

HOLLIES (AQUIFOLIACEAE) OF NORTH AMERICA NORTH OF MEXICO

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ABSTRACT

Included here are descriptions, keys to species, synonymy, and geographic distributions of Aquifoliaceae in North America north of Mexico. The family in this area comprises 20 species of *Ilex* (now including *Nemopanthus*). Three of the species are not native in North America, but are becoming naturalized. Notes are included on natives as well as non-native taxa that have significant populations outside of cultivation. One species (*Ilex curtissii*) and one subspecies (*Ilex opaca* subsp. *arenicola*) are resurrected. This treatment consolidates the delineation and nomenclature of North American taxa and provides a new key for their identification.

The Aquifoliaceae is a widespread, diverse, ecologically and horticulturally significant family of woody plants. One or more species, wherever they grow, are known widely to the public. Several species and their cultivars are widely used as ornamentals, and arboreta and botanical gardens often have living collections. Hollies are important food sources for birds and small mammals. In spite of wide public recognition and horticultural use, there has been no comprehensive study of the family since when the only monograph appeared more than 120 years ago (Loesener 1901). From then until now, the estimated number of species in the family has increased by more than 50% (Chen 2023).

AQUIFOLIACEAE Bercht. & J. Presl, 1825 (nom. cons.)

Dioecious shrubs or trees with glabrous or pubescent twigs and smooth bark (except on very old specimens); lenticels prominent. Leaves alternate, simple and petiolate, with pinnately netted venation, evergreen or deciduous; stipules small, linear and soon deciduous. Inflorescences axillary, cymose, paniculate, umbellate, fascicled, or flowers solitary. Plants dioecious. Flowers radially symmetrical, imperfect by abortion of stamens or pistil, calyx lobes free or fused together basally; corolla lobes entirely free or fused together basally, usually whitish but rarely yellowish, greenish, pink or red; sepals 3-11; petals 3-9; stamens as many as the corolla lobes and alternate with them, anthers dorsifixed, longitudinally dehiscent; ovary compound and superior, 3-9 locular, ovules 1-2 per locule, anatropous, placentation pendulous; stigma capitate or discoid, usually more or less lobed, subsessile or sessile, and persistent. Fruit a subspherical, usually red, purple or black drupe with 4 or more endocarps (pyrenes), mainly bird-dispersed. Flowers in spring; fruits in autumn.

In the Aquifoliaceae floral characteristics traditionally have been essential for generic circumscription. However, the prevailing current practice is to recognize only a single genus, *Ilex*, in the family, regardless of floral differentiation. Estimates range from 500 to 600 species of *Ilex* worldwide. Since the only monograph of the family is more than 120 years old, there have been major regional treatments (e.g., Hu 1949-1950; Chen 2023) and many new species have been described (e.g., Rodríguez 2022). The family is critically in need of an updated worldwide monograph.

Centers of diversity are in the regions of southeast Asia and meso/northern South America; diversity is extremely low in Africa and western Oceania. *Ilex* is widespread; other genera previously included in the family are currently either merged with *Ilex* (*Nemopanthus*) or reassigned to other families (*Phelline* on New Caledonia; *Sphenostemon* on Borneo).

The fundamental inflorescence of the family is axillary-cymose, often simplified by reduction. Nonfunctional, reduced androecia and gynoecia are present in the flowers of the opposite sex. Since functionally bisexual flowers have never been experimentally verified, the term polygamodioecious (which crept into the literature — Brizicky 1964) is not applicable. Hollies are strictly dioecious. Many species that are geographically, ecologically, or phenologically isolated in nature can and do hybridize when brought together under artificial conditions.

Within a single species, reproductively isolated populations often vary from more widespread phenotypes, and variation is sometimes clinal or ecophenic. Parthenogenesis (J.M. Herr Jr., pers. comm., described a possible mechanism) and resulting parthenocarpy apparently occur, and there is anecdotal evidence that pollen from some species can trigger fruit and seed development in other species without genetic recombination. This raises the possibility that populations could result from a single pistillate plant.

Embryos (at least in North American species) typically are immature when fruits ripen and typically require several subsequent cool-warm temperature oscillations to provide time for embryo maturation. That, of course, provides extended time for seed dispersal. Seeds (in pyrenes) are primarily bird-dispersed. Since birds disperse the seeds of all hollies widely, local environmental conditions will determine which species' seeds or seedlings will succeed in various habitats.

Plants of some species (notably *Ilex paraguayensis* of South America and *Ilex vomitoria*) are used to brew caffeine-rich drinks. The very light-colored wood of *Ilex opaca* is used for specialty inlay work. A number of species and cultivars are used in ornamental horticulture and landscaping.

ILEX L., Sp. Pl. 125. 1753; Gen. Pl. 45. 1754. (Ilex, the Latin common name for *Quercus ilex*, the cork oak)

Prinos L., Sp. Pl. 330. 1753; Gen. Pl. 398. 1754.

Aquifolium Miller, Gard. Dict., abr. ed., 4. 1754.

Illicioides Dum. Cours., Bot. Cult. 4: 127. 1802.

Nemopanthus Raf., Amer. Monthly Mag. & Crit. Rev. 4: 357. 1819 (nom. cons.).

Ageria Raf., Sylv. Tellur. 46. 1838.

Additional generic synonyms have been proposed.

Shrubs or trees. Leaves persistent or deciduous, margins entire to crenate, serrate, spinose or involute, often lighter in color underneath. Flowers from leaf axils of current year's growth, or on new branches from last year's nodes. Calyx lobes 4-11 (rarely 3), gamosepalous, persistent in fruit (except deciduous from fruits of *I. amelanchier* and taxa in the Nemopanthoid segregate, noted in the key below). Corolla lobes 4-10, apo- or gamopetalous (sometimes barely the latter in *I. opaca* and *I. aquifolium*), with oblong to obovate lobes, whitish or yellow, rotate or completely free (Nemopanthoids only); filaments alternate with and free (*I. collina*, *I. mucronatus* only) or adnate to corolla lobes. Pistillate flowers single to many in cymose axillary inflorescences, staminate flowers cymose and more numerous. Flowers in our area mostly white or cream, nectariferous, and often pollinated by bees. Drupes red, black, yellow, orange or dark purple, 3-9-carpellate, with the same number of stony endocarps/pyrenes. $2n = 36, 40$.

The number of perianth segments is more variable in staminate than in pistillate flowers. There is a tendency for species with a variable number of perianth segments to have more corolla lobes than calyx lobes. Geographic distributions indicated below mainly are from personal collections and personally annotated herbarium specimens, supplemented with electronic specimen images from North American herbaria.

