glands near to lamina base, puberulous, glabrescent. *Inflorescence* of axillary little-branched panicles, 4–10 cm long, the rachis and branches densely brown tomentellous; bracts and bracteoles ovate, early caducous. *Receptacle* campanulate, slightly gibbous, 2–3 mm long, ferruginous pubescent on exterior; pedicels 0.5 mm long; calyx lobes lanceolate, acute, 1 mm long, tomentellous. Petals lanceolate, glabrous. *Stamens* c. 8 with short tooth-like staminodes opposite. *Ovary* densely pilose. *Style* glabrous, equalling stamens; stigma truncate. *Fruit* not seen.

Distr. Known only from Brunei, Sabah, and Sarawak. Fig. 13.

Ecol. Forests on well-drained soil, hillsides, 50–300 m altitude.

**10. *Parinari prancei* KOSTERM.** Reinwardtia 10 (1985) 124.

Trees to 25 m tall, the young branches densely brown lanate and pilose, lenticellate. *Stipules* caducous (not seen). *Leaves* rigidly coriaceous, elliptic, 9–21 by 6.5–12 cm, glabrous and shiny above when mature, lanate when young, with conspicuous stomatal crypts filled by lanate pubescence beneath, broadly apiculate at apex, rounded to broadly subcuneate at base; midrib  $\pm$  plane above, prominent beneath; primary veins 14–16 pairs, plane or slightly impressed above, prominent beneath, arcuate near margins, secondary venation parallel and forming a ladder-like reticulum; petioles 10–12 mm long, densely ferruginous lanuginose when young, eglandular. *Inflorescences* of axillary little branched small panicles or racemes, to 3 cm long, the rachis and branches densely appressed tomentellous; bracts and bracteoles caducous. *Receptacle* campanulate-cupuliform, 3–4 mm long, appressed tomentellous on exterior; pedicels 1.5 cm long; calyx lobes triangular, acute, 1.5 mm long, tomentellous. *Fruit* ellipsoid, c. 4 by 6 cm diam.; epicarp densely lenticellate; mesocarp fleshy, 2 mm thick; endocarp woody, very hard and thick, marbled, densely lanate within.

Distr. *Malesia*: E. Papua New Guinea (Milne Bay Prov., Northern Prov.). Fig. 14.

Ecol. Lowland rain-forest to 400 m altitude.

**11. *Parinari rigida* KOSTERM.** Reinwardtia 7 (1965) 53, f. 6a, b; 163. — *Parinari ashtonii* KOSTERM. Reinwardtia 7 (1965) 53, f. 7; 164.

Trees to 30 m tall, unbuttressed, the young branches tomentellous, glabrescent, inconspicuously lenticellate. *Stipules* caducous (not seen). *Leaves* rigidly coriaceous, elliptic to oblong ovate, 7.5–23 by 3–8

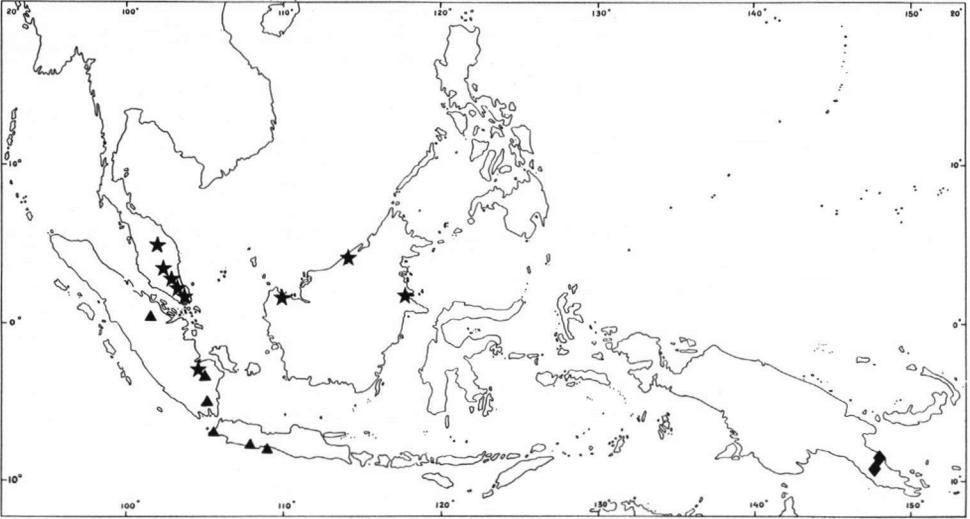


Fig. 14. Distribution of *Parinari prancei* KOSTERM. (diamonds), *P. rigida* KOSTERM. (stars), and *P. sumatrana* (JACK) BENTH. (triangles).

cm, those near to inflorescence much smaller than others, broadest below mid point, glabrous and shiny above, sometimes slightly bullate, the lower surface with stomatal crypts filled with pubescence, with 2 glandular areas at junction of midrib and petiole below, shortly and broadly acuminate at apex, the tip 3–17 mm long, rounded or subcordate at base; midrib plane or impressed for upper portion above, prominent and appressed pilose beneath when young; primary veins 13–20 pairs, slightly impressed above, prominent beneath, slightly curved at margins only; secondary venation flattened or rounded, parallel; petioles thick, 3–10 mm long, grey-pilose pubescent, rugose, with 2 small glands on mid point of upper side. *Inflorescences* of narrow terminal panicles to 13 cm long, the rachis and branches tomentose; bracts and bracteoles lanceolate, to 2 mm long, early caducous. *Receptacle* campanulate, slightly gibbous, 5 mm long, densely villos-tomentose on exterior; pedicels c. 1 mm long; calyx lobes elongate triangular, 2–2.5 mm long. Petals spatulate. *Stamens* 6–8. *Ovary* densely villos. *Style* equalling stamens; stigma capitate. *Fruit* irregularly ellipsoid, 5 cm long, to 4 cm diam., tapered towards base almost into a stipe; epicarp densely lenticellate; mesocarp thin fleshy; endocarp thick, woody, marbled, lanate within.

*Distr. Malesia:* S. Malay Peninsula, Sumatra, Borneo (Sarawak, E. Kalimantan). Fig. 14.

*Ecol.* Heath and swamp forests, lowland forest; 0–1400 m altitude.

**12. *Parinari sumatrana* (JACK) BENTH.** in Hook., Niger Fl. (1849) 335; BLUME, Mus. Bot. Lugd.-Bat. 2 (1852) 97; MIQ. Fl. Ind. Bat. 1, 1 (1855) 353; *ibid.* (1858) 1084; Suppl. Sumatra (1860) 115; *ibid.* (1861) 306; C. MUELL. in Walp., Ann. 4 (1857) 644; Flora 41 (1858) 255; Hook. f. Fl. Brit. India 2 (1878) 309; MIERS, J. Linn. Soc. Bot. 17 (1879) 336; K. & V. Bijdr. 5 (1900) 340, *p.p. excl. P. costatum auct. non BLUME*; MERR. J. Arn. Arb. 33 (1952) 239; BACKER & BAKH. f. Fl. Java 1 (1964) 522, *p.p. excl. P. costatum*; KOSTERM. Reinwardtia 7 (1965) 176. — *Petrocarya sumatrana* JACK, Mal. Misc. 2 (7) (1822) 67 [repr. Calc. J. Nat. Hist. 4 (1843) 165]. — *Lepidocarpa ovalis* (KORTH.) BLUME ex MIQ. Fl. Ind. Bat. 1, 1 (1855) 353. — *Ferolia sumatrana* (JACK) O. KTZE, Rev. Gen. Pl. 1 (1891) 216. — *Parinarium auct. non BLUME*; BACKER, Schoolf. Java 1 (1911) 445, *p.p.* — Fig. 15.

Trees to 30 m tall, without buttresses or small ones to 50 cm; the young branches densely tomentellous, glabrescent, lenticellate. *Stipules* oblong, to oblong-ovate, 5–12 mm long by 3–5 mm wide at base, membranaceous, early caducous, pilose on exterior. *Leaves* chartaceous to subcoriaceous, elliptic to oblong elliptic, 7–14(–21) by 3–7.5 cm, obtuse to shortly broad acuminate at apex, the tip up to 3 mm long, rounded to subcordate at base; glabrous and shiny above, with deep-set stomatal crypts beneath obscured by dense caducous lanate pubescence when young; midrib plane to slightly impressed above, pilose towards base, prominent beneath; primary veins

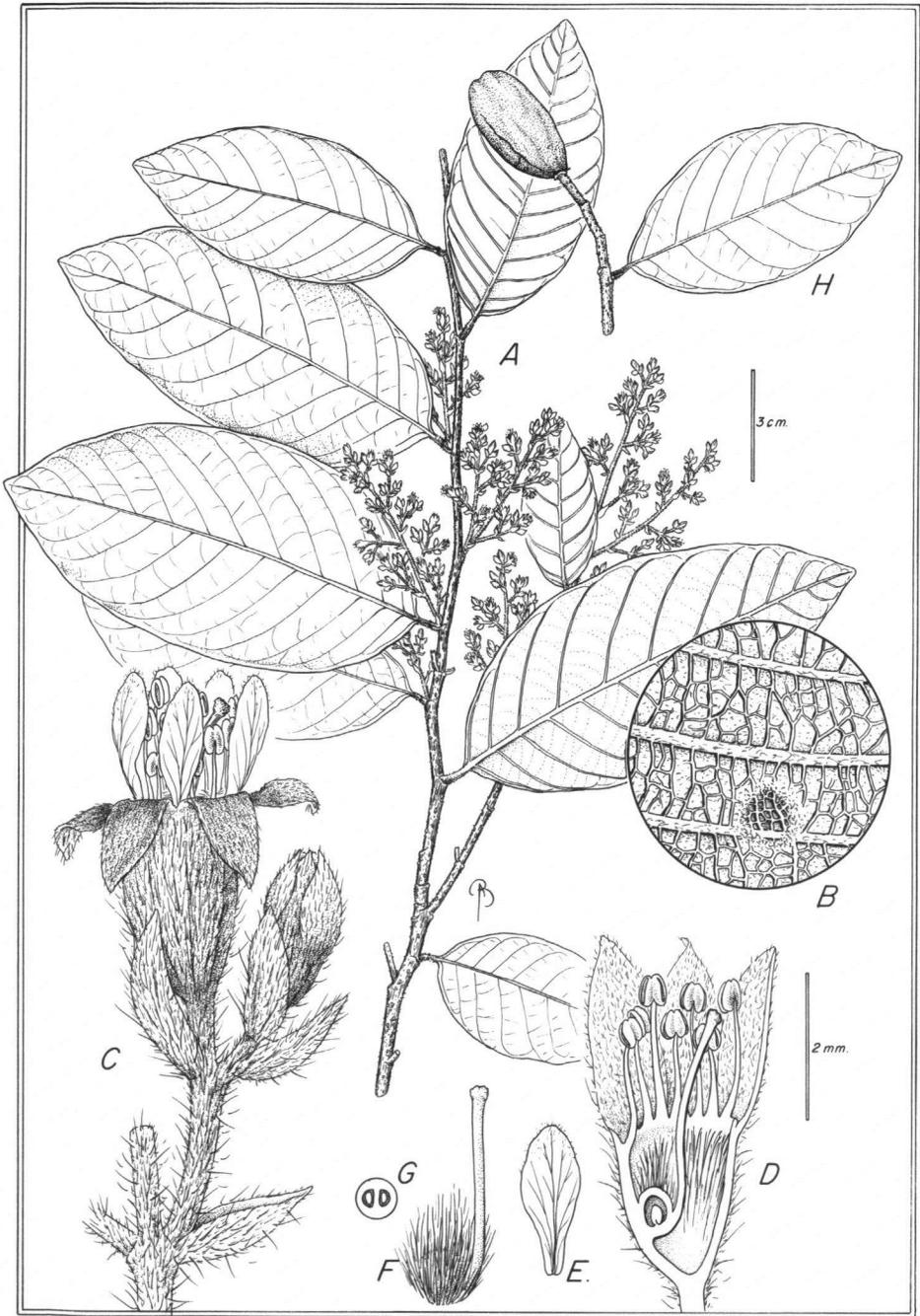


Fig. 15. *Parinari sumatrana* (JACK) BENTH. A. Habit; B. leaf undersurface with pubescence removed in small area to show stomatal cavities; C. flower; D. flower section; E. petal; F. ovary and style; G. ovary section; H. young fruit (KOSTERMANS 21859).

