

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

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THE ORDER CELASTRALES, as delimited here, includes the families Celastraceae, Hippocrateaceae, and Aquifoliaceae, as well as several other allied families (e.g., Siphonodontaceae, Stackhousiaceae) not represented in the southeastern United States. The Staphyleaceae, usually regarded as members of either Celastrales or Sapindales, are excluded from both these orders, and will be treated within Cunoniales (or Saxifragales *sensu lato*), where they seem to belong (cf. C. G. G. J. van Steenis, Fl. Males. I. 6: 49. 1960).

CELASTRACEAE R. Brown in Flinders, Voy. Terra Austr. 2: 554. 1814,  
"Celastrinae," nom. cons.

(STAFF-TREE FAMILY)

Usually glabrous trees or shrubs, rarely woody vines, sometimes gutta-percha [or rubber] bearing; nodes unilacunar. Leaves simple, membranaceous to coriaceous, opposite or alternate [rarely minute or rudimentary], petiolate, deciduous or persistent; stipules minute, usually caducous. Inflorescences axillary and/or terminal, cymose (usually dichotomously branched) or racemose, or the flowers solitary and/or fascicled in the leaf axils. Flowers small, regular, hypogynous, perigynous, or semi-epigynous, bisexual or unisexual by abortion (the plants then monoecious or dioecious), pediceled (except *Gyminda*). Sepals 4 or 5, small, connate about half of their length or more, or nearly distinct, usually imbricate.

<sup>1</sup>Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of George R. Cooley and the National Science Foundation and under the direction of Carroll E. Wood, Jr., and Reed C. Rollins. This treatment follows the pattern established in the first paper in the series (Jour. Arnold Arb. 39: 296-346. 1958) and continued through those in volumes 40-44 (1959-1963). The area covered is bounded by and includes North Carolina, Tennessee, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with any supplementary material in brackets. References which the author has not seen are marked by an asterisk.

The author is indebted to Carroll E. Wood, Jr., for his many valuable suggestions; to Harry Ahles, George R. Cooley, Wilbur H. Duncan, and James W. Hardin, for checking herbarium records on the distribution of some genera of Celastraceae, especially *Paxistima*, in the southeastern United States; and to Mrs. Gordon W. Dillon, for her help in preparation of the manuscript. The illustration of *Euonymus* was drawn by Dorothy H. Marsh, in part from fresh fruiting material sent by R. B. Channell.

Petals 4 or 5, distinct, inserted under the disc, usually imbricate. Stamens 4 or 5 [very rarely 8–10], distinct, alternipetalous, inserted under or on the disc at its exterior margin, reduced or wanting in ♀ flowers; filaments short; anthers basi- or dorsifixed, introrse, longitudinally dehiscent. Nectariferous disc intrastaminal, usually conspicuous, variously shaped, rarely wanting. Gynoecium syncarpous, 2–5-carpellate, rudimentary in ♂ flowers; stigma single, ± lobed, or stigmata 2–5; style single or wanting; ovary superior, distinct or ± immersed in and sometimes fused with the disc, or semi-inferior, 2–5-locular; placentation axile; ovules usually 2, more rarely 1 or 4–6 [to many] in a locule, pendulous from the top or ascendent from the base of the placenta, anatropous, usually apotropous, 2-integumented. Fruit a loculicidal [rarely septicidal] capsule or a drupe [berry or samara], (1)2–5-locular, the locules 1- or 2–6-seeded. Seeds often arillate; endosperm present [rarely absent]; embryo straight, axile; cotyledons large, foliaceous, often green; radicle short, superior or inferior. TYPE GENUS: *Celastrus* L.

A primarily pantropical family of 50–55 genera and over 800 species, extending with several genera into the temperate zones, to which a few are restricted. Six genera occur in our area. The genus *Paxistima* Raf. (also incorrectly spelled *Pachystima* or *Pachistima*; see Wheeler, p. 293) is excluded from the flora of the southeastern United States.<sup>2</sup>

Pollination by insects seems to be the rule. Data on floral biology and anatomy, as well as on embryology are sparse, pertaining to a few genera and species. Chromosome counts made for four genera (eight species) are  $2n = 32$  and 64, 46, and 80. Though sparse, these numbers may suggest that both aneuploidy and polyploidy have been of importance in the evolutionary development of Celastraceae.

The family is closely related to Hippocrateaceae and Aquifoliaceae. A relationship with Siphonodontaceae and Stackhousiaceae has also been assumed (Takhtajan).

<sup>2</sup> The occurrence of *Paxistima Canbyi* Gray in North Carolina was first recorded by Chapman (Fl. So. U.S. ed. 2. 613. 1889) on the authority of M. A. Curtis. Apparently on the same basis the species was included by Small (Fl. SE. U.S. 735. 1903; Man. SE. Fl. 818. 1933), who repeatedly mentioned the occurrence of the species in North Carolina. Massey (1940) was not able to verify this but concluded that "considering the distribution of limestone, this species should be sought more extensively in southern Ohio, northern Kentucky, northeastern Tennessee, and possibly in western Maryland and south central Pennsylvania." No collections of *P. Canbyi* from North Carolina have been available until J. W. Hardin recently investigated a report of the species in Mitchell County, North Carolina. He found (1963) that this species was introduced, apparently from West Virginia, into the Green & Taylor nursery, now abandoned; the plants are growing well and the population is expanding, but still without competition from the native vegetation; it remains to be seen whether the plants survive the invasion of the forest in the years to come. "In the meantime, although *Pachystima Canbyi* is now thriving in this location in western North Carolina and without constant cultivation, we still cannot call it a definite member of the native southeastern flora."

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## KEY TO THE GENERA OF CELASTRACEAE

General characters: *woody plants with opposite or alternate leaves with minute, usually caducous stipules; flowers small, bisexual or unisexual, 4- or 5-merous, usually with a conspicuous nectariferous disc, in axillary dichasial cymes or few-flowered fascicles, more rarely in terminal thyrses; stamens alternipetalous; ovary usually superior, 2-5-locular, sometimes ± immersed in the disc, the placentae axile, the ovules usually 2 or 1; fruit either a loculicidal capsule with arillate seeds or a drupe.*

- A. Plant scandent, woody, dextrorsely twining; leaves alternate; flowers in terminal or axillary raceme-like thyrses; capsule subglobular, ca. 1 cm. in diameter, orange or yellow; seed covered with a scarlet aril. 2. *Celastrus*.
- A. Plant nonscandent, shrubby, sometimes prostrate or creeping, or arborescent; flowers in axillary dichasial cymes or fascicles.
- B. Leaves opposite; flowers in axillary dichasially branched cymes.
- C. Plant deciduous, leaves membranaceous (rarely subcoriaceous); anther-halves diverging; ovary locules 2-6(10?)-ovulate; fruit a 3-5-lobed, -valved, sometimes tuberculate capsule; seed covered with a scarlet aril; occurring north of central Florida. 1. *Euonymus*.
- C. Plant evergreen, leaves thin-coriaceous; anther-halves parallel; ovary locules 1-ovulate; fruit a small drupe; seed exarillate; subtropical Florida.
- D. Flowers slender pediceled, 2-bracteolate at base of pedicel, bisexual; sepals connate nearly half their length; stigmata 4, narrow, spreading, raised on a short style; ovary 4-locular; ovule ascendent from the base of the placenta; drupe red,

- obliquely obovoid, 3–6 mm. long, excentrically crowned with a persistent style. . . . . 4. *Crossopetalum*.
- D. Flowers sessile in the forks of dichasia, 2-bracteolate just under the calyx, unisexual, the plants dioecious; sepals nearly distinct; stigmata 2, broad, sessile; ovary 2-locular; ovule pendulous from the top of the placenta; drupe black or dark blue, ellipsoidal, 6–8 mm. long, crowned with the persistent stigmata. . . . . 5. *Gyminda*.
- B. Leaves alternate; flowers in axillary few-flowered fascicles or solitary.
- E. Leaves fleshy-coriaceous, with indistinct venation on the upper surface; flowers 5-merous, with a 3-carpellate gynoecium; fruit a red ellipsoidal to obovoid capsule, 8–12 mm. long, dehiscent by 3 valves; seed arillate. . . . . 3. *Maytenus*.
- E. Leaves thin-coriaceous, conspicuously veined on the upper surface; flowers 4-merous, with a 2-carpellate gynoecium; fruit a scarlet subglobular drupe 5–6 mm. in diameter, containing 2 stones; seed exarillate. . . . . 6. *Schaefferia*.

