

THE GENERA OF FAGACEAE IN THE  
SOUTHEASTERN UNITED STATES<sup>1</sup>

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FAGACEAE Dumortier, Anal. Fam. 11, 12. 1829, "Fagineae," nom. cons.  
(BEECH FAMILY)

Deciduous to evergreen trees or shrubs of various habitats; sap watery; branches usually terete, slender, with numerous usually pale lenticels. Leaves with variable vernation, alternate [or verticillate in 3's], simple, occasionally distichous, petiolate, the blade entire, cleft or variously lobed, pinnately veined; stipules narrow, mostly deciduous. Plants monoecious [dioecious in *Nothofagus*]; flowers imperfect [rarely perfect]; inflorescences of pendulous to erect aments, or reduced spikes, heads, or cymules, or reduced to a solitary flower. Staminate flowers bracteate, the perianth with 4-8 imbricate lobes; stamens 4-20(-40); filaments filiform, free; anthers basifixed or dorsifixed, 2-loculate, the locules parallel and contiguous, dehiscence longitudinal, extrorse or introrse [a rudimentary gynoeceum sometimes present]. Carpellate flowers subtended by an involucre (generally of many adnate and imbricate bracts) that partly or wholly incloses the fruit; perianth 3-8-lobed, uniseriate or biseriate, occasionally with rudimentary stamens; gynoeceum 3-6-carpellate, syncarpous, with as many locules and styles as carpels; the style stigmatic along the upper surface, or stigma a terminal pore; ovary inferior and adnate to the lobed perianth, with 1 or 2 pendulous, anatropous, semianatropous or amphitropous, 2[1]-integumented ovules per locule, the ovules  $\pm$  basal with one often aborting. Fruit a nut, usually 1-seeded by abortion, subtended by or inclosed in the muricate, bristly, scaly, or spiny involucre. Seed with a straight embryo, without endosperm, the cotyledons thick, fleshy, generally folded. Embryo sac development of the Polygonum type. Base chromosome numbers 12, 13. TYPE GENUS: *Fagus* L.

<sup>1</sup>Prepared for a generic flora of the southeastern United States, a project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of the National Science Foundation (Grant GB-6459X, principal investigator, Carroll E. Wood, Jr.). This treatment follows the format established in the first paper of the series (Jour. Arnold Arb. 39: 296-346. 1958). The area covered includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with additional information in brackets. References which I have not seen are marked by an asterisk.

I am grateful to Dr. Wood for his thorough review of the manuscript and his numerous suggestions and additions in the course of this study. Dr. E. C. Abbe has kindly read the manuscript and has offered a number of useful and much-appreciated comments. Mrs. Nancy Dunkly has helped greatly in checking the bibliography and typing the manuscript. The illustrations are by Virginia Savage.

A family of eight genera and 400–500 species distributed throughout the temperate regions of the world, in mountainous tropical areas from Central America south to Colombia and the West Indies, and in Old World tropical areas, except tropical and southern Africa. Five genera are found in the continental United States, with *Fagus* L., *Castanea* L., and *Quercus* L. in our range. *Chrysolepis* Hjelmqv. is restricted to the Pacific coast region of the United States, and the chiefly Southeast Asian genus *Lithocarpus* Blume has a single species in California and Oregon.

The Fagaceae and the closely related Betulaceae (including Corylaceae) have generally been considered as constituting the order Fagales (Wettstein, Tippo, Rendle, Hutchinson). Current opinion among phylogenists is that the Fagales are derived from hamamelidaceous stock, which (fide Takhtajan) may serve as a link between the Magnoliales and the Amentiferae. Bessey, however, placed the Fagaceae with the Betulaceae and Juglandaceae and considered all three to be derived from a sapindaceous line. The Fagaceae have also been considered to have been derived from epigynous rosaceous stock (Berridge, 1914), but this view has not been accepted by later taxonomists. Hjelmqvist (1948), followed by Takhtajan (1969), preferred to place the Fagaceae and Betulaceae in separate but closely related orders. Cronquist (1968), in addition to including the Betulaceae and Fagaceae in the order Fagales, added the Balanopaceae. The affinities of this last family appear to be with the Fagales, but it should be studied further to determine its relationships more exactly.

Using evidence primarily from the carpellate inflorescences and fruit, Forman (1966) has postulated the lines of evolution of the cupules in the Fagaceae and has established intergeneric and specific relationships based on his findings. The basic structure of the carpellate inflorescence is considered to be a three-flowered dichasium (FIGURE 1). In the least specialized condition, each of the flowers and subsequent fruits is surrounded by several lobed involucre. In *Chrysolepis* the three trigonous fruits are enclosed by five free outer valves and two inner ones. From this condition it is supposed that the ancestral type had fruits that were trigonous (versus irregular or rounded) in section and that each of the three fruits of the basic dichasium was surrounded by three free valves, a condition that has not been found in any of the extant Fagaceae. Progressive specialization resulted in reduction in the number of involucre lobes and, later, fusion of the lobes to form the rounded cupular involucre found in *Quercus*, the *C. fissa* group of *Castanopsis*, and some species of *Lithocarpus*. Specialization was also accompanied by a reduction (by abortion) of the basic three-flowered dichasium to a single flower. The change from trigonous to  $\pm$  irregular and/or to rounded fruits appears to have occurred concurrently with the reduction and fusion of the involucre.

These trends are illustrated diagrammatically in FIGURE 1 and are further noted under each of the three generally recognized subfamilies (cf. Oersted, 1871; Schwarz, 1936; Forman, 1964), which can be separated as follows:

- Inflorescence of single- or many-flowered, axillary dichasial clusters. . . . . Fagoideae.  
 Inflorescence of aments of dichasial clusters or of solitary flowers.  
 Stigmas terminal, minute, punctiform; styles cylindrical; staminate flowers often with a rudimentary gynoecium; stamens usually 12; anthers minute, dorsifixed or versatile. . . . . Castaneoideae.  
 Stigmas on the inner surface of the generally flattened styles; staminate flowers without a rudimentary gynoecium; stamens usually 6; anthers large and  $\pm$  basifixed. . . . . Quercoideae.

The subfamily Fagoideae includes only *Fagus* and *Nothofagus*. In *Fagus* the staminate flowers are in many-flowered heads, the carpellate dichasia lack the central flower of the basic three-flowered dichasium, and the styles are elongate and tapering, while in *Nothofagus* Blume the staminate flowers typically are in sessile to short-pedunculate one- to three-flowered dichasia, the central flower is always present in the carpellate dichasia, and the styles are short. That fruiting structures apparently have not evolved as rapidly as the floral parts, may be seen in the persistence of both free involucre valves and trigonous fruits. These tendencies are demonstrated in *Nothofagus*, some species of which exhibit the less specialized features, while others have more advanced characters, and many clearly show transitional features (cf. FIGURE 1). *Fagus* has 3(4)-colporate, suboblate-subprolate pollen grains, and *Nothofagus* has (4-)6(-7)-aperturate, obovate pollen grains.

Of the four genera in the Castaneoideae, only *Castanea* Mill. occurs in our range. The Old World *Castanopsis* Spach (approximately 110 species) is separated from *Castanea* mainly on floral and fruiting characters (see *Castanea*). Recently segregated from *Castanopsis*, *Chrysolepis* Hjelmqv. is distinguished by free involucre lobes and fruits (three per involucre) separated from each other by inner valves. *Lithocarpus* Blume (*Pasania* Oersted), including ca. 100 species distributed mainly in Malesia and the Pacific Islands and *L. densiflorus* (Hook. & Arn.) Rehd. in southwestern Oregon and in California, is distinguished by having each carpellate flower of a dichasium surrounded by its own involucre, which never shows vertical divisions or lobation. Langdon (1949) suggested several evolutionary trends in the floral structures in this subfamily, including a noticeable reduction in the inflorescence, apparently from a primary many-flowered dichasial type, and a reduction in floral members. There are also various transitional stages between hypogyny and epigyny that should be studied anatomically.

Forman (1966) concluded that reduction of the basic three-flowered carpellate dichasium to a single flower took place by suppression of the lateral flowers and that reduction by fusion of the four-valved cupule, first to a two-valved one and then to a single cup with no signs of valves, has occurred. The reduction of the individual flower-cupules within a dichasium is seen in *Lithocarpus* as eventually leading to a single flower and, consequently, a single fruit that closely resembles that of *Quercus*. This convergent evolution has led many workers to think that *Lithocarpus* and

FAGACEAE

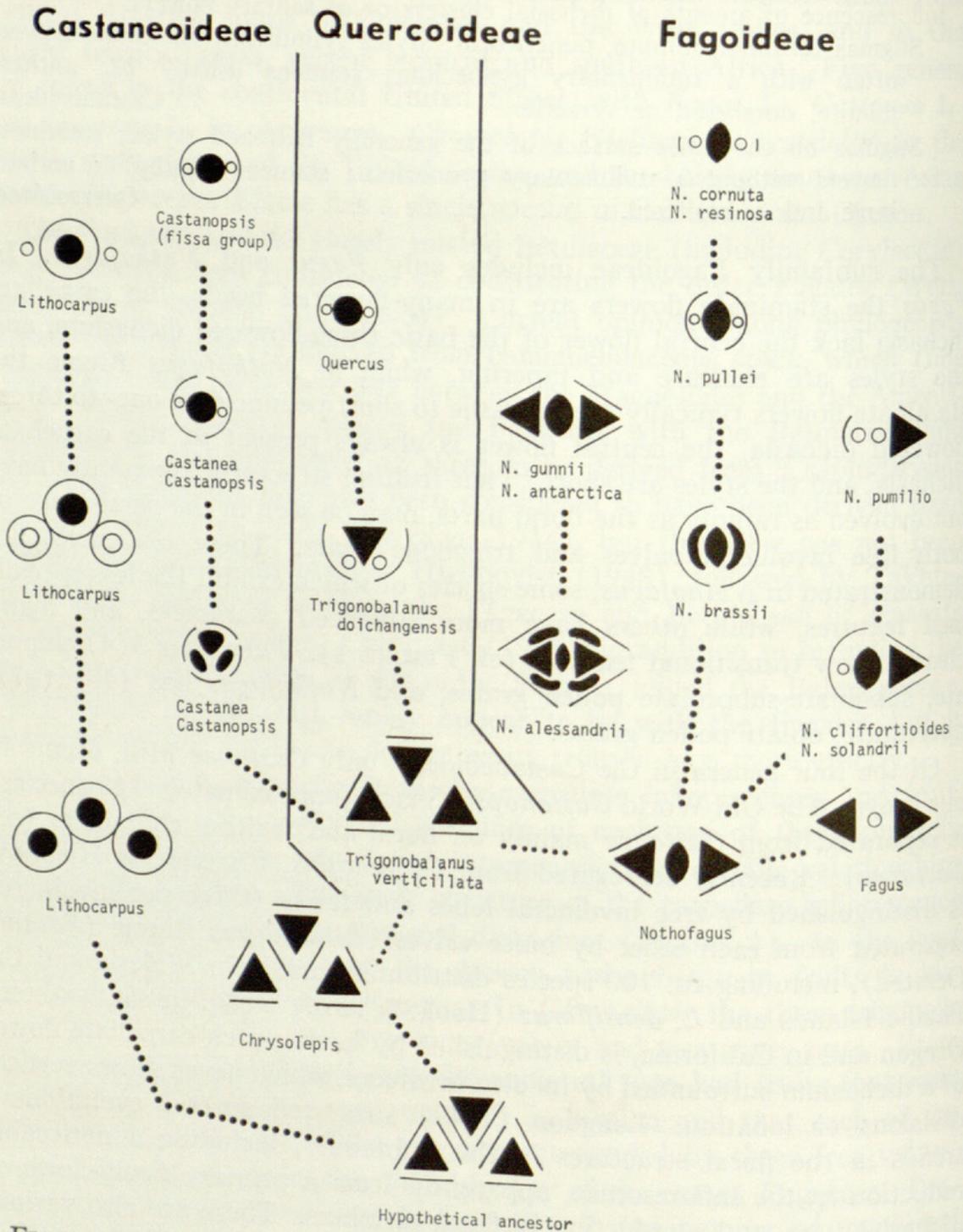


FIGURE 1. Diagrammatic scheme showing possible evolutionary relationships within the Fagaceae, based upon the involucre, flower number, and fruit shape. The basic carpellate inflorescence is considered to be a three-flowered dichasium. Shapes used indicate approximate shape of fruits in cross section, small un-darkened circles represent abortive flowers, and lines inclosing fruits represent the Fagaceae. Based mainly on Forman (1966) and van Steenis (1953).

*Quercus* are congeneric, but these workers have failed to consider the total biology of the two genera.

The reduction in the number of valves by lateral fusion is best seen

in *Castanea* and *Castanopsis*. A four-valved cupule, usually with three fruits is considered to have undergone fusion of the lateral valves to form a two-valved cupule, and, along with this, the number of flowers has been reduced to one per cupule. Further reduction can be seen in the "fissa-group" of *Castanopsis*, in which the two-valved cupule has given way to a completely fused, one-flowered cupule (cf. FIGURE 1).

The subfamily Quercoideae includes only *Quercus* (300–350 species) and the recently described *Trigonobalanus* Forman (2 species: *T. doi-changensis* (A. Camus) Forman, of northern Thailand, and *T. verticillata* Forman, of Borneo and Celebes).

Evolutionary tendencies in the Quercoideae are toward a reduction of the carpellate clusters of flowers to either a pair of flowers or a solitary one; toward a change in shape and reduction of the number of fruits per cupule; and toward a reduction by fusion of the cupular valves to form a single valveless cupule. Forman (1964) considered *Trigonobalanus* to be less advanced than *Quercus* and perhaps close to the ancestral stock of the Fagaceae, an idea based primarily on the carpellate flowers, i.e., the flowers borne in clusters of 3(–7) as compared with the presumably derived condition of the paired or solitary carpellate flowers in *Quercus*. In addition, the 1–3(–7) trigonous fruits of *Trigonobalanus* are borne in a 3–5-valved cupule. In *Quercus*, a reduction of the flowers from 3 to 1 apparently has occurred, along with a change in fruit shape from triangular to round. Reduction of the cupule valves and their probable fusion to form the single valveless cupule of *Quercus* are further specializations.

Fagaceous remains (largely leaves and leaf fragments) have been recognized in the Upper Cretaceous, and these indicate that the family was once far more widespread than the extant members are.

The Fagaceae are of considerable economic importance. Members of this family, because of their abundance and very suitable wood, are one of the most important sources of hardwood timber. The wood, valued for its tough, hard, strong, yet attractive appearance, is used in various phases of construction, furniture making, and in quality tools. *Quercus Suber* L., cork oak, native to the Mediterranean region is the source of commercial cork. Edible nuts and, to a limited degree, lumber are obtained from *Castanea*. Species of *Fagus* are also used as lumber sources, and the beech-nuts are highly sought after by various animals, both domestic and wild.

#### REFERENCES:

- ARMSTRONG, J. M., & A. N. WYLIE. A new basic chromosome number in the family Fagaceae. *Nature* 205: 1340, 1341. 1965. [ $n = 13$  in *Nothofagus Menziesii*, *N. solandrii* var. *cliffortioides*, & *N. fusca*.]
- BAILEY, I. W. Notes on the wood structure of the Betulaceae and Fagaceae. *Forestry Quart.* 8: 178–185. 1910.
- BAILLON, H. Castanéacées. *Hist. Pl.* 6: 217–259. 1877. (English ed. 6: 220–262. 1880.)
- BENSON, M. Contributions to the embryology of the Amentiferae. — Part I. *Trans. Linn. Soc. Bot.* 3: 409–424. pls. 67–72. 1894.

