

THE GENERA OF TAXACEAE IN THE
SOUTHEASTERN UNITED STATES¹ROBERT A. PRICE²TAXACEAE S. F. Gray, Nat. Arr. Brit. Pl. 2: 222. 1821, "Taxideae,"
nom. cons.

(YEW FAMILY)

Evergreen dioecious (or rarely monoecious) trees or shrubs. Foliage leaves entire, linear to linear-lanceolate, spirally arranged (often apparently 2-ranked) [or opposite in *Amentotaxus*], short-petiolate, with 2 stomatal bands on the abaxial surface; resin canal single, abaxial to the vascular bundle (or absent in *Taxus*, *Pseudotaxus*, and *Austrotaxus*). Wood without resin canals, axial wood parenchyma present or absent, helical thickenings present on the tracheid walls [apparently absent in *Austrotaxus*]. Pollen cones (microsporangiate strobili) apparently simple, borne singly in the axils of foliage leaves [or compound and

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The illustrations were drawn by Linda Vorobik under the supervision of the author. The illustrations of *Torreya taxifolia* are based on living material from the University of California Botanical Garden, on seeds collected in Georgia by the staff of Callaway Gardens, and on *W. F. Jacobs 8528* (uc) and *R. K. Godfrey 55449* (uc). The longitudinal and cross sections of the seed of *Torreya* are redrawn from photographs in Coulter & Land, while the arillate seed of *Taxus floridana* was redrawn from an original illustration supplied by Robert Godfrey.

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aggregated in *Amentotaxus* and *Austrotaxus*]; microsporophylls several per strobilus, more or less whorled, each with [2 or] 3–9 microsporangia borne in a radial arrangement (*Taxus*, *Pseudotaxus*) or developing fully only on the abaxial side (*Torreya*, *Amentotaxus*); pollen grains nonsaccate, lacking prothallial cells. Ovules arillate, borne singly at the ends of short axillary shoots³ bearing decussate [or spirally arranged] scale leaves; archegonia usually few per ovule, not clustered. Seeds with a stony coat, largely surrounded by the fleshy aril; embryo straight, cotyledons 2 (or occasionally 1 or 3). Chromosome number $2n = 22$ or 24 [14 in *Amentotaxus*]. (Including Amentotaxaceae Kudo & Yamamoto, Austrotaxaceae Nakai, Torreyaceae Nakai; Taxineae L. & A. Richard.) TYPE GENUS: *Taxus* L.

A small family of five genera and perhaps 20 species, the Taxaceae are widely distributed in the Northern Hemisphere in moist, forested habitats from the subarctic of Eurasia and North America to subtropical or even tropical areas of Central America and southeastern Asia. The monotypic *Austrotaxus* Comp-ton is endemic to New Caledonia, while *Taxus* L. ranges south of the equator on Sumatra and Celebes (Florin, 1963). Only the two most widespread genera, *Torreya* Arnott and *Taxus*, occur in North America, including the southeastern United States. The monotypic *Pseudotaxus* Cheng (*Nothotaxus* Florin) is endemic to eastern China, while *Amentotaxus* Pilger has four species in southeastern Asia, occurring from central and southern China, including Taiwan and Hongkong, to southern Vietnam and extreme eastern India (Alvin *et al.*; Ferguson, 1985; Florin, 1963). *Amentotaxus* is also known from fossils of Tertiary age in western North America and Europe, but it had disappeared from these areas by the Late Miocene or Early Pliocene (Alvin *et al.*; Florin, 1963).

The Taxaceae, both fossil and extant, are unique among the conifers in having arillate ovules borne singly at the ends of lateral short shoots, but with no evidence of a biaxial ovulate cone or ovuliferous scales. Thus Florin (1938–1945, 1948a) proposed that they form an evolutionary lineage separate from the conifers. However, the Taxaceae have the specialized pattern of proembryogeny typical of the modern conifers (Dogra; Doyle, 1963), and they share derived features of wood anatomy and pollen and leaf morphology with other modern families of conifers, particularly the Cephalotaxaceae, a monogeneric family native to eastern Asia. On the bases of overall similarity and preliminary phylogenetic analyses (Hart), it seems most likely that the Taxaceae are conifers, most closely related to *Cephalotaxus* Sieb. & Zucc. ex Endl., that have secondarily lost the coniferous ovulate cone organization, although there are no intermediates indicating how the ovules have come to be terminal in position.

Cephalotaxus (plum-yew, with nine species in Fu's treatment) is very similar to the Taxaceae in appearance and in a number of morphological features. It differs most prominently from the Taxaceae in having its young ovules borne

³In *Taxus* and *Torreya* the ovule-bearing short shoots are axillary to scale leaves borne on very short axillary shoots, while in the other genera they arise from the axils of foliage leaves (Florin, 1948a). In *Torreya* there are usually two ovuliferous shoots on each dwarf axillary shoot, but only one ovule generally matures.

in pairs along a cone axis. Each pair of ovules is subtended by a bract and is associated with a small outgrowth that has been interpreted as an extremely reduced ovuliferous scale (Florin, 1951; Singh, 1961). Generally only one or two ovules mature per cone. The ovular integument differentiates into an inner stony layer and an outer fleshy layer, making the seed similar in structure and appearance to those of *Torreya* and *Amentotaxus*, but there is no evidence of a separate aril in the development of the ovule (Singh, 1961).