## Subfamily CELASTROIDEAE

## Tribe CELASTREAE

1. *Euonymus* Linnaeus, Sp. Pl. 1: 197. 1753; Gen. Pl. ed. 5. 91. 1754.

Deciduous [or evergreen] shrubs [sometimes climbing by aërial root-lets] or trees, with green, usually quadrangular branchlets [sometimes corky ridged or warted]. Leaves opposite [rarely whorled or alternate], membranaceous [to coriaceous], crenate-serrate or serrulate, with gland-tipped teeth [rarely prickly or entire], usually petioled; stipules caducous [rarely persistent]. Inflorescences axillary [and terminal], simple or compound dichasially branched (1)3–15(31)-flowered peduncled cymes with minute caducous bracts. Flowers 4- or 5-merous, hypogynous (or semi-epigynous?), bisexual (rarely also unisexual by abortion, the plants then polygamo-monoecious or -dioecious). Sepals connate about half their length. Petals ovate-orbicular to suborbicular [to linear], sometimes shortly clawed, greenish white to purple [or greenish yellow]. Stamens inserted on the margin of a conspicuous fleshy usually 4- or 5-lobed nectariferous disc; filaments subulate, very short [more rarely  $\pm$  elongate, or wanting]; anthers basifixed, broad, the anther-halves connivent [or confluent] at apex and much divergent to subhorizontal toward the base, 2[1]-locular at anthesis, dehiscent by 2 lateral [or 1 continuous subapical] slit. Gynoecium 3–5-carpellate; stigma small, indistinctly 3–5-lobed; style short, stoutish; ovary superior (or semi-inferior?), [2]3–5-locular,  $\pm$  immersed in, except the top, and fused at base with the disc; ovules 2–6(10)[–12] in a locule,  $\pm$  ascendent or rarely pendulous, superposed or collateral [or in 2 rows], apotropous, the nucellus thin. Fruit a leathery capsule, usually pink to red or purple, subglobular or oblate [or obovoid, obconical or obpyramidal], smooth or “tuberculate” [or echinate], usually [2]3–5-locular, -lobed [-angled or -winged, or rarely round in cross-section], and -valved; locules 2–6(10?)-seeded. Seed partially or com-

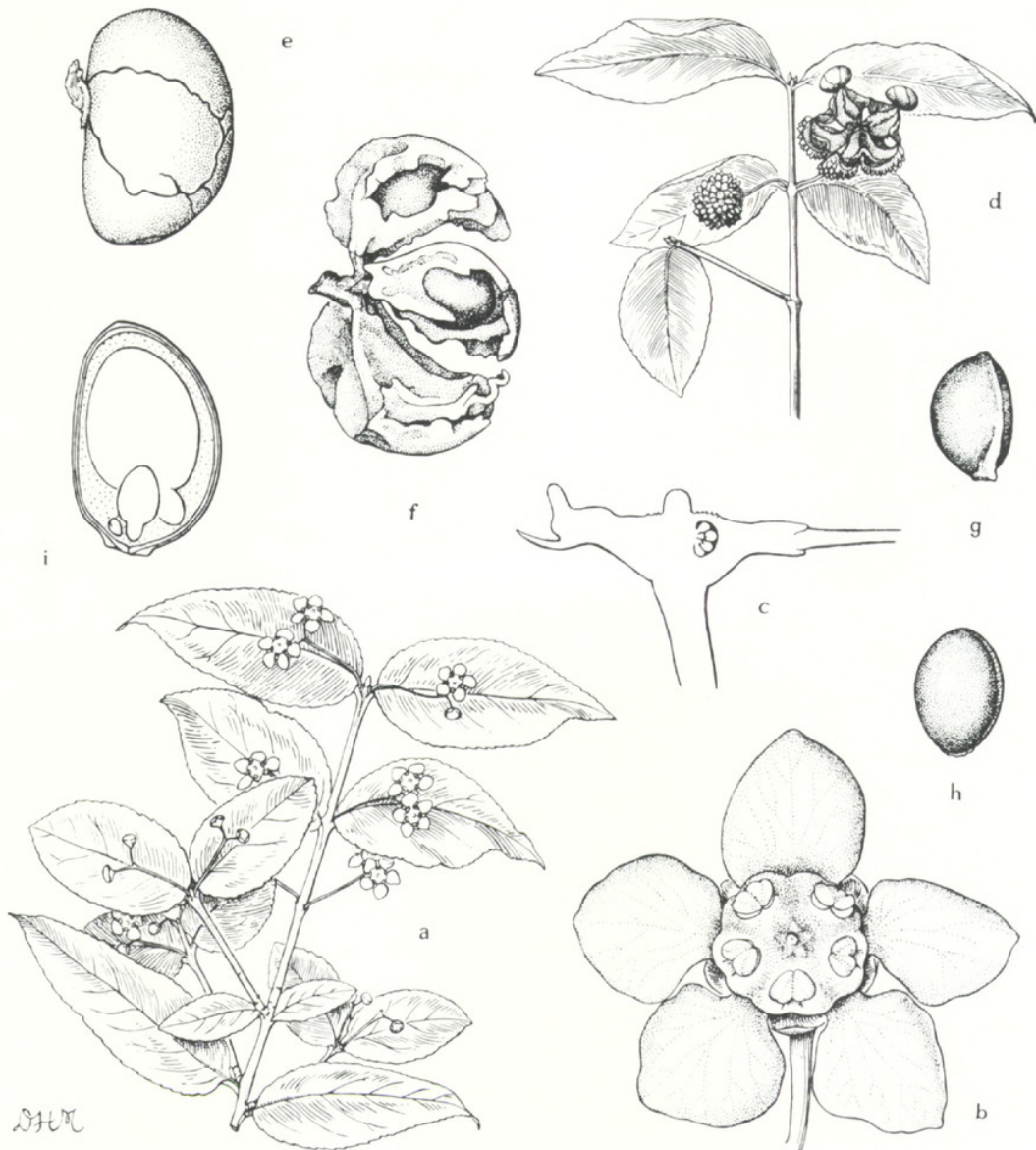


FIG. 1. *Euonymus*. *E. americanus*: a, flowering branchlet, from above,  $\times 1$ ; b, flower,  $\times 10$ ; c, flower in diagrammatic vertical section, to show insertion of petal and stamen (anther removed) and ovary immersed (except papillate top) in disc,  $\times 16$ ; d, fruiting branchlet bearing incompletely developed capsule and open loculicidal capsule with two clusters of seeds,  $\times 1$ ; e, cluster of four arillate seeds from a single locule, arils squeezed together,  $\times 6$ ; f, three lower seeds of same cluster separated to show varying development of aril,  $\times 6$ ; g, h, two views of seed, showing raphe, the micropyle below,  $\times 6$ ; i, seed in diagrammatic vertical section in plane of raphe, showing two seed coats and three of four embryos embedded in endosperm (stippled),  $\times 12$ .

pletely covered by a scarlet or orange aril; seed coat leathery, orange- or reddish-brown [to black, or whitish]; endosperm abundant, fleshy; embryo large, the cotyledons roundish to oblong, usually green; the radicle inferior or superior. LECTOTYPE SPECIES: *E. europaeus* L.; see N. L. Britton, N. Am. Trees 630. 1908. (Name from Greek, *eu*, good, and

*onoma*, name, i.e., of good name, famous, apparently applied ironically to the genus, the plants having had the bad reputation of poisoning cattle.)

— SPINDLE-TREE.

A genus of nearly 180 species of the North Temperate Zone and the Tropics, concentrated in eastern Asia, a few in Europe, Africa, Madagascar, and Australia, completely absent in South America and the West Indies; five to seven unsatisfactorily known species in Central America (south to Costa Rica), four in the United States, and three in our area. Blakelock's classification, which recognized subgenera *EUONYMUS* and *KALONYMUS* Beck emend. Blakel. with six sections and 14 series, is followed here. All American species belong to subg. *EUONYMUS*, characterized by small, ovoid, acute winter buds, filamented (*vs.* subsessile) stamens, anthers two-locular at anthesis and dehiscing by two distinct slits, and unwinged capsules. The sections are based primarily on the shape and degree of lobation and the character of the surface of the capsules.

