

A TAXONOMIC REVISION OF *PODOCARPUS*  
 II. THE AMERICAN SPECIES OF *PODOCARPUS*:  
 SECTION *STACHYCARPUS*

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*With four plates*

SPECIES OF *Podocarpus* belonging to section *Stachycarpus* have small yew-like leaves, spread apart distichously, are without hypoderm, with transfusion tissue, and have no accessory transfusion tissue. They may be distinguished from those of *Taxus* by the presence of the single resin canal, absent in *Taxus*. All American species are hypostomatic, but there are several species in the Old World near the extreme western limit of the range of this section with unequally amphistomatic leaves. (In this region there might be confusion with certain species of *Dacrydium* which are usually not distichous though some are without hypoderm.)

In differentiating the species in this section it has been found that the plants are so similar in leaf anatomy that it is impossible to distinguish the American species from each other through internal differences. The greatest variation is observed in the number of layers of palisade tissue but this character is somewhat subject to ecological conditions such as altitude and exposure. There is no sclerenchymatous tissue, nor isolated sclerids whatever, aside from that belonging to the vascular bundle and its associated transfusion tissue. Externally, some usable differences are readily visible — groove vs. ridge or flat surface above the midvein, size and shape of leaves. But to make positive identification, seed cones and seeds are necessary. Unfortunately, not many of the specimens collected are with seeds. It is therefore possible that some of the varieties may represent distinct species but a great deal of field observation by botanical collectors and foresters is necessary to delimit the natural ranges of the species and varieties, and to amplify the descriptions of the mature trees as well as the reproductive parts.

KEY TO THE NEW WORLD SPECIES OF *PODOCARPUS* BELONGING  
 TO SECTIONS *STACHYCARPUS* AND *POLYPODIOPSIS*

- Leaves flat, attached spirally, distichous, linear or oblong-linear, sometimes falcate; with a single midvein and resin canal, without a layer of hypodermal cells, with well developed palisade tissue and with stomates confined to lower (abaxial) surface.....Section *Stachycarpus*.  
 Leaves flat above or with a slight ridge above the midvein (figs. 13–17, 21, 22).  
     Leaves nearly flat above, 15–24 mm. long, about 1.5 mm. wide; seeds ovoid, 20 mm. long, 13–14 mm. wide, very little flattened, borne singly or with several on a spike which is a strobilar axis bearing numerous ovules at the time of pollination. South of Equator.....1. *P. andinus*.



Leaves with a slight ridge above the midvein.

Leaves usually 15–24 mm. long, up to 3.5–4.5 mm. wide, falcate; seeds 9–10 mm. long, with a fleshy coat drying as in a plum, the ovules numerous and borne on an axis resembling a spike, as in *P. andinus* (figs. 13, 17, 21–23). North of Equator.....2. *P. Harmsianus*.

Leaves less than 18 mm. long, seldom more than 2 mm. wide; seeds unknown, ovules borne as in *P. andinus* (figs. 14–16), single crested.

South of Equator.....3. *P. utilior*.

Leaves with groove above midvein (fig. 20). North of Equator.

Female reproductive branch bearing ordinary leaves fully or nearly same size as foliage leaves; leaves 5–20 mm. long, 2–4 mm. wide, acute or obtuse.

Leaves 12–20 mm. long, 2.5–4 mm. wide, mostly acute; dry seed up to 15 mm. long, 8–10 mm. wide, with single flattened crest 3–4 mm. long (figs. 24 & 25).....4. *P. montanus*.

Leaves 5–12 mm. long, 2–3 mm. wide, mostly obtuse; seed about 12 mm. long, 8–9 mm. wide, bearing 2 distinct, bluntly rounded crests (figs. 27 & 28).....5. *P. montanus* var. *densifolius*.

Leaves 7–14 mm. long, 2.5–3.5 mm. wide, mostly obtuse (groove sometimes broad and open); dry seed about 10–13 mm. long, 6–8 mm. wide, crest of fused spines or appearing single, relatively long and slender (figs. 19, 29–31).....6. *P. montanus* var. *meridensis*.

Female reproductive branch bearing small bracts or scales, leaves 15–25 mm.

long, 2.5–3.5 mm. wide; seed 10–11 mm. long with cylindrical crest 2 mm.

long (figs. 32–34).....7. *P. Standleyi*.

Leaves ovate, sessile, opposite, 4-ranked but spread out in a single plane; with stomates on both sides, with hypoderm, a single midvein and 3–11 resin canals.

.....Section *Polypodiopsis*.  
8. *P. Rospiglosii*.

1. *Podocarpus andinus* Poeppig ex Endlicher Syn. Conif. 219. 1847; Gay in Flora Chilena 5: 403. "1849" [1852]; Gordon, Pinetum 351. 1875; Pilger in Pflanzenreich IV. 5 (Heft 18): 64. 1903; Reiche in Engler & Drude, Veg. der Erde 8: 63–64. 1907; Florin in Svenska Vet.-Akad. Handl. ser. 3, 10: 262. 1931; Covas in Rev. Argent. Agron. 6: 24. 1939.

*Podocarpus spicata* sensu Poeppig, Nov. Gen. Sp. 3: 18. 1845, non R. Br.

*Podocarpus valdiviana* Senilis, Pinaceae 160. 1866.

*Prumnopitys elegans* Phil. in Linnaea 30: 731. 1860; Carrière, Traité Conif. 682. 1867; Dallimore & Jackson, Handb. Conif. 60. 1923, 1931.

*Stachycarpus andina* Van Tiegh. in Bull. Soc. Bot. France 38: 173. 1891.

*Taxus spicata* Dombey ex Gordon, Pinetum 351. 1875.