- BENTHAM, G., & J. D. HOOKER. Cupuliferae. Gen. Pl. 3: 402-410. 1883. [Includes tribes Betuleae, Coryleae, & Quercineae.]
- BERRIDGE, E. M. The structure of the flower of the Fagaceae, and its bearing on the affinities of the group. Ann. Bot. 28: 509-526. 1914.
- BERRY, E. W. Tree ancestors. vi + 270 pp. Baltimore. 1923. [*Fagus*, 119-128; *Quercus*, 129-140; *Castanea*, 140-145.]
- BRETT, D. W. The inflorescence of *Fagus* and *Castanea* and the evolution of the cupules of the Fagaceae. New Phytol. 63: 96-117. 1964.
- ČELAKOVSKY, L. Über die Cupula von *Fagus* und *Castanea*. Jahrb. Wiss. Bot. 21: 128-162. pl. 5. 1890.
- COUPER, R. A. Southern Hemisphere Mesozoic and Tertiary Podocarpaceae and Fagaceae and their paleogeographic significance. Proc. Roy. Soc. London B. 152: 491-500. 1960. [Includes maps.]
- DAVIS, D. E., & N. D. DAVIS. Guide and key to Alabama trees. viii + 136 pp. Wm. C. Brown Co., Dubuque, Iowa. 1965. [*Castanea* 42, 53; *Fagus*, 51; *Quercus*, 88-99.]
- EICHLER, A. W. Cupuliferae. Blüthendiagramme 2: 20-32. 1878.
- ERDTMAN, G. On the pollen morphology of *Trigonobalanus* (Fagaceae). Bot. Not. 120: 324-333. 1967.
- FORMAN, L. L. *Trigonobalanus*, a new genus of Fagaceae, with notes on the classification of the family. Kew Bull. 17: 381-396. 1964.
- . On the evolution of cupules in the Fagaceae. *Ibid.* 18: 385-419. 1966a.
- . Generic delimitation in the Castaneoideae. *Ibid.* 421-426. 1966b.
- & D. F. CUTLER. Additional notes on *Trigonobalanus* Forman (Fagaceae). *Ibid.* 21: 331-334. 1967. [*Trigonobalanus* in Malaya & Sarawak; further notes on the anatomy of the vegetative organs.]
- FOWELLS, H. A. Silvics of forest trees of the United States. U. S. Dep. Agr. Forest Serv. Agr. Handb. 271. 1965. [*Fagus*, 171-180; *Quercus*, 557-640; distribution maps by E. L. LITTLE, JR.]
- GROOM, P. The medullary rays of Fagaceae. Ann. Bot. 26: 1124, 1125. 1912.
- HJELMQVIST, H. Studies on the floral morphology and phylogeny of the Amentiferae. Bot. Not. Suppl. 2(1): 1-171. 1948. [Fagaceae, 77-121; *Chrysolepis*, 117.]
- . Some notes on the endosperm and embryo development in Fagales and related orders. Bot. Not. 110: 173-195. 1957.
- . Notes on some names and combinations within the Amentiferae. *Ibid.* 113: 373-380. 1960. [*Chrysolepis*, 377.]
- HUTCHINSON, J. The genera of flowering plants. vol. 2. xi + 659 pp. Clarendon Press, Oxford. 1967. [Fagaceae, 126-132.]
- JARETZKY, R. Zur Zytologie der Fagales. Planta 10: 120-137. 1930.
- JAYNES, R. A., ed. Handbook of North American nut trees. vii + 421 pp. Northern Nut Growers Association, Knoxville, Tenn. 1969. [*Quercus*, 336-342; *Fagus*, 342, 343; *Castanea*, 264-286.]
- KUPRIANOVA, L. A. The palynology of the Amentiferae. (In Russian.) 214 pp. 48 pls. Bot. Inst. Komarov. Akad. Nauk SSSR. Moskava-Leningrad. 1965.
- KURZ, H., & R. K. GODFREY. Trees of northern Florida. xxxiv + 311 pp. Gainesville, Florida. 1962. [*Castanea*, 57-59; *Fagus*, 60-62; *Quercus*, 62-104.]
- LANGDON, L. M. Ontogenetic and anatomical studies of the flower and fruit of the Fagaceae and Juglandaceae. Bot. Gaz. 101: 301-327. 1939.
- . The comparative morphology of the Fagaceae. I. The genus *Nothofagus*. *Ibid.* 108: 350-371. 1947.

- LEBEDENKO, L. A. The ontogeny of root and stem wood in certain representative of Fagales. (In Russian.) Dokl. Akad. Nauk SSSR 127: 213-216. 1959.\*
- LITTLE, E. L., JR. Check list of native and naturalized trees of the United States (including Alaska). U. S. Dep. Agr. Agr. Handb. 41. 472 pp. 1953. [*Castanea*, 92-94; *Fagus*, 183, 184; *Quercus*, 311-361.]
- LUBBOCK, J. A contribution to our knowledge of seedlings. vol. 2. 646 pp. New York. 1892. [Cupuliferae, 526-541; includes genera from Fagaceae & Betulaceae.]
- MARTIN, A. C. The comparative internal morphology of seeds. Am. Midl. Nat. 36: 513-660. 1946. [Fagaceae, 638, 646.]
- POOLE, A. L. The development of *Nothofagus* seed (including a preliminary account of the embryogeny, etc.). Trans. Roy. Soc. New Zealand 80: 207-212. 1952.
- PRANTL, K. Beiträge zur Kenntnis der Cupuliferen. Bot. Jahrb. 8: 321-334. 1887.
- . Fagaceae. Nat. Pflanzenfam. III. 1: 47-58. 1888.
- REHDER, A. Bibliography of cultivated trees and shrubs. xl + 825 pp. Jamaica Plain, Mass. 1949. [Fagaceae, 112-135.]
- SARGENT, C. S. Cupuliferae. Silva N. Am. 8: 1-190; 9: 1-30. 1895.
- . Manual of the trees of North America (exclusive of Mexico). ed. 2. xxvi + 910 pp. Boston & New York. 1922. [Fagaceae, 227-308; includes map.]
- SCHWARZ, O. Entwurf zu einem natürlichen System der Cupuliferen und die Gattung *Quercus* L. Notizbl. Bot. Gart. Berlin 13: 1-22. 1936.
- SEARS, P. B. Postglacial migration of five forest genera. Am. Jour. Bot. 29: 684-691. 1942. [Includes *Quercus* & *Fagus*.]
- SHIMAJI, K. Anatomical studies on the wood of the Japanese *Pasania*, *Castanea* and *Castanopsis*. (With a key to the 22 Japanese representative species of the Fagaceae.) Bull. Tokyo Univ. Forests 55: 81-99. 1959.\*
- STEENIS, C. G. G. J. VAN. Results of the Archbold Expeditions: Papuan *Nothofagus*. Jour. Arnold Arb. 34: 301-374. 1953.
- . Additional note on *Nothofagus*. *Ibid.* 35: 266-267. 1954.
- TAYLOR, L. A. Plants used as curatives by certain southeastern tribes. Part I. Plants used medicinally. xi + 88 pp. Botanical Museum, Harvard University. 1940. [*Castanea pumila*, 16; *Quercus borealis* var. *maxima* = *Q. rubra*, 16, 17; *Q. marilandica*, 17; *Q. rubra* = *Q. falcata*, 17, 18; *Q. stellata*, 18.]
- TIPPO, O. Comparative anatomy of the Moraceae and their presumed allies. Bot. Gaz. 100: 1-99. 1938. [Fagaceae, 38-42.]
- VINES, R. A. Trees, shrubs and woody vines of the southwest. xii + 1104 pp. Austin, Texas. 1960. [Fagaceae, 147-202.]
- WALKER, D., & G. WITTMANN. Notes on the pollen morphology of *Nothofagus* Bl. subsection *Bipartitae* Steen. Pollen Spores 7: 457-464. 1965.
- WEST, E., & L. ARNOLD. The native trees of Florida. xx + 212 pp. Gainesville, Florida. 1946. [Fagaceae, 33-53.]
- WODEHOUSE, R. P. Hayfever plants. xx + 245 pp. Chronica Botanica, Waltham, Mass. 1945. [*Fagus*, 75, 76; *Quercus*, 76-81.]
- U. S. DEP. AGR. FOREST SERV. Woody-plant seed manual. U. S. Dep. Agr. Forest Serv. Misc. Publ. 654. 1948. [*Castanea*, 112; *Fagus*, 174, 175; *Quercus*, 297-304.]

## KEY TO THE GENERA OF FAGACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *Trees or shrubs with alternate, simple leaves with small usually caducous stipules; flowers unisexual; staminate flowers in erect or pendulous aments or heads, the perianth 4-8-lobed; carpellate flowers 1-4 in an involucre, the perianth 4-8-lobed, the ovary inferior, 3-6-loculate with 1-2 ovules per locule; involucre becoming indurated in fruit, lobed or entire; fruit usually a nut, 1-seeded by abortion; seed without endosperm.*

- A. Staminate flowers in dense many-flowered, pendulous heads; the fruit triangular; germination epigeous; bark smooth; buds lanceolate, sharp-pointed. . . . . 1. *Fagus*.
- A. Staminate flowers in erect to pendulous aments; the fruit subglobose, turbinate or variously compressed, never triangular; germination hypogeous; bark scaly or furrowed, usually rough; buds usually rounded, ovoid or ellipsoid.
  - B. Staminate flowers in erect aments; carpellate flowers borne on androgynous aments, the ovary 6(-9)-loculate, styles usually 6, stigmata terminal, minute, punctiform; involucre with fasciculate spines, inclosing usually 1-3 fruits, splitting into 2-4 valves at maturity. . . . . 2. *Castanea*.
  - B. Staminate flowers in  $\pm$  pendulous aments; carpellate flowers borne separately, the ovary 3(4-5)-loculate, the styles generally 3, stigmatic on the inner surface; involucre cupuliform with numerous usually imbricate scales, partially inclosing the single fruit. . . . . 3. *Quercus*.

## Subfamily FAGOIDEAE [Oersted]

- 1. *Fagus* Linnaeus, Sp. Pl. 2: 997. 1753; Gen. Pl. ed. 5. 432. 1754.

Deciduous trees of low or moderate elevations and generally moist habitats in temperate regions of the Northern Hemisphere; bark smooth, usually pale; wood hard, close-grained; branchlets terete with acute, often lustrous, chestnut-brown buds, the inner bud scales accrescent, marking the base of the branchlets with persistent ring-like scars. Leaves convex and plicate in vernation, deciduous [or persistent], usually dentate, coriaceous to subcoriaceous, petiolate; leaf-scars small, elevated, subelliptic, with marginal rows of minute vascular bundle scars; stipules linear-lanceolate, infolding the leaf in bud, fugacious or rarely persistent. Flowers vernal (shortly after the leaves unfold). Staminate flowers short-pedicellate, borne in globose, many-flowered heads (dichasia, fide Brett, 1964) on long drooping peduncles with (0-)2(3) bracteoles, the inflorescences arising from base of shoots of the year or from axils of their lowest leaves; perianth 4-8-lobed, the lobes imbricate in aestivation, ovate, rounded, with 8-40 stamens inserted on the base of the perianth; filaments slender, exerted; anthers basifixed, introrse, obtuse or sagittate at base; pollen 3(4)-colporate, suboblate to subprolate. Carpellate flowers in 2-4-flowered pedunculate clusters in axils of upper leaves of the year, sessile, surrounded by numerous awn-shaped hairy bracts, the outer bracts often bright red, longer than flowers, the inner shorter and united below to form a 4-lobed involucre; perianth urceolate, villous, with 4 or 5 linear-lanceolate acute lobes, the tube triangulate and adnate to the 3-locular ovary; styles 3,

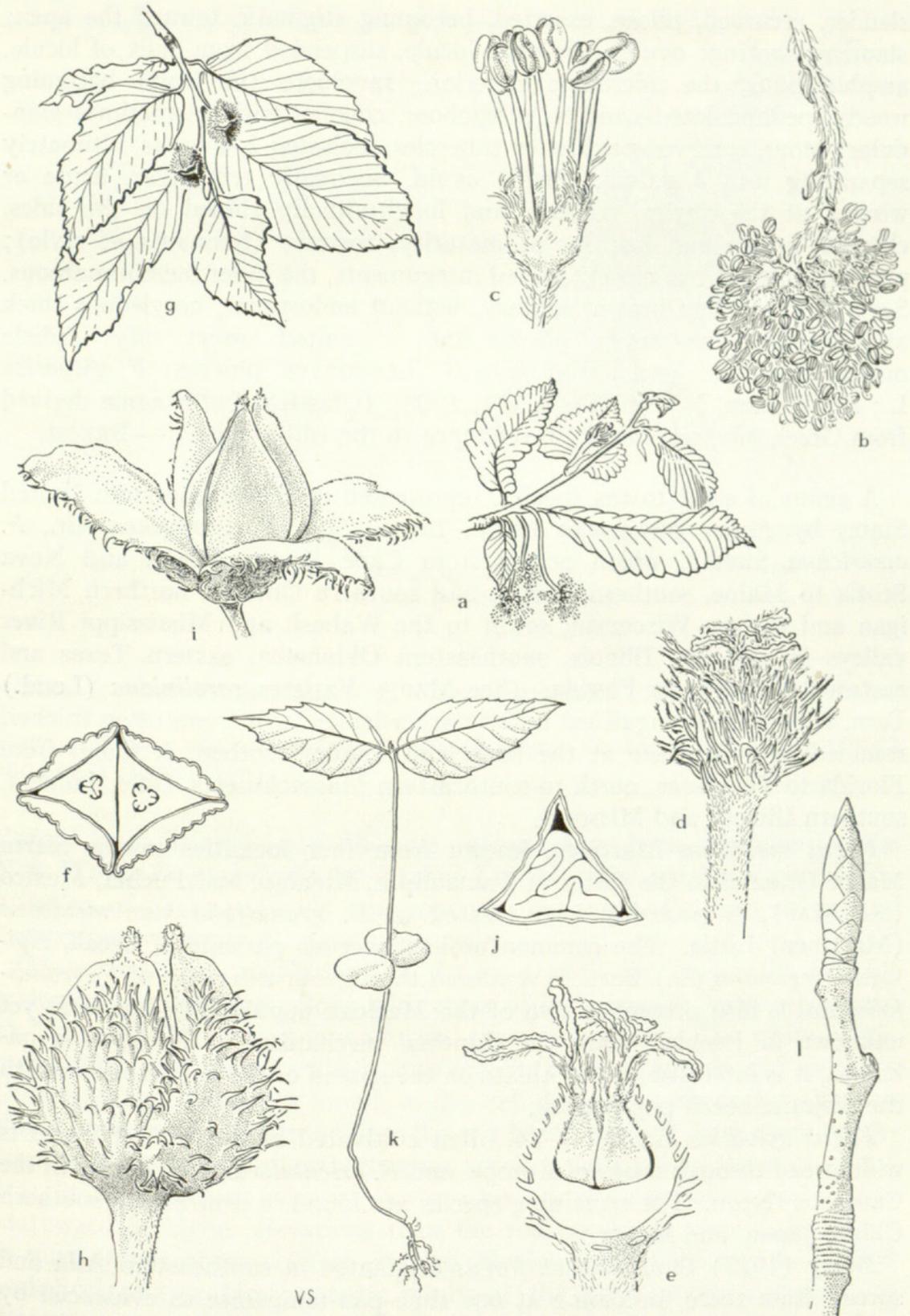


FIGURE 2. *Fagus*. a-l, *F. grandifolia*: a, flowering branchlet,  $\times \frac{1}{2}$ ; b, staminate inflorescence,  $\times 2$ ; c, staminate flower,  $\times 6$ ; d, carpellate inflorescence,  $\times 3$ ; e, carpellate inflorescence with part of involucre removed to show flowers,  $\times 4$ ; f, carpellate inflorescence in semidiagrammatic cross section to show ovules,  $\times 6$ ; g, fruiting branchlet,  $\times \frac{1}{3}$ ; h, involucre and two fruits,  $\times 2$ ; i, involucre bracts unfolding to show mature fruits,  $1\frac{1}{2}$ ; j, fruit in cross section to show cotyledons,  $\times 2$ ; k, seedling,  $\times \frac{1}{2}$ ; l, winter twig showing bud,  $\times 1\frac{1}{2}$ .

slender, recurved, pilose, exserted, becoming stigmatic toward the apex; stamens wanting; ovules 2 in each locule, suspended from apex of locule, amphitropous, the micropyle superior. Involucre (in fruit) becoming woody, pedunculate, ovoid to subglobose, covered with [sometimes glandular] stout, recurved prickles or tubercles, inclosing 2–4 fruits, ultimately separating into 4 valves. Fruits ovoid, unequally triangular, acute or winged at the angles, concave and longitudinally ridged on the sides, chestnut-brown and lustrous at maturity, rostrate (remnants of style); pericarp thin, of two closely united integuments, the inner membranaceous. Seed dark chestnut-brown, solitary, without endosperm; cotyledons thick and fleshy, plano-convex, plicate and  $\pm$  united, sweet, oily; radicle minute, superior; germination epigeal. LECTOTYPE SPECIES: *F. sylvatica* L.; see Britton, N. Am. Trees 271. 1908. (Classical Latin name derived from Greek *phagein*, to eat, in reference to the edible nuts.) — BEECH.

