

THE CASUARINACEAE IN THE SOUTHEASTERN UNITED STATES¹

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CASUARINACEAE R. Brown in Flinders, Voy. Terra Austral. **2**: 571. July–Aug. 1814. “Casuarineae.” [Mirbel, Ann. Mus. Natl. Hist. Nat. **16**: 451. 1810, “Casuarinées”], nom. cons.

(BEEFWOOD FAMILY, SHE-OAK FAMILY)

A unigeneric family of evergreen [shrubs and] trees with minute, whorled, basally connate, scalelike leaves and thin, ridged and grooved [or quadrangular], articulated branchlets. Plants monoecious or dioecious, with reduced anemophilous flowers, the staminate flowers whorled in terminal, simple [or compound], bracteate spikelets; the carpellate flowers whorled in bracteate, globose to ellipsoid heads, usually on short, lateral branchlets. Ovules semi-anatropous, bitegmic, crassinucellate. Infructescence woody and cone-like, bearing winged, indehiscent samaras, each enclosing a single seed without endosperm. TYPE GENUS: *Casuarina* Adanson.

1. **Casuarina** Adanson, Fam. Pl. **2**: 481, 534. 1763.

Plants to ca. 25(–45) m tall, to ca. 70 cm [–1 m] in diameter. Trichomes unicellular or uniseriate, often branched. Calcium oxalate crystals often single or clustered in parenchymatous tissues, sometimes in phloem fibers. Leaves in whorls of [4 or] 5–16, the free tip of each protruding as the extension of a cauline ridge, linear to narrowly elliptic-lanceolate or narrowly deltoid [or ovate], erect or recurved, usually pubescent along the margins but

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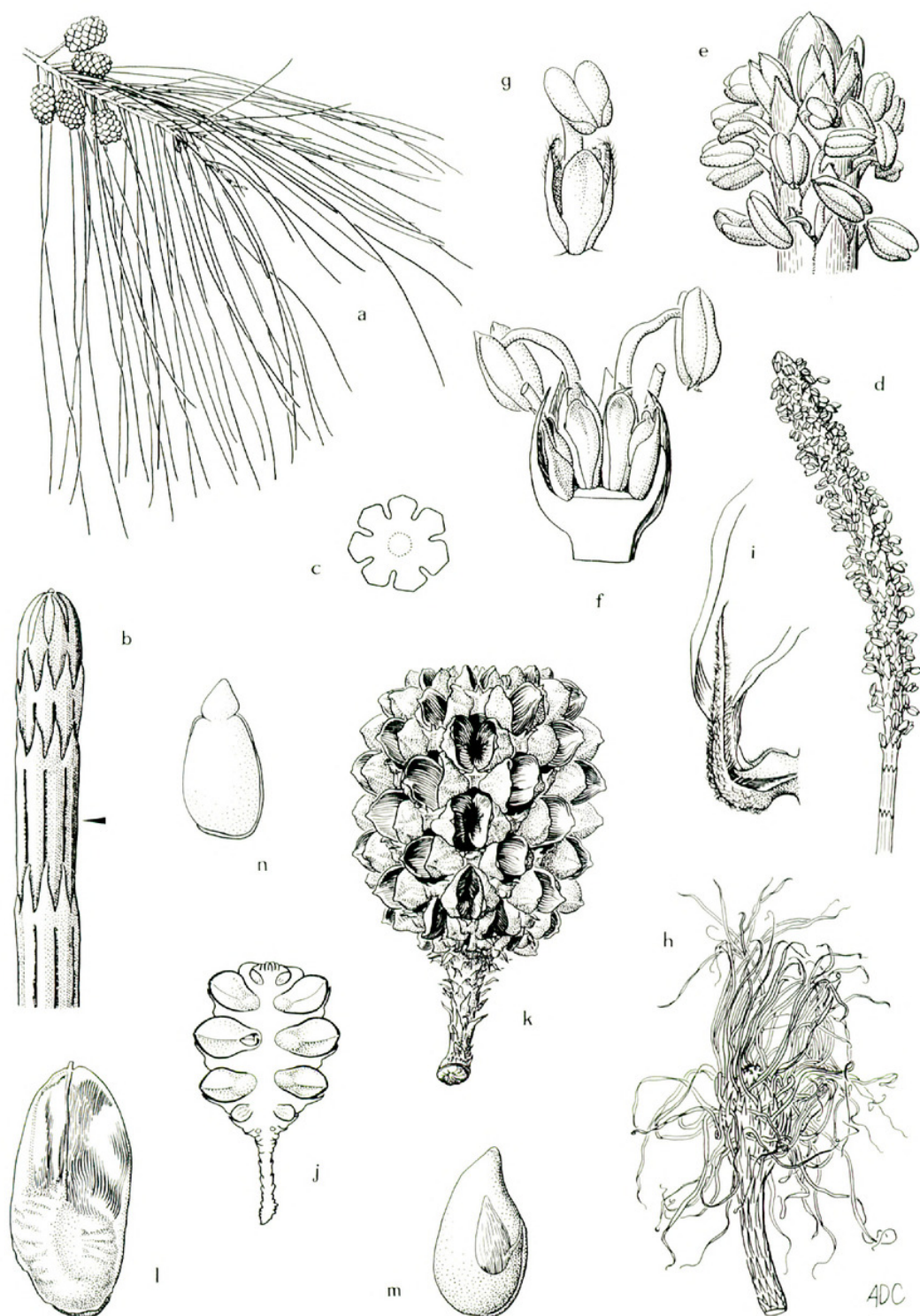