Until the early 1900's the Taxaceae were often treated as including both the Cephalotaxaceae and the Podocarpaceae (Pilger, 1903, 1916b), primarily on the grounds that these groups have fleshy structures surrounding the seed and often have the ovuliferous scales greatly reduced. The Podocarpaceae are very diverse in their ovulate-cone morphology. Cones of some species are highly reduced and bear only a single ovule, while the more primitive members of the family have prominently biaxial ones with a number of ovules (Quinn; Sporne). The Podocarpaceae have a unique binucleate cellular stage in their early embryogeny, and all but two of the genera have an epimatium (an unusual structure generally interpreted as a modified ovuliferous scale that partially folds around the ovule) as the fleshy structure associated with the seed (Florin, 1958b; Quinn). The aril surrounding the seed of the Taxaceae arises as an outgrowth at or just below the base of the ovular integument (Coulter & Land; Keng; Loze). Elsewhere among the conifers, a comparable structure occurs only in the podocarpaceous genus *Phyllocladus* L. & A. Rich. (Sporne), a highly derived group otherwise very dissimilar from the Taxaceae. The Taxaceae and Podocarpaceae also differ in wood anatomy, pollen structure, and chemistry, and there is thus little evidence of a close relationship between the two families (see Florin, 1958b; Hegnauer, 1962, 1986; Phillips).

Two tribes are often recognized in the Taxaceae, following the treatment of Janchen. In plants of tribe Torreyae Janchen, including *Torreya* and *Amentotaxus*, the microsporangia are borne abaxially on the microsporophylls (vs. radially arranged in tribe Taxeae) and the aril tightly invests the mature seed and is largely adnate to the seed coat (Florin, 1948a; Keng). In these two genera the free portion of the aril is displaced toward the apex of the ovule by intercalary growth, while in the three genera of tribe Taxeae (*Taxus*, *Pseudotaxus*, and *Austrotaxus*) the entire aril remains free from the ovular integument and forms a cuplike structure around the seed (Florin, 1948a). The genera of tribe Taxeae also lack the foliar resin canal present in *Torreya*, *Amentotaxus*, and the outgroup *Cephalotaxus* (Gaussen). *Austrotaxus* is unique in the family in having the microsporangia partially connate (Saxton; Wilde) and in apparently lacking helical thickenings on the tracheid walls (Greguss, 1955; Phillips). It has recently been found, however, to produce taxane alkaloids, which had previously been known only from *Taxus* (Guéritte-Voegelein *et al.*).

Chromosome numbers have been reported for three of the genera of Taxaceae. Counts of $2n = 24$ have been obtained for four species of *Taxus* (Dark; Sax & Sax; Sugihara, 1946b). This is presumably the primitive chromosome number for the family, since it has also been obtained for several species of the outgroup genus *Cephalotaxus* and is apparently the primitive number for the conifers generally (Ehrendorfer; Khoshoo, 1961, 1962). Eleven of the chro-

mosomes in *Taxus* are metacentric or submetacentric, while the shortest one is subtelocentric (Dark; Sax & Sax).

The chromosome number $2n = 22$ has been obtained from two species of *Torreya*, *T. nucifera* (L.) Sieb. & Zucc. (see, for example, Tahara, Terasaka) and *T. californica* Torrey (see Gaussen). All of the chromosomes of *T. nucifera* are apparently metacentric or submetacentric (Terasaka). The count of $2n = 22$ has also been reported for *Amentotaxus argotaenia* (Hance) Pilger by Sugihara (1946a), but his illustration is unclear. In contrast, Chuang & Hu provided an excellent illustration of the chromosomes of *A. formosana* Li (as *A. argotaenia*), with $2n = 14$, equaling the lowest chromosome number known for any gymnosperm (see Khoshoo, 1961). All of the chromosomes in this species are clearly heterobrachial, and two are markedly shorter than the rest (Chuang & Hu). Counts for other populations of *Amentotaxus* and for *Austrotaxus* and *Pseudotaxus*, as yet unstudied, are much needed.

The proembryogeny of the Taxaceae is similar to that of other groups of conifers, including *Cephalotaxus* and members of the Podocarpaceae (see reviews in Dogra; Doyle, 1963; Doyle & Brennan; Singh, 1978). After cell walls are formed, there is a single upper tier of cells that are open at the top, with an irregularly storied group of cells below. There is a trend among the gymnosperms toward reduction in the number of free-nuclear mitotic divisions in the proembryo prior to cell wall formation. Eight sets of free-nuclear mitoses are found in *Ginkgo*, and there are still higher numbers in the cycads, while six sets or fewer occur in the conifers (Dogra; Singh, 1978). There are usually four sets of free-nuclear mitoses in *Cephalotaxus*, *Taxus*, *Pseudotaxus*, *Amentotaxus*, and *Austrotaxus* (Buchholz, 1940; Chen & Wang, 1978, 1984a, b; Saxton; Singh, 1961, 1978; Sterling, 1948; Sugihara, 1946a, b), while in *Torreya* the number of such divisions has been reduced to two or three sets, yielding a four- or eight-celled proembryo (see review in Doyle & Brennan). Each of these genera frequently exhibits simple polyembryony. Cleavage polyembryony has been documented in *Torreya* (Chen & Wang, 1984a; Doyle & Brennan), but not in the other genera of Taxaceae and only as a rare event in species of *Cephalotaxus* (Singh, 1961).

