

A TAXONOMIC REVISION OF THE GENUS *PODOCARPUS*

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SUMMARY

In connection with the forthcoming revision of the Coniferae for the Flora Malesiana, the author thought it necessary to revise the genus *Podocarpus*. Although this genus has a substantial representation in Malesia (30 species), the revision is too involved to be appropriate with the Flora Malesiana *per se*. One new subgenus and 17 new sections are described, and 94 species are enumerated, of which 11 species and 1 variety are described as new, and 3 varieties have been raised to specific rank. Two keys are given to the 18 sections; each section has a key to the species.

INTRODUCTION

The genus *Podocarpus* which ranges across most of the tropical and antarctic forest zones of the world as well as in subtropical Asia, has recently undergone and needs further to undergo the addition and subtraction of a substantial number of species (De Laubenfels, 1969). The rather large remainder (94 species) which has its greatest concentration in Malesia (30 species) requires a division into subgenera and sections. Buchholz & Gray (1948) revised the former larger entity treated under this name but provided only letters for their subdivisions ('subsections') of *Podocarpus* s. str. With three major groups corresponding respectively to Africa, Asia, and America they included a fourth partly overlapping the Austral group, the distinctions being based on number and position of leaf resin canals, accessory transfusion tissue in the leaf, the 'Florin ring' around stomates, and bracts beneath the female receptacle. Later Gray (1953, 1955) added two more small divisions based on variations in the leaf resin canals. The characters of leaf resin canals have not proven in many cases in the genus to be a reliable distinction but distinct groupings of species in terms of a variety of characters including those mentioned are possible.

A clear nearly equal division of *Podocarpus* into two subgenera, each with several sections, can be made based on certain features of the ovule-bearing shoot and the leaf epidermis. Subgenus *Podocarpus* (A, C, & D of Buchholz & Gray, 1948) lacks the two foliola (lanceolate bracts) below the receptacle which characterizes the other subgenus, *Foliolatus* (B of Buchholz & Gray), but retains the 'Florin ring' which is lacking in *Foliolatus*. Other characters including the arrangement of foliar resin canals and the shape of the upper leaf surface as well as the possibility of a crest on

the fruit, also tend to separate the two genera. On the other hand, both have a similar range of leaf shapes and foliage bud tips.

Subgenus *Podocarpus* is associated with the antarctic forests of Tasmania, New Zealand, and Chile and extends into the tropical highlands of Africa and America, rarely penetrating into tropical lowlands. Two endemic highland species extend the range of this subgenus a short way into the Pacific tropics in northeastern Australia and New Caledonia where there is a slight geographic overlap with the other subgenus. Subgenus *Foliolatus*, on the other hand, is concentrated in the Asian and Pacific tropics and is by no means restricted to highland areas. Several of its species occur in subtropical parts of eastern Asia and of Australia.

A further subdivision of the genus *Podocarpus* into 18 sections of from 1 to 10 species each can be made with each group of species sharing one or more special characteristics. The distinctions between the sections include characters of fleshiness and shape of the fruit, placement of pollen cones and shape of the microsporophylls, form and organization of the foliage buds, shape of the leaf, leaf accessory transfusion tissue, and certain variations in the leaf resin canals. More consistent observations are available for the external morphology of the leaf where, when an important character does exist internally, it can often be detected externally in some way. The more limited availability of mature pollen cones and fruit restrict the usefulness of their distinctive characters, particularly since the sporadic out of season pollen cone structure that may appear may not be at all typical. Where possible, therefore, an emphasis is placed on the form of the leaf and foliage bud.

Subgenus *Podocarpus*

Receptacle without subtending foliola. Stomata with a 'Florin ring'. Either marginal together with other leaf resin canals or only one which lies below the vascular bundle. In many cases a channel over the vascular bundle on the upper surface of the leaf, rarely a ridge. Often a crest on the distal end of the seed coat.

The 41 species of this subgenus are divided into 9 sections of from 1 to 7 species each. Only slight geographic overlap is the rule among these sections, but in the isolated Guyana Highlands area 4 sections are represented.

KEY TO THE SECTIONS

- 1 a. Marginal resin canals in the leaves, one or more vascular resin canals [pollen cones solitary to groups of 3] 2
- b. No marginal resin canals in the leaves, one vascular resin canal [female receptacle fleshy] 3
- 2 a. Female receptacle becoming fleshy; seed with its covering about 9–12 × 6–7 mm; pollen cones more or less sessile 1. Section *Podocarpus*
- b. Female receptacle leathery; seed with its covering at least 14 × 9 mm; one to three pollen cones usually on a peduncle 2. Section *Scytopodium*

- 3a. Pollen cones one to many on a peduncle (occasionally a sessile cluster) 4
 b. Pollen cones strictly solitary, usually sessile 6
- 4a. Pollen cones clustered 3 or more, usually pedunculate; apex of seed coat blunt or with a small crest; upper surface of leaf usually with a slight groove [leaf with accessory transfusion tissue] **5. Section Capitulatis**
 b. Pollen cones 1–3 on a peduncle; apex of seed coat with a prominent beak; upper surface of leaf usually flat or ribbed 5
- 5a. Leaf without accessory transfusion tissue, less than 5 cm long; seed coat not becoming fleshy, less than 1 cm long **3. Section Australis**
 b. Leaf with accessory transfusion tissue, at least 6 cm long; seed coat becoming large and fleshy, more than 2 cm long **4. Section Crassiformis**
- 6a. Tips of outer bud scales imbricate and overlapping; upper surface of leaf with a groove **6. Section Pratensis**
 b. Tips of outer bud scales spreading or, if not, upper surface of leaf with a distinct ridge 7
- 7a. Bud scales foliaceous, much longer than diameter of bud, adult leaves lanceolate **7. Section Lanceolatis**
 b. Bud scales short, hardly longer than diameter of bud; adult leaves not lanceolate 8
- 8a. Pollen cone up to 1.5 cm long; adult leaves up to 3.5 cm × 8 mm, upper surface usually with a ridge **8. Section Pumilis**
 b. Pollen cone at least 3 cm long; adult leaves normally more than 5 cm × 8 mm, upper surface usually with a groove **9. Section Nemoralis**

1. Section Podocarpus

Leaves with a resin canal along each margin and 1–5 resin canals near the vascular bundle, with well developed accessory transfusion tissue, mostly flat or with a groove on the upper surface, linear to narrowly lanceolate. Pollen cones usually sessile and solitary or paired. Ripe receptacles becoming greatly enlarged and bright red. Globular fruit with a blunt apex about 9–12 × 6–7 mm, seed coat leathery. Foliage buds small and globular, formed of a cluster of small long triangular scales with spreading tips. Trees of tropical mountain and subtropical forests.

Distribution. Eastern to Southern Africa.

KEY TO THE SPECIES

- 1a. Leaves less than 5 mm wide, mostly less than 6 cm long, many with short rows of stomates on the upper surface **1. P. elongatus**
 b. Leaves more than 5 mm wide, mostly more than 6 cm long, very rarely a few isolated stomates or none on the upper surface **2. P. latifolius**

1. *Podocarpus elongatus* (Aiton) L'Hér. ex Pers., Syn. 2 (1807) 580. – *Taxus elongatus* Aiton, Hort. Kew. 3 (1789) 415. – *Taxus capensis* Lam., Encycl. 3 (1789) 229.
2. *Podocarpus latifolius* (Thunb.) R.Br. ex Mirbel, Mém. Mus. Hist. Nat. Paris 13 (1825) 75. – *Taxus latifolius* Thunb., Prod. Fl. Cap. (1800) 117. – *P. thunbergii* Hook. f., Lond. J. Bot. 1 (1842) 657. – *Nageia latifolia* (Thunb.) Kuntze, Rev. Gen. Pl. 2 (1891) 800. – *P. milanjanus* Rendle, Trans. Linn. Soc. II, 4 (1894) 61. – *P. ulugurensis* Pilger, Not. Bot. Gart. Mus. Berlin 12 (1934) 82.

2. Section *Scytodium* de Laubenfels, *sect. nov.*

Receptacula strobili foeminei coriacea; tegimentum seminis carnosum; folia ductibus resiniferis marginalibus instructa. – Type species: *P. madagascariensis* Baker.

Leathery rather than fleshy ripe receptacles distinguish section *Scytodium* along with marginal leaf resin canals and a fleshy ripe seed coat. In most of the species the fruit is conspicuously asymmetrical with a blunt crest displaced towards the ventral side. The one to three pollen cones are usually produced on a naked peduncle, otherwise sessile. Foliage buds are globular with tightly overlapping triangular scales usually with the tips of some spreading. Leaves are linear to lenticular mostly with a slight ridge over the vascular bundle. The numerous peripheral leaf resin canals of the rare *P. rostratus* were the basis of Gray's 'subsection E' but they are lacking in one particularly small-leaved specimen ('*P. perrieri*') while one specimen of the equally rare *P. capuronii* does have them ('*P. woltzii*'). *Podocarpus rostratus* also lacks the accessory transfusion tissue of the remaining species. Trees of highland rain-forest.

Distribution. Highlands of Madagascar and Tanganyika and in eastern South Africa.