Key to the species

1. Petals distinct, linear, not imbricate or valvate before anthesis; stamens distinct from corolla; sepals of staminate flowers narrowly lanceolate, ephemeral or obsolete; fruiting pedicels much longer than leaf petioles; pistillate sepals deciduous from mature fruit. (Rare in the high Appalachians, or limited to northern regions; this is the Nemopanthoid segregate.)
 2. Leaves with regularly glandular-serrate margins, gradually acuminate and apically glandular; sepals broadly subulate, 0.3 mm wide basally or wider; endocarps 5.2 mm long or longer, dorsally and usually laterally ribbed **Ilex collina**
 2. Leaves entire or remotely toothed (rarely regularly toothed or lobed), apically obtuse with mucro; sepals lacking, or linear to setaceous; 0.1 mm wide at most; endocarps 5.2 mm long or shorter, dorsally smooth or ribbed, laterally smooth **Ilex mucronata**
1. Petals united at base (the corolla shed as a unit), ovate or broadly oblong, imbricate in bud; stamens adnate to corolla at its base; fruiting pedicels various in length; calyx lobes broadly triangular or ovate, persistent after flowering (staminate flowers) and on fruit (except *I. amelanchier*).
 3. Leaves persistent through at least one winter season.
 4. Leaf margins strongly spinose-dentate, or leaves with a robust apical spine.
 5. Flowers and fruit borne on primary twigs of current season's growth **Ilex opaca**
 5. Flowers and fruit from the axils or spur branches of previous season's growth.
 6. Spines 4 or more along each side of leaves **Ilex aquifolium**
 6. Spines 0 to 3 along each side of leaves **Ilex cornuta**
 4. Leaf margins crenate, serrate or entire; leaf apices lacking strong spines.
 7. Leaf margins entire, or with an occasional tooth.
 8. Leaves punctate-glandular beneath **Ilex krugiana**
 8. Leaves not glandular beneath.
 9. Leaves 7 mm or less wide, petioles 0.5-2.6 mm long **Ilex myrtifolia**
 9. Leaves more than 1 cm wide, petioles 5 mm long or longer **Ilex cassine**
 7. Leaf margins obviously crenate or serrate.
 10. Leaves not glandular beneath.
 11. Leaves remotely spinulose-serrate to entire.
 12. Leaves 7 mm or less wide, petioles 0.5-2.6 mm long **Ilex myrtifolia**
 12. Leaves more than 1 cm wide, petioles 5 mm long or longer **Ilex cassine**
 11. Leaves regularly crenate **Ilex vomitoria**
 10. Leaves glandular beneath.
 13. Sepals 4 (rarely 3 or 5) **Ilex crenata**
 13. Sepals regularly 5 or more.
 14. Calyxes entire or erose; leaves entire or remotely spinulose-serrate **Ilex coriacea**
 14. Calyxes ciliate; leaves remotely crenate distally **Ilex glabra**
 3. Leaves deciduous each autumn.
 15. Plant in fruit.

16. Calyx lobes 5 or more.
 17. Endocarps smooth, lacking longitudinal dorsal ribbing.
 18. Calyces ciliate **Ilex verticillata**
 18. Calyces not ciliate **Ilex laevigata**
 17. Endocarps dorsally and longitudinally grooved or ribbed.
 19. Leaf margins remotely serrulate to subentire; plants of Coastal Plain swamps, marshes, ponds and other wet habitats ... **Ilex amelanchier**
 19. Leaf margins obviously and strongly serrate; plants of various upland, well-drained habitats; never in lowland wet habitats.
 20. Leaves acute to abruptly acuminate, petioles averaging less than 10 mm long **Ilex ambigua**
 20. Leaves long-acuminate to attenuate, petioles averaging more than 10 mm long **Ilex montana**
16. Calyx lobes 4, or calyces absent from fruit.
 21. Calyces often absent on fruits; leaf margins serrulate to subentire; leaves evenly pubescent over their lower surfaces **Ilex amelanchier**
 21. Calyces obvious on fruits; leaf margins obviously crenate or serrate; pubescence of lower leaf surfaces, if present, confined to the main veins.
 22. Pedicels far exceeding the subtending petioles; leaves definitely serrate and at least abruptly acuminate **Ilex longipes**
 22. Pedicels about as long as, or shorter than leaf petioles; leaves cuneate and not acuminate.
 23. Leaves narrowly elliptic, oblanceolate, or obovate, less than 1 cm wide at their widest point; plants native in northern Florida and extreme southeast Georgia **Ilex curtissii**
 23. Leaves broader, averaging 1 cm or more wide; plants ranging widely, from the Florida Panhandle to the Midwest and eastward **Ilex decidua**
15. Plant in flower.
 24. Staminate flowers present.
 25. Corolla lobes ciliate (sometimes remotely so).
 26. Leaf apices gradually acuminate to attenuate; petioles averaging more than 1 cm long **Ilex montana**
 26. Leaf apices obtuse, acute or abruptly acuminate; petioles averaging less than 1 cm long **Ilex ambigua**
 25. Corolla lobes not ciliate.
 27. Calyces and corollas 4-lobed.
 28. Lower leaf surfaces densely pubescent, usually with an obvious, light-colored network of veins **Ilex amelanchier**

28. Lower leaf surfaces' pubescence, if any, confined to the main veins;
veins on leaf undersides not forming an obvious, light-colored network.
29. Leaves definitely serrate and at least abruptly acuminate **Ilex longipes**
29. Leaves cuneate and not acuminate.
30. Leaves narrowly elliptic, oblanceolate, or obovate, less
than 1 cm wide at their widest point; plants native only in
northern Florida and extreme southeast Georgia **Ilex curtissii**
30. Leaves broader, averaging 1 cm or more wide; plants
ranging widely, from the Florida Panhandle to the Midwest
and eastward **Ilex decidua**
27. Calyces and corollas predominately 5- or more lobed.
31. Calyces ciliate **Ilex verticillata**
31. Calyces not ciliate.
32. Leaves tomentose underneath **Ilex amelanchier**
32. Leaves glabrous or glabrate underneath **Ilex laevigata**
24. Pistillate flowers present.
33. Corolla lobes (at least some of them) ciliate.
34. Leaf apices gradually acuminate to attenuate; petioles averaging
more than 1 cm long **Ilex montana**
34. Leaf apices obtuse, acute or abruptly acuminate; petioles averaging
less than 1 cm long **Ilex ambigua**
33. Corolla lobes not ciliate.
35. Pedicels pubescent.
36. Pedicels less than 7 mm long **Ilex verticillata**
36. Pedicels more than 7 mm long **Ilex amelanchier**
35. Pedicels glabrous.
37. Calyx lobes 4.
38. Lower leaf surfaces densely pubescent, usually with a
light-colored, obvious network of veins **Ilex amelanchier**
38. Pubescence of lower leaf surfaces (if present) confined
to the main veins; lower leaf surfaces lacking an obvious
network of light-colored veins.
39. Pedicels considerably longer than subtending leaf petioles;
leaves definitely serrate and at least abruptly acuminate **Ilex longipes**
39. Pedicels as long as, or shorter than petioles;
leaves cuneate and not acuminate.
40. Leaves narrowly elliptic, oblanceolate, or obovate,
less than 1 cm wide at their widest point; plants native
only in northern Florida and extreme southeast Georgia **Ilex curtissii**

40. Leaves broader, averaging 1 cm or more wide; plants ranging widely, from the Florida Panhandle to the Midwest and eastward ***Ilex decidua***

37. Calyx lobes 5 or more.

41. Lower surfaces of leaves evenly pubescent ***Ilex amelanchier***
 41. Lower surfaces of leaves pubescent on the main veins, or not pubescent.
 42. Calyxes ciliate ***Ilex verticillata***
 42. Calyxes not ciliate ***Ilex laevigata***

1. ***Ilex ambigua*** (Michx.) Torr., Fl. New York 2: 2. 1843. Carolina Holly, Sand Holly

Prinos ambiguus Michx., Fl. Bor. Amer. 2: 236. 1803.

