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

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BETULACEAE S. F. Gray, Nat. Arr. Brit. Pl. 2: 243. 1821, "Betulideae," nom. cons.

(BIRCH FAMILY)

Small to large, columnar or pyramidal to spreading deciduous trees or shrubs; sap watery; branching excurrent to deliquescent; trunks and branches terete to irregularly longitudinally fluted, the branchlets terete, slender, often distichous, uniform or differentiated into long and short shoots. Bark close or exfoliating

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The illustrations were prepared by Arnold D. Clapman under an earlier grant from the National Science Foundation. Carroll Wood or Kenneth R. Robertson made the dissections and supervised the drawings. The materials used were from plants in the Arnold Arboretum, as well as from wild plants, with additional items from the Arnold Arboretum and Gray herbaria (A, GH). Dr. Elizabeth Wood collected some of the specimens for the illustration of *Alnus*.

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in thin layers, thin, smooth, often marked with prominent lenticels, sometimes becoming thick, corky, and rough, furrowed or scaly with age, often strongly tanniferous; young twigs glabrous to pubescent, sometimes covered with resinous glands, terminal buds lacking; leaf scars raised, with 3 vascular bundle scars; winter buds stipitate or sessile, narrowly to broadly ovoid, terete or sometimes angular in cross section, divergent, held parallel to the twig, or appressed, acute to rounded at apex, covered with 2 smooth, valvate (stipular) scales or few to many smooth or longitudinally striate imbricate ones [or occasionally naked]; nodes trilacunar; wood light brown to nearly white, diffuse porous, close grained, moderately soft to very hard; pith relatively small, homogeneous, triangular to circular in cross section. Leaves simple, petiolate, alternate, spirally arranged, 3-ranked to distichous; blades ovate to deltoid, elliptic, obovate, or suborbicular, coarsely to finely toothed, glabrous to sparingly pubescent adaxially, glabrous to tomentose and sometimes covered with resinous glands abaxially; venation pinnate, the secondary veins craspedodromous [or semicraspedodromous], divergent and straight to strongly ascending, the tertiary (cross) veins usually prominent; leaves conduplicate in bud, open and convex but becoming conduplicate as they expand, or open and concave; stipules present, free, broadly ovate to narrowly linear, deciduous. Plants monoecious, the flowers imperfect, anemophilous, much reduced. Inflorescences consisting of pendulous or erect catkins of reduced, 3-flowered cymules, or reduced to compact clusters of several minute flowers (florets); staminate catkins terminal or lateral on the branchlets, borne on either long or short shoots, solitary or in small to large racemose clusters, precocious [or developing during the current season], when formed the previous season exposed or enclosed in buds during the winter, elongate, cylindrical, pendulous, conspicuously bracteate, the scales and flowers densely to loosely arranged, the scales consisting of [(1–)]3–5 fused bracts; carpellate inflorescences terminal or lateral on the branchlets, borne on either long or short shoots, solitary or in small [to large] racemose clusters, precocious or developing during the current season, when formed the previous season exposed or enclosed in buds during the winter, consisting of short to moderately long, erect to pendulous, bracteate catkins or of small, compact clusters of flowers subtended by leafy involucres; scales and flowers densely to loosely arranged, the bracts [(1–)]3–5 per scale, becoming variously fused and often large and subfoliaceous or woody in the infructescences. Staminate flowers small, the perianth lacking or of 1–4(–6) minute tepals; stamens (1–)4(–6), in 1 whorl, sometimes appearing to be more due to development of part or all of additional flowers of the reduced cymule; filaments short, separate or partially to wholly connate, or sometimes divided part or all the way to the base; anthers tetrasporangiate, 2-locular, dorsifixed, extrorse, entire or partially to wholly divided from the apex, opening by longitudinal slits; pollen grains smooth or slightly granular, spheroidal to oblately flattened, angular, 15–45 μm in diameter, aspidote, poroid, the apertures (3 or) 4–7, circular to elliptic, equatorial, evenly spaced; rudimentary gynoecium usually absent. Carpellate flowers small, perianth usually lacking or highly reduced and adnate to the ovary; ovary compound, of 2 (or 3) carpels, inferior or nude (i.e., apparently inferior on the basis of vascular traces, but lacking a perianth), 2- (or 3-)locular below, unilocular above, with 2 (or 3) linear styles, these stigmatic above; ovules axile, 1 or 2 per locule, pendulous, anatropous, crassinucellar, unitegmic or bitegmic; staminodes usually absent; fertilization chalazogamous; endosperm nuclear, becoming cellular. Infructescences woody and strobiluslike or consisting of elongate to compact or irregular foliaceous clusters, the scales (bracts) persistent or deciduous, variously lobed and toothed. Fruits nuts, nutlets, or 2-winged samaras (sometimes with the wings reduced), maturing and dispersed the same season as or the season following pollination. Seed single, pendulous; endosperm present but thin at maturity; embryo large, straight, as long as the seed, the cotyledons small and flat, or greatly thickened, plano-convex, and oily; radicle superior. Embryo-sac development of the Polygonum type. Germination epigeal or hypogeal. Base chromosome numbers 7, 8. (Including Corylaceae Mirbel, Elem. **2:** 906. 1815, nom. cons., and Carpinaceae Kuprianova, Taxon **12:** 12. 1963.) Type genus: *Betula* L.

A family of six genera and about 150 species, primarily of the boreal and cool-temperate zones of the Northern Hemisphere, but also represented at high elevations from Mexico southward through Central America to northern Argentina. Despite its small size, the family includes dominant trees of forests of temperate Asia, northern Europe, northwestern North America, mountainous parts of Mexico, Central America, and northern South America, and the circumboreal region. Five of the genera occur in North America and are represented by one or more species in the southeastern United States. The remaining genus, *Ostryopsis* Decne. (most closely related to *Corylus* L.), consists of two species of shrubs restricted to northern and western China.

The Betulaceae are woody plants easily distinguished by their simple, pinnately veined, usually ovate, sharp-toothed leaves, their long, dense staminate catkins that often develop the season before anthesis, and (except in *Corylus* and *Ostryopsis*) their strobiluslike infructescences. The family is held together on the basis of many characters, including habit; leaf structure, venation, and arrangement; trichome morphology; wood anatomy; inflorescence morphology; ovary structure; ovule morphology and position; pollen morphology; embryo structure; chalazogamous fertilization; germination pattern; and serological reactions.

The Betulaceae are usually treated as a single family closely allied with the Fagaceae and placed with it in the order Fagales, although Hjelmqvist (1957, 1960) and Takhtajan (1969, but not 1980) placed the family in its own order, Betulales, on the basis of embryological differences, especially the presence of endosperm in the Betulales (since then shown to exist in both groups, as discussed below). The earliest natural post-Linnaean systems treated the genera of the Betulaceae, together with the elms, oaks, willows, and other amentiferous trees, as members of a single large assemblage (e.g., "Castaneae" of Adanson, "Amentaceae" of Jussieu). Adanson segregated the betulaceous and fagaceous genera into one of three "sections" of the Castanieae, corresponding to the modern Fagales. In most of the important subsequent work until that of Prantl (e.g., De Candolle; Regel (1861, 1868); and Spach (1841, 1842a–c)), the group was divided into two families, Betulaceae and Corylaceae Mirbel, following the lead of Linnaeus, who had placed *Betula* (including *Alnus* Miller) in the Monoecia Tetrandia, and *Carpinus* (including *Ostrya* Scop.) and *Corylus* in the Monoecia Polyandria. De Candolle, in his monograph of the Corylaceae, further divided that family into two tribes, Coryleae Meisner and Carpineae Döll. However, Prantl treated the entire group as a single family, Betulaceae, composed of two tribes, Coryleae Meisner and Betuleae, the system followed by Winkler in the most recent family monograph. Koehne also adopted this arrangement, but he elevated the tribes to subfamily status; this treatment has been accepted by a number of modern authors, including Jury, Rendle, Takhtajan (1980), and Thorne (1983). Bentham & Hooker combined the Betulaceae and Fagaceae into the single family Cupuliferae, in part based on a misunderstanding of the nature of the bracts subtending the fruits in these families (Abbe, 1974), but few have followed this path. The family is still sometimes divided into two families, the Betulaceae and the Corylaceae, and Kuprianova has proposed the further splitting of the Coryloideae into two families, Corylaceae and Carpinaceae, following De Candolle's tribes Coryleae and Carpineae. Particularly in Europe, the two-family scheme has been adopted by many authors, including Airy Shaw in Willis, Dahlgren (1975, 1977, 1980, 1983), Hjelmqvist (1957, 1960), Hutchinson (1959, 1967), and Jury. In America, it has been used by Mohlenbrock & Thomson, Rehder (1940), and Small (1903, 1933). Some of these treatments based recognition of two families in part on the belief that a fundamental difference exists in the staminate inflorescences of the two groups (there being three flowers, each consisting of one to six stamens per bract in the Betulaceae, and one flower, consisting of many stamens per bract in the Corylaceae). However, it has now been established that no such difference in staminate inflorescence structure exists in these two groups (see below). Most modern authors (e.g., Cronquist, 1981, 1988; Melchior; Takhtajan (1969, 1980); and Thorne, 1968, 1973, 1983) maintain the family as a single group. When one family is recognized, the name Betulaceae is conserved against Corylaceae.

The Betulaceae are treated here as consisting of a single family subdivided into two natural subfamilies, the Betuloideae and the Coryloideae (Regel) Koehne, these corresponding to the tribes Betuleae and Coryleae recognized by Prantl and Winkler. To reflect the substantial differentiation between *Carpinus* and *Ostrya* Scop. on the one hand, and *Corylus* and *Ostryopsis* on the other, the Coryloideae are further divided into two tribes, the Coryleae and the Carpineae Döll.

In an early analysis of generic affinities within the family, Anderson & Abbe found that species differences are consistently smaller than generic differences and are approximately equal from genus to genus. These authors noted an exception, however, in the case of *Carpinus* and *Ostrya,* which they concluded show less divergence than occurs among some of the subgroups within the genus *Betula.*

Where best to place the Betulaceae within the angiosperms has been a source of continuing disagreement, in part because of an unclear fossil record of the ancestors of the group. The Englerian tradition, following earlier authors such as Jussieu, placed the amentiferous families together in a relatively low position in the dicotyledons (see Stern). Bessey, perhaps in an overreaction to the apparent phylogenetic inaccuracy of the Englerian arrangement, gave the Betulaceae an exaggeratedly advanced level (in the Sapindales). Cronquist (1981, 1988), Melchior, Takhtajan (1969, 1980), and Thorne (1973, 1983) all placed the Fagales, along with other "core" orders of the Amentiferae, in a position more advanced than the magnoliids, less advanced than the rosids, and with close ancestral ties to the Hamamelidales. Dahlgren, in his early treatments (1975, 1977), adopted a similar scheme but placed the Hamamelidanae somewhat nearer the rosid groups. However, in the most recent versions of his system (1980, 1983), he joined the Fagales with the Juglandales, Saxifragales, and Rosales in the Rosiflorae. Taking a radically different view, Meeuse (1975a–c) maintained that the Amentiferae, including the Betulaceae, were not derived from a group having well-developed flowers but instead represent a fundamentally distinct line of evolution in the flowering plants. However, this position has received little acceptance.

There is disagreement on the phylogenetic arrangement of genera in the family. While virtually all authors recognize a fundamental dichotomy between the Betuloideae and the Coryloideae, and most believe the Betuloideae to be the less specialized, the arrangement of the genera within these groups is unsettled. Within the Betuloideae, *Betula* has traditionally (e.g., by Bentham & Hooker; Komarov; Prantl; Regel (1861, 1868); Spach (1841); Winkler) been placed before *Alnus*. However, modern workers (e.g., Furlow, 1979, 1983a; Hall; Kikuzawa; Takhtajan, 1969, 1980) generally consider *Alnus* the less specialized, and it has been treated accordingly in a number of recent floras (e.g., those by Scoggan; Soper & Heimburger; Voss). In the Coryloideae there is more confusion, and all possible arrangements of the four genera are found in the modern literature. Winkler, in part following Prantl, viewed *Ostryopsis* as most primitive, *Ostrya* and *Carpinus* as intermediate, and *Corylus* as most advanced. Bentham & Hooker and Hutchinson (1959, 1967), on the other hand, listed *Carpinus* as least specialized, followed by *Ostryopsis, Ostrya,* and *Corylus.* On the basis of wood anatomy and leaf and bud structure, respectively, Hall and Kikuzawa considered *Corylus* to be the most primitive and *Carpinus* the most advanced, a view first proposed by Tippo. Hjelmqvist (1948), from floral and fruit structure, and Hardin & Bell, on the basis of trichome morphology, viewed *Carpinus* as the most primitive and *Corylus* as the most advanced. Obviously, a detailed examination of this problem is needed. In a preliminary cladistic study using many features of a variety of types, Furlow (1983a) concluded that *Carpinus* was the least specialized, followed by *Ostrya* and *Ostryopsis,* with *Corylus* the most specialized.

The leaves of the Betulaceae are simple and pinnately veined, with nonglandular teeth of a modified urticoid type (L. J. Hickey & Wolfe). The secondary veins are generally characterized as uniformly craspedodromous (L. J. Hickey; L. J. Hickey & Wolfe). However, venation in members (mostly Asian) of *Alnus* subg. CLETHROPSIS (Spach) Regel is semicraspedodromous (Furlow, 1979), a unique condition in the Fagales, although the phylogenetic significance of this pattern has not been investigated. The basal secondary veins tend to be crowded in most genera of the family, especially in *Corylus* (Meyerhoff). Branches of the lower secondary veins ("outer secondaries") appear in all genera and run, like the secondaries, to teeth at the margin; regular and usually prominent tertiary veins connect the secondaries.

The general structure of vegetative features in the family has been treated by Boubier, Metcalfe & Chalk, and Solereder. The leaves of all genera are pubescent abaxially, although in individual species or populations they vary from glabrous to densely tomentose. Most betulaceous leaves have at least some hair, especially along the major veins and in the axils of the secondary veins. Hardin & Bell have studied the foliage of the five North American genera of the family in detail and have identified six distinct trichome types, including unicellular and multicellular hairs of several kinds, stipitate glands, and peltate scales (sessile glands). The four hair types are found in all five of the genera, tying the family together as a unit (Hardin & Bell). Most of these trichome types are also present in the Fagaceae (Hardin & Johnson), suggesting a close relationship between the Betulaceae and the Fagaceae. Large glands are frequent on the leaves and twigs of *Alnus* and *Betula* (Bell *et al.*; Furlow, 1979). It has been shown by Dorman that in *Alnus* these glands secrete a high-molecular-weight polyterpene and by Wollenweber that their product includes flavonoid compounds.

Several authors have sought the origin and phylogeny of the Betulaceae in the structure of their flowers and inflorescences (Abbe, 1935, 1938; Hjelmqvist, 1948; Korchagina) and in their embryology (Benson; Hjelmqvist, 1957; Nawaschin). In a comprehensive investigation of the floral and inflorescence anatomy and morphology of the family, Abbe (1935, 1938) proposed that the inflorescences consist of systems of reduced three-flowered cymules and hypothesized the loss of various bracts, flowers, and flower parts in various genera, leading to the present patterns. He argued (1935), on the basis of the position of the tepals or their vestigial vascular traces, that the ovaries of all members of the family are inferior, and he proposed that the bicarpellate ovaries of the various genera have arisen in several different ways: those in *Alnus, Betula,* and *Corylus* from loss of the carpel in the radius of the adaxial tertiary bract; those in *Carpinus* and *Ostrya* from loss of the carpel in the radius of the secondary bract. Hjelmqvist (1948) disagreed with the latter interpretation, concluding that the different positions noted were probably due only to twisting of the original transverse carpels. In a third paper Abbe (1974) reviewed the floral structure of the entire Amentiferae and argued that the Betulaceae form a single evolutionary unit with three clearly divergent lines, which he assigned to the tribes Betuleae, Carpineae, and Coryleae.

The distinctive ways in which individual catkins are clustered in various genera and infrageneric groups of the Betulaceae have been discussed by Furlow (1979), Hjelmqvist (1948), Jäger, and Murai. Jäger, expanding upon the ideas of Hjelmqvist (1948), proposed that the hypothetically ancestral synflorescence of the family consists of an axis bearing a terminal cluster of staminate catkins, with lateral clusters of carpellate catkins placed below it. This type resembles the form seen today in members of *Alnus* subg. CREMASTOGYNE Schneider in Sarg. and, in somewhat reduced form, *Alnus* subg. ALNUS. Jäger has traced the evolution of various synflorescence types occurring in most extant betulaceous genera, explaining their progressions by means of translocations of the shoot innovations into the synflorescence itself, tendencies to monopodial or sympodial proliferation of the synflorescence, reduction in size and number of catkins, and winter protection of carpellate catkins by bud scales. He has also shown that these changes correlate closely with vegetative adaptations related to severity of climate. In *Alnus* subg. Alnobetula Peterm., as well as in most subgroups of *Betula,* the tendency has been toward a monopodial form with a terminal staminate cluster, the carpellate clusters being held on lateral shoot innovations. However, in *Betula* sect. Humiles W. D. Koch the axes have diversified sympodially and have been reduced to a form in which solitary staminate catkins occupy a position below the carpellate ones on lateral short shoots. Sympodial modifications and reductions are seen as well in *Carpinus* and *Ostrya.* In *Carpinus* the solitary or clustered staminate catkins are located laterally below the terminal carpellate ones, while in *Corylus* this trend reaches its ultimate configuration: the staminate clusters are positioned laterally below reduced solitary carpellate inflorescences.

