

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

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RECENT RESEARCH in the fields of floral morphology and anatomy, embryology, palynology, comparative anatomy, biochemistry, etc., has made possible more accurate determination of the systematic positions of many families and their arrangement into more natural affinity-groups or orders than was attainable at the time when the classical Englerian system was proposed. Since orders usually form the skeleton of every proposed scheme for a "natural system" of the angiosperms, the achievement of the greatest possible homogeneity seems to be of primary importance. With regard to this, the splitting of at least some very large and heterogeneous orders of the Englerian system (e.g., Geraniales, Sapindales), followed in some instances by rearrangement of the families among and/or within the segregated orders, appears to be expedient. Such changes have been carried out more or less successfully in several recent systems (e.g., Hutchinson, 1926 & 1959; Gundersen, 1950; Cronquist, 1957; Takhtajan, 1959).

Although the sequence of a number of families of the southeastern United States which have been surveyed by the author in the *Journal of the Arnold Arboretum* (vols. 43 & 44, 1962 & 1963) generally corresponds with that of Engler's system (1936), Takhtajan has been followed primarily in the delimitation of the orders. Thus, the families Rutaceae, Simaroubaceae, Burseraceae, and Anacardiaceae (as well as Meliaceae, unpublished) are regarded as members of the order Rurales; the families Sapindaceae, Aceraceae, and Hippocastanaceae (as well as several others occurring beyond

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our limits) constitute the order Sapindales; and Aquifoliaceae, Celastraceae, and Hippocrateaceae represent the order Celastrales. The families Empetraceae (Wood & Channell, Jour. Arnold Arb. 40: 162–164. 1959) and Cyrillaceae (Thomas, *ibid.* 42: 96–102. 1961) have been removed from Sapindales and are regarded as members of Ericales, views which accord with those of Takhtajan. Contrary to Takhtajan's view on Staphyleaceae as a primitive member of Sapindales, this family is here excluded from Sapindales and will be treated within Cunoniales (or Saxifragales *sensu lato*), where it seems to belong (cf. C. G. G. J. van Steenis, Fl. Males. I. 6: 49. 1960).

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SAPINDACEAE A. L. de Jussieu, Gen. Pl. 246. 1789, "Sapindi," nom. cons.  
 (SOAP-BERRY FAMILY)

Trees, shrubs, or woody (rarely herbaceous) vines climbing by axillary tendrils [or very rarely erect herbs], often containing saponine in the tissues of the stem and/or fruit. Leaves usually alternate, compound to decompose, often even-pinnate, rarely simple, exstipulate or rarely stipulate, persistent or deciduous. Plants (polygamo-) monoecious or dioecious; flowers in terminal and/or axillary thyrses [or simple or compound racemes, or rarely solitary], small, hypogynous, regular or more rarely irregular, usually unisexual by abortion, occasionally also bisexual. Sepals usually 4 or 5, distinct or  $\pm$  connate, usually unequal, deciduous or persistent, imbricate [or valvate]. Petals usually 4 or 5, distinct, clawed, often with petaloid appendages ("scales") on the interior surface just above the claw, imbricate, rarely wanting. Nectariferous disc extrastaminal (except in *Dodonaea*), continuous and regular or unilateral and oblique. Stamens 6–10[–12], often 7 or 8, distinct or connate at base, inserted within or on the disc, short and sterile or wanting in ♀ flowers; anthers versatile, introrse (extrorse only in *Melicoccus*), longitudinally dehiscent. Gynoecium syncarpous, usually 3–, rarely 2– or 4[–6]-carpellate, rudimentary in ♂ flowers; stigma simple or lobed, or stigmas 3; style short or elongate, sometimes  $\pm$  cleft at apex; ovary superior, 2–4[–6] (usually 3)-locular, the placentae axile; ovules usually 1 or 2 in each locule, campylotropous to anatropous, apotropous or more rarely epitropous. Fruit a drupe, berry, capsule (sometimes winged), or schizocarp splitting at maturity into drupelike [nutlike or samaroid] mericarps, often 1-locular and 1-seeded by abortion. Seed usually solitary in a locule, often provided with

an aril; <sup>2</sup> seed coat bony, crustaceous, or coriaceous (rarely fleshy); endosperm usually wanting or scanty; embryo usually curved. (Including Dodonaeaceae Link.) TYPE GENUS: *Sapindus* L.

A pantropical family of nearly 150 genera with about 2000 species, a few extending into warm-temperate areas. The number of genera occurring in America, Asia, and Africa (including Madagascar) is almost equal (with fewer in Australia with Oceania), but the greatest number of species is New World. The large genus *Allophylus* L. is pantropical; the primarily American *Cardiospermum* and the almost exclusively Australian *Dodonaea* have two and one species, respectively, of pantropical distribution. A few genera are extratropical (e.g., the Asiatic *Koelreuteria* Laxm. and *Xanthoceras* Bunge), while some largely tropical genera have extratropical species (e.g., *Sapindus*). The family has been subdivided by Radlkofer into 14 very natural tribes.

One of the peculiarities of the flowers of the family is the frequent presence of variously shaped, more or less petaloid, interior "appendages" to the petals. According to Leinfellner, the diversity of appendaged and unappendaged petals of Sapindaceae is a result of phylogenetically fixed lateral and/or median-ventral splittings of originally peltate-funnelform petals, sometimes also followed by various secondary connations or eventual suppression in development of the separated (split-off) parts.

Chromosome numbers known at present (23 species in 17 genera) form an aneuploid series,  $2n = 20, 22, 24, 28, 30, 32$ .

Sapindaceae are most closely related to Hippocastanaceae and Aceraceae, but are also allied to Anacardiaceae, Burseraceae, Meliaceae, Simaroubaceae, and Rutaceae. Evidence from wood anatomy (Heimsch) supports this scheme of relationships suggested by Radlkofer (1890, 1895, 1932-1934).

Indigenous to French Guiana, *Talisia pedicellaris* Radlk., which differs from *Melicoccus* (*q.v.*) mainly in the 5-merous perianth, introrse stamens, and septate ovary, was included in the flora of the Southeastern States by Small. This record was based on a poor herbarium specimen (NY) collected by Harshberger in Brickell Hammock, Miami, Florida, in December, 1910. Apparently neither Small nor Sargent, both of whom seem to have been much interested in Harshberger's discovery, ever relocated this species. Because Brickell Hammock since has been destroyed by the growth of

<sup>2</sup> Van der Pijl (p. 620) proposed the following definitions of the aril and aril-like structures: "I propose to define the aril more or less in the same way as Gaertner did of old, viz. as a secondary, usually postfloral outgrowth of the funicle and therefore entirely free from the seed. This definition is independent of whatever view we may hold with regard to the phylogenetical origin of the aril. While maintaining the old term 'arillode' for an outgrowth of the integument in the vicinity of the micropyle, I shall use the term 'arilloid' for every kind of outgrowth on or near the seed that resembles the apparently independent aril." Since only a few families and not all the genera of Sapindaceae with arillate seeds have been investigated in regard to the morphological nature of their "arils," it is preferred here to use the term aril in a broad descriptive sense, applying it to all the categories of seed out-growths defined by Van der Pijl.

metropolitan Miami, there seems to be no reason for the inclusion of *Talisia* in the flora of the southeastern United States at present.

The eastern Asiatic *Koelreuteria paniculata* Laxm.,  $2n = 22, 30(?)$ , and *Xanthoceras sorbifolium* Bunge are often grown as hardy ornamentals; the former is beginning to spread from cultivation in at least the northeastern United States (Fernald, Gray's Man. Bot. ed. 8. 990. 1950). The less hardy *K. formosana* Hayata,  $2n = 22$ , is grown in the warmer areas of the southern United States. Lychee, *Litchi chinensis* Sonn.,  $2n = 28, 30$ , a native of southeastern Asia, where it has also been in cultivation for over 2000 years, is now widely grown in tropical countries for its edible fruit pulp (seed aril) and seeds (edible when roasted). It is being cultivated commercially in Florida. The closely related *Euphoria Longana* Lam., longan,  $2n = 30$ , a native of India or southern China, widely planted in the Tropics (especially in Asia), is grown as an ornamental fruit tree (edible seed arils) in southern Florida, as well as in southern California. The caffeine-bearing seeds of the South American *Paullinia Cupana* HBK. find application in medicine (guarana, pasta guarana, guarana bread). Fruits and crushed shoots of many species of various genera are used for poisoning fish in the Tropics because of their saponine content.

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## KEY TO THE GENERA OF SAPINDACEAE

General characters: *trees, shrubs, or vines; leaves alternate, usually compound or decomposed, very rarely simple, mostly exstipulate; flowers small, regular or more rarely irregular, hypogynous, usually unisexual by abortion; perianth usually double, 4- or 5-merous; petals clawed, often with interior appendages above the claw, rarely absent; nectariferous disc usually extrastaminal; stamens often 6-8; gynoecium commonly 3-carpellate, syncarpous; ovary superior; ovules 1 or 2 in each locule, campylo- to anatropous, usually apotropous; fruits various, often 1-locular and 1-seeded by abortion.*

- A. Plants herbaceous or suffruticose, climbing by axillary tendrils; leaves usually biternate, minutely stipulate; flowers irregular; disc unilateral, 2-glandular; fruits subglobular to top-shaped bladderly capsules, 1.5-4.5 cm. long. . . . . 1. *Cardiospermum*.
- A. Plants woody, trees or shrubs; leaves never biternate, exstipulate; flowers regular; disc continuous; fruits various, never bladderly capsules.
- B. Leaves simple, covered with minute resiniferous glands, often viscous, appearing varnished; petals wanting; disc intrastaminal, minute; fruit a (2)3(4)-winged capsule. . . . . 5. *Dodonaea*.
- B. Leaves compound; petals always present; disc extrastaminal; fruits not winged.
- C. Leaves 3-foliolate, leaflets, small, up to 6 cm. long by 2.5 cm. broad; fruit an ovoid or ellipsoidal black drupe, 6-9 mm. long. . 6. *Hypelate*.
- C. Leaves usually even-pinnate; leaflets medium sized to rather large; fruits various, larger.
- D. Leaves with 6-18 entire or toothed leaflets; petals mostly appendaged.
- E. Leaflets entire, opposite or alternate, often conspicuously inequilateral, acute or acuminate at apex (if obtuse or rounded, the rachis winged); fruit of 1 or 2 (3) brown to black, drupe-like, subglobular mericarps with rudiment(s) of aborted carpel(s) at base, 1.2-2 cm. in diameter; seed not arillate. . . . . 2. *Sapindus*.
- E. Leaflets toothed or at least repand, alternate,  $\pm$  equilateral, obtuse or rounded at apex; fruit a triangular-top-shaped stipitate capsule, 10-15 mm. long and broad; seed with cup-shaped aril. . . . . 4. *Cupania*.
- D. Leaves usually with 4 (2-6) entire, opposite or subopposite leaflets; petals unappendaged.
- F. Flowers in slender simple or paniced racemes terminating lateral branches; leaves usually 4-foliolate, leaflets acute at apex; berry ellipsoidal or obovoid, about 3 cm. long and 2 cm. broad, green, the pericarp thick and firm; seed ellipsoidal; seed coat fleshy, edible. . . . . 3. *Melicoccus*.
- F. Flowers in axillary, subterminal, corymb-like thyrses; leaves 2- or 4(rarely 6)-foliolate, leaflets obtusish to rounded or notched at apex; berry usually subglobular, 10-14 mm in diameter, dark purple, the pericarp thin; seed subglobular; seed coat crustaceous. . . . . 7. *Exothea*.

