THE GENERA OF CUPRESSACEAE (INCLUDING TAXODIACEAE) IN THE SOUTHEASTERN UNITED STATES[1]

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CUPRESSACEAE Bartling, Ord. Nat. Pl. 90, 95. 1830,
"Cupressinae," nom. cons.

(CYPRESS FAMILY)

Aromatic, resinous, evergreen or sometimes winter-deciduous, monoecious (or dioecious in *Juniperus* [and *Diselma*]) trees or shrubs. Bark fibrous and

separating into long strips or exfoliating in plates. Wood with axial parenchyma, lacking resin canals [sometimes with traumatic resin canals in *Sequoia* and related genera] and ray tracheids [reported only for *Chamaecyparis nootkatensis*]. Branches erect or spreading; branchlets erect to pendulous, terete or quadrangular, sometimes flattened in frondlike horizontal sprays (in Cupressaceae *s.s.*). Foliage leaves entire to minutely serrate, linear to linear-lanceolate and spirally arranged (often apparently 2-ranked by twisting of leaf bases) [or opposite in *Metasequoia*] in the traditional Taxodiaceae, or decussately opposite or in whorls of 3 [rarely 4] and scalelike or sometimes awl or needle shaped in the Cupressaceae *s. s.*; foliar resin canals 1 [to 3]. Pollen cones (microsporangiate strobili) sessile or short stalked, solitary or variously clustered, terminal on leafy branches or short shoots (or sometimes axillary); microsporophylls spirally arranged, decussately opposite, or ternate, ca. 6 to 24 per strobilus; microsporangia 2 to 10 per sporophyll, globose or ellipsoid, longitudinally dehiscent, pendulous, free, in 1 or 2 abaxial rows; pollen spheroidal, without saccae or prothallial cells; intine thick, exine with surface microverrucate, with papilla or obscure germinal aperture; male cells approximately equal in size. Ovulate cones solitary (sometimes secondarily clustered), subglobose to ovoid [to pyramidal], terminal or axillary, maturing in 1 to 3 seasons; bract and scale components largely fused in the mature cone, with bract tip protrusive or inconspicuous; bract-scale complexes spirally arranged or decussately opposite or ternate, each with 1 to 6 [to 10, or rarely to 20 in *Cupressus*] erect [or ultimately inverted], adaxial, bottle-shaped ovules; archegonia aggregated in terminal (or lateral) complexes; scales peltate or broadly ovate to triangular-ovate or oblong, thickened or strongly flattened at maturity, imbricate or valvate, [2 to 4] 6 to ca. 20 [to 40 or more] per cone, ultimately woody and separating (or fleshy and fused into a berrylike structure in *Juniperus*). Seeds 1 to several per scale, with [1 or] 2 (or 3) lateral [or nearly terminal] wings derived from the seed coat, or wingless; seed coat varying from thin to very thick and woody, often with resin ducts; cotyledons 2 to 6 (to 9 in *Taxodium*). Chromosome number usually $2n = 22$ (occasionally 33, 44 [66 in *Sequoia sempervirens*]). (Including Taxodiaceae Warming, Haandb. Syst. Bot. ed. 2. 163. 1884; Juniperaceae Schaffner.) TYPE GENUS: *Cupressus* L.

A family of 29 genera[4] and approximately 130 to 140 species concentrated in the temperate portions of the Northern and Southern hemispheres, but with some species in boreal and austral areas and with *Juniperus procera* Hochst. extending into tropical montane areas of eastern Africa. Of the eight genera native in North America, *Chamaecyparis* Spach, *Juniperus* L., *Taxodium* Rich., and *Thuja* L. occur in the southeastern United States, while *Calocedrus* Kurz, *Cupressus* L., *Sequoia* Endl., and *Sequoiadendron* Buchh. occur only in the western part of the continent. About 16 of the genera are monotypic, although several of these had much larger ranges (and presumably greater numbers of species) in the Tertiary than they do now (Florin, 1963). The largest and most

[4]Or fewer, if one treats *Libocedrus* Endl. in the broad sense, including some or all of the segregate genera *Austrocedrus* Florin & Boutelje, *Papuacedrus* H. L. Li, and *Pilgerodendron* Florin, as was variously done by De Laubenfels (1972, 1988) and Eckenwalder (1976).

widespread genera are *Juniperus* (50 or more species) and *Cupressus* (perhaps 13 species) in the Northern Hemisphere, and *Callitris* Vent. (ca. 15 species) in the Southern Hemisphere.

Most recent treatments of the conifers have followed Pilger in recognizing seven families, with the Cupressaceae separate from the Taxodiaceae. However, many European authors (including Emberger, H. Erdtman & Norin, and Lebreton) have united these two families in the order Cupressales, and a number of authors (Eckenwalder; Hart; Price & Lowenstein) have advocated merging the two families under the earlier name Cupressaceae, as is done here. Although Pilger and subsequent authors have circumscribed families primarily on the basis of reproductive characters, especially those of the ovulate cone, the Cupressaceae and Taxodiaceae are similar in development and morphology of the bract-scale complexes (Florin, 1951) and differ primarily in phyllotaxy of leaves and cone scales. The leaves of the Cupressaceae *s.s.* are decussately opposite or whorled, while those of the Taxodiaceae are alternate (except in *Metasequoia* Miki ex Hu & Cheng, in which they are decussately opposite). The shift from spiral to decussate arrangement is hardly unique to the Cupressaceae *s.l.* Both patterns are also seen in the Taxaceae (where *Amentotaxus* Pilger has opposite leaves) and the Podocarpaceae (where *Microcachrys* J. D. Hooker has opposite leaves). The taxodiaceous genera also differ from the Cupressaceae *s.s.* in having a papilla protruding from the germinal area of the pollen grain, although this can be very obscure in some genera (G. Erdtman; Ueno, 1960a).

The two families are held together by an impressive number of morphological characters, including derived features of embryology (archegonia borne in complexes; free-nuclear mitotic divisions three or fewer in proembryogeny), palynology (pollen grains nonsaccate, lacking prothallial cells), chromosome base number ($x = 11$), and high degree of bract-scale fusion in the ovulate cone. Most genera have seeds with lateral wings derived from the seed coat (Singh, 1978), ovules are often more than two per cone scale, and microsporangia are usually more than two per sporophyll. Preliminary cladistic analyses of morphological characters (Hart) and immunological comparisons of seed proteins (Price & Lowenstein) indicate that the Cupressaceae *s.l.* are a natural group quite distinct from the other families of conifers and that the Cupressaceae *s.s.* form a monophyletic group apparently derived from within the traditional Taxodiaceae.

The Cupressaceae *s.l.* appear to be only distantly related to the other extant groups of conifers except for the monotypic *Sciadopitys* Sieb. & Zucc., Japanese umbrella pine, which has often been treated as a morphologically isolated member of the Taxodiaceae (see Eckenwalder; Liu & Su; Pilger; Sporne) or as the separate family Sciadopityaceae Hayata (Doyle & Brennan, 1971; Hart; Price & Lowenstein; Schlarbaum & Tsuchiya, 1985). *Sciadopitys* is similar to the Cupressaceae *s.l.* in having ovulate cones with substantial bract-scale fusion and several seeds per cone scale, each with two lateral wings derived from the seed coat, and nonsaccate pollen grains lacking prothallial cells. Its chromosome base number ($x = 10$) is apparently derived from that of the Cupressaceae *s.l.* by aneuploid reduction (Schlarbaum & Tsuchiya, 1985). It is unique among

conifers in having elongate "double needles"—axillary short shoots that combine features of leaf and stem in their development and morphology (Roth)—as its photosynthetic organs. It retains primitive states for embryological characters (archegonia not grouped in complexes, five sets of free-nuclear mitoses in proembryogeny—Dogra, 1980; Doyle, 1963; Liu & Su; Tahara, 1937, 1940), the derived states of which are shared by the Cupressaceae *s.l.*; it also differs in having male cells unequal in size (Tahara, 1940), pollen grains with much more prominent verrucate sculpture (Ho & Sziklai), and wood without axial parenchyma and with much larger cross-field pits (Phillips). *Sciadopitys* is very distant from the Cupressaceae *s.l.* in immunological comparisons of seed proteins (Price & Lowenstein), and it also has a long fossil record, dating back at least to the Jurassic (Florin, 1922, 1963; Manum). Thus it appears to be a well-separated sister-group of the Cupressaceae *s.l.* (Hart; Price & Lowenstein), and we treat it as the monotypic family Sciadopityaceae.

Most modern tribal and subfamilial classifications of the Cupressaceae/Taxodiaceae lineage have been devised in the context of two separate families, the Cupressaceae and the Taxodiaceae, or equivalent groups of lower rank (see, for example, Gaussen, 1967, 1968; Pilger; Pilger & Melchior; Vierhapper). The Cupressaceae *s.s.* have been divided into tribes or subfamilies in a variety of ways (compare Endlicher; Gaussen, 1968; Janchen; H. L. Li, 1953a; Moseley; Pilger). In perhaps the most widely utilized modern treatment, H. L. Li (1953a) divided the group into two subfamilies: Cupressoideae, with nine genera in the Northern Hemisphere (further divided into tribes Cupresseae, Junipereae Neger, and Thujopsideae Endl.), and Callitroideae Saxton, including the ten Southern Hemisphere genera plus *Tetraclinis* Masters in Spain and northern Africa (further divided into tribes Actinostrobeae Endl., Libocedreae H. L. Li, and Tetraclineae H. L. Li). The cupressoid genera were separated from the callitroid genera as having imbricate rather than valvate scales on the mature ovulate cones. However, the lowermost cone scales are often similar in arrangement in both groups, as was noted by De Laubenfels (1965). Moreover, the mature cone scales of *Cupressus* are nonoverlapping. The cones of the two subfamilies mostly differ in the reduced axis and usually fewer cone scales in the callitroid genera. The whorls of cone scales may be partially overlapping at the time of pollination in the Southern Hemisphere genera but come to lie at approximately the same level in the mature cone, rather than being separated along the cone axis. Reduction in cone-scale number has also occurred in several Northern Hemisphere genera (e.g., in *Microbiota* Komarov, with only two to four cone scales on a reduced axis (Krüssmann; Rushforth), in *Calocedrus*, and within *Chamaecyparis* and *Juniperus*). The presence of derived features of embryology (laterally positioned archegonial complexes and reduction of the number of free-nuclear divisions in the early proembryo) appears to support a close relationship among at least some of the Southern Hemisphere genera (*Callitris*, *Actinostrobus* Miq., and *Widdringtonia* Endl.—Dogra, 1984; Doyle & Brennan, 1972; Singh), although sampling has been very limited, and many of these genera have never been studied.

