

A SECOND REVISION OF THE GENUS *KETELEERIA* CARRIÈRE (Taxonomic notes on Pinaceae II*)

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ABSTRACT. A study of herbarium specimens of the genus *Keteleeria* Carrière, in preparation of a second volume of 'Drawings and Descriptions of Pinaceae', has led to the proposed reduction of 14 species and 1 variety to 3 species: *K. fortunei* (Andr. Murray) Carrière, *K. davidiana* (Bertr.) Beissner and *K. evelyniana* Masters.

INTRODUCTION

The genus *Keteleeria*, named by Carrière (*Rev. Hort.* 1866: 449; type species *K. fortunei*) after Jean-Baptiste Keteleer, a Belgian horticulturalist, is a small genus in Pinaceae, occurring in the warm-temperate regions of China, including Hong Kong, the islands of Hainan and Taiwan and the highlands of Laos and Vietnam. Fossils have been found in Japan (Pliocene), Europe (Oligocene-Pliocene), and western North America (Oligocene-Miocene) (see Florin, 1963; Axelrod, 1976). It appears to be closely related to the genera *Pseudolarix*, *Nothotsuga* and *Tsuga*, which in turn are grouped in one subfamily Abietoidae with *Abies* and *Cedrus* (Frankis, 1988). Arguments for these relationships are found in classical studies based on morphology and (wood-)anatomy, and in biochemical approaches, e.g. Niemann & Van Genderen (1980) and Price et al. (1987). Nevertheless, it has a number of characters which justify its status as an independent genus.

The large herbaria in Europe and the U.S.A. mostly possess collections of one or more species, among which are all types of taxa described prior to 1950. More recent collections are usually lacking, while living trees are very rare in arboreta or private gardens. After the Second World War, the flow of material and information, save the results of a few Sino-American expeditions not specifically dedicated to conifers, came virtually to a standstill; publications by Chinese botanists resumed in the 1960's and continue to the present day, but all their material has, until this study, remained in China. Flous (1936b) published the first revision of the genus; it was based on rather few collections, mainly from P and NY, also A (2 specimens), WU (2 specimens) and NAS (6 specimens), all together 43 specimens (of which 2 do not belong to the genus *Keteleeria*, but to *Abies* and *Cephalotaxus*).

For the present study, nearly all the relevant type specimens have been seen, and in addition to these the material kept in P, L, K, E, BM, KUN (partly), NY (partly), CAS (partly), BP and PE (partly) was studied—a total of 150 specimens. The few living trees the author has seen in arboreta in Europe are all of unknown origin and therefore of little use taxonomically. However, some of them provided valuable information about vegetative (re-)growth and phenology, and aided the interpretation of some morphological peculiarities found in herbarium material.

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HISTORICAL REVIEW

Andrew Murray (1862) was the first author to recognize a few specimens sent by R. Fortune to England, preserved in the British Museum (BM), as a species distinct from *Picea jezoensis*, with which Carrière had confused it, and native not to Japan but to China. He named this species *Picea fortunei* but a year later transferred it to *Abies*. Carrière (1866) as stated before, created the genus *Keteleeria*, with *K. fortunei* as the type species. This transfer, correct as it was, was based on the description of a single tree, growing near a temple at Fuzhou, in Fujian, China, and Fortune's specimens (partly lost) from it. However, Bertrand (1874: 86-87) later described new material from China, although he did not recognize Carrière's genus and named his species *Pseudotsuga davidiana*, based on two cones, some leaves and a little twig collected by A. David in 1870. Beissner (1891) transferred it correctly to the genus *Keteleeria*.

Van Tieghem (1891) enumerated four species of *Keteleeria*: *fortunei*, *davidiana*, *sacra* and *delavayi*. While *K. sacra*, a nomen nudum of A. David, has proved to be synonymous with *K. davidiana* (Bertr.) Beissner, the identity of '*Delavayi*', also a nomen nudum, is uncertain. Flous (1936b) suggested synonymy with *Keteleeria evelyniana* Masters, a view which is also held by the Chinese (Cheng & Fu, 1978). The latter species was published by Masters (1903) with a full description.

Hayata (1908a) described a new species: *Keteleeria formosana* from Taiwan, but in the same year reduced it to a variety of *K. davidiana* (Hayata, 1908b: 221). A fifth species was described by Léveillé (1910), *Keteleeria esquirolii*, together with a large number of other new species of plants. Rehder (1929, 1937) commented critically on these new names in Pinaceae and reduced all to synonyms of previously described species.

Between 1910 and 1936, most authors dealing with Chinese conifers reduced the number of accepted species to three: *K. fortunei*, *K. davidiana* and *K. evelyniana*, or only two, with the last species reduced to a synonym or a variety of the second. Orr (1933), who was probably the first to study sufficient material to observe it, stressed the remarkable polymorphy in the genus. Nevertheless, Flous (1936a) described four more species: *K. chien-peii*, *K. cyclolepis*, *K. dopiana* and *K. rouletii*. In the same year she published her '*Révision du genre Keteleeria*' (Flous, 1936b), in which these new species reappeared, together with the five species previously named and one variety. This treatise also contains a detailed, illustrated description of leaf and shoot anatomy and an iconography with accurate drawings of specimens, several made from type specimens.

Between 1936 and 1963 no additional material or information regarding the genus reached European or American botanists and no further taxa were named. Then, Chun & Tsiang (Chun, 1963), studying the flora of the island of Hainan (Guangdong), described *Keteleeria hainanensis*. Volume 13 (4) of *Acta Phytotaxonomica Sinica* (1975) was dedicated to a large number of descriptions of new taxa, many of which had apparently been described in more detail elsewhere and in Chinese only. In *Keteleeria*, Cheng & Fu (Cheng, Fu & Cheng, 1975) added three more species: *K. oblonga*, *K. pubescens* and *K. calcarea*. Volume 7 of *Flora Reipublicae Popularis Sinicae* deals with Gymnosperms, and in this important work, Cheng & Fu (1978) incorporated nine species of

Keteleeria and one variety: *K. hainanensis*, *K. evelyniana*, *K. oblonga*, *K. formosana*, *K. pubescens*, *K. calcarea*, *K. davidiana*, *K. davidiana* var. *chien-peii*, *K. fortunei* and *K. cyclolepis*. Extensive citations of literature, descriptions (in Chinese) and accurate drawings (of new material) were given for each taxon, but no comment was made on Flous's two species from Indochina.

Finally, Hsueh & Huo (1981) described the fourteenth species in the genus: *Keteleeria xerophila*.

GENERIC DESCRIPTION AND DISCUSSION

Keteleeria Carrière in Rev. Hort. 1866: 449 (1866)

Type: *K. fortunei* (Andr. Murray) Carrière

Tall, monoecious tree with long, irregular branches and broad crown; leaves solitary, linear, flat, hypostomatic or weakly amphistomatic, longitudinally ridged on both surfaces, twisted at petiolate base, persistent; male strobili in umbellate clusters arising from a single bud; female cones large, erect; seed scales persistent, cone rachis breaking off near the base, or slowly disintegrating on the tree; seed germination hypogeal; trees sprouting vigorously from coppicing.

The study of types and other specimens, literature (descriptions and figures), and growth of living plants in arboreta, has led to the conclusion, that the species of *Keteleeria* are highly polymorphic. Of 16 characters considered, only a few appear to be more or less constant. Some are shared by almost all specimens studied and are therefore of little diagnostic value, an example being the occurrence of stomata on the upper side of the leaves, which are present in varying amounts and rarely entirely absent. Most other characters are extremely variable, such as leaf length, shape of leaf apex (leaves of young or coppiced plants should be omitted from comparisons, as they are always lanceolate-acute and often much longer), size of mature female cones, pubescence of these (which, as in *Larix*, is dependent on the age of the cones) and of the young shoots, the shape of the vegetative buds, and the apical shape of the bract scales. What seem to be more or less constant characters are, first of all, the shape of the seed scales and, correspondingly, of the seed wings. Only in combination with these are the length of the leaves, their apical shape and, to a lesser degree, shoot pubescence, useful distinguishing characters. On the basis of this assessment of characters, only three species are retained in this study.