An evergreen pyramidal tree becoming 12 m. high, though often only a shrub in cultivation, with smooth dark reddish brown bark, extensively branched and with numerous branchlets. Twigs short, subalternate with many leaves, spreading pectinately. Leaves linear, thin leathery, bright green above and glaucous beneath, straight or only slightly falcate, short-mucronate, or often obtuse at the tip, somewhat narrowed at the base which is fairly broad, with midvein inconspicuous on upper side, much more prominent beneath especially toward the base, 15–24 mm. long and usually 1.5 or less than 2 mm. wide. Pollen cones borne spicately on a special lateral branch 1.5–2.5 cm. long, among leafy twigs; cones divaricate, numerous (12–20), 6–8 mm. long, sessile, in the axils of minute bracts and crowded toward tip of the branch. Microsporophylls with 2 pollen sacs, terminated by a broadly triangular upturned flat tip, with scarious and minutely denticular margin. Seed cone, a greatly modified strobilar axis appearing as a spike on the end of a special branch 2–2.5



cm. long, with leaves below, followed by scales and bearing several (3–5 or more) scattered ovules above in the axils of small bracts with only one or two of them maturing as seeds attached laterally to the strobilar axis. Seeds ovoid, with a stony inner and a fleshy outer layer resembling a drupe, 20 mm. long, 13–14 mm. wide, slightly flattened. Outer fleshy layer dries over the stony layer as in a miniature prune.

DISTRIBUTION: Central to south-central Chile.

SPECIMENS EXAMINED:

CHILE. Valdivia: Cordillera de la Costa, *Poeppig* (†A, US); Union, at banks of stream near Ranco, *Anon.* (US, with pollen cones). Chile, without detailed locality: "Austro-Andina," Feb. 1829, *Poeppig*, ISOTYPE (ex Bernhardt Herb.) (†Mo, †F); *Ruiz* 4635 (ex Herb. Lambert; US); *Germain* (†GH, with seeds); *Philippi*, in 1888 (†A, with seeds, NY [fig. 26], US). CULTIVATED: Kew, *Nicholson*, in 1884 (A); *R. N. Parker*, in 1903 (A); Hanover, Muenden, *H. Zabel* (A); Mainau Island, Lake Constance, *Schneider*, Sept. 1903 (A); Silesia, Breslau, *Baenitz*, 1170 (US, GH); "Greendale," *Anon.* (A, with excellent pollen cones); Golden Gate Park, San Francisco, *Walther*, in 1931 (CAS); *Buchholz* in 1942 (Ill.).

*Podocarpus andinus* was described by Endlicher who attributed the name and description to *Poeppig*, indicating an earlier report of this entity under the name of *P. spicatus*, a New Zealand species. Later *Philippi* described the same plant under a separate generic name as *Prumnopitys elegans*. This is clearly a superfluous name, and therefore, illegitimate, but somehow it has persisted as a horticultural trade name and is still in use. *Dallimore & Jackson* (1923, 1931) place all species of this group under *Podocarpus* except this one, which they describe under a separate genus as *Prumnopitys elegans* *Philippi*.

2. *Podocarpus Harmsianus* Pilger in *Pflanzenreich* IV. 5 (Heft 18): 68. 1903; *Dallimore & Jackson*, *Handb. Conif.* 47. 1923, 1931; *Pittier*, in *Bol. Cient. y Tecn. Mus. Com.* 1: 9. 1927; *Florin* in *Svenska Vet.-Akad. Handl.* ser. 3, 10: 262. 1931; *Macbride*, *Flora of Peru*, 1 (Field Mus. Nat. Hist. Publ. 351, Bot. ser. 13): 83. 1936; *Schnee* in *Bol. Soc. Venezol. Cienc. Nat.* 9: 184–5 (excl. fig. 3 = *P. montanus meridensis*), in part. 1944.

An evergreen tree with dark brown scaly bark becoming 15 m. high or higher with a trunk diameter up to 40 cm. Branchlets slender and somewhat loosely leaved. Leaves coriaceous, spirally arranged, distichously spread in one plane, patent, oblong-lanceolate, straight or falcate or somewhat s-shaped, acute or short angustate above and below, narrowly sessile, 15–27 mm. long, 3–5 mm. wide, pruinose when young except at midrib which is obtusely prominent above and less prominent or flat beneath where midvein separates the two bands of stomates. Pollen cones divaricate, about 15 in each spike, up to 10 mm. long and borne in the axils of minute elliptical, acute bracts (these 2 mm. long), surrounded at the base by small imbricated scales. Microsporophylls broad with a large triangular obtuse upturned apex lacerated at the margins, with two laterally placed microsporangia dehiscing laterally and horizontally. Ovulate cones greatly reduced, consisting of a slender modified branch 15–25 mm. long, clothed only with minute scales below (soon deciduous). Strobilar axis

† This symbol preceding the abbreviated name of an herbarium following the specimens examined signifies that the details of the leaves of this specimen have been examined in cross-section.



bearing one or more inverted ovules near tip, attached laterally in the axil of a bract half as long as the ovule. Seed not flattened, only slightly crested and with a thin fleshy outer seed coat not greatly wrinkled in drying.

SPECIMENS EXAMINED:

VENEZUELA: Colonia Tovar (= Tovar in Aragua): *Fendler 1289* Berlin ex Pilger LECTOTYPE; *Fendler 1289*, ISOTYPES (GH with pollen cones, Ph [fig. 13], †Mo); *Delgado 174* TOPOTYPE (†F with seed of *P. Rospiglosii* (?) in pocket, US without seed); *Delgado 206* (†US); Alto de Nor Leon, *Alfredo Jahn* TOPOTYPE with ovulate strobilus [fig. 21] (†US). Distr. Federal: Silla de Caracas, *O. Kuntze 1611* (NY, US, †F); *Steiermark 55146* (F, Ill); *Delgado 338* (Ven).

COLUMBIA: Magdalena: San Lorenzo Mts. near Santa Marta, *Viereck*, Dec. 1922, (†US with seeds and female strobilus in pocket, [figs. 17 & 23] (F). Colombia, without locality: *Karsten 287* (photo.) probably belongs here (F).

CULTIVATED: Guatemala, garden of Don Mariano Pancheco H., *Steiermark 39887* (†F); Venezuela, Colonia Tovar, *Tamayo 1575* [fig. 22] (†Ven); Colombia, Minca, *Bro. Apolinar A625* (†US); *Daniel 3349* (†US).

