

FLORA MALESIANA

SERIES I - SPERMATOPHYTA

Flowering Plants

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Revisions

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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 cylindrical 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 *Classopollis*, derived from the extinct family of *Cheirolepidaceae*. *Frenelopsis* ranges from Lower to Upper Cretaceous and was widely distributed in North America, Europe and Asia. *Classopollis* 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* (*Zonalapollenites*), *Araucariaceae* (*Araucariacites*), *Cheirolepidaceae* (*Classopollis*), *Cupressaceae* or *Taxodiaceae* (*Inaperturopollenites*) 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 the 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 peneplanation, but STEIN (*l.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 *Austrotaxus* 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 Sunda 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.

References: ANDERSON & MULLER, Rev. Palaeobot. Palynol. 19 (1975) 291–351; FLORIN, Acta Horti Berg. 20(4) (1963) 121–312; HAMILTON, U.S. Geol. Surv. Prof. Pap. 1078 (1979) 1–345; JONGMANS, Meded. Geol. Bur. Mijngedeb Heerlen 1938–1939 (1940) 263–274; JONGMANS & GOTHAN, Jaarb. Mijnwezen in Ned. Indië 1930, Verh. V.59, pt. 2 (1935) 71–201; KHAN, Austr. J. Bot. 24 (1976) 783–791; KRÄUSEL, Verh. Geol. Mijnbouw. Gen. Ned. Kol., Geol. Serie II (1929) 1–44; LACEY in Campbell (ed.), Gondwana Geology, Austr. Nat. Univ. Press (1975) 125–134; MULLER, Blumea 14 (1966) 231–235; Micropaleontology 14 (1968) 1–37; POSTHUMUS, Bull. Jard. Bot. Btzg III, 10 (1929) 374–384; Leiden Geol. Meded. 5 (1931) 485–508; SMILEY, Geol. Soc. of Malaysia, Bull. n. 3 (1970) 77–113; STEIN, Biogeographica 11 (1978) 1–168.

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 polystachyus* 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 relicts 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 ericoides* 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 polystachyus* 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.

Autecology. 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 up-growth 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 towering 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 WHITMORE 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 micropedunculatus* 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: *Altingia 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 Mt 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 ridleyi* 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).

Anatomy. The most important wood anatomical surveys of *Coniferales* are by E.W.J. PHILLIPS, Identification of softwoods, For. Prod. Res. Bull. London 22 (1948, repr. 1966), and by P. GREGUSS, Identification of living Gymnosperms on the basis of xyotomy, Budapest (1955), Xyotomy of the living conifers, Budapest (1972). Additional data for Malesia and adjacent regions can be found in R. KANEHIRA, Identification of Philippine woods by anatomical characters, Taihoku (1924) 231–244; H.H. JANSSONIUS, Mikrographie des Holzes der auf Java vorkommenden Baumarten 6 (1936) 469–494; H. DESCH, Mal. For. Rec. 15 (1954) 630–632; M. KAEISER, Phytomorphology 4 (1954) 39–47; J. VAN DER BURGH, Rev. Palaeobot. Palyn. 15 (1973) 73–275; S. HAYASHI c.s., Micrographic atlas of Southeast Asian timber, Kyoto (1973); T. FURUNO, Res. Rep. Foreign Wood 6, Shimane Univ., Matsue (1977); J.H. FUNDTER & J.H. WISSE, Meded. Landbouwhogeschool Wageningen 77-9 (1977); K. OGATA, Identification of Southeast Asian timbers (in Japanese), Jap. Ass. Wood Technology (1985).

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 KAEISER, *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. NAPP-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 ranalean 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 harmomegathic 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-tectate 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 (orbicules), 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 sacci 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 sacci than in *Pinaceae*. Pollen grains of *Dacrycarpus* are provided with 3 sacci, those of *Nageia*, *Podocarpus*, and *Prumnopitys* with 2. *Phyllocladus* and *Falcatifolium* pollen also have 2 sacci, 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 sacci (*Acmopyle*, *Parasitaxus*) or 3 sacci (*Microcachrys*, *Pherosphaera*). In the latter two genera and in *Dacrycarpus* sometimes grains occur which have 4, 5 or 6 sacci 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)

5–44, illus., (1965) 9–82, text; POCKNALL, New Zeal. J. Bot. 19 (1981) 67–95, 259–266, 267–272; SIVAK, Pollen et Spores 17 (1975) 349–421; STAPLIN c.s., Rev. Palaeobot. Palyn. 3 (1976) 297–310; TENGNÉR, Bot. Notis. 118 (1965) 450–452; VAN CAMPO, C. R. Acad. Sc. Paris 272 (1971) 2071–2074; WALKER, The evolutionary significance of the exine, Linn. Soc. Symp. Ser. I (1976) 251–308; WEND, J. Inst. Polyt. Osaka City Univ. II (1960) 109–136; WODEHOUSE, Pollen grains (1935). — R.W.J.M. VAN DER HAM.

Phytochemistry & Chemotaxonomy. Chemical characters of *Coniferales* were summarized twice in 'Chemotaxonomie der Pflanzen' (HEGNAUER, 1962, vol. 1: 293–440, 478–482; 1986, vol. 7: 462–554, 801–802). Here rather extensive bibliographies can be found for all families of *Gymnospermae*, *Cycadopsida*, *Coniferopsida*, *Taxopsida* and *Chlamydospermae*.

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 C₁₈- and C₂₀-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 diterpenic acids predominate. Colophony or rosin 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 ellagitannins 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, oleanane 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 phytoecdysones 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-, cupressuflavone-, 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 bisnorditerpenoid lactones such as nagilactone, and accumulation of large amounts of phytoecdysones such as the maki-strones and the podedcdysones 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 diaspores: red to pink fleshy parts of *Dacrydium*, *Phyllocladus*, and *Podocarpus* diaspores 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-O-methylrhamnose) as building stones. Acofriose is also present in mucilages of *Cycadaceae*.

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. Pinosylvin 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-glycoflavones 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. I, 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 Malaya for ornamental purpose. Finally *Pinus merkusii* is widely used for reforestation 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 of 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 Malesian 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 wing(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**

ARTIFICIAL KEY TO THE FAMILIES
based on vegetative characters

1. Leaves spirally attached, sometimes distichous.
2. Leaves (needles) in bundles of 2-3 with a basal sheath (*Pinus*) **Pinaceae**
2. Leaves not in bundles with a basal sheath.
3. Leaves needle-like or scale-like.
4. Leaves scale-like (*Dacrycarpus*, *Dacrydium*) **Podocarpaceae**
4. Leaves needle-like, triangular or quadrangular in cross-section.
5. Tree with a very dominant primary trunk with regularly placed whorls of lateral branches. Seeds dry, in large bracteate cones (*Araucaria cunninghamii*) **Araucariaceae**
5. Tree quite irregularly branched. Seeds few, in reduced cones (*Dacrycarpus*, *Dacrydium*, *Falcatifolium*)
Podocarpaceae
3. Leaves distinctly flattened and often broad.
6. Leaves bifacially flattened, linear, less than 2.5 mm wide, with a basal constriction (*Taxus*) **Taxaceae**
6. Leaves if linear either bilaterally flattened, or more than 2.5 mm wide, or without a basal constriction (*Dacrycarpus*, *Falcatifolium*, *Phyllocladus*, *Podocarpus*, *Prumnopitys*) **Podocarpaceae**
1. Leaves decussate, often distichous.
7. Leaves scale-like (*Libocedrus*) **Cupressaceae**
7. Leaves broad and many-veined.
8. Leaves sessile, clasping, lanceate from a broad base (*Araucaria hunsteinii*) **Araucariaceae**
8. Leaves broad, not with a stem-clasping base.
9. Terminal bud hemispherical (*Agathis*) **Araucariaceae**
9. Terminal bud acute (*Nageia*) **Podocarpaceae**

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 Malesia) 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

LINNÉ, Gen. Pl. ed. 5 (1754) 462; Sp. Pl. 2 (1753) 1040; PILGER, Pfl. R. IV, 5, Heft 18 (1903) 110; in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 208; FLORIN, Acta Horti Berg. 14 (1948) 378; GAUSSEN, Gymn. Act. & Foss. fasc. 15, ch. 25 (1979) 2. — Fig. 2, 3.

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 stomata-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

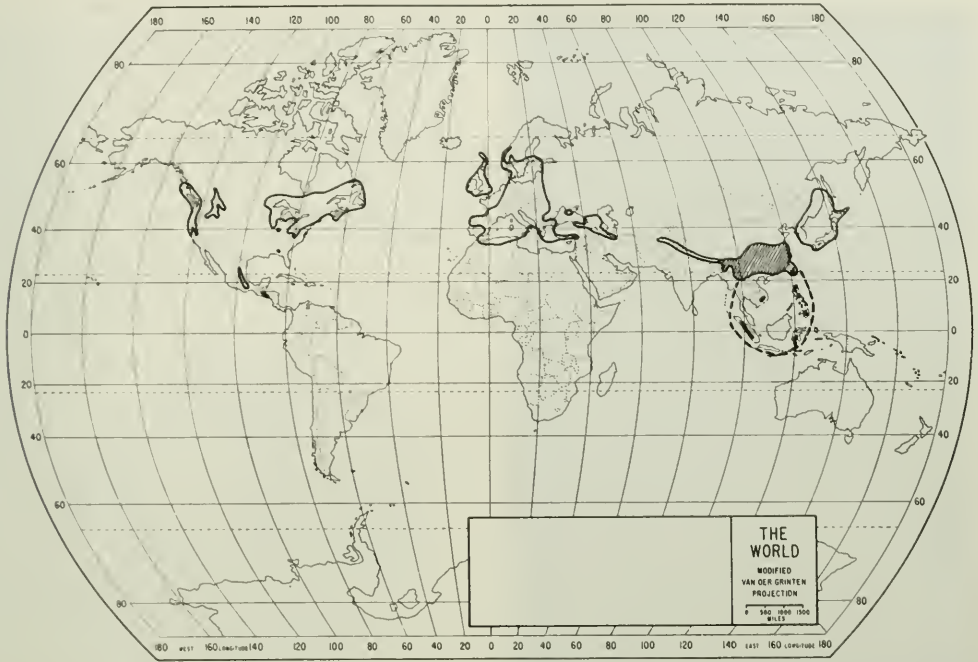


Fig. 1. Range of the genus *Taxus* L. (solid line) and *T. sumatrana* (MIQ.) DE LAUB. (broken line and hatched).

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.

Seedling 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.

Taxonomy. 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 woodwork such as chests and coffins. It is also desirable for fence posts, flooring, and mallois. The well-marked reddish brown heartwood contrasts pleasingly with the pale yellowish sapwood.

1. *Taxus sumatrana* (MIQ.) DE LAUB. Kalikasan 7 (1978) 151. — *Cephalotaxus sumatrana* MIQ. Fl. Ind. Bat. 2 (1859) 1076. — *Podocarpus celebicus* HEMS. Kew Bull. (1896) 39. — *Cephalotaxus celebica* WARR. Monsonia 1 (1900) 194. — *Cephalotaxus manni* (non HOOK.f.) PRITZEL ex DIELS, Bot. Jahrb. 29 (1900) 214; WILSON, J. Arn. Arb. 7 (1926) 40. — *T. baccata* (non L.) MASTERS, J. Linn. Soc. Bot. 26 (1902) 546, p.p. — *T. baccata* ssp. *cuspidata* var. *chi-*

ensis PILGER, Pfl. R. IV, 5, Heft 18 (1903) 112; in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 210. — *T. baccata* ssp. *wallichiana* (non ZUCC.) PILGER, Pfl. R. IV, 5, Heft 18 (1903) 112; BÜNNEMEIER, Trop. Natur 10 (1921) 55, f. 8; STEEN, Bull. Jard. Bot. Bitz III, 13 (1934) 194; STEUP, Trop. Natur Jub. no. (1936) 41, f. 1. — *T. baccata* var. *sinensis* HENRY in Elwes & Henry, Trees Gr. Brit. & Irel. 1 (1906) 100. — *T. wallichiana* (non ZUCC.) Foxw. Philip. J. Sc.



Fig. 2. *Taxus sumatrana* (MIQ.) DE LAUB. on the peak of Mt Bonthain, Celebes, 1700 m alt. (Photogr. J. VAN ZIJLL DE JONG, 1933).

6 (1911) Bot. 166; MERR. En. Philip. Fl. Pl. 1 (1923) 5; YAMAMOTO, J. Soc. Trop. Agric. 10 (1938) 182, f. 42. — *Tsuga mairei* LEMÉE & LÉVEILLÉ, Le Monde des Plantes, année 16 (2me sér.) n. 88 (May 1914) 20; Bull. Acad. Int. Geog. Bot. 16 (1914) 20. — *T. cuspidata* var. *chinensis* (PILGER) REHDER & WILSON in Sargent, Pl. Wils. 2 (1914) 8, *p.p.* — *T. cuspidata* (non SIEB. & SUCC.) KANEH. FORMOS. Trees (1917) 616. — *T. chinensis* (PILGER) REHDER, J. Arn. Arb. 1 (1919) 51; *ibid.* 4 (1923) 119; DALLIMORE & JACKSON, Handb. Conif. (1923) 71; WILSON, J. Arn. Arb. 7 (1926) 41; *ibid.* 8 (1927) 88; HAND.-MAZZ. Symb. Sin. 7 (1929) 2; HU & CHUN, Icon. Pl. Sin. 2, 8 (1929) pl. 53; BEAN, Trees & Shrubs Brit. Is. 3 (1933) 476; ORR, Not. R. Bot. Gard. Edinb. 18 (1933) 124; *ibid.* 19 (1937) 261; KANEH. Formos. Trees rev. ed. (1936) 31; REHDER, Man. Cult. Trees & Shrubs 2 (1940) 3; METCALF, Fl. Fukien 1 (1942) 23; FANG, Icon. Pl. Omeiens. 11, 2 (1946) t. 190; LAW, Bot. Bull. Acad. Sin. 1, 2 (1947) 143. — *T. wallichiana* var. *chinensis* (PILGER) FLORIN, Acta Horti Berg. 14 (1948) 378, pl. 5; GAUSSEN, Gymn. Act. & Foss. fasc. 15, ch. 25

(1979) 16. — *T. speciosa* FLORIN, Acta Horti Berg. 14 (1948) 382, pl. 6; LI & KENG, Taiwania 1 (1954) 29, pl. 2. — *T. mairei* (LEMÉE & LÉVEILLÉ) HU & LIU, Illus. Nat. & Introd. Lign. Pl. Taiwan 1 (1960) 16; GAUSSEN, Gymn. Act. & Foss. fasc. 15, ch. 25 (1979) 16, f. 858. — *T. celebica* (WALL.) LI, Woody Fl. Taiwan (1963) 34; HARRISON, Handb. Conif. & Ginkgo (1967) 598. — *T. yunnanensis* CHENG, CHENG & FU, Acta Phytotax. Sin. 13 (4) (1975) 86. — Fig. 2, 3.



Fig. 3. *Taxus sumatrana* (MIQ.) DE LAUB. Habit, female, with fruit, $\times 1$ (DE LAUBENFELS P668).

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 tadji*, 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 be-

yond 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.*) *Acropyle* 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 preglacial expansion of the genus. REYMANOWNA (1975) recently recognized *Dacrydium* and *Stachycarpus* (*Prumnopiys*) 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, *Saxegothaea*, 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).

References: COUPER, Proc. R. Soc. Lond. ser. B, 152 (1960) 491–500, maps; FERGUSON, Palaeogeogr., Palaeoclimatol., Palaeoecol. 3 (1967) 73–110; FLORIN, Acta Horti Berg. 20 (4) (1963) 121–312, 68 maps; REYMANOWNA, XIIth Intern. Bot. Congr., Leningrad; Abstracts (1975) 99.

Ecology. Mostly trees of moist forests at all elevations and well into the middle latitudes both as major canopy trees and as understory 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 mycorrhizae and that nitrogen fixation did not occur. BECKING (Ann. Inst. Pasteur. 111, 1966, 295) indicated that the mycorrhizae 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 no doubt to dispersal by birds or fruit bats which eat the fleshy fruit. Co-ordination 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 variously 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 fungus in the family *Coryneliales*, in Malesia recorded for *Podocarpus crassigemis*. 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 *Dacrydium* 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 archaegonium 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 archaegonium 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. GAUSSEN (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 and *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 trees in this family 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, uninerved 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 leafy) 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

L.C. RICH. *ex* MIRBEL, Mém. Mus. Hist. Nat. Paris 13 (1825) 76, *nom. cons.*;
 L.C. & A. RICH. *Comm. Bot. Conif. & Cycad.* (1826) 129, t. 3, f. 12; L.C. RICH.
Ann. Sci. Nat. V, 20 (1874) 37; PILGER, *Pfl. R.* IV, 5, Heft 18 (1903) 94, f. 18;
Bot. Jahrb. 54 (1916) 33; in *E. & P. Nat. Pfl. Fam.* ed. 2, 13 (1926) 249; DE
 LAUB. *J. Arn. Arb.* 50 (1969) 277; GAUSSEN, *Gymn. Act. & Foss.* fasc. 13, ch.
 20 (1974) 13, f. 675-9, map (f. 679bis); KENG, *Ann. Bot. n.s.* 26 (1962) 69, 14
 fig.; *Gard. Bull. Sing.* 20 (1963) 123, 127; *Ann. Bot.* 38 (1974) 757; *Taxon* 24
 (1975) 289; *Pl. Syst. Ecol., Suppl.* 1 (1977) 235; *J. Arn. Arb.* 59 (1978) 249, 43

fig., 4 maps; VAN ROYEN, *Alpine Fl. New Guinea* 2 (1979) 8. — *Podocarpus* LABILL. *Nov. Holl. Pl. Sp.* 2 (1806) 71, t. 221, *non* L'HÉRIT. *ex* PERS. (1807). — *Brownetera* L.C. RICH. *Ann. Mus. Hist. Nat. Paris* 16 (1810) 299, *nom. nud.* — *Thalamia* SPR. *Anl. Kennt. Gewächse* ed. 2, 2 (1817) 218. — **Fig. 6–8.**

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 'phylloclades' 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 (COUPER, *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.* III, 19, n. 2, 1940, 75, map 4; *Acta Horti Berg.* 20 (4), 1963, 184, t. 17: map).

Ecol. 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).



Fig. 7. *Phyllocladus hypophyllus* Hook.f. a. Female shoot, $\times 0.5$; b. ditto, $\times 0.5$; c. ditto, $\times 2.5$; d. cladode with immature female seed cones, $\times 1.5$; e. seeds with bracts and epimatium, $\times 3$; f. seed with epimatium, $\times 3$ (a SAN 69968, b-f BELLAMY 1404).

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.

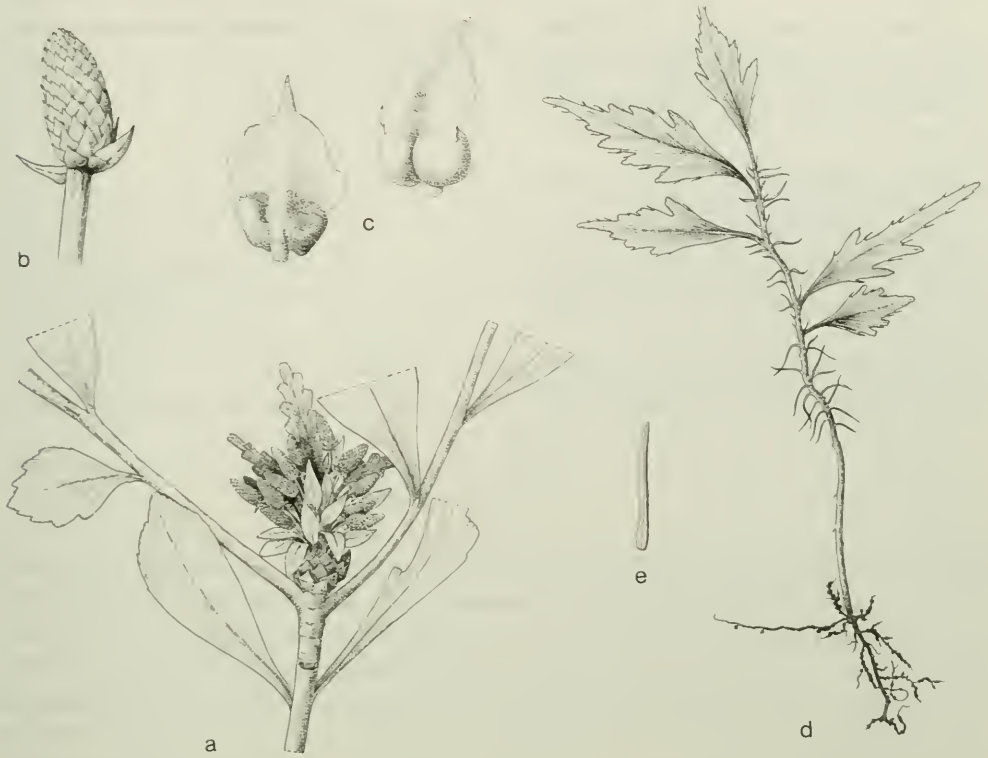


Fig. 8. *Phyllocladus hypophyllus* Hook.f. a. Male shoot, $\times 1$; b. male cone, $\times 3$; c. microsporophylls (two views), $\times 6$; d. old seedling, $\times 0.75$; e. seedling leaf, $\times 3$ (a-c DE LAUBENFELS P 636, d-e DE LAUBENFELS P645).

1. *Phyllocladus hypophyllus* Hook.f. Icon. Pl. n.s. 5 (1852) t. 889; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 372; PARL. in DC. Prod. 16, 2 (1868) 499; STAPF, Trans. Linn. Soc. Bot. 4 (1894) 249; WARB. Monsunia 1 (1900) 194, incl. var. *protracta* WARB.; PILGER, Pfl. R. IV, 5, Heft 18 (1903) 99; GIBBS, Contr. Phytogeogr. Arfak Mts (1917) 82; LANE-POOLE, For. Res. Papua & New Guinea (1925) 74; KENG, Gard. Bull. Sing. 20 (1963) 123, fig.; Ann. Bot. n.s. 27 (1963) 69, 14 figs., t. 1; DE LAUB. J. Arn. Arb. 50 (1969) 278, map 1; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 19 (1974) 17, f. 677 p.p., f. 678; KENG, J. Arn. Arb. 59 (1978) 267, map 3; VAN ROYEN, Alpine Fl. New Guinea 2 (1979) 9, f. 34. — *P. protractus* (WARB.) PILGER, Pfl. R. IV, 5, Heft 18 (1903) 99; FOXW. Philip J. Sc. 6 (1911) Bot. 165, t. 31; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 19 (1974) 17, f. 679. — *P. major* PILGER, Bot. Jahrb. 54 (1916) 211; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 19 (1974) 16, f. 677 p.p. — Fig. 6-8.

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 c.

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.

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

Ecol. 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).

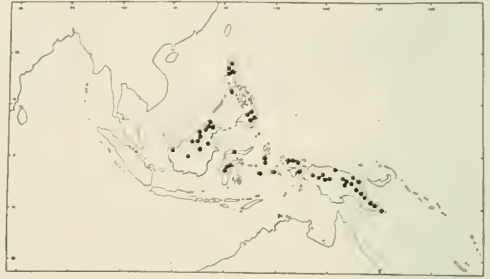


Fig. 9. Range of *Phyllocladus hypophyllus* Hook.f.

2. DACRYDIUM

SOLANDER *ex* FORST.f. *De Pl. Escul. Ins. Ocean. Austr. Comm. Bot.* (1786) 80; *Fl. Ins. Austr. Prod.* (1786) 92; *ex* LAMBERT, *Gen. Pinus* ed. 1 (1807) App. 93, t. 41; RICH. *Comm. Bot. Conif. & Cycad.* (1826) 127; ENDL. *Syn. Conif.* (1847) 224; HENKEL & HOCHSTETTER, *Synop. Nadelhölz.* (1865) 405; PARL. in DC. *Prod.* 16, 2 (1868) 493; BENTH. & HOOK.f. *Gen. Pl.* 3 (1880) 433; EICHLER in E. & P. *Nat. Pfl. Fam.* 2, 1 (1889) 106; PILGER, *Pfl. R. IV*, 5, Heft 18 (1903) 43, f. 4–6; in E. & P. *Nat. Pfl. Fam.* ed. 2, 13 (1926) 239; FLORIN, *Kongl. Svensk. Vet. Ak. Handl.* 10 (1931) 248, f. 71; CORNER, *Gard. Bull. S. S.* 10 (1939) 239, t. 5–10; DE LAUB. *J. Arn. Arb.* 50 (1969) 282, f. 1–5; *Fl. Nouv. Caléd. et Dép.* 4 (1972) 17; GAUSSEN, *Gymn. Act. & Foss.* fasc. 13, ch. 20 (1974) 11, f. 681–697, t. 85–87; VAN ROYEN, *Alpine Fl. New Guinea* 2 (1979) 33; QUINN, *Austr. J. Bot.* 30 (1982) 311. — *Lepidothamnus* PHIL. *Linnaea* 30 (1860) 730; QUINN, *Austr. J. Bot.* 30 (1982) 316, f. 7–8. — *Lagarostrobos* QUINN, *Austr. J. Bot.* 30 (1982) 316, f. 5–6. — **Fig. 14, 18, 19.**

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 foliage 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 axils 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 Australasian 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



Fig. 10. Range of the genus *Dacrydium* SOLANDER *ex* FORST.*f.* Figures above the hyphen indicate the number of endemic species, that below the hyphen the total number of species.

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

1. *Dacrydium elatum* (ROXB.) WALL. ex HOOK. London J. Bot. 2 (1843) 144, t. 2; ENDL. Syn. Conif. (1847) 226; BLUME, Rumphia 3 (1849) 221, t. 172B, f. 1 & 172C, f. 2; MIQ. Fl. Ind. Bat. 2 (1859) 1075; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 406; DE BOER, Conif. Arch. Ind. (1866) 29; PARL. in DC. Prod. 16, 2 (1868) 494; HOOK.f. Fl. Br. India 5 (1896) 648; RENDLE, J. Bot. 34 (1896) 355; PILGER, Pfl. R. IV, 5, Heft 18 (1903) 51; RIDLEY, J. Str. Br. R. As. Soc. n. 60 (1911) 55; Fl. Mal. Pen. 5 (1925) 279, f. 227; BURKILL & HOLTUM, Gard. Bull. S. S. 3 (1923) 75; CORNER, Gard. Bull. S. S. 10 (1939) 240, t. 5; Wayside Trees (1940) 721, t. 223–224; DE LAUB. J. Arn. Arb. 50 (1969) 285; KENG in Whitmore, Tree Fl. Mal. 1 (1972) 46, f. 1d; PHENGKLAI, Thai For. Bull. 7 (1973) 9, f. 5; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 48, f. 692, t. 86. — *Juniperus elata* ROXB. Fl. Ind. 3 (1832) 838. — *D. junghuhnii* MIQ. Pl. Jungh. 1 (1851) 4; Fl. Ind. Bat. 2 (1859) 1075. — *D. pierrii* HICKEL, Bull. Soc. Dendr. France 76 (1930) 74; Fl. Gén. I.-C. 5 (1931) 1070, f. 123, 2–4; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 46, f. 691, t. 87. — *D. beccarii* var. *subelatum* CORNER, Gard. Bull. S. S. 10 (1939) 243, t. 7; DE LAUB. J. Arn. Arb. 50 (1969) 303; KENG in Whitmore, Tree Fl. Mal. 1 (1972) 46, f. 1c.

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 billowy 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.

Distr. 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.

Vern. Ru, M (properly the common name for



Fig. 11. Range of *Dacrydium elatum* (ROXB.) WALL. ex HOOK. (dots) and *D. novo-guineense* GIBBS. (triangles).

Gymnostoma (Casuarinaceae); Borneo: *ouk*, Kayan, *sempilor*, Merurong 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.

2. *Dacrydium novo-guineense* GIBBS, Contr. Phytogeogr. Arfak Mts (1917) 78, f. 3; DE LAUB. J. Arn. Arb. 50 (1969) 286; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 44, f. 693.

Tree, 1.5–29 m tall, up to 50 cm diam., with ascending branches and numerous branchlets producing a dense rounded crown. *Juvenile leaves* up to at least 1 cm long, lanceolate, acute, spreading but curved so that the apex normally turns slightly inward towards the shoot, often shorter at the base of the shoot and on main axes, strongly keeled on the back, 0.2 mm thick and 0.4–0.7 mm wide, giving way abruptly to short transitional scales on plants about half a metre high, sometimes twisted to the side giving a spiral effect to the shoot. *Transitional leaves*, if present, up to c. 2 mm long and spreading slightly. *Adult shoots* cord-like, 1–2 mm diam. *Adult scale-leaves* strongly keeled on the back, acute, imbricate, 0.8–1.7 mm long and 0.4–1 mm wide. *Fertile structures* terminal, usually on short or very short lateral shoots. *Pollen cones* 5–8 mm long and 1.5 mm diam., apex of the microsporophyll less than

1 mm long. *Seed-bearing structure* formed of elongated bracts, the longest towards the apex 3 by 0.5 mm. *Seed* 5 mm long and dark brown.

DISTR. *Malesia*: Central & SE. Celebes, Moluccas (Buru, Obi), and throughout New Guinea. Fig. 11.

ECOL. Along mossy crests and in open areas from 700 to 3000 m, but mostly between 1500 and 2200 m. Rising above the mid mountain canopy or a common small tree at higher elevations rising above ferns and other scrub often after fire, sometimes dominant. On different soil types: clay, stony sand, quartzite, even peat. Very common in New Guinea.

VERN. New Guinea: *kaowié*, *kowié*, Arfak, Manikiong lang., *aru*, Wissel Lakes, Kapauko lang., *munump*, Nondugl, Minj.

NOTE. Other scale-leaved species of *Dacrydium* occur in the Antarctic forests of Tasmania, New Zealand, and Chile. *Dacrydium novo-guineense* is a tropical highland tree while, among the scale-leaved group in *Dacrydium*, only *D. elatum* occurs in tropical lowlands.

3. *Dacrydium pectinatum* DE LAUB. J. Arn. Arb. 50 (1969) 289, f. 1b–2; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 42, f. 689; DE LAUB. Kalikasan 7 (1978) 121. — *D. pectinatum* var. *robustum* DE LAUB. J. Arn. Arb. 50 (1969) 291, f. 1c.

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.

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

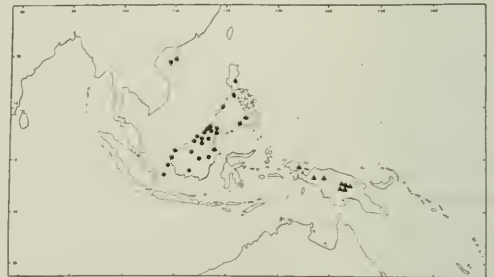


Fig. 12. Range of *Dacrydium pectinatum* DE LAUB. (dots) and *D. cornwalliana* DE LAUB. (triangles).

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 kerangas in heath forest, frequently associated with *Gymnostoma*; in Sabah also on ultrabasic soils. In Kayangeran For. Res. (Brunei) reported to occur in pure stands in the centre of peat swamps.

Vern. *Mélo*, 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.

4. *Dacrydium nidulum* DE LAUB. J. Arn. Arb. 50 (1969) 292, f. 3a; GAUSSEN, *Gymn. Act. & Foss.* fasc. 13, ch. 20 (1974) 42, f. 688.

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 epimatium 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 (Halmheira) 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.

Vern. New Guinea: *chawènum*, *kasuari*, *kwen-num*, Arfak, Maibrat lang., *tjikwal*, Hattam lang., *jammari*, Wandammen, *samiampi*, Japen, Roberbai dial., *kun*, Eipomek valley, Irian, *ibaro*, Upper Waria, *binban*, Oriomo, *nidjon*, Kebar valley, *nipaj*, Karoon lang., Arfak, *uier*, west of Hollandia, Itik lang.

Note. There is some variation between the different widely distributed populations. In the Cycloop

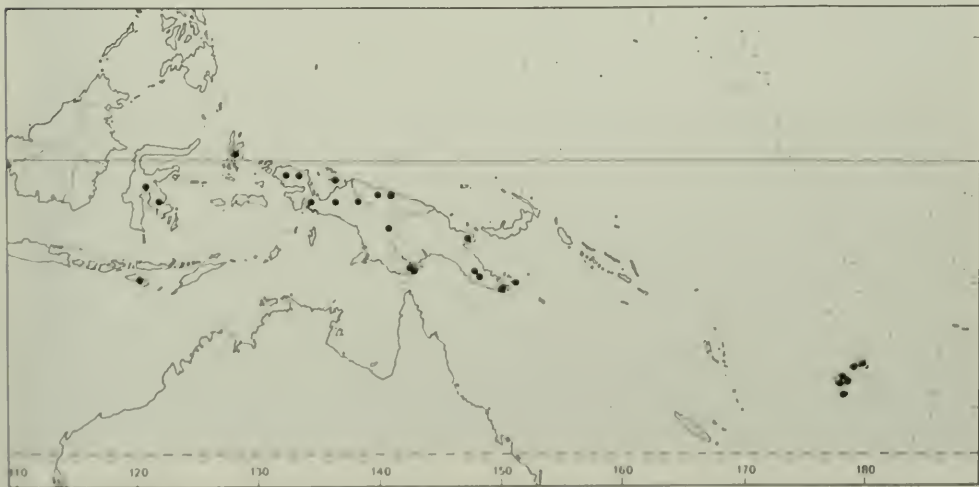


Fig. 13. Range of *Dacrydium nidulum* DE LAUB.

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.

5. *Dacrydium cornwalliana* DE LAUB., *nov. sp.* — *D. nidulum* var. *araucarioides* DE LAUB. J. Arn. Arb. 50 (1969) 295, f. 36. — **Fig. 14.**

Arbor ad 30 m alta. Folia conferta, apicium tangentum 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.

6. *Dacrydium beccarii* PARL. in DC. Prod. 16, 2 (1868) 494; PILGER, Pfl. R. IV, 5, Heft 18 (1903) 52; RIDLEY, J. Str. Br. R. As. Soc. n. 60 (1911) 56; BURKILL & HOLTUM, Gard. Bull. S. S. 3 (1923) 75; RIDLEY, Fl. Mal. Pen. 5 (1925) 280; CORNER, Gard. Bull. S. S. 10 (1939) 241, t. 6; Wayside Trees (1940) 720; DE LAUB. J. Arn. Arb. 50 (1969) 300; KENG in Whitmore, Tree Fl. Mal. 1 (1972) 46, f. 1a; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 38, f. 682 *p.p.*; VAN ROYEN, Alpine Fl. New Guinea 2 (1979) 34.

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



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. Normanby I. & New Britain), the Moluccas (Taliabu), Philippines (Mindanao; Negros; Biliran I.) and (mainly W.) Borneo to Malaya 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.

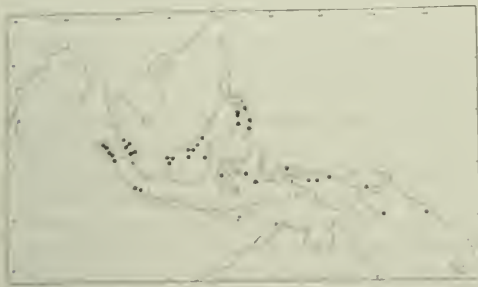


Fig. 15. Range of *Dacrydium beccarii* PARI.

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.

Vern. New Guinea: *netukuria*, New Britain, *me-joop*, Kebar valley; Taliabu: *kawau*; Borneo: *kayu embun*, Merurong Plateau, *sempilor*, Sarawak, Bintulu; Malaya: *ekor kuda*, Kedah; Sumatra: *sampmur tali*, Tapanuli.

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 diametri. Apices microsporophyllorum lanceolati, 0.5–1 mm longi, c. 0.3 mm lati. Semina matura 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 to 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.

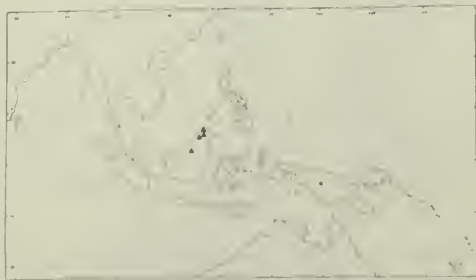


Fig. 16. Range of *Dacrydium gracilis* DE LAUB. (triangles) and *D. spathoides* DE LAUB. (dot).

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*.

8. *Dacrydium medium* DE LAUB. *Blumea* 23 (1976) 98.

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.

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



Fig. 17. Range of *Dacrydium medium* DE LAUB. (dots) and *D. magnum* 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.

9. *Dacrydium magnum* DE LAUB. *J. Arn. Arb.* 50 (1969) 299, f. 4a; GAUSSEN, *Gymn. Act. & Foss. fasc.* 13, ch. 20 (1974) 36, f. 681 *p.p.* — *D. beccarii* var.

rudens DE LAUB. *J. Arn. Arb.* 50 (1969) 303, f. 4b; GAUSSEN, *Gymn. Act. & Foss. fasc.* 13, ch. 20 (1974) 38, f. 682 *p.p.*

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.

Distr. Solomon Islands (Guadalcanal, Choiseul, S. Ysabel); in *Malesia*: Louisiades (Sudest I.) and Moluccas (Obi I.). Rare. Fig. 17.

Ecol. Locally common in the canopy of moist tropical forest between 60 and 1200 m, often along long 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.

10. *Dacrydium spathoides* DE LAUB. *J. Arn. Arb.* 50 (1969) 299, f. 3c; GAUSSEN, *Gymn. Act. & Foss. fasc.* 13, ch. 20 (1974) 44, f. 690.

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.

Distr. *Malesia*: Eastern West Irian. Fig. 16.

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

11. *Dacrydium gibbsiae* STAPP, J. Linn. Soc. Bot. 42 (1914) 192, t. 4; DE LAUB. J. Arn. Arb. 50 (1969) 306; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 34, f. 681 *p.p.* — *D. beccarii* var. *kinabaluense* CORNER, Gard. Bull. S. S. 10 (1939) 244, t. 9. — *D. sp.* STAPP, Trans. Linn. Soc. II, 4 (1894) 248.

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 on ultrabasic soils in the mountain mossy forest from 1500–3600 m.

12. *Dacrydium xanthandrum* PILGER, Bot. Jahrb. 69 (1938) 252; DE LAUB. J. Arn. Arb. 50 (1969) 304, f. 5; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 34, f. 683. — Fig. 18, 19.

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.



Fig. 18. *Dacrydium xanthandrum* PILGER. a. Female shoot with seed-bearing structure, $\times 1.5$; b. portion of twig, $\times 6$; c. seed-bearing structures and seed, $\times 1.5$ (after KOCHUMMEN FR1 29472).



Fig. 19. *Dacrydium xanthandrum* PILGER. a. Male shoot with pollen cone, $\times 0.5$; b. pollen cone, $\times 6$; c. microsporophylls, $\times 1.5$; d. juvenile shoot with leaves, $\times 1.5$; e. leaf in cross section, $\times 15$ (a–c S 37067; d–e DE LAUBENFELS P627).

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



Fig. 20. Range of *Dacrydium xanthandrum* PILGER.

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.

13. *Dacrydium comosum* CORNER, Gard. Bull. S. S. 10 (1939) 244, t. 10; Wayside Trees (1940) 721; DE LAUB. J. Arn. Arb. 50 (1969) 307; KENG in Whitmore, Tree Fl. Mal. 1 (1972) 46, f. 1b; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 36, f. 684.

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 \pm 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.

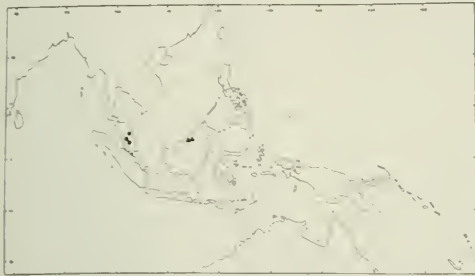


Fig. 21. Range of *Dacrydium comosum* CORNER (dots) and *D. ericoides* DE LAUB. (triangles).

14. *Dacrydium ericoides* DE LAUB., nov. sp.

Arbor ad 17 m alta. Folia linearia recta, paginis superioris 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 calcaria 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 perpendicular 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.

Distr. *Malesia*: Borneo (Sarawak, known only from Mt Dulit 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. *Sempilor*, 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.

15. *Dacrydium leptophyllum* (WASSCHER) DE LAUB., nov. comb. — *Podocarpus leptophylla* WASSCHER, Blumea 4 (1941) 414, t. 4, f. 9. — *Dacrycarpus leptophylla* (WASSCHER) GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 150.

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.

Distr. *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

DE LAUB. J. Arn. Arb. 50 (1969) 308; Fl. Nouv. Caléd. et Dép. 4 (1972) 30; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 67. — Fig. 22.

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 epimatium 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 epimatium 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 I.), 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 epimatium 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***
2. Adult leaves mostly lanceolate, sun leaves 13–20 mm long, glaucous; pollen cone 1.5–3 mm diam. **2. *F. gruezoii***
1. Adult leaves often not bent forward at the apex, the sides parallel for most of their length; pollen cones no more than 13 mm long.
3. Adult leaves weakly keeled if at all, 2–3.5 mm wide, 12–20 mm long **3. *F. papuanum***
3. Adult leaves distinctly keeled on their broader surfaces, 1–2.5 mm wide, 18–35 mm long **4. *F. angustum***

1. *Falcatifolium falciforme* (PARL.) DE LAUB. J. Arn. Arb. 50 (1969) 309; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 73. — *Podocarpus falciformis* PARL. in DC. Prod. 16, 2 (1868) 685. — *Nageia falciformis* (PARL.) O.K. Rev. Gen. Pl. 2 (1891) 800. — *Dacrydium falciforme* (PARL.) PILGER, Pfl. R. IV, 5, Heft 18 (1903) 45; FOXW. Philip. J. Sc. 6 (1911) Bot. 153; RIDLEY, J. Str. Br. R. As. Soc. n. 60 (1911) 56; PILGER, Bot. Jahrb. 54 (1916) 35; STAPP, J. Linn. Soc. Bot. 42 (1914) 191, f. 8; BURKILL & HOLTUM, Gard. Bull. S. S. 3 (1923) 76; RIDLEY, Fl. Mal. Pen. 5 (1925) 280; CORNER, Wayside Trees (1940) 722; KENG in Whitmore, Tree Fl. Mal. 1 (1972) 46, f. 2. — Fig. 22.

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, midribs 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 to 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



Fig. 22. *Falcatifolium falciforme* (PARL.) DE LAUB. Twig with male cone, $\times 1$ (after WYATT-SMITH KEP 93115).

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, Merurong 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.

It is called a 'young tree' but given as 24 m tall. This may well be a new species.

2. *Falcatifolium gruezoii* DE LAUB., nov. sp. — *Dacrydium falciforme* [non (PARL.) PILGER] FOXW. ex MERR. Philip J. Sc. 2 (1907) Bot. 257; FOXW. *ibid.* 6 (1911) Bot. 153, 1. 28, f. 1; MERR. En. Philip. 1 (1922) 4.

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 feminei 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.

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



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

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*.

3. *Falcatifolium papuanum* DE LAUB. J. Arb. 50 (1969) 312, f. 6; Blumea 17 (1969) 274; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 73, f. 698. — *Dacrydium falciforme* [non (PARL.) PILGER] LAUT. Bot. Jahrb. 68 (1937) 247.

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., *Myrtaceae* and other *Podocarpaceae*, 1500–2400 m.

Vern. *Mungag*, 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.

4. *Falcatifolium angustum* DE LAUB. J. Arn. Arb. 50 (1969) 312, f. 7a; GAUSSEN, *Gymn. Act. & Foss.* fasc. 13, ch. 20 (1974) 73, f. 699.

Tree to 20 m tall, 6–25 cm diam. *Juvenile leaves* narrowly lanceolate and gradually curved slightly forward towards the apex, c. 7 cm long and 1.2 mm near the base. *Adult leaves* less curved or straight, pungent, keeled on each side, 18–35 by 1–2.5 mm. Somewhat immature *pollen cones* 8 mm long and 2 mm diam. Seed-bearing structures unknown.

Distr. *Malesia*: Borneo (known from two locations near the coast of Sarawak). Fig. 23.

Ecol. In forests, 90–240 m, on podsolized sands and kerangas, associated with *Parastemon*, *Shorea albida*, and *Gymnostoma* sp.

4. DACRYCARPUS

(ENDL.) DE LAUB. J. Arn. Arb. 50 (1969) 315; Fl. Nouv. Caléd. et Dép. 4 (1972) 34; GAUSSEN, *Gymn. Act. & Foss.* fasc. 13, ch. 20 (1974) 133; DE LAUB. *Kalikasan* 7 (1978) 125; VAN ROYEN, *Alpine Fl. New Guinea* 2 (1979) 11. — *Podocarpus* sect. *Dacrycarpus* ENDL. *Syn. Conif.* (1847) 221; CARRIÈRE, *Traité Gen. Conif.* ed. 1 (1855) 477; ed. 2 (1867) 676; GORDON, *Pinetum* ed. 1 (1858) 289; ed. 2 (1875) 356; MIQ. *Fl. Ind. Bat.* 2 (1859) 1074; HENKEL & HOCHSTETTER, *Synop. Nadelhölz.* (1865) 403; DE BOER, *Conif. Arch. Ind.* (1866) 25; PARL. in DC. *Prod.* 16, 2 (1868) 520; DE KIRWAN, *Conif.* 2 (1868) 224; EICHLER in E. & P. *Nat. Pfl. Fam.* II, 1 (1889) 105; BEISSNER, *Nadelholzkunde* (1891) 17; PILGER, *Pfl. R.* IV, 5, Heft 18 (1903) 55; in E. & P. *Nat. Pfl. Fam.*, Nachtr. 3 (1908) 3; FOXW. *Philip J. Sc.* 6 (1911) Bot. 156; STILES, *Ann. Bot.* 26 (1912) 448; GIBBS, *Ann. Bot.* 26 (1912) 525; PILGER in E. & P. *Nat. Pfl. Fam.* ed. 2, 13 (1926) 242; HICKEL, *Fl. Gén. I.-C.* 5 (1931) 1066; WASSCHER, *Blumea* 4 (1941) 386; BUCHHOLZ & GRAY, J. Arn. Arb. 29 (1948) 56. — *Podocarpus* sect. *Dacrydioideae* BENNETT in Bennett & R.Br. *Pl. Jav. Rar.* 1 (1838) 41. — *Podocarpus* sect. *Dacrydium* BERTRAND, *Ann. Sc. Nat.* V, 20 (1874) 67. — **Fig. 26, 28, 31–33.**

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 bifacially 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***
2. 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.
3. Adult leaves bilaterally flattened.
4. Involucral leaves surrounding receptacle and mature seed (7–13 mm long); foliage leaves slender (0.6–0.8 mm wide), scarcely keeled **3. *D. cumingii***
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***
3. Adult leaves bifacially flattened.
5. Involucral leaves less than 5 mm long, not reaching the mature seed; foliage leaves 0.6–1 mm wide.
6. Seed not large (5–6 mm long); foliage leaves spreading **5. *D. expansus***
6. Seed large (7–8 mm long); foliage leaves imbricate **6. *D. compactus***
5. Involucral leaves 6–10 mm long, mostly covering the mature seed; foliage leaves 0.4–0.6 mm wide **7. *D. cinctus***

1. *Dacrycarpus imbricatus* (BLUME) DE LAUB. J. Arn. Arb. 50 (1969) 320, f. 8a; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 152, f. 724; DE LAUB.

Kalikahan 7 (1978) 126; VAN ROYEN, Alpine Fl. New Guinea 2 (1979) 13. — *Podocarpus imbricatus* BLUME, En. Pl. Jav. 1 (1827) 89; PILGER, Pfl. R. IV,

5, Heft 18 (1903) 56; KOORD. Exk. Fl. Java 1 (1911) 64, f. 2; Atlas 3 (1915) f. 585, 586; Fl. Tjibodas (1918) 3; PILGER in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 245, f. 124E; HICKEL, Fl. Gén. 1.-C. 5 (1931) 1068; STEEN. Trop. Natuur 29 (1940) 75, 1 fig.; WASCHER, Blumea 4 (1941) 388, t. III, f. 2; BACKER & BAKH, f. Fl. Java 1 (1963) 89; STEEN. Mount. Fl. Java (1972) t. 13, f. 2. — *Podocarpus cupressina* R.Br. ex MIRBEL, Mém. Mus. Hist. Nat. Paris 13 (1925) 75, *nomen*; BENNETT in Bennett & R.Br. Pl. Jav. Rar. 1 (1838) 35, f. 10; ENDL. Syn. Conif. (1847) 222; BLUME, Rumphia 3 (1847) 218, t. 172, f. 2 & t. 172B, f. 2; MIQ. Pl. Jungh. 1 (1851) 3; Fl. Ind. Bat. 2 (1859) 1074; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 403; DE BOER, Conif. Arch. Ind. (1866) 25; PARL. in DC. Prod. 16, 2 (1868) 521; EICHLER in E. & P. Nat. Pfl. Fam. 2, 1 (1887) 106; HOOK. f. Fl. Br. Ind. 5 (1896) 650; WARB. Monsunia 1 (1900) 191; K. & V. Bijdr. Booms. Java 10 (1904) 262. — *Podocarpus javanicus* (non BURM. f.) MERR. Philip J. Sc. 19 (1921) 338; En. Philip. 1 (1922) 3. — Fig. 26.

KEY TO THE VARIETIES

1. Leaves slender (0.4–0.6 mm wide); involucre leaves always spreading.
2. Leaves imbricate a. var. *imbricatus*
2. Leaves spreading b. var. *patulus*
1. Leaves robust (0.6–1 mm wide); involucre 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. Involucre 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 neriifolius* and *Altingia noronhae*, 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,

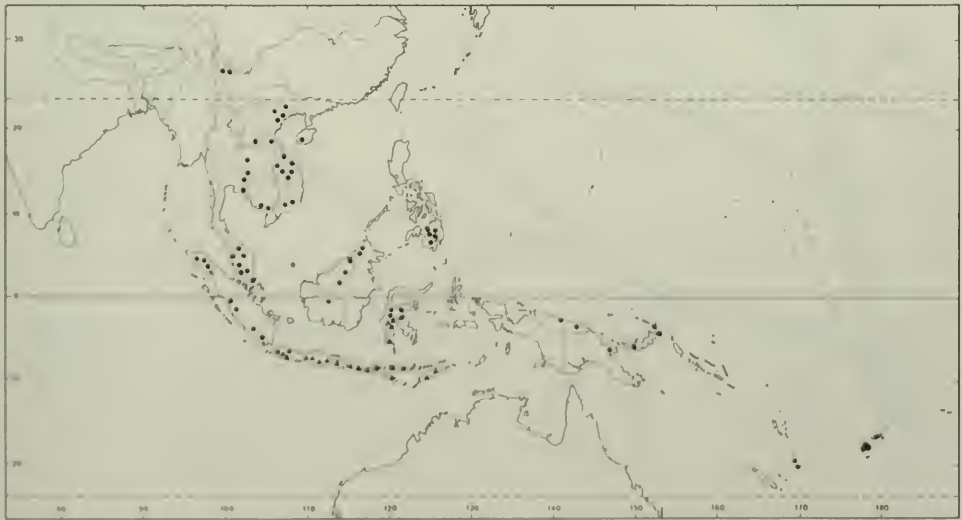


Fig. 25. Range of *Daerycarpus imbricatus* (BLUME) DE LAUB. var. *imbricatus* (triangles) and var. *patulus* DE LAUB. (dots).

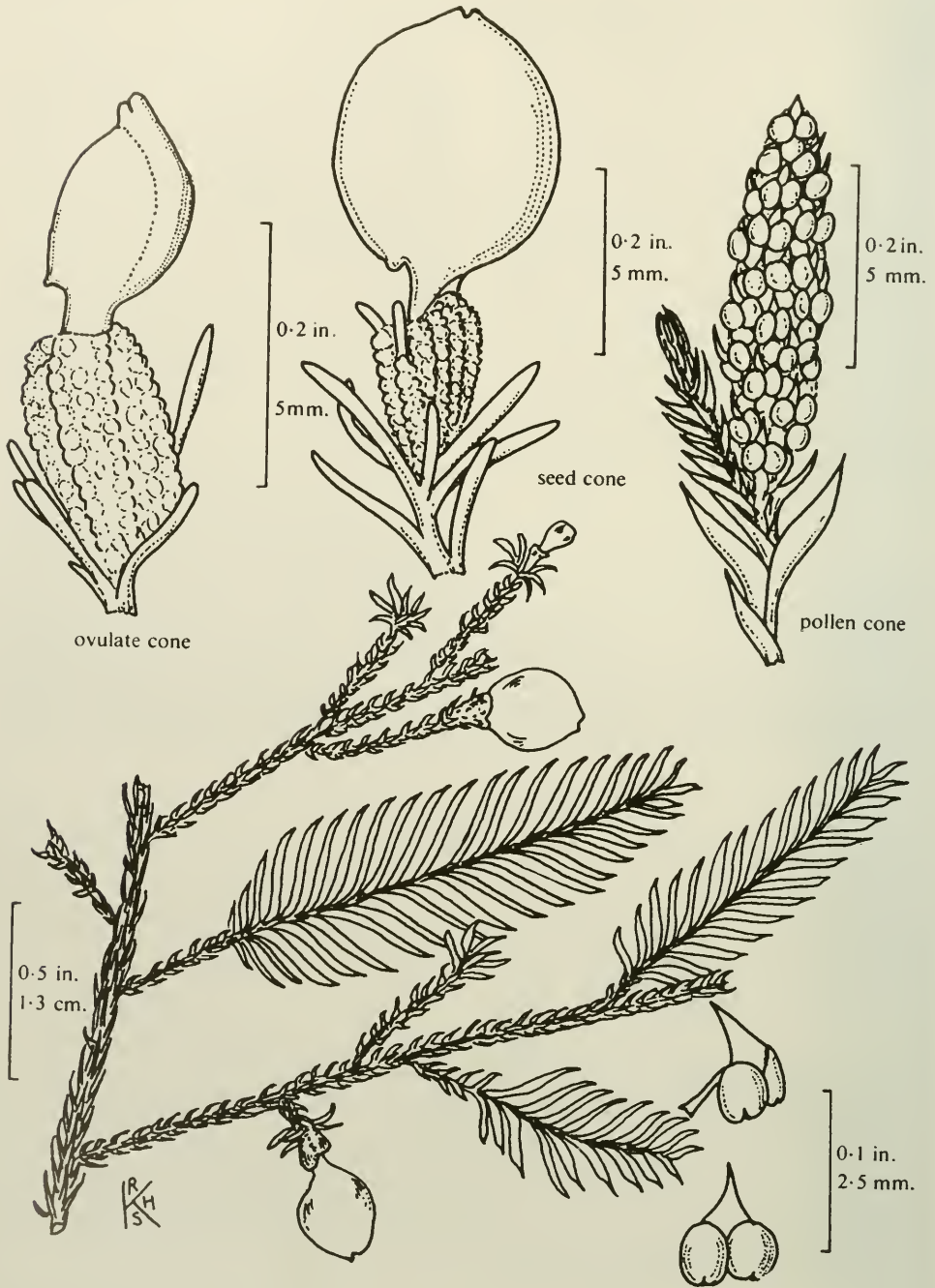


Fig. 26. *Dacrycarpus imbricatus* (BLUME) DE LAUB. var. *patulus* DE LAUB. (drawing by R.S.KENG in Whitmore, Tree Flora of Malaya 1, 1972, 51, f. 4).

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.

Vern. Java: *djamudju*, *ki hadji*, *ki putri*, *tjemoro* (*tukung*), Tjidadap, S; *kadju pakis*, *tjemara binèh*, Md.; SW. Celebes (Bonthain): *kayu angin*, *k. pa-rang*; Lesser Sunda Islands: Bali: *tarupanda*; Sum-ba: *kayu awama*, Lairondja, *kadju uamang*; Lombok: *majangnekar*; Flores: *oh-ru*, Ruteng; Timor: *hae tuni*, W. Timor, Nenas, *ai-caqueu fuie*, E. Timor, Tetun lang.

b. var. *patulus* DE LAUB. J. Arn. Arb. 50 (1969) 320, f. 8b. — *Podocarpus cupressina* RIDLEY, J. Str. Br. R. As. Soc. n. 60 (1911) 58. — *Podocarpus imbricatus sensu* GIBBS, Ann. Bot. 26 (1912) 525, t. 49, f. 1–8; STAFF, J. Linn. Soc. Bot. 42 (1914) 193; MERR. En. Born. Pl. (1921) 31; RIDLEY, Fl. Mal. Pen. 5 (1925) 283; MERR. Contr. Arn. Arb. 8 (1934) 14; CORNER, Wayside Trees (1940) 723; KENG in Whitmore, Tree Fl. Malaya 1 (1972) 51, f. 4. — *Podocarpus kawaii* HAYATA, Bull. Econ. Indochine 20 (1917) 439. — *D. kawaii* (HAYATA) GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 140, f. 726. — Fig. 26.

Tree, 5–40 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.

Vern. Malaya: *ru bukit*, Kedah; Sumatra: *ambun*, Solok, W. Coast, *balanidju*, Kerintji, *beru*, Karo Lands, *ki mèrak*, *marak*, Bencoolen, *damanik*, Simelungun, *sampinur bunga*, Karo-Toba, *talas*, Kroe, Bencoolen; Borneo: *menjilu*, Dusun lang., Kp. Tindai, Sabah, *tampilas*, Sensurun, Sabah, Dusun lang.; Celebes: *mozi*, Mt Wuka Tumpai, Palu.

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.

c. var. *robustus* DE LAUB. J. Arn. Arb. 50 (1969) 323, f. 8c; VAN ROYEN, Alpine Fl. New Guinea 2 (1979) 16, f. 35d–g. — *Podocarpus imbricatus sensu* Foxw. Philip J. Sc. 6 (1911) Bot. 157. — *Podocarpus papuanus* RIDLEY, Trans. Linn. Soc. London II, 9 (1916) 158; GIBBS, Contr. Phytogeogr. Arfak Mts (1917) 80, f. 4; PILGER in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 245; Bot. Jahrb. 68 (1937) 244; WASSCHER, Blumea 4 (1941) 402, t. 4, f. 3. — *Podocarpus javanica sensu* MERR. Philip J. Sc. 19 (1921) 338; En. Philip. 1 (1922) 3, *pro specimina*. — *Podocarpus cupressina sensu* LANE-POOLE, For. Res. Terr. Papua & New Guinea (1925) 73. — *D. papuana* (RIDLEY) GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 142, f. 731. — *D. steupii* (*non* DE LAUB.) DE LAUB. Kalikasan 7 (1978) 127.

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.

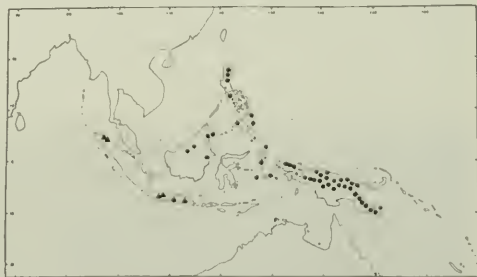


Fig. 27. Range of *Dacrycarpus imbricatus* (BLUME) DE LAUB. *var. robustus* DE LAUB. (dots) and *var. curvulus* (MIQ.) DE LAUB. (triangles).

Ecol. Scattered and, in New Guinea, very common in primary and secondary rain-forest, canopy tree, or sometimes emergent, often co-dominant, in mossy forest associated with *Nothofagus* and *Phyllocladus*, also in *Lithocarpus-Castanopsis* mixed forest co-dominant, (500–)700–3000 m, a specimen from Borneo reported from 240 m.

Vern. Borneo: *pierur*, Sarawak, Kelabit lang.; Philippines: *tupi*, Cotabato, Mindanao; West New Guinea: *upé*, Wissel Lakes, Kapauko lang., *bethica*, Arfak, Hattam lang., *jamari*, Wondiwoi Mts, Wandammen lang., *kaowie*, *kowite*, Ransiki, Manikiong lang., *nifoop*, Kebar lang., *toromoai*, Dojodial, Cycloop Mts; East New Guinea: *gubin*, *kubin*, Hagen Togoba, *iljo*, Enga lang., *kuibelpiti*, Wagi, Minj, *lou*, Wabag lang., *pau*, Lake Inim,

Enga lang., *tibuidi*, Anga Valley, Mendi lang., *uba*, Chimbu, Masul, *umba*, Waimambuno, *paupeepeen*, Mt Ne.

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 involucreal 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.

d. var. *curvulus* (MIQ.) DE LAUB. J. Arn. Arb. 50 (1969) 326, f. 8d; GAUSSEN, *Gymn. Act. & Foss.* fasc. 13, ch. 20 (1974) 154. — *Podocarpus cupressina* var. *curvula* MIQ. Pl. Jungh. 1 (1851) 4; Fl. Ind. Bat. 2 (1859) 1074. — *Podocarpus imbricatus* var. *curvula* (MIQ.) WASSCHER, *Blumea* 4 (1941) 398. — Fig. 28.

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. Involucreal 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; Diëng). 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.

2. *Dacrycarpus steupii* (WASSCHER) DE LAUB. J. Arn. Arb. 50 (1969) 328; GAUSSEN, *Gymn. Act. & Foss.* fasc. 13, ch. 20 (1974) 158, f. 728; VAN ROYEN, *Alpine Fl. New Guinea* 2 (1979) 16, f. 35a–c. — *Podocarpus steupii* WASSCHER, *Blumea* 4 (1941) 405, t. 4, f. 4. — *Podocarpus papuanus* (non RIDLEY) STEUP, *Trop. Natuur* 27 (1938) 145.

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. Involucreal leaves becoming spreading, 3–4 mm long.

Distr. *Malesia*: Central E. Borneo (G. Beratus,



Fig. 28. *Dacrycarpus imbricatus* (BLUME) DE LAUB. var. *curvulus* (MIQ.) DE LAUB. on Mt Bandahara, Sumatra, 2500 m. Habit of branch with female cones (Photogr. W.J.J.O. DE WILDE, 1972).

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.

Vern. New Guinea: *miejoop*, *nak*, Kebar lang., *apè*, Wissel Lakes, Kapauko lang., *pau*, Wabag, Enga lang.

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.

3. *Dacrycarpus cumingii* (PARL.) DE LAUB. J. Arn. Arb. 50 (1969) 329; GAUSSEN, *Gymn. Act. & Foss. fasc. 13*, ch. 20 (1974) 156, f. 727; DE LAUB. *Kalikasan* 7 (1978) 128. — *Podocarpus cumingii* PARL. in DC. *Prod.* 16, 2 (1868) 521; WASSCHER, *Blumea* 4 (1941) 407, t. 4, f. 5. — *Nageia cumingii* (PARL.) O. K. Rev. Gen. Pl. 2 (1891) 800. — *Podocarpus imbricatus* var. *cumingii* (PARL.) PILGER, *Pfl. R.* IV, 5, Heft 18 (1903) 56.

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. *Involucral 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: *sangu*, Gajo, Mt Leuser; Philippines: *igem*, Davao, Mindanao.

4. *Dacrycarpus kinabaluensis* (WASSCHER) DE LAUB. J. Arn. Arb. 50 (1969) 330; GAUSSEN, *Gymn. Act. & Foss. fasc. 13*, ch. 20 (1974) 154, f. 725. — *Podocarpus imbricatus* var. *kinabaluensis* WASSCHER, *Blumea* 4 (1941) 400, t. 4, f. 2. — *Podocarpus imbricatus* (non BLUME) GIBBS, *Ann. Bot.* 26 (1912) 525, *p.p.*, t. 49, f. 1–9.

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. *Involucral 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. cumingii*, differing particularly in the distinctly shorter involucral leaves. Foliage leaves of *D. cumingii* when collected from exposed parts of the tree approach this species in robust form. The receptacle colour of *D. cumingii* is poorly documented and may well become purple also.

5. *Dacrycarpus expansus* DE LAUB. J. Arn. Arb. 50 (1969) 334, f. 7b; GAUSSEN, *Gymn. Act. & Foss. fasc. 13*, ch. 20 (1974) 162, f. 733.

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.

Distr. *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. steupii*, a species which is also associated with dis-



Fig. 30. Range of *Dacrycarpus expansus* DE LAUB. (squares) and *D. compactus* (WASSCHER) DE LAUB. (dots).

turbed habitats. This latter species differs in the form of the foliage leaves and the involucral leaves.

6. *Dacrycarpus compactus* (WASSCHER) DE LAUB. J. Arn. Arb. 50 (1969) 336, f. 9c; GAUSSEN, Gymn. Act. & Foss. fasc. 13, ch. 20 (1974) 158, f. 730; VAN



Fig. 31. A boggy hollow, filled with the tall grass *Deschampsia klossii* RIDLEY (c. 1 m high) with on the edge tall *Dacrycarpus compactus* (WASSCHER) DE LAUB. in dense, very mossy shrubberies of mixed composition. About 1 km north of Lake Habbema, West New Guinea, 3300 m (Photogr. L.J. BRASS, 1938).

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.



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).

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.

Vern. *Kadznam, kaibigl, Minj, kaipik, Kubur, Minj, umbwa*, Lake Aunde, Chimbu, Waimambano, *umba-nistogo*, Chimbu, Lake Aunde.

7. *Dacrycarpus cinctus* (PILGER) DE LAUB. *J. Arn. Arb.* 50 (1969) 332, f. 9a; GAUSSEN, *Gymn. Act. & Foss. fasc.* 13, ch. 20 (1974), 160, f. 732; VAN ROYEN, *Alpine Fl. New Guinea* 2 (1979) 17, f. 35h, t. 79. — *Podocarpus cinctus* PILGER, *Bot. Jahrb.* 69 (1938) 253; WASSCHER, *Blumea* 4 (1941) 409, t. 4, f. 6. — *Podocarpus dacrydiifolia* WASSCHER, *l.c.* 410, t. 4, f. 7. — *D. dacrydiifolia* (WASSCHER) GAUSSEN, *Gymn. Act. & Foss. fasc.* 13, ch. 20 (1974) 148, f. 729. — Fig. 33.

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. 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.

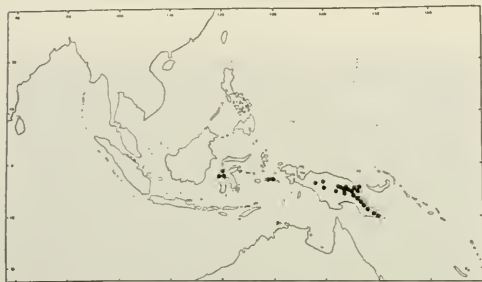


Fig. 34. Range of *Dacrycarpus cinctus* (PILGER) DE LAUB.

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 Waitape), 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.

Vern. Celebes: *sareh*, Upper Binuang, Ulu Sahu; New Guinea: *djasiha*, Asaro, Kefamo, *gu-gra-goin*, Goroka, Hagen lang., *jumbiri*, Mt Giluwe, Mendi lang., *kaiwilpitti*, Waghi, Minj, *kubil-kaibigl*, *kubuk-kajbek*, Kubor Ra., Minj, *kubin*, Hagen, Togoba, *ma-u*, Finisterre Ra., Naho lang., *pau*, Hagen-Wabag, Enga lang., *piepienie*, Mt Ne, Tari, Hula lang., *u(m)ba*, Chimbu lang. at various places.

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.

5. PRUMNOPITYS

PHILIPPI, *Linnaea* 30 (1860) 731; DE LAUB. *Fl. Nouv. Caléd. et Dép.* 4 (1972) 55; *Blumea* 24 (1978) 189. — *Stachycarpus* (ENDL.) TIEGH. *Bull. Soc. Bot. Fr.* 38 (1891) 162; GAUSSEN, *Gymn. Act. & Foss. fasc.* 13, ch. 20 (1974) 81. — *Podocarpus sect. Taxoideae* BENNETT in Bennett & R.Br. *Pl. Jav. Rar.* 1 (1838) 40. — *Podocarpus sect. Stachycarpus* ENDL. *Syn. Conif.* (1847) 218; HENKEL & HOCHSTETTER, *Synop. Nadelhölz.* (1865) 399; PARL. in DC. *Prod.* 16, 2 (1868) 518; EICHLER in E. & P. *Nat. Pfl. Fam.* 2, 1 (1889) 105; PILGER, *Pfl. R.* IV, 5, Heft 18 (1903) 63; GIBBS, *Ann. Bot.* 26 (1912) 537; BUCHHOLZ & GRAY, *J. Arn. Arb.* 29 (1948) 58. — *Podocarpus sect. Prumnopitys* (PHILIPPI) BERTRAND, *Ann. Sc. Nat.* V, 20 (1874) 65. — *Podocarpus subg. Stachycarpus* (ENDL.) ENGLER in E. & P. *Nat. Pfl. Fam., Nachtr.* 1 (1897) 21; PILGER in E. & P. *Nat. Pfl. Fam. ed.* 2, 13 (1926) 242; WASSCHER, *Blumea* 4 (1941) 380. — **Fig. 36, 38, 39.**

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*

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.

Distr. 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.

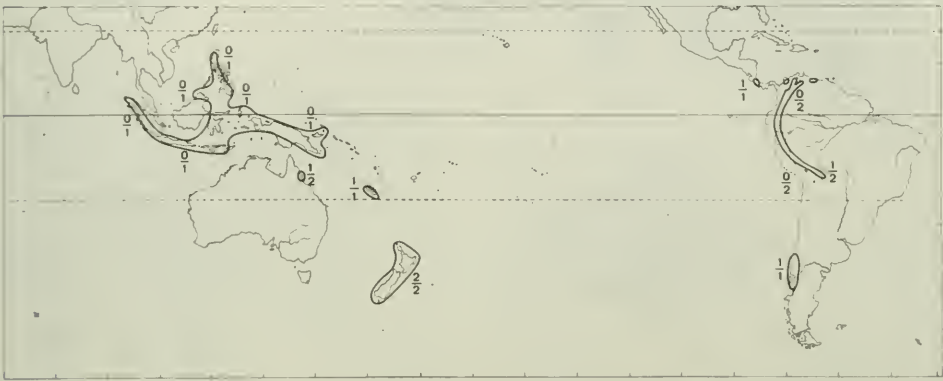


Fig. 35. Range of the genus *Prumnopitys* PHILIPPI. Figures above the hyphen indicate the number of endemic species, that below the hyphen the total number of species.

1. Section *Sundacarpus*

(BUCHHOLZ & GRAY) DE LAUB. *Blumea* 24 (1978) 190. — *Podocarpus* sect. *Sundacarpus* BUCHHOLZ & GRAY, *J. Arn. Arb.* 29 (1948) 57; FLORIN, *Acta Horti Berg.* 20 (4) (1963) 190, f. 20 (map). — *Stachycarpus* sect. *Sundacarpus* (BUCHHOLZ & GRAY) GAUSSEN, *Gymn. Act. & Foss.* fasc. 13, ch. 20 (1974) 81.

1. *Prumnopitys amara* (BLUME) DE LAUB. *Blumea* 24 (1978) 190. — *Podocarpus amara* BLUME, *En. Pl. Java* 1 (1827) 88; BENNETT in Bennett & R.Br. *Pl. Jav. Kar.* 1 (1838) 40; ENDL. *Syn. Conif.* (1847) 217; BLUME, *Rumphia* 3 (1849) 213, t. 170; MIQ. *Fl. Ind. Bat.* 6 (1859) 1073; HENKEL & HOCHSTETTER, *Synop. Nadelholz.* (1865) 395; DE BOER, *Conif. Arch. Ind.* (1866) 20; PARR. in DC. *Prod.* 16, 2 (1868) 516; BLERTRAND, *Ann. Sc. Nat.* 5, 20 (1874) 67; TIEGH. *Bull. Soc. Bot. Fr.* 38 (1891) 38; WARB. *Monshnia* 1 (1900) 192; PILGER, *Pfl. R.* IV, 5, Heft 18 (1903) 68, t. 13A–D; K. & V. *Bijdr.* 10 (1904) 263; FOXW. *Philip.*

J. Sc. 6 (1911) Bot. 159; KOORD. *Exk. Fl. Java* 1 (1911) 64, f. 1; HALL, *f. Meded. Rijksherb. n.* 14 (1912) 34; KOORD. *Atlas* 3 (1915) t. 590, 591; MERR. *En. Philip.* 1 (1922) 2; KOORD. *Fl. Tjibodas* (1922) 2; LANE-POOLE, *For. Res. Terr. Papua & New Guinea* (1925) 73; PILGER in E. & P. *Nat. Pfl. Fam.* ed. 2, 13 (1926) 245, f. 131A–D; WASSCHER, *Blumea* 4 (1941) 381; ORR, *Trans. Bot. Soc. Edinb.* 34 (1944) 11; GRAY & BUCHHOLZ, *J. Arn. Arb.* 32 (1951) 93; BACKER & BAKH, *f. Fl. Java* 1 (1963) 89. — *Podocarpus eurlyncha* MIQ. *Fl. Ind. Bat.* 2 (1856) 1074; DE BOER, *Conif. Arch. Ind.* (1866) 24, t. 3, f. 2; PARR.

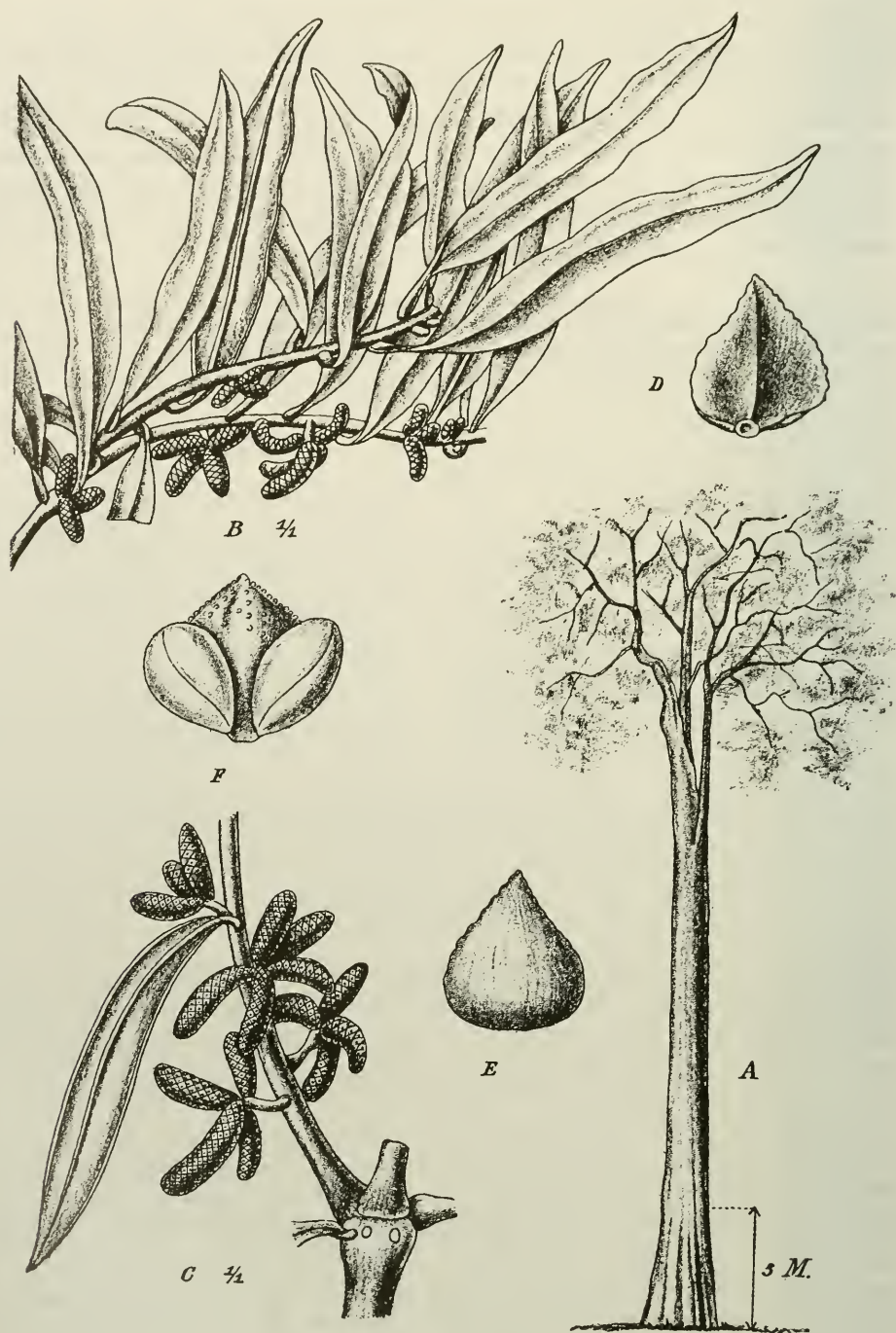


Fig. 36. *Prumnopitys amara* (BLUME) DE LAUB. A. Habit of tree; B, C. twigs with pollen cones; D-F. microsporophylls (different views) (from KOORD. Atlas 3, 1915, t. 590).

in DC. Prod. 16, 2 (1868) 518; WARB. *Monsunia* 1 (1900) 193. — *Podocarpus dulcamara* SEEM. Bonplandia 9 (1861) 253; *ibid.* 10 (1862) 365. — *Nageia amara* (BLUME) O. K. Rev. Gen. Pl. 2 (1891) 800. — *Nageia eurhyncha* (Miq.) O. K. l.c. 800. — *Podocarpus pedunculata* BAILEY, Queensl. Agr. J. 5 (1899) 390, t. 144; Queensl. Fl. 5 (1902) 1498; BAKER & SMITH, Res. Pines Austr. (1910) 441; Hardwoods Austr. (1919) 429. — *Stachycarpus amara* GAUSSEN, Gymn. Act. & Foss. fasc. 12 (1973) f. 635, 646; *ibid.* 13, ch. 20 (1974) 105, f. 715 (map). — Fig. 36, 38, 39.