## Tribe PAULLINIEAE HBK. emend. Radlk.

1. *Cardiospermum* Linnaeus, Sp. Pl. 1: 366. 1753; Gen. Pl. ed. 5. 171. 1754.

Herbaceous or suffruticose vines climbing by axillary tendrils; nodes trilacunar. Leaves biternate, sometimes also 3-foliolate with 3-lobed leaflets, or subbipinnate, petioled, minutely stipulate; leaflets usually coarsely toothed. Plants (polygamo-) monoecious or dioecious; flowers in axillary, corymb-like, reduced thyrses bearing two opposite tendrils below the summit of the peduncle, small, irregular, unisexual by abortion, sometimes also bisexual. Sepals 4 [5], the two exterior nearly half as long as the interior, imbricate. Petals 4, short clawed, appendaged, the petaloid scales of the two upper petals equilateral, cucullate crested, bearing below the apex a tongue-like "appendage" pointing downward, those of the two lower petals inequilateral, with a dorsal, winglike crest. Disc unilateral, with a gland opposite each of the two upper petals. Stamens 8, of unequal length, deflexed, shorter and sterile in ♀ flowers; filaments slightly connate at base; pollen medium sized, 3-colpate, heteropolar (one polar area bulging, the other ± flat or slightly concave), triangular in polar view, reticulate. Gynoecium 3-carpellate, rudimentary in ♂ flowers; stigmas 3, filiform, spreading; style short; ovary 3-locular, the placentae axile; ovules solitary in each locule, anatropous, apotropous, ascendent, 2-integumented, with a thick nucellus. Fruit a membranaceous or subchartaceous bladderly capsule, subglobular, obovoid or top shaped, 3-angled and slightly 3-lobed, septifragal [or septicial]. Seeds subglobular, black, with an inconspicuous aril (arillode, "pseudoaril") leaving a whitish, reniform to semicircular abscission scar ("hilum," "pseudohilum") in the micropylar area; testa thick-crustaceous; endosperm very scanty or wanting(?); embryo curved; cotyledons fleshy, unequal (the shorter, exterior one incurved, the longer, interior transversely biplicate); radicle short. TYPE SPECIES: *C. Halicacabum* L. (Name from Greek, *cardia*, heart, and *sperma*, seed, in allusion to the heart-shaped abscission scar on the seeds of the type species.) — BALLOON-VINE, HEART-SEED, HEART-PEA.

A largely tropical American genus of 12 species; *Cardiospermum grandiflorum* Sw. also occurs in tropical West Africa (introduced?), and two species of pantropical distribution extend into our area. *Cardiospermum Halicacabum* var. *Halicacabum*,  $2n = 22$ , usually an annual vine with biternate leaves and seeds with a heart-shaped to reniform "hilum," occurs sporadically in waste places, moist thickets, and cultivated grounds in our area and west to Texas and Oklahoma, north to Missouri, Ohio, Illinois, Pennsylvania, and New Jersey. It is considered to be an introduced and naturalized species. The perhaps indigenous var. *microcarpum* (HBK.) Blume, sometimes regarded as a distinct species, *C. microcarpum* HBK., differing in its somewhat smaller leaves and leaflets and smaller fruits more or less truncate at the apex, has been collected in the hammocks,

pinelands, and swamps of the Florida Keys and peninsular Florida as far north as Lake County. The closely related *C. Corindum* L. (*C. keyense* Small), a suffruticose vine with usually biternate, rarely subbipinnate leaves, and seeds with a semicircular "hilum," occurs in hammocks on the Florida Keys, where it apparently is indigenous. Some authors include this species in *C. Halicacabum*.

Our knowledge of the genus as a whole in regard to biology, floral anatomy, embryology, and cytology is almost exclusively based on studies on *Cardiospermum Halicacabum*. The tendrils below the summit of the peduncle are regarded as modified lowermost lateral branches of the inflorescence. Since the flowers usually are unisexual, and the occasional bisexual ones are proterandrous (Nair & Joseph), cross-pollination should be the rule if *Cardiospermum* is dioecious, as has been assumed. Recently, however, Hauman characterized the genus as monoecious. Although observations made on herbarium material agree with Hauman's view, at least in regard to *C. Corindum* and *C. grandiflorum*, further field observations are necessary. It is possible that both mono- and dioecism occur within the genus and even within the species. The conditions of pollination and fertilization in monoecious plants should also be investigated. Insect-pollinators have not been specified, but bees probably take part in pollination, since "Balloon vine is reported as the source of considerable honey in Texas" (Pellett). The placentation of the ovaries is axile in the ovule-bearing region, although a tendency toward a parietal condition has been indicated (Nair & Joseph). There is no positive knowledge in regard to the fruit-dispersing agents. Although Radlkofer (1895, p. 295) and Engler (p. 265) assumed winds to be responsible for the transportation of capsules for long distances, Guppy (1906) believed that granivorous birds "probably carry about the seeds of *Cardiospermum halicacabum*."

Fossil leaves (resembling those of *Cardiospermum Halicacabum*, but coriaceous) from two Oligocene localities in Colorado have been referred by MacGinitie (pp. 143, 144) to this genus.

The genus is most closely related to the tropical American *Urvillea* HBK., which extends into Texas with at least two species. Relationships with *Serjania* Schum. and *Paullinia* L. are also unquestionable.

The common balloon-vine, *Cardiospermum Halicacabum* (as well as *C. Corindum* and *C. grandiflorum* in the Tropics) is often cultivated as an ornamental. Roots, stems, and leaves of this species, as well as of *C. Corindum*, find various applications in local medicine in tropical countries. The leaves and young stems of *C. Halicacabum* are eaten in the East Indies.

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Under family references see DAVID (pp. 693-698), ENGLER (pp. 265, 268, 269), GUÉRIN (pp. 337-340), GUPPY (1906, p. 417), HAUMAN (pp. 284-287), LUBBOCK (pp. 357-359), MACGINITIE (pp. 143, 144), VAN DER PIJL (pp. 620-636), RADLKOEFER (1867, pp. 25, 26; 1895, pp. 295, 306-308; 1932, pp. 317-414), and SELLING (pp. 218, 220).



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## Tribe SAPINDEAE

2. *Sapindus* Linnaeus, Sp. Pl. 1: 367. 1753; Gen. Pl. ed. 5. 171. 1754.

Evergreen or deciduous trees or shrubs. Leaves even-, rarely odd-pinnate, [very rarely simple] (petiolate, exstipulate; leaflets (4) 6–18, entire; rachis winged or wingless. Plants monoecious or dioecious; flowers in ample terminal thyrses with minute deciduous bracts and bractlets, regular, small, unisexual by abortion. Sepals 4 or 5, unequal, the two outer smaller than the inner, connate at base, imbricate, deciduous. Petals 4 or 5, equal, longer than the sepals, unguiculate, with a single bifid scale or 2 scales above the claw on the interior surface, or without scales, imbricate. Nectariferous disc annular, fleshy, lobulate. Stamens 8(–10), inserted within the disc, exerted in the ♂, short and with rudimentary anthers in ♀ flowers. Gynoecium 2–4 (usually 3)-carpellate, rudimentary in ♂ flowers; stigma small, 3-lobed; style short, columnar, 2–4 (usually 3)-sulcate; ovary sessile, 2–4 (usually 3)-locular and -lobed; ovules solitary in each locule, ascendent, campylotropous, apotropous, 2-integumented, with a thick nucellus. Fruit a schizocarp of 3 mericarps (or more commonly of 1 or 2, with rudiments of the aborted locules); mericarps drupelike, yellow to black, subglobular or obovoid, 1-locular, 1-seeded; the flesh resinous, rich in saponine, crustaceous when dried; endocarp pergamentaceous, silky-hairy inside around the seed insertion. Seed globular or obovoid, exarillate; seed coat bony, smooth, black or dark brown; endosperm wanting; embryo curved; cotyledons fleshy, superposed, the dorsal cotyledon incurved, almost inclosing the transversely conduplicate ventral cotyledon; radicle short, inferior, directed toward the hilum. TYPE SPECIES: *S. Saponaria* L. (Name a contraction of Latin, *sapo*, soap, and *indicus*, Indian, i.e., Indian soap, referring to the saponaceous properties and use of the fruits in the West Indies for washing linen.) — SOAPBERRY.

A primarily tropical genus of about 13 species distributed in the Americas (three species), eastern and southeastern Asia (six), Oceania exclusive of Australia (three), and Hawaii (one). At least two species are extratropical. All three American species (included with a few Asiatic and Oceanic ones in sect. *SAPINDUS* [§ *Eusapindus* Radlk.]) occur in our area. The primarily tropical American *Sapindus Saponaria*, southern soapberry, a tree with winged leaf rachises (unwinged in f. *inaequalis* (DC.) Radlk.) and unappendaged petals, ranging from northern Argentina to Peru, north to Mexico and the West Indies, is known from hammocks in southern peninsular Florida (Dade, Monroe, and Collier counties) and on the Keys. It is also considered to be indigenous and represented by a distinct form, f. *microcarpus* Radlk., in the Philippines and some southern Pacific islands (including New Guinea), as well as (f. *inaequalis*) on the Mascarene and Hawaiian Islands, but is introduced and naturalized in some parts of Africa. The extratropical *S. marginatus* Willd., Florida soapberry, with narrowly margined or marginless leaf rachises and with appendaged petals, a rare and possibly rather primitive species, occurs on the Coastal Plain from central Florida (Manatee County) to eastern Georgia (Liberty and Chatham counties). It has been recorded from Cuba, but the records are apparently referable to *S. Saponaria* f. *inaequalis*, which resembles *S. marginatus* in the wingless rachises and usually falcate leaflets but lacks appendages on the petals. Since no authentic records indicating an overlap of the ranges of *S. Saponaria* and *S. marginatus* at the present time have been available, the intergradation between the two species "along their boundary in Florida," presumed by LaMotte (1935, p. 35), appears to be questionable. The also extratropical *S. Drummondii* Hook. & Arn. (*S. Saponaria* var. *Drummondii* (Hook. & Arn.) Benson), western soapberry, very closely related to and perhaps only a variant of *S. marginatus*, ranges from western Louisiana and central Arkansas north to southwestern Missouri, west to Kansas, southern Colorado, western and southern New Mexico, and Arizona, and from Texas to northern Mexico. It appears to intergrade with *S. Saponaria* in Baja California, where the ranges of both species overlap (LaMotte, p. 35).

