

THE GENERA OF OLACACEAE IN THE
SOUTHEASTERN UNITED STATES¹

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OLACACEAE Mirbel ex A. P. de Candolle, Prodr. 1: 531. 1824,
"Olacineae," nom. cons.

(OLAX FAMILY)

Trees or shrubs, sometimes sprawling, mostly glabrous, photosynthetic root parasites [or free-living autotrophs]; unarmed or armed with spines [or hooks]. Leaves alternate, simple, entire, sometimes undulate, evergreen, pinnately veined, petiolate, lacking stipules. Inflorescences axillary few-flowered dichasia, racemes, panicles, or fascicles; bracts sometimes calyciform. Flowers perfect [or infrequently imperfect, and the plants then dioecious], sometimes heterostylous, actinomorphic, mostly small. Calyx 4- or 5-lobed or indistinct and adnate to the ovary [sometimes accrescent and colorful]. Petals 4 or 5, free or connate into a cup or tube, mostly valvate in aestivation. Stamens the same number as the petals and opposite them or 2

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[3] times as many and in 2 whorls; staminodia absent [or present]; filaments free or adnate to the corolla [or connate into a tube]; anthers 2-locular, opening by longitudinal [or apical] slits; disc usually present, annular, more or less adherent around the base (*Ximenia*) or apex (*Schoepfia*) of the ovary. Gynoecium of 2-5 united carpels; ovary superior and sessile or inferior, 2- to 5-locular above and below [or 1-locular above]; style simple, terminal, usually elongate, sometimes heterostylous; stigma terminal, entire or 2- to 5-lobed; ovules 1 per locule, pendent from an axile [or free-central] placenta, anatropous or rarely apotropous, tenuinucellar, the micropyle superior, the integuments absent or 1 or 2. Fruit usually a 1-seeded drupe, the endosperm abundant, *ab initio* cellular or Helobial in formation, the embryo straight, minute, apical. TYPE GENUS: *Olax* L.

A morphologically diverse family of about 27 genera and 260 species of the tropics and subtropics. Eight genera are restricted to the New World, six to Asia/Malesia, and five to Africa; three genera occur in both Africa and the Americas, and three are present both in Africa/Madagascar and Asia/Malesia; *Ximenia* and *Schoepfia* are pantropical. Approximately eight genera are monotypic, six have only two or three species, and six have more than ten species. The largest genus in the family is *Heisteria* Jacq., with ca. 65 species in the Americas and three in tropical West Africa. *Olax* is composed of about 50 species of Africa, India, Asia, Malesia, New Guinea, Australia, and Micronesia. The third largest genus is *Schoepfia*, with about 38 species; none of the other genera exceeds 20 species.

In the most recent complete treatment of the family (Sleumer, 1935), three subfamilies are recognized: Dysolacoideae Engler (with four tribes), Olacoideae (with two tribes), and Schoepfioideae Engler (with only one genus). This scheme was modified somewhat by Schultze-Motel, who included subfamily Dysolacoideae (and its tribes) within subfamily Schoepfioideae; in addition, the genus *Octoknema* Pierre, treated as a distinct family in *Die natürlichen Pflanzenfamilien*, is included in the Olacaceae as tribe Octoknemeae of subfamily Schoepfioideae.

The placement of Olacaceae at the ordinal and higher levels is confusing, both taxonomically and nomenclaturally, because phylogenists have frequently differed widely in their circumscription of related families, suborders, orders, superorders, and classes. The situation is compounded because there are a number of small genera and families that are frequently allied with Olacaceae. Eighteenth- and nineteenth-century botanists grouped the Olacaceae, in different systems of classification, with numerous families, including Berberidaceae, Humiriaceae, Meliaceae, Pittosporaceae, Rutaceae, Sapotaceae, Styracaceae, and Theaceae. The original suggestion of Robert Brown (1810) that these plants might be allied with Santalaceae was ignored until adopted by both Baillon and Engler. This alignment has been followed in most, although not all, subsequent systems of classification, and for some time there has been general agreement that Olacaceae are closely related to Opiliaceae, Santalaceae, Loranthaceae, Viscaceae, and Misodendraceae. These are considered to be the base families of the order Santalales by Cron-

quist, Dahlgren, Kuijt, Schultze-Motel, Takhtajan, and Thorne. Kuijt (1968) stated that "Olacaceae thus emerge as the plexus from which all other Santalalean families take their origin." Hutchinson, Metcalfe and Chalk, and Reed place the Olacaceae, Opiliaceae, and some other small families in the order Olacales, which is still allied with Santalales. Phylogenists concur that the Santalales/Olacales complex is allied with Celastrales and Rhamnales.