A genus of eight to ten species, represented in the southeastern United States by *Fagus grandifolia* Ehrh.,  $2n = 24$ ,<sup>2</sup> (*F. ferruginea* Ait., *F. americana* Sweet), which occurs from Cape Breton Island and Nova Scotia to Maine, southern Quebec and southern Ontario, northern Michigan and eastern Wisconsin, south to the Wabash and Mississippi River valleys in southern Illinois, southeastern Oklahoma, eastern Texas and eastward to northern Florida. (See MAP.) Varietas *caroliniana* (Loud.) Fern. & Rehd., distinguished by its darker leaves, which are often thicker, rounded or subcordate at the base, and smaller toothed, is found from Florida to Tennessee, north to southeastern Massachusetts, Ohio, Indiana, southern Illinois, and Missouri.

*Fagus mexicana* Martínez, known from four localities in the Sierra Madre Oriental in the states of Tamaulipas, Hidalgo, and Puebla, Mexico (see MAP), is probably best treated as *F. grandifolia* var. *mexicana* (Martínez) Little. The common orobanchaceous parasite of beech, *Epifagus virginiana* (L.) Bart., is scattered throughout the range of *F. grandifolia* and is also present in two of the Mexican populations, but is as yet unknown in Puebla. Since the dispersal mechanism of *Epifagus* is unknown, it is interesting to speculate on the spread of the parasite to or with the disjunct beech populations.

*Fagus sylvatica* L.,  $2n = 24$ , often cultivated in the United States is widespread through much of Europe, and *F. orientalis* Lipsky occurs in the Caucasus region. The remaining species are found in central and southern China, Japan, and Korea.

Berry (1923) thought that *Fagus* originated in southeastern Asia and spread from there, becoming at one time pan-temperate as evidenced by the abundant fossilized material known from Europe, Russia, Japan, and the western United States. From a study of pollen from peat bogs, Sears found postglacial evidence that *Fagus* occurred farther west in the United States than the present limits of the genus. Numerous fossilized leaves in

<sup>2</sup> Aufderheide (1931) reported the haploid number of *F. grandifolia* as 6, but in view of later counts of  $n = 12$ , the  $n = 6$  count must be considered questionable.



MAP 1. Present distribution of *Fagus grandifolia*. Distribution in United States mostly generalized; disjunct populations in Tamaulipas, Hidalgo, and Puebla, Mexico, are var. *mexicana*. Based mainly on Little in Fowells (1965) and Fox & Sharp (1954).

Europe from Miocene and Pliocene deposits have been attributed to the New World *F. grandifolia* by Tralau (1962). The present disjunct distribution of *Fagus* probably represents the remnants of a once widespread pan-temperate genus of numerous species.

Three series of populations of *Fagus grandifolia*, each with distinct ecological requirements, along with areas of introgression, were recognized by Camp (1951) but not given formal taxonomic status. The white beech, best seen in moist river valleys, is found in the southeastern and southern United States. Typically found on the well-drained southern Appalachian slopes on usually stabilized talus, the red beech extends from there northward to Canada. The northern gray beech is adapted to the cool, moist area at the southern edge of the northern coniferous forest and occurs southward at higher elevations than the red beech. It commonly occurs in pure stands above 650 m. in New England and Canada. A detailed ecological and/or biosystematic study of the three series is needed to determine not only the exact relationships of the various populations, but the status of var. *caroliniana* and var. *mexicana*.

*Fagus grandifolia* and *Acer saccharum* are the climax species in much of the deciduous forest formation from west of the Allegheny mountains to New York, Ohio, and Wisconsin. The shade-tolerant beech is often found in nearly pure stands in many areas within its range, e.g., higher

altitudes in the southern Appalachians (Russel, 1953). *Fagus* in our range is generally more abundant on the moister northern slopes and on soil with pH 4.1 to 6.0.

The anemophilous flowers appear in late April or early May, shortly after the leaves begin unfolding. Cross pollination is generally necessary for seed production, plants of most species of *Fagus* being moderately to largely self-sterile. Individual trees seem to show varying degrees of self-fertility in successive years, but this needs to be carefully studied and documented. Neilson & Schaffalitzky (1954) reported proterandry in *F. sylvatica* and *F. grandifolia* varying in degree with the weather, warm dry spring conditions resulting in shorter periods of proterandry. They found the stigmas of *F. sylvatica* to be receptive to pollen for approximately 10–14 days. Artificial hybrids between *F. sylvatica* (♀) and *F. grandifolia* (♂) were produced, the progeny showing intermediate leaf characters and some tendency toward hybrid vigor.

The fruits require only one growing season to mature and are shed when the first heavy frost causes the involucre valves to separate. Germination takes place in early spring to early summer of the following year. Seed production is somewhat sporadic, with good crops every two to three years. Dispersal is mainly by rodents or large birds. Although seed germination and seedling development are common in beech stands, vegetative reproduction by root suckers is often encountered. In open areas, beech trees develop a thick, short trunk with large, low spreading limbs and a broad, rounded crown. The thin, pale bark is very susceptible to fire injury and overexposure to sunlight (sunscalding).

A number of forms of *Fagus* are cultivated. Of these the copper beech, *F. sylvatica* f. *atropunicea* (Weston) Domin, is probably most frequently grown as an ornamental in the United States. Several of the Asian species are also cultivated to a limited extent in the Northeast. In New England and Canada, *Fagus grandifolia* is susceptible to attack by the beech scale insect, *Cryptococcus fagi*, which is soon followed by the fungus *Nectria coccinea* var. *faginata*. Several species of the fungus *Fomes* occur on the beech in our range.

The wood is hard, strong, and very close grained but not very durable. It is used in the manufacture of chairs and tool handles and is perhaps the principal wood used for clothespins (Strausbaugh & Core, 1953).

#### REFERENCES:

- Under family references see also BERRY, 119–128; FORMAN, 1966a; FOWELLS, 171–180; HJELMQVIST, 82–86; KURZ & GODFREY, 60–62; LANGDON, 303–316; LITTLE, 183, 184; SEARS, 689; STEENIS; VINES, 198, 199; WEST & ARNOLD, 34.
- AUFDERHEIDE, H. Chromosome numbers in *Fagus grandifolia* and *Quercus virginiana*. Butler Univ. Bot. Stud. 2: 45–52. 1931.
- BANDULSKA, H. On the cuticles of some recent and fossil Fagaceae. Jour. Linn. Soc. Bot. 46: 427–441. 1924.
- BENNINGHOFF, W. S., & A. I. GEBBEN. Phytosociological studies of some beech-

- maple stands in Michigan's Lower Peninsula. Pap. Mich. Acad. Sci. Arts Lett. I. **45**: 83-91. 1960.
- BERRY, E. W. Notes on the ancestry of the beech. Pl. World **19**: 68-77. 1916. [Includes maps.]
- BLINKENBERG, C., H. BRIX, M. SCHAFFALITZKY DE MUCKADELL, & H. VEDEL. Controlled pollinations in *Fagus*. Silvae Genet. **7**: 116-122. 1958. [Includes map.]
- CAMP, W. H. A biogeographic and paragenetic analysis of the American beech (*Fagus*). Am. Philos. Soc. Yearb. **1950**: 166-169. 1951.
- CLOWES, F. A. L. The structure of mycorrhizal roots of *Fagus sylvatica*. New Phytol. **50**: 1-16. figs. 1-7. 1951.
- DOMIN, K. On the variability of the beech. Acad. Tchèque Sci. Bull. Int. **33**: 65-75. pls. 1-2. 1932.
- DU RIETZ, G. E. Problems of bipolar plant distribution. Acta Phytogeogr. Suec. **13**: 215-282. 1940. [Includes *Fagus* & *Nothofagus*.]
- ETTINGSHAUSEN, C. F. VON. Über Tertiäre *Fagus*-Arten der südlichen Hemisphäre. Sitz-ber. Akad. Wiss. Math.-Naturw. Wien **100**(Abt. 1): 114-137. pls. 1, 2. 1891.
- FOX, W. B., & A. J. SHARP. La distribución de *Fagus* en México. Soc. Bot. Méx. Bol. **17**: 31-33. 1954. [Includes map.]
- FRIESNER, R. C. A preliminary study of growth in the beech, *Fagus grandifolia*, by the dendrographic method. Butler Univ. Bot. Stud. **5**: 85-94. 1941.
- FRITTS, H. C. An analysis of radial growth of beech in a central Ohio forest during 1954-55. Ecology **39**: 705-720. 1958. [*F. grandifolia*.]
- & N. Holowaychuk. Some soil factors affecting the distribution of beech in a central Ohio forest. Ohio Jour. Sci. **59**: 167-186. 1959.
- GARRISON, H. J. Floral morphology and ontogeny of *Fagus grandifolia* Ehrh. Ph.D. Thesis, Pennsylvania State University. 1956. [Unpublished.] [See also Diss. Abstr. **17**: 2777, 2778. 1957.]
- GRAY, J. Temperate pollen genera in the Eocene (Claiborne) flora, Alabama. Science **132**: 808-810. 1960. [*Fagus*, 809.]
- HARLEY, J. L., & C. C. MCCREADY. A note on the effect of sodium azide upon the respiration of beech (*Fagus sylvatica*) mycorrhizas. New Phytol. **52**: 83-85. 1953.
- , ———, & J. K. BRIERLEY. The uptake of phosphate by excised mycorrhizal roots of the beech. [I.] New Phytol. **49**: 388-397. 1950; II. Distribution of phosphorus between host and fungus. *Ibid.* **51**: 56-64. pls. 1, 2. 1952; III. The effect of the fungal sheath on the availability of phosphate to the core. *Ibid.* 342-348; IV. The effect of oxygen concentration upon host and fungus. *Ibid.* **52**: 124-132. 1953; V. The examination of possible sources of misinterpretation of the quantities of phosphorus passing into the host. *Ibid.* **53**: 92-98. 1954; VI. Active transport of phosphorus from the fungal sheath into the host tissue. *Ibid.* 240-252; VII. Active transport of P<sup>32</sup> from fungus to host during uptake of phosphate from solution. *Ibid.* **54**: 296-301. 1955; VIII. Translocation of phosphorus in mycorrhizal roots. *Ibid.* **57**: 353-362. 1958. [BRIERLEY coauthor of IV-VIII; MCCREADY of I-V, VIII.]
- , ———, & J. A. GEDDES. The salt respiration of excised beech mycorrhizas. I. The development of respiratory response to salts. New Phytol. **53**: 427-444. 1954.
- , ———, J. K. BRIERLEY, & D. H. JENNINGS. The salt respiration of

- excised beech mycorrhizas. II. The relationship between oxygen consumption and phosphate absorption. *New Phytol.* **55**: 1-28. 1956.
- JACKSON, B. D. A note on nomenclature. *Jour. Bot. London* **34**: 352, 353. 1910. [Earliest publication of *F. americana*.]
- JOHNSSON, H. Chromosome numbers of twin plants of *Quercus Robur* and *Fagus silvatica*. *Hereditas* **32**: 469-472. 1946.
- LANGDON, L. M. The comparative morphology of the Fagaceae. 1. The genus *Nothofagus*. *Bot. Gaz.* **108**: 350-371. 1947.
- LITTLE, E. L., JR. Mexican beech, a variety of *Fagus grandifolia*. *Castanea* **30**: 167-170. 1965. [*F. grandifolia* var. *mexicana*.]
- LOGAN, L. A. An ecological study of the American beech along the southwestern border of its distribution. Ph.D. thesis, University of Missouri, Columbia, Missouri. [Unpublished.] [See also *Diss. Abstr.* **20**(9): 3487. 1960.]
- MARTÍNEZ, M. Una nueva especie forestal (*Fagus mexicana* sp. nova). *Anal. Inst. Biol. Méx.* **11**: 85-89. 1940.
- MIRANDA, F., & A. J. SHARP. Characteristics of the vegetation in certain temperate regions of eastern Mexico. *Ecology* **31**: 313-333. 1950. [*F. mexicana*, 325-327.]
- MYCZKOWSKI, S. The influence of ecological factors upon the formation of the habit of beech, *Fagus silvatica* L. (In Polish; English summary.) *Ann. Sect. Dendrol. Soc. Bot. Pologne* **10**: 233-251. 1955.\*
- NIELSEN, P. Chr., & M. SCHAFFALITZKY DE MUCKADELL. Flower observations and controlled pollinations in *Fagus*. *Zeitschr. Forstgen. Forstpflanzenzücht.* **3**: 6-17. 1954.
- POTZGER, J. E., & A. N. LIMING. Secondary succession in stands of red maple-sweet gum-beech forests in Ripley County, Indiana. *Butler Univ. Bot. Stud.* **11**: 50-59. 1953. [*F. grandifolia*.]
- RICE, H. P. A rough-barked American beech. *Jour. Forestry* **46**: 48. 1948.
- ROBINSON, R., & H. SMITH. Anthocyanins of the leaf of the copper beech (*Fagus sylvatica*) and the fruit of the cultivated strawberry (*Fragaria virginiana*). *Nature* **175**: 634. 1955.
- RUSSELL, N. H. The beech gaps of the Great Smoky Mountains. *Ecology* **34**: 366-374. 1953.
- SCHAFFALITZKY DE MUCKADELL, M. Experiments on developments in *Fagus silvatica* by means of herbaceous grafting. *Physiol. Pl.* **9**: 396-400. 1956.
- STRAUSBAUGH, P. D., & E. L. CORE. Flora of West Virginia. xxxi + 1075 pp. *West Virginia Univ. Bull.* 1952-64. [*F. grandifolia*, 298]
- THORUP, S. Breaking dormancy of beech. *Physiol. Pl.* **10**: 728-731. 1957. [Use of Rindite, consisting of ethylene chlorhydrine, ethylene dichloride and carbon tetrachloride, employed for breaking dormancy in *F. silvatica*.]
- TRALAU, H. Late-Tertiary *Fagus* species of Europe. (In German; English summary). *Bot. Not.* **115**: 147-176. 1962. [Includes maps.]
- TROTTER, A. The physiognomy of trees and the plasticity of the beech (*Fagus*). (In Italian; English summary.) *Monti Boschi* **4**: 339-348. 1953.\*
- WARD, R. T. The beech forests of Wisconsin; their phytosociology and relationships to forests of the state without beech. *Ecology* **39**: 444-457. 1958. [*F. grandifolia*; includes map.]
- . Some aspects of the regeneration habits of the American beech. *Ibid.* **42**: 828-832. 1961. [*F. grandifolia*; includes map.]
- WILLIAMS, A. B. The composition and dynamics of a beech maple climax community. *Ecol. Monogr.* **6**: 319-408. *figs. 1-16*. 1936.

