

THE GENERA OF STERCULIACEAE IN THE SOUTHEASTERN UNITED STATES ¹

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STERCULIACEAE Bartling, Ord. Nat. Pl. 255, 340. 1830, nom. cons.

(STERCULIA FAMILY)

Trees, shrubs, or herbs [rarely vines]; pubescence of stellate and/or simple hairs; inner bark usually fibrous; mucilage cells and/or cavities and/or ducts in the axis and/or leaves and reproductive organs. Leaves alternate, usually simple and palmately veined at base, petioled [rarely sessile]; stipules caducous or persistent. Inflorescences bracteate cymes or thyrses, axillary and/or terminal, rarely opposite the leaves, sometimes reduced to fascicled or solitary flowers. Flowers bisexual or unisexual by abortion, regular, usually hypogynous, pediceled to sessile, usually bracteolate, sometimes with an involucre of 3 or 4 distinct bract(let)s. Sepals usually 5, connate [rarely distinct], often nectariferous at base within, valvate. Petals usually 5, distinct, sometimes adnate at base to the staminal tube, usually clawed, sometimes hooded (with a terminal appendage), convolute, or absent. Stamens 5–15 [–45], usually connate into a staminal tube, often on an androgynophore, sterile in ♀ flowers, the antipetalous ones 5 (or in 5 fascicles of 2 or 3), fertile, the antisepalous ones 5, usually sterile or wanting, rarely fertile; anthers extrorse, usually dorsifixed, 2- or rarely 3-locular, the locules parallel or divergent [rarely separated, or exceptionally superposed], sometimes of unequal size, longitudinally dehiscent; pollen usually small to medium sized, oblate to prolate, often nearly spherical, 3–8-colp(oid)ate, mostly reticulate. Gynoecium 5-carpellate [rarely up to 60-carpellate], syncarpous, rarely apocarpous, or 1-carpellate, rudimentary in ♂ flowers;

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stigmata 1-5; styles as many as carpels, distinct or variously connate; ovary superior, usually 5-locular with axile placentae, or rarely 1-locular with a submarginal placenta; ovules [1] 2 to many in a locule, ascendent to pendulous, hemianatropous to anatropous, epitropous to apotropous, 2-integumented, with a thick nucellus. Fruit various, often capsules, follicles, or schizocarps, with many- to 1-seeded locules. Seed [sometimes arillate or winged] with [or without] endosperm; embryo axial, straight or curved, the cotyledons plane or plicate and/or coiled around the radicle. Germination epigeous [or hypogeous]. (Including Byttneriaceae R. Br.). TYPE GENUS: *Sterculia* L.

An almost exclusively pantropical family of 65 or 70 genera (about 1000 species), with a few extensions into warm-temperate areas; six of 12 genera indigenous to tropical America restricted to that region; four genera (one naturalized) in our area; three additional genera extending northward from Mexico to Texas or California and Arizona.²

The family has usually been subdivided into eight to ten tribes. Evidence from wood and petiole anatomy favors the establishment of two subfamilies: Sterculioideae (including only Sterculieae) and Byttnerioideae (including the remaining tribes), with at least one tribe intermediate in petiolar anatomy. Floral anatomy emphasizes the great uniformity of the family in regard to the development and structure of the androecium. In contrast, "Pollen morphology is in favour of referring Erioleneae and Dombeyeae to Malvaceae, Fremontodendreae [Fremontieae] to Bombacaceae and parts of the rest of Sterculiaceae to Tiliaceae" (Erdtman, p. 421). Thus emended, the Sterculiaceae would be very homogeneous palynologically, but the limits between the families of the Malvales would become even weaker and more uncertain than they are at present. It seems desirable, at least for the present, to treat the family within the generally accepted limits, with its subdivision into tribes.

Sterculiaceae are closely related to Tiliaceae, Malvaceae, and Bombacaceae. Evidence from floral anatomy and embryology suggests that the family is the most primitive in the Malvales. On the same basis the Sterculieae (with pentacyclic flowers, numerous stamens fertile in both series, apocarpous gynoecia, and many-ovulate locules) are regarded as the most primitive, and Hermannieae (with tetracyclic flowers, a reduced number of stamens and ovules, and a tendency to perigyny) the most advanced tribe of Sterculiaceae. In respect to perianth structure the Helicterae DC. (with irregular almost two-lipped flowers) and Byttnerieae DC. (with hooded and terminally or \pm abaxially "appendaged" petals of complex structure) appear to be the most highly specialized tribes of Sterculiaceae.

Data on floral biology are few, but the family in general appears to be adapted to insect-pollination. Nectaries, when present, seem to be located

² In addition, *Guazuma ulmifolia* Lam. (as *G. tomentosa* HBK.) has been recorded from one locality in Dade County, Florida (Moldenke). This record is in need of verification and insufficient as a basis for the inclusion of *Guazuma* Adans. in our flora.

at the base of the sepals (Brown) where they sometimes form an extrastaminal disc lining the calyx base and the receptacle around the ovary or the androgynophore. Foetid, indol- or scatol-scented flowers, usually dark purple or chocolate in color, are apparently pollinated by flies. Some of these flowers are of the "lantern type," with fly-traps for small flies. The nectariferous, irregular flowers of *Helicteres Isora* L. are supposedly pollinated by large Apidae or by small honey birds. In *Theobroma Cacao* L. pollination by thrips, ants, midges, and aphids has been recorded. Proterandry and the relative positions of the extrorse anthers and stigmata, characteristic of the family, seem to secure cross-pollination. Heterostyly is known in *Melochia* and *Waltheria* (q. v.). Cleistogamous flowers occur in a few species of *Ayenia* (Cristóbal). In *Theobroma Cacao*, individual trees are either self-incompatible, or cross-incompatible, or self-incompatible but cross-compatible only with the pollen of self-compatible trees (cf. Cope in Cuatrecasas).