Species belonging to at least five genera, including the two in our area, are known to be green-leaved root-parasites. One species, *Heisteria longipes*, is autotrophic (Kuijt, 1969). More studies of additional genera and species are needed.

Chromosome numbers have been reported from only a few species: *Ximenia americana*, $2n = 26$; *Lepionurus sylvestris* Blume, $2n = 20$; *Olax nana* Wallich, $2n = 24$; *Schoepfia fragrans* Wallich, $2n = 24$; *Heisteria parvifolia*, $2n = 38$; and *Strombosia glaucescens* var. *lucida*, $2n = 40$.

The pollen of the Olacaceae is quite diverse. The grains may be 3-colpate, 3-colporate, 3-colporoidate, 3- or 4- (or 5-)porate (angulaperturate), 6-forate (3-diploforate), or brevicolporate. The texture of the exine varies from smooth, minutely verrucose, finely reticulate, or tectate-perforate to prominently reticulate or with massive crustose ornamentation around the mesocolpal areas. Lobreau-Callen presents a detailed comparison between pollen of the Olacaceae and Icacinaceae and also has a table comparing pollen type, secondary xylem perforations, and nodal anatomy.

The number of integuments of the ovule varies from two to none in the Olacaceae, and this has been used as a primary character in defining the subfamilies and tribes. In other families that include parasitic species there is a general correlation between the parasitic habit and a reduction in the number of integuments; this also appears to be the case in the Olacaceae, although information is far from complete. An unusual morphological peculiarity of some members of the Olacaceae is the presence of more than two cotyledons in the embryo. Tribes Colueae and Heisterieae usually have three or four cotyledons, the Olaceae and *Schoepfia* may have two or three, and *Octoknema* (see above) can have up to eight. The related Opiliaceae usually have three or four cotyledons, and the Loranthaceae frequently have two to six. The vascular anatomy of the Olacaceae is also diverse. The leaf bundles are unilacunar, trilacunar, or rarely pentalacunar, and the secondary xylem varies from primitive to advanced with regard to type of perforations, pore distribution, imperforation of elements, wood parenchyma, and ray types (Reed).

Although it might appear from the number of references listed below that Olacaceae have been studied rather extensively (and, for a tropical family, they have been), the family is poorly known in comparison with others in the Santalales. The morphological, anatomical, palynological, and cytological diversity that has been observed thus far, as well as the hemiparasitic nature of some (most?) species, the interesting phylogeographical patterns, and the possibility of well-developed breeding systems and dispersal mechanisms, is tantalizing and indicates that much can be learned from further research, especially that which includes detailed field observations.

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KEY TO THE GENERA OF OLACACEAE IN THE SOUTHEASTERN UNITED STATES

General characters: *Mostly evergreen trees and shrubs, glabrous, armed with spines or not, free-living autotrophs or photosynthetic root parasites; leaves alternate, simple, entire, stipulate; inflorescences few-flowered axillary dichasia, racemes, panicles, or fascicles; flowers usually perfect, sometimes heterostylous, actinomorphic, small; perianth of 4 or 5 small sepals and free or connate petals; androecium of 4 or 5 antepetalous stamens or 8–10 in 2 whorls; gynoecium of 2–5 united carpels; ovary superior or rarely inferior, 2- to 5-locular, each locule with 1 anatropous ovule pendulous from an axile placenta, integuments absent or 1 or 2; fruit a 1-seeded drupe with abundant endosperm and a straight, minute, apical embryo.*

Branches armed with spines; corollas 6–8 mm long; stamens twice as many as the corolla lobes; ovary superior; fruit yellow, 2–3 cm in diameter. . . . 1. *Ximenia*.
 Branches unarmed; corollas 2–3 mm long; stamens the same number as the corolla lobes; ovary inferior; fruit red to black, 5 mm in diameter. 2. *Schoepfia*.

1. *Ximenia* Linnaeus, Sp. Pl. **2**: 1193. 1753; Gen. Pl. ed. 5. 500. 1754.