Other classifications have associated *Libocedrus* and its segregate genera with the thujoid genera of the Northern Hemisphere, which share elongate cone

scales and flattened ultimate branch systems (De Laubenfels, 1953, 1988; Janchen; Pilger; Vierhapper). However, the northern genera appear to differ in wood anatomy (Boutelje; Peirce, 1937). Distribution of tropolone and biflavonoid compounds (H. Erdtman & Norin; Gadek & Quinn, 1985), and preliminary data on anatomical characters such as details of pitting of the foliar transfusion tracheids (Gadek & Quinn, 1988) only partially agree with H. L. Li's (1953a) classification. Thus several recent authors (De Laubenfels, 1988; Gadek & Quinn, 1985, 1988) have questioned whether Li's subfamilies are natural groups, and additional morphological and macromolecular comparisons will be necessary to resolve their phylogenetic relationships.

The nine taxodiaceous genera (with *Sciadopitys* excluded) comprise only about 12 or 13 species and represent remnants of a group that was larger and more widespread in the Mesozoic and Tertiary (Florin, 1963; Miller, 1977, 1988). Many of the extant genera had wider geographic distributions in the past, as is indicated by the fossil record, and several occur back to the Cretaceous. One genus *Athrotaxis* D. Don, is now endemic to Tasmania, five (*Cryptomeria* D. Don, *Cunninghamia* R. Br., *Glyptostrobus* Endl., *Metasequoia*, and *Taiwania* Hayata) to eastern Asia, and three (*Sequoia, Sequoiadendron,* and *Taxodium*) to North or Central America.

Classifications of the Taxodiaceae have tended to emphasize form and development of the bract-scale complexes in the ovulate cone, but there are a number of differences in the details of the treatments (see Eckenwalder; Gaussen, 1967; Hida, 1957, 1962; Janchen; Liu & Su; Pilger & Melchior; Vierhapper), and a rigorous tribal or subfamilial treatment seems premature. Most authors group *Sequoia* with *Sequoiadendron* and *Taxodium* with *Glyptostrobus,* and recent researchers (Eckenwalder; Gaussen, 1967; Miller, 1988; Miller & Crabtree) have emphasized the similarities of *Athrotaxis, Cunninghamia,* and *Taiwania.* Preliminary cladistic analysis of a broader set of characters (Hart) and immunological comparison of seed proteins (Price & Lowenstein; Price, unpublished data) tend to support the groupings noted above, but place *Athrotaxis* in a more isolated position. These analyses differ primarily in the placement of *Metasequoia* and *Cryptomeria* relative to the other genera, associating *Metasequoia* with the other winter-deciduous genera *Glyptostrobus* and *Taxodium* (Hart) or with *Sequoia* and *Sequoiadendron* (Price & Lowenstein), and *Cryptomeria* with *Taiwania* and *Cunninghamia* (Hart) or with *Glyptostrobus* and *Taxodium* (Price & Lowenstein).

Chromosome numbers are often very stable within families of conifers (Ehrendorfer; Khoshoo, 1961), in marked contrast to the situation in the angiosperms. With the removal of *Sciadopitys* to its own family, the genera of Cupressaceae *s.l.* are apparently all characterized by a base number of $x = 11$.[5] Counts have been obtained for all species of the nine taxodiaceous genera and for species of 16 of the cupressaceous genera, including all ten Northern Hemisphere ones (see particularly Hair; Khoshoo, 1961; L.-C. Li; Mehra & Khoshoo; Sax & Sax). The great majority of the species have the diploid number $2n =$

[5]*Fokienia Hodginsii* (Dunn) Henry & Thomas has been reported by Chen to have a chromosome number of $2n = 24$, but L.-C. Li & Hu have more recently obtained $2n = 22$ for the species.

22. Two monotypic genera are polyploid: *Sequoia sempervirens* (Lamb.) Endl. is a hexaploid with $2n = 66$, while *Fitzroya cupressoides* (Molina) Johnston has been reported by Hair to have $2n = 44$. Triploid or tetraploid counts have been obtained for forms (primarily cultivated) of several species of *Juniperus* and also for occasional variants of the otherwise diploid *Cryptomeria japonica* (L. f.) D. Don and *Chamaecyparis pisifera* (Sieb. & Zucc.) Endl. Karyotypic comparisons of the taxodiaceous genera were reviewed by Schlarbaum & Tsuchiya (1984), who noted some differences in arm lengths and ratios and presence or position of secondary constrictions. *Cunninghamia* and *Taiwania* differ from the other taxodiaceous genera in having more diversity in chromosome size and a greater number of submetacentric (vs. metacentric) chromosomes, in agreement with the relationship between these genera indicated by their similarity in cone-scale development (Hida, 1957; Liu & Su).

The Cupressaceae *s.l.* are unusual among the conifers in having archegonia grouped tightly in complexes, usually with a well-defined jacket layer (Dogra, 1984; Liu & Su; Singh). The archegonial complexes are usually located near the micropyle, but are positioned along the sides of the gametophyte in at least some of the Southern Hemisphere genera of Cupressaceae *s.s.* (*Actinostrobus, Callitris,* and *Widdringtonia*—see Doyle & Brennan, 1972; Singh) and in *Sequoia* and *Sequoiadendron* (Liu & Su) and toward the chalazal end in *Athrotaxis* (Brennan & Doyle). There are three sets of free-nuclear mitoses in the proembryogeny of most genera, but the number is reduced to two in *Athrotaxis* and *Callitris* (and probably *Actinostrobus* and *Widdringtonia*). Wall formation accompanies the first mitotic division in *Sequoia*, a very unusual feature among the conifers (Singh). Cleavage polyembryony of various types occurs as a regular part of development in most genera of the Cupressaceae *s.l.* except for *Athrotaxis, Thuja,* and *Thujopsis,* in which it occurs only sporadically (Dogra, 1984; Doyle & Brennan, 1971, 1972).

The Cupressaceae are wind pollinated, as are the other conifers, and have a pollination-drop mechanism of pollen capture, which is seen in most other gymnosperms and is evidently the primitive state among the conifers (see Doyle, 1945; Singh). Dispersal of the seeds is usually by wind or gravity, except in *Juniperus,* where the fleshy cones are eaten by birds or mammals, and *Taxodium,* where the thickened seed coat may aid in distribution by water (Fowells).

Many taxodiaceous and cupressaceous genera have been shown to have vesicular-arbuscular mycorrhizae and to lack root nodules, while *Sciadopitys* is more similar to the Podocarpaceae and Araucariaceae in having root nodules (Khan & Valder).

Chemical studies have been conducted on wood and leaves of many of the genera of Cupressaceae *s.l.*, with greatest emphasis on the Northern Hemisphere and Australian groups (see reviews in H. Erdtman & Norin; Hegnauer, 1962, 1986). Biflavonoid composition has been studied in virtually all of the genera worldwide (Gadek & Quinn, 1983, 1985; Geiger & Quinn, 1975, 1982). Compounds of the amentoflavone and hinokiflavone series are widespread among gymnosperms generally and have been found in most genera of the family, although the latter series is apparently absent in the Australian genera *Callitris*

and *Actinostrobus* (Gadek & Quinn, 1983). The cupressuflavone series is of more limited distribution, occurring in the Araucariaceae, one genus of the Podocarpaceae (*Lepidothamnus* Phil.), and portions of the Cupressaceae *s.s.* (Gadek & Quinn, 1985; Geiger & Quinn, 1982). Cupressuflavone is a major component in *Calocedrus, Cupressus, Juniperus,* and *Tetraclinis,* and a lesser one in *Platycladus* Spach and individual species of *Chamaecyparis* and *Thuja* (but not others), all of these indigenous to the Northern Hemisphere. Taiwaniaflavone, an unusual biapigenin biflavoid found only in *Taiwania, Calocedrus,* and *Neocallitropsis* Florin, is probably a convergent feature, since the three genera are very dissimilar in morphology.

The cytotoxic lignans podophyllotoxin and/or desoxypodophyllotoxin, which have been used in both traditional and modern medicine as antitumor agents, are found in the leaves of a variety of cupressaceous genera, including *Austrocedrus, Callitris, Calocedrus, Chamaecyparis, Juniperus,* and *Thujopsis* (Cairnes *et al.*; H. Erdtman & Norin; Hegnauer, 1986). The related but noncytotoxic compound savinin is present in the wood of several species of *Juniperus* and also in *Taiwania* (H. Erdtman & Norin; Hegnauer, 1986).

Diverse terpene compounds are found in the wood, leaves, and other plant parts of the Cupressaceae *s.l.* and are responsible for much of the aromatic nature of the plants. Most of the monoterpene compounds in the Cupressaceae *s.l.* occur widely in other conifers, while sesquiterpenes of the cedrane, thujopsane, widdrane, and cuparane types are particularly characteristic of the Northern Hemisphere genera of Cupressaceae *s.s.* and also of *Widdringtonia* (H. Erdtman & Norin). Several of these compounds have recently been reported to occur in low concentration in the foliar resin of *Cryptomeria* (Yatagai & Sato), and detailed studies may find them to be more widely distributed among the taxodiaceous genera.

Tropolones structurally related to the terpenes are important heartwood components of several genera of the Cupressaceae *s.s.*, particularly those of the Northern Hemisphere. These compounds, notable for their fungicidal activity, are apparently absent from the other conifers (H. Erdtman & Norin; Hegnauer, 1986). Tropolones are characteristic of *Calocedrus, Cupressus, Platycladus, Tetraclinis, Thuja, Thujopsis,* and most but not all species of *Chamaecyparis* and *Juniperus* (H. Erdtman & Norin). They are found in *Austrocedrus* and the related *Papuacedrus* but are apparently absent in the other Southern Hemisphere genera.

Alkaloids are relatively uncommon components in the conifers and in the Cupressaceae *s.l.* are well documented only for *Athrotaxis*, all species of which contain homoerythrinane compounds (Hegnauer, 1986, 1988).

Many genera of Cupressaceae *s.l.*, especially species of *Chamaecyparis, Cryptomeria, Cupressus, Juniperus, Metasequoia, Platycladus, Sequoia,* and *Thuja,* are important as ornamental trees or shrubs (L. H. Bailey; Bean; Dallimore & Jackson; Ouden & Boom; Krüssmann). *Sequoia* and *Sequoiadendron* are among the largest trees in the world and are centers of attraction in several national and state parks in California. Wood of many genera of Cupressaceae *s.l.* is resistant to insect and fungal attack and thus has been highly sought for uses requiring durability. Wood of various species of *Juniperus, Thuja,* and *Cha-*

maecyparis has been important for shingles, and that of *Sequoia* for outdoor uses such as decks and fences.