The androecium in Sterculiaceae is basically obdiplostemonous. The traces for the antipetalous stamens, arising conjointly with those of the petals, divide first into three bundles each, a median and two laterals, which sometimes undergo a further secondary division (multiplication). Consequently, there are usually three (sometimes more or fewer) stamens opposite each petal (alternate with the sepals in apetalous flowers). The traces for the antisepalous stamens usually remain unbranched (single), sometimes becoming nonfunctional. Correspondingly, there characteristically are only five stamens (usually sterile), one opposite each sepal. All members of the androecium usually are connate into a staminal tube of various lengths. Thus, the androecium in Sterculiaceae seems to have evolved along the lines of cohesion and reduction (Rao, 1952).

The most significant embryological features of the family include the secretory type of anther tapetum; the multicellular archesporium of the ovule, with only one functional cell; Polygonum-type embryo sac; hooked synergids and usually ephemeral antipodals; nuclear endosperm becoming cellular at a late stage of seed development; and embryo development of the *Urtica* (exceptionally *Polygonum*) variation of the Asterad type. Polyembryony has been recorded in *Cola nitida*. Apotropous ovules occur at least in *Melochia* and *Waltheria*.

Chromosome counts recorded for about 20 genera (40 species) are $2n = 14, 16, 20, 24, 32, 36, 38, 40, 46, \text{ca. } 50, \text{ and } 120$, suggesting that diploidy, polyploidy, and aneuploidy have been of importance in the evolution of Sterculiaceae. It is notable that chromosome numbers of 20 or 40 occur in 60 per cent of the genera investigated. The lowest number, $2n = 14$, has been found in *Melochia* and *Waltheria*.

Theobroma Cacao, native to tropical America and widely cultivated there and in the Tropics of the Old World, especially in West Africa, yields seeds which are the source of cocoa, chocolate, and cocoa butter. The seeds contain the alkaloid theobromine, as well as traces of caffeine. Species of the tropical African *Cola* Schott & Endl., mainly *C. nitida* (Vent.) Schott & Endl. and *C. acuminata* (Beauv.) Schott & Endl., furnish edible seeds,

kola nuts, which contain caffeine and a heart-stimulating glucoside, kolanin, and which are used in medicine as a cerebral, cardiac, and nerve stimulant and in industry for beverage purposes. Some species of several genera yield bast fibers and/or lumber of local importance (e.g., *Guazuma*, *Sterculia* L., *Cola*). A few species of *Dombeya* Cav., *Fremontia* Torr. (*Fremontodendron* Cov.), *Brachychiton* Schott & Endl., *Sterculia*, and some other genera are grown as ornamentals in southern Florida.

REFERENCES:

- ALEXANDER, E. J. *Dombeya Cayeuxii* of hybrid origin. *Addisonia* 23: 1, 2. pl. 737. 1954.
- ARÈNES, J. Sterculiacées. In: H. HUMBERT, Fl. Madagascar Comores. 131^e Famille. 539 pp. Paris. 1959.
- BAILLON, H. Malvacées. Hist. Pl. 4: 57–160. 1873. [Sterculiaceae included in Malvaceae, 57–82, 103, 104, 121–137.]
- BENTHAM, G. Notes on Malvaceae and Sterculiaceae. Jour. Linn. Soc. Bot. 6: 97–123. 1862 (15 May). [Sterculiaceae, 110–123.]
- & J. D. HOOKER. Sterculiaceae. Gen. Pl. 1: 214–228. 1862 (July); 982–984. 1867.
- BODARD, M. Polyembryonie chez *Cola nitida*. VIII^e Congr. Int. Bot. Rapp. Commun. Sects. 7, 8: 259–261. 1954. [Two or 3 separate or completely fused seedlings from a seed; origin unknown.]
- . Propositions nouvelles sur la classification des Sterculiées. Univ. Dakar Ann. Fac. Sci. 4: 57–60. 1959.
- BROWN, W. H. The bearing of nectaries on the phylogeny of flowering plants. Proc. Am. Philos. Soc. 79: 549–595. 1938. [Includes *Dombeya*, *Helicteres*.]
- CAMMERLOHER, H. Blütenbiologie I. Sammlung Borntraeger 15. 199 pp. pls. 1, 2. Berlin. 1931. [*Sterculia javanica* R. Br. and *S. laevis* Wall., multicellular glandular "sugar-hairs" on adaxial side of sepals or forming a ring around base of androgynophore.]
- CANDOLLE, A. P. DE. Byttneriaceae. Prodr. 1: 481–502. 1824. [= Sterculiaceae.]
- CHATTAWAY, M. M. The wood of Sterculiaceae. I. Specialization of the vertical wood parenchyma within the sub-family Sterculieae. New Phytol. 31: 119–132. pls. 4, 5. 1932.
- . Tile-cells in the rays of the Malvales. *Ibid.* 32: 261–273. pl. 9. 1933.
- . Ray development in the Sterculiaceae. Forestry Great Britain 7: 93–108. 1933.
- . The wood anatomy of the Sterculiaceae. Philos. Trans. Roy. Soc. London B. 228: 313–366. 3 pls. 1937.* [Author's summary in Trop. Woods 53: 62, 63. 1937.]
- CUATRECASAS, J. Cacao and its allies. A taxonomic revision of the genus *Theobroma*. Contr. U. S. Natl. Herb. 35: 379–614. pls. 1–12. 1964. [Includes: Anatomy of the wood, by W. L. Stern, 439–442; Pollen morphology, by G. Erdtman, 442–446; Cytology, 446, and Pollen incompatibility, 447–449, by F. W. Cope; extensive bibliography, 599–605, supplemented by numerous references in footnotes, 439, 446, 447.]
- DEHAY, C. L'appareil libero-ligneux foliaire des Sterculiacées. Ann. Sci. Nat. Bot. XI. 2: 45–132. 1941. [Thirty-one genera, 86 spp.]
- DUMONT, A. Recherches sur l'anatomie comparée des Malvacées, Bombacées,