Ilex mollis A. Gray, Man. Bot. 306. 1848.

Ilex dubia (G. Don) B.S.P., Prelim. Cat. Anthop. Pterid. New York 11. 1883. Of some authors.

Ilex caroliniana (Walt.) Trel., Trans. Acad. Sci. St. Louis 5: 347. 1892 (non Miller 1768).

Ilex buswellii Small, Bull. Torr. Bot. Club 51: 382. 1924.

Shrubs or small trees. Leaves elliptic to broadly ovate, abruptly to gradually acuminate, petioles of oldest mature leaves averaging less than 1 cm long, glabrous to densely pubescent, apices obtuse to acuminate, margins serrate to crenate-serrate, bases attenuate, cuneate or obtuse; petioles to 1 cm long, glabrous to densely pubescent. Pistillate flowers solitary, staminate flowers 1-6 at a node, pedicellate or from peduncles 0.6-1.5 mm long; pedicels and peduncles glabrous or pubescent; perianth segments ciliate. Pistillate calyx lobes 3-7, corolla lobes 4-5, pedicels 0.5-5.5 mm long. Staminate calyx lobes 3-6, 0.8-1.3 mm long; corolla lobes 3-6, 1.4-2.7 mm long; pedicels 1.4-10 mm long. Fruits 5-11 mm broad, red; endocarps 4-5, dorsally and occasionally laterally ribbed.

Various well-drained, forested habitats: AL, AR, FL, GA, IL, KY, LA, MS, NC, OK, SC, TN, TX, VA, doubtfully native in eastern MI; northeastern Mexico.

Populations south and west of the Appalachians are often isolated and exhibit considerable phenotypic latitude. Heavily pubescent forms [f. *channellii* Edwin; f. *mollis* (Gray) C.F. Reed] occur throughout the range of the species; sunny and/or xeric conditions seem to favor the phenotypic expression of pubescence. Plants of Florida sometimes referred to *Ilex buswellii* Small are simply *Ilex ambigua* phenotypes that result from more xeric conditions. (Krakow, pers. comm.).

On the edge of the Blue Ridge Escarpment exists a unique series of upland forest-habitat *I. ambigua* populations that are elevationally and geographically isolated from *I. montana* and *I. ambigua* populations in the wider region. They are uniformly dwarf (less than 20cm tall) shrubs, and their short stature seems to be unrelated to frequency of forest fire. I have observed them from Polk Co., North Carolina to Pickens Co., South Carolina. Since they are unique in growth habit and are reproductively isolated from *I. ambigua* and *I. montana* populations, they probably warrant taxonomic recognition.

2. ***Ilex amelanchier*** M.A. Curtis ex Chapm., Fl. S. U.S., ed. 2, 270. 1872. Sarvis Holly

Ilex dubia (G. Don) B.S.P., Prelim. Cat. Anthop. Pterid. New York 11. 1883. (!NY)

Shrubs. Leaves deciduous, elliptic, ovate or obovate, to 8.3 cm long and 5.5 cm wide, tomentose but becoming glabrate and strongly rugose with age above, tomentose beneath, apices acute or abruptly acuminate, often mucronate, margins finely and sometimes remotely serrulate (occasionally with one to several isolated dentate teeth), bases cuneate to truncate; petioles to 1.4 cm long, tomentose. Pistillate flowers pedicellate, 1-2 per node; staminate flowers solitary, cymose or umbellate; perianth segments entire to subciliate. Pistillate calyx lobes 4-5, 0.8-1 mm long; corolla

lobes 4-5, 0.8-1.2 mm long; corolla lobes 3-5, 2-3 mm long; pedicels to 3.8 mm long, glabrous or pubescent. Fruits 6-10 mm broad, red; endocarps 2-4, dorsally ribbed, laterally unribbed. Early in the growing season, veins on the underside of leaves typically form a conspicuous, light-colored network. Later in the season, the network often fades and becomes obscure.

Pond margins, river swamp sloughs, blackwater swamp forests, cypress ponds, low pinelands and savannas, Coastal Plain: AL, FL, GA, LA, MS, NC, SC.

Hu (J. Arnold Arb. 30: 248) stated that "in *Ilex* the calyx is always persistent." *Ilex amelanther* and the nemopantheoids are exceptions, as the calyx often is absent on fully mature fruits. It has been established that this species is closely related to one species previously included in *Nemopanthus* (Powell et al. 2000). *Ilex/Nemopanthus collina* apparently was not included in the aforementioned study, so its close evolutionary affinities remain uncertain.

3. ***Ilex aquifolium* L.**, Sp. Pl. 125. 1753. English Holly, and many other common names.

Ilex aquifolium var. *vulgaris* Ait., Hort. Kew. 1: 169. 1789.

Ilex vulgaris A. Gray, Brit. Arr. Brit. Pl. 2: 491. 1831.

Shrubs or small trees to 6 m tall, with 4-merous flowers and fruits. Marginal spinose teeth/lobes more numerous than those of *Ilex cornuta*. Pistillate inflorescences are more complex and fruits are smaller than those of *I. opaca*.

Mesic woodlands; naturalized: CA, OR, WA; Canada: BC, ON. Native in Europe, escaped from nursery operations and managed landscapes, and considered to be a developing ecological disaster in some native woodlands.

Various selections of *Ilex* \times *aquipernyi* Gable ex Whittm. (= the hybrid between *Ilex pernyi* and *Ilex aquifolium*) are encountered in horticultural use and will not fit the key to species here.

This species is prominent in Celtic and Norse mythology.

4. ***Ilex cassine* L.**, Sp. Pl. 125. 1753. Cassena, dahoon

Ilex caroliniana Mill., Gard. Dict. ed. 8, no. 3. 1768.

Ilex dahoon Walt., Fl. Carol. 241. 1788.

Ilex dahoon Eaton, Man. Bot. ed. 7, 349. 1836.

Ilex dahoon var. *laurifolia* (Nutt.) Göpp., Index Semin. WROCL Wratislav. 1852: 4. 1852.

Ilex dahoon var. *ligustrina* Alph. Wood, Amer. Bot. Fl. 207. 1870.

Ilex mexicana (Turcz.) Black ex Hemsl., Biol. Cent. Amer. 1: 187. 1880.

