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NEW AND MAINTAINED GENERA IN THE CONIFER FAMILIES PODOCARPACEAE AND PINACEAE

C. N. PAGE

ABSTRACT. The taxonomic status of various genera of Coniferae in the Podocarpaceae and Pinaceae is considered. The genera *Nageia* Endl., *Afrocarpus* (Buchh. & Gray) C. N. Page, stat. nov. (Podocarpaceae), *Cathaya* Chun & Kuang and *Hesperopeuce* Lemmon (Pinaceae) are maintained, whilst new genera proposed are *Sundacarpus* (Buchh. & Gray) C. N. Page, stat. nov. and *Retrophyllum* C. N. Page, gen. nov. (Podocarpaceae) and *Nothotsuga* Hu ex C. N. Page, gen. nov. (Pinaceae). The hybrid formula at generic level x *Hesperotsuga* C. N. Page, nothogen. nov. is proposed for hybrids of intergeneric status between *Hesperopeuce* Lemmon and *Tsuga* Carr., typified by *Hesperopeuce mertensiana* (Bong.) Rydb. x *Tsuga heterophylla* (Raf.) Sarg. Inter-generic affinities of the groups in question are discussed.

INTRODUCTION

Recent general accounts of conifer species (e.g. Gaussen, 1966–67, 1974; Callen, 1976; Mitchell, 1972; Silba, 1984, 1986; Krussmann, 1985; Rushforth, 1987) or of species of major conifer genera (e.g. Ostenfeld & Larsen, 1930; Little, 1952, Critchfield & Little, 1966; Mirov, 1967; Liu, 1971, 1982; Whitmore, 1980; Silba, 1981; Farjon, 1984; de Laubenfels, 1985) show that specific delimitations in many major groups of Coniferae are relatively well defined, to which only a few new species have been added in recent years (e.g. Bailey, 1970, 1987; Page & Rushforth, 1980; Grierson, Long & Page, 1980; de Laubenfels & Silba, 1987).

Despite the relatively complete knowledge of species descriptions in conifers, much less is known about interrelationships between species. Further, apart from the particularly valuable major contributions of Florin (e.g. Florin, 1931, 1951, 1963), there have been rather few taxonomic studies in conifers directed mainly towards problems at generic level. Thus the generic status especially of some of the smaller and more geographically obscure taxa has remained more uncertain, and knowledge of their generic interrelationships rather little explored.

The following account results from attempts to consider the possible affinities and taxonomic status that should be accorded to some of the smaller taxa in the Podocarpaceae and Pinaceae, from the standpoint of the Coniferae as a whole, making changes where necessary to try to achieve evolutionarily more natural generic groupings.

These proposals support and validate the nomenclature adopted elsewhere (Page, in press).

PODOCARPACEAE

Taxonomic activity in the last quarter-century or so has done much to recognize separate generic entities within the largely tropical conifer family Podocarpaceae (e.g. Buchholz & Gray, 1948; Garden & Johnson, 1950; Gray & Buchholz, 1951; Gray, 1953; Florin, 1958, 1963; Hair & Beuzenberg, 1958; Gaussen, 1970, 1974; de Laubenfels, 1969, 1978a, 1985, 1987; Quinn, 1982) and a number of small genera (e.g. *Microstrobos*, *Prumnopitys*, *Acmopyle*, *Dacrycarpus*, *Falcatifolium*, *Parasitaxus*, *Halocarpus*, *Lepidothamnus*, *Lagarostrobos*) are mostly recognized in subsequent lists and floras (e.g. Wasscher, 1941; de Laubenfels, 1972, 1978b; Silba, 1984, 1986; Rushforth, 1987; Page, in press). The diagnoses of many of these genera often depend heavily on vegetative aspects of the plants, in a group whose reproductive aspects offer a rather limited array of features. Most, nevertheless, appear to be fairly natural groupings which prove to have good geographic and probably evolutionary cohesion. There is also support for many of these divisions from independent approaches including cytology (e.g. Hair & Beuzenberg, 1958; Hair, 1963) and phytochemistry (e.g. Quinn & Gadek, 1981; Markham et al., 1985).

The following proposals aim to recognize four other groups of this nature in the Podocarpaceae, at similar, generic rank.

Sundacarpus (Buchh. & Gray) C. N. Page, **stat. nov.**

Basionym: *Podocarpus* sect. *Sundacarpus* Buchh. & E. Gray in J. Arn. Arb. 29:57 (1948).

Syn.: *Stachycarpus* sect. *Sundacarpus* (Buchh. & E. Gray) Gaussen in Trav. Lab. For. Toulouse 2(1):107 (1974) (comb. inval.).

Prumnopitys sect. *Sundacarpus* (Buchh. & E. Gray) de Laub. in Blumea 24:190 (1978).

Type: *Sundacarpus amara* (Blume) C. N. Page.

A monoecious, columnar, evergreen tree, of ultimately very large size and rapid growth, with distantly-spaced, ascending or horizontally spreading branches, of markedly whorled habit when young. Leaves flattened, with narrowly downcurved margins, linear to linear-elliptic, straight, large, 55–150 × 8–14mm, cuneately narrowed at the base into a short petiole and with a short, elongate obtuse-tipped caudate-acuminate distal prolongation of the leaf tip, particularly marked in young plants, the midrib single, grooved above and prominent below the leaf, with two pale-coloured lengthwise stomatal bands below; the leaves distant, spirally arranged on leading shoots but regularly pectinate in alternating ranks on lateral shoots, the leaves articulated to the shoots at abscission zones from which they are regularly shed, leaving smooth, rounded leaf scars. Branches mostly patent, the branchlet systems horizontally flattened and articulated at their basal junctions.