The microsporangiate strobili of the Taxaceae are diverse in structure and have been the subject of varied morphological interpretations (see, for example, Florin, 1948a; Sporne; Wilde). In *Amentotaxus* the strobili are compound structures with some 20 to 30 small strobilar units arranged in a more or less decussate fashion along the axis (Keng; Wilde). The outgroup *Cephalotaxus* also has compound microsporangiate branches, with each lateral strobilus in the axil of a bract, indicating that a compound strobilus may be primitive in the Taxaceae (Wilde). No bracts are evident subtending the lateral units in *Amentotaxus*, each of which bears eight to 12 microsporophylls in *A. argotaenia*. *Austrotaxus* also has an unusual spikelike strobilar structure, in which the very reduced sporangia-bearing structures occur in the axils of spirally arranged bracts along the cone axis. Based on the pattern of vasculature, Wilde has interpreted the axillary structures as highly reduced lateral cones in which the sporophyll stalks are virtually absent and the sporophylls and sporangia are partially fused. *Pseudotaxus* seemingly has simple pollen cones in the axils

of foliage leaves, but two scale leaves are positioned on the axis between whorls of sporophylls (Florin, 1948b; Wilde), possibly indicating reduction from a more complex structure. *Taxus* has pollen cones rather similar to those of *Pseudotaxus* (but lacking sterile scales between the sporophylls), while *Torreya* has simple axillary pollen cones without sterile scales.

The radial arrangement of microsporangia in *Taxus* and *Pseudotaxus* is very unusual among the conifers and is somewhat reminiscent of the arrangement of sporangia in *Equisetum* L. (Sporne). Radially arranged microsporangia are also sometimes found at the apices of strobili in *Cephalotaxus* and *Amentotaxus*, in which the sporangia are usually fully developed only on the abaxial surface (Wilde). By analogy, Wilde has thus suggested that the sporangia-bearing structures of *Taxus* and *Pseudotaxus* may be equivalent to reduced lateral cones. In *Torreya*, however, the sporangial initials are radially arranged, and those on the adaxial side abort early in development to give the asymmetric arrangement seen at maturity (Coulter & Land).

The bark of *Taxus* and *Torreya* is unusual in having fibers with prominent crystals of calcium oxalate on the outer cell walls (Chang; Lotova). Crystalliferous fibers apparently are also present in *Amentotaxus* but are absent in *Austrotaxus* and in the outgroup *Cephalotaxus* (Outer & Toes).

Resin canals are absent in both the bark and the wood of Taxaceae and Cephalotaxaceae (Chang; Phillips; Suzuki, 1979a), although they are present in the leaves and arils of *Torreya* and *Amentotaxus*, as well as in the leaves and fleshy seed coat of *Cephalotaxus* (Keng; Singh, 1961). Individual resiniferous parenchyma cells are apparently present in the wood of *Cephalotaxus* (Greguss, 1972) and also in that of *Torreya* (Bliss), in accord with the distinctive odor of the wood in several species of the latter. Resiniferous parenchyma cells are evidently absent from the stem wood of *Taxus* but may be present in the root wood (Bliss).

Helical thickenings on the secondary walls of the axial tracheids are a notable feature of the wood in Taxaceae and *Cephalotaxus* (Greguss, 1955; Penhallow; Phillips). Apparently they are usually absent in *Austrotaxus* (Gaussen; Greguss, 1955), although according to Phillips they were reported for this genus by Prince. The form and distribution of helical thickenings on the tracheids of Taxaceae are strikingly similar to those of *Cephalotaxus* but differ from those found in some of the Pinaceae (Penhallow; Yoshizawa *et al.*).

Leaf anatomy has proved particularly useful in differentiating the genera of Taxaceae (Ferguson, 1978; Florin, 1931, 1948b, 1951) and has often allowed unequivocal identification of fossil leaves. *Amentotaxus* is notable for the star-like arrangement of subsidiary cells around the guard cells, with some of the subsidiary cells shared by adjacent stomata. The outer surface of the subsidiary cells is prominently thickened and papillate in *Taxus* but unthickened in *Pseudotaxus*. The stomata are monocyclic in *Torreya* and *Amentotaxus* and are usually so in *Pseudotaxus*, while they are amphicyclic in *Taxus* and *Austrotaxus*.

The pollen grains of Taxaceae are nonsaccate and lack prothallial cells, as is also the case in the Cephalotaxaceae, Sciadopityaceae, and Cupressaceae (including Taxodiaceae) (Erdtman, 1957, 1965; Singh, 1961, 1978; Ueno, 1959, 1960; Wodehouse). Presence of pollen saccae (as in most Pinaceae and Po-

docarpaceae and several extinct groups of conifers) and two prothallial cells (as in Pinaceae and *Ginkgo*, with secondarily higher numbers in Araucariaceae and most Podocarpaceae) are apparently the primitive states among the conifers (see Florin, 1951; Millay & Taylor; Singh, 1978). The sculpture and structure of the pollen grains of the Taxaceae are similar in general features to those of the Cephalotaxaceae and Cupressaceae (Owens & Simpson; Ueno, 1959), although unique features have recently been ascribed to *Amentotaxus* (Xi, 1986a, b). The Taxaceae are wind pollinated, as are virtually all gymnosperms, and have a pollination-drop mechanism of pollen capture, as is the case in *Ginkgo* and a number of groups of conifers, including the Cephalotaxaceae and Cupressaceae (Doyle, 1945; Singh, 1978).