9–14 pairs, arcuate, prominulous above, prominent beneath; petioles 4–8 mm long, with 2 conspicuous glands near middle, lightly canaliculate, glabrescent. *Inflorescence* of short axillary panicles 2–6 cm long, the rachis and branches brown tomentose; bracts and bracteoles membranous, tomentellous on exterior, puberulous within, caducous. *Receptacle* conical-campanulate, 3 mm long, densely pilose on exterior, almost sessile. Petals spatulate, bluish. Calyx lobes elongate-triangular, 2 mm long, acute, pilose on both surfaces. Fertile *stamens* 8, unequal. *Ovary* densely pilose. *Style* glabrous, equalling stamens, the stigma truncate. *Fruit* ellipsoid, 4 by 2.5 cm, epicarp densely lenticellate; mesocarp 3–4 mm thick; endocarp marbled in cross section, hard, 5 mm thick, densely lanate within.

Distr. *Malesia*: Sumatra, W. Java. Fig. 14.

Vern. Java: *kanjere badak*.

Note. This species is distinct from others by the predominantly axillary inflorescences. The material described as *Lepidocarpa ovalis* has much larger, more pointed leaves than most of the collections, but KOSTERMANS is correct in placing that name in synonymy under *P. sumatrana*.

13. *Parinari costata* (KORTH.) BLUME, *Mélang. Bot.* 2 (1855) 10; *Miq. Fl. Ind. Bat.* 1, 1 (1855) 354; *ibid.* (1858) 1084; *Suppl. Sumatra* (1860) 115; C. MUELL. in *Walp.*, *Ann.* 4 (1857) 644; *Flora* 41 (1858) 255; *Hook. f. Fl. Brit. India* 2 (1878) 309; KING, *J. As. Soc. Beng.* 66 (1897) 277; RIDLEY, *Agr. Bull. Str. & Fed. Mal. St.* 1 (1902) 145; BRANDIS, *Indian Trees* (1906) 278; BURK. *J. Str. Br. Roy. As. Soc. n.* 73 (1916) 200; MERR. *J. Str. Br. Roy. As. Soc. n.* 76 (1917) 81; *Enum. Born. Pl.* (1921) 290; RIDLEY, *Fl. Mal. Pen.* 1 (1922) 666; MERR. *Enum. Philip. Fl. Pl.* 2 (1923) 236; BURK. *Dict.* (1935) 1667; HEYNE, *Nutt. Pl. Ned. Ind. ed.* 3 (1950) 697; KOSTERM. *Reinwardtia* 7 (1965) 179, f. 17a, b; PRANCE & WHITM. *Tree Fl. Malaya* 2 (1973) 333.

For further synonyms, see under the subspecies.

#### KEY TO THE SUBSPECIES

1. Inflorescence and flowers densely ferruginous villous pubescent. Often at high altitudes

b. *ssp. rubiginosa*

1. Inflorescence and flowers sparsely to densely grey or brown appressed pubescent. Lowlands.

2. Primary leaf veins 16–26 pairs; mature leaves 9–15.7 cm long, oblong (index 2.3–3.65). Fruit exocarp usually densely verrucose

c. *ssp. polyneura*

2. Primary leaf veins 10–16 pairs; mature leaves 5–10.5 cm long, elliptic (index 1.7–2.7), rarely oblong. Fruit exocarp usually sparsely verrucose

a. *ssp. costata*

a. *ssp. costata*. — *Lepidocarpa costata* KORTH. *Ned. Kruidk. Arch.* 3 (1855) 387; *Miq. Fl. Ind. Bat.* 1, 1 (1855) 354, in *syn.*, *sphalm.* *Lepidocarya costata*. — *Ferolia costata* (KORTH.) O. Ktze, *Rev. Gen. Pl.* 1 (1891) 216.

Tree to 60 m tall, trunk buttressed up to 2 m, the young branches densely appressed tomentellous, glabrescent, with small conspicuous lenticels. *Stipules* lanceolate, membranaceous, 3–7 mm long, pilose on exterior, early caducous. *Leaves* coriaceous or rigidly chartaceous, elliptic, subovate-elliptic to oblong (leaf index 1.7–2.7), 5–10.5 by 1.8–4 cm, glabrous above when mature but with sparse lanate covering when very young, with stomatal cavities filled with grey lanate pubescence beneath, acuminate at apex, the tip 3–5 mm long, round to sub-cuneate at base; midrib prominulous above, tomentellous towards base, prominent beneath; primary veins 10–16 pairs, arcuate, prominulous above, prominent beneath; secondary veins rounded or only slightly flattened; petioles 5–9 mm long, slender, tomentellous when young, soon glabrous, usually eglandular or with 2 inconspicuous median glands. *Inflorescences* of predominantly axillary or terminal few-flowered lax panicles to 8 cm long, the rachis and branches appressed grey to brown appressed tomentellous; bracts and bracteoles lanceolate, c. 2 mm long, caducous. *Receptacle* campanulate, slightly gibbous, grey-brown pubescent on exterior, 3–3.5 mm long; pedicels 0.5–1 mm long; calyx lobes ovate, acute, 1.5–2 mm long, grey tomentellous on exterior. Petals white, spatulate, 1.5–2 mm long, caducous, glabrous. *Stamens* 7–8, with small tooth-like staminodes opposite, slightly unequal; style glabrous; stigma capitate. *Fruit* ellipsoid, to 3.5 by 4.5 cm; epicarp usually sparsely verrucose; mesocarp 2 mm, fleshy; endocarp hard, marbled, 3–5 mm thick, fibrous, densely lanate within.

Distr. *Malesia*: Malay Peninsula, Sumatra, Borneo, Philippines (Mindanao, Culion, Samar). Fig. 16.

Ecol. Lowland forest, hillsides, ridges; altitude up to 300 m.

Vern. Malay Peninsula: *kemalau, mambatu, merbatu*; Borneo: *augok*, Piak, *bugan*, Iban.

b. *ssp. rubiginosa* (RIDLEY) PRANCE, *Brittonia* 39 (1987) 368. — *Parinarium helferi* *Hook. f. Fl. Brit. India* 2 (1878) 311, *excl. syn.* *Parinarium sumatranum sensu* KURZ; BRANDIS, *Indian Trees* (1906) 278; KOSTERM. *Reinwardtia* 7 (1965) 175. — *Parinari rubiginosa* RIDLEY, *J. Str. Br. Roy. As. Soc. n.* 75 (1917) 29; *Fl. Mal. Pen.* 1 (1922) 668; *Foxw. Mal. For. Rec.* 3 (1927) 175; BURK. *Dict.* (1935) 1667; KOSTERM. *Reinwardtia* 7 (1965) 168, f. 10; PRANCE & WHITM. *Tree Fl. Malaya* 2 (1973) 336. — *Parinarium costatum* BLUME *var. rubiginosum* RIDLEY, *J. Fed.*

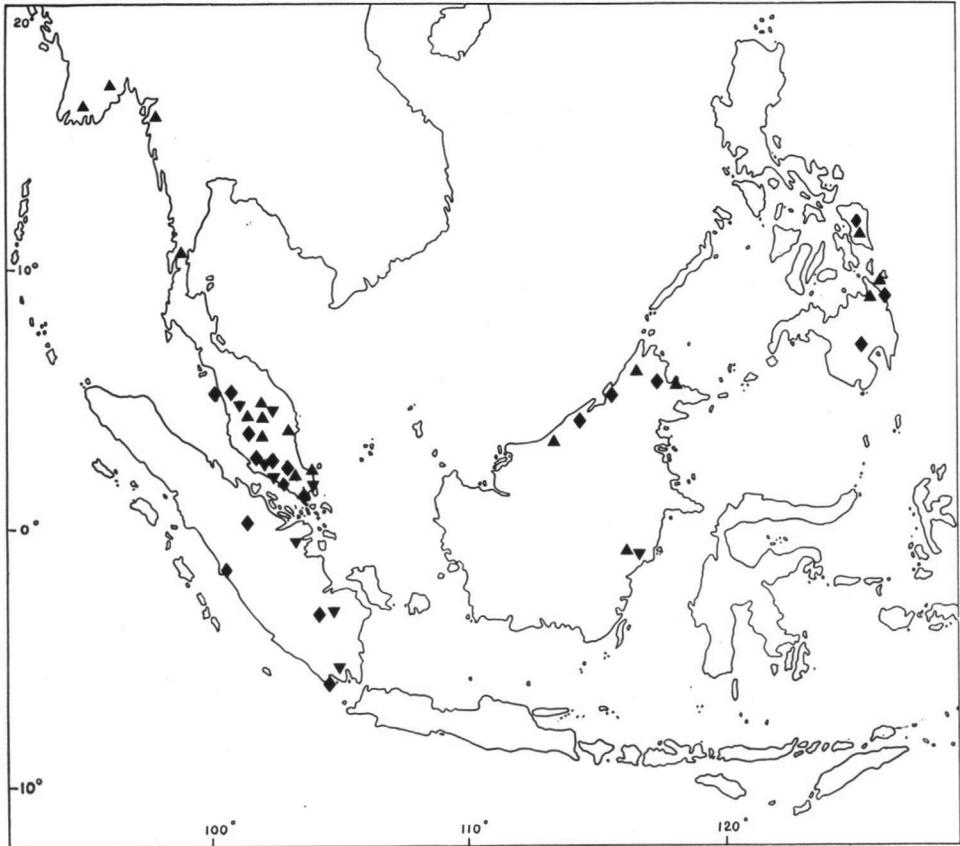


Fig. 16. Distribution of *Parinari costata* (KOSTERM.) BLUME (diamonds), *P. costata* ssp. *rubiginosa* (RIDLEY) PRANCE (triangles), and ssp. *polyneura* (MIQ.) PRANCE (inverted triangles).

Mal. St. Mus. 6 (1915) 143. — *Parinari bicolor* MERR. Philip. J. Sc. 10 (1915) Bot. 309; Enum. Philip. Fl. Pl. 2 (1923) 235; KOSTERM. Reinwardtia 7 (1965) 172, f. 12.

Leaves 4–11.5 by 1.6–4.3 cm, oblong elliptic to oblong lanceolate; primary veins 11–19 pairs; petioles 4–8 mm long, thickly tomentose. Inflorescence dense to lax, ferruginous villous pubescent. Fruit exocarp sparingly lenticellate.

Distr. Burma; *Malesia*: Malay Peninsula, Borneo (Sabah, Sarawak, Kalimantan), Philippines (Mindanao, Bucas Grande I.). Fig. 16.

Ecol. In lower montane forests of Malay Peninsula and Borneo (750–1500 m) and lowland forests of the Philippines.