Keteleeria fortunei (Andr. Murray) Carrière in Rev. Hort.: 449 (1866). Figs 1, 2, 5.

Syn.: *Picea fortunei* Andr. Murray in Proc. Roy. Hort. Soc. London 2: 419–425, f. 85–97 (1862) (*'fortunei'*).

Abies fortunei (Andr. Murray) Andr. Murray, Pines and Firs of Japan: 49, f. 83–95 (1863).

Pinus fortunei (Andr. Murray) Parl. in A. DC., Prodr. 16 (2): 430 (1868).

Pseudotsuga jezoensis (Carrière) Bertr. in Ann. Sci. Nat. sér. 5, 20: 87 (1874).

Abietia fortunei (Andr. Murray). A. H. Kent, Veitch's Man. Conif. [ed. 2]: 485, f. 123 (1900).

Keteleeria cyclolepis Flous in Bull. Soc. Hist. Nat. Toulouse 69: 402–403, f. 1–11 (1936).

Keteleeria oblonga Cheng & Fu in Acta Phytotax. Sin. 13 (4): 82 (1975).

Keteleeria sp. Masters in J. Linn. Soc. Bot. 26: 556 (1902).

Keteleeria jezoensis (Lindley) Flous in Bull. Soc. Hist. Nat. Toulouse 70: 338 (1936) pro syn.

Keteleeria esquirolii auct. non Léveill : Flous in Bull. Soc. Hist. Nat. Toulouse 70: 324–325, f. 1–13, quoad *R. C. Ching* 7244 et *Y. Tsiang* 7249 (W. C. Cheng det., non leg.).

The specimens preserved at BM as ‘type specimen’ and ‘type collection’—*R. Fortune* No. 50 (1852), Foo-Chow-Foo, China, and *R. Fortune* No. 50 (1848–1851), China respectively, cannot be the same material on which Murray based his *Picea fortunei*. Both are branches with leaves and male strobili (Fig. 1), whereas Murray stated ‘The inflorescence not observed’. His description and figures show acute or apiculate, not obtuse leaves and a mature female cone. Murray was not specific as to which of Fortune’s specimens he had seen, furthermore he failed to designate one as the type of his species. For these reasons a lectotype is designated here.

Lectotype: Fujian: Fuzhou (Foo-chow-foo), 1848–1852, *R. Fortune* 52 (ovul. cone, leaf) (BM).

Habit: tree, max. height 30m, d.b.h. 1–1.5m; trunk monopodial, straight, often short and branching low; branches of first order heavy, long, spreading wide; branches of second order spreading horizontally or ascending; crown broad, often dome-shaped; bark (young trees) thin, scaly, flaking, greyish brown, later becoming thicker and fissured, dark grey-brown. *Branchlets*: slender, firm, light reddish brown or yellowish brown; surface prominently ridged and grooved, glabrous, or rarely with some short hairs in grooves; leaf scars small, circular; pulvini usually weakly developed. *Vegetative buds*: ovoid-conical or subglobose, 3–5mm long, 2–4mm wide, not resinous; bud scales triangular, obtuse and appressed, dull brown with grey margins, persisting several years. *Leaves*: spirally arranged, usually pectinate in two lateral sets, at 45–90° from the shoot, (12–)15–30(–40)mm long, 2–4mm wide, slightly twisted and narrowed at base, narrowly linear to ligulate, flattened, with a raised midrib on both surfaces, apex obtuse, rarely somewhat acute (but acute on young or coppiced plants); stomata absent or a few near the apex above, in two broad bands separated by the midrib below; colour green, greenish white below; resin canals 2, marginal, small. *Male strobili*: lateral or terminal, in clusters from one bud, peduncled, 1–1.5cm long, yellow, with brown perular scales. *Female cones*: lateral or sub-terminal, erect; peduncles 2–5cm long, leaved; shape cylindrical, with obtuse apex, 6–18 × 3.5–6.5cm, colour (immature): strobili at first purplish red, cones green or glaucous green, sometimes tinged with purple, ripening to greyish-brown; conerachis deciduous with cone, but cones remain for several years on the branches. *Seed scales*: subcordate-orbicular, with convex, rounded or nearly straight upper margin, at mid-cone 1.8–3.2cm long and 2–3.3cm wide; surface smooth, usually striated longitudinally, in immature cones often puberulent, soon glabrous; upper margin erose-denticulate in young cones, later finely denticulate or entire; base short pedicellate. *Bract scales*: ligulate-spathulate, apex cuspidate, sometimes weakly trilobate, 1–1.5cm long, included or slightly exserted, visible when seed scales are opened. *Seeds*: oblong, grooved with resin vesicles, 10–13 × 5–6mm,

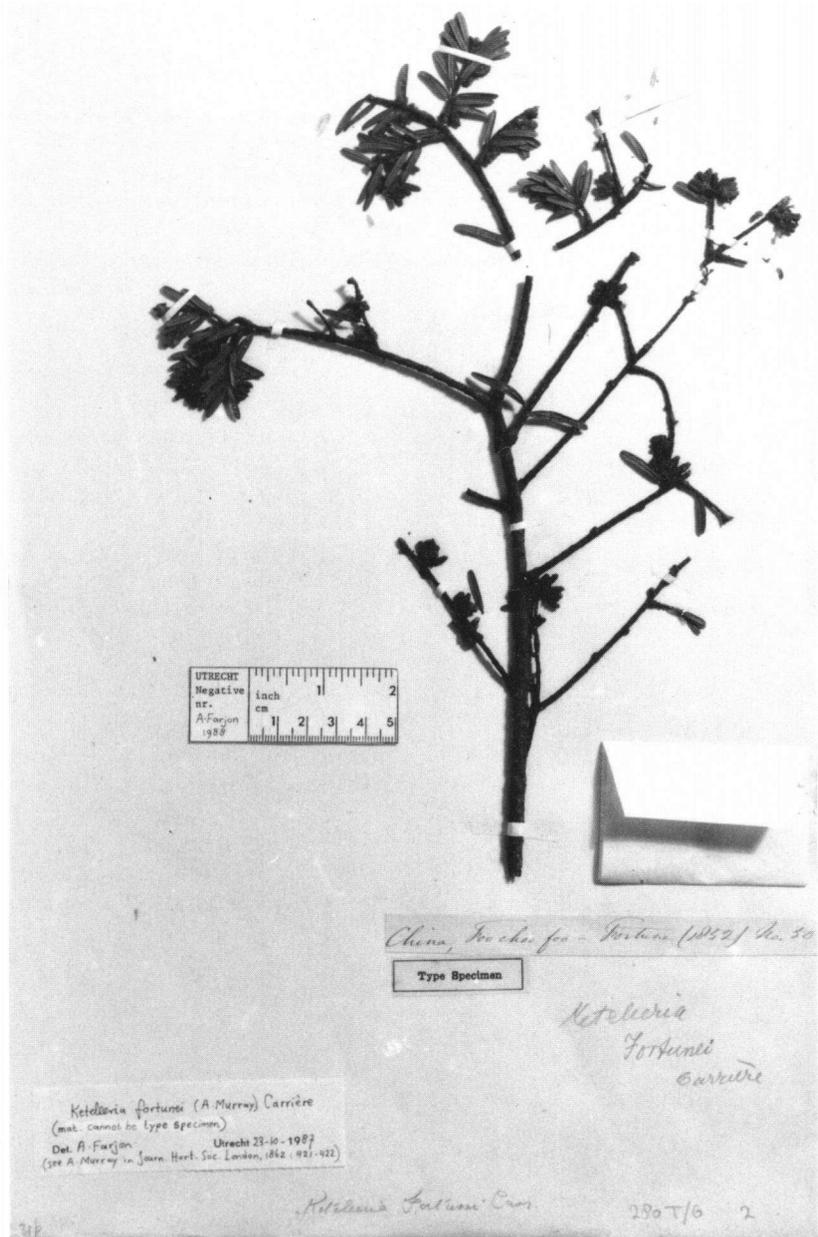


FIG. 1. *Keteleeria fortunei*. Specimen at BM of R. Fortune 50, incorrectly labelled 'type specimen'.