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KEY TO THE GENERA OF CUPRESSACEAE (INCLUDING TAXODIACEAE) IN THE SOUTHEASTERN UNITED STATES

General characters: *Monoecious (or dioecious) evergreen or winter-deciduous trees or shrubs; foliage leaves alternate (often appearing 2-ranked) and linear to linear-lanceolate, or opposite to whorled and needlelike, awl-shaped, or scale-like; pollen cones with spirally arranged, opposite, or whorled microsporophylls, each sporophyll with 2 to 10 globose abaxial microsporangia; pollen nonsaccate, lacking prothallial cells; ovulate cones subglobose to ovoid or oblong; bracts and ovuliferous scales strongly fused in mature cones; scales peltate to ovate or oblong, alternate or opposite or whorled, bearing 1 to 6 [to 20] erect [or inverted] adaxial ovules; archegonia clustered; seeds with 2 (or 3) lateral wings [or 1 nearly terminal one] or wingless; cotyledons 2 to 6 (to 9); chromosome base number* x = *11.*

A. Foliage leaves alternate, linear to linear-subulate; branchlets winter deciduous. . . . . .1. *Taxodium.*
A. Foliage leaves opposite or whorled, mostly reduced and scalelike; branchlets evergreen.
    B. Branchlets forming flattened sprays.
        C. Cones globose; cone scales peltate. . . . . 2. *Chamaecyparis.*
        C. Cones ovoid or ellipsoid; cone scales not peltate.
            D. Branchlets flattened in horizontal plane; seeds laterally winged; immature cone scales only slightly fleshy. . . . . .3. *Thuja.*
            D. Branchlets flattened in vertical plane; seeds wingless; immature cone scales very fleshy. . . . . *Platycladus.*[6]
    B. Branchlets not forming flattened sprays.
        E. Cone scales less than 1 cm long, fleshy, fused into indehiscent, berrylike structures. . . . . .4. *Juniperus.*
        E. Cone scales more than 1 cm long, woody at maturity, with evident borders, separating to release seeds. . . . . 5. *Callitris.*

1. **Taxodium** Richard, Ann. Mus. Hist. Nat. Paris **16:** 298. 1810.

Winter-deciduous [to evergreen] trees, pyramidal to narrowly conical when young, the crown often broad in older individuals; trunk much enlarged at base, often buttressed. Bark light- to reddish-brown, fibrous, ridged, often peeling in strips. Roots horizontal, often with cone-shaped "knees" projecting from water. Branches erect or spreading; branchlets dimorphic, those near the apex of the shoot persistent and with prominent axillary buds, those lower on the shoot without evident axillary buds and deciduous; winter buds globose, scaly. Juvenile leaves linear-lanceolate, whorled or spirally arranged; adult

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[6]*Platycladus orientalis* (L.) Franco, native to eastern Asia, is commonly planted in our region and may occasionally escape (Little, 1979; Small) but needs further documentation before being considered naturalized (Wunderlin, pers. comm.).

leaves spirally arranged, either 2-ranked by twisting of leaf bases, thin and linear-lanceolate, or 5- to 8-ranked, linear-subulate and keeled, closely appressed to the branches (the 2 leaf forms on the same or different trees). Pollen cones small, ovoid, in long, drooping racemes or panicles terminating the previous year's shoots; microsporophylls 6 to 10 [to 15], broadly ovate to peltate; microsporangia (2 to) 4 to 9 (or 10), globose, pendulous, in 2 rows at base of the abaxial side of the microsporophyll; pollen with evident papilla. Ovulate cones terminal on short, scaly branchlets near ends of previous year's branchlets, maturing in 1 year; immature bract-scale complexes spirally imbricate, each with (1 or) 2 (or 3) erect, bottle-shaped ovules; mature ovulate cones subglobose to somewhat ovoid; cone scales thick, woody, peltate, 4-sided, with mucronulate umbo; resin vesicles with blood-red resin prominent on interior portions of cone scale. Seeds usually 2 on the adaxial side of each cone scale, erect, attached laterally to the stalk of the scale by a large, pale hilum; seed coat thick, woody, lustrous, with 3 small, unequal corky wings; cotyledons 3 to 9. Chromosome number $2n = 22$. TYPE SPECIES: *Taxodium distichum* (L.) Rich. (Name from Greek, in allusion to the yewlike leaves of the type species.)— BALD CYPRESS, SWAMP CYPRESS.

A genus of two closely related species or perhaps a single polymorphic one, native to swampy and riverine areas of the southeastern and central United States and from extreme southern Texas south through much of Mexico to Guatemala. The genus was widespread in Europe and western North America in the Tertiary, becoming extinct in these areas with climatic deterioration in the Pliocene (Florin, 1963).

There has been considerable disagreement concerning the number of species to recognize within *Taxodium*. Britton (1926), Dallimore & Jackson, and Rehder (1940) each recognized three species (*T. distichum* Rich. (bald cypress), *T. ascendens* Brongn. (pond cypress), and *T. mucronatum* Ten. (Tule tree, Montezuma cypress), although substantial intergradation has been reported, particularly between pond and bald cypresses.

Watson (1983, 1985), after reviewing morphological, anatomical, biochemical, and cytological data, concluded that the differences between the pond and bald cypresses are minor, showing considerable overlap and being subject to environmental modification. Watson thus suggested varietal status (as var. *imbricarium* (Nutt.) Croom) for the pond cypress, and this treatment is adopted here.

Montezuma cypress is somewhat more distinct in morphology and ecology and is allopatric in distribution (reaching extreme southern Texas from Mexico and Guatemala) and is thus usually treated as the separate species *Taxodium mucronatum*, although it may be more appropriately treated as a third variety, *T. distichum* var. *mexicanum* (Carr.) Gordon. It differs in being semievergreen, retaining its annual leafy shoots until after the new shoots have leafed out in winter or spring, and being considerably less cold hardy in cultivation than the other taxa. It has sometimes been reported to have larger, more glaucous ovulate cones (Henry & McIntyre) and longer pollen-cone-bearing branches, but more thorough sampling indicates considerable overlap for these features

(Brown, 1984; Little, 1980; Martínez, 1963). The smaller branches tend to be more drooping in the Montezuma cypress, and knees are only occasionally present (Martínez, 1950, 1963). Kaieser (1953) reported that the horizontal walls of the ray parenchyma cells are thinner in the Mexican taxon, while there is little difference in the wood anatomy of the bald and pond cypresses. Isozyme electrophoresis of population samples would be very useful in assessing the degree of genetic differentiation of Montezuma cypress from the other taxa.

Taxodium distichum var. *distichum*, bald cypress, swamp cypress, $2n = 22$, is a large tree (to 50 m) with the trunk angular at the base and the leaves two-ranked on the annual branchlets. The bark is usually thin and smooth, and the knees are usually slender. *Taxodium distichum* var. *distichum* is native on the Coastal Plain from southern Delaware to Florida, west to the valley of the Devil River in Texas, and northward in the Mississippi Embayment through Louisiana and Arkansas to southeastern Missouri and Tennessee, western and northwestern Kentucky, southern Illinois, and southwestern Indiana. The species occurs in riverine swamps that are usually inundated for several months of the year and in low, saturated stream-bank habitats and wet depressions in pine barrens. It attains its largest size in the Gulf and south Atlantic coastal areas, where it tends to form pure stands in the great river swamps. The species commonly occurs with water tupelo or tupelo (*Nyssa aquatica* L., *N. sylvatica* Marsh.) and also grows in drier habitats with red maple, water ash, and sweet gum.

Taxodium distichum var. *imbricarium* (Nutt.) Croom (*T. ascendens* Brongn., *T. imbricarium* (Nutt.) Harper, *T. distichum* var. *nutans* auct., non (Aiton) Sweet), pond cypress, $2n = 22$, is a smaller tree (to ca. 25 m in height) that occurs on the Atlantic and Gulf Coastal plains from southeastern Virginia to southeastern Louisiana. Its trunk has rounded ridges, and its appressed, subulate leaves are ca. 5–12 mm long on both annual and perennial branchlets. The bark tends to be thicker and more strongly furrowed than in var. *distichum*, and the knees, if present, are short and rounded.

Watson (1983) summarized the ecological differences between the bald and pond cypresses. Pond cypress tends to grow in pine-barren ponds, often underlain by limestone, whereas bald cypress generally occurs in riverine swamps. Additionally, the habitat of the pond cypress has a decreased water flow and is more prone to drought and fire; the pH is lower, and nutrients are less available. Neufeld and Watson (1983) have suggested that the pond cypress is a recent derivative of the bald cypress that evolved in response to harshening environments along the Coastal Plain, with the smaller, closely appressed leaves helping to reduce water loss.

Taxodium has often been considered to be closely related to the East Asian genus *Glyptostrobus*, which is similar in its habitat, possession of knees, pattern of cone-scale development, relatively large number of cotyledons (averaging ca. 5 or 6), and winter-deciduous branchlets (Britton, 1926; Henry & McIntyre; Hida, 1957; Pilger & Melchior). *Metasequoia* is also similar to *Taxodium* in being winter deciduous and having the pollen cones in a racemose arrangement, and it groups with *Taxodium* and *Glyptostrobus* in Hart's preliminary cladistic analyses. In contrast, immunological comparisons of seed proteins by Price &

Lowenstein indicate that *Taxodium* is most similar to *Glyptostrobus* and *Cryptomeria* and that *Metasequoia* is most similar to *Sequoia* and *Sequoiadendron*.

Taxodium is a very distinct genus, differing from the other winter-deciduous members of the family in a number of vegetative and reproductive characters. The knees of *Glyptostrobus* are curved and bent rather than conical and erect as in *Taxodium* (Henry & McIntyre). The older perennial branchlets of *Glyptostrobus* bear scalelike leaves that remain green for several years and have rows of white stomatal dots on the surface, whereas those of *Taxodium* bear elongate linear-subulate leaves that become brown and corky in the second year. The cones of *Glyptostrobus* are pyriform and terminal on the branchlet, have scales that are elongate and imbricate at maturity and lack prominent resin pockets, and have the bract and cone-scale united at the base but free at the tip. The body of the seed is small and ovoid, bearing a single long, nearly terminal wing. In contrast, the mature cones of *Taxodium* are globose to ellipsoid, are borne laterally on the major branchlets, and have peltate scales with the edges meeting but not overlapping. The seed body is larger, much thicker walled, and three-angled, with only small, corky wings in the angles. *Metasequoia* differs from *Taxodium* in a number of features, notably in its smaller, more flattened cone scales, its opposite rather than spirally arranged leaves and cone scales, and its strongly compressed seeds that are more than two (usually five to eight) per scale, each with two lateral wings and only two cotyledons (Florin, 1952; Stebbins).