Male clones clustered in small groups of 3–5 or more, on short, naked, axillary peduncles, ovoid-cylindric, tapering, 6–30 × 2–3·5mm, surrounded at the base by sterile scales. Pollen with 2 air-bladders. Female cones solitary or in twos or threes, mostly terminal on long, naked, axillary branchlets articulated to the main axis, fleshy, drupe-like, 12–15 × 10–11mm, with a minutely asymmetrically apiculate apex, bloomed blue-black at maturity, subtended by several diminutive but not fleshy scales, and lacking an inflated receptacle.

A monotypic genus, from Sumatra and the Philippines to north Queensland and New Ireland.

Sundacarpus amara (Blume) C. N. Page, **comb. nov.**

Basionym: *Podocarpus amara* Blume, Enum. Pl. Java 88 (1827); *Prumnopitys amara* (Blume) de Laub., Blumea 24:190 (1978).

Syn.: *Podocarpus eurhyncha* Miquel, Fl. Ind. Bot. 2:1074 (1856).
Podocarpus pedunculata Bailey in Qld. Ag. J. 5:390 (1899).

De Laubenfels (1978a) discussed the nomenclatural history of *Podocarpus amara* Blume and separated this taxon from *Podocarpus*, where it had been grouped as the separate monotypic section *Sundacarpus* of *Podocarpus* by Buchholz & Gray (1948). De Laubenfels rightly recognized that the taxonomic position of *Podocarpus amara* needed to be reassessed, and transferred it to the genus *Prumnopitys* Phillippi, making it a separate monotypic section *Sundacarpus* (Buchh. & E. Gray) de Laub. of that genus. Further descriptive details of this species are given by Wasscher (1941) and de Laubenfels (1978b).

Sundacarpus seems, however, a morphologically highly distinctive taxon which is well worthy of separate generic rank. It differs from *Podocarpus* especially in the lack of the inflated fleshy receptacle in the female cone characteristic of *Podocarpus*, as well as in its unique vegetative structure. The latter, with large, linear to linear-elliptic leaves, which are regularly pectinately arranged in alternating ranks on lateral shoots, to which they are articulated by pronounced abscission zones, leaving large, rounded leaf scars, also distinguishes *Sundacarpus* clearly from *Prumnopitys*.

Retrophyllum C. N. Page, **gen. nov.**

Syn.: *Podocarpus* sect. *Polypodiopsis* Bertrand in Ann. Sci. Nat. V. 20:65 (1874).
Decussocarpus de Laub. in J. Arn. Arb. 50:340 (1969), nom. illeg. (Art. 63).
Decussocarpus sect. *Decussocarpus* de Laub. in J. Arn. Arb. 50:341 (1969).
Nageia sect. *Polypodiopsis* (Bertrand) de Laub. in Blumea 32:210 (1987).

Type: *Retrophyllum vitiense* (Seeman) C. N. Page.

Arbores parvae vel magnae. Folia unicostata, amphistomatica, in ramulis lateralibus in series duas patentar et pectinatim disposita, ea unae seriei peiolo contorto inverta, ea alterae seriei normalia. Coni feminei receptaculis carnosis carentes.

Dioecious, mostly columnar, large to very small evergreen trees, of ± rhythmic growth. Leaves on leading shoots mostly highly reduced, those on lateral shoots flattened, small, c.6–25 × 2·5–5mm and up to 5 times as long as broad on adult branches, larger on juvenile plants, lanceolate to ± narrowly-ovate, amphistomatic, each with a slender midrib, thick, fleshy-coriaceous, rigid, narrowed abruptly to an acute-acuminate spinose apex, sessile and sharply narrowed to a decurrent base, crowded, spirally arranged on leading shoots and ± obliquely inserted into opposite-subopposite and decussate, spreading, regular pectinate rows on lateral shoots, the petioles twisting through c.90°, the twists uniquely in opposite directions on opposite sides of each lateral axis failing to form a mirror-image of each other, the branchlet systems flattened, pinnate, each seasonal segment of elongate and strongly linear outline.

Male cones usually single or in groups of 2–5, mostly on short, naked, axillary peduncles or also at the apex of minor foliage branchlets, elliptic-cylindric with ± apiculate apex, 6–10 × c.2mm, surrounded at the base by a few sterile scales. Pollen with 2 air-bladders. Female cones solitary or occasionally paired, each terminal on short, naked, axillary branchlets or terminal on foliage branchlets, fleshy, drupe-like, ovoid-pyriform, with a ± apiculate apex, c.12–20 × 8–18mm, bloomed dark red-violet at maturity, subtended by several diminutive scales, swollen receptacles absent.

As construed here, a small genus of five or more species, two in New Caledonia, one in Fiji and at least two in South America (Peru, Colombia, Venezuela and west Brazil).

Retrophyllum vitiense (Seem.) C. N. Page, **comb. nov.**
Basionym: *Podocarpus vitiensis* Seeman in J. Bot. 1:33 t. 2 (1863).
Syn.: *Nageia vitiensis* (Seeman) O. Kuntze in Rev. Gen. Pl. 2:800 (1891).
  Decussocarpus vitiensis (Seeman) de Laub. in J. Arn. Arb. 50:347 (1969).

Retrophyllum comptonii (Buchh.) C. N. Page, **comb. nov.**
Basionym: *Podocarpus comptonii* Buchh. in Bull. Mus. Hist. Nat. Paris, sér. 2, 21:284 (1949).
Syn.: *Decussocarpus comptonii* (Buchh.) de Laub. in J. Arn. Arb. 50:341 (1969).
  Nageia comptonii (Buchh.) de Laub. in Blumea 32:211 (1987).

Retrophyllum minor (Carr.) C. N. Page, **comb. nov.**
Basionym: *Nageia minor* Carr., Traite Gen. Conif. ed. 2:641 (1867).
Syn.: *Podocarpus minor* (Carr.) Parl., DC. Prodr. 16:509 (1868).
  Decussocarpus minor (Carr.) de Laub. in J. Arn. Arb. 50:346 (1969).
  P. palustris Buchh. in Bull. Mus. Hist. Nat. Paris, sér. 2, 21:284 (1949).