Small trees. Leaves persistent, lanceolate, oblanceolate, elliptic, oblong or obovate, to 11 cm long and 5.1 cm wide, glabrous or pubescent above and beneath, apices emarginate, obtuse, acute or abruptly acuminate, margins entire to remotely spinulose-serrate, bases attenuate, cuneate or obtuse; petioles to 1.6 cm long, glabrous, puberulous or tomentose. Pistillate flowers solitary, cymose, paniculate or umbellate; calyces ciliate, corollas eciliate. Pistillate calyx lobes 4-5, to 0.3-0.7 mm long; corolla lobes 4-5, 1.5-2.3 mm long, peduncles to 2.7 cm long, pedicels 1.5-10 mm long, glabrous or tomentose. Staminate flowers in many-flowered panicles or umbels. Staminate calyx lobes 4-5, 0.7-1 mm long; corolla lobes 4, 1.2-2.2 mm long. Staminate pedicels to 2.3-5.3 mm long. Fruits 4-8 mm broad, red (rarely yellow); endocarps 3-5, dorsally and laterally ribbed.

Ponds, swamps, savannas, seepages in the outer Coastal Plain; AL, FL, GA, LA, NC, SC; Caribbean.

The yellow-fruited form has not yet been assigned a valid epithet. Natural hybrids of these plants with those of *Ilex opaca* are referred to ***Ilex* \times *attenuata* Ashe** (non T. & G. ex S. Wats. 1878; non Steyerl. 1988.). *Ilex* \times *attenuata* 'East Palatka' is a popular cultivar.

5. ***Ilex collina*** E.J. Alexander, Castanea 6: 30. 1941. Long-stalked Mountain Holly

Nemopanthus collinus (Alex.) R.C. Clark, J. Arn. Arbor. 55: 437. 1974.

Ilex longipes Chapm. ex Trel. Often misapplied to this species.

Tall shrubs. Leaves elliptic to oblanceolate, obovate or occasionally suborbicular, gradually acuminate, regularly glandular-serrate and glandular apically. Perianth apopetalous and aposepalous. Sepals broadly subulate and 0.3 mm wide or wider, semi-persistent on fruit; petals linear or lanceolate, flared at base and often with a small basal lobe. Fruiting pedicels 11-43 mm long. Fruits ripening red (rarely yellow); endocarps dorso-longitudinally ribbed and usually laterally ribbed as well, 5.2-6.3 mm long, 2.6-4 mm broad.

Appalachian bogs and wet woods at intermediate to high elevations: NC, TN, VA, WV; reported from GA.

Of conservation concern. This is a Pleistocene relic occurring in widely separated populations and requiring relatively open, high elevation wet habitats. Pistillate plants often fruit heavily, but no one has reported success in germinating seed, and seedling recruitment appears to be nil in populations I have observed. Plants of this species which I have had in cultivation for many years are intolerant of competition. *Nemopanthus collinus* f. *vantrumpii* M. Brooks is a yellow-fruited form. Ants (*Camponotus*) but not bees have been observed pollinating.

Sterile specimens of this species are superficially similar to specimens of *Ilex montana*. However, the glandular-serrate characteristic of *Ilex collina* leaves is easy to see with a hand lens; leaves of *Ilex montana* are serrate but lack glands on the tips of the teeth.

6. ***Ilex coriacea*** (Pursh) Chapm., Fl. S. U.S. ed. 1, 270. 1860. Sweet Gallberry

Shrubs. Leaves elliptic, oblanceolate, ovate or obovate, to 7.6 cm long and 3.5 cm wide, glabrous above except for puberulous midribs, punctate-glandular and glabrous or puberulous beneath, apices acute or abruptly acuminate, margins involute, remotely spinulose-serrate or entire, bases attenuate or cuneate; petioles to 1.0 cm long, puberulous. Pistillate flowers solitary to 6 per node in verticels or compressed racemes, peduncles less than 1 mm long; staminate flowers in 3-many-flowered verticels; calyces and corollas entire or erose. Pistillate calyx lobes 6-11, 0.7-1.1 mm long, dorsally convex in fruit; corolla lobes 4-10, 1.8-2.5 mm long; pedicels to 14 mm long, puberulous. Staminate calyx lobes 6-9, 0.4-1.7 mm long; corolla lobes 5-9, 1.8-2.3 mm long, pedicels 3-11 mm long, glabrous or puberulous. Fruits 5-10 mm broad, black (rarely red); endocarps 6-10, unribbed.

Low woods, seepages, swamp ecotones, savannas, pocosins, in the Coastal Plain: AL, FL, GA, LA, MS, NC, SC, TX, VA; Caribbean.

Although this species generally flowers slightly earlier than *Ilex glabra*, intermediates between *I. coriacea* and *I. glabra* occur only rarely. Both species are the sources of gallberry honey.

7. ***Ilex cornuta*** Lindl. & Paxt., Flower Gard. 1: 43. 1850. Chinese Holly, Horned Holly

Ilex furcata Lindl. ex Goepp., Gartenflora 3: 322. 1854.

Ilex fortunei Lindl., Gard. Chron. 1857: 868. 1857.

Ilex cornuta var. *fortunei* (Lindl.) S.Y. Hu, J. Arnold Arb. 30: 356. 1949.

Tree; native in eastern Asia. Leaves thick and coriaceous, with 2 (or very rarely more) lobes on each side, the lobes tipped with very strong indurate spines; apex indurate-spinose. Pistillate inflorescence umbelliform, many-flowered; staminate inflorescence not seen. Flowers and fruits 4-merous, red; fruits are larger than those of *I. opaca* and *Ilex aquifolium*.

Woodlands: CA, FL, LA, NC, SC, TN; probably escaping from cultivation elsewhere.

Although there are frequent anecdotal mentions of staminate ‘Burfordii’ plants in the horticultural literature, this writer has not observed staminate plants. Pistillate cultivars (*I. cornuta* f. *burfordii* DeFrance) are often used in managed landscapes, and although cultivated pistillate plants are routinely planted far from plants of any *Ilex* species, they routinely set heavy fruit (and seed) crops, apparently parthenogenetically. Offspring from the viable seed invariably display the parental species (not the form’s) phenotype. Since hollies are bird-dispersed, we may expect this species to become more common. I have not observed whether the offspring from f. *burfordii* are pistillate or staminate or both.

8. ***Ilex crenata*** Thunb. in J. Murr., Syst. Veg. ed. 14, 168. 1784. Japanese Holly

This native of eastern Asia has been documented as escaped in AR, CT, DE, MD, NC, NJ, OR, OH, PA, and probably in other States. Although native Asian populations are more variable, the relatively small-leaved plants known to occur in North America are shrubs that occasionally assume the form of small trees. Plants in our region have distally crenate-serrulate leaves.

Since plants of both species are evergreen and leaves are somewhat similar, plants of *Ilex crenata* could easily be confused with plants of *Ilex vomitoria*. Here are differences -- *Ilex crenata* leaves are glandular underneath; leaves of *Ilex vomitoria* are not glandular underneath. *Ilex crenata* has black fruit (red or yellow in *I. vomitoria*). In fresh specimens, the undersides of *I. vomitoria* twigs of the current season’s growth are gray above and beneath and distally purple; by contrast, undersides of *I. crenata* twigs of the current season’s growth in are brown on their upper sides and quite green underneath.