FIGURE 1. **Casuarina**. a-n, *C. equisetifolia*: a, fruiting branch (infructescences immature), $\times \frac{1}{4}$; b, tip of photosynthetic branchlet, $\times 12$; c, diagrammatic cross section of internode at level marked on "b," hairs omitted from grooves in stem, stele outlined by dots, $\times 18$; d, staminate inflorescence, $\times 2$; e, tip of same, showing 4 whorls of flowers, $\times 8$; f, single node showing 4 of a whorl of 7 flowers, each in a leaf axil, anthers of 2 flowers removed, adaxial side seen, $\times 12$; g, single staminate

often becoming glabrous, with 1[–3] median vein(s). Branchlets whorled, with the ridges of an internode aligned with grooves on the adjacent internodes, puberulent or tomentose, often becoming glabrous or nearly so [usually glabrous in the *Gymnostomae*], the indument usually most concentrated in or confined to the grooves, sometimes glaucous; stomata transverse, distributed mostly on the branchlets, rubiaceous or nearly so, with a variable number of polar cells. Wood with growth rings poorly defined or absent; vessel elements mostly solitary, with simple or scalariform, steeply oblique to transverse perforation plates, often with gum deposits, tertiary spiral thickenings, and tyloses; ground tissue usually composed of vasicentric tracheids intergrading with fiber-tracheids, the fibrous elements often with tertiary spiral thickenings; xylem parenchyma apotracheal banded and usually diffuse; rays highly variable, uniseriate to broadly multiseriate, often of the aggregate type. Each staminate flower subtended by a bract covering 2 small, sometimes slightly protruding bracteoles, the bracts deltoid to subulate or narrowly lanceolate [rarely orbicular], arranged like the sterile leaves and basally connate [sometimes these whorls separated by exposed sections of internode], usually with shaggy pubescence, especially along the margins; the paired bracteoles enclosing 2 perianth segments (sometimes called petals or inner bracteoles), the adaxial one larger and usually forming a hood over the anther and the other segment [the abaxial segment sometimes not developing], both sometimes broken off by growth of the exerted single stamen; stamen with the filament bent in the bud, anthers broadly oblong-elliptic, the epidermis degenerating and replaced with a fibrous layer, the 2 locules tending to separate at the often apiculate ends, dehiscing by longitudinal lateral slits. Pollen grains 2-nucleate when released, medium sized, usually oblate to oblate-spheroidal, rounded to semi-angular in polar view, (2 or) 3(–7)-porate or -pororate, the usually protruding pores often operculate, exine with or without columellae, nearly psilate to rugulate or spinulose. Whorls of carpellate flowers alternating with adjacent whorls and condensed into capitula, each flower subtended by a pair of minute, pubescent bracteoles within a usually tomentose, subulate to broadly deltoid or broadly orbicular bract (the broader shapes perhaps reflecting changes with development of the infructescence), sometimes with an attenuate apex; gynoecium 2-carpellate; ovary flattened, with 1 fertile locule and a small sterile locule; ovules 2[–4] with 1 maturing,

