RHIZOPHORACEAE (Ding Hou, Leyden)\(^1\)

Evergreen trees or shrubs, mangrove species with various remarkable root formations. Branching (in the mangrove genera) mostly sympodial; branchlets swollen at the nodes, solid and pithy, hollow in Crossostylis, Gymnotroches, and Pellacalyx. Innovation continuous, but flushwise in Anisophyilla. Leaves decussate and stipulate, rarely alternate and exstipulate (Anisophyilla and Combretocarpus), usually isomorphic, rarely dimorphic (Anisophyilla spp.), gland-like cork warts sometimes occurring as small black spots on the lower surface; young leaves involute or convolute. Nervation generally pinnate, more rarely curvinerved and with 1–2 intramarginal veins (Anisophyilla). Stipules conspicuous, interpetiolar, caducous, opposite, except in Pellacalyx overlapping each with one free margin, in Malaysia with colleters at the base inside, leaving an annular scar. Inflorescences axillary, simple or branched, usually cymose (lax or condensed and cluster-like), racemose or fascicled, rarely consisting of a solitary flower. Flowers usually bisexual, rarely unisexual or polygamous and plants monocious (Anisophyilla and Gymnotroches), sustained at the base by connate or cupular bracteoles or ebracteolate. Calyx 3–16–lobed, lobes valvate, persistent. Petals free, equal in number to the calyx lobes and alternating with them, usually fleshy and conduplicate, sometimes embracing 2 (Bruguiera) or 1 stamen, entire, 2-fid, lacerate or fringed with appendages at the apex, usually clawed, caducous during or after anthesis, rarely persistent. Stamens free or epipetalous ones adnate to the petals in Anisophyilla sp. (or adnate to the calyx tube in Pellacalyx), in one whorl (except in P. symphiodiscus), usually twice the number of the petals and one opposite and one alternating with the petals, in Bruguiera in pairs opposite and embraced by the petals, in Rhizophora apiculata 3 times and in Crossostylis spp. 3–4 times as many stamens as petals, in Kandelia indefinite in number, in some species some stamens may be aborted and staminaloid, free or connate at the base; anthers typically 4-celled, rarely multi-locellate (Rhizophora), dorsiﬁxed, dehiscing longitudinally and intorsre, in Rhizophora opening with a large ventral valve. Disk fleshy, annular, and crenate or flat, or lobed, rarely absent. Ovary inferior, rarely semi-inferior or superior (Gymnotroches, Cassipourea), 2–12-celled, rarely 1-celled by suppression of the septa; style simple with simple or ± lobed stigma, or styles free, persistent. Ovules (1–)2–∞ in each cell, pendulous, attached axile or in 1–celled ovaries on the columella-like axis running from base to apex, anatropous with micropyle upward and outward. Fruit always bearing the persistent calyx and often other floral remains, a berry or a drupe or dry and rather hard-shelled (Anisophyilla), indehiscent, rarely (in extra-Mal. spp.) a capsule and dehiscent, winged in Combretocarpus. Seeds pendulous, 1–∞, sometimes (in extra-Mal. spp.) arillate, viviparous in mangroves, germinating in the ordinary way in inland species; albumen fleshy or small and soon obsolete (in Rhizophoraceae); embryo straight or curved.

Distribution. Mainly in the Old World, 16 genera\(^2\) with an estimated 120 spp.

Four mangrove genera are restricted to the littoral zone of the tropics extending slightly into the

(1) The introductory matter on ecology by C. G. G. J. VAN STEENIS.
(2) Recently ARAÎES has described two new genera from Madagascar (Not. Syst. 15, 1954, 2–3; Fl. Madag. fam. 150, 1954, 4 & 6, f. 1 5–11). Petalodactylis differs merely from Cassipourea s.l. by 2 short styles and cannot be maintained. Richeopsis has been reduced to Scolopia (Flac.) by CAPURON (Ess. Intr. Fl. For. Madag. 1957, p. 123).
Fig. 1. Inside the Rhizophora mangrove forest at low tide at the mouth of the Pahoturi R., Western Division, Papua: *Rh. mucronata* LAMK (dark stems), *Rh. apiculata* BL. (pale stems). The dark horizon on the roots is caused by the mud and marks the high tide level. April 1936 (L. J. Brass, Archbold Expeditions).
subtropics: *Rhizophora* is pantropical, *Bruguiera* and *Ceriops* occur from tropical Africa through Malaysia to Australia and the Pacific (Micronesia and Samoa), *Kandelia* is restricted to SE Asia and West Malaysia.

The other genera occur all inland as constituents of the tropical rain-forest, only very occasionally occurring also in the seasonal forest (*Carallia brachiata*). Among them *Anisophyllum* is pantropical (very rare in America and absent from Australia and the Pacific), and *Cassipourea* nearly so (absent E of Ceylon to W. America). *Carallia* occurs from Madagascar to S. China and Australia, *Gynotroches* and *Pellacalyx* are restricted to SE. Asia and Malaysia. The others possess a still more restricted area viz Macaristica in Madagascar, *Poga* and *Anopxyis* in tropical W. Africa, *Blepharistemma* in India, *Combretocarpus* in W. Malaysia, *Sterigmapetalum* in tropical S. America, and *Crossostylis* in Melanesia and Polynesia. The latter genus might also occur in E. Malaysia and has, for that reason, been entered in the key without being described further.

The genus is small and some of them, for instance *Kandelia, Combretocarpus, Blepharistemma, etc.* are even monotypic. The largest genus is *Cassipourea* with about 70 spp. (cf. Alston, Kew Bull. 1925, 241-276). The distribution towards the north and south shows the family to be restricted to the tropical zone and the warm subtropical zone both in the inland genera and the mangroves.

On the northern hemisphere the mangroves extend on all coasts north to latitudes varying between 24° and 31° N.

In the Riuksius and S. Japan mangrove go north as far as 31° 20' N, according to Ito (Ann. Bot. 13, 1899, 465) (*Kandelia, Bruguiera, Rhizophora*).

In Florida and Bermuda they extend to c. 28° N, in California to 24° 38' N.

In the southern hemisphere the situation is very different between the west coasts of the continents and the east coasts.

On the east coast of S. America they go south to about the tropic of Capricorn. On the east coast of Africa* Rh. mucronata* extends to 30° S, *Bruguiera* gymnorrhiza to 30° (or even 32°?) S and *Ceriops* tagal to 26° S. In East Australia mangrove *Rhizophoraceae* go as far south as the far northern corner of New South Wales at 29° S.

On the westcoast of South America *Rhizophora* seems only to extend south as far as 4° S. On the west coast of Africa *Rh. racemosa* G. F. W. Mey. goes to 6° S and *Rh. harrisonii* Leechm. and *Rh. mangle* L. to 9° S. From West Australia I have no data but I would not be surprised that it will be found there also at small southern latitude. In all these cases the west coasts are very dry or even arid caused by northern directed cold oceanic currents.

Ecology (inland species). They represent constituents of the mixed Malaysian rain-forest, generally avoiding the seasonal areas and rarely found on the mountains above the upper limit of the tropical zone at 1000 m. The (extra-Malaysian) *Pellacalyx parkinsonii* and *P. axillaris* have been found up to 1200 m and 1300 m respectively, *Anisophyllum grandis* up to 1250 m, *A. disticha*, *Carallia brachiata*, and *C. eugeniodis* up to 1800 m, and *Gynotroches axillaris* up to 2250 m.

Though many species are common they are generally of humble size and either shrubs or small or medium-sized trees of the substage. Only a few spp. reach the upper canopy and sizes between 40-50 m have been recorded for *Carallia brachiata*, *Gynotroches axillaris*, *Pellacalyx lobbii*, and *Anisophyllum sp.* They may flower and fruit from a very early age onwards and share this tendency with the mangrove genera (see under *Carallia* and *Gynotroches*).

In contrast with the mangrove species none of the inland species occurs gregariously with the exception of *Combretocarpus rotundatus* which is a typical constituent of the lowland swamp- and peat-forests of Sumatra and Borneo.

Germination of representatives of the inland genera has not yet been described. The structure of the seeds in *Anisophyllum* and *Combretocarpus* is even not known with certainty. The seeds in the large-fruited species, for instance *A. grandis* and *A. griffithii*, must be a very curious one, as their enormous seeds are enveloped in exceedingly hard and woody pericarps. The structure of the seeds is in the dry state almost woody, including both embryo and its thick envelop which we assume to represent endosperm and which forms one solid whole with the embryo. In *Gynotroches* and *Carallia* the embryo is almost filliform extending from one end of the seed to the other. Germination experiments are urgently needed for getting a clear picture of both structure and mode of germination.

Ecology (mangrove species). By their wide distribution, their gregarious coastal occurrence and practical application, and their morphological and biological peculiarities, the four littoral genera deserve a more ample treatment in this Flora than is usual in the general paragraphs preceding the taxonomic revision. These four genera, *Rhizophora*, *Bruguiera*, *Ceriops*, and *Kandelia*, form a considerable part of the tropical and semi-tropical forest fringe along the shores called at variance mangrove, bakau (M) or tidal forest (vloedbos, Ny).

(1) Precise data on African mangroves were kindly supplied by Mr. J. R. Laundon.

(2) The main works on the Malaysian mangrove are:

Mangroves form a rather uniform, evergreen fringe of forest which is most profusely developed on low muddy shores, in estuaries and lagoons and is less abundant along sandy or rocky beaches and on old coral-reefs covered with a thin sheet of sand or mud. In the latter localities the height of the stands is low, trees are dwarfed and crooked, and the fringe is often narrow and sparse. This is in part due to the poor soil of these habitats and in part to the fact that different species are concerned. Whereas for example Rh. apiculata Bl. and Rh. mucronata Lamk may attain a height of 35-40 m in favourable localities in lagoons and estuaries, with straight stems (fig. 1, 7), Rh. stylosa Griff., which is bound to the sandy beach, is always a small insignificant tree (fig. 5, 13).

It should be added here at once, in order to avoid confusion with field-workers, that in very many places mangroves are poor at present due to excessive cutting by man (fig. 3). After excessive cutting they may also change their composition and clear fellings of Rhizophora are sometimes replaced by regrowth of Avicennia, commercially an inferior timber. In many localities, notably near the larger towns, the mangroves have almost disappeared or/and degraded into low, seral thickets of Acanthus, Clerodendron, and Acrostichum. In other cases the destruction has even gone further and mangroves have been replaced by fish-ponds or stands of naturalized exotics, as for example in many places along Manila Bay by Prosopis, a spiny leguminous tree doubtless imported from Mexico.

In the field it should therefore always been verified whether a poor mangrove is due to natural factors or in minor or major degree to previous anthropogenous destruction.

The number of trees and shrubs participating in the mangrove forest is a very limited one and reversely the mangrove plants are generally bound to this habitat and are not found inland. Backer (Krakatau 1929, 174) and I (Tijd. K.N.A.G. 52, 1935, 381) have given a list of the Malaysian mangrove species, the total being approximately 60.

Seen from a distance the mangrove makes the impression of a dark-green more or less monotonous type of forest. On entering it on foot with ebb its eerie aspect appears at once from the oppressing heat, the damp atmosphere, the bare, stinking mud, covered with stilt-rooted trees (fig. 1, 2, 7), and several kinds of other root formations (knee-like roots (fig. 16, 22), knobs, snake-like roots, erect peg- or torpedo-shaped pneumatophores), the mud teeming with crabs, fishes, shells, worms and their holes, mud-heaps and shallow pools, the air with plenty mosquitoes, the silence only interrupted now and then by the sudden rush of monkeys through the gloomy foliage, the thud of a fruit falling in the mud, or the forlorn cry of a passing seabird. For a tourist the place is singularly uninviting, but for the biologist it is a most fascinating biotope and the secrets of its life and life conditions are certainly far from being exhausted. Entering the mangrove on board a small prahu during high tide (fig. 4), gliding through the silent waters of the creeks, bordered now by the flooded forest which is nearly submerged up to the flatish underside of the tree crowns, the aspect is less fascinating and appears more monotonous, as the foliage of the trees is much alike even of representatives of very different families, all of them having dark-green, elliptic to obovate, medium-sized blades of the laurel type but rather coriaceous and slightly fleshy. Flowers are not particularly striking, and those which are, as e.g. of Sonneratia and Dolichandrone, are nocturnal.

On closer observation, however, it appears that each mangrove species has its own niche in accordance with its own claims to habitat and life cycle. Hence, mangroves differ in composition from place to place.

As in these low coastal regions and deltas there is always an intricate mosaic surface relief with deeper and more shallow places, higher grounds are interspersed with creeks, and soil types vary from place to place from more sandy and firm to muddy and less firm or deep soft mud, the particular niches for the species are also available in a mosaic-like pattern. Moreover, rapid changes may occur in these coastal areas where creeks may be silted up, lagoons may be shut off from the open sea by bars, and deposits of silt may be replaced or covered by those of sand.


Mead, J. P.: The mangrove forests of the Westcoast of the Federated Malay States. 1912.


1 In the following publications identification keys are given to the species of the mangrove formation, either based on vegetative or floral characters or on both. Unfortunately none is complete for the whole of Malaysia:

Becking, J. H. L. G. Den Berger & H. W. Meindersma (Tectona 15, 1922, 569-573, trees only).


The main factors responsible for the ecological preference of the mangrove species are the following three which may occur combined in a limited number of combinations:

1. **Soil type**, firm or soft, sandy or clayey in various proportions.
2. **Salinity** and its variation both daily and to yearly average, roughly corresponding to the frequency, depth, and duration of being flooded.
3. **Resistance to currents and surf of the mangrove species**.

From the side of the species conditions involved are the **conditions of germination and upgrowth of seedlings** and various degree of resistance (ecological amplitude) to these single factors, some being more restricted (stenecous), others allowing for a wider range (euryecous).

Preference for soil types is markedly shown in the genus *Rhizophora*, *Rh. mucronata* being typical in general for deep soft mud, *Rh. apiculata* ('conjugata') being rather intermediate or indifferent, and *Rh. stylosa* being bound to sandy beaches and coral reefs (eventually covered by a thin sheet of mud or sand). Fig. 5, 13. **BUNNING** (Flora 137, 1944, 341-342) rightly concluded that the major factor for the zonation of the mangrove is caused by the soil types (their mineralogical and physical condition), but not primarily by salinity.

Preference for salinity or inundation is illustrated by the fact that if the free connection with the sea (hence the tides) of estuaries or lagoons is suddenly shut off by a bar and the salinity decreases through water from the inland, *Rhizophora* forest may suddenly die off and its regeneration prohibited to be replaced by a less saline species typical for the back-mangrove, e.g. by *Lumnitzera* (LUYTJES i.e., p. 580). **Watson** observed a case of suffocation of *Bruguiera cylindrica* on stiff clays in Malaya and its dying off over a considerable surface, see p. 467.

Along coast before a hinterland which is subject to a seasonal climate, coastal waters receive during the rainy season a large amount of freshwater diminishing salinity in the littoral zone considerably in the vicinity of the mouths of large rivers.
Possibly the salinity which is naturally closely bound to the rhythm of inundation is not the primary factor as it is interwoven with the amount of oxygen brought in by freshly oxygenated surface water of the tides which, as just shown above, is necessary for the root system prohibiting suffocation.

Preference to water current velocity can easily be observed along creeks with the daily recurrence of the rush of the tides. They are often fringed with *Nypa*, the massive and dense root-system of which is better fitted to resist erosive forces of swift running water than that of most other mangroves; from this it derives its advantage in these places, from which it must not be rashly inferred that *Nypa* is bound to such localities, which is by no means the case. The phenomenon may also easily be observed in the bends of the creeks where water velocity is higher in the outward bend than along the inner bend, and where consequently one species may be gregarious along the inner bends and another along the outer bends. Current and soil type go here naturally hand in hand, as silt deposits will be more coarse-grained (sandy) along the outer bend.

Along the tropical shores the three factors mentioned, soil type, salinity & inundation, and resistance against currents are running roughly parallel with the main shore and those of the islands, and are responsible for the ecological preference, manifesting itself in a girdling or zonation of the mangrove species. *Watson* gave an instructive map of how such a zonation may be observed in a tidal estuary (l.c. p. 128, map).

The circumstances concerned with tides are naturally different in different localities: maxima and minima of the tides, their average values, turbulence of waters by wind and currents, soils, and other physical fore-shore conditions.

Schemes trying to identify conditions for the species which are responsible for the zonation are therefore apt to be of local value.

In Malaya *Watson* (l.c. p. 129 seq.) attempted to avoid to form inundation classes based on the actual number of times or even days that the ground is flooded in each month, and adopted a classification based rather on the nature of the tide that inundates the area. For Port Swettenham he distinguished the following five classes:

<table>
<thead>
<tr>
<th>Class</th>
<th>Flooded:</th>
<th>Height above Admiralty Datum</th>
<th>Days flooded p/month</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>All high tides</td>
<td>8'</td>
<td>56-62</td>
</tr>
<tr>
<td>2</td>
<td>Medium high tides</td>
<td>8-11'</td>
<td>45-59</td>
</tr>
<tr>
<td>3</td>
<td>Normal spring tides</td>
<td>11-13'</td>
<td>20-45</td>
</tr>
<tr>
<td>4</td>
<td>Spring high tides</td>
<td>13-15'</td>
<td>2-20</td>
</tr>
<tr>
<td>5</td>
<td>Abnormal or equinoctial tides</td>
<td>15-</td>
<td>0-2</td>
</tr>
</tbody>
</table>

He correlated the species typical for the different tidal classes with the following (here abbreviated) comment:

Class 1: *Inundated by all high tides.*—It is unlikely that any species can survive complete daily inundation except, perhaps, *Rhizophora mucronata* on the banks of streams, and then only if its head remains above water. On the sea this class is sterile.

Class 2: *Inundated by medium high tides.*—Here belong the *Avicennias* and *Sonneratias*. Bordering the river *Rh. mucronata* predominates.

Class 3: *Inundated by normal high tides.*—Includes the greater part of the mangrove area and the majority of the species will thrive under these conditions, but the *Rhizophoras* predominate. *Rh. mucronata* being found near the streams and, on firm soils, often associated with *Ceriops tagal*. *Rh. apiculata* reaches its optimum development and forms pure stands. *Bruguiera parviflora* grows well, often in mixture with *Rhizophora*.

Class 4: *Inundated by spring tides.*—*Rhizophoras* are replaced by *Bruguieras*. On particularly stiff soil *B. cylindrica* forms dense pure stands. On the better drained soils, particularly near the rivers, *B. parviflora* is common, with occasional *B. sexangula*, the latter rarely gregarious. Prawn heaps result in better aeration and the bringing to the surface of shell remains and sand.

Class 5: *Occasionally inundated by exceptional or equinoctial tides.*—*Bruguiera gymnorrhiza* is definitely established here, often with a dense growth of the mangrove fern. *Rh. apiculata* is sometimes present as an old tree. On the land side bordered by pure growth of *Onosperma filamentosa*.

The subject has in Java specially been studied by DE HAAN l.c. in Segara Anak near Tijlatjap (S. Java). Salinity is naturally varying both daily and with the seasons. In the dry season it is higher than in the wet season; and during the daytime it is highest at ebb when it increases in proportion to evaporation to decrease again with flood. Different species are different in their tolerance against these rather sudden changes in salinity; samples examined in Dec. 1928 (wet season) at high tide gave for *Rh. mucronata*, *Rh. apiculata*, *Bruguiera gymnorrhiza*, and *B. parviflora* c. 10-30/o NaCl, for *Xylocarpus* and *Nypa* 1-30/o, and for *Bruguiera eriopetala* (= *B. sexangula*) 1-10/o. It appears that *Xylocarpus* and *Nypa* are rather indifferent to salt percentage.
As to inundation frequency de Haan *l.c.* distinguished 6 classes, namely: *A.* salinity 10–30%/oo (1) Soils flooded 1–2 times per day, at least 20 days per month total, (2) *Ditto* 10–19 days per month, (3) *Ditto* 9 days per month or less, (4) Only a few times each year;—*B.* salinity 0–10%/oo (5) Soils slightly influenced by the tides, (6) Soils only subject to seasonal water levels in the wet period. Species tolerance to inundation by sea-water decreases hence from class 1 to class 6, that is from the outer mangrove to the inner.

And the species concerned are in this sequence: outer zone: either *Avicennia* or *Sonneratia* on soft-muddy young silts or *Rhizophora* on rather firmer silts, middle zone: *Bruguiera gymnorrhiza*, third zone: *Xylocarpus, Heritiera*, inner zone: *Bruguiera caryophylloides* (= *B. cylindrica*), *Scyphiphora, Lumnitzera*.

The 5th and 6th class are rather gradual transitions to the ± freshwater swamp forest at the back of the inner mangrove proper, with *Cerbera* and *Oncosperma*. Of course the soil increases in firmness going inland.

Depending on the physiographical structure of the coast the mangrove will differ from place to place and it will be much broader in one place than in another. Along straight coastlines and absence of streams the mangrove fringe is mostly rather narrow, 25–50 m; where there are streams and deltas bringing abundant clay and sand it may be much wider and in lagoons it may attain many km in depth, depending on the gradient of the sloping land.

The zonation depends on the circumstances: very often either *Sonneratia* or *Avicennia* are the pioneers, but in places as inside estuaries which are protected from turbulent water and surf *Rhizophora* belongs to the first colonists. Fig. 1, 2, and 7.

On reefs and rocky shores seeds and seedlings are deposited in crevices and between boulders and grow where they can attain foothold and are sufficiently sheltered against heavy surf. This biotope is therefore very heterogenous and shows no or less distinct zonation. This is the situation prevailing in many Pacific islands.

With large estuaries and low gradient where rivers are sluggish, the influence of the tides goes far up river and specially the inner mangrove species are able to disperse and grow upstream fringing the banks of the creeks and river itself to considerable distances inland, gradually thinning out in quantity and in number of species, sorted out according to capacity to stand freshwater conditions. In S. Sumatra for example mangroves are found upstream the Musi as far as Palembang. Mr Brass records to have found mangrove vegetation 85 miles upstream the Kikori River in Papua in a straight line! In the Fly River he found mangrove from the coast as far as Ellengowan Isl. 320 km upstream!, viz *Bruguiera* and *Sonneratia*. The tidal portion of the Hooghly River near Calcutta is also about 300 km long.

It has not been exactly examined whether the roots of these upstream mangrove fringes are growing under pure freshwater conditions all the year round. And this would be interesting since it has been shown by Hardenberg (Natuurwet. Tijd. Ned. Ind. 104, 1948, 341, fig. 2) that these large, sluggish, tropical rivers contain far upstream a bottom layer of salt or brackish water. This is caused by a natural bar of sand and mud, convex towards the open sea, before the river mouth; this bar is gradually sloping down seaward and steep towards the river mouth. With each high tide sea-water is driven behind it and extends,
through its higher gravity, below the upper sheet of seaward bound freshwater. It is most remarkable that these sheets of different salinity do not get mixed immediately but are separated by rather sharp 'spring horizons'. It has been found that in some Bornean rivers the brackish lower sheet may extend upstream over a considerable distance. The brackish sheet will follow the lowest course of the river bottom, i.e. that of the main current, coming closest to the river banks along the outer bends. Additional field observations must show whether indeed the upstream mangrove is found specially along these bends and whether their roots are in contact with brackish bottom water.

In passing it may be remarked here that mangrove plants are decidedly not absolutely bound to salt or brackish water; *Acanthus ilicifolius* and *Acrostichum aureum* are occasionally found inland in pure freshwater (analyzed!) (cf. VAN STEENIS, Arch. Hydrobiol. Suppl. 11, 1932, 262–263; Trop. Natuur 26, 1937, 206). And it has been reported and is still observable in various temperate greenhouses that man-

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Fig. 4. *Rhizophora* forest from the seaside at high tide, some seedlings in front. Otimmer, Tenimber Isl. (BUWALDA).

groves are cultivated under freshwater conditions, as for example shown in the Hamburg Botanic Gardens by HANS WINKLER (Ber. Deut. Bot. Ges. 49, 1931, 87), n'en déplaise the negative results with *Rhizophora* obtained by BENECKE and ARNOLD in Münster i/W who maintain that *Rhizophora* is an obligatory halophyte (Planta 14, 1931, 471–481).

Already a century ago TEYSMANN planted and maintained many mangrove species with success in a freshwater swamp and along the ponds in the Bogor Botanic Gardens at 250 m above sea-level and at c. 70 km distance from the sea (cf. Nat. Tijd. Ned. Ind. 14, 1857, 368), anticipating VON FABER's statement that the mangroves are facultative halophytes. *Sonneratia caseolaris*, *Bruguiera gymnorrhiza*, *B. sexangula*, and others are still cultivated in Kebun Raya Indonesia, Bogor, where they flower and fruit freely and even regenerate. Fig. 23.

In mapping mangroves it appears sufficiently clear that they avoid coastal areas with strong wave action and those which are subject to strong tidal currents. This is natural as frequently agitated waters prohibit generally a stable accumulation of mud or sand, hence a stable soil for the seedlings to grow up and *ditto* for the mature trees to maintain themselves. In other words, mangroves prefer shore conditions

(1) Accordingly HARDENBERG points to the well-known fact that marine fishes are found in abundance far upstream in these rivers.
which are favourable for accretion (accumulation and extension of soil and land). Their rather superficial root system does not allow otherwise and they follow rather than precede soil accumulation. This can be easily read from the mangrove map of Malaysia drawn by Foxworthy (Ann. Bot. Gard. Btsg Suppl. 3 1910, 319-344).