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 into an elongated tapering 'drip 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 outer 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 (Bonthain), Philippines (Mindanao, Luzon), Borneo (only in Sabah!), and Sumatra (Central N., Batak region, rare in S. Palembang). Fig. 37.

Ecol. 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-*



Fig. 37. Range of *Prumnopitys amara* (BLUME) DE LAUB.

xylum, *Macaranga*, *Ficus*, sometimes emergent as a colossal tree, often on latosols, 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 buttressed (Pinosok 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.

Vern. Sumatra: *kuta-béa*, *sitoba*, *sitobu*, Toba-Batak, *besi*, Karo-Batak, *buluh*, Pasemah, Palembang; Java: *ki bima*, *ki manang pait*, *ki marak*, *ki mèrak*, *ki pait*, *ki putri* (confusion with *Podocarpus neriifolius*), S; *tadji*, Tengger, *tjemoro*, Madiun (confusion with *Casuarina*), J; Borneo: *sempilau*, Kinabatangan; Lesser Sunda Islands: *pinis*, Flores, *kayu santen*, Batulante, Sumbawa; West New Guinea: *bublugie*, Wissel Lakes, Kapauko lang., *irbouska*, Manikiong, Ransiki, *du-on*, *nepa*, *niepa*, *nipah*, Kebar lang., *niwup*, Kebar Valley, Andjaidial., *tjermes*, Ransiki, Hattam lang.; East New Guinea: *kaibiltugl*, Wahgi, Minj, *kepim*, Pokaris, Wabag, Enga lang., *kumburum*, Mt Entaldam, Telefomin, *la-u*, Poget logging area, Wabag, *levekus*, Telefomin, *migimi*, Ogeramngang, *powa*, Pomagos R.C. Mission, Weng lang., *singai*, Bulolo, Garaina dial., *taso*, Wonatabe, *til*, Hagen, Togoba, *tsula*, Chimbu, Masul; New Britain: *nelil*, Mt Talawe. *Black pine*, Queensland.

Note. The leaves are variously reported as bitter ('amara'), to which also the Sundanese name 'pait' refers, bittersweet ('dulcamara'), or sweet tasting. This and the groove over the midvein 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 eurhyncha*. 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).



Fig. 39. *Prumnopitys amara* (BLUME) DE LAUB. Ripe seed red (Photogr. BW 2318).

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

GAERTN. De Fruct. & Sem. (1788) 191; GORDON, Pinetum (1858) 134; O. K. Rev. Gen. Pl. 2 (1891) 798; FLORIN, Acta Horti Berg. 20 (4) (1963) 190, f. 21 (map); DE LAUB. Blumea 32 (1987) 209. — *Decussocarpus* DE LAUB. J. Arn. Arb. 50 (1969) 340; Fl. Nouv. Caléd. et Dép. 4 (1972) 48; Kalikasan 7 (1978) 130. — Fig. 41.

Diocious, 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*
 1. Leaves small, with a single rib 2. Sect. *Polypodiopsis*

1. Section *Nageia*

DE LAUB. *Blumea* 32 (1987) 209. — *Podocarpus* sect. *Dammaroides* BENNETT in Bennett & R.Br. *Pl. Jav. Rar.* 1 (1838) 41. — *Podocarpus* sect. *Nageia* ENDL. *Syn. Conif.* (1847) 207; MIQ. *Fl. Ind. Bat.* 2 (1859) 1071; HENKEL & HOCHSTETTER, *Synop. Nadelhölz.* (1865) 378; DE BOER, *Conif. Arch. Ind.* (1866) 12; PARL. in DC. *Prod.* 16, 2 (1868) 507; BERTRAND, *Ann. Sc. Nat.* V, 20 (1874) 66; PILGER, *Pfl. R.* IV, 5, Heft 18 (1903) 59; GIBBS, *Ann. Bot.* 26 (1912) 533; PILGER in E. & P. *Nat. Pfl. Fam. ed.* 2, 13 (1926) 242; WASSCHER, *Blumea* 4 (1941) 415; BUCHHOLZ & GRAY, *J. Arn. Arb.* 29 (1948) 56; GAUSSEN, *Gymn. Act. & Foss.* fasc. 14, ch. 21 (1976) 11. — *Decussocarpus* sect. *Dammaroides* (BENNETT) DE LAUB. *J. Arn. Arb.* 50 (1969) 348; Kalikasan 7 (1978) 130.

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.

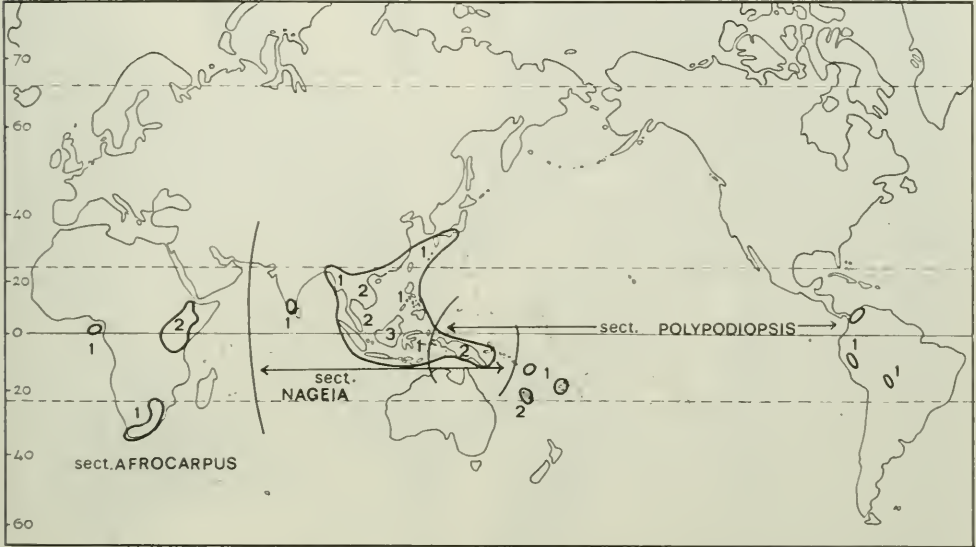


Fig. 40. Range of the genus *Nageia* GAERTN. and its three sections, with the number of species.

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. molleyi*
- 1. Fruit lacking a fleshy receptacle. Large-leaved 3. *N. maximus*

1. *Nageia wallichiana* (PRESL) O. K. Rev. Gen. Pl. 2 (1891) 800; DE LAUB. Blumea 32 (1987) 210. — *Podocarpus latifolius* (non THUNB. 1794) BLUME, En. Pl. Jav. 1 (1827) 89; WALL. Pl. As. Rar. (1830) 26; HORSFIELD in Bennett & R.Br. Pl. Jav. Rar. 1 (1838) 41; LOUDON, Arb. & Fruct. Brit. 4 (1838) 2100, f. 1995; HASSK. Cat. Hort. Bog. (1844) 70; ENDL. Syn. Conif. (1847) 208; MIQ. Pl. Jungh. 1 (1851) 1; Fl. Ind. Bat. 2 (1859) 1071; HENKEL & HOCHSTETTER, Synop. Nadelholz. (1865) 379; DE BOER, Conif. Arch. Ind. (1866) 12; PARI. in DC. Prod. 16, 2 (1868) 508; HOOK.f. Fl. Brit. India 5 (1896) 649. — *Podocarpus wallichianus* PRESL, Bot. Bemerk. (1844) 110; PILGER, Pfl. R. IV, 5, Heft 18 (1903) 59; RIDLEY, J. Str. Br. R. As. Soc. n. 60 (1911) 57; HICKEL, Fl. Gén. 1.-C. 5 (1931) 1068; KING in Whitmore, Tree Fl. Malaya 1 (1972) 53, f. 5d-f;

PHENGLAI, Thai For. Bull. Bot. 7 (1973) 17, f. 11; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 18. — *Podocarpus blumei* ENDL. Syn. Conif. (1847) 208; HENKEL & HOCHSTETTER, Synop. Nadelholz. (1865) 380; PARI. in DC. Prod. 16, 2 (1868) 508; BECC. Malesia 1 (1877) 178; WARB. Monsunia 1 (1900) 193; PILGER, Pfl. R. IV, 5, Heft 18 (1903) 60, t. 9; K. & V. Bijdr. 10 (1904) 261; KOORD. Exk. Fl. Java 1 (1911) 67; FOXW. Philip. J. Sc. 6 (1911) Bot. 158, t. 28, f. 2; KOORD. Atlas 3 (1915) f. 588; RIDLEY, Fl. Mal. Pen. 5 (1925) 281; PILGER in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 245, t. 134B; Bot. Jahrb. 68 (1937) 245; CORNER, Wayside Trees (1940) 717; WASSCHER, Blumea 4 (1941) 416; BACKER & BAKH.f. Fl. Java 1 (1963) 89; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 20, f. 736. — *Podocarpus agathifolia* BLUME, Rumphia 3 (1849) 217, t. 173. —

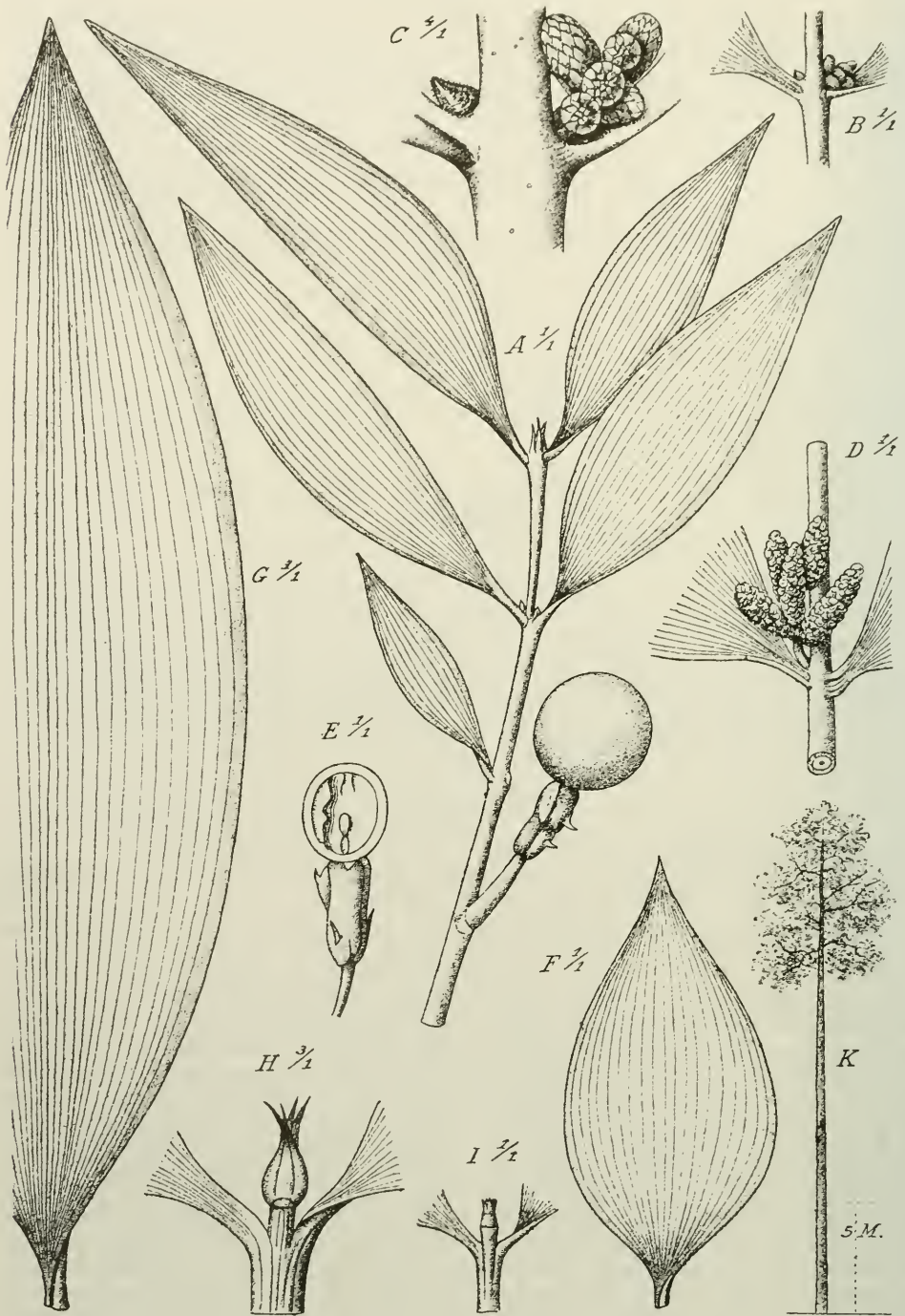


Fig. 41. *Nageia wallichiana* (PRESL) O.K. A. Twig with seed; B, C. twig portion with young pollen cones; D. ditto with mature pollen cones; E. longitudinal section of seed; F. leaf of a mature tree; G. leaf of a young tree; H, I. terminal foliage buds; K. habit of tree (from KOORD. Atlas 3, 1915, t.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

N. blumei (ENDL.) GORDON, Pinetum (1858) 138. — *Podocarpus latifolia* f. *ternatensis* DE BOER, Conif. Arch. Ind. (1866) 14. — *Decussocarpus wallichianus* (PRESL) DE LAUB. J. Arn. Arb. 50 (1969) 349; Kalikasan 7 (1978) 131. — Fig. 41.

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 8–18 by 3–4 mm. Apex of the microsporophyll 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.

Distr. 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.

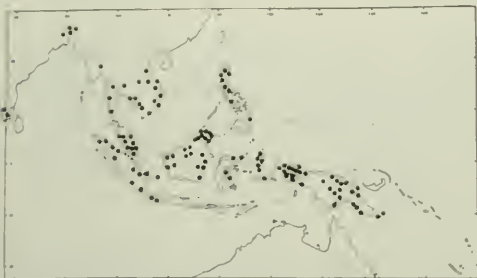


Fig. 42. Range of *Nageia wallichiana* (PRESL) O.K.

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 Thailand buttresses are recorded, at Argunt 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.

Vern. Malaya: *podo kebal musang gunung*; Sumatra: *kayu bulu soma*, Asahan, Batak lang., *labu rimba*, Sibolga, *lanang*, Pasamah, Palembang, *medang sepaling*, Bencoolen, *setebal*, Banjarmasin, Palembang, *sibulu somak*, Simelungun; W. Java: *ki bima*, *ki putri*, S; Borneo: *kebal musang*, Tawau, *manggilan*, Tambunan, Dusun lang., *mengilan*, Sabah, Serudong, *salung puteh*, Merurong Plateau; Philippines: *mala almaciga*, Tag.; Celebes: *molosambongé* = *tombolito*, Buladu, N. Cel., *tandangguli*, Malili; Lesser Sunda Islands: *tilu tuna*, Flores; Moluccas: *damar laki laki*, Obi; West New Guinea: *augom(m)a*, Wariki, Manikiong lang., *bararang*, Meos Num, Pom lang., *kabeirefo*, Tiwara, Irahutu lang., *mangurif*, Biak lang., *mejerka*, Sidai, Arfak Sidai dial., *misorvira*, Tairi, Borowai lang., *mop*, Mandobo lang., *mungkas*, Beriat, Tehid lang., *neusuwierie*, Esania lang., *nibwau*, Kebar Valley, Andjai dial., *nipa*, Kebar lang., *niwob*, Kebar dial., *manakasap*, Japen, Sambar lang., *nidjet*, Sidai, Amberbaken lang., *orsonkobu*, Warsamson, Mooi lang., *waramira*, Mimika, *wok*, Muju lang.; East New Guinea: *durwe*, Wagu, *newango*, *mewongo*, Maipa village, Mekeo lang., *ososo biri biri*, Oomsis, *waswayangumi*, Waskuk.

2. *Nageia motleyi* (PARL.) DE LAUB. *Blumea* 32 (1987) 210. — *Dammara motleyi* PARL. En. Sem. Hort. Bot. Mus. Florent. (1862) 26; SEEM. J. Bot. 1 (1863) 36; PARL. in DC. Prod. 16, 2 (1868) 377. — *Podocarpus beccarii* PARL. in DC. Prod. 16, 2 (1868) 508; WARB. *Monsunia* 1 (1900) 193; PILGER, Pfl. R. IV, 5, Heft 18 (1903) 59. — *N. beccarii* (PARL.) GORDON, Pinetum ed. 2 (1875) 186. — *Agathis motleyi* (PARL.) WARB. *Monsunia* 1 (1900) 185. — *Podocarpus motleyi* (PARL.) DÜMMER, J. Bot. 52 (1914) 240; WASSCHER, *Blumea* 4 (1941) 421, t. 4, f. 11; GAUSSEN, *Gymn. Act. & Foss.* fasc. 14, ch. 21 (1976) 22, f. 737; KENG in Whitmore, *Tree Fl. Mal.* 1 (1972) 51, f. 5. — *Decussocarpus motleyi* (PARL.) DE LAUB. J. Arn. Arb. 50 (1969) 352.

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 microsporophylls 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.

Distr. Southernmost Thailand; in *Malesia*: Ma-

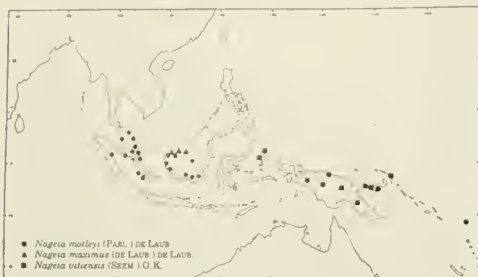


Fig. 43. Range of three species of *Nageia*.

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

Ecol. Scattered in primary and secondary rain-forest, 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 hillsides in *bindang*-dipterocarp forest and at Lawas at 1000 m on podsollic sandy loam.

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

3. *Nageia maximus* (DE LAUB.) DE LAUB. *Blumea* 32 (1987) 210. — *Decussocarpus maximus* DE LAUB. *J. Arn. Arb.* 50 (1969) 353. — *Podocarpus maximus* (DE LAUB.) GAUSSEN, *Gymn. Act. & Foss. fasc.* 14, ch. 21 (1976) 14, f. 742.

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.

Vern. *Landin paya*, Naman For. Res.

2. Section *Polypodiopsis*

(BERTRAND) DE LAUB. *Blumea* 32 (1987) 210. — *Podocarpus sect. Polypodiopsis* BERTRAND, *Ann. Sc. Nat.* V, 20 (1874) 65; WASSCHER, *Blumea* 4 (1941) 423; BUCHHOLZ & GRAY, *J. Arn. Arb.* 29 (1948) 57; GRAY, *ibid.* 43 (1962) 67; GAUSSEN, *Gymn. Act. & Foss. fasc.* 14, ch. 21 (1976) 27. — *Decussocarpus sect. Decussocarpus* DE LAUB. *J. Arn. Arb.* 50 (1969) 341.

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.

4. *Nageia vitiensis* (SEEM.) O. K. *Rev. Gen. Pl.* 2 (1891) 800; DE LAUB. *Blumea* 32 (1987) 210. — *Podocarpus vitiensis* SEEM. *Bonplandia* 10 (1862) 366; *J. Bot.* 1 (1863) 33, t. II; *Fl. Vitiensis* (1868) 266, t. 78; TIEGH. *Bull. Soc. Bot. Fr.* 38 (1891) 169; PILGER, *Pfl. R.* IV, 5, Heft 18 (1903) 63; GIBBS, *J. Linn. Soc. Bot.*

39 (1909) 182; *Ann. Bot.* 26 (1912) 533, t. 49, f. 14–16, t. 50, f. 17–18, t. 53, f. 72–73; STILES, *Ann. Bot.* 26 (1912) 533; PILGER in *E. & P. Nat. Pfl. Fam.* ed. 2, 13 (1926) 245; WASSCHER, *Blumea* 4 (1941) 425; GRAY, *J. Arn. Arb.* 43 (1962) 72; GAUSSEN, *Gymn. Act. & Foss. fasc.* 14, ch. 21 (1976) 38, f. 747. —

Podocarpus filicifolius GRAY, J. Arn. Arb. 43 (1962) 74, *p.p.*; DE LAUB. *Blumea* 15 (1967) 440; GAUSSEN, *Gymn. Act. & Foss. fasc.* 14, ch. 21 (1976) 40. — *Decussocarpus vitiensis* (SEEM.) DE LAUB. J. Arn. Arb. 50 (1969) 342.

Tree, 12–43 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 midvein 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 micropylar 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.

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

Ecol. 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* rain-forest, from sea-level up to 1800 m.

Uses. In Fiji a valuable timber tree.

Vern. *Mugo*, Wissel Lakes, Kapauko lang., *lehil*, Mt Tangis, New Britain.

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

L'HERIT. *ex* PERSOON, *Synops.* 2 (1807) 580, *nom. cons.*, *non* LABILL. (1806); ENDL. *Gen. Pl. n.* 1800 (1810); L.C. & A. RICH. *Comm. Bot. Conif. & Cycad.* (1826) 124; BLUME, *En. Pl. Jav.* 1 (1827) 88; BENNETT in Bennett & R.Br. *Pl. Jav. Rar.* 1 (1838) 35; ENDL. *Syn. Conif.* (1847) 206; BLUME, *Rumphia* 3 (1849) 212; MIQ. *Fl. Ind. Bat.* 2 (1859) 1071; HENKEL & HOCHSTETTER, *Synop. Nadelhölz.* (1865) 377; DE BOER, *Conif. Arch. Ind.* (1866) 12; PARL. in DC. *Prod.* 16, 2 (1868) 507; BENTH. & HOOK. *f. Gen. Pl. III*, 1 (1880) 434; EICHLER in E. & P. *Nat. Pfl. Fam.* 2, 1 (1887) 104; BEISSNER, *Nadelholzk.* (1891) 193; PILGER, *Pfl. R. IV*, 5, Heft 18 (1903) 54; K & V. *Bijdr.* 10 (1904) 259; PILGER in E. & P. *Nat. Pfl. Fam.*, *Nachtr.* 3 (1908) 4; KOORD. *Exk. Fl. Java* 1 (1911) 63; RIDLEY, *J. Str. Br. R. As. Soc. n.* 60 (1911) 56; FOXW. *Philip. J. Sc.* 6 (1911) Bot. 155; KOORD. *Fl. Tjibodas* (1918) 2; RIDLEY, *Fl. Mal. Pen.* 5 (1925) 280; PILGER in E. & P. *Nat. Pfl. Fam.* ed. 2, 13 (1926) 240; WASSCHER, *Blumea* 4 (1941) 360; BUCHHOLZ & GRAY, *J. Arn. Arb.* 29 (1948) 54; DE LAUB. *Fl. Nouv. Caléd. et Dép.* 4 (1972) 59; GAUSSEN, *Gymn. Act. & Foss. fasc.* 14, ch. 21 (1976) 3; DE LAUB. *Kalikasan* 7 (1978) 133; *Blumea* 30 (1985) 251. — Fig. 46, 62.

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 common 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 secondary 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 accessory 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 typically *c.* 25 mm long emerge from the primary bud simultaneously with the elongation of the secondary foliage buds, each pollen cone developing from a secondary bud which resembles the secondary foliage bud (which, however, is always 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 structure falls as soon as the pollen is shed, the basal scales usually not falling separately. 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 structure 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.

Distr. 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.

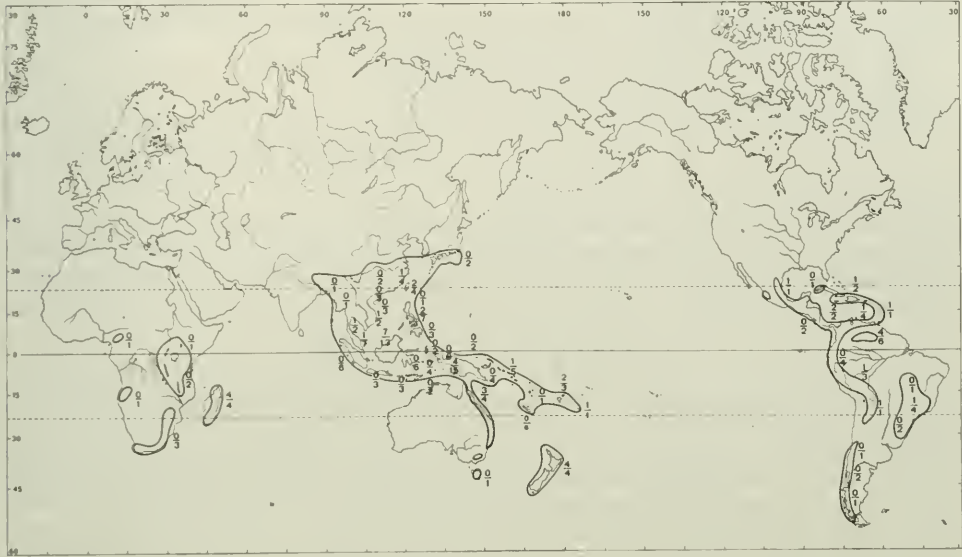


Fig. 44. Range of the genus *Podocarpus* L'HÉRIT. ex PERSOON. Figures above the hyphen indicate the number of endemic species, that below the hyphen the total number of species.

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 bud scales erect and free, secondary bud scales acute to acuminate.
- 4. Secondary bud scales broadly acute, primary bud scales 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*
- 4. Secondary bud scales acuminate, primary bud scales more than four times as long as broad; adult leaves acuminate, abruptly expanded at the base. *Spp.* 9–10..... 2. *Sect. Acuminatus*
- 3. Primary foliage bud scales imbricate, forming a globular ball; secondary bud scales blunt. *Spp.* 11–12 3. *Sect. Globulus*

2. Pollen cones normally solitary (only rarely grouped) (external bud scales erect and free; leaves not at all acuminate).
5. Foliage buds much longer than wide (with long lanceolate scales), secondary bud scales 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 bud scales 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 bud scales 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 bud scales 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 bud scales imbricate, forming a ball or pyramid with few or none of their apices raised, bud no longer than diameter.
2. Primary bud scales 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 bud scales 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 bud scales with completely free apices, bud usually longer than diameter.
3. Adult leaves distinctly acuminate; primary bud scales 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 bud scales 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
4. *Sect. Longifoliolatus (P. gibbsii)*
7. Leaves at least 8 mm wide, 4 cm long, midrib on upper side c. 0.3 mm high
1. *Sect. Foliolatus (P. borneensis)*
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. gibbsii)*
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. laubenfelsii*)

1. Section Foliolatus

DE LAUB. *Blumea* 30 (1985) 264.

Primary foliage budscales erect, triangular to shortly lanceolate; secondary scales acute, 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.

Distr. 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. neriifolius*, 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. neriifolius*), 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. neriifolius*
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*

1. Midrib on the upper side of the leaf at least 1 mm wide or indistinctly raised or both.
 5. Midrib prominently raised above, 0.3 mm high, often drying to a channel below (leaves distinctly thicker than usual for the genus). Primary bud scales may reach at least 1 cm long.
 6. Leaves more than 10 cm long. Female peduncle 9–15 mm. Primary bud scales and leaves deflexed
 5. P. *deflexus*
 6. Leaves less than 10 cm long. Female peduncle 2 mm. Primary bud scales and leaves erect 6. P. *borneensis*
 5. Upper surface of leaf flat or nearly so, lower surface generally lacking a channel (leaves not thicker than usual for the genus). Bud scales never as long as 1 cm.
 7. Leaves lanceolate or narrowly linear 7. P. *levis*
 7. Leaves oblong, not tapering 8. P. *spathoides*

1. *Podocarpus neriifolius* D.DON in Lambert, Gen. Pinus ed. 1 (1824) 21; Prod. Fl. Nep. (1825) 55; SPRENG. Syst. Veg. 3 (1826) 889; BENNETT in Bennett & R.Br. Pl. Jav. Rar. 1 (1838) 40; ENDL. Syn. Conif. (1847) 215; PARL. Bot. Mag. 78 (1852) t. 4655; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 381; PARL. in DC. Prod. 16, 2 (1868) 514; EICHLER in E. & P. Nat. Pfl. Fam. 2, 1 (1887) 104; Hook.f. Fl. Br. Ind. 5 (1888) 649; STAPF, Trans. Linn. Soc. II, Bot. 4 (1894) 249; WARB. Monsunia 1 (1900) 193; PILGER, Pfl. R. IV, 5, Heft 18 (1903) 80; K. & V. Bijdr. 10 (1904) 265; MERR. Philip. J. Sc. 1 (1906) Suppl. 24; Foxw. Philip. J. Sc. 2 (1907) Bot. 258; GIBBS, J. Linn. Soc. 39 (1909) 183; Foxw. Philip. J. Sc. 6 (1911) Bot. 162; RIDLEY, J. Str. Br. R. As. Soc. n. 60 (1911) 57; KOORD. Exk. Fl. Java 1 (1911) 65, f. 3; GIBBS, Ann. Bot. 26 (1912) 549, t. 51, f. 48–51, t. 53, f. 78; KOORD. Atlas 2 (1915) t. 589; Fl. Tjibodas 1 (1922) 3; RIDLEY, Fl. Mal. Pen. 5 (1925) 281; PILGER in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 247; HICKEL, Fl. Gén. 1.-C. 5 (1931) 1069; WASSCHER, Blumea 4 (1941) 437, incl. var. *polyantha* WASSCHER, l.c. 455; GRAY, J. Agn. Arb. 39 (1958) 460, 467; BACKER & BAKH.f. Fl. Java 1 (1963) 90; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 187, f. 805; DE LAUB. Kalikasan 7 (1978) 139. — *Nageia neriifolia* (D.DON) O.K. Rev. Gen. Pl. 2 (1891) 800. — *P. neglecta* BLUME, Rumphia 3 (1849) 213; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 396; DE BOER, Conif. Arch. Ind. (1866) 21, t. II, 2; PARL. in DC. Prod. 16, 2 (1868) 516; WARB. Monsunia 1 (1900) 193. — *Nageia neglecta* (BLUME) O.K. Rev. Gen. Pl. 2 (1891) 800. — *P. discolor* BLUME, Rumphia 3 (1847) 213; MIQ. Fl. Ind. Bat. 2 (1859) 1074; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 396; DE BOER, Conif. Arch. Ind. (1866) 23, t. III, 1; PARL. in DC. Prod. 16, 2 (1868) 518; EICHLER in E. & P. Nat. Pfl. Fam. 2, 1 (1887) 104; WARB. Monsunia 1 (1900) 193. — *Nageia discolor* (BLUME) O.K. Rev. Gen. Pl. 2 (1891) 800. — *P. leptostachya* BLUME, Rumphia 3 (1849) 214; MIQ. Fl. Ind. Bat. 2 (1859) 1073; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 392; DE BOER, Conif. Arch. Ind. (1866) 19, t. II, 1; PARL. in DC. Prod. 16, 2 (1868) 515; WARB. Monsunia 1 (1900) 193. — *Nageia leptostachya* (BLUME) O.K. Rev. Gen. Pl. 2 (1891) 800. —

P. junghuhniana MIQ. Pl. Jungh. 1 (1851) 2; Fl. Ind. Bat. 2 (1859) 1073. — *P. polyantha* (WASSCHER) GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 191, f. 811. — *P. decipiens* GRAY, J. Arn. Arb. 36 (1955) 204; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 225, f. 844.

Tree (3–)5–30(–45) m tall, 10–100 cm diam., clear bole up to 20 m; crown often dome-shaped. Foliage buds 2–5 mm long, occasionally longer, the primary scales often spreading. Juvenile leaves 15–24 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. Midrib 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. Simalur I.), throughout Java and Borneo (incl. Karimata I.), the Philippines (Mindanao), Celebes, the Lesser Sunda Islands (Bali, Flores), the Moluccas (Obi, Ceram, Halmaheira), and New Guinea (incl. New Britain, New Ireland, Rossel I.,



Fig. 45. Range of *Podocarpus neriifolius* D.DON.

Manus I., Biak, Job I., and Numfoor), common in many islands. Fig. 45.

Ecology. 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 hill-tops, 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 (*Tristania*) 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 *Pometia* 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.

Vern. *Brown pine*, E; Malaya: *jati bukit*, Pahang; Sumatra: *ambai ayam*, Indragiri, *hatang*, Tapanuli, *kayu tadji*, Palembang, *minangkas*, Bencoolen, *naru dotan*, Simalur I., *sito bu hotang*, Karo-Batak; Java: *antoh*, J, Japara, *ki bima*, *ki merak*, *ki pantjar*, *ki putri*, S; Borneo: *belah buloh*, Lawas, Sarawak, *djadjaruman*, Sampit, *ki beling*, Sabah; Celebes: *kurniah*, Nokilalaki; Lesser Sunda Islands: *hadjo ketong*, *hadju pinis rona*, Flores; Moluccas: *bitao*, Halmaheira; West New Guinea: *aiwimuwuwamee*, Biak lang., *bung*, Mayu lang., *buskagidji*, *buts-gagyi*, Andai, Manikiong lang., *gedorra*, Fakfak, Esania lang., *kayu tjina merah*, Kp. Baros, *korrikan*, Tehid lang., *uwa*, Amberbaken lang., *wajar*, Mandobo lang., *wasabraren*, Numfoor I.; East New Guinea: *isumberi*, Nindewari, *sipiri*, Kikori R., *sirau*, Bulolo, Gairana dial.

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 bud-scales 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.

2. *Podocarpus rubens* DE LAUB. *Blumea* 30 (1985) 266. — *P. neriifolius* var. *timorensis* WASSCHER, *Blumea* 4 (1941) 451. — *P. pilgeri* (non FOXW.) VAN ROYEN, *Alpine Fl. New Guinea* 2 (1979) 29, f. 39A. — Fig. 46.



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

Ecology. Scattered as a medium-sized, substage tree in primary rain-forest mostly above 1500 m but as



Fig. 47. Range of *Podocarpus rubens* DE LAUB.

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*.

Vern. West New Guinea: *bebi-è*, Wissel Lakes, Kapauko lang., *ungpop*, Arfak, Hattam lang.; East New Guinea: *bin*, Ingembit village, W. Distr., *kaip*, Wabag, Enga lang., *nelil*, Mt Tangis, New Britain, *sukou*, Wigote, Wapi lang.

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 I. 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. crassigemmis* and could represent a new allied species.

3. *Podocarpus archboldii* N.E.GRAY, J. ARN. Arb. 39 (1958) 452; GAUSSEN, *Gymn. Act. & Foss.* fasc.

14, ch. 21 (1976) 177; DE LAUB. *Blumea* 26 (1980) 140.

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 1–1.4 cm, apex broadly acute, base abruptly narrowed to a petiole up to 5 mm long, midrib above blunt, 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.

Distr. *Malesia*: New Guinea. Fig. 48.

Ecol. Scattered and locally common in the canopy of mixed mid-mountain rain-forest with *Castanopsis* from 720 to 2200 m.

Vern. West New Guinea: *mu*, *soa*, Kebar lang.; East: *sarau*, Bululo, Geraina.

Note. Sterile specimens strongly resemble *P. neriifolius* but strictly lack acuminate leaf tips and the upper midrib has sloping, not vertical sides. Unlike *P. neriifolius* the pollen cones are sometimes pedunculate and the fruit receptacle sometimes has an extra lateral bract.

4. *Podocarpus insularis* DE LAUB. *Blumea* 30 (1985) 266.

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 bud scales 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 *Malesia*: 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.

Vern. East New Guinea: *dala*, *tunum*, Milne Bay, Daga lang., *ida-ayebo*, Kutubu lang.

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.

5. *Podocarpus deflexus* RIDLEY, Fl. Mal. Pen. 5 (1925) 283; WASSCHER, Blumea 4 (1941) 427; GRAY, J. Arn. Arb. 39 (1958) 450; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 175, t. 802.

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.



Fig. 48. Range of *Podocarpus archboldii* N.E. GRAY (A), *P. deflexus* RIDLEY (D), and *P. borneensis* DE LAUB. (B).

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 monoecious inasmuch as a random field inspection of about a dozen trees showed every single one to bear male buds (fruiting specimens have been collected at a different time of year).

6. *Podocarpus borneensis* DE LAUB. Blumea 30 (1985) 266. — *P. polystachus* var. *rigidus* WASSCHER, Blumea 4 (1941) 460; GRAY, J. Arn. Arb. 39 (1958) 471.

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–)4–7.5 (–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 axillary 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, Kenya 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.

7. *Podocarpus levis* DE LAUB. Blumea 24 (1978) 496.

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 channeled, 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 Salhutu & Mt Hori), 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.



Fig. 49. Range of *Podocarpus insularis* DE LAUB. (east of line) and *P. levis* DE LAUB. (west of line).

Vern. Celebes: *marisa*, Donggala, *sanru*, Malili; New Guinea: *kayu tjina*, Meos Noom, *wasiwarare*, Japen I.

8. *Podocarpus spathoides* DE LAUB. *Blumea* 30 (1985) 267.

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 (Lousiades: 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*

DE LAUB. *Blumea* 30 (1985) 267.

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 bud scales 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 *sp.*, 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 bud scales and acuminate leaves.

KEY TO THE SPECIES

1. Seed and its covering at least 11 by 8 mm, 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*

9. *Podocarpus ledermannii* PILGER, Bot. Jahrb. 54 (1916) 210; in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 248; WASSCHER, Blumea 4 (1941) 456; N.E.GRAY, J. Arn. Arb. 39 (1958) 447; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 173, t. 827; DE LAUB. Blumea 26 (1980) 140. — *P. idenburgensis* N.E.GRAY, J. Arn. Arb. 39 (1958) 447; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 171, t. 826. — *P. ridleyi* N.E.GRAY, J. Arn. Arb. 39 (1958) 426, f. 1.

Tree, 4–26(–33) m tall, 8–60 cm diam. Foliage buds 4–8 mm long by 3–4 mm in diam., the primary bud 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. *Malesia*: New Guinea and New Britain. Fig. 51.

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

Vern. West New Guinea: *sua*, Kebar, *bèbieai*, Kapauko lang.; East New Guinea: *babako*, Aijura, Anona; New Britain: *neleel*, Cape Gloucester, *nelil*, Mt Talawe.

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.

10. *Podocarpus micropedunculatus* DE LAUB. Blumea 30 (1985) 268.

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 bud scales 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. *Malesia*: 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).

Ecol. Scattered in understory of *Agathis* forest or forming a major element in thickets along the margins of clearings, mostly on sandy, podzolic soils, kerangas, sandstone, humic peaty podsols 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

DE LAUB. Blumea 30 (1985) 268.

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 acuminate, 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*

11. *Podocarpus globulus* DE LAUB. *Blumea* 30 (1985) 269.

Tree, 3.5–27 m tall, to 18 and more cm diam. *Juvenile leaves* 7.5–16 by 1.5–2.4 cm, abruptly acuminate. *Adult leaves* linear, narrowing more or less abruptly at the base to a 2–3 mm 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.

12. *Podocarpus teysmannii* MIQ. *Fl. Ind. Bat.* 2 (1859) 1072; DE BOER, *Conif. Arch. Ind.* (1866) 14, t. 1; PARL. in *DC. Prod.* 16, 2 (1868) 516; WARB. *Monsunia* 1 (1900) 193; PILGER, *Pfl. R.* IV, 5, Heft



Fig. 52. Range of *Podocarpus globulus* DE LAUB. (G) and *P. teysmannii* MIQ. (T).

18 (1903) 81. — *Nageia teysmannii* (MIQ.) O. K. *Rev. Gen. Pl.* 2 (1891) 800. — *P. neriifolius* var. *teysmannii* (MIQ.) WASSCHER, *Blumea* 4 (1941) 453; N.E. GRAY, *J. Arn. Arb.* 39 (1958) 468; GAUSSEN, *Gymn. Act. & Foss. fasc.* 14, ch. 21 (1976) 189.

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 (West coast 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*, West coast.

4. Section Longifoliolatus

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

Primary foliage bud scales 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 bud scales 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

15. *P. bracteatus*

4. Leaves mostly less than 10 mm wide; foliola at base of receptacle up to 3.4 mm long; bud for pollen cone c. 2 mm in diameter; pollen cone with a short peduncle to 2 mm . . . 16. *P. pseudobracteatus*
3. Leaves less than 8 mm wide; scales at base of pollen cone broad and rounded; fruit blunt

17. *P. atjehensis*

13. *Podocarpus gibbsii* N.E.GRAY, J. Arn. Arb. 39 (1958) 429; GAUSSEN, *Gymn. Act. & Foss. fasc. 14*, ch. 21 (1976) 155, t. 803.

Tree 2.5–20 m tall. Foliage buds 4–9 mm long. *Juvenile leaves* linear, acute, 4–9 cm by 5–9 mm. *Adult leaves* linear to ovate, 2–5 cm by 4–7 mm, acute to almost rounded at the apex, narrowed at the base to a 1–3 mm petiole; midrib above weakly developed, 0.5–0.7 mm wide and 0.1–0.2 mm high and often collapsing upon drying leaving a weak depression with a narrow ridge in the centre, upper hypoderm continuous. *Pollen cones* 1–1.5 cm, sessile, solitary or occasionally a pair; apex of microsporophyll triangular, up to 0.8 mm long. *Seed-bearing structure* on a peduncle at least 3 mm long; foliola 4 mm long; receptacle formed of two unequal bracts; mature seed unknown.

Distr. *Malesia*: Borneo (Sabah: Mt Kinabalu). Fig. 53.



Fig. 53. Range of *Podocarpus gibbsii* N.E.GRAY (G) and *P. atjehensis* (WASSCHER) DE LAUB. (A).

Ecol. Mossy ridges between 1200 and 2400 m, mostly or always on ultrabasic soil.

Note. The leaves generally resemble those of *P. pilgeri*, a species which is not otherwise similar at all.

14. *Podocarpus confertus* DE LAUB. *Blumea* 30 (1985) 271.

Tree 1–36 m tall. Foliage buds 6–10 mm long. *Juvenile leaves* up to 20 by 1.2 cm. *Adult leaves* linear to linear-lanceolate, 5–12 cm by 7–11 mm, acute, narrowing at the base to a 3–6 mm petiole; midrib above obtuse, 1 mm wide and 0.2–0.3 mm high, collapsing when dry to form a narrow irregular ridge or becoming completely flat, upper hypoderm

continuous. *Pollen cones* 3–4.5 cm, sessile, solitary or occasionally in pairs; apex of microsporophyll triangular, 0.3–0.5 mm long. *Seed-bearing structure* on a 5–13 mm peduncle; foliola 5–6 mm long; receptacle 8–12 mm, formed of two unequal bracts. *Seed* with its covering 10–11 by 6–6.5 mm.

Distr. *Malesia*: Borneo (Sabah: Mt Silam). Fig. 54.

Ecol. In dense local populations on various poor soils some or most of which are ultrabasic; subdominant in somewhat open and sometimes stunted forest from 90 to 1200 m.

15. *Podocarpus bracteatus* BLUME, *En. Pl. Jav.* 1 (1827) 88; BENNETT in Bennett & R.Br. *Pl. Jav. Rar.* 1 (1838) 40; ENDL. *Syn. Conif.* (1847) 216; BLUME, *Rumphia* 3 (1849) 214, t. 172, f. 1; MIQ. *Pl. Jungh.* 1 (1851) 2; *Fl. Ind. Bat.* 2 (1859) 1072; HENKEL & HOCHSTETTER, *Synop. Nadelhölz.* (1865) 391; DE BOER, *Conif. Arch. Ind.* (1866) 16; PARL. in DC. *Prod.* 16, 2 (1868) 515; EICHLER in E. & P. *Nat. Pfl. Fam.* 2, 1 (1887) 104; WARB. *Monsunia* 1 (1900) 192. — *P. neriifolius* var. *bracteatus* (BLUME) WASSCHER, *Blumea* 4 (1941) 449; GAUSSEN, *Gymn. Act. & Foss. fasc. 14*, ch. 21 (1976) 189, t. 806. — *P. bracteatus* var. *brevipes* BLUME, *Rumphia* 3 (1849) 214; MIQ. *Pl. Jungh.* 1 (1851) 2; HENKEL & HOCHSTETTER, *Synop. Nadelhölz.* (1865) 392; PARL. in DC. *Prod.* 16, 2 (1868) 515. — *P. neriifolius* var. *brevipes* (BLUME) PILGER, *Pfl. R.* IV, 5, Heft 18 (1903) 81; GAUSSEN, *Gymn. Act. & Foss. fasc. 14*, ch. 21 (1976) 187. — *P. neriifolius* (non D.DON) STEEN. *Mt. Fl. Java* (1972) t. 13, f. 1.

Tree 10–40 m tall, 15–100 cm diam. Foliage buds 5–12 mm long. *Juvenile leaves* up to 23 by 2 cm. *Adult leaves* distinctly lanceolate, 6–14 cm by 9–14 mm, narrowly acute, narrowing at the base to a 2–4 mm petiole, sometimes with 5 vascular resin canals, midrib above a sharp ridge 0.4 mm wide and 0.3 mm high, sometimes collapsing when dried into a trough. *Pollen cones* 3.5–6 cm by 3–4 mm, sessile but elongating when mature through the scaly base as well as the zone of microsporophylls and the scales then following, the elongated scaly base up to 8 mm long, solitary or occasionally in pairs; apex of microsporophyll c. 1 mm long. *Seed-bearing structure* on a 10–20 mm peduncle; foliola 4–5 mm long; receptacle 10–14 mm long, often with two fertile

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.

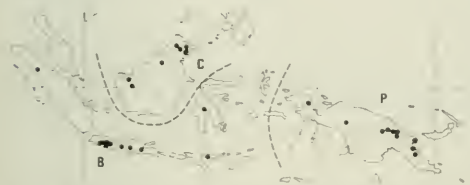


Fig. 54. Range of *Podocarpus confertus* DE LAUB. (C), *P. bracteatus* BLUME (B), and *P. pseudobracteatus* DE LAUB. (P).

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.

Vern. 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 nerifolius* 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 bud scales, and a more distinctly lanceolate shape.

16. Podocarpus pseudobracteatus DE LAUB. *Blumea* 26 (1980) 142. — *P. archboldii* var. *crassiramosus* N.E. GRAY, *J. Arn. Arb.* 39 (1958) 453.

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.

Vern. East New Guinea: *kaip*, Wabag, Enga lang., *kebu*, Tari Gap, *puling*, Togoba, Chimbu.

17. Podocarpus atjehensis (WASSCHER) DE LAUB. *Blumea* 30 (1985) 271. — *P. nerifolius* var. *atjehensis* WASSCHER, *Blumea* 4 (1941) 450; N.E. GRAY, *J. Arn. Arb.* 39 (1958) 466; GAUSSEN, *Gymn. Act. & Foss. fasc.* 14, ch. 21 (1976) 189.

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. glaucus*; 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 inasmuch 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. wangii*, 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*
 3. Leaves crowded (overlapping). Fruit crested 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*

18. *Podocarpus pilgeri* FOXW. Philip. J. Sc. 2 (1907) Bot. 259; *ibid.* 6 (1911) Bot. 160; PILGER, Bot. Jahrb. 54 (1916) 38; in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 248; N.E. GRAY, J. Arn. Arb. 39 (1958) 459; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 185, t. 810; DE LAUB, Kalikasan 7 (1978) 135. — *P. celebica* (non HEMSL.) WARB. Monsunia 1 (1900) 192; PILGER, Pfl. R. IV, 5, Heft 18 (1903) 78. — *P. costalis* (non PRESL) FOXW. Philip. J. Sc. 6 (1911) Bot. 161. — *P. schlechteri* PILGER, Bot. Jahrb. 54 (1916) 209; in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 248; LAUT. Bot. Jahrb. 63 (1930) 474; PILGER, Bot. Jahrb. 68 (1936) 246; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 187. — *P. wangii* CHANG, Sunyatsenia 6 (1941) 26.

Tree 1–25 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 Nettoti in low *Xanthomyrtus-Podocarpus* crest forest.

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

Fig. 55. Range of *Podocarpus pilgeri* Foxw.

kaibelugt, Wahgi, Minj, *kebu*, Mt Ne, *monopana*, Mairi, Natabung, *puling*, Hagen, Wankl, *sosumehi*, Dunantina, *sula*, Chimbu, Masul, *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.

19. *Podocarpus lophatus* DE LAUB. Kalikasan 7 (1978) 137. — *P. brevifolius* (non STAPF) FOXW. Philip. J. Sc. 6 (1911) Bot. 160, t. 29, f. 2; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) t. 801 p. p.

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.

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

Ecol. Mossy forest at 1800 m.

20. *Podocarpus rotundus* DE LAUB. Kalikasan 7 (1978) 136.

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 without a crest.

Distr. *Malesia*: E. Borneo (Mt Beratus near Balikpapan) and Philippines (Luzon: Mt Banajao in Ilaguna Prov. and Iucban in Tayabas Prov.), 3 collections. Fig. 56.

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

Fig. 56. Range of *Podocarpus lophatus* DE LAUB. (L) and *P. rotundus* DE LAUB. (R).

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; WASSCHER, *Blumea* 4 (1941) 468; N.E. GRAY, *J. Arn. Arb.* 39 (1958) 440; GAUSSEN, *Gymn. Act. & Foss. fasc.* 14, ch. 21 (1976) 163, t. 825; DE LAUB. *Kalikasan* 7 (1978) 138.

Decumbent shrub to small or medium-sized tree, 2–15 m tall, up to 20–25 cm diam. Foliage buds 1–1.5 mm long and 1.5 mm in diam.; primary bud-scales 0.6 mm wide. *Juvenile leaves* oval, 2–3.5 cm by 5–7 mm. *Adult leaves* ovate, the widest part somewhat beyond the centre, 1–2 cm by 3–6 mm, round and very blunt at the apex, narrowing at the base to a 2–3 mm petiole, revolute, crowded, flushing red, at least sometimes glaucous; midrib above a distinct ridge 0.2 mm wide. *Pollen cones* 1–2 cm long, often elongating in the basal scaly part to 1–2 mm. *Female receptacle* becoming purple when mature. *Seed* with its covering with a distinct crest.

Distr. Solomon Islands; in *Malesia*: New Guinea

Fig. 57. Range of *Podocarpus glaucus* Foxw.

(also on Arfak Mts, and incl. Manus in Admiralty Is.), Moluccas (W. Ceram), and Philippines (Mindoro). Fig. 57.

Ecol. 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.

Vern. West New Guinea: *nipa*, Kebar, *bèbiai*, Kapauko lang.

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

6. Section *Macrostachyus*

DE LAUB. *Blumea* 30 (1985) 273.

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 as 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).

Ecol. Locally common at high elevations or on mossy ridges. One species, *P. costalis*, largely confined to a group of small islands 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 Singgalang, 2800 m) placed with *P. bracteatus* (*sect. Longifolius*), 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*

22. *Podocarpus crassigemmis* DE LAUB. *Blumea* 26 (1980) 141. — *P. archboldii* (non N.E. GRAY) GAUSSEN, *Gymn. Act. & Foss. fasc.* 14, ch. 21 (1976) 177, t. 828; VAN ROYEN, *Alpine Fl. New Guinea* 2 (1979) 30, t. 41.

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.



Fig. 58. Range of *Podocarpus crassigenmis* DE LAUB.

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.

Vern. East New Guinea: *a-pul*, *kaboga*, *morumba*, Mt Giluwe, Mendi lang., *baula*, Kundiawa, Chimbu, *iamuka*, Tomba, *jamekang*, Hagen, Tomba, *juba*, *kamga*, *puling*, Hagen, Togoba, *kabor*, Anga Valley, Mendi lang., *kabiltugl*, *kaibelparu*, *kaibig*, Wahgi, Minj, *kaip*, Kepilam, Enga lang., *nonofan*, Mairi, Watabung, *ronohanini*, Asaro, Kefamo, *(t)sula*, Chimbu, Masul.

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 (LAL 51011) of which the leaves were infected with *Corynelia uberata* FRHS, widely distributed in the Old World.

23. *Podocarpus brassii* PILGER, Bot. Jahrb. 68 (1937) 246; WASSCHER, Blumea 4 (1941) 469; N.E. GRAY, J. Arb. Arb. 39 (1958) 440; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 163, t. 824; VAN ROYEN, Alpine Fl. New Guinea 2 (1979) 24, t. 37, 38.

KEY TO THE VARIETIES

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



Fig. 59. Range of *Podocarpus brassii* PILGER (east of line), *P. brevifolius* (STAPE) FOXW. (B), and *P. costalis* PRESL (C).

Ecol. Common and sometimes dominant near the tree line, often an emergent in alpine scrub, often flat-topped, also a gnarled treelet 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, Ibiwara 2700 m, Wissel Lakes 2000 m.

Vern. East New Guinea: *bacela*, Kundiawa,

Chimbu, *baugwa*, Waimambano, Chimbu, *chuga*, Chimbu dial., *kaibigl-tuga, ra*, Kubor, Minj, *kaipil*, Wahgi, Minj, *maja*, Mairi, Mondo, *tsulo*, Masul, Chimbu.

b. var. *humilis* DE LAUB. *Blumea* 30 (1985) 274.

Decumbent shrub to small tree up to 5 m high. *Pollen cones* 3.5–4.5 mm diam.; apex of the microsporophyll triangular, 1 mm long.

Distr. *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.

24. *Podocarpus brevifolius* (STAPF) FOXW. Philip J. Sc. 6 (1911) Bot. 160, t. 29, f. 2; PILGER, Bot. Jahrb. 54 (1916) 40; WASSCHER, *Blumea* 4 (1941) 466; N.E. GRAY, J. Arn. Arb. 39 (1958) 441; GAUSSEN, *Gymn. Act. & Foss. fasc.* 14, ch. 21 (1976) 165, t. 801, *p.p.* — *P. neriifolius* var. *brevifolius* STAPF, *Trans. Linn. Soc. Bot.* 11, 4 (1894) 249.

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.* 3 mm long; receptacle 6–8 mm long. *Seed* with its covering 10–12 (including a small crest) by 6.5 mm.

Distr. *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.

25. *Podocarpus costalis* PRESL, *Epim. Bot.* (1849) 236; PILGER, *Pfl. R.* IV, 5, Heft 18 (1903) 78; FOXW. Philip J. Sc. 6 (1911) Bot. 161, *p.p.*; N.E. GRAY, J. Arn. Arb. 39 (1958) 456; GAUSSEN, *Gymn. Act. & Foss. fasc.* 14, ch. 21 (1976) 183, t. 831. — *P. polystachyus* (*non* R.Br.) LI & KENG, *Taiwania* 5 (1954) 34, t. 5; LI, *Woody Fl. Taiwan* (1963) 41, f. 5; GAUSSEN, *Gymn. Act. & Foss. fasc.* 14, ch. 21 (1976) t. 812, *p.p.*

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.

Distr. S. Taiwan (Orchid I.); in *Malesia*: Philip-pines (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*

DE LAUB. *Blumea* 30 (1985) 274.

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 they 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; foliolar 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 bud scales often completely adpressed; receptacle often with a third lateral smaller sterile bract 26. *P. rumphii*
 1. Pollen cone clusters usually on a small peduncle; foliage bud scales always spreading at the tips; receptacle never with a third lateral sterile bract 27. *P. laubenfelsii*

26. Podocarpus rumphii BLUME, *Rumphia* 3 (1849) 214; MIQ. *Fl. Ind. Bat.* 2 (1859) 1073; HENKEL & HOCHSTETTER, *Synop. Nadelhölz.* (1865) 393; DE BOER, *Conif. Arch. Ind.* (1866) 15; PARL. in DC. *Prod.* 16, 2 (1868) 515; BECC. *Malesia* 1 (1877) 179; EICHLER in E. & P. *Nat. Pfl. Fam.* 2, 1 (1887) 104; WARB. *Monsunia* 1 (1900) 192; PILGER, *Pfl. R.* IV, 5, Heft 18 (1903) 81; FOXW. *Philip. J. Sc.* 2 (1907) Bot. 258; MERR. *Interpr. Rumph.* (1917) 75; FOXW. *Philip. J. Sc.* 6 (1911) Bot. 164; WASSCHER, *Blumea* 4 (1941) 432; N.E. GRAY, *J. Arn. Arb.* 39 (1958) 455; GAUSSEN, *Gymn. Act. & Foss. fasc.* 14, ch. 21 (1976) 179, t. 815; DE LAUB. *Blumea* 24 (1978) 496; Kalikasan 7 (1978) 141. — *Nageia rumphii* (BLUME) F.V.M. *Descr. Not.* 1 (1877) 93. — *P. koordersii* PILGER ex K. & V. *Bijdr. Booms.* 10 (1904) 268; KOORD. *Exk. Fl. Java* 1 (1911) 66; K. & V. *Atlas Baumart. Java* 3 (1915) t. 587; WASSCHER, *Blumea* 4 (1941) 431; N.E. GRAY, *J. Arn. Arb.* 39 (1958) 433; BACKER & BAKH. *f. Fl. Java* 1 (1963) 90; GAUSSEN, *Gymn. Act. & Foss. fasc.* 14, ch. 21 (1976) 159, t. 804. — *P. philippinensis* FOXW. *Philip. J. Sc.* 6 (1911) Bot. 163, t. 30; N.E. GRAY, *J. Arn. Arb.* 39 (1958) 434; GAUSSEN, *Gymn. Act. & Foss. fasc.* 14, ch. 21 (1976) 159.

Tree 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 out-

ward 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 I. (Java Sea), Borneo (Sabah, incl. Selangan Is.), Philippines (Luzon: Agusan del Norte), Celebes, Lesser Sunda 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, 5–200 (600–1550) m.

Uses. Reported to be a good timber tree.



Fig. 60. Range of *Podocarpus rumphii* BLUME.

Vern. Borneo: *kayu china*, Sabah, Selangan; Philippines: *malakanayan*, Luzon, Agusan; Celebes: *sandu*, Malili; Lesser Sunda Islands: *mermolos*, *moak*, Flores, *e-tama*, Timor, Bunaq lang.; Molucas: *kayu china*, *rangundjela*, Aru Is., P. Wokam; West New Guinea: *aibemmunowame*, *aiwimunwame*, Fakfak, Biak lang., *eswasa*, *weswaze*, Arguni Bay, Irahutu lang., *manulit*, Misool I., *onen*, Warsamson R., Mooi lang., *osien*, Sorong, Mooi lang., *djera*, *si-era*, Mimika, *wasabrarán*, Numfoor, Biak lang.

Note. Generally homogeneous throughout its range but the transition from large juvenile to small adult leaves mostly takes the form of long slender leaves towards the west and shorter broader leaves further east, especially in the Aru region. The Aru specimens apparently lack the usual continuous upper hypoderm as well.

27. *Podocarpus laubenfelsii* TIONG, *Blumea* 29 (1984) 523.

Tree, 14–35 m tall, 20–60 cm diam. Foliage buds

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.

Distr. *Malesia*: Borneo (Sarawak: Lawas; Sabah: Trusmadi & Kinabalu; E. Kalimantan: Kutei). 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*

DE LAUB. *Blumea* 30 (1985) 275.

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 bud scales 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 bud scales 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; *foliola* 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 28. *P. polystachyus*
 2. Seed and its covering more than 10 mm in diameter. Midrib above blunt 29. *P. macrocarpus*
1. Adult leaves lanceolate, narrowly acute at the apex, upper midrib indistinct 30. *P. ridleyi*

28. *Podocarpus polystachyus* R.Br. ex ENDL. Syn.

Conif. (1847) 215; MIQ. Fl. Ind. Bat. 2 (1859) 1072; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 392; PARL. in DC. Prod. 16, 2 (1868) 515; WARB. Monsunia 1 (1900) 192; PILGER, Pfl. R. IV, 5, Heft 18 (1903) 79; MERR. Philip J. Sc. 3 (1908) Bot. 394; FOXW. Philip. J. Sc. 6 (1911) Bot. 161; RIDLEY, Fl. Mal. Pen. 5 (1925) 282, t. 228; WASSCHER, Blumea 4 (1941) 456, t. 5, f. 14a–c; N.E.GRAY, J. Arn. Arb. 39 (1958) 469, f. 4; KENG in Whitmore, Tree Fl. Mal. 1 (1972) 49, f. 3, *p.p.*; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 191, t. 812, *p.p.*; DE LAUB. Kalikasan 7 (1978) 142. — *P. neriifolius* D.DON in Lamb., Pinus 1 (1824) 21, *p.p.*; HOOK. f. Fl. Brit. India 5 (1888) 649, *p.p.* — *P. thevetiaefolia* BLUME, Rumphia 3 (1849) 213; MIQ. Fl. Ind. Bat. 2 (1859) 1074; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 397; DE BOER, Conif. Arch. Ind. (1866) 22, t. 2; PARL. in DC. Prod. 16, 2 (1868) 518; BECC. Malesia 1 (1877) 180; WARB. Monsunia 1 (1900) 192; PILGER, Pfl. R. IV, 5, Heft 18 (1903) 79; WASSCHER, Blumea 4 (1941) 462; N.E.GRAY, J. Arn. Arb. 39 (1958) 457; BACKER & BAKH. f. Fl. Java 1 (1963) 90; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 183, t. 829. — *Nageia thevetiaefolia* (BLUME) F.V.M. Descr. Not. Pap. Pl. 1 (1877) 93. — *Nageia polystachyus* (R.Br. ex ENDL.) O. K. Rev. Gen. Pl. 2 (1891) 800. — Fig. 62.

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, $\times 1.4$ (Photogr. A. ELSNER, 1965).

apiculate, sometimes mixed with more typical adult leaves. *Adult leaves* linear to oval, 3–10 cm by 6–13 mm, more or less acute to rounded at the apex, narrowed abruptly at the base to a 1–3 mm peduncle, margin flat or nearly so; midrib above a sharp ridge 0.3–0.4 mm wide and 0.2 mm high. Buds for pollen cones sessile. *Pollen cones* 2–4 cm long, clustered in groups of up to at least five. *Seed-bearing structure* on a 1–6 mm peduncle; foliola 1–1.5 mm long, falling; *receptacle* 7–10 mm long. *Seed* with its covering 7–9 by 5–7 mm.

Distr. Southernmost Peninsular Thailand; in *Malesia*: Malay Peninsula, Riouw-Lingga & Banka Is., Borneo (W. Kalimantan: Pasir Pandjang & Karimata I.; Sarawak; Brunei; Sabah), Philippines (Palawan; Luzon: Tayabas & Ilocos Norte Prov.), Moluccas (Obi, Waigeu), West New Guinea (Vogelkop Peninsula). Fig. 63.



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

Ecol. 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 hightide 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.

Vern. Malaya: *jati bukit*, Selangor; Lingga: *kayu karamat*; Borneo: W. Kalimantan: *mayu serai*, Bt. Besar, *tentada*, Matan; Sarawak: *landin*, Bintulu;

Brunei: *anggeriting*; Sabah: *kandabang*, Bajau l'tan, *kayu china*, Sibuboh For. Res., *saumah*, Manadahan; New Guinea: Vogelkop: *arbudjin*, Maibrat lang., *rabudien*, Lake Ajamaru.

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.

29. *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.



Fig. 64. Range of *Podocarpus macrocarpus* DE LAUB. (M) and *P. ridleyi* (WASSCHER) N.E. GRAY (R).

Ecol. Scattered and sometimes common in cloud forests, c. 2000–2100 m. One collection reported at 700 m is doubtful.

30. *Podocarpus ridleyi* (WASSCHER) N.E. GRAY, J. Arn. Arb. 39 (1958) 435; GAUSSEN, Gymn. Act. & Foss. fasc. 14, ch. 21 (1976) 159, t. 814. — *P. nerii-folius* var. *ridleyi* WASSCHER, Blumea 4 (1941) 453; KENG in Whitmore, Tree Fl. Mal. 1 (1972) 49, f. 3, p.p.

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. over sandstone, 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*.

Maps of fossil distributions are given in FLORIN (1963).

References: FLORIN, Acta Horti Berg. 20 (4) (1963) 121–312, 68 maps; GAUSSEN, Gymn. Act. & Foss. fasc. 11, ch. 14 (1970) 42–56, f. 555–558; MACARTHUR, The genus *Araucaria* in its geographical aspects, Univ. W. Austr., Geogr. Lab. Econ. Dept., Research Rep. 5 (1949); STOCKEY, Canad. J. Bot. 59 (1981) 1932–1940.

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 'pro-suspensor' 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.)

References: BOWEN & WHITMORE, *Commonw. For. Rev.* 59 (1980) 307; B. GRAY, *J. Ecol.* 63 (1975) 273-289; HAVEL, *J. Ecol.* 59 (1971) 203-213; ISMAIL BIN HAJI ALI, *Mal. For.* 27 (1964) 354-360; WHITMORE, *A first look at Agathis*, Oxford (1977); *Econ. Bot.* 34 (1980) 1.

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

JUSS. *Gen. Pl.* (1789) 413; RICHARD, *Comm. Bot. Conif. & Cycad.* (1826) 153; D. DON, *Trans. Linn. Soc.* 18 (1841) 163; LINK, *Linnaea* 15 (1841) 541; ENDL. *Gen. Pl. Suppl.* 2 (1842) 26; *Syn. Conif.* (1847) 184; CARR. *Traité Gén. Conif.* (1855) 413; *Man. Pl.* 4 (1857) 360; GORDON, *Pinetum* ed. 1 (1858) 21; HENKEL & HOCHSTETTER, *Synop. Nadelholz.* (1865) 2; PARL. in DC. *Prod.* 16, 2 (1868) 369; BENTH. & HOOK. *Gen. Pl.* 3 (1880) 423; EICHLER in E. & P. *Nat. Pfl. Fam.* 2, 1 (1889) 67; SEWARD & FORD, *Trans. R. Soc. Lond.* 198 (1906) 317; BARSALI, *Atti Soc. Tosc. Sci. Nat., Mem.* 25 (1909) 145; DALLIMORE & JACKSON, *Handb. Conif.* (1923) 150; PILGER in E. & P. *Nat. Pfl. Fam.* ed. 2, 13 (1926) 263; GAUSSEN, *Gymn. Act. & Foss.* fasc. 11, ch. 14 (1970) 7; DE LAUB. *Fl. Nouv. Ca-*

léd. et Dép. 4 (1972) 80; SILBA, Phytologia Mem. 8 (1986) 38. — *Dombeya* LAMK. Enc. Méth., Bot. 2 (1786) 301, t. 828, *non* L'HÉRIT. *nec* CAV. — *Columbea* SALISB. Trans. Linn. Soc. 8 (1807) 317. — *Colymbea* SPRENG. Syst. Veg. 4, 2 (1827) 888 (refers to SALISBURY, but 'corrects' the spelling); STEUD. Nom. Bot. ed. 2, 1 (1840) 399. — **Fig. 67, 68.**

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 India–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 (FLORIN, K. Svensk. Vet. Ak. Handl. III, 19, 1940, 81, map 5).

KEY TO THE SECTIONS

1. Juvenile leaves bifacially flattened, cotyledons 2, pollen cones lateral 1. *Sect. Araucaria*
 1. Juvenile leaves acicular, cotyledons 4, pollen cones terminal 2. *Sect. Eutacta*

1. Section *Araucaria*

Sect. Colymbea ENDL. Gen. Pl. Suppl. 2 (1842) 26; Syn. Conif. (1847) 185; CARR. Traité Gén. Conif. (1855) 414; Man. Pl. 4 (1857) 360; GORDON, Pinetum ed. 1 (1858) 21; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 2; PARL. in DC. Prod. 16, 2 (1868) 370 ('*Columbea*'); EICHLER in E. & P. Nat. Pfl. Fam. 2, 1 (1889) 69; SEWARD & FORD, Trans. R. Soc. Lond. 198 (1906) 317; PILGER



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

in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 263; WILDE & EAMES, Ann. Bot. n.s. 16 (1952) 44 ('*Columbea*'); GAUSSEN, Gymn. Act. & Foss. fasc. 11, ch. 14 (1970) 7. — *Sect. Intermedia* WHITE, J. Arn. Arb. 28 (1947) 260; WILDE & EAMES, Ann. Bot. n.s. 16 (1952) 44; GAUSSEN, Gymn. Act. & Foss. fasc. 11, ch. 14 (1970) 7. — *Sect. Bunya* WILDE & EAMES, Ann. Bot. n.s. 16 (1952) 44. — *Subg. Colymbea* ANTOINE, Conif. nach Lambert, Loudon & Anderen (1846) 99; CARR. Traité Gén. Conif. 2 (1867) 596.

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. Eutaeta* in epigeal 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. Eutaeta* 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. bidwillii*. *Sect. Bunya* was established for *A. bidwillii* 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. STOCKFY (Canad. J. Bot. 59, 1981, 1932) argues for the usefulness of these monotypic sec-

tions based on a variety of fossil material, but the differences with the residual *sect. Araucaria* hardly seems sufficiently important.

1. *Araucaria hunsteinii* K.SCH. Fl. Kaiser Wilhelms Land (1889) 11, t. 4, f. 8; WARB. *Monsunia* 1 (1900) 187, t. 10, f. B; SEWARD & FORD, *Trans. R. Soc. Lond.* 198 (1906) 324, f. 9; BARSALI, *Atti Soc. Tosc. Sci. Nat.*, Mem. 25 (1909) 158; WILDE & EAMES, *Ann. Bot. n.s.* 16 (1952) t. 2, f. 10; GAUSSEN, *Gymn. Act. & Foss. fasc.* 11, ch. 14 (1970) 16, f. 536; HOWCROFT, *For. Genet. Res. Inf. n.* 8, FAO *For. Occ. Pap.* 1987/2 (1987) 31; SILBA, *Phytologia Mem.* 8 (1986) 41. — *A. schumanniana* WARB. *Monsunia* 1 (1900) 187, t. 10, f. A; WILDE & EAMES, *Ann. Bot. n.s.* 16 (1952) t. 2, f. 11; GAUSSEN, *Gymn. Act. & Foss. fasc.* 11, ch. 14 (1970) 15, f. 535. — *A. klinkii* LAUT. *Bot. Jahrb.* 50 (1914) 48, f. 1; LANE-POOLE, *For. Res. Terr. Papua New Guinea* (1925) 72; WILDE & EAMES, *Ann. Bot. n.s.* 16 (1952) t. 2, f. 7; t. 3; GAUSSEN, *Gymn. Act. & Foss. fasc.* 11, ch. 14 (1970) 15, f. 534 left.

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. *Microsporophyll* 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 ovoid with only the numerous lanceolate spurs visible, mature seed cones obovoid 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 no wider than the seed 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.

Distr. 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.



Fig. 66. Range of *Araucaria hunsteinii* K.SCH.

Ecol. Emergent in the submontane oak forest on well drained sites over a variety of soils from 520 to 2100 m. This is the tallest tree of Malesia. There has been much speculation concerning the origin of the disjunct gregarious stands. Natural regeneration

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.

Vern. *Pa'a*, Watut-Bulolo, *pai*, Waria-Kaisinik, *gerau*, Waria, *bimu*, Toma, *yanguman*, Agaun, *yomejo*, Kotte-Pindui, *karina*, Bembi-Madang, *rassu*, Ongoruna, *nd'uk*, Wareng, *kembaga*, *saa'vara*, Taiora, *sowes*, Erave, Mt Matmuri.

NOTE. HOWCROFT (*l.c.*: 5, 31) has distinguished a glaucous variety that corresponds to *A. klinkii*. Not only are fresh leaves glaucous, but the cones are also gray-blue due to a white exudate on their surface.

2. Section *Eutacta*

ENDL. Gen. Pl. Suppl. 2 (1842) 26; Syn. Conif. (1847) 186; CARR. Traité Gén. Conif. (1855) 418; Man. Pl. 4 (1857) 361; GORDON, Pinetum ed. 1 (1858) 26; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 9; PARL. in DC. Prod. 16, 2 (1868) 372; EICHLER, in E. & P. Nat. Pfl. Fam. 2, 1 (1889) 69; SEWARD & FORD, Trans. R. Soc. Lond. 198 (1906) 318; BARSALI, Atti Soc. Tosc. Sci. Nat., Mem. 25 (1909) 157; PILGER in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 265; FRANCO, Port. Acta Biol. Sist. ser. B, Julio Henriques (1949) 24; WILDE & EAMES, Ann. Bot. n.s. 16 (1952) 43; GAUSSEN, Gymn. Act. & Foss. fasc. 11, ch. 14 (1970) 7; DE LAUB. Fl. Nouv. Caléd. et Dép. 4 (1972) 81. — *Sect. Eutassa* (SALISB.) BENTH. & HOOK. Gen. Pl. 3 (1800) 437. — *Eutassa* SALISB. Trans. Linn. Soc. 8 (1807) 316. — *Eutacta* LINK, Linnaea 15 (1841) 543 (refers to SALISBURY, but 'corrects' the usage). — *Subg. Eutacta* (LINK) ANTOINE, Conif. nach Lambert, Loudon & Anderen (1846) 99; CARR. Traité Gén. Conif. ed. 2 (1867) 604.

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.

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

2. *Araucaria cunninghamii* Ait. ex D. DON in Lamb. Pinus ed. 2, 3 (1837) t. 79; SWEET, Hort. Brit. 2 (1830) 475, *nomen*; LAMB. Pinus ed. 3 (1832) no pages, *nomen*; LOUD. Arb. & Fruct. Brit. 4 (1838) 2443, t. 2303–2305 *et suppl.* 2603, f. 2545; FORBES, Pin. Wob. (1839) 157, t. 52; ANTOINE, Conif. nach Lambert, Loudon & Anderen (1846) 102, t. 43 & 44; ENDL. Syn. Conif. (1847) 187; CARR. Traité Gén. Conif. (1855) 419; Man. Pl. 4 (1857) 361; GORDON,

Pinetum ed. 1 (1858) 27; HENKEL & HOCHSTETTER, Synop. Nadelholz. (1865) 9; PARL. in DC. Prod. 16, 2 (1868) 372; SEBOLD, Flor. Jap. 2 (1870) t. 139; SEWARD & FORD, Trans. R. Soc. Lond. 198 (1906) 325, f. 8c; BARSALI, Atti Soc. Tosc. Sci. Nat., Mem. 25 (1909) 167; WHITE, J. Arn. Arb. 10 (1929) 200; *ibid.* 28 (1947) 259; FRANCO, Bot. Soc. Brot. 2, 23 (1949) 162; GAUSSEN, Gymn. Act. & Foss. fasc. 11, ch. 14 (1970) 32; REILLY, Dept. For. Qld. Res. Pap.



Fig. 67. *Araucaria cunninghamii* AIT. ex D.DON var. *papuana* LAUT. in West New Guinea, Kebar Valley, Vogelkop Peninsula, 600 m alt. (Photogr. J.F.U.ZIECK, 1954).

n. 4 (1974); SILBA, Phytologia Mem. 8 (1986) 40. — *Eutacta cunninghamii* (AIT.) LINK, Linnaea 15 (1841) 543; CARR. Traité Gén. Conif. ed. 2 (1867) 608. — *Eutassa cunninghamii* SPACH, Hist. Nat. Veg. Phan. 11 (1842) 362. — Fig. 67, 69.