The Betulaceae are generally uniform in fruit structure, but each genus has distinctive modifications associated with dispersal by means of wind, water, or animals. The tiny, lateral-winged samaras of *Alnus* and *Betula* are carried great distances and in large numbers by air currents. In certain species of *Alnus,* these wings have been reduced or lost and the fruits are apparently dispersed mostly by water; they have been shown to float for long periods (McVean). The fruits of *Carpinus* and *Ostrya* are also scattered by wind, but with the aid of greatly expanded bracts rather than wings on the fruits themselves. The fruits of these genera are widely called both achenes and nutlets, but since their walls are quite bony and tightly attached to the enclosed seed, the latter is more appropriate (see Hjelmqvist, 1948). The most striking fruit modifications of the Betulaceae are seen in the dramatic adaptations of *Corylus* fruits for zoöchory (Stebbins; Stone).

The seeds of all the genera are similar in internal structure (with axile and investing embryos), a type regarded as advanced in the angiosperms (A. C. Martin). In the Betuloideae the embryos are somewhat less investing than in the Coryloideae, and thus they may be considered less specialized. In both groups several ovules are initially laid down (Hagerup), but only one of these develops. In the Coryloideae (as well as in the Fagaceae (Benson; Hjelmqvist, 1948)), but not in the Betuloideae, several embryo sacs may develop.

The wood of the Betulaceae has been studied by Bailey (1910, 1911, 1912), Forsaith, Hall, Hoar, and others. Bailey (1911) discussed the presence of aggregate rays in the wood of the Betulaceae and related families and proposed a phylogenetic series involving the development of large multiseriate rays from uniseriate ones. In a second paper (1912) he developed this concept further and demonstrated reversals to uniseriate rays in various species. Hoar concluded, on the basis of the presence of aggregate rays, that the family was extremely primitive in the dicots. A study of the wood anatomy of the Betulaceae by Hall showed the family to be "anatomically natural and closely knit" (p. 262) but with clear distinctions between the Betuloideae and Coryloideae. However, Hall did not speculate on whether these groups should be considered one family or two. He found the Betuloideae to be more primitive than the

Coryloideae in having relatively large vessels lacking spiral thickenings and having scalariform perforation plates. He also concluded that true tracheids were present in the Betuloideae and absent in the Coryloideae. However, Kasapligil and Yagmaie & Catling have shown the wood of *Carpinus* and *Corylus* to contain tracheids. Within the Betuloideae *Alnus* was seen by Hall as less specialized than *Betula* in terms of the number and spacing of the bars of the perforation plates and in the presence of opposite, as well as alternate, intervascular pitting. Within the Coryloideae he noted a trend of specialization leading from *Corylus* to *Carpinus* and then to *Ostrya,* this involving reduction in the number of bars of the perforation plates, an increased presence of spiral thickenings on vessel walls, and other characters.

Brunner & Fairbrothers concluded from serological investigations of the six genera (but based on very limited sampling) that these groups held together well and should be treated as a single family. Petersen & Fairbrothers showed the Betulaceae as a whole to be closely related to members of the Fagaceae, Myricaceae, and Juglandaceae on serological grounds, with members of the Anacardiaceae, Aceraceae, Moraceae, Oleaceae, and other families of rosid affinity forming a very distant group. Other than this, there is little positive chemical evidence demonstrating relationships between the Betulaceae and other amentiferous families (Mears).

The Betulaceae are well known cytologically (Jaretzky; Wetzel, 1927, 1928, 1929; Woodworth, 1929a–c, 1930a, b, 1931). Chromosomally, the family consists of groups that do not correspond to the tribes or subfamilies (Raven). The base chromosome number of *Betula* and *Corylus* is 14, while that of *Carpinus, Ostrya,* and *Ostryopsis* is eight. *Alnus,* usually placed in the $x = 14$ group with *Betula* and *Corylus,* was suggested by Furlow (1979), after a count by Chiba, to have a base number of seven, the probable original base number of the Fagales (Raven). This number had previously been predicted for the family by Woodworth (1931) and by Wanscher. An allozyme study of *A. viridis* subsp. *crispa* ($2n = 28$) by Bousquet and colleagues (1987) indicated that this species could be treated either as a diploid or a diploidized autotetraploid. Additional study of *A. incana* subsp. *rugosa* by these authors also revealed diploidlike expression for all polymorphic allozyme loci (Bousquet *et al.,* 1988), and additional indirect evidence for a base number of seven has been provided by Brown & Al-Dawoodie, who found that meiotic behavior in hybrid birches suggests that $2n = 42$ trees actually represent hexaploids.

The Betulaceae are an ancient group, extending back in the fossil record to the Upper Cretaceous on the basis of both leaves and pollen. Fossils assigned to the family become abundant in strata of Paleocene and Eocene age in both the New and the Old worlds. This record has been summarized by Crane (1981), Crane & Stockey, Crepet, and Wolfe (1973). Members of the Betuloideae first occur in the Upper Cretaceous (Maestrichtian); coryloid types in the lower Paleocene. Evidence that *Betula* had diverged from *Alnus* by the mid-Eocene is provided by Crane & Stockey, and fossil evidence from northwestern North America indicates that the subgenera of *Alnus* had differentiated and were present in the New World during the Miocene if not before (Wolfe, 1969).

The ancestor of the Betulaceae is not obvious from the features of other extant families. On the basis of floral structure, Abbe (1938) tentatively suggested the Fagaceae as the most likely candidate, but in spite of the similarities, there are important differences between the two families, including the structure of the carpellate inflorescences and the presence of a "stem cupule" around the fruits. Takhtajan (1969) believed that the Betulaceae share a common ancestry with the Fagaceae but are not derived directly from them. Hjelmqvist (1948) concluded that the Betulaceae are not closely related to the Fagales, but that they show significant connections to the Juglandaceae in floral coalescence, chalazogamy, and other basic features. He believed that the two major subgroups of the family are closely related, although one probably did not originate directly from the other: the distinctive lines of specialization within each group, such as differences in the fruits and the involucre, indicated rather that they had developed from a common ancestor.

Tippo first suggested that the Betulaceae may have been derived from hamamelidaceous stock, and many modern workers have adopted this position. Endress (1967, 1977) emphasized that the Hamamelidales combine features of the mainly insect-pollinated Cunoniales and Rosales with those of the wind-pollinated Fagales and argued that the Betulaceae and Fagaceae may be derived from a *Corylopsis*-like hamamelid ancestor. Ehrendorfer concluded that the Hamamelidae, including the Hamamelidales and the Fagales, can be regarded as remnants of an ancient stock of dicots linking the Magnoliidae and the Rosidae-Dilleniidae, but with tendencies toward anemophily and floral reduction.

Doyle has suggested that the ancestor of the more advanced Hamamelidae (including the Betulaceae) may have been a member of the Normapolles complex, known from its psilate, complex-walled, tricolporate pollen, which first appeared during the Cretaceous and reached a peak in the Santonian, and which seems to have been adapted for wind pollination. However, the pollen of modern Betulaceae is much more specialized than that of the modern Hamamelidales (L. J. Hickey & Doyle; Walker & Doyle). This has been used to support the view that some groups of modern Amentiferae (e.g., the Juglandaceae) may have a rosid, rather than a hamamelid, ancestor.

There is fossil evidence that the unlobed, pinnately veined leaves of the Hamamelidae are of secondary derivation from a platanoid ancestor with palmately veined and lobed leaves (L. J. Hickey & Wolfe; Wolfe, 1973). In *Corylus* the basal secondary veins often tend toward an actinodromous condition, rising abruptly toward the apex, where there is a suggestion of lobing. This intriguing pattern (which can sometimes also be seen to varying degrees in other Betulaceae—e.g., in *Alnus viridis* subsp. *sinuata* (Rydb.) Löve & Löve) resembles that of the hamamelidaceous *Corylopsis* (Wolfe, 1973) and may represent a remnant of a primitive venation pattern. However, such venation is also explicable by relatively minor structural adjustments to the ordinary form of the extant Fagales (similar distortions to the apical parts of the leaves of several species of *Alnus* have been reported by Furlow, 1979). Kasapligil (p. 85) explained the pattern in *Corylus* as "due to the auriculate condition of the cordate [base] of blades and the abrupt acuminate form of the leaf apices." Wolfe (1973) pointed out that in toothed primitive Juglandaceae, the secondary veins vary from a craspedodromous pattern, the teeth being entered along the apical side by a branch from the secondary vein. He concluded (p. 351) that these leaf features "do not conform to any known specialization of venation elsewhere in the Hamamelididae but rather are highly similar to members of Rosidae." The similar pattern in *Alnus* subg. CLETHROPSIS may provide a significant connection. Wolfe thought that, although the paleobotanical and palynological evidence favors a Normapolles ancestor for the Juglandaceae, it would be difficult to reconcile such an origin for the Fagales with a close relationship between the Fagales and the Hamamelidales, as has been implied by most modern classifications. He offered the alternate hypothesis that the Betulaceae and their closely related amentiferous allies may have converged on the Normapolles group in their pollen morphology. These patterns will become clearer only as additional paleobotanical evidence accumulates.

Although the family is old, it is neither particularly unspecialized nor greatly advanced. On the basis of wood anatomy, Hall found the Betulaceae to be moderately specialized relative to other woody angiosperm families. Sporne, in reviewing the degree of specialization of the flowers of a number of amentiferous taxa, found that for the Betulaceae 60 percent of the included characters could be considered primitive, compared with values of 88, 70, and 46 percent for the Magnoliaceae, Fagaceae, and Hamamelidaceae, respectively. Moseley, in a similar comparison but using both floral and vegetative characters, arrived at a figure of 43 percent for the Betulaceae, with values ranging from 27 (Ulmaceae) to 64 percent (Myricaceae).

The most obvious evolutionary trends within the Betulaceae are those related to fruit dispersal, as discussed above, and those correlated with apparent adaptations for survival in cold climates. The latter include shrubby growth forms, small leaves with few lateral veins, protection of the carpellate catkins during the winter by bud scales, and presence of true bud scales on the winter buds (Furlow, 1979; Jäger; Kikuzawa). These trends are identifiable in all of the genera of the family. Some of the related anatomical reductions involve retention of juvenile characteristics (Forsaith; Hall).

Members of the Betulaceae are economically important as timber trees, as the source of hazelnuts and filberts (*Corylus*), as ornamental trees and shrubs, and as an aid in soil nitrification and stabilization (*Alnus*). Some are important as causes of pollen allergies in regions where they grow abundantly (Dalen & Voorhorst; Lewis *et al.*; Løwenstein *et al.*; Solomon & Durham; Wodehouse, 1945). The bark of some contains substances of medicinal value (Lewis & Elvin-Lewis; Moerman). Wood of *Betula* and *Alnus* is widely used in the manufacture of furniture, paneling, boxes, and small wooden objects; that of *Carpinus* and *Ostrya* is used for making wooden tools such as mallets. In the past the bark of *Betula* has served as a commercial source of oil and methyl salicylate. The wood of several of the genera is used in the manufacture of high-quality charcoal.

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KEY TO THE SUBFAMILIES, TRIBES, AND GENERA OF BETULACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *monoecious, anemophilous, deciduous trees or shrubs; leaves simple, petiolate, pinnately veined, serrate or doubly serrate to subentire, ovate, elliptic, or obovate, alternately arranged, with deciduous stipules; staminate flowers reduced to (1–)4(–6) stamens and an equal number of tiny, scalelike tepals (or these absent), borne in scale-covered, pendulous catkins generally formed the growing season before anthesis; carpellate flowers usually consisting of a single inferior ovary composed of 2 (or 3) carpels, adnate to several tepals (when present), containing 2 locules below and 1 above, with 2 (or 3) linear stigmatic style branches, the ovules 2, parietal, borne near the summit, (except in* Corylus*) in usually uncrowded catkinlike, bracteate clusters; infructescences often strobiluslike, with large, conspicuous bracts; fruits 2-winged samaras, nutlets, or nuts.*

A. Staminate flowers with several scalelike tepals, carpellate flowers without a perianth; carpellate flowers 2 or 3 per bract in the inflorescence; ovules apparently unitegmic; infructescences 10–40 mm long, conelike, composed of many small, crowded, woody or coriaceous scales, each derived from several fused inflorescence bracts, these deciduous with the fruits or persistent; fruits small and laterally winged (the wings sometimes reduced to ridges) (subfamily Betuloideae).
  - B. Stamens generally 4, entire; carpellate flowers 2 per bract; infructescence scales with (4 or) 5 lobes, greatly thickened, woody, and persistent long after release of the fruits. .... 1. *Alnus.*
  - B. Stamens 2, bifid below the anthers; carpellate flowers 3 per bract; infructescence scales with (1–)3 lobes, thickened but not woody, deciduous with the release of the fruits. .... 2. *Betula.*

A. Staminate flowers lacking tepals, carpellate flowers bearing several scalelike tepals; carpellate flowers 2 per bract in the inflorescence; ovules bitegmic; infructescences larger, consisting of relatively uncrowded clusters with large subfoliaceous bracts, these deciduous with the fruits; fruits tiny to moderately large nuts, not winged (subfamily Coryloideae).
  - C. Leaves narrowly ovate to elliptic, veins 10 or more; infructescences elongate, loosely arranged spikes of 3 or more pairs of leafy bracts, these each either subtending or enclosing a single nutlet (tribe Carpineae).
    - D. Infructescence bracts flat, open, 1- to 3-lobed and variously toothed. .... 3. *Carpinus.*
    - D. Infructescence bracts forming inflated bladders, these completely enclosing the fruits. .... 4. *Ostrya.*
  - C. Leaves broadly ovate to suborbicular, veins 8 or fewer; infructescences irregular clusters of several small to moderately large nuts, these each surrounded by an involucre of several coarsely toothed leaflike bracts, the involucre sometimes long and tubular (tribe Coryleae). .... 5. *Corylus.*

Subfamily BETULOIDEAE

Tribe BETULEAE

1. **Alnus** Miller, Gard. Dict. abr. ed. 4. [alph. ord.] 1754.

Small to large shrubs [or small to medium-sized pyramidal to round-crowned trees], usually with several trunks; branching excurrent to deliquescent, when excurrent, often becoming deliquescent in age; trunks and branches terete, the branchlets and twigs subdistichous to diffuse; twigs sometimes differentiated into pronounced long and short shoots (subg. ALNOBETULA). Bark close, thin and smooth [to thick, furrowed, and corky], when smooth usually dark and marked with prominent pale lenticels, these sometimes becoming elongate horizontally; young twigs glabrous or sparingly pubescent, often covered with resinous glands; leaf scars triangular to crescent shaped, with 3 more or less equidistant, deeply crescent-shaped vascular bundle scars; winter buds long stalked or subsessile, narrowly to broadly ovoid or elliptic, terete, often held more or less parallel to the twig, the apex acute to rounded, with 2 valvate (stipular) or several imbricate scales [or sometimes naked]; wood fine grained, nearly white, turning reddish upon exposure to air, moderately soft, moderately light in weight; pith triangular in cross section. Leaves 3-ranked to subdistichous, borne on long [or short] shoots; blades thin [to very leathery], ovate to elliptic or obovate, doubly serrate, serrate, serrulate [or subentire], abaxially glabrous to tomentose, sometimes covered abaxially with resinous glands; secondary venation craspedodromous [or semicraspedodromous], mostly divergent and straight; leaves open and convex in bud, becoming conduplicate and plicate upon expansion; stipules broadly ovate [to narrowly linear]. Staminate catkins terminal [or lateral in leaf axils near the ends of branchlets], [solitary or] in racemose clusters, formed during the previous growing season and exposed [or enclosed in buds] during the winter, expanding before or with the leaves [or (in subg. CLETHROPSIS) formed and expanding during the same growing season], crowded, the scales ovate, consisting of 5 fused bracts; carpellate catkins lateral, below the staminate, either on short shoots or laterally in leaf axils on long shoots, [solitary or] in small [to large] racemose clusters, developing and maturing at the same time as the staminate, exposed or enclosed within buds during the winter, short, ovoid to ellipsoid, firm and erect to subpendulous, crowded, the scales composed of 5 fused bracts. Staminate flowers 3 per scale in the catkins, each with (3 or) 4(–6) scalelike tepals and an equal number of stamens, these borne opposite the tepals, undivided; pollen grains flattened, 19–27 μm in diameter, strongly aspidote, with (3 or) 4 or 5 (or 6) elliptic equatorial apertures connected by conspicuous pairs of thickened bands (arci). Carpellate flowers sessile, normally 2 per scale, rarely with 1 or more staminodes or vestigial tepals (the latter, when present, adnate to the ovary); ovule 1 by abortion, unitegmic. Infructescences ellipsoid, ovoid [or short-cylindrical], strobiloid, conelike, borne [singly or] in racemose clusters, erect and subsessile or pendulous on long, thin peduncles, the bracts connate into woody, 5-lobed scales, these persistent until after dispersal of the fruits. Fruits small, ellipsoid to ovoid, rostrate samaras, maturing and dispersed the same season as [or the season following] pollination, the styles persistent, the wings 2, lateral, membranaceous, reduced in some species, the pericarp thin. Seeds with membranaceous testa and flat cotyledons; germination epigeal. Chromosome numbers $2n = 14, 28, 42, 56$. LECTOTYPE SPECIES: *Alnus glutinosa* (L.) Gaertner; see Furlow, Rhodora **81:** 74. 1979. (The ancient Latin name for the alder, used by Virgil, Pliny, and others; derived from *alo,* to nourish, in reference to its usual close association with water.)—ALDER.