- Tiliacées, Sterculiacées. Ann. Sci. Nat. Bot. VII. 6: 129-242. pls. 4-7. 1887. [Sterculiaceae, 198-224, 240.]
- EDLIN, H. L. A critical revision of certain taxonomic groups of the Malvales. New Phytol. 34: 1-20, 122-143. 1935. [Sterculiaceae and Byttneriaceae distinct families, both derived from Tiliaceae, 124, 125, 136, 137; Scytopetalaceae most primitive within Malvales, 136, 137; Fremontieae belong in Bombacaceae.]
- FAIRCHILD, D. Florida plant immigrants. A tree that is famous for its smell. Occ. Pap. Fairchild Trop. Gard. 12: 4-6. 1943. [*Sterculia foetida* L., odor of flowers very offensive.]
- FREYTAG, G. F. A revision of the genus *Guazuma*. Ceiba 1: 193-225. 1951. [Four spp. in 3 sects.; *G. tomentosa* HBK. a distinct sp.]
- GAZET DU CHATELIER, G. Recherches sur les Sterculiacées. Revue Gén. Bot. 52: 174-191, 211-233, 257-284, 305-332. 1940. [Comparative morphology of the flowers and petiolar anatomy; for critical notes see C. DEHAY, Bull. Soc. Bot. France 89: 76-78. 1942.]
- GEHRIG, M. Beiträge zur Pharmakognosie der Malvales. Anatomie des Laubblattes. Diss. 84 pp. 5 pls. Basel. 1938.*
- GERMAIN, R. Sterculiaceae. Fl. Congo 10: 205-316. 1963. [*Dombeya* Cav., *Melhania* Forsk., by P. BAMPS.]
- GRAY, A. Byttneriaceae. Gen. Pl. U. S. 2: 82-88. pls. 134, 135. 1849. [*Melochia*, *Hermannia* L.]
- GRISEBACH, A. H. R. Flora of the British West Indian islands. i-xvi + 789 pp. London. 1859-1864. [*Ayenia*, sects., 91, 92; *Melochia*, sects., 93, 94; *Waltheria*, 94, 95.]
- HARVEY, M. A revision of the genus *Fremontia*. Madroño 7: 100-110. 1943.
- LAKELA, O., & F. C. CRAIGHEAD. Annotated checklist of the vascular plants of Collier, Dade, and Monroe counties, Florida. 95 pp. Fairchild Trop. Gard. & Univ. Miami Press, Coral Gables. 1965. [Sterculiaceae, 61.]
- LEINFELLNER, W. Zur Entwicklungsgeschichte der Kronblätter der Sterculiaceae-Buettnerieae. Österr. Bot. Zeitschr. 107: 153-176. 1960. [Ten genera, 25 spp.]
- MARTIN, A. C. The comparative internal morphology of seeds. Am. Midl. Nat. 36: 513-647. 1946. [Endosperm fleshy to firm-fleshy; embryo usually "spatulate," "folded" in *Ayenia*, "investing" in *Firmiana simplex*.]
- MOLDENKE, H. N. A contribution to our knowledge of the wild and cultivated flora of Florida — 1. Am. Midl. Nat. 32: 529-590. 1944. [Sterculiaceae, 543; *Guazuma tomentosa*, Moldenke 3781, "Dade Co.: at edge of canal along Tamiami Trail, 25 miles west of Miami."]
- PIJL, L. VAN DER. On the flower biology of some plants from Java with general remarks on fly-traps (species of *Annona*, *Artocarpus*, *Typhonium*, *Gnetum*, *Arisaema* and *Abroma*). Ann. Bogor. 1: 77-99. 1953. [*Abroma augustum* (L.) L. f., 90-95; also *Ayenia glabrescens* K. Schum. and *Sterculia rubiginosa* Vent., 95.]
- RADFORD, A. E., H. E. AHLES, & C. R. BELL. Guide to the vascular flora of the Carolinas. 383 pp. Chapel Hill, N. C. 1964. [Sterculiaceae, 229, 230.]
- RAO, C. V. Contributions to the embryology of Sterculiaceae — I. Jour. Indian Bot. Soc. 28: 180-197. 1949. [Five genera, 6 spp.]
- . Floral anatomy of some Sterculiaceae with special references to the position of stamens. *Ibid.* 237-245. 1949. [Three genera.]
- . Pollen grains of Sterculiaceae. *Ibid.* 29: 130-137. 1950a. [Nine genera in 5 tribes; key to the genera, based on pollen.]

- . Contributions to the embryology of Sterculiaceae — II. *Waltheria indica* Linn. *Ibid.* 163–176. 1950b.
- . Contributions to the embryology of Sterculiaceae. III. *Melochia corchorifolia* L. *Ibid.* 30: 122–131. 1951.
- . Floral anatomy of some Malvales and its bearing on the affinities of families included in the order. *Ibid.* 31: 171–203. 1952. [Sterculiaceae, 171–179, 196, 197.]
- . Contributions to the embryology of Sterculiaceae. IV. Development of the gametophytes in *Pterospermum suberifolium* Lam. *Ibid.* 251–260. 1953. [Primitive embryological characters: multicellular archesporium and the development of 2 or 3 embryo sacs in an ovule.]
- . Contributions to the embryology of Sterculiaceae — V. *Ibid.* 32: 208–238. 1954. [Eight genera, 10 spp.; seed structure in *Pterospermum*.]
- ROBYNS, A. Sterculiaceae. In: R. E. WOODSON, JR., & R. W. SCHERY, Flora of Panama. Ann. Missouri Bot. Gard. 51: 69–107. 1964.
- RUFF, O. Phylogenie des Columniferen-Astes der Dicotylen. Bot. Arch. 31: 1–139. 1930. [Sterculiaceae, 17, 18, 45–47, 137, 138.]
- SAUNDERS, E. R. On carpel polymorphism. IV. Ann. Bot. 45: 91–110. 1931. [= Floral anatomy of Sterculiaceae, 10 genera.]
- SCHULTZE-MOTEL, W. Malvales. In: H. MELCHIOR, A. Engler's Syllabus der Pflanzenfamilien. ed. 12. 2: 304–316. 1964. [Sterculiaceae, 313–315.]
- SCHUMANN, K. Sterculiaceae. In: C. F. P. MARTIUS, Fl. Brasil. 12(3): 1–114. pls. 1–24. 1886a.
- . Vergleichende Blütenmorphologie der cucullaten Sterculiaceen. Jahrb. Bot. Gart. Berlin 4: 286–332. pls. 3, 4. 1886b. [Byttneriaceae.]
- . Sterculiaceae. Nat. Pflanzenfam. III. 6: 69–99. 1890.
- SHENSTONE, F. S., & J. R. VICKERY. Occurrence of cyclo-propene acids in some plants of the order Malvales. Nature 190: 168, 169. 1961. [*Brachychiton*, 2 spp., seeds; *Sterculia foetida*, leaves and seeds.]
- WINKLER, H. Beiträge zur Morphologie und Biologie tropischer Blüten und Früchte. Bot. Jahrb. 38: 233–271. 1907. [Sterculiaceae, 248–258.]