It is uncertain whether plants of *Ilex crenata* var. *radicans* (Nakai ex H. Hara) Ohwi, Bull. Nat. Sci. Mus. Tokyo 33: 78. 1953, occur in North America.

9. ***Ilex curtissii*** (Fern.) Small, Man. Southeast. Fl. 815. 1933 Curtiss’s possumhaw

Ilex decidua var. *curtissii* Fern., Bot. Gaz. 33: 155. 1902.

Shrubs or small trees. Typification of this taxon rests on three duplicate specimens of *A.H. Curtiss* 6736, collected on 24 Oct 1900. Two of these specimens (isolectotypes!) are at GH; the third is at GA. The type specimens and other specimens recently examined show that this taxon includes only plants with consistently small, narrow, elliptic, oblanceolate to obovate leaves (See Fig. 1, below). I have recently re-examined images of these three specimens and numerous other specimens of *Ilex decidua* sensu lato in this part of the USA. More specimens of this taxon are available now than were available when I began studying hollies, decades ago.

To my considerable surprise, plants congruent with the type specimens of *Ilex curtissii* have a well-defined documented geographic range, allopatric with respect to *Ilex decidua*, and extending in Florida from Jefferson to Levy counties, north and east to Columbia, Baker, and Nassau counties and in Georgia to Charlton and Lowndes counties. I also have seen specimens referable to *Ilex curtissii* from Pasco, Hillsborough, and Polk counties, Florida. Also interesting is that within its range, *I. curtissii* apparently occurs in a range of habitats where one might expect to find *Ilex decidua*. It is obvious that some environmental factor(s) have favored the evolution and persistence of this consistently very small-leaved phase. Careful study of this species might reveal other discontinuities between this species and *Ilex decidua*.

The range boundary between plants of *Ilex curtissii* and *Ilex decidua* is sharp, and there are very few morphological intermediates. From the evidence I’ve seen, *I. decidua* but not *I. curtissii* occurs in the Florida Panhandle. Other rather small-leaved specimens of *I. decidua* from other states (sometimes very far) outside of this range are not congruent with the type material; usually, the leaves

are too large or not a conformational shape. Also, the incongruent specimens do not display any coherent geographic range.

Distribution: Northern Florida and extreme southeastern Georgia, as indicated above; various habitats, on riverbanks and seasonally wet woods and depressions, to drier habitats in upland woods, sometimes over thin soil.

10. **Ilex decidua** Walt., Fl. Carol. 241. 1788. Possumhaw
Ilex cuthbertii Small, Man. Southeast. Fl. 815. 1933.
Ageria retusa Raf., Sylv. Tellur. 46. 1838.

Shrubs or small trees. Leaves deciduous, elliptic, oblanceolate or obovate, to 7 cm long and more than 3 cm wide, puberulous above at least on midrib, usually puberulous at least on midrib and glaucous beneath, apices bluntly acute or rarely abruptly acuminate with a mucronate, obtuse or retuse tip, margins crenate and usually involute, bases attenuate to obtuse; petioles to 1.5 cm long, usually puberulous. Pistillate flowers pedicellate, 1-2 per node, staminate flowers solitary, cymose or umbellate; perianth segments eciliate. Pistillate calyx lobes 4, 0.9-1.2 mm long; corolla lobes 4 (rarely 5), 2.3-3 mm long, glabrous. Staminate calyx lobes 4-7, ca. 0.8 mm long; corolla lobes 4-6, 2-3 mm long; pedicels 1.5-20 mm long, glabrous. Fruits 3-10 mm broad, red or yellow, endocarps 4 (rarely fewer by abortion), dorsally and occasionally laterally ribbed. $2n = 40$ (Darlington & Wylie 1955; Federov 1969).

Various upland and lowland habitats, often in alluvial or circumneutral soil: AL, AR, FL, GA, IL, IN, KA, KY, LA, MD, MS, MO, NC, OK, SC, TN, TX, VA; northeast Mexico.



Figure 1. *Ilex decidua* var. *curtissii*, one of the three isotypes. "Woods along the Suwannee River, near Branford, Fla.," A.H. Curtiss 6736 (GH). Image courtesy of SERNEC and the Gray Herbarium.

11. ***Ilex glabra*** (L.) A. Gray, Gray's Man., ed. 2, 264. 1856. Bitter Gallberry
Prinos glaber L., Sp. Pl. 330. 1753.

Soboliferous shrubs. Leaves elliptic, persistent or semipersistent, elliptic, oblanceolate or obovate, to 5.9 cm long and 2.8 cm wide, glabrate above, punctate-glandular or (rarely) not and glabrous beneath, apices acute to obtuse, margins involute, remotely crenate distally, bases attenuate or cuneate; petioles to 0.9 cm long, puberulous. Pistillate flowers solitary or in 2-3-flowered cymes, peduncles 6-7 mm long; staminate flowers solitary or in 2-many-flowered often umbelliform racemes or panicles; calyces ciliate, corollas ciliate or not. Pistillate calyx lobes 5-9, 0.4-1.0 mm long, not noticeably dorsally convex against fruit.; corolla lobes 4-7, 1.9-2.8 mm long; pedicels to 11 mm long, puberulous; Staminate calyx lobes 5-9, 0.4-0.9 mm long; corolla lobes 4-7, 1.3-2.8 mm long, pedicels 1.8-5.3 mm long, glabrous or puberulous. Fruits 3.5-8 mm broad, black, red, or rarely opalescent; endocarps 2-6, unribbed.

Low woods, seepages, salt marsh margins, swamp ecotones, savannas, pocosins; Coastal Plain and other coastal regions, rare in Valley & Ridge and Piedmont: AL, CT, DE, FL, GA, LA, MD, ME, MA, MI, NJ, NY, NC, RI, SC, VA; Nova Scotia.

These plants are grown as ornamentals and are somewhat tolerant of salt spray; hence, they are occasionally planted along winter-treated paved roadways. White-fruited forms are identified as *Ilex glabra* f. *leucocarpa* Woods (Rhodora 58: 25. 1956). See also the notes under *I. coriacea*.

12. ***Ilex krugiana*** Loes. in Engl., Bot. Jahrb. 15: 317. 1892. Tawnyberry Holly

Shrubs or small trees. Leaves persistent, elliptic, oblong or ovate, to 7 cm long and 3.5 cm wide, glabrous above, glandular-punctate beneath, apices acuminate, margins entire, bases broadly cuneate or obtuse; petioles to 2.3 cm long, glabrous. Pistillate flowers individually pedicellate, 1-4 per node; staminate flowers pedunculate, in (2)3-7 flowered umbels; calyces entire to ciliolate, corollas entire to erose. Pistillate calyx lobes 3-5, to 1.3 mm long; corolla not seen; pedicels 4-7 mm long, glabrous. Staminate calyx lobes 3-4, to 1 mm long; corolla lobes 4, 2-2.3 mm long; peduncles 2-4 mm long, glabrous, pedicels 2-3 mm long, glabrous. Fruits 4-4.5 mm broad, brownish-purple; endocarps 2-4, smooth.