WRIGHT, J. W., R. T. BINGHAM, & K. W. DORMAN. Genetic variation within geographic ecotypes of forest trees and its role in tree improvement. *Jour. Forestry* 56: 803-808. 1958. [*F. grandifolia*.]

Subfamily CASTANEOIDEAE Oersted

2. *Castanea* Miller, *Gard. Dict. Abridg. ed. 4. 1: ord. alph. 1754.*

Large to small, erect to spreading deciduous trees or shrubs of the temperate Northern Hemisphere, with large taproots and furrowed, brownish bark; branchlets terete, the terminal buds covered by 2 pairs of slightly imbricate scales, the outer pair lateral, the inner accrescent, becoming oblong-ovate and leaving narrow ringlike scars upon falling. Leaves convolute in vernalization, elliptic to oblong-elliptic, the veins terminating at the tips of the usually coarse serrations, deciduous, petiolate; stipules paired, ovate to linear-lanceolate, acute at apex, scarious to herbaceous, infolding the leaf in bud, usually caducous; leaf-scars semioval, slightly elevated, with an irregular marginal row of small vascular bundle scars. Flowers in  $\pm$  erect catkin-like staminate or androgynous racemes or spikes (false panicles fide Camus); staminate inflorescences  $\pm$  erect, vernal (appearing with the unfolding of the leaves), borne in the axils of the lower leaves of the year; androgynous inflorescences usually erect, shorter than the staminate, borne in the axils of later leaves. Staminate flower subtended by a minute ovate bract; perianth deeply divided into 6 ovate lobes, the lobes imbricate in bud, slightly puberulous, pale stramineous, with 6-18 (-20) exerted stamens, filaments filiform, incurved in bud, free; anthers small, ovoid to subglobose, dorsifixed, introrse, 2-locular, with longitudinal dehiscence, pollen usually 3-colporoidate, prolate to subprolate; rudimentary ovary occasionally present. Carpellate flowers at base of androgynous inflorescences, sessile, solitary or 2 or 3 within an involucre of closely imbricate, pubescent to tomentose scales and  $\pm$  branched spines; involucre subtended by a bract with two lateral bractlets; perianth urceolate, with 6 short obtuse lobes, pubescent, with 6-8 rudimentary stamens; styles usually 6 (-9), linear, spreading, pubescent below the middle, tipped by the minute punctiform stigmas; ovary incompletely (3-)6(-9)-loculate, each locule with 2 axile, collateral, semianatropous, and descending ovules. Involucre at maturity of fruit subspherical to oblong, pubescent and spiny on the outer surface, with elongated, ridged, branched spines fasciculate between the deciduous scales, inclosing 1-3 (rarely more) fruits, and splitting into 2-4 valves at maturity, the inner surface of the involucre with a lustrous pubescence. Fruits maturing in one season,  $\pm$  ovoid and variously compressed, acute apically and beaked by the persistent perianth and styles, usually bright chestnut-brown and lustrous, with a large basal scar. Seed usually solitary, the abortive ovules borne apically; embryo straight, the cotyledons thick, fleshy,  $\pm$  undulate and ruminant, inclosing remnants of endosperm between the folds, often sweet; germination hypogeal. LECTOTYPE SPECIES: *Fagus Castanea* L. = *C. sativa* Mill.; see Britton, *N. Am. Trees* 271. 1908. (The ancient Latin name of the

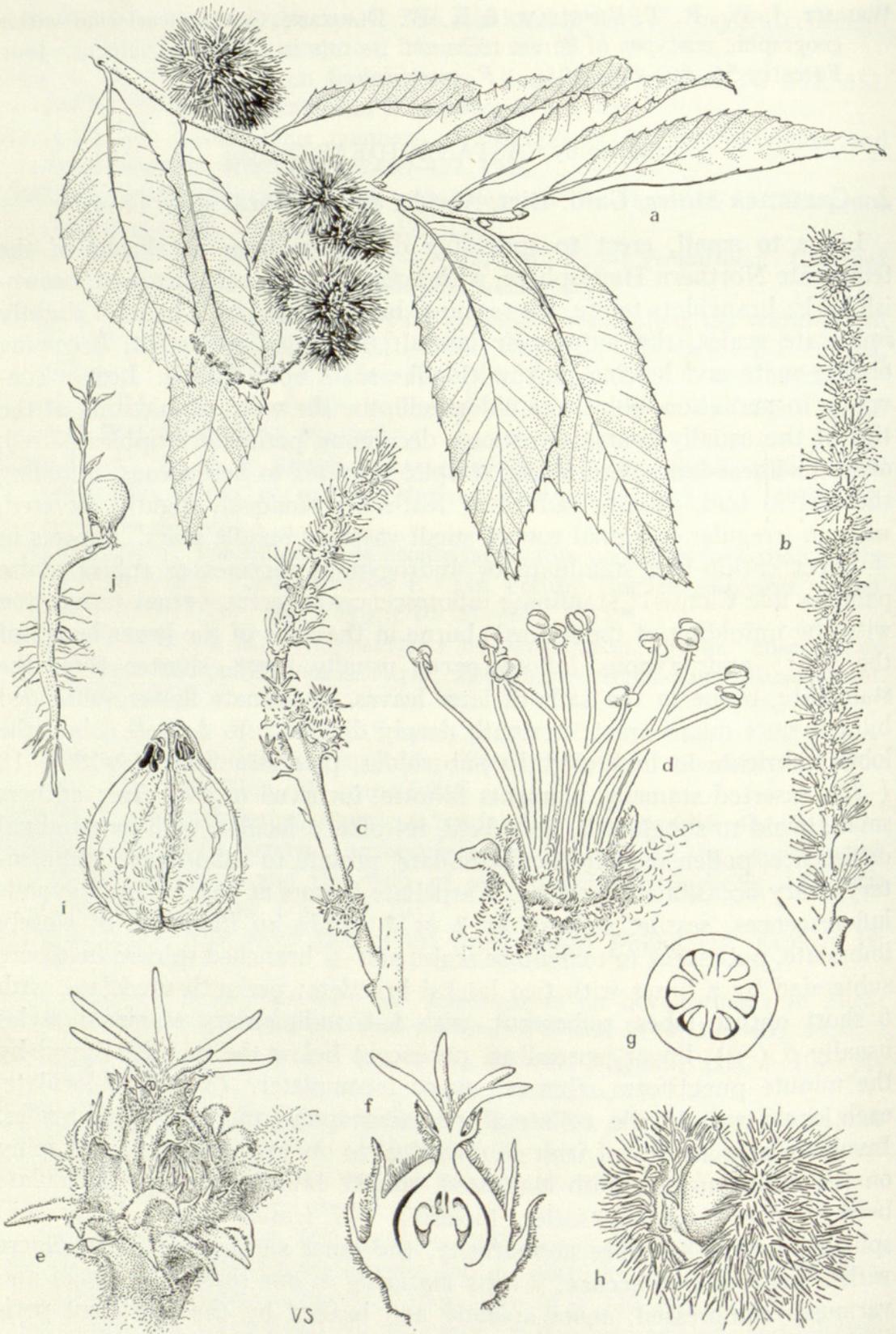


FIGURE 3. *Castanea*. a-j, *C. pumila*: a, fruiting branchlet,  $\times \frac{1}{2}$ ; b, staminate inflorescence,  $\times 1$ ; c, androgynous inflorescence,  $\times 1\frac{1}{2}$ ; d, staminate flower,  $\times 10$ ; e, carpellate flower,  $\times 6$ ; f, carpellate flower in semidiagrammatic longitudinal section showing two of the six locules,  $\times 6$ ; g, ovary in semidiagrammatic cross section,  $\times 10$ ; h, involucre with fruit,  $\times 1$ ; i, embryo with aborted ovules at the apex,  $\times 2$ ; j, seedling, showing large taproot,  $\times \frac{1}{2}$ .

European chestnut, derived from its Greek name, *kastanea* or *kastanos*.)  
— CHESTNUT.

About 12–14 species, widely distributed in eastern North America, southern Europe, northern Africa, southwestern Asia, central and northern China, Korea, and Japan. Characterized by having 6(–9) styles, the ovary 6–9-locular, the carpellate flowers borne at the base of androgynous catkins, the fruits maturing in one season, and the leaves deciduous, *Castanea* is closely related to the Old World *Castanopsis* (D. Don) Spach, which has three styles, the ovary three-locular, the carpellate flowers on separate catkins, the fruits maturing in two years, and the leaves persistent.

Dode (1908) divided *Castanea* into three sections: CASTANEA (§ *Eucastanon* Dode, BALANOCASTANON, and HYPOCASTANON, based on the number of fruits per involucre, the presence or absence of a persistent beak on the fruits, and their shape. Section HYPOCASTANON includes only *C. Henryi* Rehd., of China.

Section CASTANEA, including about six species with *C. dentata* (Marsh.) Borkh.,  $2n = 24$ , American chestnut, in our range, demonstrates the disjunction shown by a number of relict Arcto-Tertiary genera between the eastern United States (*C. dentata*), southern Europe (*C. sativa* Mill.,  $2n = 24$ ), and southeastern Asia (*C. crenata* Sieb. & Zucc.,  $2n = 24$ , *C. mollissima* Blume,  $2n = 24$ , *C. Seguinii* Dode, and *C. Davidii* Dode). Section CASTANEA is characterized by involucre each containing three fruits, rarely more, by the middle fruit being as wide as or wider than long, and by the fruits usually being conspicuously beaked.

*Castanea dentata*, formerly a dominant large tree in the eastern deciduous forest, ranges west from central Maine to New York, extreme southern Ontario, and southeastern Michigan, south to Ohio, southern Indiana, southern Illinois, western Kentucky, central Tennessee, northern Mississippi, Alabama, Georgia and northwestern Florida. Easily recognized by the large, oblong-lanceolate leaves which are coarsely serrate and by the very characteristic fruits, *C. dentata* can still be found throughout most of its original range in the form of stump sprouts that have been produced persistently for many years in spite of the attacks of the chestnut blight. The sprouts rarely reach flowering age, for usually when about 8–12 years old, they contract the blight and soon die (Neilstaedt, 1953). A few fruiting trees still survive in the wild, but most are in cultivation in areas isolated from the natural range of the species (cf. Thompson).

The natural replacement of *Castanea dentata* in the oak-chestnut forest of the eastern United States has been studied by several workers (cf. Keever, 1953; Nelson, 1955; Woods & Shanks, 1957, 1959). Replacement is mainly by species that were associated with *C. dentata* during its dominance. The main replacement species are *Q. rubra* L., *Q. prinus* L., *Q. alba* L., *Acer rubrum* L., and *Liriodendron tulipifera* L. Although other tree species, many of which were subordinate to the dominant species of *Quercus* and *C. dentata*, can be found, this association is apparently becoming an oak-oak association.

Section *BALANOCASTANON* Dode, restricted to the eastern United States, has one (rarely two) fruit per cupule, the fruit longer than broad and usually beaked. The taxa of this section need careful study to determine their exact status. *Castanea ozarkensis* Ashe, Ozark chinquapin, a tree with gray, glabrous branchlets, leaves broadly lanceolate to oblong, coarsely toothed, minutely pubescent to glabrate beneath, the involucre spines pubescent, and the seed not flattened, is found in woods and on rocky slopes from Mississippi and Louisiana to Arkansas, Oklahoma, and southern Missouri. The closely related *C. pumila* Mill. var. *pumila*,  $2n = 24$ , Allegheny chinquapin, occurs in dry woods and thickets from New Jersey and eastern Pennsylvania, southwest to Tennessee, Arkansas, and eastern Texas, and east to Florida. The generally shrubby *C. pumila* can be distinguished from *C. ozarkensis* by the pubescent branchlets, the leaves oblong, serrate, whitish-downy beneath, the involucre spines pubescent and much longer than in *C. ozarkensis*. Varietas *Ashei* Sudw. (*C. Ashei* (Sudw.) Sudw.) found mainly on the Coastal Plain from northern Florida northward to southeastern Virginia, and westward to eastern Texas and Arkansas, has the clusters of involucre spines remotely arranged, leaving conspicuous open areas on the involucre. A third species, *C. alnifolia* Nutt. var. *alnifolia*, trailing chinquapin, found in Georgia, Florida, Alabama, and Mississippi, typically occurs in dry, sandy soils. Frequently spreading by underground rootstocks, var. *alnifolia* is a low, often trailing shrub. Varietas *floridana* Sarg. (*C. floridana* (Sarg.) Ashe, *C. Margaretta* (Ashe) Ashe), Florida chinquapin, is a small tree of upland woods, flatwoods, and hammocks in the Coastal Plain from North Carolina to northern Florida and westward to southeastern Louisiana. Kurz & Godfrey (1962) consider both this variety and *C. pumila* var. *Ashei* to be distinct species. *Castanea paucispina* Ashe, a poorly known plant described from eastern Texas (Newton County) and also attributed (fide Camus) to adjoining western Louisiana, is closely related to *C. alnifolia* but is separated from it by having a shorter, pubescent fruiting axis and the spines sparsely arranged on the involucre. *Castanea*  $\times$  *alabamensis* Ashe, a hybrid of *C. dentata* and *C. alnifolia* var. *floridana*, occurs only in northern Florida. Another hybrid, *C.*  $\times$  *neglecta* Dode (*C. dentata*  $\times$  *C. pumila*) is of questionable status.

Although the species of *Castanea* are monoecious, cross pollination apparently is necessary for the production of viable seed. Solitary trees are frequently sterile, although the involucre may develop. A plausible explanation (which someone, hopefully, will prove or disprove) is that pollination may stimulate (chemically) the development of the involucre and ovary wall but that fertilization occurs only if the gametes are from another plant. Cross pollination is promoted by the staminate catkins maturing earlier than the androgynous catkins of the same plant. Clapper (1954) found that *C. mollissima* and *C. crenata* are self-sterile, but artificial hybrids between them show some self-compatibility. Self-sterility in *C. mollissima* was determined by McKay (1942) to be due to incompatibility, the pollen tube growing normally in cases of self-pollination,

but growth ceasing as the tube approached the egg, and no fertilization taking place. The two to three per cent fruit set was attributed to apomixis.

In a series of experiments to determine whether *Castanea* species are wind pollinated or insect pollinated, as suggested by some workers because of the rather conspicuous staminate spikes and the slightly odorous flowers, Clapper (1954) found them to be largely wind pollinated and concluded that this is more efficient than insect pollination and that insects are not essential for pollination. The stigmas were found to be receptive a few days after anthesis and most receptive 10–12 days after the beginning of anthesis. He also concluded that pollination was more effective in the morning than in the afternoon, apparently because of differences in humidity. From a series of interspecific crosses, it was determined that early flowering is dominant over late flowering.

Chestnut blight, caused by the ascomycete *Endothia parasitica* (Murr.) Anderson & Anderson, was first discovered in 1904 in the New York Zoological Park. Within 50 years it swept throughout the natural range of *Castanea dentata*, the species most susceptible to it. *Castanea sativa* is also proving to have little resistance against infection, but species of sect. BALANOCASTANON, as well as several species of *Quercus*, *Acer*, *Carya*, and *Rhus*, are susceptible in varying lesser degrees. The Asiatic species of *Castanea* show considerable resistance, but all serve as host to the blight fungus.

Following infection through a wound in the trunk or branches, the spores of *Endothia* germinate, and the mycelium rapidly spreads through the inner bark and cambium. Upon sporulation, a girdling canker (either appearing swollen or sunken) is usually formed, resulting in the death of the affected branch or the entire tree. Two types of spores are produced: relatively long-lived, one-celled, sticky, conidiospores produced during moist conditions, and larger, short-lived, two-celled ascospores. Conidiospores are spread by birds, insects, and to a lesser extent by rain, while ascospores are wind dispersed.