KEY TO THE SPECIES

- 1a. Fruit at least 20 × 12 mm [crest off center, blunt]; leaves at least 4 cm × 3 mm 2
- b. Fruit less than 18 × 11 mm; leaves less than 5 cm × 3.5 mm 3
- 2a. Widest part of leaf near its center 3. *P. madagascariensis*
- b. Widest part of leaf well before its center 4. *P. henkelii*
- 3a. Fruit 16–18 mm long with a large symmetrical crest; pollen cone at least 2 cm × 3.5 mm; adult leaves at least 2.5 cm 5. *P. capuronii*
- b. Fruit less than 16 mm long with a blunt off center crest; pollen cone less than 2 cm × 3 mm; adult leaves less than 2 cm 4
- 4a. Leaves oval, 2.5–3.5 mm wide 6. *P. humbertii*
- b. Leaves narrowly linear, 0.5–1.5 mm wide 7. *P. rostratus*

3. *Podocarpus madagascariensis* Baker, J. Linn. Soc. 12 (1885) 447.
4. *Podocarpus henkelii* Stapf ex Dallimore & Jackson, Handb. Conif. (1923) 47. — *P. ensiculus* Melville, Kew Bull. (1954) 566.
5. *Podocarpus capuronii* de Laubenfels, Adansonia 2, 11 (1971) 713. — *P. woltzii* Gaussen, Bull. Soc. Hist. Nat. Toulouse 110 (1974) 123.
6. *Podocarpus humbertii* de Laubenfels, Adansonia 2, 11 (1971) 714.
7. *Podocarpus rostratus* Laurent, Ann. Fac. Sc. Marseille 23 (1915) 60. — *P. perrieri* Gaussen & Woltz, Bull. Soc. Hist. Nat. Toulouse 111 (1975) 320.

3. Section *Australis* de Laubenfels, *sect. nov.*

Folia sine textura transfundenda accessoria mesophyllae et sine ductibus resiniferis marginalibus, usque ad 4.5 cm longa; strobilus masculus pedunculatus; fructus minus 1 cm longus, apicibus rostratis. — Type species: *P. totara* D. Don.

Leaves without accessory transfusion tissue and without marginal resin canals distinguish this section. The leaves are in most cases no more than 4.5 cm long but elsewhere with equally small leaves only in *P. rostratus* is accessory transfusion tissue also lacking. One to three pollen cones produced on a short naked peduncle. Seed coats mostly elongated into a distal beak inclined in most cases to the ventral side and sometimes with distinct lateral ridges, the whole leathery-coated fruit less than 1 cm long. Ripe receptacles greatly enlarged and bright red. Linear leaves with blunt to apiculate apices, mostly flat across the upper surface but in some cases a weak ridge and in others a weak groove. Foliage buds small and pyramidal, formed of a cluster of small long-triangular scales with spreading tips. Section *Australis* corresponds to 'subsection D' of Buchholz & Gray. Prostrate plants of tundra or rocky mountainous locations or trees of temperate rainforest.

Distribution. Southeastern Australia, New Zealand, New Caledonia, and southern Chile.

KEY TO THE SPECIES

- 1a. Leaf apex acute and pungent, leaves mostly more than 15 mm long with two distinct white stripes below; trees or erect shrubs 2
- b. Leaf apex rounded, leaves mostly less than 20 mm long with stripes not distinct below; prostrate 5
- 2a. Fruit at least 8 × 6 mm; upper surface of leaf with a distinct rib [pollen cone 2.5 mm in diameter; trees] 11. *P. nubigenus*
- b. Fruit less than 8 × 4 mm; upper surface of leaf flat 3

- 3a. Adult leaves less than 2.5 mm wide and length at least 10 × width; pollen cone 2.5 mm in diameter and less than 20 mm long; erect shrub **10. *P. lawrencii***
 b. Adult leaves at least 2.5 mm wide and length less than 9 × width; pollen cone more than 3 mm in diameter and central cone of a cluster at least 25 mm long; trees **4**
- 4a. Adult leaves mostly less than 25 × 3.5 mm; pollen cones mostly clustered; bark thick **8. *P. totara***
 b. Adult leaves mostly more than 25 × 3.5 mm; pollen cones solitary; bark papery **9. *P. cunninghamii***
- 5a. Fruit at least 7 × 3 mm with a large blunt crest bent towards the dorsal side; pollen cones solitary; adult leaves usually more than 15 mm, upper surface sulcate **14. *P. gnidioides***
 b. Fruit less than 6 × 3 mm with a small central crest; pollen cones usually clustered; adult leaves less than 15 mm, upper surface flat **6**
- 6a. Pollen cone 10–18 mm; leaf apex often with a minute mucro **12. *P. nivalis***
 b. Pollen cone 4–6 mm; leaf apex never mucronate **13. *P. alpinus***

8. *Podocarpus totara* D. Don in Lamb., Pinus ed. 3 (1832) 189.

9. *Podocarpus cunninghamii* Colenso, Visit Ruahine Range (1884) 58. — *P. hallii* Kirk, For. Fl. New Zeal. (1889) 14 (see also 301). — (*P. laeta* Hoibr. ex Endl., Syn. Conif. (1847) 214, no type specimen, probably belongs here. There is a 1869 specimen from cultivation in Paris with this name.)

10. *Podocarpus lawrencii* Hook. f., Lond. J. Bot. 4 (1845) 151. — *P. acutifolius* Kirk, Trans. & Proc. New Zeal. Inst. 16 (1883) 370.

11. *Podocarpus nubigenus* Lindley, J. Hort. Soc. 6 (1851) 264.

12. *Podocarpus nivalis* Hook. f., Icon. Pl. 6 (1843) 582. — *P. montana* Colenso, Trans. New Zeal. Inst. 27 (1895) 395.

13. *Podocarpus alpinus* R. Br. ex Hook. f., Lond. J. Bot. 4 (1845) 150. — *P. parvifolia* Parl. in DC. Prod. 16, 2 (1868) 514.

14. *Podocarpus gnidioides* Carrière, Traité Conif. ed. 2 (1867) 656.

4. Section *Crassiformis* de Laubenfels, *sect. nov.*

Fructus pluris quam 2 cm longis, pluris grandioribus quam receptaculum, dorsalis et lateralis costis instructum, apex elongatus; strobili masculi pedunculati; folia textura transfundenda accessoria mesophyllae instructa, pluris quam 6 cm longis. — Type species: *P. smithii* de Laubenfels.

The large beaked and ribbed fruit of section *Crassiformis*, more than 2 cm long and many times as large as the receptacle with a beak distinctly inclined to the ventral side, makes it the most distinct section in the whole genus. The seed and fruit are the largest and the seed coat is the thickest in the genus. One to three pollen cones at least 3 cm × 4 mm produced on a naked peduncle. Leaves more than 6 cm long with accessory transfusion tissue. The tiny receptacle becomes enlarged, fleshy, and bright red when ripe while the seed coat is also fleshy but a darker colour when ripe. The elliptic acute leaves have a distinct blunt rib on the upper surface and one resin canal below the vascular bundle. Foliage buds large and globular, formed by triangular to rounded scales with slightly spreading tips. Trees of primary rainforest.

Distribution. Northeastern Queensland.

15. *Podocarpus smithii* de Laubenfels, *spec. nov.*

Arbor ad circa 30 m alta. Folia juvenilia ad 16 cm × 21 mm. Gemma globulosa, squamis triangularis vel rotundatis 2–3 mm longis. Folia adulta ovata, acuta, 6–11 cm × 10–14 mm, glauca, petiolis brevis, costis paginis superis prominentibus. Strobili masculi 3–4.5 cm × 4–6 mm, 1–3 in apice pedunculi 2–9 mm longi, microsporophyllis patentis, falcatis, elongatis, 2 mm longis. Strobili foeminei in apice pedunculi 6–9 mm longi, receptaculis squamis binis incrassatis 5–6 mm longis, fructibus 1–2 apicalibus, globosis, 3 cm × 15 mm. Semina globosa, 15 × 10 mm, apicibus acutis. — Typus: *de Laubenfels P464* (holo, A), Mt Lewis, Queensland. (Named for the late Lindsay Smith.)

5. Section *Capitulatis* de Laubenfels, *sect. nov.*

Strobili masculi fasciculates saltem 3–6, plerumque pedunculati; fructus globuli minores quam 1 cm, apicis obtusis. Folia textura transfundenda accessoria mesophyllae instructa. — Type species: *P. glomeratus* D. Don.

The usual clustering of more than three pollen cones on a naked peduncle is an unique feature of section *Capitulatis* within its subgenus. Pollen cones no more than 2.5 mm in diameter, mostly less than 3 cm long. The small globular leathery-coated fruits less than 1 cm long have a blunt apex. Ripe receptacles greatly enlarged and bright red. Although the linear to lanceolate leaves are in most species small, they do have accessory transfusion tissue. There is one resin canal beneath the vascular bundle. Leaves vary from a slight ridge above the vascular bundle in some species to a groove in others. Foliage buds mostly small, bud scales triangular or lanceolate with slightly spreading tips. Only in the transitional species, *P. sellowii*, are sessile solitary or groups of no more than three pollen cones occasionally found. This species has leaves more than twice as wide as the up to 5 mm wide leaves and has foliage buds elongated much more than the up to 2.5 mm buds of the remaining species of the section, as well as growing in the rainforest environment which characterizes other

American sections of *Podocarpus* but contrasts with the distinctly seasonal areas of the remaining species of section *Capitulatis*. Trees or shrubs.

