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37. PODOCARPACEAE

By A. Farjon.

Shrubs or trees, evergreen, dioecious or monoecious, with smooth, scaly bark exfoliating in flakes. Foliage branches persistent, glabrous, terminating in a conspicuous vegetative bud. Leaves persistent or falling, arranged helically, small and scale-like (not in Mesoamerica) or larger with a distinct, flat lamina longer than wide. Pollen cones solitary or grouped with few together, (in our area) axillary to leaves from small buds, catkin-like and elongated at anthesis, consisting of a thin rachis and helically arranged microsporophylls each bearing two pollen sacs. Pollen mostly winged more or less like that of *Pinus*. Seed cones lateral or terminal, usually pedunculate, mostly greatly reduced at maturity with only a single seed fertilized and developing; the bracts and seed scales are either completely reduced (*Prumnopitys*), transformed into a swollen, succulent, coloured 'receptacle' (*Podocarpus*) or relatively well developed with more seeds per cone (not in Mesoamerica). The single seed is surrounded by a dry (*Podocarpus*) or succulent (*Prumnopitys*) sarcotesta or epimatium. A family with 18 genera and c. 185 species world-wide; its distribution is mostly pan-tropical but with outliers into the temperate zone especially in the southern hemisphere.

1. Leaves usually longer than 25 mm and wider than 3.5 mm, all spreading at different angles.

1. Podocarpus

1. Leaves not more than 25 × 3.5 mm, pectinately arranged.

2. Prumnopitys

1. Podocarpus L'Hér. ex Pers.

By A. Farjon.

Trees (Mesoamerica), dioecious, attaining 35 m and 1.5 m d.b.h., with spreading branches. Vegetative buds with two distinct layers of scales, the outer usually overlapping the inner scales. Leaves short petiolate, with a distinct flat lamina tapering at both ends and a single central midvein; hypostomatic. Pollen cones solitary (Mesoamerica), catkin-like, substantially elongated at anthesis. Seed cones pedunculate, developing a single hard, dry (Mesoamerica) seed subtended by a swollen, succulent, usually orange or red 'receptacle' formed from the fusion of infertile bract/seed scale complexes. The receptacle shrinks and shrivels substantially and turns dark in sicco. The epimatium enclosing the seed reduces to a small crest near the apex of the seed in the species of Mesoamerica. A large genus of 107 species with a largely pan-tropical distribution; 4 species in Mesoamerica, all of which are tall rainforest trees.

Bibliography: Buchholz, J.T. & Gray, N.E. *J. Arnold Arbor.* 29(2): 123-150, pl. 1-8 (1948).

The above cited revision is outdated for several reasons. The generic concepts in this family have changed substantially in recent decades; two genera instead of one are now recognised in Mesoamerica. Several new species have since been described in *Podocarpus*, two for Mesoamerica. The taxonomy in this revision is to an extent based on

characters observed in the cross-sectional anatomy of leaves only, some of which are no longer seen as taxonomically reliable. This has led to the adoption of an unusually narrow species concept in that revision. On the other hand, the two species described more recently by D.J. de Laubenfels were based on very limited herbarium collections (e.g. no seed cones were known) and were at the time poorly compared with other species and/or collections. The material available for these two species remains limited and acceptance of one of them here remains provisional.

1. Vegetative bud scales much longer than wide, acuminate, spreading.

2. Leaves acuminate, midvein prominent abaxially, lying in a shallow groove adaxially.

1. Podocarpus costaricensis

2. Leaves acute, midvein prominent only in the proximal half of the leaf, more or less flat towards the apex.

3. Podocarpus matudae

1. Vegetative bud scales short, triangular-apiculate or rounded-obtuse, imbricate.

3. Vegetative bud scales rounded-obtuse, leaves adaxially with a prominent midvein lying in a shallow groove.

2. Podocarpus guatemalensis

3. Vegetative bud scales triangular-apiculate, leaves flat, adaxially without a prominent midvein but with a deep medial groove.