Heavy surf through wave action and wind cause a great difference between the shore vegetation of the ocean-facing S. and SW. sides of Java and Sumatra and the Java–South-China Sea shores on the N. and NE. sides of the same islands. On open ocean-faced sides mangrove is very scarce and found only in closed estuaries or on leeward sides of islands.

Recently Hosokawa demonstrated this also with a mapping of mangrove in Micronesia where it is specially developed on the leeward side of the islands (Mem. Fac. Sc. Kyushu Un. E2, 1957, 106, f. 1-2).

Watson (I.c. p. 5) observed the same in Malaya. He says: —"There is a distinct difference between the west and east coasts of Malaya, silting conditions being more favourable along the west coast. On the more exposed east coast wave action is more severe, particularly during the north-east monsoon, so that any fresh water brought down by the rivers is speedily dispersed. Mangrove forms are, therefore, unable to establish themselves along the beach and are confined to the river mouths, whilst the sandy beaches themselves are flanked by a narrow belt of Casuarina equisetifolia which extends practically unbroken from Singapore northwards to far beyond the limits of Malayan territory."

"Where the flow of the river is sluggish the tendency is for banks of sand to be deposited at the mouth through the combined action of the currents and the north-east monsoon, the channel being forced thereby further and further south. The newly formed natural breakwater is speedily covered on its sea-ward edge with a dense growth of Casuarina, and subsequently on its protected side by mangrove forms brought down by the river. The bank continues to advance in a southerly direction, until exceptional circumstances breach it and allow the water to escape by a new mouth. The old channel then rapidly silts up and soon becomes stocked with mangrove species which persist until a new bank is formed and again breached. The new channel is then in its turn converted into a mangrove swamp and the old one is invaded by inland forms." "Nearly all of the east coast rivers show this tendency. It is most marked at Rumpin, Merchong, and Bebar, where successive folds in the ground running parallel to the coast and bearing a few straggling Casuarina on the ridges and decadent mangrove in the hollows, provide unmistakable evidence of former banks and swamps. The last mentioned river demonstrates this process particularly clearly, the abnormal floods at the beginning of 1927 having broken through the Casuarina bank about 5 miles above the mouth of the previous channel, which is now beginning to silt up and be invaded by mangrove."

"On the west coast the mangrove is almost continuous from Kedah to Singapore. It varies in width from a few chains to a maximum of c. 19 km at the mouth of the Larut River in the Matang District of Perak; but the mangroves follow the rivers much further inland, extending along the banks of the Perak River up to Telok Anson, at c. 50 km from the sea."

"Changes of current and unusually heavy seas may sweep away the mud banks before the forest is fully formed, or even the mature forest may be eroded."

Watson reported (I.c. p. 157): —"that disastrous floods on the east coast of the Malay Peninsula in the beginning of 1927 did considerable damage to the mangrove growing in the rivers, much of which was washed away or killed by excessive deposits of sand or silt. Large numbers of trees died as a result of prolonged inundation by practically fresh water, specially of Brugula gymnothiza. It is assumed to be a simple case of drowning; Nypa scarcely suffered from either immersion or silt." Foxworthy recorded from Manila Bay also that seedlings of Rhizophora are occasionally killed by excess of fresh water.

Land reclamation capacity has been attributed to the still-roots and pneumatophores and other root formations projecting above the soil, attributing to them not only the faculty of calming waters and favouring thus precipitation of mud and holding back (accumulating) debris from the retreating flood water, but also attributing to them to act in this manner on any coast line.

This idea has been defended by H. H. M. Bowman (Proc. Am. Phil. Soc. 66, 1917, 667-670) who claims to have projected dikes, jetties, etc. in Florida and Venezuela by planting mangroves on the fore-shore as ballast retainers. Recently J. H. Davis (Carnegie Inst. Wash. Publ. 517, 1940, 303-412) stated "that it may be possible to use mangrove, by means of plantings, to extend the coast and form islands."

Already a century ago Junguhhn (Java I, 1853, 255) showed that the mangrove follows the silting up of a coastal area rather than precedes and initiates the accumulation of mud or other soil, and that it establishes itself merely on accretant coasts.

Bisschop Grevelink (Pl. Ned.-Ind. 1883, p. 166) pointed out that cause and condition should not be confounded and that mangrove settles only in places outside the heavy surf and current in the quiet bays, estuaries, lagoons; the same opinion is held by Backer (Schoolif. 1911, cliv, p. 478), F. C. Van Heurn (Studien, 1923, p. 65-71), Mead (I.C. p. 1), Watson (I.C. p. 1, 5), Brown & Fischer (I.C. p. 17), Becking c.s. (I.c.) and has been explained by myself (Natuurwet. Tijd. N.I. 101, 1941, p. 82-85). Watson observed: —"that as silt deposits remain bare until they have attained a definite condition of elevation and consistency, it is scarcely correct to regard the mangrove as the causative agent in the silting process. The large expanse of unclothed mud of shoals and banks exposed at low water suggests that it is necessary
for the banks to remain uncovered for several days together before any form of land vegetation can establish itself. It is considered that the limit of tree growth is to be found round about the neap highwater mark, above which the ground remains unsubmerged for at least two days in every month. In rivers and sheltered situations the Rhizophoras may occupy flats that are covered by even the lowest neap tides, but here the superior length of the radicle enables them even the seedlings to keep their heads above water.)

This observation fits also with the practical experience of engineers who, in the thirties, tried to prevent the silting up of the Deli River channel in the harbour of Belawan (Deli) by building a dam (dike) from dredged mud. This was regularly damaged and washed away by the heavy surf and current and had to be paved ('metalised'). For further protection the foreshore of the dam was planted on both sides with a fringe of mangrove seedlings but this succeeded only on the side of the silted channel. It appeared impossible to force an accumulation of silt by mere planting of mangroves.

It is of course true that in many places the mangrove has been devastated by man’s cutting of fire-wood and that in those places replanting of mangrove will generally have success.

It is also true that the underwater foreshore conditions may change and may turn a formerly regressing part of the shore into an accrescent one enabling mangrove to settle. The reverse may also happen. In delta areas the underwater surface relief of shoals and gullies may vary and change from place to place on the same coast and may vary in the course of time in one place. It is comparable to the situation on the sand beach where similar conditions, accretion or regression, will be responsible for the origin of dunes: here also the wealth of the pescaprae beach flora is dependent on the supply of sand deposits and not reversely the amount of accumulated sand to the presence of sand-catching beach plants.

It should be admitted that where silt or sand are accumulating by the grace of suitable foreshore conditions plants may accelerate the process by adding mechanically towards a favourable upsetting through quieting waters and acting as a barrier during ebbing time; this is practiced in the N. of the Netherlands by building palissades on accrescent muddy coasts. The similar function of the mangrove root formations is, obviously, a secondary one.

Along certain mud shores, notably the west coast of Malaya and the east coast of N. Sumatra there occurs a narrow strip of sand beach on the mud where the surf strikes the coast. This fan of sand is sometimes slowly rolled landwards while the mangrove mud is exposed on the seaward side: in fact here we have simply a narrow belt of sand piled up on top of the mangrove mud, the mud being never more than a few feet below the surface of the sand even at the top of the beach. By this slow retreat of the sand fan mangroves are buried by sand. I found this remarkable situation near Pantatjermin, E of Medan (Deli), and it has also been reported by Chapman (1940, p. 323) from Jamaica. From the air the foreshore of such a coast with a sand beach might be interpreted as sandy, though the sands represent only a very narrow strip of sand veneer. This misinterpretation, I am told by Mr Corner, has proved to be disastrous in landing attempts of tanks by Allied Forces on the west coast of Malaya at the end of the last world war, the tanks finding a soft mud instead of a firm, sandy bottom.

Mangrove and climate.—It has been considered occasionally (Schimper l.c. p. 87–88) that mangrove, being little or not developed in arid or seasonal areas, would require ombrophilous conditions for its full development. The largest development of mangroves is indeed found in the everwet parts of Malaya.

Besides, as has been mentioned on p. 431 mangrove is absent before the arid west coasts of the S. hemisphere tropics of America and Africa (and probably Australia).

The correlation between mangrove growth and climate is still often interpreted as a direct one, but this rash conclusion is essentially wrong. The arid climate is not the cause of the absence of mangrove but merely the condition.

This follows partly from the observation that not in all ombrophilous tropics mangroves are found; they are absent from steep shores or those with turbulent coastal waters, etc.

For the explanation why they avoid arid shores we have to consider that the occurrence of mangrove is primarily controlled by accretion of silt or sand and this again is controlled by the winds, the tides, the currents before the coast, the foreshore underwater relief and its shoals, and in no mean degree by the amount of silt transported by the rivers to the shore where it is deposited by its gravity and through the coagulating power of the sea-water on soil particles. Inadequacy of any of these factors will prohibit or limit growth of mangrove. Coasts which offer suitable conditions but fall off steeply towards the deep sea can only bear a very narrow fringe. Coasts along shallow seas but without accretion of silt or big rivers bringing silt will possess a poor mangrove development or none.

The situation in the seasonal parts of Malaya, for instance the Lesser Sunda Islands, is a generally poor development of mangrove but not on account of the dry climate, but on account of the deficiency of the other conditions. In the first place this area is generally provided with steep coasts and a heavy surf. Besides, during the dry monsoon the coasts are subject to strong winds and consequently have agitated coastal water. Finally, in these islands large streams which transport a regular supply of silt to the coast are absent; most rivers are ‘flood-rivers’ filled only during the rainy season.

If under seasonal conditions there are, however, local sheltered bays and estuaries where silt is deposited in sufficient quantity, the mangrove may appear in luxuriant stands not falling short of those found under ombrogenous conditions, e.g. in the south of Central Java (Tjilatjap), the southeast of Java.
WATSON rightly remarked (I.c. p. 1) that the absence of mangroves along arid shores is due to the absence of rich silt carrying rivers in such places.

The conclusion is that Rhizophoraceae and other mangroves follow the coastal silt deposits independent of the dryness of the climate.

**Characteristics of mangrove.**—As has been alluded to above the characteristic appearance of the mangrove is in part due to the remarkable root formations which are obviously tolerant to withstand the peculiar conditions for nutrition, assimilation of water and oxygen in anaerobic mud, besides serving for anchorage on an unstable substratum. *Rhizophora* stems are provided with a cone of branched stilt- or prop-roots (fig. 12), and generally additional similar, also forked aerial roots stick out or hang down to reach eventually the soil (fig. 11); the stembase is obconical and a taproot is absent or feebly developed (fig. 7). *Sonneratia* and *Avicennia* possess a horizontal root system provided with erect, asparagus-, peg-, or torpedo-shaped 'pneumatophores' (fig. 23). *Bruguiera* and *Lumnitzera* show upward knee-like bends in the roots (fig. 16, 22), in Xylocarpus moluccensis the horizontal roots possess knobs producing thick-conical 'pneumatophores', in *X. granatum* these roots have an upper thickening which appears as a sharp ridge above the silt. *Ceriops*, however, does not very much show in the way of root formations save for large lenticels in the uncovered parts of the roots and stem base.

Another characteristic, unique in the plant world, is the frequent occurrence of vivipary in mangrove trees in which either the fruit is enlarged (*Aegiceras*) or the elongating hypocotyl pierces the apex of the fruit in the 4 genera of Rhizophoraceae: Fig. 6, 9, 17, 18, 24, and 26.

Further features differentiating the mangrove vegetation from the rain-forest is the paucity of species
and their gregarious occurrence which can easily be observed both in the field and from aerial photographs, the absence of palms (save the stemless *Nypa*), the almost absence of lianas, the general scarcity of epiphytes and parasites, the almost absence of undergrowth, and the absence of storeys with substage layers. These characteristics hold for the proper mangrove and are generally less well pronounced towards the inner transition to the coastal forest behind.

**Epiphytes and undergrowth.—**Though it should be admitted that mangroves have, in general, less epiphytes if compared with rain-forest, Schimper's assumption that they would be deficient in them is erroneous. Beccari already mentioned their occurrence in Sarawak (cf. Wanderings p. 83, amongst others of *Rhododendron brookeanum* Low), Rutten in E. Borneo (Tijd. K.N.A.G. 28, 1911), and Hun. Winkler in SE. Borneo (Bot. Jahrb. 50, 1914, Suppl. 190-191). Ridley described many epiphytic orchids from the mangrove in Malaya. I found some in the Anambas Isl. mangrove (Bull. Jard. Bot. Btg III, 12, p. 162) and Steup mentioned them from the Riouw mangroves (Trop. Nat. 30, 1941, 90). From Java they were mentioned by Beùmée (Exc. guides 4th Pac. Sc. Congr. 1928, C 3, p. 11-13) to occur in Segara Anak near Banjumas; Backer & Posthumus (Varenfl. Java 1939, 325) emphasized that the occurrence of epiphytic ferns in the mangrove is restricted to areas which are not subjected to a rather strong to strong dry annual period and lack, for that reason, near Djakarta, Pasuruan, etc. From East New Guinea and Melanesia mangrove epiphytes (mosses, pteridophytes, orchids, etc.) were recorded by Schlechter (1914) and from West New Guinea by Koch. Brown & Fischer L.C. p. 24 found epiphytes fairly common in Philippine mangroves. Hosokawa found a similar condition in Micronesia. I have tried to give a preliminary enumeration (Tijd. K.N.A.G. 52, 1935, 382).

There seems no doubt that the typical mangrove with epiphytes is bound to ombrogenous conditions. Within these the (older) inner mangrove is richer than the (younger) outer one. Epiphytes may grow very close above the waves and subject to salt spray with wind at high tide. Also ant-inhabited epiphytes occur in the mangrove (*Hydnophytum, Myrmecodia, Pachycentria, Polypodium sinuosum*).

Some epiphytic plants are even restricted to the mangrove, as for example *Humata parvula* (Wall.) Mett. on 'old mossy mangrove' in S. Malaya and Borneo, and orchids as *Dendrobium rhizophoret* J.J.S., *D. prostratum* Ridl., *D. calibotrys* Ridl., and *Bulbophyllum xylocarp* J.J.S., and a Melastomataceae *Plethiandra sessilifolia* Ridl.

The only parasites I know from the mangrove are *Viscum orientale* and *Amyema gravis*, both *Loranthaceae*. As far as known the latter species is confined to this formation. More lorantheaceous representatives will occur in the mangrove, as they also freely occur on trees of the *Barringtonia* formation; their exact number is difficult to ascertain from Danser's works on that family as he omitted to mention the host plants save in certain exceptional cases.

Among the lianas the only true ones of the outer mangrove are *Derris heptaphylla* and *D. heterophylla*; in the inner mangrove several representatives are found of the *Asclepiadaceae* (*Cynanchum carnosum, Finlaysonia maritima, Gymnanthera paludosa*, and *Sarcobatus bankii*).

Undergrowth may consist in local, open places of few grasses (*Xerochloa imberbis, Diplachne poly-stachya*) or sedges (*Fimbristylis ferruginea, Cyperus malaccensis*). A submerged water-plant of the pools and creeks is *Cryptocoryne ciliata*.

Low shrubs or tall herbs appearing in open places are *Acanthus spp.*, *Acrostichum aureum*, and *Clerodendron inermis*. These may gain ground in clearings and cuttings, specially invading the colossal mud heaps accumulated by mangrove crabfish and finally form dense thickets in which regeneration of the mangrove proves difficult.

According to measurements by Bunning (Flora 137, 1944, 342) inside well-developed mangrove the light intensity at the bottom is about 1-5% of the open.

**The mangrove as a primary vegetation type.—**The thesis is defended here that the mangrove cannot merely be subordinated as an edaphic (seral) subtype of the tropical rain-forest on the argument that the back-mangrove may sometimes contain an increasing number of coastal trees if one proceeds inland. There is only a narrow transition zone, in Sumatra characterized by a strip of a tall, spiny palm: *Onco-sperma horrida*.

It is certainly interesting that several mangroves (with the exception of *Rhizophora*) can successfully be planted and grown in freshwater mud in greenhouses. In Kebun Raya Indonesia at 250 m there is an artificial freshwater swamp where *Bruguiera gymnorrhiza*, *Sonneratia caseolaris*, &c. flower and fruit freely and produce natural regeneration (fig. 23). This might induce the viewpoint that their restricted occurrence in the littoral zone is merely a question of resistance against the extreme littoral environment combined with low competitive power as compared with the freshwater swamp forest trees immediately behind the coast. But this argument derived from cultivated plants holds for representatives of nearly all vegetation types for which the range of edaphic tolerance is always much wider than that exhibited under natural conditions.

Mangroves are certainly bound to specific edaphic conditions, but as I have tried to demonstrate (Proc. Int. Bot. Congr. Stockholm 1950, p. 638, 1954) all vegetation types are, in last instance, edaphic. Structurally the mangrove forest differs markedly from both the dryland rain-forest and from the freshwater swamp- and peat-forest in that it lacks substage *strata* and in that its subtypes, when fully
developed mostly consist of one or a few dominant species. In this the mangrove forest structure approaches that of some forest types of the temperate and cold zones.

The second important reason why the mangrove cannot be considered to represent an edaphic subtype of the rain-forest is because it is independent of the climate and is found under both everwet and seasonal conditions, though it should be admitted that under the latter the mangrove is generally poorer and more stunted, but as has been shown above for other than climatic reasons.

An additional argument, significant but not conclusive for assigning primary rank to the mangrove, is the high percentage of genera and species confined to it and provided with a unique set of structures, morphological and physiological, fitting to the environment.

By some authors it has been held that the mangrove is a pioneer forest only, preceding the stable rain-forest. This is inferred from the fact that certain coasts show a very rapid land increase (for human concepts of time) in which the mangrove fringe is continuously pushed seaward, sending out its pioneer specimens forward while the back-mangrove is simultaneously gradually replaced by the mixed coastal rain- or swamp-forest. This land increase may average a dozen or several dozen metres per year (E. Sumatra, N. Java, S. New Guinea), leaving the hinterland interspersed with old, + parallel strand dikes.

Elsewhere land is secularly sinking and the rain-forests are drowned and replaced by a landwards retreating mangrove; this process goes sometimes at such a rate that even the peat-forest, which bordered the mangrove on the land side, is gradually washed away by the sea.

Many are the vicissitudes of this shore vegetation and in Malaya it has been found that freshwater swamp forest has (probably often) replaced mangrove, as shown by subfossil mangrove timber and by marine diatoms in Telok Forest Reserve (Wyatt-Smith, Mal. For. 17, 1954, 25–26).

But there are also coasts which are, at present, stable and neither regressive nor accretive, and there the mangrove behaves not different from other climax types and comes up fully to the age class criterion which is the test for a climax: in the full grown stand all year classes of all species are present, with no further potential participants (Luytjes Lc. p. 580; Watson Lc.; Noakes, Mal. For. 18, 1955, 26).

It is true that many (specially outer) stands of mangroves are about even-aged and represent a pioneer stage of the mangrove itself, but that is no proof for accepting the mature mangrove forest as consisting of nomad species. These pioneer stands mostly consists of one species in an immature environment: there will always be an immature environment fringing the seaside with a border of pioneer stands.

It is due to the bare-soil habitat, the very restricted number of species, and their rapid growth, that the stabilization of a mature mangrove forest on a stable soil type is performed in a very much shorter period than for example a climax of the very much mixed rain-forest.

The mangrove forest formation is a type sui generis with its own stable type of regeneration.

Morphology. (1) Root system. As alluded to above the mangroves present a number of remarkable root structures worthy of special mention. A taproot is generally insignificant or absent. In Rhizophora the root system is mainly consisting of lateral adventitious prop-roots; they originate from the hypocotyl and later the stem in an upward sequence (fig. 9, 10, 11 and 12), sticking obliquely down or hanging down as rather thick, repeatedly di- or trichotomously branched aerial roots finally striking ground and rooting. The highest of these branched adventitious roots may originate on the lower branches of the crown and may attain more than 10 m in length! According to Goebel and Warmbier extreme heat and drought would be responsible for the drying of the tips of the stilt-roots. These would then in a subsequent growth period be replaced by secondary adventitious roots originating somewhat above the dead root tip. This process would be repeated, resulting in the sympodially branched stilt-roots. Docters van Leeuwen (Ber. Deutsch. Bot. Ges. 29, 1911, 476–478) has offered a much more reasonable, though very curious explanation of the drying of the root tips which he observed to be damaged by a boring beetle of the Scolytidae! Normal stilt-roots should remain unbranched. Fig. 11.

In Bruguiera the horizontal cable roots produce knee- or elbow-shaped, negative-geotropic, supra-terranean bends acting as ‘pneumatophores’. Ceriops does not have much in the way of special root structures, but may occasionally have stilt-roots at the stem base. Kandelia has merely a thickened stem base, but with pneumatophores and true buttresses. It is worthy of note that the inland Carallia brachiata sometimes produces stilt-roots (fig. 32) at the stem base under marshy conditions!

Seedlings and very young trees of Rhizophora have some coppicing power, but contrary to what some believe the aerial roots from the branches play no part in reproduction. Bruguiera spp. do not coppice. This capacity is, however, strongly developed in Combretocarpus (cf. p. 481).

The underground root system of all mangroves is flat, densely branched, and superficial, the horizontal main roots (cable roots) are anchored by vertically descending small lateral roots (anchor roots); besides they (or the pneumatophores respectively) produce an extensive net of very fine nutrition (‘absorption’) roots in the uppermost mud stratum. The structure differs from species to species in detail, but the scheme is apparently not essentially different from that worked out by Trol for Sonneratia (cf. vol. 4, p. 281, fig. 1). The cable and anchor roots give the tree mechanical fastening in the substratum, the fine nutritional roots serve for nutrition and assimilation of oxygen from the uppermost silt layer which is distinctly better aerated than the silt lower down. If the substratum is silted up, new nutritional roots are produced above the old ones, thus keeping pace with the accumulation of silt. The results obtained by Trol with Sonneratia in Malaysia (cf. vol. 4, p. 281–282, fig. 2) are in general corroborated by Chapman for Avi-
cennia in Jamaica (J. Linn. Soc. Lond. Bot. 52, 1944, p. 407–533) and there seems good reason to assume the general validity for various root formations of other mangroves.

(2) Foliage and stipules. The foliage of the mangroves is generally dark green and glossy, more or less coriaceous to fleshy, elliptic to ovate as common to the laurel type of rain-forest. They are said to have frequently a downward hanging position, specially in the daytime, which is assumed to be an ecological adjustment to avoid overheating. No critical experiments or observations are known to me to sustain this idea.

The leaves of both the mangrove and inland Rhizophoraceae show the occurrence of characteristic dark glandlike dots which appear to be corked epithem cells. The vernation of the leaves in the Malaysian Rhizophoraceae is either convolute (fig. 6j) in the genera Bruguiera and Rhizophora or involute (fig. 6i) in the genera Ceriops, Carallia, Gynotroches, and Pellacalyx. In Kandelia it could not be examined due to lack of adequate material.

The interpetiolar stipules of the mangrove Rhizophoraceae are large and caducous and are cigar-like clasping one another, each having one free margin (fig. 6k). It has sometimes been assumed that they serve for bud protection but this again has, as far as I know, not been verified by some simple experiments: it would be easy for people on the spot to cut away stipules in various stages of development to see whether the terminal bud will succeed without them.

A peculiar phenomenon is the occurrence of glandular emergences (colleters) in the axil of the stipules; they were first described by ALSTON in African Cassipourea, later by METCALF & CHALK in Carallia, but appear to occur in all Malaysian genera, both of the mangrove and inland. The resin exuded by them during the time the flush expands lends a certain varnish to the innovations which is specially conspicuous in Carallia brachiata.

(3) Branching. The mode of branching is often sympodial which adds to a flat undersurface of the crown; with low tide this flattened appearance is very distinct.

(4) Flowering of mangrove trees takes often place at an early stage (3–4 years) if sufficient light is available in seedling trees of all genera. This capacity is shared by the inland genera.

(5) Vivipary and embryology. Among mangrove plants, both of the Rhizophoraceae and belonging to taxonomically quite different families, there is a distinct tendency towards a viviparous development of the seed, which finds its extreme in the Rhizophoras. The endosperm plays only a short role and is soon obsolete. In the myrsinaceous Aegiceras corniculatum the embryo ruptures the testa and fills the pericarp which then starts to enlarge in proportion to the growth of the embryo; after the enlarged fruit is fallen the embryo pierces the pericarp. In the verbenaceous Avicennia there is a similar development, but the embryo may or may not pierce the pericarp while the fruit is still on the tree. In Bruguiera the apex of the

Fig. 6. a. Bruguiera parviflora (ROXB.) W. & A. seedling, the pericarp + calyx are pierced at both sides, \( \times \frac{1}{2} \), b. Br. sexangula (LOUR.) Poir., young seedling, \( \times \frac{1}{2} \), c. Rhizophora mangle L., ditto, \( \times \frac{1}{2} \), d. Rh. mucronata LAMK, fruit from which the seedling has fallen out, the basis of the cotyledonary body just protruding from the fruit calyx, \( \times \frac{1}{2} \), e. ditto, cotyledonary body removed, in the same position, \( \times \frac{1}{2} \), f. ditto, developing seed with widely opened micropyle, \( \times 2 \), g. ditto, older stage, \( \times 2 \), h. young germlet with the dumb-bell shaped cotyledonary body, \( \times 2 \).—Vernation of l. involute leaves, j. convolute leaves, k. clasping stipules (all in schematic cross section) (a–h after SCHIMPER).
hypocotyl pierces the fruit apex and the hypocotyl grows cigar-like out of it, to fall together while still attached. In *B. parviflora* the fruit base is frequently pierced by the growing plumule, the pericarp persisting as a cuff round the seedling (fig. 6a). In *Bruguiera* the cotyledons are only connate at the base but they serve by their glandular epidermal tissue for assimilating nutrients from the pericarp and feeding the hypocotyl. In *Rhizophora* vivipary has advanced so far that the hypocotyl may attain a considerable length and when ripe fall out of the fruit; its plumule is entwined in a single, club-shaped cotyledonary body (fig. 6d–e), formed by the fleshy connate cotyledons. This serves for sucking nutrients from the pericarp for the growth of the hypocotyl; it often protrudes from the fruit and is demarcated against the hypocotyl by an articulation. When mature this articulation is ruptured and the hypocotyl crowned by the plumule (fig. 6c) falls out of the fruit (*Rhizophora, Ceriops*) or the hypocotyl falls together with the fruit (*Bruguiera, Kandelia*). Fig. 6a, 17, 26c.