Hammocks and pinelands, FL Everglades and Keys; Caribbean.

13. ***Ilex laevigata*** (Pursh) A. Gray, Man. Bot., ed. 2, 264. 1856. Smooth Winterberry

Prinos laevigatus Pursh, Fl. Amer. Sept. 1: 220. 1814.

Tall shrubs. Leaves deciduous, elliptic, oblanceolate or obovate, to 11 cm long and 4.5 cm wide, subrugose and glabrate to pubescent, apices obtuse to acuminate, often mucronate, margins minutely or appressed-serrate to subentire, bases cuneate to obtuse; petioles to 1.4 cm long, glabrous or pubescent. Pistillate flowers solitary, staminate flowers solitary or in pedunculate 2-4-flowered cymes; calyx lobes eciliate or (very rarely) sparsely ciliate, corollas eciliate. Pistillate calyx lobes 5-8, 0.5-1 mm long; corolla lobes 5-8, 1.8 mm long; pedicels 2.3-10 mm long, glabrous. Fruits 5-8 mm broad, red or yellow, endocarps 4-8, dorsally and laterally unribbed.

Savannas, bogs, pond margins, low woods: AL, CT, DE, ME, MD, MA, NH, NC, NJ, NY, PA, RI, SC, VA.

Yellow-fruited forms are referred to *Ilex laevigata* f. *herveyi* B.L. Robinson.

14. ***Ilex longipes*** Chapm. ex Trel., Trans. Acad. Sci. St. Louis 5: 346. 1889. Buckbush, Georgia Holly

Ilex decidua var. *longipes* (Chapm. ex Trel.) Ahles, J. Elisha Mitch. Sci. Soc. 80: 173. 1964.

Ilex decidua subsp. *longipes* (Chapm. ex Trel.) A.E. Murr., Kalmia 13: 8. 1983.

Shrubs. Leaf margins definitely serrate, apices at least somewhat acuminate, bases cuneate to attenuate. A detailed diagnostic description of this species is lacking here, because during the period (1960s-1980s) when the author was carefully measuring many holly specimens, this taxon was considered to be a less than well-defined variety of *Ilex decidua*. After several decades more of observing this group of plants in the field and herbaria, I consider it to comprise a valid species.

Woodlands: SC, GA, AL, MS, TN, AR, TX.

Ilex longipes is a recognizable and consistent morphological entity that displays a core distribution on the southern Cumberland Plateau/Sand Mountain (TN, AL and GA), where it entirely replaces *I. decidua* and displays habitat differentiation. Outside of the core distribution, intermediates between *I. longipes* and *I. decidua* do occur. Although pistillate pedicel length is a reliable difference between the two species, it does not appear that there is a discontinuous difference between staminate pedicel length between the two species. However, the length of the filaments of *Ilex decidua* tend to be less long or slightly longer than leaf petioles, and *Ilex longipes* staminal filaments tend to be longer.

During field work on the Alabama Cumberland Plateau (Sand Mountain) in the 1960s, the author verified the northern Alabama common name of Buckbush for *Ilex longipes*. More recently, some botanists have adopted the common name of Georgia Holly. There is a multi-specimen population sample of *Ilex longipes* from Chapman's Tennessee topotype locality ("Mts. above Cowan") on deposit in EKY.

15. ***Ilex montana*** Torr. & Gray ex Gray, Man. Bot. N. U.S. 276. 1848 (non Griseb. 1861). Mountain Holly

Ilex monticola Gray, Man. Bot. N. U.S. 306. 1848 (non Tul. 1857).

Ilex mollis Gray, Man. Bot. N. U.S. ed. 5, 306. 1867.

Ilex amelanchier var. *monticola* Alph. Wood, Amer. Bot. Fl. 1: 208. 1870

Ilex beadlei Ashe, Bot. Gaz. 24: 377. 1897.

Ilex ambigua var. *montana* (Torr. & Gray) Ahles, J. Elisha Mitch. Sci. Soc. 80: 173. 1964.

Large shrubs or multi-stemmed small trees. Leaves narrowly to broadly ovate, apices gradually acuminate to attenuate, and petioles of oldest mature leaves more than 1 cm long. Other characteristics as given above for *Ilex ambigua*. $2n = 40$ (Darlington & Wylie 1955; Federov, 1969).

Well-drained upland woods, mostly in the Appalachian system; AL, KY, GA, MD, MA, NC, NJ, NY, PA, SC, TN, WV, VA.

This species with strong Appalachian affinity is closely related to *Ilex ambigua*, which is a more widespread and more variable taxon. Throughout its range, occasional highly pubescent forms of *I. montana* (such as *I. beadlei*) approximate the leaf morphology of *I. ambigua*. A reasonable way to determine or annotate these specimens would be "*Ilex beadlei*, the highly pubescent phase of *Ilex montana* T. & G. ex Gray." The transition from *I. ambigua* to *I. montana* morphology is sharp in the Blue Ridge Escarpment region of the Carolinas and southwestern Virginia, but the transition is more gradual in the northern Tennessee Valley and Kentucky. *Ilex ambigua* plants with relatively long petioles occur in the Ozarks and Ouachitas, but the leaves are not gradually acuminate.

16. ***Ilex mucronata*** (L.) Powell, Savonlainen, & Andrews, Kew Bull. 55: 345. 2000. Mountain Holly, Catberry, Faux Houx

Vaccinium mucronatum L., Sp. Pl. 350. 1753.

Nemopanthus fascicularis Raf., J. Phys. Chim. Hist. Nat. Arts 89: 96. 1819 (and

Nemopantes Raf., an orthographic variant).

Nemopanthus canadensis DC., Mem. Soc. Phys. Genève 1: 44. 1821.

Nemopanthus mucronatus (L.) Trel., Transact. Acad. Sci. St. Louis 5: 349. 1892

Ilicioides mucronata Britt., Mem. Torr. Bot. Club 5: 217. 1894.

Tall shrubs or small trees, often strongly soboliferous. Leaves usually oblong or elliptic but varying to ovate, sublanceolate or oblanceolate; margins normally entire, but occasionally with marginal teeth. Leaf apices obtuse to acute or abruptly acuminate, or sometimes emarginate by abortion of the mucro. Perianth apopetalous and aposepalous. Sepals linear or setaceous, 0.1 mm or less wide; staminate sepals very quickly deciduous and pistillate sepals deciduous before the fruit matures. Petals linear or narrowly lanceolate. Fruiting pedicels 7-34 mm long. Fruits ripening bluish-black (rarely yellow); endocarps dorso-longitudinally smooth or ribbed, laterally unribbed, 3.8-5.2 mm long, 2.5-3.2 mm broad. $2n = 40$.

Bogs: CT, IN, MA, MD, ME, MI, MN, OH, NH, NJ, NY, PA, RI, VT, WV, WI; Canada: NB, NL, NS, ON, PE, QC.

