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 ovules, but in the great majority of genera the ovule is inverted. The fertile scale cups the developing seed and may even completely surround it with only the micropyle protruding at the time of pollination. Fleshiness, either of the cone bracts or of the fertile scale (or both) is common and the whole female structure may be reduced to only one or a few fertile units and a few sterile units. This can yield plum-like fruits or, in other cases, structures resembling those of the cashew (*Anacardium occidentale*).

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

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

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

Fossil and present-day distributions suggest that the *Podocarpaceae*, as we know it, developed in cool moist Antarctic forests early in the Mesozoic period. Modern genera were already differentiated before the parts of Gondwanaland became isolated. Several genera had reached India and Kerguelen where they eventually disappeared, but two genera still survive in Africa. All of the important genera were included in the South American landmass where one interesting endemic genus, *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).


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 Phycocymycetes. 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. Coordination of fruiting times is for many species in tropical regions not well developed because at any given time it is often possible to find examples at any and all stages of reproduction and the collection of ripe fruit is 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 crassigemmis. Their fruiting bodies can often be seen erupting from leaves or stems in Podocarpus or Nageia, but this does not seem to be particularly harmful. One species of Korthalsella (Viscaceae), a dwarf mistletoe, is also parasitic in Podocarpaceae: K. dacrydii has been reported both on Dacrycarpus and on 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 archegonium 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. *Saxegothaecae*, *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
2. Foliage of individual leaves.
3. Foliage in the form of scales, needles, or linear leaves less than 2 mm wide.
4. Leaves not bilaterally flattened ................................................................. 2. Dacrydium
5. Leaves bilaterally flattened ........................................................................ 3. Falcatifolium
6. Foliage dimorphic, leaves of ultimate branchlets longer and narrower than on main shoots may be bilaterally flattened ......................................................... 4. Dacrycarpus
7. Foliage in the form of broad flat leaves more than 2 mm wide.
8. Leaves bilaterally flattened ........................................................................ 3. Falcatifolium
9. Leaves bifacially flattened.
10. Leaves with a groove over the midvein, (spirally placed,) lacking hypoderm, with a sweet taste
11. Leaves flat or with a ridge over the midvein, with hypoderm, without a sweet taste.
12. Leaves opposite, many with multiveined leaves ............................................. 6. Nageia
13. 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
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
4. Foliage as bilaterally flattened linear to oval-shaped leaves; fertile structure on a distinct scale lateral shoot ................................................................................................................. 3. Falcatifolium
5. Inverted seed enclosed by a leathery modified fertile scale, not turning, cone in most cases reduced to several scales, becoming fleshy or not.
6. 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
7. Leaves bifacially flattened; fertile bract separate from fruit, becoming fleshy or not.
8. Fertile structure produced on a scale (rarely leafy) shoot; covering of seed more or less fleshy.
9. Leaves spirally placed, single veined, linear; seed nearly oval with slightly asymmetrical micropylar end, fertile axis never fleshy .......................................................... 5. Prumnopitys
10. 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
11. Fertile structure produced on a naked peduncle subtending a fleshy (or leathery) receptacle, covering of seed leathery (rarely somewhat fleshy) ......................................................... 7. Podocarpus

1. PHYLLOCLADUS

Small to large trees up to 30 m tall, with smooth, dark, platy bark which is reddish or yellowish and fibrous within. Primary branches tend strongly to be in false whorls and secondary branching is abundant. The ultimate foliar shoots are flattened into cladodes or '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 epimatum. 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 (Floren, 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 epimatum, 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. Floren regarded the later developing aril as having nothing to do with the epimatum (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. Keng).
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. 7. *Phyllocladus hypophyllus* Hook.f. a. Female shoot, ×0.5; b. ditto, ×0.5; c. ditto, ×2.5; d. cladode with immature female seed cones, ×1.5; e. seeds with bracts and epimatium, ×3; f. seed with epimatium, ×3 (a SAN 69968, b–f BELLAMY 1404).
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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.](image-url)
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 epimatum 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
preceeding 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**
3. 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.
2. Microsporophylls triangular; female terminal (occasionally on short lateral branches); leaves bent forward, up to 5 mm long and length about 5 times width.
3. Leaves blunt (may be apiculate), width less than twice thickness.
4. 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**
5. 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**
6. Leaves spreading (nearly straight), 0.3–0.4 mm wide, less than twice thickness, length about 25 times width. **6. D. beccarii**