Distribution. South central Chile, southern Brazil, and the Andean highlands from northern Argentina to Ecuador.

KEY TO THE SPECIES

- 1a. Leaves more than 7 mm wide (the narrowest on leaves 4–6 cm long) [upper surface with a slight raised groove]; foliage bud scales elongated, foliaceous; fruit 5–7 mm in diameter and 7–10 mm long; pollen cones clustered 3–6 on a 8–15 mm peduncle and 8–15 mm long or one or two sessile in leaf axils and 15–30 mm long 22. *P. sellowii*
- b. Leaves mostly less than 6 mm wide (to 8 mm wide on leaves 8–12 cm long); foliage bud scales triangular or rounded, no more than twice as long as wide; fruit less than 6 mm in diameter and 8 mm long; pollen cones always clustered (mostly 3–6) 2
- 2a. Pollen cones 20–35 mm, clusters sessile or with a peduncle to 2 mm and never aggregated; fruit elongated; leaf 3–8 mm wide [never pungent], upper surface with a narrow ridge; foliage bud and bud scales about twice as long as wide 21. *P. salignus*
- b. Pollen cones 6–15 mm, peduncle of cluster at least 6 mm and clusters sometimes aggregated on a short scaly shoot; fruit oval; leaf less than 6 mm wide, upper surface flat or with a slight groove; foliage bud at least as wide as long . . . 3
- 3a. Leaves pungent, glaucous underneath; foliage bud scales acuminate with erect tips 4
- b. Leaves blunt to pungent, not or only slightly glaucous underneath; foliage bud scales short triangular or rounded and maybe completely imbricate 5
- 4a. Leaves broadly linear, 1.5–5 cm; female peduncle 3–5 mm 16. *P. glomeratus*
- b. Leaves long attenuate, 5–12 cm; female peduncle 5–10 mm 19. *P. parlatorei*
- 5a. Leaf apex round and never pungent [leaves broadly linear, not revolute, with continuous hypoderm, 3.5–5 mm wide; bracts below pollen cone clusters deciduous] 18. *P. transiens*
- b. Leaf apex acute 6
- 6a. Leaves broadly linear, revolute, with interrupted hypoderm, 3–5.5 mm wide; bracts below pollen cone clusters not deciduous 17. *P. sprucei*
- b. Leaves linear-lanceolate, not revolute, with continuous hypoderm, 2–3 mm wide; bracts below pollen cone cluster deciduous 20. *P. lambertii*

16. *Podocarpus glomeratus* D. Don in Lamb., *Pinus* 2 (1824) 21. — *P. rigida* Klotzsch ex Endl., *Syn. Conif.* (1847) 211 (given as a synonym but the type specimen is *P. sprucei*). — *P. cardenasii* Buchholz & Gray, *J. Arn. Arbor.* 29 (1948) 142.

17. *Podocarpus sprucei* Parl. in DC., Prod. 16, 2 (1868) 510 [this is also the var. β of *P. montanus* of Willdenow, Sp. Pl. IV, 4 (1805) 857].
18. *Podocarpus transiens* (Pilger) de Laubenfels, *stat. nov.* – *P. lambertii* var. *transiens* Pilger, Pflanzenreich IV, 5 (1903) 86.
19. *Podocarpus parlatorei* Pilger, Pflanzenreich IV, 5 (1903) 86. – *P. angustifolia* Parl. in DC., Prod. 16, 2 (1868) 512, non Griseb. (1866).
20. *Podocarpus lambertii* Klotzsch ex Endl., Syn. Conif. (1847) 211.
21. *Podocarpus salignus* D. Don in Lamb., Pinus 2 (1824) 20. – *P. chilinus* L.C. Rich., Comm. Bot. Conif. (1826) 11.
22. *Podocarpus sellowii* Klotzsch ex Endl., Syn. Conif. (1847) 209.

6. Section *Pratensis* de Laubenfels, *sect. nov.*

Gemma globulosa squamis imbricatis; folia paginae suprae canalis instructa; strobili masculi solitarii, plerumque sessiles; fructus cristati. – Type species: *P. oleifolius* D. Don.

The globular foliage buds with imbricate scales and broad distinctly grooved leaves along with solitary sessile pollen cones distinguish section *Pratensis*. There is a distinct crest on the distal end of the globular leathery-coated fruits which are about 1 cm long. The juvenile leaves tend to be distinctly lanceolate but the adult leaves are broadly acute to rounded at the apex. The leaves, which come in many sizes, have accessory transfusion tissue and one resin canal beneath the vascular bundle. Where known the ripe receptacles are purple. Associated with disturbed open park-like situations in moist mountain forests often near tree line.

Distribution. Southeastern Mexico to Guyana and Peru.

KEY TO THE SPECIES

- 1a. Leaves elongated, length at least $12 \times$ width, pendulous, groove raised on upper surface [pollen cone 2×4 mm, sessile; fruit $7-8 \times 5$ mm on a $7-18$ mm peduncle] 24. *P. pendulifolius*
- b. Leaves oval to broadly linear, length less than $8 \times$ width, not pendulous, groove on upper surface not raised 2
- 2a. Leaves at least 25×5 mm; pollen cones about 30×3 mm, sessile or with a short peduncle; fruit at least 8×4 mm on a $5-20$ mm peduncle 23. *P. oleifolius*
- b. Leaves less than 25×5 mm; pollen cone about 15×1.5 mm, always sessile; fruit about 7×4 mm on a 2 mm peduncle 25. *P. tepuiensis*

23. *Podocarpus oleifolius* D. Don in Lamb., Pinus 2 (1824) 20. — *P. macrostachyus* Parl. in DC., Prod. 16, 2 (1868) 510.

24. *Podocarpus pendulifolius* Buchholz & Gray, J. Arn. Arbor. 29 (1948) 138.

25. *Podocarpus tepuiensis* Buchholz & Gray, J. Arn. Arbor. 29 (1948) 134.

7. Section *Lanceolatis* de Laubenfels, *sect. nov.*

Squamae gemmarum elongatae foliaceae; folia adulta acuta, plerumque lanceolata; strobili masculi solitarii, sessiles. — Type species: *P. coriaceus* L.C. Rich.

The distinctly elongated foliaceous bud scales 3–16 mm long, along with broad and distinctly lanceolate adult leaves, as well as solitary sessile pollen cones, distinguish section *Lanceolatis*. Upper leaf surfaces and fruit apices are variable, the leaves in some species have a strong groove, others are weakly grooved, and still others have a ridge; fruits vary from blunt to weakly crested. The leaves have accessory transfusion tissue and one resin canal beneath the vascular bundle. The globular leathery-coated fruit range from less than to somewhat more than 1 cm long. The ripe receptacle in one species is known to be dark blue while those of two others have been reported to be red. Occasional specimens of *P. sellowii* of section *Capitulatis* would correspond to the characters of this section. Trees of dense highland rainforest.

Distribution. Eastern and central Mexico through the Lesser Antilles and Venezuela to highland Bolivia.

KEY TO THE SPECIES

- 1a. Upper surface of leaf with a distinct rib; fruit at least 12 × 8 mm [leaf 4–12 cm × 10–16 mm; pollen cone about 5 cm × 4 mm] 29. *P. matudai*
- b. Upper surface of leaf flat or with a groove; fruit less than 10 × 7 mm 2
- 2a. Leaf at least 8 cm × 7 mm, flat or a weak groove; pollen cone at least 4 cm × 3 mm; fruit with a weak crest or none, more than 8 × 6 mm 3
- b. Leaf less than 8 cm × 9 mm, with a distinct groove; pollen cone (where known) 10 × 2.5 mm; fruit with a distinct crest, less than 8 × 5 mm 4
- 3a. Pollen cone sessile; leaf not pendulous, with a weak raised groove 26. *P. coriaceus*
- b. Base of pollen cone elongated-scaly; leaf often pendulous, flat or slightly raised above vascular bundle 28. *P. salicifolius*
- 4a. Peduncle of fruit 12 mm (pollen cone unknown); outer bud scales more than 10 mm 27. *P. steyermarkii*
- b. Peduncle of fruit 3–4 mm; outer bud scales about 5 mm 30. *P. rusbyi*

26. *Podocarpus coriaceus* L.C. Rich., *Comm. Bot. Conif.* (1826) 14. — *Nageia coriacea* (L.C. Rich.) Kuntze, *Rev. Gen. Pl.* 2 (1891) 800. — *Taxus (?) lancifolia* Wikström, *K. Vet. Akad. Handl.* (1827) 76.
27. *Podocarpus steyermarkii* Buchholz & Gray, *J. Arn. Arbor.* 29 (1948) 133.
28. *Podocarpus salicifolius* Klotzsch & Karsten ex Endl., *Syn. Conif.* (1847) 209. — *P. pittieri* Buchholz & Gray, *J. Arn. Arbor.* 29 (1948) 130.
29. *Podocarpus matudai* Lundell, *Phytologia* 1 (1937) 212. — *P. reichei* Buchholz & Gray, *J. Arn. Arbor.* 29 (1948) 131.
30. *Podocarpus rusbyi* Buchholz & Gray, *J. Arn. Arbor.* 29 (1948) 134.