Taxodium develops three unusual structures in response to flooding: buttswells, buttresses, and knees. The term "buttswell" refers to the enlarged basal portion of the trunk, while buttresses are longitudinal ridges on the buttswell. Variation in size and shape of these structures is associated with fluctuations in exposure of the areas to air or water during the early part of the growing season, with the height of the buttresses tending to correspond to the average depth of flooding. According to Kurz & Demaree, buttress development results from the simultaneous presence of water and air, while individuals grown under permanently flooded conditions or in well-drained soils not subject to flooding fail to develop buttswells or buttresses.

The well-known "cypress knees" are usually emergent, cone-shaped structures produced as extensions of the roots and may be as tall as 3–4 m (Brown, 1984). They may arise as small swellings on the upper surfaces of shallow adventitious roots (Shaler; Whitford) or may be formed from shallow roots growing upward and then bending sharply downward, with the geniculate point becoming the "knee" (Brown & Montz). Various functions have been attributed to the knees. One suggestion has been that they act as pneumatophores ("breathing organs") that funnel oxygen into the root system (Dickeson & Brown; Mattoon; Shaler). More recent experiments have shown, however, that little if any gas exchange occurs (Kramer *et al.*), and that no stomata, lenticels, or conducting tissues are found on the surface of the knees (Brown, 1984). Other possible functions include the storage of starch, which accumulates there in significant amounts (Brown & Montz), and stabilization of the plant during severe storms (Lamborn, 1890a). Removal of the knees appears to have little adverse affect on the trees, at least over the short term (Mattoon).

Despite considerable variation in the extent of buttressing, buttswells, and knees, some authors have attempted to use these features to distinguish bald cypress from pond cypress. Watson (1983) pointed out that their magnitude appears to be ecophenically determined since they generally do not develop if the stem is not exposed to flooding; they are thus of limited taxonomic utility.

Many bald-cypress trees reach considerable size and age. One in Louisiana measured ca. 13 m in circumference and 26.7 m in height (Brown & Montz). Some individuals of Montezuma cypress also attain great size and have multiple stems at the base. At Santa Maria de Tule in Oaxaca, the famous "Tule tree" is reported to have the largest diameter of any tree (ca. 12 m), although it appears to represent three individuals that have grown together (Cronemiller; Little, 1980). This tree has been estimated to be anywhere from 1000 to 3000 years old (Krüssmann).

The wood of *Taxodium* is known for its durability in contact with soil and severe weather. The heartwood is so durable that it has been called "the wood eternal" and has been used in several types of heavy construction. The Seminole Indians in Florida have also used the wood in construction and for fenceposts, stockades, and dugout canoes. More recently, it has been valued for interior woodwork, cooperage, fence posts, and railroad ties (Little, 1980). The wood of pond cypress is purportedly heavier and stronger than that of var. *distichum* (Harper, 1902). Wood production from *T. distichum* peaked at more than one billion board feet in 1913 but has subsequently declined substantially because of heavy cutting (Mattoon; Sternitzke). In recent years second-growth bald cypress has again built up in abundance in the southeastern United States.

The resin of *Taxodium mexicanum* has been used in Mexico as a cure for wounds, ulcers, and toothaches (Henry & McIntyre).

Taxodium is of some horticultural importance in the eastern United States and Europe and is frequently planted along watercourses and farms as a windbreak in China. Cultivars of *Taxodium* are hardy as far north as Massachusetts, New York, and Michigan and grow best in deep, sandy loam with plentiful moisture and good drainage (Fowells).

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2. **Chamaecyparis** Spach, Hist. Nat. Veg. Phan. **11:** 329. 1841.

Pyramidal monoecious evergreen trees (rarely shrubs) with nodding leading shoots and a slender, spikelike crown from a thickened trunk. Branchlets slender, flattened (gradually becoming terete in later years if not shed), distichous and forming horizontal sprays. Bark reddish- [to grayish-]brown, irregularly ridged, often peeling in strips or scales. Wood soft [or hard], whitish to pinkish [to yellowish], aromatic [or not aromatic]. Leaves entire, aromatic when crushed; juvenile leaves whorled, linear-lanceolate, acuminate; adult leaves decussate, scalelike, dimorphic, the facial pair flattened, ovate to rhombic, acuminate to obtuse, with a central gland [or eglandular]; the lateral pair rounded or strongly keeled. Cones borne terminally on lateral branchlets, opening in early spring from buds formed the previous year; pollen and ovulate cones borne on separate branches. Pollen cones ovoid to oblong, quadrangular; microsporophylls ca. 8 to 12 (to 20), decussate; microsporangia 2 to 4 (to 6); pollen microverrucate, with obscure germinal aperture. Ovulate cones globose [to ellipsoid], maturing in 1 year [2 in *C. nootkatensis*], bearing 4 to 8 [rarely to 16] decussate, peltate scales; ovules bottle shaped, erect, [1 or] 2 [to 8] per scale. Maturing cones more or less erect, glaucous, ultimately red-brown. Seeds 1 or 2 [rarely to 8] per scale, ovate, with 2 broad lateral wings; cotyledons 2. Chromosome number $2n = 22$. LECTOTYPE SPECIES: *Chamaecyparis thyoides* (L.) BSP.; see Britton, N. Am. Trees, 102. 1908. (Greek name from *chamai,* on the ground, and *kyparissos,* cypress, alluding to the affinity of the genus to *Cupressus,* true cypress.)—FALSE CYPRESS, CYPRESS.

A genus of six species in North America and eastern Asia. Three species are native to eastern Asia and three (*Chamaecyparis thyoides* (L.) BSP., *C. nootkatensis* (D. Don) Spach, and *C. Lawsoniana* (A. Murray) Parl.), to North America, with the latter two restricted to the Pacific Coast region. The Asian species are *C. formosensis* Matsum. in Taiwan, *C. obtusa* (Sieb. & Zucc.) Endl. in Japan and Taiwan, and *C. pisifera* (Sieb. & Zucc.) Endl. in Japan.

Chamaecyparis is generally thought to be closely related to the widespread Northern Hemisphere genus *Cupressus* L., which also has globose cones with peltate scales, and has sometimes been treated as a subgenus or section of the latter genus. It differs in having smaller ovulate cones (ca. 6–15 vs. ca. 15–40 mm in diameter), more heavily flattened branchlets, entire (vs. minutely ciliate) foliage leaves, and a shorter reproductive cycle (usually one vs. two years until ovulate-cone maturation). A small-coned species native to China has sometimes been treated as *Chamaecyparis funebris* (Endl.) Franco, but its biflavo-
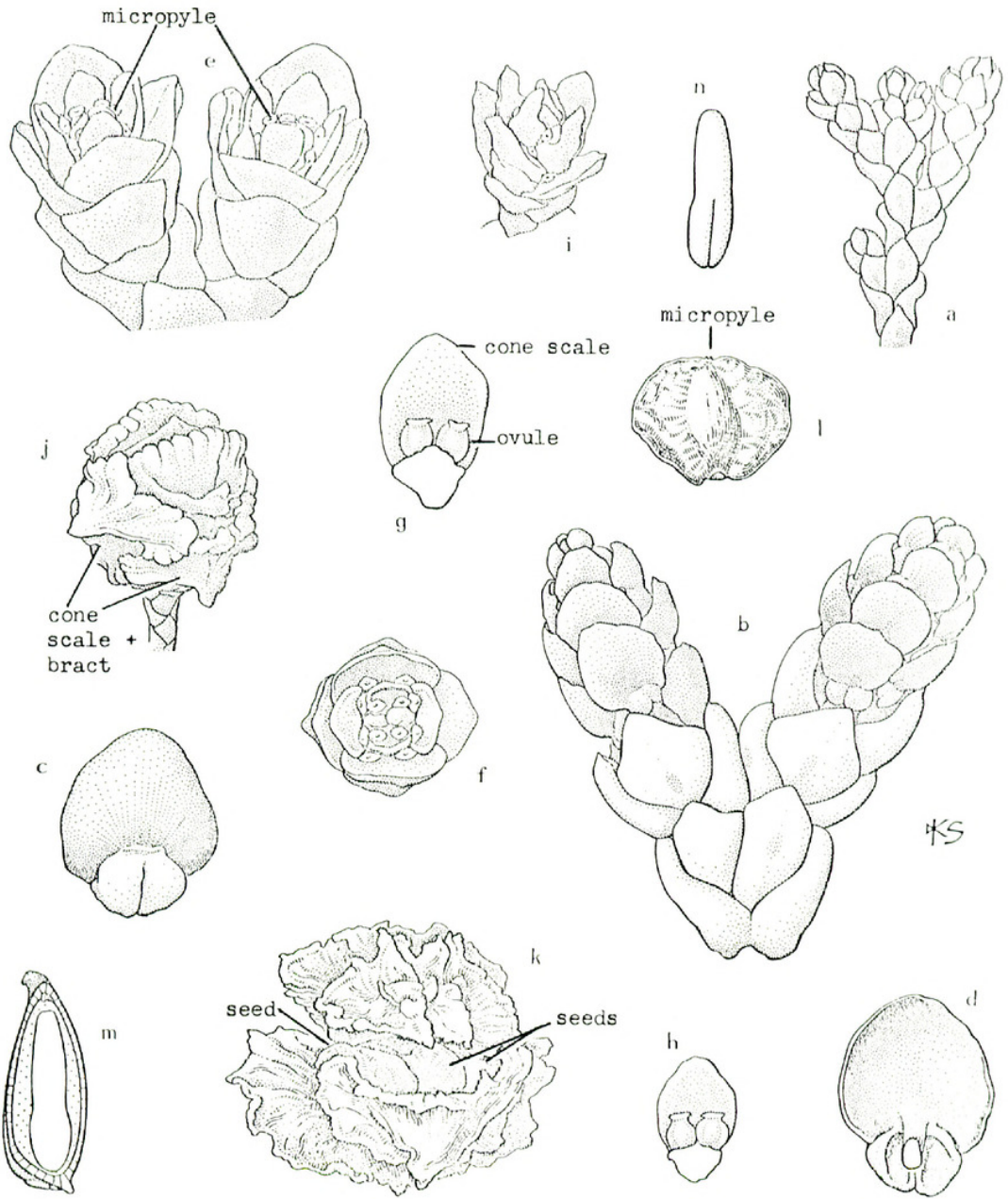
FIGURE 1. **Chamaecyparis.** a–n, *C. thyoides*: a, branchlet tip, showing lateral and facial leaves, × 5; b, detail of branchlet tip with two terminal microsporangiate strobili, × 12; c, microsporophyll with two sporangia (abaxial view), × 25; d, microsporophyll (adaxial view), showing dehisced sporangia, × 25; e, two ovulate cones at time of pollination, × 12; f, cone from "e," seen from above to show arrangement of cone scales and orthotropous ovules, × 12; g, one of lowermost pair of cone scales (adaxial view), showing two ovules at time of pollination, × 12; h, one of uppermost pair of cone scales (adaxial view) at time of pollination, × 12; i, young ovulate cone after pollination, the scales beginning to thicken and close, × 6; j, mature, unopened ovulate cone, showing fused bracts and scales, × 3; k, mature, open ovulate cone, three winged seeds visible on cone scale nearest viewer, × 5; l, winged seed, with micropyle facing upward, × 6; m, diagrammatic longitudinal section of mature seed, with embryo unshaded, gametophytic storage tissue dotted, seed coat hatched, × 10; n, embryo dissected from seed, showing two cotyledons, × 10.