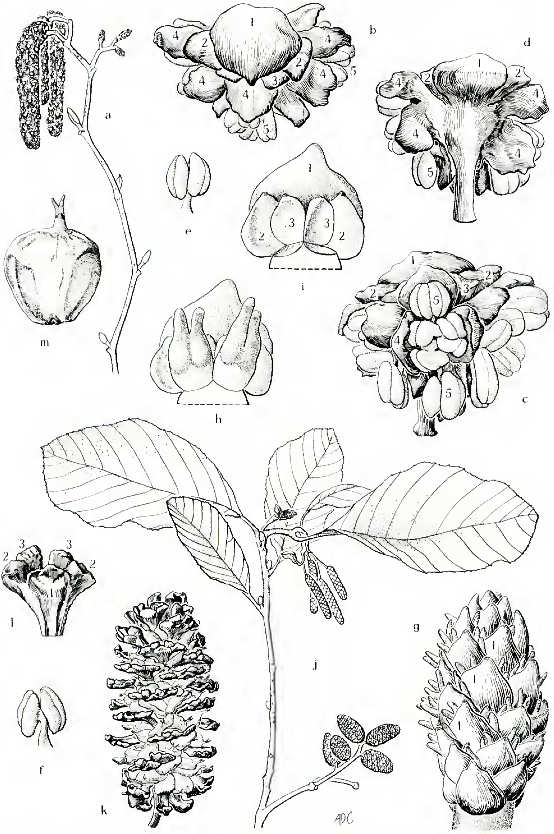

FIGURE 1. **Alnus.** a–m, *A. serrulata*: a, flowering branchlet, pendent staminate catkins at upper left, carpellate catkins at upper right, × ½; b, flowering staminate cymule oriented as on catkin in "a," primary, secondary, and tertiary bracts (1, 2, 3) visible along with tepals of 3 flowers (4) and tips of anthers of 2 of these (5), × 8; c, staminate cymules of

About 25 species of forested parts of the temperate and boreal Northern Hemisphere and Central America south to northern Argentina at high elevations. The alders resemble the birches but are easily distinguished from them by their infructescences, which consist of persistent woody scales with five lobes (vs. thin, deciduous, three-lobed scales). Except in members of subg. ALNOBETULA (which have subsessile buds with several true scales), they are also distinctive in having stipitate buds with two stipular scales. The fruits, borne two to a scale, are laterally winged, although the wings are sometimes reduced (occasionally to mere ridges).

The alders have been variously combined and split at the generic level by many authors. Linnaeus and his immediate followers combined *Alnus,* as used by Tournefort and Linnaeus himself in the first edition of *Genera Plantarum,* with *Betula,* while Czerepanov, Ledebour, Murai (1963), Spach (1841), and others have treated the present subgenera as genera. However, historically and currently the genus has most widely been held to constitute a single natural entity. In addition to the family monographs, taxonomic work in *Alnus* has included a series of descriptive papers by Callier (1892, 1911, 1918), synopses by Czerepanov and Murai (1964), and a revision of the American taxa by Furlow (1979).

The genus is diverse, including four distinct lines of specialization. These are sometimes given generic status but are here treated as subgenera (ALNUS, ALNOBETULA, CLETHROPSIS (Spach) Endl., and CREMASTOGYNE Schneider in Sarg.). Subgenera ALNUS and ALNOBETULA are further divided into sections, detailed below. Seven native (and several naturalized) species representing three of the four subgenera occur in North America north of Mexico, with an additional two being distributed throughout the mountains of Mexico, Central America, and northern South America (Furlow, 1979). Species of subg. CREMASTOGYNE, characterized by stipitate two-scaled buds, solitary axillary staminate and carpellate catkins, long-pedunculate infructescences, and fruits with broad hyaline wings, are restricted to south-central Asia.

Subgenus ALNUS is characterized by a shrubby or arborescent habit, winter buds with long stalks and two valvate (stipular) scales, inflorescences borne in racemose clusters, and development of both carpellate and staminate inflorescences (which are exposed during the winter) during the growing season prior to anthesis. Its most unspecialized segment (sect. PHYLLOTHYRSUS Spach) con-

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3 flowers, adaxial view, central flower seen from above, its 4 tepals (4) and 4 stamens (5) visible, bracts at top of illustration as in "b" (1, 2, 3), ×8; d, staminate cymule, abaxial surface, 2 lateral flowers seen from side, tepals (4) and stamens (5) partly visible, bracts as in "b" and "c," ×8; e, f, stamens, showing short filaments and partial division of anthers, ×8; g, carpellate catkin at anthesis, each scale subtending 2 flowers, only primary bracts (1) and paired stigmas visible, ×10; h, adaxial view of carpellate cymule with 2 flowers (ovaries undeveloped), bracts partially visible, ×20; i, scale with flowers removed to show primary, secondary, and tertiary bracts (1, 2, 3), ×20; j, late-season branchlet with mature infructescences and next season's carpellate catkins above and staminate ones pendent, ×½; k, infructescence with mature fruits (stippled), ×3; l, mature infructescence scale, abaxial surface, showing 5 lobes derived from primary, secondary, and tertiary bracts (1, 2, 3), ×6; m, mature fruit, style remnants at summit, ×8.

sists of large trees of western North America, Mexico, and Central America (*Alnus acuminata* HBK., *A. jorullensis* HBK., *A. oblongifolia* Nutt., and *A. rubra* Bong.), while sect. ALNUS (subg. *Gymnothyrsus* (Spach) Regel; sect. CLETHRA W. D. Koch) includes shrubby, more northern forms. In the United States and Canada sect. ALNUS is represented by four taxa. *Alnus incana* (L.) Moench subsp. *rugosa* (Du Roi) Clausen and subsp. *tenuifolia* (Nutt.) Breitung, large shrubs of riverbanks and marshy areas, occur throughout the cooler portion of the Temperate Zone across the continent. In the East subsp. *rugosa,* speckled or tag alder, characterized by dark, lenticel-speckled bark and ovate to elliptic, coarsely doubly serrate leaves, is more or less confined to the region north of the glacial boundary. Subspecies *tenuifolia,* thinleaf or white alder, distinctive in its lighter bark and smaller leaves with more evenly spaced and less acute teeth, is distributed across much of northwestern Canada and through the western mountains as far south as central California and New Mexico. Additional subspecies occur at equivalent latitudes in Europe and Asia. *Alnus serrulata* (Aiton) Willd., smooth alder, occurs throughout the Atlantic and Gulf coastal plains, in the southern Appalachians and the Ozark Highlands, and northward in the Mississippi Embayment. Its leaves are large, somewhat leathery, elliptic to obovate, and serrulate or finely and irregularly doubly serrate. The distribution of this species is essentially coastal, but it reaches north to central Ohio and Indiana in the interior, and to New York and Massachusetts in the East. Disjunct populations occur along the St. Lawrence River and the lower Great Lakes to southern Lake Michigan. The remaining species, *A. rhombifolia* Nutt., white alder, is a small tree of riverbanks and canyons in mountains of the western United States.

Subgenus ALNOBETULA consists of shrubby species of regions with cold climates. It has sometimes been segregated as a separate genus, *Alnaster* Spach (*Alnobetula* Schur, *Semidopsis* Zumaglini, *Duschekia* Opiz; see Furlow, 1979). In this group the buds are subsessile and covered by several imbricate scales. Both staminate and carpellate catkins are formed the season before anthesis, but only the staminate ones are exposed during the winter. In North America it is represented by the circumpolar *Alnus viridis* (Chaix) DC. in Lam. & DC. In the Northeast the transcontinental, far-northern subsp. *crispa* (Aiton) Turrill, green alder, occurs along the Appalachian Mountains at progressively higher elevations southward to central New York and Massachusetts, with disjunct populations in southern Pennsylvania (Wherry) and on the summit of Roan Mountain on the Tennessee–North Carolina border (Brown; Clarkson; A. Gray, 1842). It grows along streambanks and also in rocky and drier sites in colder climates. This subspecies is recognizable by its medium-sized, ovate, serrulate or finely serrate, usually glutinous leaves and its subsessile buds with more than two scales.

In western Canada, and southward in the mountains of the Northwest, subsp. *crispa* is replaced by subsp. *sinuata* (Regel) Löve & Löve, Sitka alder, a large shrub with larger, broader, thinner, more coarsely toothed leaves. This subspecies occurs along streams and frequently covers moist mountain slopes near the timberline, especially where landslides have created open areas. Subspecies *fruticosa* (Rupr.) Nyman is distributed from coastal Alaska to British Columbia, Washington, Oregon, and northern California, as well as across the Bering Strait in northeastern Asia (Furlow, 1983b). Its vegetative morphology somewhat resembles that of subsp. *crispa,* with which it has sometimes been confused in the past. Subspecies *viridis* is distributed throughout the mountains of western Europe.

The predominantly Asian subg. CLETHROPSIS is represented in America by a single species, *Alnus maritima* Muhl. ex Nutt., a small tree of stream banks, marshes, and the shores of shallow lakes. Its distribution is limited to two widely disjunct populations, one on the Delaware-Maryland-Virginia peninsula and the other in south-central Oklahoma (Furlow, 1979; Stibolt). Members of subg. CLETHROPSIS are unique in that they bloom in autumn, rather than in spring. They also differ from other native species in having essentially naked buds, leaves with semicraspedodromous venation, and solitary carpellate inflorescences borne in the axils of foliage leaves. This group was considered to be the most primitive one in *Alnus* by Murai (1963) and Takhtajan (1969) on the bases of morphology and phytogeography. However, Furlow (1979) concluded that many of its distinctive structural and life-history features represent derived conditions, and he placed it in a moderately advanced position in the family. Van Steenis, following Regel, has treated populations of the Asian *A. japonica* (Thunb.) Steudel as conspecific with American *A. maritima.* However, no critical comparison of the two has been made to determine the soundness of that arrangement.

Alnus serrulata, a common shrub along open streambanks throughout the region, was erroneously called *A. rugosa* by Britton & Brown (1896, 1913), Robinson & Fernald, and Small (1903, 1933) (see also Fernald, 1945a), and misapplication of the name *A. rugosa* continues in a few floras and herbaria. *Alnus incana* subsp. *rugosa,* a related taxon reaching its southern limit in West Virginia in the mountains and in Maryland on the Coastal Plain, hybridizes with *A. serrulata* where their ranges overlap, and extensive and often unrecognized hybrid swarms are formed (Furlow, 1979; Steele). From the results of a serological study (based on limited material taken entirely from the region of geographic overlap), Villamil & Fairbrothers concluded that the two taxa constitute a single species. Woodworth (1929a, 1930a) described apomixis from populations of *A. serrulata* (which he called *A. rugosa*) taken from this swarm. However, in a later paper (1931), he showed that populations located away from the region of intergradation have normal cytological characteristics. The two species are not difficult to distinguish in the field outside the region of overlap. *Alnus serrulata* has elliptic to obovate leaves, often with rounded apices and with very small teeth, while *A. incana* subsp. *rugosa* has ovate to elliptic leaves with acute apices and usually coarse, doubly serrate margins. The species are also distinguishable by the dark, rather shiny red-brown bark marked by prominent light-colored lenticels in *A. incana* and the dull, uniform light gray or light brown-gray bark with inconspicuous lenticels in *A. serrulata.*

The least-well-understood segments of the genus, with respect to the diversification and relationships of the genus as a whole and to the circumscription of individual species and infrageneric groups, are those occurring in Latin America and China. The Latin American species, all members of subg. ALNUS sect. PHYLLOTHYRSUS, were mostly described by Bartlett and Fernald (1904a), who were later followed by Standley. Furlow's (1977, 1979) study of this complex showed the many species and varieties to constitute two species consisting of a number of somewhat incompletely differentiated geographic and ecological races. He concluded that this group demonstrated many of the most unspecialized characters in the genus and represented remnants of a very old introduction from Asia, possibly dating from the Miocene or earlier. The relationships of the Asian taxa, particularly of species of subgenera CLETHROPSIS and CREMASTOGYNE, to the better-known American and European species, have not been taken sufficiently into account by Western taxonomists. These species will need to be studied thoroughly before many questions regarding the origin and diversification of the genus can be answered.

The shrubby habit of the northern and eastern North American alders is regarded as a specialized condition that evolved in response to harsh northern winters. The species of more equable regions (e.g., the Pacific Northwest, the mountains of Latin America, and the foothills of the Himalayas) become large trees and develop relatively thick, corky bark. It has been shown by both Forsaith and Hall that some shrubby species of *Alnus* retain juvenile wood characters, suggesting that the shrub habit was derived through neoteny. The existence of the shrub habit in several divergent lines within the genus suggests that it has arisen independently several times.

Leaves of species other than those in subg. CLETHROPSIS are rather uniform in morphology, varying mostly in size, general shape, and size of the serrations. Occasionally forms with deeply cut leaves occur naturally (see Hylander, 1957a), and these have attracted horticultural interest. In leaf venation and margins species of subg. CLETHROPSIS differ both from other *Alnus* subgroups and from other Fagales. The teeth are small, distant, and single (although on the basis of secondary vein endings, they are apparently derived from a doubly serrate form). The secondary veins branch before reaching the tooth: one of the branches enters the tooth along its apical edge, and the other connects with another vein or ends in the adjacent tooth. The tertiary (cross) veins are poorly developed in relation to those in other species.

The leaves of *Alnus*, like those of the other Betulaceae, bear trichomes of various types, including simple hairs, which are sometimes extremely dense on the abaxial surface, as well as both stipitate and sessile glands (Furlow, 1979; Hardin & Bell). In some taxa (e.g., *A. jorullensis* subsp. *lutea* Furlow and *A. viridis* subsp. *crispa*) these glands are large and conspicuous under magnification and have been given diagnostic status (e.g., by Standley). However, the great variability in the presence and prominence of the glands, like the variation in leaf pubescence, renders their use for identification largely ineffective (Furlow, 1979).

The wood anatomy of *Alnus* is the least specialized in the family (Hall). It is similar to that of *Betula* (e.g., some species have opposite intervascular pitting, perforation plates with many scalariform bars, and vessels usually frequent and small (Furlow, 1979; Hall)), although certain species are characterized by more advanced features. *Alnus viridis* appears to be the most specialized of the American species, while *A. incana* and *A. serrulata* are of intermediate advancement (Furlow, 1979) and *A. maritima* contains a mixture of primitive and advanced features.

The structure of the flowers and inflorescences of *Alnus,* together with their various adaptive trends, have been elucidated by Abbe (1935, 1938) and Hjelmqvist (1948). The staminate catkins consist of helically arranged cymules of three sessile flowers. Subtending each cluster are one primary, two secondary, and (usually) two tertiary bracts. Each flower consists of from (one to) four to six tepals and stamens (usually four in subg. ALNUS), with the stamens opposite and adnate to the tepals at the base. Where six tepals are present, these are borne in two whorls of three (Abbe, 1935). The thecae are connate or slightly separated by a short, forked connective. The short carpellate catkins consist of extremely crowded cymules of two flowers (apparently reduced from three, as seen in *Betula*) and are subtended by a scale made up of the same five bracts that subtend the staminate cymules. The ovaries were characterized as "nude" (apparently inferior on the basis of vascular traces, but lacking a perianth) by Abbe (1935). The staminate inflorescences are comparable to those of *Betula,* except that the tertiary bracts have been retained. In comparison to *Betula,* the carpellate cymules are specialized in having lost the secondary (central) flower, but primitive in having retained their tertiary bracts.

A simple progression of forms in the genus leads from racemose clusters of catkins (the carpellate borne below the staminate) to solitary axillary catkins by reduction (Furlow, 1979; Jäger; Hjelmqvist, 1948; Murai, 1964). In subgenera ALNUS and ALNOBETULA the staminate and carpellate catkins occur in separate clusters on different shoots; however, the carpellate catkins are produced on new growth in the spring in subg. ALNOBETULA, while they are formed the season before anthesis in subg. ALNUS. *Alnus maritima* has clustered staminate and solitary carpellate catkins (occurring on the same shoot). Murai (1963) viewed this condition as primitive; however, Furlow (1979) argued that the solitary carpellate inflorescences of subg. CLETHROPSIS are most likely of secondary origin by reduction of flowering branch systems such as those seen in subg. ALNUS.

The genus has been studied cytologically by Gram and colleagues, Jaretzky, Poucques, Wetzel (1927, 1928, 1929), and Woodworth (1929a, c; 1930a). All of the American species for which data are available have chromosome numbers of $2n = 28$. Other members of the genus form a polyploid series of $2n = 14$, 28, and 56, with several counts of $2n = 42$, these apparently having originated through hybridization between $2n = 28$ and $2n = 56$ types (see Furlow, 1979). The base chromosome number of *Alnus* ($x = 7$) is based on a single report (Chiba), but this is also supported indirectly by other cytological evidence (Brown & Al-Dawoodie) and the results of allozyme studies (Bousquet *et al.,* 1987a, 1988), which show plants with $2n = 28$ to behave genetically as tetraploids.