8. Section *Pumilis* de Laubenfels, *sect. nov.*

Gemmae globulosae squamarum rectarum; folia minoria quam 3.5 cm × 8 mm, coriacea, rigida, elliptica vel apiculata; strobili masculi solitarii, sessiles, minores quam 15 mm; fructus cristati. — *Type species: P. aristulatis* Parl.

The globular foliage buds about 2 mm long with triangular bud scales with slightly spreading apices, the less than 3.5 cm × 8 mm rigid leaves either elliptic or apiculate or both, and the pollen cones less than 15 mm long distinguish section *Pumilis* along with the solitary sessile pollen cones and the crested fruit. The leaves have one resin canal beneath the vascular bundle and accessory transfusion tissue, while there is generally a weak ridge on the upper surface. The leathery-coated fruits are approximately 7 mm long and there are fragmentary reports of red ripe receptacles. Dwarf trees of cloud forests.

Distribution. Greater Antilles (except Puerto Rico) and the Guyana Highlands.

KEY TO THE SPECIES

- 1a. Leaves acute, usually apiculate [upper surface with a weak ridge]; pollen cone 3–4 mm in diameter 2
- b. Leaves rounded at the apex, blunt; pollen cone 2.5 mm in diameter 4
- 2a. Adult leaves less than 4.5 mm wide (to 5 cm long) [always apiculate] 33. *P. angustifolius*
- b. Adult leaves at least 4.5 mm wide (less than 4 cm long) 3
- 3a. Leaves ovate, to 10 mm wide, always apiculate 31. *P. aristulatis*
- b. Leaves lenticular, 4.5–5.5 mm wide, blunt and apiculate leaves mixed 32. *P. urbanii*
- 4a. Leaves 4–6 mm wide, upper surface with a distinct ridge 34. *P. roraimae*
- b. Leaves 5–8 mm wide, upper surface with a distinct groove 35. *P. buchholzii*

31. *Podocarpus aristulatis* Parl. in DC., Prod. 16, 2 (1868) 513. – *P. buchii* Urban, Fedde's Repert. 19 (1924) 298. – *P. leonii* Carabia, Carib. For. 2 (1941) 92. – *P. victorinianus* Carabia, Carib. For. 2 (1941) 92.
32. *Podocarpus urbanii* Pilger, Pflanzenreich IV, 5 (1903) 89.
33. *Podocarpus angustifolius* Griseb., Cat. Pl. Cubensis (1866) 217. – *P. ekmanii* Urban, Fedde's Repert. 18 (1922) 17.
34. *Podocarpus roraimae* Pilger, Notizbl. Bot. Gart. Berlin 5 (1913) 299.
35. *Podocarpus buchholzii* de Laubenfels, Flora Venez. 11, 2 (1982) 31.

9. Section *Nemoralis* de Laubenfels, *sect. nov.*

Gemmae globulosae squamarum plerumque rectorum; folia plures quam 5 cm × 8 mm, elliptica vel linearia; strobili masculi solitarii, sessiles, pluris quam 3 cm longis. – Type species: *P. brasiliensis* de Laubenfels.

The globular foliage buds generally about 2–3 mm long, the elliptic or linear leaves more than 5 cm × 8 mm, and the pollen cones more than 3 cm long, together with the solitary sessile pollen cones distinguish section *Nemoralis*. The triangular bud scales in most species have erect free apices but in *P. guatemalensis* they are imbricate. The leaves have one resin canal beneath the vascular bundle and accessory transfusion tissue. The ripe receptacles vary from purple to bright red and the leathery-coated fruits mostly about 1 cm long have in most species a distinct crest at the distal end. Trees of primary rainforest.

Distribution. Belice to Trinidad and the Planalto of Brazil to Bolivia.

KEY TO THE SPECIES

- 1a. Leaves never lanceolate, adult leaves acuminate or broadly rounded at the apex and often with more or less parallel margins [upper surface with a groove; fruit about 5 mm in diameter, with a crest] 2
- b. Juvenile leaves conspicuously lanceolate, adult leaves acute or narrowly rounded at the apex and margins tapering towards both ends 4
- 2a. Adult leaves broadly acute or rounded [to 12 mm wide] 36. *P. brasiliensis*
- b. Adult leaves acuminate 3
- 3a. Leaves less than 13 mm wide, apex apiculate 39. *P. purdieanus*
- b. Leaves at least 18 mm wide, apex narrowly rounded 41. *P. magnifolius*
- 4a. Upper surface of leaves with a blunt ridge; tips of bud scales mostly imbricate; fruit with a distinct crest [5–6 mm in diameter] 38. *P. guatemalensis*

- b. Upper surface of leaves with a groove; tips of bud scales spreading; fruit without a crest 5
 5a. Fruit 8 mm in diameter; groove on leaf well developed 40. *P. celatus*
 b. Fruit 5–6 mm in diameter; groove on leaf weak and raised . . . 37. *P. trinitensis*

36. *Podocarpus brasiliensis* de Laubenfels, *Flora Venez.* 11, 2 (1982) 31.

37. *Podocarpus trinitensis* Buchholz & Gray, *J. Arn. Arbor.* 29 (1948) 135.

38. *Podocarpus guatemalensis* Standley, *Proc. Biol. Soc. Wash.* 37 (1924) 49. — *P. pinetorum* Bartlett, *Publ. Carnegie Inst. Wash.* 461 (1935) 21. — *P. allenii* Standley ex Woodson & Schery, *Ann. Mo. Bot. Gard.* 28 (1941) 409.

39. *Podocarpus purdieanus* Hook., *Icon. Pl.* 7 (1844) 624.

40. *Podocarpus celatus* de Laubenfels, *Flora Venez.* 11, 2 (1982) 35.

41. *Podocarpus magnifolius* Buchholz & Gray, *J. Arn. Arbor.* 29 (1948) 133.

Subgenus *Foliolatus* de Laubenfels, *subg. nov.*

Basis receptaculi strobilis foemineis foliolis instructum; stomata foliorum sine orbe florinis; folia sine ductibus resiniferis marginalibus sed plerumque 3 ductibus vascularibus instructa. —
 Type species: *P. nerifolius* D. Don.

Receptacle with two subtending foliola; stomata without a 'Florin ring'; 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; the distal end of the leathery seed coat mostly without a crest.

The 53 species of subgenus *Foliolatus* are divided into 9 sections of from 2 to 10 species each. Except for section *Spinulosus* in Australia, which is transitional in various ways, the sections broadly overlap one another in their ranges, often with ecological differences to be sure.

KEY TO THE SECTIONS

- 1a. Pollen cones solitary or in groups of 3 or fewer 2
 b. Pollen cones regularly in clusters of more than 3 7
 2a. Pollen cones regularly in threes or a mixture of threes and fewer [pollen cones usually at least 2.5 mm in diameter; midrib more than 0.3 mm wide; ripe receptacle usually red] 3

- b. Pollen cones normally solitary (only rarely grouped) [external bud scales erect and free; leaves not at all acuminate] 5
- 3a. Primary foliage bud scales imbricate, forming a globular ball; secondary bud scales blunt **12. Section Globulus**
- b. Primary foliage bud scales erect and free, secondary bud scales acute to acuminate 4
- 4a. Secondary bud scales broadly acute, primary bud scales generally less than 4 times as long as broad; adult leaves not acuminate, usually not abruptly expanded at the base **10. Section Foliolatus**
- b. Secondary bud scales acuminate, primary bud scales more than 4 times as long as broad; adult leaves acuminate, abruptly expanded at the base **11. Section Acuminatis**
- 5a. Foliage buds much longer than wide [with long lanceolate scales], secondary bud scales acuminate; bracts below the receptacle usually at least 3 mm long [ripe receptacle red] **13. Section Longifoliolatus**
- b. Foliage buds less than twice as long as wide, secondary bud scales not acuminate; bracts below the receptacle usually less than 2.5 mm long [midrib less than 0.3 mm wide] 6
- 6a. Pollen cones less than 3 mm in diameter, apex of the microsporophyll less than 0.5 mm long; foliage bud less than 2 mm in diameter **14. Section Gracilis**
- b. Pollen cones more than 3.5 mm in diameter, apex of the microsporophyll more than 1 mm long; foliage bud mostly more than 2 mm in diameter [ripe receptacle usually purple or black] **15. Section Macrostachyus**
- 7a. Leaves with one resin canal; pollen cones pedunculate, less than 10 mm long [ripe receptacle purple]; prostrate shrubs **18. Section Spinulosus**
- b. Leaves with at least 3 resin canals; pollen cones sessile, more than 10 mm long; trees and bushes 8
- 8a. Outer bud scales imbricate, apex of scales slightly if at all raised; ripe receptacle red; midrib on the upper side of the leaf broad and flat **16. Section Rumphius**
- b. Outer bud scales erect and free; ripe receptacle usually purple; midrib narrow and in most species prominently raised **17. Section Polystachyus**

10. Section Foliolatus de Laubenfels, *sect. nov.*

Squamae primariae gemmarum rectae, squamae secundariae acutae; apices foliorum adultorum plerumque non acuminati; costa in paginis superis foliorum saltem 0.3 mm lata; strobili masculi saltem 2.5 mm diametri, solitarii vel 2–3 fasciculati, in pedunculis nudis brevibus vel sessili. – *Type species: P. neriifolius* D. Don.