Little is known about the floral biology of the genus. The flowers usually are unisexual, and the plants have been characterized as (polygamo-)dioecious, although Hauman considers *Sapindus Saponaria* to be monoecious. At least some herbarium specimens of *S. marginatus* and *S. Drummondii* show monoecism. Possibly both di- and monoecism may occur within a species.

Fruit dispersal by frugivorous bats has been observed in Trinidad, as well as in Java (Van der Pijl, 1957, p. 632). In addition, "the indications of West Indian beach-drift and the stranding of the seeds in a germinable condition on the shores of Bermuda point unmistakably to the agency of the current . . . the buoyancy [of seeds] arising from the fact that the kernel [embryo] incompletely fills the seed-cavity. When, however, the cavity is entirely occupied, the seed sinks" (Guppy, 1917).

"The genus seems to have first appeared in late Lower Cretaceous time

in western America as *Sapindopsis magnifolia* Fontaine of the Fuson of Crook County, Wyoming, and *S. variabilis* Fontaine from the same beds. These forms, as figured, may represent a *Eusapindus*-like ancestor to the genus" (LaMotte, 1935, p. 36). Several more definitely outlined species of *Sapindus* are known in western North America from the Paleocene, Eocene, and Miocene. The Eocene species were, in general, large leaved like the living *S. Saponaria* and *S. Mukorossii* Gaertn. (a native of Japan and southeastern China). *Sapindus oregonianus* Knowlton, known from the Miocene of Nevada, Oregon, and Idaho, seems to have been especially close to *S. Mukorossii*, which, in turn, is considered by LaMotte to be the most primitive living species of sect. SAPINDUS.

The genus is closely related to the African *Deinbollia* Schum. & Thonn., which reportedly differs from *Sapindus* mainly in fruits devoid of saponine.

The flesh of fruits of *Sapindus Saponaria* and other species rich in saponine has been used as a substitute for soap in tropical countries. Bony seeds of several species are strung for necklaces and bracelets.

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#### Tribe MELICOCCEAE Blume emend. Radlk.

#### 3. *Melicoccus* P. Browne, Civ. Nat. Hist. Jamaica 210. 1756.

Large, usually glabrous, evergreen trees. Leaves alternate, 4 (rarely 6) [or 2]-foliolate, occasionally simple on the lower branches, petioled, exstipulate; leaflets opposite or subopposite, subsessile, membranaceous to subcoriaceous, entire, usually conspicuously inequilateral; rachis and petiole sometimes winged. Flowers manifestly pediceled, in terminal (and sometimes axillary) slender, simple or paniced racemes with minute subulate or abortive caducous bracts, small, greenish white to white, 6-8 mm. in diameter (when expanded), regular, hypogynous, unisexual by abortion, (polygamo-)dioecious (or monoecious?). Sepals 4, nearly distinct, subequal, petaloid, usually deciduous, imbricate. Petals 4, oblong-ovate to obovate, very shortly clawed, nearly twice as long as the sepals,

nonappendaged [or with an interior bifid scale above the claw], imbricate. Nectariferous disc extrastaminal, large, flat, glabrous, yellow [or red], with undulate to crenate margins. Stamens 8, as long as or longer than the petals in ♂, short and with nonfunctional anthers in ♀ flowers; filaments filiform, much longer than the anthers in ♂ flowers; anthers extrorse, attached to the filaments above the base on the adaxial side, oblong-ovate in outline, sagittate-cordate at the base, 2-locular at anthesis. Gynoecium 2(3)-carpellate, syncarpous, rudimentary in ♂ flowers; stigma large, peltate, 2(3)-lobed; style short, stoutish; ovary superior, sessile, obovoid or ellipsoid, glabrous, 1-locular to imperfectly 2-locular (when 3-carpellate); ovules 2 (3), ascendent from the base, campylotropous, apotropous. Fruit an ellipsoid to subglobular "berry" 2–4 cm. long, with green to yellowish, leathery pericarp, usually 1-locular and 1-seeded. Seed ellipsoid, 1.5–2 cm. long, exarillate; the outer seed coat fleshy, white, yellowish, or yellowish pink, sour-sweet or sour, the inner seed coat leathery to crustaceous; endosperm wanting; embryo straight; cotyledons fleshy, orbiculate, planoconvex; radicle minute, inferior. TYPE SPECIES: *M. bijugatus* Jacq. (*Melicocca bijuga* L.).<sup>3</sup> (Name derived from Greek, *meli*, honey, and *coccus*, grain, seed, berry, i.e., honey-seed or honey-berry, apparently referring to the usually pleasant, sour-sweet taste of the seed coat.) — SPANISH LIME, GENIP.

A genus of two species of tropical continental America. *Melicoccus bijugatus*,  $2n = 32$ , native to northern South America (Surinam to Colombia) and perhaps to Central America (north to Nicaragua), has been widely naturalized from cultivation in the West Indies and perhaps elsewhere in tropical America. It has been grown in southern Florida as an ornamental and shade fruit-tree (the fleshy seed coat and roasted seeds are edible) and appears to have become established in subtropical Florida.<sup>4</sup> *Melicoccus lepidopetalus* Radlk., differing from our species in the unijugate leaves and appendaged petals, has been recorded from Bolivia and Paraguay.

Since little is recorded about the biology of the genus, Lunan's observations (1814) on *Melicoccus bijugatus* are of special interest: "This tree sheds its leaves annually, in the spring, when the new leaves and blossoms make their appearance together; and, in rainy weather, the progress of its

<sup>3</sup>The genus *Melicoccus*, established as monotypic by Browne, was given a combined specific-generic description and is therefore validly published. Since Browne did not use binary nomenclature, the single species remained unnamed until 1760, when Jacquin (*Enum. Syst. Pl. Ins. Carib.*, p. 19) published *Melicoccus bijugatus*. Although Jacquin did not provide a specific description, the binomial is valid and legitimate, for he gave a complete reference to Browne. In 1762, however, Linnaeus (*Sp. Pl. ed. 2. 1: 495*) changed both the generic and specific names and introduced *Melicocca bijuga*, the binomial which has been in general use ever since. There was, however, no justification for these changes, and the correct name for the species is *Melicoccus bijugatus* Jacq.

<sup>4</sup>Monroe County: Cudjoe and Little Knock'emdown keys (cf. Dickson, Woodbury, & Alexander, p. 197); Upper Matecumbe Key, *F. C. Craighead*, 13 May 1962 (FLAS). Hendry County?: hammock, 20 mi. se. of La Belle, *T. H. Carlton*, 4 Apr. 1932 (FLAS).

vegetation is so rapid that the new leaves are completely budded and unfolded in the short space of forty-eight hours, the old foliage, yet in a green state, which ornamented the tree only yesterday, is forced off and strewed withering on the ground. When the blossoms open they diffuse their agreeable fragrance to a very considerable distance, and attract towards them, during that time, swarms of bees and humming birds to feed upon their honey. It has been observed that these trees, when young, bear blossoms two or three years without being succeeded by any fruit; and it is also remarkable that the leaves of old trees lose their foliated margin [wings] upon the common middle rib, which is only to be seen in the leaves of the young ones."

The genus is closely related to the tropical continental American *Talisia* Aubl. which extends as far north as the Yucatán Peninsula, Mexico (two species).

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Tribe CUPANIEAE Reichenb. emend. Radlk.

4. *Cupania* Linnaeus, Sp. Pl. 1: 200. 1753; Gen. Pl. ed. 5. 93. 1754.

Evergreen trees or shrubs. Leaves usually even-pinnate, rarely odd-pinnate (in cultivated specimens), petioled, persistent, exstipulate; leaflets (2) 6-14 [20], usually alternate [or subopposite], medium sized, chartaceous,  $\pm$  dentate to subentire, shortly petioluled. Plants (polygamo-) dioecious; flowers pediceled, in axillary [or terminal] thyrses with usually small bracts and bractlets, small, regular, unisexual by abortion. Sepals 5, distinct, in 2 series, broadly imbricate. Petals 5, whitish [or yellowish], as long as [or shorter than] the sepals, [or rarely wanting], each provided with 2 scales above the claw, imbricate. Disc continuous, annular, crenulate to lobulate, puberulous [tomentose or glabrous]. Stamens 8(-10), inserted within the disc, exerted in  $\delta$ , short and sterile in  $\text{♀}$  flowers. Gynoecium 2-4 (usually 3)-carpellate, rudimentary in  $\delta$  flowers; stigmas 3 [or stigma 3-lobed], style nearly as long as [or shorter than] the ovary, [sometimes 3-fid at apex]; ovary 2-4 (usually 3)-locular, usually pubescent outside [and sometimes also within], ovules solitary in each locule, ascendent from near the base of the axile placenta, campylotropous, apotropous. Fruit a stipitate, turbinate-triangular [laterally 3-lobed, sometimes also 3-winged], (2)3(4)-locular capsule, apiculate with remnants of the style, loculicidally dehiscent. Seed ellipsoidal to subglobular, covered to half its

length by a cup-shaped, fleshy aril; seed coat crustaceous [or coriaceous]; embryo thick, curved; cotyledons fleshy, plano-convex; radicle short, inflexed. TYPE SPECIES: *C. americana* L. (The name commemorates Francis Cupani, 1657–1710, a Sicilian monk, physician, and botanist.)

A tropical American genus of nearly 45 species, extending south to Argentina and Peru, north to Mexico and southern Florida. *Cupania glabra* Sw. of the West Indies, Mexico, and Central America (as far south as Costa Rica) occurs in hammocks on the Florida Keys (Big Pine Key). The species was first collected by Blodgett in the 1840's on Key West, but the specimen was identified only in 1901 by Britton. The species was thought to have been exterminated in Florida until it was rediscovered by Small in 1921 on Big Pine Key, where it has since been collected by several botanists.

Two fossil species, *Cupania oregona* Chaney & Sanborn (resembling the living South American *C. vernalis* Cambess.) and *C. Packardii* Chaney & Sanborn (resembling the living South American *C. americana* L.) are known from the Goshen and Chalk Bluff floras (Upper Eocene-Lower Oligocene) of central Oregon. Several species of the presumably very closely related fossil *Cupanites* Schimper are represented by leaves in the Eocene of the southeastern United States and by both leaves and fruits in certain European Tertiary deposits (cf. Berry, 1916, p. 269).