Trees or shrubs, mostly root parasites; branches of three types: long-shoots with elongate internodes, determinate spine-tipped short-shoots arising from leaf axils of long-shoots, and short spur-shoots produced at the base of each spine branch. Leaves ovate or elliptic [lanceolate, obovate, or orbicular], subcoriaceous, glabrous or glabrescent, the apices emarginate and mucronate, the bases cuneate to obtuse; petioles short, slender, grooved. Inflorescences few-flowered cymes or clusters produced mostly from the axils of a leaf or bract on short-shoots. Flowers fragrant, perfect [or imperfect], pedicellate. Calyx lobes 4 (or 5), small, subtending the corolla, initially valvate in aestivation, not accrescent. Petals 4 (or 5), yellowish to white, free to the base, reflexed, abaxially glabrous, adaxially bearded with 2 dense rows of long trichomes, the petal apices each with a knob that in bud interlocks with those of other petals, valvate in aestivation. Stamens [4 or] 8(–10), partially obscured by the corolla trichomes, 4 (or 5) antepetalous and 4 (or 5) anteseptal; filaments free, elongate, dorsifixed near the base of the anthers; anthers linear, 2-locular, opening laterally, evidently dehiscent while still in bud; pollen grains tricolporate, binucleate when shed. Disc prominent, surrounding base of ovary. Ovary superior, elongate-conical, base swollen,

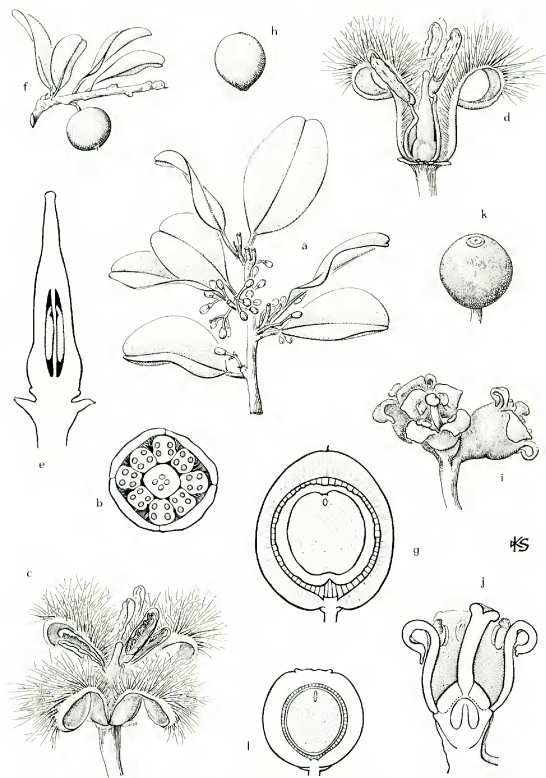


FIGURE 1. *Ximenia* and *Schoepfia*. a-h, *X. americana*: a, tip of branch with flower buds, some leaves removed, $\times \frac{3}{4}$; b, cross section of flower bud with four petals (note adaxial trichomes), eight anthers (the locules stippled), and gynoecium with four ovules, $\times 12$; c, open flower, six anthers shown, two having fallen off, $\times 5$; d, flower, two petals and four stamens removed, $\times 5$; e, gynoecium in vertical section (note two pendent, anatropous ovules, and disc at base of ovary), $\times 12$; f, branchlet. i, j, k, *Schoepfia*: i, flower, $\times 5$; j, gynoecium, $\times 12$; k, fruit, $\times 5$.

slightly constricted above, 4-locular; style shorter than to equaling ovary; stigma entire, small; ovules linear, anatropous, solitary in each locule, pendent from an axile placenta at top of locule, with 1 integument and a dorsal raphe. Fruit a yellow [red, orange, or purple], 1-seeded, ovoid to ellipsoid, or subglobose drupe; endocarp crustaceous or subligneous, ovoid, minutely pitted, light reddish-brown; seed filling endocarp, seed coat white, thin and spongy; endosperm abundant, rich in oil; embryo minute, apical. LECTOTYPE SPECIES: *X. americana* L.; see N. L. Britton & C. F. Millspaugh, Bahama Fl. 112. 1920, and A. S. Hitchcock & M. L. Greene, Int. Bot. Congr. Cambridge Nomencl. Prop. Brit. Bot. 195. 1929. (Name commemorating Francisco Ximenes (died 1612), a Dominican priest who translated "Cuatro libros de la naturaleza y virtudes de las plantas y animales que estan recevidas en el uso de medicina en la Nueva-España," by Francisco Hernández, published in Mexico in 1615, the first book on plants published in the New World; see Quinby.)