The alders are anemophilous and produce abundant pollen at anthesis (Wodehouse, 1935), which in temperate North America occurs before (subg. ALNUS) or at the same time as (subg. ALNOBETULA) the unfolding of new leaves, or in late summer (subg. CLETHROPSIS) just after the new catkins mature. The latter condition has been interpreted as precocious and therefore derived (Furlow, 1979). In Latin American populations (subg. ALNUS sect. PHYLLOTHYRSUS) anthesis occurs mostly in December and January (very early spring). The shrubby northern species often form extensive thickets that give the impression of clonal growth. However, genotypes in such populations have been found to be randomly distributed in *Alnus incana* subsp. *rugosa* (Huenneke), suggesting that they result from seeding, rather than from vegetative reproduction. In all species the tiny fruits are abundantly produced and widely distributed. In some species, as in *Betula*, the fruits are winged and are carried by the wind. In others (e.g., *A. serrulata*) the wings have been reduced to ridges, in which case dispersal may be primarily by water currents. Allozyme studies by Bousquet and colleagues (1987a–c, 1988) have shown low inbreeding with high levels of gene flow within populations of both *A. incana* subsp. *rugosa* and *A. viridis* subsp. *crispa*. Little population differentiation was noted in these studies (1987b, 1988), suggesting relatively high interpopulational gene flow as well. Members of the genus hybridize readily where species occur together. However, most species are separated by habitat or geography, and except at the intersections of the ranges of the various taxa, extensive genetic mixing does not occur. Lists of named hybrid taxa in the genus are provided by Murai (1964) and Winkler.

Alnus (and *Betula*) appear earlier in the fossil record than the other Betulaceae (Crane & Stockey; L. J. Hickey & Doyle; Wolfe, 1973), but the precise time and place of origin of the genus, like those of the family, are a matter of speculation. Takhtajan (1969) believed that the group developed in southwestern Asia, while Murai (1964) placed its origin in the area of present-day Japan. Furlow (1979) concluded that the alders most likely originated in temperate Asia, with diversification there followed by progressive migrations east and west into Europe and the New World. The species of *Alnus* currently inhabiting North America appear, from fossil and phytogeographic evidence, to have entered from both the east and the west at several different times (Furlow, 1979; McKenna; cf. Löve & Löve). The ancestors of both *A. maritima* and the Latin American taxa may have entered in the early Tertiary from Asia. Using fossil pollen, Graham (1973a) concluded that *Alnus* and other woody mesophytic genera from northwestern North America migrated to southern Latin America during the Miocene. Graham (1973a) and Martin & Harrell have reviewed the evidence covering the introduction of this element into southern Mexico and Central America (cf. Deevey; Dressler; Miranda & Sharp).

Fossils suggest that subgenera ALNUS and ALNOBETULA had already differentiated and were present in western North America by the Miocene (Wolfe, 1969). However, a recent study employing allozyme data (Bousquet *et al.*, 1988) placed the time of divergence of *Alnus incana* subsp. *rugosa* from *A. viridis* subsp. *crispa* populations at only about one million years ago. The American subspecies of *Alnus viridis* and (to a lesser extent) *A. incana* are only very slightly differentiated morphologically from their Eurasian races, and it seems likely that they may be of recent (possibly post-Pleistocene) introduction, especially in the West (cf. Hultén). However, as noted by Bousquet and colleagues (1988), Furlow (1979), and others, it is possible that these species, at least in part, survived Pleistocene glaciations in refugia in northern North America. *Alnus serrulata*, closely related to *A. incana* on the basis of morphology (Furlow, 1979), may have entered from Europe at an earlier time. However, alder pollen is not known in the pre-Pleistocene sediments of the Atlantic and Gulf coastal plains where *A. serrulata* would be expected to have existed during the Pleistocene (J. Gray).

The alders associate symbiotically with species of the actinomycete *Frankia,* which lead to the formation of nodules on the roots of the plants and fix atmospheric nitrogen (Bond; Bond *et al.*; Dalton & Naylor; Hawker & Fraymouth). The importance of alders in plant succession is well documented for different species and a variety of physical settings (e.g., Crocker & Major; Fremstad; Newton *et al.*; Reiners *et al.*; Tarrant, 1968; Ugolini). During the past two decades foresters and plant physiologists have shown great interest in the nitrogen-fixing ability of actinorhizal plants, and an extensive literature has developed related to research into details of the process and the biology of the organisms involved, including identification, isolation, cultivation, morphogenesis, ultrastructure, ecology, nitrogen-fixing activity, inheritance, metabolism, chemosystematics, growth, reaction to various environmental factors, nutritional requirements, infection of hosts, and host-endophyte interactions. Some of this work represents biotechnological research aimed at the "genetic improvement" of alders and their symbionts (see Gordon *et al.*; Hall & Maynard; Hall, McNabb, Maynard, & Green; Hall, Miller, Robison, & Onokpise; Normand & Lalonde). Of special interest is the genetic recombination of large tree species, especially *Alnus glutinosa,* European black alder, *A. rubra,* red alder, *A. cordata* (Loisel.) Loisel., Italian alder, *A. incana* (L.) Moench subsp. *incana,* European white alder, and other species. This activity is in part due to a recent interest in the possible use of alders in intensive silviculture (see Dickman; Gordon & Dawson; Tarrant, 1983). Symposium papers dealing with this subject have been published by Gordon & Wheeler, Gordon, Wheeler, & Perry, and Torrey & Tjepkema (1979, 1983). The articles cited illustrate the range and scope of current work in this field.

Alders are not seriously bothered by diseases or insect pests, although various insects feed on their foliage (Sargent, 1896). In the Southeast cottony scale insects are frequent parasites of *Alnus serrulata.* Hepting reviewed the many fungal diseases known to affect *Alnus,* but he concluded that most are of little or no economic importance. The most serious pathogen of tree-sized alders in North America is heart rot (*Fomes ignarius* (L.) Kickx), which usually appears only in trees over 40 years old (Hepting; Worthington *et al.*). A species of *Taphrina* affects the carpellate catkins of many species, resulting in curled, straplike enlargements of the infructescence bracts.

The shrubby species of *Alnus* in eastern North America are mostly opportunistic plants that rapidly colonize disturbed habitats. In other parts of the world, the genus includes large trees that are important components of the mature natural vegetation. In the Pacific Northwest *A. rubra* is a dominant tree of floodplain forests, where it has considerable commercial value. Throughout the mountains of Mexico and Central America, *A. acuminata* and *A. jorullensis* become large trees and serve locally as a source of lumber.

Alders have been put to a great many uses by many cultures throughout the centuries. Various groups of North American Indians, as well as white settlers in the New World, utilized the astringent properties of alder bark for a wide variety of medicinal purposes, including the treatment of burns, infections, leukorrhea, toothaches, and indigestion (see Lewis & Elvin-Lewis; Moerman). The triterpenes betulin and lupeol, extracted from bark and wood of *Alnus rubra,* have recently been found to have antitumor activity in laboratory animals (Sheth *et al.*). In regions where alders make up a significant part of the vegetation, their pollen is an important cause of hay-fever allergies (Chamberlain, 1927; Florvaag & Elsayed; Florvaag, Elsayed, & Apold; Florvaag, Elsayed, & Hammer; Lewis *et al.*; Løwenstein *et al.*; Solomon & Durham). In Europe and America the wood, which is fine grained, although rather soft and not very durable, has been used for beams and piles, shipbuilding, cabinetry, boxes, and the manufacture of a wide variety of small wooden objects, ranging from toys and tool handles to wooden shoes. The wood was formerly greatly valued for the production of high-quality charcoal for gunpowder manufacture. One of the most important present uses in the United States and Canada, especially in the Pacific Northwest, is as a source of pulpwood for making paper (Worthington *et al.*). The U. S. Forest Service has published two symposium volumes (Briggs *et al.*; Trappe *et al.*) dealing with aspects of alder taxonomy, ecology, and silviculture, with particular reference to *A. rubra.* Several species, especially the European *Alnus glutinosa, A. incana* subsp. *incana,* and *A. cordata* in the East and *A. rubra* in the Northwest, are occasionally cultivated as ornamentals.

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2. **Betula** Linnaeus, Sp. Pl. **2:** 982. 1753; Gen. Pl. ed. 5. 422. 1754.

Small to large, conical, pyramidal, or round-crowned trees [or small to large shrubs], often with several trunks; branching excurrent (becoming deliquescent in age) [or in shrubby forms mostly excurrent]; trunks and branches terete, the branchlets and twigs subdistichous; twigs usually differentiated into pronounced long and short shoots. Bark thin and smooth, dark brown to chalky white, often exfoliating in very thin layers, becoming thicker and scaly or furrowed in age, marked with prominent lenticels, these frequently becoming much elongated horizontally; young twigs glabrous or sparingly pubescent, often covered with resinous glands, sometimes aromatic when crushed; leaf scars crescent shaped to suboval, with 3 nearly equidistant circular to elliptic vascular bundle scars; winter buds sessile, slender, terete, divergent or appressed along the lower half, the apices acute, with several smooth imbricate scales, only the outer 3 generally visible; wood fine grained, nearly white to reddish brown, moderately hard, moderately heavy; pith circular or remotely triangular in cross section. Leaves subdistichous, usually borne on short shoots; blades thin, ovate to deltoid, elliptic [or suborbicular], doubly serrate [or serrate to shallowly lobed], glabrous to abaxially tomentose, sometimes covered abaxially with resinous glands; secondary venation craspedodromous, the veins mostly divergent and straight; leaves in bud open and convex, becoming conduplicate and plicate during expansion; stipules broadly ovate. Staminate catkins terminal [or lateral in leaf axils near the ends of branchlets], [solitary or] in small racemose clusters, formed the previous growing season and exposed [or enclosed in buds] during the winter, expanding with the leaves, densely arranged, the scales ovate, consisting of 3 fused bracts; carpellate catkins lateral on the branchlets, below the staminate, mostly borne on short shoots, usually solitary, developing at the same time as the staminate, enclosed within buds during the winter and expanding with the leaves, ovoid to cylindrical, firm and erect, scales and flowers crowded, the scales compact, consisting of 3 fused bracts. Staminate flowers 3 per scale in the catkin, consisting of [(1 or)] 2–4 scalelike tepals and [(1 or)] 2 or 3 [(or 4)] stamens, these divided nearly to the base (giving the impression of twice as many stamens with 1-locular anthers); pollen grains flattened, 15–30(–40) μm in diameter, with 3(–7) elliptic equatorial apertures. Carpellate flowers sessile, [(1–)]3 per scale, consisting of a single 2-locular ovary with 2 linear styles, sometimes with 1 or more staminodes; ovule 1 by abortion, unitegmic. Infructescences cylindrical to ovoid, strobiluslike, erect or pendulous on short peduncles, the bracts connate into coriaceous or somewhat woody [(1- or)] 3-lobed scales, these usually readily deciduous with the fruits. Fruits small, ellipsoid to ovoid, rostrate samaras, maturing and dispersed the same season as pollination, styles persistent, the wings lateral, membranaceous, the pericarp thin. Seeds with membranaceous testa and flat cotyledons; germination epigeal. Chromosome numbers $2n = 28, 42, 56, 70, 84$. LECTOTYPE SPECIES: *Betula alba* L.; see N. L. Britton, N. Am. Trees, 246. 1908. (The Latin name for birch used by Pliny; from *batuere,* "to beat," for the birch rods used by Roman lictors to beat back crowds of people.)—BIRCH.

About 35 species of small to large trees and shrubs of the Temperate and Boreal zones of the Northern Hemisphere. Like *Alnus,* the genus is highly diversified, especially in the Old World. In the United States and Canada it includes about 17 species, which occur in the area south to the Gulf Coastal Plain in the East and to Colorado and central California in the mountains of the West. The species hybridize freely; 16 named hybrids are listed by Kartesz & Kartesz. The birches occupy a variety of habitats, characteristically including peat lands; stream banks; lake shores; cool, damp woods; cool, moist slopes in coves; and (in cooler regions) drier, more open sites.

Spach (1841) treated the birches as two genera, *Betula* and *Betulaster,* the latter an Asian group distinguished by many-veined, acuminate-toothed leaves, fruits with exceptionally wide wings, and carpellate inflorescences (and fruiting catkins) borne in racemose clusters. In his monograph of the Betulaceae, Regel (1861) recognized these two major groups as parts of *Betula* but did not clearly denote their rank or names. He indicated that these were subgenera in his subsequent (1865) revision of *Betula* and *Alnus,* but he again failed to provide a suitable name (erroneously referring to Spach's genus *Alnaster,* a segregate of *Alnus*). In his revision for De Candolle's *Prodromus,* Regel (1868) named these taxa properly at the rank of section. In his 1865 revision, he further divided the two major groups into seven taxa bearing only the rank of "Gruppe." Winkler (1904) treated the two major taxa as sections of *Betula,* subdividing these into four subsections corresponding to various of Regel's subgroups, and W. D. J. Koch, Koehne, Schneider, and others have since elevated most of them to sections, the arrangement adopted by Kuzeneva and the one used here.[3] Endlicher (1842, 1847) is frequently cited as the author of sections or subgenera in *Betula,* but he did not indicate ranks for his names either in the text or in his subsequent references to it (see Brizicky). In a recent synopsis of the genus, Fontaine recognized 52 species, 24 varieties, eight natural hybrid species, and 23 cultivars and artificial hybrids.

Section COSTATAE (Regel) Koehne consists of large, mesophytic trees, often with dark (close or exfoliating) bark; large, thin leaves; infructescence scales

[3]Sections COSTATAE (Regel) Koehne and HUMILES W. D. Koch have not yet been treated at the subgeneric level—perhaps a better course, considering their high degree of differentiation (equivalent to that of the subgenera of *Alnus*).

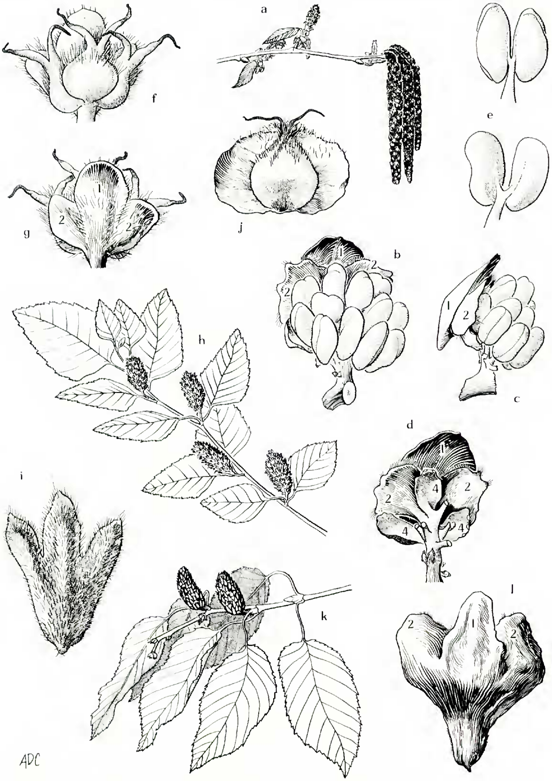

FIGURE 2. **Betula.** a–j, *B. nigra*: a, flowering branchlet with 2 ascending carpellate catkins and 3 pendent staminate ones, × ½; b, staminate cymule, oblique view of adaxial side, showing stamens of 3 flowers (tepals not visible) and tips of primary and secondary bracts (1, 2), portion of axis of catkin below, ×8; c, same, side view, primary and secondary bracts at left, ×8; d, staminate cymule, seen as in "b," anthers removed, to show primary (1) and secondary bracts (2), 1 tepal (4) of each of 3 flowers, and partial filaments of each of 6 stamens, ×8; e, 2 views of stamens, showing half-anthers, ×12;

with long, narrow lobes; and fruits with relatively narrow wings. Three species of this group occur in the southeastern United States. *Betula nigra* L., river birch, red birch, a large (to 30 m) tree usually with spreading clusters of trunks (each up to 1 m in diameter), distinctive rhombic-ovate leaves, and creamish to reddish exfoliating bark on young branches (dark, scaly bark on older trunks), is found throughout the region, except in peninsular Florida and certain areas of the Gulf Coastal Plain, including Alabama, Mississippi, Louisiana, and Arkansas (see Coyle *et al.,* 1983b; Duncan; Koevenig). This species grows on stream banks and on bottomlands. Cribben & Ungar, Fritts & Kirtland, and McClelland & Ungar have shown that in Illinois and Ohio river birch is predictably present on acid soils, especially along streams heavily affected by coal-mine drainage, and largely absent from alkaline soils. However, Wolfe & Pittillo found no such relationship in western North Carolina and concluded that in their area, the availability of continuous moisture constituted the most important limiting factor. *Betula nigra* is unique among our species in that its fruits mature, are released, and germinate in early summer, apparently an adaptation associated with the floodplain habitat (which is frequently inundated in the spring). *Betula alleghaniensis* Britton, yellow birch, and *B. lenta* L., cherry birch, sweet birch, black birch, are more northern, occurring in suitable habitats from southern Newfoundland to southeastern Manitoba and southward along the Appalachians to northern Georgia and northern Alabama (*B. lenta* only). *Betula alleghaniensis* (incorrectly spelled "*alleghanensis*" by Britton & Brown, 1913) is a large forest tree, usually with a single trunk, reaching a height of about 35 m and a trunk diameter of 1.5 m. Its leaves are large, thin, ovate, and doubly serrate. The bark of young branches is usually yellowish and exfoliates in ragged curls, but Dancik and Dancik & Barnes (1971) have shown this character to be inconsistent. The bark of older trunks becomes dark and scaly. *Betula lenta* has somewhat similar characteristics, but it is smaller and its dark cherrylike bark does not exfoliate. The two species can be distinguished by their infructescence scales, which in *Betula alleghaniensis* have pubescent, more elongate, and often more strongly ascending lateral lobes and in *B. lenta* glabrous, more expanded, more divergent ones. The bark and twigs of both species contain wintergreen oil (methyl salicylate), which can be detected by chewing fresh twigs. *Betula alleghaniensis* is an important constituent of the hemlock-hardwoods forest in the northern Appalachians, occurring on a variety of soil types and in various drainage conditions. In the southern Appalachians it occurs only at elevations over 1000 m. The yellow birch has been widely known in the past as *B. lutea* Michx. f., a superfluous and therefore illegitimate name (Michaux, after first misapplying the name *B. excelsa* to the

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f, adaxial side of carpellate cymule of 3 naked flowers, tips of primary and secondary bracts visible, ×8; g, bract complex, abaxial side, the 2 secondary bracts (2) partially united with the primary one (1), style tips of cymule visible, ×8; h, branchlet with mature infructescences, ×½; i, abaxial side of 3-lobed bract complex of mature carpellate cymule (primary bract and 2 secondary bracts partially united (see g), ×6; j, mature achene with membranaceous lateral wings, ×6. k, l, *B. lenta*: k, branchlet with mature infructescences, ×½; l, abaxial side of bract complex of mature fruiting cymule (cf. g, i), ×6.

yellow birch, substituted the epithet *lutea,* which he considered more descriptive; see Brayshaw, 1966a).