Retrophyllum piresii (Silba) C. N. Page, **comb. nov.**
Basionym: *Decussocarpus piresii* Silba in Phytologia 54:461, t. 1 (1983).
Syn.: *Nageia piresii* (Silba) de Laub. in Blumea 32:211 (1987).

Retrophyllum rospigliosii (Pilg.) C. N. Page, **comb. nov.**
Basionym: *Podocarpus rospigliosii* Pilger in Notizbl. Bot. Gard. Berlin 8:273 (1923).
Syn.: *Decussocarpus rospigliosii* (Pilger) de Laub. in J. Arn. Arb. 50:347 (1969).
  Nageia rospigliosii (Pilger) de Laub. in Blumea 32:211 (1987).

Retrophyllum is a particularly distinctive and apparently highly natural genus, differing from all other members of the Podocarpaceae in its unique vegetative features, with reduced and inclined leaves on leading shoots and those on lateral shoots photosynthetically dominant. The pectinate leaf arrangements, with petioles which twist to orientate the leaves on one side of each shoot with the adaxial surfaces uppermost, whilst on the opposite side of the same shoot, the leaves are arranged with their adaxial surfaces downwards, thus failing to form mirror images of one another, is a curious feature unique not only in the Podocarpaceae, but, indeed, in the Coniferae as a whole.

Retrophyllum has n = 10 chromosomes, thus also differing cytologically from the taxa with which it has been previously grouped: *Nageia* with n = 13 and *Afrocarpus* with n = 12 (Hair, 1963; Hair & Beuzenberg, 1958; Quinn, 1970).

The generic name *Decussocarpus* was proposed by de Laubenfels (1969) for a genus that included *Podocarpus vitiensis* Seem. as its type, within which de Laubenfels separated the species recognized here as *Retrophyllum* as his section *Decussocarpus*. Later, de Laubenfels (1987) adopted the earlier name *Nageia* for this genus. The name *Decussocarpus* is thus a *nomen superfluum* and can therefore, regrettably, not be used for the genus here defined, for which the name *Retrophyllum* is here proposed, reflecting the unique vegetative morphology of this genus.

Nageia Gaertner, De Fruct. et Sem. 191 (1788).
Basionym: *Podocarpus* sect. *Nageia* Endl., Syn. Conif. 207 (1847).
Syn.: *Podocarpus* sect. *Dammaroideae* Bennett, Pl. Jav. Rar. 41 (1838).
Decussocarpus sect. *Dammaroides* (Bennett) de Laub. in J. Arn. Arb. 50:348 (1969).
Nageia sect. Nageia de Laub. in Blumea 32:209 (1987).
Type species: *Nageia nagi* (Thunb.) O. Kuntze.

Monoecious or mostly dioecious, columnar, evergreen trees, of ± non-rhythmic growth. Leaves, including those on leading shoots large, flattened, broadly ovate-elliptic to oblong-lanceolate, amphistomatic or hypostomatic, each without a central midrib but with many fine parallel lengthwise veins converging towards the apex, thick, coriaceous, usually ± rigid, cuneatly narrowed at the base into a short petiole, and narrowed at the tip into a subobtuse or acuminate apex, distant, spirally arranged or in decussate pairs on leading shoots, opposite-subopposite and spreading on lateral shoots, the petioles twisting through 90°, the twists normally forming a mirror-imge of each other on opposite sides of lateral axes, the shoots with annual resting buds with acute scales.

Male cones single or clustered in small spicate groups of 3–6 on short, naked, axillary peduncles, ovoid-cylindric, 7–19 × 5–7mm, surrounded at the base by sterile scales. Pollen with 2 air-bladders. Female cones solitary or occasionally in twos, each terminal on short, naked, axillary branchlets, ovule inverted and enveloped by the fleshy fertile scale, becoming drupe-like, globose, up to 20mm diam., bloomed blue-black at maturity, subtended by several diminutive dry or slightly fleshy scales; the receptacle usually scarcely thicker than the peduncle, or rarely more so and somewhat fleshy.

As defined here, *Nageia* appears to be a very natural and coherent genus, widely scattered from north-east peninsular India, south-east China (Kwangtung, Chekiang, Fukien), Taiwan, Hainan Island, Okinawa, Ryukyu Islands and southern Japan, Thailand, Cambodia, Indo-China, southward through Malaysia, Philippines, Moluccas, Sarawak, Borneo to New Guinea and New Britain.

Nageia nagi (Thunb.) O. Kuntze in Rev. Gen. Pl. 2:798 (1891).
Basionym: *Myrica nagi* Thunb., Fl. Japon 76 (1784).
Syn.: *Podocarpus nageia* R. Br. ex Mirbel in Mem. Mus. Paris 13:75 (1825).
Podocarpus nagi (Thunb.) Makino in Bot. Mag. Tokyo 17:113 (1903).
Decussocarpus nagi (Thunb.) de Laub. in J. Arn. Arb. 50:357 (1969).

Nageia formosensis (Dummer) C. N. Page, **comb. nov.**
Basionym: *Podocarpus formosensis* Dummer in Gard. Chron., ser. 3, 52:295 (1918).
Syn.: *Podocarpus nankongensis* Hayata in Ic. Pl. Formosana 7:39 (1918).
P. koshuensis (Kaneh.) Kaneh., Formos. Trees (rev. ed.) 36 (1926).

Nageia wallichiana (Presl) O. Kuntze in Rev. Gen. Pl. 2:800 (1891).
Basionym: *Podocarpus wallichianus* Presl, Bot. Bemerk. 110 (1844).
Syn.: *Decussocarpus wallichianus* (Presl) de Laub. in J. Arn. Arb. 50:349 (1969).