KEY TO THE GENERA OF STERCULIACEAE

General characters: *trees to herbs; hairs simple and/or stellate; leaves alternate, simple, petioled, stipulate; inflorescences cymose; flowers small, regular, hypogynous, bisexual or rarely unisexual; perianth 5-merous, sepals and petals distinct, the latter sometimes wanting; stamens 5 to many, monadelphous, the antisepalous 5 sterile or wanting, rarely fertile; gynoecium usually 5-carpellate, syncarpous, rarely apocarpous, or 1-carpellate, ovules 2 to many in a locule; fruit simple or rarely aggregate.*

- A. Plants arborescent; leaves large, the blade commonly 15–20 cm. long and 20–30 cm. broad, usually deeply 3–5-lobed, long petioled; inflorescences ample thyrses 20–50 cm. long; flowers apetalous, unisexual; stamens (10–)15, on a conspicuous androgynophore; fruit of 5 stalked follicles 6–9 cm. long, leaflike after dehiscence, with 2 seeds on each margin. 1. *Firmiana*.
- A. Plants herbaceous, suffruticose, or rarely fruticose; leaves not more than 8 cm. long usually unlobed; inflorescences small or flowers solitary; flowers petaliferous, bisexual; stamens 5; fruit simple, capsular.
 - B. Flowers axillary, solitary or in fascicles of 2 or 3; petals long clawed, ± hooded, inflexed and attached by the tips to the apex of staminal

- tube, the corolla appearing parachute-like; androgynophore present; anthers 3-locular; capsule covered with short subcylindrical prickly-like protuberances; seeds coarsely reticulate. 2. *Ayenia*.
- B. Flowers in dense headlike or umbel-like inflorescences; petals short clawed, adnate at base to the staminal tube, \pm spreading; androgynophore wanting; anthers 2-locular; capsule and seed smooth.
- C. Corolla orange-yellow; gynoecium 1-carpellate, stigma brushlike, style 1, ovary 1-locular; capsule inclosed in persistent calyx, 1(2)-seeded, 2-valved. 4. *Waltheria*.
- C. Corolla pink to purple, or white, very rarely yellowish; gynoecium 5-carpellate, stigmata 5, subulate to subclavate, styles 5, connate at base to half their length, ovary 5-locular; capsule subtended by persistent calyx, 5-10-seeded, 5-10-valved. 3. *Melochia*.

Tribe STERCULIEAE

1. *Firmiana* Marsili, Saggi Sci. Lett. Accad. Padova 1: 106. 1786.

Deciduous trees [rarely shrubs], with minute stellate-tomentose pubescence. Leaves large, membranaceous, palmately 5-7-veined and -lobed, deeply cordate [or truncate to rounded] at base, long petioled; stipules caducous. Inflorescences large axillary and terminal thyrses; bracts caducous. Flowers regular, hypogynous, apetalous, unisexual by abortion (the plants monoecious), pedicels articulate in the upper half. Calyx with a short [rarely rather long], campanulate to urceolate tube with a dense transverse band of long hairs in the throat and a nectariferous disc around the androgynophore, the 5 lobes longer [or shorter] than the tube, somewhat fleshy, yellow-green [to yellow-orange, or white], reflexed. Stamens usually 15; anthers subsessile to sessile on margin of a \pm campanulate to subcylindrical (in δ) or saucer-like (in ♀ flowers) staminal tube at the apex of a conspicuous androgynophore, forming a globular clump concealing the pistillodium in δ , and encircling the ovary base and indehiscent in ♀ flowers, 2-locular, the locules contiguous, often unequal; pollen medium sized, prolate-spheroid, 3-colpate, reticulate. Gynoecium nearly apocarpous, but appearing syncarpous, the densely pubescent, closely appressed carpels usually connate by the upper part of the styles; rudimentary in δ flowers; stigmata 5, subpeltate, spreading, closely appressed adaxially and appearing as a single 5-lobed stigma; styles 5, connate for a short distance near their apices; ovaries 5, each with 4 submarginal, sessile, anatropous, nearly horizontal ovules. Fruit of 5 stalked membranaceous follicles, each opening before maturity into a leaflike body exposing 2-4 seeds on its margins. Seeds subglobular; the outer seed coat brown, subcoriaceous, subreticulately wrinkled, the inner crustaceous; endosperm copious, firm, fleshy; embryo straight, axial; cotyledons thin, suborbicular, cordate at base; radicle short, stoutish, inferior. TYPE SPECIES: *Sterculia platanifolia* L. f. = *F. simplex* (L.) W. F. Wight. (Named in commemoration of Count K. J. von Firmian, 1716-1782, Austrian statesman, Governor of Lombardy under Maria Theresa.)

An Asiatic genus of about ten species, primarily tropical, ranging from the western Himalaya to eastern China, the Philippines, Malesia, and Papuasia. *Firmiana simplex* (*F. platanifolia* (L. f.) Schott & Endl.), Chinese parasol tree or phoenix tree, $2n = 40$, indigenous to subtropical and warm-temperate China (Yunnan to Kwantung, north to Shensi and Hopeh) is grown as an ornamental in our area and has become naturalized locally, mostly in the Coastal Plain, from northern Florida to North Carolina, southern Alabama, and Louisiana. It is a fast-growing tree with smooth gray-green bark, occurring on roadsides, in city lots, thickets, and mixed deciduous woods.