Section *EUONYMUS* (§ *Biloculares* Rouy & Fouc. emend. Blakel.) includes about 70 Old World and two (or three) American species, all with two-ovulate locules and smooth fruits. The primarily northeastern American *Euonymus atropurpureus* Jacq., wahoo or burning bush, a large shrub or small tree with four-merous purple flowers, occurs in thickets along streams and in rich damp woods from southern Ontario to southern Minnesota, southeastern South Dakota (and locally in Montana), south to Nebraska, Kansas, Oklahoma, northeastern Texas, Arkansas, and Tennessee, with scattered stations in North Carolina, Georgia, Alabama, Mississippi, and northernmost Florida (Gadsden County). *Euonymus occidentalis* Nutt. ex Torr., differing in part in its five-merous flowers, occurs from Washington to California. *Euonymus europaeus*,  $2n = 64$ , with greenish-white petals and 3-5-flowered inflorescences, often grown as an ornamental, has been recorded as naturalized in at least the northeastern United States.

Primarily of eastern Asia, sect. *ECHINOCOCCUS* Nakai emend. Blakel., characterized by five-merous flowers (in our species), 4-6(-10?)-ovulate locules, and tuberculate fruits, includes five North American species, two in our area. *Euonymus americanus* L. (including *E. angustifolius* Pursh), strawberry-bush,  $2n = 64$ , an upright or straggling (very rarely creeping)  $\pm$  stoloniferous shrub with rather variable, rarely obovate thickish leaves, densely minutely pustulate branchlets, flowers about 1 cm. in diameter, distinctly clawed petals, and (3-)5-locular capsule is common throughout much of our area.<sup>3</sup> It occurs in rich lowland woods and thickets, in ravines

<sup>3</sup> Two poorly known variants of uncertain taxonomic status have been described as varieties of *Euonymus americanus*. The var. *angustifolius* (Pursh) A. Wood, with narrowly lanceolate to sublinear leaves (as against lanceolate or ovate, rarely obovate, ones in var. *americanus*) was described from Georgia and is also known from at least North Carolina and/or Tennessee (French Broad River), and northernmost Florida (Apalachicola River). The var. *sarmentosus* Nutt., a prostrate, usually creeping shrub, rarely seen with flowers (Meehan), seems to be of rare occurrence in some parts of our area (at least in Tennessee and Arkansas). Perhaps it represents a distinct

and bottoms, and on river bluffs from New York west to southern Illinois and southeastern Missouri, south to eastern Texas and Highlands County, Florida. The primarily northeastern American *E. obovatus* Nutt., running strawberry-bush, a creeping shrub with upright flowering shoots 3–6 dm. high, thin, usually obovate leaves, smooth branchlets, flowers 6–7 mm. in diameter, nonclawed petals, and usually three-locular capsules, reaches its southern limits in Tennessee and southwestern North Carolina, where it occurs in rich, moist or dry woods, on moist shaded banks, or on rocky bluffs.

The Asiatic *Euonymus alatus* (Thunb.) Sieb., of sect. MELANOCARYA (Turcz.) Nakai emend. Blakel., an ornamental shrub with spreading, usually corky-winged branches and smooth four-parted capsules, has become established locally in at least Connecticut, West Virginia, and Kentucky.

Flowers of the genus usually are bisexual and proterandrous, but the occasional occurrence of unisexual flowers (the plants consequently monoecious or dioecious) has been recorded at least in European species. Hymenoptera and Diptera, especially short-tongued bees and flies, seem to be the main pollinators. The attractive arillate seeds are dispersed by birds. Seeds in many (perhaps most) species have a long dormant period, requiring stratification before germination. Apomixis (adventitious polyembryony from the inner integument of the ovule, perhaps rarely from the endosperm) is known in *Euonymus latifolius* (L.) Mill., *E. americanus*, and *E. alatus*, as well as in several eastern Asiatic species. Fertilization is necessary for the development of adventitious embryos.

Berkeley, on the basis of four species, interpreted the "broad flat structure surrounding the ovary" [the disc] as a floral tube and considered the ovary to be semi-inferior, the flowers semi-epigynous. The occurrence of fibriform vessel elements in the wood of the stem and of secretory cells (sacs) containing gutta-percha in the phloem of the roots (and sparingly of the axis) is notable.

Reported chromosome numbers (four species) are  $2n = 32$  and 64. The lower number was found in *Euonymus japonicus* Thunb. and *E. Fortunei* (Turcz.) Hand.-Mazz., representing the presumably primitive sect. ILICIFOLIA, while the higher pertains to *E. europaeus* and *E. americanus*, of two presumably advanced but not closely related sections.

The genus is closely related to the West Indian *Torralsasia* Krug & Urb. and the New Guinean *Xylonymus* Kalkm.

Many species are grown as ornamentals. At least *Euonymus verrucosus* Scop. and *E. europaeus* are cultivated in the Soviet Union as sources of gutta-percha. The seeds (containing the glucoside evonosid, a heart poison) and the vegetative organs of at least the European species and *E. atropurpureus* are said to be poisonous.

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population of the species which seems to be more pronouncedly stoloniferous than the typical variety. In the study of the variants the common occurrence of apomixis (adventitious embryony) in *E. americanus* should be taken into consideration.



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The large number of references has been greatly reduced here. Under family references see ANDERSSON, BERKELEY, HOU (pp. 243-254), LOESENER (1942, pp. 115-124), MEZ (pp. 333, 334), REHFUS (1914; 1917, pp. 310-323), and SARGENT.

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## 2. *Celastrus* Linnaeus, Sp. Pl. 1: 196. 1753; Gen. Pl. ed. 5. 91. 1754.

Scandent, usually dextrorsely twining shrubs with alternate, elliptic to suborbicular or obovate, serrulate to serrate [or subentire], deciduous

[rarely persistent] leaves. Inflorescences few- or many-flowered terminal and/or axillary, sometimes raceme-like, thyrses [or simple to compound dichasia] with minute caducous bracts. Flowers small, greenish [white], hypogynous or perigynous, [bisexual or] unisexual (the plants dioecious), with articulate pedicels. Calyx campanulate, 5-lobed, the lobes imbricate, persistent in fruit. Petals 5, inserted under the margin of the disc. Stamens 5, inserted on [or under] the margin of the disc, abortive and sterile in ♀ flowers; filaments subulate [or linear]; anthers introrse, ovate [oblong] in outline, apiculate, cordate at base, dorsifixed and usually versatile, laterally or introrsely dehiscent by 2 longitudinal slits. Nectariferous disc membranaceous and cupuliform [or fleshy and flat], shallowly 5-lobed [or entire]. Gynoecium usually 3(4)-carpellate, rudimentary in ♂ flowers; stigma usually 3(4)-lobed [the lobes sometimes bifurcate]; style short; ovary superior, usually incompletely [completely] 3-locular, with axile placentae at the very base; ovules 2 [1] in each locule, ascendent, usually with a cup-shaped aril at base, the nucellus thin. Fruit a small orange to yellow subglobular [to cylindrical] leathery capsule, about 1 cm. in diameter, tipped by the persistent style, usually incompletely 3-locular, 3-valved; locules 2(1)-seeded. Seed ascendent, ellipsoidal, usually ± plano-convex, obtuse at base, attenuate toward the apex, inclosed in a fleshy crimson aril open at apex; seed coat thin, brown, leathery; endosperm copious; embryo broad-spatulate; radicle inferior. LECTOTYPE SPECIES: *C. scandens* L.; see Britton & Brown, *Illus. Fl. No. U.S. ed. 2. 2*: 492, 493. 1913. (Name from Greek, *kelastros*, the ancient name of an evergreen tree, presumably *Phillyrea latifolia* L., Oleaceae, applied by Linnaeus to this genus.)

A primarily tropical genus of about 30 (or more) species, widely distributed in eastern Asia, Malaysia, Australia, Oceania, Madagascar, and continental America. Hou (1955) established subg. *CELASTRUS* (flowers unisexual, ovary locules 2-ovulate, fruits usually 3–6-seeded), with 23 species in the Old World and one in eastern North America, and subg. *RACEMOCELASTRUS* Hou (flowers bisexual, ovary locules 1-ovulate, fruits usually 1-seeded) ranging from central Mexico to South America (seven species).

