FLORA MALESIANA

series i - Spermatophyta

Flowering Plants

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CONIFERALES (D.J. de Laubenfels, Syracuse, N.Y.)

General Introduction

In spite of generalized impressions sometimes advanced about the decline and decrease of the Gymnosperms through the enormous development of the Angiosperms in the Cretaceous and their rapidly accelerated development in the Tertiary, it must be realized that this impression is confusing as far as Coniferales are concerned.

It is of course a truism that the Gymnosperms are completely outnumbered in genera and species by the Angiosperms, the latter occupying terrain earlier beset by Gymnosperms. It must be realized, however, that possibly the almost entirely woody Gymnosperms did never have the potential for producing such immense numbers of genera and species as now found among the Angiosperms. This statement is also valid for the Coniferales.

The Coniferales were only part of the Cretaceous richness in Gymnosperms and whereas many Gymnosperm groups became extinct or lived on with meagre remains, Coniferales — though proportionally with few genera and few species — still represent a most essential part of the world’s standing timber and involve a huge biomass through their sociability and their morphology: usually a large size and the little tapering of their cylindric boles.

The ‘decline idea’ is thus not valid for the Coniferales and this is further validated by their extremely wide ecological capacity, as they thrive from the Arctic to the Antarctic, in all major parts of the globe, in the lowland, the hills and the mountains, and in the tropics from the seashore almost to the alpine zone, a colossal range, among the Angiosperms shared or approached by only very few families, e.g. Ericaceae and Fagaceae.

This universal presence is also due to their most diverse ecological capacities. Coniferales are represented on the permafrost of the taiga as well as in hot semi-deserts, on all sorts of soils, from mineral-rich to mineral-poor, even in peat-swamps, enabling them to stand all sorts of environmental conditions.

In the forest vegetation they show not seldom a high power of competition, often leading to dominance or codominance, often coupled with longevity.

Some are aggressive and tend to fill gaps in the vegetation by possessing nomad ecology.

Seed is mostly produced in ample quantity; seedlings may be shade-tolerant or -intolerant. A number of species are distinctly fire-resistant. From these facts can be concluded that Coniferales are not just ‘on the decline’, but that they form still a most successful super-order of the Gymnosperms.

Distribution. With 12 genera the Coniferales are well represented in the Malesian tropics, while elsewhere in the world only in the rich Sino-Japanese flora is there a substantially larger concentration of conifer genera; nearby Taiwan for example has 15 genera (only four of which are shared with Malesia, viz. Nageia, Podocarpus, Taxus, and Pinus). Eight wide ranging conifer genera of Antarctic affinities are today well established throughout Malesia up to the westernmost margins and four of these extend well beyond onto the continental part of Asia (Dacrycarpus, Dacrydium, Nageia, and Podocarpus). All are strictly confined to rain-forest habitats.

Seven of these have seeds dispersed by birds, the eighth (Agathis) has small seeds with large membranous wings. Except for the genus Phyllocladus, these genera are well represented at low and medium elevations and it is not necessary to imagine long-range dispersal between isolated mountain peaks as far as altitude is concerned. We have, however, to keep in mind that through the insular physiography of Malesia there may have been the necessity of crossing sea barriers. Unfortunately too little is known in detail about the precise distribution of land and sea in the course of the Tertiary.

Two Holarctic conifer genera (Taxus, Pinus) penetrate into western Malesia and two more Antarctic genera are at present confined to the eastern half of Malesia (Libocedrus, Araucaria). The fossil record, although incomplete, suggests that the situation was quite different as late as the Miocene.
Fossil record. Palaeozoic floras of Permo-carboniferous age are known from Sumatra and New Guinea. The Sumatra material shows affinities to Euramerican floras and, by the presence of Gigantopteris especially to the Cathaysian flora of Southeast Asia (Jongmans & Gothan, 1935). In New Guinea fossil floras of Gondwana type as well as with a Cathaysian character are found (Jongmans, 1940; Lacey, 1975), leading Hamilton (1979) to suspect that at that time New Guinea was situated at mid-latitudes with land connections both to Sumatra and the Australian continent.

A Mesozoic flora dated as Neocomian (Lower Cretaceous) has been described by Smiley (1970) from the Malay Peninsula. Although considerably poorer in species than the Palaeozoic ones, it is of interest because of the presence of two conifer genera, Frenelopsis of Cupressaceous affinity preserved as macrofossils and the fossil pollen genus Classopolis, derived from the extinct family of Cheirolepidaeae. Frenelopsis ranges from Lower to Upper Cretaceous and was widely distributed in North America, Europe and Asia. Classopolis is cosmopolitan and ranges from the Jurassic to the Upper Cretaceous. The general composition of this Lower Cretaceous flora clearly suggests links to Eurasian and North American floras.

Muller (1968) has described a rich and well preserved Upper Cretaceous microflora from Sarawak, NW. Borneo, in which Caytoniales (Caytonipollenites), Podocarpaceae (Zonalipollenites), Araucariaceae (Araucariacites), Cheirolepidaeae (Classopolis), Cupressaceae or Taxodiaceae (Inaperturipollenites) and a rich assemblage of bisaccate pollen grains of Pinaceous or Podocarpaceous affinity represent the Coniferalean element. Although most of these genera are cosmopolitan, the presence of bisaccate genus Rugubivesiculites is of considerable interest, since this has been recorded only from the northern hemisphere.

Tertiary floras from Malesia, which include both macro- and micro-floras, are mainly restricted to the post-Eocene and, for the Angiosperm component, show a composition not unlike the present one (Kräusel, 1929; Posthumus, 1929, 1931; Anderson & Muller, 1975). However, the reliability of identification of many of these records, especially the older leaf remains, is questionable. An exception may be made for wood of Dipterocarpaceae, for which family also fossil pollen records are available, showing that, at least in the post-Eocene, this family was well established in West Malasia.

For Gymnosperms the situation is different and the presence of pollen of Ephedra, Pinus, Picea and Tsuga in the Oligocene and Miocene of NW. Borneo, accompanied by pollen of Alnus, its disappearance from the record at the end of the Miocene, followed by immigration of Phyllocladus and Dacrycarpus in the Plio-Pleistocene suggests considerable change in the coniferous elements in West Malesia (Muller, 1966; Stein, 1978). Dacrydium pollen, which was absent in the Upper Cretaceous-Paleocene assemblages studied by Muller (1968) from Sarawak is first recorded for the Oligocene.

Muller (l.c.) has attributed the disappearance of the Asian-montane element to peneploanalysis, but Stein (1.c.) believes that they also may have suffered from competition with other forest elements in submontane habitats. Significantly, Pinus has survived longest in NW. Borneo and is still present today in N. Sumatra and the Philippines.

Khan (1976) has established the presence of pollen of the following typical southern conifers in the Upper Miocene and Pliocene of New Guinea: Dacrydium, Dacrycarpus and Microcachrys, the latter disappearing from the record at the end of the Pliocene. Here the southern conifers are accompanied by Nothofagus.

This evidence indicates that, in Borneo, boreal conifers have been replaced by Antarctic ones, immigrating from the direction of New Guinea. Dacrydium may have reached western Malesia already in the Oligocene, while Phyllocladus and Dacrycarpus only reached Borneo in the Pliocene. In New Guinea the latter two were present earlier. This reflects the collision of the northwest moving Australian plate with the Celebes-Borneo area in the mid-Tertiary (Hamilton, 1979; Stein, 1978). Before this period Antarctic conifers may have been absent in West Malesia which has remained, at least since the Cretaceous, within reach of the Southeast Asian continent, as indi-
cated by the presence of boreal conifers, both in the Cretaceous and Tertiary of the Malay Peninsula and Borneo. New Guinea presumably had been in close contact with Australia since the Palaeozoic.

From Florin’s masterwork (1963) one could deduce that Cryptomeria-like conifers should have occurred in Malesia, since they are found fossil in the Triassic of both Asia and Australia, fading away in the early Cretaceous. Similarly, relatives of Austrotaxis of New Caledonia, Athrotaxis of Tasmania and various Cupressaceae, especially Libocedrus, all genera with Holarctic affinities, must have occurred in the Cretaceous of Malesia, inasmuch as these genera flourish beyond to the east and south. There are also reports of fossils belonging to Podocarpaceae and Araucariaceae from Holarctic regions and they could have migrated through Malesia at the same time, but only fossil Araucaria pollen is known from the Upper Cretaceous of Borneo.

The main conclusion from the fossil record is that, at least from the Lower Cretaceous onwards till the Oligocene, virtually no southern conifers reached West Malesia where in the Upper Cretaceous and, more strikingly, in the Oligocene and Miocene a distinct Asian conifer element was present. Only at the mid-Tertiary collision of Australia + New Guinea with West Malesia did an invasion of southern conifers take place, in stages leading to the present-day distribution pattern. However, it is clear that large gaps in our knowledge still exist and it seems most desirable to have reliable records from the Upper Cretaceous and Lower Tertiary of Java, Celebes, the Lesser Sundas Islands and New Guinea to allow a further confirmation of what is at present still a very tentative picture.

I appreciated very much the collaboration of the late Dr. J. Muller (Leiden) in framing this paragraph on the fossil record.


Ecology. As mentioned above, the ecology of conifers shows a considerable variation and a summary may facilitate and stimulate the reader to delve in the text for further details.

No main vegetation type, except aquatics and very dry seasonal lowland, is in Malesia devoid of conifers. Though varying in density, they form an essential part of the forest and other vegetation. In the collecting numberlists of the Indonesian Forestry Service they form from one half to two percent of the total, depending on the area. Biomass of standing timber will attain probably a much higher percentage.

Conifers are among the tallest tree species in Malesia. Many possess massive straight boles, mostly cylindrical, rising to or over the canopy with a height of 40–50 m. Some reach still larger dimension and tower as emergents over the canopy, equalling the tallest size of the largest Dipterocarpaceae; notably species of the genera Agathis, Araucaria and Pinus may reach 70–75 m in height, the occasional record being a tree of Araucaria hunsteinii of 89 m (B.Gray, J. Ecol. 63, 1975, 273).

Small conifers are also well represented in Malesia. Mature specimens of no more than 1 m in height are found of Nageia maximus in Bornean swamp forests and of Podocarpus micropedunculatus on the edges of clearings in and near Brunei. Small conifers are also found in scrub in the mountains, e.g. Dacrydium medium on G. Tahan (Malaya). Colonies of prostrate Podocarpus brassii var. humilis occur on the mountains of New Guinea. Stunted specimens of many other species are found in poor, rocky habitats in the mountains.

Altitude. Lowland species are for example Podocarpus polystachys which may be locally com-
mon (e.g. in Malaya) on sandy bluffs on the seashore and on low limestone outcrops. *Dacrydium pectinatum* and *D. micropedunculatum* can be locally common on low lying sand shoals (e.g. in S. Borneo), while the former along with *Agathis borneensis* may form nearly solid stands on lowland podsols (kerangas) or lowland peat-forest in Borneo almost at sea-level. The latter occurs sometimes in such quantity as to be worthy of exploitation for timber.

A genus 'descending' to low altitude is *Pinus*: in West Luzon and in Mindoro. *Pinus merkusii* reaches sometimes as low as 50 m altitude as a pioneer in pyrogenous grasslands and up to 150 m on volcanic ash streams (lahars) and lavastreams in N. Sumatra. Descent has also been reported for *Araucaria cunninghamii* on steep rocky ridges and spurs, occasionally as low down as 75–100 m, the 'normal' low parameter being c. 500 m.

With increasing elevation conifer populations become more frequent. At high altitudes species become fewer but it is not uncommon to find subalpine forest, whether or not turned into mossy forest, dominated by one or a few species of conifers. For example, the summit forest on Mt Leuser (N. Sumatra) is often dominated by a drooping conifer, *Dacrycarpus imbricatus var. curvulus*; on Mt Suckling (Papua New Guinea) *Araucaria cunninghamii* is the dominant conifer.

**Climate.** As mentioned above, in Malesia conifers shun the seasonally very dry lowlands of eastern Java and the Lesser Sunda Islands. They are also rather rare in the mountain rain-forest in this climatically seasonal belt, but *Dacrycarpus imbricatus* is found as far as Timor as a distinct constituent of the mountain forest; after devastation single trees may even survive as relics in pyrogenous grassland, adorned with beards of *Usnea*.

**Soils.** Many conifers prefer nutrient-poor soils, and are often even confined to them, but there are also species which are mostly found on richer latosols, e.g. *Dacrycarpus imbricatus* which grows excellently on young volcanic soils.

As mentioned above, quite a number of conifers grow, sometimes in great quantity, on alluvial sandflats or on podsolized sands and sandstone (kerangas) and in peat-swamps, but they are not always limited to such habitat, as both *Dacrydium pectinatum* and *Agathis borneensis* are also commonly met as scattered individuals in middle elevation rain-forest.

Some conifers, particularly of the genus *Podocarpus*, thrive on ultrabasic bedrock in Malesia (as well as in New Caledonia), dense stunted forest with plenty of *Podocarpus confertus* in Borneo and *Podocarpus ridleyi* in Malaya are examples.

On Mt Soroako (Celebes) scattered specimens of *Agathis*, *Dacrydium*, *Podocarpus* and *Nageia* are found on ultrabasic bedrock. This may also be true for localized populations of *Podocarpus deflexus* of Malaya and N. Sumatra.

More precise data about possibly specialized soil types are unknown for a number of species with restricted ranges, e.g. *Podocarpus levis* in Central Malesia, *Dacrydium medium* in Malaya and Sumatra, *Dacrydium ericoide* in Borneo, *Dacrydium spathoides* in New Guinea, and *Agathis flavescens* in Malaya.

A curious conifer taxon is *Dacrydium cornwalliana* which is found in the mountains of West New Guinea (BW 697) restricted to deep black peat, reminding of the habitat of some *Dacrydium* and *Dacrycarpus* species occurring in peat under temperate conditions in New Zealand; both the former species and *Dacrycarpus steupii* are the only peat-swamp forest trees of Malesia so far known. Fig. 14.

As to limestone, it can in general be said that conifers are rare on this bedrock. In western Malesia *Podocarpus polystachys* occurs on low limestone outcrops; in Borneo and Celebes *Agathis* is also found on soils derived from limestone, and *Dacrycarpus imbricatus* is found on similar soils on Mt Perdido in Timor.

**Antecology.** In general Malesian conifers are constituents of the rain-forest and as such are dark-germinators, their seedlings growing up under very low light intensity. Germination and upgrowth of seedlings in shade is also the rule for high altitudes, but pioneering of conifers on disturbed, pyrogenous open land, at 2500–3000 m altitude was observed for *Libocedrus* and *Phyllocladus* by HooGLAND.
A clear exception are the species of *Pinus, P. merkusii* and *P. kesiya*, which are light-demanding germinators. They may form permanent, dominant climax stands on very steep, rocky mountain slopes where no litter remains to prohibit germination. One can observe this on the Leuser massif in N. Sumatra at some 2500 m altitude. This occurrence is rare, the main occurrence is of a temporary nature, pioneers starting a succession, viz. bare soil of talus, volcanic mudstreams (lahars), lavastreams, earth- and rockslides, places torn open by earthquakes, and further man-made pyrogenous grassland. In the latter they occupy in W. Luzon and N. Sumatra large surfaces which are consequently converted into large, mostly savannah-like stands of *Pinus*. Under undisturbed conditions secondary forest and finally new primary forest will grow up among the pines, the litter and shade of which prohibits their own regeneration. But as *Pinus* is a long-lived pioneer, under such conditions the pines — which may possibly reach an age of 200–300 years — will remain tapering over the later primary forest.

Seed of many tropical Malesian conifers rather soon loses its germination power, in line with other rain-forest trees. That of *Araucaria hunsteinii* is down to zero in ten weeks. According to WHITEMORE the viability of seed of *Agathis* drops rapidly and also that of *Araucaria cunninghamii*. This is also valid for *Pinus merkusii*. On the other hand seed in *Podocarpaceae* may require as much as a year to germinate.

To the autecology also belongs the matter of the mycorrhiza, but unfortunately little is known of this relation. It is certain that one of the exomycorrhiza of *Pinus merkusii* is a *Boletus*, but it seems that for *Pinus* and probably other conifers more genera of fungi are involved. BEVEGE (1968) and HONG (Mal. Flor. 41, 1978, 225) have established that in the species of *Araucaria* an unidentified species of *Endogone* forms an endotrophic mycorrhiza.

Sociology. Mostly conifers occur scattered through the forest, but a number of species have a tendency to occur socially in places. By their large mature size they are then often observed as emergents. It must be remarked, however, that occurrences are often local: *Agathis* is for instance in Celebes above some 1600–2000 m (where it rather suddenly becomes abundant) and in the Moluccas present in most mountain forests and also in the north of West New Guinea, where it is tapped on a commercial scale, but in Papua New Guinea it is very scarce and local.

The same can be said of *Araucaria* in New Guinea, especially *A. hunsteinii*, which is found as an upper-canopy dominant in the Bulolo area and a few other places, but is elsewhere absent and not found in West New Guinea. In most instances we are ignorant about the underlying cause.

As mentioned above, *Podocarpus polystachyus* is locally common to subdominant in sandy lowland in Malaya and Borneo, and so are *Dacrydium pectinatum* and *Podocarpus micropediumculatus* in Borneo, where the former, sometimes together with *Agathis borneensis*, may form local stands on lowland podsols (kerangas) or in lowland peat-forest, with very acid soil conditions. *Agathis borneensis* may also form locally dense stands in the upper canopy. In passing we remark that hardly ever conifers are found in forest dominated by dipterocarps, with the possible exception of the heath-forest in Borneo. In the West Javanese mixed mountain forest (e.g. on Mt Gedeh) there are three large emergents very common: *Allingia excelsa* (*Hamam.*), together with two conifers, *Dacrycarpus imbricatus* and *Podocarpus bracteatus*. But on Mt Tjeremai, a volcano in W. Central Java, there is between c. 1800–2500 m a very large gregarious dominant stand of *Dacrycarpus imbricatus* only. It remains unclear to what factor in the past this has to be ascribed.

In other islands other species of conifers may be very common or gain subdominance in the higher mountains. In Sumatra for example *Dacrydium elatum* — used for Christmas trees — and on Mts Leuser *Dacrycarpus imbricatus* var. *curvulus*, the drooping pine. A similar role in mountain forest is found with the dense stunted forests of *Podocarpus confertus* in Borneo and of *Podocarpus rideyi* in Malaya on ultrabasic bedrock. Localized subdominance is found: *Podocarpus deflexus* and *Agathis flavescens* in Malaya, *Dacrydium medium* in Malaya and Sumatra, and *Dacrydium ericoides* in Borneo.

Mostly conifers occur scattered in the mixed broad-leaved rain-forest, not infrequently represented by several species; e.g. KALKMAN & VINK found on the Doma Peaks in Central New Guinea.
Libocedrus papuana as an emergent, accompanied by Dacrycarpus expansus, Phyllocladus hypophyllus, and Podocarpus pseudobracteatus (Blumea 18, 1970, 119).


Despite the seemingly homogeneous microscopic structure of the vesselless wood of conifers, there are a number of highly diagnostic wood anatomical differences at various levels of the taxonomic hierarchy which can be profitably used for identification and which can help in the reconstruction of a natural classification. In the Malesian representatives of the Coniferales a number of genera can be immediately recognized on unique, single or combined characters:

Pinus — Vertical and horizontal resin ducts present, cross field pits (i.e., pits from tracheids to ray parenchyma cells) fenestriform or pinoid, ray tracheids present. (N.B.: resin ducts and ray tracheids are absent from all other Malesian Coniferales.)

Agathis and Araucaria — Pits on tracheids alternate and in a closely spaced honeycomb-like pattern ('araucaroid').

Taxus — Tracheids with distinct spiral thickenings.

Libocedrus — Cross field pits strictly cupressoid (i.e., with narrow, included apertures).

Podocarpaceae — The distinction of Podocarpaceae from Libocedrus is fairly subtle: cross field pits in Podocarpaceae often include cupressoid types but almost invariably also other types such as taxodioid, pinoid, or piceoid pits. Most Malesian Podocarpaceae and Libocedrus have fairly common to abundant axial parenchyma in their wood, a feature absent from the other conifers. However, Phyllocladus and at least some temperate species of Dacrydium lack axial parenchyma. Presence or absence of parenchyma has been used as an important character for sectional delimitation in Podocarpus sensu lato by Kaeser, l.c., but some of her observations have been contradicted in a more detailed study by R.N. Patel, New Zeal. J. Bot. 5 (1967) 307–321. The evidence available from the literature at present suggests that the wood anatomical variation pattern within the Podocarpaceae does not coincide with generic delimitation; further studies of well-authenticated samples are needed to assess the taxonomic significance of the wood anatomical variation in this family.

Leaf anatomy can also play a useful role in identification and classification of the Coniferales, as exemplified in the study by J.T. Buchholz & N.E. Gray, J. Arn. Arb. 29 (1948) 49–76 on the systematics of Podocarpus sensu lato and by J.W. Lanyon, A card key to Pinus based on needle anatomy, Min. Conservation, N.S.W., Australia (1966), also including the two anatomically distinct Malesian species Pinus merkusii and P. kesiya. The extensive leaf anatomical literature on conifers is summarized in K. Napf-Zinn, Encyclopedia of Plant Anatomy 8 (1), Berlin (1966). — P. Baas.

Palynology. In general gymnospermous pollen is distinguished from angiospermous pollen by the alveolate-granular structure of the sexine, the lamellate structure of the nexine, and the presence of one distal aperture. With the exception of some primitive ranalian groups Angiosperms have pollen with a columellate sexine, a non-lamellate nexine, and 3 or more equatorial apertures, or have pollen with attributes that can be derived from this basic pattern. The structure of the sexine seems at present the most reliable character.
The only aperture in pollen of Coniferales is always distal. Mostly it is a thin area (leptoma) in the exine, which is often further distinguishable by a different ornamentation. In Araucariaceae this area is large and circular, in Cupressaceae and Taxaceae small and circular; in Pinaceae and Podocarpaceae it is mostly large and oblong. When large, the thin area may also have a hromomegathic function beside participating in the germination process. Sometimes an aperture is difficult to trace.

A remarkable feature of some Coniferales pollen types is the presence of air bladders (wings, sacci) at the distal pole beside the aperture. Araucariaceae, Cupressaceae and Taxaceae have none, but most Pinaceae (except Larix, Pseudotsuga) and Podocarpaceae (except Saxegothaea) have 2 or 3 of them. Grains without bladders are more or less spherical; those with bladders have a spherical, lens-shaped, or oblong corpus.

Most Coniferales pollen is medium-sized (25–50 μm). Pinaceous grains measure (40–)50–70 (–80) μm; the corpus of the likewise saccate podocarpaceous grains are mostly smaller (up to 50 μm). Both cupressaceous and taxaceous grains range from 18 to c. 36 μm. Araucariaceous grain size varies from 40–60 μm (Agathis) to 60–90 μm (Araucaria). In addition Araucaria pollen differs from that of Agathis by the presence of a proximal annular thickening.

There is a great deal of variation with regard to wall stratification and structure. Araucariaceae, Cupressaceae, and Taxaceae have a thick intine compared with the exine. In Cupressaceae the intine is even very thick, often comprising much more than half of the grain volume. A thick intine has the capacity of swelling after moistening and probably plays an important role in the germination process. In Pinaceae and Podocarpaceae the intine is proportionally less thick. The nexine is lamellate in all Coniferales. The sexine is alveolate-granular in Araucariaceae, Cupressaceae, and Taxaceae, in Larix and Pseudotsuga of the Pinaceae, and in Saxegothaea of the Podocarpaceae; in all the rest of the Pinaceae and the Podocarpaceae the sexine offers a columellate-tecitate appearance superficially like the situation in Angiosperms, essentially being a variation of the alveolate structure. In Pinaceae, Podocarpaceae, and in most Araucariaceae pollen the sexine is thicker than the nexine, at least at the proximal side (cappa). In Cupressaceae, Taxaceae, and part of Araucariaceae pollen the nexine is the thickest layer. In the latter three families the surface of the sexine has a perine-like covering, consisting of small (< 1 μm) granules (orubicules), which is absent in Pinaceae and Podocarpaceae.

Air bladders or sacci form a remarkable aspect of the pollen wall of most Pinaceae and Podocarpaceae. Sacci develop by proliferation of the alveolate layer of the wall. Probably they function in both flight and harmomegathy of a grain. All Pinaceae have 2 sacci, except Larix and Pseudotsuga which are devoid of them and are fundamentally different from other Pinaceae. Tsuga mostly has pollen with one distal saccus encircling the aperture. In Podocarpaceae the genus Saxegothaea has no sacchi and is therefore, and also on account of other features, considered as related to the Araucariaceae. In Podocarpaceae there is more variation in respect to the number, shape, and size of the sacchi than in Pinaceae. Pollen grains of Dacrycarpus are provided with 3 sacchi, those of Nageia, Podocarpus, and Prumnopitys with 2. Phyllocladus and Falcatifoliium pollen also have 2 sacchi, but in the first they are very small and in the latter they are narrowly connected around the aperture. In Dacrydium a type occurs which has one fully radiosymmetric saccus around the aperture. Dacrydium has also the Podocarpus-like bisaccate type. Saccate pollen of the extra-Malesian podocarpaceous genera has 2 sacchi (Acemopyle, Parasitaxus) or 3 sacchi (Microcachrys, Pherosphaera). In the latter two genera and in Dacrycarpus sometimes grains occur which have 4, 5 or 6 sacchi due to aberrant tetrad configuration.

Pollen of the extra-Malesian Cephalotaxaceae and Taxodiaceae is largely similar to that of Cupressaceae and Taxaceae.

Coniferales are probably strictly wind-pollinated, the pollen being not sticky, smooth-surfaced, and sometimes provided with sacci. In the former two characters Coniferales pollen resembles some wind-pollinated Angiosperms (e.g. Gramineae, Betulaceae).

References: Erdtman, Pollen and spore morphology/plant taxonomy, Gymnospermae (1957)

General characters of Coniferales are: cuticular waxes of the so-called estolide-type; lignin which usually lacks the syringyl component; seeds which store predominantly starch or oils with unusual fatty acids, i.e. bi-tetra-unsaturated C_{18} and C_{20} acids with an isolated double bond in 5-position; accumulation of cyclitols such as pinitol, sequoyitol and (or) 0-methylmucoinositol in leaves, bark and wood; storage of shikimic and (or) quinic acid in leaves; accumulation of lignans (phenylpropanoid dimers) and (or) agatharesinol-type norlignans in wood, bark, traumatic resins and leaves (here sometimes as glycosides); production and exudation after injury of oleo-resins or gum-resins.

Oleo-resins and gum-resins are deposited in schizogenic canals and cavities which seem to be lacking only in some representatives of Taxaceae. Oleo-resins are mixtures of essential oils and resins; turpentine is the essential oil produced by distillation of oleo-resins obtained from several species of Pinus. Gum-resins are mixtures of essential oil, resin and mucilage; Araucaria is the main producer of gum-resins among Coniferales. The predominant constituents of the essential oils of most Coniferales are mono- and sesquiterpenoids; some members of Podocarpaceae and other families produce appreciable amounts of steam-volatile diterpene hydrocarbons and hence yield diterpene-rich essential oils. The resins of Coniferales are mainly composed of diterpenoids; often diterpene acids predominate. Colophony or resin is the resin part of pine oleo-resins and Manila copal is the hard oleo-resin from Agathis dammara. Amber or succinite is the fossil resin of pines and Kauri copal is fossilized Agathis resin.

Tannins are ubiquitous in Coniferales. They are represented in the taxon exclusively by the so-called condensed tannins and their building stones, the catechins and proanthocyanidins. Gall- and ellagittannins are totally lacking.

Other classes of compounds which seem to be totally absent from Coniferales are iridoid compounds, cardenolides and steroidal saponins. The same seems to be true of triterpenoids of the ursane, oleane and lupane classes, and hence of corresponding saponins.

Triterpenoids are represented in Coniferales by lanostane-type tetracyclic, onocerane-type tetra- and pentacyclic, and hopane-type pentacyclic compounds. Steroids are represented by the ubiquitous phytosterols; moreover, the frequent occurrence of phytocetylsones in rather high concentrations is somewhat typical of the taxon. In the products of steroid and triterpenoid metabolism Coniferales strongly resemble Pteridophytes.

Polyphenolic compounds other than lignans and tannins are accumulated by all conifers but, besides the general occurrence of flavonoids as a group, most classes of compounds and many individual compounds are restricted to taxa of lower levels such as infrageneric, generic and suprageneric entities. The same is true of alkaloids and several other classes of chemical constituents. Some examples to illustrate the situation follow.

Agathisflavone-, amentoflavone-, cupressusflavone-, robustaflavone- and hinokiflavone-type biflavones seem to be nearly ubiquitous in leaves of Gymnosperms, but are lacking in Pinaceae which yielded hitherto only one biflavonoid, the flavone-flavonol dimer abiesin.

Cephalotaxin-type alkaloids occur in all species of Cephalotaxus.

All members of the genus Taxus (but not the other representatives of Taxaceae) produce taxane-type diterpenoids which are often esterified with the so-called Wintersteiner acid, which is a dime-
thylamino derivative of a hydroxydihydrocinnamic acid; the resulting nitrogen-containing constituents, such as the taxines and related compounds, are the 'Taxus alkaloids'; they are accompanied in Taxus by the cyanogenic glucoside taxiphyllin. The latter too seems not to occur in other genera of Taxaceae, but is present in Metasequoia and in some species of Juniperus.

In Podocarpaceae several tendencies concerning secondary metabolism are recognizable: essential oils with appreciable amounts of diterpene hydrocarbons, ferruginol- and totarol-type phenolic diterpenes, bitter and biologically highly active mono- and bisnor-diterpenoid lactones such as nagilactone, and accumulation of large amounts of phytoecdysones such as the maki-stones and the podedcysones are examples of such family-characteristic tendencies. At the same time the family is the only representative of conifers which makes use of anthocyanins to advert its diasporas: red to pink fleshy parts of Dacrydium, Phyllocladus, and Podocarpus diasporas contain an array of anthocyanins; anthocyanins may also be present in young leaves and strobili; the latter feature is not restricted to Podocarpaceae, however.

Antibiotically active carvacrol and thymol derivatives and tropolone-type mono- and sesquiterpenic compounds are present in the wood of many Cupressaceae, including Libocedrus s.l.

Exudates of many species of Araucaria contain larger amounts of mucilage than most other conifers; they are true gum-resins; Anderson and Munro observed 20–80% of mucilage in Araucaria-exudates with 10–20% of uronic acids, 50–70% galactose and up to 7% of the rather unusual sugar acofriose (3-0-methylrhamnose) as building stones. Acofriose is also present in mucilages of Cycadaeae.

An array of low-molecular phenolic compounds, such as hydroxyacetophenones, stilbenes, dihydrostilbenes and phenylpropanoids (monolignols) is known from Pinaceae; they occur free and as glycosides and often have a taxon-characteristic distribution, and hence can be useful as taxonomic characters. Pinosylin and its monomethyl ether have been interpreted as phytoalexins of Pinus because their synthesis is induced in the softwood after infection; normally these antifungal compounds are present in Pinus only in hardwoods and in barks.

Flavonoid patterns were taxonomically exploited by many phytochemists; flavonoids yielded characters applicable at all levels of the taxonomic hierarchy. Just one example: C-glycosflavones have not yet been traced in Araucariaceae, Cephalotaxaceae, Cupressaceae and Taxaceae, and seem to be restricted in Pinaceae to Abies, Keteleeria, Tsuga and Larix; moreover, they were detected in Podocarpaceae in some species of Podocarpus.

In recent times detailed analyses of essential oils were performed during biosystematic studies of a number of American conifers; the results proved to be rather promising; in many instances a better understanding of complex population structures was made possible by such investigations.

As a whole Coniferales are chemically well characterized by the general presence of several classes of chemical constituents and by the total absence of others. Moreover, secondary metabolites yielded a large number of characters applicable at different levels of the taxonomic hierarchy. — R. Hegnauer.

Systematics. Generic delimitation. Four genera replace earlier broad treatments of the genus Podocarpus, all of which I recognized in 1969 (J. Arn. Arb. 50: 274–369); in part they had formerly been distinguished as sections of this genus. Certainly there exist substantial relationships between them, but it must be well recognized that this is no sufficient reason for adopting a one-genus concept for the whole. As a matter of fact the morphological differences between these sharply distinct genera are at least of equal taxonomic 'weight' as compared to the differences between many other groups of northern hemisphere coniferous genera unequivocally distinguished. On the other hand I cannot adhere to the recent splitting of the genus Libocedrus. For further argumentation I refer to the text under the genera in the taxonomic part.

Cultivation. A fairly large number of exotic conifers are cultivated in Malesia, in part for testing them for forestry purposes, reforestation, in part as ornamentals in gardens and parks. It falls outside the scope of this Flora to treat the cultivated exotics like the native species, none
of them is naturalized. Quite some have been incorporated in Backer & Bakhuizen van den Brink’s Flora of Java (Vol. 1, 1963, 87–95) which may be useful for their identification. A more general work that I can advise for identifying cultivated conifers is W. Dallimore & A.B. Jackson, A handbook for Coniferae and Ginkgoaceae, 4th ed., revised by S.G. Harrison (1966).

Of native conifers several are in cultivation for various purposes. Agathis philippinensis is frequently cultivated as a wayside tree in W. Java and probably elsewhere, and occasionally found in parks. Araucaria cunninghamii is frequently planted in parks and gardens as an ornamental tree. Araucaria hunsteinii, of which very large dominating complexes are found in some places in the Bulolo area in Papua New Guinea, is exploited from native growths, but the cleared territory is replanted with it on a large scale, because of the valued timber used for plywood. Dacrydium elatum is, according to Corner, widely planted in the hills in Malay for ornamental purpose. Finally Pinus merkusii is widely used for reafforestation and in addition for timber and the tapping of resin for the turpentine industry; notable huge complexes are found at Aek na Uli on the eastern hills around Lake Toba in N. Sumatra; large complexes are also found in S. Celebes; it is also used as an ornamental in parks and gardens.

In nurseries, especially of Agathis, a single specimen of an older seedling already provided with mycorrhiza is planted in the centre of the beds in order to speed upgrowth of seedlings.

An important point for silviculturists is the fact that, as mentioned above, the seed of many tropical conifers soon loses germination power. For Pinus merkusii, which is distributed on a large scale, very special care must be taken to keep the sundried seed in sealed metal containers with charcoal; even with these precautions a rather rapid loss of germination power takes place. This has been subject to extensive study. Keeping seed storage cooled is also applied.

The timber of the large-sized species of all genera is most valuable, but only few are planted for this purpose on a large scale. This is in part due to the fact that most species growth is slow, with the exception of Pinus species. It depends also for what purpose the timber is used, for pulp, sawn timber or high quality veneer. Whitmore mentioned for Agathis in Java a rotation period of 30 years for pulp, and 50 years for veneer. For Araucaria in New Guinea a rotation period of 60 years is reckoned for plywood.

Economic uses. As mentioned above all larger species of all genera provide excellent timber. In addition, species of Agathis are tapped large-scale, especially in the Moluccas and New Guinea, and to a less extent in Borneo and Celebes, for the resin (‘copal’ or ‘manila copal’, wrongly ‘damar’). In addition to the resin obtained from living trees, large bodies of subterranean resin of vanished trees are collected. The market for manila copal declined after the introduction of oil-based synthetics but there is still a use for special purposes.

The resin of Pinus merkusii, and to a less extent that of P. kesiya, is collected for the turpentine industry. In N. Sumatra, in the vicinity of Takengon, there was a large factory for this purpose. See C. Brandts Buys c.s. (Meded. Proefstation Boschwezen 19, 1928).

References in synonymy. A remark must be made about the references in the synonymy of the species. I have omitted in many cases the mention of names without description or notes which occur in so many local plant lists and casual enumerations. This was made especially urgent by the fact that the names used in these lists, e.g. of Agathis and Podocarpus, are often wrong according to my classification. To account for all these ‘non’ or ‘sensu’ names would have caused an unnecessarily complicated synonymy. If collectors’ numbers were cited in these local lists, proper identity of these records can easily be checked by means of the ‘Identification Lists of Malayan Specimens’ n. 61 (1982), which was issued separately by the Rijksherbarium, Leiden.

**KEY TO THE FAMILIES**

*based on sexual characters*

1. Ovules strictly terminal on short fertile shoots, erect, wingless. Pollen sacs usually several on each microsporophyll. Two single trace cotyledons .................................................. Taxaceae

1. Ovules produced on axillary structures of a fertile shoot.
2. Seed usually cupped by a fringing epimatium or the inverted seed even completely enclosed by a leathery or fleshy structure, rarely naked and rarely erect, solitary, wingless. Reduced cone bracts often fleshy. Two pollen sacs on each microsporophyll. Cotyledons usually two fused pairs, occasionally more.

**Podocarpaceae**

2. Seed produced on an erect, woody, rarely fleshy scale which is often fused with the fertile bract, erect or inverted, occasionally solitary, more often two or more per fertile scale, usually with one or more wings(s).

3. Fertile bract and scale fused, sometimes indistinguishable. Seeds solitary or in variable numbers. More than two pollen sacs on each microsporophyll. Cotyledons usually 2-4.

4. Seed inverted, solitary; large mature seed cones disarticulate. Leaves spirally placed or opposite-decussate and distant. Cotyledons four or two fused pairs. **Araucariaceae**

4. Seed erect, solitary or in variable numbers; small mature seed cone does not disarticulate. Leaves crowded, opposite-decussate or whorled. Cotyledons two or occasionally more, not fused. **Cupressaceae**

3. Fertile bract separate from scale and not woody. Seeds two per scale, inverted, each with a single wing.

Two pollen sacs per microsporophyll. Leaves spirally placed. Cotyledons more than two. **Pinaceae**

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**TAXACEAE**

The affinity of *Taxaceae* has been much debated, with many authors favouring a separate order, *Taxales*, for it, a position with which I tend to agree. Further questions are raised concerning the grouping of other families with *Taxaceae*, as against the other conifer families, based on the lack of seed cones, fleshiness of the mature fruit, or lack of a fertile seed scale. *Cephalotaxaceae* (not in Malaysia) has a reduced seed cone structurally organized quite differently from other conifers and vegetatively strongly resembling *Taxaceae*, so I would group these two together. All other conifer families show seed structures easily derivable from a compound cone with ovules produced on the upper face of a fertile scale which grows in the axil of a bract. Although *Taxaceae*, perhaps joined by
Cephalotaxaceae, can be set apart from the conifers proper, all can agree that taxads and conifers are more closely related to one another than to any other recognized group.

Distribution. Of the five genera recognized for the Taxaceae, only Taxus reaches Malesia. Four are distinctly Holarctic in distribution, including Taxus, which is much the most widespread and reaches into tropical highlands. The fifth, monotypic Austrotaxus, appears on the other side of Malesia in New Caledonia, a distinct fragment of Gondwanaland, obviously a most curious relict on the southern hemisphere (Florin, Acta Horti Berg. 20 (4), 1963, 260, f. 61: map).

1. TAXUS


Evergreen trees or (prostrate) shrubs. Bark thin, smooth, purple-red, peeling in large thin flakes. Leaves spirally placed (but usually twisted into a single plane), linear to linear-lanceolate, acute, distinctly constricted at the base where the leaf twists into a horizontal position and then widening again in the decurrent part, penetrated by a single vascular strand marked on the lower surface by a blunt ridge which separates two bands of stomata and on the upper stoma-free surface by a sharp narrow ridge. Foliage and fertile buds small and globular, formed by several small keeled overlapping scales, the lower ones of which remain small while the higher ones expand with growth to become round and membranous. Usually dioecious. The fertile structures produced in the axils of ordinary leaves. Pollen cone solitary above a basal cluster of sterile scales, each peltate microsporophyll with a symmetrical whorl of 6–8 inverted pollen sacs, one microsporophyll in a terminal position and up to a dozen spirally placed lateral microsporophylls. Seed-bearing structure compound with one or more short ovule-bearing shoots produced subterminally on a very short fertile axis covered by minute keeled spirally arranged scales, each fertile shoot consisting of several decussate pairs of keeled scales which expand as the seed matures into a broad membranous oval shape and together cover the base of the ripened fruit. A small basal aril gradually grows to cup the single erect terminal seed, finally becoming fleshy and bright red. Mature seed flask-shaped, slightly wider than thick with the wider margin slightly keeled.

Distr. Seven species on the northern hemisphere middle latitudes and some tropical highlands, almost completely allopatric, but possibly some overlap between two species in the eastern Himalayas; one species in Malesia, and that one more common in subtropical parts of China. The genus has a predominantly northern hemisphere distribution, Central America and S. Celebes being the stations at lowest latitude. Fig. 1.

Fossil remains are known from Europe (middle Jurassic to Pliocene) and eastern Asia (Miocene to Pliocene).

Ecol. Understory or canopy plants of moist temperate or tropical mountain forest. From near sea-level in their northernmost occurrence in Norway they reach to nearly 3000 m in subtropical and tropical mountains.
and do not go below 1200 m in tropical latitudes. As an undershrub they can be locally quite common, but the trees in this genus rarely take a dominant canopy role. Growth is generally quite slow but dense and specimens are often prized as ornamentals. Even the forms which are capable of becoming immense trees usually appear as shrubs or at best as small trees when under cultivation.

Pollination is strictly by wind dispersal. Fruits are taken by birds and probably other animals. The seeds are bitter and poisonous when broken into, so that the seeds are normally ingested intact and efficiently dispersed in animal droppings. Seeds germinate readily in moist shady places.

Seeding foliage is essentially similar to that of the adult. Vigorous young plants tend to have leaves larger than those of fully mature specimens, up to two and three times as large and sometimes more lanceolate and falcate.

Taxon. All seven species are closely related and some, at least, hybridize readily. As a result some authors such as Pilger prefer to recognize but one species with several subspecies. I would need to know more about the relationships between the taxa before I could take a strong position in this case.

Uses. The tough, dense wood has excellent qualities and has been in demand for many uses. Best known is its service for bows and decorative woodland such as chests and coffins. It is also desirable for fence posts, flooring, and mallots. The well-marked reddish brown heartwood contrasts pleasingly with the pale yellowish sapwood.


Fig. 1. Range of the genus Taxus L. (solid line) and T. sumatrana (Miq.) de Laub. (broken line and hatched).
Fig. 2. *Taxus sumatrana* (Miq.) de Laub. on the peak of Mt. Bontain, Celebes, 1700 m alt. (Photogr. J. van Zijl de Jong, 1933).


![Fig. 3. *Taxus sumatrana* (Miq.) de Laub. Habit, female, with fruit, x 1 (de Laubenfels P668).](image)

Large, slow-growing tree to as much as 45 m high and over 1 m diam., but considerably shorter on exposed ridges. Leaves on juvenile specimens or on vigorous shoots linear lanceolate and often falcate with a prominent bend near the base and also sometimes with a slight reverse curve near the apex which is narrowly acute and often slightly spiculate, 2–4 cm long by 2–2.5 mm wide at the widest part below the centre of the leaf. Leaves on older specimens or from exposed positions more nearly linear and straight and abruptly narrowed at the apex, 1.5–2.5 cm by 1.5–2 mm, with slightly recurved margins. *Pollen cones*
globular on a short stalk, about 4 mm in diameter. Mature seed c. 6 by 5 mm, and 4 mm thick.

Distr. Eastern Himalayas, N. Burma, SE. China, Taiwan, South Vietnam; in Malesia: Sumatra (from Karoland southwards to Benkulen), Philippines (Luzon: Lepanto, Benguet, Laguna, Tayabas; Mindanao; Davao), Celebes (Central and SW.: Bonthain Peak). Fig. 1, 4.

Ecol. Moist subtropical forests and tropical highland ridges and mossy forests in the canopy and locally dominant; 1400–2300 m.

Uses. A magnificent timber tree, but occurring too locally to be of importance and too slow-growing for cultivation.

Vern. Tampinur batu, Karo, kaju radji, Mt Dempo.

Note. The extensive synonymy partly stems from the discontinuous distribution, but several authors insist that two types exist in China. Whereas immense trees are seen in undisturbed forests of Taiwan and in Malesia, on the mainland only smaller trees are normally seen with one type reported mostly at lower elevation and another at higher elevation. Both types, however, often appear from the same collection area and I was able to collect both from a single large Formosan tree, part from low on the tree and part from high up. It appears that trees rarely get beyond their early stages of growth in lowland China, while highland trees, as is usual elsewhere, are of much reduced stature.

Fig. 4. Range of Taxus sumatrana (Miq.) de Laub.

PODOCARPACEAE

Monoecious or dioecious trees and shrubs, some prostrate (and one parasitic on another member of the family, Parasitaxus, in New Caledonia). Each cotyledon, of which there are usually two but in a few cases more, a fused pair with a corresponding bifid tip. Foliage buds ranging from a loose cluster of reduced leaves to a complex specialized structure (in Podocarpus). Leaves of many shapes and sizes. Pollen produced in small cones with many microsporophylls, each of which have two inverted dorsal pollen sacs above which is a small sterile tip. Male cones may be solitary in the axils of ordinary leaves, sometimes many adjacent cone subtending leaves, or they may be terminal or clustered on special structures involving sterile scales, or in a few cases they may arise in the axils of scales at the base of a new foliage shoot. The pollen for all genera (except extra-Mal. Saxegothaea) is provided with two or more bladders or ‘wings’, a trait shared with many genera of Pinaceae. More than two are found only in Dacrycarpus (and extra-Mal. Microcarpus and Microcachrys). The basic seed producing structure in Podocarpaceae is a compound terminal or lateral cone in which fertile scales arise in the axils of cone bracts. The cone is further often subtended by a specialized shoot with scales or modified leaves or even a naked peduncle. The bract is usually a small scale but may be larger and in some cases
hardly differs from foliage leaves. The fertile scale or epimatium is a highly modified shoot and in this family bears a single naked ovule on its upper surface. In one genus there is no scale while this and one other genus have erect ovules, but in the great majority of genera the ovule is inverted. The *fertile scale* cups the developing seed and may even completely surround it with only the micropyle protruding at the time of pollination. Fleshiness, either of the cone bracts or of the fertile scale (or both) is common and the whole female structure may be reduced to only one or a few fertile units and a few sterile units. This can yield plum-like fruits or, in other cases, structures resembling those of the cashew (*Anacardium occidentale*).

**Distribution.** There is a strong Antarctic relationship with a broad extension into Malesia for the 172 known species in 13 genera (in *Malesia* 7 genera with 61 spp.). Of six local and generally primitive genera, four are in the Antarctic zone and two are in New Caledonia. Three wide-ranging genera extend also into the tropical American highlands and two of these further range across the tropical African highlands. All seven of the wide-ranging genera are common in Malesia, only one of which (*Falcatifolium*), however, is confined to the Asian tropics; five are in New Zealand. A few species reach into moist subtropical forests of eastern Asia.

**Fossils.** The early fossil record is quite limited unless one includes forms that merely resemble the *Podocarpaceae* and whose relationships range from uncertain to highly doubtful. Suggestive macrofossils and pollen of the Jurassic indicate that the family was probably already present in India as well as in the far southern latitudes including New Zealand and W. Antarctica, that is to say Gondwanaland. Similar finds continue through the Cretaceous except for India, where Podocarpaceous fossils no longer occur. In the Eocene and Oligocene, fossils of this family become more abundant in the higher southern latitudes and can often be assigned to modern genera. Fossils, particularly pollen, show that some of the presently endemic genera such as (*extra-Mal.*) *Ac-mopyle* and *Microcachrys* were formerly of much greater distribution.

Some recent authors insist that fossils of *Podocarpaceae* occur in boreal regions. Ferguson (1967) identified *Podocarpus* among Cenozoic fossils from Europe, suggesting a recent wider pre-glacial expansion of the genus. Reymanowna (1975) recently recognized *Docrydium* and *Stachy-carpus* (*Prumnopitys*) from the Jurassic of Europe. Furthermore, I have been told by palynologists that typical *Podocarpaceae* type pollen is well represented in northern latitudes. On the other hand, Florin (1963), after having examined both such alleged macrofossils and pollen fossils, expressed strong scepticism concerning their relationship to *Podocarpaceae* while pointing out that southern hemisphere strata are rich in Podocarpaceous remains. Certainly if any such plants ever existed beyond subtropical China and India, they have since disappeared completely while primitive forms of the family now survive only in the far south where they also have a respectable fossil history.

Fossil and present-day distributions suggest that the *Podocarpaceae*, as we know it, developed in cool moist Antarctic forests early in the Mesozoic period. Modern genera were already differentiated before the parts of Gondwanaland became isolated. Several genera had reached India and Kerguelen where they eventually disappeared, but two genera still survive in Africa. All of the important genera were included in the South American landmass where one interesting endemic genus, *Saxegothena*, is also still found, but some of the other genera have since become extinct there. Probably all the recognized living genera had already differentiated before the Tertiary as a major element of the Antarctic flora. Only in Malesia and probably only in late Tertiary times have members of this family descended into the lowlands of the tropics to any significant extent. They are still a major element not only in the Antarctic forests and in the Malesian highlands, but also in the tropical highlands of Africa and America.
Maps of fossil distribution are given by Couper (1960) and Florin (1963).


Ecology. Most trees of moist forests at all elevations and well into the middle latitudes both as major canopy trees and as understorey plants, rarely in areas with a marked dry season. A few species are scrubby or even prostrate and as such may be found beyond the tree line, on rocky outcrops or other specialized habitats. The family is well represented in, but not confined to difficult soils such as sand and ultrabasics as well as in mossy forests.

There are nodules regularly present on the roots, but their function is unclear. Furman (Amer. J. Bot. 57, 1979, 910) showed that they contained endotrophic mycorrhizal fungi and that nitrogen fixation did not occur. Becking (Ann. Inst. Pasteur. 111, 1966, 295) indicated that the mycorrhizal fungi were Phycomycetes. Growth is possible in sterile soil without mycorrhizae.

Most genera are dioecious and pollination is by wind. Individuals are usually scattered but locally common and the large quantities of pollen that are often produced seem to be able to reach effectively across considerable distances. Seedlings are found scattered and even quite isolated from seed sources due to doubt to dispersal by birds or fruit bats which eat the fleshy fruit. Coordination of fruiting times is for many species in tropical regions not well developed because at any given time it is often possible to find examples at any and all stages of reproduction and the collection of ripe fruit is usually reported for a given species at disparate dates. I have even seen two stages on the same tree.

Growth is distinctly cyclic and in some genera there are elaborate terminal buds and similar buds for pollen cones. Seed-bearing structures are usually produced on the latest shoots while pollen cones frequently emerge from shoots of the previous cycle. Sometimes leaves of only the last cycle persist on a tree but more common is the display of three or four cycles of growth.

Seeds germinate on or near the surface of the forest floor. The cotyledons remain at least partly inside the seed coat absorbing nourishment from the endosperm while the radicle penetrates the soil and begins forming a root system. Eventually the linear cotyledons shed the emptied seed coat and persist at the base of the growing shoot for a variable length of time. When functioning leaves are established, the cotyledons will be shed. Even if the adult leaves have some other form, the first foliage leaves in almost all taxa are bifacially flattened, often with an abrupt transition where the adult foliage is distinct.

Various parasites are known for this family. Members of Podocarpaceae are the exclusive hosts of three genera of fungi in the family Coryneliales, in Malesia recorded for Podocarpus crassigemmis. Their fruiting bodies can often be seen erupting from leaves or stems in Podocarpus or Nageia, but this does not seem to be particularly harmful. One species of Korthalsella (Viscaceae), a dwarf mistletoe, is also parasitic in Podocarpaceae: K. dacrydii has been reported both on Dacrycarpus and on Dacrydiurn in various parts of Malesia (Wasscher, Blumea 4, 1941, 320, 1 map).

Embryology. The fertilized egg undergoes four or five mitoses resulting in up to 16 to 32 free nuclei. Most of these are then walled off and cluster at the base of the archegonium forming a pro-embryo of several tiers of cells. Those in the lowest tier are embryonic and divide to form binucleate cells of which there may be but one to in some genera as many as 16. The next tier of cells elongates into a 'prosuspensor' consisting of from 3 to 25 cells, the number of cells being roughly proportional to the size of the seed and therefore the length needed to reach the centre of the female gametophyte (later to become endosperm). A third tier of cells is not completely walled off and is left behind to degenerate as the embryonic mass is projected away. At the apex of the embryo there may be one or a few cells forming a 'cap'. Unless there are five mitoses (i.e. Nageia and Prumnopitys — both with large seeds) a larger number of suspensor cells means fewer embryonic cells. In the majority of cases the embryonic mass divides, along with the secondary...
suspensor which it generates, into several competing units, the common conifer condition known as cleavage polyembryony. Simple polyembryony resulting from more than one fertilized archae-gonium also occurs. Growth of the embryo begins when the nuclei of the binucleate cells divide and then form groups of four cells. Probably an actual developed embryo derives from but a single binucleate cell so that, when there are more, they are competitive. The reduction of the number of embryonic cells often to a single cell in the genus *Podocarpus* appears to be a derived character. The binucleate embryo stage itself is unique in *Podocarpaceae*, while the number of mitoses leading to the pro-embryo is intermediate between a large number for *Araucariaceae* and non-coniferous Gymnosperms on the one hand and a smaller number for most other conifers on the other. *Sciadopitys* in the *Taxodiaceae* has five, while *Cephalotaxus* and most of the *Taxaceae* also have four.

**Chromosomes.** According to *Hair & Beuzenberg* (*Nature* 181, 1958, 1584) the chromosomes in *Podocarpaceae* are remarkable. Basically the number for the great majority is in effect \( n = 10 \) while for *Phyllocladus* it is \( n = 9 \) (and for *extra*-Mal. *Halocarpus* \( n = 8 \)). For a great many species in most genera, however, there are two kinds of chromosomes. One type, always present, is median to submedian, while the other, sometimes present, is subterminal to subtelocentric. Two of the latter always correspond to one of the former indicating either a progressive splitting of some of the chromosomes or less likely a progressive pairwise fusion of some or all of the chromosomes. *Phyllocladus* and the genera with bilaterally flattened leaves (*Dacrycarpus*, *Falcatifolium*, and *Acmopyle*) have only the one kind of chromosome. The large genera *Dacrydium*, *Nageia*, and *Podocarpus* are partly with one kind and partly mixed. The other six (mostly small) genera always have mixed chromosome types. The result is a wide range of actual chromosome numbers from \( n = 8 \) to \( n = 19 \).

Occasionally hybrids have been noted or suspected. Many species occur side by side in nature without any apparent hybridization.

**Taxonomy.** Two recent works have treated all of what is recognized as a single family here. *Gaussin* (Les Gymnosperms actuelles et Fossiles, fasc. 13 & 14, 1974 & 1976) separates each of the three most distinct genera into families of their own, *viz.* *Saxegothaeaceae*, *Phyllocladaceae*, and *Pherosphaeraceae*. He recognizes one section of *Nageia* (*Afrocarpus*) as a distinct genus, while grouping the rest of this genus as *Parasitaxus* with *Podocarpus*. There are eight genera in *Podocarpaceae* as he envisions it. In my taxonomic revision (*J. Arn. Arb.* 50, 1969, 274–369) I recognize a single family and 13 genera (including the recently published *Halocarpus* by implication only).

*Uses.* The wood of these trees is light coloured, usually yellowish, is durable, easy to work, and generally similar to pine though rather harder. It is extensively used for lumber where sufficiently dense stands of good-sized trees occur, mostly outside of Malesia. In Borneo wood of *Nageia* is sometimes mixed with *Agathis* (‘dammar’) in commercial cuttings. Specimens of many genera are selected for planting around native settlements although the specimens seen in urban areas within Malesia usually come from China or Japan. In fact, natives in many areas so prize the wood for construction that, as I have been told on several occasions and have confirmed through experience, it is often necessary to go some distance from the nearest village to find mature wild trees. In some species the fruits are edible and I have found a few in tropical America that were locally appreciated but I have not discovered any such example in Malesia.

*Note.* Conifers lack flowers and even where brightly coloured fruit occurs it tends to be very transitory, thus conifers tend to be bypassed by collectors. Most genera are dioecious and separate collections of male and female are necessary. It is often desirable to have a juvenile specimen (low branches in the shade usually have the juvenile form) to appreciate the range of foliage form. Sometimes immense numbers of recently shed pollen cones are encountered on the forest floor and these are worth collecting.
VEGETATIVE KEY TO THE GENERA

1. Foliage in the form of 'cladodes' or flattened shoots ........................................ 1. Phyllocladus
1. Foliage of individual leaves.
2. Foliage in the form of scales, needles, or linear leaves less than 2 mm wide.
3. Foliage not dimorphic.
   4. Leaves not bilaterally flattened ........................................ 2. Dacrydium
   4. Leaves bilaterally flattened ........................................ 3. Falcatifolium
3. Foliage dimorphic, leaves of ultimate branchlets longer and narrower than on main shoots may be bilaterally flattened ........................................ 4. Dacrycarpus
2. Foliage in the form of broad flat leaves more than 2 mm wide.
5. Leaves bilaterally flattened ........................................ 3. Falcatifolium
5. Leaves bifacially flattened.
6. Leaves with a groove over the midvein, (spirally placed,) lacking hypoderm, with a sweet taste
   5. Prumnopitys
6. Leaves flat or with a ridge over the midvein, with hypoderm, without a sweet taste.
7. Leaves opposite, many with multiveined leaves ........................................ 6. Nageia
7. Leaves spirally placed, uninnerved ........................................ 7. Podocarpus

GENERAL KEY TO THE GENERA

1. Foliage in the form of cladodes; several ovules erect within a leathery or fleshy cone... 1. Phyllocladus
1. Foliage of individual leaves; one to rarely several subterminal inverted seeds (ovules) projecting almost wholly beyond remainder of fertile structure.
2. Inverted naked seed turning gradually as it matures to a nearly erect posture, cupped at the base by a thin epimatium, cone reduced to modified leaves which become fleshy when mature.
3. Foliage as scales, needles, or small linear bifacially flattened leaves; fertile structure terminal on ordinary but sometimes short lateral foliage shoots ........................................ 2. Dacrydium
3. Foliage as bilaterally flattened linear to oval-shaped leaves; fertile structure on a distinct scaly lateral shoot ........................................ 3. Falcatifolium
2. Inverted seed enclosed by a leathery modified fertile scale, not turning, cone in most cases reduced to several scales, becoming fleshy or not.
4. Leaves needles, scales, or small bilaterally flattened linear forms; fertile bract fused along one side of fruit, subtended by a small warty receptacle that becomes fleshy when mature ....... 4. Dacrycarpus
4. Leaves bifacially flattened; fertile bract separate from fruit, becoming fleshy or not.
5. Fertile structure produced on a scaly (rarely leathly) shoot; covering of seed more or less fleshy.
6. Leaves spirally placed, single veined, linear; seed nearly oval with slightly asymmetrical micropylar end, fertile axis never fleshy ........................................ 5. Prumnopitys
6. Leaves opposite, often multiveined, oval; seed (usually) with a pronounced curving beak at the micropylar end, fertile axis in some cases a fleshy receptacle .......... 6. Nageia
5. Fertile structure produced on a naked peduncle subtending a fleshy (or leathery) receptacle, covering of seed leathery (rarely somewhat fleshy) ........................................ 7. Podocarpus

1. PHYLLOCLADUS

Small to large trees up to 30 m tall, with smooth, dark, platy bark which is reddish or yellowish and fibrous within. Primary branches tend strongly to be in false whorls and secondary branching is abundant. The ultimate foliar shoots are flattened into cladodes or ‘phyloclades’ which involve a central axis and several alternate side ‘shoots’. In outline these cladodes can be oval, triangular, deeply lobed, or compound and small marginal hooks representing reduced leaves can sometimes be seen. Shoots which are to continue growth, whether a secondary axis or a lobed cladode, terminate in a globular bud formed of overlapping triangular scales. These in turn develop into short shoots covered with linear lanceolate caducous scale-leaves in the axils of which new cladodes or fertile structures may be produced. Seedlings bear spirally arranged, single-veined, linear, acute bifacially flattened leaves up to 1 cm long followed gradually by smaller, more lanceolate forms until the adult scales are produced. Specimens are variously found to be dioecious or predominantly of one sex or fully monoecious. The cylindrical pollen cones are clustered each in the axil of a scale of a secondary shoot and are each subtended by a short to long, mostly naked stalk and by a few sterile scales. Seed cones appear singly or grouped either terminally or laterally in the axil of a scale on a naked stalk, at the base of a cladode, or terminally or laterally on a reduced or unreduced cladode. The cone consists of a few to many thickened spirally arranged scales, some of which bear a single erect ovule on the upper surface. The developing seed is surrounded to at least half its length by a symmetrical or nearly symmetrical filmy white aril or rough-edged epimatium. Seeds are oval and wider than thick, protrude from the bright red ripe cone, have a crooked micropyle at the tip, and are dark brown to black.

Distr. Five closely related species, three in New Zealand, one in Tasmania, and one in the highlands of Malesia. Fig. 5.

Fossils have been reported from the Eocene to Quaternary in New Zealand and from the Oligocene in New South Wales and Victoria (Australia); fossil pollen of Oligocene age was found in Australia, New Zealand and western Antarctica (Coupér, Proc. R. Soc. Lond. ser. B, 152, 1960, 491). The Malesian extension of the range was probably only reached in the late Tertiary. It is now extinct in Australia (Florin, Kongl. Svensk. Vet. Ak. Handl. 111, 19, n. 2, 1940, 75, map 4; Acta Horti Berg. 20 (4), 1963, 184, t. 17: map).

Ecot. Upland tropical and temperate rain-forest, often mossy forest, as a large canopy tree to stunted forms near the tree line.

Note. The unique cladodes and fewer chromosomes set Phyllocladus apart from other Podocarpaceae but, as Singh (Embryology of Gymnosperms, 1978, 257) points out, they share such common features as winged pollen with a prothallial tissue, an epimatium, and binucleate embryo cells. Other significant common traits are a solitary ovule per fertile bract, two pollen sacs per microsporophyll, and fused pairs of cotyledons as well as fleshiness of the mature cone and a mature seed of essentially identical form as those of other genera with naked seeds in the family. The erect seed with an aril has suggested a transitional position towards Taxaceae but the ovule is not terminal as in this group and the aril is not fleshy. Florin regarded the later developing aril as having nothing to do with the epimatium (Acta Horti Berg. 15, 1951, 267) but this position requires
Fig. 5. Range of the genus *Phyllocladus* L.C.Rich ex Mirbel with the number of species.

Fig. 6. Branch with male cones of *Phyllocladus hypophyllus* Hook.f. (Photogr. I. Polunin, 1978, received from H. King).
the loss of any epimatium-type structure and the subsequent development of the morphologically similar (asymmetrical) aril in the corresponding location. In fact the erect position of the ovule may tend to suppress or delay the development of the epimatium which elsewhere arches over and around the base of inverted ovules. The only other genus of the family with an erect ovule has no epimatium at all while that of Phyllocladus, though eventually well developed, is retarded, appearing only after fertilization. The genus is a comfortable member of the Podocarpaceae and a distinct family, as Keng (Taxon 24, 1975, 289) proposed, does not seem justified. The intriguing thesis of Keng (Ann. Bot. 38, 1974, 757) that the cladodes probably represent a relic of ancient progymnosperm telomic branch systems seems hardly sustainable in the light of the above as well as the further fact that perfectly typical coniferous leaves are produced in the juvenile phase.

Large short-boled trees to shrubs near the tree line, up to at least 30 m tall. Bark dark brown to reddish, hard with large lenticels, light brown and granular within, breaking off in large, more or less rectangular scales. Foliar buds well developed, longer and less compact on younger plants, becoming more globular on older plants. Juvenile leaves 5–8 mm long and adult scale leaves 2–3 mm long. Cladodes on young plants deeply lobed and with distinct marginal hooks representing the reduced leaves, gradually becoming more compact, diamond-shaped to more or less oval with more or less wavy margins, 3–8 by 2–3 cm, the larger sizes mostly on young sterile specimens, marginal lobes c. 5 mm wide, often glaucous especially on the lower side, aggregated alternately on lateral branches of limited growth. Pollen cones usually produced on different plants than seed cones, each in the axil of a scale at the base of a growing shoot, in clusters up to 15, sometimes mixed with reduced cladodes, cylindrical, 12–15 mm long and 3 mm diameter with a naked peduncle 5–25 mm long, Apex of the microsporophyll triangular, irregularly toothed. Seed cones in an apical notch of a bilobed cladode or terminal on a reduced cladode or on a naked stalk. 

Fig. 8. Phyllocladus hypophyllus Hook.f. a. Male shoot, ×1; b. male cone, ×3; c. microsporophylls (two views), ×6; d. old seedling, ×0.75; e. seedling leaf, ×3 (a–c de Laubenfels P 636, d–e de Laubenfels P 645).
1 cm long, occasionally more than one together, ovoid and, like new cladodes, more or less purple, bearing up to 15 scales, of which usually 1–3 are fertile, becoming bright red when mature and then drying to a leathery brown. Seed shiny brown, 5–7 mm long.

Dist. Malesia: Philippines, Borneo, Celebes, Moluccas, New Guinea. Fig. 9.

Ecio. Moist mountain forests sometimes as low as 900 m up to tree line at 3200–4000 m. Scattered in the forest at lower elevation where trees may be quite large. More common but of reduced stature at higher elevations.

Note. The lower elevation occurrences are apparently examples of the phenomenon 'temporary settlement' from established higher elevation populations as described by van Steenis in his Mountain Flora of Java (1972).

Fig. 9. Range of *Phyllocladus hypophyllus* Hook.f.

### 2. DACRYDIUM


Usually dioecious shrubs to large trees as much as 40 m tall. Bark hard and smooth with fissures and breaking off in plates, with numerous small lenticels, reddish brown and weathering to gray, slightly fibrous within. Profusely branched with the major side branches in many species curving gradually upward candelabra-like and the ultimate branches aggregated into dense tufts, others less formal or even drooping. The apex of a resting shoot shoot loosely covered by a cluster of short leaves or scales. Leaves spirally placed. Juvenile leaves awl-shaped, spreading sharply from a briefly decurrent base at about a 75° angle and the tip in nearly every species bent more or less forward in a gradual curve, lanceolate or linear-lanceolate, acute to apiculate, strongly keeled on the dorsal (abaxial) side and slightly or not at all on the axial side, roughly tetragonal to triangular in cross section, normally longer and occasionally more slender than the mature leaves. Leaves on mature plants more variable among the...
species, from small keeled adpressed scales 1 mm long to linear leaves or needles as much as 2 cm long, straight to strongly incurved at the tip, tetragonal in cross section or keeled on the dorsal side and flat or even strongly concave on the axial surface, in some cases as much as six times as wide as thick, apex blunt to narrowly acute. Where adult leaves differ sharply from the juvenile leaves the transition may be gradual or almost abrupt and juvenile shoots mixed with adult foliage are often seen. *Fertile structures* usually start with a few reduced leaves and are placed either terminally or laterally, often both, but in the species without lateral structures they may nevertheless be on short lateral branches. The cylindrical *pollen cones* may be solitary with a few reduced sterile leaves on a subtending axis or they may be clustered with one or more lateral cones in the axes of reduced leaves beside an often slightly larger terminal cone. Microsporophylls either with a triangular apex tapering from the pollen sacs or with a lanceolate apex sharply narrower than the pollen sacs. *Seed-bearing structure* with slightly enlarged scale-shaped bracts or with bracts resembling normal leaves and distinctly longer than the reduced leaves which they follow and more or less expanded at their base. The entire seed-bearing structure with the exception of the apical part of the bracts has been observed in the majority of species to become greatly enlarged, fleshy, and red when mature. In two middle latitude (New Zealand) species (the genus *Lagarostrobus QuinN*) the fertile bracts are not subterminal as in the remaining species, where usually one or in some species two or more may be fertile. The solitary ovule of a fertile bract is cupped by an epimatium which represents the fertile scale and which lies between the ovule and the subtending fertile bract. In a few species the ovule apex at pollination is only slightly inverted and faces inward towards the fertile axis, but in most species it is strongly inverted while in all species it gradually turns upward as the seed develops until it reaches a nearly upright position. *Seeds* become dark brown and have the same shape as those of *Phyllocladus*.

**Distr.** In all 25 *spp.*, from Southeast Asia through Malesia (not in Java and the Lesser Sunda Islands) to New Caledonia and Fiji, Tasmania, New Zealand and southern Chile. Within *Malesia* (14 *spp.*) the greatest variety is found in Borneo (7 *spp.*), followed by New Guinea (6) and Malaya (5), while both New Caledonia and New Zealand have 4 endemic species each. Fig. 10.

*Fossils* indicate that *Dacrydium* has a long fossil record, dating back to the Middle Jurassic and Upper Cretaceous floras of western Antarctica; in fact a centre of development was in the Australian–New Zealand–Antarctic region during the Upper Mesozoic. Obviously the centre of development was in the Austral-Asian region. Its withdrawal from Australia did not take place before the Miocene (*Florin, Kongl. Svensk. Vet. Ak. Handl.* III, 19, n. 2, 1940, 74; *Acta Horti Berg.* 20 (4), 1963, 186, f. 18: map).

*Taxon.* The genus can be loosely divided into four subgroups (those with scale leaves, those with leaves much wider than thick, those with broadly triangular apices to the microsporophylls, and those with none of these characters) each of which is widely distributed in Malesia and somewhat beyond. The seemingly most primitive forms are concentrated in New Zealand with one in Tasmania.

*Note.* *Dacrydium* includes species whose leaves, progressing from acicular juvenile forms to mature scales, correspond to common early Mesozoic fossil foliage forms. Similar examples are also found in other families. A primitive clustering of pollen cones is found in the genus but the seed cones show an intermediate stage of development for the family. The most primitive seed cone form in *Dacrydium* is a rather loose structure with bracts resembling foliage leaves, rather than the compact cone of several other genera and of
preceding fossil conifers. Other seed-bearing structures are further reduced to fewer fertile units and an exposed subterminal seed placement anticipating the more formal structure in the more advanced genera of the family. The rotation of the seed as it matures is a specialized trait.

**KEY TO THE SPECIES**

1. Adult leaves in the form of imbricate scales [microsporophylls triangular].

2. Mature seed completely exposed above short (to 2 mm) cone bracts; juvenile leaves nearly straight, up to twice as wide as thick; adult scales appearing gradually on trees several meters high.  
   1. *D. elatum*  

2. Mature seed base overlapped by elongated (3 mm) cone bracts; juvenile leaves strongly bent forward and slightly inward, about three times as wide as thick, adult scales appearing almost abruptly on small specimens about half a metre high.  
   2. *D. novo-guineense*

1. Adult leaves spreading linear or lanceolate needles or leaves.  

3. Microsporophylls triangular; female terminal (occasionally on short lateral branches); leaves bent forward, up to 5 mm long and length about 5 times width.  

4. Leaves blunt (may be apiculate), width less than twice thickness.  

5. Mature seed fully exposed above short cone bracts [leaves robust (0.3–0.4 mm thick)]  
   3. *D. pectinatum*

5. Mature seed barely overtopping elongated cone bracts.  

6. Leaves spreading their tips bent parallel to the branch or directed outward, blunt or with a small apiculus, becoming triangular in cross section and about as thick as wide, 0.2–0.3 mm thick  
   4. *D. nidulum*

6. Leaves crowded and more or less touching near their tips which on mature plants curve inward towards the branch, distinctly apiculate, nearly twice as wide as thick, 0.3–0.4 mm thick  

5. *D. cornwalliana*

4. Leaves acute, width more than twice thickness  
   1. *D. elatum* (occasional specimens)  

3. Microsporophylls sharply narrowed above the pollen sacs and lanceolate; female may be lateral in some species; leaves acute, in many species to more than 5 mm long and length generally at least 8 times width.  

7. Leaves triangular in cross section, width no more than three times thickness.  

8. Leaves spreading (nearly straight), 0.3–0.4 mm wide, less than twice thickness, length about 25 times width  
   6. *D. beccarii*
8. Leaves bent forward, 0.4–0.6 mm wide and width 2–3 times thickness, length no more than 12 times width.

9. Leaves mostly 0.4 mm wide; male 6–7 mm long; microsporophyll barely 1 mm long; mature seed exposed ........................................ 7. D. gracilis

9. Leaves up to 0.6 mm wide; male more than 7 mm long; microsporophyll 1.5–2 mm long; mature seed partly covered by elongated cone bracts.

10. Leaves slightly bent forward, length up to 10 times width; male 7–9 mm long ... 8. D. medium

10. Leaves strongly bent forward, length more than 10 times width; male about 12 mm long 9. D. magnum

7. Leaves distinctly concave on the underside or wide and flat, width at least 8 times thickness.

11. Leaves at least 3 mm long.

12. Female terminal, bracts about as long as leaves, mature seed partly covered; leaves up to 7 mm long, apex abrupt and bent forward.

13. Leaves 3–5 mm long, only slightly bent (male unknown) .................. 10. D. sphaeroides

13. Leaves 5–7 mm long, strongly bent; microsporophyll very long (5–6 mm) ..... 11. D. gibbsiae

12. Female mostly lateral, bracts much smaller than leaves, mature seed exposed; leaves at least 6 mm long.

14. Leaves slightly bent forward and concave, lanceolate, narrowly acute.

15. Leaves 6–10 mm long, 0.5–0.8 mm wide ........................................ 12. D. xanthandrum

15. Leaves at least 10 mm long, 0.7–1.3 mm wide ............................. 13. D. comosum

14. Leaves straight and flat, linear, more or less abrupt at the apex, up to 10 mm long 14. D. erieoides

11. Leaf about 1 mm long, strongly bent forward ............................... 15. D. leptophyllum


Large tree, 8–40 m high, 0.1–1 m diam., with many slender, more or less erect branches and crowds of branchlets forming tufts which together construct a great billyow dome. Juvenile leaves linear-lanceolate, pungent, spreading but curved forward parallel to the branch, keeled on four sides, to at least 14 mm long, 0.3 mm wide and 0.2 mm thick, gradually becoming shorter and slightly broader with the leaves at the bases of ultimate shoots and on more vigorous shoots noticeably smaller and less spreading. Transitional forms which are sometimes fertile have spreading leaves slightly bent forward towards the acute tip, triangular in cross section, 0.3–0.4 mm wide, 0.2 mm thick, and 2–4 mm long, the leaves on vigorous shoots more nearly scale-like. Adult foliage shoots cord-like, 1–2 mm diam., leaves in the form of imbricate triangular scales 1–1.5 by 0.4–0.6 mm, sharply keeled on their exposed surface. Juvenile shoots sometimes mix with adult shoots thus giving a false impression that leaves change abruptly as the tree matures. The fertile structures are terminal. Pollen cones small, 4–5 mm long and 1–1.2 mm in diam. Apex of microsporophyll 0.5–0.8 mm long. The seed-bearing structure, even when produced on needle-bearing branches, is subtended by a scaly peduncle several mm long with scales about 1 mm long. The seed cone consists of about a dozen slightly elongated bracts 1.5–2 mm long. The solitary seed is 4–4.5 mm long.

Dis. Indochina and Thailand; in Malesia: Malaya (very common, incl. Penang I.), Sumatra (only local in Westcoast Res., Batak Lands), Borneo (Sarawak, Sabah, rather rare). Fig. 11.

Ecol. Scattered in moist rain-forest, from sea-level but mostly above several hundred m to 1,700 m, growing most abundantly in open situations indicating a preference for disturbed conditions. It also appears to prosper on difficult soils (sandstone, granite, kerangas). Hardy and popular under cultivation in fully exposed sites. Does not enter into high mountain scrub.

Vein. Ru, M (properly the common name for
Flora Malesiana [ser. 1, vol. 10]

Gymnostoma (Casuarinaceae); Borneo: ouk, Kayan, sempilor, Merulong Plateau.

Note. Dacrydium beccarii var. subelatum was established for trees bearing the intermediate foliage, a condition which appears to be persistent on certain individuals, some of them growing on high mossy ridges. Actually fruiting specimens with intermediate foliage occur sporadically throughout the range of D. elatum (de Laubenfels, Blumea 23, 1976, 97). Corner thought that this variety was somehow transitional, even suggesting that D. beccarii — of which he made it a part — might be a hybrid between D. comosum and D. elatum. Indeed, the individuals on high mossy ridges may well be hybrids between D. beccarii and D. elatum as they seem always to occur where the ranges of these two species approach one another. In any case, all such plants can be distinguished by much shorter leaves on vigorous shoots than for D. beccarii and generally variable leaf size.


Small to large tree, 3 to 40 m tall, with numerous branchlets forming a dense rounded crown. Juvenile leaves up to 18 mm long, slightly curved, pungent, strongly keeled and quadrangular in cross section, 0.2 mm wide and thick, gradually becoming shorter and thicker. Adult leaves keeled on four sides but less strongly on the axial side, abruptly acute to blunt, slightly curved, 2–5 by 0.4–0.8 mm wide and thick. Fertile structures terminal. Pollen cone 6–12 mm long and 2 mm diam., apex of microsporophyll 1–1.2 mm long. The seed-bearing structure subtended by a short zone of small leaves c. 2 mm long while the cone bracts themselves may be up to 3 mm long. Seed 4–4.5 mm long.

Dist. Hainan; in Malesia: Billiton, Borneo (incl. Karimata & Natuna Is.) and Philippines (Lu-

Fig. 11. Range of Dacrydium elatum (Roxb.) Wall. ex Hook. (dots) and D. novo-guineense Gibbs. (triangles).

Fig. 12. Range of Dacrydium pectinatum de Laub. (dots) and D. cornwalliana de Laub. (triangles).
zon: Sierra Madre; Mindanao: Zamboanga, 2 coll.), in Borneo common. Fig. 12.

Ecol. Scattered large individuals are found in primary rain-forest other than dipterocarp forest from sea-level to 1500 m but mostly below 600 m, while dense stands are found in boggy areas and nearly pure stands of stunted trees occur in shallow sandy soils, especially on so-called 'padangs', and on ke-rangas in heath forest, frequently associated with Gymnostoma; in Sabah also on ultrabasic soils. In Kayangeran For. Res. (Brunel) reported to occur in pure stands in the centre of peat swamps.

Vern. Melo, Natuna; Borneo: malur, Mangar, melur, Singkawang, tjemantan, Sampit, sempilor, Sarawak, Sabah.

Note. This species closely resembles the lowland form of D. nidulum from which it differs by the more robust leaves and by the fully exposed mature seed. Dacrydium balansae in New Caledonia and D. cupressinum in New Zealand are also similar. The variety was created for markedly shorter leaves, a condition which, it turns out, is related to more difficult environments and all variations can be seen in local populations across environmental gradients.


Tree 10 to 30 m tall, 18–50 cm diam., with numerous branchlets forming a dense crown. Juvenile leaves up to 2 cm long, slightly curved forward, acute, triangular in cross section, 0.2 mm wide and less thick. Adult leaves not crowded (leaf tips distant from adjacent leaves), nearly straight to distinctly curved so that the apex is parallel with the shoot, abruptly acute to blunt, often apiculate, 1–5 mm long but mostly 2–3.5 mm, triangular in cross section, strongly keeled on the back, 0.3–0.7 mm wide and 0.2–0.3 mm thick. Fertile structures terminal but pollen cones may also be lateral. Pollen cones 8–18 mm long and 1–1.6 mm diam. Microsporophylls 0.8–1.2 mm long. Seed-bearing structure subtended by leaves distinctly shorter than normal foliage leaves, as short as 1.5 mm; cone bracts increasing towards the apex where one or two may be fertile, up to 4 mm long and completely surrounding the epimatum but surpassed by the apex of the mature seed which is 3.5–4 mm long and glossy brown.

Distr. W. Polynesia (Fiji); in Malesia: throughout New Guinea (incl. Normanby & Japen Is.) to the Moluccas (Halmahera) and Central & SE. Celebes and the Lesser Sunda Islands (Sumba). Common in the western parts of New Guinea, but elsewhere populations are mostly rather isolated. Fig. 13.

Ecol. A canopy tree of primary and sometimes secondary rain-forest from sea-level to 1200 m but mostly under 600 m.


Note. There is some variation between the different widely distributed populations. In the Cycloop
Mts and in Fiji the leaves are not apiculate and, particularly in Fiji, the leaves are nearly straight. Variations in length seem to be mainly a function of age or exposure, with younger and protected plants tending to have longer leaves.


Arbor ad 30 m alta. Folia conferta, apicum tangens incurvum apiculatum, latiora quam crassa, 0.3–0.4 mm crassa. Type: Versteegh BW 3041 (L., holo), Wissel Lakes, West Irian.

Tree 10–30 m tall, with elongated dense fastigiate crown. Juvenile leaves up to 12 mm long, strongly curved forward parallel to the branch and soon becoming incurved, 0.4–0.5 mm wide and 0.2–0.3 mm thick, sharply apiculate. Adult leaves crowded and touching near their tips, spreading but then incurved towards the tip which is directed somewhat inward towards the branch, distinctly apiculate, 2–5 mm long, the longer examples on protected branches or younger trees, strongly keeled on the back and slightly concave on the ventral side but with a small ridge over the midvein, 0.6–0.8 mm wide and 0.3–0.4 mm thick. Fertile structures terminal, often on short lateral shoots but pollen cones may also be lateral. Pollen cones c. 12 mm long and 1.8 mm in diam. Microsporophylls c. 0.8 mm long. Seed-bearing structure as in *D. nidulum*, becoming fleshy and red when ripe, seed c. 5 mm long.

**Distr.** Malesia: West and Central New Guinea. Fig. 12.

Ecol. Dominant to nearly pure stands in swamp forests and perhaps also mossy heath forests between 1450 and 2300 m altitude.


Shrub of 1 m or a small tree up to 20 m, rarely to

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Fig. 14. *Dacrydium cornwalliana* de Laub., edge of forest on black peat; in the background mixed forest with amongst others *Libocedrus*. Wissel Lakes, New Guinea, 1700 m (Photogr. F.W. Rappard, 1955).
35 m tall. Profusely branched with the branches turned upward, often forming a dense umbrella- or dome-shaped crown. Juvenile leaves nearly straight at first on fresh growth, becoming gradually curved forward, up to 17 mm long, strongly keeled on three sides, nearly flat on the axial surface, 0.2 mm wide and 0.1 mm thick, linear-lanceolate, pungent, crowded so that shoots resemble a furry animal's tail. Adult leaves spreading, bent slightly forward but the apiculate tips still directed slightly outward, triangular in cross section, 0.3–0.4 mm wide, 0.2 mm thick, crowded, linear-lanceolate, 5–10 mm. Fertile structures both lateral and terminal. Pollen cones subtended by a cluster of sterile 1–2 mm bracts, the cone 7–10 mm long and 2.5–3 mm diam. Apex of the microsporophyll a lanceolate spur about 1 mm long and 0.3 mm wide at the base. Seed-bearing structure subtended by about a dozen reduced leaves c. 1 mm long, the seed cone itself formed of a similar number of bracts up to 2 mm long and not completely covering the epimatium, often two and occasionally even three seeds which are fully exposed at the apex of the structure. Seeds shiny, dark brown, c. 4 mm long.

**Distr.** Solomon Islands (Guadalcanal); through **Malesia**: New Guinea (incl. Normandy 1. & New Britain), the Moluccas (Tahabu), Philippines (Mindanao; Negros; Biliran 1.) and (mainly W.) Borneo to Malay and N. Sumatra. In the eastern part of the range there are only widely separated occurrences, and even in the western part they are somewhat discontinuous. Fig. 15.

**Ecol.** Most common on mossy ridges where it is often dominant and also found rising above a low mixed mountain scrub, from 600–2500 m. A variety of soils such as sandy peat and andesite have been indicated.


**7. Dacrydium gracilis** de Laub., nov. sp.

Arbor ad 30 m alta. Folia linearia lanceolata, dorsis carinatis, apices apiculatis, 3–9 mm longa, 0.4 mm lata, 0.2 mm crassa. Strobili masculi 6–7 mm longi, 2 mm diametris. Apices microsporophyllorum lanceolati, 0.5–1 mm longi, c. 0.3 mm lati. Semina muta non obscurata. Type: de LAUBENFELS P716 (L., holo), Mt Kinabalu.

Tree 7–30 m tall, up to 40 cm diam. Juvenile leaves at least 12 mm long, curved so that the tip is nearly parallel to the branch, pungent, triangular in cross section, lanceolate, up to 0.4 mm wide, at the base 0.2 mm thick. Adult leaves nearly straight, spreading at about a 45° angle but curved so the apex is parallel with the branch, apiculate, 3–9 mm long, the longer leaves on younger plants or lower on the tree, the shorter leaves on older and exposed trees, triangular in cross section, 0.4 mm wide, 0.2 mm thick. Fertile structures usually lateral. Pollen cones 6–7 mm long and 2 mm in diam., subtended by a cluster of leaves 3–5 mm long and usually distinctly shorter than normal foliage leaves. Together the two pollen sacs are 0.7–0.8 mm wide but the apex of the microsporophyll is a lanceolate spur 0.5–1 mm long and c. 0.3 mm wide. Seed-bearing structure also subtended by a cluster of reduced leaves c. 1 mm long, the bracts of the seed cone up to 3 mm long and more or less covering the epimatium, the usually solitary seed itself fully exposed. Fully mature seeds unknown.

**Distr.** Malesia: Borneo (Sabah: Mt Kinabalu and nearby to the centre of Borneo; Sarawak). Fig. 16.

**Ecol.** Scattered in the canopy of moist mountain rain-forest between 950 and 1800 m, in Sarawak also in heath forest on sandstone. Rather rare.

**Note.** Leaves smaller and much more gracile than those of the similar *D. magnum* which also occurs in lower elevation forest. The crown has a rather typical shape of a forest tree, not the striking form of the usually open growth species, *D. beccarii*.

Shrub of 1 m or a small, often gnarled tree, sometimes up to 20 m tall. Densely branched to form a compact oval shape. Juvenile leaves spreading widely but sometimes distinctly curved forward so that the apiculate apex is more or less parallel to the branch, lanceolate, up to 20 mm long, strongly keeled on three sides, nearly flat on the axial surface, up to 0.6 mm wide, 0.3 mm thick. Adult leaves on younger trees nearly straight and up to 8 mm long but with greater age the leaves become shorter and sharply curved forward or even slightly inward, apiculate, linear-lanceolate, 3–6 mm long but nearly uniform on a branch, 0.5–0.6 mm wide, 0.3 mm thick. Fertile structures mostly terminal. Pollen cones with basal leaves hardly different from foliage leaves, 7–9 mm long, 2.5 mm diam. Apex of the microsporophyll a linear-lanceolate spur 1.5–2 by 0.5 mm with the broadly acute apex strongly curved inwards so as to appear rounded and blunt. Seed-bearing structure subtended by a zone of reduced leaves about 2 mm long, the cone bracts longer and partly covering the seed. The brown seeds about 5 mm long.

Disttr. Malesia: Malaya (G. Tahan complex) and N. Sumatra (Gajo Lands: G. Leuser & Bandahara). Fig. 17.

Fig. 17. Range of Dacyridium medium de Laub. (dois) and D. magnun de Laub. (triangles).

Ecol. Rising above and often dominant in low mountain scrub on what appears to be rather poor soils between 960 and 2100 m in Malaya and 1800–2600 m in Sumatra; not rarely associated with Baeckea and Leptospermum.

Vern. Sangu, Gajo.

Note. The shortest leaved specimens resemble D. pectinatum foliage, a species which grows under similar conditions at lower elevations, but the fertile material more closely resembles several other species.


Tree, 8–30 m tall, 5–60 cm diam. Branches dense, spreading, upturned. Juvenile leaves spreading widely, slightly curved forward at the tip, pungent, triangular in cross section, gracile, up to at least 18 mm long. Adult leaves spreading at about a 45° angle and strongly curved forward so that the apiculate tip is parallel to the branch or bent slightly inward, forming a compact rope-like branch system, linear-lanceolate, 3–6 mm long but nearly uniform on a branch, 0.3–0.4 by 0.2–0.3 mm. Fertile structures mostly terminal but occasionally on short lateral branches, the subtending leaves hardly distinguishable from ordinary foliage leaves. Pollen cones 10–16 mm long and 2 mm in diameter. Apex of the microsporophyll a lanceolate spur 1.5–2 mm long and 0.5 mm wide at the base. Seed-bearing structure formed of more or less straight and slightly spreading leaf-like bracts which cover the base of the seed. The ripe fruit reported to be brown but possibly an old fruit as has been observed in other species. Seed 5 mm long, often two seeds per cone.

Disttr. Malesia: Islands (Guadalcanal, Choiseul, S. Yasabel); in Malesia: Louisiades (Sudent 1.) and Moluccas (Obi 1). Rare. Fig. 17.

Ecol. Locally common in the canopy of moist tropical forest between 60 and 1200 m, often along ridge crests where it has a somewhat reduced stature.

Note. The variety rudens was applied to collections from Tagula I. that tend to be more gracile than elsewhere but otherwise are not distinct.


Tree 26–34 m tall, 50 cm diam. Bark exuding red sap. Juvenile leaves spreading at about a 60° angle, nearly straight but slightly bent forward at the pungent tip, to at least 6 mm long, linear-lanceolate, c. 1 mm wide, 0.2 mm thick, keeled on the dorsal side, slightly concave on the axial side. Adult leaves spreading at about a 45° angle, straight or slightly bent forward at the apiculate tip, 2–4 mm long, linear-lanceolate, 0.8–0.9 mm wide, 0.2 mm thick, keeled on the dorsal side, distinctly concave on the axial side. Pollen cones unknown. Seed-bearing structure terminal, often on a short side branch, subtended by reduced leaves less than 2 mm long, the cone bracts straight, slightly spreading, up to 3 mm long and 0.5 mm wide, covering the lower part of the seed. Mature seed 4 mm long, often two seeds per cone.

Disttr. Malesia: Eastern West Irian. Fig. 16.

Ecol. Canopy tree in moist, mossy mountain rain-forest at 2150–2200 m.

Small tree, 2–12 m tall. Juvenile leaves spreading widely, slightly curved forward towards the apiculate tip, at least 12 mm long, slightly wider than thick. Adult leaves robust, the acute tip bent to be parallel to the branch or even curved slightly inward, crowded, linear or linear-lanceolate, 5–8 mm long, concave on the axial side, strongly keeled on the dorsal side, 0.8 to at least 1 mm wide, 0.2–0.3 mm thick. Fertile structures terminal, often on a short lateral branch. Pollen cones 20–25 mm long and 4.5–7 mm diam.; microsporophyll lanceolate, 5–6 mm long, 1.5 mm wide at the base. Seed-bearing structure consisting of bracts slightly narrower than ordinary foliage leaves and increasing slightly in length towards the apex where one or two may be fertile, spreading slightly and completely covering the epimatium but surpassed by the apex of the mature seed which is 4.5 mm long.

**Distr.** Malesia: N. Borneo (Mt Kinabalu). Common on the slopes.

**Ecol.** Co-dominant un ultrabasic soils in the mountain mossy forest from 1500–3600 m.


Shrub to tree, 2–36 m tall, up to 70 cm diam. Juvenile leaves spreading widely, bent slightly forward, linear-lanceolate, up to 2 cm long, 0.8 mm wide, strongly keeled on the dorsal side, slightly keeled and slightly convex on the axial side, about 0.2 mm thick, apiculate. Adult leaves spreading widely, straight or slightly bent forward but the tips still directed outwards, lanceolate to linear-lanceolate, 6–10 mm long or shorter at the base of the shoot, apiculate, strongly keeled on the dorsal side, slightly keeled and slightly concave on the axial side, 0.5–0.8 mm wide, 0.2 mm thick. Fertile structures both terminal and lateral. Pollen cone subtended by a cluster of reduced leaves which are c. 2 mm long, cone 5–13 mm long and 2–2.5 mm diam.; apex of the microsporophyll a lanceolate spur 0.6–1.2 mm long and 0.3 mm wide at the base. Seed-bearing structure subtended by a shoot up to 4 mm long with reduced leaves c. 2 mm long or when terminal sometimes following normal leaves; fertile bracts similar to leaves, spreading, 2–3 mm long; the shiny brown seeds c. 4 mm long, fully exposed, often in pairs.

**Distr.** Solomon Islands (Bougainville); in Malesia: New Guinea (incl. New Britain), Central E. Guinea and New Britain. (Bougainville), in Malesia: New Guinea (incl. New Britain), Central E. Guinea and New Britain. (Bougainville).
Celebes (2 coll.), Philippines (Mindoro, 1 coll.), Borneo (Sabah; Central Kalimantan: Bt. Raya; Sarawak: Mt Mulu, Mt Murud), N. Sumatra (Atjeh, 1 coll.), and Malaya. Locally discontinuous. Fig. 20.

Ecol. Locally common or even dominant and shrubby on mossy ridges with peaty soils over clay, sand, granite, sandstone, or dacite, or scattered larger individuals in nearby primary forest from (500–) 1000–2700 m.

Vern. Sabah: kerapui, Dusun, Sensuron, seringoun, Bokan, Mt Alab, arun gunong, Atjeh.

Note. See comments under D. beccarii. The distinctly bifacially flattened leaves, generally concave on the axial surface, contrast strongly with the fine and distinctly more crowded leaves of D. beccarii. The difference is particularly noticeable on young plants. Fertile structures, like new shoots, are normally produced as is usual in the family after a period of rest but the examples of terminal seed-bearing structures without the usual subtending short shoot with reduced leaves apparently have appeared without the intervening rest period.


Shrub c. 2–4 m tall, 5 cm diam., on exposed ridge, to a tree at least 12 m tall. Densely branched with branches all turning upward and the aggregated tufts forming a nearly flat to umbrella-like crown. Juvenile leaves spreading perpendicular to the branch and then curving forward or parallel with the branch, pungent, lanceolate, up to 33 mm long and c. 0.8 mm wide at the base, 0.2 mm thick, sharply keeled on the dorsal side, nearly flat or slightly concave on the axial side. Adult leaves similar to juvenile leaves except that the upper part is usually straight so that the apices are directed somewhat outward, 12–20 mm long, 0.6–1 mm wide but slightly expanded at the basal attachment, 0.2 mm thick. Fertile structures mostly lateral, subtended by a small cluster of reduced leaves which are c. 4 mm long. Pollen cones 8–10 mm long and c. 3 mm diam.; apex of the microsporophyll a narrow lanceolate spur 1.5–2 mm long and c. 0.5 mm wide. Seed-bearing structure consisting of several lanceolate bracts c. 2 mm long, one or two of which are usually fertile. The light brown, fully exposed seeds are 4–5 mm long.