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Fig. 10. Range of the genus *Dacrydium* Solander ex Forst. Figures above the hyphen indicate the number of endemic species, that below the hyphen the total number of species.
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. magnus
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. ericoideum
11. Leaf about 1 mm long, strongly bent forward ........................................................ 15. D. leptophyllum

Large tree, 8–40 m high, 0.1–1 m diam., with many slender, more or less erect branches and crowds of branchlets forming tufts which together construct a great 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 l.), 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
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.


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.


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.


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 curving, 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-
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 Kayangaran For. Res. (Brunel) 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.


Tree 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.

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

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


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

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.


*Arbor ad 30 m alta. Folia conferta, apicum 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.


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

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Fig. 14. *Dacrydium cornwalliana* DE LAUB., edge of forest on black peat; in the background mixed forest with amongst others *Libocedrus*. Wissel Lakes, New Guinea, 1700 m (Photogr. F.W. RAPPARD, 1955).
35 m tall. Profusely branched with the branches turned upward, often forming a dense umbrella- or dome-shaped crown. *Juvenile leaves* nearly straight at first on fresh growth, becoming gradually curved forward, up to 17 mm long, strongly keeled on three sides, nearly flat on the axial surface, 0.2 mm wide and 0.1 mm thick, linear-lanceolate, pungent, crowded so that shoots resemble a furry animal's tail. *Adult leaves* spreading, bent slightly forward but the apiculate tips still directed slightly outward, triangular in cross section, 0.3–0.4 mm wide, 0.2 mm thick, crowded, linear-lanceolate, 5–10 mm. *Fertile cones* 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.

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

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**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, mejoop, Kebar valley; Taliabu: kawaui; Borneo: kau embun, Merurong Plateau, sempilor, Sarawak, Bintulu; Malaya: ekor kuda, Kedah; Sumatra: sampinur tali, Tapanuli.

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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, 0.1–1 mm longi, c. 0.3 mm lati. Semina matura non obscura.* Type: *de LAUBENFELS* P716 (L., holo), Mt Kinabalu.

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

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

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**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*. 

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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).

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

 Vern. Sangu, Gajo.

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


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

Distr. Solomon Islands (Guadalcanal, Choiseul, S. Ysabel); in Malesia: Louisiades (Sudest 1.) and Moluccas (Obi 1.). Rare. Fig. 17.

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

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


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

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

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

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


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


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

Dist. Solomon Islands (Bougainville); in Malesia: New Guinea (incl. New Britain), Central E. Solomon Islands.
Flora Malesiana


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

Celebes (2 coll.), Philippines (Mindoro, 1 coll.), Borneo (Sabah; Central Kalimantan: Bt. Raya; Sarawak: Mt Mulu, Mt Murud), N. Sumatra (Atjeh, 1 coll.), and Malaya. Locally discontinuous. Fig. 20.

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

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

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

Fig. 19. *Dacrydium xanthandrum* PILGER. a. Male shoot with pollen cone, ×0.5; b. pollen cone, ×6; c. microsporophylls, ×1.5; d. juvenile shoot with leaves, ×1.5; e. leaf in cross section, ×15 (a–c S 37067; d–e DE LAUBENFELS P627).
14. Dacrydium ericoides de Laub., nov. sp.
   Arbor ad 17 m alta. Folia linearia recta, paginis superis planis, apicis abruptis apiculatis, 5–10 mm longa, 0.7–1 mm lata, 0.2 mm crassa, doris carina-
tis. Strobili fere laterali, masculi 7–10 mm longi, 2–2.5 mm diametri, apicis microsporophyltorum calcarea 1 mm longa. Type: BRUNI G 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 Meruong Plateau in N. Sarawak), Fig. 21.
Ecol. Locally common in primary forest on exposed mossy ridges at 1000 to 1500 m.
Vern. Semipilor, 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 leaves are usually terminal and are subtended by nearly typical leaves not greatly reduced as in D. ericoides, while the leaves are distinctly bent forward and not straight.