The inflorescences are either predominantly staminate or carpellate with a few flowers of the opposite type appearing by the end of blooming; both kinds of inflorescences occur on the same tree. Flowers intermediate between staminate and carpellate have also been observed occasionally. The staminate inflorescences seem to flower before the carpellate. Although insect-pollination may safely be assumed for the genus (presence of a nectariferous disc, petaloid sepals, etc.), no data on pollinators are available. Cross-pollination is favored by the unisexual flowers and the somewhat earlier expansion of the staminate ones, but some self-pollination is very probable. In both floral anatomy and embryology *Firmiana* seems to be very similar to *Sterculia* L. Chromosome counts for three species are $2n = 40$. The seeds, which remain firmly attached to the margins of the opened, leaflike, apparently deciduous follicles, are probably dispersed by wind.

The genus is closely related to *Scaphium* Schott & Endl. (follicles two-seeded), *Pterocymbium* R. Br. (follicles with a single basal seed), and *Sterculia* (follicles leathery to woody, seeds dropping off the carpels, radicle opposite the hilum).

The caffeine-containing seeds of *Firmiana simplex* are sometimes roasted and used to make a tea in China. The timber finds application in the paper industry, and the phloem fibers are utilized in making cordage.

REFERENCES:

- Under family references see DUMONT (pp. 198–201, under *Sterculia*), GAZET DU CHATELIER (pp. 211–259), RADFORD *et al.* (p. 229), RAO (1954, as to *Sterculia colorata*), SAUNDERS (pp. 118, 119, under *Sterculia*), and SCHUMANN (1890, p. 97).
- KOSTERMANS, A. J. G. H. A note on some African Sterculiaceae. Bull. Jard. Bot. Bruxelles 24: 335–338. 1954. [*Erythropsis* Lindl. ex Schott & Endl. congeneric with *Firmiana*; some African spp. of *Sterculia* and *Firmiana* transferred to *Hildegardia* Schott & Endl.]
- . The genus *Firmiana* Marsili (Sterculiaceae). (Revised.) Reinwardtia 4: 281–310. 1957. [For an earlier publication see Commun. Forest Res. Inst. Indon. 54: 3–33. 1956.*]
- . Miscellaneous botanical notes 2. Reinwardtia 5: 375–418. 1961. [*Firmiana*, 2 new names and 1 new combination, 383–390.]
- KOZIMA, H., T. ARAKI, K. WAKIDA, T. TAKAHASHI, & Y. MATSUO. Chemical constituents of the young leaves of *Firmiana platanifolia* Schott et Endl. (In Japanese.) Jour. Chem. Soc. Jap. Pure Chem. Sect. 82(1): 134. 1961.*

- MORRISON, B. Y. *Firmiana simplex*. Natl. Hort. Mag. 38: 58, 59. 1959. [An estimate of horticultural value.]
- NYI [YEN], T. K. Observations on the sex differentiation and flower anatomy of *Firmiana simplex*. Contr. Biol. Lab. Sci. Soc. China 5(3): 1-25. 1929.
- YEN, T. K. Carpel dehiscence in *Firmiana simplex*. Bot. Gaz. 93: 205-212. 1932.

Tribe BYTTNERIEAE DC.

2. **Ayenia** Linnaeus, Sv. Vet.-Akad. Handl. 17: 23. pl. 2. 1756.

Usually decumbent [prostrate or erect] subshrubs [or deciduous shrubs, rarely small trees], \pm pubescent with simple and/or stellate hairs [or glabrous]. Leaves small (to 1×0.7 cm.) [to rather large, 21×10 cm.], membranaceous [rarely coriaceous], 3-5-veined at base, toothed [or entire], petioled; stipules small, subulate, persistent at least in part [or caducous]. Flowers pediceled, axillary, solitary or in fascicles of 2 or 3 [to 12, or arranged in axillary or terminal, simple, peduncled, sometimes fascicled or paniced cymes], small 2-3 [-7] mm. long, pink to red, bisexual [rarely unisexual, or sometimes cleistogamous]. Sepals 5, oblong-lanceolate, connate at base. Petals 5, slender clawed, \pm rhombic (in ours), \pm hooded in the upper part, cleft and 2-dentate [or entire] at apex, with [or without] a clavate [to linear] abaxial appendage below the cleft, inflexed toward center of flower and attached by means of teeth to apex of staminal tube, the whole corolla resembling a parachute with the style protruding through its center. Androgynophore usually conspicuous [rarely wanting]. Stamens 5, antipetalous, staminodia 5, antisepalous, all connate into a \pm campanulate staminal tube; upper parts of filaments of fertile stamens distinct, reflexed; upper parts of staminodia distinct, \pm triangular [sometimes hooded], recurved; anthers with 3 contiguous locules; pollen small to medium sized, oblate-spheroid, 3-aperturate, reticulate [rarely spinuliferous]. Gynoecium usually 5-carpellate, syncarpous; stigma subcapitate, 5-lobed; style single; ovary 5-locular, minutely tuberculate, with axile placentae; ovules 2, hemianatropous, somewhat curved toward the placenta, superposed in each locule, the lower one rudimentary (in ours). Fruit a small, subglobular, usually 5-locular capsule covered with short, subcylindrical [or wartlike to trigonous] protuberances, both septicidally and loculicidally dehiscent, 10-valved. Seed solitary in each locule, narrowly ovoid, slightly curved, abruptly narrowed into a subcylindric-conical beak at apex; seed coat crustaceous, dark brown, with a few broad longitudinal and transverse ribs forming a few-meshed reticulum [or corrugated to smooth], minutely black-verruculose; chalazal knot round, subbasal, close to hilum; endosperm wanting; embryo straight; cotyledons bisect [or bilobed?], plicate, spirally rolled around an elongated superior radicle. TYPE SPECIES: *A. pusilla* L. (Name commemorating Louis de Noailles, 1739-1777, Duc d'Ayen, later Maréchal de Noailles, promoter of sciences, amateur gardener, and owner of a famous garden in St. Germain; see Linnaeus, Schwed. Akad. Wiss. Abh. 18: 25. 1757.)

