THE GENERA OF ULMACEAE IN THE SOUTHEASTERN UNITED STATES [1]

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ULMACEAE Mirbel, Elém. Phys. Vég. Bot. 2: 905. 1815, nom. cons.

(ELM FAMILY)

Trees or shrubs with watery sap; leaves with conduplicate vernation, alternate [rarely opposite], simple, the blade usually oblique at base, entire to variously serrate, petiolate; stipules paired, lateral or intrapetiolar, caducous; flowers perfect to imperfect (often by abortion of either androecium or gynoecium), actinomorphic to slightly zygomorphic, solitary, cymose, or in axillary fasciculate aggregations, usually borne on branchlets of the previous season (Ulmeae) or of the current season (Celteae). Perianth herbaceous, subcampanulate, (2–)4–8(–9)-lobed, the lobes free or variously fused, imbricate [valvate], persistent. Stamens erect in bud, hypogynous, arising from the base of the perianth, usually the same number as and opposite the perianth lobes [or sometimes more], the filaments distinct, the anthers bilocular with longitudinal dehiscence, extrorse or introrse; pollen 2–5(–6) aperturate (-porate, -colpate or -rupate), oblate to oblate-spheroidal. Gynoecium composed of 2 connate carpels; styles 2, linear, stigmatose along the upper inner surface, ovary superior, usually 1-loculate (occasionally 2-loculate in *Ulmus*), sessile to stipitate, the ovule 1, anatropous or amphitropous, pendulous from the apex of the locule, with 2 integuments. Fruit a samara, dry or thinly fleshy, often winged or appendaged, the seed with a straight embryo and without endosperm, or fruit a drupe, the seed with a curved embryo with

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folded or rolled cotyledons and usually with scanty endosperm. Embryo sac of the Polygonum type (*Celtis*) or of the Adoxa and Drusa types (*Ulmus*). Chromosome numbers, $x = 10, 11, 14$. (Celtaceae Link.) TYPE GENUS: *Ulmus L.*

A family of about 15 genera and 150–200 species distributed throughout much of the Northern Hemisphere and reaching into subtropical and tropical areas. Four genera are represented in the continental United States: *Ulmus*, with six species in the southeastern United States; *Celtis*, with five species in our range; *Planera*, a monotypic genus of the southeastern United States; and *Trema*, largely tropical, but with two species reaching into southern and central Florida. Additional New World genera include *Lozanella* Greenman, *Ampelocera* Klotzsch, and *Mirandaceltis* A. J. Sharp, all essentially tropical.

The Ulmaceae, one of five families in the order of Urticales, is distinguished from its nearest new world relatives the Moraceae, Cannabaceae, and Urticaceae by watery sap, leaves usually oblique at the base, flowers usually perfect, stamens erect in bud, fruit a samara or drupe, and seed with little or no endosperm. Using floral morphology and anatomy, Bechtel demonstrated the Ulmaceae to be the most primitive family in the order Urticales. In *Ulmus*, the flowers show evidence of suppression of a whorl of stamens and of one of the perianth whorls. Although the floral parts are cyclic in most ulmaceous genera, those of *Ulmus* are spirally arranged. In the gynoecium of Ulmaceae the many abortive vascular strands suggest suppression of carpels, the bicarpellate condition possibly having been derived from a polycarpellate condition. Tippo, using data from wood anatomy, confirmed this phylogenetic arrangement. It was pointed out that ring porosity appeared more commonly in the Ulmaceae (essentially temperate) than in the Moraceae (essentially tropical).

Dumortier divided the family into tribes Celteae (incorrectly Celtideae) and Ulmeae, but Engler raised the two divisions to subfamilial status. A third subfamily infrequently recognized is Barbeyoideae, but many workers place the monotypic genus *Barbeya* Schweinf. in a family of its own, Barbeyaceae Rendle.

The two tribes (subfamilies) can generally be separated by their pollen, the Ulmeae usually having 4- or 5-porate, -colpate, or -rupate grains, the Celteae usually having 2- or 3-porate grains. The only exception is *Zelkova* (Celteae) which typically has the *Ulmus* type of pollen.

Fairly abundant in the fossil record, fruits, as well as leaves, of *Ulmus* and *Celtis* have been found in large numbers. *Zelkova*, *Hemiptelea*, and *Pteroceltis* also are known as fossils.

The wood of *Ulmus* is of limited importance in the manufacture of furniture. The bark of *U. rubra*, high in mucilage content, has been used in medicinal preparations. Numerous cultivars of *Ulmus*, many resulting from efforts to produce disease resistant forms, are grown domestically as ornamentals.

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KEY TO THE GENERA OF ULMACEAE

A. Flowers usually perfect; fruits either flattened or ± dry with fleshy protuberances; embryo straight, cotyledons flat or longitudinally folded (ULMEAE).
  B. Fruit a flat, winged samara; leaves usually biserrate; flowers appearing either before or after the leaves. ..... 1. *Ulmus*.
  B. Fruit ovoid, wingless with numerous fleshy protuberances; leaves mostly serrate; flowers appearing with the leaves. ..... 2. *Planera*.
A. Flowers usually imperfect; fruits drupaceous; embryo curved, cotyledons variously folded (CELTEAE).
  C. Carpellate flowers solitary or in few-flowered fascicles; anthers extrorse; plants often spinose. ..... 3. *Celtis*.
  C. Carpellate flowers in axillary, subsessile cymes; anthers introrse; plants unarmed. ..... 4. *Trema*.