FIG. 2. *Keteleeria fortunei*. 1, tree, Hunan; 2, shoot ($\times 0.25$); 3, cone ($\times 0.35$); 4, shoot with female strobilus ($\times 0.5$); 5, seed scale ($\times 0.5$) with seeds; 6, seeds ($\times 0.5$) div. loc.; 7, leaves ($\times 0.5$); 8, leaf apices ($\times 1.5$); 9, shoot with male strobili ($\times 0.5$). 2, 3, 4, 7 from *W. R. Price* 1256; 5 from *W. T. Tsang* 21071; 9 from *Fortune* 50.

dull brown, on one side covered by the seed wing; seed wings \pm cuneate, with oblique end, 13–20 \times 8–12mm, yellowish-brown (Fig. 2).

In SE China, scattered in extreme SE Yunnan, Guangxi, Guizhou, N Guangdong, S Hunan, SW Jiangxi, Fujian and Zhejiang, also in Hong Kong. GUANGXI. Lingyun-Hsien, near Guiloh, 28 vii 1933, *A. N. Steward & C. C. Cheo* 720 (type of *K. cyclolepis*, holo. NY; iso. BM, BP, P); Tianyang, 680m, 1964, *Chinese coll.* 54163 (type of *K. oblonga*, holo. PE).

GUIZHOU. Lohu, x 1930, *Y. Tsiang* 7249 (P).

GUANGDONG. Tai-mo Shan, Tapu Distr., 5 vii 1932, *W. T. Tsang* 21071 (BM, P).

FUJIAN. Xiamen, ix 1912, *W. R. Price* 1256 (K); Fuzhou, Kushan Monastery, 19 xi 1934, *L. Chen* 15 (K); Fuzhou (Foo-chow-foo), 1848–1852, *Fortune* 50 (BM as 'type specimen', P as No. 50 'Herb. E. Drake'); *ibid.*, 1848–1852, *Fortune* 52 (ovul. cone, leaf) (lecto. BM); *ibid.*, 1848–1852, *Fortune* s.n. (ovul. cone) (BM).

HONG KONG. Cult. in Bot. Gard., 1888, *C. Ford & M. F. Masters* 386 (K); Kowloon Island, 30 xi 1976, *C. N. Page* 10334 (E); *ibid.*, *K. D. Rushforth* 420 (E, U); *ibid.*, *K. D. Rushforth* 421 (E).

Cultivated specimens: Bot. Gard. Sydney, Australia (K); Villa Rovelli, Pallanza, Italy (L); Villa Serbelloni, Bellagio, Italy (L).

Keteleeria fortunei occurs in the hills or low mountains of SE China, in the 'red and yellow earth region' (Wang, 1961), at elevations of 380–1200m. The climate is humid, warm-temperate to subtropical, with annual precipitation of 1300–2000mm. It occurs in two forest formations: mixed mesophytic forest, and, more usually, evergreen broad-leaved forest. Besides many angiosperm trees, such as evergreen sclerophyllous oaks and lauraceous trees, a few additional gymnosperms are also found in the latter formation: *Pseudotsuga sinensis*, *Cryptomeria japonica*, *Cephalotaxus fortunei*, and *Taxus chinensis*.

The type material of *K. cyclolepis* Flous consists of specimens with fragmentary, relatively small cones, of which Flous (1936a) only gives a description and figure of a single seed scale. All specimens I have seen (NY, BM, BP, P) have cones with more or less orbicular to slightly oblong seed scales, with convex, rounded upper margins, and short, ligulate-linear leaves with obtuse apices. When young the shoots are sparsely pubescent, reddish brown, with ovoid-conical buds. There is nothing to justify the status of a separate species for this material.

According to Cheng & Fu (1978), Flous (1936b) incorrectly cited two specimens of *K. cyclolepis* Flous (*R. C. Ching* 7244 and *Y. Tsiang* 7249) as the two specimens seen for *K. esquirolii* Léveillé. This is in accordance with the characters of specimen *Y. Tsiang* 7249 (P): it has a cone quite different from that of Léveillé's type specimen *J. Esquirol* 542 (E), which Flous apparently had not seen. Her key separating the two species on distinctions between cuspidate or trilobate bracts and few or many stomata on the upper side of the leaves is incorrect. Description and figures on pages 324–327 of Flous (1936b) are therefore indeed attributable to the same species as *Steward & Cheo* 720, the type of *K. cyclolepis* Flous.

K. oblonga Cheng & Fu was said to be characterized by oblong or broad-oblong seed scales, non-trilobate bracts, and shoots with black 'papils' (the last character probably referring to the darker pulvini). The holotype from Guangxi has a somewhat distorted but well-developed female cone, of which the seed scales are orbicular-oblong, with a length-width ratio of c.1.3. Variation in this ratio in the material of *K. fortunei* studied ranges from 0.9–1.3, while the upper margin of the seed scales can be broadly obtuse, rounded or truncate, but is always convex. Non-trilobate bracts are described by Murray (1862) for *K. fortunei*, but sometimes weakly trilobate bracts are found. Darker coloured

pulvini have been observed in other specimens and are not a good differentiating character. This variation falls entirely within that of *K. fortunei*.

Keteleeria davidiana (Bertr.) Beissner, Handb. Nadelholzkunde: 424 (1891). Figs 3, 5.

Syn.: *Pseudotsuga davidiana* Bertr. in Bull. Soc. Philom. Paris, sér. 6, 9: 38 (1872) nom. nud.; in Ann. Sci. Nat. Bot., sér. 5, 20: 86-87 (1874).

Abies davidiana (Bertr.) Franchet in Nouv. Arch. Mus. Hist. Nat. Paris, sér. 2, 7: 98, t. 13 (1884); Plantae Davidianae 1: 288-290, t. 13 (1884).

Abies sacra David ex Franchet, ibid., p. 100; resp. 290.

Podocarpus sutchuenensis Franchet in J. Bot. (Morot) 13: 265 (1899).

Keteleeria sacra (Franchet) Beissner, Handb. Nadelholzkunde: 426 (1891).

Pinus sacra (Franchet) Voss in Mitt. Deutsch. Dendrol. Ges. 16: 94 (1907).

Keteleeria davidiana var. *sacra* (Franchet) Beissner & Fitschen in Beissner, Handb. Nadelholzkunde ed. 3: 185 (1930).

Keteleeria formosana Hayata in Gard. Chron., ser. 3, 43: 194 (1908).

Keteleeria davidiana var. *formosana* (Hayata) Hayata in J. Coll. Sci. Imp. Univ. Tokyo 25 (19): 221, f. 11 (1908).

Keteleeria esquirolii Léveillé in Repert. Sp. Nov. Reg. Veg. 27/28: 60-61 (1910).