A tropical American genus of about 70 species, extending north to California, Arizona, New Mexico, Texas, and Florida, and south to Argentina and Uruguay, centered in Mexico and northern Central America, with a secondary center in Bolivia, Paraguay, and central and eastern Brazil; one species of sect. *AYENIA* in our area.

Grisebach subdivided the genus into three sections differing mainly in the structure of the petals, the length of the distinct parts of filaments, the characters of the surface of fruits and seeds, and in the sculpture of the pollen. Cristóbal's species concept, although perhaps a little too narrow, is followed here.

The Cuban *Ayenia euphrasiifolia* Griseb. occurs in pinelands on the Florida Keys and in southernmost peninsular Florida (Dade and Monroe counties).³ It is closely related to and perhaps not specifically distinct from the Cuban-Bahamian *A. tenuicaulis* Urb. Four Mexican species range into Texas, New Mexico, and Arizona, and one reaches California.

The pink to red, sometimes foetid flowers are pollinated by small insects. The petals perfectly separate the stigma from the anthers, preventing self-pollination. Unisexual flowers occur at least in the Brazilian *A. angustifolia* St. Hil. & Naud. Cleistogamous flowers with reduced petals and androgynophore and mostly introrse anthers have been recorded in four species (Cristóbal).

The comparative morphology and ontogeny of the cucullate petals in Byttnerieae (Schumann, Leinfellner) suggest that in *Ayenia* (§ *Ayenia*) the petal blade is reduced to a clavate [or linear] appendage, while the hooded rhombic portion of the petal ("face" or "mask") is homologous with the upper part of the claw.

Chromosome counts made for eleven species are $2n = 20$ and 40, the latter number occurring in three species. Fruits in *Ayenia*, which dehisce first septicidally and then loculicidally, as well as along the adaxial (ventral) suture, the valves detaching themselves from a persistent central column, may be regarded as a capsule type transitional to the schizocarp. There seem to be no special adaptations for seed dispersal, and seed dispersing agents are unknown.

The genus is closely related to the pantropical *Byttneria*, which differs mainly in petals with an evident apical portion (corresponding to the petal blade) not attached to the staminal tube.

REFERENCES:

Under family references see DUMONT (p. 217), GRISEBACH (pp. 91, 92), LAKELA & CRAIGHEAD (p. 61), LEINFELLNER (pp. 158-162), and SCHUMANN (1886a, pp. 101-108, pls. 23, 24; 1886b, pp. 294-297; 1890, pp. 83-85).

CRISTÓBAL, C. L. Revisión del género *Ayenia* L. (Sterculiaceae). (English summary.) Op. Lilloana 4: 1-230. 1960.

³ No other species seems to occur in Florida. Small's record of *A. pusilla* from that area (Man. SE. Fl. 863. 1933) apparently was based either on misidentifications or on a very broad interpretation of that species, which has been recorded only from Ecuador and northern Peru (Cristóbal, p. 191). All specimens from Florida labeled as *A. pusilla* were annotated by Cristóbal as *A. euphrasiifolia*.

- . Nueva contribución al estudio del género *Ayenia* L. (Sterculiaceae). *Anales Instituto Biol. México* 32: 191–200. 1961. [One new Mexican sp. and several new records from Mexico, Central America, and Colombia; first record of cleistogamous flowers in *A. fruticosa* Brandegees.]
- . Notas sobre el género *Ayenia*. *Lilloa* 31: 207–212. 1962. [A new sp. from Colombia described; 1 sp. from Cuba redescribed and illustrated.]

Tribe HERMANNIEAE Schott & Endl. emend. Benth.

3. **Melochia** Linnaeus, Sp. Pl. 2: 774. 1753; Gen. Pl. ed. 5. 304. 1754.

Herbs to shrubs [or rarely trees]; pubescence of simple and/or stellate hairs. Leaves narrow to broad, palmately 3–5-veined at base, serrate, petioled; stipules small, persistent at least in part. Inflorescences few-flowered umbel-like peduncled cymes or many-flowered dense headlike thyrses composed of 2- or 3-flowered dichasia or monochasia, or thyrses sometimes secondarily arranged into interrupted spikelike panicles, axillary and/or terminal (rarely opposite the leaves); bracts persistent or caducous. Flowers small, bisexual, heterostylous, often with an involucre of 3 or 4 distinct bract(let)s at base, pediceled or sessile. Calyx \pm campanulate, 5-dentate to -cleft, persistent, nectariferous at base. Petals 5, pink to purple, usually yellow or white at base, or white, or rarely yellowish, spatulate to oblong, clawed, adnate at base or higher up to staminal tube, longer than the sepals, marcescent. Stamens 5, antipetalous, the staminal tube cylindrical, inflated after fertilization; free part of filaments elongated in short-styled, very short in long-styled flowers; 5 obsolete, toothlike staminodia sometimes present in short-styled flowers; anthers 2-locular, the locules contiguous before and \pm divaricate after fertilization; pollen medium sized, spheroid to oblate-spheroid, 3-colpate, finely reticulate. Gynoecium 5-carpellate, syncarpous; stigmata 5, subulate or filiform to \pm clavate, papillose, or shortly and racemosely branched; styles 5, distinct or connate to half their length; ovary sessile to short stipitate, 5-locular, the placentation axile; ovules 2 in each locule, superposed, ascendent, anatropous, apotropous. Fruit a 5-locular, loculicidal and/or septicidal capsule [rarely a schizocarp], the locules 1- or 2-seeded. Seed obovoid, nearly round in cross-section or \pm angular on adaxial (ventral) surface, with a prominent humplike chalazal knot and thin threadlike raphe; outer seed coat thin, membranaceous, usually obliterated, the inner crustaceous; endosperm fleshy; embryo straight, spatulate, cotyledons large, foliaceous; radicle short, inferior. LECTOTYPE SPECIES: *M. corchorifolia* L.; see Medicus, *Künstl. Geschl. Malven-Fam.* 10. 1787, and Britton & Millspaugh, *Bahama Fl.* 277. 1920.⁴ (Name from *melokhiya* or *melukhiye*, an Arabic

⁴ Hitchcock & Green (*Int. Bot. Congr. Cambridge* 1930. *Nomencl. Propos. Brit. Bot.* 172. 1929) proposed *Melochia pyramidata* L. as the lectotype species, reasoning that it was "the only one of the original species included in Section *Eu-Melochia* Griseb. by K. Schumann." They overlooked, however, a few earlier circumstances.