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 hori-

zontal 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.

var. papuana LAUT. Bot. Jahrb. 50 (1913) 51; SILBA, Phytologia Mem. 8 (1986) 40. — *A. beccarii* WARB. Monsonia 1 (1900) 187; GIBBS, Arfak (1917) 83, f. 5. — *A. cunninghamii* auct. non AIT.: BECC. Malesia 1 (1877) 180; F.V.M. Vict. Nat. 4 (1887) 121; Descr. Not. 9 (2) (1890) 65; LANE-POOLE, For. Res. (1925) 73; HOWCROFT, For. Genet. Res. Inf. n. 8, FAO For. Occ. Pap. 1979/1 (1979) 9. — **Fig. 67, 69.**

Bark, particularly of younger plants, dark plum to red-brown, weathering on older plants to gray or blackish. *Juvenile leaves* up to 23–27 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, *sumgwa*, Manikiong, *alloa*, Marconi R., *kiriwi*, Wandammen, *ningwik*, Tambuni Valley, *makut*, Pikipik, *domooimerr*, *tororomooi*, Dajo, *jarujosuwa*, Tanahmerah, *flabbito*, Wapi, *d'li*, Telefomin, *escera*, Foie, *sari*, Bembu, *bontuan*, Kaigorin, *wariri*, Gurumbu, *nimola*, Esa'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

SALISB. Trans. Linn. Soc. 8 (1807) 311, t. 15, *nom. cons.* (unnecessarily); RICHARD, Comm. Bot. Conif. Cycad. (1826) 83, t. 19; WARB. *Monsunia* 1 (1900) 182; SEWARD & FORD, Trans. R. Soc. Lond. 198 (1906) 310; DALLIMORE & JACKSON, Handb. Conif. (1923) 138; PILGER in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 266; MEIJER DREES, Bull. Jard. Bot. Btzg III, 16 (1940) 455; FRANCO, An. Inst. Sup. Agron. 18 (1951) 101; GAUSSEN, Gymn. Act. & Foss. fasc. 11, ch. 14 (1970) 75; DE LAUB. Fl. Nouv. Caléd. et Dép. 4 (1972) 126; WHITM. Trop. For. Pap. 11 (1977) 3; Pl. Syst. Evol. 135 (1980) 46, f. 1–5; SILBA, Phytologia Mem. 8 (1986) 31. — *Dammara* LINK, Enum. Hort. Berol. Alt. 2 (1822) 411, given in synonymy with *Agathis* [*non* GAERTN. Fruct. Sem. Pl. 2 (1790) 100, t. 103, f. 1, *Burseraceae*]; ENDL. Syn. Conif. (1847) 188; BLUME, Rumphia 3 (1847) 211; CARR. Traité Gén. Conif. (1855) 424; Man. Pl. 4 (1857) 363; GORDON, Pinetum ed. 1 (1858) 77; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 209; PARL. in DC. Prod. 16, 2 (1868) 374. — **Fig. 70–85.**

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

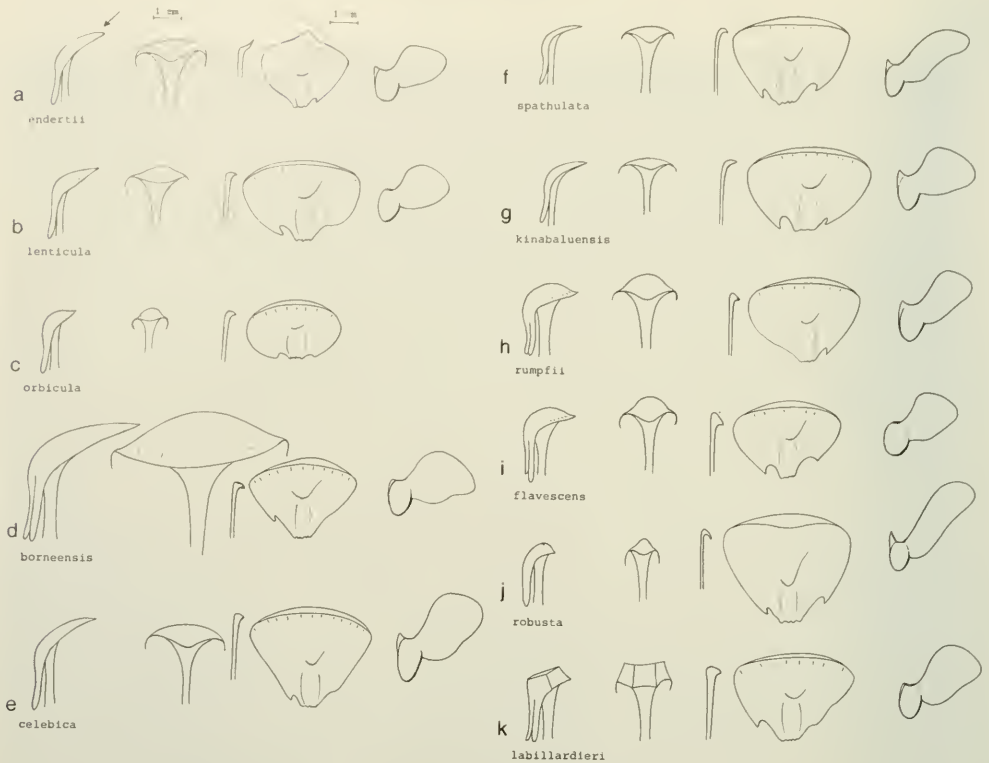


Fig. 70. *Agathis* cone elements. From left to right: lateral profile of microsporophyll, facial view of microsporophyll (from the angle indicated by arrow in the first figure), lateral profile of seed scale, facial view of seed scale (upper seed-bearing face), and seed. Microsporophylls in mm, scales 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 only slightly angled to completely blunt. *Spp.* 1-8 1. Sect. **Agathis**
- 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. Dorsal part of the microsporophyll sharply angled. *Spp.* 10-11 3. Sect. **Prismobracteata**

1. Section *Agathis*

Sect. *Macrobracteatae* MEIJER DREES, Bull. Jard. Bot. Btzg III, 16 (1940) 457.
 — Sect. *Microbracteatae* MEIJER DREES, *l.c.* 461.



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 **1. *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 **2. *A. celebica***
4. Adult leaves acute to broadly rounded at the apex. Pollen cones 9–12 mm in diameter. Pollen cone 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 **3. *A. spatulata***
2. Leaves glaucous on the underside, no more than 6 cm long. Pollen cones less than 4 cm long. Microsporophylls 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 **4. *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 **5. *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 **6. *A. philippinensis***
7. Seed bluntly rounded opposite the wing. Mature pollen cone 2–3.5 cm long by 7–10 mm in diameter. Seed cone bract 2.6–2.9 cm high. Adult leaves 3–4 cm long **7. *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

8. *A. kinabaluensis*

1. *Agathis borneensis* WARB. *Monsunia* 1 (1900) 184, t. 80; DALLIMORE & JACKSON, *Handb. Conif.* (1923) 143; MEIJER DREES, *Bull. Jard. Bot. Btzg III*, 16 (1940) 459; GAUSSEN, *Gymn. Bot. Act.* & FOSS, fasc. 11, ch. 14 (1970) 96, t. 573; DE LAUB. *Blumea* 25 (1979) 532, t. 1; WHITM. *Pl. Syst. Evol.* 135 (1980) 54, t. 1 f. 3, t. 2. f. 3, t. 4; VELDKAMP & DE LAUB. *Taxon* 33 (1984) 345; SILBA, *Phytologia Mem.* 8 (1986) 32. — *Pinus dammara* LAMB. *Descr. Pinus* 1 (1803) 61, t. 38 (& 38a), *nom. rej.*; VELDKAMP & DE LAUB. *Taxon* 33 (1984) 337. — *A. loranthifolia* SALISB. *Trans. Linn. Soc. Lond.* 8 (1807) 312, t. 15, *nom. superfl.* — *Dammara loranthifolia* (SALISB.) LINK, *Enum. Hort. Berol. Alt.* 2 (1822) 411. — *Dammara orientalis* LAMB. *Descr. Pinus* 2 (1824) 15, *nom. superfl.*; GORDON, *Pinctum ed. 1* (1858) 79. — *A. dammara* (LAMB.) RICHARD, *Comm. Bot. Conif. & Cycad.* (1826) 83, t. 19. — *Abies dammara* (LAMB.) DEST.

Tabl. Ecol. Bot. ed. 3 (1829) 356. — *Dammara orientalis var. orientalis* CARR. *Traité Gén. Conif.* (1855) 426; HENKEL & HOCHSTETTER, *Synop. Nadelhölz.* (1865) 210. — *A. beccarii* WARB. *Monsunia* 1 (1900) 184, t. 8F; DALLIMORE & JACKSON, *Handb. Conif.* (1923) 142; MEIJER DREES, *Bull. Jard. Bot. Btzg III*, 16 (1940) 458, f. 1. — *A. macrostachys* WARB. *Monsunia* 1 (1900) 183, t. 8A. — *A. rhomboidales* WARB. *l.c.* 184, t. 8C; MEIJER DREES, *Bull. Jard. Bot. Btzg III*, 16 (1940) 460; HARRISON in Dallimore & Jackson, *Handb. Conif. ed. 4* (1966) 103. — *A. alba* FOXW. *Philip. J. Sc.* 4 (1909) Bot. 442. — *A. latifolia* MEIJER DREES, *Bull. Jard. Bot. Btzg III*, 16 (1940) 459. — *A. dammara ssp. dammara* WHITM. *Pl. Syst. Evol.* 135 (1980) 56 (WHITMORE described *A. celebica* and *A. philippinensis*). — **Fig. 72, 73.**

Huge tree to 55 m tall. *Juvenile leaves* ovate-lanceolate, up to 14 by 4 cm. *Adult leaves* ovate with

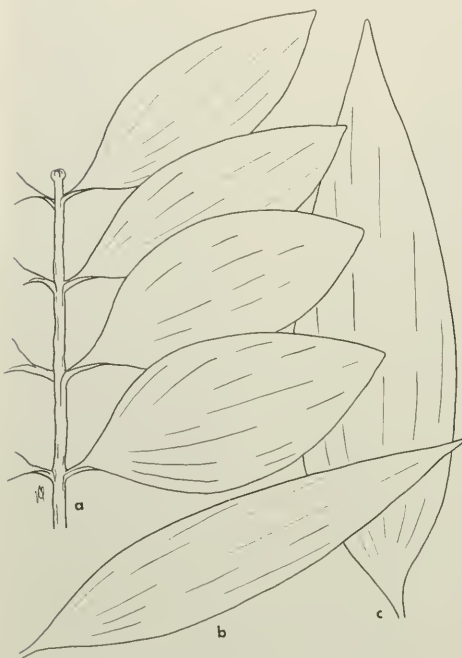
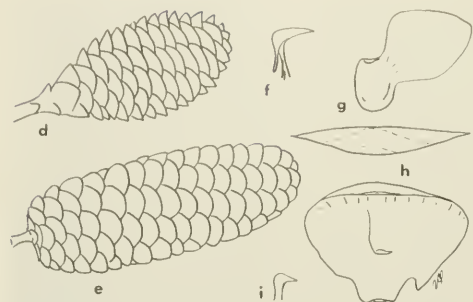


Fig. 73. *Agathis borneensis* WARB. a. Mature foliage shoot; b. leaf variation of shaded branches or alternating with a; c. juvenile leaf; d. young seed cone; e. mature pollen cone, all $\times 0.4$; f. profile view of microsporophyll, $\times 1.25$; g. seed; h. end view and facial view of the seed cone scale; i. profile view of the upper edge of the same.

a more or less acute apex, 6–12 cm by 20–35 mm, tapering at the base to a c. 5 mm petiole. The most common foliage leaf c. 7 by 3 cm but branches with relatively long and narrow leaves often interspersed with the more usual type and more general on younger trees. Resin ducts in pairs one above the other between most vascular strands rather than the

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.

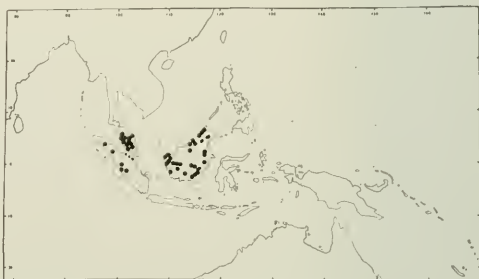


Fig. 74. Range of *Agathis borneensis* WARB.

Ecol. 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 daging*, *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, *bembuëng*, SE. Borneo, *nuju*, Dajak, *enghatan*, Sanggan, *pisau*, *putut*, 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 subspecies under this species, there would be no reason to reject the name *Agathis dammara*.

2. *Agathis celebica* (KOORD.) WARB. *Monsunia* 1 (1900) 185; DALLIMORE & JACKSON, *Handb. Conif.*

(1923) 143; MEIJER DREES, Bull. Jard. Bot. Btzg III, 16 (1940) 461; DE LAUB. Kalikasan 7 (1978) 146; Blumea 24 (1978) 504, f. 2; SILBA, Phytologia Mem. 8 (1986) 32. — *Dammara alba* RUMPH. ex HASSK. Tijd. Nat. Gesch. Phys. 9 (1842) 179; PARL. in DC. Prod. 16, 2 (1868) 374. — *Dammara rumphii* PRESL, Epim. Bot. (1851) 236, *nom. superfl.* — *Dammara orientalis* var. *pallens* CARR. Traité Gén. Conif. (1855) 426. — *Dammara orientalis* var. *alba* KNIGHT ex HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 211. — *Dammara alba* var. *alba* HASSK. Abh. Naturf. Ges. Halle 9 (1866) 180. — *Dammara alba* var. *celebica* HASSK. l.c. — *Dammara celebica* KOORD. Meded. Lands Pl. Tuin 19 (1898) 263. — *A. dammara* auct. non RICHARD: WARB. Monsunia 1 (1900) 182, t. 9, f. 1; HARRISON in Dallimore & Jackson, Handb. Conif. ed. 4 (1966) 98; DE LAUB. Blumea 24 (1978) 503, f. 1. — *A. alba* auct. non FOXW.: MERR. Rumph. Herb. Amb. (1917) 76; MEIJER DREES, Bull. Jard. Bot. Btzg III, 16 (1940) 466; DALLIMORE & JACKSON, Handb. Conif. ed. 3 (1948) 178. — *A. beckingii* MEIJER DREES, Bull. Jard. Bot. Btzg III, 16 (1940) 463. — *A. hamii* MEIJER DREES, l.c. 462, f. 1. — *A. loranthifolia* auct. non SALISB.: MEIJER DREES, l.c. 464. — *A. celebica* ssp. *celebica* VELDkamp & WHITM. in Veldkamp & De Laub. Taxon 33 (1984) 345. — *A. dammara* ssp. *dammara* auct. non WHITM.: WHITM. Pl. Syst. Evol. 135 (1980) 57, p.p.

Huge tree to 65 m tall. Juvenile leaves ovate-ranceolate, 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.

DISTR. *Malesia*: Celebes and Moluccas to Palawan in the Philippines and probably other parts of southern Philippines. Fig. 75.

Ecol. A forest emergent scattered and locally common in lowland rain-forest from near sea-level to 1200 m.



Fig. 75. Range of *Agathis celebica* (KOORD.) WARB.

Vern. *Dammar*, *dammar radja*, *M*, *hulontuu*, *Malili*, *kawo*, *Maliki*, *kisi*, *Buru*, *salu*, *Ternate*, *dayungon*, *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 on Ambon, it is the species which RUMPHINUS (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 spatulata* DE LAUB., sp. nov.; SILBA, Phytologia Mem. 8 (1986) 37, *nom. inval.* — *A.*

robusta ssp. *nesophila* WHITM. Pl. Syst. Evol. 135 (1980) 64.

Arbor magna ad 60 m alta. Folia adulta acuta 9–10 cm × 20–30 mm ad spatulata 7–9 cm × 18–20 mm. Strobili masculini 9–13 mm diametri, 4–7 cm longi, apicis microsporophyllis 1,5–2 mm latis, 1,3–1,5 mm longis. Squamae femineae 35–42 mm latae, 27–32 mm altae, marginibus rotundibus apicis costis acutis. 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, subtended 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 spatulata* 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; SILBA, 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 acumi-

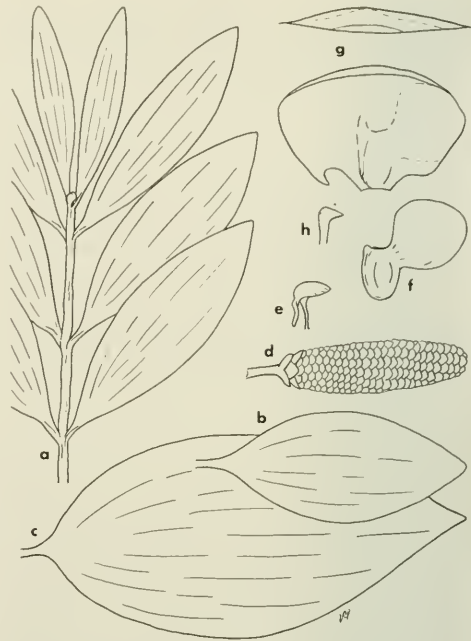


Fig. 77. *Agathis lenticula* DE LAUB. a. Mature foliage shoot; b. extreme leaf shape; c. juvenile leaf; d. mature pollen cone, all $\times 0.4$; e. profile view of microsporophyll, $\times 1.25$; f. seed; g. end view and facial view of the seed cone scale; h. profile view of the upper edge of the same.

nate 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. *Tanggilan, 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



Fig. 78. Range of *Agathis lenticula* DE LAUB. (circles) and *A. orbicula* DE LAUB. (dots).

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. *Tumuh*, Murut, *tubu*, Kenyah, *bulok*, Iban.

6. *Agathis philippinensis* WARB. *Monsunia* 1 (1900) 185, t. 8E; DALLIMORE & JACKSON, *Handb. Conif.* (1923) 147; MEIJER DREES, *Bull. Jard. Bot. Botg III*, 16 (1940) 468; SILBA, *Phytologia Mem.* 8 (1986) 36. — *Dammara rumpffii* auct. non PRESL: PRESL, *Epim. Bot.* (1841) 236. — *A. regia* WARB. *Monsunia* 1 (1900) 183, t. 8B; DALLIMORE & JACKSON, *Handb.*

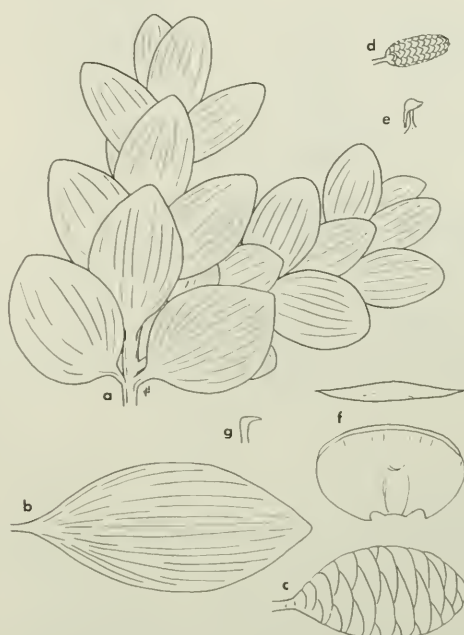


Fig. 79. *Agathis orbicula* DE LAUB. a. Mature foliage shoots; b. juvenile leaf; c. young seed cone; d. mature pollen cone, all $\times 0.4$; e. profile view of microsporophyll, $\times 1.4$; f. end view and facial view of the seed cone scale; g. profile view of the upper edge of the same.

Conif. (1923) 147. — *A. alba* auct. non FOXW.: FOXW. *Philip. J. Sc.* 4 (1909) Bot. 442. — *A. dammara* auct. non RICHARD: DE LAUB. *Kalikasan* 7 (1978) 144; *Blumea* 24 (1979) 499, f. 1. — *A. dammara* ssp. *dammara* auct. non WHITM.: WHITM. *Pl. Syst. Ecol.* 135 (1980) 56, p.p., t. 5, f. 1 & 2.

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.



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

Distr. *Malesia*: Philippines to Celebes and Halmaheira. Fig. 80.

Ecol. Scattered and often emergent in upland rain-forest, mostly 1200–2200 m, occasionally as low as 450 m in Halmaheira, 900 m in Celebes and far to the north in Luzon to 250 m.

Vern. *Dammar*, *M*, *goga*, *solo*, *tjoga*, Manado, *molewaun*, Teliwang, *almaciga*, Philippines, *dayungon*, Samar, *dingan*, Misamis.

Note. Reports by foresters of 'different' trees in the southern parts of the Philippines may well apply to *A. celebica* which has been collected there. Most Philippine collections are of nondescript leaves and (rarely) immature cones.

7. *Agathis flavescens* RIDLEY, Kew Bull. (1914) 332; J. Fed. Mal. St. Mus. 6 (1915) 3; DALLIMORE & JACKSON, Handb. Conif. (1923) 143; MEIJER DREES, Bull. Jard. Bot. Botz III, 16 (1940) 464; SILBA, Phytologia Mem. 8 (1986) 33. — *A. dammara* ssp. *flavescens* (RIDLEY) WHITM. Pl. Syst. Evol. 135

(1980) 59. — *A. celebica* ssp. *flavescens* (RIDLEY) VELDKAMP & WHITM. ex VELDKAMP & DE LAUB. Taxon 33 (1984) 346.

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 Malaya.

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

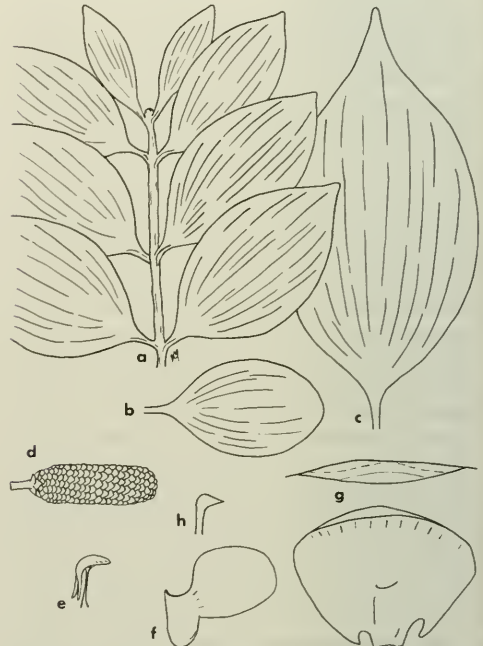


Fig. 81. *Agathis kinabaluensis* DE LAUB. a. Mature foliage shoot; b. extreme leaf shape; c. juvenile leaf; d. mature pollen cone; all $\times 0.4$; e. profile view of microsporophyll, $\times 1.25$; f. seed; g. end view and facial view of the seed cone scale; h. profile of the upper edge of the same.

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 kinabaluensis* 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. *Mature 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. *Tumu*, 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.

Arboris. Squama feminea projectioni apici instructa. Strobilus femineus 5–6 × 6–7 cm. Strobilus masculinus sessilis. Typus: Agathis australis.

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.

9. *Agathis endertii* MEIJER DREES, Bull. Jard. Bot. Botz III, 16 (1940) 470; HARRISON in Dallimore & Jackson, Handb. Conif. ed. 4 (1966) 99; DE LAUB. Blumea 25 (1979) 534, f. 2; SILBA, Phytologia Mem. 8 (1986) 33. — Fig. 82.

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. *Mature 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 trian-

gular 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.

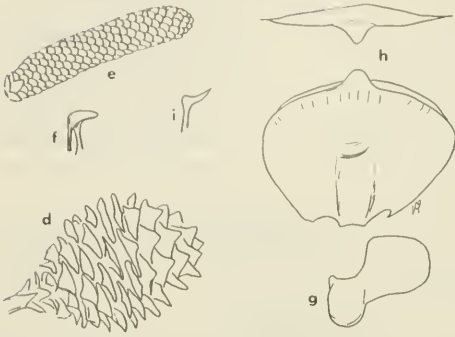
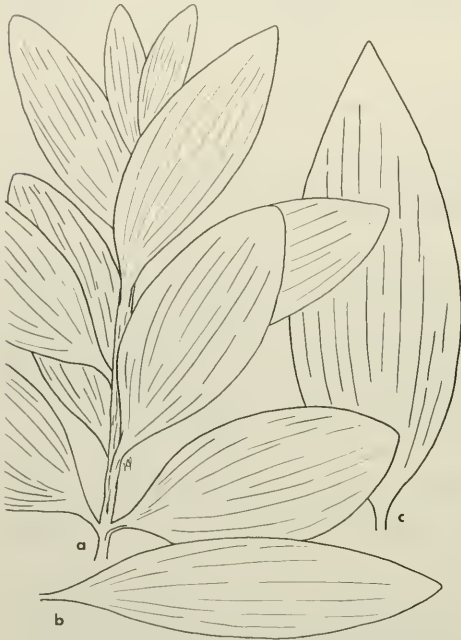


Fig. 83. Range of *Agathis endertii* MEIJER DREES.



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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 $\times 0.4$; f. profile view of microsporophyll, $\times 1.25$; g. seed; h. end view and facial view of the seed cone scale; i. profile view of the upper edge of the same.

3. Section *Prismatobracteatae*

MEIJER DREES, Bull. Jard. Bot. Btzg III, 16 (1940) 470.

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.

Distr. 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. **11. *A. robusta***



Fig. 84. *Agathis labillardieri* WARB. a. Twig with pollen cones; b. seed cone, both $\times 0.4$.

10. *Agathis labillardieri* WARB. *Monsunia* 1 (1900) 183; MEIJER DREES, *Bull. Jard. Bot. Btzg* III, 16 (1940) 471; HARRISON in Dallimore & Jackson, *Handb. Conif.* ed. 4 (1966) 99; WHITM. *Pl. Syst. Evol.* 235 (1980) 60; SILBA, *Phytologia Mem.* 8 (1986) 34. — Fig. 84, 85.

Huge tree to 60 m. *Juvenile leaves* ovate and acuminate, 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 facies 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



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).

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.

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. *Dammar*, *M*, *pen*, Pidgin, *legatulus*, Mooi lang., *aisjier*, Arguni, *idjir*, Irahutu, *tar*, Kebar, *waiui*, Pousami, *kessi*, Roberai, Kuri, *fuko*, Manikiong, *uto*, Kapauku, *warkai*, Kamora, Kokonao, *osier*, Itik, *sao*, Kwerba, *wel*, Iwer, *nu*, Wagu, *aglo*, Orne, *koba*, E. Sepik.

11. *Agathis robusta* (MOORE) BAILEY, Synops. Queensl. Fl. (1883) 498; WARB. *Monsunia* 1 (1900) 185; BAKER & SMITH, *Pines of Austr.* (1910) 376; DALLIMORE & JACKSON, *Handb. Conif.* (1923) 148; FRANCO, *An. Inst. Sup. Agron.* 18 (1951) 105, f. 2-10; HYLAND, *Brunonia* 1 (1978) 105, f. 1; SILBA, *Phytologia Mem.* 8 (1986) 37. — *Dammara robusta* MOORE ex F.V.M. Quart. J. Trans. Pharm. Soc. Vict. 2 (1806) 173. — *Dammara palmerstonii* F.V.M. Vict. Natur. 8 (1891) 45. — *A. palmerstonii* (F.V.M.) BAILEY, Queensl. Dept. Agric. Bot. Bull. 3 (1891) 17; DALLIMORE & JACKSON, *Handb. Conif.* (1923) 147. — *A. robusta* var. *robusta* WHITM. *Pl. Syst. Evol.* 135 (1980) 63. — *A. robusta* var. *nesophila* auct. non WHITM.: WHITM. *l.c.* f. 6.

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.

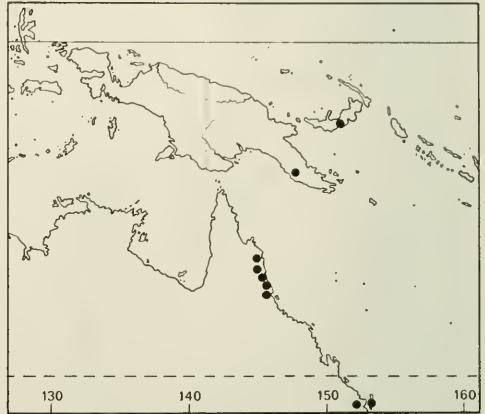


Fig. 86. Range of *Agathis robusta* (MOORE) BAILEY.

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

ENDL. Syn. Conif. (1847) 42; CARR. Traité Gén. Conif. (1855) 84; MASTERS, J. Linn. Soc. Bot. 30 (1895) 20; WARB. Monsunia 1 (1900) 189; DALLIMORE & JACKSON, Handb. Conif. (1923) 300; LI, J. Arn. Arb. 34 (1953) 17; FLORIN & BOUTELJE, Acta Horti Berg. 17 (1954) 31; DE LAUB. Fl. Nouv. Caléd. et Dép. 4 (1972) 145; SILBA, Phytologia Mem. 8 (1986) 108. — *Libocedrus* subg. *Eulibocedrus* PILGER in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 389. — *Papuacedrus* LI, J. Arn. Arb. 34 (1953) 25; FLORIN & BOUTELJE, Acta Horti Berg. 17 (1954) 31; BOUTELJE, *l.c.* 198, t. 4, pl. 7 & 8; VAN ROYEN, Alp. Fl. New Guinea 2 (1979) 1. — *Austrocedrus* FLORIN & BOUTELJE, Acta Horti Berg. 17 (1954) 28. — **Fig. 88, 89.**

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* cylindrical, 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 *sp.* 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 humous 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.



Fig. 87. Range of the genus *Libocedrus* ENDL. with the number of species, all endemic.

Notes. The relationships of *Libocedrus* are emphatically with the Holarctic *Thuja* group of genera (*Tjujoideae*) within *Cupressaceae* making it phytogeographically much like the everywhere associated *Nothofagus* whose relatives are also in the north. Like the other members of *Tjujoideae*, 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 LI (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 *Cupressaceae* 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.

1. *Libocedrus papuana* F.v.M. Trans. R. Soc. Vict. n.s. 1 (1889) 32; WARB. Monsonia 1 (1900) 189; K.SCH. & LAUT. Fl. Schutzgeb. Südsee (1901) 156; Nachtr. (1905) 51; KOORD. Nova Guinea 8 (1911) 613; LAUT. Bot. Jahrb. 50 (1913) 52, f. 2A–G; LANE-POOLE, For. Res. Terr. Papua New Guinea (1925) 74; SILBA, Phytologia Mem. 8 (1986) 109. — *Thuja pa-*

pauana (F.v.M.) Voss, Mitt. Deut. Dendr. Ges. 1907 (1908) 88. — *L. torricellensis* SCHLTR ex LAUT. Bot. Jahrb. 50 (1913) 52, f. 2H–N. — *Papuacedrus papuana* (F.v.M.) LI, J. Arn. Arb. (1953) 25; FLORIN & BOUTELJE, Acta Horti Berg. 17 (1954) 32, pl. 2, t. 1–3; HARRISON in Dallimore & Jackson, Handb. Conif. ed. 4 (1966) 323; VAN ROYEN, Alp. Fl. New



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).

Guinea 2 (1979) 2, f. 33. — *Papuacedrus torricelensis* (SCHLTR) LI, J. Arn. Arb. 34 (1953) 25; FLORIN & BOUTELJE, Acta Horti Berg. 17 (1954) 31, pl. 2, t. 4-6; HARRISON in Dallimore & Jackson, Handb. Conif. ed. 4 (1966) 323. — Fig. 88, 89.

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 \pm 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 part-way 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*, *oleh*, *Chimbu*, *Masul*, *dza-gosa*, *dzasihanini*, *hanini*, *Asaro*, *Kefamo*, *guta*, *juta*, *Mairi*, *Watabung*, *kaibel-kombam*, *kaipil*, *ongol*, *Wahgi*, *Minj*, *mandilasop*, *mondalasap*, *mondolasop*, *wrenak*, *Mendi*, *ab*, *aiap*, *aip*, *hap*, *kap*, *Enga*, *Kepilam*, *aioba*, *hohoba*, *Lei area*, *bit*, *Yogom*, *iwunturra*, *Manki*, *ye-enka*, *Nauti*, *sukou*, *Wapi*, *Migote*.

var. *arfakensis* (GIBBS) DE LAUB., *stat. nov.* — *L. arfakensis* GIBBS, *Arfak* (1917) 84, f. 6a, b; DALLIMORE & JACKSON, *Handb. Conif.* (1923) 301; SILBA, *Phytologia Mem.* 8 (1986) 108. — *Papuacedrus arfakensis* (GIBBS) LI, *J. Arn. Arb.* 34 (1953) 25; FLORIN & BOUTELJE, *Acta Horti Berg.* 17 (1954) 32,



Fig. 90. Range of *Libocedrus papuana* F.v.M. var. *papuana* (dots) and var. *arfakensis* (GIBBS) DE LAUB. (triangles).

t. 3; HARRISON in Dallimore & Jackson, Handb. Conif. ed. 4 (1966) 322.

Apex of lateral leaves at first spreading but soon

constricted to the position on older trees close to the base of the following facial leaves but between their base and tip the lateral leaves expanded outward as much as 3 mm and overall as much as 10 mm long, thus producing a strongly convex shape, gradually becoming smaller until they become indistinguishable from the type variety on older and exposed trees.

Distr. *Malesia*: from the Wissel Lakes through the Vogelkop Peninsula and probably including the material from Batjan and Ternate. Fig. 90.

Ecol. Like the type variety from 1600 to 2500 m, but as low as 840 m along the north coast of the Vogelkop Peninsula.

Vern. *Autibo*, *dautibo*, *dautie*, *matu*, *matu-dautie*, *Kepauko*, *wonga*, Arfak area, *bootsjeka*, *butsga*, Manikiong, *pomoan*, Manikiong, Hattam, *duwak*, *nipau*, *tuwa*, Kebar, *sowa*, *swa*, Kebar, And-jai, *araun*, *eis*, Karoon.

Note. Despite the strikingly different juvenile leaves, intermediate specimens exist, especially at higher elevations and it has not been possible to separate specimens taken from older plants.

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

LINN. Gen. Pl. ed. 1 (1737) 731; Sp. Pl. (1753) 1000; LAMBERT, *Pinus* (1803); PARL. in DC. Prod. 16, 2 (1868) 378; ENGELMANN, Trans. St. Louis Acad. Sc. 4 (1880) 161; MASTERS, J. Linn. Soc. 35 (1904) 560; SHAW, Publ. Arn. Arb. 5 (1914) 24, t. 1-39; PILGER in E. & P. Nat. Pfl. Fam. ed. 2, 13 (1926) 331, t. 177, 178; GAUSSEN, Gymn. Act. & Foss. fasc. 6 (1960) 11, t. 324-369, pl. 24-29; MIROV, Genus *Pinus* (1967); SILBA, Phytologia Mem. 8 (1986) 129. — Fig. 91-93.

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).

KEY TO THE SPECIES

1. Leaves two per bundle. Mature seed cone ovate 1. *P. merkusii*
 1. Leaves three per bundle. Mature seed cone globular 2. *P. kesiyi*

1. *Pinus merkusii* JUNGH. & DE VRIESE in De Vriese, Pl. Nov. Ind. Bat. Or. (1845) 5, t. 2; Bot. Zeit. 4 (1846) 13; ENDL. Syn. Conif. (1847) 176; CARR. Traité Gén. Conif. (1855) 380; GORDON, Pinetum ed. 1 (1858) 169; MIQ. Fl. Ind. Bat. 2 (1859) 1069; HENKEL & HOCHSTETTER, Synop. Nadelhölz. (1865) 43; DE BOER, Conif. Archip. Ind. (1866) 5; PARL. in DC. Prod. 16, 2 (1868) 389; VIDAL, Sin. Atlas (1883) 43, t. 98, f. B; Rev. Pl. Vasc. Filip. (1886) 296; MERR. For. Bur. Bull. Philip. 1 (1903) 15; FOXW. Philip. J. Sc. 6 (1911) Bot. 169; SHAW, Publ. Arn. Arb. 5 (1914) 23, t. 198-200; DALLIMORE & JACKSON, Handb. Conif. (1923) 415; GAUSSEN, Gymn. Act. & Foss. fasc. 6 (1960) 146, t. 344, 2 & 3; CRITCHF. & LITTLE, U.S. Dept. Ag. Misc. Publ. 991 (1966) 15, map 39; MIROV, Genus Pinus (1967) 284, f. 3-51-52, t. 3-68-69, 553; COOLING, Fast Growing Timber Trees Low. Tropics 4 (1968) 126; STEEN, Fl. Males. Bull. n. 25 (1971) 1948; PHENGLAI, Thai For. Bull. 7 (1973) 1, f. 1; SILBA, Phytologia Mem. 8 (1986) 149. — *P. sylvestris* auct. non L.: LOUR. Fl. Coch. 2 (1790) 579. — *P. sumatrana* JUNGH. Bot. Zeit. 4 (1846) 698. — *P. finlaysoniana* BLUME, Rumphia 3 (1849) 210. — *P. latteri* MASON, J. Asiat. Soc. 1 (1849) 74. — *P. merkusii* var. *tonkinensis* CHEV. Rev. Bot. Appl. Ag. Trop. 24 (1944) 7. — *P. merkusiana* COOLING & GAUSSEN, Trav. Lab. For. Toulouse (1970) 1. — Fig. 91-93.

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. *Foliage buds* long and narrow with awl-shaped scales. *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 umb. *Seed* 7.5 by 4.5 mm, with a deciduous wing 25 by 8 mm.

DISTR. 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



Fig. 94. Range of *Pinus merkusii* JUNGH. & DE VRIESE.

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 batu*, *dammar bunga*, *hejam*, *hujam*, *ujam*, *ujem*, Atjeh, *higi*, Kerintji, *kaju tussam*, *tussam*, Battok, Tapanuli; Philippines: *tapulao*, Sambal, Luzon, *agoo*, *aguu*, *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 uninodal. 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.

2. *Pinus kesiya* ROYLE ex GORDON in Loudon, Gard. Mag. 16 (1840) 8; HARRISON in Dallimore & Jackson, Handb. Conif. ed. 4 (1966) 436; STYLES & BURLEY, Comm. For. Rev. 51 (1972) 241; BURLEY, Proc. IUFRO Breeding Symp. Gainesville (1972) 38; PHENGKLAI, Thai For. Bull. 7 (1973) 3; QUIMBO, Canopy 4 (9) (1978) 9, 14; PADOLINA, Canopy 4 (10) (1978) 5; STYLES, Canopy (Aug. 1979) 5; in Armitage & Burley, Trop. For. Pap. 9 (1980) 199. — *P. taeda auct. non L.*: BLANCO, Fl. Filip. (1837) 767; MERR. Bur. Govt. Lab. Publ. Philip. 27 (1905) 82. — *P. insularis* ENDL. Syn. Conif. (1847) 157; PRESL, Epim. Bot. (1851) 37; PARL. in DC. Prod. 16, 2 (1868) 390; VIDAL, Sin. Atlas (1883) 43, t. 98, f. C; Rev. Pl. Vasc. Filip. 1 (1903) 15; Philip. J. Sc. 5 (1910) Bot. 325; WHITE, For. Bur. Bull. 10 (2) (1911) 26, t. 2, 3; FOXW. Philip. J. Sc. 6 (1911) Bot. 170; SHAW, Genus Pinus (1914) 60, t. 23, f. 208–210; WU, Acta Phytotax. Sinica 5 (1956) 145; RAIZADA & SAHNI, Ind. For. Rec. 5 (1960) 114, t. 5, f. 3; BACK & BAKH, f. Fl. Java 1 (1963) 91; CRITCHF. & LITTLE, U.S. Dept. Ag. Misc. Publ. 991 (1966) 14, map 38; MIROV, Genus Pinus (1967) 297; ROJO, Sylvatrop 3 (1978) 31; DE LAUB, Kalikasan 7 (1978) 148; ROJO, Canopy (March 1979) 10; SILBA, Phytologia Mem. 8 (1986) 145. — *P. khasyana* GRIFF. Notul. Pl. Asiat. 4 (1854) 18, t. 367, 368, with ref. to descr.: 2 (1848) 58. — *P. kasya* PARL. in DC. Prod. 16, 2 (1868) 390; BRANDIS, For. Fl. NW & Central India (1874) 508; KURZ, Fl. Burma 2 (1877) 499; GAMBLE, Man. Ind. Timber (1881) 397. — *P. khasia* ENGELMANN, Trans. St. Louis Acad. Sc. 4 (1880) 179. — *P. khasya* HOOK. f. Fl. Br. India 5 (1888) 652; GAMBLE, Man. Ind. Timber 2 (1902) 708; MERR. For. Bur. Philip. 1 (1903) 15; BRANDIS, Indian Trees (1906) 690; DALLIMORE & JACKSON, Handb. Conif. (1923) 400; BUIC NGOC-SANH, Adansonia 2 (1962) 337; GAUSSEN, Gymn. Act. & Foss. fasc. 6 (1960) 154, f. 345, 5, 7, incl. var. *insularis* (ENDL.) GAUSSEN, l.c. f. 345, 6; NGUYEN KHA, Ann.

Sci. For. 23 (1966) 261; MIROV, Genus Pinus (1967) 295.

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. Pollen 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.

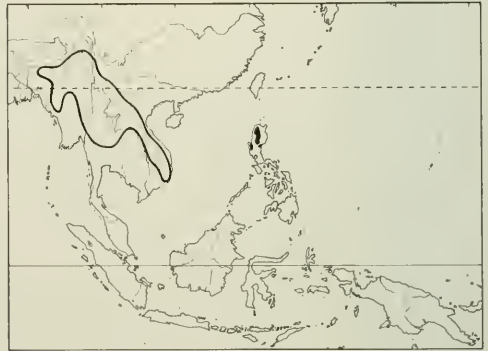


Fig. 95. Range of *Pinus kesiya* ROYLE ex GORDON.

Ecol. Most often in open pure stands following fire, but also mixed with oaks and Ericaceous 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*, *saleng*; *boo boo*, *bot bol*, *bulbul*, *l.*, *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

Callitris sp. mentioned from New Guinea by H.J. LAM, Nat. Tijd. Ned. Ind. 89 (1929) 304, 354; *Sargentia* 5 (1945) 143, 168, is according to VAN STEENIS, Acta Bot. Neerl. 2 (1953) 299 = *Gymnostoma* sp. (*Casuarinaceae*).

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 (*Reinwardtia* 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 '*Thuya 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)¹

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 raceme-like and unbranched, (supra- or extra-)axillary and/or terminal, sometimes thyrsoid or fasciculate, rarely flowers solitary. Bracts present; bracteoles basal, rarely (*Salomonina*, *Epirixanthes*) absent. *Flowers* bisexual, more or less zygomorphous, rarely actinomorphic. *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 (alae) 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 *Salomonina* 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. *Salomonina* 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 (§ *Melchiora*) 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-

(1) For this revision the 1970 manuscripts have been used of three former students of Professor Van Steenis: F. C. Roest (*Polygala* sect. *Chamaebuxus*), L. P. Rijfkoogel (*Securidaca*), and Mrs. H. M. Y. J. André de la Porte-Janss (*Salomonina*, *Epirixanthes*).

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, ornithochory, anemochory, diplochory, epizoochory. Ornithochory also occurs in *Diclidanthera*, *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 *Bredemeyera*, *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 *Salomonina*.

References: HEUBL, Mitt. Bot. Staatssamml. München 20 (1984) 222; VAN ROOSMALEN, Fr. Guianan Fl. (1985) 360; VERKERKE, J. Arn. Arb. 66 (1985) 385.

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 octolocular, uniovulate ovary of the other *Polygalaceae*. The ontogeny of bi- and trisporangiate 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 (*Diclidanthera*; and a rare abnormality in *Xanthophyllum*) is a derived character.

References: CHODAT, Monogr. I (1891); CRONQUIST, Integr. Syst. (1981) 763; HUTCHINSON, Gen. Fl. Pl. 2 (1967) 338; LEINFELLNER, Oest. Bot. Z. 120 (1972) 51; VAN DER MEIJDEN, Leiden Bot. Ser. 7 (1982) 3; VENTAKESH, Bull. Torrey Bot. Club 83 (1956) 19–26; VERKERKE, Blumea 29 (1984) 409–421; J. Arn. Arb. 66 (1985) 353–394; VERKERKE & BOUMAN, Bot. Gaz. 141 (1980) 277–282.

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 *Moutabeae* (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 *Moutabeae*).

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 *Trigoniaceae*, especially *Trigoniastrum*.

References: BRIDGWATER & BAAS, IAWA Bull. n.s. 3 (1982) 115–125; DICKISON, Bot. J. Linn.

Soc. 67 (1973) 103–115; METCALFE & CHALK, *Anatomy of the Dicotyledons 1* (1950) 133–138; STYER, *J. Arn. Arb.* 58 (1977) 109–145.

Palyngology. 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 ('synorate') 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 mesocolpia 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 *Salomonina* 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 synorate type in *Polygalaceae*.

References: ERDTMAN, Bot. Notis. (1944) 80–84; Pollen morphology and plant taxonomy, Angiosperms (1952) 332–333; HUYNH, Pollen et Spores 10 (1968) 11–55; LARSON & SKVARLA, Pollen et Spores 3 (1961) 21–32; MULLER, Ann. Missouri Bot. Gard. 66 (1979) 593–632; VAN ROYEN & VAN STEENIS, *J. Arn. Arb.* 33 (1952) 91–95; SIMPSON & SKVARLA, Amer. J. Bot. 68 (1981); THANIKAIMONI, Pollen et Spores 8 (1966) 265–284. — R.W.J.M. VAN DER HAM.

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, $\text{C}_{30}\text{H}_{46}\text{O}_7$, an acid-labile derivative of oleanolic acid; it was shown to be mainly sapogenin of roots of several members of *Bredemeyera*, *Carpolobia*, *Polygala* and *Securidaca*. Closely related sapogenins are polygalacic acid from *Polygala paenea* and bredemolic acid from *Bredemeyera floribunda*. Mono-, di- and trimethoxycinnamic 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 -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 infrafamiliar 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 *Trigoniaceae*, *Vochysiaceae*, *Malpighiaceae* as well as the *Tremandraceae* and the *Krameriaceae*. Wood anatomical evidence (BRIDGWATER & BAAS, 1982) supports a close affinity of *Polygalaceae*, *Xanthophyllum* and *Trigoniaceae*, but not with the other families. VAN DER MEIJDEN (1982) found no arguments to include *Tremandraceae* and *Krameriaceae*. Although there seemed to be little evidence for the inclusion of *Krameriaceae* in the order (SIMPSON & SKVARLA, 1981; SIMPSON, 1982), the first author recently supported the classification of *Krameriaceae* 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 septa, 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.

References: BRIDGWATER & BAAS, IAWA Bull. n.s. 3 (1982) 115–125; BUSE-JUNG, Thesis, Kiel (1979); CHODAT, Monogr. I (1891); CRONQUIST, Integr. Syst. (1981) 763; DICKISON, J. Linn. Soc. Bot. 67 (1973) 103–115; LEINFELLNER, Oest. Bot. Z. 120 (1972) 51; VAN DER MEIJDEN, Leiden Bot. Ser. 7 (1982); SIMPSON, Taxon 31 (1982) 517–528; SIMPSON & SKVARLA, Amer. J. Bot. 68 (1981) 277–294; STYER, J. Arn. Arb. 58 (1977) 100–145; VERKERKE, Blumea 29 (1984) 409–421; J. Arn. Arb. 66 (1985) 353–394.

Bibliographical note. R. CHODAT published a monograph of the family in two parts in Mém. Soc. Phys. Hist. Nat. Genève, 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).

KEY TO THE GENERA

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**
2. All sepals subequal, not petaloid, much shorter than the petals. Keel apically inappendiculate. Stamens 2–6. Fruit either indehiscent, or laterally dehiscent and then the margins dentate or spinose. Seed exarillate.
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. Salomonina**
3. Saprophytic, echlorophyllous plant with scale-like leaves. Fruit indehiscent, enclosed by the sepals. Pericarp fleshy. Style straight or very short. Disk present (but indistinct), adnate to the base of the ovary, semi-annular or as a lobe. Anthers 3 or 5, rarely 2 or 4. Rachis terete **4. Epirixanthes**
1. Shrubs, trees or lianas.
4. Sepals united at base, upper part of calyx caducous by a circumcission. 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 **5. Eriandra**
4. Sepals free, caducous or 3 or 5 persistent. Petals free from the sepals. Ovary 1- or 2-locular. Seeds without an aril, or aril lobed.
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**
5. Petals 3 or with an additional pair of much-reduced ones. Lateral sepals (alae) petaloid and at least twice as large as the other sepals. Ovary 1- or 2-locular, each locule containing a single ovule.
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

LINNÉ, Sp. Pl. 2 (1753) 701; Gen. Pl. ed. 5 (1754) 315; DC. Prod. 1 (1824) 321; BENTH. & HOOK. Gen. Pl. 1 (1862) 136; HASSK. in Miq. Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 151; CHODAT, Monogr. I (1891); *ibid.* II (1893); E. & P. Nat. Pfl. Fam. 3, 4 (1896) 330; BLAKE, N. Amer. Fl. 25 (1924) 305; MUKHERJEE, Bull. Bot. Soc. Beng. 12 (1961, '1958') 29; HUTCH. Gen. Fl. Pl. 2 (1967) 340; ADEMA, Blumea 4 (1966) 256. — *Chamaebuxus* (DC.) SPACH, Hist. Nat. Vég. Phan. 7 (1838, '1839') 125; OPIZ, Oekon. Neuigk. Verh. (1839) 526. — *Badiera* (non DC.) HASSK. Cat. Hort. Bog. (1845) 227, *p.p.* — *Semeiocardium* (non ZOLL.) HASSK. in Miq. Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 150. — **Fig. 1–16.**

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 (alae) 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 oblanceolate. *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.

Distr. 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 infragenetic 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. Pseudosemiocardium* 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. exsuarrosa*, 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. vauthieri* 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.

References: BRANTJES, Pl. Syst. Evol. 141 (1982) 41–52; FAEGRI & VAN DER PIJL, Princ. Poll. Ecol. 3rd ed. (1979) 165, f. 6; HEUBL, Bot. Mitt. München 20 (1984) 234; MILLER, J. Arn. Arb. 52 (1971) 267; VENKATESH, Bull. Torrey Bot. Club 83 (1956) 19.

Tax on. In view of the surprisingly great variation in species-constant characters of diverse flowering and fruiting parts, it has been tried to split this large genus into a number of smaller genera. The large genus concept as adopted by R. CHODAT (Monogr. 1, 1891, 93), the only author who revised all species, is still adopted, some minor questions regarding the status of some American groups set aside. CHODAT's infrageneric division of the genus, however, was unsuccessful, as had been pointed out by S.F. BLAKE in his revision of the North American species (1924), and more recently by ADEMA (1966) for the Malesian ones. This is probably due to the fact that two of CHODAT's major characters to define his sections, viz. the presence or absence of sepals at fruiting state, and of carinal appendages, are not constant in the different lineages: parallel developments (reductions *c.q.* reversions of character states) will have been developed in many of these lineages. Until a new revision of the tropical American species has been made, it will be impossible to make a balanced reconsideration of the status of the diverse groups of species within and outside the borderlines of this genus.

In the Indo-Australian area a great diversity of species is present, probably caused by diverse migration lines. Perhaps the Australian genus *Comesperma* should also be included in *Polygala*; see note under 4. *P. papuana*.

KEY TO THE SECTIONS AND SPECIES

1. Lateral sepals (alae) caducous at the beginning of fruit-setting. Disk present. Leaves usually with distinct petioles.
 2. Annual herbs up to 30 cm high. Flowers, fruits and seeds up to 3 mm long. *Spp.* 1–3. — 1. *Sect. Pseudo-semeiocardium*
 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.
 5. Fruit much longer than wide, at base with 3 small, persistent sepals. Seed very long-hairy, without aril. Upper sepal flat. Lianas. *Sp.* 4. — 2. *Sect. Melchiora* 4. *P. papuana*
 5. Fruit about as long as wide, without persistent sepals. Seed glabrous or shortly hairy, partly covered by an aril. 'Upper' sepal saccate. Shrubs or small trees. *Spp.* 5–8. — 3. *Sect. Chamaebuxus*
 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. arillata*
 1. Lateral sepals (alae) persistent. Disk (apparently) absent. Leaves hardly petiolate. Annual to perennial herbs, sometimes woody at base. *Spp.* 9–20. — 4. *Sect. Polygala*
 9. Lateral sepals (alae) broadly ovate, hairy.
 10. Alae yellowish. Ovary and fruit hairy all over. Capsule narrowly winged. Stigma not recurved at apex, with 2 minute lobes 9. *P. javana*
 10. Alae green. Ovary and fruit only hairy at margin. Stigma strongly recurved at apex, at inner 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*

12. Alae 3–10 mm long. Stem eglandular. Capsule winged. Style not or hardly widened at apex, without a tuft of hairs.
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.
14. Alae 6–7 mm long. Capsule hairy along margin. Racemes in the forks (but terminal on side-branches). Bracts and bracteoles persistent **11. *P. persicariaefolia***
14. Alae 3–4 (in fruit up to 5) mm long. Capsule glabrous. Racemes mostly terminal. Bracts and bracteoles early caducous **12. *P. longifolia***
11. Alae asymmetric, falcate, not petaloid (green).
15. Capsule and vegetative parts stiffly hairy. Appendages of keel little incised. Stigma apically neither widened nor sharply reflexed **14. *P. exsuarrosa***
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 sharply reflexed.
16. Capsule c. 2 mm long. Alae c. 3 mm long. Style apically widened, at one side with the stigmatic lobe **15. *P. polifolia***
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 *Pseudosemeiocardium*

ADEMA, *Blumea* 14 (1966) 256. — *Semeiocardium* (*non* ZOLL.) HASSK. in *Miq. Ann. Mus. Bot. Lugd.-Bat.* 1 (1863) 150. — *Polygala sect. Semeiocardium* [*non* (ZOLL.) HASSK.] CHODAT, *Monogr.* II (1893) 41.

Small, erect, branched, annual herbs. *Flowers* in terminal or axillary multiflowered unbranched racemes. *Sepals* caducous before fruit-setting. *Keel* with 2 hardly incised appendages, or inappendiculate. 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*.

1. *Polygala tatarinowii* REGEL, *Bull. Soc. Nat. Mosc.* 34 (1861) 523, t. 7, f. 10, 11; FORBES & HEMSLEY, *J. Linn. Soc.* 23 (1888) 62; CRAIB, *Not. R. Bot. Gard. Edinb.* 11 (1919) 187; GAGNEP, *Fl. Gén. 1.-C. Suppl.* 1 (1938) 226, f. 1–6; MAKINO, *Ill. Fl. Japan* (1954) 383; MUKHERJEE, *Bull. Bot. Soc. Beng.* 12 (1961) 34;

OHWI, *Fl. Japan* (1965) 587; ADEMA, *Blumea* 14 (1966) 256, f. 1; *ibid.* 18 (1970) 564; IQBAL DAR, *Fl. W. Pakist.* 52 (1973) 2, f. 1a–c; CHRTEK & KRISA, *Fl. Iranica* 124 (1977) 2; HUI-LIN LI *c.s.* *Fl. Taiwan* 3 (1977) 568, pl. 727; HARA, *En. Fl. Pl. Nep.* 2 (1979) 51. — *P. triphylla* (*non* BUCH.-HAM. *ex* D.DON,

1825) ROYLE, III. (1839) t. 19D, *non* BURM.f. 1768, *et auct. var. pro parte*; MERR. En. Philip. 2 (1923) 384. — *Semeiocardium hamiltonii* HASSK. in Miq. Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 151, *p.p.* — Fig. 1a-h.

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, ciliate, 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 alae obovate, 5-nerved. Upper petals oblong, slightly longer than the keel; the keel inappendiculate, apically minutely papillose. Filaments free for c. 1/4. Ovary orbicular; style curved and widened in apical half, obliquely truncate. Capsule symmetric, \pm 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 tuberculate, shortly hairy, at micropylar side with an obliquely lobed aril, at chalazal side inappendiculate.

DISTR. Iran to 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 tuberculate, almost globular, at chalazal side with a minute appendage.

2. *Polygala malesiana* ADEMA, Blumea 14 (1966) 257, f. 3, 4. — *P. triphylla* BUCH.-HAM. ex D. DON var. *glaucescens* [*non* WALL. Cat. (1831) 4182] BENN. Fl. Br. India 1 (1872) 201; KING, J. As. Soc. Beng. 59, ii (1890) 130. — *P. cardiocarpa* (*non* KURZ) RIDLEY, Fl. Mal. Pen. 1 (1922) 139, *p.p.*; MERR. En. Philip. 2 (1923) 383; MUKHERJEE, Bull. Bot. Soc. Beng. 12 (1961) 36, *p.p.* — Fig. 1i-k.

Herb up to 25 cm. Stem glabrous, ribbed, 2- or 3-chotomously branched. Leaves mostly in pseudowhirls of 3, broadly elliptic to ovate, 10-55 by 9-25 mm, acute, base attenuate, laxly short-hairy, ciliate, 0.5-1 cm petioled. Racemes terminal or in a fork, including the peduncle 3-7.5 cm; bracts and bracteoles early caducous. Flowers 1.5-2 mm long, white with rosa crest. Sepals blunt, the alae 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 obovate; style curved and widened in apical half, obliquely truncate apically. Capsule symmetric, obovate, c. 2.5 mm long, apically notched, not mucronate, winged; wing cross-veined, distinctly widening

apically. Seed ellipsoid, tuberculate, shortly hairy, at micropylar side with an obliquely lobed aril, at chalazal side with an appendage one third as long as the seed; this somewhat narrower than the seed, truncate, ending in an orbicular, hollow, membranous lamella, which makes an angle of c. 45° with the seed.

DISTR. Malesia: Malay Peninsula (Perak, Pahang, Selangor), Lesser Sunda Islands (Sumba, Flores), SE. Celebes (Tukangbesi Is.), Philippines (Bohol), Moluccas (Buru, Ceram, Kai and Aru Is.), and West New Guinea (Sorong and Vogelkop Peninsula).

ECOL. In Malaya and Celebes noted from limestone (should also be from Sumba), in open terrain, below 300 m.

NOTE. *Polygala isocarpa* CHODAT (*P. umbonata* CRAIB) differs in a number of small but constant characters, especially in the style, which is somewhat inflated and apically not widened, and in the chalazal appendage of the seed, of which the kidney-shaped, basal, hollow membranous lamella makes a right angle to the seed.

3. *Polygala cardiocarpa* KURZ, J. As. Soc. Beng. 41, ii (1872) 293; CHODAT, Monogr. 11 (1893) 42, *nomen*; CRAIB, Not. R. Bot. Gard. Edinb. 11 (1919) 187, 188; RIDLEY, Fl. Mal. Pen. 1 (1922) 139, *p.p.*; CRAIB, Fl. Siam. En. 1 (1931) 100; ADEMA, Blumea 14 (1966) 260, f. 6. — *Heterosamara birmanica* (O. K.) CHODAT, Bull. Herb. Boiss. 3 (1895) 128. — *P. palustris* LACE, Kew Bull. (1915) 344; MUKHERJEE, Bull. Bot. Soc. Beng. 12 (1961) 36. — Fig. 1l-n.

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, ciliate, 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 obovate, 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 \pm ellipsoid, tuberculate, 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 Is.).

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

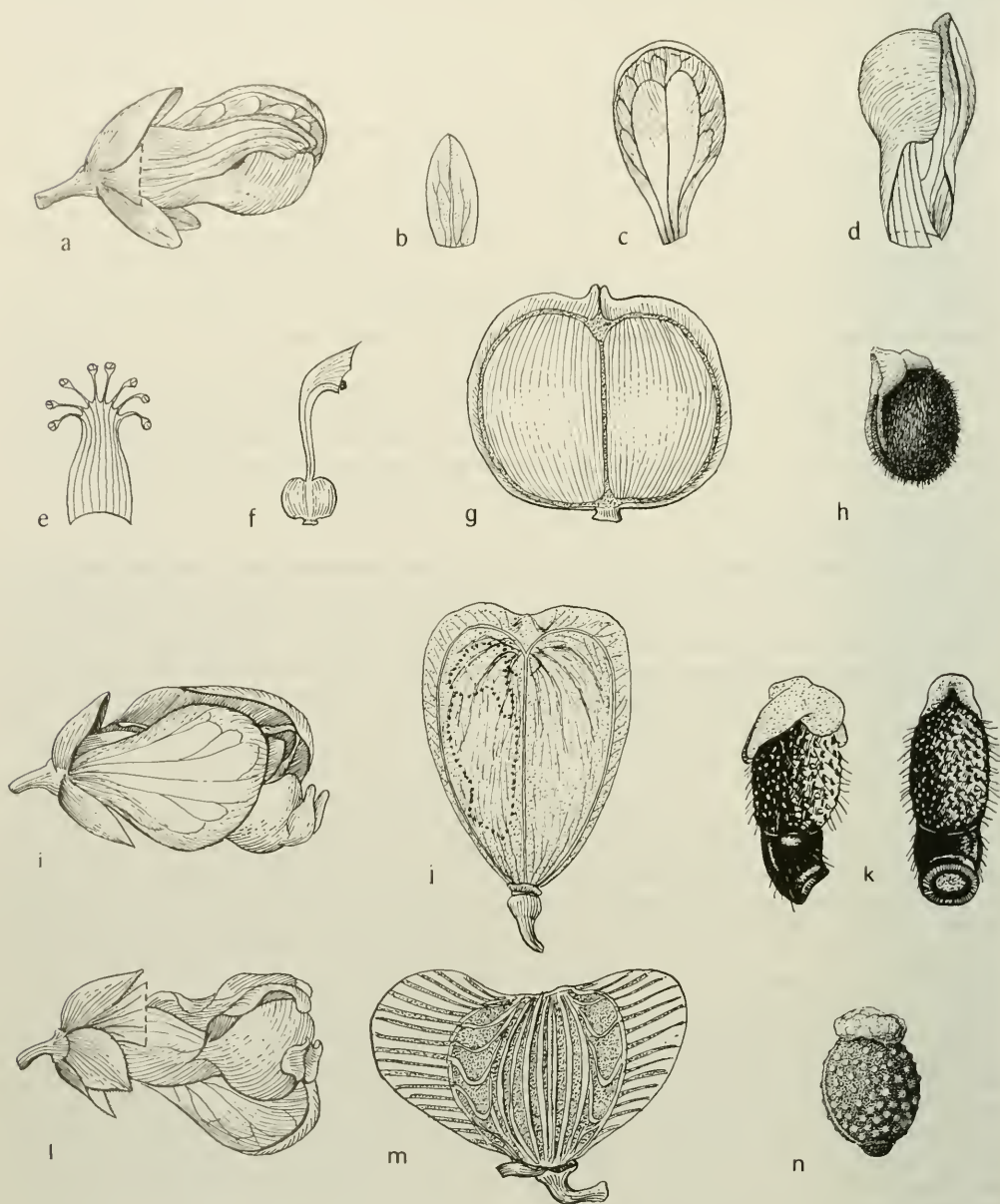


Fig. 1. *Polygala tatarinowii* REGEL. a. Flower; b. upper sepal; c. ala; d. keel enveloping staminal tube, at right one petal; e. staminal tube laid open; f. pistil; g. fruit; h. seed. — *P. malesiana* ADEMA. i. Flower; j. fruit; k. seed, lateral and ventral view. All $\times 15$. — *P. cardiocarpa* KURZ. l. Flower; m. fruit; n. seed. All $\times 10$ (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.*

Bredemeyera sect. Melchiora STEEN. Acta Bot. Neerl. 17 (1968) 380 (Typus: *Bredemeyera papuana* STEEN.).

Liana. Flowers in short axillary racemes. Lateral *sepals* (alae) caducous before fruit-setting, other sepals persistent below the fruit. Keel inappendiculate. 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.

4. *Polygala papuana* (STEEN.) MEIJDEN, *comb. nov.* — *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 petioled. 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.

Distr. *Malesia*: New Guinea.

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 (*l.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. Pro-*

sthemasperma F.v.M. 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 (*l.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 (*l.c.*) dismissed the difference in the calyx as 'rather trivial', whereas CHODAT 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*.

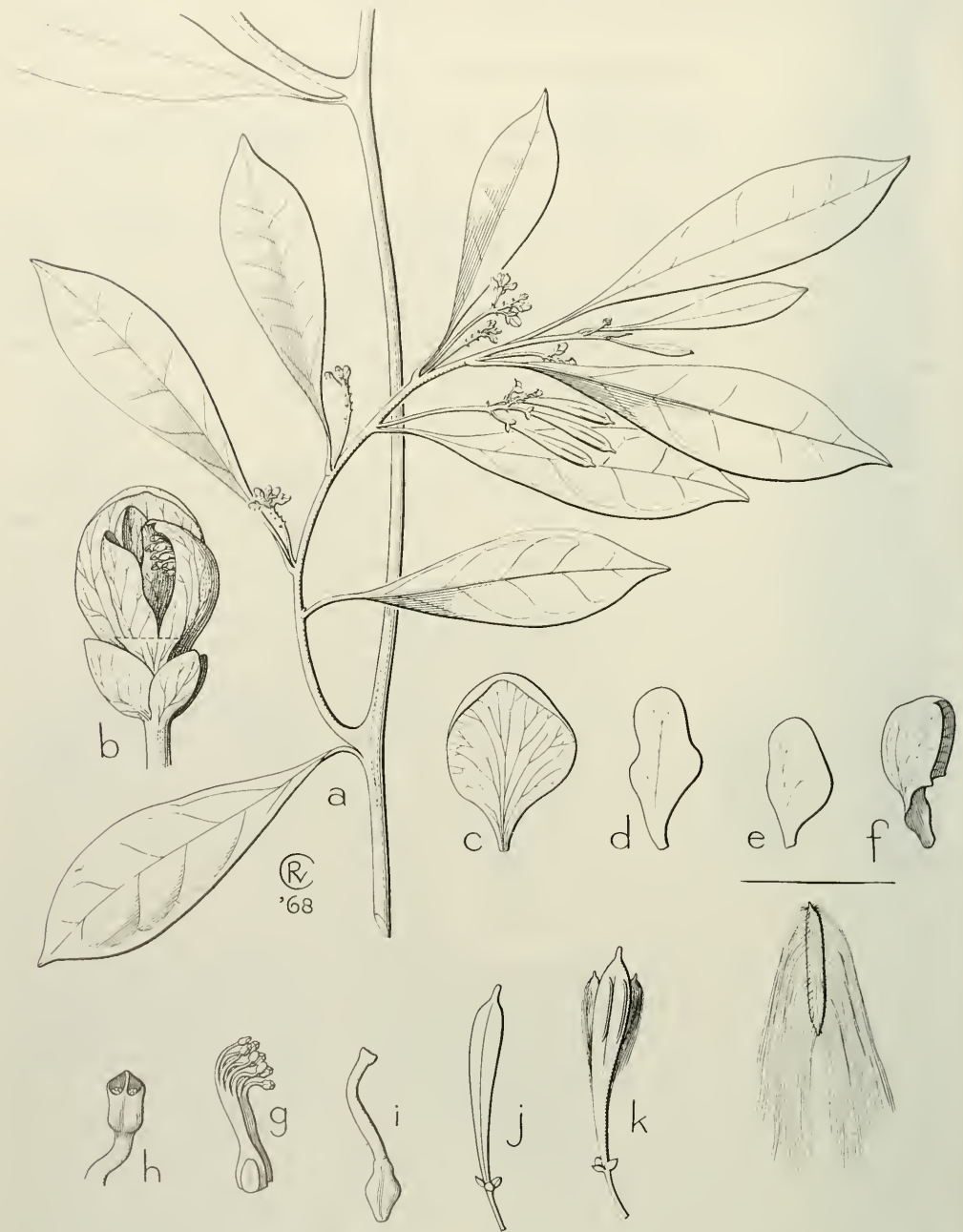


Fig. 2. *Polygala papuana* (STEEN.) MEIJDEN. a. Habit, $\times 0.66$; b. flower; c. lateral petal; d. upper petal; e. ditto; f. keel; g. stamens; all $\times 4$; h. anther, $\times 16$; i. ovary and style, $\times 4$; j. young fruit, k. ripe fruit; $\times 1.3$; l. seed, $\times 2.5$ (a, e, j-l DOCTERS VAN LEEUWEN 10387, b-d, f-i LEDERMANN 9395).

3. Section Chamaebuxus

DC. Prod. 1 (1824) 331; CHODAT, Monogr. II (1893) 93. — *Chamaebuxus* (DC.) SPACH, Hist. Vég. Phan. 7 (1838) 125 ('1839'); OPIZ, Oekon. Neuigk. Verh. (1839) 526. — *Badiera sensu* HASSK. Cat. Hort. Bog. (1844) 227, p.p.

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.) spatulate, 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 inappetent but chalazal area often slightly protruding; (sub)glabrous or (not in Mal.) completely covered with hairs at least twice as long as the seed.

5. *Polygala oreotrephe*s BURTT, Not. R. Bot. Gard. Edinb. 29 (1969) 148, fig.; STONE, Fed. Mus. J. 26 (1981) 131. — *P. monticola* (non H.B.K., 1823) RID-

LEY, J. Linn. Soc. Bot. 38 (1908) 303; Fl. Mal. Pen. 1 (1922) 138; HEND. Gard. Bull. S. S. 4 (1927) 93; J. Fed. Mal. St. Mus. 13 (1927) 2; SYM. J. Mal. Br. R.

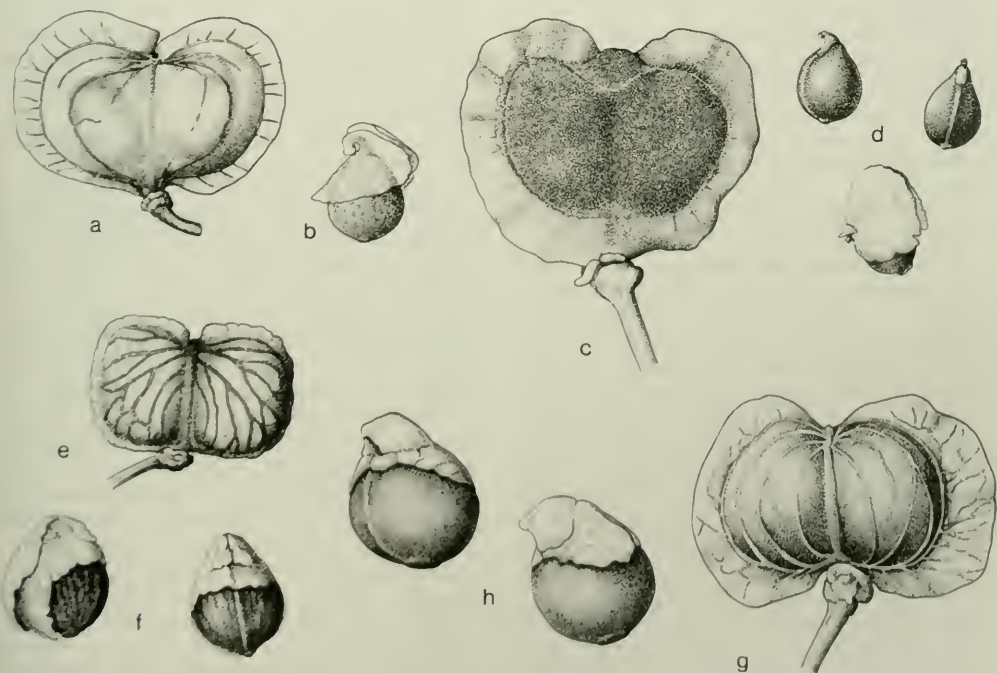


Fig. 3. *Polygala oreotrephe*s BURTT. a. Capsule; b. seed. — *P. sumatrana* MIQ. c. Capsule; d. seeds. — *P. venenosa* JUSS. ex POIR. e. Capsule; f. seeds. — *P. arillata* BUCH.-HAM. ex D. DON. g. Capsule; h. seeds. All $\times 5$ (a, b MAXWELL 78-320, b, c MORLEY 437, e, f PNH 117264, g, h MAXWELL 74-782).

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 alae 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 chalaza 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.

6. *Polygala sumatrana* MIQ. Fl. Ind. Bat., Suppl. (1861) 392; CHODAT, Bull. Herb. Boiss. 4 (1896) 234. — *P. glaucocarpa* RIDLEY, J. Fed. Mal. St. Mus. 84 (1917) 16. — Fig. 3c, d.

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 alae 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 transverse-ly 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 chalaza and the raphe distinctly visible.

Distr. *Malesia*: West, Central and East Sumatra. Ecol. Mountain forests, 1000–2200 m.

7. *Polygala venenosa* Juss. ex POIR. in Lamk, Encycl. 5 (1804) 493; DC. Prod. 1 (1824) 331; HASSK. Flora 25² (1842) Beibl. 2, 31; MIQ. Fl. Ind. Bat. 1, 2 (1858) 126; O.K. Rev. Gen. Pl. 1 (1891) 45, incl. var. *eramosa* O. K.; CHODAT, Monogr. II (1893) 98; RIDLEY, Trans. Linn. Soc. II, 3 (1893) 276; STAPP, *ibid.* 4 (1894) 131; MERR. Philip. J. Sc. 2 (1907) Bot. 277; BACKER, Schoolfl. Java (1911) 77; HALL.f. Meded. Rijksherb. 12 (1912) 26; KOORD. Exk. Fl. Java 2 (1912) 450; RIDLEY, J. Fed. Mal. St. Mus. 8⁴ (1917) 16; MERR. En. Botn. (1921) 324; RIDLEY, Fl. Mal. Pen. 1 (1922) 137; MERR. En. Philip. 2 (1923) 385; BURK. Gard. Bull. S. S. 3 (1923) 34; KOORD. Fl. Tjibodas 2 (1923) 132; BURK. Gard. Bull. S. S. 3 (1925) 345; HEND. J. Mal. Br. R. As. Soc. 5 (1927) 242; MERR. Pl. Elm. Born. (1929) 133; CRAIB, Fl. Siam. En. 1 (1931) 104, incl. var. *robusta*; MERR. Contr. Arn. Arb. 8 (1934) 84; HEND. Mal. Nat. J. 4 (1949) 29; MUKHERJEE, Bull. Bot. Soc. Beng. 12 (1961) 31; BACKER & BAKH.f. Fl. Java I (1963) 198; STEEN. Mount. Fl. Java (1972) pl. 41-5, incl. ssp. *pulchra* (HASSK.) STEEN., pl. 41-6. — *P. pulchra* HASSK. Flora 25² (1842) Beibl. 2, 32; CHODAT, Monogr. II (1893) 100; BACKER, Schoolfl. Java (1911) 77; KOORD. Exk. Fl. Java 2 (1912) 450; RIDLEY, Fl. Mal. Pen. 1 (1922) 137; RIDLEY, J. Str. Br. R. As. Soc. n. 87 (1923) 53; BACKER & BAKH.f. Fl. Java 1 (1963) 198. — *Badiera venenosa* (POIR.) HASSK. Cat. Hort. Bog. (1844) 227. — *Badiera pulchra* (HASSK.) HASSK. l.c. 227. — *Chamaebuxus venenosa* (POIR.) HASSK. Pl. Jav. Rar. (1848) 294; in Miq. Pl. Jungh. 1 (1851) 26, incl. var. *robusta*, *gracilis*, *aptera*; in Miq. Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 154, incl. subvar. *obovata* & *elliptica*, var. *minor*. — *Chamaebuxus pulchra* (HASSK.) HASSK. Pl. Jav. Rar. (1848) 294; in Miq. Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 152. — *P. sinassan* MIQ. Fl. Ind. Bat., Suppl. (1861) 392. — Fig. 3e, f.

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 obovate. 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 micropylar 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.