noid pattern supports its original placement in *Cupressus* (Gadek & Quinn, 1987).

Chamaecyparis nootkatensis is unusual in the genus in having less-flattened branchlets and a longer reproductive cycle; it is also divergent in its biflavonoid profile and tropolone composition (H. Erdtman & Norin; Gadek & Quinn, 1985). This species also is notable for producing intergeneric hybrids with *Cupressus* in cultivation. Leyland cypress (× *Cupressocyparis Leylandii* (Jackson & Dallim.) Dallim. = *Chamaecyparis nootkatensis* × *Cupressus macrocarpa* Gordon) apparently originated in England from spontaneous crosses in both directions (Osborn). More recently, hybrids between *Chamaecyparis nootkatensis* and *Cupressus glabra* Sudw. and *C. lusitanica* Miller, respectively, have also been reported from cultivated plants in England (Mitchell).

Our sole species, *Chamaecyparis thyoides* (including *C. Henryae* H. L. Li, *C. thyoides* var. *Henryae* (H. L. Li) Little), Atlantic white cedar, white cedar, swamp cedar, "juniper," occurs in swamps and wet woods near the Atlantic and Gulf coasts from southern Maine to northern Florida and westward to southeastern Mississippi. In the northern part of its range, it often occurs in pure stands, while in the south it frequently grows with bald cypress. It can be distinguished by its adult leaves that are usually glandular and not conspicuously whitened below, and by its branchlets that are irregularly arranged rather than held in the horizontal plane. In segregating the southern populations of the species (from Florida through Mississippi) as *C. Henryae*, H. L. Li cited a number of morphological differences (e.g., smoother bark with twisting ridges, lighter-colored microsporophylls, and less-glaucous ovulate cones), but the divergence between northern and southern populations is apparently clinal rather than abrupt (Hardin; E. L. Little, 1966). Thus, E. L. Little (1966) reduced *C. Henryae* to varietal status under *C. thyoides* and later (1979) placed it in synonymy.

Chromosome counts of $2n = 22$ have been reported for four species of *Chamaecyparis* (Khoshoo, 1961; Kuo *et al.*; Sax & Sax); evidently no count has ever been made for *C. thyoides*. Natural interspecific hybridization has not been reported, but artificial crosses have been attempted in several combinations (Fukuhara; Yamamoto, 1981a, b). Meiotic irregularities have been reported in hybrids between *C. obtusa* and *C. pisifera* (Fukuhara), while a high percentage of nonviable seedlings was obtained in crosses of *C. Lawsoniana* and *C. pisifera* (Yamamoto, 1981a).

Among species of *Chamaecyparis*, significant differences have been reported in distributions of foliar terpenoids (Von Rudloff; Yatagai *et al.*) and heartwood tropolones (H. Erdtman & Norin), but more comprehensive population studies are needed. *Chamaecyparis nootkatensis* appears to be unique in the genus in having the tropolone nootkatin and the biflavonoid cupressuflavone, which are widespread in the genus *Cupressus* (H. Erdtman & Norin; Gadek & Quinn, 1985).

Most species of *Chamaecyparis* are utilized as ornamentals, with *C. Lawsoniana* (Port Orford cedar), *C. pisifera* (Sawara cypress), and *C. obtusa* (Hinoki cypress) being of particular importance. Hinoki cypress has religious significance in Japan and was often planted outside Shinto temples and used for

construction of temples and palaces (Wilson). The durable wood of the North American species has been valued for construction of boats and houses and for cooperage and shingles (Sargent, 1896, 1926). *Chamaecyparis thyoides* has historically been an important timber tree in the eastern United States, but large trees have been greatly depleted by logging (Jarvis; Tangley). Submerged logs of the species are so resistant to decay that they have been "mined" from swamps (Jarvis).

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3. **Thuja** Linnaeus, Sp. Pl. 2: 1002. 1753; Gen. Pl. ed. 5. 435. 1754.

Evergreen, pyramidal, monoecious trees or sometimes shrubs; leading shoot erect; trunk often lobed and buttressed, sometimes dividing into 2 or more upright secondary stems. Bark reddish brown [to grayish], thin, fissured on older trees, peeling in irregular patches and fibrous shreds. Wood soft, pale, with light brown [to dark brown] aromatic heartwood. Branches horizontal at first, becoming ascendent; branchlets slender, pendulous, forming flattened, frondlike, horizontal sprays, gradually becoming terete, the smaller leafy branchlets deciduous after several seasons. Foliage fragrant; juvenile leaves in spirally arranged whorls, linear-lanceolate, acuminate, spreading or reflexed, retained on adult plants of some cultivars; adult leaves decussately opposite, scalelike, closely imbricate (except on rapidly growing shoots), the facial leaves ovate, acute tipped (to ovate-lanceolate on rapidly growing shoots), with a central gland [or eglandular], the lateral leaves folded over the facial ones, keeled. Buds small, naked, hidden by the leaves. Cones terminal and solitary, appearing in early spring; pollen and ovulate cones usually produced on dif-

ferent branchlets. Pollen cones nearly sessile, cylindrical or globose; microsporophylls ca. 4 to 6 [to 12], decussate, short stalked and more or less peltate, each with 2 to 4 microsporangia; pollen with obscure germinal aperture. Ovulate cones maturing in 1 season, terminal on short lateral branchlets, ovoid or oblong, with 8 to 12 imbricately arranged, oblong [to broadly ovate] scales, the central 4 to 6 fertile and bearing 2 (sometimes to 4) erect, bottle-shaped ovules; mature cones more or less erect; scales brownish, somewhat woody, with a minute [or more prominent] spine near the apex. Seeds (1 or) 2 (or 3) per scale, thin and flattened, with resin blisters in the thin seed coat, the membranaceous wings nearly encircling the whole seed, notched at the micropylar end; cotyledons 2. Chromosome number $2n = 22$. LECTOTYPE SPECIES: *Thuja occidentalis* L.[7] (From the Greek name of a resin-bearing conifer.)— ARBORVITAE, WHITE CEDAR.

A genus of five species, two in North America and three in Asia. *Thuja plicata* D. Don, western red cedar, is native to northwestern North America; *T. occidentalis* L. to the eastern deciduous forest area. *Thuja Standishii* (Gordon) Carr., *T. koraiensis* Nakai, and *T. sutchuensis* Franchet are native to portions of eastern Asia.

Thuja occidentalis, arborvitae, northern white cedar, white cedar, swamp cedar, $2n = 22$, is found from Nova Scotia westward to southeastern and central Manitoba, southward to the Great Lakes States and very locally south, barely reaching our region in mountainous areas of North Carolina and Tennessee. The species is common in the northern portion of its range, occurring over great areas of swampy forest land, where it forms largely impenetrable forests, as well as along rocky stream banks and drier limestone ridges, with best growth on neutral to alkaline substrates (Fernald; Fowells; Sargent, 1926). At the southern end of its distribution in western Virginia and Tennessee, arborvitae is less abundant, occurring only at higher elevations, usually on limestone or dolomitic cliffs. A number of floras (Britton, 1908; Coker & Totten; Little, 1980; Sargent, 1896, 1926) report the species from North Carolina, but there are apparently no natural populations remaining in the state (Clebsch; Radford *et al.*).

Thuja occidentalis differs from the other North American species (*T. plicata*) in usually having four rather than six fertile scales in the ovulate cone; these are also less prominently spine tipped. *Thuja plicata* is a larger tree, reaching 30–40(–70) (vs. 15–20(–25)) m in height, with more lustrous leaves that are more prominently whitened below.

The generic relationships of *Thuja* have not yet been determined with certainty. It has been suggested that it is most closely related to the monotypic eastern Asian genus *Thujopsis* Sieb. & Zucc. (Hart), which is similar in its tropolone profile (H. Erdtman & Norin) and embryogeny (Dogra, 1984) but differs in having subglobose ovulate cones with three to five (vs. usually two) seeds per scale and more spreading, hatchet-shaped lateral leaves. *Platycladus orientalis* (L.) Franco (*Biota orientalis* (L.) Endl., *Thuja orientalis* L.) has often

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[7]The genus was effectively lectotypified when Spach (Hist. Nat. Veg. Phan. **11**: 333. 1841) transferred the only other Linnaean species, *Thuja orientalis,* to *Platycladus* Spach.

been treated in the genus *Thuja* and may also be closely related, but is distinct from *Thuja* and *Thujopsis* in having fleshier immature cone scales, hard-coated, unwinged seeds, regularly occurring cleavage polyembryony, and vertically rather than horizontally oriented sprays of branchlets (Dallimore & Jackson; Singh & Oberoi).

Chromosome counts of $2n = 22$ have been reported for three of the five species of *Thuja* (*T. occidentalis, T. plicata,* and *T. Standishii*) by Sax & Sax. All of the chromosomes were more or less isobranchial in a cultivar of *T. occidentalis* studied by Mehra & Khoshoo.

