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Taxaceae: The Genera and Cultivated Species

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I. Abstract

Past and present research and literature are assembled into a review of the Taxaceae. Five genera and 13 cultivated species are described, including keys and illustrations.

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II. Introduction

The Taxaceae are a small group of gymnosperms constituting less than 2% of all gymnosperm species, with one of its genera, *Taxus*, a very widely cultivated ornamental shrub in the northern hemisphere.

Most taxa in the Taxaceae are rare or restricted in their distribution, although several species of *Taxus* are natively abundant and widely cultivated. *Torreya taxifolia* Arn. and *Taxus floridana* Nutt. are endangered plants restricted to Florida and Georgia (Godfrey & Kurz, 1962; Ward, 1979). *Taxus globosa* Schldl. is a rare endemic of central Mexico. *Austrotaxus* and *Pseudotaxus* are known only from New Caledonia and the Zhejiang (Chekiang) Province, China, respectively. *Torreya californica* grows only in northern California and southern Oregon. Three other species of *Torreya* are restricted to several provinces in China, and *Torreya nucifera* grows only in Japan and Korea.

The Taxaceae are characterized by a unique reproductive structure that has fueled prolonged and insightful discussion about interpretation and origin of the complex compound megasporangiate strobilus of other conifers (Buchholz, 1934, 1948; Chamberlain, 1935; Coulter & Chamberlain, 1917; Florin, 1931, 1948c, 1951, 1954; Gausson, 1979; Janchen, 1949; Keng, 1969; Pilger, 1903, 1916a, 1916b, 1926; Robertson, 1907; Sahni, 1920; Saxton, 1934; Sugihara, 1943, 1946; Sporne, 1965; Wang et al., 1979). The examination and analysis of this structure has kept plant morphologists busy for nearly two centuries. Controversy has centered on the nature of the megasporangial enclosure or ovular integument and the interpretation of the ovuliferous scale. The ovuliferous scale should not be confused with the "cone scale," which is actually an entire branch system consisting of the ovuliferous scale and bract. The ovuliferous scale is now prevalingly considered to be a sporophyll-bearing branch in the axil of the bract from the axis of the strobilus (Bierhorst, 1971; Chamberlain, 1935; Florin, 1954; Foster & Gifford, 1974; Sporne, 1965).

In the case of the Taxaceae, the megastrobilus is not a cone as it is in most other conifers; rather, it consists of a solitary ovule, terminal on an axillary shoot (axis of the strobilus). The ovule is surrounded by an aril, which is an outgrowth of the funiculus as in angiosperm genera such as *Celastrus*. The Taxaceae aril is the fleshy part of the megasporophyll and the apex of the axillary shoot (Chamberlain, 1935; Coulter & Chamberlain, 1917; Florin, 1954; Wilde, 1944). This contrasts with the strobilus in *Juniperus* and in the other gymnosperm family with a fleshy reproductive structure, the Podocarpaceae. In these the fleshy structure comprises part or all of the ovuliferous scale, sometimes fused with the subtending fertile bract.

The microsporangiate strobilus of gymnosperms is simple, but within the Taxaceae and the Cephalotaxaceae there are clear examples of compound pollen strobili, and those that appear simple are currently interpreted to be reduced compound structures (Keng, 1969; Wilde, 1944, 1975). The microsporophylls within this compact structure are peltate or apically thickened, a distinctive feature of the Taxaceae and the Cephalotaxaceae but also present in the Araucariaceae. The sporangiophores or stalks may be lacking and a lamina or leafy component may or may not be present. The Taxaceae are dioecious with few exceptions, a condition not uncommon among conifers.

The family is further distinguished, vegetatively, by a combination of flattened, strongly decurrent leaves with the stomatal bands only on the lower or abaxial leaf surface, mature and juvenile leaves of similar form, and resin canals lacking or reduced in size and number. In most species of Taxaceae the mature plants are profusely branching, spreading shrubs or small trees.

New discoveries and continued floristic work, particularly in China, have added to our body of knowledge on the Taxaceae (Buchholz, 1948; Chen & Wang, 1978, 1984; Cheng,

1934, 1947; Cheng & Fu, 1975; Cheng et al., 1978; Ching, 1927; Chun, 1925; Ferguson, 1984; Florin, 1948a; Hu, 1927, 1934; Hu, 1964; Lan & Zhang, 1984; Laubenfels, 1972, 1978, 1988; Lee, 1935, 1973; Li, 1963, 1975; Morikawa, 1928; Nakai, 1938; Price, 1990; Rehder, 1919; Wilson, 1916). The purpose of this paper is to assemble currently available knowledge on the Taxaceae into descriptions of the genera and keys and descriptions for the species cultivated in North America.

III. Systematic Treatment

TAXACEAE S. F. Gray, Nat. Arr. Br. Pl., vol. 2: 222. 1821. Yew family. Type genus: *Taxus* L., Sp. Pl. 1040. 1753.

Evergreen, dioecious (sometimes monoecious in *Torreya* and *Taxus canadensis*) trees or shrubs; bark thin and flaking to thick and rough or tight, red-brown to dark brown, calcium oxalate crystalline fibers sometimes present; wood lacking resin, with helical thickenings on secondary walls of axial tracheids (often absent in *Austrotaxus*); branches spreading to erect and ascending; branchlets opposite or alternate, glabrous, brown to green, completely covered by the decurrent bases of the leaves. Leaves persistent (2-)3-4 years, usually 2-ranked, usually papillose, prominently long-decurrent, alternate (opposite in *Amentotaxus*), linear to linear-lanceolate, attenuate, acuminate or cuspidate, glabrous, sometimes papillose on the midrib or margins; petioles 1-2 mm long or lacking, margins entire, revolute, upper (adaxial) surface dark green, lower (abaxial) surface dark green to dull yellow or yellow-green; hypostomatic, the stomata in 2 longitudinal, glaucous or pale-green to fulvous bands, single-veined, the midrib a ridge, groove, or not evident on upper surface, raised on lower surface, resin in a single canal (*Amentotaxus*), scattered in the parenchyma (*Torreya*) or lacking.

Pollen strobili (male cones, pollen cones, microstrobili, microsporangiata strobili) simple (at least appearing so) or compound, terminal or axillary; solitary or elongate in clusters of 2-4, sessile or subsessile, globose or oblong-cylindrical when young, oblong-cylindrical or oblong-conical when mature, 2-10 mm long; sterile scales 8 to many below the microsporophylls (with 2 additional sterile scales among the microsporophylls in *Pseudotaxus*); microsporophylls 3-14 (numerous in *Torreya*), perisporangiata and radially symmetrical (in *Taxus*, *Pseudotaxus*, and *Austrotaxus*) or hyposporangiata (only the abaxial sporangia fully developing) and dorsiventral (in *Amentotaxus* and *Torreya*), 1-3 mm long, stalked (except in *Austrotaxus*) and peltate or apically thickened; microsporangia (2-)3-9, the pollen lacking bladders or wings (except for remnants in *Amentotaxus argotaenia*), globose or subglobose, scabrous or slightly granular, the exine in 2 layers of equal thickness.

Ovulate strobili (female cones, seed cones, megastrobili, megasporangiata strobili) consisting of a solitary ovule that is terminal, sessile or on a peduncle to 1.5 cm long; sterile scales persistent, 6-14, spirally arranged or opposite and decussate; mature ovule or seed surrounded by an aril (a fleshy part of the megasporophyll that develops from the axis or apex of the ovule-bearing axillary shoot); aril globose to ovoid or oblong, 5-30 × 10-15 mm, sweet, pulpy, red, white, green, or purple; seed dry and nutlike, with 2 cotyledons. Chromosome number, $n = 12$, sometimes 11 (in *Torreya californica* and *T. nucifera* and possibly in *Amentotaxus formosana*) or rarely 7 (in *A. argotaenia*) or uncounted (*Austrotaxus*, *Pseudotaxus*).

The Taxaceae are a family of five genera and 25 species (including 2 artificial hybrids) distributed in the northern hemisphere except for the monotypic *Austrotaxus*, which occurs in New Caledonia, and one species of *Taxus* in Indonesia (Fig. 1). Three species of *Taxus* and



Fig. 1. Native distribution of the Taxaceae.

two species of *Torreya* represent the family in North America. Florin (1963), in his thorough examination of the fossil record, explained the wide, mostly disjunct distribution of the family through partial extinction during climatic changes of the Tertiary and Pleistocene, while Sporne (1965) tentatively suggested dispersal by avian species as a possible explanation, the fleshy aril supposedly being a favored food of birds.

The Taxaceae are distinguished from other conifer families (except for Cephalotaxaceae) by compound pollen strobili or simple structures derived from compound pollen strobili, peltate microsporophylls, and solitary, terminal ovules embedded in a fleshy closed or open aril. In the past, *Cephalotaxus* and *Podocarpus* s.l. were included in the Taxaceae (Pilger, 1903, 1916b) on account of their reduced ovuliferous scales and fleshy ovulate strobili. In recognition of differing origins of these features of the female reproductive structure, the two genera are now placed in the Cephalotaxaceae and the Podocarpaceae, respectively. The fleshy structure in *Cephalotaxus* is the outer layer of the integument of the ovule (Singh, 1961) and, in the Podocarpaceae, the "aril" is formed from outgrowths of the megasporophyll and part or all of the ovuliferous scale, sometimes even including the bract (Florin, 1954; Keng, 1969; Buchholz, 1934; Wilde, 1944). Cephalotaxaceae, Podocarpaceae, and Taxaceae also differ in other aspects of their reproductive morphology, chemistry, pollen, leaves, and wood. *Amentotaxus* has been considered by some to be sufficiently distinct from the other genera of the Taxaceae to be recognized as a separate family, the Amentotaxaceae (Kudo & Yamamoto, 1931; Yamamoto, 1932; Chuang & Hu, 1965; Xi, 1986a, 1986b), and by others (Pilger, 1926; Koidzumi, 1942) as a member of the Cephalotaxaceae. The distinctly compound pollen strobili, pollen characteristics and deviation in chromosome number are largely responsible for these considerations. However, leaf and ovulate strobilus morphology and many other characteristics that are similar to other Taxaceae, particularly *Torreya*, suggest retention of *Amentotaxus* in the Taxaceae (Florin, 1948, 1951; Janchen, 1934; Keng, 1969; Koidzumi, 1932; Li, 1952).

The compound pollen strobilus in *Amentotaxus* and *Austrorotaxus* easily distinguishes these genera from all other conifers. The pollen strobilus is less obviously compound in *Pseudotaxus* and reduced to a simple structure in *Taxus* and *Torreya*. The interpretation of the simple pollen strobilus as reduced from a more primitive, compound structure is currently accepted (Keng, 1969; Wilde, 1975) over earlier considerations (Florin, 1948c, 1951; Sporne, 1965) of the simple pollen strobilus as primitive.

The presence, absence, and placement of resin varies among genera and has been considered an important character in the evolutionary history of the Taxaceae. Applying the principles that the root is more likely to bear ancestral features and that the resin canal is primitive among conifers (Jeffrey, 1903) led Bliss (1918) to contend that the Taxaceae are the most modern gymnosperm family. Various stages in the decreasing organization of the resin cells, culminating in their disappearance altogether, are represented in several extant members. Resin is organized into a canal in the leaves of *Amentotaxus* (Keng, 1969), appears in scattered cells in the foliar parenchyma of *Torreya*, is found only in the roots and wounded stems of *Taxus* (Bliss, 1918), and is lacking in *Pseudotaxus* and *Austrotaxus*.

The principal area of disagreement among gymnosperm taxonomists concerning the Taxaceae has been the evolutionary position of the family in relation to other groups of conifers. Florin (1948c, 1951, 1954) caused much of the controversy with his assertion that the single, terminal ovule of the Taxaceae (often referred to as the "uniaxial cone," in order to distinguish it from the reduced strobilus of the Podocarpaceae) is a primitive feature. He drew support for this position largely from the appearance of a similar ovulate strobilus in a Jurassic fossil conifer, the bladderless pollen of Taxaceae, and the intermingling of sterile and fertile scales in the pollen strobili of *Pseudotaxus*. Most other researchers before (Chamberlain, 1935; Wilde 1944; Pilger, 1926,) and after (Hart, 1987; Keng, 1969; Price, 1990; Wang et al., 1979) have considered this unique female reproductive structure to be reduced from a compound or biaxial cone. The Taxaceae can now be considered a more recently derived conifer family with some of its own specializations rather than an early offshoot from conifers. Hart's (1987) preliminary cladistic analysis supports this theory and positions the Cephalotaxaceae and the Taxaceae as sister groups. On the other hand, Miller (1988), as a result of his cladistic analysis of extant conifers, found the Taxaceae to be a distinct clade that diverged early in conifer evolution. Keng (1969) proposed the recent derivation of the Taxaceae from an ancestral group that contained features similar to present-day *Taxus*, *Amentotaxus*, and *Cephalotaxus*.