8. *Polygala arillata* BUCH.-HAM. ex D.DON, Prod. Fl. Nep. (1825) 199; WALL. Pl. As. Rar. 1 (1830) 100; MIQ. Fl. Ind. Bat. 1, 2 (1858) 125; BENN. Fl. Br. India 1 (1872) 200, *p.p.*; FORBES & HEMSLEY, J. Linn. Soc. 23 (1886) 59; CHODAT, Monogr. II (1893) 94; TRIMEN, Fl. Ceyl. 1 (1893) 79; BURK. Rec. Bot. Surv. India 4 (1910) 98; HAND.-MAZZ. Symb. Sinic. 7 (1933) 633; KANJILAL & DAS, Fl. Assam 1, 1 (1935) 87; GAGNEP. Fl. Gén. I.-C. Suppl. 1 (1938) 231; BANERJI, J. Bomb. Nat. Hist. Soc. 51 (1953) 555; KITAMURA, Fl. Pl. Nepal Himal. (1955) 170; SMITINAND, Thai For. Bull. 2 (1955) 3; MUKHERJEE, Bull. Bot. Soc. Beng. 12 (1961) 31; SMITINAND, Nat. Hist. Bull. Siam Soc. 20 (1961) 43; LAUENER, Not. R. Bot.

Gard. Edinb. 26 (1965) 343; KANAI, Fl. E. Himal. (1966) 173; HANSEN *c.s.* Dansk Bot. Ark. 25 (1967) 83; KANAI, Phot. Pl. E. Himal. (1968) f. 138; MURATA, Acta Phyt. Geobot. 25 (1973) 116; HARA, En. Fl. Pl. Nepal 2 (1979) 50. — *Chamaebuxus arillata* (D.DON) HASSK. in Miq. Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 153; KURZ, Fl. Burma 1 (1877) 79, *p.p.* — *P. tonkinensis* CHODAT, Monogr. II (1893) 97. — *Crotalaria duboisii* LÉV. Bull. Soc. Bot. Fr. 51 (1904) 291, *cf.* LAUENER, *l.c.* — **Fig. 3g, h.**

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, cuspidate, base attenuate to obtuse, thinly hairy to glabrous, beneath somewhat glaucescent, up to 1.5 cm petioled. *Racemes* terminal, axillary or extra-axillary, erect or rarely pendulous at apex, including the 6–12.5 cm long peduncle, dense. 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 obovate. 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 micropylar 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 karensium* 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*

Polygala sect. Orthopolygala CHODAT, Monogr. II (1893) 120, *nom. illeg.*

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-



E. Vjisma '66

Fig. 4. *Polygala javana* DC. Habit, $\times 0.7$ (TEIJSMA *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.) inappendiculate. 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 inappendiculate.

9. *Polygala javana* DC. Prod. 1 (1824) 327; W. & A. Prod. 1 (1834) 38; MIQ. Fl. Ind. Bat. 1, 2 (1858) 124; THWAITES, En. (1864) 22; HASSK. in Miq. Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 180; BENN. Fl. Br. India 1 (1872) 201; TRIMEN, Fl. Ceyl. 1 (1893) 80; BACKER, Schoolfl. Java (1911) 79; Onkruidfl. Suiker. (1934) 394, Atlas t. 375; MUKHERJEE, Bull. Bot. Soc. Beng. 12 (1961) 44, *excl. var.*; BACKER & BAKH.f. Fl. Java 1 (1963) 198; ADEMA, Blumea 14 (1966) 261; MATTHEW, Fl. Tamil. Carnatic 1 (1981) 70. — *P. tinctoria* (non VAHL) HASSK. in Miq. Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 181, *p.p.* — Fig. 4, 5.

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, \pm 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* \pm 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, \pm quadrangular, apically notched, with a narrow, membranous, veined margin, hairy. *Seeds* \pm globular, at micropylar side with an unequally 3-lobed aril, black, hairy.

Distr. Sri Lanka and S. India; in *Malesia*: Java



Fig. 5. *Polygala javana* DC. a. Flower; b. upper sepal; c. ala; all $\times 4$; d. keel enveloping staminal tube, at right one petal; e. opened staminal tube; f. pistil; all $\times 6$; g. fruit, $\times 4$; h. seed, $\times 6$ (a–f TEUSMANN 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.

10. *Polygala japonica* HOUTT. Handl. 10 (1779) t. 62 f. 1; DC. Prod. 1 (1824) 324; BENTH. Fl. Austr. 1 (1863) 138; CHODAT, Monogr. II (1893) 353; F.M. BAILEY, Queensl. Fl. 1 (1899) 78; MERR. & ROLFE, Philip. J. Sc. 3 (1908) Bot. 106; GAGNEP. Fl. Gén. 1.-C. 1 (1909) 255; MERR. En. Philip. 2 (1923) 384; YAMAZUTA, List Manch. Pl. (1930) 176; MASAMUNE, Yakusima (1934) 263; MAKINO, Ill. Fl. Japan (1954) 382; OHWI, Fl. Japan (1965) 587; ADEMA, Blumea 14 (1966) 263, f. 8; Proc. R. Soc. Queensl. 80 (1969) 126; HORIKAWA, Atlas Jap. Fl. 1 (1972) 155; WILLIS, Pl. Vict. 2 (1972) 342; WALKER, Fl. Okinawa (1976) 623; HUI-LIN LI c.s. Fl. Taiwan 3 (1977) 558, f. 726; THOMPSON, Fl. New South Wales

112 (1978) 14. — *P. vulgaris* (non L.) THUNB. Fl. Jap. (1784) 277. — *P. veronicaea* F.v.M. Trans. Vict. Inst. 1 (1855) 117; CHODAT, Monogr. II (1893) 355 ('*veronicaefolia*'); DOMIN, Bibl. Bot. 89 (1927) 855; BURB. Fl. Austr. Cap. Terr. (1970) 244, t. 237. — *P. khasyana* HASSK. in Miq. Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 176. — *P. sibirica* (non L.) HASSK. l.c. 260; BENN. Fl. Br. India 1 (1872) 205, p.p.; EWART, Fl. Vict. (1931) 715. — *P. sibirica* L. var. *japonica* (HOUTT.) T. ITO, J. Coll. Sc. Univ. Tokyo 12 (1899) 311. — *P. luzoniensis* MERR. Philip. J. Sc. 1 (1906) Suppl. 202. — *P. hondoënsis* NAKAI, Bot. Mag. Tokyo 36 (1922) 21. — **Fig. 6.**

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, subsessile, 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 $\times 7$ (a–f SHAW MAYER s.n.; g, h BORGMANN 326).

finely punctate-dotted. *Racemes* supra-axillary, the free part 1–3 mm long, rather few-flowered. Bracts and bracteoles early caducous. *Flowers* 5–7 mm long, mauve or purple to deep lavender. *Sepals* mucronate, the outer shortly hairy, the alae elliptic, 3–5-nerved. Upper *petals* oblong, rarely (JACOBS 7428) absent or very much reduced, hairy inside in basal half; keel articulate, with 2 much-incised appendages. *Filaments* (nearly) connate to apex. *Ovary* broadly obovate, glabrous; style (nearly) straight, subapically at inner side with 2 small, spaced (1 mm) stigmatic lobes, the lower one \pm knob-like. *Capsule* broader and somewhat shorter than the alae, c. 4–5 by 5 mm, emarginate apically, with a rather wide (c. 1 mm), veined membranous margin which is apically often wider than basally. *Seeds* \pm ovoid, at micropylar side with an unequally 3-lobed aril, black, hairy.

Distr. 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.

Ecol. Roadsides, grasslands, trodden ground in

the mountains, 1200–2600 m; in Japan from 0–1500(–2000) m.

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.

11. *Polygala persicariaefolia* DC. Prod. 1 (1824) 326; WALL. Pl. As. Rar. 2 (1831) 79, t. 184; HASSK. in Miq. Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 178; OLIV. Fl. Trop. Afr. 1 (1868) 129; BENN. Fl. Br. India 1 (1872) 202; F.V.M. Descr. Not. Pap. Pl. 7 (1887) 26; CHODAT, Monogr. 11 (1893) 331; F.M. BAILEY, Queensl. Fl. 1 (1899) 78; K.SCH. & LAUT. Fl. Schutzgeb. Südsee, Nachtr. (1905) 326; F.M. BAILEY, Compr. Cat. Queensl. Pl. (1913) 43; MERR. En. Philip. 2 (1923) 384; CRAIB, Fl. Siam. En. 1 (1931) 103; MERR. Pap. Mich. Ac. Sc. 20 (1935) 100; GAGNEP. Fl. Gén. I.-C. Suppl. 1 (1938) 236; BANERJI, J. Bomb. Nat. Hist. Soc. 51 (1953) 555; *ibid.* 55 (1958) 251; MUKHERJEE, Bull. Bot. Soc. Beng. 12 (1961) 45; BACKER & BAKH.f. Fl. Java 1 (1963) 199; BANERJI,



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 $\times 7.5$ (a–f PRINGGO ATMODOJO 123; g, h HUBOT 32).

Rec. Bot. Surv. India 19² (1965) 25; KANAI, Fl. E. Himal. (1966) 173; ADEMA, Blumea 14 (1966) 265, f. 9; Proc. R. Soc. Queensl. 80 (1969) 128; MATTHEW, Fl. Tamil. Carnatic 1 (1981) 72. — *P. buchanani* BUCH.-HAM. ex D. DON, Prod. Fl. Nepal. (1825) 199, *nom. superfl., illeg.* — *P. wallichiana* WIGHT, Ill. 1 (1831) 49, t. 22A. — *P. rufa* SPAN. Linnaea 15 (1841) 167, lc. 40 (*ined.*). — *P. septemnervia* MERR. Philip. J. Sc. 1 (1906) Suppl. 202. — Fig. 7.

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 petioled, 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 \pm orbicular, 5-veined. Upper *petals* oblong, hairy inside in basal half; keel auriculate and there 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.

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

12. *Polygala longifolia* POIR. in Lamk. Encycl. 5 (1804) 501; DC. Prod. 1 (1824) 325; F.v.M. Descr. Not. Pap. Pl. 6 (1885) 4; CHODAT, Monogr. II (1893) 358; BURK. Rec. Bot. Surv. India 4 (1910) 98; BACKER, Schoolfl. Java (1911) 79; MERR. En. Philip. 2 (1923) 384; CRAIB, Fl. Siam. En. 1 (1931) 103; BANERJI, J. Bomb. Nat. Hist. Soc. 51 (1953) 555; KITAMURA, Fl. Pl. Nepal Himal. (1955) 171; MUKHERJEE, Bull. Bot. Soc. Beng. 12 (1961) 40; BACKER & BAKH.f. Fl. Java 1 (1963) 199; LAUENER, Not. R. Bot. Gard. Edinb. 26 (1965) 344; ADEMA, Blumea 14 (1966) 266, f. 11; Proc. R. Soc. Queensl. 80 (1969) 127; WALKER, Fl. Okinawa (1976) 623; HARA, En. Fl. Pl. Nepal 2 (1979) 50; GILLI, Ann. Naturhist. Mus. Wien 83 (1980) 452; ANON. Icon. Corm. Sin. Suppl. 2 (1983) 183, f. 8783. — *P. leptalea* DC. Prod. 1 (1824) 325; BENTH. Fl. Austr. 1 (1863) 139; HASSK. in Miq. Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 173; BENN. Fl. Br. India 1 (1872) 202; F.M. BAILEY, Queensl. Fl. 1 (1899) 78; DOMIN, Beitr. Fl. & Pfl. Geogr. Austr. 1 (1927) 855. — *P. oligophylla* DC. Prod. 1 (1824) 325; CHODAT, Monogr. II (1893) 353. — *P. discolor* BUCH.-HAM. ex D. DON, Prod. Fl. Nepal. (1825) 199. — *P. pyramidalis* LÉV. Bull. Soc. Bot. Fr. 51 (1904) 291. — *P. riukiensis* OHWI, J. Jap. Bot. 12 (1936) 661; MASAMUNE, En. Trach. 5 (1955) 148. — Fig. 8.

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, sessile, 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), lilac, 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

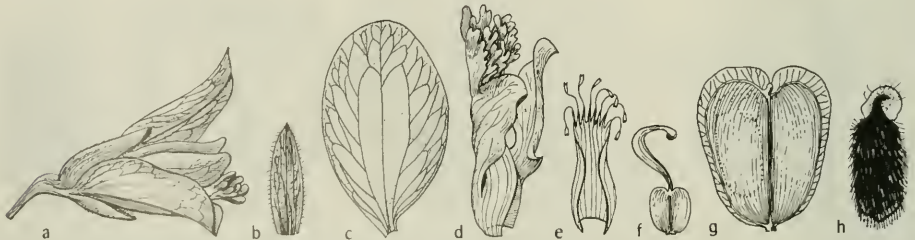


Fig. 8. *Polygala longifolia* POIR. a. Flower; b. upper sepal; c. ala; d. keel enveloping staminal tube, at right one petal; e. opened staminal tube; f. pistil; g. fruit; all $\times 7$; h. seed, $\times 7.5$ (BRASS 32360).



Fig. 9. *Polygala paniculata* LINNÉ. a. Inflorescence, $\times 8$; b. flower; c. upper sepal; d. ala; e. keel enveloping staminal tube, at right one petal; f. opened staminal tube; g. pistil; h. fruit; all $\times 10$; i. seed, $\times 12.5$ (ELBERT 218).

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, Indochina, 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, FI) is said to hail from Java, but this is certainly an error, cf. Fl. Males. I, 1 (1950) xxix.

13. *Polygala paniculata* LINNÉ, Syst. ed. 10 (1759) 1154; Amon. 5 (1759) 402; CHODAT, Monogr. 11 (1893) 229; K. SCH. & LAUT. Fl. Schutzgeb. Südsee, Nachr. (1905) 285; BACKER, Schoolfl. Java (1911) 79; BACKER & SLOOTEN, Handb. Thee. (1924) 159; BACKER, Onkruidfl. Suiker. (1930) 393, Atlas t. 374; SINCLAIR, Gard. Bull. Sing. 14 (1953) 31; BACKER & BARKH. f. Fl. Java 1 (1963) 78; ADEMA, Blumea 14 (1966) 267; HANSEN c.s. Dansk Bot. Ark. 25 (1967) 84; ADEMA, Proc. R. Soc. Queensl. 80 (1969) 128;

STONE, Micronesica 6 (1970) 362; HENTY & PRITCH. Div. Bot. Lae, Bot. Bull. 7 (1973) 136; HUI-LIN LI c.s. Fl. Taiwan 3 (1977) 558; GILLI, Ann. Naturhist. Mus. Wien 83 (1980) 452; A.C. SMITH, Fl. Vit. Nova 3 (1985) 723. — *P. variabilis* (non H.B.K.) HASSK. Retzia (1855) 149. — *P. fernandesiana* PAIVA, Bol. Soc. Brot. III, 53 (1981) 1460. — Fig. 9.

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 $\pm 1/8$. Ovary \pm 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, \pm 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).

Ecol. Waste places and fields, often abundant, on different soil types, avoiding the driest areas, 0–2250 m.

14. *Polygala exsuarrosa* ADEMA, Blumea 14 (1966) 268; Proc. R. Soc. Queensl. 80 (1969) 125. — *P. arvensis* var. *squarrosa* BENTH. Fl. Austr. 1 (1863) 141, non *P. squarrosa* L.f., 1781. — Fig. 10.

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-

angular, patently 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 quadrangular, 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 I., Brisbane); in *Malesia*: SE. Moluccas, Aru Is. (Trangan), New Guinea (Cyclops Mts: 1 coll.; Papua: W. Distr., 1 coll.).

Ecol. Sandy savannah in hilly country, a few metres above sea-level.

Note. Similar to the Australian species *P. eriocephala* BENTH.; its affinity with that species should be further examined.

15. *Polygala polifolia* PRESL, Rel. Haenk. 2 (1835) 101; MERR. En. Philip. 2 (1923) 384; HUI-LIN LI c.s. Fl. Taiwan 3 (1977) 558 (*'polyfolia'*). — *P. brachystachya* DC. Prod. 1 (1824) 326, non POIRET, 1816, nom. illeg.; MUKHERJEE, Bull. Bot. Soc. Beng. 12 (1961) 43 (*'brachistachyos'*), nec BLUME, 1825. — *P. telephoides* (non WILLD.) W. & A. Prod. 1 (1834) 36; THWAITES, En. Pl. Zeyl. (1864) 22; BENN. Fl. Br. India 1 (1872) 205; TRIMEN, Fl. Ceyl. 1 (1893) 80;

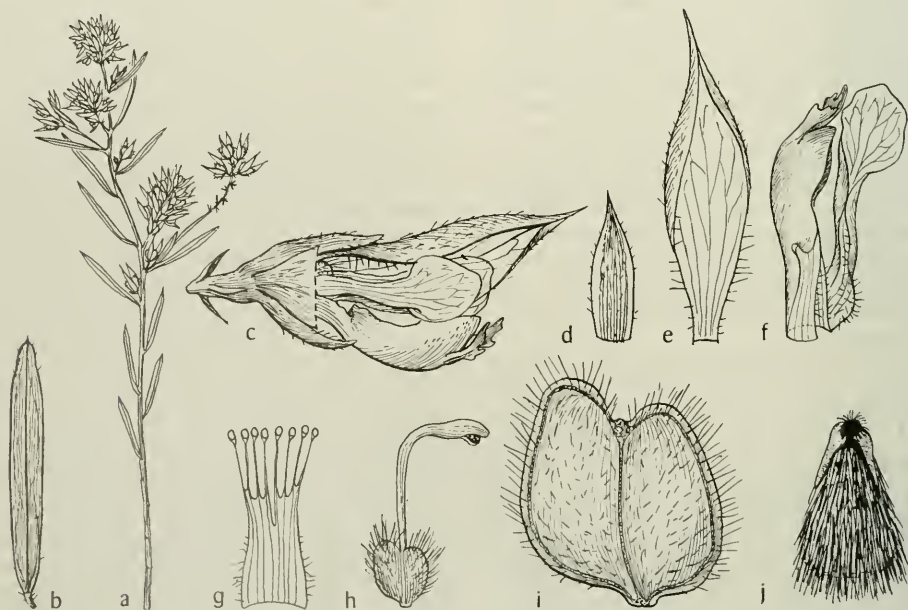


Fig. 10. *Polygala exsuarrosa* ADEMA. a. Habit, $\times 0.5$; b. leaf, $\times 2$; c. flower, one ala cut away; d. upper sepal; e. ala; f. keel enveloping staminal tube, at right one petal; g. opened staminal tube; h. pistil; i. fruit; j. seed. All $\times 10$ (BUWALDA 5344).



Fig. 11. *Polygala polifolia* PRESL. 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 $\times 10$ (RAHMAT SI TOROES 4561).

ADEMA, Blumea 14 (1966) 269, *in syn.*; NAKAJIMA, Hokuriku J. Geobot. 18 (1970) 124; MATTHEW, Fl. Tamil. Carnatic 1 (1981) 74. — *P. buxiformis* HASSK. in Miq. Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 161. — *P. chinensis* (non L.) BENN. Fl. Br. India 1 (1872) 204; F.V.M. Descr. Not. Pap. Pl. 9 (1890) 55; CHODAT, Monogr. II (1893) 385; K.SCH. & LAUT. Fl. Schutzgeb. Südsee, Nachtr. (1905) 284; GIBBS, J. Linn. Soc. Bot. 42 (1914) 59; MERR. En. Born. (1921) 324; ADEMA, Blumea 14 (1966) 269, f. 15; YAMAZAKI, J. Jap. Bot. 49 (1974) 227; WALKER, Fl. Okinawa (1976) 623. — *P. warburgii* CHODAT *ex* WARB. Bot. Jahrb. 13 (1891) 346; CHODAT, Monogr. II (1893) 315. — *P. simadae* MASAMUNE, J. Soc. Trop. Agr. 3 (1931) 114; En. Trach. 5 (1955) 148. — *P. arvensis* (non WILLD.) ADEMA, Blumea 14 (1966) 269, *in syn.*; BURTT, Not. R. Bot. Gard. Edinb. 32 (1972) 404; IQBAL DAR, Fl. W. Pakist. 52 (1973) 7, f. 3a-c. — 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 \pm spatulate, emarginate, shorter than the keel; keel auriculate, at apex with 2 much-incised appendages. Staminal tube split halfway, with 2 single filaments and 2 bundles of 3 fully connate filaments with sessile anthers. Ovary broadly elliptic, ciliolate 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, cilio-

late, 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. CHIRIFK) 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*, *linarifolia*, 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.

16. *Polygala chinensis* LINNÉ, Sp. Pl. 1 (1753) 704; MERR. Trans. Am. Phil. Soc. 24² (1935) 228; *non auct. var.*; MUKHERJEE, Bull. Bot. Soc. Beng. 12 (1961) 38, *excl. var. linearifolia et hirsuta*. — *P. glomerata* LOUR. Fl. Cochinch. (1790) 426; DC. Prod. 1 (1824) 326; MIQ. Fl. Ind. Bat. 1, 2 (1858) 125; BACKER, Schoolfl. Java (1911) 78; MERR. En. Born. (1921) 324; En. Philip. 2 (1923) 353; BACKER & SLOOTEN, Handb. Thee. (1924) 158; BACKER & BAKH.f. Fl. Java 1 (1963) 198; ADEMA, Blumea 14 (1966) 270, f. 16; BURTT, Not. R. Bot. Gard. Edinb. 32 (1972) 403. — *P. telephoides* WILLD. Sp. Pl. 3 (1803) 876; *non auct. plur.* — *P. arvensis* WILLD. Sp. Pl. 3 (1803) 876; ROXB. Fl. Ind. (ed. Carey) 3 (1832) 218; W. & A. Prod. (1834) 236; WALP. Rep. 1 (1842) 233; HASSK. in Miq. Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 162; MATTHEW, Fl. Tamil. Carnatic 1 (1981) 65; *non BENTH.* 1864, *nec BURTT*, 1972. — ? *P. tranquebarica* MART. Denkschr. Bot. Ges. Regensb. 1 (1815) 186. — *P. densiflora* BLUME, Bijdr. (1825) 59; HASSK. in Miq. Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 166; CHODAT, Monogr. II (1893) 380; K.SCH. & LAUT. Fl. Schutzgeb. Südsee, Nachtr. (1905) 284. — *P. toxoptera* TURCZ. Bull. Soc. Nat. Mosc. 27² (1854) 348. — Fig. 12.

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* c. 4.5 mm long, white with green alae. *Sepals* lanceolate, acuminate and with a long mucro, ciliate, alae asymmetric, 5-nerved. Upper *petals* spatulate, 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 Indochina; in *Malesia*: Malay Peninsula (Penang), Sumatra, Java (very common in W. Java, much less so in Central and E. Java), Lesser Sunda Islands

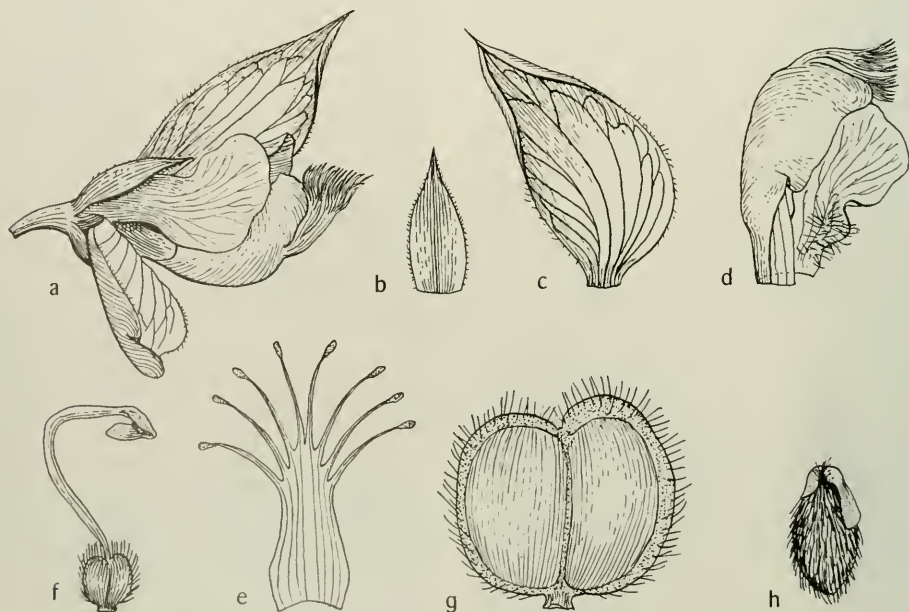


Fig. 12. *Polygala chinensis* LINNÉ. a. Flower; b. upper sepal; c. ala; d. keel enveloping staminal tube, at right one petal; e. opened staminal tube; f. pistil; g. fruit; h. seed. All $\times 7$ (ADELBERT 313).

(Sumbawa, Sumba, Flores), SE. Borneo and Sarawak, Philippines (Luzon, Jolo, Mindanao), New Guinea.

Ecol. 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. glaucoides*. 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*.

17. *Polygala wightiana* W. & A. Prod. (1834) 38; WALP. Rep. 1 (1842) 232; HASSK. in Miq. Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 170; CHODAT, Monogr. II (1893) 358; ADEMA, Blumea 14 (1966) 272, f. 17; Proc. R. Soc. Queensl. 80 (1969) 128; MATTHEW, Fl. Tamil. Carnatic 1 (1981) 74. — Fig. 13.

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).

Ecol. In open grassland obviously with a preference for areas subject to a dry season, 0–500 m.

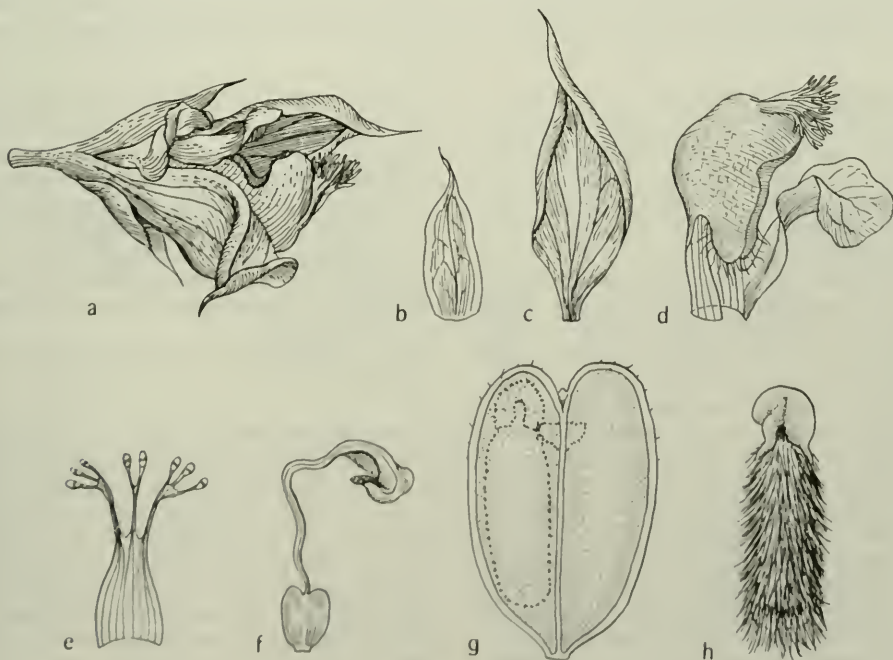


Fig. 13. *Polygala wightiana* W. & A. a. Flower; b. upper sepal; c. ala; d. keel enveloping staminal tube, at right one petal; e. opened staminal tube; f. pistil; g. fruit; h. seed. All $\times 10$ (WALLICH 4190).

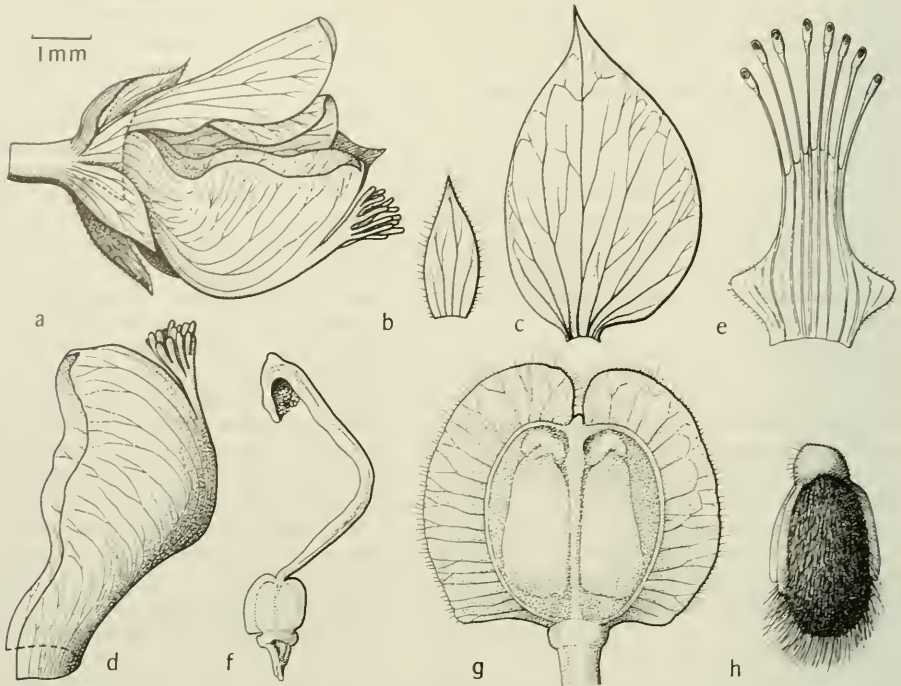


Fig. 14. *Polygala rhinanthoides* BENTH. a. Flower; b. upper sepal; c. ala; d. keel enveloping staminal tube, at right one petal; e. opened staminal tube; f. pistil; g. fruit; h. seed. Scale bar 1 mm.

18. *Polygala rhinanthoides* BENTH. Fl. Austr. 1 (1863) 140; CHODAT, Monogr. II (1893) 384; F.M. BAILEY, Queensl. Fl. 1 (1899) 79; BANKS & SOL. III. Bot. Voy. Endeav. 1 (1900) 9, t. 14; F.M. BAILEY, Compr. Cat. Queensl. Pl. (1913) 43; DOMIN, Bibl. Bot. 89 (1927) 856; ADEMA, Proc. R. Soc. Queensl. 80 (1969) 128. — Fig. 14.

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 I.); in Malesia: Papua New Guinea (W. Distr.: 3 coll.).

Ecol. Open savannah woodland and grassland at low altitude.

19. *Polygala glaucoides* LINNÉ, Sp. Pl. 1 (1753) 705; BENN. Fl. Br. India 1 (1872) 203, *excl. var.*; TRIMEN, Fl. Ceyl. 1 (1893) 80, *excl. var.* — *P. elongata* WILLD. Sp. Pl. 3 (1803) 879; DC. Prod. 1 (1824) 332; SPRENG. Syst. Verz. 3 (1826) 167; W. & A. Prod. 1 (1834) 38; THWAITES, En. (1864) 22; HASSK. in Miq. Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 172; BENN. Fl. Br. India 1 (1872) 203, *p.p.*; CHODAT, Monogr. II (1893) 387, *excl. fig.*; MUKHERJEE, Bull. Bot. Soc. Beng. 12 (1961) 36; *non* ADEMA, 1966. — *P. brachystachya* BLUME, Bijdr. (1825) 59, *nom. illeg.*; KING, J. As. Soc. Beng. 59, ii (1890) 130; RIDLEY, Fl. Mal. Pen. 1 (1922) 139, *non* DC. 1824, *nec* POIR.

1816. — *P. humilis* SPAN. *Linnaea* 15 (1841) 167; WALP. Rep. 1 (1842) 234; MIQ. Fl. Ind. Bat. 1, 2 (1858) 125; HASSK. in Miq. Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 160. — *P. macrostachya* HASSK. l.c. 171. — *P. eunekes* HASSK. l.c. 172. — *P. chinensis* L. var. *brachystachya* (BLUME) BENN. Fl. Br. India 1 (1872) 204; BACKER, Schoofl. Java (1911) 78. — *P. chinensis* L. var. *linearifolia* (non WILLD.) CHODAT, Monogr. II (1893) 381; MUKHERJEE, Bull. Bot. Soc. Beng. 12 (1961) 40; KANAI, Fl. E. Himal. (1966) 173. — *P. linearifolia* (non WILLD.) ADEMA, Blumea 14 (1966) 274, f. 19, p.p., excl. syn.; Proc. R. Soc. Queensl. 80 (1969) 126, p.p.; THOMPSON, Fl. New South Wales 112 (1978) 15; HARA, En. Fl. Pl. Nepal 2 (1979) 50. — Fig. 15.

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 \pm as long as the keel, spatulate, inside hairy in basal half; keel with 2 bundles of shortly incised appendages. *Ovary* \pm orbicular,

notched, ciliate with crispate 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's *P. glaucoides* 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*.

20. *Polygala triflora* LINNÉ, Sp. Pl. 1 (1753) 705. — *P. linearifolia* WILLD. Sp. Pl. 3 (1803) 877; DC. Prod. 1 (1824) 326 ('*linearifolia*'); non ADEMA, 1966. — *P.*

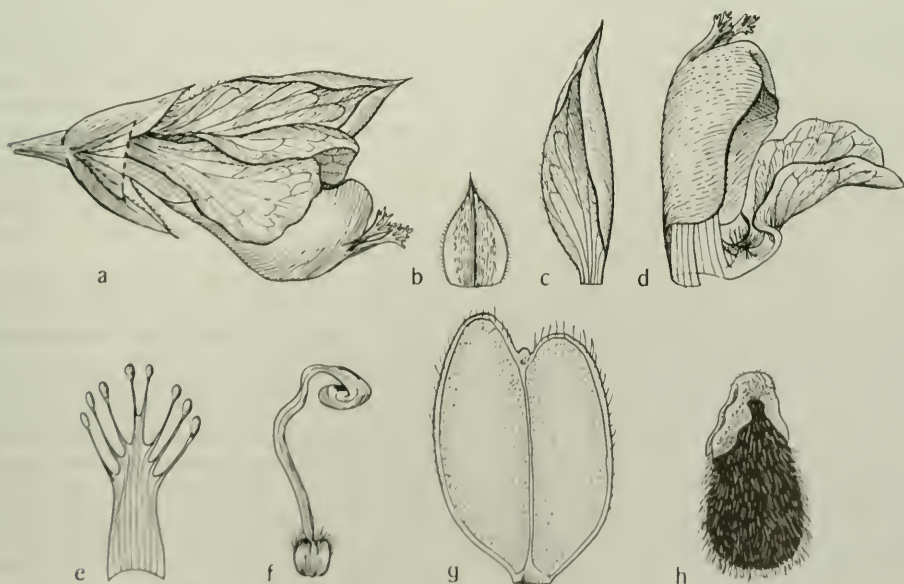


Fig. 15. *Polygala glaucoides* LINNÉ. a. Flower, one ala cut away; b. upper sepal; c. ala; d. keel enveloping staminal tube, at right one petal; e. opened staminal tube; f. pistil; g. fruit; h. seed. All $\times 10$ (FENIX BS 26016).

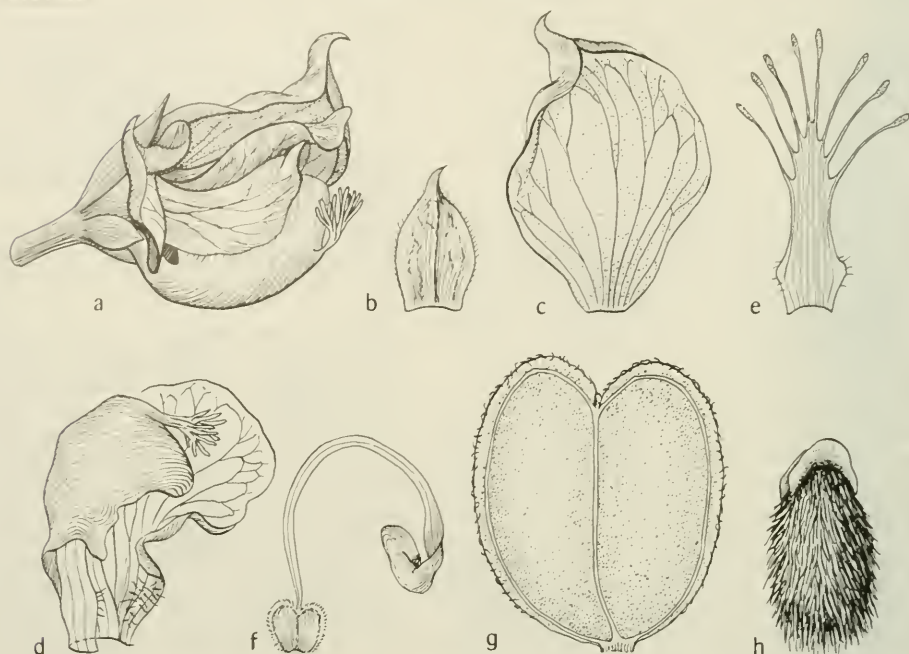


Fig. 16. *Polygala triflora* LINNÉ. a. Flower; b. upper sepal; c. ala; d. keel enveloping staminal tube, at right one petal; e. opened staminal tube; f. pistil; all $\times 10$; g. fruit; h. seed; both $\times 10$ (BACKER 23143).

prostrata WILLD. Sp. Pl. 3 (1803) 876. — *P. monspeliaca* (non L.) BLANCO, Fl. Filip. (1837) 557. — *P. arvensis* (non WILLD.) BENTH. Fl. Austr. 1 (1864) 140; F.M. BAILEY, Queensl. Fl. 1 (1899) 79. — *P. elongata* (non WILLD.) BENN. Fl. Br. India 1 (1872) 203, *p.p.*; K.SCH. & LAUT. Fl. Schutzgeb. Südsee, Nachtr. (1905) 289; MERR. Philip. J. Sc. 13 (1918) Bot. 20; EN. Philip. 2 (1923) 383; ADEMA, Blumea 14 (1966) 273, *p.p.*; *ibid.* 17 (1969) 269; MATTHEW, Fl. Tamil Carnatic 1 (1981) 66. — *P. chinensis* L. var. *triflora* (L.) BENN. Fl. Br. India 1 (1872) 204. — *P. glaucoides* L. var. *triflora* (L.) TRIMEN, Fl. Ceyl. 1 (1893) 81. — Fig. 16.

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, spatulate, 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 Malesia: 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 Malesia 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

LINNÉ, Syst. Nat. ed. 10 (1759) 1155, *nom. cons.*, *non* LINNÉ, 1753, *nec* MILL. 1754; DC. Prod. 1 (1824) 340; HASSK. in Miq. Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 190; BENN. Fl. Br. India 1 (1872) 207; CHODAT in E. & P. Nat. Pfl. Fam. 3, 4 (1896) 340; HUTCH. Gen. Fl. Pl. 2 (1967) 342. — *Elsota* ADANS. Fam. 2 (1763) 358; O.K. Rev. Gen. Pl. 1 (1891) 46; S.F. BLAKE, N. Austr. Fl. 25 (1924) 370. — *Corytholobium* MART. *ex* BENTH. Ann. Naturk. Mus. Wien 2 (1838) 93. — *Lophostylis* HOCHST. Flora 25 (1842) 229. — **Fig. 17.**

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, petioled. *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 (alae) 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, \pm 2-lobed stigma. *Fruit* a samara with a coriaceous wing (wing sometimes reduced), sometimes a second reduced wing present. *Seed* inappendiculate, glabrous, with thick cotyledons.

Distr. About 80 species, mainly in South and Central America, some in tropical Africa and in Southeast Asia and *Malesia*; not in Australia.

Ecol. 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 inappendiculate. Fruit (without the wings) orbicular. **4. *S. ecristata***
1. Flowers pink to deep purple. Staminal tube completely glabrous, all filaments free for 1/4. Fruit only with a single large wing.
 3. Leaf tip 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-violacea***
 3. Leaf tip 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. inappendiculata***

1. *Securidaca inappendiculata* HASSK. Flora 25² Jav. Rar. (1848) 295; WALP. Rep. 5 (1845) 1; KURZ, (1842) Beibl. 2, 32; Cat. Hort. Bog. (1844) 227; Pl. J. As. Soc. Beng. 43, ii (1874) 79; For. Fl. Burma 1

(1877) 80; CRAIB, Fl. Siam. En. 1 (1931) 104; HEND. J. Mal. Br. R. As. Soc. 17 (1939) 35; RAIZADA, J. Bomb. Nat. Hist. Soc. 48 (1952) 668; CHUN, Acta Phytotax. Sin. 7 (1958) 7; BACKER & BAKH.f. Fl. Java 1 (1963) 199; CHUN, Fl. Hainanica (1964) 368; BANERJI, Bull. Bot. Surv. India 10 (1968) 234; HARA, En. Fl. Pl. Nepal 2 (1979) 51; ANON. Icon. Corm. Sin. Suppl. 2 (1983) 172. — *S. paniculata* ROXB. [Hort. Beng. (1814) 53, *nomen*;] Fl. Ind. ed. Carey 3 (1832) 219, *non* LAMK, 1806. — *Lophostylis javanica* MIQ. Fl. Ind. Bat. 1, 2 (1858) 128. — *S. scandens* HAM. in Wall. [Cat. (1831) 4195, *nomen*] *ex* BENTH. Fl. Hongk. (1861) 45, *non* JACQ. 1760, *nec* POIR. 1806; SASAKI, Cat. Gov. Herb. Formosa Dept. For. (1930) 299. — *S. tavoyana* WALL. [Cat. (1831) 4196, *nomen*] *ex* BENN. Fl. Br. India 1 (1872) 208; FORBES, J. Linn. Soc. Bot. 23 (1886) 63; GAGNEP. Fl. Gén. I.-C. 1 (1909) 261; BACKER, Schoolfl. Java (1911) 79; KOORD. Exk. Fl. Java 2 (1912) 451; RIDLEY, Fl. Mal. Pen. 1 (1922) 141; MERR. Lingn. Sc. J. 5 (1927) 105; KANJILAL, Fl. Assam 1, 1 (1935) 98; MASAMUNE, Fl. Kainantensis (1943) 151; GAGNEP. Fl. Gén. I.-C. Suppl. 1 (1943) 238; HUNDLEY, List Trees, Shrubs etc. from Burma 3 (1961) 18. — *S. bracteata* BENN. Fl. Br. India 1 (1872) 208; KING, J. As. Soc. Beng. 59, ii (1890) 133; RIDLEY, Fl. Mal. Pen. 1 (1922) 141. — *Elsota bracteata* (BENN.) O.K. Rev. Gen. Pl. 1 (1891) 46. — *Elsota tavoyana* (BENN.) O. K. l.c. — *S. yaoshannensis* HAO in Fedde, Rep. 40 (1963) 213; ANON. Icon. Corm. Sin. Suppl. 2 (1983) 172.

KEY TO THE SUBSPECIES

1. Greatest width of leaf halfway. Pedicel (sub)glabrous **a. ssp. inappendiculata**
 1. Greatest width of leaf in basal half. Pedicel densely shortly hairy **b. ssp. corymbosa**

a. ssp. inappendiculata

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 orbicular, the wing up to 13 by 3 cm, narrowly attached, stalk-like constricted in basal 1/3 part; second wing absent; fruiting pedicel up to 22 mm. *Seed* globose.

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.

b. ssp. corymbosa (TURCZ.) MEIJDEN, *stat. nov.* — *S. corymbosa* TURCZ. Bull. Soc. Nat. Mosc. 27² (1854) 2, 360; MERR. Sp. Blanc. (1918) 214; En. Philip. 2 (1923) 385; BROWN, Min. Prod. Philip. For. 3 (1921) 56; Useful Pl. Philip. 2 (1950) 280; SASAKI, Cat. Gov. Herb. Formosa Dept. For. (1930) 299; RIDLEY, Kew Bull. (1938) 115; MASAMUNE, En. Phan. Born. (1942) 378. — *S. volubilis* auct. (*non* LINNÉ, 1753) BLANCO, Fl. Filip. (1837) 555. — *S. complicata* auct. (*non* H.B.K. 1823) BLANCO, Fl. Filip. ed. 2 (1845) 388. — *S. cumingii* HASSK. in Miq. Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 190. — *Elsota corymbosa* (TURCZ.) O. K. Rev. Gen. Pl. 1 (1891) 46.

Distr. *Malesia*: Philippines (Luzon, Mindoro, Negros).

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.

2. Securidaca atro-violacea ELMER, Leafl. Philip. Bot. 5 (1913) 1671; MERR. En. Philip. 2 (1923) 385.

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 hydathode, glabrous to sparsely 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.

Distr. *Malesia*: Philippines (Palawan).

Ecol. Disturbed forests on ultrabasic soil (RIDS-DALE), 100–600 m.

3. Securidaca philippinensis CHODAT, Bull. Herb. Boiss. 4 (1896) 233; BROWN, Min. Prod. Philip. For. 3 (1921) 58; Useful Pl. Philip. 2 (1950) 280; MERR. En. Philip. 2 (1923) 385.

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 cuneate, 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. *Sepals* ciliate, the outer densely shortly 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 ecristata* 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, shortly hairy at both sides; petioles 3–5 mm, shortly 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, shortly hairy pedicels. *Sepals* 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.



Fig. 17. *Securidaca ecristata* KASSAU. a. Habit flowering plant, $\times 0.5$; b. flower; c. keel; d. staminal tube with lateral and upper petals; e. gynoecium; f. staminal tube; all $\times 6$; g. habit fruiting plant, $\times 0.5$ (a–f MULLAR NGF 9917, g CLIMENS 8388).

3. SALOMONIA

LOUR. Fl. Coch. 1 (1790) 14, *nom. cons.*, *non* HEISTER *ex* FABRICIUS, Enum. 20 (1759); VAHL, En. Pl. 1 (1805) 8 ('*Salmonea*'); DC. Prod. Fl. Nep. (1825) 200; WIGHT, Ill. 1 (1840) 47; MIQ. Fl. Ind. Bat. 1, 2 (1858) 126; BENTH. Fl. Hongk. (1861) 43; BENTH. & HOOK. Gen. Pl. 1 (1862) 136; BENTH. Fl. Austr. 1 (1863) 138, *p.p.*; HASSK. in Miq. Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 144; BENN. Fl. Br. India 1 (1872) 206, *p.p.*; BOERL. Handl. 1 (1890) 76; CHODAT in E. & P. Nat. Pfl. Fam. 3, 4 (1896) 452, *p.p.*; BACKER & BAKH.*f.* Fl. Java 1 (1963) 199; BURBIDGE, Dict. Austr. Pl. Gen. (1963) 260; HUTCH. Gen. Pl. 2 (1967) 341, *p.p.*

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 inappendiculate. *Stamens* 4 or 6, rarely 5, monadelphous; anthers bisporangiate by abortion of the outer microsporangiae, 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, inappendiculate; 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.

Ecol. 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 *Salomonina*. 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 *Salomonina*) has never been mentioned. The androecium is very different: the strongly curved style with the anthers tightly enclosing the stigma in *Salomonina* 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 *Salomonina* was given by LOUREIRO to honour the famous Jewish King Salomo, 'the first botanist'.

KEY TO THE SPECIES

1. All leaves shortly but distinctly petiolate, broadly ovate, never ciliate. Wall of cells of capsule with protruding, reticulate venation. Lower sepals equal to or somewhat smaller than the other sepals. Keel outside at lower side minutely papillose **1. *S. cantoniensis***
1. Leaves subsessile except the basal ones, ovate to ovate-lanceolate, margin glabrous or often set with stiff ciliae. Walls of cells of capsule without reticulate, protruding venation, often shortly sparsely hairy. Lower sepals distinctly larger than the other sepals. Keel not papillose outside **2. *S. ciliata***

1. *Salomonina cantoniensis* LOUR. Fl. Coch. 1 (1790) 14; VAHL, En. Pl. (1805) 8; DC. Prod. 1 (1824) 334; WALL. Cat. (1831) 4192; HASSK. in Miq. Pl. Jungh. 2 (1852) 123; MIQ. Fl. Ind. Bat. 1, 2 (1858) 127; BENTH. Fl. Hongk. (1861) 44; HASSK. in Miq. Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 144; BENN. Fl. Br. India 1 (1872) 206; KING, J. As. Soc. Beng. 59, ii (1890) 132; CHODAT in E. & P. Nat. Pfl. Fam. 3, 4 (1896) 330; BACKER, Schoofl. Java (1911) 76; KOORD. Exk. Fl. Java 2 (1912) 453; MERR. En. Born. (1921) 324; RIDLEY, Fl. Mal. Pen. 1 (1922) 139; MERR. En. Philip. 2 (1923) 385; BACKER & SLOOT. Theonkr. (1924) 160; HEYNE, Nutt. Pl. (1927) 901; MERR. Sarawak Mus. J. 3 (1928) 524; HAND.-MAZZ. Symb. Sin. 7 (1933) 634; BACKER, Onkruidfl. Suiker. (1934) 397; HEND. Mal. Nat. J. 4 (1949) 28; BANERJI, J. Bomb. Nat. Hist. Soc. 55 (1958) 251; BACKER & BAKH.f. Fl. Java 1 (1963) 199; BANERJI, Rec. Bot. Surv. India 19² (1966) 25; RAO, New Phyt. 63 (1964) 281; HARA, En. Fl. Pl. Nepal 2 (1979) 51; ANON. Icon. Corm. Sin. Suppl. 2 (1983) 184. — *S. edentula* DC. Prod. 1 (1824) 334; D.DON, Prod. Fl. Nepal. (1825) 200; WALL. Cat. (1831) 4194; HASSK. in Miq. Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 146; BENN. Fl. Br. India 1 (1872) 206; BANERJI, J. Bomb. Nat. Hist. Soc. 51 (1953) 554; KANAI, Fl. E. Himal. (1966) 173. — *S. petiolata* D.DON, Prod. Fl. Nepal. (1825) 200, *nom. superfl.* — *Polygala trinervata* HAM. ex WALL. Cat. (1831) 4192B. — *Polygala undulata* ROXB. [Hort. Beng. (1814) 98, *nomen*.] Fl. Ind. ed. Carey 3 (1832) 219, cf. ADEMA, Blumea 14 (1966) 276. — *S. trinervata* STEUD. Nom. ed. 2, 2 (1841) 373. — *S. subrotunda* HASSK. in Miq. Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 146.

Herb up to 30(–40) cm. Lateral stems often long and patent, stem glabrous, 0.5–1 mm wide, the wings up to 0.8 mm wide. *Leaves* broadly ovate, 4–15 by 3–10 mm, slightly cordate at base, acutish and mucronate at apex, 3–5-nerved, glabrous; petiole 0.5–2 mm. *Flowers* 1.7–2.3(–2.6) mm long, white to light violet. *Sepals* subequal, 0.5–0.8 mm long. Keel at lower side densely minutely papillose. *Anthers* 4 or 6, rarely 5, c. 0.15 mm long. *Capsule* c. 1 by 1.5–2 mm, walls of cells with protruding reticulate venation; spines up to 0.5(–0.75) mm long.

DISTR. E. India and Nepal, Bangla Desh, Burma, Thailand, S. Vietnam to S. China (Yunnan); in *Malaysia*: Sumatra (also Nias, Riouw, Banka), Malay

Peninsula (also Langkawi Is.), Java (also Madura I.), Lesser Sunda Islands (Sumbawa, Timor), Borneo, Celebes, Philippines (Luzon, Panay, Mindanao), Moluccas (Ceram, Ambon, Tanimbar Is.) and Misool I.; not recorded from New Guinea. Records for Japan and Australia are erroneous.

Ecol. Sunny or slightly shaded open places in grasslands, bracken, deciduous jungle or primary forests, usually on wet sand, clay or rock, not common, but locally abundant, 0–1500 m.

Not e. Mixed collections of this and the next species are not uncommon.

2. *Salomonina ciliata* (L.) DC. Prod. 1 (1824) 334; HASSK. in Miq. Pl. Jungh. 2 (1852) 123; MIQ. Fl. Ind. Bat. 1, 2 (1858) 127; HASSK. in Miq. Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 144; BENN. Fl. Br. India 1 (1872) 206; MERR. Philip. J. Sc. 7 (1912) Bot. 237; Fl. Manila (1912) 279; Sp. Blanc. (1918) 214; En. Born. (1921) 324; RIDLEY, Fl. Mal. Pen. 1 (1922) 140; MERR. En. Philip. 2 (1923) 386; SASAKI, Cat. Gov. Herb. (1930) 299; CRAIB, Fl. Siam. En. 1 (1931) 60, 90; ALSTON, Fl. Ceyl. Suppl. 6 (1931) 16; MASAMUNE, Yakusima (1934) 264; HOSOKAWA, Mat. Bot. Micron. 18 (1938) 155; GAGNEP. Fl. Gén. I.-C. Suppl. 1 (1939) 224; BACKER & BAKH.f. Fl. Java 1 (1963) 199; LAUENER, Not. R. Bot. Gard. Edinb. 26 (1965) 344; FOSBERG & SACHET, Micronesica 11 (1975) 83; HARA, En. Fl. Nepal 2 (1979) 51. — *Polygala ciliata* LINNÉ, Sp. Pl. 1 (1753) 701. — *S. oblongifolia* DC. Prod. 1 (1824) 334; WIGHT & ARN. Nov. Act. Ac. Caes. Leop.-Car. 18 (1836) 322; BENTH. Fl. Hongk. (1861) 44; Fl. Austr. 1 (1863) 138; BENN. Fl. Br. India 1 (1872) 207; KURZ, J. As. Soc. Beng. 43, ii (1874) 79; F.V.M. Austr. Pl. 1 (1882) 8; VIDAL, Phan. Cuming. (1885) 36; KING, J. As. Soc. Beng. 59, ii (1890) 132; TRIMLEN, Fl. Ceyl. 1 (1893) 83; PRAIN, Bengal Pl. 1 (1903) 156; RIDLEY, Fl. Mal. Pen. 1 (1922) 140; BANERJI, J. Bomb. Nat. Hist. Soc. 51 (1953) 554; MASAMUNE, Sc. Rep. Kanazawa Univ. 3 (1955) 149; OHWI, Fl. Japan (1965) 587; HUI-LIN LI, Fl. Taiwan 3 (1977) 558, pl. 728; GILLI, Ann. Naturhist. Mus. Wien 83 (1980) 452; ANON. Icon. Corm. Sin. Suppl. 2 (1983) 185. — *S. vexillifolia* D.DON, Prod. Fl. Nepal. (1825) 201, *nom. superfl.*; BENN. Fl. Br. India 1 (1872) 207, '*vexilliflora*', — *S. obovata* WIGHT, Ill. 1 (1831) 49, t. 22B. — *S. cordata* WIGHT, l.c. 1. 22C; WIGHT & ARN. Nov. Act. Ac.

Caes. Leop.-Car. 18 (1836) 322; TRIMEN, Fl. Ceyl. 1 (1893) 83. — *Amorpha pedalis* BLANCO, Fl. Filip. (1837) 553; ed. 2 (1845) 387; ed. 3, 2 (1879) 348; cf. MERR. Sp. Blanc. (1918) 214. — *S. stricta* SIEB. & ZUCC. Abh. Ak. Wiss. München 4, 2 (1845) 152; MAKINO, Ill. Fl. Japan (1954) 382. — *S. arnottiana* MIQ. Analecta 3 (1852) 3. — *S. canarana* MIQ. l.c.; HASSK. in Miq. Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 147. — *S. horneri* HASSK. in Miq. Pl. Jungh. (1852) 123; MIQ. Fl. Ind. Bat. 1, 2 (1858) 127; HASSK. in Miq. Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 149. — *S. angulata* GRIFF. Notul. 4 (1854) 539; l.c. t. 585, f. 16. — *S. ramosissima* TURCZ. Bull. Soc. Nat. Mosc. 27² (1854) 352; F.-VILL. Nov. App. (1880) 14. — *S. rigida* HASSK. in Miq. Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 148. — *S. setoso-ciliata* HASSK. l.c. 149. — *S. uncinata* HASSK. l.c. 148; KOORD. Exk. Fl. Java 2 (1912) 453. — *S. longiciliata* KURZ, J. As. Soc. Beng. 41, ii (1872) 292. — *S. cavaleriesi* LÉV. Bull. Soc. Bot. Fr. 51 (1904) 291. — *S. cantoniensis* auct.: HOSOKAWA, J. Agric. Kyushu Univ. 4, 6 (1935) 434; WALTER & RODIN, Contr. U.S. Nat. Herb. 30 (1949) 461; STONE, Micronesia 6 (1970) 362.

Herb up to 25 cm, branched or unbranched. Stem glabrous to sparingly ciliate, ribbed, c. 0.5 mm wide, the wings up to 0.5 mm wide. Leaves elliptic or ovate to oblong or ovate-lanceolate, 3–9 by 1–5 mm, truncate to attenuate at base, acutish and mucronate at apex, the margin glabrous to densely long-ciliate, usually 3-nerved; petiole up to 0.5 mm or in the basal leaves up to c. 1 mm. Flowers 1.5–2 mm long, pink

to purple. *Sepals* unequal, the lower ones distinctly larger than the other sepals, 1–1.5 mm long. Keel not papillose. *Anthers* 4, c. 0.15 mm long. *Capsule* 0.8–1 by 1.5–2 mm, walls of cells smooth, sometimes sparsely minutely hairy, not veined; spines at margin up to 0.5 mm long.

Distr. Sri Lanka, Bangla Desh, S. & E. India, Burma, Thailand, Indochina, China, Japan, S. Korea, Taiwan, Ryukyu Is., Marianas (Guam), Carolines (Yap), Australia (N. Australia, Queensland); in *Malesia*: Sumatra (incl. Banka & Billiton), W. Java (also Madura I.), Borneo (N. Sarawak, Brunei, Sabah; also Karimata I.), Celebes, Philippines (Luzon), Moluccas (Sula & Tanimbar Is.), New Guinea.

Ecol. Sunny or slightly shaded open places in grasslands or sometimes in deciduous forest, *Melaleuca* forest, teak forest, sand dunes, swamps; usually on wet fine quartz sand or on clay; locally rather common, 0–1250 m.

Note. Mixed collections of this and the former species are not uncommon.

Excluded species

Salomonina seguinii LÉV. Bull. Soc. Bot. Fr. 51 (1904) 291 = *Polygala furcata*, cf. LAUENER, Not. R. Bot. Gard. Edinb. 26 (1965) 343.

Salomonina martinii LÉV. Bull. Soc. Bot. Fr. 51 (1904) 290 = *Polygala tatarinowii* REGEL.

4. EPIRIXANTHES¹

BLUME, Cat. (1823) 25, 82; NEES, Flora 8 (1825) 133; ENDL. Gen. Pl. (1839) 728; REUTER in DC. Prod. 11 (1847) 44; MIQ. Fl. Ind. Bat. 1, 2 (1858) 127; BENTH. & HOOK. Gen. Pl. 1 (1862) 135; HASSK. in Miq. Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 143; JOHOW in Pringsh. Bot. Jahrb. 20 (1889) 479; CHODAT in E. & P. Nat. Pfl. Fam. 3, 4 (1896) 342; PENZIG, Ann. Jard. Bot. Btzg 17 (1901) 142, t. 20–26; STEEN. Trop. Natuur 23 (1934) 51, f. 10; Bull. Bot. Gard. Btzg III, 17 (1948) 461; BACKER & BAKH.f. Fl. Java 1 (1963) 200. — *Salomonina sect. Epirixanthes* (BLUME) BENN. Fl. Br. India 1 (1872) 207; KING, J. As. Soc. Beng. 59, ii (1890) 132. — *Salomonina auct. plur. pro parte*. — **Fig. 18.**

Echlophyllous, small, erect, little-branched herbs with small, bract-like, erect leaves; roots not aromatic. Stems without nodal glands, terete, ribbed, un-

(1) In 1966 a preliminary study has been performed by H.M.Y.J. ANDRÉ DE LA PORTE-JANSS (Leiden). That manuscript was sent to T. WENDT (then Gray Herbarium, Cambridge, U.S.A.; at present Collegio de Postgraduados, Chapingo, Mexico) during his study of the genus. We received WENDT's unpublished manuscript in 1985 during the preparation of the *Polygalaceae* treatment for this flora. The present treatment is largely in accordance with that of WENDT. In nomenclatural sense, WENDT must be seen as the author of the two new species, viz. *E. pallida* and *E. kinabaluensis*, which are published here for the first time.

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. papuana*) 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 \pm boat-shaped, inappendiculate 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* \pm 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).

Distr. E. India to China and throughout *Malesia* as far as the Solomon Is. (San Cristobal); rare but very locally abundant. In all 5 spp.

Ecol. On humous 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 *Epirixanthes*) 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 I, 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. *Epirixanthes* means flower growing on roots. BLUME described *Epirixanthes* as '*radicibus arborum innascentes*'. Though ZOLLINGER in 1854 already wrote '*inter folia emortua*', MIQUEL in 1858 called the *Epirixanthes* 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 *Epirixanthes* could be one for a crossword puzzle. BLUME started with *Epirixanthus*, which is thus the correct spelling. Later, however, he spelled the name *Epirhizanthes* on herbarium sheets. Ever since we can find all sorts of etymological variants: *Epirrhizanthes*, *Epirrhizanthé*, *Epirizanthes*, *Hyperixanthes* and *Epicryanthes*. 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. 2. *E. papuana*
 3. Bracteoles absent. Apex of fruits not 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*

1. *Epirixanthes elongata* BLUME, Cat. (1823) 82; NEES, Flora 8 (1825) 133; REUTER in DC. Prod. 11 (1847) 44; ZOLL. Syst. Verz. 3 (1855) 58; MIQ. Fl. Ind. Bat. 1, 2 (1858) 128; HASSK. in Miq. Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 143; PENZIG, Ann. Jard. Bot. Btzg 17 (1901) 142, t. 24–26; PILGER in E. & P. Nat. Pfl. Fam., Nachtr. 3 (1908) 190; WIRZ, Flora 1 (1910) 395; BACKER, Schoolfl. Java (1911) 75; MERR. En. Born. (1921) 325; STEEN. Trop. Natuur 23 (1934) 51, f. 10; PILL, Rec. Trav. Bot. Néerl. 31 (1934) 761; SMITINAND, Thai For. Bull., Bot. 2 (1955) 2; BACKER & BAKH.f. Fl. Java 1 (1963) 200; HANSEN c.s. Dansk Bot. Ark. 25, 2 (1967) 83. — *E. linearis* BLUME, Cat. (1823) 82; REUTER in DC. Prod. 11 (1847) 44; MIQ.

Fl. Ind. Bat. 1, 2 (1858) 128. — *Salomonina aphylla* GRIFF. Proc. Linn. Soc. 1 (1844) 221; Trans. Linn. Soc. 14 (1845) 112; BENN. Fl. Br. India 1 (1872) 207; KING, J. As. Soc. Beng. 59, ii (1890) 132; CHODAT in E. & P. Nat. Pfl. Fam. 3, 4 (1896) 342; JOSEPH, Bull. Bot. Surv. India 12 (1970) 73, f. 1–5. — *Salomonina parasitica* GRIFF. Not. 4 (1854) 538, t. 1598, f. 5. — *E. tenella* HOOK.f. Trans. Linn. Soc. 23 (1862) 158; C. MÜLL. in Walp. Ann. 7 (1868) 243. — *Salomonina elongata* (BLUME) KURZ ex KOORD. Exk. Fl. Java 2 (1912) 453; RIDLEY, Fl. Mal. Pen. 1 (1922) 140. — *E. aphylla* (GRIFF.) MERR. Philip. J. Sc. 13 (1918) Bot. 142. — Fig. 18.

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 full-grown; bracteoles absent. *Flowers* 2–2.5 mm long, yellowish white. *Sepals* free, subequal, c. 1 mm long, ciliolate-papillose. *Anthers* 5, rarely 4, sessile or stipitate. Disk lobe present adaxially at the base of the ovary, difficultly 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; gynoeceum at first longer than the androeceum, later equally long. *Fruit* reniform to broadly elliptic, c. 0.6 by 0.9 mm, enclosed by the slightly longer sepals.

DISTR. E. India, S. Burma (Tavoy), N. Vietnam, S. China; in *Malesia*: Malay Peninsula, Sumatra, W. Java, Borneo, Moluccas (Ambon, Ceram).

2. *Epirixanthes papuana* J.J. SMITH in Fedde, Rep. 10 (1912) 286; Nova Guinea Bot. 8 (1914) 897; STEEN. Trop. Natuur 23 (1934) 51; BACKER & BAKH.f. Fl. Java 1 (1963) 200. — *Salomonina cylindrica* (BLUME) KURZ, p.p.: K.SCH. & LAUT. Nachtr. Fl. Schutzgeb. Südsee (1905) 285.

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* connate for 1/2–3/4, subequal, glabrous. *Stamens* usually 3 and then anthers 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; gynoeceum shorter than androeceum. *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. *Malesia*: N. Sumatra (incl. Enggano I.), W. Java, Borneo, Philippines (Luzon), Moluccas (Talaud, Ceram), New Guinea. Also in the Solomon Is. (San Cristobal).

3. *Epirixanthes cylindrica* BLUME, Cat. (1823) 82; NEES, Flora 8 (1825) 133; REUTER in DC. Prod. 11 (1847) 44; ZOLL. Syst. Verz. 3 (1855) 58; MIQ. Fl. Ind. Bat. 1, 2 (1858) 128, t. 15; HASSK. in Miq. Ann. Mus. Bot. Lugd.-Bat. 1 (1863) 143; BECC. Malesia 3 (1890) 325; KING, J. As. Soc. Beng. 59, ii (1890) 132; PENZIG, Ann. Jard. Bot. Btzig 17 (1901) 142, t. 20–23; MERR. Philip. J. Sc. 1 (1906) Suppl. 203; PILGER in E. & P. Nat. Pfl. Fam., Nachtr. 3 (1908) 190; BACKER, Schoolfl. Java (1911) 76; WENT, Nova Guinea Bot. 8 (1909) 169; KOORD. Exk. Fl. Java 2 (1912) 453; MERR. En. Born. (1921) 325; En. Philip. 2 (1923) 386; STEEN. Trop. Natuur 23 (1934) 52; HEND. Mal. Nat. J. 4 (1949) 27; BACKER & BAKH.f. Fl. Java 1 (1963) 200. — *Salomonina cylindrica* (BLUME) KURZ, J. As. Soc. Beng. 43, ii (1874) 79; CHODAT in E. & P. Nat. Pfl. Fam. 3, 4 (1896) 342; K.SCH. & LAUT. Nachtr. Fl. Schutzgeb. Südsee (1905) 285, p.p.; RIDLEY, Trans. Linn. Soc. 11, Bot. 9 (1916) 19.

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 acutish 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* connate ± halfway, unequal, slightly cucullate, c. 1.5 mm long. *Anthers* 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; gynoeceum somewhat shorter than the androeceum. *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.

4. *Epirixanthes kinabaluensis* WINDI, sp. nov.

A E. cylindrica bracteis (ovatus-lanceolatis, 2–2.5 × 0.5–0.6 mm, parum crassinervatis ad basin, gradatim attenuatis et mucronatis, gemmis florum partiter expositis, persistentibus tempore fructificationis differt. — *Typus:* CLEMENS 30039 (A holo; BO, G, I, NY, UC). See note 1 under the genus.

Herb up to 30 cm, glabrous. Stem simple or branched, 1–2.5 mm wide, tinged reddish. *Leaves* 2–3.5 mm long, slightly swollen at base, brown.

Spike 1.5–6 cm by 4–5 mm, very dense, rounded at apex. Bracts (ovate-)lanceolate, 2–2.5 by 0.5–0.6 mm, at base slightly thickened along midrib, very gradually narrowed into the acute and finely mucronate apex, not fully covering the flower buds, patent with upturned apex at flowering time, persistent until the fruit has fallen, then reflexed and eventually caducous; bracteoles absent. *Flowers* c. 2 mm long, milk-white with yellow-brown calyx. *Sepals* halfway connate, unequal, slightly cucullate, 1.5 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 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.

Dist. *Malesia*: Sumatra, Borneo.

Note. Very closely allied to *E. cylindrica*, from which it differs only by the narrower and longer bracts.

5. *Epirixanthes pallida* WENDT, *sp. nov.*

Sepala libera. Bractea 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, whitish. *Sepals* free, unequal, the larger ones slightly cucullate, 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* elliptic, style shorter than the ovary, subcylindrical, c. 0.2 mm long, unequally 2-lobed, the larger upper lobe stigmatic, the lower one tooth-like and hollow at apex; gynoecium somewhat shorter than androecium. *Fruit* broadly elliptic or nearly didymous, c. 0.6 by 0.8 mm, at base tightly enclosed by the disk, the whole enclosed by the slightly longer sepals.

Dist. *Malesia*: Borneo, Celebes.

Note. A distinct species, easily recognizable by its relatively large bracts which imbricately cover the upper part of the spike but are very early caducous.

5. ERIANDRA

ROYEN & STEEN. *J. Arn. Arb.* 33 (1952) 91, t. 1; STEEN. *Blumea* 12 (1964) 319; HUTCH. *Gen. Fl. Pl.* 2 (1967) 343.

Tree. Twigs apparently without nodal glands. *Leaves* alternate, petioled. *In-florescences* fasciculate, axillary, short; bracts and bracteoles \pm 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 circumcission, 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-orbicular. *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.

Distr. Solomon Islands; in *Malesia*: New Guinea. Monotypic.

Ecol. Primary and secondary rain-forests, 0–150(–660) m.

Notes. In flowering and fruiting characters resembling the tropical American genus *Diclidanthera* MART., a genus of small trees and lianas differing in the 5-locular ovary (and fruit), the glabrous anthers, the constricted corolla tube and the exarillate seed. As the nearly regular flowers and the many-celled ovary are probably derived in the family, it is probable that both genera are closely allied.

STYER (J. Arn. Arb. 58, 1977, 124) studied the anatomy of *Eriandra*, and compared his results with those of the South American genera *Barnhartia* GLEASON, *Moutabea* AUBL. and *Diclidanthera*. He concluded (*l.c.* 139) that *Eriandra*, although a tree, has a 'lianos ancestry'.

1. *Eriandra fragrans* ROYEN & STEEN. J. Arn. Arb. 33 (1952) 91, t. 1; STEEN. Blumea 12 (1964) 319.

Tree up to 32 m, 70 m dbh. Twigs glabrous. *Leaves* oblong to (ob)lanceolate, 7–40 by 3–10 cm, narrowly cuneate at base, acutish or shortly acuminate at apex, coriaceous, glabrous above, slightly hairy on midrib beneath, in basal part beneath with 1–4 indistinct glands 0.2 mm diam.; midrib sunken above in basal half, nerves 5–16 pairs, finely prominent at both sides; petiole 1–2.5 cm, flattened above, wrinkled below, apically with a pair of indistinct glands 0.2 mm diam. Axis of raceme-like *fascicle* 2–20 mm long, shortly hairy to glabrous, at the nodes near the bracts with a pair of inconspicuous, tiny, slightly prominent glands. *Flowers* 5–6 mm long, white, fragrant, on 1–5 mm long pedicels. *Sepals* obovate-spathulate, 4–5.5 mm long, glabrous except for the

margin, the outer ones ciliate to base, the inner ones ciliate only apically. *Petals* free over c. 3 mm, the free parts reflexed during flowering; glabrous except for the ciliate incurved margins. *Staminal tube* glabrous outside, hairy inside; anthers elliptic, 3-locular in upper half, 4-locular at base, c. 1 mm long, hairy all round. *Ovary* glabrous; style 3–4 mm long, densely hairy. *Fruit* 2–4 cm diam., apically with a hairy remnant of the style. *Seeds* elliptic, c. 1.5 by 1 cm; aril c. 0.2 mm thick; indumentum of testa very dense, 1–2 mm thick.

Distr. Solomon Islands (New Georgia, Kolombangara); in *Malesia*: New Guinea.

Ecol. Primary and secondary rain-forests, usually in the valley bottoms or on plains near the coast, usually on well-drained sandy clay, sometimes on limestone, 0–150(–660) m.

6. XANTHOPHYLLUM

ROXB. Pl. Corom. 3 (1820, '1819') 81, *nom. cons.*; BENN. Fl. Br. India 1 (1872) 208; CHODAT, Bull. Herb. Boiss. 4 (1896) 254; in E. & P. Nat. Pfl. Fam. 3, 4 (1896) 343; GAGNEP. in Desv. J. Bot. 21 (1908) 241; GAGNEP. Fl. Gén. I.-C. 1 (1909) 242; CHODAT in Merr. Pl. Elm. Born. (1929) 133; HUTCH. Gen. Fl. Pl. 2 (1967) 339; NG, Tree Fl. Mal. 1 (1972) 352; MEIJDEN, Leiden Bot. Ser. 7 (1982). — *Pelae* [HERMANNUS, Fl. Zeyl. (1717) 24 ('*Paetae*')] ADANSON, Fam. 2 (1763) 448, *nom. rejic.* — *Eystathes* LOUR. Fl. Coch. 1 (1790) 235, *nom. rejic.* — *Jakkia* BLUME, Cat. (1823) 17; Bijdr. (1825) 60 ('*Jackia*'), *non Jackia* WALL., *nec Jackia* SPRENGEL. — *Skaphium* MIQ. Fl. Ind. Bat., Suppl. (1861) 357. — *Bannisterodes* [L., Fl. Zeyl. (1747) 192 ('*Bannisterioides*')] O. K. Rev. Gen. Pl. 1 (1891) 45, *nom. illeg.* — **Fig. 19–26.**

Shrubs or trees. Twigs terete, sometimes with annular or cap-like nodal glands. Axillary buds 2–8, serial, each with 2 bud-scales. *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 inappendiculate. *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 tetrasporangiate, opening introrsely with slits. Disk annular. *Gynoeceium* 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 irregularly 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 triadelphous. Embryo flat, covered by copious endosperm. *Spp.* 64–68 III. Subg. **Triadelphum**
 3. Stamens monadelphous or free. Embryo thick, without or with little endosperm.
 4. Stigma peltate. Twigs at the nodes with a pair of annular glands. *Sp.* 63 II. Subg. **Coriaceum**
 4. Stigma small, slightly bilobed. Nodal glands absent on the twigs. *Spp.* 1–62 I. Subg. **Xanthophyllum**

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-papillose 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-papillose 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**
7. Ovules 8–16. Petals (sub)glabrous outside.
8. Sepals and inflorescence axis with hairs c. 1 mm long..... **50. X. trichocladum**
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-papillose 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.
14. Ovary glabrous.
15. Ovules 4. Anthers 0.3–0.4 mm long.
16. Petiole (6–)7–11(–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**
15. Ovules 8–18. Anthers at least 0.7 mm long.
17. 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
14. Ovary hairy.
19. Ovules 8–16.
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. pseudoadenotus
22. Ovary and style patently hairy. Petiole 4–9 mm long. Nerves 6–13 pairs.... **45. X. pulchrum**
19. Ovules 4.
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*.
24. Axillary bud situated in the leaf axil, sessile.
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. monticulum*
31. Filaments more or less straight, without appendage above base. Fruit (unknown in 58. *X. novoguinese*) 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 nearly 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. novoguinese*) 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. novoguinese*
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, \pm 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 \pm 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. brigittae*
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
34. X. ceraceifolium
42. Petiole 8–18 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. adenotus**
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 over most of its length.
46. Petals \pm 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**
49. Nerves 3–7 pairs. Filaments free at base.
50. Petiole glabrous or hairy only in the upper groove. Finer venation beneath not very distinct
54. X. eurhynchum
50. Petiole densely hairy all round. Finer venation at lower side very distinctly prominent
53. X. retinerve
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. retinerve
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 shortly hairy.
55. Petiole glabrous or hairy only in the upper groove. Finer venation 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 venation beneath very distinctly prominent. Fruit rather sparsely hairy, smooth **53. X. retinerve**
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**

58. Ovules 4.
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. Gynoecium somewhat shorter than the carina. Laminar glands numerous **26. X. tenuipetalum**
65. Anthers 1–1.2 mm long. Gynoecium 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. brigittae**
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*
79. Leaf-blade in upper half with at least 6 glands situated on the margin. Anthers shortly hairy along slits and at base.
80. Filaments and style densely and rather shortly patently hairy 65. *X. celebicum*
80. Filaments and style glabrous 64. *X. ellipticum*
78. Stamens either free or all connate except between upper petals.
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*
82. Petals reddish orange when dry. Twigs without nodal glands. Filaments with short, straight hairs near base. 52. *X. laeve*
81. Petals nearly equal in size and form.
83. Pedicel 1.5–4 mm. Stamens shorter 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*
84. Filaments connate to nearly halfway. Petals 9.5–12 mm long. Outer sepals 4–5.5 mm long, inner sepals 6–7 mm long 75. *X. ecarinatum*
83. Pedicel at least 8 mm. Stamens longer than petals.
85. Petals 14–16 mm long. Stamens 17–22 mm long. Anthers hairy from base to apex, 1–1.3 mm long 69. *X. suberosum*
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*
86. Petals 7–7.5(–8) mm long. Style glabrous in upper half. Laminar glands 0–2(–4) 71. *X. stipitatum*
77. Fruiting.
87. Fruit small, less than 2 cm diam., 1- (or 2-) seeded (mature fruit not known in 52. *X. laeve* and 67. *X. contractum*).
88. At least 6 glands situated on the leaf margin itself, in upper part of the leaf-blade.
89. Pedicel 3–6(–8) mm 64. *X. ellipticum*
89. Pedicel 7–9.5 mm 65. *X. celebicum*
88. Laminar glands absent from margin of leaf-blade.
90. 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*
91. Twigs without nodal glands. Pedicel 8–15 mm. (Fruits unknown) 52. *X. laeve*
87. Fruit large, many-seeded.
92. Pericarp strongly wrinkled outside when dry.
93. Fruit globular to pear-shaped, black 76. *X. chartaceum*
93. Fruit ellipsoid, attenuate at apex and base when dry, orange to brown .. 75. *X. ecarinatum*
92. Pericarp remaining smooth when dry.
94. Fruit black. Seeds with copious albumen, with thin cotyledons 69. *X. suberosum*
70. *X. amoenum*
71. *X. stipitatum*
94. Fruit not black. Seeds (nearly) without albumen, with very thick cotyledons.
95. Seeds sticking to the pericarp when dry 74. *X. papuanum*
95. Seeds sticking together in drying, leaving shining reddish marks on inner side of the pericarp 73. *X. obscurum*

I. 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 oblanceolate to \pm 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 c. 1.5–2 cm diam. *Seed(s)* 1 (or 2), rarely up to 4; testa 1- or 2-layered; albumen present or not; embryo globular, plumule not differentiated.