Vern. *Merbatu*, Malay (= Malesian standard timber name for various genera); Borneo: *mengkudur*, Balikpapan.

c. ssp. *polyneura* (MIQ.) PRANCE, Brittonia 39 (1987) 368. — *Parinari polyneurum* MIQ. Fl. Ind. Bat., Suppl. Sumatra (1860) 115; *ibid.* (1861) 306; HOOK. f. Fl. Brit. India 2 (1878) 309; KING, J. As. Soc. Beng. 60 (1897) 278; K. & V. Bijdr. 3 (1901) 340; KOSTERM. Reinwardtia 7 (1965) 167, f. 9a, b; PRANCE & WHITM. Tree Fl. Malaya 2 (1973) 336. — *Ferolia polyneura* (MIQ.) O. KRZE, Rev. Gen. Pl. 1 (1891) 216.

Leaves 9–15.7 by 3.7–6.3 cm, oblong (index 2.3–3.65); primary veins 16–26 pairs; petioles 3–7 mm long, thick, tomentose. Inflorescence lax, inflorescence and flowers with grey appressed tomentellous pubescence. Fruit exocarp usually densely verrucose.

Distr. *Malesia*: Malay Peninsula (Kelantan, Perak, Pahang, Malacca), Singapore, Sumatra, Borneo. Fig. 16.

Ecol. Lowland forest and occasionally in hills and seasonal swamps.

## Excluded species

7520] *ex* HOOK. *f.* Fl. Brit. India 2 (1878) 311;KOSTERM. *Reinwardtia* 7 (1965) 178, *f.* 16. =*Parinari wallichiana* R.Br. [in Wall., *Cat.* (1832)*Dipterocarpus cornutus* DYER (*Dipterocarpaceae*).

## 6. ATUNA

RAFIN. *Sylva Tellur.* (1838) 153; KOSTERM. *Reinwardtia* 7 (1969) 421; PRANCE & WHITM. *Tree Fl. Malaya* 2 (1973) 323; SMITH, *Fl. Vit. Nova* 3 (1985) 47. — *Atunus* RUMPH. *Herb. Amb.* 1 (1741) 171, t. 66; LAMK, *Encycl. Méth.* 1 (1783) 329, *non Atunus* RUMPH. (1743); PANIGRAHI & PUROHIT, *Taxon* 32 (1983) 122. — *Cyclandrophora* HASSK. *Flora* 25<sup>2</sup>, *Beibl.* 1 (1842) 47; STEEN. *Bull. Jard. Bot. Btzig III*, 17 (1948) 461; KOSTERM. *Candollea* 20 (1965) 118. — *Moquilea sect. Cyclandrophora* (HASSK.) ENDL. *Gen. Pl. Suppl.* 3 (1843) 103. — *Parinarium subg. Cyclandrophora* (HASSK.) BLUME, *Mélang. Bot.* 2 (1855) 10; repr. *Flora N.R.* 16 (1858) 255. — *Parinarium subg. Macrocarya* MIQ. *Fl. Ind. Bat.* 1, 1 (1855) 354. — *Parinarium sect. Cyclandrophora* (HASSK.) C.MUELL. in *Walp.*, *Ann.* (1857) 644. — *Entosiphon* BEDD. *Madr. J. Lit. Sci. ser.* 3, 1 (1864) 44. — *Parinarium subg. III* HOOK. *f.* *Fl. Brit. India* 2 (1878) 308, *p.p.* — *Petrocarya auct. non* SCHREB.: JACK, *Mal. Misc.* 2 (7) (1822) 68 [repr. HOOK. *Comp. Bot. Mag.* 1 (1836) 220; *Calc. J. Nat. Hist.* 4 (1843) 164]. — *Parinari auct. non* AUBL. (*Parinarium auct. non* JUSS.): BENTH. in *Hook.*, *Niger Fl.* (1849) 333, *p.p.*; BLUME, *Mus. Bot. Lugd.-Bat.* 2 (1852) 94; BENTH. in *Benth. & Hook.f.*, *Gen. Pl.* 1 (1865) 607; BOERL. *Handl. Fl. Ned. Ind.* 1 (1890) 431, 424; FOCKE in *E. & P. Nat. Pfl. Fam.* 3, 3 (1891) 60; KOORD. *Exk. Fl. Java* 2 (1912) 338; RIDLEY, *Fl. Mal. Pen.* 1 (1922) 666. — **Fig. 19.**

Small to large trees, ultimate shoots with complicated system of divaricate branching. *Stipules* large, prominently keeled, lateral, persistent or subpersistent. *Leaves* almost glabrous on both surfaces, often with minute papillae on venation giving beaded appearance, without stomatal crypts, with a pair of glands on midrib at or near base of lower surface. *Petioles* eglandular. *Inflorescence* a raceme, or sparsely branched, contracted panicle. *Bracts* and *bracteoles* persistent, eglandular, not enclosing groups of flower buds. *Flowers* hermaphrodite. *Receptacle* obconical to cylindrical, as long as or exceeding calyx lobes, hollow, hairy inside throughout, throat blocked by retrorse hairs. *Calyx lobes* 5, broadly ovate to lanceolate, tomentellous on both surfaces. *Petals* 5, glabrous, exceeding calyx lobes. *Stamens* 10–20, posterior, inserted unilaterally on margin of disk; filaments free, exserted; staminodes forming a barely visible denticulate margin to throat. *Ovary* inserted at mouth of receptacle tube, pilose on exterior; carpel bilocular with 1 ovule in each loculus. *Fruit* large; epicarp glabrous, densely verrucose-crustaceous; mesocarp transversely fibrous; endocarp hard, thick, shortly and sparsely hairy inside, breaking up irregularly at germination. *Cotyledons* large and strongly ruminant. *Germination* cryptocotylar, eophylls alternate.

Distr. About 11 species in Southern India, Thailand, E. to Fiji and Samoa in the Pacific; in *Malesia* 5 species in the Malay Peninsula throughout Indonesia, and New Guinea.

Vern. *Merbatu*, Malay = Malesian standard timber name for various genera.

KEY TO THE SPECIES  
(including species of India and the Pacific)

1. Leaf apex rounded; primary veins 6–8 pairs. *Fiji* ..... **A. elliptica** (KOSTERM.) KOSTERM.
1. Leaf apex acuminate or acute; primary veins usually more than 10 pairs. *India, Malesia, or Pacific: Fiji, only A. racemosa.*
2. Receptacle tube cylindrical and narrow.
  3. Leaves broadly elliptic, 8–10 cm broad; rounded at base; apex shortly acuminate, the acumen 2–3 mm long ..... **1. A. latifrons**
  3. Leaves oblong, 2.5–6 cm broad; subcuneate to rounded at base; apex with long thin acumen 4–22 mm long.
    4. Receptacle 8–13 mm long. Leaf apex long acuminate; base rounded ..... **2. A. nannodes**
    4. Receptacle 5–7 mm long. Leaf apex short acuminate, the acumen 3–10 mm long; base cuneate
      - 3. A. penangiana**
2. Receptacle tube funnel-shaped to campanulate.
  5. Leaves broadly ovate, thickly coriaceous, cordate at base, 4.5–12 cm long ..... **4. A. cordata**
  5. Leaves usually elliptic, chartaceous to thinly coriaceous, usually rounded at base (if cordate then exceeding 10 cm in length).
    6. Fertile stamens 12–14. Inflorescence sericeous or sparsely pilose. *India.*
      7. Inflorescence sparsely pilose. Leaves elliptic-lanceolate, with 8–10 pairs of primary veins. *India*
        - A. indica** (BEDD.) KOSTERM.
      7. Inflorescence densely sericeous. Leaves lanceolate, with 12–16 pairs of primary veins. *India*
        - A. travancorica** (BEDD.) KOSTERM.
    6. Fertile stamens 15–20. Inflorescence tomentellous. Not in *India* ..... **5. A. racemosa**

**1. *Atuna latifrons*** (KOSTERM.) PRANCE & WHITE, Phil. Trans. Roy. Soc. Lond. 320 (1987) 132. – *Parinarium latifolium* HEND. Gard. Bull. Str. Settl. 7 (1933) 102, *nom. illeg., non latifolium* EXELL. – *Parinari latifrons* KOSTERM. Reinwardtia 7 (1965) 54. – *Cyclandrophora latifolia* (HEND.) PRANCE in Kosterm., Candollea 20 (1965) 121. – *Atuna latifolia* (HEND.) KOSTERM. Reinwardtia 7 (1969) 421.

Small tree to 5 m tall, the young branches densely lanate-tomentellous becoming glabrous, obscurely lenticellate. *Stipules* lanceolate, to 11 mm long, acute, keeled, sparsely appressed pubescent. *Leaves* chartaceous, broadly elliptic, 11–13 by 8–10 cm, glabrous and shiny above, slightly bullate, glabrous beneath except for sparsely pilose venation, apex very shortly abrupt acuminate, the acumen 2–3 mm long, rounded at base with base contracted into petiole; midrib prominent on both surfaces, slightly pilose towards base above, pilose beneath; primary veins 12–14 pairs, prominulous inset in a groove above, prominent and pilose beneath, venation prominulous; petioles thick, 5–7 mm long, terete, densely brown lanate when young. *Inflorescences* of axillary little-branched panicles or spikes, to 5 cm long, densely brown sericeous; bracts and bracteoles to 15 mm long, ovate-lanceolate, acute, densely sericeous on exterior, appressed puberulous within. *Receptacle* tube narrowly cylindrical, 7–11 mm long,

sericeous on exterior, sessile; calyx lobes lanceolate to oblong-ovate, 5–10 mm long, unequal, densely sericeous on exterior, tomentellous within. Petals obovate narrowed to base, 10–11 mm long. *Stamens* c. 20, inserted on faucal annulus 2 mm high with tooth-like staminodes opposite, the filaments 10–12 mm long. *Ovary* densely strigose. *Style* slender, glabrous; stigma truncate. *Fruit* unknown.

Distr. Known only from Malay Peninsula on Kedah-Perak border. Fig. 17.

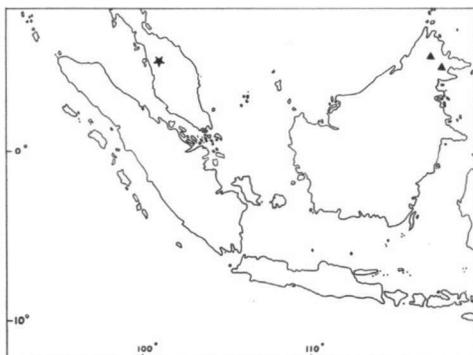


Fig. 17. Distribution of *Atuna latifrons* (KOSTERM.) PRANCE & WHITE (star) and *A. cordata* COCKBURN ex PRANCE (triangles).

2. *Atuna nannodes* (KOSTERM.) KOSTERM. Reinwardtia 7 (1969) 422; PRANCE & WHITM. Tree Fl. Malaya 2 (1973) 325. — *Parinari nannodes* KOSTERM. Reinwardtia 7 (1965) 50, f. 4. — *Cyclandrophora nannodes* (KOSTERM.) KOSTERM. & PRANCE, Candollea 20 (1965) 122.

Trees to 20 m, usually smaller, unbuttressed; the young branches sparsely appressed hirsutulous-strigose, soon glabrous, obscurely lenticellate. *Stipules* narrowly lanceolate, acute, 6–12 mm long, strigose to glabrous, subsistent. *Leaves* thinly coriaceous, oblong-lanceolate, 6.7–19 by 2.5–5.5 cm, glabrous on both surfaces, sometimes slightly bullate above, long slender acuminate at apex, the acumen 7–22 mm long, rounded at base; midrib prominulous above, prominent beneath; primary veins 10–12 pairs, arcuate, prominulous on both surfaces or sometimes prominent beneath; petioles 2–4 mm long, glabrescent, eglandular, the lower part swollen, usually curved. *Inflorescences* axillary racemes 3–7 cm long, the rachis densely sericeous-tomentellous; bracts and bracteoles lanceolate, 3–7(–13) mm long, persistent, sericeous. *Receptacle* cylindrical, 8–13 mm long, densely sericeous on exterior, sessile; calyx lobes to 6 mm long, unequal, acute, sericeous on exterior. Petals white, spatulate to ovate, 8–12 mm long, narrowed to base. *Stamens* 18–20, black to purple, the filaments 10–15 mm long, slightly unilateral with tooth-like staminodes opposite. *Style* to 15 mm long, glabrous; stigma capitate. *Ovary* pilose. *Fruit* ellipsoid, 3–4 by 1.5 cm, slightly tapered to base, crustaceous verrucose on exterior; mesocarp 2–2.5 mm, fibrous, hard, endocarp thin.