Keteleeria chien-peii Flous in Bull. Soc. Hist. Nat. Toulouse 69: 400-402, f. 1-11. (1936).

Keteleeria davidiana var. *chien-peii* (Flous) Cheng & Fu in Flora Reip. Pop. Sin. 7: 48 (1978).

Keteleeria calcarea Cheng & Fu in Acta Phytotax. Sin. 13 (4): 82 (1975).

Keteleeria pubescens Cheng & Fu in Acta Phytotax. Sin. 13 (4): 82 (1975).

Keteleeria xerophila Hsueh & Hao in Acta Bot. Yunnanica 3: 249-250, f. 1-5 (1981).

Abies sacra David, J. Trois. Voy. Chin. 2: 29 (1875) nom nud.

Type: Sichuan: Longan-fou, 1870, *A. David* 36 (?) (holo. P).

Habit: tree, max. height 40-50m, d.b.h. 2-2.5m; trunk monopodial, usually straight and columnar, but often forked in the crown; branches of first and second order long, heavy, spreading and ascending; crown broad conical or domed, often open in old trees; bark on young trees thin, flaking, greyish brown, on old trees rough and scaly, fissured in lower part of the trunk, dark grey-brown. *Branchlets*: slender, firm, light reddish brown or yellowish brown, becoming grey; surface ridged and grooved; young shoots usually densely brown pubescent, but soon glabrous; leaf scars small, circular; pulvini distinct, weak or absent. *Vegetative buds*: ovoid-globose, 3-5 × 2-4mm, not resinous; bud scales triangular, obtuse, appressed, dull brown with grey margins, persisting several years. *Leaves*: spirally arranged, usually pectinate, directed forward, crowded near end of shoot, (15-)20-50(-55)mm long, 2.5-4.5mm wide, slightly twisted and/or narrowed at base, narrowly linear, ligulate-linear, or lanceolate in young plants, flattened, with slightly recurved margins, obtuse or truncate (in young plants acute) at apex, with a longitudinal midrib on both surfaces; stomata none or a few near the apex above, in two broad bands below; colour (glaucous-) green above, greenish-white stomatal bands below; resin canals 2, marginal near edges of leaf, small. *Male strobili*: sublateral or

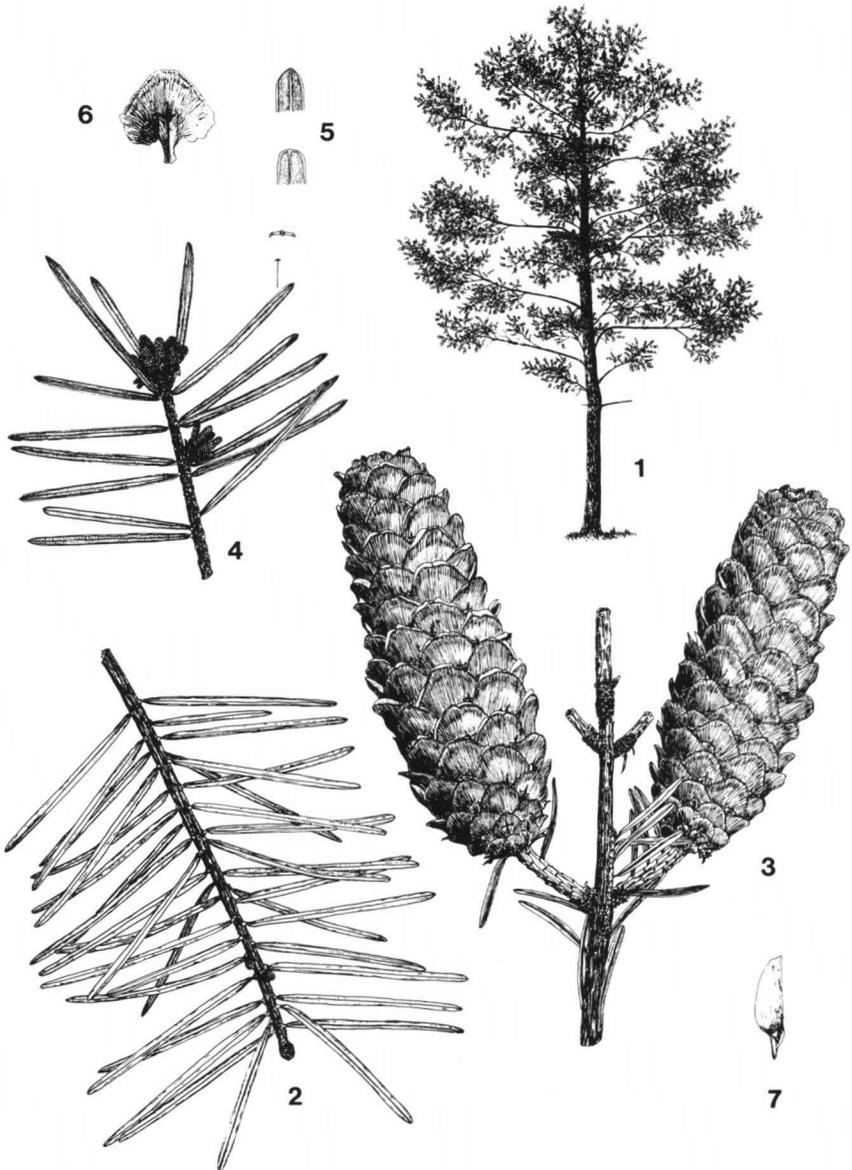


FIG. 3. *Keteleeria davidiana*. 1, tree, Tung Valley, Sichuan; 2, shoot ($\times 0.5$); 3, cones ($\times 0.35$); 4, shoot ($\times 0.5$) with male strobili; 5, leaf apices ($\times 1.5$); 6, seed scale ($\times 0.35$), abaxial side with bract; 7, seed ($\times 0.35$). 2 from *E. H. Wilson* 3018; 3, 6 from Yu Ping Hua 435; 4 from *Abbé Delavay* 570; 7 from *E. H. Wilson* 797.

terminal, in clusters from one bud, pedunculate, 1–1.5cm long, yellow with brown perular scales. *Female cones*: lateral or sub-terminal, erect, solitary or paired; peduncles 1.5–6cm long, leaved as shoots, at an angle to the axis of the cone; cones short or long cylindrical, with obtuse apex, (5–)8–21cm long, with opened scales 3.5–6cm wide, colour: young strobilus purplish red, immature cone glaucous-green, ripening to light or dark brown; cone rachis deciduous with cone, or slowly disintegrating, narrowly conical, grooved, brown. *Seed scales*: subcordate, with often reflexed apical end or margin, at mid-cone 2.6–3.2cm long and 2.2–2.8cm wide; abaxial surface striated, sometimes pubescent in young cones, but soon glabrous, adaxial surface without marks of seed wings, with central rib or line; upper margin erose-denticulate in young cones, becoming entire; base short pedicellate. *Bract scales*: narrowly spatulate, with cuspidate or tridentate apex, 1.5–2cm long, straight, slightly exerted with opened seed scales. *Seeds*: oblong, grooved with resin vesicles, 10–15 × 6–8mm, dull brown, on one side covered by the seed wing; seed wing semi-trullate, 25–30 × 10–12mm, lustrous light brown (Fig. 3).

In NE Yunnan, NE & SE Sichuan, SE Gansu, S Shaanxi, NW Guizhou, SW Hubei, SW Hunan, N Guangxi, and also Taiwan.

YUNNAN. Xiping-hsien, 1978, *Hsueh* 1290 (type of *K. xerophila*, holo. PE); sine loc., 1883, *Abbé Delavay* s.n. (sev. sheets) (P); sine loc., iv 1883, *Abbé Delavay* 570 (P).