KEY TO THE SECTIONS

1. Tertiary nerves scalariform. Testa sticking to the inner side of the fruitwall in drying. Albumen absent. *Spp.* 1–13 1. *Sect. Xanthophyllum*
 1. Tertiary nerves finely reticulate. Testa sticking to the rest of the seed in drying. Albumen present, though sometimes scarce. *Spp.* 14–62 2. *Sect. Eystathes*

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 exerted.

1. *Xanthophyllum flavescens* ROXB. Pl. Corom. 3 (1820) 82, t. 284, f. 2; WALL. Cat. (1831) 4198; ROXB. Fl. Ind. ed. Carey 1 (1832) 221; WALP. Rep. 1 (1842) 248; DRURY, Handb. Ind. Fl. 1 (1864) 56; KURZ, J. As. Soc. Beng. 42, ii (1873) 79, 80; Prelim. Rep. For. Pegu (1875) 26; For. Fl. Burma 1 (1877) 81; PRAIN, Bengal Pl. (1903) 236; BRANDIS, Indian Trees (1906) 44, *excl. syn.*; MEIJDEN, Leiden Bot. Ser. 7 (1982) 64. — *X. excelsum* (BLUME) MIQ. Fl. Ind. Bat. 1, 2 (1858) 129; Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 274; BINNEND. Ann. Jard. Bot. Btzg 1 (1876) 172; KING, Mat. Fl. Mal. Pen. (1890) 142, *p.p.* (*sub X. affine*); K. &

V. Icon. Bog. 1, 1 (1897) 11, *p.p.* (*sub X. affine* β *excelsa*); BOERL. Cat. Hort. Bog. (1899) 58; K. & V. Bijdr. Booms. 5 (1900) 298; RACIB. Ann. Jard. Bot. Btzg 17 (1900) 53; BOORSMA, Bull. Dép. Agr. Ind. Néerl. 16 (1908) 3; GAGNEP. in Desv. J. Bot. 21 (1908) 253; Fl. Gén. 1.-C. 1 (1909) 246; BACKER, Schoolfl. Java (1911) 80; KOORD. Exk. Fl. Java 2 (1912) 453; MERR. En. Born. (1921) 326, *p.p.*; RIDLEY, Fl. Mal. Pen. 1 (1922) 143, *p.p.* (*sub X. affine*); MERR. En. Philip. 2 (1923) 386, *p.p.*; BURK. Gard. Bull. S. S. 3 (1923) 35, *p.p.*; ENDERT, Tectona 18 (1925) 97; DOCTERS VAN LEEUWEN, Zoocécidia

(1926) 273; HEYNE, Nutt. Pl. (1927) 901; CRAIB, Fl. Siam. En. 1 (1931) 105; BURK. Dict. (1935) 2268; GAGNEP. Fl. Gén. 1.-C. Suppl. 1 (1939) 222; MASAMUNE, En. Phan. Born. (1942) 380; WYATT-SMITH, Mal. For. Rec. 17 (1952) 80, 363, *p.p.*; *ibid.* 23² (1963) f. 10, *p.p.* (*sub X. affine*); BACKER & BAKH.f. Fl. Java 1 (1963) 201; NG, Fed. Mus. J. n.s. 13 (1971) 137; Tree Fl. Mal. 1 (1972) 354, f. 1, *p.p.* — *Jakkia excelsa* BLUME, Bijdr. (1825) 62 ('*Jackia*'); G. DON, Gen. Hist. 1 (1831) 368. — *Monnina excelsa* (BLUME) SPRENGEL, Syst. Veg. 3 (1827) 265; STEUD. Nom. ed. 2, 2 (1841) 157. — *X. adenopodum* MIQ. Fl. Ind. Bat., Suppl. (1861) 393; Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 277. — *Banisterodes excelsum* (BLUME) O. K. Rev. Gen. Pl. 1 (1891) 46, *nom. illeg.* — *X. affine* var. *adenopodum* (MIQ.) K. & V. Icon. Bog. 1, 1 (1897) 11. — *X. glandulosum* MERR. Philip. Gov. Lab. Bur. Bull. 35 (1905) 34; GAGNEP. in Desv. J. Bot. 21 (1908) 252; MERR. En. Philip. 2 (1923) 485. — *X. floriferum* ELMER, Leafl. Philip. Bot. 5 (1913) 1674. — *X. multiramosum* ELMER, l.c. 1676; MERR. Philip. J. Sc. 27 (1925) 29. — *X. loheri* MERR. l.c. 29. — *X. pallidum* RIDLEY, Kew Bull. (1938) 113; MASAMUNE, En. Phan. Born. (1942) 380.

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-blade 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 grooved, thickened on the nodes and there with usually distinct, protruding glands, brownish, densely minutely patently hairy. *Flowers* usually with 3 together. *Pedicele* (2.5–)3–4.5 mm, rarely longer, densely minutely half-patently 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, or white and 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 patently 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 basal part; ovules 8–12, rarely 6. *Fruit* 1- to often 2-locular, the second chamber often reduced and seemingly enveloped by the pericarp; usually globose, up to c. 2 cm diam., smooth to irregularly low-tuberculate, rarely densely tuberculate, rather dull to somewhat shiny, yellowish to brownish; pericarp usually hard; pedicel 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 *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 eglandular.

2. *Xanthophyllum bullatum* KING, J. As. Soc. Beng. 59, ii (1890) 142; BURK. & HEND. Gard. Bull. S. S. 4 (1928) 222; NG, Tree Fl. Mal. 1 (1972) 356, f. 1; CORNER, Gard. Bull. Sing. Suppl. 1 (1978) 146; MEUDEN, Leiden Bot. Ser. 7 (1982) 66.

Shrub or small tree, 3–4.5 m high, 6 cm dbh. Twigs appressedly hairy. *Petiole* c. 12–22 mm, rather densely minutely appressedly 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 appressedly to patently minutely hairy, light to very dark brownish, with large, protruding nodal glands. *Pedicele* 5–7 mm, very densely minutely appressedly reddish brown hairy. *Sepals* minutely appressedly 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 appressedly 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 sparsely shortly hairy at base; anthers 0.8–1.2 mm long, ciliate along slits. *Ovary* slightly ribbed; style glabrous in basal part, apically shortly 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).

3. *Xanthophyllum sulphureum* KING, J. As. Soc. Beng. 59, ii (1890) 143; GAGNEP. in Desv. J. Bot. 21 (1908) 252 ('*sulphureum*'); RIDLEY, Fl. Mal. Pen. 1 (1922) 145; WYATT-SMITH, Mal. For. Rec. 17 (1952) 81, 363; NG, Tree Fl. Mal. 1 (1972) 363, f. 4, *excl.* FRI 8041; MEIJDEN, Leiden Bot. Ser. 7 (1982) 67, f. 10c.

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 patently 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. *Pedice*l c. 4 mm, rather stout, very densely patently brownish pubescent. *Sepals* densely brownish patently shortly 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) patently 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 tuberculate; pericarp hard.

Distr. Malesia: Malay Peninsula (Perak, Kelantan, Pahang).

4. *Xanthophyllum cockburnii* MEIJDEN, Leiden Bot. Ser. 7 (1982) 67.

Tree, 20 m high, 30 cm dbh. Axillary buds densely

patently 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 patently 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 reddish brown pubescent, with rather large nodal glands. *Pedice*l 4.5 mm. *Sepals* densely patently reddish brown hairy; 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.

5. *Xanthophyllum hosei* RIDLEY, Kew Bull. (1938) 113; MASAMUNE, En. Phan. Born. (1942) 380; MEIJDEN, Leiden Bot. Ser. 7 (1982) 69.

Small tree, up to 3.5 m high, dbh 3 cm. Twigs minutely appressedly hairy, soon glabrescent, or glabrous. *Petiole* 7–10 mm, minutely appressedly hairy. *Leaf-blade* 12–21 by 4.5–10 cm, base rounded to more or less obtuse, apex rather suddenly cuspidate 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, sparsely minutely appressedly 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 appressedly hairy, internodes (except at very base) very short, c. 0.5–1 mm long, thus giving the inflorescence a very dense-flowered appearance. *Pedice*l 2.5–4 mm, grooved, densely minutely appressedly hairy. *Sepals* glabrous to sparsely minutely appressedly hairy inside; outer sepals 2.1–2.5 by 2.5–2.8 mm, with 2–4 glandular spots, minutely densely appressedly hairy outside; inner sepals 3.5–3.8 by 2.2–2.6 mm, rather distinctly keeled and there densely minutely appressedly hairy, further more or less glabrous outside. *Petals* yellowish when dry, the

longest one c. 8.5 mm; carina sparsely appressedly hairy outside in middle part, glabrous inside; other petals ciliate to halfway, further glabrous. *Stamens*: filaments wide at base, sparsely appressedly hairy adaxially and abaxially to \pm 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 appressedly hairy till the apex; ovules 7–10. *Fruit* (very young) not ribbed, finely pustulate; style persistent, recurved; sepals persistent.

Distr. *Malesia*: Borneo (Sarawak).

6. *Xanthophyllum ferrugineum* MEIJDEN, Bot. J. Linn. Soc. 67 (1973) 118; Leiden Bot. Ser. 7 (1982) 69.

Tree, up to 25 m high, up to 40(–60) cm dbh. 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; 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 appressedly greyish hairy. *Sepals* possibly persistent in fruit, medium-brown with light brown margin when dry; outer sepals 3.7–4.8 by 3.5–4 mm, (sub)glabrous outside, often with (sometimes minute) glandular spots; inner sepals 4–5 by 4–4.2 mm, thickened in middle basal part, minutely appressedly 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 appressedly hairy all round, apically often greyish hairy in 4 short rows; ovules 8–14. *Fruit* (immature) partly enclosed by the persistent sepals, ovoid, finely tuberculate, dull, yellowish brown.

Distr. *Malesia*: Borneo (Sarawak, Brunei, Sabah, Tawau).

7. *Xanthophyllum affine* KORTL. ex MIQ. Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 271; KURZ, J. As. Soc. Beng. 42, ii (1873) 80; BENN. Fl. Br. India 1 (1874) 209; KURZ, For. Fl. Burma 1 (1877) 82; F.-VILL. Nov. App. (1880) 14; KING, J. As. Soc. Beng. 59, ii (1890) 142, *p.p.*; CHODAT in E. & P. Nat. Pfl. Fam. 3, 4

(1896) 345; K. & V. Icon. Bog. 1, 1 (1897) 11, *p.p.* (*alpha genuina*, t. 11, *p.p.*, excl. f. 12–14; RIDLEY, J. Str. Br. R. As. Soc. n. 33 (1900) 45; BRANDIS, Indian Trees (1906) 44; GAGNEP. in Desv. J. Bot. 21 (1908) 253; RIDLEY, J. Fed. Mal. St. Mus. 4 (1909) 5; J. Str. Br. R. As. Soc. n. 59 (1911) 73; MERR. En. Born. (1921) 326, *p.p.* (*sub X. excelsum*); RIDLEY, Fl. Mal. Pen. 1 (1922) 143, *p.p.*; BURK. Gard. Bull. S. S. 3 (1923) 35, *p.p.* (*sub X. excelsum*); MERR. En. Philip. 2 (1923) 386, *p.p.* (*sub X. excelsum*); BAKER, J. Bot. 62 (1924) Suppl. 7; BURK. & HEND. Gard. Bull. S. S. 3 (1925) 345; HEND. *ibid.* 4 (1928) 222; WATSON, Mal. For. Rec. 5 (1928) 249; CHODAT in Merr. Pl. Elm. Born. (1929) 133; CRAIB, Fl. Siam. En. 1 (1931) 105; BURK. Dict. (1935) 2268, *p.p.*; KEITH, N. Born. For. Rec. 2 (1938) 225; DOCTERS VAN LEEUWEN, Ned. Kruidk. Arch. 51 (1941) 166, 167; MASAMUNE, En. Phan. Born. (1942) 379; WYATT-SMITH, Mal. For. Rec. 17 (1952) 80, 363, *p.p.* (*sub X. excelsum*); BALAN MENON, *ibid.* 19 (1956) 34; WYATT-SMITH, *ibid.* 23² (1963) f. 10, *p.p.*?; MEIJER, Bot. News Bull. Sandakan 7 (1967) 88; NG, Fed. Mus. J. n.s. 13 (1971) 137; Tree Fl. Mal. 1 (1972) 354, f. 1, *p.p.*; CORNER, Gard. Bull. Sing. Suppl. 1 (1978) 146, 211 (*excl. n. 29341*); MEIJDEN, Leiden Bot. Ser. 7 (1982) 70, f. 2, 3A g–i, 10C, 11. — *Banisterodes affine* (MIQ.) O. K. Rev. Gen. Pl. 1 (1891) 46, *nom. illeg.* — *X. sarawakense* CHODAT, Bull. Herb. Boiss. 4 (1896) 262 (*'sarawakensis'*); GAGNEP. in Desv. J. Bot. 21 (1908) 252; MASAMUNE, En. Phan. Born. (1942) 381. — *X. excelsum* var. *affine* (MIQ.) BOERL. Cat. Hort. Bog. (1899) 59; HEYNE, Nutt. Pl. (1927) 901.

Tree, rarely a shrub, up to 15(–30) m, up to 40(–95) cm dbh. 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 densely 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 bulate 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 appressedly to half-patently, sometimes patently hairy outside, inside appressedly 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 appressedly 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* globular 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 Banka), Malay Peninsula, Borneo (Sarawak, Brunei, Sabah), Philippines (Palawan, Culion, Busuanga).

Notes. Very variable, and probably not homogeneous; for a discussion, see VAN DER MEIJDEN, *l.c.* 71-73.

Most authors have included *I. X. flavescens* in this species; see note under that species.

8. *Xanthophyllum pubescens* MEIJDEN, Leiden Bot. Ser. 7 (1982) 73. — *Xanthophyllum spec. B* NG, Tree Fl. Mal. 1 (1972) 365, f. 5.

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 patently 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).

9. *Xanthophyllum resupinatum* MEIJDEN, Bot. J. Linn. Soc. 67 (1973) 120; Leiden Bot. Ser. 7 (1982) 74.

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 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 appressedly greyish hairy. *Pedicel* slightly grooved, 4-5 mm, very densely minutely appressedly 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 appressedly 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).

10. *Xanthophyllum schizocarpon* CHODAT in Merr. Pl. Elm. Born. (1929) 136; MASAMUNE, En. Phan. Born. (1942) 381; MEIJDEN, Leiden Bot. Ser. 7 (1982) 74.

Tree, 10-25 m, 35 cm dbh. Twigs minutely appressedly 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 appressedly hairy to glabrous. *Leaf-blade* 4.5-12 by 1.5-4.5 cm; above

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 grooved, 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, \pm 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 patently 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 globular, 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).

11. *Xanthophyllum velutinum* CHODAT, Bull. Herb. Boiss. 4 (1896) 259; MEIJDEN, Leiden Bot. Ser. 7 (1982) 75.

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 patently brownish hairy in the basal part; flowers with 3 together. *Pedicel* 1.5–6.5 mm, ribbed, very densely patently 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 out-

side, 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 slits. *Ovary* sessile, distinctly ribbed, glabrous or sometimes hairy on 2 ribs down to halfway; 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).

12. *Xanthophyllum rufum* BENN. Fl. Br. India 1 (1874) 210; KING, Mat. Fl. Mal. Pen. (1890) 144; MAINGAY, Kew Bull. (1890) 113; GAGNEP. in Desv. J. Bot. 21 (1908) 252; RIDLEY, Fl. Mal. Pen. 1 (1922) 145; WATSON, Mal. For. Rec. 5 (1928) 249; BURK. Dict. (1935) 2269; WYATT-SMITH, Mal. For. Rec. 17 (1952) 81, 362; BALAN MENON, *ibid.* 19 (1956) 34; WYATT-SMITH, *ibid.* 23² (1963) f. 5, 9; MEIJER, Bot. News Bull. Sandakan 7 (1967) 87; NG, Tree Fl. Mal. 1 (1972) 361, f. 4; MEIJDEN, Leiden Bot. Ser. 7 (1982) 76, f. 3A-1, 12. — *Banisterodes rufum* (A.W. BENNETT) O. K. Rev. Gen. Pl. 1 (1891) 46, *nom. illeg.* — *X. flavum* RIDLEY, Kew Bull. (1925) 77. — *X. heteropleurum* CHODAT in Merr. Pl. Elm. Born. (1929) 134; MASAMUNE, En. Phan. Born. (1942) 380; NG, Tree Fl. Mal. 1 (1972) 363. — **Fig. 19.**

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 patently 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, subsistent. *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-

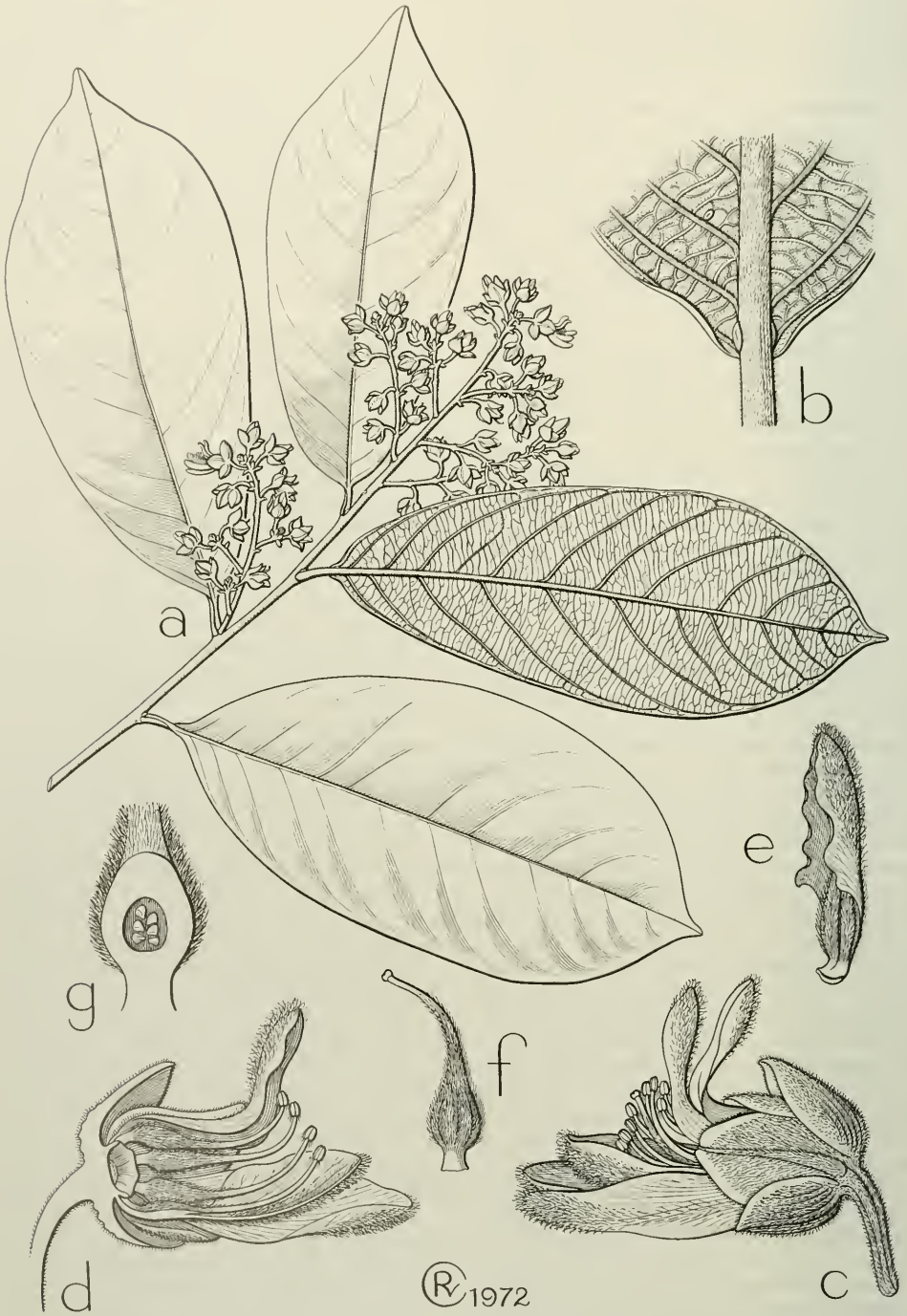


Fig. 19. *Xanthophyllum rufum* BENN. *a*. Habit, $\times 0.5$; *b*. base of leaf, $\times 2$; *c*. flower; *d*. flower, longitudinal section, gynoecium removed; *e*. carina with two stamens enclosed; *f*. gynoecium; all $\times 3$; *g*. ovary, longitudinal section, $\times 6$ (SAN 36554).

bescent 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 tuberculate; pericarp rather thick, hard; not rarely some sepals present.

Distr. 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.

13. *Xanthophyllum macrophyllum* BAKER, Kew Bull. (1896) 21; AIRY SHAW, Kew Bull. (1940) 252; MASAMUNE, En. Phan. Born. (1942) 380; MEIJER, Bot. News Bull. Sandakan 7 (1967) 88; MEIJDEN, Leiden Bot. Ser. 7 (1982) 78.

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 decurrent-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 intramarginal nerve; glands mostly rather few, scattered, 0.4–0.5 mm diam. *Inflorescences* sometimes unbranched, shorter than the leaves; axes grooved, appressedly brown-velvety; bracts often opposite, with 2 small indistinct glands. *Pedicele* 2–12 mm, appressedly brown-velvety. *Sepals* shortly appressedly 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 appressedly 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.

Distr. Malesia: Borneo (Sarawak, Sabah).

2. Section *Eystathes*

(LOUR.) MEIJDEN, Bot. J. Linn. Soc. 67 (1973) 117; Leiden Bot. Ser. 7 (1982) 81. — *Eystathes* LOUR. Fl. Coch. 1 (1790) 235.

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 over 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 tuberculate. *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*
1. Testa without a hard inner layer. Albumen very thin. Embryo without flattened areas near the base. Radicle not exerted. *Spp.* 58–62. 2b. *Subsect. Eystathes*

2a. Subsection Jakkia

(BL.) MEIJDEN, Leiden Bot. Ser. 7 (1982) 81. — *Jakkia* BLUME, Cat. (1823) 17.

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 exerted.

14. *Xanthophyllum nigricans* MEIJDEN, Bot. J. Linn. Soc. 67 (1973) 119; Leiden Bot. Ser. 7 (1982) 82.

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 patently 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 concolorous, 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 ciliolate 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* globular, up to 1.3 cm diam., dull, slightly wrinkled, brownish; pedicel up to 3 mm long.

DISTR. *Malesia*: Borneo (Brunei, Sabah).

15. *Xanthophyllum borneense* MIQ. Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 277; MASAMUNE, En. Phan. Born. (1942) 379; MEIJDEN, Leiden Bot. Ser. 7 (1982) 82. — *X. glabrescens* RIDLEY, Kew Bull. (1938) 113; MASAMUNE, En. Phan. Born. (1942) 380.

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 acutish; 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, gla-

brous. *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* globular to broadly ovoid, c. 1.8 cm diam., smooth, brown; pedicel c. 5 mm.

DISTR. *Malesia*: Borneo (Sarawak, Sabah, SE. Borneo).

16. *Xanthophyllum ovatifolium* CHODAT, Bull. Herb. Boiss. 4 (1896) 258; MEIJDEN, Leiden Bot. Ser. 7 (1982) 83.

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).

17. *Xanthophyllum tenue* CHODAT in Merr. Pl. Elm. Born. (1929) 135; MASAMUNE, En. Phan. Born. (1942) 382; MEIJER, Bot. News Bull. Sandakan 7 (1967) 88; MEIJDEN, Leiden Bot. Ser. 7 (1982) 83.

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, shortly patently 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 patently minutely hairy in basal half; beneath mostly rather dull, yellowish green, glabrous to minutely patently 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, sparsely 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* globular, up to 1.8 cm diam., dull, wrinkled, light greenish brown; pericarp soft, thin; pedicel mostly up to 7 mm, reddish.

Distr. Malesia: Borneo (Sarawak, Sabah, Tawau, N. Kalimantan).

Ecol. Submontane rain-forest, 500–1200 m.

18. *Xanthophyllum subcoriaceum* (CHODAT) MEIJDEN, Bot. J. Linn. Soc. 67 (1973) 120; Leiden Bot. Ser. 7 (1982) 85. — *X. ellipticum* var. *subcoriaceum* CHODAT in Merr. Pl. Elm. Born. (1929) 134; MEIJER, Bot. News Bull. Sandakan 7 (1967) 88.

Shrub or small tree, up to 15 m, 20 cm dbh. Axillary buds 2 (or 3), (0.5–)1–2.7 mm long. *Petiole* 5–8.5 mm. *Leaf-blade* 5–12 by 1.5–5.5 cm, base sometimes more or less rounded, margin mostly strongly curved upwards when dry, apex cuspidate to acuminate; above sometimes slightly bullate between secondary nerves, dull, light greyish green to olive-green, secondary nerves mostly indistinct, venation mostly indistinct, sometimes scarcely visible, less often finely prominent; lower side yellowish green, secondary nerves (3 or) 4–6 pairs, forming a distinct intramarginal nerve, venation usually obscure; glands (0–)2–12, situated at some distance from the

midrib, 0.2–0.4 mm diam. *Inflorescences* unbranched, \pm as long as the leaves; axes angular, light brown, sparsely appressedly shortly hairy; lowermost bracts sometimes leaf-like. *Pedicel* 2.5–3.5 mm, mostly light brown, glabrous to sparsely minutely appressedly hairy. *Sepals* (nearly) glabrous outside; outer ones 1.6–1.8 by 1.4–1.8 mm; inner ones 2–2.5 by 2–2.5 mm. *Petals* white, when dry orange, faintly ciliate apically, outside glabrous except at base, longest one 8–10 mm. *Stamens*: anthers 0.5–0.7 mm long, sparsely hairy at base. *Ovary* 0.5–1.5 mm stipitate, subglabrous to rather densely appressedly hairy, rather soon partly glabrescent; style sparsely appressedly hairy; ovules 4. *Fruit* at first \pm ellipsoid with a sharp beak because of subsistent style, when mature globular, c. 1.7 cm diam., smooth, light green to brown, rather dull to shiny; pericarp thin; pedicel up to 5(–7) mm, mostly light brown.

Distr. Malesia: Borneo (Sarawak, Brunei, Sabah: Mt Kinabalu & Tawau).

19. *Xanthophyllum neglectum* MEIJDEN, Bot. J. Linn. Soc. 67 (1973) 119; Leiden Bot. Ser. 7 (1982) 86. — *X. palembanicum* (non MIQ.) KEITH, N. Born. For. Rec. 2 (1938) 225.

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 sparsely very shortly hairy especially in the upper groove. *Leaf-blade* 5–12 by 1.8–5.5 cm, 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 patently 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 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.

Distr. Malesia: Borneo (E. Sabah, F. Kalimantan).

20. *Xanthophyllum pauciflorum* MEIJDEN, Bot. J. Linn. Soc. 67 (1973) 119; Leiden Bot. Ser. 7 (1982) 87.

Tree, up to 21 m, 25 cm dbh. Twigs \pm 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-papillose, 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 patently hairy. *Pedicel* 1.5–2.5(–3) mm, very shortly patently hairy. *Sepals* with a small apical tuft; outer ones 2–2.2 by 1.5–1.8 mm, very sparsely very shortly hairy outside; inner ones c. 2.7 by 3 mm, glabrous outside. *Petals* yellowish, when dry yellowish orange, very sparsely hairy to glabrous outside, apically slightly tufted and distinctly ciliate, basally rather densely hairy at both sides, the longest one 7.5–8.5 mm long. *Stamens*: anthers c. 0.4 mm long, with few hairs at base. *Ovary* appressedly hairy; ovules 4. *Fruit* (immature) ovoid-globular, olive-brown, smooth, with a distinct remainder of the style, roughly pubescent, glabrescent.

Distr. *Malesia*: Borneo (Sarawak: Mersing Hill).

21. *Xanthophyllum tardicrescens* MEIJDEN, Bot. J. Linn. Soc. 67 (1973) 120; Leiden Bot. Ser. 7 (1982) 87.

Small tree, up to 6 m, 6 cm dbh. Twigs dull, bearing 1 or 2 (or 3) leaves per shoot. Axillary buds 2 (or 3?), smaller than 1 mm. *Petiole* 3.5–5 mm. *Leaf-blade* 7–16 by 2–5 cm, base rounded-truncate to -cordate; above dark greyish green, very dull, secondary nerves slightly sunken, venation obscured; beneath olive-greenish, dull, secondary nerves 3 or 4 pairs, the basal nerves long, reaching often beyond the middle of the leaf, or forming an intramarginal nerve, venation not distinct; glands 6–12, scattered, 0.2–0.3 mm diam. *Inflorescences* unbranched, \pm as long as the leaves; axes grooved, not flattened, nearly glabrous, light brown; flowers often with 2 or 3 together; bracts relatively long-persistent. *Pedicel* 3.5–4.5 mm, sparsely very shortly appressedly hairy. *Sepals* sometimes apically with tiny glandular spots; outer ones 2 by 2.1 mm; inner ones 2.3 by 2.3 mm. *Petals* white, the upper ones with a yellow spot, when dry yellowish orange, the longest one 7–8 mm; carina nearly glabrous outside; other petals glabrous. *Stamens*: filaments connate over 0.7–1 mm, very shortly hairy above base, further glabrous; anthers probably c. 0.7 mm long. *Ovary* very shortly stipitate, more or less appressedly hairy; ovules 4. *Fruit* (immature) smooth, slightly shiny, yellowish green, sparsely appressedly hairy, glabrescent; pericarp very thin.

Distr. *Malesia*: Borneo (Sarawak: Semengoh).

22. *Xanthophyllum parvifolium* MEIJDEN, Bot. J. Linn. Soc. 67 (1973) 119; Leiden Bot. Ser. 7 (1982) 88.

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-papillose, 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 \pm 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 patently hairy, further glabrous; anthers 0.35–0.4 mm long, with few short hairs at base. *Ovary* c. 1 mm stipitate, appressedly hairy; style rather sparsely appressedly hairy in lower half, further glabrous; ovules 4. *Fruit* very shortly stipitate, globular, up to 1.1 cm diam., dull, light brown, very sparsely shortly appressedly hairy; pericarp rather thin; pedicel slender, 6.5–10 mm, completely glabrous.

Distr. *Malesia*: Borneo (Sarawak: Sabal For. Res., Lambir hills).

23. *Xanthophyllum philippinense* CHODAT, Bull. Herb. Boiss. 4 (1896) 261; MERR. En. Philip. 2 (1923) 387; MEIJDEN, Leiden Bot. Ser. 7 (1982) 88, f. 10A.

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 \pm 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 appressedly 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), exerting 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. *Seed(s)* 1 or 2.

Distr. Malesia: Philippines (Luzon, Mindoro, Mindanao).

Ecol. In open flowers the stigma is exerted from the carina. This may mean that cross-pollination is obligatory.

24. *Xanthophyllum ancolanum* MIQ. Fl. Ind. Bat., Suppl. (1861) 394; CHODAT, Bull. Herb. Boiss. 4 (1896) 261; MIQ. Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 275, incl. *f. angustifolia* MIQ.; MEIJDEN, Leiden Bot. Ser. 7 (1982) 89. — *X. palembanicum* MIQ. Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 277. — *X. sumatranum* MIQ. l.c. 275; BAKER, J. Bot. 62 (1924) Suppl. 7.

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 shortly hairy, apically sometimes with glands. *Leaf-blade* 10–26 by (2.5–)3.5–10.5 cm, apex shortly acuminate to cuspidate; 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 ramiflorous), 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 patently 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 appressedly hairy outside; other petals very sparsely hairy outside to glabrous. *Stamens:* filaments connate over (0.7–)2–2.5 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-patently hairy; style exerted 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: Lampong Distr.: Muaradua).

Ecol. Montane rain-forest, 500–1200 m.

25. *Xanthophyllum brigittae* MEIJDEN, sp. nov. — Fig. 20.

Gemmae axillares 2,5–3,5 mm longae. *Folia basi cordata incurvata; glandulae sparsae; nervis laterali-bus* 14–20-jugis; *petiolo* 15–18 mm longo. *Petala inaequalia, petalo longissimo* 16 mm longo; *carina subglabra, extus sparse appresse pilosa. Filamenta (sub)libera; antherae* 1 mm longae. *Ovarium sparse appresse pilosum; stylum appresse pilosus; ovula* 4. *Fructus ignotus.* — *Typus:* W.J.J.O. DE WILDE & B.E.E. DE WILDE DUYFJES 15060 (L).

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 transversally 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 appressedly 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 appressedly 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 appressedly 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 transversally 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 VAN 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 51. *X. erythrostachyum* GAGNEP. 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.

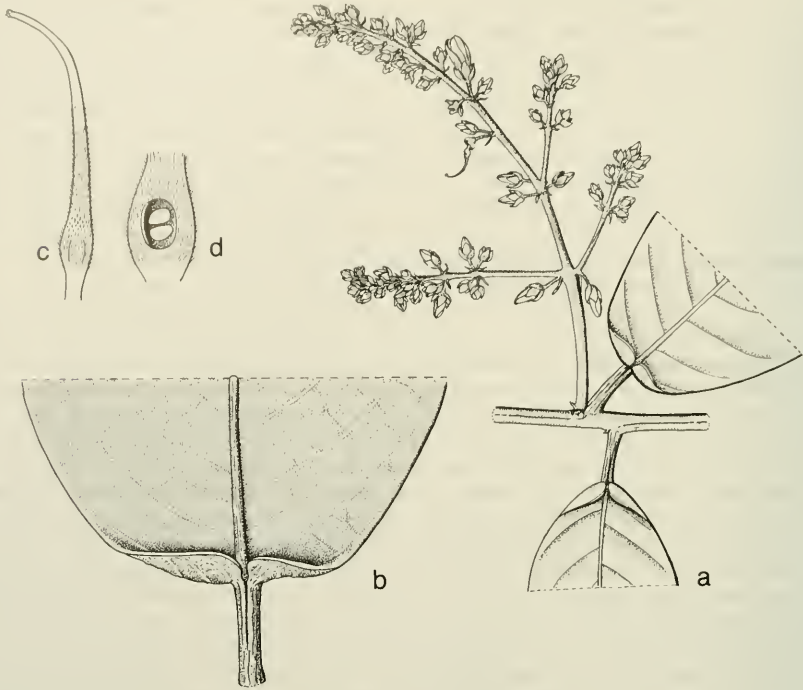


Fig. 20. *Xanthophyllum brigittae* MEIJDEN. a. Habit, $\times 0.5$; b. leaf base, $\times 1.5$; c. gynoecium, $\times 3$; d. ovary, longitudinal section, $\times 6$ (DE WILDE & DE WILDE-DUYFJES 15728).

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.

26. *Xanthophyllum tenuipetalum* MEIJDEN, Bot. J. Linn. Soc. 67 (1973) 120; Leiden Bot. Ser. 7 (1982) 89, f. 9a. — *X. affine* (non MIQ.) KOORD. Minah. (1898) 344.

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 ciliate along slits, sparsely and shortly hairy at base. *Ovary* appressedly hairy; style rather sparsely hairy; ovules 4. *Fruit* globular, 1.8–2 cm

diam., slightly shiny, light brown, faintly appressedly hairy; pericarp rather thin; pedicel up to 6 mm.

Distr. *Malesia*: N. & S. Celebes (Minahassa; Malili; Kendari; Muna I.), Moluccas (Taliabu & Kai Is.), West New Guinea (Vogelkop Peninsula).

27. *Xanthophyllum impressum* MEIJDEN, Leiden Bot. Ser. 7 (1982) 90.

Tree, up to 23 m, 20 cm dbh. Axillary buds, when resting, mostly more or less enclosed between the base of the petiole and a low ridge of the twig, 1–1.8 by 1.5–2 mm, for c. 1 mm of its length uncovered; scales strongly thickened, especially at base, but leaving a narrow scar. *Petiole* 10–14 mm, sometimes with glands. *Leaf-blade* 10–20 by 3.5–9 cm, apex acutish to shortly acuminate; above rather dull, greyish green; beneath light yellowish green, papillose, secondary nerves c. 8 or 9 pairs, not forming an intramarginal nerve; glands scattered, probably rather numerous but often seemingly absent, up to 0.2 mm diam., exceptionally larger. *Inflorescences* up to 20 cm long; axes reddish brown, densely minutely appressedly hairy; lower bracts (sub)opposite. *Pedicel* 1.5–4 mm, grooved, appressedly shortly hairy. *Sepals*: outer sepals 2–2.5 by 2.6–3.3 mm; inner sepals 3.2–3.7 by 3.2–3.3 mm. *Petals* white, the upper ones with a yellow spot, when dry orange to dark red, sometimes with incrustations, the longest one 8.5–10.5 mm; carina densely more or less appressedly hairy outside; other petals glabrous outside. *Stamens*: filaments widened and thickened above base, there appressedly hairy, further glabrous; anthers 0.6–0.7 mm long, hairy to (sub)glabrous at base. *Ovary* nearly sessile, half-patently hairy; ovules 4. *Fruit* globular, c. 1.7 cm diam., dull, smooth, light brownish, appressedly hairy.

Distr. *Malesia*: E. Borneo (E. Sabah, E. Kalimantan), Philippines (Catanduanes).

28. *Xanthophyllum griffithii* HOOK.f. ex A.W. BENNETT, Fl. Br. India 1 (1874) 210; KING, Mat. Fl. Mal. Pen. (1890) 136; MAINGAY, Kew Bull. (1890) 114; BRANDIS, Indian Trees (1906) 45; GAGNEP. in Desv. J. Bot. 21 (1908) 251; RIDLEY, Fl. Mal. Pen. 1 (1922) 149; BURK. & HEND. Gard. Bull. S. S. 3 (1925) 346; HEND. *ibid.* 4 (1928) 222; BURK. Dict. (1935) 2269; WYATT-SMITH, Mal. For. Rec. 17 (1952) 80, 362; NG, Tree Fl. Mal. 1 (1972) 357, f. 2, *excl. var. curtisii et var. montanum*; Mal. For. 38 (1975) 85, f. 8.1 A–E, 8.2; MEIJDEN, Leiden Bot. Ser. 7 (1982) 92. — *Banisterodes griffithii* (HOOK.f. ex A.W. BENNETT) O. K. Rev. Gen. Pl. 1 (1891) 46, *nom. illeg.* — *X. parvum* CHODAT, Bull. Herb. Boiss. 4 (1896) 264. — *X. gracile* CHODAT, l.c. 256; K. & V. Bijdr. Booms. Java 5 (1900) 302; BACKER, Schoofl. Java (1911) 80; KOORD. Exk. Fl. Java 2 (1912) 454. — *X. pseudosti-*

palaceum MERR. Philip. J. Sc. 10 (1915) Bot. 316; En. Philip. 2 (1923) 387.

Tree, up to 27 m, 40 cm dbh. Twigs glabrous to minutely patently hairy. Axillary buds erect to half-patent, (1.5–)3–8 mm long, not thickened at base, glabrous to densely minutely hairy; enclosing a pair of nearly similar buds of second order (those at base of a new twig often half-patent). *Petiole* 4–12 mm, sometimes with 1 or 2 glands in apical part. *Leaf-blade* 4–12(–15) by 1–4.5(–9) cm, apex sometimes cuspidate; 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 reddish brown, densely minutely patently hairy; lower bracts opposite. *Pedicel* 1–4.5 mm, grooved, densely minutely appressedly hairy. *Sepals* sometimes with 2 glands in apical part; outer sepals 1.6–2.5 by 2.1–2.7 mm; inner sepals 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 appressedly hairy outside; other petals glabrous to appressedly hairy outside in apical part. *Stamens*: 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 appressedly hairy; ovules 4. *Fruit* globular, up to 1.5 cm diam., more or less smooth brown, appressedly 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*

1. Axillary buds erect, flattened against the twig, basally convex b. *ssp. erectum*

a. *ssp. angustifolium* (NG) MEIJDEN, Leiden Bot. Ser. 7 (1982) 94. — *X. griffithii* var. *angustifolium* NG, Fed. Mus. J. n.s. 13 (1971) 137. — *X. parvum* CHODAT. — *X. gracile* CHODAT. — *X. pseudostipulaecum* MERR.

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. *Petiole* 4–8(–9) mm. *Leaf-blade* 4–8(–10) by 1–4(–5) cm, in juvenile shoots up to 10 by 2.5 cm; beneath glaucous-papillose to (nearly) smooth and

not glaucous, secondary nerves 4 or 5 (or 6) pairs; glands 0.2–0.3 mm diam. *Pedice*l 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, Borneo (Sarawak, Sabah, E. Kalimantan), Philippines (Luzon).

Ecol. Usually in submontane rain-forest, up to 1400 m.

b. ssp. erectum MEIJDEN, Leiden Bot. Ser. 7 (1982) 94. — *X. griffithii* HOOK.f. ex A.W.BENNETT, excl. *Mergui coll.*

Axillary buds erect or nearly so and flattened in their upper part against the twig, ovate to ovate-lanceolate, rarely elliptic, (3–)4–8 mm long, basally convex, slightly wrinkled, glabrous to densely minutely hairy. *Petiole* 6–12 mm. *Leaf-blade* 5–12(–15) by 2–4.5(–9) cm; beneath glaucous-papillose, secondary nerves c. 5 or 6 pairs; glands c. 0.2 mm diam. *Pedice*l 1–2(–3) mm. *Petals*: longest one (6.5–)7–8 mm. *Stamens*: anthers 0.4(–0.5) mm long. *Fruit* up to 1.5 cm diam.

Distr. *Malesia*: Malay Peninsula (common).

29. *Xanthophyllum monticolum* MEIJDEN, Leiden Bot. Ser. 7 (1982) 95. — *X. griffithii* var. *montanum* NG, Fed. Mus. J. n.s. 13 (1971) 137; Tree Fl. Mal. (1972) 359, f. 2.

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, slit-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. *Pedice*l 3.5–5 mm, slightly grooved, very densely appressedly hairy. *Sepals*: outer sepals 2.6–3 by 2.5–3 mm; inner sepals 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 appressedly hairy outside, subglabrous inside; other petals outside in basal part shortly appressedly 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* globular, 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.

30. *Xanthophyllum vitellinum* (BLUME) DIETR. Syn. Pl. 2 (1840) 1277; WALP. Rep. 1 (1842) 248; HASSK. Cat. Hort. Bog. (1844) 227; Pl. Jav. Rar. (1848) 296; MIQ. Fl. Ind. Bat. 1, 2 (1858) 129; HASSK. in Miq. Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 193; MIQ. l.c. 272; TEJSM. & BINN. Cat. Hort. Bog. (1866) 218; CHODAT, Monogr. 1 (1891) t. 9, f. 1, 2; t. 12, f. 4c–e; BURCK, Wand. Bot. Tuin Btzg (1892) 31; WIESNER, Ann. Jard. Bot. Btzg, Suppl. 2 (1898) 97, t. 3; BOERL. Cat. Hort. Bog. (1899) 58; K. & V. Bijdr. Booms. Java 5 (1900) 294; VALETON, Icon. Bog. 1, 4 (1901) 9, t. 79; GAGNEP. in Desv. J. Bot. 21 (1908) 251; Fl. Gén. I.-C. 1 (1909) 243; BACKER, Schoolfl. Java (1911) 80; KOORD. Exk. Fl. Java 2 (1912) 453; MERR. En. Born. (1921) 326; BAKER, J. Bot. 62 (1924) Suppl. 7; DOCTERS VAN LEEUWEN, Zooecidia (1926) 273, 274; GAGNEP. Fl. Gén. I.-C. Suppl. 1 (1939) 218; BACKER & BAKH.f. Fl. Java 1 (1963) 200; MEIJDEN, Leiden Bot. Ser. 7 (1982) 97. — *Jakkia vitellina* BLUME, Cat. (1823) 17, 64; NEES, Fl. Bot. Zeit. 8 (1825) 120 ('*Jackia*'); BLUME, Bijdr. (1825) 61 ('*Jackia*'); G.DON, Gen. Hist. 1 (1831) 368. — *Jakkia longifolia* BLUME, Bijdr. (1825) 61 ('*Jackia*'); G.DON, Gen. Hist. 1 (1831) 368 ('*Jackia*'). — *Monnina longifolia* (BLUME) SPRENGEL, Syst. Veg. 3 (1827) 265. — *Monnina vitellina* (BLUME) SPRENGEL, l.c. 265; STEUDEL, Nom. ed. 2, 2 (1841) 157. — *X. longifolium* (BLUME) DIETR. Syn. Pl. 2 (1840) 1277; HASSK. Cat. Hort. Bog. (1844) 228; MIQ. Fl. Ind. Bat. 1, 2 (1858) 129; HASSK. in Miq. Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 194. — *Monnina macrophylla* STEUDEL, Nom. ed. 2, 2 (1841) 157, *nom. illeg.* — *X. paniculatum* MIQ. Fl. Ind. Bat., Suppl. (1861) 393; BAKER, J. Bot. 62 (1924) Suppl. 7. — *X. flavescens* (non ROXB.) F.-VILL. Nov. App. (1880) 14; VIDAL, Sinopsis (1883) 13. — *X. griffithii* (non A.W.BENNETT) ROLFE, J. Bot. 23 (1885) 210; VIDAL, Rev. Pl. Vasc. Filip. (1886) 51; CERON, Cat. Pl. Herb. Manila (1892) 19. — *X. hookerianum* KING, J. As. Soc. Beng. 59, ii (1890) 139; RIDLEY, Fl. Mal. Pen. 1 (1922) 144; BURK. Dict. (1935) 2268; NG, Tree Fl. Mal. 1 (1972) 359. — *X. kunstleri* KING, J. As. Soc. Beng. 59, ii (1890) 139; Ann. R. Bot. Gard. Calc. 5 (1896) 137, pl. 162; RIDLEY, J. Str. Br. R. As. Soc. n. 33 (1900) 45; BURK. & HEND. Gard. Bull. S. S. 3 (1925) 346; WATSON, Mal. For. Rec. 5 (1928) 249; BURK. Dict. (1935) 2268; NG, Tree Fl. Mal. 1 (1972) 359. — *X. curtisii* KING, J. As. Soc. Beng. 59, ii (1890) 138; RIDLEY, Fl. Mal. Pen. 1 (1922) 146; BURK. Dict. (1935) 2269; KORIBA, Gard. Bull. Sing. 17 (1958) 19, 51, f. 1; F. HALLÉ c.s. Trop. Trees & Forests (1978) 56; CORNER, Gard. Bull. Sing. Suppl. 1 (1978) 146, 211. — *Banisterodes longifolia* (BLUME)

O. K. Rev. Gen. Pl. 1 (1891) 46, *nom. illeg.* — *Banisterodes vitellinum* (BLUME) O. K. l.c. 46, *nom. illeg.* — *X. robustum* CHODAT, Bull. Herb. Boiss. 4 (1896) 262; MERR. EN. BORN. (1921) 326; En. Philip. 2 (1923) 387; MASAMUNE, En. Phan. Born. (1942) 381; MEIJER, Bot. News Bull. Sandakan 7 (1967) 88. — *X. robustum* var. *elmeri* CHODAT in Merr. Pl. Elm. Born. (1929) 136; MASAMUNE, En. Phan. Born. (1942) 381. — *X. griffithii* var. *curtisii* (KING) NG, Tree Fl. Mal. 1 (1972) 359, f. 2.

Shrub or tree, up to 30 m, 36 cm dbh. Axillary buds varying from narrowly triangular with strongly thickened base and then often 1.5–3 mm long, to rhomboid-ovate or ovate-oblong and then often 6–11 mm long. *Petiole* 8–14(–16) mm, very often with a pair of glands in apical half. *Leaf-blade* 8–20(–30) by 3.5–11 cm, sometimes a few leaves of a twig smaller; above greyish green to yellowish brown; midrib protruding to nearly flat in basal half; beneath: secondary nerves (6 or) 7–9(–11) pairs, in apical half forming an indistinct intramarginal nerve; glands mostly more than 10, near midrib or scattered, 0.2–0.4 mm diam., basal glands mostly present. *Inflorescences* branched, 8–30 cm long, branches often in pairs in lower part; axes basally mostly strongly flattened, grooved, glabrous to densely shortly patently or less often appressedly hairy; in basal part flowers with up to 3 together, solitary in apical part; lower bracts nearly opposite. *Pedicel* 1.5–5.5 mm, very rarely longer, grooved, densely shortly patently (sometimes appressedly) hairy. *Sepals* basally often more or less thickened and wrinkled; outer sepals (1.7–)2–3.3(–3.9) by 1.9–4 mm; inner sepals (2.6–)3–5.3(–5.7) by (2.5–)3–4(–5) mm. *Petals* dark yellow to white, when dry orange to dark reddish and often with white incrustations, the longest one (7–)8–12, exceptionally up to 15.5 mm; carina densely appressedly hairy outside; other petals glabrous outside or with a few hairs at apex. *Stamens*: 8, very rarely 9; filaments free or connate over up to 0.7 mm, widened above base and with a knob-like, rather densely hairy appendage at inner side, further glabrous; anthers 0.4–0.6(–0.7) mm long. *Ovary* subsessile or up to 1 mm stipitate, half-patently hairy; style hairy in basal half, little hairy upwards; ovules 4. *Fruit* globular, up to 1.8 cm diam., often wrinkled when dry, rather dull or rarely shiny, usually light brown, sometimes dark reddish brown, hairy; pericarp rather thin.

DISTR. *Malesia*: Sumatra (incl. Siberut & Simalur Is.), Malay Peninsula (incl. Penang), Java, Borneo, Philippines (Babuyan, Luzon, Mindanao). One of the most common species.

NOTE. Three collections from Sumatra, Riouw District (bb 24833, 27509, 30108) and an (otherwise different) collection from Borneo (S 23996) have an unusual type of axillary buds. The buds are globular

to ovoid, 1.5–2.5 mm long, rather strongly thickened in the middle and apical part. Such buds also occur in the sterile collection SF 20520 from the Anambas Is., in which, however, most axillary buds are very large and flat, c. 10–12 by 5–6 mm, resembling those of 40. *X. heterophyllum*.

31. *Xanthophyllum incertum* (BLUME) MEIJDEN, Leiden Bot. Ser. 7 (1982) 99, f. 3A-e. — *Guatteria incerta* BLUME, Fl. Java (1830) 100, t. 49B. — ? *X. acuminatissimum* MIQ. Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 276. — *Monoon incertum* (BLUME) MIQ. *ibid.* 2 (1865) 19.

Small tree, to 10 m. Axillary buds narrowly triangular to lanceolate, (2–)4.5–10(–11) mm long, more or less wrinkled; buds of second order rarely present. *Petiole* (6–)8–10(–12) mm. *Leaf-blade* 6–16(–22) by 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, reddish 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 shortly 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-)appressedly 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* patently hairy; style nearly glabrous to rather densely appressedly hairy; ovules 4. *Fruit* globular, c. 1.5 cm diam., ± shiny, brown, densely patently hairy; pedicel up to 3.5(–6) mm.

DISTR. *Malesia*: Central Sumatra (Toba Lands, Pajakumbuh, Mt Sago), West and Central Java.

Ecol. Montane rain-forest, (200–)500–1300 m.

32. *Xanthophyllum adenotus* MIQ. Fl. Ind. Bat., Suppl. (1861) 393; Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 275; MEIJDEN, Leiden Bot. Ser. 7 (1982) 100. — *X. cordatum* KORTII, ex MIQ. Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 274; MERR. EN. BORN. (1921) 325; RIDLEY, Kew Bull. (1925) 77; CHODAT in Merr. Pl. Elm. Born. (1929) 133, *incl. f. aequale* CHODAT; KEITH, N. Born. For. Rec. 2 (1938) 225; MASAMUNE,

En. Phan. Born. (1942) 379; MEIJER, Bot. News Bull. Sandakan 7 (1967) 87. — *X. arsatii* C.E.C. FISCHER, Kew Bull. (1932) 176; MASAMUNE, En. Phan. Born. (1942) 379.

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–)5–10(–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 appressedly 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 appressedly 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 3–5.5 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 appressedly 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* globular, 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–)5–15 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.

b. var. **lineare** MEIJDEN, Leiden Bot. Ser. 7 (1982) 101.

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).

33. **Xanthophyllum palawanense** ELMER, Leaf. Philip. Bot. 5 (1913) 1673; MEIJDEN, Leiden Bot. Ser. 7 (1982) 101. — *X. cordatum* (non MIQ.) MERR. En. Philip. 2 (1923) 386.

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 shortly 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 rather 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).

34. *Xanthophyllum ceraceifolium* MEIJDEN, Bot. J. Linn. Soc. 67 (1973) 117; Leiden Bot. Ser. 7 (1982) 102.

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).

35. *Xanthophyllum petiolatum* MEIJDEN, Leiden Bot. Ser. 7 (1982) 103.

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 pustulate; 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 constricted 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.).

36. *Xanthophyllum clovis* (STEEN. ex MEIJDEN) MEIJDEN, Leiden Bot. Ser. 7 (1982) 103. — *X. vitellinum* var. *clovis* STEEN. ex MEIJDEN, Bot. J. Linn. Soc. 67 (1973) 120.

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 \pm 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-papillose, 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, \pm grooved, densely very shortly, \pm 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 halfway. *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 I.), 3 collections.



Fig. 21. *Xanthophyllum bracteatum* CHODAT. a. Habit, $\times 0.5$; b. flower; c. flower, longitudinal section, gynoecium removed; d. gynoecium, all $\times 3$; e. ovary, longitudinal section, $\times 6$; f. carina, $\times 4$; g. base of leaf with glands, $\times 2.5$ (EDAÑO BS 28512).

37. *Xanthophyllum reflexum* MEIJDEN, Leiden Bot. Ser. 7 (1982) 104.

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. *Petiole* 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 \pm 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, \pm 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).

38. *Xanthophyllum angustigemma* MEIJDEN, Leiden Bot. Ser. 7 (1982) 104.

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. *Petiole* 10–14 mm. *Leaf-blade* c. 6–12 by 2.5–5.8 cm; above greyish green to brownish green; beneath glaucous-papillose, 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.

39. *Xanthophyllum bracteatum* CHODAT, Bull. Herb. Boiss. 4 (1896) 258; MERR. En. Philip. 2 (1923) 386; MEIJDEN, Leiden Bot. Ser. 7 (1982) 105, f. 15. — Fig. 21.

Axillary buds (ob)ovate-oblong to linear-lanceolate, 7–20 by 1.5–6 mm, basally slightly wrinkled, acute, more or less flat. *Petiole* 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-papillose, 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 pustulate, 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).

40. *Xanthophyllum heterophyllum* MEIJDEN, Leiden Bot. Ser. 7 (1982) 107. — *X. pseudostipulaceum* (non MERR.) MEIJER, Bot. News Bull. Sandakan 7 (1967) 87; WEBERLING, Beitr. Biol. Pfl. 50 (1974) 279, f. 1, II.

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 nerved, more or less shiny, sometimes in middle part with 1–4 rather indistinct glands, base shortly attenuate, apex rounded to obtuse. *Petiole* 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 \pm 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 known, these are either vegetative or in fruit.

41. *Xanthophyllum korthalsianum* MIQ. Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 277; MEIJDEN, Leiden Bot. Ser. 7 (1982) 107.

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 nerved. *Petiole* 7-10 mm, glands present or not. *Leaf-blade* 8-14 by 2.5-5 cm; above often slightly bullate between the secondary nerves, mostly dark green, secondary nerves finely prominent to obscure, venation obscure to finely prominent; beneath glaucous-papillose, secondary nerves 6-8 pairs, forming a \pm 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* patently 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.

42. *Xanthophyllum discolor* CHODAT, Bull. Herb. Boiss. 4 (1896) 257; RIDLEY, Fl. Mal. Pen. 1 (1922) 147; WATSON, Mal. For. Rec. 5 (1928) 249; BURK. Dict. (1935) 2268; WYATT-SMITH, Mal. For. Rec. 23² (1963) f. 8; NG, Tree Fl. Mal. 1 (1972) 356, f. 1; MEIJDEN, Bot. J. Linn. Soc. 67 (1973) 118, incl. *ssp. macranthum* MEIJDEN; Leiden Bot. Ser. 7 (1982) 108, f. 3A-q. — *X. macranthum* CHODAT ex ELMER, Leaf. Philip. Bot. 5 (1913) 1674, *nomen*. — *X. hypoleucum* MERR. Pl. Elm. Born. (1929) 135 (excl. BS 44034); KEITH, N. Born. For. Rec. 2 (1938) 225; MASAMUNE, En. Phan. Born. (1942) 380; MEIJER, Bot. News Bull. Sandakan 7 (1967) 88. — *X. flavovirens* ELMER, Leaf. Philip. Bot. 10 (1939) 3776, *nom. inval. (anglice)*.

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 bullate between the secondary nerves, light to dark greyish green, midrib mostly slightly sunken, sometimes a little prominent, venation rather indistinct; beneath glaucous-papillose 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, appressedly 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 up to 2 mm; anthers 2-2.5 mm long, minutely hairy all over. *Ovary* sessile to distinctly stipitate, appressedly whitish hairy; ovules 8-15. *Fruit* globular, 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.

b. ssp. macranthum MEIJDEN, Bot. J. Linn. Soc. 67 (1973) 118; Leiden Bot. Ser. 7 (1982) 109, f. 3A-q.

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.

43. *Xanthophyllum penibukanense* HEINE, Mitt. Bot. Staatssamml. München 6 (1955) 215; Pfl. Clemens Kinab. (1953) 50; MEIJER, Bot. News Bull. Sandakan 7 (1967) 88; MEIJDEN, Leiden Bot. Ser. 7 (1982) 110, f. 9b.

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 \pm prominent, secondary nerves and venation very distinct, sometimes even more distinct than beneath; glaucous-papillose 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 appressedly 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, appressedly hairy. *Sepals* sparsely hairy along the midrib to (nearly) glabrous outside, often some with rather distinct glandular spots; outer sepals 2.7–2.9 by 2.1–2.4 mm; inner sepals 3.1–3.3 by 3–3.2 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 connate over up to 2.5 mm; anthers c. 1.2–1.8 mm long, often minutely hairy all over. *Ovary* 1–2 mm stipitate, glabrous to densely appressedly whitish hairy; style thinly appressedly hairy in basal part, further glabrous; ovules 8–12. *Fruit* sometimes distinctly stipitate, globular, c. 1.5 cm diam., \pm shiny, brownish, glabrous or nearly so; pericarp thin; pedicel up to 10 mm.

Distr. *Malesia*: Borneo (Sarawak, E. Kalimantan).

Ecol. Mostly found in mountain forests, 500–1500 (–1800?) m.

Note. Very variable in the indumentum of the ovary.

44. *Xanthophyllum pseudoadenotus* MEIJDEN, Leiden Bot. Ser. 7 (1982) 110. — *X. stapfii* CHODAT, Bull. Herb. Boiss. 4 (1896) 260, *p.p.*, *pro specim.* HAVILAND 1620.

Small tree, up to 9 m, 12 cm dbh. Axillary buds oblong, 3–6 mm long, basally strongly thickened, obtuse, probably glabrous; secondary and adven-

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-papillose, 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 appressedly hairy (hairs 0.1 mm long). *Pedicel* 5–6 mm, minutely appressedly 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. 15 mm. *Stamens*: filaments c. 1.5 mm connate; anthers 2 mm long, ciliate along slits. *Ovary* minutely appressedly hairy (hairs 0.1–0.2 mm long); style glabrous in apical part; ovules 9–11. *Fruit* globular, c. 1.5 cm diam., minutely appressedly 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.

45. *Xanthophyllum pulchrum* KING, J. As. Soc. Beng. 59, ii (1890) 141; Ann. R. Bot. Gard. Calc. 5 (1896) 138, pl. 164; GAGNEP. in Desv. J. Bot. 21 (1908) 252; RIDLEY, Fl. Mal. Pen. 1 (1922) 146; BURK. & HEND. Gard. Bull. S. S. 3 (1925) 346; NG, Tree Fl. Mal. 1 (1972) 361, f. 3; CORNER, Gard. Bull. Sing. Suppl. 1 (1978) 27, 147, 211; MEIJDEN, Leiden Bot. Ser. 7 (1982) 111. — *X. stapfii* CHODAT, Bull. Herb. Boiss. 4 (1896) 260 (*excl.* HAVILAND 1620); in E. & P. Nat. Pfl. Fam. 3, 4 (1896) 345 ('*stapferi*'); MERR. En. Born. (1921) 326; MASAMUNE, En. Phan. Born. (1942) 381. — *X. densiflorum* CHODAT, Bull. Herb. Boiss. 4 (1896) 256; MERR. En. Born. (1921) 325; MASAMUNE, En. Phan. Born. (1942) 379.

Small shrub to small tree, up to 8 m. Twigs glabrous to minutely patently hairy. Axillary buds ovate, 1.8–3.5 (–5?) 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 cuculate-rounded, apex acutish, rarely rounded; above rarely bullate between midrib and secondary nerves, greyish green, midrib slightly sunken to flat, rarely

indistinctly prominent; beneath glaucous-papillose, 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. *Pedice*l 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*: anthers (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* globular, 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–)1–3.6 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. *Anthers* 1.3–1.8 mm long.

Distr. Malesia: Sumatra, Malay Peninsula (incl. Penang I.).

b. *ssp. stapfii* (CHODAT) MEIJDEN, Leiden Bot. Ser. 7 (1982) 112. — *X. stapfii* CHODAT. — *X. densiflorum* CHODAT.

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. *Anthers* (1.7–)2.1–2.5(–3.6) mm long.

Distr. Malesia: Borneo (Sarawak, Kalimantan).

46. *Xanthophyllum beccarianum* CHODAT, Bull. Herb. Boiss. 4 (1896) 257; Monogr. I (1891) t. 9, f. 3; MERR. En. Born. (1921) 325; MASAMUNE, En. Phan. Born. (1942) 379; MEIJER, Bot. News Bull. Sandakan 7 (1967) 87; MEIJDEN, Leiden Bot. Ser. 7 (1982) 112.

Tree, up to 12 m, 17 cm dbh. Twigs very densely patently hairy (hairs up to 1 mm). Axillary buds tri-

angular, 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-papillose, 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. *Pedice*l 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* patently hairy; style glabrous in apical half; ovules 13. *Fruit* (immature) apically pointed; pedicel *c.* 10–12 mm.

Distr. Malesia: Borneo (Sarawak).

47. *Xanthophyllum pedicellatum* MEIJDEN, Leiden Bot. Ser. 7 (1982) 113.

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 glaucous-papillose, 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. *Pedice*l (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* globular, *c.* 2.2 cm diam., light brownish, hairy; pericarp thin.

Distr. Malesia: Borneo (E. Sabah).

48. *Xanthophyllum purpureum* RIDLEY, Kew Bull. (1938) 114; MEIJDEN, Leiden Bot. Ser. 7 (1982) 114. — *X. molle* RIDLEY, Kew Bull. (1938) 114.

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.

Petiole c. 5 mm, densely hairy. *Leaf-blade* (6-)10-20 by (1.5-)2.5-9 cm, base cordate to rounded-attenuate, rarely cuneate, apex acutish; above green, midrib slightly sunken to flat; beneath glaucous-papillose, more or less densely hairy all over or only on nerves, secondary nerves (5 or) 6 or 7 pairs, not or only in apical part forming an intramarginal nerve; glands 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. *Pedicel* 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 rosa-violet, when dry orange-red, ciliate at base and apex, further glabrous, the longest one 11-12(-14?) mm. *Stamens*: filaments free or 0.4 mm connate; 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).

49. *Xanthophyllum reticulatum* CHODAT in Merr. Pl. Elm. Born. (1929) 136; MEIJDEN, Leiden Bot. Ser. 7 (1982) 114.

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 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).

50. *Xanthophyllum trichocladum* CHODAT in Merr. Pl. Elm. Born. (1929) 137; MASAMUNE, En. Phan. Born. (1942) 382; MEIJER, Bot. News Bull. Sandakan 7 (1967) 87; MEIJDEN, Leiden Bot. Ser. 7 (1982) 115.

Shrub or small tree, up to 12 m, 13 cm dbh. 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 to as long as the leaves or sometimes with one side-branch at very base; axes very densely brownish patently pubescent (most hairs 0.5-0.8 mm long); flowers often turned upside-down. *Pedicel* 5-7 mm, very densely brownish hairy (hairs up to 1 mm long); pedicels of flower buds at first curved downwards, of open flowers turned upwards and often half-twisted, rarely straight, pedicels of fruits curved downwards again. *Sepals* very densely brownish pubescent outside (hairs up to 1 mm long); outer sepals 3.2-3.8(-4) by 2.7-3.2 mm; inner sepals 3.2-4.2(-5.6) by 3.2-4.2 mm. *Petals* pink, the upper ones with a yellow spot, when dry dark reddish, the longest one 13(-16) mm; carina glabrous to sparsely appressedly hairy outside along central veins; other petals glabrous except for a few hairs at base, sometimes sparsely ciliate in basal part. *Stamens*: filaments free or 0.1-0.5(-1.5) mm connate; anthers 2.2-3 mm long, faintly hairy at base, ciliolate along slits. *Ovary* patently hairy; ovules 11-16. *Fruit* globular, c. 1.5 cm diam., densely hairy; pericarp rather thin; sepals subsistent in fruit.

Distr. Malesia: Borneo (Sarawak, E. Sabah, Samarinda).

51. *Xanthophyllum erythrostachyum* GAGNEP. in Desv. J. Bot. 21 (1908) 250; Bull. Soc. Bot. Fr. 56 (1909) 36; MEIJDEN, Leiden Bot. Ser. 7 (1982) 115, excl. STEENIS 10075. — *X. forbesii* BAKER, J. Bot. 62 (1924) Suppl. 7, nom. superfl.

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 minutely hairy near base, near apex very sparsely appressedly 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 (Lamongan Distr.), one collection.

52. *Xanthophyllum laeve* MEIJDEN, Bot. J. Linn. Soc. 67 (1973) 118 ('*laevis*'); Leiden Bot. Ser. 7 (1982) 116.

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 appressedly 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 appressedly hairy; ovules 8. *Fruit* unknown.

Distr. *Malesia*: NE. Sumatra (Sibolangit), 2 collections.

53. *Xanthophyllum retinerve* MEIJDEN, Leiden Bot. Ser. 7 (1982) 117.

Tree, up to 12 m, 20 cm dbh. Twigs sparsely shortly appressedly hairy, glabrescent; axillary region shortly densely appressedly hairy. Axillary buds mostly 3, inconspicuous, shortly densely appressedly 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 c. 6.5 mm; carina appressedly hairy outside; other petals sparsely hairy apically. *Stamens*: anthers 0.3–0.4 mm long. *Ovary* (sub)sessile, faintly ribbed, densely shortly appressedly hairy; ovules 4. *Fruit* globular, up to 2.2 cm diam., smooth, rather dull, brown, sparsely appressedly hairy; pericarp c. 4 mm thick, rather hard; pedicel up to 4 mm.

Distr. *Malesia*: Malay Peninsula (Perak; Trengganu; Fraser's Hill).

54. *Xanthophyllum eurhynchum* MIQ. Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 277; KING, J. As. Soc. Beng. 59, ii (1890) 137; GAGNEP. in Desv. J. Bot. 21 (1908) 252; BAKER, J. Bot. 62 (1924) Suppl. 7; MEIJDEN, Leiden Bot. Ser. 7 (1982) 117, f. 3A-a,b. — *X. maingayi* HOOK. f. ex A.W. BENNETT, Fl. Br. India 1 (1874) 210; KING, Mat. Fl. Pen. (1890) 136; GAGNEP. in Desv. J. Bot. 21 (1908) 252; BURK. Gard. Bull. S. S. 3 (1923) 35; WYATT-SMITH, Mal. For. Rec. 17 (1952) 362; BALAN MENON, *ibid.* 19 (1956) 34; NG, Tree Fl. Mal. 1 (1972) 360, f. 3; CORNER, Gard. Bull. Sing. Suppl. 1 (1978) 146, 147, 211. — *Banisterodes maingayi* (A.W. BENNETT) O. K. Rev. Gen. Pl. 1 (1891) 46, *nom. illeg.* — *X. verrucosum* CHODAT, Bull. Herb. Boiss. 4 (1896) 263; RIDLEY, Fl. Mal. Pen. 1 (1922) 147; HEND. Gard. Bull. S. S. 4 (1928) 222; WATSON, Mal. For. Rec. 5 (1928) 249; WYATT-SMITH, *ibid.* 17 (1952) 364. — *X. palembanicum* (*non* MIQ.) KING, J. As. Soc. Beng. 59, ii (1890) 137; GAGNEP. in Desv. J. Bot. 21 (1908) 251; RIDLEY, Fl. Mal. Pen. 1 (1922) 149; BURK. & HEND. Gard. Bull. S. S. 3 (1925) 346; WATSON, Mal. For. Rec. 5 (1928) 249; CRAIB, Fl. Siam. En. 1 (1931) 105; BURK. Dict. (1935) 2269.

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 patently 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 appressedly 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 appressedly hairy with hairs of different length; ovules 4. *Fruit* globular 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 appressedly hairy.

Distr. S. Thailand; *Malesia*: Malay Peninsula (also Penang and Singapore), Sumatra.

KEY TO THE SUBSPECIES

1. Fruit with distinct warts arranged in longitudinal rows a. *ssp. eurhynchum*
1. Fruit more or less smooth, transversely wrinkled or finely rugose or irregularly grooved b. *ssp. maingayi*

a. *ssp. eurhynchum* MEIJDEN, Leiden Bot. Ser. 7 (1982) 119, f. 3A-b. — *X. eurhynchum* MIQ. — *X. verrucosum* CHODAT.

Fruit globular, 1.5-1.8 cm diam., strongly warty, densely appressedly hairy between the warts.

Distr. S. Thailand; in *Malesia*: Malay Peninsula (incl. Penang I.), Sumatra.

b. *ssp. maingayi* (HOOK.f. ex A.W.BENNETT) MEIJDEN, Leiden Bot. Ser. 7 (1982) 119, f. 3A-a. — *X. maingayi* HOOK.f. ex A.W.BENNETT, Fl. Br. Ind. 1 (1874) 210. — *X. palembanicum* (non MIQ.) KING.

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.

Distr. S. Thailand; in *Malesia*: Malay Peninsula (incl. Singapore).

55. *Xanthophyllum wrayi* KING, J. As. Soc. Beng. 59, ii (1890) 138; Ann. R. Bot. Gard. Calc. 5 (1896) 138, pl. 164; GAGNEP. in DESV. J. Bot. 21 (1908) 251; RIDLEY, Fl. Mal. Pen. 1 (1922) 148; BURK. & HEND. Gard. Bull. S. S. 3 (1925) 346; HEND. *ibid.* 4 (1928) 222; WATSON, Mal. For. Rec. 5 (1928) 249; BURK.

Dict. (1935) 2268; NG, Tree Fl. Mal. 1 (1972) 363, f. 5; CORNER, Gard. Bull. Sing. Suppl. 1 (1978) 147, 211; MEIJDEN, Leiden Bot. Ser. 7 (1982) 119, f. 3A-c. — *X. puberulum* RIDLEY, J. Str. Br. R. As. Soc. n. 73 (1916) 139; HEND. Gard. Bull. S. S. 4 (1928) 222.

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. *Petiole* (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 cordate; above often slightly bullate 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 \pm 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 mm, densely minutely patently hairy. *Sepals*: outer sepals 2.1-3 by 1.5-2.1 mm, sometimes with small glands; inner sepals 2.8-4 by 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 triadelphous, 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 globular, 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.

Distr. Peninsular Thailand; in *Malesia*: Malay Peninsula (incl. Penang I.).

56. *Xanthophyllum venosum* KING, J. As. Soc. Beng. 59, ii (1890) 139; RIDLEY, Fl. Mal. Pen. 1 (1922) 222; MEIJDEN, Leiden Bot. Ser. 7 (1982) 120, f. 3A-d.

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. *Petiole* (12-)15-21(-27) mm, glabrous to sparsely minutely hairy, not transversely

wrinkled, 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. *Pedice* 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 sparsely 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.

57. *Xanthophyllum malayanum* MEIJDEN, Bot. J. Linn. Soc. 67 (1973) 118; NG, Tree Fl. Mal. 1 (1972) 365; CORNER, Gard. Bull. Sing. Suppl. 1 (1978) 146; MEIJDEN, Leiden Bot. Ser. 7 (1982) 121.

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 cuspidate; 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. *Pedice* 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, exerted 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 exerted.

58. *Xanthophyllum novoguineense* MEIJDEN, Leiden Bot. Ser. 7 (1982) 122.

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. *Pedice* 2.5 mm, grooved, rather densely minutely more or less patently 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.

Distr. *Malesia*: New Guinea (Sorong in W, Sepik in Central), 4 collections.

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.

59. *Xanthophyllum ngii* MEIJDEN, Bot. J. Linn. Soc. 67 (1973) 119; NG, Tree Fl. Mal. 1 (1972) 365, f. 5; MEIJDEN, Leiden Bot. Ser. 7 (1982) 122, f. 3B-a.

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 acuminate; 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 halfway 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 shortly hairy; lower bracts (sub)opposite. *Pedice*l 3–4.5 mm, very densely more or less appressedly shortly hairy. *Sepals* shortly rather sparsely appressedly hairy outside, (sub)glabrous inside; outer sepals 2.2–2.9 by 2–2.8 mm; inner sepals 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, shortly appressedly 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* 1 (or '1–more' according to Ng, l.c.), up to 2 cm diam.

Distr. Malesia: Southern half of Sumatra, Malay Peninsula.