In his *Genera Plantarum* (ed. 5. 1754, p. 304) Linnaeus attributed *Melochia* to Dillenius, referring to plate 176 of *Hortus Elthamensis* on which Dillenius's *Melochia corchori folio* (*M. corchorifolia* L.) was figured. Thus Linnaeus himself seems to

name for *Corchorus olitorius* L., widely cultivated as a potherb in the eastern Mediterranean, particularly in Egypt, since ancient times.)

A pantropical, predominantly American genus of about 60 species, with one extending into warm-temperate regions; four species (one naturalized) in our area.

The three predominantly American sections of the genus established by Grisebach are delimitable by the shape and/or the kind of dehiscence of fruits and sometimes by the type of inflorescence and presence or absence of a floral involucl. The fourth, the Indo-Malayan-Pacific sect. *VISENIA* (Houtt.) Benth. & Hook. differs in the arborescent habit and usually apically winged seeds of its species.

Section *MELOCHIA* (§ *Riedlea* (Vent.) Griseb.; *Riedlea* Vent.). Capsules sessile, subglobular, slightly 5-lobed, the lobes rounded; inflorescences dense, many-flowered, peduncled to sessile headlike thyrses; flowers sessile, with an involucl. About 30 (or more) species, centered in tropical America, a few in the Old World, two endemic on Madagascar; *M. melissifolia* Benth. in America and Africa.

The paleotropical *Melochia corchorifolia*, chocolate weed, with pedunculate, usually terminal inflorescences and long-petioled leaves glabrous or with scattered hairs on the veins beneath, has become naturalized in old, especially sandy, fields, cultivated grounds, and waste places in the Coastal Plain, from southern peninsular Florida north to southeastern North Carolina and west to southeastern Texas. In the New World it is also recorded from Panama, suggesting that it may become a pantropical weed. *Melochia villosa* (Mill.) Fawc. & Rendle (*M. hirsuta* Cav., *Riedlea hirsuta* (Cav.) DC.), with sessile axillary and terminal inflorescences forming interrupted spikelike thyrses and short-petioled leaves silky-pubescent or glabrescent beneath, is widely distributed in tropical America. It reaches southern Florida, where it occurs on moist sands in marshy lands, flatwoods, and pinelands. In the Old World this species has become naturalized at least on Madagascar.

Section *MOLUCHIA* (Medic.) Brizicky (§ *Eumelochia* Griseb.; *Moluchia* Medic.). Capsules \pm stipitate, pyramidal, deeply 5-lobed, the lobes wing-

have indicated the type of this genus, and the generic description does not contradict this assumption. In 1787, Medicus, considering *M. corchorifolia* to be the typical species of *Melochia* established the segregate genus *Moluchia*, clearly based on *Melochia pyramidata*, and thus effectively typified *Melochia*. In choosing *M. corchorifolia* as the lectotype species, Britton and Millspaugh formally accomplished the typification of the genus, which had already been indicated by Linnaeus and effected by Medicus.

With this typification the following nomenclatural changes in two of three sections recognized by Grisebach are necessary:

Melochia sect. **Melochia** (*Melochia* sect. *Riedlea* (Vent.) Griseb. Fl. Brit. W. Indian Is. 93. 1859.) TYPE SPECIES: *M. corchorifolia* L.

Melochia sect. **Moluchia** (Medic.) Brizicky, stat. nov. (*Melochia* sect. *Eumelochia* Griseb. Fl. Brit. W. Indian Is. 93. 1859. *Moluchia* Medic. Künstl. Geschl. Malven-Fam. 10. 1787.) TYPE SPECIES: *M. pyramidata* L. (*Moluchia herbacea* Medic., nom. superfl.).

like; inflorescences 3–10-flowered umbel-like peduncled [sometimes paniced] cymes; flowers pediceled, without an involucl. About nine species, eight American, one endemic on Madagascar.

Melochia tomentosa L. (*Moluchia tomentosa* (L.) Britt.), with axillary cymes and tomentose leaves and capsules, occurs in pinelands in southernmost Florida (Dade County) and ranges widely in tropical America. *Melochia pyramidata* L., with inflorescences opposite the glabrous leaves and capsules with scattered minute stellate hairs, has also been reported from Dade County, Florida (Lakela & Craighead). Widely distributed in tropical America (north to Mexico and Texas), it has been introduced into the Old World, where it seems to have become a pantropical weed. In Texas the flowers of this species open at noon and close in late afternoon [from a collector's field note].

The nectaries and the bright-colored petals indicate insect-pollination, but pollinators have not been observed. Heterostyly seems to be common within the genus. Floral anatomy and embryology have been investigated only in *M. corchorifolia*. The single chromosome count recorded is $2n = 14$ (in *M. bracteosa* F. Hoffm. = *M. melissifolia* Benth. var. *bracteosa* (F. Hoffm.) K. Schum., from West Africa). Although fruits in *Melochia* mostly are septicidal and/or loculicidal capsules, types intermediate to schizocarps ("pentacocous capsules") also occur (sect. *MOUGEOTIA* (HBK.) Griseb.). Seed-dispersal agents are unknown, except in the species of sect. *VISENIA*, the usually winged seeds of which are said to be dispersed both by wind and ocean currents. The very wide distribution of *M. pyramidata* and *M. corchorifolia* is due mainly to human agency.

Melochia is closely related to *Waltheria* L. The genus is in need of a modern revision.