flower, from abaxial side, showing 2 lateral bracteoles, abaxial “petal,” and tip of adaxial “petal,” $\times 12$; h, carpellate inflorescence, $\times 3$; i, single primary bract with carpellate flower, the minute ovary with a bracteole on either side; styles only partly shown, $\times 12$; j, developing infructescence, in vertical section, showing 6 developing fruits, one in diagrammatic section to show 2 ovules (note primary bract subtending each fruit, heavy secondary bract behind each fruit), $\times 2$; k, infructescence from which fruits have fallen (note pairs of greatly enlarged secondary bracts (bracteoles; cf. i), each above a primary bract), $\times 2$; l, mature fruit, $\times 6$; m, seed, with delicate seed coat and rudiment of aborted ovule, $\times 10$; n, embryo, oriented as in seed (radicle up), $\times 10$.

the micropyle superior; style short, surmounted by 2 long, exserted, reddish stigmas. Infructescence globose to cylindrical; bracts becoming variably deformed and woody, often apiculate at the apex; bracteoles enlarging greatly, becoming woody, usually conspicuously puberulent toward the apex on both sides, their jutting, rounded to acute [to truncate or acuminate] apices becoming the most conspicuous components of the infructescence [sometimes bearing an abaxial projection], coming superficially to resemble paired valves of a capsule enclosing the seedlike samara. Samara flat, elliptic to obovate, rounded to acute at the apex, sometimes apiculate due to the persistent base of the style, conforming to the outline of the enclosing bracteoles and thickened at the basal end, membranaceous-winged at the opposite end, the wing traversed by a dark-colored nerve. Seed solitary, the pericarp adhering to the seed coat; endosperm originally nuclear with cell formation proceeding from the micropylar end, eventually completely consumed by the embryo; embryo straight, with flat cotyledons and a superior radicle. (Including *Gymnostoma* L. A. S. Johnson; type species *G. nodiflorum* (Thunb.) L. A. S. Johnson.) TYPE SPECIES: *C. equisetifolia* [L. ex] J. R. & G. Forster.² (Name from the resemblance of the branchlets to the plumage of the cassowary bird, *Casuaris*.) Rumphius, the acknowledged originator of the generic name, mentioned the common name "Casuaris-Boom, a foliorum forma." He remarked further that the pattern of striations in the wood resembles feathers even more than does the foliage.

A genus of approximately 55 species distributed mostly in or near Australia including New Caledonia and Fiji, with the southernmost species in Tas-

²The correct name for the species long known as *Casuarina equisetifolia* has been a matter of controversy. Linnaeus published the name *Casuarina equise[ti]folia* in the *Amoenitates Academicæ* (4: 143. 1759), but arguments for setting the valid publication at both an earlier and a later date have been made. In the Linnaean dissertation (Stickman's *Herbarium Amboinense*, 1754), on which the work of 1759 is based, Fosberg and Sachet (see also Fosberg) noticed that the misspelled name *Casaarina litorea* preceded *C. equisetifolia*. Citing ICBN Art. 42, they stated that reference to the description and figure in Rumphius's pre-Linnaean *Herbarium Amboinense* validated both the generic and the specific names. Fosberg proposed amending Art. 23 of the ICBN to consider the Rumphian names in Stickman's dissertation as invalidly published. In response, Voss and Greuter asserted that under Art. 34.1(a) most botanists would consider these names as already invalid "since they were not accepted by Linnaeus upon publication." The XIII Botanical Congress referred the matter to the editorial committee (Taxon 30: 906. 1981), with the result that Stickman's Rumphian names will appear in the 1982 edition of the ICBN as an example of names not accepted by the author in the original publication. (However, note that *C. equisetifolia* appeared as a replacement for *C. litorea* in 1759, not 1754.)