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


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
3. 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.
2. 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


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
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.


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

Tree 4–12 m tall. Juvenile leaves to 7.5 cm by 7 mm, falcate with the apex curved forward more or less parallel with the branch; lanceolate. Adult leaves in the shade smaller, 3.5 cm by 6–7 mm; sun leaves even smaller, 13–20 cm 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.

Notes. See note under F. falciforme.


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


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 (Flörin, 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. *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. *D. kinabaluensis*

3. Involucral leaves 6–10 mm long, mostly covering the mature seed; foliage leaves 0.4–0.6 mm wide.
5. Seed not large (5–6 mm long); foliage leaves spreading
6. Seed large (7–8 mm long); foliage leaves imbricate

5. *D. expansus*  
6. *D. compactus*

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
7. Seed large (7–8 mm long); foliage leaves imbricate

6. *D. cinctus*

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KEY TO THE VARIETIES

1. Leaves slender (0.4–0.6 mm wide); involucral leaves always spreading.

2. Leaves imbricate ............ a. var. imbricatus

3. Leaves spreading ............ b. var. patulus

1. Leaves robust (0.6–1 mm wide); involucral leaves sometimes clasping the receptacle.

3. Leaves imbricate ............ d. var. curvulus

2. Leaves spreading ............ a. var. imbricatus

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

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

Ecol. Most 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.
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: djamadju, ki hadji, ki putri, tjemoro (tukung), Tjidadap, S; kadju pakis, tjemara binèh, Md.; SW. Celebes (Bonthain): katus angin, k. parang; Lesser Sunda Islands: Bali: tarupanda; Sumb: katu wawama, Lainondja, kadju wamang; Lombok: majangmekar; Flores: oh-ru, Ruteng; Timor: haae tuni, W. Timor, Nenas, ai-caqueu fuie, E. Timor, Tetun lang.


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.

*Ecol.* Scattered and in 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 on sea-level in Fiji.


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


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

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

Fig. 27. Range of *Daecrycaspis imbricatus* (Blume) de Laub. var. robustus de Laub. (dots) and *var. curvulus* (Miq.) de Laub. (triangles).

*Ecol.* Scattered and in common 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.


Note. Specimens from Borneo and the Philippines have been identified as *D. steupii* where the foliage leaves fall within the size range of this species because in these areas the distichous habit is lost rather early causing the foliage to resemble *D. steupii* closely. Unlike *D. steupii*, however, the leaves range to the smaller sizes of *D. imbricatus*. The involucral leaves in these areas, unlike elsewhere in *D. imbricatus*, are at least 5 mm long and curved upward. Perhaps this material represents a distinct variety. *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. Involucral leaves 2.5—4.5 mm long and more or less clasping the receptacle.

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

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

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


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

Distr. *Malesia*: Central E. Borneo (G. Beratus,
near Balikpapan, once), Central Celebes (Latimodjong Mts) and throughout New Guinea. Fig. 29.

![Fig. 29. Range of three species of the genus Dacrycarpus.](image)

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


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


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


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 (Sahabat: 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.


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


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

**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.


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 Woltape), 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: djasita, Asaro, Kefamo, gu-gra-goin, Goroka, Hagen lang. jumbiri, Mt Giluwe, Mendi lang., kaiwilppiti, Wghi, Minj, kubil-kaibigl, kubuk-kajbek, Kubor Ra., Minj, kubin, Hagen, Togoba, ma-u, Finisterre Ra., Naho lang., pau, Hagen-Wabag, Enga lang. piepipie, 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


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.

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

Tree 10–60 m high, 12–140 cm diam. Bark surface checkered by numerous cracks. Cotyledons 3 fused pairs. Foliage buds small, globose, with overlapping, rounded, keeled scales up to 2 mm long. Juvenile leaves oblong, 4–12 by up to 2 cm, more or less abruptly narrowing at the base to a 3–5 mm long petiole, narrowly abruptly at the apex to an elongated tapering ‘drip tip’ which is 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 midrib 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 micropyyle, 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, Halmahera, Morotai), Lesser Sunda Islands (Timo, 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. Palimbang). 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 Dysos-

xytum, Macaranga, Ficus, sometimes emergent as a triangular or subcylindrical 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.