Nageia motleyi (Parl.) de Laub. in Blumea 32:210 (1987).
Basionym: *Dammara motleyi* Parlatore, Enum. Sem. Hort. Bot. Mus. Florent. 26 (1862).
Syn.: *Agathis motleyi* (Parl.) Warburg in Monsunia 1:185 (1900).
Podocarpus motleyi (Parl.) Dummer in J. Bot. 52:240 (1914).
Decussocarpus motleyi (Parl.) de Laub. in J. Arn. Arb. 50:352 (1969).

Nageia maximus (de Laub.) de Laub. in Blumea 32:210 (1987).
Basionym: *Decussocarpus maximus* de Laub. in J. Arn. Arb. 50:353 (1969).

Nageia fleuryi (Hickel) de Laub. in Blumea 32:210 (1987).
Basionym: *Podocarpus fleuryi* Hickel in Bull. Soc. Dendrol. France 75:75 (1930).
Syn.: *Decussocarpus fleuryi* (Hickel) de Laub. in J. Arn. Arb. 50:355 (1969).

Nageia differs from all other Podocarpaceae in its distinctive, broadly-lanceolate multi-veined leaves which are unique in conifers. It differs from *Retrophyllum* not only in this character, but also in lacking the unique and unusual opposing petiole rotations of *Retrophyllum*, the leaves of *Nageia* forming mirror-images on opposite sides of each lateral shoot, and in the tendency in a few species towards having somewhat fleshy receptacles to the female cones. Its annual growth is much less rhythmic and less morphologically differentiated than is that of *Retrophyllum*, and the leaves on leading shoots are unreduced and photosynthetically functional, unlike those of *Retrophyllum*.

Its cytological distinction from other allied genera is also substantial. *Nageia* has $n=13$ chromosomes, thus differing from *Retrophyllum* with n = 10 and *Afrocarpus* with n = 12 (Hair, 1963; Hair & Beuzenberg, 1958; Quinn, 1970).

The name *Nageia* has been recently adopted by de Laubenfels (1987) for the genus previously named *Decussocarpus* (de Laubenfels, 1969), which includes the three genera here separated as *Nageia*, *Retrophyllum* and *Afrocarpus*. The name *Nageia* is therefore retained here for that part of the former genus *Decussocarpus* which includes the type of *Myrica nagi* Thunb. (= *Podocarpus nagi* (Thunb.) Makino), after the species of *Retrophyllum* and *Afrocarpus*, as here defined, have been excluded.

Afrocarpus (Buchh. & E. Gray) C. N. Page, **stat. nov.**
Basionym: *Podocarpus* sect. *Afrocarpus* Buchh. & E. Gray. in J. Arn. Arb. 29:57 (1948).
Syn.: *Decussocarpus* sect. *Afrocarpus* (Buchh. & E. Gray) de Laub. in J. Arn. Arb. 50:224 (1969).
Nageia sect. *Afrocarpus* (Buchh. & Gray) de Laub. in Blumea 32:211 (1987).
Type: *Afrocarpus falcata* (Thunb.) C. N. Page.

Dioecious, columnar, tall evergreen trees. Leaves flattened, leathery, narrowly lanceolate-elliptic, amphistomatic, each with a single midrib, and single resin canal, long, tapering, 25–150 × 5–15mm, thick, hard, coriaceous, with acute acuminate apices, spirally to subopposite or decussately arranged, and generally spreading or sometimes assurgently arranged all around the shoots, the petioles twisting through 90°, the twists forming a mirror-image of each other on opposite sides of lateral axes. Branchlets often square in section and deeply ridged.

Male cones solitary or more rarely in groups of 2–3, on short, naked, axillary peduncles, 10–30 × 2–4mm, surrounded at the base by a small number of sterile scales. Pollen with two air-bladders. Female cones solitary, each terminal on a short, naked or leafy axillary branchlet, thinly fleshy or shining, subglobose to obovoid, c.10–20mm diam., bloomed yellow green to purple-black at maturity, inserted directly on the peduncle, subtended by several diminutive or sometimes spreading scales, the whole structure lacking an inflated receptacle, the outer layer of the seed coat forming a hard and woody shell at maturity.

A genus from equatorial Africa (Congo, Ethiopia and Uganda) discontinuously southward to south and south-east Africa and the Cape.

Afrocarpus falcata (Thunb.) C. N. Page, **comb. nov.**
Basionym: *Taxus falcata* Thunb., Prod. Pl. Capensis 117 (1800).
Syn.: *Podocarpus falcatus* (Thunb.) R. Br. ex Mirb. in Mem. Mus. Hist. Nat. Paris 13:75 (1825).
Nageia falacata (Thunb.) O. Kuntze in Rev. Gen. Pl. 2:800 (1891).
Decussocarpus falcatus (Thunb.) de Laub. in J. Arn. Arb. 50:359 (1969).

Afrocarpus gracilior (Pilger) C. N. Page, **comb. nov.**
Basionym: *Podocarpus gracilior* Pilger in Pflanzenr. IV, 5, Heft 18:71 (1903).
Syn.: *Decussocarpus gracilior* (Pilger) de Laub. in J. Arn. Arb. 50:359 (1969).

Afrocarpus mannii (Hook. f.) C. N. Page, **comb. nov.**
Basionym: *Podocarpus mannii* Hook. f. in J. Linn. Soc. 7:218 (1864).
Syn.: *Nageia mannii* (Hook. f.) O. Kuntze in Rev. Gen. Pl. 2:800 (1891).
Decussocarpus mannii (Hook. f.) de Laub. in J. Arn. Arb. 50:359 (1969).

Afrocarpus usambarensis (Pilger) C. N. Page, **comb. nov.**
Basionym: *Podocarpus usambarensis* Pilger, Pflanzenreich IV 5 (Heft 18):70 (1903).

Afrocarpus dawei (Stapf) C. N. Page, **comb. nov.**
Basionym: *Podocarpus dawei* Stapf, Fl. Trop. Afr. 6(2):342 (1917).