Tribe ULMEAE [Dumort.]

1. Ulmus Linnaeus, Sp. Pl. 1: 225. 1753; Gen. Pl. ed. 5. 106. 1754.

Trees (or infrequently shrubs) of various habitats, the bark usually deeply furrowed; branches unarmed, slender, terete, often with corky wings; leaf buds axillary, covered with numerous ovate to rounded chestnut-brown, glabrous to pubescent, closely imbricated scales, the inner scales accrescent and replacing the stipules, deciduous, leaving ring-like scars. Leaves distichous, petiolate, simply or doubly serrate, pinnately veined, deciduous to subpersistent [rarely persisting until new growth]; stipules lateral, linear-lanceolate to obovate, entire, free or connate at the base, scarious, inclosing the leaf in bud, caducous. Flowers perfect [rarely imperfect, the plants then polygamous], vernal to autumnal, minute, articulate on slender 2-bracteolate pedicels, produced in axillary subsessile or pedicellate cymes or racemes. Perianth uniseriate, campanulate, slightly to deeply (4–)5(–9)-lobed, membranaceous, marcescent. Stamens with the filaments filiform to ± flattened, exserted after anthesis; anthers oblong, emarginate, subcordate at the base, dorsified below the middle, extrorse. Style deeply 2-lobed, divergent, the lobes papillate and stigmatic on the inner face, ovary sessile or stipitate, compressed, glabrous or hirsute, usually 1-locular by abortion, rarely 2-locular; ovule amphitropous, micropyle extrorse, superior. Fruit a ± flattened samara, ovate to oblong, often oblique, sessile or stipitate, surrounded at the base by the marcescent calyx, often beaked by the remnants of the persistent styles, occasionally marked vertically by the thickened line of union of the two carpels, and

with a thin reticulate-venulose, membranaceous, light brown, broad or narrow wing [± unwinged], the wing often ciliate on the margin. Seed ovate, compressed, marked on the abaxial edge with the thin raphe, without endosperm; seed coat membranaceous, light or dark brown,

FIG. 1. **Ulmus.** a–h, *U. americana*: a, mature leaf × ½; b, branchlet with flowers, × ½; c, flower at time of shedding of pollen, × 5; d, flower with receptive stigmas, × 5; e, gynoecium in partial section to show ovule, × 5; f, mature fruit, × 1; g, seed, × 4; h, embryo, × 4. i–k, *U. rubra*: i, mature leaf, × ½; j, branchlet with nearly mature fruit and expanding leaves, × ½; k, mature fruit, × 1. l, *U. crassifolia*, leaf, × 1. m, *U. alata*, mature leaf, × ½.

rarely produced into a narrow wing. Embryo straight; cotyledons flat or slightly convex, fleshy, much longer than the superior radicle, the hilum oblong-linear, pale. (Including *Microptelea* Spach, *Chaetoptelea* Liebmann.) TYPE SPECIES: *U. campestris* L. = *U. glabra* Hudson; see

R. Melville, Jour. Bot. 76: 261–265. 1938, and A. Rehder, Bibl. Cult. Trees & Shrubs 135. 1949.[2] (Ancient Latin name for elm.) — ELM.

A genus of 25–30 species widely distributed through temperate and boreal regions of the Northern Hemisphere, with central and northern Asia the apparent center of distribution. Six species occur in eastern North America, but the genus is noticeably absent from western North America. *Ulmus* is found throughout Europe, extends south to the mountains of northern Africa, east to Turkey and the Caucasus Mountains, Pakistan, and the western Himalayas, to Siberia, Manchuria, and northern China to Japan. The genus has been divided into various subgenera, sections, and series (Spach, 1841; Planchon, 1848; Schneider, 1904); in the most recent subgeneric classification, Rehder (1949) recognized five sections, each represented in our range by at least one species.

KEY TO THE SECTIONS OF ULMUS IN THE SOUTHEASTERN UNITED STATES

A. Flowers vernal, appearing before the leaves; perianth with short, often unequal lobes.
  B. Flowers subsessile to very short pedicellate, not pendulous; samaras not ciliate on the margins. ..... Sect. ULMUS.
  B. Flowers long pedicellate, often unequally so, becoming pendulous; samaras marginally ciliate.
    C. Flowers fasciculate, the floral axis only slightly elongating; samaras glabrous on the sides; branches without corky wings. ..... Sect. BLEPHAROCARPUS.
    C. Flowers racemose, the floral axis slender and elongating; samaras pubescent on the sides; branches often with corky wings. ..... Sect. CHAETOPTELEA.
A. Flowers autumnal or appearing considerably after the leaves; perianth with the lobes deeply divided, often to the base.
  D. Flowers fasciculate, not pendulous, 4–5(–8)-merous; leaves subpersistent to ± persistent. ..... Sect. MICROPTELEA.
  D. Flowers in pendulous racemes, 6–9-merous; leaves deciduous. ..... Sect. TRICHOPTELEA.