The primarily northeastern American *Celastrus scandens*, climbing or false or American bittersweet, waxwork,  $2n = 46$ , with ovate to elliptic leaves and terminal inflorescences, occurs in thickets, woods (most frequently in stands of young trees), fence-rows, and along streams, usually in rich soil, from southern Quebec west to southern Manitoba, south to Oklahoma and central Texas, Arkansas, Tennessee, northern Alabama, and western North Carolina, although it is scattered and rare in the states of our area.<sup>4</sup> This species "is related to the eastern Asiatic center of

<sup>4</sup>Fernald (*Gray's Man. Bot. ed. 8. 984. 1950*), Small (*Man. SE. Fl. 818. 1933*), and some other authors, include also Georgia and Louisiana, or Mississippi (Small), in the range of *Celastrus scandens*. The occurrence of *C. scandens* in Louisiana is doubtful, since C. A. Brown (*Louisiana trees and shrubs, 1945, p. 169*) says, "Reported

dispersion rather than to the one in Central America" (Hou, 1955, p. 224). The Asiatic *C. orbiculatus* Thunb.,  $2n = 46$ , with suborbicular to obovate leaves and axillary inflorescences, often grown as an ornamental, has become naturalized in at least the Northeastern States, south to Virginia. Recently it has also been noted by Hoffman as naturalized in Tennessee in the Great Smoky Mountains National Park.

Little is recorded regarding floral biology in the genus. Hymenopterous insects, especially bees, seem to be the main pollinators, although wind may also be involved (cf. Wyman, pp. 84, 85).

Apomixis (adventitious embryony from the inner integument), and perhaps "false polyembryony" (supposed on the basis of the occasional occurrence of two nucelli in an ovule), and parthenocarpy have been recorded in *Celastrus scandens* (Andersson). Birds are considered to be the seed dispersing agents. Seeds in *C. scandens* which mature in the fall seem to have a long dormancy period and should be stratified to accelerate germination. Vegetative reproduction by suckers seems to be common.

Chromosome numbers are known only for the two species mentioned here. The artificial hybrid *C. scandens*  $\times$  *orbiculatus* is less vigorous than the parents, sparingly fertile, and smaller fruited than either parent. The occurrence of natural hybrids between some species in eastern Asia seems probable (Hou, 1955 p. 225).

The flowers are regarded by Berkeley as perigynous, the cup-shaped disc (free from the ovary) being interpreted as a floral tube.

The genus is closely related to the pantropical *Maytenus* Molina.

*Celastrus scandens*, *C. orbiculatus*, and a few other species are grown as ornamentals. All are strangling vines, and our species may cause distinctive injuries to the stem and branches of young trees (Lutz). Leaves of *C. scandens* are said to be poisonous to horses.

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from West Feliciana Parish by R. S. Cocks. There are no specimens of this in the Tulane herbarium. The material so labeled is the star vine, *Schizandra coccinea* Michx. The author has searched for this plant in the state but never found it." No herbarium material of this species from Mississippi and Georgia nor documented published records from these states have been available to me; therefore the occurrence of *C. scandens* in these states cannot be confirmed at present. Suspecting that the herbarium specimen of this species collected in the southern part of Columbia County, Florida, (Hitchcock 267) may represent *Schisandra glabra* (Brickell) Rehd., rather than *Celastrus scandens*, I am reluctant to include Florida in the range of the species until Hitchcock's specimen is located and checked and/or the species is re-collected in northern Florida.

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3. **Maytenus** Molina, *Sagg. Stor. Nat. Chili* 177. 1782; emend. Bosc, *Nouv. Dict. Hist. Nat.* **14**: 211. 1803.

Evergreen, usually glabrous shrubs or small trees. Leaves alternate, fleshy-coriaceous [or membranaceous to coriaceous], entire [or toothed], short-petiolate; stipules minute, caducous [or wanting]. Inflorescences compact fascicles or flowers solitary [or in dichasial cymes, short thyrses, or racemes] in leaf- or more rarely in cataphyll-axils. Flowers short-pedicelled, small, usually hypogynous, [bisexual or] unisexual by abortion, the plants monoecious or dioecious. Sepals (4) 5, small, connate at least at base, persistent. Petals (4) 5, greenish white or white [or yellow, or red], longer than the sepals, spreading. Stamens (4) 5, inserted on or under the margin of the disc, shorter than the petals, reduced and sterile in ♀ flowers; filaments subulate, distinct; anthers ovate-suborbicular in outline, half as long as the filaments, introrse. Nectariferous disc conspicuous, fleshy, flattish and (4)5-angular [to -lobed] in ♂, annular and fused with the base of the ovary in ♀ flowers. Gynoecium [2]3(–5)-carpellate, rudi-

mentary in ♂ flowers; stigma [2]3(-5)-lobed; style very short or wanting; ovary superior,  $\pm$  immersed in and fused at least at base with the disc, short-conical, slightly 3(-5)-angular, incompletely [or completely] 3(-5)-locular, with axile placentae at base; ovules 1 [2] in each locule, ascendent, apotropous. Fruit an ellipsoidal or obovoid, usually slightly 3(-5)-angular, coriaceous, red (our species) capsule 8-12 mm. long, 1[-3]-locular, 3(-5)-valvate, (1)3(-5)[-6]-seeded. Seed ascendent, ovoid-ellipsoidal, 3-5 mm. long, covered entirely [or partly] by a fleshy scarlet [white] aril; seed coat crustaceous [coriaceous]; endosperm fleshy [or wanting]; embryo with the radicle inferior. TYPE SPECIES: *M. boaria* Molina. (Derived from *maytén*, the vernacular Chilean name of the type species.)

A pantropical genus of over 200 species. In accordance with a broad concept of the genus (cf. Hou), *Maytenus* is here delimited to include *Gymnosporia* (Wight & Arn.) Benth. & Hook. and *Moya* Griseb. The subgeneric classification of the inclusive genus has not yet been established, but all the American species (except four formerly included in *Moya*) belong to *Maytenus* proper, i.e., to subg. MAYTENUS. The primarily South American sect. TRICERMA (Liebm.) Loes., including seven species, is represented in our area by *Maytenus phyllanthoides* Benth., a shrub or small tree with rather small fleshy-leathery obovate to oblanceolate leaves, elsewhere known from Mexico (Baja California and Sonora to Yucatán and Puebla), Central America (?), coastal southwestern Texas, and Cuba. It occurs in the hammocks and coastal sand dunes on the Florida Keys, northward along the coasts of peninsular Florida to Levy County (Seahorse Key) on the west, and Palm Beach County on the east.

Little is known concerning the floral biology, pollination, seed germination, and other biological features of either our species or the genus in general. Birds seem to be dispersal agents. The only chromosome number reported is  $2n = 80$  for *Maytenus Vitis-Idaea* Griseb. (Argentina, Uruguay, Paraguay, and Bolivia), a close relative of *M. phyllanthoides*.

The genus differs from *Celastrus* mainly in the nonscandent habit, the flowers largely in compact axillary fascicles or solitary, and the ovary  $\pm$  immersed in and fused at least at base with the disc.

#### REFERENCES:

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## Subfam. CASSINOIDEAE Loes.

## Tribe CASSINEAE

4. *Crossopetalum* P. Browne, Civ. Nat. Hist. Jamaica 145. *pl.* 17. *fig.* 1. 1756.