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 midrib 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 euryrhyncha. Gray & Buchholz (1951) report that the leaves occasionally have a lateral pair of vascular resin canals in addition to the conspicuous central canal beneath the vascular bundle. Two collectors...
Fig. 38. *Prumnopitys amara* (Blume) de Laub. G, H. Twigs with pollen cones; I. twig with seeds; K, L. twig and leaf of a young tree; M. leaf of an adult tree; N–P. pollen cones with details; Q, R. seed, also in cross section (from Koord. Atlas 3, 1915, t. 591).
report seeds with distinctive sculpturing on their surface but this is not evident in the corresponding preserved specimens. The normally three rather than two fused pairs of cotyledons is unique. The limited occurrence in Borneo is curious.

6. NAGEIA


— Fig. 41.

Dioecious, erect shrubs or trees, 1–54 m tall. Bark tan to brown within and dark brown to black on the surface but often weathering to gray, peeling in irregular shaped plates to short vertical strips. Leaves opposite-decussate (or mixed with some leaves spirally placed), distinctly narrowed to a decurrent base. Juvenile leaves mostly larger than the adult leaves which are otherwise similar, twisted at the base so as to appear distichous, in most cases amphistomatic with
the abaxial face uppermost on the left side of the shoot and the axial face upper-most 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**


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 twits), 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.

**KEY TO THE SPECIES**

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

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2. *Nageia motleyi* —

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3. *Nageia maximus* —

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Fig. 41. *Nageia wullichiana* (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).
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 pelewan (*Tristiana*) 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 Arguni Bay (New Guinea) even high buttresses; this seems to occur occasionally.

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


Tree to 34 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 lancedolate to acuminate, at least 2 mm long. Seed-bearing structure solitary on a scale 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-
laya, throughout Sumatra and Borneo (Sarawak & SE. Borneo). Fig. 43.

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


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

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

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


2. Section *Polypodiopsis*


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

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

7. PODOCARPUS


Usually dioecious shrubs to large trees up to 45 m tall. Yellowish to reddish brown soft fibrous bark weathering to gray, more or less fissured and peeling in short to long vertical strips. Vigorous branching of the primary stem tends
to produce false whorls, otherwise branching is less regular to irregular. Growth is by flushes with new leaves sometimes distinctly red rather than the more 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, uninnerved, 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.
There are two slightly overlapping subgenera with 95 spp. across the lower and southern latitudes, throughout the southern temperate forests, all of the tropical highland forests, and throughout the Asian–Malesian tropical lowland forests with a few species reaching other tropical lowlands and others the Asian subtropics. In *Malesia* only subg. *Foliolatus* is represented. Fig. 44.

**Subgenus Foliolatus**

DE LAUB. Blumea 30 (1985) 263.

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

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

**KEY TO THE SECTIONS**

1. Pollen cones solitary or in groups of 3 or fewer.
2. Pollen cones regularly in threes or a mixture of threes and fewer (pollen cones usually at least 2.5 mm diam.; midrib more than 0.3 mm wide; ripe receptacle usually red).
3. Primary foliage budscales erect and free, secondary budscales acute to acuminate.
4. Secondary budscales broadly acute, primary budscales generally less than four times as long as broad; adult leaves not acuminate, usually not abruptly expanded at the base. *Spp.* 1–8 1. Sect. *Foliolatus*
5. Secondary budscales acuminate, primary budscales more than four times as long as broad; adult leaves acuminate, abruptly expanded at the base. *Spp.* 9–10
6. Sect. *Acuminatus*
7. Primary foliage budscales imbricate, forming a globular ball; secondary budscales blunt. *Spp.* 11–12
8. Sect. *Globulus*
2. Pollen cones normally solitary (only rarely grouped) (external budscales erect and free; leaves not at all acuminate).