Distr. Malesia: Malaya (known only from the crest separating Selangor and Pahang and on the G. Tahan massif; Pine Tree Hill; Ulu Kali; Ginting Highland). Fig. 21.

Ecol. On exposed ridges as a local dominant in stunted mossy forest between 1440 and 2200 m.
14. Dacrydium Ericoides de Laub., nov. sp.

Arbor ad 17 m alta. Folia linearia recta, paginis superis planis, apicis abruptis apiculatis, 5–10 mm longa, 0.7–1 mm lata, 0.2 mm crassa, dorsis carinatis. Strobili fere laterali, masculi 7–10 mm longi, 2–2.5 mm diametri, apicis microsporophyllorum calcarea 1 mm longa. Type: Brunig S 8722 (L, holo), Merurong Plateau, Sarawak.

Tree 10–17 m tall, 25–30 cm diam., with drooping twigs. Leaves linear, straight, spread out more or less perpendicularly to the shoot except on new growth, narrowing abruptly at the apex to an apiculate tip, flat on the upper surface but becoming slightly concave towards the apex, stomata on the upper surface in two bands separated over the midvein, sharply keeled on the lower surface, 5–10 mm long, 0.7–1 mm wide, 0.2 mm thick. Fertile structures usually lateral, subtended by a cluster of reduced leaves which are 2–3 mm long. Pollen cones 7–10 mm long and 2–2.5 mm diam. Apex of the microsporophyll a lanceolate spur c. 1 mm long and 0.7 mm wide. Seed bracts 3–4 mm long with sometimes two fertile. Mature seed unknown.

Dist. Malesia: Borneo (Sarawak, known only from Mt Duiti and the Merurong Plateau in N. Sarawak). Fig. 21.

Ecol. Locally common in primary forest on exposed mossy ridges at 1000 to 1500 m.

Vern. Semiplor, Bintulu.

Note. The spreading straight linear leaves contrast rather strikingly with other members of the genus and rather resemble the juvenile foliage of Cupressaceae. Earlier I had included it in D. spathoides where the shorter leaves are also more or less linear and much wider than thick, but in this species the fertile structures are usually terminal and are subtended by nearly typical leaves not greatly reduced as in D. ericoides, while the leaves are distinctly bent forward and not straight.


Leaves diverging widely from the stem but sharply bent forward parallel to the stem or even directed inward, lanceolate, pungent, 1–1.5 mm long, 0.2–0.3 mm wide, 0.1 mm thick, strongly keeled on the dorsal side, flat or slightly concave on the axial side. Leaves on vigorous branches larger, up to 3 mm long and 0.6 mm wide. Fertile material unknown.

Dist. Malesia: West New Guinea (known only from the top of Mt Goliath), at 3000–3600 m.

Note. The original description expressed uncertainty between Dacrydium and Podocarpus sect. Dacrycarpus for this unique taxon, but unfortunately settled for the latter. The tiny leaves are typical for Dacrydium and the primary branches show no sign of the dimorphism which characterizes Dacrycarpus.

3. FALCATIFOLIUM


Dioecious shrubs to large trees to 36 m tall with thin more or less smooth brownish bark with scattered lenticels, reddish and somewhat fibrous within, breaking off in occasional flakes on larger specimens. Loosely and irregularly branched. Leaves spirally placed, single veined, and alternating with elongated appressed scales which are loosely clustered at the shoot apices to form foliar buds between episodes of growth. Seedling leaves narrowly lenticular, apiculate, bifacially flattened, giving way abruptly to distinct juvenile leaves in about the second year of growth. Juvenile and adult leaves distichous, bilaterally flattened and falcately curved away from the branch with the apex in most cases oppositely curved in the direction of shoot growth. Reproductive struc-
tures on short scaly shoots which are either axillary or terminal and may bear a few reduced leaves. Pollen cones cylindrical, solitary or clustered; microsporophyll a small acuminate spur above the two pollen sacs. Seed-bearing structures solitary, consisting of up to about a dozen large acuminate scales which become greatly swollen, red, and fleshy when mature; normally one subapical scale fertile with a cup-shaped epimatum which has a distinct hump opposite the base of the included seed positioned well beyond the subtending fleshy scale so that the solitary seed and its basal humped epimatum are fully exposed; the inverted ovule gradually turning upward as it matures into a nearly erect seed; the mature seed with two lateral weak ridges along its wider sides which come together in an apical ridge, otherwise the seed is more or less egg-shaped.

**Distr.** New Caledonia (1 sp.); in Malesia: New Guinea, Moluccas (Obi 1.), N. & Central Celebes, Philippines (Mindoro), Borneo, Riouw-Lingga Arch. (Lingga), and Malaya.

**Note.** Obviously related to Dacrydium but differing in the dimorphic foliage with specialized fertile shoots and the exposed hump of the epimatum opposite the base of the seed. In Dacrydium the base of the seed lies close to its attachment and is always well covered by the subtending bract.

**Key to the Species**

1. Adult leaves normally bent at least slightly forward at the apex, tapering from at least the centre of the leaf; pollen cones at least 17 mm long.
2. Adult leaves linear-lanceolate, sun leaves at least 20 mm long, not glaucous; pollen cone 2.5–3.5 mm diam. ........................................ 1. F. falciforme
3. Adult leaves mostly lanceolate, sun leaves 13–20 mm long, glaucous; pollen cone 1.5–3 mm diam. ................................................ 2. F. gruezoii


Large shrub from 1.5 m to occasionally a large tree as much as 36 m tall, more commonly 5–12 m, 4–40 cm diam. Seedling leaves widening gradually from a petiole several mm long to margins parallel in the middle of the leaf, apex more abrupt, acute, apiculate, midrib a low blunt ridge above and a narrow sharp ridge below, slightly revolute, 4–9 by 2–3.5 mm. Juvenile leaves on the first branches only slightly longer and wider than the seedling but soon becoming as much as 12 cm long and more gradually becoming as much as 12 mm wide, the lanceolate apex strongly curved so as to become parallel to the shoot, midrib on either side a weak ridge. Adult shade leaves spreading at a large angle with more or less parallel margins in the centre of the leaves and broadly lanceolate apex which curves strongly forward but still at an angle from the shoot, 4–7 cm by 5–9 mm. Adult sun leaves much more abrupt at both ends so as to form a broad lens shape almost a parallelogram with rounded corners, 2–4 cm long by 5–7 mm wide, the apex sometimes not bent forward. Pollen cones 2–4 cm long by 2.5–3.5 mm diam. Receptacle of seed-bearing structure 4–5 mm long; mature seed 6–7 mm long, 5 mm wide, and 3.5–4 mm thick, becoming black.

**Distr.** Malesia: Malaya, Riouw-Lingga Arch. (Lingga: P. Tanda) and Borneo (mainly Sarawak and Sabah). Fig. 23.

**Ecol.** Locally common along ridges as a bushy tree or in the subcanopy of primary rain-forest, often
It is called a 'young tree' but given as 24 m tall. This may well be a new species.


*Arbor 4–12 m alta. Folia juvenilia ad 7.5 cm longa, 7 mm lata, falcata et apice versus apex ramorum curvo, lanceolata; folia adulta umbrae minora, 3.5 cm longa, 6–7 mm lata; folia solis plus minora, 13–20 mm longa, 3.5–6 mm lata, acuta, apiculata, glauca. Strobili masculi 1.7–6 cm longi, 1.5–3 mm diametri. Strobili feminii receptaculo 2 mm, semina 7 mm longo. Type: GRUEZO WM 4052 (L., holo; CALP, iso), Naujan, Paitan access, Paitaraan (Mt Halcon area), Mindoro Oriental, Philippines.

Tree 4–12 m tall. Juvenile leaves to 7.5 cm by 7 mm, falcate with the apex curved forward more or less parallel with the branch; lanceolate. *Adult leaves* in the shade smaller, 3.5 cm by 6–7 mm; sun leaves even smaller, 13–20 by 3.5–6 mm, acute, apiculate, glaucous. *Pollen cones* 1.7–6 cm long and 1.5–3 mm diam. *Receptacle* of the seed-bearing structure 2 mm long; seed 7 mm long.

*Dist. Malasia*: Philippines (Luzon: Tayabas, Nueva Ecija; Mindoro: Panay; Mindanao: Davao, Surigao); Celebes: Manado (Poso; Gorontalo; Palu); Moluccas (Obi). Fig. 23.

on podsol sands and kerangas, but occasionally on deeper fertile soils a somewhat emergent forest giant, from 400–2100 m.

*Vern.* Kayu china, Sabah, Lahad Datu, iguh gawah, Iban, Meruong Plateau.

*Notes.* In the forests of Mt Kinabalu the juvenile plants have smaller leaves than elsewhere, but otherwise there do not appear to be any differences. Several collections of more or less juvenile material have been made in Celebes and Central Moluccas (Obi), but these resemble more *F. gruezoii* of the Philippines. A single specimen from high kerangas on the Usan Apan Plateau in Sarawak has leaves in the form of adult shade leaves, but these are only 6 by 2 mm.

Fig. 22. *Falcifolium falciforme* (Parl.) De Laub. Twig with male cone, x 1 (after Wyatt-Smith KEP 93115).

Fig. 23. Range of four species of the genus *Falcifolium*.

*Ecol.* In exposed locations along ridges or on the borders of open areas, 1600–2200 m in the Philippines, 1200–1400 m in Celebes, 700 m in Obi.

*Note.* See note under *F. falciforme*.


Tree 6–22 m tall, 8–40 cm diam. Seedling leaves 6–18 by 0.6–0.8 mm. Juvenile leaves the same as the smaller adult leaves, glaucous beneath. Adult leaves falcate and then more or less linear in the distal part of the leaf or tapering slightly, narrowing almost abruptly to an apiculate apex, the apex occasionally bent slightly forward, 10–20 by 2–4 mm. Pollen cones 5–13 mm long and 2–2.5 mm diam. Receptacle and seed each 6–7 mm long.

**Distr.** Malesia: New Guinea. Fig. 23.

**Ecol.** Understory tree of moist mountain forests, often associated with *Nothofagus spp*, *Myriaceae* and other *Podocarpaceae*, 1500–2400 m.

**Vern.** Mungagi, Hagen Togoba, *tugl*, Wahgi, Minj.

*Note.* An entire plant scarcely 20 cm tall with tiny leaves mentioned and illustrated in the type description from the Vogelkop either represents perhaps a reduced form of exposed ridges or a distinct new species.


Dioecious shrubs or trees, to 41 m tall. Bark hard, dark brown or blackish but weathering to gray, surface rough with occasional lenticels, inside pink to reddish brown and granular or slightly fibrous, on older trees breaking off in small thick, somewhat vertically elongated plates or sometimes short strips. Leaves amphistomatic, spirally placed, broadly decurrent, apiculate. Leaves on primary shoots as well as on the basis of foliage shoots and fertile structures bilaterally flattened, keeled on the dorsal side, lanceolate or sometimes triangular, often nearly appressed, mostly 1.5–3 by 0.5–0.8 mm, but wider on the decurrent part, up to at least 4 mm long on young plants and mostly 1–2 mm long at the base of foliage shoots or fertile structures. The apex of resting shoots a
loose cluster of reduced leaves. *Juvenile type of leaves* on special shoots that generally do not continue growth after reaching a resting stage, bilaterally flattened and usually slightly keeled on both faces, falcate and then curved forward towards the apex so that the apiculate tip is oriented more or less parallel with the shoot, otherwise linear or less often lanceolate, spreading at about a 60° angle, the centre of the leaf either straight or gradually curving to the tip, distinctly shorter towards either end of the shoot so that the whole shoot has a feather-like appearance, mostly 6–12 mm long and c. 1 mm wide, usually distichous, gradually changing to an adult form but often fertile at intermediate stages of this transition. *Final adult forms* not distichous, generally shorter and more robust than the juvenile leaves, more or less uniform along the shoot, the apiculate tip still bent forward parallel to the shoot, in some species nearly identical with the leaves of primary shoots. *Fertile structures* terminal on short, mostly lateral shoots, the seed-bearing structures usually on a considerably longer shoot than that of the pollen cone. Immature *pollen cones* at first sometimes nearly spherical, then becoming somewhat elongated but finally elongating abruptly with a slight decrease in diameter at maturity, then mostly c. 6–10 mm long and 2–3 mm diam., sometimes longer. Apex of microsporophyll triangular, acute to apiculate, c. 1.2 by 0.8 mm. *Shoots for female structures* 3–17 mm long. Leaves at the base of the seed-bearing structure sharply elongated to form an involucre which often surrounds the immature seed-bearing structure but which in the shorter examples becomes spreading as the structure grows. *Seed-bearing structure* composed of a small warty receptacle, 2.5–4 mm long, 2.5 mm diam., which becomes greatly enlarged, fleshy, and first orange then red or in other species purple when ripe, later turning brown, bearing one or two protruding short sterile leaf-like bracts and one or two subterminal fertile bracts. *The inverted ovules* completely surrounded by the epimatium and fused as a rib along one side with the fertile bract whose short free tip forms a small off-centre crest over the mature structure. *Mature seed* nearly spherical (or oval) but remaining covered by the leathery epimatium and scale, forming an erect or somewhat oblique structure which in most species is c. 5–6 mm long and 4.5–5.5 mm diam., dark in colour.

**Distr.** Ranging from northern Burma and southernmost China to Fiji and New Zealand 9 *spp.*; in Malesia abundant with 7 *spp.*, reaching their greatest variety in New Guinea with 5 *spp.* Fig. 24.

*Fossils* are known from N. Antarctica (Graham Land) and New Zealand (Middle Jurassic) and S. Patagonia (Upper Cretaceous to Oligocene) where the genus is now extinct. In the Eocene found in New Zealand, and since the Oligocene also in SE. Australia, where it became extinct (FLORIN, Kongl. Svensk. Vet. Ak. Handl. III, 19, n. 2, 1940, 70; Acta Horti Berg. 20 (4), 1963, 188, f. 19: map).

**Note.** Sterile specimens strongly resemble *Dacrydium* and hence the generic name. The fusion of the fertile scale with the epimatium is a unique trait of the genus while the seeds of *Dacrydium* are furthermore naked. In most cases sterile specimens can be readily distinguished from *Dacrydium* by the distinctly dimorphic foliage.
Fig. 24. Range of the genus *Dacrycarpus* (ENDL.) DE LAUB. Figures above the hyphen indicate the number of endemic species, that below the hyphen the total number of species.

**KEY TO THE SPECIES**

1. Involucral leaves short (2.5–5 mm long) and mostly spreading so that the immature receptacle becomes or more frequently is always exposed; adult leaves scale-like or equally keeled on four sides, 1–3 mm long.
2. Adult leaves less than 2 mm long, more or less in the form of scales ................. 1. *D. imbricatus*
3. Adult leaves at least 2 mm long, in the form of short needles .............................. 2. *D. steupii*

1. Involucral leaves curved to surround the young fertile structure (3–13 mm long) and still covering at least the entire immature receptacle before it enlarges when ripe; adult leaves not scale-like nor equally keeled on four sides, 1–6 mm long.
2. Adult leaves bilaterally flattened.
3. Involucral leaves surrounding receptacle and mature seed (7–13 mm long); foliage leaves slender (0.6–0.8 mm wide), scarcely keeled ................................................................. 3. *D. cunningii*
4. Involucral leaves reaching the base only of the mature seed (5–8 mm long); foliage leaves robust (0.8–1 mm wide), strongly keeled .................................................. 4. *D. kinabaluensis*
5. Adult leaves bifacially flattened.
6. Involucral leaves less than 5 mm long, not reaching the mature seed; foliage leaves 0.6–1 mm wide.
7. Seed not large (5–6 mm long); foliage leaves spreading ........................................ 5. *D. expansus*
8. Seed large (7–8 mm long); foliage leaves imbricate ........................................... 6. *D. compactus*
9. Involucral leaves 6–10 mm long, mostly covering the mature seed; foliage leaves 0.4–0.6 mm wide


KEY TO THE VARIETIES

1. Leaves slender (0.4–0.6 mm wide); involucral leaves always spreading.
2. Leaves imbricate ............ a. var. imbricatus
2. Leaves spreading ............ b. var. patulus
1. Leaves robust (0.6–1 mm wide); involucral leaves sometimes clasping the receptacle.
3. Leaves spreading ............ c. var. robustus
3. Leaves imbricate ............ d. var. curvulus

a. var. imbricatus

Majestic columnar tree to 50 m tall, up to 2 m diam., crown large, often dome-shaped. Leaves of primary shoots imbricate; leaves of juvenile foliage shoots distichous, nearly linear, up to 10–17 mm long by 1.2–2.2 mm wide at the centre of a shoot, gradually losing the distichous habit as the tree matures, but shoots with more or less bilaterally flattened leaves distinctly longer in the middle of the shoot almost always present on even the oldest trees. Terminal shoots on young plants often elongated whip-like up to 20 cm. Leaves on older trees eventually becoming mostly scale-like, imbricate, distinctly keeled on the dorsal side, long-triangular, 1–1.8 by 0.4–0.6 mm. Involucral leaves becoming spreading, acicular, 2.5–4 mm long, rarely to 5 mm. Ripe receptacle red.

Distr. Malesia: Java, all Lesser Sunda Islands (Bali–Timor) and SW. & Central Celebes. Fig. 25.

Ecol. Mostly scattered and common in primary and secondary rain-forest, not rarely as an emergent, and co-dominant in West Java with Podocarpus nerifolius and Alltingia noronhiae, on the south slope of Mt Tjeremai volcano characterizing the zone between 2400–2700 m without other co-dominants, a situation not yet explained (van Steenis, 1972), in Timor found under more or less seasonal conditions in isolated specimens laden with Usnea in grassland after deforestation, mostly between 1000–2500 m.
Fig. 26. *Daucrycarpus imbricatus* (Blume) de Laub. *var. patulus* de Laub. (drawing by R.S.Keng in Whitmore, Tree Flora of Malaya 1, 1972, 51, f. 4).
but in Lombok reported as low as 200 m and in Celebes ascending to 3000 m. Probably exterminated at lower elevations in Java by deforestation. Male flowers at Tjibodas in Aug.—Sept. Sometimes the stem of full-grown trees produces sprouts at the base (van Steenis, 1940).

Uses. A most valuable timber tree.


Tree, 5–45 m tall, 10–100 cm diam. Adult foliage leaves not imbricate, spreading sharply, acicular, distinctly keeled on four sides, 0.8–1.5 by 0.4–0.6 mm. Involucral leaves to 3 mm long, spreading.

Distr. Northern Burma and southernmost China, through Southeast Asia to Malesia: Sumatra, Malaya, Borneo, Philippines (Luzon, Mindanao), Central Celebes, along the N. coast of New Guinea (incl. New Britain and New Ireland), and New Hebrides to Fiji. Common, but not in Java. Fig. 25.

Ecol. Scattered and common in primary and secondary rain-forest, mostly between 700 and 2500 m, in N. Sumatra at c. 400 m on sinterlimestone near sulphur springs near Tinggi Radja, up to c. 3000 m in Borneo, and occasionally to near sea-level in Fiji.


Note. Only in Celebes is there an overlap with var. imbricatus with possibly transitional forms. In Borneo, Mindanao, and along the northern coast of New Guinea specimens approach var. robustus in form. Specimens from the western and eastern parts of the range are identical and easily distinguishable from other varieties.


Tree, 5–45 m tall, 5–130 cm diam. Adult foliage leaves like var. patulus but distinctly more robust, 1.2–1.8 by 0.6–0.8 mm. Involucral leaves to 3 mm long and spreading or in some areas to 5 mm and more or less clasping the receptacle.

Distr. Malesia: Borneo (Sarawak, once), Philippines (Luzon, Mindanao), Moluccas (Morotai, Ceram), and throughout New Guinea. Fig. 27.

Fig. 27. Range of Dacrycarpus imbricatus (BLUME) DE LAUB. var. robustus DE LAUB. (dots) and var. curvulus (MIQ.) DE LAUB. (triangles).

**Note.** Specimens from Borneo and the Philippines have been identified as *D. steupii* where the foliage leaves fall within the size range of this species because in these areas the distichous habit is lost rather early causing the foliage to resemble *D. steupii* closely. Unlike *D. steupii*, however, the leaves range to the smaller sizes of *D. imbricatus*. The involucral leaves in these areas, unlike elsewhere in *D. imbricatus*, are at least 5 mm long and curved upward. Perhaps this material represents a distinct variety.


Shrubby pyramidal tree to 8 m tall and sometimes procumbent. Foliage shoots curved downwards but main branches curved upwards. Adult foliage leaves like var. *imbricatus* but distinctly more robust, 1.2–2 by 0.8–1 mm. Involumcular leaves 2.5–4.5 mm long and more or less clasping the receptacle.

**Distr.** *Malesia*: North Sumatra (Atjeh: Leuser complex & G. Bandahara) and western half of Java (Priangan; Dieng). Fig. 27.

**Ecol.** In N. Sumatra pure stands on exposed mossy mountain peaks, on blangs and steep slopes, between 2000 and 3420 m.

**Vern.** *Tjamarah*, J, at variance for *Casuarina* which does not occur so far west in Java.


Conical tree, 4–36 m tall, 15–100 cm diam. Leaves of primary shoots spreading slightly. Leaves of juvenile foliage shoots distichous, nearly linear, soon losing the distichous habit as the tree matures. Leaves on older trees eventually becoming nearly quadrangular in cross section, widely spreading, tapering slightly, uniform in size along a shoot, 2–3 by 0.4–0.6 mm. Involumcular leaves becoming spreading, 3–4 mm long.

near Balikpapan, once), Central Celebes (Latimodjong Mts) and throughout New Guinea. Fig. 29.

Fig. 29. Range of three species of the genus Dacrycarpus.

Ecol. Locally common, particularly in disturbed forests, or in poorly drained areas where it may form nearly pure stands, in boggy grasslands and reed-swamps, on sandy clay, once on a rocky riverbank, once on a limestone hillock in mossy forest (Mt Beratus), 860–3420 m, but mostly c. 1500–2000 m. 


Note. The spreading needles give this species a rather distinct appearance from D. imbricatus var. robustus which it otherwise strongly resembles. In New Guinea it has a markedly distinct ecology.


Tree, 8–25 m tall, up to 18–75 cm diam. Leaves of primary shoots spreading slightly, often curved so that the apex is directed inward slightly towards the axis. Leaves of juvenile foliage shoots distichous, nearly linear. Leaves of older trees similar but mostly not distichous, often more robust and scarcely keeled on the lateral faces, 3–6 by 0.6–0.8 mm. In addition to primary shoots and purely foliage shoots there are intermediate shoots with leaves 2–3 mm long, strongly keeled on four sides, but distinctly bilaterally flattened. The intermediate shoots bear foliage shoots and fertile shoots but are caducous like the foliage shoots and unlike the primary shoots. Pollen cones usually normal but on one specimen from low elevation up to 4 cm long. Involutacular leaves greatly elongated resembling the foliage leaves but curved, not straight, 7–13 mm long, completely surrounding the developing fertile structure which scarcely surpasses them when fully mature. Ripe receptacle reddish.

Distr. Malesia: N. Sumatra (Leuser complex, 2 coll.), Borneo (Sarawak, rare), Philippines (Luzon, Negros, Panay, Mindanao). Fig. 29.

Ecol. Locally common from 1000 to 3314 m, but mostly between 1850 and 2650 m in mossy primary forest. Locally it occurs above D. imbricatus most of whose varieties do not enter the mossy forest. 

Vern. Sumatra: sangi, Gajo, Mt Leuser; Philippines: igem, Davao, Mindanao.


Shrub or small, sometimes gnarled tree, 2–13 m tall, 15–30 cm diam. Leaves of primary shoots nearly imbricate with the apex often curved slightly inward. Leaves of juvenile foliage shoots distichous, nearly linear. Leaves on older trees similar but soon becoming not distichous and more robust, distinctly keeled on the lateral faces, 3–6 by 0.8–1 mm. Together with primary shoots and foliage shoots are intermediate shoots with leaves 2–5 mm long and triangular or quadrangular in cross section. The intermediate shoots bear foliage shoots and fertile shoots but are also deciduous. Involutacular leaves greatly elongated resembling the foliage leaves but more distinctly curved, 5–8 mm long, reaching only the lower part of the seed when it is mature. Ripe receptacle blue or purple. Seed with its covering 6–7 mm long and 5–6 mm diam.

Distr. Malesia: Borneo (Sabah: Mt Kinabalu). Fig. 29.

Ecol. Common, sometimes in nearly pure stands in dwarf mountain scrub from 2700 m to the tree line at c. 4000 m. 

Note. On Mt Kinabalu D. imbricatus does not occur above c. 2000 m, leaving a considerable gap before D. kinabaluensis is seen, which represents the mossy forest zone. In fact, D. kinabaluensis rather strongly resembles D. cunningii, differing particularly in the distinctly shorter involucral leaves. Foliage leaves of D. cunningii when collected from exposed parts of the tree approach this species in robust form. The receptacle colour of D. cunningii is poorly documented and may well become purple also.


Tree 9–25 (–30) m tall, 22–58 cm diam. Leaves of
primary shoots on young plants nearly imbricate but on older plants spreading and then curved forwards. Leaves of juvenile foliage shoots distichous, nearly linear, soon losing the distichous habit as the tree matures. Leaves on older trees eventually becoming wider than thick but distinctly keeled on the upper and lower surfaces, spreading but the upper half curving forwards, uniform in size along the shoot, tapering slightly, 1.5–3 by 0.4–0.8 mm or a little larger on younger trees. Involucral leaves loosely surrounding the young fertile structure but covering only the receptacle of the mature seed with its covering, which is c. 3–3.5 mm long.

Dist. Malesia: Central Highlands of Papua New Guinea. Fig. 30.

Ecol. Locally common or even in pure stands (e.g. at Wabag), or co-dominant, sometimes emergent, often in disturbed situations, e.g. on edges of treefern grassland, 1300–2750 m.

Vern. Pa‘u, pau, Kepilan, Enga lang.

Note. Not associated with moist habitats like D. sieupii, a species which is also associated with disturbed habitats. This latter species differs in the form of the foliage leaves and the involucral leaves.

CoNiFERALES

ROYEN, Alpine Fl. New Guinea 2 (1979) 20, f. 36, t. 80. — Podocarpus compacta Wasscher, Blumea 4 (1941) 411, t. 4, f. 8a, b. — Podocarpus papuanus (non Ridley) Pilger, Bot. Jahrb. 68 (1936) 244. — Fig. 31, 32.

Irregular tree 2–20 m tall, up to 25–60 cm diam. Leaves of primary shoots spreading slightly, often curved so that the apex is directed inward towards the axis. Leaves of juvenile foliage shoots not distichous, lanceolate, strongly keeled laterally, 2–2.5 by 0.6 mm. Leaves on older trees becoming similar to the leaves on primary shoots, spreading but curved through most of their length, strongly keeled on the dorsal side, 1–2.5 by 0.6–1 mm. Pollen cones on a 3 mm or more often longer shoot. Involucral leaves robust, curving to surround the receptacle, strongly keeled on the dorsal side and more or less triangular in cross section, 4–5 by 0.8–1.2 mm. Ripe receptacle purple to black. Seed with its covering 7–8.5 mm long and 7–8 mm diam.

Distr. Malesia: New Guinea. Common in E., but rare in W. New Guinea (Habbema Lake, Quarles Lake, 2 coll.). Fig. 30.

Ecol. Common on the higher peaks near the tree line, sometimes forming pure stands or emerging above a subalpine shrubbery, or scattered in alpine grassland, often in isolated specimens and obviously fire-resistant, in Podocarpus-Libocedrus forest, rarely on wet peaty soil (Lake Aunde), 2800–3950 m, but mostly above 3400 m.


Often flat-crowned tree up to 33 m, 20–90 cm diam., or a shrub 2–4 m tall. Leaves of primary shoots spreading slightly, straight or more often curved forward, 5–6 mm long on young plants, becoming 3–4 mm long on adult plants and 2–3 mm long at the base of foliage shoots and fertile structures. Leaves of juvenile foliage shoots not disti-

Fig. 32. Dacrycarpus compactus (Wasscher) de Laub. Detail of female branch with cones. Mt Amungwiwa, New Guinea, 3050 m (Photogr. P. van Royen 11072, June 1976).

Fig. 33. Dacrycarpus cinctus (Pilger) de Laub. Detail of female branch with cones. Papua New Guinea, Southern Highlands District, 27 miles from Mendi, 2743 m (Photogr. Womersley LAE 55322, Sept. 1972).
chous or perhaps slightly so, linear-lanceolate, the upper half curved forward, 0.5–0.8 mm wide. Leaves on older trees eventually becoming similar to the leaves of primary shoots but somewhat narrower and curved like the juvenile leaves, 2–5 by 0.4–0.6 mm, uniform along a shoot, often glaucous. Pollen cone sometimes on long shoots. Involucral leaves resembling the foliage leaves but curved throughout their length, completely surrounding the developing seed with its covering which rises slightly above them when mature, 6–10 mm long. Receptacle bright red when ripe. Seed with its covering 7 mm long and 6–7 mm diam.

Distr. Malesia: Central Celebes, Moluccas (Central Ceram: G. Binaja), and throughout New Guinea. Fig. 34.

Fig. 34. Range of Daecycarpus cinctus (PILGER) DE LAUB.

5. PRUMNOPSIS


For further synonyms see under section Sundacarpus.

Densely branched dioecious trees to 60 m tall. Bark smooth, fibrous, and reddish to yellowish brown, often darker on the surface but weathering to gray, on older trees breaking off in irregular more or less quadrangular plates 3–5 mm thick and 3–10 cm across, with scattered lenticel-like mounds. Foliage buds

Ecol. In New Guinea extremely common and often dominant, or co-dominant with Nothofagus, Libocedrus, Elaeocarpus and Podocarpus, in mountain forest and mossy forest, on Mt Binaja in orchard-like pure stands with a mossy ground cover, rarely in muddy parts of swamps (Iowasi swamp near Woitape), a canopy tree or sometimes emergent, often thick-trunked, the foliage glaucous or not, 1800–2850 m, occasionally as high as 3600 m, in Ceram from 1300–3000 m, in Celebes reported as low as 900 m.


Note. Collectors complain that this species grades into D. compactus and indeed in the zone of overlap between these two species specimens of D. cinctus have shorter and more robust leaves resembling D. compactus, while the common glaucousness of D. cinctus has been observed to disappear above 2950 m. The two species are substantially different, however, and both become much less common in the elevations where they overlap (2900–3400 m). Perhaps hybridization occurs where they overlap.
small and inconspicuous with overlapping triangular scales. *Leaves* spirally placed, bifacially flattened, linear, uninerved, without hypoderm, hypostomatic, narrowed at the decurrent base with a twist where the leaf leaves the stem so that the leaves appear distichous. *Pollen cones* axillary and solitary or grouped on scaly spike (or even compound structures). *Seed* with its covering solitary and subterminal or grouped along a scaly or leafy shoot, inverted and completely covered by a fleshy epimatium with an apical crest; the seed with a slightly asymmetrical ridge at the micropylar end.

**Dist.** 10 spp. in two slightly geographically overlapping sections, with the type section extending from Australia and New Caledonia to New Zealand and from Chile to Venezuela and Costa Rica. The monospecific section *Sundacarpus* is confined to Malesia and NE. Queensland. Fig. 35.

**Uses.** Several species are important timber trees.

![Fig. 35. Range of the genus Prumnopitys Philippi. Figures above the hyphen indicate the number of endemic species, that below the hyphen the total number of species.](image)

1. **Section Sundacarpus**


Fig. 36. Prumnopitys amara (Blume) de Laub. A. Habit of tree; B, C. twigs with pollen cones; D–F. microsporophylls (different views) (from Koord. Atlas 3, 1915, t. 590).

Tree 10–60 m high, 12–140 cm diam. Bark surface checkered by numerous cracks. Cotyledons 3 fused pairs. Foliage buds small, globose, with overlapping, rounded, keeled scales up to 2 mm long. Juvenile leaves oblong, 4–12 by up to 2 cm, more or less abruptly narrowing at the base to a 3–5 mm long petiole, narrowing abruptly at the apex to an elongated tapering 'tip' which is c. 2 mm wide and up to 20 mm long, apex rounded to acute. Mature leaves becoming longer and narrower, linear, narrowed at the base to a c. 5 mm long petiole, usually slightly acuminate and acute, a distinct groove over the mid-vein above, broadly raised below, 5–15 cm by 6–14 mm. Pollen cones 15–35 by 2.5–3.5 mm, solitary and terminal or grouped to at least seven on an auxiliary 1–7 mm peduncle with several sterile basal scales. Apex of microsporophyll acute, triangular, keeled, c. 0.8 mm long. One to several ovules scattered laterally along a 3–5 mm scaly shoot, the scales triangular to rounded, decurrent, spreading, 1.5–2 mm long, the sterile scales deciduous. Ovule and its covering oval, longer than its bract (fertile scale) and distinctly crested at its apex, dark blue and glaucous. Growing seed and its covering elongated at both the micropylar end and the forwardly bent apex; mature seed and its covering nearly spherical, with a small obtuse crest, c. 25 mm diam., becoming reddish and then dark purple and glaucous. Seed c. 20 mm diam., with an indistinct ridge and minute apiculus formed from the micropyle, the smooth surface hard shell c. 1 mm thick, the fleshy covering c. 3 mm thick becoming wrinkled as it dries and often falling off.

Distr. NE. coastal Queensland; in Malesia: through and very common in New Guinea (incl. New Britain & New Ireland), Moluccas (Buru, Halmaheira, Morotai), Lesser Sunda Islands (Timor, Flores, West Sumbawa, Lombok), throughout Java, Central and SW. Celebes (Bontbain), Philippines (Mindanao, Luzon), Borneo (only in Sabah!), and Sumatra (Central–N., Batak region, rare in S. Palembang). Fig. 37.

Loc. Scattered and often common in primary and secondary rain-forest, in New Guinea very common, often in Fagaceous forest, sometimes in mossy forest, in submontane forest at c. 900 m with Dyso-

...xylum, Macaranga, Ficus, sometimes emerging as a colossal tree, often on laterosols, rarely on sandy soils or on marshy ground, (sea-level–)500–2000 (–2300) m, according to SMYTHIES (in sched.) to 3000 m in Sabah.

A few times it is mentioned that the tree is butted (Pinosos Plateau and Mt Cyclops, New Guinea), or spurred, a rare feature in Podocarpaceae.

Uses. A fine timber tree, often of large dimension. In New Guinea mentioned to be used for joinery and furniture.


Note. The leaves are variously reported as bitter ('amara'), to which also the Sundanese name 'pai' refers, bittersweet ('dulcamara'), or sweet tasting. This and the groove over the mid-vein most readily distinguishes it from similar-leaved associated Podocarpus species while the lack of hypoderm also gives a distinct texture to the leaves. The striking form of the juvenile leaves led to the description of Podocarpus eurycynthia. GRAY & BUCHHOLZ (1951) report that the leaves occasionally have a lateral pair of vascular resin canals in addition to the conspicuous central canal beneath the vascular bundle. Two collectors
Fig. 38. Prumnopitys amara (Blume) de Laub. G, H. Twigs with pollen cones; I. twig with seeds; K, L. twig and leaf of a young tree; M. leaf of an adult tree; N–P. pollen cones with details; Q, R. seed, also in cross section (from Koord. Atlas 3, 1915, t. 591).
report seeds with distinctive sculpturing on their surface but this is not evident in the corresponding preserved specimens. The normally three rather than two fused pairs of cotyledons is unique. The limited occurrence in Borneo is curious.

6. NAGEIA


Dioecious, erect shrubs or trees, 1–54 m tall. Bark tan to brown within and dark brown to black on the surface but often weathering to gray, peeling in irregular shaped plates to short vertical strips. Leaves opposite-decussate (or mixed with some leaves spirally placed), distinctly narrowed to a decurrent base. Juvenile leaves mostly larger than the adult leaves which are otherwise similar, twisted at the base so as to appear distichous, in most cases amphistomatic with
the abaxial face uppermost on the left side of the shoot and the axial face uppermost on the right side (in a few species the leaves are hypostomatic and without this unique orientation). *Pollen cones* sessile or terminal, solitary or grouped, cylindrical (or oval). Each inverted *seed* completely covered by the fertile scale (epimatium), one or occasionally two subterminal on a scaly shoot, the usually persistent leathery covering becoming more or less fleshy when ripe.

**Distr.** There are 12 *spp.* in the three sections through most of the tropical forests of the world, throughout *Malesia*, where two sections overlap each other. Fig. 40.

**KEY TO THE SECTIONS**

1. Leaves large, broad, ovate to broad-lanceolate, with many longitudinal veins........ 1. *Sect. Nageia*
2. Leaves small, with a single rib.................................................. 2. *Sect. Polypodiopsis*

**1. Section Nageia**


Erect shrubs or trees, 1–48 m tall. Bark smooth, on trees peeling in large thin irregular shaped plates with scattered lenticels. *Foliage buds* a compact cluster of lanceolate deciduous scales abruptly wider than the shoot and distinctly acute, when terminal often 2–3 mm beyond the last leaf bases, 3–6 mm long, lateral buds sessile. Primary shoots not differentiated from ultimate shoots. *Leaves* with many parallel vascular bundles (one of which is medial) converging towards the acute to acuminate apex, more or less elliptic but juvenile leaves very acuminate and adult leaves sometimes more or less blunt, distichous, amphistomatic with equal basal twists (or hypostomatic with opposite basal twists), narrowed to a short broad petiole. *Fertile shoots* arising in the axils of leaves from sessile buds essentially the same as foliage buds, one to several pairs of deciduous scales below the first pollen cone or the female receptacle. *Pollen cones* cylindrical, solitary or grouped with one terminal and others forming sessile decussate pairs about 5 mm apart, each cone in the axil of a sterile scale but the terminal three often fused at their bases. In some species a part of the fruit-bearing shoot becoming enlarged and eventually fleshy forming a receptacle, otherwise a part of the shoot often remaining attached to the seed when it falls. *Seed* smooth, nearly spherical but elongated on the micropylar end into a small asymmetrical beak.

**Distr.** There are 5 *spp.* from southern India and Bangladesh across Indochina and *Malesia* to New Britain and through southern China to southern Japan; in *Malesia* 3 *spp.* Fig. 40.
Notes. Sterile specimens often confused with Agathis with very similar leaves, but in Agathis the parallel vascular bundles do not markedly converge towards the leaf apex and the terminal bud is globular, not acute, but very blunt-rounded.

The key to the three species is inadequate for identification of sterile material, but the leaf-size and length of the petiole may be helpful, though sizes overlap.

Fig. 40. Range of the genus Nageia Gaertn. and its three sections, with the number of species.

KEY TO THE SPECIES

1. Fruit with fleshy receptacle.
2. Pollen cones grouped on a peduncle. Leaves at least 6 cm long ........................................ 1. N. wallichiana
2. Pollen cones solitary, sessile. Leaves mostly less than 5 cm long ........................................ 2. N. motleyi
1. Fruit lacking a fleshy receptacle. Large-leaved .................................................. 3. N. maximus

Fig. 41. *Nageia wallichiana* (Presl) O.K. A. Twig with seed; B, C. twig portion with young pollen cones; D. *ditto* with mature pollen cones; E. longitudinal section of seed; F. leaf of a mature tree; G. leaf of a young tree; H, I. terminal foliage buds; K. habit of tree (from Koord. Atlas 3, 1915, t. 588).

Tree, 10–54 m high, 7–60 cm diam., clear bole to 30 m. Leaves quite variable both on juvenile and adult plants with the larger leaves growing in the shade, 6–14(–23) by 2–5(–9) cm, 2 to at least 6 times as long as broad; petiole 5–10 mm. Pollen cones in groups of up to at least 7 on a 2–10 mm peduncle; mature cone 8–15 by 3–4 mm. Apex of the microspermophyll lanceolate, 2–3 mm long. Seed-bearing structure solitary on a 8 to at least 20 mm peduncle with caducous scales or occasionally reduced leaves. Receptacle with 4–7 sterile, deflexed, slightly enlarged bracts, 7–18 mm long before becoming ripe and fleshy, dark purple or black when ripe. Seed with its covering 15–18 mm diam.

Dist. Southeast Asia (S. extremity of the Decan Peninsula, Assam, Burma, Thailand, Indochina, Yunnan); in Malesia: Sumatra, Malaya, Banka I., W. Java, Lesser Sunda Islands (Flores), Borneo (incl. Karimata I.). Philippines (Luzon, Sibuyan, Mindoro, Panay, Samar), N. & Central Celebes, Moluccas (Obi, Ternate, Morotai, Ceram), New Guinea (incl. Meos Num, Biak, Japen, and Normanby Is.). Fig. 42.

Fig. 42. Range of Nageia wallichiana (Presl) O.K.

Ecol. Scattered and often common in primary rain-forests, nowhere reported gregarious or dominant, from very low elevation (5 m) ascending occasionally as high as 2100 m.

Collected in peat-swamps in Sumatra and Borneo, or dry parts of them, in the lowland, in Sarawak on basalt ridges and submontane kerangas, in E. Borneo (G. Beratus) in mossy forest on sandstone, in Sabah in sandy pelawan (Tristania) forest, in New Guinea on clay or sandy ridge forest, sometimes associated at submontane altitude with Anisoptera, Cinnamomum, Sloanea, Castanopsis, or with Araucaria-Podocarpus-Fagaceae at 700 m. In Thai land buttresses are recorded, at Argung Bay (New Guinea) even high buttresses; this seems to occur occasionally.

Uses. The tree yields a good timber. In Obi planks are used for house construction. In the Fly R. area it is used for smaller canoe logs.


Tree to 54 m high. Leaves 3–5(–7.5) by 1.5–2.2 (–2.8) cm, 1.5–3 times as long as broad; petiole 2–3 mm. Pollen cones solitary and sessile in the leaf axils, 15–20 by 5–6 mm. Apex of microspermophyll lanceolate to acuminate, at least 2 mm long. Seed-bearing structure solitary on a scaly 2–5 mm peduncle, Receptacle with 5–9 sterile, spreading, slightly enlarged bracts, 8–12 mm long before becoming ripe and fleshy. Seed with its covering 13–16 mm diam.

Dist. Southernmost Thailand; in Malesia: Ma-
Flora Malesiana

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Fig. 43. Range of three species of Nageia.

laya, throughout Sumatra and Borneo (Sarawak & SE. Borneo). Fig. 43.

Ecol. Scattered in primary and secondary rainforest, from very low altitude (15 m) to c. 500 m. It occurs on slopes and hills on dry soil, but also in Borneo in two different situations: in Sarawak it is collected on deep peat in a mixed ramin-peat swamp, but also on ridges and hill sides in bindang-dipterocarp forest and at Lawas at 1000 m on podsol sandy loam.

Vern. Malaya: podo kebal musang; Sumatra: kayu bawa, setebal, Palembang; Sarawak: medang buloh, Simunjan.


Erect shrub to tree, 1–10 m high. Leaves (8–)16–34 by (3–)6–9.5 cm, acuminate, 2.5–3.5 times as long as broad; petiole 4–10 mm. Pollen cones in groups of up to 9 on a 3–10 mm peduncle, 12–20 by 2.5–3 mm. Apex of microsporophyll more or less lanceolate, 0.5–1 mm long. Seed-bearing structure solitary or grouped to as many as five on a scaly shoot c. 6 mm long, the individual peduncles up to 12 mm long, not forming a fleshy receptacle. Seed and its cover 16–18 mm diam.

Distr. Malesia: Borneo (Sarawak, very local), a few collections. Fig. 43.

Ecol. Locally common in the understory of moist rain-forest on ridge in Bako National Park and in peat-swamp forest, from near sea-level to 120 m.


2. Section Polypodiopsis


Erect shrubs or trees, 2–43 m high. Foliage buds a loose cluster of rounded scales; at the apex of foliage shoots not destined to continue growth there are found only a few very reduced leaves. Leaves with a single vascular bundle, lanceolate, oval to nearly linear, acute or rounded at the apex, less than 5 times as long as wide, amphistomatic, distichous when juvenile and adult (adult leaves sometimes not distichous), sessile or with a very short petiole. A part of the not fleshy fertile shoot remaining attached to the seed and its covering when it falls. Seed ovate or globular with an elongated beak at the micropylar end.

Distr. There are 5 spp. from the Moluccas across New Guinea to Fiji and from Peru and western Brazil to Venezuela. Fossils have been reported from southern Australia, New Zealand, and S. Chile [FLORIN, Acta Horti Berg. 20 (4) (1963)]. One species in Malesia. Fig. 40.


Tree, 12–45 m high, up to 50–130 cm diam. Bark smooth, peeling in thin plates. Primary shoots with thin dispersed decussate rounded deciduous scales 1–2 mm long and broadly decurrent. *Foliage shoots* lateral or terminal with leaves somewhat smaller towards the extremities and a few very reduced leaves or scales at the base, usually not continuing growth after a resting period but sometimes producing a second cycle of growth or sometimes converting to a primary shoot. *Leaves* distichous, narrowed abruptly at the twisted base, broadly decurrent, linear-lanceolate to ovate, blunt, an indistinct rib marking the mid-vein on either surface, juvenile leaves up to 40 by 8 mm and consistently lanceolate, adult leaves 15–25 by 3–5 mm. *Pollen cones* subtended by a few crowded sterile scales similar to but smaller than those of the primary shoots, occasionally solitary in the axils of leaves but usually at the base of a foliage shoot or the upper portion of primary shoots, solitary or clustered (with one terminal) on scaly shoots or sometimes compound clusters, ovate when immature but elongating upon maturity and cylindrical, 12–24 by 2–2.5 mm. Apex of the microsporophylls triangular, at least 1 mm long. *Ovuliferous shoot* solitary in positions similar to the pollen cones, 6–10 mm long, scaly with the subterminal fertile scale or scales slightly larger. *Seed* with its covering globular but elongated into a curved beak towards the micro- pylar end which lies close to the attachment of the seed to the fertile shoot, the other (distal) end with a small crest which may persist on the mature seed whose coat becomes deep red and fleshy when ripe. *Seed* itself blunt on the base, 13–16 mm long including the beak, 8–10 mm diam.

*Distribution*. Fiji Is., Solomon Is. (Santa Cruz group); in *Malesia*: throughout New Guinea (incl. New Britain) and the Moluccas (Morotai). Fig. 43.

*Ecology*. Scattered and locally common in montane rain-forest, near the Wissel Lakes common, in New Britain co-dominant with *Gymnostoma*, in New Guinea sometimes frequent in *Agathis-Quercus* rainforest, from sea-level up to 1800 m.


*Note*. The stem is at the base sometimes recorded as fluted or spur-buttressed. *Henty (in sched.*) found the leaves and bark aromatic.

### 7. PODOCARPUS


Usually dioecious shrubs to large trees up to 45 m tall. Yellowish to reddish brown soft fibrous bark weathering to gray, more or less fissured and peeling in short to long vertical strips. Vigorous branching of the primary stem tends
to produce false whorls, otherwise branching is less regular to irregular. *Growth*

is by flushes with new leaves sometimes distinctly red rather than the more com-
mon shades of lighter green. Distinct resting buds are formed at the apex of each
leafy shoot and consist of two kinds of usually deciduous scales. *Primary scales*

which cover the resting shoot apex are produced in a cluster of 4 or 5 generally
unequal, keeled, mostly acute, triangular to lanceolate, partly overlapping
scales, mostly 1.5–2 mm wide at the base, the width related to the vigour of the
shoot. *Secondary scales* surround the newly growing shoot and are broader,
membranous, and blunt to acuminate. The growth and emergence of the sec-
ondary bud can produce striking changes in the appearance of the foliage bud.
On vigorous shoots the foliage bud is typically c. 4 mm diam., while weaker
shoots have buds 2–3 mm diam., but larger or smaller buds characterize certain
sections of the genus. *Leaves* spirally placed, bifacially flattened, uninerved, the
midrib flat or prominent, either with a distinct hypoderm or well developed ac-
cessory transfusion tissue but mostly with both, hypostomatic, or rarely with a
few upper stomata, more or less narrowed at the base into a short petiole. *Pollen cones*
produced in an axillary or occasionally terminal structure corresponding
to a foliage shoot. The primary pollen cone bud is sessile or produced on a short
naked peduncle and consists of 3 (4) small, more or less equal scales and appears
usually concurrently with the development of foliage buds which it resembles,
but is usually somewhat smaller with the individual scales typically c. 1 mm wide
at the base (wider in some sections). One or more cylindrical pollen cones typi-
cally c. 25 mm long emerge from the primary bud simultaneously with the elon-
gation of the secondary foliage buds, each pollen cone developing from a sec-
ondary bud which resembles the secondary foliage bud (which, however, is al-
ways solitary within the primary foliage bud). The typical pollen cone is up to
4 mm diam. before the elongation which accompanies pollen shedding and
2.5–3.5 mm diam. after shedding. In a few species the scaly base of the pollen
cone also elongates along with the fertile part at anthesis. The whole male struc-
ture falls as soon as the pollen is shed, the basal scales usually not falling separ-
ately. The *seed-bearing structure* is axillary mostly on new foliage shoots and
consists of a naked peduncle commonly c. 5–15 mm long surmounted by two
(to five) thickened adnate bracts which form a *receptacle* typically 7–12 mm
long which in most species becomes fleshy and greatly enlarged upon maturity,
one or more of the bracts in a subterminal position may be fertile. The inverted
*ovule* is completely enclosed in the leathery epimatium which often forms a crest
at the distal end where it folds over the base of the ovule and the resulting struc-
ture is completely exposed above the receptacle. The *seed* is usually glaucous
when immature and more or less green when mature (rarely with the seed cover
becoming fleshy or flushed with red), the seed cover normally persistent even
after drying.
There are two slightly overlapping subgenera with 95 spp. across the lower and southern latitudes, throughout the southern temperate forests, all of the tropical highland forests, and throughout the Asian–Malesian tropical lowland forests with a few species reaching other tropical lowlands and others the Asian subtropics. In Malesia only subg. Foliolatus is represented. Fig. 44.

**Subgenus Foliolatus**

*De Laub.* Blumea 30 (1985) 263.

Receptacle with two subtending foliola (lanceolate bracts); stomata without a ‘Florin ring’ (Buchholz & Gray, 1948); leaves with accessory transfusion tissue, never with resin canals at the leaf margins but in most cases at least three resin canals below or beside the vascular bundle; in most cases a ridge over the vascular bundle on the upper leaf surface, never a channel; juvenile leaves generally similar to adult leaves. Female receptacle becoming fleshy when mature but seed cover remaining leathery and greenish.

**Distr.** From Central China and Japan to eastern Nepal, across all of Malesia to eastern Australia and Tonga 53 spp. in 9 mostly overlapping sections. In Malesia: 8 sections with 30 spp.

**Key to the Sections**

1. Pollen cones solitary or in groups of 3 or fewer.
2. Pollen cones regularly in threes or a mixture of threes and fewer (pollen cones usually at least 2.5 mm diam.; midrib more than 0.3 mm wide; ripe receptacle usually red).
3. Primary foliage budscales erect and free, secondary budscales acute to acuminate.
4. Secondary budscales broadly acute, primary budscales generally less than four times as long as broad; adult leaves not acuminate, usually not abruptly expanded at the base. *Spp.* 1–8 1. Sect. Foliolatus
5. Secondary budscales acuminate, primary budscales more than four times as long as broad; adult leaves acuminate, abruptly expanded at the base. *Spp.* 9–10 2. Sect. Acuminatus

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**Fig. 44.** Range of the genus *Podocarpus* L'Hérit. ex Persoon. Figures above the hyphen indicate the number of endemic species, that below the hyphen the total number of species.
2. Pollen cones normally solitary (only rarely grouped) (external budscales erect and free; leaves not at all acuminate).

5. Foliage buds much longer than wide (with long lanceolate scales), secondary budscales acuminate. Bracts below the receptacle usually at least 3 mm long (ripe receptacle, red). **Spp. 13–17**

4. **Sect. Longifoliolatus**

5. Foliage buds less than twice as long as wide, secondary budscales not acuminate. Bracts below the receptacle usually less than 2.5 mm long (midrib less than 0.3 mm wide).

6. Pollen cones less than 3 mm diam., apex of the microsporophyll less than 0.5 mm long. Foliage bud less than 2 mm diam. **Spp. 18–21**

5. **Sect. Gracilis**

6. Pollen cones more than 3.5 mm diam., apex of the microsporophyll more than 1 mm long. Foliage bud mostly more than 2 mm diam. Ripe receptacle usually purple or black. **Spp. 22–25**

6. **Sect. Macrostachyus**

1. Pollen cones regularly in clusters of more than 3.

7. Outer budscales imbricate, apex of the scales slightly if at all raised. Midrib on the upper side of the leaf broad and flat. Ripe receptacle red. **Spp. 26–27**

7. **Sect. Rumphius**

7. Outer budscales erect and free. Midrib narrow and in most species prominently raised. Ripe receptacle usually purple. **Spp. 28–30**

8. **Sect. Polystachyus**

VEGETATIVE KEY TO THE SECTIONS

1. Primary budscales imbricate, forming a ball or pyramid with few or none of their apices raised, bud no longer than diameter.

2. Primary budscales overlapping and forming a ball or in some cases meeting pyramid-like at the bud apex but the scale apices never recurved outward; leaf hypoderm absent or occasionally slightly developed; leaf midvein generally more than half a mm wide but never a full mm ............. **3. Sect. Globulus**

2. Primary budscales mostly in the form of a pyramid with usually one or more scales recurved outward at the apex; leaves with continuous upper hypoderm and well developed lower hypoderm; leaf midvein more or less one mm wide ................................ **7. Sect. Rumphius**

1. Primary budscales with completely free apices, bud usually longer than diameter.

3. Adult leaves distinctly acuminate; primary budscales mostly more than four times as long as wide

2. **Sect. Acuminatus**

3. Adult leaves not acuminate but where transitional leaves may be slightly acuminate, the primary budscales less than four times as long as wide.

4. Foliage buds at least twice as long and generally much longer than basal diameter (leaves not at all acuminate).

5. Leaves lanceolate, widest near the base.

6. Midrib on upper side of leaf at least 0.2 mm high, often prominent ............. **4. Sect. Longifoliolatus**

6. Midrib on upper side of leaf less than 0.2 mm high, indistinct................ **8. Sect. Polystachyus (P. ridleyi)**

5. Leaves more or less linear, not widest near the base (buds only sometimes more than twice as long as basal diameter).

7. Leaves less than 7 mm wide, 5 cm long, midrib on the upper side less than 0.2 mm high

3. **Sect. Polystachyus**

8. **Sect. Foliolatus (P. gibsii)**

7. Leaves at least 8 mm wide, 4 cm long, midrib on upper side c. 0.3 mm high

4. **Sect. Foliolatus**

4. Foliage buds less than twice as long as basal diameter.

8. Basal diameter of foliage bud 1–2 mm (midrib on upper side of leaf 0.2 mm high and less than 0.5 mm wide).

9. Midrib on upper side of leaf 0.2 mm wide ...................................... **5. Sect. Gracilis**

9. Midrib on upper side of leaf at least 0.3 mm wide ................................ **8. Sect. Polystachyus**

8. Basal diameter of foliage bud at least 2 mm, usually considerably more.

10. Midrib on upper side of leaf less than 0.2 mm high and 0.7 mm wide.

11. Leaf midrib 0.2–0.3 mm wide ....................................................... **6. Sect. Macrostachyus**

11. Leaf midrib at least 0.5 mm wide.

12. Leaf less than 7 mm wide, 5 cm long; basal diameter of foliage bud less than 3 mm; leaf midrib 0.5–0.7 mm wide, distinct ......................... **4. Sect. Longifoliolatus (P. gibsii)**

12. Leaf at least 8 mm wide, 5 cm long; basal diameter of foliage bud 3–4 mm (P. levis) or leaf midrib broad and indistinct (P. spathoides) .................. **1. Sect. Foliolatus**
10. Midrib on upper side of leaf at least 0.2 mm high and 0.3 mm wide but where less than 0.5 mm wide it is at least 0.3 mm high.
13. Leaf midrib at least 0.3 mm high ........................................ 1. Sect. Foliolatus
13. Leaf midrib 0.2–0.3 mm high.
14. Leaf midrib 0.5–0.6 mm wide ........................................ 8. Sect. Polystachyus (P. macrocarpus)
14. Leaf midrib 0.8–1.2 mm wide ........................................ 7. Sect. Rumphius (P. laubefielsi)

1. Section Foliolatus


Primary foliage budscales erect, triangular to shortly lanceolate; secondary scales aëufe, the secondary bud when it first appears generally a pyramid whose apex is formed of a cluster of crowded scale tips. Leaves mostly with more or less parallel sides and mostly acute, only in a few cases acuminate; upper midrib a blunt ridge at least 0.3 mm wide, broader but less prominent below; usually three vascular resin canals, sometimes more. Buds for pollen cones mostly 2–3 mm long, either sessile or on a short peduncle, the secondary pollen cone buds when they first appear a round ball of overlapping imbricate scales. Pollen cones mostly solitary or in groups of no more than 3. Apex of the microsporophyll a small triangular spur c. 0.3–0.5 mm long over a base c. 1 mm wide. Foliola of the female structure mostly c. 2 mm long. Receptacle normally formed of two bracts, one of which is fertile and longer than the other or both fertile and equal, the fertile bracts 8–10(–12) mm long before becoming fleshy, in most species the ripe receptacle is known to be red. Seed with its covering 7–12 mm long by 5–8 mm diam., in most species more particularly 9–10 mm long and 6–7 mm diam., globular, apex mostly blunt. Peduncle mostly 5–10(–15) mm long but shorter in some species.

Dist. From Nepal throughout Malesia to the Solomon Islands, Fiji and Tonga 10 spp. The range is greatly dominated by the impressive, wide distribution of P. nerifolius, the most widespread species of the genus, which covers virtually the entire Asian–Pacific wet tropical forest zone. The one highland species, P. rubens, is also widely distributed, otherwise the species are more local but combine to form a nearly continuous slightly overlapping series from Sumatra to Tonga. All but 2 spp. lie within Malesia.

Ecol. Scattered either in primary rain-forest (but rarely encountered in the dipterocarp forest: P. nerifolius), generally prominent in ridgetop mossy forests at moderate elevations (most species), or widespread in mountain forests at higher elevations (P. rubens). One species is confined to riverbanks.

Note. Sect. Foliolatus consists of a group of closely related species which lack the specialized characteristics which distinguish each of the remaining sections of the genus.

Key to the species

1. Midrib on the upper side of the leaf prominent, at least 0.3 mm high and less than 1 mm wide (primary budscales no more than 5 mm long).
2. Juvenile leaves acuminate, midrib bold with vertical sides. Primary budscales 1–1.5 mm wide.
3. Leaf at least 7 cm by 10 mm, not apiculate, new leaves green to reddish, midrib 0.4–0.8 mm wide (where only 0.4–0.5 mm wide the leaf usually acuminate). Pollen cones normally sessile. Ripe receptacle red.
   1. P. nerifolius
3. Adult leaf no more than 6 cm by 10 mm, often apiculate, new leaves bright red, midrib 0.3 mm wide. Pollen cones often on a short peduncle. Ripe receptacle often purple ............... 2. P. rubens
2. Juvenile leaves never acuminate, midrib with sloping sides. Primary budscales 2 mm wide (pollen cones usually pedunculate).
4. Leaf at least 7 cm by 10 mm, linear-oblong (midrib 0.5 mm wide). Pollen cone usually solitary. Receptacle often with three fleshy bracts ......................... 3. P. archboldii
4. Adult leaf no more than 9 cm by 9 mm, elliptic. Pollen cones usually in clusters of 2–3. Receptacle of two bracts only ........................................ 4. P. insularis
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Tree (3-)5–30(-45) m tall, 10–100 cm diam., clear bole up to 20 m; crown often dome-shaped. Foilage buds 2–5 mm long, occasionally longer, the primary scales often opening. Juvenile leaves 15–24 cm by up to 2.4 cm, acuminate and acute, narrowing abruptly at the base to a short petiole, becoming linear-lanceolate and c. 1.6 cm wide on older fast-growing saplings in open forest situations. Leaves of mature trees similar with a short petiole up to 6 mm. Shade leaves acuminate, 8–12 by 1.2–1.8 cm. More exposed leaves linear-lanceolate, 12–18 by 1.1–1.5 cm or on particularly large trees more nearly linear and 7–10 by 1–1.1 cm. Michironia abruptly raised on the upper side of the leaf at least 0.3 mm high and usually 0.6–0.8 mm wide but as little as 0.4 mm wide on less vigorous leaves or in the Borneo region on most leaves. Pollen cones solitary or in groups of two or most commonly three, sessile. Receptacle bright red when mature.

Distr. From Nepal, Sikkim, Assam (Khasya), Thailand and Indochina through Malesia to the Solomon and Fiji Islands; in Malesia: Malaya, Sumatra (incl. Simulur I.), throughout Java and Borneo (incl. Karimata I.), the Philippines (Mindanao), Celebes, the Lesser Sunda Islands (Bali, Flores), the Moluccas (Obi, Ceram, Halmahera), and New Guinea (incl. New Britain, New Ireland, Rossel I.,...
Manus I., Biak, Job L., and Numfoor), common in many islands. Fig. 45.

Ecot. Scattered and locally common in primary rain-forests from near sea-level to c. 2100 m. In most areas it appears as an understory tree with occasional much larger, emergent specimens in the canopy but in other areas, such as Java, Fiji, etc. it is normally a canopy tree.

Habitats vary: rarely riverine, often on rocky hilltops, in mossy forest, twice recorded from limestone, and twice from swampy forest. Also as to soils there is diversity: in Sarawak it is found on kerangas in heath forest and on sandstone ridges, but also on andesitic laterites, which is the common latosol in Java, and sandy clay. In the Morobe District (New Guinea) it is recorded from ultrabasic.

As to associates it is recorded from pelawan (Tristani a) forest on sandstone ridges in S. Borneo; in the Javanese mountain forest its codominants are Dacrycarpus imbricatus and Altingia noronhae; in New Britain it occurs in the hills with Pomelia and Calophyllum, in the montane forest in New Ireland with Fagaceae, Eugenia and Schizomeria; in the Morobe District (New Guinea) it is associated with Anisoptera and Flindersia in the canopy.

Field notes. The bole is columnar, as usual; very rarely buttresses were recorded on field labels, 120 by 60 cm and 200 by 40 cm; sometimes the base was slightly spurred.

Uses. A valuable timber tree, used for construction.


Notes. Much the most widespread species of the genus, but other species are very commonly identified under this name causing confusion as to its exact character and retarding the recognition of the other species.

In spite of the great geographic range, only slight variation exists within the species. The most distinct element is in the substantially isolated occurrence in Fiji where primary foliage budscales can reach 5 mm and where extra vascular resin canals are often found in the leaves (P. decipiens). In Borneo the midrib on the upper surface of the leaf is weak while from India to southeastern Asia the leaves are more commonly lanceolate and the foliage buds are usually no more than 2 mm long with barely spreading primary scales.


Fig. 46. Podocarpus rubens de Laub. Twig with seed-bearing structure showing two fruits on their receptacles (after NGF 6980).

Tree 2–30 m tall, 4–36 cm diam. Foliage buds 2–3 mm long, the primary scales erect or slightly spreading. Developing leaves bright red. Juvenile leaves linear, narrowly acuminate, becoming apiculate, 6–8 by 1.1–1.4 cm, narrowing at the base to a 2–3 mm petiole. Adult leaves linear to elliptic, 3–6 by 0.6–1 cm, apex acute to rounded and often apiculate, base same as juvenile leaves, margin revolute, midrib above 0.3 mm high with vertical sides, 0.3 mm wide. Pollen cones solitary or in threes, sessile or on a short peduncle. Receptacle becoming first red then purple.

Distr. Malevia: Central to S. Sumatra, Celebes (Central: Latimodjong & Kambuno Mts.; SW: G. Bontaim), Lesser Sunda Islands (Timor: G. Mutis), and New Guinea (incl. Normanby & New Britain). Fig. 47.

Ecot. Scattered as a medium-sized, substage tree in primary rain-forest mostly above 1500 m but as
low as 800 m on smaller islands or locally common to dominant as a small tree on ridges between 2000 and 3000 m or occasionally higher. Mostly on latosols, in New Guinea in Fagaceous mossy forest, rarely in swampy forest on peaty soils with Dacrydium.


Notes. The bright red colour of a new flush of leaves which has been seen in this species can make the trees quite conspicuous. Herbarium specimens can resemble *P. pilgeri* but the upper midrib of the leaf rises c. 0.3 mm with vertical sides, while that of *P. pilgeri* is hardly 0.2 mm high with sloping sides. Leaves of *P. pilgeri* which approach *P. rubens* in size are from shady situations and are distinctly thin and delicate while those whose texture resembles the coarse rigid leaves of *P. rubens* are no more than 4–6 mm wide. The always solitary pollen cone of *P. pilgeri* is distinctly more slender and the ripe receptacle is red. Unique in the section is that most specimens of *P. rubens* have some leaves with a narrow-acuminate or more or less apiculate apex.

The specimens of *P. rubens* from Ambon have a continuous upper hypoderm while elsewhere there are only scattered upper hypoderm cells and vascular sclereids.

Specimens assigned to *P. rubens* from Normanby 1. and New Britain have quite blunt leaves with a less prominent midrib. In all other ways they conform to the species but it is possible that they represent a different taxon.

The specimen Ichlas 166 from a high elevation in Sumatra seems too long and narrow to be placed comfortably here, even though more typical specimens exist nearby at lower elevation. The foliage bud is rather robust and the lateral resin canals are quite large. It resembles *P. brevifolius* and *P. crassigeninis* and could represent a new allied species.


Tree 10–40 m tall, 30–100 cm diam., clear bole up to 12–24 m, sometimes slightly fluted. Foliage buds 2–4 mm long, the primary scales slightly spreading. *Juvenile leaves* to at least 18 by 1.6 cm, otherwise like adult leaves. *Adult leaves* linear to linear-lanceolate, 7–12 by 1.4 cm, apex broadly acute, base abruptly narrowed to a petiole up to 5 mm long, midrib above blunter, 0.3 mm high, with sloping sides, 0.5 mm wide. *Pollen cones* solitary, sessile or on a peduncle to at least 4 mm. *Receptacle* often with a third lateral bract smaller than the second bract, red when mature.


Small to medium-sized tree, 3–39 m tall, up to 20–60 cm diam., bole up to 24 m. Foliage buds 2.5–3 mm long and up to 3.5 mm diam., the primary budscales strongly spreading. *Juvenile leaves* linear, to 15 by 1.4 cm. *Adult leaves* elliptic, 5.5–9 cm by 7–9 mm, apex acute, narrowed at the base to a 3–4 mm petiole; midrib above 0.3 mm high with vertical sides, 0.3 mm wide. *Pollen cones* solitary or in threes, sessile or with a short peduncle. *Receptacle* red when mature.

Distr. New Hebrides and all Solomon Islands; in *Maislea*: New Guinea and adjacent islands: Rossel, Sudest, Misima, Woodlark, Fergusson, and New Britain. Fig. 49.

Ecol. A good-sized lesser canopy tree, scattered and locally common in wet rain-forest, also in *Nothofagus* forest with undergrowth of *Nastus*, from near sea-level to 1680 m, and smaller trees from low ridge habitats.


Note. This species is distinguished by its rather small and narrow elliptic leaves with narrow but prominent midrib with nearly vertical slides and by the robust compact foliage buds with outward curling scales. Dried specimens sometimes develop a rich red-brown colour on the underside.

Small tree, 5–10 m tall, to 10 cm diam. Foliage buds c. 3 mm long but with the primary budscales up to 12 mm long and curling sharply outward with bluntly rounded apices, the secondary scales much shorter, broader, and rounded. *Juvenile leaves* up to 26 by 1.2–1.5 cm. *Adult leaves* linear to linear-lanceolate, 11–22 cm by 8–10(–13) mm, acute or slightly rounded at the apex, narrowing gradually more or less to a petiole, cuticle thick, often with five vascular resin canals, sharply bent at the base so as to hang downward, midrib above 0.4 mm high and 1 mm broad with indistinct margins, midrib beneath drying to a channel below. *Pollen cones* in groups of three, sessile or with a 2 mm peduncle. Primary pollen cone budscales 2 mm wide. *Receptacle* formed by two fertile bracts and a third shorter sterile bract crowded more or less to one side between the other two. *Seed* 11–12 by 6–8 mm.

**Distr. Malesia**: N. Sumatra (Gajo Lands: G. Ketambe) and Malaya (G. Tahan). Fig. 48.

![Range of Podocarpus archboldii N.E.Gray (A), P. deflexus Ridley (D), and P. borneensis de Laub. (B).](image)

**Ecol.** Rising above and locally dominant in dwarf mountain scrub, 1500–2100 m.

**Note.** A rather distinctive species, its large smooth leaves and large fruit resembling among others *P. rumphii* and *P. solomonensis* in other sections of the genus but differing in the key characters of those sections. This species, unlike most of the genus, appears to be monoeccious inasmuch as a random field inspection of about a dozen trees showed every single one to bear male buds (fruited specimens have been collected at a different time of year).


Small to medium-sized tree, (2–)5–12(–23) m tall, 2.5–21 cm diam. Foliage buds 4–10 mm long, the primary scales erect. *Juvenile leaves* linear, to 16 by 1.4 cm. *Adult leaves* linear to ovate, (2.5–)5–7.5 (–9) cm by 8–13 mm, narrowing at the base to a 3–5 mm petiole, more or less acute but usually slightly rounded at the apex, thick, with abundant auxiliary sclereids, midrib above prominent, 1 mm wide and 0.3 mm high, often drying to a channel below, often crowded around the foliage bud. *Pollen cones* solitary or in threes, sessile or on a short peduncle. *Seed-bearing structure* on a 2 mm peduncle, *receptacle* red when mature. *Seed* with a small crest.

**Distr. Malesia**: Borneo (incl. Karimata Is.). Fig. 48.

**Ecol.** Locally common or even dominant (Meru­rong Plateau) on mossy rocky ridges, or scattered in nearby forest, in high kerangas forest and on white, sandy soils, 700–2070 m, one collection from a swamp at 360 m.

**Vern.** Bisit, Sarawak, Kenyana lang., bubung, Iban lang., buloh, Merurong Plateau.

**Note.** As in *P. deflexus* the leaves are thicker than usual for the genus and the lower midrib dries to a channel. The abundant foliar sclereids is a character shared apparently with *P. novaecaledoniae* in this section.


Tree, 8–25 (–35) m tall, 16–40 cm diam. Foliage buds 3–9 mm long, the primary scales spreading. *Juvenile leaves* up to 20 by 1.5 cm, narrowly acute. *Adult leaves* linear-lanceolate, 8–14 by 1–1.4 cm, acute or narrowly rounded at the apex, narrowing at the base to a 4–9 mm petiole, stiff, upper hypodermal fibres in a continuous layer, upper midrib a low blunt ridge 0.3–0.5 mm wide and 0.1–0.2 mm high which furthermore often collapses upon drying so that the leaf appears smooth or even channelled, often with five vascular resin canals. *Pollen cones* typical of the section or longer, up to 8 cm long, solitary or in groups of up to three. *Receptacle* often with two bracts fertile and then sometimes with a third shorter sterile bract on one side between the other two, red when mature; foliola 2–4 mm long. *Seed* with its covering 12–13 by c. 8 mm.

**Distr. Malesia**: E. Borneo (once: Berau), Celebes, Moluccas (Talaud Is.; Karakelong, Mt Piapi; Ambon; Mt Salihutu & Mt Horti), and West New Guinea (Meos Noom & Japan Is.). Fig. 49.

**Ecol.** Scattered and locally common in primary rain-forest, from sea-level to 1650 m. In E. Borneo on limestone.

Tree, 3–20 m tall, to 30 cm diam. Foliage buds 2–6 mm long, the primary scales spreading. Juvenile leaves up to 23 mm wide. Adult leaves linear, 5–13 by 0.8–2 cm, apex acute or rounded, narrowing abruptly at the base to a 3–5 mm petiole, midrib above broad and obtuse. Pollen cones in threes on a short peduncle.

Distr. Solomon Islands; in Malesia: E. New Guinea (Louisiades: Rossel I.), N. Moluccas (Morotai: G. Pare), and Malaya (G. Ledang = Mt Ophir; type), all isolated occurrences. Fig. 50.

Fig. 50. Range of Podocarpus spathoides de Laub.

Ecol. Scattered and locally common at 1000–1200 m in the western two stands and near sea-level in the east.

Note. In Malaya and Rossel I. the foliage buds are no more than 3 mm long, the others are twice as long. In Malaya the trees grow in a summit scrub and are only 3–4 m high, elsewhere collectors report 12–20 m high trees. Perhaps intermediates exist or alternatively more than one similar taxon may be involved here.

2. Section Acuminatus


Primary foliage buds of variable diameters, at least 4 mm long, often much longer; primary scales erect, lanceolate, with free tips, as long as the bud itself, up to 3 mm wide at the base in vigorous buds but c. 1.5 mm wide in weaker buds; secondary budscales acuminate, the secondary bud when it first appears a loose cluster of free scales whose tips resemble the surrounding primary scales. Leaves with parallel margins, distinctly acuminate, narrowing more or less abruptly at the base, midrib above at least 0.5 mm wide and 0.3 mm high, broader and less prominent beneath, usually three vascular resin canals, occasionally more. Buds for pollen cones c. 3–5 mm long, either sessile or on a short peduncle, secondary scales acuminate, the secondary pollen cone bud when it first appears is briefly a round ball of overlapping imbricate scales. Pollen cones 3–5 cm long or longer, occasionally solitary but mostly in groups of three. Apex of the microsporophyll a triangular spur 0.5–0.7 mm long over a broader base. Peduncle of seed-bearing structure variable. Receptacle of the seed formed of one or two fertile bracts of variable sizes and one shorter sterile bract, the ripe receptacle red. Seed with its covering of variable size, globular, apex blunt or a slight crest.

Distr. From Borneo to Queensland 3 spp., of which 2 in Malesia: in Borneo and New Guinea respectively. Ecol. Low elevation primary rain-forest understory trees, in one case also common along disturbed forest margins.

Note. The only section with both acuminate secondary budscales and acuminate leaves.
1. Seed and its covering at least 11 by 8 cm, not crested. Adult leaves mostly more than 17 mm wide. Female peduncle at least 4 mm long. Plant lacking rhizomes ........................................ 9. P. ledermannii

1. Seed and its covering less than 11 by 8 mm, slightly crested. Adult leaves less than 17 mm wide. Female peduncle c. 1 mm long. Plant with rhizomes ........................................ 10. P. micropedunculatus


Tree, 4–26(–33) m tall, 8–60 cm diam. Foliage buds 4–8 mm long by 3–4 mm in diam., the primary buds scales more or less spreading. Juvenile and adult shade leaves linear, 11–22 by 2–2.4 cm, narrowing abruptly to an acuminate apex and at the base to a 4–10 mm petiole; leaves more exposed to the sun no more than 16–18 mm wide, weakly acuminate if at all and narrowing less abruptly at the base; midrib above broad and rounded, 1.5–2 mm wide and c. 0.6 mm high, sometimes collapsing on dried specimens to a small narrow ridge. Pollen cones c. 4.5 cm long, grouped on a 3–4 mm peduncle. Seed-bearing structure on a 4–15 mm peduncle; foliola 2 mm long; receptacle 9–16 mm long. Seed with its covering 11–13 by 9–10 mm, slightly crested.

Distr. Maleisia: Borneo (Sarawak: Marudi For. Res.; Brunei; Sabah: Papar, Tawao). Fig. 51.

Fig. 51. Range of Podocarpus ledermannii Pilger (L) and P. micropedunculatus De Laub. (M).

Ecot. Scattered and locally common in primary rain-forest understory at low elevation to at least 1800 m.


Note. Leaves in the type collection are at the short and broad extremes for the species. Leaves in two examples were found to have two large additional vascular resin canals and one of these also had a continuous upper hypoderm.


Shrub or small tree, 1–7(–13) m tall, 5–20 cm diam., with rhizomes which spread under the forest litter. Foliage buds 6–15 mm long by 1.5–3 mm diam. Juvenile leaves 14–18 by 1.5–2.1 cm. Adult leaves 8–17 by 1–1.5 cm; petiole 3–5 mm; midrib above 0.5–0.8 mm wide and 0.4 mm high, drying to a channel below. Pollen cones 3.5–7.5 cm, sessile or with a short peduncle. Primary pollen cone budscales 4–5 mm long. Seed-bearing structure on a 1 mm peduncle; foliola 3–4 mm; receptacle 8–10 mm long. Seed with its covering 8–10 by 6 mm with a small crest.

Distr. Maleisia: Borneo (Sarawak: Marudi For. Res.; Brunei; Sabah: Papar, Tawao). Fig. 51.

Ecot. Scattered in understory of Agathis forest or forming a major element in thickets along the margins of clearings, mostly on sandy, podzolic soils, ke-rangas, sandstone, humic peaty podsol of raised beaches, and peat-swamp forest, from sea-level to occasionally as much as 500 m. Sometimes associated with Dryobalanops rappa or Shorea albida.

Vern. Sarawak: kayu china; Sabah: kayu tjina.

Note. Propagation by rhizomes is a remarkable character otherwise unknown among erect conifers and obviously facilitates rapid appropriation of disturbed situations.

3. Section Globulus


Primary foliage bud a globular head of completely imbricate scales, gradually expanding with
the growth of a new shoot until the secondary bud, also globular, erupts; primary budscales acute to more or less rounded, c. 1.5–2 mm long; secondary scales oval and blunt. Leaves with parallel sides or somewhat lanceolate, slightly rounded at a narrow apex to broadly rounded and sometimes acuminated, midrib above blunt, 0.2 mm high and at least 0.5 mm broad, broader and indistinct below, 3 vascular resin canals. Buds for pollen cones sessile or on a short peduncle, the primary scales c. 1.5 mm long; the secondary pollen cone bud similar to the secondary foliage bud. Pollen cones mostly 2.5–4.5 cm long (smaller in some species), solitary or in groups of three. Apex of the microsporophyll mostly a small triangle less than 0.5 mm long (longer in P. nakaii).

Seed-bearing structure on a peduncle of variable length; receptacle formed of two bracts, one of which is longer and mostly 7–9 mm long (longer in P. lucienii) or both are fertile and equal, where known the ripe receptacle red. Seed with its covering 8–10 mm long by 5.5–6 mm diam. (or larger in some species), globular, apex blunt or in some species with crest.

Distr. From Vietnam and Formosa to Borneo and New Caledonia 6 spp.; in Malesia: 2 spp., in Sumatra/Malaya and Borneo respectively.

Ecol. Mostly short trees of low (to 2000 m) elevation tropical forest either in the understory of primary or secondary rain-forest (occasionally larger and in the canopy), on exposed mossy ridges, or in short open forest.

Note. The gap between Borneo and New Caledonia is largely filled by the related sect. Rumphius which overlaps this section geographically only slightly. The primary budscales in sect. Rumphius rather than being completely imbricate and overlapping more or less meet at their apices with usually one or more actually curling outward at their apex while, in addition, the pollen cones in sect. Rumphius are normally in clusters of more than three and all the species of sect. Rumphius occur as large canopy trees.

Key to the Species

1. Seed and its covering with a small crest; foliola 2 mm long. Adult leaves not acuminate, 9–15 mm wide
   11. P. globulus

1. Seed and its covering without a crest; foliola less than 1 mm long. Adult leaves distinctly acuminate, 14–21 mm wide
   12. P. teysmannii


Tree, 3.5–27 m tall, to 18 and more cm diam. Juvenile leaves 7.5–16 by 1.5–2.4 cm, abruptly acuminated. Adult leaves linear, narrowing more or less abruptly at the base to a 2–3 cm petiole, acute to rounded apex, 3.5–8 by 0.9–1.5 cm, midrib above 0.5–0.7 mm wide. Pollen cones 2.5–4.5 cm, solitary or occasionally in threes, sessile or on a short (1 mm) peduncle. Seed-bearing structure on a 3–4 mm peduncle; foliola 2 mm and early deciduous. Seed with its covering with a brief crest.

Distr. Malesia: northern part of Borneo (Sarawak; Sabah: Mt Silam). Fig. 52.

Ecol. In primary rain-forest or mossy forest on ridges and peaks from 300 to 1500 m apparently where the forest is not dominated by dipterocarps. In some cases at least, an ultrabasic soil is indicated.

Vern. Sapiro, Lawas, Murut lang.


Tree, 4–12 m tall, up to 30 cm diam. Juvenile leaves to 16 by 2.7 cm. Adult leaves linear, 9–13 by 1.4–2.1 cm, acuminate, narrowing more or less abruptly at the base to 4–7 mm petiole, midrib above 0.6–0.8 mm wide. Pollen cones 2.5 cm, solitary or occasionally paired, sessile. Seed-bearing structure
on a 6–11 mm peduncle; foliola 1 mm and early deciduous.

**Distr.** *Malesia*: Malaya and Sumatra (Westcoast Res.), incl. Riouw-Lingga and Banka Is. Fig. 52.

**Ecol.** Understory tree of primary or secondary rain-forest from sea-level to occasionally as high as 1140 m, in Banka on granite sand.

**Vern.** Sumatra: *kalek rotan*, Westcoast.

4. Section Longifoliolatus

**DE LAUB.** Blumea 30 (1985) 269.

Primary foliage budscales erect, narrowly lanceolate with free tips, occasionally as little as 4 mm long on weak shoots but mostly at least 6 mm long and often much longer; secondary budscales acuminate, the secondary bud when it first becomes visible a cluster of erect scale tips shorter than the primary scales. **Leaves** either linear and no more than 11 mm wide or narrowly lanceolate, narrowing gradually at the base, midrib above variable in width and mostly c. 0.3 mm high but lower in some species, broader and less prominent beneath (and in some species drying into a channel), in most species more than 3 vascular resin canals, frequently a well-developed or continuous upper hypoderm, especially where there are no extra resin canals. **Buds for pollen cones** 3–4 mm long, mostly sessile but with a short peduncle in a few species, the primary scales mostly 1.5 mm wide at the base, occasionally wider; secondary scales mostly acuminate, the secondary pollen cone bud when it first appears sometimes still a ball of overlapping scales but more often with the scale tips starting to separate. **Pollen cones** variable in length, slightly greater in diameter than usual for the genus where the apex of the microsporophyll is longer than usual, solitary or sporadically in groups of 2 or 3. Apex of the microsporophyll usually a spur c. 0.5 mm long on a wider base but longer in some species and shorter in others. **Seed-bearing structure** on a peduncle (2–)7–15(–20) mm long; foliola in all species to over 3 mm and only sometimes as little as 2 mm in any species. **Receptacle** formed of at least two bracts at least one of which is fertile and longer, while often, or in some species usually, two are equal, with one to three smaller bracts crowded between them and sometimes one or two of these smaller bracts fertile, the larger bracts variable in size between the species but at least 9 mm long; where known the ripe receptacles are red to dark red. **Seed** with its covering also variable in size, at least 8 mm long by 6 mm diam., globular, in some species with a weak crest.

**Distr.** Mostly in highly localized stands from Sumatra to Fiji, 10 spp., 5 of which are in *Malesia.*

**Ecol.** Mostly small or stunted trees (or even decumbent) in more or less specialized habitats, particularly over ultrabasic soils.

**Notes.** This section can be divided roughly into two parts, one with more or less parallel-margined leaves with extra resin canals and normally at least two fruits on each fertile structure as well as small pollen cones 10–28 mm long and a strong relationship to ultrabasic soils; the other part with lanceolate leaves, which only in some cases have extra resin canals and normally only one fruit in each fertile structure as well as larger pollen cones 3–4.5(–6) cm long and a relationship to a variety of habitats. In all species the foliage buds on vigorous shoots surpass 8 mm, a condition found in the subgenus only elsewhere in sect. *Acuminatus*. The female foliola usually or always at least 3 mm long are rare elsewhere in the genus.

**KEY TO THE SPECIES**

1. Pollen cones less than 3 cm long; leaf elliptic, somewhat revolute, adult leaves less than 5 cm long
   13. *P. gibbsii*

1. Pollen cones more than 3 cm long; leaf mostly lanceolate or linear-lanceolate, not revolute, adult leaves at least 5 cm long.
   2. Leaf linear-lanceolate or linear, midrib broad and blunt on the upper side (no crest on fruit)
      14. *P. confertus*
   2. Leaf lanceolate, midrib sharp and narrow on the upper side.
3. Leaves more than 7 mm wide; scales at base of pollen cone long triangular; fruit with a crest.
4. Leaves mostly over 10 mm wide; foliola at base of receptacle more than 3 mm long; bud for pollen cone 4–5 mm in diameter; pollen cone initially sessile, when mature with an elongated scaly base


17. *Podocarpus atjehensis*
bracts and additional bracts between them. Seed with its covering including a small crest, 11–14 by 7 mm.

**Distr. Malesia:** N. & Central Sumatra (rare), throughout Java and the Lesser Sunda Islands (Flores: Mt Ranaka). Fig. 54.

Fig. 54. Range of *Podocarpus conferlilus* de Laub. (C), *P. bracteatus* Blume (B), and *P. pseudobracteatus* de Laub. (P).

**Ecol.** Scattered in the canopy of moist mountain rain-forest from 1000 to 2600 m or occasionally as low as 400 m.

**Uses.** An excellent timber tree.

**Ver.** Sumatra: *kayu unung unung*, Toba Batak; Java: *bima*, J (Pekalongan), *ki marak, ki pantjar, ki putri*, S.

**Note.** The most common *Podocarpus of the mountain forests of Java*. *Podocarpus neriifolius* also occurs there, but rarely above 1600 m, while *P. bracteatus* is common to over 2000 m. Sterile specimens of the two are sometimes similar, but *P. bracteatus* has a narrower midrib, longer budscales, and a more distinctly lanceolate shape.


Tree 1–15 m tall, 5–20 cm diam. Foliage buds 5–14 mm long. *Juvenile leaves* linear-lanceolate, up to 22 by 1.7 cm. *Adult leaves* linear-lanceolate to lanceolate or exceptionally elliptic, 6–15 cm by 7–12 mm, narrowly acute, tapering more or less abruptly at the base to a 2–4 mm petiole; midrib above a prominent narrow ridge with nearly vertical sides, 0.4–0.5 mm wide and 0.3–0.4 mm high. *Pollen cones* 4–4.5 cm, on a short peduncle up to 2 mm long, solitary; apex of the microsporophyll 0.5–0.7 mm long. *Seed-bearing structure* on a 2–5 mm peduncle; foliola 2.5–3 mm long, often thick and lanceolate; receptacle 7–11 mm long, formed of two bracts and becoming first orange, then red, then almost black when ripe. Seed with its covering 10–11 by 8–9 mm, blunt.

**Distr. Malesia:** New Guinea. Fig. 54.

**Ecol.** Scattered and locally common in the understory of mossy *Castanopsis-Nothofagus* forest and *Dacrydium* swamp forest, sometimes entering the alpine shrubbery, from 1740 to 2850 m.


Tree 8–15 m tall, 20 cm diam. Foliage buds 6–14 mm long. *Adult leaves* linear-lanceolate to lanceolate, 7–11 cm by 6–8 mm, narrowly acute, narrowing somewhat gradually at the base to a 3–4 mm petiole, cuticle thick, sometimes with lateral vascular resin canals distinctly larger than the median canal, midrib above a prominent ridge with nearly vertical sides, 0.2–0.3 mm wide, 0.2 mm high. *Pollen cones* 3.5 cm, sessile, solitary; apex of the microsporophyll a small triangular spur c. 0.2 mm long. *Seed-bearing structure* on a 8–16 mm peduncle; foliola 2–4 mm long; *receptacle* 10–11 mm long, formed of two unequal bracts, becoming red when mature. Seed with its covering, including a blunt apex, 9–11 by 7–8 mm.

**Distr. Malesia:** N. Sumatra (Gajo Lands: Kemiri & Bandahara Mts) and West New Guinea (Wissel Lakes). Fig. 53.

**Ecol.** In local forest populations, probably on poor soils, in N. Sumatra at 2500–3300 m, near Wissel Lakes at 1800 m.

5. Section Gracilis

**De Laub.** Blumea 30 (1985) 272.

Primary foliage bud small, up to 2 mm diam., but smaller in some species; primary scales erect or slightly spreading, triangular to lanceolate, up to 3 mm long and 1 mm wide at the base, only 0.6 mm wide in *P. glaucescens*; secondary scales also acute, the secondary bud when it first appears a cluster of free bud tips. Leaves linear to ovate, acute to rounded at the apex, particularly delicate with remarkably blunt apices when growing in the shade, generally distinctly rigid when growing in exposed situations; midrib above distinct but gracile with sloping sides and about the size of
an ordinary pencil line (up to 0.3 mm wide), broader and blunt to nearly flat below, three vascular resin canals. **Buds for pollen cones** sessile and quite small, the primary scales no more than 1.5 mm long with free tips; secondary scales about twice as long as broad, the secondary pollen cone bud when it first appears a spherical ball cupped by the primary scales. **Pollen cones** slender, mostly 2—3.5 cm long and c. 3 mm diam. before shedding pollen but 2—2.5 mm diam. after shedding, solitary, often elongating in the scaly base as well as in the zone of microsporophylls when mature. Apex of the microsporophyll a small triangular spur 0.3—0.5 mm long over a base c. 1 mm wide. **Seed-bearing structure** on a peduncle (3—5)10(—16) mm long. Foliola 1.5 mm long. **Receptacle** formed of two bracts, the fertile bracts 7—8(—10) mm long, sterile bracts shorter, becoming red in some species and purple in others when mature. **Seed** with its covering globular, 7—8 mm long without a small crest and 8—9 mm long in species with a crest, mostly 5.5—6 mm diam. (less in *P. affinis* from Fiji).

**Distr.** From southern China through Malesia to Fiji, but not in Malaya, Sumatra, and Java, 5 spp. Two species widespread and the other three quite rare and outside the range of the other two. Four of the five species occur in the Philippines.

**Ecol.** Mossy mountain forests either on isolated peaks or at high elevation.

**Note.** A group of closely related species, some of which could conceivably be considered varieties instead as certain variations of a like nature are also known within *P. pilgeri*. For example, *P. lophatus* has crowded leaves and a crest on the fruit, characters shared with *P. glaucus* but otherwise it corresponds with *P. pilgeri*. On the other hand, *P. wangi*, here included in *P. pilgeri*, has very small foliage buds and a purple ripe receptacle, characters also shared with *P. glaucus*.

**KEY TO THE SPECIES**

1. Leaves over 2 cm long; foliage bud at least 1.5 mm long.
2. Leaves less than 8 mm wide, not always blunt (sun growth leaves acute).
3. Leaves dispersed. Fruit not Crested
   — 18. *P. pilgeri*
   — 19. *P. lophatus*
2. Leaves more than 8 mm wide, always blunt (dispersed; fruit not crested)
   — 20. *P. rotundus*
1. Leaves less than 2 cm long (less than 6 mm wide, always blunt, crowded); foliage bud less than 1.5 mm long (fruit crested)
   — 21. *P. glaucus*


Tree 1—2.5 m tall, 8—60 cm diam.; bole to 12 m, rarely fluted. Foliage buds 2.5—3 mm long (or sometimes shorter). **Juvenile leaves** linear, up to 7 cm by 9 mm, broadly acute and apiculate. **Adult shade leaves** ovate, widest part closer to the apex, 2—4 cm by 5—8 mm, abruptly rounded at the apex, narrowing more gradually at the base to a short 2—3 mm petiole; exposed leaves elliptic, 2.5—4 cm by 4—6 mm, acute, revolute, with intermediate forms towards shade leaves common; midrib above on all leaves 0.2 mm wide and high. **Pollen cones** often elongating in the basal scaly part to 3 mm. **Female receptacle** becoming red when mature (dark violet has also been reported). **Seed** with its covering without a crest.

**Distr.** S. China; in Malesia: Philippines (Negros Occidental, Mindanao), Central Celebes, and common in New Guinea. Fig. 55.

**Ecol.** Scattered and locally common in moist and often mossy forest, (700—)1200—1300 m, as a medium-sized tree, but dwarfed on ridges and at high elevation. Mostly in the understory, in beech forest with mossy undergrowth, associated with *Phyllocladus* and *Myrsine*, in New Guinea in elfin woodland on Mt Hunstein and on Mt Nettio in low Xanthomyrus-Podocarpus crest forest.

**Vern.** West New Guinea: bempop, Hattam lang.; East New Guinea: gihura, Asaro, Kefamo, iamugang, Goroka, Toboga, janega, Hagen, Toboga,
CoNiFERALES

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New Borneo I

Juvenile situations, (1978) covering

less.

with

rounded

20.

Podocarpus pilgeri Foxw.

Fig. 55. Range of Podocarpus pilgeri Foxw.

kaibelugi, Wahgi, Minj, kebu, Mt Ne, monopana, Mairi, Nataubung, puling, Hagen, Wankl, sosumehi, Dunantina, sula, Chimbu, Masai, yamga, Hagen, Minj, yazib, Nondugl, Minj.

Note. The great variability of the leaves can be confusing and the position on the tree of leaf collections should be noted.


Small tree. Foliage buds 3 mm long. Adult leaves densely crowded, thick, elliptic, 3 cm by 5 mm, slightly revolute, acute, narrowed at the base to a short 2 mm petiole; midrib above a distinct ridge c. 0.2 mm wide. Pollen cones unknown. Seed with its covering with a distinct crest.

Disr. Malesia: Philippines (Luzon: Mt Tapulao), one locality only. Fig. 56.

Ecol. Mossy forest at 1800 m.


Tree 5–15 m tall. Foliage buds 2–3 mm long. Juvenile leaves linear, up to 10 cm long. Adult leaves oval to slightly linear, 2–5 cm by 8–11 mm, very rounded at the apex even when growing in exposed situations, sometimes apiculate, narrowed at the base to a 2 mm petiole; midrib above a small ridge 0.2 mm wide and high. Pollen cone elongating through the base to produce a scaly section 3–10 mm long. Female receptacle becoming red when mature. Seed with its covering with a crest.

Disr. Malesia: L. Borneo (Mt Beratus near Balikpapan) and Philippines (Luzon: Mt Banajao in Laguna Prov. and Iucban in Tayabas Prov.), 2 collections. Fig. 56.

Ecol. Dwarf mossy forest, on Mt Beratus at c. 1000 m, in Luzon up to 2200 m.

Fig. 57. Range of Podocarpus glaucus Foxw.