SICHUAN. Longan-fou, 1870, *A. David* 36(?) (type of *K. davidiana*, holo P); S of Jinchuan, iii 1925, *J. F. Rock* 12027 (K, P); near Sanko-shi, iii 1925, *J. F. Rock* 12056 (E, K, P); Tung Valley (Shimian), 1914, *E. H. Wilson* 3018 (K); near Kangding (Tachien-lu), 11 viii 1930, *W. C. Cheng* 1819 (BM, CAS); Sima-kong, 1909, *Légendre* 599 (P); Tchen-keou-tin, E Sichuan, 1200m, 14 iv 1893, *R. P. Farges* 1292 (P); E Sichuan, 1885–1888, *A. Henry* 7098 (BM, K, P); near Muli, SW Sichuan, viii 1922, *G. Forrest* 22180 (E).

SHAANXI. Hanzhong, S Shaanxi, vi 1873, *A. David* s.n. (P).

GUIZHOU. near Guiyang, 9 vii 1930, *Y. Tsiang* 8479 (type of *K. chien-peii*, holo. NY; iso. BM, E, K, PE); sine loc., 1930, *Y. Tsiang* 7137 (K); Pa-yang, vi 1905, *J. Esquirol* 542 (type of *K. esquirolii*, holo. E); near the border of Yunnan, 20 viii 1957, Yu Ping Hua 435 (KUN).

HUBEI. Yichang, Nan-t'ao, ii 1887, *A. Henry* 3276 (K); *ibid.*, x 1887, *A. Henry* 3878 (BM, P); *ibid.*, x 1887, *A. Henry* 3878A (K); W Hubei, v 1907, *E. H. Wilson* 797 (BM, K); *ibid.*, xi 1907, *E. H. Wilson* 797A (BM, E, K); *ibid.*, 1900, *E. H. Wilson* 312 (K); *ibid.*, 1907, *E. H. Wilson* 420 (E, K); sine loc., iii 1889, *A. Henry* 7576 (BM, K); sine loc., 1934, *H. C. Chow* 19 (E); *ibid.*, 1934, *H. C. Chow* 1615 (E).

GUANGXI. Miu Shan, 20 vi 1928, *R. C. Ching* 6187 (type of *K. pubescens*, holo. PE, iso. NY); loc. ?, no date, det. as *K. calcarea* Cheng & Fu 5 ix 1960, *Chinese coll.* 808004 (PE).

TAIWAN. Shinguki, Shinkocho, xi 1902, *N. Konishi* s.n. (type of *K. formosana*, holo. BM); Kinkasyo, 1912, *W. R. Price* 285 (K); Tahoku Prov., 666m, 18 v 1918, *E. H. Wilson* 10140 (BM, K); Taipei Bot. Gard., xi 1922, *A. T. Hsieh* s.n. (P); *ibid.*, xi 1976, *C. N. Page* 10200 (E).

(Prov. unknown). Tsui-gai, 1903, *J. Cavalerie* 1192 (E).

Keteleeria davidiana occurs from hills to low mountains throughout much of E China, at elevations of (300–)600–1000(–1300)m. It grows on the red and yellow earth, which are acid, podzolic soils poor in nutrients, or on brown forest soils. The climate is humid, continental warm-temperate to subtropical, with annual precipitation of 1000–2000mm. It is a constituent of the mixed mesophytic forest formation (Wang, 1961) together with many genera and species of broad-leaved deciduous trees, and some other gymnosperms such as *Pinus massoniana*, *P. bungeana*, *Cunninghamia lanceolata*, *Cupressus funebris*, *Torreya grandis*, and *Podocarpus nakaii* (Taiwan). In northern Taiwan trees usually occur as isolated individuals or in small groves only on steep ridge crests (C.N. Page, pers. comm.). It also occupies the evergreen broad-leaved forest formation (Guizhou, Taiwan), with numerous (sclerophyllous) evergreen tree species and *Pinus* spp. It rarely forms pure stands. It occurs in the

parts of China where deforestation has been going on for millennia, leaving very little of the primeval forest. *Keteleeria* survives coppicing and, like many species of *Pinus*, appears to act as a pioneer in secondary vegetation.

According to Li (1963: 45, fig. 7) the characters of *K. formosana* (see also Hayata, 1908a, b) are close to those of *K. davidiana* s. str., the only differences being the usually quite glabrous young shoots and the smaller cones. The holotype (BM) is far too fragmentary to confirm these characters. Indeed most of the material studied from Taiwan has rather small cones, but Kanehira (1936) gives a photograph of a much longer cone. These variable characters are insufficient to distinguish the Taiwan plants from the mainland specimens of *K. davidiana*. Shape of the seed scales and leaves of old plants are found to be identical with those of *K. davidiana*. (In discussing the matter, C. N. Page, Edinburgh, and M. P. Frankis, Newcastle-upon-Tyne, were inclined to retain the Taiwan material at some infraspecific rank as a distinct taxon, but I see no definite morphological arguments to follow them in this treatment. We have as yet no knowledge of possible non-morphological differences between the two provenances).

K. esquirolii Léveillé was based on *Esquirol* 542 (E) from Guizhou with a young, not fully developed cone, which is therefore rather small and has 'erose-dentate' seed scale margins. The other differences from *K. davidiana*, as described by Léveillé, such as the non-trilobate bracts and the absence of 'conspicuous puberulous seed scales' (sic!) are either inaccurately observed (see also Rehder, 1929: 109-110; 1937: 254), or of little taxonomic merit.

K. chien-peii Flous, based on *Y. Tsiang* 8479 from Guizhou, was reduced to a variety of *K. davidiana* by Cheng & Fu (1978: 48). The only other specimen cited by Flous (1936b) as belonging to this species, *R. C. Ching* 6187 from Guangxi, was later designated as the type of *K. pubescens* Cheng & Fu (Cheng, Fu & Cheng, 1975). Neither the mucronate leaves of *K. chien-peii*, nor the pubescence of the seed scales of *K. pubescens* are constant characters, not even in the collections cited here! The authors had seen only one specimen of each 'species' (NY and PE respectively); if they had seen the other collections with identical numbers, in other herbaria, they would have observed that *Y. Tsiang* 8479 at E had obtuse leaves and that *R. C. Ching* 6187 in NY (still green when collected on 20 vi 1928) had only faint pubescence at the base of the seed scales, as normally observed in several specimens of *K. davidiana*.

K. calcarea Cheng & Fu, based on *Chinese collectors* 241, from Guangxi, near Guilin (holo. PE n.v.) was said to differ from *K. davidiana* in having globose terminal buds. However, such buds are found commonly in specimens of both *K. davidiana* and *K. fortunei*. Yellowish young shoots (in sicco) and pubescence of the seed scales are no real differentiating characters from *K. davidiana* as found in locations outside Guangxi and Guizhou (from the latter province is *Y. Tsiang* 7137 (K, PE) cited with *K. calcarea* by Cheng, Fu & Cheng, 1975). The drawings and descriptions in Cheng & Fu (1978) match almost exactly the type specimen of *K. davidiana*, including the obovate-globose terminal buds and the truncate, sometimes slightly notched leaf apices.

The holotype of *K. xerophila* Hsueh & Hao, described from Xiping-hsien in Yunnan, matches the description and type material of *K. chien-peii* Flous exactly, having cones 7-11cm long, rhombic-orbicular seed scales with recurved upper margins and usually mucronate leaf apices. The leaves are rather

long (4.5–6cm in the specimens described), but it is not known whether coppiced or young trees (which have longer leaves than old trees) were among the specimens studied by the authors. The seeds, according to the drawings accompanying the description (Hsueh & Hao, 1981, fig. 5) have rather short wings; no comment was made about the seeds in the protologue. It seems appropriate to consider this species synonymous with *K. davidiana*.