The genus is very closely related to the tropical American *Matayba* Aubl.

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Tribe DODONAEAE HBK. emend. Radlk.

#### 5. *Dodonaea* Miller, Gard. Dict. Abr. ed. 4. 1754.

Evergreen shrubs [sometimes low and ericoid] or small trees, mostly resinous-viscous. Leaves alternate [rarely subopposite], simple [or pinnate], usually subchartaceous, entire or repand [or ± toothed], with ± numerous parallel lateral veins, usually appearing varnished, viscous, ±

covered with resiniferous glands, petioled to sessile, exstipulate. Plants (polygamo-) monoecious or dioecious; flowers pediceled, [solitary or] in terminal [or axillary] thyrses [or panicles] with small bracts, small, regular, unisexual by abortion, often (in ours) also bisexual. Sepals 3–7, usually 4 or 5 (more rarely 3), connate at base, valvate or narrowly imbricate, usually deciduous. Petals wanting. Stamens distinct, 6–10[–12] in ♂ and bisexual, sterile or wanting in ♀ flowers; filaments very short; anthers linear-oblong in outline, obtusely quadrangular in cross section, apiculate at apex, much longer than the filaments; pollen medium sized, 3-colpate, prolate-spheroidal, subtriangular in polar view, smooth or minutely reticulate. Nectariferous disc intrastaminal, obsolete (minute) in ♂, stipelike in bisexual and ♀ flowers. Gynoecium 2–4[–6] (usually 3)-carpellate, rudimentary in ♂ flowers; stigmas 2–4, usually 3, small; style filiform, sometimes 2–4-fid at apex, at least 3 times as long as the ovary, deciduous; ovary 2–4[–6] (usually 3)-locular, slightly raised on a short, gynophore-like disc, mostly densely covered with resiniferous glands; placentation axile; ovules 2 in each locule, superposed (the upper ascendent, apotropous, the lower pendulous, epitropous), sessile on the outgrowths of the placenta, campylotropous, 2-integumented, with a thick nucellus. Fruit a chartaceous [membranaceous or coriaceous], septifragal [or septicidal] capsule, usually 3–, rarely 2– or 4[–6]-locular, the locules boat shaped, manifestly [or narrowly] winged, 2(or by abortion 1)-seeded. Seeds lenticular or obovoid [or subglobular], with a callus-like outgrowth of the carpel wall around the abscission scar; seed coat crustaceous [or coriaceous]; endosperm wanting; embryo coiled; cotyledons linear; radicle elongated. TYPE SPECIES: *Ptelea viscosa* L. = *D. viscosa* (L.) Jacq. (Named in honor of Rembert Dodoens, or Dodonaeus, 1518–1585, Dutch physician and herbalist.) — HOPBUSH, VARNISH-TREE.

A primarily Australian genus of nearly 60 species, with one in Madagascar, three in Hawaii, and one (*Dodonaea viscosa*) pantropical. *Dodonaea viscosa* (including *D. jamaicensis* DC., *D. microcarya* Small),  $2n = 28, 32$ , extremely variable in shape and size of leaves, size of capsules, and size and shape of seeds, occurs in our area primarily in coastal habitats and hammocks from the Florida Keys northward to Volusia and Hernando counties, Florida. The taxonomy of this perplexing complex apparently has been based almost exclusively on the study of herbarium material, and the numerous varieties and forms have been distinguished primarily on the basis of vegetative characteristics. The lines between taxa are weak, and there seem to be many transitional specimens. The limits of variability of leaves (size and shape) on individual plants have not been studied, but may be rather broad, since in some instances two sheets of the same collection of *D. viscosa* have been cited as different varieties. As delimited by Sherff the species comprises three pantropical varieties (including 11 forms) and var. *Stokesiana* F. Br. restricted to Fiji, the New Hebrides, Society, and Tubuai (Austral) islands of the southern Pacific. The lack of field observations and ecological and cytological data for this complex

makes impossible any conclusion regarding the nature and delimitation of infraspecific categories of *D. viscosa*.

On the basis of Sherff's treatment, all three pantropical varieties, sometimes regarded as distinct species, are represented in Florida. *Dodonaea viscosa* var. *viscosa* f. *viscosa* (var. *vulgaris* Benth. f. *repanda* (Schum. & Thonn.) Radlk.), a shrub with oblong or obovate leaves 7–15 cm. long by 1.5–4 cm. broad and subcircular to oblate capsules 1.5–2.5 cm. broad, seems to be restricted to the mainland in our area, while var. *linearis* (Harv. & Sond.) Sherff f. *angustifolia* (Benth.) Sherff (var. *angustifolia* Benth.; *D. jamaicensis* DC.), a shrub or small tree (?), with linear-oblong to narrowly oblanceolate leaves 6–9 cm. long by 0.5–1 cm. broad and capsules 1.2–1.6 cm. broad, has been collected both on the mainland and the Keys. The var. *arborescens* (Cunn.) Sherff (var. *spathulata* Benth.), a shrub or small tree with spatulate leaves, is represented on the mainland by the rare f. *arborescens*, with narrowly spatulate, sinuate-dentate leaves, and by similar but more frequent f. *spathulata* (Smith) Sherff in which the leaves are entire or slightly sinuate; on the Keys (very rarely on the mainland?) occurs the very distinctive f. *elaegnoides* (Rudolphi ex Ledeb. & Adlerst.) Brizicky<sup>5</sup> (*D. microcarya* Small), a small tree with subcoriaceous, broadly spatulate to obovate-cuneate leaves 3.5–5 cm. long by 1.6–3 cm. broad and small, oblate capsules only 0.8–1[–1.6] cm. broad. Forma *elaegnoides* (f. *Ehrenbergii*) is known also from the Bahamas, Cuba, Hispaniola, and the Lesser Antilles. Sherff comments (1947, p. 304), "It cannot be emphasized too strongly that in certain localities the f. *Ehrenbergii* may easily appear widely and specifically different from f. *arborescens*. Future authors of floristic works restricted to such localities will perhaps, therefore, be tempted to treat it so." In view of the broad tropical distribution of the infraspecific taxa of *D. viscosa*, these apparent geographical restrictions within our area are of interest.

Both dioecism and monoecism have been recorded in *Dodonaea viscosa*; apparently the former is more frequent. Delpino concluded that pollination is by wind. Parthenocarpy has been reported by Joshi. Both Radlkofer and Engler considered wind to be mainly responsible for fruit dispersal in *D. viscosa*, but Guppy (1917, p. 207) concluded "that if we placed the agencies of dispersal in their order of effectiveness they would be, first granivorous birds, then currents, and lastly man."

About 15 fossil species of *Dodonaea*, represented by leaves and/or fruits have been described from the Tertiary deposits (Oligocene and Miocene) of various parts of western Europe. A few species, based on leaves or fruits, are known from the Lower Eocene (e.g., *D. Wilcoxiana* Berry, *D. Knowltonii* Berry) and the Middle and Upper Eocene (e.g., *D.*

<sup>5</sup> *Dodonaea viscosa* (L.) Jacq. var. *arborescens* (Cunn.) Sherff forma *elaegnoides* (Rudolphi ex Ledeb. & Adlerst.) Brizicky, comb. nov. Basionym: *D. viscosa* (L.) Jacq. var. *spathulata* Benth. f. *elaegnoides* (Rudolphi) Radlk. Pflanzenreich IV. 165 (Heft 98g): 1371. 1934. *Dodonaea viscosa* var. *arborescens* (Cunn.) Sherff f. *Ehrenbergii* (Schlechtend.) Sherff, Am. Jour. Bot. 32: 214. 1945; *D. elaegnoides* Rudolphi ex Ledeb. & Adlerst. Diss. Bot. Sist. Pl. Doming. Decad. 18. 1805; *D. Ehrenbergii* Schlechtend. Linnaea 18: 36. 1844.



*viscosoides* Berry) of the southeastern United States (Mississippi, Tennessee, Louisiana), the Oligocene of Colorado (*D. umbrina* MacGinitie), the Miocene of southern California (*D. californica* Axelrod), the Pliocene of Bolivia, and the late Tertiary of Brazil. Axelrod states that material of *D. californica* "cannot be separated from the living *Dodonaea viscosa* . . . . In fact, the affinity of the Miocene to the modern species is so much closer that it seems desirable to recognize a new species."

A modern revision of the genus, eventually of *Dodonaea viscosa*, based on population studies accompanied by cytological investigations, is very desirable.

The genus is most closely related to the Australian *Distichostemon* F. Muell.

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#### Tribe DORATOXYLEAE Radlk.

#### 6. *Hypelate* P. Browne, Civ. Nat. Hist. Jamaica 208. 1756.

Evergreen trees or shrubs. Leaves 3-foliolate, petioled, exstipulate; leaflets relatively small, 3.5-6 cm. long by 1.3-2.5 cm. broad, obovate-cuneate or oblanceolate, sessile, entire, thin-coriaceous, with close, paral-

lel, lateral veins. Plants monoecious; flowers slender pediceled, in axillary or subterminal, loosely branched, few-flowered, long-peduncled thyrses (as long as or longer than the leaves) with small caducous bracts and bractlets, small, regular, unisexual by abortion. Sepals (4) 5, reddish, unequal, the two exterior smaller than the interior, imbricate, deciduous. Petals (4) 5, white, as long as the sepals, unappendaged, flabellate veined, imbricate. Disc annular, fleshy, shallowly 5-lobed, (7)8-sulcate, glabrous. Stamens (7) 8, inserted on the lobes of the disc, exerted in ♂, short and with sterile anthers in ♀ flowers. Gynoecium 3-carpellate, rudimentary in ♂ flowers; stigma obtuse, 3-lobed; style short, curved near apex; ovary 3-locular; placentae axile; ovules 2 in each locule, superposed (the upper ascendent and apotropous, the lower pendulous, epitropous), campylotropous. Fruit a small (ca. 8–9 mm.) drupe, black, subglobular, slightly 3-sulcate, crowned with remnants of the persistent style; flesh thin, sweet, containing saponine; stone thick-crustaceous, 1-locular by abortion, 1-seeded. Seed ellipsoidal or obovoid, exarillate; seed coat thin, leathery, rugulose, reddish brown; endosperm wanting; embryo curved; cotyledons thin, curved, the exterior nearly infolding the circinate interior; radicle long, incumbent, directed toward the fruit apex. TYPE SPECIES: *H. trifoliata* Sw. (The ancient Greek name for *Ruscus* [Liliaceae], butcher's broom, applied by Browne to this genus.) — WHITE IRONWOOD.

A monotypic genus of the West Indies and the hammocks or rarely pinelands (Big Pine Key) of southernmost Florida (Florida Keys). This large shrub or small tree (occasionally up to 12 m. tall and 45 cm. in diameter) is one of the rarest tropical plants indigenous to our area (cf. *Cupania*).