The differences between the Colombian and Venezuelan specimens of *Podocarpus Harmsianus* seem to be only slight. More intensive study may reveal differences sufficient to warrant a variety. If so, the Venezuelan plants should be considered as representing the typical form of the species.

Pilger cited two specimens under the original description of this species, listed alphabetically — Colombia without locality *Karsten 287* and Venezuela, Colonia Tovar (= Tovar in Aragua), *Fendler 1289*. The first specimen cited has been selected as the type by Macbride for the collection of photographs. This arbitrary choice by Macbride is unfortunate, since the *Karsten* specimen is sterile, without locality and has now been destroyed with the Berlin collections.

A study of Pilger's description reveals that the whole of the text applies to the Venezuelan plant, for this is the only one that included pollen cones. The *Karsten* photograph shows longer leaves, suggesting a seedling or juvenile specimen. Only about half of the description could apply to this sheet. Duplicates of the *Fendler* specimen are found in American herbaria and one of these (GH) includes the reproductive parts. We, therefore, designate *Fendler 1289* as the lectotype of this species.

3. *Podocarpus utilior* Pilger in Fedde, Rep. Nov. Spec. 1: 189. 1905; Weberbauer in Veg. der Erde 12: 74. 1911; Florin in Svenska Vet.-Akad. Handl. ser. 3, 10: 262. 1931; Macbride, Flora of Peru, 1 (Field Mus. Nat. Hist. Publ. 351, Bot. Ser. 13): 84. 1936.

*Podocarpus montanus* sensu Britton in. Bull. Torrey Bot. Club 16: 13. 1889, not (Willd.) Lodd.

An evergreen tree up to 20 m. or more high with many branches, the branchlets spreading or erect to spreading, very leafy. Leaves borne spirally but spreading out distichously in one plane, crowded, patent, small, thick, linear, coriaceous, often somewhat widest above the middle, acute or obtuse, oblique at base, sessile or very short-petioled, 10–18 mm. long, about 1.5–2.5 mm. broad, midrib slightly prominent above, with streaks beneath, except along the midrib, but not glaucescent. Leaves of seedlings and young trees probably larger. Pollen cones unknown. Seed cones reduced to a special branch 15–30 mm. long surrounded at the base



by a few deciduous scales and ending in a strobilar axis bearing 4–6 bracted inverted ovules in spiral arrangement, the ovules prominently crested with a single spine-like point. Seeds unknown.

SPECIMENS EXAMINED:

PERU: Junin: Tarma, Mt. Yananga, east of Haucapitana, photo. of *type* and fragment *Weberbauer 2114* (†F Neg. no. 11580, fragment from Florin ex Berlin Herb. †, [figs. 14, 15]); Oxapampa, *Soukup 1802* (GH, †US, †Ill with female strobili [fig. 16]). The following sterile specimens may be referred to *P. utilior* mostly on the basis of geography and agreement in leaf structure even though larger: Ayacucho: Ocarapa, *Killip and Smith 22480* (†A, †F, NY, US); Junin, Pichis Trail, *Killip and Smith 25746* (†US seedling).

BOLIVIA: Yungas, *Rusby 1960* (†NY, Mich); Huainachoirisa, *Williams 1535* (†NY); Santa Cruz: Samaipata, *Carriker* (†Ph, this specimen has no ridge above midvein, is actually somewhat concave-depressed above).

CULTIVATED: Berlin Bot. Gard., *Rehder* in 1885 (A); ex Gord. Herb. (A); Naples, Hort. Bot. Neapol., *Engelmann* in 1868 (Mo).

As the name implies, this tree is locally used as a source of lumber. Figure 20, supplied by Mr. J. Soukup, shows recent logging operations at Oxapampa. These large logs 1.75 m. in diameter are presumably of this species but this is not a certainty since *P. Rospiglosii* is known to occur also in this locality. The latter is a much smaller tree.

While mature seeds have not been available, fig. 15 of the type specimen of *P. utilior* shows some of the ovules beginning to enlarge, bearing single long spine-like crests. Partially enlarged ovules of *P. Harmsianus* have not shown traces of the crested condition. Its mature seeds are crestless or show a very blunt crest; also this tree is not known to approach the size of *P. utilior* shown in fig. 20. The seeds of *P. Harmsianus* which mature are usually subterminal, those of *P. utilior* show several lateral ovules developing.

The leaves of these two species are very similar. Those of *P. utilior* are smaller in general and are much smaller in the type specimen than those of *P. Harmsianus*. Presumably, reproductive branches taken far up near the top of a large tree would have smaller leaves. The collections of *Soukup 1802* are reproductive in the U. of Ill. specimen (fig. 16) and have leaves larger than the type. Presumably the size of the leaf of *P. utilior* varies greatly depending upon the position on the tree and upon the size of the plant, so that shrubby specimens may have much larger leaves than mature trees. In this condition they may be indistinguishable from those of *P. Harmsianus*, but the latter have not been found to be as small as the type of *P. utilior*, on any specimens. Small seedlings of both of the species have been seen, and have long, relatively slender leaves.

On the assumption that only a single species has been found in Peru, we are including the material of seedlings and shrubby plants collected by Killip & Smith with rather large leaves under *P. utilior*. This decision is also supported on the basis of geography. With no collections before us from central and southern Colombia or Ecuador with a ridge above the midvein of the leaves, we feel convinced that this geographic discontinuity indicates two distinct but closely related species.



Prior to Pilger's monograph (1903) only a single species in this group was recognized. All specimens are referred to *P. taxifolius* = *P. montanus*. No distinction has been made with respect to a groove vs. ridge above the midvein. However, the plant now known as *P. utilior* was found in cultivation in European gardens — this or *P. Harmsianus*. Gordon in the Pinetum (1858 and 1875) describes the species as known to him "with a slight rib along the upper surface." Witness also the cultivated specimens cited above: Rehder in 1885 from the Berlin Botanical Gardens and a specimen from the Gordon Herbarium. Both of these have the ridge.