Two tribes have been distinguished in the Taxaceae (Janchen, 1949). The tribe, Torreyaee Janchen, consisting of *Amentotaxus* and *Torreya*, has arils adnate to the seed, abaxially positioned microsporangia, and leaves that contain resin. In tribe Taxaceae the arils are free from the seed, the microsporangia are radially arranged, and the leaves lack resin. Both tribes show a tendency toward reduction in the number of free nuclei divisions during mitosis, *Torreya* being the most advanced genus in having only two or three divisions, and the only genus with cleavage polyembryony (Buchholz, 1934; Chen & Wang, 1978, 1984; Chowdhury, 1962; Coulter, 1905; Dogra, 1980; Doyle & Brennan, 1971; Singh, 1978).

Only *Torreya* and *Taxus* are cultivated to any extent in the United States. Although *Torreya* is grown mostly only in botanical gardens, nearly all species of *Taxus* are cultivated as ornamentals with *T. baccata*, *T. cuspidata*, and the hybrid between them, *T. ×media*, planted in profusion throughout the Northeast and Midwest. The seeds of *Torreya* are economically important in China.

Key to the genera of Taxaceae

1. Pollen strobili in racemes; leaves 5–9 mm wide.
 2. Leaves opposite; pollen strobili terminal or subterminal; tracheids with spiral thickenings *Amentotaxus*
 2. Leaves spirally arranged; pollen strobili axillary; tracheids lacking spiral thickenings. *Austrotaxus*
1. Pollen strobili solitary; leaves <5 mm wide.
 3. Arils closed at the apex, concealing the seed; branchlets opposite; leaves lacking elevated midrib on adaxial surface *Torreya*

3. Arils open at the apex, revealing the seed; branchlets alternate; leaves with prominent midrib on adaxial (upper) surface.
4. Arils white; pollen strobili with sterile scales; leaves with papillae only at the margins *Pseudotaxus*
4. Arils red; pollen strobili lacking sterile scales; leaves with papillae, if present, along the midrib of the abaxial surface *Taxus*

A. AMENTOTAXUS

AMENTOTAXUS Pilg., Bot. Jahrb. Syst. 54: 41. 1916. Type species: *A. argotaenia* (Hance) Pilg., Bot. Jahrb. Syst. 54: 41. 1916. (Fig. 2)

Small trees or shrubs 2–10 m tall with few thin, spreading or erect branches; branchlets opposite, pale yellow-green to brown or dark brown; buds 2 mm long, brown, the scales persistent, acuminate. Leaves persistent (2–)3 years, opposite, leathery, linear-elliptic to linear-lanceolate, 3.3–12.5 cm × 6–9 mm, constricted at base to a short petiole, acute, margins slightly revolute, petiole 1 mm long, midrib prominent, raised and 0.5 mm wide on upper surface, less raised and 1.5 mm wide on lower surface; the 2 stomatal bands glaucous or fulvous, each 2–3 times the width of the green margins, ca. 2 mm wide.

Pollen strobili compound, terminal, in groups of 1–5, erect, quickly becoming pendulous, 3–7(–12) cm long; microsporophylls 8–10, dorsiventral, peltate, hyposporangiate, each bearing 3–5(–8) sporangia.

Ovules on peduncles 1–1.5 cm long, subtended by 10 persistent, decussate, ovate, keeled scales; arils ovoid or ellipsoid, 1.5–2.5 × ca. 1.5 cm, open at the apex, red-yellow, becoming dark purple, resinous. Chromosome number, $n = 11$.

Amentotaxus is a genus of three or four species endemic to eastern Asia. *Amentotaxus* has been allied with *Cephalotaxus* as a member of the Cephalotaxaceae, the sister family and best outgroup to the Taxaceae (Hart, 1987; Keng, 1969). As mentioned previously, *Amentotaxus* has also been placed in its own family, but now may best be considered most closely allied to *Torreya* of the Taxaceae (Li, 1952; Hart, 1987; Keng, 1969; Price, 1990), although Xi (1986a, 1989b), on the basis of pollen studies, prefers an independent Amentotaxaceae. A very different pattern of ovule development, paired ovules with subtending bract and minute ovuliferous scale, and lack of a clearly separate aril as in the Taxaceae are important characteristics of the Cephalotaxaceae that prevent inclusion of *Amentotaxus* despite some similarity in other features.

The pollen strobilus of *Amentotaxus* lacks bracts but otherwise strongly resembles the compound arrangement of the pollen strobilus of *Cephalotaxus*. The microsporangia are dorsiventral, but occasionally radial symmetry is displayed, at least near the strobilus apex, a condition also observed in the Cephalotaxaceae (Wilde, 1975).

The *Amentotaxus* leaf contains a unique arrangement of subsidiary cells that are greater in number, bear thicker papillae, and attend several neighboring monocyclic stomata (Keng, 1969; Florin, 1931, 1951). Foliar resin is present in the leaves and arils as in *Torreya* and the Cephalotaxaceae, although *Amentotaxus* is the only genus of the Taxaceae that has its resin organized into a duct or canal (Ferguson, 1978; Jeffrey, 1903; Keng, 1969; Singh, 1961).

In addition to these features of the pollen strobili and leaves, there are at least five characteristics of the wood anatomy (Miller, 1973), some pollen characteristics (Xi, 1986a, 1986b), and a seed protein peptide pattern (Hu et al., 1986) that are unique to *Amentotaxus*. Amentoflavone and five other chemical components have been identified from the foliage of *A. argotaenia* (Hance) Pilg. (Geiger & Quinn, 1975; Ma et al., 1986). The chromosome number for

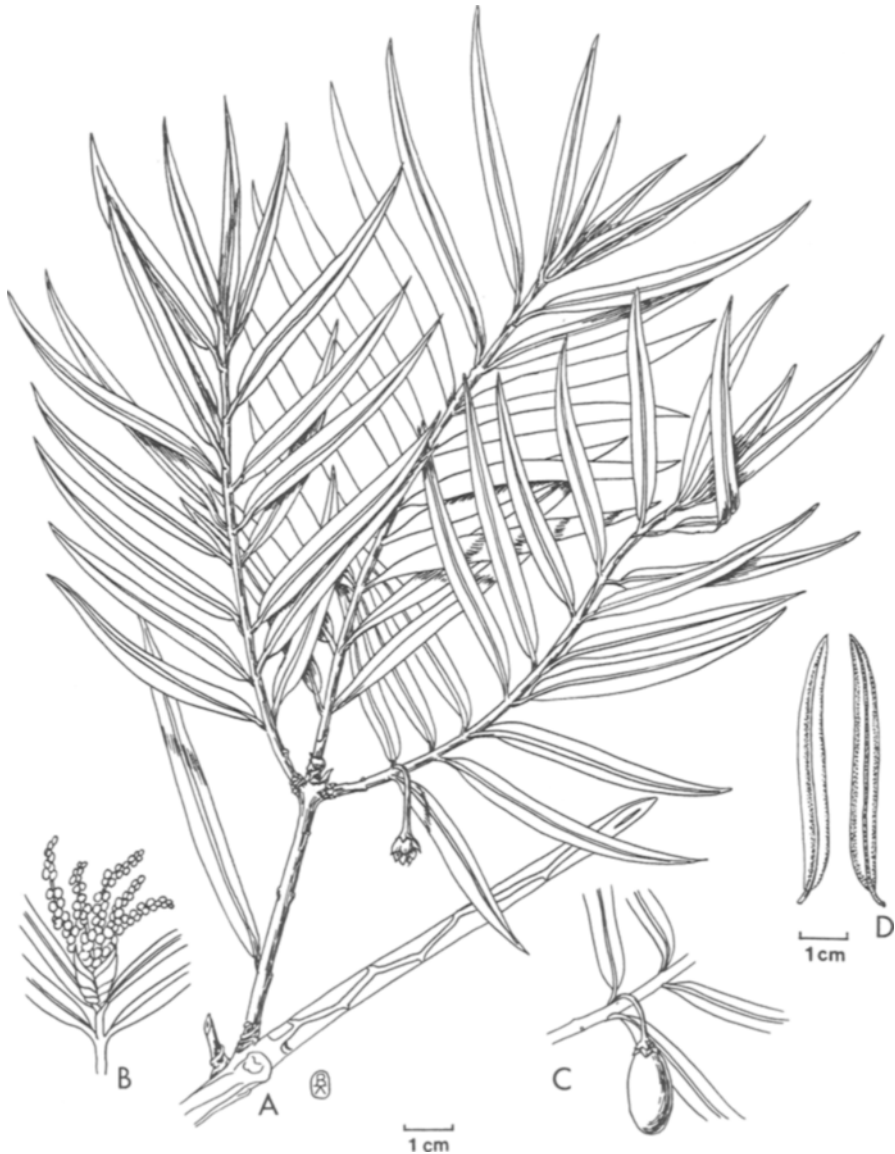


Fig. 2. *Amentotaxus argotaenia* Pilger. **A.** Branchlets, the mature megastrobilus having fallen, an immature megastrobilus remaining. **B.** Pollen strobili. **C.** Megastrobilus and aril. [After *Y. Sugihara s.n.* (11 Jul 1941) (A) and *W. T. Tsang 20351* (A).] **D.** Adaxial (left) and abaxial (right) leaf surfaces.

Amentotaxus has been reported as $n = 11$ (Suigihara, 1946)—a common occurrence in conifers where the often-shorter 12th chromosome is eventually lost (Khoshoo, 1961)—but also as $n = 7$ in *A. formosana* H. L. Li (Chuang & Hu, 1965), the lowest chromosome number ever reported in the gymnosperms (chromosome number $n = 7$ is frequent in the Gnetales).

Li (1952) recognized four species, on the basis of size and shape of the leaves and width and color of the stomatal bands, while suggesting that the number of racemes of microstrobili and size and shape of the seed may be taxonomically important. Geographical distribution is also significant, as these four entities occupy isolated and restricted ranges in China and southern Taiwan. Subsequent authors (Chang & Hu, 1965; Ferguson, 1978; S. Y. Hu, 1964; Keng, 1969; Miller, 1973; Gaussen, 1979) have cast doubts on the distinctness of these taxa at least at the species level. Ferguson (1984) proposed a new species, *A. assamica* D. Ferg., and lumped one of Li's species, *A. cathayensis*, with *A. argotaenia*; and Lan and Zhang (1984) described a variety of *A. argotaenia* from the Guizhou province. All species of the genus occur at relatively high altitudes in damp or shady places such as along stream banks or ravines.

Amentotaxus is easily distinguished from *Austrotaxus* by its opposite leaves and from all other genera in the family by its terminal racemes of pollen strobili.

Although the foliage attracts ornamental interest, the lack of available plant material has prevented cultivation in the United States.

1. Species Not in Cultivation

AMENTOTAXUS ARGOTAENIA (Hance) Pilg., Bot. Jahrb. Syst. 54: 41. 1916.

Podocarpus argotaenia Hance, Bot. Brit. For. 21: 357. 1883.

P. insignis Hemsley, J. Bot. 28: 357. 1885.

Cephalotaxus argotaenia (Hance) Pilg. in Engl., Pflanzenz. 18: 104. 1903.

A. cathayensis H. L. Li, J. Arnold Arbor. 33: 195. 1952.

A. ASSAMICA D. Ferg., Kew Bull. 40: 115–116. 1984.

A. FORMOSANA H. L. Li, J. Arnold Arbor. 33: 196. 1952.

Podocarpus argotaenia sensu Matsum. & Hayata, J. Coll. Sci. Imp. Univ. Tokyo 22: 399. 1906.