Several preliminary comparisons have been made of terpenoid profiles from foliage of *Thuja* species (Banthorpe *et al.*; Von Rudloff, 1975; Yatagai *et al.*). *Thuja Standishii* is quite different from *T. occidentalis* and *T. plicata* in its monoterpene profile, while *Platycladus orientalis* is apparently quite similar to the latter two species based on the preliminary data of Banthorpe and colleagues. *Thuja plicata* shows very limited variation in leaf terpenoids and isozymes (Copes; Von Rudloff & Lapp; Von Rudloff *et al.*; Yeh) and apparently went through a genetic bottleneck during Pleistocene glaciation, while *T. occidentalis* seems to be more variable at the isozyme level (Walker).

Thuja occidentalis differs from three of the other species of the genus in having cupressuflavone present in its leaves, in addition to biflavonoids of the amentoflavone and hinokiflavone series (Gadek & Quinn, 1985).

The rate and pattern of root development in *Thuja occidentalis* were found to vary in relation to swampy versus calcareous substrate (Habeck). An increased rate of stem growth and greater wood strength were also found in plants growing on relatively dry limestone substrates by Harlow.

Thuja occidentalis and *T. plicata* are valued for their light, durable wood, which has been used for construction and to make fenceposts, railroad ties, and shingles. American Indian tribes have used the thick sapwood layers of both to make woven baskets and logs of *T. plicata* to make canoes and totem poles. The bark is rich in tannin, and the leaf oil has been used medicinally. *Thuja occidentalis* was one of the first North American trees cultivated in Europe, having been planted in Paris by about 1536. It was named arborvitae (tree of life) after tea brewed from the bark (which is rich in vitamin C) saved the crew of the French explorer Jacques Cartier from scurvy (Little, 1980). Several species of *Thuja* are cultivated as ornamentals, and diverse cultivars of *T. occidentalis* have been selected (Dallimore & Jackson; Krüssmann).

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4. **Juniperus** Linnaeus, Sp. Pl. **2**: 1038. 1753; Gen. Pl. ed. 5. 461. 1754.

Dioecious (rarely monoecious), evergreen, erect to prostrate shrubs, or pyramidal to open-crowned trees. Bark reddish-brown, usually thin and scaly, falling off in longitudinal strips [rarely thick and broken into plates]. Wood fragrant, close grained, with heartwood brownish to reddish-brown. Branches spreading or upright; branchlets rounded to nearly quadrangular or triangular, grooved and somewhat flattened. Leaves aromatic, entire or minutely denticulate; juvenile leaves in whorls of 3, linear-lanceolate to subulate, spreading; leaves of mature plants either also needlelike and in whorls of 3 (having the spreading portion linear-lanceolate, with rigidly pointed apex, eglandular, entire, abscising at the juncture with the stem [or retained on the decurrent leaf base], the abaxial surface concave and grooved, with 1 or 2 whitened stomatal bands) or in sect. SABINA mainly scalelike and decussately opposite (acute to acuminate or sometimes blunt tipped, closely appressed, imbricate, entire or minutely denticulate, glandular or eglandular, firmly attached to the decurrent base). Buds naked or covered with scalelike leaves, ovate to acute. Cones axillary or terminal on short branchlets from buds of the previous autumn. Pollen cones (microsporangiate strobili) solitary [or in clusters of 3 to 6 in *J. drupacea*], ovoid to oblong; microsporophylls decussate or ternate, (6 to) 10 to 20 per cone, ovate to peltate, entire to denticulate; microsporangia (2 or) 3 to 6 [rarely to 8] per sporophyll, globose, attached to the abaxial edge of the sporophyll; pollen with obscure germinal aperture. Ovulate cones ovoid to globose, maturing in 1, 2, or 3 years, subtended by several whorls of persistent scalelike bracts, with 3 to 8 [or 9] decussate or ternate fleshy scales, these alternating with or bearing on their inner surfaces 1 or 2 [rarely 3] erect ovules; mature ovulate cones berrylike, succulent or ultimately dry and fibrous, blue, blue-black [or reddish to brownish], resinous, with scales strongly fused and their suture lines seldom evident [rarely conspicuous], obscurely or conspicuously umbonate. Seeds 1 to 3 [rarely to 14] per cone, ovoid, terete or angled, wingless, often grooved or pitted by pressure from resin vesicles in the cone; seed coat thick and bony. Cotyledons 2 [to 6]. Chromosome number $2n = 22$

(sometimes $3n = 33$ [$4n = 44$]). (Including *Sabina* Miller, *Arceuthos* Antoine & Kotschy.) LECTOTYPE SPECIES: *Juniperus communis* L.; see Britton, N. Am. Trees, 107. 1908. (Classical Latin name for juniper.)—JUNIPER, RED CEDAR.

The largest genus of Cupressaceae, with 50 or more species in North and Central America, Eurasia, and northern and eastern Africa, very widely distributed from the arctic to the mountains of the subtropics, and with one species, *Juniperus procera* Hochst., occurring on tropical mountains from 14°N to 12°S in eastern Africa (Florin, 1963). Junipers are often dominant plants in subdesert vegetation—for example, in the Great Basin area of the western United States. Of the 13 species native to the United States (Zanoni), *Juniperus Ashei* Buchh., *J. communis* L., and *J. virginiana* L. are native in the Southeast. Three sections are usually recognized in the genus, with sects. JUNIPERUS and SABINA (Miller) Spach represented by native species in our area. Section CARYOCEDRUS Endl. contains only a single species, *J. drupacea* Labill., native to Greece and Asia Minor and cultivated as an ornamental in Europe and the United States. This species, occasionally segregated in the monotypic genus *Arceuthos* Antoine & Kotschy, has very large (ca. 2–2.5 cm in diameter) and relatively woody ovulate cones with the coats of the three seeds connate, as well as clustered pollen cones, but is otherwise quite similar to sect. JUNIPERUS, having all leaves ternate and needlelike and the cones axillary.

Gaussen's (1967, 1968) informal classification treats the three sections as subgenera and divides them into ten sections (which were not formally described), largely on the bases of geography, cone color, number of seeds per cone, and presence or absence of teeth on the leaf margin. The genus has also been divided into eight informal species groups, generally following the "sections" of Gaussen, by Rushforth. Given the probability of repeated convergence for cone color and seed number, it is likely that several of the species groups in sect. SABINA are artificial, and no subsectional groups are recognized in Zanoni's treatment of the North and Central American species.

Section JUNIPERUS (sect. *Oxycedrus* Spach) (foliage leaves needlelike, ternate, eglandular, with blade jointed to the leaf base and abscising at the juncture with the stem; winter buds evident; cones solitary, axillary, with microsporophylls and cone scales ternate; ovulate cones one- to three-seeded, ripening in two or three years) comprises eight species (Dallimore & Jackson; Rushforth), primarily from northern or mountainous areas of North America, Eurasia, northern Africa, the Canary Islands, and the Azores. The only North American species is the very widespread *Juniperus communis* L. (*J. nana* Willd., nom. illeg.; *J. sibirica* Burgsd.), common juniper, ground juniper, mountain juniper, $2n = 22$, a prostrate or spreading shrub or sometimes a columnar to irregularly branched tree with a single white stomatal band generally wider than the adaxial leaf margins. It is native to much of northern North America, occurring south in the higher mountains to North and South Carolina and Georgia in the east and New Mexico and California in the west, and from coastal Greenland across Europe and northern and central Asia. Franco divided the species into four subspecies on the basis of habit and leaf morphology; he referred the eastern North American forms to subsp. *depressa* (Pursh) Franco (var. *depressa* Pursh)

because the stomatal band is narrower than the leaf margin. In our region the species is found primarily on barren rocky slopes and is a matted, prostrate shrub or very rarely a dwarfed tree (Coker & Totten).

Section SABINA Spach (adult leaves mostly scalelike and decussately opposite [or sometimes all ternate and needlelike], often with an abaxial gland, with the leaf base clearly decurrent on the stem and not jointed and abscising at the stem juncture; winter buds indistinct; cones terminal on elongating branchlets, usually solitary; ovulate cones maturing in one [or two] years, usually one- or two- [more rarely to 14-]seeded) comprises 40 or more species widely distributed in North and Central America and the Caribbean, southern and central Europe to eastern Asia, and northern and east-central Africa. The North American species have often been divided into entire- and denticulate-leaved groups (Gaussen, 1967, 1968; Hall, 1952c; Rushforth; Zanoni & Adams, 1976). The majority of them are denticulate leaved, while *Juniperus horizontalis* Moench, *J. scopulorum* Sarg., *J. virginiana,* the Mexican *J. Blancoi* Martínez, and several Caribbean species have entire scale leaves and may form a natural group (Zanoni & Adams, 1976). The denticulate-leaved species in North America tend to occur in more xeric habitats (Hall, 1952c).

Juniperus virginiana L. (*Sabina virginiana* (L.) Antoine), eastern red cedar, red cedar, savin, $2n = 22$ (rarely $3n = 33$; Stiff), is named in allusion to its red heartwood. It is very widely distributed in the eastern half of the United States and southeastern Canada. It is a tree reaching 10–15(–30) m in height, with the trunk occasionally up to 1 m in diameter. In the Atlantic States the species often occurs on dry, gravelly slopes and rocky ridges, especially on calcareous soils. In Kentucky, Tennessee, northern Alabama, and Mississippi it covers great areas of rolling limestone hills, forming nearly pure stands of small bushy trees. The "cedar glades" in the Nashville Basin of Tennessee, noted for their unusual flora (Quarterman), are dominated by the species. Eastern red cedar is also often found in abandoned fields and along fence rows. In coastal areas of the eastern Gulf States, it often grows in deep swamps (where it tends to become a large tree), as well as on coastal sands. In southwestern Texas, Arkansas, and Louisiana it attains its largest size on rich alluvial bottomlands.