4. Podocarpus oleifolius

1. Podocarpus costaricensis de Laub., *Phytologia* 68: 67 (1990). Holotype: Costa Rica, *de Laubenfels 810* (MO).

Tree 20-30 m tall, erect, monopodial, to 1 m d.b.h. but most known trees more slender; bark reddish-brown, scaly and exfoliating. Foliage branches with prominent leaf scars and fine grooves from decurrent leaf bases. Terminal vegetative buds with spreading acuminate scales 10-15 mm; axillary buds small, with triangular, keeled, acute to acuminate scales 2-3 mm with free tips. Leaves lanceolate, flat, (4-)6-10(-13) cm × (7-)10-18(-22) mm, mostly with an acuminate apex. Midvein (costa) prominent on the abaxial side and extending to the leaf apex, lying in a groove on the adaxial side. Pollen cones axillary, solitary, 20-55 × 4-5 mm. Seed cones axillary, not observed. *Tropical lowland to montane evergreen rainforest*. CR (*G. Herrera 7736*, K); P (*Cuadros et al. 3963*, MO). 70-1600 m. (Endemic.)

According to de Laubenfels (1990) this species is the only species in Costa Rica with long acuminate vegetative bud scales; its leaf apices are also (mostly) acuminate. The only other species in Mesoamerica with similar bud scales is *Podocarpus matudae*; its leaves are usually gradually tapering to an acute apex and only occasionally acuminate; they are also often narrower but there is considerable variation in this. The midvein has characteristics similar to that species. Although now known from a few more collections than the four cited by de Laubenfels, its seed cones are still unknown; they probably are similar to those of *P. matudae*. This new species is disjunct from *P. matudae*, which has not been recorded with certainty south of Guatemala, and at present remains only known from a limited area in Costa Rica and from one locality (Parque Nacional de Darién) in Panama.

2. Podocarpus guatemalensis Standl., *Proc. Biol. Soc. Washington* 37: 49 (1924). Holotype: Guatemala, *Standley 25090* (US).

Podocarpus allenii Standl., *P. guatemalensis* Standl. var. *allenii* (Standl.) J.

Buchholz & N. E. Gray, *P. guatemalensis* Standl. var. *pinetorum* (Bartlett) J. Buchholz & N.E. Gray, *P. pinetorum* Bartlett.

Tree 20-35 m tall, erect, monopodial; trunk up to 1-1.5 m d.b.h.; bark smooth, reddish-brown turning dark grey and fissured. Branches spreading, forming a broad or sometimes pyramidal crown. Foliage branches finely grooved from decurrent leaf bases. Terminal vegetative buds semi-globose or ovoid, with short, keeled, acute, sometimes apiculate scales c. 3 mm; axillary buds small, with ovate scales. Leaves lanceolate to linear-lanceolate, straight or slightly curved, sometimes falcate, 4-16 cm × 6-18 mm (largest on saplings and shaded lower branches), leaf apex acute or sometimes obtuse. Midvein (costa) with a more or less prominent ridge abaxially, with a narrow ridge in a groove adaxially. Pollen cones axillary, solitary, cylindrical, 10-15 mm. Seed cones axillary, on short peduncles, receptacle 6-8 mm, succulent, reddish turning brown; seed ellipsoidal, 7-8 × 5 mm, smooth with a small, apical crest, light brown or grey-brown. *Tropical lowland to submontane evergreen rainforests*. B (*Gentle 3159*, K); CR (*Herrera 4037*, K); H (*Liesner & Mejía 26372*, MO); P (*McPherson 11944*, MO). 100-600 m. (Mexico, Mesoamerica, Colombia, Venezuela.)

Bartlett (1935) described from Mountain Pine Ridge, Belize a new species *Podocarpus pinetorum*, comparing it with the type of *P. guatemalensis* (*Standley 25090*, US) which apparently came from a shrubby young plant with longer, falcate leaves. He "reluctantly separated [it] from *P. guatemalensis*" because he realized that it might just represent the more mature form of that species. Likewise, Standley (1941) expressed doubts about the distinction between his new species *P. allenii* from Panama and *P. guatemalensis* on similar grounds. Leaves of these large Panaman trees measured only 3.5-4.5 cm × 7-8 mm, but leaves of seedlings and saplings measured 9-12 cm × 9-14 mm. These two species were reduced by Buchholz & Gray (1948) to varieties of *P. guatemalensis*, mainly on the basis of asserted differences in leaf anatomy, particularly the presence of sclereids and their position in the mesophyll. Orr (1944) found sclereids only in *P. oleifolius* among American species of *Podocarpus* but he did not examine leaves of these two taxa and only juvenile leaves of *P. guatemalensis*. As Buchholz & Gray admit, there may be a correlation with leaf form (juvenile versus adult) as well as environment (lowland versus upland) and taxonomic distinction on the basis of these characters in limited samples may not be justified.