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

4. Sect. Longifoliolatus

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

6. Pollen cones less than 3 mm diam., apex of the microsporophyll less than 0.5 mm long. Foliage bud less than 2 mm diam. Spp. 18–21 .............................................. 5. Sect. Gracilis

6. Sect. Macrostachys

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

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


VEGETATIVE KEY TO THE SECTIONS

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

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

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

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

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

2. Sect. Acuminatus

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

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

5. Leaves lanceolate, widest near the base.

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

6. Midrib on upper side of leaf less than 0.2 mm high, indistinct... 8. Sect. Polystachys (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

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

4. Sect. Longifoliolatus (P. gibbsii)

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. Polystachys

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. Macrostachys

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


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. nerifolius, the most widespread species of the genus, which covers virtually the entire Asian–Pacific wet tropical forest zone. The one highland species, P. rubens, is also widely distributed, otherwise the species are more local but combine to form a nearly continuous slightly overlapping series from Sumatra to Tonga. All but 2 spp. lie within Malesia.

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

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

KEY TO THE SPECIES

1. Midrib on the upper side of the leaf prominent, at least 0.3 mm high and less than 1 mm wide (primary budscales no more than 5 mm long).
2. Juvenile leaves acuminate, midrib bold with vertical sides. Primary budscales 1–1.5 mm wide.
3. Leaf at least 7 cm by 10 mm, not apiculate, new leaves green to reddish, midrib 0.4–0.8 mm wide (where only 0.4–0.5 mm wide the leaf usually acuminate). Pollen cones normally sessile. Ripe receptacle red.
   1. P. nerifolius
3. Adult leaf no more than 6 cm by 10 mm, often apiculate, new leaves bright red, midrib 0.3 mm wide. Pollen cones often on a short peduncle. Ripe receptacle often purple .......................... 2. P. rubens
2. Juvenile leaves never acuminate, midrib with sloping sides. Primary budscales 2 mm wide (pollen cones usually pedunculate).
4. Leaf at least 7 cm by 10 mm, linear-oblong (midrib 0.5 mm wide). Pollen cone usually solitary. Receptacle often with three fleshy bracts ................................. 3. P. archboldii
4. Adult leaf no more than 9 cm by 9 mm, elliptic. Pollen cones usually in clusters of 2–3. Receptacle of two bracts only ................................. 4. P. insularis

Tree (3)–35–50(–45) m tall, 10–100 cm diam., clear bole up to 20 m; crown often dome-shaped. Foliate 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 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 (Khaya), Thailand and Indochina through Malesia to the Solomon and Fiji Islands; in Malesia: Malaysia, Sumatra (incl. Simulur I.), throughout Java and Borneo (incl. Karimata I.), the Philippines (Mindanao), Celebes, the Lesser Sunda Islands (Bali, Flores), the Moluccas (obi, Ceram, Halmahera), and New Guinea (incl. New Britain, New Ireland, Rossel I.,

Fig. 45. Range of Podocarpus neriifolius D.Don.
Manus I., Biak, Job I., and Numfoor), common in many islands. Fig. 45.

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

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

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

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

Uses. A valuable timber tree, used for construction.


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

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


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

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

Distr. Malaya: 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.

Ecol. 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.


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 rip 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 ICNLS 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.


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.


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


Small to medium-sized tree, 3–39 m tall, up to 20–60 cm diam., bole up to 24 m. Foliage buds 2.5–3 mm long and up to 3.5 mm diam., the primary budscales strongly spreading. Juvenile leaves linear, to 15 by 1.4 cm. Adult leaves elliptic, 5.5–9 cm by 7–9 mm, apex acute, narrowed at the base to 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, Ferguson, and New Britain. Fig. 49.

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


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

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

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

![Fig. 48. Range of *Podocarpus archboldii* N.E.Gray (A), *P. deflexus* Ridley (D), and *P. borneensis* de Laub. (B).](image)

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

Note. A rather distinctive species, its large smooth leaves and large fruit resembling among others *P. rumphii* and *P. solomoniensis* 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).


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 auxiliary scleroids, 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 (Meru-rong 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.


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 scleroids is a character shared apparently with *P. novaecaledonae* in this section.


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

Distr. Malesia: E. Borneo (once; Berau), Celebes, Moluccas (Talaud Is.: Karakelong, Mt Piapi; Ambon: Mt 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.