21. Podocarpus glaucus Foxw. Philip. J. Sc. 2 (1907) Bot. 258; ibid. 6 (1911) Bot. 159, t. 29, f. 1; Pilger in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 248; W ...
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(Also on Arfak Mts, and incl. Manus in Admiralty Is.), Moluccas (W. Ceram), and Philippines (Mindoro). Fg. 57.

Ecot. A medium-sized tree in the forest or more often dwarfed or even decumbent on mountain crests in stunted mossy forests, often locally common, (500-)1000–2800 m. Recorded from stony, sandy clay and from a limestone ridge associated with Gymnostoma and Rhododendron, near Kiunga and Wissel Lakes (New Guinea) on peaty soil.


Note. Sterile young plants resemble P. pilgeri, but with crowded leaves.

6. Section Macrostachyus


Primary foliage bud mostly at least 4 mm diam. on vigorous shoots, but 3–3.5 mm diam. on weaker shoots, and generally somewhat smaller in some species, about as long or somewhat longer than the diameter, none more than 5 mm long; primary scales triangular and erect or lanceolate and often with outwardly curling tips and thus longer than the bud itself; secondary scales acute or apiculate, the secondary bud when it first appears a nest of scale tips which elongates into a loose pyramid. Mature leaves only c. 5–8 mm wide and mostly less than 6 cm long, acute to rounded at the apex, narrowed gradually at the base, mostly revolute, tough, midrib above narrow but distinct, 0.2–0.4 mm wide and 0.1–0.2 mm high, broader and blunt below, sometimes drying to a channel, three vascular resin canals. Buds for pollen cones sessile (or in P. crassigemmis on a short peduncle), the secondary pollen cone bud when it first appears more exposed and still a globular ball. Pollen cones 2.5–5.5 cm long and up to 7 mm diam. before shedding pollen, but 4–5 mm diam. after shedding and even smaller in one variety which does not have the usual lanceolate 2–3(–4) mm apex of the microsporophyll, solitary or occasionally in pairs. Seed-bearing structure of various sizes, usually with a short peduncle 2–6 mm long and foliola c. 2 mm long; where known the fully ripe receptacles are dark purplish black passing through red in ripening.

Distr. In isolated populations from southern Cambodia and islands south of Taiwan to New Guinea, 5 spp., of which 4 in Malesia (two widespread examples in New Guinea).

Ecot. Locally common at high elevations or on mossy ridges. One species, P. costalis, largely confined to a group of small plants at low elevation.

Note. A similar habitat and general distribution to sect. Gracilis but members of sect. Macrostachyus have robust leaves where those of sect. Gracilis are delicate. One sterile specimen from Sumatra (Ichlas 166, Mt Singgagang, 2800 m) placed with P. bracteatus (sect. Longifoliiatus), resembles P. brevifolius of the present section also, but more information is needed.

KEY TO THE SPECIES

1. Foliage bud at least 3 mm in diameter. Leaves elliptic.
2. Seed with its covering not crested, more than 9 mm diameter.
3. Leaf at least 7 times as long as wide. Pollen cone pedunculate .................. 22. P. crassigemmis
3. Leaf less than 4 times as long as wide. Pollen cone sessile ...................... 23. P. brassii
2. Seed with its covering crested, less than 8 mm diameter. (Leaf less than 7 mm wide) 24. P. brevifolius
1. Foliage bud less than 3 mm in diameter. Leaves more or less linear blunt. (Fruit crested, less than 7 mm diameter) .................. 25. P. costalis


Tree (3–)8–38 m tall, 10–75 cm diam., bole occasionally fluted. Sometimes pagoda habit. Foliage buds 3–5 mm long, the primary scales up to 8 mm long, on juvenile plants to over 10 mm, strongly curling outward. Juvenile leaves linear-lanceolate, nar-
rowly acute, up to 20 by 1.4 cm. Adult leaves elliptic, 3–11 cm by 4.5–12 mm, acute to narrowly acute, narrowing at the base to a 2–5 mm petiole, revolute, midrib above a sharp ridge 0.2–0.4 mm wide and 0.2 mm high. Buds for pollen cones on a 1–7 mm peduncle, primary scales up to 4.5 mm long. Pollen cones occasionally in pairs. Seed-bearing structure on a 5–14 mm peduncle; receptacle 10–15 mm long. Seed with its covering 11–14 by 9–10 mm.

**Distr.** *Malesia*: New Guinea (except Vogelkop Peninsula). Fig. 58.

**Ecol.** Common or subdominant in the canopy of high mountain mossy forest, or emergent, often in *Nothofagus* and *Phyllocladus* forest, rarely in secondary forest and occasionally in grassland, (1800–)2100–3400 m.


**Note.** Leaves from lower parts of trees substantially larger than those from higher or more exposed parts of the same tree can at the same time bear fertile material.

In the Goroka Subdistrict STEVENS found two trees (LAE 5101) of which the leaves were infected with *Corinhiela hetera PIESI*, widely distributed in the Old World.


**KEY TO THE VARIETIES**

1. Apex of microsporophyll lanceolate, at least 2 mm long. Tree ...................... a. var. brassii

2. Apex of microsporophyll triangular, less than 1 mm long. Small tree to prostrate shrub

b. var. humilis

**a. var. brassii**

Tree 3–30 m tall, up to 75 cm diam. Foliage buds 4–5 mm long, primary scales erect and up to 5 mm (or more) long. Juvenile leaves linear, 2.5–4 cm by 5–7.5 mm, acute or even apiculate, narrowing abruptly at the base. Adult leaves oval, 1–2.5 cm by 4–7 mm, broadly acute, narrowing more or less abruptly at the base to a 1–2 mm petiole, revolute, glaucous on the underside; midrib above a sometimes indistinct ridge 0.2 mm wide and 0.1 mm high. *Pollen cone* 6–7 mm diam.; apex of the microsporophyll lanceolate or slightly rounded at the tip, 3–4 mm long. Seed-bearing structure on a 1–9 mm peduncle; receptacle 6–9 mm with the apex of the otherwise adnate bracts spreading. Seed with its covering 10–13 by 9 mm.

**Distr.** *Malesia*: New Guinea (except Vogelkop Peninsula). Fig. 59.

**Ecol.** Common and sometimes dominant near the tree line, often an emergent in alpine scrub, often flat-topped, also a gnarled treetheet in fire-induced grasslands or in coppices on edge of grassland, on limestone fields, rarely in mossy forest, commonest between 3000 and at least 3750 m, but also occasionally lower: Mt Ambua 2600 m, Ibiware 2700 m, Wissel Lakes 2000 m.

**Vern.** East New Guinea: *bacela*, Kundiawa,
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Decumbent shrub to small tree up to 5 m high. 

*Poll. cones* 3.5–4.5 mm diam.; apex of the microsporophyll triangular, 1 mm long.

Dist. *Malesia*: New Guinea (except Vogelkop Peninsula). Fig. 59.

Ecol. High elevation scrub, 2600–3600 m, prostrate in open areas, sometimes with pools, on Mt Capella forming dense mats 3 m square, 15–30 cm high.

Note. Definitely not a stunted alpine form, being found at lower elevations than the other (larger) variety which actually occurs as a tree in the alpine scrub at or near the tree line. Only the pollen cone and the prostrate habit that often develops distinguish the two varieties so that herbarium specimens cannot always be assigned with confidence to their proper variety.


Small, often gnarled, sometimes conical tree 2–7.5 m tall. Foliage bud 3.4–4 mm long, primary scales erect, spreading at their tips, occasionally somewhat longer than the bud itself. *Juvenile leaves* 5–8 cm by 6–9 mm, narrowly acute. *Adult leaves* elliptical, 2–5 cm by 4–6.5 mm, acute, narrowed at the base to a broad 1–2 mm petiole, slightly revolute; midrib above a narrow ridge 0.2 mm wide and 0.1 mm high. *Seed-bearing structure* on a 2–4 mm peduncle; foliola c. 1.5 mm long and early caducous; receptacle 12–15 mm long, reported to be red when mature. *Seed* with its covering 9–10 (including a small crest) by 6–7 mm.

Dist. *Malesia*: N. Borneo (Sabah: Mt Kinabalu). Fig. 59.

Ecol. Scattered and locally common in or under dwarf forest, (2100–)2650–3750 m, on granite rocks.

Note. Reports of occurrences in various other places have all proven to be distinctly different species.


Small tree c. 1–5 m high, possibly higher. Foliage buds 2–4 mm long, primary scales erect. *Juvenile leaves* up to at least 9 by 1.3 cm, acute or more or less rounded at the apex. *Adult leaves* linear, 4–7 cm (or as little as 2.5 cm on short side branches) by 5–10 mm, broadly acute or more usually rounded at the apex, sometimes with a small blunt apiculus, narrowing more or less abruptly at the base to a 2–3 mm petiole, slightly revolute; midrib above a distinct ridge 0.3 mm wide and 0.2 mm high. *Seed-bearing structure* on a 4–6 mm peduncle; foliola c. 1.5 mm long and early caducous; receptacle 12–15 mm long, reported to be red when mature. *Seed* with its covering 9–10 (including a small crest) by 6–7 mm.

Dist. S. Taiwan (Orchid 1); in *Malesia*: Philippines (N. Luzon, on Bucas and other isles between Luzon and Taiwan and possibly on the northcoast of Luzon). Fig. 59.

Ecol. Coastal bluffs near sea-level to at least 300 m.

Note. Popular in cultivation in the Philippines and often confused with *P. polystachyus* because of a similar habitat and similar sized leaves. The leaves of *P. costalis* are slightly revolute while those of *P. polystachyus* are not.

7. Section Rumphius


Primary foliage bud globular, up to 4 mm long; primary scales as long as the bud, triangular, crowded together more or less into a pyramid usually with the very tip of some or all of the scales bent away from the apex of the pyramid; secondary scales acute to slightly acuminate, the secondary bud when it first appears in most cases a spherical ball as in sect. *Globulus* but in *P. laubenfelsii* the scale tips may already be free. *Leaves* linear, sometimes larger than average for the genus, acute or on juvenile specimens sometimes slightly acuminate, narrowing more or less abruptly at
the base to a 4–16 mm petiole, stiff, mostly with a continuous upper hypoderm, midrib blunt above, at least 0.7 mm wide, broader and sometimes almost flat below, usually three vascular resin canals. *Buds for pollen cones* 1.5–2 mm long, either sessile or on a short peduncle, the primary scales 1–1.5 mm wide at the base; secondary scales rounded, the secondary pollen cone buds when first appear a round ball of overlapping imbricate scales. *Pollen cones* 2 to at least 4 cm long, usually in groups of more than three. Apex of the microsporophyll a small triangular spur 0.2 mm long over a wider base. *Seed-bearing structure* on a (2.5–)6–16 mm peduncle; foliolae 1–1.5 mm long; *receptacle* mostly formed of two bracts, the longer fertile one 9–15 mm long or both fertile and equal, in *P. rumphii* a third lateral smaller bract often found; where known the ripe receptacle becomes red. *Seed* with its covering globular, at least 8 mm long, larger in *P. rumphii*.

**Distr.** One very widespread species from the fringes of Asia through New Guinea and two localized species, one in northern Borneo and the other in northern Queensland. In *Malesia* 2 spp.

**Ecol.** Scattered, often widely separated stands involving large, primary rain-forest canopy trees at generally low elevation.

**Note.** A transitional section which shares multiple clustered pollen cones with sect. *Polystachyus*, but lacks the purple fruit of that section and shares the spherical developing pollen cone buds with sect. *Globulus* along with generally broad and blunt upperside of the midribs. The ecology and large linear leaves are somewhat distinct.

**KEY TO THE SPECIES**

1. Pollen cones sessile; foliage budscales often completely adpressed; receptacle often with a third lateral smaller sterile bract ................................................................. **26. P. rumphii**
2. Pollen cones clusters usually on a small peduncle; foliage budscales always spreading at the tips; receptacle never with a third lateral sterile bract ................................................................. **27. P. laubenfelsii**

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Trees 12–45 m tall, up to 35–75 cm diam. Foliage buds 2.5–4 mm long, the tips of the primary scales meeting at the apex with one or two often bent outward at the tip. *Juvenile leaves* 19–26 by 1.9–2.6 cm, acute or slightly acuminate. *Adult leaves* on smaller trees and lower branches of taller trees linear, 12–22 by 1.1–1.9 cm, acute or slightly acuminate, narrowing distinctly at the base to a 4–16 mm petiole, stiff; leaves from the exposed parts of taller trees 9–14 cm by 9–14 mm, acute, with a 4–10 mm petiole; upper side of midrib of all leaves a blunt ridge 0.7–1.2 mm wide and 0.3 mm high, often collapsing when dried to a flat surface or a small irregular ridge. Buds for pollen cones sessile. *Pollen cones* in groups of up to at least five, 3.5–4.5 cm long; microsporophylls somewhat elongated and tightly crowded. *Receptacle* frequently with a third lateral bract smaller than the other two. *Seed* with its covering glaucous, 12–15 by 10–12 mm.

**Distr.** Hainan; in *Malesia*: Malaya (Genting Highl.), S. Central Java (Nusa Kambangan), Bawean 1. (Java Sea), Borneo (Sabah, incl. Selangon Is.), Philippines (Luzon: Agusan del Norte), Celebes, Lesser Sundia Islands (Flores, Timor) Moluccas (Obi, Weda, Aru Is.), New Guinea (incl. Misool & Numfoor Is.). Fig. 60.

**Ecol.** Locally common in primary rain-forest but rather in widely separate localities, frequently on islands, in Java on limestone, 5–2000–600–1550 m. **Uses.** Reported to be a good timber tree.
2.5–4 mm long, the tips of the primary scales generally spreading. Juvenile leaves 11–24 by 1.7–2.4 cm. Adult leaves linear to linear-lanceolate, 7–19 by 1–1.8 cm, narrowly acute to acuminate, narrowing more or less abruptly at the base to a 6–14 mm petiole, upper side of midrib a blunt ridge 0.8–1.2 mm wide and 0.2–0.3 mm high. Buds for pollen cones on a peduncle to 6 mm long or less commonly sessile. Pollen cones grouped (3) 4 (5), 2–4 cm long; microsporophylls more or less elongated. Seed with its covering at least 8 mm long but fully mature examples unknown.

Dist. Malesia: Borneo (Sarawak: Lawas; Sabah: Trusmadi & Kinabalu; E. Kalimantan: Kutel). Fig. 61.

Fig. 61. Range of Podocarpus laubenfelsii Tiong.

Ecol. Scattered in primary rain-forest, in mossy forest, a large emergent on rocky ridge on kerangas, dominant in heath forest, also in waterlogged acid soil of Agathis forest. 600–1600 m.

8. Section Polystachyus


Foliage bud on vigorous shoots mostly 2–2.5 mm diam. and on weaker shoots 1–1.5 mm diam., larger in P. macrocarpus, up to 4.5 mm long in species with more or less linear leaves and 4–9 mm long in species with distinctly lanceolate leaves; primary foliage budscales erect, sometimes slightly spreading, triangular to lanceolate, up to 1.5 mm wide at the base in vigorous buds and 1 mm wide in weaker buds; secondary budscales more or less rounded or slightly acuminate, the secondary bud when it first appears a cluster of scale tips or when with particularly short primary scales may still be more or less in a ball. Leaves linear and almost blunt to lanceolate, sometimes in the same species at different stages of growth; midrib prominent above, usually less than 0.6 mm wide, broader and blunter below, usually three vascular resin canals but occasionally more (or less). Buds for pollen cones up to 3 mm long, either sessile or on a short peduncle; the secondary pollen cone buds when they first appear a round ball of overlapping scales. Pollen cones variable in length among the species but most commonly 2–4 cm long, normally in clusters of up to five; apex of the microsporophyll similarly variable in length but most commonly a small
spur 0.2–0.3 mm long over a wider base. Seed-bearing structure on a variable-sized peduncle, mostly 3–12 mm long but shorter in some species; foliolas mostly 1.5–2 mm long; receptacle normally formed of two unequal bracts with one fertile but occasionally both are fertile and equal, the fertile bracts mostly 7–12 mm long (longer in P. fasciculatus), in most species known to become purple after passing through red when ripening. Seed with its covering of various sizes, globular and blunt.

**Distr.** Central China and southern Japan through Malesia to eastern Australia, 9 spp. Most of these species occur in or near China. In *Malesia* 3 spp.

**Ecol.** Scattered in (subtropical and) highland tropical forests but one species occurs on tropical sandy coastal bluffs or low elevation limestone outcrops.

**Note.** In two species only pink ripe receptacles have been reported but in this section just as in familiar *Rubus* fruits, a crop of pink or red fruit is later seen to become purple or in other cases fruit bats strip off the fully ripe fruit leaving only the less ripe red, so reports of red or pink may not be conclusive. Isolated specimens may well have pollen cones in clusters of no more than 3 but a normal flush of pollen cone production will have larger clusters well represented and collectors should note this.

**KEY TO THE SPECIES**

1. Adult leaves linear and more or less rounded at the apex, not lanceolate, upper midrib prominent.

2. Seed and its covering less than 8 mm in diameter. Midrib above sharp


Tree 1–20 m tall, 3–45 cm diam., most commonly c. 6 m. Foliage buds 1.5–3 mm long. Juvenile leaves generally within the upper range of adult leaf size, linear to linear-lanceolate, acute and almost

**Fig. 62. Podocarpus polystachyus R.Br. ex Endl. Pollen cones. × 1.4 (Photogr. A. Eisener, 1965).**
Flora Malesiana

**Podocarpus macrocarpus** de Laub. Kalikasan 7 (1978) 140.

Tree 10–20 m tall, up to 30 cm diam. Foliage buds 2–4 mm long and the same in diameter; the longer buds with distinctly spreading upper parts of the primary scales; the secondary bud when it first appears may still be a globular ball with the shorter examples of primary budscales. **Juvenile leaves** linear-lanceolate, 8–15 by 1–1.4 cm, acute. **Adult leaves** linear to linear-lanceolate, 6–10 cm by 8–13 mm, acute but often slightly rounded at the apex, narrowed at the base more or less to a 2–4 mm petiole, thick with nearly continuous upper hypoderm and more or less shiny on the upper surface; midrib above a blunt ridge 0.5–0.6 mm wide and 0.2–0.3 mm high. Buds for pollen cones sessile. **Pollen cones** 2.5 cm long, grouped in clusters of up to at least four. **Seed-bearing structure** on a 3–12 mm peduncle; receptacle 10–12 mm long. **Seed** with its covering 15–17 by 10–13 mm.

**Distr. Malesia**: Philippines (northern Luzon). Fig. 64.

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**Podocarpus polystachyus** R. Br. ex Endl.

Ecoul. The main occurrences are at low altitudes and fall apart for the major part into three ecologies. First, the principal habitat is sandy beaches, often gregariously bordering the sea at high tide mark and sandy coastal bluffs and low outcrops, also mentioned for sandy ridges in the mangrove. On coastal granite and limestone rocks the trees are gnarled. Second, it is often frequent on lowland coastal kerangas and sandy 'pandangs' (degraded heath forest) and sandy heath forest (Menchali For. Res., Pahang). These two habitats are typical in the Sunda Land. Third, on limestone hills inland, for instance in Malaya and the Philippines, in Obi, Waigeu, and the Vogelkop Peninsula in New Guinea at 180, 280 and 550 m, at 1000 m in Palawan. In East Malesia these occurrences are scattered.

The bole is sometimes recorded to be fluted. The tree is found in Obi exceptionally tall, 40 m, with a clear bole of 25 m and 38 cm diam., and buttresses of 1 by 1.5 m. A most interesting ecology.


Note. Often cultivated (e.g. in Medan in gardens and parks) and remarkably similar to the also widely cultivated *P. macrophyllus* whose native range and ecology nevertheless is quite distinct. The leaves of *P. macrophyllus* usually have narrow but definitely revolute margins which narrow gradually towards the base while the leaves of *P. polystachyus* are not revolute and narrow abruptly at the base. Gray (1958) reported that the leaves of *P. polystachyus* have upper hypodermal fibres 70 μm diam., while in *P. macrophyllus* these are less than 20 μm.

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**Fig. 63.** Range of *Podocarpus polystachyus* R. Br. ex Endl.

**Fig. 64.** Range of *Podocarpus macrocarpus* de Laub. (M) and *P. ridleyi* (Wasscher) N.E. Gray (R).

Tree 4–24 m tall, 20–30 cm diam. Foliage buds 4–8 mm long. *Juvenile leaves* linear-lanceolate, 11–20 by 1.1–1.6 cm, narrowly acute. *Adult leaves* linear-lanceolate to lanceolate, 5–12 cm by 7–14 mm, acute, narrowed at the base more or less to a 2–3 mm petiole, slightly revolute, with a continuous upper hypoderm, sometimes with five vascular resin canals; midrib above a low ridge 0.2–0.5 mm wide and 0.1–0.2 mm high. Buds for pollen cones sessile or on a 1 mm peduncle. *Pollen cones* 1.5–2 cm by 2 mm, clustered to at least four; apex of the microsporophyll a tiny triangular spur 0.1 mm long. *Seed-bearing structure* on a 3–12 mm peduncle; receptacle 8–9 mm long, known to turn pink. *Seed* with its covering 7 by at least 4 mm.  

**Distr.** *Malesia*: Malay Peninsula. Fig. 64.  
**Ecol.** Localized and more or less dominant on several isolated peaks with poor soils in a somewhat stunted rain-forest, 480–1300 m. On ridge in Panti For. Res. ov. standstone, on Mt Ophir on granite.

### ARAUCARIACEAE

Monoecious, medium-sized to very large trees (rarely shrubby in very exposed situations). Either four independent *cotyledons* or two fused pairs (which may be retained in the seed after germination). The growing point of foliage shoots quite distinct between the two genera, being just a few highly reduced leaves in *Araucaria* and a highly organized bud formed of overlapping scales in *Agathis*. The leaves vary from scales or needles to broad leathery forms with many parallel veins sometimes on the same plant at different stages of growth. *Pollen* produced in cylindrical cones from one to as much as twenty cm long with numerous pedunculate spirally placed microsporophylls each with several to many pendent elongated pollen sacs attached to the lower side of an enlarged shield-like apex which also projects apically more or less overlapping the adjacent microsporophylls. *Pollen cones* solitary, terminal or lateral, on branches separate from those bearing seed cones, subtended by a cluster of more or less modified leaves in the form of scales, deciduous when mature. Pollen globular, without ‘wings’. *Seeds* produced in large, well-formed cones which disintegrate when mature, dispensing the seeds in most cases with the help of wing-like structures; the seed cone terminal on a robust shoot or peduncle with more or less modified leaves that change in a brief transition zone at the base of the cone into cone bracts, formed of numerous spirally-placed bract complexes, usually maturing in the second year. Individual seed cone bract leathery or woody and fused with the fertile scale which bears one large inverted seed on its upper surface.

**Distribution.** The 40 species in two genera are well represented in *Malesia* (13 spp.) and extend eastward and southward into Fiji, New Caledonia (18 spp.), Australia, and New Zealand, with 2 spp. also in the cooler parts of South America, giving the family a distinct Antarctic relationship. Only one species of *Araucaria* (in South America) occurs completely outside of the tropics, while the majority of the species in the family belong in the lowland tropics and others grow in the tropical highlands.

**Fossils.** Early coniferous fossils are often characterized as ‘Araucarioid’ because of the morphological resemblance of fossil foliage shoots to certain well-known juvenile forms of *Araucaria*,...
but there is no reason to conclude that these actually belong in *Araucariaceae*. Acceptable fossils of *Araucariaceae*, however, from Jurassic and Cretaceous age are well represented in the general areas of their modern occurrences, often at higher latitudes to be sure, and also in India and South Africa. More surprising is the apparent occurrence of fossils belonging to the family during the same time span but far away in North America and Europe (Florin, 1963; Gaussen, 1970). A close relationship of English Jurassic fossils specifically to *Araucaria bidwillii* is indicated by Stockey (1981). Wherever the family may have originated, it became well established in the southern hemisphere in Mesozoic times and has since disappeared from whatever northern occurrences it may have had. The genus *Agathis* is first recorded in the Oligocene of Australia and New Zealand and today extends into the Asian tropics, while no convincing fossils have ever been found in any other part of the world for this genus.

Tertiary records of the two modern genera of *Araucariaceae* are all well south of the equator across all of the southernmost land areas including the Palmer Peninsula of Antarctica. Speculation about tropical origins or early penetration of the tropics is not supported by any evidence and it is at least as likely that the occupation of the Malesian region took place during Plio-Pleistocene times alongside advancing members of *Podocarpaceae*.


Ecology. Canopy trees or emergents of moist forests at a wide range of elevations starting at sea-level in the tropics and extending to tropical highlands and to intermediate elevations in the middle latitudes. (One species in New Caledonia grows in drier forests and open places.) Some species clearly follow disturbances and others just as clearly do not. Many contrasting soil types are associated with different species.

Most or probably all species are monoecious and pollination is by wind. Frequent reports of dioeciousness result from a single sex stage, inasmuch as many species produce seed cones well before pollen cones appear. Dense stands are common for many but by no means all species and the large amounts of pollen are adequate to reach substantial distances effectively. Seeds are carried only short distances by wind in most cases and germinate in large numbers near their parent tree. The occurrence of isolated specimens shows that seeds sometimes are carried across substantial distances.

Growth occurs in distinct episodes and where distinct terminal buds are not evident whole units of growth tend eventually to be shed as a unit. Leaves normally persist for several years and may be shed separately from branch units in some cases. Cyclic growth results in false whorls of branches and a tendency for highly formal tree architecture.

A number of pests and diseases specific and otherwise of *Agathis* have been reported by Whitmore (1977) mostly outside of Malesia. In particular a moth genus, *Agathiphaga*, specifically attacks cones, while a coccid, *Coniferococcus agathidis*, causes defoliation. Problems mostly arise when normally dispersed trees are concentrated in plantations. Gaussen (1970: 62 & 66) lists a variety of pests of *Araucaria*, mostly associated with cultivated examples. Notable are a 'pine bark weevil' (*Aesiotes notabilis*) and the 'hoop pine borer' (*Calymnaderus*). Termites of the genus *Coptotermes* do serious damage to *A. hunsteinii*.

Embryology. The fertilized egg undergoes at least five mitoses resulting in 32 or more free nuclei before cell walls form. The resulting cluster of cells deep inside the egg (proembryo) is then organized into three parts. The cells closest to the archaegonium elongate to form a massive 'prosuspensor' while those on the opposite side form a temporary 'cap'. The cells at the centre of the proembryo become the embryo proper, which does not undergo cleavage as in many other conifers. Simple polyembryony resulting from more than one fertilized archaegonium, however, may occur. The large number of proembryo cells and the massive embryonic 'cap' are distinct for
Araucariaceae within the conifers. The chromosome number is n = 13. No hybridization is suspected.

**Taxonomy.** Two well marked genera are recognized.

Uses. The large size of individuals in many species in this family along with the excellent quality of the wood has made them prime candidates for lumber production where sufficiently dense stands occur. The wood is light coloured, yellowish or brownish, straight grained, easily worked, durable, and generally similar to pine but somewhat harder than the more familiar types. The wood is sometimes intermingled and hardly distinguishable from material of Podocarpaceae. Important stands of Agathis have been exploited in Borneo and stands of Araucaria in New Guinea (ismail, 1964; Gray, 1975; Havel, 1971), as well as many locations outside of Malesia. Heavy exploitation has reduced the economic importance of this family. Some attempts have been made to establish tree plantations, but this effort is in the early stages of development (Whitmore, 1977, 1980; Bowen & Whitmore, 1980). Large quantities of pitch have been gathered, particularly from certain species of Agathis where it is known as 'dammar'. Both fossil pitch with darker colours and fresh pitch which is much lighter have been produced. Immense dammar trees sometimes have some form of steps built into their trunks to enable collectors to reach the accumulating pitch. Specimens of various species make handsome ornamentals and are widely used in landscaping in the warmer parts of the world. (The seeds of several Araucaria species are in great demand as food.)


**Note.** The great size of trees in this family has led to an emphasis on collection of juvenile foliage specimens and immature cones and when this is not admitted by the collectors the result can be misleading. Because the seed cones shatter on maturity and the pollen cones are deciduous, it is next to impossible to collect attached mature fertile material. Fallen cone scales and pollen cones abound below mature trees and should be collected.

**Key to the Genera**

1. Seed coat fused with cone-scale complex, apex of fertile scale forming a 'ligule', bract usually with membranous wings. Leaves spirally placed, crowded and broadly attached, variable in form from broad to scales and needles, amphistomatic ........................................ 1. Araucaria

1. Seed coat independent and extended into a wing, scale completely fused with bract which is thin but not wing-like. Leaves opposite decussate, dispersed, and narrowed to a basal petiole, broad and more or less oval, hypostomatic ........................................ 2. Agathis

**1. Araucaria**

Monoecious or sometimes (temporarily?) dioecious small to immense trees mostly with limited and very formal branching elements consisting of long sweeping primary branches in false whorls along the main trunk often turned apically upward candelabra-like, then in most species only one additional rank of branches. The first branches sooner or later deciduous and in open situations replaced by adventitious branches thus producing a variety of double-crown forms. Apex of a resting shoot a cluster of incompletely formed leaves. Leaves spirally placed, broadly attached, crowded, multi-veined when broad and even sometimes in the needle-shaped examples, becoming uniform in size along a branch, but sometimes quite variable in the juvenile forms, amphistomatic. Pollen cones subtended by a cluster of reduced, leaf-like, sterile bracts, often broadened at their bases and where the mature leaves are needle-like these bracts are at least somewhat broader and flatter. Fertile bract of the seed cone broad and often extended laterally into membranous wings, the apex provided with a prominent narrow spur above the thickened apical margin. Seed-bearing scale only partly fused with the associated bract, its apex a free acute scale-like ‘ligule’ ± reaching the base of the spur on the fertile bract. Seed coat fused with its scale.

**Distr.** Across New Guinea, coastal Queensland, New Caledonia, Norfolk Island, S. & Central Chile, and southern Brazil 19 spp. in two sections. Fig. 65.

**Fossils.** In Jurassic times there was evidently an important centre of development and distribution in the Inda-Australia-Antarctic region, from whence it subsequently spread to the Kerguelen and southern Cape Colony on one hand and to Patagonia on the other. The close of the Mesozoic era seems to have witnessed its disappearance from Peninsular India, South Africa and New Zealand. Both sections had an Eocene centre in Antarctica and southern South America, one of which survives still on both sides. The oldest find of Araucaria was from probably Late Triassic in N. Central India (then situated in the southern hemisphere) where it remained until the Early Cretaceous whereupon it disappeared (Flörin. K. Svensk. Vet. Ak. Handl. III, 19, 1940, 81, map 5).

**KEY TO THE SECTIONS**


1. Section Araucaria

Fig. 65. Range of the genus *Araucaria* Juss. with the number of species.


Cotyledons 2, either hypogeal or epigeal, each cotyledon apparently formed of two fused units. Juvenile leaves narrow but distinctly flattened, spreading, often twisted into a horizontal plane; mature leaves broad and often with an acuminate tip. Pollen cones lateral. Ligule elongated and more or less constricted above the seed; cross section of the cone scale complex narrowed to a distinct and generally elongated neck above the seed, margins of the bract with or without broad membranous lateral wings.

**Distr.** In E. New Guinea, coastal Queensland, S. Central Chile and S. Brazil 4 non-overlapping spp., of which 1 in *Malesia*.

**Ecol.** Trees of moist forests mostly rising above the associated trees and often colonizing disturbed areas and protecting the regrowth into that area of other trees.

**Notes.** Sect. *Intermedia* was established for *Araucaria klinkii* (= *A. hunsteinii*) because it differs from the rest of sect. *Araucaria* while resembling sect. *Elatella* in epigal cotyledons and broad membranous wings on the cone scales, but it does have two cotyledons and the spreading flat juvenile leaves of sect. *Araucaria*. One could also add that mature leaves have the hooked tip seen elsewhere only on some species of sect. *Elatella* but the apex of the cone scale complex and the laterally placed pollen cones conform to sect. *Araucaria*. Young plants of *A. hunsteinii* are indistinguishable from those of *A. butwillii*. Sect. *Bunya* was established for *A. butwillii* because the cone scale complex has thick woody wings as opposed to no wings in the two American species, and because of the double vascular supply to the bract and scale. The mature seed also separates from the scale complex. Stockey (Canad. J. Bot. 59, 1981, 1932) argues for the usefulness of these monotypic sec-
flora. Based on a variety of fossil material, but the differences with the residual sect. *Araucaria* hardly seems sufficiently important.


Forest emergent 50–89 m tall with a clear bole of 35–60 m and up to 2 m diam. Branches in loose false whorls of 5 or 6 and sometimes rising towards their apex where the leaf-bearing shoots are clustered, forming a rounded crown on the upper part of the tree. In open sites after the first branches are shed a second set of smaller adventitious branches develop on the middle part of the bole. Outer bark reddish brown, rough, peeling in horizontal strips leaving a thick dark red corky flaky underbark which weathers to shades of brown. Much colourless resin is produced. Two cotyledons c. 35 by 1.5–2.5 mm at the base, tapering gradually to the narrow blunt apex, flat, their surface similar to the shorter broader acute first leaves which contain half a dozen parallel vascular strands evenly spaced, while the vascular strands of the cotyledons are separated into two groups by a slight gap along the centre. Juvenile leaves linear-ovate, narrowed to a decurrent base and tapering to a slightly acuminate pungent apex, very variable in size, less than 2 by 1 mm during resting phases to at least 2.5 by 0.5 cm in the first flush of growth and becoming larger and more lanceolate as the plant matures, twisting sharply at the base to attain a horizontal position. Adult leaves produced in full sunlight, often in five distinct rows, narrowed slightly at the base to a broad decurrent portion 10–15 mm long, ovate-lanceolate, nearly uniform along all but the ends of the branch, 7–15 by 1.2–2 cm, an asymmetrical dorsal ridge prolonged from the junction of the two subtending leaves, ventrally concave, inflexed at the narrow acute apex. Pollen cones clustering near the ends of foliage branches each in the axil of a leaf, subtended by a cluster of reduced leaves the first few more or less decussate and up to 25 mm long but not always remaining attached when the cone falls, the mature cone linear, 16–22 by 1.8–2.5 cm. *Microsorophyll* on a c. 4 mm peduncle, the apical part 5–10 by 2–2.5 mm and more or less linear but narrowing to an acute apex, slightly keeled on the dorsal side, margins membranous and somewhat serrate, expanded at the base on the other side of the peduncle to accommodate about 10 pollen sacs. Seed cones terminal on robust short branches, subtended by numerous reduced leaves, the immature cone devoid of the numerous lanceolate spurs visible, mature seed cones ovoid to cylindrical with the apex conical to slightly depressed, 18–25 by 12.5–16 cm, the exposed slightly expanded outer edge of each seed scale complex more or less rhomboidal in outline, the included seed 3–4 by 0.8–1 cm imbedded in the complex with the ligule extending another 2 cm but without the cone and tapering at first only slightly and then more so near the acute free apex, the thick part of the fertile bract sharply expanded above the seed to its widest and thickest part at the level of the free tip of the ligule and then forming a blunt rhomboidal end or apophysis that is visible on the surface of the mature cone and includes a narrow lateral ridge on each side and terminates in a spur 9–15 mm long which is often broken off before the cone reaches maturity, the two edges of the cone bract expanded into broad blunt membranous wings each as much as 4 cm wide.

**Disf.** *Malesia*: E. New Guinea, in several large stands in large valleys and numerous small stands which are often clustered and with higher mountain areas intervening between the regions of occurrence (B.Gray, Papua New Guinea Dept. For. Res. Bull. 1, 1973, 1–56). Fig. 66.

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**Fig. 66.** Range of *Araucaria hunsteinii* K.SCH.
does occur under forest conditions, but most vigorous germination is associated with open disturbed conditions and it is generally believed that prehistoric disturbance played a major role in producing the current distribution. Heavy commercial exploitation, pressure on regeneration by feral pigs, and anthropogenic fires have all caused serious reductions in many stands.

Uses. The basis of a major plywood industry at Bulolo which results from the fine quality of the wood and the impressive log sizes. The firm, light wood is easily worked and is yellowish brown in colour with attractive purplish streaks in the heartwood. 

2. Section Eutacta


Cotyledons 4, epigeal. The first leaves following the cotyledons small elongated triangular scales with juvenile leaves appearing on lateral shoots or much later on the leader. Juvenile leaves acicular, four angled in cross section, straight or falcate and never twisted into a horizontal plane. Adult leaves acicular (to broad and concave towards the ventral side and with an asymmetrical dorsal ridge prolonged from the junction of the two subtending leaves), never with an acuminate tip. Pollen cones terminal. Ligule narrowing abruptly above the seed generally without any constriction; the thickened apex of the bract (apophysis) directly above the apex of the seed; margins of the bract with broad membranous lateral wings.

Dist. NE. coastal Australia (1 sp.), New Guinea (1 var.), Norfolk Island (1 sp.), New Caledonia (incl. Loyalty Is.) (13 spp.); in Malesia only the one variety in New Guinea.

Fig. 67. Araucaria cunninghamii Ait. ex D.Don var. papuana Laub. in West New Guinea, Kebar Valley, Vogelkop Peninsula, 600 m alt. (Photogr. J.F.U. Zieck, 1954).


Forest emergent, 30–60 m tall, with a clear bole of 20–40 m and up to 2 m diam. Major branches tend to be in false whorls and tend to be rather straight, growing upwards at a slight angle but gradually declining with weight, persisting in open growth situations. Subsequent ramification more complex and denser than in any other Araucaria giving the tree the appearance of a cypress when young and a spruce when older. Outer bark at first in nearly smooth horizontal peeling strips or hoops which become smaller and rough with maturity, red in the interior but weathering to dark brown or black. There is a thick white resinous exudate. Cotyledons linear, c. 2 cm by 1.5–1.8 mm, narrowing to an acute apex, with several evenly spaced vascular strands. Juvenile leaves straight, linear-lanceolate, pungent, bilaterally flattened but laterally keeled, briefly decurrent forming a sharp rib on the stem, quite variable in size being tiny at the base of a shoot, most often c. 1 by 0.1 cm, on vigorous shoots up to 2.5 by 25 cm; leaves on the leader, particularly at the seedling stage, reduced to triangular spreading bifacially flattened scales c. 2 mm long. Leaves on older plants gradually becoming
falcately curved forward and acicular. Adult leaves crowded and curved so that their sharply pointed apices are directed slightly inward, four-angled but about twice as wide as thick, the ultimate leafy branches c. 5 mm in diameter with lanceolate leaves c. 5 by 1.5 mm; vigorous branches at least 1 cm in diameter with leaves 7–9 by 2 mm. Pollen cones terminal on foliage shoots, sometimes rather short shoots, subtended by a cluster of numerous leaf-like bracts about the same size as the leaves but distinctly thinner and more crowded, the cone 4–8 cm long and 8–10 mm in diameter, linear but tapering slightly to a more or less blunt apex, formed of numerous microsporophylls. Each microsporophyll on a stalk 2–3 mm long, the apex extended into a triangular flat apical part 1.2–1.8 mm long, slightly keeled on the dorsal side, margins narrow and slightly serrate, with five or more pendant pollen sacs along the base. Seed cones terminal on robust shoots with a more or less abrupt transition to the fertile scales whose apical spines are like the leaves but bent backward, the mature spine-covered cones ovoid shaped, 6–10 by 5–7 cm. The cone scales complex less the spine 23–29 mm long and including the membranous wings c. 34 mm wide, the thickened end or apophysis up to 24 mm wide with a tetragonal central part c. 5 mm thick and bearing a strong central ridge, from the upper part of the seed to the apophysis the thickened scale extended laterally by firm lobes; a ligule covering the seed, 7–9 mm wide, narrowing sharply above the seed apex and then elongated into a triangular free apex c. 2 mm long and touching the edge of the apophysis; membranous wings bluntly rounded and c. 12 mm wide; seed completely imbedded between the scale and the ligule but indicated by an almond-shaped bulge 2 by 0.7 cm and tapering towards the micropyle at the base of the cone scale.

**Distr.** There are two varieties, the type in Australia and the other in New Guinea.


Bark, particularly of younger plants, dark plum to red-brown, weathering on older plants to gray or blackish. Juvenile leaves up to 21–27 mm long, even on ultimate branches, contrasting sharply with Australian material: where planted side by side the Australian seedlings have leaves no more than half as long. Generally reported to be slightly bigger and more vigorous (trees 50–70 m, pollen cone 9–10 cm long, seed cone 7–12 by 6–8 cm). Pollen cones produced in the middle part of the mature tree and seed cones in the upper part.

**Distr.** *Malesia*: New Guinea, scattered in isolated to extensive stands from one end of the island to the other, both in the central range and along the north coast, including Japen and Ferguson Is. (B.Gray, Papua New Guinea Dept. For. Res. Bull. 1, 1973, 1–56). Fig. 68.

**Fig. 68.** Range of *Araucaria cunninghamii* Ait. ex D.Don var. papuana Laut.

**Ecol.** Emergent in rain-forests from 60–2745 m in a variety of rain-forest soils usually along ridges, but occasionally in swampy conditions, most often in the submontane oak forest. The higher elevation occurrences are in the more southerly part of New Guinea. Vigorous regeneration has been noticed in abandoned gardens and on old burn sites confirming that *A. cunninghamii* is a pioneer tree and a nurse for the invasion of rain-forest. On the other hand lumbering, fire, pigs, and agriculture all contribute to the destruction of natural stands.

**Uses.** The same as for *A. hunsteinii*, with which it often grows. The heartwood is difficult to distinguish from the sapwood.

**Vern.** Pien, Pidgin, ungwa, Kapauku, sngwga, Maniklong, allou, Marconi R., kirivi, Wandammen, ningwik, Tambuni Valley, makut, Pikpik, donoomerr, tororomooi, Dajo, jarusuwua, Tanahmerah, flabbiito, Wapi, d’ti, Telefomin, escera, Foie, sari, Bembé, bentuan, Kaigorin, wariri, Gurumbu, nimola, Es’ala.

**Note.** Howcroft (l.c.) has noted in some areas of New Guinea trees that have more gracile foliage, particularly in the juvenile stage. These differences could well correspond to the type variety which therefore might include New Guinea within its range. While noting that there are slight differences, recent authors have chosen not to use the variety in describing New-Guinea material perhaps because in its original description the distinctions actually given are not valid.
Fig. 69. *Araucaria cunninghamii* Ait. ex D.Don var. *papuana* Laut. Tree, 49 m high, on slopes of Mt Cycloop above Lake Sentani in West New Guinea, 700 m (Photogr. F.W.Rappard, 1956).
2. AGATHIS


Monoecious trees often of immense size with clear straight boles below the globular crown, the large branches often turning irregularly upward; young trees with a conical shape. Bark at first quite smooth and light gray to reddish brown, peeling with large thin irregular flakes that gradually become thicker leaving a pitted somewhat rough reddish brown surface on larger trees. The two cotyledons are broad and lanceolate with an acute apex, the several vascular strands at least at first divided into two groups. Following the cotyledons the leaves are little more than triangular scales with a distinct central vein and several lateral veins. The first full leaves appear in pairs on lateral shoots. Juvenile leaves distinctly larger than adult leaves, particularly those adult leaves exposed to the sun, more or less acute, varying among the species from oval and acuminate to lanceolate. Adult leaves bluntly acute to rounded at the apex, rarely acuminate or lanceolate, oval to linear, sometimes lens-shaped, with considerable variation even along a single shoot where for example the first leaves may be substantially narrower than the later ones, generally somewhat reduced on seed cone bearing shoots, narrowed at the base to a brief broad petiole which is often twisted to place the leaves in a horizontal position, opposite decussate, decurrent, dispersed along the branch so that individual leaves do not overlap, with many parallel veins that converge no more than slightly towards the apex, resin canals alternating with the veins, more or less hypostomatic. Foliage buds globular, tightly covered with several pairs of overlapping scales. Pollen cones appearing mostly on larger trees well after the seed cones first appear, lateral and often in the axils of both of an opposite pair of leaves or occasionally terminal, subtended by several pairs of scales which form the sessile to briefly pedunculate pollen cone buds with the lowest pair sometimes expanded into reduced spreading leaves, more or less cylindrical with numerous small spirally placed microsporophylls. Seed cone bracts also spirally placed, their thickened
Fig. 70. Agathis cone elements. From left to right: lateral profile of microsporophyll, facial view of microsporophyll (from the angle indicated by arrow in the first figure), lateral profile of seed scale, facial view of seed scale (upper seed-bearing face), and seed. Microsporophylls in mm, scales and seeds in cm. — Lateral scallops of the seed scale and shape of seed wing shown are representative; these delicate structures show considerable variation. Orientation of the upper edge of the seed scale varies to which part of the cone it is in. Fully developed seed scales are formed in the middle part of the cone; numerous imperfectly formed scales occur towards the cone base and apex. Seed cone scales and seeds are laterally asymmetrical and both left-handed and right-handed cones are produced. — N.B.: under h, read philippinensis instead of rumpfii.

apical margin blunt or in some species with a projecting flattened ‘beak’, the lateral margins thin and broadly expanded but not membranous, normally indented near the base to form a ‘scallop’ which is usually much larger on one side than the other or more often one side has only a kink, quite variable especially near either end of the cone but more regular in the central fertile part, deciduous when mature. Seed scale complex fused with the bract. Inverted seed attached along its base, more or less flattened and oval-shaped, the margin on one side greatly expanded from the basal part into an oval membranous wing, the other margin blunt or more often with a rudimentary wing or sporadically the seed with two wings (cones and their elements come in both left and right handed versions). Seed cone oval to spherical.
Fig. 71. Range of the genus Agathis Salisb. Figures above the hyphen indicate the number of endemic species, that below the hyphen the total number of species.

Distr. Three sections with 21 spp. from Malaya and the Philippines across New Guinea and the coast of Queensland to Fiji and northern New Zealand; in Malesia 11 spp. There is a gap in the Solomons. Fig. 71.

Fossils: Fossil wood attributed to Agathis has been found in the Upper Cretaceous and Tertiary of New Zealand and from the Jurassic to the Tertiary in Australia, as well as in the Tertiary of Western Australia. Cone scales have been found in the northern hemisphere but the identification is uncertain (Florin, K. Svenska Vet. Ak. Handl. III, 19, 1940, n. 2, 82; Acta Horti Berg. 20 (4), 1963, 180, f. 15 map).

Ecol. The majority belong to lowland rain-forests.

**KEY TO THE SECTIONS**

1. Dorsal part of the microsporophyll not at all angled.
2. Seed scale with a distinct beak (seed cone small, 5–6 cm diam. by 6–7 cm long). *Sp.* 9 2. Sect. Rostrata

1. **Section Agathis**


Fig. 72. Flaky bole of *Agathis borneensis* Warb. in heath forest on podsolized white sandy terrace, c. 20 m alt., Brunei (Photogr. P.S. Ashton, May 1959).
Large trees. Pollen cones with spoon-shaped microsporophylls without angled creases, rarely sessile. Seed cones in most cases at least 7 cm long and the seed bracts always blunt along their apical margins.

Distr. In the same territory as the genus less the more southerly areas 13 spp., of which 8 in Malesia.

KEY TO THE SPECIES

1. Juvenile (and more accessible) leaves not at all acuminate, adult leaves at least 6 cm long or else glaucous on the underside.

2. Leaves not glaucous on the underside, at least 6 cm long. Pollen cones at least 4 cm long. Microsporophylls slightly acute and nearly as long as wide or large (over 5 mm long).

3. Pollen cone at least 2 cm in diameter. Microsporophyll c. 6 mm wide, over 5 mm long, and blunt, resin canals in the leaves paired. A. borneensis

3. Pollen cone more than 14 mm in diameter. Microsporophyll no more than 2.5 mm wide, 2 mm long, and slightly acute, resin canals in the leaves solitary.

4. Adult leaves never broadly rounded at the apex. Pollen cones 12–14 mm in diameter. Apex of microsporophyll at least 2 mm long and wide. Seed bract at least 42 mm wide and 32 mm high with more or less straight margins and the apex bluntly ridged. A. celebica

4. Adult leaves acute to broadly rounded at the apex. Pollen cones 9–12 mm in diameter. Apex of microsporophyll less than 2 mm wide and 1.5 mm long. Seed bract less than 42 mm wide and 32 mm high with more or less rounded margins and the apex sharply rigid. A. spatulata

2. Leaves glaucous on the underside, no more than 6 cm long. Pollen cones less than 4 cm long. Microsporophyll blunt (much wider than long), less than 2 mm long.

5. Adult leaves lens-shaped, 5–7 cm long. Pollen cones 3–4 cm by 9–10 mm. Microsporophyll 2–2.5 mm wide. Seed cone c. 6 cm in diameter, spherical. A. lenticula

5. Adult leaves orbicular, blunt, 2.4–4 cm long. Pollen cones 8–14 by 4–6 mm. Microsporophyll 1.2–1.5 mm wide. Seed cone c. 4.5 cm in diameter, elongated. A. orbicula

1. Juvenile leaves distinctly acuminate. Adult leaves less than 6 cm long and not glaucous on the underside.

6. Adult leaves not acuminate. Microsporophyll helmet-shaped, the stalk attached near the centre of the apical part, at least 2 mm wide. Apex of the seed cone bract bluntly ridged.

7. Seed sharply angled opposite the wing. Mature pollen cone mostly at least 3.5 cm long by 10 mm in diameter. Seed cone bract 2.8–3.2 cm high. Adult leaves at least 4.5 cm. A. philippinensis

7. Seed bluntly rounded opposite the wing. Mature pollen cone 2.3–5 cm long by 7–10 mm in diameter.

8. Seed cone bract 2.6–2.9 cm high. Adult leaves 3–4 cm long. A. flavescens

6. Adult leaves acuminate or small and blunt. Microsporophyll shingle-shaped, the stalk attached below the centre of the apical part, 1.6–1.8 mm wide. Apex of the seed cone bract sharply ridged. A. kinabaluensis


Huge tree to 55 m tall. Juvenile leaves ovate-lanceolate, up to 14 by 4 cm. Adult leaves ovate with
prevailing solitary duct elsewhere in the genus. *Mature pollen cones* oblong, 4–7 cm by 20–25 mm, rounded at the apex, subtended by a 2–10 mm peduncle, the apex of the microsporophyll spoon-shaped, 5.5–6.5 by 4–5 mm, the apex a broad semi-circle. *Mature seed cones* oval, 6–8.5 by 5.5–6.5 cm. *Seed bract* roughly triangular but well rounded at the upper corners, a low thick ridge along the apical margin, a strongly hooked 6 mm scallop on one side of the base, the other side with no more than a kink, 26–28 by 36–40 mm. *Seed* c. 12 by 9 mm, blunt at one upper corner and a broadly rounded wing c. 20 by 16 mm at the other corner.

**Distr.** Malesia: throughout Borneo and more restricted areas in Malaya and N. Sumatra. Fig. 74.

Fig. 74. Range of *Agathis borneensis* Warb.

Ecology. Scattered in upland rain-forest from low elevations to 1200 m throughout its range and in dense nearly pure stands on low-lying sandy peat soil in many parts of Borneo and in one area in Malaya. It is of interest to note that *Dacrydium pectinatum* has a similar ecology.

**Vern.** Malaya: dammar, dammar dagang, dammar minyak, tulong, M; Sumatra: hedje, Tapanuli; Borneo: bindang, Sarawak, bulu, Iban, salang, Kedayah, tambunan, Sabah, manggilam, Dusun, bangalan, bengalan, Sampit, Pilau, toga, W. Kutai, bembueng, SE. Borneo, miju, Dakaj, enghatan, Sunggan, pisau, puit, Sintang.

Note. If the proposal to reject *Pinus dammara* Lamb. in favour of *Agathis borneensis* Warb. is not accepted, the proper name of this species would be *Agathis dammara* (Lamb.) Richard, a name heretofore (incorrectly) associated with different species of Celebes, the Moluccas and the Philippines (see under *A. celebica* and *A. philippinensis*). If various closely related species were combined as varieties or sub-species under this species, there would be no reason to reject the name *Agathis dammara*.

Huge tree to 65 m tall. Juvenile leaves ovate-lanceolate, up to 15 by 4.6 cm. Shade leaves on mature trees acute and roughly 9 by 3 cm. Leaves from fully exposed branches well rounded at the apex but still tapering, not blunt, 6–8 by 2–3 cm, tapering at the base to a 5–10 mm petiole. Pollen cones after shedding pollen 4–6 by 1.2–1.4 cm or possibly even larger, subtended by a short peduncle c. 3 mm long, normally axillary but sometimes terminal (A. beckingii). The apical part of the microsporophyll spoon-shaped, spreading, with the stalk attached well behind its centre, c. 2.5 mm by 2 mm and slightly angled at the apex. Seed cone oval, 9–10.5 by 7.5–9.5 cm. Seed bract with a low thick ridge along the apical margin exposed in the unopened cone to within a few mm of its lateral margins, roughly triangular in shape, the lateral margins nearly straight with a small scallop 4–8 mm above the base on one side, the upper corners more or less angular and rigid, 32–36 by 42–45 mm. Seed c. 14 by 9 mm with a short acute projection on one upper corner and a broad rounded wing c. 24 by 16 mm at the other.

**Vern.** *Dammara, dammar radja, M. hulontu, Malili, kawo, Maliki, kisi, Buru, salo, Ternate, dayungan, Samar, Philippines.*

**Note.** Whitmore (1980) insists that he can find no difference between this and *A. philippinensis* among others and certainly the vast majority of the collected materials (shade leaves and immature reproductive organs) is enigmatic. Whitmore’s descriptions show he is dealing with immature material and the notion that pollen cones continue growth after shedding their pollen is inadmissible. Groups of both species grow side by side at Bogor, where properly mature material can be compared and sharp differences easily seen. Because this is the only species known from Ambon, it is the species which Rumphius (Herb. Amb. 2, 1741, 174, t. 57) has in mind and, like the closely related *A. borneensis*, which occupies similar habitats west of the Makassar Strait, is an important producer of the resin known as dammar.

**3. Agathis spathulata** de Laub., sp. nov.; Silba, Phytologia Mem. 8 (1986) 37, nom. inval. — *A.

Arbor magna ad 60 m alta. Folia adulta acuta 9–10 cm × 20–30 mm ad spatulata 7–9 cm × 18–20 mm. Sirobili masculini 9–13 mm diametri, 4–7 cm longi, apicis microsporophyllis 1,5–2 mm latis, 1,3–1,5 mm longis. Squamae feminae 35–42 mm latae, 27–32 mm aliae, marginibus rotundibus apicis costis acuis. Holotypus: de Laubenfels P741 (L).

Huge tree to 60 m tall. Juvenile leaves ovate-lanceolate, not at all acuminate, up to 13 by 4.5 cm. Adult leaves bluntly acute, 9–10 cm by 20–30 mm to broadly rounded and 7–9 cm by 18–20 mm, tapering at the base to a 5–10 mm petiole. Mature pollen cones 4–7 cm by 9–13 mm, subtending by a 2–9 mm peduncle, the apex of the microsporophyll spoon-shaped without ridges, 1.5–2 by 1.3–1.5 mm, broadly acute. Seed cone oval, 8.5–10 by 6.5–7.5 cm. Seed bract with a thin sharp ridge along the apical margin, broadly rounded at the upper corners, a small 6 mm scallop on one side of the base and a larger 10 mm scallop on the other, 27–32 mm high by 35–42 mm broad. Seed c. 10 by 6 mm, with a sharp projection on one upper corner and an elongated bent wing c. 24 by 10 mm at its widest at the other corner.

Distr. Malesia: SE. New Guinea, E. Highland, near Obura. Fig. 76.

Fig. 76. Range of Agathis spathulata de Laub. (squares) and A. labillardieri Warb. (dots).

Ecol. Scattered as a rain-forest emergent or surviving in small exposed groves between 900 and 1980 m.

Vern. Asong, muwaka, ogapa.

Note. The seed cone scale and seed, though smaller, resemble those of A. robusta, a lowland species, but the pollen cone in particular is quite different.

4. Agathis lenticula de Laub. Blumea 25 (1979) 537, f. 4; Sélba, Phytologia Mem. 8 (1986) 34. — Fig. 77.

Large tree to 45 m tall. Juvenile leaves to 11 cm by 47 mm, ovate, tapering to an acute, scarcely acuminate apex and more sharply at the base. Adult leaves lens-shaped, more or less acute, 5–7 cm by 18–24 mm, tapering to a 3–7 mm petiole, glaucous on the underside. Mature pollen cones 3–4 cm by 9–10 mm, subtended by a 2–6 mm peduncle, the apex of the microsporophyll spoon-shaped and spreading, 2–2.5 by 1.5–2 mm, apex blunt. Seed cone nearly spherical, c. 7 by 6 cm. Seed bract with a thin sharp ridge along the apical margin, lateral margins broadly rounded with a strongly hooked scallop 7 mm above the base on one side, c. 27 mm high by 38–45 mm broad. Seed c. 11 by 7 mm with a slight blunt to no projection on one upper corner and a broadly rounded wing c. 8 by 14 mm at the other corner.

Distr. Malesia: Sabah (Mt Kinabalu and the Crocker Range). Fig. 78.

Ecol. Emergent in mountain rain-forest, 1140–1680 m.

Vern. Tanggigan, tengilan, tungilan, Dusun.

Note. This species occurs just below A. kinabaluensis on Mt Kinabalu where the two can easily be compared in the field. The distinctive leaf shapes are readily apparent but in herbarium specimens the
A glaucous leaf undersurface is generally not detectable. Other differences are the larger pollen cones with blunt, not angled, microsporophylls and the lack of a sharp projection at the upper corner of the seed. Besides A. orbicula and A. endertii, other Agathis species with glaucous leaf undersides occur far to the east beyond Malesia.

5. Agathis orbicula de Laub. Blumea 25 (1979) 540, f. 5; Silba, Phytologia Mem. 8 (1986) 36. — Fig. 79.

Tree to 40 m tall. A light yellow resin is produced in some abundance. Juvenile leaves ovate and bluntly acute, to 6.5 cm by 28 mm. Adult leaves ovate to orbicular, broadly rounded to slightly angled at the apex, 24–40 by 12–24 mm, tapering sharply at the base to a 3–7 mm petiole, glaucous on the underside. Mature pollen cones 8–14 by 4–6 mm, subtended by a 2–6 mm peduncle, the apex of the microsporophyll helmet-shaped, 1.2–1.5 by 1–1.2 mm, apex blunt. Seed cone oval, c. 7 by 4.5 cm. Seed bract with an acute ridge along the apical margin, ovate with a 4 mm scallop spreading nearly perpendicularly to each side of the base, c. 20 mm high and 33 mm broad. Seed unknown but leaving a blunt impression suggesting a shape like that of A. lenticula.

Distr. Malesia: S. Sabah to Central Sarawak. Fig. 78.

Ecol. Scattered in rain-forests and kerangas on low mountains and plateaus between 450 and 1050 m.

Vern. Tumah, Murut, tubu, Kenyah, bulok, Iban.


Huge tree to 60 m tall. Abundant white resin produced. Juvenile leaves ovate and distinctly acuminate, to 7 by 3 cm. Adult leaves ovate, very slightly to distinctly acute, 4–6 by 1.5–2 cm, the smaller leaves, which probably derive from more exposed position, being the least acute, tapering at the base to a 5–8 mm petiole. Mature pollen cones 2.5–4.5 cm by 10–11 mm, subtended by a short peduncle, the apex of the microsporophyll helmet-shaped with the stalk attached close to its centre, 2–2.5 by 1.5–2 mm, the apex very slightly angled. Seed cone oval, 7–9 by 12 cm. Seed bract with a low thick ridge along apical margin, broadly rounded at the upper corners, a small 3–6 mm scallop on one side of the base, 28–32 mm high by 35–45 mm broad. Seed c. 11 by 6 mm, broadly acute at one upper corner and with a wing c. 20 by 11 mm at its widest at the other corner.
Small to medium-sized tree to 12 m tall. **Juvenile leaves** ovate-lanceolate and slightly acuminate, up to 8 cm by 32 mm. **Adult leaves** ovate and, unlike most adult *Agathis* leaves, often wider before the middle, 3–4 cm by 10–20 mm, rounded and blunt at the apex or very slightly angled, tapering at the base to a 3–5 mm petiole. ** Mature pollen cones** 20–35 by 8–9 mm, subtended by a 2–8 mm peduncle, the apex of the microsporophyll helmet-shaped, 2 by 1.8 mm, the apex slightly angled. **Seed cone** oval, 6–7 by 7–8 cm. **Seed bract** with a thick ridge along the apical margin, broadly rounded at the upper corners, a large scallop more than one cm from the base on one side and a smaller c. 6 mm scallop on the other, 26–29 by 35–37 mm. **Seed** oval, c. 11 by 9 mm, blunt at one upper corner and with a broad wing 17 by 14 mm at its widest at the other corner.

**Distr.** *Malesia*: the two or three highest peaks in Peninsular Malay.

**Ecol.** Scattered trees above a low summit scrub, 1200–1800 m, the leaves often yellow, suggesting adaptation to difficult nutrient conditions.

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**Fig. 80.** Range of *Agathis philippinensis* Warb.

**Fig. 81.** *Agathis kinabaluensis* de Laub. a. Mature foliage shoot; b. extreme leaf shape; c. juvenile leaf; d. mature pollen cone; all ×0.4; e. profile view of microsporophyll, ×1.25; f. seed; g. end view and facial view of the seed cone scale; h. profile of the upper edge of the same.
Note. This species corresponds in Malaya to *A. philippinensis* which it strongly resembles, differing in smaller cones, somewhat differently shaped leaves and seeds and especially by the blunt corner of the seed opposite the wing.

8. *Agathis kinabalauensis* de Laub. Blumea 25 (1979) 535; Silba, Phytologia Mem. 8 (1986) 34. — Fig. 81.

Small to large tree to 36 m tall. *Juvenile leaves* ovate and strongly acuminate, to 9 cm by 44 mm. *Adult leaves* ovate, slightly acuminate or occasionally on the smaller leaves round and blunt, 3.5–7 cm by 18–32 mm, tapering at the base to a 4–7 mm petiole. *Matue pollen cones* 18–30 by 8–10 mm, nearly sessile to a 4 mm peduncle at the base, the apex of the microsporophyll spoon-shaped, spreading slightly, 1.6–1.8 by 1.2–1.6 mm, the apex very slightly angled. *Seed cone* oval, 7.5–8.5 by 11 cm. *Seed bract* with a prominent narrow ridge along the apical margin, broadly rounded at the upper corners, a smaller 4 mm and a larger 6 mm scallop on either side of the base, 28–32 by 40–45 mm. *Seed c. 11 by 7 mm*, prominently acute at one upper corner and with a broad wing 20 by at least 12 mm at the other corner.

**Distr.** *Malesia*: Mt Kinabalu in Sabah.

**Ecol.** In or rising slightly above the mossy forest and rather small where the forest is stunted, 1500–2400 m.

**Vern.** *Tunu*, Murut.

Note. This species in Borneo corresponds in many ways with *A. philippinensis* but is nevertheless substantially different.

2. **Section Rostrata** de Laub., sect. nov.


Small to large trees. *Leaves* ovate and slightly angled at the apex to round and blunt, the leaf undersides distinctly glaucous, solitary resin canals between the vascular bundles. *Juvenile leaves* more acute. *Pollen cones* more or less sessile. *Microsporophylls* spoon-shaped, more or less acute and spreading. *Seed cones* spherical to oval and rather small, 5–6 by 6–7 cm. *Seed bract* with a distinct projection or beak near the centre of the ridged apical margin. *Seeds* broadly oval with a blunt projection at one upper corner and a broad wing at the other corner.

**Distr.** There are 3 spp., widely separated, in New Zealand (1 sp.), in New Caledonia (1), and in *Malesia*: Borneo (1).

Note. The projection on the seed bract corresponds to the ligule in *Araucaria* and other conifers and for *Agathis* is a primitive trait.


Tree to at least 48 m. *Juvenile leaves* apparently lanceolate. *Adult leaves* ovate and broadly acute to semicircular and blunt at the apex, 5–8 cm by 17–36 mm with considerable variation on individual specimens, tapering to a 3–6 mm petiole, glaucous on the underside. *Matue pollen cones* 26–38 by 7 mm, sessile, the apex of the microsporophyll spoon-shaped, spreading, 2.5 by 2 mm, the apex slightly angled. *Seed cone* oval, 4.5 by 7 cm. *Seed bract* with a prominent narrow ridge along the apical margin surmounted by a spreading blunt more or less triangular projection c. 8 by 3 mm, somewhat rounded at the upper corners, a small 4 mm scallop on one side at the base, at least 25 mm by 30 mm. *Seed c. 11 by 8 mm*, a short acute projection on one upper corner, a broad wing c. 18 by 14 mm at its widest at the other corner.

**Distr.** *Malesia*: Borneo. Fig. 83.

**Ecol.** In more or less isolated populations from near sea-level to 1440 m, often associated with sandstone kerangas.

**Vern.** *Bulok*, Iban.

Note. The leaves more or less resemble in particular *A. borneensis* (but lack the paired resin canals) so that sterile specimens cannot be readily identified in this otherwise quite distinct species.
3. Section Prismatobracteatae


Large trees. Microsporophylls with sharp creases dividing the apical part into three or more facies. Pollen cones with a short peduncle. Seed bracts always blunt along their apical margins. Leaves not glaucous underneath.

Dist. From New Guinea and New Britain to Queensland, New Caledonia and Vanuatu (New Hebrides) 5 spp.; in Malesia: 2 spp.

Key to the Species

1. Apical part of pollen cone prismatic with a series of lateral facies surrounding a flat hexagonal upper face
   10. A. labillardieri
1. Apical part of pollen cone divided into three lateral facies

Fig. 82. Agathis endertii Meijer Drees. a. Mature foliage shoot; b. leaf variation; c. juvenile leaf; d. young seed cone; e. mature pollen cone, all ×0.4; f. profile view of microsporophyll, ×1.25; g. seed; h. end view and facial view of the seed cone scale; i. profile view of the upper edge of the same.

Fig. 83. Range of Agathis endertii Meijer Drees.

Huge tree to 60 m. *Juvenile leaves* ovate and acuminated, to 10 by 6 cm. *Adult leaves* ovate to oval lanceolate, acute, 6–9 cm by 20–24 mm, narrowing to a 5–7 mm petiole. *Mature pollen cones* 25–35 by 10–15 mm, subtended by a 2–6 mm peduncle, the apical part of the microsporophyll prismatic with a series of lateral faces surrounding a flat hexagonal upper face 1–1.5 mm wide and long and crowded so that only the upper face is exposed. *Seed cone* oval, 8.5–10 by 7.5–9 cm. *Seed bract* with a low thick ridge along the apical margin exposed in the unopened cone to within a few mm of its margins, roughly triangular in shape with nearly straight lateral margins, with a distinct scallop c. 8 mm above the base on one side, slightly rounded at the upper corners, 30–32 by 38–42 mm. *Seed* c. 12 by 7 mm with a short broadly acute projection on one upper corner and a broad rounded wing c. 20 by 15 mm at the other.

Fig. 84. *Agathis labillardieri* Warb. a. Twig with pollen cones; b. seed cone, both × 0.4.

Fig. 85. Cones of *Agathis labillardieri* Warb. of a specimen growing in Sarmi on the north coast of West New Guinea (Photogr. H.R. KARSTEL, 1957).
Distr. *Malesia*: throughout the western part of New Guinea and eastward to the margins of the Sepik Valley. Fig. 76.

Ecol. From near sea-level to 1350 m or occasionally to 1800 m, often on ultrabasic soil and locally very common.

Vern. *Dannmar, M, pen, Pidgin, legatulhus, Mooi lang., aisi, Arguni, idjir, Irahatu, tar, Kebar, waiui, Pousami, kessi, Roberai, Kuri, fuko, Manikiong, uto, Kapaku, warkai, Kamora, Kokonao, osier, lik, sao, Kwerba, we1, lwer, nu, Wagu, aglo, Orne, koba, E. Sepik.


Tree to 48 m. Juvenile leaves ovate and acuminate, up to 13 by 3.8 cm. Adult leaves ovate and acute to rounded at the apex, 5–9.5 cm by 10–26 mm, tapering to a 3–10 mm petiole. Mature pollen cones 4–8.5 cm by 7–9 mm, subtended by a 2–9 mm peduncle, apex of microsporophyll sharply angled to form three lateral facies, c. 1 mm wide and long, the slightly angled along its margin front (apical) face directed inward to the bases of the next microsporophylls ahead on either side. Seed cone oval to elongated, 9–15 by 8–10 cm. Seed bract with a thin sharp ridge along the apical margin, rounded at the upper corners, the curving lateral margins with a larger scallop c. 10–12 mm above the base on one side and a smaller one 5–8 mm above the base on the other side, 30–45 by 39–46 mm. Seed c. 10 by 6 mm with a long acute projection on one upper corner and a long bent wing c. 30 by 12 mm at the other.

Distr. In four localized clusters, one in the central part of New Britain, another east of Port Moresby in Papua New Guinea, the largest in the rainforests of northern Queensland, and the last in southern Queensland on Fraser I. and the nearby mainland. Fig. 86.

Fig. 86. Range of *Agathis robusta* (Moore) Bailey.

Ecol. Locally common on a variety of soils in exposed positions following disturbance from near sea-level in Australia and 400 m further north to 900 m throughout its range.

Vern. Naveil, New Britain.

**CUPRESSACEAE**

Both *Cupressaceae* and the closely related *Taxodiaceae* are important Holarctic families which also have representatives in the southern hemisphere. A few species of both extend into habitats on the margins of the tropics or into tropical highlands. Of 18 genera of *Cupressaceae* only *Libocedrus* reaches into Malesia. Occasional reports of *Callitris* in New Guinea have been based on similar appearing specimens of *Casuarina*. 
1. LIBOCEDRUS


Monoecious evergreen trees or shrubs. Bark smooth but fissured, peeling in strips or flakes, fibrous, rich brown but weathering to blackish or gray. **Leaves** in alternating whorls of 3 or 4 soon reduced to opposite decussate, those of the seedling single veined and linear, c. 1 cm long, changing abruptly on lateral branches and throughout mature trees to specialized scale forms. **Scale-bearing branches** with small dorsally keeled facial scales alternating decussately with larger marginal leaves that are strongly bilaterally flattened and sometimes extend outward wing-like, the basal margins of each pair meeting between the succeeding facial leaves, the whole branch system further differentiated dorsiventrally with a convex upper surface bearing few or even no stomata and a concave lower surface where the stomata are concentrated, the leaf differentiation diminishing (or more or less disappearing) on older more exposed plants. Foliage buds nothing more than the last pair of developing leaves. **Fertile structures** solitary, terminal, often on short lateral branches. **Pollen cones** cylindric, composed of decussate or more or less crowded scales each with 2–6 inverted pollen sacs. **Seed cones** woody, composed of two oval opposed fertile scales each bearing two erect ovules at their bases and two small triangular lateral sterile scales. The bracts are mostly fused to the outer surface of the scales, the apex of the bract a short to elongated acute spreading projection. **Seed** an elongated cone with two very unequal wings, a narrow wing along one side and an elongated more or less expanded wing at least twice as long as the seed on the other side and extending beyond and more or less outward from the seed apex (micropyle).

**Distr.** There are 7 spp. of Antarctic forests and tropical highlands including New Guinea, New Caledonia, New Zealand, and S. Central Chile with adjacent parts of Argentina. In **Malesia**: 1 sp. with 2 varieties endemic to New Guinea and nearby islands. Fig. 87.

**Fossils.** Foliage shoots and wood from the Eocene of Patagonia and Chile (Florin, K. Svenska Vet. Ak. Handl. II, 19, nr. 2, 1940, 82).

**Ecol.** A wide range of forest and rain-forest habitats from lowland tropics to the tropical tree line and throughout the Antarctic forests (in Chile prospering on the dry margins of the forest). Pollination and seed dispersal strictly by wind. Seedlings germinating in abundance in rich humus soils.

**Uses.** The aromatic wood is similar to that of Juniperus in appearance and uses, with light coloured sapwood and reddish brown to purplish heartwood. Where large enough it is much appreciated for construction and furniture while the bark is sometimes used for roofing.
Notes. The relationships of *Libocedrus* are emphatically with the Holarctic *Thuja* group of genera (*Thuajoideae*) within *Cupressaceae* making it phytogeographically much like the everywhere associated *Nothofagus* whose relatives are also in the north. Like the other members of *Thuajoideae*, the leaves are strongly differentiated into lateral and facial types and even further like many of these genera the branches are also differentiated dorsiventrally (the Holarctic genus *Calocedrus* was for a long time included within *Libocedrus*). Attempts as in Lj (1953) to attach *Libocedrus* to southern hemisphere cypresses (*Callitroideae*) by ignoring the highly specialized foliage forms and describing the seed cones as 'valvate' are inadmissible. The so-called valvate appearance is due to the few cone scales, the lowermost scales of any Cupressaceous seed cone being the same so that this appearance occurs wherever the number of scales is reduced, as in *Chamaecyparis nootkatensis*.

The species of New Guinea and of Chile have been placed into separate genera based on slight differences. The upper surface of the leaves of the Chilean species are so constricted that little or no space is left for stomata, making them more or less hypostomatic while other species are clearly amphistomatic but with rather few upper stomata. The New Guinea species was separated on the basis of spirally placed microsporophylls. In fact, simple opposite decussate pollen cones occur alongside crowded cones whose microsporophylls appear to be whorled or perhaps spirally placed. Florin & Boutelje (1954) carefully examined these cones and found each two decussate pairs of microsporophylls brought to the same level but certainly not spirally placed. On the other hand, they adduced some other minor distinctions for the New Guinea material, in particular that the stomate bands are more or less separated by narrow irregular stomate-free zones, a character not seen elsewhere in the genus. In my opinion these otherwise very similar species should not be separated generically by such unimportant distinctions.

Fig. 88. View south over the Archbold Expedition camp and Lake Habbema to snow-capped Mt Wilhelmina, from an altitude of 3265 m. Open forest of Libocedrus papuana F.v.M. in foreground centre and big, moss-cushioned Podocarpus compacta; alt. of Lake Habbema 3225 m, Mt Wilhelmina 4750 m (Photogr. L.J. Brass, August 1938).


Trees 2–50 m tall, rarely shrubby, pyramidal or spreading or even slightly pendulous with age. Leaves on older and more exposed trees becoming quite small, facial scales rhomboidal, acute, up to half as long as the lateral scales, c. 1 mm long, the lateral scales nearly straight, their base between the outermost edges of the next lower facial scales, spreading slightly and then straight or weakly convex, tips extending slightly beyond the outermost edges of the next higher facial scales and either straight or slightly spreading or (when convex) slightly incurved and ± touching the base of the next lateral leaves but below the tips of the next facial leaves, down to c. 2 mm long. Branches darker above and often glaucous below. Pollen cones 4–25 mm long by 2–3 mm in diameter, the upper part of the microsporophyll roughly triangular, c. 1.5 mm long, with 2–4 pollen sacs. Seed-bearing scale broadly lanceolate to almost elliptic, at least slightly rounded at the tip, 8–12 mm long and 4–6 mm wide, narrowing at the base and sometimes slightly constricted along the side where touched by the smaller lateral scales which are about half as long and ± lanceolate. Bracts broadly fused to the dorsal side of their corresponding scale on its lower half with a short spreading acute to obtuse tip. The woody mature cone brown or blackish, often with ridges radiating from the bracts to the margins of the scale. Seed 2–3 mm long, the wing twice as long and spreading upward with a bend partway along the outer edge towards the straight inner edge forming an acutish rounded apex.

var. papuana

Apex of lateral leaves becoming widely spreading on young plants up to 6 mm from the stem and often
Fig. 89. *Libocedrus papuana* F.v.M. var. *papuana*. A. sterile twig; B. fertile twig; C. pollen cone; D. seed cone; E. scales with pollen sacs (from LAUT. Bot. Jahrb. 50, 1913, 52, f. 2).

Falcately bent outwards but the tip always turned upwards, up to 13 mm from base to tip, gradually becoming smaller and less spreading as the tree matures.

**Distr.** *Malesia*: most of the length of *New Guinea* along the central range but also on the Huon Peninsula, the Torricelli Mts, and the Cycloop Mts, grading into the other variety towards the western end of *New Guinea*, particularly at higher elevations. Fig. 90.

**Ecol.** A tree of mountain rain-forests and especially the mossy forest from 1500 m to the tree line in the central range, sometimes emerging from the alpine scrub to as high as 3800 m, as low as 620 m along the north coast. Above 3300 m a stunted tree less than 10 m tall.

**Vern.** Tera, Garaina; gamuga, kamgenkuna, Togoba, Hagen, ogeleh, oeh, Chimbu, Masul, dzagosa, dzasihanini, hanini, Asaro, Kefamo, guita, juta, Mairi, Watabung, kaibel-kombam, kaipil, ongol, Wahgi, Minj, mondilasop, mondolasap, mondolosap, wrenak, Mendi, ab, aiap, aip, hap, kap, Enga, Kepilam, aioba, hohoba, Lei area, bit, Yogom, iwunturra, Manki, ye-enka, Nauti, sukou, Wapi, Migote.

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PINACEAE

The pine family is one of the most characteristic families of the holarctic realm of which family a few genera reach the margins of the tropics in highlands, but only Pinus extends into tropical lowlands including Malesia.

1. PINUS


Evergreen monoecious trees or rarely shrubs. Bark smooth or rough, particularly on older trees, peeling in flakes often of very irregular shape. Leaves linear or lanceolate, often with minute serrations, spirally placed, soon replaced by scales in the axils of which appear reduced shoots in the form of bundles enclosed around their base by a sheath of scale leaves, adult leaves in the bundles linear, pungent, needle-like, the cross section of each leaf forming a sector of the circle formed by the entire bundle. Pollen cones numerous, axillary, cylindrical, subtended by a cluster of overlapping scales similar to the foliage bud, microsporophylls scale-like with two inverted pollen sacs. Seed cones terminal
Fig. 91. *Pinus merkusii* JUNGH. & DE VRIESE in primary forest habitat on slope of Mt Bandahara, Leuser Nature Park, Sumatra, 2000 m alt. (Photogr. W.J.J.O. DE WILDE, 1972).
on short scaly shoots, more or less cylindrical, consisting of numerous fertile scales which become woody, ripening in the second or third year, the apiculate bract fused with the scale, two inverted ovules on each scale. *Seed* egg-shaped, with a firm outer shell, usually with an expanded wing which is attached to the broad base of the seed.

**Distr.** Over one hundred species across the middle and higher latitudes of the northern hemisphere and southward into Central America, Cuba, and Hispaniola as well as into *Malesia*, where two important pines of southeastern Asia (belonging to subg. *Diploxylon*) extend their range. Absent from the Indian subcontinent, but occurring throughout the Himalayan range.

**Fig. 92.** *Pinus merkusii* JUNGH. & DE VRIESE in fire-prone grassland, blang area along the Gajo-road, Sumatra (Photogr. J.C. VAN DER MEER MOHR, 1925).

**Ecol.** A wide range of forest and savanna habitats most characteristically following disturbance and thus even as large trees surrounded by rain-forest in some cases. Frequently occurring as a fire climax woodland or scattered in fire-prone grasslands. Pollination and seed dispersal by wind or in many cases the seed are gathered by birds or rodents or even collected for human food.

**Note.** Pines are leading sources of lumber and pulpwood and some species such as the two described here yield large amounts of pitch and are tapped to make turpentine. Use as ornamentals is widespread and pines are favourite subjects of afforestation. The widespread use of pines in tropical tree plantations derives from the detailed information available for their silviculture and not because they are of particularly good quality wood. The fact is that much tropical pine wood production is of very poor quality and it is to be hoped that knowledge of the production of better quality woods will increase in the future.
Fig. 93. Pinus merkusii JUNGH. & DE VRIESE. a. Twig with seed cone; b. twig with pollen cones; c. growing shoot; d. pair of needles; e. tips of needles, enlarged; f, g. pollen cones (from DE VRIESE, Pl. Nov. Ind. Bat. Or., 1845, 5, t. 2).
1. Leaves two per bundle. Mature seed cone ovate ........................................... 1. P. merkusii
1. Leaves three per bundle. Mature seed cone globular ........................................... 2. P. kesya


Large tree 40–50 m tall, occasionally to 70 m. Pyramidal with heavy horizontal branches and thick fissured bark in most areas but in some regions trees have more slender, somewhat ascending branches and much thinner, smoothish bark resembling that in the upper crown of thick-barked populations. These two types hold true in artificial plantings. The reddish bark of young trees changes to dark brown weathering to gray on older trees. Needles in pairs, 16–19 cm by 1 mm, abruptly pointed, stomata on all faces, falling in the second year. Basal sheath 12–18 mm long, reddish. Pollen cones 18–25 by 5 mm. Seed cone cylindrical before opening, 5–11 by 3 cm and twice as thick after opening, generally falling soon after shedding seeds. Apophysis broadly tetragonal in shape with a smooth, almost depressed umbo. Seed 7.5 by 4.5 mm, with a deciduous wing 25 by 8 mm.

Dist. In Malesia common throughout the mountains of Atjeh in Sumatra and scattered further south in Tapanuli with an isolated outlier near Mt Kerintji at c. 2° south of the equator and the only natural occurrence of pine south of the equator. The same or a closely related pine is scattered throughout SE. Asia from E. Burma to the South China Sea and two small areas in the Philippines, one on Mindoro and the other near the west coast of Luzon in Zambales Prov. Fig. 94.

Ecol. From low elevations to 2000 m, generally on poor quality acid podzolic soils over sandstone or fresh volcanic ash, sometimes on deeply leached acid basalt, rarely successfully competing on richer forest soils. Most stands show a clear relationship to fire or other disturbance and the pine can be seen to be expanding in recently disturbed areas. In Sumatra the habitat experiences heavy year-round precipitation, but the pine areas themselves definitely favour the drier sites. The Tapanuli populations, which have thin bark, are more sensitive to fire and do not descend below 1000 m. Elsewhere, including the Philippine islands, this pine grows in strongly seasonal environments.

Vern. Sumatra: dammar butu, dammar hunga, hejam, hujam, ujam, ujem, Atjeh, higi, Kerintji, ka-tu tusam, tussam, Battok, Tapanuli; Philippines: tapula, Sambal, Luzon, agoo, agui, salit, Philip. islands.

Note. The similar pines of the southeastern Asian mainland and the Philippines differ in certain ways from those of Sumatra. The mainland pines, which grow in areas with a distinct dry season much stronger than any seasonality in Sumatra, have a distinct grass stage for the seedling, a character not seen
at all in Sumatra. The needles are 19–24(–27) cm long, the seed cones have a more typical taper of most pines, not the unusual cylindrical Sumatran shape, and their umbos tend to be distinctly raised on an apophysis distinctly wider than high. Seeds are nearly twice as heavy. Sumatran pines have a multinodal leader (several nodes in each year's growth) while the mainland form is uninode. The new species, *P. merkusiana*, proposed for the mainland population, was described without a type specimen, but the earlier name, *P. latteri*, is already available. The varietal name *tonkinensis* is also available. Like Sumatra, mainland areas have an 'upland' thin-barked form to which the varietal name applies should further nomenclatural divisions be needed.


Tree to 35–45 m, the crown expanding on older trees. Bark reddish brown, thick and deeply reticulately fissured, breaking off in small thick irregular plates and thus sometimes becoming smoother and plate-like. Branchlets smooth, bright brown. Buds oblong cylindrical and non-resinous with brown lanceolate scales free at the tips. *Needles* in threes, rarely pairs, 12–24 cm by 0.5 mm, acuminate, stomata on most surfaces, falling after two years. Basal sheath 5–18 mm long, greyish brown. *Pollenn cones* 18–30 by 5 mm. *Seed cone* ovoid to conical before opening, 4.5–10 by 3–5 cm, very persistent. *Apophysis* wider than long, pyramidal, the umbo with a small expanded and usually deciduous mucro. *Seed* 5–8 by 3 mm with a deciduous wing 20 by 8 mm.

**Distr.** Across SE. Asia to E. India (Khasia) and a short way into China; in *Malesia*: Philippines (common in the northern part of Luzon). Fig. 95.

![Fig. 95. Range of *Pinus kesiya* Royle ex Gordon.](image-url)

**Ecol.** Most often in open pure stands following fire, but also mixed with oaks and Ericaceae species at intermediate elevations from 300 to 2700 m, often on steep slopes. Generally in the same area as *P. merkusii*, but usually at higher elevations. A few specimens in the Philippines have been considered hybrids between these two species, but actual hybridization has not been verified.

**Vern.** Al-al, parua, saleg; boo boo, bot bot, bulbul, II., tapulao, Zambales.

**Note.** *Pinus timorensis* (an earlier name) was thought by some to be equal to *P. kesiya* (*P. insularis*) although the description is inadequate to confirm this. There are no native pines in Timor; perhaps this was a cultivated tree.
Doubtful or Excluded


Podocarpus elata R.Br. — Engler, Bot. Jahrb. 7 (1886) 445, mentioned a specimen from Timor (Kupang Bay) to belong to this Australian species. Pilger did not mention this specimen in his monograph and Wasscher did not see it either (cf. Blumea 4, 1941, 471).

Podocarpus palembanica Miq. Fl. Ind. Bat. Suppl. (1860) 252, 289. According to de Boer (Conif. Arch. Ind., 1866, 4) it is not a conifer because of its non-coniferous wood. Kostermans (Reinwardti 2, 1953, 362) observed its stipules and nerves and identified it as a juvenile specimen of Ganua sp., later referred tentatively to a distinct species by van den Assem (Blumea 7, 1954, 482): Ganua palembanica (Miq.) van den Assem & Kosterm. (Sapotaceae).

Thuja javanica Burm. f. Fl. Ind. (1768) 202, t. 64, f. 3. — Podocarpus javanicus (Burm. f.) Merr. Philip. J. Sc. 19 (1921) 338, pro nomen. Burman’s description and figure are based on a specimen of Java. In L there is a specimen in herb. van Royen, with a label ‘Thuja javanica è Java. Monoic.’ which seems to be in Burman’s handwriting and which can provisionally be accepted as the type specimen. According to Hallier f. (Meded. Rijksherb. n. 37, 1918, 92) it belongs to Juniperus chinensis, a conifer already cultivated in Java in early days.
POLYGALACEAE (R. van der Meijden, Leiden)

Herbs (sometimes saprophytic), shrubs, lianas or trees. Stipules absent but stem sometimes provided with a pair of glands at the nodes. Leaves simple, entire, usually spirally arranged, sometimes alternate, (semi)decussate or verticillate, sometimes scale-like or absent. Inflorescence usually racem-like and unbranched, (supra- or extra-)axillary and/or terminal, sometimes thyrsoid or fasciculate, rarely flowers solitary. Bracts present; bracteoles basal, rarely (Salomonia, Epirixanthes) absent. Flowers bisexual, more or less zygomorphous, rarely actinomorphous. Sepals 5, free and quincuncial, or the lower (abaxial) 2 connate, sometimes all connate, subequal or the lateral ones larger and then often wing-like (ala) and petaloid. Petals 3 or 5, free or variously united, occasionally also with the calyx, usually adnate to the base of the staminal tube or the filaments, subequal or more often unequal with the lower petal often keel-like and frequently pouched, lobed, or crested. Stamens 2–10, usually 8, filaments usually more or less connate except between the upper stamens, often adnate to the petals; anthers basifixed, tetra- or bi-, rarely trisporangiate, 1- or 2-locular, opening by a single and often oblique pore or by a longitudinal introrse slit. Ovary superior, usually 2-locular but occasionally 1-, 3-, 5-, 7- or 8-locular, sessile or sometimes stipitate; style simple but often variously dilated or lobed at apex, usually articulate with the ovary and nearly always deciduous in fruits. Ovules 1 per cell and subapical, or (in Xanthophyllum) 4—more in a 1-locular, bicarpellate ovary with 2 parietal placentas, anatropous, bitegmic and crassinucellate. Fruit various, a berry, capsule, samara or drupe.

Distribution. About 15 genera and over 1000 species, widespread in temperate and tropical regions of the world, especially well-developed in South America and South Africa. In Malesia 6 genera, of which Polygala and Securidaca (not in Australia) are cosmopolitan, Xanthophyllum and Salomonia Indo-Australian, Epirixanthes Indo-Malayan. The sixth genus is Eriandra which belongs to the tropical American tribe Moutabeae, of which 3 genera are known in South America; Eriandra occurs in New Guinea and the Solomon Islands and represents a marked example of disjunct, tropical trans-Pacific affinities.

Ecology. Very diverse, in wet or dry, open or closed, warm or rather cold habitats, in the lowlands or on mountains up to 3600 m; greatly varying in habit. Epirixanthes is a genus of small saprophytic (not parasitic) plants on humous soil in deep shade among litter of the rain-forest. Salomonia is an unseemly herb of open places. In Polygala there are woody shrubs in the undergrowth of the rain-forest, but most species are herbs of open country, several even preferring a seasonal climate; one species (§ Melichora) is a climber of the rain-forest, like Securidaca. The species of Xanthophyllum and the monotypic Eriandra are trees of the rain-forest, sometimes of lofty size.

In some species of Polygala the occurrence of endomycorrhiza (VA-mycorrhiza) has been demonstrated (Heubl, 1984).

Pollination. Most species seem to be adapted to cross-pollination, but thusfar actual observations have only been reported for some Polygala species (see there). In Epirixanthes the structure of the flowers seems fit for cross-pollination (see there). Self-pollination, however, has been re-
ported for species in diverse genera, also for those species in which cross-pollination has been reported, or is suspected to be possible. It may be concluded tentatively that self-pollination is an effective second-chance possibility for reproduction in the *Polygalaceae*.

**Dispersal.** Corresponding to the diversity in fruit and seed types there is a great variation in dispersal types (*Verkerke*, 1985). Especially in *Polygala* many dispersal types occur: myrmecochory, orinthochory, anemochory, diplochory, epizoochory. Orinthochory also occurs in *Dielidanthera, Carpolobia, Atroxima*, and probably in some *Xanthophyllum* species. *Moutabea* fruits have endozoochorous dispersal by monkeys (*Van Roosmalen*, 1985); this may also be true for some *Xanthophyllum* species. Myrmecochory (or perhaps also anemochory) probably occurs in *Bredeneyera, Comesperma, and Epirixanthes*; anemochory also in *Monnina* and *Securidaca* (*Van Roosmalen, l.c.*), but in the latter also hydrochory is possible. Epizoochory is the possible means of dispersal for *Salomonia*.


**Morphology.** Recently the morphology and ontogeny of ovules, fruits and seeds have been described (and reviewed) by *Verkerke*; of *Polygala*: *Verkerke & Bauman* (1980); of *Xanthophyllum*: *Verkerke* (1984); of the remaining genera: *Verkerke* (1985). *Leinfellner* (1972) demonstrated that there is no principal difference in the ontogeny of the unilocular, multiovulate ovary of *Xanthophyllum* and the bi- to octoloculate, uniovulate ovary of the other *Polygalaceae*. The ontogeny of bi- and trisperangiate anthers of *Polygala* has been described by *Chodat* (1891) and *Venkatesh* (1956). Stipular outgrowths or nodal glands are pseudostipules in the sense of *Weberling* (*Van der Meijden*, 1982: 3). Contrary to the idealistic opinion of *Chodat* (l.c.) (also adopted by *Hutchinson*, 1967) and *Cronquist* (1981), the primitive number of stamens is 8; the presence of 10 stamens (*Dielidanthera*; and a rare abnormality in *Xanthophyllum*) is a derived character.


**Vegetative anatomy.** The *Polygalaceae* exhibit an interesting diversity in their leaf and wood anatomy, which has only fragmentarily been explored, especially for the Malesian genera. Hairs if present are unicellular, or more rarely uniseriate. The lower epidermis is papillate in a number of species. Stomata may be of the anomocytic, paracytic or anisocytic type (all three types occur within the genus *Xanthophyllum*). An adaxial hypodermis is frequently present in the woody species with coriaceous leaves. The vascular pattern in petiole and midrib ranges from a single collateral bundle to a closed cylinder with accessory bundles (again the whole range of the family is represented in *Xanthophyllum*). The nodes are unilacunar. Unusual tracheoidal idioblasts in the leaf mesophyll are characteristic for *Xanthophyllum*.

The secondary xylem of the trees and climbers is characterised by largely solitary vessels with simple perforations, fibres with distinctly bordered pits and heterocellular rays which are usually narrow (1–2-seriate), but may be much wider in the *Moutabea* (e.g. *Securidaca*). Axial parenchyma is mainly paratracheal in *Polygala*, apotracheally diffuse and diffuse-in-aggregates plus vasicentric to loosely aliform in *Securidaca*, and apotracheally banded plus vasicentric in *Xanthophyllum*. Included phloem occurs in the wood of *Securidaca* (and other *Moutabea*).

Despite the anatomical distinctness of *Xanthophyllum* (mainly through its tracheoidal idioblasts), vegetative anatomy clearly witnesses affinity with other *Polygalaceae* (epidermal characters, overall leaf histology, solitary vessels and fibre type in the wood; the parenchyma distribution in some *Xanthophyllum* species is reminiscent of that of *Securidaca*). In its wood anatomy *Xanthophyllum* also recalls *Trigonioeae*, especially *Trigoniostrum*.

**References:** *Bridgwater & Baas, IAWA Bull. n.s.* 3 (1982) 115–125; *Dickison, Bot. J. Linn.*
Pollonymology. Pollen grains in Polygalaceae are mostly suboblate to prolate, sometimes equatorially constricted (Epirixanthes cylindrica), and measure from 25 to 62 μm. The apertural system is zonocolporate (‘stephanocolporate’) in all genera, the number of apertures ranging from 5 (Xanthophyllum papuanum) to 17, or up to 42 in Polygala. The endoapertures may be fused (‘syrnorate’) to form one broad, equatorial endoaperture, bordered by endexinous costae. In this way, the circle-shaped endoaperture divides a grain into two rigid halves, in which the colpi are no longer active in harmomegathic functioning. Volume accommodation in such a grain, and possibly also in grains with poorly separated pores, is achieved by folding of the flexible parts of the mesocolpa which cross the endoapertural zone (Muller, 1979). Similar apertural systems and harmomegathic mechanisms occur in the genus Utricularia of the unrelated family Lentibulariaceae (Thanikaimoni, 1966; Huynh, 1968).