60. *Xanthophyllum lanceatum* (Miq.) J.J. SMITH, Ic. Bogor. 4 (1912) 109, t. 334; GORTER, Indische Mercur 34 (1911) 410 ('*lancoelatum*?'); Tropenfl. 16 (1912) 50; HEGI, Fl. Mitteleur. 5-1 (1925) 87 ('*lancoelatum*?'); HEYNE, Nutt. Pl. (1927) 901; BURK. Dict. (1935) 2268; MEIJDEN, Leiden Bot. Ser. 7 (1982) 124, f. 10A. — *Skaphium lanceatum* Miq. Fl. Ind. Bat., Suppl. (1861) 357; KURZ, J. As. Soc. Beng. 40, ii (1871) 46; SCHEFFER, Nat. Tijd. Ned. Ind. 34 (1874) 105. — *X. glaucum* WALL. [Cat. (1831) 4199] ex HASSK. Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 193; KURZ, J. As. Soc. Beng. 42, ii (1873) 80; A.W. BENNETT, Fl. Br. India 1 (1874) 209; KURZ, For. Fl. Br. Burma 1 (1877) 81; KING, Mat. Fl. Mal. Pen. (1890) 136; GAGE, Rec. Bot. Surv. India 3 (1904) 24; WILLIAMS, Bull. Herb. Boiss. II, 5 (1905) 219; BRANDIS, Indian Trees (1906) 44; GAGNEP. in Desv. J. Bot. 21 (1908) 251; Fl. Gén. I.-C. 1 (1909) 245; RIDLEY, J. Str. Br. R. As. Soc. n. 59 (1911) 73; *ibid.* n. 73 (1916) 140; Fl. Mal. Pen. 1 (1922) 147; WATSON, Mal. For. Rec. 5 (1928) 249; CREVOST & PETELOT, Bull. Econ. Indochine (1929) 138; CRAIB, Fl. Siam. Ed. 1 (1931) 105; BURK. Dict. (1935) 2268; GAGNEP. Fl. Gén. I.-C. Suppl. 1 (1939) 219; HEND. J. Mal. Br. R. As. Soc. 17 (1939) 36; STADLEMAN, For. Southeast Asia

(1966) 186; Ng, Tree Fl. Mal. 1 (1972) 357, f. 1. — *Banisterodes glaucum* (WALL. ex HASSK.) O. K. Rev. Gen. Pl. 1 (1891) 46, *nom. illeg.* — *X. microcarpum* CHODAT, Bull. Herb. Boiss. 4 (1896) 263.

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 sparsely 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 acuminate; 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. *Pedice*l 2–3.5 mm, ± densely patently shortly hairy. *Sepals*: outer sepals 1.7–2.2 by 1.5–2 mm; inner sepals 2.2–2.7 by 2–2.9 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 greyish 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 Is.).

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.

61. *Xanthophyllum lateriflorum* MIQ. Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 318; MEIJDEN, Leiden Bot. Ser. 7 (1982) 129.

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), \pm 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-papillose, 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. *Infructescences* shorter than the leaves, unbranched; axes minutely hairy. *Fruit* (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 Distr.), 5 collections; insufficiently known species.

62. *Xanthophyllum virens* ROXB. Pl. Corom. 3 (1820) 81, t. 284, f. 1; SPRENGEL, Syst. Veg. 2 (1825) 219 ('*virescens*'); WALL. Cat. (1831) 4197; ROXB. Fl. Ind. ed. Carey 2 (1832) 221; DIETR. Syn. Pl. 2 (1840) 1277 ('*virescens*'); WIGHT, Ill. Ind. Bot. 1 (1840) 49, 50, t. 23, f. 10 (*sub X. flavescens, sphalm.*); DRURY, Handb. Indian Fl. 1 (1864) 56; BEDD. Fl. Sylv. Anal. Gen. 3 (1869) xix, pl. III, f. 2, 1–3; KURZ, J. As. Soc. Beng. 42, ii (1873) 79, 80; Prelim. Rep. For. Pegu (1875) 26; For. Fl. Br. Burma 1 (1877) 81; GAGNEP. in Desv. J. Bot. 21 (1908) 251; CRAIB, Fl. Siam. En. 1 (1931) 107; GAGNEP. Fl. Gén. 1.-C. Suppl. 1 (1939) 219; PURKAYASTHA in Chowdhury & Ghosh, Indian Woods 1 (1958) 60; MEIJDEN, Leiden Bot. Ser. 7 (1982) 130, f. 10A. — *X. flavescens* var. *virens* (ROXB.) A.W. BENNETT, Fl. Br. India 1 (1874) 209; CRAIB, Bull. Misc. Inf. Kew (1911) 14. — *X. affine* (*non* MIQ.) RIDLEY, J. Fed. Mal. St. Mus. 10 (1920) 82.

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 papillose, 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 patently 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; pedicel 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*

MEIJDEN, Leiden Bot. Ser. 7 (1982) 133.

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, \pm 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 exerted.



Fig. 22. *Xanthophyllum ramiflorum* MEIJDEN. *a-b*. Habit, $\times 0.7$; *c*. base of leaf with glands, $\times 2$; *d*. part of twig with axillary bud; *e*. flower; *f*. flower, longitudinal section, gynoceium removed; *g*. lower petal; *h*. gynoceium; all $\times 4$; *i*. ovary, longitudinal section, $\times 8$ (S 16051).

63. *Xanthophyllum ramiflorum* MEIJDEN, Blumea 18 (1970) 392; Leiden Bot. Ser. 7 (1982) 133, f. 16. — *X. spec.*: ANDERSON, Gard. Bull. Sing. 20 (1963) 152; WHITM. Trop. Rain For. Far East (1975) 147. — Fig. 22.

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-papillose, 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 patently 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 connate over c. 1.5–2 mm, densely shortly patently 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, ± globular, up to 1.2 cm diam., pustulate, 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*

MEIJDEN, Leiden Bot. Ser. 7 (1982) 135.

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, connate parts c. 3–4 mm high. *Ovary* usually black, glabrous; style glabrous or hairy; stigma peltate; ovules 8–14. *Fruit* indehiscent, 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, nerved, green, plumule undifferentiated, radicle exerted.

64. *Xanthophyllum ellipticum* KORTH. ex MIQ. Ann. Mus. Bot. Lugd.-Bat. 1 (1864) 276; A.W. BENNETT, Fl. Br. India 1 (1874) 211; KING, Mat. Fl. Mal. Pen. (1890) 140; CHODAT in E. & P. Nat. Pfl. Fam. 3, 4 (1896) 344; RIDLEY, J. Str. Br. R. As. Soc. n. 33 (1900) 45; GAGNEP. in Desv. J. Bot. 21 (1908) 253; MERR. En. Born. (1921) 326; CHODAT in Merr. Pl. Elm. Born. (1929) 133, *excl. var.*; FISCHER, Kew Bull. (1933) 487; KEITH, N. Born. For. Rec. 2 (1938) 225; MASAMUNE, En. Phan. Born. (1942) 379; MEIJER, Bot. News Bull. Sandakan 7 (1967) 88; FOX, Sabah For. Rec. 7 (1970) 65; NG, Fed. Mus. J. n.s. 13 (1971) 137; Tree Fl. Mal. 1 (1972) 357, f. 3; CORNER, Gard. Bull. Sing. Suppl. 1 (1978) 146, 211; MEIJDEN, Leiden Bot. Ser. 7 (1982) 135, f. 3A–p, 17. — *Banisterodes ellipticum* (KORTH. ex MIQ.) O. K. Rev. Gen. Pl. 1 (1891) 46, *nom. illeg.* — *X. citrifolium* CHODAT, Bull. Herb. Boiss. 4 (1896) 255;

in E. & P. Nat. Pfl. Fam. 3, 4 (1896) 345; MASAMUNE, En. Phan. Born. (1942) 379; ANDERSON, Gard. Bull. Sing. 20 (1963) 152. — *X. kingii* CHODAT, Bull. Herb. Boiss. 4 (1896) 255; RIDLEY, Fl. Mal. Pen. 1 (1922) 143; WATSON, Mal. For. Rec. 5 (1928) 249; CRAIB, Fl. Siam. En. 1 (1931) 106; BURK. Dict. (1935) 2268; WYATT-SMITH, Mal. For. Rec. 17 (1952) 80, 361; *ibid.* 23² (1963) iii, 12, 57. — Fig. 23.

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* KÖRTH. ex MIQ. a. Habit, $\times 0.5$; b. flower and inflorescence axis; c. flower, longitudinal section, gynoecium removed; d. carina with two stamens enclosed; e. gynoecium; all $\times 3$; f. ovary, longitudinal section, $\times 6$; g. part of twig with young inflorescence, $\times 4.5$ (S 25564).

(4-)6-10. *Inflorescences* often several together on the secondarily thickened nodes, shorter than the leaves. *Pedicel* c. 3-4 mm, rather sparsely to rather densely minutely (woolly-)hairy. *Sepals* mostly nigrescent, glabrous to minutely hairy inside; outer sepals 3-3.8 by 1.8-2.2(-2.7) mm; inner sepals 3.8-4.8(-6) by 2.3-3.2(-4.5) mm. *Petals* white to light yellow, when dry light brown to dark orange, inside minutely hairy only above base; carina 6-7(-8) mm long; other petals 8-9 mm long, lateral petals 3-4 mm wide, upper petals 1.5-2 mm wide. *Stamens*: filaments glabrous; anthers 0.4-0.6 mm long, shortly hairy at base, ciliate along slits, often cohering around the stigma. *Ovary* subsessile; style glabrous; ovules 8-14. *Fruit* sessile, globular, 1.5-2.2 cm diam., smooth, dark reddish, somewhat shiny; pericarp thin, brittle; pedicel 3-6(-8) mm long. *Seed* often (sub)apical.

Distr. S. Thailand; in *Malesia*: Malay Peninsula (incl. Singapore, Penang I.), Sumatra (incl. Simalur, Nias; Riouw: Karimun Is.), Borneo.

65. *Xanthophyllum celebicum* MEIJDEN, Leiden Bot. Ser. 7 (1982) 137.

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* triadelphous; filaments densely rather shortly hairy; anthers 0.6 mm long, sparsely hairy at base, ciliate along slits. *Ovary* shortly stipitate, slightly pustulate; style rather densely shortly more or less patently (\pm 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.

66. *Xanthophyllum montanum* MEIJDEN, Leiden Bot. Ser. 7 (1982) 137, f. 10B.

Tree, up to 30 m, 60 cm dbh. Nodal glands elliptic, 0.3-0.6 mm long. *Petiole* 3.5-5 mm, indistinctly transversely wrinkled. *Leaf-blade* (4-)6-9 by 1-2.5(-3.5) cm, apex gradually acuminate; above brownish green, midrib sunken; beneath concolor-

ous, 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 Sumatran 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.

67. *Xanthophyllum contractum* MEIJDEN, Leiden Bot. Ser. 7 (1982) 138.

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 pustulate, 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*

MEIJDEN, Leiden Bot. Ser. 7 (1982) 139.

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* nigrescent. *Petals* (sub)equal, spatulate-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, nerved, plumule undifferentiated, radicle exserted.

69. *Xanthophyllum suberosum* C.T. WHITE, J. Arn. Arb. 10 (1929) 229; MEIJDEN, Leiden Bot. Ser. 7 (1982) 141, f. 18. — Fig. 24.

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, glands 10-14, sometimes more, mostly \pm 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 sepals 3.5-5.5 by 3.5-4 mm; inner sepals 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 very 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.

Distr. *Malesia*: New Guinea (incl. Meos Num, Biak & Japen Is.).

70. *Xanthophyllum amoenum* CHODAT, Bull. Herb. Boiss. 4 (1896) 259; in E. & P. Nat. Pfl. Fam. 3, 4

(1896) 344; GAGNEP. in Desv. J. Bot. 21 (1908) 252; MASAMUNE, En. Phan. Born. (1942) 379; WYATT-SMITH, Mal. For. Rec. 17 (1952) 80, 363; *ibid.* 23² (1963) f. 8; ANDERSON, Gard. Bull. Sing. 20 (1963) 152; MEIJER, Bot. News Bull. Sandakan 7 (1967) 87; NG, Tree Fl. Mal. 1 (1972) 356, f. 1; MEIJDEN, Leiden Bot. Ser. 7 (1982) 141, f. 3A-n. — *X. stipitatum* var. *nitidum* CHODAT in Merr. Pl. Elm. Born. (1929) 137; MASAMUNE, En. Phan. Born. (1942) 381. — *X. stipitatum* var. *pachyphyllum* CHODAT in Merr. Pl. Elm. Born. (1929) 137; MASAMUNE, En. Phan. Born. (1942) 381.

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; glands 6-10(-20), scattered, 0.1-0.4(-0.5) mm diam. *Pedicel* 8-15 mm, rather densely minutely lanate. *Sepals*: outer sepals 2.5-3 by 1.8-2.2 mm, minutely rather densely hairy at both sides; inner sepals 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

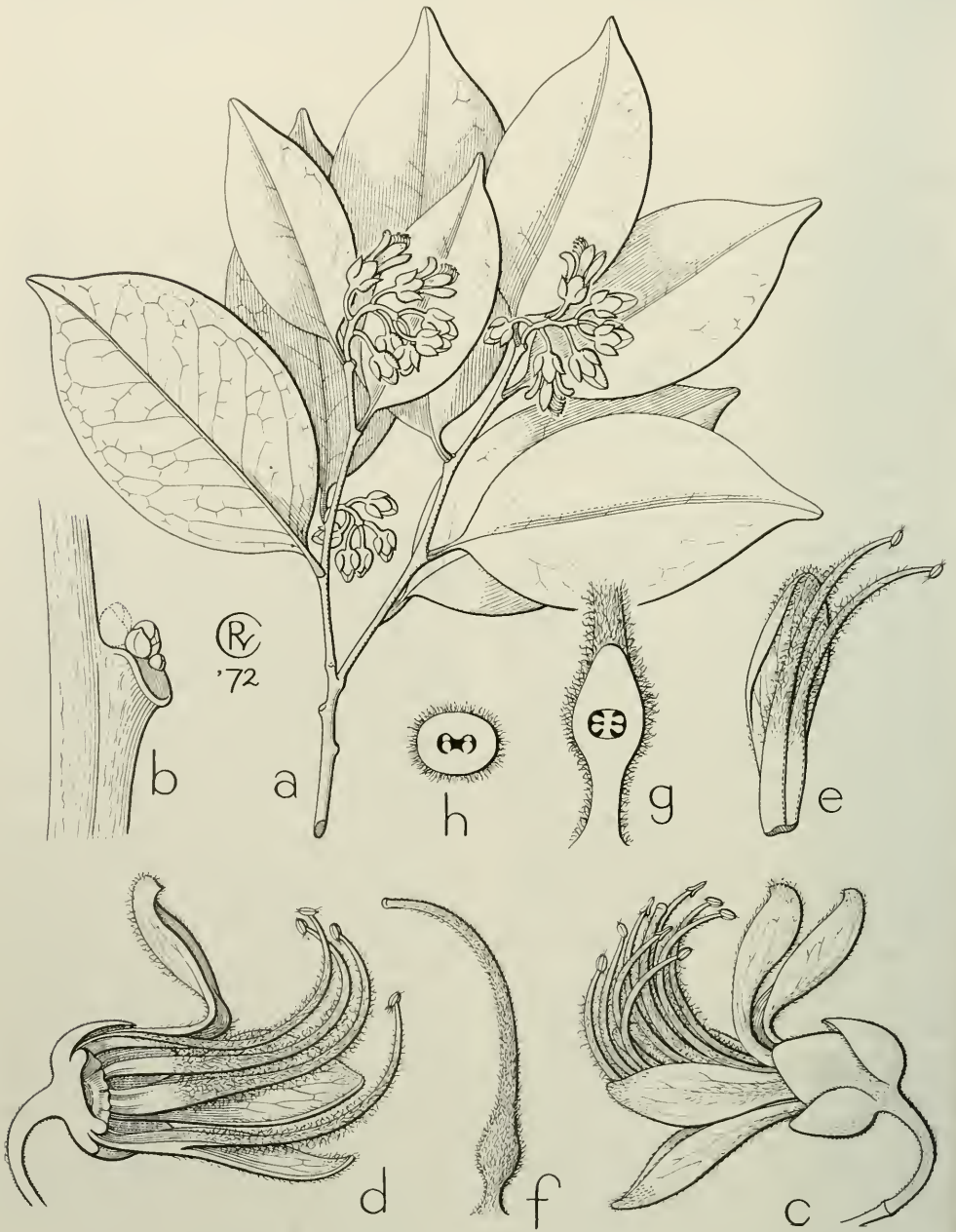


Fig. 24. *Xanthophyllum suberosum* C.T. WHITE. a. Habit, $\times 0.7$; b. part of twig with axillary buds; c. flower; d. flower, longitudinal section, gynoecium removed; e. lower petal; f. gynoecium, longitudinal and cross section, $\times 4$ (VAN ROYEN 3201).

diam., sometimes bluish waxy, hairy or apparently glabrous; pericarp 1–10 cm thick. *Seeds* 6 or more.

Distr. Malesia: Malay Peninsula, Central Sumatra, Borneo.

71. *Xanthophyllum stipitatum* A.W.BENNETT, Fl. Br. India 1 (1874) 210; KING, Mat. Fl. Mal. Pen. (1890) 140; CHODAT in E. & P. Nat. Pfl. Fam. 3, 4 (1896) 345; RIDLEY, Fl. Mal. Pen. 1 (1922) 145; HEND. Gard. Bull. S. S. 4 (1928) 222; WATSON, Mal. For. Rec. 5 (1928) 249; CHODAT in Merr. Pl. Elm. Born. (1929) 137, *incl. var. borneense* CHODAT; BURK. Dict. (1935) 2268; WYATT-SMITH, Mal. For. Rec. 17 (1952) 81, 361; BALAN MENON, *ibid.* 19 (1956) 34; MEIJER, Bot. News Bull. Sandakan 7 (1967) 87; NG, Tree Fl. Mal. 1 (1972) 363, f. 5; CORNER, Gard. Bull. Sing. Suppl. 1 (1978) 147; MEIJDEN, Leiden Bot. Ser. 7 (1982) 142. — *Banisterodes stipitatum* (A.W.BENNETT) O. K. Rev. Gen. Pl. 1 (1891) 46. — *X. amoenum* (non CHODAT) KEITH, N. Born. For. Rec. 2 (1938) 225.

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 intramarginal 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. *Pedice*l 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 cm thick; pedicel up to c. 1.5 mm. *Seeds* c. 4–12.

Distr. Malesia: Malay Peninsula, 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.

Distr. Malesia: Malay Peninsula (incl. Singapore), Central Sumatra, Borneo.

b. var. glabrum MEIJDEN, Leiden Bot. Ser. 7 (1982) 144.

Stamens: filaments forming a 'tube' by their intertwined hairs. *Ovary* glabrous or with a few appressed hairs; style thinly hairy basally.

Distr. Malesia: E. Borneo (Kalimantan: Long Petah).

V. Subgenus *Brunophyllum*

MEIJDEN, Bot. J. Linn. Soc. 67 (1973) 117; Leiden Bot. Ser. 7 (1982) 144.

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*), plumule usually differentiated into a number of small scales, radicle fully enveloped by the cotyledons or just exerted at base.



Fig. 25. Inflorescence of *Xanthophyllum brevipes* MEIJDEN, collected in Arboretum, Semengoh For. Res., Sarawak (S 26838) (Photogr. P.SIE, 1971).

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* more than 10, flattened-ovoid, c. 1 cm long; albumen

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, transversally flattened, cordate at base; cotyledons thickened; plumule not differentiated; radicle slightly exerted.

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 babylonica* because of its pendant twigs.

73. *Xanthophyllum obscurum* A.W.BENNETT, Fl. Br. India 1 (1874) 211; KING, Mat. Fl. Mal. Pen. (1890) 141; RIDLEY, J. Str. Br. R. As. Soc. n. 33 (1900) 45; Fl. Mal. Pen. 1 (1922) 144; HEYNE, Nutt. Pl. (1927) 902; HEND. Gard. Bull. S. S. 4 (1928) 222; WATSON, Mal. For. Rec. 5 (1928) 249; WYATT-SMITH, Mal. For. Rec. 17 (1952) 81, 363; BALAN MENON, *ibid.* 19 (1956) 34; WYATT-SMITH, *ibid.* 23² (1963) f. 8; NG, Tree Fl. Mal. 1 (1972) 361, f. 3; Mal. For. 38 (1975) 89, f. 8.1 F–J, 8.3, 8.4; CORNER, Gard. Bull. Sing. Suppl. 1 (1978) 147, 211; MEIJDEN, Leiden Bot. Ser. 7 (1982) 145, f. 3B-b, 10B. — *X. insigne* A.W.BENNETT, Fl. Br. India 1 (1874) 211; KING, Mat. Fl. Mal. Pen. (1890) 144. — *X. scortechinii* KING, J. As. Soc. Beng. 59, ii (1890) 140; Ann. R. Bot. Gard. Calc. 5 (1896) 138, pl. 163; GAGNEP. in Desv. J. Bot. 21 (1908) 253; RIDLEY, Fl. Mal. Pen. 1 (1922) 143; HEND. Gard. Bull. S. S. 4

(1928) 222; WATSON, Mal. For. Rec. 5 (1928) 249; BURK. Dict. (1935) 2268; WYATT-SMITH, Mal. For. Rec. 17 (1952) 81, 361; BALAN MENON, *ibid.* 19 (1956) 34; WYATT-SMITH, *ibid.* 23² (1963) f. 5; NG, Tree Fl. Mal. 1 (1972) 363, f. 3. — *Banisterodes insignis* (A.W.BENNETT) O. K. Rev. Gen. 1 (1891) 46, *nom. illeg.* — *Banisterodes obscurum* (A.W.BENNETT) O. K. *l.c.*, *nom. illeg.*

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 sparsely hairy. *Sepals* black; outer sepals 2.8–5.5 by 2.8–6 mm; inner sepals 4–7.5 by 3.5–7 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* globular, 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 visible 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. Southernmost Thailand; in *Malesia*: Malay Peninsula (incl. Singapore & Penang I.), Sumatra, Borneo.

74. *Xanthophyllum papuanum* WHITM. *ex* MEIJDEN, Bot. J. Linn. Soc. 67 (1973) 119; WHITM. Guide For. Br. Sol. Is. (1966) 92, 151; PAIJMANS, Land Research Ser. 29 (1971) 107; VERSTEEGH, Meded. Landb. hogesch. Wageningen 71-19 (1971) 63; EDDOWES, Commerc. Timbers P.N.G. (1977) 46 ('Boxwood'); MEIJDEN, Leiden Bot. Ser. 7 (1982) 147, f. 3B-c, 19. — *X. affine* (*non* MIQ.) K.SCH. & HOLLR. Fl. Kaiser Wilhelm Land (1889) 68; K.SCH. & LAUT. Fl. Schutzgeb. Südsee (1901) 388. — **Fig. 26.**

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 darker 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 without vessel-like elements; top of radicle hardly exerted at base.

Distr. Solomon Islands; in *Malesia*: New Guinea (incl. Ferguson I. in E, and Salawati, Numfoor, Japen & Mios Waar Is. in W), Moluccas (Ceram), Central Celebes (Palopo).

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, $\times 0.7$; *b.* flower and part of inflorescence axis; *c.* flower, longitudinal section, gynoecium removed; *d.* lower petal with three stamens; *e.* gynoecium; all $\times 4$; *f.* ovary, longitudinal section, $\times 8$ (HOOGLAND 5072).

75. *Xanthophyllum ecarinatum* CHODAT, Bull. Herb. Boiss. 4 (1896) 254; in E. & P. Nat. Pfl. Fam. 3, 4 (1896) 344; MERR. En. Born. (1921) 325; MASAMUNE, En. Phan. Born. (1942) 379; MEIJER, Bot. News Bull. Sandakan 7 (1967) 87; MEIJDEN, Leiden Bot. Ser. 7 (1982) 148, f. 3B-d. — *X. kalimantanum* MEIJDEN, Bot. J. Linn. Soc. 67 (1973) 118.

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 sepals (3–)4–5.5 by (1.5–)2.5–3.5 mm; inner sepals (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.

Distr. Malesia: Borneo (Sarawak, Sabah, Kalimantan).

76. *Xanthophyllum chartaceum* MEIJDEN, Bot. J. Linn. Soc. 67 (1973) 118; Leiden Bot. Ser. 7 (1982) 149. — *X. spec. E*, NG, Tree Fl. Mal. 1 (1972) 366.

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.

Distr. Malesia: Malay Peninsula, Central Sumatra (Indragiri).

Note. Because of its thin nigrescent 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 hebecarpum CHODAT, Bull. Herb. Boiss. 4 (1896) 263; RIDLEY, J. Str. Br. R. As. Soc. n. 73 (1916) 139; Fl. Mal. Pen. 1 (1922) 149, was identified by SYMINGTON, Kew Bull. (1937) 318 as *Ryparosa kunstleri* KING (*Flacourtiaceae*); SLEUMER, Fl. Males. 1, 5 (1954) 48.

Xanthophyllum subglobosum ELMER, Leaf. Philip. Bot. 5 (1913) 1676, *incl. var. longifolium* ELMER, was identified by MERRILL, En. Philip. 2 (1923) 485 as *Siphonodon celastrineus* GRIFFITH (*Celastraceae*); DING HOU, Fl. Males. 1, 6 (1964) 395.

Excluded

Semeiocardium ZOLL. Nat. Tijd. Ned. Ind. 17 (1858) 245, the type of a monospecific genus, was by ZOLLINGER assigned to *Balsaminaceae*, but later referred to *Polygalaceae* by HASSKARL (in Miq. Ann. Mus. Bot. Lugd.-Bat. 1, 1863, 142). Still later CHODAT reduced it to *Polygala triphylla* (MONOGR. 1, 1891, 41). BACKER (Gard. Bull. S. S. 9, 1938, 70) showed that ZOLLINGER was correct.

CRUCIFERAE (B. Jonsell, Stockholm)

Herbs, sometimes subshrubs. *Leaves* spirally arranged, basal ones often in a rosette, exstipulate, 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, spatulate to clawed, imbricate or contorted. *Stamens* 6, tetradynamous (rarely 4 or 2), episepalous usually free; anthers usually 2-theous 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 siliqua 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 buckeri* 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.

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*.

References: CARLQUIST, *Aliso* 7 (1971) 365–384; INAMDAR & RAO, *Feddes Rep.* 94 (1983) 183–190; IVERSEN, BAGGERUD & BEISVAAG, *Z. Pflanzenphysiol.* 94 (1979) 143–154; KOWAL & CUTLER, *Kew Bull.* 30 (1975) 503–507; METCALFE & CHALK, *Anatomy of the Dicotyledons* 1 (1950) 79–87; PANT & KIDWAI, *Ann. Bot. (N.S.)* 31 (1967) 513–521; RAO & INAMDAR, *Bot. Mag. Tokyo* 96 (1983) 15–28.

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 tritenuate 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).

References: CHIGURIAEVA, *Pollen morphology of Cruciferae*, in Kuprijanova, *Pollen and spores morphology of the recent plants. Proc. III Int. Palyn. Conf.* (1973) 93–98; ERDTMAN, *Pollen morphology and plant taxonomy, Angiosperms* (1952) 133–134; ERDTMAN, PRAGLOWSKI & NILSSON, *An introduction to a Scandinavian Pollen Flora II* (1963). — R.W.J.M. VAN DER HAM.

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 unliked 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.

References: HEGNAUER, *Chemotaxonomie der Pflanzen* 3 (1964) 586–607; VAUGHAN *c.s.* (ed.), *The biology and chemistry of the Cruciferae* (1976) 191–330.

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 *Stenopetaleae* and *Heliophilleae*, 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.

References: FEDOROV (ed.), *Chromosome numbers of flowering plants* (1969); MANTON, *Ann. Bot. n.s.* 1 (1932) 438–462.

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 *Lepidieae* (*Lepidium* and *Capsella*) and *Arabideae* (*Cardamine* and *Rorippa*).

References: HEDGE in Vaughan *c.s.* (ed.), *The biology and chemistry of the Cruciferae* (1976) 1–45; SCHULZ, *Cruciferae*, in Engler & Prantl (ed.), *Die natürlichen Pflanzenfamilien* ed. 2, 17b (1936) 227–658.

Cultivated species. The following species have been reported as cultivated only, and are not treated separately: *Aromoracia rusticana* G.M. & SCHERB. See BACKER & BAKH. *f. Fl. Java* 1 (1963) 188. — *Brassica chinensis* L. See HEYNE, *Nutt. Pl. Ned. Indië* (1927) 677; OCHSE & BAKH. *Indische Groenten* (1931) 162; STONE, *Fed. Mus. J.* 26 (1981) 81. — *B. napus* L. See HEYNE, *Nutt. Pl. Ned. Indië* (1927) 677; OCHSE & BAKH. *Indische Groenten* (1931) 168. — *B. oleracea* L. See KOORD. *Meded. Lands Plantentuin* 19 (1898) 341; *Exk. Fl. Java* 2 (1912) 284; HOCHR. *Candollea* 2 (1925) 367; HEYNE, *Nutt. Pl. Ned. Indië* (1927) 677; OCHSE & BAKH. *Indische Groenten* (1931) 169; DOCTERS VAN LEEUWEN, *Verh. Kon. Akad. Wet. Amsterdam* sect. II, 31 (1933) 166; BACKER & BAKH. *f. Fl. Java* 1 (1963) 188. — *B. rapa* L. (*B. campestris* L.). See KOORD. *Exk. Fl. Java* 2 (1912) 284; HOCHR. *Candollea* 2 (1925) 367; HEYNE, *Nutt. Pl. Ned. Indië* (1927) 678; OCHSE & BAKH. *Indische Groenten* (1931) 174; BACKER & BAKH. *f. Fl. Java* 1 (1963) 188; GILLI, *Ann. Naturhist. Mus. Wien* 83 (1980) 429. — *B. rugosa* PRAIN. See KOORD. *Exk. Fl. Java* 2 (1912) 286; HEYNE, *Nutt. Pl. Ned. Indië* (1927) 678. — *Cochlearia officinalis* L. See BACKER, *Schoolfl. Java* (1911) 57; KOORD. *Exk. Fl. Java* 2 (1912) 283. — *Iberis amara* L. See BACKER & BAKH. *f. Fl. Java* 1 (1963) 188. — *I. umbellata* L. See BACKER & BAKH. *f. Fl. Java* 1 (1963) 188. — *Lobularia*



Fig. 1. *Brassica juncea* (L.) CZERN. 1. Habit, $\times 0.6$; 2. flower, $\times 6$; 3. petal, $\times 6$; 4. silique, $\times 2$; 5. seed, $\times 12$ (1-3 DRUMMOND & HEMSLEY 3360; 4, 5 CONRADS 230; drawn after African material). Courtesy Fl. Trop. E. Afr., Crucif. (1982) 4, f. 1.

maritima (L.) DESV. See BACKER & BAKH.f. Fl. Java 1 (1963) 192. — *Matthiola incana* (L.) R.BR. See BACKER & BAKH.f. Fl. Java 1 (1963) 192. — *Sinapis alba* L. See KOORD. Meded. Lands Plantentuin 19 (1898) 342; Exk. Fl. Java 2 (1912) 284.

In addition the following species has been reported, probably as occasional, but it is in L represented only by indeterminable material: *Barbarea vulgaris* R.BR. See BACKER, Schoolfl. Java (1911) 55; KOORD. Exk. Fl. Java 2 (1912) 288; BACK. & BAKH.f. 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*
 2. Silicule with more than two seeds, triangular in outline 4. *Capsella*
1. Fruit a siliqua, *i.e.* more than three times as long as broad. Ovary \pm cylindrical.
 3. Siliqua corky-spongy, non-dehiscent 2. *Raphanus*
 3. Siliqua opening by two valves.
 4. Siliqua narrowing into a conical beak (rostrum), terminated by the style 1. *Brassica*
 4. Siliqua without a rostrum, \pm abruptly terminated by the style.
 5. Siliqua 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*
 5. Siliqua with a thin replum; valves opening without coiling 6. *Rorippa*

1. BRASSICA

LINNÉ, Sp. Pl. (1753) 666; Gen. Pl. ed. 5 (1754) 299; ENDL. Gen. Pl. (1839) 882; B. & H. Gen. Pl. 1 (1862) 84; BAILLON, Hist. Pl. 3 (1871) 248; PRANTL in E. & P. Nat. Pfl. Fam. III, 2 (1891) 177; SCHULZ, Pflanzenr. IV-105, Heft 70 (1919) 21; in E. & P. Nat. Pfl. Fam. ed. 2, 17b (1936) 321. — Fig. 1.

Annual, biennial or perennial herbs, rarely subshrubs, glabrous or with hispidulous simple hairs. *Leaves* undivided to pinnatipartite. *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, ovules numerous, usually uniseriate. *Fruit* a siliqua, readily dehiscent, terete or slightly laterally compressed, in transverse section \pm biconvex, attenuate into a conical to filiform beak with 0–3 seeds; valves rather thick, convex, with prominent midnerve 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.*

1. *Brassica juncea* (L.) CZERN. Consp. Pl. Chark. (1859) 8; BACKER, Fl. Batavia (1907) 49; MERR. Fl. Manila (1912) 214; KOORD. Exk. Fl. Java 2 (1912) 286; MERR. Int. Rumph. Herb. Amb. (1917) 240;

SCHULZ, Pflanzenr. IV-105, 70 (1919) 55; OCHSE & BAKH. Ind. Groenten (1931) 164, f. 99–101; BURK. DICL. (1935) 361; BACKER & BAKH.f. Fl. Java 1 (1963) 188; HENTY, Harmful Pl. PNG, Bot. Bull. Lae 12

(1980) 43. — *Sinapis juncea* LINNÉ, Sp. Pl. (1753) 668. — *Sinapis timoriana* DC. Syst. Nat. 2 (1821) 616; MIQ. Fl. Ind. Bat. 1, 2 (1858) 93; DECNE, Herb. Timor. Descr. (1835) 97; BOERL. Handl. Fl. Ned. Ind. 1, 1 (1890) 59; QUIS. Medic. Pl. Philip. (1951) 332. — *B. besseriana* ANDRZ. ex TRAUTV. Bull. Soc. Nat. Moscou 33 (1860) 134; KOORD. Meded. Lands Plantentuin 19 (1898) 341. — *B. integrifolia* (WEST) RUPR. Fl. Ingrica 1 (1860) 96; MERR. En. Philip. 2 (1923) 207. — Fig. 1.

Annual herb, glabrous or somewhat hispid at bases of stem and petioles, somewhat glaucous. *Stem* erect, usually 30–150 cm high, with long ascending branches in upper part. Basal and lower *leaves* petioled, not auriculate, with obovate attenuate blade up to 20 by 10 cm, rather coarsely and irregularly dentate, and 1–3 pairs of small lateral lobes; median and upper leaves ± distinctly petioled, not auriculate, obovate and obtuse or oblanceolate and acute, usually 5–10 cm long, irregularly dentate. *Racemes*

corymbiform, rather loose, with numerous flowers; in fruit lax, up to 50 cm long; pedicels ascending, 5–12 mm long. *Sepals* green, oblong, 4–6 mm long. *Petals* bright yellow, clawed, with obovate blade, 6–10 mm long. *Anthers* 1.5–2.5 mm long. *Ovary* with 10–20 ovules. *Siliquae* linear, often somewhat torulose, sometimes inflated, 25–75 by 2–3.5 mm, attenuate into a narrowly conical seedless beak, 6–12 mm long; valves with distinct ± keeled midnerve. *Seeds* dark brown, globose, 1–1.5 mm in diameter, with a distinct fine reticulum.

Distr. Wild origin unknown, perhaps E. Europe or SW. Asia; widely spread with cultivation in Asia, S. Europe, Africa and America; in *Malesia*: Malay Peninsula, Java, Borneo (Brunei, Sarawak), Celebes, Moluccas, Philippines, New Guinea.

Ecol. Weed of waste land, open places, cultivations (sometimes in gardens); mostly at 2000–3000 m.

Note. *Brassica juncea* has in later years become the world's most important mustard crop.

2. RAPHANUS

LINNÉ, Sp. Pl. (1753) 669; Gen. Pl. ed. 5 (1754) 300; ENDL. Gen. Pl. (1839) 886; B. & H. Gen. Pl. 1 (1862) 101; PRANTL in E. & P. Nat. Pfl. Fam. III, 2 (1891) 179; BAILLON, Hist. Pl. 3 (1871) 250; SCHULZ, Pflanzenr. IV-105, 70 (1919) 194; in E. & P. Nat. Pfl. Fam. ed. 2, 17b (1936) 347.

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 semi-globose 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.

1. *Raphanus sativus* LINNÉ, Sp. Pl. (1753) 669; BACKER, Fl. Batavia (1907) 50; MERR. Fl. Manila (1912) 214; KOORD. Exk. Fl. Java 2 (1912) 287; HEYNE, Nutt. Pl. Ned. Ind. (1927) 679; OCHSE & BAKH. Ind. Groenten (1931) 178; BURK. Dict. (1935) 1566; BACKER & BAKH. f. Fl. Java 1 (1963) 188; QUIS. Medic. Pl. Philip. (1951) 336; STONE, Fed. Mus. J. 26 (1981) 80. — *R. caudatus* LINNÉ, Mant. Pl. (1767) 95; MIQ. Fl. Ind. Bat. 1, 2 (1858) 93.

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, petioled, 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 corymbiform 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, \pm dark-veined, 15–20 mm long with obovate, emarginate to rounded blade, 5–6 mm broad. *Anthers* \pm 2.5 mm long. *Siliqua* 20–90 by 7–15 mm; lower segment much reduced; upper segment of \pm 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

LINNÉ, *Sp. Pl.* (1753) 644; *Gen. Pl. ed. 5* (1754) 291; ENDL. *Gen. Pl.* (1839) 879; B. & H. *Gen. Pl.* 1 (1862) 87; BAILLON, *Hist. Pl.* 3 (1871) 284; PRANTL in E. & P. *Nat. Pfl. Fam.* III, 2 (1891) 160; THELL. *Die Gattung Lepidium* (1906); SCHULZ in E. & P. *Nat. Pfl. Fam. ed. 2*, 17b (1936) 407; HEWSON, *Brunonia* 5 (1982) 73. — *Papuzilla* RIDLEY, *Trans. Linn. Soc. Lond.* II, Bot. 9 (1916) 17; SCHULZ in E. & P. *Nat. Pfl. Fam. ed. 2*, 17b (1936) 410; P. ROYEN, *Mt. Fl. New Guinea* 3 (1982) 2014. — **Fig. 2.**

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 septate, 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. 1. *L. sativum*
2. Leaves deeply divided. Siliculae with prominent wings 2. *L. virginicum*
2. Leaves undivided, serrate. Siliculae wingless 5. *L. maccowngel*
1. Inflorescences very short with 5 or fewer flowers inserted at base of spines.
 3. Subshrub, more than 20 cm high 5. *L. maccowngel*
 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. minutiflorum*
 4. Cushions less than 5 cm thick. Leaves mostly deeply pinnatifid with up to 7 pairs of lobes

3. *L. laeteviride*

1. *Lepidium sativum* LINNÉ, Sp. Pl. (1753) 644; HEYNE, Nutt. Pl. Ned. Ind. (1927) 676; BURK. Dict. (1935) 1331; BACKER & BAKH, f. Fl. Java I (1963) 188.

Annual herb with slender taproot, up to 70 cm high, erect, simple or much branched, glabrous or with scattered minute hairs. *Leaves* membranous, petioled, very sparsely pubescent, up to 10 cm long, imparipinnati- or bipinnatifid, with 2–4 pairs of lateral lobes; lobes linear, lanceolate or oblanceolate, up to 3 cm long; uppermost leaves sometimes simple, serrate. *Racemes* terminal, with rather conspicuous whitish flowers, in fruit loose, up to 25 cm long; pedicels in fruit 3–6 mm long, ascending to almost erect, straight, glabrous. *Sepals* green with membranous margins, elliptic, 1–1.5 mm long. *Petals* white or violet, spatulate to slightly clawed, with rounded apex, 1.7–3 mm long. *Stamens* 6, with a single small nectary between each of them. *Ovary* elliptic, emarginate, with projecting style. *Siliculae* elliptic in outline, 4.5–6.6 mm long, 3–4 mm broad, with prominent apical wings, deeply emarginate; style distinct, with stigma completely within or just level with the top of the sinus. *Seeds* wingless, reddish brown, 2–3 mm long, c. 1.5 mm broad.

Distr. Probably native in Ethiopia and neighbouring countries to the west and north, and in the Near East; spread by cultivation or inadvertently to many parts of the world; in *Malesia* introduced: Java, Flores, probably elsewhere.

Ecol. Occurs as an occasional escape from cultivation; uncertain whether naturalized anywhere in the area.

2. *Lepidium virginicum* LINNÉ, Sp. Pl. (1753) 645; MERR. En. Philip. 2 (1923) 207; BACKER & BAKH, f. Fl. Java I (1963) 187.

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.

Distr. Native of North America; widespread as a weed; in *Malesia* 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.

3. *Lepidium laeteviride* (P.ROYEN) HEWSON, Brunonia 5 (1982) 74. — *Papuzilla laeteviridis* P.ROYEN, Nova Guinea, Bot. 19 (1964) 430; Mt Fl. New Guinea 3 (1982) 2014, f. 615, pl. 154. — Fig. 2.

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 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. *Malesia*: Papua New Guinea (Morobe District, Sarawaket Range, Mt Bangeta).

Ecol. On overgrown screes and among boulders at c. 4100 m.

4. *Lepidium minutiflorum* (RIDLEY) HEWSON, Brunonia 5 (1982) 74. — *Papuzilla minutiflora* RIDLEY, Trans. Linn. Soc. Lond. II, Bot. 9 (1916) 16, f. 7–14, pl. 1; MERR. & PERRY, J. Arn. Arb. 24 (1943) 207; P.ROYEN, Nova Guinea, Bot. 19 (1964) 428; Mt. Fl. New Guinea 3 (1982) 2014, f. 614.

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-)pinnate 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 equalling sepals, linear. *Stamens* 2 (median)



Fig. 2. *Lepidium laeteviride* (P. ROYEN) HEWSON. a. Habit, $\times 4$; b. flower, $\times 12$; c. ditto, calyx removed; d. petals; e. ovary; f. ovary, lateral view; all $\times 16$; g. fruit; h. seeds; i. fruit valve; all $\times 4$ (P. ROYEN 20026).

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 (Mts Carstensz & Wilhelmina), Papua New Guinea (W. Sepik District: Mt Capella).

Ecol. Screes, wet open places, tussock grassland, heaths; 3100–4350 m.

5. *Lepidium maccowagei* HEWSON, *Brunonia* 5 (1982) 75. — *Papuzilla minutiflora* auct. non RIDLEY: P. ROYEN, Mt. Fl. New Guinea 3 (1982) 2014, *p.p.*, as to Papua New Guinea specimens.

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 exerted. Seeds wingless, red-brown, 2–2.5 by 1.1–1.5 mm.

Distr. *Malesia*: Papua New Guinea (Southern Highlands: Mt Giluwe, Kaguba).

Ecol. Screes, stream-edges, etc., at lower altitudes along roadsides; 2750–3500 m.

4. CAPSELLA

MEDICUS, *Pflanzengatt.* 1 (1792) 85; ENDL. *Gen. Pl.* (1839) 878; B. & H. *Gen. Pl.* 1 (1862) 86; BAILLON, *Hist. Pl.* 3 (1871) 287; SCHULZ in E. & P. *Nat. Pfl. Fam.* ed. 2, 17b (1936) 453.

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, \pm 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.

1. *Capsella bursa-pastoris* (L.) MEDICUS, Pflanzen-gatt. 1 (1792) 85; BACKER, Schoolfl. Java (1911) 58; KOORD. Exk. Fl. Java 2 (1912) 291; MERR. En. Philip. 2 (1923) 208; BACKER & BAKH.f. Fl. Java 1 (1963) 192; EVERAARTS, Weeds Veget. Java (1981) 51, f. 38.

Annual to short-lived perennial herb, 5–50 cm high. *Stems* 1–few, erect or ascending, simple or sparsely branched. Rosette *leaves* numerous, petiolate, imparipinnatifid 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, \pm 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

LINNÉ, Sp. Pl. (1753) 654; Gen. Pl. ed. 5 (1754) 295; ENDL. Gen. Pl. (1839) 865; B. & H. Gen. Pl. 1 (1862) 70; PRANTL in E. & P. Nat. Pfl. Fam. III, 2 (1891) 184; BAILLON, Hist. Pl. 3 (1871) 234; SCHULZ, Bot. Jahrb. 32 (1903) 280; in E. & P. Nat. Pfl. Fam. ed. 2, 17b (1936) 527. — *Pteroneurum* DC. Syst. Nat. 2 (1821) 269. — **Fig. 3.**

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*
 2. Leaves tripartite, terminal leaflet not more than 3 times as long as the lateral ones 2. *C. africana*
1. Most leaves with two or more pairs of lateral leaflets.
 3. Leaflets oblanceolate in outline. Plants usually very slender with internodes much longer than leaves 3. *C. altigena*
 3. Leaflets ovate to orbicular in outline. Plants not very slender, with most internodes equalling or shorter than leaves.
 4. Petals at least 6 mm long 4. *C. keysseri*
 4. Petals not exceeding 4 mm.
 5. Pedicels of siliquae patent at an angle with stem exceeding 45° (usually c. 60°). Seeds at least 1.1 mm long 5. *C. flexuosa*
 5. Pedicels of siliquae erect to erecto-patent (angle with stem c. 45° or less). Seeds shorter than 1.1 mm 6. *C. hirsuta*

1. *Cardamine papuana* (LAUT.) O.E.SCHULZ, Bot. Jahrb. 55 (1918) 271, f. 1E; MERR. & PERRY, J. Agr. Arb. 24 (1943) 207; P.ROYEN, Mt. Fl. New Guinea 3 (1982) 2021. — *C. africana* L. *ssp. borbonica* (PERS.) O.E.SCHULZ *var. papuana* LAUT. in K.Sch. & Laut. Fl. Deut. Schutzgeb. Südsee, Nachtr. (1905) 271; PULLE, Nova Guinea 8 (1911) 641. — Fig. 3.

Perennial, rhizomatous, glabrous (rarely pubescent) herb with 15–50 cm high, erect or ascending shoots, appearing solitarily or with 2 or 3 together. *Stems* unbranched or with a few rather long branches in the upper part. *Leaves* tripartite or unifoliolate (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 petiolules (in partite leaves); lateral leaflets ovate, acute, sparsely serrate or dentate, 0.5–3 by 0.2–2 cm on 1–4 mm long petiolules. *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, 8–12 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.

Distr. Malesia: New Guinea (throughout), rather widely distributed.

Ecol. Wet cliffs, rocky banks of streams in forests; 500–3100 m.

2. *Cardamine africana* LINNÉ, Sp. Pl. (1753) 655; SCHULZ, Bot. Jahrb. 32 (1903) 414; KOORD. Exk. Fl. Java 2 (1912) 290; BOLDINGH, Zakfl. Landb. Java (1916) 67; KOORD. Fl. Tjibodas 3 (1923) 80; RIDLEY, J. Mal. Br. R. As. Soc. n. 87 (1926) 52; HENTY & PRITCHARD, Weeds New Guinea, Div. Bot. Lae, Bot. Bull. 7 (1973) 96. — *C. borbonica* PERS. Syn. Pl. 2 (1807) 195. — *Pteroneurum javanicum* BLUME,



Fig. 3. *Cardamine papuana* (LAUT.) O.E.SCHULZ. a. Habit, $\times 0.6$; b. siliqua, $\times 2$; c. seed, scale bar 1 mm (SCHODDE 5540). Del. K.G. FORSS.

Bijdr. (1825) 51; ZOLL. & MOR. Syst. Verz. (1845/46) 35; MIQ. Fl. Ind. Bat. 1, 2 (1858) 93. — *C. javanica* (BLUME) MIQ. Ill. Arch. Ind. (1871) pl. X; BOERL. Handl. Fl. Ned. Ind. 1, 1 (1890) 58; BACKER, Schoolfl. Java (1911) 56. — *C. africana* L. ssp. *borbonica* (PERS.) SCHULZ, Bot. Jahrb. 32 (1903) 414; DOCTERS VAN LEEUWEN, Verh. Kon. Akad. Wet. Amsterdam,

sect. II, 31 (1933) 167; BACKER & BAKH.f. Fl. Java 1 (1963) 191; STEEN. Mt. Fl. Java (1972) pl. 13/6; P.ROYEN, Mt. Fl. New Guinea 3 (1982) 2021; STREIMANN, Canberra Nat. Bot. Gard. (1983) 100 ('var. *borbonica*').

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 petiolules; 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 sepals, 3–12 mm long, $\pm 1/3$ 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. Ubiquitous in tropical montane areas. In Africa from Ethiopia south to South Africa (Cape Province) and westwards to Mt Cameroun; also in Fernando Póo, São Tomé, Comores, Madagascar and Réunion. 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 damp, shady places; 200–2400 m.

3. *Cardamine altigena* O.E.SCHULZ, Bot. Jahrb. 62 (1929) 479; MERR. & PERRY, J. Arn. Arb. 24 (1943) 207; HOOGLAND, Blumea Suppl. 4 (1958) 227; P. ROYEN, Mt. Fl. New Guinea 3 (1982) 2021, f. 616, pl. 154.

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 petiolules; lateral leaflets trifid to oblanceolate, 0.2–0.7 by 0.1–0.5 cm, petiolules c. 1 mm. *Racemes* terminal, with 3–10 flowers, often very slender; pedicels straight, erect 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, $\pm 1/3$ 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.

4. *Cardamine keysseri* O.E.SCHULZ, Bot. Jahrb. 62 (1929) 480; P. ROYEN, Mt. Fl. New Guinea 3 (1982) 2025, f. 617, pl. 156.

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; petiolules 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 sepals, 7–8 mm long, \pm 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.

Distr. *Malesia*: New Guinea (throughout), rather widespread.

Ecol. Sandy or gravelly streambanks, moist forest clearings, moist eroded soil, in gardens; 900–4000 m.

5. *Cardamine flexuosa* WITH. Arr. Brit. Pl. ed. 3, 3 (1796) 578; SCHULZ, Bot. Jahrb. 32 (1903) 473; KOORD. Exk. Fl. Java 2 (1912) 290; BOLDINGH, Zakfl. Landb. Java (1916) 67; RIDLEY, J. Fed. Mal. St. Mus. 8, 4 (1917) 15. — *Pteroneurum decurrens* BLUME, Bijdr. (1825) 51. — *C. decurrens* (BLUME) ZOLL. & MOR. Syst. Verz. (1845/46) 35; MIQ. Fl. Ind. Bat. 1, 2 (1858) 93; Ill. Arch. Ind. (1871) pl. X; BOERL. Handl. Fl. Ned. Ind. 1, 1 (1890) 58; BACKER, Voerl. Schoolfl. (1908) 11; Schoolfl. Java (1911) 56. — *C. regeliana* MIQ. Ann. Mus. Bot. Lugd.-Bat. 2 (1865) 73; MERR. En. Philip. 2 (1923) 208; RIDLEY, J. Mal. Br. R. As. Soc. n. 87 (1926) 52.

Mostly perennial, diffusely branching herb; from the base usually many erect to ascending, curved or flexuose 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 sparsely pubescent, mostly numerous, imparipinnate with a terminal and 2 or 3 pairs of lateral leaflets, 2–10 cm long; petiole non-auriculate; 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 petiolules; 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 siliquae, 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. Circumpolar in northern temperate region. Also in some montane areas further south. In *Malesia*: N. Sumatra (Atjeh), Java, Celebes (Menado), Philippines (Mindanao, Luzon), Moluccas (Buru, Ceram).

Ecol. Moist places in forests, among rocks and boulders, at streams, in clearings; 1000–2200 m.

6. *Cardamine hirsuta* LINNÉ, Sp. Pl. (1753) 655; BOERL. Handl. Fl. Ned. Ind. 1, 1 (1890) 58; KOORD. Nat. Tijd. Ned. Ind. 62 (1902) 234; SCHULZ, Bot. Jahrb. 32 (1903) 464; BACKER, Schoolfl. Java (1911) 56; KOORD. Exk. Fl. Java 2 (1912) 290; RIDLEY, Trans. Linn. Soc. Lond. II, Bot. 9 (1916) 17; KOORD.

Fl. Tjibodas 3 (1923) 80; HOCHR. Candollea 2 (1925) 371; BURK. & HEND. Gard. Bull. S. S. 3 (1925) 345; DOCTERS VAN LEEUWEN, Verh. Kon. Akad. Wet. Amsterdam, sect. II, 31 (1933) 168; BACKER & BAKH.f. Fl. Java 1 (1963) 191; STEEN. Mt. Fl. Java (1972) pl. 13/5; HENTY & PRITCHARD, Weeds New Guinea, Div. Bot. Lae, Bot. Bull. 7 (1973) 96, fig.; GILLI, Ann. Naturhist. Mus. Wien 83 (1980) 429; EVERAARTS, Weeds Veget. Java (1981) 53, f. 39. — *C. flexuosa auct. non WITH.*: STONE, Fed. Mus. J. 26 (1981) 80.

Usually annual, branching from the base but not or very sparsely above (occasionally perennial and then branched above and devoid of leaf-rosette). *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-auriculate, 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 siliquae 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, Bencoolen), Java, Borneo (Sabah), Philippines (Luzon), New Guinea (throughout).

Ecol. Moist, open ground in montane forests, clearings, etc.; 850–3000 m. Weed in gardens, flowerbeds, also at low altitudes.

6. RORIPPA

SCOP. Fl. Carniol. (1760) 520; JONSELL, Symb. Bot. Upsal. 19² (1968); STUCKEY, Sida 4 (1972) 279. — *Nasturtium* R. BR. in Ait., Hort. Kew. ed. 2, 4 (1812) 109; ENDL. Gen. Pl. (1839) 863; B. & H. Gen. Pl. 1 (1862) 68; PRANTL in E. & P. Nat. Pfl. Fam. III, 2 (1891) 184; BAILLON, Hist. Pl. 3 (1871) 232; SCHULZ in E. & P. Nat. Pfl. Fam. ed. 2, 17b (1936) 551. — *Trochiscus* GILLI, Ann. Naturhist. Mus. Wien 83 (1980) 430. — **Fig. 4.**

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. *Leaves* membranous, usually pinnatifid to pinnate, often auriculate. *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 \pm twice as long as the sepals. *Stamens* 6, distinctly tetradynamous, with usually linear filaments; anthers ovate to oblong, yellow, blunt. *Nectarial tissue* \pm 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 gynophore, 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. <i>R. benghalensis</i> |
| 1. Racemes ebracteate (rarely with a few bracts at the lowest pedicels). | |
| 2. Siliquae not more than 1.5 mm thick | 7. <i>R. heterophylla</i> |
| 2. Siliquae more than 1.5 mm thick. | |
| 3. Pedicels of fruits straight. | |
| 4. Seeds not over 0.8 mm long | 9. <i>R. micrantha</i> |
| 4. Seeds longer than 0.8 mm. | |
| 5. Cauline leaves numerous; seeds distinctly reticulate (c. 150 areoles per face) | 2. <i>R. hackeri</i> |
| 5. Cauline leaves absent or few; seeds very finely reticulate (over 300 areoles per face) | 3. <i>R. peekelii</i> |
| 3. Most pedicels of fruits curved. | |
| 6. Petals white. Seeds coarsely reticulate | 1. <i>R. nasturtium-aquaticum</i> |
| 6. Petals yellow. Seeds with very fine surface patterns. | |
| 7. Ripe siliquae inflated, semiglobose | 6. <i>R. schlechteri</i> |
| 7. Ripe siliquae \pm ellipsoid to sausage-shaped, not inflated. | |
| 8. Seeds with warty processes. Very tall and stout plants | 5. <i>R. hybosperma</i> |
| 8. Seeds without processes. Moderately high plants | 4. <i>R. palustris</i> |

1. *Rorippa nasturtium-aquaticum* (L.) HAYEK, Sched. Fl. Stir. Exs. 3-4 (1905) 22. — *Sisymbrium nasturtium-aquaticum* LINNÉ, Sp. Pl. (1753) 657. — *Nasturtium officinale* R. BR. in Ait., Hort. Kew. ed.

2, 4 (1812) 110; MRO. Fl. Ind. Bat. 1, 2 (1858) 73; BOERL. Handl. Fl. Ned. Ind. 1, 1 (1890) 58; KOORD. Meded. Lands Plantentuin 19 (1898) 342; BACKER, Schoolfl. Java (1911) 55; KOORD. EXK. Fl. Java 2



Fig. 4. Harvest of *Rorippa nasturtium-aquaticum* (L.) HAYEK (Photogr. W.F. WINCKEL, 1918).

(1912) 288; MERR. En. Philip. 2 (1923) 208; HEYNE, Nutt. Pl. Ned. Ind. (1927) 680; OCHSE & BAKH. Ind. Groenten (1931) 176, f. 108; BURK. Dict. (1935) 1534; QUIS. Medic. Pl. Philip. (1951) 335; BACKER & BAKH.f. Fl. Java I (1963) 191; GILLI, Ann. Naturhist. Mus. Wien 83 (1980) 430; LENCH & OSBORNE, Fresh-water Pl. Papua New Guinea (1985) 105. — *Rorippa officinalis* (R.BR.) P.ROYEN, Mt. Fl. New Guinea 3 (1982) 2029. — Fig. 4.

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 2–9 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.

2. *Rorippa backeri* (O.E.SCHULZ) JONSELL, Bot. Notis. 132 (1979) 536. — *Nasturtium backeri* O.E.SCHULZ, Notizbl. Bot. Gart. Berlin 9 (1925) 84; BACKER & BAKH.f. Fl. Java I (1963) 191; STEEN. Mt. Fl. Java (1972) pl. 12/7.

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, lyrato-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, lyrato-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 distantly 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 $\pm 90^\circ$, 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. *Siliquae* linear, straight or fairly curved, 30–50 by 1.7–2.2 mm; valves rather firm; style 0.8–1.2 by c. 0.4 mm; stigma flat, slightly broader than style. *Seeds* dark brown, broadly oblong to subspheroid in outline, 1.2–1.4 by 0.9–1.1 mm, regularly reticulate-foveolate.

Distr. Malesia: Java (eastern part: Mts Merbabu, Wilis, Jang & Idjen: Suket).

Ecol. In burnt forests, thickets, locally common; 1600–3000 m. *Fl. fr.* throughout the year.

3. *Rorippa peekelii* (O.E.SCHULZ) P.ROYEN, *Mt. Fl. New Guinea* 3 (1982) 2032. — *Nasturtium peekelii* O.E.SCHULZ, *Bot. Jahrb.* 55 (1918) 270, f. 1D; VON MALM in Fedde, *Rep.* 41 (1937) 295; SCHULZ in E. & P. *Nat. Pfl. Fam.* ed. 2, 17b (1936) 555, f. 337D; VELDKAMP, *Blumea* 28 (1982) 166. — *Nasturtium novo-guineense* GILLI, *Ann. Naturhist. Mus. Wien* 83 (1980) 429. — **Fig. 5.**

Annual to shortlived perennial herb with taproot, glabrous, 20–60 cm high. *Stems* one to few, \pm straight, spreading, sometimes prostrate-ascending, usually with few erecto-patent branches from the lower parts. Basal *leaves* mostly numerous, in a \pm dense rosette, 4–13 by 1–5 cm, petiolate, lyrato-pinnate with 1–3 pairs of oblong, lateral lobes, 0.4–2.5 by 0.2–1.5 cm; terminal lobe elliptic-ovate, 1.5–5 by 1–3 cm; margins sinuate to irregularly serrate; cauline leaves similar but smaller, the uppermost without side-lobes, petiolate, without or with rather small auricles, sometimes in axillary rosettes; margins crenate to acutely serrate. *Racemes* ebracteate, terminal, in flower very condensed with 20–50 flowers, in fruit very prolonged, up to 30 cm long; pedicels divaricate at 60–90°, straight, rather thin, 4–13 mm long. *Sepals* elliptic-oblong, 2–3.7 mm long. *Petals* white, broadly spatulate, 3–4 mm long. *Stamens* 6; anthers c. 0.7 mm long. *Ovary* nar-

rowly cylindrical with c. 0.3 mm long style. *Siliquae* linear, straight, 23–30 by 1.4–2 mm; valves rather firm; style 0.7–2.5 by 0.4–0.5 mm; stigma \pm 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.

Distr. Malesia: E. Timor (Mts Mutis & Tatamailau), Papua New Guinea (W., E. & S. Highlands), Bismarck Archipelago (New Ireland).

Ecol. Along streams on rocks and beaches, a weed in gardens and along damp tracks. In New Guinea 1350–3500 m altitude, in Timor 1600–2850 m.

4. *Rorippa palustris* (L.) BESS. *Enum. Pl. Volhyniae* (1822) 27; JONSELL, *Symb. Bot. Upsal.* 19² (1968) 157. — *Sisymbrium amphibium* L. var. *palustre* LINNÉ, *Sp. Pl.* (1753) 657. — *Nasturtium palustre* (L.) DC. *Syst. Nat.* 2 (1821) 121; BLUME, *Bijdr.* (1825) 50; MIQ. *Fl. Ind. Bat.* 1, 2 (1858) 93; BACKER, *Schoolfl. Java* (1911) 55. — *Rorippa islandica* (OED.) BORB. *Bal. Fl.* (1900) 392; BACKER & BAKH.f. *Fl. Java* 1 (1963) 190. — *Nasturtium homalospermum* O.E.SCHULZ, *Bot. Jahrb.* 55 (1918) 270, f. 1C, *incl. var. macrocarpum*; in E. & P. *Nat. Pfl. Fam.* ed. 2, 17b (1936) 551, f. 337C. — *Nasturtium indicum auct. non DC.*: K.SCH. & LAUT. *Fl. Deut. Schutzgeb. Südsee* (1901) 334, *p.p.*

Annual or shortlived 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, lyrato-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. *Siliquae* 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.

Distr. Over the whole north temperate area; widespread in many montane regions in subtropics 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. Moist or marshy places, ditches and other



Fig. 5. *Rorippa peekelii* (O.E.SCHULZ) P.ROYEN. a. Habit, $\times 0.7$; b. fruiting raceme, $\times 0.7$; c. silique, $\times 2$; 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.

5. *Rorippa hybosperma* (O.E.SCHULZ) JONSELL, *comb. nov.* — *Nasturtium hybospermum* O.E. SCHULZ, Bot. Jahrb. 55 (1918) 268, f. 1B; in E. & P. Nat. Pfl. Fam. ed. 2, 17b (1936) 551, f. 337b. — *Nasturtium indicum auct. non DC.*: K.SCH. & HOLLR. Fl. Kaiser Wilh. Land (1889) 49; WARB. Bot. Jahrb. 13 (1891) 317; K.SCH. & LAUT. Fl. Deut. Schutzgeb. Südsee (1901) 334, *p.p.*

Annual herb with taproot, glabrous, 50–150 cm high. *Stem* solitary, erect or in basal part ascending, shining, mostly rather stout, with many long erectopatent branches. *Leaves* petiolate, auriculate, 3–17 by 1–8 cm, lyrato-pinnate with 1–3 pairs of oblong-elliptic lateral lobes, 0.8–4 by 0.3–1.5 cm; terminal lobe elliptic-ovate, 1.5–7 by 0.8–2.5 cm; margins crenulate-serrulate. *Racemes* terminal on stem and side-branches, ebracteate or with a few bracts in the lowest part, in flowers very condensed, in fruit rather loose, sometimes branched, up to 25 cm long; pedicels patent, the lower somewhat curved, 5–10 mm long. *Sepals* elliptic, 1.5–1.8 mm long. *Petals* yellow, spatulate, 2–2.5 mm long. *Stamens* 6; anthers c. 0.5 mm long; filaments narrowly subulate. *Ovary* cylindrical with a c. 0.3 mm long style. *Siliquae* sausage-shaped, often curved, 12–17 by 1.5–2.7 mm; valves thin; style 0.9–1.5 by 0.2–0.3 mm, with a broader stigma. *Seeds* yellow brown, spheroid, finely colliculate and with prominent irregular warts around the margin, c. 1.2 mm long.

Distr. *Malesia*: Philippines (N. Mindanao: Dulawan), New Guinea (West; East: Nuru, Sepik, Lae).

Ecol. Along streams and rivers and in marshes in the lowland. Also a weed in moist places.

6. *Rorippa schlechteri* (O.E.SCHULZ) P.ROYEN, Mt. Fl. New Guinea 3 (1982) 2031. — *Nasturtium schlechteri* O.E.SCHULZ, Bot. Jahrb. 55 (1918) 266, f. 1A; in E. & P. Nat. Pfl. Fam. ed. 2, 17b (1936) 554, f. 337A; VELDKAMP, Blumea 28 (1982) 166. — *Trochiscus macrocarpus* GILLI, Ann. Naturhist. Mus. Wien 83 (1980) 430.

Annual to short-lived perennial with taproot, 15–50 cm high. *Stem* solitary, erect, unbranched or with rather few, comparatively long branches. *Leaves* indistinctly petiolate, auriculate, 1.5–15 by 0.9–3.5 cm, lyrato-pinnate with 1–3 pairs of oblong lateral lobes, 0.2–1.5 by 0.1–0.6 mm; terminal lobe elliptic-ovate, 0.8–4 by 0.3–2.5 mm; margins irregularly dentate. *Racemes* terminal and on side-branches, ebracteate, in flower very condensed, in fruit rather loose, up to 15 cm long; pedicels patent to reflexed, 3–10 mm long. *Sepals* oblong, 1.5–2 mm long. *Petals* yellow, spatulate, 1.7–2.5 mm

long. *Stamens* 6; anthers c. 0.5 mm long; filaments linear. *Ovary* ellipsoid with c. 0.2 mm long style. *Siliquae* inflated, semiglobose to broadly ellipsoid, 5–9 by 3–6 mm; valves thin; style 0.6–0.9 by c. 0.3 mm, with flat, slightly broader stigma. *Seeds* red-brown, spheroid, 0.8–1 mm, minutely foveolate.

Distr. *Malesia*: Papua New Guinea.

Ecol. Moist or marshy places, various kinds of disturbed moist ground; c. 200–2600 m.

Vern. *Heleki*, Okapa, *heyenka*, Tairora, *kemu kembili*, Kaugel.

7. *Rorippa heterophylla* (BLUME) WILLIAMS, Fl. Trinidad & Tobago 1 (1929) 24. — *Nasturtium heterophyllum* BLUME, Bijdr. (1825) 50; MIQ. Ill. Arch. Ind. (1871) pl. IX; BOERL. Handl. Fl. Ned. Ind. 1, 1 (1890) 58; BACKER, Fl. Batavia (1907) 47; Schooffl. Java (1911) 55; KOORD. Exk. Fl. Java 2 (1912) 288; HEYNE, Nutt. Pl. Ned. Ind. (1927) 680; OCHSE & BAKH. Ind. Groenten (1931) 175, f. 107; BURK. Dict. (1935) 1534. — *Cardamine sublyrata* MIQ. Ann. Mus. Bot. Lugd.-Bat. 2 (1848) 178. — *Nasturtium indicum* (L.) DC. *var. javana* BLUME, Bijdr. (1825) 50; MIQ. Fl. Ind. Bat. 1, 2 (1858) 93. — *Nasturtium diffusum auct. non DC.*: MIQ. Fl. Ind. Bat. 1, 2 (1858) 93; BOERL. Handl. Fl. Ned. Ind. 1, 1 (1890) 58. — *Nasturtium indicum auct. non (L.) DC.*: BOERL. Handl. Fl. Ned. Ind. 1, 1 (1890) 58; BACKER, Fl. Batavia (1907) 47; Schooffl. Java (1911) 55; MERR. Fl. Manila (1912) 213; KOORD. Exk. Fl. Java 2 (1912) 289; RIDLEY, Trans. Linn. Soc. Lond. II, Bot. 9 (1916) 16; MERR. Interpr. Rumph. Herb. Amb. (1917) 240; RIDLEY, Fl. Mal. Pen. 1 (1922) 119; MERR. En. Philip. 2 (1923) 208; KOORD. Fl. Tjibodas 3 (1923) 80; HOCHR. Candollea 2 (1925) 370; HEYNE, Nutt. Pl. Ned. Ind. (1927) 680; BURK. Dict. (1935) 1534; H.J.LAM, Blumea 5 (1945) 570; QUIS. Medic. Pl. Philip. (1951) 335; BACKER & BAKH. f. Fl. Java 1 (1963) 190. — *R. indica* (L.) HIERN *var. apetala* (LOUR.) HOCHR. Candollea 2 (1925) 370. — *R. dubia* (PERS.) HARA, J. Jap. Bot. 30 (1955) 196; BACKER & BAKH. f. Fl. Java 1 (1963) 190.

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-pinnatifid 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.

Ecol. Open, moist ground, often cultivated places; 250–1500 m.

8. *Rorippa benghalensis* (DC.) HARA, J. Jap. Bot. 49 (1974) 132. — *Nasturtium benghalense* DC. Syst. Nat. 2 (1821) 198; SCHULZ in Fedde, Rep. 33 (1934) 281.

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).

Ecol. Weed in settled areas, perhaps only incidental.

9. *Rorippa micrantha* (ROTH) JONSELL, Svensk Bot. Tidskr. 68 (1974) 384; Fl. Trop. E. Afr., Cruciferae (1982) 55, f. 19. — *Sisymbrium micranthum* ROTH, Nov. Pl. Sp. (1821) 324.

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 petiole, 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.).

Ecol. Weed in settled areas, perhaps only incidental.

MAGNOLIACEAE (H.P. Nootboom, Leiden)

Trees or shrubs, glabrous or with an indumentum of single hairs. *Leaves* spirally arranged, simple, entire or 2–10-lobed, penninerved, 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, dehiscent 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, biseriata on the ventral suture. *Fruit* apocarpous, sometimes syncarpous; fruiting carpels opening along the dorsal and/or ventral suture, or circumscissile, 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 Malasia 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 blossom 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 protogyny 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 (TIEN, 1974).

References: THIEN, Amer. J. Bot. 61 (1974) 1037–1045; TRESEDER, Magnolias (1978).

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 *Liriodendroideae* and in tribe *Magnolieae* of *Magnolioideae* 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 *Micheliaceae* 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.

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 spatheaceous 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 spatheaceous 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* (l.c.) 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 Ranalean 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 conerescent. 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 conerescent. But only the outer layers of the exocarpium are really conerescent, 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 conerescence of the carpels has apparently developed independently in different lineages of *Magnoliaceae*. Species with free and conerescent 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 endoreticulum 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 synergids and antipodal cells are ephemeral. The endosperm is cellular from the beginning, and embryogeny conforms to the *Myosurus* variation of the *Onagra* type or is irregular (HAYASHI, 1964, 1966; BHANDARI, 1971; DAVIS, 1966).

References: BHANDARI, J. Arn. Arb. 52 (1971) 1–40, 285–304; BOUMAN, Acta Bot. Neerl. 26 (1977) 213–223; CANRIGHT, Amer. J. Bot. 39 (1952) 484–497; *ibid.* 47 (1960) 145–155; CORNER, Seed of Dicotyledons (1976) 177; DAVIS, Systematic embryology of the Angiosperms (1966) 167; ERBAR & LEINS, Beitr. Biol. Pflanzen 56 (1982) 225–241; Bot. Jahrb. 103 (1983) 433–449; HAYASHI, Sci. Rep. Tohoku Univ. ser. IV Biol., 30 (1964) 89–98; *ibid.* 32 (1966) 111–118; VAN HEEL, Blumea 27 (1981) 499–522; *ibid.* 28 (1983) 231–270; SKIPWORTH, Phytomorphology 20 (1970) 228–235; TIFFNEY, Bot. J. Linn. Soc. 75 (1977) 299–323; TUCKER, Amer. J. Bot. 47 (1960) 266–277; *ibid.* 48 (1961) 60–71; UEDA, Bot. Mag. Tokyo 99 (1986) 333–349.

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 *Manglietia* while the most advanced are found in *Elmerrillia*, *Michelia* (*Tsoongiodendron*), and in some scattered species of *Magnolia*.

The stomata are paracytic in *Magnolioideae* (but in rare cases NONG VAN TIEP, 1980: 519, found also anomocytic stomata in *Manglietia*) and paracytic as well as anomocytic in *Liriodendroideae*. 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 encased in sclerenchymatous sheaths, and the veinlets terminate in sclerified elements. *Manglietia* 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. *Manglietia* leaves are characterized by sclerified epidermal and hypodermal layers, sclerified arm parenchyma in the mesophyll, unignified 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 *Manglietia* 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 *Alcimandra*, *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 International 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, except 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. Talauma sect. Blumiana* by its silica-bearing vessels and the pronounced heterogeneity of the rays. *Magnolia subg. Talauma sect. Aromadendron* differs from the rest of *subg. Talauma* in that the pores are almost twice the size of the investigated Asian species of *subg. Talauma*. 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 *Kmeria* 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. Talauma* exhibits the largest assemblage of primitive characters. The tropical *Magnolia paenetauma* from Hainan exhibits a great number of primitive features. Also in the external morphology the species of *sect. Gwillimia*, to which this species belongs, resemble the species of *subg. Talauma* so closely that they cannot be distinguished in absence of fruits.

References: BARANOVA, *Taxon* 21 (1972) 447–469; CANRIGHT, *J. Arn. Arb.* 36 (1955) 119–140; CHOWDHURY, *J. Indian Bot. Soc.* 43 (1964) 334–342; GOTTWALD, *Wood Sci. Technol.* 6 (1972) 121–127; METCALFE & CHALK, *Anatomy of the Dicotyledons* ed. 2, 3 (1987) 24–33; NONG VAN TIEP, *Feddes Rep.* 91 (1980) 497–576; TUCKER, *Bot. J. Linn. Soc.* 75 (1977) 325–356.

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, hexaploid, 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).

References: EHRENDORFER *c.s.* *Taxon* 17 (1968) 337–468; TRESEDER, *Magnolias* (1978); WHITAKER, *J. Arn. Arb.* 14 (1933) 376–385.

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 benzyloisoquinolines, bisbenzyloisoquinolines, aporphines, oxoaporphines, 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. Talauma* (quercitol). The sporadic occurrence of lignans (lirioresinol), 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 *Polycarpicae*.

In the meantime much additional phytochemical research was performed with members of the genera *Alcimandra*, *Elmerrillia*, *Liriodendron*, *Magnolia subg. Magnolia* and *Talauma*, and *Michelia*. In each instance alkaloids were isolated, some being new compounds and some already known from other members of *Polycarpicae*. All, however, belong to the phenyltetrahydroisoquinoline class. The oxoaporphine 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 germacranolide, eudesmanolide, elemnanolide, 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. Cyanogenic 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 *Polycarpicae* 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*, *Lauraceae*, *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 *Polycarpicae* — *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 suprategal 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. tsiampacca 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. Maingola*.

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.

Reference: PRAGLOWSKI, World Pollen and Spore Flora 3 (1974).

The family can easily be divided into two subfamilies, *Magnolioideae* and *Liriodendroideae*, the latter not in Malesia.

SUBFAMILY MAGNOLIOIDEAE

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 conerescent into a syncarp. Testa free from the endocarp, externally ariloid.

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**
 1. Growth monopodial. Flower buds arising on brachyblasts in the axils of the leaves 2. **Tribus Michelieae**

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, unignified vein-sheath cells, absence of either sclerified veinlet terminal cells or a sclerified leaf margin 2. **Manglietia**
 2. Ovules 2 in each carpel (4 in *Magnolia kachirachirai*), 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. Fruit a woody loculicidal capsule composed of few (2–8) conerescent carpels. Tepals 9–15, subequal. Ovules about 4–8 in each carpel. Stipules free from the petiole 3. **Pachylarnax**

1. **MAGNOLIA**

LINNÉ, Sp. Pl. (1753) 535; Gen. Pl. ed. 5 (1754) 240; DANDY, Kew Bull. (1927) 259; in Hutch. Gen. Fl. Pl. 1 (1964) 55; in Treseder, Magnolias (1978) 29; NOOT, Blumea 31 (1985) 83; *ibid.* 32 (1987) 343. — Type: *M. virginiana* LINNÉ, E. United States.

Talauma Juss. Gen. Pl. (1789) 281; DANDY, Kew Bull. (1927) 259; in Hutch. Gen. Fl. Pl. 1 (1964) 55. — *Magnolia* sect. *Talauma* BAILLON, Adansonia 7 (1866) 3, 66; NOOT, Blumea 31 (1985) 83. — *Magnolia* subg. *Talauma* PIERRE, Fl. For. Cochinch. 1 (1881) sub t. 1. — *Violaria* Post & O. K. Lexic. Gen. Pl. (1903) 588, p.p. — Type: *T. plumierii* (SCHWARTZ) A.DC. (*Magnolia plumierii* SCHWARTZ).

Aromadendron BLUME, Bijdr. (1825) 10; Fl. Java Magnol. (1829) 25 ('*Aromadendrum*'); DANDY, Kew Bull. (1927) 259; in Hutch. Gen. Fl. Pl. 1 (1964) 55.

— *Violaria* POST & O. K. Lexic. Gen. Pl. (1903) 588, *p.p.* — *Talauma sect. Aromadendron* MIQ. Ann. Mus. Bot. Lugd.-Bat. 4 (1868) 70 (excl. *T. vrie-seana*). — Type: *A. elegans* BLUME.