Keteleeria evelyniana Masters in Gard. Chron., ser. 3, 33: 194 (1903). Figs 4, 5. Syn.: *Keteleeria dopiana* Flous in Bull. Soc. Hist. Nat. Toulouse 69: 404–406, f. 1–11 (1936).

Keteleeria rouletii Flous in Bull. Soc. Hist. Nat. Toulouse 69: 406–408, f. 1–13 (1936).

Keteleeria hainanensis Chun & Tsiang in Acta Phytotax. Sin. 8 (3): 259–260 (1963).

Keteleeria evelyniana var. *pendula* Hsueh in Acta Phytotax. Sin. 21 (3): 253 (1983).

Keteleeria delavayi Van Tieghem in Bull. Soc. Bot. France 38: 412 (1891), nom. nud.

Keteleeria davidiana auct. non Beissner: Pax in Repert. Sp. Nov. Reg. Veg., Beih. 12: 304 (1922); Wilson in J. Arnold Arb. 7: 53 (1926), p.p.; Hand.-Mazz. in Symb. Sin. 7: 10 (1929), p.p.; Orr in Notes RBG Edinb. 88: 139, quoad *Forrest* 7386, 10230, 11114, 11425, 11436, 13727, 17788, 18373, 21042, 21428, 28228, 30907, 30961.

Type: Yunnan: near Yuan-chiang (Jianchuan), 1898, *A. Henry* 11815, (holo. NY).

Habit: tree, max. height 30–40m, d.b.h. 1–1.5m; trunk monopodial, usually straight, sometimes forked in the crown; branches of first and second order long, curved, spreading, ascending near the top; crown broad conical, irregular in old trees; bark on young trees thin, flaking, greyish brown, later becoming rough and scaly, dark grey-brown. *Branchlets*: slender, firm, light reddish brown or yellowish brown, turning grey-brown; surface ridged and grooved, soon flaking, pubescence on young shoots only, weak or absent; leaf scars small, circular; pulvini weak or absent. *Vegetative buds*: ovoid-globose or ovoid-conical, 4–6mm long, 3–4mm wide, not resinous; bud scales triangular, obtuse, appressed, dull brown, persisting several years. *Leaves*: spirally arranged, usually pectinate, on terminal shoots sometimes assurgent, directed forward, (20–)30–65(–80)mm long, 2–4mm wide, slightly twisted or only narrowed at base, linear, often falcate, lanceolate in young or coppiced plants, flattened (especially leaves of young plants), apex usually mucronate, sometimes obtuse (acute in young plants); stomata usually in several lines near central rib above, in two broad bands separated by a midrib below; colour glaucous- light or dark green above, greenish-white stomatal bands below; resin canals 2, marginal, small. *Male strobili*: lateral or terminal, pedunculate, clustered from one bud, 1–1.5cm long, yellow, with brown perular scales. *Female cones*: lateral or sub-terminal, usually solitary, erect; peduncles at an angle to the cone axis, 2–6cm long, leaved as shoots; cone long cylindrical when fully developed, with obtuse apex, (4–)9–20(–25)cm long, with opened seed scales (3–)4–6.5(–9?)cm wide; young strobilus light red, cone green or purplish when immature, ripening to light brown, often lustrous; cone rachis deciduous with cone, or slowly disintegrating, narrowly conical, grooved, brown. *Seed scales*: subcordate-

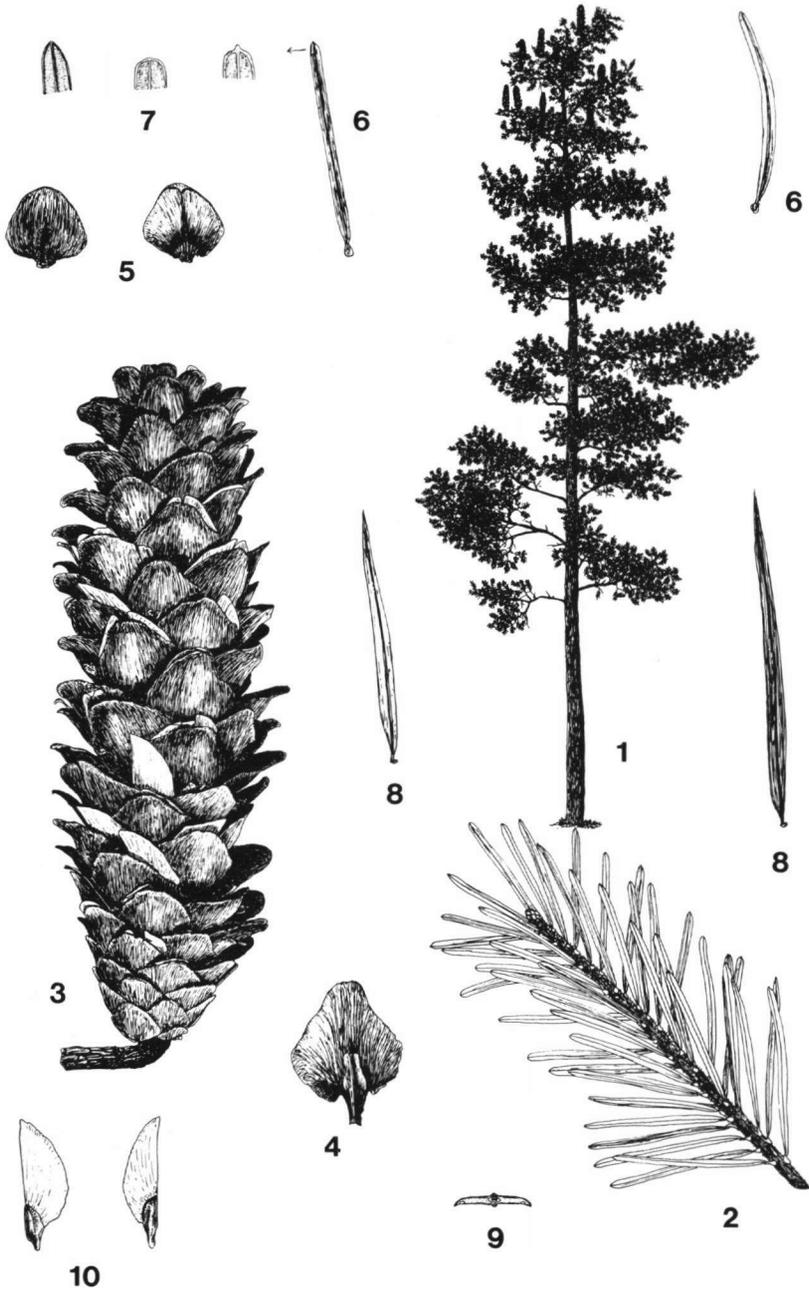


FIG. 4. *Keteleeria evelyniana*. 1, tree, near Kunming, Yunnan; 2, shoot ($\times 0.35$); 3, cone ($\times 0.35$); 4, seed scale ($\times 0.35$) with bract; 5, seed scales ($\times 0.25$) from cone apex; 6, leaves ($\times 0.5$); 7, leaf apices ($\times 1.5$); 8, leaves ($\times 0.5$) of coppiced tree; 9, cross-section of leaf ($\times 2$); 10, seeds (0.35). 2, 6 from *Sino-American Exped.* 79; 3, 5, 10 from *M. E. Poilane* s.n.; 4 from *A. Henry* 11355; 8 from *A. Chevalier* 40439.

oblong, with narrowed apex and more or less concave margins, straight or recurved, at mid-cone 3–4cm long, 2.5–3cm wide; abaxial surface striated, glabrous; adaxial surface without clear marks of seed wings, with central line; upper margin erose-denticulate in young cones, later entire or erose; base short pedicellate. *Bract scales*: ligulate-spathulate, with cuspidate or trilobate apex, 1–1.5cm long, straight, slightly exerted with opened seed scales. *Seeds*: oblong, grooved with resin vesicles, 9–14 × 7mm, dull brown, on one side covered by the seed wing; seed wing semi-trullate, 20–30 × 12–15mm, lustrous yellowish-brown (Fig. 4).