All early references give Peru as the origin of *P. montanus*. The original type specimen of *Taxus montanus* Willd. has a distinct groove above the midvein, clearly shown in the photograph. These earliest collections actually came from near Loja in Ecuador and from Colombia, not Peru. No Peruvian specimen of *P. montanus* has been found among those available in American collections. However, all plants that agreed with the early descriptions, grown from seeds of Peruvian origin passed under the name of the only described species and it may be inferred that the plant now known as *P. utilior* was actually in cultivation in Europe for more than a half century before *P. utilior* was described.

Macbride included *P. montanus* in his Flora of Peru based upon material collected by Humboldt on Mt. Saraguro across the border in Ecuador. It might, therefore, be encountered in northern Peru but has not been collected there thus far.

4. *Podocarpus montanus* (Willd.) Loddiges, Cat. 37. 1836; Pilger in Pflanzenreich IV. 5 (Heft 18): 67. 1903, *in part*, in Nat. Pflanzenfam., ed. 2, 13: 245. 1926, *in part*; Dallimore & Jackson, Handb. Conif. 51. 1923, 1931, *in part*; Florin in Svenska Vet.-Akad. Handl. ser. 3, 10: 262. 1931; Macbride, Flora of Peru, 1 (Field Mus. Nat. Hist. Publ. 351, Bot. Ser. 13): 83. 1936.  
*Podocarpus montanus* var. *diversifolius* Dallimore & Jackson, Handb. Conif. 51. 1923, 1931.  
*Podocarpus Harmsianus* sensu Schnee in Bol. Soc. Venezol. Cienc. Nat. 9: 184-6. 1944, not Pilg.  
*Dacrydium distichum* Don ex Lamb. Pinus, ed. 2, 2: 120. 1828.  
*Nageia montana* O. Kuntze, Rev. Gen. 2: 800. 1891.  
*Podocarpus taxifolia* Kunth, in Humb. and Bonpl., Nov. Gen. 2: 2, pl. 97. 1817; L.C. & A. Richard, Comm. Bot. Conif. 15. 1826; Endlicher, Syn. Conif. 219. 1847; Gordon, Pinetum 288. 1858, 355. 1875, *in part*; Carrière, Traité Conif. ed. 2, 672. 1867; Parlatore in DC. Prodr. 16(2): 518. 1868; Uribe, Flora de Antioquia Medellín 44. 1940.  
*Podocarpus Humboldtii* Hort. ex Gordon, Pinetum 288. 1858, 355. 1875.  
*Prumnopitys taxifolia* Hort. ex Dallimore & Jackson, Handb. Conif. 51. 1923, 1931.  
*Stachycarpus taxifolia* Van Tiegh. in Bull. Soc. Bot. France 28: 173. 1891.  
*Taxus montana* Willd. Spec. Plant. 4(2): 857. 1805, not Nuttall.  
*Torreya Humboldtii* Hort. ex Lindl. & Gord. in Jour. Hort. Soc. 5: 355. 1850; Knight ex Gord. Pinetum 355. 1875.

An evergreen tree up to 25 m. tall with wide-spreading branches bearing numerous alternate branchlets with taxoid foliage. Leaves spirally arranged and spread out distichously in one plane, linear, sometimes oblique or falcate, apex acute, broadly acute or mucronately acute, gradually narrowed at the subsessile base, sub-petioled, 10-18 mm. long, 2.5-3.5 mm.



wide, dark green above, paler beneath, with a distinct groove above the midvein which is slightly prominent beneath between two broad bands of stomates. Pollen cones numerous (up to 25) spicately arranged on the end of a special branch 3–5 cm. long, each cone borne in the axil of a small ovate bract (this 2–3 mm. long). The cones patent about 10 mm. long, sessile toward the end of the special branch but with peduncles up to 3 mm. long in the lowest cones. Microsporophylls broad with a pair of ovoid sporangia dehiscing horizontally, the upturned apex of the sporophylls triangular from a broad base, obtusely rounded with a scarious margin. Pollen 2-winged. Seed cone reduced to the end of a small branch 4–6 cm. long bearing ordinary leaves below, and only a few bracted inverted ovules at its tip, only the terminal ovule developing into a fleshy seed, the strobilar axis not becoming fleshy. Seed ovoid-globose, sessile, 14 mm. long, 8–9 mm. thick, tipped with a single, somewhat flattened crest, the fleshy outer layer wrinkled upon drying.

Type specimen not seen. Plate 97, vol. 2, Humboldt & Bonpland (1817) shows presumed type specimen; locality, according to Kunth: Quindiu Pass (in Colombia near 4° 38' N. Lat.; 75° 42' W. Long.)

DISTRIBUTION: central cordillera in Colombia and Ecuador.

SPECIMENS EXAMINED:

COLOMBIA: Cauca, western slopes of Paramo de Moras, *Lehmann 3763* (†US); Musillo, Central Cordillera, *Dawe 747* (NY, US); Caldas, San Felix near Salamma, *Bro. Thomas 2050* (US); Colombia (New Granada) without specific locality: *Rev. Holton* in 1854 ex Torrey Herb. [fig. 18] (†NY); *Triana 511* (†US); *Mutis 641, 3858, 4414* (US); *Bro. Ariste Joseph A897* (†US).

ECUADOR: Loja, between Tambo Cachiyacu and Nudo de Sabinillas, *Steyermark 54472* (F with seeds, [figs. 24 & 25], Ill).

It should be noted that we have included *Dawe 747* bearing the annotation that this is an important timber tree of the central cordillera in Colombia as representative of the species. Dallimore & Jackson mention this Dawe collection under a trinomial *P. montanus diversifolius* (they may have intended *densifolius* Kunth) which has leaves that are shorter than those of Costa Rican collections, but somewhat longer than those of the variety *densifolius* (see below). Unfortunately no seeds are included among the Dawe specimens, which therefore lack the completeness necessary for more definite classification.

The combination *P. montanus* var. *diversifolius* Dallimore & Jackson is a superfluous name, in any case illegitimate whether it belongs under the variety *densifolius* Kunth or under the species.