The Taxaceae are one of several gymnospermous groups in which dioecy is coupled with a seed-dispersal syndrome involving mammals or birds as vectors (Givnish). *Taxus* exhibits a typical pattern of characters related to bird dispersal, with the attracting aril becoming sweet and red when the seeds ripen, while the seed itself is toxic and protected by a hard coat. The large, edible seeds of *Torreya*, with their dull purplish, resinous aril, are well suited to mammal dispersal. The seeds of *Torreya taxifolia* are highly sought after by squirrels (U. S. Fish & Wildlife Service). Field studies are needed to determine the dispersal mechanisms in the other genera, although preliminary morphological and chemical data tend to suggest bird dispersal in the other two genera of Taxaceae.

Studies of the natural-product chemistry of the Taxaceae have been largely restricted to the genera *Taxus* and *Torreya*, with the exception of preliminary studies of the biflavonoid composition of *Amentotaxus* and *Pseudotaxus* (see reviews in Geiger & Quinn, 1975, 1982; Hegnauer, 1986) and of a few of the compounds extractable from the wood of *Pseudotaxus Chienii* (Cheng) Cheng (Ma *et al.*, 1982) and the leaves of *Amentotaxus argotaenia* (Ma *et al.*, 1986). What is known of the chemistry of the Taxaceae does not provide evidence favoring its treatment as a group separate from the other families of conifers (Hegnauer, 1962, 1986).

Only the amentoflavone series of biflavonoids appears to be present in the Taxaceae and Cephalotaxaceae, in contrast to the much greater diversity of biflavonoid structures found in the Araucariaceae, Cupressaceae (including Taxodiaceae), and Podocarpaceae (Geiger & Quinn, 1975; Hegnauer, 1962, 1986). Kayaflavone, the sole biflavonoid reported from four species of *Torreya* (see Geiger & Quinn, 1975; He *et al.*, 1983; Ma *et al.*, 1985), has not been found in *Amentotaxus*, *Pseudotaxus*, or *Taxus*, while the parent compound amentoflavone is the only biflavonoid reported to date from *Amentotaxus*. Mono-, di-, and trimethyl ethers of the series, including sciadopitysin, ginkgetin, and sequoiaflavone have been isolated from *Taxus baccata* (M. S. Y. Khan *et al.*; Morelli), while only sciadopitysin was reported from several other species of *Taxus* by Ma and colleagues (1985).

Leaf oils have apparently been investigated only in *Torreya*, in large part because foliar resin canals are absent in the other genera except for *Amentotaxus*. The major monoterpene components of *Torreya* leaf resin, including limonene, α -pinene, and myrcene, are also of wide occurrence elsewhere among

the conifers (He *et al.*, 1986; Hegnauer, 1962, 1986; Yatagai & Sato). A series of more unusual resin sesquiterpenes has also been isolated from the stem wood of *Torreya nucifera* (see reviews by Burke; Hegnauer, 1986), but only limited comparative studies have been conducted within the genus.

Taxus is notable for the highly poisonous taxane alkaloids, an unusual class of diterpene alkaloids that is characteristic of its leaves, stems, and seeds (Lythgoe; R. W. Miller). Some of these alkaloids, most notably taxol, have been the subject of considerable interest because of their potent antimitotic activity and potential utility as anticancer chemotherapeutic agents (Guéritte-Voegelein *et al.*; R. W. Miller). Taxane alkaloids had been considered to be unique to *Taxus* (Hegnauer, 1986, 1988) but have recently also been found to occur in *Austrotaxus* (Guéritte-Voegelein *et al.*). They are not present in *Torreya* but need to be thoroughly sought after in *Pseudotaxus*. A biosynthetically unrelated class of cytotoxic alkaloids is characteristic of *Cephalotaxus*, and these compounds are also under investigation for their anticancer activity (Chu; Huang & Xue). Alkaloids are of quite restricted distribution among conifers outside of the Taxaceae and Cephalotaxaceae, having been found only in a few members of the Pinaceae and in *Athrotaxis* D. Don (Cupressaceae *sensu lato*) (Hegnauer, 1988).

Taxus, which is widely grown as an ornamental hedge or tree in North America and Europe, is the only genus of Taxaceae with major economic importance. *Torreya* is of lesser importance as an ornamental, but it is valued in Asia for its wood, edible seeds, and seed oil. *Amentotaxus* and *Pseudotaxus* are of potential horticultural interest, but only *A. argotaenia* has been introduced into cultivation outside of China (Rushforth).

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KEY TO THE GENERA OF TAXACEAE IN THE
SOUTHEASTERN UNITED STATES

General characters: dioecious (rarely monoecious) evergreen shrubs or trees; foliage leaves alternate, appearing 2-ranked [or less commonly opposite], linear to linear-lanceolate, short-petiolate; pollen cones with whorled or tightly clustered microsporophylls; each sporophyll with [2 or] 3–9 abaxial or radially arranged microsporangia; pollen nonsaccate, lacking prothallial cells; ovules borne singly, terminating short axillary shoots; seeds arillate, with hard coat; cotyledons 2 (rarely 1 or 3).

- A. Seed ca. 2–5 cm long, completely surrounded by a greenish or purplish aril; leaves sharply pointed, aromatic when bruised, with a resin canal. 1. *Torreya*.
- A. Seed < 1 cm long, partially enclosed by a cup-shaped red aril; leaves not sharply pointed or strongly aromatic, without a resin canal. 2. *Taxus*.