Plants of this species comprise an important component of the shrub zone in many *Sphagnum* bogs north of the continental glacial boundary. *Nemopanthus mucronatus* f. *chrysocarpa* (Farwell) Fern. (Rhodora 42: 307. 1940) is a yellow-fruited form, the name not formally transferred into *Ilex*.

17. *Ilex myrtifolia* Walt., Fl. Carol. 241. 1788. Myrtle-leaved Holly

Ilex dahoon var. *myrtifolia* (Nutt.) Chapm., Fl. S. U.S. 269. 1860.

Ilex cassine var. *myrtifolia* (Walt.) Sarg., Garden & Forest 2: 269. 1889.

Shrubs or small trees. Leaves persistent, lanceolate, narrowly elliptic or oblong, to 4 cm long and 0.7 cm wide, glabrous or minutely strigillose on midribs beneath; petioles 0.5-2.6 mm long. Pistillate flowers solitary or in 2-3-flowered cymes, peduncles 2-7 mm long. Pistillate calyx lobes 4-6, 0.5-1 mm long; corolla lobes 4, 1.9-2.7 mm long, pedicels 2-7 mm long, strigillose. Staminate flowers in umbelliform or cymose inflorescences; peduncles 2-7 mm long, pedicels 1.6-4.7 mm long, calyx lobes 4-6, 0.4-1 mm long, corolla lobes to 2.6 mm long. Fruits 4-8 mm broad, red (rarely yellow); endocarps 3-5, dorsally and laterally ribbed.

Cypress ponds, pocosins, savannas in the Coastal Plain: AL, FL, GA, LA, MS, NC, SC.

Yellow-fruited plants are referred to *Ilex myrtifolia* f. *lowei* Blake (Rhodora 26: 231. 1924). Intermediate populations of both hybrid and introgressive origin involving *I. cassine* and *I. myrtifolia* are referred to *Ilex cassine* var. *angustifolia* Ait. (Hort. Kew. 1: 170. 1789). Such intermediate populations are often encountered. Plants of this species growing farther inland tend to be tardily winter-deciduous.

18. *Ilex opaca* Ait., Hort. Kew. ed. 1, 169. 1789. American Holly

Ilex canadensis Michx., Arbust. Amer. 64. 1785.

Ilex laxiflora Lam., Encycl. 3: 147. 1789.

Ageria opaca (Ait.) Raf., Sylva Tellur. 47. 1838.

Ilex aquifolium var. *opaca* (Ait.) Laurentius, Laur. Gärtneri 40: 42. 1868.

Leaves persistent, oblanceolate, elliptic or obovate, glabrate or glabrous when mature, apices acute or acuminate, spinose-mucronate, margins spinose-dentate or occasionally subentire or entire, bases cuneate to obtuse; petioles to 1.5 cm long, puberulous. Pistillate flowers 1-2 per node; staminate flowers solitary, racemose, umbellate, cymose, or in many-flowered bracteolate panicles; calyces ciliate, corollas eciliate. Pistillate calyx lobes 4, to 1.8 mm long, glabrous or puberulous. Staminate calyx lobes 4-5, 0.5-1.2 mm long; corolla lobes 4, 1.7-3.7 mm long, pedicels to 14 mm long, glabrous or puberulous. Fruits 5-13 mm broad, red or yellow; endocarps 4-6, dorsally and laterally ribbed.

Two subspecies.

18a. ***Ilex opaca*** subsp. ***opaca***

Single to few-trunked tree, to about 30m tall, typically a subcanopy inhabitant. **Leaves** to more than 12 cm long and 7.5 mm wide. Pistillate inflorescence solitary, cymose or racemose, pistillate pedicels and/or peduncles to 12 mm long. Staminate flowers solitary, racemose, umbellate, cymose, or in many-flowered bracteolate panicles. Endocarps 4-6. $2n = 36$ (Federov 1969).

The yellow-fruited form is referred to *Ilex opaca* f. *xanthocarpa* Rehd. (Mitt. Deutsch. Dendrol. Ges. 1907: 73. 1907). Plants with a high percentage of entire leaves have been referred to *I. opaca* f. *subintegra* Weatherby ex Rehder (Rehd., Man. CuIt. Trees Shrubs 543. 1923).

Upland or low woods, swamps, maritime forests: AL, AR, DE, FL, GA, IL, IN, KY, LA, MA, MD, MI, MO, MS, NC, NJ, NY, OH, OK, PA, RI, SC, TN, TX, VA, WV.

Intermediates between typical *Ilex opaca* and *Ilex cassine* are referable to *Ilex* \times *attenuata* Ashe (J. Elisha Mitch. Sci. Soc. 40: 44. 1924). Various cultivar selections of this hybrid are often planted and will not fit the key to species here. For example, the common cultivar 'East Palatka' would key here to *Ilex cornuta* f. *burfordii*. Keys simply cannot account for all cultivars!

The light-colored wood of these plants is popular for specialty inlay purposes.

18b. ***Ilex opaca*** subsp. ***arenicola*** (Ashe) A.E. Murr., *Kalmia* 12: 21. 1982. Scrub Holly, Dune Holly

Ilex arenicola Ashe, J. Elisha Mitchell Sci. Soc. 40: 44. 1924.

Ilex cumulicola Small, Bull. Torr. Bot. Club. 51: 382. 1924.

Ilex opaca var. *arenicola* (Ashe) Ashe, Charleston Mus. Quart. 1(2): 31. 1925.

Ilex pygmaea McFarlin, Rhodora. 34: 17. 1932.

Ilex arenicola var. *obovata* McFarlin, Rhodora 34: 234. 1932.

Ilex arenicola var. *paucidens* McFarlin, Rhodora 34: 235. 1932.

Shrubs or trees to 15 m tall. Leaves to 6 cm long and 3.1 cm wide, somewhat smaller than typical leaves of subsp. *opaca*, with margins usually (sometimes much) more involute. Pistillate inflorescence solitary or of two pedunculate flowers, pistillate pedicels and/or peduncles to 7 mm long. Staminate flowers (specimens in USF Herbarium, courtesy of SERNEC), cymo-umbelliform. Fruits red, occasionally yellow. Endocarps 4.

Pine and oak scrub ecosystems; upland, xeric, sandy habitats: central Florida northward, excluding northwest peninsular Florida and the Florida Panhandle.

Of conservation concern, this subspecies replaces typical *Ilex opaca* in the xeric sand scrub of central and northern Florida.

Whether this entity warrants recognition at specific rank is problematic. *Ilex opaca* subsp. *opaca* is a wide-ranging taxon and displays genetic variability. Numerous cultivars have been selected for foliage, fruit, and growth habit. In addition, typical *I. opaca* succeeds in habitats ranging from river swamp forests to xeric uplands.