SW Sichuan, Yunnan, where it probably intergrades with *K. davidiana*, the central mountains of Hainan (*K. hainanensis* Chun & Tsiang), and Laos and Vietnam, as far south as the Plateau of Lang-bian near Dalat.

YUNNAN, near Yunnan-sen, 12 iii 1899, *Ducloux* 530 (P); *ibid.*, *Ducloux* 530-bis (P); *ibid.*, iii 1920, *J. Cavalerie* s.n. (K); *ibid.*, iii 1920, *J. Cavalerie* 4621 (E); *ibid.*, *J. Cavalerie* 8063 (E); near Yunnan-fu (Kunming), 1950–2400m, 19–21 ii 1914, *H. Handel-Mazzetti* 87 (K); *ibid.*, 19 ii 1914, *C. Schneider* 61 (K, P); *ibid.*, 1906, *E. E. Maire* 1395 (E); *ibid.*, xi 1906, *E. E. Maire* 1736 (E, K); *ibid.*, 17 ii 1917, *C. Schneider* 118 (K); *ibid.*, 9 iii 1919, *C. Schneider* 4031 (K); *ibid.*, 1906, *E. E. Maire* 1800 (E); Lijiang Shan, viii 1922, *J. F. Rock* 6321 (P); *ibid.*, no date, *J. F. Rock* 10892 (E); *ibid.*, 1933, *McLaren* P28 (BM); *ibid.*, 1933, *McLaren* 44 (BM); *ibid.*, Sun-kwei Pass, 2700m, vii–viii 1932, *J. F. Rock* 25208 (K, NY); *ibid.*, xi 1910, *G. Forrest* 7386 (E); *ibid.*, xi 1932, *J. F. Rock* 25433 (E); near Lijiang, 1929, *J. F. Rock* 18529 (NY); *ibid.*, vi 1922, *G. Forrest* 21428 (E); Yangbi-xian, 1650m, 14 vi 1984, *Sino-American Exped.* 79 (CAS); Hocking Valley, v 1913, *G. Forrest* 10230 (BM, E); Chuntien Plateau, ix 1913, *G. Forrest* 11425 (E); Dali Range, 1917–1918, *G. Forrest* 17788 (E); Tatsien-lu, 11 viii 1930, *W. C. Cheng* 1819 (NY); Tchehai, 2550m, iv 1923, *E. E. Maire* 298 (K); Yung-pei, xii 1921, *G. Forrest* 21042 (E); Tong Shan, ix 1913, *G. Forrest* 11114 (E); NW Yunnan, Shunpi-Yangpi divide, iv 1917, *G. Forrest* 13727 (E); NW Yunnan, N'mai-Nu (Salween) divide, viii 1919, *G. Forrest* 18373 (E, K); Long-yu Shan, Mung-hua, no date, *McLaren* 77A (E, K); Lunan, no date, *A. Henry* 10744, 10744A (NY); near Jianchuan, 1898, *A. Henry* 11815 (type of *K. evelyniana*, holo. NY); NW Yunnan, 1929, *J. F. Rock* 18529 (E); W Yunnan, no date, *G. Forrest* 28228 (E); Yunnan, v 1913, *G. Forrest* 10230 (BM, E, K); *ibid.*, xii 1918, *G. Forrest* 17788 (E, K); *ibid.*, x 1913, *G. Forrest* 11436 (E); E. Yunnan, 1936, *McLaren* 120 (E); Yunnan, no date, *Chinese collector* s.n. (E); sine loc., no date, *G. Forrest* 30907, 30961 (E); *ibid.*, *A. Henry* 11355 (NY).

HAINAN, Tungfan-hsien, no date, *Y. Tsiang* 17237 (type of *K. hainanensis*, iso. PE).

LAOS, Ko-inh, Xam Nua, 24 ix 1920, *M. E. Poilane* 1959 (type of *K. dopiana*, holo. P); Plateau de Jaures, 1903, *De Spire* 494 (P); *ibid.*, no date, *M. E. Poilane* 16188 (P); Boloven Plateau, no date, *M. E. Poilane* s.n. (L); near Xiang-khoang, 1000m, 8 iv 1932, *A. F. G. Kerr* 20971 (BM, P); *ibid.*, ix 1917, *Mieville* 37070 (P); Ban Sat, 1200m, iv 1932, *Colani* s.n. (P); Prov. Tran-ninh, ix–xii 1917, *Mieville* 37068 (P).

VIETNAM, Dalat, Lang-bian Mts, no date, *A. Chevalier* 30025 (type of *K. roulletii*, holo. P); *ibid.*, 3 v 1919, *A. Chevalier* 40542 (4 sheets from diff. plants, P); *ibid.*, 3 iv 1919, *A. Chevalier* 40439 (P); *ibid.*, 10 ii 1914, *A. Chevalier* 30669 (P); *ibid.*, 20 vi 1922, *M. E. Poilane* 3929 (P); *ibid.*, 1100–1500m, no date, *A. Krenpf* s.n. (P); near Dalat, 1911, *H. Lecomte & A. Finet* s.n. (P); *ibid.*, xi 1967, *S. H. Vu-Van-Cuong* 1152 (P); Donai, Bi-Doup Mts, 19 x 1940, *M. E. Poilane* 31049 (P).

Keteleeria evelyniana is one of the few species of Pinaceae occurring in near tropical environments (the others are species of *Pinus*). It is found in mountainous areas in SE Asia at elevations of 700–2700m (–3000m according to Wilson, 1926), but generally not above 2000m. The soil is mainly red earth (in China and Laos); the climate is humid, tropical to temperate at high altitudes, often with more than 2000mm precipitation annually. It is a minor constituent of the evergreen broad-leaved forest formation, which occurs in mountains above the tropical lowland rainforest. In Yunnan and N Laos, it also occurs in mixed evergreen oak forest, with *Cunninghamia lanceolata* (Yunnan), *Podocarpus* spp, *Cephalotaxus fortunei*, Lauraceae, Magnoliaceae, etc.