Distr. *Malesia*: Malay Peninsula (Trengganu and Pahang southward), Borneo (Sabah, Sarawak). Fig. 18.

Ecol. Well drained forests to 500 m altitude.  
Vern. *Merbatu*, Malay.

3. *Atuna penangiana* (KOSTERM.) KOSTERM. Reinwardtia 7 (1969) 422; PRANCE & WHITM. Tree Fl. Malaya 2 (1973) 326. — *Cyclandrophora penangiana* KOSTERM. & PRANCE, Candollea 20 (1965) 124. — *Parinari asperula* auct. non MIQ.: KING, J. As. Soc. Beng. 66 (1897) 281, p.p.

Trees to 20 m tall, unbuttressed, the young branchlets glabrescent, obscurely lenticellate. *Stipules* lanceolate, acute, to 7 mm long, glabrous, stiff, subsistent. *Leaves* thinly subcoriaceous, oblong to oblong lanceolate, 3.7–13 by 2–5.5 cm, glabrous on both surfaces, acuminate at apex, the acumen 3–10 mm, cuneate at base; midrib flattened prominulous above, prominent beneath; primary veins 10–13 pairs, arcuate, prominulous on both surfaces; petioles 3–5 mm long, eglandular, glabrescent, smooth, not swollen or curved. *Inflorescences* axillary racemes 3–7 cm long, the rachis densely appressed pilose; bracts and bracteoles sericeous to 10 mm long, persistent. *Receptacle* cylindrical, 5–7 mm long, sericeous pubescent on exterior; calyx lobes acute, 4–5 mm long, slightly unequal. *Stamens* c. 20, the filaments to 8 mm long with tooth-like staminodes opposite. *Style* to 10 mm long, stigma capitate. *Ovary* pilose. *Fruit* (immature) ellipsoid, epicarp crustaceous, verrucose.

Distr. *Malesia*: Malay Peninsula (Penang, Perak, Johore, Kelantan and Trengganu). Fig. 18.

Ecol. Well drained forests to 500 m altitude.

Vern. *Membatu*, Malay.

Note. The two species *Atuna nannodes* and *A. penangiana* are hard to separate. The larger flowers of *A. nannodes* seem consistent and the species generally has leaves with a much longer apex. These may be one variable species.

4. *Atuna cordata* COCKBURN ex PRANCE, Brittonia 39 (1987) 364. — *Atuna cordata* COCKBURN, Trees of Sabah 2 (1980) 82, *nom. inval.*

Tree to 40 m tall, the trunk often with thick buttresses; young branches glabrescent, inconspicuously lenticellate. *Stipules* to 1.7 cm long, very early caducous. *Leaves* coriaceous, broadly ovate, 4.5–12 cm long, 3–9.5 cm wide, abruptly acuminate at apex, the acumen 1–3 mm long, cordate at base, glabrous and shiny above, glabrous beneath; midrib prominulous above, prominent beneath; primary veins 9–12 pairs, lightly prominulous above, prominulous and glabrous beneath; petioles 1–3 mm long, short and thick, glabrous. *Inflorescences* of terminal and subterminal racemes 4–8 cm long, borne in single or more often in paired branches, densely tomentellous on exterior, puberulous within; bracts and bracteoles ovate, tomentellous, early caducous. *Receptacle* 5–7 mm long, conical to campanulate, tomentellous on exterior, sessile; calyx lobes slightly unequal, tomentellous on both surfaces. Petals c. 7 mm long,

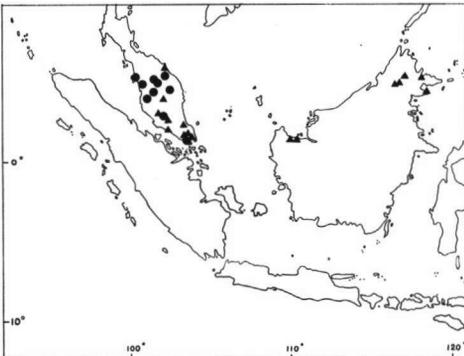


Fig. 18. Distribution of *Atuna nannodes* (KOSTERM.) KOSTERM. (triangles), *A. penangiana* (KOSTERM.) KOSTERM. (dots).

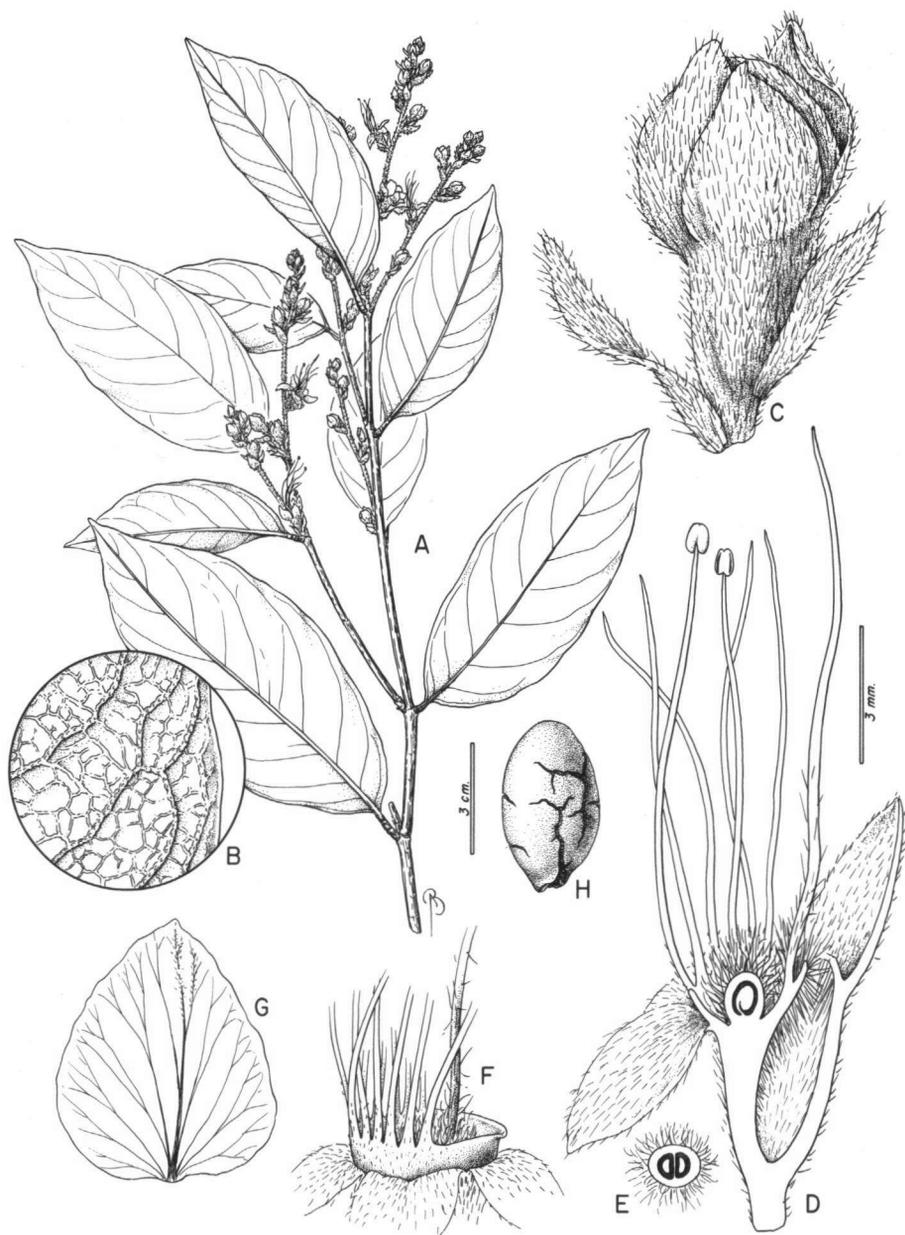


Fig. 19. *Atuna racemosa* RAFIN. ssp. *excelsa* (JACK) PRANCE. A. Habit; B. leaf undersurface; C. flower bud; D. flower section; E. ovary section; F. base of stamens; G. petal; H. fruit (A–G WHITMORE 3542, H AGAMA 4222).

obovate, glabrous. *Stamens* c. 10, inserted on one side of ring, the filaments 10–12 mm long. *Ovary* densely pilose. Style slender, hirsutulous on lower portion. *Fruit* 6 cm long, 5 cm wide, ovoid; epicarp crustaceous verrucose, mesocarp 5 mm thick, fibrous, hard, endocarp thin.

Distr. *Malesia*: Borneo (Sabah). Fig. 17.

Ecol. Hill forests on ultrabasic rock.

5. *Atuna racemosa* RAFIN. *Sylva Tellur.* (1838) 153; MERR. *Index Rafin.* (1949) 136; KOSTERM. *Reinwardtia* 7 (1969) 422. — Fig. 19.

For further synonyms, see under the subspecies.

#### KEY TO THE SUBSPECIES

1. Leaves 10–25(–35) cm long, usually elliptic, oblong or lanceolate but sometimes ovate, chartaceous or thickly coriaceous, the apex long finely acuminate, 6–25 mm long; petioles thick. Flowers 10–17 mm long. Medium to large trees often with fluted bole . . . . . a. *spp. racemosa*
1. Leaves 4.5–12 cm long, usually ovate or oblong-ovate, subcoriaceous or coriaceous, the apex bluntly acuminate, 3–10 mm long; petioles thin. Flowers 8–11 mm long. Large trees with cylindrical bole . . . . . b. *spp. excelsa*

a. *spp. racemosa*. — *Atunus alba* RUMPH. *Herb. Amb.* 1 (1741) 171, t. 66, non *Atunus litorea* RUMPH. *Herb. Amb.* 3 (1743) 96, t. 63. — *Cyclandrophora glaberrima* HASSK. *Flora* 25 (2), Beibl. 1 (1842) 47; *ibid.* 27 (1844) 583; *Cat. Hort. Bog.* (1844) 269. — *Parinari glaberrimum* (HASSK.) HASSK. *Tijd. Nat. Ges. Phys.* 10 (1843) 147; C.MUELL. in *Walp.*, *Rep.* 5 (1845/46) 647; in *Walp.*, *Ann.* 4 (1857) 645; BLUME, *Mus. Bot. Lugd.-Bat.* 2 (1852) 98; MIQ. *Fl. Ind. Bat.* 1, 1 (1855) 355; K. & V. *Bijdr.* (1900) 338, *incl. var. lanceolatum* (TEUSM. & BINN.) K. & V., *p.p. quoad spec. Java*; BURK. *Dict.* (1935) 1696; BACKER & BAKH., *f. Fl. Java* 1 (1964) 522. — *Parinarium scabrum* HASSK. *Tijd. Nat. Ges. Phys.* 10 (1843) 147, *nomen*; *Cat. Hort. Bog.* (1844) 269, *nomen*; *Flora* 27 (1844) 585; C.MUELL. in *Walp.*, *Rep.* 5 (1845/46) 647; in *Walp.*, *Ann.* 4 (1857) 645; BLUME, *Mus. Bot. Lugd.-Bat.* 2 (1852) 95, *p.p.*; MIQ. *Fl. Ind. Bat.* 1, 1 (1855) 354, t. 5; K. & V. *Bijdr.* 5 (1900) 337, *p.p.*; BACKER, *Schoolfl. Java* (1911) 445; RIDLEY, *Fl. Mal. Pen.* 1 (1922) 669. — *Parinarium lanceolatum* TEUSM. & BINN. *Cat. Hort. Bog.* (1854) 253, 255, *nomen*. — *Parinarium amboinense* TEUSM. & BINN. *l.c.* 254, *nomen*. — *Parinarium margarata* A.GRAY, *Bot. Wilkes U.S. Expl. Exped.* 1 (1854) 489, t. 55; C.MUELL. in *Walp.*, *Ann.* 4 (1857) 646. — *Parinarium laurinum* A.GRAY, *Bot. Wilkes U.S. Expl. Exped.* 1 (1854) 490, t. 55; C.MUELL. in *Walp.*, *Ann.* 4 (1857) 646; MERR. *Philip. J. Sc.* 10 (1915) *Bot.* 210;