A. argotaenia sensu Yamamoto, Bot. Mag. (Tokyo) 40: 453. 1926.

A. YUNNANENSIS H. L. Li, J. Arnold Arbor. 33: 197. 1952.

A. argotaenia sensu Hu, non Pilg., Bull. Chin. Bot. Soc. 2: 8. 1935.

2. Representative Specimens

Austrotaxus argotaenia. TAIWAN: Taito-cho, 11 Jul 1941, Y. Sugihara s.n. (A). CHINA: Hong Kong, Tungchung, Y. W. Taam 2080 (BH); Ma on Shan, D. J. de Laubenfels P572 (A); Hubei, Shennugia, B. Bartholomew et al. 533 (A); Hupeh, Hengshan Hsian, E. H. Wilson 2107 (A); Kwantung, Tsengshing, Nwaam Kwan Shan, W. T. Tsang 20351 (A); Kwantung, Y. W. Taam 594 (A), 552 (A), T. M. Tsui 83 (A), 8 Aug 1922, C. O. Levine s.n., (A); Sichuan, Omei-hsien, H. K. Hu 9209 (A).

Austrotaxus formosana. TAIWAN: Taririku, 27 Dec 1925, R. Kanehira s.n. (A, BH), 19 Feb 1925, R. Kanehira & S. Sasaki s.n. (A, BH), 11 May 1924, R. Kanehira s.n. (A). INDIA: Annam, Kantum, 29 May 1947, M. E. Poilane s.n. (A).

Austrotaxus cathayensis. CHINA: (probably western Sichuan), E. H. Wilson 3005 (HOLOTYPE: A).

Austrotaxus yunnanensis. CHINA: Yunnan, Faa Douu, Si-chour-hsien, K. M. Feng 12050 (A); Chung dzai, Har-li-po, K. M. Feng 12792 (A).

B. AUSTROTAXUS

AUSTROTAXUS Compton, J. Linn. Soc. Bot. 45: 427-428. 1922. Type species: *A. spicata* Compton, J. Linn. Soc. Bot. 45: 427-428. 1922. (Fig. 3)

Trees 12-25 m tall with a dense crown; branchlets opposite or irregularly arranged, stout, 3-6 mm diam., red-brown, dark brown or gray; buds ovoid, 2-3 mm long, red-brown, the scales deciduous, ovate, strongly keeled toward the apex, acute, deciduous. Leaves persistent 3(-4) years, spirally arranged, slightly thickened, linear, gradually tapered at either end, 6-13 cm × 4-8 mm, acute, margins revolute, dull green, midrib prominent on lower surface, grooved on upper surface, 1 mm wide; the stomatal bands inconspicuous but wider than the midrib and margins, 2-2.5 mm wide.

Pollen strobili axillary, erect or horizontal, compound, 5-10 clustered together on a 1-2 cm subterminal portion of the branchlet, 0.5 cm long when closed to 1.3 cm long when open for pollen dispersal; microsporophylls 1-5, radially symmetrical, perisporangiate, each bearing 2-4 closely united sporangia.

Ovules sessile or on short peduncles to 2 mm long; subtending scales persistent, 15-20, spirally arranged, imbricate, ovate to flabelliform, slightly keeled, 1-2 × 1.5-4 mm; arils oblong-cylindrical, 1.5 cm long, open at the apex, orange; seeds hard, ovoid, 4-6 mm long, ca. 3 mm wide, 2-angled at the apex. Chromosome number unknown.

This rare genus consists of a single species endemic to New Caledonia. The compound pollen strobili of *Austrotaxus* have a unique arrangement whereby the stalks of the microsporophylls are vestigial, the microsporangia of each microsporophyll are fused to each other and partially adnate to the microsporophyll itself (Saxton, 1934; Wilde, 1975).

Austrotaxus may also be distinguished by its apparent lack of spiral thickenings on the tracheid walls that is so distinctive of Taxaceae wood (Greguss, 1955). The stomata are amphicyclic as in *Taxus*, unlike the monocyclic stomata of *Amentotaxus*, *Pseudotaxus*, and *Torreya* (Florin, 1948c). Taxane alkaloids—the same class of diterpene alkaloids that has produced the cancer-mitigating compound, taxol, from *Taxus brevifolia* Nutt.—have been identified in the leaves of *Austrotaxus* (Gueritte-Voegelien et al., 1987).

Austrotaxus is not cultivated to any extent in this country.

1. Species Not in Cultivation

AUSTROTAXUS SPICATA Compton, J. Linn. Soc. Bot. 45: 427-428. 1922.

2. Representative Specimens

NEW CALEDONIA: Mt. Ignambi, *H. E. Moore 10476* (A), *P. S. Green 1784* (A); Mt. Pannie, *D. J. de Laubenfels P579* (A); Mandjelia, *G. McPherson 2753* (A); between Farino and Table Unio, *J. T. Buchholz 1519* (BH); La Foa, *L. H. MacDaniels 2345* (BH), *2371* (BH).

C. PSEUDOTAXUS

PSEUDOTAXUS W. C. Cheng, Res. Notes Forest. Inst. Nat. Centr. Univ. Nanking Dendrol. Ser. 1: 1. 1947. Type species: *P. chienii* (W. C. Cheng) W. C. Cheng, Res. Notes Forest. Inst. Nat. Centr. Univ. Nanking Dendrol. Ser. 1: 1. 1947. (Fig. 4)

Nothotaxus Florin, Acta Horti Berg. 14: 394. 1948.

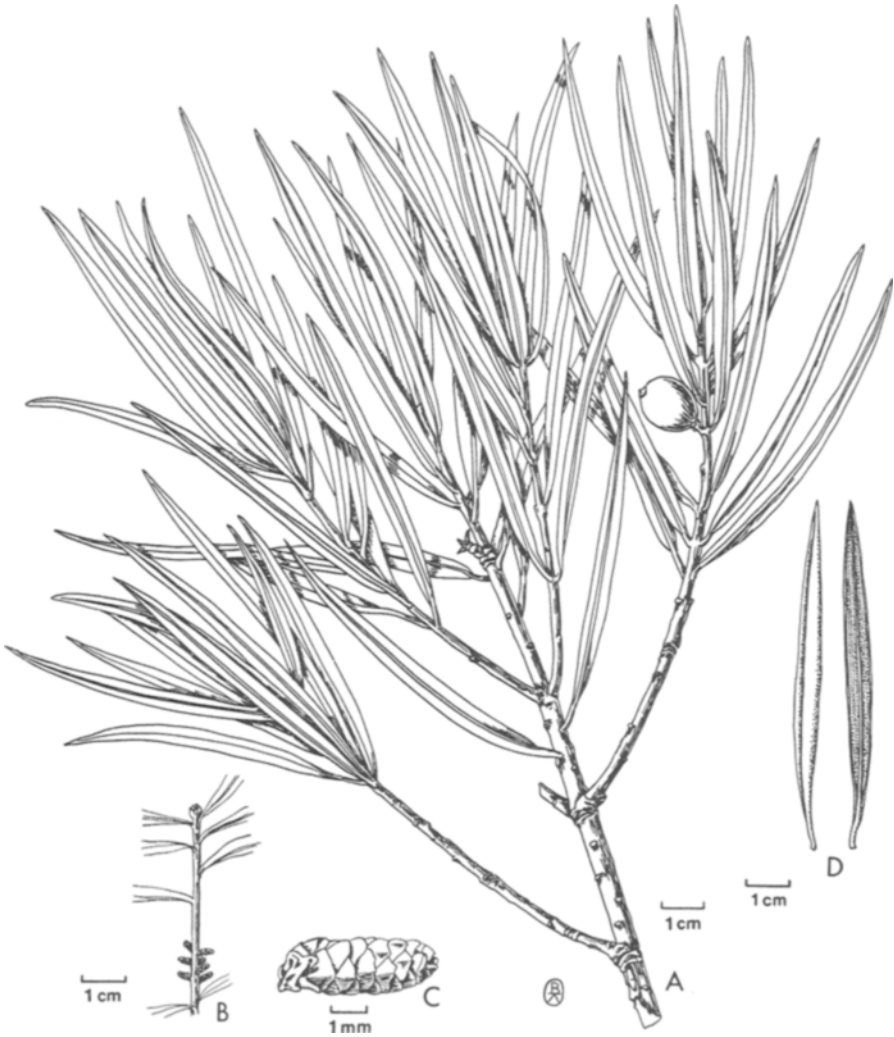


Fig. 3. *Austrotaxus spicata* Compton. **A.** Branchlets with megastrobilus and aril. **B.** Branchlet with pollen strobilus. **C.** Pollen strobilus. **D.** Adaxial (left) and abaxial(right) leaf surfaces. [After *H. E. Moore 10476 (BH)* and *P. S. Green 1784 (BH)*.]

Shrubs 2–4 m tall with branches in whorls; branchlets in 3's or subopposite or alternate, dark-brown to yellow-green; buds ovoid, 2 mm long, yellow-brown, the bud scales persistent, ovate to triangular-lanceolate, keeled, 1–1.5 × 1 mm, yellow-brown to gray-brown. Leaves persistent 3(–4) years, spirally arranged, linear, 12–25 × 2–4 mm, abruptly acuminate to cuspidate, papillose at the margins, petiole 1–2 mm long, midrib prominent on upper surface, the stomatal bands 0.5–1 mm wide, each nearly twice the width of the margins, glaucous.

Pollen strobili axillary, simple (or at least appearing so), 2–3 × 2–3 mm, with 8 spreading, decussate ovate or obovate, sterile scales below and 2 sterile scales among the microsporo-

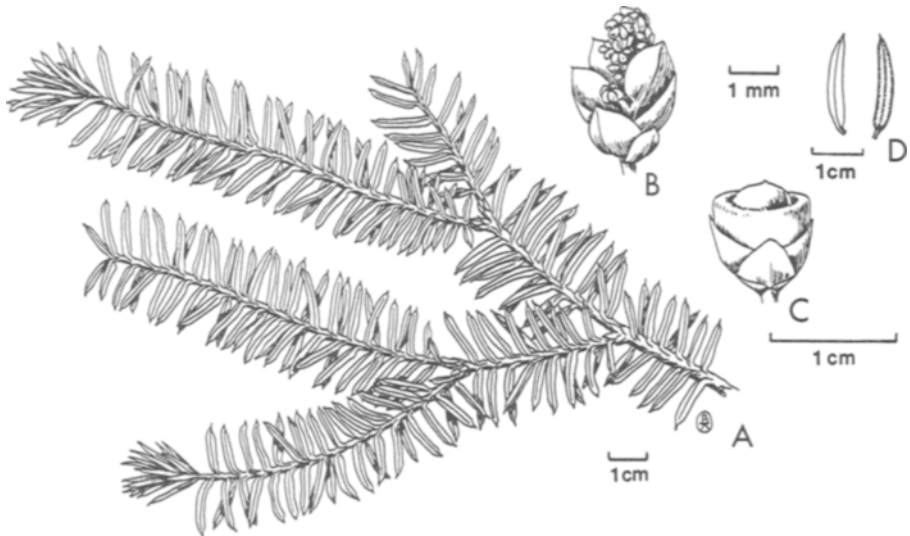


Fig. 4. *Pseudotaxus chienii* (Cheng) Cheng. A. Branchlet. B. Pollen strobilus. C. Megastrobilus and aril. D. Adaxial (left) and abaxial (right) leaf surfaces. [After S. Chen 1384 (A).]

phylls; microsporophylls 10, perisporangiate (rarely hyposporangiate near strobilus apex), radially symmetrical, peltate, each with (2-)4-6 united sporangia.

Ovules nearly sessile, subtended by 14-16 decussate, ovate, acute scales, the uppermost 5 mm long and hiding the young ovule; arils open apically, 5-7 mm long, white; seeds broadly ovoid, slightly compressed, 5×4 mm, with elliptic or rhombic-elliptic hilum. Chromosome number unknown.

A monotypic genus endemic to the Zhejiang province in eastern China, *Pseudotaxus* resembles *Taxus* but has more scales subtending the ovule, has a white aril, lacks microscopic papillae surrounding the foliar stomatal guard cells, and has monocyclic rather than amphicyclic stomata (Florin, 1948b, 1948c). The presence of two sterile scales in the middle of the pollen strobilus is unique in the family and is evidence for the trend of reduction in taxaceous pollen strobili (Wilde, 1975). There may be flavonoid differences, although no biflavones have been detected in *Pseudotaxus*, and three crystalline compounds have been identified in the wood (Ma et al., 1982, 1985). Whether or not taxane alkaloids are present in the leaves is unknown.

Pseudotaxus, which was only recently discovered and controversially named in 1947 (Florin, 1948d), is rare and is probably not cultivated even in its native China.

1. *Species Not in Cultivation*

PSEUDOTAXUS CHIENII (W. C. Cheng) W. C. Cheng, Res. Notes Forest. Inst. Nat. Centr. Univ. Nanking Dendrol. Ser. 1: 1. 1947.