3. *Podocarpus matudae* Lundell, *Phytologia* 1: 212 (1937). ("matudai").

Holotype: Mexico, Chiapas, *Matuda 698* (MICH).

Podocarpus matudae Lundell var. *macrocarpus* J. Buchholz & N. E. Gray, *P. matudae* Lundell var. *reichei* (J. Buchholz & N.E. Gray) de Laub. & Silba, *P. reichei* J. Buchholz & N.E. Gray.

Large tree to 30 m or taller, up to 1.5 m d.b.h.; trunk monopodial, erect, eventually with scaly bark. Foliage branches slender, straight, with fine grooves from decurrent leaf bases. Terminal vegetative buds with more or less spreading, long acuminate scales up to 12 mm; axillary buds small, with acuminate scales 3-4 mm. Leaves lanceolate, flat, 5-14(-20?) cm × 8-17 mm (both measurements largest on shaded branches of young, vigorous trees; smallest on canopy branches of old, slow growing trees), coriaceous, short petiolate, tapering to an acute or more or less acuminate apex. Midvein (costa) prominent on the abaxial side and on the proximal half of the adaxial

side, becoming flat towards the apex, lying in a shallow groove on the adaxial side. Pollen cones axillary, solitary, cylindrical, 3-4.5 cm × 4-5 mm when full-grown. Seed cones axillary, on short peduncles; receptacle 6-12 mm, succulent, red turning purplish-brown; seed 8-12 mm, broadly ovoid, with an inconspicuous crest, drying dark brown. *Montane subtropical cloud forests*. Ch (*Matuda s.n.*, K); ES (*Martínez 1082*, MO); H (*Mejía 443*, MO). 1100-2370 m. (Mexico, Mesoamerica.)

Lundell (1937) briefly described *Podocarpus matudae* as a new species from Chiapas, Mexico, based on *E. Matuda 698* with rather short and broad leaves. No mention was made of the vegetative buds while apparently the seed cones were not present in Matuda's specimens seen by Lundell. Buchholz and Gray (1948) added a new species from south-central Mexico, *P. reichei*, but also cited this new species from a collection made in Costa Rica. The leaves are similar, if we ignore their observations about presence or absence of sclereids in the mesophyll as an informative character, but the seed cones (seeds) are larger than those in *P. matudae*. However, Buchholz & Gray (1948) also described, from Chiapas and Guatemala, a new variety *P. matudae* var. *macrocarpus*, with (maximum) seed dimensions exceeding those of *P. reichei* and with 4-6 cm long pollen cones. Maturity of these organs is crucial for proper comparison, as often they are not full grown on the specimens examined. In all this material the buds with their long acuminate scales are most characteristic and we consider it to belong to a single species occurring from central Mexico to Costa Rica. De Laubenfels & Silba (1990) described a variety with leaves up to 20 cm from Jalisco, Mexico, but no information is given about the range of sizes found in leaves from this area or whether these long leaves occurred only on vigorous shoots of shaded plants or not.

4. *Podocarpus oleifolius* D. Don in Lambert, *Descr. Pinus* 2: 20 (1824).

Holotype: Peru [not Chile], *Pavon y Jiménez s.n.* (B).

Podocarpus macrostachyus Parl., *P. monteverdeensis* de Laub., *P. oleifolius* D. Don var. *costaricensis* J. Buchholz & N. E. Gray, *P. oleifolius* D. Don var. *macrostachyus* (Parl.) J. Buchholz & N. E. Gray, *P. oleifolius* D. Don var. *trujillensis* J. Buchholz & N. E. Gray.

Tree 20-25(-30) m tall, to 1 m d.b.h., monopodial, erect, branching densely; bark yellowish-brown, eventually scaly. Foliage branches with prominent leaf scars and decurrent grooves. Terminal vegetative buds subglobose, with short, rounded or ovate scales 3-4 mm long; axillary buds globose, with thick, rounded, carinate scales 2-3 mm. Leaves lanceolate to linear-lanceolate, straight (sometimes slightly curved), petiolate at base, gradually narrowing towards the acute or more or less obtuse apex, extremely variable in size dependent on growth of shoot, usually 4-9 cm × 7-12 mm but as small as 1.5 cm × 5 mm and as large as 15 cm × 20 mm, coriaceous. Midvein (costa) a more or less prominent ridge abaxially, often with a central groove continuing to the apex, on the adaxial side not elevated above the surface of the lamina but forming a narrow medial groove. Pollen cones axillary, solitary, c. 3 cm × 3-4 mm. Seed cones axillary, on short peduncles; receptacle 6-10 mm, succulent, red; seed ovoid-globose 7-8 mm, with an inconspicuous crest. *Montane to high montane tropical rain and cloudforests*. Ch (???)G (Stevens et al. 25436, MO);H (*Farjon 296*, E); ES (*Tucker 1034*, K); N (*Stevens 6724*, MO); CR (*Aguilar 3969*, K); P (*Gentry & S. Mori 13771*, MO). 2000-2800 m. (Mexico, Mesoamerica, Colombia, Venezuela, N. Peru.)