Orr (1933), in his discussion of the conifer specimens collected by George

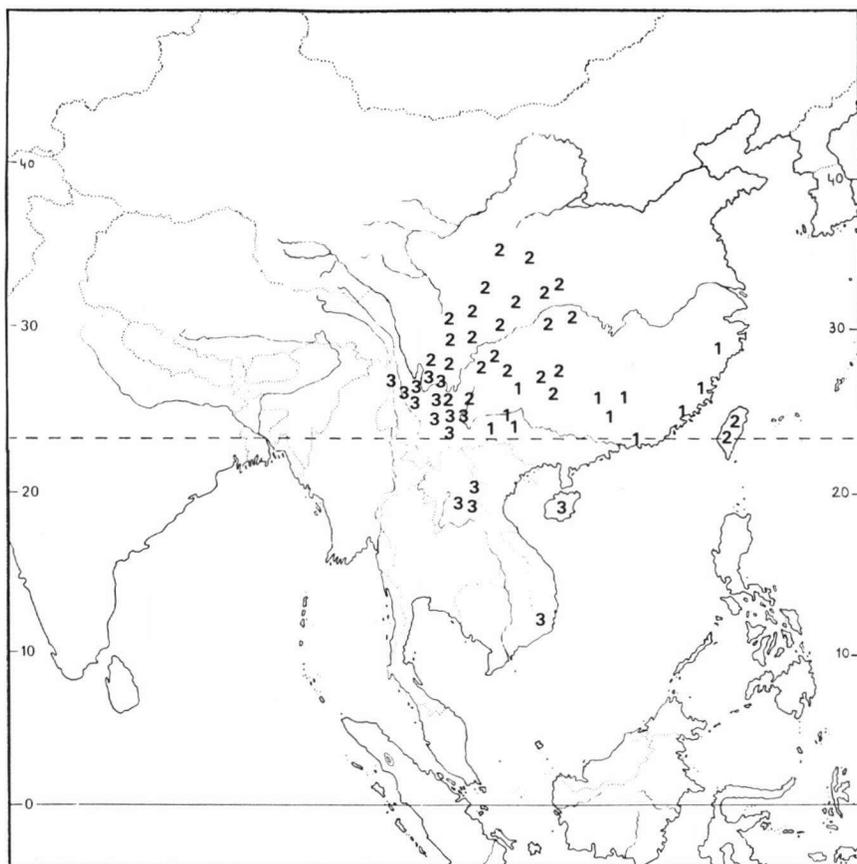


FIG. 5. Distribution of *Keteleeria* species: 1, *K. fortunei*; 2, *K. davidiana*; 3, *K. evelyniana*.

Forrest in China, treated all his material (in E) from Yunnan and Sichuan as belonging to *K. davidiana*. All collections, except *Forrest* 22180, are from Yunnan. Other collectors referred to (Maire, Henry, Wilson) were also active, at least partly, in Yunnan and several of their collections preserved at E are from that province. Careful examination of all these specimens has led to the conclusion that *Forrest*'s specimens from Yunnan, cited by Orr, belong to *K. evelyniana*.

Flous (1936a) described *K. dopiana* with *Poilane* 1959 (P) from N Laos as type, a specimen with a bisected (for mounting purposes) and fragmented cone. Flous (1936b) regarded the somewhat obtuse, not mucronate, leaves as the main point of difference in keying out her species, but this does not hold true even if compared with other collections from the same area. The seed scales have the characteristic concave margins and narrowed apex usually found in *K. evelyniana*; *Poilane* 16188 (with intact cone), cited by Flous (1936b) under *K. dopiana*, has the same characters.

K. rouletii Flous is based on an even poorer type specimen: *A. Chevalier* 30025 (P), from S Vietnam. The cone is represented only by its (disintegrated)

basal part and must have been very large when intact, nevertheless Flous (1936a,b) gave as its characteristics: globose, 5–8cm long, 4cm wide. Under this species she cited several other collections of Chevalier (Flous, 1936b), one of which has three small, but fully developed, cones, while *Chevalier* 40374 consists of two sheets with branches of *Cephalotaxus oliveri* Masters. De Ferré (1952) has corrected the mistake regarding the cones, by adding three more collections, two of which are from N Laos and one from S Vietnam, and by giving a good drawing of a complete cone which is in every respect equal to a typical cone of *K. evelyniana*, and quite similar to other specimens from Laos and Vietnam. Some specimens from Laos and Vietnam have \pm acute leaf apices, others are more obtuse, one specimen is evidently secondary growth from a coppiced plant.

Chun & Tsiang (Chun, 1963) described *K. hainanensis* with *Y. Tsiang* 17237 (PE) as type, from the island of Hainan. Cheng & Fu (1978) illustrated a somewhat truncate cone which, according to the original Latin description, was not completely developed, for this reason the maximum length of 18cm given for this taxon is not typical. Morphology of the cone, seed scales and bract scales, as well as the seeds, matches that of *K. evelyniana*. The leaves as described in the protologue and in the Flora are rather enigmatic. Whereas Chun & Tsiang (Chun, 1963) gave measurements of 6–14cm length and 4.5–6mm width for the linear-lanceolate leaves, Cheng & Fu (1978) reduced these to 5–8cm and 3–4mm respectively. Furthermore, they depict a small shoot with such leaves and clusters of male strobili (l.c., p. 37, f 6). *Y. Tsiang* 17237 (iso. PE) has leaves with a maximum length of 10cm and a maximum width of 5mm. These long, lanceolate leaves evidently represent those of coppiced plants, of which the vigorous young shoots display such large, rather thin and flat leaves. The wood and seed scales preserved in an envelope with this specimen are senescent material. *Chevalier* 40439 (P), from S Vietnam, represents such a branch, and the like have also been observed in a number of young or coppiced plants in Dutch and British arboreta. At Edinburgh, a 6-year old plant of *Keteleeria* sp. had already produced male strobili once (C.N. Page, pers. comm.), so it is most probable that such material was incorporated in the original description of *K. hainanensis* together with an incompletely developed cone.

Recently, Hsueh (1983) described *K. evelyniana* var. *pendula* with *H. G. Zhang* 823 (YNFC n.v.) as the type, from the vicinity of Huaning, Yunnan. Its botanical characteristics are not significantly different from typical *K. evelyniana*, with the exception of its long, pendulous branches. The tree, from which herbarium specimens were collected and which is represented by a photograph, shows evidence of coppicing: the hanging branches are secondary shoots. Their pendulous habit should be regarded as an odd form, which occasionally occurs (e.g. *Picea abies*, *Pseudotsuga menziesii*) and has been preserved in cultivars.

CONCLUSION

The three species of the genus *Keteleeria* Carrière retained in this study are those accepted by most authors in the early 1930's: *K. fortunei*, *K. davidiana* and *K. evelyniana*. Of these, the first is the most distinct species. Of the other two it may be argued that *K. evelyniana* ought to be regarded as a subspecies of *K.*

davidiana, as the differences are more subtle; furthermore there has arisen some doubt from the material studied as to whether both species are truly sympatric in parts of Yunnan: some interbreeding may occur, accounting for intermediate forms. Nevertheless, much of the material appears distinct enough regarding the same, and only constant, characters also differentiating *K. fortunei* and *K. davidiana*: i.e. those making up the morphology of the mature female cones. Other characters do not consistently separate any group of specimens studied, which could reasonably make up a species, but some may be helpful in support of the characters of the female cones. Geographically, the three species occupy distinct parts of the range of the genus, with probably some overlap (Fig. 5), especially between *K. fortunei* and *K. davidiana*. *K. evelyniana* is essentially a Yunnan species, but has a few (relict?) outposts on high plateaux and mountains deep into tropical SE Asia. The three species can be keyed out as follows:

- 1. Seed scales of mature female cones subcordate-orbicular (broadest point above the middle), with convex, rounded or truncate upper margins; bract scales usually with a cuspidate apex; leaves short, not exceeding 4cm; shoots usually glabrous**K. fortunei**
- + Seed scales subcordate (broadest point below the middle), with a more or less obtuse-acute, concave or recurved apex; leaves often longer, but variable2
- 2. Seed scales subcordate, length-width ratio 1 or only slightly more, lateral margins straight; leaves linear, with usually obtuse or truncate apex; shoots more or less densely brown pubescent**K. davidiana**
- + Seed scales subcordate-oblong, length-width ratio larger than 1, lateral margins usually concave; leaves linear-falcate, with usually more or less mucronate apex; pubescence on shoots weak or absent**K. evelyniana**

It should be observed, that only the seed scales of the central part of well-developed, ripe female cones show these diagnostic characters fully; likewise, only shoots and leaves on branches of mature trees, not of relatively young plants or regrowth of coppiced plants, should be studied for determination of the species in this polymorphic genus.

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