A very extensive breeding program was started soon after the devastating results of the chestnut blight became obvious. Breeding efforts were centered around *Castanea crenata*, the Japanese chestnut, and *C. mollissima*, the Chinese chestnut. Several disease-resistant hybrids have resulted, some suitable for commercial nut growing, others for ornamental trees. Clapper (1954) and Graves (1960, 1962) have presented techniques and results of some of the major breeding programs.

*Castanea dentata* was formerly an important timber tree in the eastern United States. The wood, brown, soft, light, open-grained, very durable, and easy to work, was widely used both indoors and in outside construction. The wood of *Castanea* species is high in tannin and was the major tanning agent for leather. Commercial chestnut growing in the United States has had to rely on Asiatic species and hybrids since the virtual elimination of the American chestnut.

## REFERENCES:

- See also under family references BERRY 140-145; FORMAN; KURZ & GODFREY, 57-59; HJELMQVIST; HUTCHINSON; LANGDON; SARGENT; VINES, 191-202; and WEST & ARNOLD, 33.
- ARRETINI, C. Bio-morphological aspects of flowering in young chestnut plants (*Castanea sativa* Mill.). (In Italian; English summary.) *Monti Boschi* 8: 323-331. 1957.\*
- BEATTIE, R. K., & J. D. DILLER. Fifty years of chestnut blight in America. *Jour. Forestry* 52: 323-329. 1954.
- BERRY, F. H. Relative resistance of some chestnut species and hybrids inoculated with the blight fungus. *North. Nut Growers Assoc. Rep.* 51: 46, 47. 1960. [*Endothia parasitica*.]
- BROOKS, A. B. *Castanea dentata*. *Castanea* 2: 61-67. 1937. [Range of *C. dentata*; also mentions introduced spp.]
- BUTTERICK, P. L. The chestnut in North Carolina. *Econ. Paper North Carolina Geol. Econ. Surv.* 56: 7-10. *pls.* 1, 2. 1925.\*
- CAMUS, A. Les chataigniers. 2 vols.: Texte, 604 pp. 28 *figs.*; Planches, 76 *pls.* + XXXIV *pls.* Paul Lechevalier, Paris. 1929. [Monograph of *Castanea* & *Castanopsis*.]
- CLAPPER, R. Chestnut breeding, techniques and results. I. Breeding material and pollination techniques. *Jour. Hered.* 45: 106-114. 1954; II. Inheritance of characters, breeding for vigor, and mutations. *Ibid.* 201-208.
- DERMEN, H., & J. D. DILLER. Colchipoidity of chestnuts. *Forest Sci.* 8: 43-50. 1962. [*C. dentata*, *C. mollissima*, & *C. crenata*.]
- DILLER, J. D. Is our American chestnut developing blight resistance? *North. Nut Growers Assoc. Rep.* 47: 29-31. 1956.
- . The present status of screening the American chestnut for blight resistance. *Ibid.* 51: 47-50. 1960.\*
- . Chestnut blight. U. S. Dep. Agr. Forest Pest Leaflet. 94. 7 pp. 1965. [Excellent account of chestnut blight.]
- GRAVATT, G. F. The chestnut situation in Europe. *North. Nut Growers Assoc. Rep.* 49: 67, 68. 1958.\*
- GRAVES, A. H. Relative blight resistance in species and hybrids of *Castanea*. *Phytopathology* 40: 1125-1131. 1950.
- . Hastening flowering in a chestnut seedling. *North. Nut Growers Assoc. Rep.* 49: 90-94. 1958.\* [*C. Henryi*.]
- . Some outstanding new chestnut hybrids. I. *Bull. Torrey Bot. Club* 87: 192-204. 1960; II. *Ibid.* 89: 161-172. 1962.
- GRAVES, H. S. Notes on the rate of growth of red cedar, red oak, and chestnut. *Forestry Quart.* 3: 349-353. 1905.
- HOLM, T. Medicinal plants of North America. 88. *Castanea dentata* (Marsh.) Borkh. and *C. pumila* (L.) Mill. *Merck's Rep.* 24: 85-87. 1915.
- ILLICK, J. S. Replacement of the chestnut. *Jour. Forestry* 19: 105-114. 1921.
- JAYNES, R. A. Chestnut chromosomes. *Forest Sci.* 8: 372-377. 1962.\*
- KEEVER, C. Present composition of some strands of the former oak-chestnut forest in the southern Blue Ridge Mountains. *Ecology* 34: 44-54. 1953.
- KRIBS, D. A. Salient lines of structural specialization in the wood rays of dicotyledons. *Bot. Gaz.* 96: 547-557. *pl.* 8. 1935. [Includes *C. pumila*.]
- LANGDON, L. M. The Castaneae, variations of floral and inflorescence morphology. (Abstr.) *Am. Jour. Bot.* 36: 798. 1949.

- MATTOON, W. R. The origin and early development of chestnut sprouts. *Forestry Quart.* **7**: 34-37. 1909.
- MCCORMICK, J. F., & R. B. PLATT. A half century of succession in an Appalachian forest following the chestnut blight. (Abstr.) *ASB Bull.* **17**: 54. 1970. [Replacement of *C. dentata* by various genera, especially *Carya*.]
- McKAY, J. W. Self-sterility in the Chinese chestnut (*Castanea mollissima*). *Proc. Am. Soc. Hort. Sci.* **41**: 156-160. 1942.
- . Heterosis in chestnuts. (Abstr.) *Genetics* **33**: 116. 1948. [*C. mollissima* × *C. crenata*.]
- . Seed and seedling characters as tools in speeding up chestnut breeding. *Proc. Am. Soc. Hort. Sci.* **75**: 322-325. 1960.
- & F. H. BERRY. Introduction and distribution of Chinese chestnuts in the United States. *North. Nut Growers Assoc. Rep.* **51**: 31-36. 1960.\* [*C. mollissima*.]
- MURRILL, W. A. A serious chestnut disease. *Jour. N. Y. Bot. Gard.* **7**: 143-153. 1906. [First report of chestnut blight in U. S.]
- NEINSTAEDT, H. Tannin as a factor in the resistance of chestnut, *Castanea* spp., to the chestnut blight fungus, *Endothia parasitica* (Murr.) A. & A. *Phytopathology* **43**: 32-38. 1953. [*C. dentata*, *C. crenata*, & *C. mollissima*.]
- NELSON, R. M. Growth and mortality of chestnut sprouts. *Jour. Forestry* **30**: 872, 873. 1932.
- NELSON, T. C. Chestnut [*Castanea dentata*] replacement in the southern highlands. *Ecology* **36**: 352, 353. 1955. [*C. dentata* in North Carolina.]
- RICHARDS, E. C. M. A study of reforested chestnut cut-over land. *Jour. Forestry* **15**: 609-614. 1917.
- SOLIGNAT, G. Observations sur la biologie du chataignier. *Ann. Amel. Pl.* **8**: 31-58. 1958.\*
- STOUT, A. B. Why are chestnuts self-fruitless? *Jour. N. Y. Bot. Gard.* **27**: 154-158. 1926.
- THOMPSON, P. W. A unique American chestnut grove. *Mich. Academician* **1**: 175-178. 1969. [Outside natural range of *C. dentata*, near Frankfort, Michigan.]
- VILKOMERSON, H. Flowering habits of the chestnut. *North. Nut Growers Assoc. Rep.* **31**: 114-116. 1941.\*
- WOODS, F. W., & R. E. SHANKS. Replacement of chestnut in the Great Smoky Mountains of Tennessee and North Carolina. *Jour. Forestry* **55**: 847. 1957. [*C. dentata*.]
- & ———. Natural replacement of chestnut by other species in the Great Smoky Mountains National Park. *Ecology* **40**: 349-361. 1959. [*C. dentata*.]

#### Subfamily QUERCOIDEAE Oersted

### 3. *Quercus* Linnaeus, Sp. Pl. 2: 994. 1753; Gen. Pl. ed. 5. 431. 1754.

Evergreen or deciduous trees or shrubs of varied habitats, often with astringent properties, the sap watery, the bark pale and scaly or dark and furrowed, the wood usually hard and close-grained or brittle and either diffuse or ring porous with both uniseriate and multiseriate rays, the pith star-shaped in section and continuous; branchlets slender, lenticellate, often fluted or ± prominently 5-angled; winter buds clustered at end of branchlets, the scales chestnut-brown, closely imbricate in 5 ranks, slightly ac-

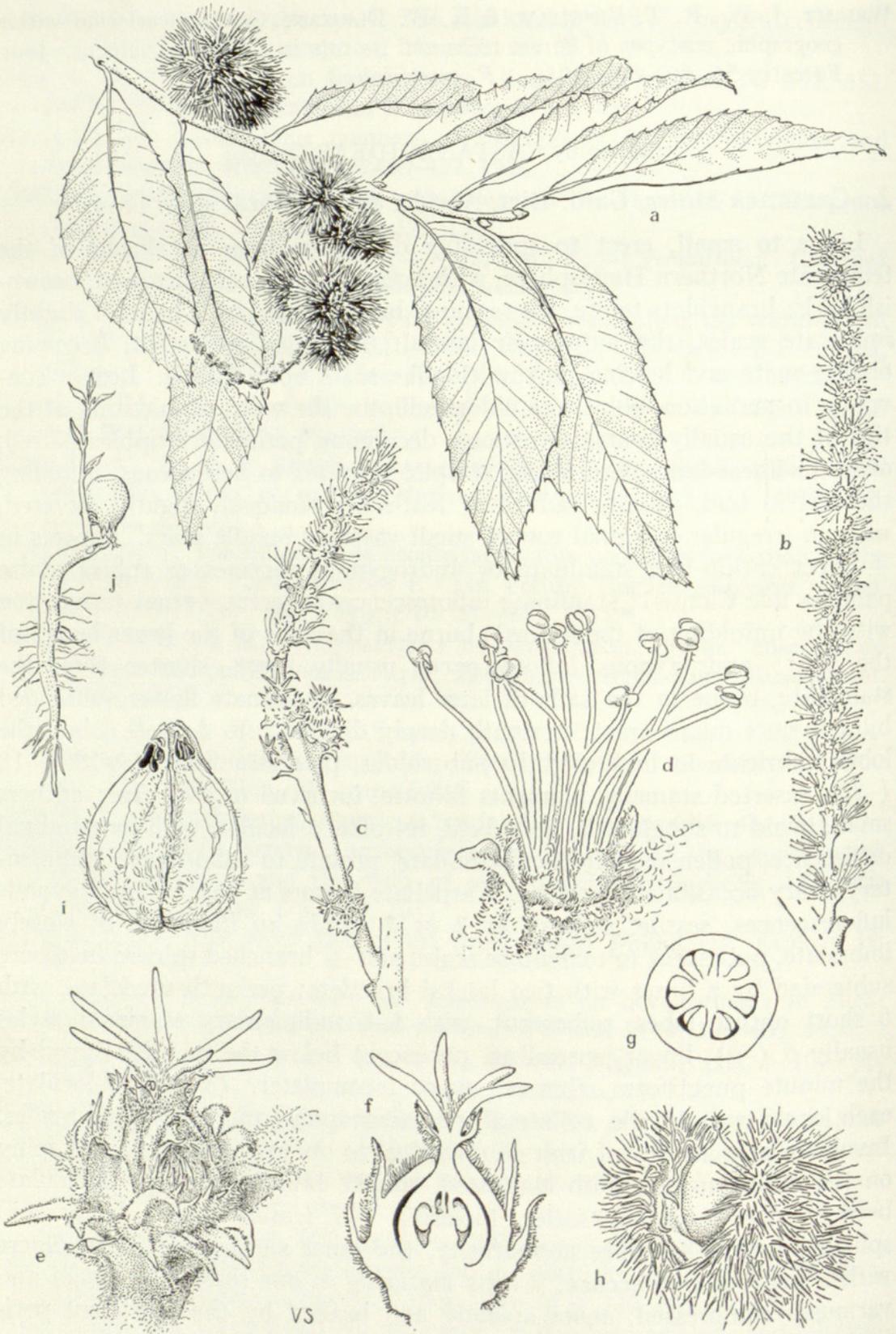


FIGURE 3. *Castanea*. a-j, *C. pumila*: a, fruiting branchlet,  $\times \frac{1}{2}$ ; b, staminate inflorescence,  $\times 1$ ; c, androgynous inflorescence,  $\times 1\frac{1}{2}$ ; d, staminate flower,  $\times 10$ ; e, carpellate flower,  $\times 6$ ; f, carpellate flower in semidiagrammatic longitudinal section showing two of the six locules,  $\times 6$ ; g, ovary in semidiagrammatic cross section,  $\times 10$ ; h, involucre with fruit,  $\times 1$ ; i, embryo with aborted ovules at the apex,  $\times 2$ ; j, seedling, showing large taproot,  $\times \frac{1}{2}$ .

European chestnut, derived from its Greek name, *kastanea* or *kastanos*.)  
— CHESTNUT.

About 12–14 species, widely distributed in eastern North America, southern Europe, northern Africa, southwestern Asia, central and northern China, Korea, and Japan. Characterized by having 6(–9) styles, the ovary 6–9-locular, the carpellate flowers borne at the base of androgynous catkins, the fruits maturing in one season, and the leaves deciduous, *Castanea* is closely related to the Old World *Castanopsis* (D. Don) Spach, which has three styles, the ovary three-locular, the carpellate flowers on separate catkins, the fruits maturing in two years, and the leaves persistent.

Dode (1908) divided *Castanea* into three sections: CASTANEA (§ *Eucastanon* Dode, BALANOCASTANON, and HYPOCASTANON, based on the number of fruits per involucre, the presence or absence of a persistent beak on the fruits, and their shape. Section HYPOCASTANON includes only *C. Henryi* Rehd., of China.

Section CASTANEA, including about six species with *C. dentata* (Marsh.) Borkh.,  $2n = 24$ , American chestnut, in our range, demonstrates the disjunction shown by a number of relict Arcto-Tertiary genera between the eastern United States (*C. dentata*), southern Europe (*C. sativa* Mill.,  $2n = 24$ ), and southeastern Asia (*C. crenata* Sieb. & Zucc.,  $2n = 24$ , *C. mollissima* Blume,  $2n = 24$ , *C. Seguinii* Dode, and *C. Davidii* Dode). Section CASTANEA is characterized by involucre each containing three fruits, rarely more, by the middle fruit being as wide as or wider than long, and by the fruits usually being conspicuously beaked.

*Castanea dentata*, formerly a dominant large tree in the eastern deciduous forest, ranges west from central Maine to New York, extreme southern Ontario, and southeastern Michigan, south to Ohio, southern Indiana, southern Illinois, western Kentucky, central Tennessee, northern Mississippi, Alabama, Georgia and northwestern Florida. Easily recognized by the large, oblong-lanceolate leaves which are coarsely serrate and by the very characteristic fruits, *C. dentata* can still be found throughout most of its original range in the form of stump sprouts that have been produced persistently for many years in spite of the attacks of the chestnut blight. The sprouts rarely reach flowering age, for usually when about 8–12 years old, they contract the blight and soon die (Neilstaedt, 1953). A few fruiting trees still survive in the wild, but most are in cultivation in areas isolated from the natural range of the species (cf. Thompson).

The natural replacement of *Castanea dentata* in the oak-chestnut forest of the eastern United States has been studied by several workers (cf. Keever, 1953; Nelson, 1955; Woods & Shanks, 1957, 1959). Replacement is mainly by species that were associated with *C. dentata* during its dominance. The main replacement species are *Q. rubra* L., *Q. prinus* L., *Q. alba* L., *Acer rubrum* L., and *Liriodendron tulipifera* L. Although other tree species, many of which were subordinate to the dominant species of *Quercus* and *C. dentata*, can be found, this association is apparently becoming an oak-oak association.