Section ULMUS (§ *Madocarpus* Dumort.), an extensive Eurasian group, is represented in North America only by *Ulmus rubra* Muhl. (*U. fulva* Michx.), slippery elm, $2n = 28$. Occurring from southwestern Maine westward through southern Ontario to eastern North Dakota, southward to western Oklahoma and central and southeastern Texas, and eastward to central Georgia and northwestern Florida, *U. rubra* is commonly found in lowlands, especially in rich soil along stream banks and on low,

[2] The Linnaean name for the type species of the name *Ulmus* is *U. campestris* L. Since it has been used for three other species (*U. glabra* Hudson, *U. carpinifolia* Ruppius ex Suckow, and *U. procera* R. A. Salisbury) this name is now considered a *nomen ambiguum* to be rejected under Art. 69 of the Code (see Report of Standing Committee on Stabilization, Synop. Prop. Bot. Nomencl. XI Internatl. Bot. Congr., Seattle, 1969. Append. E, p. 113. 1969.). The correct name for this species appears to be *U. glabra* Huds. (cf. Melville, 1938, and Rehder, 1949).

rocky hillsides. In addition to the sectional characters, *U. rubra* is characterized by the ciliate leaves being scabrous above and by the very mucilaginous inner bark. Sterile, scabrous-leaved specimens of *U. americana* may be confused with this species but are distinguishable by the hardly mucilaginous bark.

Section BLEPHAROCARPUS Dumort. comprises a small group of European species and a single North American one, *Ulmus americana* L., American, soft, water, or white elm, $2n = (28)\ 56$. It occupies a broad range from Newfoundland west to southern Manitoba and eastern Saskatchewan, south to North Dakota, southeastern Montana, western Nebraska, western Oklahoma and central Texas, and in the east to Florida. It is readily identified by the flowers borne in close fascicles with elongating, pendulous pedicels, and a marginally ciliate, elliptic samara. The leaves may be smooth to scabrous above.

Fernald recognized four forms based on combinations of two pairs of vegetative characters: f. *pendula* (Ait.) Fern., with pubescent branchlets and the leaves smooth above; f. *laevior* Fern., with the branchlets as well as the upper leaf surfaces smooth; f. *alba* (Ait.) Fern., with pubescent branchlets and the leaves harshly scabrous above; and f. *intercedens* Fern., with glabrous branchlets and the leaves harshly scabrous above. All four can be found in our range, but attempts to distinguish them can end in frustration, for both smooth and scabrous leaves can be found on the same tree (Thieret). Varietas *floridana* (Chapm.) Little (*U. floridana* Chapm.), Florida elm, differing from var. *americana* only in degree in several quantitative characters (cf. Kurz & Godfrey, p. 113) is found on the Coastal Plain from eastern North Carolina to central Florida.

Natural hybrids of *Ulmus americana* are rare. Artificial hybrids have been made between this species and both *U. pumila* L., $2n = 28$, and *U. laevis* Pallas (cited as *U. pedunculata* Fougeroux by Winieski), but seed production from the crosses was very low and germination of the hybrid seeds even lower. Sax (1933) postulated that *U. americana* rarely crosses successfully with other *Ulmus* species because of an inability of the chromosomes to pair, since most species are diploid ($2n = 28$), while most American elms are tetraploids. Much of the genetic research with the elms, especially *U. americana*, has been concerned with the development of various races and hybrids which would hopefully be resistant to the Dutch elm disease and/or phloem necrosis. The closest relative of *U. americana* is the European *U. laevis* Pallas, $2n = 28$.

Section CHAETOPTELEA (Liebm.) Schneid., a New World section of only three species, is represented in our range by *Ulmus Thomasii* Sarg. and *U. alata* Michx., both of which frequently have corky-winged branchlets. *Ulmus Thomasii*, rock elm, $2n = 28$, is known from western Vermont west to southern Ontario, central Michigan, Wisconsin, northern Minnesota, and southeastern South Dakota, south to northern and eastern Nebraska and eastern Kansas, east to Missouri and Tennessee (and locally in northwestern Arkansas), and northeastward to Ohio and New

York. *Ulmas alata*, wahoo, winged, or cork elm, occurs from Virginia to Kentucky, southern Indiana, southern Illinois, and Missouri, south to central Oklahoma, eastern and southeastern Texas, and east to central Florida. Both species are commonly found on dry, rocky uplands, slopes, or cliffs. The two are easily distinguished by the broadly elliptic samaras and larger, distinctly petiolate leaves of *U. Thomasii*, in contrast with the lanceolate-ovate samaras and small, subsessile leaves of *U. alata*. The third member of this section is *U. mexicana* (Liebm.) Planch. (*Chaetoptelea mexicana* Liebm.), which occurs in mountainous areas from southern Mexico southward to Panama.

Section MICROPTELEA (Spach) Benth. & Hook. includes only the closely related but widely separated *Ulmus parvifolia* Jacq., of eastern Asia, and *U. crassifolia* Nutt., cedar, basket, or southern rock elm, of the southern United States. The latter is found in southwestern Tennessee, Arkansas, and southern Oklahoma, south to central and southern Texas, Louisiana, and western Mississippi. An isolated station was recently discovered in northern Florida (Suwanee County), and intervening stations should be looked for in Alabama and eastern Mississippi. It is questionably known from Nuevo León, Mexico. The older branches frequently have corky wings. This species, along with its Asian counterpart, is usually a tall tree reaching to 25 m. and is often free of branches for half its height. The frequently thick bark usually peels off in scales, exposing the brownish inner bark. Although described as a member of the following section, the poorly known *U. monterreyensis* C. H. Muller of Nuevo León, Mexico, is vegetatively very similar to *U. crassifolia*, but fruits and additional flowering material are needed before it can be placed properly.