Primary foliage bud scales are erect and acute, triangular to shortly lanceolate; secondary bud scales also acute. Leaves are broad and generally not acuminate with a blunt ridge above the vascular bundle at least 0.3 mm wide. Pollen cones at least 2.5 mm in diameter, solitary or in groups of no more than three, either sessile or on a short peduncle. The apex of the microsporophyll is never more than 1 mm long. In

most species the ripe receptacle is known to be red. Fruit 7–12 mm long but most often at least 10 mm, apex blunt. Trees of a variety of moist habitats mostly in lower forest zones but with one widespread highland forest species (*P. rubens*).

Distribution. Nepal through Sumatra, the Philippines, and New Guinea to Tonga.

KEY TO THE SPECIES

- 1a. Midrib on the upper side of the leaf prominent, at least 0.3 mm high and less than 1 mm wide [primary bud scales no more than 5 mm long] 2
- b. Midrib on the upper side of the leaf at least 1 mm wide or indistinctly raised or both 5
- 2a. Juvenile leaves acuminate, leaf midrib bold with vertical sides; primary bud scales 1–1.5 mm wide 3
- b. Juvenile leaves never acuminate, leaf midrib with sloping sides; primary bud scales 2 mm wide [pollen cones usually pedunculate] 4
- 3a. Leaf at least 7 cm × 10 mm, not apiculate, new leaves green to reddish, midrib 0.4–0.8 mm wide (there only 0.4–0.5 mm wide the leaf usually acuminate); pollen cones normally sessile; ripe receptacle red 42. *P. neriifolius*
- b. Adult leaf no more than 6 cm × 10 mm, often apiculate, new leaves bright red, midrib 0.3 mm wide; pollen cones often on a short peduncle; ripe receptacle often purple 43. *P. rubens*
- 4a. Leaf at least 7 cm × 10 mm, linear-oblong [midrib 0.5 mm wide]; pollen cone usually solitary; receptacle often with three fleshy bracts 44. *P. archboldii*
- b. Adult leaf no more than 9 cm × 9 mm, elliptic; pollen cones usually in clusters of 2–3; receptacle of two bracts only 45. *P. insularis*
- 5a. Midrib prominently raised above, 0.3 mm high, often drying to a channel below (leaves distinctly thicker than usual for the genus); primary bud scales may reach at least 1 cm long 6
- b. Upper surface of leaf flat or nearly so, lower surface generally lacking a channel (leaves not thicker than usual for the genus); bud scales never as long as 1 cm . 7
- 6a. Leaves more than 10 cm long; female peduncle 9–15 mm; primary bud scales and leaves deflexed 46. *P. deflexus*
- b. Leaves less than 10 cm long; female peduncle 2 mm; primary bud scales and leaves erect 47. *P. borneensis*
- 7a. Leaves lanceolate or narrowly linear 8
- b. Leaves oblong, not tapering 9
- 8a. Leaves at least 8 cm × 10 mm; fruit at least 12 mm; pollen cone at least 3 cm 48. *P. levis*
- b. Leaves less than 8 cm × 5 mm; fruit less than 8 mm; pollen cone less than 12 mm 49. *P. novae-caledoniae*
- 9a. Leaves blunt, 8–20 mm wide, usually over 8 cm long; pollen cones in clusters of 3 50. *P. spathoides*
- b. Leaves apiculate, 7–9 mm wide, less than 8 cm long; pollen cone apparently solitary 51. *P. pallidus*

42. Podocarpus neriifolius D. Don in Lamb., Pinus ed. 1, 2 (1824) 21. – *Nageia neriifolia* (D. Don) Kuntze, Rev. Gen. Pl. 2 (1891) 800. – *P. neglecta* Blume, Rumphia 3 (1847) 213. – *Nageia neglecta* (Blume) Kuntze, Rev. Gen. Pl. 2 (1891) 800. – *P. discolor* Blume, Rumphia 3 (1847) 213. – *Nageia discolor* (Blume) Kuntze, Rev. Gen. Pl. 2 (1891) 800. – *P. leptostachya* Blume, Rumphia 3 (1847) 214. – *Nageia leptostachya* (Blume) Kuntze, Rev. Gen. Pl. 2 (1891) 800. – *P. junghuhniana* Miq., Pl. Jungh. 1 (1851) 2. – *P. decipiens* Gray, J. Arn. Arbor. 36 (1955) 204.

43. Podocarpus rubens de Laubenfels, *spec. nov.*

Arbor 2–30 m alta. Gemma 2–3 × 2–3 mm, squamis exterioribus triangularibus basibus 1 mm latis. Folia evolventia rubra; adulta 3–6 cm × 6–10 mm, linearia vel lenticula, apicibus acutis vel rotundatis saepe apiculatis, marginibus revolutis, costis superis prominentibus, 0.3 mm latis, 0.3 mm altis, subtis latioribus. Strobili masculi 2–3.5 cm × 2.5–3.5 mm, solitarii vel terni, sessili vel pedunculis brevibus. Strobili feminei pedunculatis 4–9 mm longis, foliolis basalibus 1.5 mm longis, receptaculis 6–8 mm longis, fructibus ovoideis 8–9 × 5–6 mm. – Typus: *Womersley & Millar NGF 6980* (holo, L; iso, A, BO, BRI, K, LAE, SING), Wahgi-Sepik Div., New Guinea.

44. Podocarpus archboldii N.E. Gray, J. Arn. Arbor. 39 (1958) 452.

45. Podocarpus insularis de Laubenfels, *spec. nov.*

Arbor 3–39 m alta. Gemma 2.5–3 × 2.5–3.5 mm, squamis exterioribus triangularibus basibus 2 mm latis, apicibus patulis. Folia 5.5–9 cm × 7–9 mm, lenticula, costis superis prominentibus, 0.3 mm latis, 0.3 mm altis. Strobili masculi 3–3.5 cm × 4 mm, solitarii vel terni, sessili vel pedunculis brevibus. Strobili feminei pedunculatis 7–10 mm longis, foliolis basalibus 2 mm longis, receptaculis 8–10 mm longis, fructibus ovoideis, 9–10 × 6–7 mm. – Typus: *Brass 27987* (holo, L; iso, A, K, LAE, US), Sudest I. (Tagula).

46. Podocarpus deflexus Ridley, Fl. Mal. Pen. 5 (1925) 283.

47. Podocarpus borneensis de Laubenfels, *spec. nov.*

Arbor (2–)5–12(–23) m alta. Gemma 4–10 mm longa, 2–3 mm diametra, squamis exterioribus lanceolatis vel linearis, basis 1.5 mm latis. Folia adulta crassa, lineares vel ovata, (2.5–)4–7.5(–9) cm × 8–13 mm, apicibus acutis vel obtusis, costis superis prominentibus, 1 mm latis, 0.3 mm altis subtis latioribus minus prominentibus plerumque canaliculatis in siccatis. Strobili masculi 3–5 cm × 2.5–3 mm, solitarii vel terni, sessili vel pedunculis brevibus. Strobili feminei pedunculatis 2 mm longis, foliolis basalibus 2 mm longis, receptaculis 6 mm longis, fructibus ovoideis cristatis 6 × 5 mm. – Typus: *de Laubenfels P702* (holo, L; iso, A, K, RSA, SAN, US), B. Tawai, Sabah.

48. *Podocarpus levis* de Laubenfels, *Blumea* 24 (1978) 496.

49. *Podocarpus novae-caledoniae* Vieillard, *Ann. Sc. Nat.* IV, 16 (1862) 56.

50. *Podocarpus spathoides* de Laubenfels, *spec. nov.*

Arbor 3–20 m alta. Gemma 2–6 × 2–3 mm, squamis exterioribus triangularibus basibus 1.5 mm latis. Folia linearia, 5–13 cm × 8–20 mm, apicibus acutis vel rotundatis, basibus abruptis attenuatis in petiolis 3–5 mm longis, costis superis obtusis, latis, subtus prominentibus, latioribus. Strobili masculi terni, pedunculis brevibus maturi ignoti. Strobili feminei pedunculis 2–6 mm longis, receptaculis 5 mm longis, foliolis basalibus 1.5 mm longis, fructibus 7 × 5 mm. — Typus: *de Laubenfels P600* (holo, L; iso, A, K, KLU, LAE, RSA, US), G. Ledang, Malaya.

51. *Podocarpus pallidus* N.E. Gray, *Bishop Mus. Bull.* 220 (1959) 46.

11. Section *Acuminatis* de Laubenfels, *sect. nov.*

Folia et squamae secundariae gemmarum acuminatae; squamae primariae elongatae; bases foliorum abruptae expansae; costa in paginis superis foliorum saltem 0.5 mm latis, 0.3 mm altis; strobili masculi 3 fasciculati, saltem 2.5 mm diametri. — Type species: *P. ledermannii* Pilger.

Both acuminate leaves and acuminate secondary bud scales distinguish section *Acuminatis* along with elongated erect lanceolate primary bud scales at least twice as long as the bud diameter and at least 4 mm long, upper leaf midribs at least 0.5 mm wide and 0.3 mm high, and pollen cones in groups of no more than three and about 2.5 mm in diameter. Occasionally more than three resin canals are seen in the leaves. Pollen cones are sessile or in *P. ledermannii* grouped on a short peduncle. Apices of the microsporophylls are not more than 0.7 mm long. The ripe receptacles are red. The fruit range from about 10 mm long with a small crest in *P. micropedunculatus* to about 20 mm long and with a blunt apex in *P. dispermus*. Understorey trees in primary rainforest at low elevation.