Betula uber (Ashe) Fern., known for many years only from herbarium material (Mazzeo), was rediscovered in 1975 in a single southwestern Virginia population (Ogle & Mazzeo; Reed). On the basis of leaf shape, the presence of wintergreen oil in its bark, and other characters, it had been speculated that this birch could represent a relative or hybrid of *B. pumila* L. (now occurring 500 miles to the north) or a variant or hybrid of *B. lenta* (see A. G. Johnson). However, wood anatomy clearly places *B. uber* in sect. COSTATAE, not with the dwarf birches, and additional evidence suggests that it is not closely related to other sympatric species of that section (e.g., *B. lenta*) (Hayden & Hayden). This view is supported by discriminant analysis (Sharik & Ford).

The mostly circumboreal sect. BETULA (sect. *Albae* (Regel) Schneider) consists of small to medium-sized trees with rather large, thin leaves and fruits with relatively wide wings (wider than the body of the fruit). A characteristic feature of trees in this group is their white bark, which often peels apart in sheets due to its alternating layers of tabular cells with thick walls and larger ones with thin walls, the latter containing grains composed largely of the triterpenoid betulin, which also makes the bark waterproof (Metcalfe & Chalk). The birches of northern North America with white bark (including *Betula papyrifera* Marsh., *B. populifolia* Marsh., and *B. cordifolia* Regel) are often little differentiated from each other and from races of this complex in Europe and Asia, and they commonly hybridize in nature. *Betula papyrifera,* paper birch, canoe birch, is transcontinental in distribution across the Boreal Zone, extending south in cool forests at high elevations in the Appalachians. Although individuals of this species are relatively short lived (about 150 years), they sometimes reach a height of 30 m and a trunk diameter of nearly 1 m. Their distinctive features include pinkish to chalky-white exfoliating bark marked with dark, horizontal lenticels; ovate, doubly serrate, acute to acuminate leaves with rounded or cuneate bases; and infructescence scales having relatively wide, rather angular ascending lobes of about the same length. *Betula populifolia,* gray birch, occurs from Quebec to southwestern Ontario and south to Delaware, northern Pennsylvania, and northern Indiana. It is distinguished from *B. papyrifera* by its close bark, deltoid to rhombic leaves with long-acuminate tips, and cone scales with very short central lobes.

The only white-barked birch to enter our range is *Betula cordifolia,* heartleaf birch. This species, sometimes treated as *B. papyrifera* var. *cordifolia* (Regel) Fern., occurs from Labrador and central Ontario to northern New York, Michigan, Wisconsin, and northern Indiana, and south along the Appalachians as small disjunct populations as far as Mount Mitchell in the Black Mountains of North Carolina (listed as *B. papyrifera* in Radford). It is similar in aspect to *B. papyrifera* but differs in its cordate leaves with more lateral veins, reddish bark, narrower and longer infructescence-scale lobes, larger fruits, and other characters. It is found at higher elevations than *B. papyrifera* throughout its range. Its different chromosome number ($2n = 28$ or 56 in *B. cordifolia,* $2n = 56$, 70, or 84 in *B. papyrifera*; Grant & Thompson; Löve & Löve, 1966), plus results from a discriminant analysis of morphological characters (Grant &

Thompson), support recognition of *B. cordifolia* at the species level. This interpretation is also supported by a study of betulin content of the bark of *B. cordifolia* (O'Connell *et al.*).

Populations of a shrubby, small-leafed white birch, *Betula minor* (Tuckerman) Fern., occasionally occur with *B. cordifolia* and *B. glandulosa* (discussed below) from Labrador south to the Gaspé Peninsula and the Laurentian Mountains, Quebec, with disjunct populations in northern New England and the Adirondack Mountains. This birch was treated as a variety of *B. papyrifera* by Tuckerman, as a subspecies of *B. pubescens* by Löve & Löve (1966) and as conspecific with *B. fontinalis* by Scoggan. It has long been suspected of representing a hybrid. Lepage concluded that its holotype represents a hybrid plant, but that Canadian populations, which he named *B. saxophila* Lepage, constitute a natural species. Löve & Löve (1966) determined that plants near the summit of Mount Washington had a chromosome number of $2n = 56$. However, at least one of the putative parents (*B. glandulosa*) has never been reported with a number higher than $2n = 28$, and the other (*B. minor*) has usually been found also to be diploid. Therefore, if *B. minor* actually represents a hybrid, it may be of alloploid origin.

From western Ontario to northeastern British Columbia and south in the mountains of the western United States to northern New Mexico and California, *Betula papyrifera* is replaced by *B. fontinalis* Sarg., water birch, a tall, shrubby race with darker, mostly nonexfoliating bark, smaller leaves, and cone scales with broad, ascending lateral lobes. The name *B. occidentalis* Hooker, often applied to this species, is illegitimate because both the original description and the specimens cited in the protologue are mixed (Dugle, 1969). A fifth species, *B. resinifera* (Regel) Britton, Alaska birch, occurs from central Canada to Alaska. This species resembles *B. papyrifera,* but it is smaller in stature, reaching a height of only about 12 m, and it differs in its more acuminate leaves and in details of the shape of its infructescence-scale lobes.

Two additional species with white bark, *Betula caerulea* Blanch., blue birch, and *B. caerulea-grandis* Blanch., big blue birch, have been a source of confusion and controversy. *Betula caerulea-grandis,* which occurs from southern Quebec to Nova Scotia and in adjacent areas of New England and New York, resembles *B. papyrifera* in size, bark morphology, and general aspect, but its leaves are glabrous with more extended apices and more rounded or strongly cuneate bases, and its infructescence scales, like those of *B. populifolia,* have a short central lobe. *Betula caerulea* is similar in habit but smaller, reaching a height of only 8 or 9 m, and it has somewhat smaller and more sharply cuneate leaves. Sargent (1922) suggested that both of these forms are hybrids of *B. papyrifera* and *B. populifolia,* while Fernald (1922) concluded that *B. caerulea-grandis* was a "good" species, and that *B. caerulea* represented a hybrid between it and *B. populifolia* (cf. Fernald, 1950a). From a morphological analysis of the complex, Brayshaw (1966b) found that *B. caerulea* and *B. caerulea-grandis* fall between *B. populifolia* and *B. papyrifera* in many characters and concluded that the blue birches represent extremes of a hybrid swarm between those species. A paper and thin-layer chromatographic analysis of the northeastern white-barked birches by Koshy and colleagues demonstrated close flavonoid relationships among *B. caerulea, B. populifolia, B. caerulea-grandis, B. cordifolia,* and *B. papyrifera* and showed patterns supporting this conclusion. However, Brittain & Grant (1967a), Grant & Thompson, and Guerriero and co-workers, in further morphological and cytological studies, concluded that *B. caerulea* and *B. caerulea-grandis* represent hybrids between *B. populifolia* and *B. cordifolia.* Dehond & Campbell's recent multivariate analysis of a single community in Maine containing *B. papyrifera, B. cordifolia, B. populifolia,* and *B. caerulea-grandis* suggested that *B. caerulea-grandis* represents a hybrid between *B. populifolia* and *B. cordifolia,* with *B. papyrifera* apparently not entering into the hybridization. These results have been substantiated by a study of betulin content in the bark of trees of the same population (O'Connell *et al.*).

Section HUMILES W. D. Koch (subsect. *Nanae* (Regel) Winkler), the "dwarf birches," are shrubs of the cold circumpolar region that are characterized by small, rounded leaves with few veins and by staminate catkins that are borne laterally and (usually) singly, enclosed in buds during the winter prior to anthesis. The usually solitary carpellate catkins emerge with new growth from the apical buds of short shoots. *Betula pumila* L., bog birch, an upright spreading shrub to ca. 4 m in height with leaves to ca. 7 cm long, is a common and variable species throughout bogs and fens of cool northeastern North America. A scarcely distinct more northern variety, *B. pumila* var. *glandulifera* Regel (*B. glandulifera* (Regel) Dugle), is marked by pubescent, somewhat gland-dotted branchlets and often smaller, more glandular leaves. This variety occurs from Newfoundland to the Yukon, extending southward in the western mountains to Oregon. A second dwarf species, *B. glandulosa* Mich., is found from Greenland and Labrador to western Canada and south in the Rocky Mountains. It is distinguished by its much smaller (to 3 cm long) leaves, its stems that are warty with large resinous glands, and its ascending lateral infructescence-scale lobes. This species reaches its southernmost limit in the East on the summits of high peaks, including Mount Washington (New Hampshire) and Mount Marcy (New York). A third member of this group, *B. nana* L., usually a prostrate shrub with tiny leaves, is circumpolar across the high latitudes of Europe, Asia, and North America. A similar species, *B. Michauxii* Spach, occurs in Nova Scotia and Newfoundland. It differs from *B. nana* primarily in the shape of the infructescence bracts (often lacking the side lobes) and in its wingless fruits (Fernald, 1950b; Rousseau & Raymond). In a preliminary multivariate analysis of these species, Furlow (1984) found that *B. Michauxii* differs very little from *B. nana* and concluded that it did not deserve specific status. *Betula rupestris,* an intriguing birch apparently related to this complex, was described by Rafinesque in 1819 (p. 229) from northern Kentucky on "the cliffs and on the sandstone rocks of the Kentucky river in Estill County." Although no specimen of this record exists today, Rafinesque's description agrees almost perfectly with that of *B. pumila,* not presently known farther south than central Ohio.

Birches and alders share many features, but they are easily distinguished by the bracts of their infructescences, which are three-lobed and deciduous in *Betula* and five-lobed and persistent in *Alnus.* In vegetative morphology, including the structure of their leaves, buds, shoots, and bark, and their broad-winged fruits, species of *Betula* resemble those of *Alnus* subg. ALNOBETULA.

However, the leaves are distinct in that they lack uniseriate-stalked glandular trichomes (Hardin & Bell). Like the alders, some birches have cut-leaved forms (Hylander, 1957b). In pollen morphology the two genera are distinct, with grains of *Alnus* normally bearing four or five apertures and those of *Betula* most frequently having three and lacking the prominent arci characteristic of alder pollen. Overall, the genus is much more homogeneous morphologically than *Alnus* is.

The birches are a difficult group taxonomically because of their high vegetative variability and frequent hybridization. Particular confusion has centered around the variable white-barked birches of the circumpolar *Betula alba* complex, the North American representatives being considered geographic races of a single species, *B. pubescens* Ehrh. (*B. alba* L.) (e.g., by Fernald, 1902), or separate species or hybrids (see Fernald, 1945b; Grant & Thompson; Hitchcock; Hultén). The response of several American authors (e.g., Britton; Butler) to the observed diversity was to name numerous new species (see Dugle, 1966). Others (e.g., Fernald, 1902) have recognized the American forms as varieties of the European species. Gleason and Gleason & Cronquist (1963) suggested that *B. papyrifera* and *B. pubescens* might better be considered parts of a single circumboreal species, but they, as well as Fernald (1950a) and most other modern authors, have maintained the American plants as separate species. Recent cytological research has begun to elucidate some of the subtle relationships of American representatives of the complex (see the review of Dugle, 1966). Several of the races differ in chromosome number and on the basis of meiotic irregularities (Woodworth, 1931) are possibly of hybrid origin. However, the American *B. papyrifera* is interfertile with both of the European white-barked species, *B. pubescens* Ehrh. (*B. alba*) and *B. pendula* Roth (*B. verrucosa* Ehrh.), even though a sterility barrier exists between the two European species (Johnsson, 1949).

Many morphological and cytological studies have dealt with variation within and among separate and (mostly) mixed populations of the European white-barked birches, *Betula pubescens* and *B. pendula.* The most comprehensive reviews of this work are those of Natho (1959, 1964). Jentys-Szaferowa (1949, 1950, 1952), using simple statistical and graphic methods, analyzed morphological variation in Polish populations, and Gardiner & Jeffers and Gardiner & Pearce, employing multivariate statistics, examined leaf-shape variation in populations in Scotland. These studies have shown both species to be extremely variable and suggest that they hybridize whenever they occur together. Jentys-Szaferowa (1950) noted that, because of this high variability, *B. pubescens* and *B. pendula* cannot be separated on the basis of any single character, but that each one is held together on the basis of combinations of characters and represents a natural group.

The cytogenetics of the European white-barked birches has been studied extensively (see the reviews of Brown & Al-Dawoodie, 1979; Gardiner, 1984; and Johnsson, 1974). Helms & Jørgensen first pointed out that the chromosome number of *Betula pubescens* is $2n = 56$, while that of *B. pendula* is $2n = 28$. This fact was discussed further by Woodworth (1931), and Johnsson (1945) noted the presence of nonchromosomal sterility barriers between the species.

Nevertheless, triploid ($2n = 42$) plants have been widely reported in mixed populations (see Brown & Al-Dawoodie, 1977, 1979; Brown & Williams; Eifler, 1956, 1958; Gardiner & Pearce; Helms & Jørgensen). Lindquist has noted that some of the triploid plants described by Helms & Jörgensen lack intermediate characters and thus might represent autopolyploids.

A result of some of this work has been the formal recognition (e.g., by Gunnarsson) of many simple variants and putative hybrids as separate species or varieties. In a more moderate treatment of the European birches, Lindquist consolidated the variants of *Betula pendula* into three varieties that correspond with major phytogeographic regions. From a study of *B. pubescens* in relation to the subspecies recognized in *Flora Europaea* (Walters), Gardiner (1984) concluded that two main races of that species occur in Europe, an arctic and southern montane group corresponding to subsp. *tortuosa* (Ledeb.) Nyman, and a common lowland form corresponding to subsp. *pubescens*. A third subspecies recognized in *Flora Europaea*, subsp. *carpathica* (Willd.) Ascherson & Graebner, differs little from subsp. *tortuosa*.

The taxonomy of the *Betula alba* complex has long been complicated by disagreement over the correct name of *B. alba* itself, as well as those of the other white-barked birches with which it occurs. According to Winkler (1904, 1930), Linnaeus circumscribed *B. alba* in such a way that he included both of the white-barked species of northern and central Europe in his concept (although Linnaeus's name "Betula foliis ovatis acuminatis serratis" and the listed synonym from *Flora Lapponica*, "Betula foliis cordatis serratis," together with his herbarium material, seem in fact to apply well to only one element of the complex). The major components of *B. alba* were separated by Roth as *B. alba* and *B. pendula* Roth. However, European authors have since mostly used the later name *B. pubescens* Ehrh. for the species with pubescent leaves and upright branches (*B. alba* as interpreted by Roth) (see Fernald, 1945b, p. 309, who condemned "the very doubtful Germanic practice of rejecting all Linnaean names of European species if they included what are now considered two or more species . . ."). Many nineteenth-century workers (e.g., W. D. J. Koch; Lamarck & De Candolle) at the same time incorrectly applied the name *B. alba* to what should have been called *B. pendula*, and many (although not all) recent systems substitute *B. verrucosa* Ehrh. for *B. pendula* (see Fernald, 1902, 1945b). Recent European authors have mostly used *B. alba* in the sense of a "collective species" or *Grossart* (a named species complex; *cf.* Natho, 1964; Winkler, 1930), ignoring its nomenclatural priority for one of the elements of that complex. In the present treatment, the name *B. pubescens* has been employed to follow prevalent current usage, pending final clarification of the issue.

Taxonomic confusion also exists with regard to the dwarf birches (see Furlow, 1984; Lepage). The various North American taxa of this complex have been combined and split into a large number of species and infraspecific taxa. The most comprehensive recent analysis of these problems is found in the work of Dugle (1966), who studied the relationships and hybridization patterns among the various taxa occurring in western Canada. Using statistical analyses of morphological characters in combination with chromatographic and cytological procedures, Dugle recognized and described the variation patterns of two species

(*Betula glandulosa* and *B. glandulifera*) and four hybrids of dwarf birches. Similar work is needed for the eastern American and European segments of the complex, followed by a comprehensive taxonomic revision of the entire group.

Several studies have been made of the vegetative variability of the three southeastern species. Coyle and colleagues (1983a) have described clinal variation and population differentiation in *Betula nigra* based on measurements of leaf characters. Dancik and Dancik & Barnes (1971) have shown that the bark of *B. alleghaniensis* varies from light colored and exfoliating to dark and close in certain populations. Trees exhibiting the latter characters were at first thought to represent hybrids between *B. alleghaniensis* and *B. lenta* but after study were judged to be dark-barked variants of *B. alleghaniensis*. Further work (Dancik & Barnes, 1975; Sharik & Barnes, 1979) has shown that the two species vary considerably, both within and among populations (often more so within populations), but with discernible trends for many characters over latitudinal and altitudinal gradients.