Exine stratification is mostly obscure using light microscopy. Larson & Skvarla (1961) demonstrated the presence of ectexine, endexine, and a columellate infratectal layer in Polygala with electron microscopy. The tectum is mostly smooth, pitted, or perforate, sometimes somewhat fossulate or scabrate. Large perforations (‘aperturoid depressions’, ‘lacunae’) may occupy the poles.

Pollen of the family Polygalaceae is very distinct. Supposed relationships with other families within the Polygalales are not supported by pollen morphological evidence. Pollen of the family Krameriaceae is certainly dissimilar to that of Polygalaceae (Erdtman, 1944, 1952; Simpson & Skvarla, 1981). On the other hand, the distinct pollen type represents a strong argument for inclusion of Xanthophyllum as a genus within Polygalaceae. Also in ascertaining the systematic position of Diclidanthera (Erdtman, 1944) and Eriandra (Van Royen & Van Steenis, 1952) pollen morphology turned out to provide circumstantial or even deciding evidence.

It is not yet possible to key out all Malesian genera of Polygalaceae on the strength of pollen characters. Only one rough separation can be made: pollen of Epirixanthes, Eriandra, Securidaca, and Xanthophyllum mostly has 12 or less apertures, while grains in Polygala and Salomonia rarely have less than 12. Pollen of Epirixanthes is characterized by its heavy equatorial belt and involute colpus margins. These features probably represent derived states in Polygalaceae. Pollen of Securidaca has clearly separated endoapertures. This state may be considered as primitive, comparing with the syrnorate type in Polygalaceae.


Phytochemistry & Chemotaxonomy. Chemical characters of the family were summarized and discussed by Hegnauer (Chemotaxonomie der Pflanzen 5, 1969, 352–361, 459). A supplement will be included in volume 8. Glycosides releasing methyl salicylate on hydrolysis and saponins with triterpenic acids as their sapogenins are rather common in the family, especially in roots. The most characteristic genuine sapogenin of the family seems to be presenegenin, C_{35}H_{46}O_{5}, an acid-labile derivative of oleanolic acid; it was shown to be mainly sapogenin of roots of several members of Bredemeyera, Carpoolobia, Polygala and Securidaca. Closely related sapogenins are polygalacic acid from Polygala paenea and bredemolic acid from Bredemeyera florbunda. Mono-, di- and trimethoxy-cinnamic acids as well as ferulic and sinapic acid occur widely; usually they are esterified with free sugars such as saccharose or with the sugar part of the bidesmosidic saponins. Leaf flavonoids seem mostly to be glycosides of quercetin and kaempferol. Polygalitol (= aceritol = 1,5-anhydroglucitol) is a characteristic hexitol derivative of roots of many polygalaceous plants; it occurs free and combined with sugars. Seeds usually store mainly proteins and fatty oils, but no starch. There is still little known about the chemistry of
polygalaceous seed oils, but very unusual oils were shown to be produced by *Monnina emarginata* and *Polygala virgata*. Three groups of secondary metabolites have still to be mentioned notwithstanding the fact that they are known only from a few species of *Polygala* at present. These are polyhydroxylated xanthenes, and naphthalin- and bibenzyl-γ,γ-butyrolactone-type lignans such as podophyllotoxin (e.g. *Polygala polygama*) and suchilactone (e.g. *Polygala chinensis*). Moreover, the Central American *Polygala paniculata* yielded a number of rutaceous coumarins and a diester of khellactone.

The taxonomic relevance of chemical characters was discussed by Hegnauer in 1969. It may be added now that the occurrence of isoprenylated coumarins and an obvious total lack of iridoids agree well with the assumption of sapindalean (*sensu lato*) affinities. Tannins too seem to be totally lacking in *Polygalaceae*; this, however, does not contradict the just mentioned assumption, because within *Sapindales s.l.* a strong tendency to replace tannins by other types of secondary metabolites is apparent. Finally it should not be forgotten that several chemical characters may prove valuable in future for infrafamilial classification. — R. Hegnauer.

**Taxonomy.** Cronquist's circumscription of the order *Polygalales* (1981: 763) reflects the general opinion of systematists; next to the *Polygalaceae* (with *Xanthophyllum* as a separate family) it includes the *Trigonieae, Vochysiaceae, Malpighiaceae* as well as the *Tremandraceae* and the *Kramerieae*. Wood anatomical evidence (Bridgwater & Baas, 1982) supports a close affinity of *Polygalaceae, Xanthophyllum* and *Trigonieae*, but not with the other families. Van der Meijden (1982) found no arguments to include *Tremandraceae* and *Kramerieae*. Although there seemed to be little evidence for the inclusion of *Kramerieae* in the order (Simson & Skvarla, 1981; Simpson, 1982), the first author recently supported the classification of *Kramerieae* next to *Polygalaceae*, mainly based on serological evidence (Buse-Jung, 1979).

Splitting off *Xanthophyllum* as a separate family has been based on incomplete or erroneous knowledge of the genus. Of the three characters mentioned by Cronquist (l.c.), two do not hold: filaments are often partly and sometimes halfway connate in *Xanthophyllum*, and seeds with copious endosperm occur in four of the seven subgenera. Thus *Xanthophyllum* differs in a single though compound character from other *Polygalaceae*, viz. in the structure of the ovary (which ontogenetically is largely similar to other *Polygalaceae*, cf. Leinfellner, l.c.); this differs in the reduced septs, in the doubling of the number of ovules per carpel, and in the height of insertion of the ovules. On the other hand *Xanthophyllum* has a number of striking similarities with other *Polygalaceae* in the structure of the flowers, as well as in some vegetative characters (the presence of laminar and nodal glands). Also studies on the morphology of ovules, fruits and seeds (Verkerke, 1984, 1985), of foliar anatomy (Dickison, 1973) and wood anatomy (Bridgwater & Baas, 1982) do not present arguments to split *Xanthophyllum* from the *Polygalaceae*.

Mainly based on differences in floral structure, Chodat (1891) distinguished three tribes in the family, *Polygaleae, Moutabeae* and *Xanthophylleae*. Both the studies of Styer (1977) and Verkerke (1984, 1985) revealed that the differences between *Moutabeae* and *Polygaleae* are unclear; the results of vegetative and of seed anatomy do not correspond with differences in the flowers. Therefore a formal subdivision of the family is not presented.


**Bibliographical note.** R. Chodat published a monograph of the family in two parts in Mém. Soc. Phys. Hist. Nat. Geneve, Suppl. 1890 (1891) 1–143, t. 1–12 and *ibid.* 31 (1893) 1–500, t. 13–35. Because of frequent mention of this basic work and the complicated reference, I refer to this work in simpler form, as follows: Chodat, Monogr. I (1891) and Chodat, Monogr. II (1893).
1. Herbs, sometimes woody at base.
2. Lateral sepals larger than the 3 outer ones and petaloid, about as long as the petals. Lower petal (keel) appendiculate apically (except P. tatarinowii). Stamens 8. Fruit laterally dehiscent, the margins entire. Seed with a lobed aril at micropylar side ........................................... 1. Polygala

3. Autotrophic plant with (small) green leaves. Fruit laterally dehiscent, dentate or spinose along the margins, far exceeding the sepals. Pericarp pergamentaceous. Style S-curved at base, long. Disk absent. Anthers 4 or 6, rarely 5. Rachis of inflorescence winged ........................................... 3. Salomonia

4. Sepals united at base, upper part of calyx caducous by a circumcision. Petals basally adnate to the calyx. Ovary 7- or 8-locular. Fruit (by abortion) often 4- or 5-locular. Seeds completely enclosed in an aril ........................................... 2. Securidaca

5. Petals 5. Lateral sepals not petaloid and less than twice as large as the other sepals. Ovary and fruit 1-locular with 4 or more ovules ........................................... 6. Xanthophyllum

6. Ovary and fruit 1-locular. Fruit a distinct samara, indehiscent. Twigs with a pair of glands at the nodes. Seeds without appendages, glabrous ........................................... 2. Securidaca

6. Ovary and fruit 2-locular. Capsule dehiscent, without a large wing. Nodal glands absent, rarely (6. P. sumatrana) pseudostipules present. Seeds either with a lobed aril, or very long-hairy ... 1. Polygala

1. POLYGALA


Annual or perennial herbs, shrubs, small trees or rarely lianas. Stems or twigs rarely with nodal glands, these sometimes transformed into spines. Leaves alternate or verticillate, sometimes (sub)opposite, rarely caducous, sometimes scale-like or apparently absent. Inflorescences raceme-like or rarely paniculate, (supra-)axillary, terminal (and then often overtopped by side-branches) or lateral, sometimes in dense heads. Sepals 5 or the lower pair connate, unequal, caducous or persistent in fruit, the two lateral ones (alaee) at least twice as large as the other ones and often petaloid. Petals 3, unequal, halfway adnate to the staminal tube and sometimes mutually connate into a single 3-lobed petal; some-
times with an additional pair of reduced lateral petals; lower petal (keel) boat-shaped, clawed, its blade entire or 3-lobed or basally auriculate, at apex with or less often without 2 entire or variously incised appendages (crest). *Stamens* 8, rarely 6, monadelphous or partly dia- or triadelphous; anthers usually bisporangiate by abortion of the outer microsporangia, or sometimes tri- or tetrasporangiate, sessile or on a free filamentous stalk, opening by an apical pore or a V-shaped introrse slit common to both cells. *Disk* annular or variously reduced or often apparently absent. *Ovary* 2-celled, each locule with a single subapical ovule; style tip various, often 2-lobed, the apical lobe often sterile and variously dilated, the stigmatic lobe lateral or subapical. *Capsule* 2-celled or very rarely 1-celled by abortion, compressed contrary to the sept, often more or less winged, sometimes with a double wing, dehiscing by a marginal split, reniform to ob lanceolate. *Seeds* various, usually at micropylar side with a lobed or unlobed appendage (aril) and/or with an elongate appendage, at the opposite chalazal side sometimes with a variously shaped appendage, rarely appendages at both sides lacking; glabrous to hairy, or rarely with a coma of hairs.

**Dist.** A polytypic genus comprising at least 500 spp. in tropical, subtropical, temperate and montane regions. The majority of species grow in tropical South and Central America, where *Polygala* also has its greatest infrageneric diversity. Both in North America and in South Africa secondary centres of speciation occur. Eurasia, North Africa, Malesia and Australia are rather poor in species. In *Malesia* the species can be referred to four little-related sections. *Sect. Melchiora* is monotypic and endemic to New Guinea, *sect. Pseudosemeiocardium* is common in Southeast Asia, *sect. Chamaebuxus* occurs over all continents except tropical South and Central America, and the largest (probably unnatural) *sect. Polygala* covers the same area as the genus. The majority of species in Malesia have rather restricted areas, with some notable exceptions, *e.g.*, *P. persicariaefolia*, which also occurs in tropical Africa, and *P. paniculata*, an American species which is now a pantropical weed. Two species are endemic in Malesia.

**Ecol.** Species of *sect. Chamaebuxus* belong to the undergrowth of rain-forests, in Malesia occurring in submontane and montane forests, between 400 and 3000 m altitude. The single species of *sect. Melchiora* is a true liana of the tropical rain-forest. The remaining herbaceous species are heliophilous species growing in open terrains, in open woodland, with a preference for grasslands in seasonal areas; this is especially true for 9. *P. javana*, 12. *P. longifolia*, 14. *P. exsquarrosa*, 17. *P. wightiana*, and 18. *P. rhinanthoides*, which are all restricted to areas subject to a distinct or pronounced dry season.

**Pollination.** Self-pollination probably occurs in all species, although the flowers of the majority are attractive to insects. Many large-flowered species show structures which seem to be adaptations to pollinating insects (*Faegri & van der Pijl, 1979, for P. chamaebuxus*), but in those species, too, self-pollination seems to occur frequently.

In a number of species pollen grains are deposited directly on the stigma, often already in the unopened flower (*Venkatesh, 1956*). In many species the style tip bears special pockets in various ways in which the pollen grains are deposited from the anthers. At that time the stigma can theoretically still be pollinated with foreign pollen grains, as for instance in *P. lutea* (*Miller, 1971*) and *P. vulgaris* (*Heubl, 1984*). According to *Heubl’s* observations, however, a visiting insect will effect self-pollination. Yet there are rather reliable records of hybrids of the latter species in nature (*Heubl, l.c.*), and F₁-plants of artificially produced hybrids are often fertile. This must mean that cross-pollination (rarely) occurs in *P. vulgaris*. Only *Brantjes* (1982) observed and described cross-pollination in the two Brazilian species *P. monticola* H.B.K. and *P. vauhthieri* *Chodat*. The pollination mechanism of those species is a very precise one, and if cross-pollination fails, the flowers are effectively self-pollinated.

Perhaps such examples of precision cross-pollination can be discovered in many other *Polygala* species, because it is rather unlikely that the great variation in style tips and stigma forms could have evolved in complete absence of gene-exchange. It is also possible that many species in which formerly cross-pollination was rare, have lost this possibility.
PoLYGALACEAE

18. (reductions at American revision some TESH, fruiting 1.

2. Annual herbs up to 30 cm high. Flowers, fruits and seeds up to 3 mm long. Spp. 1–3. — 1. Sect. Pseudosemioocardium

3. Keel without appendages at apex. Seed without tubercles, without black appendage at chalazal side. 1. P. tatarinowii

3. Keel with a pair of appendages near apex. Seed tuberculate, with a small or large black appendage at chalazal side.

4. Capsule narrowly winged, longer than wide. Seed at chalazal side with a cylindrical appendage one third as long as the seed itself .......................................................... 2. P. malesiana

4. Capsule broadly winged, much wider than long. Seed at chalazal side with a small, knob-like appendage. 3. P. cardiocarpa

2. Shrubs, small trees, or lianas. Flowers, fruits and seeds at least 5 mm long.


6. Flowers 5–6 mm long. Style straight to near stigma. Seed nearly completely covered by the aril 5. P. oreotrophes

6. Flowers at least 10 mm long. Style curved in apical half. Seed usually covered up to halfway by the aril.

7. Capsule covered by a white layer of dense papillae, the wall not with prominent veins. Racemes in the forks .......................................................... 6. P. sumatrana

7. Capsule without white layer, with prominent longitudinal veins. Racemes (supra-)axillary. 8. Appendages of the keel undivided. Racemes mostly reflexed or patent from the base 7. P. venenosa

8. Appendages of the keel divided into 7–10 ± connate lobes. Racemes erect or very rarely pendulous 8. P. arilifata


10. Alae green. Ovary and fruit only hairy at margin. Stigma strongly recurved at apex, at lower side with one stigmatic lobe .......................................................... 18. P. rhinanthoides

9. Lateral sepals (broadly) elliptic or narrower, glabrous or hairy marginally, or rarely covered by stiff hairs.

11. Alae nearly symmetric, petaloid (coloured).

12. Alae 1.5–2 mm long. Stem set with small, shortly stalked glands. Capsule unwinged. Style obliquely cup-shaped at apex, at one end with a tuft of hairs ............................................. 13. P. paniculata
13. Alae mucronate. Style (nearly) straight, (sub)apically with 2 small stigmatic lobes. Filaments nearly completely connate ........................................... 10. P. japonica
13. Alae rounded at apex. Style curved in apical half, with one stigmatic lobe. Filaments free for at least one third.
11. Alae asymmetric, falcate, not petaloid (green).
15. Capsule glabrous or hairy only at margin. Plants not stiffly hairy. Appendages of keel divided into a number of filiform or finger-shaped lobes. Stigma apically widened or simply reflexed.
16. Capsule c. 2 mm long. Alae c. 3 mm long. Style apically widened, at one side with the stigmatic lobe
16. Capsule (3–)3.5–5 mm long. Alae 4–6 mm long. Style apically strongly reflexed.
17. Plant with stiffly erect, long inflorescences. Apical part of the style very asymmetrically winged.
Free parts of filaments triadelphous ........................................... 17. P. wightiana
17. Plant with short inflorescences or, if with long ones, then these ascending. Style apically symmetrically winged. Free parts of filaments not connate.
18. Appendages of the keel finely divided into hair-like segments. Capsule almost orbicular, c. 4 by 4 mm ........................................... 16. P. chinensis
18. Appendages of the keel divided into finger-shaped lobes. Capsule somewhat longer than wide, 2.5–4 by 2.5–3.5 mm.
19. Upper petals shorter than the keel, 2.5–3.5 mm long. Capsule at the margin both with curved as well as with short straight hairs. Inflorescences 0.5–2 cm long ........................................... 20. P. triflora
19. Upper petals slightly longer than the keel, 2.5–4.5 mm long. Capsule at the margin with curved hairs only. Inflorescences 0.5–7 cm long ........................................... 19. P. glaucoides

1. Section Pseudo-semeiocardium


Small, erect, branched, annual herbs. Flowers in terminal or axillary multflowered unbranched racemes. Sepals caducous before fruit-setting. Keel with 2 hardly incised appendages, or appen- diculate. Disk annular or consisting of 1 or 2 lobes. Style ± tubular, curved in upper half, widened apically, at inner side with a single stigmatic lobe. Capsule orbicular to obovate, narrowly winged. Seeds black, shortly hairy, at micropylar side with a small appendage or with a lobed aril, at chalazal side with or without an appendage.

Distr. Southeast Asia and Malesia.

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1825] ROYLE, Ill. (1839) t. 19D, non Bum.f. 1768, et auct. var. pro parte; MERR. En. Philip. 2 (1923) 384.

Herb up to 25 cm. Stem glabrous, faintly ribbed. Leaves ovate to obovate, 2-35 by 1-20 mm, acute, base attenuate, laxly short-hairy, ciliolate, 0.5-1 cm petioled. Racemes terminal, including the peduncle 1-10.5 cm; bracts and bracteoles early caducous. Flowers c. 1.5-2 mm long, glabrous, rosa-red to purple. Sepals blunt, the alate obovate, 5-nerved. Upper petals oblong, slightly longer than the keel; the keel inapandulate, apically minutely papillose. Filaments free for c. 1/4. Ovary orbicular; style curved and widened in apical half, obliquely truncate. Capsule symmetric, ± quadrangular with rounded edges, apically to orbicular, c. 2 mm long, very narrowly winged all round (wings not visibly cross-veined), the truncate apex mucronate. Seed ellipsoid, not tuberculatc, shortly hairy, at micropylar side with an obliquely lobed aril, at chalazal side inapandulate.

Distr. Irran; N. China, Korea, E. Siberia, Japan and Taiwan; in Malesia: Philippines (Luzon, Mindanao) and New Guinea (Sepik); apparently very rare.

Ecol. Open grassland, ascending to 2000 m.

Note. Polygala furcata ROYLE from N. India, Thailand and S. China differs in the following characters: keel with unlobed appendages, capsule not mucronate, seed tuberculatc, almost globular, at chalazal side with a minute appendage.


Herb up to 25 cm. Stem glabrous, ribbed, 2- or 3-chotomously branched. Leaves mostly in pseudowhors of 3, broadly elliptic to ovate, 10-55 by 9-25 mm, acute, base attenuate, laxly short-hairy, ciliolate, 0.5-1 cm petioled. Racemes terminal or in a fork, including the peduncle 3-7.5 cm; bracts and bracteoles early caducous. Flowers c. 1.5-2 mm long, white or rosa sepals. Sepals blunt, the alate obovate, 5-nerved. Upper petals oblong, about as long as the keel; keel with 2 broad 2-tipped appendages. Filaments free for 1/4-1/2, hairy along the upper suture. Ovary obcordate; style curved and widened in apical half, obliquely truncate apically. Capsule asymmetric, broadly obcordate, c. 2.5 by 3.5 mm, provided with 2 unequal cross-veined wings. Seed ± ellipsoid, tuberculatc, shortly hairy, at micropylar side with a minute oblique appendage covered by a rather small, obliquely lobed aril, at chalazal side with a minute appendage.

Distr. Burma, Thailand; in Malesia: Malay Peninsula (Langkawi ls.).

Ecol. Apparently restricted to limestone rocks. In Langkawi at very low altitude, in Southeast Asian mainland ascending to 2000 m.


Herb up to 25 cm. Stem glabrous, somewhat ribbed, towards apex trichotomously branched. Leaves ovate to elliptic, 6-55 by 4-30 mm, acute, base attenuate, laxly short-hairy, ciliolate, 0.5-1.5 cm petioled. Racemes terminal or in a fork, including the peduncle 1.5-14 cm; bracts and bracteoles early caducous. Flowers c. 3 mm long, glabrous, orange-yellow to bright yellow. Outer sepals short-mucronate, alae broadly obovate, rounded, 3-nerved. Upper petals oblong, slightly longer than the keel; keel with 2 rounded appendages. Filaments free for 1/4-1/2, Ovary obcordate, the upper cell smaller; style curved and widened in apical half, obliquely truncate apically. Capsule asymmetric, broadly obcordate, c. 2.5 by 3.5 mm, provided with 2 unequal cross-veined wings. Seed ± ellipsoid, tuberculatc, shortly hairy, at micropylar side with a minute oblique appendage covered by a rather small, obliquely lobed aril, at chalazal side with a minute appendage.

Distr. Burma, Thailand; in Malesia: Malay Peninsula (Langkawi ls.).

Ecol. Apparently restricted to limestone rocks. In Langkawi at very low altitude, in Southeast Asian mainland ascending to 2000 m.
Fig. 1. Polygala tatarinowii REGEL. a. Flower; b. upper sepal; c. ala; d. keel enveloping staminal tube, at right one petal; e. staminal tube laid open; f. pistil; g. fruit; h. seed. — P. malesiana ADEMA. i. Flower; j. fruit; k. seed, lateral and ventral view. All × 15. — P. cardiocarpa KURZ. l. Flower; m. fruit; n. seed. All × 10 (a–h Ramos & Edaño BS 40317, i–k Jensen 169, l–n Curtis 3686).
Note. Similar to *P. furcata* Royle from N. India, Thailand and S. China, especially in the seed. The latter has narrowly winged capsules without prominent venation.

2. Section Melchiora (Steen.) Meijden, *comb. nov.*


Liana. *Flowers* in short axillary racemes. Lateral *sepals* (alae) caducous before fruit-setting, other sepals persistent below the fruit. *Keel* inapplicable. Disk indistinct, annular, slightly sunken in apex of pedicel, at upper side slightly protruding. *Ovary* apically elongated into a sterile part; style articulate with the ovary, curved in apical half, apically slightly 2-horned, stigma elliptic, terminal. *Capsule* much elongated, unwinged. *Seed* at micropylar and chalazal side with small appendages, completely set with hairs at least as long as the seed.

For distribution, ecology and taxonomy see the species.


— *Bredemeyera papuana* Steen. Acta Bot. Neerl. 17 (1968) 380. — Fig. 2.

Liana, glabrous in all parts except sepals and seed. Twigs slightly angular. *Leaves* obovate-oblong to obovate-lanceolate, rarely lanceolate, c. 3.5–8.5 by 1.5–3 cm, shortly acuminate, gradually attenuate at base, nerves c. 5–7 pairs, 0.5–1.5 cm petaled. *Racemes* axillary, 1 or 2 together, including the peduncle 2–6 cm long. *Bracts* and bracteoles persistent (?). *Flowers* 4.5–6.5 mm long, white with red keel, on 3–5 mm long pedicels. *Sepals* adnate over 0.5–1 mm to the petals, ± orbicular shortly ciliate, the alae broadly obovate. *Upper petals* obliquely obovate to oblong; keel emarginate. *Filaments* halfway free. *Ovary* obovate, apically with a 1 mm long sterile part. *Capsule* obovate-linear, c. 18–22 by 2–2.5 mm, shortly acuminate at apex, gradually narrowed towards base, unwinged. *Seed* 5–7 by c. 1 mm, completely covered by white silky hairs c. 1.5 cm long.


*Ecol.* Thin vine in disturbed forest below 300 m.

*Note.* Recent Australian authors (Thompson, Fl. New South Wales 112, 1978, 2; Pedley, Austrobaileya 2, 1984, 7) claimed that this species belongs to the genus *Comesperma*. They agree with van Steenis (i.c.) that *Comesperma* differs from the South American genus *Bredemeyera* in a single character; in the latter the carinal appendage bears the coma-hairs; in *Comesperma* the coma-hairs are present all over the seed or in two rows. It is dubious whether other differences exist. However, it is uncertain whether *Comesperma* itself is a good genus. Some *Comesperma* species (viz. those of sect. *Prosthemosperma* F.v.N. Pl. Vict. 1862, 186) have no coma-hairs and no elongated capsule. *Comesperma* can only be upheld if it could be proven that this is a reversion (by reduction) of the evolution. If, however, these 'abnormal' *Comesperma* species represent the primitive character of fruit and seed, the genus cannot be upheld against *Polygala*. Thus far this important question has been neglected. On the other hand it should be noted that two species of *Polygala* sect. *Chamaebuxus* (P. wattersii Hance and *P. mariesii* Hemsley, both from China) have 'typical' *Comesperma* fruits and seeds, but definitely do not belong to this group as can be demonstrated by the differences in floral characters. Thus there is good reason to assume that *Comesperma* should be merged into *Polygala*. The same may be true for *Bredemeyera*, but the present state of knowledge on this genus is still incomplete. In view of the weak differences of *Bredemeyera* and *Comesperma* with *Polygala*, there is no good reason to combine both (under *Bredemeyera*) as van Steenis (i.c.) proposed. As a consequence *Bredemeyera papuana* is best considered for the present to be a species of *Polygala*.

The affinity of *P. papuana* with the typical representatives of *Comesperma* is unclear. Surprisingly, Pedley (i.c.) dismissed the difference in the calyx as 'rather trivial', whereas Cho Dat used this character as the main one for his subdivision of the genus *Polygala*. As far as I am aware only one other species (*P. acicularis* Oliv. from tropical Africa) has caducous alae and persistent sepals. At present it seems better to keep *P. papuana* in a separate section, separate from *Comesperma* when considered as a section from *Polygala*. 
Fig. 2. Polygala papuana (Steen.) Meijden. a. Habit, × 0.66; b. flower; c. lateral petal; d. upper petal; e. ditto; f. keel; g. stamens; all × 4; h. anther, × 16; i. ovary and style, × 4; j. young fruit, k. ripe fruit; × 1.3; l. seed, × 2.5 (a, e, j–l Docters van Leeuwen 10387, b–d, f–i Ledermann 9395).
3. Section Chamaebuxus


Little-branched shrubs or small trees up to 6 m high, or low chamaephytes with woody base, sometimes very spiny. Nodal glands sometimes present. Inflorescences mostly extra-axillary and unbranched, raceme-like, rarely branched, or very short, 1-2-flowered and axillary. Flowers mostly turned upside-down. Sepals caducous before fruit-setting, the adaxial one saccate. Keel with 2 fleshy, not or little-incised, rarely with strongly incised appendages. Disk annular or consisting of a single lobe. Style straight or curved in apical half, apically obliquely 2-fid, the apical lobe sterile, the stigmatic lobe subapical. Capsule about as wide as long or didymous, or sometimes (not in Mal.) spathulate, unwinged or narrowly winged. Seed at micropylar side with a short curved appendage and from there usually with a distinct, unlobed aril, at chalazal side inapplicable but chalazal area often slightly protruding; (sub)glabrous or (not in Mal.) completely covered with hairs at least twice as long as the seed.


Fig. 3. Polygala oreotrephes BURTT. a. Capsule; b. seed. — P. sumatrana MIQ. c. Capsule; d. seeds. — P. venenosa JUSS. ex POIR. e. Capsule; f. seeds. — P. aritlata BUCH.-HAM. ex D. DON. g. Capsule; h. seeds. All x5 (a, b MAXWELL 78-320, b, c MORLEY 437, e, f PNH 117264, g, h MAXWELL 74-782).
Flora Malesiana [ser. 1, vol. 10]

As. Soc. 14 (1936) 347; Hend. Mal. Nat. J. 4 (1949) 30, f. 18. — Fig. 3a, b.

Erect, simple or branched shrub, 30–90 cm high. Twigs slightly angular, (sub)glabrous. Leaves oblong to lanceolate, 5–16 by 1–5 cm, acuminate or cuspidate, base attenuate, glabrous to hairy, chartaceous, petioled (petiole 0.5–2 cm). Racemes terminal, 1–4 together, erect, including the peduncle 4–16 cm, dense. Bracts and bracteoles early caducous. Flowers 5–6 mm long, white and yellow, later crimson and pink, on 1–3 mm long pedicels. Sepals rounded, usually ciliate, the abaxial one not strongly saccate, the ala elliptic to nearly orbicular. Upper petals lanceolate; keel with 2 deltoid, massive, wrinkled appendages. Filaments free for c. 1/4. Disk ± annular, abaxially protruding backwards. Ovary ± quadrangular with rounded edges; style straight or with slightly recurved apex, subapically at inner side with a knob-like stigmatic appendage and there laterally with 2 triangular, wing-like appendages. Capsule ± didymous, c. 7 by 12 mm, winged, with faintly protruding concentric nerves, coriaceous, purple, glabrous. Seed elliptic or orbicular, at micropylar side with a small appendage, black, glabrous, (nearly) completely covered by the smooth, orange to scarlet aril, the slightly protruding calaza and the raphe distinctly visible.

Distr. Malesia: Malay Peninsula and Borneo (Sarawak: Murud), apparently very rare in the latter locality.

Ecol. Mountains, 1100–2500 m.


Erect, dichotomously branched small shrub. Twigs slightly angular, thinly strigose, glabrescent, at the nodes often with small, triangular pseudostipules. Leaves oblong to linear-lanceolate, 4.5–15 by 1.5–3.5 cm, cuspidate, base attenuate, thinly strigose, up to 2 cm petioled. Racemes terminal between 2 opposite twigs or leaves, erect, later pendulous, including the peduncle 3.5–7.5 cm, lax. Bracts and bracteoles early caducous. Flowers c. 15 mm long, white to pink and later violet, with yolk-yellow appendages on the keel, on 4–11 mm long pedicels. Sepals rounded, ciliate, the ala obovate-oblong. Upper petals lanceolate; keel with 2 large fleshy entire appendages. Filaments free for c. 1/4. Disk annular, abaxially protruding. Ovary ± quadrangular with rounded edges; style straight in basal half, in upper half falcate, apically weakly 2-fid, at inner side with the stigmatic lobe. Capsule broadly obovate, c. 9–10 by 11–14 mm, winged (wings not transversely veined), without protruding nerves, coriaceous, very densely covered by white, orbicular, flat papillae. Seed elliptic, at micropylar side with a small appendage, reddish brown, glabrous, up to about halfway covered by the smooth aril, the slightly protruding calaza and the raphe distinctly visible.


Erect, sparingly dichotomously branched shrub or small tree, 0.7–5 m high. Twigs terete, (sub)glabrous, fleshy or not, at the nodes sometimes with small pseudostipules. Leaves elliptic to lanceolate, 7–33 by 4–13 cm, acuminate, base attenuate, thinly strigose to glabrous, glaucescent beneath, 0.5–3 cm petioled. Racemes extra-axillary, mostly reflexed from the base, including the peduncle 2–26 (50) cm long, lax to dense; rachis straight and thick or thin and flexuous. Bracts and bracteoles early caducous. Flowers 13–20 mm long, upper petals white or magenta and turning violet, crest yellow and turning...
dark violet to brownish, on 6–15(–20) mm long pedicels. *Sepals* white or yellowish, rounded, ciliate, alae ovobate. Upper *petals* lanceolate; keel with 2 large massive, wrinkled appendages. *Filaments* free for about one third. Disk annular, sometimes abaxially protruding. *Ovary* obreniform to orbicular; style straight in lower half, in upper half falcate, apically weakly 2-fid, at inner side with the stigmatic lobe. *Capsule* obreniform to didymous, 5–8 by 7.5–12 mm, winged or unwinged, with more or less protruding concentric ribs, coriaceous, greenish purple to deep purple, glabrous. *Seeds* elliptic, at micro-pylyar side with a small appendage, purplish black, glabrous, to halfway or nearly completely covered by the smooth, orange to scarlet aril, the slightly protruding chalaza and the raphe distinctly visible.

**Distr.** *Malesia*: Peninsular Thailand (Pattani), Malay Peninsula, Sumatra, Java, Borneo, Philippines.

**Ecol.** Undershrub or tree in forests, 0–2400 m.

**Taxon.** Van Steenis (1972) distinguished two ecological races: *ssp. pulchra*, with rather small leaves, non-fleshy stems, and lax inflorescence with thin, flexuous axes, and *ssp. venenosa* with fleshy leaves and stems, dense inflorescence with thick, straight axes, the first occurring in submontane altitudes on stony, well-drained places in light forest on slopes and ridges, the latter in the depth of primary and secondary forest in deep moist humus, stream valleys and riparian. Also in Java intermediate forms occur. Outside Java the distinction between both types is less distinct or even obscure.


Erect, dichotomously branched shrub or small tree, 1.5–6 m high. Twigs terete, glabrescent. *Leaves* oblong to ovate-lanceolate, 5–20 by 1.5–8 cm, cuspitate, base attenuate to obtuse, thinly hairy to glabrous, beneath somewhat glaucescent, to 1.5 cm petiolate. *Racemes* terminal, axillary or extra-axillary, erect or rarely pendulous at apex, including the 6–12.5 cm long peduncle. Bracts and bracteoles early caducous. *Flowers* 11–20 mm long, yellow, turning orange and red, on 2–7(–9) mm long pedicels. *Sepals* rounded, ciliate, alae ovobate. Upper *petals* lanceolate, keel with 2 much-incised appendages. *Filaments* free for one third. Disk annular. *Ovary* orbicular, sometimes ciliate; style straight in lower half, curved in upper half, apically weakly 2-fid, at inner side with the stigmatic lobe. *Capsule* ± orbicular or somewhat asymmetric, 8–10 by 12–15 mm winged, with prominent concentric ribs, coriaceous, glabrous. *Seeds* globular, at micro-pylyar side with a distinct appendage, black, glabrous or sparsely hairy up to halfway covered by an irregularly lobed and apically rather strongly projecting aril, the little protruding chalaza and the raphe distinctly visible.

**Distr.** India and Sri Lanka, Nepal, Bhutan, S. China, Hongkong, Burma, Thailand, Indochina; in *Malesia*: Philippines (Palawan; see Hansen, l.c.).

**Ecol.** Undershrub in forests from 1000–3000 m, in Palawan at 850 m.

**Note.** *Polygala trichocolpa* Chodat with about the same distribution (but not yet found in Malesia) differs in the branched inflorescence and in the typical, galeate (helm-shaped) aril. *Polygala karvensium* Kurz, from Burma to Vietnam and Yunnan, differs in the geniculate style which is nearly recurved in the apical half and is strongly thickened subapically, and in the unribbed capsule.

4. Section Polygala


Little- to much-branched annuals to perennial herbs or low chamaephytes with woody base, or (not in Mal.) shrubs or small trees, sometimes nearly aphyllous. *Inflorescences* raceme-like, ter-
Fig. 4. Polygala javana DC. Habit, ×0.7 (Teijsmann s.n.).
minal, (supra-)axillary, or in the forks, unbranched, many or few-flowered. Sepals persistent in fruit, the lowest pair sometimes (not in Mal.) partly or wholly connate, or very rarely (not in Mal.) all or only the lateral ones caducous before fruit-setting. Keel with usually much-incised appendages or rarely (not in Mal.) inapplicable. Disk apparently absent. Style and stigma variously shaped. Capsule mostly more or less orbicular, sometimes elongated, usually narrowly or sometimes widely winged. Seeds various, usually at micropylar side with a 2- or 3-lobed aril, sometimes (not in Mal.) with a translucent appendage along the raphe to the chalazal side; glabrous or hairy, rarely set with very long hairs, in the Malesian spp. at chalazal side inapplicable.


Perennial, erect, branched herb, up to 80 cm high. Stem terete, becoming woody at base, set with short curved hairs. Leaves mostly obovate-oblong, 5–35 by 2–12 mm, subsessile, mucronate, with recurved margins shortly hairy at both sides, in transmitted light finely punctate-dotted. Racemes supra-axillary, often leaf-opposed, the free part 2–8 cm long. Bracts persistent, ± rhomboid, 1–2 mm long, hairy. Flowers 8–10 mm long, with purple crista and yellowish alae. Sepals mucronate, hairy on both sides, ciliate, the alae broadly ovate, flabellate-veined. Upper petals oblong, hairy inside in basal half; keel auriculate and there sometimes hairy, with 2 much-incised appendages. Filaments free for 1/8–1/3. Ovary ± quadrangular with rounded sides, apically notched, hairy all over; style straight in lower half, curved in upper half, subapically at inner side with 2 small, spaced, stigmatic lobes, slightly widened between the lobes. Capsule smaller than the alae, ± quadrangular, apically notched, with a narrow, membranous, veined margin, hairy. Seeds ± globular, at micropylar side with an unequally 3-lobed aril, black, hairy.

Dist. Sri Lanka and S. India; in Malesia: Java

Fig. 5. Polygala javana DC. a. Flower; b. upper sepal; c. ala; all ×4; d. keel enveloping staminal tube, at right one petal; e. opened staminal tube; f. pistil; all ×6; g. fruit, ×4; h. seed, ×6 (u–f Feßmann s.n., g. H. Backer 36532).
(from Semarang eastwards, incl. Madura & Kangean Is.), Lesser Sunda Islands (Bali, Lombok, Sumba, Sumbawa, Flores, Timor).

Ecol. Characteristic for areas subject to a strong dry season, in teak forests, between grass, several times on limestone, below 250 m, once at 700 m in Sumba.


Perennial, prostrate or ascending, branched undershrub 10-20 cm high, mostly developing a woody, rhizomatous, erect root crown or stem base. Stem terete, becoming woody at the base, set with short curved hairs. Leaves ovate to elliptic, the lower ones proportionally broadest, 5-15 by 3-8 mm, sub-sessile, acute, with slightly recurved margin, prominent-reticulate veined, mostly minutely hairy on at least midrib and margin, in transmitted light faintly

Fig. 6. Polygala japonica Houtt. a. Flower; b. upper sepal; c. ala; d. keel enveloping staminal tube, at right one petal; e. opened staminal tube; f. pistil; g. fruit; h. seed. All ×7 (a–f SHAW MAYER s.n.; g, h BORGGMANN 326).
Polygalaceae


Note. Closely allied to P. sibirica L., which occurs from Central Europe to Central China and NE. India (Khasya). This differs in the following characters: leaves mostly longer and narrower, ovary orbicular and ciliate, stigmas closer together, capsule oblong with narrower wing.

Ecol. Roadsides, grasslands, trodden ground in the mountains, 1200–2600 m; in Japan from 0–1500 (–2000) m.

Dist. NE. India, Burma, Sri Lanka, Indochina, China, Japan, Korea and E. Siberia, also in the Ryukyu Is. and Taiwan, in E. Australia southwards to NE. Victoria; in Malesia: Philippines (Luzon, Mindoro) and New Guinea.

Fig. 7. Polygala persicariaefolia DC. a. Flower; b. upper sepal; c. ala; d. keel enveloping staminal tube, at right one petal; e. opened staminal tube; f. pistil; g. fruit; h. seed. All × 7.5 (a–f PRINGGO ATAMOXO 123; g, h IHOFT 32).

Annual, erect, mostly branched herb, up to 70 cm high. Stem terete, set with short curved hairs. Leaves lanceolate to linear-lanceolate, 15–50 by 3–10 mm, shortly petiolated, mucronate, with flat margin, thin, shortly hairy to (sub)glabrous, in transmitted light finely punctate-dotted. Racemes in the forks and terminal on the lateral branches, 1–10 cm long, rather few-flowered. Bracts persistent, lanceolate, c. 1 mm long, shortly hairy. Flowers 6–7 mm long, light violet turning purple, with whitish alae. Sepals blunt, ciliolate or the alae sometimes completely glabrous, alae broadly elliptic to ± orbicular, 5-veined. Upper petals oblong, hairy inside in basal half; keel auriculate and sometimes hairy, with 2 much-incised appendages. Filaments free for 1/4–1/2. Ovary elliptic, ciliate; style straight in lower half, curved in upper half, subapically at inner side with 2 closely approximate stigmatic lobes. Capsule somewhat smaller than the alae, c. 5 mm long, broadly elliptic, emarginate, with a rather narrow, veined, sparsely ciliate wing widening apically. Seeds oblong, at micropylar side with a small, unequally 3-lobed aril, black, hairy.

Distr. Africa (Angola via South Africa to Ethiopia), SE. Asia (India, Upper Burma, Thailand), S. China (Yunnan), also in Australia (N. Queensland); in Malesia: Sumatra (northern half), E. Java (Mt Idjen), Lesser Sunda Islands (Bali, Lombok, Flores, Timor, Alor), Philippines (Luzon) and throughout New Guinea.

Ecot. In waste and often arid or stony places, mainly in grasslands, along roadsides, on old lava-streams, etc., (300–)500–1500(–1800) m.


Annual, erect, little-branched herb up to 80 cm high. Stem ribbed, glabrous or upwards set with short, curved hairs. Leaves proportionally few, linear to linear-lanceolate, the lowest ones slightly broader, 10–55 by 1–6 mm, subsessile, acute, with recurved margins, (sub)glabrous, 1-nerved. Racemes mostly terminal, 2–20 cm long, dense. Bracts and bracteoles early caducous. Flowers 3–4, in fruit up to 5 mm long (including the alae), ilac, turning purple, when dry whitish. Outer sepals acute, glabrous to ciliate, alae elliptic to obovate, rounded, 3-nerved, glabrous. Upper petals oblong, glabrous or rarely hairy inside in basal half; keel not auriculate, glabrous or rarely sparsely hairy outside, apically with 2 rather few-divided appendages. Filaments free for...
1/4–1/2. Ovary elliptic, glabrous; style strongly curved, (sub)apically at inner side with a single, relatively large, knob-shaped stigmatic lobe. Capsule shorter than the alae, broadly elliptic to obovate, c. 3–3.5 mm long, emarginate, with a narrow, veined, glabrous wing widening apically. Seeds oblong, at micropylar side with a small, unequally 3-lobed aril, dark, hairy.

Distr. Sri Lanka, India, Nepal, Thailand, Indo-China, China, Ryukyu Is. and northern Australia; in Malesia: N. Sumatra, N. Borneo, SW. Celebes, Philippines (Luzon), Lesser Sunda Islands (Sumba), Moluccas (Kai Is.), and throughout New Guinea.

Ecol. Mainly grasslands (often burned), 0–1400 m; obviously with a preference for areas subject to a dry season.

Note. The type specimen, collected by Commerson (P, Fl) is said to hail from Java, but this is certainly an error, cf. Fl. Males. 1, 1 (1950) xxix.


Annual, erect, mostly much-branched herb, up to 50 cm high. Stem terete, set with numerous small shortly stalked glands. Leaves lanceolate to linear-lanceolate, 5–20 by 1–4 mm, shortly petioled, acute, margin slightly recurved, (sub)glabrous, 1-nerved, the lowest ones in one or more pseudowhorls of 4–5. Racemes all terminal, 2–15 cm long. Bracts and bracteoles early caducous. Flowers whitish or often purple tinged, 1.5–2 mm long, glabrous. Sepals lanceolate, obtuse, the alae weakly 3-nerved. Upper petals lanceolate; keel not auriculate, with 2 ± 6-fid appendages. Filaments free for ± 1/8. Ovary ± orbicular; style straight to near apex, there curved and strongly widened in an asymmetrical, wide cup, terminally with a hair tuft, diametrically opposed to this with the stigmatic lobe. Capsule somewhat longer than the alae, ± elliptic, c. 2 mm long, slightly notched, not winged. Seeds oblong, at micropylar side with a one-sided, deeply 2-fid aril, black, hairy.

Distr. Native in tropical America, from Brazil to Mexico. Introduced in Central tropical Africa (PAIVA, l.c.) and Indo-Australia. In Malesia unintentionally introduced as early as 1845 or 1846.
(Backer, 1930) and since then abundantly naturalized throughout. Also in NE. Australia, Taiwan, and S. Japan (Okinawa), further widespread in Melanesia (Bismarcks, Solomons, New Hebrides, New Caledonia), Micronesia (Carolines), Polynesia (Fiji, Samoa, Marquesas, and recently in Hawaii).

Ec. Waste places and fields, often abundant, on different soil types, avoiding the driest areas, 0–2250 m.


Annual, erect or ascending, branched herb up to 15 cm high. Stem terete, set with long erect and short curved hairs. Leaves linear to linear-lanceolate, 5–15 by c. 1 mm, subsessile, mucronate, with recurved margin, sparingly set with long hairs, 1-nerved. Racemes supra-axillary, usually not more than 1 cm long, very dense. Bracts persistent, lanceolate, c. 1 mm long, hairy. Flowers 4–5 mm long, whitish with green alae. Sepals lanceolate, acuminate, hairy, the alae asymmetric, 3-nerved. Upper petals spatulate to oblong, hairy inside in basal half; keel auriculate, with 2 little-incised appendages. Filaments free for 1/3, the staminal tube adaxially split for 1/4 into two bundles of 4 filaments. Ovary asymmetrically quad-rangular, patent hairy; style straight in basal half, curved in upper half, apically obliquely 2-fid, the upper part sterile, the stigmatic lobe situated at inner side. Capsule much shorter but somewhat wider than the alae, c. 2–2.5 mm long, asymmetrically quad-rangular, deeply notched apically, narrowly winged, set with stiff, long hairs. Seeds ovoid, at micropylar side with an unequally 3-lobed aril, black, densely set with rather long appressed hairs.

Distr. Australia (Northern Territory; Queensland: Thursday 1., Brisbane); in Malesia: SE. Moluccas, Aru Is. (Trangan), New Guinea (Cyclops Mts: 1 coll.; Papua: W. Distr., 1 coll.).

Ec. Sandy savannah in hilly country, a few metres above sea-level.

Note. Similar to the Australian species P. eterocephala Benth.; its affinity with that species should be further examined.


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Fig. 10. Polygala exsquarrosa Adema. a. Habit, × 0.5; b. leaf, × 2; c. flower, one ala cut away; d. upper sepal; e. ala; f. keel enveloping staminal tube, at right one petal; g. opened staminal tube; h. pistil; i. fruit; j. seed. All × 10 (Buwalda 5344).

Fig. 11.

Annual, erect to prostrate, branched herb up to 50 (70) cm high. Stem terete, set with short curved hairs. Leaves elliptic to lanceolate, 2–20 by 1–7 mm, subsessile, acute to mucronate, with slightly recurved margin, sparsely hairy to subglabrous, 1-nerved. Racemes supra-axillary, up to 1 cm long, few-flowered and cluster-like. Bracts persistent, minute, acute, ciliate. Flowers c. 2.5–3 (–3.5) mm long, light to deep blue, turning violet, alae green and often partly red. Sepals lanceolate, acuminate, ciliate, alae asymmetric, 5-nerved. Upper petals ± spathulate, emarginate, shorter than the keel; keel auriculate, at apex with 2 much-increased appendages. Staminal tube split halfway, with 2 single filaments and 2 bundles of 3 fully connate filaments with sessile anthers. Ovary broadly elliptic, ciliate and sometimes minutely hairy; style curved in apical half, apically widened, stunted, on one side with a sterile, more or less pronounced tip, the other side (situated at inner side) with a more or less pronounced stigmatic lobe. Capsule shorter but wider than the alae, c. 1.5 mm long, almost orbicular, very narrowly winged, ciliolate, further glabrous to sparsely hairy. Seeds oblong, at micropylar side with an unequally 3-lobed aril, black, hairy.

Distr. Pakistan, Sri Lanka, India, Bangla Desh, Thailand, Indochina, China (and Hongkong), Taiwan, Ryukyu Is., Micronesia (Ponape) and northern Australia; in Malesia: Sumatra, Malay Peninsula (Johore), Java, Lesser Sunda Islands (Sumba), Celebes, Philippines (Mindoro, Luzon, Mindanao), Moluccas (Ceram, Ambon), New Guinea. Ecol. Along roadsides, in grasslands, in waste places, 0–750 (–1800 m).

Notes. Unfortunately Mukherjee’s revision of the Indian and Burmese species of *Polygala* has been neglected by ADEMA, and following him, by subsequent authors. As a result it was not until BURTT (l.c.) showed that MERRILL (l.c.) correctly assigned the name *P. chinensis* L. to the next species, that that name was commonly used for the present species. Based on ADEMA’s revision (1966), BURTT chose the name *P. arvensis* Willd. for it. Examination of the type material of both *P. arvensis* Willd. and *P. telephoides* Willd. (in B) revealed, however, that those names also should be attributed to the next species. As *P. brachystachya* DC. (the name which MUKHERJEE chose) is a later homonym of POIRET’S name, it cannot be accepted, thus preventing future confusion with *P. brachystachya* BLUME, which is a synonym of *P. glaucoides* L. As the type of *P. polifolia* (in PRC, kindly examined by Dr. J. CHRIFF) certainly belongs to the present species, this name must be chosen as the correct one.

The synonymy of this and the following species is very complicated, and must remain partly unclear, not only for the name *chinensis*, but likewise for the names *arvensis*, *brachystachya*, *elongata*, *lurinifolia*, and *telephoides*. ADEMA (l.c.) did not succeed in unraveling this complex synonymy, and added a new series of mistakes in this matter.

The only sheet from Java is an old specimen from Krawang without indication of the collector; besides
it has monstrous flowers. It is suspected to be mislocalized because no later collections have been made of this species in Java.


Perennial, erect or ascending, mostly branched herb or undershrub up to 75 cm high, becoming woody at base, with a thickened root crown. Stem terete, becoming woody at base, set with curved short hairs and with straight long hairs. Leaves very variable, from broadly elliptic to lanceolate, 5–65 by 2–20 mm, shortly petioled, acute to mucronate, with slightly recurved margin, sparsely shortly hairy, few-nerved. Racemes supra-axillary, up to 1.5 cm long, few-flowered and cluster-like. Bracts caducous before or during anthesis, minute, lanceolate, ciliate. Flowers 4.5 mm long, white with green alae. Sepals lanceolate, acuminate and with a long mucro, ciliate, alae asymmetric, 5-nerved. Upper petals spathulate, about as long as the keel, inside hairy in basal half; keel more or less auriculate, with 2 bundles of filiform appendages. Filaments ± halfway free. Ovary orbicular, emarginate, ciliate; style strongly curved in the apical half, subapically strongly reflexed with the stigmatic lobe inside. Capsule shorter but somewhat wider than the alae, c. 4 by 4 mm, somewhat asymmetrically orbicular, notched, with a narrow distinctly ciliate wing. Seed ovoid, at micropylar side with an unequally 3-lobed aril, black, hairy.

Distr. NE. India to S. China, Thailand and Indo-China; in Malesia: Malay Peninsula (Penang), Sumatra, Java (very common in W. Java, much less so in Central and E. Java), Lesser Sunda Islands.

Fig. 12. Polygala chinensis LINNÉ. a. Flower; b. upper sepal; c. ala; d. keel enveloping staminal tube, at right one petal; e. opened staminal tube; f. pistil; g. fruit; h. seed. All ×7 (ADELBERT 313).
(Sumbawa, Sumba, Flores), SE. Borneo and Sarawak, Philippines (Luzon, Jolo, Mindanao), New Guinea.

Ecot. Waste places, rubber estates, grasslands, roadsides, largely restricted to everwet areas, from 0–1300 m, in Java several times reported from limestone.

Notes. The name *P. chinensis* L. has been misapplied in nearly all cases, most often for *P. polifolia*, but also for *P. triflora* and *P. glaucoidea*. Therefore, Burtt (1972) rejected the name for the present species, addressing it as *P. glomerata*. I cannot follow this illegal procedure.

For remarks on synonymy, see under *15. P. polifolia*.


Annual, erect or ascending, little-branched herb up to 40 cm high. Stem terete, glabrous. Leaves linear-lanceolate, 7–20 by 1–2 mm, subsessile, acute, mucronate, with slightly recurved margin, glabrous, 1-nerved. *Racemes* supra-axillary, the free part 5–17 cm long. Bracts persistent, lanceolate, minute, glabrous. *Flowers* c. 4 mm long, pale yellow to red with green alae. *Sepals* lanceolate, mucronate, apically sparsely ciliate, alae asymmetric, 3-nerved. Upper *petals* spatulate, somewhat longer than the keel, inside hairy in lower half, keel auriculate and there hairy, with two bundles of much-incised appendages. *Staminal tube* split halfway, with 2 partly connate filaments and 2 bundles of 3 largely connate filaments. *Ovary* elliptic, notched, (sub)glabrous; style strongly curved in apical half, subapically strongly recurved with the stigmatic lobe inside and with 2 wings, one below the stigma at lateral side, one median at the outer side of the curve. *Capsule* somewhat shorter than the alae, elliptic, strongly notched, c. 3.5 mm long, narrowly winged, (sub)glabrous. *Seeds* oblong to cylindrical, at micropylar side unequally shortly 3-lobed, black, hairy.

Distr. India (Deccan Peninsula; apparently rare) and Australia (N. Queensland); in *Malesia*: Lesser Sunda Islands (Flores).

Ecot. In open grassland obviously with a preference for areas subject to a dry season, 0–500 m.

Fig. 13. *Polygala wightiana* W. & A. a. Flower; b. upper sepal; c. ala; d. keel enveloping staminal tube, at right one petal; e. opened staminal tube; f. pistil; g. fruit; h. seed. All × 10 (Wallich 4190).

Annual, erect to ascending, little-branched herb up to 70 cm high. Stem terete, set with short curved and few long erect hairs. *Leaves* lanceolate to linear-lanceolate, 15–55 by 2–10 mm, subsessile, mucronate, with recurved margin, more or less hairy, 1-nerved or with very weak secondary nerves. *Racemes* (supra-)axillary, shorter to much longer than the leaves, the free part 1–10 cm long. Bracts persistent, minute, acute, hairy. *Flowers* 5–7 mm long, bright green or bluish, turning pinkish to purple with green alae. *Outer sepals* lanceolate, acute, shortly hairy, the alae broadly ovate, rounded, mucronate, many-nerved, hairy. *Upper petals* elliptic-spathulate, somewhat shorter than the keel; keel not auriculate, with 2 bundles of much incised short appendages. *Filaments* halfway free. *Ovary* ± quadrangular, notched at both ends, ciliate; style strongly curved in apical half, subapically strongly reflexed with the stigmatic lobe inside and with a small tooth at the outer side of the curve. *Capsule* about as long as the alae, somewhat larger than broad to somewhat broader than long, c. 5 by 5–6 mm, deeply emarginate, broadly winged, the wings 1–2 mm wide and thinly veined and with patent ciliate hairs, fruit further glabrous. *Seeds* ellipsoid, at micropylar side with an unequally 3-lobed aril, black, hairy.

**Distr.** Australia (Northern Territory, Queensland, Thursday Island.); in *Malesia*: Papua New Guinea (W. Distr.: 3 coll.).

**Ecol.** Open savannah woodland and grassland at low altitude.

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Erect to prostrate, usually much-branched herb, sometimes woody at base, up to 40 cm high. Stem terete, set with short, curved hairs. Leaves obovate-oblong to lanceolate, 3–45 by 1–8 mm, subsessile, mucronate, with recurved margin, shortly hairy, usually 1-nerved. Racemes usually supra-axillary, the free part (0.5–)3–5(–10) cm long. Bracts usually persistent, minute, ciliate. Flowers (2.5–)3–4.5(–5) mm long, yellow with green and partly red alae. Sepals lanceolate, acuminate and with a short mucro, ciliate, alae asymmetric, 5-nerved. Upper petals slightly longer than to ± as long as the keel, spatulate, inside hairy in basal half; keel with 2 bundles of shortly incised appendages. Ovary ± orbicular, notched, ciliate with crissate hairs; style strongly curved in apical part, subapically strongly reflexed with the stigmatic lobe inside. Capsule shorter than the alae, usually symmetric, broadly elliptic, 3–3.5 by 2.5–3 mm, notched, narrowly winged, the wings with short curved hairs only. Seeds ellipsoid, at micropylar side with an unequally 3-lobed aril, black, hairy.

Distr. Sri Lanka, continental SE. Asia, N. Australia; in Malesia: W. Sumatra, Malay Peninsula (Singapore), Java, Lesser Sunda Islands (Timor), Celebes.

Ecol. In grassy places at low altitudes, probably in drier places than the next species.

Notes. This and the next species are rather similar. Adema (l.c.), unaware of the identity of Linnaeus’ *P. glaucoideas* and *P. triflora*, unfortunately interchanged their names, and furthermore mixed the material of both species. After re-examination of the material of both, it appeared that their ranges are largely exclusive (although I have seen less material than Adema). Literature citation and distribution area as cited above must be somewhat inaccurate.

For additional remarks on the synonymy, see the note under 15. *P. polifolia*.


Fig. 15. *Polygala glaucoideas* Linn. a. Flower, one ala cut away; b. upper sepal; c. ala; d. keel enveloping staminal tube, at right one petal; e. opened staminal tube; f. pistil; g. fruit; h. seed. All × 10 (FLNIX BS 26016).
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Fig. 16. Polygala triflora Linne. a. Flower; b. upper sepal; c. ala; d. keel enveloping staminal tube, at right one petal; e. opened staminal tube; f. pistil; all ×10; g. fruit; h. seed; both ×10 (Backer 23143).


Erect to prostrate, usually much-branched herb, sometimes woody at base, up to 40 cm high. Stem terete, set with short, curved hairs. Leaves lanceolate to linear-lanceolate, 5–50 by 1–5 mm, subsessile, mucronate, with recurved margins, shortly hairy, 1-nerved. Racemes usually supra-axillary, the free part 0.5–2 cm long. Bracts usually persistent, minute, ciliate. Flowers (3.5–)4–5 mm long, yellow or dull orange, with green and partly red alae. Sepals lanceolate, acuminate and with a short mucro, ciliate, alae asymmetric, 5-nerved. Upper petals slightly to distinctly shorter than the keel, spathulate, inside hairy in basal half; keel with 2 bundles of shortly incised appendages. Ovary quadrangular with rounded edges, stiffly hairy in upper part along the margin; style strongly curved in apical part, subapically strongly reflexed with the stigmatic lobe inside. Capsule shorter than the alae, usually asymmetric, usually broadly elliptic, 3.5–4 by 2.5–3.5 mm, notched, narrowly winged, the wings with both short curved hairs as well as with long stiff hairs. Seeds ellipsoid, at micropylar side with an unequally 3-lobed aril, black, hairy.

Distr. Sri Lanka, continental SE. Asia, Australia; in Maleisia: N. Sumatra, N. Borneo, Celebes, Moluccas (Ternate), Philippines (Palawan, Luzon, Mindanao), New Guinea.

Ecol. Open, grassy places, probably in climatologically wetter places than *P. glaucoides*, 0–1200 m.

Notes. Adema (l.c.) made some mistakes with this and the preceding species; see there. He stated that its occurrence in Maleis was uncertain, until 1969 when he mentioned its occurrence from New Guinea. My revision revealed that a considerable part of the collections identified by Adema as the former species, proved to belong to the present one. As holds for the preceding species, literature citation and distribution area of *P. triflora* must be somewhat inaccurate.

A single sheet from Java (in L.) probably is wrongly labelled and collected in Sumatra.

For further notes on the synonymy, see under 15. *P. polifolia*.
2. SECURIDACA


Big lianas to straggling shrubs. Twigs terete, sometimes twisted, glabrescent, at the nodes often with a pair of slightly protruding glands. Leaves alternate or distichous, peltioed. Inflorescences raceme-like or usually paniculate, (supra-)axillary or terminal, at the nodes usually with a pair of protruding glands; bracts and bracteoles early caducous. Sepals 5, unequal, caducous before fruit-setting, ciliate, the lateral ones (alaie) at least twice as large as the other ones and petaloid, unguiculate, auriculate. Petals 3, halfway adnate to the staminal tube or with an additional pair of reduced petals; upper petals spathulate, lower one (keel) boat-shaped, unguiculate, at apex with or rarely without a slightly 2-lobed, obliquely cup-shaped, hardly incised appendage (crest). Stamens 8, monadelphous; anthers bisporangiate by abortion of the outer microsporangia, sessile or on a free filamentous stalk, opening by an apical, oblique pore common to both cells. Disk annular, distinct after flowering. Ovary asymmetrical, 1-celled (by abortion of the second cell), 1-ovuled; style subterminal, curved in apical half, with a terminal, ± 2-lobed stigma. Fruit a samara with a coriaceous wing (wing sometimes reduced), sometimes a second reduced wing present. Seed inapplicable, glabrous, with thick cotyledons.

Disir. About 80 species, mainly in South and Central America, some in tropical Africa and in Southeast Asia and Malesia; not in Australia.
Ecél. Primary and secondary forests, along streams and in ravines, 0–1500 m.

Key to the Species

1. Flowers yellow. Staminal tube hairy inside, split in apical half, the filaments of the 2 parts connate to apex. Fruit with a second, smaller wing.

2. Keel glabrous, apically with a nearly undivided crest. Fruit (without wing) elliptic. 3. S. philippinensis

2. Keel slightly hairy inside, apically inapplicable. Fruit (without the wings) orbicular. 4. S. cristata

1. Flowers pink to deep purple. Staminal tube completely glabrous, all filaments free for 1/4. Fruit only with a single large wing.

3. Leaflet rounded to emarginate, at apex of midrib with a distinct hydathode. Vegetative parts almost glabrous. Outer sepals glabrous except for margin. Wing of fruit broadly attached to halfway, without stipe-like constriction. 2. S. atro-violaraca

3. Leaflet acute to cuspidate, without apical hydathode. Young twigs, petioles and lower side of leaves shortly hairy. Outer sepals shortly hairy. Wing of fruit narrowly attached, stipe-like constricted in basal 1/3 part. 1. S. inapplicable

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KEY TO THE SUBSPECIES

1. Greatest width of leaf halfway. Pedicel (sub)gla-
bru s .......................... a. ssp. inapplicata
1. Greatest width of leaf in basal half. Pedicel dense-
ly shortly hairy ................................ b. ssp. corynosa

a. ssp. inapplicata

Twigs with rather inconspicuous glands at the nodes. Leaves ovate to (ovate-)oblong, 5-12 by 2.5-5.5 cm, base rounded to acute, apex acute to cuspidate, above sparsely shortly hairy, beneath densely shortly hairy; petiole 3-8 mm, shortly hairy. Inflorescences branched, nodal glands indistinct. Flowers 5-7(--8) mm long, pink to deep purple, on 6-14 mm long pedicels. Sepals sparsely to densely shortly hairy, the alae about as long as the keel. Upper petals shorter than the keel, glabrous; keel apically crested, reduced lateral petals mostly present. Filaments free for 1/4. Samara basally obliquely elliptic, the wing 3-4 cm long, broadly attached to halfway, not constricted; second wing absent; fruiting pedicel up to 10 mm. Seed ovoid.

Distr. From India through Burma, S. Thailand and Nepal to China; in Malesia: Sumatra, Malay Peninsula, W. Java (very rare), Borneo.

Ecol. Rain-forests below 1000 m.


Ecol. Low and medium altitudes in rain-forest.

Note. The Philippine populations differ slightly but constantly vegetatively from the other populations. Although always separated as a distinct species, the absence of differences in flower or fruit is an argument to assume a close affinity between both taxa. In view of the replacing areas it seems appropriate to distinguish them as subspecies.


Twigs with rather inconspicuous glands at the nodes. Leaves elliptic to oblong, 5-7 by 2-4 cm, base rounded to broadly cuneate, apex emarginate to rounded, at apex of midrib with a distinct hya-
thode, glabrous to sparingly shortly hairy; petiole 4-8 mm, shortly hairy. Inflorescences raceme-like or with a few side-branches, nodal glands indistinct. Flowers 5-7 mm long, purple on 5-8 mm long, glabrous pedicels. Sepals ciliate, the alae about as long as the keel. Upper petals somewhat shorter than the keel, ciliate; keel apically crested; reduced lateral petals present. Filaments free for 1/4. Samara basally obliquely elliptic, the wing 3-4 cm long, broadly attached to halfway, not constricted; second wing absent; fruiting pedicel up to 10 mm. Seed ovoid.


Ecol. Disturbed forests on ultrabasic soil (Rids-
dale), 100-600 m.


Twigs with rather inconspicuous glands at the nodes. Leaves ovate to ovate-oblong, 4.5-6.5(-9.5) by 2.5-3.5(--4.5) cm, base rounded to broadly cu-
neate, apex acute to acuminate, nearly glabrous above, densely shortly hairy beneath; petioles c. 5 mm, shortly hairy. Inflorescences branched, nodal glands rather distinct at base of bracteoles. Flowers 5-8 mm long, yellow, on 5-9(--11) mm long shortly
hairy pedicels. 

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Hairy pedicels. *Securidaca* ciliate, the outer densely short-hairy, alae about as long as the keel, ciliate only. Upper petals about as long as the keel, usually hairy inside; keel glabrous, apically crested; reduced lateral petals usually present. Filaments hairy inside in basal part, at c. 1/4 split into two connate groups; anthers sessile. *Samara* basally elliptic, the wing 5–7.5 cm long; reduced second wing up to 2 mm wide. **Seed** oblong.

**Distr.** Malesia: Borneo (Sarawak), Celebes, Moluccas (Ambon, Buru), Philippines (Luzon, Leyte, Bohol, Negros, Panay, Mindanao, Palawan).

**Ecol.** Primary and secondary forests at low and medium altitudes (Merrill).

4. **Securidaca ecrisitata** Kassau in Fedde, Rep. 35 (1934) 160, incl. var. nitida. — *S. bracteata* var. *papuana* F.v.M. Descr. Not. Pap. Pl. 8 (1886) 41. — Fig. 17.

Twigs with rather inconspicuous glands at the nodes. Leaves ovate-oblong to ovate-lanceolate, 3.5–7(–9) by 1.5–2.5 (–3.5) cm, base rounded to broadly cuneate, apex acuminate to cuspidate, short-hairy at both sides; petioles 3–5 mm, short-hairy. Inflorescences unbranched or sometimes with few side-branches, nodal glands rather distinct at base of bracteoles. Flowers 3–5 mm long, yellow, on 5–6(–7) mm long, short-hairy pedicels. *Securidaca* ciliate, the outer shortly hairy, the alae about as long as the keel. Upper petals rather densely hairy inside in basal half, the keel slightly hairy inside basally, apically inappendiculate; reduced lateral petals present, very small. Filaments hairy at both sides in basal half, at c. 1/4 split into two connate groups; anthers sessile. Samara basally globose, the wing 3–8 cm long; second reduced wing distinct. **Seed** globose.

**Distr.** Malesia: New Guinea.

**Ecol.** Rain-forest below 1500 m.

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**Fig. 17. Securidaca ecrisitata Kassau.** a. Habit flowering plant, ×0.5; b. flower; c. keel; d. staminal tube with lateral and upper petals; e. gynoecium; f. staminal tube; all ×6; g. habit fructing plant, ×0.5 (a–f Millar NGF 9917, g Clemens 8388).
3. SALOMONIA


Small erect annual herbs with aromatic roots. Stems without nodal glands, angular with 3 transparent wings. Leaves alternate, shortly petioled or sessile, glabrous or ciliate, 1–5-nerved. Inflorescence spike-like, terminal, the axes without nodal glands, winged; bracts early caducous or sometimes persistent, bracteoles absent. Sepals 5, unequal, much smaller than the petals, connate at very base, persistent, 1-nerved. Petals 3, unequal, asymmetric, halfway adnate to the staminal tube, the upper ones halfway connate to the lower one (keel) and slightly shorter than this; lower petal broad at base, narrowed in the middle, obliquely cup-shaped in apical part and completely enclosing stamens and stigma, apically inappendedulate. Stamens 4 or 6, rarely 5, monadelphous; anthers bisporangiate by abortion of the outer microsporangia, sessile, opening by an introrse slit common to both cells. Disk absent. Ovary 2-celled, compressed contrary to the sept, each locule 1-ovuled; style strongly curved upwards at base and gradually recurved towards the slightly upturned apex; stigma 2-lobed, completely enclosed by the anthers in flower. Capsule transversally elliptic, laterally compressed, pergamentaceous, far exceeding the sepals, at the margin of each cell with a double row of 6–10 short or long teeth or spines. Seed elliptic, laterally flattened, glabrous, inappendedulate; albumen nearly absent in the ripe seed; embryo translucent, delicate, containing oil (even in dry state).

**Distr.** Sri Lanka, India, Nepal, China, Japan, S. Korea, Taiwan, Ryukyu Is., Micronesia (Kusaie), Indochina, Thailand, throughout Malesia to northern Australia. There are 3 spp., of which 2 widespread and 1 endemic in SE. Thailand and neighbouring Cambodia.

**Eccl.** Sunny, open, usually wet places on sand, clay or rock, sometimes in deciduous or light forests, 0–1500 m.

**Taxon.** CHODAT (1896) and HUTCHINSON (1967) included Epirixanthes in Salomonia. The genera share indeed a number of derived characters indicating a close affinity. Probably because of the small and rather complex flowers the differences between both have generally escaped the attention of most botanists. The presence of a disk in Epirixanthes (absent in Salomonia) has never been mentioned. The androecium is very different: the strongly curved style with the anthers tightly enclosing the stigma in Salomonia versus the straight or very short style of Epirixanthes with longer or shorter stamens not enclosing the stigma. The fruits are also different (dehiscent versus indehiscent) and, of course, the habit differs as a result of the different ecology of both (auto- versus heterotrophy).

**Note.** The name Salomonia was given by LOUREIRO to honour the famous Jewish King Salomo, 'the first botanist'.

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4. EPIRIXANTHES


Echlophyllous, small, erect, little-branched herbs with small, bract-like, erect leaves; roots not aromatic. Stems without nodal glands, terete, ribbed, un-
winged. Leaves sessile, erect, up to 4 mm long, glabrous or minutely ciliate, 1-nerved. Inflorescences terminal, spike-like, very dense, the axes without nodal glands, terete; bracts persistent or early caducous; bracteoles absent or (in E. pampa) present and persistent. Sepals 5, unequal, distinctly shorter than the petals, free or variously connate, persistent in fruit, glabrous to minutely ciliate. Petals 3, unequal, glabrous or apically papillose, asymmetric, halfway adnate to the staminal tube, the upper ones halfway connate to the lower one (keel) and about as long as this; free part of lower petal ± boat-shaped, inapplicable at apex. Stamens 2, 3 or 5, rarely 4, filaments completely connate or partly free; anthers bisporangiate by abortion of the outer microsporangia, sessile or on a free filamentous stalk, c. 0.2 mm long, opening by an introrse slit common to both cells or opening irregularly introrsely. Disk either semi-annular, enclosing the lower and lateral side of the ovary and accrescent during fruit-setting, or present only at adaxial (upper) side of the ovary as a lobe not accrescent in fruit. Ovary 2-locular, orbicular to elliptic and laterally slightly flattened, glabrous, each locule with a single apical epitropous ovule; style either rather long and straight and apically with a slightly 2-lobed stigma, or short and more or less bifurcate with a larger fertile upper lobe and a smaller sterile apically hollow lobe. Fruit indehiscent, largely enclosed by the sepals, broadly ellipsoid, apically rounded or faintly bilobed, with a fleshy pericarp. Seeds ± ellipsoid, glabrous, with a soft, thickened tissue at micropylar side (aril?), along the raphe, and most distinctly so at chalazal side; albumen nearly absent in ripe seeds; embryo translucent, delicate, containing oil (even in dry state).

Dist. E. India to China and throughout Matesia as far as the Solomon Is. (San Cristobal); rare but very locally abundant. In all 5 spp.

Eccl. On humid soil between litter, in different types of rain-forests, sometimes locally abundant and together with other small saprophytes (Burmanniaceae, Triuridaceae); 0–1800 m.

According to Richards (Trop. Rainforest, 1952) the saprophytes (including Epixranthex) prefer intense shade and are not able to survive even a slight drying of the forest floor.

The fleshy disk at the base of the fruit might serve as a ‘fruit-aril’ and serve for dispersal by ants.

Pollination. At the beginning of flowering cross-pollination seems to be possible, because the stigma is then out of reach of the anthers. In later stages, however, either the filaments stretch a little so that the anthers surround the stigma (E. elongata), or (in the other species) ovary and style grow out a little so that the stigma is situated just at the base of the bursting anthers. At that time self-pollination is likely to occur. Wirz (Flora 1, 1910, 395, f. 6) recorded that pollen grains germinated in the anthers, and directly grew into the stigma.

Taxon. Allied to Salomonia; see there.

Notes. 1. There is much more in a name than Shakespeare’s Julia could suppose. Epixranthex means flower growing on roots. Blume described Epixranthex as ‘radicibus arborum innassences’. Though Zollinger in 1854 already wrote ‘inter flora emortua’, Miquel in 1858 called the Epixranthex species ‘rhizoparasitae’, Chodat in 1896 wrote ‘schmarotzende Pflanzen’, Henderson in 1949 described them as ‘parasitic plants’ and even in 1967 Hutchinson is misled by the name by calling it ‘parasitic’ on roots.

2. The spelling of the name Epixranthex could be one for a crossword puzzle. Blume started with Epixranthex, which is thus the correct spelling. Later, however, he spelled the name Epirhizanthes on herbarium sheets. Even since we can find all sorts of etymological variants: Epirhizanthes, Epirhizante, Epixranthex, Hyperixanthes and Epiryranthes. In this revision only the correct spelling is used (H.M.Y.J. André de La Porte-Janss).
KEY TO THE SPECIES

1. Sepals free. Bracts caducous before the flowers are full-grown.
2. Style longer than the ovary. Bracts cuspidate ........................................... 1. E. elongata
   2. Style much shorter than the ovary. Bracts rounded .................................... 5. E. pallida
1. Sepals connate for 1/4–3/4. Bracts persistent till or after the fruits have fallen.
3. Flowers subtended by a bract and a pair of subulate bracteoles. Fruits fully enclosed by the sepals
   4. Bracts lanceolate, 2–2.5 by 0.5–0.6 mm ......................................................... 4. E. kinabaluensis
   4. Bracts elliptic to obovate, 1.5–2 by 0.8–1.2 mm ............................................... 3. E. cylindrica


Herb, up to 25 cm. Stem simple or branched in up-

Fig. 18. Epirixanthes elongata Blume. (Photogr. A. Elsener, Borneo, 28 May 1964).
per half, 0.5–2 mm wide, violet or reddish, set with minute clavate hairs or papillae. Leaves 2–3.5 mm long, ciliate-pilose, usually violet. Spike 0.5–6 cm by 2–3 mm, rather dense, acutish at apex. Bracts ovate, c. 1.2 by 0.5 mm, cuspidate, ciliolate-papillose, erect, caducous before the flowers are fully grown; bracteoles absent. Flowers 2–2.5 mm long, yellowish white. Sepals free, subequal, c. 1 mm long, ciliolate-papillose. Antlers 5, rarely 4, sessile or stipitate. Disk lobes present adaxially at the base of the ovary, definitely discernible, not accrescent after flowering. Ovary ± orbicular; style longer than the ovary, c. 0.6 mm long, straight or apically slightly curved upwards, apically widened into the slightly 2-lobed stigma; gynoecium at longer than the androecium, later equally long. Fruit reniform to broadly elliptic, c. 0.6 by 0.9 mm, enclosed by the slightly longer sepal.

**Distr.** E. India, S. Burma (Tavoy), N. Vietnam, S. China; in **Malesia**: Malay Peninsula, Sumatra, W. Java, Borneo, Moluccas (Ambon, Ceram).


Herb to 25 cm, generally purplish red in most of its parts except the corolla. Stem often repeatedly branched in apical part, 1–3 mm wide, glabrous. Leaves 1.5–2.5 mm long, glabrous. Spike 0.5–6 (–12) cm by 2.5–4.5 mm, very dense, rounded at apex. Bracts elliptic to obovate, 1–2 by c. 1 mm, rounded apically, glabrous, patent with slightly upturned apex, persistent till or after the fruits have fallen, at last reflexed; bracteoles always present, subulate, c. 1 mm long. Flowers 1.5–2.7 mm long, white but purple in bud. Sepals 2–4 mm, unequal, slightly cuculate, c. 1.5 mm long. Anters 3 or 5, rarely 4, sessile. Disk rather distinct, enclosing the lower and lateral side of the ovary and adnate to it, expanding gradually in fruit and then visible as a rim near the base of it. Ovary broadly elliptic; style shorter than the ovary, subcylindrical, c. 0.1 mm long, unequally 2-lobed, the larger upper lobe stigmatic, the lower one tooth-like and hollow at apex; gynoecium somewhat shorter than the androecium. Fruit broadly elliptic, c. 1 by 1 mm, at base tightly enclosed by the disk, the whole enclosed by the somewhat shorter sepals.

**Distr.** Burma; in **Malesia**: Sumatra, W. Java, Borneo, New Guinea.

**Note.** Closely allied to the next species; see there.


Herb, up to 25 cm, (sub)glabrous. Stem simple or branched, 1.5–2 mm wide. Leaves 2–4 mm long, slightly thickened at base, minutely sparsely papillose. Spike 0.5–6 cm by 4.5–5.5 mm, very dense, rounded at apex. Bracts elliptic to obovate, 1.5–2 by 0.8–1.2 mm, not thickened at base, at apex acute and finely mucronate, imbricately covering the flower buds, patent with slightly upturned apex, persistent till or after the fruits have fallen, at last reflexed; bracteoles absent. Flowers c. 2.5 mm long. Sepals 1/2–3/4, subequal, glabrous. Stamenus usually 3 and then antlers sessile, rarely 2 and then filaments free to halfway. Disk very indistinct, semi-annular, enclosing and fully adnate to the basal part of the lateral and lower side of the ovary, hardly accrescent in fruit. Ovary broadly elliptic; style up to 0.1 mm long; stigma very asymmetrical, 0.2 mm long, the upper stigmatic lobe oblique, rounded, the lower lobe narrower and longer, directed a little downwards, hollow at apex; gynoecium shorter than the androecium. Fruit broadly obovate, 0.7–0.9 by 0.7–0.9 mm, at base tightly enclosed by the fully adnate and very indistinct disk, the whole enclosed by the slightly longer sepals.

**Distr.** Moluccas; in **Malesia**: Sumatra, W. Java, Borneo, New Guinea.

**Note.** Closely allied to the next species; see there.

### 4. Epirixanthes kinabaluensis Wendt, sp. nov.

A E. cylindrica bactrea tovatus-lanceolatis, 2–2.5 x 0.5–0.6 mm, parum crassimarginatis ad basim, gradatim attenuatis et mucronatis, gynemo floribus partitum expositis, persistetibus temporibus floriferis ascendunt et differunt. — Type: Siemens 30039 (A holo; BO, G, K, NY, UC). See note 1 under the genus.

Herb up to 30 cm, glabrous. Stem simple or branched, 1.25 mm wide, tinged reddish. Leaves 2–3.5 mm long, slightly swollen at base, brown.
5. **Eriandrea pallida** Wendt, sp. nov.

- **Sepal libera**. Bracteae ellipticae, 2–3 × 1–1.5 mm, compressae ad basin, obtusae, marginibus hyalinis, pallidae, imbricatae apicem spicae tectae, ante tempus florendi caducae. Stylus brevis. — Typus: Brooke 10498 (L). See note 1 under the genus.

Herb up to 15 cm, glabrous, straw-coloured. Stem simple or branched in upper half, 2–2.5 mm thick. Leaves 2–4 mm long, swollen at base. Spike 1–5 cm long, 2.5–3 mm thick, very dense, rounded at apex. Bracts elliptic, 2–3 by 1–1.5 mm, at base compressed along the midrib, at apex obtuse, the margin nearly hyaline, pallid in dry state, imbricately covering the younger part of the spike and completely hiding the flower buds, caducous at the beginning of flowering, thus leaving the fruiting calyx exposed; bracteoles absent. Flowers c. 1.8 mm long, white. Sepals free, unequal, the larger ones slightly cuculate, 0.8–1 mm long. Anthers 5, sessile. Disk rather distinct, enclosing the basal part of the lower and lateral side of the ovary and adnate to it, expanding gradually in fruit and then visible as a rim near the base of it. Ovary broadly elliptic; style shorter than the ovary, subcylindrical, c. 0.1 mm long, unequally 2-lobed, the upper lobe stigmatic, the lower one tooth-like and hollow at apex; gynoecium somewhat shorter than the androecium. Fruit broadly elliptic, c. 1 by 1 mm, at base tightly enclosed by the disk, the whole enclosed by the somewhat shorter sepals.

Distr. Malesia: Sumatra, Borneo.

Note. Very closely allied to *E. cylindrica*, from which it differs only by the narrower and longer bracts.

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5. **ERIANDRA**


Tree. Twigs apparently without nodal glands. Leaves alternate, petioled. Inflorescences fasciculate, axillary, short; bracts and bracteoles ± persistent; bracts at very base with a pair of inconspicuous glands. Sepals 5 (or 4), equal, connate in basal half and adnate to the base of the petals, caducous as a whole together with the petals at the beginning of fruit-setting by a circumcision, the connate basal part persistent. Petals 5 or 4, connate for 3/4, basally adnate to the sepals and halfway to the staminal tube, equal, the free parts half-ornicular. Stamens (8–)10, monadelphous; anthers hairy all round, tetrasporangiate, the inner microsporangia fused in upper half, shorter than the outer ones; dehiscing at inner side by a sickle-shaped slit common to both loculi. Disk annular, inconspicuous, hairy. Ovary globose, 7–8-locular, each locule with 1 ovule; style terminal, straight; stigma capitate, slightly lobed. Fruit a fleshy globular berry, apically with a remnant of the style, basally with a remnant of the calyx tube. Seeds c. 4, flattened, radially, completely enveloped by an aril; testa very densely hairy; albumen fleshy.
6. XANTHOPHYLLUM


Shrubs or trees. Twigs terete, sometimes with annular or cap-like nodal glands. Axillary buds 2–8, serial, each with 2 budscapes. Leaves alternate (or spiral), sometimes shifted-decussate, stalked, nearly always with glands beneath, mostly near base of blade. Inflorescence axillary, branched or sometimes unbranched, panicle- or raceme-like. Flowers solitary or in lower half with 3 (rarely more) together. Sepals 5, free, usually slightly unequal, usually caducous after flowering. Petals 5, usually unequal, free; lower petal (carina) usually boat-shaped, clawed, apically inapplicable. Stamens nearly always...
8, rarely 7, 9, or 8–10; 4 epipetalous, 2 placed at the base of the carina and adnate with it or not, 2 alternipetalous and opposite the lateral sepals; filaments free or connate basally, rarely halfway connate, very rarely triadelphous; anthers tetrasperangiate, opening introrsely with slits. Disk annular. Gynoeicum usually as long as androecium; ovary usually shortly stipitate, syncarpous, composed of 2 median carpels, 1-locular or sometimes semi-2-locular; style terminal; stigma slightly bilobed or sometimes peltate; ovules 2-seriate, 4 or (6–)8–c. 20, very rarely c. 40. Fruit indehiscent (or very rarely irregually 2-valved, not in Mal.), globular or rarely ellipsoid, c. 1–15 cm, usually with a hard pericarp. Seed(s) 1 or 4–20, inappendiculate, glabrous; embryo large, flat or thick; albumen copious to nearly absent.

**Distr.** About 94 species in tropical Southeast Asia, northwards to S. China and Hainan, throughout Malesia to Australia (N. Queensland); 76 spp. do not occur outside Malesia; 2 are endemic to Queensland.

Not a single species crosses WALLACE's plant-geographical demarcation line. Although only 7 spp. occur east of this line, at subgeneric level the greatest variation is found there. For that reason it is assumed that the genus originated in Austro-Malesia.

**Ecol.** By far the majority of the species grow in the tropical lowland rain-forest, mostly below 500 m. About 10 spp. (of which 3 extra-Malesian ones) are usually found between 500–1200(–1500) m, but sometimes also lower. About a dozen species are sometimes found in freshwater swamp forests, but they are not confined to that habitat, except 63. X. ramiflorum. Also nearly all of the continental Southeast Asian species seem to be confined to the rain-forest; 60. X. lanceatum is restricted to stream banks and swamps; 62. X. virens occurs in monsoon forests, tolerating rather long dry periods. Otherwise the ecology is for all species 'rain-forest', not specifically repeated.

**Note.** From the subdivision of the genus it appears that both the fruit and seed, and the flower structure are important for specific distinction, in addition to vegetative characters. Unfortunately the mature fruit is yet unknown in several species (spp. 4, 16, 25, 34, 35, 36, 37, 38, 41, 51, 52, 58) and flowers are unknown from spp. 40, 49, 61, 67, 68, and 76. Besides, specimens in fruit seldom carry flowers too, and the reverse. These factors have complicated the key and necessitated to enter many species twice or even thrice.

**KEY TO THE SUBGENERA**

1. Fruit 4–more-seeded.
2. Embryo thick, covered by little endosperm. Spp. 72–76 ......................... V. Subg. Brunophyllum
2. Embryo flat, covered by copious endosperm. Spp. 69–71 ........................ IV. Subg. Exsertum
1. Fruit 1- (exceptionally 2)-seeded.
3. Stamens monadelphous or free. Embryo thick, without or with little endosperm.

**KEY TO THE SPECIES**

1. Petiole and lower side of leaves densely patently hairy, at least on the midrib.
2. Venation of 3rd order scalariform.
3. Inflorescence axis at the nodes with 2 crateriform or cup-like glands.
4. Leaves glaucous-papillosse beneath, with 6–8 pairs of secondary nerves; laminar glands indistinct or only the basal ones distinct .......................... 3. X. sulphureum
4. Leaves smooth beneath, with 12 or 13 pairs of secondary nerves; laminar glands numerous, distinct 4. X. cockburnii
3. No glands present at the nodes of the inflorescence axis.
5. Leaves glaucous-papillosse beneath. Ovary and fruit hairy all round or in 4 rows in upper half

12. X. rufum
5. Leaves smooth beneath. Ovary and fruit glabrous or hairy in 2 rows in upper half.
6. Inflorescence brownish hairy. Sepals persistent in fruit, the outer c. 2—3 mm long, the inner c. 3.5—5 mm long. 
11. X. velutinum
6. Inflorescence axis greyish white-hairy. Sepals caducous in fruit, the outer c. 4 mm long, the inner 5—6 mm long. 
8. X. pubescens

2. Venation of 3rd order finely reticulate.
7. Ovules 4. Carina appressedly hairy outside, other petals appressedly hairy apically 57. X. malayanum
8. Sepals and inflorescence axis with hairs c. 1 mm long 50. X. trichoelatum
8. Sepals and inflorescence axis with hairs 0.1—0.2 (—0.4) mm long.
9. Leaf-blade bullate between the tertiary nerves 49. X. reticulatum
9. Leaf-blade flat or only the midrib raised in a shallow depression.
10. Pedicel 2.5—4.5 (—5) mm long. Anthers 0.9—1.4 mm long. Flowers 11—12 mm long
48. X. purpureum
10. Pedicel 7.5—14 mm long. Anthers 1.5—2.2 mm long. Flowers 12.5—16.5 mm long.
11. Petiole 5—6 mm long. Flowers 16—16.5 mm long. Anthers c. 2.2 mm long 46. X. beccarianum
11. Petiole 1.5—2.5 (—3) mm long. Flowers c. 12.5 mm long. Anthers 1.5—1.6 mm long
47. X. pedicellatum

1. Petiole and lower side of leaves shortly appressedly hairy or glabrous.
12. Leaves glaucous-papilllose beneath.
13. Venation of 3rd order scalariform. Ovary hairy on median ribs. Fruits irregularly 4-sulcate
10. X. schizocarpon
13. Venation of 3rd order reticulate. Ovary glabrous or, if hairy, not especially hairy on the ribs. Fruit not 4-sulcate.

15. Ovules 4. Anthers 0.3—0.4 mm long.
16. Petiole (6—)17—11 (—14) mm. Axillary buds very densely shortly hairy, not soon glabrescent. Inner sepals c. 2.5 mm long. Anthers hairy at base 14. X. nigricans
16. Petiole 5—6.5 mm. Axillary buds soon glabrescent. Inner sepals c. 4 mm long. Anthers glabrous or with very few hairs at base 15. X. borneense
17. Ovules 8—18. Anthers at least 0.7 mm long.
18. Axillary buds 3—7 mm long
43. X. penibukanense
17. Axillary buds up to 1 mm long.
18. Petiole (5—)8—12 mm long. Flowers up to 8.5 mm long. Fruit 1-seeded, up to 1.2 cm long
63. X. ramiflorum
18. Petiole 1.5—3 mm long. Flowers 15—16 mm long. Fruit 10-or more-seeded, at least 5 cm long
72. X. brevipes

20. Petiole distinctly transversely wrinkled.
21. Petiole 8—15 mm long, gradually widened into the attenuate leaf base. Lower pair of nerves reaching beyond the middle of the leaf-blade 43. X. penibukanense
21. Petiole 3—6 (—7) mm long, abruptly ending into the cuneate or cordate leaf base. Nerves in the lower part of the leaf blade not reaching the middle of the blade 42. X. discolor
20. Petiole not transversally wrinkled.
22. Ovary and style appressedly hairy. Petiole (8—)10—14 mm long. Nerves 11—14 pairs
44. X. pseudoadoenotus
22. Ovary and style patently hairy. Petiole 4—9 mm long. Nerves 6—13 pairs
45. X. pulchrum
23. Axillary buds at least 4 mm long.
24. (Upper) axillary bud situated (1.5─3)─15 mm above the leaf axil and placed on a 0.5─1.5 mm long stalk .............................................................. 41. X. korthalsianum

Note: Compare also 61. X. lateriflorum.


25. Scales of axillary bud at apex with 2 distinct thickenings .......................... 36. X. clovis

25. Scales of axillary bud not thickened at apex.

26. Petiole 26─31 mm .......................... 35. X. petiolatum

26. Petiole (excl. attenuate leaf base) up to 17 mm.

27. Axillary buds half-patent to patent, with their flat side perpendicular to the twig 39. X. bracteatum

27. Axillary buds erect, usually with their flat side pressed against the twig.

28. Petals 6─8 mm long. Outer sepals 1.5─2.5 mm long, inner side 2.5─3.5 mm long. Anthers 0.4─0.5 mm long ............................. 28. X. griffithii

28. Petals c. 13 mm long. Outer sepals c. 3─4 mm long, inner sepals 3.5─5.5 mm long. Anthers c. 0.7 mm long .......................... 38. X. angustigemma

23. Axillary buds at most 1.5 mm long.

29. Leaf-blade 1.5─5(─6) by 0.5─1.5(─2) cm. Flowers solitary or in an up to 3-flowered inflorescence, 10─11 mm long, on 10─11 mm long pedicels ............................. 22. X. parvifolium

29. Leaf-blades, at least averagely, more than 5 cm long. Inflorescences either with more than 6 flowers, or the flowers 7.5─8.5 mm long on 1.5─3 mm long pedicels.

30. Inflorescence unbranched, bearing only 3─6 flowers. Fruit (immature) apically pointed 20. X. pauciflorum

30. Inflorescence at least basally branched, with more than 6 flowers (sometimes seemingly unbranched if lower bracts resemble leaves). Fruit apically rounded.

31. Filaments of upper stamens slightly S-curved, above base with a blunt appendage directed inwards. Fruit globular, 1.1─1.7 cm diam.

32. Axillary buds more or less enclosed between the base of the petiole and a low ridge of the twig, not projecting outwards, wider than high. 27. X. impressum

32. Axillary buds projecting outwards, at least twice as long as wide ...... 29. X. monticolum

31. Filaments more or less straight, without appendage above base. Fruit (unknown in 58. X. novoguineense) broadly ellipsoid or apple-shaped, 3.5─8 cm diam.

33. Petiole 3─5 mm long. Axillary buds 2 or 3. Nerves c. 8─14 pairs. Fruit broadly ellipsoid to narrowly globular, up to 3.5 cm diam., pericarp up to 3 mm thick ............. 60. X. lanceatum

33. Petiole 6─10 mm long. Axillary buds 1 or 2. Nerves 5─8 pairs. Fruit (unknown in 58. X. novoguineense) large, up to 8 cm diam., apple-shaped, pericarp up to 30 mm thick.

34. Petals c. 7 mm long. Pedicel 1.5─2.5 mm long ..................... 58. X. novoguineense

34. Petals 10─12 mm long. Pedicel 3─4.5 mm long ....................... 59. X. ngii

12. Leaves smooth beneath.

35. Ovary hairy all round, not glabrous at lateral side.

36. Most axillary buds, at least in upper half of the twigs, 3 mm long or longer.

37. Axillary buds (8)─11─20(─30) by 6─12(─14) mm, ± 1─3 times as long as wide, flat, at base attenuate and not thickened, at apex rounded to obtuse. (Flowers unknown) ........... 40. X. heterophyllum

37. Axillary buds up to 11 mm long and basally thickened, or more than 3 times as long as wide and ± acute, or smaller than 8 mm.