Distribution. New Guinea, New Britain, northwestern Borneo and northern Queensland.

KEY TO THE SPECIES

1a. Fruit less than 11 × 8 mm, slightly crested; adult leaves less than 17 mm wide; female peduncle about 1 mm long; plant with rhizomes

54. *P. micropedunculatus*

b. Fruit at least 11 × 8 mm, not crested; adult leaves mostly more than 17 mm wide; female peduncle at least 4 mm long; plant lacking rhizomes 2

- 2a. Pollen cones pedunculate; leaves less than 24 mm wide; fruit less than 15 mm long 52. *P. ledermannii*
 b. Pollen cones sessile; leaves at least 24 mm wide; fruit more than 15 mm long
 53. *P. dispermus*

52. *Podocarpus ledermannii* Pilger, Bot. Jahrb. 54 (1916) 210. — *P. idenburgensis* N.E. Gray, J. Arn. Arbor. 39 (1958) 447.

53. *Podocarpus dispermus* White, Contr. Arn. Arbor. 4 (1933) 10.

54. *Podocarpus micropedunculatus* de Laubenfels, *spec. nov.*

Arbor 1–7(–13) m alta, rhizomis instructa. Gemma 6–15 × 1.5–3 mm, squamis exterioribus lanceolatis patentibus basibus 1–1.5 mm latis. Folia adulta linearia acuminata, 8–17 cm × 10–15 mm, costis superis prominentibus, 0.5–0.8 mm latis, 0.4 mm altis, subtus latioribus et canaliculatis. Strobili masculi solitarii vel terni, 3.5–7.5 cm × 2.5–3.5 mm, breviter pedunculati vel sessiles. Strobili feminei pedunculis 1 mm longis, receptaculis 8–10 mm longis, foliolis basalibus 3–4 mm longis, fructibus ovoideis cristatis 8–10 × 6 mm. — Typus: *de Laubenfels P564* (holo, A; iso, K, SING, US), Marudi, Sarawak.

12. Section *Globulus* de Laubenfels, *sect. nov.*

Gemmae globosae, 1.5–3 mm × 1.5–3 mm, squamis imbricatis; costa in paginis superis foliorum prominens obtusa vel debila, saltem 0.5 mm lata; strobili masculi solitarii vel terni. — Type species: *P. globulus* de Laubenfels.

The completely imbricate primary foliage bud scales with pollen cones in groups of not more than three distinguish section *Globulus* along with the blunt to weak ridge on the upper leaf surface at least 0.5 mm wide. Foliage buds are 1.5–3 × 1.5–3 mm, the primary scales bluntly triangular and the secondary scales round and blunt. Leaves are linear to lanceolate, occasionally acuminate, with blunt to narrowly rounded apices. Pollen cones are sessile or grouped on a peduncle no more than 2 mm long. The apex of the microsporophyll is 1 mm long or less. Where known the ripe receptacles are red. Fruits are mostly about 10 mm long but in some species may reach 15 mm and are blunt to crested. Understory or canopy trees of primary rainforest and mossy forests of moderate elevation occasionally to 2000 m.

Distribution. Vietnam and Taiwan to Sumatra and Borneo and in New Caledonia.

KEY TO THE SPECIES

- 1 a. Fruit with a distinct crest [juvenile leaves acuminate] 2
 b. Fruit without a crest 3

- 2a. Leaves less than 8 cm, linear, apex rounded to acute; small crest on fruit
55. *P. globulus*
- b. Leaves at least 7 cm, linear-lanceolate, apex acute; large crest on fruit
56. *P. nakai*
- 3a. Adult leaves distinctly acuminate, broad; bracts at the base of the female receptacle less than 1 mm long 57. *P. teysmannii*
- b. Leaves not at all acuminate; bracts at the base of the female receptacle at least 1 mm long 4
- 4a. Leaves linear-lanceolate with a rounded apex 58. *P. annamiensis*
- b. Leaves oblong with a rounded or acute apex 5
- 5a. Adult leaves less than 9 mm wide, apex rounded or broadly acute; female peduncle length, receptacle length, and seed diameter all less than 9 mm
59. *P. sylvestris*
- b. Adult leaves more than 10 mm wide, apex very blunt; female peduncle length, receptacle length, and seed diameter all more than 9 mm 60. *P. lucienii*

55. *Podocarpus globulus* de Laubenfels, *spec. nov.*

Arbor 3.5–27 m alta. Gemma 2–3 × 2–3 mm. Folia linearia, 3.5–8 cm × 9–15 mm, apicibus acutis vel rotundatis, costis superioribus prominentibus 0.5–0.7 mm latis, 0.2 mm altis. Strobili masculi 2.5–4.5 cm × 3–4 mm, solitarii vel aliquando terni, sessiles vel breviter (1 mm) pedunculati, apicibus microsporophyllorum triangularibus, 1 mm longis. Strobili feminei pedunculis 3–4 mm longis, receptaculis 9 mm longis, foliolis basalibus 2 mm longis, fructibus 9 mm (crista brevi inclusa) × 5.5 mm. — Typus: *de Laubenfels P688* (holo, L; iso, A, K, P, RSA, SAN, US), Mt Silam, Sabah.

56. *Podocarpus nakaii* Hayata, *Icon. Pl. Form.* 6 (1916) 66.

57. *Podocarpus teysmannii* Miq., *Fl. Ind. Bat.* 2 (1859) 1072.

58. *Podocarpus annamiensis* N.E. Gray, *J. Arn. Arb.* 39 (1958) 451.

59. *Podocarpus sylvestris* Buchholz, *Bull. Mus. Nat. Hist. Paris* 2 (1949) 285.

60. *Podocarpus lucienii* de Laubenfels, *Brittonia* 12 (1960) 80.

13. Section *Longifoliolatus* de Laubenfels, *sect. nov.*

Gemma minus quam 4 mm diametri × (4–)6 mm plus longi, squamis primariis lanceolatis, squamis secundariis acuminatis; folia linearia minoris quam 11 mm lata vel anguste lanceolata; strobili masculi solitarii, minoris quam 4.5 mm diametri; foliola plerumque saltem 3 mm longa. — Type species: *P. longifoliolatus* Pilger.

- long; bud for pollen cone 4–5 mm in diameter; pollen cone initially sessile, when mature with an elongated scaly base 67. *P. bracteatus*
- b. Leaves mostly less than 10 mm wide; foliola at base of receptacle less than 3 mm long; bud for pollen cone about 2 mm in diameter; pollen cone with a short peduncle to 2 mm 68. *P. pseudobracteatus*
- 9a. Fruit crested; foliola at base of receptacle 4–10 mm long; apex of microsporophyll about 1 mm long 69. *P. degeneri*
- b. Fruit blunt; foliola at base of receptacle 2–4 mm long; apex of microsporophyll about 0.2 mm long 70. *P. atjehensis*

61. *Podocarpus longifoliolatus* Pilger in Engler, Pflanzenreich 4, 5 (1903) 79.

62. *Podocarpus decumbens* N.E. Gray, J. Arn. Arbor. 36 (1955) 202.

63. *Podocarpus polyspermus* de Laubenfels, Fl. Nouv. Caléd. et Dép. 4 (1972) 60.

64. *Podocarpus salomoniensis* Wasscher, Blumea 4 (1941) 430.

65. *Podocarpus gibbsii* N.E. Gray, J. Arn. Arbor. 39 (1958) 429.

66. *Podocarpus confertus* de Laubenfels, *spec. nov.*

Arbor 1–36 m alta. Gemma foliata 6–10 × 2–3 mm, squamis lanceolatis ad 2 mm latis. Folia linearia vel lineari-lanceolata, 5–12 cm × 7–11 mm, apicibus acutis, costis paginis superis obtusis 1 mm latis, 0.2–0.3 mm altis. Strobili masculi solitarii vel aliquando bini, sessiles, 3–4.5 cm × 2.5–3.5 mm, apicibus microsporophyllorum triangularibus, 0.3–0.5 mm longis. Strobili feminei pedunculis 5–13 mm longis, receptaculis 8–12 mm longis, foliolis basalis 5–6 mm longis, fructibus 10–11 × 6–6.5 mm, sine cristis. — Typus: *de Laubenfels P691* (holo, L; iso, A, K, P, RSA, SAN, US), Mt Silam, Sabah.

67. *Podocarpus bracteatus* Blume, En. Pl. Jav. 1 (1827) 88.

68. *Podocarpus pseudobracteatus* de Laubenfels, Blumea 26 (1980) 142.

69. *Podocarpus degeneri* (Gray) de Laubenfels, *stat. nov.* — *P. neriifolius* var. *degeneri* N.E. Gray, J. Arn. Arbor. 39 (1958) 467.

70. *Podocarpus atjehensis* (Wasscher) de Laubenfels, *stat. nov.* — *P. neriifolius* var. *atjehensis* Wasscher, Blumea 3 (1941) 450.

14. Section *Gracilis* de Laubenfels, *sect. nov.*

Costa paginae superae folii prominens, gracilis, minus quam 0.3 mm lata; gemma minus quam 2 × 3 mm; squamae primariae minus quam 1 mm latae, apicibus liberis, rectis vel patulis; strobili masculi solitarii, minus quam 3 mm in diametro. – *Type species*: *P. pilgeri* Foxw.