KANEHIRA, *Bot. Mag. Tokyo* 45 (1931) 282. — *Petrocarya glaberrima* (HASSK.) MIERS, *J. Linn. Soc. Bot.* 17 (1879) 336. — *Ferolia glaberrima* (HASSK.) O. Ktze, *Rev. Gen. Pl.* 1 (1891) 216. — *Ferolia scabra* (HASSK.) O. Ktze, *l.c.* 216. — *Petrocarya scabra* (HASSK.) MIERS, *J. Linn. Soc. Bot.* 17 (1897) 336. — *Parinarium elatum* KING, *J. As. Soc. Beng.* 66 (1897) 280; RIDLEY, *Fl. Mal. Pen.* 1 (1922) 669. — *Parinarium hahlii* WARB. *Tropenpfl.* 6 (1902) 370. — *Parinarium mindanaense* PERK. *Fragm. Fl. Philip.* (1904) 119. — *Parinarium curranii* MERR. *Philip. J. Sc.* 4 (1909) *Bot.* 264. — *Parinarium warburgii* PERK. ex MERR. *J. Str. Br. Roy. As. Soc. n.* 76 (1917) 82. — *Cyclandrophora elata* (KING) KOSTERM. *Candollea* 20 (1965) 122. — *Cyclandrophora scabra* (HASSK.) KOSTERM. *l.c.* 126. — *Cyclandrophora laurina* (GRAY) KOSTERM. *l.c.* 135. — *A. elata* (KING) KOSTERM. *Reinwardtia* 7 (1969) 421; PRANCE & WHITM. *Tree Fl. Malaya* 2 (1973) 324. — *Atuna scabra* (HASSK.) KOSTERM. *Reinwardtia* 7 (1969) 422.

Trees to 45 m tall, usually smaller, the bole often fluted, young branches glabrous or appressed strigose. *Stipules* lanceolate, stiff, to 20 mm long, acute, glabrous to strigose, subsistent. *Leaves* usually chartaceous, more rarely stiffly coriaceous, broadly ovate, elliptic, oblong or even lanceolate, 10–25 (–35) by 3.5–11 cm, acuminate at apex, the acumen 6–25 mm long, rounded to subcordate at base, glabrous on both surfaces when mature, sometimes sparsely strigose beneath on lower portion when young; midrib prominent on both surfaces; primary veins 10–13 pairs, prominulous above, prominent beneath, straight or arcuate; the venation conspicuously papillose and often giving leaf a scabrous appearance; petioles thick, 3–7 mm long, glabrous or pilose glabrescent. *Inflorescences* of axillary racemes or little branched with up to 3 racemose branches on short main peduncle, 5–15 cm long, the rachis tomentellous to sericeous; bracts and bracteoles ovate, acute, to 8 mm long, caducous. *Receptacle* turbinate-campanulate, 5–10 mm long, tomentose to sericeous on exterior; pedicels 0.5–1 mm long, calyx lobes 4–7 mm long, ovate to ovate-oblong, densely tomentellous on both surfaces. Petals ovate-oblong, to 10 mm long, blue or white. *Stamens* 15–20, pale blue, to 15 mm long with tooth-like staminodes opposite. *Ovary* densely villous. *Style* equalling filaments, stigma small. *Fruit* ellipsoid to subglobose, to 7.5 cm diam.; epicarp crustaceous verrucose; mesocarp to 11 mm thick, endocarp thin, 1–3 mm, densely pilose within.

Distr. A wide range from Thailand to the Pacific: Admiralty, Caroline, and Solomon Islands, Fiji, Tonga, Samoa; in *Malesia*: Malay Peninsula (Perak), Singapore, Sumatra, Borneo (Sarawak, Brunei), Sulawesi, Philippines, Ambon, Ternate, Ceram, New Guinea, New Britain. Fig. 20.

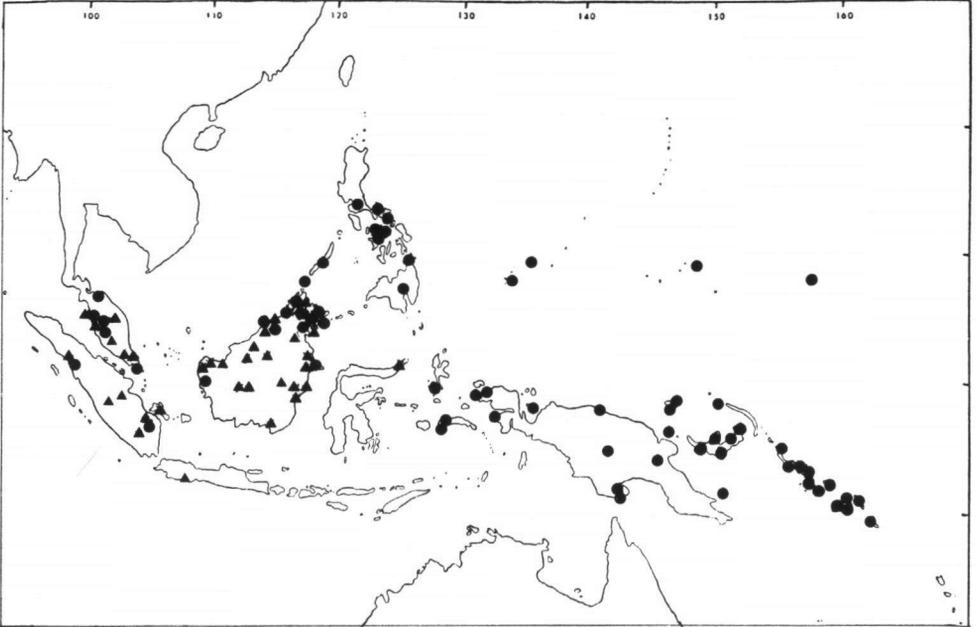


Fig. 20. Distribution of *Atuna racemosa* RAFIN. *ssp. racemosa* (dots) and *ssp. excelsa* (JACK) PRANCE (triangles). *Atuna racemosa ssp. racemosa* also occurs in Tonga, Fiji, and Samoa outside the area shown in the map.

**Ecol.** Usually occurring in well-drained lowland or hill forest, up to 600 m altitude, but also found on riverbanks, freshwater or brackish swamps and even in mangrove.

**Uses.** The fruit (cotyledon) is grated and made into a putty for caulking canoes, widely used in Pacific islands. An oil is extracted from the seeds used variously in different areas, e.g. to scent coconut oil and for hairdressing. The leaves are used to thatch the outside walls of houses in Fiji. The wood is used locally for posts and poles, but is not of good quality.

**Vern.** *Jangong, membatu*, Malay; *kisokka*, Jav.; Borneo: *belibu, senumpol*, Iban, *kukut*, Sarawak, *merampangi, tatambu*, Sabah, *torog*, Orang Sungei, K'tangan; Sulawesi: *lomo*, Makassar; Philippines: *aluma*, Ceb., *botabon, butabul, getabon*, Tagb., *botga*, Bik., *pantog-usa*, Kuy., *pinax, tabontaba, takoutaban*, Bis., *tabong, Bag., tabon-tabon*, C. Bis., Bik., Mbo., *samake*, Bug.; New Guinea: *asikua, asista*, Saki, *bata-bata, koewao*, Kwerba, *dela*, Mooi, *kan*, Oriomo, *low tukwa, lowtukwa*, Manikiong, *mangosowai*, Japen; New Britain: *latita, tita*; New Georgia: *jjj, tawai, tita*, Uso; Caroline Is.: *agaratim, ais, eis, eritem, grihing*, Palau, *adidi*, Yap, Solomon Is.: *do-omu, oso, saia, tij*, Kwara'ae; Fiji: *makita*; Tonga: *hea, seea*; Samoa: *ifi-ifi*.

**Note.** KOSTERMANS included *Cyclandrophora glaberrima* as a synonym of *Atuna excelsa* rather than where it is placed here. There seems little doubt based on the original description and herbarium material at Leiden bearing HASSEKARL's writing that *C. glaberrima* is equal to *Atuna racemosa ssp. racemosa* as defined here. The original description of *C. glaberrima* indicates leaves that are far too large for *ssp. excelsa*. *Atuna excelsa* was distinguished by KOSTERMANS by its coriaceous leaves and short petioles. However, many sheets which he determined as *A. racemosa* have equally short petioles and there is much variation in leaf texture. Therefore it is not possible to maintain *A. elata*. Similarly the distinction of *A. scabra* was the scabrous texture of the leaves and their more lanceolate shape. Many collections of *A. racemosa* are equally scabrous (e.g. LAE 52392 from New Guinea) and there is so much variation in leaf shape that it would be quite impossible to separate *A. scabra* on that feature. This was already placed under *Parinari glaberrimum* by BACKER and BAKHUIZEN VAN DEN BRINK (*l.c.* 1964).

**b. *ssp. excelsa* (JACK) PRANCE, *stat. nov.*** – *Petrocarya excelsa* JACK, Mal. Misc. 2 (7) (1822) 68 [repr. HOOK. Comp. Bot. Mag. 1 (1836) 220; Calc. J. Nat. Hist. 4 (1843) 164]; WALP. Rep. 2 (1843) 7. – *Parina-*

*rium jackianum* BENTH. in Hook., Niger Fl. (1849) 335; MIQ. Fl. Ind. Bat. 1, 1 (1855) 356; C. MUELL. in Walp., Ann. 4 (1857) 644; HOOK. f. Fl. Brit. India 2 (1878) 312. — *Parinarium asperulum* MIQ. Fl. Ind. Bat., Suppl. Sumatra (1860) 115, *nomen*; *ibid.* (1861) 307, *descr.*; HOOK. f. Fl. Brit. India 2 (1878) 310; KING, J. As. Soc. Beng. 66 (1897) 281; K. & V. Bijdr. (1900) 337, *p.p.*; RIDLEY, Fl. Mal. Pen. 1 (1922) 670. — *Ferolia asperula* (MIQ.) O. KTZE, Rev. Gen. Pl. 1 (1891) 216. — *Ferolia jackiana* (BENTH.) O. KTZE, *l.c.* — *Parinarium spicatum* KING, J. As. Soc. Beng. 66 (1897) 279; RIDLEY, Fl. Mal. Pen. 1 (1922) 669. — *Parinarium maingayi* KING, J. As. Soc. Beng. 66 (1897) 280; RIDLEY, Fl. Mal. Pen. 1 (1922) 669. — *Parinarium villamilii* MERR. Philip. J. Sc. 10 (1915) Bot. 308; Enum. Philip. Fl. Pl. 2 (1923) 236. — *Cyclandrophora villamilii* (MERR.) PRANCE ex KOSTERM. Candollea 20 (1965) 126. — *Cyclandrophora excelsa* (JACK) KOSTERM. *l.c.* 128. — *Cyclandrophora asperula* (MIQ.) PRANCE ex KOSTERM. *l.c.* 130. — *Atuna villamilii* (MERR.) KOSTERM. Reinwardtia 7 (1969) 422. — *Atuna excelsa* (JACK) KOSTERM. *l.c.* 422; PRANCE & WHITM. Tree Fl. Malaya 2 (1973) 324. — Fig. 19.