38. Axillary buds erect, flattened against the twig, very densely shortly hairy ...... 37. X. reflexum

38. Axillary buds half-patent to patent, glabrous or sparsely shortly hairy.

39. Axillary buds at base narrow, not thickened.

40. Leaf base cordate with upturned margins. Leaves with 14─20 pairs of nerves. Petals 16 mm long 25. X. brigitteae

40. Leaf base attenuate and flat. Leaves with 5─7 pairs of nerves. Petals 10─12 mm long 31. X. incertum

39. Axillary buds at base wide and strongly thickened.
41. Inflorescence unbranched. Petiole 4–6.5 mm. Leaves with 3–5 pairs of nerves. 19. X. neglectum
41. Inflorescence branched. Petiole 8–14 mm. Leaves with 7 or more pairs of nerves.
42. Petiole (18–)25–30 mm. Leaf-blade 22–42 cm long, finer nervation beneath indistinct
43. Petiole 8–15 mm, exceptionally longer. Nervation at lower side of leaf-blade distinctly prominent, or leaf-blade much shorter than 20 cm.
43. Leaf-blade up to 3 times as long as wide. Petiole 8–14(–16) mm. Nerves (6 or) 7–9(–11) pairs. Leaf base never cordate. Anthers 0.4–0.6(–0.7) mm long ................. 30. X. vitellinum
43. Leaf-blade c. 4–6 times as long as wide. Petiole (8–)15–18(–24) mm, if shorter than 15 mm, then leaf base cordate. Nerves (9–)13–20 pairs. Anthers (0.6–)0.7–1.2 mm long.
44. Leaf base cuneate to rounded, or cordate with the margins curved upwards and connate above the apex of the petiole. Petals (8.5–)9.5–12.5(–14.5) mm long. Anthers (0.6–)0.7–0.9(–1) mm long ........................................... 32. X. adenosum
44. Leaf base cordate, flat, or only with little upturning margins. Petals 15–18.5 mm long. Anthers 1.1–1.2 mm long ........................................... 33. X. palawanense
36. Most axillary buds up to c. 2 mm long.
45. Midrib sunken above most of its length.
46. Petals ± equal in size and form. Fruit black, 2–6 cm diam., seeds 4–12. (Compare also 70. X. amoenum) ..................................................... 71. X. stipitatum
46. Petals unequal. Fruit not black, up to 2 cm diam., 1-seeded.
47. Flowering.
48. Upper petals hairy inside to near apex ............................... 55. X. wrayi
48. Upper petals hairy inside only at base.
49. Nerves 12–20 pairs. Filaments 1–3 mm connate ....................... 56. X. venosum
50. Petiole glabrous or hairy only in the upper groove. Finer nervation beneath not very distinct
54. X. eurhynchum
50. Petiole densely hairy all round. Finer nervation at lower side very distinctly prominent
53. X. retnerve
47. Fruiting.
51. Fruit neither densely set with thick warts, nor ribbed.
52. Petiole glabrous or hairy only in the upper groove. Fruit densely hairy, smooth to slightly wrinkled or 2–4-sulcate, sometimes finely rugose, up to 1.5 cm diam. ....... 54. X. eurhynchum
52. Petiole densely hairy all round. Fruit rather sparsely hairy, smooth, up to 2.2 cm diam.
53. X. retnerve
51. Fruit densely set with thick warts, or verrucose and ribbed.
53. Fruit apically shortly but distinctly beaked, strongly verrucosely ribbed .... 56. X. venosum
53. Fruit apically rounded, densely set with thick warts .......... 54. X. eurhynchum, 55. X. wrayi
45. Midrib flat above or prominent, then sometimes with a groove in basal half.
54. Region of the twig above the leaf axil as well as the 2–4 very small and inconspicuous axillary buds densely short hairy.
55. Petiole glabrous or hairy only in the upper groove. Finer nervation beneath not very distinct. Fruit either densely set with thick warts or densely hairy and smooth to slightly wrinkled or 2–4-sulcate
54. X. eurhynchum
55. Petiole densely hairy all round. Finer nervation beneath very distinctly prominent. Fruit rather sparsely hairy, smooth .......................... 53. X. retnerve
54. Twigs glabrous above the leaf axil. Axillary buds glabrous or sparsely hairy and soon glabrescent.
56. Axillary buds (2 or) 3–7, the upper one situated at least 1–2 mm above the leaf axil.
57. Upper axillary buds placed on a 1–2.5 mm long stalk. (Flowers unknown) 61. X. lateriflorum
57. Upper axillary buds sessile on the twig ............ .... 62. X. virens
56. Axillary bud(s) seemingly 1, or 2, rarely 3, close together in the leaf axil.
58. Ovules 8–12. (Compare also 7. X. ferrugineum) ...................... 51. X. erythrostachyum
59. Inflorescence branched.
60. Leaf-blade c. 4–6 times as long as wide. Petiole (8–)15–18(–24) mm. Nerves (9–)13–20 pairs.
   Anthers (0.6–)0.7–0.9(–1) mm long ........................................ 32. X. adenotus
60. Leaf-blade up to c. 3 times as long as wide. Petiole 8–14(–16) mm. Nerves (6 or) 7–9(–11)
   pairs. Anthers 0.4–0.6(–0.7) mm long .................................... 30. X. vitellinum
59. Inflorescence unbranched or sometimes with a side-branch at base.
61. Ovary (half-)patently hairy, fruit patently hairy.
62. Nerves c. 8–10 pairs. Pedicel of flowers 4.5–6 mm, of fruits 8–11 mm long. Petals 13–19
   mm long. Anthers 0.8–1.2 mm long ...................................... 24. X. ancolanum
62. Nerves 3–5 pairs. Pedicel of flowers c. 2 mm, of fruits c. 4.5 mm long. Anthers 0.3–0.4 mm
   long ................................................................. 19. X. neglectum
61. Ovary and fruit appressedly hairy.
63. Inner sepals 2–2.5 mm long.
64. Leaf base truncate to cordate. Carina auriculate. Filaments for 0.7–1 mm connate
   ................................................................. 21. X. tardicrescens
64. Leaf base cuneate to rounded. Carina gradually enlarged, not auriculate. Filaments free
   ................................................................. 18. X. subcoriaceum
63. Inner sepals 2.8–4.5 mm long.
65. Anthers 0.4–0.7 mm long. Gynoeicum somewhat shorter than the carina. Laminar glands
   numerous ............................................................ 26. X. tenuipetalum
65. Anthers 1–1.2 mm long. Gynoeicum 0.5–2 mm longer than the carina. Laminar glands 1–6.
66. Leaf base cordate with upturned margins. Nerves 14–20 pairs. Petiole 15–18 mm
   ................................................................. 25. X. brigitteae
66. Leaf base attenuate and flat. Nerves 5–7 pairs. Petiole 6–10 mm  .................................. 23. X. philippinense
35. Ovary glabrous, at least at the lateral sides.
67. Nerves of 3rd order scalariform.
68. Inflorescence axis at the nodes with 2 crateriform glands.
69. Leaf base cuneate to rounded. Leaf-blade 5–25 by 2–12 cm. Nerves 4–10 pairs 1. X. flavescens
69. Leaf base cordate. Leaf-blade 20–50 by 6.5–20 cm. Nerves 14–20 pairs .......................... 2. X. bullatum
68. No glands present on inflorescence axis.
70. Ovary and fruit hairy on 4 ribs in apical half, hairs brown ........................ 13. X. macrophyllum
70. Ovary and fruit glabrous or hairy in 2 rows, hairs greyish.
71. Midrib flat beneath (prominent above) ................................. 9. X. resupinatum
71. Midrib prominent beneath (prominent to sunken above).
72. Inflorescence axis branched or unbranched, very densely set with flowers or scars of pedicels
   ................................................................. 5. X. hosei
72. Inflorescence axis branched, except in upper part not densely set with flowers or scars of pedicels.
73. Pedicels 1–1.5(–4) mm. Sepals thickened basally, not fleshy, when dry medium brown with light
   coloured margin; outer sepals very sparsely minutely hairy ....................... 6. X. ferrugineum
73. Pedicels (2–)4–10 mm long. Sepals, if thickened, somewhat fleshy, without a lighter coloured
   margin; outer sepals more densely hairy .................................. 7. X. affine
67. Nerves of 3rd order reticulate.
74. Ovules 4.
75. Petiole distinctly transversally wrinkled, 3.5–4.5(–6.5) mm. Nerves 3 or 4 pairs. Inflorescence and
   pedicels (sub)glabrous .................................................. 16. X. ovatifolium
75. Petiole smooth, 6–11 mm. Nerves 4–6 pairs. Inflorescence and pedicels more or less densely shortly
   hairy ................................................................. 17. X. tenue
74. Ovules 8 or more.
76. Laminar glands rather numerous and distinct, 0.5–1 mm diam., nearly all situated in the ‘axil’ of
   secondary nerves and midrib. (Flowers and ripe fruits unknown) .......................... 68. X. hildebrandii
76. Laminar glands scattered or situated at the margin, not in the ‘axil’ of secondary nerves and midrib.
77. Flowering (flowers unknown in 67. X. contractum and 76. X. chartaceum).
78. Stamens triadelphous, i.e., 6 stamens connate in 2 groups, and the remaining 2 stamens connate.
79. Laminar glands sometimes situated near margin of leaf-blade but never present on the margin itself. Anthers completely glabrous .......................... 66. X. montanum
80. Leaf-blade in upper half with at least 6 glands situated on the margin. Anthers shortly hairy along slits and at base.
81. Petals unequal, the lower middle one (carina) very distinct from the upper ones.
82. Petals black when dry. Twigs at the nodes with rather distinct annular glands. Filaments partly set with lanate hairs ........................................ 73. X. obscurum
83. Pedicel at least 8 mm. Stamens longer than petals.
84. Filaments (nearly) free. Petals 7–8.5 mm long. Outer sepals 2.5–3.5 mm long, inner sepals 3–4.5 mm long ........................................ 74. X. papuanum
85. Petals 7–12 mm long. Stamens 11–13(–16) mm long. Anthers glabrous or with a few hairs at base, 0.7–0.9 mm long.
86. Petals (8–)9–11(–12) mm long. Style hairy to apex. Laminar glands 6–10(–20) .......................... 70. X. amoenum
87. Petals 7–7.5(–8) mm long. Style glabrous in upper half. Laminar glands 0–2(–4) ......... 71. X. stipitatum
77. Fruiting.
88. At least 6 glands situated on the leaf margin itself, in upper part of the leaf-blade.
89. Midrib prominent above. ........................................ 67. X. contractum
90. Midrib sunken above.
91. Twigs at the nodes with distinct annular glands. Pedicel 4–5.5 mm ...... 66. X. montanum
92. Pericarp strongly wrinkled outside when dry.
93. Fruit globose to pear-shaped, black ........................................ 76. X. chartaceum
94. Fruit black. Seeds with copious albumen, with thin cotyledons ......... 69. X. suberosum
95. Seeds sticking together in drying, leaving shining reddish marks on inner side of the pericarp 73. X. obscurum
1. Subgenus Xanthophyllum

Nodal glands absent. Axillary buds sometimes very long, usually thickened basally, subacute, sometimes hairy. Petiole sometimes with glands, sometimes hairy. Leaf-blade sometimes hairy, base rarely cordate; tertiary nerves finely reticulate, or scalariform. Inflorescence usually branched. Sepals usually densely minutely greyish hairy out- and inside, sometimes with longer or differently coloured hairs, the inner ones often subglabrous in marginal area and often slightly keeled. Petals unequal, ciliate above base; carina unguiculate, boat-shaped, auriculate or not, usually densely hairy outside; lateral and upper petals narrow, usually oblongo-elliptic to ± linear, more or less flat, slightly constricted basally, usually glabrous outside, usually slightly hairy inside above insertion of filaments, upper petals often reflexed. Ovary sometimes semi-2-locular, glabrous to hairy; style usually hairy; stigma small, slightly 2-lobed, very rarely wider than apex of style; ovules 4 to c. 20. Fruit indehiscent, usually globular, usually 1.5—2 cm diam. Seed(s) 1 (or 2), rarely up to 4; testa 1-2-layered; albumen present or not; embryo globular, plumule not differentiated.

KEY TO THE SECTIONS


1. Section Xanthophyllum

Twigs usually densely patently hairy, sometimes glabrous. Petiole usually more or less smooth, sometimes with glands. Leaf-blade: tertiary nerves scalariform, prominent. Petals: carina usually shortly unguiculate. Ovary sometimes semi-2-locular (the marginal areas of the carpels touching the other ones along their length), glabrous, sometimes hairy in 2—8 rows, rarely hairy all round; ovules 6—16, or (not in Mal.) 4—10, in 7. X. affine very rarely 5. Fruit globular or sometimes pointed or 4-sulcate, smooth or sometimes tuberculate. Seed(s) 1 or occasionally 2 (in 1. X. flavescens often 2); testa reduced, without hard inner layer, sticking to the pericarp in drying, the raphe widely branched, hypostase not developed; albumen absent in ripe seed; radicle not exserted.


Tree, 8–36 m high, up to 1 m dbh. Twigs glabrous. Petiole (5)–7–15 mm, often seemingly longer when leaf base is attenuate, mostly in apical half with two rather distinct glands. Leaf-blade (5.2)–7–18–(25) by (2.3)–3–7–(12) cm, base often long attenuate with the margins of the leaf-base curved upwards and gradually grading into the ridges of the petiole; above yellowish green to yellowish brown; beneath: secondary nerves (4)–6–8–(10) pairs, usually forming a rather distinct intramarginal nerve, venation sometimes indistinct; glands 1–10, scattered, 0.3–0.6–(0.9) mm diam., basal glands usually absent if petiole bears glands. Inflorescences often several together on one thickened node, rarely unbranched, as long as or longer than the leaves; axes slender, somewhat flattened, slightly groove, thickened on the nodes and there with usually distinct, protruding glands, brownish, distinctly patent hairy. Flowers usually with 3 together. Pedicle (2.5)–3–4.5 mm, rarely longer, distinctly minutely half-patent greyish hairy. Sepals: outer sepals 2.3–3–(3.6) by 1.4–2.7 mm; inner sepals 3–4.1 by 2.3–3.7 mm. Petals bright yellow, white or the upper petals with a yellow spot, or fully white, when dry yellowish, the longest one (6–)7–8–(8.5) mm long; carina basally more or less densely hairy, in upper part outside densely patent hairy to glabrous, inside rather densely hairy to glabrous; lateral petals usually glabrous outside, mostly glabrous inside, upper petals reflexed, ciliate basally or up to 2/3 their length, usually glabrous outside, inside patently hairy or at base only. Stamens: filaments very rarely c. 1 mm connate; anthers (0.4–)0.5–0.6(–0.65) mm long. Ovary glabrous to hairy in apical region on 4 ribs, very rarely (in one coll.) loosely hairy all over, often semi-2-locular; style sometimes glabrous in basar part; ovules 8–12, rarely 6. Fruit 1- to often 2-locular, the second chamber often reduced and seemingly enveloped by the pericarp; usually gloular, up to c. 2 cm diam., smooth to irregularly low-tuberculater, rarely densely tuberculate, rather dull to somewhat shiny, yellowish to brownish; pericarp usually hard; pedicle up to 6(–7) mm long. Seed(s) 1 or 2.

Distr. Throughout tropical continental SE Asia; in Malesia: Sumatra (incl. Simalur, Banka), Malay Peninsula, Borneo, Philippines (Luzon, Mindoro, Palawan, Masbate, Guimaras, Negros, Mindanao).

Note. Closely resembling 7. X. affine, and nearly always combined with that species in one taxon. The only reliable character distinguishing it from the latter species is the presence of nodal glands in the inflorescence. Due to the variability of X. affine it is difficult to identify sterile collections of both species. Differences are found in the petiole; in X. flavescens the petiole is glabrous and often bears a pair of glands, in X. affine the petiole is minutely hairy, and eglanular.


Shrub or small tree, 3–4.5 m high, 6 cm dbh. Twigs appressed hairy. Petiole c. 12–22 mm, rather densely minutely appressed hairy. Leaf-blade 20–50 by 6.5–25 cm; base cordate; above yellowish green, bullate between midrib and secondary nerves, midrib strongly prominent to flat, secondary nerves rather strongly prominent, venation finely prominent; beneath creamish brown to light brownish green, minutely hairy on the nerves, secondary nerves 14–20 pairs, protruding, mostly forming a nearly complete, rather distinct intramarginal nerve, venation sometimes rather obscure; glands rather few and mainly along the margin, or numerous and scattered, 0.3–0.6 mm diam., basal glands (1 or sometimes 2 pairs) at very base on midrib. Inflorescences shorter than the leaves, mostly elongate and often very densely set with flowers; axes appressed to patently minutely hairy, light to very dark brownish, with large, protruding nodal glands. Pedicel 5–7 mm, very densely minutely appressed reddish brown hairy. Sepals minutely appressed reddish brown hairy; outer sepals c. 4.5 by 3 mm, with or without protruding glands; inner sepals c. 6.5 by 3.7 mm, keeled. Petals white, when dry yellowish, the longest one 12 mm long; carina in apical part rather shortly appressed hairy outside, minutely so.
inside, further glabrous; other petals glabrous outside, glabrous or ciliate at base, shortly hairy or not inside in basal part, the lateral petals strongly bent, the upper petals strongly $S$-curved. **Stamens**: filaments glabrous or sparingly hairy at base; anthers 0.8–1.2 mm long, ciliate along slits. **Ovary** slightly ribbed; style glabrous in basal part, apically rather appressedly hairy; ovules 8–10. **Fruit** globular, up to 2 cm diam., dull, rather smooth, light brown; pericarp rather thin, not very hard.

**Distr.** **Malesia**: Malay Peninsula (Perak, Trengganu, Selangor).


Small to large tree, 30–50 m high. Twigs finely reticulately wrinkled, brownish hairy, glabrescent. Axillary buds up to 2.8 mm long but often much smaller, rounded, densely hairy. **Petiole** 9–13 mm, very densely patent hairy. **Leaf-blade** 9–20 by 2.8–7.5 cm; above yellowish green, dull, midrib basally slightly prominent to slightly sunken and rather densely hairy, upwards sunken and glabrous, nerves and venation rather obscure; beneath glaucous-papillose, rather densely hairy especially on the nerves, secondary nerves 6–8 pairs, forming a rather distinct intramarginal nerve; basal glands perhaps always present but mostly hidden by the very prominent midrib and then scarcely visible, rarely not so and then distinct, c. 0.5 mm diam., other glands apparently few or possibly absent. **Inflorescences** shorter than the leaves; axes rather smooth, very densely brownish hairy, with distinct, large, prominent 'cap-like' nodal glands. **Pedicel** c. 4 mm, rather stout, very densely patent hairy pubescent. **Sepals** densely brownish patent hairy slightly hairy at both sides; outer sepals 4 by 3.7 mm; inner sepals 5 by 4.2 mm, some with glandular spots, distinctly keeled. **Petals** yellow, when dry yellowish, the longest one 11 mm; carina very densely (nearly velvety) patent hairy pubescent outside, densely pubescent inside in apical part; other petals woolly-tufted outside. **Stamens**: filaments nearly glabrous; anthers 0.5 mm long, cohering around the style. **Ovary** containing 16 ovules. **Fruit** globular, c. 2 cm diam., light brownish, dull, finely turbuculate; pericarp hard.

**Distr.** **Malesia**: Malay Peninsula (Pahang, near Johore border, Upper Anak Endau R.). Once collected.


Tree, 20 m high, 30 cm dbh. Axillary buds densely patent hairy. **Petiole** 8–12 mm, densely hairy. **Leaf-blade** 11–17 by 3.5–7 cm, base rounded to obtuse; above slightly bullate between midrib and secondary nerves, greenish or brownish yellow, midrib rather obscure, finely prominent to flat, secondary nerves obscure; beneath creamish to greenish yellow, rather densely patent hairy on the nerves, secondary nerves 12 or 13 pairs, forming a complete intramarginal nerve, fine venation obscure; glands c. 15–20, 0.2–0.4 mm diam., those at very base distinct, situated on midrib. **Inflorescences** shorter than to as long as the leaves; axes very densely redish brown pubescent, with rather large nodal glands. **Pedicel** 4.5 mm. **Sepals** densely patent hairy brownish; outer sepals 3.8–4 by 3 mm; inner sepals 3.8–4 by 3–3.3 mm, keeled. **Petals** white, when dry yellowish, the longest one 11 mm; carina light yellowish velutinous outside, rather densely hairy inside in apical part; other petals glabrous or slightly hairy apically, not ciliate at base. **Stamens**: anthers 0.8–0.85 mm long, minutely hairy. **Ovary** containing 8 ovules. **Fruit** unknown.

**Distr.** **Malesia**: Malay Peninsula (Pahang, near Johore border, Upper Anak Endau R.). Once collected.


Small tree, up to 3.5 m high, dbh 3 cm. Twigs minutely appressed hairy, soon glabrescent, or glabrous. **Petiole** 7–10 mm, minutely appressed hairy. **Leaf-blade** 12–21 by 4.5–10 cm, base rounded to more or less obtuse, apex rather suddenly cuspitate to acuminate; above slightly bullate between midrib, secondary nerves, and intramarginal nerve, dark greyish green, midrib sunken, rather wide, other nervation finely prominent; beneath lighter coloured, sparingly minutely appressed hairy in basal part especially on the nerves, secondary nerves 7–11 pairs, forming a distinct, (nearly) complete intramarginal nerve; glands 8 to very numerous, scattered, (0.2–)0.3–0.4 mm diam., basal glands larger. **Inflorescences** branched or unbranched, up to 12 cm long; axes slightly thickened, curved, smooth, dull, minutely very densely appressed hairy, internodes (except at very base) very short, c. 0.5–1 mm long, thus giving the inflorescence a very dense-flowered appearance. **Pedicel** 2.5–4 mm, grooved, densely minutely appressed hairy. **Sepals** glabrous to sparingly minutely appressed hairy inside; outer sepals 2.1–2.5 by 2.5–2.8 mm, with 2–4 glandular spots, minutely densely appressed hairy outside; inner sepals 3.5–3.8 by 2.2–2.6 mm, rather distinctly keeled and there densely minutely appressed hairy, further more or less glabrous outside. **Petals** yellowish when dry, the
longest one c. 8.5 mm; carina sparsely appressed hairy outside in middle part, glabrous inside; other petals ciliate to halfway, further glabrous. *Stamens:* filaments wide at base, sparsely appressed hairy adaxially and abaxially to ± halfway, further glabrous; anthers 0.85–1 mm long, ciliate along slits. *Ovary* nearly sessile, ribbed; style glabrous in basal 1/3 part, upwards rather densely appressed hairy till the apex; ovules 7–10. *Fruit* (very young) not ribbed, finely pustulate; style persistent, recurved; sepal persistent.

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


Tree, up to 25 m high, up to 40–(60) cmdbh. Twigs glabrous. *Petiole* 9–14 mm. *Leaf-blade* 8–20 by 3–7 cm; above bright yellow to yellowish green, nerves finely prominent to rather obscure but mostly more distinct above than beneath; midrib not very prominent, secondary nerves c. 5–7 pairs, finely prominent to rather obscure, intramarginal nerve indistinct, tertiary nerves finely prominent to obscure, fine venation mostly obscure; glands rather few, mainly situated near margin, 0.4–0.6 mm diam., basal glands similar. *Inflorescences* shorter than the leaves; axes more or less flattened, yellowish brown, densely to rather sparsely shortly patently hairy. *Pedicel* 1–1.5(–4) mm, densely minutely appressed greyish hairy. *Sepals* possibly persistent in fruit, medium-brown with light brown margin when dry; outer sepal 3.7–4.8 by 3.5–4 mm, (sub)glabrous outside, often with (sometimes minute) glandular spots; inner sepal 4–5 by 4–4.2 mm, thickened in middle basal part, minutely appressed hairy especially on the midrib, glabrous along the margin. *Petals* yellow, or white and the upper petals with a yellow spot, when dry yellowish, the longest one 8.5–10 mm long; carina very densely patently pubescent outside, densely pubescent in apical part inside; other petals glabrous or with few hairs in apical part outside. *Stamens:* anthers 0.5–0.7 mm long, minutely hairy. *Ovary* smooth or ribbed, glabrous, rarely sparsely appressed hairy all round, apically often greyish hairy in 4 short rows; ovules 8–14. *Fruit* (immature) partly enclosed by the persistent sepal, ovoid, finely tuberculate, dull, yellowish brown.

**Distr.** *Maesia:* Borneo (Sarawak, Brunei, Sabah, Taiwan).


Tree, rarely a shrub, up to 15(–30) m, up to 40–95 cmdbh. Twigs mostly very densely, sometimes rather sparsely, patently to appressedly minutely greyish hairy, glabrescent. Axillary buds 2 (or 3), often seemingly single, the upper bud often stalked, rarely supra-axillary for more than 0.5 mm. *Petiole* (5)–6–11(–17) mm, more or less minutely greyish hairy all round or at the upper side only, eglandular. *Leaf-blade* rarely linear-lanceolate, 6.5–18(–35) by (2)–3–8(–13) cm, base cuneate to rounded-attenuate, sometimes attenuate with the margins of the leaf-blade curved upwards and gradually grading into the ridges on the petiole, apex sometimes cuspidate; above sometimes slightly bulbate between secondary nerves, yellowish to rather dark greyish green, often with a lighter strip along midrib and base of secondary nerves, midrib prominent to flat, rarely slightly sunken, in basal part often with a groove and often minutely hairy; beneath concolorous or more brownish, sometimes more or less densely minutely hairy in basal part, secondary nerves 5–16 pairs, usually forming a more or less distinct intramarginal nerve in the apical half, intramarginal nerve rarely (nearly) complete to the base; glands very variable in number and size, usually dis-
tinct. Inflorescences shorter than the leaves; axes smooth, minutely greyish hairy; bracts sometimes with distinct glands. Pedicel (2-)4–11 mm, rarely longer, densely minutely greyish hairy. Sepals persistent or not in fruit, sometimes with small glands; outer sepals 1.7–5.5 by 1.8–4.7 mm; inner ones 2.1–7.8 by 2.1–5.2 mm. Petals white (or rarely pink), the upper ones with an orange-yellow spot, when dry yellowish, the longest one 6–17 mm; carina appressed to half-patently, sometimes patently hairy outside, inside appressed hairy or sometimes glabrous; other petals sometimes quite glabrous, usually hairy outside at base, upper petals hairy inside or only at base. Stamens: filaments glabrous to sparsely appressed hairy in basal part; anthers 0.5–1.3 (–1.6) mm long. Ovary often semi-2-locular, smooth to distinctly ribbed, sometimes tuberculate, glabrous or sometimes greyish hairy in 2(–4) rows in apical part; ovules usually 8–12, very rarely 6 or 5, rarely up to 16. Fruit globose or somewhat longer than wide, rounded or slightly but sometimes rather sharply beaked apically, up to 1.5 cm diam., smooth to pustulate or tuberculate, sometimes ribbed, creamish to brown; pericarp not very thick; sepals (sub)persistent in fruit or not.

Distr. SE. Asia (Khasya, Laos, Thailand); in Malesia: Sumatra (also Banda), Malay Peninsula, Borneo (Sarawak, Brunei, Sabah), Philippines (Palawan, Cullon, Busuanga).

Notes. Very variable, and probably not homogeneous; for a discussion, see Van der Meijden, l.c. 71–73.

Most authors have included 1. X. flavescens in this species; see note under that species.


Shrub or small tree, up to 12 m, 5 cm dbh. Twigs more or less brownish hairy. Axillary buds densely patently rather shortly hairy. Petiole 10–12 mm, hairy like twig. Leaf-blade 15–28 by 5.5–9.5 cm; above greenish, more or less densely hairy on the nerves, glabrescent, midrib flat to slightly prominent; beneath lighter coloured, rather densely patent-ly hairy, secondary nerves 8 or 9 pairs, forming a more or less distinct intramarginal nerve; glands (2–)7–14(–18), scattered, (0.5–)0.6–0.8(–1) mm diam. Inflorescences up to 10 cm long; axes densely patently greyish hairy; in basal part flowers with 3 together; bracts with 2 large glands. Pedicel 5–8 mm, very densely minutely greyish patently hairy. Sepals densely to very densely patently greyish hairy outside; outer sepals 3.8–4 by 2.7–4 mm; inner sepals 5.2–6.1 by 3.8–4.5 mm, slightly keeled. Petals white, the upper ones with a yellow spot, when dry yellowish, the longest one 12–13 mm; carina very densely shortly half-patently whitish hairy outside, in apical part rather densely hairy inside; other petals glabrous or basally ciliate, or the upper petals minutely hairy inside above the base. Stamens: anthers 1.1–1.5 mm long, sometimes cohering around the stigma, ciliate along slits. Ovary containing 8–13 ovules. Fruit (immature) obovoid, dull, finely pustulate.

Distr. Malesia: Malay Peninsula (Pahang, Johore).


Tree, up to 25 m, 40 cm dbh. Twigs glabrous. Axillary buds very inconspicuous, ± enclosed between basal part of the petiole and the twig. Petiole 4.5–7 mm, often appearing longer because of the narrow leaf base, transversely wrinkled. Leaf-blade 6–12.5 by 2.7–5.5 cm, attenuate into a narrow petiole-like part; above (very) shiny, greenish to dark olive-greenish, midrib distinctly prominent; beneath yellowish brown to greenish brown, very shiny, midrib flat to faintly sunken, rarely faintly prominent or a narrow crest, secondary nerves 4–7 pairs, forming an incomplete, indistinct intramarginal nerve, tertiary nerves rather indistinct to obscure; glands very few, mostly situated above the middle, 0.3–0.7 mm diam. Inflorescences shorter than the leaves; axes grooved, densely minutely appressed greyish hairy. Pedicel slightly grooved, 4–5 mm, very densely minutely appressed greyish hairy. Sepals dark brown to blackish; outer ones c. 3 by 2.4–3 mm, with scattered, indistinct, small glandular spots, sometimes with 2 protruding glands halfway; inner sepals c. 4–4.8 by 2.8–3.5 mm, slightly keeled, with few glandular spots. Petals white, when dry dark brownish, the longest one 7–9 mm; carina very densely half-patently greyish pubescent outside, ± hairy inside in apical part; other petals glabrous. Stamens: anthers 0.5–0.7 mm long, faintly hairy. Ovary dark brownish, ribbed, slightly appressed hairy on the ribs in apical part, or glabrous; ovules 9–14. Fruit 1.2 cm diam., blackish, slightly shiny, finely pustulate; pericarp rather thin, hard.

Distr. Malesia: Borneo (Sarawak, E. Sabah, N. Kalimantan).


Tree, 10–25 m, 35 cm dbh. Twigs minutely appressed hairy in younger parts to glabrous. Axillary buds 2 or 3, the upper one 0–3 mm above the axil. Petiole 5–7 mm, minutely appressed hairy to glabrous. Leaf-blade 4.5–12 by 1.5–4.5 cm; above
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greyish green, midrib sunken; beneath glaucous-papillose, minutely appressedly hairy on nerves, secondary nerves 6 or 7 pairs, not forming an intramarginal nerve, finer venation indistinct; glands numerous, scattered. c. 0.2 mm diam., basal glands (if present) c. 0.5 mm diam. Inflorescences often shortly supra-axillary, often 2 per leaf axil, unbranched, shorter than the leaves; axes faintly brownish, minutely appressedly hairy; lower bracts opposite. Pedicel 6–8 mm, slightly grooved, minutely densely more or less appressedly greyish hairy. Sepals: outer ones 2.5–3.8 by 2.3 mm; inner ones 3.1–4.3 by 3.2 mm, ± keeled. Petals yellow, when dry yellowish, the longest one 6–7 mm; carina rather densely appressedly hairy outside, shortly hairy inside in apical part; lateral petals glabrous inside, further like the upper ones, upper petals glabrous to shortly hairy outside, shortly patent hairy inside up to 2/3. Stamens: 8 (or 9); anthers c. 0.3 mm long. Ovary slightly ribbed, brownish, appressedly hairy on median ribs; ovules 6–8. Fruit irregularly globose, c. 1.5 cm diam., mostly wider than high, irregularly 4-sulcate, dull, light greenish to yellowish brown; pericarp hard and irregular in thickness.

Distr. Malesia: Borneo (Sarawak: Mersing Hill & Lambir; Sabah: Tawau).


Tree, 5–25 m, 60 cm dbh. Twigs densely set with short and long hairs, longer hairs 0.3–0.8 mm long. Axillary buds 1–3 mm long, hairy like the twig. Petiole (4)–8–14(–16) mm, hairy like the twig. Leaf-blade (6)–9–22 by 3–9 cm, apex cuspidate or sometimes acuminate; above greyish green, in basal part sometimes sparsely hairy especially on the nerves and midrib, midrib distinctly sunken, nerves and intramarginal nerve slightly sunken to flat and rather obscure, venation obscure; beneath brownish, hairy like the twig, rarely rather sparsely hairy, secondary nerves 8–11 (or 12) pairs, strongly prominent, forming a strongly prominent intramarginal nerve; glands (7–)10 or more, scattered, (0.2–)0.3–0.4–0.6 mm diam., basal glands 0.9–1.2 mm long. Inflorescences about as long as the leaves; axes ribbed, very densely patent brownish hairy in the basal part; flowers with 3 together. Pedicel 1.5–6.5 mm, ribbed, very densely patent brown pubescent, rarely shortly hairy. Sepals persistent in fruit, greyish hairy; outer sepals 2.1–3.2 by 1.7–3 mm, with 2–4 glandular spots; inner sepals 3.5–5.3 by 2.4–3.4 mm, distinctly keeled. Petals white or yellow, when dry brownish orange, the longest one 9.5–10.5 mm long; carina more or less densely appressedly hairy outside, sparsely appressedly hairy inside in middle part; other petals ciliate in basal half, glabrous outside, upper petals reflexed. Stamens: filaments rather sparsely appressedly hairy till apex; anthers (0.75–)0.8–1.2 mm long, usually cohering around the stigma, ciliate along slit. Ovary sessile, distinctly ribbed, glabrous or sometimes hairy on 2 ribs down to half-way; style reflexed at end of anthesis; ovules (6–)8–12. Fruit (immature) ovoid, very sharply beaked, with 8 or more distinct ribs, finely pustulate to tuberculate, dull, greyish brown; pericarp thick, hard; pedicel crowned by persistent sepals.

Distr. Malesia: Borneo (Sarawak, Brunei, Sabah).


Tree, up to 32 m, 40 cm dbh. Twigs rufous-hairy. Axillary buds to 1.8 mm long, but often much smaller, densely pubescent. Petiole 7–21 mm, densely patent pubescent, more or less glabrescent, apically often with large glands. Leaf-blade 8–25 by 4–13 cm, base sometimes cordate; above bright (neon-like) yellow-green to light greyish green, midrib and nerves slightly sunken, venation indistinct; beneath light brownish to brownish green, papillose, rather densely hairy, secondary nerves 5–9 pairs, forming a rather distinct intramarginal nerve in apical or rarely also in basal part; glands very numerous, c. 0.1 mm diam., basal glands large, situated on the midrib at the very base of the leaf and then obscure, or at very apex of the petiole and then conspicuous. Inflorescences sometimes unbranched, shorter than to as long as the leaves; axes finely ribbed, very densely rufous-hairy; bracts conspicuous, persistent, often with distinct glands, bracteoles small, subpersistent. Pedicel 4.5–7(–10) mm, ribbed, very densely rufous-hairy. Sepals persistent or not, sometimes present under fully ripe fruits (then up to c. 12 mm long), very densely rufous-hairy outside, glands present or not, inconspicuous; outer sepals c. 4–6 by 4–6 mm, mostly slightly ribbed; inner sepals c. 5–7 by 4–6 mm, keeled. Petals white, the upper ones with a yellow spot, when dry yellowish, the longest one 12–15 mm; carina very densely yellowish brown pu-
Fig. 19. *Xanthophyllum rufum* Benn. a. Habit, $\times 0.5$; b. base of leaf, $\times 2$; c. flower; d. flower, longitudinal section, gynoecium removed; e. carina with two stamens enclosed; f. gynoecium; all $\times 3$; g. ovary, longitudinal section, $\times 6$ (SAN 36554).
subtomentous outside, inside hairy in apical part; other petals pubescent outside in apical part or only apically tufted. Stamens: filaments glabrous; anthers 0.4—0.6 mm long, shortly hairy at base or glabrous. Ovary very densely rufous-pubescent all round or pubescent in 4(-8) rows, the median rows mostly longer than the lateral ones; style very densely rufous-pubescent in apical part; ovules 12—14. Fruit globular, up to 1.8 cm diam., often with 2—4, sometimes hairy ridges running down from the style-scar, yellowish green, dull, finely tuberculculate; pericarp rather thick, hard; not rarely some sepals present.

Dist. Malesia: Sumatra, Malay Peninsula, Borneo.

Note. In most Bornean collections the ovary is hairy all round (or sometimes hairy in 8 rows), and the sepals are more or less persistent in fruit ("X. heterophyllum" CHODAT). In Malaya ("X. rufum") and Sumatra ("X. flavum" RIDLEY) the ovary is usually hairy in 4 rows, and the sepals are soon dropping off. These differences are not consistent in Malaya, however, as sometimes the ovary is hairy all round, or the sepals are persistent. Apart from those I did not find other differences; therefore it is not necessary to distinguish varieties based on these conspicuous but minor and grading differences.


Shrub or tree, up to 25 m, up to 30 cm dbh. Twigs glabrous. Petiole 10—18 mm, with (0—)2(-4) very distinct glands. Leaf-blade (10—)14—28 by (3.8—)4.5—10 cm, base often curved upwards and de-current-attenuate; above sometimes slightly bullate between the secondary nerves, greenish, midrib slightly to distinctly prominent, rarely slightly sunken, nerves finely prominent; beneath mostly brownish green, secondary nerves 7—10 pairs, forming a nearly complete rather prominent intra-marginal nerve; glands mostly rather few, scattered, 0.4—0.5 mm diam. Inflorescences sometimes unbranched, shorter than the leaves; axes grooved, appressed brown-velvety; bracts often opposite, with 2 small indistinct glands. Pedicel 2—12 mm, appressed brown-velvety. Sepals shortly appressed brownish hairy outside, ribbed inside; outer sepals 5—6.5 by 3.8—6.2 mm; inner sepals 6—7.2 by 3.7—6.2 mm. Petals yellow, or white and the upper ones with a yellow spot, when dry yellowish to dark-brown, the longest one 13—16 mm long; carina appressed velvety outside, more or less densely hairy inside in apical part; other petals glabrous or hairy outside in apical part. Stamens: anthers 0.55—0.75—(0.8) mm long, shortly hairy. Ovary sessile or shortly stipitate, creamish brown, often about 8-ribbed when dry, the median ribs most prominent and hairy over 1/3—2/3 their length, the other ribs hairy in apical part only; ovules 6—14. Fruit c. 2 cm diam., brownish to blackish, ribbed in apical part, thick-walled.

Dist. Malesia: Borneo (Sarawak, Sabah).

2. Section Eystathes


Twigs sometimes hairy. Axillary buds sometimes 3—7, sometimes erect. Leaves sometimes shifted-decussate. Leaf-blade: tertiary nerves finely reticulate, mostly distinctly protruding. Inflorescences: bracts sometimes opposite in basal part. Petals: carina usually distinctly unguiculate. Stamens: filaments sometimes connate up to 3 mm, rarely occasionally triadelphous, sometimes with a knob-like appendage at inner side. Ovary mostly densely hairy all round, rarely glabrous; stigma very rarely wider than the apex of the style; ovules 4 or 8—16 (rarely more, exceptionally 5 or 6). Fruit mostly globular, smooth or rarely tuberculculate. Seed(s) 1 or occasionally 2, very rarely up to 4; testa with or without a hard inner layer; albumen thin but distinct; radicle exerted or not.

KEY TO THE SUBSECTIONS

1. Testa with a hard inner layer. Albumen forming a distinct layer. Embryo laterally near the base with 2 flattened areas. Radicle exerted. Spp. 14—57

2a. Subsect. Jakkia

2b. Subsect. Eystathes

1. Testa without a hard inner layer. Albumen very thin. Embryo without flattened areas near the base. Radicle not exerted. Spp. 58—62
Twigs and inflorescence axes without nodal appendages. Axillary buds mostly 2 (seemingly single) and close together, rarely up to 4 or the upper one supra-axillary. Seed 1 or seeds occasionally 2; testa with a hard inner layer; albumen forming a rather thin, distinct layer, which is very thin at the lateral sides of the cotyledons near the base of the embryo; embryo laterally near the base with 2 flattened areas, radicle exserted.


Small tree, up to 15 m, 20 cm dbh. Twigs finely longitudinally wrinkled. Axillary buds 2 or 3 (or 4), 1.5–2.2 mm long, very densely shortly patent light-brown hairy. Petiole (6–)7–11(–14) mm. Leaf-blade 3.5–12 by 1.2–5.5 cm; above greyish olive-green (to brownish); beneath concorolous, or bluish because of thin waxy layer, (glaucous-)papillose, secondary nerves 5 or 6 (or 7) pairs, forming a more or less distinct intramarginal nerve; glands rather scarce or sometimes apparently absent, situated on or near the midrib, 0.1–0.2 mm diam., basal ones often slightly larger. Inflorescences unbranched, shorter than the leaves; axes flattened, angular, black, very sparsely appressedly hairy; flowers with 1–3 together. Pedicel 2–2.5 mm, black, nearly glabrous. Sepals glabrous outside, densely very shortly more or less patently hairy inside at base, further glabrous inside; outer sepals 1.8 by 1.7 mm; inner sepals 2.5 by 2.1 mm. Petals white, when dry dark reddish, very sparsely appressedly hairy outside, faintly ciliate apically, the longest one 8 mm long. Stamens: anthers c. 0.3 mm long. Ovary black, glabrous; style glabrous or basally very sparsely appressedly hairy; ovules 4. Fruit globose, up to 1.3 cm diam., dull, slightly wrinkled, brownish; pedicel up to 3 mm long.

**Distr. Malesia**: Borneo (Bunyei, Sabah).


Small tree, up to 5 (–8?) m high. Twigs more or less reticulately wrinkled. Axillary buds 2 (or 3), 1.2–1.8(–3) mm long. Petiole c. 5–6.5 mm. Leaf-blade 4–16 by 1.5–7 cm, margin undulate, apex acute; above slightly bullate to flat between secondary nerves, greenish to brownish; beneath glaucous-papillose, secondary nerves 4–6 pairs, forming a rather distinct intramarginal nerve; glands numerous, scattered, 0.1–0.2 mm diam. Inflorescences unbranched, about as long as the leaves; axes flattened basally, angular, dull, light brownish, glabrous. Pedicel 1.5–2.5 mm, dull, brownish, glabrous. Sepals glabrous outside; outer sepals 3 by 2.1 mm; inner sepals 3.8 by 2.8 mm. Petals light brownish or orange when dry, minutely ciliate apically, the longest one 10–11 mm long; carina sparsely appressedly minutely hairy outside. Stamens: anthers c. 0.3 mm long, glabrous or with very few short hairs at base. Ovary completely glabrous; style very sparsely more or less appressedly hairy; ovules 4. Fruit globose to broadly ovoid, c. 1.8 cm diam., smooth, brown; pedicel c. 5 mm.

**Distr. Malesia**: Borneo (Sarawak, Sabah, SE Borneo).


Axillary buds 2 (or 3), 1–1.8 mm long. Petals 3.5–4.5(–6.5) mm; glands present or not. Leaf-blade 3.5–9.5 by 1.4–6 cm, apex sometimes cuspidate; above rather dull, brownish to greenish, midrib little prominent at base; beneath dull, secondary nerves c. 3 or 4 pairs, not forming an intramarginal nerve; glands 8–20, usually situated halfway between margin and midrib, 0.4–0.5 mm diam., basal glands usually present, 0.5–0.6 mm diam. Inflorescences shorter than the leaves, unbranched; axes slightly flattened, brownish, glabrous to very sparsely appressedly hairy. Pedicel 7–8 mm, glabrous. Sepals glabrous outside; outer ones c. 2.8 by 1.7 mm; inner ones 3–3.5 by 1.8–2 mm. Petals white, when dry light brownish, ciliate at apex and base, further glabrous, the longest one 9–10 mm. Stamens: anthers 0.3–0.4 mm long, glabrous. Ovary glabrous; style sparsely appressedly hairy basally; ovules 4. Fruit unknown.

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


Tree, up to 25 m, 40 cm dbh. Twigs glabrous to rather densely very shortly patently hairy. Axillary buds 2 (or 3), 1.5–2.5 mm long, shortly hairy, some-
times irregular and larger because of cork-forming in apical region. *Petiole* 6–11 mm, not transversely wrinkled, sparingly patent hairy to glabrous; glands absent or small. *Leaf-blade* (5–)7–16 by (2–)2.5–6.5 cm; above slightly bullate to flat between secondary nerves, dull, greyish green to light reddish brown, midrib glabrous to patentely minutely hairy in basal half; beneath mostly rather dull, yellowish green, glabrous to minutely patent hairy, midrib slightly prominent to flat, secondary nerves 4–6 pairs, mostly forming a rather indistinct intramarginal nerve, venation mostly not very prominent, sometimes rather indistinct; glands (0–)4–25, often situated near midrib, 0.3–0.5(–0.7) mm diam.; basal glands often present, relatively large. *Inflorescences* much shorter than the leaves, unbranched; axes slightly angular, sparingly to rather densely patently shortly hairy. *Pedicel* (2.5–)4–6(–10) mm, rather sparsely to densely minutely hairy. *Sepals* nearly glabrous outside; outer sepals 2.1–2.8 by 1.3–2.5 mm, inner sepals 2.5–4(–4.5) by 1.5–3.2 mm. *Petals* yellowish or white, when dry orange, the longest one 8–9(–11.5) mm; carina sparsely to rather densely appressedly hairy outside, inside hairy to halfway or up to the apex; other petals glabrous to sparsely hairy outside, lateral petals hairy inside to halfway, upper petals hairy inside to apex. *Stamens* : filaments nearly free or connate over up to 1.5 mm; anthers c. 0.4 mm long. *Ovary* glabrous or less often rather sparsely appressedly hairy and probably soon glabrescent; style glabrous or less often sparsely appressedly hairy in basal part; ovules 4. *Fruit* gloular, up to 1.8 cm diam., dull, wrinkled, light greenish brown; pericarp soft, thin; pedicle mostly up to 7 mm, reddish.

*Disstr.* *Malesia*: Borneo (Sarawak, Sabah, Tawau, N. Kalimantan).

Ecot. Submontane rain-forest, 500–1200 m.


Shrub or small tree, up to 15 m, 20 cm dbh. Axillary buds 2, elliptic to ovate-oblong, 1.5–4(–6) mm long, acute, light yellowish brown. *Petiole* 4–6.5 mm, glabrous to sparingly very shortly hairy especially in the upper groove. *Leaf-blade* 5–12 by 1.8–5.5 mm, margin undulate; above dull, greyish green; beneath rather dull, sometimes slightly waxy, secondary nerves 3–5 pairs, forming a rather indistinct intramarginal nerve; glands 2–8, not in basal part, 0.2–0.3(–0.4) mm diam. *Inflorescences* unbranched, 1.5–5(–8) cm long, shorter than the leaves, bearing 3 or 4–7 flowers; axes c. 0.5 mm diam., slightly flattened basally, light brown, rather sparsely patentely shortly hairy. *Pedicel* c. 2 mm, slightly grooved, rather densely patently shortly hairy. *Sepals*: outer ones 2.2–2.5 by 2–2.3 mm; inner ones 2.8–3.5 by 2.2–3.5 mm. *Petals* white or yellowish, when dry light brownish, the longest one 7–10 mm; carina nearly glabrous to rather densely hairy outside, shortly hairy at both sides basally; other petals nearly glabrous except for some hairs at the base and apex. *Stamens*: filaments of abaxial 4 stamens basally widened and slightly thickened; anthers 0.3–0.4 mm long. *Ovary* patently hairy; ovules 4. *Fruit* (immature) ovoid, dull greyish green, hairy, slightly wrinkled when dry; pericarp rather soft; pedicel up to 4.5 mm, light brown.

*Disstr.* *Malesia*: Borneo (L. Sabah, E. Kalimantan).


Tree, up to 20 m, 20 cm dbh. Axillary buds 2, elliptic to ovate-oblong, 1.5–4(–6) mm long, acute, light yellowish brown. *Petiole* 4–6.5 mm, glabrous to sparingly very shortly hairy especially in the upper groove. *Leaf-blade* 5–12 by 1.8–5.5 mm, margin undulate; above dull, greyish green; beneath rather dull, sometimes slightly waxy, secondary nerves 3–5 pairs, forming a rather indistinct intramarginal nerve; glands 2–8, not in basal part, 0.2–0.3(–0.4) mm diam. *Inflorescences* unbranched, 1.5–5(–8) cm long, shorter than the leaves, bearing 3 or 4(–7) flowers; axes c. 0.5 mm diam., slightly flattened basally, light brown, rather sparsely patentely shortly hairy. *Pedicel* c. 2 mm, slightly grooved, rather densely patently shortly hairy. *Sepals*: outer ones 2.2–2.5 by 2–2.3 mm; inner ones 2.8–3.5 by 2.2–3.5 mm. *Petals* white or yellowish, when dry light brownish, the longest one 7–10 mm; carina nearly glabrous to rather densely hairy outside, shortly hairy at both sides basally; other petals nearly glabrous except for some hairs at the base and apex. *Stamens*: filaments of abaxial 4 stamens basally widened and slightly thickened; anthers 0.3–0.4 mm long. *Ovary* patently hairy; ovules 4. *Fruit* (immature) ovoid, dull greyish green, hairy, slightly wrinkled when dry; pericarp rather soft; pedicel up to 4.5 mm, light brown.

*Disstr.* *Malesia*: Borneo (L. Sabah, E. Kalimantan).

Tree, up to 21 m, 25 cm dbh. Twigs ± as thick as the petioles, only a few internodes long. Axillary buds 2, 0.5–1.3 mm. Petiole 3.5–4.5 mm. Leaf-blade 4.8–8(–9) by 1.2–2.2(–3.5) cm, apex cuspidate to acuminate; above olive- to dark-green, rather dull; beneath glaucous-papilllose, secondary nerves 4–6 pairs, not forming an intramarginal nerve; glands 2–7, 0.1(–0.2) mm diam. Inflorescences unbranched, much shorter than the leaves, bearing only 3–6 flowers; axes slender, slightly flattened, glabrous to sparsely very shortly patent hairy. Pedicel 1.5–2.5(–3) mm, very shortly patent hairy. Sepals yellowish, rather apically orange, outside. 0.2–0.3 × cordate; nerves 3–6 pairs, rather indistinct, forming an indistinct intramarginal nerve, venation rather indistinct; glands rather numerous, scattered, very small though relatively distinct, up to 0.1 mm diam. Flowers solitary in the upper leaf axils or twigs terminating in a 1–3-flowered inflorescence; this unbranched, shorter than to ± as long as the leaves, up to c. 0.5 mm diam., up to 3.5 cm long, glabrous. Pedicel 10–11 mm, glabrous. Sepals purplish, (sub)glabrous outside, outer ones c. 2 by 1.6 mm, inner ones 3–3.4 by 1.8–2.3 mm. Petals light orange, when dry orange brown, very sparsely hairy at base and at very apex, further glabrous, the longest one 10–11 mm. Stamens: filaments widened and slightly thickened above their base and there densely rather shortly patent hairy, further glabrous; anthers 0.35–0.4 mm long, with few short hairs at base. Ovary c. 1 mm stipitate, appressed hairy; style rather sparsely appressed hairy in lower half, further glabrous; ovules 4. Fruit very shortly stipitate, globarul, up to 1.1 cm diam., dull, light brown, very sparsely shortly appressed hairy; pericarp rather thin; pedicel slender, 6.5–10 mm, completely glabrous.

**Distr. Malesia**: Borneo (Sarawak: Semengoh).


Tree, up to 25 m, 30 cm dbh. Twigs forming very short shoots bearing 2 or 3 leaves, the young ones very slender, c. 0.5 mm diam. Axillary buds 2, 0.7–1.2 mm long. Petiole 2–2.5 mm. Leaf-blade 1.6–5(–6) by 0.5–1.6(–1.9) cm, base rounded to cuneate; above shiny, yellowish or greenish brown, midrib flat or slightly prominent, nervation finely prominent to obscure; beneath glaucous-papilllose, yellowish to reddish brown, secondary nerves 1–3 pairs, rather indistinct, forming an indistinct intramarginal nerve, venation rather indistinct; glands rather numerous, scattered, very small though relatively distinct, up to 0.1 mm diam. Flowers solitary in the upper leaf axils or twigs terminating in a 1–3-flowered inflorescence; this unbranched, shorter than to ± as long as the leaves, up to c. 0.5 mm diam., up to 3.5 cm long, glabrous. Pedicel 10–11 mm, glabrous. Sepals purplish, (sub)glabrous outside, outer ones c. 2 by 1.6 mm, inner ones 3–3.4 by 1.8–2.3 mm. Petals light orange, when dry orange brown, very sparsely hairy at base and at very apex, further glabrous, the longest one 10–11 mm. Stamens: filaments widened and slightly thickened above their base and there densely rather shortly patent hairy, further glabrous; anthers 0.35–0.4 mm long, with few short hairs at base. Ovary c. 1 mm stipitate, appressed hairy; style rather sparsely appressed hairy in lower half, further glabrous; ovules 4. Fruit very shortly stipitate, globarul, up to 1.1 cm diam., dull, light brown, very sparsely shortly appressed hairy; pericarp rather thin; pedicel slender, 6.5–10 mm, completely glabrous.


Twigs often with numerous adventitious buds on older nodes. Petioles 6–10 mm, often grading into the narrow leaf base, mostly in middle part with glands. Leaf-blade 7–14 by 2.5–6 cm, apex acutish; above shiny to rather dull; beneath ± concolorous, rather dull, secondary nerves c. 5–7 pairs, apically hardly distinguishable; glands 1–6, 0.4–0.6 mm diam. Inflorescences unbranched or with one side-branch, up to 5 cm long, often several together in the leaf axils; axes rather dark, sparsely minutely hairy; lower bracts (sub)opposite. Pedicel c. 3.5 mm, reddish brown, densely minutely hairy. Sepals: outer ones c. 2.5 by 2 mm; inner ones c. 3.5 by 3 mm. Petals orange when dry, the longest one c. 12 mm; carina faintly appressed hairy outside near apex; other petals nearly glabrous. Stamens: filaments
widened but hardly thickened above their base and there densely more or less woolly hairy, further glabrous; anthers c. 1.2 mm long. Ovary c. 2 mm stipitate, appressedly hairy; style very long (c. 10 mm), exserting over c. 2 mm from the carina, faintly appressedly hairy; ovules 4. Fruit c. 2 cm diam., smooth, light brown, faintly hairy; pedicel 2.5–6(–8) mm, minutely hairy. Seeds 1 or 2.


Ecol. In open flowers the stigma is exserted from the carina. This may mean that cross-pollination is obligatory.


Shrub or small tree, up to 4 m, 4 cm dbh. Twigs glabrous to densely short hairy. Axillary buds c. 1–2.5 mm long, hairy; older nodes often with numerous adventitious buds. Petiole (5–)7–15 mm, not transversely wrinkled, glabrous to densely short hairy, apically sometimes with glands. Leaf-blade 10–26 by (2.5–)3.5–10.5 cm, apex shortly acuminate to cuspitate; above greyish green, rather dull; beneath green, secondary nerves 8–10 pairs, at least in apical part forming an intramarginal nerve; glands mostly rather numerous, scattered, 0.2–0.5 mm diam., basal glands often present. Inflorescences situated at end of young twigs, but also axillary and on old nodes (plant partly rami divulous), 1 (or 2) in each axil, erect to strongly reflexed, unbranched, or sometimes with a side-branch; axes 1–11 cm long, dark, rather sparsely shortly hairy; lower bracts (sub)opposite. Pedicel 4.5–6 mm, dark, rather sparsely minutely patent hairy. Sepals dark purple; outer ones 2.5–3.8 by 2.1–3.1 mm; inner ones 4.2–5.2 by 3–3.9 mm. Petals when dry light to dark orange; the longest one 13–19 mm long; carina long unguiculate, sparsely very shortly appressed hairy outside; other petals very sparsely hairy outside to glabrous. Stamens: filaments c. 2.5–3.2 mm, slightly widened and hardly thickened above base; anthers 0.8–1.2 mm long, very shortly hairy at base. Ovary c. 2 mm stipitate, half-patent hairy; style exserted from the carina for less than 0.5 mm, sparsely hairy in 2 rows; ovules 4. Fruit (immature) shortly stalked, more or less globular, slightly beaked, brownish, hairy; pedicels 8–11 mm.

Distr. Malesia: Sumatra (North: Gajolands; Mt Bandahara; Central: N. of Padang; South: Lampung Distr.: Muaraud). Ecol. Montane rain-forest, 500–1200 m.}

25. Xanthophyllum brigitiae MEIJDEN, sp. nov. — Fig. 20.


Shrub, c. 2 m high. Twigs glabrous. Axillary buds ovate-oblong, 2.5–3.5 mm long, hardly thickened basally, sparsely shortly hairy; older nodes with numerous small adventitious buds. Petiole 15–18 mm, distinctly transversely wrinkled, apically with a pair of indistinct glands. Leaf-blade 25–50 by 9–12 cm; base cordate with the margins curved upwards above the base of the petiole; apex slightly acuminate; above greyish green, rather dull; beneath green, secondary nerves 14–20 pairs, in apical part forming a rather indistinct intramarginal nerve; glands indistinct, few, scattered, c. 0.1 mm diam., basal glands usually present, 0.3 mm diam. Inflorescences numerous in the upper part of young twigs and also on older nodes, 1 or 2 in each axil, patent or slightly reflexed, unbranched or basally sometimes with a side-branch; axes 4–10 cm long, dark, rather sparsely shortly hairy; lower bracts subopposite. Pedicel 3–4 mm, brown, densely shortly appressed hairy. Sepals purplish brown, shortly hairy; outer ones c. 3 by 2.5 mm; inner ones c. 4.5 by 3 mm. Petals whitish with pink to lilac tips when fresh, light to dark orange when dry, the longest one c. 16 mm; carina unguiculate, sparsely shortly appressed hairy outside; other petals (sub)glabrous outside. Stamens: filaments free or connate for 0.1 mm, hardly widened and not thickened above base; anthers 1 mm long, very shortly hairy at base. Ovary c. 1.5 mm stipitate, shortly appressed hairy to near apex; ovules 4. Fruit unknown.

Distr. Malesia: N. Sumatra (Gajolands; Mt Leuser National Park).

Notes. Like 24. X. ancolanum, differing in the longer, distinctly transversely wrinkled petioles, the more numerous secondary nerves, the leaf base with its upturned margin (like in 32. X. adenotus) and its (nearly) free filaments.

Half a century ago V. A. STEENIS collected (also on Mt Leuser) a fragment of this species (van Steenis 10075, BO!), thrown down by monkeys, with a single flower and a small part of a single leaf. I erroneously attributed this to 31. X. erythrostachyum AGAP. noting, however, that the single flower possessed 4 instead of 11 ovules. Having now a fine collection at hand, it turned out that the original count of the ovules in van Steenis' collection was correct.
The present species is named in honour of Ms. BRIGITTA DE WILDE-DUYFJES who ardently assisted her husband in the botanical exploration of the Leuser National Park in the Gajolands of N. Sumatra.


Tree, up to 30 m, 40 cm dbh. Axillary buds 2 (or 3), 0.5–2.5 mm long, basally wrinkled, in apical part smooth or slightly keeled. Petiole 6–9 mm, often appearing somewhat longer because of the attenuate leaf base, always with 2 rather distinct glands usually situated in the middle part or at the (very) base. Leaf-blade 9–20 by 3.5–11 cm; above slightly bullate between the secondary nerves, shiny, dark to brownish green, nervation often very distinct; beneath slightly shiny, secondary nerves c. 6–8 pairs, apically difficult to count, forming an irregular and fine intramarginal nerve or ending in the venation; glands mostly very numerous, scattered, c. 0.3–0.5 mm diam. Inflorescences also in lower leaf axils, unbranched or rarely with one short branch, up to 7 cm long; axes rather slender, smooth, very densely shortly more or less appressedly hairy; flowers with 3 together or in the apical part solitary; lower bracts (sub)opposite. Pedicel 2–4 mm, very densely nearly appressedly shortly hairy. Sepals: outer sepals 1.8–2.9 by 1.9–3 mm; inner sepals 2.9–3.5 by 2.6–3.2 mm. Petals rather thin, white (or yellow?) when fresh, when dry light brown or orange, not covering the stamens in anthesis, the longest one 10.5–12.5 mm; carina long-unguiculate, apically ciliate, rather sparsely to rather densely more or less appressedly woolly hairy outside in apical region and slightly so near the base, inside glabrous; other petals ciliate at very apex, near base sparsely to rather densely hairy on either side. Stamens 8, occasionally 9; filaments connate over 0.1–0.5 mm, rather densely more or less appressedly woolly hairy in basal half, glabrous upwards; anthers (0.5–)0.6–0.7 mm, sparsely ciliolate along slits, sparsely and shortly hairy at base. Ovary appressed hairy; style rather sparsely hairy; ovules 4. Fruit globular, 1.8–2 cm
PoLYGALACEAE

b. or Sta-

4(12-15) by 1-4.5(-9) cm, apex sometimes cupuliate; above dark green to brownish; beneath lighter coloured, smooth to glaucous-papillose, secondary nerves 4-6 pairs, usually forming an indistinct intramarginal nerve in apical half; glands 4-20, scattered but often near midrib, 0.2-0.3 mm diam. Inflorescences up to 10 cm long, at very base with 2 side-axes or with a pair of buds of second order; axes often red-brown, densely minutely patent hairy; lower bracts opposite. Pedicel 1-4.5 mm, grooved, densely minutely appressed hairy. Sepals sometimes with 2 glands in apical part; outer sepal 1.6-2.5 by 2.1-2.7 mm; inner sepal 2.6-3.3 by 2.1-3 mm. Petals white, the upper ones with a yellow spot, when dry dark red to orange-red, the longest one (5-)7-8 mm long; carina densely more or less appressed hairy outside; other petals glabrous to appressed hairy outside in apical part. Stamen: filaments widened above base and with a knob-like, densely hairy appendage at inner side, further glabrous; anthers (0.3-)0.4(-0.5) mm long. Ovary 0.5-2 mm stalked, more or less appressed hairy; ovules 4. Fruit globular, up to 1.5 cm diam., more or less smooth brown, appressed hairy; pedicel up to 4 mm.

Distr. SE, Asia and Malesia.

Note. Van der Meijden (l.c.) distinguished 3 subspecies, of which the typical one (from Burma, Mergui) occurs outside Malesia.

KEY TO THE SUBSPECIES

1. Axillary buds half-patent, flat
   a. ssp. angustifolium
   b. ssp. erectum


Axillary buds half-patent, elliptic to lanceolate, 1.5-8 mm long, at base often stalk-like constricted, more or less flat, wrinkled, glabrous or soon glabrescent. Pedicel 4-8(-10) mm. Leaf-blade 4-8(-10) by 1-4(-5) cm, in juvenile shoots up to 10 by 2.5 cm; beneath glaucous-papillos to (nearly) smooth and
not glaucous, secondary nerves 4 or 5 (or 6) pairs; glands 0.2–0.3 mm diam. *Pedicel* 1.5–4.5 mm. *Petals*: longest ones 6.5–7.8 mm. *Stamens*: anthers 0.4 mm long. *Fruit*: c. 1.1 cm diam.

**Distr. Malesia**: Central Sumatra (Indragiri), Malay Peninsula, Bornéo (Sarawak, Sabah, E. Kalimantan), Philippines (Luzon).

**Ecol.** Usually in submontane rain-forest, up to 1400 m.


Tree, up to 10 m, 20 cm dbh. Axillary buds often appressed against the petiole, (1)–1.8–2.9 mm long, base wrinkled, apex acute. *Petiole* 9–14 mm. *Leaf-blade* 8–16 by 2–5(–7.5) cm; above usually dark green, sometimes brownish; beneath glaucous-papillose, secondary nerves 6–8 (or 9) pairs, in apical part forming a weak intramarginal nerve; glands 4–16, mostly in basal half near midrib, 0.2–0.3 mm diam., basal glands sometimes present, silt-like, c. 0.8 mm long. *Inflorescences* up to 12 cm long; axes angular, basally flattened, grooved, very densely minutely patently yellowish brown hairy; flowers solitary or in basal part with 2 together; lower bracts (sub)opposite. *Pedicel* 3.5–5 mm, slightly grooved, very densely appressed hairy. *Sepals*: outer sepal 2.6–3 by 2.5–3 mm; inner sepal 4.4–5.5 by 3–4.5 mm. *Petals* whitish, when dry dark orange red, the longest one 10.5 mm long; carina rather densely appressed hairy outside, subglabrous inside; other petals outside in basal part shortly appressed hairy, further glabrous. *Stamens*: filaments widened above base and with a knob-like, rather densely hairy appendage at inner side, further glabrous; anthers 0.5–0.7 mm long. *Ovary* half-patently hairy, up to 1.5 mm stipitate, inserted on a rather wide, minutely hairy receptacle; ovules 4. *Fruit* globose, c. 1.7 cm diam., dark, shortly patently hairy; pericarp rather soft.

**Distr. Malesia**: Malay Peninsula (Cameron Highlands, Fraser’s Hill, G. Benom).

**Ecol.** Submontane rain-forest, 1000–1500 m.


Small tree, to 10 m. Axillary buds narrowly triangular to lanceolate, (2—)4.5—11 mm long, more or less wrinkled; buds of second order rarely present. 

Pedicel (6—)8—10—(12) mm. Leaf-blade 6—16—(22) mm. petals 2.3—5.5—(8) cm, apex cuspidate; above dark green, shiny; beneath green, secondary nerves 5 or 6 (or 7) pairs, in apical part forming an intramarginal nerve; glands few, 0.2 mm diam., basal glands sometimes present. Inflorescences branched or unbranched, up to 7 cm long; axes densely shortly hairy; in basal part flowers with 3 together; lower bracts (sub)opposite. Pedicel 1.5—2 mm, densely shortly more or less appressedly hairy. Sepals sometimes with tiny glandular spots; outer sepals 2.8—3.5 by 3.1—4.1 mm; inner sepals 4.3—5.6 by 3.1—4.2 mm. Petals pinkish, redish white or pale yellowish and purplish, when dry orange, the longest one 10.5—11.5 mm; carina shortly and rather sparsely appressedly hairy outside; other petals more or less glabrous or sometimes sparsely hairy outside in apical part. Stamens: filaments free or connate over 0.5—(1) mm, widened above base and with a knob-like, shortly (half-)appressed hairy appendage at inner side, further glabrous; filament of lateral alternipetalous stamens hairy to base in two rows; anthers 0.6—0.9 mm long. Ovary patent hairy; style nearly glabrous to rather densely appressedly hairy; ovules 4. Fruit globose, c. 1.5 cm diam., ± shiny, brown, densely patent hairy; pedicel up to 3.5—(6) mm.

Distr. Malesia: Central Sumatra (Toba Lands, Pakajumbuh, Mt Sago), West and Central Java.

Ecol. Montane rain-forest, (200—)500—1300 m.
Flora Malesiana [ser. I, vol. 103]


Shrub or small tree, up to 10 m, 25 cm dbh. Twigs glabrous or rarely minutely patently hairy. Axillary buds oblong or sometimes ovate-lanceolate, (1.3-)3–6(–10.5) mm long, the longer ones strongly thickened at base and usually suddenly widened and flattened upwards, usually glabrous, the smaller ones less distinctly flattened and usually rather densely shortly hairy; buds of second order often present. Petiole (8–)15–18(–23) mm, glabrous to rather densely minutely hairy, usually with 2 small, prominent glands. Leaf-blade (linear-)lanceolate, (9-)22–47 by (1.3-)15–10(–20) cm; base usually cordate with the margins curved upwards and connate above the apex of the petiole, or flat and rounded to broadly cuneate, apex acutish; above usually slightly bullate between secondary nerves and intramarginal nerve, greyish green to brown; beneath usually brownish, glabrous to minutely patently hairy all over, secondary nerves (9-)13–20 pairs, mostly forming a distinct, nearly complete intramarginal nerve; glands 2–6(–20), usually near the midrib (if few, only present in basal part), 0.3–0.4 mm diam. Inflorescences sometimes also axillary on the older nodes; axes slightly angular, slightly grooved, main axis basally usually sparsely minutely appressed hairy, side axes and main axis in upper part more densely hairy; flowers solitary or very rarely with 2 together; lower bracts opposite. Pedicel (1-)1.5–2(–3.5) mm, more or less distinctly grooved, densely minutely appressed to patently hairy. Sepals often with minute, rather distinct glands; outer sepals (2.1-)2.8–3.8(–4.1) by (2.4-)3–4.9 mm; inner sepals 3.5 by (2.8-)3.4–4.6 mm. Petals pinkish to pale violet, the upper petals with a yellow spot, when dry dark red, the longest one (8.5-)9.5–12.5(–14.5) mm; carina rather densely appressed hairy outside, inside sparsely minutely hairy in apical part only, further glabrous; other petals very sparsely minutely hairy above base outside, sparsely patently hairy outside near apex, inside glabrous to hairy up to ± halfway. Stamens: filaments free or connate over 1(–2) mm, widened above base and especially those of abaxial stamens with a more or less distinct (half-)patently hairy knob-like thickening at inner side, further glabrous; anthers (0.6–)0.7–0.9(–1) mm long, ciliate along slits. Ovary (half-)patently hairy; style (rather) sparsely half-patently hairy in basal half, very sparsely hairy in apical half; glabrous near apex; ovules 4. Fruit gloular, 1.5–1.8 cm diam., rather dull, light to reddish brown, distinctly hairy; pericarp thin, brittle.

Distr. Malesia: Sumatra, Borneo.

Key to the varieties

1. Leaf-blade (4.5–)5–10(–20) cm wide. Secondary nerves 13–20 pairs, forming a nearly complete intramarginal nerve. a. var. adenotus
   1. Leaf-blade 2–5.2 cm wide. Secondary nerves 9–14 pairs, forming a weak, irregular intramarginal nerve. b. var. lineare

a. var. adenotus
Axillary buds (1.8-)3–6(–10.5) mm long. Petiole (10-)15–21 mm, glabrous or hairy. Leaf-blade (15-)22–47 by (4.5-)15–15 cm, base cordate to cuneate. Secondary nerves 13–20 pairs, forming a distinct, nearly complete intramarginal nerve. Flowers: upper petals glabrous or hairy inside to about halfway.

Distr. Malesia: Sumatra, Borneo.


Axillary buds at upper side partly enclosed by a distinct ridge formed by the twig, 1.3–2.2 mm long. Petiole (8-)10–12(–18) mm, glabrous. Leaf-blade linear-lanceolate with more or less parallel sides over most of its length, (9-)13–30 by (1.3-)2–5.2 cm, base rounded to obtuse. Secondary nerves 9–14 pairs, forming a weak, irregular intramarginal nerve. Flowers rather small in all parts; upper petals shortly patently hairy inside to about halfway. Fruit unknown.

Distr. Malesia: Borneo (Sabah).


Small tree, up to 8 m, 5 cm dbh. Twigs sparsely minutely hairy, glabrescent, older nodes often strongly thickened and with numerous adventitious buds. Axillary buds oblong, 6–9 mm long, basally narrowed and strongly thickened, sparsely shortly hairy, glabrescent. Petiole 15–18 mm, more or less densely shortly hairy, with 2(–4) more or less distinctly protruding small glands. Leaf-blade ovate-oblong to ovate-lanceolate, rarely elliptic, c. 20–40 by (6-)8–12(–15) cm, base cordate, the margins at base flat or only little upturned, apex gradually narrowed to shortly acuminate; above often slightly bullate between secondary nerves and intramarginal nerve, dark green to greenish brown; beneath sparsely minutely hairy on the nerves in basal part, secondary nerves 9–12 pairs, often irregular, forming a nearly complete, somewhat irregular, intramarginal nerve; glands few, situated in middle and basal part, 0.2(–0.4) mm diam. Inflorescences sometimes also on older shoots from adventitious buds, up to 22 cm.
long; axes angular, slightly grooved, densely shortly patently hairy; lower bracts opposite. *Pedicel* 2–3.5 mm, grooved, densely shortly half-patently hairy. *Sepals*: outer sepals 3.5–4.3 by 4.3–5 mm; inner sepals 5–5.9 by 4.3–4.5 mm. *Petals* dark red when dry, the longest one 15–18.5 mm; carina rather densely slightly appressedly hairy outside, glabrous inside except at base; other petals minutely sparsely appressedly hairy in basal part out-and-inside, further glabrous. *Stamens*: filaments widened and slightly thickened above base and only there densely half-patently hairy; anthers 1.1–1.2 mm long, ciliate along slits. *Ovary* stipitate for 1–1.5 mm, half-patently hairy; style densely hairy in basal part, upwards sparsely hairy to near apex; ovules 4. *Fruit* globular, c. 1.7 cm diam., dull brown, rather distinctly half-patently hairy; pericarp rather thin, brittle; pedicel up to 5–6 mm.

**Distr.** *Malesia*: Southern Philippines (Palawan, Sulu Is.: Tawitawi, Jolo).


Small tree, up to 15 m, 16 cm dbh. Axillary buds elliptic to oblong, 5–7 mm long. *Petiole* (18–)25–30 mm. *Leaf-blade* 22–42 by 7–15.5 cm; above rather dull, greenish, beneath dull, concolorous, secondary nerves c. 8–10 pairs, little prominent, in apical part forming an indistinct intramarginal nerve, venation obscure; glands 2–8, 2 situated at the very base and 0.6–1 mm diam., the other ones (if present) scattered, sometimes close to midrib, 0.5 mm diam. *Inflorescences* much shorter than the leaf; axes strongly flattened basally, grooved, brown, minutely hairy; lower bracts (sub)opposite. *Pedicel* 2.5–3.5 mm, grooved, densely shortly patently hairy. *Sepals*: outer sepals 2.8–3.5 by 3.6–4.4 mm; inner sepals 4.5–4.9 by 3.6–4.7 mm. *Petals* yellowish, when dry dark red with large incrustations, glabrous inside, the longest one 9–10.5 mm; carina appressedly hairy outside. *Stamens*: filaments widened above base and with a distinct, rather shortly (half-)appressedly hairy knob-like thickening at inner side, further glabrous; anthers 0.6 mm long. *Ovary* nearly sessile, appressedly hairy; ovules 4. *Fruit* unknown.

**Distr.** *Malesia*: Borneo (Sarawak: Semengoh; Sabah).


Tree, 14 m. Twigs minutely patently hairy. Axillary buds erect, oblong, c. 11–12 by 4 mm, base broad, rounded, apex rounded. *Petiole* 26–31 mm. *Leaf-blade* 6–13.5 by 4–7 cm, base rounded, apex rounded to slightly obtuse; above: midrib sunken in apical half, slightly prominent in basal half, second-

ary nerves slightly sunken; beneath glaucous-papillose, secondary nerves 6–8 pairs, forming an indistinct intramarginal nerve in apical part, venation hardly protruding; glands 1–3, situated in middle and apical part, mostly c. 0.4 mm diam., basal glands sometimes present, rather large. *Inflorescences* up to 15 cm long; axes dark, patently, extremely shortly hairy; lower bracts opposite. *Pedicel* 4 mm, grooved, densely very shortly half-patently hairy. *Sepals*: outer sepals 2.9 by 3.3 mm, slightly pubescent; inner sepals 4 by 3.3 mm. *Petals* dark red when dry, the longest one 11.5 mm; carina densely appressedly hairy outside; other petals glabrous to sparsely shortly hairy outside. *Stamens*: filaments connate over 0.5–0.8 mm between upper and lateral petals, connate over c. 1.5 mm between lateral petals and carina, the free parts constituted at very base and then widened and with a distinct densely hairy knob-like thickening at inner side, further glabrous; anthers 0.7 mm long. *Ovary* c. 1.5 mm stipitate, appressedly hairy; ovules 4. *Fruit* unknown.

**Distr.** *Malesia*: Borneo (Brunei: Andalau For. Res.).


Tree, up to 14 m. Axillary buds with the form of a clove; scales 6.5–12 mm long, at base slightly enlarged and convex, distinctly enlarged at the rounded to ± emarginate apex, and there with 2 more or less distinctly prominent knob-like appendages; buds of second order c. 5–6 mm long, hardly thickened at apex. *Petiole* 9–17 mm. *Leaf-blade* 8.5–18 by 3.5–6.5 cm; above greenish to brownish; beneath glaucous-papilllose, secondary nerves c. 7 or 8 pairs, forming an indistinct intramarginal nerve in apical half; glands few to rather numerous, mostly near the midrib, c. 0.2–0.3 mm, basal ones up to 0.5 mm diam. *Inflorescences* up to 20 cm long; axes dark, minutely patently hairy; in basal part flowers in clusters of up to 7 together; lower bracts opposite. *Pedicel* 4.5 mm, ± grooved, densely very shortly, ± appressedly hairy. *Sepals*: outer sepals 3 by 3.2 mm; inner sepals 4.1 by 4.1 mm, with tiny glandular spots at apex. *Petals* dark red when dry, the longest one 8.5 mm; carina appressedly hairy outside; other petals glabrous outside, the upper ones sparsely ciliate to half-way. *Stamens*: filaments widened above base and with a distinct densely appressedly hairy knob-like appendage at inner side, further glabrous; anthers 0.5 mm long. *Ovary* subsessile, half-patently hairy; style hairy in two rows to near apex; ovules 4. *Fruit* unknown.

**Distr.** *Malesia*: Borneo (Brunei, Sabah, Labuan l.), 3 collections.
Fig. 21. *Xanthophyllum bracteatum* Chodat. a. Habit, ×0.5; b. flower; c. flower, longitudinal section, gynoecium removed; d. gynoecium, all ×3; e. ovary, longitudinal section, ×6; f. carina, ×4; g. base of leaf with glands, ×2.5 (Edaño BS 28512).

Small tree, up to 10 m, 12 cm dbh. Twigs minutely patently hairy. Axillary buds erect, appressed against twig, scales laterally flattened, triangular, 3–4.5 mm long, minutely densely patently hairy. *Petciole* 9–10 mm, densely minutely hairy. *Leaf-blade* 11–18 by 3.5–5.5 cm; above rather dull, dark greenish to yellowish brown, midrib ± sunken, nervation rather obscure; beneath nearly concolorous, secondary nerves c. 6–9 pairs, not very distinct, in apical part forming an indistinct intramarginal nerve, venation rather obscure; glands 2 (or 3), situated near base, 0.4–0.7 mm diam. *Inflorescences* shorter than the leaves; axes dark, very densely more or less patently hairy; lower bracts opposite. *Pedicel* 2.5–3 mm, ± grooved, very densely shortly patently hairy. *Sepals*: outer sepals 2.2–2.5 by 3.4–3.6 mm; inner sepals 3.8–3.9 by 3.6–4.9 mm. *Petals* yellowish white, when dry dark red, the longest one 13–14 mm; carina densely more or less appressedly hairy outside; other petals glabrous. *Stamens*: filaments widened above base and with a knob-like shortly (half-)-appressedly hairy appendage at inner side, further glabrous; anthers 0.7–0.8 mm long, hairy or nearly glabrous at base. *Ovary* subsessile, half-patently hairy; ovules 4. *Fruit* unknown.

**Distr.** *Malesia*: Borneo (Sarawak: Semengoh).


Axillary buds erect or nearly so, mostly flattened against twig; scales ovate-lanceolate, 6–9 mm long, not thickened at base; buds of second order distinct, 3.5–5 mm long. *Petciole* 10–14 mm. *Leaf-blade* c. 6–12 by 2.5–5.8 cm; above greyish green to brownish green; beneath glaucous-papilllose, secondary nerves c. 5–7 pairs, usually forming an indistinct intramarginal nerve in apical part; glands rather numerous, scattered, 0.1–0.2 mm diam. *Inflorescences* about as long as the leaves; axes dark, minutely patently hairy; in basal part flowers with 3 together; lower bracts opposite. *Pedicel* 3.5–4 mm, very densely whitish shortly patently hairy. *Sepals*: outer sepals 3.2–3.7 by 2.9–3.3 mm; inner sepals 3.7–5.4 by 2.3–3.2 mm. *Petals* dark red when dry, the longest one c. 13 mm; carina densely half-patently hairy outside; other petals faintly hairy along midrib outside. *Stamens*: filaments c. 2 mm connate, the free parts constricted at very base and then widened and slightly thickened, only there densely half-patently hairy; anthers 0.7 mm long. *Ovary* half-patently hairy; ovules 4. *Fruit* unknown.

**Distr.** *Malesia*: Philippines (Luzon, Samar), 2 collections.


Axillary buds (ob)ovate-oblong to linear-lanceolate, 7–20 by 1.5–6 mm, basally slightly wrinkled, acute, more or less flat. *Petciole* 5–11(–14) mm, sometimes with glands. *Leaf-blade* 9.5–25 by 3–8 cm, rounded-attenuate to cordate; above (yellowish) green, midrib nearly flat to distinctly prominent; beneath glaucous-papilllose, secondary nerves 10–12 pairs, forming a rather distinct intramarginal nerve; glands scattered, numerous, 0.1–0.2 mm diam. *Inflorescences* up to 10 cm long; axes (rather) densely minutely patently hairy, smooth to pubulate, angular, reddish; flowers solitary or in basal part with up to 3 together, sometimes turned upside-down; lower bracts opposite. *Pedicel* 5–7 mm, slender, very densely patently shortly whitish hairy. *Sepals*: outer sepals c. 3 by 2.1 mm; inner sepals c. 5–5.5 by 4–4.5 mm. *Petals* dark red when dry, the longest one c. 14–17 mm; carina rather densely more or less appressedly hairy outside in middle and apical part; other petals nearly glabrous outside. *Stamens*: filaments connate over 1–3 mm, widened and hardly thickened above base, basally rather densely whitish hairy in 2 rows; anthers c. 1–1.2 mm. *Ovary* more or less patently whitish hairy; ovules 4. *Fruit* (immature) globular, yellowish brown; pericarp thin.

**Distr.** *Malesia*: Philippines (Luzon).


Tree, up to 33 m, 70 cm dbh. Axillary buds elliptic to oblong, (8–)11–20(–30) by 6–12(–14) mm; scales flat, wrinkled, indistinctly nervel, more or less shiny, sometimes in middle part with 1–4 rather indistinct glands, base shortly attenuate, apex rounded to obtuse. *Petciole* 7–15 mm. *Leaf-blade* (3–)4.5–12 (–19) by (1.8–)2.5–5(–7.5) cm, apex shortly acuminate to cuspidate; above ± shiny, brownish green; beneath yellowish brown, secondary nerves 7–10(–12) pairs, not forming an intramarginal nerve; glands few to many, mostly situated in middle and apical part, 0.2–0.4 mm diam. *Inflorescences* branched; axes densely patently shortly hairy; lower bracts opposite. *Flowers* unknown. *Fruit* globular, up to 1.7 cm diam., shiny, brown, slightly hairy; pericarp rather soft; pedicel 1.5–2.5 mm, densely shortly patently hairy. *Seed* 1; 3 ovules abortive.

**Distr.** *Malesia*: Borneo (Sarawak, Brunei, Sabah).

**Note.** Although quite a number of collections are noted, these are either vegetative or in fruit.

Tree, up to 21 m, 23 cm dbh. Axillary buds inserted (1.5–)3–15 mm above the axils on 1–2 mm long stalks; scales elliptic to linear-lanceolate, 6–18 by 1.5–8 mm long, faintly nervet. Petiole 7–10 mm, glands present or not. Leaf-blade 8–14 by 2.5–5 cm; above often slightly bulate between the secondary nerves, mostly dark green, secondary nerves finely prominent to obscure, venation obscure to finely prominent; beneath glaucous-papilllose, secondary nerves 6–8 pairs, forming a ± distinct intramarginal nerve; glands either not numerous, mostly situated near midrib, and c. 0.3 mm diam., or numerous, scattered, and 0.1–0.2 mm diam. Inflorescences shorter to much longer than the leaves, the lower branches distinctly supra-axillary, (sub)opposite; axes densely minutely hairy, more or less grooved, angular. Pedicel 1.5–2 mm, grooved, densely patently minutely hairy. Sepals glabrous inside except for a few hairs at the very base; outer sepals c. 2 by 2 mm; inner sepals c. 3.5 by 3 mm. Petals incompletely known, carina and lateral petals unknown; upper petal probably c. 8.5 mm long, sparsely hairy at apex. Stamens: unknown. Ovary whitish hairy (short and long fine hairs mixed); style and stigma unknown; ovules 4. Fruit unknown.

Distr. Malesia: Central Sumatra, Borneo (Sarawak, SE. Kalimantan), 4 collections.


Very low shrub or small tree, 1–10 m, up to 10 cm dbh. Axillary buds narrowly triangular, c. 2.5–6 mm long, basally and centrally thickened, acute, shiny. Petiole 3–6(–7) mm, often rather shiny. Leaf-blade 3.8–25 by 1.6–10 cm, base obtuse to cordate or cuneate, apex acutish; above rarely faintly bulate between the secondary nerves, light to dark greyish green, midrib mostly slightly sunken, sometimes a little prominent, venation rather indistinct; beneath glaucous-papilllose to nearly smooth, secondary nerves (5 or) 6–13 pairs, forming a mostly rather in-

distinct intramarginal nerve; glands numerous, scattered, c. 0.1 mm diam., the basal ones often somewhat larger. Inflorescences unbranched or rarely with one branch, much shorter than to three times as long as the leaves; axes mostly very slender, mostly less than 1 mm thick, (rather) sparsely minutely hairy; in basal part flowers usually with 3 together; bracts small, either with 2 large glands (in Bornean material) and then rather long-persistent, or eglandular (in Malayan and Philippine collections) and then soon caducous; lower bracts (sub)opposite. Pedicel 2–25 mm, slightly grooved, apparently to patently, sparsely to rather densely hairy, rarely glabrous. Sepals rarely glabrous outside; outer sepals (1.5–)2–4 by (1.3–)2–3.5 mm, without or with (in most Bornean material) very distinct glands; inner sepals 3–6 by 4–6 mm. Petals white or pinkish, when dry brownish to dark reddish, nearly glabrous, apically with few hairs, basally inside slightly hairy, the longest one 11–23 mm. Stamens: filaments free or connate over to upper 2 mm; anthers 2–2.5 mm long, minutely hairy all over. Ovary sessile to distinctly stipitate, appressedly whitish hairy; ovules 8–15. Fruit globose, up to 1.8–3 cm diam., dull, light brownish; pericarp thin, rather brittle.

Distr. Malesia: Malay Peninsula, Borneo, Philippines.

KEY TO THE SUBSPECIES

1. Inflorescence less than half as long as the leaves. Inner sepals 3–3.8 mm long. Longest petals 11–15 mm ............... a. ssp. discolor
1. Inflorescence 0.5–3 times as long as the leaves. Inner sepals 5–6 mm long. Longest petals 15–23 mm ............... b. ssp. macranthum

a. ssp. discolor — X. discolor CHODAT. — X. hypoleucum MERR.

Very low shrub or small tree, up to 10 m. Secondary nerves (5 or) 6 or 7(–9) pairs. Inflorescences mostly much less than (rarely up to) half as long as the leaves, often few-flowered. Pedicel 2–8.5 mm. Sepals: outer sepals (1.5–)2–2.5 by (1.3–)2–2.5 mm; inner sepals 3–3.8 by 4–4.5 mm. Longest petals 11–15 mm. Fruit up to 1.8 cm diam.

Distr. Malesia: Malay Peninsula (Johore; Singapore), Borneo.


Low shrub or small tree up to 8 m. Secondary nerves 6–13 pairs. Inflorescences half as long to three times as long as the leaves, many-flowered. Pedicel 10–25 mm. Sepals: outer sepals 2.8–4 by 2.2–3.5 mm; inner sepals 5–6 by 4.2–6 mm. Longest petals 15–23 mm. Fruit up to 3 cm diam.
Distr. Malesia: throughout the Philippines.


Small shrub or tree, up to 12 m, 30 cm dbh. Axillary buds ovate-oblong, 3.2–7 mm long, acute, flat, but basally strongly thickened, there often with exuberant cork-forming which may hide the scale completely, greyish to cream-coloured, more or less shiny. Petiole 8–15 mm, often seemingly much longer because of the long-attenuate leaf base. Leaf-blade (5–)7–28 by 2.3–10 cm, base long-attenuate, above dark green, shiny, midrib slightly sunken to slightly prominent basally, further ± prominent, secondary nerves and venation very distinct, sometimes even more distinct than beneath; glaucous-papilllose beneath, secondary nerves c. 4–6 pairs, first nerves reaching to halfway or further, intramarginal nerve in apical part rather distinct; glands very numerous, scattered, 0.1–0.2 mm diam. Inflorescences unbranched, shorter than the leaves; axes minutely rather sparsely appressed hairy to nearly glabrous; in basal part flowers with up to 3 together. Pedicel 2.5–6 mm, more or less smooth, minutely sparsely to densely, appressed hairy. Sepals sparsely hairy along the midrib to (nearly) glabrous outside, often some with rather distinct glandular spots; outer sepal 2.7–2.9 by 2.1–2.4 mm; inner sepal 3.1–3.3 by 3.2–3.2 mm. Petals creamish white to light purplish, the upper ones with a yellow spot, when dry orange, glabrous outside, apically and basally sparsely ciliate, the longest one 11–13 mm. Stamens: filaments c. 1.5 mm conuate; anthers 2 mm long, ciliate along slits. Ovary minutely appressed hairy (hairs 0.1–0.2 mm long); style glabrous in apical part; ovules 9–11. Fruit globular, c. 1.5 cm diam., minutely appressed hairy; pericarp thin, brittle; pedicel up to 7 mm.

Distr. Malesia: Borneo (Sarawak, Sabah).

Note. Resembling 45. X. pulchrum ssp. stapfii, differing in the shorter, appressed hairs of inflorescence and flowering parts, in the greater number of secondary nerves which form a distinct intramarginal nerve, in the longer pedicel, and in the smaller sepals.


Small shrub to small tree, up to 8 m. Twigs glabrous to minutely patently hairy. Axillary buds ovate, 1.8–3.5 (–57) mm long, very thick (mostly not especially basally), obtuse, light brown and often more or less reddish, often irregular because of cork-forming. Petiole 4–9 mm, the young ones nearly smooth, not transversely wrinkled, glabrous to minutely densely patently hairy all round, the older ones soon becoming transversely cracked, more or less corky; glands often present, mostly rather distinct. Leaf-blade (5.5–)7.5–30 by 2.4–11.5 cm; base rounded-cordate, rarely rounded, obtuse, or cuneate-rounded, apex acutish, rarely rounded; above rarely bullate between midrib and secondary nerves, greyish green, midrib slightly sunken to flat, rarely

titious buds often present, numerous. Petiole (8–)10.5–14 mm, smooth. Leaf-blade 13–32 by 5–10.5 cm, base attenuate to cordate, apex acutish; above dark green, often slightly bullate between the secondary nerves, midrib prominent, often with a groove from halfway down; beneath glaucous-papilllose, secondary nerves 11–14 pairs, forming a rather distinct complete intramarginal nerve; glands numerous, smaller than 0.1 mm diam. Inflorescences 1.5–6 cm long, also arising from adventitious buds on older nodes, unbranched; axes minutely appressed hairy (hairs 0.1 mm long). Pedicel 5–6 mm, minutely appressed hairy (hairs 0.1 mm long). Sepals: outer sepals 2 by 2 mm; inner sepals 3.2 by 2.7 mm. Petals subglabrous, brownish orange when dry, the longest c. 1.5 mm. Stamens: filaments c. 1.5 mm conuate; anthers 2 mm long, ciliate along slits. Ovary minutely appressed hairy (hairs 0.1–0.2 mm long); style glabrous in apical part; ovules 9–11. Fruit globular, c. 1.5 cm diam., minutely appressed hairy; pericarp thin, brittle; pedicel up to 7 mm.

Distr. Malesia: Borneo (Sarawak, Sabah).

Note. Resembling 45. X. pulchrum ssp. stapfii, differing in the shorter, appressed hairs of inflorescence and flowering parts, in the greater number of secondary nerves which form a distinct intramarginal nerve, in the longer pedicel, and in the smaller sepals.


Small tree, up to 9 m, 12 cm dbh. Axillary buds oblong, 3–6 mm long, basally strongly thickened, obtuse, probably glabrous; secondary and adventi-
indistinctly prominent; beneath glaucous-papillosse, secondary nerves (6 or) 7–12 (or 13) pairs, forming mostly an indistinct intramarginal nerve in apical half; glands numerous, scattered, c. 0.1–0.2 mm diam. Inflorescences at end of young twigs but also axillary, not rarely on old nodes, unbranched, shorter than the leaves, many-flowered; axes stiff, minutely patently hairy; in basal part flowers with up to 3 together. Pedicel 2.5–3.5(–4.5) mm, finely grooved, very densely minutely patently hairy. Sepals often with rather distinct glands; outer sepals 2.1–5 by 2.7–4.2 mm; inner sepals 3.2–6 by 3.2–4.9 mm. Petals pink or whitish, when dry red or brownish orange, slightly hairy apically and basally inside, further glabrous, the longest one 13–18 mm. Stamens: andthers (1.3–)1.7–2.5(–3.6) mm long, faintly hairy at base, sparsely ciliate along slits. Ovary up to 2 mm stipitate, patently light brownish pubescent; style glabrous in apical part; ovules 12–16. Fruit gloular, up to 2 cm diam.; pericarp thin.

Distr. Malesia: Sumatra, Malay Peninsula, Borneo.

**KEY TO THE SUBSPECIES**

1. Secondary nerves 6 or 7 pairs. Longest petals 12–16 mm. Anthers 1.3–1.8 mm long
   
   a. ssp. pulchrum

1. Secondary nerves 7–13 pairs. Longest petals 15–18 mm. Anthers (1.7–)1.3–3.6 mm long
   
   b. ssp. stapfii

a. ssp. pulchrum — X. pulchrum King.

Petiole 4–6.5 mm. Secondary nerves (6 or) 7 pairs. Outer sepals 2.1–4 by 2.7–3.9 mm, inner sepals 3.2–4.7 by 3.4–4.3 mm. Longest petals 12–16 mm.

Distr. Malesia: Sumatra, Malay Peninsula (incl. Penang l.).


Petiole (4–)5–9 mm. Secondary nerves 7–12 (or 13) pairs. Outer sepals 3.4–5 by 3.1–4.2 mm, inner sepals 3.6–6 by 3.2–4.9 mm. Longest petals 15–18 mm.

Distr. Malesia: Borneo (Sarawak, Kalimantan).


Tree, up to 12 m, 17 cm dbh. Twigs very densely patently hairy (hairs up to 1 mm). Axillary buds triangular, 0.5–4.5 mm long, basally strongly thickened, acutish. Petiole 5–6 mm, very densely hairy. Leaf-blade 9.5–19 by 4–8 cm, base cordate, apex acutish; above dark green; beneath glaucous-papillosse, rather sparsely hairy, midrib rather densely hairy, secondary nerves c. 6–8 pairs, forming an indistinct intramarginal nerve in apical part; glands numerous, scattered, c. 0.1 mm diam. Inflorescences unbranched, shorter than the leaves; axes densely minutely hairy (hairs up to 0.4 mm); in basal part flowers with up to 3 together, sometimes turned upside-down. Pedicel 7.5–9.5 mm, densely patently minutely hairy (hairs up to 0.25(–0.4) mm). Sepals nearly glabrous (very shortly hairy); outer sepals 2.5–2.7 by 3–3.6 mm, with rather distinct glandular spots; inner sepals 3.2–4 by 2.8–3.4 mm. Petals orange-red when dry, glabrous except for the ciliate base, the longest one c. 16–16.5 mm long, minutely hairy at base along margin, further glabrous. Stamens: anthers 2.2 mm long. Ovary patenty hairy; style glabrous in apical part; ovules 13. Fruit (immature) apically pointed; pedicel c. 10–12 mm.

Distr. Malesia: Borneo (Sarawak).