Section TRICHOPTELEA Schneid. contains *Ulmus serotina* Sarg., September elm, probably the sole member of this section, which ranges from southern Illinois, Kentucky, and Tennessee, south to northern Alabama, northwestern Georgia, Arkansas, and eastern Oklahoma. Flowering and fruiting later than *U. crassifolia*, *U. serotina* is usually found in bottom lands and on limestone hills.

Of the numerous species and cultivars in cultivation (see Green), three appear to be naturalized and spreading from cultivation. The English elm, *Ulmus procera* Salisb. (§ *Ulmus*), naturalized from southern New England and New York southward to Virginia, has been reported by Crutchfield from Roanoke Island, North Carolina. The other European introduction in eastern North America, *U. glabra* Huds. (*U. campestris* L., pro parte) (§ *Ulmus*), Wych elm, has not been reported as being naturalized in our range. The third species, *U. pumila* L., (§ *Ulmus*), dwarf or Siberian elm, introduced from Asia and apparently stabilized from Minnesota to Kansas and in Utah, has also been reported from North Carolina by Crutchfield. This species has been planted in the northeastern and midwestern United States in parks, along boulevards, and on farms for windbreaks. It has mistakenly been called *U.*

parvifolia, Chinese elm, a species of eastern Siberia, northern China, and Japan which is not cultivated to any extent in the United States.

Pollination in *Ulmus* is clearly by wind, and, within our range, the elms contribute to both the early spring hayfever or tree-fever and the late-summer hayfever seasons. *Ulmus alata*, *U. americana*, and possibly *U. rubra*, all producing prodigious amounts of pollen, cause hayfever mainly in February and March in the Virginias and Carolinas (Wodehouse). Flowering about the same time as the ragweeds, *U. crassifolia* usually complicates late summer hayfever. *Ulmus serotina*, does not appear to be significant as a hayfever plant.

Although the flowers of *Ulmus* are perfect, cross pollination is apparently necessary to insure good seed production. It has not been clearly established whether the plants are partially or wholly self-incompatible or whether the proterogyny or proterandry reported in several species accounts for the lack of self fertilization. Further study of the floral maturation patterns is needed.

The base chromosome number for *Ulmus* appears to be 14 ($2n = 28$). Chromosome numbers for at least 13 species have been reported, with most *U. americana* and possibly some *U. glabra* at the tetraploid level, $2n = 56$. According to Sax, *U. americana* is probably an autotetraploid. Ehrenberg, in a study of the pollen of *U. glabra*, reported partial sterility in 47.2 per cent of the plants studied. The embryo sacs are tetrasporic and of the Adoxa or Drusa types or a modified form of the two.

First appearing in the Upper Cretaceous, *Ulmus* became abundant and widespread in the rocks of the early Tertiary (over 28 Eocene species described). Apparently reaching its maximum distribution during the Miocene (ca. 30 species), *Ulmus* was widespread in Europe, both eastern and western North America, and Asia. Pleistocene deposits have yielded some eight species, most of which are still extant.

Although many species of elms have corky flanges (wings) on the branches, the nature of these has been studied only in *U.* × *hollandica* Mill. in which the wings are produced by a symmetrical longitudinal splitting of the cork into bands which project like wings from the stem surface (Smithson). The corky wings found in *U. alata* and *U. crassifolia* have not been investigated.

Of the many diseases of elms, none has received as much attention as the Dutch elm disease, so called because much of the early work on it was done in Holland. Discovered in France in 1918 and now occurring over most of western Europe, it reached the United States about 1930, probably in a shipment of elm burl logs imported for veneer. It has now spread throughout the northeastern United States and has reached Ontario and Quebec and at least as far west as Illinois and as far south as Tennessee. *Ulmus* species vary in susceptibility, but *U. americana*, widely planted as a street tree in northeastern North America, is especially vulnerable and is possibly threatened with extinction. The disease is caused by an ascomycete, *Ceratocystis ulmi* (*Ceratostomella ulmi*), a yeast-like stage of which spreads through the vessels. It both produces

a toxin and stimulates the production of tyloses in the vessels, blocking water flow and causing wilting and death of the infected parts. The fungal spores are carried by the bark beetles *Scolytus multistriatus* and *Hylurgopinus rufipes* (and perhaps others), which lay their eggs in dead or injured bark of the trunk and branches of elms. The larvae tunnel under the bark in a characteristic feather-like pattern. The fungus sporulates in cracks in the bark, beneath dying bark, and in the beetle tunnels, and the sticky spores are carried by the emerging adult beetles to uninfected branches of the same or other trees where the beetles feed for a time before breeding. The spores enter the healthy tissues through the feeding wounds made by the beetles in the thin bark of young shoots. No satisfactory control has yet been found, but control of the beetles through spraying and removal and burning of diseased trees is widely practiced in cities. Several clones have been reported to be resistant to the disease: a highly regarded one is *U. carpinifolia* 'Christine Buisman', which, although showing considerable resistance to phloem necrosis as well, is unusually susceptible to a dieback caused by *Nectria cinnabarina*.