The staminate and carpellate flowers occur in separate inflorescences on the same plant. The occurrence of occasional bisexual flowers seems to be possible. Nothing is known in regard to pollination.

The wood is very heavy, hard, very durable in contact with the soil, and has been valued in Florida for posts; it is also used elsewhere in shipbuilding and for handles of tools.

The genus is closely related to the monotypic Cuban *Euchorium* Ekm. & Radlk. and to *Exothea* Macfad.

#### REFERENCES:

- See also under family references RADLKOFER (1895, p. 358; 1933, pp. 1407–1410), and SARGENT (1922, pp. 716, 717).  
SARGENT, C. S. *Hypelate*. *Silva N. Am.* 2: 77, 78. pls. 80, 81. 1891.

#### 7. *Exothea* Macfadyen, Fl. Jamaica 1: 232. 1837.

Evergreen trees. Leaves even-pinnate, 2–6[–8] (most often 4)-foliolate, very rarely 3- or 1-foliolate, petiolate, exstipulate; leaflets opposite usually thin, entire, obscurely veined, lustrous on the upper surface, sessile or shortly petiolulate. Plants (polygamo-)dioecious; flowers shortly pediceled, in axillary, subterminal, corymb-like thyrses with minute, decid-

uous bractlets, small (ca. 1 cm. in diameter), regular, unisexual by abortion, rarely also bisexual. Sepals 5, connate at base, tomentulose, reflexed after blooming, persistent, imbricate. Petals 5, whitish, short-unguiculate, unappendaged, 1-nerved, about as long as the sepals, imbricate. Nectariferous disc fleshy, patelliform, lobulate, puberulous, orange to red. Stamens 7-10, usually 8, inserted on the disc in small depressions near its margin, as long as or somewhat longer than the petals in  $\delta$  and bisexual, short and sterile in  $\text{♀}$  flowers. Pollen small, 3-colpate, spheroidal, spinulose. Gynoecium 2-carpellate, rudimentary in  $\delta$  flowers; stigma large, obtuse, subbilobed or indistinctly 3-4-lobed; style short, stoutish; ovary sessile, pubescent, 2-locular; ovules 2 in each locule, collateral, suspended from the summit of the axile placentae, anatropous, epitropous. Fruit a berry, dark purple to black, juicy (crustaceous and brownish when dried), crowned with remnants of the style, surrounded at the base by reflexed sepals, usually nearly globular, 1.2-1.6 cm. in diameter, 1-locular and 1-

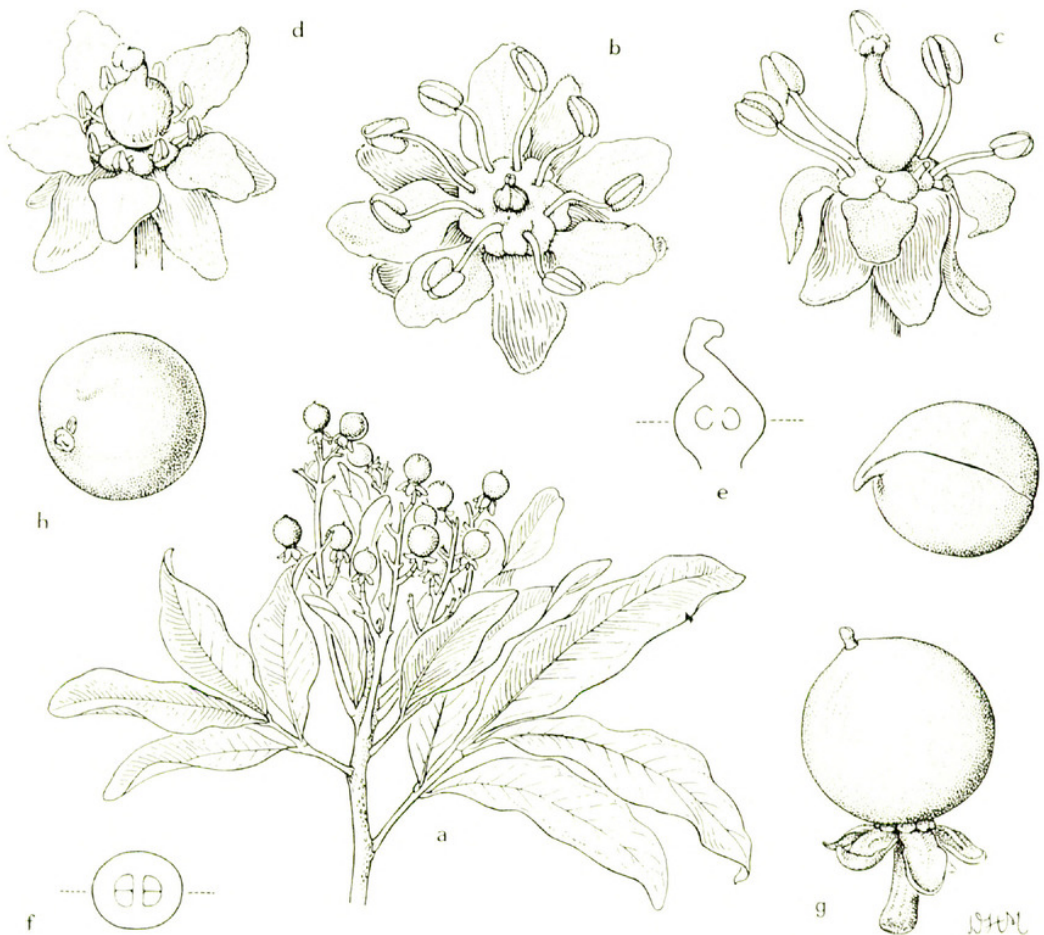


FIG. 1. *Exothea paniculata*: a, twig with immature fruits,  $\times \frac{1}{2}$ ; b, staminate flower, showing disc and pistillodium,  $\times 4$ ; c, bisexual flower, two stamens removed,  $\times 4$ ; d, carpellate flower, showing staminodia,  $\times 4$ ; e, gynoecium in vertical section in plane marked by broken line in "f."  $\times 6$ ; f, gynoecium in horizontal section in plane marked by broken line in "e." showing the four ovules,  $\times 6$ ; g, fruit,  $\times 2$ ; h, seed,  $\times 2$ ; i, embryo, lateral view,  $\times 2$ ; e, f, diagrammatic.

seeded by abortion, rarely transversely ellipsoidal, 2-lobed, 2-locular and 2-seeded. Seed globular, exarillate; seed coat thin, crustaceous, reddish brown, lustrous; endosperm wanting; embryo curved; cotyledons fleshy, plano-convex, puberulous; radicle superior, very short, incumbent, turned toward the small hilum and inclosed in a lateral cavity of the seed coat. TYPE SPECIES: *E. oblongifolia* Macfad. = *E. paniculata* (Juss.) Radlk. (Name derived from Greek, *exotheo*, to remove, in allusion to the separation of this genus from Amyrideae, with which group it was thought to be related.) — INKWOOD, BUTTERBOUGH.

A tropical American genus of three species, distributed in the West Indies, southern Florida, Mexico, and Central America, south to Costa Rica. *Exothea paniculata* occurs in hammocks and on calcareous soils and shell mounds (kitchen middens) in southern peninsular Florida (northward on the east coast to Volusia County) and on the Florida Keys, southward beyond our limits in the West Indies and Central America. Apparently birds are responsible for fruit dispersal. The wood is very hard and heavy, resistant to the attacks of teredo, therefore valuable for piles; it is also used for cabinet-work, boat-building, and small articles.

The genus is closely related to *Hypelate* and *Euchorium*.

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- See also under family references RADLKOFER (1895, p. 358; 1933, pp. 1411-1415), SARGENT (1922, pp. 714-716), and WEST & ARNOLD (p. 133).  
SARGENT, C. S. *Exothea*. *Silva N. Am.* 2: 73-76. pls. 78, 79. 1891.

#### ACERACEAE A. L. de Jussieu, Gen. Pl. 250. 1789, "Acer," nom. cons. (MAPLE FAMILY)

Trees or shrubs distinguishable from the closely related Sapindaceae by the opposite, largely simple leaves; regular flowers; often intrastaminal nectariferous disc; regularly 2-carpellate gynoecium; and schizocarpous fruit (a "double samara") splitting into 2 winged mericarps. TYPE GENUS: *Acer* L.

A family of two genera, chiefly of the Temperate Zone of the Northern Hemisphere. In contrast to the polymorphic and widely distributed *Acer*, *Dipteronia* Oliv. (differing from *Acer* in naked buds, pinnately multifoliate leaves, ample thyrses, and mericarps winged all around) is known only from central and western China (two species), although, in the Tertiary it was represented in western North America by *D. insignis* (Lesq.) R. W. Br., similar to the extant *D. sinensis* Oliv.

A close relationship of Aceraceae to Sapindaceae has generally been assumed, an assumption fully supported by evidence from external and internal morphology, palynology, and biochemistry. The relationship to Hippocastanaceae also is unquestionable, but that to Staphyleaceae, presumed by some taxonomists (cf. Takhtajan), has not been demonstrated satisfactorily.

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1. *Acer* Linnaeus, Sp. Pl. 2: 1054. 1753; Gen. Pl. ed. 5. 474. 1754.