Taxus chienii W. C. Cheng, Contr. Biol. Lab. Sci. Soc. China 4: 240. 1934.

Nothotaxus chienii (W. C. Cheng) Florin., Acta Horti. Berg. 14: 394. 1948.

2. Representative Specimen

CHINA: Zhejiang, Lungtsuan, Maoshan, *S. Chen 1384* (A) (ISOTYPE).

D. TAXUS

TAXUS L., Sp. Pl. 1040. 1753. Type species: *T. baccata* L., Sp. Pl., 1040. 1753. (Fig. 5)

Dioecious (except for *T. canadensis* Marsh.) trees or shrubs 3–9 m, rarely to 25 m tall; bark scaly, red-brown, purple-brown or chestnut-brown; branches irregularly arranged, erect or spreading; branchlets slender, yellow-green or olive green to red-orange or orange-brown, the second-year shoots often remaining green, at least in part; winter buds ovoid, conical or obovoid, 1.5–3 mm long, the apex acute or obtuse, often 2–4-angled at the apex, the scales imbricate, usually persistent [mostly deciduous in *T. chinensis* (Pilg.) Rehder)], thickened and slightly to strongly keeled especially toward the apex. Leaves persistent (3–)4 years, usually pectinate and 2-ranked, leathery, linear, abruptly narrowed at the petiole, 2–4.5 cm × 1–3 mm, acuminate to cuspidate or almost mucronate-apiculate, dark green to yellow-green on upper surface, petiole distinct, 1–2 mm long, widening into a broad decurrent base; dark green to yellow-green on upper surface, midrib usually prominently raised on the upper surface, sometimes also raised on the lower surface, with or without cuticular papillae, the stomatal bands each about twice the width of the margin, 0.2–1 mm wide, pale green or yellow-green, resin ducts lacking.

Pollen strobili simple, solitary, subsessile, the peduncles to 1 mm long, axillary on first-year branchlets, globose before expansion then short oblong-cylindrical, 2.5 mm diam. when closed, 4 × 2 mm at pollen release, green, yellow-green, or yellow; sterile scales all basal, ca. 10; microsporophylls 6–14, perisporangiate, radially symmetrical, peltate, each bearing 4–9 microsporangia.

Ovules solitary or occasionally paired in the axils of bracts on short branchlets or stalks which themselves are axillary on the first-, second- or occasionally third-year branchlet, sessile, subtending scales about 12–20, decussate, ovate to flabellate, concave, membranous, often rugose, nearly enclosed at maturity by the aril; arils open at the apex, 5–10 × 5–7 mm, green when young, sometimes remaining so, becoming orange or usually bright scarlet red at maturity; seeds hard, ovoid, 5–7 × 4–5 mm, becoming 2–4-angled at the apex, the hilum slightly depressed, ovate, triangular or square. Chromosome number, $n = 12$.

Taxus is a genus of 12 species (including two artificial hybrid species) distributed mainly in the Northern Hemisphere (Fig. 6). It is a taxonomically troublesome genus because of the variability and overlapping nature of the limited number of morphological features that are used to distinguish species. The genus might also be considered monospecific with clear-cut geographical subspecies as Pilger (1926) and others have treated it. It is convenient here, as in most treatments, to recognize the taxa at the specific level, although identification based on morphological characters is uncertain.

The species of *Taxus* occupy distinct geographical regions of the world, with four species in North America, one in Europe, and the remainder native to Southeast Asia (Fig. 6). The species ranges do not overlap except in Southeast Asia where, depending on taxonomic interpretation, there are at least four species present. The most widespread of the Asian species, *T. chinensis* (Pilg.) Rehder, is endemic to China, occurring mainly in the central and southern provinces. Cheng et al. (1978) have accepted two varieties, *T. chinensis* var. *chinensis*, which has papillae on the midrib of the abaxial surface of the leaf, and *T. chinensis* var. *mairei* (Lemée & A. Leveille) W. C. Cheng & L. K. Fu, which lacks papillae. These are the same taxa

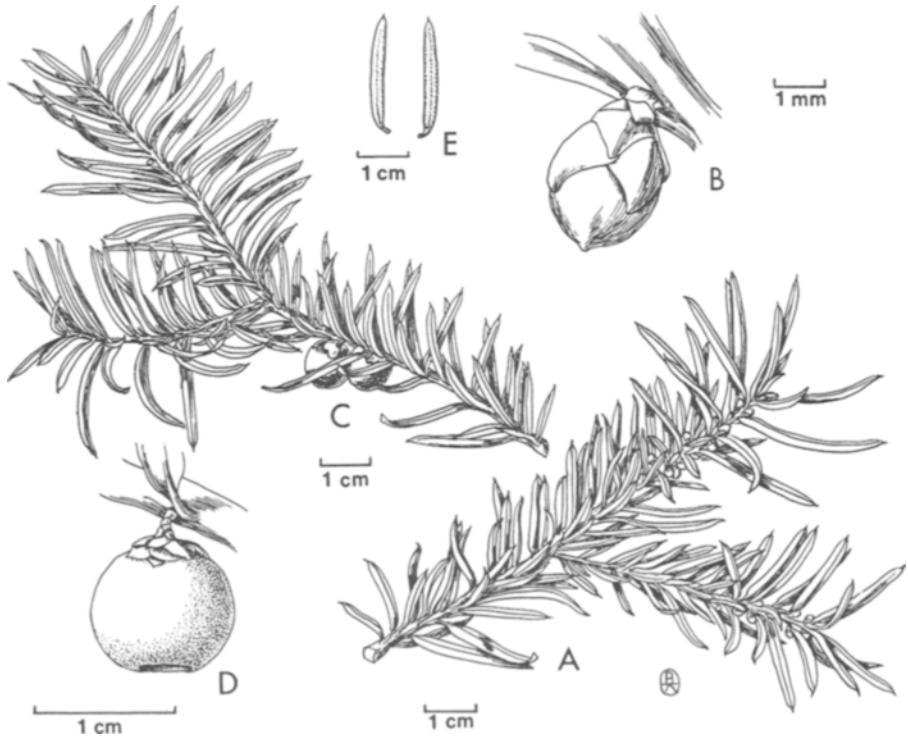


Fig. 5. *Taxus cuspidata* Siebold & Zucc. A. Branchlets bearing pollen strobili. B. Unopened pollen strobilus. C. Branchlet bearing megastrobili. D. Megastrobilus and aril. E. Adaxial (left) and abaxial (right) leaf surfaces. [From live material.]

that Hu (1964) earlier recognized as species. *Taxus chinensis* var. *mairei* has been collected in every province that the typical variety has, but is also found farther south and east in the provinces of Jiangxi (Kiangsi), Zhejiang (Chekiang), Guangdong (Kwantung), Fujian (Fukien), and Taiwan. *Taxus wallichiana* Zucc., principally of the eastern Himalayas and southern Tibet, in the wider sense, extends to western China (Yunnan province), the Philippines, and Celebes. Cheng and Fu (Cheng et al., 1975) have described *T. yunnanensis* from the Yunnan Province, and Li (1963, 1975) proposed *T. celebica* (Warb.) Li from the Celebes. However, Laubenfels (1978) merged *T. celebica* into *T. sumatrana* (Miq.) Laubenf., which he described from the high elevations of the Philippines, Celebes, and Sumatra. This Southeast Asian complex needs further collecting and systematic study.

Bud scales and leaf apices, features traditionally used to separate taxa, are variable and the differences slight, as is seen in Figure 7. Presence or absence of papillae on the lower surface of the leaves and variability in the persistence of the bud scales are two other features that have been used with limited success in the analyses of taxa in Southeast Asia (Cheng et al., 1978; Ferguson, 1978; Hu, 1964). Differences in stomatal band width and stomate density among several species have been reported (Nicolosi & Lineberger, 1982). Pollen morphology and leaf chemistry have not produced reliable characters (Baxter et al., 1958; Graf et al., 1958; Jones & Lynn, 1933; Nicolosi & Lineberger, 1982; Xi, 1986a).



Fig. 6. Native distribution of *Taxus* L.

Taxus differs from *Torreya* in its obviously alternate leaves and open red aril; from *Pseudotaxus* by its red aril, lack of sterile scales among the microsporophylls, and fewer scales subtending the ovule; from *Austrotaxus* by its simple pollen strobili and smaller leaves; and from *Amentotaxus* by its alternate leaves and simple, axillary pollen strobili. It is distinguished from *Cephalotaxus* by its shorter, alternate leaves and open, red aril.

The microsporangia of *Taxus*, as with *Pseudotaxus*, are distinctive among conifers in that they are radial (as opposed to being positioned only abaxially on the sporangiophore), which has led Wilde (1975) to suggest that the pollen strobilus is a reduced lateral one. The leaves of *Taxus* are distinctive because of the expanded, papillose subsidiary cells of stomata being amphicyclic as in *Austrotaxus* and resin canals lacking as in *Pseudotaxus* and *Austrotaxus* (Florin, 1948c). Cyanogenic glycosides probably contribute greatly to the toxicity of *Taxus* plant parts. Other biflavonoid compounds of the amentoflavone series, including sciadopitysin, have unknown effects (Khan et al., 1976; Ma et al., 1985; Morelli, 1976).

The compound in *Taxus* with the greatest current significance for man is a cancer cell-inhibiting, oxygen-rich diterpene called taxol. First isolated in the late 1960s (Wani et al., 1971) from the bark of *T. brevifolia* Nutt., it was available in short supply because six trees, each 100 years old, were required for the treatment of a single patient—a quantity that posed an immediate threat to the prosperity of this northwestern North American endemic. However, with the discovery of taxol precursors in related species, especially *T. baccata*, and in 1994 the development of the capability to completely synthesize taxol (Nicolaou et al., 1994c; Holten et al., 1994), the future of *T. brevifolia* became more secure. Further work by chemists continues to yield many derivative compounds, called taxoids, that are now commonly used in chemotherapy treatments for many types of cancer (Nicolaou et al., 1996).

The identification of *Taxus* species is nearly impossible in cultivation, where the most reliable information, native geographical distribution, is unavailable. Yew is a popular and useful ornamental plant that is easily propagated, resulting in an abundance of named cultivars, most of which cannot be identified without comparing the plants side by side.

The yew is planted for a variety of horticultural purposes and is particularly popular as a planting next to buildings and as hedges. This is true despite the fact that foliage and seeds are poisonous to some animals and humans and that the dark green foliage can cast a somber atmosphere to a planting site if these shrubs are planted in great abundance (Brown & Hull,

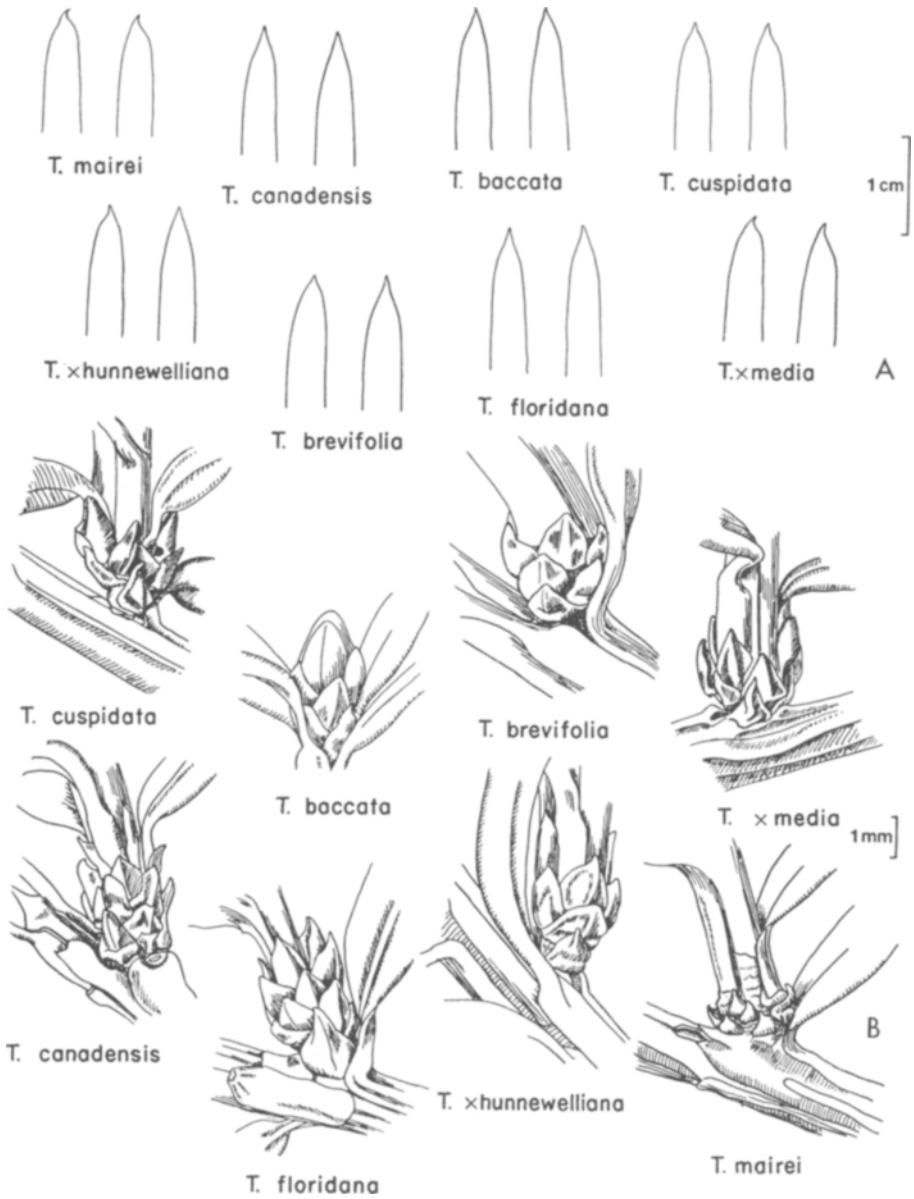


Fig. 7. Leaf apices and buds of seven species of *Taxus*.