Afrocarpus gaussenii (Woltz) C. N. Page, **comb. nov.**
Basionym: *Podocarpus gaussenii* Woltz in Bull. Soc. Bot. Fr. 116:349 (1969).

The adoption of *Afrocarpus* at generic rank and the combinations of the six above-cited species into this genus were earlier proposed by Gaussen (1974). All, however, were invalidly published (see *Index Kewensis* suppl. 16, p.12, 1981).

The species of *Afrocarpus*, all endemic to the African continent, have always been in a somewhat anomalous position in the Podocarpaceae. Older treatments simply group them all as *Podocarpus*, but modern treatments define *Podocarpus* as having fleshy receptacles to the female fruit, which the species of *Afrocarpus* do not. In lacking this character, they resemble *Retrophyllum* and most species of *Nageia*, but differ from both these genera quite strongly in vegetative characters, which seem much more akin to those of *Podocarpus*, for they lack the unusual fine parallel venation of *Nageia* and the small, curiously rotated leaves of *Retrophyllum*, whilst also differing from *Podocarpus* in seedling morphology and anatomy (Ferre et al., 1975).

The cytological distinction of *Afrocarpus* from other allied genera is also substantial. *Afrocarpus* has $n=12$ chromosomes, differing from *Retrophyllum* with $n=10$, *Nageia* with $n=13$ and the African species of *Podocarpus* with $n=11$ (Hair, 1963, Hair & Beuzenberg, 1958, Quinn, 1970).

De Laubenfels (1969) separated all the podocarps typified by mainly non-fleshy peduncles and mostly amphistomatic leaves from *Podocarpus* as the single genus *Decussocarpus*, while later (de Laubenfels, 1987) changing the name of the whole group to the earlier name *Nageia*. Such a generic unity of the separated African members with the Malesian and Indo-Pacific ones has, however, met with little recognition by botanists concerned principally with African trees or vegetation (e.g. Palmer & Pitman, 1972; Lind & Morrison, 1974; Moll, 1981; Hilliard, 1985). This view is perhaps not surprising when the similarity in general tree form and vegetative appearance of the African members to the remaining species of true *Podocarpus* within that continent is considered. Indeed, the species grouped here as *Afrocarpus* are in some respects intermediate in taxonomic position between *Podocarpus*, as typified by the African species, and *Nageia* and *Retrophyllum*, whilst in other respects, differing sharply from both. In lacking the highly specialized, but different, leaf morphologies of *Nageia* and *Retrophyllum*, as well as the fleshly peduncle and hypostomatic leaves of *Podocarpus*—themselves probably evolutionarily advanced features (the fleshly peduncle related to improved animal disperal)—*Afrocarpus* seems, in my view, to reflect the least specialized condition of any, both in its vegetative and reproductive features. It also has the chromosome base number considered by Stiff (1952) to be the most primitive within the family. I thus propose that the phylogenetically most realistic treatment is to group the species of *Afrocarpus* as a section of neither *Podocarpus*, *Retrophyllum* nor *Nageia*, but to treat *Afrocarpus* as a distinctive genus in its own right, which is phylogenetically primitive to these other genera. Its modern distribution, entirely African, would suggest *Afrocarpus* to be a relict genus of gondwanan origin.

PINACEAE

Although most genera of the Pinaceae are well-defined and widely accepted, there has been a particular lack of general agreement concerning the affinities and homogeneity of the near allies of *Tsuga*, including the genera recognized here as *Cathaya*, *Nothotsuga* and *Hesperopeuce*.

One view (e.g. Silba, 1984, 1986) is to group all these taxa into the single genus *Tsuga*. Taxonomically their fit into this genus seems, however, uncomfortable, making the genus complex to define by the inclusion of a few species which differ taxonomically from the much larger group of more morphologically uniform taxa. It also seems to greatly oversimplify the probable biological reality of the apparently complex generic interrelationships of the atypical taxa, which seem each to be not the same as those of each other, nor to be the same as are those of other *Tsuga*.

The alternative view, adopted here, is to recognize *Cathaya*, *Nothotsuga* and *Hesperopeuce* as separate genera which, whilst each has some affinity with *Tsuga*, each has also diverse affinities with other pinaceous genera.

The following genera have thus been maintained or are proposed.

Cathaya Chun & Kuang in Bot. Zhur. 43:464 (1958).

Moderately tall, pyramidal, monoecious, evergreen trees. Leaves linear, flattened, flexible, dark green, lustrous above, hypostomatic, 25–50mm long, with finely fimbriate-ciliate margins in juvenile foliage, abundant and spirally arranged, borne from slightly prominent leaf-cushions on long leading shoots; sparse, clustered and ± whorled on short, lateral spur shoots, which include mostly leaves of much shorter length. Winter buds ovoid, obtuse, lustrous, non-resinous.

Male cones solitary or in small groups, oblong-ovoid, large, c.15–25mm or more long, 8–9mm diam., short-stalked or subsessile, terminal on short, lateral spur shoots, subtended by numerous scarious leafy bracts. Pollen with two air-bladders. Female cones maturing in the first year but long-persistent thereafter, spreading or pendulous, solitary, broadly ovoid-oblong, small, 2·5–5cm long with a small number (12–16) of broadly rounded, thinly rigid, concave, persistent, linearly-striated scales; the bracts not protruding beyond the scales at maturity, the peduncles with awl-like, forward-swept leaves which overtop the young cone buds, the seed wings smaller and narrower than those of the corresponding seed-scales.

Cathaya appears to be a distinctive genus within the Pinaceae, endemic to China (Kwangsi, Hunan? and Szechuan), with fossil (Tertiary) representatives also elsewhere. Its sole known living species is *Cathaya argyrophylla* Chun & Kuang (1958).

Cathaya differs from *Tsuga* especially in its sub-dimorphic to dimorphic shoot structure, with much of its foliage clustered and ± whorled on short, lateral, spur shoots, in its grouped male cones, which are also far larger than those of *Tsuga*, and in the possession of 2-bladdered pollen grains, lacking the characteristic frill found throughout the species of *Tsuga*, whilst differing also from the non-winged pollen grains of *Pseudotsuga*.