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

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

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

**Distr.** From Borneo to Queensland 3 spp., of which 2 in *Malesia*: in Borneo and New Guinea respectively.

**Ecol.** Low elevation primary rain-forest understory trees, in one case also common along disturbed forest margins.

**Note.** The only section with both acuminate secondary budscales and acuminate leaves.
KEY TO THE SPECIES

1. Seed and its covering at least 11 by 8 cm, not crested. Adult leaves mostly more than 17 mm wide. Female peduncle at least 4 mm long. Plant lacking rhizomes ............................................. 9. P. ledermannii
2. Seed and its covering less than 11 by 8 mm, slightly crested. Adult leaves less than 17 mm wide. Female peduncle c. 1 mm long. Plant with rhizomes ............................................. 10. P. micropedunculatus


Tree, 4--26(--33) m tall, 8--60 cm diam. Foliage buds 4--8 mm long by 3--4 mm in diam., the primary budscales 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: Borneo (Sarawak: Marudi For. Res.; Brunei; Sabah: Papar, Tawao). Fig. 51.


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

Distr. 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.


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.

3. Section Globulus


Primary foliage bud a globular head of completely imbricate scales, gradually expanding with
the growth of a new shoot until the secondary bud, also globular, erupts; primary budscales acute to more or less rounded, c. 1.5–2 mm long; secondary scales oval and blunt. Leaves with parallel sides or somewhat lanceolate, slightly rounded at a narrow apex to broadly rounded and sometimes 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. nakai). 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 understorey of primary or secondary rain-forest (occasionally larger and in the canopy), on exposed mossy ridges, or in short open forest.

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

**KEY TO THE SPECIES**

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

11. P. globulus

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


Tree, 3.5–27 m tall, to 18 and more cm diam. Juvenile leaves 7.5–16 by 1.5–2.4 cm, abruptly 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.


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

Fig. 52. Range of *Podocarpus globulus* DE LAUB. (G) and *P. teysmannii* MIQ. (T).
on a 6–11 mm peduncle; foliola 1 mm and early deciduous.  

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

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

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

### 4. Section Longifoliolatus

**De Laub.** Blumea 30 (1985) 269.

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

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

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

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

**Key to the Species**

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

1. Pollen cones more than 3 cm long; leaf mostly lanceolate or linear-lanceolate, not revolute, adult leaves at least 5 cm long.  
2. Leaf linear-lanceolate or linear, midrib broad and blunt on the upper side (no crest on fruit)  
14. P. confertus

2. Leaf lanceolate, midrib sharp and narrow on the upper side.
3. Leaves more than 7 mm wide; scales at base of pollen cone long triangular; fruit with a crest.
4. Leaves mostly over 10 mm wide; foliola at base of receptacle more than 3 mm long; bud for pollen cone 4–5 mm in diameter; pollen cone initially sessile, when mature with an elongated scaly base

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*


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.


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.


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


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

Distr. Malesia: New Guinea. Fig. 54.

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


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

Distr. Malesia: N. Sumatra (Gajo Lands: Kemiri & Bandahara Mts) and West New Guinea (Wisser 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


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 by 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
5. Leaves more than 8 mm wide, always blunt; (dispersed; fruit not crested) ........ 20. P. rotundus

1. Leaves less than 2 cm long (less than 6 mm wide, always blunt, crowded); foliage bud less than 1.5 mm long (fruit crested) ................................................................. 21. P. glaucus


Tree 1–25 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 beach forest with mossy undergrowth, associated with Phyllocladus and Myrsine, in New Guinea in elfin woodland on Mt Hunstein and on Mt Nettoto in low Xantho-
myrus-Podocarpus crest forest.

Vern. West New Guinea: bempop, Hattam Lang.; East New Guinea: gihura, Asaro, Kefamo, iamu-
gang, Goroka, Togoba, jamega, Hagen, Togoba,
kaibeltugl, 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.


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.


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 Laguna Prov. and Lucban in Tayabas Prov.), 3 collections. Fig. 56. Ecol. Dwarf mossy forest, on Mt Beratus at c. 1000 m, in Luzon up to 2200 m.