1951; Graf et al., 1958). The pulp of the juicy aril is sweet and edible and can be used in jams, as long as the toxic seed is removed. Several authors have discussed cultivar growth habit, identification, and nomenclature, and have attempted comprehensive compilations of cultivars (Bailey, 1933; Chadwick, 1951; Chadwick & Keen, 1976; Cope, 1986; Cope & Vance, 1991; Dallimore, 1908; Den Ouden & Boom, 1965; Hatfield, 1921; Krussmann, 1979, 1983, 1985; Rehder, 1940; Wyman 1964). An excellent yew collection, now nearly 50 years old, of various cultivars from seven species of *Taxus* is maintained at Secrest Arboretum, Wooster, Ohio. The *Taxus* cultivars most commonly cultivated in the United States and Canada include *T. baccata* 'Fastiglata' and 'Repandens'; *T. cuspidata* 'Capitata', 'Green Wave', 'Nana', and 'Thayerae'; and *T. ×media* 'Brownii', 'Densiformis', 'Hatfieldii', 'Henryi', 'Hicksii', 'Hill', 'Nigra', 'Runyan', Sebian, and 'Wardii' (Cope & Vance, 1991). These and other, less common cultivars are listed in the Appendix according to growth rate, habit, and color.

1. Species Not in Cultivation

TAXUS GLOBOSA Schldl., Linnaea 12: 496. 1838.

T. baccata L. subsp. *globosa* (Schldl.) Pilg. in Engl., Pflanzenr. 4: 114. 1903.

T. mexicana Senilis, Pinaceae: 174. 1866.

T. SUMATRANA (Miq.) Laubenf., Kalikasan 7: 117–152. 1978.

Cephalotaxus sumatrana Miq., Flor. Ned. Ind. 2: 1076. 1859.

Taxus celebica (Warb.) H. L. Li, Woody Fl. Taiwan: 34. 1963.

Cephalotaxus celebica Warb., Monsunia 1: 194. 1900.

T. WALLICHIANA Zucc., Abh. Math-Phys. Cl. Konigl. Bayr. Akad. Wiss. Munch. 3: 803. 1843.

T. baccata L. subsp. *wallichiana* (Zucc.) Pilg. in Engl., Pflanzenr. 18: 112. 1903.

T. YUNNANENSIS W. C. Cheng & L. K. Fu in W. C. Cheng et al., Acta Phytotax. Sin. 13: 86–87. 1975.

2. Representative Specimens

Taxus globosa. EL SALVADOR: Chalatenango, *J. M. Tucker 1073* (BH, A). HONDURAS: Yoja, Santa Barbara Mts., 21 Mar 1949, *A. J. Chable s.n.* (A). GUATEMALA: El Progress, *J. K. Steyermark 43487* (A). MEXICO: Oaxaca, Tetillan, 11 Dec 1907, *C. Conzatti s.n.* (A); Tamaulipas, Gomez Farias, *A. J. Sharp et al. 50178* (A); Nuevo Leon, El Cerado, Puertos, *C. J. Mueller & K. Mueller 1337* (A); Hidalgo, Aqua Blanca, Dec 1945, *M. Martinez s.n.* (A); Hidalgo, Barranca, *C. G. Pringle 10808*.

T. sumatrana. PHILIPPINES: Luzon, Mt. Banaho, *D. J. de Laubenfels P668* (A); Luzon, Mt. Panai, January 1948, *M. D. Sulit s.n.* (A); Bengiut, *M. S. Clemens 17112* (A); TAIWAN: Tai Shu Shan, *D. J. de Laubenfels P670* (A), *P671* (GH).

T. wallichiana. CHINA: Sichuan, Mt. Omei, *W. K. Hu 8176* (A), *T. C. Lee 3237* (A), *W. P. Tang 18420* (A). BURMA: *F. K. Ward 9375* (A). NEPAL: Khola, 5 Aug 1983, *H. Ohba et al. s.n.* (A). INDIA: Dharmsala, Dharnkat, *R. R. Stewart 1938* (BH).

T. yunnanensis. CHINA: Yunnan, Xieniupindi, *Anonymous 0227* (A); Shangchung, *Anonymous 0419* (A); Champu-tung, *C. W. Wang 67414* (A); Yanghi-xian, *B. Bartholomew et al. 388* (A).

3. *Cultivated Species*Key to the cultivated species of *Taxus*

1. Bud scales deciduous; arils 4–7 mm long; rare in cultivation. *T. chinensis*
1. Bud scales persistent; arils normally >7 mm long.
 2. Leaves mostly acuminate; bud scales obtuse, not sharply keeled *T. baccata*
 2. Leaves cuspidate; bud scales acute, sharply keeled.
 3. Plants monoecious; arils globose or subglobose, 6–8 mm diam *T. canadensis*
 3. Plants dioecious; arils ovoid or ellipsoid, usually 13 mm diam.
 4. Plants endemic to small region in Florida, rare in cultivation; leaves often widely spaced on the branchlets *T. floridana*
 4. Plants native to northwestern North America or Asia or common in cultivation; leaves mostly close together on the branchlets.
 5. Leaves 2-ranked, flat and forming a V-trough on upper side of branchlet; native to northwestern North America, infrequently cultivated *T. brevifolia*
 5. Leaves scattered along branchlet and lacking V-trough on upper side of branchlet; native to Asia and commonly cultivated *T. cuspidata* and its hybrids, *T. ×hunnewelliana* and *T. ×media*

TAXUS BACCATA L., Sp. Pl. 1040. 1753. Common names: English yew, common yew.

Tree 12–20 m tall or densely branched shrub; bark scaly, flaky, red-brown to purple-brown; branchlets all green or all brown or mixed, first-year shoots always green; buds ovoid, almost globose, the scales persistent, only slightly keeled, obtuse. Leaves directed slightly forward along the shoot, 2–3(–4.5) cm × 3 mm, upper surface dark green, the lower surface yellow-green; petiole short, yellow-green, apex acuminate to acuminate-cuspidate, midrib prominent on upper surface. Arils 1 or 2 on a shoot, 1 cm × 6 mm, bright red; seeds ellipsoid, 6–7 × 5 mm, green-brown to brown, usually 2-angled or flattened at the apex.

A native of northern and middle Europe and the Mediterranean area (Asia minor, Caucasia, North Africa), English yew is cultivated extensively in Europe, North America, and, to some extent, Asia, North Africa, and Australia. The English yew has a long history of cultivation, having been grown by the Druids and nearly always present around ancient cemeteries and churches. Historically the wood of English yew has been used for furniture and bows. Horticulturally, it continues to be used for a variety of purposes, but most often as hedges and plantings next to buildings. Zone 5.

Representative specimens: HUNGARY: *S. Javorka 935* (BH). UNITED STATES (CULTIVATED): Virginia, Williamsburg, *J. T. Baldwin 12194* (BH); New York, Chataqua Co., Brocton, *J. F. Cornman 15* (BH); Massachusetts, Jamaica Plain, *S. Elsik et al. 872* (BH), 6119 (BH).

TAXUS BREVIFOLIA Nutt., N. Amer. Sylva 3: 86. 1849. Common names: Pacific yew, western yew.

T. baccata L. var. *brevifolia* Koehne, Deut. Dendrol.: 6. 1893.

T. baccata L. subsp. *brevifolia* Pilg. in Engl., Pflanzenr. 4: 113. 1903.

T. bourcier Carriere, Rev. Hort. 4: 228. 1854.

T. lindleyana Lawson ex Carriere, Traite Gen. Conif.: 523. 1855.

T. lindleyana A. Murr., Edinburgh New Philos. J., ser. 2, 1: 294. 1855.

Tree 5–25 m tall with slightly pendulous branches; bark scaly, dark red-brown; branchlets yellow-green to light brown, first-year shoots green; buds ovoid, the scales persistent but loose, sometimes yellow-brown. Leaves loosely spaced on the shoot, distinctly 2-ranked,

1.2–1.8 cm × 1–2 mm; light green on upper and lower surfaces, petiole yellow-green, sometimes longer than in other species, apex cuspidate, midrib raised on upper surface. Arils ovoid, 1 cm × 6–7 mm, scarlet; seeds ovoid, 5–6 mm long, 2–4 angled.

A native of western North America, British Columbia to California and Montana, Pacific yew was introduced into cultivation in Britain in 1854. It is planted there and in North America mostly in botanical gardens as specimen plantings. Zone 5.

Representative specimens: UNITED STATES: California, Trinity Co., *L. S. Rose 55089* (BH); Idaho, Latah Co., *W. C. Muenschner 13* (BH). UNITED STATES (CULTIVATED): New York, Tompkins Co., 23 Aug 1983, *J. Appling s.n.* (BH); Ohio, Hunting Valley, 12 Dec 1942, *E. D. MacDonald s.n.* (BH).

TAXUS CANADENSIS Marshall, *Arbust. Amer.* 151. 1785. Common names: Canada yew, American yew, ground-hemlock.

T. baccata L. subsp. *canadensis* Pilg. in *Engl., Pflanzenr.* 4: 113. 1903.

T. minor Britton, *Mem. Torrey Bot. Club* 5: 19. 1893.

T. baccata L. var. *minor* Michaux, *Fl. Bor.-Amer.* 2: 245. 1803.

T. baccata L. var. *procumbens* Loudon, *Arbor. et Frutic. Brit.* 4: 2067. 1838.

Monoecious or dioecious shrub to 2 m tall, with many ascending branches, the main stems often prostrate and rooting; bark scaly, brown; branchlets red-brown, the tips drooping slightly, first-year shoots green; buds ovoid or conical, green, small, the scales persistent, greater in number than the other species, keeled, acute or obtuse. Leaves crowded in a flat plane forming a deep V along the shoot, shorter near tips of the branchlets, 1–2 cm × 1–2 mm, light or dull green on upper surface, yellow-green on lower surface, sometimes becoming slightly red or purple in the winter sun, petiole 0.5–1 mm long; apex more cuspidate than acuminate, midrib inconspicuously raised on upper surface. Arils globose or subglobose, 6–8 × 6 mm, orange to scarlet; seeds ovoid, 5 × 4 mm, mostly 2-angled at the apex.

A native of eastern United States and Canada, south to Virginia, west to Manitoba and Iowa, this yew is cultivated occasionally in North America as a low cover or specimen planting. Outside North America it is typically found only in botanical gardens. *Taxus canadensis* is reported to be monoecious in most floras and manuals, but this has not been substantiated by examination of herbarium specimens. This species was introduced into cultivation in Britain in 1800. Zone 3.

Representative specimens: UNITED STATES: New York, Cortland Co., *A. J. Eames 5447* (BH); Maine, Piscataquis Co., *M. L. Fernald 297* (BH). UNITED STATES (CULTIVATED): New York, Monroe Co., 19 Aug 1917, *L. H. Bailey s.n.* (BH); Wellesley, Mass., 8 Aug 1932, *L. H. Bailey s.n.* (BH).