In tree-habit, *Cathaya* is very pine-like, and indeed Gaussen (1966–67, 1971) has pointed to some intermediacy of *Cathaya* between *Tsuga* and *Pinus*. *Cathaya* has also been suggested to resemble *Pseudolarix* in its shoot morphology, *Keteleeria* in its leaf morphology, and *Pseudotsuga* in its female cone and wood anatomy (Greguss, 1955). Indeed, the female cone scale shape and that of its slightly exerted bracts, are a feature shared between *Cathaya* and only the Chinese species of *Pseudotsuga*, although it differs from this genus especially in pollen morphology and in such vegetative features as its obtuse buds, whilst the awl-shaped leaves surrounding the base of the female cone bud and overtopping it, seem unique to *Cathaya*. The bladdered pollen grain of *Cathaya* is of the *Pinus*-type, and this feature, plus its sub-dimorphic shoot morphology links *Cathaya* and *Hesperopeuce*. On wood structure, Xie (1957, quoted in Hu & Wang, 1984) suggests that *Cathaya* is intermediate between *Pseudotsuga* and *Larix* and Yatsenko-Khmelevsky & Budkevich (1958) consider its wood anatomy closer to *Picea* than to *Pseudotsuga*, whilst showing links, on this evidence, also with *Abies*, *Pinus* and *Larix*. The occasional grouping of the male cones appears to link *Cathaya* with *Keteleeria*, *Nothotsuga* and *Pseudolarix*, whilst the size and shape of the short-stalked male cones is more reminiscent of those of *Abies*, *Picea* and *Pinus*. The bracteate bases to the male cones approach those of *Hesperopeuce*.

This diffuseness of apparent inter-generic links between *Cathaya* and other living genera of Pinaceae, results in lack of close taxonomic fit of *Cathaya* into any other single genus of the family. For these reasons, *Cathaya* is maintained here as a distinctive genus within the Pinaceae.

In describing *Cathaya* as a new genus, Chun & Kuang (1958) also assigned to this genus a Pliocene fossil cone formerly described as *Keteleeria loehri*, whilst subsequently, according to Ferguson (1967), two more European species of *Cathaya* cone and leaf fragment material have been described from Pliocene sediments east of the Black Sea (Svechnikova, 1964). The genus is also known from Tertiary (?Oligocene) deposits of East Germany (H. Walther, pers. comm.), whilst pollen grains which might be this genus are also indicated from Iceland by Einarsson (1963). The past far wider occurrence of *Cathaya* thus seems highly likely.

Hesperopeuce Lemmon in Bienn. Rept. Calif. State Board Forestry 3:126, 69 (1890).

Syn.: *Tsugo-Picea* Campo-Duplan & Gaussen in Trav. Lab. For. Bot. Toulouse 1(4) art. 24: 8 (1948) (nom. illeg.).

Tall, conical or spreading, often massive, monoecious evergreen trees, the branches dense in young trees, massive on old plants. Long and ± short shoots present, minutely to densely pubescent, the short shoots often stout, densely crowded and mostly ascending, bearing much of the vegetative foliage. Leaves long, mostly 12–26mm, ± curved and thick, angular-triangular in section, ± grooved above, the midrib inconspicuous below, acute, simple and blunt or ± bevelled at the tip, narrowed towards the base but scarcely petiolate, mid to dark green, dull, glaucous, amphistomatic, radially arranged and assurgent, set on shining projections with cushion-like bases (pulvini) which are persistent after the leaves fall. Winter buds ovoid, obtuse, lustrous, non-resinous.

Male cones deltoid-globular to conical-campanuloid, eventually long-stalked (c.5mm long) and ± ascending, grouped in ± whorls of 5–12, each axillary in a leaf of the previous season, often coloured, their basal bud scales ultimately widely-spreading, papery and often semi-persistent after the male cones have abscised. Pollen winged. Female cones maturing in first year and shed in second or third year, mostly sub-terminal on long shoots of previous year, solitary, sessile, at first sub-erect, remaining so, or becoming eventually sub-pendulous, ovoid-cylindric, 32–70 × 10–15mm (closed), 23–35mm (open), thus several times longer than broad, with numerous, rounded, leathery or papery linearly striated scales, the scales often densely short-pubescent at first, often becoming strongly recurved at maturity, the bracts long, acute or sometimes slightly lobed, exerted at post-pollination but not protruding beyond the scales at cone maturity.

Thus defined, *Hesperopeuce* is endemic to western North America from southern Alaska to central California, especially at snowline.

Hesperopeuce mertensiana (Bong.) Rydb. in Bull. Torrey Bot. Cl. 39:100 (1912).

Basionym: *Pinus mertensiana* Bong. in Mem. Acad. Sci. St. Petersb. 2:163 (1933), *Abies mertensiana* (Bong.) Lindb. & Gard. in J. Hort. Soc. Lond. 5:211 (1850); *Tsuga mertensiana* (Bong.) Carr., Traite Conif. ed. 2:250 (1867), *Tsugo-Picea hookeriana* (Murr.) van Campo-Duplan & Gaussen (nom. illeg.).

Hesperopeuce differs from *Tsuga* especially in its thick, rather stiff, angular, assurgent amphistomatic leaves, its sub-dimorphic shoot morphology, its long, ovoid-cylindric cones with longer bracts and pubescent scales regularly reflexing at post-maturity, the cones being sub-erect before and long after pollination, with exerted bracts at post-pollination; and the highly tannin-rich, dark, furrowed bark of its trunk which, in wild trees, is much darker than that of most species of *Tsuga*. *Hesperopeuce* also has distinctly-bladdered pollen grains—a feature not found in *Tsuga*.