Wood of the dwarf northern birches, like that of the shrubby alders, exhibits primitive (juvenile) characters (e.g., many small vessels and numerous tracheids), while that of species of sects. COSTATAE and BETULA is more specialized (Hall). The most specialized wood is present in members of sect. BETULASTER Regel (cf. Roskam).

The staminate inflorescences of *Betula* are similar to those of *Alnus* except that they lack the two tertiary bracts subtending the cymules (Abbe, 1935, 1938, 1974). As in *Alnus,* the number of stamens and tepals in each flower differs among the species—i.e., generally three or four in members of sect. COSTATAE, two or three in sect. BETULA, and one or two in sect. HUMILES. In sect. BETULASTER, the number of stamens has been reduced to two, but four tepals have been retained, a condition seen also in *Alnus* but not elsewhere in *Betula* (Abbe, 1935). The carpellate cymules of *Betula* differ from those of all other Betulaceae in that they usually retain all three flowers; the secondary one is absent in the other genera (Abbe, 1935).

As in *Alnus,* various lines of *Betula* have become specialized in the grouping, number, and position of the staminate and carpellate catkins (Hjelmqvist, 1948; Jäger). The staminate catkins are produced the season before blooming in all sections except sect. HUMILES. The carpellate ones develop with the new growth in all sections. The number of both staminate and carpellate catkins in each cluster has been reduced from four or more in subg. BETULASTER to one in sect. HUMILES (cf. Jäger). Accompanying this reduction are alterations in branching that place the staminate catkins (which occur near the ends of branches and above the carpellate clusters in subg. BETULASTER and sects. COSTATAE and BETULA of subg. BETULA) below the terminal carpellate ones on short shoots in sect. HUMILES (Jäger). These changes parallel modifications, interpreted as adaptations to cold climates, seen in *Alnus* subg. ALNOBETULA (Furlow, 1979).

Little chemosystematic work has been attempted with woody plants in general in comparison with herbaceous groups. However, a surprising number of studies have been undertaken in *Betula.* An early flavonoid study was conducted by K. E. Clausen (1960b) to identify hybridization between *B. papyrifera* and *B. pumila*. Other work, in addition to that of Koshy and colleagues (described above), has included an extensive series of investigations of northern European birches by Pawlowska (1980a–c, 1982a, 1982b, 1983a, b) to demonstrate relationships of flavonoid occurrence among various species, species segregates, and putative hybrids. An electrophoretic analysis of pollen proteins in *B. populifolia* by Payne & Fairbrothers showed a high level of variation in proteins among populations in that species and suggested that local population differentiation was occurring. In a study of ten *Betula* species of the Soviet Far East, Baranov and co-workers found triterpene data to be taxonomically useful in the identification and separation of groups and subgroups of various species.

Species of *Betula* form a polyploid series, with chromosome numbers of $2n = 28, 56, 70, 84$, and 112, plus dysploid numbers in some hybrids (Woodworth, 1929b; Dugle, 1966; Poucques; Wetzel, 1927, 1928, 1929; Barnes & Dancik). Of the southeastern species, *B. nigra* and *B. alleghaniensis* are diploids ($2n = 28$), while *B. alleghaniensis* is hexaploid ($2n = 84$). Meiosis is normal in the diploids and somewhat abnormal in *B. alleghaniensis* (Woodworth, 1929b). Although the European *B. pubescens* (*B. alba*) and two of its northeastern American races, *B. papyrifera* and *B. fontinalis*, form a circumpolar complex having distributional and morphological patterns similar to those of *Alnus incana*, these birches represent different polyploidy levels ($2n = 56$, 70, and 84, respectively), lending support to their continued treatment as separate species. The European species, *B. pendula* Roth, and its American and Asian counterparts, *B. populifolia* and *B. japonica* Sieb., are diploids ($2n = 28$), but these forms are more differentiated morphologically than are the members of the *B. pubescens* group. Consequently, there has been little tendency to treat them as conspecific. In both complexes the segments should be examined in relation to modern species concepts to determine whether they might better be treated as a single species.

The birches are anemophilous and produce large quantities of pollen (Wodehouse, 1935). In all subgroups of the genus, the carpellate catkins appear with the new growth, and anthesis occurs as the leaves unfold. Achenes are produced in large numbers and are carried for considerable distances by the wind.

Natural hybridization is common (Alam & Grant; Johnsson, 1945), and many of the resulting hybrids have been named (see L. P. V. Johnson; Kartesz & Kartesz; Winkler, 1904). In eastern North America *Betula alleghaniensis* and *B. lenta* have been shown to hybridize (Sharik & Barnes, 1971). These species, as well as *B. papyrifera* and *B. populifolia*, also hybridize with *B. pumila* in the North where their ranges overlap (Cousins). Through artificial crosses hybridization between *B. papyrifera* and *B. populifolia* has been studied by Alam & Grant, who found the progeny to resemble *B. papyrifera* more closely than *B. populifolia* in juvenile leaf characters. Seeds from single trees of various taxa of *Betula* often give rise to offspring of two or more ploidy levels, and there "appears to be little barrier to cross fertilization between *Betula* plants with different levels of polyploidy" (Grant, 1969, p. 81). He suggested that this feature may have permitted the genus to take advantage of new ecological niches that opened up following the Pleistocene.

The earliest pollen and leaf material of *Betula* is from the Upper Cretaceous, and fossils of *Betula* are widespread and highly diversified by the Middle Eocene (Crane & Stockey). Differentiation of subgenera and sections appears to have occurred largely in response to major climatic differences (Jäger; Kikuzawa). A cladistic analysis of the birches by Roskam, done as part of a study of coevolutionary patterns in the birches and their gall-midge parasites, indicated that sect. COSTATAE is the most plesiomorphic subgroup and the sister group of *Alnus* subg. ALNOBETULA, with which the tree birches share many characters. However, it seems unlikely that *Betula* sect. COSTATAE is closely related to *Alnus* subg. ALNOBETULA. If the shrubby growth form indeed represents adaptation to cold climates, as is strongly suggested by morphological and phytogeographic patterns in both genera, it is improbable that unspecialized birches could have evolved directly from one of the most highly specialized groups of alders, or vice versa. In a preliminary cladistic analysis by Furlow (1983), all of *Alnus* and all of *Betula* appear as sister groups. Within *Betula*, sect. COSTATAE is most closely related to sect. BETULASTER.

Birches serve as important sources of food for browsing animals (LeResche & Davis; Oldemeyer). Palo, Pehrson, & Knutsson and Palo, Sunnerheim, & Theander have shown that phenolic compounds become much more concentrated in the twigs and bark of white-barked birches during the winter and have correlated this fact with striking examples of weight loss and reduced food consumption in vertebrate herbivores feeding on birch twigs and branches in the winter. They suggested that phenolic compounds may constitute a major chemical defense in birches against browsing animals.

In areas recently exposed by logging or natural causes, *Betula papyrifera* and *B. alleghaniensis* often exhibit symptoms of distress and gradually die from the top downward. This occurrence, known as "decadence," has generally been attributed to suddenly changing environmental conditions. During the 1930's, a disease with similar symptoms (termed "dieback") appeared in New Brunswick and rapidly spread throughout the Northeast, although there had been no alteration of the surrounding forest. By 1905 at least 80 percent of the merchantable birch had been killed in the Maritime region of Canada to as far west as New Hampshire (Clark; Clark & Barter). Dieback, which affects *B. alleghaniensis* more severely than *B. populifolia*, and which in Europe and in ornamental plantings also affects especially *B. pendula*, has since spread westward through New York, Ontario, Michigan, and Minnesota. Various explanations have been proposed, but thus far no single climatic or biotic cause has been identified. It has been suggested by Ball & Simmons and Houston that a population is first weakened by adverse environmental conditions, such as a period of drought, then is invaded and eventually decimated by the bronze birch borer, *Agrilus anxius* Gory, a native buprestid beetle. Others (e.g., Berbee; Cooper & Massalsk) believe, on the basis of the nature of dieback symptoms, that the initial causative agent of decline may be a virus, with borer invasion following in the weakened trees.

Many insect species feed on or otherwise affect birches, the most detrimental being the bronze birch borer. Others include the gypsy moth, tent caterpillars, leaf miners, and scale insects. Fungal diseases result in the destruction of large numbers of trees and are therefore of considerable economic consequence

(Hepting). The most important of these include heartwood rots caused by various species of *Fomes* and *Poria,* especially *Fomes ignarius* (L.) Kickx (Basham & Morawski; Campbell & Davidson), and nectria canker (*Nectria galligena* Bres.), the most damaging external stem disease of yellow birch and paper birch (Hepting).

The pollen of birches, in regions where they are numerous, is a significant cause of hay fever (Lewis & Imber; Lewis *et al.*; Løwenstein *et al.*; Wodehouse, 1945). During the past two decades considerable progress has been made in Europe to elucidate the basis of this ailment (Apold *et al.*; Berlin; Vik & Elsayed; Vik *et al.*). This research has revealed that the allergenic reaction to *Betula* pollen is related to that caused by *Alnus* and *Corylus* pollen. The responsible allergens have been partly identified (Dalen & Voorhorst; Løwenstein *et al.*). It has been shown that in children, birch-pollen allergies are sometimes related to food allergies (Dreborg & Foucard; Halmepuro *et al.*; Lahti *et al.*; Løwenstein & Eriksson). Birch sap has also been shown to cause a contact dermatitis in persons sensitive to birch pollen (Lahti & Hannuksela).

The wood of the birches has many uses (reviewed by Lines). In eastern North America *Betula alleghaniensis* and *B. lenta* are important sources of hardwood timber employed in the manufacture of doors and windows, flooring, cabinetry, interior molding, wood paneling, barrels, shoe lasts, furniture, and plywood. These and other species, especially *B. papyrifera,* are also widely used for making small specialty products, including wooden toys, athletic equipment, broom handles, clothespins, ice-cream sticks, spools, bobbins, and toothpicks. Wood of various species has long been utilized to make charcoal for gunpowder and for filtration purposes.

In the northern Appalachians *Betula lenta* is sometimes tapped during the spring in the same way sugar maple trees are tapped, the collected sap being fermented to produce a naturally carbonated birch beer. A tea is made from the bark and twigs of this species by steeping them in hot water (Fernald *et al.*; Sargent, 1896). *Betula lenta* was formerly a major commercial source of methyl salicylate, the chief constituent of wintergreen oil, widely used as a flavoring and as a component of pharmaceuticals, including aromatic cascara sagrada fluid extract (sweet cascara). Its chief medicinal use has been as a rubefacient and, in the past, as an antirheumatic (Lewis & Elvin-Lewis). Today, methyl salicylate is largely produced synthetically. Infusions of the bark of various birch species were widely used by North American Indians as treatments for infections, colds, pulmonary problems, burns, leukorrhea, and other ailments (Lewis & Elvin-Lewis; Moerman). Twigs of *Betula lenta* and *B. alleghaniensis* have been used in modern times as chewing sticks for cleaning the teeth (Lewis & Elvin-Lewis).

A pyroligneous oil is obtained by distillation from the bark and wood of *Betula pendula* and other species. This material has been widely used in northeastern Europe in the preparation of leather and in the manufacture of lotions, ointments, and medicines. Birch wood is a common source of high-quality firewood and of pulp for manufacturing paper in regions where the trees are plentiful. Birch bark, rich in oil and starch, has been used for centuries by people in times of famine as a source of food. Many species, especially those with white bark (*B. pendula, B. pubescens, B. populifolia,* and *B. papyrifera*), as well as *B. nigra,* are utilized horticulturally (of these, *B. pendula* is by far the most widely used in the United States). The bark of *B. papyrifera,* which is waterproof and easily workable because of its betulin and oil content, was extensively employed by northern North American Indians as a covering material for canoes, houses, and bundles, and as a material for making various articles of clothing.

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Subfamily CORYLOIDEAE (Regel) Koehne

Tribe Carpineae Döll

3. **Carpinus** Linnaeus, Sp. Pl. **2:** 998. 1753; Gen. Pl. ed. 5. 432. 1754.

Small [to large] usually spreading trees, mostly with a single trunk; branching mostly deliquescent; trunk and branches irregularly longitudinally ridged and fluted, the branchlets and twigs conspicuously distichous; twigs differentiated into long and short shoots. Bark close, thin, smooth, bluish- to brownish-gray, becoming thicker and scaly or furrowed in age, the lenticels generally inconspicuous; young twigs glabrous or sparingly pubescent; leaf scars narrowly crescent shaped to suboval, with 3 circular to elliptic vascular bundle scars; winter buds sessile, ovoid, 4-angled in cross section, usually appressed, the apices acute, with many smooth, imbricate scales; wood fine grained, nearly white to light brown, extremely hard, very heavy; pith circular to slightly angular in cross section. Leaves distichous, borne on long and short shoots; blades thin, narrowly ovate to ovate, elliptic, or obovate, doubly serrate [to

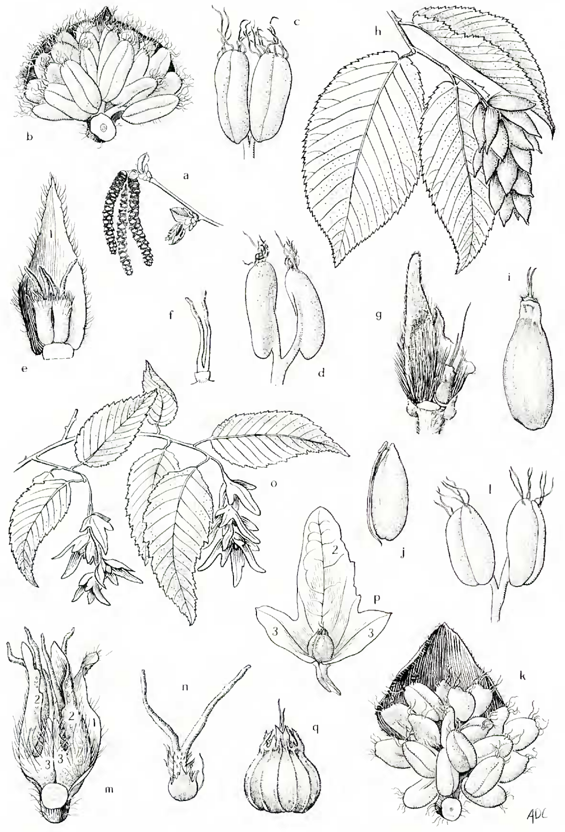

FIGURE 3. **Ostrya** and **Carpinus.** a–j, *O. virginiana*: a, flowering branchlet, pendent staminate catkins above, carpellate catkin partly hidden by expanding leaves below, × ½; b, adaxial side of staminate cymule with bract (composed of primary bract united with 2 secondary ones) visible behind, portion of axis of catkin below, × 8; c, d, 2 views of stamens, showing division of anther and upper part of filament into halves, × 15; e,

serrulate], glabrous to tomentose abaxially, sometimes with small glands abaxially; secondary venation craspedodromous, divergent and straight; leaves in bud concave, plicate, not conduplicate; stipules broadly ovate. Staminate catkins lateral, from axillary buds on short shoots, solitary [or in small racemose clusters], borne below the carpellate catkins, formed the previous growing season and [exposed or] enclosed in buds during the winter, expanding with the leaves, the scales broadly ovate [to elliptic], relatively uncrowded [to crowded], each consisting of 3 fused bracts; carpellate catkins terminal on short shoots from leafy new growth, solitary, developing at the same time as the staminate ones, enclosed within buds during the winter and expanding with the leaves, more or less erect, uncrowded [to crowded], with paired flowers subtended by a primary scale and each surrounded by a 3-lobed scale consisting of 3 fused bracts. Staminate flowers 3 per scale, each flower consisting of 3(–6) stamens, several such clusters crowded together on a pilose torus at the base of the scale; stamens short, the anthers divided into 2 1-locular parts, pilose at the apex, the filaments often divided partway to the base; pollen grains spheroidal to slightly flattened, 20–45 μm in diameter, slightly aspidote, with 3(–6) circular to slightly elliptic equatorial apertures. Carpellate flowers sessile, 2 per primary scale; ovary 1, 2-locular, with 2 linear styles; perianth of several scalelike tepals, these adnate to the ovary and apparent as a membranaceous or short-fringed margin at the apex; sometimes with 1 or more staminodes; ovule 1 by abortion, bitegmic. Infructescences elongate, pendulous, consisting of a loose racemose [to densely imbricate] cluster of pairs of expanded, [(1- to)] 3-lobed and variously toothed foliaceous bracts, each bract subtending a single fruit, splitting away with the adnate fruit. Fruits small, ovoid, longitudinally ribbed nutlets, usually crowned with the persistent tepals and styles, maturing and dispersed the same season as pollination; pericarp relatively thick and bony; seeds with membranaceous testa and somewhat thickened cotyledons; germination epigeal. Chromosome numbers $2n$ = 16, 32, 64. LECTOTYPE SPECIES: *Carpinus Betulus* L.; see N. L. Britton, N. Am. Trees, 241. 1908; N. L. Britton & A.