Trees or shrubs. Leaves opposite, simple and usually palmately 3-9 [-11]-nerved and -lobed, or rarely pinnately compound, 3-7-foliolate [or palmately 3-5-foliolate], membranaceous or subcoriaceous [or coriaceous], deciduous [rarely persistent]; nodes 3[4, 5]-lacunar. Inflorescences usually terminal raceme- or corymb-like thyrses, racemes, corymbs, or umbel-like fascicles on short, few-leaved or leafless branchlets developing from the apical and/or lateral buds, before, with, or after leaves. Flowers small or minute, regular, usually hypogynous, ♂ sometimes perigynous, greenish yellow or yellow, rarely red [or white], unisexual by abortion, sometimes also bisexual. Sepals 5(4), ± distinct, or more rarely connate, imbricate. Petals 5 (4), distinct, not rarely sepal-like, imbricate, rarely wanting. Nectariferous disc thick, annular, often lobed, sometimes deeply 5-parted, extra- or intrastaminal, rarely wanting. Stamens 4-10, usually 7 or 8, distinct, hypogynous or perigynous (at least in ♂ flowers) or inserted in the middle of the disc, commonly exerted in ♂, short and generally abortive or rarely wanting in ♀ flowers; filaments filiform; anthers oblong or linear in outline, nearly basifixed, 2-locular at anthesis, introrse, longitudinally dehiscent; pollen medium sized, 3-colpate, prolate, the surface reticulate to striate [or exceptionally spinulose]. Gynoecium syncarpous, usually 2-carpellate (sometimes 3- or 4-, rarely to 8-carpellate), rudimentary or wanting in ♂ flowers; stigmas 2, spreading, often recurved, short to elongate and narrow; style single, elongate to very short; ovary superior, usually 2-locular, much compressed perpendicular to the partition; ovules 2 in each locule, collateral or superposed, campylotropous to anatropous, 2-integumented, with a thick nucellus, nearly sessile, the funicle very short and broad. Fruit a winged schizocarp ("double samara"), composed of 2 mericarps (samaras) separating after maturity from the

persistent axis (carpophore), the nutlike, usually 1-seeded, body ("nutlet") of each mericarp produced on the back into a chartaceous or coriaceous, reticulated,  $\pm$  obovate (sometimes  $\pm$  falcate) wing thickened on the lower margin. Seed without endosperm; testa membranaceous; embryo conduplicate, sometimes coiled [rarely straight]; cotyledons foliaceous or fleshy, variously irregularly plicate or rarely flat, incumbent or accumbent on the elongated descending radicle turned toward the hilum. Germination usually epigeous (hypogeous in *A. saccharinum*). (Including *Negundo* Boehm. in Ludw., *Rulac* Adans., *Saccharodendron* (Raf.) Nieuwl., *Crula* Nieuwl., *Argentacer* Small, and *Rufacer* Small). LECTOTYPE SPECIES: *A. Pseudo-Platanus* L.; see N. L. Britton, N. Am. Trees 638. 1908. (The classical Latin name of the maple; etymology obscure.) — MAPLE.

A genus of nearly 150 species, primarily of the North Temperate Zone, a few extending into the subarctic in Europe (e.g., *Acer platanoides* L., up to 63° N. Lat. in Sweden) and North America (e.g., *A. glabrum* Torr., up to 59° N. Lat. in Alaska), as well as into the Tropics in Central America (*A. Skutchii* and *A. Negundo* in Guatemala) and in Asia (*A. niveum* Blume in the mountains of Java, Sumatra, Celebes, and Timor). The genus is centered in eastern Asia where about two-thirds of the species and several endemic sections occur. The species in general are components of various associations and forest types of deciduous and mixed forests of moderately warm and humid climates. Only *A. monspessulanum* L. and its allies seem to have become adapted to the arid conditions of the Mediterranean region.

The classification of *Acer* followed here is basically that of Pax (1902), emended by Rehder (1905, 1940). The genus is subdivided into 14 sections, five of which occur in our area. The monotypic and endemic sect. GLABRA Pax (presumably related to the eastern Asiatic sect. ARGUTA Rehd.) is represented by *A. glabrum* Torr., and the otherwise eastern Asiatic sect. PALMATA Pax by *A. circinatum* Fusch in Pacific North America. The sections are based on the characteristics most adequately known at present: type of inflorescence; floral structures; gross morphology of fruits, especially of the nutlets (seed-bearing portions); number and arrangement of the scales of winter buds; and external (and partially internal) features of leaves.

In the early Tertiary, the genus was widely distributed throughout the boreal zone, and the ranges of some sections were much more extensive than at present. Thus, in the Oligocene, and perhaps even the Eocene, species of sect. RUBRA, which is now restricted to eastern North America and Honshu, Japan, occurred in Eurasia and North America (as far north as Greenland). In the Miocene this section was still represented in Pacific North America (e.g., *Acer Chaneyi* Knowl., from Oregon), and in the Pliocene and even the Quaternary in northern Italy. Members of the now exclusively American sect. SACCHARINA Pax have been described from the Miocene of Hungary (e.g., *A. Jurenakii* Stur.) Fossil species of sect. NEGUNDO have been recorded from the Oligocene (Colorado) and the

Miocene (Oregon) of North America, and from the Miocene of Europe (Bohemia) and eastern Asia (Shantung Prov., China).

KEY TO THE SECTIONS OF ACER IN THE SOUTHEASTERN UNITED STATES

- A. Leaves simple, palmately 3-5-lobed or -cleft; plants usually monoecious; flowers 5-merous, entomophilous; stamens usually 7 or 8, rarely 5 or 6.
- B. Flowers in thyrses or racemes; petals and disc present; leaves 3 (or slightly 5)-lobed (our spp.); winter buds with 2 outer scales.
  - C. Inflorescences slender, upright, subcylindrical thyrses; petals linear or linear-spatulate; disc extrastaminal; nutlets of the samaras convex, strongly ribbed; bark of trunk and branches brown or darker, not striped; leaves coarsely serrate. . . . . Sect. ACER.
  - C. Inflorescences slender, pendulous racemes; petals obovate; disc intrastaminal; nutlets of the samaras somewhat flattened, ribless; bark of young trunk and branches green, with longitudinal pale or dark stripes; leaves finely doubly-serrate. . . . . Sect. MACRANTHA.
- B. Flowers in corymbs or fascicles; petals and/or disc present or absent; winter buds with several to many imbricate scales; leaves 3-5-lobed or -cleft.
  - D. Flowers on long, filiform, pendulous pedicels, in  $\pm$  many-flowered, umbel-like corymbs produced from the terminal buds of the leading shoot and short lateral branchlets, appearing with or a little before the leaves; plants monoecious; petals wanting; disc extrastaminal; leaf lobes entire or sparingly coarsely sinuate-dentate or lobulate, the the sinuses between lobes rounded. . . . . Sect. SACCHARINA.
  - D. Flowers subsessile or pediceled (the pedicels not pendulous), in 3-7-flowered umbel- or headlike clusters produced from aggregated lateral buds, appearing long before the leaves; plants monoecious or dioecious; petals and an intrastaminal disc present, or both wanting; leaf lobes serrate or coarsely dentate, the sinuses between lobes usually acute; if rounded, the middle lobe considerably narrowed toward its base. . . . . Sect. RUBRA.
- A. Leaves pinnately compound, 3-7(-11)-foliolate; plants dioecious; flowers 4- or 5-merous, anemophilous, the staminate fascicled and pendulous on long, filiform pedicels, the pistillate in slender, drooping racemes; petals and disc wanting (our sp.); stamens 4-6; winter buds with 2 outer scales. . . . . Sect. NEGUNDO.

The Eurasian-North American sect. ACER (§ *Spicata* Pax, §§ *Gemmata*, *Microcarpa*, and *Trilobata* Pojark.), comprising about 30 species and centered in eastern Asia, is represented in our area by *Acer spicatum* Lam., mountain maple,  $2n = 26$ , which occurs from Newfoundland and southeastern Labrador to Hudson Bay, Manitoba, and Saskatchewan, and southward in cool, damp, rocky woods at higher elevations in the Appalachians to western North Carolina, eastern Tennessee, and northern Georgia. This species is closely related to the Japanese-Manchurian *A. ukurunduense* Trautv. & Mey. The Pacific North American *A. macrophyllum* Pursh,  $2n = 26$ , usually placed here, perhaps represents a section of its own. The European *A. Pseudo-Platanus* L., sycamore-maple,  $2n =$

52, much planted as an ornamental in the Northeastern States, has become established there locally, and the eastern Asiatic *A. Ginnala* Maxim.,  $2n = 26$ , is locally established from Maine to Connecticut and western New York. Section ACER, as delimited here, seems to be somewhat heterogeneous.

The almost exclusively eastern Asiatic sect. MACRANTHA Pax, including about 20 species, is represented in North America only by *Acer pensylvanicum* L., striped maple,  $2n = 26$ , a primarily northeastern species extending into our area along the Appalachians, usually in cool, damp soil at elevations above 3000 feet, to Tennessee, North Carolina, and northern Georgia. It seems to be closely related to the Manchurian-Korean *A. tegmentosum* Maxim.

The entirely North American sect. SACCHARINA Pax (*Saccharodendron* Nieuwl.) consists of two to six species (depending upon the taxonomy adopted). The species concept followed here is that based on population studies by Desmarais (1952), who regarded *Acer saccharum* Marsh. emend. Desm. as a complex species comprised of six subspecies (five formerly regarded as distinct species), four of which occur in our area. The subspecies have been distinguished mainly on the basis of the general leaf outline, the types of which appear to have definite geographical patterns and to show some correlation with the color and the degree (amount) and type of the pubescence of the lower leaf-surface. All these characters intergrade in the areas where the ranges of the subspecies overlap.

The northeastern American *Acer saccharum* subsp. *saccharum* (*A. saccharodendron* K. Koch; *A. nigrum* var. *glaucum* (Schmidt) Fosb.; *Saccharodendron barbatum* Nieuwl., not *A. barbatum* Michx.), sugar maple,  $2n = 26$ , extends southward into our area, being abundant in eastern Tennessee and western North Carolina, but sparse in central North Carolina, northeastern Alabama, and northeastern Georgia. "It attains its greatest abundance in the northern part of its range, forming in some places almost pure stands. Farther south along the Appalachians, it is still an important element of the flora, but grows with many other species of trees. From the Appalachians west its abundance gradually decreases, until it is replaced by subsp. *nigrum*" (Desmarais). Subspecies *nigrum* (Michx. f.) Desm. (*A. nigrum* Michx. f.; *S. nigrum* (Michx. f.) Small), black maple,  $2n = 26$ , ranges from southern Quebec to southern Minnesota southward, reaching its southern limit in Arkansas, Tennessee, and western North Carolina. Its occurrence in Georgia and Alabama (cf. Fernald, Gray's Man. Bot. ed. 8. 987. 1950) should be verified. Records from Louisiana are possibly based on planted specimens. "The black maple, covering a wide range, is really abundant only in Illinois and Iowa, where it forms pure stands in the valleys along the rivers. It is a very variable group, and seems to be gradually eliminated by subsp. *saccharum* where the two grow together" (Desmarais). Intermediates between subsp. *saccharum* and subsp. *nigrum* have been grouped by Desmarais into a "*saccharum-nigrum*" cline. Subspecies *floridanum* (Chapm.) Desm. (*A. barbatum* Michx. fide Fernald; *A. floridanum* (Chapm.) Pax; *A. nigrum* var. *floridanum* (Chapm.) Fosb.; *S. floridanum* (Chapm.) Nieuwl.), Florida



maple, occurs on the Coastal Plain and in the Piedmont, from southeastern Virginia south to central Florida (Hillsborough County), west to Louisiana, north to Arkansas and Tennessee, and beyond our limits in the Ozark Plateau of Missouri and along the Mississippi Valley in southern Illinois and western Kentucky. Subspecies *leucoderme* (Small) Desm. (*A. leucoderme* Small; *A. nigrum* var. *leucoderme* (Small) Fosb.; *S. leucoderme* (Small) Nieuwl.), chalk-maple, is a tree mostly of the deep valleys of the southern Appalachians and Piedmont, as well as at the inner edge of the Coastal Plain, from western North Carolina south to northernmost Florida (Gadsden and Liberty counties), west to Louisiana, north to Arkansas and Tennessee. Generally rare and local, it is apparently most abundant in Georgia and Alabama. This subspecies presents a homogeneous population intermediate between subsp. *nigrum* and *floridanum*, with which it is often confused. Subspecies *Schneckii* (Rehd.) Desm. (*A. saccharum* var. *Schneckii* Rehd.), "intermediate between *saccharum*, *floridanum*, and *grandidentatum* . . . is found along a zone where the ranges of *saccharum* and *floridanum* meet" (Desmarais). Although apparently unrecorded from our area, its occurrence in at least the northwestern part seems to be possible. The range of subsp. *grandidentatum* (Torr. & Gray) Desm. (*A. grandidentatum* Torr. & Gray, including *A. sinuosum* Rehd.), bigtooth maple, lies to the west and northwest of our area, and there are no authentic records of its occurrence east of Comanche County, Oklahoma. Since the subspecies of *A. saccharum* distinguished by Desmarais, "although treated on the same level in the nomenclatural system, are not of equal rank and do not have the same relationships" (Desmarais), further taxonomic changes are to be expected.