The links of *Hesperopeuce* with other genera, however, seem particularly diverse and distinctive, to the extent of *Hesperopeuce* occupying a morphologically intermediate position between several genera, no other single one of which it is typical. Van Campo-Duplan & Gaussen (1950) and Gaussen (1966–67) viewed *Hesperopeuce* as sufficiently intermediate between *Tsuga* and *Picea* as to suggest it to be a recent hybrid, citing *Tsuga heterophylla* and *Picea sitchensis* in western North America as its likely parents.

Van Campo-Duplan & Gaussen (1948) also noted the southern populations of *Hesperopeuce mertensiana* as especially distinctive, indicating the possibility that these might represent backcross hybrids of *Hesperopeuce mertensiana* to *Picea*, giving such plants the polynominal *Tsugo-Piceo-Picea crassifolia* (Flous) Van Campo-Duplan & Gaussen (nomen illeg.).

Although, in my view, affinities do exist with both *Tsuga* and *Picea* (and perhaps more with *Picea breweriana* than *P. sitchensis*), the total of affinities of *Hesperopeuce* seem very much more complex and diverse than with just these genera, and the plant to be very much more ancient than a recent hybrid. The papery but semi-persistent basal bud scales to the male cone spreading widely at maturity are reminiscent of those of *Cathaya* and of *Abies bracteata*, primitive within *Abies*, whilst the short, very dense pubescence of the cone scales compares only with that of some *Abies* (*A. lasiocarpa*, *A. procera* and *A. magnifica*) and that of *Cedrus*. The linearly striated scales to the female cone are seen elsewhere in *Cathaya* and *Nothotsuga* as well as in some *Tsuga*, *Pseudotsuga*, *Picea* and *Larix*, whilst the habit of the female cone scales (especially the basal ones) reflexing strongly on maturity, is reminiscent of some *Tsuga* and *Picea* but especially of more primitive *Larix*, which they also more nearly resemble in size. During the brief period of exertion of the bracts beyond the scales of the female cone subsequent to pollination, the form of the cone (which is also erect at this stage) resembles the mature cones of *Nothotsuga*. Most especially, however, in many vegetative aspects, notably in most features of its shoot morphology, including especially its semi-dimorphic, assurgent shoots, leaf texture, structure and arrangement, cone-scale pubescence (noted above), mature tree habit and bark characters, *Hesperopeuce* seems to me consistently to link strongly with *Cedrus*, and perhaps especially with *Cedrus atlantica* and *C. brevifolia*—an inter-generic affinity which seems not to have been hitherto suggested. The freshly-dried cones of *H. mertensiana* have been independently noted to also have a characteristic scent especially similar to that of *Cedrus* heartwood (M. Frankis, pers. comm.). Its unusual snowline ecology (Sudworth, 1908; Franklin & Dyrness, 1973; Arno, 1984) also much more closely parallels that of *Cedrus* and some species of *Pinus* than it does that of any *Tsuga* or most *Picea* (and is approached in America perhaps in the latter genus only by *P. breweriana*).

The taxonomic affinities of *Hesperopeuce mertensiana* thus seem to me to be both diverse and distinctive, with no good taxonomic fit into any other single genus of conifers. To incorporate it into its own genus therefore seems the taxonomically and biologically most realistic way of reflecting this phylogenetic situation.

The variability of its populations, noted by Clausen (1965), might suggest some hybridity, or that present populations of *Hesperopeuce* may be survivors of past wider and more variable ones. The present southern geographic extensions of its range into the Sierra Nevada (Parsons, 1972) suggest that even in America, the range of *Hesperopeuce* may have changed substantially through the Pleistocene (Ritchie, 1984), probably involving major geographic shifts, perhaps including southern montane islands (Wells, 1983), in a manner analogous to that of the *Pinus balfouriana-P. longaeva* group (Bailey, 1970) or *Picea sitchensis* (Page & Hollands, 1987).

An even wider past range of *Hesperopeuce* is, indeed, indicated by fossil evidence. Fossil pollen grains and leaves attributed to *Tsuga* occur as a number of forms in the Tertiary to Lower Pleistocene of Europe (Ferguson, 1967), some of which according to Oszast (1960) appear, on evidence of pollen morphology, to be *T. mertensiana*, and hence the present genus. If so, this genus may have been present in Europe as early as the Miocene, in a vegetation in which it occurred with other now-relict and distantly-scattered conifer genera, including *Sciadopitys*, *Cunninghamia* and *Sequoia*.

There thus seems no reason to regard *Hesperopeuce* as necessarily purely a local hybrid taxon originating recently between extant American species of other genera. Rather, it is relict, with diverse intergeneric affinities.

Such a more ancient origin of *Hesperopeuce* need not rule out, however, the occasional occurrence of hybrids between it and other genera today, a phenomenon which has, and probably still does, play an important role in conifer evolution (Page & Hollands, 1987). The occurrence of single, scattered plants which are probably genuine modern hybrids between *Hesperopeuce mertensiana* (Bong.) Rydb. and *Tsuga heterophylla* (Raf.) Sarg., in the wild and in cultivation, hitherto considered as an interspecific hybrid under the name *Tsuga* × *jeffreyi* (Henry) Henry, would seem to represent such a case, and provide no reason to preclude the recognition of *Hesperopeuce* as a separate genus. Such hybrids are themselves of evolutionary interest, for they seem to be relatively common in nursery-raised seed from wild *Hesperopeuce mertensiana*. The very slow growth of such hybrid plants and their considerable lack of heterosis perhaps indicates very poor competitive survival rates under field conditions, as well as considerable genetic distance between their parents. This situation contrasts markedly, for example, with the high degree of heterosis in the intergeneric *Chamaecyparis-Cupressus* cross of × *Cupressocyparis leylandii* (Jackson & Dallimore) Dallimore.