Section *BALANOCASTANON* Dode, restricted to the eastern United States, has one (rarely two) fruit per cupule, the fruit longer than broad and usually beaked. The taxa of this section need careful study to determine their exact status. *Castanea ozarkensis* Ashe, Ozark chinquapin, a tree with gray, glabrous branchlets, leaves broadly lanceolate to oblong, coarsely toothed, minutely pubescent to glabrate beneath, the involucre spines pubescent, and the seed not flattened, is found in woods and on rocky slopes from Mississippi and Louisiana to Arkansas, Oklahoma, and southern Missouri. The closely related *C. pumila* Mill. var. *pumila*,  $2n = 24$ , Allegheny chinquapin, occurs in dry woods and thickets from New Jersey and eastern Pennsylvania, southwest to Tennessee, Arkansas, and eastern Texas, and east to Florida. The generally shrubby *C. pumila* can be distinguished from *C. ozarkensis* by the pubescent branchlets, the leaves oblong, serrate, whitish-downy beneath, the involucre spines pubescent and much longer than in *C. ozarkensis*. Varietas *Ashei* Sudw. (*C. Ashei* (Sudw.) Sudw.) found mainly on the Coastal Plain from northern Florida northward to southeastern Virginia, and westward to eastern Texas and Arkansas, has the clusters of involucre spines remotely arranged, leaving conspicuous open areas on the involucre. A third species, *C. alnifolia* Nutt. var. *alnifolia*, trailing chinquapin, found in Georgia, Florida, Alabama, and Mississippi, typically occurs in dry, sandy soils. Frequently spreading by underground rootstocks, var. *alnifolia* is a low, often trailing shrub. Varietas *floridana* Sarg. (*C. floridana* (Sarg.) Ashe, *C. Margaretta* (Ashe) Ashe), Florida chinquapin, is a small tree of upland woods, flatwoods, and hammocks in the Coastal Plain from North Carolina to northern Florida and westward to southeastern Louisiana. Kurz & Godfrey (1962) consider both this variety and *C. pumila* var. *Ashei* to be distinct species. *Castanea paucispina* Ashe, a poorly known plant described from eastern Texas (Newton County) and also attributed (fide Camus) to adjoining western Louisiana, is closely related to *C. alnifolia* but is separated from it by having a shorter, pubescent fruiting axis and the spines sparsely arranged on the involucre. *Castanea* × *alabamensis* Ashe, a hybrid of *C. dentata* and *C. alnifolia* var. *floridana*, occurs only in northern Florida. Another hybrid, *C.* × *neglecta* Dode (*C. dentata* × *C. pumila*) is of questionable status.

Although the species of *Castanea* are monoecious, cross pollination apparently is necessary for the production of viable seed. Solitary trees are frequently sterile, although the involucre may develop. A plausible explanation (which someone, hopefully, will prove or disprove) is that pollination may stimulate (chemically) the development of the involucre and ovary wall but that fertilization occurs only if the gametes are from another plant. Cross pollination is promoted by the staminate catkins maturing earlier than the androgynous catkins of the same plant. Clapper (1954) found that *C. mollissima* and *C. crenata* are self-sterile, but artificial hybrids between them show some self-compatibility. Self-sterility in *C. mollissima* was determined by McKay (1942) to be due to incompatibility, the pollen tube growing normally in cases of self-pollination,

but growth ceasing as the tube approached the egg, and no fertilization taking place. The two to three per cent fruit set was attributed to apomixis.

In a series of experiments to determine whether *Castanea* species are wind pollinated or insect pollinated, as suggested by some workers because of the rather conspicuous staminate spikes and the slightly odorous flowers, Clapper (1954) found them to be largely wind pollinated and concluded that this is more efficient than insect pollination and that insects are not essential for pollination. The stigmas were found to be receptive a few days after anthesis and most receptive 10–12 days after the beginning of anthesis. He also concluded that pollination was more effective in the morning than in the afternoon, apparently because of differences in humidity. From a series of interspecific crosses, it was determined that early flowering is dominant over late flowering.

Chestnut blight, caused by the ascomycete *Endothia parasitica* (Murr.) Anderson & Anderson, was first discovered in 1904 in the New York Zoological Park. Within 50 years it swept throughout the natural range of *Castanea dentata*, the species most susceptible to it. *Castanea sativa* is also proving to have little resistance against infection, but species of sect. BALANOCASTANON, as well as several species of *Quercus*, *Acer*, *Carya*, and *Rhus*, are susceptible in varying lesser degrees. The Asiatic species of *Castanea* show considerable resistance, but all serve as host to the blight fungus.

Following infection through a wound in the trunk or branches, the spores of *Endothia* germinate, and the mycelium rapidly spreads through the inner bark and cambium. Upon sporulation, a girdling canker (either appearing swollen or sunken) is usually formed, resulting in the death of the affected branch or the entire tree. Two types of spores are produced: relatively long-lived, one-celled, sticky, conidiospores produced during moist conditions, and larger, short-lived, two-celled ascospores. Conidiospores are spread by birds, insects, and to a lesser extent by rain, while ascospores are wind dispersed.

A very extensive breeding program was started soon after the devastating results of the chestnut blight became obvious. Breeding efforts were centered around *Castanea crenata*, the Japanese chestnut, and *C. mollissima*, the Chinese chestnut. Several disease-resistant hybrids have resulted, some suitable for commercial nut growing, others for ornamental trees. Clapper (1954) and Graves (1960, 1962) have presented techniques and results of some of the major breeding programs.

*Castanea dentata* was formerly an important timber tree in the eastern United States. The wood, brown, soft, light, open-grained, very durable, and easy to work, was widely used both indoors and in outside construction. The wood of *Castanea* species is high in tannin and was the major tanning agent for leather. Commercial chestnut growing in the United States has had to rely on Asiatic species and hybrids since the virtual elimination of the American chestnut.

## REFERENCES:

- See also under family references BERRY 140-145; FORMAN; KURZ & GODFREY, 57-59; HJELMQVIST; HUTCHINSON; LANGDON; SARGENT; VINES, 191-202; and WEST & ARNOLD, 33.
- ARRETINI, C. Bio-morphological aspects of flowering in young chestnut plants (*Castanea sativa* Mill.). (In Italian; English summary.) *Monti Boschi* 8: 323-331. 1957.\*
- BEATTIE, R. K., & J. D. DILLER. Fifty years of chestnut blight in America. *Jour. Forestry* 52: 323-329. 1954.
- BERRY, F. H. Relative resistance of some chestnut species and hybrids inoculated with the blight fungus. *North. Nut Growers Assoc. Rep.* 51: 46, 47. 1960. [*Endothia parasitica*.]
- BROOKS, A. B. *Castanea dentata*. *Castanea* 2: 61-67. 1937. [Range of *C. dentata*; also mentions introduced spp.]
- BUTTERICK, P. L. The chestnut in North Carolina. *Econ. Paper North Carolina Geol. Econ. Surv.* 56: 7-10. *pls.* 1, 2. 1925.\*
- CAMUS, A. Les chataigniers. 2 vols.: Texte, 604 pp. 28 *figs.*; Planches, 76 *pls.* + XXXIV *pls.* Paul Lechevalier, Paris. 1929. [Monograph of *Castanea* & *Castanopsis*.]
- CLAPPER, R. Chestnut breeding, techniques and results. I. Breeding material and pollination techniques. *Jour. Hered.* 45: 106-114. 1954; II. Inheritance of characters, breeding for vigor, and mutations. *Ibid.* 201-208.
- DERMEN, H., & J. D. DILLER. Colchipoidity of chestnuts. *Forest Sci.* 8: 43-50. 1962. [*C. dentata*, *C. mollissima*, & *C. crenata*.]
- DILLER, J. D. Is our American chestnut developing blight resistance? *North. Nut Growers Assoc. Rep.* 47: 29-31. 1956.
- . The present status of screening the American chestnut for blight resistance. *Ibid.* 51: 47-50. 1960.\*
- . Chestnut blight. U. S. Dep. Agr. Forest Pest Leaflet. 94. 7 pp. 1965. [Excellent account of chestnut blight.]
- GRAVATT, G. F. The chestnut situation in Europe. *North. Nut Growers Assoc. Rep.* 49: 67, 68. 1958.\*
- GRAVES, A. H. Relative blight resistance in species and hybrids of *Castanea*. *Phytopathology* 40: 1125-1131. 1950.
- . Hastening flowering in a chestnut seedling. *North. Nut Growers Assoc. Rep.* 49: 90-94. 1958.\* [*C. Henryi*.]
- . Some outstanding new chestnut hybrids. I. *Bull. Torrey Bot. Club* 87: 192-204. 1960; II. *Ibid.* 89: 161-172. 1962.
- GRAVES, H. S. Notes on the rate of growth of red cedar, red oak, and chestnut. *Forestry Quart.* 3: 349-353. 1905.
- HOLM, T. Medicinal plants of North America. 88. *Castanea dentata* (Marsh.) Borkh. and *C. pumila* (L.) Mill. *Merck's Rep.* 24: 85-87. 1915.
- ILLICK, J. S. Replacement of the chestnut. *Jour. Forestry* 19: 105-114. 1921.
- JAYNES, R. A. Chestnut chromosomes. *Forest Sci.* 8: 372-377. 1962.\*
- KEEVER, C. Present composition of some strands of the former oak-chestnut forest in the southern Blue Ridge Mountains. *Ecology* 34: 44-54. 1953.
- KRIBS, D. A. Salient lines of structural specialization in the wood rays of dicotyledons. *Bot. Gaz.* 96: 547-557. *pl.* 8. 1935. [Includes *C. pumila*.]
- LANGDON, L. M. The Castaneae, variations of floral and inflorescence morphology. (Abstr.) *Am. Jour. Bot.* 36: 798. 1949.

- MATTOON, W. R. The origin and early development of chestnut sprouts. *Forestry Quart.* **7**: 34-37. 1909.
- MCCORMICK, J. F., & R. B. PLATT. A half century of succession in an Appalachian forest following the chestnut blight. (Abstr.) *ASB Bull.* **17**: 54. 1970. [Replacement of *C. dentata* by various genera, especially *Carya*.]
- McKAY, J. W. Self-sterility in the Chinese chestnut (*Castanea mollissima*). *Proc. Am. Soc. Hort. Sci.* **41**: 156-160. 1942.
- . Heterosis in chestnuts. (Abstr.) *Genetics* **33**: 116. 1948. [*C. mollissima* × *C. crenata*.]
- . Seed and seedling characters as tools in speeding up chestnut breeding. *Proc. Am. Soc. Hort. Sci.* **75**: 322-325. 1960.
- & F. H. BERRY. Introduction and distribution of Chinese chestnuts in the United States. *North. Nut Growers Assoc. Rep.* **51**: 31-36. 1960.\* [*C. mollissima*.]
- MURRILL, W. A. A serious chestnut disease. *Jour. N. Y. Bot. Gard.* **7**: 143-153. 1906. [First report of chestnut blight in U. S.]
- NEINSTAEDT, H. Tannin as a factor in the resistance of chestnut, *Castanea* spp., to the chestnut blight fungus, *Endothia parasitica* (Murr.) A. & A. *Phytopathology* **43**: 32-38. 1953. [*C. dentata*, *C. crenata*, & *C. mollissima*.]
- NELSON, R. M. Growth and mortality of chestnut sprouts. *Jour. Forestry* **30**: 872, 873. 1932.
- NELSON, T. C. Chestnut [*Castanea dentata*] replacement in the southern highlands. *Ecology* **36**: 352, 353. 1955. [*C. dentata* in North Carolina.]
- RICHARDS, E. C. M. A study of reforested chestnut cut-over land. *Jour. Forestry* **15**: 609-614. 1917.
- SOLIGNAT, G. Observations sur la biologie du chataignier. *Ann. Amel. Pl.* **8**: 31-58. 1958.\*
- STOUT, A. B. Why are chestnuts self-fruitless? *Jour. N. Y. Bot. Gard.* **27**: 154-158. 1926.
- THOMPSON, P. W. A unique American chestnut grove. *Mich. Academician* **1**: 175-178. 1969. [Outside natural range of *C. dentata*, near Frankfort, Michigan.]
- VILKOMERSON, H. Flowering habits of the chestnut. *North. Nut Growers Assoc. Rep.* **31**: 114-116. 1941.\*
- WOODS, F. W., & R. E. SHANKS. Replacement of chestnut in the Great Smoky Mountains of Tennessee and North Carolina. *Jour. Forestry* **55**: 847. 1957. [*C. dentata*.]
- & ———. Natural replacement of chestnut by other species in the Great Smoky Mountains National Park. *Ecology* **40**: 349-361. 1959. [*C. dentata*.]

#### Subfamily QUERCOIDEAE Oersted

### 3. *Quercus* Linnaeus, Sp. Pl. 2: 994. 1753; Gen. Pl. ed. 5. 431. 1754.

Evergreen or deciduous trees or shrubs of varied habitats, often with astringent properties, the sap watery, the bark pale and scaly or dark and furrowed, the wood usually hard and close-grained or brittle and either diffuse or ring porous with both uniseriate and multiseriate rays, the pith star-shaped in section and continuous; branchlets slender, lenticellate, often fluted or ± prominently 5-angled; winter buds clustered at end of branchlets, the scales chestnut-brown, closely imbricate in 5 ranks, slightly ac-

crescent, caducous, leaving ring-like scars upon falling. Leaves usually with involute, convolute or revolute vernation, deciduous or persistent until spring or persistent for 2–4 years, simple, usually distinctly petiolate, the blade entire, variously lobed or dentate, often variable on the same branch, membranaceous to coriaceous, pinnately veined, the prominent primary veins extending to the margins or beyond as bristles, or veins anastomosing within; stipules obovate to lanceolate, scarious, often caducous, or those of the upper leaves occasionally persisting to the next year; leaf-scars slightly elevated, semiorbicular, usually broader than high. Flowers vernal, with or slightly after unfolding of leaves; staminate inflorescences in pendulous, fasciculate aments from axils of leaves of the previous year, from axils of the inner scales of the terminal bud, or from axils of leaves of the current year. Staminate flowers solitary or in clusters of 2 or 3, bracts absent or, if present, caducous; perianth campanulate, 3–6-lobed, usually divided to near the base; stamens (2–)4–12, inserted on a slightly thickened torus, the filaments free, filiform, exerted, the anthers usually ovate-oblong to subglobose, glabrous to rarely pubescent, 2-loculate, ex-torse, pollen 3-colporate or 3-colporoidate, usually subprolate to prolate. Carpellate flowers solitary or in erect few-flowered spikes from the axils of the leaves of the current year, each flower inclosed by an involucre of many imbricate [or annular] scales, the involucre subtended by a caducous bract and 2 bractlets and later becoming the cupule of the fruit; perianth urceolate, with 6 short lobes, the perianth tube adnate to the incompletely 3(–4–5)-loculate ovary; styles usually 3, short or elongate, erect or incurved, often dilated above, stigmatic on the inner face or at the apex, usually persistent in fruit, stamens wanting [or abortive stamens as many as the lobes]; ovules 2 per locule, collateral, anatropous or semi-anatropous, descending. Fruit a nut (acorn) maturing in one or two growing seasons, ovoid, subglobose, or turbinate, usually short-pointed at the apex, generally 1-seeded by abortion, marked at the base by a large conspicuous circular scar; pericarp crustaceous or coriaceous, glabrous or with a pale tomentum on the inner surface, partially to completely inclosed in the accrescent cupule (involucre); cupule scales loosely or closely imbricate, flattened or variously thickened [rarely united into concentric rings], occasionally with a fringed margin. Seed with the aborted ovules at the base or at the apex, rarely lateral; cotyledons thick, fleshy, usually plano-convex and entire; often undulate on the back; radicle superior, included within the base of the cotyledons, hilum minute, basal or apical, germination hypogeal.  $x = 12$ . (*Quercus* Raf., *Cerris* Raf., *Scolodrys* Raf., *Macrobalanus* (Oersted) Schwarz, *Erythrobalanus* (Spach) Schwarz.) LECTOTYPE SPECIES: *Q. Robur* L.; see Britton, N. Am. Trees 278. 1908. (Classical Latin name for oak.) — OAK.