Subsp. *arenicola*, however, consistently displays adaptation we might attribute to a uniquely xeric series of habitats, in its size, somewhat reduced leaf size, xeromorphic foliage, and somewhat reduced inflorescences. Some specimens in Florida herbaria are intermediate between the two subspecies. I also have observed a few specimens approaching the morphology of subsp. *arenicola* from xeric habitats in DE, NJ and LA. The northern range of subsp. *arenicola*, from Flagler and Marion counties south to Pasco, is within the range of subsp. *opaca*, although the southern part of the former's range (Manatee to Glades counties) is outside the range of subsp. *opaca*.

Xeric sand ridge habitats are not uncommon in the southeastern Coastal Plain. However, Florida pine-oak scrub habitats are unique habitats, noted for endemic taxa. The biological uniqueness of these habitats strongly suggests that environmental factors are strongly selective. It is significant that only in these unique Florida ecosystems has the extreme phenotype (and the ecological tolerance to environmental extremes) of subsp. *arenicola* become consistent. However, gene flow between populations of both subspecies almost certainly occurs.

During preparation of this manuscript, I have re-examined specimens of subsp. *arenicola* I examined decades earlier, as well as other specimens collected more recently. Since I have been unable to discern morphological discontinuities (including reproductive morphology) between the two partially sympatric subspecies, I suggest that the differences are, to a degree, environmentally induced. It would help if experimental data were available (e.g., morphological transects, reciprocal transplants, germination and isozymes studies) that might indicate the extent to which genetic and physiological divergence has occurred in the two *opaca* entities. On the other hand, the difference between these two *opaca* phases is far from random or desultory and apparently has evolutionary significance. Taking all of these perspectives into consideration, a reasonably conservative approach is to rank the *arenicola* plants at the subspecies level.

The publication of *Ilex arenicola* Ashe preceded the publication of *Ilex cumulicola* Small by a single month.

19. ***Ilex verticillata*** (L.) A. Gray, Man. Bot., ed. 2, 264. 1856. Black alder, Winterberry Holly, Apalanche, Aulne Blanche

Prinos verticillata L., Sp. Pl. 330. 1753.

Ilex verticillata var. *padifolia* (Willd.) Torr. & Gray ex S. Wats., Bibl. Index N. Amer. Bot. 1: 160. 1878.

Ilex verticillata var. *tenuifolia* (Torr.) S. Wats., Bibl. Index N. Am. Bot. 1: 160. 1878.

Ilex verticillata var. *cyclophylla* B.L. Rob., Rhodora 2: 105. 1900.

Ilex bronxensis Britt., Man. Fl. N. U.S. 604. 1901.

Ilex verticillata var. *fastigiata* (Bickn.) Fern., Rhodora 23: 274. 1922.

Shrubs, rarely small trees. Leaves deciduous, elliptic, oblanceolate or obovate, to 13 cm long and 6 cm wide, usually strongly rugose, apices obtuse to acuminate, margins serrate or doubly serrate, bases cuneate or obtuse; petioles to 1.6 cm long, glabrous to densely tomentose. Calyces ciliate. Pistillate flowers solitary, cymose or fasciculate, 1-4 flowers per node; staminate flowers in many-flowered or reduced umbels; calyces abundantly ciliate, corollas eciliate. Pistillate calyx lobes 5-8, to 1.3 mm long; corolla lobes 5-8, 1.3-2.4 mm long; pedicels 1-4.5 mm long, glabrous or pubescent. Staminate calyx lobes 4-7, to 1.3 mm long; corolla lobes 5-8, 1.5-2.4 mm long; pedicels to 4 mm long, glabrous or pubescent. Fruits 4-9 mm broad, red or yellow; endocarps 2-7, dorsally and laterally unribbed. $2n = 36$ (Darlington & Wylie 1955; Federov 1969).

Upland or low woods, seepages, streambanks, bogs and pond margins, various geological provinces: AL, AR, CT, DE, GA, IL, IN, KY, LA, MD, MA, ME, MI, MN, MO, NC, NH, NJ, NY, NC, OH, PA, RI, SC, TN, TX, VA, VT, WV.; Canada: NB, NL, NS, ON, PE, QC.

Leaves of northern populations are noticeably smaller than those of southern populations. Yellow-fruited forms may be referred to *Ilex verticillata* f. *chrysocarpa* Robinson or to *I. verticillata* f. *aurantiaca* (Moldenke) Rehder, which has deeper golden-colored fruit. This species has the widest native geographic range of any North American *Ilex* species. Artificially produced hybrids between this and a closely related east Asian species *Ilex serrata* Thunb. have reported (pers. comm., Warren Hill) to have been produced at the U.S. National Arboretum.

20. ***Ilex vomitoria*** Ait, Hort. Kew. ed. 1(1): 170. 1789. Yaupon

Ilex floridana Lam., Tab. Encycl. 1: 356. 1792.

Ilex cassena Michx., Fl. Bor.-Amer. 2: 229. 1803.

Ilex dahoon sensu Pursh, Fl. Am. Sept. 117. 1816.

Ilex caroliniana (Lam.) Loes., Bot. Centralbl. 47: 163. 1891.

Shrubs or small trees. Leaves persistent, lanceolate, elliptic or ovate, to 5.5 cm long and 2.8 cm wide, glabrous above and beneath except sometimes puberulous on midribs; apices obtuse, margins crenate, bases cuneate, truncate or obtuse; petioles to 4.8 mm long, puberulous. Pistillate flowers solitary to 4 per node, individually pedicellate; staminate flowers in many-flowered fascicles or sessile umbelliform inflorescences, rarely solitary; calyces and corollas ciliate or eciliate. Pistillate calyx lobes 3-5, 0.4-0.8 mm long; corolla lobes 3-5, 1.6-2 mm long; pedicels 1.6-2.9 mm long, glabrous or puberulous. Staminate calyx lobes 3-4, 0.3-0.7 mm long; corolla lobes 4, 1.7-2.6 mm long; pedicels 2.0-2.8 mm long, glabrous or proximally puberulous. Fruits 4.6 mm broad, red (rarely yellow), endocarps 2-4, dorsally ribbed, laterally ribbed or not. $2n = 40$ (Darlington & Wylie 1955; Federov 1969).

Sandy or dry woods and thickets, upper margins of salt marshes: AL, AR, FL, GA, LA, MS, OK, NC, SC, TX, VA; Chiapas, Mexico (*Ilex vomitoria* var. *chiapensis* A.J. Sharp !isotypes, TENN); reported in Cuba.

The Chiapas plants have been described at varietal and subspecific rank, but specimens are rare, which complicates critical study. The yellow fruited form of *Ilex vomitoria* has not received a formal epithet.

Yaupon has become a popular ornamental; escapes from cultivation should be expected. Native Americans formerly brewed the caffeine-containing foliage into a drink, which is seeing a modest revival in popularity at the present time. This taxon is a member of a species complex native from North America to MesoAmerican uplands and the Caribbean. The entire complex warrants careful study.

Some plants in the Arkansas-Oklahoma contact region between the two species are intermediate between *Ilex vomitoria* and *Ilex decidua*. The only observed difference between the two in that region apparently is whether plants are deciduous or not, and that is not always clear.

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