The populations of the southeastern Coastal Plain (from eastern North Carolina west to southeastern Texas) have often been treated as a separate species, *Juniperus silicicola* (Small) Bailey (*Sabina silicicola* Small; *Juniperus barbadensis* auct., non L.), but detailed comparisons of morphology and terpenoid chemistry by Adams (1986) indicate that they are better treated as var. *silicicola* (Small) Silba. Varietas *silicicola* has been distinguished as having shorter scale leaves, longer pollen cones, smaller ovulate cones, and more slender twigs, but there is considerable overlap in these characters, and multivariate comparisons fail to separate the geographic groups cleanly (Adams, 1986). Multivariate comparison of terpenoid profiles gives discrete but closely adjoining inland and coastal groups. Adams noted that coastal populations tend to have cinnamon-colored rather than brownish bark and a rounded rather than pyramidal crown. On the basis of both morphology and chemistry, populations from Texas and Louisiana, previously mapped as the coastal form by Little (1971), appear to fit into var. *virginiana* better than into var. *silicicola.*
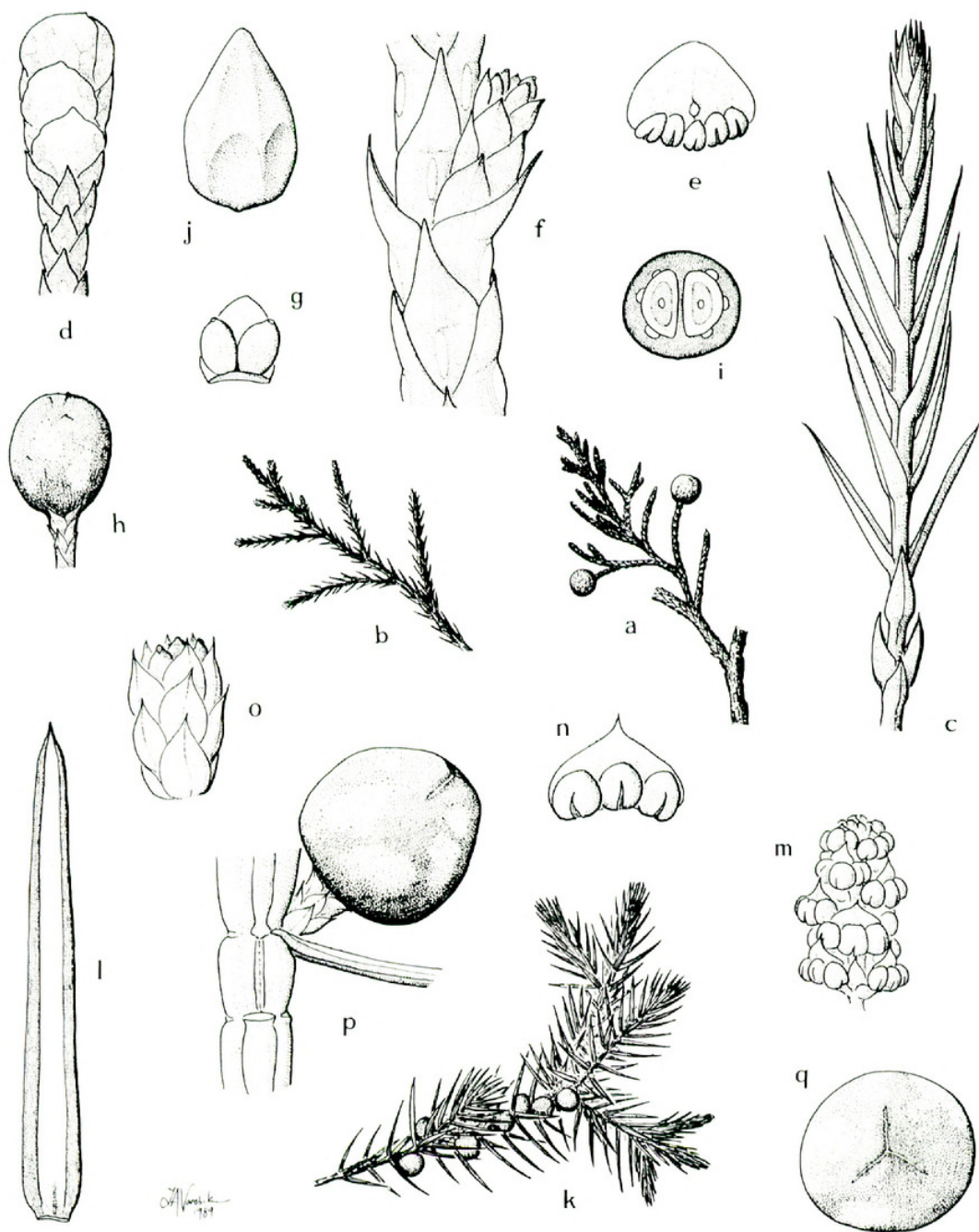
FIGURE 2. **Juniperus.** a–j, *J. virginiana*: a, branchlets with only scale leaves, bearing mature ovulate cones, × ¾; b, branchlet with scale and needle leaves, × ¾; c, detail of branchlet with needle leaves, showing decurrent leaf bases, × 5; d, microsporangiate strobilus before shedding of pollen, subtended by numerous scale leaves, × 5; e, microsporophyll (abaxial view), showing dehisced sporangia, × 10; f, branchlet with ovulate cone near time of pollination, × 7; g, cone scale (adaxial view) with 2 erect ovules near time of pollination, × 10; h, mature ovulate cone with fused cone scales, × 3; i, cross section of mature cone, only 2 seeds maturing—note resin vesicles outside seeds, × 3; j, seed, showing pits and ridges, × 5. k–q, *J. communis*: k, branch, showing ternate leaves and axillary ovulate cones, × ¾; l, detail of abscised portion of leaf in adaxial view, showing broad stomatal band, × 5; m, microsporangiate strobilus after shedding of pollen, × 5; n, microsporophyll (abaxial view), × 10; o, short axillary shoot with young

The geographic distribution of *Juniperus virginiana* adjoins or partially overlaps those of several other entire-leaved species: *J. horizontalis* to the north, *J. scopulorum* to the west, and a taxonomically complex Caribbean group of species (Adams, 1983a; Adams & Hogge; Adams, Jarvis, Slane, & Zanoni) to the south. Hybridization with *J. horizontalis* and *J. scopulorum* has been suggested on the basis of morphological variation patterns (Fassett, 1944b, 1945b; Hall, 1952c; Schurtz). Terpenoid profiles are suggestive of past introgression from *J. scopulorum* into *J. virginiana* (Adams, 1983b; Comer *et al.*; Flake, Urbatsch, & Turner). Hybridization of *J. virginiana* and *J. horizontalis* on the edge of the Driftless Area in Wisconsin has been well documented by multivariate analyses of morphology and terpenoid chemistry, as well as electrophoretic-banding patterns of peroxidase enzymes (Palma-Otal *et al.*)

Juniperus virginiana is most similar in morphology to *J. scopulorum* and the Caribbean species complex. *Juniperus scopulorum* tends to differ from *J. virginiana* and the Caribbean species in having its cones mature in the second rather than the first year. Morton noted some variation for this character in *J. scopulorum* and suggested that it be treated as a variety of *J. virginiana,* but this view has not been accepted by most later authors. Other characters that have been used to separate these species (Fassett, 1944a, b; Hall, 1952c; Rehder, 1940) include the degree of overlap of the mature scale leaves (much greater in *J. virginiana*), the width of the leaf epidermal cells (greater in *J. scopulorum*), the shape of the leaf glands (more elongate in *J. scopulorum*), and the number of sporophylls per pollen cone (lower in *J. scopulorum*), although the variation patterns are complex in both and comparisons based on wide sampling are needed. The terpenoid distribution in the two taxa is distinctly bimodal and provides support for their treatment as separate species (Adams, 1983b; Comer *et al.*; Flake, Urbatsch, & Turner), partially intergrading in the northern and southern Great Plains.

As many as six species closely related to *Juniperus virginiana* have been recognized from the islands of the Caribbean (see discussions in Adams, 1983a, 1986; Adams & Hogge; Adams, Jarvis, Slane, & Zanoni), although some authors (Dallimore & Jackson; Silba) have placed most of these taxa in synonymy under *J. barbadensis* L. *Juniperus bermudiana* L., a rare species endemic to Bermuda, differs from *J. barbadensis* and *J. virginiana* in its stouter ultimate branches, averaging 1.5 mm or more in width. Preliminary studies (Adams, 1983a; Adams & Hogge) have indicated significant differences in terpenoid distribution among some of the Caribbean taxa and between the Caribbean taxa and the morphologically similar *J. virginiana* var. *silicicola*. A detailed monographic treatment of this group is much needed.

Juniperus Ashei Buchh. (*J. mexicana* Spreng., nom. illeg.), Ashe juniper, rock cedar, mountain cedar, $2n = 22$, occurs on upland limestone or dolomite outcrops in the Ozark Mountains of northwestern Arkansas, southwestern Mis-

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ovulate cone at apex, showing 3 ovules near time of pollination, × 10; p, portion of branchlet with mature ovulate cone—note remnant leaf bases fused to larger stem, × 3; q, apical view of ovulate cone, showing suture lines between 3 fused cone scales, × 3.

souri, and adjacent Oklahoma, in the Arbuckle Mountains of southern Oklahoma, in extreme southwestern Arkansas, and more broadly in west-central Texas (where it often forms dense stands on the Edwards Plateau) and northeastern Mexico. It is a small, bushy tree differing from *J. virginiana* in its more irregular or rounded branching habit, its minutely serrulate rather than entire leaves, and its typically rounded rather than elongate leaf glands. There have been a number of reports of hybridization or morphological intergradation between *J. Ashei* and *J. virginiana* (e.g., Hall, 1952a, c; 1955), but these have not been substantiated by subsequent comparison of terpenoid profiles (Adams, 1975a, 1977; Adams & Turner; Flake, Von Rudloff, & Turner). The disjunct northern populations of *J. Ashei,* well within the distribution of *J. virginiana,* are very similar in terpenoid profiles to populations of *J. Ashei* in the main portion of its range (Adams, 1975a). *Juniperus Ashei* is apparently most similar to the Mexican species *J. saltillensis* Hall in both morphology and terpenoid patterns (Adams, 1975a, 1977; Zanoni & Adams, 1976). The terpenoids of *J. Ashei* appear to represent a subset of those in the latter species, which may be its progenitor (Adams, Von Rudloff, Zanoni, & Hogge, 1980).

Juniperus is a very distinct genus in the Cupressaceae on the basis of its unique fleshy cones with fused cone scales; it has sometimes been placed in a monogeneric tribe or subfamily. Its affinities to other genera are not well established on the basis of morphology, but the genus is similar to *Cupressus* in its distribution of tropolones (H. Erdtman & Norin) and biflavonoids (Gadek & Quinn, 1985).