It is current usage to accept, teleologically, the striking vivipary of the mangroves as a ‘special adaptation’ to the environment, though what ‘profit’ is exactly meant by this trend of thought is not disclosed. It is termed ‘adaptation’ as it is exhibited in one environment by various not related plants. As a matter of fact vivipary with such intricate designs is not found in any other vegetation type. But on the other hand it appears that certainly not all mangroves possess it; none of these remarkable features occurs for example in *Sonneratia* which is, among the mangroves, taxonomically the closest ally of the *Rhizophoraceae* and ecologically a pioneer! Also none of these characters is found among the representatives of the *Barringtonia* formation which grows under rather similar conditions of the shore, though not under permanent inundation, and none is found among the trees of the swamp- and peat-forests which are often found immediately behind the mangrove. Consequently a generalization seems out of question and the term ‘adaptation’ seems rather an excuse for ignorance than explanatory.

**Seedling stage and dispersal.** As is usual among shore plants dispersal is mainly waterborne. Drift capacity over relative short distances is undeniable. The idea that the hypocotyls would fall from the seed tree (at ebb tide) torpedo-like penetrating into the mud and grow into seedlings in that same place is a popular opinion, but seems to be wrong and to happen only in exceptional cases. To my knowledge there have been made no pertinent observations in nature to the effect that one has actually seen fruits falling, sticking in the mud, remaining in a vertical position, and growing up. The ‘torpedo-act’ would therefore be possible in very soft exposed mud and then the chance that they will soon sag sideways is likely. On stiff clays and on sand (*Rhizophora stylosa*) it seems out of question that it may happen even occasionally. Furthermore all fruits falling when the mud is covered with a good sheet of water will not have the force to penetrate into the mud as the water will act as a distinct brake on their falling speed.

C. D. de la Rue & T. J. Muzik have made a plea to the contrary (Science 114, 1951, 169) and assume *Rhizophora* mainly ‘plant themselves’ but they counted the erect seedlings as being borne from ‘self-planting’ and those which are curved they assumed derived from fruits which took root while lying flat. It is quite possible, however, that the latter may get an erect position and remain straight by the uplifting power of the water in conjunction with their own drifting capacity. I agree entirely with the excellent observations and considerations by Egler (Carib. For. 9, 1948, no 4) and by B. D. Lawrence (Am. J. Bot. 36, 1949, 426–427) on the self-erecting habit of *Rh. mangle* which seems the usual way of seedling growing up. As a matter of fact hypocotyls are dispersed by floating horizontally in the water (though some have been observed floating in a vertical position). It is true that sometimes a seed tree is surrounded by seedlings as children under a mother (fig. 5), but we should not jump to the conclusion that they are *per se* its own children. The observation is that the hypocotyls drift freely in the water; the hypocotyl produces small roots near its tip and they get attached to the mud during ebb tide in a horizontal position. When the anchorage is obviously firm enough, the hypocotyl bends itself upwards and soon gains the erect position (fig. 6c). That this happens often nearly an already existing tree is due to the fact that this offers obviously a suitable ecology for growth of mangrove, and secondly in that mature hypocotyls are easily caught between the projecting root structures of existing trees with other drifting debris. Spring ebb is possibly the most suitable time for the hypocotyls to fasten their rootlets for anchorage.

For no obvious reason the main root of the seedling in *Rhizophora* and *Ceriops* is abortive and lateral roots take its function (fig. 9–10).

According to Guppy fruits or seedlings may drift for several months and retain their vitality. In Malaya, however, it is maintained (Res. Pamphl. For. Res. Inst. Mal. 15c, 1957, 7) that observations on natural regeneration in the mangrove indicate that recruitment of seedlings of *Rhizophora, Bruguiera*, and *Ceriops* species, in deep flooding blanks of the Perak mangrove, proceeds slowly with seed from nearby trees and not from seed which has been waterborne for any distance. Recruitment of *Sonneratia* and *Avicennia* species may occur with seed which has been waterborne for a considerable distance.

Champion C.S. have pointed out (Geogr. J. 76, 1940, 320) that a successful colonization of seedlings depends either upon a very shallow sea in those cases where there is only a small tidal rise, otherwise there must be a considerable tidal rise and fall so that they are exposed for some hours during the day, as unless the seedling portion is out of the water the seedling soon dies.
Accordingly the length of the hypocotyl must play a considerable role in the colonization and is obviously responsible for the fact that *Rhizophora mucronata*, the hypocotyls of which may attain 60 cm in length (according to Corner even 3 feet), are able to grow in the deepest water (or places subject to deepest fall and rise of the water level with the tides), and is henceforth the principal seaward pioneer.

The waterborne dispersal is certainly one of the factors responsible for the generally wide distribution of mangroves. Obviously the megatherm character of the *Rhizophoraceae* has prohibited species to migrate freely between oceans which are separated by N-S directed continents, as Indo-Pacific species do not occur in the Atlantic, *vice versa*, but those of the Caribbean occur also in West Africa. Schimper (I.c. p. 193) has already pointed to the agreement between the littoral flora of the Caribbean and West Africa and the marked difference between the West African and East African coastal floras, the latter being a depauperated Indo-Malaysian one. The situation is obviously radically different from that found in the distribution of the seagrasses (see p. 382).

The relation between the mangroves of the Caribbean and those of the Pacific coast of North America are less clear and can not be explained before a critical detail identification of Pacific *Rhizophorae* has been undertaken. If the tentative assumptions made under the genus *Rhizophora* (see p. 450) are right it would seem that at least two Caribbean *Rhizophorae* occur on the Pacific American coast and their distribution must have been effected before the closing of the isthmus of Panama.

From the rather restricted area of a few rhizophoraceous mangrove species we also may infer that there are limitations to either the long-distance dispersal capacity or the ecology. It is for example difficult to explain why *Kandelia candel* is so extremely rare in Malaysia, as the number of ecological niches offered by Malaysian coastal areas certainly includes the one suitable for *Kandelia*. *Bruguiera exaristata* and *B. hainesii* are other examples of geographically relatively restricted species.

Another argument for the relative difficulty in dispersal for the seaborne mangroves is the remarkable fact that no mangroves are known to occur native in the Hawaiian islands, although they can grow there in certain localities, as has been shown by extensive planting experiments initiated by the Hawaiian Sugar Planters' Association in 1922. This peculiarity is even more remarkable if it is remembered that of the *inland* genus *Crossostylis* representatives have been found eastwards in the Pacific in truly oceanic islands as far as southeast Polynesia, although their means of dispersal would appear far inferior to those of the mangroves!

**Physiology.** The extreme habitat of the mangrove vegetation has led to several assumptions, some of which have been mentioned in passing in the foregoing paragraphs. Schimper (Pfl. Geogr. 1898) classified the mangroves among the 'xerophytes', accepting a low rate of transpiration and growth. His (+ teleological) argument was that this must be so in order to avoid too high salt concentration in the tissues. He believed to have circumstantial evidence for this viewpoint in morphological 'adaptations' to xerophyli, *viz* fleshy or lepidote leaves, hairy leaves, isolateral leaves, thickened epidermis and cuticle, slime cells and thin-walled water tissue, sunken stomata, *etc.*. Holtermann (Einfl. Klimas, &c. 1907), and specially von Faber (Proc. 4th Pac. Sc. Congr. 1929, 3, 1930, 113–120) have shown, however, that mangroves are strong transpirators and besides show abundant guttation. Concentration of salt is avoided by exuding it and the water supply and water stream through the plant consists of salt water.

As has been shown by Mrs Reinders-Gouwentak in an excellent digest of later literature in this Flora (vol. 4, p. 513–515) on the relation between wood anatomy and water relations later authors are not in full agreement with von Faber's results and are of opinion that his evaporation figures are overestimated. But growth measurements by silviculturists have shown mangroves to be not particularly slow growers. And it can be maintained that their classification with xerophytes is definitely erroneous.

It would be most interesting to make a comparative study of the physiology of the mangrove *in situ* and that in the Botanic Gardens, Bogor, where the same species have grown up in fresh-water.

It seemed an appealing idea of Schimper to base a wholesale ecological classification of the plant kingdom on correlating the water supply of substratum and climate with the morphology of plants, but it appears more and more that this simple device has to be abandoned, both for the halophytes, mangroves, and desert plants themselves, of which show a high rate of transpiration.

In the foregoing paragraphs the other major physiological problem of the *Rhizophoraceae*, viz their respiration under anaerobic soil conditions has already been touched upon and reference has been made to the work of Troll and Chapham who I believe have found a reasonable explanation for the way how the root systems of Sonneratia and Avicennia are provided with sufficient oxygen, from which it follows that the respiratory function of the supraterranean 'breathing roots' has formerly been exaggerated. This pattern will, *mutatis mutandis*, probably hold in its basic design for other mangroves; there is here a need for further investigation.

**Galls.** Docters van Leeuwen (Zoocccidia Neth. Ind. 1926, 402, fig. 746–747) reported a leaf-gall caused by a gall-midge in *Anisophylla disticha* and a flower-gall caused by a gall-midge in *Carallia lucida* (= *C. brachia*). I have also seen those two kinds of galls in the above-mentioned species. Besides, I have found a fruit-gall in *Anisophylla beccariana* where the ovary is swollen into a fruit-like body.

**Flower biology.** Though the flowers are, for example in *Bruguiera*, *Kandelia*, and *Rhizophora*, not small, very little actual observation has been recorded and this remains an urgent desideratum.
Many representatives possess a distinct disk and their flowers will contain honey. Further there are in certain genera unisexual or polynamulous flowers which might require insect pollination.

GEHRMANN (Ber. Deut. Bot. Ges. 29, 1911, 308–318) and PORSCH (Jahrb. Wiss. Bot. 63, 1924, 611) assume occasional visits by birds in addition to anemophily in Bruguiera. The first author studied in the Botanic Gardens, Bogor, March 1911, the structure of the flowers of B. gymnorrhiza. He found the anthers pressed between the petal lobes with a tension in the snakelike curved filaments. This tension can be released by touching with a needle or hair the sensitive inner basis of the petal after which the anther will start forward and explodes into a cloud of powdery pollen. This can also be attained by shock. The cupular calyx basis is filled with honey. No flower visitors were observed.

DOCTORS VAN LEEUWEN (Ann. Jard. Bot. Btsg 37, 1927, 11) did not observe bird’s visits, though the red calyx and abundance of honey would suit them. But visits by Xylocoma (wood bees) and wind might also be capable of setting free the pollen. In the flowers of Rhizophora stylosa he observed once a small bee (I.c. p. 24).


The group of the tidal genera is readily separated from the 3 groups (see MARCO, METCALFE & CHALK) of inland genera by the heavy-barred scalariform perforations of the vessels, the scalariform intervacular pitting, the libriform fibers, the scanty (except in Kandelia) vascentric parenchyma, and the structure of the fine-celled rays (JANSSONIUS, MARCO, METCALFE & CHALK). Four of the 5 inland genera are rather readily separated from the Macarisiaceae (MARCO) but METCALFE & CHALK do not quite agree. Pellacalyx cannot be placed satisfactorily into any group of the family (MARCO, METCALFE & CHALK).—C.A.R.-G.

**Taxonomy.** The family was established by R. BROWN as order Rhizophoreae including Rhizophora L., Bruguiera Lamk., and Carallia Roxb. (in Flinders' Voy. II, 1814, App. iii, p. 549).

Endlicher separated two inland genera Cassiporeoa and Dryptopetalum (= Gymnotroches) from the mangrove genera and accommodated them in a subdivision Legnotidoeae (Gen. Pl. 1840, p. 1184), but he left Carallia in the Rhizophoreae sens. strict. He maintained this division in his Enchr. Bot. (1840) 634–635, where he added that the Legnotidoeae differed from the Rhizophoreae by albuminous seeds and superior ovary.

These two subdivisions were raised to family rank by BLUME (Mus. Bot. I, 1849, 126, 131), followed by MIQUEL (Fl. Ind. Bat. 1, 1, 1855, 581, 591), but Carallia was (rightly) transferred to the Legnotidoeae which then consisted merely of inland genera.

BENTHAM & HOOKER f. maintained the two groups Rhizophoreae and Legnotidoeae as tribes of one family but added a third tribe, Anisophylleae, including two inland genera Anisophyllum and Combretocarpus (Gen. Pl. 1, 1865, 687). This system was recently still followed by RIDLEY, who raised these three tribes each to family rank (Fl. Mal. Pen. 1, 1822, 692, 696, 700).

It was also followed by BAILLON, who, however, split the Legnotidoeae into two separate tribes ('series') (Hist. Pl. 6, 1876, 284–304).

Corner distinguished the same three groups as BENTHAM & HOOKER f., but was of opinion that the Anisophylleae deserved family rank against the Rhizophoreae proper, subdividing the latter into two subfamilies Rhizophoreae and Legnotidoeae (Ways. Trees 1940, 122, 520).

SCHIMPER had a quite different opinion as compared with preceding authors, in assuming that the remarkable structure of the fruit and mode of germination of the mangrove genera were mere adaptations to the tidal habitat, which would represent therefore artificial characters. He suggested a different system and rearranged the genera according to what he assumed to represent natural relationships; he kept the subfam. Anisophylloeae in the circumscription of BENTHAM & HOOKER f. and kept also one inland tribe Macarisiaceae in about the circumscription of BAILLON, but he assembled Carallia and Pellacalyx with Bruguiera in a subtribe and added Gymnotroches and Circusostylis to the Rhizophora-Ceriops-Kandelia affinity (in Engl. & Pr. Nat. Pfl. Fam. 3, 7, 1898, 49–50).

This mixing of inland and subtribes as advocated by SCHIMPER is not sustained by the wood anatomy and other anatomical characters, as pointed out by SOLEREDER (Syst. Anat. Diot. 1908, 384, Ergänz. Bd 1908, 137), MOLL & JANSSONIUS (Mikr. Holz. Jahv. 3, 1918, 323), and DEN BERGER (Hand. 4e N.I. Nat. Congr. 1926, 403–404, 1927). SCHIMPER’s clearly wrong classification provides again a good example of what danger is involved if a taxonomist introduces preoccupied theoretical ideas in a classification.

MARCO (Trop. Woods 44, 1935, 1–21) in a comprehensive study of the wood anatomy classified the family into 3 divisions, leaving Pellacalyx and Poga unclassified, as he could not refer them to any of these divisions. He considered the mangrove division, Rhizophoreae, to form wood-anatomically, a well-defined, homogeneous, natural division readily separable from other groups of this or any other family;
it might even deserve family rank. In his opinion BENTHAM & HOOKER’s Legnotideae are, wood-anatomically, heterogeneous and unnatural. Therefore he split it into two divisions, Gynotrocheae and Macariseae, adding the Anisophylleae (Anisophylyea & Combretocarpus) to the Gynotrocheae, as a separate section.

METCALFE & CHALK (Anat. Dic. 1, 1950, 610) confirmed in general MARCO’s scheme, but remarked that the material they examined provided less convincing evidence of the clear distinction between Gynotrocheae and Macariseae. They confirmed also that MARCO’s unclassified genera Poga and Pallacalx do not fit very well into any of their proposed groups though these genera have many characteristics in common, even in detail, with other members of the Rhizophoraceae.

DESF had a similar opinion (Mal. For. Rec. 152, 1954, 447-454) and assumed that Pallacalx shows wood-anatomically a distinct alliance with both Carallia and Gynotroches, all belonging together to the Legnotiidae sens. lat.

Affinities with other families. R. BROWN, L., BENTHAM (J. Proc. Linn. Soc. Bot. 3, 1859, 65), LINDLEY (Veg. Kingd. 1846, 726), BAILLON, L., and HUTCHINSON (Fam. Fl. Pl. 1, 1926, 185) have discussed the multiple affinity of this family. It shows relationships with Myrtaceae, Lythraceae, Cunoniaceae, Combretaceae, and Melastomataceae in one way or another.

ERICA (Pollen Morph. & Pl. Tax. 1952, 379) has examined pollen grains of 12 species from 10 genera of Rhizophoraceae. He stated that “grains ± similar to those in Rhizophoraceae occur for instance in certain lythraceous genera (cf. also Dialypetalanthaceae and Santalaceae). The grains in Combretaceae, Cunoniaceae, Lecythidaceae, Melastomataceae, Sonneratiaeae, etc. are ± different.” The pollen structure gives obviously no clear conclusion either for the subdivision of the family or for its affinity. Anisophylyea has no aberrant pollen type justifying a separate rank.

Resemblance with Rubiaceae. There is an astonishing outward, vegetative morphological resemblance between Rhizophoraceae and Rubiaceae, both families sharing in the majority of genera, decussate leaves, interpetiolar stipules provided with callieters, and an inferior ovary.

In Rhizophoraceae the caducous stipules have overlapping margins (except in Pallacalx where they are flat), each stipule having one free margin (fig. 6k). In Rubiaceae they are generally flat, often persistent, and not overlapping, though in Mastixiodendron the situation is exactly the same as in Rhizophoraceae (except that each stipule is inserted between the leaves and besides intra-axillary in one axill!). In Tironius spp. the situation varies with the spp. and may be overlapping as in the Rhizophoraceae, or one stipule may embrace entirely the other, or the stipules may be connate and are cuscullately caducous, or they may be valvate.

The families can of course easily be distinguished by the structure of the corolla (sympetalous in Rubiaceae and choripetalous in Rhizophoraceae) and the androecium (isomorous in Rubiaceae and twice or more the number of flower parts in Rhizophoraceae). Besides the petals of Rhizophoraceae have a distinct tendency to produce fringes or appendages and are generally erose, emarginate, or 2-lobed.

Uses. Nearly all Rhizophoraceae have a heavy, dense, and hard, often red timber, but none of them seems to be capable to withstand use in the open, except for the proper heart-wood of some mangroves which is said to be durable in the soil below the water level.

The timber of some inland genera seems to be of better quality for building purposes and cabinet work. Mangrove timber is frequently used for short time purposes, poles in fisheries, piles for mining, for tobacco drying sheds, etc.

Its main use is for fire-wood, fuel in locomotives, etc. and for making charcoal. Chinese coastal people in Malaya and Sumatra (e.g. on Rupat Isl. near Bengkalis and in Aru Bay) are using large, stone-built permanent kilns of which the filling and burning takes one month, one filling delivering nearly 8000 piculs charcoal. NOAKES described the charcoal industry in the Matang mangrove and recorded that the art of building good brick kilns was introduced by the Siamese (Mal. For. 13, 1950, 80-83).

The bark of nearly all species of mangrove species is used for tanning purpose (bakau: Rhizophora, Bruguiera; tēngar: Ceriops) and may contain up to more than 40% tanning substance in air-dry bark. The tannin is sometimes extracted and concentrated into cutch. In general the impression of HEYNE is (Nutt. Pl. 1927, 1162 seq.) that the quality of the tan is less good than that derived from Acacia bark, partly caused by the red colour of leather tanned with bakau bark. The bark is also used for tanning nets and fishing lines but is not judged of excellent quality. Large studies on the use of mangrove have been published by R. WIND (Med. Proefst. Boschwezen Ned. Ind. no 9, 1924) and T. A. BUCKLEY (Publ. Dep. For. Malaya no 7, 1929).

Tēngar bark is also used for the purpose of dyeing, phlobaphene colouring-matter being associated with the tan, and has been used in the batik industry; it is preferred for black colours to Melastoma. For more details and for minor uses (as food or medicinal purposes) see under the species.

The mangrove forests are of distinct value for the timber industry in the widest sense for various reasons: species are few and gregarious, the terrain is not fit for many other purposes (save in some cases for fish-ponds1, the coastal situation near large towns and harbours needing timber and fuel is favourable, and extraction and transport is relatively easy.

The total surfaces covered by mangrove are rather considerable; in Malaya (West Coast) estimated at

(1) In North Java these fish-ponds (‘tambaks’) cover c. 75.000 ha.
about 1400 sq. km, in Riouw-Indragiri at 1750 sq. km, in Papua the area from the Purari mouth to the Torama River is estimated to contain 800–1200 sq. km mangrove forest.

The stands are often heavy: a good mangrove forest may contain in certain cases, according to MERRITT (in Mindoro) 500–1000 trees per ha 10–30 cm thick and 6–14 m high. In Subuguay Bay (Mindanao) FOXWORTHY found in 1912 old stands to contain the enormous amount of 300–650 m²/ha (stacks), and also in Mindanao he found virgin mangrove forest to contain 149 trees per ha over 25 cm diam. with a cubic content of 130 m³/ha. According to WATSON (I.c. p. 167) the average yield of 250 m³/ha (stacks) is optimistic for future yield of productive areas; in Riouw it is according to JONKER (Tect. 26, 1933, 730) 100–200 m²; planted forest 40 years old would yield 400 m³.

The rotation period in Malaya was originally estimated at 20 years, later 40 years, but the latest and obviously final working plan by NOAKES is planned at 30 years.

Cutting and management of mangrove must be planned from place to place in accordance with available rejuvenation, the course of the creeks, occurrence of Acrostichum and Acanthus which may hamper upgrowth of seedlings or sometimes be favourable for nursing them. Care should be taken that a felling is not followed by a succession of the inferior Avicennia or Bruguiera parviflora. Sometimes it is advisable to leave seed trees ('standards'). The planting of mangroves can be performed both by using young seedlings or fruits (see Jong, Tect. 27, 1934, 290). Extraction of timber is sometimes done by rail but mostly by water transport. Drainage ditches or canals are sometimes necessary for improving stands or specific composition.

KEY TO THE GENERA

**Based on fertile material**

1. Plants of mangrove forests. Seeds germinating in the fruit while the latter is still attached to the tree; hypocotyl protruding from the fruit.
   2. Calyx always 4-lobed. Petals entire, without appendages. Anthers multi-locellate, finally dehiscing with a large ventral valve
      1. Rhizophora
   2. Calyx 5–16-lobed. Petals 2-lobed, multifid, or with apical appendages. Anthers 4-locular, dehiscing with lengthwise slits.
      3. Calyx 8–16-lobed, lobes subulate-lanceolate, pointed. Petals bilobed or emarginate
         3. Ceriops
      4. Calyx lobes linear-oblong, c. 15 mm long. Petals c. 1½ cm long. Stamens indefinite. Hypocotyl smooth
         4. Kandelia

1. Plants of inland habit. Seeds not germinating in the fruit when the latter is still attached to the tree.
   5. Leaves alternate, exstipulate. Styles free.
      5. Anisophylla
   6. Flowers bisexual, 3-merous. Fruit 3-winged. Leaves pinate-nerved
      6. Combretocarpus

5. Leaves decussate, stipulate. Styles simple.
   7. Free part of the calyx divided to the base, inside glabrous in the lower part. Disk annular or cup-shaped surrounding the base of the style. Stamens attached to the disk. Stipules imbricate and overlapping.
   8. Fruits globose to ellipsoid, indehiscent. Seeds not embedded in a thin pulp. Petals eroze, fimbriate, or fringed with filamentous appendages in the upper part. Stamens usually three or more times the number of petals.
      9. Branchlets solid. Flowers usually in peduncled rarely in sessile cymes, pedicelled or not, not articulate. Petals eroze or fimbriate. Persistent calyx lobes terminating the fruit. 7. Carallia
      9. Branchlets hollow. Flowers in fascicles; pedicels with distinct articulation. Petals fringed with filamentous appendages. Persistent calyx lobes at the base of the fruit
      8. Gynotroches
   9. Free part of the calyx forming a distinct tube and divided only at the upper part; lower part of the tube hairy inside. Disk none. Stamens attached to the mouth of the calyx tube. Stipules flat, not imbricate.
      9. Pellacalyx

**KEY TO THE GENERA**

*Mainly based on vegetative characters*

1. Leaves decussate. Stipules interpetiolar.
2. Stipules imbricate, one margin of each free. Free part of the calyx not forming a tube or forming an obscure one much shorter than the lobes.

(1) See footnote on p. 448.
4. Leaves acute or pointed at the apex, lower surface usually with scattered black dots.
5. Leaf tip mucronate by the extending midrib. Trees supported by conspicuous stilt roots. Calyx lobes always 4. Anthers multilocellate ........................................ 1. Rhizophora
7. Flowers bracteolate. Calyx lobes 8–16, lobes subulate-lanceolate, pointed. Petals fringed with white hairs on the margins sometimes also on the dorsal surface, each embracing 2 stamens. Mangrove trees ........................................................................ 2. Bruguiera
8. Flowers bracteolate. Calyx lobes 5 or 6–7, lobes deltoid, acute to acuminate. Petals glabrous, each embracing 1 stamen. Inland trees ........................................................................ 7. Carallia
9. Leaves obtuse or slightly notched at the apex, lower surface without black dots.