As an objection to the genus being validated by reference to Rumphius, Friis noted that "Although the Code is not absolutely clear on this point it has consistently been stressed by Rickett and Stafleu . . . that monotypic new genera cannot be validated by references to pre-Linnaean literature only." If Rumphius's description does not validate the generic name, it cannot validate the combination *Casuarina litorea* either according to Art. 43.1.

In contrast to Friis, Bullock found Stickman's or Linnaeus's (1754, 1759) "Generis proprii, singularis arbor, Equiseti Structura" insufficient as a validating description. He suggested that Adanson gave valid publication to *Casuarina* and that the Forsters did so for *C. equisetifolia*.

mania and the northernmost in southeastern Asia. The original eastern and western limits are defined by the only naturally widespread species, *Casuarina equisetifolia*. This appears to be indigenous around the Indian Ocean and eastward to part of Polynesia, where the extent of introduction by humans and subsequent naturalization is unclear (Smith), an uncertainty common to the history of this and various other species in tropical and subtropical regions.

Casuarina equisetifolia, *C. Cunninghamiana* Miq., and *C. glauca* Sieber ex Sprengel are cultivated and have become naturalized in the southeastern United States, mostly in Florida. Reports of *C. lepidophloia* F. Mueller (*C. cristata* Miq.) in Florida apparently result from misidentifications of *C. glauca* (see Bailey, Morton). Other species have been introduced, but either they are now absent or their presence is not well documented (e.g., a list of several such species appears in Eick).

The most common species, *Casuarina equisetifolia* (*C. litorea* [Rumph. ex] L. and many other synonyms) (with at least three taxonomic varieties), Australian pine, beefwood, was available from a nursery in Florida at least as early as 1887, as were several other species that have been less successful. Trees of *C. equisetifolia* differ from the other species naturalized in Florida in having an open, irregular crown; prominent ribs on the branchlets; infructescences usually more than 13 mm in diameter vs. narrower in *C. Cunninghamiana* (infructescences of *C. glauca* do not develop in Florida); and samaras usually 6–8 mm long vs. 3–4.5 mm in *C. Cunninghamiana*. *Casuarina equisetifolia* is usually monoecious, highly tolerant of salty soil, and prolific in fruit production. It flowers in Florida from late winter to October, with individual trees flowering twice per season. About 45–50 days pass between pollination and fertilization (Swamy).

Casuarina glauca, native to Australia (where it is called swamp oak) and restricted to South Florida in the southeastern United States, is dioecious and tolerant of salt; it has a strong tendency to sucker. In order to combine its attractive, dark green, dense, erect crown with a root system that does not sucker, scions of this species are grafted onto rootstocks from *C. equisetifolia*. Branchlets of *C. glauca* usually have 12–16 leaves per whorl vs. 6–8 in *C. equisetifolia*, and 6–11 in *C. Cunninghamiana*. *Casuarina glauca* has the thickest branchlets (usually more than 0.85 mm vs. a narrower diameter) and the longest internodes (usually 8–13 mm vs. usually less than 10 mm in *C. equisetifolia* and *C. Cunninghamiana*). That *C. glauca* hybridizes with *C. Cunninghamiana* is well established by anatomical, morphological, and serological criteria (Bailey *et al.*, El-Lakany *et al.*, El-Osta *et al.*, Saleh & El-Lakany). The other two possible hybrid combinations may occur in Florida as well.

Casuarina Cunninghamiana is native to eastern Australia, where it is called “River-[She]-Oak” from its tendency to line streams in pure stands, although it also grows well on drier sites. This is the least salt tolerant among the species in Florida. Trees of this species may attain the largest sizes to be found in *Casuarina*—in Australia the trunk sometimes exceeds a meter in diameter. *Casuarina Cunninghamiana* has ascending branches and a py-

ramidal crown; it sometimes suckers from the roots. Distributed from South Florida northward and westward to Tallahassee and to southern Louisiana, these (at least usually) dioecious trees flower from late summer through November, and occasionally later (e.g., in February.)