According to DeFilipps, the most recent monographer, eight species and 12 taxa mostly of tropical and subtropical regions of the Americas, with *Ximения americana* L. occurring pantropically and *X. Caffra* Sonder in Africa and Madagascar. Most taxa of the genus are xeromorphic and occur in dry, rather severe habitats, such as savannas and scrublands. The genus is represented in our area by *X. americana*, tallow-wood, hog plum, a spinescent, straggly shrub or small tree that occurs fairly frequently in hammock margins, scrublands, coastal sand dunes, sand ridges, shell mounds, and pinelands throughout much of peninsular Florida and the Florida Keys; it is largely absent from the Everglades except on the Everglade Keys. DeFilipps recognized three varieties of *X. americana*: var. *americana* (pantropical—Florida, the West Indies, Mexico and Central America, South America, Africa, Asia, Malesia, Australia, and Pacific Islands); var. *argentinensis* DeFilipps (Argentina); and var. *microphylla* Welw. ex Oliver (Africa).

Ximения americana is a facultative root-parasite, and plants can grow indefinitely from seed in greenhouse cultivation in pots that do not contain a host plant. In cultivation, parasitism seems to cause neither a visible increase nor a decrease in vigor of either the parasite or host, and under certain conditions haustoria are produced that either attack the parasite's own root system or attach themselves to nonliving objects such as stones, plastic, and charcoal. The haustoria of *X. americana* may be up to 3 cm in diameter, the

with leaves and nearly mature fruit (note small spine at tip of branchlet), $\times \frac{1}{2}$; g, fruit in vertical section, mesocarp stippled in rows, endocarp wall hatched, fleshy inner layer unshaded, endosperm stippled, minute apical embryo unshaded, $\times 2$; h, endocarp removed from fruit, $\times 1$. i-1, *S. Schreberi*: i, cluster of three flowers, $\times 5$; j, flower in vertical section, apex of ovary covered by large disc, $\times 10$; k, fruit, a drupe from an inferior ovary, $\times 2$; l, fruit in vertical section, mesocarp unshaded, endocarp wall hatched, inner layer unshaded, endosperm stippled, embryo near apex unshaded, $\times 3$.

largest of any North American root parasite! Hundreds of haustoria can be produced on the roots of a host species in a single season, and some reports indicate that *X. americana* can cause serious damage in Southeastern forests. (See DeFilipps, Heckel, and Musselman & Mann for information on the parasitic nature of *Ximения*.)

The flowers of *Ximения americana* are very fragrant, sometimes likened to jasmine (*Jasminum*, Oleaceae), and are presumably insect pollinated. The only report of compatibility for the species (Zapata & Kalin Arroyo) showed that 334 flowers artificially self-pollinated on seven trees produced no fruit, while artificial cross-pollination of ten flowers on two trees resulted in the production of one fruit.

According to DeFilipps (1976), the fruits of *Ximения americana* have two types of dispersal mechanisms, which account for its wide geographic distribution. First, the fleshy drupes are eaten by various animals, such as birds and monkeys; second, the pit (endocarp) has an air-filled tissue beneath the outer wall, and the fruits can be water-borne for several months. The seedlings of *X. americana* are unusual in that the first-formed leaves (cataphylls) grow downward into the seed to the space between the petioles of the cotyledons, although no fusion of tissue takes place (see Musselman & Mann). Tomlinson (family references) gives a detailed description of the phenology and growth pattern of the species.

Ximения belongs to subfamily Dysolacoideae Engler (ovules anatropous with a dorsal raphe and one or two integuments; calyx not accrescent in fruit; ovary superior), which according to Sleumer (1935, family references) includes 16 genera in four tribes. *Ximения* is the only genus in tribe Ximeneae Engler (hemiparasitic, spinescent trees or shrubs; leaves and bark lacking resin canals or latex tubes; stamens usually twice as many as the petals, half antepetalous, half antepetalous; ovules with one integument).

The endocarps of *Ximения americana* are rich in oil, and it has been suggested that the species could be grown as a crop in hot, dry areas with poor soil, but this has not yet proven to be feasible.