5. *Podocarpus montanus* var. *densifolius* (Kunth) comb. nov.

*Taxus montanus* var. (without name) Willd. Sp. Pl. 4(2): 857. 1805.

*Podocarpus taxifolia* var.  $\beta$ : *densifolia* Kunth in Humb. and Bonpl. Nov. Gen. 2: 2. 1817.

*Podocarpus taxifolia densifolia* (Kunth) Gordon, Pinetum 289, 1858. 355, 1875; Carrière, Traité Conif. ed. 2, 673, 1867.

An evergreen tree differing from the above species in its more crowded, shorter, more obtuse leaves, 6–12 mm. long, 2–3.5 mm. wide, dark green above, paler but not glaucous beneath; ovules borne as in the above species but double crested. Seeds about 14 mm. long, 8–9 mm. wide, with a pair of blunt crests.



Type specimen not seen; presumed to be *Link* in Berlin Herb., Photograph in Collection of American types in European Herbaria, Neg. #11575, (F).

Type locality: a few authors including Gordon cite Humboldt in giving the Mountains of Saraguro between Ona and Loja by error in Peru; actually this is in Ecuador. Both the species and the variety appear to be found here and in Colombia and have been collected since in the two regions.

SPECIMENS EXAMINED:

COLOMBIA: Bogota, *Purdie*, sent to Hooker about 1849 (ex Bentham Herb.) with ♀ strobilus, seed in packet (†NY [fig. 27]); *Purdie*, sent to Torrey and Gray, no date (NY, G); Cundinamarca, Sibate, shrub or young tree, *Pennell* 2436 (Ph, GH, †NY, [fig. 28] US, F).

ECUADOR: Azuay, beyond Sayousi on trail to Cajas, *Penland & Summers* 1082 (F).

6. *Podocarpus montanus* var. *meridensis* var. nov.

*Podocarpus montanus* Pilger, Pflanzenreich IV. 5 (Heft 18): 67. 1903, in part, in Nat. Pflanzenfam. ed. 2, 13: 245. 1926, in part.

*Podocarpus Harmsianus* Schnee in Bol. Soc. Venezol. Cienc. Nat. 9: 184-5. 1944, not Pilger.

*Podocarpus montanus* Schnee, ibid. in part.

Semine quam in *P. montano* ejusque var. *densifolio* minore differt; seminis crista saepius processibus spinosis geminis confluentibus efformata, vel processibus totis coalescentibus semen *P. montani* valde diminutum mentiente; foliis *P. montani* var. *densifoli* persimilibus vel statura intermediis, canaliculo per costam interdum magis aperto.

SPECIMENS EXAMINED:

VENEZUELA: Lara, between Buenos Aires and Páramo de las Rosas, *Steyermark* 55459 (F, Ill); Trujillo, Cerra de La Mesa de Esmujaque, *Schnee* 50 (Ven, †Ill); *Schnee* 55 (Ven, †Ill); Merida, Timotes, *Delgado* 366 (†Ven [fig. 29]); Arriba de Chachopo, *Schnee* 33 (Ven, †Ill); Tachira, below Páramo de la Negra, above La Grita, *Steyermark* 57103 (F, Ill TYPE [fig. 19]); *Klugh* in 1944 (†Ven [fig. 30]).

COLOMBIA: Magdalena, Cerro Pintado, Sierra Perija, *Carricker* 49 (US).

This variety of *P. montanus* with leaves that are very similar to or intermediate between the species and var. *densifolius* in size, appears to be widely distributed and somewhat more frequently encountered than the others, with an eastward extension to Lara in Venezuela. However, the seed is not intermediate in size, but is smaller, and furnishes a more distinctive characteristic in its crest. The crest is composed of a pair of partially fused spine-like projections, or these spines may be completely fused resembling the seeds of *P. montanus*, but the entire seed is much smaller. Schnee (1944) was led astray by these spines, regarding them as characteristic of the seeds of *P. Harmsianus* Pilg. of which seeds had not been seen thus far; where actually collected, the specimens had been referred to *P. montanus* by some Venezuelan botanists. As shown in our key, *P. Harmsianus* and *P. utilior* have a ridge on the upper side of the leaf, while the members of the *montanus* group have a distinct groove over the midvein. However, this groove may be somewhat open (fig. 7) in the specimens of var. *meridensis*.



It is possible that both the varieties under *P. montanus* should be regarded as distinct species. There is considerable variation among specimens both as to the leaf and seed characters. We feel that careful observation of these characters by foresters and collectors is desirable before establishing these entities as distinct species, and that our treatment of the specimens before us will serve adequately to bring them to the attention of collectors.

7. *Podocarpus Standleyi* nov. sp.\*

*Podocarpus montanus* sensu Pilger in Pflanzenreich IV. 5 (Heft 18): 67. 1903; in Nat. Pflanzenfam. ed. 2, 13: 245. 1926, in part; sensu Standley, Flora Costa Rica, Field Mus. Nat. Hist. Publ. 391, Bot. ser. 18: 64. 1937.

Arbor sempervirens 25 m. alta, ramulis foliosis alternatum patentibus numerosis; foliis linearibus spiraliter dispositis, uno plano patentibus, saepius falcatis, deorsum acutis vel mucronatio-acutis, ad basim gradatim angustatis, late breviterque subpetiolatis, 12–25 mm. longis (pro more 14–18), 2.5–3.5 mm. latis, supra ad costam, manifeste canaliculatis, costa subtus prominente utrinque zona stomatifera notata; foliis hypostomaticis, regione chlorenchymatis subinde cum epidermate finitima (i.e., strato hypodermico nullo), ducto resinifero sub vena unico; strobilis ♂ in ramulo proprio spicatum dispositis, numerosis (ad 20), apicalibus sessilibus, infernis subsessilibus, in anthesi (i.e., pollinis effusi tempore) ca. 10 mm. longis, bracteis minutis ovatis fultis; microsporophyllis latis, sporangiis 2 ovoideis, basi latis, in apicem triangularem excurvatis, margine libero laevi, scarioso, denticulato; microsporangiiis transversim dehiscentibus, polline alato; strobilis ♀ in apice ramuli spiralis 15–25 mm. longis fultis, foliis minimis vel squamis praeditis quam foliis eufoliaceis multo minoribus; ovulis inter sessilibus paucis bracteatis, ad apicem ramuli proprii insidentibus in axin strobili confluenti, terminali semen unicum praebenti maturum; seminibus globoso-ovoides, crista gracili cylindrico-conica 2 mm. longa coronatis, semine toto 10.5 mm. longo, ca. 6 mm. lato, haud complanato, sicco extus tantum minute ruguloso.