Using mostly characters of the bracteoles in the infructescence, Miquel (1868) divided *Casuarina* into the sections (EU-)CASUARINA and ACANTHOPITYS. Benthams and Mueller retained ACANTHOPITYS but split section CASUARINA into sections TRACHYPITYS and LEIOPITYS. The latter contains the three species naturalized in Florida and, because it contains the type species of the genus, should be called section CASUARINA. Refinement of Benthams and Muellers classification with an anatomical characterization of the sections appeared in Moseleys monograph on the wood anatomy of the Casuarinaceae. Poisson accepted Benthams sections, collected them as his *Divisio Casuarinae Cylindricae seu Cryptostomae*, and proposed the new *Divisio Casuarinae Tetragonae seu Gymnostomae* (corresponding to Loews "Typus nodiflorae") for seven species from New Caledonia, Sumatra, and some other nearby islands. These differ from the Cryptostomae in having quadrangular stems with only four leaves per sheath (*vs.* stems usually cylindrical with pilose grooves and more than four leaves per sheath); sparse, pseudoverticillate branches; usually compound staminate inflorescences; and squared (*vs.* rounded) infructescences with exserted bracteoles and 8-ranked scales, which are broadened at the base.

The genus *Gymnostoma*, recently segregated from *Casuarina* by L. A. S. Johnson, seems to correspond closely to the Gymnostomae in description and distribution. Stating that the new genus "is not formally based on" Poissons taxon, Johnson published *Gymnostoma* with little elaboration in a note that is preliminary to an upcoming revision of the Casuarinaceae in which he will recognize four genera.

Others have agreed that *Casuarina* can be divided. Anticipating Johnsons publication, Chanda found *Gymnostoma* to differ from *Casuarina* by having "distinctly striate" (*vs.* striate, faintly striate, or nonstriate) punctitegillate pollen. Kershaw (also in anticipation of *Gymnostoma*) did not fully confirm Chandas distinction, but concluded that pollen of *Gymnostoma* tended to be smaller, and to have a larger polar index, fewer pores with smaller protrusions, and less frequent cracks in the exine. The chromosome number is known for only one species of Gymnostomae, *C. papuana* S. Moore, $2n = 16$; all counts in the Cryptostomae are different (Barlow, 1959a). Stomata of Gymnostomae are sunken, are separated vertically by only one or no subsidiary cells, are not restricted to cauline grooves or adaxial surfaces of leaves, and have thicker lamellae in the guard cells (Flores, 1977). Moreover, Moseleys study of the wood anatomy of Casuarinaceae supports the recognition of *Gymnostoma*. (For more detailed general comparisons of these two groups see Christophel; Flores, 1977; and Smith.)

Other than by providing limited evidence that the Gymnostomae comprise a distinct group, Barlows (1959a) informal subdivision of *Casuarina* on the basis of chromosome counts hardly coincides with any of the infrageneric

classifications mentioned above. Barlow divided the Cryptostomae into groups A and B. Members of group A (including the species in Florida) are like the Gymnostomae in having few chromosomes ($n = 9$, but see Darlington & Wylie) and a distribution not limited to Australia. The $n = 8$ or 9 of the Gymnostomae or Cryptostomae Group A are thought to be the base numbers from which the diploid numbers, $2n = 20-28$ (and to 56 with polyploidy), in the entirely Australian group B were derived. Barlow (1959a, b) found species of the problematic *Casuarina* "Distyla complex," which was revised by Macklin and belongs to group B, all to have diploid numbers of 22, and he found sexual tetraploid individuals in most of them. Triploid carpellate plants of two species of the Distyla complex yield mixed triploid and tetraploid progeny, with a high frequency of heteroploid double embryos. In such cases haploid pollen fertilizes unreduced eggs, producing tetraploid embryos, and initiates pseudogamous development of unreduced triploid synergids. Apomictic embryos derive (without pseudogamous initiation) from triploid parents in two other species (Barlow, 1959b). Palynological characters serving to distinguish Barlow's groups were tabulated by Kershaw, who found the sequence *Gymnostoma*, group A, group B, and the Distyla complex to "form a series of increasing morphological complexity."