Tribe TORREYEAE Janchen

1. *Torreya* Arnott, Ann. Nat. Hist. 1: 130. 1838, nom. cons.

Evergreen dioecious (rarely monoecious) trees with branches seemingly in whorls. Bark fissured. Wood with little or no axial parenchyma, persistently aromatic. Foliage leaves spirally arranged (appearing 2-ranked due to twisting of the leaf bases), linear to linear-lanceolate, sharply pointed at apex, strongly aromatic when bruised [or slightly so in *T. grandis*]; abaxial surface with 2 narrow, whitened [or sometimes brownish] stomatal bands with sunken stomata; resin canal single, abaxial to the vascular bundle. Pollen cones short-stalked, borne singly in leaf axils of the current year; microsporophylls in ca. 6–8 whorls of 4 per strobilus, distal to a series of tightly clustered decussate scale leaves; sporangia abaxial, usually 3–5 per sporophyll. Ovules borne singly, terminating short secondary lateral shoots, generally with 2 such ovuliferous shoots borne in the axils of scale leaves on a primary dwarf shoot axillary to a foliage leaf, usually only 1 ovule maturing per associated foliage leaf. Seeds ca. 2–5 cm long, surrounded by the resinous greenish or purplish aril, maturing the second year; seed coat heavily sclerified, adnate to the surrounding aril except at the distal tip; gametophytic storage tissue irregularly channeled (“ruminant”); embryo distal, very small when seed is shed. Chromosome number $2n = 22$. (*Tumion* Raf.) TYPE SPECIES: *Torreya taxifolia* Arnott. (After John Torrey, 1796–1875, noted American botanist.)—TORREYA, STINKING CEDAR.

A genus of seven species in moist temperate areas of eastern Asia and North America, with two native to the United States (*Torreya californica* Torrey in California and *T. taxifolia* Arnott in Florida and adjacent Georgia), one to Japan (*T. nucifera* (L.) Sieb. & Zucc.), and four to central and southern China (see the recent treatment in Cheng & Fu) and adjacent Burma (Florin, 1963). *Torreya* had a more extensive Northern Hemisphere range during Mesozoic and Tertiary times. The oldest fossils of the genus, from Great Britain and southern Scandinavia, are of middle Jurassic age, and the genus persisted in central and southern Europe until the Pliocene (Florin, 1958a, 1963).

Torreya most closely resembles *Amentotaxus* (and *Cephalotaxus*) in having large, drupelike seeds and elongate leaves with a single resin canal. *Torreya* differs from these genera and the remainder of the Taxaceae in having narrower stomatal bands with sunken stomata on the abaxial leaf surface (Ferguson, 1978; Florin, 1931), a pungent aromatic odor when its foliage is bruised, simple rather than compound microsporangiate strobili, and highly channeled (“ruminant”) gametophytic storage tissue in its seeds. The last feature is unique among the gymnosperms and is caused by the irregular growth of megagametophytic tissue into the surrounding nucellar and integumentary tissues (Coulter & Land). It has given rise to the name “California nutmeg” for *Torreya californica*.

Torreya is apparently not divisible into clearcut infrageneric groups supported by multiple characters but has been divided into sect. NUCIFERAE Hu, with only slightly channeled seed-storage tissue (*T. nucifera* and *T. grandis* Fortune only), and sect. TORREYA (sect. *Ruminatae* Hu), with prominent channeling of the seed tissue (Cheng & Fu).