The poorly known *Acer Skutchii* Rehd. occurs in the mountains of Tamaulipas, Mexico, and Zacapa and Quiché, Guatemala. Combining the leaf outline of subsp. *nigrum* (but the leaves glaucous, glaucescent, or green on the lower surface), the pubescence of subsp. *Schneckii*, and fruits larger and smoother than those of *A. saccharum*, it should be studied in the light of variation in *A. saccharum*. It is considered to be an Arcto-Tertiary element in the Mexican [and Guatemalan] montane biota (Martin & Harrell).

Section SACCHARINA is supposed to be closely related to sect. GONIOCARPA Pojark. (§ *Campestris* sensu Pax, exclusive of *Acer campestre* L.<sup>6</sup>) of the Mediterranean region.

Section RUBRA Pax (*Rufacer* Small, *Argentacer* Small) includes two eastern North American and one endemic Japanese species, *Acer pycnanthum* K. Koch, closely related to *A. rubrum*. The red maple, *A. rubrum* L., (*Rufacer rubrum* (L.) Small),  $2n = 78, 104$  (flowers in umbel-like clusters, usually red, rarely yellow, pediceled; sepals distinct; petals and disc present; wings of samaras slightly divergent), ranges from Newfoundland, the Gaspé Peninsula, southern Quebec, and Ontario, southward, in a wide

<sup>6</sup> Following Pojarkova (1936) and Fernald (Gray's Man. Bot. ed. 8. 986. 1950), the writer regards *Acer campestre* L. as a member of sect. PLATANOIDEA Pax. Consequently, the sectional name *Campestris* Pax is replaced by GONIOCARPA Pojarkova.

variety of habitats, throughout our area, except the extreme southeastern part of peninsular Florida (Dade County) and the Florida Keys, westward to Texas and Oklahoma. Two doubtful varieties, var. *Drummondii* (Hook. & Arn.) Sarg. (*Rufacer Drummondii* (Hook. & Arn.) Small) and var. *tridens* A. Wood (var. *trilobum* K. Koch; *Rufacer carolinianum* (Walt.) Small), occur on the Coastal Plain south to Florida. The taxonomy of this polymorphic species remains obscure; extensive population studies are desirable. The existence of chromosomal races within *A. rubrum* has been suggested (Taylor, Duffield). The silver maple, *Acer saccharinum* L. (*A. dasycarpum* Ehrh.; *Argentacer saccharinum* (L.) Small),  $2n = 52$  (flowers in headlike clusters, usually yellow, rarely red, subsessile; sepals connate; petals and disc wanting; wings of samaras much divergent), a characteristic bottomland species similar in its silvical features and general range to the red maple, occurs in the Piedmont and at moderate elevations in the mountains, as well as on the Coastal Plain, especially in river valleys, locally throughout our area south to northern Florida and west to Louisiana. "The likelihood of the formation of distinct races within relatively small distances (about 100 miles) in the climatically uniform Middle West" is presumed (Wright, 1949, pp. 301, 302). The position of sect. RUBRA within the genus seems to be rather isolated. Anatomically it seems to be close to sect. GLABRA Pax (cf. Warsow).

The eastern Asiatic-North American sect. NEGUNDO (Boehm. in Ludw.) Maxim.<sup>7</sup> emend. Rehd., 1940 (*Negundo* Boehm., *Acer* subg. *Negundo* (Boehm.) Momotani), includes three species, one American. *Acer Negundo* L. (*Negundo aceroides* Moench, *N. Negundo* (L.) Karst.), box-elder, ash-leaved maple, water maple,  $2n = 26$ , ranging throughout most of the United States, north to southern Canada and south to Mexico and Guatemala, occurs scattered in the valleys of the lower mountains, along sandy banks and bottoms in the Piedmont, and along the larger rivers on the Coastal Plain, throughout our area south to central Florida (Hernando County). This polymorphic species includes several apparently intergrading varieties (sometimes regarded as distinct species) which differ mainly in the shape, thickness, and dentation of the leaflets, and the hairiness of leaflets and/or branchlets and fruits. Its closest allies are *A. cissifolium* (Sieb. & Zucc.) K. Koch,  $2n = 26$ , from Japan, and *A. Henryi* Pax,  $2n = 26$ , from central China, both with petaliferous flowers with an intrastaminal disc. The position of the section within the genus seems to be rather isolated, and its relationships are obscure.

Although the flowers of *Acer* usually are unisexual by abortion, occasional bisexual (morphologically, at least) flowers and rarely even individuals

<sup>7</sup> In his *Bibliography of Cultivated Trees and Shrubs* (1949, p. 428a), Rehder cited Pax (Bot. Jahrb. 6: 327. 1885) as the author of the sectional name *Negundo*. In a footnote he pointed out that it could not be attributed to K. Koch, since Koch used the informal "term 'Gruppe' for his four divisions which are published with descriptions but without names; in Gruppe 4 the name '*Negundo* Mnch. meth. 334' is obviously cited as a synonym and is not intended as the name of the group." Although correct in regard to Koch, Rehder apparently overlooked the earlier publication of the name by Maximowicz (Bull. Acad. Sci. St. Pétersb. III. 26: 450. 1880).

with prevailingly bisexual flowers occur. In general, however, polygamy seems to be relatively rare within the genus. In most species the plants are monoecious (dioecism being of extremely rare occurrence, e.g., in *A. platanoides*, *A. Pseudo-Platanus*) and entomophilous, bees being recorded as most frequent pollinators. *Acer saccharinum* and *A. rubrum* are either monoecious or dioecious and pollinated by insects and wind; and *A. Negundo* is dioecious and wind pollinated. Cross-pollination seems to be the rule, bisexual flowers being proterogynous (e.g., in *A. Negundo*  $\times$  *platanoides*; see Beskaravainaya) and close-pollination in monoecious plants being obstructed by differences in position of staminate and carpellate flowers on the tree and by their expansion at different times (male-female or vice versa) (cf. Mushegian, Stout). Some species have been found to be self-fertile (e.g., *A. campestre*, *A. Ginnala*, *A. Pseudo-Plantanus*, and perhaps *A. rubrum*), others self-sterile (e.g., *A. platanoides*, *A. saccharinum*, *A. spicatum*; cf. Pjatnitzki). Parthenocarpy and rarely apomixis have been recorded in *A. Negundo* and its hybrids with *A. platanoides*.

Chromosome numbers have been investigated in about 31 species, all of which are diploid (*A. platanoides* also sometimes triploid) with  $2n = 26$ , except three tetraploids (*A. Pseudo-Platanus*, *A. saccharinum*, and *A. carpinifolium*), and *A. rubrum* ( $2n = 78, 104$ ). It has been suggested that the basic number 13 might have arisen either through multiplication of an original chromosome set of 5 (Takizawa, 1952) or from one of 12 (Meurman).

With the exception of *Acer*  $\times$  *Bornmuelleri* Borbas (*A. campestre*  $\times$  *monspeulanum*), all of about 18 known intra- or intersectional hybrids are either artificial or of spontaneous garden or nursery origin. The at least partly fertile artificial hybrid, *A. Negundo*  $\text{♀}$   $\times$  *platanoides*  $\text{♂}$ , reported from the U.S.S.R., is of special interest as being between species of presumably very remotely related sections.

Floral anatomy, investigated in 11 species (Hall, 1951, 1961), revealed eight different anatomical types mostly corresponding to Pax's sections. On the basis of leaf anatomy (studied in 85 species by Warsow), a few changes in Pax's classification have subsequently been made by Rehder (1905, 1940), Pojarkova (1936), and Momotani (1962). Petiole anatomy, investigated in 55 species (in great detail in 42 species by Watari), though variable and complicated, seems mostly to be in agreement with Koidzumi's delimitation of the sections (slightly different from that of Pax) and is hardly in favor of any generic segregation. Fruit histology (Momotani, 1961) for about 55 species seems to support the classification of the genus used here. Seed proteins have been investigated in 45 species (Momotani, 1962), but the data are quite incomplete in terms of the whole genus; further investigations in this field are very desirable.

Many species, domestic and foreign, yield valuable timbers. The sap of *A. saccharum* is the source of maple syrup and sugar of considerable economic importance. Numerous species are of high ornamental value as garden and park plants and/or shade trees (cf. Mulligan).

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HIPPOCASTANACEAE A. P. de Candolle, Prodr. 1: 597. 1824, nom. cons.  
(HORSE-CHESTNUT FAMILY)

Trees or shrubs distinguishable from the closely related Sapindaceae by the opposite, 5–11-foliolate, palmately compound leaves; relatively large, showy, irregular flowers in ample terminal thyrses [or panicles]; and capsules with large chestnut-like seeds. (Paviaceae Horaninow, 1834; Aesculaceae Lindley, 1836.) TYPE GENUS: *Aesculus* L.

A family of two closely related genera, *Aesculus*, of the North Temperate Zone, and *Billia* Peyr., of tropical America (southern Mexico to northwestern South America). Hippocastanaceae, the closely related Aceraceae, and perhaps the Bretschneideraceae are regarded as having been derived independently and on different lines from the ancestral Sapindaceae (cf. Hardin, 1957d).

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1. *Aesculus* Linnaeus, Sp. Pl. 1: 344. 1753; Gen. Pl. ed. 5. 161. 1754.