Shrub to tree, 3.5–23 m, 60 cm dbh. Twigs densely patently brownish hairy, glabrescent. Axillary buds narrowly triangular, 1.5–3.5 mm long, hairy. Petiole 1.5–2.5(–3) cm, very densely patently hairy. Leaf-blade (5–)9–11 by (1–)1.5–3(–4) cm, base cuneate to rounded or slightly cordate, apex usually acutish; above dark green, shiny, beneath glaucose-papillosse, hairy mainly on midrib, secondary nerves c. 7 or 8 pairs, forming an indistinct intramarginal nerve or not; glands very numerous, scattered, c. 0.1 mm diam. Inflorescences unbranched, as long as the leaves; axes densely minutely patently hairy, some hairs up to 0.5 mm. Pedicel (9–)10–15 mm, minutely patently hairy. Sepals very sparsely minutely hairy outside, glabrous inside except at very base; outer sepals c. 2–2.5 by 2 mm; inner sepals c. 3–3.5 by 2–2.4 mm. Petals pinkish, when dry orange-red, glabrous except for ciliate base, the longest one 12.5 mm. Stamens: anthers 1.5–1.6 mm long, sparsely minutely hairy at base. Ovary nearly sessile, half-patently brownish pubescent; style glabrous in apical part; ovules 9–11. Fruit gloular, c. 2.2 cm diam., light brownish, hairy; pericarp thin.

Distr. Malesia: Borneo (E. Sabah).


Shrub or small tree, up to 5 m, 10 cm dbh. Twigs very densely patently hairy. Axillary buds narrowly triangular, (1.5–)3–5 mm long, basally thickened.
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Shrub or small tree, up to 12 m, 13 cmdbh. Twigs very densely patently hairy. Axillary buds ovate-oblong, (1.5–)2.5–5(–6) mm long, densely hairy. *Petiole* c. 4–7 mm, very densely hairy. *Leaf-blade* 11–31 by 3–9 cm, base cordate, covering upper side of petiole, apex acutish; above green, dull, hairy on the midrib; midrib distinctly sunken, rarely flat, secondary nerves and intramarginal nerve faintly sunken, rarely slightly prominent, venation little prominent; beneath glaucous-papillose, pubescent all over, secondary nerves c. (9–12) pairs, forming a distinct intramarginal nerve; glands very numerous, scattered, c. 0.1 mm diam. *Inflorescences* unbranched, shorter than the leaves, often curved downwards; axes sparsely minutely hairy (hairs up to 0.2 mm long); in basal part flowers with 3 together. *Pedicle* 2.5–5 mm, minutely densely hairy (hairs up to 0.2–0.3 mm). *Sepals* rather densely minutely hairy outside (hairs 0.1 mm), subglabrous inside, often with tiny, rather indistinct glandular spots; outer sepals 1.8–3 by 2.1–2.6 mm; inner sepals 2.7–4.3 by 2.7–3.5 mm. *Petals* (light) purple to rosacea-violet, when dry orange-red, ciliate at base and apex, further glabrous, the longest one 11–12(–147) mm. *Stamens*: filaments free or 0.4 mm conuate; anthers 0.9–1.4 mm long, glabrous to shortly hairy at base. *Ovary* subsessile or c. 1.5 mm stipulate, patently hairy; style glabrous in apical half; ovules 8–14. *Fruit* globular, 1.2–1.5 cm diam., usually with remnant of style, hairy; pericarp thin; pedicel curved.

**Distr.** Malesia: Borneo (Sarawak, Sabah, NE. Kalimantan).


Small tree, 2.5–15 m. Twigs very densely patently hairy (hairs up to 1 mm long). Axillary buds narrowly triangular, 4–6(–7.5) mm long, hairy. *Petiole* c. 5 mm, densely pubescent. *Leaf-blade* 7–19 by 3.5–5.5 cm, base obtuse to rounded, apex acutish; above dark green, midrib, secondary nerves and part of finer nervation sunken, midrib hairy at very base; beneath green, smooth or indistinctly papillose, hairy on midrib and on basal part of nerves, secondary nerves c. 8 pairs (difficult to count), tertiary nerves strongly protruding, blade bullate in-between; finer nerves not strongly prominent; glands numerous, scattered, c. 0.1 mm diam. *Flowers* unknown. *Inflorescences* 0.8–4.5 cm long, unbranched; axes shortly sparsely hairy (hairs up to 0.25 mm long). *Fruit* globular, c. 1.5 cm diam., sessile, with remnant of style, hairy; pedicel 5–10.5 mm, minutely patently hairy (hairs up to 0.2 mm long). *Seed* 1; abortive ovules 11–13.

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


Axillary buds 0.8–1.5 mm long, minutely hairy, glabrous. *Petiole* 3–4 mm. *Leaf-blade* 10–20.5 by 4–5.5 cm, base cordate to cordate-truncate, apex distinctly acuminate; upper side dull, greyish green, midrib prominent, nervation rather obscure; beneath greenish, secondary nerves 8–10 pairs, rather indistinct, forming an indistinct intramarginal nerve in upper part, venation rather obscure; glands numerous, 0.2–0.3 mm diam. *Inflorescences* unbranched or with one side-branch, up to 8 cm long; axes angular, orange, rather sparsely appressedly minutely hairy. *Pedicel* 4–4.5 mm, rather densely appressedly minutely hairy. *Sepals*: outer sepals 2.7–3 by 1.8–2.2 mm, with rather distinct glands; inner sepals
3.5–4 by 2.7–3.2 mm. Petals whitish tinged with rosa, when dry reddish orange, the longest one 13 mm; carina outside glabrous to rather sparsely patently hairy near base, near apex very sparsely appressed hairy, further glabrous; other petals glabrous. Stamens: filaments 0.3 mm connate; anthers 1–1.2 mm long, glabrous at base, ciliate along slits. Ovary appressedly rather shortly brownish hairy; ovules 11. Fruit unknown.

Distr. Malesia: S. Sumatra (Lampong Distr.), one collection.


Shrub or small tree, 3–6 m. Axillary buds c. 1 mm long. Petiole 5–7 mm. Leaf-blade 4.5–13.5 by 1.9–5.3 cm, apex cuspidate; above greenish to reddish brown, dull, midrib sunken, hardly visible, nerves obscure to slightly protruding; beneath light greenish to reddish brown, secondary nerves c. 5 pairs, rather indistinct to slightly protruding, forming an indistinct intramarginal nerve, venation indistinct; glands rather few, near midrib, 0.3–0.4 mm diam. Inflorescences branched or unbranched, shorter than the leaves; axes glabrous, more or less smooth. Pedicel 8–15 mm, grooved, dark, glabrous. Sepals: outer sepals 1.8–2.1 by 2.4 mm; inner sepals 2.8–3 by 2.8 mm. Petals white with red spots, when dry reddish orange, the longest one 11–13 mm; carina shortly sparsely appressed hairy outside, shortly hairy inside; other petals sparsely hairy outside near apex. Stamens: anthers c. 0.5 mm long. Ovary glabrous or with a few hairs; style very sparsely more or less appressed hairy; ovules 8. Fruit unknown.

Distr. Malesia: NE. Sumatra (Sibolangit), 2 collections.


Tree, up to 12 m, 20 cmdbh. Twigs sparsely short­ly appressed hairy, glabrescent; axillary region shortly densely appressed hairy. Axillary buds mostly 3, inconspicuous, shortly densely appressed hairy, the upper one 1–2 mm supra-axillary, sometimes more distinct and up to 0.8 mm long. Petiole 6–16 mm, appressedly shortly hairy. Leaf-blade 7–14 by 2.5–5 cm, apex shortly acuminate to cuspidate; above (greenish) brown, midrib sunken to slightly prominent; beneath reddish brown, sometimes glaucous, sparsely shortly hairy, secondary nerves 5–7 pairs, sometimes forming an indistinct intramarginal nerve; glands 0–2, mostly close to midrib, 0.2(–0.4) mm diam. Inflorescences up to 10 cm long, with 2 opposite branches directly above base; axes densely appressedly shortly hairy; lower bracts of side axes opposite. Pedicel 2–2.5 mm, densely appressedly shortly hairy. Sepals sometimes with tiny glands; outer sepals 1.4–1.5 by 1.3–1.4 mm; inner sepals 2.1–2.2 by 2.2–2.3 mm. Petals white, when dry orange-red, glabrous inside, the longest one 6.5 mm; carina appressedly hairy outside; other petals sparsely hairy apically. Stamens: anthers 0.3–0.4 mm long. Ovary (sub)essisi, faintly ribbed, densely shortly appressedly hairy; ovules 4. Fruit globular, up to 2.2 cm diam., smooth, rather dull, brown, sparsely appressed hairy; pericarp c. 4 mm thick, rather hard; pedicel up to 4 mm.

Distr. Malesia: Malay Peninsula (Perak; Treng­ganu; Fraser’s Hill).


Shrub or tree, 3–20 m, up to 20 cm dbh. Twigs glabrous to minutely patently hairy, mostly soon glabrescent; axillary region shortly densely patent­ly hairy. Axillary buds 2–4, usually less than 0.5 mm long, mostly very densely hairy, the upper one sometimes slightly supra-axillary. Petiole 3–9(–11), exceptionally up to 14 mm, glabrous to shortly rather densely hairy in the upper groove, rarely (in some Sumatran coll.) shortly hairy all round; glands mostly indistinct. Leaf-blade rarely linear-lanceolate, (2.5–)3.5–15(–18) by (1–)2–5(–7) cm, apex acuminate to cuspidate; above sometimes slightly bullate between the secondary nerves, greyish green, midrib slightly sunken or sometimes flat to slightly prominent; beneath rather dull, mostly glabrous, yellowish green, secondary nerves 3–5 (or 6) pairs, forming a rather distinct intramarginal nerve; glands (0–)2–7(–11), 0.1–0.3
(--0.4) mm diam. Inflorescences solitary or with 2 together, mostly unbranched or sometimes with a few short side axes at base; axes angular to terete, minutely hairy; flowers solitary or in basal part with 3 together; bracts and bracteoles relatively long-persistent. Pedicel (1 -- 2) -- (4 -- 7.5) mm, densely minutely hairy. Sepals: outer sepals 1.6 -- 2.3 by 1.4 -- 2.3 mm; inner sepals 2.6 -- 3.6 by 2 -- 3.3 mm. Petals: white, when dry: yellowish, the longest one 7 -- 8.5(--9) mm; carina mostly bent outwards in open flowers, thus exposing the stamens, rather densely appressed hairy outside, inside minutely hairy in apical part, ciliate in basal half; other petals glabrous to sparsely hairy outside at apex. Stamens: anthers (0.4--) 0.5 mm long. Ovary (sub)sessile, more or less ribbed, more or less appressed hairy with hairs of different length; ovules 4. Fruit globose to broadly ellipsoid, sometimes irregularly 2 -- 4-sulcate, 1.2 -- 1.8 cm diam., more or less smooth to strongly warty, light brown, velvety to densely appressed hairy.

**Key to the subspecies**

1. Fruit with distinct warps arranged in longitudinal rows .................. a. ssp. eurynchum

1. Fruit more or less smooth, transversely wrinkled or finely rugose or irregularly grooved b. ssp. maingayi


Fruit globose, 1.5 -- 1.8 cm diam., strongly warty, densely appressed hairy between the warps.

**Dist.** S. Thailand; in *Malesia*: Malay Peninsula (incl. Penang 1.), Sumatra.


Fruit broadly ellipsoid, often irregularly formed, 1.2 -- 1.5 cm diam., sometimes 2 -- 4-sulcate, surface at lateral sides usually with depressions of irregular size or transversely wrinkled, sometimes finely rugose, very densely shortly velvety.

**Dist.** S. Thailand; in *Malesia*: Malay Peninsula (incl. Singapore).


Shrub to small tree, up to 10 m. Twigs shortly densely patently to appressedly hairy, rarely glabrous except for the densely hairy area above the leaf axil. Axillary buds 2 or 3, densely hairy, up to c. 0.5 mm long. Pediole (5--)7--11(--14) mm, usually not transversely wrinkled, densely minutely hairy all round, rarely hairy only in the upper groove, often with rather distinct prominent glands. Leaf-blade 10--30 by 3.5--13 cm, base rarely coriaceous; above often slightly binate between the secondary nerves, mostly greyish green, midrib deeply sunken and mostly hairy in basal part; beneath yellowish green, rather dull, minutely hairy or rarely glabrous, secondary nerves 8--15 pairs, forming a distinct intramarginal nerve; glands (2--)4--14, often (very) close to the midrib, sometimes present only in upper part, (0.3--)0.5--0.7 mm diam. Inflorescences shorter than to ± as long as the leaves; axes strongly ribbed, flattened at base, densely minutely hairy; in basal part flowers with 3 together; bracts and bracteoles relatively long-persistent. Pedicels 2.5--7(--7) mm, densely minutely hairy. Sepals: outer sepals 2.1--3 by 1.5--2.1 mm, sometimes with small glands; inner sepals 2.5--4 by 2.2--2.5 mm. Petals white to lilac, the upper ones with a yellow spot, when dry yellowish, the longest one 5.8--7.5(--8) mm; carina densely minutely hairy in apical part outside and inside; other petals sparsely hairy outside in apical part, lateral petals minutely hairy inside above insertion of filaments, upper petals rather densely patently hairy inside up to apex. Stamens: filaments connate over 0.5--2 mm or sometimes triadphous, sparsely minutely hairy in basal part to densely more or less patently hairy in middle part; anthers 0.4--0.5 mm long. Ovary patently to appressedly hairy; style patently hairy in basal part, in apical half sparsely hairy to glabrous; ovules 4. Fruit more or less globose, up to c. 1.5 cm diam., verrucately ribbed to strongly tuberculate-warty, apically rounded or with the style scar sunken; pedicel 2--6 mm.

**Dist.** Peninsular Thailand; in *Malesia*: Malay Peninsula (incl. Penang 1.).


Shrub to small tree, up to 10 m. Twigs rather densely hairy in axillary area, further glabrous to sparsely minutely hairy. Axillary buds 2--4, up to 0.5 mm long, hairy. Pediole (12--)15--21(--27) mm, glabrous to sparsely minutely hairy, not transversely
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winkled, often with glands. Leaf-blade 12.5–40 by 4.5–12(–13) cm, base cuneate to rounded or cordate; above often slightly bullate between the secondary nerves, greenish to yellowish brown, midrib deeply sunken; beneath yellowish green, mostly glabrous, secondary nerves 12–20 pairs, forming a distinct intramarginal nerve; glands mostly numerous, scattered, 0.1–0.2 mm diam. Inflorescences sometimes also on older nodes, shorter than the leaves; axes strongly flattened basally, ribbed, densely minutely hairy; in basal part flowers with 3 together; bracts and bracteoles relatively long-persistent. Pedicel 2–4 mm, minutely hairy. Sepals: outer sepals 2.3–3.3 by 2.1–3.3 mm, often with glands; inner sepals 2.8–4 by 2.5–4 mm. Petals light purple, when dry pale yellow, the longest one 8.5–11.5 mm; carina sparingly minutely appressedly hairy outside, glabrous inside; other petals slightly hairy basally, further glabrous. Stamens: filaments connate over (0.5–)1–3 mm, rarely some filaments free; anthers 0.5–0.9 mm long. Ovary (sub)sessile, ribbed, appressedly hairy; ovules 4. Fruit ovoid, c. 2 by 1.5 cm, apically shortly but distinctly beaked, strongly verrucately ribbed; pedicel 3–5 mm, minutely hairy.

Distr. Malesia: Malay Peninsula.


Tree, up to 10 m, 10 cm dbh. Twigs very densely brownish patently hairy with a mixture of very small and long hairs. Axillary buds nearly completely covered by indumentum, narrowly triangular, possibly up to 2.5 mm long. Petiole 4–10 mm, very densely patently pubescent. Leaf-blade 5–24 by 1.5–8.5 cm, base obtuse to slightly cordate, apex obtuse to cupuldate; above greyish green to light brownish, midrib and nerves sunken, venation obscure; beneath concolorous, rather densely patently pubescent, secondary nerves 5–8 pairs, forming a distinct intramarginal nerve; glands 2–8, up to 0.1 mm diam. Inflorescences unbranched or basally with a pair of side axes, shorter than to as long as the leaves; axes strongly, flattened and ribbed at base, densely rather shortly hairy, mixed with longer patent hairs; bracts and bracteoles small, relatively long-persistent. Pedicel 2.5–5.5 mm, ribbed, minutely densely patently hairy. Sepals: outer sepals 2.4–3 by 2.1–3.1 mm; inner sepals 3.4–3.8 by 2.9–3.5 mm. Petals purplish, when dry brownish orange, the longest one 7.5–10 mm; carina minutely hairy outside, inside minutely appressedly hairy in apical and basal part; other petals minutely patently hairy in apical part outside, upper petals inside glabrous to rather densely patently hairy. Stamens: filaments free or 1 mm connate, exserted from the carina in open flowers; anthers c. 0.5–0.7 mm long. Ovary more or less patently pubescent; ovules 4. Fruit (immature) shortly beaked or apically rounded, verrucately ribbed.

Distr. Malesia: Malay Peninsula (Pahang, Johore).

2b. Subsection Eystathes

Twigs and inflorescence axes sometimes with minute nodal appendages. Axillary buds (2 or) 3–5(–7), often all distant and supra-axillary. Seed(s) 1(–4); testa without a hard inner layer; albumen very thin; embryo without flattened areas near the base, radicle not exserted.


Tree, up to 30 m, 40 cm dbh. Axillary buds 0.8–1.6 mm long, faintly keeled. Petiole 6–10 mm. Leaf-blade 4–13.5 by 1.3–6.5 cm; above green; beneath light green, papillose, secondary nerves c. 6–8 pairs, forming an indistinct intramarginal nerve or not; glands rather numerous, scattered, c. 0.2–0.4 mm diam., basal glands c. 0.6–1.5 mm diam. Inflorescences up to c. 8 cm long; axes light brownish, slender, rather thinly minutely hairy; in basal part flowers with 3 together. Pedicel 2.5 mm, grooved, rather densely minutely more or less patent hairy. Sepals: outer sepals 2.4 by 2.1 mm; inner sepals 2.9 by 2.5 mm. Petals yellowish orange when dry, the longest one c. 7 mm; carina woolly hairy outside in apical half; other petals outside with a few hairs at apex and at base. Stamens: anthers 0.35–0.4 mm long. Ovary appressedly hairy; ovules 4. Fruit unknown.


Note. Part of the flowers of the type collection have abnormally developed ovules; these vary in number from 1–3 and they are placed basally in the ovary and have a distinct funiculus. The majority of the ovaries, however, contained 4 laterally inserted, sessile ovules.


Tree, up to 35 m, 65 cm diam. at 5 m. Nodal appendages extremely small, present on very short
straight ridges adjoining the insertion of the petiole. Axillary buds 0.5-1(-1.5) mm long, blackish, rather densely hairy. *Petiole* 7.5-10 mm. *Leaf-blade* 6-17 by 1.7-6.5 cm, base rounded to narrowly cuneate, margin slightly undulate, apex acutish to shortly acuminata; above yellowish green or brownish, midrib nearly flat to slightly protruding, sometimes at very base a little sunken; beneath glaucous-papillose, secondary nerves 5-8 pairs; glands 6-12, situated half-way between midrib and margin or near midrib, 0.3-0.5 mm diam., the basal ones mostly larger. *Inflorescences* about as long as the leaves; axes flattened at base, blackish, rather densely hairy; lower bracts (sub)opposite. *Pedicel* 3-4.5 mm, very densely more or less appressedly shortly hairy. *Sepals* rather sparsely appressedly hairy outside, (sub)glabrous inside; outer sepalas 2.2-2.9 by 2.8-8 mm; inner sepalas 3.1-3.6 by 2.5-3.2 mm. *Petals* brownish orange when dry, the longest one 10-12.5 mm; carina shortly appressedly hairy outside along median veins, further glabrous outside. *Stamens*; anthers 0.3-0.4 mm long, sparsely hairy at base. *Ovary* subsessile, rather sparingly hairy; style sparsely appressedly hairy at very base only, further glabrous; ovules 4. *Fruit* more or less apple-shaped, up to 8 cm diam., the very short pedicel enveloped by the pericarp; pericarp very hard, in mature fruit up to 3 cm thick when dry. *Seed* (or '1-more' according to Ng, l.c.), up to 2 cm diam.

**Distr.** *Malesia*: Southern half of Sumatra, Malay Peninsula.


Low shrub or small tree, 3-12 m, 18-20 cm dbh. Twigs often sparsely appressedly hairy when young, soon glabrescent. Nodal appendages bluntly conical to triangular, up to 0.2 mm long but often smaller.

Axillary buds 2-3, up to 2 mm long, sessile or the upper very shortly stipitate, acutish, often distinctly keeled, more or less densely shortly hairy. *Petiole* 3-5 mm, ± indistinctly transversely wrinkled, brownish, often sparingly thinly hairy when young, glabrescent. *Leaf-blade* 5-14 by 1.4-4(-5.5) cm, margin more or less distinctly undulate, often a little incurved, apex acutish, rarely shortly acuminata; above yellowish green to brown, midrib flat to slightly prominent in apical half, in basal half with a central groove; beneath light yellowish or brownish, papillose, midrib glaucous or sometimes sparsely appressedly hairy, secondary nerves mostly hardly distinct from finer veins, c. 8-14 pairs, not forming an intramarginal nerve; glands mostly numerous, 0.2-0.3 mm diam., but sometimes larger (up to 0.8 mm) and then of irregular form. *Inflorescences* mostly longer to much longer than the leaves, basally branched but sometimes seemingly unbranched if lower bracts resemble normal leaves; axes mostly distinctly flattened basally, rust-brown, more or less densely patently shortly hairy; in basal part flowers with 3-5 together, solitary in apical part. *Pedicel* 2.3-5.5 mm, ± densely patently shortly hairy. *Sepals*: outer sepals 1.7-2.2 by 1.5-2 mm; inner sepals 2.2-2.7 by 2.2-2.9 mm. *Petals* pinkish or white, the upper ones often with a yellow spot, when dry yellowish, the longest one 6-9 mm long; carina rather densely (woolly) hairy outside; other petals hairy at very apex. *Stamens* 8, rarely in some flowers 9; anthers 0.3-0.5 mm long. *Ovary* appressedly hairy; ovules 4. *Fruit* broadly ellipsoid to globular, 1.2-3.5 cm diam., mostly brown, pericarp often wrinkled when dry, rather thick, soft. *Seed(s)* 1 or 2.

**Distr.** Continental SE. Asia (Bangla Desh, Burma, Thailand, Cambodia, Laos, S. Vietnam); in *Malesia*: S. Sumatra (Palembang), Malay Peninsula (incl. Langkawi l.s.).

**Ecol.** Confined to streambanks and swamps.

**Note.** A common species with the largest distributional area within this subsection, and little variation in its characters except in the size of the ripe fruit.


Shrub or small tree, 5-6 m. Axillary buds (2 or) 3(-5), distant, the upper one 3-5(-15) mm supra-
axillary, usually shortly stipitate (stalk up to 3 mm), ± oblong, c. 1–2 mm long (excl. stalk), more or less acute. *Petiole* 3.5–4.5(–6) mm. *Leaf-blade* 4–8 by 1.5–3.5 cm, apex acuminate to cuspidate; above dark green; beneath glaucous-papilllose, secondary nerves c. (5–)7 or 8 pairs, not forming an intramarginal nerve; glands c. 6–8(–10), usually near midrib, 0.1–0.3 mm diam., basal ones somewhat larger. *Flowers* unknown. *Inflorescences* shorter than the leaves, unbranched; axes minutely hairy. *Frutiu* (immature) globular, rather sparsely minutely appressedly hairy; pedicel 3–3.5 mm, minutely appressedly hairy. *Seed* (immature) 1; abortive ovules 3.

**Distr.** *Malesia*: S. Sumatra (Palembang, Lampung Dist.), 5 collections; insufficiently known species.


Tree, up to 30 m, 1 m dbh. Nodal appendages c. 0.1 mm long. Axillary buds 3–7, 0.5–1.6 mm long, the upper one (2–)3–10(–20) mm supra-axillary. *Petiole* (5–)6–12 mm, often in apical part with small, usually not protruding glands. *Leaf-blade* (6.5–)10–23 by 2.5–7.5 cm, margin slightly undulate, often somewhat irregular, apex acutish; above dark or greyish green, midrib prominent to flat, in basal part with a central groove; beneath usually brownish to yellowish green, smooth to papilllose, secondary nerves 7–10 pairs, forming an indistinct intramarginal nerve; glands either 0–3 (or 4) and often of an irregular form, or numerous and 0.1–0.2 mm diam., basal glands larger. *Inflorescences* usually 2 per leaf axil, 5–20 mm supra-axillary, as long as or longer than the leaves, much-branched, the basal branches 1–3 together; axes flattened basally, sparsely minutely hairy at the nodes with minute appendages; flowers 1–7 together; lower bracts opposite. *Pedicel* 2.5–5.5 mm, minutely patent to appressedly hairy, sometimes subglabrous. *Sepals*: outer sepals 1.4–2.2 by 1–1.9 mm; inner sepals (1.9–)2.3–3.3 by 1.6–3.5 mm. *Petals* white or pinkish, the upper ones with a yellow spot, when dry yellowish orange, the longest one 6.5–11 mm; carina sparsely to densely appressedly hairy outside, inside sparsely hairy in apical part; other petals glabrous or sparsely hairy at apex. *Stamens*: anthers 0.3–0.5 mm long. *Ovary* appressedly hairy; style rarely only basally hairy; ovules 4. *Fruit* globular, c. 1.5 cm diam., smooth, dull, greyish, appressedly hairy apically; pericarp rather thick; pedicle 4–6 mm (see note).

**Distr.** Continental SE. Asia (Bangla Desh, Burma, Thailand); in *Malesia*: Malay Peninsula (Kelantan, Perak).

**Ecol.** Outside Malesia in (usually submontane) monsoon forest.

**Notes.** The Malayan collections are either sterile or only in fruit; as they have longer pedicels, they may not belong to this species.

In some collections all flowers examined had 7 stamens only; instead of 2 carinal stamens only a single one is present in those flowers.

### II. Subgenus Coriaceum


Nodal glands distinct, c. 0.3 mm diam. Axillary buds indistinct when resting. *Leaf-blade*: tertiary nerves coarsely reticulate, sometimes partly scalariform. *Inflorescences* inserted in older nodes, unbranched, few-flowered, axes up to 1.5 cm, with minute nodal glands. *Sepals* glabrous except for ciliate margin. *Petals* glabrous in apical half out- and inside, lateral petals and carina spoon-shaped, upper petals narrower. *Stamens* monadelphous. *Ovary* glabrous; style glabrous; stigma peltate; ovules 8–12. *Fruit* indehiscent, stipitate, ± globular, apically pointed, 1.2 cm diam. *Seed* 1; testa 2-layered, less than 0.1 mm thick inner layer hard; albumen forming a rather distinct, thin layer which is very thin at lateral sides of cotyledons; embryo more or less globular, green, plumule undifferentiated, radicle exserted.
Fig. 22. *Xanthophyllum ramiflorum* MEIJDEN. a–b. Habit, × 0.7; c. base of leaf with glands, × 2; d. part of twig with axillary bud; e. flower; f. flower, longitudinal section, gynoecium removed; g. lower petal; h. gynoecium; all × 4; i. ovary, longitudinal section, × 8 (S 16051).

Tree, up to 30 m, 27 cm dbh. Axillary buds 2, very indistinct when resting, apparently sunken into the tissue of the twig, the upper one when bursting with 2 broadly ovate c. 1–1.5 mm long persistent scales. *Petiole* (5–)8–12 mm. *Leaf-blade* coriaceous, 7–20 by 3–8 cm, apex obtuse to subacute; above brownish, midrib slightly sunken to flat; beneath pale glaucous-papilllose, secondary nerves c. 8 pairs, not forming an intramarginal nerve; glands numerous, c. 0.3 mm diam. *Inflorescences* solitary or up to 9 together in the axils of the lower leaves and those of the already fallen ones, 1–10-flowered; axes up to 1.5 cm long, thin, glabrous; nodal glands very indistinct; bracts small, scale-like. *Pedicel* 8–10 mm, glabrous. *Sepals* dark reddish when dry; outer sepals c. 4–4.2 by 2.6 mm; inner sepals 4.5–4.8 by 3–3.3 mm. *Petals* white, the upper ones with a purple mark, when dry yellowish, minutely peltately hairy in basal half outside and inside, further glabrous; carina like the lateral petals but a little shorter; lateral petals 7.5–8.5 by 7 mm; upper petals up to 7 by 2 mm. *Stamens* 8, exceptionally 7, up to c. 5 mm long; filaments conenate over c. 1.5–2 mm, densely shortly peltately hairy up to about halfway; anthers c. 0.7–0.8 mm long, minutely ciliate, very shortly hairy at base. *Ovary* light brownish, glabrous; style c. 5 mm, glabrous; stigma peltate, oblique, rather large; ovules 8–12. *Fruit* stipitate, ± gloobular, up to 1.2 cm diam., postulate, dull, reddish brown, the style-scar more or less protruding and excentric. 

Distr. *Malesia*: Borneo (Sarawak, Brunei). 

Ecol. Confined to the lowland 'padang' peat-swamp forest on a very poor, sandy, wet soil.

III. Subgenus Triadelphum


Nodal glands usually distinct, 0.3–0.7 mm diam. Axillary buds seemingly single, small, the scales usually not fully covering the bracts of young inflorescences, 0.4–1(–1.5) mm long. *Leaf-blade*: tertiary nerves coarsely reticulate. *Inflorescences* unbranched, axes slightly angular, dark, glabrous to sparsely hairy, with usually distinct nodal glands. *Sepals* glabrous outside, usually minutely hairy inside. *Petals* (sub)glabrous outside, lateral petals and the somewhat short carina spoon-shaped, upper petals narrower. *Stamens* triadelphous, conenate parts c. 3–4 mm high. *Ovary* usually black, glabrous; style glabrous or hairy; stigma peltate; ovules 8–14. *Fruit* indescent, usually stipitate, 1–2 cm diam. *Seed* 1; testa 2-layered, c. 0.2 mm thick, inner layer c. 0.1 mm thick, hard; albumen copious, (nearly) separated into 2 halves; embryo flat, named, green, plumule undifferentiated, radicle exserted.


Shrub or tree, up to 30 m, 40 cm dbh. Twigs glabrous to minutely hairy. *Petiole* (4–)5–7 mm, glabrous to minutely hairy. *Leaf-blade* 5–20 by 2–7 cm, margin often irregular, sometimes shallowly crenate because of glands; above usually brownish, midrib narrowly sunken; beneath more or less concolorous, secondary nerves 5–9 pairs, forming a rather distinct intramarginal nerve; glands rather numerous, c. 0.4–0.8 mm diam., scattered but at least 8 present on the leaf margin itself, other glands
Fig. 23. Xanthophyllum ellipticum Korth. ex Meij. a. Habit, ×0.5; b. flower and inflorescence axis; c. flower, longitudinal section, gynoecium removed; d. carina with two stamens enclosed; e. gynoecium; all ×3; f. ovary, longitudinal section, ×6; g. part of twig with young inflorescence, ×4.5 (S 25564).

Tree, 25 m. Older nodes usually with a cluster of adventitious buds. Petiole 5–7 mm, not transversally wrinkled, more or less smooth. Leaf-blade 8–15 by 3–6 cm; above green, midrib sunken; beneath concolorous, secondary nerves 5 or 6 pairs, not forming an intramarginal nerve; glands present only in apical half of the leaf-blade, c. 0.2 mm diam., scattered but up to 6 present on the leaf margin itself, other glands c. 8–12. Inflorescences up to 4 cm long; nodal glands rather distinct. Pedicel 5–7 mm, rather sparsely minutely woolly hairy. Sepals sparsely minutely hairy inside; outer sepals 4 by 2.5 mm; inner sepals 4.9 by 2.4 mm. Petals brownish orange when dry, the longest one 7.5 mm long; carina inside in middle part shortly appressedly sparsely hairy; other petals inside densely appressedly shortly hairy. Stamens triadephous; filaments densely rather shortly hairy; anthers 0.6 mm long, sparsely hairy at base, ciliate along slits. Ovary shortly stipitate, slightly pubescent; style rather densely shortly more or less patently (± woolly) hairy; ovules 13. Fruit globular, c. 1.5 cm diam., smooth, dark reddish; pericarp thin; pedicel 7–9.5 mm.

Distr. Malesia: Central Celebes (Malili), one collection.


Tree, up to 30 m, 60 cm dbh. Nodal glands elliptic, 0.3–0.6 mm long. Petiole 3.5–5 mm, indistinctly transversally wrinkled. Leaf-blade (4–)6–9 by 1–2.5(–3.5) cm, apex gradually acuminate; above brownish green, midrib sunken; beneath concolorous, secondary nerves c. 6–8 pairs, forming an intramarginal nerve; glands (2–)4–8(–15), present in middle and apical part, absent from margin itself but (in Sumatr. coll.) rather close to the margin, or (in Bornean coll.) rather closely together and not near the margin, 0.3–0.6 mm diam. Inflorescences up to 3 cm long; nodal glands elongate, usually very distinct. Pedicel c. 5 mm, sparsely minutely woolly hairy. Sepals minutely hairy inside; outer sepals c. 3.1 by 2.3 mm; inner sepals 3.5–4.3 by 2.3–2.8 mm. Petals yellowish brown when dry, the longest one 6–6.5 mm long; carina inside minutely hairy above base, upper petals minutely hairy inside. Stamens: filaments minutely hairy in basal part; anthers 0.6 mm long, glabrous. Ovary 0.5–0.7 mm stipitate, glabrous; style glabrous or only at base very sparsely minutely hairy; ovules 8–12. Fruit globular, up to 0.9 cm diam., yellowish to greenish brown, smooth, dull; pericarp thin; pedicel 4–5.5 mm.

Distr. Malesia: Sumatra (near Lake Toba), Borneo (Sabah: Mt Kinabalu).

Ecol. Submontane rain-forests, 900–1600 m.


Tree, flowering on older twigs from adventitious axillary buds. Nodal glands indistinct, elongated. Petiole 9–10 mm. Leaf-blade 14–20 by 6.5–8 cm, apex obtuse to very shortly acuminate; above yellowish green, midrib protruding; beneath: secondary nerves 8 or 9 pairs, not forming an intramarginal nerve; glands c. 12–18, mostly at 2–5 mm from the margin, some scattered, 0.2–0.3 mm diam. Inflorescences up to 4 cm long; nodal glands present but very indistinct. Flowers unknown. Fruit (immature) c. 3 mm stipitate, ovoid, c. 2 by 1.2 cm, more or less fleshy, finely pubescent, light reddish, glabrous; pericarp hard; pedicel 5–6 mm, glabrous. Seed 1 (sub)apical, developing from one of the 12 opposite ovules which are situated only in the apical half of the young fruit.

Distr. Malesia: Borneo (Sarawak, Brunei).

68. Xanthophyllum hildebrandii MEIJDEN, Leiden Bot. Ser. 7 (1982) 139, f. 10B.

Petiole c. 6 mm, not transversally wrinkled. Leaf-blade c. 15 by 5–7 cm, papery thin; above dull, midrib sunken; beneath reddish brown, secondary nerves c. 7 pairs, in apical half forming a rather indistinct intramarginal nerve; glands numerous, mostly situated very close to midrib and a few scattered, 0.5–1.1 mm diam. Inflorescences 1 or 2 together; nodal glands distinct; axes up to 10 cm long, sparsely shortly woolly hairy. Flowers unknown. Fruit (very young) c. 2.5 mm stipitate, ovoid, apically with gland-like pustules, black, glabrous; pedicel 7–10 mm, dark, minutely woolly hairy. Seed (immature)
1, (sub)apical, developing from one of c. 12 ovules situated in apical 2/3 part of the fruit.

Distr. *Malesia*: Borneo (Sabah: Mt Kinabalu, Dallas), one collection only.

Note. Dedicated to the late Mr. F.H. Hildebrand who cleverly recognized many inadequate specimens of the genus by means of macroscopical characters of the wood of the twigs.

IV. Subgenus Exsertum


Presence of nodal glands uncertain. Axillary buds 2–4, usually seemingly single, black when dry. *Leaf-blade*: tertiary nerves coarsely reticulate. *Inflorescences* unbranched, up to 6–8 cm long, axes slightly angular, black when dry, rather sparsely woolly hairy, sometimes with indistinct nodal glands. *Sepals* nigrrescent. *Petals* (sub)equal, spathulate-lanceolate, apex flat, (sub)glabrous outside, densely lanately ciliate. *Stamens*: filaments free, longer than petals, rather densely woolly hairy. *Ovary* black when dry, hairy inside, outside glabrous or hairy; stigma small, bilobed; ovules 8–16. *Fruit* indehiscent, globular, 2–6 cm diam., black when dry. *Seeds* c. 4–12, more or less bean-shaped, testa with rather thick and soft, fibrous outer layer and a hard inner layer; albumen copious, (nearly) separated into 2 halves; embryo flat, elliptic, curved, plume undifferentiated, radicle exserted.


Tree, up to 25 m, up to 70 cm dbh. *Petiole* 6–7 mm, black, sometimes glaucous. *Leaf-blade* 4.5–11 by 2–5.5 cm; above olive-green, midrib narrowly sunken, nervation mostly rather indistinct; beneath reddish olive-green, secondary nerves c. 7–9 pairs, forming an indistinct intramarginal nerve, glabrous 10–14, sometimes more, mostly 1–2½ halfway between midrib and margin, or near the margin, 0.1–0.3 mm diam., basal ones c. 0.3–0.4 mm diam. *Pedicel* 8–11 mm, rather sparsely shortly lanate. *Sepals* sparsely minutely hairy outside, rather densely shortly lanate. *Sepals* sparsely minutely hairy outside, rather densely shortly hairy inside; outer sepal 3.5–5.5 by 3.5–4 mm; inner sepal 5–7.5 by 4–5 mm. *Petals* 14–16 mm long, white, when dry dark reddish, rather sparsely hairy outside, subglabrous inside. *Stamens*: filaments 17–22 mm, glabrous at base, further densely woolly hairy; anthers 1–1.3 mm long, hairy from base to apex. *Disk* densely hairy, with a small number of patent hairs on upper and lower lobes. *Ovary* very densely (velvety) hairy; style rather sparsely woolly hairy; ovules 10–16. *Fruit* (immature) c. 2 cm diam., shortly stipitate, finely pustulate, dark, distinctly bluish-waxy, hairy; pericarp c. 1–4 mm thick; pedicel slender, c. 15–18 mm.


Tree, up to 35 m, up to 80 cm dbh. Axillary buds 2 or 3, the upper one up to 2 mm long. *Petiole* 4.5–10.5 mm. *Leaf-blade* 4–14 by (1–)2–7 cm; above deep brown to reddish brown, midrib narrowly sunken, nervation rather obscure to rather distinct; beneath sometimes waxy, secondary nerves 5–7, not forming an intramarginal nerve; glans 6–10(–20), scattered, 0.1–0.4(–0.5) mm diam. *Pedicel* 8–15 mm, rather densely minutely lanate. *Sepals*: outer sepal 2.5–3 by 1.8–2.2 mm, minutely rather densely hairy at both sides; inner sepal 4–4.5 by 1.8–2.4 mm, hairy outside along midrib, inside densely hairy at base, further more or less glabrous. *Petals* (8–)9–11(–12) mm long, white (‘3 lower with yellow centre’; HAVILAND 2112), when dry dark reddish, glabrous outside, inside lanate especially in basal and apical part. *Stamens*: filaments 11–13(–16) mm; anthers 0.7–0.9 mm long, glabrous or with a few hairs at base. *Disk* glabrous. *Ovary* stipitate, (glabrous or) densely lanate; style lanate; ovules 8–16. *Fruit* globular or less often ovoid, up to c. 5 cm
Fig. 24. *Xanthophyllum suberosum* C.T. White.  

*a*. Habit, ×0.7;  
*b*. part of twig with axillary buds;  
*c*. flower;  
*d*. flower, longitudinal section, gynoecium removed;  
*e*. lower petal;  
*f*. gynoecium; all ×2;  
*g–h*. ovary, longitudinal and cross section, ×4 (van Royen 3201).
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Tree, up to 50 m, 1.20 m dbh. Axillary buds 2(–4), c. 2 mm long. Petiole 3–8 mm. Leaf-blade (2.5–)4–13 by (1–)2–7 cm; above mostly greyish brown to dark brown, sometimes reddish brown, midrib slightly sunken, nerves mostly obscure; beneath concolorous, sometimes more or less waxy, secondary nerves 5 or 6 pairs, not forming an inframarginal nerve, finely prominent to rather obscure; glands few, 0–2(–4) per leaf, near the base and in the middle, 0.1–0.2 mm diam. Pedicel c. 8–12 mm, dark, minutely lanate. Sepals densely minutely hairy inside at base, further almost glabrous; outer sepals 1.8–3 by 1.8–2 mm; inner sepals 3–3.5 by 2–2.5 mm. Petals 7–7.5(–8) mm long, dark reddish when dry, glabrous outside, hairy inside at base and sometimes also in apical part. Stamens: filaments 11–13 mm, shortly rather densely lanate, glabrous in apical part, free or (in var. glabrum) forming a ‘tube’ by their intertwined hairs; anthers c. 0.8 mm long, glabrous. Disk glabrous. Ovary densely lanate or rarely (sub)glabrous; style glabrous in upper half; ovules 8–12. Fruit c. 2–6 cm diam., often apparently sterile, shortly to long-stipitate, black, often waxy, glabrous or hairy; pericarp 0.5–1.5 mm thick; pedicel up to c. 1.5 mm. Seeds c. 4–12.

Dist. Malesia: Malay Peninsula, Central Sumatra, Borneo.

Key to the varieties

1. Filaments forming a ‘tube’ by their intertwined hairs. Ovary (sub)glabrous... b. var. glabrum

1. Filaments free, hairy. Ovary densely lanate

a. var. stipitatum

a. var. stipitatum — X. stipitatum A.W. Bennett, incl. var. borneense ChOdAt.

Stamens: filaments free, hairy. Ovary densely lanate; style densely hairy basally.

Dist. Malesia: Malay Peninsula (incl. Singapore), Central Sumatra, Borneo.


Stamens: filaments forming a ‘tube’ by their intertwined hairs. Ovary glabrous or with a few pressed hairs; style thinly hairy basally.


V. Subgenus Brunophyllum


Nodal glands usually distinct, c. 0.3–0.5 mm diam. Leaf-blade: tertiary nerves coarsely reticulate. Inflorescences unbranched. Sepals glabrous to minutely hairy outside, usually woolly-ciliate, usually minutely hairy inside. Petals unequal with the carina boat-shaped, or equal, (sub)glabrous outside. Stamens 8(–10), filaments free or up to 6 mm connate, densely woolly hairy. Ovary glabrous to hairy; style glabrous or hairy at base; stigma peltate; ovules 8–18(–23). Fruit indehiscent, pear-shaped to ovoid, large. Seeds 8–more, large; testa 2-layered, outer layer usually thick (thin in 76. X. chartaceum), soft, inner layer hard; embryo broadly triangular-ovoid and with little albumen, to flattened-ovoid and covered by much albumen; cotyledons cordate, usually seemingly peltate (except in 72. X. brevipes), plunule usually differentiated into a number of small scales, radicle fully enveloped by the cotyledons or just exerted at base.
72. Xanthophyllum brevipes MEIJDEN, Bot. J. Linn. Soc. 67 (1973) 117; Leiden Bot. Ser. 7 (1982) 144. — Fig. 25.

Tree, up to 35 m, 40 cm dbh. Twigs (sometimes?) all curved downwards, pendent. Nodal glands often indistinct. Petiole 1.5–3 mm. Leaf-blade 2.6–7.5 by 0.7–2.6 cm, apex acuminate to cuspidate; above brown to olive-green, midrib sunken; beneath olive-greenish brown, papillose, secondary nerves c. 10 pairs, little more distinct than finer nerves, forming an indistinct intramarginal nerve; glands more than 10, in a row between margin and midrib, c. 0.1 mm diam. Inflorescences 2–5-flowered; axes hardly thicker than pedicel, glabrous. Pedicel c. 7 mm, glabrous. Sepals minutely ciliate, further glabrous; outer sepals c. 3.5 by 3.5 mm; inner sepals c. 4 by 4.5 mm. Petals unequal, white, when dry orange-brown, faintly ciliate, the longest one 15–16 mm; carina unguiculate, boat-shaped, ciliate only at base; lateral petals narrowly boat-shaped; upper petals more or less straight, with cup-shaped apex. Stamens: filaments c. 0.5 mm connate, rather densely shortly hairy in basal part; anthers c. 1 mm long, glabrous. Ovary shortly stipitate, orange-brown, glabrous; style glabrous; ovules 18. Fruit pear-shaped (to broadly ovoid?), up to 4 cm diam., strongly wrinkled when dry, shiny, brown; pericarp probably very fleshy; pedicel 12–15 mm, blackish, shiny. Seeds nearly absent from lateral sides of cotyledons, at the broad side of these forming a layer equal in thickness to each cotyledon; embryo elliptic in side view, transversely flattened, cordate at base; cotyledons thickened; plumule not differentiated; radicle slightly exserted.

Distr. Malesia: Borneo (Sarawak, Brunei). Note. Ashton mentioned in a fieldnote that the habit of the tree is very reminiscent of old specimens of Salix babyonica because of its pendant twigs.

Tree, up to 47 m, 70 cm dbh. Twigs often strongly thickened on the nodes and with adventitious buds. Nodal glands usually distinct, sometimes elongate, c. 0.5 mm diam. Petiole 5–11–(15) mm. Leaf-blade (4–)7.5–17 by (1.5–)3.5–9 cm, apex rounded to obtuse or sometimes very shortly acuminate; above dark or greyish reddish brown, rarely green, midrib flat to protruding; beneath concolorous or darker than above, midrib prominent or flat, secondary nerves c. (3–)6–9 pairs, sometimes in upper part forming an intramarginal nerve; glands 2–16, usually situated near or on the margin of the leaf, (0.2–)0.5–0.7 (–1.2) mm diam. Inflorescences sometimes also on the older nodes, shorter than the leaves; axes angular, black, glabrous to sparsely shortly lanate. Pedicel 3–11 mm, glabrous to sparingly hairy. Sepals black; outer sepals 2.8–5.5 by 2.8–6 mm; inner sepals 4–7.5 by 3.5–7.7 mm. Petals unequal, white or purple, the upper ones with a yellow or green spot, when dry black, inside glabrous or rather densely woolly hairy above insertion of filaments and at apex, the longest one 14–19 mm; carina boat-shaped, 9.5–16 mm long; lateral petals more or less spatulate, distinctly longer than upper petals and carina; upper petals more or less linear, flat to slightly channelled, curved upwards. Stamens 7.5–12 mm long; filaments connate for (0.1–)1–3 mm, glabrous in basal part, free parts of filaments lanate in basal part, hairs often intertwined, thus forming a filamental 'tube', glabrous upwards; anthers 0.7–1.7 mm long, glabrous to minutely hairy, free or attached to each other around the stigma. Ovary black, glabrous; style black, glabrous; ovules 8–18. Fruit globose, very large, the largest up to 14 cm diam., dull pinkish brown, with numerous small dark spots; pericarp 0.5–2 cm thick. Seeds 8–16, sticking together in drying like a ball, each c. 2–6 cm wide; testa 2-layered, outer layer thick, soft, fibrous, inner layer c. 0.1 mm thick; albumen nearly absent, usually visibly only at base; embryo thick, triangular in side view, plumule and radicle situated in the very centre of the embryo, the plumule differentiated into a number of decussate scales; cotyledons seemingly peltate, peripherically with numerous vessel-like elements forming a regularly reticulate pattern.

Distr. Solomon Islands; in Malesia: N. Papua: Malay Peninsula (incl. Singapore & Penang), Sumatra, Borneo.

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Tree, up to 43 m, up to 1.1 m dbh. Petiole 5–9 mm. Leaf-blade 5–14 by 2.8–9.3 cm; above greyish mid-green, rarely yellowish brown, midrib mostly sunken, sometimes flat, rarely prominent; beneath concolorous, secondary nerves 5 or 6 pairs; glands 6–10 (–14), in middle part close to the midrib, in upper part often along margin and midrib, 0.4–0.5 mm diam. Inflorescences ± as long as to longer than the leaves; axes angular, brown, rather densely shortly lanate; in basal part flowers with 3 (–7) together. Pedicel 3–4 mm, ribbed, densely shortly lanate. Sepals brownish, shortly lanate outside; outer sepals 2.5–3.5 by c. 2 mm; inner sepals 3–4.5 by c. 2.5 mm. Petals (sub)equal, obovate-lanceolate, 7–8.5 mm long, with slightly cupped apex, white, when dry orange-brown, outside with a few woolly hairs along midrib, woolly-ciliate especially at apex, inside woolly hairy. Stamens 8 or 9, the middle carinal stamen rather often developed; filaments free or 0.1 mm connate, densely lanate to apex; anthers 0.7–0.8 mm long, sparsely woolly hairy. Ovary 0.5–0.7 mm stipitate, inside glabrous to sparsely hairy, outside densely shortly lanate on median rib, further glabrous; style basally shortly lanate, upwards nearly glabrous; ovules 14–16. Fruit pear-shaped, c. 5–15 cm long, 3–12 cm diam., reddish brown to greyish greenish brown, often with dark spots; pericarp c. 0.5 cm thick, hard; pedicel up to 5 mm. Seeds mostly more than 8, rarely less, sticking to the pericarp in drying, broadly triangular-ovoid, up to 5 cm wide when dry; testa 2-layered, outer layer thick, soft, not fibrous, inner layer less than 0.1 mm thick, hard; albumen nearly absent, usually visible only at the base; embryo thick, triangular in side view, plumule and radicle situated below the centre of the embryo, plumule differentiated into a number of decussate scales; cotyledons seemingly peltate, peripherically with vessel-like elements; top of radicle hardly exserted at base.


Note. In a number of collections all flowers examined have 9 stamens: 3 instead of 2 stamens are placed before the adaxial petal.
Fig. 26. *Xanthophyllum papuanum* Whitm. ex Meijden. a. Habit, ×0.7; b. flower and part of inflorescence axis; c. flower, longitudinal section, gynoecium removed; d. lower petal with three stamens; e. gynoecium; all ×4; f. ovary, longitudinal section, ×8 (Hoogland 5072).

Tree, up to 25 m, 16 cm dbh. Petiole (1.5—)4—6.5 mm. Leaf-blade (ovate-)oblong, (3—)7—17 by (1—)2.8—7 cm, apex acuminate to cuspidate; above dark reddish brown to dark olive-green, midrib slightly prominent to flat, or sunken in basal part; beneath concolorous, secondary nerves 5—7 pairs, forming a rather indistinct intramarginal nerve; glands 0—8, situated in middle and apical part, (0.1—)0.2—0.4 mm diam. Inflorescences (much) shorter than the leaves; axes lanate; flowers solitary or in basal part with up to 3 together. Pedicel (1.5—)3—4 mm, dark, sparsely lanate. Sepals black when dry; outer sepal (3—)4—5.5 by (1.5—)2.5—3.5 mm; inner sepal (3.5—)6—7 by (1.5—)2.5—4 mm. Petals subequal, 9.5—12 mm long, white, the upper ones with a yellow spot, when dry nearly black, ciliate to apex, inside hairy above insertion of filaments. Stamens 8 (—10); filaments connate over c. 5—6 mm, glabrous at base, upwards densely (woolly) hairy; anthers 0.5—0.65 mm long, glabrous to sparsely woolly hairy at base. Ovary stipitate for 2.5—3 cm, dark, glabrous or with a few rather long hairs; style glabrous to rather sparsely lanate; ovules 12—18 (—23). Fruit ellipsoid, up to 11 by 6 cm, attenuate at base and apex, often more or less smooth, orange to dark brown; pericarp rather soft, c. 0.5 mm thick. Seeds 8 or more, like those of 74. X. papuanum, but albumen forming a thin layer along outer side of the cotyledons.

Dist. Malesia: Borneo (Sarawak, Sabah, Kalimantan).


Tree, up to 30 m, 1 m dbh. Petiole 3—4 mm. Leaf-blade 4.5—11.5 by 2—4.2 cm, papery thin, base nearly cordate to cuneate, apex acuminate to cuspidate; above very dark green, midrib flat to slightly prominent; beneath ± glabrous, concolorous, secondary nerves c. 5—7 pairs; glands very few, up to 3, c. 0.1 mm diam., very indistinct. Flowers unknown. Inflorescences short; axes black, glabrous. Fruit globular to more or less pear-shaped, up to 8.5 cm long, strongly wrinkled, when dry black, probably glabrous; pericarp rather thick, hard. Pedicel c. 5 mm, black, glabrous. Seeds 8 or more, like those of 74. X. papuanum, but both layers of the testa much thinner, and albumen forming a thin layer along the outer side of the cotyledons.

Dist. Malesia: Malay Peninsula, Central Sumatra (Indragiri).

Note. Because of its thin nigerescent leaves with few laminar glands, its habit is atypical in Xanthophyllum. As its flowers may be atypical too (i.e. in being possibly 'regular'), flowering material may have been collected already but identified wrongly.

Excluded

Xanthophyllum glaucescens Miq. Fl. Ind. Bat., Suppl. (1861) 394; Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 274, has been identified by Hildebrand and Kostermans as Litsea insignis (Blume) Boerl. (Lauraceae).


Xanthophyllum subglobosum Elmer, Leafl. Philip. Bot. 5 (1913) 1676, incl. var. longifolium Elmer, was identified by Merril, En. Philip. 2 (1923) 485 as Siphonodon celastrinus Griffith (Celastraceae); Ding Hou, Fl. Males. 1, 6 (1964) 395.
CRUCIFERAE (B. Jonsell, Stockholm)

Herbs, sometimes subshrubs. Leaves spirally arranged, basal ones often in a rosette, extipulate, petiolate to sessile and amplexicaul, entire to variously divided. Inflorescences terminal or sometimes axillary racemes, in flower mostly condensed and often corymbose, in fruit elongate, usually ebracteate. Flowers bisexual, actinomorphic or slightly zygomorphic, hypogynous, cyclic, tetramerous, heterochlamydous. Sepals 4, free, usually equal, spathulate to clawed, imbricate or contorted. Stamens 6, tetradynamous (rarely 4 or 2), epipetalous usually free; anthers usually 2-thecous opening lengthwise. Nectarial glands variously arranged at the filament bases. Ovary superior, sessile or stipitate, of seemingly two united carpels, secondarily divided into two locules by a thin membranous septum (sometimes transversely locular by intrusions from the fruit wall); placentation parietal, ovules usually many, anatropous or campylotropous; stigma bifid or connate. Fruit a bivalved dehiscent silique or silicula (see key), sometimes a nutlet, lomentaceous or otherwise constricted. Seeds virtually devoid of endosperm, with cotyledons incumbent, accumbent or variously folded.

Distribution. A cosmopolitan family with about 380 genera and more than 3000 species, especially diversified in the Mediterranean and the Irano-Turanian regions as well as in parts of Southern Africa, North America and montane South America. The family is comparatively sparse in the tropics, mainly confined to montane and arid areas.

The family includes a number of important crops and spices, notably in the genera Brassica, Sinapis, Raphanus, Crambe, Lepidium, Rorippa, some now cultivated in montane parts of the tropics.

Several cosmopolitan weeds belong to the family (within Lepidium, Coronopus, Capsella, Thlaspi, Arabis, Sisymbrium, Rorippa, Camelina, and others) and may appear as casual aliens virtually anywhere.

In Malesia there are 6 genera with a total of 24 species. The genus Papuzilla (3 spp.), regarded as a New Guinean endemic, is here included within Lepidium. In each of the genera Cardamine and Rorippa 3 spp. are endemic to New Guinea and some adjacent areas, and Rorippa backeri is an endemic of Java.

The affinities of the endemic Rorippa species is with Australia and New Zealand, while the Cardamine species belong to an alliance of tropical montane species around the widespread C. africana.

The remaining 14 species may all have been introduced by man and partly naturalized.

Ecology. The native species are montane (some secondarily at lower levels). Natural occurrences are open forests, rocky outcrops, riverbanks, mostly places without a closed vegetation cover. Many are favoured by clearings, fires, road building, etc.

Dispersal. All Malesian species (except Raphanus sativus) disperse by small seeds without special devices. Some seeds are mucilaginous (get sticky with water), which may facilitate transport with birds and other agents.

Morphology. In spite of its size, the family is remarkably uniform. Lignification is rarely substantial except in basal parts, the hypocotylar region and roots. The herbaceous life-form seems to be primary, at least so far as many woody groups seem to have evolved from herbaceous forms. Annuals are common in many genera.

In floral parts little specialization is to be found, but not rarely reductions as to stamens, petals and nectaries. The position of the nectaries varies in relation to the filament bases (and is of taxonomic importance) but no particular elaboration is found.

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Variation and specialization are important and often drastic as to fruits and diaspores, which means that without developed fruits many species are not determinable.

The seeds are variously ornamented, often winged. The testa is rather uniformly built from one-cell-thick layers: epidermis (which may contain mucilage), subepidermis (which may be absent), palissade layer (usually with pigmented wall thickenings) and a parenchymatous pigmented layer. The ripe seed is almost filled up by the embryo; endosperm is reduced to a one-cell-thick 'aleurone' layer adjacent to the testa. The folding of the cotyledons and their position in relation to the radicle is of taxonomic importance.

Vegetative anatomy. Wood anatomy is quite variable within the family and largely associated with stem width. The xylem in thin-stemmed species forms a closed cylinder and the cambium forms a continuous ring. In thicker stems sclerenchymatous tissue separates the xylem bundles and the cambium cylinder is mostly discontinuous. In woody species medullary rays may also separate the xylem bundles. The variation largely reflects degrees of adaptations to arid conditions and occurs within genera and species as well as intra-individually according to age. Even in strongly lignified species the wood elements are of little advanced types, making it probable that woodiness has evolved comparatively recently in the family.

Secretory cells containing myrosinase (myrosin cells) are widely distributed in the family, but in various organs in various genera. Their distribution has been regarded to be of some taxonomic value.

Hairs are always unicellular, but shape varies from unbranched to forked, stellate, T-shaped, etc. and is of considerable taxonomic interest at various levels.

The stomata are mostly of a characteristic type with one small and two larger subsidiary cells: so-called anisocytic or cruciferous stomata. This type is, however, by no means restricted to the Cruciferae.


Palynology. As with macromorphology, the pollen morphological variation within Cruciferae is small in proportion to the number of genera and species. Shape of the grains ranges from suboblate to subprolate, but prolate and perprolate shape is easily attained by invagination of the long colpi under dry conditions (e.g. during transport through the air). The grains are small to medium-sized (10–45 μm), rarely somewhat larger.

The apertural system is nearly always 3-colpate. Seldom also 2-, 4-, 5-, 6-, or 7-colpate grains occur. Erdtman (1952) records the rare occurrence of inaperturate pollen, which probably represents a kind of tritennate apertural system.

Exine stratification is mostly distinct, sexine and nexine being clearly distinguishable. A reticulate tectum with up to 1 μm broad muri is usually present. Columellae may be distinct or not, which mainly depends on their size.

On the strength of extensive material (200 out of about 380 genera) Chiguriaeva (1973) established 5 main pollen types within Cruciferae. Most characters used in this subdivision are quantitatively determined and the various pollen types occur together in most tribes of the family. Besides, compared with the pollen morphological range in the whole family, relatively much variation appeared to be present within single species. Thus, pollen morphology seems of little significance for taxonomy in Cruciferae. As to be expected, cruciferous pollen keys out very difficultly (Erdtman c.s., 1963).

Phytochemistry. The family is rather uniform and highly characteristic also from the chemical point of view. Particularly the seeds but also other organs contain glucosides with sulphur and nitrogen in their molecules, so-called mustard oil glucosides, or glucosinolates, compounds unique to the family. The enzyme myrosinase, localized in particular cells, will split the glucosinolates when cell walls are crushed in the presence of water into three compounds, among those the pungent mustard oils. They are either isothiocyanates of usually pleasant flavour or thiocyanates with a strong, often garlic-like odour (e.g. in *Lepidium* and *Thlaspi*).

Very important in the seeds are also lipid acids, particularly unsaturated ones with 18, 20 or 22 carbon atoms. Particular for the family and very widespread is the erucic acid, which because of unlike properties should be kept at a minimum in strains of *e.g. Brassica* cultivated as oil seed crops. Others of those fatty acids (oleic, linolenic and linoleic acids) are of utmost economic importance. Among alkaloid-like compounds sinapin, a protoalkaloid of bitter taste, is very common in the family and concentrated in the seeds. Proteins are of importance in the seeds, while starch is lacking.


Chromosomes. By far the most widespread basic number is *x* = 8, but dysploidy occurs within several genera (*e.g. Brassica*) and may account for *x* = 7, which prevails in a few genera (*e.g. Thlaspi, Sisymbrium*); *x* = 5 is known from *Arabidopsis*, the southern hemispheric tribes *Stenopetalae* and *Heliophileae*, and on polyploid level in *Crambe*. Polyploidy, often combined with aneuploidy, is extensive in most of the large genera, *e.g. Cardamine*. The chromosomes are small and do not readily lend themselves to structural studies.


Taxonomy. The uniformity of this large family makes subdivision difficult. A number of tribal classifications have been proposed, most of them ending up with 15–20 tribes, 9 of those distinct and largely restricted to limited parts of the southern hemisphere. They include few genera and mostly also few species. Among widespread tribes, rich in genera and species, *Brassicaceae* (with *Brassica* and *Raphanus* in the Malesian flora) is the only one really distinct, and not been disagreed upon as to its circumscription. Most of the other tribes have been rather schematically delimited and may contain a nucleus of closely related genera to which others seem to have been more arbitrarily added. According to Schulz's system the Malesian genera should be included within *Lepidaceae* (*Lepidium* and *Capsella*) and *Arabideae* (*Cardamine* and *Rorippa*).


Fig. 1. Brassica juncea (L.) Czern. 1. Habit, ×0.6; 2. flower, ×6; 3. petal, ×6; 4. silique, ×2; 5. seed, ×12 (1–3 Drummond & Hemsley 3360; 4, 5 Conrads 230; drawn after African material). Courtesy Fl. Trop. E. Afr., Crucif. (1982) 4, f. 1.
**Cruciferae (Jonsell)**


In addition the following species has been reported, probably as occasional, but it is in L. represented only by indeterminable material: *Barbara vulgaris* R.Br. See Backer, Schoolfl. Java (1911) 55; Koord. Exk. Fl. Java 2 (1912) 288; Back. & Bakh. *fl.* Fl. Java 3 (1968) 643.

**Key to the genera**

1. Fruit a siliqua, *i.e.* less than three times as long as broad. Ovary ovoid to pyriform.
2. Silicule with two seeds, orbicular, elliptic in outline .................................................. 3. *Lepidium*
3. Silicule opening by two valves.
   4. Silicule without a rostrum, ± abruptly terminated by the style .............................. 1. *Brassica*
   5. Silicule with a thickened replum (*i.e.* thickened edge of the septum of the siliqua, on which the seeds grow), explosively dehiscent by coiling valves .......................... 5. *Cardamine*

**1. Brassica**


Annual, biennial or perennial herbs, rarely subshrubs, glabrous or with hispidulous simple hairs. *Leaves* undivided to pinnatifid. *Racemes* terminal, usually ebracteate, corymbiform to paniculate, with many rather large flowers, in fruit elongate, lax. *Sepals* erect, connivent or spreading, the inner larger and somewhat saccate. *Petals* yellow or white, spatulated to clawed. *Stamens* 6, the lateral ones often ascending, filaments linear. Lateral nectaries prismatic or reduced, median ones semiglobose to filiform, often large. *Ovary* cylindrical, sometimes on a gynophore; stigma semiglobose to slightly bilobed, ovoids numerous, usually uniseriate. *Fruit* a siliqua, readily dehiscent, terete or slightly laterally compressed, in transverse section ± biconvex, attenuate into a conical to filiform beak with 0–3 seeds; valves rather thick, convex, with prominent midnerves and inconspicuous side-nerves. *Seeds* usually globose, reticulate, not mucilaginous.

**Distr.** As indigenous mostly Mediterranean; a number of the nearly 40 spp. have widely spread as weeds, some of them in connection with cultivation.

**Ecol.** Natural habitats are open, rather dry places like seacliffs, etc. In the tropics only as weeds of cultivation, roadsides, waste places, etc.

2. RAPHANUS


Annual to perennial herb, ± hispid with simple hairs. Leaves lyrate-pinnatifid to pinnatifid. Racemes terminal, ebracteate, ± corymbiform, with many rather large flowers, in fruit elongate, lax. Sepals erect, the inner larger and somewhat saccate. Petals white, yellow or ± violet, clawed. Stamens 6; filaments linear; anthers linear, obtuse. Lateral nectaries very small, median semiglobose or filiform. Ovary biarticulate; lower segment very short, upper segment long with 2–20 ovules; stigma capitate. Fruit a transversely articulate siliqua; lower segment usually stalk-like, very short, seedless; upper segment indehiscent, cylindrical, in transverse section circular, ± constricted between the seeds, sometimes lomentaceous; beak narrow, seedless. Seeds ovoid to globose, reticulate to smooth.

Distr. About 8 spp., native in the Mediterranean area; 2 spp. are almost cosmopolitan weeds.


Annual or usually biennial herb with thickened napiform to cylindrical taproot, hispid especially in lower parts. Stem erect, usually branched, 15–150 cm high. Basal and lower cauline leaves lyrate-pinnatifid to -pinnatisect, petiolate, not auriculate, up to 15 cm long; terminal lobe large, at least half as long as the whole leaf, elliptic to ovate, acute, ± cuneate, ± coarsely dentate; lateral lobes in up to 7 pairs (but usually much fewer), small, oblong or narrowly triangular, ± dentate; upper leaves shortly to indistinctly petiolate, undivided, oblong to lan-
ceolate, acute, cuneate, serrate to dentate. **Racemes** loosely corymbose to paniculate with many flowers on 10–20 mm long pedicels, in fruit elongate, lax with up to 30 mm long pedicels. **Sepals** lanceolate, obtuse, 5–10 mm long. **Petals** white, yellow or lilac, ± dark-veined, 15–20 mm long with obovate, emarginate to rounded blade, 5–6 mm broad. **Anthers** ± 2.5 mm long. **Silique** 20–90 by 7–15 mm; lower segment much reduced; upper segment of ± spongy to corky consistency, not or slightly constricted between the 1–12 seeds; beak conical, 10–20 mm long.

**Seeds** brownish, ellipsoid to globose, 1.5–4 mm long, finely reticulate.

**Distr.** Only known as a cultivated species, which has probably originated from hybrids between forms of *R. raphanistrum* L. In *Malesia* as a weed (probably escaped from cultivation) at least in Java, probably elsewhere. Cultivated also in the Malay Peninsula and the Philippines, probably elsewhere.

**Ecol.** Cultivated land, waste places, roadsides; usually 1800–2200 m altitude.

### 3. LEPIDIUM


Annual or perennial, small to medium-sized herbs or subshrubs with taproot, often finely pubescent with simple hairs. **Stems** erect or ascending, sometimes procumbent, freely branching. **Leaves** membranous or coriaceous, simple to imparipinnatifid. **Racemes** terminal or axillary, ebracteate, densely corymbose, with small to minute flowers, in fruit narrowly cylindrical, contracted or elongate but usually rather dense. **Sepals** elliptic, not saccate, greenish. **Petals** usually whitish, somewhat longer or shorter than the sepals, or often lacking. **Stamens** 6, 4, or 2, median and/or lateral ones reduced; filaments usually linear to subulate. **Nectarial glands** usually 6 or 4, adjacent to the bases of the lateral filaments. **Ovary** flat, dorsiventrally compressed, elliptic in outline, ovules 2. **Fruit** a silicula, dehiscent, flat, strongly compressed, narrowly septic, usually orbicular to elliptic in outline, winged (especially distally) or not, with the short style as an apical notch. **Seeds** single in each locule, very finely reticulate, mucilaginous, usually reddish brown, rather flat, elliptic to obovate in outline, sometimes narrowly and unilaterally winged.

**Distr.** Worldwide; a number of the c. 150 spp. are cosmopolitan weeds.

**Ecol.** Largely open, wet or dry ground without closed vegetation, in elevated regions. Very often in disturbed places.

### Key to the species

1. Inflorescences terminal with numerous flowers. Spines absent.
2. Leaves deeply divided. Siliculae with prominent wings ................. 1. *L. sativum*
2. Leaves undivided, serrate. Siliculae wingless .......................... 2. *L. virginicum*
1. Inflorescences very short with 5 or fewer flowers inserted at base of spines.
3. Subshrub, more than 20 cm high ........................................... 5. *L. maceowagei*
3. Cushion forming, rhizomatous, partly woody herbs, less than 15 cm high.
4. Cushions over 5 cm thick. Leaves mostly serrate or incised with up to 4 pairs of lobes. 4. L. minitiflorum
4. Cushions less than 5 cm thick. Leaves mostly deeply pinnatifid with up to 7 pairs of lobes

3. L. laeteviride

**Distr.** Native of North America; widespread as a weed; in *Malaysia* known from E. Java (Mt Tengger) and the Philippines (Luzon).

**Ecol.** In Java naturalized in young forest at c. 1500 m. Elsewhere a weed in settled areas.


**Perennial, mat- or cushion-forming, rhizomatous herb with persistent old leaf bases. Stems** up to 3.5 cm long, sparingly branched, puberulent, and with a few leaf-opposed, up to 1 cm long spines. **Leaves** coriaceous, sessile; basal ones in a rosette, sparsely puberulent, bipinnatifid with up to 7 pairs of lobes, acute, without spines; cauline leaves obovate, entire or acutely serrate. **Racemes** axillary at the base of spines with 1–3 minute flowers, in fruit hardly elongating, up to 10 mm long; pedicels 2–3 mm long, patent, sparsely pubescent. **Sepals** green with hyaline margins, c. 1 mm long. **Petals** white, shorter than sepals, 0.6–0.8 mm long. ** Stamens** 2 (median), with 4 linear nectaries, one on either side of each stamen. **Ovary** elliptic with inconspicuous style. **Siliculae** in outline broadly ovate to obovate, 3–3.5 by 2.5–3.5 mm, with very narrow wing in upper third, shallowly emarginate; style very short, stigma sessile or nearly so. **Seeds** wingless, dark brown, 1.5–2 by 0.8–1.3 mm.

**Distr.** *Malaysia*: Papua New Guinea (Morobe District, Sarawaket Range, Mt Bangea).

**Ecol.** On overgrown screes and among boulders at c. 4100 m.


**Annual or short-lived perennial herb with taproot, 20–80 cm high with one to few erect-ascending stems, branching above, puberulent with thin falcate hairs. Leaves** membranous, lowest ones lyrate-pinnatifid, up to 7 cm long, median and upper ones mostly oblanceolate, acutely serrate. **Racemes** terminal with minute flowers, rather dense in fruit, up to 15 cm long; pedicels in fruit 3.5–5.5 mm long, patent, straight, glabrous. **Sepals** greenish, c. 1 mm long. **Petals** white, longer or shorter than sepals, very narrow. ** Stamens** 2 (median) with triangular nectaries. **Ovary** elliptic, emarginate, style not projecting. **Siliculae** wingless, suborbicular, 3–3.5 by 2.7–3.5 mm, rather widely and deeply emarginate; style short with stigma completely contained within sinus. **Seeds** narrowly winged, red-brown, c. 1.5 by 0.9 mm.


**Perennial, mat- or cushion-forming rhizomatous herb with persistent old leaf bases. Stems** up to at least 12 cm, intricately branched, puberulent, with numerous leaf- or bract-opposed, up to 1.2 cm long spines. **Leaves** coriaceous, sessile, up to 25 mm long, glabrous to sparsely puberulent, impari- (or rarely bi-)pinmate with 2–4 pairs of lobes, or undivided, acutely serrate or entire. **Racemes** axillary at the base of spines with 1–3 minute flowers, in fruit little elongating, to 5 mm long; pedicels 2–4 mm long, straight, patent, puberulent. **Sepals** green with hyaline margins, 1–1.5 mm long. **Petals** white, shorter than or equaling sepals, linear. ** Stamens** 2 (median).
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with 4 shield-like nectaries, one on either side of each stamen. *Ovary* elliptic with very short style. *Siliculae* broadly to cordate in outline, 2.5–5 by 2–4 mm, with narrow wing in upper third, not or indistinctly narrowly and shallowly emarginate; style 0.5–1 mm long, stigma exerted from the sinus. *Seeds* wingless, dark brown, 1–2 by 0.5–1.3 mm.

**Distr.** Malesia: West New Guinea (Mis Carstensz & Wilhelmina), Papua New Guinea (W. Sepik District: Mt Capella).

**Ecot.** Screes, wet open places, tussock grassland, heaths; 3100–4350 m.


Subshrub with taproot, 20–35 cm high or more, woody, branched, puberulent, with numerous leaf-opposed, up to 1.3 cm long spines. *Leaves* coriaceous, sessile, up to 14 by 5 mm, glabrous to puberulent, ovate to obovate, acutely serrate. *Raceme* reduced to a single flower at the base of a spine; pedicels 3–5 mm long, straight, patent, puberulent. *Sepals* green with hyaline margins, 0.7–1 mm long. *Petals* white, shorter than or equalling sepals, linear. *Stamens* 2 (median) with 4 linear nectaries, one on either side of each stamen. *Ovary* elliptic with very short style. *Siliculae* broadly elliptic to obovate, 3.5–6.5 by 2.5–3.8 mm, with narrow wing in upper third, narrowly and shallowly emarginate; style c. 0.3 mm long, just level with the top of the sinus or slightly exserted. *Seeds* wingless, red-brown, 2–2.5 by 1.1–1.5 mm.

**Distr.** Malesia: Papua New Guinea (Southern Highlands: Mt Giliwe, Kaguba).

**Ecot.** Screes, stream-edges, *etc.*, at lower altitudes along roadsides; 2750–3500 m.

4. **CAPSELLA**

Annual to short-lived perennials, small to medium-sized with taproot. Hairs simple, or forked, or branched. **Racemes** terminal, ebracteate, corymbose, with small flowers, in fruit loose. **Sepals** somewhat spreading, not saccate. **Petals** white, sometimes reddish or yellowish, ± clawed, rarely absent. **Stamens** 6; filaments linear; anthers ovoid, obtuse. **Nectaries** as semicircular glands at each side of each lateral stamen. **Ovary** dorsiventrally flattened, obovate in outline, with 10–40 ovules in each locule. **Fruit** a silicula, dehiscent, flat, with narrow septum, obtriangular to obcordate, valves keeled. **Seeds** numerous, not mucilaginous.

**Distr.** About 5 **spp.**, mainly European; doubtfully congeneric species in other parts of the world; in *Malesia* introduced.


Annual to short-lived perennial herb, 5–50 cm high. **Stems** 1–few, erect or ascending, simple or sparsely branched. Rosette **leaves** numerous, petiolate, imparipinnatipartite to coarsely dentate, oblanceolate in outline, 3–15 cm long; cauline leaves rather few, smaller, oblong to lanceolate, undivided (lower leaves sometimes lyrate-pinnatifid), sagittate and clasping, coarsely to finely distantly dentate or entire. Stem and leaves with simple and branched hairs. **Racemes** dense, with numerous small flowers, in fruit elongate, loose, sparsely hairy or glabrous; pedicels spreading to divaricate, 5–20 mm long. **Sepals** green, mostly pubescent, oblong (sometimes with a tinge of purple), c. 1.5 mm long. **Petals** white, clawed, distinctly exceeding sepals, 1.8–3 mm long. **Silicula** obtriangular, with straight or slightly concave margins, ± emarginate, 5–10 mm long, 2.5–8 mm broad; style c. 0.3 mm long. **Seeds** reddish brown, oblong, 0.8–1 by c. 0.4 mm, minutely verrucose.

**Distr.** Almost cosmopolitan as a weed, probably native in Europe, introduced in *Malesia*, recorded from highlands of E. Java, Philippines (Luzon) and E. New Guinea; probably more widespread.

**Ecol.** Weed of cultivated soil in mountain areas; 2000–2500 m.

**Vern.** Shepherd’s purse (E).

### 5. **CARDAMINE**


Annual, biennial or perennial, small to large herbs, with a taproot and often with creeping or tuberous rhizomes. Hairs often present, simple. **Stems** erect, ascending, sometimes basally rooting. **Racemes** mostly terminal, ebracteate, densely to laxly corymbose, with a few to numerous small to medium-sized flowers, in fruit at least basally elongate and lax. **Sepals** not saccate, not spreading; margins hyaline. **Petals** white, cream, violet or purple, spatulate to clawed, sometimes lacking. **Stamens** 6–4, rarely fewer; filaments linear to subulate. **Nectaries** horseshoe-shaped or a close ring-shaped tissue around the lateral stamen and usually as a conical gland outside each median pair of stamens. **Ovary** cylindrical, usually with a short narrower style; stigma flat; ovules...
4–40. Fruit a siliqua, dehiscent, linear, straight, tapered towards the narrow style; stigma flat; fruit disrupting explosively by the valves coiling from the base upwards; replum swollen; valves without prominent nerves. Seeds uniseriate, flattened, usually broadly elliptic to oblong, minutely rugose to colliculate, not mucilaginous.

Distr. In subarctic, temperate, and montane tropical areas all over the world; c. 130 spp., of which 6 spp. in Malesia.

Ecol. Most species grow in moist places, many in or along running water, in marshes, etc. Quite a few form undergrowth in rather dense forests. Very few species are widely spread as weeds, though many are locally favoured by human interactions (clearings, ditches, etc.).

Note. Specific delimitation is notoriously difficult in this genus through frequent hybridization and occurrence of polyploids.

**KEY TO THE SPECIES**

1. Leaves tripartite or undivided.
2. Leaves undivided or terminal leaflet at least 6 times as long as the lateral ones .......... 1. *C. papuana*
3. Leaflets oblanceolate in outline. Plants usually very slender with internodes much longer than leaves
4. Leaves tripartite, terminal leaflet not more than 3 times as long as the lateral ones .... 2. *C. africana*
5. Most leaves with two or more pairs of lateral leaflets.

3. Leaflets ovate to orbicular in outline. Plants not very slender, with most internodes equalling or shorter than leaves.

4. Leaves at least 6 mm long ............................................................. 4. *C. keysseri*

5. Petals at least 6 mm long ............................................................. 1. *C. papuana*

6. Petals not exceeding 4 mm.

5. Pedicels of siliqueae patent at an angle with stem exceeding 45° (usually c. 60°). Seeds at least 1.1 mm long .... 5. *C. flexuosa*

6. Pedicels of siliqueae erect to erecto-patent (angle with stem c. 45° or less). Seeds shorter than 1.1 mm

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Perennial, rhizomatous, glabrous (rarely pubescent) herb with 15–50 cm high, erect or ascending shoots, appearing solitary or with 2 or 3 together. Stems unbranched or with a few rather long branches in the upper part. Leaves tripartite or unifoliate (side-lobes reduced); basal leaves (often not present) up to 12 cm long with 9 cm long petioles; cauline leaves rather few, up to 8 cm long, without or with only slightly auriculate, 2–8 cm long petioles; terminal leaflet ovatotriangular, acute to acuminate, at base cuneate or rounded (rarely truncate), distantly serrate-dentate, 3–12 by 1–4 cm on 5–20 mm long petioles (in partite leaves); lateral leaflets ovate, acute, sparsely serrate or dentate, 0.5–3 by 0.2–2 cm on 1–4 mm long petioles. Racemes terminal (but often surpassed by upper leaves) with 5–15 flowers on 0.5–5 cm long peduncles, in fruit condensed or loose, 1–6 cm long; pedicels straight, erecto-patent, 5–12 mm long. Sepals green with hyaline margins, oblong, 2.5–4 mm long. Petals white, broadly spathulate, usually notched, 2 or 3 times longer than sepals, 6–12 mm long, ± half as broad. Stamens 6, with linear filaments; anthers c. 0.8 mm long. Ovary cylindrical with indistinctly demarcated style and somewhat expanded stigma. Siliqua straight, linear, 20–40 by 1.5–2 mm; style 0.5–1.7 by 0.3–0.5 mm. Seeds dark to light brown, oblong in outline, 1.7–2 by 1–1.3 mm, smooth.


Ecol. Wet cliffs, rocky banks of streams in forests; 500–3100 m.

Flora Malesiana

Fig. 3. Cardamine papuana (Laut.) O.E. Schulz. a. Habit, × 0.6; b. siliqua, × 2; c. seed, scale bar 1 mm (Schodde 5540). Del. K.G. Forss.


Perennial rhizomatous herb with 10-80 cm high, erect or ascending shoots appearing solitary or clus-
tered. Stems often basally rooting, unbranched or with a few branches, most from the lower parts, glabrous or basally puberulent. Leaves tripartite (rarely with one additional small pair of leaflets), glabrous or hispidulous above; basal leaves up to 15 cm long with up to 8 cm long petioles, soon disappearing; cauline leaves few to numerous, 5–20 cm long, in lower leaves with proportionally very long (up to 12 cm), slightly auriculate petioles; terminal leaflet broadly to narrowly ovate or subtriangular, acute to acuminate (but the tip often obtuse with a short point), at base truncate or rounded (in upper leaves also cuneate), often oblique, crenate, serrate or incised (especially plants from New Guinea), 1.5–7.5 by 0.8–4 cm on 2–20 mm long petioles; lateral leaflets of similar shape as the terminal, slightly to considerably smaller, 0.5–6.5 by 0.2–3 cm on 0.5–10 mm long petioles. Racemes terminal with 5–20 flowers on 1–25 cm long peduncles, in fruit condensed or loose, 2–25 cm long; pedicels straight, erecto-patent, 4–30 mm long. Sepals green with hyaline margins, elliptic, 1.4–4.5 mm. Petals white to pale violet, spatulate, broadly obtuse, at least twice as long as sepal, 3–12 mm long, ± 1/3 as broad. Stamens 6 with subulate filaments; anthers 1–1.5 mm long. Ovary cylindrical with short narrower style and somewhat expanded stigma. Siliqua straight, linear, 20–55 by 1.3–2.5 mm, tapered towards style, which is 0.6–2.5 by c. 0.4 mm. Seeds red or dark brown, broadly elliptic or oblong in outline, 1.5–2.5 by 1–1.5 mm, smooth.

Distr. Ubiquist in tropical montane areas. In Africa from Ethiopia south to South Africa (Cape Province) and westwards to Mt Cameroon; also in Fernando Poo, Sao Tome, Comores, Madagascar and Reunion. In America in many Caribbean islands, Central America and NW. South America; in Asia in India and Sri Lanka; in Malesia: Sumatra (northern parts: W., E. coast, Tapanuli, Atjeh), Java (W., E.), Lesser Sunda Islands (Bali, Lombok, Sumbawa), Ceram, Papua New Guinea.

Ecol. Undergrowth in montane forests, often also in clearings, along roads and paths. Usually in shady places; 200–2400 m.


Perennial, slender herb with 20–50 cm long stems, ascending to largely prostrate and running with rooting nodes from which more stems may arise. Stems glabrous with few, slender branches. Leaves glabrous or sparsely ciliate, imparipinnate with 1–3 pairs of lateral leaflets (rarely leaflets lacking); basal leaves 2–7 cm long with 1.5–3 mm long petioles, soon disappearing; cauline leaves distantly inserted, rather few, up to 6 cm long with non-auriculate, up to 2 cm long petioles; terminal leaflets trifid, orbicular or reniform, in upper leaves oblanceolate, obtuse, 0.5–1.5(–3) by 0.1–1.2(–2) cm, on 0–8 mm long petioles; lateral leaflets trifid to oblanceolate, 0.2–0.7 by 0.1–0.5 cm, petioles c. 1 mm. Racemes terminal, with 3–10 flowers, often very slender; pedicels straight, erecto to erecto-patent, 8–15 mm long. Sepals green to reddish white with hyaline margins, oblong, 1.8–2.7 mm long. Petals white, spatulate, obtuse, 3.5–6 mm long, ± 1/3 as broad. Stamens 6, tetradynamous, with subulate filaments; anthers 0.3–0.5 mm long. Ovary cylindrical with indistinct style and flat stigma. Siliqua straight linear, 13–35 by 1.3–1.8 mm; style 0.4–2 by c. 0.5 mm. Seeds red-brown, oblong in outline, 1.4–1.7 by c. 1.1 mm, smooth.

Distr. Malesia: New Guinea (throughout), widespread in high mountain areas.

Ecol. Preferably in or near running water; along streams, in wet grassy slopes; 1700–4000 m.


Annual to probably short-lived perennial herb with 10–40 cm high, ascending main stem, basally prostrate and rooting at nodes, from which one to several new stems may arise. Stems in lower parts mostly hispidulous without or with rather few, usually arcuate branches. Leaves glabrous or with a few scattered hairs, imparipinnate with 2–4 pairs of lateral leaflets; basal leaves 4–8 cm long with 1–4 cm long petioles, soon disappearing; cauline leaves often numerous, up to 9 cm but mostly much smaller with non-auriculate petioles; leaflets trifid, acute (often with a point), at base attenuate, cuneate (rarely truncate), 0.3–2.5 by 0.2–1.4 mm; terminal leaflet often larger and proportionately narrower than the lateral; petioles 0–15 mm. Racemes terminal with 5–10 flowers on up to 4 cm long peduncles, in fruit up to 10 cm long; pedicels straight, erecto-patent, 4–10 mm long. Sepals green to reddish with hyaline margins, oblong, 2.5–3.5 by c. 1.2 mm. Petals white, spatulate, obtuse or emarginate, 2–3 times longer than sepal, 7–8 mm long, ± half as broad. Stamens 6 of nearly equal length with subulate filaments; anthers c. 0.8 mm long. Ovary bottle-shaped, with short distinct style and slightly expanded stigma. Siliqua straight linear, 20–38 by 1–2 mm; style 0.5–1.4 by c. 0.5 mm. Seeds red-brown, elliptic in outline, 1.4–1.8 by 1.2–1.4 mm, smooth.


Ecol. Sandy or gravelly streambanks, moist forest clearings, moist eroded soil, in gardens; 900–4000 m.

Mostly perennial, diffusely branching herb; from the base usually many erect to ascending, curved or flexuous stems, in lower parts sometimes prostrate and rooting, 10–50 cm high with few to numerous scattered hairs. Basal leaves rarely persistent; cauline leaves nearly glabrous to sparingly pubescent, mostly numerous, imparipinnate with a terminal and 2 or 3 pairs of lateral leaflets, 2–10 cm long; petiole non-aureiculate; leaflets narrowly to broadly ovate or orbicular in outline, obtuse, truncate to cuneate, usually crenate and often shallowly trifid; terminal leaflets 0.7–3.5 by 0.7–2 cm on distinct petioles; lateral leaflets 0.4–1.5 by 0.3–1.5 cm on 1.5–7 mm long petiolules. Racemes terminal with 5–20 flowers, in fruit rather lax, up to 12 cm long; pedicels in fruit patent (angle to stem over 45°), 6–12 mm long with patent to erect siliqueae, angled upwards at junction with the pedicel. Sepals green with narrow hyaline margins, oblong, obtuse, c. 1.5 mm long. Petals white, spatulate, 2.5–4 mm long. Stamens 6, distinctly tetradynamous; anthers 0.3–0.4 mm long. Ovary cylindrical with a rather short style, narrower than the ovary, and a flat stigma. Siliqua straight, linear, 18–30 by 0.8–1.2 mm; style 0.7–2 by c. 0.3 mm. Seeds reddish brown, often with a vestigial wing, broadly oblong in outline, 1.1–1.4 by 0.8–1.1 mm, nearly smooth.

Distr. Circumboreal in northern temperate region. Also in some montane areas further south. In Malesia: N. Sumatra (Atjeh), Java, Celebes (Mendo), Philippines (Mindanao, Luzon), Moluccas (Buru, Ceram).

Ecot. Moist places in forests, among rocks and boulders, at streams, in clearings; 1000–2200 m.


Usually annual, branching from the base but not or very sparsely above (occasionally perennials and then branched above and devoid of leaf-roseate). Stems erect or in tall specimens curving, 5–30 cm high, glabrous or with scattered hairs. Basal leaves forming a distinct rosette, cauline leaves rather few; all leaves imparipinnate, with a terminal and 2–6 pairs of lateral leaflets, 1.5–10 cm long (including petiole); petiole non-aureiculate, with a few straight hairs at base; leaflets rhombic, ovate, orbicular or reniform, truncate to broadly cuneate (in upper parts also narrowly cuneate), entire to deeply crenate, occasionally with secondary lobes, glabrous or with scattered hairs; terminal leaflet 0.5–1.5 by 0.3–2 cm, distinctly petioled, the lateral ones oblique, 0.2–1 by 0.2–1.1 cm, nearly sessile or with a petiole up to the length of the leaflet. Racemes terminal, very dense, with several small whitish flowers, in fruit rather lax (up to c. 10 cm long); pedicels in fruit erect to suberect (angle to stem usually c. 45° or less), 3–8 mm long with erect siliqueae overtopping the flowers. Sepals green with narrow white margins, oblong, obtuse, c. 1.5 mm long. Petals white, narrowly spatulate, usually 2–3 mm long (rarely absent). Stamens 4–6; anthers c. 0.4 mm long. Ovary cylindrical with a very short style narrower than the ovary, and a flat stigma. Siliqua glabrous, linear, 12–27 by c. 1 mm; style 0.5–1 by c. 0.4 mm. Seeds reddish brown with a vestigial wing, broadly oblong to suborbicular in outline, c. 1 by 0.8 mm, smooth.

Distr. Native at least in Europe, and probably in some tropical mountain areas (Ethiopia, E. Africa, Cameroun). Widespread as a weed in most parts of the world and probably naturalized in many areas; in Malesia: possibly native in some mountain areas, elsewhere a weed or naturalized; Malay Peninsula (incl. also Singapore), Sumatra (N. parts, Bengkulu), Java, Borneo (Sabah), Philippines (Luzon), New Guinea (throughout).

Ecot. Moist, open ground in montane forests, clearings, etc.; 850–3000 m. Weed in gardens, flowerbeds, also at low altitudes.
6. RORIPPA


Annual to perennial, small to rather tall herbs with a taproot, sometimes also with root-runners or adventive roots from the stem-nodes, practically glabrous to pubescent with simple, pointed hairs. Stems prostrate to erect, usually much branched. Racemes terminal, less often axillary, with or without bracts, nearly corymbose, with numerous, rather small to small flowers, in fruit cylindrical and loose. Sepals greenish, elliptic, not saccate, spreading. Petals yellow or white, equalling or up to ± twice as long as the sepals. Stamens 6, distinctly tetracydynamous, with usually linear filaments; anthers ovate to oblong, yellow, blunt. Nectarial tissue ± surrounding the lateral filament bases, usually also extending outside the median ones but sometimes lacking there. Ovary spheroid to narrowly cylindrical, with numerous ovules. Fruits terete, very variable in shape (globose to narrowly linear), without or rarely with a very short gyrophone, usually with a short but distinct style and flat to slightly bifid stigma, dehiscent by 2 valves with or without very fine midnerve. Seeds many to numerous, not mucilaginous, finely and variously sculptured, yellowish to dark brown, ellipsoid to spheroid, wingless, 0.5–1.5 mm diameter.

**KEY TO THE SPECIES**

1. Racemes bracteate ........................................ 8. *R. henghalensis*
2. Racemes ebracteate (rarely with a few bracts at the lowest pedicels).
3. Siliquae not more than 1.5 mm thick .......... 7. *R. heterophylla*
4. Siliquae more than 1.5 mm thick. ........ 9. *R. micrantha*
5. Pedicels of fruits straight.
6. Seeds not over 0.8 mm long. .......... 1. *R. nasturtium-aquaticum*
7. Pedicels longer than 0.8 mm.
8. Cauline leaves numerous; seeds distinctly reticulate (c. 150 areoles per face) .......... 2. *R. backeri*
9. Cauline leaves absent or few; seeds very finely reticulate (over 300 areoles per face) .......... 3. *R. peckelii*
10. Most pedicels of fruits curved.
13. Ripe siliquae inflated, semi-globose.
14. Ripe siliquae ± ellipsoid to sausage-shaped, not inflated.


Perennial, practically glabrous herb. Stems juicy and hollow, prostrate to ascending, usually rooting at the lower nodes, richly branched, 10–100 cm long. Leaves petiolate, auriculate, pinnatisect, oblong in outline, up to 10 cm long; lateral leaflets in 2–2 pairs, sessile, narrowly obovate, elliptic or nearly orbicular, entire to faintly dentate; terminal leaflet of similar shape, often somewhat larger. Racemes mostly terminal, ebracteate with numerous small white flowers, in fruit rather loose but short, usually c. 10 cm long; pedicels spreading to somewhat reflexed, 8–12 mm long. Sepals green, elliptic, c. 2 mm long. Petals white, often with a violet tinge, obovate, c. 4 mm long. Anthers c. 0.7 mm long. Ovary narrowly ellipsoid, with short but distinct style. Siliqua broadly linear, often curved and torulose, 10–18 by 2–2.5 mm, 7–12 times as long as broad, with seeds arranged in two distinct rows; style 0.8–1.8 by c. 0.5 mm, with a slightly expanded stigma; valves rather thin, bulging when seeds are ripe. Seeds shining, dark red-brown, nearly orbicular in outline, 1–1.3 mm long, covered by a distinct rather high reticulum, which forms 25–50 areoles at each side of the seed.

Distr. Native in Europe and West Asia, perhaps also in Ethiopia; widely cultivated (‘watercress’) and spread with European settlements to temperate and montane areas throughout the world; in Malesia: Java (especially West, rarer in Central and East), Lesser Sunda Islands (Flores), Borneo (Sabah), Philippines (Luzon), Papua New Guinea. Probably naturalized in many more areas than so far recorded.

Ecol. Along streams, ditches and all sorts of running water, on shores or floating in shallow water; c. 350–2500 m. Forms often large mats which very rarely produce flowers.