Treub's classic monograph of the embryology of three species of *Casuarina* is a source of numerous surprises, not all of which have withstood subsequent research (Frye, Juel, Swamy). Among his apparently accurate observations are that the branching pollen tube reaches the embryo sac (i.e., megagametophyte) by growth through the placenta and chalaza (chalazogamy) rather than by the more typical passage through the micropyle (porogamy); a massive sporogenous tissue produces several megaspores and several (to 20 or 25) embryo sacs (according to Swamy, probably leading occasionally to polyembryony); tracheids develop in the sporogenous tissue of some species; and the embryo sacs elongate basally into the chalaza. Frye reported that in *C. stricta* Aiton the chalazogamous pollen tube grows within the embryo sacs, but Swamy thought that the tube passed only between them.

Among Treub's probably inaccurate observations are that antipodal cells, and sometimes synergids, are absent (the embryo sac is of the eight-celled Polygonum type); the endosperm begins to divide before fertilization; the sporogenous tissue develops from two distinct groups of cells; the unfertilized egg is enclosed in a cellulose wall; the tip of the pollen tube becomes detached and is carried along by growth of the embryo sac; and the sperm is probably released into the embryo sac far from the egg.

Treub listed several supposedly primitive embryological features of *Casuarina* and segregated it as the subdivision Chalazogames, establishing the Porogames for the other angiosperms. *Casuarina* represented to him a fundamental split within the flowering plants and not, he emphasized, a group intermediate to the gymnosperms. Chalazogamy and multiple megaspores and embryo sacs were accepted as primitive by both Engler and Wettstein, who, from this and other observations—primarily the incomplete, anemophilous flowers and the vegetative resemblances to some gymno-

sperms—regarded *Casuarina* as primitive, not far removed from the gymnosperms, and placed the Casuarinaceae in the Archichlamydeae and Monochlamydeae, respectively. Wettstein explained that imperfect flowers with uniseriate perianths could have arisen from reproductive clusters on gymnosperms like *Ephedra*, with the carpellate flowers and whorls of staminate flowers of *Casuarina* as intermediates. Nevertheless, he thought that *Casuarina* probably represented a line of descent from the gymnosperms distinct from the origin of the other angiosperms.

Such incomplete, usually anemophilous flowers are now interpreted by most botanists to be specialized reductions from more complex, insect-pollinated ancestors. Wood, phloem, and pollen all indicate that *Casuarina* is fairly specialized (Erdtman, Moseley, Tippo). Its embryological oddities are also not strong evidence for labeling *Casuarina* as primitive. Chalazogamy probably evolved from porogamy, and the production of many megaspores occurs in diverse angiosperms (Moseley, Tippo). Both characteristics are found in the hamamelidalean families (Swamy, Tippo), to which the Casuarinaceae are allied by most who have considered their placement.

Similarity to the hamamelidalean assemblage is apparent not only in the small anemophilous flowers and the embryological characteristics, but also in the wood anatomy (Metcalf & Chalk, Moseley, Tippo) and pollen (Erdtman). The Betulaceae have received the most attention as the possible closest relatives of *Casuarina*, with likenesses apparent in the pollen (Erdtman, Kedves *et al.*), aspects of the embryology (Benson *et al.*), and paired vascular traces in the filaments (Eames). Poisson listed many similarities between *Casuarina* and the Myricaceae; Erdtman noticed palynological resemblance to this family and to Juglandaceae. Nonetheless, most authors perceive the Casuarinaceae as sufficiently isolated to comprise an order, the Casuarinales (or Verticillatae), which is placed in the subclass Hamameli[d]idae or superorder Hamamelidiflorae (Cronquist, Takhtajan, Thorne).