Trees to small shrubs. Leaves opposite, palmately compound, 5–11 (usually 5–7)-foliolate, manifestly petiolate, deciduous; leaflets thin to subcoriaceous [or coriaceous], variable in size and shape, the central leaflet usually the largest, usually petiolulate [or sessile], serrulate to serrate or doubly-serrate [rarely nearly entire.] Plants andromonoecious; flowers showy, irregular, ♂ and bisexual, pediceled, in terminal thyrses composed of cincinni each of which is subtended by a small bract. Sepals 5, whitish, yellowish, or reddish, connate to  $\frac{2}{3}$  or more [or less] of their length into an equally or unequally 5-lobed [sometimes 1- or 2-lipped] campanulate to tubular calyx often oblique and gibbous at base on the upper side. Petals 4 or 5, subequal or unequal (the upper pair longer and narrower than the lateral), clawed (the claw often wide, with involute margins clasping a staminal filament), white to yellow, scarlet or red. Disc annular or lobed, usually one sided. Stamens usually 6–8 [rarely 5], exerted or included; filaments white; anthers yellow, orange or reddish, usually glandular at the tip and at the base of each anther half; pollen medium sized, 3-colpate, subprolate or prolate, striate-reticulate. Gynoecium rudimentary and stalked in ♂ flowers; stigma terminal, small, simple or obscurely 3-lobed; style single, subulate, elongate, often arcuate, deciduous; ovary sessile, 3-locular (rarely 2- or 4-locular); ovules 2 in each locule, superposed, sessile, campylotropous (or amphitropous?), 2-integumented, with a thick nucellus. Fruit subglobular or obovoid, variable in size; pericarp leathery, thick or thin, pale to dark brown; smooth, tuberculate or spiny; seeds usually 1–3 (occasionally 4–6), dark chestnut-brown to light orange-brown, with a pale “hilum” (pseudohilum) of variable size; embryo large, filling the seed cavity at maturity (nuclear endosperm abundant in early stages); cotyledons unequal, thick, hemispherical, usually inseparable (conferruminate), incurved on a short radicle lying in a pocket formed by an infolding of the testa; plumule distinctly 2-leaved. LECTOTYPE SPECIES: *A. Hippocastanum* L.; see N. L. Britton, N. Am. Trees 657. 1908. (The ancient Latin name of some oak, applied by Linnaeus to this genus; etymology of name obscure.) — HORSE-CHESTNUT, BUCKEYE.

A genus of about 13 species in five sections, of disjunct distribution in the North Temperate Zone in North America (7), Asia (5), and the Balkan Peninsula of Europe (1 species). One Asiatic species, *Aesculus assamica* Griff., extends into the Tropical Zone as far south as northern Siam and northwestern Indochina. Five species occur in our area; <sup>8</sup> *A. californica* (Spach) Nutt. ex Torr. & Gray (§ CALOTHYRSUS (Spach) Koehne) is restricted to California, and *A. Parryi* Gray (§ PARRYANAE Wiggins) to northwestern Baja California.

Including only a single distinctive species, sect. MACROTHYRSUS (Spach) Koehne (Deutsche Dendrol. 384. 1893), comprises spreading shrubs or small trees with elongate columnar inflorescences (20–30[–50] cm. long);

<sup>8</sup> In taxonomic treatment and distribution of the taxa Hardin's *Revision* (1957d) is followed here.

petals 5, white, subequal; and stamens 3–4 times the length of the petals. *Aesculus parviflora* Walt. (*A. macrostachya* Michx.), bottlebrush buckeye,  $2n = 40$ , apparently is endemic to Georgia and Alabama. It occurs “in the Coastal Plain of southwestern Georgia and southeastern Alabama (along the Apalachicola River), and through central Alabama from Clarke, Butler, and Monroe Counties north and off the Coastal Plain into Franklin, Blount, and Etawah Counties.” Early records of the occurrence of this species in eastern Georgia, South Carolina, and Florida have been questioned, but the type specimen of *A. macrostachya* was collected “ad ripas amnis *Savannah*, juxta urbiculum *St. Augusti* [Augusta, Richmond County, Georgia]” (Michaux, Fl. Bor.-Am. 1: 220. 1803). This species is stoloniferous and is usually found in dense colonies or clones in rich woods on calcareous soils, on shady hillsides, on river and stream bottoms, or on rocky and sandy banks. The species seems to be most closely related to those of the Asiatic-western American sect. CALOTHYRSUS.

The exclusively eastern North American sect. PAVIA (Mill.) Walp. (Repert. Bot. Syst. 1: 423. 1842) comprises four highly variable, closely related, sympatric species characterized by broad pyramidal inflorescences (10–15[–25] cm. long); petals 4, yellow or red, nearly equal or mostly unequal; and stamens included or exerted to twice the length of the petals. Hybridization and introgression between the species seem to be common; flowering dates for all four species overlap.

Of wide range, *Aesculus glabra* Willd. var. *glabra*, Ohio buckeye,  $2n = 40$ , a tree 10–30 m. tall, or a shrub, with exerted stamens, yellowish, nearly equal petals, fruits usually spiny-tuberculate, and leaves with 5–7 oval-oblong to elliptic-obovate leaflets, occurs in our area in northern Alabama, central Tennessee (with outlying stations in eastern Tennessee, central Alabama, and east-central Mississippi), and western Arkansas. It extends to Missouri, Iowa, Indiana, southern Michigan, eastern Pennsylvania, and Kentucky. The distinctive var. *arguta* (Buckl.) Robins., a shrub or small tree, the leaves with 7–11 narrow leaflets attenuate at both ends, intergrades with var. *glabra* in western Arkansas; its principal range is beyond our limits in Kansas, Oklahoma, and Texas. Both varieties usually grow in fertile bottomlands of rivers and streams, or in rich calcareous soils on hillsides and in flat woodlands.

Primarily Appalachian, *Aesculus octandra* Marsh. (*A. flava* Ait.), yellow or sweet buckeye,  $2n = 40$ , usually a large tree 20–30 m. tall, with included stamens, yellow, unequal petals, stipitate glands on the pedicels, and smooth or somewhat scaly or pitted fruits, ranges from northern Georgia, northeastern Alabama, and central Tennessee, through eastern Tennessee, western South and North Carolina, western Virginia, eastern Kentucky, and West Virginia to southwestern Pennsylvania and southern Ohio, thence along the Ohio River bluffs to southern Indiana and Illinois. A plant of rich forest soils, “it is often a dominant, or more often the co-dominant, with *Tilia heterophylla*, *Liriodendron tulipifera*, and *Acer saccharum*, in the cove forests of the Blue Ridge, Smoky, and Cumberland Mountains.”

Usually a shrub 1–3 m. tall, more rarely a tree to 15 m., *Aesculus sylvatica* Bartr. (*A. neglecta* of many authors, not Lindley), the Georgia buckeye, further characterized by yellow to often reddish petals and eglandular pedicels, occurs mainly in the Piedmont from southern Virginia south through the Carolinas and Georgia to northeastern Alabama and northward into eastern Tennessee, growing in many different habitats and soil types. “Many populations of *A. sylvatica* are quite variable in many characters, as a result of introgression from *A. Pavia* or *A. octandra*, or both. . . . The great variation in the [petal] color (yellow to red), characteristic of many populations is thought to be due to introgression with *A. Pavia*” (Hardin 1957d; cf. 1957a, b). *Aesculus Pavia* L., red buckeye,  $2n = 40$ , also a shrub or small tree, with scarlet, red, yellowish-red, or yellow petals, the petals stipitate-glandular on the margins and surface, occurs from central Florida (Orange County) northward to eastern North Carolina and westward to eastern Texas, extreme southeastern Oklahoma, Arkansas, western Tennessee, southeastern Missouri, and southern Illinois. It is usually a plant of well-drained soils in pinelands, mixed pine and broad-leaved forests, and oak-hickory flatwoods. *Aesculus Pavia* has often been separated into several varieties or even species. “When the entire species is examined, however, there is no real degree of discontinuity which would separate any of the variants. . . . A conspicuous clinal variation exists from east to west in two characters, the calyx length and the pubescence of the lower leaf-surface. The calyx becomes shorter and more campanulate westward, and there is a gradual increase westward in the percentage of shrubs in a population with tomentose or woolly leaves.” The yellow color of the petals “in eastern populations, and west to Texas, is considered a result of the influence of *A. sylvatica* and *A. glabra* through introgression. On the other hand, the populations of *A. Pavia* [representing a variant] in the extreme western part of its range are typically yellow.”

This section is considered by Hardin to have been evolved on a line independent from that of the four other more or less interrelated sections, and its closely related species “were presumably derived from an ancestral form (or forms) which was a relic of the Arcto-Tertiary forest that persisted through late Tertiary and Pleistocene in the Appalachian refugium.” The genus itself presumably was derived from a *Billia*-like ancestor, and Central or South America is supposed to be its center of origin.

Although only staminate and bisexual flowers have been recorded in our species, at least in *Aesculus Hippocastanum* occasional carpellate flowers with the stamens either losing their anthers before dehiscence or having more or less closed anthers with nonfunctional (shriveled) pollen seem to occur. The bisexual flowers are either proterogynous (e.g., *A. Hippocastanum*, *A. glabra*) or proterandrous (e.g., *A. parviflora*). Close-pollination in an inflorescence seems to be prevented by the expansion of male and bisexual flowers at somewhat different times, apparently in a male-bisexual sequence. An extensive study of the floral biology of our species, however, has not been available. *Aesculus Hippocastanum* is believed to be self-fertile. Bumblebees are considered to be the main pollinators in all the

species except *A. parviflora*, which appears to be pollinated by moths. The reported occurrence of polyembryony in *A. Hippocastanum* (see Penzig, p. 222) should be verified. Chromosome numbers, known in six species representing four sections and in a few hybrids, are invariably  $2n = 40$ , except  $2n = 80$  in *A. × carnea* Hayne (*A. × rubicunda* Loisel.), an amphiploid intersectional hybrid between *A. Hippocastanum* and *A. Pavia*, and  $2n = 60$  in *A. × plantierensis* André, a sterile backcross between *A. × carnea* and *A. Hippocastanum*. Both of these hybrids are of garden origin. Intraspecific hybrids are known only within sect. PAVIA. Hardin (1957b) mentions seven hybrids, both under cultivation and/or in natural populations. Two of these, both of garden origin, are triparental, i.e., *A. × arnoldiana* Sarg. (*A. glabra* × [*A. octandra* × *A. Pavia*]), and *A. woerlitzensis* Koehne (*A. octandra* × [*A. Pavia* × *A. sylvatica*]), the latter apparently also occurring wild.

Many species, varieties, and hybrids of *Aesculus* (e.g., *A. Hippocastanum* of southeastern Europe, *A. × carnea* Hayne, *A. parviflora*, and species of § PAVIA) are planted for ornament or shade, and a few species are a source of commercial timber. The glucoside aesculin, present in all organs, but especially in the bark and bud scales of *A. Hippocastanum*, seems to have some application in plant cytology (see Sharma). All species of our area are considered poisonous to livestock.

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