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. *Gynoeceium* sessile or in some species stipitate; carpels many to few, usually free but connate in *sect. Talauma*, *sect. Gynopodium*, 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 dehiscent; in some species of *sect. Gynopodium* the carpels connate but tearing apart when maturing and dehiscent 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. candollei*, by the midrib being not prominent on the upper surface. *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
(only in Malesia)

1. Stipules free from the petiole. Midrib not prominent above.
 2. Fruits with free carpels 1. *Sect. Maingola*
 2. Fruits with connate carpels 2. *Sect. Aromadendron*
1. Stipules adnate to the petiole. Midrib prominent above 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. Gynoeceium 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 1. *M. macklottii*
4. Scars of perianth and stamens along 10–20 mm of the torus under the fruit. Stamens c. 6 mm long, the c. 5 mm long connective appendage not included 4. *M. uvariifolia*
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. Petiole 8–25 mm. Pedicel 0–10 mm. Alveoles in general more than 0.5 mm diam. Reticulation on the upper surface quite distinct.
6. Leaves mostly narrowly elliptic; primary nerves in 11–16 pairs. Pedicel 5–10 m. Outer tepals 4, 4.5–7 cm, inner tepals 15–33. Connective appendage 12–15 mm 6. *M. elegans*
6. Leaves mostly obovate; primary nerves in 8–12 pairs. Pedicel absent. Outer tepals 3, c. 2 cm long, inner tepals c. 15, connective appendage 10–12 mm 7. *M. bintuluensis*
5. Tepals at most 12. Carpels free or connate in fruit. Connective appendage 0.5–15 mm.
7. Stamens c. 10, 4 mm long, the connective appendage c. 7 mm. Carpels c. 6. Pedicel absent, scars of stamens and perianth at most 1 mm 10. *M. pahangensis*
7. Stamens more than 10 and longer than 4 mm. Carpels in general many.
8. Petiole 2.5–5 cm. Pedicel 7–8 mm. Gynophore 5–10 mm. Carpels connate in fruit. 8. *M. ashtonii*
8. Petiole 3–17 mm. Pedicel 0–5 mm. Gynophore 0–5 mm. Carpels free or connate in fruit.
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*
9. 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. Stamens (5–)7.5–12 mm, the 2–3 mm long connective appendage not included. Scars of tepals and stamens along 5–9 mm of the torus. Carpels many (rarely less than 15) 1. *M. macklottii*
10. 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. Stamens c. 5 mm, 0.5–1 mm long connective appendage not included. Scars of perianth and stamens along 1 mm of the torus 5. *M. phaulantha*
11. 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 2. *M. carsonii*

I. Subgenus *Magnolia*

Ripe fruits consisting of free carpels which dehisce along the dorsal suture. Anthers dehiscing introrsely. Flowers neither precocious nor with a much reduced calyx-like whorl of outer tepals. Leaves in Asia evergreen.

Only one section indigenous:

I. Section *Maingola*

DANDY, Curtis Bot. Mag. 155 (1948) *sub* t. 16; NOOT, Blumea 31 (1985) 88; *ibid.* 32 (1987) 346.

KEY TO THE SPECIES

1. Carpels many, or at least 15 (rarely in *M. macklottii* 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. macklottii*
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. Brachyblast 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. Brachyblast 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*

1. *Magnolia macklottii* (KORTH.) DANDY, Kew Bull. (1927) 263; BACKER & BAKH, f. Fl. Java 1 (1963) 97; NOOT, in Whitmore & Tantra, Tree Fl. Indonesia, Sumatra Checklist (1986) 141; Blumea 32 (1987) 347. — *Manglietia macklottii* KORTH, Ned. Kruidk. Arch. 2, Versl. (1851) 97; MIQ, Fl. Ind. Bat. 1, 2 (1858) 15, excl. coll. Haleban; Suppl. (1860) 153; Ann. Mus. Bot. Lugd.-Bat. 4 (1868) 71, excl. coll. Haleban. — Type: KORTHALS (L; BO), Sumatra, Mt Singalan.

M. javanica K. & V. Bijdr. 4 (1896) 315; Exk. Fl. Java 2 (1912) 239; KOORD.-SCHUM, Syst. Verz. 1, Fam. 95 (1913) 2; K. & V. Atlas 4 (1918) t. 800; RANT, Nat. Tijds. Ned. Ind. 89 (1929) 446. — *M. pealiana* (non KING) K. & V. Bijdr. 4 (1896) 148, 314 (err. 'pealii'). — Lectotype: KOORDERS 4520 (L; BO).

Michelia beccariana (AGOSTINI), Atti Com. Accad. Fisiocrit. Siena IX, 7 (1926) sep. 23. — *M. beccariana* (AGOSTINI) NOOT, in Whitmore & Tantra, Tree Fl. Indonesia, Sumatra Checklist (1986) 141, nom. inval. — Type: BECCARI P.S. 116 (FI; BM, K, photo in L), Sumatra, Mt Singalan.

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 appressedly to patently long soft hairy, rarely nearly glabrous, 3–9 cm. *Leaves* appressedly 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. *Brachyblast* appressedly 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 as 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* cylindric, distorted by the abortive carpels, 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.

a. var. *macklottii*. — *M. javanica* K. & V.

Leaves mostly elliptic. Flower buds and carpels glabrous.

Distr. *Malesia*: Sumatra (W. coast, G. Singgalan, Palembang); W. Java, Borneo (Sabah, Tawau).

Ecol. Rare in primary vegetation; 80–1500 m. Vern. Java: *tjampacca rimbo, t. gunung*.

b. var. *beccariana* (AGOSTINI) NOOT, Blumea 32 (1987) 348. — *Michelia beccariana* AGOSTINI. — *M. aequinoctialis* DANDY.

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.).

Ecol. Rare in the mountains; 1000–2600 m; fl. Feb.–Aug., fr. May–June.

Note. The collection from Perak was identified as *M. maingayi* KING. It rather belongs to *M. macklottii* var. *beccariana* but demonstrates the close affinity between the two taxa.

2. *Magnolia carsonii* DANDY ex NOOT, Blumea 32 (1987) 348, f. 1. — *Carson's Magnolia* W. MEIJER, The Magnoliaceae of Sabah, Bot. Bull. Sandakan 11 (1968) 7, fig. — *M. 'carsonii'* DANDY ex COCKBURN, Sabah For. Rec. 10 (1980) 56, t. 17, nomen. — Type: SAN A 1680 (L; SING).

Drymis-leaved Magnolia W. MEIJER l.c. 8, fig. — *M. 'drymifolia'* DANDY ex COCKBURN, l.c. 55, nomen. — Type: NOOTEBOOM 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. *Brachyblast* 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 gynop-



Fig. 1. *Magnolia carsonii* DANDY ex NOOT. var. *carsonii*. a. Habit, $\times 1$; b. fruit, $\times 3$ (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

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

b. var. *drymifolia*

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 larger 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.

Distr. Malesia: Borneo (Sabah, Kinabalu, Crocker Range).

Ecol. Locally rather common, especially in Sosopodon For. Res.; 1200–1800 m; *fl. fr.* probably Jan.–Dec.

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 glaucous underneath, 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 \pm 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 Palimasan).

Ecol. Primary and secondary mountain forest; 1000–2850 m; *fl. fr.* probably Jan.–Dec.

Note. Undersurface of leaves often papillate.

3. *Magnolia maingayi* KING, *J. As. Soc. Beng.* 58, ii (1889) 369; *Ann. Bot. Gard. Calc.* 3 (1891) 208, t. 45 B; C. CURTIS, *J. Str. Br. R. As. Soc. n.* 25 (1894) 71; MERR. *Enum. Born.* (1921) 251; excl. coll. BECCARI 2661, 3660; RIDLEY, *Fl. Mal. Pen.* 1 (1922) 13; BURK. *Dict.* (1935) 1393; W. MEIJER, *Bot. Bull. Sabah* 11 (1968) 9; COCKBURN, *Sabah For. Rec.* 10 (1980) 55. — Type: MAINGAY 17 (?; iso L).

Treeclet 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, glabrescent, glabrous 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 cm; 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.



Fig. 2. *Magnolia carsonii* DANDY ex NOOT. var. *drymifolia* NOOT. a. Habit, $\times 0.7$; b. flower, $\times 1$; c. reduced leaf from spathaceous bracts, $\times 0.7$ (NOOTEBOOM 4612).

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.

Vern. Borneo: *analwei*, *leka*, Kelabit.

4. *Magnolia uvariifolia* DANDY ex NOOT. Blumea 32 (1987) 358, f. 6. — *Uvaria-leaved Magnolia* W. MEIJER, Bot. Bull. Sandakan 11 (1968) 9. — *M. 'uvariifolia' (sic!)* DANDY ex COCKBURN, Sabah For. Rec. 10 (1980) 55, *nomen*. — Type: CLEMENS 28439 (L; BO, NY). — Fig. 3.

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.

Distr. *Malesia*: Borneo (Sarawak, Kapit, 3rd Div.; Sabah, G. Alab, Tambunan, Penampang, Kinabalu; SE. Kalimantan, Berouw).

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 uvarufoha* DASDY ex NOOT. a. Habit, $\times 0.6$; b. ovary, $\times 1.5$; c. anthers, $\times 6$; d. fruit, $\times 0.8$.

maingayi which, however, differs in the mostly longer and denser indumentum and in the flower buds and carpels being hairy.

5. *Magnolia phaulantha* DANDY ex NOOT. *Blumea* 32 (1987) 359. — Type: FRI bb 29194 (L; A, SING).

Tree 10 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, Masamba, Malili, Rantelema, 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*

(JUSS.) PIERRE, *Fl. For. Cochinch.* 1 (1881) *sub* t.1; NOOT. *Blumea* 31 (1985) 89; *ibid.* 32 (1987) 360.

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*

(BLUME) NOOT. *Blumea* 31 (1985) 89. — *Aromadendron* BLUME, *Bijdr.* (1825) 10; *Fl. Java Magnol.* (1829) 25. — *Talauma sect. Aromadendron* MIQ. *Ann. Mus. Bot. Lugd.-Bat.* 4 (1868) 70.

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*
3. Nerves in 11–16 pairs. Petiole 8–25 mm. Fruit 5–7 by 3–5 mm.
4. Tepals 18–36 6. *M. elegans*
4. Tepals 12 9. *M. borneensis*

6. *Magnolia elegans* (BLUME) H.KENG, Gard. Bull. Sing. 31 (1978) 129; NOOT. in Whitmore & Tantra, Tree Fl. Indonesia, Sumatra Checklist (1986) 141; Blumea 32 (1987) 361. — *Aromadendron elegans* BLUME, Bijdr. (1825) 10; Fl. Java Magnol. (1829) 26, t. 7, 8; MOR. Syst. Verz. (1846) 36; KORTH. Ned. Kruidk. Arch. 2, Versl. (1851) 97; MIQ. Fl. Ind. Bat. 1, 2 (1858) 16; RIDLEY, Fl. Mal. Pen. 1 (1922) 17, f. 3; BURK. Gard. Bull. S. S. 6 (1930) 454; Dict. (1935) 241; BACKER & BAKH.f. Fl. Java 1 (1963) 98. — *Talauma elegans* (BLUME) MIQ. Ann. Mus. Bot. Lugd.-Bat. 4 (1868) 70; K. & V. Meded. Lands Plantent. 17 (1896) 167; RIDLEY, J. Str. Br. R. As. Soc. n. 33 (1900) 38; BACKER, Schoolfl. Java (1911) 13; KOORD. Exk. Fl. Java 2 (1912) 239; KOORD.-SCHUM. Syst. Verz. 1, Fam. 95 (1913) 4; BAKER f. J. Bot. 62, Suppl. (1924) 2, excl. parte; *ibid.* 64, Suppl. 1 (1926) 142. — Type: BLUME (L; BO).

Aromadendron glaucum KORTH. Ned. Kruidk. Arch. 2, Versl. (1851) 98. — *Talauma glaucum* (KORTH.) MIQ. Ann. Mus. Bot. Lugd.-Bat. 4 (1868) 70, excl. syn. *Manglietia oortii*. — *M. glauca* (KORTH.) PIERRE, Fl. For. Cochinch. 1 (1881) sub t. 2, non *M. glauca* L. (1759). — *Talauma elegans* var. *glaucum* (KORTH.) P. PARMENT. Bull. Sc. Fr. Belg. 27 (1896) 277, 336. — *Aromadendron elegans* var. *glaucum* (KORTH.) DANDY, Kew Bull. (1928) 183. — Type: KORTHALS (L; NY).

Manglietia oortii KORTH. Ned. Kruidk. Arch. 2, Versl. (1851) 97; MIQ. Fl. Ind. Bat. 1, 2 (1858) 15; *ibid.* Suppl. 1 (1860) 153, excl. coll. TEIJSMANN. — *Manglietia oortii* MIQ. Suppl. (1860) 153, excl. coll. Haleban. — Type: KORTHALS (L; NY), Singalan.

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. *glaucum*'), 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 uppersurface but on the uppersurface hardly distinct from the venation; reticulation densely netted, prominent on both surfaces, the marginal vein included in the reticulation. Petiole 8–20(–25) mm. *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 ellip-

tic, slightly shorter and much narrower. *Stamens* 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 gynophore 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, gynophore also c. 5 mm long but rarely shorter to nearly absent.

Distr. *Malesia*: Sumatra incl. Banka, Malay Peninsula (Penang, Selangor, Perak, Singapore), W. Java.

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*, *kayu sulung*, *kedondong tunjuk*, *medang mempau*, *m. pauh*, *M. utup-utup*, Batak.

7. *Magnolia bintuluensis* (AGOSTINI) NOOT. [in Whitmore & Tantra, Tree Fl. Indonesia, Sumatra Checklist (1986) 141, *nom. inval.*] Blumea 32 (1987) 362. — *Talauma bintuluensis* AGOSTINI, Atti Com. Accad. Fisiocrit. Siena IX, 7 (1926) sep. 26; NOOT. in Whitmore & Tantra, Tree Fl. Indonesia, Sumatra Checklist (1986) 143. — Type: BECCARI P.S. 2661 (F1; K). Syntype: BECCARI P.S. 3660.

Aromadendron nutans DANDY, Kew Bull. (1928) 183; W. MEIJER, Bot. Bull. Sandakan 11 (1968) 5; COCKBURN, Sabah For. Rec. 10 (1980) 53, t. 16. — *M. maingayi* (non KING) RIDLEY, Enum. Born. (1913) 72, *p.p.*; MERR. Enum. Born. (1921) 251, *p.p.* — *M. nutans* (DANDY) H.KENG, Gard. Bull. Sing. 31 (1978) 129. — Type: BECCARI P.S. 3660 (K; F1).

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 3–7.5 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 uppersurface, 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; gynophore absent. *Fruits* ellipsoid, c. 3–4.5 by 2–3.5 cm, no pedicel or



Fig. 4. *Magnolia ashtonii* DANDY ex NOOT. a. Habit with flower, $\times 0.6$; b. ovary, $\times 1.8$; c. anthers, $\times 1.8$; d. fruit, $\times 0.6$ (a, c S 7895 ASHTON, b BRUN 5503, d S 12449).

gynophore. Scars of perianth and stamens along c. 3 mm of the torus.

Distr. *Malesia*: Sumatra (Indragiri, Biliton), Malay Peninsula (Johore), Borneo (Sarawak, Brunei, Sabah, Kalimantan).

Ecol. Rare, 21 collections in total. As far as recorded often in (coastal) swamp, kerangas, in E. Kalimantan in *Agathis* forest on sandy waterlogged soil; 0–1000 m. Fr. Feb.–Sept.

Vern. Sumatra: *kedondong kijai*; Borneo: *medang pelam*, W. Kalimantan, *triburus*, Sarawak, Land Dyak.

8. *Magnolia ashtonii* DANDY ex NOOT. *Blumea* 32 (1987) 363, f. 7. — *Ashton's Aromadendron* W. MEIJER, Bot. Bull. Sandakan 11 (1968) 5, t. — *Aromadendron 'ashtonii'* DANDY ex COCKBURN, Sabah For. Rec. 10 (1980) 53, *nomen*. — *M. ashtonii* NOOT, in Whitmore & Tantra, Tree Fl. Indonesia, Sumatra Checklist (1986) 141, *nomen*. — Type: S 7895 (ASHTON) (L; A, K, SING). — Fig. 4.

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 densely punctulate, 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).

9. *Magnolia borneensis* NOOT. *Blumea* 32 (1987) 366, f. 8. — *Borneo Aromadendron* W. MEIJER, Bot. Bull. Sandakan 11 (1968) 5. — *Aromadendron 'borneensis'* DANDY ex COCKBURN, Sabah For. Rec. 10 (1980) 53, *nomen*. — Type: PAYMANS 173 (L; K, SING). — Fig. 5.

Tree 23–40 m by 40–112 cm; twigs glabrous; stip-

ules 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) cm. *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 ultrabasic in Palawan; from low up to 1800 m; fl. Feb.–Aug., fr. Feb.–Nov.

Vern. *Asam*, *M. jalat*, *uwun*, 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*.

10. *Magnolia pahangensis* NOOT. *Blumea* 32 (1987) 367. — Type: KIP FRI 9030 (L; SING).

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. leriau), only known from the type.



Fig. 5. *Magnolia borneensis* Noot. a. Habit, $\times 0.9$; b. ovary, $\times 5$; c. stamen, $\times 1.8$ (PAIJMANS 173).

3. Section Blumiana

BLUME, Fl. Java Magnol. (1829) 32; NOOT, Blumea 31 (1985) 89; *ibid.* 32 (1987) 367. — *Blumea* NEES, Flora 8 (1825) 152.

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 third 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 styler 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 (villous) 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. persuaveolens*
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. persuaveolens*
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*

11. *Magnolia candollii* (BLUME) H. KENG, Gard. Bull. Sing. 31 (1978) 129 ('*decandollii*'); NOOT, Blumea 32 (1987) 369. — *Talauma candollii* BLUME, Verh. Bat. Gen. K. W. 9 (1823) 147. — Lectotype: BLUME s.n. (L.), Salak. — Fig. 6.

For further synonymy see under the varieties.

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

- diam. at top 5–13 mm. Stamens 12–30 mm. Carpels 10–c. 100, with an up to 15 mm long woody styler 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!).
3. Twigs diam. 3–7 mm. Peduncle diam. at top 2–9 mm. Carpels c. 5–100. **a. var. candollii**
3. Twigs diam. 5–12 mm. Peduncle diam. at top 8–20 mm. Carpels c. 40–200.
4. Carpels c. 200. Stamens c. 10 mm. Petiole 2–4 cm **d. var. beccarii**
4. Carpels c. 40–150. Stamens 12–30 mm. Petiole 1.5–11 cm.
5. Leaves (at least when young) hairy beneath. Carpels c. 50–100. Stamens 13–30 mm. Petiole 2.5–11 cm **e. var. singapurensis**
5. Leaves glabrous beneath. Carpels c. 40–150. Stamens 12–20 mm. Petiole 1.5–6.5 cm
- c. var. angatensis**

a. var. candollii. — *M. candollii* (BLUME) H. KENG, Gard. Bull. Sing. 31 (1978) 129 ('*decandollii*'). — *Talauma candollii* BLUME, Verh. Bat. Gen. K. W. 9 (1823) 147; Bijdr. (1825) 9; Fl. Java Magnol. (1829) 32, t. 9, 12A; Hook. Curtis Bot. Mag. 72 (1846) t. 4251; MIQ. Fl. Ind. Bat. 1, 2 (1858) 14; Ann. Mus. Bot. Lugd.-Bat. 4 (1868) 68, *excl. parte*; KURZ, J. As. Soc. Beng. 43, ii (1874) 47; For. Fl. Burma 1 (1877) 24; K. & V. Bijdr. 4 (1896) 166; BACKER, Fl. Batavia 1 (1907) 8; KOORD. Exk. Fl. Java 2 (1912) 240, t. 48; KOORD.-SCHUM. Syst. Verz. 1, Fam. 95 (1913) 3; RIDLEY, Contr. Fl. Born. (1913) 72, *p.p.*; MERR. Enum. Born. (1921) 251, *p.p.*; BURK. Dict. 2 (1935) 2120; GAGNEP. Fl. Gén. I.-C. Suppl. 1 (1938) 31; H. KENG, Tree Fl. Malaya 2 (1973) 293; NOOT. in Whitmore & Tantra, Tree Fl. Indonesia, Sumatra Checklist (1986) 143; Blumea 32 (1987) 369, f. 9. — *Blumia candollii* (BLUME) NEES, Flora 8 (1825) 152. — *Manglietia candollii* (BLUME) WALL. Cat. (1832) 6497. — Lectotype: BLUME *s.n.* (L), Salak.

Talauma candollii BLUME *var. latifolia* BLUME, Bijdr. (1825) 9. — Lectotype: BLUME *s.n.* (L), Noesa Kambangan.

M. rumphii SPRENG. Syst. Veget. 4, 2 (1827) 217. — [*Sampacca montana* RUMPH. Herb. Amb. 2 (1741) 204, t. 69.] — *Liriodendron liliiferum* LINNÉ, Sp. Pl. ed. 2, 1 (1762) 755. — *M. pumila auct. non* ANDR.: DC. Syst. 1 (1817) 458, *p.p.*; Prod. 1 (1824) 81, *p.p.* — *Talauma rumphii* BLUME, Bijdr. (1825) 10; Fl. Java Magnol. (1829) 39; MIQ. Fl. Ind. Bat. 1, 2 (1858) 14; MERR. Interpr. Rumph. (1917) 224. — *Talauma pumila* BLUME, Fl. Java Magnol. (1829) 38, *pro syn.* LINNÉ. — *M. liliifera* (LINNÉ) BAILLON,

Hist. Pl. 1 (1868) 141, *excl. parte*; DRUCE, Bot. Exch. Club Soc. Br. Is. 3 (1914) 421. — *Talauma liliifera* (LINNÉ) O. K. Rev. Gen. Pl. 1 (1891) 6, *excl. var., non T. liliifera* KURZ (1874). — Type: RUMPHIUS t. 69.

Talauma mutabilis BLUME, Fl. Jav. Magnol. (1829) 35, t. 10, 11, 12B; KORTH. Ned. Kruidk. Arch. 2, Versl. (1851) 98; MIQ. Fl. Ind. Bat. 1, 2 (1858) 14; Suppl. 1 (1860) 152; (1861) 366; Hook. *f.* & THOMS. Fl. Br. India 1 (1872) 40; F.-VILL. Nov. App. (1880) 3; KING, J. As. Soc. Beng. 58, ii (1889) 373; Ann. Bot. Gard. Calc. 3 (1891) 203, t. 44; CRAIB, Fl. Siam. Enum. 1 (1925) 25. — Lectotype: BLUME *s.n.* (L), Bantam.

Talauma mutabilis BLUME *var. acuminata* BLUME, Fl. Java Magnol. (1829) 36, t. 11, *excl. sciagr.* — Lectotype: BLUME *s.n.* (L), Parang.

Talauma mutabilis BLUME *var. longifolia* BLUME, Fl. Java Magnol. (1829) 37; FINET & GAGNEP. Fl. Gén. I.-C. 1 (1907) 33. — *Talauma longifolia* (BLUME) RIDLEY, J. Fed. Mal. St. Mus. 17 (1916) 38; Fl. Mal. Pen. 1 (1922) 16; CRAIB, Fl. Siam. Enum. 1 (1925) 25, *excl. parte*. — Lectotype: BLUME *s.n.* (L).

Talauma mutabilis BLUME *var. splendens* BLUME, Fl. Java Magnol. (1829) 38, t. 11 ('*sciagraphia*'). — *M. splendens* REINW. *ex* BLUME, Fl. Jav. Magnol. (1829) 38 *nom. syn., non M. splendens* URB. (1899). — Type: REINWARDT (L).

Talauma rubra MIQ. Fl. Ind. Bat. 1, 2 (1858) 14; Suppl. 1 (1860) 153; Ann. Mus. Bot. Lugd.-Bat. 4 (1868) 69; NOOT. in Whitmore & Tantra, Tree Fl. Indonesia, Sumatra Checklist (1986) 143. — Type: TEIJSMANN HB 470 (U; BO, L), Sumatra, Lolong.

Manglietia celebica MIQ. Ann. Mus. Bot. Lugd.-Bat. 4 (1868) 72. — *Talauma miqueliana* DANDY, Kew Bull. (1927) 262. — Type: TEIJSMANN & DE VRIESE (L; BO), Celebes.

Manglietia sebassa KING, J. As. Soc. Beng. 58, ii (1889) 370; Ann. Bot. Gard. Calc. 3 (1891) 211, t. 54; RIDLEY, Fl. Mal. Pen. 1 (1922) 14. — *Talauma sebassa* MIQ. [Fl. Ind. Bat. Suppl. 1 (1860) 153, *nomen*] *ex* DANDY, Kew Bull. (1928) 192; H. KENG, Tree Fl. Malaya 2 (1973) 294; NOOT. in Whitmore & Tantra, Tree Fl. Indonesia, Sumatra Checklist (1986) 143. — Type: TEIJSMANN 3983 (U; BO, L), Sumatra, Moeara Enim.

Talauma forbesii KING, J. As. Soc. Beng. 58, ii (1889) 373; Ann. Bot. Gard. Calc. 3 (1891) 206, t. 45A. — *M. forbesii* KING, Ann. Bot. Gard. Calc. 3 (1891) 206, *nom. syn.* — Type: FORBES 8153 (CAL, *n.v.*; BM, K, GH), Sumatra.

Talauma kunstleri KING, J. As. Soc. Beng. 58, ii (1889) 373; RIDLEY, Fl. Mal. Pen. 1 (1922) 16. — *M. kunstleri* KING, Ann. Bot. Gard. Calc. 3 (1891) 204, *nom. syn.* — Type: KING's coll. 6383 (BM, K).

Talauma inflata P. PARMENT. Bull. Sc. Fr. Belg. 27 (1896) 208, 273, t. 8, f. 10. — *Talauma undulatifolia*

AGOSTINI, Atti Com. Accad. Fisiocrit. Siena ser. IX, 7 (1926) sep. 26. — Type: BECCARI PS 76 (MEL; BM, BO, L).

Talauma javanica P. PARMENT. Bull. Sc. Fr. Belg. 27 (1896) 208, 274. — Type: ZOLLINGER 2809 (MEL, n.v.; A, BM, BO).

Talauma gitingensis ELMER, Leafl. Philip. Bot. 4 (1912) 1497; DANDY, Kew Bull. (1927) 420. — Type: ELMER 12443 (n.v.).

Talauma oreadum DIELS, Bot. Jahrb. 54 (1916) 240; A.C. SMITH, J. Arn. Arb. 23 (1942) 441; CROFT in Womersley, Handb. Fl. Papua New Guinea (1978) 129, t. 66. — *Aromadendron oreadum* (DIELS) KANEH. & HATUS. Bot. Mag. Tokyo 57 (1943) 147. — Type: LEDERMANN 9114 (K), Sepik Gebiet: Etappenberg, 850 m.

Talauma reticulata MERR. Philip. J. Sc. 17 (1920) 249. — Type: BS 35187 (K), Dinagat I.

Talauma borneensis MERR. J. Str. Br. R. As. Soc. n. 85 (1922) 173. — Type: RAMOS 1533 (L, BO), Sandakan and vicinity.

Talauma sumatrana AGOSTINI, Atti Com. Accad. Fisiocrit. Siena ser. IX, 7 (1926) sep. 28. — Type: BECCARI PS 918 (FI; L), Sumatra, Padang; Sgei Balu.

M. pachyphylla DANDY, Kew Bull. (1928) 186. — Type: FB 3864 CURRAN (K; NY, US).

Talauma athliantha DANDY, l.c. 189. — Type: RIDLEY (K), Sumatra, Berastagi.

Talauma gitingensis var. *glabra* DANDY, l.c. 189. — Type: BS 39436 RAMOS (BM; BO, US).

Talauma gitingensis 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: BURKILL & HANIFF 16053 (K; BO, SING).

Talauma soembensis DANDY, Kew Bull. (1928) 193. — Type: IBOET 311 (BO; L), Soemba, Boendohero.

Champaca turbinata NOR. Verh. Bat. Gen. K. W. 5, 4 (1791) 12, *nomen*.

M. fragrans REINW. ex BLUME, Cat. Gewassen Lands Plantent. Buzg (1823) 79, *nomen*.

M. odoratissima REINW. ex BLUME, l.c., *nomen*.

M. pumila auct. non ANDR.: BLUME, Bijdr. (1825) 9, p.p. — *Talauma pumila* auct. non ANDR.: BLUME, Fl. Jav. Magnol. (1829) 38, p.p.; MIQ. Fl. Ind. Bat. 1, 2 (1858) 14, p.p.; Ann. Mus. Bot. Lugd.-Bat. 4 (1868) 69; RIDLEY, J. Mal. Br. R. As. Soc. 1 (1923) 51.

Talauma mutabilis var. *acuminatissima* T. & B. Cat. Hort. Bogor. (1866) 177, *nomen*.

Talauma mutabilis var. *brevifolia* T. & B. l.c., *nomen*.

Talauma mutabilis var. *latifolia* T. & B. l.c., *nomen*.

Talauma mutabilis var. *leiocarpa* T. & B. l.c., *nomen*.

Talauma macrophylla BLUME ex MIQ. Ann. Mus. Bot. Lugd.-Bat. 4 (1868) 68, *nom. syn.*

Talauma villariana ROLFE, J. Linn. Soc. Bot. 21 (1884) 307, *pro syn.* F.-VILL. *excl. typus*; MERR. Philip. J. Sc. 1 (1906) Suppl. 52; Philip. J. Sc. 5 (1910) C 348; Sp. Blanc. (1918) 12 ('*villarii*'); Enum. Philip. 2 (1923) 152, p.p.

Talauma elegans auct. non MIQ.: 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 appressedly 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) appressedly 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–)3.5–15(–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 densely long 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; spatheaceous 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 ± elliptic, 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. Seed(s) 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).

DISTR.—Sikkim, Assam (Khasi Hills), Thailand,



Fig. 6. *Magnolia candollii* (BLUME) H.KENG var. *candollii* 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.

Vern. Sumatra: *djato*, Karo, *medang abu*, Kerinci, *si tekwok*, Pahang; Java: *kembang tundjung*, *ketundjung*, *tjempaka gonda*, *t. gondoh*, *t. gondok*, *t. gunung*, *t. putih*; Lesser Sunda Islands: *longkor*, Flores; Borneo: *tjempaka telur*, Pontianak, *talahuma*, Iban; Philippines: *anobling*, Luzon; Sulawesi: *danoan*, *wasian-batu*, *wasian-watu*, Minahasa; New Guinea: *adjai dia diwarmom*, Kebar Valley.

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.

b. var. obovata (KORTH.) NOOT. *Blumea* 32 (1987) 374. — *Talauma obovata* KORTH. Ned. Kruidk. Arch. 2, Versl. (1851) 98, non *M. obovata* THUNB.; MIQ. *Fl. Ind. Bat.* 1, 2 (1858) 14; Ann. Mus. Bot. Lugd.-Bat. 4 (1868) 69; RIDLEY, *Contr. Fl. Borneo* (1913) 72, *excl. spec. Bangka*; MERR. *Enum. Born.* (1921) 251, *excl. parte*. — Lectotype: KORTHALS *s.n.* (L; BO; syntype: L), G. Pamatton.

Talauma betongensis CRAIB, [*Fl. Siam. Enum.* 1 (1924) 24, *nomen*] *Kew Bull.* (1925) 7; DANDY, *Kew Bull.* (1928) 189. — *M. betongensis* (CRAIB) H. KENG, *Gard. Bull. Sing.* 31 (1978) 129. — Type: KERR 7449 (K; BM).

Talauma oblanceolata RIDLEY, *Fl. Mal. Pen.* 5 (1925) 286, *excl. pl. e Borneo et Bangka*; DANDY, *Kew Bull.* (1928) 192; H. KENG, *Tree Fl. Malaya* 2 (1973) 294. — Type: RIDLEY 15590 (SING, K).

Talauma levissima DANDY, *Kew Bull.* (1928) 191. — Type: RIDLEY 9047 (K; SING).

Talauma sclerophylla DANDY, *J. Bot.* 66 (1928) 47. — Type: HAVILAND 3148 (BM; K).

Talauma candollei auct. non BLUME: RIDLEY, *Contr. Fl. Born.* (1913) 72, *p.p.*; MERR. *Enum. Born.* (1921) 251, *p.p.*

Manghetia glauca auct. non BLUME: RIDLEY, *Fl. Mal. Pen.* 1 (1922) 14, *pro coll. Bell & Haniff*.

Treelet, 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, intramarginal vein present; reticulation rather coarse, sometimes obscure (*T. levissima* 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.

Vern. Borneo: *tala umah*, Iban.

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.

c. var. angatensis (BLANCO) NOOT. *Blumea* 32 (1987) 375. — *M. angatensis* BLANCO, *Fl. Filip.* (1837) 859; ed. 3, 2 (1878) 243. — *Talauma angatensis* (BLANCO) VIDAL, *Cat. Pl. Prov. Manila* (Nov. 1880) 17; F.-VILL. *Nov. App.* (Dec. 1880) 3; VIDAL, *Sin. Philip. Atl.* (1883) t. 3; *Rev. Pl. Vasc. Filip.* (1886) 38; CERON, *Cat. Pl. Herb.* (1892) 9; MERR. *Bur. Gov. Lab. Philip. Publ.* 35 (1906) 7; Sp. Blanc. (1918) 146; *Enum. Philip.* 2 (1923) 151. — Type: BLANCO (*n.v.*).

Talauma villariana ROLFE, *J. Linn. Soc. Bot.* 21 (1884) 307, *excl. syn.*; VIDAL, *Rev. Pl. Vasc. Filip.* (1886) 38; CERON, *Cat. Pl. Herb.* (1892) 9; MERR. *Enum. Philip.* 2 (1923) 152, *excl. maj. parte*. — *Talauma mutabilis auct. non BLUME*: F.-VILL. *Nov. App.* (1880) 3, *excl. parte et tab. 148*. — Type: VIDAL 5 (K, I), Bulacan. VIDAL 5 in A is different and belongs to *var. candollei*.

Talauma luzoniensis WARB. *ex PERKINS*, *Fragm. Fl. Philip.* (1904) 171; MERR. *Bur. Gov. Lab. Philip. Publ.* 35 (1906) 8; *Philip. J. Sc.* 3 (1909) C 406. — Type: WARBURG 11767 (?B, *n.v.*).

Talauma grandiflora MERR. *Bur. Gov. Lab. Philip. Publ.* 29 (1905) 13; *ibid.* 35 (1906) 7. — Type: FB 314 (*n.v.*, photo BM).

Talauma oblongata MERR. *Bur. Gov. Lab. Philip. Publ.* 35 (1906) 8. — Type: MERRILL 1003 (*n.v.*).

Talauma gigantifolia auct. non MIQ.: F.-VILL. *Nov. App.* (1880) 4.

Tree to 18 m by 45 cm diam.; twigs appressedly pubescent to glabrous, diam. 5–12 mm. *Leaves* glabrous, (narrowly to broadly) 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 stylar spines to c. 7 mm long.

Distr. *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.

d. var. beccarii (RIDLEY) NOOT. *Blumea* 32 (1987) 375. — *Talauma beccarii* RIDLEY, *Kew Bull.* (1912) 381; *Contr. Fl. Born.* (1913) 72; MERR. *Enum. Born.* (1921) 251. — Type: BECCARI 3959 (K; FI), Sarawak, colline del Sadong.

Tree (7–)15–30 m 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.

Distr. *Malesia*: Borneo (Sarawak, 1st & 3rd Div., Kapit Distr., 4th Div., Marudi; Sabah, Lahad Datu; E. Kalimantan, Berouw, Sangkuliran I., W. Kalimantan, Amai Ambit).

Ecol. Forest; to 800 m.

Vern. Borneo: *talauma*, Iban.

Field notes. Flowers yellow or cream coloured.

e. var. singaporensis (RIDLEY) NOOT. *Blumea* 32 (1987) 376. — *Talauma singaporensis* RIDLEY, *Kew*

Bull. (1914) 323; *Fl. Mal. Pen.* 1 (1922) 16; DANDY, *Kew Bull.* (1928) 192; H. KENG, *Tree Fl. Malaya* 2 (1973) 293; NOOT, in Whitmore & Tantra, *Tree Fl. Indonesia, Sumatra Checklist* (1986) 143. — *M. singaporensis* (RIDLEY) H. KENG, *Gard. Bull. Sing.* 31 (1978) 129. — Lectotype: RIDLEY 5091 (SING; BM), Singapore, Chan Chukang.

Talauma kuteinensis AGOSTINI, *Atti. Com. Accad. Fisiocrit. Siena ser. IX*, 7 (1926) sep. 30. — Type: BECCARI PB 2102 (FI).

Talauma lanigera auct. non HOOK. f. & THOMS.: RIDLEY, *J. Str. Br. R. As. Soc. n. 33* (1900) 38.

Talauma obovata auct. non KORTH.: RIDLEY, *Contr. Fl. Born.* (1913) 72, *pro spec. Bangka*; MERR. *Enum. Born.* (1921) 251, *pro coll. Low*.

Talauma oblanceolata RIDLEY, *Fl. Mal. Pen.* 5 (1925) 286, *quoad pl. Borneo et Banca*.

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 incurved, (5–)12–17 mm long. *Fruits* 10–15 by 6–7 cm.

Distr. *Malesia*: Sumatra, Simalur I., Banka, Malay Peninsula (incl. Singapore), Borneo (Sarawak, Kuching, Semengoh Arb., 3rd Div., Kapit Distr., Kutein; Sabah, Sandakan, Sgei Labuk, Sipiting, Ulu Mendalong; E. Kalimantan, 3 coll.).

Ecol. Primary rain-forest; 0–600 m.

12. *Magnolia gigantifolia* (Miq.) NOOT. *Blumea* 32 (1987) 377. — *Talauma gigantifolia* MIQ. *Fl. Ind. Bat.* 1, 2 (1858) 15; *Suppl.* (1860) 153; (1861) 366; T. & B. *Cat. Hort. Bogor.* (1866) 177; MIQ. *Ann. Mus. Bot. Lugd.-Bat.* 4 (1868) 70; BOERL. *Cat. Hort. Bogor.* (1899) 7; RIDLEY, *Contr. Fl. Born.* (1913) 72; MERR. *Enum. Born.* (1921) 251; *Pl. Elm. Born.* (1929) 60; NOOT, in Whitmore & Tantra, *Tree Fl. Indonesia, Sumatra Checklist* (1986) 143. — Type: TEIJSMANN HB 463 (U; BO, L), West coast Sumatra, Sungei Pagoe.

Talauma megalophylla MERR. *J. Str. Br. R. As. Soc. n. 85* (1922) 172. — Type: RAMOS 1509 (A; K), Sandakan and vicinity.

Talauma magna AGOSTINI, *Atti Com. Accad. Fisiocrit. Siena ser. IX*, 7 (1926) sep. 31. — Type: BEC-

CARI PS 498 (FI; L). ad Ayer mancier, Provincia di Padang in Sumatra occid.

Talauma elmeri MERR. ex SODERBERG, Svensk Bot. Tidskr. 30 (1936) 538, *nomen*.

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, 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 spines. *Fruit* 13–18 by c. 8 cm.

Distr. *Malesia*: Sumatra (Padang, Palembang, Lampong, Banka), Borneo (Sarawak; Sabah, Sandakan, Tawao; E. Kalimantan, Blu-u, Nunukan, Berouw).

Ecol. Primary forest, on sandy (loam) soil; below 300 m.

Vern. Sumatra: *kayu klappoh, k. tangihah*.

Field notes. The flowers are reported to be from pale white via light red to dark brown, the fruits pale yellowish.

13. *Magnolia lasia* NOOT. Blumea 32 (1987) 377. — Type: KATO c.s. 7830 (L; KYO).

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 *idem*, rather fine. Petiole glabrous or slightly long villous, 4–10 cm long, stipular scar from halfway to up to the apex. Peduncle densely very long villous, 3–more than 20 cm 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 styler 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: *tatal umar*, Iban.

14. *Magnolia persuaveolens* DANDY, Kew Bull. (1928) 186. — *Talauma persuaveolens* DANDY, Taxon 21 (1972) 468. — *Michelia ?spec.* STAPP, Trans. Linn. Soc. Lond. II, Bot. 4 (1894) 128. — Type: Low (K), Kinabalu.

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 styler 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: RSNB 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 glaucous, 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.

Distr. *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.

b2. var. pubescens NOOT. *Blumea* 32 (1987) 379. — Type: BEAMAN 9131 (L; MSC, UKMG).

As *var. rigida*, but twigs, leaves, and carpels densely appressedly pubescent. Nerves in c. 10 pairs. Flowers not known.

Distr. *Malesia*: Borneo (Sabah, Kinabalu), only the type.

Ecol. Altitude 1950–2000 m.

15. *Magnolia sarawakensis* (AGOSTINI) NOOT. *Blumea* 32 (1987) 380. — *Talauma sarawakensis* AGOSTINI, *Atti Com. Accad. Fisiocrit. Siena ser. IX*, 17 (1925) sep. 29. — *Talauma intonsa* DANDY, *Kew Bull.* (1928) 191. — Type: BECCARI PB 3331 (FI; K). The isotype in K is the holotype of *Talauma intonsa* DANDY.

Twigs densely long villous, glabrescent in patches, diam. 5–7 mm. *Leaves* in innovations with same indumentum, soon glabrous, glaucous 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.

Distr. *Malesia*: Borneo (Sarawak, Batang Lupar; Sabah, SE. Kinabalu, Bt Kulung; W. Kalimantan, Singkadjian; E. Kalimantan, Lilit Buan, Teputse).

Ecol. Dipterocarp forest on ultramafic soil; 750 m (once recorded, Bt Kulung).

16. *Magnolia villosa* (MIQ.) H.KENG, *Gard. Bull. Sing.* 31 (1978) 129. — *Talauma villosa* MIQ. [Fl. Ind. Bat. Suppl. (1860) 153, *nomen*] Fl. Ind. Bat. Suppl. (1861) 366; H.KENG, *Tree Fl. Malaya* 2 (1973) 293; NOOT, in Whitmore & Tantra, *Tree Fl. Indonesia, Sumatra Checklist* (1986) 144. — *Talauma rabiana* CRAIB *var. villosa* (MIQ.) P.PARMENT. *Bull. Sc. Fr. Belg.* 27 (1896) 271. — Type: TEIJSMANN HB 3690 (L; BO), Sumatra, Moeara Enim.

Talauma lanigera Hook.f. & THOMS. *Fl. Br. India* 1 (1872) 40; KING, *J. As. Soc. Beng.* 58, ii (1889) 372; *Ann. Bot. Gard. Calc.* 3 (1891) 202, t. 42; RIDLEY, *Fl. Mal. Pen.* 1 (1922) 15. — Type: GRIFFITH 65 (K).

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. Peduncle densely (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).

Distr. *Malesia*: Sumatra (West, Taram, E. of Pajakumbuh), Malay Peninsula (Penang; Perak; Genting highlands; Malacca; Lingga Arch.), Borneo (Sabah, Lamag distr.).

Ecol. Primary forest (once recorded); 450–1000 m.

17. *Magnolia mariusjacobsia* NOOT. *Blumea* 32 (1987) 381, f. 10.

Treelet 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 decurrent 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*.

Distr. *Malesia*: Borneo (Sarawak, 3rd Div., Kapit Distr.).

Ecol. Primary forest on sandstone, on low hills.

Field notes. Outer perianth leaves green, inner ones cream coloured.

2. MANGLIETIA

BLUME, Verh. Bat. Gen. K. W. 9 (1823) 149; Bijdr. (1825) 8; Fl. Java Magnol. (1829) 22; DANDY, Kew Bull. (1927) 259; in Hutch. Gen. Fl. Pl. 1 (1964) 54; NOOT, Blumea 31 (1985) 91. — *Magnolia* sect. *Manglietia* (BLUME) BAILLON, Adansonia 7 (1866) 66. — Type: *M. glauca* BLUME.

Paramanglietia HU & CHENG, Acta Phytotax. Sin. 1 (1951) 255. — Type: *P. aromatica* (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.
 3. Underside of leaves densely minutely reddish-brown appressedly hairy. Nerves in 10–15 pairs 3. *M. calophylla*
 3. Underside of leaves glabrous. Nerves in 14–20 pairs 4. *M. sabahensis*
1. Stipules higher adnate to petiole, stipular scar clearly present.
 4. Innovations, peduncles, stipules and underside of leaves rufous woolly pubescent .. 2. *M. lanuginosa*
 4. 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. dolichogyna*
 5. Fruits ellipsoid or ovoid, only slightly longer than wide 1. *M. glauca* (var. *glauca*)

1. *Manglietia glauca* BLUME, Verh. Bat. Gen. K. W. 9 (1823) 150; Bijdr. (1825) 8; Fl. Java Magnol. (1829) 22, t. 6; KORTH, Ned. Kruidk. Arch. 2, Versl. (1851) 97; MIQ, Fl. Ind. Bat. 1, 2 (1858) 15; Ann. Mus. Bot. Lugd.-Bat. 4 (1868) 71; K. & V. Meded. Lands Plantent. 17 (1896) 150; BACKER, Schoolfl. Java (1911) 14; KOORD. Exk. Fl. Java 2 (1912) 238, f. 47; KOORD.-SCHUM. Syst. Verz. 1, Fam. 95 (1913) 1; BACKER & BAKH.F. Fl. Java 1 (1963) 97; NOOT, Blumea 31 (1985) 92. — *Micheha doltsopa* auct. non BUCH.-HAM. ex DC.: SPRENG, Syst. Verz. 4, 2 (1827) 217; HASSK. Cat. Hort. Bog. (1844) 178. — *Magnolia*

blumei PRANTL in E. & P. Nat. Pfl. Fam. 3, 2 (1888) 16. — Type: BLUME, Salak (n.v.)

M. macklottii auct. non KORTH.: MIQ, Fl. Ind. Bat. 1, 2 (1858) 15, p.p. — *M. oortii* auct. non KORTH.: MIQ, Suppl. (1860) 153. — Type: TEUSMANN HB 466, Haleban.

M. sumatrana MIQ, Suppl. (1860) 153, nomen; *ibid.* (1861) 367; Ann. Mus. Bot. Lugd.-Bat. 4 (1868) 71. — *M. oortii* (non KORTH.) MIQ, Fl. Ind. Bat. 1, 2 (1858) 15, p.p. — *M. glauca* var. *sumatrana* DANDY, Kew Bull. (1928) 188. — Type: TEUSMANN HB 468, Bukit Silit (L; BO).

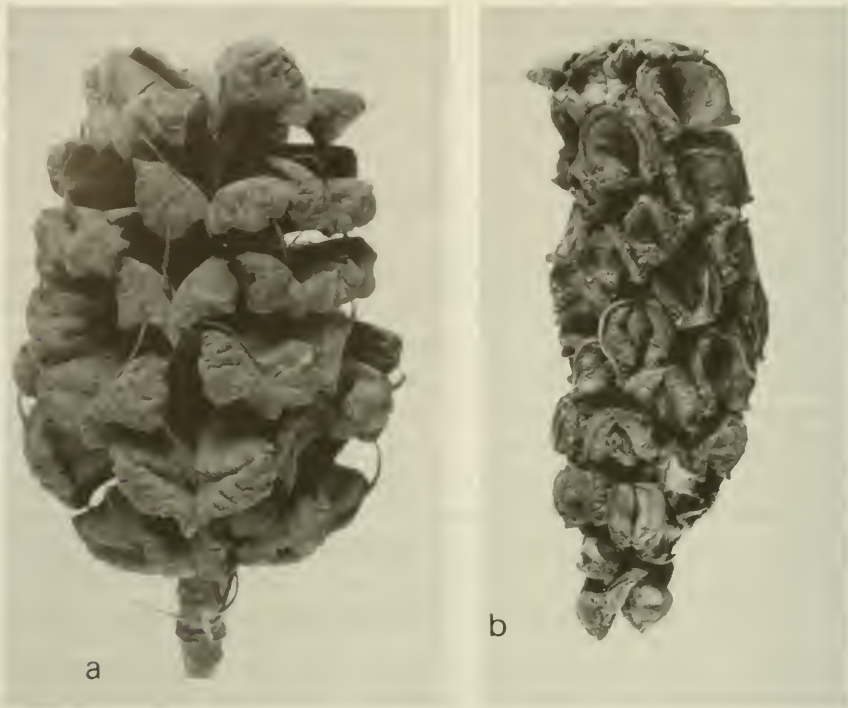


Fig. 7. Fruits of *a. Manglietia glauca* BLUME and *b. M. dolichogyna* DANDY *ex* NOOT., both $\times 1$ (*a* KOORDERS 4449, *b* CLEMENS 26279).

M. pilosa P. PARMENT. Bull. Sc. Fr. Belg. 27 (1896) 217, 292. — *M. singalanensis* AGOSTINI, Atti Com. Accad. Fisiocrit. Siena, ser. IX, 7 (1926) sep. 22. — Type: BECCARI PS 334 (L, FI), Sumatra, Mt Singalan. — Fig. 7a.

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. sumatрана* 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. sumatрана*, without scars or with one scar 15–40 mm, pedicel glabrous, or appressedly hairy in *var. sumatрана*, 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 (Acheh, G. Ketambe;

Sumatera Utara, E. Coast and Tapanuli; W. coast; Lampung, G. Tanggamus), 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*, *tjepoko kantil*; Bali: *tjim-paka*; 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; NOOT, Blumea 31 (1985) 93. — *M. sumatrana* MIQ. — *M. pilosa* P. PARMENT.

Peduncle and pedicel 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.

Distr. *Malesia*: W. Sumatra (G. Singalan, G. Talang, G. Merapi, G. Silit and Padang Panjang).

Ecol. In forests; 600–1300 m; *fl. fr.* Sept.–Oct., *fr.* June.

Vern. *Sikibus*.

Field notes. Flowers yellow or white, fruit black.

2. Manglietia lanuginosa (DANDY) NOOT, Blumea 31 (1985) 94. — *M. glauca* var. *lanuginosa* DANDY, Kew Bull. (1928) 187. — Type: FRI bb 8531 (BO).

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*.

Distr. *Malesia*: Sumatra (around lake Toba: Deli, Simelungun & Karolands, Tapanuli).

Ecol. Primary forest; 1000–1500 m; *fl. fr.* Feb.–Nov.

Vern. *Aduwang*, *antuang*, *modang sanggar*.

Field notes. Flowers cream or green, sweet scented; fruit grey-green becoming brown.

3. Manglietia calophylla DANDY, J. Bot. 66 (1928) 46; NOOT, Blumea 31 (1985) 94. — *M. glauca* (non BLUME) RIDLEY, J. Fed. Mal. St. Mus. 8, 4 (1917) 14. — Type: ROBINSON & KLOSS 200 (BM; SING), Sumatra, Korinchi Peak.

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 indumentum of very small glistening reddish brown hairs

beneath (often only to be seen with a magnification of more than $\times 50$), 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.

Distr. *Malesia*: Sumatra (W. Coast, G. Kerinci).

Ecol. Primary mountain forest; 2000–2200 m; *fl. fr.* Oct., *fr.* May–Aug.

Field notes. Flowers white or yellow.

4. Manglietia sabahensis DANDY ex NOOT, Blumea 31 (1985) 95. — '*Sabah Manglietia*' DANDY ex MEIJER, Bot. Bull. Herb. Sabah 11 (1968) 11, *nomen*. — *M. 'sabahensis'* DANDY ex COCKBURN, Trees of Sabah 2 (1980) 56, *nomen*. — Type: CLEMENS 34192 (L; A, BO), Kinabalu, Colombon basin, 4500 ft. — **Fig. 8.**

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.

Distr. *Malesia*: Borneo (Sabah, Kinabalu).

Ecol. In forest; c. 1300 m; *fr.* June–Aug.

5. Manglietia dolichogyne DANDY ex NOOT, Blumea 31 (1985) 95. — *M. glauca* (non BLUME) KING, J. As. Soc. Beng. 58, ii (1889) 370; Ann. Bot. Gard. Cale. 3 (1891) 213, t. 56, *excl. fr.*; RIDLEY, Fl. Mal. Pen. 1 (1922) 14, *p.p.*; BURK. Dict. (1935) 1407. — '*Long-pistillate Manglietia*' MEIJER, Bot. Bull. Herb. Sabah 11 (1968) 10. — *M. 'dolichogyne'* DANDY ex COCKBURN, Trees of Sabah 2 (1980) 56, *nomen*. — Type: SAN 41051 (L; SAN). — **Fig. 7b.**

Tree up to 21 m and 60 cm diam. Stipular scar on petiole to 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, $\times 0.6$; b. fruit, $\times 0.6$; c. ovary, $\times 0.9$; d. anther, $\times 3.8$ (a, b CLEMENS 40979, c, d CLEMENS 40769).

Stamens many, c. 10 mm, incl. the c. 3 mm long acute connective appendage. *Ovary* conical or cylindrical, dorsal face of carpels 2–3 mm along suture, style c. 2 mm long. Ripe *fruits* cylindrical 4–7.5 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. *Seeds* flat ellipsoidal, c. 6 by 4 mm. Otherwise as *M. glauca*.

Distr. *Malesia*: Malay Peninsula (Perak, Taiping, road to Fraser's Hill, near Gap Valley), Borneo (Sabah, Tenom, Tambunan, Kinabalu).

Ecol. Primary forest; 450–1500 m; *fl.* March–May, *fr.* June–Feb.

Field notes. Outer tepals dark purple on green, inner tepals lemon with purple tinge; flowers pale yellow.

Excluded species

Manglietia ? *minahassae* K. & V. Meded. Lands Plantent. 19 (1898) 328, *nomen*; KOORD.-SCHUM. Syst. Verz. 3, 1 (1914) 41, *nomen* = *Madhuca burckiana* (KOORD.) LAMK (*Sapotaceae*).

3. PACHYLARNAX

DANDY, Kew Bull. (1927) 260; in Hutch. Gen. Fl. Pl. 1 (1964) 55; NOOT. Blumea 31 (1985) 97. — Type: *P. praecalva* DANDY. — Fig. 9.

Trees. Stipules free from the petiole. *Flowers* terminal, solitary, bisexual. *Tepals* 9–15, 3–5-merous, subequal. *Anthers* introrse; connective produced into a short appendage. *Gynoecium* sessile; carpels few (2–8), concrescent; ovules about 4–8 in each carpel. *Fruit* a thick-walled woody loculicidal capsule, the carpels dehiscent along the dorsal suture and sometimes separating towards the apex.

Distr. There are 2 *spp.*, of which one in Assam and one in Indochina and in *Malesia* (Sumatra and the Malay Peninsula).

1. *Pachylarnax praecalva* DANDY, Kew Bull. (1927) 260, *excl. plantae ex Annam*; H.KENG, Tree Fl. Malaya 2 (1973) 289, t. 4; NOOT. Blumea 31 (1985) 97, f. 4, 5. — Type: HANIFF 4067 (K; SING), Penang. — Fig. 9.

Tree 10–60 m by 30–100 cm, glabrous in all its parts. Stipules free from the petiole. *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. *Flowers* terminal on an incrassate peduncle of 0.5–20 mm (sometimes the peduncle becoming much

longer); 1–3 (rarely many) spathaceous bracts under each flower, pedicel very short. *Tepals* 9(–10), ± similar, the outermost oblanceolate to oblong, 2.5–3.5 cm long. *Stamens* c. 17–20 mm long with an acute connective appendage; gynoecium elongate-obovoid; carpels 2–4; ovules 4–8. *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. *Seeds* black with enveloping pink aril.

Distr. Annam (Bana near Tourane); *Malesia*: Sumatra (W. coast), Malay Peninsula (Kedah, Penang, Selangor).

Ecol. In primary forest; 360–1800 m; *fl. fr.* probably the whole year round.

2. Tribus Micheliaceae

LAW YUH-WU, Acta Phytotax. Sin. 22 (1984) 89.

Growth monopodial. Flower buds arising on brachyblasts in the axils of the leaves. Genera: *Michelia* (incl. *Paramichelia* and *Tsoongiodendron*) and *Elmerrillia*.



Fig. 9. *Pachylarnax praecalva* DANDY. a. Habit, $\times 0.7$; b. fruit, $\times 0.7$; c. ovary, $\times 2.2$; d. anther, $\times 3$ (CURTIS 3012).

KEY TO THE GENERA

1. Gynoecium sessile 4. *Elmerrillia*
 1. Gynoecium distinctly stipitate 5. *Michelia*

4. ELMERRILLIA

DANDY, Kew Bull. (1927) 261; in Hutch. Gen. Fl. Pl. 1 (1964) 56; NOOT, Blumea 31 (1985) 100. — Type: *E. papuana* (SCHLTR) DANDY.

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. tsiampacca*
 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. tsiampacca*.
 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 dehiscing 4. *E. tsiampacca*
 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 dehiscing.
 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. tsiampacca* var. *glaberrima*) 4. *E. tsiampacca*

1. *Elmerrillia ovalis* (Miq.) DANDY, Kew Bull. (1927) 261; NOOT, Blumea 31 (1985) 101. — *Talauma ovalis* Miq. Ann. Mus. Bot. Lugd.-Bat. 4 (1868) 69; KOORD. Meded. Lands Plantent. 19 (1898) 331; Suppl. Fl. N.O. Celebes 2 (1922) t. 8. — Type: FORSTEN s.n. (L; BO), Celebes near Tondano.

Talauma vrieseana Miq. Ann. Mus. Bot. Lugd.-Bat. 4 (1868) 70. — *Magnolia vrieseana* (Miq.) BAILLON ex PIERRE, Fl. For. Cochinch. 1 (1881) sub t. 2. — *E. vrieseana* (Miq.) DANDY, Kew Bull. (1927) 262. — Type: DE VRIESE & TEJSMANN s.n. (L), N. Celebes.

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 appressedly hairy, rarely sparsely patently 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 same indumentum as twigs, (1–)2.4–4.5(–7) cm. Brachyblast glabrous or yellowish villous; spatheaceous bracts (sparsely) pubescent to glabrous. Flowers (creamy) white; tepals c. 16 in 2 or 3 whorls, more or less coriaceous, the longest 25–35 mm. Stamens 8–14 mm long; carpels puberulous, 4(–6)-ovuled, concrescent. Fruit ellipsoidal, the ripe carpels disintegrating, losing their apical portions and thus shedding the 1–4 seeds.

Distr. *Malesia*: Sulawesi (incl. Muna), Moluccas (Morotai, Ambon).

Ecol. 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).

2. *Elmerrillia platyphylla* (MERR.) NOOT, Blumea 31 (1985) 102. — *Michelia platyphylla* MERR. Philip. J. Sc. 13 (1918) Bot. 11; Enum. Philip. 2 (1923) 153. — Type: FB 26866 (K), Leyte.

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; spatheaceous 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.

Distr. *Malesia*: Philippines (Leyte, Agusan; Mindanao, Zamboanga).

Ecol. Secondary forest at low altitudes.

3. *Elmerrillia pubescens* (MERR.) DANDY, Kew Bull. (1927) 261; NOOT, Blumea 31 (1985) 102. — *Talauma*

pubescens MERR. Philip. J. Sc. 3 (1908) Bot. 133; Enum. Philip. 2 (1923) 152. — Type: CLEMENS 686 (iso BO), Mindanao.

Tree c. 15–40 m high and up to 80 cm diam. Twigs densely fulvously pubescent or tomentose, glabrescent. Stipules densely fulvously 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 same indumentum as twigs, 20–25 mm. Brachyblast densely fulvously tomentose or pubescent, 3–5 cm; spatheaceous 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 c. 2 cm; carpels c. 8 mm long, concrescent, tearing apart towards the outside when mature, longitudinally dehiscent, 1–4-seeded.

Distr. *Malesia*: Philippines (Mindanao, Lanao lake, Mt Katanglad, Mt Apo).

Ecol. Altitude c. 2000 m; fl. fr. Jan.–Dec.

Vern. *Hangilon*, Bukidnon.

4. *Elmerrillia tsiampacca* (LINNÉ) DANDY in Pragnowski, World Pollen & Spore Flora 3 (1974) 5; NOOT, Blumea 31 (1985) 103, f. 6–8. — *Michelia tsiampacca* LINNÉ, Mant. (1767) 78; Miq. Fl. Ind. Bat. 1, 2 (1858) 18, p.p.; Ann. Mus. Bot. Lugd.-Bat. 4 (1868) 73; MERR. Interpr. Rumphius (1917) 224. — *Michelia champacca* auct. non LINNÉ: LINNÉ, Syst. ed. 10, 2 (1759) 1082, p.p. — *Michelia celebica* KOORD. Meded. Lands Plantent. 19 (1898) 328, 631, nom. ill.; Suppl. Fl. N.O. Celebes 2 (1922) t. 9. — *E. celebica* (KOORD.) DANDY, Kew Bull. (1927) 261. — Type: *Sampacca sylvestris* RUMPH. Herb. Amb. 2 (1741) 202, t. 68.

Talauma papuana SCHLTR, Bot. Jahrb. 50 (1913) 70. — *E. papuana* (SCHLTR) DANDY, Kew Bull. (1927) 261; CROFT in Womersley, Handb. Papua New Guinea (1978) 130, t. 65. — Type: SCHLECHTER 19001 (not seen).

Michelia forbesii Baker f. J. Bot. 61 (1923) Suppl. 2. — Type: FORBES 442a (K; P), Sogeri.

Michelia arfakiana AGOSTINI, Atti Com. Accad. Fisiocrit. Siena, ser. IX, 7 (1926) sep. 25. — Type: BECCARI PP 890 (FI), Mt Arfak.

E. mollis DANDY, Kew Bull. (1928) 184. — *Michelia mollis* (DANDY) McLAUGHLIN, Trop. Woods 34 (1933) 36. — Type: ENDERT 5252 (K; BO, L), Borneo, W. Kutei.

E. papuana var. *adpressa* DANDY, Kew Bull. (1928) 185. — Type: LEDERMANN 13089 (K; L), Sepik region.

E. papuana var. *glaberrima* DANDY, l.c. — Type: LEDERMANN 9505 (K), Sepik.

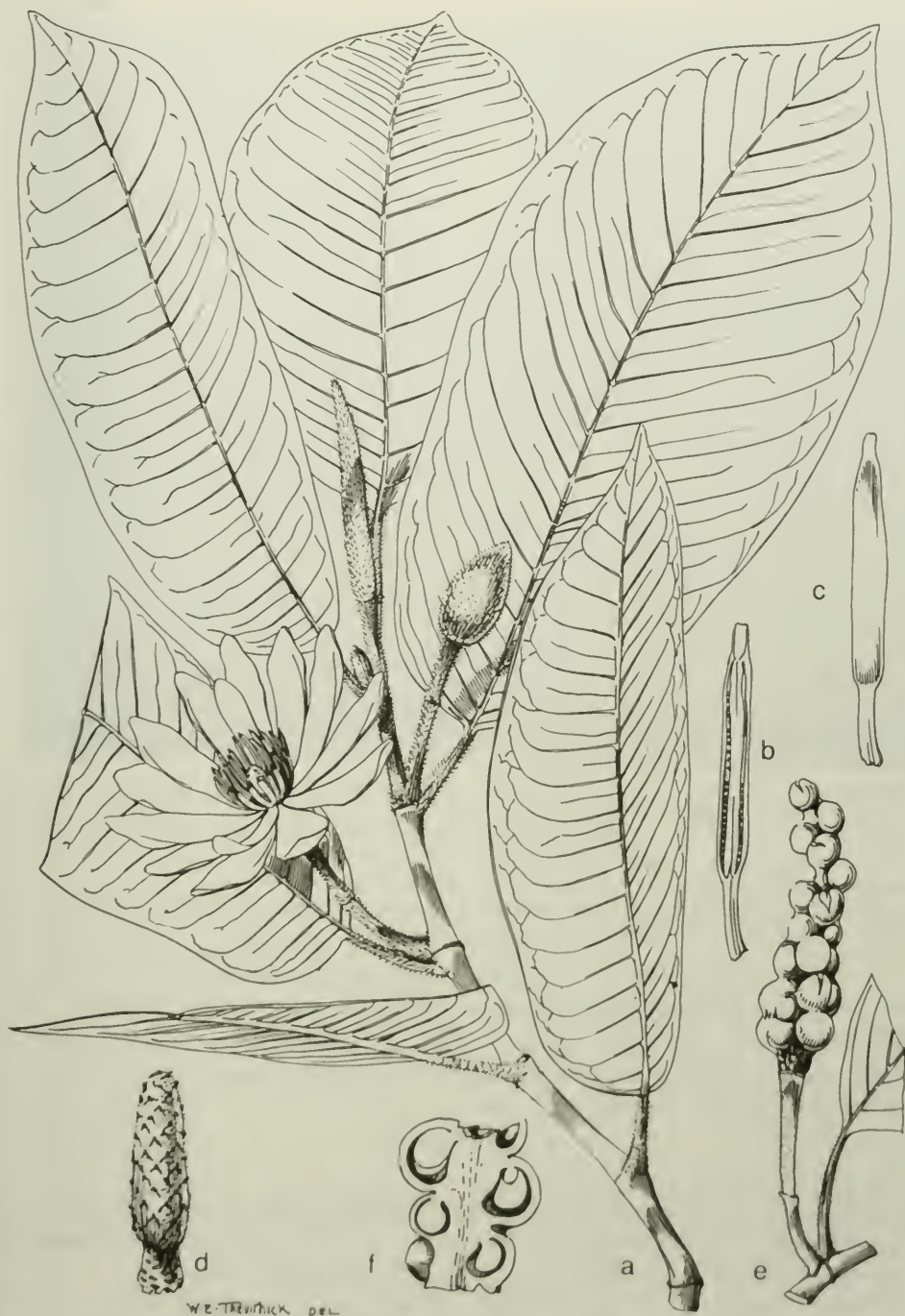


Fig. 10. *Elmerrillia tsampaca* (LINNÉ) DANDY var. *tsampaca*. a. Habit, $\times 0.6$; b-c. stamens, $\times 4$; d. ovary, $\times 2$; e. young fruit, $\times 2$; f. ditto, longitudinal section, $\times 4$.

E. sericea C.T. WHITE, J. Arn. Arb. 10 (1929) 212.

— Type: BRASS 661 (A; K), Sogeri. — **Fig. 10, 11.**

Tree to 60 m high and 150(–200) cm diam. Twigs (densely) ferruginously or fulvously (woolly) pubescent or tomentose when young, rarely glabrous. Stipules with same indumentum. *Leaves* often appressedly pubescent above in innovations, soon glabrescent, hairy beneath but glabrous in *var. glaberrima*, sometimes glaucous, (narrowly) elliptic, rarely ovate (often so in Sulawesi), 10–46 by 4–15 cm; acumen 5–17 mm; base cuneate to rounded, rarely subcordate; nerves in 11–28 pairs, meeting in an often hardly distinct intramarginal vein; reticulation rather fine to very fine. Petiole 7–35 mm. *Brachyblast* densely pubescent (glabrous in *var. glaberrima*), 15–40(–60) mm. *Flowers* white to yellow; *tepals* (10–)12–c. 15, glabrous or the outer ones pubescent, 20–35 mm long. *Stamens* 10–14 mm; carpels many (c. 50), pubescent or puberulous, glabrous in *var. glaberrima*. *Fruit* cylindrical, 4–9 by 1.5–2 cm.

Distr. *Malesia*: Sumatra (Mentawai I., Siberut), Borneo, Central & N. Sulawesi, Moluccas (Ambon, Buru), New Guinea (incl. Biak & Japen), New Britain.

Ecol. On fertile soil in forest; 0–1800 m; *fl. fr.* Jan.–Dec.

KEY TO THE INFRASPECIFIC TAXA

1. Leaves 10–30 cm; nerves in (11–)14–22(–24) pairs. Hairs underneath the leaf blade not curved towards their base. *Tepals* (12–)c. 15. *Sulawesi, Moluccas, New Guinea* **a. ssp. tsiampacca**
2. Young twigs and stipules hairy; ovary puberulous. **a1. var. tsiampacca**
2. Entire plant glabrous **a2. var. glaberrima**
1. Leaves 16–46 cm; nerves (14–)17–18 pairs. Hairs underneath the leaf blade usually (uncinately) curved towards the base. *Tepals* (10–)12. *Sumatra, Borneo* **b. ssp. mollis**

a. ssp. tsiampacca. — All synonyms except *E. mollis* DANDY.

Tree to 60 m high and 150(–200) cm diam. *Leaves* beneath very densely, often minutely appressedly or patently hairy, 10–30 by 3–15 cm. Petiole 12–35 mm.

Distr. *Malesia*: Central & N. Sulawesi, Moluccas (Ambon, Buru), New Guinea (incl. Biak & Japen), New Britain.

a1. var. tsiampacca. — 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.

Vern. *Sulawesi*: *tjempaka utan, t. u. aloes, uru tanduk, wasian, w. rintek, w. sela*; *New Guinea*: *balantalogo, Mooi lang., boska, Manikiong lang., arimot, pui, Biak, hui, Sogeri, wasau, wuka, Morobe, kaule, Kainantu, bibau, Hattam lang., war-mei, Waskuk lang., pubitza, Garaina lang., rap, Sepik, biendjung.*

a2. var. glaberrima (DANDY) NOOT. *Blumea* 31 (1985) 107, f. 6c. — *E. papuana var. glaberrima* DANDY.

Distr. *Malesia*: New Guinea (Kebar Valley, Idenburg R., Sepik R., Morobe Distr.).

Ecol. Primary forest; up to 1200 m.

Vern. *Maner, 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 mm. Carpels with 2 ovules.

Distr. *Malesia*: Sumatra (Mentawai I., Siberut), Borneo.

Ecol. In forest at low and medium altitude. In Sabah 1500–1800 m. *Fl. fr.* Jan.–Dec.

Vern. Sumatra: *minjaran*; M; Borneo: *arau, miharo*, Dyak.

5. MICHELIA

LINNÉ, *Sp. Pl.* (1753) 536; *Gen. Pl.* ed. 5 (1754) 240; DANDY in *Hutch. Gen. Fl. Pl.* 1 (1964) 56. — *Champaca* ADANS. *Fam. Pl.* 2 (1763) 365, 537. — *Sampacca* O. K. *Rev. Gen. Pl.* 1 (1891) 6. — Type: *M. champaca* LINNÉ.

Liriopsis SPACH, *Hist. Natur. Veget., Phanerog.* 7 (1839) 460, *non Liriopsis* REICHB. (1828). — *Magnolia sect. Liriopsis* BAILLON, *Hist. Pl.* (1868) 142, note 4. — Type: *L. fuscata* (ANDR.) SPACH.



Fig. 11. *Elmerillia tsiampaca* (LINNÉ) DANDY var. *mollis* (DANDY) NOOT. Twig with flower, deflorated flower, and bud showing the stipular nature of the spathaceous bract; \pm natural size (NOOTEBOOM 4518A).

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 sublatorse (to introrse). *Gynoeceium* stipitate, carpels many to few (rarely 1), free or connate; ovules 2 to many; fruiting carpels free or conrescent.

DISTR. About 30 *spp.*, in Southeast Asia from India and Sri Lanka eastwards to S. Japan and Taiwan and southeastwards 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*

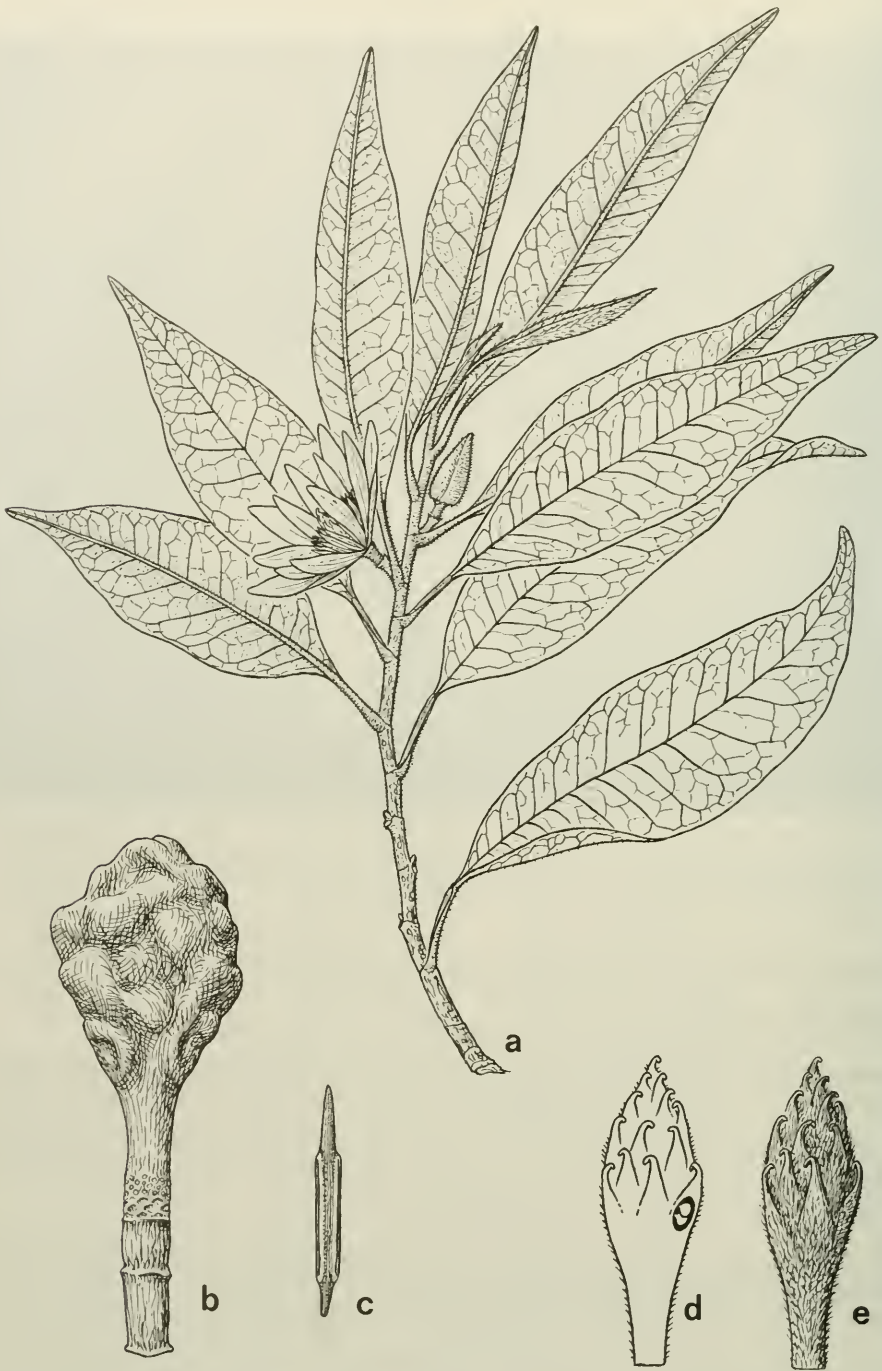


Fig. 12. *Michelia scortechinii* (KING) DANDY. *a.* Habit, $\times 0.7$; *b.* young fruit, $\times 2$; *c.* anther, $\times 4$; *d-e.* ovary, $\times 4$ (*a, c-e* SF HOLTUM 31244; *b* GRASHOFF 335).