Usually evergreen shrubs or small trees. Leaves opposite, rarely some [or all] alternate or whorled, chartaceous to thin-coriaceous, entire, or more often serrulate to serrulate-crenate or spinose-dentate [rarely rudimentary and caducous], short-petiolate; stipules minute, subulate or rudimentary (punctiform). Inflorescences short [rarely rather ample] axillary, simple or compound (once to four times forked) dichasial cymes. Flowers very small, hypogynous, bisexual, 2-bracteolate at the base of the slender pedicels. Sepals 4, connate into a 4-lobed calyx, persistent. Petals red or purplish [greenish or white], spreading to reflexed. Stamens 4, distinct, inserted between the lobes of the disc; filaments subulate, short; anthers small, suborbicular in outline, introrsely or laterally dehiscent. Nectariferous disc  $\pm$  annular to low-cupuliform, usually  $\pm$  4-lobed. Gynoecium [2]4-carpellate; stigmas [2] 4, narrow, spreading; style usually short [rarely wanting]; ovary superior, [2]4-locular; ovule 1 in each locule, ascendent from the base of the axile placenta, apotropous. Fruit a red drupe, usually obliquely obovoid, 3–6 mm. long, excentrically apiculate by the persistent style, 1(2)-seeded; mesocarp fleshy, thin; endocarp bony or crustaceous. Seed small, obovoid, exarillate; seed coat membranaceous, pale brown, obsoletely minutely reticulate, with a branched raphe; endosperm fleshy, usually copious [sparse to wanting]; embryo spatulate; cotyledons ovate or suborbicular-ovate; radicle inferior. (*Rhacoma* L. Syst. Nat. ed. 10. 2: 896. 1759, nom. illeg.; a proposal to conserve this almost universally used name has been rejected. Including *Myginda* Jacq.) TYPE SPECIES: *Rhacoma Crossopetalum* L. = *Crossopetalum Rhacoma* Crantz. (Name from Greek, *crossos*, fringe, and *petalon*, petal, i.e., referring to the fimbriate petals of the type species.)

A tropical American genus of nearly 25 species, best represented in the West Indies and Central America, a few species in northern South America, and two in the southernmost part of our area.

The West Indian *Crossopetalum Rhacoma* (*C. austrinum* J. R. Gardn., *Rhacoma Crossopetalum* L.), a shrub or small tree with relatively small obovate or elliptic, usually serrulate-crenate leaves, occurs in hammocks and on coastal sand dunes on the Florida Keys and in southernmost peninsular Florida (Dade County). *Crossopetalum ilicifolium* (Poir.) Kuntze (*C. floridanum* J. R. Gardn., *Myginda ilicifolia* Poir., *Rhacoma ilicifolia* (Poir.) Trel.), a prostrate shrub with coriaceous spiny-toothed leaves 10–15(20) mm. long, occurs in pinelands in the same areas of subtropical Florida<sup>5</sup> and beyond in the Bahamas and Hispaniola.

<sup>5</sup> A recent record (Hayes) of this species from a locality in the Coastal Plain of eastern North Carolina is apparently based either on an introduced plant or on a

The genus appears to be closely related to *Cassine* L. (*Elaeodendron* Jacq. f.) and more remotely allied to *Gyminda* Sargent.

REFERENCES:

Under family references see LOESENER (1942, pp. 183-185), METZ (pp. 380, 381), URBAN (pp. 69-79), and WEST & ARNOLD (p. 127).

HAYES, D. W. Two remarkable range extensions (*Rhabdadenia corallicola* and *Rhacoma ilicifolia*). *Castanea* 11: 61, 62. 1946. [Both collected by W. A. Dayton in acid soil at Blackland Branch Station near Wenona, Washington Co., N.C.]

5. *Gyminda* Sargent, *Garden Forest* 4: 4. 1891.

Dioecious glabrous evergreen shrubs or small trees. Leaves opposite, thin-coriaceous, entire or crenulate [serrate], short-petiolate; stipules minute, membranaceous, lanceolate to linear-lanceolate, caducous. Inflorescences short, simple to compound (1-4 times forked), peduncled axillary cymes. Flowers very small, hypogynous, unisexual by abortion, minutely 2-bracteolate just below the calyx, sessile. Sepals 4, nearly distinct, persistent. Petals 4, white, longer than the sepals, spreading or reflexed. Stamens 4, alternipetalous, distinct, inserted between the lobes of the disc, wanting in ♀ flowers; filaments subulate; anthers suborbicular in outline, laterally-introrsely dehiscent. Disc fleshy, 4-lobed in ♂, crenulate, adnate to the base of ovary in ♀ flowers. Gynoecium 2(3)-carpellate, rudimentary in ♂ flowers; stigmata 2, ample, commissural, peltate, nearly semiorbicular, sessile, persistent on fruit; ovary superior, 2(3)-locular; ovule 1 in each locule, pendulous from the top of axile placenta, anatropous, apotropous. Fruit an ellipsoidal to obovoid drupe, 6-8 mm. long, black or dark blue, crowned with persistent stigmata, 2(3)-locular (1 locule often rudimentary), (1)2(3)-seeded; mesocarp fleshy, thin; stone bony. Seed ellipsoidal or cylindrical-ellipsoidal, exarillate; seed coat membranaceous, finely foveolate-reticulate; endosperm fleshy, thin; embryo spatulate, the cotyledons ovate or oblong, the radicle subcylindrical, superior. TYPE SPECIES: *G. latifolia* (Sw.) Urb. (Name an anagram of *Myginda*, to which this plant had been referred.)

A genus of two or three (?) species of subtropical North America, the West Indies, and Central America south to Costa Rica. The West Indian *Gyminda latifolia* (*G. Grisebachii* Sarg.), false-boxwood, occurs in hammocks on the Florida Keys. Records of this species from Mexico may perhaps refer to the closely related Central American *G. Tonduzii* Loes. The latter seems to be rather variable in the shape and size of leaves, and some specimens (forms?) with smaller and more rounded leaves (than those usually seen) can easily be confused with *G. latifolia*, as often also are sterile (and rarely flowering) specimens of *Crossopetalum Rhacoma*.

The genus is most closely related to and perhaps congeneric with the                      mistake in labeling. At present there hardly is a reason to regard *C. ilicifolium* as either native to or naturalized in North Carolina.



monotypic Jamaican *Tetrasiphon* Urb., which differs from *Gyminda* only in its four-carpellate gynoecium, four oblong-linear stigmata, and fibrous innermost layers of mesocarp. The genus also shows a relationship to *Maurocenia* Mill., *Cassine* L. (*Elaeodendron* Jacq. f.), and *Crossopetalum*. It differs from *Cassine* and *Crossopetalum* in its pendulous ovules and, if combined with either of these, would be an anomalous group with regard to this characteristic.

REFERENCES:

Under family references see LOESENER (1942, p. 182), METZ (pp. 377, 378), SARGENT (pp. 678, 679), URBAN (pp. 80-83), and WEST & ARNOLD (p. 127).

SARGENT, C. S., *Gyminda*. *Silva N. Am.* 2: 13, 14. *pl.* 54. 1891.

6. *Schaefferia* Jacquin, Enum. Syst. Pl. Ins. Carib. 10. 1760.

Dioecious, evergreen, usually glabrous shrubs or trees. Leaves alternate,  $\pm$  coriaceous, entire [rarely toothed], short-petiolate; stipules subulate or rudimentary. Flowers small, hypogynous, unisexual by abortion, manifestly pediceled, in axillary few-flowered fascicles or solitary. Sepals 4, nearly distinct, persistent. Petals 4, much longer than the sepals, yellowish or whitish, spreading or reflexed, cochleate-imbricate. Stamens 4, hypogynous, shorter than the petals, wanting in  $\text{\textit{f}}\text{\textit{e}}\text{\textit{m}}\text{\textit{a}}\text{\textit{l}}$  flowers; filaments subulate; anthers broad-elliptic-subquadrangular, dorsifixed near base, hardly versatile, introrsely dehiscent. Nectariferous disc indistinct and adnate to the base of ovary in  $\text{\textit{f}}\text{\textit{e}}\text{\textit{m}}\text{\textit{a}}\text{\textit{l}}$ , wanting in  $\text{\textit{m}}\text{\textit{a}}\text{\textit{l}}$  flowers. Gynoecium 2-carpellate, rudimentary in  $\text{\textit{m}}\text{\textit{a}}\text{\textit{l}}$  flowers; stigmata 2, commissural, large, usually 2-lobed to -fid, spreading or reflexed; style very short, stoutish, or wanting; ovary superior, sessile, 2-locular; ovule 1 (2) in each locule, ascendent from the base of the axile placenta, apotropous. Fruit a small, scarlet, subglobular, thin-fleshed drupe, nearly 5-6 mm. in diameter, indistinctly 2-lobed, crowned by the persistent style and/or bases of stigmata; stones (pyrenes, "nutlets") 2, or 1 by abortion, somewhat obovoid, plano-convex, with rough  $\pm$  tuberculate cartilaginous endocarp. Seed ellipsoidal or ovoid, plano-convex, exarillate; seed coat membranaceous, smooth, brownish; endosperm copious; embryo spatulate, the radicle inferior. TYPE SPECIES: *S. frutescens* Jacq. (Named for Jacob Christian Schaeffer, 1718-1790, distinguished German naturalist and mycologist.)