Phloem necrosis, caused by the virus *Morsus ulmi*, is even more deadly and has been known to kill an elm in a single season. The virus attacks the phloem, eventually destroying the phloem elements, interrupting the food supply to the roots, and causing in the more advanced stages small and even large roots to die. It is transmitted by the elm leaf-hopper, *Scaphiodeus luteolus*, which can be controlled by various insecticides. An American disease, cephalosporium wilt, caused by the imperfect fungus *Dothiorella ulmi*, causes foliage wilting and dieback of the young branches. Judicious pruning can usually control and eradicate this threat.

Elms are attacked by numerous insect pests, including the elm leaf-curl aphid, *Ariosoma ulmi*; the leaf beetle, *Galerucella luteola*; the elm borer, *Saperda tridentata*; the elm lace bug, *Corythucha ulmi*; and the gypsy moth, *Porthetria dispar*.

The wood of elm is heavy, tough, strong, often flexible, durable under water, often difficult to split, and fairly attractive in appearance. The sapwood is usually yellowish or cream colored with brown or grayish-brown heartwood. The wood of all the species in our range is ring porous. A minor lumber source, elm wood is used in shipbuilding, panelling, crates, and in some furniture. At one time it was commonly used for wheel hubs. High in mucilage content, the inner bark of *U. rubra*, and to a lesser extent that of *U. americana*, has been used in various decoctions in folk and Indian medicine in the southeastern United States.

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Many popular or semipopular articles about *Ulmus* and numerous references concerning the Dutch elm disease have been omitted. Under family references see BAILLON, 187; BERNARD, 1108–1112; BERRY, 146–153; FOWELLS, 724–742; GIBSON, 379–394; JONGMANS, 23–66; KURZ & GODFREY, 109–115; VINES, 208–214; WEST & ARNOLD, 58–60.

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2. **Planera** J. F. Gmelin, Linn. Syst. Nat. ed. 13. 2: 150. 1791.

Deciduous trees or large shrubs of wet habitats, usually less than 20 m. tall, with scaly bark, the inner bark reddish brown; branchlets slender, terete, unarmed, puberulous; lenticels pale, scattered; leaf scars small, ± orbicular; buds axillary, minute, subglobose, covered with thin, closely imbricate scales. Leaves petiolate, ovate-oblong, coarsely serrate, acute to rounded at apex, oblique to rounded at base, pinnately veined, the veins ± conspicuously anastomosing beneath; stipules free, lateral, ovate, caducous. Plants polygamous, flowers perfect or often functionally imperfect, fasciculate at the nodes of the one-year-old branches, articulate, short-pedicellate, the pedicels ebracteolate, the lower flowers often staminate. Perianth campanulate, 4- or 5-lobed from midway to near the base, the lobes rounded apically, greenish yellow, subscarious, submarcescent. Stamens as many as the perianth lobes in staminate flowers, in carpellate flowers often reduced or wanting; filaments filiform, exserted; anthers introrse, ovate, emarginate apically, cordate basally, dorsifixed below the middle; pollen 4–5-porate, -colpate or -rupate. Gynoecium often rudimentary in staminate flowers; styles 2, elongate, papillo-stigmatic on the inner faces, united at the base, wanting in staminate flowers; ovary ovate, stipitate, tuberculate, 1-loculate, the ovule anatropous to shortly amphitropous. Fruit obliquely ovate to oblong, ± compressed, keeled on the back, with numerous fleshy protuberances, often inclosed basally by the marcescent calyx, often beaked by the persistent style. Seeds plano-compressed, ovoid, often oblique, testa membranaceous, endosperm absent. Embryo straight; cotyledons ± thick, flat, slightly unequal, the apex of the larger hooded and slightly infolding the smaller, the radicle minute, directed toward the linear hilum. TYPE SPECIES: *P. aquatica* J. F. Gmelin (*Anonymos aquatica* Walt., nom. invalid., cf. ICBN 1966. Art. 20, 43.) (Named for the German botanist Johann Jakob Planer, 1743–1789.) — WATER ELM, PLANER TREE.

A monotypic genus of the southeastern United States ranging along the Coastal Plain from southeastern North Carolina south to northern Florida, west to eastern Texas, and north in the Mississippi Embayment to southeastern Oklahoma, southeastern Missouri, southern Illinois, western Kentucky, and western Tennessee. *Planera aquatica* appears to be restricted to swamps, margins of sluggish streams or rivers and alluvial flood plains. It is frequently found growing in permanent water up to a meter deep, but can withstand long periods of inundation at greater depths (McAtee).

Flowering begins in February and continues into April, with the fruits maturing approximately one month following anthesis. The seed viability has been reported to be very high (McAtee). The seeds are a major food source for waterfowl, especially mallard ducks. A study conducted in Louisiana from October through December on 171 mallard ducks revealed that 45.5 per cent of their total subsistence consisted of seeds of

P. aquatica (McAtee). Other species of ducks occasionally feed upon the seeds, but not as a major food supply (McAtee, Mabbott). The seeds apparently remain viable in standing water, thus supplying waterfowl with an overwintering food.

Several species of *Planera* have been described on the basis of fossil leaves and leaf fragments. *Planera longifolia* and *P. Ungeri* are attributed to the Upper and Middle Miocene in the central Rocky Mountain area (Lesquereux, 1878, 1883), and *P. Ungeri* has been reported by Heer from Alaska. Berry (1924) considered the genus to be an old one, with four Upper Cretaceous species distributed from western Greenland to North Carolina. Also three or four Eocene species are known only from North America and the Arctic localities. *Planera* is also represented in the Miocene of Europe and North America and in the Pliocene of Europe and Asia.