Such intergeneric hybrids between *Hesperopeuce* and *Tsuga* might consequently now be best transferred to an intergeneric status. Such a taxon thus requires a new name, for which the following is proposed:

× **Hesperotsuga** C. N. Page, **nothogen. nov.** (*Hesperopeuce* Lemmon × *Tsuga* Carr.).
Synonym: *Tsugo-Piceo-Tsuga* Van Campo-Duplan & Gaussen, Trav. Lab. For. Toulouse 1(4) art. 24:11 (1948) (nomen dubium).

× **Hesperotsuga jeffreyi** (Henry) C. N. Page, **comb. nov.**
Basionym: *Tsuga pattoniana* (Jeffrey) Engelm. var. *jeffreyi* Henry in

Elwes & Henry, Trees Gt Brit. & Ireland 2:231 (1907), *Tsuga* × *jeffreyi* (Henry) Henry in Henry & Flood in Proc. Roy. Irish Acad. 35B:55 (1919).

Syn.: *Tsuga mertensiana* var. *jeffreyi* (Henry) Schneider in Silva Tarouca, Uns. Freil.-Nadelh. 294 (1913).
T. pattoniana var. *jeffreyi* Henry in Elwes & Henry, Trees Gt Brit. & Irel. 2:231 (1907).

According to Murray (1863), this hybrid (*Hesperopeuce mertensiana* (Bong.) Rydb. × *Tsuga heterophylla* (Raf.) Sarg.) was first raised at Edinburgh Royal Botanic Garden in 1851 from seed collected by the Oregon Botanical Association on the Mount Baker range in British Columbia by Jeffrey. A tree of this hybrid, perhaps dating from this introduction, still grows in Edinburgh.

Nothotsuga H.-H. Hu ex C. N. Page, **gen. nov.**
Nothotsuga H.-H. Hu 'Discussions of the Taxonomy of Seed Plants' [in Chinese]: 64 (1951 n.v.), (nom. nud.); *Tsuga* subgen. *Palaeotsuga* Miki, Proc. Jap. Acad. 30:977 (1954).

Tsugae L. affinis sed foliis longis acutis hypostomaticis, conis femineis erectis pedunculatis, bracteis longis exsertis subspathulatis, conis masculinis terminalibus aggregatis praecipue distinguitur.

Tall, monoecious evergreen trees. Shoots all of one type, slender, glabrous or rarely with a very sparse scattered pubescence. Leaves narrowly linear-elliptic, long, flattened, petiolate, the margins entire, the midrib prominent below, the apex simple, usually acute, dark green above, light green below, amphistomatic, the stomata numerous on both surfaces but denser below, spreading into two somewhat contorted ranks, set on shining projections with prominent cushion-like bases (pulvini) which are persistent after the leaves fall. Winter buds long, ovoid-conic, acute to acuminate lustrous, non-resinous, with keeled bud-scales.

Male cones clustered, terminal from a bud of the previous season. Female cones solitary, with a stiffly erect straight peduncle, oblong-ovoid, about twice as long as broad, erect, with a small number of broad, rhombic-ovate, woody scales, the bracts small, simple, subspathulate-acute, erect, exerted beyond the scales at maturity, erose-denticulate on their upper margins, the peduncles ± long and often leaf-bearing.

Thus defined, *Nothotsuga* is a distinctive genus of Pinaceae endemic to China, known from Hunan, Kweichow, Kwangtung and Kwangsi.

Nothotsuga longibracteata (Cheng) H.-H. Hu ex C. N. Page, **comb. nov.**
Basionym: *Tsuga longibracteata* Cheng, Contrib. Biol. Lab. Sci. Soc. China, Bot. Ser. 7:1 (1932).
Syn.: *Nothotsuga longibracteata* (Cheng) H.-H. Hu, 'Discussions of the Taxonomy of Seed Plants' [in Chinese]: 64 (1951, n.v.) comb. inval.

Nothotsuga differs from *Tsuga* especially in its ovoid-conic acute buds, entire-margined, long, acute leaves which, although flattened, are hypostomatic; erect, stiffly pedunculate female cones with long, exerted, subspathulate bracts; and terminally clustered male cones. It also has pollen with paired air-bladders, not found in *Tsuga* (Campo-Duplan & Gaussen, 1950).

First described by Cheng (op. cit.) the taxonomically anomalous position of this rather little known taxon of localized distribution, has been recognized previously by several authors. Hu (1951) placed it as a separate genus *Nothotsuga* (cited as a nomen nudum by Cheng *et al.*, 1978), while it was regarded as a generic intermediate between *Tsuga* and *Keteleeria* by Gaussen (1966), citing *Tsuga chinensis* (Franch.) Pritzel and *Keteleeria evelyniana* Masters as its likely parents. Although fragmentary, there is fossil evidence that plants of probable nearest affinity with *Tsuga longibracteata* and hence with this genus occurred in the Pliocene of both Japan and the USSR (Miki, 1954; Karakaev, 1958). Miki (1954) assigned its fossils to a separate (fossil) subgenus *Palaeotsuga*.

In my view, *Nothotsuga*, like *Cathaya* and *Hesperopeuce*, occupies a position linking it with several other genera of Pinaceae, none of which it is wholly typical. Its vegetative foliage especially would seem to link it with both *Tsuga* and *Keteleeria* as stressed by Gaussen (1966), but (as with *Hesperopeuce*) it is clearly not a modern hybrid and to me its female cone more resembles *Keteleeria* or *Abies* in erect habit, *Pseudotsuga* in size, shape, and number of scales, and *Larix* in exerted, simple bracts and *Larix* and *Keteleeria* in long, leafy cone peduncles. Further, the unusual grouping of the male cones into clusters appears to link it also with *Pseudolarix* and, more distantly, perhaps with *Cathaya*.

I thus propose that the phylogenetically most realistic treatment for a plant with such diverse affinities and hence without good fit into any other genus, is, as with *Hesperopeuce* and *Cathaya*, to treat *Nothotsuga* as well worthy of independent generic rank.

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