A tropical American genus of nine species, ranging from Peru, northern Argentina, and Uruguay, northward to the West Indies, southernmost Florida, western Texas, and northern Mexico; one species in the subtropical part of our area.

*Schaefferia frutescens*, Florida boxwood, yellow-wood, distributed in the West Indies, Venezuela and Colombia, and northward in Central America to southern Mexico, occurs in hammocks on the Florida Keys and in extreme southeastern peninsular Florida. According to Sargent (1891),

the ripe fruits possess an acrid disagreeable flavor but are greedily eaten by many birds. *Schaefferia cuneifolia* Gray, a small shrub, occurs in the arid region of western Texas and northern Mexico.

Loesener (1942) assumed *Schaefferia* to be closely related to *Crosso-petalum* but to approach Aquifoliaceae in its discless staminate flowers. The genus also resembles the latter family in the general structure of the fruits (convergent evolution?).

#### REFERENCES:

Under family references see LOESENER (1942, p. 189), METZ (pp. 383, 384), SARGENT (pp. 689, 690), URBAN (pp. 84-87), and WEST & ARNOLD (p. 128).

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HIPPOCRATEACEAE A. L. de Jussieu, Ann. Mus. Hist. Nat. Paris **18**: 486, 1811, "Hippocrateaceae," nom. cons.

#### (HIPPOCRATEA FAMILY)

Woody vines with slender, scandent branches [or shrubs, or slender trees], often with  $\pm$  anomalous wood, frequently with latex ducts in all organs [or only in the axis], differing from Celastraceae mainly in the almost exclusively opposite leaves; extrastaminal nectariferous disc; usually 3-merous androecium; usually extrorse anthers often dehiscing by transversally confluent slits; occurrence of pollen tetrads in some taxa; usually 6-8[2-20]-ovulate locules; pleurotropic ovules; and frequent occurrence of peculiar, usually 3-locular, deeply 3-parted capsules with large, dorsiventrally flattened, radially divergent segments containing endospermless seeds winged from the base. TYPE GENUS: *Hippocratea* L.

A pantropical family of about 21 genera with nearly 400 species. It is centered and almost equally represented (with regard to the genera) in America and Africa, with a few taxa in Asia and Australasia. Only *Hippocratea* is represented in the subtropical part of our area.

No data on floral biology or anatomy are available; those on embryology pertain to six genera. Pollen has been studied in 44 species of 14 genera (mostly African, three Afro-American, one pantropical). Chromosome counts for ten species in seven genera (two Afro-American, one pantropical) invariably have been  $2n = 28$  in the genera with berry- or drupelike fruits (e.g., *Salacia* L., *Salacighia* Loes., of subfam. Salacioideae Hallé), and  $2n = 56$  in the genera with capsular fruits (e.g., *Campylostemonia* Welw.; *Hippocratea*, *sensu stricto*; and *Loeseneriella* A. C. Sm., of subfam. Hippocrateoideae). Polyploidy apparently has been of importance in the evolutionary development of the family.

The peculiar shape of the capsules of the members of subfam. Hippocrateoideae is due to a disproportionate growth of the ovary after fertiliza-

tion. While the size of the axis of the ovary and the lower placentiferous parts of the locules remains almost unchanged during the process of fruit development, the tips of the locules expand greatly, forming segments [or lobes] up to 50–100 times longer than the length of the central placentiferous part of the mature fruit. Since the basal placentiferous parts of the locules (including the funicles) remain permanently united with the persistent fruit axis after dehiscence of the expanded locular tips, such a fruit is to be classified as a somewhat modified capsule, rather than as an apocarpous or schizocarpous fruit.

The taxonomy of the Hippocrateaceae has been based primarily on the gross morphology of the reproductive organs, on some characters of the inflorescence, and, in some cases, on palynological data. Differences in evaluation of these characters have resulted in varying numbers of recognized genera, e.g., nine (including *Campylostemon* and *Cheiloclinium* Miers [placed in Celastraceae] in Loesener, 1942) or 21 (Smith, 1940, 1941, 1945; Wilczek, 1960; Hallé, 1962). The generic concepts of the last three authors are accepted here, but it is likely that additional data on floral anatomy, embryology, cytology, etc., will create a basis for a considerable reduction in the number of genera.

This very natural group is closely related to and sometimes included in (most recently by Blakelock) the Celastraceae, which name is conserved over Hippocrateaceae when the two are united. A relationship to Siphonodontaceae and Stackhousiaceae is also presumed.

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1. **Hippocratea** Linnaeus, *Sp. Pl.* 2: 1191. 1753; *Gen. Pl.* ed. 5. 498. 1754.

Latex-bearing vines with scandent, usually opposite branches. Leaves opposite, membranaceous to subcoriaceous, petiolate, persistent; stipules minute, subulate, caducous. Inflorescences axillary, corymbose-paniculate, dichotomously branched, peduncled cymes, usually with 1 or 2 short, few-flowered branchlets in each dichotomy, with minute bracts and bractlets. Flowers small, regular, hypogynous, bisexual, pediceled. Sepals 5, connate at least at base, imbricate [or valvate]. Petals 5, distinct, yellowish [or whitish], thickish, much longer than the sepals, spreading, with a transverse tomentulose band below the apex within [or tomentulose except at the base], narrowly imbricate [or valvate]. Disc extrastaminal, conspicuous, fleshy, annular-pulvinate, subcylindrical or truncate-conical [or  $\pm$  cup shaped], puberulent [or glabrous] without. Stamens 3, suberect, spreading, or reflexed; filaments strap shaped, dilated toward and often contiguous at base, often adnate to the upper margin of the disc; anthers basifixed, oblate-spheroidal, dehiscing by horizontal (transverse) extrorse-apical slits; pollen 3- or 4-porate, in compound tetrads (polyads) of 16 grains. Gynoecium syncarpous, 3-carpellate; stigma small, punctiform or

inconspicuously 3-lobed; style short, subulate; ovary 3-locular, 3-lobed, sessile, completely immersed in and fused with the disc, at least at the base; ovules usually 6[-8] in a locule, 2-ranked,  $\pm$  ascendent, anatropous. Fruit a 3-locular, deeply 3-parted capsule, with divergent, dorsiventrally (vertically) flattened segments (the greatly expanded tips of the locules), each dehiscing loculicidally along an inconspicuous median suture; pericarp membranaceous to thin-coriaceous. Seeds 5 or 6 in each capsule segment, each with a basal wing jointed at the base with a fleshy, nearly obdeltoid funicle, the embryoniferous apical portion of seed coriaceous, flattened, the wing membranaceous, with a marginal and a submedian longitudinal nerve; endosperm wanting; embryo straight; cotyledons large, distinct, fleshy, flat; radicle minute, inferior. TYPE SPECIES: *H. volubilis* L. (Named for Hippocrates, 460-377 B.C., eminent Greek physician, "Father of Medicine.")

A genus of one American and two African species. The tropical American *Hippocratea volubilis* (*H. scandens* Jacq., *H. ovata* Lam.) occurs in hammocks and mangrove swamps in southernmost peninsular Florida (Dade, Monroe, Collier, and Lee counties) and on the Florida Keys, in the West Indies, and from central Mexico, south to Peru, Bolivia, northern Argentina (Misiones), Paraguay, and southern Brazil. Within its extensive range the species exhibits numerous variations on which many supposedly distinct species have been based (see A.C. Smith, 1940, for a complete synonymy).