1. Petiole longer than 5 mm. The other characters different or the tepals more than 6.
2. Young twigs glabrous. Terminal buds hairy at the apex only. Carpels 1–4. Stipules free from the 15–35 mm long petiole. Leaves glabrous, 9–35 cm long 4. *M. montana*
2. Young twigs hairy, at least directly under the terminal bud. Carpels 8 or more.
3. Stipules adnate to the petiole for one third or more than one third of its length.
4. Leaves 8–12 by 2.5–3.5 cm. Petiole 6–16 mm 1. *M. scortechinii*
4. Leaves 10–35 by 4–11 cm. Petiole 14–50 mm.
5. Tepals 15, from light yellow to orange, 20–45 mm long. Carpels c. 30, fertile. Leaves 10–30 cm 3. *M. champaca*
5. Tepals c. 12, white, 30–55 mm long. Carpels c. 10, sterile. Leaves 15–35 cm 7. *M. alba*
3. Stipules free from petiole or adnate to its base only (in *M. salicifolia* sometimes up to one third).
6. Leaves 15–35 by 5.5–11 cm. Petiole 15–50 mm. Tepals c. 12, white, 30–55 mm. Carpels sterile, c. 10 7. *M. alba*
6. Leaves 4–16 by 2.3–6 cm. Petiole 5–20 mm. Tepals white to yellow, 10–40 mm. Carpels fertile.
7. Brachyblast 10–17 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 2. *M. koordersiana*
7. Brachyblast 3–7 mm. All the tepals the same, 9–17. Twigs and stipules pubescent or puberulous. Leaves glabrous or hairy beneath, 4–13 by 1.5–4 cm. Carpels 8–16 or c. 30.
8. Tepals 20–40 mm. Leaves 9–13 by 2.3–4 cm, often glaucous beneath. Carpels c. 30 5. *M. salicifolia*
8. Tepals 10–15 mm. Leaves 4–12 by 1.5–3.5 cm, not glaucous beneath. Carpels 8–c. 16 6. *M. philippinensis*

1. *Michelia scortechinii* (KING) DANDY, Kew Bull. (1927) 262; H. KENG, Tree Fl. Malaya 2 (1973) 288; NOOT, Blumea 31 (1985) 111, f. 9. — *Manglietia scortechinii* KING, J. As. Soc. Beng. 58, ii (1889) 370; RIDLEY, Fl. Mal. Pen. 1 (1922) 14. — *Paramichelia scortechinii* (KING) DANDY in Praglowski, Pollen & Spore Flora 3 (1974) 21. — Type: SCORTECHINII 764 (BM, K, SING). — Fig. 12.

Tree to 37 m high and c. 50 cm diam. Twigs zigzag, ferruginously pubescent to tomentose when young. Stipules adnate to the petiole for at least half its length, to 30 mm long. Leaves (densely) ferruginously 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 ferruginously 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 ferruginously pubescent. Fruiting carpels conerescent.

Distr. *Malesia*: Sumatra (W. Coast, Bengkulu, Palembang), Malay Peninsula (Perak, Pahang, Cameron Highlands).

Ecol. Primary forest; 650–1300 m; fl. fr. April–May.

2. *Michelia koordersiana* NOOT, Blumea 31 (1985) 111, f. 10. — Fig. 13

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 zig-

zag. Stipules with same indumentum 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.

3. *Michelia champaca* LINNÉ, Sp. Pl. (1753) 536; BLUME, Bijdr. (1825) 7; Fl. Java Magnol. (1829) 9, t. 1; BLANCO, Fl. Filip. (1837) 462; KORTU, Ned. Kruidk. Arch. 2 (1851) 96; MRO, Fl. Ind. Bat. 1, 2 (1860) 101, 153; Ann. Mus. Bot. Lugd.-Bat. 4 (1868) 72, excl. var.; K. & V. Bijdr. 4 (1869) 159; Atlas 4 (1918) t. 799; KOORD. Exk. Fl. Java 2 (1912) 241; MERR. Enum. Born. (1921) 251; Enum. Philip. 2 (1923) 152; BACKER, Schoolfl. Java (1911) 16; RIDLEY, Fl. Mal. Pen. 1 (1922) 15; BURK. Diet. (1935) 1465; CORNER, Wayside Trees (1940) 434; BACKER & BAKIJ, Fl. Java 1 (1963) 98; NOOT, Blumea 31 (1985) 113. — Type: HERMANN Fl. Zeyl. 144 (BM).

M. suaveolens PERS., Syn. 2 (1806) 94, p.p. excl. syn. RIEDEL et RUMPH. — *M. blumeri* STEUD.



Fig. 13. *Michelia koordersiana* NOOT. a. Habit, $\times 0.6$; b. fruit, $\times 0.6$; c. ovary, $\times 4$; d. anther, $\times 6$ (VAN DER ZWAAN for THORENAAR T345).

Nomencl. ed. 2, 2 (1841) 139. — *M. tsiampacca* L. var. *blumei* MORITZ in Zoll. Syst. Verz. (1846) 36. — Type: RUMPH. Herb. Amb. 2 (1741) t. 67.

M. tsiampacca BLUME, Bijdr. (1825) 7, non *M. tsiampacca* LINNÉ (1767). — *M. velutina* BLUME, Fl. Java Magnol. (1829) 17, non *M. velutina* DC. (1824); MIQ. Fl. Ind. Bat. 1, 2 (1858) 17; K. & V. Bijdr. 4 (1896) 162; BACKER, Schoolfl. Java (1911) 16; KOORD. Exk. Fl. Java 2 (1912) 241; H. KENG, Tree Fl. Malaya 2 (1973) 288 pro coll. KEP FRI 6943. — *Champangca velutina* O. K. Rev. Gen. Pl. 1 (1891) 6. — *M. pilifera* BAKH.f. Blumea 12 (1963) 61; BACKER & BAKH.f. Fl. Java 1 (1963) 98. — Type: BLUME s.n. (L).

M. pubinervia BLUME, Fl. Java Magnol. (1829) 14, t. 4. — *M. rufinervis* BLUME, Bijdr. (1825) 8, non *M. rufinervis* DC. (1817). — *M. champaca* MIQ. Fl. Ind. Bat. 1, 2 (1858) 16, p.p., non *M. champaca* LINNÉ (1753); BISSCHOP GREVELINK, Pl. Ned. Ind. (1882) 277, p.p. — *M. champaca* LINNÉ var. *pubinervia* (BLUME) MIQ. Ann. Mus. Bot. Lugd.-Bat. 4 (1868) 72. — Type: BLUME 670 (L; BO).

Talauma villosa MIQ. forma *celebrica* MIQ. Ann. Mus. Bot. Lugd.-Bat. 4 (1868) 70. — Type: DE VRIESE & TEJSMANN s.n. (L; BO).

M. montana auct. non BLUME: BAKER.f. J. Bot. 62 (1924) Suppl. 2.

Huge forest tree 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; spatheaceous bracts pubescent. Flowers light yellow becoming dark orange; tepals 15, 20–45 mm long. *Stamens* 6–8 mm, incl. the up to 1 mm connective appendage; carpels c. 30, the c. 3 mm long gynophore densely pubescent.

DISTR. 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.

a. 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.

b. var. *pubinervia*

a. var. *champaca*. — All synonyms except those under var. *pubinervia*.

DISTR. Commonly cultivated throughout the tropics. Probably originally from India, where it is cultivated on the temple ground of Jains and Hindus.

USES. See BURKILL, Dict. ed. 2 (1966) 148.

VERN. *Tjampacca* (India: *cempaka*) or *t. kuning* is the common name in most of its area. Further: *djeumpa*, Aceh, *djempa*, Gajo, *kantil*, *lotjari*, *petjari*, J, *kembang konèng*, *tjampacca mera*, Mad., *t. barak*, *t. warangan*, Bali, *hépaka*, *képaka*, Sawu, *sampacca*, *s. modarag*, *t. mariri*, Ald., Cel., *bunga edja*, Mak., *bunga matjela*, Bug., *kupa haja*, Ceram, *kupa pokur*, *papokur*, *pupukuljo*, *walatol*, Ulis, *hapaka*, *tjapaka*, N. Halmheira, *t. goratji*, Ternate, Tidore.

b. var. *pubinervia* (BLUME) MIQ. Ann. Mus. Bot. Lugd.-Bat. 4 (1868) 72; NOOT. Blumea 31 (1985) 115. — *M. pubinervia* BLUME. — *M. tsiampacca* BLUME. — *M. montana* auct. non BLUME: BAKER.f.

DISTR. *Malesia*: Sumatra (Aceh; Bengkulu, Lake Ranau), Malay Peninsula (Kedah, Langkawi Is.; Bt. 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 sekar*, J, *kadju kempheug*, Md, *lungjung*, J; Sumbawa: *tengkel*.

4. *Michelia montana* BLUME, Verh. Bat. Gen. K. W. 9 (1823) 153; Bijdr. (1825) 7; Fl. Java Magnol. (1829) 15, t. 5; MIQ. Fl. Ind. Bat. 1, 2 (1858) 17; Suppl. 1 (1860) 153; Ann. Mus. Bot. Lugd.-Bat. 4 (1868) 73; BACKER, Schoolfl. Java (1911) 15; KOORD. Exk. Fl. Java 2 (1912) 241; RIDLEY, Fl. Mal. Pen. 1 (1922) 15; BURK. Dict. (1935) 1491; CORNER, Wayside Trees (1940) 434; BACKER & BAKH.f. Fl. Java 1 (1963) 98; NOOT. Blumea 31 (1985) 116, f. 11. — *Sampangca montana* O. K. Rev. Gen. Pl. 1 (1891) 6. — Lectotype: BLUME 575 (L, NY).

M. eucarisata MIQ. Fl. Ind. Bat. Suppl. [(1860)

153, *nomen*] (1861) 368. — *M. montana* BLUME var. *subvelutina* MIQ. Ann. Mus. Bot. Lugd.-Bat. 4 (1868) 73. — Lectotype: TEJSMANN HB 4457 (L; BO).

Tree becoming over 40 m tall and over 2 m diam. Twigs glabrous. Stipules pubescent at the apex only, exceptionally entirely pubescent, free from petiole. *Leaves* glabrous, spirally arranged, more or less elliptic, 9–30(–35) by 4–13(–20) cm; acumen 2–20 mm; base attenuate; nerves in 9–15 pairs, conspicuous, intramarginal vein rather conspicuous; reticulation dense, prominent on both surfaces. Petiole often thickened towards its base, 15–35 mm. *Brachyblast* 5–20 mm, glabrous to (rarely) densely pubescent; spathaceous bracts glabrous except the margins towards the apex. Outer *tepals* 3, rather thin, 15–30 mm, greenish or greenish white; inner *tepals* creamy or white, 6, thick, coriaceous, 14–40 mm. *Stamens* incl. the c. 2 mm long connective appendage 10–13 mm; carpels 1–4, with the 4–8 mm long gynophore reddish puberulous when dry, green *in vivo*. Fruiting carpels free.

Distr. *Malesia*: Sumatra (Aceh; W. coast; Lampung; Palembang; Banka), Malay Peninsula (Perak; Pahang; Cameron Highlands), Borneo (Sabah; E. Kalimantan), Java (common), Bali. Fig. 14.

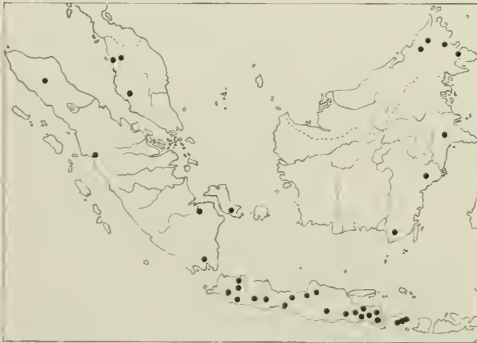


Fig. 14. Range of *Michelia montana* BLUME.

Ecol. Primary forest, on different soils, from low altitude up to 1700 m. *Fl. fr.* Jan.–Dec.

Uses. Very good timber (often used instead of *Tectona grandis*).

Vern. Sumatra: *cempaka utan*, *medang plàm*, *m. tanah*; Borneo: *tjempaka wilis*; Java: *kembang marsèhe*, *k. marsiki*, *kitaleus*, *sekar*, *cempaka baros*, *c. jahé*, *t. putih*, *tjoko rekitje*, M; *mangkl*, *manglit*, Sund., J., *kembang mondhung*, Mad., *basé*, Bali.

Note c. The sapwood reportedly has a ginger smell.

5. *Michelia salicifolia* AGOSTINI, Atti Com. Accad. Fisiocrit. 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 ferruginously pubescent. Stipules with same indumentum, adnate to base of petiole only. *Leaves* spirally arranged, appressedly finely ferruginously 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 ferruginously 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 ferruginously tomentellous. Fruiting carpels free.

Distr. *Malesia*: Sumatra (W. Coast, G. Singal- lang; Aceh, G. Leuser).

Ecol. Altitude 1500–2000 m. Apparently rare. *Fl. fr.* March, July.

6. *Michelia philippinensis* (P. PARMENT.) DANDY, Kew Bull. (1927) 263; NOOT. Blumea 31 (1985) 118. — *Magnolia philippinensis* P. PARMENT. Bull. Sc. Fr. Belg. 27 (1896) 206, 270. — *M. parviflora* MERR. Bur. Gov. Lab. Publ. 35 (1906) 70, *non M. parviflora* DC. (1817). — *M. cumingii* MERR. & ROLFE, Philip J. Sc. 3 (1908) Bot. 100; MERR. Enum. Philip. 2 (1923) 153. — Type: CUMING 783 (MEL; A, BM, K, L, NY).

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 indumentum, 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 indumentum 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.

7. *Michelia* × *alba* DC. Syst. (1817) 449; MERR. Interpret. Rumph. (1917) 223; Enum. Philip. 2 (1923) 152; BURK. Dict. (1935) 1464; CORNER, Wayside Trees (1940) 433, t. 142, pl. 129, 130; BACKER & BAKH.f. Fl. Java 1 (1963) 98. — Type: this species is based on *Sampaca domestica* IV *alba* RUMPH. Herb. Amb. 2 (1741) 200.

M. longifolia BLUME, Verh. Bat. Gen. K. W. 9 (1823) 155; Bijdr. (1825) 7; Fl. Java Magnol. (1829) 12, t. 2; K. & V. Meded. Lands Plantent. 17 (1896) 157; BACKER, Schoolfl. Java (1911) 15; KOORD. Exk. Fl. Java 2 (1912) 205; MERR. Fl. Manila (1912) 205 ('*longiflora*'); RIDLEY, Fl. Mal. Pen. 1 (1922) 15. — *Sampaca longifolia* O. K. Rev. Gen. Pl. 1 (1891) 6. — Type: BLUME *s.n.* (L).

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.

Ecol. Up to 1200 m altitude. Fl. Jan.–Dec.

Uses. The beautiful and nicely scented flowers are sold on the market. The tree is grown as an ornamental.

VERN. *Djeumpa gadèng*, Aceh, *tjempaka putih*, M., *t. bodas*, Sund., *petjari putih*, *t. putih*, Jav., *sampaka kulo*, *s. mopoesi*, *t. momero*, *t. mawuro*, Alf. Cel., *bunga èdga kébo*, *paténé*, Mak., *bunga èdja maputè*, Bug., *t. bobudo*, Ternate, *t. bubolo*, Tidore.

NOTE. FRI bb 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.

8. *Michelia figo* (LOUR.) SPRENG. Syst. 2 (1825) 643; NOOT. Blumea 31 (1985) 120. — Type: LOUREIRO. — For further synonymy see NOOT. (1985).

Shrub. Twigs pubescent to tomentose, often zigzag. Stipules adnate to the petiole for nearly its whole length, long ferruginously 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

Phelima NOR. in Verh. 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 iryaghedi* (GAERTN.) WARB. (*Myristicaceae*). HASSKARL, Cat. Pl. Hort. Bot. Bogor. Cult. Alt. (1844) 174 referred *Phelima* to *Pyrrhosa horsfieldii* (BLUME) HASSK., which is a synonym of *H. iryaghedi*.

Spermabolus TEJISM. & BINN. Cat. Hort. Bog. (1866) 178, *nomen*, with one species, *S. fruticosus* TEJISM. & BINN., *nomen*, is *Anaxagorea* A.ST.HIL. (*Annonaceae*).

LINACEAE (A.M.N. van Hooren & H.P. Nootboom, 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 & NOOTBOOM (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.

Ixonanthaceae — Trees. Tufted hairs absent. Stipules lateral. Leaves spirally arranged. Flowers perigynous. Petals persistent in fruit, imbricate (*extra*-Mal. also contorted). Disk intrastaminal. Filaments free, inserted outside and against the disk. Style 1, simple. Fruit a capsule. Seed not persistent, with an obvious basal wing or suprahilar 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 *Hugoniaceae* (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 mesotestal construction in the *Hugonioideae*. The genus *Indorouchera* of the *Hugonioideae* may yield the most primitive pollen type in *Linaceae*.

References: CORNER, The seeds of dicotyledons I (1976); CRONQUIST, An integrated system of classification *etc.* (1981); DAHLGREN, Bot. Notis. 128 (1975) 119–147; EXELL & MENDONÇA, *Consp. florae Angolensis* 1, 2 (1951) 242–249, 390–392; HEIMSCH & TSCHABOLD, Bot. Gaz. 133 (1972) 242–253; NARAYANA & RAO, J. Ind. Bot. Soc. 57 (1978) 258–266; OLTMANN, Pollenmorphologisch-systematische Untersuchungen innerhalb der Geraniales. Diss. Bot. 11 (1971); SAAD, Pollen et Spores 4 (1962) 65–82; TAKHTAJAN, Flowering plants. Origin and dispersal (1969) 226.

SUBFAMILY HUGONIOIDEAE

Trees or lianas, rarely shrubs. Hairs, if present, simple, uniseriate, or multi-seriate 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 axile fascicle, few- to many-flowered, rarely 1-flowered. *Flowers* actinomorphic, pentamerous, bisexual, hypogynous, sometimes heterodistylous. *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 dorsoversatile, 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 capitate. Ovules 2 per cell, axile, 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 (*Hebepetalum*, *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 cristatque 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 *Linoideae* (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 unligified 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*.

References: HEIMSCH, Lilloa 8 (1942) 83–198, pl. 1–17; HEIMSCH & TSCHABOLD, Bot. Gaz. 133 (1972) 242–253; METCALFE & CHALK, Anatomy of the dicotyledons 1 (1950) 268–279; VAN WELZEN & BAAS, Blumea 29 (1984) 453–479. — P. BAAS.

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 pantoporate. *Indorouchera* has inaperturate grains, which, however, actually represent a tritenuate condition.

In most genera the exine shows differentiation in sexine and nexine. In *Indorouchera* 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-tectate sexine.

The macromorphologically distinct subfamilies *Linoideae* and *Hugonioideae* can be separated in a pollen morphological way too. Pollen of *Linoideae* is tricolpate, pantocolpate, or pantoporate, and has a more or less granulate sexine, while that of *Hugonioideae* is tricolporate (*Hugonia*, *Philbornea*) or inaperturate (*Indorouchera*), and mostly has a more or less baculate or a columellate-tectate sexine (SAAD, 1962). Generally speaking, subfamily *Linoideae* has more primitive pollen characters than subfamily *Hugonioideae*, although *Indorouchera* may yield the most primitive pollen type in *Linaceae*.

Following SAAD (*l.c.*) the pollen of the *Linaceae* is primitive within the *Geraniales*. Relationship of the *Linaceae* with *Ixonanthaceae*, as well as with *Erythroxylaceae* and *Humiriaceae*, is supported by pollen morphology (OLTMANN, 1971). However, pollen also indicates the distinctness of the *Linaceae* within this group of families. Pollen of *Ctenolophonaceae* appeared to be dissimilar to that of *Linaceae*.

References: OLTMANN, Pollenmorphologisch-systematische Untersuchungen innerhalb der Geraniales. Diss. Bot. 11 (1971); SAAD, Pollen et Spores 4 (1962) 65–82. — R.W.J.M. VAN DER HAM.

Phytochemistry. See HEGNAUER, Chemotaxonomie der Pflanzen 4 (1966) 393.

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*
1. All parts glabrous. Styles 3–4(–5). Ovary 3(–4)-celled, only one, rarely 2 locules distinct in the fruit. Drupe usually with one developed seed.
 2. Resin absent. Leaves spirally arranged. Flowers in rather lax racemes or panicles 2. *Philbornea*
 2. Buds and stipules often covered by resin. Leaves distichously arranged. Flowers in axillary fascicles, subtended by often densely packed, imbricate bracteoles 3. *Indorouchera*

1. HUGONIA

LINNÉ, Gen. Pl. ed. 5 (1754) 305; Sp. Pl. (1753) 675; STAPF in Hook. Ic. Pl. (1906) t. 2822; HALL, f. Beih. Bot. Centralbl. 39, 2 (1923) 43; HUB. WINKLER in E. & P. Nat. Pfl. Fam. ed. 2, 19a (1931) 108; VAN HOOREN & NOOTEBOOM, Blumea 29 (1984) 553, map. — *Durandea* PLANCH. in Hook. Lond. J. Bot. 6 (1847) 594, *nom. cons.*; HUB. WINKLER in E. & P. Nat. Pfl. Fam. ed. 2, 19a (1931) 108. — *Hugonia sect. Durandea* (PLANCH.) BAILLON. Hist. Pl. 5 (1874) 48. — Fig. 1, 3.

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)-

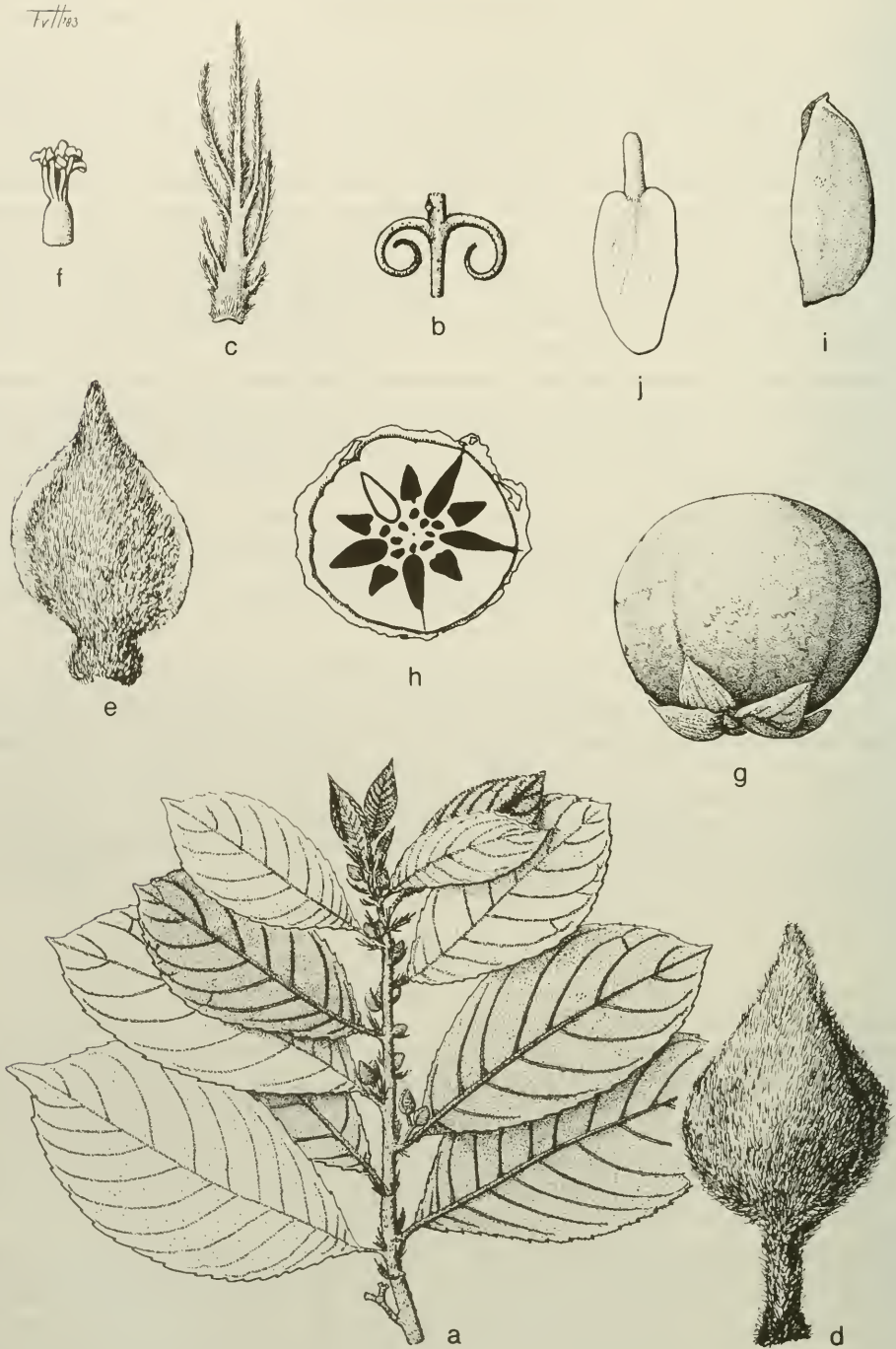


Fig. 1. *Hugonia costata* MIQ. a. Habit, $\times 0.5$; b. climbing hooks, $\times 0.5$; c. stipules from inside, $\times 3$; d. flower bud; e. innermost sepal; f. pistil (in bud), all $\times 5$; g. fruit, $\times 1.5$; h. fruit in CS, $\times 1.5$; i. seed, $\times 3$; j. embryo, $\times 3$ (a, c-j 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 allopatric 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).

KEY TO THE SECTIONS AND THE SPECIES

1. Young parts, twigs, stipules, petiole and nerves densely tomentose. Stipules digitately lacinate or pinnately lobed. Sepals 5–15 mm long. Petals 12–30 by 4–10 mm. *Drupe* usually indehiscent, sometimes finally septical. *Sect. Hugonia* 1. *H. costata*
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*

1. *Hugonia costata* MIQ. Illustr. (1871) 67; BOERL. Handl. Fl. Ned. Ind. 1 (1890) 139; HALL.f. Beih. Bot. Centralbl. 39, 2 (1923) 45; VAN HOOREN & NOOTBOOM, Blumea 29 (1984) 555. — Fig. 1.

Liana. Tomentum appressed to patent, hairs up to 1 mm. Twigs densely tomentose when young, glabrescent. *Climbing shoots* often patent, some growing out to 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 lacinate up to 1/3, with 7–10 lobules. *Leaves* sparsely to densely tomentose, narrowly elliptic to obovate, 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, acumen 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, 1–1.5 cm, sometimes reduced to 1 flower, densely tomentose; bracts caducous, narrowly ovate to obovate, 10–15 by 2–3.5 mm, deeply digitately lacinate 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- (or 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. *Seed(s)* 1 or 2, exarillate, ventrally attached, flattened obovoid, 11.5 by 4.5 mm, c. 1 mm thick; hilum not obvious; testa thin, 2-layered. Embryo straight; cotyledons obovate, 7 by 4 mm; radicle cylindrical, 3 by 0.8 mm. Endosperm copious, slightly granular.

Distr. Malesia: Sumatra (Palembang, Padang), Malay Peninsula (Ibis For. Res.), Borneo (Sabah, Kutai, E. Kalimantan). Fig. 2.

Ecol. Typically matures in late building gaps, well drained ridges, and flat upland areas; in Malaya 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.

2. *Hugonia jenkinsii* F.V.M. Fragm. 5 (1865) 7; VAN HOOREN & NOOTBOOM, Blumea 29 (1984) 555 (with complete synonymy). — *Durandea pallida* K. SCH. in

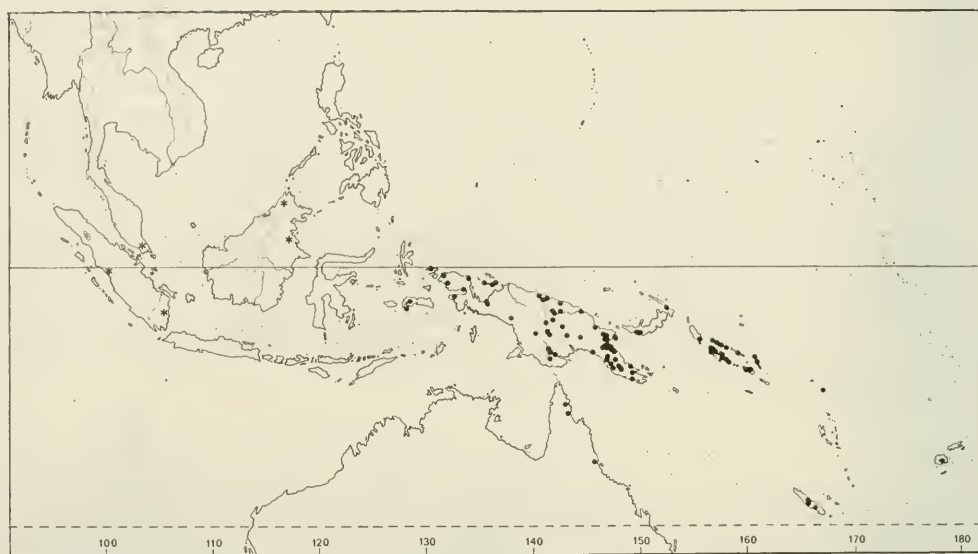


Fig. 2. Range of *Hugonia costata* MIQ. (stars) and *H. jenkinsii* F.v.M. (dots).

K.Sch. & Hollr. Fl. Kaiser Wilhelm Land (1889) 56. — *Ancistrocladus pentagynus* WARB. Bot. Jahrb. 13 (1891) 383. — *H. pentagyna* (WARB.) K.SCH. in K.Sch. & Laut. Fl. Deut. Schutzgeb. Südsee (1900) 373; HUB. WINKLER in E. & P. Nat. Pfl. Fam. ed. 2, 19a (1931) 100, f. 48. — *Durandea rotundata* K.SCH. in K.Sch. & Laut. Fl. Deut. Schutzgeb. Südsee, Nachtr. (1905) 278. — *Durandea pentagyna* (WARB.) K.SCH. *l.c.* — *Durandea jenkinsii* (F.v.M.) STAPF in Hook. Ic. Pl. (1906) t. 2822. — *H. robinsonii* MERR. Philip. J. Sc. 11 (1916) Bot. 277. — *Durandea pentagyna* var. *rotundata* (K.SCH.) LAUT. Bot. Jahrb. 52 (1915) 117. — *Durandea robinsonii* (MERR.) HALL. f. Beih. Bot. Centralbl. 39, 2 (1923) 41. — Fig. 3.

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 reticulatofan; 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–)1.5–14 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* heterodistylous, 7–9 by 5–9 mm. *Sepals* ± orbicular to transversely broadly elliptic, (1.8–)2–3(–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* shortly 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

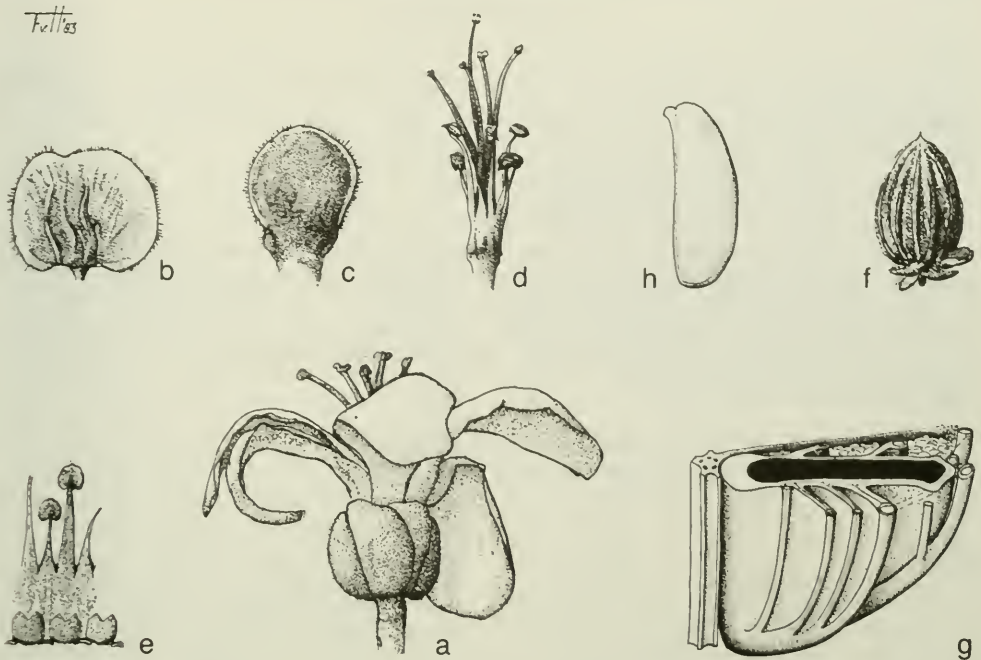


Fig. 3. *Hugonia jenkinsii* F.v.M. a. Flower, $\times 4$; b. inner sepal, $\times 5$; c. outer sepal, $\times 5$; d. flower, sepals and petals removed, $\times 4$; e. stamens with glandular thickenings at base of tube, $\times 5$; f. fruit, $\times 1.5$; g. pyrene, $\times 6$; h. seed, $\times 3$ (a-h 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 ob-

vious; 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.

Vern. New Guinea: *agref*, Vogelkop, *abus*, Sepik, Waskuk, *camuraka*, Sepik, Wagu, *quamo*, Wikahiri.

2. PHILBORNEA

HALL.f. Arch. Néerl. Sc. Ex. Nat. IIIB, 1 (1912) 110; in Fedde, Rep. 13 (1914) 414; HUB.WINKLER in E. & P. Nat. Pfl. Fam. ed. 2, 19a (1931) 109; VAN HOOREN & NOOTEBOOM, Blumea 29 (1984) 556. — Fig. 4.

Lianas with hooks. Indumentum absent. Stipules simple, entire. *Leaves* spirally arranged, rarely some leaves opposite. *Inflorescences* a rather lax flowered axillary or terminal raceme, sometimes ramiflorous. Bracts and bracteoles present. *Sepals* basally shortly connate, subequal. Disk absent; nectary glands not obviously present. Styles 3. Ovary 3-loculed. *Drupe* indehiscent, 1-seeded with 2 reduced locules. *Seed* ventrally attached, with arillode. Embryo straight. Endosperm scanty, fleshy.

Distr. Monotypic. *Malesia*: Sumatra, Borneo, Philippines.

Ecol. Periodically inundated soil and near rivers in the lowland.

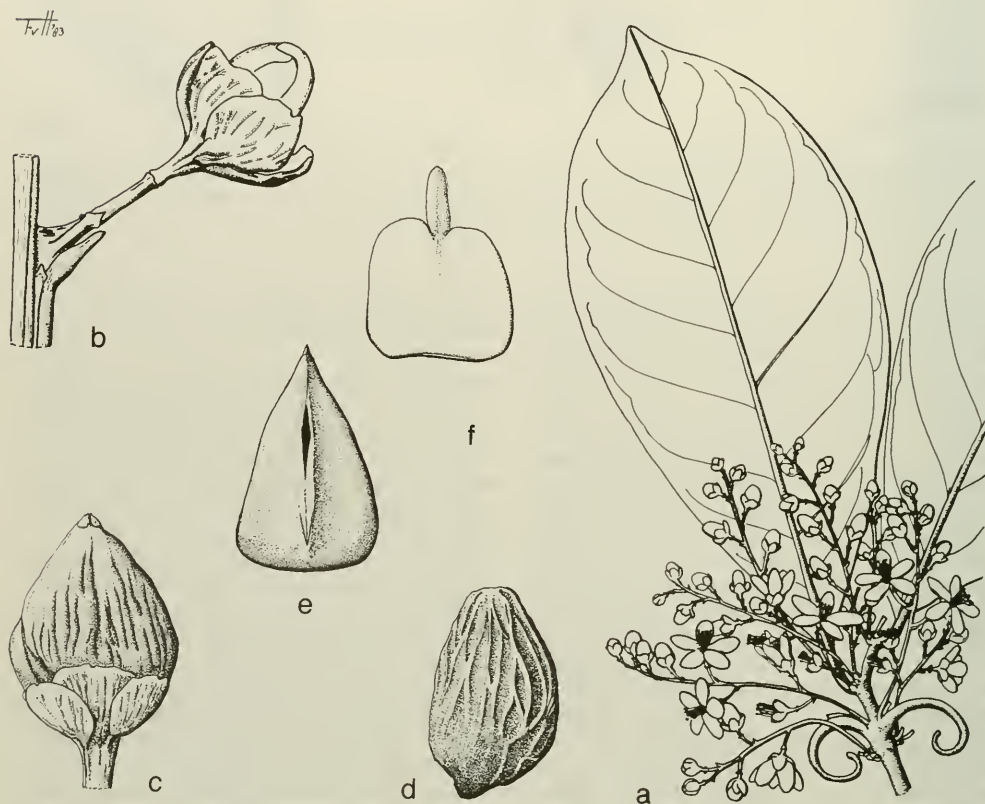


Fig. 4. *Philbornea magnifolia* (STAPF) HALL.f. a. Habit, $\times 0.5$; b. bract, bracteoles, and flower bud, $\times 5$; c. fruit; d. fruit, exocarp removed; e. seed; f. embryo; all $\times 3$ (a after STAPF, b KOSTERMANS 21142, c-f RAHMAT SI BOEEA 5362).

1. *Philbornea magnifolia* (STAPF) HALL.f. Arch. Néerl. Sc. Ex. Nat. IIIB, 1 (1912) 110; in Fedde, Rep. 13 (1914) 415; VAN HOOREN & NOOTEBOOM, Blumea 29 (1984) 556. — *Durandea magnifolia* STAPF in Hook. Ic. Pl. (1906) t. 2822; in Fedde, Rep. 5 (1908) 268. — *P. palawanica* HALL.f. Arch. Néerl. Sc. Ex. Nat. IIIB, 1 (1912) 110; in Fedde, Rep. 13 (1914) 415. — 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, acumens 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, \pm 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, \pm 0.3 mm thick; endocarp leathery in basal and sterile half, tougher and with prominent, subreticulate, firm, \pm 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 arilode; testa 0.2 mm thick; tegmen somewhat thinner. Embryo straight; cotyledons transversely broadly ovate, \pm 6 by 6 mm; radicle cylindric, 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

HALL.f. Beih. Bot. Centralbl. 39, 2 (1923) 50; HUB. WINKLER in E. & P. Nat. Pfl. Fam. ed. 2, 19a (1931) 109; BACKER & BAKH.f. Fl. Java 1 (1963) 241; VAN HOOREN & NOOTEBOOM, Blumea 29 (1984) 557. — Fig. 6–8.

Glabrous lianas, with hooks. Buds often covered with resin. Stipules simple, entire or dentate, often covered with resin. Leaves distichously arranged. Flowers in fascicles in the axils of (often fallen) leaves, rarely solitary, heterodistylous. Bracts absent. Pedicel densely beset with often numerous, \pm spirally arranged, persistent, imbricate bracteoles and often covered with resin. Sepals free, unequal. Petals very thin. Nectary glands absent. Ovary 3(–4)-loculed;

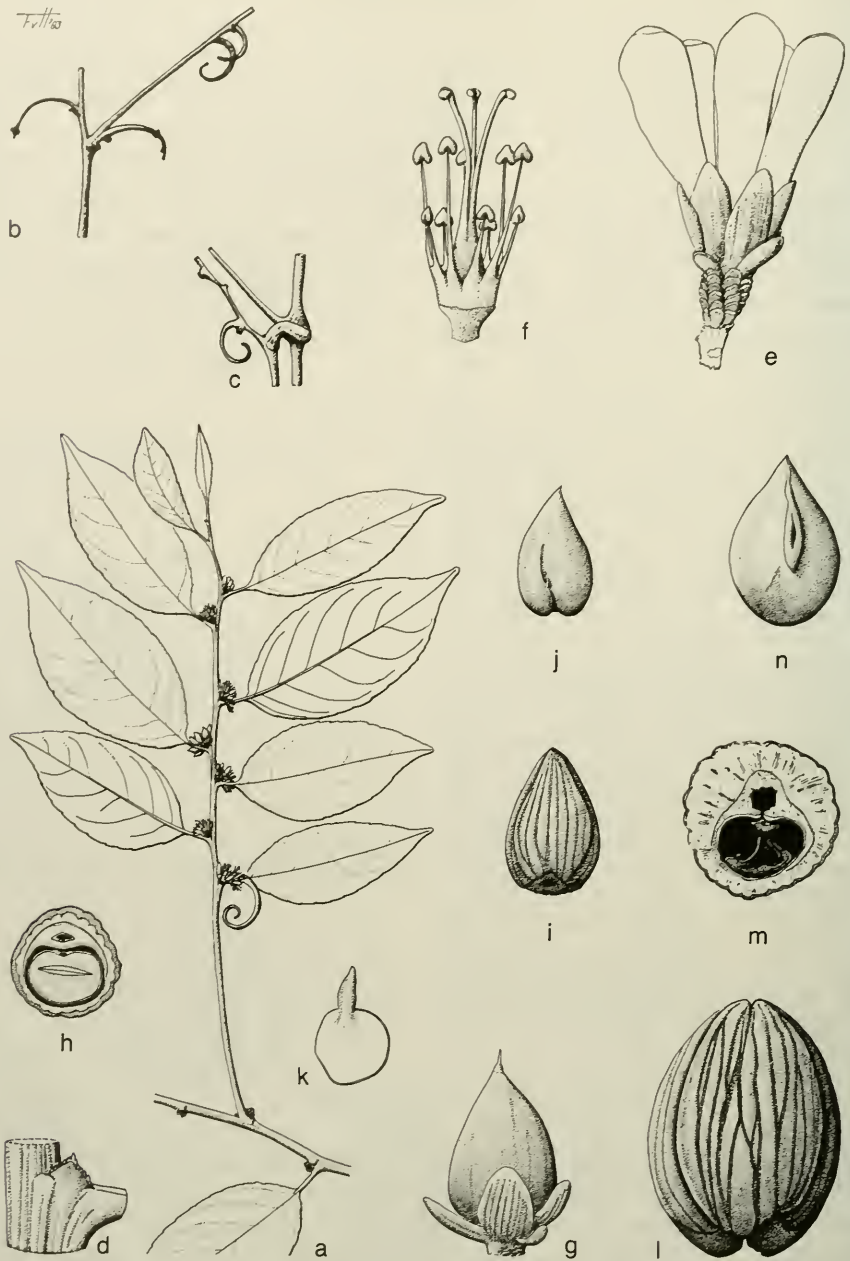


Fig. 6. *Indorouchera contestiana* (PIERRE) HALL.f. a. Habit; b. twig with climbing hooks provided with reduced inflorescence at apex; c. climbing hook, thickened after grasping a twig; all $\times 0.5$; d. stipule, $\times 12$; e. flower and bracteoles, $\times 12$; f. flower, sepals and petals removed, $\times 8$; g. fruit; h. fruit in CS; i. fruit, exocarp removed; j. seed; k. embryo; all $\times 12$. — *I. griffithiana* (PLANCH.) HALL.f. l. Fruit, exocarp removed; m. fruit in CS; n. seed; all $\times 12$ (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*

1. *Indorouchera griffithiana* (PLANCH.) HALL. *f.* Beih. Bot. Centralbl. 39, 2 (1923) 50, *incl. var. coriacea* HALL. *f.*, *l.c.* 52; HUB. WINKLER in E. & P. Nat. Pfl. Fam. ed. 2, 19a (1931) 109; BACKER & BAKH. *f.* Fl. Java 1 (1963) 242; COCKBURN, Tree Fl. Malaya 1 (1972) 306; Trees of Sabah 1 (1976) 204; VAN HOOREN & NOOTEBOOM, Blumea 29 (1984) 557. — *Roucheria griffithiana* PLANCH. Hook. Lond. J. Bot. 6 (1847)

143; *ibid.* 7 (1848) 527; WALP. Ann. 1 (1849) 97; HOOK. *f.* Fl. Br. India 1 (1874) 414; BOERL. Handl. 1 (1890) 140; KING, J. As. Soc. Beng. 62, ii (1893) 190; BOERL. Feestbundel (1894) 91, tab.; *l.c.* Bog. 1 (1897) 25, t. VII, f. 1–22; KOORD. Nat. Tijd. Ned. Ind. 60 (1901) 384; BACKER, Schoolfl. Java (1911) 163; KOORD. Exk. Fl. Java 2 (1912) 415; RIDLEY, Fl. Mal. Pen. 1 (1922) 323; Kew Bull. (1926) 60. — *Flacourtia*



Fig. 7. *Indorouchera griffithiana* (PLANCH.) HALL. *f.* in blossom, Njarumkop (NW, Kalimantan) (Photograph by Father A. EISENER, 9 April 1964)

?*camptoceras* MIQ. Fl. Ind. Bat., Suppl. (1861) 288; BOERL. Feestbundel (1894) 91; Ic. Bog. 1 (1897) 27; KOORD. Exk. Fl. Java 2 (1912) 415; HALL.f. Beih. Bot. Centralbl. 39, 2 (1923) 50; SLEUMER, Fl. Males. 1, 5 (1954) 77. — *Hugonia sumatrana* MIQ. Illustr. (1871) 68; BOERL. Feestbundel (1894) 91; Ic. Bog. 1 (1897) 27. — Fig. 61-n, 7, 8.

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, heterodistylous. *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 obovate, (5–)6.5–8.5 by 1.5–3 mm; base obtuse to very short-ly 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, cylindrical, obovoid or globular, 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 cylindrical to flattened, straight to slightly curved, 1.1–1.5 by 0.4–0.5 mm.

Distr. India (Nicobar Is.), Thailand; in *Malesia*: Sumatra, Malay Peninsula, Borneo, Java. Fig. 9.

Ecol. 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).

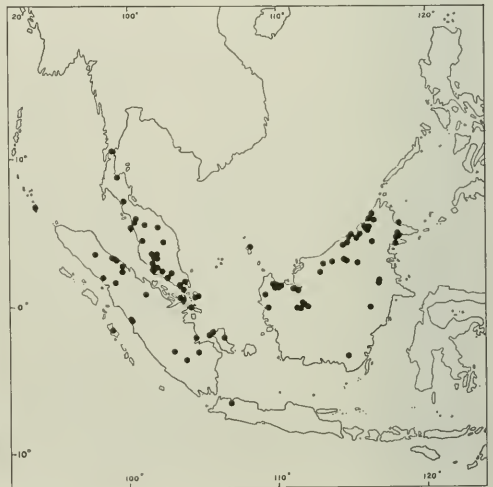


Fig. 9. Range of *Indorouchera griffithiana* (PLANCH.) HALL.f.

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 BURKILL, Dict. 2 (1935) 1949. In Sarawak used for parang handles.

Vern. Sumatra: *andor pijom*, Tapanuli, *akar tandu*, *takkolan*, East Coast, *olor nanas*, *olor silayur*, *surango etem*, Simalur. Malay Peninsula: *akar garam garam*, *a. tenggadin*, Selangor. Borneo: *wa bakar*, Iban, *akar katjap*, Brunei, *dingkai*, Sabah, *akar tuai*, Kenyah.

2. *Indorouchera contestiana* (PIERRE) HALL f. Beih. Bot. Centralbl. 39, 2 (1923) 52; HUB. WINKLER in E. & P. Nat. Pfl. Fam. ed. 2, 19a (1931) 110; VAN HOOREN & NOOTEBOOM, Blumea 29 (1984) 558. — *Roucheria contestiana* PIERRE, Fl. For. Coch. (1893) t. 281; GUILLAUMIN, Fl. Gén. I.-C. 1 (1911) 586, f. 61-5 & 61-6. — *I. rhannifolia* HALL f. Beih. Bot. Centralbl. 39, 2 (1923) 52; HUB. WINKLER in E. & P. Nat. Pfl. Fam. ed. 2, 19a (1931) 110. — Fig. 6a-k.

Liana, up to 10 m, sometimes a shrub up to 4 m. Stem \pm 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 \pm 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. Stamens 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. Drupe ovoid, 4–4.5 by 2.5–3 mm; exocarp thin-fleshy, c. 0.2 mm thick;

mesocarp chartaceous, \pm lengthwise grooved, c. 0.2 mm thick; endocarp woody, crescent-shaped in CS, \pm 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, \pm 1.5 mm long; aril indistinct, short, \pm thickened below the hilum; testa thin. Embryo 2.8–3 by 1.3–1.5 mm; cotyledons straight, broadly elliptic to \pm 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.

Distr. 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 BURKILL, Dict. (1935) 1949. For details on chemical contents see HEGNAUER, Chemotaxonomie der Pflanzen 4 (1966) 397. On the label of CINS 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: *kut kut puteh*, 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*: *Cyrrilopsis* KUHLM. 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.*).

References: EXELL & MENDONÇA, Bol. Soc. Brot. ser. 2a, 25 (1951) 105; FORMAN, Kew Bull. 19 (1965) 521–526; HALLIER *f. Beih. Bot. Centralbl.* 39, 2 (1923) 1–178; NOOTEBOOM, *Adansonia* II, 7 (1967) 161–168; *Fl. Males.* I, 6 (1972) 970, f. 1; PLANCHON in *Hook. Lond. J. Bot.* 6 (1847) 588–603; PLANCHON & KLOTZSCH, *Abh. Kön. Ak. Wiss. Berlin* 1856, *Physik. Abh.* (1857) 235; VAN WELZEN & BAAS, *Blumea* 29 (1984) 453–479; HUB. WINKLER in *E. & P. Nat. Pfl. Fam. ed.* 2, 19a (1931) 123, f. 55 & 56. — C.G.G.J. VAN STEENIS (1985).

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*, *Cyrrilopsis*, *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.

References: BURGESS, *Sabah For. Rec.* 6 (1966) 247–248; DESCH, *Mal. For. Rec.* 15 (1957) 156–157; METCALFE & CHALK, *Anatomy of the Dicotyledons* 1 (1950) 268–273; METCALFE, LESCOT & LOBREAU, *Adansonia sér.* II, 8 (1968) 337–351; ROJO, *Adansonia sér.* II, 8 (1968) 73–83; VAN WELZEN & BAAS, *Blumea* 29 (1984) 453–479. — P. BAAS.

Palynology. Pollen of *Ixonanthaceae*, which is described by LOBREAU (1969: 526, *Cyrrilopsis*) and OLTMANN (1971), is subprolate to prolate (*Cyrrilopsis*, *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 columellae.

The thickness of this columellate layer clearly exceeds that of tectum and nexine together. Sculpture is mostly somewhat scabrate. *Cyrillopsis* has a rugulate or striate exine. Pollen of *Ixonanthes* is characterized by the presence of distinct supracteal 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 *Iringia*) by MULLER (1972), which latter opinion is accepted here. METCALFE *c.s.* (*l.c.*) consider pollen of *Ixonanthaceae*, *Allantospermum*, and *Iringiaceae* 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*.

References: BORTENSCHLAGER, ERDTMAN & PRAGLOWSKI, Bot. Notis. 119 (1966) 160–168; LOBREAU, Pollen et Spores 11 (1969) 499–555; METCALFE, LESCOT & LOBREAU, Adansonia sér. II, 8 (1968) 337–351; MULLER, Fl. Males. 1, 6 (1972) 972; OLTMANN, Pollenmorphologisch-systematische Untersuchungen innerhalb der Geraniales. Diss. Bot. 11 (1971). — R.W.J.M. VAN DER HAM.

1. IXONANTHES

JACK, Mal. Misc. 2, 7 (1822) 51; ENDL. Gen. Pl. (1840) 1055, '*Ixonanthes*'; HALL *f.* Beih. Bot. Centralbl. 39, 2 (1923) 6; HUB. WINKLER in E. & P. Nat. Pfl. Fam. ed. 2, 19a (1931) 124, f. 55, 56A–E; KOOL, Blumea 26 (1980) 195. — *Emmenanthes* HOOK. *f.* & ARN. Bot. Beech. Voy. (1836) 217. — *Brewstera* M.J. ROEMER, Syn. Monogr. 1 (1846) 141. — *Pierotia* BLUME, Mus. Bot. Lugd. Bat. 1 (1850) 179; *ibid.* 1 (1851) 396. — *Discogyne* SCHLTR, Bot. Jahrb. 52 (1915) 123. — Fig. 1–3.

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, subsistent; anthers (basi-)dorso-versatile with a large peltate connective, introrse with 2 longitudinal slits, finely verru-



Fig. 1. View on *Ixonanthes* forest, seen from the resthouse at Malili, Central Celebes (Photogr. J. VAN ZIJLL 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, subsistent in fruit; stigma mushroom-shaped, margin slightly lobed, fleshy. *Capsule* septicial 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 septa 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, \pm half as long as the dorso-ventrally appressed, \pm asymmetrically elliptic cotyledons. Germination epigeal.

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, $\times 0.5$; b. branching of inflorescence, $\times 3$; c. flower bud; d. ditto, perianth removed, both $\times 10$; e. fruit, $\times 3$; f. ditto in CS, $\times 4$; g. ovule, with 3-lobed arillode, $\times 15$; h. stipules, $\times 2$ (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. Brewstera* 1. *I. icosandra*
1. Petioles 10–25 mm. Leaf margins entire, eglandular. Primary branches of the inflorescence paired. Stamens 10. Seeds with a basal wing, suprahilar arillode absent. *Sect. Ixonanthes*.
 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 *Brewstera*

(M.J.ROEMER) HALL.f. Beih. Bot. Centralbl. 39, 2 (1923) 7. — *Brewstera* M.J.ROEMER, Syn. Monogr. 1 (1846) 141.

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.

1. *Ixonanthes icosandra* JACK, Mal. Misc. 2, 7 (1822) 53; MIQ. Fl. Ind. Bat. 1, 2 (1859) 494; Illust. (1870) 68, *incl. var. cuneata* MIQ.; HOOK.f. Fl. Br. India 1 (1874) 416; KING, J. As. Soc. Beng. 62, ii (1893) 191; HOCHR. Pl. Bogor. Exsic. (1912) 40; GUILLAUMIN, Fl. Gén. I.-C. 1 (1911) 584; RIDLEY, Fl. Mal. Pen. 1 (1922) 325, f. 31, *incl. var. obovata* RIDLEY; HALL.f. Beih. Bot. Centralbl. 39, 2 (1923) 7; CORNER, Wayside Trees (1940) 221, f. 60; GUILLAUMIN, Fl. Gén. I.-C. ed. 2, 1 (1945) 501; MERR. J. Arn. Arb. 33 (1952) 227; COCKBURN, Tree Fl. Mal. 1 (1972) 307; KOOL, Blumea 26 (1980) 197, f. 2. — *Brewstera crenata* M.J.ROEMER, Syn. Monogr. 1 (1846) 141, *nom. illeg.* — *Pterotia lucida* BLUME, Mus. Bot. Lugd. Bat. 1 (1850) 180. — *I. lucida* BLUME, *ibid.* 1 (1851) 396. — *I. dodecandra* GRIFF. J. As. Soc. Beng. 23 (1854) 632, t. 1 ('*subdodecandra*'). — *Macharista isoxandra* PLANCH. [in Herb. Hook.] ex CHOISY, Mém. Soc. Phys. & Hist. Nat. 14 (1855) 168, *nom. inval.* — *I. cuneata* MIQ. Suppl. (1896) 484. — *I. obovata* HOOK.f. Fl. Br. India 1 (1874) 417. — Fig. 2.

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 obovate oblong, 6–19 by 3–6.5 cm, pergamentaceous, base tap-

ering; 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-dorso-versatile. 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.

Distr. 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 stiltroots. 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 whitish, yellow, green, sticky. Fruits green to dark brown, sticky.

Uses. Sometimes used for house-building.
 Vern. *Kayu leja-leja*, Sum. E. Coast, *kassi
 branah, kayu ratuh, pempaaga*, Palembang, *kayu*

beluks, Banka, *buah tui, pagar anak, sankau merah*,
 Malaya, *injau belukar*, Pahang, *jenjulang, men-
 julong, punggong kijang*, Kedah.

2. Section *Ixonanthes*

Emmenanthes HOOK.f. & ARN. Bot. Beech. Voy. (1836) 217. — *Ixonanthes*
sect. Emmenanthes HALL.f. Beih. Bot. Centralbl. 39, 2 (1923) 8.

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 incrasate, 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 suprahilar arillode; wing oblong, fairly stiff, concolorous, with a distinct dark-coloured raphe.

2. *Ixonanthes petiolaris* BLUME, Mus. Bot. Lugd. Bat. 1 (1851) 396; MIQ. Fl. Ind. Bat. 1, 2 (1859) 494; Illust. (1870) 69; KOOL, Blumea 26 (1980) 199, f. 1d, 3b. — *Pierotia reticulata* BLUME, Mus. Bot. Lugd. Bat. 1 (1850) 180; *ibid.* 1 (1851) 396, non *I. reticulata* JACK. — *I. multiflora* STAFF ex RIDLEY, Kew Bull. (1930) 75. — *I. philippinensis* ELMER, Leaf. Philip. Bot. 10 (1939) 3758, *descr. angl.* — Fig. 3.

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, pergamentaceous 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 hyalinous, chartaceous in fruit. *Filaments* ultimately up to 15 mm; anthers dorso-versatile. *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; septa 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*.

Ecol. 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 redbrown, 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.

3. *Ixonanthes reticulata* JACK, Mal. Misc. 2, 7 (1822) 51; MIQ. Fl. Ind. Bat. 1, 2 (1859) 494; Illust. (1870) 69; HANCE, J. Bot. 14 (1876) 243; KING, J. As. Soc. Beng. 62, ii (1893) 192; RIDLEY, Fl. Mal. Pen. 1 (1922) 326; HALL.f. Beih. Bot. Centralbl. 39, 2 (1923) 9; CORNER, Wayside Trees (1940) 222, f. 60; MERR. J. Arn. Arb. 33 (1952) 228; BROWNE, For. Trees Sarawak Brunei (1955) 175; COCKBURN, Tree Fl. Mal. 1 (1972) 307; KOOL, Blumea 26 (1980) 200, f. 3A. — *Hypericinea macrocarpa* WALL. Cat. (1831) 4833, *nomen*. — *Gordonia decandra* ROXB. Fl. Ind. ed. Carey 2 (1832) 573. — *Emmenanthus chinensis* HOOK.f. & ARN. Bot. Beech. Voy. (1836) 217. — *I. chinensis* (HOOK.f. & ARN.) CHAMP. in R.Br. Proc. Linn. Soc. 2 (1850) 100, and many later authors. — *I. khasiana* HOOK.f. Fl. Br. India 1 (1874) 416. — *I. hancei* PIERRE in Laness. Pl. Util. Col. Fr. (1886) 306. — *I. cochinchinensis* PIERRE, Fl. For. Coch. 4 (1893) t. 284A; GUILLAUMIN, Fl. Gén. I.-C. 1 (1911) 584; ed. 2, 1 (1945) 501. — *I. grandiflora* HOCHR. Pl.

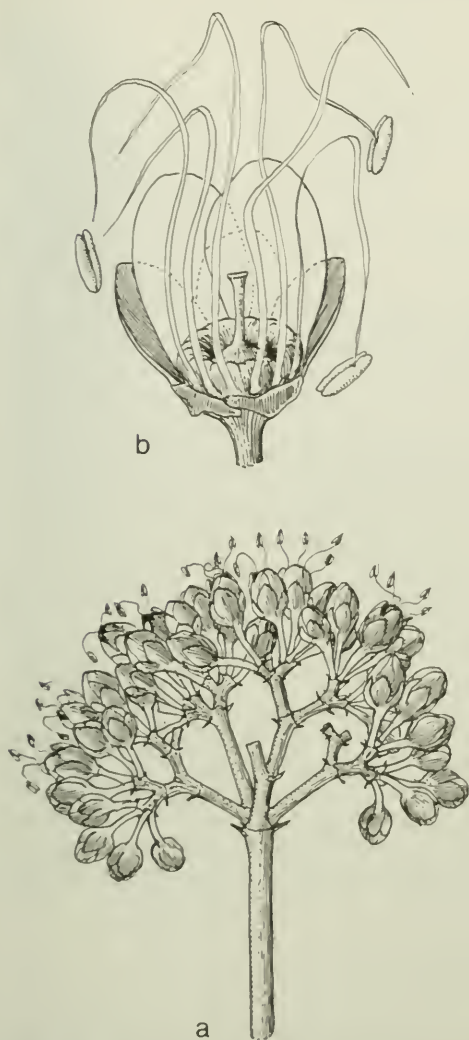


Fig. 3. *Ixonanthes petiolaris* BLUME. a. Inflorescence, $\times 2$; b. flower, $\times 6$ (SAN 40370).

Bog. Exsicc. (1904) 39; MERR. Enum. Born. (1921) 313; HEYNE, Nult. Pl. Ned. Ind. (1927) 854. — *Discogyne papuana* SCHLTR, Bot. Jahrb. 52 (1915) 123. — *I. longipedunculata* MERR. Philip. J. Sc. 17 (1921) Bot. 264. — *I. crassifolia* HALL.f. Beih. Bot. Centralbl. 39, 2 (1923) 10. — *I. beccarii* HALL.f. l.c. — *I. petiolaris* (non BLUME) HALL.f. l.c. 8, pro syn. — *I. grandifolia* RIDLEY, Kew Bull. (1930) 74. — *I. pa-*

puana (SCHLTR) HUB. WINKLER in E. & P. Nat. Pfl. Fam. ed. 2, 19a (1931) 126, t. 55, 56 A-E.

Treelet or tree up to 40 m, bole up to 1 m diam. Lenticles 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, pergamentaceous 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; septa 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 (Kwangsi, Kwantung, 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*, Malaya, *jinjagong*, *sansak china*, Penang, *ingeran* or *inggi burong*, *nyiran burong*, *pagar anak*, *sakit hudang*, Selangor, *angaran buron*, Trengganu, *djurung*, Palembang, *sentulu*, N. Borneo, *langudai*, *perepat rumba*, Sabah, *kanju junong*, Brunei, *redin*, S. Sarawak, *lura*, Celebes, *keseruok*, New Guinea, *Tehid 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*.

CTENOLOPHONACEAE

(A.M.N. van Hooren & H.P. Nooteboom, Leiden)

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; BAILLON, 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 & NOOTEBOOM (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 *Malpighiaceae* and found that it is very different from both *Humiriaceae* and *Malpighiaceae*, but also from other *Linaceae*, and they supported the status of a family of its own, adding that close affinities are still unknown.

References: BAILLON, *Hist. Pl.* 11 (1892) 445; BECCARI, *Malesia* 1 (1877) 119; CRONQUIST, *Integrated system etc.* (1981) 759; ENGLER, *Nat. Pfl. Fam.* 3, 1 (1889) 237; *ibid.*, *Nachtr.* 3 (1907) 204; EXELL, *J. Bot.* 65 (1927) *Suppl.* 1: 50; EXELL & MENDONÇA, *Conspectus flora Angolensis* 1, 2 (1951) 248, 392; HALLIER *f. Arch. Néerl.* III B, 1 (1912) 109; *Meded. Rijksherb.* 35 (1918) 28; HEIMSCH, *Lilloa* 8 (1942) 83; VAN HOOREN & NOOTEBOOM, *Blumea* 29 (1984) 547; HUTCHINSON, *Fam. Fl. Pl.* 1 (1959) 265; ed. 3 (1973) 324; MASTERS, *Fl. Br. India* 1 (1875) 577; OLIVER, *Trans. Linn. Soc.* 28 (1873) 516; PIERRE, *Fl. For. Coch.* (1893) t. 281; VAN WELZEN & BAAS, *Blumea* 29 (1984) 477; HUB.WINKLER in *E. & P. Nat. Pfl. Fam.* ed. 2, 19a (1931) 122.

1. CTENOLOPHON

OLIVER, *Trans. Linn. Soc.* 28 (1873) 516; HUB.WINKLER in *E. & P. Nat. Pfl. Fam.* ed. 2, 19a (1931) 122; BULLOCK, *Kew Bull.* 14 (1960) 41; VAN HOOREN & NOOTEBOOM, *Blumea* 29 (1984) 547. — **Fig. 1, 2.**

Trees. Hairs stellately tufted and simple. Stipules interpetiolar, caducous. *Leaves* entire, opposite, petiolate, simple, pinnately nerved. *Inflorescence* an axillary or terminal cymoid panicle. Bracts present, bracteoles absent. *Flowers* bisexual, 5-merous, actinomorphic, hypogynous. *Sepals* basally shortly connate, quincuncially imbricate, subequal, indurate, swollen and persistent in fruit, with stellate hair tufts. *Petals* free, contorted, caducous, often shortly clawed. *Disk* extrastaminal. *Stamens* 10, free, inserted halfway the disk, alternately longer and shorter, the longer epipetalous and the shorter episepalous; 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, epitropous. *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.

Distr. Two species, one (*C. engleriana* MILDBR.) 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 Moluccas, 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, more rarely 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 solitary vessels with scalariform perforations, fibres with distinctly 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 monogeneric family *Ctenolophonaceae*. Its stomatal type removes it from the *Linaceae* complex, but other leaf anatomical characters 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, Bot. Gaz. 133 (1972) 242–253; METCALFE & CHALK, Anatomy of the Dicotyledons 1 (1950) 268–273; SAAD, Bot. Notis. 115 (1962) 44–57; VAN WELZEN & BAAS, Blumea 29 (1984) 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 *englerianus* type. Contrary to the rounded subspherical *parvifolius* type, the *englerianus* type shows distinct thickenings 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 difficult to determine, especially in the *englerianus* type. A thick nexine can mostly be observed. The infratactal layer appears labyrinthine, sometimes exhibiting granulate-columellate 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 (*l.c.*) actually represents only superficial similarity. Pollen of *Ctenolophon* cannot be convincingly connected with that of other families, which supports attribution 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.*, *l.c.*). The *englerianus* type (*Ctenolophonidites*) occurred in Africa nearly uninterruptedly 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.*, *l.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 occurred in the Paleocene and the Eocene, while it is known from Borneo starting from the Upper Eocene continuing 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 easterly contact between both types. Possibly, the Indian *englerianus* 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. englerianus* and *C. parvifolius* is very small. The occurrence of intermediate pollen between the *englerianus* and the *parvifolius* type is suggestive of introgression between the two species, although independent origin of the *englerianus* type on Samar cannot be excluded.

References: GERMERAAD, HOPPING & MULLER, Rev. Palaeobot. Palynol. 6 (1968) 189–348; MORLEY, Proc. Indon. Petr. Ass., 6th Ann. Conv. (1977) 255–276; MULLER, Bot. Review 47 (1981) 73–74; SAAD, Bot. Notis. 115 (1962) 49–57; THANIKAJMONI, CARATINI, VENKATACHALA, RAMANUJAM & KAR, Trav. Sect. Sci. et Techn. Inst. Franç. Pondichéry 19 (1984) 23, 80. — R.W.J.M. VAN DER HAM.

Notes. 1. The African species *C. englerianus* MILDBR. 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. englerianus*, 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.

1. *Ctenolophon parvifolius* OLIVER, Trans. Linn. Soc. 28 (1873) 516, t. 43, f. 1–7; MAST. Fl. Br. India 1 (1875) 577; BECC. Malesia 1 (1877) 120; KING, J. As. Soc. Beng. 62, ii (1895) 106; RIDLEY, Fl. Mal. Pen. 1 (1922) 423; BURK. Dict. (1935) 695; ed. 2 (1966) 705; DESCH, Man. Mal. Timbers 2 (1954) 15; BULLOCK, Kew Bull. 14 (1960) 41; MEIJER, Bull. Herb. For. Dep. Sandakan 10 (1968) 151, fig.; COCKBURN, Gard. Bull. Sing. 24 (1969) 6; Tree Fl. Malaya 1 (1972) 306; Sabah For. Rec. 10 (1976) 205; ANDERSON, Checklist Trees Sarawak (1983) 239; VAN HOOREN & NOOTBOOM, Blumea 29 (1984) 547. — *C. grandifolius* OLIVER, Trans. Linn. Soc. 28 (1873) 517, t. 43, f. 8–10; MAST. Fl. Br. India 1 (1875) 577; BECC. Malesia 1 (1877) 119; KING, J. As. Soc. Beng. 62, ii (1895) 106; RIDLEY, Fl. Mal. Pen. 1 (1922) 423. — *C. philippinensis* HALL. f. ex SCHNEIDER, Philip. Bur. For. Bull. 14 (1916) 127, *nomen*; MERR. Enum. Philip. 2 (1923) 326. — **Fig. 1, 2.**

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 \pm parallel margins, 5–15 by 2–6 cm; base broadly cuneate, sometimes rounded; margin often \pm thickened; apex broadly acute to obtusely acuminate, sometimes rounded, acumen to 2.5 cm; nerves (5–7–10(–12) pairs, slightly curving upwards to near the margin, often meeting in 1 (or 2) looped intramarginal 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 ramiflorous, 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, 1–3.5 by 0.5–1.7 mm; base with a row of bristles within. Pedicel articulate, grooved, swollen in fruit, 1–1.5(–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, 1–2.5 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. *Pistil* up to halfway the style covered with straight, up to 2 mm long simple hairs; style straight, rather stout, slightly flattened, equalling to up to 3 mm exceeding the long stamens, sometimes as long as the short stamens, 5–10 mm long. *Ovary* \pm 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 obovoid, 12–20 by 5–9 mm,

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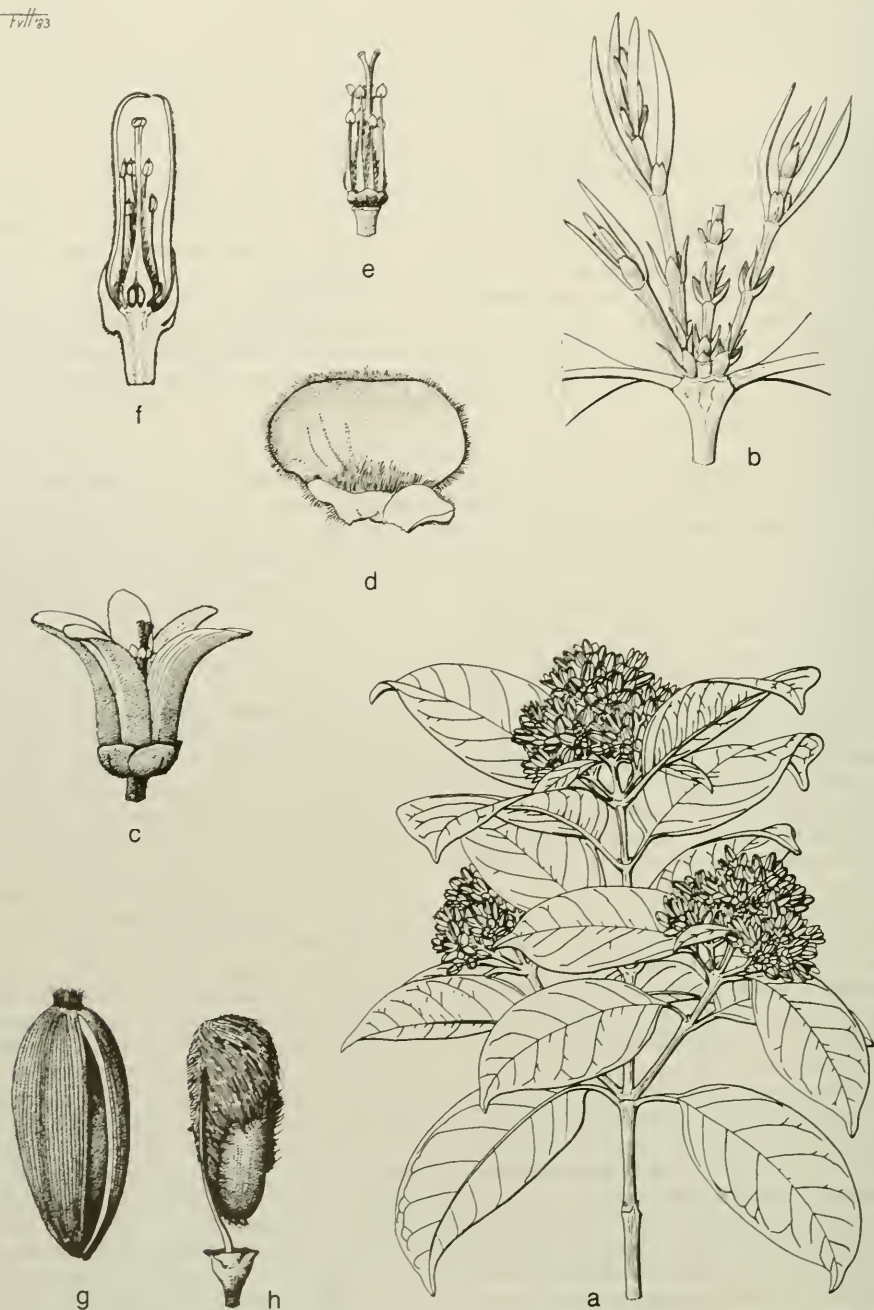


Fig. 1. *Ctenolophon parvifolius* OLIVER. a. Habit, $\times 0.5$; b. innovations, with bud scales, stipules and plicate leaves; c. flower, $\times 3$; d. sepal from inside, $\times 12$; e. flower (sepals and petals removed), $\times 3$; f. flower in LS, $\times 5$; g. fruit, $\times 2$; h. seed, $\times 2$ (a from OLIVER (1873), b DUMAS 1513, c-f SAN 4595, g, h LAMBACH 1251).



Fig. 2. *Ctenolophon parvifolius* OLIVER. A large mature tree at Dolok Puhutan Lajan, Tapanuli, E. Central Sumatra (Photo G.A.L. DE HAAN, 1939; coll. no. 697).

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, 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.

Distr. Malesia: Sumatra, Malay Peninsula, Borneo, Philippines (Samar, Leyte, Mindanao), and New Guinea (incl. Japen I.). Fig. 3.

Ecol. Mixed primary forest, also in heath and swamp forest, indifferent to soils (latosols, 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 reddish brown 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

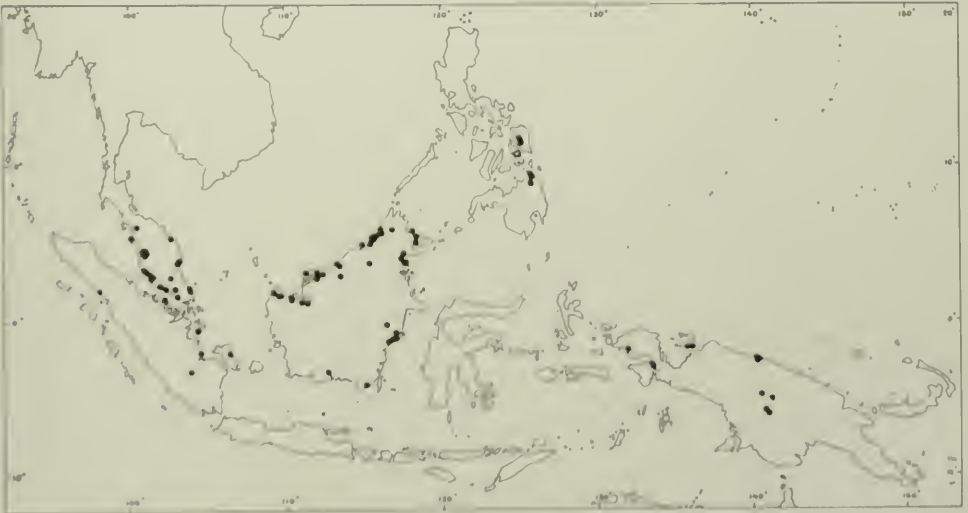


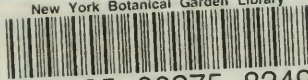
Fig. 3. Localities of *Ctenolophon parvifolius* OLIVER.

bright red. Style pinkish. Fruit yellow to pink, later brown. Seed brown or glossy black; arilloid white to orange or brilliant vermilion.

Uses. The hard and very durable timber is used for house construction and as general purpose timber (SCHNEIDER, 1916; RIDLEY, 1922; DESCH, 1954; BURKILL, 1966).

Vern. Sumatra: *babi kurus*, *batu*, *djambu ayer*, *jinkinai*, *kaju batu*, *k. bawang*, *kalek bung cung*, *klawar*, *medang tembatu*, *petjah pangan*; Malay Peninsula: *bunga tanjong hutan*, *kumus beruang*,

mata ulat, *membatu hitam*, *perichat*, Malaya; *ban(g)kal*, *bankal paya*, *kas*, Mersing; *karu karu*, *kelabau*, Perak; *kelat*, *k. bukit*, *pompong paya*, Pahang, *kelat hitam*, *mertas*, Kuala Lumpur, *mertas kuning*, Kuala Trengganu; *jambu paya*, Johore; Borneo: *belama'a*, *tamana'a*, Sarawak: *litoh*, Iban; *besi*, *obah*, Sabah; *merandi*, W. Kalimantan; *jarmgin*, *kayu batu*, *latak manuk*, E. & SE. Kalimantan. New Guinea: *gun*, Iwur I.; *kodawu*, *kodowu*, *kotawu*, Ingembit I.; *mamdai*, *tora*, Ormu dial., *dnok*, *nook*, Tehid I.; *samber*, *sosopi*, Japen dial.



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