SPECIMENS EXAMINED:

COSTA RICA: Volcan de Poas: Mts. of Canton de Dota, *Tonduz* 10333, TYPE, immature ♂, ♀ cones with seed [fig. 33] in packet (†US); *Tonduz* 10743, ♀ cone [fig. 32] (US); *J. D. Smith* 6857 (†GH, US [fig. 34]); *Standley* 34836 (US); *Haupt* in 1940 (†LA); *Roever* 5074 (NJU); La Laguna, *Tonduz* 11913 (US); *Standley* 42347 (†F, US); San José, Cerro de las Vueltas, *Standley & Valerio* 43581 (†F, US); Cartago, Camp Empalme, along Pan American Hy., *Little* 6030 (F).

In describing *P. Standleyi* we are restricting Pilger's description of *P. montanus*. Pilger had broadened the description in including Costa Rican plants. The seed is much smaller than in *P. montanus*, has a cylindrical spine-like crest, and is borne on a specialized reproductive branch which has only scales rather than foliar leaves. Compare figs. 32 and 33 with figs. 24 and 25. The leaves of *P. Standleyi* become much larger and are very glaucous beneath. (fig. 34).

\* Named in honor of Paul C. Standley, Curator of the Herbarium, Chicago Natural History Museum, in recognition of his outstanding contributions to our knowledge of the flora of Costa Rica.



## LITERATURE CITED

1. BERTRAND, C. E. Anatomie Comparée des Tiges des feuilles chez les Gnétacées et les Conifères. Ann. des Sci. Nat. ser. V. 20: 5-153. 1874.
2. BUCHHOLZ, J. T. Embryogeny of the Podocarpaceae. Bot. Gaz. 103: 1-37. 1941.
3. DU TOIT, ALEX. L. Our wandering continents. Edinburgh and London. 1937.
4. ENGLER, A. in Engler & Prantl, Nat. Pflanzenfam. ed. 1, Nachträge zu II-IV, p. 21. 1897.
5. FLORIN, R. Untersuchungen zur Stammesgeschichte der Coniferales u. Cordaitales. Erster teil. Morphologie und Epidermisstruktur der Assimilationsorgane bei den rezenten Koniferen. Svenska Vet.-Akad. Handl. ser. 3, 10. Stockholm. 1931.
6. ———. Die Koniferen des Oberkarbons u. des unteren Perms. Palaeontographica 85 (B1-7): 1938-1944.
7. FULLING, EDMUND H. Identification, by leaf structure, of the species of *Abies* cultivated in the U. S. Bull. Torrey Bot. Club 61: 497-524. 1934.
8. GRIFFIN, E. M. Conifer leaves with regard to transfusion tissue and to adaptation to environment. Transactions of the New Zealand Institute 40: 43-72. 1907.
9. LANJOUW, J. On the standardization of herbarium abbreviations. Chronica Botanica, 5: 142-150. 1939.
10. MAHLERT, ADOLPH. Beiträge zur kenntnis der Anatomie des Laubblätter der Coniferen mit besonderer Berücksichtigung des Spaltöffnungs-Apparates. Bot. Centralbl. 24: 54-59, 85-88, 118-122, 149-153, 180-185, 214-218, 243-249, 278-282, 310-312. 1885.
11. ORR, M. Y. The leaf anatomy of *Podocarpus*. Trans. Proc. Bot. Soc. Edinburgh 34 (1): 1-54. 2 plates. 1944.
12. PILGER, R. Taxaceae. Engler Pflanzenr. IV. 5 (Heft 18): 1903.
13. ———. Coniferae. Nat. Pflanzenfam. ed. 2, 13: 1926.
14. WASSCHER, J. The genus *Podocarpus* in the Netherlands Indies. Blumea 4: 359-481. 1941.
15. WILDE, MARY L. A new interpretation of coniferous cones. I. Podocarpaceae. Ann. Bot. n.s. 8: 1-41. 1944.
16. WORSDELL, W. C. On "transfusion tissue": its origin and function in the leaves of gymnospermous plants. Trans. Linn. Soc. (Second series) 5: 301-319. 1897.

## EXPLANATION OF FIGURES

All photomicrographic illustrations of leaf sections for this investigation were made from unstained leaf sections cut free hand from the leaves of herbarium specimens, mounted in glycerine. Figures 11 and 12 showing the presence and absence of the Florin ring (Fl) are exceptions which were removed after maceration and stained with safranin, mounted in balsam, outer side up and photographed under high magnification.

SYMBOLS: *e*, epidermis; *h*, hypoderm; *sc*, sclerid; *p*, palisade tissue; *r*, resin canal; *tr*, transfusion tissue; *act*, accessory transfusion tissue; *Fl*, Florin ring.

## PLATE I

FIG. 1. *Podocarpus Cummingii* Parl. R. M. Holman 0004 (DS). Transverse section of leaf showing epidermis and hypoderm interrupted by stomates on both sides of leaf. This leaf is flattened vertically and has stomates in rows of 2-5 on 4 sides. Resin canal (*r*) beneath vascular bundle is large, bundle has a very small amount of transfusion tissue at the right and left and there is no accessory transfusion tissue. × 48.