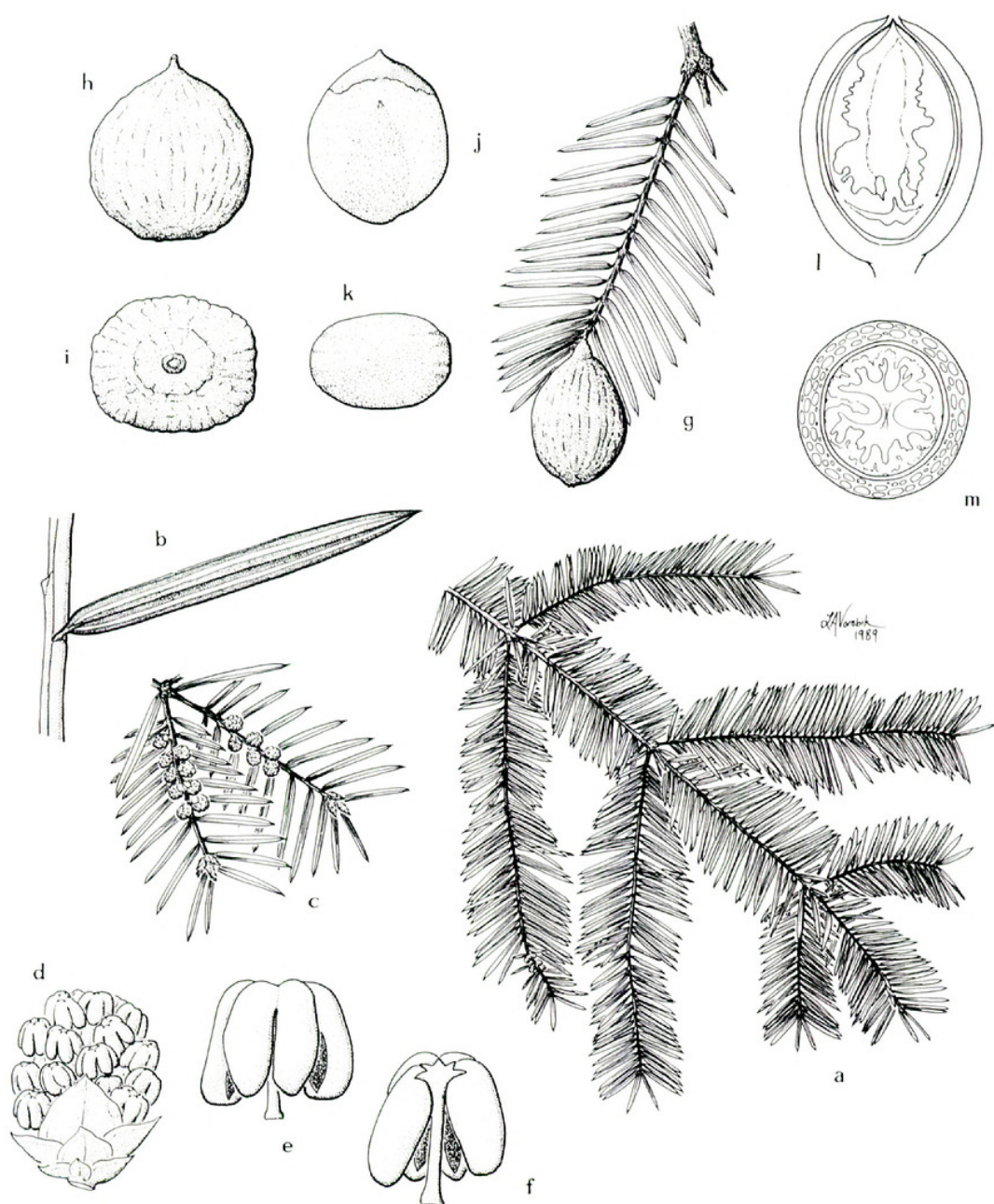


FIGURE 1. Tribe Torreyaee. a-m, *Torreya taxifolia*: a, leafy shoot, $\times \frac{1}{3}$; b, detail of leaf in abaxial view, $\times 1\frac{1}{2}$; c, shoots bearing microsporangiate strobili, $\times \frac{1}{2}$; d, detail of microsporangiate strobilus with subtending bracts, $\times 5$; e, f, microsporophyll in abaxial and adaxial views, $\times 20$; g, shoot bearing mature seed, $\times \frac{1}{2}$; h, i, dry seed with aril, longitudinal and radial views, $\times \frac{1}{2}$; j, k, seed with aril removed, longitudinal and radial views, $\times \frac{1}{2}$; l, longitudinal section of mature seed showing "ruminant" gametophytic tissue, $\times \frac{3}{4}$; m, cross section of moist arillate seed, showing resin canals in the aril and "ruminant" gametophytic tissue, $\times \frac{3}{4}$.

Our sole species, *Torreya taxifolia* Arnott (*Tumion taxifolium* (Arnott) Greene), Florida torreya, stinking cedar, gopherwood, is a very narrow endemic restricted to moist, wooded slopes and limestone bluffs in the vicinity of the Apalachicola River in three counties (Gadsden, Liberty, Jackson) of north-

western Florida and in adjacent Decatur County, Georgia (Kral; Little, 1978; Stalter & Dial). The species was already significantly diminished in population size by the early 1900's because of cutting for lumber and fenceposts (Britton; Coulter & Land) and is now critically endangered because of the effects of a fungal blight. It is a listed endangered species at both the state and federal levels (U. S. Fish & Wildlife Service). At some point between 1954 and 1962, fungal disease(s) of the leaves and stems began to attack the native populations (Godfrey & Kurz). Several fungal pathogens have been isolated from diseased trees (Alfieri *et al.*; U. S. Fish & Wildlife Service), but the causative agent is still unknown. Drought and habitat degradation may have played a significant role in making the wild trees less resistant to fungal attack (Savage; Stalter & Dial). By 1981, essentially all wild individuals had been infected and all of the wild trees over 3 m tall had died back except for stump sprouting (Stalter & Dial). Only approximately 100 wild individuals were alive as of 1981. Further propagation of cultivated trees outside the native range will be needed to avoid the extinction of the species.

Torreya taxifolia differs from the other North American species, *T. californica*, in having yellowish brown rather than reddish brown second-year twigs and generally shorter leaves (2.5–4 cm vs. 3–8 cm) that are less flat on the adaxial surface. The stomatal bands are also less deeply sunken into the leaf in *T. taxifolia* than in *T. californica* and the other species of the genus (Krüssmann). The two species also evidently differ in their volatile oil chemistry, as indicated by differences in the odor of the bruised stems and foliage, described as pungently aromatic in *T. californica* and foul-smelling in *T. taxifolia* (Krüssmann; Sargent).

No systematic investigation of crossability in *Torreya* has been conducted. An apparently spontaneous hybrid of *T. californica* and *T. nucifera* was mentioned by Krüssmann.

The various species of *Torreya* are attractive ornamentals in cultivation. *Torreya californica* is the hardiest and most widely cultivated species of the genus in North America and Great Britain, while *T. nucifera* and *T. grandis* are grown primarily in their native countries in Asia, where several cultivars have been selected (Bean; Krüssmann). The large seeds of several species are highly esteemed food items. Seeds of *T. californica* were gathered by a number of tribes of native Americans, while those of *T. nucifera* are both eaten and used as a commercial source of cooking oil in eastern Asia (Burke). The very durable wood of *Torreya* has been valued for furniture, cabinetry, and fence posts (Burke; Dallimore & Jackson), and thus few large trees remain outside of cultivation.