Tree to 45 m tall, the trunk buttressed up to 2 m, not fluted, the young branches sparsely strigose, glabrescent, obscurely lenticellate. *Stipules* lanceolate, 8–15 mm long, acute, sparsely strigose, subsistent. *Leaves* rigidly chartaceous to coriaceous, ovate to oblong-ovate or less frequently oblong, 4.5–12 by 2–5 cm, acuminate at apex, the acumen 3–10 mm long, subcordate, rounded or subcuneate at base, glabrous on both surfaces; midrib prominent on both surfaces; primary veins 9–13 pairs, arcuate, prominent above, prominent beneath, the venation papillose giving a beaded appearance; petioles slender, 3–6 mm long, puberulous, glabrescent or glabrous. *Inflorescences* of axillary racemes to 7.5 cm long, or little branched with 2 or more racemose branches on short main peduncle, the rachis and branches densely short sericeous; bracts and brac-

teoles oblong, c. 3 mm long, persistent. *Receptacle* turbinate-campanulate, 4–7 long, sericeous on exterior; calyx lobes ovate, equal, to 4 mm, sericeous on exterior, tomentellous within. Petals white to bluish white, oblong, to 5 mm long, caducous. *Stamens* 13–18, to 8 mm long with tooth-like stamino-odes opposite. *Ovary* pilose. *Style* glabrous, equaling filaments, glabrous above, stigma small. *Fruit* subglobose to slightly pyriform, 5–7 cm diam. or 5–7 by 3.5–4.5 cm; epicarp crustaceous, verrucose; mesocarp fibrous, 5–8 mm thick, endocarp thin, densely pilose within.

Distr. *Malesia*: Malay Peninsula (Kedah and Trengganu southward), Sumatra, Java, Borneo, N. Sulawesi. Fig. 20.

Ecol. Lowland forests on well drained soils extending to 750 m altitude on ridges and hillsides.

Vern. Malay Peninsula: *kemalau ulat*, *merbatu*; Sumatra: *kemiling utan*, *klappa soepai*, *pelec kambing*, *salak*; Borneo: *membatu*, Sabah, *mahadiu*, Bantjar, *temalang*.

Notes. KOSTERMANS is probably correct in interpreting *Petrocarya excelsa* JACK as the species described here. The original description is quite detailed and fits this taxon better than any other *Atuna*.

KOSTERMANS treated these two subspecies as separate species. They were differentiated by small characteristics of leaf shape, the acumen and the base. While there do seem to be two elements involved in this complex, there is a complete graduation of any single character such as leaf length, apex length, petiole thickness, leaf shape or flower size. *Ssp. excelsa* is much commoner in Sundaland and *ssp. racemosa* in the Sahul shelf and Pacific islands, but the two subspecies have considerable geographical overlap with *ssp. racemosa* occurring sporadically on the Malay Peninsula. Since all characters merge and are only weakly correlated, these two species are reduced to subspecies, a rank more in accord with their variational and geographical patterns.

## 7. MARANTHES

BLUME, Bijdr. (1825) 89; KOSTERM. Candollea 20 (1965) 196; PRANCE, Bol. Soc. Brot. sér. 2, 40 (1966) 183; Brittonia 20 (1968) 203; Fl. Neotrop. 9 (1972) 201; PRANCE & WHITM. Tree Fl. Malaya 2 (1973) 329; WHITE, Bull. Jard. Bot. Nat. Belg. 46 (1976) 294; Distr. Pl. Afr. 10 (1976) 313; Fl. Zamb. 4 (1978) 41; LETOUZEY & WHITE, Fl. Cameroun 20, Fl. Gab. 24 (1978) 29. — *Exitelia* BLUME, Fl. Jav. 1, Praef. (1828) vii, *nom. illeg.* — *Grymania* PRESL, Epim. Bot. (1851) 193, *p.p. quoad G. salicifolia tantum.* — *Parinari sect. Sarcostegia* BENTH. in Hook., Niger Fl. (1849) 335, *excl. P. jackiana (Petrocarya excelsa).* — *Parinari subg. Sarcostegia* (BENTH.) MIQ. Fl. Ind. Bat. 1, 1 (1855) 355, *excl. P. jackiana*;

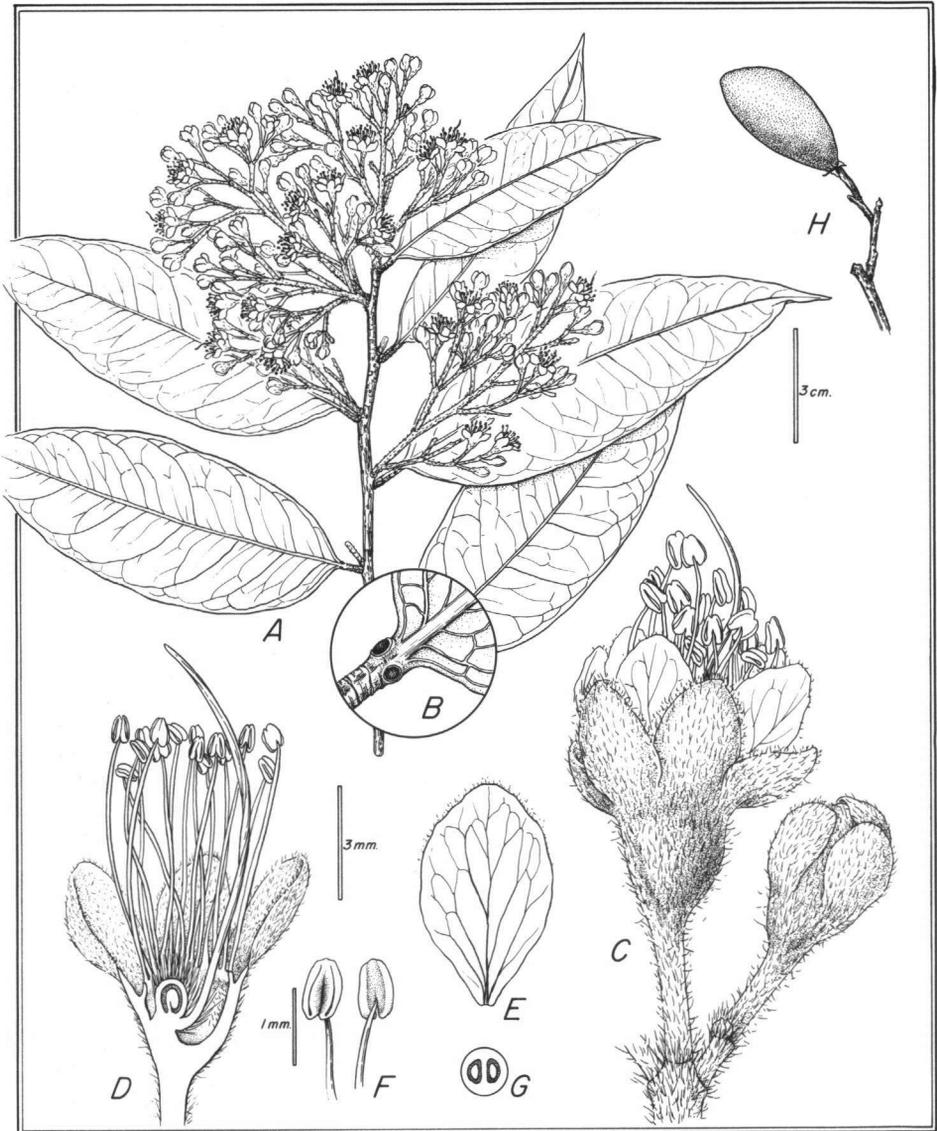


Fig. 21. *Maranthes corymbosa* BLUME. A. Habit; B. leaf base and glands; C. flower and bud; D. flower section; E. petal; F. anthers; G. ovary section; H. fruit (A-G SULIT 19, H SINCLAIR 10687).

HAUMAN, Bull. Jard. Bot. Brux. 21 (1951) 185. — *Parinari subg. Exitelia* BLUME, Mélang. Bot. 2 (1855) 10; HASSK. Flora 16 (1858) 255. — *Parinari sect. Exitelia* (BLUME) C.MUELL. in Walp., Ann. 4 (1857) 645. — Fig. 21.

Medium-sized to large trees. *Stipules* deltate, intrapetiolar, stiff, caducous. *Leaves* glabrous on both surfaces when mature (or lanate in African species), with dense caducous cobweb-like indumentum when young, without stomatal crypts; with paired glands at junction of lamina and petiole. Petioles eglandular. *Inflorescence* a many-flowered corymbose panicle. Bracts and bracteoles eglandular, caducous, not enclosing flower buds in small groups. *Flowers* hermaphrodite. *Receptacle* obconical, narrowed into pedicel, solid, almost completely filled with nectariferous tissue, short tomentose to glabrous on exterior, glabrous within, calyx lobes suborbicular, deeply concave, unequal. Petals 5, not clawed. *Stamens* 25–40, inserted on margin of disk, unilateral with tooth-like staminodes opposite to almost in a complete circle; filaments far exerted beyond calyx lobes, in a tangled mass. *Ovary* inserted laterally at mouth of receptacle; carpel bilocular with 1 ovule in each loculus. *Style* pubescent at base only, curved upwards, exerted. *Fruit* a large fleshy drupe; epicarp smooth, glabrous, not lenticellate; mesocarp fleshy; endocarp very hard, fibrous with a rough exterior, densely tomentose within, with 2 lateral plates which break away on germination. Germination phanerocotylar. *Cotyledons* fleshy, pale green; cataphylls absent; first 2 eophylls opposite, the others alternate or opposite.

Distr. In tropical Africa 10 species, one native to Central America and one widespread species in *Malesia*, NE. Australia and W. Pacific.