1. RHIZOPHORA


Trees. Stems supported by numerous, branched stilt-roots provided with a root cap; tap-root abortive. Leaves decussate, entire, coriaceous, petioled, usually black-dotted below, glabrous; midrib protruding at the tip into a (caducous) macro; nerves and veinlets obscure beneath, visible or distinct above. Stipules lanceolate, more or less red when fresh. Inflorescences peduncled, simple or di- to trichotomously branched cymes. Flowers bisexual, bracteolate. Calyx deeply 4-lobed, coriaceous, accrescent and reflexed in fruit, surrounded at the base by cup-shaped bracteoles. Petals 4, lanceolate, caducous, inserted at the base of the disk. Stamens 8–12, sessile or with very short filaments, inserted on the margin of the crenulate disk; anthers areolate, elongated, pointed, triangular in cross section, multilocellate, opening with a large ventral valve. Ovary semi-inferior, 2-celled; each cell with 2 ovules; style obscure to 6 mm long, stigma simple or obscurely 2-lobed. Fruits ovoid with a granular or roughened surface. Seeds 1, very rarely 2–3. Cotyledons connate into a fleshy body continuous with but set off from the hypocotyl, in old fruits protruding from the fruit; hypocotyl clavate, elongate, perforating the apex of the fruit and falling out of it.

Distr. About 6(–9) spp., widely distributed along tropical coasts, throughout Malaysia.

Ecol. In coastal swamps and along tidal streams; the most important and widest spread of the man-

(1) The genus Crossostylis Forst. (Haplopetalum A. Gray) has also been entered in the key though it is hitherto only recorded from Melanesia (Solomons, New Hebrides, New Caledonia, Fiji, and Samoa) as far east as the Marquesas in Polynesia. It might occur in East Malaysia.
Fig. 7. Forest of *Rhizophora apiculata* Bl., with falling tide, at Pangkalan Susu, Aru Bay, in the estuary of the Besitang River, NE. Sumatra, April 1937.
grove genera. Several botanists have said that the Rhizophoras occur to the exposed sea-face; this is not so, and they are generally found well behind the Avicennias, which are the pioneers extending into the sea. Only R. stylosa, occurring on sandy reefs and sandy beaches, faces the open sea. The Rhizophoras make in Malaya about 70-90% of the stock of the mangrove belt, filling the estuaries with a closed forest of straight cylindrical boles and compact ellipsoid crowns, raised commonly about 20 m from the ground; exceptional trees are sometimes over 30 m tall, with a clear bole of 25 m and a maximum diameter of 60 cm.

Noakes (Work. Plan Matang 1952, 59) recorded that "regeneration is always present beneath mature bakau, whether or not there has been a regeneration felling, but little of it survives the final felling."

Morph. According to Docters Van Leeuwen (Ber. Deut. Bot. Ges. 29, 1911, 476-478) the branching of the stilt-roots seems to be abnormal and caused by a Scolytid beetle damaging the root tips; above the hole one or more adventitious roots develop, the tips of which may be attacked in turn, and so forth, giving a sympodial branching.

Uses. The wood is used for timber, fire-wood, and the making of charcoal. The bark contains up to 30% tannin of its dry weight. Browne (1955, p. 297) cited some chemical analysis from bark which appears to contain high percentages of pentosans and furfurol, the ash consisting mostly of lime and CaCO3.

In Java Rhizophora is sometimes planted along littoral fishponds for protecting the dykes and banks by the extensive root system.

Taxon. Rhizophora is subdivided into two sections:


Specific distinction.—As to the species of Rhizophora it is very clear that in the E. African-Indo-Australian area there are three well distinguished species. In the Atlantic Ocean tropics there are also three (other) good species (Keay I.C.) which all occur also in the Caribbean as recently found by Dr Jonker.

Specific identification of the Rhizophoras of the Pacific Ocean as far West as Fiji is still unsatisfactory. Formerly it was held that there would be only R. mangle the area of which would then touch the areas of R. mucronata and R. stylosa in Fiji.

Salvoza (I.C. 225) recorded in the Pacific R. mangle only from Hawaii as introduced!

In the Pacific Ocean he distinguished R. brevistyloa Salv. (obviously closely allied to the Caribbean R. harrisoni (cf. Keay; non sens. Salvoza) from the Pacific coast of America.

The second species he distinguished in the Pacific basin, ranging from the Pacific coast of America westwards to Polynesia and Melanesia is R. samoensis Salv. put in the key close to R. mangle.

Finally he distinguished a third Pacific species R. lamarkii Montr. from New Caledonia which he puts very close to R. apiculata; this is known only from very few specimens.

I have some doubt about these distinctions; it may well appear that two of the Caribbean species (R. mangle and R. harrisoni) occur also on the Pacific coasts of America (in slightly different forms).

It falls beyond the scope of this revision to make a closer study of the situation in the Pacific which should preferably be performed in a combined study of living plants and adequate herbarium material.

Nomencl. In the Species Plantarum Linnaeus inserted 5 species among Rhizophora, 4 of which have later been transferred to Bruguiera and Kandelia, the only one remaining in Rhizophora being R. mangle. This is, consequently, the type species.

Under R. mangle there are several references, partly relating to Caribbean plants, partly to those from Malabar (Pee-Kandel Rheede). This mixture led also to the definition of Rhizophora as having 12 stamens (in R. mangle there are 8) obviously derived from the characters of R. apiculata (Rheede's plate).

Keay in his careful study of the W. African species (Kew Bull. 1953, 124) records 2 specimens from the Linnean Herbarium, probably entered posterior to 1755: one is possibly R. mangle, the other R. mucronata. Keay found good reason to typify R. mangle with the specimen in the Sloane herbarium (BM) which is the basis of a reference mentioned by Linnaeus.

**KEY TO THE SPECIES**

1. Inflorescences 2-flowered, shorter than the petiole, in the axils of leaf scars of last year's or season's growth. Bracteoles at the base of the flower completely connate, cup-shaped. Petals glabrous...

1. R. apiculata

1. Inflorescences 2-16-flowered, longer than the petiole, in the axils of the leaves on the twigs of current year's or season's growth. Bracteoles only connate at their base. Petals hairy.

2. Style obscure or very short up to 11/2 mm...

2. R. mucronata

2. Style filiform 4-6 mm...

3. R. stylosa
Fig. 8. *Rhizophora stylosa* GRIFF. a. Habit, × 2/3, b. lengthwise section of flower (petals and stamens removed), × 2, c–c". petal from outside, inside, and laterally, × 3, d. stamen, × 3, e. opened stamen, × 3, f. fruit, × 1/2.—*Rh. mucronata* LAMK. g. Lengthwise section of flower (petals and stamens removed), × 2, h–h". petals from outside, inside, and laterally, × 3, i. stamen, × 4, j. old stamen, × 4 (a–e JENSEN 239, b VAN STEENIS 971, f VAN STEENIS 17997, g–j CUADRA A 854).

Tree up to over 30 m tall and 50 cm diam.; bole 10-12 m. Branching primarily sympodial. Leaves elliptic-oblong to sub lanceolate, 7-18 by 3-8 cm, acute to apiculate, base cuneate; midrib ± tinged reddish beneath; petiole 1 1/2-2 cm, tinged reddish. Stipules 4-8 cm long. Inflorescences 2-flowered, peduncle thick, 1 1/2-1 1/2 cm. Flowers sessile, developing from the cupular involucro after the falling of the sustaining leaf; yellow; mature buds elliptic; 14 mm long; bracteoles at the base of the flower cup-shaped, fleshy, crenulate. Calyx lobes brown-yellow to reddish, ovate, concave, acute, 10-14 by 6-8 mm. Petals 8-11 by 1 1/2-2 mm, lanceolate, glabrous, membranous, covering the epipetalum only on the back. Stamens mostly 12, 4 epipetalous, and 4 pairs epispalous (sometimes 1 or 2 pairs with only 1 stamen), 6-7 1/2 mm long, sessile, acute. Superior part of the ovary 1 1/2-2 1/2 mm high, enclosed by the disk, bluntly conical; style 1 1/2-1 mm, 2-lobed. Fruit obovate, rather rough, 2-2 1/2 cm long, brown, the protruding part of the cotyledons red, 12-20 mm long. Hypocotyl cylindric-club-shaped, ± blunt, green with purple, up to 38 cm by 12 mm before falling.

Distr. Tropical SE. Asia (also Ceylon) throughout Malaysia to Micronesia (Marianas, Ponape, Guam, Yap) and New Britain.

![Fig. 9. Detached fruits with hypocotyl and seedlings of *Rhizophora mucronata* Lamk, E. Java, March 1914 (P. Arens).](image-url)

Ecol. Gregarious on deep soft mud of estuaries flooded by normal high tides and forming often 90% of the crop, avoiding bottoms which are harder and mixed with sand. Bark grey, with vertical fissures rather than horizontal, sometimes producing aerial roots from the branches. Crabs are sometimes, according to Watson, a menace to the upgrowth of the seedlings by devouring or removing the bark of the seedlings until they are...
completely girdled or even bitten right through. In the Malay Peninsula judged to be a slow grower attaining 30 cm diam. in 35 years.

Uses. This most important species has red-brown, heavy, and hard heart-wood. The trees are standing in places very densely and make a pure forest up creeks and in estuaries behind the protecting belt of Avicennia. The timber of both R. apiculata and R. mucronata is used indiscriminately. A great advantage of Rhizophora in the eyes of fire-wood dealers is that it can easily be split. Besides it has a high caloric value.

 Branched still-roots are used for anchors weightened by a stone.

Fig. 10. Root system of young saplings of Rhizophora mucronata Lamk., E. Java, March 1917 (P. ARENS).


Notes. Many authors have for this species adopted the specific name R. conjugata L. (Sp. Pl. 1, 443) which was based on Rhizophora, etc. LINNÉ, Fl. Zeyl. (1748) 81, no 181. The type of the latter is an unpublished plate by HERMANN (t. 279) which is preserved in the Br. Mus.

Part of the plate is a flowering branch with two opposite flowers; each of them is in the leaf axil of the terminal node, which had led LINNAEUS to describe them as 'flowers in twins' (calyces gemini). It is unmistakably a Bruguiera, but it can hardly be identified with certainty whether it is B. gymnorrhiza or B. sexangula. TRIMEN (J. Linn. Soc. Bot. 29, 1888, 142) had identified the plate as B. gymnorrhiza. However, the tips of petals are obtuse and glabrous and quite similar to those of B. sexangula.

At the lower part of the flowering branch, an infructescence is drawn consisting of two 'cylindric, subulate, very long and nodding fruits' (fructus cylindrici, subulati, longissimi, nutantes). These two 'fruits' as described by LINNAEUS are actually hypocotyls of Rhizophora. One of the 'fruits' is detached from the pedicel and had been placed upside down. To which species they belong is uncertain.

In the Linnean Herbarium there is further a specimen which according to SAVAGE (Cat. 1945, 84) bears LINNAEUS's handwriting. It is sterile and provided with the doubtful locality 'Chin'; it has not yet been identified. It is neither a Rhizophora nor a Bruguiera. It does not agree with LINNAEUS's description of R. conjugata and it may have been added to his Herbarium after 1753. It can not serve for more precise typification.

Merely on the basis of literature and without having studied the drawing and specimen at London MERRIL has proposed to use R. conjugata L. as the basionym for what is called here B. gymnorrhiza (L.) Lamk. (cf. Philip. J. Sc. 9, 1914, Bot. 118), with which BACKER (l.c. 7) and I disagree.

As R. conjugata L. is based on a drawing composed of flowers and fruits of two species of entirely different genera, the specific interpretation of which must remain distinctly uncertain by the inadequacy of the drawing, which has led in the past already to confusion and error, I reject it in agreement with Art. 65 and 66 of the 1956 Code.

VAN DER MEER Mohr (1929, l.c.) found near Medan three fruits each with two hypocotyls.
Flora Malesiana


Tree up to 27 m tall, rarely over 30 m by 70 cm diam. Branching not distinctly sympodial. Leaves broad-elliptic to oblong, (8'/2–)11–18–(23) cm by 5–10'/2–(13) cm, apex ± blunt to ± acute, base cuneate; midrib green beneath; petiole 2'/2–3'/2 cm, green. Stipules 5'/2–8'/2 cm long. Inflorescences 2–3 times forked, each arm with an apical involucre, 2–5–(12)–flowered; peduncles 2'/2–5 cm; pedicles 4–8 mm. Free parts of the bracteoles at the base of the flower distinctly 2-lobed, lobes deltoid, acute or obtuse. Buds emerging from the bracteolar involucrane long before the falling of the sustaining leaf. Mature buds widest near the base. Calyx 13–19 mm long, deeply lobed, lobes ovate, in anthesis pale yellow, c. 13–15 by 5–7 mm. Petals 9 mm long, densely hairy along the margins, partly clasping the epipetalous stamens with these margins, sparsely hairy on the back, hairs up to 3 mm. Stamens 8, sessile, 4 epipetalous, 4 epipetalous, anthers 6–8 mm long. Free part of the ovary high-conical, in anthesis already emerging far beyond the disk, 2'/2–3 mm high; style 1'/2–1'/2 mm, 2-lobed. Mature fruit elongate ovoid, with hardly contracted apex and often rugose base, dull brown-green, 5–7 by 2'/2–3'/2 cm; cotyledons 2–4 cm protruding; mature cotyledons green; hypo-cotyl cylindrical, strongly rugose, 36–64 by 1'4/4 cm.

Distr. On the coasts of Old World tropics: East Africa, Madagascar, Seychelles, Mauritius, SE. Asia, Riai, through Malaysia to N. Australia, Molasesia (Fiji, New Caledonia, New Hebrides), and Micronesia (Guam, Palau, Pomp, Ogiwal), introduced in Hawaii (Salvoza, l.c.).

Ecol. In similar localities as *R. apiculata* but more tolerant for sandy and firmer bottoms. Generally gregarious near and on the banks of tidal creeks and in estuaries, seldom more than a few chains from tidal water; optimal development with rather deep inundation classes and soils rich in humus and somewhat firmer than those of *R. apiculata*. Bark dark, almost black, with horizontal fissures (Watson). Occasionally planted along coastal fish-ponds for protecting the banks.

Crabs are great enemies to seedlings and damage plantations when they are made. It has been found in the Philippine Islands that seedlings dried for several days in the shade, before planting are more or less spared by them; Burkill queries whether the arrest of growth due to this unnatural drying can have led to an accumulation of protecting tannin in the tissues.

Uses. The timber is used for fuel and charcoal.

The heart-wood is dark orange-red. The bark is rich in tannin, used for tanning and dyeing, and occasionally medicinally in cases of haematuria. In Malaya the poles are in considerable demand.
Fig. 12. Well developed *Rhizophora apiculata* Bl., with its cone of branched stilt-roots. Rantau Pandjang, E. Sumatra (H. H. Th. Schreuder).
for piling and for frames of houses in and about the swamps; for fish-traps, being preferred over other available trees in certain localities; and particularly for firewood. The bark is rich in tannin, associated with which is a substance darkening gradually. It served as a deep brown or black dye (samak bakau) and its chief function was to toughen fishing-lines and ropes, for which Ceriops bark is preferable. See for the cutch industry Burkill, p. 1898-1902.

Vern. Bakau bèlukap, b. gelukap, b. jangkar, b. hitam, b. kurap, b. mèrah, bèlukap, Mal. Pen., bangka itam, b. u, Atjeh, dongoh korap, N. Simalur, bakau itam; b. korap, b. mèrah, M. bako, djankar, J. lènggayong, S.; Celebes: bèlukap, Bugin., lolaro, Manado; Philippines: bakàuan-bàbàe, Tag. (common name), bakàu (many lang.), bakhàu, C. Bis., bangkàu, Tag.; nanàsi èsàtì, Karakelong; New Guinea: korikì, Duru, paho, Babo, togo (for fruit), torìor, Kanoria, totoa, Motu, kamo, Binandele, kul, Hagen.


3. Rhizophora stylosa Griff. Not. Pl. As. 4 (1854) 665; Ic. 4 (1854) t. 640; Back. Schoolfl. (1911) 482; Ridl. Fl. Mal. Pen. 1 (1922) 693; Back. cm long. Inflorescences 3-4 times forked, each arm with an apical bracteolar involucre, (4-)5-8(-16)-flowered; peduncle 2½-5 cm; pedicels ½-1 cm. Buds emerging from the involucre long before the falling of the sustaining leaf. Mature buds widest near the base. Calyx in anthesis pale yellow, lobes 9-12 by 3-5 mm. Petals c. 8 mm long, densely villose along the margins rarely also on the back, partly enclosing the epipetalous stamen with these margins, hairs 3-6 mm. Stamens 8, 4 epipetalous, 4 episepalous, anthers 5-6 mm long, apiculate, filament distinct, short. Superior part of the ovary depressed-conical, in anthesis enclosed by the disk, hardly 1½ mm high; style filiform 4-6 mm, shortly and obscurely 2-toothed. Mature fruit obpyriform, with strongly contracted apex, not rugose, brown, 2½-4 by 1½-2½ cm; cotyle-
dons emerging for 1½-2½ cm from the calyx,
terrace, facing the open sea, obviously better resisting the surf than the other species.

Excluded

*Rhizophora aegiceras* GMELIN, Syst. 1 (1791) 747, based on RUMPH. Herb. Amb. 3, t. 82 = *Aegiceras corniculatum* (L.) BLANCO, cf. MERR. Int. Rumph. (1917) 413 (Myrsinac.).


*Rhizophora corniculata* LINNÉ in Stickman, Herb. Amb. (1754) 13; AMOON. Acad. 4 (1759) 123, based on RUMPH. Herb. Amb. 3, t. 77 = *Aegiceras corniculatum* (L.) BLANCO, cf. MERR. Sp. BLAN. (1918) 299 (Myrsinac.).

*Rhizophora obtusa* DENNST. Schlüss. Hort. Mal. (1818) 15, 24, 32, based on RHEEDE, Hort. Mal. 6, t. 36 = *Aegiceras* (Myrsinac.).

### 2. BRUGUIERA


Buttressed trees up to 40 m, with kneed pneumatophores, sometimes with aerial roots when young. *Leaves* decussate, entire, usually coriaceous, glabrous, black-dotted beneath, petioled. Stipules lanceolate, 2–4 cm long, glabrous. *Flowers* bisexual, ebracteolate, articulated at the base with the pedicel, solitary or in 2–5-flowered, peduncled cymes. *Calyx* coriaceous, accrescent, 8–14–(15)-lobed, lobes subulate-lanceolate, acute. *Petals* each embracing a pair of stamens, 2-lobed rarely emarginate, caducous. Disk distinctly cup-shaped and adnate to the calyx tube. *Stamens* twice the number of petals, paired, epipetalous, filaments filiform, unequal in length; anthers linear. *Ovary* inferior, adnate to the lower part of the calyx tube, 2–4-celled, each cell with 2 ovules; style filiform, stigma obscurely 2–4-lobed. *Fruit* included in or adnate to the calyx tube, usually 1-celled, 1(–2)-seeded; cotyledons conenate at the base; hypocotyl terete or obscurely ribbed, blunt, perforating the apex of the fruit and falling with it.

Distr. Species 6, widely distributed from tropical East Africa (*B. gymnorrhiza*) to Asia, throughout Malaysia to Australia, and Polynesia (*B. gymnorrhiza* to Samoa, and the Marshall Isl.).

Ecol. In tropical mangrove forests, ascending tidal parts of rivers. *Bruguieras* grow in less frequently inundated situations than the *Rhizophoras*, and rely to a greater extent (*B. cylindrica* probably almost entirely) on distribution by surface water following heavy rains. *B. parviflora* is less discriminating than any other mangrove species and forms pure crops under a great variety of conditions.

The calyx falls with the fruit but becomes soon detached, except in *B. parviflora*.

Uses. The wood is seldom used for timber, but is profusely used for fuel and charcoal; the bark is less suitable for tanning than that of *Rhizophora*. Fig. 14. Localities of *Rhizophora stylosa* GRIFF.

green; hypocotyl cylindric, up to 54 cm by 12–16 mm before falling.

Distr. Formosa, throughout Malaysia: Philippines, Java, Malay Peninsula, Celebes, Moluccas, New Guinea, to Melanesia (Solomon Isl., Fiji), New Britain, and N. Australia. Fig. 14.

Ecol. Exclusively along sandy shores and coral

"
Fig. 15. Fully developed *Bruguiera* forest at Nusa Kambangan, S. Central Java, with Prof. Skottsberg standing amidst the luxuriant regeneration, 1929 (Jeswiet).
Fig. 16. Stem-base with knee-roots of Bruguiera cf. gymnorrhiza (L.) Lamk. Nusa Kambangan (Jeswiet).
Taxon. Blume, l.c. 140, segregated the many-flowered species from those with solitary flowers and established the former group as a new genus Kanilia. Miquel, l.c. 588, reduced Kanilia to a section of Bruguiera, dividing the genus into two sections Mangium. Miq. and Kanilia (Bl.) Miq. which he distinguished chiefly by the shape of the calyx tube, the anthers, and number of floral parts. Through the recently described B. hainesii and B. exaristata the distinction between these sections is obscured and they should in my opinion be omitted.

Note. In his Schlüss. Hort. Mal. (1818) Dennstedt gave three indexes, the first containing Rheede's vernacular names with their Latin equivalents, the second giving the Latin plant names with references to Rheede's work, the third tabulating Rheede's plates, volume by volume and plate by plate, with their Latin equivalents. In the third index a genus name has not been repeated for successive species and has from the second species onwards been indicated by a dash indicating the repetition. This has led to an error under Bruguiera on p. 32 of the 'Schlüssel' where tab. 31–32 = Bruguiera gymnorrhiza is followed by tab. 33–36 with four Rhizophoras but where the generic name Rhizophora has been omitted and erroneously been replaced by a dash, which formally consequently refers to Bruguiera. From this omission it can not be concluded that Dennstedt's intention was to reduce the genus Rhizophora to Bruguiera as the lists further agree inter se. In case Dennstedt made a new combination in his 'Schlüssel' he added consistently 'mihi', this was not done here except for his new species Rhizophora obtusa. Therefore, it cannot be inferred that he actually made four new combinations under Bruguiera.

Fig. 17. Bruguiera exaristata Ding Hou. a. Habit, × 2/3, b–d. petals, lateral, ventral (with 2 stamens), and dorsal, × 3, e. stamen, × 3, f. lengthwise section of flower (petals and stamens removed), × 2, g. cross-section of ovary, × 2, h–i. hypocotyls, × 2/3.—Br. hainesii Rogers. j. Flower beyond anthesis, × 3, k. petals from outside, × 3, l. hypocotyl with calyx, × 2/3.—Br. sexangula (Lour.) Poir. m. Petal, from outside, × 3.—Br. gymnorrhiza (L.) Lamk. n. Petal, from outside, × 3 (a, e–i Brass 808, b–d van Royen 4826, j, i Symington CP 51661, k F.M.S. 3, m Koorders 6293, n Hoogland 4182).
KEY TO THE SPECIES

1. Flowers solitary. Bristle in the sinus between the petal lobes not exceeding the lobe tips or minute to absent.
2. Tips of the petal lobes acute, each with 3 or 4 bristles 2–3 mm long, distinctly exceeding the lobe tips
   1. B. gymnorrhiza
   2. Tips of the petal lobes obtuse, without or each with 1 or 2, rarely 3 short bristles usually less than 11/4 mm, not or hardly exceeding the apex.
3. Leaves usually oblong-elliptic, flat, 8–13 by 3–6 cm, base acute to obtuse. Petals 13–15 mm long, the lobe tips with 1–3 bristles usually less than 11/4 mm; a distinct bristle in the sinus between the lobes.
   2. B. sexangula
3. Leaves usually obovate (rarely elliptic), with revolute margins, 5–91/2 by 3–41/2 cm, base acuminate. Petals 9–11 mm long, exaristate, without (or very rarely with an obscure) bristle in the sinus of the lobes
   3. B. exaristata
1. Peduncles 2–5-flowered (in some specimens of B. hainesii a few solitary flowers have been observed along with 2–3-flowered peduncles). Bristle in the sinus of the petal lobes far exceeding the lobe tips.
4. Calyx lobes 11/4–11/2 the length of the calyx, erect or slightly spreading in fruit. Petals 11/2–2 mm long.
   4. B. parviflora
4. Calyx lobes half length of the calyx, reflexed in fruit. Petals 4–9 mm long.
5. Mature flowers 10–12 mm long. Petals 3–4 mm long. Calyx tube 2 mm diam., lobes 8, completely reflexed in fruit.
   5. B. cylindrica
5. Mature flowers 18–22 mm long. Petals 7–9 mm long. Calyx tube 5 mm diam., lobes 10, patent at right angles in fruit.
   6. B. hainesii


Buttressed tree up to 36 m by 40–65 cm. Branching mostly sympodial. Bark grey to almost black, roughly fissured, usually with large corky lenticels on buttresses and base of stems. Leaves elliptic-oblong, coriaceous, 81/2–22 by (41/2)–5–7(–9) cm, acute, base cuneate, rarely obtuse; nerves 9–10 pairs, visible beneath, obscure above; petiole 2–41/2 cm, pruinose, often reddish. Stipules c. 4 cm long, often reddish. Flowers in anthesis 3–31/2 cm long, generally nodding; pedicel 1–21/2 cm, pruinose, bright red on the outside curve. Calyx red to pink-red, lobes (10–)12–14–16, usually 3 by the length of the calyx, obliquely ascending in fruit, tube usually ribbed at the upper part. Petals 13–15 mm long, lobe 11/2–11/2 the length of the petal, acute, each with 3 or 4 bristles 2–3 mm exceeding the tip, outer margins fringed with white silky hairs especially at the base, rarely the upper part glabrous. Stamens 8–11 mm long, anthers linear, 4–5 mm. Style c. 15 mm, angular towards the base; stigmatic arms 3–4, filiform, 11/2–11/4 mm. Fruit not ribbed, 2–21/2 cm long. Seeds 1–2. Hypocotyl cigar-shaped, slightly angular, with a blunt narrowed apex, 15–25 by 11/2–2 cm.