FIG. 2. *Podocarpus amarus* Blume. C. E. Lane-Poole s.n. (A). Transverse section of central portion of leaf, showing absence of hypoderm with palisade layer abutting heavily cutinized epidermis. The large vascular bundle shows well developed transfusion tissue (*tr*) and accessory transfusion tissue (*act*), the latter extending to the margin of the leaf.

The air chambers found below near the resin canal (*r*) might be confused as additional resin canals, which our sections have usually shown to be single. Stomates are confined to lower (abaxial) surface.  $\times 48$ .

FIG. 3. *Podocarpus falcatus* (Thunb.) R.Br. Whitford 27 (US). Transverse section of leaf showing epidermis and hypoderm (*h*) interrupted above and below except at margins and midvein, with large wing-like expansions of transfusion tissue (*tr*) extending nearly halfway to leaf margin but without traces of accessory transfusion tissue. Vascular sclerids are shown above and below bundle and a single resin canal (*r*) near phloem. Stomates are equally distributed on both sides of leaf.  $\times 48$ .

FIG. 4. *Podocarpus Rospiglosii* Pilger. Archer 541 (US). Transverse section of lower portion of half of leaf, showing epidermis and interrupted hypoderm. There are stomates on both sides of leaf. The vascular bundle with 3 resin canals (*r*) below, shows (as in FIG. 3) wing-like expansions of transfusion tissue (*tr*) and is likewise without accessory transfusion tissue.  $\times 48$ .

FIG. 5. *Podocarpus elongatus* L'Herit. Transverse sections of midvein and half of leaf showing epidermis (*e*), hypoderm (*h*) continuous above, interrupted below where the stomates are found. Vascular bundle shows a single resin canal with well developed vascular sclerids below phloem. Transfusion tissue (*tr*) is found on each side of vascular bundle; accessory transfusion tissue (*act*) extends toward margin of leaf where a marginal resin canal (*r*) may be seen.  $\times 48$ .

FIG. 6. *Podocarpus Totara* D. Don. R. J. Matthews s.n. (UC). Transverse section of half of leaf showing continuous hypoderm above, interrupted below, where the stomates are found. The palisade tissue is developed only on upper side. There are no accessory sclerids of any kind; resin canal (*r*) is single near vascular bundle; transfusion tissue (*tr*) is present at left and right of bundle but no accessory transfusion tissue is present; instead the mesophyll cells are slightly elongated.  $\times 48$ .

## PLATE II

FIG. 7. *Podocarpus montanus* var. *meridensis* Buchh. & Gray. Klugh s.n. (Ven). Transverse section of central portion of leaf showing epidermis, absence of hypoderm, and well developed palisade tissue bordering directly upon epidermis. Stomates are confined entirely to lower surface of leaf. Vascular bundle has no sclerids; has only small areas of transfusion tissue (*tr*) and no accessory transfusion tissue or sclerids of any kind. This leaf has a groove above midvein, much more open in this variety than in most leaves of the *montanus* group.  $\times 48$ .

FIG. 8. *Podocarpus macrophyllus* (Thunb.) D. Don. Cult. Jamaica. Transverse section of central portion of leaf showing hypoderm above and below, interrupted above where there are no stomates and absent below except at leaf margin and beneath midvein. Vascular bundle with transfusion tissue (*tr*) and well developed accessory transfusion tissue (*act*) which extends to margin of leaf. There are three resin canals (*r*) beneath vascular bundle but no vascular sclerids or other accessory sclerids.  $\times 48$ .

FIG. 9. *Podocarpus oleifolius* (?) Steyermark 53431. Transverse section of leaf at one side of vascular bundle, showing epidermis and continuous hypoderm above (at right) interrupted hypoderm below (at left) where stomates are confined, and accessory transfusion tissue (*act*) at center. The palisade tissue shows several palisade and accessory sclerids (*sc*) in mesophyll below palisade layer.  $\times 48$ .



FIG. 10. *Podocarpus nubigenus* Lindl. *C. Junger* 73 (Mo). Transverse section near vascular bundle showing hypoderm continuous above, below only at midvein and interrupted elsewhere below where stomates occur; a single resin canal (*r*) beneath vascular bundle, with transfusion tissue on each side but no accessory transfusion tissue. In the position of the latter several large sclerids (*sc*) are shown.  $\times 48$ .

FIG. 11. *Podocarpus oleifolius* (?) *Steyermark* 53431. Part of lower epidermis after maceration stained and mounted under high magnification, showing the Florin ring (*Fl*) a thin furrow giving a non-staining circle in the cuticular layer above subsidiary cells.  $\times 212$ .

FIG. 12. *Podocarpus novae-caledoneae* Vieill. *Franc* 96 (LA). Lower epidermis, same treatment as FIG. 11 showing absence of Florin ring.  $\times 212$ .

FIG. 13. *Podocarpus Harmsianus* Pilger. *Fendler* 1289 (Ph.). Specimen from lectotype collection showing leaves with ridge above midvein.  $\times 2/3$ .

#### PLATE III\*

FIGS. 14-16. *Podocarpus utilior* Pilg. FIGS. 14 and 15 parts of photograph of type specimen *Weberbauer* 2114 (F) enlarged to natural size. FIG. 16 *Soukup* 1802 (Ill) bearing female cones.

FIG. 17. *Podocarpus Harmsianus* Pilg. *Viereck* in Dec. 1922 (US) showing female cones and numerous ovules near time of pollination, mature seeds and leaves with ridge above midvein.

FIG. 18. *Podocarpus montanus* (Willd.) Lodd. *I. F. Holton* in 1854 (NY) showing leaves with groove above midvein and spicate arrangement of pollen cones.

FIG. 19. *Podocarpus montanus* var. *meridensis* Buchh. & Gray. *Steyermark* 57103 type (Ill.) Leaves have groove above midvein (lower sides shown here) and seeds borne at ends of leafy branches.

#### PLATE IV\*

FIG. 20. Logging operations at Oxapampa, Peru, showing very large trees, presumably *P. utilior* Pilg. Photo. supplied by J. Soukup.