Juniperus has been the subject of an increasing number of detailed taxonomic studies using multivariate analyses of terpenoid chemistry, as well as morphology (see, for example, Adams, 1983a, b, 1986; Adams & Hogge; Adams, Von Rudloff, Hogge, & Zanoni; Adams, Von Rudloff, & Hogge; Zanoni & Adams, 1975, 1976), and preliminary revisions have been presented for the Mexican and Guatemalan (Zanoni & Adams, 1979) and North American (Zanoni) taxa of sect. SABINA. Species delimitation is often very difficult in the genus, and overall monographic treatment is much needed. Problems in distinguishing species are partially due to the relatively cryptic characters of leaves, stems, cones, and seeds used to separate them and to our poor knowledge of certain species. To a large degree, however, they are due to the complexity of variation within species and the limited divergence or convergence among them. Fassett's (1944a, b; 1945a, b) work on *J. virginiana, J. horizontalis,* and *J. scopulorum* illustrates the problems in attempting to discriminate among closely related species by the use of univariate comparisons of morphological characters—problems that have been obviated in part by multivariate analysis and the use of independent chemical data sets. Fassett found that quantitative variation within individual populations can be substantial, and that characters yielding statistically significant differences among species often show a considerable degree of overlap. Zones of past or present hybridization in the areas where the species meet also add to the taxonomic complexity.

As in the rest of the family, *Juniperus* most frequently has a chromosome number of $2n = 22$. Counts have been obtained for at least 23 species (see especially Hall, Mukherjee, & Crowley, 1973, 1979; Khoshoo, 1961; Mehra;

Mehra & Khoshoo; Sax & Sax) of which 19 are reported to be diploid or preponderantly diploid. Triploid or tetraploid plants have been found predominantly in horticultural variants (e.g., in *J. chinensis* L. and *J. squamata* Buch.-Ham.); their frequency in wild populations is unclear. Some species differ in karyotype; e.g., one chromosome pair is markedly heterobrachial in *J. horizontalis* and *J. procera,* while all of the chromosomes are more or less isobrachial in *J. communis, J. virginiana,* and several other species (Mehra; Mehra & Khoshoo; Mujoo & Dhar; Ross & Duncan).

As discussed by Lemoine-Sébastian (1968), evolution within the genus *Juniperus* has been marked by repeated reductions in the numbers of both cone-scale whorls and ovules, culminating in several species with a single apparently terminal ovule enveloped by one whorl of cone scales. Seeds with very hard coats contained in fleshy, "berrylike" cones are effective adaptations for seed dispersal by birds or sometimes mammals (Holthuijzen & Sharik, 1984, 1985; Phillips). As in a number of other groups of conifers, animal dispersal of seeds is coupled with a dioecious breeding system (Givnish).

Several species of junipers (e.g., *Juniperus virginiana*) are hosts for cedar-apple rust (*Gymnosporangium* spp.), which produces conspicuous gall-like growths on the plant (illustrated in Coker & Totten) and is a serious pathogen of cultivated apples and other woody Rosaceae.

The wood of *Juniperus* is fragrant, very durable, and little damaged by insects. Wood and bark of several North American species have been found to be very effective termiticides (Adams, McDaniel, & Carter). The wood of *J. virginiana* has been much used for pencils, although incense cedar (*Calocedrus decurrens* (Torrey) Florin) is now much more widely employed for this purpose because of heavy exploitation of red cedar (Hemmerly). Red cedar wood has been widely used for fenceposts and furniture, especially moth-resistant cedar chests for storage of clothing. In the western United States junipers are also highly valued for their aromatic firewood. The essential oil (cedarwood oil) from the heartwood of *Juniperus* species has been widely utilized in compounding fragrances for soaps, perfumes, and industrial uses, as well as in microscopy as a mountant (Adams, 1987; Hemmerly). Leaf or fruit oils of *Juniperus* have been used medicinally and can possess powerful diuretic properties. Many species of junipers are grown as ornamentals, and a large number of habit and color variants have been selected, particularly in *J. chinensis, J. communis,* and *J. virginiana* (Dallimore & Jackson; Krüssmann; Ouden & Boom). Juniper "berries" from *J. communis* are used as flavoring agents in cooking and in the production of the alcoholic beverage gin (the name shortened from Dutch *jenever,* traceable back to Latin *juniperus*).

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5. **Callitris** Ventenat, Dec. Gen. Nov. 10. 1808.

Evergreen monoecious trees or shrubs with spreading or erect branches. Bark grayish, furrowed [brownish and fibrous in *C. Macleayana*]. Wood very dense, not distinctively colored. Juvenile leaves needlelike, in whorls of four; adult leaves scalelike, triangular, in whorls of 3, with bases decurrent and fused to the stem. Pollen cones solitary or clustered near branchlet tips; microsporophylls in whorls of 3 [rarely 4], each with (2 or) 3 (or 4) sporangia. Ovulate cones globose [to ovoid or conical], terminal on short, thickened stalks, bearing 6 [sometimes 8 in *C. Macleayana*] cone scales in 2 alternating and unequal whorls of 3, appearing to form a single whorl at maturity; cone scales thickened, triangular-ovate, valvate and opening out from the very reduced cone axis (columella); ovules [6 to] 18 to 36 [to 54] per cone, in 3 intersecting rows arranged around the columella and at the base of the cone scales. Seeds flattened, irregularly tetrahedral, bearing [1 or] 2 or 3 lateral wings; cotyledons 2 (rarely 3). Chromosome number $2n = 22$. (Including *Octoclinis* F. Mueller; *Frenela* Mirbel.) LECTOTYPE SPECIES: *Callitris rhomboidea* (R. Br.) A. & L. Rich.; see Bullock, Taxon **6**: 227. 1957. (From Greek *kallistos*, beautiful, and *treis*, three, in reference to the arrangement of leaves and cone scales.)—CYPRESS PINE.

A genus of approximately 15 species, 13 in Australia and two in New Caledonia. *Callitris* is divided into sect. OCTOCLINIS Bentham, including only *C. Macleayana* (F. Mueller) F. Mueller, and sect. CALLITRIS (sect. *Hexaclinis* Bentham). *Callitris Macleayana* is unusual in having some ovulate cones (those on shoots retaining the juvenile leaf type) with eight rather than six scales, both numbers often occurring on the same tree; loosely fibrous rather than dense, vertically furrowed bark; and only one elongate wing on the seed rather than two or three smaller ones (Baker & Smith; Clifford & Constantine; Garden).

Callitris columellaris F. Mueller var. *campestris* Silba (*C. glaucophylla* J. Thompson & L. Johnson; *C. glauca* R. Br. ex Baker & Smith, nom. illegit.), white cypress pine, $2n = 22$, has escaped from cultivation and has become locally naturalized in sand-pine (*Pinus clausa*) scrub in Brevard, Indian River, Orange, Osceola, and Seminole counties in eastern Florida (Judd, pers. comm.; Little, 1979; Wunderlin, pers. comm.). It is characterized by usually glaucous, unkeeled leaves and generally solitary ovulate cones with rugose but not verrucate scales that separate to near the base at maturity.

The nomenclature and species circumscription in the *Callitris columellaris* complex has been controversial. Franco chose a specimen referable to *C. columellaris* var. *columellaris* as a lectotype for *C. Hugelii*, a new combination based on *Frenela Hugelii* Carr., which would be an earlier name for the species. Blake has contended, however, that the specimen chosen was an inappropriate neotype probably representing a different species from that described in the protologue.

Several authors (Baker & Smith; Garden; Lacey; Thompson; Thompson & Johnson) have recognized three ecogeographic species in the *Callitris columellaris* complex: *C. glaucophylla* (*C. glauca*) in inland areas of the southern two thirds of Australia, *C. intratropica* Baker & Smith in the tropical zone of northern Australia, and *C. columellaris* s.s. in coastal areas of Queensland and

New South Wales. Other authors (Blake; Clifford & Constantine; Dallimore & Jackson; Venning, 1979, 1986) have emphasized morphological intergradation among these taxa, however, and they are treated here as varieties following Silba. There appear to be genetically based differences in plant habit and in foliage color and density among the three varieties (Lacey; Thompson & Johnson). In particular, the inland var. *campestris* usually has more glaucous foliage than the other varieties (hence the name "white cypress pine"), while var. *columellaris* has denser, dark green leaves and a more irregular branching pattern. Varieties *campestris* and *columellaris* are quite similar in cone size, while var. *intratropica* (Baker & Smith) Silba has been distinguished on the basis of its smaller cones (usually less than 1.8 cm wide) with narrower upper cone scales (Thompson & Johnson). It is uncertain whether plants from southern Queensland, between the generalized geographic ranges given for vars. *intratropica* and *campestris* by Thompson & Johnson, were included in the morphological comparisons (see Blake). Differences in leaf and wood chemistry among the taxa have been reported based on limited sampling (see Baker & Smith; Lacey; Thompson & Johnson), but thorough range-wide comparisons are needed to assess their validity.

The widespread south Australian species *Callitris Preissii* Miq. can also approach *C. columellaris* in morphology and leaf-oil chemistry (Adams & Simmons), and the taxa have been reported to produce fertile hybrids (Thompson & Johnson).

Chromosome counts for six species of *Callitris*, all $2n = 22$, were given by Mehra & Khoshoo. Similar karyotypes are seen in these species, with the chromosomes having median or submedian centromeres. Natural hybridization has been reported for three of these taxa, *C. Preissii, C. verrucosa* (A. Cunn. ex Endl.) F. Mueller, and *C. columellaris* var. *campestris*, in all possible combinations (Adams & Simmons; Garden; Thompson & Johnson).

Morphologically, *Callitris* shows the greatest similarity to the western Australian genus *Actinostrobus* Miq., which differs most prominently in having its ovulate cones subtended by a number of closely imbricate bracts. These are lacking in *Callitris*. Both genera have decurrent leaves in whorls of three and ovulate cones of six basally fused cone scales; they also have similar biflavonoid profiles, lacking in cupressuflavone and hinokiflavone derivatives (Gadek & Quinn, 1985). The southern African *Widdringtonia* Endl., which is similar to *Callitris* and *Actinostrobus* in embryology, differs in having decussately opposite foliage leaves, only four scales per ovulate cone, and a much more complex biflavonoid profile.

The sesquiterpene alcohol guaiol is a very characteristic component of the heartwood of *Callitris*, often crystallizing from cut stumps (Baker & Smith); within the Cupressaceae s.l. it has otherwise been reported only from the New Caledonian genus *Neocallitropsis* (H. Erdtman & Norin).

Several species of *Callitris* are important timber trees in Australia, furnishing hard, durable, termite-resistant wood for construction. The bark is rich in tannin. Resin exuding from the inner bark of cut stumps is similar to sandarac (obtained from *Tetraclinis*) and has been used in the manufacture of varnishes and incense (Lacey). In Australia various species of *Callitris* are widely planted

as windbreaks and ornamental trees and are particularly valuable for their drought resistance.

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