A genus of approximately 500–600 species in the mild-temperate regions of the Northern Hemisphere and in higher altitudes of the tropics, in the New World distributed southward to Mexico, Central America, and Colombia, and in the West Indies. In the Old World the genus is dis-

tributed from Manchuria, China, and Japan, southward to the East Indies and the Philippine Islands, and to southern India, westward along the Himalayas to western Asia, and through the Mediterranean region into western and northern Europe. It is absent from central and southern Africa, New Guinea, Australia, and the Pacific Islands. Approximately 30 species occur in the southeastern United States.

Although numerous infrageneric names of various ranks have been proposed for the American oaks by several workers, Trelease (1924) in his comprehensive treatment arranged them in three sections and more than 100 series. Three subgenera are recognized here: *ERYTHROBALANUS* (Spach) Oersted, restricted to the New World; *QUERCUS* (subg. *Lepidobalanus* (Endl.) Oersted) of both Old and New Worlds; and *CYCLOBALANOPSIS* (Oersted) Schneider, of eastern Asia. The differences between the two subgenera in North America are summarized in the following key.

Leaves entire or lobed, the lobes rounded or, if toothed, only mucronate-tipped, never aristate-tipped; styles short, abruptly flaring; acorns annual, cup scales usually prominently thickened basally and loosely appressed apically, acorn wall (pericarp) glabrous within; aborted ovules generally basal; bark usually soft gray and scaly, rarely black and deeply furrowed; wood pale, the larger vessels often plugged by tyloses, the smaller summer vessels thin-walled and rounded. . . . . subg. *QUERCUS*.

Leaves entire or lobed, the lobes not rounded and, when toothed, aristate-tipped or, if entire, aristate-tipped from the veins; styles long, gradually flaring; acorns generally biennial, rarely annual, cup scales scarcely thickened basally and usually tightly appressed apically, acorn wall (pericarp) tomentose within; aborted ovules usually apical; bark rather hard, dark and furrowed, scarcely scaly; wood usually reddish, the vessels seldom filled with tyloses, the smaller summer vessels always thick-walled and rounded. . . subg. *ERYTHROBALANUS*.

Subgenus *QUERCUS* (*Lepidobalanus* Endl. ex Oersted; sect. *Lepidobalanus* (Oersted) Sargent; subg. *Macrobalanus* Oersted; *Macrobalanus* (Oersted) Schwarz; sect. *Leucobalanus* Engelm.; subg. *Leucobalanus* (Engelm.) Trelease) is represented in the eastern United States by approximately 16 species, many of which are confined to the Gulf Coastal Plain. The 57 series of subg. *QUERCUS* proposed by Trelease do not contribute significantly to an understanding of relationships and are not considered here, for the sections recognized by Rehder (1949) seem to represent more natural groups in this subgenus. Sections *CERRIS* Dumort., *SUBER* [Reichenb.] Spach, *GALLIFERA* Spach, and *QUERCUS* (§ *Robur* Dumort.) are confined to the Old World; our species are members of sects. *ILEX* and *PRINUS*.

Section *ILEX* Loudon, characterized by the evergreen habit; leaves usually entire, coriaceous; styles short, dilated toward the rounded apex; involucre with appressed scales; and fruit usually annual, is disjunctly distributed between the southeastern United States, southern Europe (*Quercus Ilex* L.), and southeastern Asia (*Q. phillyraeoides* Gray). Nearly restricted to the Atlantic and Gulf coastal plains, *Q. virginiana* Mill. extends from southeastern Virginia to southern Florida and western Cuba,

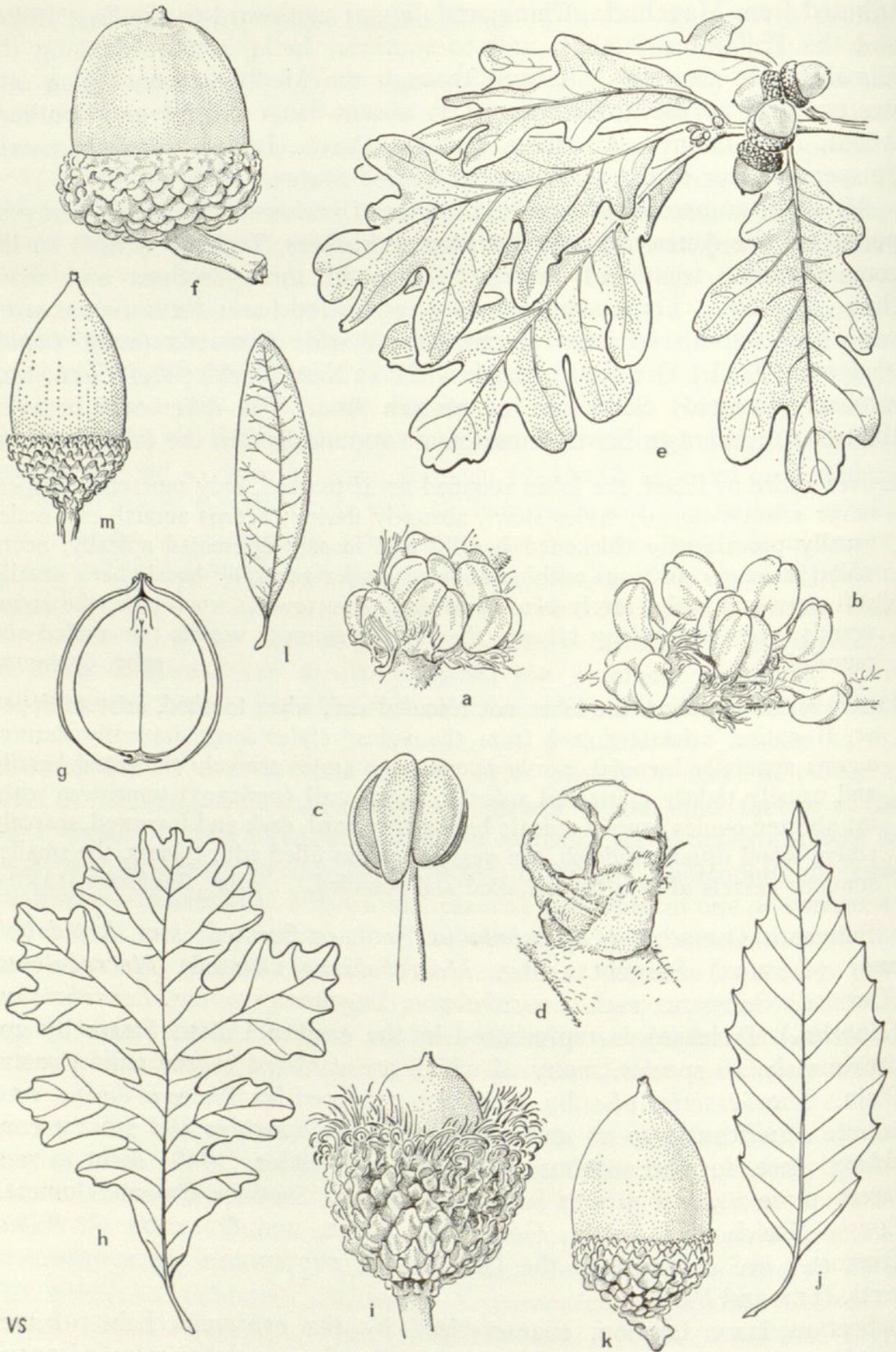


FIGURE 4. *Quercus* subgenus *Quercus*. a-d, *Q. prinus*: a, staminate flower prior to anthesis,  $\times 10$ ; b, staminate flower at anthesis,  $\times 10$ ; c, stamen showing longitudinal dehiscence,  $\times 20$ ; d, carpellate flower,  $\times 15$ . e-g, *Q. alba*: e, fruiting branchlet,  $\times \frac{1}{3}$ ; f, mature acorn,  $\times 1\frac{1}{2}$ ; g, mature acorn in semidiagrammatic longitudinal section showing basally aborted ovules,  $\times 1\frac{1}{2}$ . h, i, *Q. macrocarpa*: h, leaf,  $\times \frac{1}{2}$ ; i, mature acorn,  $\times 1$ . j, k, *Q. muhlenbergii*: j, leaf,  $\times 1$ ;

and west to central and southern Texas and northeastern Mexico. Three varieties are recognized: var. *virginiana* (*Q. minima* (Sarg.) Small, *Q. pygmaea* (Sarg.) Ashe), var. *fusiformis* (Small) Sarg. (*Q. fusiformis* Small), and var. *maritima* (Michx.) Sarg. (*Q. maritima* (Michx.) Willd., *Q. geminata* Small, *Q. Rolfsii* Small, *Q. succulenta* Small).

Section PRINUS Loudon, with some 14 species in the United States, is distinguished by the deciduous, variously lobed to dentate leaves; the short styles, broad at the apex; the involucre scales appressed or rarely the upper free and subulate (*Q. macrocarpa*); and the annual fruit. The species that occur in our range include *Q. alba* L.; *Q. stellata* Wang., with var. *stellata* (*Q. Ashei* Sterrett, *Q. similis* Ashe), var. *Margaretta* (Small) Sarg. (*Q. Margaretta* Ashe ex Small, *Q. Boyntoni* Beadle), and var. *mississippiensis* (Ashe) Little (*Q. mississippiensis* Ashe); *Q. lyrata* Walt.; *Q. macrocarpa* Michx.; *Q. bicolor* Willd. (*Q. platanooides* (Lam.) Sudw.); *Q. oglethorpensis* Duncan; *Q. Chapmanii* Sarg.; *Q. Durandii* Buckl. (*Q. austrina* Small, *Q. sinuata* Walt.); *Q. Prinus* L. (*Q. montana* Willd.); *Q. prinoides* Willd.; and *Q. Muehlenbergii* Engelm. (*Q. Castanea* Muhl., *Q. acuminata* (Michx.) Sarg., *Q. Alexanderi* Britton, *Q. Brayii* Small). Approximately five species belonging here are found in the western United States, and four (perhaps more) species occur in eastern Asia.

Subgenus QUERCUS has fewer species (ca. 19) in Central America than subg. ERYTHROBALANUS. In both subgenera the Mexican species are poorly known, poorly represented in herbaria, and in need of careful study.

Subgenus ERYTHROBALANUS (Spach) Oersted (§ *Erythrobalanus* Spach, *Erythrobalanus* (Spach) Schwarz, § *Melanobalanus* Engelm.) is confined to the New World, mainly to the southern and eastern parts of the United States, Mexico and Central America. Trelease (1924) recognized 190 species (plus numerous subspecific taxa), which he distributed among 73 series, many of these with only one to three species! Muller (1942), in a taxonomic survey of the Central American species of *Quercus*, recognized many of Trelease's series, but he reduced to synonymy more than he recognized and, in addition, reduced many of the species described by Trelease. Since the series seem to be largely artificial, no attempt is made here to account for them. Muller concluded that the difficulties in delimiting subgeneric categories in subg. ERYTHROBALANUS lie in the poorly known Mexican species. For convenience, the species discussed here have been grouped mainly on the basis of leaf characters that do not necessarily reflect natural relationships. These relationships need to be worked out carefully.

*Quercus chrysolepis* Liebm., of southwestern Oregon south along the coastal ranges and the Sierra Nevada to northern Lower California and western Nevada, and *Q. tomentella* Engelm., of the California Channel Islands and Guadalupe Island off Baja California, are somewhat intermediate between subg. ERYTHROBALANUS and subg. QUERCUS. Both have

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k, mature acorn,  $\times 1\frac{1}{2}$ . l, m, *Q. virginiana*: l, leaf,  $\times 1$ ; m, mature acorn,  $\times 1\frac{1}{2}$ .

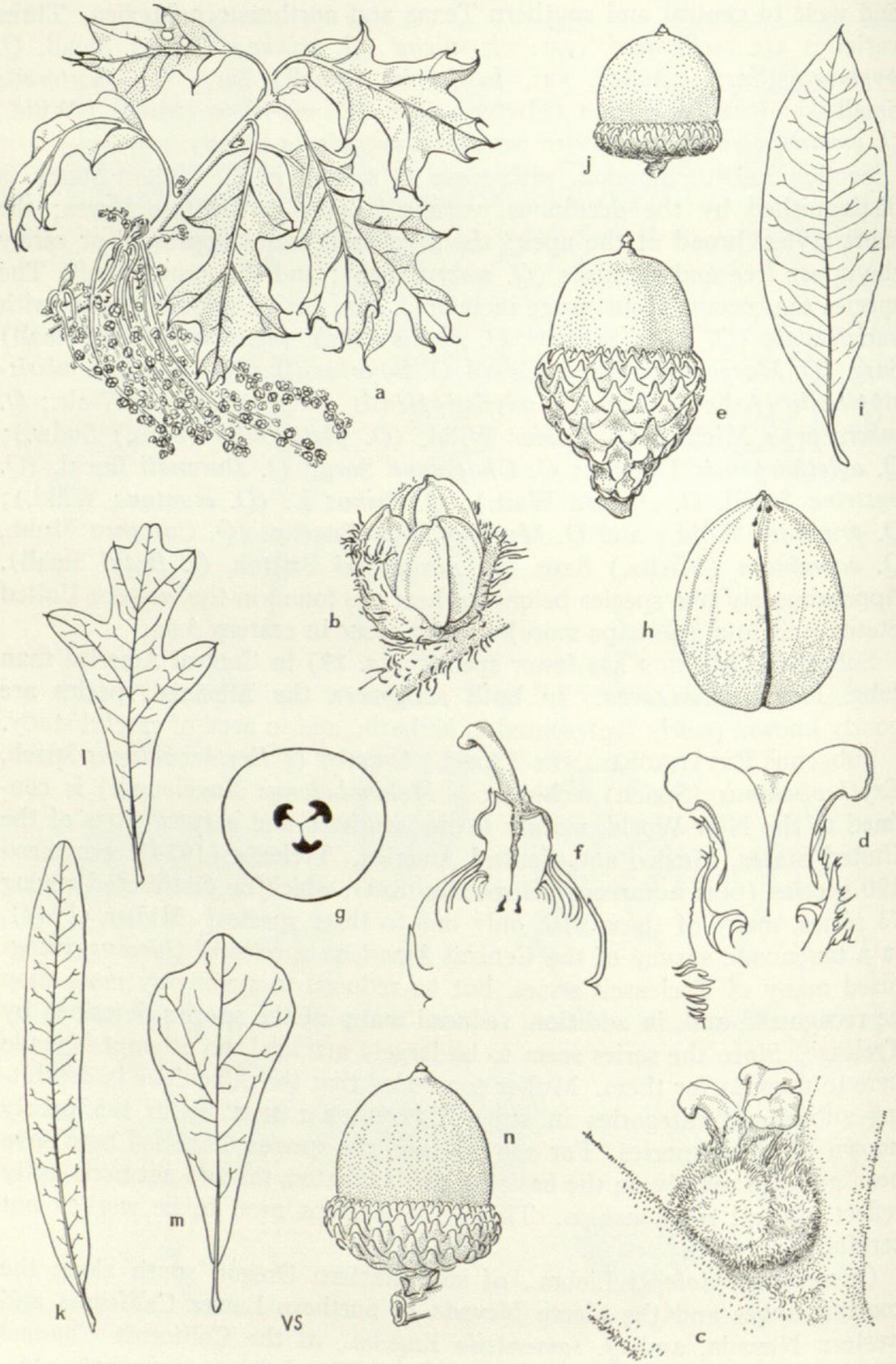


FIGURE 5. *Quercus* subgenus *Erythrobalanus*. a-e, *Q. ilicifolia*: a, branchlet with staminate inflorescences,  $\times 1$ ; b, staminate flower,  $\times 12$ ; c, carpellate flower,  $\times 12$ ; d, first year receptive carpellate flower in semidiagrammatic longitudinal section showing absence of ovules,  $\times 20$ ; e, mature acorn,  $\times 1\frac{1}{2}$ . f-h, *Q. rubra*: f, second year carpellate flower in semidiagrammatic longitudinal section

entire persistent leaves that are involute in bud, usually 6–8 stamens, and abortive ovules that are basal or lateral. Although *Q. chrysolepis* was placed by Rehder in subg. QUERCUS, and some of its characters are intermediate between the subgenera, both species seem best referred to ERYTHROBALANUS because of the silky tomentum on the inner surface of the acorn wall and the biennial fruits.