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

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


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

6. Section Macrostachyus


Primary foliage bud mostly at least 4 mm diam. on vigorous shoots, but 3–3.5 mm diam. on weaker shoots, and generally somewhat smaller in some species, about as long as or somewhat longer than the diameter, none more than 5 mm long; primary scales triangular and erect or lancetolate 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).

Ecological. 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. Longifoliatus), resembles P. brevifolius of the present section also, but more information is needed.

KEY TO THE SPECIES

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


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

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

Fig. 58. Range of Podocarpus crassigemmis 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.


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

In the Goroka Subdistrict Stevens found two trees (LAE 51011) of which the leaves were infected with Corynelia uberata Fries, widely distributed in the Old World.


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 Pilot (east of line), P. brevifolius (Staaff) 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, Ibiware 2700 m, Wissel Lakes 2000 m.

Vern. East New Guinea: bacela, Kundiawa,
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 or at near the tree line. Only the pollen cone and the prostrate habit that often develops distinguish the two varieties so that herbarium specimens cannot always be assigned with confidence to their proper variety.


Small, often gnarled, sometimes conical tree 2–7.5 m tall. Foliage bud 3.4–4 mm long, primary scales erect, spreading at their tips, occasionally somewhat longer than the bud itself. Juvenile leaves 5–8 cm by 6–9 mm, narrowly acute. Adult leaves elliptical, 2–5 cm by 4–6.5 mm, acute, narrowed at the base to a broad 1–2 mm petiole, slightly revolute; midrib above a narrow ridge 0.2 mm wide and 0.1 mm high. Seed-bearing structure on a 2–4 mm peduncle; foliola c. 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.


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: Philippines (N. Luzon, on Bucas and other isles between Luzon and Taiwan and possibly on the northcoast of Luzon). Fig. 59.

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

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

7. Section Rumphius

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. laubefelsii 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; foliola 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*.

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

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

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

**Key to the Species**

1. Pollen cones sessile; foliage budscales often completely adpressed; receptacle often with a third lateral smaller sterile bract ................................................................. 26. *P. rumphii*

1. Pollen cone clusters usually on a small peduncle; foliage budscales always spreading at the tips; receptacle never with a third lateral sterile bract ........................................ 27. *P. laubenfelsii*


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

**Dist.** 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.
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.

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**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 buds 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 budscales more or less rounded or slightly acuminate, the secondary bud when it first appears a cluster of scale tips or when with particularly short primary scales may still be more or less in a ball. **Leaves** linear and almost blunt to lanceolate, sometimes in the same species at different stages of growth; midrib prominent above, usually less than 0.6 mm wide, broader and blunter below, usually three vascular resin canals but occasionally more (or less). **Buds for pollen cones** up to 3 mm long, either sessile or on a short peduncle; the secondary pollen cone buds when they first appear a round ball of overlapping scales. **Pollen cones** variable in length among the species but most commonly 2–4 cm long, normally in clusters of up to five; apex of the microsporophyll similarly variable in length but most commonly a small.
spur 0.2—0.3 mm long over a wider base. **Seed-bearing structure** on a variable-sized peduncle, mostly 3—12 mm long but shorter in some species; 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. fasciculus*), 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 (sub)tropical 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*
3. Seed and its covering more than 10 mm in diameter. Midrib above blunt .......... 29. *P. macrocarpus*


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

Fig. 62. *Podocarpus polystachyus* R.Br. ex Endl. Pollen cones, ×1.4 (Photogr. A. ELSENBER, 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; f oliola 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 high tide mark and sandy coastal bluffs and low outcrops, also mentioned for sandy ridges in the mangrove. On coastal granite and limestone rocks the trees are gnarled. Second, it is often frequent on lowland coastal kerangas and sandy ‘pandangs’ (degraded heath forest) and sandy heath forest (Menchali For. Res., Pahang). These two habitats are typical in the Sunda Land. Third, on limestone hills inland, for instance in Malaya and the Philippines, in Obi, Waigeu, and the Vogelkop Peninsula in New Guinea at 180, 280 and 550 m, at 1000 m in Palawan. In East Malesia these occurrences are scattered.

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


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


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 Lab. (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.

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 standstone, on Mt Ophir on granite.