Distr. Tropical South and East Africa, Madagascar, Seychelles, Ceylon, SE. Asia, Riuikiu; throughout Malaysia, to Australia, Micronesia (Palau, Yap, Marshall Isl., &c.), and Polynesia (Samoa, Fiji).
Fig. 18. *Bruguiera sexangula* (Lour.) Poir. (Kebun Raja Indonesia).
Ecol. One of the largest trees of the mangrove, as a rule on somewhat dry, well aerated soil towards the landward side, often dominating as a tall forest with occasional stems up to 36 m by 65 cm. In the interior of islands it is sometimes pure but more often associated with R. apiculata. On the sea face it is only found following erosion.

B. gymnorrhiza marks the final stage in the development of the littoral forests and the beginning of the transition to ordinary inland types. It is the largest and probably the longest lived of the mangroves. It can stand any amount of shade and is frequently able to establish itself in pure bakau stands when the shade is too dense for Rhizophora seedlings to develop. Watson considers it a 'cuckoo species', leaving the nursing of its progeny to be carried out by others. After telling its re-generation is very often scant or absent and there is danger of overgrowth by Aerocistichum, but once seedlings have established themselves the fern acts rather as a nurse, forcing the seedlings up.

Uses: The red, hard timber is used for firewood and for charcoal, less so for piles, house-posts and rafters. Rumphius says that the leaves and peeled hypocotyls are eaten in the Moluccas after having been soaked in water and boiled, which he deems a poor food.

In Djakarta the starchy central part of the hypocotyls is treated with sugar and the sweet meat sold as 'manisan kandèka'. The fruits are sometimes used as an adstringent in the betel-quid, when not available is available.


Note. For a discussion of the rejection of the combination 'B. conjugata (L.) Merr.' see under Rhizophora apiculata Bl.

DOCTERS VAN LEUWEN found in specimens cultivated in Kebun Raya Indonesia a fruit with 2 hypocotyls (Costerus & Smith, Ic. 1923).


Tree up to 33 m by 65—80 cm, buttresses up to 1 m high; kned roots 45 cm. Bark smooth, grey to pale-brown, with a few large corky lenticels especially on the buttresses, sometimes with stilt roots. Branching mostly sympodial. Leaves elliptic to elliptic-oblong, usually oblanceolate, 8–13(–16) by 3–5 cm, acute to obtuse, wedge-shaped at both ends, flat; nerves 7–11 pairs visible to obscure on both surfaces; petiole 1½–2 cm, not pruinose. Stipules green or yellowish, 3½–4 cm long. Flowers generally nodding, at anthesis 2½–4 cm long. Pedicels 6–12 mm, green, yellow, or brownish, not pruinose. Calyx 10–12 lobed, yellow, yellow-brown or reddish, never bright red, tube 1–1½ cm long, outside distinctly ridged to the base. Petals 1½ cm long, densely fringed with hairs along the outer margins from the base to the apex; lobes half the length of the petal, apex reflexed and obtuse, each near the top with a few (1–3) bristles up to 1½ mm long and not or hardly exceeding the apex; a distinct bristle in the sinus between the lobes. Staminodes 7–14 mm, anthers linear, 3–5 mm. Style filiform, 1½–2¼ cm long, arms 3–4, at most 1½ mm. Hypocotyl thick, rather angular, with narrowed blunt ends, 6–8 by 1½ cm, straight.


Ecol. As of B. gymnorrhiza, mainly in the back mangrove in places which are infrequently submerged, but generally preferring wetter soils in association with B. cylindrica and B. parviflora. According to Burkill it has been suggested that it is a hybrid between B. cylindrica and B. gymnorrhiza; there is nothing to sustain this idea and its large area of distribution and fertility indicate its good specific status. According to Watson the
rarest Bruguiera in Malaya; it is the only one which occasionally stands on stiff-roots.

Uses. As B. gymnorrhiza. The tree yields firewood and poles and is suitable for making charcoal. Fruit is said to be used in an application for shingles, and root or leaves are used for burns. In Celebes the fruits are eaten after having been soaked and boiled.


Note. For a discussion of the evaluation of Rhizophora conjuncta L. I refer to Rhizophora apiculata Bl.

In Hawaii introduced Aug. 1922 by the Hawaiian Sugar Planters' Association and ten years later growing naturalized in the salt marshes near Heeia, Oahu (Degener, l.c.).

3. Bruguiera exaristata DING HOU, Nova Guinea, n.s. 8 (1957) 166, f. 1–2.—Fig. 17a–l.

Small tree up to 10 m by 25 cm. Bark dark-grey and cracked. Leaves obovate, rarely elliptic, 5–9 1/2 by 3–4 1/2 cm, acute, base acuminate, margin sometimes revolute; nerves 7 pairs, distinct; petiole 1 1/2–2 1/2 cm. Stipules c. 2 cm long. Peduncle 7–12 mm. Flowers at anthesis 2 1/2–2 1/2 cm long. Calyx 8–(10)-lobed, 10–15 mm tube, distinctly ridged externally down to the base. Petals 9–11 mm long, densely fringed with white appressed hairs at the base and along the outer margins, lobes 1/3 the length of the petal, obtuse, without bristles at the apex and in the sinus, very rarely with a minute, obscure one in the sinus. Filaments 10 mm, anthers 5 mm long, apical. Style c. 14 mm long, stigma obscurely 3-lobed. Hypocotyl cylindric, obtuse at both ends, obscurely ridged, 4 1/2–6 cm by 6–8 mm.

Distr. Northern Australia (Northern Territory, Queensland) and Malaysia: South New Guinea (Kapa Kapa, Merauke) and Lesser Sunda Islands (Timor). Fig. 19.

Ecol. In mangroves or growing at the rear of other mangroves and along creeks (Mossman River, Queensland).


Tree up to 24 m by 15–30(–55) cm. Bark smooth, grey, with a few small, obscure lenticels. Leaves elliptic, 7 1/2–13 by 2 1/2–4 cm, apex acute, base cuneate; nerves about 10 pairs, faintly visible on both surfaces; petiole 1 1/2–2 cm. Stipules c. 4 1/2 cm long. Cymes 3–7-flowered. Peduncle c. 2 cm, 2–5-flowered. Flowers yellowish green. Pedicels 6–13 mm. Calyx tube ridged; 7–9 mm long. lobes 8, about 1/4–1/5 as long as the tube. Petals 1 1/2–2 mm long, the lobes 1/3 the length of the petal, each with 3 bristles c. 1/2 mm, white hairy at the lower margin. Stamens 1 1/2 mm, anthers slightly oblong, 1/3 mm long. Style c. 1 1/4–1 1/2 mm long, obscurely lobed, stigmas 2–3. Fruit-calyx-tube 1 1/2–2 1/2 cm long, lobes erect, not accrescent. Hypocotyl cylindric, smooth, 7 1/2–13 by 1/4 mm; plumeul piercing the base of the fruit which remains on the seedling as a cull.

Distr. SE. Asia, throughout Malaysia to Melanesia (New Hebrides, Solomon Isl.) and Australia (N. Queensland and Northern Territory), introduced in Hawaii (Degener, l.c.).

Ecol. Mostly on the inner side of the mangrove, not infrequently found associated with B. cyclindrica, but more often with Rhizophoras where it is at its best. Occasionally it forms pure, solid stands. It distinctly increases as a result of exploitation of immature areas. It often establishes itself on soils formerly occupied by Rhizophora and is frequently common on river-banks where excessive pole

Fig. 19. Localities of Bruguiera exaristata DING HOU.
Fig. 20–21. Pure forest of *Bruguiera parviflora* W. & A. as seen from the outside near Palu Piai (E. Sumatra), c. 10 years old (H. H. Th. Schreuder) and inside, with mud mark of high tide in Malaya (J. Wyatt-Smith).
cutting has been indulged in by fishermen. And then it may become a nurse for the Rhizophoras. If it grows mixed with *B. gymnorrhiza* it is evidently under conditions which suit it as then it attains its largest size. It is much more tolerant of submer-

gence than *B. cylindrica*. Though quick to establish itself, WATSON finds it a slow grower and among the *Bruguieras* it has the shortest life, particularly when it grows in pure stands as it frequently does in the wetter parts. WATSON calls it an 'opportunist species' occurring under a variety of conditions. For that reason the forester encourages it if he cuts as frequently as every twenty years.

Uses. By its small dimensions not of much use, but employed for (inferior) fire-wood and for mining and on the Selangor coast for fishing-stakes and traps, but in Perak fishermen say that, like *B. cylindrica*, it has a peculiar odour which frightens fish away. Sometimes poles are used for rafters.

Bark is deficient in tannin. Malays sometimes use the germinating embryo as a vegetable.

Vern. Lĕnggadai, lĕnggadis, mĕngkadai, Mal. Pen., langgadé, Atjeh, lĕnggadal, Ban, Borneo, mĕngêlangan, Pal., tandjang, I., tĕngit, M (Palo); Philippines: hañgarai, lañgarai, Tag. & other lang. bakaw-an-laláki, mañgalai, potósan, Tag., hânggalai, Tag., Mbo., hiñgalai, hiñgarai, Tag., P. Bis., arum, Bag., biosan, bubutigan, S. L. Bis., hanagalai, hângai, C. Bis.

Fig. 22. *Bruguiera* forest with knee-roots in sandy mangrove at low tide, near Kiojoh, south coast of Enggano Isl. (Lütjeharms).

Tree up to 23 m by 20–30 cm, buttresses small, up to 1 m. Bark grey, with a few small, corky lenticels. Leaves thin, elliptic, 7–17 by 2–8 cm, acute, base cuneate; nerves c. 7 pairs, distinct, rarely obscure on both surfaces; petiole 1–4/2 cm. Stipulae 2 1/2–3 1/2 cm long. Cymes 3-flowered. Peduncle 6–8 mm. Flowers greenish, at anthesis 10–12 mm long. Pedicels 1–4 mm. Calyx tube smooth, 4–6 by 2 mm, lobes 8, about as long as the tube. Petals 3–4 mm long, the lobes c. 1/8 as long as the petal, with 2 or 3 bristles at the apex, outer margins usually fringed with white hairs in the lower part. Stamens 1 1/2–2 1/2 mm long, anthers oblong, 1/2 mm long, slightly apiculate. Calyx tube in fruit 10–12 mm long, the lobes reflexed, not accrescent. Hypocotyl cylindric, often curved, 8–15 cm by 5 mm.

Distr. SE. Asia, throughout Malaysia to N. Queensland.

Ecol. Generally not higher than 20 m, essentially gregarious on stiff clay behind *Avicennia* on the seaface; it gives way to species on better drained soils, existing gregariously by virtue of its ability to grow in newly formed soils unsuitable to other mangroves.

The almost entire absence of aeration in the dense clay habitually occupied by *B. cylindrica* makes the tree more than usually dependent on its pneumatophores for an adequate supply of oxygen, and particularly susceptible to prolonged submersion. Suffocation on a much more extensive scale has occurred in the centre of Trong Island, in the Matang For. Res., Perak, where its progressive dying off over an area that had grown to over 40 ha has recently been checked by the cutting of an extraction canal, which has allowed the accumulated surface water to drain away towards the landward side.

Fig. 23. Spontaneous seedlings of *Bruguiera sexangula* (LOUR.) POIR. between pneumatophores of *Sonneratia casauralis* (L.) ENGL. in the fresh-water swamp of the Botanic Gardens, Bogor (II.Q.F.), Oct. 1956 (JACOBS).

There is good reason to believe that *B. cylindrica* is a legitimate precursor of the *Rhizophoras* in most situations where accretion is proceeding on the sea-face. It is a prolific seed-bearer and healthy forests can be relied upon to regenerate themselves even after clear felling (WATSON).

According to SETTEN the pure stands in Malaya are found normally above reach of the ordinary tides and are inundated only with spring tides. The stocking of the young stands is extremely dense and these pole woods may contain from 55,000–70,000 stems per ha. SETTEN says that berus holds the doubtful honour of achieving
pride of place as the slowest growing of any commercial tree species in Malaya. From seed it takes 11-12 years to attain 6 m height, c. 16-17 years to attain 9 m by 5 cm diam. and c. 60 years to attain 30 cm diam. Its rotation should be longer than 30 years now accepted for average rotation in Malaya of mangrove forest. Heavy early thinnings are necessary to increase the rate of growth.

Uses. Timber mainly used for fire-wood; it is reddish, heavy, and close-grained. The bark is thin and of too poor quality for tanning purpose. According to Heyne the young radicles are in some areas occasionally eaten with sugar and coconut. Fisherman say that the wood has a peculiar odour which frightens away fish; and many do not like to use it for making fish-traps.

Vern. Bakau belukap, b. bėrus, b. putih, bėrus, b. kēṭijil, bosang, Mal. Pen., hurus, M, tandjang, t. sukun, J, lindur, Md; Philippines: bakāsan, biyas, busāin, pututān, taŋgālan, taŋgālab-babāę, Tag, biyas, Pang, bius, Mag, Sul, kalapīnai, Ilk, laŋgarai, Mag., magotūngog, magtuŋgud, S. L. Bis.

6. Bruguiera hainesii C. G. Rogers, Kew Bull. (1919) 225; Craib, Fl. Siam. En. 1 (1931) 596; Wyatt-Smith, Mal. For. 16 (1953) 157, f. 3; Ding Hou, Nova Guinea, n.s. 8 (1957) 168.—Rhizophora caryophylloides (non Burt. f.) Griff. Inc. 4 (1854) t. 642.—Fig. 17—I.

Tree up to 33 m by 70 cm. Bark brown to grey, with large corky yellow-brown lenticels from base to top. Leaves elliptic-oblong, 9-16 by 4-7 cm, acute, base cuneate; petiole 2½-4 cm. Stipules 3½-2 cm long. Cymes 2-3-flowered. Peduncle short, 7-13 mm. Pedicels 6-8 mm. Flowers in anthesis 1½-2½ cm long. Calyx pale green, 10-lobed, tube 5 mm diam., slightly ridged outside in the upper part, lobes as long as the tube. Petals 7-9 mm long, villose at the lower margins, slightly pilose at the upper part of the lobes, lobes ⅓ as long as the petal, with 2-4 bristles at the apex. Calyx lobes patent at right angles in fruit. Hypocotyl cigar-shaped or slightly clavate, slightly curved, up to 9 cm by 11 mm.

Distr. ?India (fide Griffith Lc.), S. Burma (Mergui), Siam (Chantaburi, Surat), and Malaysia: Malay Peninsula (Klang Isl., Selangor), and Papua (Port Moresby).

Ecol. On dry side or inland of mangrove, only inundated for a few hours at fairly high spring tides.

Vern. Bėrus mata buaya, M.

Excluded Bruguiera nubicola Pritz. Icon. Ind. 2 (1866) 51, nomen, spalhm. = Bougneria nubicola Decne (Plantaginac.).

3. CERIOPS

ARN. Ann. Mag. Nat. Hist. 1 (1838) 363.—Fig. 24-25.

Small to medium-sized trees. Stems with appressed stilt-roots up to 1 m tall. Leaves decussate, clustered at the end of the twigs, entire, coriaceous, glabrous, not black-dotted beneath; nerves obscure on both surfaces. Stipules lanceolate. Inflorescences solitary, sub sessile to shortly peduncled, (2-4) ~flowered, condensed cymes. Bracteoles 2 at the base of the flower, partly connate, cupular, the free part ovate. Calyx deeply 5-6-lobed, ovate and acuminate. Petals white, 5 or 6, each embracing 2 stamens, inserted at the margin of the disk, sometimes cohering at the base by the uncinate-hairy margins, apex marg inate or truncate, fringe-like divided or with 3 clavate appendages (occasionally only 2). Disk cupular, shallowly lobed, lobes ep isepalous. Stamens twice the number of calyx lobes, inserted in the sinuations of the disk. Ovary semi-inferior, 3-celled, each cell with 2 ovules; style terete, simple; stigma simple or obscurely 2-3-lobed. Fruits ovoid, for the greater part superior. Hypocotyls clavate, tapering to the apex, ridged and sulcate.

Distr. Species 2, distributed in the tropics of the Old World, from eastern Africa throughout Malaysia to Micronesia, Melanesia, and N. Australia.

Ecol. Typical constituents of the inner mangrove.

Key to the Species

1. Petals with 3 clavate appendages at the apex. Anthers obtuse at the apex, c. 1/4-1/6 the length of the filament. Calyx lobes on the fruits reflexed or widely patent. Hypocotyl 15-25(35) cm 1. C. tagal
1. Petals fringe-like divided at the apex. Anthers apiculate, longer than the filament or rarely as long as it. Calyx lobes in fruit erect or ascending. Hypocotyl 9-15 cm long . . . . 2. C. decandra

Fig. 24. Ceriops tagal (PERR.) C. B. ROBINSON. a. Habit, \( \times \frac{2}{3} \), b. flower, corolla removed, \( \times 3 \), c. petals, inside, \( \times 5 \), d. stamens, \( \times 13 \), e. hypocotyl, \( \times \frac{2}{3} \).—C. decandra (ROXB.) DING Hou. f. Petal, inside, \( \times 13 \), g. stamen, \( \times 13 \), h. hypocotyl, \( \times \frac{2}{3} \) (a-d HOOGLAND 4315, e SAUNDERS 95, f-g VERSTEEG 1892, h KOORDERS 29925).

Shrub or tree up to 15(-25) m by 20 cm, often degenerating into a bushy shrub under unfavourable conditions. Stem base often with small stilt-roots. Bark light grey, fairly smooth with fine lenticular fissures. Leaves obovate to obovate-oblong, rarely elliptic-oblong, 5-111/2 by 2-71/2 cm, obtuse or sometimes slightly emarginate, base cuneate, margins often wavy; petioles 11/2-31/2 cm. Stipules 11/4-21/2 cm long. Inflorescences often on the terminal nodes of the new shoot, usually resinosus, (2-)34-10-flowered. Calyx lobes erect in flower, widely patent, reflexed in fruit, ovate, acuminate, 4-5 mm long; tube c. 2 mm high. Petals oblong, white, turning brown, coherent at the base with uncinate hairs, limb c. 31/2 mm long, with 3 clavate, apical appendages c. 11/2 mm long. Stamens 3-5 mm long, white, anther and shorter, anthers slightly ovoid, sagittate, much shorter than the filaments. Superior part of the ovary 11/2 mm high, style 2 mm, entire. Fruit ovoid, 11/2-21/2 cm long, calyx lobes soon reflexed; hypocotyl club-shaped, sharply angular, 15-25(-35) cm long. Seeds 1(-2).

Distr. Eastern Africa, Madagascar, Seychelles, Ceylon, India, Burma (Andamans), Siam (Koh-chang, Koh-kong, Koh-chick), Indo-China (Cambodia, Cochinchina), Formosa, throughout Malaysia to Micronesia (Carolines: Palau, Yap), Australia (Northern Territory: Darwin, South Bay, Melville Bay; Queensland: Stradbroke Isl.), and Melanesia (?) New Ireland, Solomons, and New Caledonia).

ecol. On well drained soils, within the reach of occasional tides in the inner mangrove. Fishermen exploit it so much in Malaya that well grown trees are rare, according to BURKILL. On the whole it is much more common than C. decandra. It is very interesting that one can break a seedling into halves and regeneration of a new plant occurs from either half, according to CUBITT.

It sometimes occurs as undergrowth in Rhizophora or Brugulera mangrove forest, but in other places occurs in thin-stemmed, very dense, gregarious monospecific stands on well-drained soils, cf. HEYNE, p. 1167.

In Siam recorded with aerial roots from the branches and according to BECKING also in Indonesia sometimes with aerial roots.

Uses. In Malaya the bent branches are often used as knees for boats and the trunks for house-building. Watson regards it as the most durable of all the mangroves. It also makes an excellent fire-wood. In Indonesia it is used for pit-props (coal mines of P. Laut) and various other purposes. The heart-wood is yellow to orange without any sharp distinction against the sap-wood.

The Malays use the bark for tanning fishing lines, nets, and sails. It is used as dye in the batik industry for colouring red, or black in combination with indigo, as is done in Pattani and Kelantan, for cotton and matting, cf. BURKILL, p. 517.

The tannin is not suitable for medicinal use, though occasionally used; a fragment of the bark or the old calyx is placed in the betel-quid as an astringent.

Vern. Têngar, têngoh, tangar, M, tingi(h), J; Philippines; tâgdî, Tag. & various lang., lîgasên, tagasa, tâgdî-lâlêkî, tânhôl, tîgassan, Tag., mag-tângod, tângôd, tûngîg, P. Bis., pakat, Tagb., rûngôn, ruûngôn, Sbl., tâgôd, tûngôg, S. L. Bis., tûngông, Sub., tonggi, Kuy, tûngûd, Sulu; palun, parun, Ambon (Alf.), bido-bido, Galela.

Notes. Perrottet's original description is very poor and applies to both species of Ceriops and I have not seen a type specimen. Merrill (1923) said that C. tagal is abundant in Zambanga Prov. (Mindanao), the type locality of PERROTTET where C. decandra seems to be absent. The febrifugal medicinal use of C. tagal, stressed by PERROTTET, is another argument to accept PERROTTET's name as such use is not made of the bark of C. decandra.

Ceriops paciflora BTH. has tentatively been reduced to C. tagal, with which it agrees in all characters save the 2-flowered cymes and slightly larger flowers (calyx c. 6 mm). It is only known from the type locality: New Ireland, Barclay (K).

Ceriops somalensis Chiov. was said to differ from C. tagal in having short filaments and triangular-tipped petals. Obviously these observations are deficient and made on too young material. The fragments of Senini 134 received through the courtesy of the Firenze Herbarium have very long filaments below the young fruit. I suppose the petals have been drawn upside down and the absence of the 3 apical appendages is due to inaccurate observation; I had no buds available.

Kanehira (En. Micr. 1935, 377) recorded this species under the wrong name C. roxburghiana from Micronesia; his description and figure in his Fl. Micr. (1933) 255, 447, fig. 119 leave no doubt about the identity.

I have observed one fruit with 2 hypocotyls. Occasionally there are only 2 appendages to a petal (cf. Koord. Atlas 1, 1913, t. 107, fig. E).

cf. Sealy, Kew Bull. 1956, p. 376 (1957).—Fig. 24f–h.

Small tree up to 15 m tall, 15–20 cm diam. Leaves obovate or obovate-elliptic-oblong, 4 1/2–10 by 2 1/2–5 cm, apex obtuse, rounded or ± emarginate, base cuneate; petiole 1 1/2–2 1/2 cm. Stipules 1 1/2–2 1/2 cm. Inflorescences usually in the axils of several nodes at the upper part of a branch, 3–5-flowered, head-like condensed. Calyx lobes erect both in flower and in fruit, ovate, acute, 3–4 mm, tube c. 2 mm high. Petals white, turning brownish, with broad base, folded longitudinally, hardly or not cohering, c. 2 1/2 mm long, fringe-like divided at the apex. Siamens 1 mm long, ± equal, anthers ovoid, seemingly much longer than the filaments as the erect anthers are dorsifixed. Fruit ovoid-conical, c. 1 1/4 cm long, calyx lobes obliquely erect or ascending; cotyledons red, finally protruding from the fruit for c. 2–4 mm; hypocotyl club-shaped, sharply angular and sulcate, 9–15 cm.

Distr. India, Burma, Siam, Indo-China ( Cochinchina), and Malaysia: Malay Peninsula (E. coast), Banka, Java, Borneo, Philippines, Celebes, Moluccas (Ceram), and New Guinea, not yet found in Sumatra and the Lesser Sunda Islands. 

Ecol. Edges of mangrove swamps, but relatively rare, and much less common than C. tagal.

Uses. For fire-wood.

Vern. Têngal, têngar, M., tingi, J., bakau lali,
Sarawak, landing-landing, Sarawak (Lawas); Philippines: tañgál, Tag., Bik., matañgál, tagasa, Tag., bulabadiang, tuñgûg, P. Bis., tuñgung, C. Bis., palun, parun, Ambon, bido-bido, Halmahera.

Note. According to Wyatt-Smith the fruits of the Ceriops species can be distinguished in the field by the following characters: C. tagal: hypocotyl hardly ridged and warty over its whole length; calyx smooth; lobes reflexed in fruit. C. decandra: hypocotyl distinctly ridged, only warty at the apex; calyx distinctly warty; calyx lobes erect in fruit.