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Tribe TAXEAE

2. *Taxus* Linnaeus, Sp. Pl. 2: 1040. 1753; Gen. Pl. ed. 5. 462. 1754.

Dioecious (rarely monoecious) shrubs or trees. Bark reddish brown, becoming scaly with age. Wood without axial parenchyma. Foliage leaves spirally arranged (often appearing 2-ranked), linear, with 2 yellowish or grayish, abaxial stomatal bands; resin canals absent. Pollen cones short-stalked, borne singly in axils of foliage leaves; microsporophylls densely clustered, ca. 5–15 per strobilus, each with 4–9 radially arranged sporangia. Ovules borne singly in the axils of foliage leaves, each terminating an ovuliferous dwarf shoot borne laterally on a very short vegetative shoot in the axil of the foliage leaf. Seeds ca. 0.5[–1] cm long, largely surrounded by the cuplike reddish [rarely yellow] aril, which is not adnate to the highly sclerified seed coat; cotyledons 2 (rarely 3). Chromosome number $2n = 24$. LECTOTYPE SPECIES: *Taxus baccata* L.⁴ (Classical Latin name for yew.)—YEW.

A genus of perhaps eight or nine poorly differentiated allopatric taxa, treated most often as separate species but sometimes as geographic subspecies (Pilger, 1903, 1926). The species of *Taxus* are very difficult to distinguish by either gross morphology or leaf anatomy (Florin, 1931; Kwei & Hu; Pilger, 1903). A thorough revision making use of comparative biochemistry as well as morphology is much needed. Four species are native to North America, of which two, *T. canadensis* Marsh. and *T. floridana* Chapman, occur in our region. *Taxus brevifolia* Nutt. is widely distributed but relatively uncommon in the extreme western United States and Canada, while the poorly known *T. globosa* Schlecht. is endemic to Mexico and Guatemala. *Taxus baccata* L. (English yew, Irish yew) is native to Europe, Asia Minor, and north Africa, while *T. cuspidata* Sieb. & Zucc. (Japanese yew) and two or three other species are native to eastern Asia and the Himalayas (Cheng & Fu; De Laubenfels, 1988). Given the fact that the genus apparently dates back to the Jurassic (Florin, 1958a; Harris, 1976b), it is remarkable how little morphological differentiation is seen among its extant members.

Taxus canadensis (*T. baccata* subsp. *canadensis* (Marsh.) Pilger; *T. baccata* var. *canadensis* (Marsh.) A. Gray, 1856; *T. baccata* var. *minor* Michx., 1803; *T. minor* (Michx.) Britton), Canada yew, American yew, ground hemlock, $2n = 24$, is native to an area extending from Newfoundland to Manitoba, south to portions of Iowa, Illinois, Indiana, eastern Kentucky, Virginia, and extreme northern Tennessee and North Carolina. It is usually found under cool, moist conditions on well-drained soil as an understory plant in coniferous or mixed-mesophytic forest. In the southern part of its range, it almost always occurs on upland sites. In our area it has only recently been found in Pickett County, Tennessee, on protected northern slopes on the western edge of the Cumberland Plateau (Gonsoulin) and under montane forest conditions in Ashe and Watauga

⁴The genus was effectively lectotypified by Siebold & Zuccarini, Fl. Japon. Fam. Nat. 2: 108. 1846, when they transferred the only other Linnaean species, *Taxus nucifera*, to the newly described genus *Torreya*.