The distinct but very gracile midribs up to no more than 0.3 mm wide, the foliage buds less than 2 mm in diameter, and solitary pollen cones up to 3 mm in diameter distinguish section *Gracilis*. The primary bud scales are up to 1 mm wide and 3 mm long with free tips. Shade leaves are particularly delicate and blunt. The scaly base of the pollen cone often elongates upon maturity. The apex of the microsporophylls are no more than 0.5 mm long. Ripe receptacles are variously reported as red or purple. Fruits 7–10 mm long and blunt or bluntly crested. Trees of mossy forests.

Distribution. Southern China across Malesia to Fiji (not in southwestern Indonesia).

KEY TO THE SPECIES

- 1 a. Leaves less than 2 cm long [less than 6 mm wide, always blunt, crowded; foliage bud less than 1.5 mm long; fruit crested; mature receptacle purple] 75. *P. glaucus*
- b. Leaves over 2 cm long 2
- 2 a. Leaves more than 8 mm wide, always blunt [dispersed; foliage bud at least 2 mm long; fruit not crested] 74. *P. rotundus*
- b. Leaves less than 8 mm wide, not always blunt (sun growth leaves acute) 3
- 3 a. Leaves crowded (overlapping) [fruit crested, bud 3 × 2 mm] 73. *P. lophatus*
- b. Leaves dispersed 4
- 4 a. Foliage bud at least 1.5 × 1.5 mm; fruit not crested 71. *P. pilgeri*
- b. Foliage bud 1–1.5 × 1 mm; fruit crested 72. *P. affinis*

71. *Podocarpus pilgeri* Foxw., Philip. J. Sc. 2 (1907) Bot. 259. – *P. celebicus* Warb., *Monsunia* 1 (1900) 192, non Hemsl. (1896). – *P. schlechteri* Pilger, Bot. Jahrb. 54 (1916) 209. – *P. wangii* Chang, *Sunyatsenia* 6 (1941) 26.

72. *Podocarpus affinis* Seemann, Fl. Vitiensis (1868) 266.

73. *Podocarpus lophatus* de Laubenfels, *Kalikasan* 7 (1978) 137.

74. *Podocarpus rotundus* de Laubenfels, *Kalikasan* 7 (1978) 136.

75. *Podocarpus glaucus* Foxw., Philip. J. Sc. 2 (1907) Bot. 258.

15. Section *Macrostachyus* de Laubenfels, *sect. nov.*

Folia revoluta, coriacea, costis paginis superis parvis, 0.2–0.3 mm latis; strobili masculi solitarii plus quam 4 mm in diametro, apicibus microsporophyllorum lanceolatis. – Type species: *P. crassigemmis* de Laubenfels.

Solitary pollen cones more than 4 mm and usually about 6 mm in diameter with lanceolate microsporophyll apices distinguish section *Macrostachyus* (the var. *humilis* of *P. brassii* lacks these characters) along with tough revolute leaves whose upper midribs are narrow (0.2–0.3 mm) but distinct. Foliage buds are no more than 5 mm long but in several species up to 4–5 mm in diameter. Primary bud scales are mostly 1.5–2 mm wide, erect or sometimes strongly spreading. Secondary bud scales are acute or apiculate. Leaves are linear to lenticular, blunt to acute, generally smaller than usual for the genus, the adult leaves being mostly less than 5 cm long. Pollen cones sessile or occasionally on a short peduncle. Seed structure mostly with short peduncles about 4–6 mm long and foliola about 2 mm long. Where known the fully ripe receptacles are dark purplish black, passing through red in ripening. Fruits vary from somewhat less to somewhat more than 1 cm long, blunt or the smaller fruits with a small crest at the distal end. Trees or shrubs of high mossy forests but one (*P. costalis*) largely confined to a group of small islands at low elevation.

Distribution. Thailand-Cambodian coastal mountains, islands south of Formosa, Mt Kinabalu, and the interior of New Guinea.

KEY TO THE SPECIES

- 1a. Foliage bud at least 3 mm in diameter; leaves elliptic 2
 b. Foliage bud less than 3 mm in diameter; leaves more or less linear and blunt [fruit crested, less than 7 mm in diameter] 5
 2a. Fruit crested, less than 8 mm in diameter [leaf less than 7 mm wide] 78. *P. brevifolius*
 b. Fruit not crested, more than 9 mm in diameter 3
 3a. Leaf at least 7 times as long as wide; pollen cone pedunculate 76. *P. crassigemmis*
 b. Leaf less than 4 times as long as wide; pollen cone sessile 77. *P. brassii*
 4a. Apex of microsporophyll lanceolate, at least 2 mm long; tree 77. *P. brassii* var. *brassii*
 b. Apex of microsporophyll triangular, less than 1 mm long; small tree to prostrate shrub 77a. *P. brassii* var. *humilis*
 5a. Leaves more than 2.5 mm long, usually more than 4 mm; pollen cone sessile; fruit with a small crest 79. *P. costalis*
 b. Leaves less than 3.5 mm long; pollen cone pedunculate; fruit with a large (broad) crest 80. *P. tixieri*

76. *Podocarpus crassigemmis* de Laubenfels, *Blumea* 26 (1980) 26.

77. *Podocarpus brassii* Pilger, *Bot. Jahrb.* 68 (1937) 246.

77a. *Podocarpus brassii* var. *humilis* de Laubenfels, *var. nov.*

Frutex decumbens vel arbor parva ad 5 m alta. Strobili masculi 2.5–5 cm × 3.5–4.5 mm. Apices microsporophyllorum triangularis, 1 mm longi. – Typus: *Barker LAE 67278* (holo, L; iso, LAE), Mt Capella, Telefomin Dist., New Guinea.

78. *Podocarpus brevifolius* (Stapf) Foxw., *Philip. J. Sc.* 6 (1911) Bot. 160. – *P. nerifolius* var. *brevifolius* Stapf, *Trans. Linn. Soc. Bot.* II, 4 (1894) 249.

79. *Podocarpus costalis* Presl, *Epim. Bot.* (1849) 236.

80. *Podocarpus tixieri* Gaussen, *Gymn. Act. et Foss. Fasc.* 14 (1976) 155.

16. Section *Rumphius* de Laubenfels, *sect. nov.*

Strobili masculi fere in fasciculis ad pluribus quam tres dispositi; gemma globosa, squamis imbricatis vel apicibus rectis, triangularibus; costa paginis superis foliorum crassis, pluribus quam 0.7 mm latis; strobili feminei foliolis 1–1.5 mm, receptaculis rubris. – Type species: *P. rumphii* Blume.

The pollen cones usually in clusters of more than three, the bud scales imbricate or slightly raised at the apex, the red receptacle, and the upper midrib more than 0.7 mm wide and nearly flat distinguish this section along with short foliola 1–1.5 mm long and three vascular resin canals in the leaves. The foliage bud scales are short triangular. The leaves are linear and generally more than 12 cm long, often with continuous upper hypoderm, with an acute apex or on more or less juvenile specimens the apex may be acuminate. Pollen cone clusters are sessile or on a short peduncle. The apex of the microsporophyll is only 0.2 mm long. Fruit globular and blunt, 12–18 mm long. Trees of primary rainforest at low elevation.

Distribution. From Malaya and Hainan through most of Malesia except Sumatra and to northern Queensland.

KEY TO THE SPECIES

- 1a. Pollen cone clusters usually on a small peduncle; foliage bud scales always spreading at the tips 83. *P. laubenfelsii*
 b. Pollen cones sessile; foliage bud scales often completely adpressed 2

- 2a. Seed large, more than 10 mm in diameter, 12 mm long; receptacle often with a third lateral smaller sterile bract 81. *P. rumphii*
 b. Seed less than 10 mm in diameter, 12 mm long; receptacle never with a third lateral sterile bract 82. *P. grayii*

81. *Podocarpus rumphii* Blume, Rumphia 3 (1847) 214. — *Nageia rumphii* (Blume) Kuntze, Rev. Gen. Pl. 2 (1891) 800. — *P. koordersii* Pilger ex Koord. & Valetton, Meded. Lands Plantentuin 68 (1904) 268. — *P. philippinensis* Foxw., Philip. J. Sc. 6 (1911) Bot. 163.

83. *Podocarpus grayii* de Laubenfels, *spec. nov.*

Gemma globosa, 2–3 × 2–3 mm, squamis imbricatis vel congruentibus pyramidalibus, squamis exterioribus aliquando apicibus curvatis. Folia juvenilia linearia lanceolata, 16–23 cm × 14–19 mm. Folia adulta petiolis 4–10 mm, laminis linearibus vel lineari-lanceolatis, acutis, 9–18 cm × 8–14 mm, costis paginis superis obtusis, 0.8–1.2 mm latis, 0.2 mm altis. Strobili masculi sessiles vel 1 mm pedunculati, 1–4 fasciculati, 2–3 cm × 3–4 mm, apicibus microsporophyllorum triangularibus, 0.2 mm longis. Strobili feminei pedunculis 6–8 mm longis, receptaculis 9–12 mm longis, foliolis 1 mm longis, fructibus 10–12 × 7–9 mm. — Typus: *Brass 20203* (holo, L; iso A, BRI, K), Annan R., Cape York, N. Queensland. (Named for the late Netta E. Gray.)