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adaxial side of carpellate cymule, showing primary bract (1) and 2 flowers (only styles visible), each with sheath composed of secondary bract united with 2 tertiary ones, ×15; f, carpellate flower at anthesis, showing 2 receptive styles and hardly developed ovary crowned by rudimentary perianth, ×15; g, carpellate cymule in young fruit, inflated surrounding bracts (secondary united with tertiary) removed from developing fruit at right to show persistent styles and collarlike perianth topping ovary, ×5; h, branchlet with nearly mature infructescence, each fruit surrounded by inflated bracts (cf. e, g), ×½; i, mature fruit with persistent rudimentary perianth and styles at top, ×4; j, seed, with aborted ovule at upper left, ×4. k–q, *C. caroliniana*: k, adaxial side of staminate cymule, showing stamens of 3 flowers with bract (composed of united primary and secondary bracts) behind, portion of axis of catkin below, ×8; l, stamen, showing half-anthers and partly divided filament, ×15; m, carpellate cymule, from adaxial side, showing primary bract (1) and 2 flowers (only styles visible), each surrounded by 3-lobed bract composed of a secondary bract (2) united with 2 tertiary ones (3), ×15; n, carpellate flower, the hardly developed ovary with minute perianth, ×15; o, branchlet with nearly mature infructescences, each fruit subtended by 3-lobed bract, ×½; p, mature fruit adnate to 3-lobed bract (united secondary (2) and tertiary (3) bracts), portion of axis splitting away, ×1½; q, mature fruit topped by accrescent perianth and persistent styles, ×4.

Brown, Illus. Fl. No. U. S. & Canada, ed. 2. **1:** 606. 1913. (The Latin name used by Pliny and other ancient writers for the hornbeam; possibly derived from *carpentum,* the name of a horse-drawn vehicle made from its wood.)—HORNBEAM, IRONWOOD.

A genus of about 25 species of small to large trees mostly of the North Temperate Zone, but with a few extending into Central America along the Sierra Madre and in the Old World in the mountains from the North Temperate Zone to India and Iran. *Carpinus Betulus* is a large and important forest tree throughout much of Europe (where it attains trunk diameters of up to 4 m). In mountainous Mexico and Central America *C. tropicalis* (J. D. Sm.) Lundell forms a dominant canopy component. Some of the Asian species also become large trees. However, *C. caroliniana* Walter subsp. *virginiana* (Fern.) Furlow, of the northeastern United States and adjacent Canada, and subsp. *caroliniana,* found throughout the Coastal Plain (Fernald, 1935; Furlow, 1987b), consist of smaller forms of the forest understory, often near streams, where they occupy a subdominant position.

Carpinus was treated taxonomically by Spach, De Candolle, and Winkler (1904). De Candolle divided the family Corylaceae into tribes CARPINEAE and CORYLEAE, the latter containing only *Corylus* (as followed in the present treatment). He further divided *Carpinus* into two genera, *Carpinus* and *Distegocarpus* Sieb. & Zucc., the latter an Asian group (*D. japonica* Blume, *D. cordatus* Blume) characterized by elongate, stipitate, more densely imbricate staminate floral bracts and crowded infructescences composed of numerous broad unlobed scales (as opposed to broadly ovate, subsessile, more or less uncrowded staminate bracts and open infructescences of relatively few distinctly three-lobed scales in *Carpinus*). Winkler (1904) treated these segregates as sections of *Carpinus,* and this remains the most frequently used treatment today. In a further revision of the genus (1914), he named a number of new species and varieties, based largely on the shape and size of the leaves and the infructescence bracts. Rafinesque modified the name of the genus, which he considered too similar to *Pinus,* to *Carpinum,* and this variant is sometimes cited as a synonym. Additional study is needed to determine whether sect. DISTEGOCARPUS (Sieb. & Zucc.) Sarg. is distinct enough to warrant continued recognition.

Numerous Asiatic species of *Carpinus* have been described in recent decades. In an early enumeration of Chinese *Carpinus,* Hu (1933) reported 23 species. Lee (1935) listed 24 species in *Forest Botany of China,* and 52 in the supplement to this work (1973). In *Flora Reipublicae Popularis Sinicae* Li & Cheng listed 25 species, together with an additional 15 infraspecific taxa. Although it is doubtful that all of these taxa deserve formal recognition, some of them appear to represent good species. The genus as a whole is in need of a comprehensive taxonomic revision.

In North America *Carpinus* consists of two species, *C. caroliniana* Walter and *C. tropicalis* J. D. Smith, each with several geographic races (Furlow, 1987a). Fernald (1935) first distinguished an Atlantic and Gulf Coastal Plain race, with small, blunt-toothed leaves, from the widespread Appalachian and continental form. Furlow (1987a) analyzed this complex using multivariate statistics and concluded that the Latin American hornbeams constitute a divergent group, most likely not derived from the species in the eastern United States, and recognizable as a separate species. The Coastal Plain populations of the United States were shown to form a distinctive and cohesive subgroup of *C. caroliniana.* This and the Appalachian race were recognized formally at the level of subspecies.

Carpinus caroliniana, American hornbeam, ironwood, blue beech, is easily recognized by its smooth, gray, often fluted stems, normally ovate to elliptic sharp-toothed leaves, and racemose infructescences of pairs of uncrowded, leaflike, three-lobed bracts, each subtending a small triangular nutlet. The staminate (but not the carpellate) catkins develop in the autumn, although they are enclosed in buds throughout the winter prior to anthesis. The carpellate catkins are produced on the first new growth in the spring. Both the staminate and carpellate catkins (except in sect. DISTEGOCARPUS) are much more uncrowded than those of *Alnus* or *Betula.*

Leaves of *Carpinus* closely resemble those of *Ostrya.* Both lack peltate scales (sessile glands), and they have similar kinds of trichomes. However, they differ in the structure of their stipitate glands: in *Carpinus* the stalks are uniseriate, rather than multiseriate, and the heads are more globose (Bell *et al.*; Hardin & Bell). The color and degree of development of these glands in *C. caroliniana* were shown by Furlow (1987a, b) to be of value in characterizing the subspecies.

The wood, which overall has been regarded as rather advanced in the Betulaceae, has both primitive features (e.g., numerous vessels of small diameter) and advanced ones (e.g., spiral thickenings on the vessels, homogeneous rays) (Hall). In some characters (e.g., structure of the perforation plates), relatively primitive states are present in some species and more advanced ones in others. Hall concluded that true tracheids were absent in *Carpinus,* although he noted fiber tracheids in all genera of the family. Recently, Yagmaie & Catling reported the presence of true tracheids in the wood of *Carpinus.*

Staminate inflorescences of *Carpinus* and *Ostrya* are much more difficult to interpret than those of members of the Betuloideae because the flowers lack tepals and the cymules lack tertiary bracts (see Abbe, 1935, 1974). In *Carpinus* the catkins consist of clusters ("partial inflorescences") of about 18 stamens. From the patterns observed in the Betuloideae and in *Corylus,* and from MacDonald's anatomical observations in *Ostrya* (see below under *Corylus*), such clusters have been interpreted as highly reduced cymules of three flowers, each consisting of six stamens (Abbe, 1974). The carpellate cymules consist of two ovaries subtended by one primary, two secondary, and four tertiary bracts (Abbe, 1935). As the infructescence develops, the primary bract abscises and the united secondary and two tertiary bracts associated with each fruit develop into a characteristic wing by which the fruits are dispersed (see FIGURE 3p).

Species of *Carpinus* form a straightforward polyploid series of $2n = 16$, 32, and 64 (in *C. caroliniana,* $2n = 16$).

In most species both the staminate and carpellate catkins are produced along with growth of the new leaves. The fruits, attached to expanded winglike bracts that dehisce from the infructescences with them, are dispersed by the wind.

The paleobotanical history of the genus has been reviewed by Crane (1981) and by Berger. Fossils referred to the Coryloideae first appear in the Paleocene. The genus *Paleocarpinus* Crane, from the upper Paleocene, morphologically links *Carpinus* with *Corylus* on the basis of fruit and bract characters (Crane, 1981, p. 131). Crane proposed that this fossil "may approach the generalized *Carpinus* form envisaged by Hjelmqvist as having given rise to the extant genera of Coryleae." He further showed that modern betulaceous characters began to differentiate in the Upper Cretaceous, with genera such as *Carpinus* greatly diversifying in the late Paleogene and early Neogene, and concluded (p. 131) that this shows that the "strong morphological adaptation for dispersal exhibited by most extant species" had not developed before that time. He proposed that the primary diversification took place in Eurasia, perhaps in relation to vegetation changes following climatic deterioration during the Eocene and Oligocene (cf. Wolfe, 1973).

The origin of populations of *Carpinus* in the mountains of Mexico and Central America (Hernández X. *et al.*) has been the subject of considerable speculation. Some workers (Deevey; Dressler; Miranda & Sharp) considered these populations to be closely related to those of the eastern United States, while others (e.g., Martin & Harrell) emphasized obstacles to the dispersal of mesophytic plants between these areas. Furlow (1987a, b) has shown by means of multivariate analyses that the taxa in Latin America are distinct morphologically and concluded on this basis, as well as on that of phytogeographic evidence, that Latin American *Carpinus* has more likely been derived from an extinct western taxon. Clinal variation and population differentiation have been demonstrated for several characters of *C. caroliniana* (Wardell & Winstead; Winstead *et al.*). Furlow (1987a) showed that these and other characters vary geographically in complex ways, and that the patterns are related to climatic factors—in different ways in different regions.

There are no serious insect pests or fungal pathogens associated with *Carpinus*, although many fungi including mildews and rusts attack the leaves (Hepting). Sargent (1896) listed a variety of insects known to feed on the leaves of members of the genus.

The very hard wood of *Carpinus* has been used, especially in Europe (where the trees are larger), for making mallet heads, tool handles, levers, and other small, hard, wooden objects. It has also been employed to make high-quality charcoal for use in manufacturing gunpowder. The branches are utilized extensively in Europe for fuel. *Carpinus Betulus* and (less frequently) *C. caroliniana* are cultivated as ornamentals, the former being available in a number of cultivars.

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Under family references see ABBE (1935, 1974); BELL *et al.*; CANDOLLE; CRANE (1981); DEEVEY; DRESSLER; HALL; HARDIN & BELL; HEPTING; HERNÁNDEZ X. *et al.*; LEE (1935, 1973); LI & CHENG; MACDONALD; MARTIN & HARRELL; MIRANDA & SHARP; RAFINESQUE; WINKLER (1904); WOLFE (1973); and YAGMAIE & CATLING.

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4. **Ostrya** Scopoli, Fl. Carniolica, ed. 2. **2:** 243. 1772, nom. cons.

Small to medium-sized, usually spreading trees, mostly with a single trunk; branching mostly deliquescent; trunks and branches terete, the branchlets and twigs conspicuously distichous; twigs differentiated into long and short shoots. Bark thin, light brownish gray to light brown, breaking into slender, shaggy vertical shreds, the lenticels generally inconspicuous; young twigs glabrous or sparingly pubescent; leaf scars narrowly crescent shaped to suboval, with 3 circular to elliptic vascular bundle scars; winter buds sessile, ovoid, somewhat laterally compressed, divergent, the apices acute, with many longitudinally striate imbricate scales; wood fine grained, nearly white to light brown, extremely hard, very heavy; pith circular to slightly angular in cross section. Leaves distichous, borne on long and short shoots; blades thin, narrowly ovate to ovate, elliptic, or obovate, doubly serrate [to serrulate], glabrous to abaxially tomentose; secondary venation craspedodromous, the veins divergent and straight; new leaves in bud concave, plicate, not conduplicate; stipules broadly ovate. Staminate catkins terminal on branchlets, [solitary or] in small racemose clusters, formed the previous growing season and exposed during the winter, expanding with the leaves, the scales relatively uncrowded, broadly ovate, each consisting of 3 fused bracts; carpellate catkins terminal on short shoots from leafy new growth, below the staminate, solitary, developing at the same time as the staminate, enclosed within buds during the winter and expanding with the leaves, more or less erect and uncrowded, the scales 3 fused bracts, these later completely fusing so as to enclose the young fruits completely in bladderlike involucres. Staminate flowers 3 per scale, each consisting of 3(–6) stamens, several such clusters crowded together on a pilose torus at the base of the scale; stamens short, the anthers divided into 2 1-locular parts, pilose at the apex, the filaments often divided partway to the base; pollen grains spheroidal to slightly flattened, 20–45 μm in diameter, slightly aspidote, with 3(–6) circular to slightly elliptic equatorial apertures. Carpellate flowers sessile, 2 per scale; ovary 1, 2-locular, with 2 linear styles; perianth of several scalelike tepals, these adnate to the ovary and apparent as a membranaceous or short-fringed margin at the apex; sometimes with 1 or more staminodes; ovule 1 by abortion, bitegmic. Infructescences consisting of loosely imbricate, pendulous, strobiloid clusters of closed bladderlike involucres derived from the encircling bracts of each flower in the catkins, each bract enclosing and deciduous with a single fruit. Fruits small, ovoid, longitudinally ribbed nutlets, maturing and dispersed during the same season as pollination, often crowned with the persistent tepals and styles; pericarp relatively thick and bony; seeds with membranaceous testa and somewhat thickened cotyledons; germination epigeal. Chromosome number $2n = 16$. TYPE SPECIES: *Ostrya carpinifolia* Scop. (The Greek name used by Theophrastus for a tree with very hard wood; from the Greek *ostryos,* "a scale," in reference to the scaly catkins.)—HOP HORNBEAM, IRONWOOD.

About five species of small trees of the North Temperate Zone. *Ostrya carpinifolia* is a common and important forest tree throughout southern Europe. In North America the genus consists of small trees of the northeastern deciduous forest and the mountains of the southwestern United States and adjacent Mexico, south to northern Central America.

Ostrya was included as a single species of *Carpinus* (*C. Ostrya*) by Linnaeus. Miller accepted this generic concept, but he separated the American species (as *C. virginiana* Miller) from the European; Michaux treated it as *C. Ostrya americana.* The genus was segregated from *Carpinus* in 1772 by Scopoli, who named the common European tree *Ostrya carpinifolia. Ostrya* has since mostly stood as a separate genus, yet on the basis of its inflorescences, infructescences, and vegetative features, the two genera are closely allied. Willdenow, in the fourth edition of *Species Plantarum,* named the American species *O. virginica.* Spach (1842b), in a revision of the genus, recognized two species, *O. italica* Micheli (including all the European forms) and *O. virginica* Willd. De Candolle also recognized these species but correctly selected the earlier name, *O. carpinifolia,* to designate the former. In 1873 K. Koch transferred Miller's name to *Ostrya.* Winkler submerged both *O. virginiana* (Miller) K. Koch and *O.*

carpinifolia as subspecies of *O. italica* but recognized the western North American *O. Knowltonii* Cov. as separate. Rafinesque, in *Florula Ludoviciana,* substituted the name *Zugilus* for *Ostrya* because he believed the name to be too similar to *Ostrea.* Four species are listed for China by Lee (1973) and Li & Cheng, although some of these may be found to be too indistinct to deserve specific status.

Ostrya virginiana is a common tree in North America from Nova Scotia to eastern Manitoba, south to Virginia, northern Georgia, Tennessee, and Oklahoma, with a disjunct population in the Black Hills (South Dakota). Although frequent in the Northeast, *O. virginiana* is seldom a major forest component. There, like *Carpinus caroliniana,* it usually occupies a subdominant position in the understory (although Greenidge has reported that the species is nearly absent from closed old-growth forests in Nova Scotia). Unlike *Carpinus,* it is characteristic of drier or better-drained, more upland sites. It is seldom seen in wet areas. *Ostrya virginiana* is much less abundant in the Southeast than farther north (Duncan, Radford), occurring—when present at all—mostly in the mountains and Piedmont.

The leaves of *Ostrya virginiana* are similar to those of *Carpinus caroliniana,* as are its infructescences and fruits, except that the infructescences are somewhat more compact, with the bracts fused into bladders that completely enclose the fruits. As in *Carpinus,* only the staminate catkins develop in the autumn, although in *Ostrya* these occur in small clusters and are exposed during the winter near the tips of lateral branchlets (short shoots). Also as in *Carpinus,* the carpellate and staminate catkins are loosely arranged at anthesis. One of the most characteristic field characters of *O. virginiana* is its light brownish-gray bark, which shreds into thin, narrow vertical strips. In the winter the trees are distinctive in their numerous small terminal clusters of dormant catkins (absent in *Carpinus caroliniana*).

Coastal Plain populations of *Ostrya virginiana* are represented by a small-leaved and somewhat pubescent geographic race (var. *lasia* Fern.). However, the *O. virginiana* complex has not been studied in detail. Two shrubbier species occur in the Southwest: *O. Knowltonii* Cov. is found in mountains and canyons from southwestern Texas to southeastern Utah (including both rims of the Grand Canyon), and *O. chisosensis* Correll occurs in the Chisos Mountains in Big Bend National Park in southwestern Texas. These two species differ somewhat from each other and from *O. virginiana* in characters of leaf shape, leaf margin, and plant pubescence. However, no comprehensive study has considered the distinctness of these species in terms of their variation patterns or their relationships to other North American taxa.

Additional populations of *Ostrya* occur in the eastern and western mountains of Mexico and northern Central America. Rose believed these segments to differ significantly from *O. virginiana* and named the Mexican group, characterized by more narrowly lanceolate and more gradually acuminate leaves, *O. mexicana* Rose. He called the southern group, with similar features but somewhat broader and more pubescent leaves, *O. guatemalensis* Rose. However, in current work (e.g., Nee) these forms are usually treated as conspecific with *O. virginiana.* The Latin American representatives are especially in need of critical taxonomic examination. The morphological differentiation and paleoecology of these segments, as well as of *O. Knowltonii* and *O. chisosensis*, need to be examined in relation to the complex as a whole.