4. KANDELIA

W. & A. Prod. (1834) 310.—Fig. 26.

Small tree. Leaves decussate, entire. Stipules linear. Inflorescences peduncled solitary, cymose, 4–9-flowered. Calyx deeply 5(–6)-lobed. Petals 5(–6), bilobed, with a long seta in the sinus, each lobe multifid. Stamens free, unequal in length,

Fig. 26. Kandelia candel (L.) Druce. a. Habit, × 2/3, b. longitudinal section of a flower (petals and stamens removed), × 3, c. petal, × 5, d. stamen, × 3, e. hypocotyl, × 1/3 (a, b, d Salim A 1727, c Cuadra A 1415, e Brooke 8826).
exserted. **Ovary** inferior, 1-celled, with 6 apical ovules. Style simple. **Fruit** ovoid, 1-seeded. **Hypocotyl** cylindric to spindle-shaped or clavate, pointed.

**Distr.** Monotypic, locally distributed in SE. to E. Asia (Kwantung, Hainan, Formosa, Riukiu, Kyushu) and **W. Malaysia** (Sumatra, Malay Peninsula, and Borneo). Fig. 27.

**Ecol.** On banks of tidal rivers in the mangrove forest.


Shrub or small tree up to c. 7 m tall. Stem base thickened, generally without proper buttresses. No pneumatophores. Bark smooth, lenticellate, greyish to reddish brown, inner bark thin, pink. **Leaves** elliptic-oblong to narrowly so, or obovate-oblong, 6-13 by 2½-6 cm, obtuse, base cuneate, margin usually reflexed; nerves 6-7 pairs, obscure beneath, distinct or slightly elevated above; petiole 1-1½ cm. **Stipules** 2 cm long. Inflorescences dichotomously branched, 4-6-9-flowered, peduncle 1½-5 cm, pedicels 2-3 mm. **Flowers** white, at anthesis 1½-2½ cm long. **Bracteoles** 2-4, connate, cup-shaped and adnate to the base of the calyx. **Calyx tube** exceeding the ovary, lobes linear, acute, reflexed after anthesis. **Petals** c. 14 mm long. **Stamens** 8-13 mm, filiform. Disk cup-shaped. **Ovary** 1-celled, with 6 ovules; ovules attached mostly at the apical part of the central axis, pendulous; style filiform, with 3 stigmas. **Fruit** green, ovoid, 1½-2½ cm long. **Hypocotyl** clavate, 15-40 cm long, terete, clavate.

**Distr.** India, Burma, Siam, Indo-China (Tonkin, Annam, and Cochinchina), China (Kwantung, Hongkong, and Formosa), Riukius, S. Japan (Kyushu: Saksumia), and **Malaysia**: NE. Sumatra, Malay Peninsula, and West N. Borneo, very local and rare. Fig. 27.

MIQUEL recorded **Kandelia** from New Guinea, but this specimen has appeared to be **Ceriops decandra**. **KURZ** recorded it from Banka (Nat. Tijd. Ned. Ind. 27, 1864, 150, 165) but though it might occur there I have seen no specimen and KURZ’s identification may have been an error.

It has also been recorded from the Philippines, by F.—**VILLAR, Nov.** App. (1880) 79 and **VIDAL, Sinopsis Atlas** (1883) 25, t. 47, f. D, and **VIDAL**’s material was, according to him, based on material from Bulacan Prov., Luzon, but neither **MERRILL** nor I have seen any material collected in the Philippine Islands. As it is known from N. Borneo and Formosa it is likely to occur there.

**Ecol.** A small tree with conically thickened stem base but without buttresses or pneumatophores, sporadic on banks of tidal rivers among other mangroves but almost everywhere scarce and obviously occupying a narrow niche in the mangrove forest, rarely common in association with **Sonneratia alba** (Batu Lima R., Brunei). In 1939 **STEUP** found **Kandelia** as pioneer on mudshoals in the mouth of Indragiri R. (Amphitrite Bay, Mandah courses) fronting **Rhizophora**.

**Uses.** Timber too small and tree too scarce to have real value, only occasionally used according to **BURKILL**.

**Vern.** **Bérus-bérus** (false Bruguiera), béras-béras, pulut-pulut, mêmepulut, pisang-pisang laut (bustard sea banana), mêm-pisang, Mal. Pen., bèus, Bajau (Borneo), lingsajong, L. laut, pulut-pulut, Brunei.

**Note.** This plant is easily distinguished by the indefinite number of stamens, multifid petals, and long, narrow calyx lobes which are completely reflexed in fruit. Two or more radicles (5 have been recorded) are not infrequently formed on one fruit (WATSON).
5. ANISOPHYLLEA


Trees and shrubs. Leaf-axils with 4–6 superposed serial buds. Leaves alternate (distichous), often inequilateral, entire, isomorphic, or dimorphous (in A. disticha and some specimens of A. scortechinii), generally curvinerved with 3–5 longitudinal nerves (including the midrib) running from base to apex, more rarely pinnate-nerved but in that case always provided with an intramarginal vein. Stipules 0. Inflorescences axillary or supra-axillary, solitary or serial (super-numerary), simple or branched, spike-like, racemose, or paniculate, ebracteate or with minute bracts, brownish pubescent. Monoeccious, flowers unisexual, poly-gamous or bisexual, in A. disticha the inflorescences either φ or σ; male flowers more or less globose, female flowers cylindric and more or less quadrangular. Calyx lobes (3–4)–(5), lobes deltoid, acute, tube adnate to the ovary. Petals entire, lobed, or lacerate. Stamens twice as many as petals, usually unequal in length, episperalous ones longest; filaments short, subulate, in some spp. the epipetalous filaments adnate to the basal part of the petal; anthers small, ovoid; abortive in the females. Disk obscure, crenulate or lobed. Ovary inferior, 3–5-celled, each cell with 1 ovule, abortive in the σ flowers and consisting of 3–4 small conical or subulate appendages homologous with the styles with the ovary suppressed. Styles (3–)4, free, subulate. Ovules pendulous. Fruits ellipsoid to pyriform, smooth or ridged, usually 1-seeded, floral parts persistent; pericarp generally consisting of 3 layers, rather hard and fibrous, in A. disticha exocarp fleshy, mesocarp and endocarp bony and ridged. Seeds with a coriaceous testa, consisting of a solid body of which the main part is formed by a thick, hard albumen; embryo linear or slightly spindle-shaped, longitudinally embedded in the seed, possibly for the greater part consisting of a hypocotyl.

Distr. About 25 spp. distributed in tropical Africa, Ceylon, India, SE. Asia, Malaysia (Sumatra, Malay Peninsula, and Borneo), with one species in tropical South America (British Guiana, viz. A. guyanensis Sandwith).

It is remarkable that the Malaysian species have such clear cut areas, A. disticha occurring throughout the Sunda shelf area (Java excepted), the others being confined to one subarea, viz Malaya: apetala, corneri, curitis, grandis, griffithii, and scortechinii, Borneo: beccariana, ferruginea, Sumatra: Anisophylea sp.

Ecology. Primary rain-forests below 1000 m, one record of 1250 and one of 1870 m.


The fruit of the W. African species A. laurina is edible and is called monkey apple, cf. Sabine, l.c.

In our area only A. disticha has a fleshy drupe but is not known to have been eaten by men.

Note. There is some doubt about the exact structure of the seed as far as could be ascertained from the Malaysian herbarium material. The pericarp consists always of three layers, the inner one being the thinnest and of hard, bony texture, the meso- and exocarp being both hard, but more fibrous, the exocarp being in some species fleshy.

The seed coat is coriaceous and envelops a solid body of endosperm and embryo, differentiated by a very thin brown layer. In cross-section both 'endosperm' and 'embryo' appear to consist of rather amorphous parenchymatic tissue. I have concluded that the outer thick layer represents the endosperm which then tightly envelops the embryo. It appeared impossible to separate embryo from endosperm and though the impression is that it almost wholly consists of the hypocotyl, this point should be left to further examination with abundant fresh material. This evaluation is contrary to Bailon's who
stated (Hist. Pl. 3, 304): 'embryonis exalbunimosi carnosi radicula macropora clavata'. According to this interpretation the thick outer seed tissue can only represent the united cotyledons (as occur in Rhizophoraceae) tightly enveloping the thick longitudinal radicle. I believe, however, that this interpretation is wrong.

**KEY TO THE SPECIES**

1. Leaves of one kind.
2. Nerves thin, pinnate, an intramarginal vein running less than 1 mm from the leaf-edge. Leaves 5–9 cm long. Fruit large. Flowers solitary, sessile.

   1. A. griffithii

3. All leaves ± rhombic, distinctly unequal-sided, the apical half much broader than the basal one. Cross-veins between the curved nerves distinctly prominent-scaliform beneath, faintly sunken in on the upper surface. Twig-ends brownish pubescent-tomentose. (Fruit small, thin-shelled, globular to broad-elliptic, c. 1 1/2–2 cm long)

   9. A. scoetechinii

3. Leaves not rhombic and not all distinctly unequal-sided. Cross-veins not distinctly prominent-scaliform beneath. Twig-ends glabrous or with a very thin, smooth, strictly appressed rusty tomentum.

4. Twigs and undersurface of the leaves initially covered by a thin, smooth indument of strictly appressed, rusty tomentum, glabrescent but vestiges almost always found along the nerves or in the nerve-axes at the base. (Venation tessellate; fruits large with a thick pericarp; endocarp woody)

   4. A. ferruginea

5. Twigs and leaves without such indument. (Leaves tessellate or not; fruits large or average; endocarp woody or not).

6. Flowers in contracted simple or compound panicles, the flowers on very short thickish side branches of both the main rachis and its main branches. Fruits very large, with a dense thin rusty tomentum consisting of very short hairs and scales. Main nerves 3–7, the inner ones separating from the midrib at c. 1 cm above the insertion of the lower ones. Dried leaves generally discoloured, the upper surface pale yellowish-greenish, the under surface cinnamon to pale brown. (Petals entire, long-hairy all over)

   5. A. grandis

7. Flowers in racemes, spikes or open panicles, in the latter case the few branches elongated and resembling the main axis.

6. Leaves nignescent, small, 5–8 by 1 1/2–2 1/2 cm. Petals split into filiform segments nearly to the base.

   6. A. curtissii

6. Leaves not nignescent, larger, at least 3 cm wide. Petals entire, glabrous or sparingly ciliate along the margin.

7. Curved main nerves about as prominent as the venation, much less prominent than the midrib. (Leaves c. 2 times as long as broad, under 10 cm long).

   2. A. beccariana

7. Curved main nerves about as prominent as the midrib. (Leaves c. 2–3 times as long as broad, mostly larger).

8. Venation prominent on both sides, but the meshes (areolae) rather irregular and not tessellate. Leaves c. 12–20 by 4–9 1/2 cm, in the herbarium usually yellowish or pale brown, mostly long-cuneate-accuminate. Flowers dark red or purple. Mature fruits spindle-shaped, acuminate at both ends, 5–6 by 2–2 1/2 cm, the pericarp c. 2 mm thick; endocarp merely a lining, woody mesocarp and exocarp both 1 mm diam.

   6. A. apetala

8. Venation prominent and tessellate on both surfaces. Leaves 7 1/2–13 by 2 1/2–5 1/2 cm, in the herbarium the upper surface rather dark brown, shorter and less abruptly acuminate on the whole. Flowers (7 always) white with 2 yellow lines. Mature fruits (5–5 1/2–7–9) by 4–5 cm, broad-ellipsoid, slightly acuminate narrowed at both ends, pear-shaped or broad-ellipsoid, the pericarp c. 5–9 mm diam.; endocarp 1 mm, mesocarp woody 4–6 mm, exocarp corky 1 1/2–3 mm.

   7. A. coronell

8. Venation prominent and tessellate on both surfaces. Leaves 8–17 by 4–7 cm, in the herbarium yellowish or pale green, acute to shortly acuminate. Flowers (inadequately known) yellow.

   Immature fruits ellipsoid, 5 1/2 by 2 1/2 cm, acuminate at both ends, pericarp c. 4 mm diam.

   8. Anisoplylea sp.

9. Curved nerves 2–4, all rising from the leaf-base. Scalariform cross-veins distinctly prominent on the under surface. Fruits globular to broadly ellipsoid (c. 15–20 by 12–17 mm), pericarp smooth outside, exocarp obviously not becoming fleshy.

   9. A. scoetechinii

9. Curved nerves 3, 2 outer ones rising from the leaf-base, 1 inner one emerging on the apical half of the blade from the midrib above and separate from the 2 outer ones. Scalariform cross-veins faintly prominent on the under surface. Fruits narrow-oblong, the hard mesocarp c. 15–18 by 5–8 mm, with (6–8) prominent lengthwise ridges (section 1), exocarp obviously fleshy, red when ripe

10. A. disticha
Flora Malesiana

Fig. 28. *Anisophyllea beccariana* Baill. a. Leaf, lower surface, \( \times \frac{3}{13} \), b. longitudinal section of the flower, \( \times 9 \), c. longitudinal section of the flower, \( \times 9 \), d. petal of the flower with staminode, \( \times 13 \).

--- *A. disticha* (Jack) Baill. e-f. Flowering branches, lower surface, \( \times \frac{3}{3} \), g. flowering branch, upper surface, \( \times \frac{2}{3} \), h-i. d. flowers, \( \times 9 \), j. petal, \( \times 13 \), k. longitudinal section of the flower, \( \times 9 \), l. dried fruit, nat. size (a, c, d Beccari P.B. 1001 (type), b Dickson 5, e, k Grashoff 1144, f, i, j Dumas 1574, g Bünnemeier 7336, l S.F. 306).

1. *Anisophyllea griffithii* Oliver, Trans. Linn. Soc. 23 (1862) 460, t. 48; Henslow in Hook f.


Tree up to 25 m by 60 cm. Bark light brown, smooth, becoming slightly ridged, cracked and rugged. Young leaves bronze and drooping (sec. CORNER); mature leaves elliptic to ovate-lanceolate, rarely lanceolate, slightly asymmetric at the base, thinly coriaceous, glabrous, shining above, rather dull below; \( \frac{5}{2} - \frac{10}{2} \) by 2-5 cm, shortly, bluntly acuminate, base cuneate, margin revolute when dry; midrib much stronger than the 6-8 pairs of pinnate nerves; leaf edge with a distinct intramarginal vein; veinlets slightly elevated beneath, visible but sometimes obscure above; petiole c. 3 mm. Inflorescences solitary or serial, sometimes 2-3-branched at the very base, spike-like, \( \pm \) zigzag, up to 7 cm long. Flowers bisexual, sessile, green, slightly obvoid, c. 4 mm long. Calyx lobes 4, deltoid, c. 1 mm long, acute. Petals oblong, fleshy. Stamens c. 1 mm long, filaments fleshy, subulate-oblong, in the epipetalous stamens for c. \( \frac{1}{3} \) adnate to the petals. Styles 4, subulate, c. 1 mm. Fruits broadly ellipsoid or subglobose, obtuse at each end, glabrous, smooth, \( \frac{4}{3} - \frac{5}{2} \) by \( \frac{3}{1} \)-4 cm, with a woody pericarp up to \( \frac{1}{1} \) cm diam. Seeds globose, \( \frac{1}{1} \)-\( \frac{1}{2} \) cm diam.


Ecol. In lowland forests up to 230 m.

Uses. The heavy durable timber is suitable for house-beams.

Vern. Delek tēmbaša, kēmpas dadeh, pēlēpap, poko kumpao dadeh, sēluang bērlĕring, M.

Note. In the available specimens I found only bisexual flowers.

2. *Anisophyllea beccariana* Baillon, Adansonia 11 (1875) 311; Merr. En. Born. (1921) 422.—Fig. 28a-d.

Medium-sized tree up to 25 m, with a narrow outline; bark rough. Leaves elliptic or ovate, chartaceous to thinly coriaceous, glabrous on both surfaces, \( \frac{7}{3} - \frac{10}{2} \) by 3-5 cm, bluntly acuminate, base acute rarely obtuse; longitudinal nerves 5, subequal at the base, elevated beneath, depressed or distinct above; veinlets reticulate, slightly elevated beneath, plane above; petiole 4-8 mm. Inflorescences in groups, branched near the base, racemose, up to 10 cm long. Flowers unisexual, bright yellow, slightly pubescent outside. Male flowers \( \frac{1}{1} \) mm long, shortly pedicelled. Calyx lobes 4, deltoid, 1 mm long. Petals oblong, \( \frac{3}{2} \) mm long, slightly emarginate, margins incurved. Stamens 8, 4 epipetalous, sterile, \( \frac{1}{2} \) mm long, antherless or glandular at the tip; 4 epispalous, fertile, \( \frac{3}{2} \) mm long; filaments thick, flat, subulate. Disk obscure. Pistil rudiments 4, subulate, \( \frac{1}{2} \) mm. Female flowers cylindric, c. \( \frac{2}{3} \) mm long, slightly pubescent outside, sessile or subsessile. Calyx lobes and petals similar as in the males. Disk none. Staminodes 8. Styles 4, free, subulate, \( \frac{2}{3} \) mm, thick, recurved. Fruit unknown.
Distr. Malaysia: Borneo (Sarawak).
Ecol. In forests from the lowland up to 650 m.
Vern. Kédaram, Paloh, pet, Kayan.

Note. The fruit-like bodies on Sar S 0250 are insect galls of the ovary which are subglobose or ellipsoid, 11/2 by 1/2 cm, with scattered lenticils.


Tree 10-13 m; young branches appressed rusty-pubescent. Leaves elliptic-oblong, rarely slightly unequal at the base, 6-8 by 2-21/2 cm, thinly coriaceous, usually glabrous on both surfaces, sometimes sparsely hairy near the base underneath, shining on both surfaces, acuminate, base cuneate; longitudinal nerves 5, starting from the apex of the petiole (sometimes 1 starting a little higher), slightly elevated beneath, plane but visible above, the marginal ones visible beneath and faint above; petiole 2-5 mm. Inflorescences spike-like, simple, c. 1 cm long. Flowers unisexual, shortly pedicelled, with a minute bract at the base. Male flowers c. 3 mm long, brownish pubescent. Calyx 4-lobed, lobes deltoid, acute, 11/2 mm long. Petals c. 3 mm long, divided almost to the base, 5-7-fid, filiform, twisted. Stamens 11/2-21/2 mm. Sterile pistil c. 1/2 mm. Female flowers (fide KING) 6 mm long. Calyx lobes reflexed, tube ribbed. Petals as in the males but larger and with more lobes. Styles as long as the petals. Fruits unknown.

Distr. Malaysia: Malay Peninsula (Penang CURTIS 746).
Note. Known only from the type collection.

HANIFF & NUR 2378 has been referred to this species by BURKILL & HENDERSON (in Gard. Bull. S. S. 3, 1925, 370) and RIDLEY Ic. However, that specimen clearly belongs to Linderia (Laurac.).

4. Anisophyllum ferruginea DING HOU, nov. sp.
Arbor, ramulis ferrugineo-tomentosissimis, gemmis 5 vel 6, in seriem verticalem dispositis. Folia oblongo-elliptica, vel oblongo-ovata, (71/2-24) 9-18/2-24 31/2-11 cm, integra, apice breviter acuminata, basi obtusa, stigmatibus vel rostratissimis, coriacea, supra glabriuscula, subtus ferrugineo-tomentosa, densum ± glabrescentes, nervis 3-5 prominentibus, venulis tessellatis. Flores parvi, unisexuales, sessiles. Fructus immaturos visus, ellipsoides. Typus Neth. Ind. For. Serv. bb 25118, Bo.

Tree up to 31 m by 40 cm. Young branches always rusty, pubescent-tomentose. Leaves oblong-elliptical to oblong-ovate, coriaceous, rusty tomentose beneath rather above, glabrescent but vestiges of indument always found on the veins or in axils of the veins at the base, (71/2-29-18/2-24) by 31/2-11 cm, shortly acuminate, base attenuated to rounded, margin rarely recurved; longitudinal nerves 3-5, prominent and elevated beneath, depressed above, sometimes a faint intramarginal vein along the margin; cross-veinlets slightly elevated, venation distinctly tessellate on both surfaces; petiole 1-11/2 cm, furrowed above. Inflorescences (inadequately known) short, branch-ed, paniculiform, densely rusty pubescent. Flowers unisexual, sessile. Male flowers c. 1 mm long. Calyx lobes (3-)4-5, deltoid, acute, c. 11/2 mm long. Petals minute, deltoid, c. 1/2 mm long, brownish hairy all over. Disk obscurely crenulate. Stamens c. 1/2 mm long, filament as long as the anther. Pistil rudiments c. 1/2 mm long, brownish hairy at the base. Female flowers slightly cylindric, quadrangular, 11/2 mm long, densely brownish hairy outside. Calyx lobes and petals similar as in the males. Staminodes almost sessile, c. 1/2 mm long. Apex of the styles slightly curved. Fruits (imma-ture) ellipsoid, obtuse at both ends.

Ecol. Lowland forests up to 450 m.
Vern. Kêpajang, sangkwak, têngoda, Dajak, bèlian landak, bulu, kêpajang landak, M.


Tree up to 25 m, with rather narrow conical crown and drooping branches and leaves. Leaves large, broadly ovate-oblong, rarely narrowly oblong-elliptic, coriaceous, glabrous, usually yellowish green above when dry, (15-)24-30 by (4-)6-11 cm, acuminate, base abruptly acute or rounded; longitudinal nerves 5 (middle 3 stronger than the 2 outer ones), elevated beneath, plane or slightly depressed above, besides 2 intramarginal veins; transverse veinlets subparallel; petiole 6-12 mm. Inflorescences irregularly and unevenly branched, up to 20 cm long, branches flattened when dry. Flowers unisexual, brownish pubescent outside, usually crowded on very short lateral branches. Male flowers shortly pedicelled. Calyx lobes 4, deltoid, acute. Petals deltoid, c. 1/2 mm long, brownish hairy all over. Stamens c. 1/2 mm long. Disk crenulate. Pistil rudiments subulate, sparsely brownish hairy in the lower part. Female flowers sessile, cylindrical, more or less quadrangular, c. 21/2 mm long. Calyx lobes and petals similar as in the males. Sterile stamens c. 1/2 mm; filaments sometimes twice as long as the anthers. Styles conical, 1/2 mm, recurved, densely brownish hairy in the lower part. Fruits pyriform, 8-12 by 5-7 cm, saccate at the base, minutely rusty-pubescent; pericarp 8-10 mm diam. Seeds very hard, solid and large.

Distr. Malaysia: Malay Peninsula (Penang, Perak).
Ecol. In forests from the lowland up to 1250 m.
Vern. Penang pear, E, dalek limau mantis.

Tree up to 14 m. Leaves broadly ovate-oblong to elliptic-oblong, 10–21 by 4–9 cm, glabrous, chartaceous to thin-coriaceous, shining above, rather dull beneath, caudate-acuminate or rarely acute, base rounded, rarely acute, margin entire; longitudinal nerves 5 (middle 3 conspicuous and elevated beneath, plane or depressed above, lateral 2 faint), besides the intramarginal veins; transverse veins faintly reticulate, petiole 6 mm. Inflorescences spike-like, serial, usually branched at the base, up to 19 cm long. Flowers unisexual, usually in groups on very short lateral stalks, brownish pubescent outside. Male flowers 2½ mm long, 1½ mm pedicelled. Calyx lobes 4, deltoid, acute, 2 mm long. Petals deltoid, acute, c. ½ mm long, entire, sometimes sparsely ciliate on the margins. Stamens 1½–1 mm. Pistil rudiments 4, subulate, ½ mm long, sparsely hairy at the base. Disk 4-lobed, each lobe crenulate. Female flowers sessile. Calyx tube cylindrical and more or less quadrangular, c. 1½ mm long. Calyx lobes and petals similar as in the males. Staminodes ¼–½ mm. Styles 4, exserted, spread and recurved, ½ mm, sparsely brownish pubescent at the base. Fruits ellipsoid or ovoid, usually tapering at each end, glabrous, with red stripes when fresh, 5–7½ by 2½ cm; pericarp woody. Seeds ellipsoid, 3 by 1 cm.


Ecol. In forests from the lowland up to 1000 m. Vern. Nipis kutil, pęparah, stial meaun, M.

8. Anisophyllea sp.

Tree up to 38 m by 60 cm. Leaves ovate to ovate-oblong or elliptic-oblong, chartaceous to thinly coriaceous, glabrous and shining on both surfaces, 8–17 by 4–7 cm, acute to shortly acuminate, bluntly tipped (tips up to 1½ cm long), base cuneate to rounded; longitudinal nerves 3–5, conspicuous and elevated on both surfaces; petiole 3–7 mm. Inflorescences branched at the base, paniculiform, up to 7 cm long, branches flattened when dry, brownish pubescent, rather stout as in A. grandis. Flowers (inadequately known) yellow, crowded on very short lateral branches. Female flowers sessile, 1½ mm long. Calyx lobes deltoid, ½ mm long; tube cylindric and more or less quadrangular, shortly pubescent outside. Petals not seen. Sterile stamens c. ½ mm long. Disk obscure. Styles 4, subulate, ½ mm long, exserted and slightly recurved, densely brownish hairy at the lower part. Fruits (immature) ellipsoid.
5½ by 2½ cm, with purple stripes when dry, pericarp 4 mm diam.


Ecol. In primary forests from the lowland up to 400 m.

Vern. Kalek sakam, medang lawang, sakam, Minangk.

Notes. This is in all probability a new species, but unfortunately all but two specimens are sterile, and the fertile ones (SWX I-45, bb 30096) bear only immature fruits and too fragmentary flowers respectively. The sheets are very homogeneous and have all been collected in a rather restricted coherent area in Central Sumatra. It is closest allied to A. coroniflora, but I have refrained from describing it; it is easily distinguished by the colour and size of the leaves.