The wood of *Planera* is considered to be of little or no use economically. In comparison with the wood of *Ulmus*, Gibson found that of *Planera* to be lighter in weight (specific gravity 0.53), poorer in fuel value, weaker, and more brittle. The wood is described as being soft, light brown in color with almost white sapwood. *Planera* differs from *Ulmus* in that the annual rings lack the rows of large open vessel-pores common in *Ulmus*.

The genus is closely related to *Ulmus* but has partially imperfect flowers and a characteristic wingless fruit with irregular fleshy protuberances. Unfortunately little is known of the genus in regard to its overall biology, i.e., floral anatomy, embryology, cytology, and ecology.

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Tribe CELTEAE Dumort., "Celtideae"

3. **Celtis** Linnaeus, Sp. Pl. 2: 1043. 1753; Gen. Pl. ed. 5. 467. 1754.

Small to moderate-sized or large trees or shrubs of variable habitats, the bark smooth or often fissured and conspicuously warty; branches un-

armed or spinose; buds scaly or naked. Leaves distichous, serrate or entire, often oblique at the base, pinnately 3(–5)-veined, petiolate, membranaceous to coriaceous, deciduous [or persistent]; stipules lateral, free, usually scarious, caducous. Plants monoecious or rarely polygamomonoecious, the flowers vernal, small, pedicellate on the branches of the year, usually functionally imperfect, rarely functionally perfect, the usually lower staminate flowers cymose or fascicled, the carpellate flowers solitary or in few-flowered fascicles from the axils of the upper leaves. Perianth imbricate, slightly to deeply 4(5)-lobed, the lobes deciduous. Stamens as many as the perianth lobes, inserted on the usually densely pilose receptacle; filaments subulate, sometimes incurved in bud and spreading elastically, exserted after anthesis; in carpellate flowers usually shorter and included and often nonfunctional, rarely wanting; anthers ovate, dorsifixed just above the emarginate base, close together and face to face in bud, extrorse. Gynoecium in staminate flowers minute and rudimentary; in carpellate flowers style short, sessile, divided into two divergent, elongate, reflexed lobes, the lobes entire or bifid, papillate-stigmatic on the inner face, deciduous; ovary ovate, sessile, 1-loculate; ovule anatropous, with two integuments. Fruit a fleshy drupe, ovoid or globose, the outer part of mesocarp thick and firm, the inner thin and fleshy, the stone thick-walled, bony, smooth or rugose. Seed filling the locule; endosperm scanty, gelatinous, nearly inclosed between the folds of the cotyledons, or wanting; seed coat membranaceous, the chalaza colored, close to the minute hilum. Embryo curved; cotyledons broad, foliaceous, conduplicate or rarely flat, variously folded, corrugate, incumbent on or embracing the short superior radicle. (*Mertensia* HBK. non L., *Momisia* F. G. Dietr., *Solenostigma* Endl.). TYPE SPECIES: *C. australis* L., of Europe and Asia. (Name the classical Latin one given by Pliny for an African lotus with sweet berries, possibly *Celtis australis*.) — HACKBERRY, SUGARBERRY, NETTLE-TREE.

A genus of 50–60 species widely distributed in temperate and tropical regions of the world, with five species in our range. Because of the common occurrence of intergrading forms, as well as ecological variations, the species are at best poorly defined and are much in need of careful biosystematic study. The species enumerated here should be considered as tentative. Many of the minor variants have been described at various subspecific levels.

Combining mainly vegetative and floral characters with geographical distribution Planchon divided *Celtis* into four subgenera, two of which, CELTIS and MOMISIA, are represented in our area. Subgenus SPONIOCELTIS, composed of three species with linear, entire stigmas, the flowers borne in cymes with the staminate and/or polygamous flowers borne near the apex of the branchlets, is disjunctly distributed in tropical America and Malesia. *Celtis Swartzii* Planch., of the Greater Antilles, is closely related to the Malesian *C. cinnamomea* Lindl., but *C. trinervia* Lam., attributed to this subgenus by Planchon appears to be placed better in

subgen. CELTIS. Subgenus SOLENOSTIGMA Planch., characterized by two-lobed or emarginate stigmas and the flowers borne in cymes, is restricted to southern Asia and Australia. The monotypic genus *Mirandaceltis* A. J. Sharp was established for *C. monoica* Hemsl., of Mexico, which differs in leaf venation and drupe size and which is perhaps somewhat intermediate between *Celtis* and the Asiatic genus *Zelkova*.