Fig. 4. Harvest of Rorippa nasturtium-aquaticum (L.) Hayek (Photogr. W.F. Winckel, 1918).
Annual or short-lived perennial herb with taproot, glabrous, 30–150 cm high. *Stems* erect, usually solitary, unbranched or with few erecto-patent branches. Basal and lower cauline *leaves* originally numerous (in older specimens lacking), 40–150 by 10–30 mm, petiolate, lyrate-pinnate with 1–4 pairs of oblong 5–12 by 2–10 mm lateral lobes; terminal lobe elliptic to ovate, 20–35 by 9–30 mm; cauline leaves numerous, 3–10 by 0.7–2 cm, lyrate-pinnatifid with long petioles, auriculate, with usually one pair of side-lobes; terminal lobe 1.5–5 by 0.7–2 cm; margins serrate to distinctly crenate. *Racemes* ebracteate, terminal, sometimes numerous from upper branches, in flower much condensed with 30–70 flowers, in fruit up to 80 cm long; pedicels divaricate at ± 90°, straight, stout, 5–8 mm long. *Sepals* oblong, 2.5–4 mm long. *Petals* white, broadly spatulate, 3.5–7 mm long. * Stamens* 6; anthers 0.6–0.8 mm long. *Ovary* narrowly cylindrical with c. 0.5 mm long style. *Siliqueae* linear, straight, 23–30 by 1.4–2 mm; valves rather firm; style 0.7–2.5 by 0.4–0.5 mm; stigma ± flat, slightly broader than style. Seeds red-brown, subglobose to oblong, very finely reticulate-foveolate, 1.1–1.3 by 0.9–1.1 mm.

**Dist.** *Malesia*: E. Timor (Mts Mutis & Tatanailau), Papua New Guinea (W., E. & S. Highlands), Bismarck Archipelago (New Ireland).

**Ecol.** Along streams on rocks and beaches, a weed in gardens and along dappled tracks. In New Guinea 1350–3500 m altitude, in Timor 1600–2850 m.


Annual or short-lived perennial herb with taproot, glabrous, 10–110 cm high. *Stems* erect, solitary or a few together, unbranched or branched in upper parts. Basal *leaves* lyrate-pinnatisect, usually evanescent; cauline leaves few to numerous, 2.5–12 by 0.7–3 cm, lyrate-pinnatisect with 2–6 pairs of lanceolate lateral lobes, shortly to indistinctly petiolate, auriculate; terminal lobe 1/3 to 1/2 of total leaf length; margin irregularly serrate-crenate. *Racemes* ebracteate, terminal, often branched, and from upper leaf axils, in flower much condensed with numerous flowers, in fruit up to 50 cm long and rather dense; pedicels somewhat curved, patent to deflexed, 3.5–7 mm long. *Sepals* oblong, 1.6–2.4 mm long. *Petals* pale yellow, spatulate, 1.6–2.6 mm long. *Anthers* 0.3–0.6 mm long. *Ovary* cylindrical with distinct style and not or slightly expanded stigma. *Siliqueae* sausage-like, often curved, 5–12 by 1.7–3 mm; valves rather firm; style 0.4–1 by c. 0.3 mm with not or slightly broader stigma. Seeds brown to light brown, spheroid, 0.6–0.9 mm, finely colliculate.

**Dist.** Over the whole north temperate area; widespread in many montane regions in sub tropics and tropics; introduced to south temperate areas and elsewhere. In *Malesia*: Java (W., E.), Lesser Sunda Is. (Alor), Moluccas (Tanimbar), New Guinea (West: Vogelkop; East: Sepik, S. Highlands).

**Ecol.** Most or marshy places, ditches and other
Fig. 5. *Rorippa peekelii* (O.E.Schulz) P.Royen.  
- a. Habit, ×0.7; 
- b. fruiting raceme, ×0.7; 
- c. siliqua, ×2; 
- d. seed, scale bar 1 mm (a Brass 30519, b Sayers NGF 21316, c d Womersley NGF 14272). Del. K.G. Forss.
kinds of disturbed moist ground; from near sea-level to c. 2100 m.


Annual herb with taproot, glabrous, 50—150 cm high. *Stem* solitary, erect or in basal part ascending, shining, mostly rather stout, with many long erecto-patent branches. *Leaves* petiolate, auriculate, 3—17 cm. *Sepals* elliptic, 1.5—1.8 mm long. *Petals* yellow, spathulate, 2—2.5 mm long. *Stamens* 6; *anthers* c. 0.5 mm long; filaments linear. *Ovary* ellipsoid with c. 0.2 mm long style. *Siliqua* inflated, semiglobose to broadly ellipsoid, 5—9 mm; valves thin; style 0.6—0.9 by c. 0.3 mm, with flat, slightly broader stigma. *Seeds* red-brown, spHERoidal, 0.8—1 mm, minutely foveolate.

**Distr.** Malesia: Papua New Guinea.

*Vern.* Heleki, Okapa, heyenka, Tairora, kemu kembiti, Kaugel.


Annual herb with taproot, nearly glabrous. *Stems* erect or ascending, one or more from the base, 5—50 cm high, not or little branched. *Leaves* in a rosette and along the stem, the lower 1.5—8 cm long with 8—60 mm long petioles, narrowly obovate in outline, undivided or lyrate-pinnatipartite with 1—3 pairs of small lateral lobes; terminal lobe ovate, 1—7 by 0.8—4 cm, dentate, obtuse, basally cuneate or truncate; upper leaves rather few, undivided, narrowly ovate. *Racemes* terminal, and on short patent side-branches, ebracteate, with many small, very condensed flowers, in fruit usually rather dense, 2—10 cm long; pedicels spreading, straight, 2—8 mm long. *Sepals* green, elliptic, c. 2 mm long. *Petals* often reduced or lacking, sometimes up to 3.2 mm long, nar-
rowly spatulate. Stamens up to 3 mm long with c. 0.7 mm long anthers. Ovary narrowly cylindrical, with very short style and flat expanded stigma. Siliqua linear, straight, 14–25 by 0.7–1.3 mm; valves rather thin; style narrow, 0.5–1.3 by c. 0.3 mm; stigma broader than style. Seeds uniseriate, red-brown, roundedly quadrangular in outline, c. 0.7 mm long, very finely colliculate.

Distr. Indigenous in East Asia, at least from Japan to Burma; introduced in other tropical areas, also in Africa and America; in Malesia: Sumatra, Malay Peninsula, Java, Lesser Sunda Islands (Timor), Philippines (Luzon, Mindanao), Moluccas (Ambon, Buru, Ceram), Celebes, Papua New Guinea.

Ecot. Open, moist ground, often cultivated places; 250–1500 m.


Annual, pubescent herb, with taproot. Stems erect or ascending, up to 50 cm high, branched at least in upper parts. Leaves obovate in outline, auriculate, lyrato-pinnatipartite, irregularly serrate-dentate, up to 15 by 3 cm, successively transgrading into smaller undivided bracts; terminal lobe ovate, 1.5–5 by 1–3 cm; lateral lobes in 1–4 pairs. Racemes terminal or axillary, at least in lower and middle parts bracteate, with numerous small light yellow flowers, in fruit rather dense, up to 7 cm long; pedicels spreading, straight, 3–7 mm long. Sepals green, elliptic, c. 1.5 mm long. Petals pale yellow, spatulate, 1–2 mm long, about as long as the sepals. Anthers c. 0.5 mm long. Ovary cylindrical with very short style and flat expanded stigma. Siliqua linear, straight, 6–17 by 1–1.5 mm; valves rather thin; style 0.3–0.8 by c. 0.4 mm; stigma flat, broader than style. Seeds biseriate, dark brown, spheroid, c. 0.5 mm long, minutely foveolate.

Distr. India to Vietnam; in Malesia: Java, Lesser Sunda Islands (Sumbawa).

Ecot. Weed in settled areas, perhaps only incidental.


Annual herb with taproot. Stems erect or ascending, up to 70 cm high but usually much shorter, branched at least in upper parts, somewhat pubescent especially basally. Basal leaves lyrate-pinnatipartite in an evanescent rosette; cauline leaves petiolate, auriculate, nearly amplexicaul, broadly oblong-elliptic in outline, imparipinnatisect to lyrate-pinnatipartite; lateral lobes usually in 2–5 pairs, sessile, elliptic to lanceolate, serrate, up to 3 cm long. Racemes terminal and axillary, ebracteate, with numerous small yellowish flowers, in fruit rather loose, up to 20 cm long; pedicels spreading, straight, 2.5–5 mm long. Sepals light to yellowish green, elliptic, 1.5–2.5 mm long. Petals pale yellow, sometimes with a violet tinge, spatulate, 2–3 mm long, usually longer than the sepals. Anthers c. 0.7 mm long. Ovary ellipsoid to cylindrical, with very short style and flat expanded stigma. Siliqua linear, straight, 14–25 by 1.8–2.5 mm; valves rather firm; style 1–2.2 by 0.5–0.8 mm; stigma broader than style and slightly bifid. Seeds red-brown, finely orbicular to broadly elliptic in outline, 0.5–0.8 by 0.4–0.8 mm, finely reticulate-foveolate.

Distr. India, widespread in Africa from Egypt to Zaire and South Africa, also in Madagascar; in Malesia: collected a few times in E. Java (Pasuruan, Besuki, etc.).

Ecot. Weed in settled areas, perhaps only incidental.
MAGNOLIACEAE (H.P. Nooteboom, Leiden)

Trees or shrubs, glabrous or with an indumentum of single hairs. Leaves spirally arranged, simple, entire or 2–10-lobed, pinninerved, evergreen or deciduous; stipules present, at first enclosing and protecting the innovations, later caducous and leaving an annular scar around the node. Flowers terminal or pseudo-axillary on a short shoot in the axils of the leaves, bisexual, rarely unisexual, pedunculate. Peduncle bearing 1 or more caducous spathaceous bracts which leave annular scars. Perianth spiral or spirocyclic, simple or differentiated in calyx and corolla, perianth members 6 or more, free, imbricate. Stamens numerous, free, spirally arranged; filaments short or more or less elongated; anthers linear, 2-locular, dehiscing introrsely, latrorsely or rarely extrorsely; connective usually more or less produced into an appendage. Gynoecium sessile or stipitate (a gynophore present); carpels numerous to few (rarely one), spirally arranged (except in Pachylarnax), free or sometimes concrescent; ovules 2 or more, biseriate on the ventral suture. Fruit apocarpous, sometimes syncarpous; fruiting carpels opening along the dorsal and/or ventral suture, or circum-scissile, rarely indehiscent. Seed(s) 1 or more in each fruiting carpel, large, in dehiscent carpels hanging from the elongated spiral vessels of the funiculus, with arilloid testa, rarely, when fruit indehiscent adherent to the endocarp; endosperm copious, oily; embryo minute.

Distribution. Seven genera in temperate and tropical SE. and E. Asia and from North America southward through the West Indies and Central America to S. Brazil.

Ecology. Several of the tropical species are found at low altitudes, many grow at medium and high altitudes, in Malesia up to c. 3500 m.

Pollination. — Thien (1974) studied the floral morphology of North American Magnoliaceae. They are all protogynous. The flowers are pollinated by beetles which enter at all stages from large bud to open flower and feed on stigmas, pollen, nectar, and the secretions of the petals. They become covered with pollen when feeding. Because the pollen is shed after the stigmas cease to be receptive, the first flowers that open often are not pollinated. There are indications that if all the flowers bloom in one flush, as rarely happens after a severe winter, no seed is set (Treseder, 1978). The timing of the flowers, including opening and closing of petals, the appression of stigmas to the gynoecium (in some species), large quantities of food, and protogyyn all suggest that the flowers are highly specialised for exclusive pollination by beetles. Despite the sharing of pollinators few hybrids have been found in nature. Not enough is known about isolating mechanisms in Magnolia to explain fully the lack of natural hybrids. Between several species artificial hybrids easily can be obtained (Thien, 1974).


Morphology. — Vegetative morphology. All Magnoliaceae are trees or shrubs with deciduous or persistent stipulate leaves. The stipules are first connate, thus forming a cap for the terminal bud and then rupture longitudinally and fall, leaving a circular scar round the twig. They can be free from the petiole or (partly) adnate to it. Growth of the twigs often is faster in the beginning of the season, thus first producing longer internodes than later. In tropical species, however, there may be no conspicuous difference in length of internodes throughout the twig. In Lirioidendronaceae and in tribe Magnoliaceae of Magnolioidae growth is sympodial, and when a flower terminates a twig, the axillary bud of the uppermost leaf or a lower leaf gives rise to the next vegetative shoot which in turn eventually will be terminated by a flower. In tribe Micheliaeae growth is monopodial, the flowers grow from the axil of a leaf and are mostly borne on a brachyblast that consists of two or several internodes.

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Flower structure and floral anatomy. — The flowers are borne on a pedicel which mostly is the ultimate internode of a brachyblast (axillary in *Elmerrillia* and *Michelia*; terminal in the other genera). The flower bud is often protected by the stipules of the uppermost leaf, especially in the genera with terminal flowers. In temperate species these stipules often are leathery and/or hairy. The brachyblast, if present, bears one to several spathaceous bracts which also surround and protect the flower bud. Essentially these bracts consist of a petiole (reduced lamina) with its stipules adnate to it, together forming a cap like the one surrounding the vegetative buds. The uppermost spathaceous bract, sometimes called bracteole, surrounds the base of the pedicel. This pedicel can be very short or (nearly) absent or long. The perianth is either spiral throughout, such as in *Magnolia stellata*, or consists of some ternate whorls. Ontogenetic studies have shown that the latter are initiated successively, although they form two tiers. Thus there is a clear transition from the spiral phyllotaxy to a whorled phyllotaxy in perianths of the *Magnoliaceae* (Tucker, 1960; Erbar & Leins, 1982, 1983). While there is often no clear differentiation of calyx and corolla such a separation may exist in some cases, e.g. in *Liriodendron*, although Ueda (1986) argues for the regular presence of a true calyx.

Vascular system. — Two vascular systems, a stelar and a cortical system of vascular bundles, are present in the floral axis of the *Magnoliaceae* (Skipworth, 1970). The cortical system arises below the flower, either directly from the stele or as branches of leaf and stipule traces. In general it provides the lateral traces of the flower appendages, while the stelar system gives rise to the median traces. This is true of bracts, perianth members, stamens, and carpels. The stamens are spirally arranged and develop either directly after the tepals and in the same 8 (7–10) parastichies like in *Magnolia stellata* (Erbar & Leins, 1982), or after a relatively long interval like in *Magnolia denudata* (I.e.) and *Michelia fuscata* (Tucker, 1960). In *Magnolia denudata* the spiral of the stamens is somewhat irregular.

A number of tropical species has broad 3-veined stamens with two pairs of linear sporangia which are deeply embedded in their surface. They are comparable to those of the *Degeneriaceae* and *Himantandraceae*. Canright (1952) describes several trends of specialisation in the stamens of the *Magnoliaceae* such as: (1) elongation of the apices; (2) differentiation of a filament; (3) reduction in number of veins from three to one; and (4) the transition from a laminal to a marginal position of the sporangia. Teratological stamens often occur, which range from broad petaloid stamens to narrow filamented ones. These different forms were found in the same flower of *Michelia champaca*. Also carpels with varying degrees of fertility were found among the stamens.

The carpels are arranged spirally on the lengthened receptacle. Their phyllotaxy was studied in *Magnolia stellata* (Erbar & Leins, 1982) and *Michelia fuscata* (Tucker, 1961). They arise in the same spirals as stamens and tepals, i.e. 8 (sometimes 7, 9) parastichies. In *Michelia* different divergence angles were found to occur in different flowers.

In contrast to the more primitive Ranalian families, the carpels of the *Magnoliaceae* and the related *Himantandraceae* (Canright, 1960) appear strongly advanced. The most significant specialisations are: (1) the closure of the fertile part of the carpel; (2) the restriction of the external stigmatic surfaces to the margins of the conduplicate style; and (3) conspicuous changes in the vascularisation of the carpels. There is also a tendency towards a reduction in the number of ovules (to two in many *Magnoliaceae*) and to lateral adherence or actual concrescence of crowded carpels. In summary the carpels of *Magnoliaceae* exhibit more or less advanced stages of phylogenetic modification. The carpels, like the stamens, are supplied by three veins. The dorsal traces commonly originate from the stelar system while the two ventral traces originate from the cortical system. Canright (1960), however, found in cleared material from *Michelia champaca* that 'not uncommonly, the basal carpels of a gynoecium are vascularized entirely by the cortical system, and the apical carpels entirely by the stelar system.'

Van Heel (1981, 1983) suggests that the carpels are basically cupuliform. His SEM studies show that carpels arise as cup-shaped (ascidiate) or partly cup-shaped organs lateral or terminal on the flower apex. According to Canright the margins of the carpels become adnate to the floral
axis. According to van Heel's observations there is no later fusion, but already in an early state there is no abaxial margin present. On the side of the floral axis the cup is deepened secondarily, and the ovules originate in it on the inside margin close to the floral axis when an ovary and a style have not yet differentiated.

Fruits. — The fruits of Magnolioideae principally consist of several to many (in Michelia montana sometimes one) free carpels spirally arranged around the receptacle. The fruiting carpels are woody and entirely free in some taxa while they are, secondarily, more or less connate in others. The young carpels are always free when initiated, and only relatively late in ontogeny they may become concrescent. Dehiscence of the mature carpels is mostly along the dorsal suture, often also along the ventral suture. Sometimes the carpels become bivalved, the 2 valves only adnate to the central axis, shedding their seeds. Sometimes the carpels form a pseudosyncarp, becoming more or less concrescent. But only the outer layers of the exocarpium are really concrescent, giving the fruit the appearance of a syncarp. In the latter case the dorsal (abaxial) parts of the carpels finally fall away leaving their base, which is inbedded in the receptacle, exposed with the seeds mostly hanging from their placenta on the elongate funicle which in that stage consists of spirally thickened vessels. In some taxa the abaxial parts of the carpels when falling also dehisce along the dorsal suture ('Tsoongiodendron', but also in some 'Talaumas' and in 'Manglietiastrum'). In Magnolia nitida and M. kachirachirai the carpels are essentially connate. When maturing they tear apart and dehisce along the dorsal suture thus giving the appearance of a common Magnolia fruit. This condition probably exists in many species with crowded carpels. The concrescence of the carpels has apparently developed independently in different lineages of Magnoliaceae. Species with free and concrescent carpels sometimes are very closely allied, judging from the other characters. In Liriodendron the fruits are free, indehiscent, samaroid (produced at the apex into a wing-like beak) and, contrary to Magnolioideae, caducous.

Seed. — In Magnolioideae the seeds are exposed, hanging from the dehiscent carpels. In Liriodendron the testa is adherent to the endocarp and the seed falls with the fruit. The seed coat is organised chiefly from the outer integument while the inner integument is represented by a layer of crushed cells. In a ripe seed the testa consists of an outer fleshy region (sarcotesta) comprising the epidermis of the outer integument, 2 or 3 layers of tangentially elongated cells, a 10–12 layered fleshy zone, 2 or 3 layers of tangentially compressed cells, and an inner stony region of 3 or 4 layers of lignified cells. In Liriodendron no sarcotesta is formed. The same tissue remains thin-layered and becomes partly sclerotic. The differences in seed coat structure between Magnolia and Liriodendron are clearly associated with differences in seed dispersal (Bouman, 1977).

The seed has such primitive features as the multiplicative sarcotesta, stomata, ligneous sclerotesta (endotesta sensu Corner), massive chalaza, copious endosperm, and minute embryo. It is advanced in the apparently functionless nature of the tegmen, perhaps in loss of rumination, and in the substitution of the aril by the sarcotesta. The specialities of the seed of Magnolioideae are the pink pellicle of the sarcotesta, the nature of the cells composing the multiple endotesta, and the tubular lignified sheath around the chalaza. The lignified cells of the sclerotesta are peculiar and need study by electron microscopy. A system of lignified filaments pervades each cell as if the endorecticulum were lignified (Corner, 1976). Tiffney (1977) studied the sclerotesta of many living and fossil species and found that it is possible to recognise morphological distinctions between the genera and in many cases between species within a genus.

Embryology. — The anther wall at the microspore mother cell stage comprises epidermis, endothecium, 2–4 middle layers, and a bilateral glandular tapetum. By the time the cytokinesis is completed in the microspore mother cells, a large number of Ubisch granules line the inner walls of the tapetum. In a fully mature anther the papillate epidermis and endothecium along with 2 or 3 middle layers persist. After meiosis II in the microspore mother cell the cytokinesis takes place by furrowing, resulting in tetrahedral or isobilateral tetrads. The mature pollen is shed at the 2-celled stage. The generative cell is surrounded by a thin sheath of finely granular cytoplasm and a delicate membrane.
The ovules are anatropous, bitegmic, and crassinucellate; the outer integument is vascularised. The hypodermal archesporium is multicellular and of hypodermal origin although ultimately only one cell functions. The primary parietal cell divides repeatedly to form the parietal tissue so that the megaspore mother cell is buried deep in the nucellus. At the end of meiosis II linear or T-shaped megaspore tetrads are formed. The chalazal megaspore functions, giving rise to the Polygonum type of embryo sac. The synergid and antipodal cells are ephemeral. The endosperm is cellular from the beginning, and embryogeny conforms to the Myosurus variation of the Onagraceae type or is irregular (Hayashi, 1964, 1966; Bhandari, 1971; Davis, 1966).


Anatomy. — Vegetative anatomy. The epidermal cells are irregular in form, less often polygonal and with sinuous, curved or nearly straight walls which are often thickened. Many members of the family have a modified subepidermal layer (hypodermis) beneath the upper epidermis, some have such a layer associated with both upper and lower epidermis, and few have it only with the lower epidermis. Many species lack specialised subepidermal cells entirely.

Hairs may be present on both the upper and lower epidermis, or only on the lower. In some species the leaves lack hairs altogether. They are uniseriate, consisting of one to several or many cells. Several types of hair base have been distinguished by Baranova (1972), of which the most primitive occurs in Magnolia while the most advanced are found in Elmerillia, Michelia (Tsoon-giodendron), and in some scattered species of Magnolia.

The stomata are paracytic in Magnoliidaeae (but in rare cases Nong Van Tiep, 1980: 519, found also anomocytic stomata in Magnolia) and paracytic as well as anomocytic in Liriodendroidae. They are confined to the lower surface. Significant thickenings on the walls of the epidermal and subsidiary cells, as well as strongly developed cuticular thickenings on the outer wall of the guard cell, occur mainly in the tropical sections of Magnolia subg. Magnolia as well as in many Asian species of Magnolia subg. Talauma. Foliar sclereids are present in certain taxa. They vary widely in form, size, wall thickness, pitting, and degree of ramification. They may be found in four tissues or cell assemblages: First, as idioblastic sclereids in the petiole and along the midrib, especially in evergreen leaves; less frequently in the mesophyll, in dermal layers and in the vein sheath system including veinlet endings.

Taxonomically the mentioned characters are of different value. Each genus shows a particular range of features, some of which can be used diagnostically to separate taxa above the genus level. The coriaceous texture of tropical leaves is achieved in various ways arising from the variable form and diverse distribution of the sclereids. Magnolia subg. Talauma species characteristically have the entire vein system of the leaf ensheathed in sclerenchymatous sheaths, and the veinlets terminate in sclerified elements. Magnolia species in contrast have parenchymatous vein sheaths near the terminations and lack sclerified terminal cells, but most of the mesophyll and epidermal cells are sclerified. Magnolia leaves are characterized by sclerified epidermal and hypodermal layers, sclerified arm parenchyma in the mesophyll, unilignified lobate vein-sheath cells, and an absence of either sclerified veinlet terminal cells or a sclerified leaf margin. No other genus combines all those features, although some do show one or more. Sterile specimens of Magnolia can easily be recognized on the basis of cleared leaf segments.

Magnolia subg. Magnolia and subg. Talauma and Michelia exhibit in many of their members sclerified terminal veinlet cells, thick sclerified leaf margins, and stellate sclereids along the midrib. Rarely those features may be diagnostic for species, but in most cases they are too common
to be useful. The foliar characteristics of *Magnolia* subg. *Talauma* include veinlets terminating in thick-walled stellate sclereids and thinner walled tracheary elements. These cell types are typically absent from temperate zone *Magnolia* sections and therefore are possibly an adaptation to climatic conditions. In all the Asian species of subg. *Talauma* examined there is a thick sclerified margin, usually including a vein. In the American species this is absent but in few of them a weak approach to this condition is seen.

The massive marginal ridge helps to identify certain species of *Magnolia* subg. *Talauma* and subg. *Magnolia*, *Manglietia* (3 spp.), and *Michelia* (3 spp.).

In *Aleimandra*, *Liriodendron*, 'Paramichelia', and most *Elmerrillia* species foliar sclereids are rare. This may indicate that these taxa have not developed vegetative modifications different from those of the related large genera (mainly after Baranova, 1972 and Tucker, 1977).

Wood anatomy (largely from H. Gottwald, a manuscript of a lecture given for the Internationale Association of Wood Anatomists in Amsterdam, which he kindly put at my disposal). Wood anatomy is homogeneous throughout the family. The secondary xylem shows a well-developed fibrous ground tissue of thin to medium thick-walled fibres, with diameters from 15 to 25 μm depending on the species. The vessels are mostly evenly distributed, for the temperate species which show (semi-)ring-porous tendencies. Vessel diameter ranges from 50 to 180 μm on average. The rays are nonstoried, mostly 3 cells wide and 0.5–1 mm high. The axial parenchyma is mainly banded and marginal (bands 1–2(–12) cells wide). Chowdhury (1964) established the annual periodicity of these parenchyma bands, even in the tropical *Michelia champaca*. For other tropical species the periodicity of the parenchyma bands remains to be studied, and is probably not annual. Only in *Magnolia* subg. *Talauma* the bands tend to fork. The paratracheal parenchyma is usually scanty or in some species virtually absent. The parenchyma cells do not contain any kind of crystals, nor are there any phenolic substances found in the vessels. There are some striking anatomical details occurring only in groups of individual taxa. Firstly the primitive vessel pitting varying from purely scalariform to opposite. The vessel perforations are mostly scalariform with only 1 to 15 bars. In the advanced taxa *Liriodendron* and sect. *Yulania* of *Magnolia* also simple vessel perforations occur, always in connection with opposite pits. A rare feature is the occurrence of amorphous silica as a coating on the cell walls including the tyloses, or as solid occlusions completely occluding the lumina. Complete solid plugs of silicium dioxide occur in all species of sect. *Blumiana* of *Magnolia* subg. *Talauma* and in the monotypic sect. *Lirianthe* of *Magnolia*. The estimated volume percentage of silica is up to 8%, based on air-dried volume; sometimes almost every vessel is filled with silicium dioxide. This means that these taxa belong to the woody species with the highest silica content known in the vascular plants. Spiral thickenings on the vessel walls are a further special feature of limited occurrence in *Magnoliaceae*. They are only weakly pronounced and hard to detect.

Some peculiar idioblastic parenchyma cells are found mainly between the marginal cells of the rays. They are thin-walled, have mostly amorphous brownish contents, and are often referred to as 'oil cells', although their chemical nature is still unknown. These enlarged cells are of irregular distribution so that their taxonomic value is limited. Silica bodies which occur in the ray cells of a few species in sect. *Maingola* of *Magnolia* and in sect. *Blumiana* of *Magnolia* subg. *Talauma*, point to their close relationship. Crystalline inclusions are found in fine wood-splits of *Magnolia* subg. *Magnolia* and subg. *Talauma*; they consist of calcium carbonate and are always of traumatic origin. The last special item concerns the occurrence of tyloses in the fibres, besides those in the vessels. This rare feature was observed in 24 species, belonging to 7 genera and subgenera.

The homogeneity of characters enhances a mixture of overlapping structural details which is detrimental to the internal classification of the family. The largest genus, *Magnolia* (without subg. *Talauma*) includes almost all structural traits which are otherwise distributed over the remaining genera.

There are only few taxa which can be distinguished anatomically such as the genus *Liriodendron*, which has neither spirals in the vessels nor tyloses in the fibres. *Magnolia* sect. *Yulania* is
characterized by simple perforations, and Magnolia subg. Talauna sect. Blumiana by its silica-bearing vessels and the pronounced heterogeneity of the rays. Magnolia subg. Talauna sect. Aromadendron differs from the rest of subg. Talauna in that the pores are almost twice the size of the investigated Asian species of subg. Talauna. They are also the largest in the whole family (Canright, 1955).

Differences are also apparent in the distribution of wood parenchyma and of characteristics of fibre tracheids. In this respect Elmerrillia falls within the range of Michelia whereas Kneria is indistinguishable from many tropical Magnolia species. There is little difference in the wood anatomy of Manglietia and many temperate Magnolia species. Although neither the primitive nor the advanced wood anatomical characters are confined to any one genus, there are many indications that the woods of the temperate species of Magnolia and Liriodendron are the most specialized. Magnolia subg. Talauna exhibits the largest assemblage of primitive characters. The tropical Magnolia paenetaulauma from Hainan exhibits a great number of primitive features. Also in the external morphology the species of sect. Gwilliamia, to which this species belongs, resemble the species of subg. Talauna so closely that they cannot be distinguished in absence of fruits.


Chromosomes. The basic chromosome number is $x = 19$. Polyploidy has been demonstrated in Magnolia. In wild species diploidy as well as tetraploidy is found. Treseder (1978: 208) reports for cultivated Magnolias besides diploid, also triploid, tetraploid, pentaploid, heptaploid, and octoploid numbers, while aneuploid numbers also are recorded.

The chromosomes are characteristically small, short rods (Whitaker, 1933). The chromosome base number of all Angiosperms is 7, the higher numbers are derived from it by palaeopolyploidy (Ehrendorfer c.s., 1968). The same basic chromosome number of 19 is found in Myristicaceae (also 21) and Monimiaceae (also 22).


Phytochemistry. Chemical characters of the family were summarized and analyzed by Hegnauer (1969). A general occurrence of essential oils deposited in large idioblasts and of alkaloids of the biosynthetic pathway resulting in the so-called benzyltetrahydroisoquinoline family of alkaloids comprising among others benzylisoquinolines, bisbenzylisoquinolines, aporphines, oxaaporphines, and protoberberines was stressed. Leaf phenolics were represented mainly by kaempferol, quercetin, rhamnetin, procyanidins, and caffeic acid. At the same time a total lack of flavonols with trihydroxylated B-ring, of ordinary flavones and of galli- and ellagitannins had been demonstrated. Other characters mentioned are strongly silicified leaves in many taxa, oil-rich seeds without starch, and a strong tendency to store cyclitols in Liriodendron (liriodendritol), Magnolia subg. Magnolia (pinitol) and subg. Talauna (quercitol). The sporadic occurrence of lignans (liriotesinol), neolignans (magnolol), coumarin glycosides (magnolioside), cyanogenic compounds (not identified), and of the sesquiterpene lactones costunolide and parthenolide was noted. The totality of known chemical characters was interpreted as being highly typical of Polycarpiceae.

In the meantime much additional phytochemical research was performed with members of the genera Alcimandra, Elmerrillia, Liriodendron, Magnolia subg. Magnolia and Talauna, and Michelia. In each instance alkaloids were isolated, some being new compounds and some already known from other members of Polycarpiceae. All, however, belong to the phenyltetrahydroisoquinoline class. The oxaaporphine liriodendrine and the quaternary aporphine magnoflorine seem to be nearly ubiquitous. New features are the rather general occurrence of biologically active sesquiterpene lactones belonging to the germacrone, eudesmanolide, elemanolide, and guaianolide groups of these constituents, and of lignans and neolignans (together called ligna-
noids). Hitherto sesquiterpene lactones were isolated from species of *Liriodendron*, *Magnolia*, and *Michelia*. All species investigated for lignanoids were shown to contain such metabolites. Today many individual compounds are known from members of *Liriodendron*, *Magnolia subg. Magnolia* and *Talauma*, and *Michelia*; they represent at least 12 different structural types. Cyanogenetic compounds were detected in *Liriodendron tulipifera* (taxifolin and triglochinin) and in *Magnolia sprengeri* cv. ‘Diva’ (taxifolin). They belong to the tyrosine-derived class of cyanogens.

From the taxonomic point of view the secondary metabolism of *Magnoliaceae* can be considered as highly characteristic of *Polycarpaceae* and closely related orders such as *Piperales* and *Aristolochiales*. They all have essential oils in idioblasts and comprise members synthesizing benzylisoquinolines. Similar lignanoids are presently known, among others, from *Aristolochiaceae*, *Eupomatiaceae*, *Laureaceae*, *Myristicaceae*, *Piperaceae*, and *Trimeniaceae*. Sesquiterpene lactones occur also in *Chloranthaceae* and *Lauraceae*. They form one of the arguments for the proposition of an evolutionary line *Polycarpaceae — Rutales — Umbelliferales s.str. — Asterales. — R. Hegnauer.*

**Palynology.** (After Praglowski, 1974). The pollen grains of *Magnoliaceae* are 1-(ana)colpate, bilateral, heteropolar. Aperture simple, with markedly thin, frequently slightly undulated margins. Colpus usually longer, occasionally as long as, or rarely shorter than the longest axis. Colpus invagination usually absent or insignificant. Exine structure in tectate grains (about 95%) consists of a continuous tectum perforatum supported by columellae which have no geometrical connection with the tectum or with the suprartectal elements. In rarely occurring semitectate grains the exine structure is microreticulate, without sculpturing. Sculpturing rugulose or absent (tectum smooth). Sexine at the proximal face thicker than nexine, usually twice or more. Columellae minute, usually indistinct.

*Elmerrillia* pollen grains show partly similarity with pollen grains of *Michelia*, but the microreticulate structure of the grains of *E. tsianpaccas ssp. mollis* is rather unique showing no resemblance to *Michelia* pollen. The reticulum is considerably coarser than that of *Pachylarnax* pollen grains.

*Michelia*, *Paramichelia*, and *Tsoongiodendron* possess pollen grains that are very similar. *Pachylarnax* possesses pollen with microreticulate exine structure consisting of thin muri encompassing very minute lumina. This rather peculiar exine structure is more delicate than that in other *Magnoliaceae*. Similarly, the rather symmetric ellipsoidal shape of the pollen makes it quite difficult to include them among typical magnoliaceous pollen.

*Alcimandra* pollen possesses an exine without sculpturing which shows sometimes resemblance with *Talauma* pollen. *Magnolia* pollen grains show a rather large morphological variation; nearly all the pollen types of subfamily *Magnolioideae* are found in *Magnolia* Pollen grains of *Elmerrillia* and *Michelia* show slight differences to that of *Magnolia*. Manglietia pollen grains show a high morphological similarity to those of *Magnolia*. *Talauma* pollen grains show features similar to those encountered in *Magnolia subg. Magnolia*. *Aromadendron* pollen grains show similarity to *Alcimandra* pollen grains, but also with those of *Magnolia sect. Mangiola*.

On palynological evidence the joining of *Michelia*, *Tsoongiodendron*, and *Paramichelia* is strongly supported. The same holds for *Manglietia*, *Magnolia*, and *Talauma*, while the joining of *Aromadendron* with *Magnolia* is not contradicted.


The family can easily be divided into two subfamilies, *Magnolioideae* and *Liriodendroideae*, the latter not in Malesia.
Leaves entire or occasionally two-lobed at the apex; stipules free from the petiole or adnate to it. Anthers introrse or latrorse. Fruiting carpels longitudinally dehiscent or circumscissile, at least the base remaining adnate to the torus, free or concrescent into a syncarp. Testa free from the endocarp, externally arilloid.

In Magnolioideae two tribes can be recognized clearly.

**KEY TO THE TRIBES**

1. Growth sympodial. Flower buds arising terminal on the twigs ................. 1. Tribus Magnolieae
2. Growth monopodial. Flower buds arising on brachyblasts in the axils of the leaves 2. Tribus Micheliace

**1. Tribus Magnolieae**

Growth sympodial. Flower buds arising terminal on the twigs, the latter growing in length from an axillary bud of one of the upper leaves. Genera: Magnolia (incl. Talauma, Alcimandra, Manglietiastrum and Aromadendron), Manglietia, Kmeria (not in Malesia), and Pachylarnax.

**KEY TO THE GENERA**

1. Fruit consisting of few to many separate free or connate carpels along the torus.
2. Ovules 4 or more in each carpel. The hair base replaces a normal epidermal cell, so that the loss of a hair leaves a pore in the cutical membrane. Leaf anatomical characters: sclerified epidermal and hypodermal layers, sclerified arm parenchyma in the mesophyll, unlignified vein-sheath cells, absence of either sclerified veinlet terminal cells or a sclerified leaf margin ......................... 2. Manglietia
3. Ovules 2 in each carpel (4 in Magnolia kachirachira), sometimes 4 in the lower carpels. The hair base consists of at least two epidermal cells. The hair does not leave a pore when falling ........ 1. Magnolia

**1. MAGNOLIA**


Blumia Nees, Flora 8 (1825) 152, non Blumea DC., nom. conserv. — Type: Talauma candollei Blume.

Alcimandra Dandy, Kew Bull. (1927) 260. — Type: A. cathcartii (Hook.f. & Thoms.) Dandy. — Fig. 1–6.

Trees or shrubs. Stipules adnate to or free from the petiole. Flowers terminal, solitary, bisexual. Tepals 9–21, 3–5-merous, subequal or more rarely the outer whorl forming a true calyx. Anthers introrse to latrorse, connective produced into a longer or shorter appendage or rarely unappendaged. Gynoecium sessile or in some species stipitate; carpels many to few, usually free but connate in sect. Talauma, sect. Glynopodium, and in some other species. Fruiting carpels free, crowded, dehiscent along the dorsal suture, in subg. Talauma the basal parts of the ripe carpels staying adnate to the torus, the apical parts falling and thus exposing the seeds which hang from the lengthened funiculus, sometimes the apical parts during or before falling dorsally dehiscing; in some species of sect. Glynopodium the carpels connate but tearing apart when maturing and dehiscing dorsally. Ovules generally 2 in each carpel, rarely 3 or 4 in the lower carpels, in few species up to 4 or 5 in all carpels. Ripe seeds often hanging from the funicles which lengthen through uncoiling of the spiral vessels.

Distr. About 120 spp. of which about one third in the New World from SE. North America to S. Brazil, the remainder in temperate and tropical SE. Asia from the Himalayas to China, Japan, Taiwan and Malesia. In Malesia represented by sect. Maingola of subg. Magnolia, and sect. Blumiana and sect. Aromadendron of subg. Talauma.

Note. Two species of subg. Magnolia are commonly cultivated in Malesia, M. coco (Lour.) DC. and M. grandiflora L. Magnolia coco (of sect. Gwillimia) differs from the species in sect. Maingola because the stipules are adnate to the petiole. The species can be distinguished from sect. Blumiana, especially from M. candollii, by the midrib not being prominent on the uppersurface. Magnolia grandiflora (of sect. Theorodon) has petals of 7 cm long or even longer while those in sect. Maingola never exceed 5 cm. The stamens in M. grandiflora are 2–3 cm long and the densely appressedly pubescent brachyblast 8 mm diam. or more.

KEY TO THE SECTIONS
(in only in Malesia)

1. Stipules free from the petiole. Midrib not prominent above
2. Fruits with free carpels
3. Stipules adnate to the petiole. Midrib prominent above
1. Sect. Maingola
2. Sect. Aromadendron
3. Sect. Blumiana

To make identification of collections without fruits possible, besides the keys to the species of each section a separate key is given to the sections Maingola and Aromadendron together.

KEY TO THE SPECIES OF SECTIONS MAINGOLA AND AROMADENDRON

1. Young twigs and underside of leaves hairy. Carpels free in fruit
2. Gynoecium hairy
3. Young twigs pubescent or pilose. Scars of perianth and stamens along 5–9 mm of the torus under the fruit. Stamens 7.5–12 mm, the 2–3 mm long connective appendage not included
1. M. macklottii
3. Young twigs densely woolly hairy. Scars of perianth and stamens along 10–15 mm of the torus. Stamens 6–9 mm long, the 1.5–2 mm long connective appendage not included. 3. M. maingayi

2. Gynoecium glabrous.

4. Scars of perianth and stamens along 5–9 mm of the torus under the fruit. Stamens 7.5–12 mm, the 2–3 mm long connective appendage not included. Outer tepals 3.5–4 cm long. 4. M. macklotii

1. Young twigs mostly and underside of leaves always glabrous. Carpels free or connate in fruit.

5. Tepals c. 18 or more. Carpels connate in fruit. Connective appendage 10–15 mm. Pedicle 8–25 mm. Pedicle 0–10 mm. Alveoles in general more than 0.5 mm diam. Reticulation on the upper surface quite distinct. 5. M. bintuluensis


7. Stamens c. 10, 4 mm long, the connective appendage c. 7 mm. Carpels c. 6. Pedicle absent, scars of stamens and perianth at most 1 mm. 7. M. pahangensis

8. Petiole 2.5–5 cm. Pedicle 7–8 mm. Gynophore 5–10 mm. Carpels connate in fruit. 8. M. ashtonii

9. Outer tepals 4, c. 4.5 cm long. Stamens 9–14 mm, the 10–15 mm long connective appendage not included. Scars of tepals and stamens under the fruit along c. 5 mm of the torus. Carpels connate in fruit. 9. M. borneensis

10. Outer tepals 3, 1.5–4 cm long. Stamens 5–12 mm, the 0.5–3 mm long connective appendage not included. Scars of tepals and stamens under the fruit along c. 1–9 mm of the torus. Carpels free in fruit. 10. M. macklotii

11. Stamens 5–10 mm, the 0.5–3 mm long connective appendage not included. Scars of tepals and stamens under the fruit along 1–3 mm of the torus. Carpels 1–15. 11. M. phaulantha

12. Stamens 5–10 mm, the 1–1.5 mm long connective appendage not included. Scars of perianth and stamens along 2–3 mm of the torus. 12. M. carsonii

1. Subgenus Magnolia

Ripe fruits consisting of free carpels which dehisce along the dorsal suture. Anthers dehiscing intransely. Flowers neither precocious nor with a much reduced calyx-like whorl of outer tepals. Leaves in Asia evergreen.

Only one section indigenous:

1. Section Maingola


KEY TO THE SPECIES

1. Carpels many, or at least 15 (rarely in M. macklotii fewer). Scars of perianth and stamens in fruit along 5–20 mm of the torus.

2. Twigs (long) yellowish pubescent, pilose, or glabrous. Scars of perianth and stamens in fruit along 5–9 mm of the torus. 1. M. macklotii

2. Twigs woolly hairy when young. Scars of perianth and stamens in fruit along 10–20 mm of the torus.
3. Fruits hairy, 5–8 cm long. Scars of perianth and stamens in fruit along 10(–15) mm of the torus. Brachylast 1–5 cm.

3. M. maingayi

3. Fruits glabrous, 7–12 cm long. Scars of perianth and stamens in fruit along 10–20 mm of the torus. Brachylast 4.5–11 cm.

4. M. uvariifolia

1. Carpels at most 15. Scars of perianth and stamens in fruit along 1–3 mm of the torus.

4. Scars of perianth and stamens in fruit along c. 1 mm of the torus. Petiole 5–10 mm. 5. M. phaulantha

4. Scars of perianth and stamens in fruit along 2–3 mm of the torus. Petiole 6–18 mm... 2. M. carsonii


M. aequinoctialis Dandy, Kew Bull. (1928) 185. — Type: Houtvester Sumatra's Oostkust 25 (BO; L), Sumatra, Karolanden.

Shrub or treelet, or tree to 23 m (–50 m, once recorded) high by 43–(50) cm diam. Twigs long yellowish pubescent or pilose, or sometimes glabrous, glabrescent when older; stipules densely yellowish pubescent to patently long soft hairy, rarely nearly glabrous, 3–9 cm. Leaves: — apressedly or patently pubescent, especially on midrib and nerves, often glabrescent, or glabrous below, ± elliptic to narrowly obovate, 12–25 by 3–9 cm; base acute; acumen c. 5–15 mm; midrib much prominent below; nerves in 12–22 pairs, much prominent in the undersurface, less so above; intramarginal vein prominent on both surfaces; reticulation densely netted and much prominent on both surfaces. Petiole 5–15 mm.

Brachylast: apressedly pubescent, rarely (nearly) glabrous, often very slender, 2.5–8 cm long; pedicel absent; spathaceous bracts only one pair. Outer tepals three, 2–3 by c. 0.7–1.5 cm; inner tepals 6, in two rows, as long or slightly shorter than outer ones, 5–10 mm broad. Stamens 20–many, filament 1.5–2 mm long, anthers 3.5–10 mm, connective appendage triangular, acute, 2–3 mm long; carpels glabrous, glaucous, or yellowish tomentose. 15–c. 50, rarely fewer than 15. Fruits: — c. 2.5 cm broad and up to 5 cm long, torus with scars of perianth and stamens 5–9 mm long. 

Distr. Malesia: Sumatra, Malay Peninsula (Perak), Java, Borneo (Sabah).

Note. The flowers are creamy, the outer tepals more greenish.


Distr. Malesia: Sumatra (W. coast, G. Singgalan, Palembang); W. Java, Borneo (Sabah, Tawau).

Ecol. Rare in primary vegetation; 80–1500 m.


Leaves mostly narrowly obovate. Flower buds and carpels hairy.

Distr. Malesia: Sumatra (Aceh, G. Leuser; Tapanuli; E. coast, Karolanden; W. coast, Padang, G. Singalan, G. Kerinci), Malay Peninsula (Perak, Maxwell's Hill, one coll.).


Note. The collection from Perak was identified as M. maingayi. It rather belongs to M. mackiottii var. beccariana but demonstrates the close affinity between the two taxa.


Drumis-leaved Magnolia W. Meijer i.e. 8, fig. — M. 'drymisfolia' Dandy ex Cockburn, i.e. 55, nomen. — Type: NOOTBOOM 4612 (L; BO). — Fig. 1, 2.

Shrub or tree to 60 m high and 70 cm diam. Twigs glabrous or hairy in innovations with apical buds glabrous or hairy. Leaves glabrous, thin or thick coriaceous, 4.5–16 by 2.5–8 cm. Petiole 6 to 18 mm. Brachylast glabrous or hairy, 2–5 mm long. Outer tepals 3(4), 15–40 mm long; inner tepals 6. Stamens c. 15–30, 7–12 mm long with a connective appendage of 1–3 mm long. Fruit sessile or gynopo-
Magnolia carsonii Dandy ex Noot. var. carsonii. a. Habit, ×1; b. fruit, ×3 (Clemens 50271).

dium to 5 mm long, carpels 1–15, glabrous; scar of perianth and stamens 2–3 mm along the torus.

KEY TO THE VARIETIES

1. Tree from 9 to 60 m, glabrous in all its parts except sometimes the inner margins of the terminal stipules. Leaves when dry rather dark reddish brown, darker above than beneath, thin coriaceous, 5–13 by 2.5–6 cm; nerves in 8–15 pairs; the larger alveoles filled with smaller ones from less prominent veins. Petiole 6–13 mm. Gynophore absent

a. var. carsonii

1. Shrub or tree to 25 m; twigs hairy directly under the terminal bud or glabrous; terminal buds hairy or sometimes glabrous. Leaves when dry olive
Magnoliaceae

greyish green or greyish brown on both surfaces, thick coriaceous, 4.5—9 by 2.5—4.5 cm; nerves in 6—12 pairs, all lesser veins forming a dense reticulation and no difference in alveoles, often the reticulation slightly obscured by the coriaceousness of the leaf and the undersurface glaucous. Petiole 10—18 mm. Gynophore 0—5 mm

**a. var. carsonii.** — *Carson’s Magnolia W. MEIJER. — M. ‘carsonii’ DANDY ex COCKBURN. — Fig. 1.*

A big tree to 60 m tall and 60 cm diam.; twigs glabrous; stipules glabrous, up to 4 cm long, sometimes long silky on the inner margin. Leaves rather dark reddish brown, darker above than beneath, glabrous, elliptic, thin coriaceous, 5—13 by 2.5—6 cm; acumen 3—10 mm; base cuneate; midrib prominent below; nerves in 8—12 (—15) pairs, much prominent below, slightly less so above, meeting in an intramarginal vein; reticulation rather densely and prominently netted on both surfaces, secondary nerves 2—c. 4 about parallel with the nerves starting from the midrib and rather obvious from the lesser veins, the alveoles near the midrib oblong, the longest diameter parallel with nerves, the large alveoles filled with the smaller ones of which the veins are less prominent. Petiole 6—13 mm. *Brachyblast* glabrous, 2.5—4 cm long, very slender; pedicel absent. Only one pair of spathaceous bracts. Outer tepals 3, 15—27 mm by c. 5 mm; inner tepals 6, about as long by 5—10 mm. *Stamens* 7—10 mm long, the 1—1.5 mm long connective appendage not included; gynophore absent; carpels glabrous, up to c. 15. *Fruits* with lenticels on the ripe carpels, often distorted by abortive carpels, mostly less than 10 carpels, sometimes only 1. fertile; scars of perianth and stamens along c. 2 (—3) mm of the torus.


**b. var. drymifolia** Noot. Blumea 32 (1987) 351, f. 2. — *Drimys-leaved Magnolia W. MEIJER. — M. ‘drymifolia’ DANDY ex COCKBURN. — Fig. 2.*

Shrub (on exposed ridges) to tree of 25 m high; twigs hairy directly under the hairy terminal bud, soon glabrescent, or rarely entire plant glabrous; stipules hairy (or rarely glabrous) in the terminal bud, glabrous or hairy in lateral buds. Leaves olive greyish green or brown on both surfaces or the undersurface bluish, thick coriaceous, glabrous, (broadly) elliptic to sometimes obovate, glossy above, often glabrescent beneath, 4.5—9 (~16) by 2.5—4.5 (~8) cm; apex not or hardly acuminate or sometimes emarginate to shortly acuminate, acumen up to 10 mm; margin thickened containing a vein; base cuneate, slightly acuminate; midrib much prominent beneath; nerves in 6—12 pairs, curved upwards and meeting in an intramarginal vein; all lesser veins forming together a dense reticulation, prominent above, slightly obscured by the coriaceousness of the leaves below, the alveoles along the midrib mostly ± isodiametric. Petiole 10—18 mm. *Flowers* erect, brachyblast stout, densely appressedly pubescent or pilose to nearly glabrous or more slender and glabrous, (2—)3—5 cm; pedicel 0—1.5 mm, when present densely appressedly pubescent; spathaceous bracts glabrous, only 1 pair. Outer tepals 3, greenish, 2—4 by c. 1 cm; inner tepals yellow, 6, c. 13—35 by 10 mm. *Stamens* up to c. 30, filament 1—3 mm, anthers 4—8 mm, connective appendage 1—2 mm; gynophore 2—5 mm or rarely absent; carpels very few (3—5 in my own collections from Bukit Raya), probably never more than 10, glabrous. *Fruits* without or with only few small lenticels, scars of perianth and stamens along 3 mm of the torus; seeds 1 or 2.

**Distr. Malesia:** Borneo (Sarawak; Sabah, Crocker Range, Kinabalu; W., Central and E. Kalimantan, Mt Palimanan).

Ecol. Primary and secondary mountain forest; 1000—2850 m; fl. fr. probably Jan.—Dec.

**Note.** Undersurface of leaves often papillate.

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Treetel or tree from 1.2 to 18 m, to 50 cm diam.; twigs, terminal buds, and petioles densely woolly hairy. Leaves long hairy below, especially on midrib and nerves, glabrous, glabrescent, above obovate to narrowly obovate or rarely elliptic, 9—26 by 3—9 (~11) cm; acumen 5—25 mm; base cuneate to more or less rounded; midrib much prominent below; nerves in 14—18 pairs, meeting in an intramarginal vein; reticulation netted, prominent below, slightly so above. Petiole 3—5 (~15) mm. *Brachyblast* densely hairy, 1—5 mm; pedicel absent; spathaceous bracts one pair, long hairy. Outer tepals 3, 20—40 by 10—12 mm; inner tepals 6, thick coriaceous, 20—25 by 10 mm. *Stamens* many, filament c. 1 mm, anthers 5—6 (—8) mm, connective appendage triangular, not very acute, tip often blunt, c. 1.5—2 mm long; gynophore absent; carpels many, densely (woolly) hairy. *Fruits* hairy, cylindrical, c. 5 (~8) by 2—3 cm, sometimes much shorter by abortion of the carpels, scars of perianth and stamens along 10 (~15) mm of the torus.
Distr. Malesia: Malay Peninsula (Perak; Pahang; Selangor, Kepong; Johore; Singapore), Borneo (Sarawak, Kapit, Ulu Mojong, 3rd Div., Bario, Kelabit plateau; Sabah, Kinabalu).

Ecol. In forest from low altitude to 1500 m; fl. fr. Jan.–Dec.


Treelet or tree from 6 to 25 m, up to 35 cm diam.; twigs and terminal buds yellowish woolly hairy. Leaves pubescent beneath, especially on midrib and nerves, glabrescent, obovate to narrowly obovate, 10–28 by 3.5–9 cm; acumen 3–15 mm; base cuneate to rounded; nerves in 13–19 pairs, prominent below and less so above, meeting in an intramarginal vein; reticulation densely netted, much prominent below, less so above. Petiole 3–13 mm. Brachyblast pilose, glabrescent, 4.5–11 cm, pedicel absent; bracts in one pair only, glabrous. Outer tepals 3, c. 35–40 by 15 mm; inner tepals 6, thick coriaceous, c. 30 by 10 mm. Stamens very many, filament c. 1 mm, anthers c. 5 mm, the connective appendage acute, 2.5–3 mm long; gynophore absent; carpels very many, glabrous. Fruits cylindrical, c. 7–14 by 2–3 cm; scars of perianth and stamens along 10–20 mm of the torus.


Ecol. Primary or secondary forest; 180–1800 m; fl. fr. Jan.–Dec.

Vern. Borneo: karampilung, SE. Kalimantan.

Note. This species is closely related to Magnolia...
Fig. 3. *Magnolia uvarifolia* Dandy ex Noot. a. Habit, ×0.6; b. ovary, ×1.5; c. anthers, ×6; d. fruit, ×0.8.
maingayi which, however, differs in the mostly longer and denser indumentum and in the flower buds and carpels being hairy.


Tree to at least 30 m by 50 cm diam., in the young parts entirely glabrous; stipules c. 2–4 cm (sometimes the inner margins long hairy); leaves (narrowly) elliptic, to slightly obovate, 6–15 by 2.5–4.5 cm; acumen 3–20 mm; base cuneate, midrib much prominent beneath; nerves in c. 10 pairs, hardly distinct from the densely netted reticulation which is prominent on both surfaces. Petiole c. 5–10 mm.

Brachyblast very slender, 2.5–4 cm; pedicel absent; flower buds glabrous. Outer tepals 3, c. 15 by 2 mm; inner tepals 6–7, slightly longer. Stamens many, filament very short, anthers c. 5 mm long, connective appendage to c. 1 mm long; gynophore absent; carpels less than 10, glabrous. Fruits often with only one or two developed carpels, c. 1 by 1 cm.

Distr. Malesia: Sulawesi (Central, Malambang, Malili, Rantelemo, Rantepao, Palu).

Ecol. Mountain forest; 1250–2200 m; fl. Apr.–Dec.

Note. This species resembles Magnolia carsonii (var. carsonii) very much and might prove to be conspecific with it.

II. Subgenus Talauma


Trees or shrubs. Stipules adnate to or free from the petiole. Tepals 9–36, subequal. Anthers introrse, connective produced into a short to very long (even longer than the anther) appendage. Gynoecium sessile or with a gynophore to 10 mm. Carpels many to few, concrescent at least at the base; fruiting carpels woody, circumscissile, the upper portions falling away either singly or in irregular masses, the lower portions persistent with the suspended seeds.

2. Section Aromadendron


Stipules free from the petiole. Outer tepals 3 or more often 4, inner tepals 8–32. Stamens with a connective appendage that is in most species very long, from slightly shorter to longer than the anthers, but in M. ashtonii it is triangular and only 2.5 mm long. Fruit a fleshy syncarp, often on a gynophore of c. 5 to rarely 10 mm long, the carpels falling off when ripe in irregular masses thus exposing the seeds which hang from the torus. Seeds 1–2 in each carpel.

Distr. Malesia: Sumatra, Malay Peninsula, Java, Borneo, Philippines (Palawan).

Key to the species

1. Leaves 4.5–7.5 by 1.5–3.5 cm. Petiole 7–10 mm. Carpels c. 6 .......................... 10. M. pahangensis
1. Leaves longer than 7.5 cm. Petiole 8–50 mm. Carpels more than 6.
2. Nerves in 8–12 pairs. Pedicel absent. Fruit ellipsoid, 3–4.5 by 2–3.5 cm. Gynophore absent. Scars of perianth and stamens along up to 3 mm of the torus ................................. 7. M. bintuluensis
2. Nerves in 11–20 pairs. Pedicel 2–10 mm. Fruit 5–9 by 3–5 cm. Gynophore 0–10 mm. Scars of perianth and stamens along 5 mm of the torus.
3. Nerves in (12–)15–20 pairs. Petiole 25–50 mm. Fruits ovoid to pear-shaped, 8–9 by 4–5 cm
8. M. ashtonii
4. Tepals 12 .......................................................................................... 9. M. borneensis


Tree to 40(-53) m high and 80(-115) cm diam.; twigs glabrous, brown or blackish brown provided with many sometimes light coloured annular stipular scars; stipules glabrous but with a tuft of hairs at the apex, the inner margins sometimes beset with long white hairs. Leaves glabrous, glossy but rarely the undersurface glaucous ("var. glauca"), mostly narrowly elliptic, sometimes elliptic, 7.5-22(-27) by 3-6(-8) cm; acumen 3-20 mm; base cuneate to sometimes rounded; midrib much prominent below; nerves in 11-16 pairs meeting in a looped intramarginal vein which is prominent on both under- and upper surfaces but on the upper surface hardly distinct from the venation; reticulation densely netted, prominent on both surfaces, the marginal vein included in the reticulation. Petiole 8-20(-25) cm. Brachyblast glabrous, 3-5(-6) cm long; spathaceous bracts one pair, c. 6 cm long, glabrous but with some hairs apically; pedicel glabrous, c. 5(-10) mm, often in N. Sumatra and the Malay Peninsula nearly absent. Tepals c. 18-36, the 4 outer sepaloid ones light yellowish green in vivo, narrowly obovate or mostly elliptic, the longest c. 4.5-7 cm long and up to 1.5(-1.8) cm broad, the others white, narrowly elliptic, slightly shorter and much narrower. Stamen 60-70, filament c. 0.5 mm, anthers 8-9 mm, the connective produced in a long setaceous, 12-15 mm long appendage; a short synophore present between stamens and carpels. Fruits ellipsoid to orbicular, c. 5-7 cm long and c. 3-5 cm diam., tepal and staminal scars along c. 5 mm of the torus, synophore also c. 5 mm long but rarely shorter to nearly absent.


Ecol. Common, mostly in lowland rain-forest but in Sumatra also to 1200 and in Aceh (G. Leuser) to 1850 m, in Java up to 1200 m. Fl. fr. Jan.–Dec. Vern. Sumatra: jelatan bulan, kau suhing, kedondong tunjuk, medang mempau, m. pahu, M. utup-utup, Batak.


Tree 6-25 m by 15-62 cm; twigs glabrous, wrinkled; terminal buds glabrous, sometimes with a tuft of hairs apically; stipules glabrous but the inner margin provided with long hairs. Leaves coriaceous, glabrous, mostly dull, the undersurface sometimes glaucous, obovate or sometimes elliptic, 8.5-18 by 3.5-7.5 cm, abruptly shortly acuminate with rounded tip, acumen c. 5-10 mm; base cuneate; midrib much prominent below; nerves prominent on the undersurface and less so above, in 8-12 pairs, intramarginal vein rather inconspicuous on the undersurface, often a second less conspicuous intramarginal vein closer to the margin present; reticulation netted and prominent on the undersurface but less so above, the smaller nerves obscured because the leaves are coriaceous and thus the reticulation rather coarse. Petiole 10-25 mm. Brachyblast 1-3 cm, mostly curved, often terminating a twig of which the upper leaves are reduced or fallen; pedicel absent; spathaceous bracts glabrous, direct under the flower. Outer tepals 3, linear oblong c. 2 cm long; inner tepals c. 15. Stamens 10-12 mm, provided with a connective appendage of hardly the same length; synophore absent. Fruits ellipsoid, c. 3.4-5.3 cm by 2-3.5 cm, no pedicel or
Fig. 4. *Magnolia ashtonii* DANDY ex NOOT. a. Habit with flower, ×0.6; b. ovary, ×1.8; c. anthers, ×1.8; d. fruit, ×0.6 (a, c S 7895 ASHTON, b BRUN 5503, d S 12449).
Magnoliaceae


Tree up to 45 m high and 60 cm diam. Twigs glabrous, rather thick, terminal buds sometimes with a tuft of hairs on the apex; stipules glabrous, c. 2 cm. *Leaves* glabrous, the undersurface distinctly punctuate, often glaucous, obovate, 12–23 by 5–10 cm; acumen 3–7 mm with blunt tip; base acute, decurrent with two ridges into the petiole; midrib much prominent on the undersurface; nerves in 15–20 pairs, distinct on both surfaces, slightly prominent below, hardly or not above; reticulation distinctly fine netted but hardly prominent on both surfaces. Petiole 2.5–5 cm, often thickened towards the base. *Brachyblast* glabrous, 2.5–3 cm (–4 cm in fruit); pedicel glabrous, 7–8 mm. Spathaceous bracts not seen. *Outer tepals* 4, ± linear, 5 by 0.6–0.8 cm; inner tepals 8, linear, 4.5 by 1 (the outermost) to 0.6 (the innermost) cm. *Stamens* c. 50, filament c. 1 mm, anthers 9–10 mm, connective appendage ± triangular, c. 2.5 mm long; gynophore distinct; carpels many (more than 100). *Fruits* ellipsoid, ovoid or pear-shaped, 8–9 by c. 4 cm, pedicel, scars of perianth and stamens, and gynophore all c. 5 mm long or gynophore up to 10 mm.

Distr. Malesia: Sumatra (Riouw, Indragiri), Borneo (Sarawak, Brunei, Sabah, W. Kalimantan). Ecol. Very rare (only 8 collections), on yellow sandy soil (once recorded); low, up to 500 m; fl. May–June; fr. Aug.–Sept. (both twice recorded).


Tree 23–40 m by 40–112 cm; twigs glabrous; stipules glabrous at both surfaces. *Leaves* glabrous, usually narrowly elliptic, rarely elliptic, 7.5–21 by 3.5–6 cm; acumen 7–10 (–15) mm; base acute to sometimes nearly rounded; midrib much prominent on the undersurface; nerves in 11–16 pairs, intramarginal vein rather inconspicuous, slightly prominent on both under- and uppersurface; reticulation very fine (about half as fine as in *M. elegans*), slightly prominent on the otherwise very smooth and somewhat glossy uppersurface, inconspicuous to slightly prominent on the rather dull and mostly darker coloured undersurface, rarely more prominent on both surfaces. Petiole rather slender, 12–17 mm. *Brachyblast* glabrous, often curved at the base, 3–5 cm long; pedicel 2–5 mm; spathaceous bracts glabrous, c. 4.5 cm long. *Outer tepals* 4, c. 4.5 by 1 cm; inner tepals 8, c. 4–4.5 by 1.5 (the outer ones)–1 (the inner ones) mm. *Stamens* c. 55, filament c. 1 mm, anthers 8–13 mm, setaceous connective appendage 10–15 mm; gynophore in the observed flowers clearly present. *Fruits* ellipsoid or ovoid, c. 5–7 by 4–5 cm, pedicel, scars of perianth and stamens, and gynophore all c. 5 mm long or gynophore reduced.

Distr. Malesia: Borneo (Sarawak, Sabah, E. Kalimantan), Philippines (Palawan, one coll.). Ecol. Rare, 14 collections in total. In primary forest, on sandy loam (once recorded) or on ultra-basic in Palawan; from low up to 1800 m; fl. Feb.–Aug., fr. Feb.–Nov.

Vern. Asum, M, jilat, wunin, Dyak.

Note. This species resembles vegetatively and in fruit very much *M. elegans* but the flowers are clearly distinct by having only 12 tepals which are also broader than in *M. elegans*. Also the reticulation is more dense. Some Bornean collections, of which the flowers are not known, as well as the collection from Palawan might belong to *M. elegans*.


Tree, 30 cm diam., glabrous in all its parts. *Leaves* (narrowly) obovate, 4.5–7.5 by 1.5–3.5 cm; acumen less than 4 mm long; base cuneate. Petiole 7–10 mm; midrib much prominent below, hardly so above; nerves in 8–12 pairs prominent on both surfaces, intramarginal vein hardly distinct from the reticulation; reticulation densely netted, much prominent above, less so beneath. *Brachyblast* glabrous, 15 mm long; spathaceous bracts only one pair, directly under the tepals, no pedicel. *Tepals* c. 20 mm long, the 4 outer ones 6–7 mm broad, the 8 (!) inner ones 3–4 mm broad. *Stamens* c. 10, filament c. 1 mm, anthers c. 3 mm, the connective appendage as broad as the anthers, c. 7 mm long. Gynophore probably present, carpels c. 6. *Fruits* not known.

Distr. Malesia: Malay Peninsula (Pahang, Bk. Ierai), only known from the type.
Fig. 5. *Magnolia borneensis* Noot. *a.* Habit, ×0.9; *b.* ovary, ×5; *c.* stamen, ×1.8 (PAIJMANS 173).
3. Section Blumiana


Distr. 6 spp., in tropical and subtropical Southeast Asia from Central Himalaya to Indochina and throughout Malesia.

**KEY TO THE SPECIES**

1. Leaves usually densely appressedly pubescent beneath, 33—more than 85 by 13—32 cm, obovate, the base usually cuneate and the margins straight for the lower half to two thirds of the blade. Nerves in 24 to more than 50 pairs. Petiole from only a few millimetres to 5 cm. Peduncle with a diam. of 10—20 mm. Stamens 20—25 mm. Fruiting carpels with a stout styril spine of c. 2 cm long ......... 12. M. gigantifolia

1. Plant different. If base cuneate, the margins straight for far less than the lower half of the leaf or leaves glabrous beneath. Fruiting carpels with a smaller spine or twigs very long villous.

2. (Young twigs), peduncle and carpels densely very long (patently) villous. Leaves glabrous, at least when mature.

3. Twigs 8—12 mm diam. Leaves 25—60 by 11—21 cm; nerves nearly straight for the major part of their length. Peduncle diam. at top 10—20 mm. Stamens c. 25 mm long. Carpels more than 100

13. M. lasia

3. Twigs 5—7 mm diam. Leaves 23—40 by 6—11 cm; nerves leaving the midrib nearly perpendicular and gradually curved upwards. Peduncle diam. probably up to 10 mm. Stamens not known. Carpels probably less than 100 ......... 15. M. sarawakensis

2. Young twigs glabrous, appressedly hairy, or tomentose, peduncle glabrous, appressedly hairy, or (villus) tomentose. Carpels glabrous or hairy.

4. Young twigs 6—7 mm diam., with young leaves (shortly) tomentose, glabrescent in patches, often part of the indumentum persistent on the leaves, especially on midrib and nerves. Peduncle 10—12 mm diam. at top, villous tomentose. Carpels 18—60, densely villous to tomentose .......... 16. M. villosa

4. Young twigs glabrous or appressedly hairy, rarely short villous (if tomentose diam. 7—12 mm or less than 5 mm and carpels glabrous).

5. Carpels 20—25(—80), densely villous-pubescent. Leaves elliptic to obovate (rarely broadly elliptic), thick coriaceous with strongly recurved margins, glaucous beneath (or undersurface obscured by the indumentum), glabrous or appressedly (finely) hairy beneath, with strongly recurved margins and rounded to bluntly acute apex. Nerves 10—16 pairs, reticulation rather coarse, alveoles more than 1 mm diam., often obscured below. Twigs diam. 6—10 mm, peduncle diam. at top 6—15 mm. Only on Mt Kinabalu

14. M. persnaseolens

5. Plant different.

6. Plant glabrous. Leaves thick coriaceous with strongly recurved margins, broadly elliptic, less than two times as long as broad, 11—18 by 6—14 cm, apex rounded to blunt acute. Nerves in 14—15 pairs, forked towards the apex. Twigs 8—10 mm diam., peduncles 9—15 mm diam. at apex 14. M. persnaseolens

6. Leaves more than twice as long as broad and plant also otherwise different.

7. Plant glabrous. Leaves nearly ten times as long as broad. Petiole not longer than 2 cm

17. M. mariusjacobsia

7. Plant usually not glabrous. If glabrous then leaves far less than 10 times as long as broad

11. M. candollii

**KEY TO THE VARIETIES**

1. Plant entirely glabrous, except sometimes long caducous silky hairs between the bracts.

2. Leaves mostly obovate, 17—50 by 8—22 cm. Petiole 2.5—7 cm. Twigs diam. 5—12 mm. Peduncle


For further synonymy see under the varieties.
diam. at top 5–13 mm. Stamens 12–30 mm. Carpels 10–c. 100, with an up to 15 mm long woody styilar spine .......... b. var. obovata
2. Plant different. Twigs and peduncle usually thinner. Petiole 1–4.5 cm. Stamens 8–13–(15) mm. Spines on carpels, if present, shorter

a. var. candollii
1. Young twigs and peduncles hairy (often glabrescent in fruit!).
2. Twigs diam. 3–7 mm. Peduncle diam. at top 2–9 mm. Carpels c. 5–100 .......... a. var. candollii
4. Carpels c. 200. Stamens c. 10 mm. Petiole 2–4 cm .......... d. var. beccarii
5. Carpels 40–150. Stamens 12–30 mm. Petiole 1.5–11 cm.
6. Leaves (at least when young) hairy beneath. Carpels c. 50–100. Stamens 13–30 mm. Petiole 2.5–11 cm .... e. var. singapurensis
7. Leaves glabrous beneath. Carpels c. 40–150. Stamens 12–20 mm. Petiole 1.5–6.5 cm

c. var. angatensis

Talauna candollii Blume var. latifolia Blume, Bijdr. (1825) 9. — Lectotype: Blume s.n. (L), Noesa Kambangan.


Talauna mutabilis Blume var. acuminata Blume, Fl. Java Magnol. (1829) 36, t. 11, excl. sciagr. — Lectotype: Blume s.n. (L), Parang.


Talauna inflata P. PARMENT. Bull. Sc. Fr. Belg. 27 (1896) 208, 273, t. 8, f. 10. — Talauna undulatifolia


Talauma reticulata Merr. Philip. J. Sc. 17 (1920) 249. — Type: BS 35187 (K), Dinagat 1.


Talauma sumatranus Agostini, Atti Com. Accad. Fisiocr. Siena ser. IX, 7 (1926) sep. 28. — Type: Beccari PS 918 (FL; L), Sumatra, Padang; Sgei Balu.

M. pachysphylla Dandy, Kew Bull. (1928) 186. — Type: FB 3864 Curran (K; NY, US).

Talauma athlithartha Dandy, l.c. 189. — Type: Ridley (K), Sumatra, Berastagi.

Talauma gittingenesis var. glabra Dandy, l.c. 189. — Type: BS 39436 Ramos (BM; BO, US).

Talauma gittingenesis var. rotundata Dandy, l.c. 190. — Type: Vidal 2554 (n.v.).

Talauma gracilior Dandy, l.c. 190. — Type: Robinson & Kloss 6040 (K).

Talauma peninsularis Dandy, l.c. 192; H. Keng, Tree Fl. Malaya 2 (1973) 294. — Type: Burkhill & Hanfie 16053 (K; BO, SING).

Talauma soembenis Dandy, Kew Bull. (1928) 193. — Type: Iboet 311 (BO; L), Soemba, Boenodhero.


M. odoratissima Reinh. ex Blume, l.c., nomen.


Talauma mutabilis var. brescifolia T. & B. I.c., nomen.

Talauma mutabilis var. latifolia T. & B. I.c., nomen.

Talauma mutabilis var. leiocarpa T. & B. I.c., nomen.


Talauma elegans auct. non Mio.: Baker f. J. Bot. 62 (1924) Suppl. 2. — Fig. 6.

Mostly a shrub or small tree, rarely a medium-sized tree to 25 m high and 50 cm diam.; twigs approx. long pilose (rarely woolly or villous when young), glabrescent, 3–5(–7) mm diam. Sometimes entire plant glabrous. Stipules adnate to petiole for its whole length, but sometimes up to halfway to up to its whole length. Leaves glabrous or (finely) approx. hairy beneath, hairs straight or sometimes circular-curved at base, in some specimens both types of hairs occur, elliptic to narrowly elliptic, sometimes somewhat ovate or obovate, (6–)13–35 (–46) by (3–)13.5–15(–20) cm; acumen 10–25(–35), ‘var. acuminata’) mm, rarely apex rounded to obtuse; base cuneate to attenuate, rarely rounded but somewhat attenuate; margins nearly meeting at their base at the upperside of the midrib; lateral nerves in (7–)10–20 pairs; intramarginal vein prominent on both surfaces; reticulation prominent on both surfaces, from rather coarse to very fine. In some collections at both sides of the midrib a furrow-like line of depression caused by the leaves being folded in bud. Petiole often conspicuously thickened towards its base, with same indumentum as twigs, 10–45 mm, stipular scars up to halfway the top. Peduncle dense ly brown pubescent, rarely glabrous, with 1 to 10 nodes, 0.7–0.8 cm long, at the top 2–6(–9) mm thick, the uppermost leaf sometimes reduced. Rarely peduncle from the axil of a leaf, up to 8 cm long, with up to 10 nodes from reduced leaves; spathaceous bracts long, brown pubescent without, rarely one of them fertile and the inflorescence bearing two flowers; pedicel 0–5 mm, with same indumentum. Outer tepals 3, sometimes pubescent towards the base c. 1.5–5(–6.5) by 1–2 cm; inner tepals 6–9, in two to three whorls, shorter than to as long as outer tepals. Stamens 8–13(–15) mm long, incl. the 1.5–2 mm long triangular connective appendage; carpels 5–more than 100, glabrous, rarely hairy and soon glabrescent. Fruits ellipsoid, 4–7.5(–15) by 2.5–6 cm, the carpels terminating in a protruding, outwards curved to 5 mm long stylar beak which often is caducous. Seeds 1 or 2 from each carpel, 6–20 mm long. When the beaks of the carpels are caducous, the fruits are quite smooth when ripe (especially in the Moluccas and New Guinea).

Distri.: Sikkim, Assam (Khasi Hills), Thailand,
Fig. 6. Magnolia candollii (Blume) H. Keng var. candolli a. Habit; b. fruit; c. carpel; all $\times 0.6$; d. ovaries, $\times 0.9$; e. anther, $\times 2.7$ (a, b van Steenis 9417, c Kostermans 7337, d, e Herb. Bog. 124717).
Cambodia, Andaman Is.; in *Malesia*: throughout.

Ecol. In all kinds of forest, on different types of soil (ultrabasic, sandy, limestone, clay, in kerangas, on volcanic tuff, sometimes on waterlogged soil); 0–1700 m, in Sumatra up to 2500 m, in Borneo (Kinabalu) and in Sulawesi to 2000 m, in New Guinea up to 2700 m. *Fl. fr. Jan.–Dec.*

Uses. Rarely recorded (Lesser Sunda Islands and Sulawesi) as very hard, durable construction wood.


Field notes. Flowers sweet-scented, white to cream coloured, often red tinged or violet at base, sometimes light red or purplish. Outer tepals often greenish.


*Talauma levisissima* Dandy, Kew Bull. (1928) 192. — Type: Ridley 9047 (K; SING).

*Talauma scelerophylla* Dandy, J. Bot. 66 (1928) 47. — Type: HAV 3148 (BM; K).


Treclet, rarely a medium-sized tree 3–20 m, up to 25 cm diam. (50 cm once recorded); twigs glabrous, diam. 5–12 mm. Leaves glabrous, (broadly to narrowly) obovate or sometimes elliptic, 17–50 by 8–22 cm; apex rounded to slightly acuminate; base mostly cuneate, often attenuate; nerves in 9–25 pairs, intra-marginal vein present; reticulation rather coarse, sometimes obscure (*T. levisissima* Dandy): Petiole 2.5–7 cm, scar of stipules up to about (nearly) half to the apex. Peduncle glabrous, 3–12 cm, diam. at top 5–13 mm, with 2–18 nodes, pedicel absent or very short; between the (upper) bracts often tufts of (very) long woolly soon caducous hairs. *Tepals* 3–10 cm, the 3 outer ones sometimes recurved in mature flowers (but evidently many flowers were not yet mature when collected); the 6 inner ones erect, in big flowers quite narrow, in small flowers often broader and fleshy. *Stamens* from c. 1.2 to c. 3 cm, the appendage (narrowly) triangular to subulate, c. 3 mm long, filament c. 3 mm: carpels c. 10–100, the styles long, becoming woody spines up to 15 mm in fruit but sometimes caducous. *Fruits* 5–15 by 4–7.5 cm, ± ellipsoid.

Distr. Sikkim, Assam (Khasia), Thailand; in *Malesia*: Malay Peninsula, Borneo (Sarawak, 3rd and 4th Div.; Sabah; E. Kalimantan).

Ecol. Primary and secondary forest; 0–1700 m; *fl. fr. Jan.–Dec.*


Field notes. Peduncles blue-green, often recorded as glaucous. Tepals cream, often recorded with purple base, sometimes (yolk-)yellow with white base. Outer tepals sometimes recorded as green. Bracts purple.


Tree to 18 m by 45 cm diam.; twigs appressed pubescent to glabrous, diam. 5–12 mm. Leaves glabrous, (narrowly) elliptic, 22–45 by 8–22
cm; acumen between 0 and 20 mm; base cuneate, acuminate; midrib much prominent at both sides; nerves in 12 to 26 pairs, with an angle of 50–70° to midrib. Petiole 1.5–6.5 cm, often much thickened at base, scars of stipules from up to halfway, and then the leaf margins decurrent into two ridges, to up to the top. Peduncle (sparsely) appressedly pubescent, often glabrescent under fruit, at the top 8–15 mm diam., 2–5 cm long, nodes 2–11; bracts glabrous but appressedly puberulous at base, to 8 cm, but often much shorter. Outer tepals 3, to 7 cm; inner tepals 6, 2.5–4.5 cm long. Stamens introrse, 12–20 mm long, including the 1–3 mm long filament and the short triangular appendage; carpels pubescent, sometimes only at base of ovary, to glabrous, c. 40 to more than 150. Fruit 6–15 by 5–7 cm, base of torus under fruit 10 to 17 mm diam., the carpels provided with persistent styler spines to c. 7 mm long.

**Dist. Malesia:** Philippines (Luzon, Mindanao, Busuanga I., Camiguin I., Dalupiri I., Negros, Palawan, Panay, Capiz prov., Samar), Sulu Archipelago, Tawi I., Moluccas (Talaud; 1 coll.).

**Ecol.** Primary forest; 0–200 m, but rarely recorded.

**Uses.** Used for construction and canoe building.

**Field notes.** Flowers white.


Tree (7–15 dm) 30–50 cm by 20–50 cm; twigs and buds glabrous or appressedly pubescent, diameter of twigs under peduncle 5–9 mm. Leaves glabrous, coriaceous with recurved margins, elliptic to obovate, 16–36 by 6–17 cm; apex slightly acuminate, base cuneate in the lower part; nerves in 16–26 pairs, slightly curved upwards but nearly straight, meeting in an intramarginal vein close to the margin. Petiole 20–40–55 mm, stipular scar (nearly) to the apex. Peduncle densely appressedly pubescent, 3–11 cm long, nodes 6–13, diam. at top 9–18 mm; bracts pubescent. Tepals 4.5–9 cm long. Stamens c. 10 mm; carpels many (c. 200) sparsely pubescent to glabrous in flower, glabrescent. Fruit with small stylar spines on the mature carpels, c. 12 by 6 cm.

**Dist. Malesia:** Borneo (Sarawak, 1st & 3rd Div., Kapit Dist., 4th Div., Marudi; Sabah, Lahad Datu; E. Kalimantan, Berow, Sangkuliran I., W. Kalimantan, Amat Ambit).

**Ecol.** Forest; to 800 m.

**Vern.** Borneo: talaua, Iban.

**Field notes.** Flowers yellow or cream coloured.


**Talauma lanigera** auct. non Hook. f. & Thoms.: Ridley, J. St. Br. R. As. Soc. n. 33 (1900) 38.


Tree 6–40 m, 20–60 cm diam.; twigs appressedly long pubescent to shortly tomentose, glabrescent, diam. 7–12 mm. Leaves with basally curled hairs beneath, glabrescent in fruiting specimens often already glabrous, (narrowly) elliptic to obovate, 30–70 by 8–25 cm; apex slightly acuminate; base cuneate; nerves in 17–29 pairs prominent at both surfaces; reticulation *idem*, rather coarse. Petiole 2.5–11 cm long, stipular scar from up to 1/3 to up to 2/3 of its length. Peduncle densely appressedly long pubescent, 5–12 cm, diam. at top 10–20 mm, nodes 5–11; bracts with same indumentum. Outer tepals glabrous, 5–8 cm long, the inner ones c. 2 cm shorter. Stamens (13–)25–30 mm; carpels glabrous or nearly so, 50–150. In fruit the stylar spine present, recurved, but top often recurved, (5–)12–17 mm long. Fruits 10–15 by 6–7 cm.

**Dist. Malesia:** Sumatra, Simalur I., Banka, Malay Peninsula (incl. Singapore), Borneo (Sarawak, Kuching, Semengoh Arb., 3rd Div., Kapit Dist., Kutein; Sabah, Sandakan, Sgei Labuk, Sipiing, Ulu Mendalong; E. Kalimantan, 3 coll.).

**Ecol.** Primary rain-forest; 0–600 m.


**Talauma megalophylla** Merr. J. St. Br. R. As. Soc. n. 85 (1922) 172. — Type: RAMOS 1509 (A; K), Sandakan and vicinity.

cari PS 498 (F1; L). ad Ayer mancior, Provincia di Padang in Sumatra occid.


Tree 6-25 m high by 7-40 cm diam.; twigs often thick, more than 10 mm diam., densely appressedly, sometimes very long-pubescent, glabrescent. Leaves often crowded towards the end of the twigs, densely appressedly pubescent, glabrescent, rarely glabrous beneath, rarely villous, often more than 10 mm diam., densely appressedly pubescent, glabrescent, rarely glabrous beneath, in innovations often also above, mostly narrowly obovate, 33-85 by 13-32 cm; acumen rounded to shortly abruptly acuminate, to 2.5 cm; base cuneate, usually for the lower half to 2/3 of the blade; nerves in 24-more than 50 pairs, intramarginal vein present; reticulation prominent on both surfaces. Petiole from only a few millimetres to 5 cm, the flat stipular scar nearly up to the top. Peduncle 2.5-15 cm, diam. 10-20 mm, nodes 5-11, densely appressedly (sometimes very long-pubescent); bracts densely appressedly pubescent. Outer tepals 3, at least towards the base densely appressedly pubescent, 7-9 cm long; inner tepals 6, glabrous, 6-7 cm long. _Stamens_ c. 20-25 mm, the triangular connective appendage 2-3 mm; carpels from c. 40 to c. 200, densely appressedly pubescent, the stigma glabrous, styles long, persistent in fruit as c. 2 cm long stout stipes. _Fruit_ 13-18 by c. 8 cm.

_Distr._ _Malesia_: Sumatra (Padang, Palembang, Lampung, Banka), Borneo (Sarawak; Sabah, Sandakan, Tawau; E. Kalimantan, Blu-u, Nunukan, Be-rouw).

_Ecol._ Primary forest, on sandy (loam) soil; below 300 m.

_Vern._ Sumatra: _kayu klappoh_, _k. tangiheh_.

_Field notes._ The flowers are reported to be from pale white via light red to dark brown, the fruits pale yellowish.


Tree 9-20 m by c. 20 cm; twigs densely very long villous when young, the indumentum falling in patches, diameter 8-12 mm. _Leaves_ glabrous, elliptic to obovate, 25-60 by 11-21 cm; apex hardly acuminate; base cuneate; nerves in 16-22 pairs, prominent at both surfaces, reticulation _identem_, rather fine. Petiole glabrous or slightly long villous, 4-10 cm long, stipular scar from halfway up to the apex. Peduncle densely very long villous, 3-10 mm long, diameter at top 10-20 mm; bracts not seen. _Tepals_ glabrous, 6-10 cm long. _Stamens_ 25-30 mm long; carpels more than 100, densely long villous with very long styles. In fruit the carpels oblong, with a slender stylar spine of c. 3 cm. Probably in ripe _fruits_ (not seen, but certainly longer than 10 cm) still vestiges of the indumentum.

_Distr._ _Malesia_: Borneo (Sarawak, 5th Div., La-

was; Sabah, Tenom & Mostyn; E. Kalimantan, near Long Bawan.

_Ecol._ Primary, secondary, and riparian forest, also kerangas; 950-1100 m. _Fl_. July (twice recorded), _fr_. March, Aug.

_Vern._ Borneo: _talal unar_, Iban.


**KEY TO THE INFRASPECIFIC TAXA**

1. _Leaves_ elliptic to broadly elliptic, at least twice as long as broad. Twigs appressedly pubescent

   a. _ssp._ _persuaveolens_  
   1. _Leaves_ broadly elliptic, less than twice as long as broad ........................................ (b. _ssp._ _rigida_)
   2. _Plant_ glabrous .................................. _bl._ _var._ _rigida_
   2. _Twigs_, leaves beneath, and carpels densely pubescent........................................... _b2._ _var._ _pubescens_

   a. _ssp._ _persuaveolens_

   Shrub 1.5-2.5 m (once recorded); twigs appressedly pubescent at least towards the apex, diam. 6-10 mm, terminal buds appressedly hairy. _Leaves_ brown when dry, coriaceous, very finely (short) appressedly hairy at least when young, glaucous beneath, ± elliptic to somewhat obovate, 9-22 by 4-8 cm; apex rounded to bluntly acute, margin rather strongly recurved, base cuneate; nerves in 10-14 pairs, slightly curved upwards and meeting in a looped intramarginal vein; reticulation prominent at both sides but often more or less obscured below, rather coarse, diameter of the alveoles much more than 1 mm. Petiole when young with same indumentum as twigs, glabrescent, 1.5-3 cm long, stipular scar up to c. 3/4 of its length. Peduncle appressedly pubescent, 4.5-10 cm, with 5-8 nodes, diam. at apex 6-7 mm. _Tepals_ 22-45 mm, the outer three somewhat longer than the inner 6. _Stamens_ 8-12 mm; carpels c. 20-25, pubescent, with rather long styles. _Fruit_ glabrous, c. 5 by 3 cm, the stylar spines persistent.

   _Distr._ _Malesia_: Borneo (Sabah, Kinabalu, 5 coll.).

   _Ecol._ Mossy forest and open places; 1200-1650 m. _Fl._ Feb.-Aug.

   _Field notes._ Flowers cream.

   _b._ _ssp._ _rigida_

   _Noot._ Blumea 32 (1987) 379. — _Type_: RSNI 845 (L; SING).

   _bl._ _var._ _rigida_

   Shrub to big tree, 3 to 25 m, diam. to 60 cm but
usually much less. Twigs glabrous, thick, blackish, diam. 8–10 mm. Leaves glabrous, thick coriaceous with strongly recurved margins, the undersurface glaucescent, broadly elliptic, always less than twice as long as broad, 11–18 by 6–14 cm; apex rounded to blunt cuneate; base attenuate; nerves in 15–16 pairs, straight, forked towards the end and meeting in a less conspicuous intramarginal vein. Petiole 23–35 mm, stipular scar from up to half to up to 3/4. Peduncle glabrous, thick, diam. 9–15 mm, with 2–12 nodes; bracts glabrous, c. 6 cm long. Tepals 5–6 cm when flower fully open, outer 3, inner 6. Stamens 18–20 mm, about as long as the ovary; carpels c. 20–80, with long styles. Fruit 6–9 by c. 5 cm, reported to become c. 12.5 cm long. Spines probably persistent, but in the herbarium often caducous.

Dist. Malesia: Borneo (Sabah, Kinabalu, 12 coll.), recorded as a common tree.

Ecol. Frequent in gullies as a big tree without buttresses, as shrub probably on ridges; 2700–3400 m; fl. fr. Jan., July, Nov.

Field notes. Petals recorded to be white or creamy, slightly purplish at base.


As var. rigida, but twigs, leaves, and carpels densely appressed pubescent. Nerves in c. 10 pairs. Flowers not known.

Dist. Malesia: Borneo (Sabah, Kinabalu), only the type.


Twigs densely long villous, glabrescent in patches, diam. 5–7 mm. Leaves in innovations with same indumentum, soon glabrous, glaucescent beneath, narrowly elliptic to obovate, 23–40 by 6–11 cm; apex acuminate; base attenuate-cuneate; nerves in 12–18 pairs, leaving the midrib nearly perpendicular and then gradually curved upwards; reticulation rather coarse, prominent at both surfaces. Petiole 15–60 mm with a stipular scar from about half to 2/3 of its length. Peduncle long villous, diam. 12 mm at the top. Flowers probably as in M. lasia, but length of stamens not known; carpels densely long villous, not many (acc. to DANDY). Fruits not known.

Dist. Malesia: Borneo (Sarawak, Batang Lupar; Sabah, SE. Kinabalu, Bt Kulung; W. Kalmantian, Singkadjian; E. Kalmantian, Lilit Buan, Taputse).

Ecol. Dipterocarp forest on ultramafic soil; 750 m (once recorded, Bk Kulung).


Tree 9–18 m by 30 cm (once recorded); twigs (shortly) tomentose, glabrescent in patches, diam. 6–7 mm. Leaves tomentose when young at both surfaces, glabrescent but often the tomentum persistent on midrib and nerves, elliptic, 19–40(–50) by 7.5–20 cm; apex (abruptly) acuminate; base cuneate-attenuate; nerves in 13–20(–25) pairs; reticulation rather fine, prominent on both surfaces. Petiole with same indumentum as twigs, 1.5–4.5(–6) cm, stipular scar from up to 1/4 to up to 3/4 of its length. Peduncule densely villous (villous) tomentose, 2.5–76 cm, diam. at top 10–12 mm; bracts densely villous tomentose. Tepals villous without or only at the base, 4–5 cm long. Stamens probably c. 15 mm; carpels 18–60, densely villous-tomentose, when ripe with a rather stout stylar spine of up to 1 cm. Fruit 10 by 6 cm (once seen).

Dist. Malesia: Sumatra (West, Taram, E. of Pajakumbuh), Malay Peninsula (Penang; Perak; Genting highlands; Malacca; Lingga Arch.), Borneo (Sabah, Lamag dist.).

Ecol. Primary forest (once recorded); 450–1000 m.


Treelcet. c. 6 m high by c. 6 cm, entirely glabrous. Twigs with many obvious scars of fallen leaves. Leaves narrowly elliptic to obovate, 27–55 by 3–7 cm, the blade long dentcurrent into the short, thickened, 1–2 cm long petiole which bears a stipular scar for its entire length; apex not acuminate, nearly rounded; nerves in c. 20–30 pairs, much prominent below and meeting in a prominent intramarginal vein; reticulation rather coarse, prominent beneath. Peduncle 1.5–2.5 cm, thickened towards the apex and there about 8 mm broad, with 2–3 scars; pedicel short to absent. Outer tepals 3, c. 5 by 3 cm, thin; inner tepals in two whorls of three each (or the inner whorl with 4–5 tepals), fleshy, the outer whorl c. 4.5, the inner 2.5–3 cm long. Stamens up to 3 (at base 4)
mm broad, 10–12 mm long including the broadly triangular connective appendage; carpels c. 25 with long styles protruding above the stamens. Only young fruits known yet, like those of *M. candollii var. candollii*.

**2. MANGLIETIA**


*Paramanglietia* Hu & Cheng, Acta Phytotax. Sin. 1 (1951) 255. — Type: *P. aromatic* (Dandy) Hu & Cheng. — Fig. 7, 8.

Trees. Stipules adnate to or free from petiole. Flowers terminal, solitary, bisexual. Tepals 9–13, 3-merous, subequal. Anthers introrse, connective produced into a short or long appendage. Gynoecium sessile. Carpels many, free, or often connate when young; ovules 4 or more in each carpel. Fruiting carpels free, crowded, dehiscent along the dorsal and sometimes also the ventral suture.

**Distr.** About 25 species in tropical and subtropical Asia from the E. Himalayas eastwards to S. China and *Malesia* (5 spp., not in the Moluccas and New Guinea).

**Key to the Species**

1. Stipules only adnate to the very base of the petiole. Stipular scar hardly or not present. Innovations, stipules, young petioles and underside of leaves never woolly pubescent

2. Peduncles appressedly hairy ................................................................. 1b. *M. glauca* var. sumatrana

2. Peduncles glabrous.


4. Innovations, peduncles, stipules and underside of leaves rufous woolly pubescent .......................... 2. *M. lanuginosa*

5. Twigs and stipules glabrous or nearly so. Hairs if present minute and appressed.

5. Fruits cylindrical, 2–3 times as long as wide; carpels mostly opening along the dorsal suture first. Ovary conical or cylindrical .......................... 5. *M. dolichogyyns*

5. Fruits ellipsoid or ovoid, only slightly longer than wide .................. 1. *M. glauca* (var. glauca)


*blumei* Prantl in E. & P. Nat. Pfl. Fam. 3, 2 (1888) 16. — Type: *Blume* Salak (n.v.)


Tree up to 35 m by 122 cm diam. Twigs warted, with many ring-formed scars of the fallen stipules, glabrous or with some hairs at the apex, in var. sumatrana appressedly hairy in innovations. Stipules glabrous or with some hairs on the apex, adnate to the petiole, c. 15–60(–90) mm. Leaves glabrous above, minutely appressedly hairy beneath, sometimes the hairs microscopically small and the leaves seemingly glabrous, glaucous, (long-)elliptic to slightly obovate, 10–35 by 5–12 cm; acumen 3–15 mm; base acute to slightly acuminate; midrib much prominent; nerves in (9–)11–16(–18) pairs, decurrent along the midrib, prominent on both sides, straight, anastomosing at some distance from the margin and merging into the venation, sometimes an intramarginal vein distinct; reticulation fine, prominent on both surfaces. Petiole glabrous, 1.5–3(–4.5) cm, stipular scar c. 3–10(–15) mm, less than one third of its length, rarely slightly longer, sometimes even up to above halfway its length. Peduncle glabrous, or appressedly hairy in var. sumatrana, without scars or with one scar 15–40 mm, pedicel glabrous, or appressedly hairy in var. sumatrana, 2–8 mm; spathaceous bracts at least one towards the base of pedicel and one at base of peduncle or higher, sometimes a third at the middle of peduncle or lower. Outer tepals 3, c. 5–6.2 by 2 cm, inner tepals 6, smaller than the outer tepals. Stamens many, filament c. 3 mm, anthers c. 6 mm, connective appendage very acute, c. 4 mm; gynoecium ovoid to orbicular, c. 15 by 7 mm. Carpels 20–c. 50, nearly entirely connate when young, c. 3 mm long along the dorsal suture, dorsal face polygonous; style free, 1.5–2 mm long. Fruits ellipsoidal or ovoid, 3.5–8(–9.5) by 2.5–5.5(–6.5) cm. Seeds flat-orbicular to ellipsoidal, often irregularly shaped, 5–8 by 4–5 mm.

a. var. glauca

Peduncle and pedicel glabrous. Fruits at most 8 by 5.5 cm. Dorsal face of carpels from 1–1.5 cm in the upper to at most 2.5 cm in the lower carpels. Twigs in innovations glabrous.