1. *Maranthes corymbosa* BLUME, Bijdr. (1825) 89; KOSTERM. Candollea 20 (1965) 107; PRANCE & WHITM. Tree Fl. Malaya 2 (1973) 330, *excl. syn. Couepia panamensis*. — *Exitelia corymbosa* (BLUME) BLUME, Fl. Java 1, Praef. (1828) vii. — *Maranthes multiflora* KORTH. Verh. Nat. Ges. Ned. Overz. Bezitt., Bot. (1839/42) 259; Ned. Kruidk. Arch. 3 (1855) 281; TEUSM. & BINN. Cat. Hort. Bog. (1866) 253. — *Exitelia multiflora* (KORTH.) WALP. Rep. 5 (1845/46) 115; MIERS, J. Linn. Soc. Bot. 17 (1879) 336, *sub Exitelles*. — *Parinarium griffithianum* BENTH. in Hook., Niger Fl. (1849) 334; Fl. Austr. 2 (1864) 426; WALP. Ann. 2 (1851/52) 463; BLUME, Mus. Bot. Lugd.-Bat. 2 (1852) 98; Mélang. Bot. 2 (1855) 10; MIQ. Fl. Ind. Bat. 1, 1 (1855) 356; *ibid.* (1858) 1084; HOOK. f. Fl. Brit. India 2 (1878) 310; MIERS, J. Linn. Soc. Bot. 17 (1879) 336; VIDAL, Sinopsis Atlas (1883) 25; MAINGAY, Kew Bull. (1890) 122; KING, J. As. Soc. Beng. 66 (1897) 283; BAILEY, Queensl. Fl. 2 (1900) 524; K. & V. Bijdr. 5 (1900) 334; K.SCH. & LAUT. Fl. Deut. Schutzgeb. Südsee (1901) 341; PERK. Fragm. Fl. Philip. (1904) 118; BRANDIS, Indian Trees (1906) 278; FOXW. Philip. J. Sc. 2 (1907) Bot. 386; BACKER, Schooffl. Java (1911) 446; RIDLEY, Fl. Mal. Pen. 1 (1922) 670; Disp. (1930) 400;

CRAIB, Fl. Siam. Enum. 1 (1931) 563. — *Grymania salicifolia* PRESL, Epim. Bot. (1849) 193; WALP. Ann. 3 (1853) 854. — *Parinarium griffithianum* BENTH. in Hook., Niger Fl. (1849) 334; Fl. Austr. 2 (1864) 426; WALP. Ann. 2 (1851/52) 463; BLUME, Mus. Bot. Lugd.-Bat. 2 (1852) 98; Mélang. Bot. 2 (1855) 10; MIQ. Fl. Ind. Bat. 1, 1 (1855) 356; *ibid.* (1858) 1084; HOOK. f. Fl. Brit. India 2 (1878) 310; MIERS, J. Linn. Soc. Bot. 17 (1879) 336; VIDAL, Sinopsis Atlas (1883) 25; MAINGAY, Kew Bull. (1890) 122; KING, J. As. Soc. Beng. 66 (1897) 283; BAILEY, Queensl. Fl. 2 (1900) 524; K. & V. Bijdr. 5 (1900) 334; K.SCH. & LAUT. Fl. Deut. Schutzgeb. Südsee (1901) 341; PERK. Fragm. Fl. Philip. (1904) 118; BRANDIS, Indian Trees (1906) 278; FOXW. Philip. J. Sc. 2 (1907) Bot. 386; BACKER, Schooffl. Java (1911) 446; RIDLEY, Fl. Mal. Pen. 1 (1922) 670; Disp. (1930) 400; CRAIB, Fl. Siam. Enum. 1 (1931) 563. — *Parinarium maranthes* BLUME, Mus. Bot. Lugd.-Bat. 2 (1852) 99; Mélang. Bot. 2 (1855) 10. — *Parinarium corymbosum* (BLUME) MIQ. Fl. Ind. Bat. 1, 1 (1855) 356; *ibid.* (1858) 1084; Ann. Mus. Bot. Lugd.-Bat. 3 (1867) 237; WALP. Ann. 4 (1857) 645; VIDAL, Cat. Pl. Len. Silv. Cult. Manila (1880) 29; MERR. Philip. J. Sc. 10 (1915) Bot. 309; Spec. Blanc. (1918) 162;

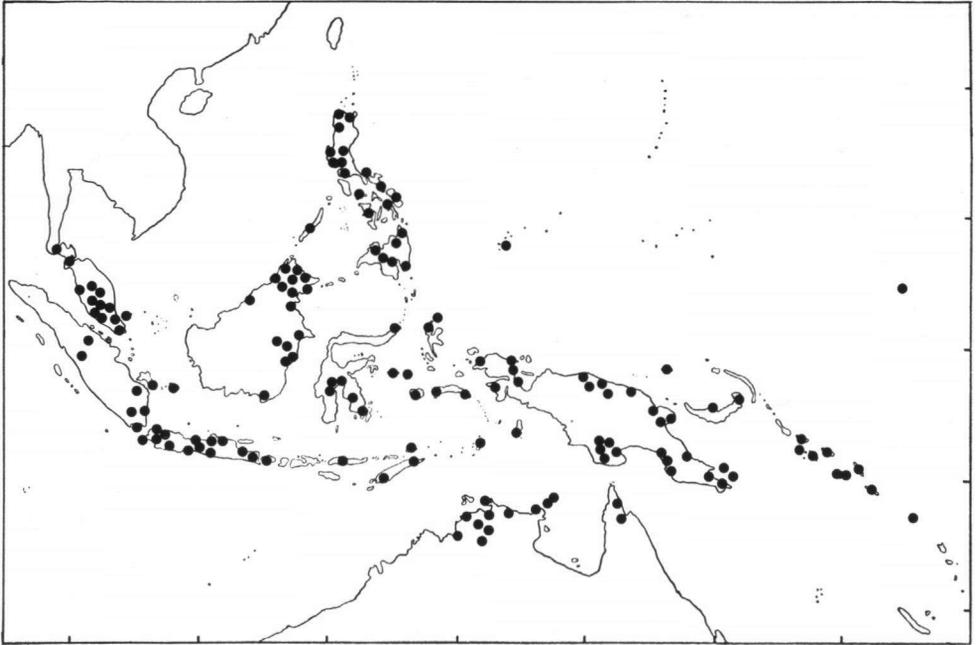


Fig. 22. Distribution of *Maranthes corymbosa* BLUME.

Enum. Born. (1921) 290; Enum. Philip. Fl. Pl. 2 (1923) 235; CRAIB, Fl. Siam. Enum. 1 (1931) 563; BURK. Dict. (1935) 1695; CORNER, Wayside Trees (1940) 527; BACKER & BAKH. f. Fl. Java 1 (1964) 522. — *Parinarium multiflorum* (KORTH.) MIQ. Fl. Ind. Bat. 1, 1 (1855) 356; *ibid.* (1858) 1084; Suppl. Sumatra (1860) 115; *ibid.* (1861) 307; C. MUELL. in Walp., Ann. 4 (1857) 646. — *Parinarium salicifolium* (PRESL) MIQ. Fl. Ind. Bat. 1, 1 (1855) 357; C. MUELL. in Walp., Ann. 4 (1857) 646. — *Maranthes speciosa* KORTH. ex MIQ. Fl. Ind. Bat. 1, 1 (1855) 357. — *Chrysobalanus ciliatus* KORTH. ex MIQ. l.c. 357. — *Petrocarya griffithiana* (BENTH.) MIERS, J. Linn. Soc. Bot. 17 (1879) 336. — *Parinarium racemosum* VIDAL, Cat. Pl. Len. Silv. Cult. Manila (1880) 29. — *Ferolia griffithiana* (BENTH.) O. KTZE, Rev. Gen. Pl. 1 (1891) 216. — *Ferolia corymbosa* (BLUME) O. KTZE, l.c. 216. — *Ferolia salicifolia* (PRESL) O. KTZE, l.c. 216. — *Parinarium nitidum auct. non* BENTH.: KOORD. Meded. Lands Planten Tuin Btzg 19 (1898) 448. — *Polyalthia pulchrinervia* BOERL. Cat. Pl. Hort. Bog. (1899) 20; Icon. Bog. 1 (1899) 106. — *Parinarium palauense* KANEHIRA, Bot. Mag. Tokyo 45 (1931) 282; Fl. Micrones. (1933) 129; J. Dept. Agr. Kyushu Imp. Univ. Fukuoka 4 (1934) 325. — Fig. 21.

Small to large tree up to 40 m, sometimes flowering when only a few metres high, trunk not but-

tered or slightly enlarged at base. *Stipules* intrapetiolar, lanceolate, acute, 5–10 mm long, sparsely pilose on exterior, glabrous within, early deciduous. *Leaves* coriaceous, usually oblong-lanceolate to oblong-elliptic, 6.5–14 by 2.5–8 cm, acuminate at apex, the acumen 8–20(–30) mm long, cuneate at base, glabrous when mature but often sparsely caducous arachnoid-lanate when young, usually with 2 conspicuous prominent glands at junction of petiole and decurrent lower surface; primary veins 7–10 pairs, arcuate, prominulous on both surfaces; midrib plane above, prominulous beneath; petioles 4–9 mm long, glabrous when mature, flattened above. *Inflorescences* of flattened many-flowered corymbose panicles, rachis and branches sparsely pilose, glabrescent. Bracts and bracteoles ovate to lanceolate, sparsely pubescent, caducous. *Receptacle* turbinate, tapering into pedicels 2–4 mm long, grey tomentose to glabrous on exterior, glabrous within, calyx lobes fleshy, ovate to elliptic, obtuse, 2.5–4 mm long, unequal. Petals white tinged pink, glabrous, 3–6 mm long, caducous. *Stamens* 25–35 inserted in several rows on one side of throat, with tooth-like staminodes opposite. *Ovary* bilocular, densely lanate and villous. *Style* glabrous except at base; stigma truncate. *Fruit* ellipsoid, 3–4 mm long, 1.5–2 cm broad, tapered towards base; epicarp thin, glabrous on exterior when mature, sometimes lanate

when young; endocarp hard, 5 mm thick, rough on exterior; densely lanate within; bilocular usually with seed in one locule only. Cotyledons plane-convex.

Distr. S. Thailand extending east to Solomon and Caroline Islands and Australia (Queensland, Northern Territory); in *Malesia*: Malay Peninsula, Sumatra, Java, Borneo, Lesser Sunda Islands, Sulawesi, Philippines, Moluccas, New Guinea, New Britain and Admiralty Islands. Fig. 22.

Ecol. Common in coastal areas on rocky and sandy hills and extremely inland up to 600 m altitude. Also in gallery forest and in Australia on sand dunes behind mangrove swamp. In Kalimantan the fruit is eaten by many bird species, including hornbills and fruit pigeons, which probably disperse the seed. The seed is also scatter-hoarded by the squirrel *Sundasciurus hippurus*. African species of *Maranthes* are bat-pollinated.

Uses. Wood used for house-building and for posts. Fruit edible.

Vern. Thailand: *chi-kat-pen*, *chi-ot-pen*, Korat; Malay Peninsula: *chana*, *lejin*, *merbatu*, *m. layang*, *mujagon*, *sau hutan*, *sunko rimau*; Sumatra: *damor lilis*, *kajie batu*, *kaju batu*, Banka, *kalek kureseng*, *k. parada*; Java: *gesing*, *kituwat*, *solo*, *sulo*, *triwulan*, *wuloh*, Jav., *taritik*, *t. monjet*, Sund.; Borneo: *bang-*

*kawang*, *bonsissian*, Malay; *bansisian*, Sabah, Tenggara; *nyalin laat*, Sarawak; *buenza*, *kajebabu*, *kajoe kambang*, *kambang*, *potang*, Kalimantan; Sulawesi: *kolaka*; Tidore: *latan*, Aru Is.; Philippines: *almag*, *delebaybai*, *kaphangan*, *kolaka*, *kolasa*, *kulingan*, *malapiga*, *malapuyan*, *sampinit*, *takdangan*, Tag., *aningat*, *binggas*, *caratacat*, *kagemkena*, *karatakat*, Ilk., *arangan*, Tagb., *dakayau*, Pang., *bakoyan*, *tapas*, P.Bis., *bongog*, *dau*, *mata-mata*, *sarangun*, S.-L.Bis., *dumaga*, Kuy., *kagangan*, *kalakangon*, *ogot*, Bag., *kamuli tingan*, Pamp., *lank angan*, Lan., *langog*, Buk., *lumalwas*, *sigadaan*, Mag., *maluktik*, Sul., *salipungan*, *salutui*, Neg., *bareraga*, *barit*, Bik., C.Bis., *laiusin*, Bik., S.C.Bis., *liusin*, Sbl., Tag., Bik., *sabongkaag*, Ilk., Ting., *tadiang manok*, Ting., Tag.; New Guinea: *badigal*, Wagu, *djuramun*, Kemptuk, *jambuan*, Kaigorin, *kaupen*, Jal, *kawol*, *kowot*, Muyu, *kwanu*, Maprik, *lakan*, *luikoko*, Bush Mekeo, *marigag*, Sinai, *mehlue*, Bemb, *morolee*, *mun*, Dagu, *naas*, *ningua*, *njali*, Nemo, *njiwa*, *niwa*, Sidei, *paguh*, Timbunke, *phu*, Wasuk, *watu*, Karopa; Solomon Is.: *asikisiki*, *giza*, *mon warlu*, *morigag*, *now-wa-ru*, *santalan*; Bougainville: *mon-warku*, Kugumaru, *marigai*, Siwai, Bouin; Palau Is.: *apgau*.