The oldest collection of it is by Teysmann (Hb 2339); his sheets were wrongly referred to the Lauraceae by Miquel who, in his Supplement Sumatra (1860, p. 142, last two lines from bottom), referred it to Cinnamomum eucalyptoides Nees; he was possibly misled by the (wrong) Malay vernacular madang kult manis.


Small tree up to 10 m. Young branches sometimes rust-pubescent. Leaves usually of one kind (rarely with a few small, stipule-like ones appressed to the twig), falcately elliptic to slightly rhomboid, thinly coriaceous, rather silvery in living condition, shining on both surfaces, glabrous, sometimes with a few scattered, appressed, brownish hairs on both surfaces and especially on the main nerves and veins, 4–15½ by 1½–6 cm, acuminate, base obliquely cuneate; longitudinal nerves usually 5, rarely more, impressed; one forked, middle 3 prominent and elevated beneath, depressed or plane above, marginal 2 slightly elevated below, visible or obscure above; cross-veinlets distinctly prominent-scariosiform beneath, faintly depressed on the upper surface. Inflorescences racemose or spike-like, 1–7 cm long. Flowers polygamous, brownish pubescent outside. Male flowers 1 mm pedicellate, minutely bracteate at the base. Calyx lobes 4(–5), ovate, c. 1 mm long, acute. Petsals 3-fid at the apex, 3½ mm long; stamens c. 1½ mm. Disk deeply lobed. Pistil rudiments conical. Bisexual flowers sessile or subsessile, cylindric, c. 2 mm long. Calyx lobes ½-fid the length of the calyx, deltoid, acute. Petals 2–3-fid at the apex. Stamens 8, equal in length. Styles conical, c. 3½ mm, rusty hairy at the base; stigmas subcapitate. Fruits ellipsoid, obtuse on both ends, 1½–2 by 1½–1½ cm; pericarp woody, persistent, 1½ mm diam.; calyx lobes reflexed. Seeds ellipsoid, 1½ by 1 cm.

Distr. Malaysia: Malay Peninsula (Dindings, Johore, Kedah, Pahang, Perak, Singapore, and Wellesley) and Lingga.

Ecol. In forests from the lowland up to 230 m. Vern. Kayu ribu-ribu, M.

Notes. In A. scortechinii, though closest allied to A. disticha, the reduced, stipule-like leaves are much less in number and less frequent than in the latter species. For this reason it has been entered in the key in two places.


A miniature tree up to 7½ m by 10 cm. Branches graceful, drooping, generally arranged in distant whorls; upright main stems only provided with the stipule-like dwarf leaves. Twigs brownish pubescent, all lateral branches provided with leaves of several successive flushes. Leaves dimorphous, thin, very distichous, closely set with touching margins, the main upright stems and branches only with small leaves. Large leaves oblong-rhomboid, subfalcate, only on the lateral branches, densely brownish pubescent on both surfaces of the young leaves, glabrescent, 1½–9 by 1½–3 cm, acute at both ends; midrib slightly elevated beneath, depressed above; 1 or 2 longitudinal nerves on each side of the midrib, visible beneath, obscure above; transverse veinlets obscure on both surfaces. Small leaves stipule-like, falcate, generally appressed to the upper side of the twig, and more or less alternating with the large leaves on the lateral twigs, stipule-like, c. 5 mm long. Inflorescences either with 2 or 9 flowers, flowers pinkish white. Pedicels of inflorescences fasciculate or racemose, up to 7 cm long, rarely branched in the axils of the large leaves, turned to the underside of the twigs. Male flowers c. 2 mm long, yellowish, shortly pedicelled, minutely bracteate at the base. Calyx deeply (3-)4–(5-)lobed, lobes deltoid, 1½ mm long, acute, brownish appressed-hairy outside. Petals obovate, irregularly 3–5-fid, 1½ mm long. Stamens small as compared with other spp. Disk deeply lobed. Pistil rudiments subulate. Female inflorescences: flowers usually solitary, very rarely in a short, up to 2 cm long, spike-like inflorescence. Female flowers sessile, c. 2 mm long. Calyx lobes and petals similar as in the males. Staminodes alternating with the disk lobes. Style columnar c. 1½ mm, glabrous; stigma capitale. Drupes bright red when fresh, oblong, hanging singly or in pairs from the underside of the twigs, sessile, 1½–2½ cm long, the stone yellow-white, 1–2 by 1½–1 cm, acute at both ends, with 6–8 grooves and ridges; hard pericarp 1½–2½ mm diam.
Distr. Malaysia: Sumatra, Lingga Isl., Malay Peninsula, and Borneo.

Ecol. Common species in low woods and secondary forests, in wet places, on granitic sands, and on ridges, sometimes occurring up to 714 m, one collection said to have been found at 1785 m (Mt Kinabalu), fl. April-Aug., fr. throughout the year.

Uses. The hard wood of the main stem is used for making walking-sticks and shafts of pikes, spears, and lances. An infusion of the leaves is used against diarrhoea and dysentery. NOORDUN reported that in Borneo the roots of this plant are boiled together with jintan itam (seeds of Nigella sativa L.) and bawang merah (Allium cepa L.) for drinking to relieve weariness; also the leaves of it are grinded with the same ingredients for external application towards the same purpose.


Notes. The size of leaves is very variable, ranging from 9 by 3 to 11/2 by 1/2 cm. All specimens from the Malay Peninsula have small leaves and their size is usually less than 31/2 by 1/2 cm. As far as could be ascertained on the available material, the male and female flowers are borne on separate inflorescences.

A specimen of A. disticha in K marked as 'Luzon, Lobb' has been cited by ROEFE (J. Bot. 23, 1885, 212) as a Philippine plant. MERRILL (Philip. J. Sc. 10, 1915, Bot. 191) has pointed out that no representative of Antisophylea is known from the Philippines and that the Lobb specimen must have been erroneously localized; it may have come from Borneo.

6. COMBRETOCARPUS

Hook. f. in B. & H. Gen. Pl. 1 (1865) 683.—Fig. 29.

Tree. Leaves alternate, entire. Stipules 0. Inflorescences solitary or rarely fasciculate (branched from the very base), inserted on a tubercular basis. Calyx lobes 3–(4). Petals 3–(4), linear, entire, rarely laciniate. Stamens 6–(8). Ovary trigonous, cuneate to the base, lepidote, inferior, 3–(4)-celled, each cell with 2 ovules. Styles 3–(4), subulate, free. Fruit trigonous-fusiform, widely 3–(4)-winged, 1-celled, 2 cells aborted, 1-seeded. Seed narrow spindle-shaped (compressed in the herb. when not well developed), a solid whole, without a sharp demarcation between endosperm and embryo under the microscope; embryo obviously central and longitudinal, fusiform.

Distr. Monotypic. Malaysia: Sumatra, Riouw (Karimon Island), Banka, Billiton, and Borneo.

Ecol. In waterlogged soils of peat-swamp and kérangas forests at low altitude.


Tree up to 25 m by 80(–100) cm, easily producing copitoppe shoots. Bark grey, usually pale, fissured. Buttresses none or small. Leaves coriaceous, obovate, elliptic, broad-elliptic, to suborbicular, 8–14/2 by 5/2–9 cm, apex rounded, base cuneate; nerves 6–10 pairs, slightly elevated beneath, flat above; petiole 7/2–15 mm. Young leaves dark red; fallen leaves usually drying grey above and yellowish below. Inflorescences 11/2–6/2 cm peduncled, including the latter up to 9 cm long; pedicels c. 6 mm. Flowers yellow. Calyx lobes ovate, obtuse, 2/2–4 by 2 mm, outside lepidote in the apical part, slightly ciliate on the margin. Petals c. 2 mm long. Stamens inserted between the lobes of the disk, filament filiform, c. 2–21/2 mm; anther ovoid, versatile. Disk annular, obscurely 6-lobed. Ovary c. 2 mm; fruit including the wings 11/2–2 by 2–3 cm, wings semicircular, membranous, with parallel, transverse veins. Seed elongate-fusiform.

Distr. Malaysia: Sumatra (Palembang, Tebingtinggi), Riouw (Karimon Isl.), Banka, Billiton, and Borneo.

Ecol. From near sea-level up to 100 m, on sandy soils, peat swamps, freshwater swamps, and along the coast.

A distinctly gregarious tree of fairly large size confined to coastal swamp forest common from Borneo to Palembang and adjacent islands, in Brunei associated with Dactylocladus & Gonystylus, in Palembang with Campnosperma & Shorea albida.

According to BROWNE (l.c. p. 7) it may be dominant in the peat-forests 'padang paya' of Sarawak and Brunei in similar places as Shorea albida var. or as a co-dominant of Sh. albida (alan);
he says it also occurs on dry kērangan soils and in the mixed swamp forest type (I.c. p. 303). Over considerable areas, particularly in Baram and Brunei, it may average more than 5 large trees per ha. Stems of old trees are in some localities hollow and produce upward curved, short 'hunger roots' in the lower part of the bole from fissures in the bark. Generally it is small-sized but this is often compensated by abundance.

In South Sumatra ENDERT (I.c.) found it in peat-forests in the Musi delta associated with Campnosperma macrophylla and Shorea sp.

Kēruntum coppices are remarkably vigorous, and posts used for fencing and similar purposes often take roots and sprout (cf. BROWNE I.c.); the young red leaves of the coppices are conspicuous. Branches of wind-blown trees may easily take root and when the old stem in the course of time disintegrates, there may be eventually 4–6 young trees standing in its place, a most remarkable way of vegetative reproduction (Browne, I.c. t. 41; DIELS & HACKENBERG, I.c. p. 295).

Uses. The reddish-brown heart-wood is fairly hard and heavy; logs sink in water. It is locally highly favoured for heavy interior construction; strength properties appear to be roughly equivalent to those of teak or mērbau, easy to saw and work. It has a reputation for durability under cover. Large supplies are available and it deserves much more attention than it now receives (BROWNE).


7. CARALLIA


Shrubs or trees, a single sp. occasionally with small stilt-roots at the base of the stem. Twigs solid. Leaves decussate, petioled, entire to dentate or serrate, papyraceous to thinly coriaceous, black-dotted beneath; midrib sulcate above, prominent below. Stipules lanceolate. Inflorescences sessile or peduncled, cluster-like condensed or lax, di- or trichotomously branched, sometimes reduced to 2, or even a single flower. Bracteoles 2, free and caducous or at least connate at the base and persistent. Flowers sessile or pedicelled. Calyx lobes 5–8, deltoid, acute to acuminate. Petals 5–8, unguicate, caducous or persistent. Stamens twice the number of petals, persistent, free or towards the base connate into a tube (C. papuana), unequal in length, the short ones oppositipetalous, the long ones oppositipetalous; filaments subulate, flat or slightly fleshy; anthers ovoid or subglobose. Disk annular, fleshy. Ovary inferior, 5–8-celled, each cell 2-ovuled, or 1-celled with a central axis and 10–12 pendulous ovules inserted at its top; style filiform or slightly conical; stigmas discoid or capitate, grooved or obscurely lobed. Fruits pulpy, globose, ellipsoid or obovoid, 1-celled, 1(–2–5)-seeded. Seeds ellipsoid or reniform, albuminous, areolate; embryo straight or curved.

Distr. About 10 spp. in Madagascar, Ceylon, India, SE. Asia, throughout Malaysia to northern Australia and Melanesia (Solomon Isl.).

Ecol. On lowland ridges, hills, and in swampy places up into the mountains to c. 1800 m.

Morph. Stilt-roots have been observed to occur occasionally in C. brachiata (Koorders, Backer, Brown); Koorders’ specimen was collected in the Kampar swamp forest in Central Sumatra. Endert observed the same in Borneo.

Nomencl. Carallia is a conserved generic name, but the citations in the Rules of Nomenclature (Paris Code 1956) are unsatisfactory.

Carallia was not described by R. Brown, in Flinders, Voy. Bot. 2, app. 3 (1814) 549, but was merely referred to as a nomen nudum. The proper description and plate had been given by Roxburgh himself three years earlier.

Kare Kandel Adans. Fam. Pl. 2 (1763) 88, 532, based on Rheed’s name and description (H.M. 5, t. 13), is an illegitimate name according to art. 68 (4) and need not to be mentioned among the rejected names of which Diatoma Lour. and Barraldeia Thouars should stand.

The leaf margin is in this genus either entire, crenulate, or dentate; juvenile specimens of some species, notably C. brachiata, are sometimes densely and sharply dentate; the taxonomic value of the leaf margin is, hence, not particularly significant.

KEY TO THE SPECIES

1. Cyme(s) and flowers sessile. (Leaves thin-coriaceous.) . . . . . . . . 1. C. corifolia
2. Cyme(s) (at least) short-peduncled. Flowers sessile or pedicelled. (Leaves papyraceous to thin-coriaceous.)
3. Bracts and bracteoles semi-amplexicaulose, not connate, caducous in or after anthesis.
4. 2. C. eugenioidea
5. Bracts and bracteoles persistent, at least connate at the base.
6. On top of the common peduncle 2 or 3 simple or forked branches, each branch densely covered by decussate and deltoid or semi-orbicular bracts or bracteoles, the internodes between which are invisible from the outside; usually some of the bracteoles with solitary, sessile flowers. Leaves entire.
7. Leaf-base usually rounded, more or less abruptly set off from the petiole. Petals with a claw c. 2½ mm long, lamina elliptic, 1½ by 1 mm, shortly fimbriate (ovate and sessile when young). Filaments fleshy, connate about halfway up into a ventrally grooved tube . . . . 3. C. papuana
8. Leaf-base cuneate-attenuate, gradually narrowed into the petiole. Petals with a claw 1 mm long, lamina transversely oblong, 0.6 by 1 mm, slightly emarginate. Filaments thin, subulate, free.
9. 4. C. pulsifilii
10. Inflorescences distinctly cymose, each pair or triplet of bracts with 2 or 3 flowers or axes with clearly visible internodes, each ultimate cyme 3–flowered, the central flower bractless, sessile, the
lateral flowers pedicelled, sustained by cup-shaped, connate or partly connate bracteoles. Leaf margins distinctly fimbriate-dentate, serrulate, denticulate, very shallowly dentate-crenate, or entire.

5. Petals sagittate, persistent. Calyx lobes inside with short hairs. Seed obovoid or ellipsoid; embryo straight.

6. Inflorescences only in the axils of the upper leaf pair on each shoot. Disk divided in the upper half into deltoid lobes. Leaves serrulate to denticulate.

5. C. borneensis

6. C. suffruticosa

5. Petals suborbicular or obovate-spathulate, caducous in or after anthesis. Calyx lobes inside glabrous. Seed reniform or curved, embryo curved.

7. Flowers 6–8 mm long, not resinous. Petals obovate-spathulate, 3–3½ by 1½–2 mm. Ovary 1-celled. Fruits obovoid, 6 by 3 mm, ridged

7. C. calophyloidea


8. C. brachiata

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**Fig. 30. Carallia coriifolia Ridl.** a. Habit, × 3/5, b. longitudinal section of flower (petals removed), × 5, c. petal, × 7.—C. eugenioidea King. d. Bud, × 4, e. longitudinal section of flower (petals removed), × 4, f. petal, × 7, g. fruit, × 2, h. seed, × 2 (a–c Haviland 1797, d, f Purseglove 4244, e, g Scortechini s.n.).
persistent. Seeds obovoid, obuse at both ends, areolate, 9 by 4½ mm; embryo straight.

Distr. Malaysia: W. Borneo (Sarawak, Sintang, Kapuas).

Ecol. Rain-forests at low altitude.


Shrub or small tree, up to 8 m. Leaves usually at the branch ends, obivate, obovate-oblong, or elliptic-oblong, 4–8 by 1½–4½ cm, shining above, rather dull beneath, thinly coriaceous, acuminate to abruptly acute, rarely rounded, base cuneate, margin entire or rarely crenulate; nerves 7–10 pairs; petiole c. 5 mm. Stipules 5–7 mm long. Inflorescences cymose, once or twice branched, 2½–5 cm peduncled. Flowers green, yellowish-green, or white; pedicels up to 7 mm, sometimes the central flower of the ultimate cyme sessile. Calyx lobes 5, deltoid, acuminated, 2–3 mm long. Petals suborbicular, 2 mm diam., shortly unguiculate. Disk fleshy, slightly crenulate. Stamens 1½–2 mm; filament subulate; anthers slightly apiculate. Ovary campanulate, 3½–5 mm long, 5-celled, each cell with 2 ovules; style 2½ mm; stigma capitate, slightly 5-grooved. Fruits slightly oblong, 4–5 by 3 mm. Seed oblong-ovoid, areolate, corrugate, 3 by 1½ mm; embryo straight.

Distr. Malaysia: Malay Peninsula and Central Sumatra (Mt Sago).

Ecol. This species has rather seldom been collected and as far as these specimens go they show a rather remarkable vertical distribution, having been found in the Malay Peninsula at low altitude (c. 200–300 m) with rather thin, narrow leaves (once noted on a quartzite ridge) and further at much higher altitude (c. 1400–1700 m) with coriaceous, more blunt, and broader leaves. The Sumatran collection was made between 1500 and 1800 m and approaches the type of leaf as found in the Malayan mountains.

Note. The single collection from Sumatra (JACOBs 4685) is a young flowering specimen, which matches the present species very well; the bracts and bracteoles are still on the inflorescences, which may be due to the young stage.

3. Carallia papuana DING HOU, nov. sp.

Affinis C. hulstijini sed foliis basi rotundatis diversa; petalas unguiculata, 2½ mm long, lamina elliptica, 15 × 1 mm, breviter fimbriata; filamenta crassiscutula, infra ad dimidium in tubum canaliculatum connata. Typus DOCTERS VAN LEEUWEN 9530, l; SING.

Small tree, 4–6 m. Leaves elliptic-oblong to ovate-oblong, chartaceous, 12–20 by 5½–8½ cm, entire, shortly acuminate, base rounded; nerves 7–12 pairs, slightly elevated on both surfaces; petiole 6–10 mm. Stipules 1½–2 cm long. Inflorescences cymose, up to c. 2 cm long, 7–11 mm peduncled. Flowers c. 3 mm long, white. Calyx lobes 5, deltoid, acuminated, sparsely short-whitish hairy inside. Petals c. 2½ mm long, obovate-spatulate, erose, unguiculate. Stamens fleshy, 2–3 mm, anthers small, oblong and obtuse. Disk thin, crenulate. Ovary 5-celled, each cell with 2 pendulous ovules; style conical, c. 2½ mm; stigma obscure. Fruit unknown.


Ecol. On hill ridge at 75 m.


Leaves narrow elliptic-oblong, 14–19½ by 5–7 cm, entire, bluntly acuminate, base cuneate-attenuate; petiole c. 1 cm. Stipules 1½–2½ cm long. Inflorescences cymose, up to 3 cm long, peduncules ½–1½ cm. Flowers 4 mm long. Calyx lobes 5 or 6, deltoid, c. 2 mm long, acute. Petals transversely oblong, unguiculate, with claw c. 1 mm long and wide. Stamens ½–1½ mm; anthers ovoid, slightly apiculate. Disk thick, crenulate. Ovary 5–6-celled; style filiform, 2 mm, stigma discoid, obscurely lobed. Fruit unknown.

Distr. Malaysia: (Moluccas: Sula Isl.) once collected.


Tree up to 24 m by 45 cm. Bark finely fissured, pale brown. Leaves broad-elliptic, suborbicular to obovate or elliptic-oblong, acuminate to shortly abruptly acuminate (tip acute or rounded), 5½–10 by 2½–7 cm, shallowly crenulate, base cuneate to broad-cuneate; nerves 6–8 pairs, slightly elevated beneath, obscure or visible above; petiole 7 mm. Stipules linear, 1½ cm long. Inflorescences cymose up to 3½ cm long, (di-)trichotomously branched, ½–2 cm peduncled, sometimes with only 2, or even a single flower, in the ultimate cymes the lateral flowers pedicelled and with 2 to 3 bracteoles united into a basal cup, central flower sessile and without bracteoles. Flowers white or pale green, 7–8 mm long. Calyx lobes 6, lanceolate, ¾–4 mm long, shortly whitish hairy within. Petals, stamens, and style exerted. Petals sagittate, 3–5 mm long, unguiculate, fimbriate, conduplicate, base acute and inflexed. Filaments filiform, 3½–5 mm; anthers ovoid, slightly apiculate. Disk cup-shaped, fleshy, halfway divided into deltoid lobes. Ovary cylindric or cuneate, 2½–4 cm long, 1-celled, with 12 ovules; ovules pendulous, borne at the top of the central axis; style filiform 4–6 mm, stigmas capitate. Fruit oblong-ellipsoid 1½ by 1 cm, crowned by the persistent floral parts, base abruptly narrowed, 1-celled, 1-seeded. Seeds oblong-ellipsoid or obovoid, 9 by 6 mm, black, slightly areolate.

Distr. Malaysia: Borneo, Philippines (Palawan, Mindanao), and (once found) in W. New Guinea (Lake Amaru).

Ecol. Primary forests at low altitude.

lobes 5, deltoid, acuminated, sparsely short-whitish hairy inside. Petals c. 2½ mm long, obovate-spatulate, erose, unguiculate. Stamens fleshy, 2–3 mm, anthers small, oblong and obtuse. Disk thin, crenulate. Ovary 5-celled, each cell with 2 pendulous ovules; style conical, c. 2½ mm; stigma obscure. Fruit unknown.

Shrub or small tree, 2—3 m. Leaves elliptic-oblong to narrow elliptic-oblong, papyraceous, 10—18 by 4—6'/2 cm, acuminate, base cuneate to subrotundate, margins distinctly fimbriate-dentate; nerves 8—13 pairs, slightly elevated on both surfaces; petiole 1—1'/2 cm. Stipules 7—10 mm long. Inflorescences cymose, 1'/2 cm, 5 mm peduncled. Flowers white or red. Bracteoles decussate, ovate, keeled, persistent. Calyx 5—7-lobed, lobes lanceolate, acuminate, 3—4 mm long, shortly hairy within. Petals sagittate, unguiculata, cuneulate, 4—6'/2 mm long, slightly emarginate, conduplicate, base acute and inflexed. Stamens 3—4 mm; anthers ovoid, obtuse, rarely slightly apiculate. Ovary 1-celled, with 10—12 ovules; style 4'/2 mm; stigma discoid. Fruits wine-red, ellipsoid, sometimes slightly curved, 15 by 6 mm, 1-celled, 1-seeded, crowned by the remains of the floral parts. Seeds oblong, slightly curved, 11 by 4 mm, brown.

Distr. Indo-China (Cochinchina) and Malay-sia: Malay Peninsula (Selangor, Perak, Trengganu). Ecol. In lowland forests.

Uses. The leaves are used by the Malayans both internally and externally. "In the form of an infusion of the leaves, it is taken internally for worms, coughs, and after childbirth as a protective medicine; in the form of a decoction it is employed for bathing in fever; and as a poultice of the pulped leaves it is applied to boils" (cf. Burkill. Dic.t. I.c.). Vern. Sisek puyoh, sisek puyu, méranti, rédip pépyohu, tulang daing.

Notes. Burkill (Gard. Bull. S.S. 4, 1927, 77) said that C. spinulosa Ridl. does not adequately differ from the C. suffruticosa Ridl. He also referred his own collection (4690) to the latter, which actually is C. brachiata. The type specimen of C. spinulosa Ridl. is Ridley 11858 which clearly belongs to C. brachiata. Sterile specimens of C. brachiata with denticulate leaves can hardly be distinguished from the present species.

7. Carallia calyphloidea Ding Hou, nov. sp. Folia lata ellipitica vel oblongo-elliptica, 6—12 X 3-6'/2 cm, integra, apice acuta vel breviter acuminata, basi cuneata vel rotundata, nervis primariis numerosis subparallelibus. Cymae usque ad 10 cm longae, pedunculis 3-6 cm longis. Calycis tubus campanulatus. Petala obovato-spatulata, 2'/2—3'/2 X 2 mm, unguiculata, irregulariter denticulata. Stanma 3-4 mm longa, antheris apiculata. Ovarium uniloculare, ovulis apice axis pendulis. Fructus obovatus, leviter costatus, 1-spermus. Semina anguste reniformia. Typus HALLIER 2199, Bo.

Leaves broadly elliptic or elliptic-oblong, 6—12 by 3-6'/2 cm, thin coriaceous, shining above, rather dull beneath, entire, acute to shortly acuminate (tip acute to obtuse), base cuneate to rounded; nerves numerous and parallel, slightly elevated on both surfaces; petiole slender, 12—15 mm. Stipules 7—10 mm long. Inflorescences distinctly cymose, up to 10 cm long, 3-6 cm peduncled, (di)trichotomously branched. Bracts and bracteoles 2 or 3, united at the base into a cup, their free parts ovate, acute. Lateral flowers of the ultimate cymes pedicelled and bracteolate, the central flowers ebracteolate and sessile. Flowers 6—8 mm long. Calyx lobes 5—6—7, lanceolate, 4 mm long. Petals obovato-spatulate, 2'/2—3'/2 by 2 mm, unguiculata, erose. Disk fleshy. Stamens 3—4 mm long, filaments subulate, flat; anthers distinctly apiculate. Ovary 1-celled, with 10—12(14) ovules, pendulous; style 4 mm long; stigma discoid, grooved and obscurely lobed. Fruits obovoid, excluding the persistent floral parts 7 by 3'/2—4 mm. Lengthwise ridged outside, 1-seeded. Seed reniform, curved, black, 5 by 3 mm, areolate.