Subgenus CELTIS (subgen. *Euceltis* Planch.), widespread, mostly throughout the mild-temperate regions of the world, is characterized by linear, entire stigmas and staminate flowers fasciculate in the axils of new leaves. Three species occur in eastern North America. *Celtis laevigata* Willd. (*C. mississippiensis* Bosc), $2n = 20$, with drupes 5–8 mm. long and narrow entire to somewhat serrate leaves, ranges from southeastern Virginia, south through Florida, and west to southern and western Texas, northeastern Mexico and southeastern Oklahoma, southern Kansas, Missouri, southern Illinois, southern Indiana, and central Kentucky. Varietas *Smallii* (Beadle) Sargent (*C. Smallii* Beadle), of questionable status, differs only in its constantly serrate leaves. Shorter, thicker leaves and more pubescence dubiously separate var. *texana* (Scheele) Sarg. (*C. texana* Scheele) from var. *laevigata*. A shrub or small tree, generally of exposed habitats, with drupes 5–8 mm. long and relatively small, often entire leaves, *C. tenuifolia* Nutt. is found from southeastern Pennsylvania to Indiana, northern Illinois, Missouri and eastern Kansas and south to eastern Oklahoma, Louisiana and northern Florida. Fernald & Schubert distinguished var. *georgiana* (Small) Fern. & Schub. (*C. georgiana* Small) on the basis of its pubescence and leaves which are coriaceous and scabrous above. A third species in our range, *C. occidentalis*, $2n = 20, 28$, has a more northern distribution, ranging from Massachusetts and New Hampshire to New York, southern Quebec, southern Ontario, central Michigan, southern Manitoba, Minnesota and central North Dakota, south to western Nebraska, northeastern Colorado, southeastern Wyoming, western Kansas and western Oklahoma, east to Arkansas, Alabama, and Georgia. Varietas *pumila* (Pursh) Gray (*C. pumila* Pursh) is based on plants with submembranaceous to membranaceous leaves which are conspicuously inequilateral at the base. Boivin (1967) described var. *Soperi* from southeastern Ontario and from northern Illinois on the basis of the leaves being regularly dentate. Other species within the continental United States which are assignable to this subgenus are *C. Lindheimeri* Engl., of central and southern Texas, and *C. reticulata* Torrey (*C. Douglasii* Planch.), of the western states (Wyoming and Idaho, west to western Washington, south to Oregon, eastern and southern California, east to Arizona, northern Mexico, New Mexico and western Texas, western Oklahoma, and Colorado).

Subgenus MOMISIA (F. G. Dietr.) Planch. with about 15 species in the Neotropics, is centered in Brazil and attains its northernmost limits in southern Florida and the southwestern United States. The flowers have linear, bifid or twice bifid stigmas, and they are borne in racemes. Typically shrubs, the species usually have solitary or paired axillary spines

in the stipular position. *Celtis iguanaea* (Jacq.) Sarg. (*Momisia iguanaea* (L.) Rose & Standl., *M. aculeata* (Swartz) Klotzsch) is reported from the southwestern coast of Florida and the Coastal Plain of Texas. The smaller- and scabrous-leaved *C. pallida* Torr. (*Momisia pallida* (Torr.) Planch.), common in central, western and southern Texas, New Mexico, Arizona, and in Mexico from Chihuahua to Baja California south to Oaxaca, is also known from the western coast of peninsular Florida.

Chromosome numbers reported for *Celtis* (six species) are $2n = 20$, 22, 26, 28, and 40. Sax noticed in *C. occidentalis* very irregular meiotic divisions with little pairing and with the univalent chromosomes irregularly distributed. Although 80 per cent of the pollen was sterile, a large number of fruits were produced. As Sax indicated, if the species contains two different basic sets of chromosomes with only a few homologous chromosomes or parts of chromosomes it could breed true only by some form of apomixis, a problem in *Celtis* that has not been investigated, but one which may be crucial in the taxonomy of the genus.

Flowering of *Celtis* species begins with or shortly after the appearance of the leaves in early April to late May. The drupes, ripening in September and October, are dark red to purple and are often sought after by animals. The fruits are eaten principally by birds, which in turn aid in the dissemination of the hard stones.

Numerous fossilized stones of the drupes of *Celtis* have been discovered in Europe, in Asia (including Japan), and in the western, midwestern, and southern United States. The first records are apparently from the early Eocene in Wyoming and the late Eocene in Georgia (United States) with only one European species. Continuing through the Oligocene, *Celtis* species are best known from the Miocene (at least nine species). Fossilized material of *Celtis* from the Pliocene is sparse, and even less is known of the genus in the Pleistocene.

Perhaps the most obvious disease of hackberries is the characteristic "witches-broom" produced by numerous proliferations at the branch tips. Although the cause is not clearly understood, a mite, *Eriophyes*, and the powdery mildew *Sphaerotheca phytophylla* are almost consistently associated with outbreaks of the deformations. No effective control is known. Although at least 17 types of insect galls occur on *Celtis occidentalis*, four caused by species of the genus *Pachypsylla* (Hemiptera) appear to be most prevalent. Damage to the trees is probably slight, even though the adults overwinter in the cracks of the bark. More serious threats, when abundant, are the spiny elm caterpillar, which is the larva of the mourning cloak butterfly, *Nymphalis antiopa*, and the larva of the hackberry butterfly, *Chlorippe celtis*, both of which feed upon the leaves. The hackberry engraver beetle, *Scolytus muticus*, often is found on the dead or dying branches.

The wood of both species is clear, light yellow with a thick, lighter-colored sapwood, but that of *C. occidentalis* is coarse grained, while that of *C. laevigata* is described as close grained. The secondary xylem is

also characterized by thin medullary rays and numerous small groups of small ducts arranged in intermediate concentric rings. In a comparison of the wood of temperate and tropical species of New and Old World *Celtis*, Cox and Grumbles independently showed that the species of temperate areas were ring-porous, while the tropical species were diffuse porous, an obvious reflection of the effects of seasonality on the trees. Only *C. occidentalis* and *C. laevigata*, of the species in our range, are large enough for the rather soft, weak wood to be utilized to any extent. The wood is used largely for posts, inexpensive furniture, boxes, crates, barrels, and other miscellaneous items. Described as a good tree for shade, species of *Celtis* are planted as yard and street trees. At least seven taxa, mainly from southeastern Asia and China, have been introduced into the United States.