The genus has often been delimited in a broad sense (cf. Loesener, 1942; Blakelock, 1958) to include all the species (over 100) of Hippocrateaceae with very similar capsular fruits and winged seeds (except *Campylostemon* Welw. and *Tristemonanthus* Loes., both with introrse stamens). In 1940, however, A. C. Smith restricted *Hippocratea* to the type species. Recently two African species (*H. myriantha* Oliver and *H. Vignei* Hoyle) have been included in *Hippocratea*, *sensu stricto* (see Hallé, 1962). Thus delimited, *Hippocratea* differs from closely related segregate genera (e.g., *Pristimera* Miers, *Prionistemma* Miers, *Elachyptera* A. C. Sm., *Reissantia* Hallé, *Loeseneriella* A. C. Sm.) both in some floral characters (e.g., petals tomentulose within in *Hippocratea*, configuration of the disc) and in the compound pollen tetrads and the presence of latex in all parts of the plant (a questionable generic character in this family). In general, the characters distinguishing *Hippocratea*, *sensu stricto*, from the closely related genera are of such a nature that they may eventually be regarded as subgeneric, in view of the rather uniform anatomy of vegetative organs and the gross morphology of fruits and seeds (cf. Aceraceae).

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Under family references see BLAKELOCK (pp. 626-629), FRITSCH (pp. 288-300, 302-310, 336-344), HALLÉ (pp. 123-131), LOESENER (1942, pp. 206-216), OBATON (pp. 108, 109), RECORD (pp. 22, 23), RECORD & HESS (p. 191), SMITH (1940, pp. 356-367), and VAN CAMPO & HALLÉ, (*pls.* 35, 36 [pp. 242-245]).

AQUIFOLIACEAE Bartling, Ord. Nat. Pl. 228, 376. 1830, nom. cons.

(HOLLY FAMILY)

Shrubs or trees, differing from Celastraceae mainly in the almost exclusively alternate leaves, the usually sympetalous rotate corolla, the absence of a nectariferous disc (but cf. *Schaefferia*); the almost exclusively one-ovulate locules, the always pendulous one-integumented ovules, and the minute "rudimentary" embryo in the vicinity of the micropyle. TYPE GENUS: *Aquifolium* Mill., nom. illeg. = *Ilex* L.

A family of three genera: the primarily pantropical polytypic *Ilex*; the monotypic *Nemopanthus* Raf., endemic in northeastern North America; and the tropical *Phelline* Labill. (ten species), endemic in New Caledonia. Only *Ilex* is represented in our area; *Nemopanthus mucronatus* (L.) Trel. occurs from Newfoundland to Minnesota, southward to northern Illinois, Indiana, Ohio, and upland West Virginia and Virginia.

Aquifoliaceae exhibit a number of primitive characters (e.g., the minute "rudimentary" embryo; the exclusively scalariform perforation plates in vessels), as well as specialized features (e.g., the often sympetalous corolla; the absence of a nectariferous disc, apparently due to abortion; the solitary, one-integumented ovules). A relationship to Celastraceae (especially to subfam. Cassinoideae) has generally been assumed, and the evidence from gross morphology of flowers and fruits, wood anatomy, and embryology seems to support this view. Pollen morphology does not furnish positive indications in favor of such a relationship (Erdtman, p. 55), but it should be noted that only two genera of subfam. Cassinoideae, the group apparently closest to Aquifoliaceae, have been investigated.

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1. *Ilex* Linnaeus, *Sp. Pl.* 1: 125. 1753; *Gen. Pl.* ed. 5. 60. 1754.

Dioecious evergreen, or more rarely deciduous, shrubs or trees of acid, often wet soils. Leaves alternate [exceptionally opposite], simple, thick-coriaceous to membranaceous, entire, crenate, serrate, or spiny toothed, petioled; stipules minute, usually caducous, more rarely persistent. Inflorescences axillary to leaves or bracts on either long- or short-shoots, single or fascicled 1- to many-flowered dichasial cymes, sometimes umbel-like and/or paniced [or racemes], or flowers solitary or in fascicles. Flowers small, hypogynous, unisexual by abortion. Sepals 4–9, connate in a 4–9-lobed (to -parted) calyx, imbricate, persistent. Petals 4–9, [rarely distinct] usually connate into a sympetalous rotate corolla, usually white, greenish-white or -yellow [rarely pink, red, or lavender], imbricate. Stamens 4–9, alternipetalous, usually adnate at base to the short corolla tube, more rarely distinct, nearly as long as the petals in ♂, abortive and sterile in ♀ flowers; filaments subulate or straplike; anthers ovoid to ellipsoidal, introrse, dorsifixed, not versatile, dehiscing by 2 lateral longitudinal slits, 2-locular at anthesis; pollen 3-colp(oro)idate, spheroidal to subprolate (or prolate?), medium sized, coarsely and densely granular on the surface. Gynoecium syncarpous, 4–9[–22]-carpellate, rudimentary in ♂ flowers; stigma mostly sessile or subsessile, large, capitate or discoid [or columnar], mostly ± lobed, persistent in fruit; style wanting or very short; ovary superior, 4–9[–22]-locular; ovules 1 (occasionally 2) in each locule, pendulous from the top of the axile placenta, anatropous, apotropous, 1-integumented, with a thickish nucellus; funiculus often with a prominent protuberance on the entire adaxial surface. Fruit a subglobular to ellipsoidal berry-like drupe, usually red, more rarely dark purple to black, occasionally yellow to whitish, containing [2]4–9[–22] unilocular stones (pyrenes, “nutlets”) shaped like citrus-fruit segments [exceptionally a single 4-locular stone]; exocarp chartaceous; mesocarp fleshy or sometimes ± coriaceous because of stone cells interspersed in its outer layers; endocarp bony or woody, rarely coriaceous, the back (and sides) of stones either completely smooth and even, or more often longitudinally striate and/or ridged and grooved, sometimes sparsely irregularly reticulate. Seed solitary (occasionally 2) in a stone, pendulous; seed coat membranaceous; endosperm copious, fleshy; embryo minute, obversely heart shaped, situated near the micropyle. (Including *Prinos* L.) LECTO-TYPE SPECIES: *I. Aquifolium* L.; see N. L. Britton, *N. Am. Trees.* 621. 1908. (Classical Latin name of the Mediterranean holly oak, *Quercus Ilex* L., applied by Linnaeus to this genus.) — HOLLY.

A primarily pantropical genus of 300–400 species, centered in eastern Asia (southern and southwestern China and Indochina) and South America (Brazil), with one species in tropical Africa, one in Australia, and one in Europe; about 14 species (all represented with us) occur in eastern North America. Since the genus is currently being studied by several workers and its classification is still in flux, the relatively simple but at least partly unnatural one of Asa Gray is followed here (Gray, *Man.* eds. 1–5. 1848–1869; Fernald, *Gray's Man. Bot. ed. 8.* 980–982. 1950).<sup>6</sup>

Subgenus *ILEX* (subg. *Euilex* Loes., subg. *Aquifolium* (DC.) Gray). Leaves persistent, thin- to thick-coriaceous, sometimes spiny toothed; short-shoots lacking; carpellate flowers usually 4-merous; drupes red; stones (pyrenes) longitudinally (2)3–5-striate (sometimes faintly so) and/or ridged and grooved or irregularly thinly reticulated on the back. The largest and most widely distributed subgenus, it is represented with us by *Ilex opaca* Ait. var. *opaca*, American holly,  $2n = 36$ , and var. *arenicola* (Ashe) Ashe (*I. arenicola* Ashe, *I. cumulicola* Small), scrub holly; *I. vomitoria* Ait. var. *vomitoria*, yaupon or cassena,  $2n = 40$ ; *I. Cassine* L., dahoon holly; and *I. myrtifolia* Walt. The principal taxonomic problems revolve around the status of *I. opaca* var. *arenicola*, of the sand scrub of peninsular Florida, which has been treated as a distinct species (correctly named *I. arenicola*), and that of the relationships of *I. Cassine* and *I. myrtifolia*, which have sometimes been regarded as varieties of a single species. *Ilex vomitoria* is notable for the caffeine content of the leaves, a concentrated infusion of which was used by the Indians of the Coastal Plain in a stimulating and emetic “black drink.” The species occurs disjunctly in Chiapas and Vera Cruz, Mexico, as the pubescent var. *chiapensis* Sharp. *Ilex* × *attenuata* Ashe, a presumed natural hybrid between *I. Cassine* and *I. opaca*, has been recorded from northwestern Florida and both Carolinas.