The chemistry of *Casuarina* remains too inadequately studied to be important in its taxonomy (Mears). The following phenolic compounds have been detected in several species or as indicated: catechin, cinnamic acids, cupressuflavone, cyanidin, delphinidin (*C. stricta*), ellagic acid, hinokiflavone, kaempferol, and quercetin. "Casuarin" from *C. equisetifolia* appears to be a mixture of d-galocatechin and d-catechin (Roux). (For tables of species and compounds see Bate-Smith, Natarajan *et al.*, and Saleh & El-Lakany.) Biflavonoids (hinokiflavone and cupressuflavone in *Casuarina*) are known from only seven families of angiosperms but are common among gymnosperms (Geiger & Quinn). Similarly, Natarajan *et al.* mentioned that juniperic acid reported from *C. stricta* is "considered to be a typical gymnosperm constituent." At least some of the other phenolic compounds are consistent with hamamelidalean affinity (Bate-Smith, *table 2*; Hegnauer; Natarajan *et al.*). In *C. Cunninghamiana* three sterols amount to over three mg per gram of dry weight of the roots (Knights & Wheeler), and haemoglobin is contained in the root nodules (Davenport).

Megafossils clearly identifiable as Casuarinaceae have been found in

Eocene and later deposits in Australia (Christophel, Lange, Patton, Pike), with the oldest (according to Christophel) most similar to *Gymnostomae*. A Gondwanalandic distribution is indicated by a Miocene fossil of a fruiting branchlet from Patagonia (Frenguelli). Less certainly identified is the fossil pollen attributed to *Casuarina*. Martin transferred the palynological form-species, *Casuarinidites cainozoicus* Cookson & Pike and *Triorites Harrisii* Couper, to *Casuarina*. The oldest specimens of the former are Paleocene (Harris). Pollen identified as *T. Harrisii* is common and widespread in Tertiary deposits in Australia and New Zealand, extending back to approximately the Danian-Maestrichtian transition (Couper).

Several authors have studied the unusual photosynthetic branchlets; the most thorough and broadly based study appears in the recent series by Flores. Her tentative opinion (1978) on the long-standing question of the homology of the ridges on the surface of the branchlets was to consider them as axial, limiting her concept of the leaves to the free, scalelike tips. The contrary and often accepted view that the ridges are the decurrent bases of leaves originated with Loew, who coined the term "phyllichnia" for them. As seen in transverse section, each ridge has near the outer surface a sclerenchymatous layer usually shaped like a "T," with the stem extending variably toward an underlying vein and halving the photosynthetic palisade layer. These veins extend into the leaf tips, are alternate with the more internal bundles of the cauline stele, are flanked by flanges of transfusion tissue, and have been reported in a few species to be surrounded by an endodermis (Boodle & Worsdell, Cordemoy). Flores (1977), however, was unable to verify the presence of Casparian strips in the alleged outer endodermis in any of the many species she studied. The inner vascular ring is surrounded by an endodermis. Succulent branchlets that sometimes develop in *Casuarina equisetifolia* probably result from exposure to salt spray along seashores (Rao).

Ovule orientation and attachment have been variably described as orthotropous to anatropous and apical to basal. In an effort to correct this confusion, Treub conducted a developmental study of the ovary of *Casuarina suberosa* Otto & Dietr., which when augmented by later studies allows some clarification. The (usually) two ovules originate parietally on opposite sides of an initially unilocular ovary; as a sterile second locule appears, the ovules become collateral on the septum. The base of the septum could be misinterpreted as the funiculus of a basally inserted orthotropous ovule. The mature ovule is erect, with its integument fused to the septum toward the top of the locule above the attachment of the bent funiculus.

Species of *Casuarina* grow in varied habitats, from rainforest to arid regions, commonly showing tolerance for dry conditions and substrates deficient in nitrogen. *Casuarina equisetifolia*, for example, forms forests on nearly soilless volcanic rock on Polynesian and Melanesian islands. Undoubtedly contributing to such tolerance are the nitrogen-fixing nodules on the roots of this and no fewer than ten other species, including the three in Florida.