## 8. KOSTERMANTHUS

PRANCE [Tree Fl. Malaya 2 (1973) 327, unpublished], Brittonia 31 (1979) 91; PRANCE & WHITE, Phil. Trans. Roy. Soc. Lond. 320 (1988) 149, f. 40, 41. — *Parinari auct. non AUBL.*: *quoad P. heteropetala* SCORTECH. ex KING et *P. myriandra* MERR., *tantum*. — *Acioa auct. non AUBL.*: KOSTERM. Reinwardtia 7 (1965) 9. — Fig. 23.

Large trees, ultimate shoots not divaricate. *Stipules* to 7 mm long, foliaceous, persistent, lanceolate to ovate. *Leaves* glabrous on both surfaces with minute papillae on veins giving a beaded appearance. *Petioles* eglandular. *Inflorescence* an unbranched or little-branched terminal or axillary raceme with shortly stalked congested cymules proximally and singly inserted flowers distally. *Bracts* and *bracteoles* small, suborbicular, persistent, eglandular, not enclosing groups of flower buds. *Flowers* hermaphrodite, strongly zygomorphic. *Receptacle* broadly obconic-campanulate, shorter than calyx lobes, asymmetric, hollow, hairy on both surfaces, but throat not blocked by retrorse hairs; calyx lobes 5, markedly unequal, suborbicular to lingulate, strongly imbricate. *Petals* 5, unequal in size and shape, the 2 posterior larger than the others, markedly unguulate and enclosing stamens in bud. *Stamens* 8–30, inserted unilaterally on margin of disk; filaments united for half to three quarters of length into a strap; staminodes 5–8, inserted opposite stamens. *Ovary* inserted laterally at mouth of receptacle; unilocular with 2 ovules. *Fruit* large, hard; epicarp glabrous,

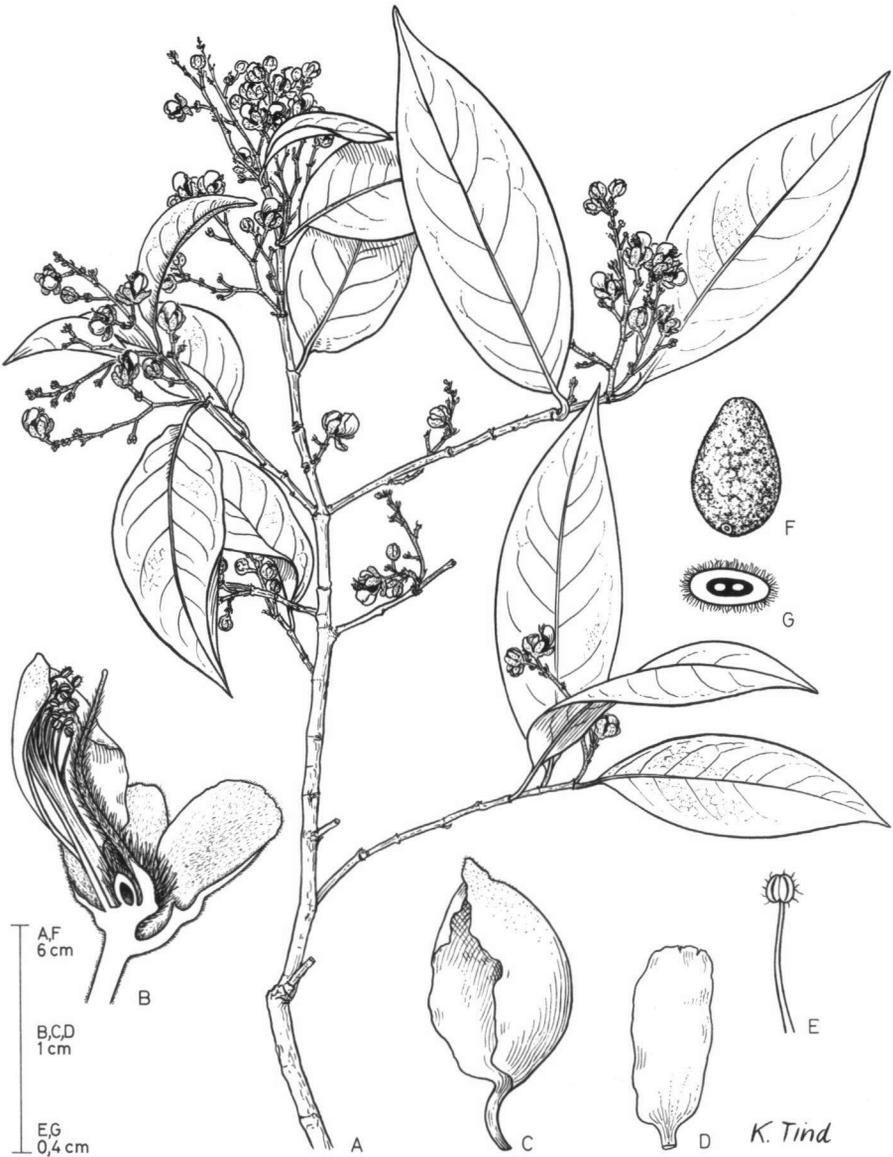


Fig. 23. *Kostermanthus heteropetalus* (SCORTECH. ex KING) PRANCE. A. Habit; B. flower section; C & D. petals; E. stamen; F. fruit; G. ovary section (A–E, G OGATA KEP 105153, F MEIJER SAN 34279).

crustaceous-verrucose; endocarp hard, thick, glabrous within, breaking irregularly on germination. *Cotyledons* slightly ruminant.

Distr. *Malesia*: Malay Peninsula, Sumatra, Borneo, Sulawesi, Philippines (Mindanao); 2 species.

## KEY TO THE SPECIES

1. Leaves coriaceous; petioles 6–12 mm long; calyx tube 2–3 mm long, broadly campanulate

1. *K. heteropetalus*

1. Leaves chartaceous; petioles 2–3 mm long; calyx tube 5 mm long, slender . . . . . 2. *K. malayanus*

1. *Kostermanthus heteropetalus* (SCORTECH. ex KING) PRANCE, *Brittonia* 31 (1979) 91; PRANCE & WHITE, *Phil. Trans. Roy. Soc. Lond.* 320 (1988) 152 – *Parinarium heteropetalum* SCORTECH. ex KING, *J. As. Soc. Beng.* 66 (1897) 283; RIDLEY, *Fl. Mal. Pen.* 1 (1922) 670; NAYARANASWAMI, *J. As. Soc. Beng. n.s.* 27 (1931) 368. – *Parinarium kunstleri* KING, *J. As. Soc. Beng.* 66 (1897) 282; RIDLEY, *Fl. Mal. Pen.* 1 (1922) 670. – *Parinarium myriandrums* MERR. *Univ. Cal. Publ. Bot.* 15 (1929) 93. – *Acioa heteropetala* (SCORTECH. ex KING) KOSTERM. *Reinwardtia* 7 (1965) 11. – Fig. 23.

Tree to 35 m tall, older trees buttressed to 1 m up trunk; young branches glabrous, lenticellate. *Stipules* 6–7 mm long, partly intrapetiolar, carinate, ovate, foliaceous, acute to acuminate, persistent to subsistent. *Leaves* coriaceous, usually elliptic-subovate to rarely lanceolate, 5–20 by 2.5–6 cm, bluntly acuminate at apex, cuneate to rounded at base, glabrous on both surfaces, minutely papillose on venation of both surfaces giving a bead-like appearance; midrib prominent above, prominent beneath; primary veins 6–10 pairs, arcuate, slender, prominent beneath; petioles 6–12 mm long, sometimes lightly alate from decurrent leaf margins, slightly flattened above, eglandular. *Inflorescences* little-branched, to 10 cm long, the rachis and branches lightly tomentellous; bracts and bracteoles ovate, acute, to 3 mm long, caducous. *Receptacle* broadly campanulate, 2–3 mm long, tomentose on both surfaces; calyx lobes fleshy, unequal, acute, to 7 mm long, pilose on both surfaces, reflexed in open flowers. *Petals* white tinged pink, fleshy, elliptic, concave, largest up to 15 mm long, tomentellous on exterior, enveloping staminal ligule, the others much smaller to 6 mm long. *Stamens* 25–30 united into a unilateral ligule for 2/3 length, to 12 mm long, glabrous; anthers pubescent. *Ovary* densely pilose. *Style* densely appressed pilose, stigma truncate. *Fruit* ovoid, unilocular 4 by 3 cm; epicarp glabrous, crustaceous; endocarp hard, thick. *Cotyledons* slightly ruminant, 1.5 by 3 cm.

Distr. *Malesia*: Malay Peninsula, Sumatra, Borneo, Sulawesi, Philippines (Mindanao). Fig. 24.

Ecol. From sea level up to 500 m altitude.

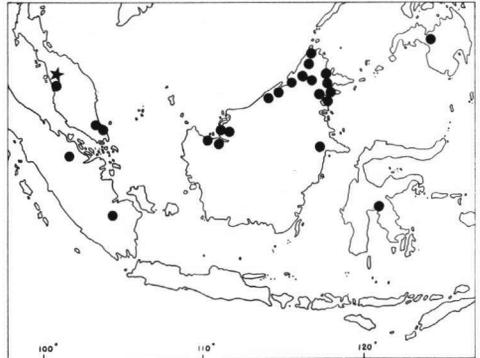


Fig. 24. Distribution of *Kostermanthus heteropetalus* (SCORTECH. ex KING) PRANCE (dots) and *K. malayanus* (KOSTERM.) PRANCE (star).

2. *Kostermanthus malayanus* (KOSTERM.) PRANCE, *Brittonia* 31 (1979) 94; PRANCE & WHITE, *Phil. Trans. Roy. Soc. Lond.* 320 (1988) 152. – *Acioa malayana* KOSTERM. *Reinwardtia* 7 (1965) 13.

Small tree to 10 m; young branches glabrous, lenticellate. *Stipules* lanceolate, acute, glabrous, subsistent, c. 5 mm long. *Leaves* chartaceous, elliptic, 14–20 by 6.5–8.5 cm, acuminate at apex, the acumen 4–10 mm long, cuneate at base, glabrous on both surfaces; midrib slightly prominent to plane above, prominent beneath, with a pair of round glands at base; primary veins 10–13 pairs, prominent above, prominent beneath; petioles 2–3 mm long, glabrous, slightly alate with decurrent leaf margins. *Inflorescence* of subterminal racemes or little branched, the rachis brown pilose pubescent; bracts and bracteoles ovate, acute, to 3 mm long, caducous. *Receptacle* slender cylindrical, 5 mm long, sessile tomentose on exterior, densely tomentose within; calyx lobes ovate, acute, 4–5 mm long, densely tomentose on exterior, glabrous within except at apex. *Petals* spatulate, 6 mm long, clawed. *Stamens* 8–10, united into a unilateral ligule for half of length. *Ovary* densely pilose. *Style* pilose for most of length. *Fruit* unknown.

Distr. *Malesia*: Malay Peninsula (Penang). Known only from the type collection.

## Insufficiently known

*Acioa percoriacea* KOSTERM. Reinwardtia 7 (1965) 14.

This species was described from a single sterile collection from the Malay Peninsula, and distinguished from *Kostermanthus heteropetalus* PRANCE by its pubescent branches and caducous pubescent leaf undersurfaces. It is impossible to evaluate until further material is collected, but almost certainly belongs within *K. heteropetalus*.