TAXUS CHINENSIS (Pilg.) Rehder, *J. Arnold Arbor.* 1: 51. 1919. Common name: Chinese yew.

T. baccata L. subsp. *cuspidata* (Siebold & Zucc.) Pilg. var. *chinensis* Pilg. in *Engl., Pflanzenr.* 18: 112–113. 1903.

T. cuspidata Siebold & Zucc. var. *chinensis* Rehder & E. Wilson, *Sarg., Pl. Wilson.* 2: 8. 1914.

T. chinensis (Pilg.) Rehder var. *mairei* (Lemee & A. Leveille) W. C. Cheng & L. K. Fu in W. C. Cheng, L. K. Fu & C. D. Chu in W. C. Cheng & L. K. Fu, eds., *Fl. Rep. Pop. Sinicae, Gymnosperms*, Tom. 7: 443–445. 1978.

T. mairei (Lemee & A. Leveille.) S. Y. Hu ex Liu, *Ill. Nat. Lign. Pl. Taiwan* 1: 16. 1960.

T. speciosa Florin, *Acta Horti Berg.* 14: 382–383. 1948.

Tsuga mairei Lemee & A. Leveille, *Monde Pl.* II, 16: 20. 1914.

Tree to 15 m tall, in cultivation a wide shrub; bark red-brown to red-orange or sometimes gray; branchlets yellow-green to light brown, first-year shoots green; buds smaller than in *T.*

baccata, the scales mostly deciduous or only partly persistent, thickened toward the base, rounded or only slightly keeled. Leaves sparse on the shoots, some curving backward, 1.2–3 cm × 2–3 mm, upper surface dark green, the lower surface gray-green to yellow-green, petiole short, yellow to yellow-green, apex abruptly acute, acute or acuminate, midrib inconspicuously raised on upper surface. Arils globose or subglobose, 4–7 mm diam., red or sometimes remaining green; seeds ovoid, 4–6 × 4 mm, 2–4-angled at the apex.

An endemic of China and Taiwan, Chinese yew is rarely cultivated in North America as a specimen planting or near buildings but is cultivated more frequently in Europe and presumably also in its native land. It was introduced into cultivation in Britain in 1908. Zone 6.

Representative specimens: CHINA: Jiangxi, *R. C. Ching* 5976 (A); Fujian, *H. H. Chung* 3581 (A); Zhejiang, *R. C. Ching* 2489 (A), *S. Chen* 1063 (A); Sichuan, *W. K. Hu* 8542 (BH), *W. P. Fung* 3796 (A). UNITED STATES (CULTIVATED): New York, Long Island, 18 Apr 1932, *L. H. Bailey s.n.* (BH); Massachusetts, Jamaica Plain, Arnold Arboretum, 25 Nov 1921, *C. M. Merrill s.n.* (BH).

TAXUS CUSPIDATA Siebold & Zucc., Fl. Japonic. Fam. Naturales 2: 108. 1846. Common name: Japanese yew.

T. baccata L. var. *cuspidata* Carriere, Traite Gen. Conif., ed. 2. 733. 1867.

T. baccata L. subsp. *cuspidata* Pilg. in Engl., Pflanzenz. 4: 112. 1903.

T. sieboldii hort.

T. cuspidata var. *capitata* hort.

Tree to 20 m tall, but mostly a shrub in cultivation; bark scaly, red-brown to dark brown; branchlets brown, first-year shoots yellow-green; buds oblong to ovoid, the scales persistent, keeled, tending to be acute. Leaves vertically arranged along the shoot forming an irregular V-shaped trough; 1.5–2.5 cm × 1.5–2.5 mm, upper surface dark or dull green, the lower surface yellow-green, petiole short, yellow to yellow-green, apex cuspidate, midrib prominent on upper surface, narrow or invisible on lower surface. Arils globose, 1 cm diam., red; seeds ovoid, 6 × 5 mm, mostly 3–4-angled at the apex.

A native of Japan, Korea, and northeastern China, Japanese yew is cultivated commonly and successfully in North America, Europe, and Asia. It was first planted in England in 1862. This popular species is utilized for many horticultural purposes including hedges, specimen plantings, and near buildings. Zone 4.

Representative specimens: JAPAN: Yamoto, 20 Jul 1953, *H. Tanaha s.n.* (BH); Ohmachi, 27 Aug 1951, *K. Uno s.n.* (BH). UNITED STATES (CULTIVATED): New York, Tompkins Co., *E. A. Cope* 528 (BH); Illinois, DeKalb Co., 28 May 1962, *J. Tate s.n.* (BH).

T. FLORIDANA Nutt., N. Amer. Sylva 3: 92. 1849. Common name: Florida yew.

Tree to 8 m tall or shrub, with crowded, short, spreading branches; bark scaly, purple-brown; branchlets red-brown, first-year and sometimes second-year shoots green; buds ovoid, the scales persistent, rounded or only slightly keeled, obtuse. Leaves forming a V-shaped trough on the shoot, 1.2–2.5 cm × 2–2.5 mm, upper surface dark green, the lower surface light green, petiole green, short, apex cuspidate, midrib obscure. Arils 1 cm × 6 mm, light red; seeds ovoid, 5–7 × 5 mm, usually 2-angled at the apex.

Florida yew is an endangered plant, endemic to the bluffs along the Apalachicola River in Gadsden and Liberty counties in northwestern Florida. It is cultivated only very rarely as specimen plantings in or near its native region. Zone 7.

Representative specimens: UNITED STATES: Florida, Liberty Co., *W. J. Dress & W. Read* 7710 (BH), *R. F. Thorne & W. C. Muenscher* 2623 (BH); Florida, Gadsden Co., 26 Apr

1936, *L. H. MacDaniels s.n.* (BH). UNITED STATES (CULTIVATED): Florida, Leon Co., *E. A. Cope 927* (BH).

TAXUS × HUNNEWELLIANA Rehder (*T. cuspidata* Siebold & Zucc. × *T. canadensis* Marshall), *J. Arnold Arbor.*, 6: 201. 1925. Common name: Hunnewell yew.

Shrubs with dense ascending branches or with vigorous growth and spreading branches; bark red-brown; branchlets brown, first-year shoots green; buds ovoid, the scales persistent, and less keeled than *T. cuspidata*, acute. Leaves 1–2.5 cm × 1.5–2.5 mm, the base more swollen and generally larger in all dimensions than *T. canadensis*, upper surface dark green, lower surface yellow-green, petiole short, apex sometimes less cuspidate than in *T. cuspidata*. Arils globose, 8–10 mm diam., red, ripening later than *T. canadensis*; seeds ovoid, 5–6 × 4–5 mm, 2–4-angled.

A chance hybrid originating about 1900 in Hunnewell Gardens, Massachusetts, this yew is cultivated mostly in botanical gardens, occasionally offered by nurseries specializing in conifers. Used in specimen plantings. Zone 5.

Representative specimens: UNITED STATES (CULTIVATED): New York, Tompkins Co., Cornell Plantations, *E. A. Cope 542* (BH); Massachusetts, Jamaica Plain, Arnold Arboretum, *G. P. DeWolf & P. Bruns 2186* (BH), *S. Elsik et al. 6122* (BH).

TAXUS × MEDIA Rehder (*T. baccata* L. × *T. cuspidata* Siebold & Zucc.), *J. Arnold Arbor.* 4: 107. 1923. Common names: hybrid yew, Anglo-Japanese yew.

Tree or shrub, often densely branched; bark red-brown to red-orange; branchlets olive-green, often red-brown above, not changing to brown (at least on the more vigorous growth); buds ovoid, the scales persistent, not as strongly keeled as *T. cuspidata*, obtuse. Leaves spreading distinctly in 2 ranks, 1.5–3 cm × 2–3 mm, upper surface green, the lower surface yellow-green, petiole short, yellow to yellow-green, apex cuspidate or cuspidate-acuminate, midrib more raised than in *T. baccata*. Arils globose, 1 cm long, red; seeds ovoid, 6 × 5 mm, 2–4-angled at the apex.

Taxus × media is a hybrid of the two most commonly cultivated species, *T. baccata* and *T. cuspidata*. This hybrid originated in 1900 in the Hunnewell Gardens in Massachusetts and is now planted more than any other yew species in North America. It is also cultivated in Europe. The plants are used extensively in horticultural plantings including hedges, specimen plantings, and plantings next to buildings. Zone 4.

Representative specimens: UNITED STATES (CULTIVATED): New York, Tompkins Co., *E. A. Cope 530* (BH), Nov 1979, *J. W. Appling 29* (BH); Massachusetts, Jamaica Plain, Arnold Arboretum, *R. Warren et al. 551* (BH); Illinois, Cook Co., *M. Nee 30082* (BH).

E. TORREYA

TORREYA Arn., *Ann. Nat. Hist.* 1: 130. 1838. Type species: *T. taxifolia* Arn., *Ann. Nat. Hist.* 1: 130. 1838. Common names: torreyia, fetid-yew (Fig. 8).

Tumion E. Greene, *Pittonia* 2: 194. 1891.

Dioecious, occasionally monoecious, small or large trees 5–30 m tall; bark gray-brown to light brown or orange-brown, smooth when young, narrowly fissured with age; branches opposite or whorled; branchlets opposite or subopposite, green the first year, changing to dark red-brown, brown or gray by the third year; buds ovoid, acute, prismatic, 3–12 mm long, the scales persistent or deciduous, few, imbricate, lustrous, ovate, keeled. Leaves persistent 3–4

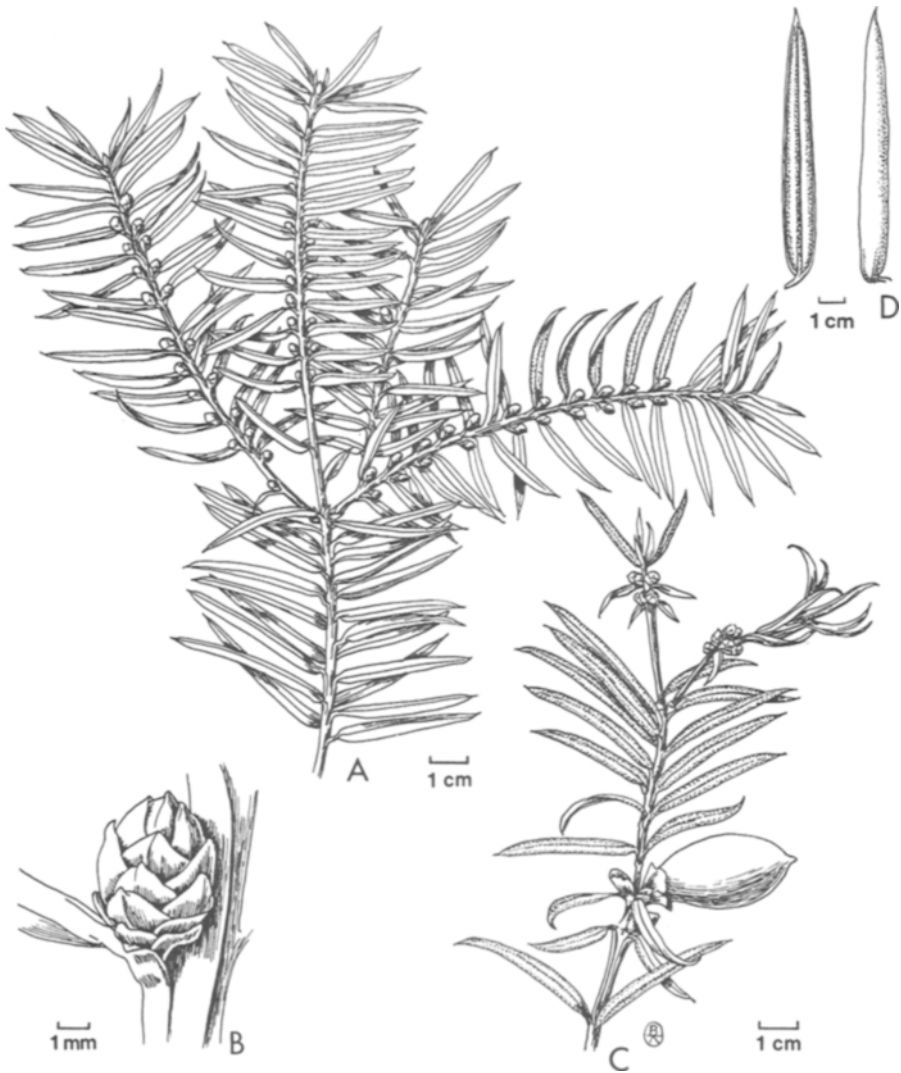


Fig. 8. *Torreya nucifera* (L.) Siebold & Zucc. **A.** Branchlets bearing pollen strobili. **B.** Pollen strobilus. **C.** Branchlet bearing young megastrobili with mature megastrobilus and aril. **D.** Adaxial (left) and abaxial (right) leaf surfaces. [From live material, *E. A. Cope 781* (BH) and *B. K. Boom 3224* (BH).]

years, spirally arranged but 2-ranked and appearing opposite by the twisting of the bases, linear-lanceolate, (1-)1.5-9 cm × 2-5 mm, often rounded at the base, acuminate to cuspidate with rigid, pale, spiny tips, petiole usually only distinguishable where it is decurrent on the branchlet, upper surface convex, often with a puffy appearance, sometimes with 2 thin longitudinal grooves, the midrib obscure or slightly impressed, lower surface broadly concave, the midrib raised, stomatal bands impressed or sunken, each much narrower than or equal to the

raised midrib, 0.2–1 mm wide, pale, becoming fulvous with age, resin canal 1, extending to the tip of the leaf in the center, below the vascular bundle, aromatic, fetid or odor lacking.