Although *Ostrya* shares many vegetative features with *Carpinus*, its habit is more treelike. As in *Corylus* but not *Carpinus*, the stipitate glands of the leaves have multiseriate rather than uniseriate stalks, and these bear more elongate heads, features not seen in other Betulaceae (Hardin & Bell). The wood is similar to that of *Carpinus*, but the vessels are of a more specialized type, with largely simple perforation plates (Hall). The genus is seen by Hall as the most advanced of the family on the basis of wood structure.

The inflorescence and flower structure of *Ostrya* is also similar to that of *Carpinus*, except that in the infructescences the secondary and two tertiary bracts of each floret are fused into a sac that envelops the fruit, rather than a flat wing that subtends it (Abbe, 1935, 1974). Even though direct evidence was lacking, Abbe (1935) hypothesized that the clusters of stamens found in staminate catkins of *Carpinus* and *Ostrya* represented the three reduced florets of a cymule comparable to those seen in the Betuloideae. This position was recently supported by the work of MacDonald, who demonstrated three growth areas in the primordia of the staminal groups in developing catkins.

All species of *Ostrya* for which counts have been made have a chromosome number of $2n = 16$.

Unlike *Carpinus*, in most species of *Ostrya* the staminate catkins are produced the season before anthesis and exposed during the winter. The carpellate catkins develop in the spring with the new shoots, with anthesis occurring as the leaves are forming. Dispersal is as in *Carpinus*, except that the bracts form closed bladderlike structures rather than flat wings.

The evolution of *Ostrya* parallels that of *Carpinus*, but the genus first appears somewhat later in the fossil record (Miocene), and fossils of *Ostrya* are not nearly so well represented (Crane). Although the disjunct populations of *Ostrya* in the mountains of Mexico have generally been considered to be conspecific with the species of the eastern United States (Miranda & Sharp; Nee), the same phytogeographic evidence cited in connection with Latin American *Carpinus* suggests that these populations may have been derived not from *O. virginiana*, but rather from an earlier and more western species.

Ostrya, like *Carpinus*, suffers from few insect pests or diseases, and none of these is regarded to be of economic importance. Sargent (1896) listed a number of insects that feed on or otherwise affect hornbeams. Hepting discussed various parasitic fungi, mostly found on *Ostrya* leaves.

The wood of *Ostrya* is employed for fuel, fence posts, and other utility purposes. It was formerly used for making items subject to prolonged friction, including sleigh runners, wagon tongues, wheel rims, spokes, windmill vanes, and airplane propellers. Because of its density, it has been used for tool handles, mallet heads, and other hard wooden objects. Millspaugh listed a tincture of the heartwood of *Ostrya virginiana* as a treatment for intermittent fever. *Ostrya virginiana*, and sometimes *O. carpinifolia*, are occasionally cultivated in eastern North America.

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Tribe CORYLEAE Meisner

5. **Corylus** Linnaeus, Sp. Pl. **2:** 998. 1753; Gen. Pl. ed. 5. 433. 1754.

Medium-sized to large shrubs [or small to medium-sized, usually spreading trees]; branching mostly deliquescent; trunks and branches terete, the branchlets and twigs subdistichous to diffuse; twigs differentiated into long and short shoots. Bark close, thin, smooth, grayish brown, breaking into vertical strips and scales with age, lenticels inconspicuous; young twigs glabrous or sparingly pubescent, sometimes with resinous glands; leaf scars suboval to triangular, with 3 nearly equidistant circular to elliptic vascular bundle scars; winter buds sessile, broadly ovoid, terete, divergent, the apices acute, with several smooth, imbricate scales; wood fine grained, nearly white to light brown, moderately hard, moderately heavy; pith circular to slightly angular in cross section. Leaves distichous, borne on long and short shoots; blades thin, broadly ovate, the base often cordate, occasionally somewhat lobed above, doubly serrate, usually pubescent and sometimes glandular abaxially; secondary venation craspedodromous, the lowest veins sometimes crowded at the base of the midrib and rising abruptly toward the apex; leaves in bud conduplicate and plicate; stipules broadly ovate. Staminate catkins lateral in bud axils on short shoots, in numerous racemose clusters of (2 or) 3–5, formed the previous growing season and exposed during the winter, expanding long before the leaves, the scales broadly ovate, relatively uncrowded, consisting of 3 fused bracts; carpellate inflorescences lateral, borne near the tips of the branchlets producing staminate catkins, developing at the same time as the staminate, enclosed within buds during the winter and expanding long before the leaves, consisting of a small cluster of flowers and bracts, only the styles protruding from the buds at anthesis, the scales 3 fused bracts. Staminate flowers 3 per scale in the catkin, congested, the tepals lacking [(or 1–4)], the stamens 4, divided nearly or entirely to the base to form 8 half-stamens, the filaments very short, fused along with 2 bractlets to the scale; pollen grains flattened, 12–30 μm in diameter, slightly to moderately aspidote, with (2 or) 3 (or 4–6) slightly elliptic equatorial apertures. Carpellate flowers sessile, 2 per scale, with 4 extremely reduced tepals (displayed as a thin irregular fringe on the ovary); ovary 1, 2-locular, with 2 linear styles; ovule 1 by abortion, bitegmic. Infructescences consisting of compact clusters of several fruits, each subtended and surrounded by an involucre of 2 hairy [or spiny] expanded foliaceous bracts, these sometimes fused into a [short to] elongate tube. Fruits relatively thin-walled, subglobose to ovoid, somewhat laterally compressed, longitudinally ribbed nuts; pericarp bony; seed with membranaceous testa, the cotyledons thick and oily; germination hypogeal, the seed being raised to the surface but remaining in the fruit. Chromosome number $2n = 28$. LECTOTYPE SPECIES: *Corylus Avellana* L.; see N. L. Britton, N. Am. Trees, 246. 1908; N. L. Britton & A. Brown, Illus. Fl. No. U. S. & Canada, ed. 2. **1:** 607. 1913. (The Latin name used by Virgil, Pliny, and other ancient writers for the European hop hornbeam; from *korus,* "helmet," for the shape of the shells of the nuts.)—HAZEL.

About 15 species of trees and shrubs of the North Temperate Zone. *Corylus Colurna* L., Turkish filbert or hazel, is a medium-sized tree of southeastern Europe and Asia Minor. The other species of Europe and North America are small to large shrubs or small trees. Two species, *C. americana* Walter, American hazel, and *C. cornuta* Marsh. (*C. rostrata* Aiton), beaked hazel, occur throughout much of the northeastern United States and adjacent Canada. In the Southeast these are mostly confined to the mountains southward to northern Alabama and Georgia. Several varieties of *C. cornuta,* including the tree-sized var. *californica* (A. DC.) Sharp, occur to the west.

Corylus was treated as a genus by Linnaeus and his predecessors. Spach (1842c) divided the genus into three sections, *Avellana* Spach (*C. Avellana* and *C. Colurna*), *Tubo-Avellana* Spach (*C. tubulosa* Willd. and *C. rostrata*), and *Acanthochlamnys* Spach (*C. ferox* Wall.). The second of these groups is characterized by an elongate tubular involucral beak, and the last by densely spiny bracts. De Candolle modified this scheme, making the first two groups subsections of sect. *Avellana.* Winkler recognized no infrageneric categories of *Corylus* in his monograph of the Betulaceae. In his synopsis, Beijerinck described 32 species, varieties, and cultivars of the genus. Lee (1973) listed 15 Chinese species, while Li & Cheng recognized seven. As in the other genera of the Betulaceae, the relatively poorly known Asian species need to be examined in relation to the genus as a whole. No infrageneric taxa are recognized here, pending detailed study of subgroups of the genus.

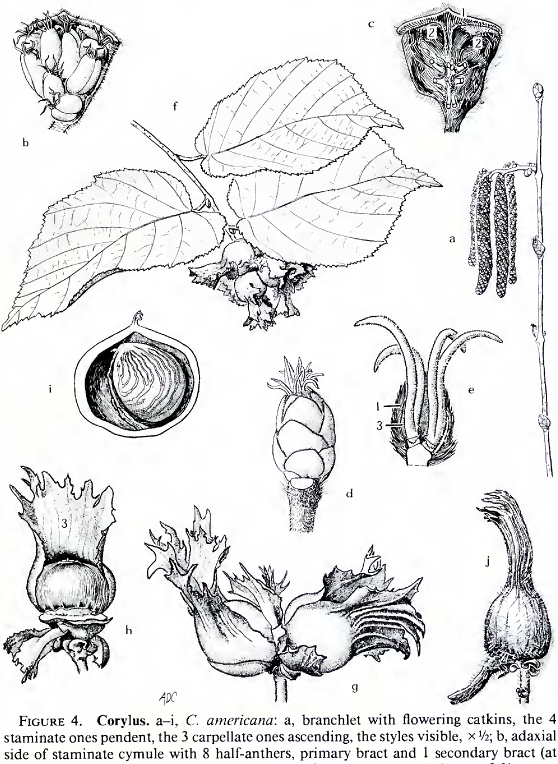

FIGURE 4. **Corylus.** a–i, *C. americana*: a, branchlet with flowering catkins, the 4 staminate ones pendent, the 3 carpellate ones ascending, the styles visible, × ½; b, adaxial side of staminate cymule with 8 half-anthers, primary bract and 1 secondary bract (at right) visible behind them, × 8; c, same, 8 half-anthers removed, bases of filaments shown, primary (1) and 2 secondary (2) bracts visible, × 8; d, carpellate catkin, × 4; e, adaxial side of carpellate cymule of 2 flowers, styles receptive, ovaries hardly developed, each ovary with delicate, rudimentary perianth, primary bract (1) and parts of tertiary bracts (3) visible behind flowers, secondary bracts absent, × 13; f, branchlet with 3 nearly mature fruits with their accrescent paired tertiary bracts, × ½; g, 2 mature fruits, each surrounded by tertiary bracts, × 1; h, mature nut with 1 tertiary bract (3) behind, the other removed, × 1; i, nut to show seed with half of pericarp removed at right and aborted ovule at upper left, × 2. j, *C. cornuta*: mature fruit with paired tertiary bracts and (at lower left) undeveloped fruits with bracts, × 1.

Corylus americana is a shrub to about 3 m tall, occurring mostly in thickets, open woods, fence rows, and forest edges, especially on well-drained soils, from Maine to Missouri and south to Georgia and Oklahoma. Its broadly ovate or roundish, doubly serrate leaves are distinctive in that they are often expanded apically to give a squarish appearance. *Corylus cornuta* is similar in habitat and distribution, but it extends farther north and west (from Newfoundland to British Columbia and south to Georgia, eastern Kansas, Colorado, and California). It is a larger plant than *C. americana,* reaching a height of about 5 m, and its leaves are narrower and more ovate. Drumke concluded that *C. cornuta* var. *californica* (A. DC.) Sharp, which becomes a small tree, is sufficiently distinct to warrant varietal status. He noted that this form grades clinally into var. *cornuta* to the north in Oregon and Washington. Useful field characters for separating the two species include the presence of reddish stipitate glands on the petioles and young twigs of *C. americana* and their absence on the petioles of *C. cornuta* (see Wiegand), and more rounded bud apices in *C. americana. Corylus cornuta* differs most noticeably from *C. americana* in the narrow, extended, tubular involucres surrounding its fruits, those of *C. americana* being short and leaflike. Drumke examined populations of these two species in their region of overlap and found them to be morphologically distinct, with little or no evidence of hybridization.

Although clearly related at the family level, the hazels are morphologically distinct both from the Betuloideae and from *Carpinus* and *Ostrya.* Their most distinctive features lie in their infructescences, which consist of a small cluster of small to moderately large nuts, each enclosed by a loose involucre of leaflike bracts. As in *Ostrya,* staminate catkins are formed during the summer and are exposed through the winter prior to anthesis. However, these are represented by numerous clusters of catkins borne on short shoots arranged evenly along the branches. The carpellate catkins develop at the same time as the staminate and consist of only a few flowers protected by the scales of special buds.

The leaves of *Corylus* resemble those of the other Betulaceae in overall aspect, but they are modified in shape and venation. As noted by L. J. Hickey & Wolfe and Wolfe (1973), the blades are frequently broader, and the lowest secondary veins, which are congested at the base of the midrib in some species, rise sharply toward the apex, a pattern also seen in *Corylopsis* of the Hamamelidaceae (see further discussion above under the family treatment). The indumentum on the leaves of *Corylus* is very similar to that of *Ostrya* and (to a slightly lesser degree) *Carpinus* (Hardin & Bell). All three genera lack peltate scales but have the five other trichome types described by Hardin & Bell. However, the stipitate glands of *Corylus* and *Ostrya* have multiseriate stalks, while those of *Carpinus* are more primitive in their uniseriate stalks (Hardin & Bell). The genus is the most specialized of the family in its fruit type (well-developed nuts) and the accompanying involucre (Stebbins; Stone).

Corylus stands apart from the remainder of the family in terms of flower and inflorescence morphology. The staminate inflorescences are similar in structure to those of the other Coryloideae except that up to four tepals are occasionally present, clearly defining the three individual flowers that make up each cymule. The carpellate catkins are much modified. The inflorescence itself is reduced to a small cluster of flowers, only one or two of which develop further. Present in each partial inflorescence are two flowers, as in *Carpinus* and *Ostrya,* plus one primary and several additional bracts. Abbe (1935) interpreted the latter to represent various of the four tertiary bracts of a cymule (the secondary bracts not developing), but Hjelmqvist (1948) believed the two secondary bracts to be present, each fused to one of the two tertiary bracts associated with every flower (cf. Abbe, 1974). The two resulting foliaceous bracts grow around the developing fruit, either free from each other, as in *Corylus americana,* or fused into a tube, as in *C. cornuta* (see Abbe, 1974). Abbe (1974) reviewed the development of present concepts regarding the nature of the involucre of *Corylus* and various misconceptions that have involved its structure and development.

All investigated species of *Corylus* have chromosome numbers of $2n = 28$.

The inflorescences are produced the season before flowering, with the staminate being exposed during the winter and the carpellate enclosed in buds. Anthesis usually occurs extremely early (January or February), even in northern areas, and well before production of the new leaves. The plants are anemophilous, producing large quantities of pollen (Wodehouse, 1935). Dispersal is (apparently) by means of small mammals that carry the nuts away.

The wood of *Corylus,* like that of *Carpinus* and *Ostrya,* contains numerous small vessels with spiral secondary thickenings (Hall). However, its vessels, like those of *Alnus* and *Betula,* have scalariform perforation plates and are thus regarded as more primitive than those of the other Coryloideae (Hall). Hall concluded that true tracheids are absent from all of the Coryloideae, although fiber tracheids are present. However, Kasapligil (1964) and Yagmaie & Catling have reported tracheids in *Corylus* wood. Kasapligil (1964) noted two distinct subgroups of the genus on the basis of wood anatomy, with one, including *C. Avellana,* mostly lacking true tracheids and having fewer and wider bars in the perforation plates of its vessels, and a second, more primitive group (including *C. Colurna*) with wood composed of both tracheids and vessels, the latter with numerous narrow scalariform perforations. He suggested, on the basis of indumentum and other characters, that this second group might also include *C. ferox,* but that a formal assignment of *C. Colurna* to sect. *Acanthochlamnys* would require additional study. According to Hall, the wood of *Corylus* is anatomically indistinguishable from that of *Ostryopsis.*

Fossil leaves from the Late Cretaceous and early Paleocene have been identified as *Corylus,* but fossil fruits of the *Corylus* type are scarce during this period (Crane, 1981). A probable small *Corylus* nut was discovered in the Danian of Greenland by Koch. By the Pliocene, the genus had become well established in North America and Europe. Zoöchory, a novelty in the Betulaceae, has been regarded by both Stebbins and Stone as a specialized condition; all of the other genera (except *Ostryopsis*) rely on wind or water for dispersal. Crane (1981) pointed out that zoöchory is related to more stable K-selective environments than is anemochory, and its development may have paralleled the evolution of suitable animal dispersal vectors during the Paleocene, these permitting the genus to diversify into new niches.

Corylus is the source of hazelnuts and filberts. The commercial filbert (*C.*

Avellana and *C. maxima* Miller) and the Turkey nut (*C. Colurna*) are cultivated as crop plants in various parts of the world, particularly Turkey, Italy, Spain, China, and Japan. In the United States these species are grown commercially in the Pacific Northwest, where they produce over 10,000 metric tons of nuts annually, about five percent of the world crop (Schery). The fruits are used mostly as dessert nuts, but they are rich in oil (up to 68 percent) and serve as a commercial source for cooking and salad oil in Europe (Eckey; Vaughn). The kernels are sometimes ground into meal used to make a sweet, cakelike bread (Fernald *et al.*). Wild hazelnuts are gathered locally in both America and Europe. The pollen of hazels causes hay-fever allergies in regions where they occur in abundance (Dalen & Voorhorst; Lewis *et al.*; Løwenstein *et al.*; Wodehouse, 1945). The wood of the tree-sized species, which is similar in structure to that of birches, is used in limited amounts for pipe stems, hoops, tool handles, carved items, molding, and boxes. *Corylus cornuta* spreads aggressively and is considered a weedy pest in northern forest plantations (Tappeiner). Cultivars of a number of species, especially the shrubby *C. Avellana* and the arborescent *C. Colurna*, are widely planted as ornamental shrubs.

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