Four other species, including *Quercus myrtifolia* Willd., of the southeastern Coastal Plain (southern South Carolina to southern Florida, west to southern Mississippi), have similar leaf characters but differ (as do the remaining species of the subgenus) in having 4–6 stamens per flower, styles finally recurved, and the abortive ovules apical. Almost grading into the above group are five species of the southeastern United States, commonly known as the willow oaks, which have mainly entire, but deciduous leaves. These are *Q. Phellos* L., *Q. incana* Bartr. (*Q. cinerea* Michx., *Q. brevifolia* (Lam.) Sarg.), *Q. imbricaria* Michx., and *Q. pumila* Walt. Formerly thought to be a distinct species, *Q. × laurifolia* Michx. (*Q. hemisphaerica* Bartr., *Q. hybrida* (Chapm.) Small, *Q. obtusa* (Willd.) Ashe, *Q. rhombica* Sarg.) has recently been considered by Burk (1963) to be the hybrid of *Q. Phellos* and *Q. nigra*.

The other species of subg. ERYTHROBALANUS have deciduous, variously lobed leaves (except some *Quercus nigra* L. and *Q. ilicifolia* Wang.) that are convolute in bud. An almost complete gradation in lobing can be found from one species to another, from an entire leaf to a slightly three to five lobed (apically) leaf, to those with five shallow lobes, and eventually to those with five to nine to eleven deep lobes. Entire to three lobed leaves can be found in *Q. nigra* L. (*Q. microcarya* Small) and *Q. ilicifolia* Wang. (*Q. nana* (Marsh.) Sarg.), while slightly three to five lobed, usually obovate leaves are generally evident in *Q. marilandica* Muenchh. (*Q. neo-ashei* Bush), *Q. arkansana* Sarg., *Q. laevis* Walt. (*Q. Catesbaei* Michx.), and *Q. georgiana* Curtis. The leaves of *Quercus falcata* Michx., including var. *falcata* (*Q. triloba* Michx., *Q. elongata* Willd., *Q. digitata* (Marsh.) Sudw.) and var. *pagodifolia* Ell. (*Q. Pagoda* Raf., *Q. pagodifolia* (Ell.) Ashe, *Q. leucophylla* (Ashe) Ashe) show a condition that continues to the more deeply lobed leaves of *Q. coccinea* Muenchh.; *Q. velutina* Lam. (*Q. missouriensis* (Sarg.) Ashe); *Q. palustris* Muenchh.; *Q. ellipsoidalis* Hill; *Q. Shumardii* Buckl., with var. *Shumardii* (*Q. Schneckii* Britton) and var. *texana* (Buckl.) Ashe (*Q. texana* Buckl.); *Q. Nuttallii* Palmer; and *Q. rubra* L. (*Q. borealis* Michx. f., *Q. maxima* (Marsh.) Ashe). In the United States, the entire-leaved species of *Quercus* occur mainly in the southern United States, and there appears to be a trend toward the more lobed condition in the northern portions of the range of the genus.

Muller (1942) recognized 27 species as belonging to this subgenus in

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showing ovule formation,  $\times 8$ ; g, second year carpellate flower in semidiagrammatic cross section,  $\times 25$ ; h, mature embryo showing apically aborted ovules,  $\times 1\frac{1}{2}$ . i, j, *Q. imbricaria*: i, mature leaf,  $\times \frac{1}{2}$ ; j, mature acorn,  $\times 1\frac{1}{2}$ . k–n, *Q. nigra*: k, l, m, variation in mature leaves,  $\times \frac{1}{2}$ ; n, mature acorn,  $\times 1\frac{1}{2}$ .

Central America (from Chiapas, Mexico, through Panama). *Quercus Humboldtii* Bonpl., the southernmost of the American species, is found from Panama southward into the Colombian Andes. The taxonomy of the species of subg. ERYTHROBALANUS in Mexico is very poorly known, perhaps due to the paucity of fruiting collections.

Hybridization among species of *Quercus* has been known and discussed for many years. Numerous hybrids have been described, but only relatively recently has the critical study of the true nature of the putative hybrids been begun. Natural, usually fertile, hybrids between recognized species of *Quercus* are common, but the total number of hybrid combinations is uncertain, for several species (e.g., *Q. rubra*) are polytypic, and some recognized forms may prove to be only variants of a polytypic species. Palmer (1948) listed what he considered to be 75 certain hybrids and approximately 15 dubious ones. Muller (1955) questioned the actual existence of so many hybrids, for many were based on minor variations that probably fall within the variability of the supposed parental species. Unfortunately, many hybrids described between 1900 and 1950 were based primarily on a few specimens with no attempt to provide quantitative data supporting the putative hybrids.

It has been clearly shown that the species that are compatible and produce fertile hybrids are the more closely related ones. Although all species of *Quercus* counted have  $2n = 24$ , natural hybridization between species of the subgenera QUERCUS and ERYTHROBALANUS is unknown and not expected to be found, although Pjatnitzky (1946) was able to cross experimentally *Q. Robur* with *Q. borealis maxima* [= *Q. rubra*] and *Q. macranthera* with *Q. borealis maxima* and produce vigorous seedlings.

Hybrid individuals or populations are usually found in areas where the ranges of two species overlap or where they once overlapped but now do not. Muller (1953) demonstrated that *Q. Havardii* Rydb. (confined to deep sandy soils) and *Q. Mohriana* Buckl. (on limestone) will only come into contact where erosion of the sandy areas exposes the limestone. Hybrids are readily produced but are confined to soils composed of a mixture of sand and limestone. Several other studies have also shown that hybrids are better suited to "hybrid" habitats than to the edaphic conditions of either parent. Hybrids between two allopatric species whose ranges now do not overlap, *Q. macrocarpa* Michx. and *Q. Gambelii* Nutt., were interpreted by Maze (1968) to have occurred during a period in the past when the two species were partially sympatric. Pleistocene migration was believed responsible for the sympatry.

Some species of *Quercus* in our range are sympatric with others of the same subgenus but have not yet been shown to hybridize with them. Among these are *Q. pumila*, *Q. myrtifolia*, *Q. Chapmanii*, *Q. Nuttallii*, and *Q. oglethorpensis*. Whether the apparent absence of hybrids is due to insufficient study or whether these species are incompatible with others remains to be seen, but the former appears to be more likely.

Flowering is vernal, the flowers appearing shortly before, with, or shortly after the new leaves. The staminate inflorescences usually develop from

axillary buds of leaves of the previous season. Development of the staminate inflorescences of *Q. alba* is initiated in early summer (late June); the inflorescence initials overwinter and then complete development the following spring. In contrast, the solitary or paired carpellate flowers are borne in the axils of the leaves of the current season. In *Q. alba* the carpellate flower primordia do not appear until late summer or early fall, overwinter, and mature the following spring as the terminal bud expands.

The lightweight pollen, produced in enormous amounts and a major contributor to pollen allergies, is dispersed by wind. Sharp & Chisman (1961) reported that the mature anthers of *Q. alba* open or close, depending upon the relative humidity, high humidity and rain often delaying or reducing pollen shedding and dispersal and, consequently, lowering acorn production. The staminate inflorescences are sensitive in varying degrees to freezing temperatures and prolonged dry winds. Nearly complete pollen dissemination requires as little as a few hours in some of the shrubby oaks and as long as several days in the larger tree species. Although not sufficiently studied, individuals of the various species of *Quercus* are cross-pollinated, for the plants are partially or wholly self-sterile.

In subg. QUERCUS, pollen-tube development and subsequent fertilization usually occur soon after pollination. In *Q. alba*, and presumably other species, pollination occurs before the ovules are completely developed. Syngamy may be delayed for a month or more in *Q. alba* (Turkel *et al.*, 1955) depending on the time of maturation of the ovule. Following fertilization, one of the six ovules (the other five abort, basally) develops along with the other parts of the carpellate flower into a mature acorn in one season. Pollination and pollen-tube development also occur in the spring in subg. ERYTHROBALANUS, but fertilization in most species does not occur until the following spring. At the time of pollination, the ovules have not differentiated, and the entire ovary is rather undeveloped. By late spring, the ovule and placenta develop meagerly, but most of the development takes place the next spring. Fertilization of one of the ovules (the other five abort, usually apically) occurs approximately a year after pollination and the acorn matures in the fall of the second year.

Acorns of subg. QUERCUS generally require little or no dormancy and germinate soon after falling, if suitable environmental factors are present. The acorns of most species (temperate) of the subg. ERYTHROBALANUS appear to require a period of dormancy before germinating the following spring. Germination in both subgenera is hypogeal, the fleshy cotyledons remaining inside the pericarp. Polyembryonic acorns with two or very rarely three embryos per fruit, are known in *Q. Prinus*, *Q. alba*, *Q. rubra*, and *Q. Robur* and probably occur in many more species of *Quercus*. The embryogeny of *Q. Robur* and *Q. velutina* follows the onagrad type but with very irregular cleavage. The bitegmic ovule is crassinucellar. The formation of short branches in the pollen tubes of *Q. Robur* is noteworthy.

Oaks are the most abundant trees over most of the eastern United States and in parts of the southern forest. The most extensive association is the oak-hickory (*Quercus-Carya*) forest found through much of the

Piedmont and Inner Coastal Plain of the Atlantic States, the Gulf Coastal Plain, and westward to eastern Texas and north throughout most of the Mississippi River Valley (Shelford, 1963). Various combinations of oak and hickory species occur throughout the association, the most frequent species being *Q. alba* L., *Q. rubra* L., *Q. velutina* Lam., *Q. stellata* Wang., *Q. marilandica* Muenchh., and *Carya cordiformis* (Wang.) Koch, *C. ovata* (Mill.) Koch, and *C. laciniosa* (Michx. f.) Loud. Braun (1950), restricting the oak-hickory forest to the Interior Highlands, centered mainly around the Ozark and Ouachita mountain region, preferred to label the remaining area as the oak-pine forest, emphasizing the sometimes transitory, sometimes persistent nature of the pines in the southeastern United States. Bourdeau (1954) attempted to determine why certain species of *Quercus* are found in some oak-hickory associations but not in others. He found that *Q. alba*, *Q. velutina*, and *Q. rubra*, generally restricted to mesic upland areas, are eliminated from drier, more rocky areas because their seedlings are not very drought resistant. They are, however, more shade tolerant than *Q. marilandica* and *Q. stellata*, which are restricted to the thin, rocky soils with periods of drought and considerable exposure.

Other associations include the *Liriodendron-Quercus* forest found in the northeastern United States, the maritime live-oak forest usually found in a narrow band along the coastline where dune areas have become relatively stable (cf. Bourdeau & Oosting), and the oak-chestnut forest of the eastern United States formerly found in our range throughout much of the Appalachian Mountains.

Vegetative reproduction is of considerable ecological importance in semiarid regions, which are often unsuitable for seedling establishment (Muller, 1951). Clonal thickets are formed by rhizomatous branches in several species of *Quercus* (*Q. Hinckleyi* Muller, *Q. Havardii* Rydb., *Q. pyrenaica* Willd., *Q. Ilex* L., and *Q. virginiana*). The dwarf *Q. pumila* also spreads in this way. Muller considers the resulting increase in longevity to be an important factor in the ability to compete with the more xeric forms.

Far too many species of *Quercus* have been described from fossil leaf fragments. Apparently the first identifiable oaks are found in Upper Cretaceous deposits. The leaves of the earliest oaks were entire, toothed, or scarcely lobed. Since deeply lobed leaves comparable to those of many species of subg. *ERYTHROBALANUS* appear much later in the fossil record, this condition is probably derived in *Quercus*. The relationship between *Quercus* and the fossil genus *Dryophyllum* is clouded with misidentifications and the lack of a comprehensive paleobotanical study of the two genera. Berry (1923) thought that *Quercus* probably diverged from ancestral *Dryophyllum* stock at the end of the Lower Cretaceous or the beginning of the Upper Cretaceous.

The oak wilt disease, caused by a heterothallic ascomycete, *Ceratocystis fagacearum* (Bretz) Hunt, is a serious menace that spread rapidly from the Midwest to the eastern and southern United States. The disease usually appears in the uppermost branches of the tree and spreads down-

ward to the trunk and roots. Wilting is caused by the great production of tyloses that block the xylem vessels, but toxins are also produced and may be the ultimate cause of death. Large masses of hyphae can be found on the outer surface of the sapwood and on the inner surface of the bark. Asexual reproduction is by conidia and sexual by ascospores from perithecia. The disease is spread by root grafts of trees growing close together or by the asexual or sexual spores being carried by insects. Most, or perhaps all species of *Quercus* are susceptible, those of subg. ERYTHROBALANUS apparently more so than species of subg. QUERCUS. Insect damage often is a serious threat and has been shown by Nichols (1968) to be the main cause of mortality of *Q. Prinus* and *Q. alba* in Pennsylvania. Heart rot, frequent in trees following fire damage, often makes the wood useless for lumber.

*Quercus* is extremely important in the hardwood lumber industry, mature oaks being among the larger hardwood trees and yielding a hard, tough, yet durable, resilient and elastic wood that is used in heavy construction, shipbuilding, and in better furniture. Of the two subgenera, QUERCUS typically has harder, stronger and more durable wood than the species of ERYTHROBALANUS, in which the wood is softer, more porous, and more open-grained. The more important timber species of subg. QUERCUS include *Q. alba*, *Q. macrocarpa*, *Q. stellata*, *Q. montana*, *Q. Prinus*, *Q. Garryana*, and *Q. bicolor*; those of subg. ERYTHROBALANUS include *Q. borealis*, *Q. velutina*, *Q. coccinea*, *Q. palustris*, *Q. laevis*, *Q. phellos*, *Q. texana*, and *Q. imbricaria*. *Quercus virginiana* reportedly has the hardest, strongest, and toughest wood of all oaks and is highly prized. As early as the 19th century the United States government was making concerted efforts to insure that adequate supplies of *Q. virginiana* would be available for naval stores. The decrease in shipbuilding demands, extensive cutting, the slow growing nature of the species, and the restricted range limit the usefulness of *Q. virginiana* as a lumber source.

Acorns have been used as a food supplement and as forage for animals, especially hogs. Among the best species of *Quercus* utilized are *Q. alba* and *Q. virginiana*, the former species used by the American Indians in making flour. Species of subg. QUERCUS generally have a low tannin content in the acorns and, consequently, are more readily edible than those of subg. ERYTHROBALANUS, which have to be leached to remove the high tannin content to make them suitable for human consumption. All acorns are high in carbohydrates.

*Quercus Suber* L., native to the Mediterranean region of southern Europe and the source of commercial cork, has been introduced into the southeastern United States, where cork growing has hardly been successful commercially. This species is also an excellent ornamental shade tree, as are a number of other oaks, including the Japanese *Q. myrsinifolia* Blume and *Q. glauca* Thunb., of subgen. CYCLOBALANOPSIS, both of which are evergreen trees grown to a limited extent in the warmer parts of our area. As with other members of subg. CYCLOBALANOPSIS, the cupule with the scales connate in concentric rings is characteristic.



Elias, Thomas Sam. 1971. "The genera of Fagaceae in the southeastern United States." *Journal of the Arnold Arboretum* 52(1), 159–195.

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