Pollen strobili simple, axillary, on the most recent year's branchlets, borne on minute recurved peduncles so that the strobili are most easily visible from the lower surface of the branchlet, 4–10 mm long, subtended by 12 or 16 keeled sterile scales arranged in 4 vertical rows; microsporophylls numerous (20–36), arranged in alternating whorls of 4, hyposporangiate (occasionally perisporangiate), dorsiventral, each with (3–)4(–6–7) microsporangia.

Ovules solitary, terminal on short shoots, the shoots paired on an abbreviated branchlet in the axil of a foliage leaf near the base of the current year's branchlet, entirely surrounded by and nearly completely adnate to the thin aril, subtended by 4 short (1–3 mm long) sterile scales, one ovule of the paired shoots often not developing; arils ovoid-oblong, drupe-like, (1.5–)2–3.5(–5) cm long, purple or tinged green, resinous, ripening the second season; seeds hard, woody, nearly as large as the aril, megagametophyte smooth to slightly or deeply ruminate. Chromosome number, $n = 11$.

Torreya is a genus of seven closely related species in North America and eastern Asia. Four of the species inhabit a band of eight provinces across central China. Of these, *T. jackii* Chun grows only in the eastern coast province of Zhejiang. The range of *T. grandis* Fortune from east to west includes Zhejiang, Fujian, Anhui, and Jiangxi to Hubei, where *T. fargesii* Franchet begins to appear. *Torreya fargesii* extends west through Sichuan to Yunnan, the province from which *T. yunnanensis* W. C. Cheng & L. K. Fu has been described. The morphological differences between these taxa are slight. *Torreya fargesii* and *T. grandis* are especially similar, distinguished principally by a ruminant megagametophyte in the seed in *T. fargesii* (Hu, 1927). There is overlap in other characters that have been used to distinguish species—e.g., grooves on the upper surface of the leaves, length of the spiny tips of the leaves, and branchlet color (Fig. 9). *Torreya jackii* is more readily discernable because of its longer, falcate leaves that terminate in a shorter, spiny tip. *Torreya yunnanensis* has recently been segregated from *T. fargesii* (Cheng et al., 1975) on the basis of the tendency of the former for longer, slightly less falcate, acuminate leaves and a different pattern of canals and ridges in the ruminant albumen. These species are not well known, as very little descriptive work has been published and only a few specimens are available in major herbaria.

A fifth Asian species, *T. nucifera* Siebold & Zucc. of Japan, is geographically separated from other species and is the most commonly cultivated species. Without this information identification is difficult, the only reasonably reliable feature being the color change of the branchlets in the third year of growth.

Torreya taxifolia Arn., the nearly extinct relict surviving in a tiny region in southeastern United States, and *T. californica* Torrey, a California endemic, show strong resemblance to the Asian torreyas but are easily distinguished from them. In contrast to torreyas from Asia, these species have a smooth or only slightly ruminant (irregular lobing, rippling or deeply grooved or channeled) megagametophyte in the seed, rather long, spiny leaf tips, and stomata that are only slightly sunken in the lower leaf surface. *Torreya californica* has considerably longer leaves than all other *Torreya* species except *T. jackii*, an endemic of a single province in China.

Torreya is unique in the Taxaceae in having embryogenesis with cleavage rather than simple polyembryony and a cell wall formed at the 4 or 8 nuclei stage (Doyle & Brennan, 1971; Tang et al., 1986), a purple aril that completely surrounds the seed, and a ruminant megagametophyte in the seed. The genus is distinguished from *Taxus* by its opposite or subopposite branchlets and lack of a prominent midrib on the upper surface of the leaf. *Torreya* is distinguished from *Cephalotaxus* by its sessile or subsessile arils, lack of a prominent mid-

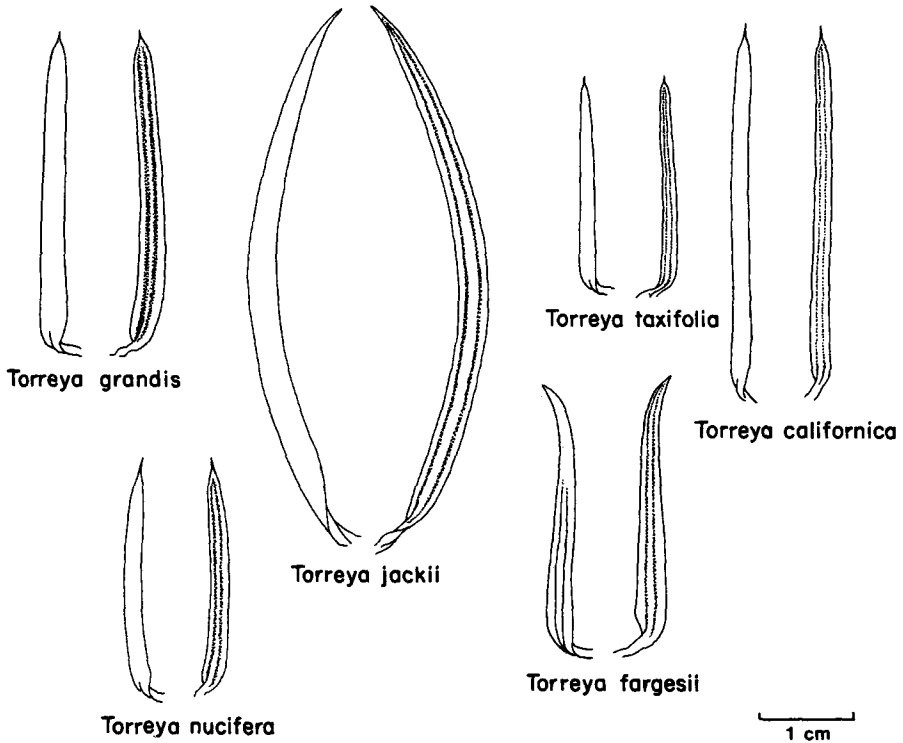


Fig. 9. Leaves of six species of *Torreya*. Left: Upper, adaxial surface. Right: Lower, abaxial surface showing stomatal bands (shaded).

rib, sunken stomatal bands that are narrower than or equal to the midrib and spine-tipped leaves.

Torreya is most closely related to *Amentotaxus*, with which it shares the characteristics of monocyclic stomata, foliar resin canal, absence of taxane alkaloids, long leaves, and large seeds (Hart, 1987; Janchen, 1950; Keng, 1969). It differs substantially from *Amentotaxus* in its simple pollen strobili, sunken stomatal bands, chromosome number, and the above-mentioned characteristics of the embryo.

Kayaflavone, which has not been found in other genera of Taxaceae, is the only biflavonoid that has been isolated from *Torreya* (He et al., 1983; Ma et al., 1985). Monoterpenes typical of other conifers and sesquiterpenes abound in the foliar resin of *Torreya*, the major components being limonene, alpha-pinene, and myrcene (He et al., 1985, 1986; Yatagai & T. Sato, 1986). Calcium oxalate is present in the bark (Chang, 1954) and the wood of *Torreya* contains resin (Bliss, 1918). The anti-cancer agent, taxol, present in *Taxus* and *Austrotaxus*, has not been identified in *Torreya*.

Torreya is rarely cultivated in this country, limited almost entirely to parks and arboreta. In China, the large oily seed is highly valued for food, and many trees have been propagated and planted for this purpose.

1. Species Not in Cultivation

T. YUNNANENSIS W. C. Cheng & L. K. Fu in W. C. Cheng et al., Acta Phytotax. Sin. 13: 87. 1975.

2. Representative Specimens

None seen.

3. Cultivated Species

Key to the cultivated species of *Torreya*

1. Leaves 3–9 cm long.
 2. Leaves falcate, to 9 cm long, the spiny tip <0.5 mm; megagametophyte ruminant *T. jackii*
 2. Leaves straight, <6.5 cm long, the spiny tip to 2 mm long; megagametophyte smooth or only slightly ruminant *T. californica*
1. Leaves mostly <3 cm long.
 3. Megagametophyte deeply ruminant; leaves with 2 longitudinal grooves on upper surface, spines at leaf tips usually <1 mm long *T. fargesii*
 3. Megagametophyte smooth or only slightly ruminant; leaves lacking longitudinal grooves (if present, extending only 1/5 of the distance toward tip) on upper surface, spines at leaf tips usually at least 1.5 mm long.
 4. Stomatal bands scarcely impressed on lower leaf surface; extremely rare; hardy only to Zone 8 *T. taxifolia*
 4. Stomatal bands impressed on lower leaf surface; less rare; hardy at least to Zone 6.
 5. Branchlets dark red-brown or brown by the third year; spines at leaf tips usually 2 mm long *T. nucifera*
 5. Branchlets light-colored or only gray by the third year; spines at leaf tips usually 1.5 mm long *T. grandis*

TORREYA CALIFORNICA Torrey, New York J. Pharm. 1(3): 49. 1852. Common names: California torreyia, California-nutmeg.

T. myristica Hook.f., Bot. Mag. 4780. 1854.

Tree, 5–30 m, conical or round-topped with slender, spreading, slightly pendulous branches; bark gray-brown to orange-brown, smooth, developing narrow furrows; branchlets green in the first year, turning brown by the third year; buds 8–10 mm long. Leaves stiff, 2.5–6 cm × 2–3 mm, acuminate or cuspidate with long (to 2 mm) spiny tips, dark green, midrib 1–1.5 mm wide; the stomatal bands 0.2–0.5 mm wide, narrower than the margins. Arils ovoid-oblong to ellipsoid, 2.5–3.5 cm long, green with purple markings; seeds 2.5–3.5 cm long, shallowly furrowed, the megagametophyte smooth or slightly ruminant.

A native of northern California, the California nutmeg is cultivated rarely in places other than parks and botanical gardens in the United States and Europe. It was introduced into cultivation in England in 1851. Zone 6.

Representative specimens: UNITED STATES: California, Mariposa Co., *W. J. Dress 4561* (BH), Butte Co., *R. T. Clausen 641* (BH). UNITED STATES (CULTIVATED): Pennsylvania, Philadelphia, 5 Aug 1969, *J. M. Fogg s.n.* (BH); Massachusetts, Jamaica Plain, Arnold Arboretum, 25 Nov 1921, *G. M. Merrill s.n.* (BH); California, San Francisco, Golden Gate Park, 28 May 1959, *E. McClintock s.n.* (BH).

TORREYA FARGESII Franchet, J. Bot. 13: 264. 1899. Common name: Farges torreyia.

Tree to 25 m tall or shrub; bark gray-brown; branchlets green the first year, becoming yellow-green the second year and finally gray. Leaves 1.5–2.5 cm long, acuminate, the spiny

tips 0.5–1 mm long; upper surface with 2 distinct grooves on either side of the midrib, the stomatal bands narrower than the green margins, pale green. Arils 1.6–2.5 cm long; seeds 1.6–2.5 cm long, globose-ellipsoid, the megagametophyte deeply ruminant almost to the middle.

A native of central and western China, this torreya is cultivated only in its native region, if at all, and rarely in botanical gardens.