REFERENCES:

Under family references see GERMAIN (pp. 255–258), GRAY (pp. 85, 86, *pl.* 134), GRISEBACH (pp. 93, 94), LAKELA & CRAIGHEAD (p. 61), RADFORD *et al.* (p. 230), RAO (1950a; 1951; 1952, p. 179), ROBYNS (pp. 77–85), and SCHUMANN (1886a, pp. 27–49, *pls.* 7–10; 1890, pp. 80, 81).

GARCKE, A. Über einige Arten von *Melochia*. Bot. Jahrb. 12(Beibl. 27): 29–32. 1890.

JONES, S. B., JR. Additional Alabama weeds. Castanea 26: 136–138. 1961. ["Currently it (*M. corchorifolia*) is one of the most troublesome weeds in cultivated fields in Mobile and Baldwin counties, but was not observed north of those counties."]

MEDICUS, F. K. Ueber einige künstliche Geschlechter aus der Malven-Familie, denn der Klasse der Monadelphien. 158 pp. Mannheim. 1787. [*Moluchia* Medic., 10–12.]

4. *Waltheria* Linnaeus, Sp. Pl. 2: 673. 1753; Gen. Pl. ed. 5. 304. 1754.

Herbs or subshrubs [or shrubs], erect, single stemmed or much branched from the base, rarely diffuse and prostrate; pubescence mainly of stellate hairs. Leaves usually oblong to ovate, 3–5-veined at base, toothed, petioled; stipules small, lanceolate-subulate, caducous. Inflorescences axillary

and terminal, peduncled to sessile, dense headlike compound cymes (or thyrses?) composed of 2- or 3-flowered sessile or subsessile dichasia or monochasia, sometimes forming short-branched or spikelike thyrses. Flowers small, bisexual, homostylous [or often heterostylous], sessile, with 1 or more bractlets at base. Calyx persistent, the tube campanulate-turbinate, slightly 5-angled, 10-veined, nectariferous at base, equaling or exceeding the 5 lanceolate-subulate lobes. Petals usually orange-yellow, spatulate, clawed, adnate at base to the staminal tube, longer than the sepals, marcescent. Stamens 5, connate into a tubular staminal tube equaling [or shorter than] the pistil; free upper parts of filaments very short [or elongated]; anthers 2-locular, the locules contiguous; pollen medium sized, usually oblate-spheroid, (3)4(-8)-colpate, reticulate. Gynoecium 1-carpellate; stigma brushlike [or clavate?]; style single, solid, excentric (sublateral); ovary sessile, 1-locular, subtruncate and hairy at apex; ovules 2, submarginal, superposed, ascendent, anatropous, apotropous. Capsule obliquely obovoid, hairy at apex, 1(2)-seeded, 2-valved. Seed obliquely obovoid, slightly compressed laterally, with a shallow adaxial raphe-bearing groove, dark brown to black except the rusty-colored round or elliptic chalazal knot; endosperm fleshy; embryo straight; cotyledons large, foliaceous; radicle short, inferior. LECTOTYPE SPECIES: *W. indica* L. (*W. americana* L.); see R. Brown in Tuckey, Narr. Exped. Congo 484. 1818.⁵ (Name commemorating Augustin Friedrich Walther, 1688-1746, professor of botany in Leipzig; see Linnaeus, Crit. Bot. 95. 1735.)

An almost exclusively tropical American genus of about 30 (or fewer) species, one pantropical and two African (one endemic on Madagascar); one species in our area.

The polymorphic, pantropical *Waltheria indica* (*W. americana* of almost all American authors), a usually \pm canescent herb or subshrub, occurs in hammocks, pinelands, and on sand dunes on the Florida Keys and in southern peninsular Florida, north to Highlands and Lee counties. It was recorded as adventive on the coast of Alabama (Small, Man. SE. Fl. 863. 1933) but does not seem to occur there at present.

Heterostyly is fairly frequent within the genus. Pollination by wasps and bees has been recorded for *W. indica* and *W. viscosissima* St. Hil. in Brazil. The floral anatomy and embryology of *W. indica* appear to be very similar to those of *Melochia corchorifolia*, but embryo development conforms to the *Polygonum* variation of the Asterad type (in contrast with the *Urtica* variation in *Melochia* and other genera of Sterculiaceae thus far investigated).⁶ The single recorded chromosome count is $2n = 14$. Seed

⁵ "Robert Brown (in Tuckey, Narr. Exp. Congo 484. 1818) appears to have been the first to unite *Waltheria americana* L. (Sp. Pl. 673. 1753) and *W. indica* L. (Sp. Pl. 673. 1753). He adopted the name *Waltheria indica* for the combined species, and this name must accordingly be retained" (Art. 57, Int. Code Bot. Nomencl. 47. 1961).

⁶ The following comment by Rao (1950b, p. 175) is enigmatic: "Embryological evidence supports the retention of the genus *Waltheria* in Sterculiaceae as indicated by Hutchinson and is against its transfer to Bombacaceae as suggested by Engler and Prantl." In the references to Rao's article "Engler, A. and Prantl, K. (1928). — Natürliche Pflanzenfamilien. 2. Auflage" is cited. This incomplete and apparently erroneous

dispersal by wild goats and perhaps by some granivorous birds (e.g., doves) has been recorded for *W. indica*.

The genus is closely related to *Melochia*. A modern revision is desirable.

REFERENCES:

Under family references see GERMAIN (pp. 258, 259), RAO (1950a & b; 1952, p. 179), ROBYNS (pp. 74-77), and SCHUMANN (1886a, pp. 50-68. *pls.* 11-14; 1890, p. 81).

DIERS, L. Der Anteil an Polyploiden in den Vegetationsgürteln der Westkordillere Perus. *Zeitschr. Bot.* **49**: 437-488. 1961. [$2n = 14$ in *W. ovata* Cav., 450.]

reference provides no clue to Rao's statement. The order Malvales (or Columniferae) has not appeared in the second edition of the *Natürlichen Pflanzenfamilien*, and the only volumes of this series published in 1928 are Bd. 2 and Bd. 5, with treatments of Algae and Fungi respectively.



Brizicky, George K. 1966. "The genera of Sterculiaceae in the southeastern United States." *Journal of the Arnold Arboretum* 47(1), 60–74.

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