That nitrogen is fixed by the microorganisms in the nodules and that the symbiosis contributes to the growth of the tree have been thoroughly demonstrated (Aldrich-Blake, Bond, Gauthier *et al.*, McLuckie, Narasimhan, Tyson & Silver). The endophyte invades a young lateral root near its base through a deformed root hair, stops the longitudinal growth of the root, comes to fill enlarged cortical cells, and initiates production of upwardly growing branch roots. The branch roots, in turn, branch from their own bases, ultimately producing a coralloid mass up to 6–7 cm in diameter (Becking, Callaham *et al.*, McLuckie, Miehe, Torrey; these studies based mostly on *Casuarina Cunninghamiana* and, to a lesser degree, on *C. equisetifolia*). As the branched, septate hyphae follow the growing end of the nodule, polyhedral resting stages are left behind in dead cortical cells. The mycelium produces terminal vesicles that probably have a role in the fixation of nitrogen. (For information on the morphology and growth of the endophyte, see Becking, Gauthier *et al.*, Miehe, Torrey, Tyson & Silver).

Similar nodules form in roots in six other nonleguminous families of angiosperms. Nodules of the Myricaceae most resemble those of *Casuarina* in also having upturned rootlets. The microbial symbionts hosted by each of these families all belong to the family Frankiaceae recently described and assigned to the Actinomycetales by Becking, who named and described the species from nodules of *Casuarina* as *Frankia casuarinae*. *Casuarina* also shares with the other nodulated nonlegumes the characteristic of vesicular-arbuscular endomycorrhizal symbiosis. Casuarinas in Florida are infected by species of *Gigaspora* and *Glomus* (Zygomycetes) (see Rose). Warcup recorded ectomycorrhizal associations for three species of *Casuarina* in Australia.

As is often noted, *Casuarina equisetifolia* sometimes grows more than ten feet a year and thus can be a rapidly regenerating source of wood on inferior soils. In India this species is cultivated in plantations and is harvested for fuel after five to seven years (Singh). (According to Morton, it is regarded favorably as a fuel for barbecues in Florida, lending a desirable flavor to the meat.) Wood of *C. equisetifolia* is hard and fine grained. Although several defects diminish its utility in cabinet work, it is commonly used for such rougher items as beams, poles, and handles for tools. Durability in salt water has made the wood of this species and *C. glauca* useful for masts, oars, spars, and docks. The pulp is suitable for manufacture of wrapping paper and coarser products (Guha & Karira).

Branchlets or seedlings of *Casuarina Cunninghamiana*, *C. glauca*, and other species have served as cattle fodder but are of low quality and even toxic (Anderson, Morton). Tannin, dyes for textiles, and ingredients in a wide variety of medicinal preparations (listed by Morton) have been derived from bark of *C. equisetifolia*.

The principal use of casuarinas in Florida has been horticultural, although the mature infructescences have been used in necklaces and for buttons. *Casuarina* has been planted along roads, in lawns, in hedges, in sandy areas (as a restraint to shifting), and in citrus groves (as a shelter).

All the species in Florida are susceptible to root rot caused by the basidiomycete *Clitocybe tabescens* (Rhoads). *Casuarina equisetifolia* (and to a

lesser extent the other species) has become an invasive pest in South Florida. It spreads rapidly, aggressively displaces native vegetation, and is difficult to eradicate. The masses of roots and fallen branchlets interfere with the nesting of sea turtles and the American crocodile. Sites invaded by *C. equisetifolia* provide poor habitats for other wildlife. (For information on *Casuarina* as a nuisance, see Craighead, Mazzotti *et al.*, Morton, Toops, Workman & Missimer.)

Zivitz found that three cases of hay fever and asthma near Miami coincided with flowering of *Casuarina equisetifolia* and "*C. lepidopholia*" (*sic*; probably *C. glauca*); he also found pollen of *C. Cunninghamiana* to be antigenic, and thus a likely source of problems in central and western Florida. Morton mentioned additional instances in which pollen from *Casuarina* has evidently caused respiratory irritation.

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