FIGS. 21-23. *Podocarpus Harmsianus* Pilg. FIG. 21 *Jahn s.n.* (US). Nor Leon (near Tovar in Aragua) female cones past time of pollination with ovules dropped away, only one subterminal ovule remaining, the special branch having scale leaves. FIG. 22 *Tamayo* 1575 (Ven.) from a cultivated specimen, at Tovar in Aragua (type locality) showing crestless seed appearing terminal, actually sub-terminal. This twig exposes lower sides of leaves. FIG. 23 *Viereck* in Dec. 1922 (US) from Colombia for comparison with FIG. 8.

FIGS. 24-25. *P. montanus* (Willd.) Lodd. FIG. 24 *Steyermark* 54472 (Ill) from Ecuador near Loja showing large leaves with groove above midvein, fruiting branch with seed in terminal position and detached seeds.

FIG. 25. Seeds with flat crests, same collection (F).

FIG. 26. *Podocarpus andinus* Poeppig. Seeds from packet of *Phillipi* in 1888 (NY).

FIGS. 27-31. *Podocarpus montanus* var. *densifolius* (Kunth) Buchh. & Gray.

FIG. 27. *Purdie s.n.* (NY) showing leafy reproductive branch bearing 2 double crested ovules and a full grown seed with 2 distinct blunt crests.

FIG. 28. *Pennell* 2436 (NY) showing foliage. Seeds from western Venezuela.

\*All figures 7/8 natural size.



FIG. 29. *Delgado* 366 (Ven.). FIG. 30 *Klugh* (Ven.). FIG. 31 *Steyermark* 57103.

FIGS. 32-34. *Podocarpus Standleyi* Buchh. & Gray. FIG. 32 *Tonduz* 10743 (US) showing leaves and female cone, clothed with scales rather than leaves. FIG. 33 *Tonduz* 10333 *type* (US), seed with crest and conical cylindrical spine. FIG. 34 *J. D. Smith* 6857 (US) showing large leaves with lower surface glaucous.

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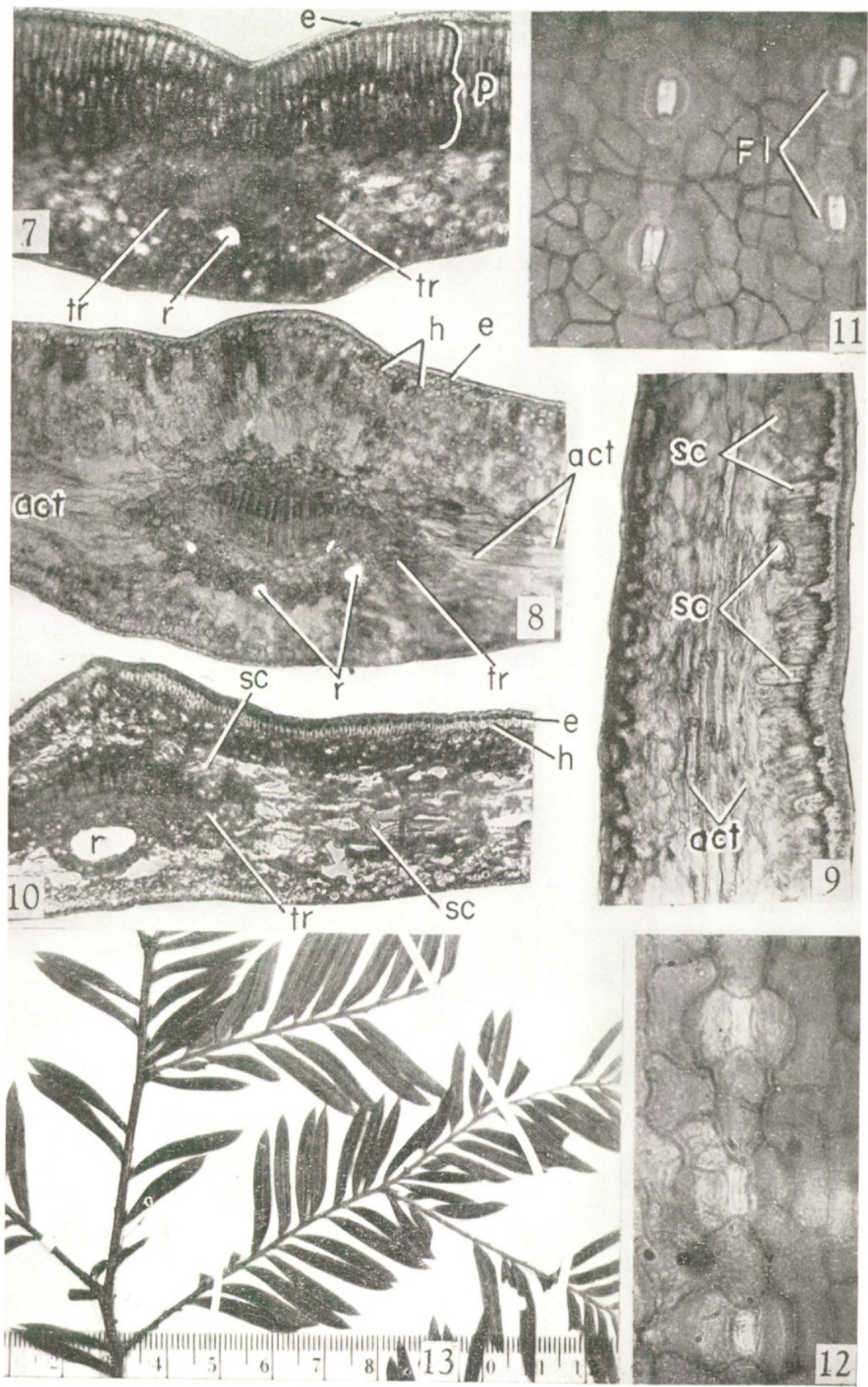
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Buchholz, J. T. and Gray, Netta E. 1948. "A Taxonomic Revision of Podocarpus: II. the American Species of Podocarpus: Section Stachycarpus." *Journal of the Arnold Arboretum* 29(1), 64–76. <https://doi.org/10.5962/p.185590>.

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