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2. *Schoepfia* Schreber, Gen. Pl. **1**: 129. 1789.

Unarmed, glabrous, evergreen root-parasitic trees [or shrubs]; distal shoots sympodially branched. Leaves alternate, subcoriaceous, entire or obscurely toothed, elliptic to ovate [obovate, oblanceolate, or spatulate], the apices acute to acuminate [rounded or obtuse]; petioles short, faintly winged. Inflorescences short axillary clusters [or racemes] of 2- or 3-flowered dichasia [or the flowers solitary]; bracts and bracteoles fused to form a 2-lobed, calyx-like structure. Flowers perfect, heterostylous [or not?], sweet scented. Calyx cup shaped, the rim entire or slightly lobed, slightly dilated. Petals 4 or 5, connate into a cylindrical-urceolate [to rotate] tube, orange, pink, red [yellow or greenish], slightly bearded just above the anthers, the tips recurved [or erect] at anthesis and sometimes pubescent. Stamens 4 or 5, adnate to the corolla tube, opposite the petals, included in long-styled flowers, very shortly exerted in short-styled flowers; anthers nearly sessile. Ovary inferior, topped by a thick disc, mostly 2-locular in 4-merous flowers and 3-locular in 5-merous flowers; each locule with an apotropous ovule pendent from an axile placenta; style 1, included in short-styled flowers, shortly exerted in long-styled flowers; stigma terminal, thicker than the style, 2- or 3-lobed. Fruit a fleshy ovoid [ellipsoid or subglobose], red [or yellow] drupe, turning black

at maturity [or not], surmounted by the persistent calyx ring; flesh reddish [or whitish]; endocarp crustaceous; seed solitary, nearly filling the endocarp; endosperm abundant; embryo minute, apical. TYPE SPECIES: *S. Schreberi* J. F. Gmelin. (Name commemorating Johann David Schoepf, 1752–1800, a German physician and botanist who traveled in North America and the West Indies.)

According to Sleumer (pers. comm. and 1980, family references), a genus of 23 species in three sections. Section SCHOEPFIA (sect. *Codonium* (Vahl) Endl.), the largest (19 species), is restricted to the tropics of Central and South America and the West Indies, with one species reaching peninsular Florida. Section SCHOEPFIOPSIS (Miers) Engler includes three species of southeastern Asia (Tibet/China border, China, Macau, Hong Kong, and Japan), and sect. ALLOSCHOEPFIA Sleumer (sect. *Euschoepfia* Engler) is composed of a single species, *S. fragrans* Wallich, which occurs in southeastern Asia and western Malesia (Nepal, Bhutan, eastern Bengal, Assam, Burma, Yunnan province of China, Thailand, Indochina, and northern Sumatra).

Schoepfia Schreberi J. F. Gmelin (*S. chrysophylloides* (A. Rich.) Planchon), graytwig, whitewood, is a shrub or tree to 10 m tall with trunks to 30–45 cm in diameter. It occurs locally, sometimes in abundance, in hammocks, pinelands, and coppices, and on limestone, coral rock, or sand, in Florida from the Everglade Keys northward along the eastern coast to Volusia County and along the western coast to Pinellas County (reports of this species from the Florida Keys may be the result of mistaking Long Key in the Everglades for the island Long Key). This is a wide-ranging species in the West Indies, Mexico, Central America, and northern and western South America.

Schoepfia Schreberi is a photosynthetic root parasite that is not host specific—it has been reported to parasitize the roots of ten different species, both dicots and monocots, in Florida and the Bahamas (Werth *et al.*, 1978, 1979; Piehl, 1973; and Musselman & Mann, 1978). The haustoria are similar to those found in other Santalales but have a distinctive conical or dome shape.

Within the Olacaceae, *Schoepfia* is very distinctive and is the only member of subfam. Schoepfioidae Engler. Reed (1955, family references), on the basis of wood anatomy and floral morphology, considered the genus to be the most specialized in the family. The calyx is mostly absent, being represented by a lobed ridge at the base of the ovary. The bract and two bracteoles that subtend each flower are united into a cup-shaped, calyciform involucre that encloses the lower part of the flower. The ovary is inferior and two- or three-locular, with each locule containing a single apotropous ovule that lacks integuments. The flowers of *S. Schreberi* are heterostylous, and other members of the genus should be examined carefully for this feature.

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