Subgenus *PRINOS* (L.) Gray, *Man. Bot. No. U. S. ed. 2.* 264. 1856 (*Prinos* L.; including subg. *Euilex* Loes. sect. *Cassinoides* Loes. *Nat. Pflanzenfam. Nachtr.* 218. 1897, in part). LECTOTYPE SPECIES: *Prinos verticillata* L. = *Ilex verticillata* (L.) Gray; see Hitchcock & Greene, *Int. Bot. Congr. Cambridge 1930. Nomencl. Propos. Brit. Bot.* 147. 1929. Leaves deciduous or persistent; carpellate flowers (4)6–8(9)-merous; stones smooth and even, rarely indistinctly 1-striate on the back. Largely a temperate eastern Asiatic-North American group of about 12 species, extending with one or two species into the West Indies and Central America. Five species, comprising three morphological groups, occur in our area. *Ilex verticillata* (L.) Gray, winterberry, black alder, or fever bush,  $2n = 36$ , and *I. laevigata* (Pursh) Gray, smooth winterberry, are deciduous shrubs or small trees with red (rarely yellow) drupes. By contrast, *I. glabra* (L.) Gray, inkberry, gallberry, or bitter gallberry;

<sup>6</sup> Following Gray's classification, Fernald mistook his subgeneric names for those of sections (cf. Brizicky, *Jour. Arnold Arb.* 44: 62, footnote 3. 1963). For much more elaborate classifications of *Ilex*, see Loesener (1901, 1942) and Hu (1949–1950; and in Dengler, 1957, pp. 31–64).



*I. coriacea* (Pursh) Chapm., large or sweet gallberry; and the West Indian *I. Krugiana* Loes., which reaches Dade County, Florida, are all black-fruited evergreen species placed by Loesener in subg. ILEX. The last species differs, however, from the former two in its epunctate leaves, four-merous flowers, and fascicled inflorescences and seems to represent a distinct, primarily South American group (sect. *Microdontae* Loes.). Although the three groups have many similarities in the morphology of flowers and fruits, their relationships are highly questionable. *Ilex glabra* and *I. coriacea* are similar in many characteristics and are often confused, although they appear to be distinct species. *Ilex glabra* is regarded by foresters as an undesirable plant in pinewoods, but it seems to be an important source of honey in the Gulf region.

Subgenus PRINOIDES (DC.) Gray, Man. Bot. No. U. S. 276. 1848 (subg. *Prinos* sect. *Prinoides* (DC.) Gray ex Loes. Nat. Pflanzenfam. Nachtr. 221. 1897). LECTOTYPE SPECIES: *Ilex prinoides* Ait. = *I. decidua* Walt.). Leaves deciduous, membranaceous to subcoriaceous, often crowded on short spurs (short-shoots); carpellate flowers 4–5(6)-merous, often crowded on short-shoots; drupes red (occasionally yellow); stones as in subg. ILEX. A temperate eastern Asiatic-North American group of about 12 species, five or six in our area. The subgenus seems to be closely related to and is often included in subg. PRINOS (cf. deciduous, red-fruited species). Our species include *Ilex montana* Torr. & Gray var. *montana* (*I. monticola* Gray), mountain winterberry or mountain holly,  $2n = 40$ , and the pubescent-leaved var. *mollis* (Gray) Britton (including *I. Beadlei* Ashe ex Kearney); *I. decidua* Walt. var. *decidua*, possum-haw,  $2n = 40$ , and a small-leaved Florida variant, var. *Curtissii* Fern. (*I. Curtissii* (Fern.) Small); *I. ambigua* (Michx.) Torr., Carolina holly; *I. longipes* Chapm. (including *I. collina* E. J. Alex., fide Edwin), Georgia holly; and the very rare *I. Amelanchier* M. A. Curtis (*I. dubia* (G. Don) BSP., 1888; not Weber, 1851, pl. fossil.), sarvis holly, of sandy swamps from Louisiana to Georgia and southeastern Virginia. *Ilex Cuthbertii* Small apparently should be included in *I. decidua*, while *I. Buswellii* Small, found in hammocks along the Caloosahatchee River in southwestern Florida, may perhaps be a small-leaved form of *I. ambigua*. *Ilex longipes* is remarkable for its fruits with pedicels 1.2–2.2 cm. long.

It is notable that several eastern North American species have counterparts in eastern Asia, e.g., *I. montana*–*I. Tsoi* Merr. & Chun; *I. decidua*–*I. aculeolata* Nakai; *I. longipes*–*I. asprella* (Hook. & Arn.) Chapm.; *I. glabra*–*I. yunnanensis* Franch.; *I. verticillata*–*I. serrata* Thunb. var. *Sieboldii* (Miq.) Rehder (Hu, 1949, p. 255).

It seems likely that diversification of inflorescence types in *Ilex* has generally been due to the reduction and simplification of an original ample compound dichasial cyme (or cymes) along several divergent or convergent lines, rather than to the elaboration of a simple dichasium. Solitary or fascicled single-flowered inflorescences and solitary or fascicled flowers seem to be the final products of lines of reduction. Within a species, the carpellate inflorescences usually are somewhat more reduced than the

staminate ones (sexual dimorphism), e.g., fascicled simple staminate dichasia, but fascicled single-flowered carpellate inflorescences in *I. Krugiana*; solitary 3–7-flowered dichasial staminate cymes, but solitary single-flowered carpellate inflorescences in *I. glabra*; fascicled staminate flowers, but solitary carpellate flowers in *I. coriacea*. No correlation between the types of inflorescence and the fruit (pyrene) characters has yet been demonstrated.

Since the species of the genus usually are dioecious, although the occasional occurrence of bisexual flowers has been recorded in *I. Aquifolium*, cross-pollination and -fertilization are the rule. Insects, especially bees, have been recorded as pollinators, but wind apparently also is a factor in pollination in some species. The nectar is said to be excreted from small papillose swellings found at the base or near the middle of the petals on their adaxial (upper) surface (Loesener, 1942, p. 45).

Although a single axile ovule in each locule is typical, the occasional occurrence of two-ovulate locules has been recorded. Herr (1959) demonstrated that the two-ovulate condition is due to the presence of a second parietal rudimentary ovule ("parietal protuberance") in the ovary locule which maintains a potentiality to develop. Also, the "funicular protuberance," considered by Herr to be a partially suppressed nonfunctional ovule, can sometimes develop into a regular ovule.

Chromosome counts made in ten species ( $2n = 36, 40$ ) possibly indicate polyploidy, with the basic numbers supposedly  $x = 9, 10$ . *Ilex*  $\times$  *attenuata* is the only wild interspecific hybrid known in eastern North America; the occurrence of many forms intermediate between the species of *Ilex* in eastern Asia, especially in south and southwest China (Hu, 1949, p. 254) may suggest more extensive hybridization in that region. Many artificial and/or natural hybrids of garden and nursery origin are known at present. Most are within subg. ILEX and involve *I. Aquifolium* as one of the parents, but a few are in subg. PRINOS (sensu Gray), e.g., *I. glabra*  $\times$  *serrata*, *I. crenata*  $\times$  *glabra*. The established hybrid *I. Aquifolium*  $\times$  *yunnanensis*, and the suspected *I. chinensis*  $\times$  *glabra* are intersubgeneric (according to the classification used here) or intersectional (according to that of Hu).

Birds are considered to be the seed dispersing agents. Parthenocarpy seems to be common in *I. laevigata* and *I. cornuta* Lindl., less so in *I. vomitoria*, but apparently is of wider distribution, since a natural tendency to parthenocarpy has also been found in several other species (e.g., *I. Aquifolium*, *I. Cassine*, *I. myrtifolia*). The rudimentary embryo of *Ilex* undergoes maturation after dispersal but prior to germination (Herr, 1962, p. 32), which usually occurs in nature from one to three years after dispersal. The percentage of germination is low, and as a rule, the seeds are very difficult to germinate.

Many foreign and indigenous species are grown as ornamentals (e.g., the European *I. Aquifolium* with its numerous varieties and hybrids, the eastern Asiatic *I. cornuta* and *I. crenata*, the domestic *I. opaca*). The berried branches of *I. Aquifolium* and *I. opaca* are in great demand for Christmas decoration, and those of *I. laevigata* and *I. verticillata* are

sometimes sold for this purpose. Leaves of the South American *I. paraguariensis* St. Hil. (and possibly of a few other closely related species) yield the maté or Paraguay tea which is much used in South America. The wood of some arborescent species is valued for lathe work, engraving, and cabinet-making.

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