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4. **Trema** Loureiro, Fl. Cochinch. 562. 1790.

Evergreen trees or shrubs of tropical forest margins and disturbed areas, the bark usually lightly fissured; branchlets terete, unarmed, variously pubescent, usually with conspicuous lenticels; buds axillary, narrowly ovate, covered with thin imbricate scales. Leaves distichous in ours, petiolate, variously serrate [to subentire], pinnately veined, usually conspicuously 3-veined at the base, the veins prominent beneath; stipules free, lateral, subpersistent to persistent [caducous?]. Plants monoecious [subdioecious], the flowers imperfect or polygamous (but then functionally imperfect), articulated with the pedicel, in axillary, subsessile cymes. Staminate flowers with the perianth 4- or 5-lobed, the lobes united near the base and induplicate-valvate or slightly imbricate; stamens 4 or 5, the filaments flattened, included to equalling the perianth lobes, the anthers introrse, ovate, dorsifixed below the middle; pollen 2-porate, suboblate, a rudimentary ovary usually present with numerous hairs at its base. Carpellate flowers with 4 or 5 flattened perianth lobes, the lobes united near the base, ± imbricate; style central, divided to the base, the two branches linear, minutely plumose-stigmatic on the inner faces; ovary sessile with numerous pilose hairs inserted at the base, 1-loculate, ovule

FIG. 2. **Trema.** a–i, *T. micrantha*: a, branch with staminate flowers, × ½; b, same, leaves removed, × 2; c, staminate flower with rudimentary gynoecium, × 5; d, node with carpellate flowers, leaf removed, × 2; e, carpellate flower, × 10; f, same, vertical section, semidiagrammatic, × 10; g, mature fruit, × 5; h, seed, × 10; i, same, in partial section to show embryo, × 10. j, *T. Lamarckiana*, leaf, × ½.

amphitropous; stamens wanting. Drupe small, ovoid or subglobose, inclosed basally by the persistent perianth, often beaked by the persistent style, smooth [pitted]; exocarp ± fleshy, endocarp hard; seed with fleshy endosperm. Embryo curved or nearly involute; cotyledons narrow, radicle folded inward and ascending. (*Sponia* Comm.) TYPE SPECIES: *T. cannabina* Lour.; for discussion of the identity of the type and appropriate synonyms see E. D. Merrill, A Commentary on Loureiro's "Flora Cochinchinensis" 132, 133. 1935. (Name Greek, *trema*, hole, in reference to the sometimes pitted drupe.)

A primarily pantropical genus of some 45 to 55 species with two, *Trema Lamarckiana* (Roem. & Schult.) Blume and *T. micrantha* (L.) Blume (*T.*

floridana Britton) occurring in our area. *Trema Lamarckiana* is found in southern Florida (Dade and Monroe counties), including the Florida Keys, and from Bermuda and the Bahamas to the Greater Antilles and into the Lesser Antilles from Saba to St. Vincent. Readily distinguished from *T. Lamarckiana* by its larger leaves which are not scabrous beneath, *T. micrantha* is widespread in the West Indies and coastal Mexico southward to Central and South America and occurs in our area from the Florida Keys northward to central peninsular Florida. The species of *Trema* are highly variable and often confusing, and the taxonomy of the genus is poorly understood.

Characterized by their spreading crowns and horizontal to slightly drooping branches, species of *Trema* are generally secondary forest trees and usually indicators of secondary succession. In a study of succession in old clearings on Barro Colorado Island (Panama), Kenoyer (1929) found that *T. micrantha*, along with *Cecropia*, *Apeiba*, *Ochroma*, and *Cordia* were the first trees to establish themselves. Other species of *Trema* have been reported as secondary forest indicators or major components in various stages of secondary succession in western Africa and Malaya. The rapidly growing trees are also found along forest margins and in disturbed areas, both natural (e.g., gravel bars) and man-made (roadsides).

Cytologically the genus is poorly known. The chromosome number of *Trema orientalis* Blume has been reported as $2n = 20, 36, 40$ and that of *T. cannabina* as $2n = 40$. Anatomically *Trema* is closely related to *Celtis*. Of the ulmaceous genera tested by Stake (1931) only *Trema* and *Celtis* had cystoliths in the upper epidermis, mainly in association with the hairs. Mucilage cells are common in the mesophyll of all species of *Celtis* and of many of *Trema*, but are lacking in the two *Trema* species in our range. Little is known of the embryology and floral biology of *Trema*.

Flowering and fruiting appear to occur throughout most of the year with the flowers often noticeable in early spring (late March and early April). The minute greenish flowers are soon followed by tiny orange to bright yellow (?) drupes. The wood has been described by Little & Wadsworth (1964) as light brown, soft, weak, lightweight and of limited use. In Puerto Rico the wood is occasionally used for fence posts and fuel and the strong fiber in the bark for cordage. The inner bark is light brown or pinkish and is tasteless to slightly bitter.

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