Buchholz & Gray (1948) described *Podocarpus oleifolius* var. *costaricensis* from Volcán de Poás; the type (Pittier 822) as well as other collections from there have short leaves and small, crested seeds. Similar specimens with small leaves are known from other localities in Mesoamerica and it is doubtful that they all belong to a single taxon distinct from the more common form of the species. They are known from both high and middle elevations. De Laubenfels (1991) considered *P. macrostachyus* and *P. oleifolius* to be distinct species, the latter restricted to South America, but they form a continuum of highly variable leaf sizes and are not consistently distinct. A small leaved, male specimen (de Laubenfels 814, MO) was designated as the type of his new species *P. monteverdeensis* from Monteverde in Costa Rica, but its morphology falls entirely within the range found in *P. macrostachyus*/*P. oleifolius* and none of the distinctions mentioned in the protologue appear to hold true if a sufficient number of collections is examined. Leaf shape and size are influenced by growth conditions and age of plants; the only consistent vegetative characters are mentioned in the key to the Mesoamerican species at the beginning of this account.

2. *Prumnopitys* Phil.

By A. Farjon.

Trees, normally dioecious, much branched, of moderate to large size. Leaves helically arranged but mostly twisted at the petiolate base to form two pectinate rows on the branches, relatively small, subfalcate, bifacially flattened, with whitish stomatal bands below. Pollen cones aggregated in axillary spikes near the ends of small foliage shoots, catkin-like, straight, yellow at anthesis. Seed cones pedunculate, grouped with 2-several on foliage branches, at maturity reduced to a single, globose or elliptic seed surrounded by a fleshy, greenish to yellowish or bluish epimatium, drupe-like, becoming pendant and lacking an inflated receptacle as in *Podocarpus*. A genus of 9 species with a disjunct distribution in South America (from Costa Rica to southern Chile) and New Caledonia, New Zealand and Queensland, Australia. One species in Mesoamerica, endemic in Costa Rica.

1. *Prumnopitys standleyi* (J. Buchholz & N.E. Gray) de Laub., *Blumea* 24 (1): 190. (1978). *Podocarpus* (section *Stachycarpus*) *standleyi* J. Buchholz & N.E. Gray. Holotype: Costa Rica, *Tonduz 10333* (US).

Tree to 25 m, evergreen, dioecious; trunk monopodial, branches spreading, foliage branches alternate, forming flat sprays. Foliage twigs slender, glabrous, initially covered in narrow decurrent leaf bases, later with thin, exfoliating bark. Leaves alternate, usually pectinately arranged in two rows and one plane, linear, twisted and slightly curved above the decurrent base and sometimes near the apex, or more or less falcate, (12)15-20(-25) × 2-3.5 mm, narrowed towards the petiolate base, apex acute to mucronate. Adaxial leaf surface (upper side) with a conspicuous longitudinal groove through the middle, dark green; abaxial surface (lower side) with a narrow longitudinal midrib, stomatiferous, stomata in numerous lines, very small, covered with a greyish-white wax. Pollen cones numerous on slender leafless twigs (spikes) towards the ends of foliage sprays, close together, each catkin-like cone on a 2-3 mm 'stalk' (bare base of the rachis), slender, 10-15 × 2-2.5 mm at anthesis. Microsporophylls numerous, helically

arranged, sub-peltate, curved upwards with a scarious-denticulate, acute apex; each bearing near the base two relatively large, transversely dehiscent microsporangia containing spherical pollen. Seed cones on small branchlets with a few reduced leaves, axillary to these, much reduced to produce a single subapical seed c. $10 \times 7-8$ mm, with a fleshy sarcotesta (epimatium), green, bluish when mature, rugose in sicco. *High montane tropical rain- and cloudforests. CR (Tonduz 10743, K). (Endemic.)*