Representative specimens: CHINA: Hubei, Tang-hsien, *E. H. Wilson 2108* (A); Yunnan, Lienfu, Kakatung, between Mekong and Yangtze Rivers, *H. F. von Handel-Mazetti 7848* (A); Yunnan, *H. T. Tsai 57582A* (A); Yunnan, Weixi, Lipiting Range, *J. F. Rock 9396* (A); Sichuan, *A. Henry 7096* (A); Tibet, Tsarung, *J. F. Rock 22656* (A).

TORREYA GRANDIS Fortune, *Gard. Chron.* 1857: 788. 1857. Common names: Chinese torreya, grand torreya, tall torreya.

T. grandis Fortune ex Gordon, *Pinetum*: 326. 1858.

T. nucifera var. *grandis* Pilg. in Engl., *Pflanzenr.* 4: 107. 1903.

Shrub or occasionally tree to 25 m tall; bark gray-brown; branchlets green the first year, yellow-green the second year and gray by the third year. Leaves 1.2–3 cm × 3 mm, the apex usually more cuspidate than acuminate, the spiny tip usually ca. 1.5 mm long, nearly rounded at the base, dark yellow-green; 2 longitudinal grooves usually present on upper surface for $\frac{1}{3}$ – $\frac{1}{2}$ the length, lacking aromatic or fetid odor. Arils obovoid, oblong-ellipsoid or cylindrical, 2–3 cm long; seeds 2–3(–5) cm long, obovoid-oblong or ellipsoid to subglobose, brown or red-brown, mucronate, the megagametophyte smooth or only slightly ruminant.

H. H. Hu (1927) and Ching (1927) described two forms and four varieties of these species on the basis of nut and leaf size and mature tree habit. These have long been grafted and grown for their nuts. Cheng and Fu (1978) described one of these as the cultivar 'Merrillii' (more properly 'Merrill') and synonymized the others under *T. grandis*.

A native of five provinces in eastern China, the edible nuts or seeds are an important food source in China. Chinese torreya is cultivated rarely in botanical gardens, having been introduced to Britain in 1855. Zone 6.

Representative specimens: CHINA: Hubei, *B. Bartholomew et al. 584* (A); Anhui, Huang Sang, *F. Y. Yuan 31039* (A); Anhui, *R. C. Ching 3036* (A); Anhui, *A. N. Steward 7143* (A); Zhejiang, King-huan, *R. C. Ching 2346* (A); Zhejiang, Sula-am-hsien, *Y. L. Keng 808* (A); Zhejiang, Tien-mo-shan, *T. Tang & W. Y. Hsia 97* (A); Zhejiang, Chu-chi-hsien, *S. Chen 326* (A), *Y. L. Keng 1188* (A).

TORREYA JACKII Chun, *J. Arnold Arbor.* 6: 144. 1925. Common name: jack torreya.

Tree 8–12 m tall, the trunk ca. 20 cm diam., or shrub with numerous ascending branches; branchlets spreading, somewhat pendulous, green-brown the first year, red-brown the second year, gray thereafter. Leaves falcate, (3.5–)5–9 cm × 4–5 mm, acuminate or attenuate, the spiny tip <0.5 mm; midrib inconspicuous, slightly impressed, aromatic. Arils obovoid, sessile or subsessile, ≥2.5 cm long, glaucous; seeds 2.5–3 cm long, the megagametophyte ruminant.

A native of China, this torreya is cultivated extremely rarely in arboreta (Arnold Arboretum may contain the only specimen cultivated in North America).

Representative specimen: CHINA: Zhejiang, Chen-chian, Ga Fong Keng, *R. C. Ching 1779* (ISOTYPE: A).

TORREYA NUCIFERA (L.) Siebold & Zucc., Abh. Math.-Phys. Cl. Konigl. Bayer. Akad. Wiss. 4: 234. 1846. Common names: Japanese torreyia, nut-bearing torreyia, kaya.

T. ignensis Doi & Morik., Bot. Mag. (Tokyo) 42: 534. 1928.

T. macrosperma Miyoshi ex Morik., Bot. Mag. (Tokyo) 42: 534. 1928.

Tree to 10 m, occasionally to 25 m tall with oval crown; branches numerous, stout, horizontally wide-spreading; bark gray to gray-brown, smooth, fissured and scaling with age; branchlets green in the first two years, dark red-brown or brown by the third year; buds shining, 3 mm long, the scales stiff. Leaves (1-)2-3.8 cm × 3-4 mm, green to blue-green, more often cuspidate than acuminate, the spiny tips to 2 mm long, stomatal bands equal in width to the midrib, pale to nearly white. Arils ellipsoid, 2.5 cm long, green, striped or tinged purple; seeds (1.6-)2-2.5 cm long, the megagametophyte smooth or only slightly ruminant. Cultivars: 'Aurea Variegata', 'Prostrata'.

A native of central and southern Japan, Japanese torreyia is cultivated in North America, Europe, and Asia. It was introduced as a cultivated plant in North America in 1860 and in England in 1764. This torreyia has been used for ornament and furniture-making; the seeds have been used as food. Two additional species earlier described from Japan (Morikawa, 1928) are included here. Zone 6.

Representative specimens: KOREA: Kyung Nam Do, *Y. C. Oh 86* (BH). JAPAN: Kamata, Tokyo-fu, *R. K. Bentlie & Y. Kurihara 10575* (BH). UNITED STATES (CULTIVATED): New York, Bronx, 8 Aug 1924, *K. R. Boynton s.n.* (BH); North Carolina, Biltmore, 28 Jul 1923, *W. H. Manning s.n.* (BH); California, Hollywood, 20 Jun 1916, *E. P. Bradbury s.n.* (BH).

TORREYA TAXIFOLIA Arn., Ann. Nat. Hist. 1: 130. 1838. Common names: Florida torreyia, stinking-cedar, gopherwood.

Tree to 12 m tall with open pyramidal crown; branches slightly pendulous; bark brown to orange-brown, scaly, irregularly fissured; branchlets green or yellow-green the second year, brown or gray thereafter; buds acute, 1 cm long, brown. Leaves linear to linear-lanceolate, 2-3.7 cm × 3 mm, rounded at the base, acuminate with sharp, piercing, spiny tips 1.5-2 mm long, rounded at the base, glossy green, aromatic, the petiole sometimes distinguishable and ca. 1 mm long, stomatal bands scarcely impressed, narrower than the midrib. Arils obovoid, 2.5-3 cm long, dark purple; seeds 2-3 cm long, the megagametophyte smooth or only slightly ruminant.

Florida torreyia is an endangered species. It is native only in Gadsden, Liberty, and Jackson Counties in Florida and Decatur County in southeastern Georgia. This species is cultivated in Florida and in botanical gardens in North America and Europe. It was introduced into cultivation in England in 1840. Zone 8. Cultivar: 'Argentea'.

Representative specimens: UNITED STATES: Decatur Co., Georgia, *R. F. Thorne et al. 3058* (BH); Liberty Co., Florida, *K. M. Wiegand & W. E. Manning 52* (BH). UNITED STATES (CULTIVATED): Leon Co., Tallahassee, Florida, *L. H. Bailey 6903* (BH).

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VI. Appendix: *Taxus* Cultivars by Growth Form

Growth Rate Dwarf (Height Not Exceeding 1 m in 10 Years)

FOLIAGE VARIEGATED YELLOW

T. baccata

- 'Elegantissima'
- 'Repandens Aurea'
- 'Pumila Aurea'
- 'Standishii'

T. cuspidata

- 'Fastigiata'

FOLIAGE GREEN

T. baccata

- 'Amersfoort'
- 'Argentea Minor'
- 'Compacta'
- 'Corona'
- 'Decora'
- 'Epacrioides'
- 'Ericoides'
- 'Fastigiata Nana'

- 'Knirps'
- 'Nana'
- 'Nutans'
- 'Page'
- 'Paulina'
- 'President'
- 'Procumbens'
- 'Prostrata'
- 'Pumila'
- 'Pygmaea'
- 'Repandens'
- 'Repens'

T. brevifolia

- 'Nana'

T. canadensis

- 'Dwarf Hedge'
- 'Fastigiata'
- 'Pyramidalis'
- 'Stricta'

T. cuspidata

- 'Bobbink'
- 'Densa'
- 'Midget'
- 'Minima'

T. ×hunnelli
'Richard Horsey'

T. ×media
'Fairview'
'Flushing'
'Heasleyi'

**Growth Rate Slow (Height Not
Exceeding 2 m in 10 Years)**

T. baccata
'Adpressa Variegata'
'Argentea Minor'

T. cuspidata
'Compacta'
'Intermedia'
'Nana'
'Vermeulen'
'Visseri'

T. ×media
'Compacta'
'Flemer'
'Newport'
'Pilaris'
'Pyramidalis'
'Sentinalis'

Growth Rate Typical of the Species

GROWTH HABIT CONICAL;
FOLIAGE VARIEGATED YELLOW

T. baccata
'Adpressa Aurea'
'Aurea'
'Aureovariegata'
'Aureoscens'
'Dovastonii'
'Dovastonii Aurea'
'Erecta Aurea'
'Semperaurea'
'Washingtonii'

T. canadensis
'Aurea'

T. cuspidata
'Aurea'
'Aureoscens'

GROWTH HABIT CONICAL;
FOLIAGE VARIEGATED WHITE

T. baccata
'Variegata'

GROWTH HABIT CONICAL;
FOLIAGE GREEN

T. baccata
'Adpressa'
'Adpressa Pyramidalis'
'Brevifolia'
'Cheshuntensis'
'Davisii'
'Erecta'
'Fowle'
'Fructoluteo'
'Glaucua'
'Hessei'
'Hibernica'
'Imperialis'
'Kadett'
'Lutea'
'Neidpathensis'
'Nigra'
'Overeynderi'
'Pyramidalis'
'Raket'
'Silver Green'
'Tardiva'

T. canadensis
'Compacta'

T. cuspidata
'Aristocrat'
'Brownii'
'Bulkii'
'Capitata'
'Green Wave'
'Hiti'
'Hoytii'
'Luteobaccata'
'Nana Pyramidalis'
'Nigra'
'Ovata'
'Robusta'
'Rustique'
'Sieboldii'
'Thayerae'

T. ×media
'Andorra'
'Brevicata'
'Brevimedia'
'Broad Beauty'
'Brownhelm'
'Brownii'
'Burr'
'Chadwick'
'Cliftonii'
'Cole'

'Coleana'
 'Dark Green Spreader'
 'Densiformis'
 'Devermannii'
 'Done Well'
 'Drulia'
 'Eddie'
 'Emerald'
 'Grandifolia'
 'Green Mountain'
 'Halloriana'
 'Hatfieldii'
 'Helleri'
 'Henryi'
 'Hill'
 'Hoogendorn'
 'Kelseyi'
 'Kobel'
 'Lodi'
 'Microphylla'
 'Mitiska Upright'
 'Moon'
 'Natrop'
 'Nigra'
 'Ovata'
 'Peterson'
 'Roseco'
 'Runyan'
 'Straight Hedge'
 'Stricta'
 'Wardii'
 'Wiltonii'

GROWTH HABIT GLOBOSE;
 FOLIAGE VARIEGATED YELLOW

T. baccata
 'Pumila Aurea'

GROWTH HABIT GLOBOSE;
 FOLIAGE GREEN

T. cuspidata
 'Wilsonii'
T. ×media
 'Dutweilleri'
 'Gem'
 'Kohlii'
 'Ohio Globe'
 'Taunton'
 'Wymanii'

GROWTH HABIT COLUMNAR

T. baccata
 'Columnaris'
 'Fastigiata'
 'Fastigiata Aurea'
 'Fastigiata Aureomarginata'
 'Fastigiata Aureovariegata'
 'Hibernica'
 'Melfard'
 'Stricta'
T. brevifolia
 'Erecta'
T. cuspidata
 'Adams'
 'Columnaris'
 'Erecta'
 'Pyramidalis'
 'Stovekenii'
T. ×media
 'Anthony Wayne'
 'Columnaris'
 'Costich'
 'Erecta'
 'Green Candle'
 'Hicksii'
 'Parade'
 'Robusta'
 'Totem'
 'Viridis'
 'Wellesleyana'

GROWTH HABIT LOW OR PROSTRATE

T. baccata
 'Cavendishii'
 'Decora'
 'Ericoides'
 'Michellii'
 'Procumbens'
 'Prostrata'
 'Repandens'
T. cuspidata
 'Bright Gold'
 'Depressa'
 'Prostrata'
T. ×media
 'Berryhillii'
 'Everlow'
 'Nidiformis'
 'Sebian'