Distr. Malesia: Sumatra (Aceh, G. Ketambe;

Fig. 7. Fruits of a. Manglietia glauca Blume and b. M. dolichogyna Dandy ex Noot., both ×1 (a Koorders 4449, b Clemens 26279).
Sumaterra Utara, E. Coast and Tapanuli; W. coast; Lampung, G. Tanganjumas, Java (common in the mountains of W. Java, less so in Central and E. Java), Lesser Sunda Is. (Bali, Sumba, Flores), Sulawesi (Central, near Malili; North, Mt. Nokilalaki). Ecol. In forest; 500–2400 m; fl. fr. Jan.–Dec. Uses. Good timber, used for building houses. Vern. Sumatra: antuang, bungo, madang bustak, m. kaladi, m. tjampago, tjampago; Java: baros, tempoko baros, tjepko kantil; Bali: tjimpaka; Sulawesi: manglid.

Field notes. Flowers cream, rarely white or yellowish green. Fruit (reddish) green to red brown.

b. var. sumatrana DANDY, Kew Bull. (1928) 188; NOTT. Blumea 31 (1985) 93. — M. sumatrana Miq. — M. pilosa P. ARMENT.

Peduncle and pedicle appressedly hairy. Fruits c. 9.5 by 6.5 cm. Dorsal face of carpels from 2 cm in upper to 3.5 cm in lower carpels. Twigs in innovations appressedly hairy. Stipules often adnate to the very base of the petiole only. 


Vern. Sikiibus.

Field notes. Flowers yellow or white, fruit black.


Tree up to 40 m high and 1 m diam. Innovations and peduncles, stipules, young petioles and undersides of leaves rufous woolly pubescent. Leaves (narrowly) elliptic, sometimes slightly obovate, 15–26 by 7–11 cm; nerves in 14–20 pairs. Petiole 2.5–4 cm, with stipular scar only towards the base. Further as M. glauca.


Vern. Aduwang, antuang, madang sanggar.

Field notes. Flowers cream or green, sweet scented; fruit grey-green becoming brown.


Tree to at least 30 m by 1 m. Stipules appressedly hairy to nearly glabrous, only adnate to the very base of the petiole. Leaves ovate, covered by a dense indument of very small glinting reddish brown hairs beneath (often only to be seen with magnification of more than x 50), 10–20 by 4–8 cm with faintly acuminate apex, recurved, bony margin and acute to nearly rounded base; midrib much prominent beneath, grooved; nerves prominent on both sides, in 10–15 pairs, anastomosing and meeting in an intramarginal vein which is hardly distinct from the finely netted reticulation on both surfaces. Petiole 2–2.5 cm. Peduncle glabrous. Flowers as in M. glauca but smaller, the tepals as far as known not longer than c. 2.5 cm. Fruits as the smaller fruits in M. glauca c. 4–5.5 by 3.5–5 cm, number of carpels c. 20. Seeds c. 4 from each carpel, flat ovoid, c. 7 by 4 mm.


Field notes. Flowers white or yellow.


Tree. Stipules glabrous, c. 7 cm long, adnate to the very base of the petiole only. Leaves glabrous, the undersurface in young leaves with an occasional very small hair, elliptic to obovate, 12–22 by 6–9 cm; base cuneate, apex acute to rounded, usually not or only very shortly acuminate; midrib sulcate above, very prominent and grooved below; nerves in 14–c. 20 pairs, meeting in an intramarginal vein which is slightly more prominent than the densely netted reticulation. Petiole 23–30 mm, stipular scar hardly visible. Outer tepals 3, c. 3 by 1–1.5 cm; inner tepals 6, narrower. Stamens c. 1 cm long; ovary ellipsoid, c. 15 by 10 mm. Fruits ellipsoid to ovoid, c. 6 by 4 cm, the carpels opening along the dorsal suture only or both along dorsal and ventral suture. Peduncle slender, c. 3 cm long, pedicel slender, c. 2 cm long. Seeds c. 4 in each carpel, 5–8 by 3–4 mm.


Tree up to 21 m and 60 cm diam. Stipular scar on petiole c. halfway. Flowers: peduncle c. 2–3 cm, pedicel 4–7 mm, spathaceous bract glabrous, outer tepals 3, c. 3.5 by 14 mm, inner tepals 6, smaller.
Fig. 8. *Manglietia sabahensis* Dandy ex Noot. a. Habit, ×0.6; b. fruit, ×0.6; c. ovary, ×0.9; d. anther, ×3.8 (a, b Clemens 40979, c, d Clemens 40769).
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\textit{Magnoliaceae} many, c. 10 mm, incl. the c. 3 mm long acute connective appendage. \textit{Ovary} conical or cylindrical, dorsal face of carpels 2–3 mm along suture, style c. 2 mm long. Ripe \textit{fruits} cylindrical 4–7.5 cm by 2–c. 2.5 cm, 2 to 3 times as long as wide, carpels c. 60, c. 1 cm along the dorsal suture, opening along the dorsal suture first and sometimes later also along the ventral suture. \textit{Seeds} flat ellipsoidal, c. 6 by 4 mm. Otherwise as \textit{M. glauca}.

\textbf{Distr.} \textit{Malesia}: Malay Peninsula (Perak, Tai- ping, road to Fraser’s Hill, near Gap Valley), Borneo (Sabah, Tenom, Tambunan, Kinabalu).

Ecol. Primary forest; 450–1500 m; \textit{fl.} March–May, \textit{fr.} June–Feb.

\textbf{Field notes.} Outer tepals dark purple on green, inner tepals lemon with purple tinge; flowers pale yellow.

\textbf{Excluded species}


3. \textbf{PACHYLARNAX}


Trees. Stipules free from the petiole. Flowers terminal, solitary, bisexual. \textit{Tepals} 9–15, 3–5-merous, subequal. \textit{Anthers} introrse; connective produced into a short appendage. \textit{Gynoecium} sessile; carpels few (2–8), concrescent; ovules about 4–8 in each carpel. \textit{Fruit} a thick-walled woody loculicidal capsule, the carpels dehiscent along the dorsal suture and sometimes separating towards the apex.

\textbf{Distr.} There are 2 spp., of which one in Assam and one in Indochina and in \textit{Malesia} (Sumatra and the Malay Peninsula).

1. \textit{Pachylarnax praecalva} \textit{DANDY, Kew Bull.} (1927) 260, \textit{excl. plantae ex Annam}; H. \textit{KENG, Tree Fl. Malaya} 2 (1973) 289, t. 4; \textit{Noot. Blumea} 31 (1985) 97, f. 4, 5. — \textit{Type: HANIFF 4067} (K; SING), Penang. — \textit{Fig. 9}.

Tree 10–60 m by 30–100 cm, glabrous in all its parts. Stipules free from the petiole. \textit{Leaves} glossy above, less so beneath, (narrowly) elliptic to obovate, 7–16 by 3–6.5 cm; apex obtuse or rounded; base cuneate or attenuate; margin recurved; midrib prominent beneath, slightly so above; nerves in 12–15 pairs, prominent on both surfaces, curved upwards and meeting in a looped intramarginal vein which is rather indistinct from the coarsely netted venation. Petiole without stipular scar, slender, 1.5–3 cm long. \textit{Flowers} terminal on an increscence peduncle of 0.5–20 mm (sometimes the peduncle becoming much longer); 1–3 (rarely many) spathaceous bracts under each flower, pedicel very short. \textit{Tepals} 9(–10), ± similar, the outermost oblanceolate to oblong, 2.5–3.5 cm long. \textit{Stamens} c. 17–20 mm long with an acute connective appendage; gynoecium elongate-ovoid; carpels 2–4; ovules 4–8. \textit{Fruit} 3.5–6 cm long, ± orbicular before opening, loculicidal, splitting into 2–4 valves, the carpels more or less separating from each other later, in the centre a columella with the attached fruits persistent. \textit{Seeds} black with enveloping pink aril.

\textbf{Distr.} Annam (Bana near Tourane); \textit{Malesia}: Sumatra (W. coast), Malay Peninsula (Kedah, Penang, Selangor).

Ecol. In primary forest; 360–1800 m; \textit{fl. fr.} probably the whole year round.

2. \textbf{Tribus Micheliae}


Growth monopodial. Flower buds arising on brachyblasts in the axils of the leaves. Genera: \textit{Michelia} (incl. \textit{Paramichelia} and \textit{Tsoongiodendron}) and \textit{Elmerrillia}.

\textit{Michelia} many.
Fig. 9. Pachylarnax praecalva DANDY. a. Habit, ×0.7; b. fruit, ×0.7; c. ovary, ×2.2; d. anther, ×3 (Curtis 3012).
**KEY TO THE GENERA**

1. Gynoecium sessile ......................................................... 4. *Elmerrillia*
1. Gynoecium distinctly stipitate ........................................ 5. *Michelia*

### 4. ELMERRILLIA


*Elmerrillia* sect. *Pseudoaromadendron* Dandy in Praglowski, World Pollen & Spore Flora 3 (1974) 5. — Type: *E. ovalis* (Miq.) Dandy. — Fig. 10, 11.

Trees. Stipules free from petiole. Flowers terminal on axillary brachyblasts, solitary or sometimes 2–3-nate, bisexual, growth monopodial. Sepals 4 (or 5); petals 5–c. 10, 3–5-merous, subequal. Anthers introrse; connective produced into a short appendage. Gynoecium sessile; carpels many, with the base sunken in the torus, free or concrescent; ovules 2–6 in each carpel. Fruiting carpels basally sunken in the torus, free, crowded, and dehiscent along the dorsal suture, finally 2-valved, or concrescent to form a fleshy syncarp. In the latter case the carpels hexagonal, the apical parts falling away, often in irregular masses, thus shedding the seeds, or carpels tearing apart towards the outside and dehiscing longitudinally.

**Distr.** There are 4 spp., all in *Malesia*.

### KEY TO THE SPECIES

*(based on flower and fruit characters)*

1. Tepals 12. Carpels free (not seen in *E. platyphylla*).
2. Twigs and stipules hairy ................................................. 4. *E. tsiamapacca*
2. Twigs and stipules glabrous ............................................ 2. *E. platyphylla*
1. Tepals (12–)17. Carpels free or concrescent. For New Guinea plants with 12 tepals and fruiting carpels free, see under *E. tsiamapacca*.
3. Undersurface of leaves glaucous (sometimes a dense indumentum of appressed hairs obscuring the glaucousness), hairy (in New Guinea sometimes glabrous: var. *glaberrima*). Fruiting carpels free, dorsally dehiscent. .................................................................................. 4. *E. tsiamapacca*
3. Undersurface of leaves not glaucous, glabrous or hairy. Fruiting carpels concrescent.
4. Twigs glabrous or yellowish villous, soon glabrescent, rarely pubescent. Nerves in (10–)14–21 pairs
   1. *E. ovalis*
4. Twigs densely fulvously pubescent or tomentose, later glabrescent. Nerves in 20–24 pairs
   3. *E. pubescens*

### KEY TO THE SPECIES

*(based on fruit characters)*

1. Fruit a syncarp, ripe carpels shedding their apical parts.
2. Young twigs and stipules glabrous or yellowish villous, soon glabrescent, rarely pubescent. Nerves in (10–)14–21 pairs ........................................ 1. *E. ovalis*
2. Twigs densely fulvously pubescent or tomentose, later glabrescent. Nerves in 20–24 pairs 3. *E. pubescens*
1. Fruit apocarpous, ripe carpels longitudinally dehiscent.
3. Twigs and leaves glabrous. Brachyblast glabrous
   2. *E. platyphylla*
3. Twigs and leaves glabrous or hairy. Brachyblast hairy (except rarely in New Guinea: *E. tsiamapacca* var. *glaberrima*)
   4. *E. tsiamapacca*


Tree to 45 m high and 100–150 cm diam. Twigs glabrous or yellowish villous, soon glabrescent, rarely pubescent. Stipules glabrous to yellowish villous. Leaves glabrous or underside minutely sparsely appressed hairy, rarely sparsely patentely pubescent, elliptic, 7–36 by 4–16 cm; acumen less than 10 mm; base cuneate (to rounded), usually attenuate; nerves in (10–)14–21 pairs, intramarginal vein often rather inconspicuous in the prominent fine reticulation. Petiole glabrous or with some indumentum as twigs, (1–)2.4–4.5(-7) cm. Brachyblast glabrous or yellowish villous; spathaceous bracts (sparingly pubescent) to glabrous. Flowers (creamy) white; tepals c. 16 in 2 or 3 whors, more or less coriaceous, the longest 25–35 mm. Stamens 8–14 long mm; carpels puberulous, 4(–6)-ovuled, congested. Fruit ellipsoidal, the ripe carpels disintegrating, losing their apical portions and thus shedding the 1–4 seeds.

Disr. Malesia: Sulawesi (incl. Muna), Moluccas (Morotai, Ambon).

Ec. In forests at low and medium altitudes, up to 1000 m; fl. fr. Jan.–Dec.

Uses. The timber is very durable and amongst others used for house-building. The trees are cultivated for timber (see Koorders, 1898).


Tree. Twigs glabrous. Stipules glabrous. Leaves elliptic, glabrous, 23–30 by 9–13 cm; acumen shorter than 10 mm; base cuneate, shortly attenuate; nerves in 18–23 pairs meeting in an intramarginal vein; reticulation rather fine. Petiole 2–3 cm. Brachyblast glabrous, 4–5 cm long; spathaceous bracts glabrous. Flowers white; tepals c. 12, the outer ones c. 25–35 mm long. Stamens c. 12 mm; ovary glabrous. Fruits unknown as yet.

Disr. Malesia: Philippines (Leyte, Agusan; Mindanao, Zamboanga).

Ec. Secondary forest at low altitudes.


Trec c. 15–40 m high and up to 80 cm diam. Twigs densely pubescent or tomentose, glabrescent. Stipules densely pubescent long tomentose or pubescent. Leaves pubescent beneath, elliptic to ovate, 15–30 by 8–14 cm; acumen less than 1 cm; base nearly rounded, slightly acuminate; nerves in 20–24 pairs, meeting in a looped intramarginal vein; reticulation fine. Petiole with some indumentum as twigs, 20–25 mm. Brachyblast densely pubescent tomentose or pubescent, 3–5 cm; spathaceous bracts densely pubescent. Flowers white; tepals c. 15, glabrous, the outer ones 27–35 mm, the inner ones gradually shorter and narrower. Stamens c. 10 mm; carpels many, 3–4 ovuled, pubescent. Fruit 3–6 by 2 cm; carpels c. 8 mm long, concrest, tearing apart towards the outside when mature, longitudinally dehiscing, 1–4-seeded.

Disr. Malesia: Philippines (Mindanao, Lanao lake, Mt Katanglad, Mt Apo).


Vern. Hangilon, Bukidnon.


Michelia forbesii Baker f. J. Bot. 61 (1923) Suppl. 2. — Type: Forbes 442a (K; P), Sogeri.


E. papuana var. adpressa Dandy, Kew Bull. (1928) 185. — Type: Ledermann 13089 (K; L), Sepik region.

E. papuana var. glaberrima Dandy, loc. — Type: Ledermann 9505 (K), Sepik.
Fig. 10. Elmerillia tsampaca (Linné) Dandy var. tsampaca. a. Habit, × 0.6; b–c. stamens, × 4; d. ovary, × 2; e. young fruit, × 2; f. ditto, longitudinal section, × 4.
Tree to 60 m high and 150(−200) cm diam. Leaves beneath very densely, often minutely appressed or patently hairy, 10−30 by 3−15 cm. Petiole 12−35 mm.


a1. var. tsiampaca. — All synonyms except E. papuana var. glaberrima Dandy. — Fig. 10.

Distr. As the subspecies.

Ecol. On fertile soil in forest; to 1400 m; fl. fr. Jan.–Dec.

Uses. The most valuable and most demanded timber in N. Sulawesi. Already becoming scarce in 1898 (Koorders). Very durable.


a2. var. glaberrima (Dandy) Noot. Blumea 31 (1985) 107, f. 6c. — E. papuana var. glaberrima Dandy.


Ecol. Primary forest; up to 1200 m.

Vern. Mamer, mamier, Kebar lang.

b. ssp. mollis (Dandy) Noot. Blumea 31 (1985) 108, f. 6d. 8. — E. mollis Dandy. — Fig. 11.

Tree to 40 m high and 80 cm diam. Leaves beneath villous, pubescent, or puberulous. Petiole 7−25 cm. Carpels with 2 ovules.

Distr. Malesia: Sumatra (Mentawei I., Siberut), Borneo.


Vern. Sumatra: minjaran; M; Borneo: arau, miharo, Dyak.

5. MICHELIA


Paramichelia H.H. Hu, Sunyatsenia 4 (1940) 142. — Type: P. baillonii (Pierre) Hu. — Fig. 12, 13.

For further synonymy see Noot. Blumea 31 (1985) 108.

Trees or shrubs. Stipules adnate to or free from petiole. Flowers bisexual. Tepals 6–21, 3–6-merous, subequal or rarely the outer whorl different. Anthers latrorse or sublatrorse (to introrse). Gynoeicum stipitate, carpels many to few (rarely 1), free or connate; ovules 2 to many; fruiting carpels free or concrecent.

Distr. About 30 spp., in Southeast Asia from India and Sri Lanka eastwards to S. Japan and Taiwan and south eastwards into Indonesia (not in Sulawesi and New Guinea). In Malesia 6 spp., 2 other spp. commonly cultivated.

KEY TO THE SPECIES

1. Petiole 3–5 mm long, stipular scar present for nearly its whole length. Leaves glabrous, 4.5–6.5 by 2–3 cm. Tepals 6

8. M. figo
Fig. 12. *Michelia scortechinii* (King) Dandy. a. Habit, × 0.7; b. young fruit, × 2; c. anther, × 4; d–e. ovary, × 4 (a, c–e SF Holtum 31244; b Grashoff 335).
1. Petiole longer than 5 mm. The other characters different or the tepals more than 6.
3. Young twigs hairy, at least directly under the terminal bud. Carpels 8 or more.
4. Stipules adnate to the petiole for one third or more than one third of its length.
5. Leaves 8–12 by 2.5–3.5 cm. Petiole 6–16 mm ................................. 1. M. scortechinii
7. Tepals 15, from light yellow to orange, 20–45 mm long. Carpels c. 30, fertile. Leaves 10–30 cm
8. 3. M. champaca
3. M. koordersiana
4. Stipules free from petiole or adnate to its base only (in M. salicifolia sometimes up to one third).
5. Leaves 15–35 by 5–11 cm. Petiole 15–50 mm. Tepals c. 12, white, 30–55 mm. Carpels sterile, c. 10
6. Tepals white to yellow, 10–40 mm. Carpels fertile.
7. Tree 10–20 mm. Outer tepals 3, membranous, inner tepals 6, coriaceous. Twigs and stipules puberulous to nearly glabrous. Leaves glabrous beneath, 6–16 by 3–6 cm. Carpels c. 10
8. 5. M. salicifolia
9. Tree 3–7 mm. All the tepals the same, 9–17. Twigs and stipules pubescent or puberulous.
10. Leaves glabrous or hairy beneath, 4–13 by 1.5–4 cm. Carpels 8–16 or c. 30.
11. Tepals 20–40 mm. Leaves 9–13 by 2.3–4 cm, often glaucous beneath. Carpels c. 30
12. 5. M. philippinensis

2. Tree to 37 m high and c. 50 cm diam. Twigs zigzag, ferrugineously pubescent to tomentose when young. Stipules adnate to the petiole for at least half its length, to 30 mm long. Leaves (densely) ferrugineously pubescent or puberulous beneath, distichously arranged, elliptic, 8–12 by 2.5–3.5 cm; apex shortly acuminate; base cuneate; nerves in 12–18 pairs, with the very fine reticulation prominent on both sides. Petiole 6–16 mm, Brachyblast 6–8 mm; spathaceous bracts densely ferrugineously pubescent. Flowers white; tepals c. 12, more or less the same, 12–18 mm long. Stamens c. 8 mm, incl. the c. 1 mm long connective appendage; carpels c. 20, densely ferrugineously pubescent. Fruiting carpels concrecent.

Distr. Malesia: Sumatra (W. coast, Bengkulu, Palembang), Malay Peninsula (Perak, Pahang, Cameron Highlands).
Ecol. Primary forest; 650–1300 m; fl. fr. probably Jan.–Dec.

2. Michelia koordersiana NOOT. Blumea 31 (1985) 111, f. 10. — Fig. 13
2. Tree to 32 m high and 62 cm diam. Twigs finely appressedly puberulous when young, or only so directly under the terminal bud, soon glabrescent, often zigzag. Stipules with same indument to nearly glabrous, not adnate to petiole, 10–15 mm. Leaves glabrous, more or less elliptic, distichously arranged, 6–16 by 3–6 cm; apex shortly acuminate, acumen (0–3)–8 mm; base cuneate; nerves in 7–13 pairs, with the fine reticulation prominent on both sides. Petiole 10–20 mm. Brachyblast appressedly pubescent, 10–17 mm. Flowers (orange) yellow; outer tepals 3, membranous, 12–22 mm; inner tepals 6, coriaceous. Stamens incl. the 0.5 mm long appendage 5–7 mm; carpels c. 10, with the c. 5 mm long gynophore minutely tomentellous or puberulous. Fruiting carpels 2–10.

Distr. Malesia: Sumatra (W. coast, Padang; E. coast, Palembang), Malay Peninsula (Selangor).
Ecol. Primary forest; 0–1000 m; fl. fr. probably Jan.–Dec.


M. staweolens PERS. SYL. 2 (1806) 94, p.p. excl. syn. RHIEMDE ET RUMPHE — M. blumei STEUD.
Fig. 13. *Michelia koordersiana* Noot. *a.* Habit, ×0.6; *b.* fruit, ×0.6; *c.* ovary, ×4; *d.* anther, ×6 (Van der Zwaan for Thorenaar T345).
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1988]


*M. monata auct. non BLUME; BAKER f. J. BoI. 62 (1924) Suppl. 2.

Huge tree forest up to 50 m high and 183 cm diam. Twigs (appressedly) pubescent, glabrescent. Stipules pubescent, adnate to petiole at least for one third of its length. Leaves spirally arranged, (long) elliptic or ovate, pubescent below especially on midrib and nerves, often glabrescent, 10–30 by 4–10 cm; acumen 7–13 (–25) mm; base cuneate to more often rounded; nerves in 14–23 pairs, intramarginal vein often hardly more prominent than fine reticulation. Petiole 14–36 (–40) mm. *Brachyblast* densely pubescent, (5–)10–18 (–25) mm long; spathaceous bracts pubescent. Flowers light yellow becoming dark orange; tepals 15, 20–45 mm long. *Stamens* 6–8 mm, incl. the upper to 1 mm connective appendage; carpels c. 30, the c. 3 mm long gynophore densely pubescent.

Disir. From India to SW. China and Indochina; in *Malesia*: Sumatra, Malay Peninsula, Java, Lesser Sunda Islands.

**KEY TO THE VARIETIES**

1. Leaves ovate with cuneate-attenuate base; the acumen often quite long. Petiole with a stipular scar up to shortly below its middle to up to its apex. Tree to c. 30 m high and 50 cm diam.

1a. var. *champaca*

1. Leaves more or less elliptic with cuneate to rounded base, the acumen often rather short, oblique. Petiole with a stipular scar from 0.3 up to 0.7 of its length. Tree to 50 m high and 180 cm diam.

1b. var. *pubinervia*

**a. var. champaca.** — All synonyms except those under *var. pubinervia*.

Disir. Commonly cultivated throughout the tropics. Probably originally from India, where it is cultivated on the temple ground of Jains and Hindus.


*M. monata auct. non BLUME; BAKER.*

Disir. *Malesia*: Sumatra (Acheh; Bengkulu, Lake Rana), Malay Peninsula (Kedah, Langkawi Is.; Br. Kaju Hitam; Kelantan, Cameron Highlands), Java (common in the mountains), Lesser Sunda Is. (Sumbawa).

Ecol. Evergreen primary forest on fertile soil; 250–1500 m, in Java mostly between 1000 and 1200 m. *Fl. fr. Jan.–Dec.*

Uses. The wood is highly esteemed for building and furniture. The properties are at least the same as of *Tectona grandis*. Because of its nice structure the value for furniture is higher than that of the wood of *M. montana*. In the beginning of this century its extinction was already feared by Koorders because of the use made of it. The trees can easily be cultivated and reach a height of c. 27 m and a diameter of c. 55 cm in 27 years (K. & V., 1896).

*Vern.* Sumatra: kemait, M; Java: baros, manglis, S; kadjeng sekaj, J; kadun kemphug, Md; langjung, J; Sumbawa: tengkel.


*M. ecuatrisata* Mq. Fl. Ind. Bat. Suppl. (1860)
5. **Michelia salicifolia** Agostini, Atti Com. Accad. Fisico-Crit. Siena IX, 7 (1926) sep. 23; Noot. Blumea 31 (1985) 118. — *M. sumatrae* Dandy, Kew Bull. (1928) 188. — Type: Beccari PS 118 (FI; BM = holotype *M. sumatrae*, K, L). Tree 25 m high and 50 cm diam. Twigs appressedly ferrugineously pubescent. Stipules with same indument, adnate to base of petiole only. *Leaves* spirally arranged, appressedly finely ferrugineously pubescent, glaucous beneath (often seemingly glabrous because the hairs are very small), narrowly elliptic (to obovate), 9–13 by 2.3–4 cm; acumen 8–13 mm; base cuneate or attenuate; nerves in 9–16 pairs, intramarginal vein rather inconspicuous in the much prominent reticulation on both surfaces. Petiole 10–15 mm. *Brachyblast* appressedly ferrugineously pubescent, 5–7 mm; spathaceous bracts rufous tomentose. *Tepals* c. 12, 20–40 mm long. *Stamens* incl. the 2 mm long connective appendage c. 15 mm long; carpels c. 30, with the gynophore appressedly ferrugineously tomentellous. Fruiting carpels free.

**Distr. Malesia**: Sumatra (W. Coast, G. Singalan; Aceh, G. Leuser).


Tree to 18 m high and 80 cm diam. Twigs often zigzag, young parts appressedly pubescent, rarely patently pubescent and nearly tomentose. Stipules with same indument, free from petiole. *Leaves* often distichously arranged (narrowly) elliptic to slightly obovate, glabrous to finely appressedly puberulous beneath (or patently pubescent when the twigs are so), 4–12 by 1.5–3.5 cm; acumen (0–)15 mm, with rounded tip; base cuneate; nerves in 8–14 pairs. Petiole 5–20 mm. *Brachyblast* 3–7 mm, with same indument as twigs; spathaceous bracts *idem*. *Flowers* creamy yellow to white; outer *tepals* 3, inner *tepals* 6–14, all 10–12 mm (once 15 mm). *Stamens* 3–5 mm; carpels 8–c. 16, with the 3–4 mm long gynophore appressedly pubescent. Fruiting carpels free.

**Distr. Malesia**: Philippines (Luzon: Benguet; Zambales; Ilocos Norte; Bataan; Rizal; Laguna; Tayabas; Batangas; Abra; Negros: Dumagueta; Mindanao: Misamis; Lanao; Todaya; Bukidnon).

**Ecol.** In forests at medium altitude, on some mountains up to 2100 m. *Fl. fr.* Jan.–Feb.


*M. longifolia var. racemosa* Blume, Fl. Java Magnol. (1829) 13, t. 3. — Type: Blume s.n. (L).

Tree to c. 30 m. Twigs appressedly greyish pubescent, glabrescent. Stipules with same indumentum, adnate to the base of the petiole. Leaves sparsely appressedly puberulous or glabrous, spirally arranged, mostly ovate, 15–35 by 5.5–11 cm; acumen 0.7–30 mm; base attenuate; nerves in 12–18 pairs; reticulation fine, prominent on both sides. Petiole 15–50 mm. *Brachyblast* densely greyish pubescent. Flowers often many, nicely scented, white; tepals c. 12, all nearly the same, 30–55 mm. *Stamens* c. 10 mm long, carpels c. 10, with the c. 5 mm long gynophore greyish puberulous. *Fruits* not known (plant sterile).

*Distr.* Commonly cultivated in tropical and subtropical countries.


Uses. The beautiful and nicely scented flowers are sold on the market. The tree is grown as an ornamental.


Note. FR Ibb 11996 from Bali has the characters of this species but produced fruits. The Head of the Forest Office in Bali, Dr. Ir. I.G.M. Tantra, told me that *M. alba* in Bali is fertile.


Shrub. Twigs pubescent to tomentose, often zigzag. Stipules adnate to the petiole for nearly its whole length, long ferrugineously pubescent. Leaves glabrous, elliptic, 4.5–6.5 by 2–3 cm; acumen 0–5 mm; base cuneate; nerves in 9–12 pairs. Petiole 3–5 mm. *Brachyblast* woolly pubescent, in Malesia c. 5 mm; spathaceous bracts long pubescent to tomentose. *Tepals* ± the same, 6 in total, c. 18–20 mm. *Stamens* c. 10 mm; carpels c. 20–30, gynophore 2 mm, both glabrous or only the gynophore pubescent.

*Distr.* China; in *Malesia*: frequently and widely cultivated as an ornamental shrub, not known to be naturalized.

*Vern.* *Cempaka muleng*, Jav.

**Excluded genera**

*Phelina* Nor. in Verb. Bat. Gen. 5, Art. 4 (1790) 3, nomen; ibid. ed. 2 (1827) 66, nomen. Based on a Javan plant, the vernacular name being given as *champaca ceylon*.

This was referred to *Michelia* Linné by Jackson, Index Kew. 2 (1894) 492, and to *Liriodendron* Linné by Dalla Torre & Harms, Gen. Siphonog. (1901) 171. According to the vernacular name, however, it was based on the species now known as *Horsfieldia iraygahedi* (Gaertn.) Warb. (Myristicaceae). Hasskari, Cat. Pl. Hort. Bot. Bogor. Cult. Alt. (1844) 174 referred *Phelina* to *Pyrrhosa horsfieldii* (Blume) Hassk., which is a synonym of *H. iraygahedi*.

LINACEAE (A.M.N. van Hooren & H.P. Nooteboom, Leiden)

In this work Linaceae sensu lato have been split into three families: Linaceae, Ixonanthaceae and Ctenolophonaceae, among which the latter deviates most.

In order to elucidate distinction of the two segregated families of Linaceae sensu lato Van Hooren & Nooteboom (Blumea 29, 1984, 550) prepared the following diagnoses:

**Linaceae** — Lianas, trees, shrubs, or herbs. Tufted hairs absent. Stipules lateral. Leaves spirally or distichously arranged. Flowers hypogynous. Petals caducous, contorted. Disk absent (or traces of an extrastaminal disk present, *l.c.* 556 *sub Philbornea*). Filaments basally connate in a tube. Styles 3-5(-6), simple. Fruit a drupe or a capsule (sometimes with indehiscent mericarps). Seed not persistent, with slightly or not developed arillode. — Stomata paracytic.


**Ctenolophonaceae** — Trees. Tufted hairs present. Stipules interpetiolar. Leaves opposite. Flowers hypogynous. Petals caducous, contorted. Disk extrastaminal. Filaments free, inserted halfway on inside of disk. Style 1, apically bifurcate, with 2 stigmas. Fruit a capsule. Seed persistent on the columella after the valves have been shed, with hairy-papillose arillode. — Stomata anomocytic.

Linaceae sensu stricto are distinguished by several flower characters from the other two families, viz. disk absent or almost so, filaments connate at base, styles 3-5, and arillode absent or hardly developed. The distinction of these families is also sustained by wood and anatomical research (*Heimsch & Tschabold, 1972*) and pollen morphological studies (*Saad, 1962; Oltmann, 1971*). *Narayana & Rao* (1978) concluded that on the basis of floral morphology and embryology Linaceae are related to *Erythroxylaceae* and *Humiriaceae*, in addition to showing affinity with Ctenolophonaceae and Ixonanthaceae. In his studies on seeds, *Corner* (1976) opposed an affinity with Geraniaceae, but suggested Malpighiaceae and possibly also Oxalidaceae as closer relatives.

Within Linaceae sensu stricto there are two distinct subfamilies, Linoideae and Hugonioideae. They can be distinguished as follows:

1. **Linoideae** — Erect herbs or small shrubs. Petals usually long-clawed. Stamens as many as petals, alternating with the same number of staminodes. Ovary 6-10-celled. Fruit usually a capsule. — Almost entirely confined to the northern hemisphere.

2. **Hugonioideae** — Trees or lianas with hooks, rarely shrubs, all ligneous. Petals not or hardly clawed. Stamens twice as many as petals. Ovary 3-5-celled. Fruit a drupe, rarely splitting finally in indehiscent mericarps. — Pantropical, but hardly on the northern hemisphere except in southern Southeast Asia.

In Malesia only Hugonioideae occur, and have not seldom been distinguished as a separate family Hugioniaceae (*e.g.* by *Exell & Mendonça, 1951; Takhtajan, 1969; Dahlgren, 1975; Cronquist, 1981*). *Corner* (*l.c.*) dwelt extensively on the anatomical structure of their seeds. In his opinion the simple tegmen of the Linoideae may be derived from the mesotental construction in the Hugioniaceae. The genus *Indorouchera* of the Hugioniaceae may yield the most primitive pollen type in Linaceae.

Subfamily Hugonioideae

Trees or lianas, rarely shrubs. Hairs, if present, simple, uniseriate, or multiserial with multicellular, glandular heads. Stipules lateral, caducous. Leaves simple, spirally or distichously arranged, pinnately nerved. Inflorescences an axillary or terminal compound panicle, raceme, corymb, or cyme, or an axe fascicle, few- to many-flowered, rarely 1-flowered. Flowers actinomorphic, pentamerous, bisexual, hypogynous, sometimes heterodistyloous. Sepals basally shortly connate or free, quincuncially imbricate, subequal or unequal, flabellately nerved, persistent, often slightly indurated and enlarged in fruit. Petals free, rarely basally clasping, shortly or not clawed, contorted, flabellately nerved, caducous. Disk absent. Stamens 10, alternately shorter and longer; filaments basally connate in a tube; anthers dorsoventral, 2-celled, introrse. Extrastaminal nectary glands adnate to staminal tube, up to 5, or absent. Ovary superior, 3–5(-8)-celled; styles 3–5(-8), free or basally connate; stigma capit. Ovules 2 per cell, axe, collateral, pendulous, epitropous. Fruit a drupe, rarely splitting in pyrenes. Seed(s) 1 or 2 per cell, arillode hardly or not developed. Endosperm dry or fleshy, copious or scanty. Embryo straight or slightly curved.

Distribution. Pantropical; 5 genera, of which 2 small (Hebeperatum, Roucheria) confined to tropical South America, 1 (Philbornea) confined to Malesia, 1 Indo-Malesian (Indorouchera), and 1 in the Old World tropics (Hugonia, incl. Durandea), including Madagascar, with some three dozen species, eastwards extending as far as the Solomon Islands, Queensland, New Caledonia, and Fiji. In Malesia in all 5 spp.

Ecology. Tropical, everwet rain-forest, mostly in the lowland but locally ascending to 1500 m on Mt Kinabalu. As to latitude up to c. 20° N and 25° S (Madagascar).

The South American representatives are trees, the Old World ones predominantly lianas, rarely shrubs in New Caledonia. Sometimes the lianoid species may remain shrubs or small trees as long as no support is available to climb. As soon as a support is present, the plants climb by means of stout, woody, curved climbing hooks (branch metamorphosis), which wind around the support and considerably thicken afterwards.

Vegetative anatomy. The Hugonioideae are leaf anatomically very strictly defined by their shared possession of subsidiary cells which are lobed underneath the stomatal guard cells and cristaque cells (cells with Ca-Oxalate crystals and a unilaterally thickened, sclerified cell wall); paracytic stomata are another constant feature of the group. This very unusual combination of characters induced Van Welzen & Baas (1984) to advocate family status for Hugoniaceae, because the Linioideae (or Linaceae) lack this combination of characters. Most Hugonioideae have lignified guard cell pairs, but Indorouchera constitutes an exception and can be separated from the other two Malesian genera on account of its un lignified cells.

The wood anatomy of the Malesian Hugonioideae is incompletely known. Indorouchera has been recorded to have exclusively scalariform perforations; in Hugonia they are simple. The fibres have distinctly bordered pits like in all members (families or subfamilies) of the Linaceae sensu lato.


Palynology. Pollen grains in Linaceae are suboblate to prolate, and measure from 20 to 90
μm. The apertural system is mostly tricolpate or tricolporate. In *Linum* also pantocolpate and pantocolporate pollen occur. *Anisadenia* and *Reinwardtia* pollen is always pantporate. *Indoroucheria* has inaperturate grains, which, however, actually represent a tritenuate condition.

In most genera the exine shows differentiation in sexine and nexine. In *Indoroucheria* the exine is a thin, homogeneous sheet, covered by small verrucae. Otherwise, the sexine is granulate or baculate. Sometimes the tips of the bacula are fused to form a columellate-tecitate sexine.

The macromorphologically distinct subfamilies *Linoideae* and *Hugonioideae* can be separated in a pollen morphological way too. Pollen of *Linoideae* is tricolpate, pantocolpate, or pantocolporate, and has a more or less granulate sexine, while that of *Hugonioideae* is tricolporate (*Hugonia, Philbornea*) or inaperturate (*Indoroucheria*), and mostly has a more or less baculate or a columellate-tecitate sexine (Saad, 1962). Generally speaking, subfamily *Linoideae* has more primitive pollen characters than subfamily *Hugonioideae*, although *Indoroucheria* may yield the most primitive pollen type in *Linaceae*.

Following Saad (*ibid.*) the pollen of the *Linaceae* is primitive within the *Geraniales*. Relationship of the *Linaceae* with *Ixonanthaceae*, as well as with *Erythroxylaceae* and *Humiriaaceae*, is supported by pollen morphology (Oltmann, 1971). However, pollen also indicates the distinctness of the *Linaceae* within this group of families. Pollen of *Cienolophonaceae* appeared to be dissimilar to that of *Linaceae*.


**KEY TO THE GENERA**

1. Indumentum present, at least on the calyx. Styles 5(–6). Ovary 5(–6)-celled, locules all distinct in the fruit. Drupe with 2–4(–5) developed seeds ...................................................... 1. *Hugonia*

2. Resin absent. Leaves spirally arranged. Flowers in rather lax racemes or panicles........ 2. *Philbornea*

3. Buds and stipules often covered by resin. Leaves distichously arranged. Flowers in axillary fascicles, subtended by often densely packed, imbricate bracteoles.......................... 3. *Indoroucheria*

**1. HUGONIA**


Indumentum present at least on calyx. Stipules palmatifid-laciniate, pinnatifid or simple, entire or dentate. Leaves spirally arranged. Flowers in axillary or terminal more or less densely flowered racemes or leafy or leafless panicles, or axillary, in few-flowered cymes or solitary, rarely ramiﬂorous. Bracts and bracteoles present or not. Sepals free, unequal, rarely subequal. Petals shortly clawed or thickened at base. Nectary glands present or not. Ovary 5(–6)-
Fig. 1. *Hugonia costata* Miq. *a*. Habit, × 0.5; *b*. climbing hooks, × 0.5; *c*. stipules from inside, × 3; *d*. flower bud; *e*. innermost sepal; *f*. pistil (in bud), all × 5; *g*. fruit, × 1.5; *h*. fruit in CS, × 1.5; *i*. seed, × 3; *j*. embryo, × 3 (*a–j* FORBES 2978, *b* FORBES 2814).
loculed; styles 5(−6). 

*Drupe* (pseudo-)indehiscent or splitting into 5 pyrenes; endocarp woody, provided with more or less prominent longitudinal ribs, either compact and forming one stone with 5(−6) fertile locules alternating with as many interlocular sterile cavities or divided into 5 thin, more or less obviously ribbed pyrenes which are separated by a fleshy mesocarp. *Seeds* 1 per locule, 2−4(−5) developed per fruit, apically attached. Embryo with fleshy endosperm.

**Distr.** About 40 spp., in the Old World reaching from Senegal in the west to Fiji in the east and from Bombay in India at 20° N as far as Madagascar at c. 25° S; in *Malesia* 2 spp., one in the west (Sumatra, Borneo) and a second one in the east (Moluccas, New Guinea).

They belong to two allogamous sections: *sect. Hugonia* possesses some 30 spp. in Africa, Mauritius, and 4 spp. in SE. Asia (Sri Lanka, Indonesia, Malesia); *sect. Durandea* (Planch.) BAillon has 4 spp. in E. Malesia, Queensland, Solomons, New Caledonia (2 or 3 endemic), and Fiji.

**Ecol.** Mixed tropical forests; 0–1500 m (Mt Kinabalu).

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**KEY TO THE SECTIONS AND THE SPECIES**


1. Young parts, stipules, petiole and nerves glabrous or with some very small scattered hairs. Stipules simple, entire or dentate. Sepals up to 3.5(−4) mm long. Petals 2.5−3.5 by 1.5−2.5 mm. Drupe splitting into 5 pyrenes. *Sect. Durandea* 2. H. jenkinsii


Liana. Tomentum appressed to patent, hairs up to 1 mm. Twigs densely tomentose when young, glabrescent. *Climbing shoots* often patent, some growing out into a leafy, sometimes fertile branch; first internodium 3−12 cm long; hooks (1−)2, subopposite or opposite, apically on the first internodium, 2.5−5 cm long, later thickening; at apex often with cataphylls. Stipules narrowly ovate to obovate, 5−10 by 2.5−3.5 mm, digitately laciniate up to 1/3, with 7−10 lobules. Leaves sparsely to densely tomentose, narrowly elliptic to ovate, sometimes asymmetric, (4−)6−18 by 2.5−7 cm; base obtuse to acute or cuneate; margin glandular-crenulate to crenate, glands caducous, conical; apex acuminate to cuspidate, acute to obtuse, acumens up to 1.5 cm; nerves 11−17 pairs, arching upwards and ending in the dense reticulation; petiole 3−14 mm, the margin with 1−3 conical glands on each side. *Inflorescence* an axillary (and terminal?) 3-flowered cyme, 1.1−1.5 cm, sometimes reduced to 1 flower, densely tomentose; bracts caducous, narrowly ovate to obovate, 10−15 by 2−3.5 mm, deeply digitately laciniate into 8 lobules. Pedicel 2−5 mm, articulate below the calyx. *Flowers* only known in bud. Buds ovoid, c. 8 by 5.5 mm. *Sepals* leathery, the 3 or 4 outer ones tomentose, boat-shaped, ovate, 9−10 by 5−6.5(−8.5) mm; inner ones 1−2 mm shorter. *Petals* boat-shaped, broadly ovate, at least 10 by 7 mm. *Staminal tube* ± thickened at base, sometimes persistent in fruit; filaments ± hairy. *Ovary* 5−(6)−loculed, glabrous, cylindrical; styles 5 (or 6), exceeding the stamens, of different length. *Drupe* broadly obovate to globular, 18−23 by 20−24 mm; base with vascular openings absorbed into a navel with slightly prominent margin; mesocarp thick-fleshy, hard and strongly irregularly wrinkled when dry, adnate to the stone; endocarp woody, very hard, with thick radial septa, 5 (or 6) narrowly elliptic to narrowly ovate (in CS), seminal cavities and as many alternating, always empty, cordate, sterile cavities, 1.7 mm diam. *Seeds* 1 or 2, excarillate, ventrally attached, flattened obvoid, 11.5 by 4.5 mm, c. 1 mm thick; hilum not obvious; testa thin, 2-layered. Embryo straight; cotyledons oblong, 7 by 4 mm; radicle cylindrical, 3 by 0.8 mm. Endosperm copious, slightly granular.

**Distr.** *Malesia*: Sumatra (Palembang, Padang), Malay Peninsula (Lebios For. Res.), Borneo (Sabah, Kutai, E. Kalimantan). Fig. 2.

**Ecol.** Typically matures in late building gaps, well drained ridges, and flat upland areas; in Malaysia on gently undulating ground in lowland forest at 100 m. Although rarely collected, according to Leighton (coll. no. 1010) locally relatively common, 8 mature individuals/km²; on Mt Kinabalu at 1500 m.

Fig. 2. Range of *Hugonia costata* Miq. (stars) and *H. jenkinsii* F.v.M. (dots).


Liana to 40 m, rarely small tree to 3 m, or climbing shrub, up to 10 cm diam. *Climbing shoots* with first internodium (2.5—6—18 cm, following internodia very short with some distichously arranged, reduced, linear to orbicular leaves, a few of these shoots with a long-peduncled, reduced inflorescence or a climbing hook, or the climbing shoot above the hooks growing out to a leafy and often fertile branch. *Hooks* distichously or subopposite, woody, (3.5—)6.5—8.5 cm long, apically often with bract-like organs, peduncles, cymes, or reduced leaves. *Stipules* entire, obtuse to acute, with or without glandular teeth, persistent or sometimes caducous, sometimes only present as a glandular tooth, subulate or triangular, 0.5—0.8 by 0.2—0.8 mm. *Leaves* glabrous (rarely some hairs on midrib), narrowly elliptic to obovate, sometimes broadly elliptic or ovate, sometimes asymmetric, (6—)11—27—(36) by (1.6—)3—9.5 (—11) cm; base cuneate, seldom rounded; margin often wavy, glandular-crenulate to crenate, apex acute to acuminate, rarely obtuse, acumen up to 2 cm; nerves 7—16 pairs, slightly arching upwards and almost reaching the margin, meeting in an often somewhat obscure intramarginal vein or in the dense reticulation; petiole 3—20 mm. Inflorescence an axillary or terminal compound panicle, sometimes a raceme; terminal panicles often leafy, cone-shaped to obovoid, (4—)12—18—(32) by (2.5—)1.5—1.4 cm with 5—25—(30) more or less closely set subinflorescences, sometimes up to 5—8 pseudoterminal panicles together; axillary panicles patent, narrowly obovoid to broadly ellipsoid, (2—)6—11—(12) by (1—)2—6.5 cm, with (4—)10—23 subinflorescences; peduncle up to 6.5 cm; cymes up to 15, 0—5 times branched; bracts persistent, obtuse deltoid, (1.5—)2—5.5 by 0.2—1 mm, with 2—6 glandular teeth. Pedicel articulate and often thickened below the flower, 1.5—3 mm. Bracteoles like the bracts but smaller. *Flowers* heterodis-tylous, 7—9 by 5—9 mm. *Sepals* ± orbicular to transversely broadly elliptic, (1.8—)2—3—4—(4) by 2—4—4.5 mm, shortly connate to free, appressed but patent in fruit, outer 2 smaller and thicker. *Petals* recurving during anthesis, narrowly elliptic to obovate, 6—9.5 by 1.5—3—4 mm; base often indistinctly 0.8 mm clawed. *Stamens* mostly persistent, obdiplostemonous, in short-styled flowers (4.5—)4.8—6 and (5—)5.5—7.5 mm, in long-styled flowers (2.5—)3.8—4.5—(4.8) and (3.8—)4.2—5—(5.8) mm; tube 1—1.5—(2) mm, partly persistent in fruit; base often irregularly thickened or marked by darker coloured
Fig. 3. Hugonia jenkinsii F.v.M. a. Flower, ×4; b. inner sepal, ×5; c. outer sepal, ×5; d. flower, sepals and petals removed, ×4; e. stamens with glandular thickenings at base of tube, ×5; f. fruit, ×1.5; g. pyrene, ×6; h. seed, ×3 (a–h BSIP 10657).

semi-ellipsoid, sometimes apically notched, staminal glands at the base of long or short stamens, these later becoming connate with each other; filaments triangular at base, apically filiform. Ovary 5-loculed, ovoid to broadly ellipsoid, 1–2 by 0.8–1.2 mm; styles 5, basally shortly connate and apically (in short- and long-styled forms) hooked or sigmoidly curved or (in long-styled forms) slightly arching to curving downwards; sometimes of different length, in short-styled flowers (1–)1.5–2.8 mm, in long-styled flowers (3–)3.2–3.5(–5.2) mm; stigma 2-lobed. Drupe 15-ribbed, ovoid to subglobose, (8–)10–13 by (7–)8–10.5 mm, splitting into 5 pyrenes; mesocarp fleshy, surrounding the pyrenes, between the pyrenes often disappearing thus giving rise to a false locule; endocarp bony, thin, 3-ribbed, ribs branching, the branches connected by bony septa, forming cavities filled with aerenchyma; septa and aerenchyma dissolving when ripe. Seed 1 or 0 in each pyrene, ventrally-apically attached by a short funicle, medially flattened, asymmetrically semi-ellipsoid. c. 8.5 by 3.5 mm; hilum and arillus not obvious; testa thin, 2-layered. Embryo c. 8 by 3 mm; radicle flattened, arched, c. 1.5 by 2.5 mm. Endosperm fleshy.

Distr. W. Pacific (Fiji), Melanesia (Solomons, New Caledonia), Queensland; in Malesia: New Guinea, Moluccas (Ceram, Ambon). Fig. 2.

Ecol. Primary and secondary forests, often on well drained places or along rivers, also along estuaries or mangroves, locally rather scarce to common; up to 2000 m. Fl. Jan.–Nov.; fr. Feb.–Nov.

Field notes. Flowers fragrant to very strong sweet-scented with yellowish green to dark green sepals and bright golden yellow to orange petals. Filaments pale olive yellow to orange with deep purple to brown anthers. Styles pale yellow to pale orange with green stigma. Fruits golden yellow to light orange becoming pinkish red, red to brown or orange brown.

Uses. In Queensland the Tully River natives use the climbing hooks as fish hooks.

2. PHILBORNEA


Ecol. Periodically inundated soil and near rivers in the lowland.

Fig. 4. Philbornea magnifolia (STAPF) HALL.f. a. Habit, × 0.5; b. bract, bracteoles, and flower bud, × 5; c. fruit; d. fruit, exocarp removed; e. seed; f. embryo; all × 3 (a after STAPF, b KOSTERMANS 21142, c–f RAHMAT SI BOEEA 5362).

Fig. 4.

Twigs often roughened by many light coloured lenticels. Climbing shoots patent, first internode 6−12 cm, following internodia very short with caducous, reduced, broadly elliptic leaves. Hooks 2, (sub)opposite, woody, 1.5−5 cm. Stipules appressed to patent, triangular, sometimes gland-like, 0.3−0.5 by 0.2−0.3 mm. Leaves obovate or elliptic, rarely ovate, 7−20(−30) by (2−)4−10(−14.5) cm, sometimes asymmetrical; base gradually decurrent to the petiole; margin glandular-crenulate; apex broadly acute to obtuse or acutely acuminate, acumen up to 2.8 cm; nerves 7−14 pairs, slightly arching upwards to and along the margin, often meeting in an intramarginal vein; reticulation dense; petiole rather stout, often thickened, (3−)6−15(−25) mm. Racemes axillary from (often fallen) leaves or scales, or terminal, sometimes with some cymes, 7−15(−28)-flowered, (2−)3.5−9.5 by (1−)1.5−4 cm. Bracts narrowly triangular to rhomboid, 0.5−2 by 0.2−0.5 mm, usually with 2 triangular glandular teeth. Pedicels articulate in or above the middle, (2−)4−10(−15) mm. Bracteoles 2, persistent, very small. Sepals basally shortly connate, membranous, ± shell-shaped, 3−4 mm diam., the inner 3 sometimes lacerate up to 2/3. Petals recurving during anthesis, elliptic to obovate, 7.5−9 by 4−4.5 mm. Stamens obdiplostemonous, the long ones 5.5−6.2 mm and basally thickened, the short ones 1−1.5 mm shorter, 4.5−4.8 mm; staminal tube 0.5−1.5 mm. Filaments basally flattened. Ovary elliptic to obovoid-pyriform, 1−1.5 by 0.7−1.5 mm; styles free, apically sometimes slightly twisted; stigmas knob-shaped, 2-lobed. Drupe lengthwise wrinkled, often flattened at one side, ovoid, 10−12 by (5−)7−10 mm, exocarp membranous; mesocarp thin-fleshy, ± 0.3 mm thick; endocarp leathery in basal and sterile half, tougher and with prominent, subreticulate, firm, ± 0.2 mm thick ribs in upper half of fertile part. Seed 1, smooth, flattened ovoid, 10−11 by 5.5−6 mm, ventrally attached by a long raphe, thickened around the raphe and along the whole length by an arillode; testa 0.2 mm thick; tegmen somewhat thinner. Embryo straight; cotyledons transversely broadly ovate, ± 6 by 6 mm; radicle cylindrical, 4.5 mm long.

Distr. Malesia: Sumatra, Borneo (Sarawak, E. Kalimantan), Philippines (Palawan). Fig. 5.

Fig. 5. Range of Philbornea magnifolia (Stapf) Hall. f.

Ecol. Periodically inundated soil and near rivers, up to 270 m.
Field notes. Petals bright yellow.

3. INDOROUCHERA


Fig. 6. Indorouchera contestiana (Pierre) Hall.f. a. Habit; b. twig with climbing hooks provided with reduced inflorescence at apex; c. climbing hook, thickened after grasping a twig; all ×0.5; d. stipule, ×12; e. flower and bracteoles, ×12; f. flower, sepals and petals removed, ×8; g. fruit; h. fruit in CS; i. fruit, exocarp removed; j. seed; k. embryo; all ×12. — l. griffithiana (Planch.) Hall.f. l. Fruit, exocarp removed; m. fruit in CS; n. seed; all ×12 (a, d, g–k Haviland 2840, b van Niel 3607, c A 441 Rahim, e, f NBFD 2113, l, m de Wilde & de Wilde-Duyfjes 16540, n Meijer 7335).
styles 3–4(–5), basally connate to free. Drupe indehiscent, 1- (rarely 2-)seeded with 2 (or 1) reduced locule(s). Seed ventrally attached, arillate. Embryo straight or slightly curved. Endosperm copious, oily.

**Distr.** 2 spp., SE. Asia (India: Nicobars; ?Burma, Thailand, Cambodia, S. Vietnam); in **Malesia**: Sumatra, Malay Peninsula, Borneo, Java.

**Ecol.** Rain-forest, also along the seashore, estuaries and on sanddunes, up to 1500 m.

**KEY TO THE SPECIES**

1. Leaves elliptic to obovate; reticulation densely parallel in the whole leaf. Petals (5–)6.4–8.5 by 1.5–3 mm. Stigma knob-shaped. Drupe 4.5–6 by 3–4.5 mm .................................................. 1. *I. griffithiana*

1. Leaves often ovate, rarely elliptic; reticulation predominantly in the basal half laxly and (irregularly) parallel, in the apical half reticulated. Petals 4–5.5 by 1–1.8 mm. Stigma clavate, recurved. Drupe 4–4.5 by 2.5–3 mm .................................................. 2. *I. contestiana*

Flora Malesiana
[ser. 1, vol. 10]


Liana, up to 30 m, rarely shrub or treelet, 4 m. Stem up to 3 cm diam. Climbing shoots with first internodium of 3–10 cm. Hooks 1 or 2 at the end of a climbing shoot or several (up to 5) distichously arranged in the axils of (often fallen) leaves or inflorescences, 3–5 cm long. Stipules triangular to ovate, 0.7–0.8 by 1.5–1.8 mm, crenate. Leaves elliptic to obovate, rarely ovate, (4–)7.5–11.5–(19) by (1–)2.5–4(–6.8) cm; base cuneate; margin glandular to crenate; apex obtusely caudate to acuminate, rarely rounded; acumen up to 2.5 cm; nerves (5–)7–10 pairs, ± arching upwards and almost reaching the margin; primary veins often subperpendicular to midrib and many of them ± parallel; reticulations densely parallel and transverse to midrib; petiole narrowly sulcate above, (0.5–)1–2 cm. Flowers (1–)3–7(–10) together, heterodistylos. Pedicels articulate, 1–3 mm; bracteoles membranous, ovate, 0.2–1(–2) by 0.2–0.9(–2) mm; Sepals elliptic to ovate or orbicular, 1.8–2.5 by (1.5–)2–2.8 mm. Petals thin, in anthesis straight, elliptic to ovobate, (5–)6.5–8.5 by 1.5–3 mm; base obtuse to very shortly clawed. Stamens in short-styled flowers 3.5–6 and 5–8 mm, in long-styled flowers 2.5–3.8 and 3.5–5.5 mm; staminal tube 0.6–1.3 mm, persistent in fruit. Ovary 3(–4)-loculed, rather smooth to 3–4-lobed when dry, cylindric, obovoid or globose, 0.8–1(–1.5) by 0.7–1(–1.5) mm; styles 3–4(–5), sometimes persistent in fruit, straight to sigmoidly curved in the middle, in short-styled flowers 1.2–2 mm, in long-styled flowers 3.2–5.5 mm; stigma flattened, knob-shaped, slightly 2-lobed. Drupe ± lengthwise ribbed when dry, ovoid to ellipsoid, 4.5–6 by 3–4.5 mm; exocarp membranous, 0.1–0.2 mm thick; mesocarp ± ribbed, fibrous-bony, 0.4–1 mm thick; endocarp bony, 0.3–0.4 mm thick. Seed(s) 1 (or 2), ventrally attached, semi-ovoid, 3–4.5 by 2.2–2.3 mm; arillus around the 1–2 mm long hilum, short, slightly thickened, funicular; testa thin. Embryo 3–4.3 by 1–2 mm; cotyledons straight or plicate, elliptic to broadly elliptic, 1.8–2.8 by 1–2 mm; radicle cylindric to flattened, straight to slightly curved, 1.1–1.5 by 0.4–0.5 mm.

Dist. India (Nicobar Is.), Thailand; in Malesia: Sumatra, Malay Peninsula, Borneo, Java. Fig. 9.

Ecoc. Rain-forests, common, but rare in Java, the Nicobar Is. and Thailand; up to 1500 m. Fl. fr. Jan.–Dec.

Fig. 8. Indorouchera griffithiana (Planch.) Hall.f. Twig with hook and flowers at Njarumkop (NW. Kalimantan) (Photogr. Father A. Elsener, 9 April 1964).

Fig. 9. Range of Indorouchera griffithiana (Planch.) Hall.f.
Field notes. Petals white to bright yellow, pale orange or reddish brown. Stamens yellow, anthers bright yellow, pistil light yellow. Drupe yellow to red, 8 mm diameter, with edible pericarp and tomato-like flavour.

Uses. According to Scholz (in Engler, Syllabus 2, 1964, 243) the plant contains saponin-like constituents. They are used in mixtures for arrow poisons. See also Burkitt, Dict. 2 (1935) 1949. In Sarawak used for parang handles.


Liana, up to 10 m, sometimes a shrub up to 4 m. Stem ± 1 cm diam. Climbing shoots patent, c. 45°, first internodium 3.5 – 7 cm, hooks 1 or 2 at the end of a climbing shoot or up to 3 in the axils of leaves or inflorescences, at the apex sometimes with reduced inflorescences, (0.5–)1.5–4.5 cm long. Stipules liguliform to shallowly triangular, 0.8–1.5 by 1–1.5 mm, entire to crenate. Leaves elliptic to ovate, 3–11.5 by 1.5–4.7 cm; base obtuse, rarely cuneate; margin glandular-crenulate; apex obtusely acuminate, rarely obtuse, acumen up to 1.5 cm; nerves (4–)5–8 pairs; veins ± perpendicular to midrib and many parallel; reticulation rather lax, irregularly parallel, predominantly in basal half and along midrib, densely reticulate in apical part of leaf; petiole 0.5–1 cm. Flowers in (1–)4–7(–14)–flowered fascicles. Pedicel articulate, 0.5–1.5 mm. Bracteoles membranous, ovate, 0.3–1–(1.5) by 0.3–1(–1.5) mm. Sepals elliptic to ovate, 1.7–2.5 by 0.7–1.6 mm. Staminens 1.8–2.2 and 2.5–3.5 mm; staminal tube 0.7–0.8 mm high. Ovary 3-loculed, rather smooth, cylindrical to ovoid, 0.8–1 by 0.6–0.7 mm; styles 2–3.5 mm; stigma clavate, recurved, slightly 2-lobed, c. 0.25 mm diam. Drupes ovoid, 4–4.5 by 2.5–3 mm; exocarp thin-fleshy, ± 0.2 mm thick; mesocarp chartaceous, ± lengthwise grooved, c. 0.2 mm thick; endocarp woody, crescent-shaped in CS, ± 0.2–0.4 mm thick. Seed(s) 1 (or 2), ventrally attached, semi-ovoid, 2.5–2.7 by 1.7–1.9 mm, often asymmetric; hilum narrowly elliptic, ± 1.5 mm long; aril indistinct, short, ± thickened below the hilum; testa thin. Embryo 2.8–3 by 1.3–1.5 mm; cotyledons straight, broadly elliptic to ± orbicular, 1.5–1.7 by 1.3–1.5 mm; radicle cylindrical to slightly flattened, 0.8–1 by 0.2–0.3 mm. Endosperm granular.

Dist. S. Vietnam, Cambodia; in Malesia: Borneo. Fig. 10.

Fig. 10. Range of Indorouchera contestiana (PIERRE) Hall.f.

Ecol. Edge of young secondary forest and of swampy forest, rare; up to 10 m altitude. Fl. fr. April–June.

Field notes. Petals yellow, fruit red.

Uses. According to Scholz (in Engler, Syllabus 2, 1964, 243) the plant contains saponin-like constituents. They are used in mixtures for arrow poisons. See also Burkitt, Dict. (1935) 1949. For details on chemical contents see Hagnauer, Chemotaxonomie der Pflanzen 4 (1966) 397. On the label of CHN 2829 is mentioned: 'a "T"-point can be made into a parang handle. The wood is tough, not excessively hard, and will not split easily.'

Vern. Borneo: kai kai pateh, Brunei.
IXONANTHACEAE (R. Kool, Leiden)

This small family of 2 or 3 Old World rain-forest genera was already recognized as a separate suprageneric taxon by Planchon (1847) and Planchon & Klotzsch (1856), who relegated it to the affinity of Ochnaceae, later correctly referred to *Linaceae* as a subfamily *Ixonanthoideae* by Hub.Winkler (1931) and finally recognized as a family of its own by Exell & Mendonça (1951).

As to the number of genera contained in the family, there is no unanimity of opinion. Forman (1965: 523) referred 8 genera to the family, but Nooteboom (1967) argued that several belong to Simaroubaceae. After careful consideration 3 genera are admitted here in *Ixonanthaceae sensu stricto*: Cyrillopsis Kuhl. from South America, Ochthocosmus Benth. (incl. Phyllocosmus Klotzsch) from tropical America and Africa, and Ixonanthes Jack from Indo-Malesia. The three genera form a close-knit group. They are all small and the wide distribution in the tropics points to a high age of the group.

We must mention that there is a, doubtful, fourth genus, *Allantospermum* Forman, which the author reckons to the *Ixonanthaceae*. It occurs with one species in Borneo and another one in Madagascar. Nooteboom (1967, 1972) included this genus in *Simaroubaceae*. The morphology, chemotaxonomy, and palynology corroborate this affinity, but the anatomy of wood and leaf (van Welzen & Baas, 1984) is just in favour of affinity with *Ixonanthaceae*.

We refrain from a long discussion of the merits of Hallier’s attempt (1923) to have *Linaceae* as a huge complex centre of affinities and confine ourselves to what is usually accepted nowadays in recognizing a few families grouped around *Linaceae sensu stricto*.

In the treatment of the family *Linaceae* (page 607, see there) the families *Linaceae*, *Ixonanthaceae*, and *Ctenolophonaceae* are opposed by concise diagnoses.

Leaf anatomy has clarified many points but a fair number remains unsolved, which should be the subject of further multidisciplinary studies (van Welzen & Baas, l.c.).


**Vegetative anatomy.** The leaves of *Ixonanthes* have paracytic stomata, a simple vascular strand in petiole and midrib with sclerenchyma forming a complete cylinder enclosing parenchymatous ground tissue adaxially, and rhomboidal crystals and druses, as more or less constant characters. Variation has been recorded in presence or absence of anticlinal division walls of the epidermal cells, mucilage cells and extent of the vascular bundle sheaths of the minor veins. This diversity partly coincides with the boundaries between the sections *Brewstera* and *Ixonanthes*.

The wood of *Ixonanthes* is characterized by solitary vessels with simple perforations, fibres with numerous distinctly bordered pits, largely apotracheal axial parenchyma bands of 2–5 cells wide, and narrow 1–3(–4)-seriate, weakly heterogeneous rays. The vessel-ray pits are large and simple.

The above characters are in fairly good agreement with the treatment of *Ixonanthes*, together with *Allantospermum*, *Cyrillopsis*, *Ochthocosmus*, and *Phyllocosmus* in one family of the *Linaceae* alliance. *Allantospermum* would fit here better than in the *Irvingiaceae*, although its wood stands out in the *Ixonanthaceae* on account of its minute, half-bordered vessel-ray pits.


**Palynology.** Pollen of *Ixonanthaceae*, which is described by Lobreau (1969: 526, Cyrillopsis) and Oltmann (1971), is subprolate to prolate (*Cyrillopsis, Ochthospermum*) or subspherical (*Ixonanthes*), and measures from 27 to 52 µm. The apertural system is always tricolporate. The colpi are long and the endoapertures have costae on their polar sides. Exine stratification can easily be observed. Tectum and nexine are thin, while the infratectal layer consists of long columnellae.
The thickness of this columellate layer clearly exceeds that of tectum and nexein together. Sculpture is mostly somewhat scabrate. *Cyrillopsis* has a rugulate or striate exine. Pollen of *Ixonanthes* is characterized by the presence of distinct supratectal spines. *Allantospermum*, which genus was at first included in *Ixonanthaceae*, has tricolporate pollen with endoapertural costae, long columellae, and a rugulate to striate sculpture. As for its pollen morphology, the genus *Allantospermum* is considered to be related to *Ixonanthaceae* by Bortenschlager c.s. (1966), Metcalfe c.s. (1968) and Oltmann (l.c.) and to *Simaroubaceae* (especially to *Irvingia*) by Muller (1972), which latter opinion is accepted here. Metcalfe c.s. (l.c.) consider pollen of *Ixonanthaceae*, *Allantospermum*, and *Irvingiaceae* together more similar to *Simaroubaceae* pollen than to that of *Linaceae*. However, Oltmann (l.c.) concluded on pollen morphological evidence that *Ixonanthaceae* (*Allantospermum* excluded) are nearest to *Erythroxylaceae* and also, but to a lesser extent, related to *Linaceae*.


### 1. Ixonanthes


Evergreen, buttressed trees or treelets growing monopodially with flushes, glabrous. Branches ascending. Bark brownish, finely fissured, rich in tannin; younger parts smooth. Stipules caducous, free, scale-like, about obliquely triangular, entire, acutish, glabrous. **Leaves** simple, spirally arranged, with slightly incrassate, entire or glandular-serrate margin, pinnately nerved, mostly obovate, tapering towards the base into a short petiole; midrib sulcate above, prominent beneath; venation obscure or slightly prominent on both surfaces; reticulations fine, irregular. **Inflorescences** axillary, dichasially corymbose. Peduncle smooth, glabrous; primary axes paired or sub-4-whorled, secondary axis paired, otherwise as the primary ones but usually much shorter; bracts scale-like, triangular, persistent, acutish, entire, smooth; bracteoles absent. **Flowers** bisexual, 5-merous, actinomorphic, perigynous. Young buds sticky. **Calyx** and **corolla** indurated and persistent in fruit, increasing in size. **Sepals** connate for up to 0.2 of their length, quincuncial, glabrous, fleshy to coriaceous in fruit. **Petals** quincuncial, almost free, glabrous, distinctly veined. **Stamens** 10 or (15—)20, in one whorl; filaments inserted outside and against the disk, irregularly coiled in bud, glabrous, subpersistent; anthers (basi-)dorso-versatile with a large peltate connective, introrse with 2 longitudinal slits, finely verru-
Fig. 1. View on *Ixanthes* forest, seen from the resthouse at Malili, Central Celebes (Photogr. J. van Zijl de Jong, 1933).

cose. *Disk* well-developed, bowl-shaped, with free margin, erect, entire or slightly lobed. *Ovary* superior, 5-celled, glabrous. *Ovules* 2 per locule, axile, one on each margin of the carpel, collateral, pendulous, epitropous. *Style* 1, irregularly coiled in bud, either elongating to 25 mm or remaining very short (up to 2.5 mm in *I. petiolaris*), glabrous, subpersistent in fruit; stigma mushroom-shaped, margin slightly lobed, fleshy. *Capsule* septicidal and septifragal, 5-celled, 5-valvate, without a central column, ovoid-conical or ellipsoid, acute or obtuse, glabrous, smooth; valves sometimes ultimately apically bifid, in transverse section W-shaped; exocarp sometimes fibrous and subtended by a thin membrane (hypoderm) folding along the septs and apparently into the 5 epicarp clefts; mesocarp dark, spongy; endocarp glossy. *Seeds* 1 or 2 per cell, either with a basal wing or with a suprahilar arillode; testa tenacious, brown; endosperm spongy, white, containing oil; embryo straight, ± half as long as the dorso-ventrally appressed, ± asymmetrically elliptic cotyledons. Germination epigean.

**Distr.** In continental Southeast Asia and Malesia 3 spp. (absent in Java, the Lesser Sunda Islands, and the Moluccas).

**Ecol.** Primary forest on various soils below 1000 m.
Fig. 2. *Ixonanthes icosandra* Jack. a. Habit, ×0.5; b. branching of inflorescence, ×3; c. flower bud; d. ditto, perianth removed, both ×10; e. fruit, ×3; f. ditto in CS, ×4; g. ovule, with 3-lobed arillode, ×15; h. stipules, ×2 (KEP FRI 3121).
Field notes. According to Corner (Wayside Trees, 1940) the withering leaves are characteristic ochre-brown.

Uses. Though they may be sizeable trees, the timber is of little value and has no features for special purposes.

KEY TO THE SECTIONS AND THE SPECIES

1. Petiole 2–3 mm. Leaf margins slightly glandular-serrate. Primary branches of the inflorescence sub-4-whorled. Stamens (15–)20. Ovules and seeds with a suprahilar arillode, without a basal wing. — Sect. Brewestera

1. Ixonanthes icosandra


2. Inflorescence dense. Flowers at anthesis 1.5–3 by 1–2.5 mm diam. Style 1.5–2.5 mm. Fruit at most 1.5(–2) cm long. Valves ultimately apically 1–2 mm deep bifid. Seeds 10–13 by 3–4 mm. 2. I. petiolaris

2. Inflorescence lax. Flowers at anthesis 3–5 by 2–7 mm. Style 15–20 mm. Fruit (2–)3–4(–4.5) cm long. Valves not bifid. Seed 18–20 by 4–9 mm. — 3. I. reticulata

1. Section Brewestera


Young inflorescence axes, petioles etc. not glaucous. Lenticels inconspicuous. Petiole pulvinate. Leaf margin slightly glandular-serrate. Peduncle slightly flattened and distally faintly grooved with four ridges; primary branches sub-4-whorled around the usually developed terminal flower of the peduncle. Disk entire. Stamens (15–)20. Ovules 2 per cell, usually only one fertile. Capsule ovoid-conical, acute. Seeds with a suprahilar arillode, without a basal wing; arillode as long as the seed, fleshy, cream-coloured.


Trees or treelets up to 30 m, bole up to 1.3 m diam. Leaf scars ± orbicular to triangular. Stipules up to 0.6 mm long. Leaves oblong to slightly oblanceolate long. 6–19 by 3–6.5 cm, pungentaceous, base tapering; apex obtuse, often retuse, apiculate; petiole 2–3 mm, pulvinate. Peduncle 6–14 cm; pedicels 3–15 mm; bracts up to 5 mm long. Flowers at anthesis 2–3 by 1–2 mm diam. Sepals elliptic, 1–1.5 by 0.8–1 mm (in fruit enlarging to 1.5–2.5 by 1–1.5 mm), c. 0.3 mm thick at the base, margin ± hyaline, subcoriaceous in fruit. Petals orbicular, 2–2.5 by 2–2.5 mm (in fruit enlarging to 3–4 by 3–4 mm), subcoriaceous in fruit. Filaments ultimately up to 15 mm long; anthers basi-dorsal-ventral. Style up to 10 mm. Ovary top-shaped, ± 5-angular, c. 0.5 by 0.7 mm. Capsule 15(–20) by 5–6 mm. Seeds ellipsoid, 10 by 2 mm; arillode adaxillary, tripartite.

Dist. Thailand; in Malesia: Sumatra and Malay Peninsula.

Ecol. Primary and secondary forests on slopes and ridges, 0–600(–900) m.

Field notes. Bole straight, sometimes with short stilts roots. Bark smooth or slightly shallowly fissured, red, fawn, brown, or grey, soft. Inner bark red, purplish red, reddish brown, or brown. Wood white, orange, yellow, brown, cream-brown, or brownish red, hard. Crown conical, dense. Flowers white, yellow, green, sticky. Fruits green to dark brown, sticky.

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Uses. Sometimes used for house-building.


2. Section Ixonanthes


Young inflorescence axes, petioles, etc. glaucous. Lenticels punctiform or slit-like. Petiole flattened, upper side more or less deeply sulcate, sometimes very narrowly winged. Leaf margin slightly incrassate, entire, eglandular. Peduncle angular to flattened, not grooved; primary branches of inflorescence paired, terminal flower of the peduncle usually developed. Disk entire or sometimes slightly 10-lobed. Stamens 10. Ovules 2 per cell, usually both fertile. Capsule short- or long-ellipsoid, obtuse. Seeds with a basal wing, without a suprabasal arillode; wing oblong, fairly stiff, concolorous, with a distinct dark-coloured raphe.


Trees or treelets up to 30 m, bole up to 50 cm diam. Young bark with punctiform lenticels, older parts striped with numerous lanceolate lenticels. Leaf scars orbicular with 3–5, sometimes distinct vascular scars. Stipules up to 0.5 mm. Leaves elliptic-oblong, 6–15 by 3–7.5 cm, pergaminate to subcoriaceous; base acute; apex slightly obtuse; petiole 1.5–2 cm. Inflorescences densely flowered. Peduncle 3.5–7 (–9.5) cm; pedicels c. 5 mm; bracts up to 1 mm. Flowers at anthesis 1.5–3 by 1–2.5 mm. Sepals elliptic to orbicular, 1–1.5 by 1–1.5 mm (in fruit enlarging to 1.5–2 by 1.5–2 mm), thickened at base, laterally with a c. 1.5 mm wide hyaline band; fleshy in fruit. Petals orbicular to elliptic, 2–2.5 by 1–1.5 mm (in fruit enlarging to 2.5–3 by 1.5–2 mm), thickened at base, margin narrowly hyaline, chartaceous in fruit. Filaments ultimately up to 15 mm; anthers dorso-ventral. Style up to 2.5 mm. Ovary flattened globose, c. 1.5 by 0.5 mm. Capsule short-ellipsoid, 1.5 (–2) by 0.8 (–1.2) cm, valves ultimately apically 1–2 mm deep bifid; sepal after dehiscence (long-)persistent, adaxially connate with the adjacent ones. Seeds 1–1.3 by 0.3–0.4 cm.

Distr. Thailand; in Malesia: Sumatra, Malay Peninsula, Borneo, Philippines (Luzon, Sulu Is.), and Central Celebes. Perhaps also in New Guinea; see the note under I. reticulata.

Ecot. In primary and secondary forests on granitic sand and on slopes and ridges, 0–800 m.

Field notes. Bole deeply fluted, buttresses gradually merging into the bole. Outer bark smooth, green, red, pale brown, yellowish brown, or black, flaking in small pieces, minutely ridged. Inner bark orange-whitish, yellow, pink, red, or reddish brown, granular, sticky, soft. Wood white or reddish brown. Sapwood white, pinkish white, honey-coloured, yellow, or brown, with distinct lamination. Crown large, spreading, medium dense. Flowers cream to green; calyx green; stamens white. Fruits green to brown.

Vern. Mara jening, meribikang, Sumatra; tinjau laut, Sum. W. Coast; kayurdori bunga, Sum. E. Coast; gerungang, jurung, Malaya; inyang burong, N. Sembilan, Selangor; inggi burong, pinang pinang, Borneo.

**Ixonanthaceae** (Kool)


Treetop or tree up to 40 m, bole up to 1 m diam. Lenticels slit-like or punctiform. Leaf scars round to ovate. Stipules up to 1 mm. Leaves elliptic, elliptic oblong, or slightly ovate, entire, 5.5–14 by 3–10 cm, pertainagraceous to coriaceous; base acute, apex slightly obtuse to emarginate; petiole 1–2.5 cm. Inflorescences lax. Peduncle (3)–5–8(–14) cm; pedicels c. 5 mm, bracts up to 1 mm. Flowers at anthesis 3–5.5 by 2–7 mm. Sepals elliptic, 4–5 by 3–4 mm (in fruit enlarging to c. 8 by 4 mm), within from top to bottom with a slightly thickened and paler band, fleshy to coriaceous in fruit. Petals orbicular to elliptic, 4–5.5 by 3–4 mm (in fruit enlarging to c. 10 by 6 mm), within from the base upwards thickened by a bundle of nerves, margin broadly hyaline, subcoriaceous in fruit. Filaments ultimately up to 2 cm. Style up to 2 cm. Ovary globose, c. 3 by 2 mm. Capsule long-ellipsoid, (2–)3–4(–4.5) cm long, valves not apically bifid; sepal after dehiscence (long) persistent, connate with the adjacent ones. Seeds 1.8–2 by 0.4–0.9 cm.

**Distr.** From Assam through Indochina to S. China (Kuangsi, Kwangtung, Yunnan, Kweichow, Hainan); throughout Malesia (but not in Java and Lesser Sunda Islands, and not yet collected in the Moluccas).

**Ecol.** Primary (rarely secondary) forests, frequently on hillsides and ridges, often on sand and granite, sandstone and kerangas, in swamp and heath forest, largely below 500 m, but occasionally found as high as 1000 m.

**Field notes.** Bole straight and fluted. Buttresses narrow, small. Bark smooth, lengthwise fissured, scaly or cracked, pink, yellowish, brown, fawn, or grey to blackish. Inner bark red, light brown, or dark orange brown, granular, soft. Wood white, dirty white, or dirty yellowish, hard, heavy. Sapwood ochre, with white or yellow lamination, medium hard. Flowers white or greenish. Stamens yellowish-brown. Ovary brown, style green.

**Vern.** Obah, Malay, jinjagong, sansak china, Penang, ugeneran or inggi burong, nyiran burong, pagar anak, sakit hudang, Selangot, angaran buron, Trengganu, djurning, Palembang, sentulu, N. Borneo, langudau, perepat rumah, Sabah, kanju junong, Brunei, redun, S. Sarawak, hura, Celebes, keseruok, New Guinea, Tchid lang.

**Note.** This species is the only one with certainty found in New Guinea. As identification of sterile collections is not possible, such collections from New Guinea are tentatively included in I. reticulata, but might belong in part to I. petiolaris.
The systematic place of the tropical lowland rain-forest tree *Ctenolophon* Oliver has a chequered history.

Originally it was referred to affinity with *Olacaceae* (Oliver, 1873; Masters, 1875; Engler, 1889; Bailon, 1892) or *Icacinaceae* (Beccari, 1877). Hallier f. (1912, 1918) held another view and arranged the genus in the Celastrales, deriving this group from *Linaceae*. Hutchinson (1959, 1973) referred the genus to the Malvales.

In a meticulous exposé of the anatomy, flower and fruit structure, Pierre (1893) concluded that the affinity of *Ctenolophon* is with the *Linaceae* and he was followed by Engler (1907), Exell (1927), and Hub.Winkler (1931).

At present *Ctenolophon* is almost unanimously recognized as belonging to the Linaceous affinity, together with *Ixonanthaceae*. Within *Linaceae* Hub.Winkler (1931) had raised the genus to the rank of a monogeneric subfamily. Later Exell & Mendonça (1951) recognized it as representing a family of its own, a view now almost unanimously accepted, as fully discussed by Van Hooren & Nootboom (1984).

In the treatment of the family *Linaceae* (page 607, see there) the families *Linaceae*, *Ixonanthaceae*, and *Ctenolophonaceae* are opposed by concise diagnoses.

On account of studies of special features some other affinities have been put forward. Heimsch (1942) found a remarkable resemblance in xylem structure with *Humiriaceae*. Cronquist (1981) referred to *Ctenolophon* as an aberrant member of *Hugoniaceae*, a view with which we cannot agree. Van Welzen & Baas (1984) compared the leaf anatomy of *Ctenolophon* with that of *Humiria* and some *Maltiphiaceae* and found that it is very different from both *Humiriaceae* and *Maltiphiaceae*, but also from other *Linaceae*, and they supported the status of a family of its own, adding that close affinities are still unknown.


1. **Ctenolophon**


Trees. Hairs stellately tufted and simple. Stipules interpetiolar, caducous. Leaves entire, opposite, petiolate, simple, pinnately nerved. Inflorescence an axillary or terminal cymid panicale. Bracts present, bracteoles absent. Flowers bisexual, 5-merous, actinomorphic, hypogynous. Sepals basally shortly connate, quincunically imbricate, subequal, indurate, swollen and persistent in fruit, with stellate hair tufts. Petals free, contortate, caducous, often shortly clawed. Disk extrastaminal. Stamens 10, free, inserted halfway the disk, alternately longer and shorter, the longer epipetalous and the shorter epispalous; anthers dorso-versatile, 2-celled, introrse; connective protruding, acute-triangular. Extrastaminal nectary glands absent. Ovary superior, 2-celled; style 1, apically
forked with 2 capitate stigmas; ovules 2 per cell, axile, collateral, pendent, epi-
tropous. Fruit a 1-celled capsule, the woody pericarp finally lengthwise splitting
into 2 valves. Seed 1, persisting after falling of pericarp and pendulous from the
top of a filiform columella; arilloid papillose, surrounding lower half of the
seed. Endosperm copious. Embryo straight.

**Dist**. Two species, one (C. engleriana Milbr.) in West Africa (Angola, Zaire, Nigeria, Gabon) and one
throughout Malesia (but not in Java and Lesser Sunda Islands and not yet reported from Celebes and Molu-
cas, where it is expected to occur). For Malesia see fig. 3.

**Ecol.** Mixed lowland rain-forest.

Vegetative anatomy. Ctenolophon has glabrous leaves, but the young shoots and floral parts have
tufted, stellate hairs. Stomata are anisocytic to anomocytic. Crystals are mainly solitary and rhomboidal,
moresrarely clusters intergrading with druses. Crystalliferous bundle sheath cells have unilateral sclerified
thickenings (cristarque cells). The petiole and midrib have a simple collateral vascular strand.

The wood of Ctenolophon is characterized by solstitial vessels with scalariform perforations, fibres with dis-
tinctly bordered pits, parenchyma which is scanty paratracheal and diffuse-in-aggregates, and heterocellular
1-3-seriate rays.

The above attributes are not very helpful in determining the phylogenetic affinity of this monogenic fam-
ily Ctenolophonaceae. Its stomatal type removes it from the Linaceae complex, but other leaf anatomical char-
acters are of common occurrence throughout the dicotyledons, including the Linaceae. The wood anatomy of
Ctenolophon is very plesiomorphic and cannot therefore be used to support or reject various suggestions
of natural affinity of the genus, although similarities with Humiriaceae have been pointed out by HEIMSCH &
TSCHABOLD (1972) and METCALFE & CHALK (1950).

**References:** HEIMSCH & TSCHABOLD, Boi. Gaz. 133 (1972) 242–253; METCALFE & CHALK, Anatomy of the
453–479. — P. BAAS.

**Palynology.** Pollen of Ctenolophonaceae shows two types: the Ctenolophon englerianus type and the
C. parvifolius type. Pollen grains of both types measure 31–66 μm. The apertural system is zonocolporate
('stephanocolporate'), the number of apertures ranging from 3–8 in the parvifolius type and 5–9 in the engler-
ianus type. Contrary to the rounded subspherical parvifolius type, the englerianus type shows distinct thick-
enings on its mesocolpia and polar areas, making this type characteristically angular and barrel-shaped.

Exine thickness ranges from 3–6 μm. Exine stratification is rather obscure in the light microscope and dif-
ficult to determine, especially in the englerianus type. A thick nexine can mostly be observed. The infratralatal
layer appears labyrinthine, sometimes exhibiting granulate-collumellate structures. The tectum is psilate or
finely perforate in the englerianus type, perforate to foveolate in the parvifolius type (THANIKAIMONI c.s.,
1984).

SAAD (1962) noted striking resemblance with pollen of some Malpighiaceae, which led him to the conclusion
that Ctenolophon may be considered as related to Malpighiaceae. Pollen morphological affinity to Linaceae
and Humiriaceae is regarded as respectively being absent and not close. Here, it is put forward that pollen
of Ctenolophon is neither close to that of Malpighiaceae, as the bipartite nature of wall stratification in both
Ctenolophon and some Malpighiaceae noted by SAAD (I.c.) actually represents only superficial similarity.
Pollen of Ctenolophon cannot be convincingly connected with that of other families, which supports attribu-
tion of family rank to the taxon.

**Fossils.** The distinctness of Ctenolophon pollen is illustrated by its extensive fossil record. Both types can
be easily recognized (MULLER, 1981; THANIKAIMONI c.s., I.c.). The englerianus type (Ctenolophonidites) oc-
curred in Africa nearly uninterrupted from the Upper Cretaceous onwards, and can be linked with the recent
area of distribution of C. englerianus. The type was also present in South America (Paleocene, Eocene) and
India (Eocene, Miocene), but disappeared from those areas in the course of the Tertiary. In recent time the
englerianus type also exists in the Philippines on Samar, in C. parvifolius (THANIKAIMONI c.s., I.c., as C.
philippinensis, PNH 6385). This Samar material is distinct from that of Africa by having mostly less apertures
(5 to 7 versus 5 to 9) and by showing a perforate rather than a psilate or finely perforate tectum. Another
collection from Samar (PNH 6146) shows pollen which seems to be intermediate between PNH 6385 and the
parvifolius type (original observation).

The parvifolius type (Retistephanocolpites) was first recorded from the Paleocene of Africa. In India it oc-
curred in the Paleocene and the Eocene, while it is known from Borneo starting from the Upper Eocene con-
tinuing up to the present (MORLEY, 1977; manuscript comm. MORLEY).
The fossil record of both types clearly demonstrates the relic nature of the present area of distribution of *Ctenolophonaceae*. It points to separation of the two types in the Upper Cretaceous in Africa (Germeraad c.s., 1968: 276). However, the Samar collections may reflect another, much more recent as well as eastward contact between both types. Possibly, the Indian *engleri anus* stock did not become extinct in the Miocene before branching off into the Malesian area. Probably the Indian *parvifolius* stock branched off into Malesia as early as the Eocene, becoming extinct in India at the Eocene-Oligocene transition. Macromorphological difference between recent *C. engleri anus* and *C. parvifolius* is very small. The occurrence of intermediate pollen between the *engleri anus* and the *parvifolius* type is suggestive of introgression between the two species, though independent origin of the *engleri anus* type on Samar cannot be excluded.


Notes: 1. The African species *C. engleri anus* Millbr. is hardly different from the Malesian species, *C. parvifolius*. The only differences observed are the simple cymose panicle and the stamens being up to 15 mm long in *C. engleri anus*, versus the compound cymose panicle and the stamens up to 10 mm in *C. parvifolius*.

2. The fruit and seed structure was wrongly described by Hutchinson and by Hub.Winkler, who said that the seed dangles from a long funicle. The so-called funicle, however, is a filiform columella on which the seed is attached apically.


Tree, 12–40 m, 15–120 cm diam., buttressed. Twigs with distinct leaf-scars and thickened at the insertion of the buds, glabrous. Innovations marginally and apically tufted-hairy, hairs to 1 mm long. Stipules boat-shaped, triangular to ovate, 1.5–2.5 (–3) by 1–1.5 mm; entire, apex rounded to emarginate. Leaves glabrous, narrowly ovate to elliptic, sometimes obovate, often with ± parallel margins, 5–15 by 2–6 cm; base broadly cuneate, sometimes rounded; margin often ± thickened; apex broadly acute to obtusely acuminate, sometimes rounded, acumens to 2.5 cm; nerves 5 (–7)–10 (–12) pairs, slightly curving upwards to near the margin, often meeting in 1 (or 2) looped inframarginal veins; reticulation rather lax to dense; petiole sulcate above, 4–10 (–15) mm. Panicles rather densely flowered, terminal and up to 7 together, or 2–3 in the axil of a leaf near the end of the twigs, sometimes ramiluflous, up to 3 times branched, broadly ovoid to depressed obovoid, 3–9 (–16) cm long. Axes patently tufted hairy, especially above the nodes. Bracts caducous just below the articulation, densely or sparsely appressedly to patently tufted-hairy without, especially on margin and midrib, more or less boat-shaped, narrowly ovate-liguliform to triangular, 1.3–3.5 by 0.5–1.7 mm; base with a row of bristles within. Pedicel articulate, grooved, swollen in fruit, 1.5–2.5 mm. Hypanthium thickened. Sepals appressed, densely appressedly to patently tufted-hairy to the inner 3 marginally) glabrous, glabrous within but inner base with a row of up to 0.8 mm long bristles, boat-shaped, obovate to depressed ovate, ciliate, 1.2–2.5 by 1.5–4.7 mm, the outer two smallest. Petals recurved and more or less twisted in anthesis, stout, thin-leathery, densely appressedly tufted-hairy without except the overlapping margin and the base, glabrous within, slightly asymmetric, narrowly elliptic to narrowly ovate, 7–12 by 2–2.5 mm; claw absent or indistinct, at most 1 by 1 mm; margin sometimes with simple hairs towards its base. Disk membranous or slightly fleshy, cup-shaped, 1–1.5 mm high; margin often more or less dentate to undulate. Stamens inserted halfway up to just below the margin of the disk, short filaments 3.7–6.5 mm, long filaments 4.5–7.5 mm. Petal up halfway the style covered with straight, up to 2 mm long simple hairs; style straight, rather stout, slightly flattened, equaling to up to 3 mm exceeding the long stamens, sometimes as long as the short stamens, 5–10 mm long. Ovary ± constricted at base, ellipsoid to ovoid, 1.5–3 by 1–2 mm. Fruit 1 celled, densely appressedly tufted-hairy, ellipsoid to obovoid, 13–24 by 6–13 mm, sometimes basally curved; pericarp woody, ribbed, smooth inside, consisting of 4 layers, 1.5–2 mm diam. Seed ellipsoid to ovoid, 12–20 by 5–9 mm,
Fig. 1. Ctenolophon parvifolius Oliver. a. Habit, × 0.5; b. innovations, with budscales, stipules and plicate leaves; c. flower, × 3; d. sepal from inside, × 12; e. flower (sepals and petals removed), × 3; f. flower in LS, × 5; g. fruit, × 2; h. seed, × 2 (a from Oliver (1873), b Dumas 1513, c–f SAN 4595, g, h Lambach 1251).
dangling from a filiform columella (10-)15–20 mm long; hilum apical, slightly protruding from testa, obtriangular, 4–7 by 2–2.5 mm; arilloid from slightly above the base up to around the hilum, oblong triangular, up to 5 by 5 mm, with hair-like papillae which are reddish when dry, surrounded by a gelatinous transparent layer. Testa 0.1–0.2 mm thick, outer layer smooth, crustaceous, dark olive-brown to purple black when dry, sometimes fissured, finally covered by a thin membrane; second and third layer reddish-brown, free from the outer wall. Endosperm fleshy, spongy. Embryo stout; cotyledons elliptic to obovate, 8–10.5 by 4.7–5 mm; radicle (1-)2–2.5 mm long.

Dist. Malesia: Sumatra, Malay Peninsula, Borneo, Philippines (Samar, Leyte, Mindanao), and New Guinea (incl. Japen l.). Fig. 3.

Ecol. Mixed primary forest, also in heath and swamp forest, indifferent to soils (litosols, humic podsols, loam, ultrabasic) and also frequent on sand (Banka, Borneo), locally common to sometimes very common in lowland and on hills, generally below 850 m, but in Borneo rarely up to 1650 m. Fl. fr. Feb.–Dec. Fig. 2.

Field notes. Bole up to 35 m; buttresses, if present, up to 4 m high and wide up to 12.5 cm thick. Bark reddish brown to black, often greyish, very variable in appearance, scaly or cracked, often peeling off, hard. Inner bark redbrown to pink, granular or fibrous. Exudate colourless to iodine-coloured, clear, slowly appearing, thick, or absent. Heartwood often reddish or brown, rather hard, heavy, sinks in water. Corolla from white to yellow, orange or
bright red. Style pinkish. Fruit yellow to pink, later brown. Seed brown or glossy black; arillloid white to orange or brilliant vermillion.

Uses. The hard and very durable timber is used for house construction and as general purpose timber (Schneider, 1916; Ridley, 1922; Desch, 1954; Burkhill, 1966).

Vern. Sumatra: bebi kurus, batu, djambu ayer, jinkinai, kaju batu, k. bawang, kalek bung cung, klawar, medang tembatu, petjah pingan; Malay Peninsula: bunga tanjong hutan, kumus beruang, mata ulat, membatu hitam, perichat, Malaya; bant(gikal, bankal paya, kas, Mersing; katu katu, kelabau, Perak; kelat, k. bukit, pompong paya, Pahang, kelat hitam, mertas, Kuala Lumpur, mertas kuning, Kuala Trengganu; jambu paya, Johore; Born: belama’a, tamana’a, Sarawak: liitoh, Iban; besi, obah, Sabah; merandi, W. Kalimantan; jarmgin, kayu batu, latak manuk, E. & SE. Kalimantan. New Guinea: gun, lwr 1.; kodau, kodowu, kotawu, In-gembit L.; mandai, tora, Ormu dial., dnok, nook, Tehid L.; sambir, sosopi, Japen dial.
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