Distr. Malaysia: W. Borneo (Sg. Smiatu; HALLIER 1264; Sg. Kenibung: HALLIER 1317; Sg. Kenepai, P. Malaju: HALLIER 8646).


Tree up to 50 m by 70 cm. Bark deeply fissured, corky, gray to dark warm-brown, ridges invariably riddled by small black ants, occasionally buttressed and with adventitious roots to 1 m tall. Leaves elliptic-oblong, broadly-elliptic, obovate to obovate-oblong, rarely suborbicular or obovate, 5–15 by 2–10 cm, papyraceous to thin-coriaceous; in the herbarium shining above, rather dull beneath, yellowish green to dark brown, entire, serrate, or denticulate, acute to shortly acuminate (acumen up to 1 cm long), base cuneate; nerves 8–12 pairs; petiole 1 cm. Stipules 1–2 cm long. Inflorescences solitary, di- or trichotomously branched, 1–6 cm long, usually shining by secreted resin; peduncles short, up to 2 cm. Flowers white or greenish, 3 mm long, shortly pedicelled or sessile. Bracteoles 2 or 3, entirely connate or rarely partially united into a cup at the base of the flower. Calyx deeply (4–6)–7–8 lobed, lobes deltoid. Petals suborbicular, obscurely bilobed, crenate, unguiculate, including the claw c. 1 mm long. Stamens c. 2 cm long, anthers ovoid, small, filament usually glabrous rarely scaly. Disk annular, obscurely crenulate. Ovary semi-inferior, the free part ovoid, 5–8-celled, each cell with 2 ovules; style filiform c. 11/2 mm, stigma discoid, obscurely grooved or lobed. Fruits globose c. 7 mm diam., translucent pink to red when ripe. Seeds reniform.

Distr. Widely distributed from Madagascar to Ceylon, India, Siam, Burma, China (Kwangtung, Hainan), Hongkong, and Indo-China (Tonkin), throughout Malaysia, to New Britain, the Solomon Isl., and northern Australia.
though of a common tree, nowhere available in quantity.

Various minor medicinal uses are known, BURKILL, l.c. 448.

Vern. Sumatra: Bĕlidah, maransi, ringgit darah, sĕpat, M, ambaradé, tinggiran bata, Batak, kuku, Gajo, maransi, tinggiran rimbo, Minangk., sĕmĕragi, Kubu Distr., hĕrkat, kandis pulan, manggris, tĕnggeris, Banka, gandang, ganding, mĕrpo, mĕrpui, tĕngkawa, bongbong, junggut kĕli, kĕsingi, mĕransi, mĕ(r)singa, mundar, siseh puyoh, Mal. Pen.; ki kukuran, ki tamijang, S, bibis, gigil, kĕ-

dalĕn, kĕlumpit, kukuran, krintjing, liris, ki kukuran, kukuang, sumjak, pututan, sĕpat, tandjang girang, t. gunung, J, kotjĕngal, Md, djanggut kĕli, M; Borneo: hĕlĕngkĕching, dabong, massulie, mundar, patjar, M, bara, bĕranggae, tulangular, Dajak, ganggang putih, tulang ular, Bandjar., kîtirkitir, Kwijau, mundar burung, Loa Djanan, sawar bubu, Bettoton, tampilas, Dusun, aru, Central E. Born.; Philippines: anosep, kamaăn, karoĕkan, kuling-manok, Tag., bakāuan-gūbat, maingua, Mang., katolit, llk., magtuñgod, malibasag, Mbo., tandul, Sulu; Celebes: Marabia = barabia, Bug., moro-

Fig. 32. Carallia brachiata (LOUR.) MERR. in the Bornean rapah-swamp forest develops occasionally abundant aerial roots at the stem-base. Kutei, E. Borneo, 1925 (ENDERT).
Flora Malesiana


8. GYNOTROCHES


Distr. Monotypic, from Burma (Upper Tenasserim) and Siam throughout Malaysia (not yet recorded from the Lesser Sunda Islands) to Micronesia (Carolines: Tjaparna, Ponape), and Melanesia (Solomons and New Britain).

Ecol. Primary and secondary forests, up to 2250 m.


Tree up to 15–30(–45) m by 30–50 cm, but very often rather small, and occasionally shrubby; 1–2 m high specimens have been found with flowers and fruit. Bark transversely fissured, grey to blackish; young branchlets hollow, brown coloured, sometimes pubescent; nodes ± swollen. Leaves variable in shape (ovate, ovate-oblong, elliptic-oblong, ovobate oblong, or lanceolate), 4½–20 by 1½–9 cm, bluntly or shortly acuminate to acute, acute rarely obtuse at the base, usually glabrous, rarely pubescent beneath or only on the nerves and veins, sometimes lepidoct on both surfaces, shining and dark brown when dry; nerves 5–9 pairs, ascending along the margins, veins prominent beneath, flat to slightly prominent above; petiole 1½–1 cm. Stipules 1½ cm long, sometimes pubescent. Bracteoles sometimes pubescent and condensed into short, tubicular glomerules. Flowers greenish-white, few to 16, subessessile to 5 mm pedicelled, bisexual, but obviously occasionally male by abortion. Calyx lobes 4–5, ovate, 1½–2½ by 1½–3 mm, with a tuft of hairs at the apex. Petals 2–2½ by 3½ mm. Disk cup-shaped or nearly flat, crenulate to 8–10-lobed. Stamens 8–10, attached on the margin of the disk or just beneath it; filaments incurved, 1–1½ mm; anthers subglobose to ovoid, obtuse or slightly apiculate. Ovary ovoid, sometimes abortive; style columnar, short, up to 2 mm; stigma discoid and 4–8-lobed or slender with spreading lobes. Berries red, then shiny black, pulpy, usually globose and c. 3 mm diam., rarely oblong and 5–7 by 3–5 mm, calyx lobes erect or completely reflexed. Seeds ellipsoid, 1½ by ½ mm, areolate.

Distr. From S. Burma (Upper Tenasserim) and S. Siam (Nakawn Sritamatarat) throughout Malaysia to Australia, Melanesia (Solomon Isl.: Ysabel & Bougainville Isl.; New Britain), and Micronesia (Carolines: Tjaparna, Ponape), not yet recorded from Central to E. Java and the Lesser Sunda Islands.

Ecol. Marshy places, swamps, particularly along creeks in tall rain-forests, slopes of partially
open virgin forests, and very common in secondary forests, from the lowland up to 2250 m.

It clearly avoids regions subject to a seasonal climate as it is absent from Central Java to Timor; in Java it is confined to the Res. of Bantam, Bogor, and Preanger, one specimen being found in an everwet forest in S. Banjumas.

HOSOKAWA found G. axillaris common in the mossy hill forest of the Micronesian islands Ponape and Kusaie together with Alsophila where it produces aerial roots from the boughs of the crowns (Mem. Fac. Sc. Kyushu Univ. E 1, 1952, 65-82).

Uses. The brownish-white timber is of little use and not durable, it is occasionally used under roof, further for blades of oars, and sometimes for rafters and house-posts.

Vern. Bulu-bulu (in common with several superficially similar trees), bēbula, junggut kētil mata kēlli, mēmalu kētil, mēmbulu, mērdulu, Mal. Pen., kata kēlli, M (Sum.), sibeuruwah, surmaunah, Simalur (Tapah dial.), kaju bula, Kubu Distr., mēngkēlli, mēnsollong, tēlundju, sabar bula, Banka, kukuran, S, kopi-kupi, Brunei, mēmōluloh, sabar baku, Sarawak; Philippines: kibal, malakulambilis-san, Tag., auai, Mbo., bayasbas, dōyok-dōyok, talingan, C. Bis.

Notes. This species is very widely distributed and is markedly variable in leaf-size and shape. Some specimens collected above 1000 m have small and obovate leaves and larger flowers and fruits. The filamentous appendages of the petals are usually in a fringe at the upper third or half, or sometimes there are 9 of them, 3 at the apex, and 3 at the margin of each side (BRASS 2475, LAM 1797). There is a remarkable variability in the structure of the ovary, namely in the placentation: the ovules are fascicled and attached at the top (ACHMAD 163), at the base (LAM 1972), or at the middle (BRASS 2495) of the axis, or even along the axis (RICHARDS 1430). The stigmas vary from discoid and obscurely grooved to deeply divided into linear and spreading lobes. The remarkable 'looseness' in floral characters of this monotypic genus suggests a promising matrix for future phylogenetical development into several more restricted, rigid types.—VAN STEENIS.

Excluded

BENTHAM omitted reference to MIQUEL’s publication and only cited the unpublished provisional name MIQUEL had attached to the type exsicata Metz 713. As far as I know no evaluation of MIQUEL’s name was ever proposed and it has fallen into oblivion. The tracing of its identity I owe to Dr R. C. BAKHUIZEN VAN DEN BRINK f.

9. PELLACALYX


Trees. Young branches hollow. Leaves decussate, entire, obscurely serrulate, or rarely serrate, densely or sparsely pubescent with stellate-hairs rarely mixed with simple ones, or simple hairs only, sometimes glabrescent or subglabrous. Stipules with not overlapping margins, minutely stellate-hairy outside. Flowers fascicled or on branched glomerules, 2–8 together, rarely solitary, with minute bracteoles. Calyx (incl. ovary) tubular, lobes (3–)4–5(–6), lower part of the tube inside always hairy. Petals densely puberulous outside, inserted on the margin of the calyx tube; apex denticulate to fringed in various degree. Stamens twice as many as petals, inflexed, inserted on the margin of calyx tube, subulate or deltoid, connate at the base or free, 1- rarely 2-seriate, unequal, 5 long, 5 short (except in P. pustulatus); anthers suborbicular. Ovary inferior, 9–10(12)-celled, each cell with 8–25 fasciculate ovules; style columnar, usually pilose; stigma discoid or capitate, obscurely 8–10-lobed. Fruit a subglobose, few- to many-seeded berry, 1 to several in each axil. Seeds oblong or ellipsoid, black; endosperm fleshy; embryo linear, axile.

Distr. Species 7 or 8, distributed in Burma, Siam, S. China (Yunnan), and Malaysia: Sumatra, Malay Peninsula, Borneo, north Celebes, and the Philippines.

In continental Asia P. yunnannensis H.H.HU seems rather disjunct from the Siam-Burmese generic frontier; it has been described on a fruiting specimen; no material was available to me.

In Malaysia 4 of the 6 species have rather restricted areas in one island or district, but they seem to me all perfectly good species.

Ecol. In forests from the lowland up to 1300 m.

KEY TO THE SPECIES

1. Flowers 4-merous, very rarely with a few 3- or 5-merous flowers together with the 4-merous ones. Calyx mostly glabrous outside, the tube inside with only very short straight hairs in the lower half. Petals denticulate at the upper end. (Flowers 2-3 mm wide).

2. Leaves usually obovate rarely obovate-oblong, 7–11(–15) by 3½–5 cm. Nerves 5–7 pairs. Stipules 3–5(–7) mm. Style not ridged . . . . . . . . . . . . . . . . . . . . . . . . . . 1. P. lobbil

2. Leaves usually obovate rarely obovate, 12–18½ by 3–6½ cm. Nerves 9–11 pairs. Stipules 10–12 mm. Style distinctly ridged . . . . . . . . . . . . . . . . . . . . . . . . . . 2. P. saccardianus

1. Flowers 5-merous, very rarely with a few 4- or 6-merous flowers together with the 5-merous ones. Calyx usually densely or sparsely stellate-pubescent, rarely glabrous outside, the tube inside with a zone of woolly or villous hairs (except in P. symphiodiscus), its bottom covered with very short straight hairs. Petals always with filamentous or subulate appendages at the upper end. (Flowers 4–6 mm wide.)

3. Calyx tube very short, not longer than broad, base acute. Calyx lobes about half as long as the tube. Free filaments isomorphic, 1-seriate, equal in size and shape . . . . . . . . . . . . . . . . . . . . . . . . . . 3. P. pustulatus

3. Calyx tube always longer than broad, base rounded or slightly truncate. Calyx lobes always shorter than the tube. Free filaments dimorphic, alternately shorter and longer, 1- or 2-seriate.

4. Stamens 2-seriate. Filaments of the outer whorl united at the base, free part of the filaments alternately spaced and slightly incurved at the apex; stamens of the inner whorl with an extremely short (knob-like) filament, inserted distant from the sinuses. Calyx tube with only short, straight hairs inside in the lower part. Undersurface of the leaves with stellate hairs mixed with simple ones. Fig. 35b-c . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 4. P. symphiodiscus

4. Stamens 1-seriate, free filaments alternately shorter and longer. Calyx tube inside with a zone of woolly or villous hairs above the straight and short ones.
5. Leaves thin, underneath distinctly pubescent with simple, long, white hairs. Nerves c. 8 pairs. Style usually exserted and glabrous at the upper third ... 5. P. parkinsonii
5. Leaves chartaceous to firmly chartaceous, underneath with densely or sparsely stellate hairs. Nerves 9–14 pairs. Style 1/8–1/2 the length of the tube, pilose or covered with short hairs throughout.
6. Leaves usually with a rather dense, rarely sparse indument of rusty, stellate or more or less lepidote hairs, very rarely subglabrous or mixed with some simple hairs. Calyx tube inside with a zone of woolly hairs. Petals 11/2–2 mm long, the upper end usually with a few short appendages up to 11/2(2½) mm. Calyx lobes reflexed in anthesis ... 6. P. axillaris
6. Leaves underside usually subglabrous with scattered, lepidote-like, minute stellate hairs. Calyx tube inside with a zone of villous hairs. Petals 2½–3½ mm long, the upper end always fringed with many rather long appendages 3–5 mm. Calyx lobes erect in anthesis ... 7. P. cristatus

1. Pellacalyx lobbii (Hook. f.) Schimp. in E. & P. Plf. Fam. 3, 7 (1893) 54.—Paesiantha lobbii Hook. f. in Benth. & Hook. f. Gen. Pl. 1 (1865) 145.—Fig. 34.

Tree up to 35(45) m by 40(65) cm, sometimes with buttresses 1½–5 m high. Bark grey to brown, regularly polygonally fissured. Leaves obovate, obovate-oblong, 7–11(15) by 3½–5 cm, entire to remotely serrulate, glabrous, sometimes lepidote above, rarely puberulous on the midrib and nerves on both surfaces, abruptly acute, base cuneate; nerves 5–7 pairs, slightly elevated beneath, plane above; petiole 6 mm. Stipules 3–5(7) mm long. Calyx (incl. ovary) narrow, 6½–8 by 2–3 mm, glabrous or sparingly pubescent with minute, stellate hairs without, green, (3–)4(5)–lobed, lobes deltoid, 1½–2 mm long, acuminate. Petals white, slightly obovate, 1½–2 mm long, slightly dentate in the upper half. Ovary 9-celled, style 3 mm long, slightly pilose. Fruit green, subglobose, c. 8 mm diam., calyx lobes erect, very rarely reflexed. Seeds ellipsoid, 1–2 by 1 mm.

Distr. Malaysia: Borneo (common), and Sumatra (Palembang, Asahan).


Uses. Wood fairly heavy, yellowish-brown, occasionally used for rafters and fuel.


Note. P. lobbii is closely related to P. saccardianus, and most specimens of it were misidentified as belonging to the latter species. They can easily be separated by the leaf shape and the floral structure.


Small tree up to 15 m by 25 cm. Young branches puberulous. Leaves elliptic-oblong to rarely obovate, 12–18½ by 3–6½ cm, entire, rarely with fascicles of hairs or serrulate, usually glabrous, rarely with minute stellate hairs on the veins, sometimes also on both surfaces of the young blades, shortly acuminate, base rounded to cuneate; nerves and veins elevated beneath, visible or slightly elevated above; petiole 8–10 mm. Stipules 10 mm long. Calyx (incl. ovary) glabrous or short-sparingly hairy outside, 5½–9 by 3 mm, (3–)4(5)–lobed, lobes deltoid, 2 mm long, acuminate, tube cylindrical c. 3 mm long. Petals obovate, 1½–2½ mm long, apex rounded sometimes slightly emarginate and denticulate. Ovary 9-celled; style distinctively ridged, 3 mm long, with short, straight hairs; stigma discoid and slightly lobed. Fruits subglobose, glabrous, 10 mm diam., greenish-yellow when ripening. Seeds 1½–2½ mm long, ellipsoid.

Distr. Malaysia: Malay Peninsula.


Vern. Huka hurgu, kauv johor, mënbuloh rimba, piango jantan, M.

Note. The leaf size and shape in P. saccardianus is more variable than in P. lobbii. Corner recorded that the leaves may be occasionally in whorls of three.

Fig. 34. Stem-base of Pellacalyx lobbii (Hook. f.) Schimp. in the forest reserve Bajunglintjir, Aug. 1919 (Endert).

Tree up to 18 m by 25 cm. Young branches sparingly puberulous. Leaves elliptic, ovate or slightly obovate, entire or rarely obscurely glandular-toothed, 11–17 by 4–7 cm, abruptly acute, base cuneate, midrib elevated beneath, depressed above; nerves 6–8 pairs, slightly elevated beneath, distinct above; petiole c. 1 cm, glabrous, or slightly pubescent. Stipules 6–8 mm long. Calyx (incl. ovary) subcampanulate, acute to the base, sparingly stellate-puberulous or glabrous; lobes 5(–6), deltoid, acute, 2–3 mm long; tube short 2 mm long, densely villous within, its bottom covered with short straight hairs, the long hairs falling off in fruit, the short ones persistent. Petals white, obovate rarely suborbicular, 2—3 1/2 mm long, apex obtuse, sometimes with 1–3 subulate appendages, base narrowed. Stamens equal. Ovary half the length of the calyx tube; style columnar, c. 3/4 the length of the calyx tube, covered with short, straight hairs, stigma capitate, Glabrous or with sparse straight hairs at the base; stigma discoid, 8–9-lobered, or 4–5-lobered and then each lobe bifid, lobes slender, reflexed. Fruits globose, 12–15 mm diam. Seeds elliptic-oblong, obtuse at both ends, 2 by 1 mm, slightly areolate.

Distr. Malaysia: Philippines (Leyte, Luzon, Mindanao, and Samar), and N. Celebes (Minahasa). Ecol. Primary forests from the lowland up to 900 m.


4. Pellacalyx symphiodiscus Stafff, Kew Bull. (1898) 224; Merr. En. Born. (1921) 422.—Fig. 35a–e.

Shrub or small tree up to 12 m tall. Branches and branchlets covered with rusty-stellate hairs. Leaves ovate-oblong to obovate-oblong, 9–19 by 3 1/2–7 cm, shortly acuminate to acute, base rounded or acute, margin with tufted hairs, sometimes glabrous; midrib and nerves elevated beneath, slightly depressed or plane above; petiole 4–10 mm, with minutely stellate hairs. Stipules 13 mm long. Calyx (incl. ovary) cylindric or slightly campanulate-tubular, 9–12 by 4–5 mm, densely stellate-hairy outside, lobes 5(–6), deltoid, c. 2 mm long, acuminate, lower part of the tube inside with short, straight hairs; pedicels 6–10 mm. Petals obovate-oblong, 1 1/2–2 1/2 mm long, top fringed with filamentous, up to c. 2 mm long appendages. Ovary half the length of the calyx tube; style columnar, c. 3/4 the length of the calyx tube, covered with short, straight hairs, stigma capitata,

Distr. Malaysia: Philippines (Leyte, Luzon, Mindanao, and Samar), and N. Celebes (Minahasa). Ecol. Primary forests from the lowland up to 900 m.


Fig. 35. Pellacalyx symphiodiscus Stafff. a. Habit, x 2/3, b. undersurface of a portion of leaf, x 5, c. longitudinal section of flower (petals removed), x 3, d. young fruit, x 4/3, e. seeds, x 13.—P. axillaris Korth. f. Longitudinal section of flower (petals removed), x 3.—P. parkinsonii Fischer. g. Longitudinal section of flower (petals removed), x 3, h. petal, x 7, i. stamen, x 11 (a, b, d, e Ramos 1427, c Haviland b.q.v.f., f Haviland & Hose s.n. = 2312, g–i Kerr 12134).
slightly grooved. *Fruits* subglobose, c. 9 mm diam., calyx lobes erect. *Seeds* ellipsoid, 1½ mm long, slightly transversely striate.

**Distr.** Malaysia: Borneo (Sarawak).

**Vern.** Mura buloh.

5. **Pellacalyx parkinsonii** FISCHER, Kew Bull. (1927) 311, with fig.; CRAIB, Fl. Siam. En. 1 (1931) 599.—Fig. 35g–l.

Tree up to c. 18 m tall. Branchlets sparsely pubescent with minutely stellate hairs. *Leaves* elliptic or elliptic-oblong, 10–19 by 5–7 cm, entire, thinly white-hairy beneath, with rather scattered, short, simple hairs above, especially on the midrib and nerves, abruptly acute, base rounded or cuneate; midrib elevated beneath, depressed above; nerves slightly elevated beneath, visible above; petiole 7–10 mm, pubescent. Pedicel c. 7 mm. *Calyx* (incl. ovary) oblong, 8–12 by 3–5 mm, minutely stellate-hairy outside; lobes 5–6, ovate, acuminate, 2–3 mm long; tube inside villous in the lower half down to c. 1 mm of the basal part which is, as the bottom, covered with very short, straight hairs. *Petals* white, obovate (sub-orbicular when young), 2–3 mm long, fringed with filamentous, c. 1¼½ mm long appendages in the upper half or third. *Ovary* c. 1½ to 1½ of the length of the calyx tube, 10-celled; style columnar, 6–8 mm, slightly exerted, covered with short, straight hairs below, glabrous in the upper third; stigma capitate, flat, slightly lobed. *Fruit* unknown.

**Distr.** Burma (Mergui, Victoria Is.), Siam (Kamala, Pato), not yet found in *Malaysia*.

**Ecol.** In forest from the lowland up to 1200 m.


Tree up to 24 m by 60 cm, trunk straight, monopodial, rather slender, buttresses up to 1 m. Branches stiffly horizontal, twigs rusty pubescent. *Leaves* drooping, oblong rarely obovate-oblong, 10–20 by 5–6 cm, densely stellately rusty-pubescent beneath, scattered hairy and glabrescent to glabrous above, acute, abruptly acute, or rarely acuminate, base obtuse to rounded, margin entire to serrulate; midrib prominently elevated beneath, slightly elevated above, nerves 9–12 pairs, ascending, elevated beneath, plane or slightly depressed above; petiole 5–8 mm. Stipules 1–1½ cm long, rusty pubescent. Inflorescence densely rusty-pubescent. Pedicels 1–2 cm. *Calyx* (incl. ovary) oblong, c. 10 mm long, base acute, densely pubescent without; lobes 5–6 deltoid, 1½ mm long; tube densely woolly hairy inside at the base. *Petals* yellowish green or white, broad-elliptic, obtuse rarely emarginate, sometimes the apex with filamentous appendages 1½(–2½) mm long, soon caducous. *Ovary* c. 1 by 4 mm, 10-celled; style 3 mm, pilose. *Fruits* ovoid or subglobose, c. 10 by 8 mm, c. 18 by 16 mm when fresh sec. *CORNER*, calyx lobes reflexed. *Seeds* oblong, obtuse at both ends, c. 1½ by 1 mm, obscurely striate.

**Distr.** Malaysia: Sumatra, Malay Peninsula, Borneo, and the Philippines (Mindanao).

**Ecol.** Common in damp lowland primary and secondary forests, especially along streams, up to 1300 m. According to *CORNER*, *l.c.*, it develops in swampy ground loop-like breathing roots like some mangrove trees. *Fl*. April–Dec., *fr.* Jan.–June. Uses. According to *HEYNE* the timber is red, hard, and heavy and would be durable under roof.


Note. *CORNER* recorded the flowers occasionally 6-merous.

7. **Pellacalyx cristatus** HEMSL. in Hook. ic. Pl. 16 (1886) t. 1546; RIDL. Kew Bull. (1938) 282.

Small tree up to c. 9 m tall. *Leaves* narrowly oblong to ovate-oblong, 10–17 by 3–5 cm, gradually acuminate, base rounded, rarely cuneate, margin serrulate to serrate; midrib elevated beneath, depressed above; nerves elevated beneath, visible above; young leaves with minute, scale-like, short, stellate hairs on both surfaces, glabrescent; petiole 7–10 mm. Stipules 1½ cm long. Pedicels c. 7 mm. *Calyx* (incl. ovary) green, 7–12 by 4 mm, with scattered, minute, scaly, stellate hairs outside; lobes 5–6, deltoid 2 mm long; tube cylindrical, slightly contracted at the middle, with a zone of villous hairs near the base. *Petals* green, elliptic, 2½–3½ mm long, the upper end fringed with filamentous appendages up to 5 mm long. *Ovary* c. 2 mm long, 10-celled; style columnar, slightly ridged, covered with short straight hairs; stigma capitate, slightly grooved. *Fruits* subglobose, c. 1 cm in diam., calyx lobes erect. *Seeds* ellipsoid, transversely striate, c. 1½ mm long.

**Distr.** Malaysia: Borneo (Dallas, Mt Kinabalu, Sarawak, and Landak).

**Ecol.** On mountain ridges, 400–900 m.

**Excluded**