83. *Podocarpus laubenfelsii* Tiong, Blumea 29 (1984) 523.

17. Section *Polystachyus* de Laubenfels, *sect. nov.*

Squamae externae gemmarum apicibus liberis patulis. Folia nunquam acuminata, costis in paginis superis prominentibus, plerumque minoribus quam 0.6 mm latis. Strobili masculi fasciculati saltem simul 3, microsporophyllis minutis. Receptaculum fructus maturitatem plerumque purpureum. — Type species: *P. polystachyus* R. Br.

The pollen cones usually in clusters of more than three, the erect or spreading bud scales, the purple ripe receptacles, and the prominent upper midribs usually less than 0.6 mm wide distinguish section *Polystachyus* along with never acuminate leaves, apices of the microsporophylls less than 0.7 mm long, and three vascular resin canals. The colour of the ripe receptacles have not been confirmed in a few species. The leaves vary from linear and almost blunt to lanceolate, sometimes on the same plant. Pollen cone clusters are sessile or in a few species shortly pedunculate. The fruits are variable in size, globular and blunt. Trees of upland rainforests, subtropical forests or in one species (*P. polystachyus*) tropical coasts and limestone bluffs.

Distribution. Southern China and Japan through Malaya to western New Guinea and northeastern Australia.

KEY TO THE SPECIES

- 1 a. Adult leaves linear and more or less rounded at the apex, not lanceolate 2
 b. Adult leaves lanceolate, narrowly acute at the apex 7
 2 a. Leaves narrowing abruptly to more or less gradually at the base, more than 6 mm wide [less than 10 times as long as wide] 3
 b. Leaves narrowing gradually at the base, less than 7 mm wide 6
 3 a. Fruit more than 10 mm in diameter 87. *P. macrocarpus*
 b. Fruit less than 10 mm in diameter 4
 4 a. Fruit more than 10 mm long, 8 mm in diameter; pollen cone less than 2 mm in diameter; most leaves mucronate 86. *P. elatus*
 b. Fruit less than 10 mm long, 8 mm in diameter; pollen cone more than 2.5 mm in diameter; leaf not mucronate 5
 5 a. Leaf not revolute, narrowing abruptly at the base 84. *P. polystachyus*
 b. Leaf with revolute margins, narrowing gradually at the base 85. *P. macrophyllus*
 6 a. Leaf at least 4 cm long, at least 10 times as long as wide 88. *P. chinensis*
 b. Leaf less than 3.5 cm long, more or less oval 89. *P. chingianus*
 7 a. Midrib indistinct [pollen cone 2 mm in diameter, without a scaly peduncle] 92. *P. ridleyi*
 b. Midrib prominent 8
 8 a. Pollen cones sessile, 3–3.5 mm in diameter 90. *P. subtropicalis*
 b. Pollen cones with a scaly peduncle, 2–2.5 mm in diameter . . . 91. *P. fasciculus*

84. *Podocarpus polystachyus* R. Br. ex Endl., Syn. Conif. (1847) 215. – *Nageia polystachya* (R. Br. ex Endl.) Kuntze, Rev. Gen. Pl. 2 (1891) 800. – *P. thevetii-folia* Blume, Rumphia 3 (1847) 213.

85. *Podocarpus macrophyllus* (Thunb.) Sweet, Hort. Sub. Lond. (1818) 211. – *Taxus macrophylla* Thunb., Nov. Acta Soc. Sc. Ups. 4 (1793) 38. – *P. sweetii* Presl, Bot. Bemerk. (1844) 110 (based on *P. macrophyllus* (Thunb.) Sweet). – *Nageia macrophylla* (Thunb.) Kuntze, Rev. Gen. Pl. 2 (1891) 800. – *P. forrestii* Craib & W.W. Smith, Notes Toy. Bot. Gard. Edinb. 12 (1920) 219.

86. *Podocarpus elatus* R. Br. ex Endl., Syn. Conif. (1847) 213. – *Nageia elata* (R. Br. ex Endl.) Mueller, Cens. (1882) 109.

87. *Podocarpus macrocarpus* de Laubenfels, Kalikasan 7 (1978) 140.

88. *Podocarpus chinensis* (Roxb.) Wall. ex Forbes, Pinet. Woburn. (1839) 212. – *Juniperus chinensis* Roxb., Fl. Ind. Orient. 3 (1832) 840, non L. (1767). – *P. macrophyllus* var. *maki* Sieb. & Zucc., Abh. Math.-Phys. Cl. K. Bayer. Ak. Wiss. 4 (1846) 232. – *P. maki* (Sieb. & Zucc.) Gaussen, Gymn. Act. et Foss. Fasc. 14

(1976) 214. — *P. japonica* Sieb. ex Endl., Syn. Conif. (1847) 217. — *P. makoyi* Blume, Rumphia 3 (1847) 215. — *Myrica esquirolii* Lév. in Fedde, Repert. 12 (1913) 537.

89. *Podocarpus chingianus* (Gray) S. Y. Hu, Taiwania 10 (1964) 32. — *P. macrophyllus* var. *chingii* N. E. Gray, J. Arn. Arbor. 39 (1958) 474.

90. *Podocarpus subtropicalis* de Laubenfels, *spec. nov.*

Gemma 4–7 × 1.5–2.5 mm, squamis exterioribus lanceolatis carinatis rectis. Folia juvenilia lineari-lanceolata, ad 18 cm × 14 mm, acuta. Folia adulta petiolis 3–6 mm longis, laminis linearibus vel lineari-lanceolatis, acute, 6–15 cm × 7–13 mm, costis paginis superis acutis, 0.3–0.5 mm latis, 0.2 mm altis. Strobili masculi sessiles, 1–5 fasciculati, 3–6 cm × 3–3.5 mm, apicibus microsporophyllis triangularibus, 0.2–0.3 mm longis. Strobili feminei pedunculis 8–14 cm longis, receptaculis 7–12 mm longis, foliolis 1–1.5 mm longis, fructibus 12–14 × 8–10 mm. — Typus: *Wilson 3007* (holo, A; iso, BM, K), Szechuan, Mt Omei.

91. *Podocarpus fasciculus* de Laubenfels, *spec. nov.*

Gemma 4–9 × 1.5 mm, squamis exterioribus lanceolatis carinatis rectis. Folia juvenilia lineari-lanceolata, 9–16 cm × 9–13 mm, acuta. Folia adulta petiolis 3–6 mm longis, laminis lineari-lanceolatis, 5–12 cm × 5–12 mm, acuta, costis paginis superis acutis, 0.3–0.5 mm latis, 0.2 mm altis. Strobili masculi 1–5 fasciculati, 2–3 cm × 2–2.5 mm, pedunculis squamiferis, 2–10 mm longis, squamis triangularis, carinatis, ad 2 × 1 mm, apicibus microsporophyllis triangularibus, 0.3 mm longis. Strobili feminei pedunculis 6–13 mm longis, receptaculis 9–16 mm longis, foliolis 2–3 mm longis, fructibus 10 × 7 mm. — Typus: *de Laubenfels P675* (holo, L; iso, A, K, P, RSA, US), Tai-shu Shan, Formosa.

92. *Podocarpus ridleyi* (Wasscher) N. E. Gray, J. Arn. Arbor. 39 (1958) 435. — *P. nerifolius* var. *ridleyi* Wasscher, Blumea 4 (1941) 453.

18. Section *Spinulosus* de Laubenfels, *sect. nov.*

Frutices prostrati ramis rectis ad 2 m altis. Strobili masculi usque ad 10 mm longi, 1–5 fasciculati vel ramis specialibus dispositi. Squamae gemmarum rectae. Folia ductis resiniferis unicus. — Type species: *P. spinulosus* (Smith) R. Br.

The pollen cones up to 10 mm long in fascicles of 1–5 or on special shoots and the single vascular resin canal distinguish section *Spinulosus* along with erect bud scales, a prostrate habit, and purple ripe receptacles. Leaves linear and acute with a narrow prominent upper midrib. Fruit variable in size, globular, with a sharp crest at the distal end. Often growing in the open subtropical forest regions.

Distribution. Southwestern and southeastern coasts of Australia.

KEY TO THE SPECIES

- 1 a. Adult leaves 2–6.5 mm, underside not glaucous; fruit with a stout beak; peduncle of pollen cone cluster 1–3 mm **93. *P. spinulosus***
 b. Adult leaves 5–12 cm, underside glaucous; apex of fruit rounded, blunt; peduncle of pollen cone cluster 10–25 mm **94. *P. drouynianus***

93. *Podocarpus spinulosus* (Smith) R. Br. ex Mirb., *Mém. Mus. Hist. Nat. Paris* 13 (1825) 75. – *Taxus spinulosa* Smith ex Rees, *Cyclop.* (1819) 35. – *P. pungens* Don ex Lamb., *Pinus* 1, 2 (1824) 23. – *P. bidwillii* Hoibr. ex Endl., *Syn. Conif.* (1847) 213. – *P. ensifolia* R. Br. ex Carrière, *Trait. Gen. Conif.* (1855) 456.

94. *Podocarpus drouynianus* Mueller, *Fragm.* 4 (1863-4) 86. – *Nageia drouyniana* (Mueller) Mueller, *Cens.* (1882) 104.

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