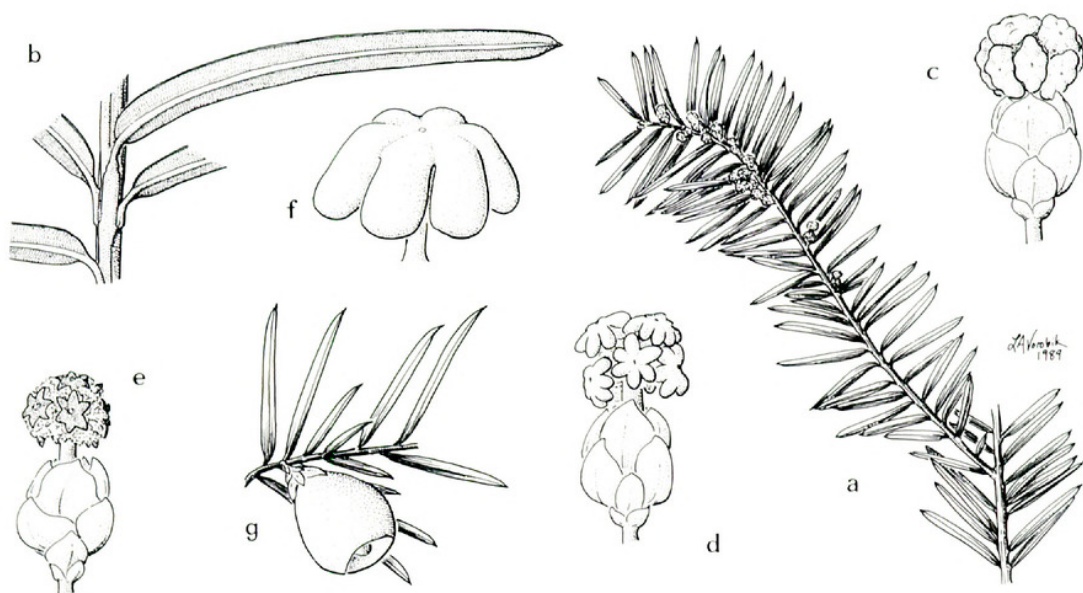


FIGURE 2. Tribe Taxeae. a-g, *Taxus floridana*: a, leafy shoot with microsporangiate strobili at time of pollen release, $\times \frac{1}{2}$; b, detail of leaf in abaxial view, $\times 2\frac{1}{2}$; c, d, e, microsporangiate strobili before, during, and after shedding of pollen, $\times 5$; f, detail of microsporophyll, $\times 20$; g, shoot with arillate ovule, $\times 1\frac{1}{2}$.

counties in extreme northwestern North Carolina (McDowell). Despite the fact that the foliage of the plant is toxic to most animals, Canada yew is a favored browse plant of deer and has been greatly reduced in numbers in much of the northeastern United States by the large resident deer populations (Martell).

Taxus floridana Chapman, Florida yew, savin, is a very rare species native only to areas of Gadsden and Liberty counties in northwestern Florida, largely in the vicinity of the Apalachicola River in the same area where *Torreya taxifolia* is native (Little, 1978). It occurs primarily on moist ravine slopes and sometimes bluffs in mixed deciduous forest, although one population has been found in an acidic bog (Kurz).

Taxus canadensis is usually a low shrub, occasionally becoming 2–3 m tall, while *T. floridana* is a small tree up to 10 m in height. The leaves of *T. canadensis* are yellowish green above, relatively flat, and ca. 1.3–2 cm long, while those of *T. floridana* are dark green above, usually falcate, and ca. 2–2.5 cm long (Rehder, 1940; Sargent). *Taxus floridana* could easily be treated as a subspecies of *T. canadensis* (or perhaps of *T. baccata*) on the basis of its morphology, but its ecological tolerances are clearly different. It would be instructive to compare their chemistry in detail to assess the extent of other genetic differences between them.

The genus *Taxus* is most similar to the monotypic Chinese *Pseudotaxus*, which differs in having a white rather than a reddish aril, ovuliferous shoots apparently borne directly in the axils of foliage leaves (vs. on dwarf axillary shoots), sterile scales present (vs. absent) between the sporophylls in the microsporangiate strobilus, and epidermal papillae only on the margins of the leaves (vs. on the subsidiary cells of the stomata) (Florin, 1948b). The New

Caledonian *Austrotaxus* is similar to *Taxus* in the general features of its ovular development (Florin, 1948a) and in the presence of taxane alkaloids (Guéritte-Voegelein *et al.*), but it differs substantially in the structure of its microsporangiate strobilus and in having much larger leaves and seeds.

Crossability among species of *Taxus* has not been investigated in a systematic manner, but hybrids between *T. baccata* and *T. cuspidata* (*T. × media* Rehder) and *T. cuspidata* and *T. canadensis* (*T. × Hunnewelliana* Rehder) have originated spontaneously in cultivation (Dallimore & Jackson; Rehder, 1923) and are now commonly planted in the United States.

Taxus is most notable chemically for the apparently ubiquitous presence of taxane alkaloids, an unusual class of diterpene alkaloids (Hegnauer, 1988; Lythgoe; R. W. Miller). Taxol, an alkaloid of this group that was isolated first from *T. brevifolia* and later from *T. baccata*, *T. cuspidata*, and *T. Wallichiana* Zucc., has been of particular interest as an antimitotic agent with activity against a number of types of cancer cells (Guéritte-Voegelein *et al.*; Kingston *et al.*; Wani *et al.*). Taxol and related compounds bind to tubulin and promote unusually rapid microtubule assembly and are thus also useful in studying the mitotic process (Bajer *et al.*; Schiff *et al.*). The well-known toxicity of virtually all parts of the yew plant (only the aril is edible) is due in large part to more immediate physiological effects of the various taxane alkaloids, although other biologically active compounds are also present. The degree of toxicity of the foliage appears to vary considerably within species.

Cyanogenic glycosides have been found in the leaves of *Taxus baccata*, *T. canadensis*, and *T. cuspidata* (Hegnauer, 1986) and presumably contribute to the toxicity of the plants. Biflavonoids and other types of glycosides may also have important pharmacological effects and are probably the active ingredients in nonalkaloidal leaf extracts used in traditional medicine in India (M. S. Y. Khan *et al.*; Vohora).

The ecdysterones, biologically active compounds related to insect-molting hormones, are another interesting class of compounds found in the foliage of at least *Taxus baccata* and *T. cuspidata* (Hegnauer, 1986).

Yews (*Taxus baccata*) have long been important plants in the history and folklore of Great Britain and Europe (Bean; Bialobok; Voliotis). The wood of *Taxus* is very strong and durable and was heavily utilized for the manufacture of bows for archery before the advent of gunpowder. The early Celts, who considered yew trees to be sacred, built temples near them in Britain and Ireland. These temples were often perpetuated by later Christian churches (Bean). Today the main economic importance of *Taxus* is as an ornamental hedge, shrub, or tree. The most widely used horticultural yews are forms of *T. baccata*, *T. cuspidata* (which is more cold tolerant), and their hybrid, *T. × media*.

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